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A new congrid eel (Teleostei: Anguilliformes: Congridae) from the Western Pacific, with an analysis of its relationships

DAVID G. SMITH[1*], EMMA S. KARMOVSKAYA[2] & JOÃO PAULO CAPRETZ BATISTA DA SILVA[3]
[1]*Smithsonian Institution, Museum Support Center, MRC-534, 4210 Silver Hill Road, Suitland, MD 20746*
smithd@si.edu; https://orcid.org/0000-0002-6354-2427
[2]*Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, 117218, Russia*
ekarmovs@ocean.ru; https://orcid.org/0000-0002-0636-4265
[3]*Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, Castelo Branco, 58051-900, João Pessoa, PB, Brazil*
jpzoologia@dse.ufpb.br; https://orcid.org/0000-0002-2373-3421
[*]*Corresponding author*

Abstract

A new species of congrid eel, *Bathycongrus villosus* **sp. nov.**, is described from the Philippines and Vanuatu. It is similar to some of the small-toothed species currently placed in *Bathycongrus* and to the species of *Bassanago*. In this paper we compare the new species to *Bassanago albescens* (Barnard, 1923) and to *Bathycongrus parviporus* Karmovskaya, 2011, which it most closely resembles. An analysis of 19 characters shows that it agrees with *Bat. parviporus* in 16 characters and with *Bas. albescens* in one. In two characters, the three species are all different. We therefore place it in *Bathycongrus*.

Key words: Taxonomy, Pisces, *Bathycongrus,* new species

Introduction

The species described here was discovered independently by two of the authors. Karmovskaya found the Vanuatu specimen among material examined at the Muséum National d'Histoire Naturelle in Paris. She wrote a preliminary description but did not publish it because of uncertainty about its relationships. It was clearly a member of the subfamily Congrinae, and within that group it resembled the genus *Bassanago* in having small, hair-like epidermal processes on the surface of the body. It differed from *Bassanago* in several other characters, however, such as the number of vertebrae, the pigment on the stomach and intestine, and the length of the gas bladder. In those characters, it was closer to certain small-toothed species currently placed in *Bathycongrus*. Smith meanwhile had discovered three specimens of an undescribed species collected from a similar deep-water habitat in the Philippines. A comparison of the specimens from the two locations showed that they appeared to represent the same species. Silva joined the project to describe and analyze the osteology. The results of the study are presented here.

Material and methods

Specimens dissected for description of skeletal anatomy in *Bassanago albescens* (Barnard, 1923) and *Bathycongrus villosus* **sp. nov.** were double stained for cartilage and bone and prepared following Dingerkus and Uhler (1977) and Taylor and Van Dyke (1985). Manual dissections were performed using scalpel, fine-tipped scissors and forceps in order to visualize all aspects of the skeleton. The dissected structures were analyzed and photographed using a Zeiss Axiocam HRc attached to a ZeissDiscovery V20 Stereomicroscope. The analysis included all bony and cartilaginous elements of the cranium, pectoral skeleton, vertebrae and caudal skeleton. The anatomical terminology followed Castle (1960), Asano (1962), Smith (1989), Eagderi & Adriaens (2014) and Silva *et al.* (2019). The

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character matrix was assembled in Mesquite v. 3.51 (Maddison & Maddison 2018). A maximum parsimony analysis by implicit enumeration was performed under TNT v. 1.5 (Goloboff, Farris, & Nixon 2008). The obtained tree was rooted in *Conger cinereus* (outgroup), a basal representative of the Congrinae. Numbers of steps, consistency indexes, retention indexes, and character mapping were obtained from Winclada v.1.00.08 (Nixon 2002). Character changes were optimized using ACCTRAN transformation. Descriptions of skeletal anatomy in *Bathycongrus parviporus* Karmovskaya, 2011 are based on those provided by Karmovskaya (2011). These specimens were single stained for bone only with Alizarin Red S.

Morphometric characters are given as follows. Total length (TL) is measured from tip of snout to end of caudal fin; preanal length from tip of snout to origin of anal fin; predorsal length from tip of snout to origin of dorsal fin; head length from tip of snout to upper end of pectoral-fin base; trunk length is preanal minus head length; depth at anus does not include height of dorsal fin; snout length from tip of snout to anterior edge of clear "spectacle" covering eye; horizontal eye diameter measured across middle of "spectacle;" postorbital length from posterior edge of "spectacle" to upper end of pectoral-fin base (= head length minus snout length and eye diameter); snout to rictus from tip of snout to posterior corner of mouth opening (rictus); gill opening from corner to corner; interbranchial is the distance between lower corners of gill openings measured across isthmus; pectoral-fin length from upper end of base to tip of longest ray. Total length was measured with a meter stick; other measurements were taken by dial calipers. Total, preanal, predorsal, head, and trunk length are given to the nearest mm; other measurements to the nearest 0.1 mm.

Meristic characters are as follows. Preanal lateral-line pores are those anterior to a vertical line drawn through the anterior edge of the anus. Total vertebrae include the hypural complex as one vertebra; preanal vertebrae include the one directly above the anal-fin origin; predorsal vertebrae include the one directly below the dorsal-fin origin; precaudal vertebrae are those anterior to the first closed hemal arch. Preanal dorsal-fin rays are those anterior to the first anal-fin ray.

Institutional abbreviations: MNHN, Muséum National d'Histoire Naturelle, Paris, France; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA. Anatomical abbreviations given in text.

***Bathycongrus villosus* sp. nov.**

Figs. 1–3; Tables 1–3

Holotype: MNHN 1997-3795 (236 mm TL, female), Vanuatu, 15º 36' S, 167º 16' E, depth 182–215 m, beam trawl, 5 October, 1994, station CP 1086, C.R.V. "Alis", MUSORSTOM 8.

Paratypes: USNM 344104 (2 females, 239–296 mm), Albay Gulf, Philippines, 13° 10' 16" N, 123° 50' 12" E to 13° 10' 14"N, 123° 52' 22 "E, depth 174–190 m, 30-m otter trawl, RV "Fishery Researcher 1", 22 Sep 1995; USNM 451061 (1 male, 252 mm, stained and partly dissected), same data as USNM 344104.

Material for comparison. *Bassanago albescens*: USNM 365200 (12, 367–508 mm), 37°24'06"S, 54°39'42"W, depth 187–327 m, 5 May 1975; USNM 404584 (21, 354–605) same data as USNM 365200; USNM 427184 (1, 343, stained and partly dissected), same data as USNM 365200. *Conger cinereus* Rüppell, in Klunzinger, 1871: CSIRO H 8518-01 (1, 382), Solomon Is., 8° 17'S, 157° 09'E, 9 Jul 1987; USNM 451062 (1, cleared and stained), Red Sea, Gulf of Aqaba, depth 0–2 m, 5 Sep 1969.

Diagnosis. A moderately elongate congrid eel of the subfamily Congrinae, with small hair-like epidermal processes on surface of body and head. Tail moderately attenuate. Dorsal-fin origin behind origin of pectoral fin. Snout slightly projecting beyond lower jaw. Upper labial flange rudimentary. Anterior and posterior nostrils tubular, posterior at mid-eye level. Teeth conical, relatively small, all about the same size, in bands tapering posteriorly on jaws; intermaxillary patch broader than long, teeth slightly exposed when mouth closed, in 3–4 transverse rows; vomerine teeth in an elongate patch, blunt conical, none enlarged, roughly in 4–5 rows anteriorly and 2 rows posteriorly. Total vertebrae 121–126, preanal lateral-line pores 26–27. Lateral-line pores tubular. Head pores small.

Description Counts and measurements of individual specimens are provided in Table 1. Values given for holotype, with those of paratypes in parentheses. Measurements as % TL: preanal length 33.9 (35.1–36.1), predorsal length 16.1 (17.6–18.7), head length 14.8 (15.5–16.3), trunk length 19.1 (18.9–20.5), depth at anus 8.1 (5.7–7.1); as % of head length: snout length 22.9 (23.4–23.8), horizontal eye diameter 20.3 (16.5–21.2), postorbital length 56.9 (55.4–59.7), snout to rictus 29.7 (30.8–33.7), gill opening 15.4 (9.4–12.2), interbranchial 28.6 (20.5–28.9), pectoral-

fin length 37.1 (32.7–35.1). Meristic characters: preanal lateral-line pores 26 (26–27), supraorbital (SO) pores 3, infraorbital (IO) pores 5, preoperculomandibular (POM) pores 10, supratemporal commissure (STC) 1 pore. Predorsal vertebrae 8 (8–10), preanal vertebrae 28 (29–30), precaudal vertebrae 36 (35–37), total vertebrae 123 (121–126). Pectoral-fin-rays 12 (13), dorsal-fin-rays 284 (268^{+}, ca 278), preanal dorsal-fin-rays 54 (50–59), anal-fin-rays 217 (205^{+}, ca 215), caudal-fin rays ca. 4+5. Branchiostegal rays 9 (10).

FIGURE 1. *Bathycongrus villosus* **sp. nov.** Holotype, MNHN 1997-3795, 236 mm TL.

TABLE 1. Morphometric and meristic characters for *Bathycongrus villosus* specimens.

Specimen	MNHN 1997-3795		USNM 344104		USNM 344104		USNM 451061	
	mm	%TL	mm	%TL	mm	%TL	mm	%TL
Total length	236		296		239		252	
Preanal	80	33.9	104	35.1	86	36.0	91	36.1
Predorsal	38	16.1	52	17.6	42	17.6	47	18.7
Head	35	14.8	48	16.2	37	15.5	41	16.3
Trunk	45	19.1	56	18.9	49	20.5	50	19.8
Depth at anus	19	8.1	16.9	5.7	17.0	7.1	15.5	6.2
	mm	%HL	mm	%HL	mm	%HL	mm	%HL
Snout	8	22.9	11.3	23.5	8.8	23.8	9.6	23.4
Eye	7.1	20.3	9.6	20.0	6.1	16.5	8.7	21.2
Postorbital	19.9	56.9	27.1	56.5	22.1	59.7	22.7	55.4
Snout to rictus	10.4	29.7	14.9	31.0	11.4	30.8	13.8	33.7
Gill opening	5.4	15.4	4.5	9.4	4.2	11.4	5.0	12.2
Interbranchial	10	28.6	10.4	21.7	10.7	28.9	8.4	20.5
Pectoral fin	13	37.1	16.0	33.3	13.0	35.1	3.4	32.7
Predorsal vertebrae	8		8		8		10	
Preanal vertebrae	28		30		29		30	
Precaudal vertebrae	36		37		35		36	
Total vertebrae	123		125+		126		121	
Preanal LL pores	26		27		26		26	
SO pores	3		3		3		3	
IO pores	5		5		5		5	
POM pores	10		10		10		10	
STC pores	1		1		1		1	
Dorsal rays	284		268+		ca 278			
Dorsal rays to anus	54		57		59		50	
Anal rays	217		205+		ca 215			

Body moderately elongate, robust, round in cross section anteriorly, tapering and compressed behind anus to tip of caudal region; tip of tail slender but not filiform; anus slightly posterior to anterior third of total length. Dorsal fin begins slightly ahead of midpoint of appressed pectoral fin. Anal fin begins immediately behind anus under the 26th–27th lateral-line pore. Pectoral fin well developed. Gill opening large, upper end slightly below midpoint of pectoral-fin base. Interbranchial nearly twice gill opening. Small villiform transparent epidermal processes over

surface of head and body, some of them pigmented by minute melanophores. Myorhabdoi absent, dorsal- and anal-fin rays segmented.

