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A new generic name for the "*Lepadichthys*" *lineatus* complex with a rediagnosis of *Discotrema*, a senior synonym of *Unguitrema*, and comments on their phylogenetic relationships (Gobiesocidae: Diademichthyinae)

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https://zoobank.org/C920DCB5-053D-4DD6-8892-3BA74E65C092

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Academic editor Ralf Britz | **Received** 17 October 2023 | **Accepted** 5 February 2024 | **Published** 28 March 2024

Citation: Fujiwara K, Motomura H, Summers AP, Conway KW (2024) A new generic name for the "*Lepadichthys*" *lineatus* complex with a rediagnosis of *Discotrema*, a senior synonym of *Unguitrema*, and comments on their phylogenetic relationships (Gobiesocidae: Diademichthyinae). Vertebrate Zoology 74 279–301. https://doi.org/10.3897/vz.74.e113955

Abstract

Rhinolepadichthys, a new genus of the gobiesocid subfamily Diademichthyinae, is described for the "*Lepadichthys*" *lineatus* complex (including *Rhinolepadichthys geminus* **comb. nov.**, *R. heemstraorum* **comb. nov.**, *R. lineatus* **comb. nov.**, and *R. polyastrous* **comb. nov.**). Detailed investigation of external morphology and osteological anatomy of the new genus and related genera suggests that *Rhinolepadichthys* represents the sister genus to *Discotrema*, based on the following putative synapomorphies: (1) presence of a hardened (potentially keratinized) cap on the surface of at least some disc papillae (vs. surface of disc papillae soft, without hardened cap); and (2) the anterolateral part of the ventral postcleithrum extended anteriorly as a well-developed rod-like process, its tip close to the base of pelvic-fin soft ray 4 (vs. only weakly pointed, or irregular). Compared with *Discotrema*, *Rhinolepadichthys* **gen. nov.** is distinguished by the presence of a row of 8–12 large papillae on the inner surface of the upper and lower lips (vs. inner surface of lips smooth, without distinct papillae); the absence (vs. presence) of a well-developed lateral process on the pterotic immediately posterior to the opening of the otic canal; the presence (vs. absence) of gill rakers on the anterior edge of ceratobranchials 1–3; the presence (vs. absence) of gill rakers on the posterior edge of ceratobranchial 4; having the upper pharyngeal teeth arranged in a loose patch on the ventral surface of the pharyngobranchial 3 toothplate, with tooth tips directed posteroventrally (vs. arranged in a single row along posteroventral edge of the pharyngobranchial 3 toothplate, with tooth tips directed posteriorly); features of the adhesive disc, including outline of disc papillae roughly hexagonal or ovoid and with a flattened surface (vs. outline circular, at least some with raised, dome-like surface); the absence (vs. presence) of a deep cavity at the center of disc region C; the absence (vs. presence) of three paired and one median cluster of small papillae (reminiscent of bunches of grapes) across the surface of the adhesive disc; and having the ventral postcleithrum entire, not divided into two separate, articulating elements (vs. ventral postcleithrum divided into an anterior and posterior element, separated via a specialized joint). Reexamination of materials of the poorly known genus *Unguitrema*, considered a close relative of *Discotrema*, revealed no morphological differences between the two genera. *Unguitrema* therefore represents a junior synonym of *Discotrema*.

Keywords

Clingfishes, Indopacific, morphology, taxonomy, Teleostei

Introduction

Lepadichthys lineatus Briggs, 1966 (Fig. 1A) was described based on two specimens collected from the Red Sea, and subsequently recorded from locations throughout the Indopacific (Briggs 1986; Randall 1995; Allen and Erdmann 2012). The generic assignment of this species has been contentious since the original description. Whereas Briggs (1966, 1986, 2001) and others (e.g., Randall 1995; Craig and Randall 2008) have considered this species a member of *Lepadichthys* Waite, 1904, several authors have instead considered it a member of *Discotrema* Briggs, 1976 (e.g., Hayashi and Hayashi 1985 [first mention]; Hayashi et al. 1986; Hayashi 1993, 2000, 2002; Hutchins 2001; Hayashi and Hagiwara 2013). In their study of *Discotrema*, Craig and Randall (2008: 73) briefly discussed the conflicting taxonomic views concerning *L. lineatus* and noted that "future study may result in its placement in a new monotypic genus." In a recent

Figure 1. Representatives of diademichthyine clingfishes. **A** *Rhinolepadichthys lineatus* (Oman: J. Randall); **B** *Rhinolepadichthys geminus* (Anilao, Philippines: J. Eyre); **C** *Rhinolepadichthys geminus* (Okinoerabu Islands, Amami Islands, Japan: K. Uehara); **D** *Discotrema crinophilum* (Amami-oshima Island, Amami Islands, Japan: KPM-NR 78755, K. Uchino); **E** *Lepadichthys frenatus* (Lord Howe Island, Australia: J. Eyre); **F** *Diademichthys lineatus* (Lembeh Strait, Indonesia: KPM-NR 147468, K. Uchino). All images except **F** with sides reversed.

molecular phylogenetic study of Gobiesocidae, Conway et al. (2020) showed that *Lepadichthys* is polyphyletic (referred to as "*Lepadichthys*" hereafter) and recovered "*L.*" *lineatus* as a close relative of *Discotrema* (Fig. 1D) and *Diademichthys* Pfaff, 1942 (Fig. 1F), and not the closest relative of any other species of "*Lepadichthys*" included in that study (Fig. 2; the type species *L. frenatus* Waite, 1904 [Fig. 1E] was not included). Subsequently, Fujiwara and Motomura (2021) demonstrated that specimens previously identified as "*L.*" *lineatus* comprised four distinct species, three of which were described as new (viz., "*L.*" *geminus* [Fig. 1B, C], "*L.*" *heemstraorum*, and "*L.*" *polyastrous*). Fujiwara and Motomura (2021) also provided a redescription of "*L.*" *lineatus*, which they identified as a senior synonym of "*L.*" *caritus* Briggs, 1969, and defined the "*L.*" *lineatus* complex (including "*L.*" *lineatus*, "*L.*" *geminus*, "*L.*" *heemstraorum*, and "*L.*" *polyastrous*) based on unique characters of the snout and lips (see Fujiwara and Motomura 2021: fig. 1), and considered this complex more closely related to *Discotrema* than *Lepadichthys* (sensu stricto = "core" *Lepadichthys* sensu Fujiwara et al. 2021). Fujiwara and Motomura (2021) also listed several differences between members of the "*L.*" *lineatus* complex and those of *Discotrema*, and suggested that a new genus should be established for the former.

The contentious taxonomic history of "*Lepadichthys*" *lineatus* and the "*L.*" *lineatus* complex encouraged us to take a closer look at the anatomy of this group in comparison to that of *Lepadichthys* (sensu stricto), and also *Discotrema* and the putatively closely related *Unguitrema* Fricke, 2014 (type species: *Unguitrema nigrum* Fricke, 2014). In doing so, we discovered further osteological differences between members of the "*L.*" *lineatus* complex and those of *Lepadichthys* (sensu stricto), and also between this complex and *Discotrema*, justifying the recognition of a new genus for the "*L.*" *lineatus* complex (described herein). In contrast, we were unable to identify morphological differences between *Discotrema* and *Unguitrema* and we conclude that the latter represents a junior synonym of the former. We also discuss the phylogenetic relationship of the new genus and conclude that it represents the sister taxon to *Discotrema*, based on a number of putative morphological synapomorphies.

Materials and Methods

Material examined as part of this study includes that listed by Conway et al. (2021: 436) and Fujiwara et al.

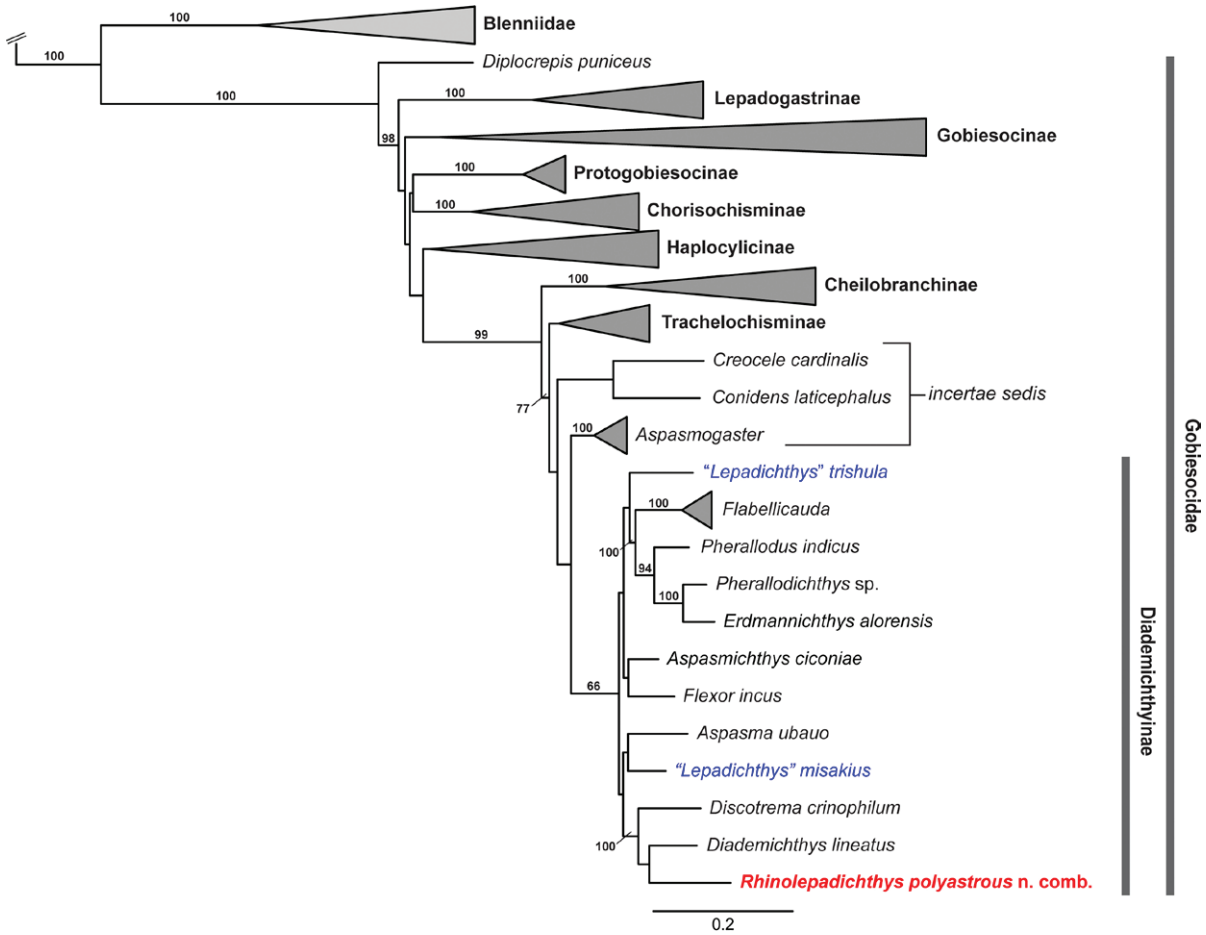

Figure 2. Phylogenetic relationships of Gobiesocidae modified from Conway et al. (2020: fig. 3) showing placement of *Rhinolepadichthys polyastrous* (red) and other species of "*Lepadichthys*" (blue). Numbers above branches represent bootstrap support values (values below 65 not shown).

(2021: 782, 2022: 495) and the additional material listed below. Features of both the adhesive disc and cephalic lateral-line canal pores were observed using versatile staining with Cyanine Blue (Saruwatari et al. 1997). Select specimens were cleared and double stained (C&S) following the protocol of Taylor and Van Dyke (1985). Observations and photographs of specimens or their parts were generally made using a ZEISS SteReo Discovery V20 stereomicroscope equipped with a Zeiss Axiocam MRc5 digital camera, or a Nikon D850 camera with an internal focus bracketing function. Images were obtained using the stacking function in the Zeiss Axiovision software or Adobe Photoshop 2023, and processed using a combination of Adobe Photoshop 2023 and Illustrator 2023. Computed tomography (CT) scans of select specimens were obtained at the Karel F. Liem Bio-Imaging Center (Friday Harbor Laboratories, University of Washington), using a Bruker SkyScan 1173 scanner (for "*Lepadichthys*" *polyastrous*), or at the National Museum of Science and Nature, using an inspeXio SMX-225CR FPD HR Plus (for "*Lepadichthys*" *geminus* and *Discotrema monogrammum*). Scans were run at 60 kV and 110 µA on a 2048×2048 pixel CCD at a resolution of 13.8 µm (for "*Lepadichthys*" *polyastrous*) or 8 µm (for "*Lepadichthys*" *geminus* and *Discotrema monogrammum*). Specimens were scanned while inside a 15 ml plastic Falcon tube, in which they were wrapped with cheesecloth moistened with ethanol (70%) to prevent movement during scanning. The resulting CT data were visualized using 3D Slicer v.4.10.2 (https://www.slicer.org) or VGSTUDIO MAX ver. 3.3, and have been deposited on MorphoSource (https://www.morphosource.org).

Osteological terminology used herein generally follows Springer and Fraser (1976), with modifications from Conway et al. (2018). In this study, a small bony element located along the ventral midline between the ventral postcleithra is referred to as an "accessory ossicle". This term was first used by Shiogaki and Dotsu (1983: figs 3C, 5B, 7B) and Hayashi et al. (1986: fig. 21) but applied inconsistently to different (non-homologous) bony elements of various sizes located at the posterior part of the adhesive disc in diademichthyine clingfishes. For example, this term was used for both the smaller ossifications located posterior to the ventral postcleithra (*Aspasma* Jordan & Fowler, 1902, *Diademichthys*, "*Lepadichthys*", *Pherallodichthys* Briggs, 1955, *Pherallodus* Shiogaki & Dotsu, 1983, and *Propherallodus* Shiogaki & Dotsu, 1983) and for part of the ventral postcleithrum (*Discotrema*). The fimbriae along the posterior margin of the ventral postcleithra were not taken into consideration by Shiogaki and Dotsu (1983) or Hayashi et al. (1986) (based on the absence of fimbriae in their illustrations) and this may have led these authors to overlook the strange configuration of the ventral postcleithra (divided into two parts) in *Discotrema* (see below). Adhesive disc terminology generally follows Briggs (1955: fig. 1). Cephalic lateral-line canal pore terminology and abbreviations follow Shiogaki and Dotsu (1983: fig. 1) and Conway et al. (2017: fig. 1). Generic membership of the Diademichthyinae used herein follows Fujiwara et al. (2023), which differs from that of Conway et al. (2020) by the exclusion of *Lissonanchus* Smith, 1966, and its junior synonym *Briggsia* Craig & Randall, 2009. Standard length is abbreviated as SL. Collection abbreviations follow Sabaj (2020).

