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Description of a New Genus and Two New Species of Indo-Pacific Clingfishes (Gobiesocidae: Diademichthyinae) with Redescription and Reassignment of Two Species Previously Assigned to *Lepadichthys* Waite, 1904

Kyoji Fujiwara[1], Kevin W. Conway[2,3], and Hiroyuki Motomura[3,4]

A new genus and two new species of Indo-Pacific clingfishes are described in this study. The new genus, *Flabellicauda*, belongs to the Diademichthyinae and can be distinguished from other genera currently placed in this subfamily by the following combination of characters: snout moderate in length and slightly pointed, not extremely long or strongly rounded; oral cleft very small, restricted to anterior tip of snout, posterior portion of both jaws covered by thick skin of snout; gill opening a tiny, narrow slit, dorsalmost point level with base of 9th to 14th (usually 12th, rarely 9th) pectoral-fin ray in lateral view; gill membrane attached to isthmus; two rows of gill filaments on gill arches 1–3; extremely small "single" adhesive disc, its length 8.1–13.5% SL; center of disc flat, without cavity; disc papillae flattened, similar in size across disc surface; preopercular lateral-line canal and associated pores absent; dorsal, anal, and caudal fins connected via thin membrane, giving appearance of single, continuous median fin around posterior part of body; and upper and lower hypural plates completely fused, forming large fan-like hypural complex. Two new species are described and assigned to *Flabellicauda*, new genus, including *F. alleni*, new species (type species of *Flabellicauda*, new genus), and *F. cometes*, new species. Two additional species previously assigned to *Lepadichthys* are transferred to *Flabellicauda*, new genus, including *F. bolini*, new combination, and *F. akiko*, new combination. Among species of *Flabellicauda*, new genus, *F. akiko* is unique in having the following characters: head sensory canal pores poorly developed, including 1 nasal and 1 postorbital pore (vs. usually 2 nasal, 2 lacrimal, and 2 postorbital pores in *F. alleni*, new species, and *F. bolini*; 2 nasal pores in *F. cometes*, new species); upper end of gill opening level with base of 9th or 10th pectoral-fin ray in lateral view (vs. 12th to 14th); disc region A with papillae at center (vs. disc region A without papillae at center); and body background color red in life, with white stripes along body (vs. body background color black or maroon in life, with white stripes along body). Although *F. alleni*, new species, is very similar to *F. bolini*, the former differs from the latter in having a higher number of gill rakers (viz., 5–8 [modally 6, rarely 5], 6–8 [6], and 6–8 [7] on the first, second, and third gill arch, respectively, and 18–24 [19] total gill rakers [first + second + third arch] in *F. alleni*, new species, vs. 4–6 [5] on the first, second, and third arch, respectively, and 12–17 [14] total gill rakers in *F. bolini*). In addition to the meristic difference, head length, pre-disc length, orbit diameter, and caudal-peduncle length and width proportions further aid to distinguish *F. alleni*, new species, from *F. bolini*. Examined specimens of *F. alleni*, new species, were collected from Sri Lanka and southeast Asia, whereas those of *F. bolini* were collected from Papua New Guinea, Vanuatu, and Fiji; the range of the two species are not known to overlap. *Flabellicauda cometes*, new species, can be easily distinguished from *F. alleni*, new species, and *F. bolini* in having the following characters: 10–12 dorsal-fin rays (vs. 12–15 [13]); 9–11 anal-fin rays (vs. 10–13 [11], rarely 10); head sensory canal pores poorly developed, including 2 nasal and 1 postorbital pores. Notes on the ecology of each of the four species of *Flabellicauda*, new genus, are also provided.

THE family Diademichthyidae was introduced by Whitley (1950) for the distinctive Urchin Clingfish *Diademichthys lineatus*. Briggs (1955) redefined it as a subfamily of the Gobiesocidae and included both *Diademichthys* and *Lepadichthys*. Later, Briggs (1976) and Fricke (2014) added *Discotrema* and *Unguitrema*, respectively, to the Diademichthyinae. In their phylogenetic investigation of the Gobiesocidae, Conway et al. (2020) recovered the Diademichthyinae as a polyphyletic group and, in order to achieve monophyly, recommended that it be expanded to include several additional genera formerly included in the Aspasminae, Diplocrepinae, and Protogobiesocinae by Briggs (1955) and Fricke et al. (2016). Following Conway et al. (2020), the total number of genera included in the Diademichthyinae is 15, which can be artificially separated into two groups based on whether they exhibit a "single" or "double" adhesive disc (see Briggs, 1955: fig. 1), a character that has traditionally been reserved for the diagnosis of subfamily-level taxa (Briggs, 1955).

The genus *Lepadichthys* was established by Waite (1904) for *Lepadichthys frenatus*, based on specimens collected at Lord Howe Island, Tasman sea, Australia. Later Regan (1921), added *L. coccinotaenia*, described based on specimens collected from the southwestern Indian Ocean (along the coast of South Africa), and Whitley (1943) added *L. sandaracatus*, described based on specimens collected from the southeastern Indian Ocean (along the coast of Western Australia). In his review of gobiesocid fishes, Briggs (1955) placed *Lepadichthys* within his Diademichthyinae, provided a rediagnosis for the genus, and also described *L. minor*, based on specimens collected from the Sulawesi Sea (western Pacific). Subsequent to Briggs's (1955) revision,

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ten species of *Lepadichthys* have been described from throughout the Indo-Pacific, including (in order of year of description): *L. bolini*, *L. ctenion*, *L. erythraeus*, *L. lineatus*, *L. caritus*, *L. springeri*, *L. akiko*, *L. bilineatus*, *L. trishula*, and *L. conwayi* (Briggs, 1962, 1966, 1969a, 2001; Briggs and Link, 1963; Allen and Erdmann, 2012; Craig et al., 2015; Fujiwara et al., 2020; Fujiwara and Motomura, 2020a). In the most recent taxonomic work on the genus, Fujiwara and Motomura (2019a) showed that *Lepadichthys misakius*, previously regarded as a junior synonym of *L. frenatus*, is a valid species, and Fujiwara and Motomura (2020a) showed that *L. springeri* is a synonym of *L. misakius*. Presently, the total number of valid species of *Lepadichthys* is 14 (Fricke et al., 2021). Though the number of species of *Lepadichthys* has increased markedly after Briggs (1955), the diagnosis of the genus has never been revised. Hence, some species currently included in *Lepadichthys* do not match the current generic diagnosis (see explanation in Fujiwara and Motomura, 2018). The results of a recent molecular phylogenetic study on clingfishes (Conway et al., 2020) showed that *Lepadichthys*, as currently defined, is likely polyphyletic based on the phylogenetic placement of the four species included in that study (*L. akiko*, *L. bolini*, *L. misakius*, and *L. trishula*).

As part of an ongoing taxonomic study of *Lepadichthys*, we observed consistent morphological variation among samples of the geographically widespread *L. bolini*, a species described by Briggs (1962) based on a single individual from Vanuatu. Further investigation revealed this material to comprise not one but instead three species, two of which are currently undescribed. Like *L. bolini* and the closely related *L. akiko*, the two new species exhibit a striking pattern in life comprising a series of white stripes along the body that contrast with a darker background color of black or maroon. In addition to this striking live color pattern, all four species exhibit a distinctive arrangement of the caudal-fin skeleton, in which the hypural complex is represented by a single, large fan-shaped element (vs. separated into an upper and lower hypural plate in the majority of other gobiesocids). These apomorphic characters, in combination with a number of others, suggest to us that these four species represent a putative monophyletic group, which, based on the results of recent molecular phylogenetic work, is not closely related to members of *Lepadichthys* (including the type species, *L. frenatus*; see discussion). In this study, we describe the new genus *Flabellicauda* to accommodate four distinctive members of the Diademichthyinae, describe two new species, and provide redescriptions of *Flabellicauda akiko* and *Flabellicauda bolini*, both new combinations.

MATERIALS AND METHODS

Counts and measurements follow Fujiwara and Motomura (2018) except for upper-jaw length, which is measured from the anterior point of the upper lip to the junction between the lateral part of the upper lip and the skin of the snout, which restricts the mouth opening laterally. Measurements were made to the nearest 0.01 mm, except for standard length (SL), which was measured to the nearest 0.1 mm. Institutional codes followed Sabaj (2020). Data obtained from holotypes are presented first within descriptions, followed by data obtained from other specimens in parentheses (if different). Adhesive disc terminology follows Briggs (1955: fig. 1), and cephalic sensory canal pore terminology follows Shiogaki and Dotsu (1983: fig. 1) and Conway et al. (2017a: fig. 1), except that we use the term otic canal instead of postorbital canal (though retain the abbreviations PO1 and PO2 for the pores associated with this canal). Features of both the adhesive disc and cephalic sensory canal pores were observed using versatile staining with Cyanine Blue (Saruwatari et al., 1997). Osteological terminology follows Springer and Fraser (1976) and Conway et al. (2019). Osteological features were assessed via radiographs for the majority of specimens, but select specimens were cleared and double stained (CS) for bone and cartilage investigation using the protocol of Taylor and Van Dyke (1985). Computed tomography (CT) scans of select specimens of *F. akiko*, *F. alleni*, new species, and *F. cometes*, new species, were also obtained at the Karel F. Liem Bioimaging Facility (Friday Harbor Laboratories, University of Washington) using a Bruker (Billerica, MA) SkyScan 1173 scanner with a 1 mm aluminum filter at 60 kV and 110 μA on a 2240 × 2240 pixel CCD at a resolution of 8.8 μm. Specimens were scanned simultaneously in a 50 ml plastic Falcon tube (Corning, NY), in which they were wrapped with cheesecloth moistened with ethanol (70%) to prevent movement during scanning. The resulting CT data were visualized, segmented, and rendered in Horos (https://horosproject.org) and Amira (FEI). The distributional map was prepared using GMT 5.3.1, using data from GSHHG (Wessel and Smith, 1996).

Flabellicauda, new genus

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Type species.—*Flabellicauda alleni*, new species.

Diagnosis.—A genus of the Gobiesocidae distinguished from other gobiesocid genera, except for *Diademichthys*, *Discotrema*, *Lepadichthys*, *Lepadicyathus*, and *Unguitrema*, by having a "single" adhesive disc, two rows of gill filaments on gill arches 1–3 (3 gills *sensu* Briggs, 1955), and the gill membrane attached to the isthmus. The new genus is distinguished from *Discotrema* and *Unguitrema* by the following combination of characters: snout slightly pointed (vs. strongly rounded in *Discotrema* and *Unguitrema*; Fig. 1A, D); center of disc flat, without cavity (vs. deep cavity present: see Briggs, 1976: fig. 1); and disc papillae flattened, similar in size across disc surface (vs. disc papillae of variable size across surface of disc, largest papillae dome-like, or pyramidal: see Briggs, 1976: fig. 1; Fricke, 2014: fig. 1c). The new genus is distinguished from *Diademichthys*, *Lepadichthys*, and *Lepadicyathus* by the following unique combination of characters: snout moderate in length (vs. extremely long in *Diademichthys*; Fig. 1A, C); oral cleft very small, restricted to anterior tip of snout, posterior portion of both jaws covered by thick skin of snout (vs. moderate, not covered by skin of snout in *Diademichthys* and *Lepadichthys*; Fig. 1A–C); preopercular lateral-line canal and associated pores absent (vs. present in *Diademichthys* and *Lepadichthys*); gill opening a tiny, narrow slit, dorsalmost point level with base of 9th to 14th (usually 12th, rarely 9th) pectoral-fin ray in lateral view (vs. moderate in *Diademichthys* [7th to 9th] and *Lepadichthys* [3rd to 9th, rarely 10th]); disc extremely

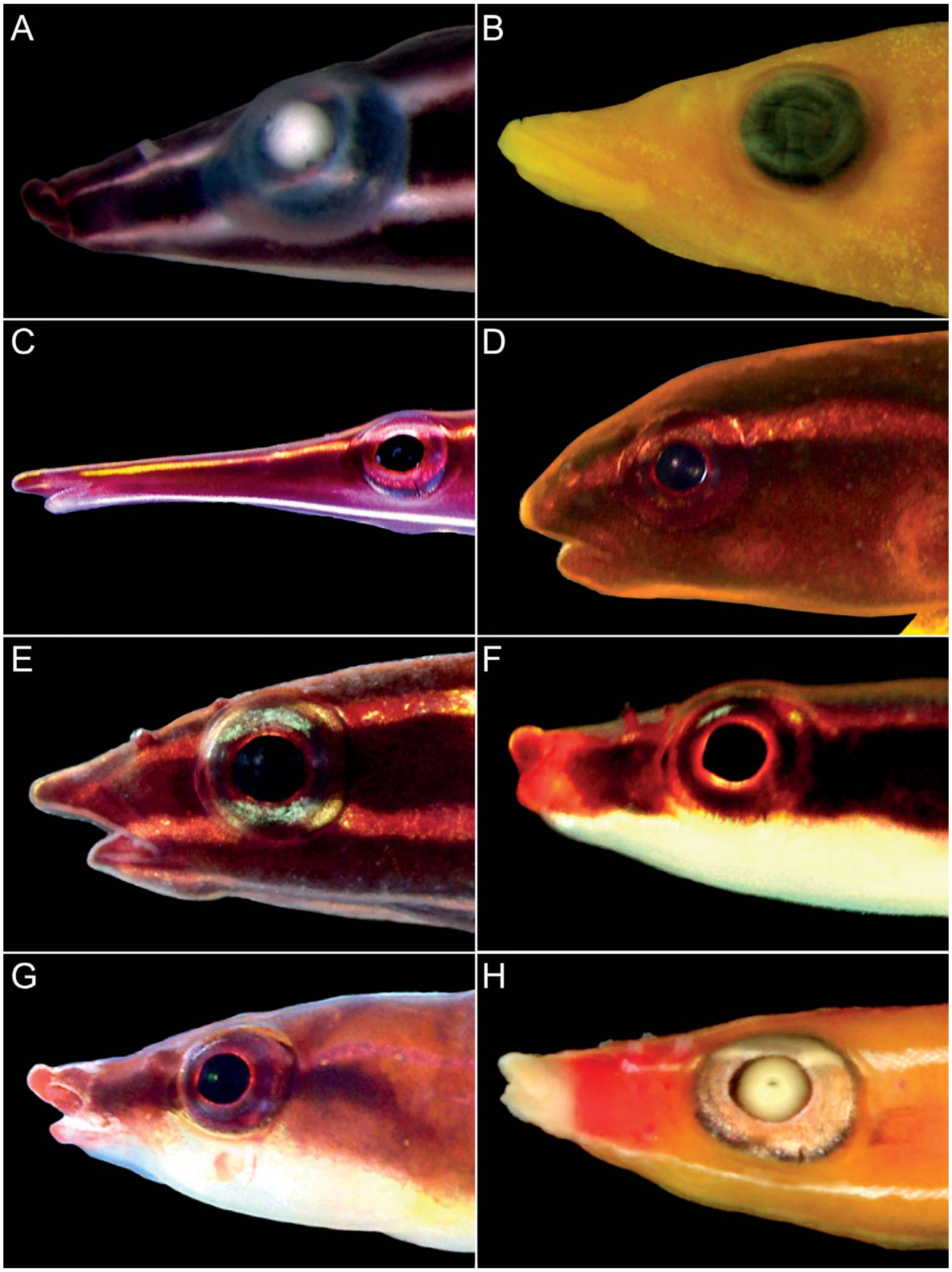

Fig. 1. Lateral view of heads of (A) *Flabellicauda alleni*, new species, WAM P. 35182-001, preserved specimen, 21.4 mm SL; (B) *Lepadichthys frenatus*, AMS I. 20256-013, preserved specimen, 35.3 mm SL; (C) *Diademichthys lineatus*, KAUM-I. 79654, 26.4 mm SL; (D) *Discotrema crinophilum*, KAUM-I. 72122, 26.3 mm SL; (E) *Lepadichthys lineatus*, KAUM-I. 128500, 22.0 mm SL; (F) *Lepadichthys minor*, KAUM-I. 70995, 18.2 mm SL; (G) *Lepadichthys trishula*, KAUM-I. 71567, 31.1 mm SL; and (H) *Lepadicyathus mendeleevi*, ZIN 53413, preserved holotype, 13.5 mm SL.

small, its length 8.1–13.5% SL (vs. moderate in *Lepadichthys* [13.9–20.8% SL] and *Lepadicyathus* [18.1–19.0% SL]); dorsal, anal, and caudal fins strongly connected with membrane, giving appearance of single, continuous median fin around posterior part of body (vs. completely separated in *Diademichthys*, connected by membrane but with distinct notch between fins in *Lepadichthys* and *Lepadicyathus*); and caudal skeleton with a single, large fan-like hypural plate (vs. caudal skeleton with upper and lower hypural plates, separated by narrow hypural diastema; Fig. 2A–D).

Etymology.—Combination of the new Latin *flabellum*, an anatomical term for a body organ or part that resembles a fan, and *cauda*, meaning tail. In reference to the unique shape of the hypural plate. Feminine.

Included species.—The genus contains four valid species: *F. akiko*, *F. alleni*, new species, *F. bolini*, and *F. cometes*, new species.

Remarks.—*Flabellicauda* belongs to the subfamily Diademichthyinae, which was recently revised ("expanded") by Conway et al. (2020) based on the shared presence of the following characters: upper-jaw teeth incisiviform, compressed laterally, with hooked tip; premaxillae separated anteriorly by large circular gap in dorsal view; and complex articulation present between posterior tip of basipterygium and anteromedial edge of ventral postcleithrum. The new genus shares several morphological characters in common with *Lepadicyathus*, including a similar arrangement of the cephalic sensory canal pores, features of the jaws (including a small mouth restricted to the anterior tip of snout; Fig. 1A,

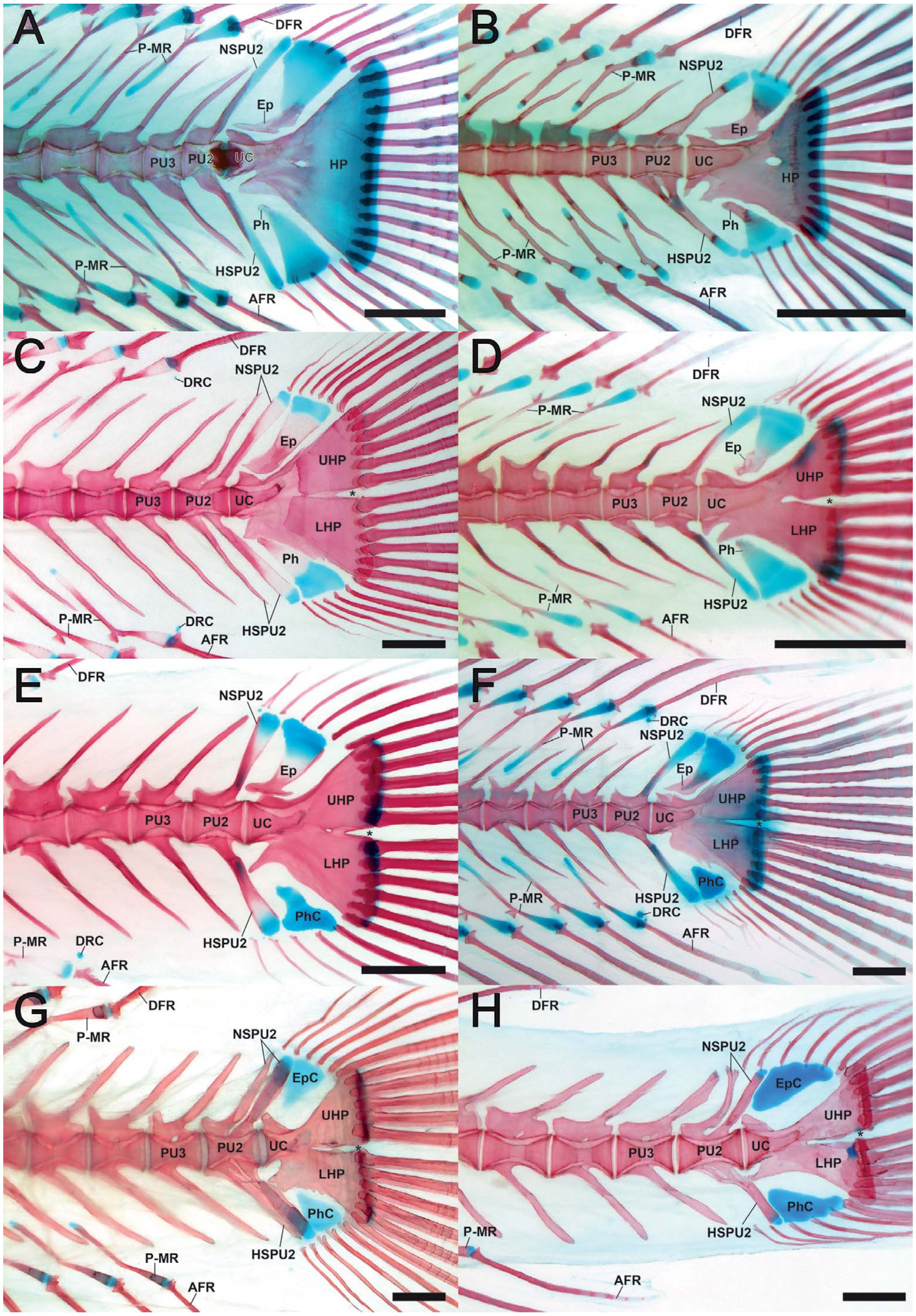

Fig. 2. Caudal skeletons of (A) *Flabellicauda alleni*, new species, FMNH 127786, 17.1 mm SL; (B) *Flabellicauda cometes*, new species, ROM 55928, 10.3 mm SL; (C) *Lepadichthys frenatus*, AMS I. 27134-018, 30.3 mm SL; (D) *Lepadichthys minor*, ROM 73449, 13.4 mm SL; (E) *Discotrema crinophilum*, ROM 85350, 25.4 mm SL; (F) *Diademichthys lineatus*, ROM 65282, 35.6 mm SL; (G) *Gobiesox funebris*, AMNH 5557, 46.7 mm SL; and (H) *Acyrtus rubiginosus*, UF 149202, 20.0 mm SL. Scale bars = 1 mm. Abbreviations: AFR, anal-fin ray; DFR, dorsal-fin ray; DRC, cartilaginous distal radial; Ep, epural; EpC, epural cartilage; HP, hypural plate; HSPU2, hemal spine of preural centrum 2; LHP, lower hypural plate; NSPU2, neural spine of preural centrum 2; Ph, parhypural; PhC, parhypural cartilage; P-MR, proximal-middle radial; PU, preural centrum; UC, ural centrum; and UHP, upper hypural plate. Asterisks indicate diastema between UHP and LHP.