Head well differentiated from trunk, deepest midway between posterior margin of eye and gill opening, its length contained 2.2–2.3 times in preanal and 6.1–6.7 in total length; snout about equal to eye diameter, projecting slightly beyond anterior end of lower jaw; rictus below middle of eye. Upper lip with reduced upturned flange; lower lip thick, with well-developed downturned flange. Anterior nostril a short tube, near tip of snout, directed anteroventrally. Posterior nostril tubular, at mid-eye level.

FIGURE 2. *Bathycongrus villosus* **sp. nov.** Paratype, USNM 344104, 296 mm TL. A, Whole; B, Head.

Lateral line not complete, ca.100 small tube-like pores along lower edge of lateral-line canal; 26–27 pores before anus. Head pores relatively small, none greatly enlarged (Fig. 3A). Supraorbital canal with three pores: the first (ethmoidal) small, on ventral side of tip of snout; the second somewhat enlarged and immediately in front of anterior nostril; the third somewhat enlarged and immediately above anterior nostril. Infraorbital canal with five pores: the first immediately behind anterior nostril; the second between anterior and posterior nostrils; the third below posterior nostril; the fourth below anterior part of eye; the fifth behind rictus and below posterior part of eye; no adnasal pore, and no pores behind eye. Preoperculomandibular canal with ten pores, seven in mandibular canal and three behind mandible; the third mandibular pore round and noticeably enlarged. Supratemporal commissure with one medial pore.

Teeth rather small, conical, all about the same size (Fig. 3B). Intermaxillary patch slightly broader than long, teeth in three to four transverse rows, slightly separated from maxillary and vomerine teeth, partially excluded from closed mouth. Maxillary and mandibular teeth in bands, wider anteriorly, roughly in five to six rows anteriorly tapering to two rows posteriorly. Vomerine tooth patch longer than broad, reaches to level of posterior nostril; teeth blunt-conical, larger posteriorly, in three to four irregular longitudinal rows.

Gas bladder terminates far behind anus. Stomach long, reaching about three-quarters of distance from gill opening to anus.

Color in life unknown. Color in preservative yellowish-brown to medium brown. Large, diffuse, darkish spot below lateral line in front of pectoral fin. Body mottled with tiny pointed melanophores. Vertical fins pigmented

in posterior caudal part but not edged in black. No traces of larval pigmentation. Peritoneum mostly pale, slightly pigmented on dorsal side; intestine dark; stomach black. Oral cavity pale; branchial cavity largely pale with some scattered melanophores.

Size range of specimens 236–296 mm TL. Three of the specimens are females with well-developed ovaries, one is a male. Apparently a small species, probably not greatly exceeding 300 mm TL.

Etymology. Referring to the small dermal villi or papillae on the head and body.

Remarks. In three of the four specimens, the dorsal-fin origin is over the eighth vertebra. In the other specimen, it is between the ninth and tenth vertebrae.

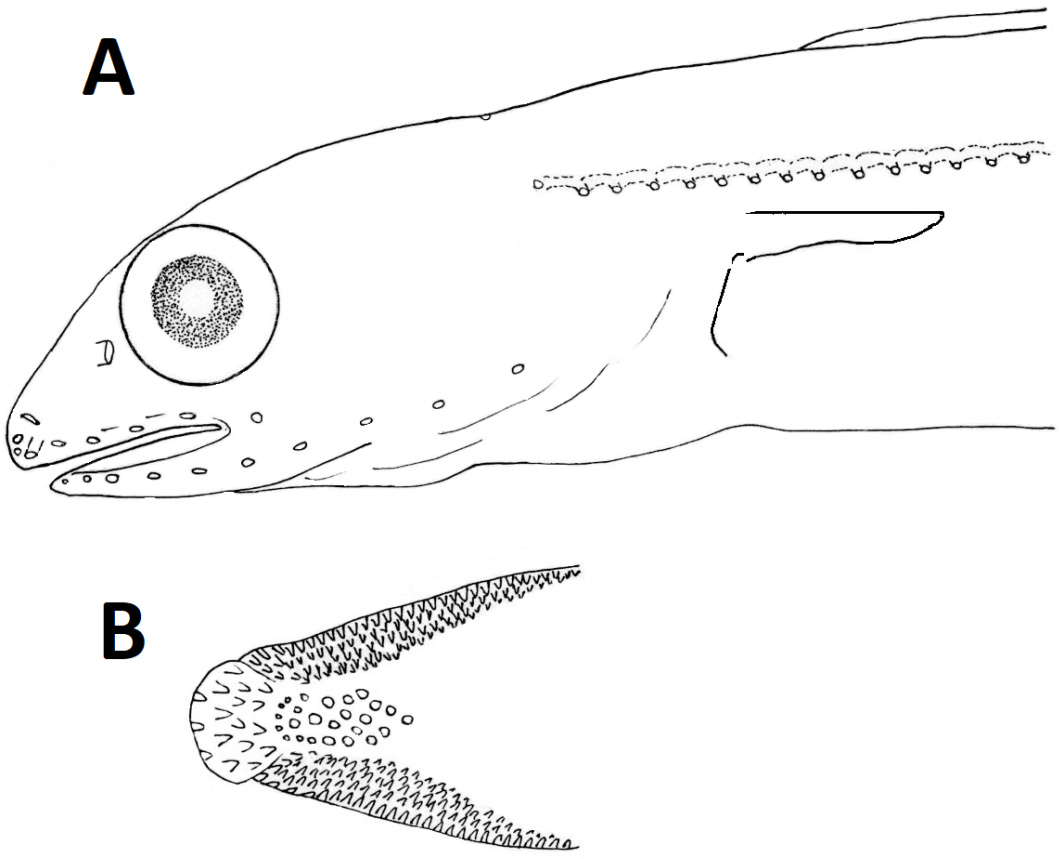

FIGURE 3. *Bathycongrus villosus* **sp. nov.** Holotype, MNHN 1997-3795, 236 mm TL. A, Head; B, Upper teeth.

Skeletal description of new species and *Bassanago albescens*

Neurocranium. (Figs. 4–7) The ethmoid region consists of the fused premaxillaries, ethmoid and vomeral bones, as the premaxillo-ethmovomerine complex (**PEV**). The premaxillo-ethmovomerine complex has a nearly oval and laterally directed lateral process (**LEP**), which is visibly smaller in *Bassanago albescens* (Figs. 4 and 6). The anteroventral surface of the premaxillo-ethmovomerine complex is anteriorly expanded and bears teeth extending posterior to the lateral process of the ethmoid in *Bas. albescens* but not in the new species (Fig. 6). Associated with the lateral portion of the premaxillo-ethmovomerine complex there is a lateral ethmoid cartilage (**LEC**) originating dorsal to the parasphenoid and extending anterolaterally. In addition, the lateral ethmoid cartilage is branched anteriorly, more evidently in the new species. The frontal (**F**) is unpaired and surrounds most of the dorsal margin of the orbital region. Additionally, the frontal bears nearly rectangular and laterally directed processes (**LFP**) in *Bas. albescens*, which are absent in the new species. The posterior portion of the roof of the braincase also includes paired parietals (**P**) and epiotics (**EP**), a short supraoccipital (**SOC**) and part of the exoccipital (**EX**). A low crest is present on the supraoccipital in the new species but is absent in *Bas. albescens* (Fig. 7). The sides are composed of the elongated pterotic (**PTO**) that reaches the posterior portion of the neurocranium (the pterotic connects to the exoccipital bone and contributes to form the posterior wall of the neurocranium), the pterosphenoid (**PTS**), the prootic

(**PRO**) and the laterally projecting sphenotic (**SPH**). The sphenotic contributes to form the anterior articular facet of the suspensorium together with the prootic (Figs. 5 and 6). The sphenotics are more pronounced in the new species when compared to *Bas. albescens* and this difference is also noticed in the rear view of the neurocranium. A small basisphenoid (**BS**) lies at the posterior end of the orbital foramen and has a marked concavity on its anteroventral portion (it bears a short anterior process in *Bas. albescens*; Fig. 5B). The dorsal part of this bone is in contact with both the frontal and the pterosphenoid, and ventrally it is associated with the parasphenoid (**PS**). The parasphenoid is bifurcated anteriorly and forms the ventral aspect of the orbit. The exoccipitals enclose much of the posterior wall of the neurocranium along with portions of the epiotics, supraoccipital, pterotics and basioccipital (**BO**). The foramen magnum (**FM**) is bordered dorsally and laterally by the exoccipitals and ventrally by the condyle of the basioccipital. The remainder of the basioccipital forms the posterior portion of the large otic bullae and contributes to the floor of the braincase along with the parasphenoid and part of the prootics. The large prootics also form the anterior part of the otic bullae (Fig. 5).

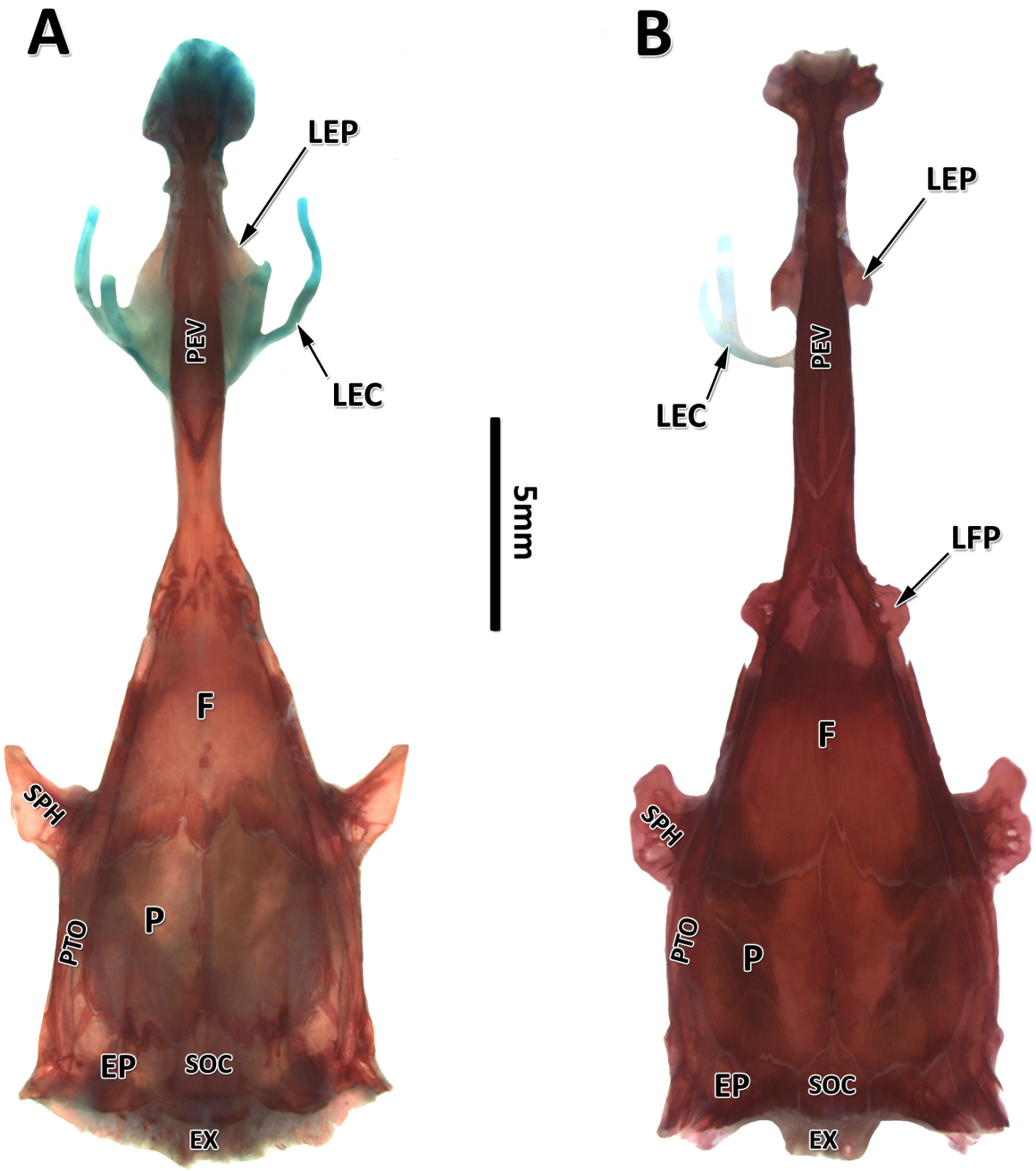

FIGURE 4. Neurocranium, dorsal view. A, *Bathycongrus villosus* **sp. nov.** B, *Bassanago albescens*. Anatomical abbreviations: epiotic (EP), exoccipital (EX), frontal (F), lateral ethmoid cartilage (LEC), lateral ethmoid process (LEP), lateral frontal process (LFP), parietal (P), premaxillo-ethmovomerine complex (PEV), pterotic (PTO), sphenotic (SPH), supraoccipital (SOC).