"*Lepadichthys*" *geminus*, **"*Lepadichthys*" *heemstraorum***, and **"*Lepadichthys*" *lineatus***: specimens listed in Fujiwara and Motomura (2021), including NSMT-P 132199, paratype of "*L.*" *geminus*, 15.9 mm SL, Ambon, Indonesia (CT; https://doi.org/10.17602/M2/M597330).

"*Lepadichthys*" *polyastrous*: specimens listed in Fujiwara and Motomura (2021) plus ROM 72940, 21 specimens, 9.4–33.4 mm SL, (1CT; https://doi.org/10.17602/M2/M29846), SAIAB 9319, 2 specimens, 23.5–25.0 mm SL, Sodwana Bay, KwaZulu-Natal, South Africa (C&S).

Discotrema crinophilum (37 specimens): USNM 215329, holotype, 22.1 mm SL, off Benga Island, Fiji; KAUM–I. 45108–45109, 2 specimens, 12.0–14.2 mm SL, KAUM–I. 72122, 25.2 mm SL, KAUM–I. 145059–145061, 3 specimens, 13.2–34.3 mm SL, KAUM–I. 145201–145206, 6 specimens, 12.0–25.9 mm SL, KAUM–I. 145211, 22.9 mm SL, KAUM–I. 145217–145218, 2 specimens, 11.2–32.5 mm SL, KAUM–I. 153204–153211, 8 specimens, 15.6–29.1 mm SL, KAUM–I. 153213–153217, 5 specimens, 19.2–29.4 mm SL, KAUM–I. 159922–159924, 3 specimens, 14.3–17.5, Amami Islands, Kagoshima, Japan; ROM 65282, 4 specimens (1C&S) 20.7–43.9 mm SL, Coral Sea, New Caledonia; ROM 85350, 25.4 mm SL, Raja Ampat, Indonesia (C&S); WAM P. 26100-009, 1 of 6 specimens, 22.2 mm SL, Christmas Island, Western Australia.

Discotrema monogrammum (6 specimens): BPBM 39040, holotype, 21.2 mm SL, BPBM 40504, paratype, 16.4 mm SL (CT; https://doi.org/10.17602/M2/M597259), Kimbe Bay, New Britain, Papua New Guinea; BPBM 36504, 2 paratypes, 15.5–21.2 mm SL, Flores, Indonesia; BPBM 36899, 2 paratypes, 18.9–19.8 mm SL, Normanby Island, Papua New Guinea.

Discotrema zonatum (1 specimen): BPBM 38972, holotype, 23.0 mm SL, Charybdis Reef, Fiji.

Unguitrema nigrum (2 specimens): NTUM 10603, holotype, 11.1 mm SL, MNHN 2015-0142, paratype, 10.0 mm SL, Madang, Papua New Guinea.

Taxonomy

Rhinolepadichthys gen. nov.

https://zoobank.org/C3BDA09B-3C4E-4689-A5EE-31C3233C0749

Type species. *Lepadichthys polyastrous* Fujiwara & Motomura, 2021

Diagnosis. A new genus of the Gobiesocidae belonging to the Diademichthyinae and distinguished from all other genera by having a row of 8–12 large papillae on the inner surface of the upper and lower lips (Fig. 3C, F).

The following characters are also diagnostic, although not unique to the new genus (details discussed in "Relationships of *Rhinolepadichthys* **gen. nov.** and *Discotrema*" [see below]): snout tip well extended, distinctly beyond tip of lower jaw (Fig. 3B, E); upper lip fused with skin of snout, therefore usually lacking a distinct groove between lip margin and snout, but if present, groove very weak, restricted to posterior portion of upper jaw only (Fig. 3A, B, D, E); anterior part of lower lip without skin lobes and fused with skin of gular area (Fig. 3C, F); absence of well-developed lateral process on pterotic immediately posterior to exit of otic canal (Figs 4A, B, 5A, B, 6); upper-jaw teeth only weakly hooked, with tip of crown blunt or rounded (Figs 4B, 5B, 7A, D); medial edge of premaxilla very weakly concave, forming indistinct, narrow oval opening anteriorly in dorsal view between premaxillae (Figs 4A, 5A); gill membrane attached to isthmus; upper pharyngeal teeth arranged in a loose patch on ventral surface of pharyngobranchial 3 toothplate, with tooth tips directed posteroventrally (Figs 4C, 5C, 7F, G); two rows and single row of gill rakers on ceratobranchials 1–3 and 4, respectively (Fig. 7E); ceratobranchial 5 edentulous (Fig. 7E, H); preopercle without lateral-line canal and associated pores (PR1–3) (Fig. 3); single adhesive disc (Fig. 8A); absence of a deep cavity at center of disc region C (Fig. 8A); absence of three paired

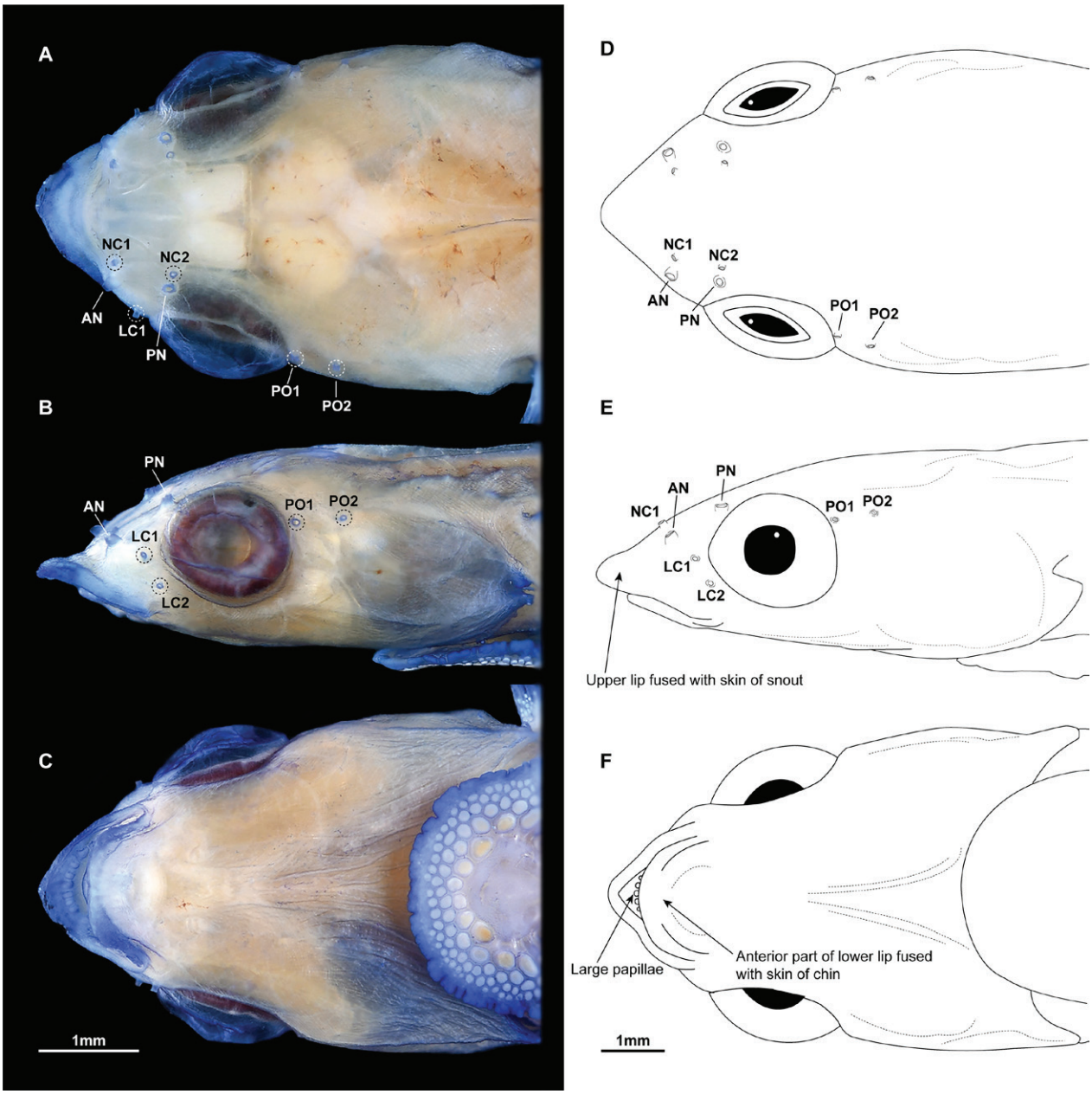

Figure 3. Heads of *Rhinolepadichthys geminus*. **A**–**C** NSMT-P 132199, 15.9 mm SL (cyanine stain); **D**–**F** KAUM–I. 145207, 21.2 mm SL (line drawing). **A**, **D** dorsal views; **B** right side in lateral view (image reversed); **E** left side in lateral view; **C**, **F** ventral views. Abbreviations: AN, anterior nostril; LC1–2, lachrymal canal pores; NC1–2, nasal canal pores; PN, posterior nostril; PO1–2 postorbital canal pores.

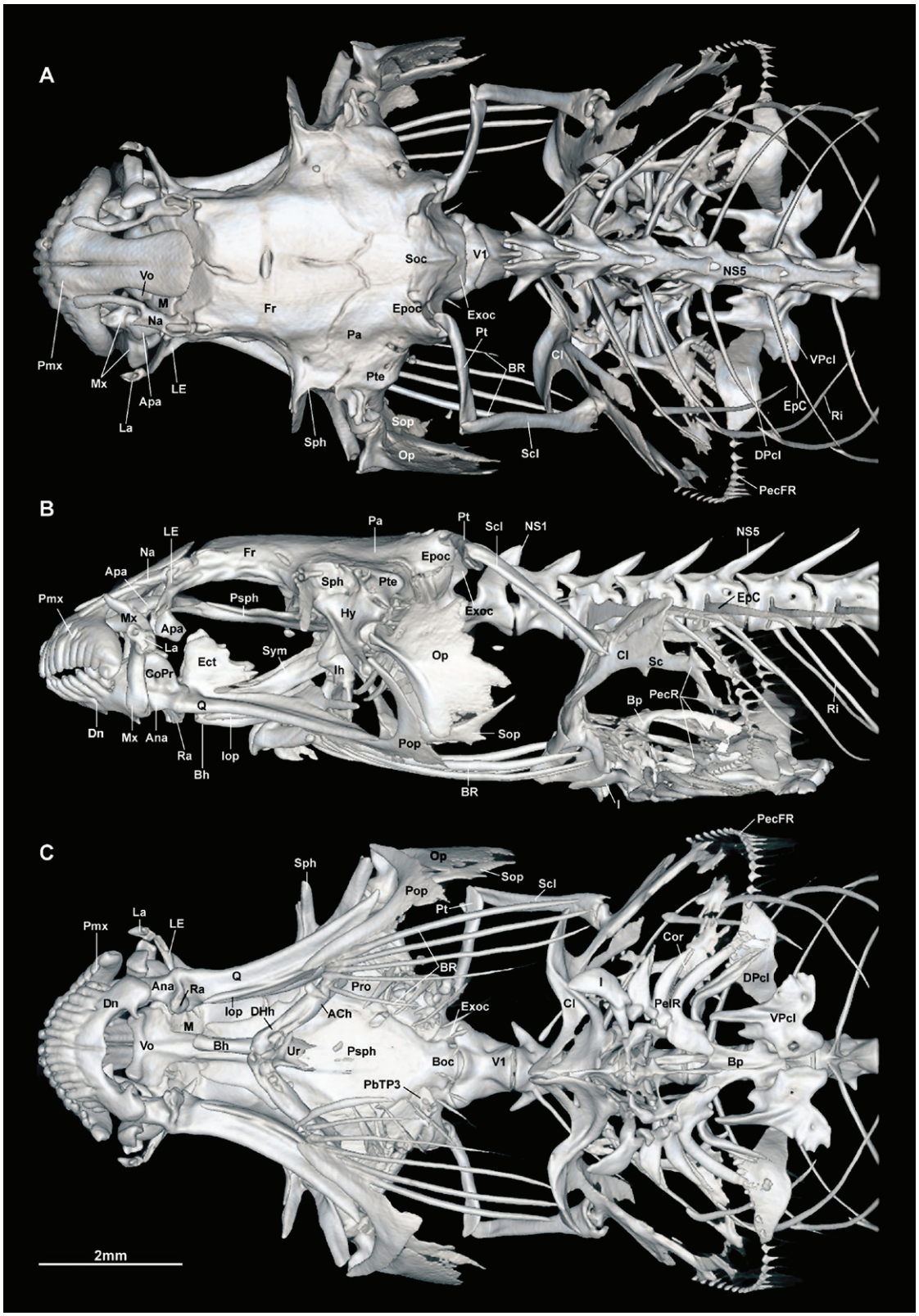

Figure 4. CT scanned anterior skeleton, including cranium, paired-fin girdles, and abdominal region of vertebral column, of *Rhinolepadichthys polyastrous* (ROM 72940, 33.4 mm SL). **A** dorsal view; **B** lateral view; **C** ventral view. Abbreviations: ACh, anterior ceratohyal; Ana, angulo-articular; Apa, autopalatine; Bh, basihyal; Boc, basioccipital; Bp, basipterygium; BR, branchiostegal rays; Cl, cleithrum; CoPr, coronoid process; Cor, coracoid; DHh, dorsal hypohyal; Dn, dentary; DPcl, dorsal postcleithrum; Ect, ectopterygoid; EpC, epicentral; Epoc, epiotic; Exoc, exoccipital; Fr, frontal; Hy, hyomandibular; I, pelvic-fin spine; Ih, interhyal; Iop, interopercle; La, lachrymal; LE, lateral ethmoid; M, mesethmoid; Mx, maxilla; Na, nasal; NS1, 5, neural spine of vertebral centrum 1, 5; Op, opercle; Pa, parietal; PbTP3, pharyngobranchial 3 toothplate; PecFR, pectoral-fin rays; PecR, pectoral radials; PelR, pelvic-fin soft rays; Pmx, premaxilla; Pop, preopercle; Pro, prootic; Psph, parasphenoid; Pt, posttemporal; Pte, pterotic; Q, quadrate; Ra, retroarticular; Ri, ribs; Sc, scapula; Scl, supracleithrum; Soc, supraoccipital; Sop, subopercle; Sph, sphenotic; Sym, symplectic; Ur, urohyal; V1, vertebral centrum 1; Vo, vomer; VPcl, ventral postcleithrum.