H), and a restricted gill opening. The two genera are potentially closely related but are distinguished by characters listed in the diagnosis (warranting separate generic status), and detailed investigation of *Lepadicyathus* is currently ongoing (K. Fujiwara, unpubl.).

Though we have not investigated the phylogenetic relationships among the four species of *Flabellicauda*, based on our preliminary observations we recognize two putative monophyletic groups each comprising a pair of putative sister taxa. This includes: (1) *F. alleni*, new species, and *F. bolini*; and (2): *F. akiko* and *F. cometes*, new species. We consider the members of the first group to represent each other's closest relatives based on an almost identical external appearance (including an identical color pattern). The second pair comprises two miniature taxa (*sensu* Weitzman and Vari, 1988) that exhibit a number of reductive characters in relation to the other two members of the genus (including lower numbers of dorsal- and anal-fin rays, and the absence of the infraorbital lateral-line canal and associated pores, LC1 and LC2). Our investigation of cleared and stained material and CT datasets did not reveal any additional osteological characters in support of these two putative monophyletic groups, and further investigation of additional characters will be needed to corroborate or refute.

KEY TO THE SPECIES OF *FLABELLICAUDA*

Selected characters distinguishing between species of *Flabellicauda* given in Table 1.

1a. 12–15 (modally 13) dorsal-fin rays; 10–13 (11, rarely 10) anal-fin rays; and 2 (rarely 1) lacrimal and postorbital pores present 2

1b. 10–12 dorsal-fin rays; 9–11 anal-fin rays; and lacking lacrimal pores and 1 postorbital pore present 3

2a. 6–8 (6, rarely 5), 6–8 (6), 6–8 (7) gill rakers on first to third gill arches, respectively; total (first + second + third arches) 18–24 (19) gill rakers; caudal-peduncle length and depth 2.7–5.3 (mean 3.8) and 4.2–6.8 (5.5) % SL, respectively; and value of caudal-peduncle length plus caudal-peduncle depth 7.0–11.8 (9.3) % SL .... ***F. alleni*, new species** (Sri Lanka and Southeast Asia, 0.6–23.1 m depth)

2b. 4–6 (5) gill rakers on first to third gill arches, respectively; total 12–17 (14) gill rakers; caudal-peduncle length and depth 4.1–5.6 (4.9) and 5.6–7.8 (6.8) % SL, respectively; and value of caudal-peduncle length plus caudal-peduncle depth 10.4–13.1 (11.8) % SL .... ***F. bolini*** (Papua New Guinea, Vanuatu, and Fiji, 0.6–12.2 m depth)

3a. Upper end of gill opening level with base of 9th or 10th pectoral-fin ray in lateral view; 1 nasal pore present; disc region A with papillae at center; head width and anterior and posterior interorbital width proportions slightly narrow; and body red with white stripes in life .... ***F. akiko*** (Japan, Palau, and Indonesia, 40–90 m depth)

3b. Upper end of gill opening level with base of 12th to 14th pectoral-fin ray in lateral view; 2 nasal pores present; disc region A without papillae at center; head width and anterior and posterior interorbital width proportions slightly wide; and body maroon with white stripes in life .... ***F. cometes*, new species** (Indo-West Pacific, 3–13 m depth)

***Flabellicauda alleni*, new species**

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Allen's Clingfish

Figures 1A, 2A, 3, 4A–E, 5, 6A–C, 7A, 8A–D, 9–15; Tables 1–4

Lepadichthys bolini (not of Briggs)—Conway et al., 2018a: 99, fig. 17 (CT-scanned skeleton; Philippines: based on 1 of ROM 55185); Fujiwara and Motomura, 2018: 92, fig. 6 (comparative material; Palau: based on BPBM 9219); Conway et al., 2020: 893, figs. 3, 4 (molecular result; Wainilu, Rinca [Komodo Region], Indonesia: based on WAM P. 34628-002).

Holotype.—USNM 360264, 26.2 mm SL, west of Cuyo Island, Palawan, Philippines, 10°51′12″N, 121°00′14″E, 0.6–1.2 m, V. Springer et al., 21 May 1978.

Paratypes.—48 specimens, 11.1–27.9 mm SL. Indonesia: USNM 211918, ca. 16 mm SL, west of Kasa Island, Maluku, 03°18′S, 128°08′E, 1.2 m, V. Springer, 4 March 1974; USNM 211939, 22.5 mm SL, Naira Island, Banda islands, Maluku, 04°20′30″S, 129°54′20″E, 3–9 m, V. Springer et al., 8 March 1974; WAM P. 35182-001, 2, 20.7–21.4 mm SL, Ampera, Alor, Lesser Sundas, 8°16′04″S, 124°25′31″E, 5 m, M. Erdmann, 4 May 2019. Malaysia: KPM-NI. 1982, 24.5 mm SL, KPM-NI. 1983, 18.5 mm SL, YCM-P 36726, 2, 19.7–20.5 mm SL, YCM-P 36727, 11.5 mm SL, YCM-P 37150, ca. 19.0 mm SL, Mabul Island, Sabah. Palau: BPBM 9219, 27.9 mm SL, Arakabesang Island, 0.6–0.9 m, J. Randall and E. Helfman, 5 June 1968; CAS 247204, 25.1 mm SL, Melekeok, Babelthuap Island, 07°21′04″N, 134°31′23″E, 1.2 m, Y. Sumang and H. Fehlmann, 23 June 1958. Philippines: FMNH 127786, 19 (2 of 19 CS), 12.5–26.5 mm SL, north of Cabilauan Island, Palawan, 12°12′32″N, 120°07′49″E, Busuanga Team, 5 March 2003; KAUM-I. 146168, 20.9 mm SL, KAUM-I. 146169, 18.2 mm SL, KAUM-I. 146170, 17.1 mm SL, USNM 451066 (formerly USNM 360264), 5, 15.0–23.1 mm SL, same as holotype; ROM 55178, 11.6 mm SL, Pasihagon, Siquijor Island, Siquijor, 09°12′17″N, 123°27′16″E, 10.4 m, R. Winterbottom and E. Downar, 10 May 1987, rotenone; ROM 55181, 11.1 mm SL, Pasihagon, Siquijor Island, Siquijor, 09°12′16″N, 123°27′16″E, 10.3 m, R. Winterbottom et al., 12 May 1987, rotenone; ROM 55183, 19.2 mm SL, Pasihagon, Siquijor Island, Siquijor, 09°12′16″N, 123°27′16″E, 18.8 m, R. Mooi et al., 14 May 1987, rotenone; ROM 55185, 4 (1 of 4 CS), 11.5–23.8 mm SL, mouth of North Basis Bay, Negros Island, Negros Oriental, 09°37′00″N, 123°10′00″E, 23.1 m, R. Winterbottom et al., 17 May 1987, rotenone; USNM 360265, 2, 12.4–13.3 mm SL, San Juan, Siquijor Island, Siquijor, 09°08′30″N, 123°29′22″E, 6.1 m, Smithsonian Team, 9 May 1978. Sri Lanka: USNM 360162, 22.9 mm SL, Trincomalee, 7.6 m, C. Koenig, 4 April 1970.

Diagnosis.—A species of *Flabellicauda* (Figs. 3, 4A–E, 5) distinguished from congeners by the following combination of characters: 12–15 (modally 13) dorsal-fin rays (vs. 11 or 12 in *F. akiko*; 10–12 in *F. cometes*, new species; Table 2); 10–13 (11, rarely 10) anal-fin rays (vs. 9 or 10 in *F. akiko*; 9–11 in *F. cometes*, new species; Table 2); upper end of gill opening level with base of 12th to 14th pectoral-fin ray in lateral view (vs. 9th or 10th in *F. akiko*); 5–8 (6, rarely 5), 6–8 (6), and 6–8 (7) gill rakers on first to third arches, respectively (vs. 4, 4 or 5, and 5, respectively in *F. akiko*; 4–6 [5], respectively in *F. bolini*; 5, 5, and no data, respectively in *F. cometes*, new species; Table 3); head sensory canal pores relatively developed, including usually 2 nasal, 2 lacrimal, and 2 postorbital pores (vs. lacking lacrimal pores and 1 postorbital pore present in *F. akiko* and *F. cometes*, new species; 1 nasal pore present in *F. akiko*; Fig. 6); disc region A without papillae at center (vs. disc region A with papillae at center in *F. akiko*; Fig. 7A, D); body black with white stripes (vs. body red with white stripes in *F. akiko*; Figs. 5, 8F–H). *Flabellicauda alleni* is most similar to *F. bolini* and in addition to the aforementioned diagnostic characters, values of head length, pre-disc length, orbit diameter, and caudal-peduncle length and width proportions also serve to distinguish between the two species (see Diagnosis of *F. bolini*).

Description.—Measurements given in Table 4. Body slender, cylindrical, compressed at caudal peduncle. Body width narrower than head width. Anus situated closer to anal-fin origin than to posterior margin of disc (disc to anus length 69.4 [62.7–78.3, mean 69.2] % of disc to anal-fin origin length). Head size medium, becoming smaller with growth (Fig. 9A), depressed anteriorly, its length and width 3.5 (2.7–

Table 1. Selected characters distinguishing among species of *Flabellicauda*.

	F. alleni, new species 11.1–27.9 mm SL $n = 49$	*F. cometes*, new species 10.1–17.3 mm SL $n = 8$	*F. bolini* 11.5–28.8 mm SL $n = 30$	*F. akiko* 10.5–14.0 mm SL $n = 5$
Dorsal-fin rays	12–15 (modally 13)	10–12	12–15 (13)	11 or 12
Anal-fin rays	10–13 (11, rarely 10)	9–11	10–12 (11, rarely 10)	9 or 10
Number of pectoral-fin ray at same level with upper end of gill membrane	12^{th} to 14^{th}	12^{th} or 13^{th}	12^{th} to 14^{th}	9^{th} or 10^{th}
Gill rakers on 1^{st} arch	5–8 (6, rarely 5)	5	4–6 (5)	4
Gill rakers on 2^{nd} arch	6–8 (6)	5	4–6 (5)	4 or 5
Gill rakers on 3^{rd} arch	6–8 (7)	—	4–6 (5)	5
Gill rakers (1^{st} + 2^{nd} + 3^{rd} arches)	18–24 (19)	—	12–17 (14)	14
Nasal canal pores	2	2	2	1
Lacrimal canal pores	2 (rarely 1)	0	2 (rarely 1)	0
Postorbital canal pores	2 (rarely 1)	1	2	1
Papillae on antero-center of disc region A	Absent	Absent	Absent	Present
Head size*	Small	—	Large	—
Head width**	Wide	Wide	Wide	Narrow
Anterior and posterior interorbital widths**	Wide	Wide	Wide	Narrow
Eye size*	Small	—	Large	—
Caudal-peduncle length (%SL)	2.7–5.3 (mean 3.8)	3.3–4.8	4.1–5.6 (4.9)	3.2–3.9
Caudal-peduncle depth (%SL)	4.2–6.8 (5.5)	5.1–6.3	5.6–7.8 (6.8)	5.3–6.0
Caudal-peduncle length + Caudal-peduncle depth (%SL)	7.0–11.8 (9.3)	9.3–11.0	10.4–13.1 (11.8)	8.5–9.5
Coloration	Body black with white stripes	Body maroon with white stripes	Body black with white stripes	Body red with white stripes
Habitat depth (m)	0.6–23.1	3–13	0.6–12.2	40–90

—, no data or need to more specimens; * and ** see Figures 9 and 15, respectively.

3.5 [mean 3.1]) and 5.5 (5.1–7.2 [6.2]) in SL, respectively. Snout moderate, its length 12.7 (9.2–13.1 [11.3]) in SL, becoming shorter with growth (Fig. 9E), its tip slightly pointed in lateral view, semi-elliptical (or duck beak-shaped) in dorsal view; dorsal profile of snout slightly concave anteriorly. Mouth terminal, small, restricted to tip of snout. Anterior tip of upper jaw slightly pointed, extending slightly beyond that of lower jaw. Upper lip fleshy, weakly expanded, lower lip thin. Posterior 2/3 of both jaws covered by thick skin on lateral surface of snout. Anterior and posterior nostrils larger than head sensory canal pores, former slightly smaller than latter; both with a membranous tube, that of former much longer than latter. Eye size moderate, becoming smaller with growth (Fig. 9D), diameter slightly smaller (slightly larger in 9 specimens) than snout length, 14.6 (8.8–15.6 [12.3]) in SL. Interorbital region flattened. Gill opening tiny, slit-like. Upper end of gill opening level with base of 12^{th} (12^{th} to 14^{th}) pectoral-fin ray in lateral view (number of pectoral-fin rays given in Table 2); lower 9^{th} (7^{th} [6 specimens], 8^{th} [20], or 9^{th} [12]) pectoral-fin-ray base attached to disc by membrane. First to third gill arches with two rows of gill filaments, 4^{th} arch without filaments (gill description based on 21 specimens). Gill rakers slender, short and pointed (gill raker counts listed in Table 3). Gill membranes on each side united ventrally, attached to isthmus. Head sensory canal pores relatively developed, including 2 nasal, 2 (1 on left side only in 2 specimens; 1 on both sides of 1 specimen) lacrimal, and 2 (1 on both sides of 2 specimens) postorbital pores; preopercular and mandibular pores absent; all pores similarly sized with minute membranous tube. NC1 located in front of anterior nostrils in dorsal view (or between anterior and posterior margins of anterior nostril); NC2 level with anterior margin (before anterior margin [7 of 41 specimens], between anterior and posterior margins [24 specimens], or level with posterior margin [2 specimens]) of posterior nostril; LC1 located in front of anterior margin of eye; LC2 located postero-ventrally below LC1 (antero-ventrally below LC1 [3 of 37 specimens] or just below LC1 [7 specimens]); PO1 located just behind posterior margin of orbit; PO2 located posterodorsal to PO1 (Fig. 6A–C).

Dorsal- and anal-fin-ray counts listed in Table 2. Origin of dorsal fin slightly anterior to vertical through anal-fin origin. Dorsal and anal fins located posteriorly, their bases relatively long, lengths 4.6 (4.4–6.4 [5.1]) and 5.4 (4.9–6.9 [5.7]) in SL, respectively; strongly connected to caudal fin by membranes, giving appearance of single, continuous median fin around posterior part of body (easily damaged). Post-dorsal-caudal length 4.9 (3.5–7.0 [5.1]) in dorsal-fin base length. Dorsal- and anal-fin heights almost equal, except anteriorly. Pectoral- and caudal-fin margins rounded. Pectoral-fin rays 28 (26 [5], 27 [8], 28 [13], 29 [11], or 30 [1]). Upper and lowermost pectoral-fin rays minute, longest ray extending beyond

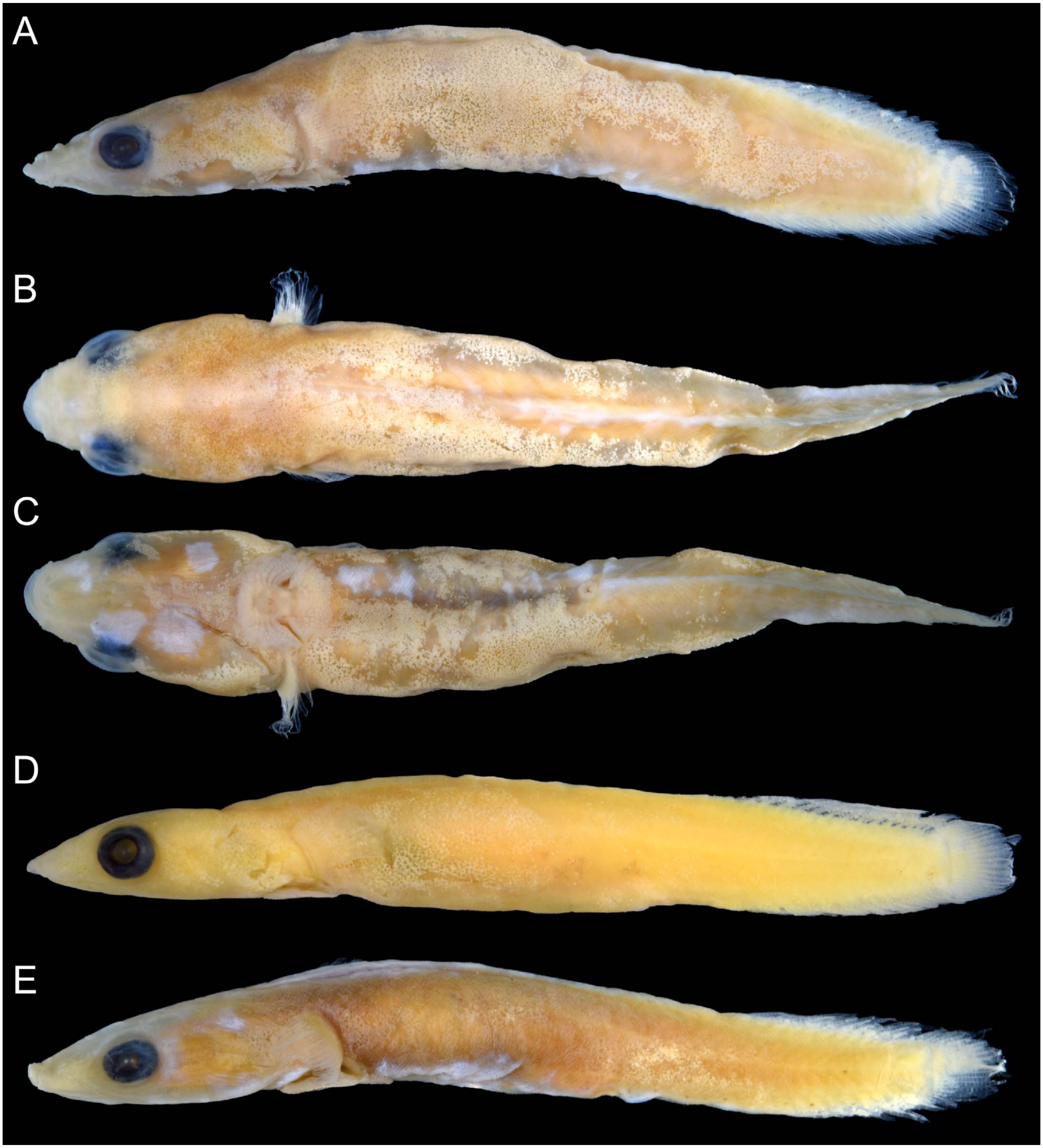

Fig. 3. Preserved specimens of *Flabellicauda alleni*, new species. (A–C) USNM 360264, holotype, 26.2 mm SL, Palawan, Philippines; (D) KPM-NI. 1982, 24.5 mm SL, Sabah, Malaysia; and (E) USNM 360162, 22.9 mm SL, Trincomalee, Sri Lanka. (A, D, E) Lateral views. (B) Dorsal view. (C) Ventral view.