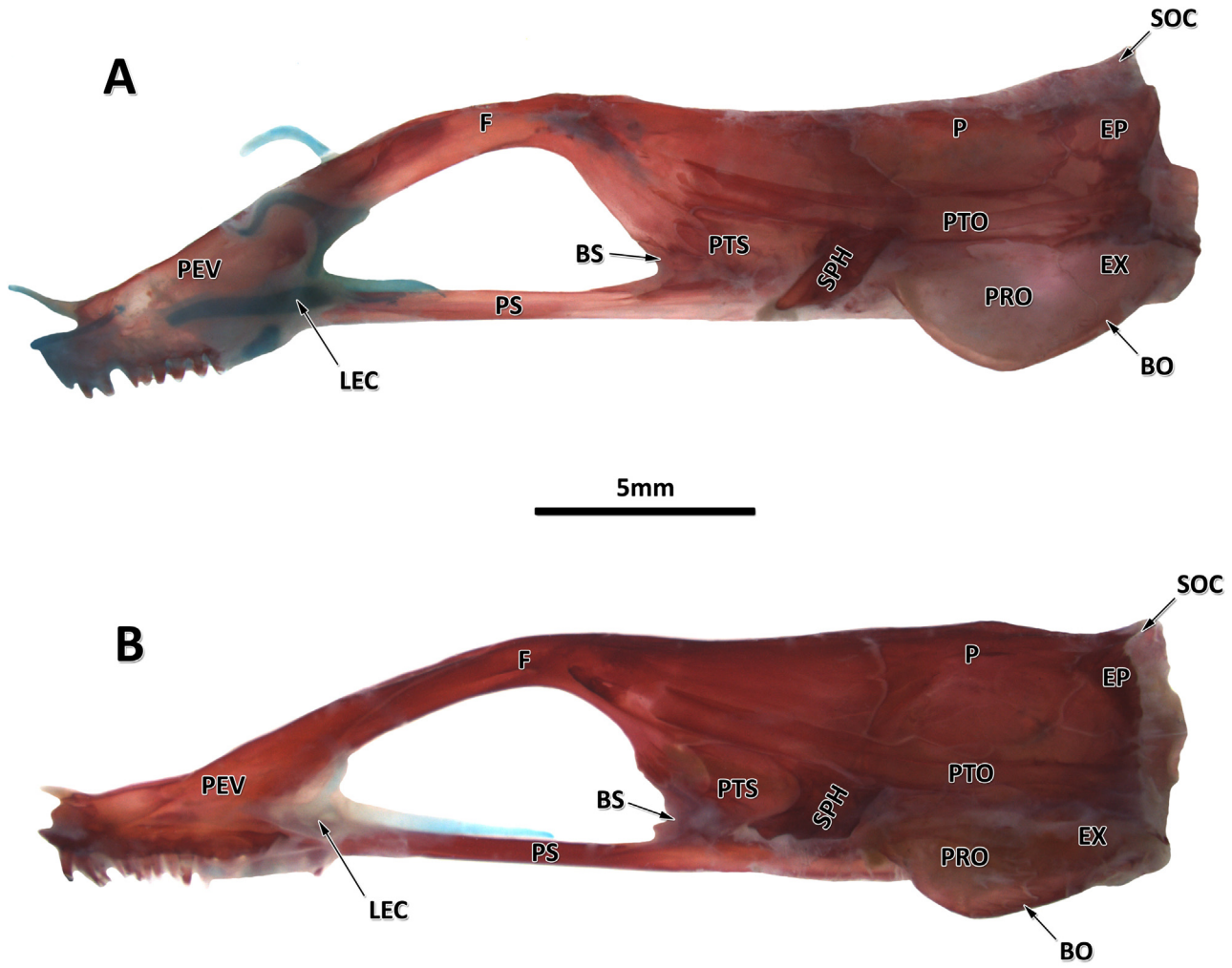

FIGURE 5. Neurocranium, lateral view. A, *Bathycongrus villosus* **sp. nov.** B, *Bassanago albescens*. Anatomical abbreviations: basioccipital (BO), basisphenoid (BS), epiotic (EP), exoccipital (EX), frontal (F), lateral ethmoid cartilage (LEC), parietal (P), parasphenoid (PS), premaxillo-ethmovomerine complex (PEV), prootic (PRO), pterosphenoid (PTS), pterotic (PTO), sphenotic (SPH), supraoccipital (SOC).

Jaws. (Fig. 8) The maxilla (**MX**) has a broad dorsal process (larger in the new species when compared to *Bas. albescens*) on its anterodorsal extremity which articulates anteromedially with the neurocranium at the premaxillo-ethmovomerine complex. Posteriorly it tapers to a square-shaped end and is connected to the angular complex via the primordial ligament (**l-prim**). The dentary (**D**) is the largest component of the lower jaw and bears the coronoid process posterodorsally. Additionally, the dentary is deeper and bears an anterior concave curvature in the new species when compared to *Bas. albescens*. The coronomeckelian is not apparent. The angular, articular and retro-articular are fused into a single bone forming the angular complex (**ART**), which is attached to the posteriormost extremity of dentary complex.

Suspensorium. (Fig. 8) The suspensorium is wider than deep and includes a hyomandibula (**HM**), a quadrate (**QU**) and an ectopterygoid (**PTG**). The ectopterygoid is connected anteriorly to the lateral ethmoid process (**LEP**) and posteriorly to the hyomandibula. The hyomandibula has three articular condyles, including an anterior one that articulates with the sphenotic and prootic, a median one that articulates with the pterotic, and a posterior one that articulates with the opercle and is situated at the posterodorsal margin of the hyomandibula.

Opercular series. (Fig. 8) The opercular series consists of four bones: opercle, subopercle, interopercle and preopercle. The anterior portion of the preopercle (**POP**) contacts the posteroventral portion of the suspensorium and its posterior margin covers the anterior margin of the interopercle (**IOP**). The interopercle is convex ventrally and its proximo-medial portion is connected to the angular complex by means of an interoperculo-angular ligament (**l-Iop-Ang**). The subopercle (**SOP**) curves around behind the opercle and encloses its posterior side in the new spe-

cies, whereas in *Bas. albescens*, it is short and does not extend beyond the posteroventral border of the opercle. The opercle (**OP**) is posteriorly widened (fan-like in shape) and has a smooth posterior margin in *Bas. albescens* but a serrated margin in the new species. It also articulates anteriorly to the posterodorsal condyle of the hyomandibula.

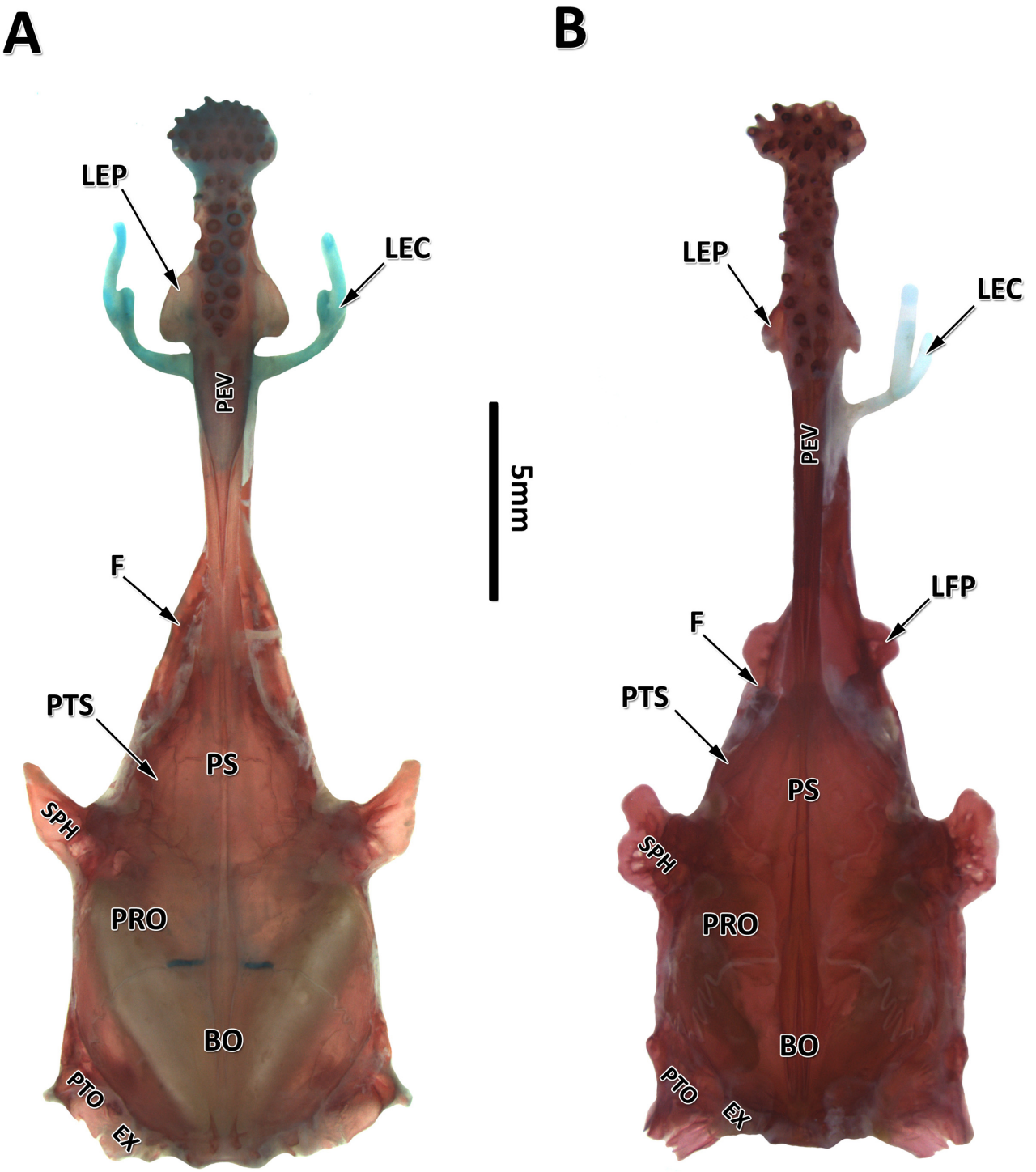

FIGURE 6. Neurocranium, ventral view. A, *Bathycongrus villosus* **sp. nov.** B, *Bassanago albescens*. Anatomical abbreviations: basioccipital (BO), exoccipital (EX), frontal (F), lateral ethmoid cartilage (LEC), lateral ethmoid process (LEP), lateral frontal process (LFP), parasphenoid (PS), premaxillo-ethmovomerine complex (PEV), prootic (PRO), pterosphenoid (PTS), pterotic (PTO), sphenotic (SPH).