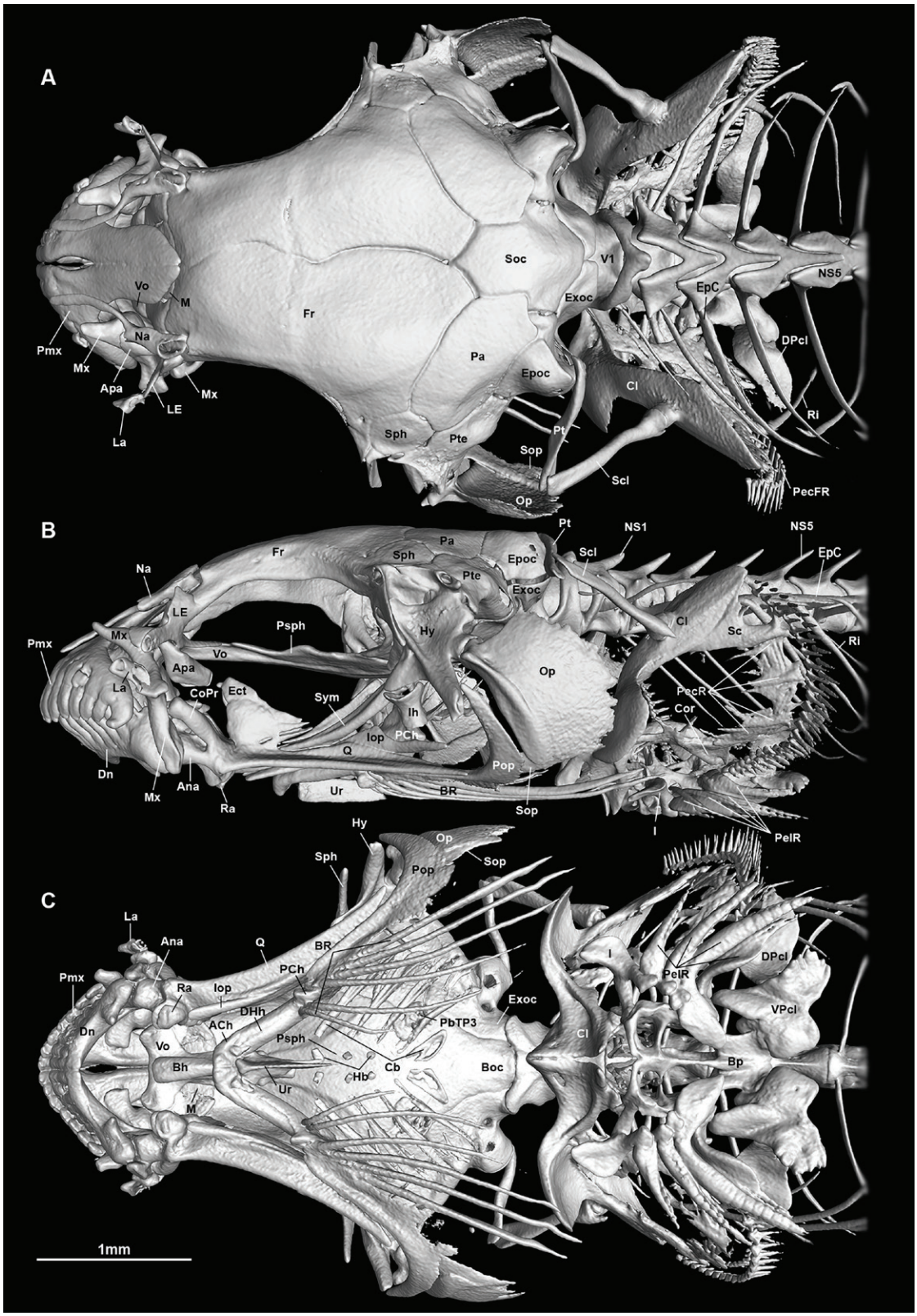

Figure 5. CT scanned anterior skeleton, including cranium, paired-fin girdles, and abdominal region of vertebral column, of *Rhinolepadichthys geminus* (NSMT-P 132199, 15.9 mm SL). **A** dorsal view; **B** lateral view; **C** ventral view. Abbreviations: ACh, anterior ceratohyal; Ana, angulo-articular; Apa, autopalatine; Bh, basihyal; Boc, basioccipital; Bp, basipterygium; BR, branchiostegal rays; Cb, ceratobranchials; Cl, cleithrum; CoPr, coronoid process; Cor, coracoid; DHh, dorsal hypohyal; Dn, dentary; DPcl, dorsal postcleithrum; Ect, ectopterygoid; EpC, epicentral; Epoc, epiotic; Exoc, exoccipital; Fr, frontal; Hb, hypobranchials; Hy, hyomandibular; I, pelvic-fin spine; Ih, interhyal; Iop, interopercle; La, lachrymal; LE, lateral ethmoid; M, mesethmoid; Mx, maxilla; Na, nasal; NS1, 5, neural spine of vertebral centrum 1, 5; Op, opercle; Pa, parietal; PbTP3, pharyngobranchial 3 toothplate; PCh, posterior ceratohyal; PecFR, pectoral-fin rays; PecR, pectoral radials; PelR, pelvic-fin soft rays; Pmx, premaxilla; Pop, preopercle; Psph, parasphenoid; Pt, posttemporal; Pte, pterotic; Q, quadrate; Ra, retroarticular; Ri, ribs; Sc, scapula; Scl, supracleithrum; Soc, supraoccipital; Sop, subopercle; Sph, sphenotic; Sym, symplectic; Ur, urohyal; V1, vertebral centrum 1; Vo, vomer; VPcl, ventral postcleithrum.

and one median cluster of small papillae across disc surface (Fig. 8A); disc papillae with a roughly hexagonal or ovoid outline and flattened surface, some larger papillae with a hardened (potentially keratinized) cap (Fig. 8A); anterolateral part of ventral postcleithrum extended anteriorly as a well-developed rod-like process, its tip close to base of pelvic-fin soft ray 4 (Figs 4C, 5C, 8B); and ventral postcleithrum entire, not divided into two separate, articulating elements (Figs 4C, 5C, 8B).

Description. See Fujiwara and Motomura (2021: 63: "Common features of the *L. lineatus* complex") for information on external morphology. Photographs and line drawing of heads, showing cephalic lateral-line canal pores plus snout and lip characters, given in Fig. 3. Features of osteology shown in Figs 4–9. Neurocranium comprising nasal, lateral ethmoid, mesethmoid, sphenotic, pterotic, epiotic, prootic, supraoccipital, basioccipital, exoccipital, frontal, vomer, parasphenoid, and parietal (Fig. 6). Nasal slender, its an-

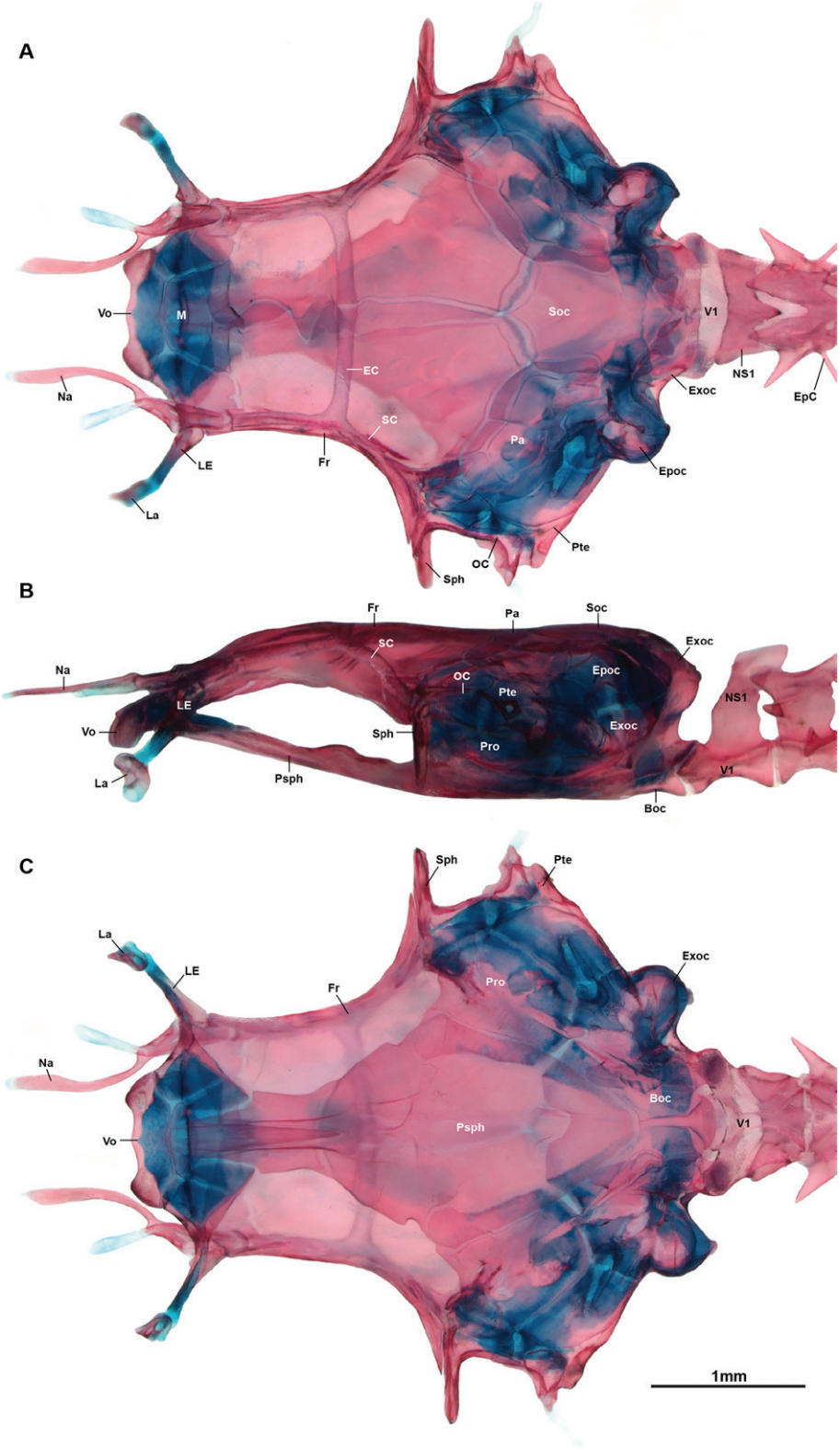

Figure 6. Neurocranium of *Rhinolepadichthys polyastrous* (SAIAB 9319, 25.0 mm SL). **A** dorsal view; **B** lateral view; **C** ventral view. Abbreviations: Boc, basioccipital; EC, epiphyseal commissure of supraorbital canal; EpC, epicentral; Epoc, epiotic; Exoc, exoccipital; Fr, frontal; La, lachrymal; LE, lateral ethmoid; M, mesethmoid; Na, nasal; NS1, neural spine of vertebral centrum 1; OC, otic canal; Pa, parietal; Pro, prootic; Psph, parasphenoid; Pte, pterotic; SC, supraorbital canal; Soc, supraoccipital; Sph, sphenotic; V1, vertebral centrum 1; Vo, vomer.

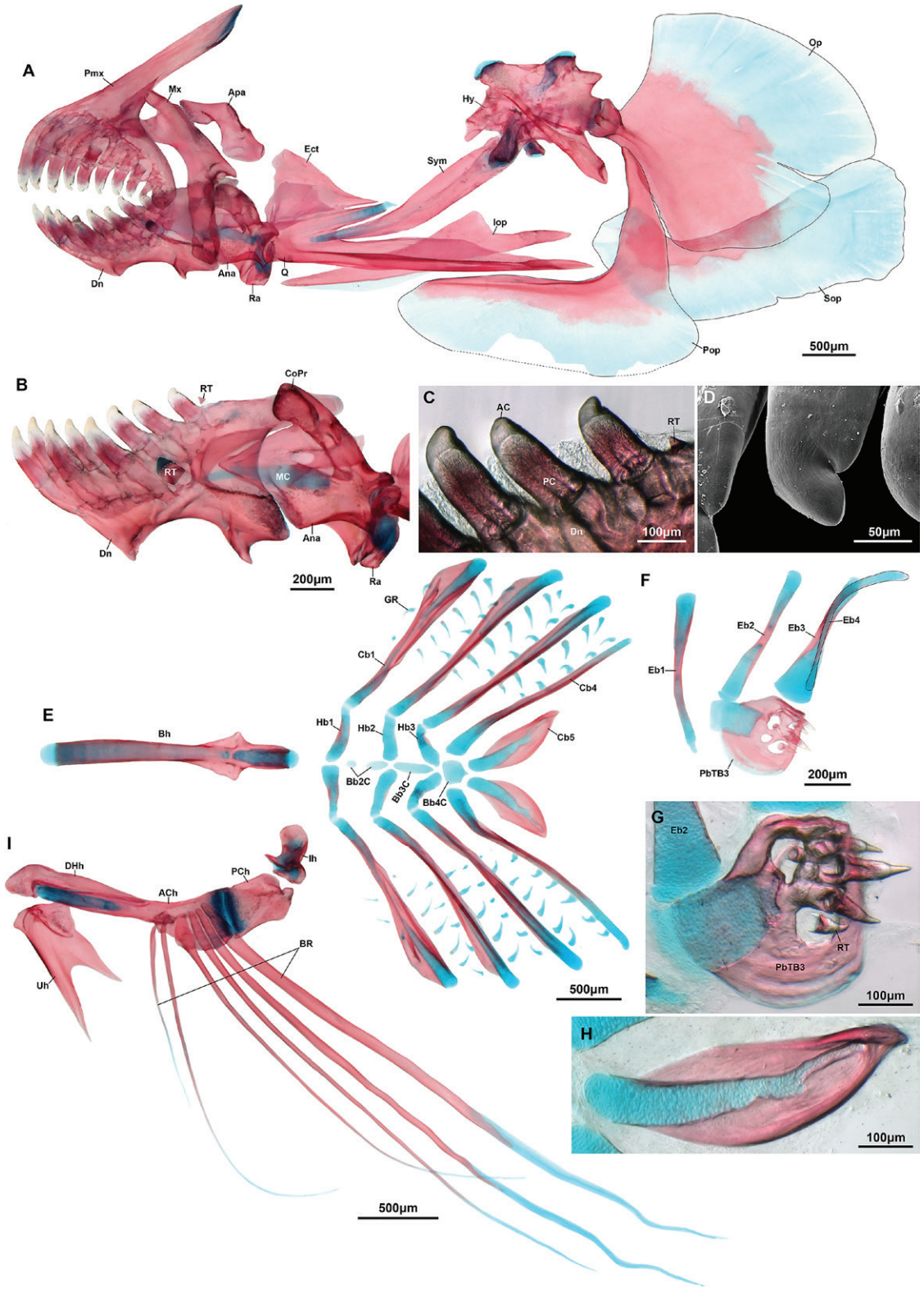

Figure 7. Viscerocranium of *Rhinolepadichthys polyastrous* (SAIAB 9319, 25.0 mm SL [except scanning electron micrograph]). **A** Hyopalatine arch and opercular series (right side) in lateral view (image reversed), outline of preopercle, opercle, and subopercle highlighted by thin black line, thin dashed line indicates damage to margin of preopercle; **B** lower jaw (left side) in lateral view; **C** close-up of posterior teeth on dentary (left side) in lateral view; **D** close-up of upper jaw teeth from Conway et al. (2015: fig. 11I); **E** lower gill-arch elements in dorsal view; **F** upper gill-arch elements (right side) in dorsal view; **G** close-up of PbTP3 (left side) in ventral view; **H** close-up of Cb5 (left side) in dorsal view; **I** hyoid bar (left side) in lateral view and urohyal. Abbreviations: AC, acrodin cap; ACh, anterior ceratohyal; Ana, angulo-articular; Apa, autopalatine; Bb2–4, basibranchial 2–4; Bh, basihyal; BR, branchiostegal rays; Cb1–5, ceratobranchial 1–5; CoPr, coronoid process; DHh, dorsal hypohyal; Dn, dentary; Eb1–4, epibranchial 1–4; Ect, ectopterygoid; GR, gill rakers; Hb1–3, hypobranchial 1–3; Hy, hyomandibular; Ih, interhyal; Iop, interopercle; MC, meckel's cartilage; Mx, maxilla; Op, opercle; PbTP3, pharyngobranchial 3 toothplate; PC, pulp cavity; PCh, posterior ceratohyal; Pmx, premaxilla; Pop, preopercle; Q, quadrate; Ra, retroarticular; RT, replacement teeth; Sop, subopercle; Sym, symplectic; Ur, urohyal.

terior tip slightly rounded, not reaching to anterior edge of premaxillae in dorsal view (Figs 4A, 5A); its posterior tip articulating with anterior part of frontal. Sphenotic with sharply pointed lateral process just below exit of supraorbital canal. Exit of otic canal forming robustly pointed lateral process on pterotic. Vomer generally T-shape, its anteriormost point slightly protracted, its posterior tip well pointed, reaching to slightly before epiphyseal commissure of supraorbital canal in ventral view. Parasphenoid narrowest anteriorly, expanded posteriorly, forming an oval shape posteriorly. Infraorbital series comprising lachrymal only, firmly attached to tip of short and slender cartilage extending from anterolateral tip of lateral ethmoid (Fig. 6).