vertical through posterior margin of disc. All soft-fin rays unbranched and segmented. Pelvic fins and pectoral-girdle elements forming a circular, extremely small, "single" adhesive disc (Fig. 7A), its length and width 9.6 (7.4–12.4 [9.7]) and 9.3 (7.9–13.4 [10.0]) in SL, respectively. Disc region B bell-shaped, equal in size to disc region A. Anterior margin of disc region A smooth, posterior margin of disc region B with fringe. Disc regions A and B with flattened papillae (disc papillae description based on 33 specimens). Center of disc region A lacking papillae; anterolateral part with 3 (3–5) rows of papillae, number of rows slightly decreasing toward apapillate center; both sides of disc region A (except margins)

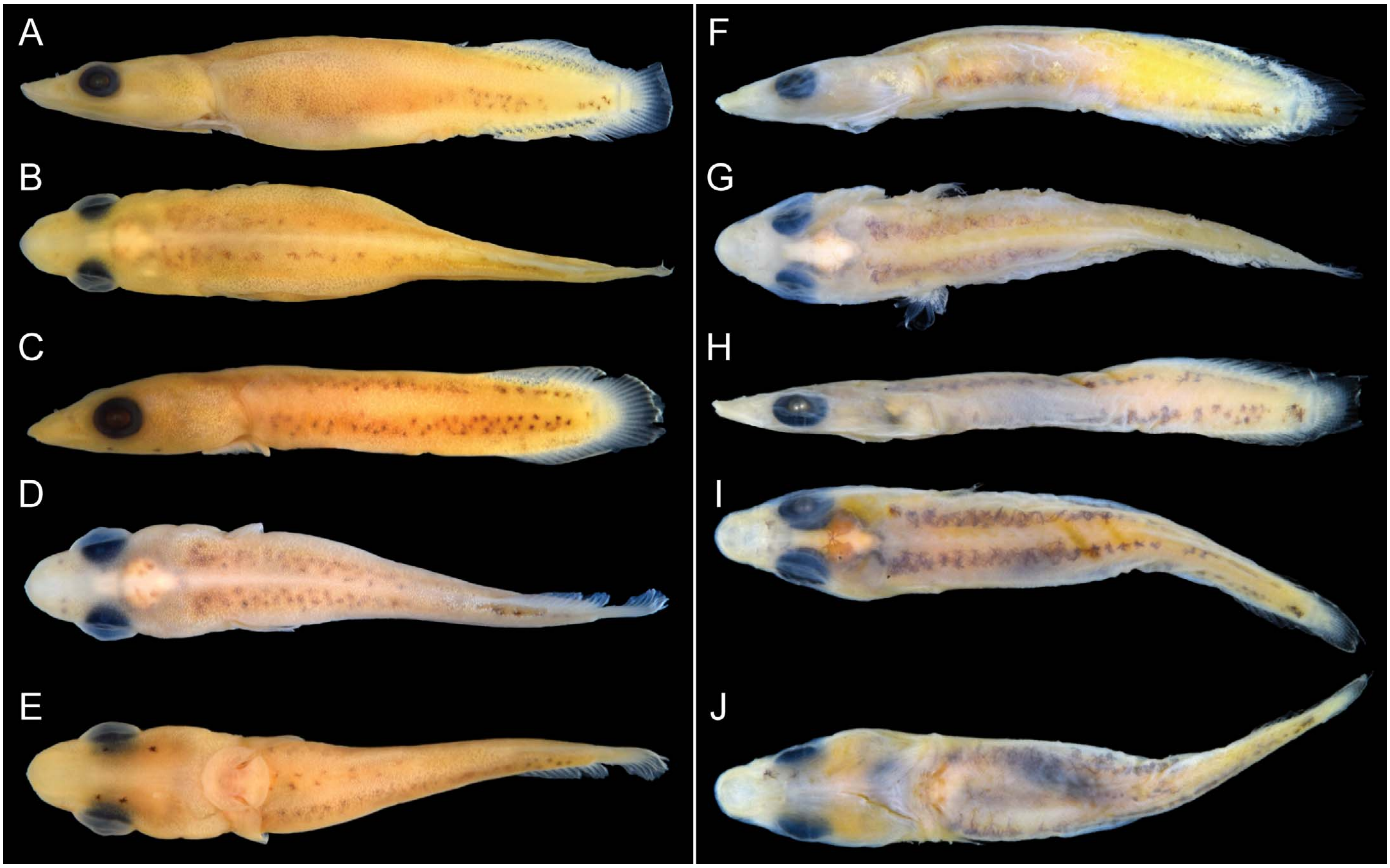

Fig. 4. Preserved small specimens of (A–E) *Flabellicauda alleni*, new species, and (F–J) *Flabellicauda bolini*. (A, B) YCM-P 36726, 19.7 mm SL, Sabah, Malaysia; (C–E) YCM-P 36727, 11.5 mm SL, Sabah, Malaysia; (F, G) CAS 224422, 16.2 mm SL, Suva, Fiji; and (H–J) CAS 224419, 13.2 mm SL, Vanua Levu Island, Fiji. (A, C, F, H) Lateral views. (B, D, G, I) Dorsal views. (E, J) Ventral views.

covered with papillae; papillae of inner rows slightly larger than papillae of outer rows. Disc region B with 5 (4–6) rows of papillae; papillae of inner rows slightly larger than papillae of outer rows; anterior part of disc region B without papillae (Fig. 7A). Disc region C lacking papillae.

Osteological description based on 3 CS specimens and CT-scanned image (Fig. 10). General osteological characters as in Figures 2A, 10–13. Vertebrae 34 (1 specimen) or 35 (3). Neurocranium depressed, comprising nasal, lacrimal, lateral ethmoid, mesethmoid, sphenotic, pterotic, epiotic, prootic, supraoccipital, basioccipital, exoccipital, frontal, vomer, parasphenoid, and parietal (Fig. 11). Posterior tip of epiotic articulating with posttemporal; sphenotic and pterotic contributing to hyomandibular facet accommodating articular heads of hyomandibular; lacrimal firmly attached to tip of slender cartilage extending from anterolateral tip of lateral ethmoid. Antero-center point of vomer slightly protracted; posterior tip of vomer pointed in ventral view. Anterior tip of nasal slightly forked, tapering posteriorly; 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 (Fig. 12). Premaxilla with laterally compressed incisiviform teeth with hook-like tip, strongly curved posteriorly (ca. 90°). Ascending process of premaxilla long, terminating slightly posterior to imaginary line through posterior tip of nasal; premaxillae separated anteriorly by large circular gap in dorsal view. Maxilla irregular, boot-shaped, with elongate part oriented along dorsal-ventral axis; connected with premaxilla via well-developed, bifurcated articular head. Anterior half of dentary with 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. Retroarticular tiny, elongate, nestled in articular facet located on posteroventral part of anguloarticular. Suspensorium comprising autopalatine, quadrate, hyomandibular, ectopterygoid, and symplectic (Fig. 12A). Autopalatine a curved cylinder, articulating with lateral ethmoid dorsally, and premaxilla 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; all bones poorly ossified, excluding articular head of opercle; subopercle without spine-like posterior tip (Fig. 12A). Gill arches comprising basihyal, 4 paired epibranchials, paired pharyngobranchial 3 and associated tooth plate, 3 paired hypobranchial elements (bone or cartilage), 5 paired ceratobranchials, and 3 basibranchial elements (bone or cartilage; Fig. 12D). Basihyal long, slender, anterior tip cartilaginous. Pharyngobranchial 3 flat, irregularly shaped

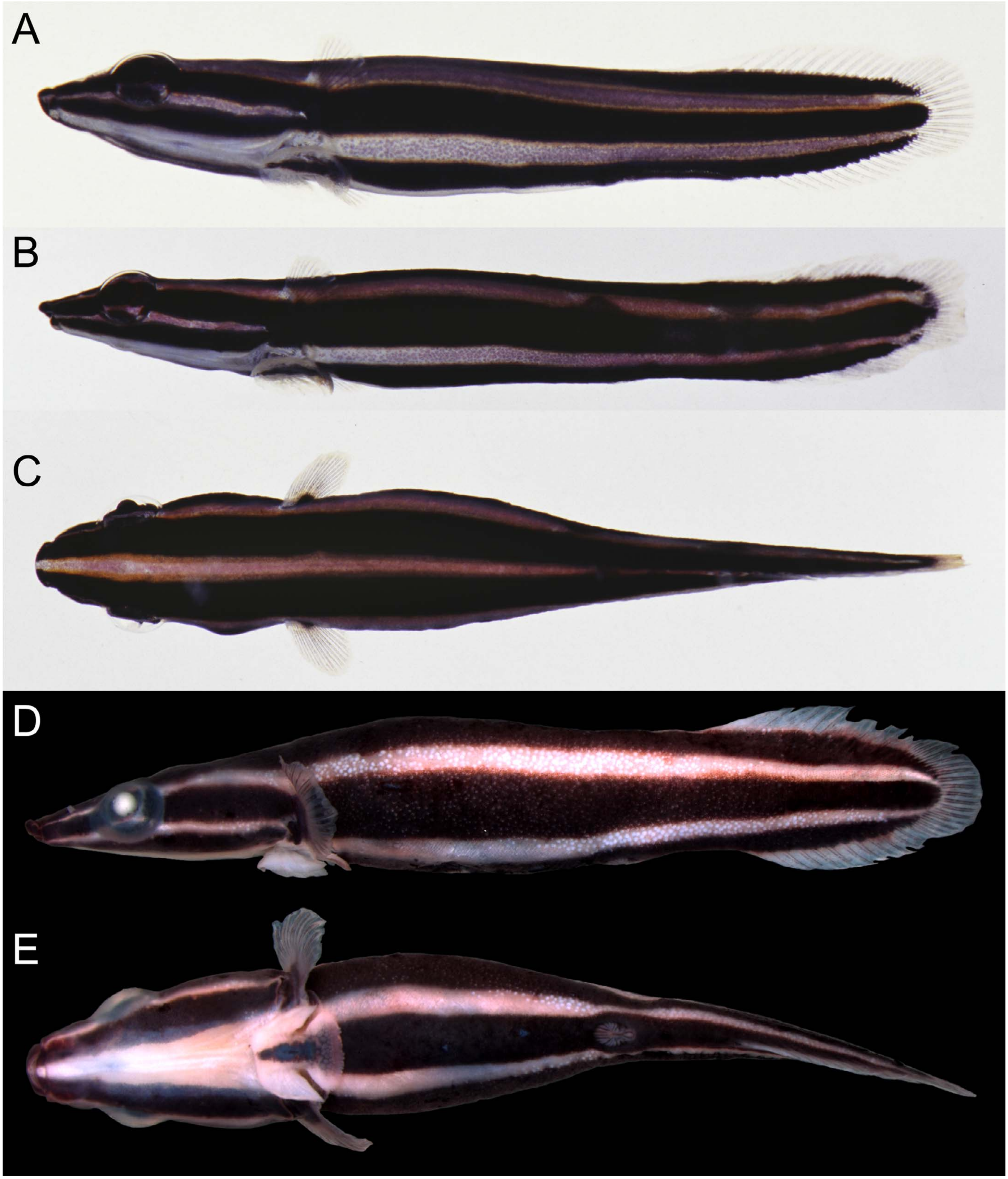

Fig. 5. Fresh coloration of *Flabellicauda alleni*, new species. (A) KPM-NI. 1983, 18.5 mm SL, Sabah, Malaysia (image reversed); (B, C) KPM-NI. 1982, 24.5 mm SL, Sabah, Malaysia (image reversed); and (D, E) WAM P. 35182-001, 21.4 mm SL, Lesser Sundas, Indonesia. (A, B, D) Lateral views. (C) Dorsal view. (E) Ventral view. (A–C) Photos by H. Senou.

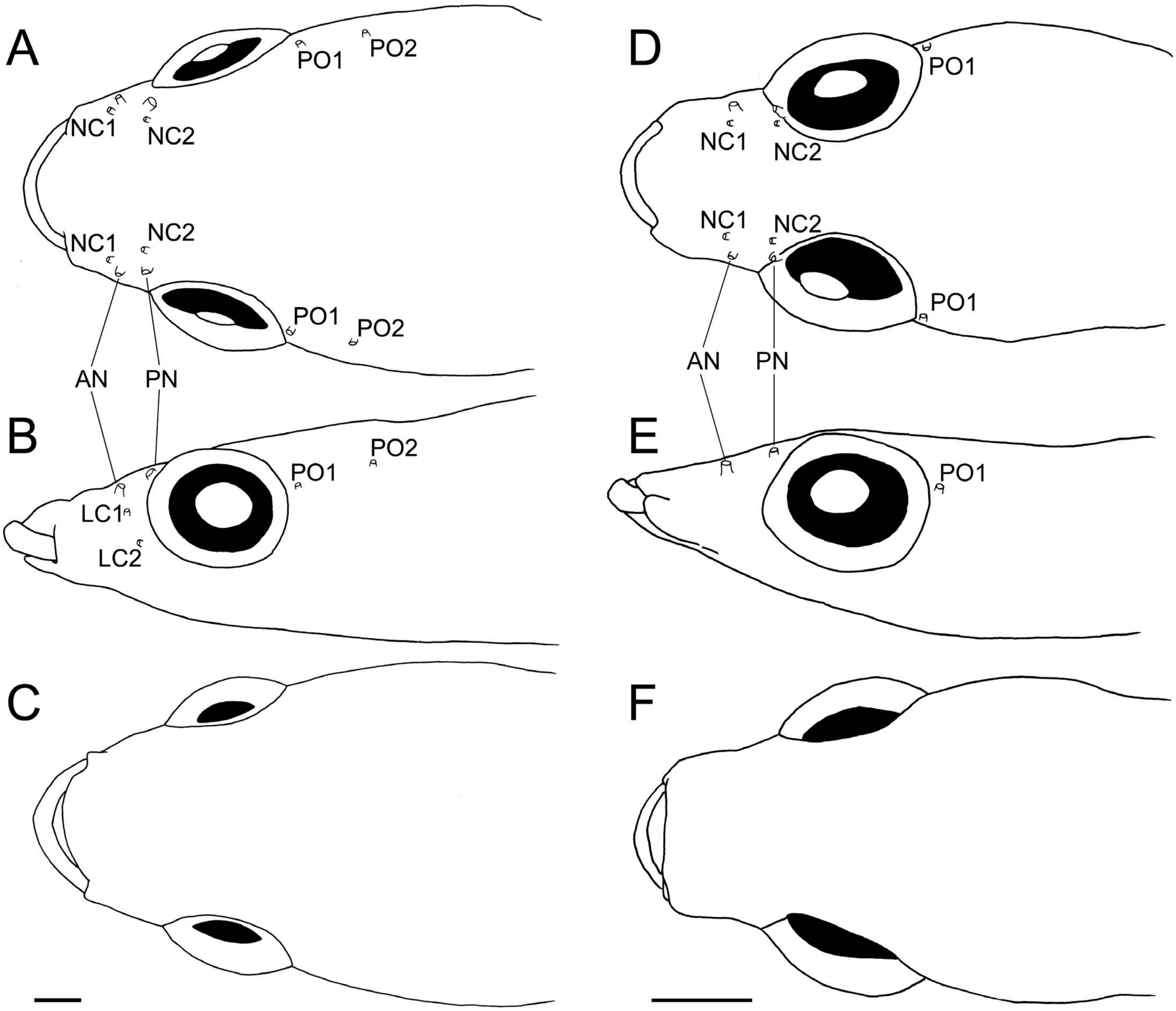

Fig. 6. Head sensory canal pores of (A–C) *Flabellicauda alleni*, new species, and (D–F) *Flabellicauda cometes*, new species. Illustrations based on (A–C) USNM 360264, holotype, 26.2 mm SL and (D–F) ROM 55929, holotype, 17.3 mm SL. (A, D) Dorsal views. (B, E) Lateral views. (C, F) Ventral views. Scale bars = 1 mm. Abbreviations: AN and PN, anterior and posterior nostrils, respectively; LC, lacrimal canal pores; NC, nasal canal pores; PO, postorbital canal pores.

