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FULL PAPER

Rediagnosis of the monotypic genus *Lepadicyathus* Prokofiev 2005 (Gobiesocidae: Diademichthyinae) and redescription of *Lepadicyathus minor* (Briggs 1955), new combination

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Abstract

A revised diagnosis is provided for the poorly known clingfish genus *Lepadicyathus* Prokofiev 2005. The genus belongs to Diademichthyinae (*sensu* Conway et al.) and is characterized by the following combination of characters: snout moderate in length, slightly pointed in lateral view; oral cleft very small, restricted to anterior tip of snout, posterior portion of both jaws covered by thick skin; gill membrane attached to isthmus; gill opening tiny, narrow slit, dorsal-most extent level with base of 12th or 13th pectoral-fin ray in lateral view; "single" adhesive disc, its size moderate, length 16.6–20.4% SL; center of disc flat, without cavity; disc papillae flattened, similar in size across disc surface; cephalic lateral-line canals moderately developed, including 2 nasal, 2 lacrimal and 2 postorbital pores; pre-opercular and mandibular lateral-line canals absent; anus situated about midway between posterior margin of disc and anal-fin origin (disc to anus length 45.8–55.5% of disc to anal-fin origin length); dorsal, anal, and caudal fins weakly connected by membrane with distinct notch between fins; premaxillae separated anteriorly by large circular gap in dorsal view; nasal bone long, anterior tip pointed, terminating close to anteromedial tip of premaxilla in dorsal view; few lower-jaw teeth (ca. 6), restricted to anterior ca. 1/4 of dentary; basibranchial elements (including cartilages) absent; caudal skeleton with upper and lower hypural plates, separated by narrow hypural diastema. As recognized herein, *Lepadicyathus* is monotypic and contains only *Lepadicyathus minor* (Briggs 1955), new combination. The species has previously been assigned to *Lepadichthys* Waite 1904 and represents a senior synonym of *Lepadicyathus mendeleevi* Prokofiev 2005, type species of *Lepadicyathus*.

Keywords *Lepadicyathus mendeleevi* · *Lepadichthys minor* · Diagnosis · Synonymy · Western Pacific Ocean

Introduction

The clingfish genus *Lepadicyathus* Prokofiev 2005 was established for *Lepadicyathus mendeleevi* Prokofiev 2005, described based on two small specimens (13.5 and 15.0

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mm standard length) collected from Papua New Guinea. Prokofiev (2005) originally placed *Lepadicyathus* within the subfamily Aspasminae (*sensu* Briggs 1955), but subsequent authors have considered this genus as a member of either the Protogobiesocinane (Fricke et al. 2016) or the Diademichthyinae (Conway et al. 2020; Fujiwara et al. 2021). In a recent study, Fujiwara et al. (2021) hypothesized a close relationship between *Lepadicyathus* and the diademichthyine genus *Flabellicauda* Fujiwara et al. 2021 based on a number of putatively derived characters, including a similar arrangement of the cephalic sensory canal pores, a "single" adhesive disc, features of the jaws (in particular the presence of thick skin over the posterior part that restricts the mouth opening to the anterior-most tip of the snout), and a restricted gill opening.

In this study, we provide a revised diagnosis for *Lepadicyathus*. Based on examination of the holotype of *Lepadicyathus mendeleevi* and other material referable to *Lepadicyathus* from throughout the western Pacific Ocean, we show that *Lepadicyathus mendeleevi* is a junior synonym of *Lepadichthys minor* Briggs 1955, which is transferred to *Lepadicyathus* and re-described as *Lepadicyathus minor*, new combination.

Materials and methods

Counts and measurements follow Fujiwara and Motomura (2018) and Fujiwara et al. (2021) except for gill-opening depth which is omitted due to the difficulty of obtaining this measurement from small specimens (<15 mm SL). Standard length (SL) was measured to the nearest 0.1 mm. Other measurements were made to the nearest 0.01 mm using needle-point calipers under a dissecting microscope. Adhesive disc terminology follows Briggs (1955: fig. 1). Cephalic lateral-line canal pore terminology follows Shiogaki and Dotsu (1983: fig. 1), Conway et al. (2017: fig. 1), and Fujiwara et al. (2021). Surface features of the adhesive disc and pores of the cephalic lateral-line canals were observed with the aid of Cyanine Blue (following Saruwatari et al. 1997). Selected specimens were cleared and double stained (C&S) for bone and cartilage investigation using the protocol of Taylor and Van Dyke (1985). Computed tomography (CT) scans of the selected specimen were obtained at the Karel F. Liem BioImaging Center (Friday Harbor Laboratories, University of Washington) using a Bruker (Billerica, MA) SkyScan scanner w1173 with a 1 mm aluminum filter at 55 kV and 143 µA on a 2,240 × 2,240 pixel CCD at a resolution of 6.7 µm. The specimen was scanned in a 15 ml plastic Falcon tube (Corning, NY), in which it was wrapped with cheesecloth moistened with ethanol (70%) to prevent movement during scanning. The resulting CT data were visualized, segmented, and rendered in 3D Slicer (https://www.slicer.org) and were deposited on MorphoSource (https://doi.org/10.17602/M2/M30731). Osteological terminology follows Springer and Fraser (1976) and Conway et al. (2019). Photographs of preserved specimens (except for the holotype and paratype of *Lepadicyathus mendeleevi*) were taken with a Nikon D850 camera using an internal focus bracketing function; sets of multifocal images were then collated into a composite image, using the software CombineZP 1.0. The distribution map was prepared using the software GMT 5.3.1, using data from GSHHG (Wessel and Smith 1996). Institutional codes follow Sabaj (2020). Comparative data on *Lepadichthys* Waite 1904 and *Flabellicauda* used in this study were obtained from Fujiwara et al. (2021).

Lepadicyathus Prokofiev 2005

(New standard Japanese name: Amatsumi-ubauo-zoku)

Lepadicyathus Prokofiev 2005: 559 (type species: *Lepadicyathus mendeleevi* Prokofiev 2005; type by original designation, monotypic)

Diagnosis. A genus of the Diademichthyinae (*sensu* Briggs 1955; Conway et al. 2020) distinguished from other gobiesocid genera by the following combination of characters: snout moderate in length, slightly pointed in lateral view; oral cleft very small, restricted to anterior tip of snout, posterior portion of both jaws covered by thick skin of snout; gill membrane attached to isthmus; gill opening tiny, narrow slit, dorsal-most extent level with base of 12th or 13th pectoral-fin ray in lateral view; "single" adhesive disc, its size moderate, length 16.6–20.4% SL; center of disc flat, without cavity; disc papillae flattened, similar in size across disc surface; cephalic lateral-line canal pores moderately developed, including 2 nasal, 2 lacrimal and 2 postorbital pores; pre-opercular and mandibular lateral-line canals absent; anus situated about midway between posterior margin of disc and anal-fin (disc to anus length 45.8–55.5% of disc to anal-fin origin length); dorsal, anal, and caudal fins weakly connected by membrane with distinct notch between fins, not giving appearance of single, continuous median fin around posterior part of body; premaxillae separated anteriorly by large circular gap in dorsal view; nasal bone long, anterior tip pointed, terminating close to anteromedial tip of premaxilla in dorsal view; lower-jaw teeth few (ca. 6), restricted to anterior ca. 1/4 part of dentary; basibranchial elements (including cartilages) absent; caudal skeleton with upper and lower hypural plates, separated by narrow hypural diastema.

Comparisons with other genera. *Lepadicyathus* exhibits the putative synapomorphic characters of the Diademichthyinae (see Conway et al. 2020: 897). This subfamily currently contains 17 Indo-Pacific genera (Conway et al. 2020, 2021; Fujiwara et al. 2021), which can be artificially separated

into two groups based on the configuration of the adhesive disc ("single" adhesive disc group and "double" adhesive disc group; see Conway et al. 2021; Fujiwara et al. 2021). *Lepadicyathus* belongs to the "single" adhesive disc group (Fig. 1a), which also includes *Diademichthys* Pfaff 1942, *Discotrema* Briggs 1976, *Flabellicauda*, *Lepadichthys*, and *Unguitrema* Fricke 2014. *Lepadicyathus* is most similar to *Flabellicauda* and *Lepadichthys*, which share a similar snout (moderate in length, slightly pointed in lateral view; Fig. 2) and features of the adhesive disc (disc papillae flattened, center of disc flat, without cavity; Fig. 1a) (vs. snout extremely long in *Diademichthys*, strongly rounded in *Discotrema* and *Unguitrema*; disc papillae variable in size and shape, largest convex, dome-like mounds, and deep cavity present on center of disc in *Discotrema* and *Unguitrema*; see Briggs 1976: fig. 1; Fricke 2014: fig. 1c; Fujiwara et al. 2021: fig. 1).