Viscerocranium of C&S specimen shown in Fig. 7. Jaws comprising premaxilla, maxilla, dentary, anguloarticular, and retroarticular (Fig. 7A–D). Premaxilla with 8 or 9 dorsoventrally elongated (roughly rectangular shape) incisiviform teeth with weakly hooked distal tip, form-

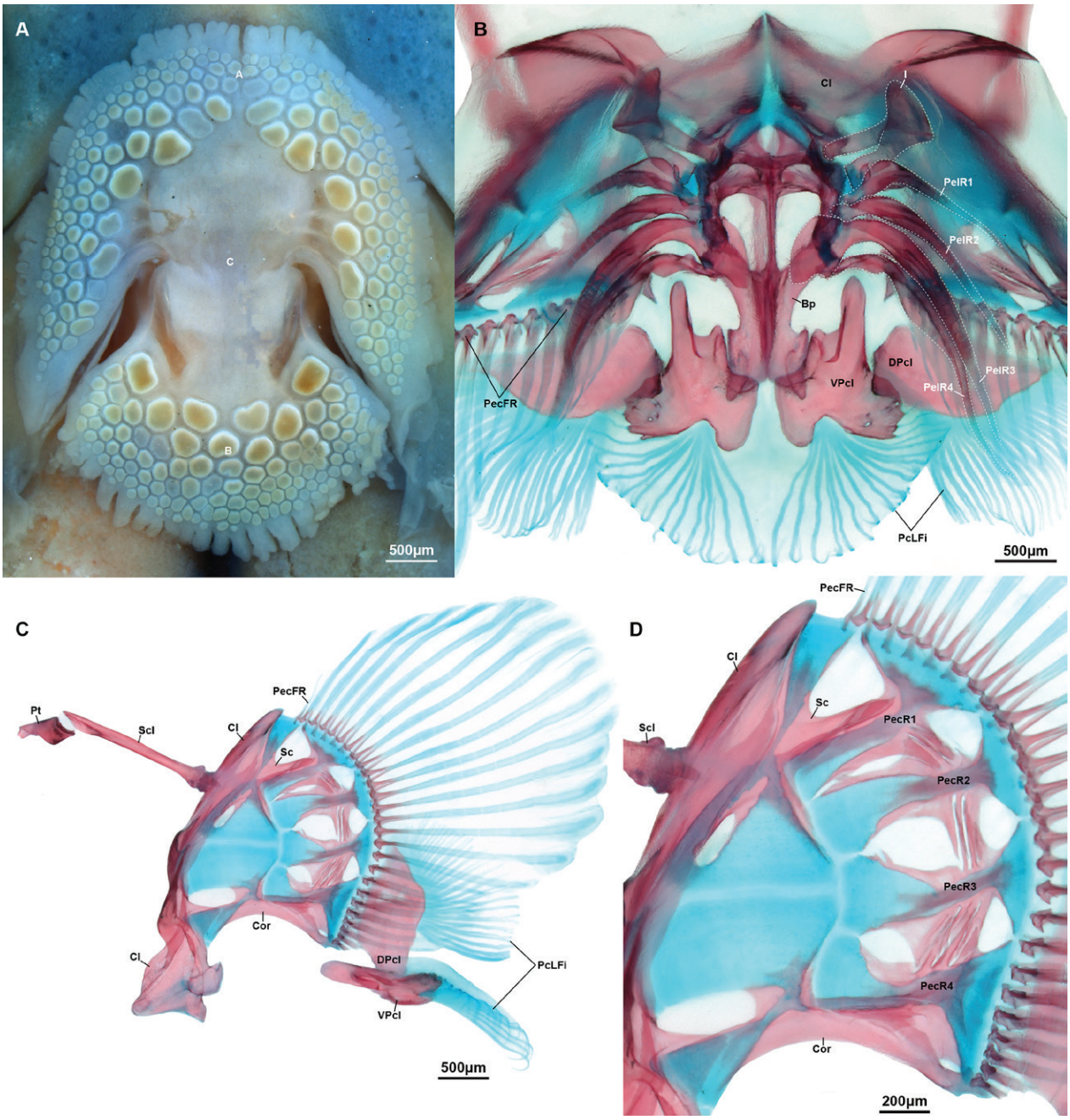

Figure 8. Surface features of adhesive disc (**A** ROM 72940, 26.5 mm SL, cyanine stain) and internal supporting skeleton of paired-fin girdles (**B**–**D** SAIAB 9319, 25.0 mm SL) of *Rhinolepadichthys polyastrous*. **B** Pelvic disc supporting skeleton, including elements of pelvic- and pectoral-fin girdle in ventral view (anterior to top of page), outline of pelvic-fin spine and rays highlighted by thin white-dashed line; **C** pectoral-fin girdle (right side) in lateral view (anterior to left, image reversed); **D** close-up of elements of pectoral-fin endoskeleton articulating with pectoral-fin rays (right side) in lateral view (anterior to left, image reversed). Abbreviations: A–C disc region A–C; Bp, basipterygium; Cl, cleithrum; Cor, coracoid; DPcl, dorsal postcleithrum; I, pelvic-fin spine; PcLFi, postcleithral fimbrae; PecFR, pectoral-fin rays; PecR1–4, pectoral radial 1–4; PelR1–4, pelvic-fin soft ray 1–4; Pt, posttemporal; Sc, scapula; Scl, supracleithrum; VPcl, ventral postcleithrum.

ing angle of ca. 45° (Fig. 7A, D; also see Conway et al. 2015: fig. 11B, H, I); teeth on anterior part of premaxilla distinctly larger than those of posterior part; ventrally directed process with rounded tip present on posteroventral tip of premaxilla. Dentary with 8 or 9 similarly sized incisiviform teeth, similar in shape to those on premaxilla; anterior 4 or 5 teeth somewhat more elongate, with tip weakly curved and directed upward, remaining teeth with hooked distal edge but usually poorly defined as a result of abrasion (Fig. 7B, C; also see Conway et al. 2015: fig. 11B, J); posteromedial face of dentary with squarish process. Anguloarticular without foramen (see Springer and Fraser 1976: fig. 3b); anterior quarter pointed, inserted into medial face of dentary; posterior part with well-developed dorsal process (termed coronoid process by Fujiwara et al. 2021), its tip rounded and directed anterolaterally. Hyopalatine arch comprising autopalatine, quadrate, hyomandibular, ectopterygoid, and symplectic (Fig. 7A). Hyomandibular generally squarish; posterodorsal part with posterior process; antero- and posteroventrally directed processes present, latter process distinctly larger than former. Ectopterygoid large, triangular, its dorsal tip approaching posteroventral tip of autopalatine. Opercular bones comprising opercle, subopercle, preopercle, and interopercle (Fig. 7A). All bones poorly ossified, excluding articular head of opercle. Subopercle without spine-like posterior tip. Gill arches comprising basihyal, 4 paired epibranchials, paired pharyngobranchial 3 and associated toothplate, 3 paired hypobranchials, 5 paired ceratobranchials, and 3 basibranchial cartilages (Fig. 7E–H). Basihyal long, slender, its anterior tip cartilaginous. Pharyngobranchial 3 toothplate squarish with two poor-

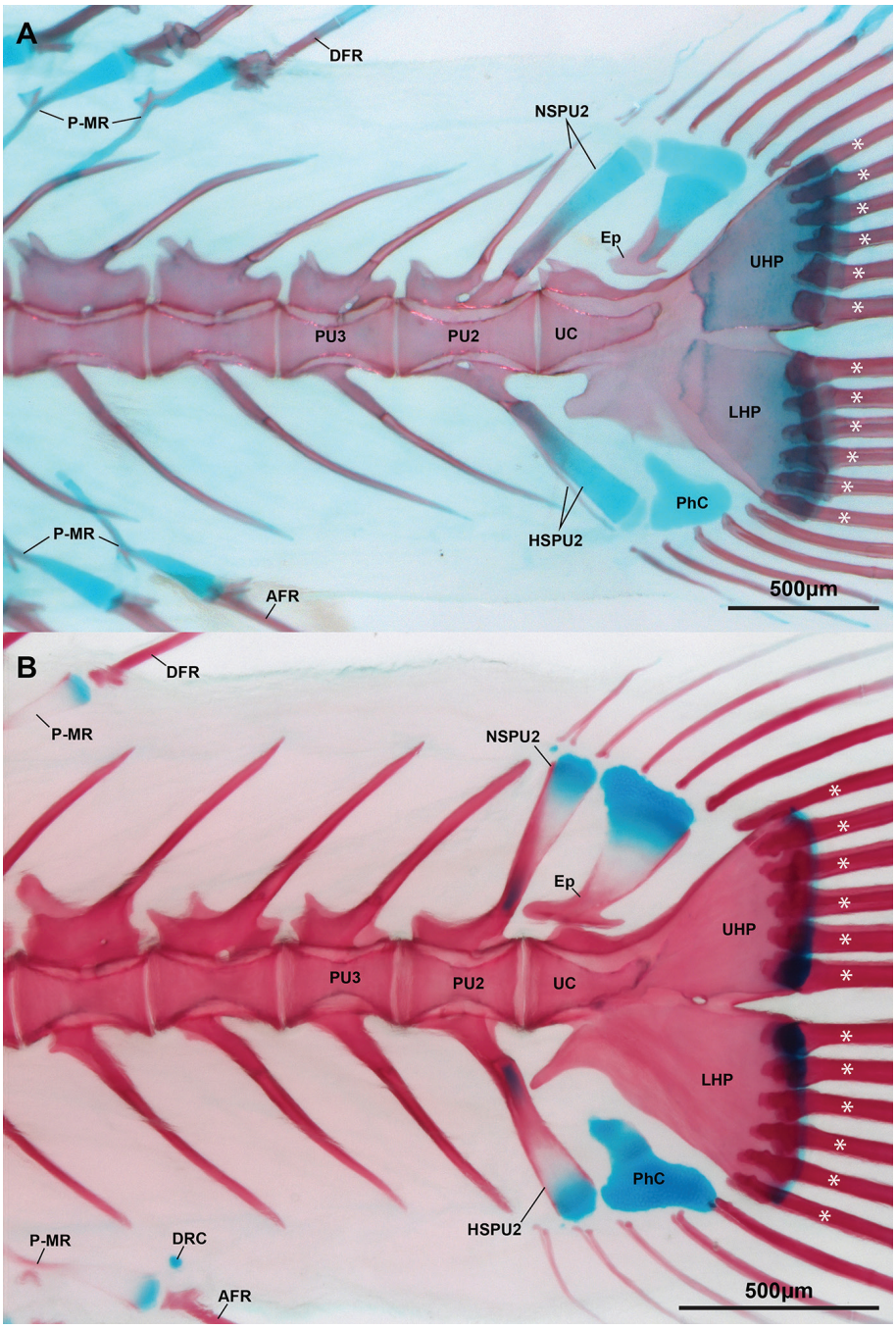

Figure 9. Caudal skeletons (left side, anterior to left) of **A** *Rhinolepadichthys polyastrous* (SAIAB 9319, 25.0 mm SL) and **B** *Discotrema crinophilum* (ROM 85350, 25.4 mm SL). Abbreviations: AFR, anal-fin rays; DFR, dorsal-fin rays; DRC, cartilaginous distal radial; Ep, epural; HSPU2, hemal spine of preural centrum 2; LHP, lower hypural plate; NSPU2, neural spine of preural centrum 2; PhC, parhypural cartilage; PU2, 3, preural centrum 2, 3; P-MR, proximal-middle radial; UC, ural centrum; UHP, upper hypural plate. White asterisks (*) indicates caudal-fin rays associated with upper and lower hypural plates.

ly defined rows of ca. 5 conical teeth on ventral surface; teeth of outer row larger than those of inner row (Fig. 7F, G). Row of small triangular gill rakers present on anterior and posterior edges of ceratobranchials 1–3, and anterior edge of ceratobranchial 4; row on anterior edge of ceratobranchial 1 short, comprising ca. 2–3 gill rakers; other rows with ca. 5–7 gill rakers (Fig. 7E). Ceratobranchial 5 lanceolate, edentulous (Fig. 7H). Hyoid bar comprising dorsal hypohyal, anterior and posterior ceratohyals, interhyal, and 6 slender branchiostegal rays (Fig. 7I). Posterior half of urohyal well forked in lateral view.

Pelvic- and pectoral-fin girdles and caudal skeleton of C&S specimen shown in Fig. 8 and Fig. 9A, respectively. Pelvic-fin girdle comprising basipterygium, and dorsal postcleithrum, and ventral postcleithrum. Pectoral-fin girdle with posttemporal, supracleithrum, cleithrum, scapula, coracoid, and 4 pectoral radials (Fig. 8). Anterior outline of basipterygia together triangular, posterior outline resembles inverted T-shape. Dorsal postcleithrum roughly triangular, with well-developed fimbriae along posterior edge. Ventral postcleithrum irregular in shape; posterolateral margin weakly serrated; posterior margin concave, with well-developed fimbriae. Complex articulation present between posterior tip of basipterygium and anteromedial edge of ventral postcleithrum. Caudal skeleton comprising upper and lower hypural plates, epural, and parhypural cartilage (Fig. 9A). Hypural plates separated by narrow diastema.

Based on *Rhinolepadichthys polyastrous* (SAIAB 9319), total number of vertebrae 33 or 34, including 17 or 18 abdominal and 16 caudal vertebrae. Ribs 13 or 14, associated with vertebrae 3–15 or 3–16. Epicentrals 20, associated with vertebrae 2–21. First dorsal-fin pterygiophore inserted between neural spines of vertebrae 19/20. First anal-fin pterygiophore inserted between hemal spines of vertebrae 21/22.