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. Hypobranchial 1 and 3 thin, perichondrally ossified bone around precursor hypobranchial cartilages 1 and 3, respectively; hypobranchial 2 cartilage without associated ossification. Ceratobranchial 5 tiny, without pharyngeal teeth. Three basibranchial elements situated between second and third hypobranchial elements and tip of ceratobranchial 4; basibranchial 3 a thin, pericondrially ossified bone around precursor basibranchial 3 cartilage; basibranchial 2 and 4 cartilages without associated ossification; basibranchial 1 cartilage absent. Hyoid bar comprising dorsal hypohyal, anterior and posterior ceratohyal, interhyal, and 6 branchiostegal rays (Fig. 12E). 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 as urohyal. Pelvic- and pectoral-fin girdles comprising basipterygium, dorsal postcleithrum, ventral postcleithrum, posttemporal, supracleithrum, cleithrum, scapula, coracoid, and 4 pectoral radials (Fig. 13). Anterior outline of basipterygia together triangular, posterior outline resembles inverted T-shape. Anteromedial tip and lateral edge of basipterygium cartilaginous; two large oval openings at center. Dorsal postcleithrum oblong shape, with well-developed fimbriae

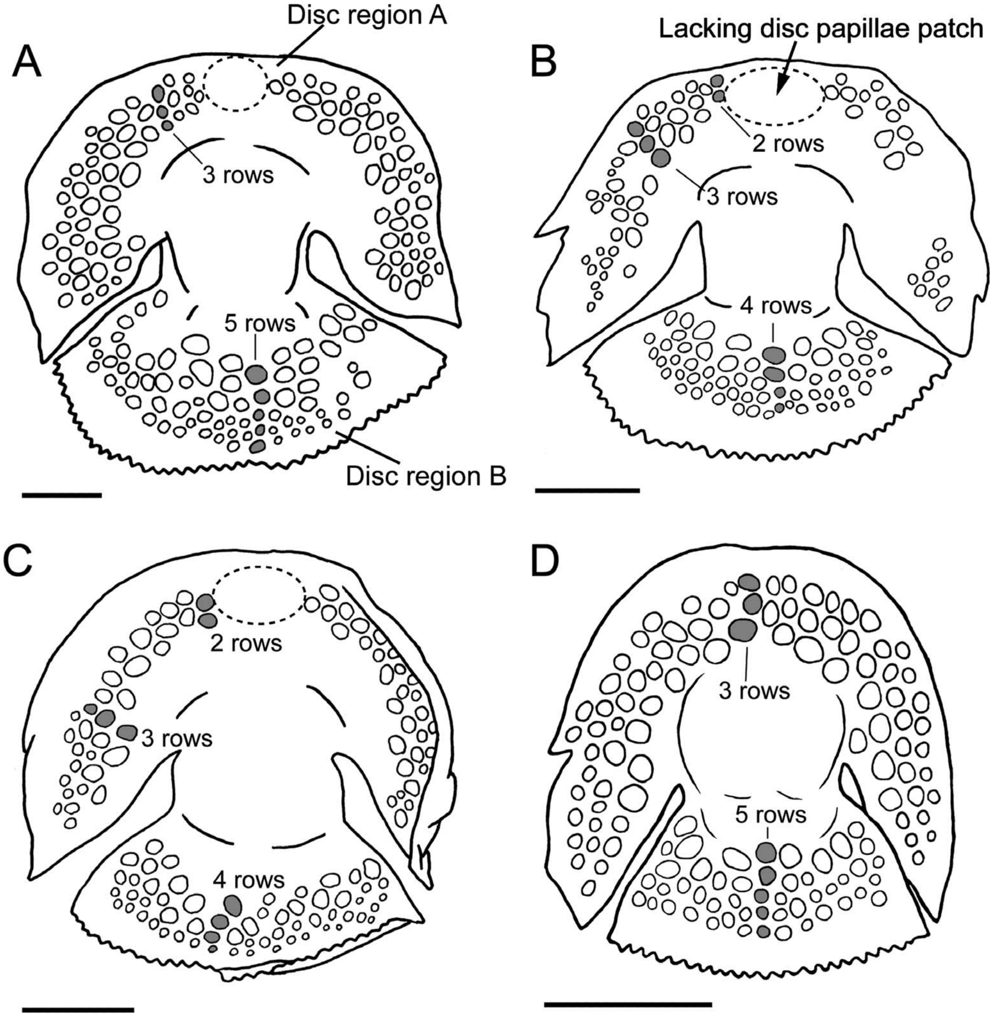

Fig. 7. Pelvic discs of (A) *F. alleni*, new species, USNM 360264, holotype, 26.2 mm SL; (B) *F. cometes*, new species, ROM 55929, holotype, 17.3 mm SL; (C) *F. bolini*, ANSP 128248, 20.6 mm SL; and (D) *F. akiko*, WAM P. 33772-002, 11.5 mm SL. Scale bars = 0.5 mm. Black dots indicate lacking disc papillae patch.

along posterior edge. Ventral postcleithrum irregular in shape; anterior margin with 2 pointed processes, outer process much larger than inner process; posterior margin concave, with well-developed fimbriae. Complex articulation present between posterior tip of basipterygium and anteromedial edge of ventral postcleithrum. Pelvic-fin rays I, 4, articulating with cartilaginous lateral edge of basipterygium; pelvic spine short, tip wide, rounded; soft rays slender, tapering distally (Fig. 13C). 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 (Fig. 13E). Scapula irregular in shape, tightly connected with dorsal surface of pectoral radial 1 (Fig. 13E). Coracoid bifurcated anteriorly, pointed posteriorly; tightly connected with ventral surface of pectoral radial 4 (Fig. 13E). Caudal skeleton comprising single hypural plate, epural, and parhypural (Fig. 2A). Upper and lower hypural plates fused, forming large fan-shaped plate; small circular opening, potential remnant of diastema between upper and lower hypural plate in other gobiesocids, at center of hypural plate; 13 (2 specimens) or 14 (2) caudal-fin rays associated with plate. Epural and parhypural thin, perichondrally ossified bone around triangular precursor cartilages.

Coloration.—Based on Figures 3, 4A–E, 5, 8A–D. Body black with white stripe on dorsal midline (Fig. 5C) and three white stripes on each side (Fig. 5A, B, D); uppermost stripe extending from snout tip, past dorsal margin of pupil and pectoral fin, to caudal-fin base, its width very narrow on snout, gradually wider from head region, widest on body, slightly tapering posteriorly; central stripe narrowest of three stripes, extending from posterior point of lower jaw (or snout tip; Fig. 5A), passing below pupil, to pectoral-fin base, both tips tapering; lowermost stripe located ventrally, united in front of pelvic disc, forming large isosceles triangle shape, its tip located on ventral surface of snout tip (Fig. 5E), posterior tip of stripe tapering and reaching caudal-fin base, its width on body same as uppermost stripe; stripe on dorsal midline tapering posteriorly and extending from snout tip to dorsal-fin origin; all stripes edged very faint yellow (sometimes distinct in life; Fig. 8A–C). Stripes of single individual from Philippines notably narrower than in other individuals (Fig. 8D). Iris black except for upper and lower portions, pupil black. Tubes of nostrils and all fins except for rays transparent, fin rays faint black. Adhesive disc white, isosceles triangle shape of black pigmentation at center, its tip located at anterior margin of disc (Fig. 5E).

Preserved coloration uniformly yellowish (Fig. 3). Black melanophores present on body of small specimens (ca. <20 mm SL), those forming two stripes (somewhat indistinct in large specimens; Fig. 4A, B), upper and lower stripes located

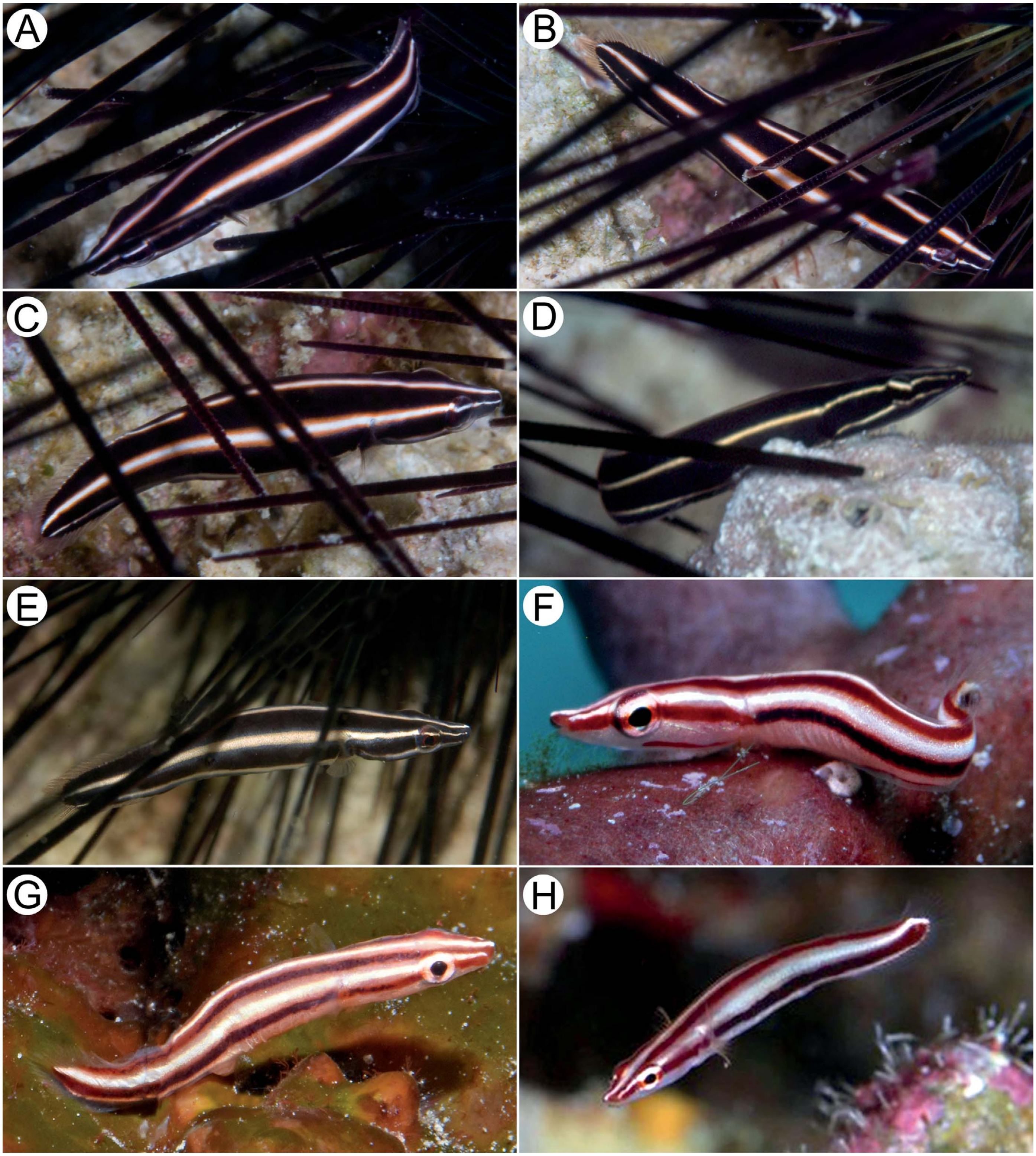

Fig. 8. Underwater photographs of (A–D) *F. alleni*, new species, (E) *F. bolini*, and (F–H) *F. akiko*. (A–C) 1.5 m depth, Rinca Island, West Flores, Indonesia. Photos by M. Erdmann. (D) 7 m depth, Bohol, Philippines. Photo by K. Yamasaki. (E) 5 m depth, Manus, Papua New Guinea. Photo by G. Allen. (F) 70 m depth, West Papua, Indonesia. Holotype. Photo by G. Allen. (G) 70 m depth, West Papua, Indonesia. Photo by M. Erdmann. (H) 40 m depth, Okinawa Island, Japan. Photo by N. Shirakawa. (A–E, G, H) Specimens not collected. (E, F) Reproduced from Allen and Erdmann (2012) with permission.

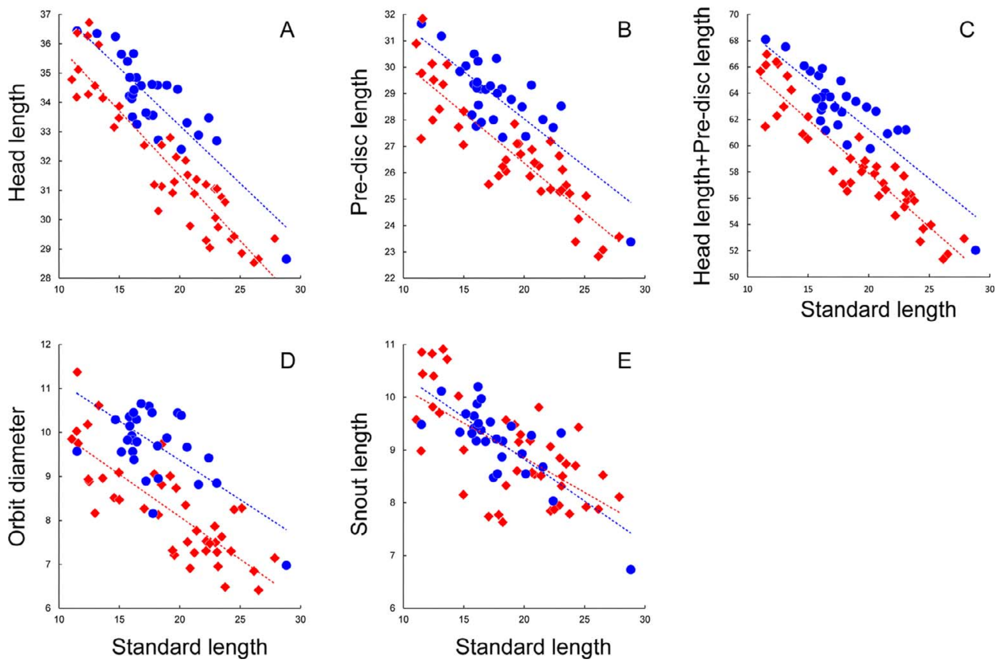

Fig. 9. Relationships of (A) head length, (B) pre-disc length, (C) head length plus pre-disc length, (D) orbit diameter, and (E) snout length (as % of standard length) to standard length (mm) in *F. alleni*, new species (red diamonds) and *F. bolini* (blue circles), showing (A–D) differences and (E) morphological change with growth.

dorsally and laterally, respectively, former extending from nape to most posterior point of dorsal-fin base, latter extending from pectoral-fin base to caudal-fin base (Fig. 4A–E).

Distribution.—Known from Sri Lanka and Southeast Asia (Philippines, Palau, Malaysia, and Indonesia; Fig. 14).

Etymology.—Named for Dr. Gerald R. Allen (WAM), for his great contributions to the systematics of tropical reef fishes of the East Indies. A noun in the genitive.

***Flabellicauda cometes*, new species**

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Comet Clingfish
Figures 2B, 6D–F, 7B, 14–17; Tables 1–4

Lepadichthys bolini (not of Briggs)—Briggs, 1969a: 464 (brief comments; Amirante Islands, Seychelles: based on ANSP 150416); Winterbottom et al., 1989: 14, fig. 63 (listed; Peros Banhos and Salomon Atolls, Chagos Archipelago: based on ROM 55928, 55929).

Holotype.—ROM 55929, 17.3 mm SL, Salomon Atoll, Chagos Archipelago, 05°21′18″S, 72°12′58″E, 3–13 m, A. Emery and R. Winterbottom, 14 March 1979, rotenone.

Paratypes.—4 specimens, 10.3–15.0 mm SL. ANSP 150416, 14.9 mm SL, Amirante Islands, Seychelles, 04°54′S, 53°23′E, 3.7 m, J. Böhlke et al., 3 March 1964; ROM 55928, 3 (1 of 3 CS), 10.3–15.0 mm SL, Peros Banhos Atoll, Chagos Archipelago, 05°26′44″S, 71°47′42″E, 3–13 m, R. Winterbottom, 6 March 1979, rotenone.

Non-type specimens.—3 specimens, 10.1–12.9 mm SL. AMS I. 18051-039, 12.9 mm SL, Tebontibike, Abaiang Islands, Gilbert Islands, Kiribati, 01°43′48″N, 172°58′48″E, D. Hoese and B. Goldman; AMS I. 20755-073, 11.4 mm SL, off Cape Melville, Queensland, Australia, 13°56′S, 144°36′E, D. Hoese et al., 9 February 1979; AMS I. 21974-001, 10.1 mm SL, Lizard Island, Queensland, Australia, 14°40′S, 145°27′E, D. Hoese et al., 11 February 1975.

Diagnosis.—A species of *Flabellicauda* (Fig. 16) distinguished from congeners by the following combination of characters: 10–12 dorsal-fin rays (vs. 12–15 [13] in *F. alleni* and *F. bolini*; Table 2); 9–11 anal-fin rays (vs. 10–13 [11, rarely 10] in *F. alleni* and *F. bolini*; Table 2); upper end of gill opening level with base of 12th to 14th pectoral-fin ray in lateral view (vs. 9th or 10th in *F. akiko*); 5 gill rakers on first and second arches (vs. 5–8 [6, rarely 5], 6–8 [6], and 6–8 [7] on first to third arches, respectively in *F. alleni*; Table 3); head sensory canal pores poorly developed, including 2 nasal and 1 postorbital pore (vs. usually 2 nasal, 2 lacrimal, and 2 postorbital pores in *F. alleni* and *F. bolini*; 1 nasal pore in *F. akiko*; Fig. 6); disc region A without papillae at center (vs. disc region A with papillae at center in *F. akiko*; Fig. 7B, D); and body maroon with white stripes (vs. body red with white stripes in *F. akiko*; Figs. 8F–H, 16F).

Description.—Measurements given in Table 4. Body slender, cylindrical, compressed at caudal peduncle. Body width narrower than head width. Anus situated closer to anal-fin origin than to posterior margin of disc (disc to anus length 63.4 [56.4–64.4] % of disc to anal-fin origin length). Head size medium, depressed anteriorly, its length and width 2.8 (2.7–2.9) and 5.3 (5.0–6.3) in SL, respectively. Snout moderate, its length 10.7 (10.9–12.3) in SL, its tip slightly pointed in lateral view, duck beak-shaped in dorsal view; dorsal profile of snout slightly concave anteriorly. Mouth terminal, small, restricted to tip of snout. Anterior tip of upper jaw slightly pointed, extending slightly beyond that of lower jaw. Upper lip fleshy, weakly expanded, lower lip thin. Posterior 2/3 of both jaws covered by thick skin on lateral surface of snout. Anterior and posterior nostrils larger than head sensory canal pores, former slightly smaller than latter; both with a membranous tube, that of former longer than latter. Eye size moderate, diameter slightly larger (slightly smaller in 2 specimens) than snout length, 10.6 (9.4–12.6) in SL. Interorbital region flattened. Gill opening tiny, slit-like.

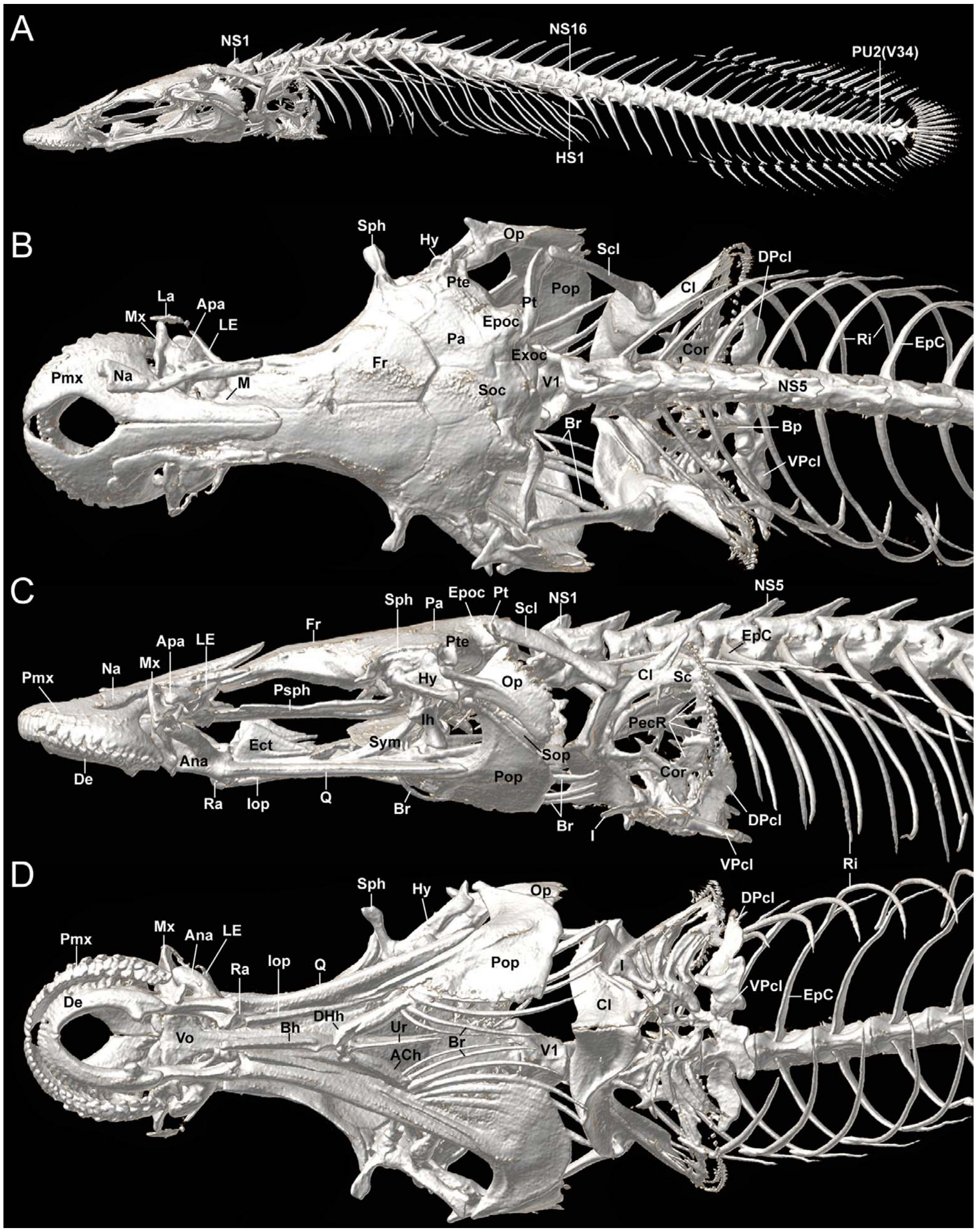

Fig. 10. CT-scanned skeleton of *Flabellicauda alleni*, new species, ROM 55185, 21.5 mm SL. (A) Lateral view of whole body. (B) Dorsal view of anterior body. (C) Lateral view of anterior body. (D) Ventral view of anterior body. Abbreviations: ACh, anterior ceratohyal; Ana, anguloarticular; Apa, autopalatine; 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; La, lachrymal; LE, lateral ethmoid; M, mesethmoid; 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; Sc, scapula; Scl, supracleithrum; Soc, supraoccipital; Sop, subopercle; Sph, sphenotic; Sym, symplectic; Ur, urohyal; V, vertebral centrum; Vo, vomer; and VPcl, ventral postcleithrum.