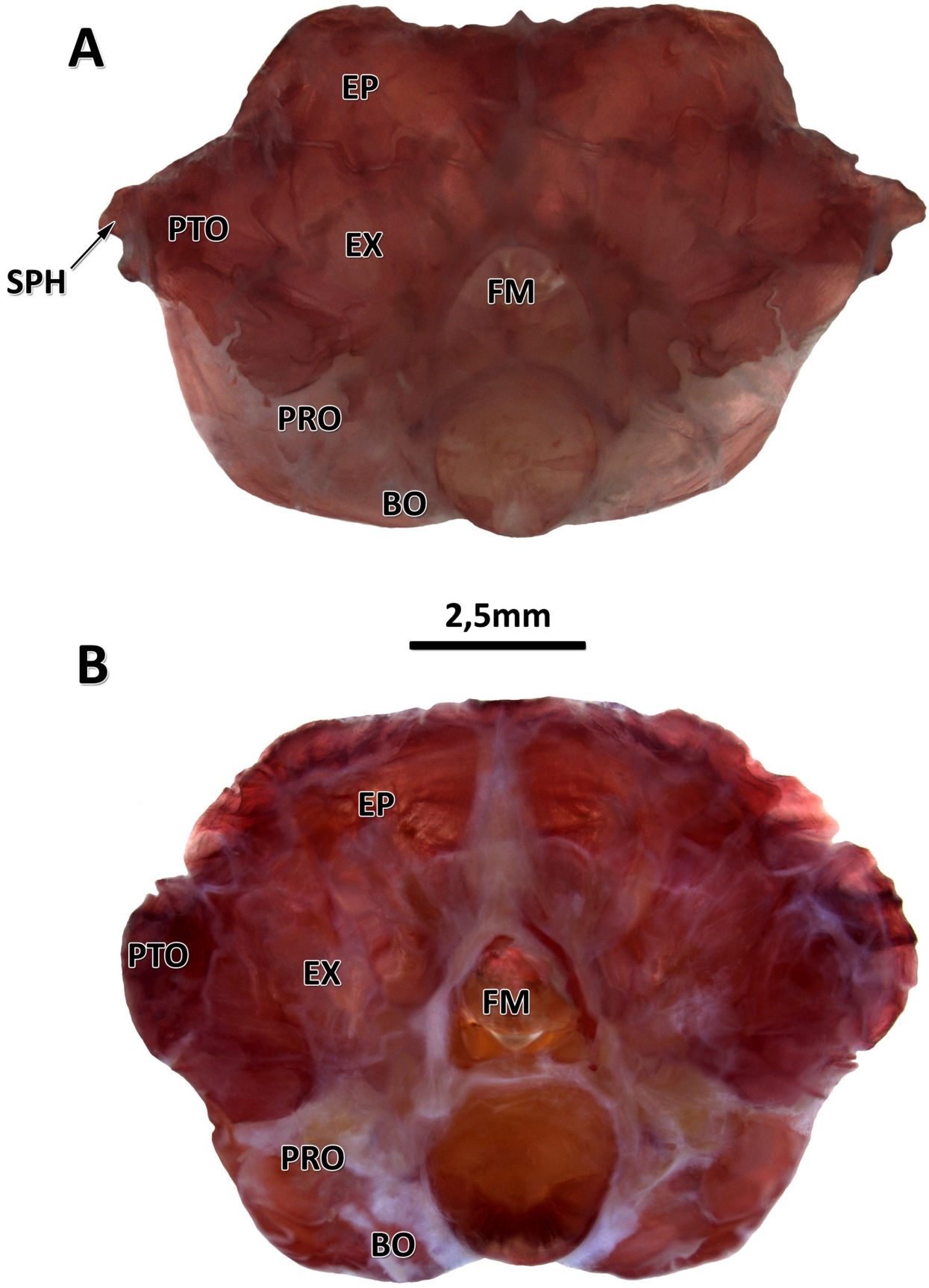

FIGURE 7. Neurocranium, posterior view. A, *Bathycongrus villosus* **sp. nov.** B, *Bassanago albescens*. Anatomical abbreviations: basioccipital (BO), epiotic (EP), exoccipital (EX), foramen magnum (FM), prootic (PRO), pterotic (PTO), sphenotic (SPH).

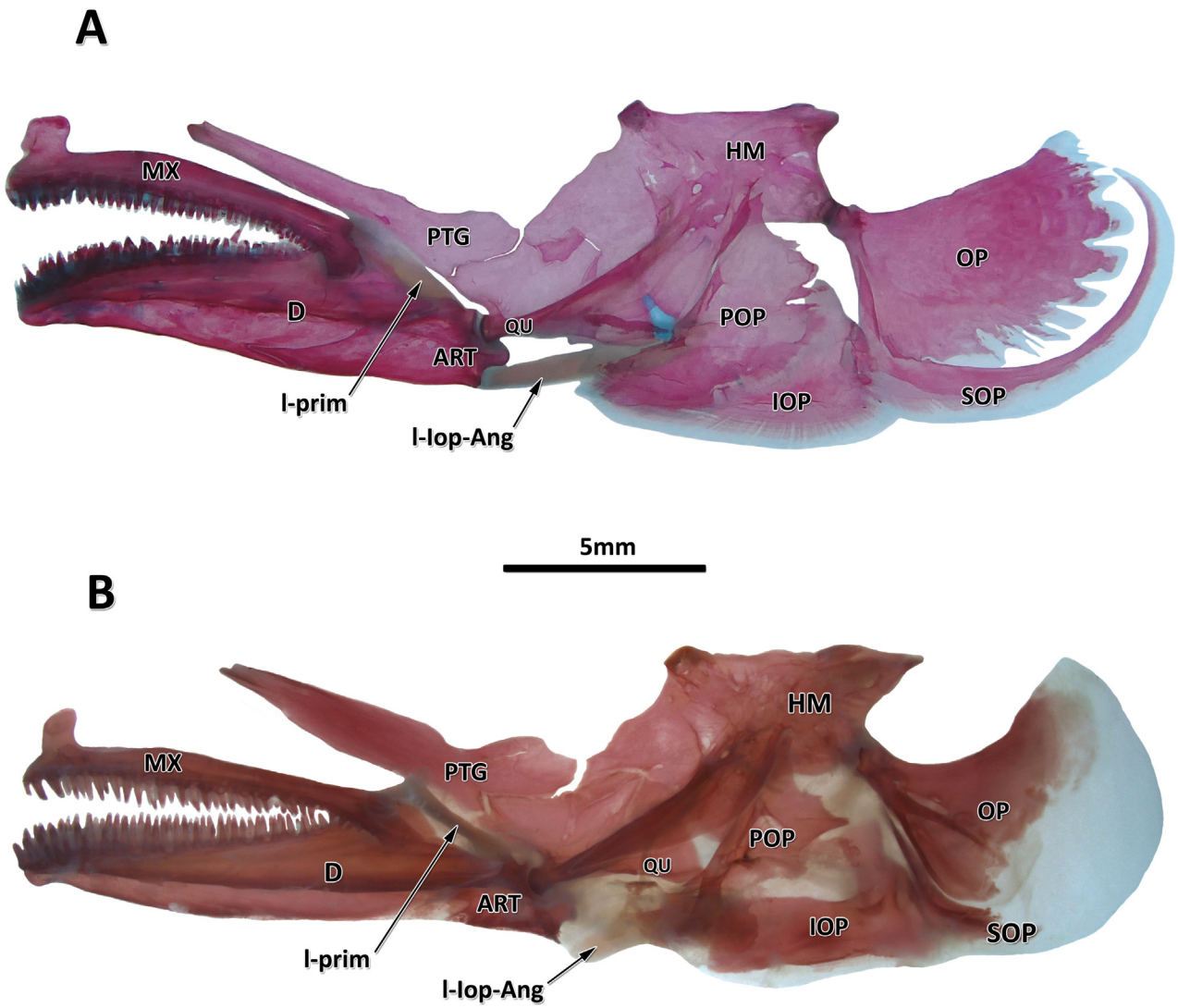

FIGURE 8. Suspensorium, jaws, and opercular apparatus. A, *Bathycongrus villosus* **sp. nov.** B, *Bassanago albescens*. Anatomical abbreviations: angular complex (ART), dentary (D), ectopterygoid (PTG), hyomandibula (HM), interopercle (IOP), interoperculo-angular ligament (l-Iop-Ang), maxilla (MX), opercle (OP), preopercle (POP), primordial ligament (l-prim), quadrate (QU), subopercle (SOP).

Hyoid. (Figs. 9–11, 13) The hyoid complex consists of the unpaired glossohyal and urohyal and paired anterior and posterior ceratohyals. Hypohyals are absent. The glossohyal (**GH**) (Fig. 13) is anteriorly expanded with an anterior cartilaginous tip and tapers posteriorly, articulating with the first basibranchial (**BB1**). It also bears a ventral crest that is connected to the lateral face of the anterior ceratohyal (**ACH**). The urohyal (Figs. 10–11) bears a dorsal ridge anteriorly for the articulation of both anterior ceratohyals. Posteriorly, the urohyal is enlarged and somewhat spoon-shaped and tapers into a pointed end (Fig. 11). In addition, the posterior portion of the urohyal in the new species is considerably larger and bears a small posterodorsal knob (Fig. 11A) that is absent in *Bas. albescens* (Fig. 11B). The anterior and posterior ceratohyals (Fig. 9) are firmly connected and separated from each other by a short patch of cartilage. The posterior ceratohyal (**PCH**) is dorsally curved and associated with eight of the ten branchiostegal rays (**BR**), the others connected to the anterior ceratohyal. The branchiostegal rays extend beyond the ventral border of the opercular series and curve dorsally posterior to the subopercle, almost reaching the dorsal portion of the opercle.

Circumorbital bones. (Fig. 12) The circumorbital bones consist of a large nasal bone (not included in the figure) anterodorsally, a preorbital bone immediately below it, and five discrete suborbital bones posteriorly. The infraorbital canal starts at the anteroventral portion of the snout and extends posteriorly, curving dorsally towards the postorbital region. The elongate and somewhat branched preorbital bone (**PRE**) is located at the anterior part of

the infraorbital canal. The posterior portion of this canal is composed of five suborbital bones (**SBO**). The suborbital bones are more elongated in *Bas. albescens* than in the new species.