Included species. The genus contains the following four valid species, previously included in the "*Lepadichthys*" *lineatus* complex by Fujiwara and Motomura (2021): *Rhinolepadichthys geminus* (Fujiwara and Motomura, 2021) **comb. nov.**, *Rhinolepadichthys heemstraorum* (Fujiwara and Motomura, 2021) **comb. nov.**, *Rhinolepadichthys lineatus* (Briggs, 1966) **comb. nov.**, and *Rhinolepadichthys polyastrous* (Fujiwara and Motomura, 2021) **comb. nov.**

Etymology. The suffix *rhino-*, meaning nose, in combination with *Lepadichthys*, a genus of the Diademichthyinae. In reference to the pointed snout in members of this genus, which distinguishes the new genus from *Lepadichthys* (sensu stricto). Gender masculine.

Discotrema Briggs, 1976

Discotrema Briggs, 1976: 339 (type species: *Discotrema crinophilum* Briggs, 1976, by original designation, monotypic)

Unguitrema Fricke, 2014: 36 (type species: *Unguitrema nigrum* Fricke, 2014, by original designation, monotypic)

Type species. *Discotrema crinophilum* Briggs, 1976 (Fig. 10E–G)

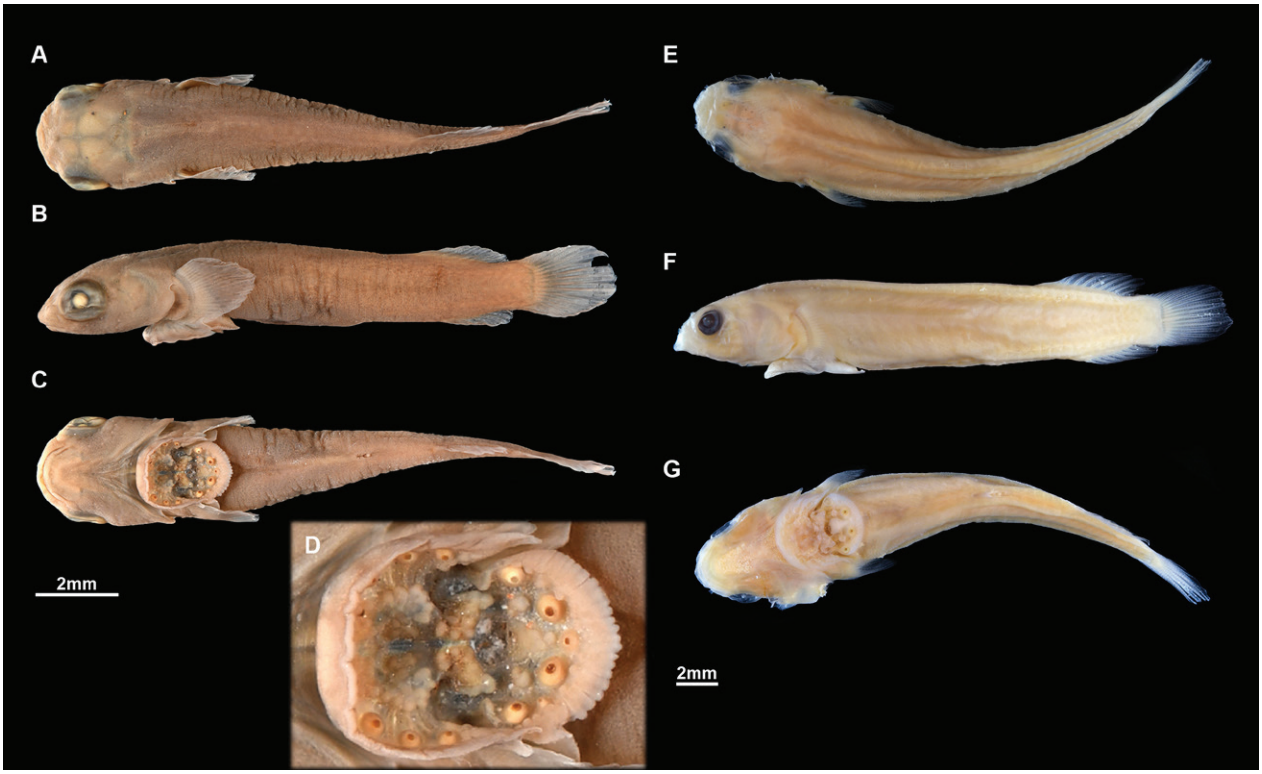

Figure 10. Photographs of preserved holotypes of **A**–**D** *Unguitrema nigrum* (NTUM 10603, 11.1 mm SL); **D** close-up of surface features of adhesive disc; **E**–**G** *Discotrema crinophilum* (USNM 215329, 22.1 mm SL). **A**, **E** dorsal views; **B**, **F** lateral views; **C**, **D**, **G** ventral views.

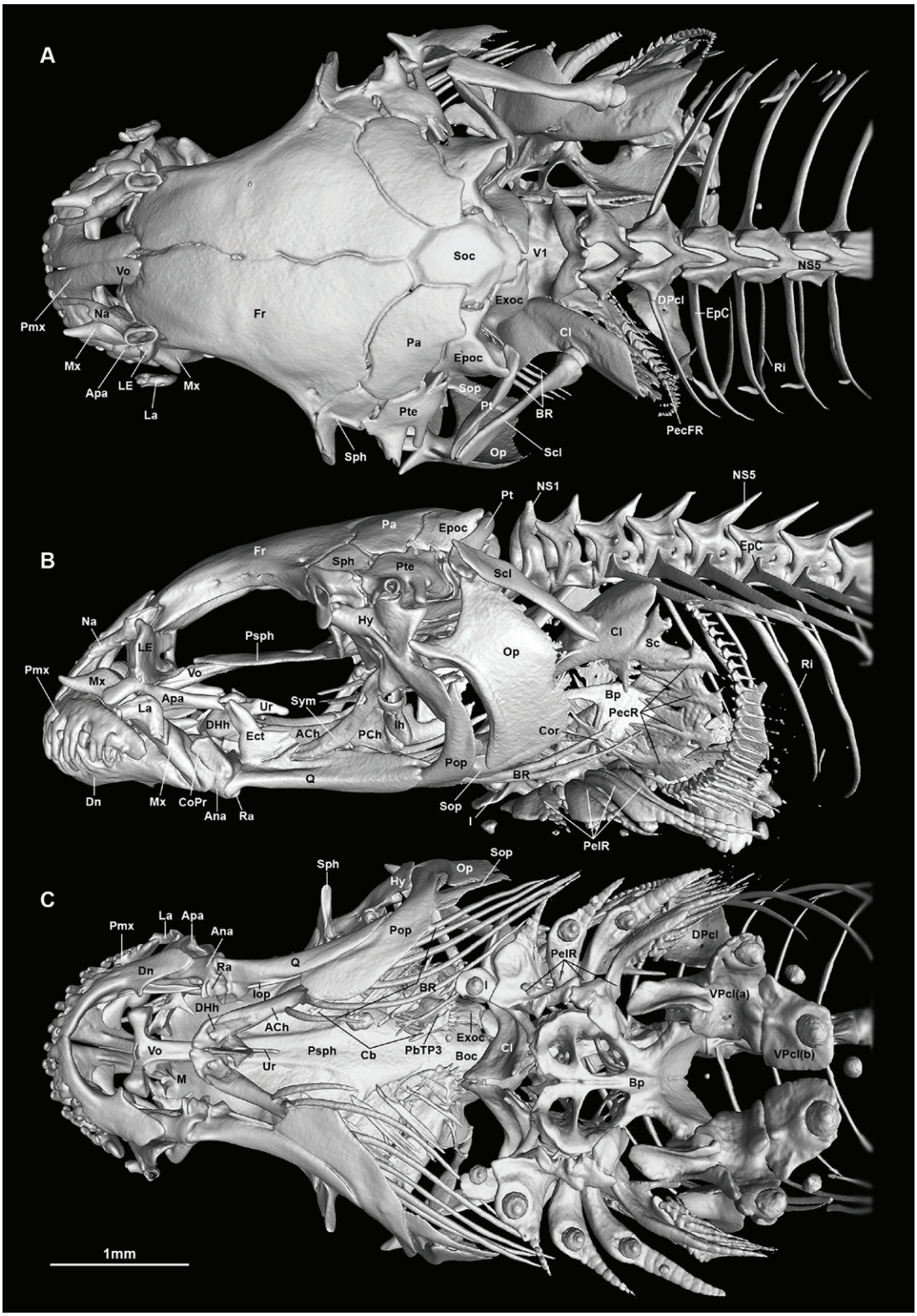

Figure 11. CT scanned anterior skeleton, including cranium, paired-fin girdles, and abdominal region of vertebral column, of *Discotrema monogrammum* (BPBM 40504, 16.4 mm SL). **A** dorsal view; **B** lateral view; **C** ventral view. Abbreviations: ACh, anterior ceratohyal; Ana, angulo-articular; Apa, autopalatine; Bh, basihyal; Boc, basioccipital; Bp, basipterygium; BR, branchiostegal rays; Cb, ceratobranchials; Cl, cleithrum; CoPr, coronoid process; Cor, coracoid; DHh, dorsal hypohyal; Dn, dentary; DPcl, dorsal postcleithrum; Ect, ectopterygoid; EpC, epicentral; Epoc, epiotic; Exoc, exoccipital; Fr, frontal; Hy, hyomandibular; I, pelvic-fin spine; Ih, interhyal; Iop, interopercle; La, lachrymal; LE, lateral ethmoid; M, mesethmoid; Mx, maxilla; Na, nasal; NS1, 5, neural spine of vertebral centrum 1, 5; Op, opercle; Pa, parietal; PbTP3, pharyngobranchial 3 toothplate; PCh, posterior ceratohyal; PecFR, pectoral-fin rays; PecR, pectoral radials; PelR, pelvic-fin soft rays; Pmx, premaxilla; Pop, preopercle; Pro, prootic; Psph, parasphenoid; Pt, posttemporal; Pte, pterotic; Q, quadrate; Ra, retroarticular; Ri, ribs; Sc, scapula; Scl, supracleithrum; Soc, supraoccipital; Sop, subopercle; Sph, sphenotic; Sym, symplectic; Ur, urohyal; V1, vertebral centrum 1; Vo, vomer; VPcl(a), ventral postcleithrum (anterior); VPcl(p), ventral postcleithrum (posterior).

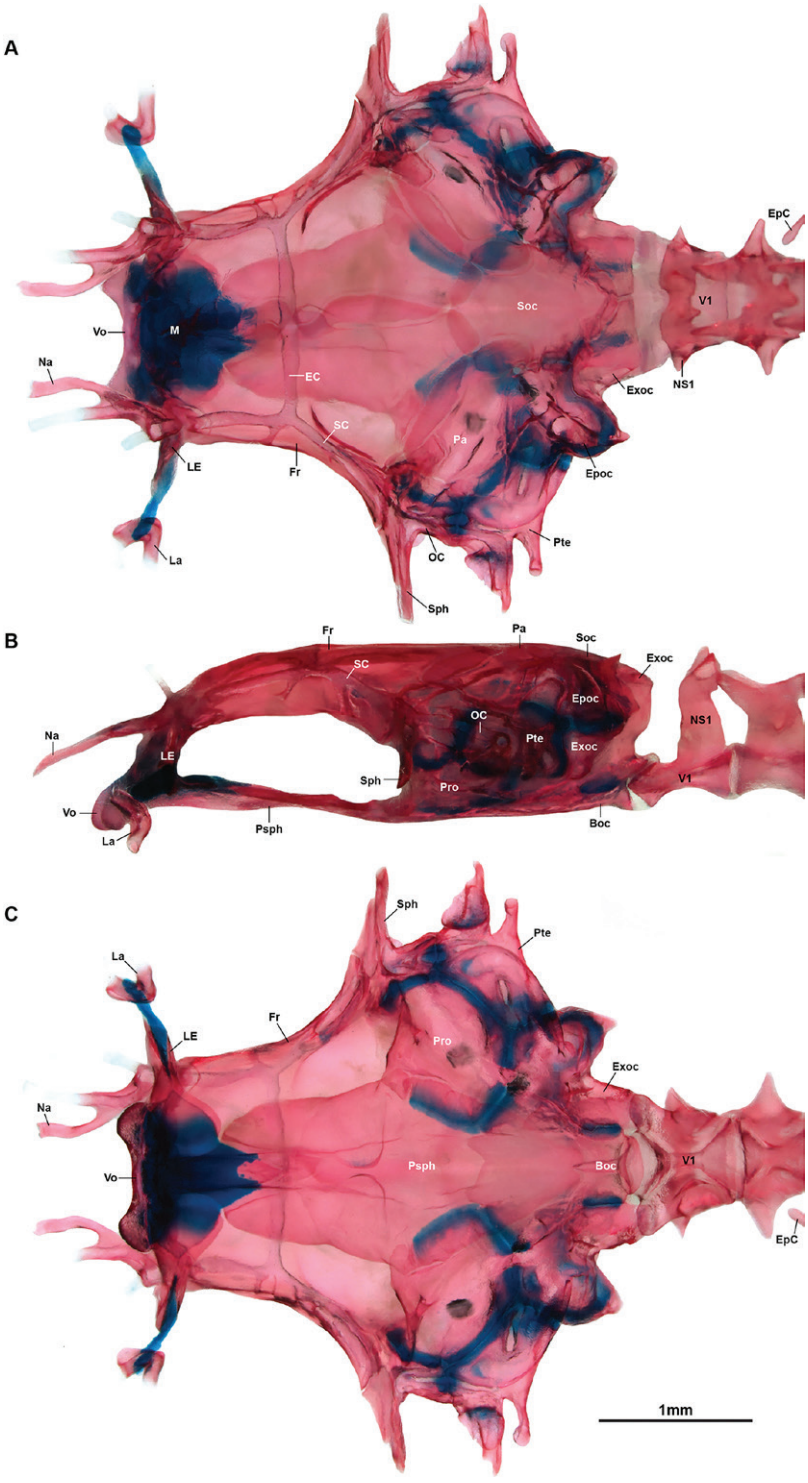

Figure 12. Neurocranium of *Discotrema crinophilum* (ROM 85350, 25.4 mm SL). **A** dorsal view; **B** lateral view; **C** ventral view. Abbreviations: Boc, basioccipital; EC, epiphyseal commissure of supraorbital canal; EpC, epicentral; Epoc, epiotic; Exoc, exoccipital; Fr, frontal; La, lachrymal; LE, lateral ethmoid; M, mesethmoid; Na, nasal; NS1, neural spine of vertebral centrum 1; OC, otic canal; Pa, parietal; Pro, prootic; Psph, parasphenoid; Pte, pterotic; SC, supraorbital canal; Soc, supraoccipital; Sph, sphenotic; V1, vertebral centrum 1; Vo, vomer.