Upper end of gill opening level with base of 13^{th} (12^{th} or 13^{th}) pectoral-fin ray in lateral view (number of pectoral-fin rays given in Table 2); lower 8^{th} (8^{th} [3 specimens] or 9^{th} [4]) pectoral-fin-ray base attached to disc by membrane. First to third gill arch with two rows of gill filaments, 4^{th} arch without filaments (gill description based on 3 specimens). Gill rakers slender, pointed and very short, somewhat indistinct (not visible in 1 of 3 specimens; gill raker counts listed in Table 3). Gill membranes on each side united ventrally, attached to isthmus. Head sensory canal pores poorly developed, including 2 nasal and 1 postorbital pore; lacrimal, preopercular, and mandibular pores absent; all pores similarly sized with minute membranous tube; NC1 located in front of anterior nostrils in dorsal view (or between anterior and posterior margins of anterior nostril); NC2 between anterior and posterior margins (before anterior margin [2 of 5 specimens] or level with anterior margin [1 specimen]) of posterior nostril; PO1 located just behind posterior margin of orbit (Fig. 6D–F).

Dorsal- and anal-fin-ray counts listed in Table 2. Origin of dorsal fin slightly anterior to vertical through anal-fin origin. Dorsal and anal fins located posteriorly, their bases relatively long, lengths 6.4 (4.4–6.7) and 7.0 (5.3–7.6) in SL, respectively; strongly connected to caudal fin by membranes, giving appearance of single, continuous median fin around posterior part of body (easily damaged). Post-dorsal-caudal length 3.3 (4.6–6.6) in dorsal-fin base length. Dorsal- and anal-fin heights almost equal, except anteriorly. Pectoral- and caudal-fin margins rounded. Pectoral-fin rays 27 (27 [2] or 28 [5]). Upper and lowermost pectoral-fin rays minute, longest ray extending beyond vertical through posterior margin of disc. All soft-fin rays unbranched. Principal caudal-fin rays segmented. Pelvic fins and pectoral-girdle elements forming a circular, extremely small "single" adhesive disc (Fig. 7B), its length and width 8.5 (8.3–9.0) and 8.0 (6.7–9.5) in SL, respectively. Disc region B bell-shaped, equal in size to disc region A. Anterior margin of disc region A smooth, posterior margin of disc region B with fringe. Disc regions A and B with

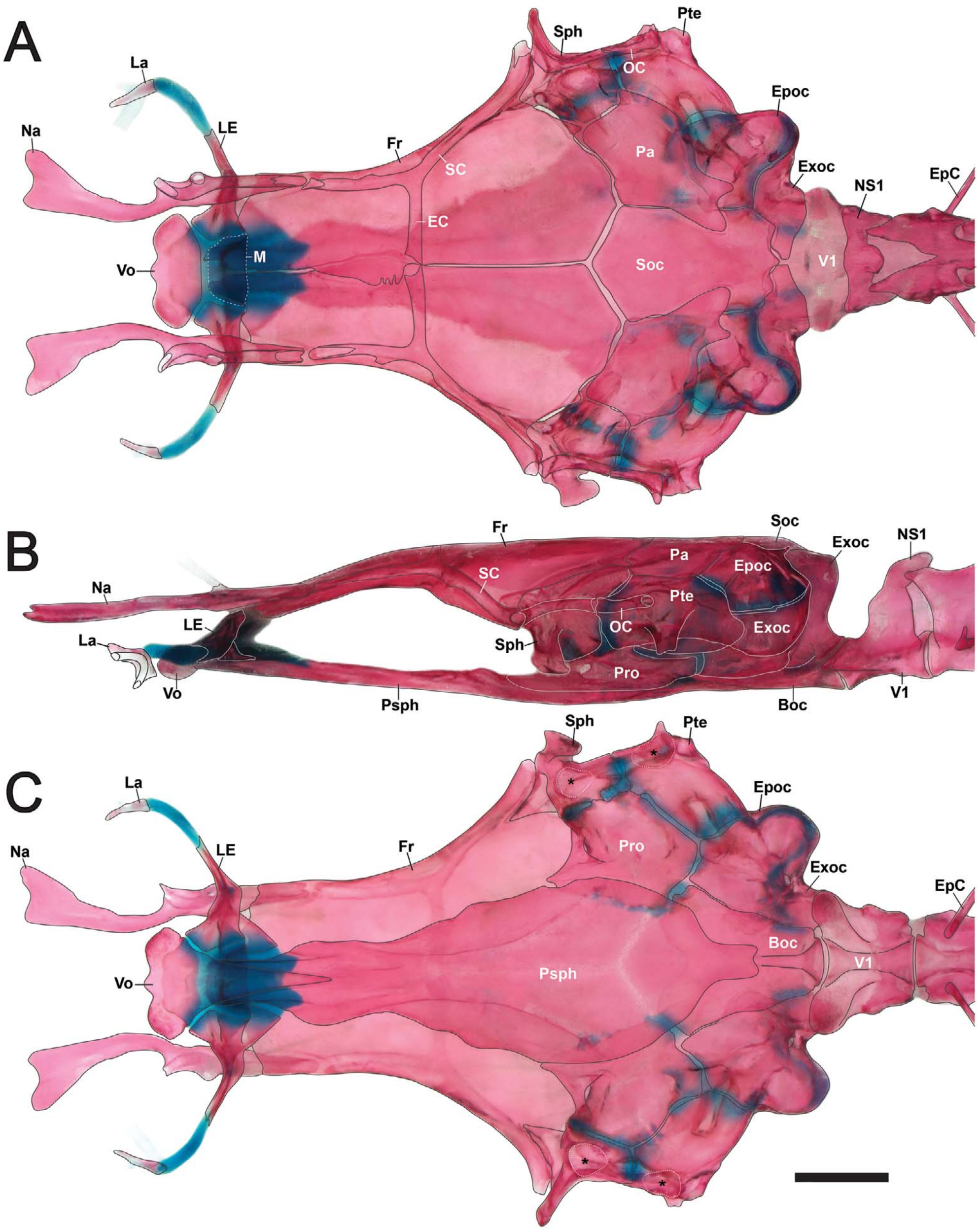

Fig. 11. Neurocranium of *Flabellicauda alleni*, new species, FMNH 127786, 16.5 mm SL. (A) Dorsal view. (B) Lateral view. (C) Ventral view. Scale bar = 1 mm. Abbreviations: Boc, basioccipital; EC, epiphyseal commissure of supraorbital canal; OC, otic canal; Pro, prootic; and SC, supraorbital canal. Other abbreviations as in Figure 10. Asterisks indicate articular condyles that accommodate articular heads of hyomandibular on sphenotic and pterotic.

flattened papillae (disc papillae description based on 5 specimens). Center of disc region A lacking papillae; anterolateral part with 2 or 3 rows of papillae, number of rows slightly decreasing toward apapillate center; both sides of disc region A (except margins) covered with papillae; papillae of inner rows slightly larger than outer rows. Disc region B with 4 (5) rows of papillae; papillae of inner rows slightly larger than papillae of outer rows, anterior part of disc region B without papillae (Fig. 7B). Disc region C lacking papillae.

Osteological description based on CS specimen (1 of ROM 55928) and CT-scanned image (Fig. 17). General osteological characters as in Figures 2B, 17. As described for *F. alleni* except for the following minor differences: ceratobranchial 5 supporting 1–2 tiny conical teeth; vertebrae 33 or 34; and 12 caudal-fin rays associated with hypural plate.

Coloration.—Based on Figure 16, fresh coloration described only from dorsal view (Fig. 16F). Body maroon with white stripe on dorsal midline and lateral side of body; stripe on dorsal midline extending from snout tip to dorsal-fin origin, its width broad anteriorly, gradually narrower toward posterior; lateral stripes extending from posterior point of jaws, past dorsal margin of eye, to posterior part of body (becoming indistinct posteriorly). Snout tip dark red, jaws reddish orange. Pupil black. Preserved coloration uniformly yellowish (Fig. 16A–E).

Distribution.—Known from the Indian Ocean (Seychelles and Chagos Archipelagoes) and western Pacific Ocean (Queensland, Australia, and Kiribati; Fig. 14).

Etymology.—From the Latin *cometes*, a comet, a reference to the bold white stripe along the dorsal midline, reminiscent of the trailing tail of a traveling comet against the night sky. A noun in apposition.

Remarks.—Our description of *F. cometes* is based only on eight individuals, collected from widely separate localities in the Indian and Pacific Oceans. We have chosen to tentatively

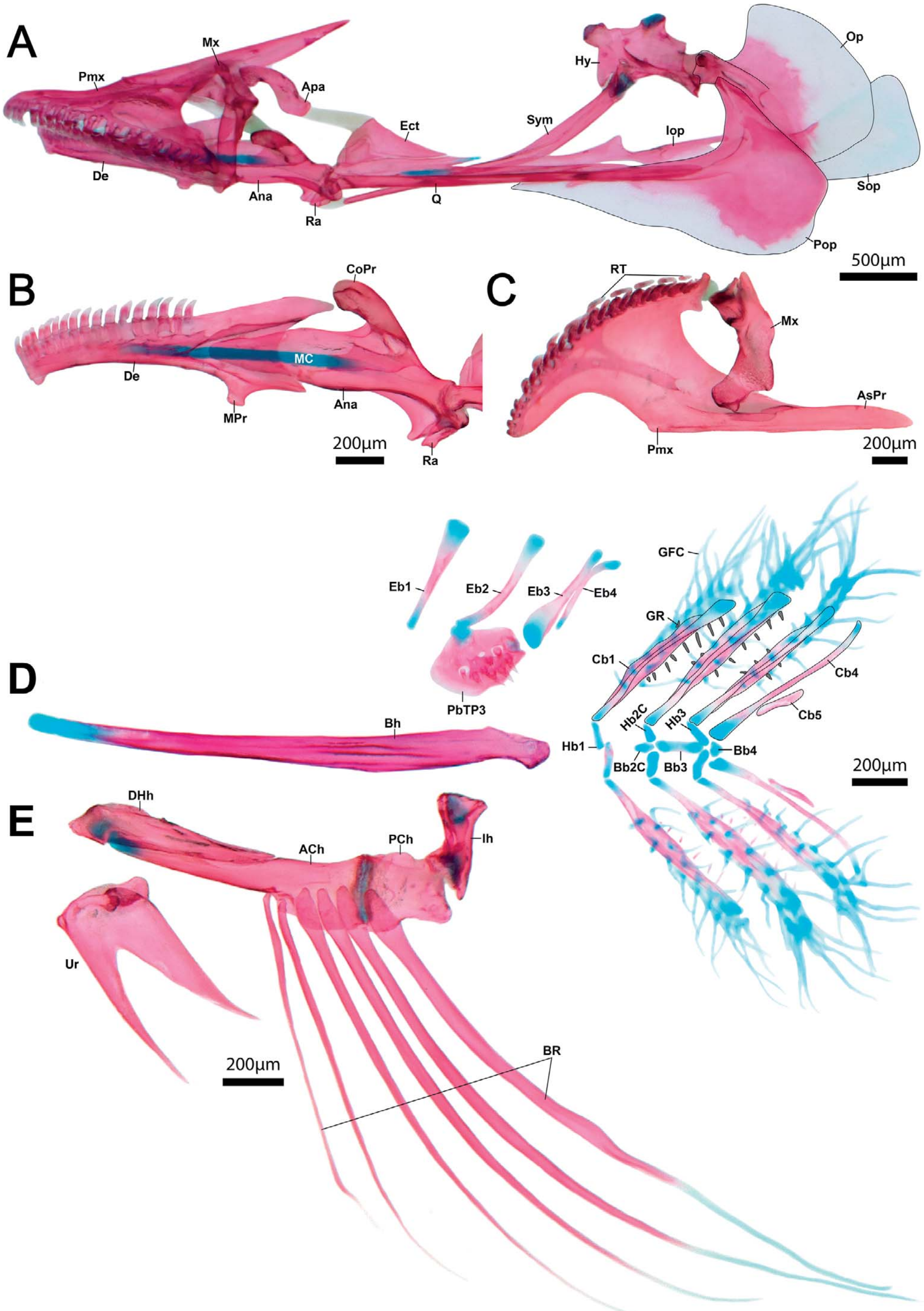

Fig. 12. Viscerocranium of *Flabellicauda alleni*, new species, FMNH 127786, 16.5 mm SL. (A) Hyopalatine arch and opercular series, right side in lateral view (image reversed); margins of opercular bones highlighted with thin black lines. (B) Lower jaw in lateral view. (C) Upper jaw in dorsal view. (D) Gill-arch elements in dorsal view; margins of ceratobranchial bones of right side highlighted with thin black lines. (E) Hyoid bar, right side in medial view and urohyal. Abbreviations: AsPr, ascending process of premaxilla; Bb, basibranchial; Cb, ceratobranchial; CoPr, coronoid process; Eb, epibranchial; GFC, gill-filament cartilage; GR, gill raker; Hb, hypobranchial; MC, Meckel's cartilage; MPr, median process of dentary; PbTP3, pharyngobranchial 3 toothplate; PCh, posterior ceratohyal; and RT, replacement teeth. Other abbreviations as in Figure 10.

identify this material as conspecific because we could not identify significant differences between specimens from these different localities. Additional investigation, including assessment of life colors (which was not possible for specimens from localities in the Pacific), is warranted.

Flabellicauda bolini (Briggs, 1962)

Bolin's Clingfish

Figures 4F–J, 7C, 8E, 9, 14, 15, 18, 19A–C; Tables 1–3, 5

Lepadichthys bolini—Briggs, 1962: 424, fig. 1 (original description; type locality: Palikulo Bay, Espiritu Santo Island, Vanuatu).

Lepadichthys species—Allen and Erdmann, 2012: 841, unnumbered fig. (brief description; Manus, Papua New Guinea: based on underwater photograph).

Holotype.—CAS 158341, 28.8 mm SL, Palikulo Bay, Espiritu Santo Island, Vanuatu, 15°29′10″S, 167°14′37″E, 0.6–3.7 m, R. Bolin and A. Persson, 7 October 1958, rotenone.

Non-type specimens.—29 specimens, 11.5–23.1 mm SL. Papua New Guinea: CAS 65629, 16.4 mm SL, Nagada Mission, 05°09′20″S, 145°47′50″E, 1.5–3.7 m, S. Poss et al., 8 May 1987; CAS 65630, 15.8 mm SL, Nagada Mission, 05°09′20″S, 145°47′50″E, 0.9–3.7 m, S. Poss et al., 1 May 1987; USNM

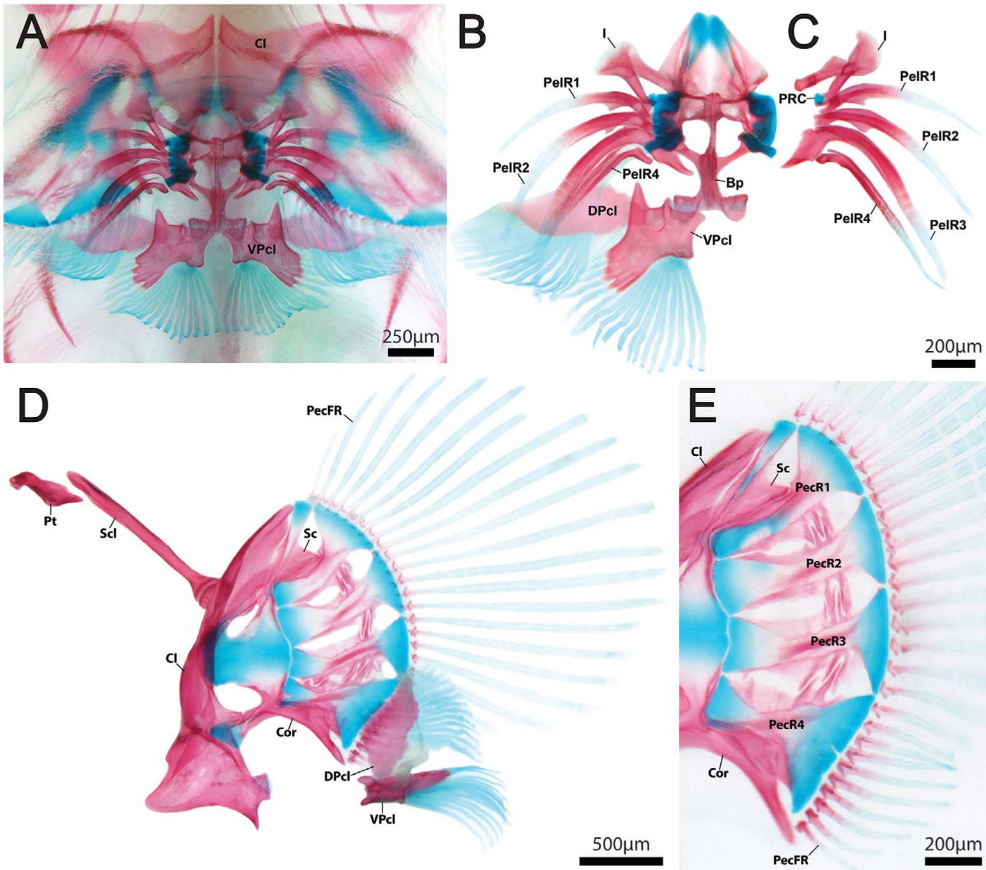

Fig. 13. Internal supporting skeleton of the paired-fin girdles of *Flabellicauda alleni*, new species, FMNH 127786, 16.5 mm SL. (A) Pelvic disc in ventral view. (B) Pelvic disc supporting skeleton, including elements of the pelvic and pectoral-fin girdle in dorsal view (anterior to top of page); postcleithra and pelvic-fin rays of the right side removed. (C) Pelvic-fin rays of right side in dorsal view (anterior to top of page). (D) Pectoral-fin girdle of right side in medial view (anterior to left). (E) 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. Other abbreviations as in Figure 10.

360161, 2, 21.6–23.1 mm SL, Kranket Island, Madang, 1.5–7.6 m, B. Collette, 30 May 1970; USNM 360164, 11.5 mm SL, Kranket Island, Madang, 05°11′30″S, 145°50′42″E, 0.9 m, V. Springer et al., 7 November 1978. Fiji: ANSP 128248, 2, 18.9–20.6 mm SL, Nukumbutho Island, Lauthala Bay, Suva, W. Smith-Vaniz, 15 April 1974; CAS 224415, 17.5 mm SL, Yadua Island, 16°38′07″S, 178°18′41″E, 1.5–6.4 m, D. Greenfield et al., 19 March 2002; CAS 224416, 19.8 mm SL, Daveita Bay, Vanua Levu Island, 16°45′35″S, 179°54′37″E, 7.6–12.2 m, D. Greenfield et al., 26 May 2003; CAS 224418, 15.9 mm SL, Navatu, Vanua Levu Island, 16°56′54″S, 178°58′14″E, 1.2–3.7 m, D. Greenfield et al., 21 March 2002; CAS 224419, 3, 13.2–18.2 mm SL, Nasau Bay, Vanua Levu Island, 16°43′39″S, 179°53′58″E, 0.9–4.6 m, K. Longenecker et al., 25 May 2003; CAS 224420, 4, 16.0–20.1 mm SL, Nananu-i-Cake Island, 17°19′28″S, 178°14′15″E, 3–15 m, D. Greenfield et al., 15 March 2002; CAS 224422, 12, 14.7–22.4 mm SL, Nasese, Suva, 18°10′24″S, 178°25′17″E, D. Greenfield et al., 10 February 2002.