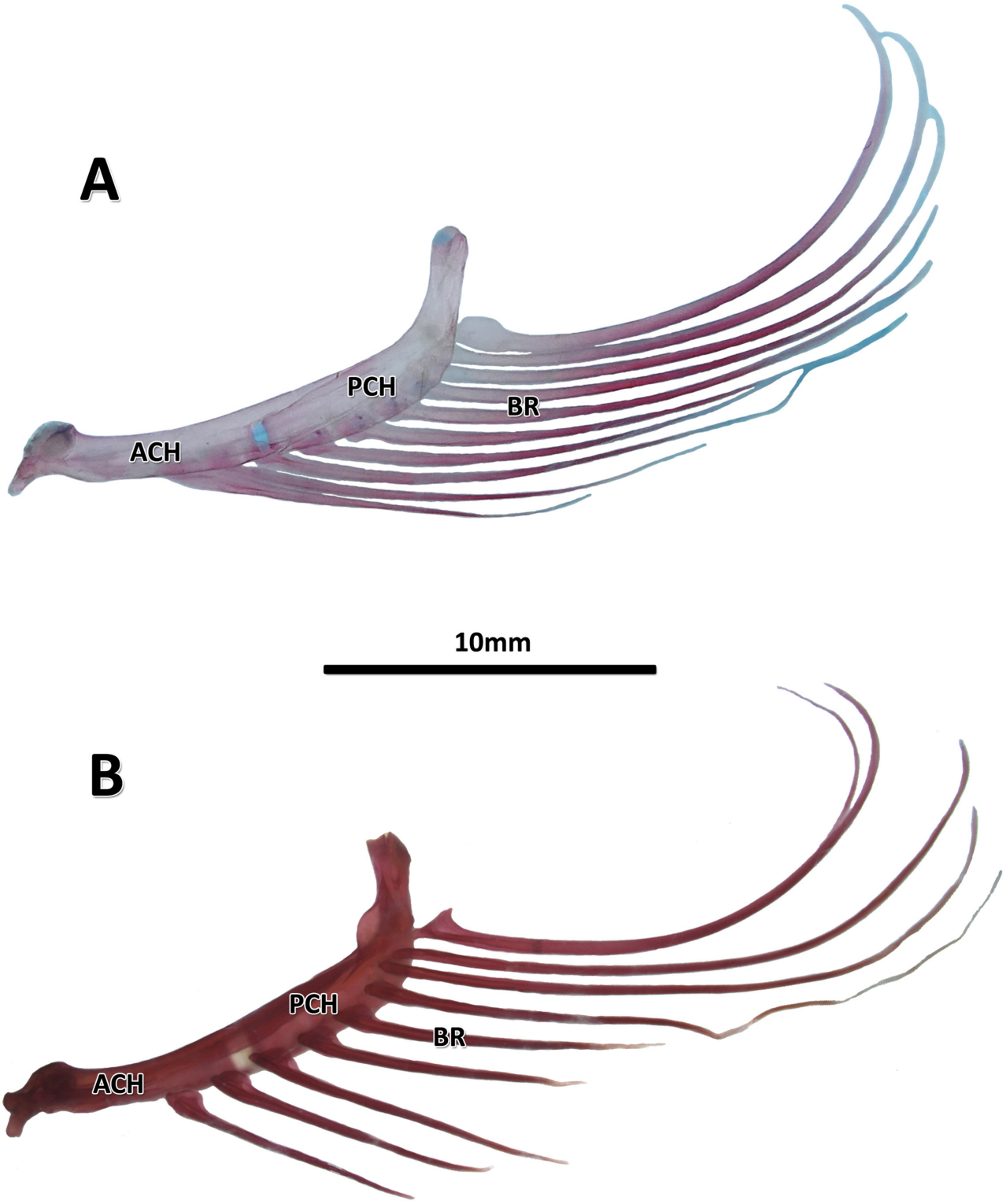

FIGURE 9. Hyoid arch: ceratohyals and branchiostegal rays. A, *Bathycongrus villosus* **sp. nov.** B, *Bassanago albescens*. Anatomical abbreviations: anterior ceratohyal (ACH), branchiostegal rays (BR), posterior ceratohyal (PCH).

Branchial arches. (Fig. 13) Branchial arches with first three basibranchials ossified (**BB1**–**3**) and fourth cartilaginous (**BB4**). There are three pairs of hypobranchials, with the first two ossified (**HB1**–**2**) (bearing posteriorly directed uncinate processes) and the third (**HB3**) cartilaginous. Hypobranchials 2 (**HB2**) bearing anteriorly directed uncinate processes in *Bas. albescens*. Five pairs of ceratobranchials (**CB1**–**5**) present and ossified. Ceratobranchial

5 (**CB5**) narrow and associated with an elongated lower pharyngeal tooth plate (**LP**). There are four pairs of ossified epibranchials (**EB1–4**), with the fourth epibranchial connected with a wide upper pharyngeal tooth plate (**UP**). Epibranchial 4 (**EB4**) also forked proximally. Two pairs of pharyngobranchials (**PB2-3**) present. Pharyngobranchial 2 (**PB2**) not obviously stouter in *Bas. albescens* and pharyngobranchial 3 (**PB3**) arched in the new species.

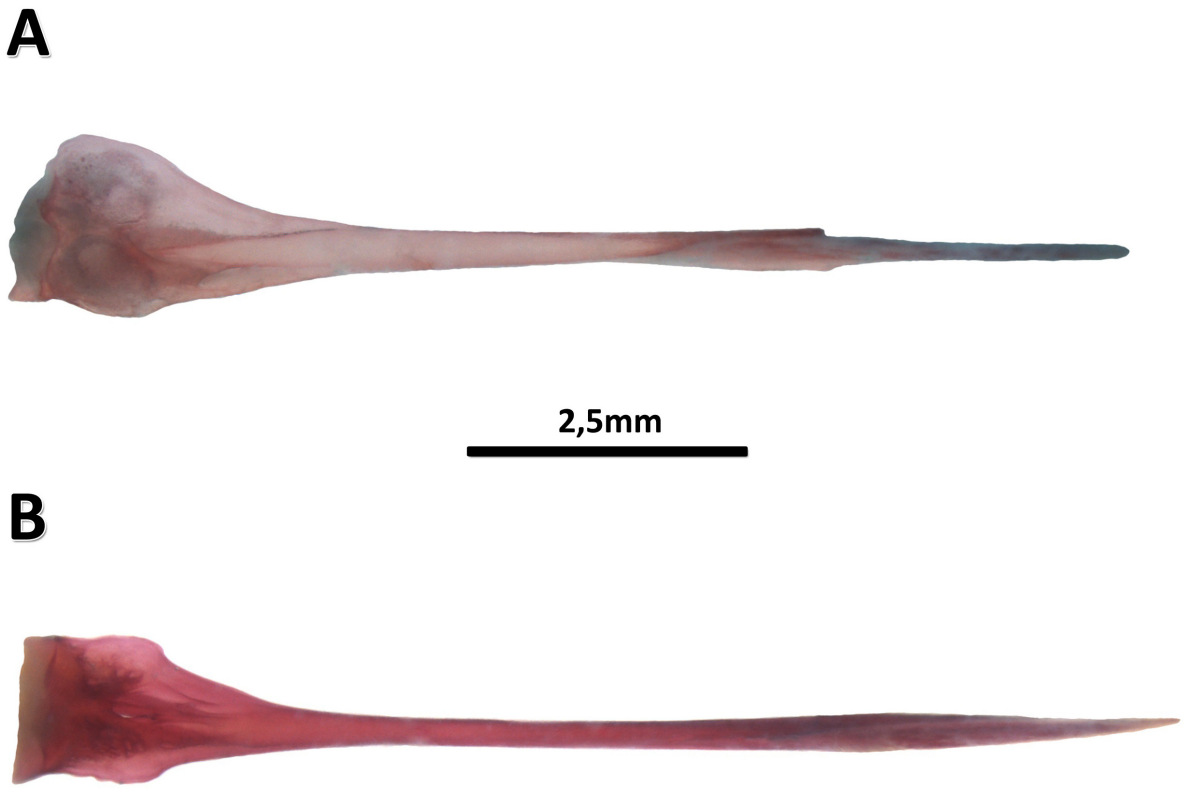

FIGURE 10. Urohyal, dorsal view. A, *Bathycongrus villosus* **sp. nov.** B, *Bassanago albescens*.

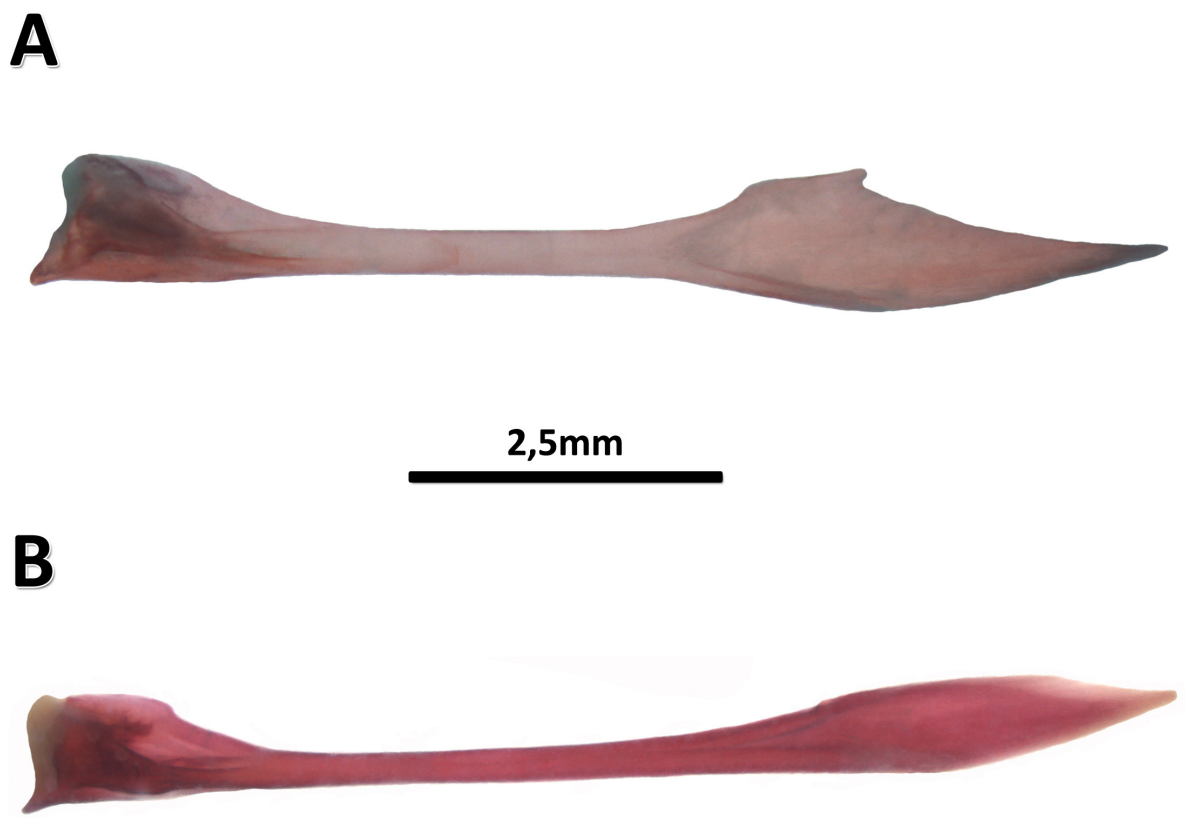

FIGURE 11. Urohyal, lateral view. A, *Bathycongrus villosus* **sp. nov.** B, *Bassanago albescens*.