Revised diagnosis. A genus of the Gobiesocidae belonging to the Diademichthyinae and distinguished from all other genera by the following unique characters: a well-developed lateral process on pterotic immediately posterior to exit of otic canal (Figs 11A, B, 12); upper pharyngeal teeth arranged in a single row along posteroventral edge of pharyngobranchial 3 toothplate, with tooth tips directed posteriorly (Figs 11C, 13E, F); a deep cavity at center of disc region C (Fig. 14A); disc papillae heterogeneous, including small, flattened papillae with a roughly hexagonal or circular outline around outer margin of disc and larger, circular papillae with a hardened (potentially keratinized) cap, with a raised, dome-like surface (Fig. 14A); three paired and one median cluster of small papillae (reminiscent of bunches of grapes) across adhesive disc (Fig. 14A); ventral postcleithrum divided into an anterior and posterior element, separated via a specialized joint (Figs 11C, 14B, D, E).

The following characters are also diagnostic, although not unique to the genus (details discussed in "Relationships of *Rhinolepadichthys* **gen. nov.** and *Discotrema*" [mostly same as those of *Rhinolepadichthys* **gen. nov.**; see below]): snout tip well extended, distinctly beyond

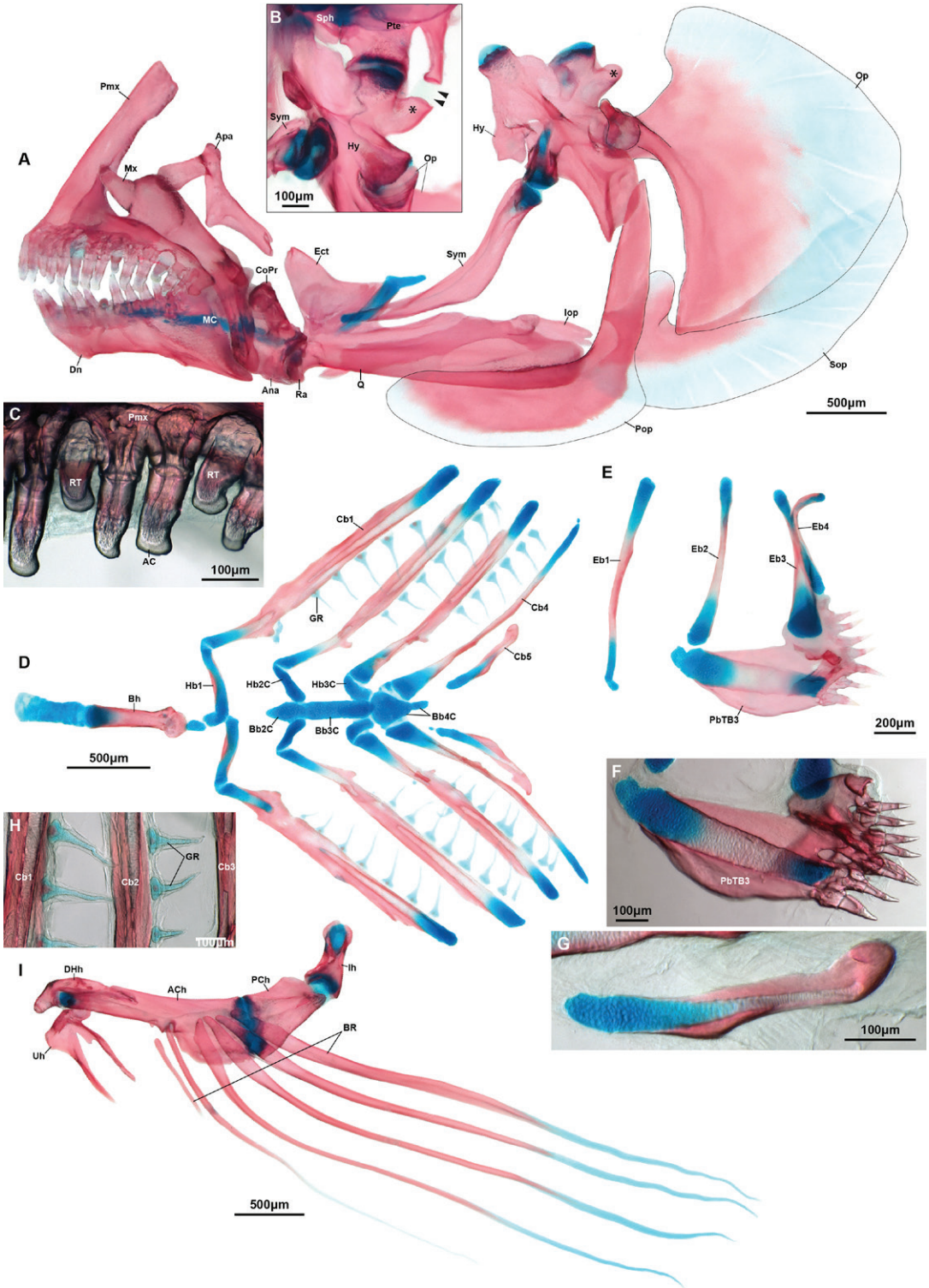

Figure 13. Viscerocranium of *Discotrema crinophilum* (ROM 85350, 25.4 mm SL mm SL). **A** Hyopalatine arch and opercular series (right side) in lateral view (image reversed), outline of preopercle, opercle, and subopercle highlighted by thin black line, posterior process of hyomandibular indicted by black asterisk (*); **B** articulation between hyomandibular and pterotic (left side) in ventral view, ligament between posterior process of hyomandibular (*) and hyomandibular process of pterotic indicted by double arrow head; **C** close-up of posterior teeth on premaxilla (left side) in lateral view; **D** lower gill-arch elements in dorsal view; **E** upper gill-arch elements (right side) in dorsal view; **F** close-up of PbTP3 (right side) in ventral view (image reversed); **G** close-up of Cb5 (right side) in dorsal view; **H** close up of gill rakers on posterior edge of ceratobranchials 1 and 2 (right side) in dorsal view; **I** hyoid bar (left side) in lateral view and urohyal. Abbreviations: AC, acrodin cap; ACh, anterior ceratohyal; Ana, angulo-articular; Apa, autopalatine; Bb2–4, basibranchial 2–4; Bh, basihyal; BR, branchiostegal rays; Cb1–5, ceratobranchial 1–5; CoPr, coronoid process; DHh, dorsal hypohyal; Dn, dentary; Eb1–4, epibranchial 1–4; Ect, ectopterygoid; GR, gill rakers; Hb1–3, hypobranchial 1–3; Hy, hyomandibular; Ih, interhyal; Iop, interopercle; MC, meckel's cartilage; Mx, maxilla; Op, opercle; PbTP3, pharyngobranchial 3 toothplate; PCh, posterior ceratohyal; Pmx, premaxilla; Pop, preopercle; Pte, pterotic; Q, quadrate; Ra, retroarticular; RT, replacement teeth; Sph, sphenotic; Sop, subopercle; Sym, symplectic; Ur, urohyal.

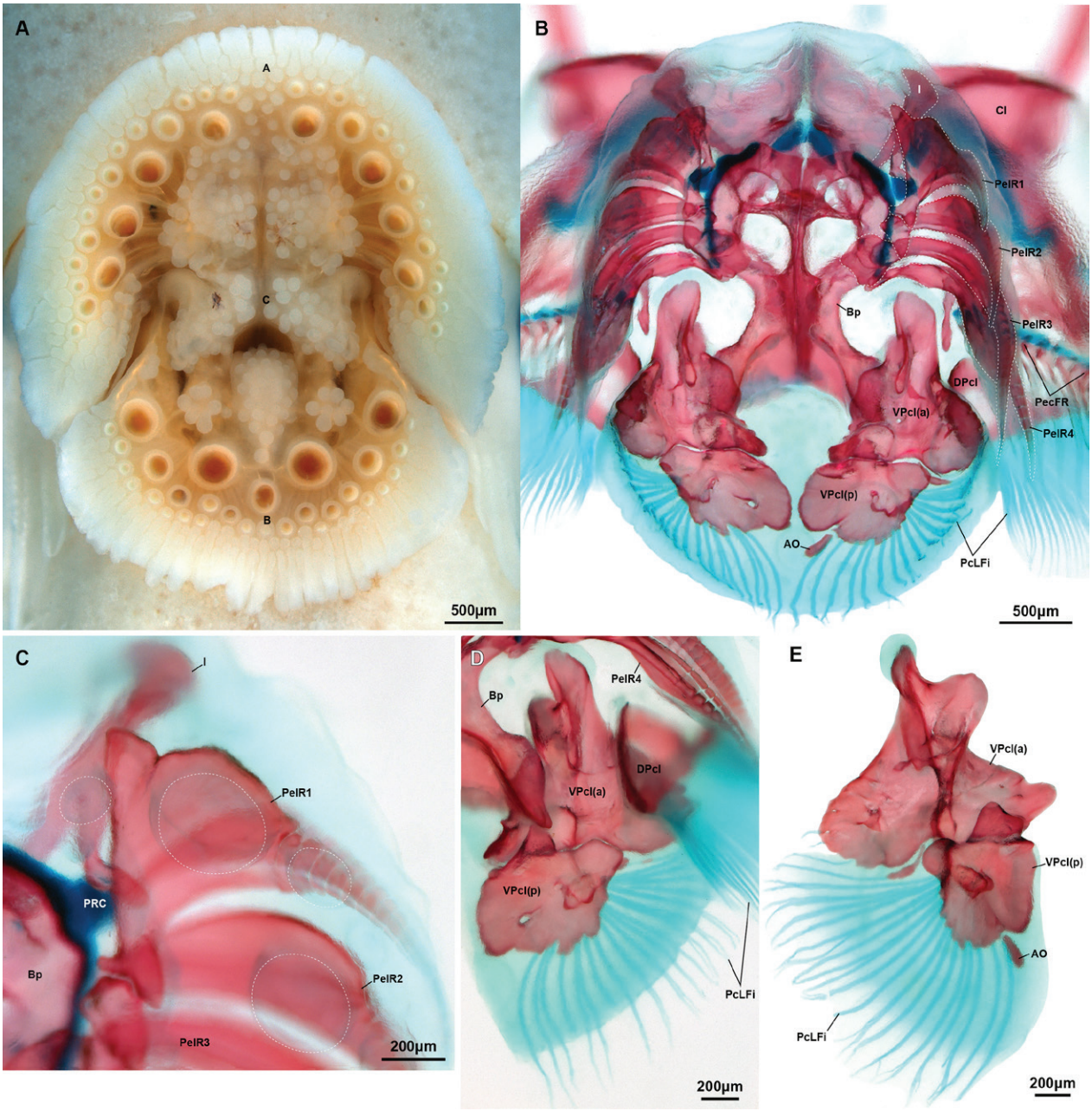

Figure 14. Surface features of the adhesive disc (**A** KAUM–I 153217, 29.4 mm SL, weak cyanine stain) and internal supporting skeleton of paired-fin girdles (**B**–**E** ROM 85350, 25.4 mm SL) of *Discotrema crinophilum*. **B** Pelvic disc supporting skeleton, including elements of pelvic- and pectoral-fin girdle in ventral view (anterior to top of page), outline of pelvic-fin spine and rays highlighted by thin white-dashed line; **C** close up of pelvic-fin ray 1, showing expanded anterior edge ventral to enlarged hardened papillae (outline show in thin white-dashed line); **D** ventral postcleithrum and surrounding elements (right side) in dorsal view (anterior to top of page); **E** dissected ventral postcleithrum (left side) in dorsal view (anterior to top of page). Abbreviations: A–C disc region A–C; AO, accessory ossicle; Bp, basipterygium; Cl, cleithrum; DPcl, dorsal postcleithrum; I, pelvic-fin spine; PcLFi, postcleithral fimbrae; PecFR, pectoral-fin rays; PelR1–4, pelvic-fin soft ray 1–4; PRC, pelvic radial cartilage; VPcl(a), ventral postcleithrum (anterior); VPcl(p), ventral postcleithrum (posterior).

tip of lower jaw (more pronounced in specimens smaller than ca. 25 mm SL) (Fig. 15B, E); upper lip fused with skin of snout, usually lacking a distinct groove between lip margin and snout, if present, groove very weak, restricted to posterior portion of upper jaw only (Fig. 15A, B, D, E); anterior part of lower lip without skin lobes and fused with skin of gular area (Fig. 15C, F); upper-jaw teeth only weakly hooked, with tip of crown blunt or rounded (Figs 11B, 13A, C); medial edge of premaxilla very weakly concave, forming indistinct, narrow oval opening anteriorly in dorsal view between premaxillae (Fig. 11A); gill membrane attached to isthmus; gill rakers present only on posterior edge on ceratobranchials 1–3 (absent from anterior edge of ceratobranchial 1–3, and from ceratobranchial 4) (Fig. 13D); ceratobranchial 5 edentulous (Fig. 13D, G); preopercle without lateral-line canal and associated pores (PR1–3) (Fig. 15); single adhesive disc (Fig. 14A); anterolateral part of ventral post-