The general appearance of *Lepadicyathus* is similar to *Lepadichthys*; however, the former differs distinctly from the latter in having a very small oral cleft (see below), a tiny gill opening (dorsal-most extent of gill opening level with base of 12th or 13th pectoral-fin ray in lateral view) (vs. gill opening moderate, level with base of 3rd to 10th in *Lepadichthys*), and lacking the pre-opercular lateral-line canal (Fig. 2) (vs. pre-opercular lateral-line canal present with 3 pores). We do not consider the four species of the *Lepadichthys lineatus* complex (*sensu* Fujiwara and Motomura 2021; *Lepadichthys geminus* Fujiwara and Motomura 2021, *Lepadichthys heemstraorum* Fujiwara and Motomura 2021, *Lepadichthys lineatus* Briggs 1966, and *Lepadichthys polyastrous* Fujiwara and Motomura 2021) as members of *Lepadichthys* (= "core" *Lepadichthys sensu* Fujiwara et al. 2021) and these have been excluded from the comparison above pending further investigation of the generic status of this group. Regardless, *Lepadicyathus* can be distinguished from the *Lepadichthys lineatus* complex by the condition of the upper lip (upper lip not fused with snout skin, distinct continuous groove present between the dorsal lip margin and snout), the shape of the snout (not extended, tip slightly beyond or about level with lower-jaw tip) and lacking oral papillae on inner surface of both lips (Fujiwara and Motomura 2021).

Lepadicyathus can be easily distinguished from all other gobiesocid genera, except for *Flabellicauda*, by the presence of thick skin covering the posterior portion of both jaws, which restricts the mouth opening to the anterior-most

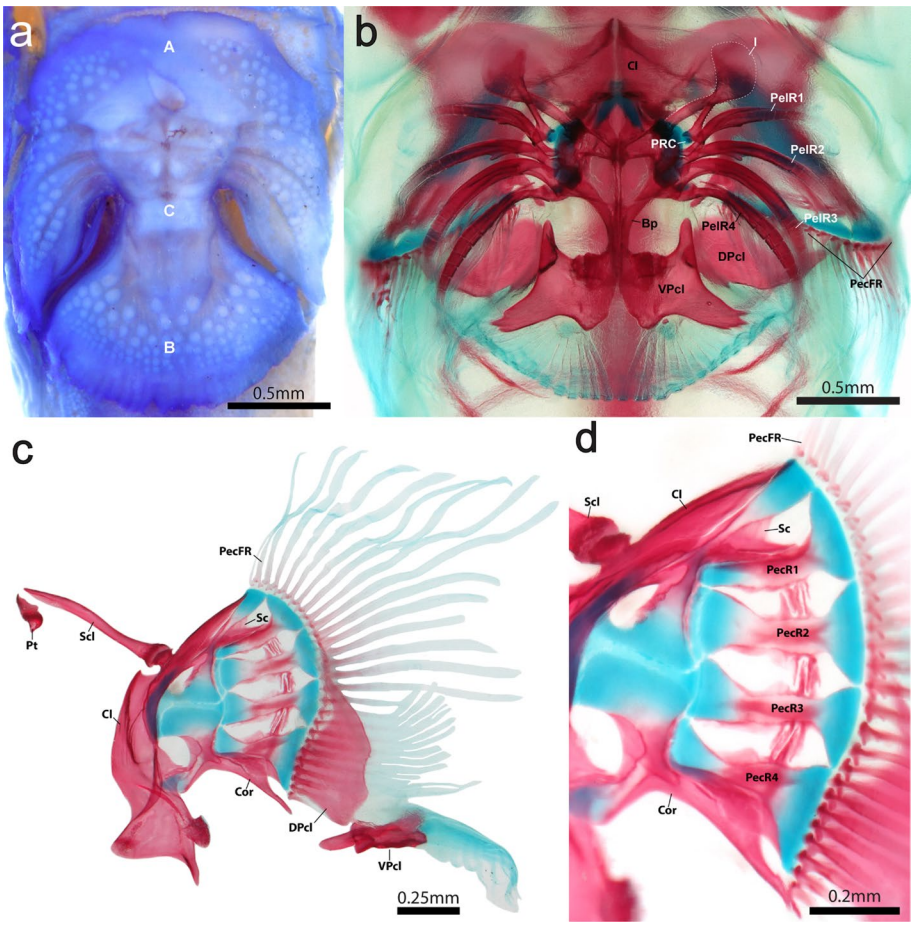


Fig. 1 Surface features of the adhesive disc (**a** ROM 47022, 18.0 mm SL, cyanine stain) and internal supporting skeleton of the paired-fin girdles (**b–d** ROM 73449, 13.4 mm SL) of *Lepadicyathus minor*. **b** Pelvic disc supporting skeleton, including elements of the pelvic and pectoral-fin girdle in ventral view (anterior to top of page). **c** Pectoral-fin girdle of right side in medial view (anterior to left). **d** Close-up of elements of the pectoral-fin endoskeleton articulating with pectoral-fin rays of the right side in medial view (anterior to left). Abbreviations: *PecFR* pectoral-fin ray; *PelR* pelvic-fin soft ray; *PRC* pelvic-radial cartilage; *A–C* disc region A–C, respectively. Other abbreviations as in Fig. 5

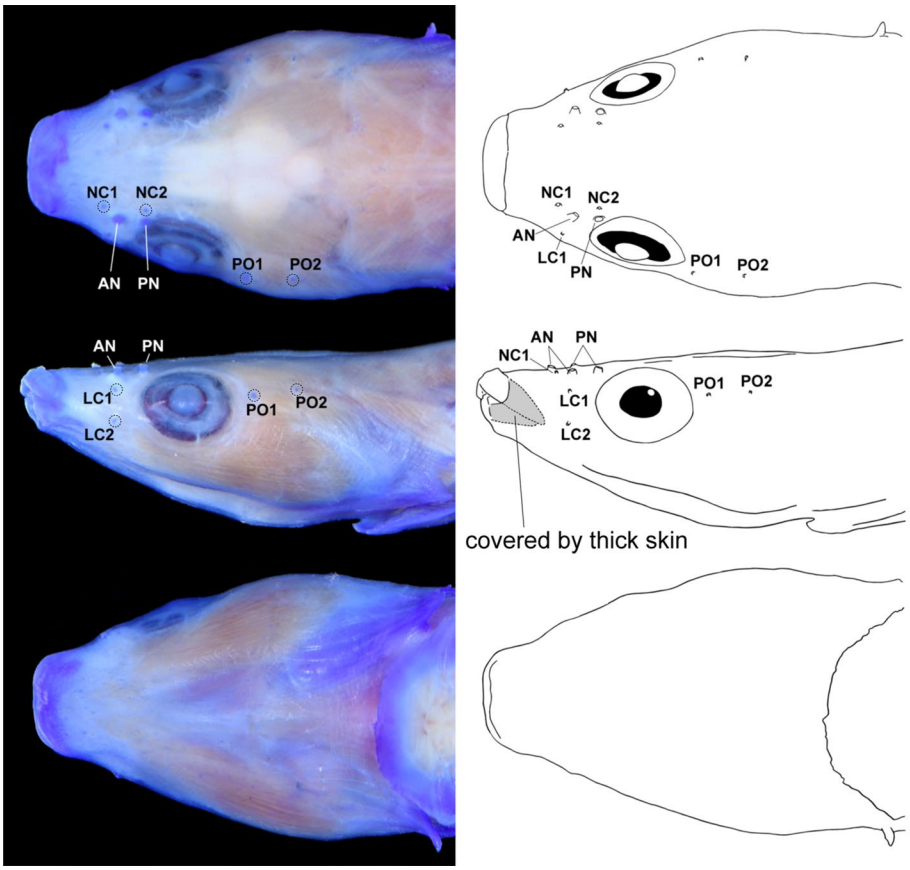


Fig. 2 Photographs (cyanine stain) and illustrations of head of *Lepadicyathus minor* (ANSP 51054, 17.0 mm SL), showing head sensory canal pores and mouth features. Abbreviations: *NC1–2* nasal canal pores; *LC1–2* lacrimal canal pores; *PO1–2* postorbital canal pores; *AN* and *PN* anterior and posterior nostrils, respectively

tip of the snout (Fig. 2; Fujiwara et al. 2021: figs. 6, 19). In all other gobiesocid genera, the mouth opening is not restricted laterally by skin of the snout, enabling a relatively wide gape. The unique confirmation of the skin surrounding the jaws of *Lepadicyathus* and *Flabellicauda* may represent a synapomorphy in support of a sister group relationship between the two genera. In addition to this character, Fujiwara et al. (2021) listed two other characters shared between *Lepadicyathus* and *Flabellicauda*, including a similar arrangement of the cephalic lateral-line canals (including the shared absence of the pre-opercular and mandibular lateral-line canals) and a restricted gill opening, but considered the two genera to be distinct based on other characters (viz., disc size, configuration of skin membrane uniting median fins, and features of the caudal-fin skeleton; see Fujiwara et al., 2021; Figs. 3a, 4), justifying separate generic status. In addition to the aforementioned characters, we note here that *Lepadicyathus* is further distinguished from *Flabellicauda* by the position of the anus, the shape of the nasal bone, the number of lower-jaw teeth, and features of the gill arch skeleton [viz., anus situated about midway between posterior margin of disc and anal-fin, disc to anus length 45.8–55.5% of disc to anal-fin origin length in *Lepadicyathus* vs. closer to anal-fin origin than to posterior margin of disc, above value is 56.4–78.3% in *Flabellicauda* (Fig. 3b); nasal bone elongate, anterior tip pointed, terminating close to anteromedial tip of premaxilla in dorsal view vs. moderate, anterior tip square to slightly rounded, terminating dorsal to posterior part of semi-circular indentation on medial edge of premaxilla (Figs. 5b, 6; Fujiwara et al. 2021: figs. 10, 11, 17); few lower-jaw teeth (ca. 6), restricted to anterior ca. 1/4 of dentary vs. dentary with ca. 18 teeth, extending along ca. 1/2 of dentary (Fig. 7b; Fujiwara et al. 2021: fig. 12B); basibranchial elements completely absent vs. 3 basibranchial elements (bone or cartilage) present (Fig. 7e; Fujiwara et al. 2021: fig. 12D)].