Diagnosis.—A species of *Flabellicauda* (Figs. 4F–J, 18) very similar to *F. alleni* and sharing the following characters: 12–15 (13) dorsal-fin rays; 10–12 (11, rarely 10) anal-fin rays; upper end of gill opening level with base of 12th to 14th pectoral-fin ray in lateral view; head sensory canal pores relatively developed, including usually 2 nasal, 2 lacrimal, and 2 postorbital pores (Fig. 19A–C); disc region A without papillae at center (Fig. 7C); and body black with white stripes (Fig. 8E). *Flabellicauda bolini* differs from *F. alleni* in having fewer gill rakers (4–6 [5] on first to third arches, respectively and 12–17 [14] total [first + second + third arches] gill rakers in *F. bolini* vs. 5–8 [6, rarely 5], 6–8 [6], and 6–8 [7], respectively and 18–24 [19] total gill rakers in *F. alleni*; Table 3). When compared at the same size, the species has slightly larger head (compared as values of head length 28.7–36.4 [34.1] % SL in *F. bolini* vs. 28.5–36.7 [31.9] % SL in *F. alleni* and pre-disc length 23.4–31.7 [28.9] % SL vs. 22.8–31.8 [26.8] % SL; Fig. 9A, B), the difference emphasized when those values combined (52.0–68.1 [63.0] % SL vs. 51.4–67.7 [58.7] % SL; Fig. 9C) and orbit diameter (7.0–12.7 [9.8] % SL vs. 6.4–11.4 [8.3] % SL; Fig. 9D) than *F. alleni*. *Flabellicauda bolini* is further distinguished from congeners by having a relatively longer and thicker caudal-peduncle length and depth proportions (4.1–5.6 [4.9] % and 5.6–7.8 [6.8] % SL, respectively in *F. bolini* vs. 3.2–3.9% and 5.3–6.0% SL, respectively in *F. akiko*; 2.7–5.3 [3.8] and 4.2–6.8 [5.5] % SL, respectively in *F. alleni*; 3.3–4.8% and 5.1–6.3 % SL, respectively in *F. cometes*; Fig. 15A, B). The value of caudal-peduncle length plus caudal-peduncle depth is also useful for distinguishing between the four species of *Flabellicauda* (10.4–13.1 [11.8] % SL in *F. bolini* vs. 8.5–9.5% SL in *F. akiko*; 7.0–11.8 [9.3] % SL in *F. alleni*; 9.3–11.0% SL in *F. cometes*; Fig. 15C).

Description.—Measurements given in Table 5. Body slender, cylindrical, compressed at caudal peduncle. Body width narrower than head width. Anus situated closer to anal-fin origin than to posterior margin of disc (disc to anus length 64.1 [60.3–72.4, mean 65.7] % of disc to anal-fin origin length). Vertebrae 33 (2 specimens), 34 (3), or 35 (6), based radiographs of 11 specimens, not including holotype. Head large, becoming smaller with growth (Fig. 9A), depressed anteriorly, its length and width 3.5 (2.7–3.1 [mean 2.9]) and 5.6 (4.8–6.2 [5.6]) in SL, respectively. Snout moderate, its

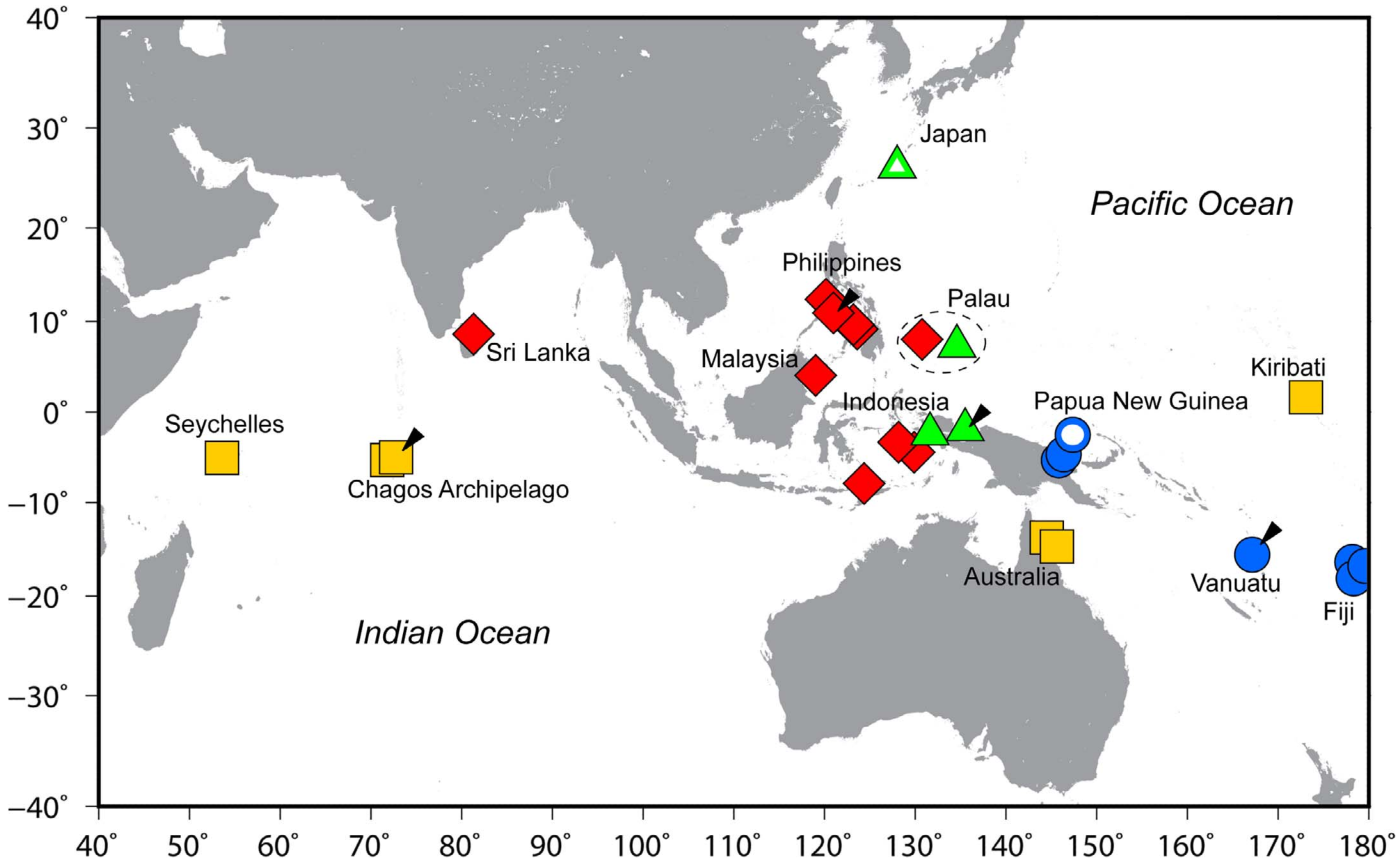

Fig. 14. Distributional map of species of *Flabellicauda*: *F. alleni*, new species (red diamonds), *F. cometes*, new species (yellow squares), *F. bolini* (blue circles), and *F. akiko* (green triangles). Closed and open symbols indicate records based on specimens examined in this study and published photographs, respectively. Arrowheads indicate type locality.

length 14.9 (9.8–12.5 [11.0]) in SL, becoming shorter with growth (Fig. 9E), its tip slightly pointed in lateral view, semi-elliptical (or duck beak-shaped) in dorsal view; dorsal profile of snout slightly concave anteriorly. Mouth terminal, small, restricted to tip of snout. Anterior tip of upper jaw slightly pointed, extending slightly beyond that of lower jaw. Upper lip fleshy, weakly expanded, lower lip thin. Posterior 2/3 of both jaws covered by thick skin on lateral surface of snout. Single row of small similarly sized teeth in both jaws; upper-jaw teeth incisiviform, compressed laterally, with hook-like tips strongly curved posteriorly (ca. 90°); lower-jaw teeth with pointed conical tips, inner surface slightly curved. Premaxillae separated anteriorly by large circular gap in dorsal view (based on radiographs of 1 specimen). Anterior and posterior nostrils larger than head sensory canal pores, former slightly smaller than latter; both with a membranous tube, that of former much longer than latter. Eye size slightly large, becoming smaller with growth (Fig. 9D), diameter slightly larger (slightly smaller in 7 specimens) than snout length, 14.3 (7.9–12.3 [10.3]) in SL. Interorbital region flattened. Gill opening tiny, slit-like. Upper end of gill opening level with base of 14th (12th to 14th) pectoral-fin ray in lateral view (number of pectoral-fin ray given in Table 2); lower 9th (8th [13 specimens] or 9th [12]) pectoral-fin-ray base attached to disc by membrane. First to third gill arches with two rows of gill filaments, 4th arch without filaments (gill description based on 26 specimens). Gill rakers slender, short and pointed (gill raker counts listed in Table 3). Gill membranes on each side united ventrally, attached to isthmus. Head sensory canal pores relatively developed, including 2 nasal, 2 (1 on left side only in 2 specimens) lacrimal, and 2 postorbital pores; preopercular and mandibular pores absent; all pores similarly sized with minute membranous tube; NC1 located in front of anterior nostrils in dorsal view (or between anterior and posterior margins of anterior nostril); NC2 before anterior margin (level with anterior margin [5 of 30 specimens], between anterior and posterior margins [18 specimens], or level with posterior margin [3 specimens]) of posterior nostril; LC1 located in front of anterior margin of eye; LC2 located just below LC1 (postero-ventrally below LC1 [18 of 29 specimens]); PO1 located just behind posterior margin of orbit; PO2 on slightly higher horizontal level of PO1 (Fig. 19A–C).

Dorsal- and anal-fin-ray counts listed in Table 2. Origin of dorsal fin slightly anterior to vertical through anal-fin origin. Dorsal and anal fins located posteriorly, their bases relatively long, lengths 5.3 (4.3–6.1 [5.1]) and 5.7 (4.7–6.6 [5.8]) in SL, respectively; strongly connected to caudal fin by membranes, giving appearance of single, continuous median fin around posterior part of body (easily damaged). Upper and lower hypural plates completely fused, forming single large fan-like hypural plate (radiographs of 10 specimens, not including holotype). Post-dorsal-caudal length 4.0 (3.7–7.0 [4.7]) in dorsal-fin base length. Dorsal- and anal-fin heights almost equal, except anteriorly. Pectoral- and caudal-fin margins rounded. Pectoral-fin rays 30 (27 [4], 28 [7], 29 [10], or 30 [5]). Upper and lowermost pectoral-fin rays minute, longest ray extending beyond vertical through posterior margin of

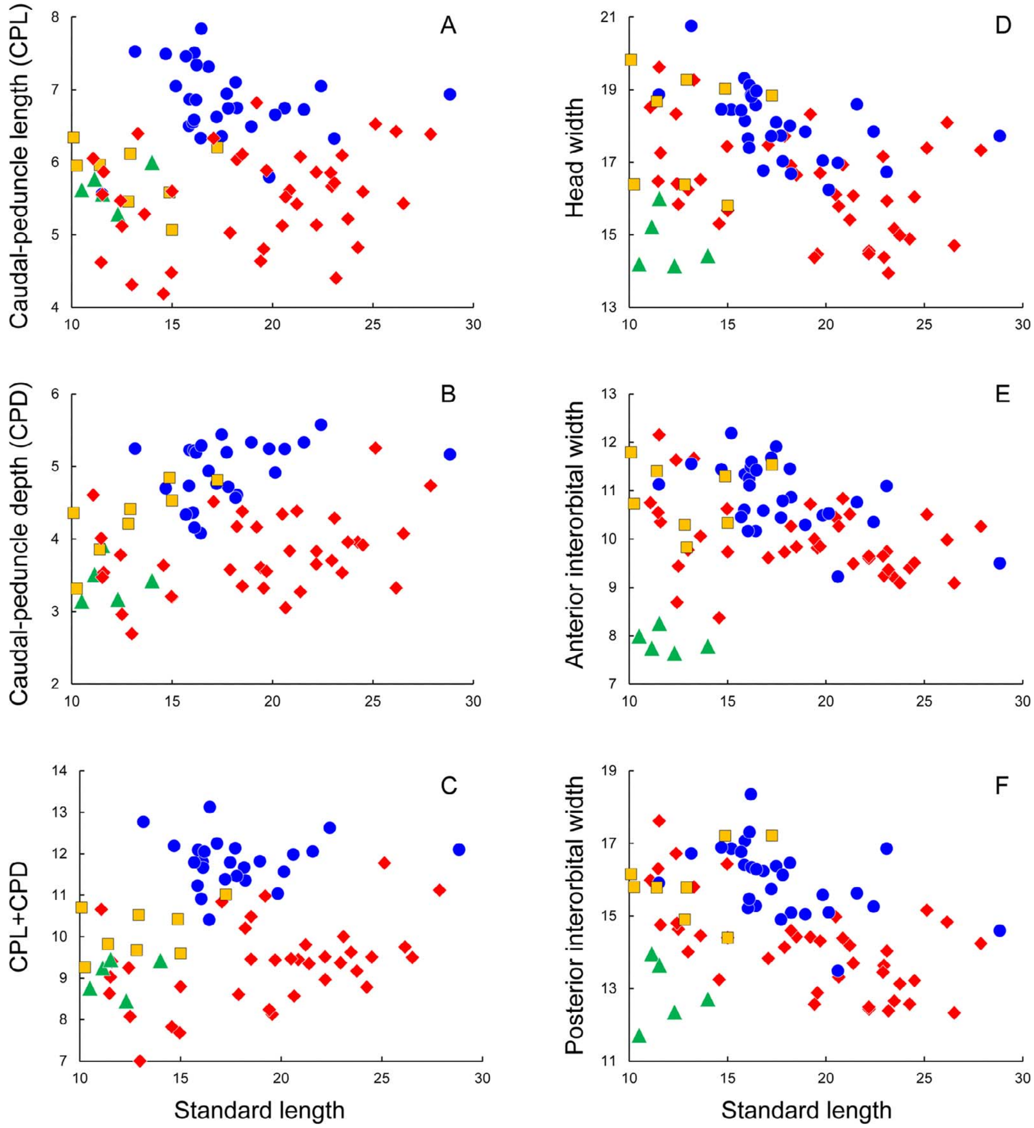

Fig. 15. Relationships of (A) caudal-peduncle length, (B) caudal-peduncle depth, (C) caudal-peduncle length plus caudal-peduncle depth, (D) head width, (E) anterior interorbital width, and (F) posterior interorbital width (as % of SL) in *F. alleni*, new species (red diamonds), *F. cometes*, new species (yellow squares), *F. bolini* (blue circles), and *F. akiko* (green triangles).

disc. All soft-fin rays unbranched and segmented. Pelvic fins and pectoral-girdle elements forming a circular, extremely small "single" adhesive disc (Fig. 7C), its length and width 9.0 (8.3–11.3 [9.4]) and 10.2 (7.4–11.2 [9.5]) in SL, respectively. Disc region B bell-shaped, equal in size to region A. Anterior margin of disc region A smooth, posterior margin of disc region B with fringe. Disc regions A and B with flattened papillae (disc papillae description based on 12 specimens). Center of disc region A lacking papillae; anterolateral part with (2 or 3) rows of papillae, number of rows slightly decreasing toward apapillate 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 (4 or 5) rows of papillae; papillae of inner rows slightly larger than outer rows, anterior part of disc region B without papillae (Fig. 7C). Disc region C lacking papillae.

Coloration.—Based on Figures 4F–J, 8E, 18. Body black with white stripes on dorsal midline and lateral side, stripe pattern very similar to those of *F. alleni* (see Coloration of *F. alleni*). Preserved coloration uniformly yellowish (Fig. 18). Black melanophores present on body of small specimens (ca. <16 mm SL), forming an upper and lower stripe (somewhat indistinct in large specimens; Fig. 4F, G); upper and lower stripes located dorsally and laterally, respectively, former extending from nape to most posterior point of dorsal-fin base, latter extending from pectoral-fin base to caudal-fin base (Fig. 4F–J).

Distribution.—Known from Papua New Guinea, Vanuatu, and Fiji (Fig. 14).

Remarks.—*Flabellicauda bolini* was originally described as *Lepadichthys bolini* by Briggs (1962) on the basis of a single specimen (CAS 158341, 28.8 mm SL; Fig. 18A–C) collected from Vanuatu. Although this species has previously been considered to be widely distributed throughout the Indo-West Pacific by several authors (e.g., Briggs, 1969a; Winterbottom et al., 1989; Fujiwara and Motomura, 2018), these previous records refer either to *F. alleni* or *F. cometes* (described

Table 2. Frequency distribution of dorsal- and anal-fin ray counts and number of pectoral-fin ray at same level with upper end of gill membrane in species of *Flabellicauda*.

	Dorsal-fin rays					
	10	11	12	13	14	15
F. alleni, new species			5	25^{H}	15	2
F. cometes, new species	3	3^{H}	2			
F. bolini			4^{H}	17	7	1
F. akiko		2	3^{H}			

	Anal-fin rays				
	9	10	11	12	13
F. alleni, new species		1	19	16^{H}	5
F. cometes, new species	3	4^{H}	1		
F. bolini		1	18^{H}	9	
F. akiko	1	4^{H}			

	Number of pectoral-fin ray at same level with upper end of gill membrane					
	9th	10th	11th	12th	13th	14th
F. alleni, new species				18^{H}	11	8
F. cometes, new species				2	6^{H}	
F. bolini				7	9	9^{H}
F. akiko	1	4^{H}				

^{H} indicates holotype

Table 3. Frequency distribution of gill raker counts in species of *Flabellicauda*.

	Gill rakers on 1st arch				
	4	5	6	7	8
F. alleni, new species		1	9^{H}	7	3
F. cometes, new species		1^{H}			
F. bolini	11	13^{H}	2		
F. akiko	1				

	Gill rakers on 2nd arch				
	4	5	6	7	8
F. alleni, new species			9^{H}	8	7
F. cometes, new species		2^{H}			
F. bolini	11	12^{H}	3		
F. akiko	1	1			

	Gill rakers on 3rd arch				
	4	5	6	7	8
F. alleni, new species			6	10^{H}	5
F. cometes, new species					
F. bolini	4	18^{H}	4		
F. akiko		2			

	Gill rakers (1st + 2nd + 3rd arches)												
	12	13	14	15	16	17	18	19	20	21	22	23	24
F. alleni, new species							3	5^{H}	3	4	2	2	1
F. cometes, new species													
F. bolini	2	4	10	5^{H}	3	2							
F. akiko			1										

^{H} indicates holotype

Table 4. Morphometric measurements (expressed as percentages of SL) of examined specimens of *Flabellicauda alleni*, new species, and *Flabellicauda cometes*, new species.