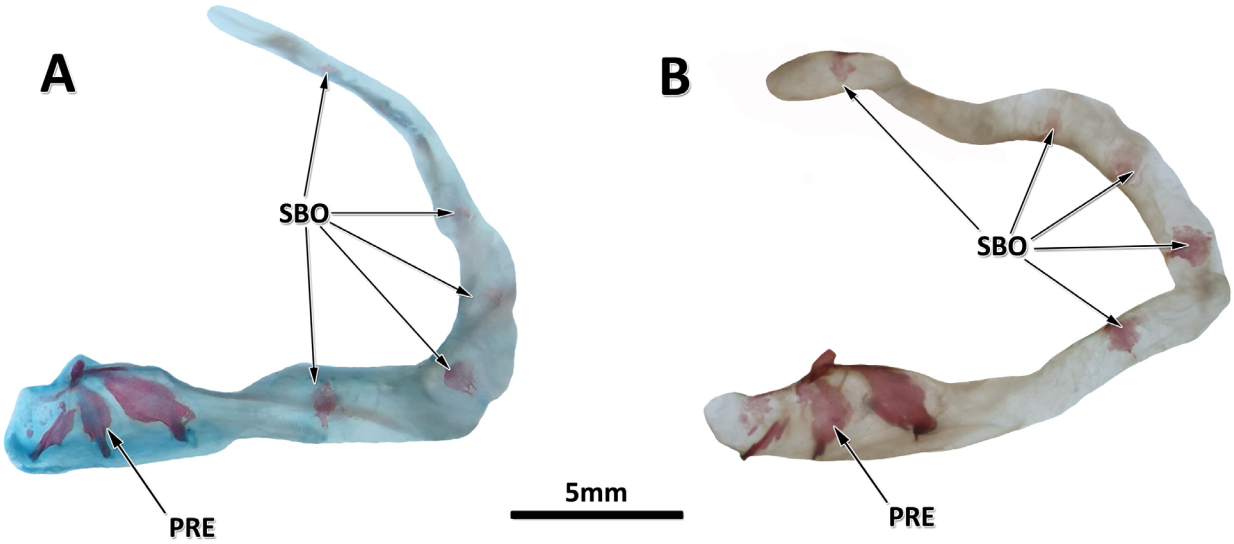

FIGURE 12. Circumorbital bones. A, *Bathycongrus villosus* **sp. nov.** B, *Bassanago albescens*. Anatomical abbreviations: preorbital bone (PRE), suborbital bones (SBO).

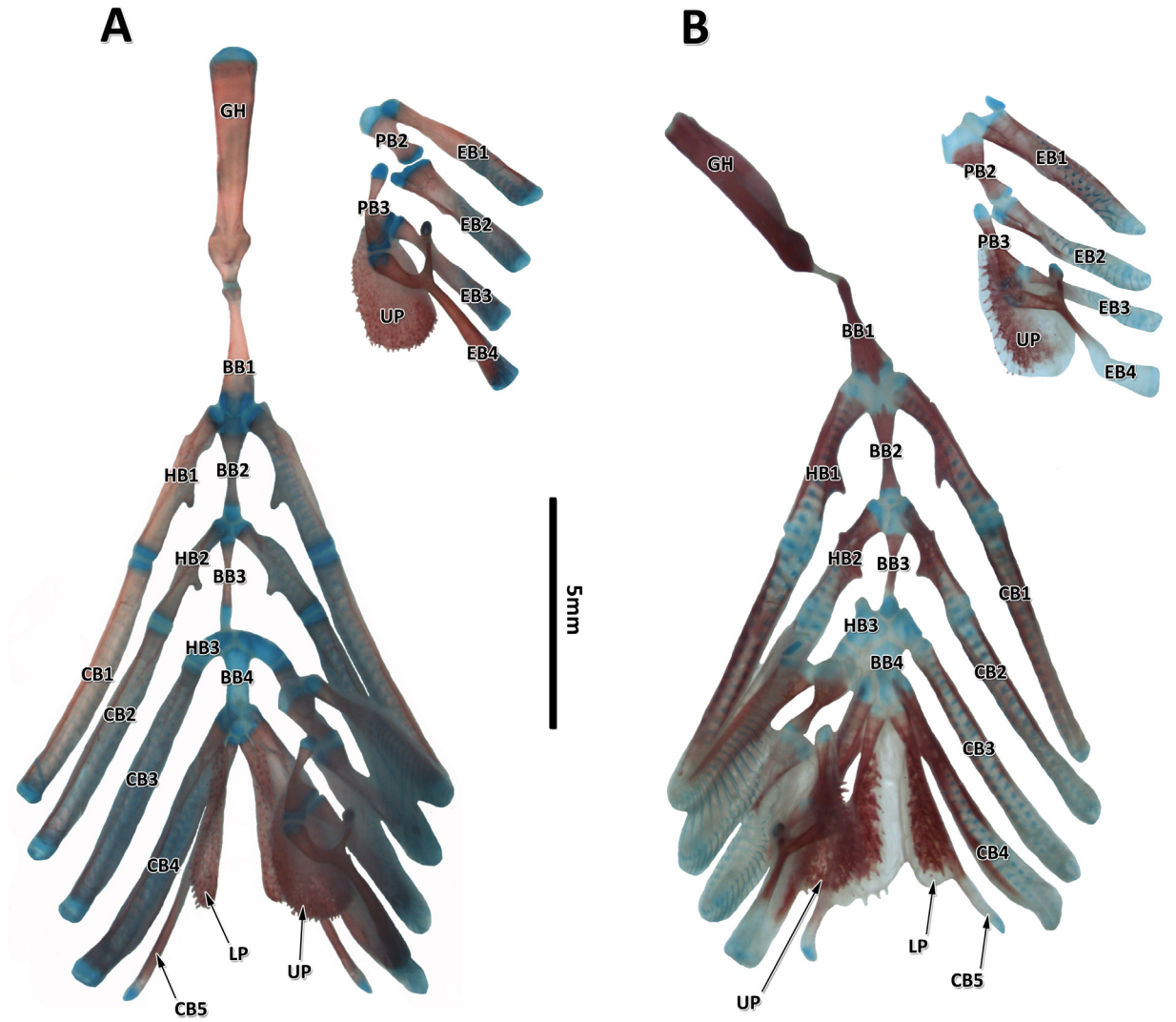

FIGURE 13. Branchial arches. A, *Bathycongrus villosus* **sp. nov.** B, *Bassanago albescens*. Anatomical abbreviations: basibranchials (BB1-4), ceratobranchials (CB1-5), epibranchials (EB1-4), glossohyal (GH), hypobranchials (HB1-3), lower pharyngeal tooth plate (LP), pharyngobranchials (PB2-3) upper pharyngeal tooth plate (UP).

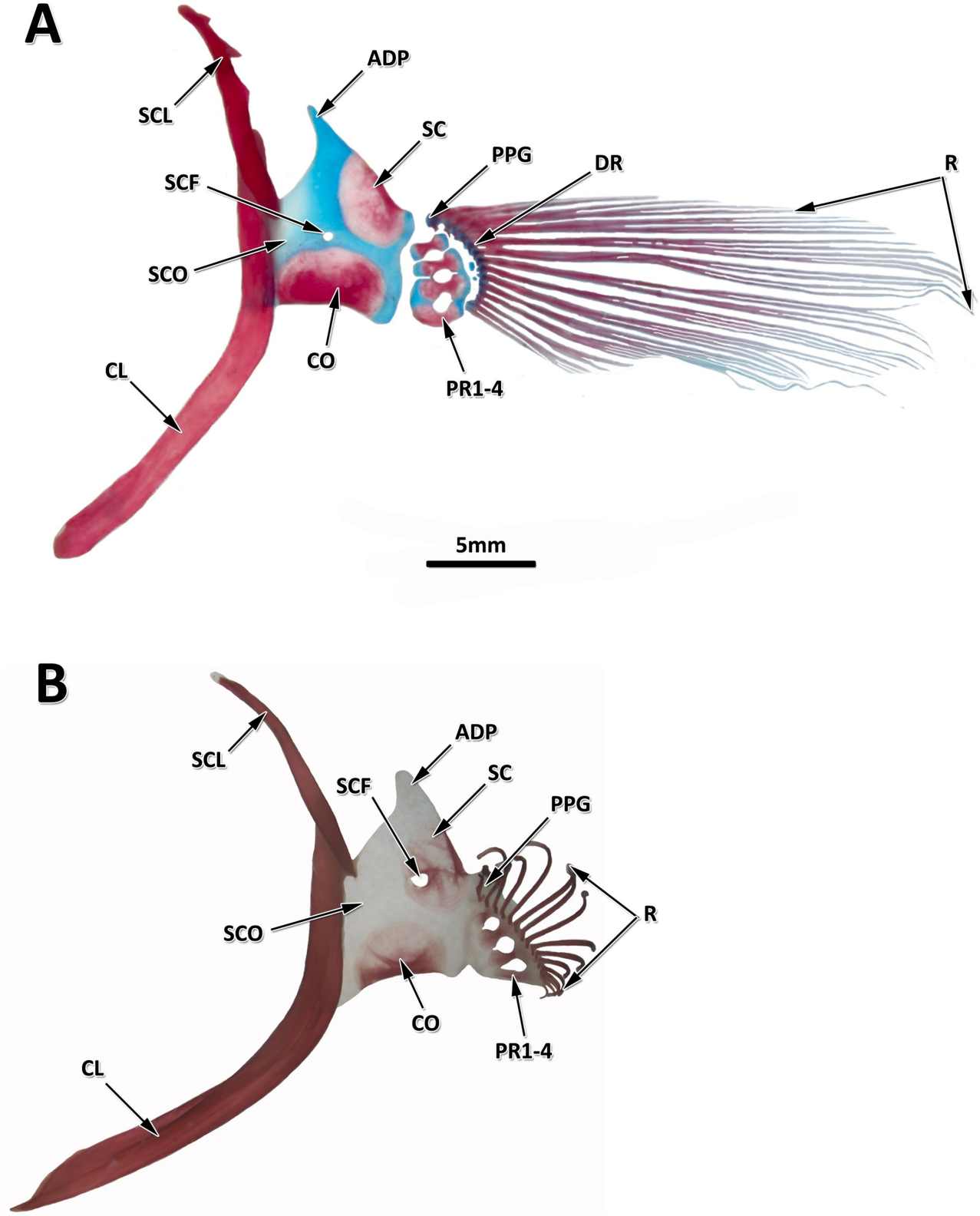

FIGURE 14. Pectoral skeleton. A, *Bathycongrus villosus* **sp. nov.** B, *Bassanago albescens*. Anatomical abbreviations: anteriorly directed process (ADP), cleithrum (CL), coracoid (CO), distal radials (DR), pectoral-fin rays (R), propterygium (PPG), proximal radials (PR1-4), scapula (SC), scapulocoracoid (SCO), scapulocoracoid fenestra (SCF), supracleithrum (SCL).

Pectoral skeleton. (Fig. 14) The cleithrum (**CL**) is stout, with half the width of the scapulocoracoid, and nearly "J" shaped. The cleithrum is expanded ventrally and culminates in a rhomboid tip (pointed tip in *Bas. albescens*). The supracleithrum (**SCL**) is narrow ventrally and enlarged and branched dorsally (supracleithrum not branched

dorsally in *Bas. albescens*). The scapulocoracoid (**SCO**) is an approximately trapezoidal cartilage associated with the dorsal portion of the cleithrum anteroventrally. A nearly triangular and anteriorly directed process (**ADP**) is present on the anterodorsal edge of the scapulocoracoid. The scapular (**SC**) and coracoid (**CO**) ossifications are embedded in the scapulocoracoid cartilage. The scapula is slightly larger than the coracoid and both ossifications are nearly ovoid. The round and reduced scapulocoracoid fenestra (**SCF**) pierces the scapulocoracoid cartilage in between the scapular and coracoid ossifications (the scapulocoracoid fenestra pierces the ventral portion of the scapula in *Bas. albescens*). There are five pectoral basals articulating with the sinuous posterior border of the scapulocoracoid cartilage, including a propterygium (**PPG**) and four proximal radials (**PR1–4**). The propterygium is rounded and cartilaginous, with ¼ the size of the first proximal radial. The proximal radials are hourglass shaped and gradually longer and stouter toward the ventral portion of the pectoral fin. They are mostly ossified and only cartilaginous on their anterior and posterior edges. There are thirteen rounded, cartilaginous distal radials (**DR**) (with about half the size of the propterygium) equally spaced along the posterior border of the proximal radials and associated with the proximal portion of the pectoral-fin rays. The pectoral-fin rays (**R**) are equal in number to the distal radials. They are also segmented and branch before reaching half of their extension.