Included species. Our comprehensive examination of Indo-Pacific clingfishes revealed that two nominal species [*Lepadicyathus mendeleevi* (type locality: Papua New Guinea) and *Lepadichthys minor* Briggs 1955 (Celebes Sea, Indonesia)] can be assigned to *Lepadicyathus*, as defined in this study. When the former was described as a new genus and species, Prokofiev (2005) did not compare *Lepadicyathus mendeleevi* to *Lepadichthys minor* based on a misinterpretation of the adhesive disc characters of Briggs (1955) (see Remarks). A direct comparison between available paratypes of *Lepadichthys minor* (3 specimens; Fig. 8a–d) and the holotype and paratype of *Lepadicyathus mendeleevi* (Fig. 9) failed to reveal any

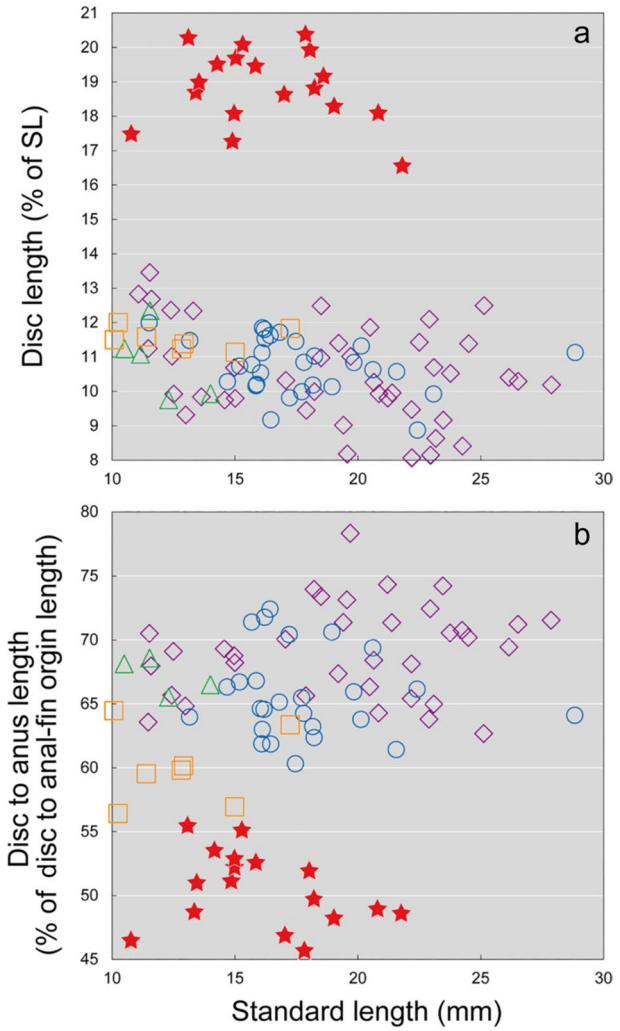


Fig. 3 Relationships of **a** disc length (as % of standard length) and **b** disc to anus length (as % of disc to anal-fin origin length) to standard length (mm), showing differences between *Lepadicyathus* (closed symbols) and *Flabellicauda* (open symbols) in *L. minor* (red stars), *F. alleni* (purple diamonds), *F. cometes* (yellow squares), *F. bolini* (blue circles), and *F. akiko* (green triangles)

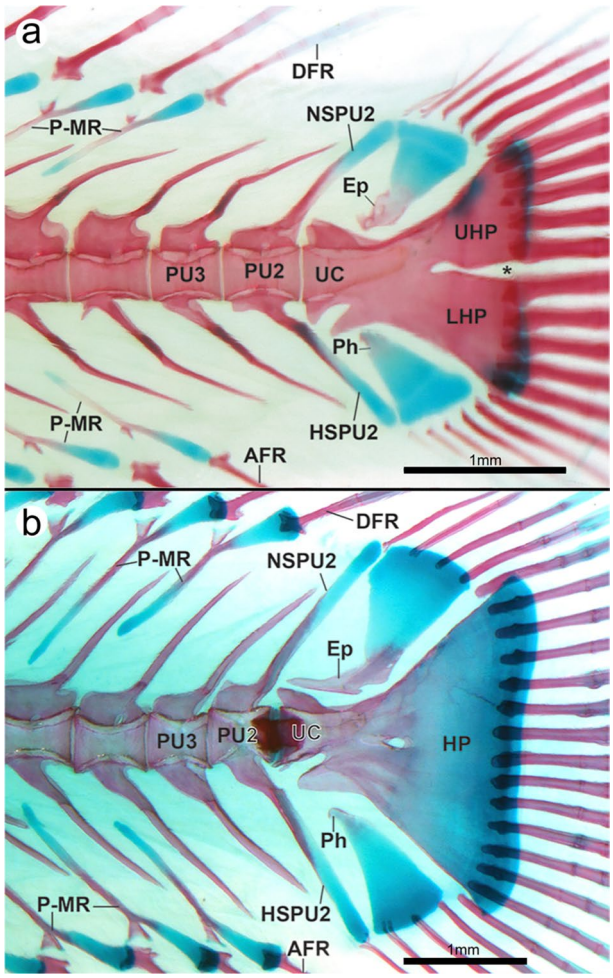


Fig. 4 Caudal skeletons of **a** *Lepadichthys minor*, ROM 73449, 13.4 mm SL; **b** *Flabellicauda alleni*, FMNH 127786, 17.1 mm SL. Scale bars = 1 mm. Abbreviations: *AFR* anal-fin ray; *DFR* dorsal-fin ray; *Ep* epural; *HP* hypural plate; *HSPU2* hemal spine of preural centrum 2; *LHP* lower hypural plate; *NSPU2* neural spine of preural centrum 2; *Ph* parhypural; *PU* preural centrum; *P-MR* proximal-middle radial; *UC* ural centrum; *UHP* upper hypural plate. *Asterisk* indicates diastema between *UHP* and *LHP*

differences between the two nominal species (Tables 1, 2). Although the holotype of *Lepadichthys minor* (ZMA 104162) was not examined as part of this study, information available from the original description (Briggs 1955) in combination with information on live coloration of *Lepadichthys minor* available from Koumans (1953) does not contain characters that would distinguish *Lepadichthys minor* from *Lepadicyathus mendeleevi*. The two nominal species are regarded herein as conspecific, *Lepadicyathus mendeleevi* representing a junior synonym of *Lepadichthys minor*. Accordingly, *Lepadicyathus* comprises only *Lepadicyathus minor*, new combination (= monotypic genus).

Lepadicyathus minor (Briggs 1955)