	Flabellicauda alleni			*Flabellicauda cometes*		
	Holotype	Paratypes		Holotype	Paratypes	Non-type specimens
	USNM 360264	$n = 41$	Means	ROM 55929	$n = 4$	$n = 3$
Standard length (mm; SL)	26.2	11.1–27.9		17.3	10.3–15.0	10.1–12.9
Head length	28.5	28.7–36.7	31.9	35.4	33.9–37.5	35.4–36.9
Postorbital length	14.7	12.1–17.2	14.6	16.5	14.6–16.8	16.1–17.1
Head depth	8.6	6.6–11.8[a]	9.2	10.7	8.9–10.0	9.3–10.4
Head width	18.1	13.9–19.6[b]	16.4	18.8	15.8–19.0	18.7–19.8
Body depth	13.2	10.8–14.6[a]	12.4	11.9	11.2–12.0	9.1–13.8
Body width	15.0	11.8–17.8[a]	14.3	15.2	15.0–15.3	15.4–16.3
Gill-opening depth	2.4	2.3–4.5[c]	3.1	3.1	3.6–3.9[j]	3.7–4.0[l]
Snout length	7.9	7.6–10.9	9.0	9.3	8.1–9.0	8.8–9.2
Snout depth	5.5	4.2–8.1[b]	6.2	6.0	5.8–6.9	6.3–7.4
Upper-jaw length	4.4	2.7–5.1	3.9	3.7	4.1–5.1	3.0–3.8
Orbit diameter	6.8	6.4–11.4	8.3	9.4	8.0–10.6	10.1–10.6
Anterior interorbital width	10.0	8.4–12.2[b]	10.0	11.5	10.3–11.3	9.8–11.8
Posterior interorbital width	14.8	12.3–17.6[b]	14.2	17.2	14.4–17.2	15.8–16.2
Least interorbital width	5.3	2.7–5.9[b]	4.4	3.5	3.0–4.1	4.4–5.5
Disc length	10.4	8.1–13.5	10.5	11.8	11.1–12.0[j]	11.4–11.6
Disc width	10.7	7.5–12.6[d]	10.2	12.5	10.5–11.1[j]	13.5–15.0
Caudal-peduncle length	3.3	2.7–5.3[e]	3.8	4.8	3.3–4.8	3.9–4.4
Caudal-peduncle depth	6.4	4.2–6.8[b]	5.5	6.2	5.1–6.0	6.0–6.3
Pre-disc length	22.8	23.1–31.8[d]	26.8	30.3	29.5–34.2[j]	30.3–31.7
Pre-anus length	61.0	61.5–70.3[d]	65.9	66.4	62.8–67.7	66.3–66.9
Disc to anal-fin origin length	40.9	35.0–45.4[e]	40.2	35.6	37.4–39.8[j]	34.8–40.1
Disc to anus length	28.4	20.8–31.9[d]	27.6	22.6	21.1–23.8[j]	20.9–23.9
Pre-dorsal-fin length	76.9	73.1–80.5[f]	76.9	79.1	77.0–80.2	76.9–77.5
Pre-anal-fin length	76.5	72.5–82.5[g]	77.9	78.5	82.3–85.6	77.4–82.0
Dorsal-caudal length	27.0	19.8–27.1[h]	24.3	22.1	20.5–23.9	20.9–25.3
Post-dorsal-caudal length	4.5	2.5–5.4[h]	3.9	4.8	3.0–3.4	3.1–4.0
Anal-caudal length	22.3	18.2–26.9[h]	21.4	18.1	15.9–20.8	17.9–21.9
Dorsal-fin base length	21.9	15.5–22.8[h]	19.8	15.7	15.8–19.7	14.9–22.8
Anal-fin base length	18.7	14.4–20.5[h]	17.6	14.3	13.2–18.9	14.9–18.0
Pectoral-fin length	Broken	7.8–12.3[i]	9.4	11.0	9.2[k]	12.6–13.4
Caudal-fin length	9.3	6.3–11.9[a]	8.6	9.5	Broken	11.0–11.8

[a, b, c, d, e, f, g, h, i, j, k, l] based on 38, 39, 32, 40, 35, 37, 34, 36, 27, 3, 1, and 2 specimens, respectively

above). Based on available material, *F. bolini* appears to be restricted to the western Pacific, from Papua New Guinea to Fiji (Fig. 14).

In their book of the reef fishes of the East Indies, Allen and Erdmann (2012) included an underwater photograph of unidentified species of *Lepadichthys* taken at Papua New Guinea (Fig. 8E). Judging from its general appearance (e.g., mouth and vertical fins shape) and the locality, the photographed individual likely belongs to *F. bolini*.

Flabellicauda akiko (Allen and Erdmann, 2012)
Minute Clingfish
Figures 7D, 8F–H, 14, 15, 19, 20; Tables 1–3, 5

Lepadichthys akiko—Allen and Erdmann, 2012: 1164, figs. 1–3 (original description; type locality: east of Point Mangguar, Cenderawasih Bay, West Papua, Indonesia); Fujiwara and Motomura, 2018: 88, figs. 1–5 (description; Okinawa Island, Japan [based on underwater photographs] and Palau [BPBM 37695, 37705]); Conway et al., 2020: 893, figs. 3, 4 (molecular result; East Kalig Island, Misool, Raja Ampat, Indonesia: based on WAM P. 35180-001).

Holotype.—MZB 20592, 10.5 mm SL, east of Point Mangguar, Cenderawasih Bay, West Papua, Indonesia, 02°25′50″S, 134°59′25″E, 70 m, M. Erdmann, 20 September 2010, clove oil.

Non-type specimens.—4 specimens, 11.1–14.0 mm SL. Indonesia: WAM P. 33772-002, 11.5 mm SL, same as type locality, 44–45 m, M. Erdmann, 15 June 2012; WAM P. 35180-001, 11.1 mm SL, East Kalig Island, Misool, Raja Ampat, 02°13′15″S, 130°33′14″E, ca. 60 m, M. Erdmann, 16 June 2015. Palau: BPBM 37695, 14.0 mm SL, Augulpelu Reef, 07°16′24.6″N, 134°31′26.4″E, ca. 90 m, J. Earle, 10 May 1997; BPBM 37705, 12.3 mm SL, same locality as BPBM 37695, ca. 90 m, R. Pyle and J. Earle, 12 May 1997.

Diagnosis.—A species of *Flabellicauda* (Fig. 20) distinguished from congeners by the following unique characters: head sensory canal pores poorly developed, including 1 nasal and 1 postorbital pore (vs. usually 2 nasal, 2 lacrimal, and 2 postorbital pores in *F. alleni* and *F. bolini*; 2 nasal pores present in *F. cometes*; Fig. 19); upper end of gill opening level with base of 9th or 10th pectoral-fin ray in lateral view (vs.

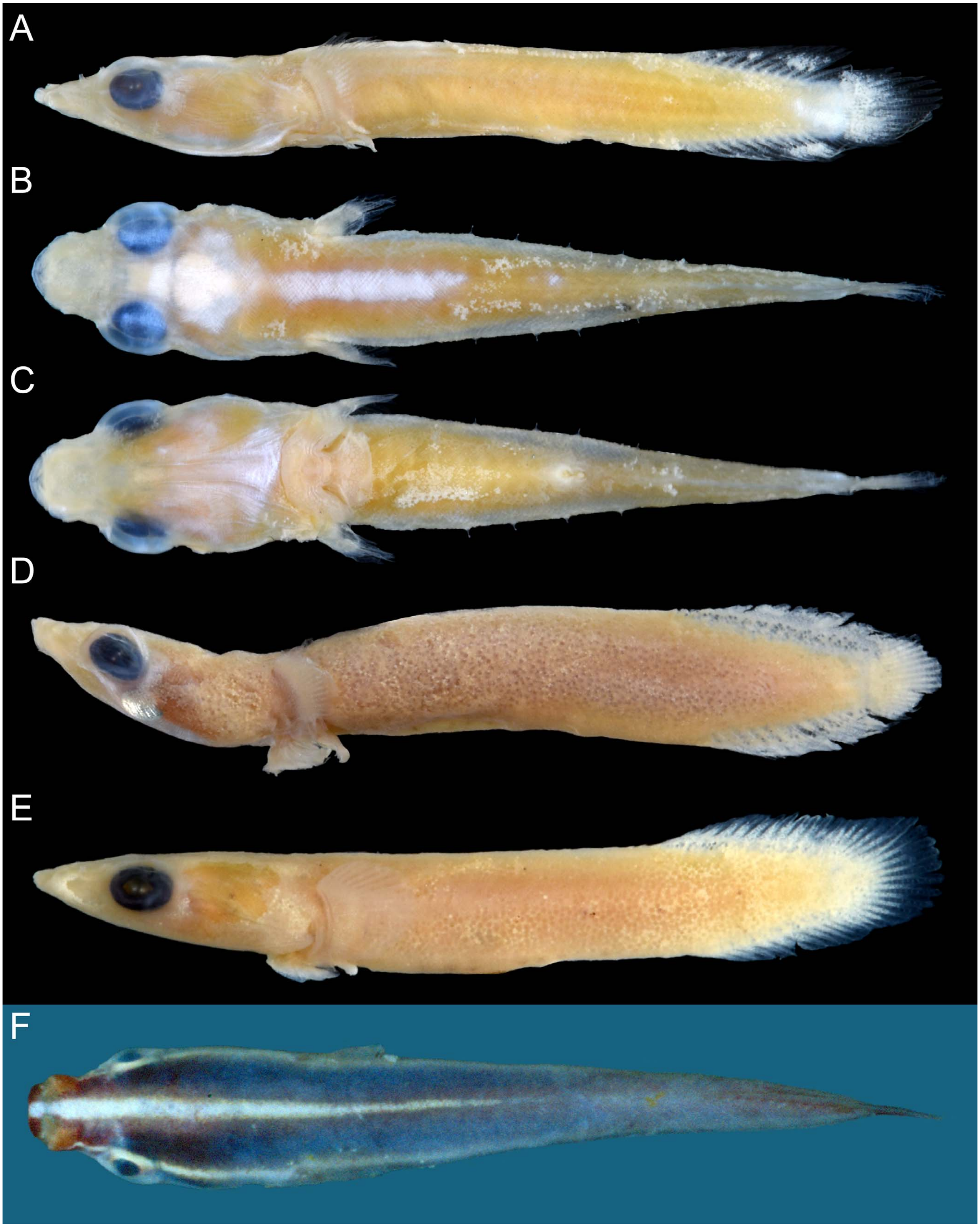

Fig. 16. Preserved (A–E) and fresh (F) specimens of *Flabellicauda cometes*, new species. (A–C) ROM 55929, holotype, 17.3 mm SL, Salomon Atoll, Chagos Archipelago; (D) ANSP 150416, 14.9 mm SL, Amirante Islands, Seychelles; (E) AMS I. 20755-073, 11.4 mm SL, Queensland, Australia; (F) ROM 55928, 15.0 mm SL, Peros Banhos Atoll, Chagos Archipelago. (A, D, E) Lateral views. (B, F) Dorsal views. (C) Ventral view.

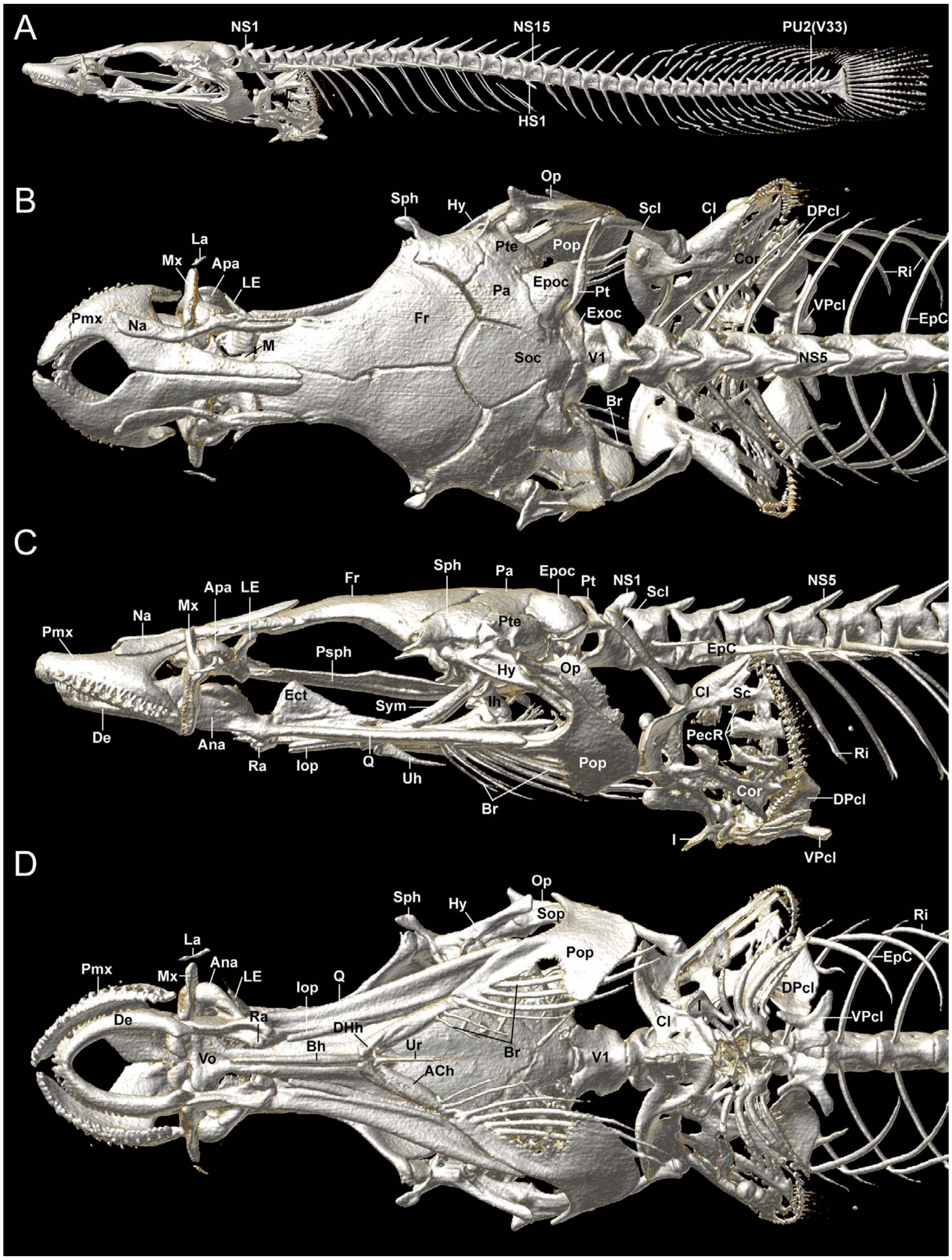

Fig. 17. CT-scanned skeleton of *Flabellicauda cometes*, new species, ROM 55928, 15.0 mm SL. (A) Lateral view of whole body. (B) Dorsal view of anterior body. (C) Lateral view of anterior body. (D) Ventral view of anterior body. Abbreviations as in Figure 10.

12th to 14th); disc region A with papillae at center (vs. disc region A without papillae at center; Fig. 7); and body red with white stripes (vs. body black or maroon with white stripes; Fig. 8F–H). In addition to the aforementioned diagnostic characters, *F. akiko* also exhibits a slightly narrower head (head width 14.1–16.0% SL), and slightly narrower anterior and posterior interorbital widths (7.6–8.3%, and 11.7–14.0% SL, respectively) when compared with congeners of similar body size (Fig. 15). A small number of meristic and morphometric characters also distinguish *F. akiko* from congeners (see Diagnosis of *F. alleni* and *F. bolini*).

Description.—Measurements given in Table 5. Body slender, cylindrical, compressed at caudal peduncle. Body width narrower than head width. Anus situated closer to anal-fin origin than to posterior margin of disc (disc to anus length 68.1 [65.5–68.6] % of disc to anal-fin origin length). Vertebrae 34 (based on CT-scanned image of WAM P. 35180-001). Head size medium, depressed anteriorly, its length and width 2.8 (2.9–3.1) and 7.0 (6.3–7.1) in SL, respectively. Snout moderate, its length 9.4 (10.1–13.3) in SL, tip slightly pointed in lateral view, duck beak-shaped in dorsal view; dorsal profile of snout slightly concave anteriorly. Mouth terminal, small, restricted to tip of snout. Anterior tip of upper jaw slightly pointed, extending slightly beyond that of lower jaw. Upper lip fleshy, weakly expanded, lower lip thin. Posterior 2/3 of both jaws covered by thick skin on lateral surface of snout; thick skin of snout visible in dorsal and ventral view as obvious bulge posterolateral to mouth (skin only weakly expanded in 2 specimens; Fig. 20E, F). Single row of small similarly sized teeth in both jaws; upper-jaw teeth incisiviform, compressed laterally, with hook-like tips strongly curved posteriorly (ca. 90°); lower-

Fig. 18. Preserved specimens of *Flabellicauda bolini*. (A–C) CAS 158341, holotype, 28.8 mm SL, Espiritu Santo Island, Vanuatu; (D) USNM 360161, 21 mm SL, Madang, Papua New Guinea; (E) ANSP 128248, 18.9 mm SL, Suva, Fiji. (A, D, E) Lateral views. (B) Dorsal view. (C) Ventral view.

jaw teeth with pointed conical tips, inner surface slightly curved. Premaxillae separated anteriorly by large circular gap in dorsal view (based on CT-scanned image of WAM P. 35180-001). Anterior and posterior nostrils larger than head sensory canal pores, former slightly smaller than latter; both with a membranous tube, that of latter very short and somewhat indistinct. Eye size moderate, diameter slightly smaller (or larger in 2 specimens) than snout length, 11.2 (9.8–16.1) in SL. Interorbital region flattened. Gill opening tiny, slit-like. Upper end of gill opening level with base of 10th (or 9th) pectoral-fin ray in lateral view (number of pectoral-fin ray given in Table 2); lower 6th (6th [1 specimen], 7th [1] or 8th [2]) pectoral-fin-ray base attached to disc by membrane. First to third gill arches with two rows of gill filaments, 4th arch without filaments (gill description based on 2 specimens, not including holotype). Gill rakers slender, very short and pointed (gill raker counts listed in Table 3). Gill membranes on each side united ventrally, attached to isthmus. Head sensory canal pores poorly developed, including 1 nasal and 1 postorbital pore; preopercular, lacrimal, and mandibular pores absent; all pores similarly sized with minute membranous tube. Nasal pore located in front of anterior nostrils in dorsal view (or between anterior and posterior margins of

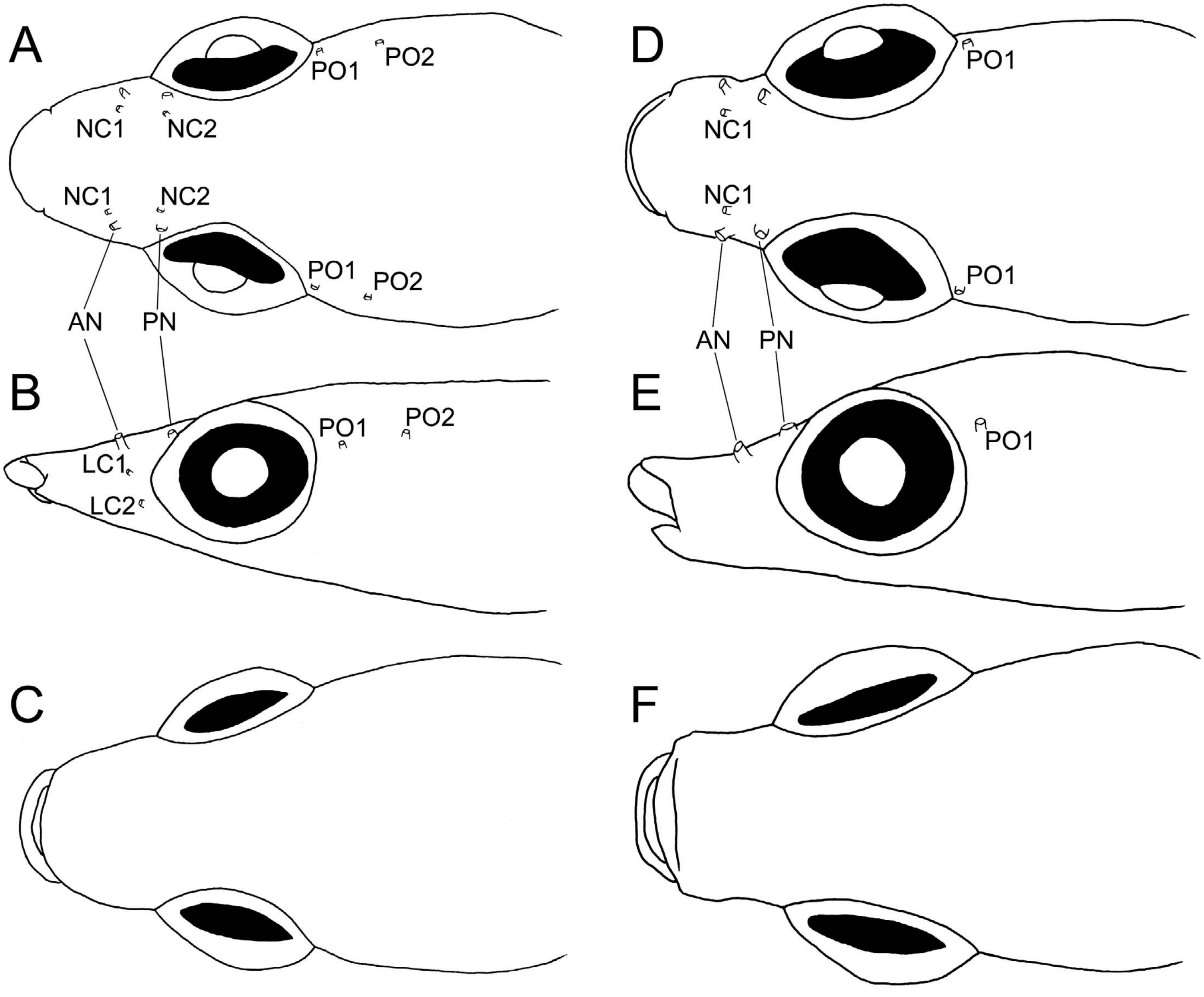

Fig. 19. Head sensory canal pores of (A–C) *Flabellicauda bolini* and (D–F) *Flabellicauda akiko*. Illustrations based on (A–C) ANSP 128248, 20.6 mm SL and (D–F) WAM P. 33772-002, 11.5 mm SL. (A, D) Dorsal views. (B, E) Lateral views. (C, F) Ventral views. Scale bars = 1 mm. Abbreviations as in Figure 6.

anterior nostril). Postorbital pore just behind posterior margin of orbit (Fig. 19D–F).