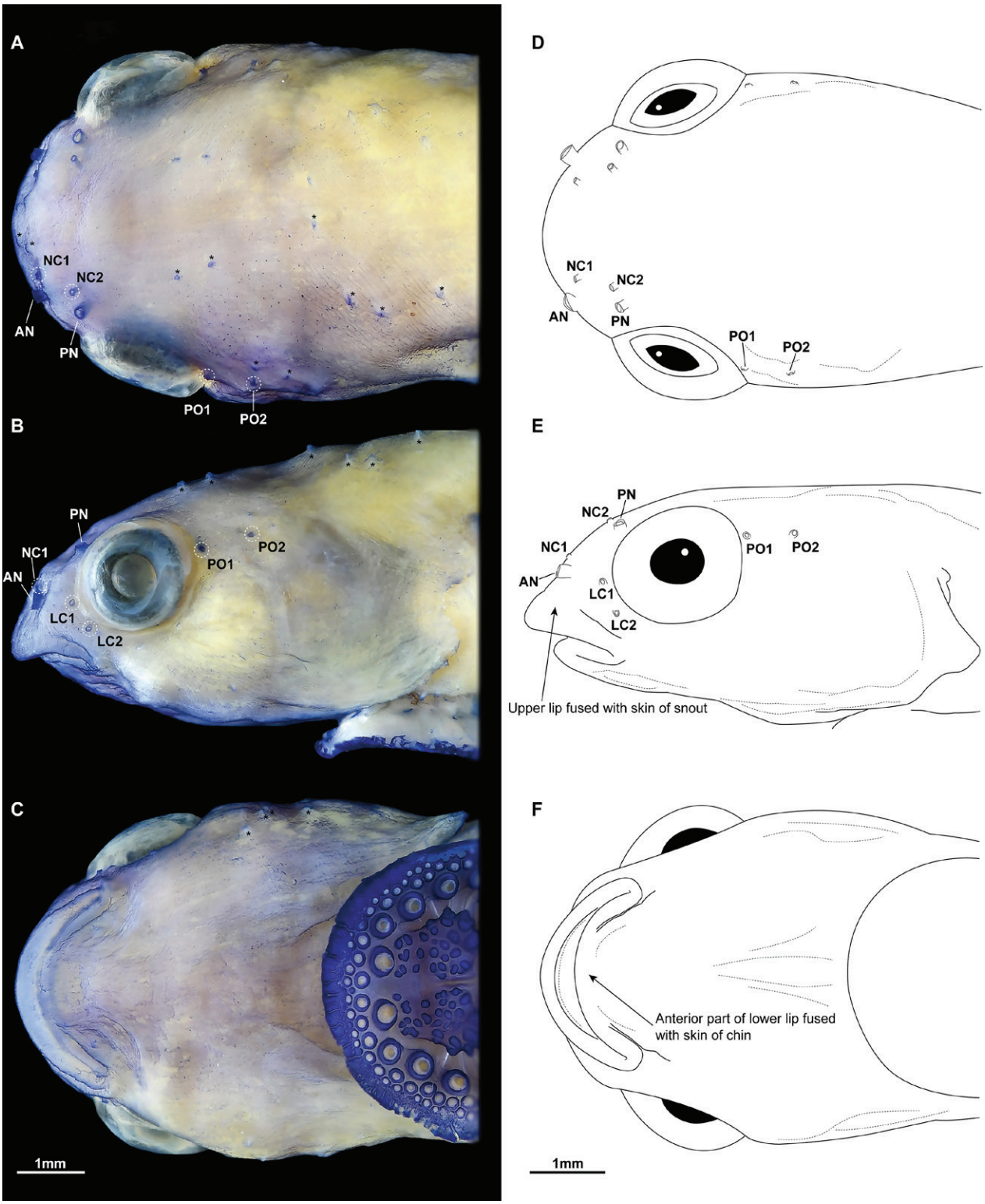

Figure 15. Heads of *Discotrema crinophilum*. **A**–**C** KAUM–I. 145201, 25.9 mm SL (cyanine stain); **D**–**F** WAM P. 26100-009, 1 of 6 specimens, 22.2 mm SL (line drawing). **A**, **D** dorsal views; **B** right side in lateral view (image reversed); **E** left side in lateral view; **C**, **F** ventral views. Abbreviations: AN, anterior nostril; LC1–2, lachrymal canal pores; NC1–2, nasal canal pores; PN, posterior nostril; PO1–2 postorbital canal pores. Black asterisks (*) indicates superficial neuromasts.

cleithrum extended anteriorly as a well-developed rod-like process, its tip close to base of pelvic-fin soft ray 4 (Fig. 11C, 14B).

Description. General body appearance as in Fig. 10. Photographs and line drawing of heads, showing cephalic lateral-line canal pores plus snout and lip characters, given in Fig. 15. Features of osteology shown in Figs 11–14, 16. Body cylindrical laterally, compressed at caudal peduncle. Anus closer to anal-fin origin than to posterior margin of disc. Head depressed anteriorly, its width wider than body width. Snout tip weakly pointed

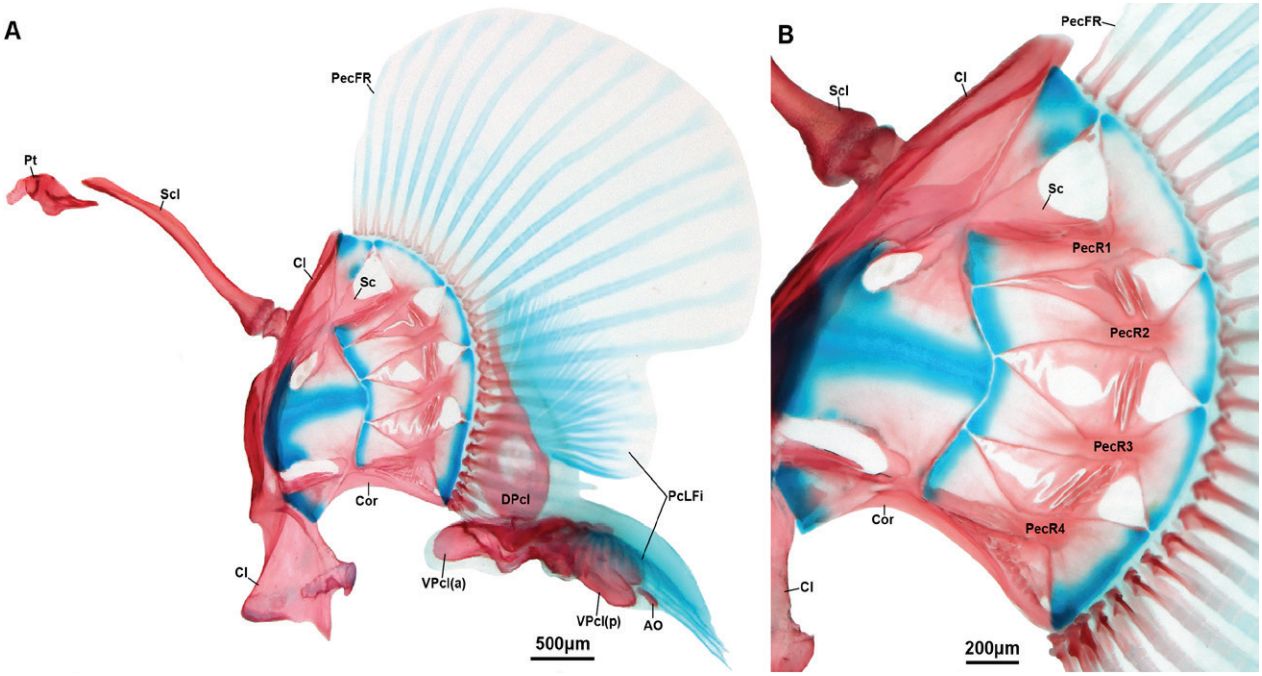

Figure 16. Pectoral-fin girdle of *Discotrema crinophilum* (ROM 85350, 25.4 mm SL). **A** Right side in lateral view (anterior to left, image reversed); **B** close-up of elements of pectoral-fin endoskeleton articulating with pectoral-fin rays (left side) in lateral view (anterior to left), dorsal postcleithrum removed. Abbreviations: AO, accessory ossicle; Cl, cleithrum; Cor, coracoid; DPcl, dorsal postcleithrum; PcLFi, postcleithral fimbrae; PecFR, pectoral-fin rays; PecR1–4, pectoral radial 1–4; Pt, posttemporal; Sc, scapula; Scl, supracleithrum; VPcl(a), ventral postcleithrum (anterior); VPcl(p), ventral postcleithrum (posterior).

(lateral view), semi-elliptical (dorsal view); no skin fold (see Hutchins 1984: fig. 2b) across dorsal surface; dorsal profile of snout rounded. Mouth terminal, its posterior tip level with vertical through anterior margin of eye lens. Posterior part of lower lip well separated from skin of gular area, with distinct groove between both structures. Anterior and posterior nostrils close to each other, located dorsolaterally; posterior nostril vertically level with anterior margin of eye; both nostrils with a membranous tube, that of former slightly longer than that of latter. Interorbital region flattened. Upper end of gill opening level with base of 4th–6th pectoral-fin ray (lateral view); lower 5th–8th pectoral-fin ray base attached to disc by membrane. First to third gill arches with 2 rows of gill filaments, fourth arch without filaments (= 3 gills sensu Briggs 1955). Cephalic lateral-line canal pores with 2 nasal (NC), 2 lachrymal (LC) and 2 postorbital (PO) canal pores (Fig. 15). NC1 located vertical through anterior nostrils (dorsal view); NC2 slightly before posterior nostrils (dorsal view); LC1 just in front of anterior margin of eye; LC2 posteroventrally below LC1; PO1 just behind posterior margin of orbit; PO2 similar horizontal level with or slightly above PO1. Dorsal and anal fins located posteriorly, their bases relatively short; not connected to caudal fin by membranes. Dorsal- and anal-fin height almost equal, except anteriorly. Pectoral- and caudal-fin margins rounded.

Structure of neurocranium (Fig. 12), lachrymal (Fig. 12), viscerocranium (Fig. 13), paired-fin girdles (Figs 14, 16), and caudal skeleton (Fig. 9B) generally similar to that described above for *Rhinolepadichthys* **gen. nov.**, except for the following differences. Pterotic with elongate lateral process immediately posterior to exit of otic canal (Figs 11, 12), tightly connected to posterior process on hyomandibular by ligament (Fig. 13B). Posterovenrally directed processes on hyomandibular somewhat expanded dorsolaterally; ectopterygoid triangular, dorsal edge weakly concave; preopercle relatively well ossified, its ventral edge rounded (Fig. 11C, 13A). Cartilaginous tip of basihyal elongate, occupying half the length of basihyal; pharyngobranchial 3 toothplate trapezoid; gill rakers present on posterior edge of ceratobranchials 1–3 only; ceratobranchial 5 rod-like (Fig. 11C, 13D–H). Posterior 3/4th of urohyal well forked in lateral view (Fig. 13I). Single small accessory ossicle variably present between ventral postcleithra (Fig. 14B, E; no accessory ossicle in BPBM 40504: Fig. 11C).

Dorsal-fin rays 7–10. Anal-fin rays 7–9. Pectoral-fin rays 23–27. Based on *Discotrema crinophilum* (ROM 85350), total number of vertebrae 35, including 18 abdominal and 17 caudal. Ribs 14, associated with vertebrae 3–16. Epicentrals 19 (left side) or 20 (right side), associated with vertebrae 2–21 (right side) or 3–21 (left side). First dorsal-fin pterygiophore inserted between neural spines of vertebrae 21/22. First anal-fin pterygiophore inserted between hemal spines of vertebrae 23/24.

Included species. The genus contains the following four valid species, *Discotrema crinophilum* Briggs, 1976, *Discotrema monogrammum* Craig & Randall, 2008, *Discotrema nigrum* (Fricke, 2014), **comb. nov.** (validity tentative, see below), and *Discotrema zonatum* Craig & Randall, 2008.

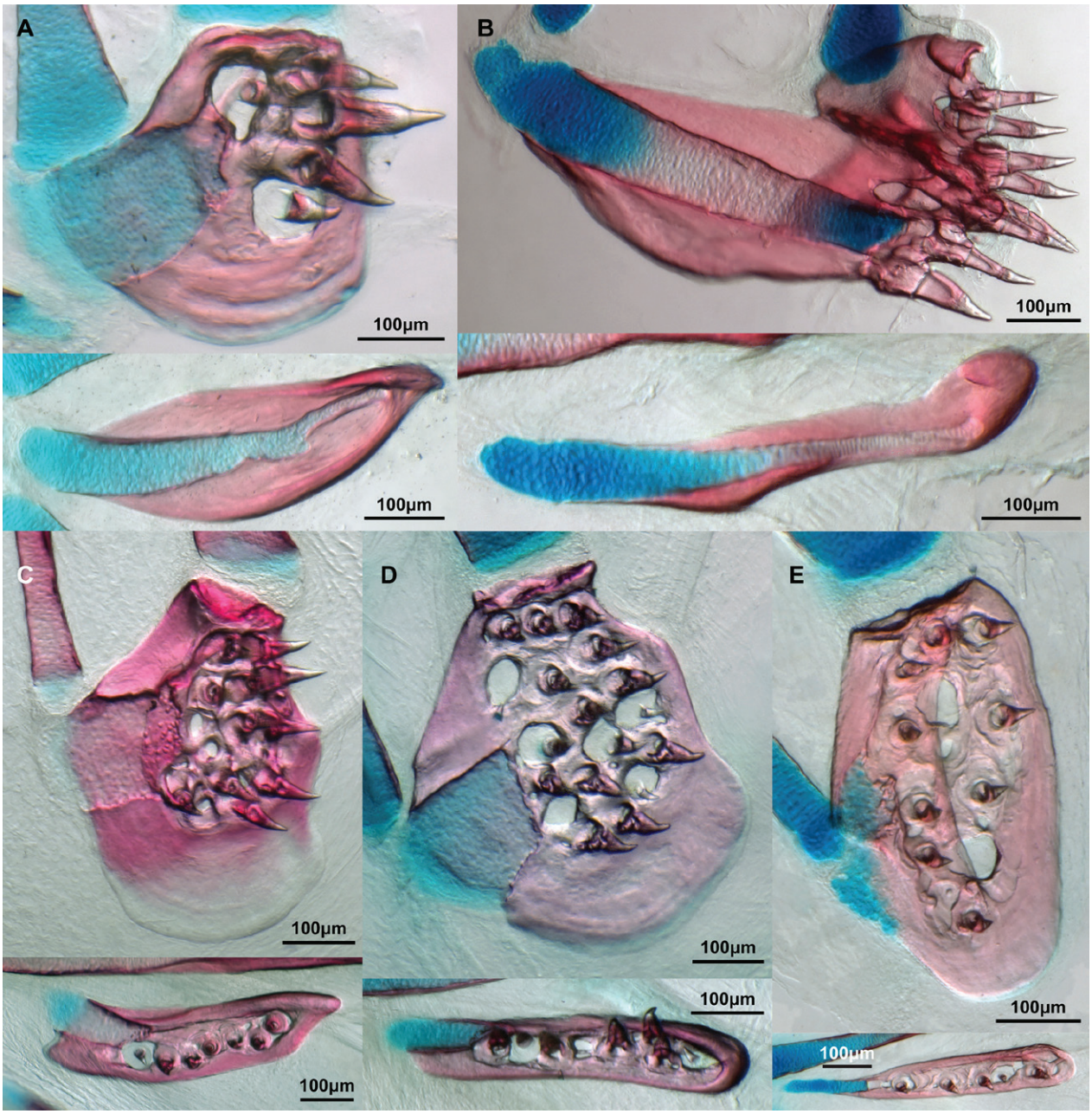

Figure 17. Elements of the upper (pharyngobranchial toothplate 3 [upper image]) and lower (ceratobranchial 5 [lower image]) pharyngeal jaws in *Rhinolepadichthys polyastrous* (**A** SAIAB 9319, 25.0 mm SL), *Discotrema crinophilum* (**B** ROM 85350, 25.4 mm SL), *Lepadichthys frenatus* (**C** AMS I. 27134-018, 32.0 mm SL), *Lepadichthys coccinotaenia* (**D** SAIAB 49396, 39.1 mm SL), and *Diademichthys lineatus* (**E** ROM 65282, 34.7 mm SL).

Discussion

Synonymy of *Discotrema* and *Unguitrema*

Fricke (2014) described *Unguitrema nigrum* as a new genus and species on the basis of two small specimens (10.0 and 11.1 mm SL) collected from Papua New Guinea. Fricke (2014) noted that the genus is superficially similar to *Discotrema*, but supposedly differed from this genus in a number of features of the adhesive disc, including the presence of a short "claw-like appendage" at the center of some papillae (vs. absence in *Discotrema*), 3 rows of papillae distally on disc region B (vs. single row), paired clusters of small papillae located on both sides of the median papillae cluster, with only 2 papillae each (vs. 5 papillae), paired cluster of small papillae located on disc region C separated by a naked patch centrally (vs. no naked patch), and some morphometric measurements, including head length and width, and the distance from disc to anus.