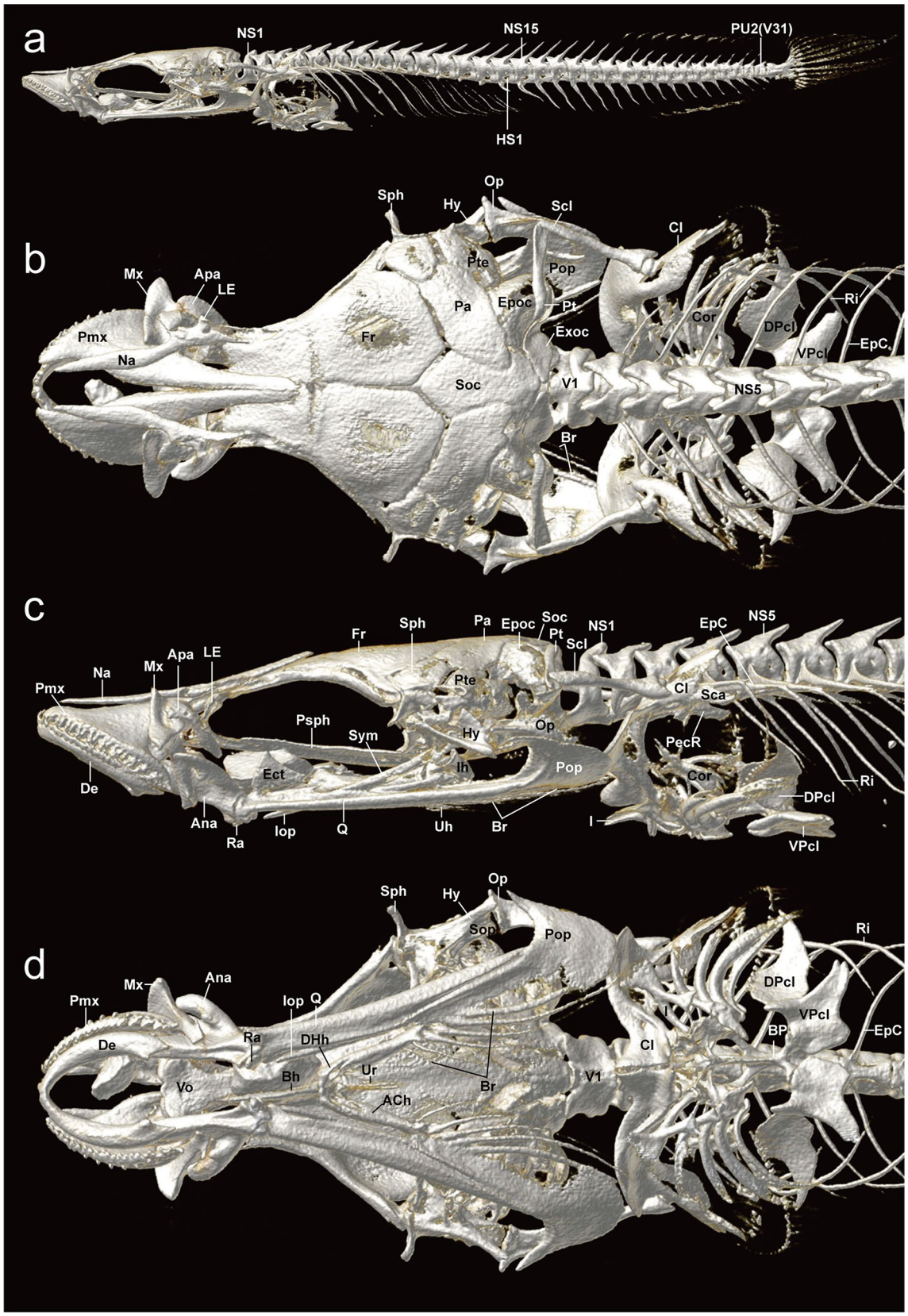
(English name: Dwarf Clingfish; new standard Japanese name: Amatsumi-ubauo)

(Figs. 1, 2, 3, 4a, 5, 6, 7, 8, 9, 10, 11; Tables 1, 2)

Crepidogaster indicus Weber 1913: 525, fig. 111 [in part (one of three paralectotypes); Muaras Reef, Celebes Sea, Indonesia]

Crepidogaster samoensis (not of Steindachner): Fowler and Silvester 1922: 124 (Pago Pago, Samoa: based on ANSP 51054); Fowler 1928: 447 (Samoa: based on ANSP 51054)

Gobiesocidae: Koumans 1953: 261 (Seram Sea, Indonesia: based on specimen deposited at RMNH)


a
NS1
NS15
PU2(V31)
HS1
b
Sph
Hy
Op
Scl
Cl
Pte
Pop
Mx
Apa
LE
Pa
Epoc
Pt
Ri
Cor
Pmx
Fr
Exoc
DPcl
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BP
EpC
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Ra
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Cl
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◂**Fig. 5** CT scanned skeleton of *Lepadicyathus minor*, ROM 73449, 10.8 mm SL. **a** Lateral view of whole body. **b** Dorsal view of anterior body. **c** Lateral view of anterior body. **d** Ventral view of anterior body. Abbreviations: *ACh* anterior ceratohyal; *Ana* anguloarticular; *Apa* autopalatine; *Bh* basihyal; *Bp* basipterygium; *Br* branchiostegal rays; *Cl* cleithrum; *Cor* coracoid; *De* dentary; *DHh* dorsal hypohyal; *DPcl* dorsal postcleithrum; *EpC* epicentral; *Ect* ectopterygoid; *Epoc* epiotic; *Exoc* exoccipital; *Fr* frontal; *HS* hemal spine of ventral postcleithrum; *Hy* hyomandibular; *I* pelvic-fin spine; *Ih* interhyal; *Iop* interopercle; *LE* lateral ethmoid; *Mx* maxilla; *Na* nasal; *NS* neural spine of ventral postcleithrum; *Op* opercle; *Pa* parietal; *PecR* pectoral radial; *Pmx* premaxilla; *Pop* preopercle; *Psph* parasphenoid; *Pt* posttemporal; *Pte* pterotic; *PU* preural centrum; *Q* quadrate; *Ra* retroarticular; *Ri* rib; *Sca* scapula; *Scl* supracleithrum; *Soc* supraoccipital; *Sop* subopercle; *Sph* sphenotic; *Sym* symplectic; *Ur* urohyal; *V* vertebral centrum; *Vo* vomer; *VPcl* ventral postcleithrum

Lepadichthys minor Briggs 1955: 137, fig. 113 [original description; type locality: Muaras Reef, Celebes Sea, Indonesia: based on ZMA 104162 (paralectotype of *Crepidogaster indicus*)]; Randall 2005: 506 (Howland Island: based on BPBM 38919); Fujiwara et al. 2020: 437 (Samoa: based on ANSP 51054); Fujiwara and Motomura 2020: 845 (Epi Island, Vanuatu: based on AMS IA. 832; Samoa: based on ANSP 51054); Fujiwara et al. 2021: 755, figs. 1F, 2D (Vanuatu: based on AMS IA. 832; Samoa: based on ANSP 51054; New Caledonia: based on BPBM 33610; Yoron Island, Ryukyu Islands, Japan: based on KAUM–I. 70995; Nha Trang Bay, Vietnam: based on ROM 73449)

Lepadicyathus mendeleevi Prokofiev 2005: 560, figs. 1–2 (original description; type locality: near village of Bongu, Madang Province, Papua New Guinea: based on ZIN 53413); Fricke et al. 2016: 57, fig. 6 (Papua New Guinea: based on ZIN 53413, 53413a); Fujiwara et al. 2021: 755, figs. 1H (Papua New Guinea: based on ZIN 53413)

Lepadichthys sp.: Haraguchi 2014: 485, unnumbered fig. (Yoron Island, Ryukyu Islands, Japan: based on KAUM–I. 58305)

Type specimens of *Lepadichthys minor*. AMS IA. 832, paratype, 19.0 mm SL, Lamen Bay, Epi Island, Vanuatu, 16°37′12″S, 168°09′00″E. ANSP 51054, 2 paratypes, 17.0 and 20.8 mm SL, Pago Pago, Samoa, 5 Apr. 1917, C. Silvester (Carnegie Samoa Expedition).

Type specimens of *Lepadicyathus mendeleevi*. ZIN 53413, holotype, 13.5 mm SL, ZIN 53413a, paratype, 15.0 mm SL, near village of Bongu, Madang Province, Papua New Guinea, 1 m depth, 14 Feb. 1977, RV *Dmitrii Mendeleev*.

Non-type specimens. 13 specimens, 10.8–21.8 mm SL. **JAPAN**: KAUM–I. 58305, 17.8 mm SL, Maehama Beach, Yoron Island, Amami Islands, Kagoshima, 27°01′15″N, 128°26′29″E, 2–5 m depth, 21 Jan. 2014, hand net, KAUM Fish Team; KAUM–I. 70995, 18.2 mm SL, Chabana, Yoron Island, Amami Islands, Kagoshima, 27°03′40″N, 128°24′31″E, 9 m depth, 15 Mar. 2015, hand net, T. Yoshida; YCM-P 33403, 15.3 mm SL, Honhaar, Ishigaki Island, Yaeyama Islands, Okinawa, A. Ono. **PHILIPPINES**: USNM 360253, 14.8 mm SL, Siit Bay, south of Negros Island, 09°04′00″N, 123°08′48″E, 2 m depth, 14 June 1978. **VIETNAM**: ROM 73449, 2 specimens, 10.8 (CT scanned) and 13.4 (C&S specimen) mm SL, north of Mun Island, Nha Trang Bay, Khanh Hoa, 12°10′19″N, 109°18′02″E, 21 May 2002, R. Winterbottom et al. **INDONESIA**: USNM 211922, 15.0 mm SL, Haria Bay, Saparua Island, 03°35′S, 128°36′E, 1.5–4.5 m depth, 5 Mar. 1974, V. Springer and M. Gomon. **AUSTRALIA**: AMS I. 33749-120, 13.1 mm SL, Boot Reef, Coral Sea Marine Park, Queensland, 09°58′50″S, 144°42′12″E, 2–6 m depth, 28 Jan. 1993, V. Springer. **NEW CALEDONIA**: AMS I. 47374-009, 18.5 mm SL, east of Hunter Island, 22°23′32″S, 172°05′25″E, 22 m depth, 4 Aug. 2017; BPBM 33610, 21.8 mm SL, Anchorage Islets, Chesterfield Islands, 19°53′30″S, 158°28′06″E, 14–15 m depth, 22 Aug. 1988, J. Randall et al. **Howland Island**: BPBM 38919, 14.2 mm SL, 0°47′56″N, 176°37′13″W, 9 m depth, 8 Feb. 2001. **FIJI**: CAS-ICH 247281, 15.8 mm SL, Nasese, Suva, 18°10′24″S, 178°25′17″E, 10 Feb. 2002, D. Greenfield et al.; ROM 47022, 18.0 mm SL, Laucala Bay, Suva, 18°10′28″S, 178°28′40″E, 11 Apr. 1983, A. Emery et al.