Vertebrae. (Fig. 15) The anteriormost vertebrae are somewhat modified, with their depth exceeding their width and bearing elaborate neural spines (**NS**). The neural spines are highly branched dorsally in *Bas. albescens* but not in the new species. The first vertebra is shortened, and its centrum articulates with the basioccipital. The subsequent vertebrae are successively larger. The epineurals (**EN**) begin on the first vertebra and are fused to the body of the vertebrae.

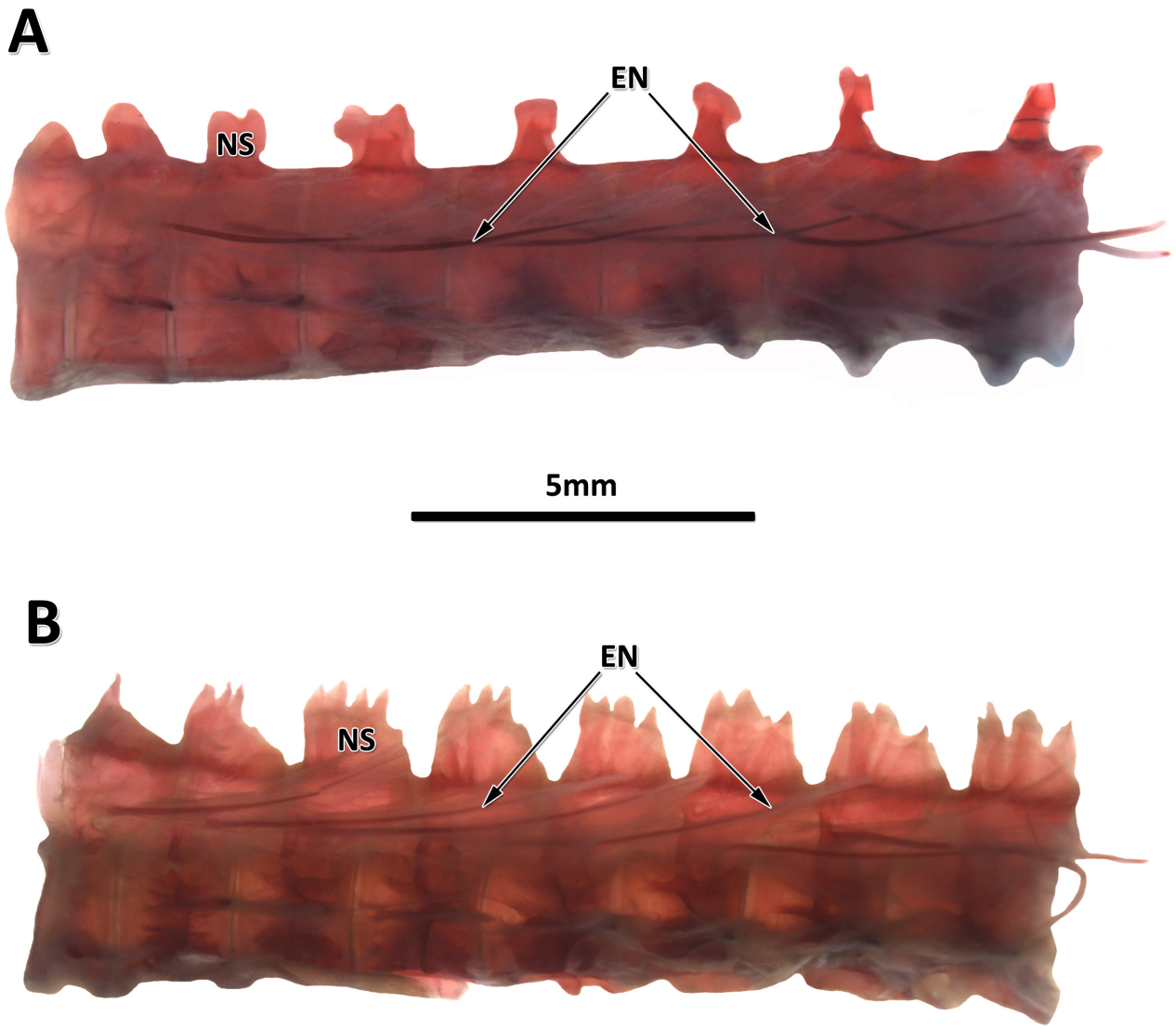

FIGURE 15. Anterior vertebrae. A, *Bathycongrus villosus* **sp. nov.** B, *Bassanago albescens*. Anatomical abbreviations: epineurals (EN), neural spines (NS).

Caudal skeleton. (Fig. 16) The caudal skeleton consists of fused dorsal hypurals 3 and 4 (**H 3–4**) and ventral hypurals 1 and 2 (**H 1–2**). The parhypural (**PH**) is fused to the hypurals 1–2 in *Bas. albescens* forming a hypural fenestra but is unfused to the hypurals in the new species. The first preural centrum (**PU1**) is situated anterior to the urostyle (**US**), which is formed by the fusion of the first and second ural vertebrae. Epurals are absent. Neural spines are lacking on the caudal vertebrae preceding the urostyle in the new species but are present in *Bas. albescens*. Four caudal rays associated with hypural 3–4 (five in *Bas. albescens*), four with hypural 1–2 and one with the parhypural.

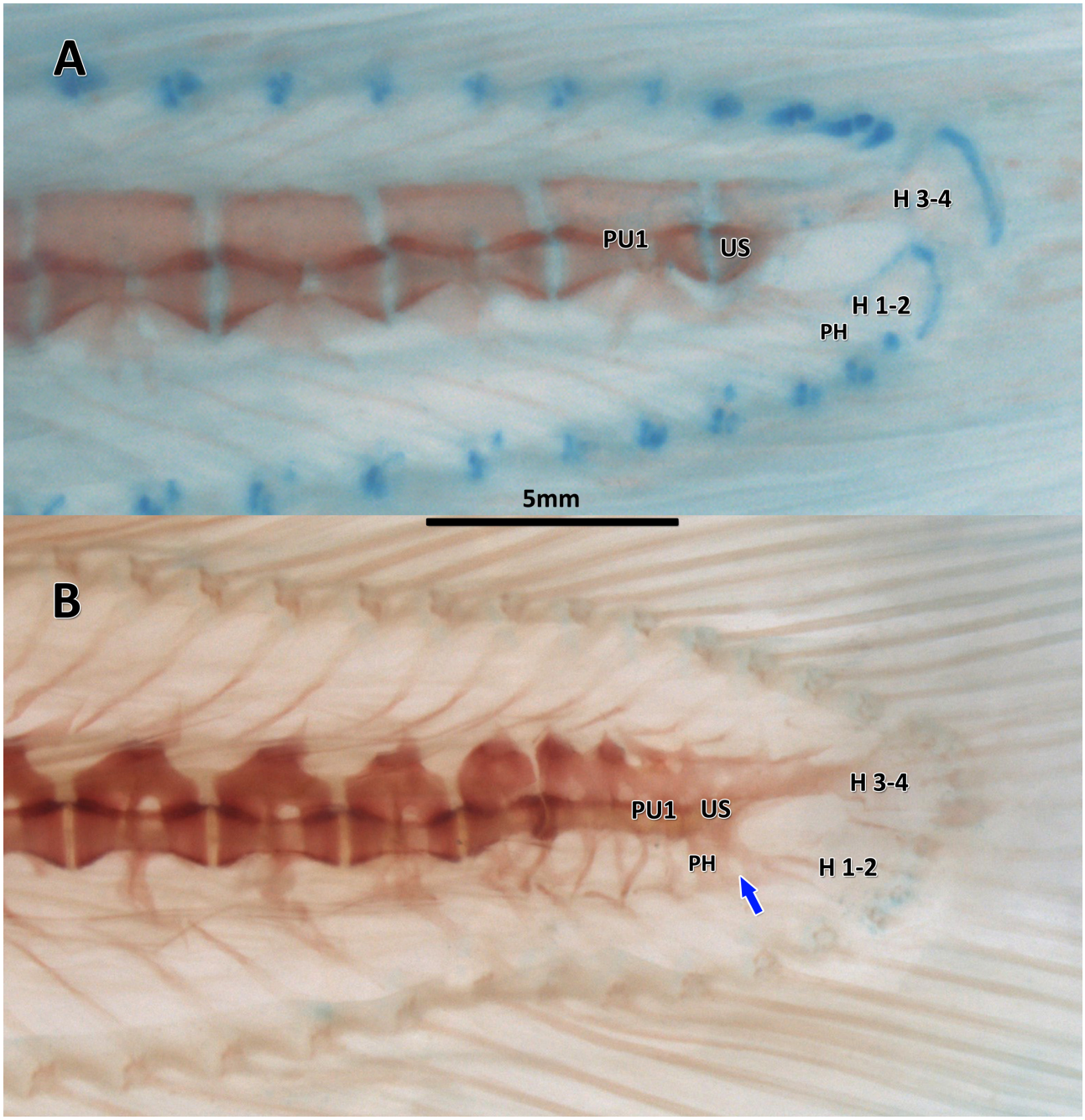

FIGURE 16. Caudal skeleton. A, *Bathycongrus villosus* **sp. nov.** B, *Bassanago albescens*. Anatomical abbreviations: first preural centrum (PU1), hypurals 1 and 2 (H1-2), hypurals 3 and 4 (H3-4), parhypural (PH), urostyle (US). Blue arrow points to the fenestra formed by the fusion of the parhypural to hypurals 1–2 in *Bassanago albescens*.

Discussion

The new species is clearly a member of the subfamily Congrinae, based on the following characters: preanal length less than 40% TL, posterior nostril at mid-eye level, tip of tail soft and flexible, dorsal- and anal-fin rays segmented.

Within this group, it is most similar to *Bassanago* and to certain small-toothed species currently placed in *Bathycongrus*. It resembles *Bassanago* in the following characters: snout slightly projecting beyond lower jaw; upper lip with reduced flange; teeth conical, small, all about the same size; head pores small; lateral-line pores tube-like; and, most distinctively, small hair-like epidermal processes on the surface of the head and body. It differs from *Bassanago* in its smaller size; shorter and stouter body with the tail tapering more abruptly; longer stomach and gas bladder; and fewer vertebrae. In addition, the species of *Bassanago* are restricted to the subtropical and temperate waters of the southern hemisphere south of 20° latitude. The new species, by contrast, is found in tropical waters of both the southern and northern hemisphere.

Of the small-toothed species of *Bathycongrus*, the new species resembles *B. bleekeri* Fowler, 1934 in the general shape of the body and tail, but that species has enlarged pores in the supraorbital and infraorbital canals, and it also has fewer vertebrae (107–113). The species *B. bimaculatus* Smith & Ho, 2018a*, B. trimaculatus* Karmovskaya & Smith, 2008, and *B. unimaculatus* Karmovskaya, 2009 are more pale in color and have distinct dark spots on the dorsal and anal fins. They also have enlarged head pores. The Atlantic species *B. dubius* (Breder, 1927) has a more elongate and gradually tapering body, and it also has enlarged head pores. The species that most resembles the new species is *Bat. parviporus*, which, as the name suggests, has small head pores. To clarify the relationships further, we have compared the new species with *Bassanago albescens* and *Bat. parviporus*. The results are shown in Table 2.