Reexamination of the holotype and paratype of *Unguitrema nigrum* as part of this study revealed that some of the disc papillae exhibit a hardened (potentially keratinized), domed cap, similar to that of *Discotrema* (Figs

10C, D, G, 14A). We did not observe short "claw-like appendages" on the disc papillae of either of the two specimens of *U. nigrum*, as illustrated in Fricke (2014: fig. 2) and it is possible, though unlikely in our opinion, that these structures have been damaged or lost independently on both types subsequent to the original description. Judging from the condition of the two specimens, a more plausible explanation is that Fricke (2014) misjudged the shape of the dome-like papillae (we note that no microscope is mentioned in the materials and methods section of Fricke 2014: 36). The examination of a number of specimens of *Discotrema* revealed variation in features of disc papillae, which overlapped with those listed for *Unguitrema* by Fricke (2014) (viz., 1–3 rows of papillae distally on disc region B; paired cluster of small papillae located on both sides of median papillae cluster with ca. 2–15 papillae each). The so-called "naked patch" on disc region C of *Unguitrema nigrum* is also present in some specimens of *Discotrema* and likely the result of papillae dislodgement (which is common in the disc bearing gobiesocids; Hayashi and Hayashi 1985; Fujiwara and Motomura 2018). We were unable to observe internal osteological characters of *Unguitrema*, but both *Unguitrema* and *Discotrema* exhibit the same condition for several externally observable osteological characters that are important in gobiesocid classification (e.g., tooth shape, cephalic lateral-line canal pore number and position). Based on the above, we conclude that there are no significant differences between *Unguitrema* and *Discotrema* that would warrant different genus-level taxa, and that the former should be regarded as a junior synonym of the latter. Although we treat *Unguitrema nigrum* as a valid species of *Discotrema* (= *Discotrema nigrum*) in this study, the validity of the species should be considered tentative based on further review of *Discotrema* (beyond the scope of this paper but forthcoming; K. Fujiwara in prep.).

Relationships of *Rhinolepadichthys* gen. nov. and *Discotrema*

Rhinolepadichthys **gen. nov.** and *Discotrema* belong to the subfamily Diademichthyinae based on the shared presence of the following characters: (1) upper-jaw teeth incisiviform, with hooked distal edge; (2) premaxillae separated anteriorly by indistinct, narrow oval opening in dorsal view; and (3) complex articulation between posterior tip of basipterygium and anteromedial edge of ventral postcleithrum. The two genera can be easily distinguished from 9 of the 13 diademichthyine genera with a double adhesive disc (viz., *Aspasma*, *Aspasmichthys* Briggs, 1955, *Aspasmodes* Smith, 1957, *Erdmannichthys* Conway, Fujiwara, Motomura & Summers, 2021, *Flexor* Conway, Stewart & Summers, 2018, *Liobranchia* Briggs, 1955, *Pherallodus*, *Pherallodichthys*, and *Propherallodus*) by having a single adhesive disc, a character shared with the remaining genera (viz., *Diademichthys*, *Flabellicauda* Fujiwara, Motomura & Conway, 2021, "*Lepadichthys*", and *Lepadicyathus* Prokofiev, 2005). *Rhinolepadichthys* **gen. nov.** and *Discotrema* are further distinguished from the four genera with a single adhesive disc by a number of external and internal features (discussed below).

Based on analyses of a concatenated seven-gene dataset (two mitochondrial and five protein-coding nuclear loci), Conway et al. (2020: figs 3, 4) recovered *Rhinolepadichthys* **gen. nov.** (as *Lepadichthys lineatus*, here reidentified as *R. polyastrous*), *Discotrema*, and *Diademichthys* as a monophyletic group, with high branch support values (100% bootstrap and 1.0 posterior probability, respectively). This monophyletic group is also supported by at least two putative morphological synapomorphies, as first identified by Fujiwara and Motomura (2021): (1) upper lip fused with skin of snout, usually lacking a distinct groove between the lip margin and snout, if present, groove very weak, restricted to the posterior portion of upper jaw only (vs. upper lip separated from skin of snout by an obvious groove along entire length of upper jaw, or separated at center of upper jaw in *Flabellicauda* and *Lepadicyathus*; see Fujiwara et al. 2021: fig. 1 and Fujiwara and Motomura 2021: fig. 1); (2) snout tip extended, its extension sometimes variable but distinctly beyond tip of lower jaw consistently (vs. not strongly extended, tip slightly beyond or about level with lower-jaw tip).

Within the putative monophyletic group comprising *Rhinolepadichthys* **gen. nov.**, *Discotrema* and *Diademichthys*, Conway et al. (2020) recovered *Rhinolepadichthys* **gen. nov.** in a sister-group relationship with *Diademichthys*, though with only low branch support (64% bootstrap in maximum-likelihood phylogram and 0.62 posterior probability in Bayesian topology; Conway et al. 2020: figs 3, 4; see Fig. 2). Further exploration of the dataset used by Conway et al. (2020) shows that the sister-group relationship between *Rhinolepadichthys* **gen. nov.** and *Diademichthys* is present in only one of the seven possible gene trees available from that study (GLYT; Fig. S1C). An alternative sister-group relationship between *Rhinolepadichthys* **gen. nov.** and *Discotrema* is supported by the analysis of two mitochondrial genes (COI, 12S; Fig. S1A, B) and two of the four remaining nuclear genes (MYH6, SH3PX3; Fig. S1D, F). The three genera are not supported as monophyletic in the gene trees for ZIC1 and SH3PX3 (Fig. S1E, F), and *Rhinolepadichthys* **gen. nov.** is not represented in the dataset for the fifth nuclear gene (ENC1). This cursory investigation of the dataset of Conway et al. (2020) suggests that the putative sister-group relationship between *Rhinolepadichthys* **gen. nov.** and *Diademichthys* reported in that study (see Fig. 2) is unlikely to represent the "final word" on the relationships of the three genera.

Despite the conflicting molecular evidence, our morphological investigation presents strong evidence that *Rhinolepadichthys* **gen. nov.** and *Discotrema* are sister taxa, based on the following putatively derived characters (potential synapomorphies): (1) the presence of a hardened (potentially keratinized) cap to the surface of at least some disc papillae (Figs 8A, 14A) (vs. surface of disc papillae soft, without hardened cap); and (2) having the anterolateral part of the ventral postcleithrum extended anteriorly as a well-developed rod-like process, its anteriormost tip close to the base of pelvic-fin soft ray 4 (Figs 4C, 5C, 8B, 11C, 14B, D, E) (vs. only weakly

pointed, or irregular). As far as we are aware, these two characters are found only in *Rhinolepadichthys* **gen. nov.** and *Discotrema* amongst the disc-bearing gobiesocids. In addition, *Rhinolepadichthys* **gen. nov.** and *Discotrema* also share a number of other characters (none unique to the pair within Diademichthyinae), including: (1) anterior part of lower lip without skin lobes and fused with skin of gular area (Figs 3C, F, 11C, F) (vs. skin lobes present in *Aspasma* and *Propherallodus*; lower lip separated from skin of gular area by an obvious groove along entire length of lower jaw in other diademichthyine genera, except *Diademichthys*, *Flabellicauda*, and *Lepadicyathus*); (2) upper-jaw teeth only weakly hooked (curved ca. 45°), with tip of crown blunt or rounded (Figs 7A, D, 13A, C) (vs. upper-jaw teeth strongly hooked [curved ca. 90°], with tip of crown forming a sharp point in all diademichthyine genera, except *Aspasma* and *Propherallodus*); (3) medial edge of premaxilla very weakly concave, forming indistinct, narrow oval opening anteriorly in dorsal view between premaxillae (Figs 4A, 5A, 11A) (vs. strongly concave, forming small to large opening between premaxillae in dorsal view in all diademichthyine genera, except *Aspasmodes*, *Liobranchia*, *Pherallodichthys*, and *Propherallodus*); (4) gill membrane attached to isthmus (vs. gill membrane free from isthmus in all diademichthyine genera, except *Aspasma*, *Aspasmichthys*, *Aspasmodes*, *Diademichthys*, *Flabellicauda*, "*Lepadichthys*", *Lepadicyathus*, *Liobranchia*, and *Pherallodichthys*); (5) absence of teeth on ceratobranchial 5 (Figs 7E, H, 13D, G, 17) (vs. presence in all diademichthyine genera, except *Flabellicauda*; condition unknown for *Erdmannichthys*; Fig. 17); (6) preopercle without lateral-line canal and associated pores (Figs 3B, E, 15B, E) (vs. preopercular portion of preoperculo-mandibular lateral-line canal with 2 or 3 pores [PR1–3 or PR1, 3] in all diademichthyine genera, except *Flabellicauda*, *Lepadicyathus*, and *Pherallodus*). Based on the characters listed above, we propose that *Rhinolepadichthys* **gen. nov.** and *Discotrema* form a putative monophyletic group.

Rhinolepadichthys **gen. nov.** is distinguished from its putative sister taxon *Discotrema*, by the presence of a row of 8–12 large papillae on the inner surface of the upper and lower lips (vs. inner surface of lips smooth, without distinct papillae) (Figs 3C, F, 15C, F; see Fujiwara and Motomura 2021: fig. 1), the absence (vs. presence) of a well-developed lateral process on the pterotic immediately posterior to the exit of the otic canal (Figs 4, 5, 6, 11, 12), the presence of two rows and single row of gill rakers on ceratobranchials 1–3 and 4, respectively (vs. single row of gill rakers on ceratobranchials 1–3 and gill rakers absent on ceratobranchial 4) (Figs 7E, 13D, H), having the upper pharyngeal teeth arranged in a loose patch on the ventral surface of pharyngobranchial 3 toothplate, with tooth tips directed posteroventrally (vs. arranged in a single row along posteroventral edge of pharyngobranchial 3 toothplate, with tooth tips directed posteriorly) (Figs 4C, 5C, 7F, G, 11C, 13E, F, 17). *Rhinolepadichthys* **gen. nov.** is further distinguished from *Discotrema* by features of the adhesive disc, including outline of disc papillae roughly hexagonal or ovoid and with a flattened surface (vs. outline circular with a raised, dome-like surface in some papillae), the absence of a deep cavity at the center of disc region C (vs. presence), the absence of three paired and one median cluster of small papillae (reminiscent of bunches of grapes) across the surface of the adhesive disc (vs. presence) (Figs 8A, 10C, D, G, 14A), and by having the ventral postcleithrum entire, not divided into two separate, articulating elements (vs. ventral postcleithrum divided into an anterior and posterior element, separated via a specialized joint) (Figs 4C, 5C, 8B, 11C, 14B, D, E).

Adhesive disc of *Rhinolepadichthys* gen. nov. and *Discotrema*

To the best of our knowledge, *Rhinolepadichthys* **gen. nov.** and *Discotrema* are the only disc-bearing gobiesocids to possess at least some adhesive disc papillae with a hardened, orange-brownish cap (Figs 8A, 10C, D, G, 14A). It is possible that the cap (or cuticle) of these hardened papillae contains a higher amount of keratin or keratin-like protein (see Green and Barber 1988) than the adjacent opaque or whitish papillae that exhibit a soft cap (similar to that of other disc-bearing gobiesocids). In *Rhinolepadichthys* **gen. nov.**, the hardened papillae are similar in shape to the papillae present in other diademichthyine clingfishes (i.e., outline hexagonal to roundish, with a flattened surface; Fig. 8A). In *Discotrema*, the hardened papillae exhibit a round outline, and the surface of each is strongly convex (Figs 10C, D, G, 14A). Notably, the two genera are also the only members of the Gobiesocidae known to adhere to the surface of crinoids (Fig. 1A, C, D), and the hardened papillae may represent an adaptation for attaching to the bodies of these invertebrates. While some species of *Rhinolepadichthys* **gen. nov.** also inhabit rocky substrate in the vicinity of sea urchins (Fig. 1B; Fujiwara and Motomura 2021: fig. 6c), members of *Discotrema* are obligate commensals of crinoids (Fig. 1D; K. Fujiwara, pers. obs.). The unique surface (enlarged papillae, with a hard, domed cap, central cavity in disc region C) and internal features (ventral postcleithrum divided into an anterior and posterior element; Figs 12C, 14B, D, E) of the adhesive disc in *Discotrema*, in comparison to *Rhinolepadichthys* **gen. nov.**, may represent a more highly specialized condition for adhering to the surface of crinoids. A detailed investigation of the anatomy of the adhesive disc of *Discotrema* was beyond the scope of this work but will form the subject of a future study by the authors.

Acknowledgments

We are grateful to A. Suzumoto and L. O'Hara (BPBM), P. Pruvost, R. Causse, Z. Gabsi, and J. Pfliger (MNHN), W.-J. Chen (NTUM), R. Winterbottom and E. Holm (ROM), D. Pitassy, S. Raredon, and K. Murphy (USNM), R. Bills, O. Gon, and M. Dwani (SAIAB), and G. Moore and M. Allen (WAM) for providing opportunities to examine specimens; the late J. Randall (BPBM), J. Eyre (San Francisco, USA), K. Uehara and T. Uehara (GT Divers), and K. Uchino and H. Senou (KPM) for sharing underwater photographs; G. Shinohara, S. Nomura, T. Kutsuna,

and Y. Shigeta (NSMT) for their efforts toward proper maintenance of the micro-CT scanner and software in the National Museum of Nature and Science, Research Wing, Tsukuba District. This study was supported in part by a Grant-in-Aid from the Japan Society for the Promotion of Science for JSPS Fellows to KF (DC1: 19J21103; PD: 22J01404); JSPS KAKENHI Grant Numbers 20H03311 and 21H03651; the JSPS Core-to-core CREPSUM JPJSCCB2020009; and the "Establishment of Glocal Research and Education Network in the Amami Islands" project of Kagoshima University adopted by the Ministry of Education, Culture, Sports, Science and Technology, Japan to HM. KWC acknowledges financial support from NSF (IOS 1256793/DBI 1702442) and Texas A&M Agrilife Research (Hatch TEX09452). APS acknowledges financial support from NSF (IOS 1256602/DBI 1701665). This is publication number 1688 of the Biodiversity Research and Teaching Collections at Texas A&M University.

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Supplementary Material 1

Figure S1

Authors: Fujiwara K, Motomura H, Summers AP, Conway KW (2024)
Data type: .jpg
Explanation notes: The least inclusive clade containing *Diademichthys*, *Rhinolepadichthys* **gen. nov.**, and *Discotrema* present in six of the seven possible gene trees available from Conway et al. (2020). **A** cytochrome oxidase 1 (COI); **B** 12S ribosomal RNA (12S); **C** glycosyltransferase (GLYT); D cardiac muscle myosin heavy chain 6 alpha (MYH6); **E** zic family member 1 (ZIC1); **F** SH3 and PX domain containing 3 gene (SH3PX3). Individual gene datasets from Conway et al. (2022) were obtained using a maximum likelihood algorithm implemented in Garli v.0.951-GUI (GTR model of nucleotide substitution).

Link: https://doi.org/vz.74.e113955.suppl1