Diagnosis. See generic diagnosis.

Description. Counts and measurements given in Tables 1, 2, general appearance in Figs. 8, 9 and 10. Body slender, cylindrical, compressed at caudal peduncle. Body width narrower than head width. Head size medium, depressed anteriorly. Snout moderate, its tip slightly pointed in lateral view, semi-elliptical shaped in dorsal view; dorsal profile of snout straight. Mouth terminal, small, restricted to tip of snout. Anterior tip of upper jaw slightly pointed, extending slightly beyond that of lower jaw. Both lips thick, fleshy, weakly expanded. Posterior ca. 2/3 of both jaws covered by thick skin on lateral surface of snout (Fig. 2). Anterior and posterior nostrils larger than head sensory canal pores, close to each other, located dorsolaterally; both with a membranous tube, that of former slightly longer than latter; posterior margin of posterior nostril level with imaginary vertical line through anterior margin of eye. Eye size moderate. Interorbital region flattened. Gill membranes on each side united ventrally, attached to isthmus. Gill opening tiny, slit-like. First to third gill arches with two rows of gill filaments, 4th arch without filaments (gill description based on 5 specimens). Gill rakers slender, short and pointed. Cephalic lateral-line canal pores relatively developed, including 2 nasal, 2 lacrimal, and 2 postorbital pores; all pores similarly sized with minute membranous tube; pre-opercular and mandibular lateral-line canals absent. NC1 located in front of anterior nostrils in dorsal view; NC2 located slightly before anterior margin of posterior nostril to level with posterior margin of posterior nostril; LC1 located in front of anterior margin of eye; LC2 located just below LC1 or slightly

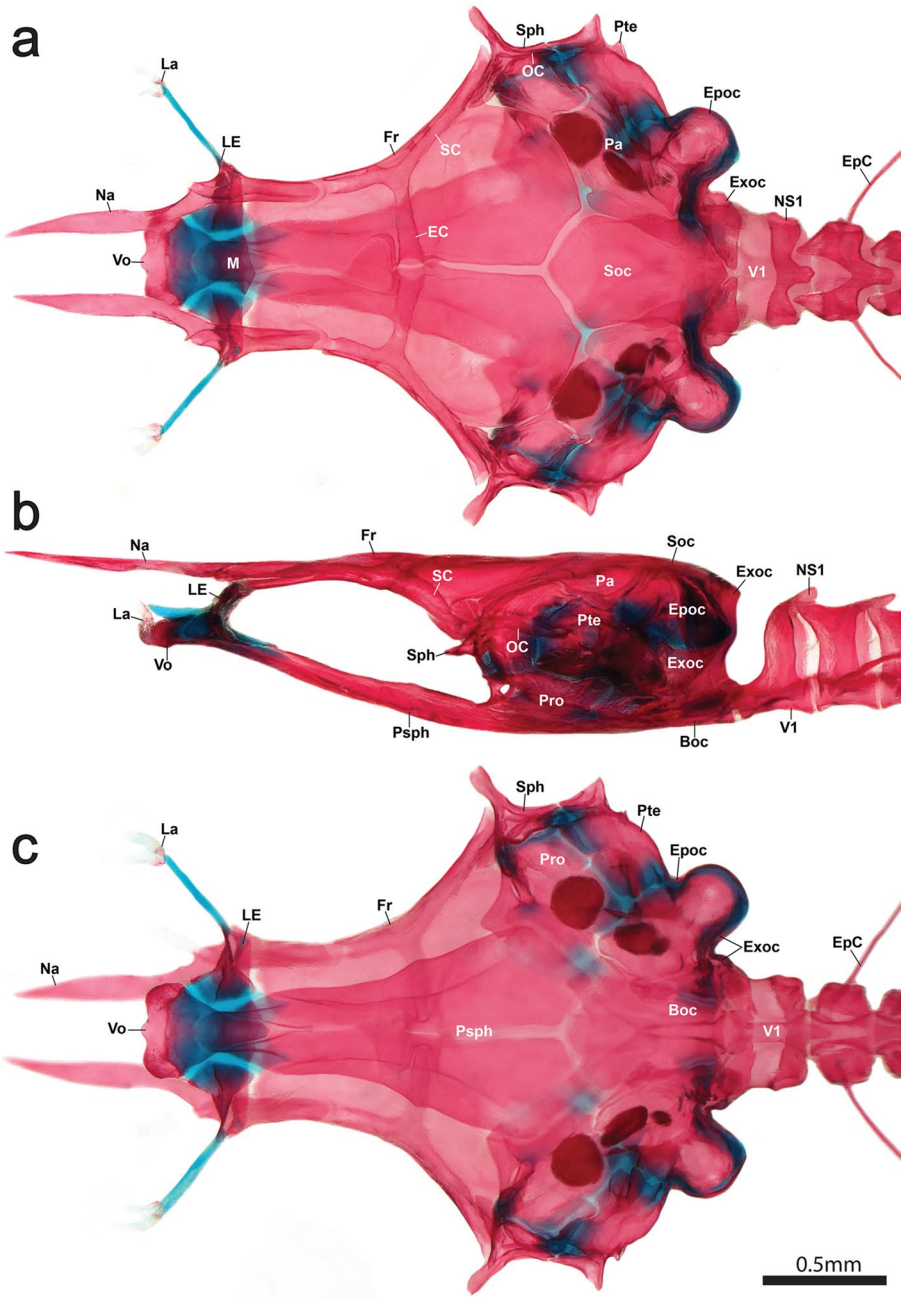

Fig. 6 Neurocranium of *Lepadicyathus minor*, ROM 73449, 13.4 mm SL. **a** Dorsal view. **b** Lateral view. **c** Ventral view. Abbreviations: *Boc* basioccipital; *EC* epiphyseal commissure of supraorbital canal; *La* lacrimal; *M* mesethmoid; *OC* otic canal; *Pro* prootic; *SC* supraorbital canal. Other abbreviations as in Fig. 5

postero-ventrally below LC1; PO1 located just behind posterior margin of orbit; PO2 close to PO1, located slightly posterodorsal to PO1 (Fig. 2).

Origin of dorsal fin slightly anterior to or even with imaginary vertical line through anal-fin origin. Dorsal and anal fins located posteriorly, their base relatively short; both fins weakly connected to caudal fin by membrane with distinct notch between fins (easily damaged). Dorsal- and anal-fin heights almost equal, except anteriorly. Pectoral- and caudal-fin margins rounded. Upper and lowermost pectoral-fin rays minute, longest ray extending beyond vertical through posterior margin of disc. All soft-fin rays unbranched and segmented. Pelvic fins and pectoral-girdle elements forming a circular, moderate sized, "single" adhesive disc (Fig. 1a). Disc region B bell-shaped, equal in size to disc region A. Anterior and posterior margins of disc region A and B, respectively, with fringe. Disc regions A and B with flattened papillae (disc papillae description based on 8 specimens, not including types). Center of disc region A lacking papillae; anterolateral part with 3 or 4 rows of papillae, number of rows slightly decreasing toward center; both sides of disc region A (except margins) covered with papillae; papillae of inner rows slightly larger than papillae of outer rows. Disc region B with 5 rows of papillae; papillae of inner