Of the 19 characters examined, the new species agrees with *Bathycongrus parviporus* in 16 and with *Bassanago albescens* in one. In two characters they are all different (Tables 2 and 3). The numbers in parentheses below refer to the character states.

TABLE 2. Character States in *Conger cinereus* (outgroup)*, Bassanago albescens*, *Bathycongrus villosus*, and *Bathycongrus parviporus*.

Character	*Conger cinereus* (outgroup)	*Bassanago albescens*	*Bathycongrus villosus*	*Bathycongrus parviporus*
1. LEP	(2) large	(1) intermediate	(2) large	(0) small
2. LFP	(0) absent	(1) present	(0) absent	(0) absent
3. BS process	(1) present	(1) present	(0) absent	(0) absent
4. Sphenotic	(1) wider	(1) wider	(0) narrower	(0) narrower
5. Supraoccipital crest	(1) present	(0) absent	(1) present	(1) present
6. Dentary	(0) convex	(0) convex	(1) concave	(1) concave
7. Opercle	(0) smooth	(0) smooth	(1) serrated	(1) serrated
8. Subopercle	(0) short	(0) short	(1) long	(1) long
9. Supracleithrum	(0) smooth	(0) smooth	(1) branched	(1) branched
10. Urohyal	(1) more expanded	(0) less expanded	(1) more expanded	(1) more expanded
11. Number of vertebrae	(1) intermediate (140–148)	(2) high (161–170)	(0) low (121–126)	(0) low (120–122)
12. Anterior vertebrae	(0) less spiny	(2) more spiny	(0) less spiny	(1) intermediate
13. Neural spines on posterior caudal vertebrae	(0) absent	(1) present	(0) absent	(0) absent
14. Parhypural	(1) partially fused to hypurals 1–2	(2) fused to hypurals 1–2	(0) unfused to hypurals 1–2	(0) unfused to hypurals 1–2
15. Dermal papillae	(0) absent	(1) present	(1) present	(0) absent
16. Gas bladder ends	(0) before anus	(0) before anus	(1) behind anus	(1) behind anus
17. Stomach	(0) pale	(0) pale	(1) dark	(1) dark
18. Peritoneum	(1) pale	(0) dark	(1) pale	(1) pale
19. Size	(0) large	(0) large	(1) small	(1) small

New species more like *Bassanago albescens*—1 character
New species more like *Bathycongrus parviporus* —16 characters
New species different from both—2 characters

TABLE 3. Data matrix of members of the eel genera *Conger, Bassanago*, and *Bathycongrus*. Characters and character states as explained in text. *Conger cinereus* is the outgroup.

Taxon/Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Conger cinereus	2	0	1	1	1	0	0	0	0	1	1	0	0	1	0	0	0	1	0
Bassanago albescens	1	1	1	1	0	0	0	0	0	0	2	2	1	2	1	0	0	0	0
Bathycongrus parviporus	0	0	0	0	1	1	1	1	1	1	0	1	0	0	0	1	1	1	1
Bathycongrus villosus	2	0	0	0	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1

1. The lateral ethmoid process on the upper jaw (Figs. 4 and 6) is long and broad and rounded in the new species and in *Conger cinereus* (outgroup) (2). Its length is about equal to the distance from the anterior end of the process to the tip of the upper jaw. In *Bassanago albescens*, it is shorter and more triangular, its length contained about three times in the distance from the anterior end of the process to the tip of the upper jaw (1). In *Bathycongrus parviporus* it is reduced, its length contained at least ten times in the antero-posterior distance of the ethmoid process (0) (Karmovskaya 2011: Fig. 4).
2. The lateral frontal process (Figs. 4 and 6) is clearly present in *Bassanago albescens* (1) but absent in the new species (0). It is also absent in *Bathycongrus parviporus* (Karmovskaya 2011: Fig. 4) and in *Conger cinereus* (0).
3. The basisphenoid (Fig. 5) has a smooth anterior margin in the new species (0), whereas in *Bassanago albescens* and *Conger cinereus* (outgroup) it has a distinct process (1). *Bathycongrus parviporus* also lacks a process (0) (Karmovskaya 2011: Fig. 4).
4. In dorsal and ventral views, the sphenotic is more slender and acute in the new species and *Bathycongrus parviporus* (Karmovskaya 2011: Fig 4) (0) than in *Bassanago albescens* (1) (Figs. 4 and 6). The condition in the outgroup is similar to that observed in *Bassanago albescens* (1).
5. In the new species, in *Bathycongrus parviporus*, and in *Conger cinereus* (outgroup) the supraoccipital bears a low crest on its posterior part (1). In *Bassanago albescens*, this crest is absent (0).
6. In the new species and in *Bathycongrus parviporus* the ventral profile of the dentary (Fig. 8) is distinctly concave (1). In *Bassanago albescens* and in *Conger cinereus* (outgroup) it is convex (0).
7. The posterior edge of the opercle is distinctly serrated in the new species (Fig. 8A) and in *Bathycongrus parviporus* (Karmovskaya 2011: Fig. 5) (1), whereas it is smooth in *Conger cinereus* (outgroup) and in *Bassanago albescens* (Fig. 8B) (0).
8. In both the new species (Fig. 8A) and *Bathycongrus parviporus* (Karmovskaya 2011: Fig. 5b), the subopercle is long, curving up behind the posterior edge of the opercle (1). In *Conger cinereus* (outgroup) and in *Bassanago albescens* (Fig. 8B), it is short, not extending behind the opercle (0).
9. The upper end of the supracleithrum in both the new species (Fig. 14A) and *Bathycongrus parviporus* (Karmovskaya 2011: Fig. 5c) is irregular in shape, with lobes and projections (1). In *Conger cinereus* (outgroup) and in *Bassanago albescens* (Fig. 14B), it is smooth (0).
10. In lateral view, the posterior part of the urohyal is more expanded dorsoventrally in the new species and has a distinct projection on the dorsal edge (Fig, 11A) (1). In *Bassanago albescens* (Fig. 11B), it is less expanded, and the dorsal edge is smooth (0). The urohyal of *Bathycongrus parviporus* and *Conger cinereus* (outgroup) is more similar to the new species, more expanded and with an irregular dorsal edge (Karmovskaya 2011: Fig. 6) (1).
11. The number of vertebrae is distinctly greater in *Bassanago albescens* (161–172) (2), intermediate in *Conger cinereus* (140–148) (Smith & Ho 2018b: Table 1) (1) and lower in the new species (121–126) and *Bathycongrus parviporus* (120–122) (0).
12. The neural spines of the anterior vertebrae form a progressive series in terms of their ornamentation. In the new species (Fig. 15A) and in *Conger cinereus* (outgroup), they are narrow and relatively simple, with little ornamentation on the dorsal edge (0). In *Bassanago albescens* (Fig. 15B), the neural arches are broader and bordered with spiny projections (2). In *Bathycongrus parviporus* (Karmovskaya 2011: Fig. 7a), the condition is somewhat intermediate in both shape and ornamentation (1).
13. *Bassanago albescens* has neural spines on the posteriormost vertebrae (Fig. 16B) (1), whereas *Conger cinereus* (outgroup), the new species (Fig. 16A) and *Bathycongrus parviporus* (Karmovskaya 2011: Fig. 8) lack them (0).
14. The parhypural is contiguous and apparently fused partially to hypurals 1-2 in *Conger cinereus* (outgroup) (1),

but completely fused to hypurals 1-2 in *Bassanago albescens* (Fig. 16B) (2). Conversely, the parhypural is unfused to hypurals 1-2 in both *Bathycongrus parviporus* and the new species (Fig. 16A) (0).

15. The small dermal papillae on the head and body are found in the new species and in *Bassanago albescens* (1). This character is absent in *Conger cinereus* (outgroup) and in the other species of *Bathycongrus*, including *Bat. parviporus* (0).
16. The gas bladder ends before the anus in *Conger cinereus* (outgroup) and *Bassanago albescens* (0), whereas in both the new species and *Bathycongrus parviporus* it extends well behind the anus (1).
17. The stomach is pale in *Conger cinereus* (outgroup) and *Bassanago albescens* (0), but dark in both the new species and *Bathycongrus parviporus* (1).
18. The peritoneum is uniformly dark in *Bassanago albescens* (0). In both the new species and *Bathycongrus parviporus*, it is pale ventrally and laterally, with a slight darkening on the dorsal side (1). The peritoneum is pale in *Conger cinereus* (outgroup) (1).
19. Both the new species and *Bathycongrus parviporus* are small, less than 300 mm in TL (1). *Conger cinereus* (outgroup) and *Bassanago albescens* grow significantly larger, reaching a TL over 600 mm (0).

Thus, the new species agrees with *Bathycongrus parviporus* in 16 characters and with *Bassanago albescens* in only one (Table 2). Moreover, in our analysis of relationships of members of the subfamily Congrinae, 11 of the 19 investigated morphological characters are optimized as unambiguous and homoplasy-free synapomorphies for the monophyletic group including the new species and *Bat. parviporus* (Fig. 17). Based on these results, we are placing this species in *Bathycongrus*. However, more comprehensive phylogenetic studies are needed to determine the interrelationships of the species within the subfamily Congrinae.

The holotype and paratypes came from widely separated locations, but there are no obvious differences between them. There are slight differences in some of the morphometric characters, but the sample size is small, and the significance is uncertain. They were collected at similar depths and may occur in the intervening area as well. Precise information on habitat is not available.

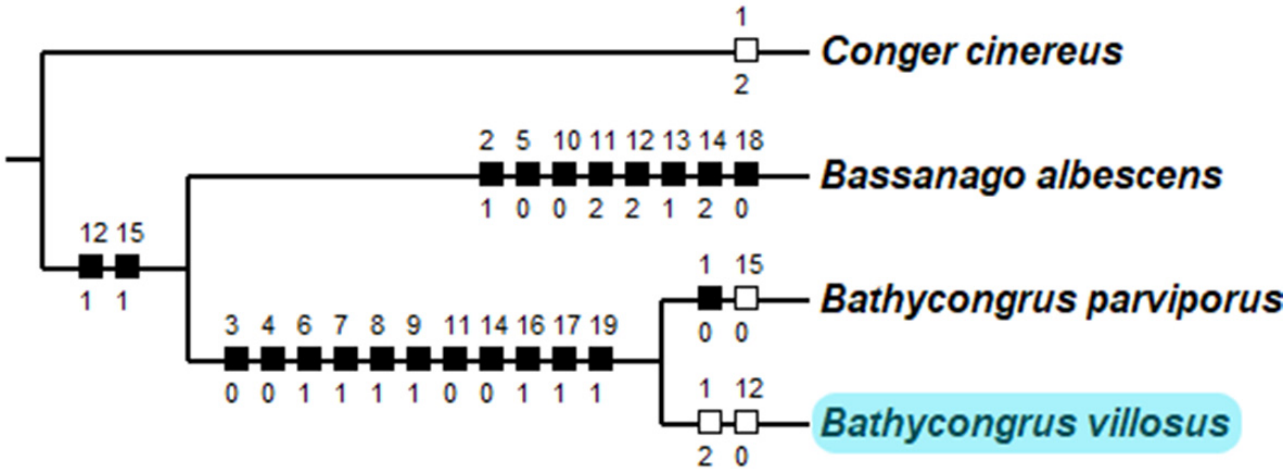

FIGURE 17. Cladogram of relationships of members of *Conger*, *Bassanago* and *Bathycongrus* derived from a matrix with four terminal-taxa and 19 equally weighted characters (L = 24; CI = 96; RI = 90).

Acknowledgments

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