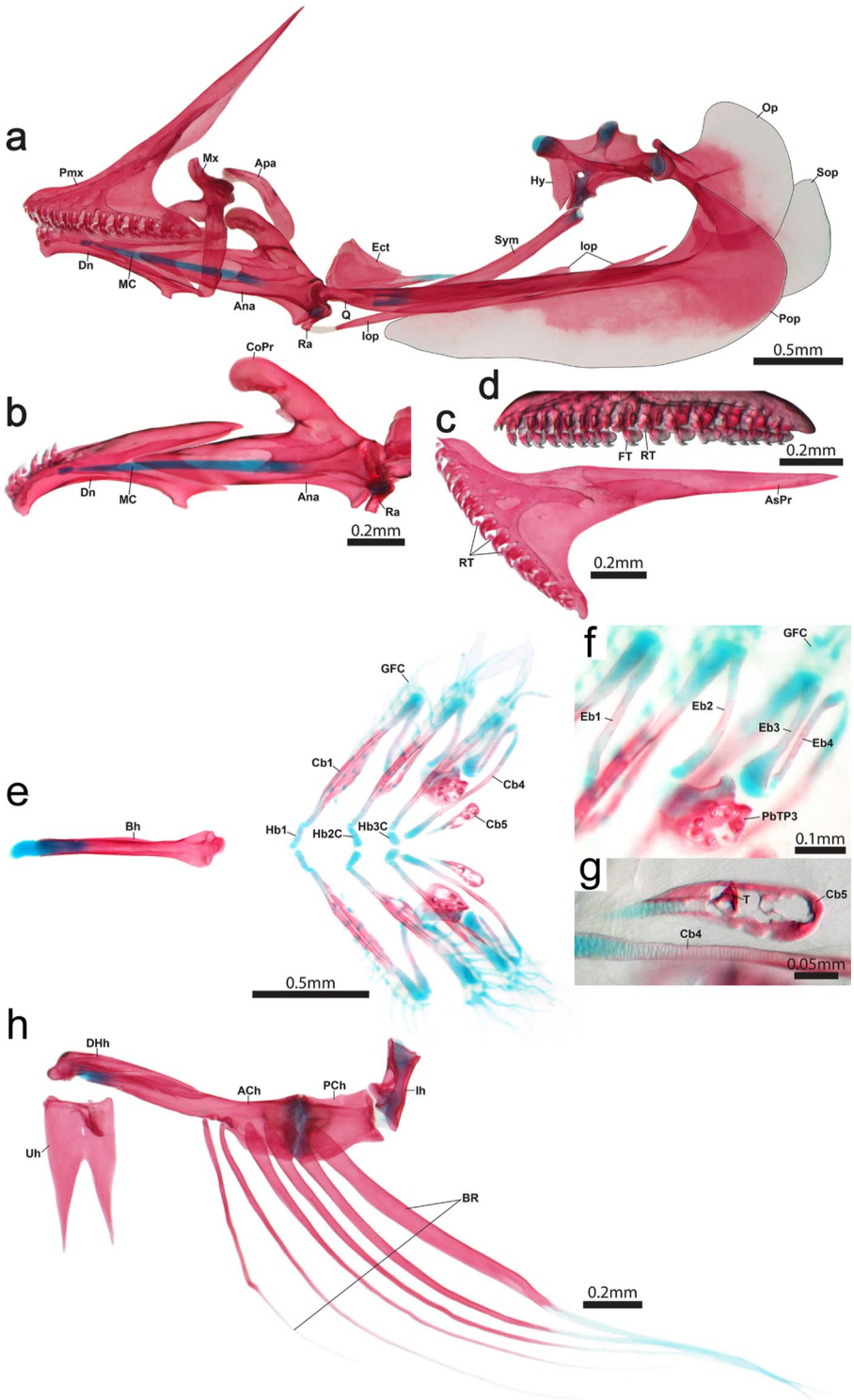

Fig. 7 Viscerocranium of *Lepadicyathus minor*, ROM 73449, 13.4 mm SL. **a** Hyopalatine arch and opercular series, right side in lateral view (image reversed). **b** Lower jaw in lateral view. **c** and **d** Upper jaw in dorsal and lateral views, respectively. **e** Gill-arch elements in dorsal view. **f** Close-up of Eb and PbTP3. **g** Close-up of Cb5. **h** Hyoid bar, right side in medial view and urohyal. Abbreviations: *AsPr* ascending process of premaxilla; *Cb* ceratobranchial; *CoPr* coronoid process; *Eb* epibranchial; *FT* functional teeth; *GFC* gill-filament cartilage; *Hb* hypobranchial; *MC* meckel's cartilage; *PbTP3* pharyngobranchial 3 toothplate; *PCh* posterior ceratohyal; *RT* replacement teeth; *T* pharyngeal teeth. Other abbreviations as in Fig. 5

rows slightly larger than papillae of outer rows; anterior part of disc region B without papillae. Disc region C lacking papillae.

Osteological description based on 1 C&S specimen (ROM 73449, 13.4 mm SL) and image resulting from CT scan (ROM 73449, 10.8 mm SL). General osteological characters as in Figs. 1b–d, 4a, 5, 6, 7. Neurocranium depressed, comprising nasal, lacrimal, lateral ethmoid, mesethmoid, sphenotic, pterotic, epiotic, prootic, supraoccipital, basioccipital, exoccipital, frontal, vomer, parasphenoid, and parietal (Figs. 5, 6). Posterior tip of epiotic articulating with posttemporal; sphenotic and pterotic contributing

Fig. 8 Preserved specimens of *Lepadicyathus minor*. **a**–**c** ANSP 51054, paratype, 17.0 mm SL, Pago Pago, Samoa; **d** ANSP 51054, paratype, 20.8 mm SL, Pago Pago, Samoa; **e** CAS-ICH 247281, 15.8 mm SL, Nasese, Suva, Fiji; **f** KAUM–I. 58305, Yoron Island, Amami Islands, Kagoshima, Japan. **a**, **d**–**f** Lateral views; **b** dorsal view; **c** ventral view

to hyomandibular facet, accommodating dorsal articular heads of hyomandibular; lacrimal firmly attached to tip of long, slender cartilage extending from anterolateral tip of lateral ethmoid. Antero-center point of vomer slightly protracted; posterior tip of vomer pointed in ventral view. Nasal long and slender; anterior tip pointed, reaching to anteromedial tip of premaxilla in dorsal view; its posterior tip articulating with anterior part of frontal; middle portion of nasal with sharp lateral process at exit of nasal canal. Jaws comprising maxilla, premaxilla, dentary, anguloarticular, and retroarticular (Figs. 5, 7a–d). Premaxilla with laterally compressed incisiviform teeth with hook-like tip, strongly curved posteriorly (ca. 90°). Ascending process of premaxilla long, terminating slightly anterior to epiphyseal commissure of supraorbital canal; premaxillae separated anteriorly by large circular gap in dorsal view. Maxilla irregular, boot-shaped, with elongate part orientated along dorsal-ventral axis; connected with premaxilla via well-developed, bifurcated articular head. Anterior ca. 1/4 part of dentary with ca. 6 pointed conical teeth, inner surface slightly curved; posteromedial face of dentary with squarish process. Anterior ca. 1/3 part of anguloarticular pointed, articulating with dentary; coronoid process of anguloarticular well-developed, tip rounded, directed anterodorsal.

Fig. 9 Preserved types of *Lepadicyathus mendeleevi* collected from near village of Bongu, Madang Province, Papua New Guinea. **a**–**c** ZIN 53413, holotype, 13.5 mm SL; **d**–**f** ZIN 53413a, paratype, 15.0 mm SL. **a**, **d** Lateral views; **b**, **e** dorsal views; **c**, **f**, ventral views

Retroarticular tiny, elongate, nestled in articular facet located on posteroventral part of anguloarticular. Suspensorium comprising autopalatine, quadrate, hyomandibular, ectopterygoid, and symplectic (Figs. 5, 7a). Autopalatine, a curved cylinder, articulating with lateral ethmoid dorsally, and maxilla anteriorly. Ectopterygoid triangular, its lower margin strongly connected with quadrate via elongate suture. Symplectic, a slender rod, articulating with posterior triangular part of quadrate anteriorly and anteroventral part of hyomandibular posteriorly. Opercular bones comprising opercle, subopercle, preopercle, and interopercle. Posterior margin of opercle, and posteroventral margin of subopercle and preopercle poorly ossified. Subopercle without spine-like posterior tip (Figs. 5, 7a). Interopercle thin, elongate bone with shallow notch along dorsal edge lateral to point of articulation between interhyal, symplectic and hyomandibular. Gill arches comprising basihyal, 4 paired epibranchials, paired pharyngobranchial 3 and associated tooth plate, 3 paired hypobranchial elements (bone or cartilage), and 5 paired ceratobranchials (Fig. 7e–g). Basibranchial elements

Table 1 Morphometric measurements (expressed as percentages of SL) of examined specimens of *Lepadicyathus minor*

	Types of *Lepadicyathus mendeleevi*		Types of *Lepadichthys minor*			Non-type specimens ($n = 7$)	Non-type specimens ($n = 6$)
	Holotype (ZIN 53413)	Paratype (ZIN 53413a)	Paratype (AMS IA. 832)	Paratype (ANSP 51054)	Paratype (ANSP 51054)	Japan and Southeast Asia	southwestern Pacific Ocean
Standard length (mm)	13.5	15.0	19.0	17.0	20.8	10.8–18.2	13.1–21.8
Head length	39.3	35.7	33.6	36.3	36.1	33.8–37.8	30.8–38.5
Post-orbital length	18.8	18.0	15.9	18.4	17.0	15.6–18.3	14.9–18.7
Head depth	10.0	9.7	11.6	10.2	10.6	9.2–12.0[a]	9.7–12.2[c]
Head width	22.1	20.3	21.0	22.4	21.2	19.3–22.3[a]	18.9–22.1[c]
Body depth	14.9	11.9	12.3	14.8	11.2	11.0–14.3[a]	13.4–15.2[c]
Body width	19.6	18.7	21.0	19.2	19.3	15.9–19.5	16.0–21.0[c]
Snout length	9.7	9.1	8.8	9.7	9.2	8.4–10.9	7.7–10.5
Snout depth	7.0	6.1	8.0	6.8	7.5	4.0–9.2	6.5–8.6[c]
Upper-jaw length	3.9	3.3	4.9	4.7	5.5	3.6–5.2	3.8–5.4
Orbit diameter	9.9	9.5	9.7	9.6	8.6	8.4–10.9	8.8–11.3
Anterior interorbital width	12.2	11.3	12.4	12.6	12.2	9.7–13.6	9.5–13.8[c]
Posterior interorbital width	17.8	16.3	19.4	16.4	18.8	17.2–19.5	15.2–20.1[c]
Least interorbital width	4.5	5.3	5.5	5.8	4.9	3.8–6.2	4.6–6.5[c]
Disc length	19.0	18.1	18.3	18.6	18.1	17.3–20.4	16.6–20.3
Disc width	18.3	16.6	18.6	16.0	16.7	14.9–17.6	16.1–18.6
Caudal-peduncle length	7.0	6.3	7.3	5.7	6.1	5.1–6.9	6.1–7.5[c]
Caudal-peduncle depth	6.6	6.9	7.8	8.4	7.5	6.4–9.1	7.4–9.0[c]
Pre-disc length	30.6	28.6	27.3	30.7	26.5	25.1–27.9	24.7–28.6[c]
Pre-anus length	68.3	65.5	63.6	65.8	62.7	61.9–64.8	60.2–66.3[c]
Disc to anal-fin origin length	35.3	37.9	38.0	36.0	37.7	31.8–36.3	32.1–36.6[c]
Disc to anus length	18.0	20.0	18.4	16.9	18.5	14.8–19.0	16.7–18.8[c]
Pre-dorsal-fin length	77.0	75.3	78.0	78.4	77.9	71.0–77.6	75.1–79.7[c]
Pre-anal-fin length	84.3	84.2	82.1	82.5	82.2	76.6–83.6	78.1–81.5[c]
Dorsal-caudal length	23.2	25.1	24.0	23.6	24.1	22.3–26.0	23.2–25.6[c]
Post-dorsal-caudal length	6.1	5.7	6.7	6.2	6.3	5.3–6.2	5.1–6.9[c]
Anal-caudal length	20.0	18.6	19.1	19.0	18.2	18.8–22.4	18.8–22.8[c]
Dorsal-fin base length	17.0	18.3	19.3	17.2	19.5	16.1–19.2	16.0–19.6[c]
Anal-fin base length	15.1	13.5	14.5	14.1	13.4	12.4–18.3	13.3–18.7[c]
Pectoral-fin length	15.9	12.7	13.5	–	–	10.8–17.4[a]	13.0–14.1[b]
Caudal-fin length	–	–	–	–	–	14.8–17.3[b]	14.0–18.3[d]

– no data; *a*, *b*, *c*, and *d* based on 6, 4, 5, and 3 specimens, respectively

(including cartilages) absent. Basihyal long, slender, anterior tip cartilaginous. Pharyngobranchial 3 flat, irregular shaped with anteromedial and posteromedial cartilaginous process, articulating with cartilaginous head of epibranchial 2 and 3, respectively. Pharyngobranchial 3 tooth plate associated (fused) with ventral surface of pharyngobranchial 3, with 2 rows of 3–4 conical teeth on ventral surface (Fig. 7f). Hypobranchial 1 thin, perichondrally ossified bone around precursor hypobranchial 1 cartilage; hypobranchial 2 and 3 cartilages without associated ossification. Ceratobranchial 5 tiny, with 1 or 2 small pharyngeal teeth (Fig. 7e, g). Hyoid bar comprising dorsal hypohyal, anterior and posterior ceratohyal, interhyal, and 6 branchiostegal rays (Figs. 5, 7h). Anterior ceratohyal tightly connected with dorsal hypohyal anterodorsally; separated from posterior ceratohyal posteriorly by thin band of cartilage. Interhyal well-developed, similar in size to posterior ceratohyal. Urohyal deeply forked posteriorly. Dorsal hypohyal elongate, similar length

Table 2 Frequency distribution of meristic counts of examined specimens of *Lepadicyathus minor*

	Dorsal-fin rays			Anal-fin rays			
	9	10	11	7	8	9	10
Japan and Southeast Asia		7			4	2	1
southwestern Pacific Ocean	2	$7^{H, Pme, Pmi}$	2^{Pmi}	1^{Pmi}	5^{Pmi}	$5^{H, Pme, Pmi}$	

	Pectoral-fin rays			Number of P1B same level with upper end of GM in lateral view		Number of P1B attached disc base by membrane*		
	26	27	28	12^{th}	13th	11th	12th	13th
Japan and Southeast Asia	4	1	1	5	1	3	2	1
southwestern Pacific Ocean	$3^{H, Pme}$	7^{Pmi}		$8^{H, Pme, Pmi}$	2^{Pmi}	3^{Pmi}	$6^{H, Pme, Pmi}$	1^{Pmi}

	Gill rakers (1st arch)				Gill rakers (2nd arch)		Gill rakers (3rd arch)	
	5	6	7	8	6	7	5	6
Japan and Southeast Asia		1		1	1	1		2
southwestern Pacific Ocean	1				1		1	1^{Pme}

H holotype of *Lepadicyathus mendeleevi*; *Pme* paratype of *Lepadicyathus mendeleevi*; *Pmi* paratype of *Lepadichthys minor*; *P1b* pectoral-fin ray base; *GM* gill membrane

*Counted from lowermost pectoral-fin ray base

as urohyal. Pelvic- and pectoral-fin girdles comprising basipterygium, dorsal postcleithrum, ventral postcleithrum, posttemporal, supracleithrum, cleithrum, scapula, coracoid, and 4 pectoral radials (Figs. 1b–d, 5). Anterior outline of basipterygia together triangular, posterior outline resembles reversed T-shape. Anteromedial tip and lateral edge of basipterygium cartilaginous; two large oval openings at center. Dorsal postcleithrum roughly triangular, with well-developed fimbrae along posterior edge. Ventral postcleithrum irregular in shape; anterior margin with pointed anterolateral process; posterior margin concave, with well-developed fimbrae. Complex articulation present between posterior tip of basipterygium and anteromedial edge of ventral postcleithrum. Pelvic-fin rays I, 4. Pelvic spine short, tip wide, rounded; base articulating with small pelvic-radial cartilage. Pelvic-fin soft rays 1–4 articulating with cartilaginous lateral edge of basipterygium; soft rays slender, tapering distally. Four pectoral radials (1–4) with cartilaginous posterior tip; bony struts along ventral (pectoral radial 1), dorsal (pectoral radial 4), or both ventral and dorsal margins (pectoral radials 2 and 3) interdigitating with struts borne on element(s) directly above and/or below. Scapula irregular in shape, tightly connected with dorsal surface of pectoral radial 1. Coracoid bifurcated anteriorly, pointed posteriorly; tightly connected with ventral surface of pectoral radial 4. Caudal skeleton comprising upper and lower hypural plates, epural, and parhypural (Fig. 4a). Hypural plates, separated by narrow hypural diastema; 5 caudal-fin rays associated with upper and lower plates, respectively; 6 upper and 6 lower procurrent caudal-fin rays. Epural and parhypural thin, perichondrally ossified bone around triangular precursor cartilages. Total number of vertebrae 32, including 14 abdominal and 18 caudal. Ribs 10, associated with vertebrae 3–12. Epicentrals 17, associated with vertebrae 2–18. First dorsal-fin pterygiophore inserted between neural spines of vertebrae 17/18. First anal-fin pterygiophore inserted between hemal spines of vertebrae 20/21.

Coloration in fresh condition (Fig. 10). Body reddish brown with white stripe on dorsal midline and two narrow white stripes on each side; upper stripe extending from anterior nostril, past dorsal margin of pupil and pectoral fin, to caudal-fin base, both tips tapering; lower stripe (sometimes indistinct) located ventrally (visible in ventral view), extending from under lower-jaw tip to base of last anal-fin rays through lower margin of eye and base of adhesive disc, middle part of stripe (from posterior margin of disc to around anus) relatively wide, both tips tapering, anterior tips of each side connected on chin; stripe on dorsal midline extending from snout tip to dorsal-fin origin, anterior part relatively wide (widest in all stripes), tapering posteriorly. ca. 20–30 small white spots (sometimes indistinct) present on posterior part of body (between stripes). Upper part of head reddish brown, lower region (below level of lower margin of eye) white; both lips reddish orange; tubes of nostrils reddish brown; iris reddish orange, pupil black. All fin membranes hyaline, rays reddish brown (especially base of dorsal- and anal-fin rays); caudal fin with large regular triangular marking centrally; adhesive disc white.

Coloration when preserved. Uniformly light brown or yellowish white. Black melanophores scattered on body

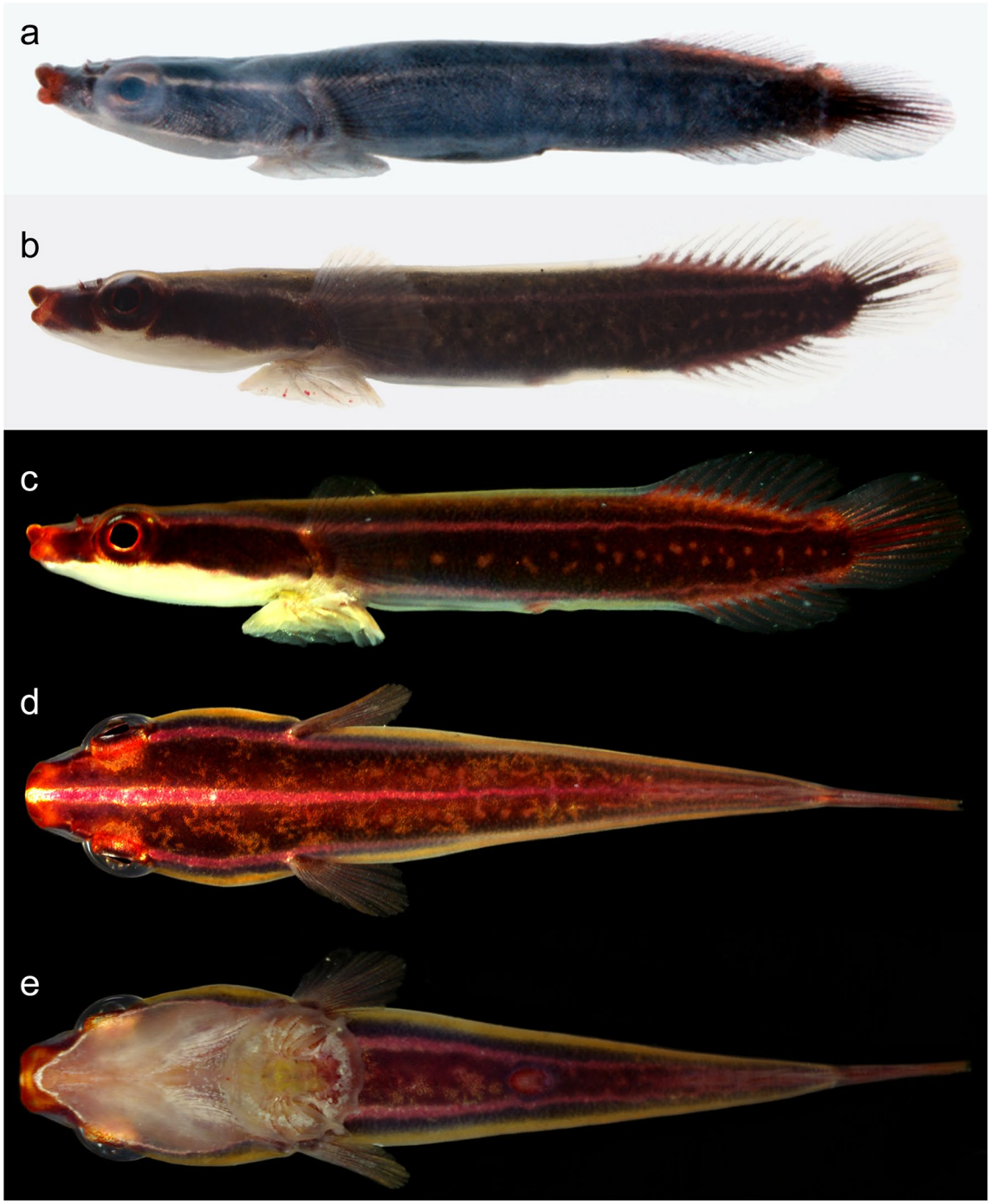

Fig. 10 Color photographs of freshly captured *Lepadicyathus minor*. **a** ROM 73449, 13.4 mm SL, Nha Trang Bay, Khanh Hoa, Vietnam; **b** KAUM–I. 58305, Yoron Island, Amami Islands, Kagoshima, Japan; **c–e** KAUM–I. 70995, 18.2 mm SL, Yoron Island, Amami Islands, Kagoshima, Japan. **a–c** Lateral views; **d** dorsal view; **e** ventral view

in 4 of 18 specimens (BPBM 38919, CAS-ICH 247281, and KAUM–I. 58305, 70995; Fig. 8e, f). Aforementioned pattern of stripes retained only in type material of *Lepadicyathus mendeleevi* (Fig. 9), which appear to have been preserved in ethanol (based on white appearance of pupil).

Distribution and habitat. Known from several locations throughout the western Pacific Ocean (Briggs 1955; Prokofiev 2005; this study). Specimens examined during the present study were collected from southern Japan (Ryukyu Islands), Philippines (Negros Island), Vietnam

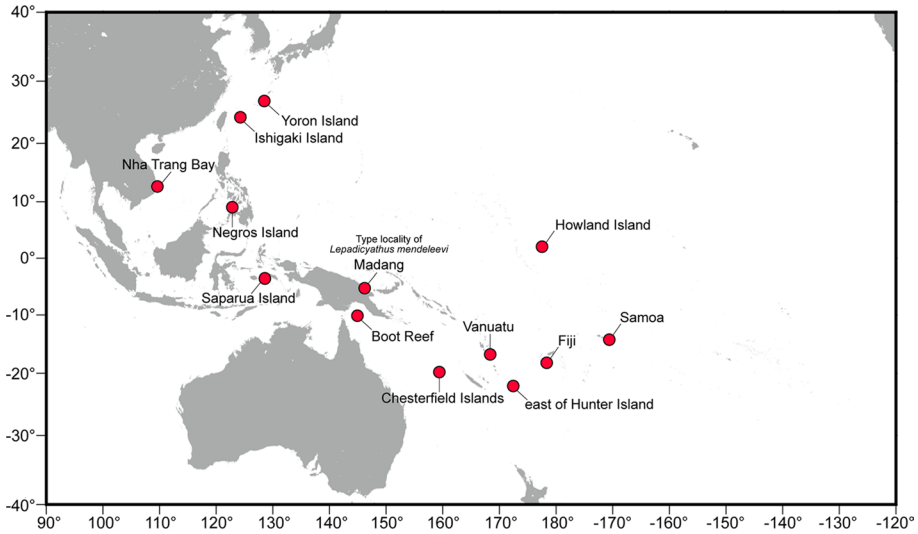

Fig. 11 Distributional map of *Lepadicyathus minor* based on examined specimens in this study

(Nha Trang Bay), Indonesia (Banda Sea), Papua New Guinea (north coast near Madang), east coast of Australia (north of Coral Sea), Vanuatu, New Caledonia, Howland Island, Fiji, and Samoa (Fig. 11) at depths of 1–22 m. According to Prokofiev (2005), *L. minor* (as *L. mendeleevi*) is associated with hydrozoan corals (species of *Millepora*).

Remarks. *Lepadicyathus minor* was originally described by Briggs (1955) as a member of *Lepadichthys* on the basis of five specimens (holotype also paralectotype of *Crepidogaster indicus*). Later, Prokofiev (2005) described *Lepadicyathus mendeleevi* as a new genus and species and included it in the subfamily Aspasminae (*sensu* Briggs 1955), characterized by a "double" adhesive disc, three gills, and the gill membrane attached to the isthmus (Aspasminae is currently placed in the synonymy of Diademichthyinae following Conway et al. 2020). This decision was based on a misinterpretation of the disc features of the new species, which exhibits a "single" disc (Fig. 9c, f) but interpreted as "double" by Prokofiev (2005). Subsequently, Fricke et al. (2016) redescribed *Lepadicyathus mendeleevi* and placed it within their new subfamily Protogobiesocinae, characterized by the laterally asymmetrical body, although such a condition could not be confirmed in the type material of *Lepadicyathus mendeleevi* or other specimens examined in this study (see also Conway et al. 2020: 900–901). In addition, the arrangement of head sensory canal pores and some meristic characters given by Prokofiev (2005) and Fricke et al. (2016) (viz., two preopercle canal pores, 11–12 dorsal-fin rays, 23–25 pectoral-fin rays, and upper end of gill membrane level with 10th pectoral-fin ray in lateral view) are also revised in this study as follows: pre-opercular lateral-line canal and associate pores absent; 9–11 dorsal-fin rays; 26–28 pectoral fin rays; and upper end of gill membrane level with 12th or 13th pectoral-fin ray in lateral view. The nominal species is regarded here as a junior synonym of *Lepadichthys minor* (= *Lepadicyathus minor*) (see Included species).

The largest individual of *Lepadicyathus minor* that we have examined is 21.8 mm SL. Though we have not confirmed that this individual is mature, following the criteria of Weitzman and Vari (1988) we consider this species miniature (i.e., not exceeding 26 mm SL), adding to the growing number of miniature gobiesocids described within the last decade (e.g., Allen and Erdmann 2012; Fricke 2014; Conway et al. 2019; Fujiwara et al. 2021).

The new standard Japanese names "Amatsumi-ubauo-zoku" and "Amatsumi-ubauo" are proposed here for *Lepadicyathus* and *Lepadicyathus minor*, respectively, in reference to small white spots on the posterior part of the body. "Amatsumi" (= "Amatsumikaboshi") is the God of Stars in Japanese mythology.

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