Dorsal- and anal-fin-ray counts listed in Table 2. Origin of dorsal fin slightly anterior to vertical through anal-fin origin. Dorsal and anal fins located posteriorly, their bases relatively short, lengths 5.7 (4.6–7.0) and 6.7 (5.1–8.1) in SL, respectively; strongly connected to caudal fin by membranes, giving appearance of single, continuous median fin around posterior part of body (easily damaged). Upper and lower hypural plates fused, forming single large fan-like hypural plate (based on CT-scanned image of WAM P. 35180-001). Post-dorsal-caudal length 4.3 (2.5–6.3) in dorsal-fin base length. Dorsal- and anal-fin heights almost equal, except anteriorly. Pectoral- and caudal-fin margins rounded. Pectoral-fin rays 27 (26 [1] or 27 [3]). 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, extremely small, "single" adhesive disc (Fig. 7D), its length and width 8.9 (8.1–10.3) and 13.5 (9.5–11.2) in SL, respectively. Disc region B bell-shaped, equal in size to disc region A. Anterior margin of disc region A smooth, posterior margin of disc region B with fringe. Disc regions A and B with flattened papillae (disc papillae description based on 3 specimens). Anterior part of disc region A with 3 rows of papillae across 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 4 (4 or 5) rows of papillae; papillae of inner rows slightly larger than papillae of outer rows, anterior part of disc region B without papillae (Fig. 7D). Disc region C lacking papillae.

Coloration.—Based on Figures 8F–H, 20 and Fujiwara and Motomura (2018: figs. 1, 4). Body red with three broad white stripes on each side; upper and lowermost stripes continuing

Table 5. Morphometric measurements (expressed as percentages of SL) of examined specimens of *Flabellicauda bolini* and *Flabellicauda akiko*.

	Flabellicauda bolini			*Flabellicauda akiko*	
	Holotype	Non-type specimens		Holotype	Non-type specimens
	CAS 158341	*n* = 28	Means	MZB 20592	*n* = 4
Standard length (mm; SL)	28.8	11.5–23.1		10.5	11.1–14.0
Head length	28.7	32.4–36.4	34.1	35.4	32.4–34.7
Postorbital length	15.6	14.1–17.6	15.8	15.9	14.4–15.7
Head depth	7.7	8.0–12.1	9.5	8.5	8.9–11.1
Head width	17.7	16.2–20.8	18.0	14.2	14.1–16.0
Body depth	12.8	11.1–14.9[a]	13.0	13.2	11.0–12.9
Body width	16.1	14.2–18.0	15.8	11.3	11.7–13.7
Gill-opening depth	4.4	2.4–4.4[a]	3.4	4.0	3.3–4.2
Snout length	6.7	8.0–10.2	9.2	10.7	7.6–9.9
Snout depth	4.8	4.9–7.4	6.4	4.3	6.0–6.8
Upper-jaw length	4.8	3.1–4.9	4.0	4.8	3.9–5.0
Orbit diameter	7.0	8.2–12.7	9.8	9.0	6.2–10.3
Anterior interorbital width	9.5	9.2–12.2	10.9	8.0	7.6–8.3
Posterior interorbital width	14.6	13.5–18.4	16.0	11.7	12.4–14.0
Least interorbital width	5.9	3.0–6.5	4.5	2.5	2.2–2.9
Disc length	11.1	8.9–12.0	10.8	11.2	9.8–12.3
Disc width	9.9	8.9–13.5	10.6	7.4	8.9–10.5
Caudal-peduncle length	5.2	4.1–5.6[b]	4.9	3.1	3.2–3.9
Caudal-peduncle depth	6.9	5.6–7.8	6.8	5.6	5.3–6.0
Pre-disc length	23.4	27.3–31.7	28.9	30.6	28.6–30.6
Pre-anus length	63.4	62.1–70.1	66.8	70.1	69.0–69.4[f]
Disc to anal-fin origin length	46.3	36.0–46.3[c]	41.5	39.1	36.8–42.9
Disc to anus length	29.7	22.7–30.8	27.3	26.7	26.0–28.1[f]
Pre-dorsal-fin length	78.7	72.8–83.2[a]	77.5	76.7	76.1–77.8
Pre-anal-fin length	80.0	74.8–83.9[c]	79.4	78.0	77.2–81.8
Dorsal-caudal length	25.0	21.3–28.1[a]	24.5	20.5	20.6–26.5
Post-dorsal-caudal length	4.7	2.8–5.5[a]	4.3	4.1	3.5–5.8
Anal-caudal length	23.3	18.5–24.0[c]	20.9	21.0	16.5–24.7
Dorsal-fin base length	19.0	16.4–23.3[a]	19.8	17.6	14.3–21.8
Anal-fin base length	17.4	15.0–21.3[b]	17.3	14.9	12.3–19.7
Pectoral-fin length	11.0	8.4–11.7[d]	9.9	12.3	10.4–12.7[f]
Caudal-fin length	Broken	7.4–11.5[e]	9.6	Broken	7.8–12.2

[a, b, c, d, e, f] based on 26, 24, 25, 19, 22, and 3 specimens, respectively

onto dorsal and ventral surface of head, respectively, visible in lateral view; uppermost stripe extending from snout tip, past dorsal margin of eye, to posteriormost point of dorsal-fin base, slightly tapering posteriorly; central stripe extending along side of body, from snout tip to caudal-fin base (or reaching center of caudal fin) through pupil, posterior third slightly expanded, tapering at posterior tip; lowermost stripe narrow (or somewhat indistinct), extending just below middle of eye to anterior margin of pelvic disc, both tips tapering; additional red stripe extending along ventral midline from posterior portion of pelvic disc to in front of anus. Slightly indistinct (distinct in life; Fig. 8F–H) bright white stripes on dorsal midline and between upper and middle red stripes. Upper and lower parts of iris white, pupil black. Tubes of nostrils, all fins, and pelvic disc transparent.

Preserved coloration uniformly yellowish (or whitish; Fig. 20), body stripes indistinct, orangish or yellowish (disappearing completely after several years in preservative: Fujiwara and Motomura, 2018: fig. 1; Fig. 20).

Distribution.—Currently known only from Okinawa Island, Japan (based on underwater photographs), Palau, and West Papua, Indonesia (Fujiwara and Motomura, 2018; Fig. 14).

Remarks.—*Flabellicauda akiko* was originally described as *Lepadichthys akiko* by Allen and Erdmann (2012) on the basis of a single specimen (MZB 20592, 10.5 mm SL; Fig. 20A–C) collected from West Papua, Indonesia. Subsequently, Fujiwara and Motomura (2018) recorded the species from Palau and Okinawa Island, Japan and also provided additional information on gill raker counts and head sensory canal pores based on the examination of addition material, which they considered to be diagnostic characters for the species. Allen and Erdmann (2012) and Fujiwara and Motomura (2018) reported pectoral-fin ray counts of 16 or 17 and 18, respectively, for *F. akiko*, but our reexamination of their material has revealed the number of pectoral-fin rays to be higher (26 or 27). The lowermost rays of the pectoral fin are embedded inside of the fleshy membrane that unites the pelvic and pectoral fins and are easily overlooked.

Fig. 20. Preserved specimens of *Flabellicauda akiko*. (A–C) MZB 20592, holotype, 10.5 mm SL, West Papua, Indonesia; (D–F) WAM P. 33772-002, 11.5 mm SL, West Papua, Indonesia. (A, D) Lateral views. (B, E) Dorsal views. (C, F) Ventral views.

DISCUSSION

***Ecological notes on* Flabellicauda.—**Allen and Erdmann (2012) were first to provide information on the ecology of *F. akiko*, based on observations and photographs of a single individual discovered attached to a sponge over a rubble substrate at 70 m depth (this specimen later became the holotype; Allen and Erdmann, 2012; Fig. 8F). Subsequently, Fujiwara and Motomura (2018) suggested that *F. akiko* is likely epibenthic, based on underwater photographs taken at Okinawa Island (Japan) that captured an individual hovering in the water column in close proximity to a sea urchin (Fujiwara and Motomura, 2018: fig. 4). Additional underwater photographs of this species included herein (Fig. 8G, H) provide further documentation of this behavior. Underwater photographs of *F. alleni* and *F. bolini* reveal these two species also spend time hovering in the water column, in all cases amongst the spines of sea urchins of the family Diadematidae (Fig. 8A–C, E; KPM-NR. 35830, 37813, 38041, 73907, 73908, 84746; all KPM-NR pictures were here identified as *F. alleni* based on locality [Philippines or Malaysia]). Whether these two species also attach to the urchin spines that they shelter within is currently unknown as we are aware of only a single underwater photograph of *F. alleni* in which the photographed individual is attached to a substrate, in this case a rock in close proximity to a sea urchin (Fig. 8D). Though gobiesocids, especially reef-associated species, are frequently encountered in close proximity or attached to marine invertebrates, including sponges, corals, gorgonians, sea urchins, and crinoids (e.g., Craig and Randall, 2008: fig. 1; Craig et al., 2015: fig. 4; Fricke and Wirtz, 2017: figs. 4, 5; Conway et al., 2018b; Fujiwara et al., 2020: fig. 8), the majority of these taxa are benthic. To the best of our knowledge, the only other epibenthic gobiesocid is *Diademichthys lineatus*, which is frequently observed and photographed hovering in the water column between the spines of diadematid sea urchins (e.g., Randall et al., 1990: 56; Randall, 1995: 349, 2005: 505; Allen and Erdmann, 2012: 839). Based on the topology presented in Conway et al. (2020: figs. 3, 4), the epibenthic behavior exhibited by the members of *Diademichthys* and *Flabellicauda* is most likely the product of convergence. It is of note that members of both genera exhibit an extremely small adhesive disc, compared to close relatives, and this reduction in overall disc size may be related (in some way) to the epibenthic behavior of these species. Though we do not have information on the behavior of *F. cometes*, we expect that this species likely also is epibenthic. Another potential parallel between the ecology of *Flabellicauda* and *Diademichthys* is the consumption of the tube feet of sea urchins. Sakashita (1992) reported tube feet of sea urchins in the stomachs of adult *D. lineatus*, and also noted that large males (~40 mm SL) consume larger quantities of tube feet than smaller males and females. We removed two partially digested tube feet from the stomach of a single individual of *F. alleni* (FMNH 127786), suggesting that at least one of the species of *Flabellicauda* consumes tube feet, and potentially those of the sea urchins in which they seek shelter.

Like the majority of gobiesocids, *F. alleni*, *F. bolini*, and *F. cometes* inhabit relatively shallow coastal waters, at depths of 0.6–23 m, 0.6–12 m, and 3–13 m, respectively. Notably, *F. akiko* occurs at much greater depths (40–90 m) than the other members of the genus and is one of only ~20 species of gobiesocid known to inhabit depths greater than 50 m (see Hastings and Conway, 2017: table 1). Underwater observations of *F. akiko* by M. Erdmann (pers. comm.) confirm that this species is an inhabitant of mesophotic coral reefs (i.e., largely tropical, light-dependent communities found between 30–150 m depth; Loya et al., 2019). Gobiesocids are rarely encountered in mesophotic coral reef ecosystems, and in addition to *F. akiko*, other mesophotic coral reef-dwelling gobiesocids include the members of the new world genus *Derilissus* (which contains five species, *D. altifrons*, *D. kremnobates*, *D. lombardii*, *D. nanus*, and *D. vittiger*; Briggs, 1969b; Fraser, 1970; Smith-Vaniz, 1971; Sparks and Gruber, 2012) and potentially also certain eastern tropical Atlantic members of the genus *Diplecogaster* (including *D. ctenocrypta* and *D. tonstricula*; Fricke et al., 2015).

***Comments on diagnostic characters of* Flabellicauda.—**In the majority of gobiesocids, the caudal-fin skeleton includes a single large hypural complex or urostyler complex (e.g., see Monod, 1968; Springer and Fraser, 1976; Hayashi et al., 1986; Fujita, 1990; Konstantinidis and Conway, 2010). At the posterior edge of this complex, adjacent to the caudal-fin diastema, is a narrow opening or notch of variable length that divides the complex into an upper and lower part (upper and lower hypural plates of recent authors; e.g., see Conway et al., 2017b: fig. 7, 2018a: fig. 10, 2018b: fig. 6; 2019: fig. 10; Fujiwara and Motomura, 2019a: fig. 3, 2019b: fig. 4; Fujiwara et al., 2018: fig. 4, 2020: fig. 3; Fig. 2C–H). Development of the caudal skeleton has not been investigated for gobiesocids, and it is unknown whether the single hypural element present in adults is derived from a single hypural cartilage or from multiple separate hypural cartilages that may undergo ontogenetic fusion. In the members of *Flabellicauda*, there is no narrow opening or notch at the center of the posterior part of the hypural complex, and the posterior edge is straight, giving the complex the overall appearance of a large triangular or fan-like element (Fig. 2A, B), reminiscent of the condition in some members of the Atherinomorpha, in which only a single fan-like hypural element is present in adult individuals (e.g., see Parenti, 1981: fig. 2F; Ghedotti, 2000: fig. 17B; Costa, 2012: figs. 2B, 3B; Thieme et al., 2021: fig. 8i, k). A small circular opening is located at the center of the hypural complex of *Flabellicauda*, and this may be homologous to the anterior part of the narrow opening or notch that divides the hypural complex into an upper and lower part in other gobiesocids. If we are correct, the condition in *Flabellicauda* may represent a peramorphic condition in which the narrow opening or notch that is present in the hypural complex of other gobiesocids has become closed posteriorly, potentially via ontogenetic fusion. Though the condition of the hypural complex in *Flabellicauda* is unique amongst diademichthyine clingfishes, Springer and Fraser (1976) have documented a similar (convergent) condition in *Alabes dorsalis*, in which only a single fan-shaped hypural element is present, though in this case without a small opening at the center (see Springer and Fraser, 1976: fig. 7).

In addition to the shape of the hypural complex, the caudal region of *Flabellicauda* is also notable because of the connection between the three median fins. This connection is established by a thin, narrow membrane of skin spanning the short gap between the posteriormost ray of the dorsal or anal fin and the anteriormost dorsal or ventral procurrent ray of the caudal fin, respectively. This thin membrane is easily damaged during collection and preservation but persists in well-preserved material and gives the impression of a single, continuous median fin around the posterior part of body in the members of *Flabellicauda*. In the majority of gobiesocids, the dorsal and anal fins are separate from the caudal fin (see Briggs, 1955: figs. 82–101, 103–112; Fujiwara, 2019: 327, 329) or in the few other cases in which these fins are connected by a thin transparent membrane (see Briggs, 1955: figs. 102, 113, 114; Fujiwara, 2019: 327, 328), the median fins appear as separate entities because the gap between the posteriormost ray of the dorsal or anal fin and the anteriormost dorsal or ventral procurrent ray of the caudal fin is much greater than in *Flabellicauda*. In *Gouania willdenowi*, the gap between the caudal and dorsal/anal fins is bridged by a high number of procurrent rays, which are housed within the same ridge of thick skin that accommodates the greatly reduced dorsal- and anal-fin rays (Konstantinidis and Conway, 2010). This arrangement also gives the external appearance of a single continuous median fin around the posterior part of the body, but this condition is different from the condition in *Flabellicauda*.

Shiogaki and Dotsu (1983) considered the number and position of cephalic lateral-line canal pores as important characteristics for defining higher groups of gobiesocids, especially genera. We have also found characters of the cephalic lateral-line canal system useful for the purpose of diagnosing *Flabellicauda* relative to other genera of the Diademichthyinae and also for diagnosis of the different members of the genus. In all four species of *Flabellicauda*, the preoperculo-mandibular lateral-line canal is absent, and this character, in combination with others, is useful to distinguish the new genus from the other diademichthyine genera that possess this structure (e.g., the preopercle houses a canal in *Aspasma*, *Diademichthys*, *Flexor*, *Lepadichthys*, *Pherallodichthys*, and *Propherallodus*; Shiogaki and Dotsu, 1983; Conway et al., 2018a; Fujiwara and Motomura, 2019b, 2020b). There is also variation in the infraorbital and otic lateral-line canal among the four members of *Flabellicauda*. In *F. alleni* and *F. bolini*, the infraorbital canal is represented by a poorly ossified tube on the lacrimal, with two canal openings (LC1 and LC2). In *F. akiko* and *F. cometes*, the infraorbital canal (and associated pores) is absent. The otic canal (and associated pore on the pterotic; PO2) is present in *F. alleni*, *F. bolini*, and *F. cometes*, but absent in *F. akiko*. The tiny *F. akiko*, the largest specimen of which is recorded at 14.0 mm SL, exhibits the greatest number of reductions to the cephalic lateral-line system of the four species of *Flabellicauda*, and these reductions may be the product of developmental truncation, associated with the evolutionary process of miniaturization (Weitzman and Vari, 1988; Hanken and Wake, 1993). Intraspecific variation is rarely documented for characters of the cephalic lateral-line system in gobiesocids but Hayashi and Hayashi (1985), Fujiwara et al. (2018), and Fujiwara and Motomura (2020b) have documented asymmetry in the number of cephalic lateral-line canal pores present on either side of the head for a small number of individuals. We have also recorded asymmetry in the number of pores in the nasal portion of the supraorbital canal, and the infraorbital canal of *F. alleni*, and the infraorbital canal of *F. bolini* (see Description). We did not observe asymmetry in the number of pores associated with the cephalic lateral-line canal system in *F. akiko* or *F. cometes*, but this may be related to the small number of specimens of each available for examination.

***Comments on* Lepadichthys.**—In a recent molecular phylogenetic study of gobiesocids, *Lepadichthys* was identified as one of several non-monophyletic genera in need of taxonomic revision (Conway et al., 2020). As a first step towards this necessary revision, we have transferred two morphologically distinct species that have previously been considered members of *Lepadichthys* to our new genus *Flabellicauda*. We have taken this step because these two species (*F. akiko* and *F. bolini*) were inferred by Conway et al. (2020) to be more closely related to members of other diademichthyine genera than to other species of *Lepadichthys* (note that Conway et al.'s material of *F. bolini* actually represents *F. alleni*). *Lepadichthys*, as currently defined and adopting the taxonomic changes herein, now contains 12 species (viz. *L. bilineatus*, *L. caritus*, *L. coccinotaenia*, *L. conwayi*, *L. ctenion*, *L. erythraeus*, *L. frenatus* [type species], *L. lineatus*, *L. minor*, *L. misakius*, *L. sandaracatus*, and *L. trishula*), and the next step in the process of taxonomic revision will require us to assess: (1) whether these 12 species represent a monophyletic group or not; and (2) whether the morphological characters used to diagnose the genus in the last taxonomic revision (Briggs, 1955) are still useful for diagnosing this group or whether they need to be revised (as has been suggested previously; Fujiwara and Motomura, 2018). This work is currently underway, and to date we have examined material representing 11 of 12 valid species of the genus (all except for *L. bilineatus*; see Material Examined).

Based on our preliminary morphological observations, we have identified what we consider to represent a "core" group of eight species that exhibit all the morphological characters used to diagnose the genus in the last revision (see Briggs, 1955; Fujiwara et al., 2020). This core group includes *L. coccinotaenia*, *L. conwayi*, *L. ctenion*, *L. erythraeus*, *L. frenatus* (type species), *L. misakius*, *L. sandaracatus*, and *L. trishula*. In addition to the morphological characters listed by Briggs (1955), these eight species also exhibit a well-developed lateral-line canal along the preopercle (with three pores) and similar mouth features (oral cleft moderate, not covered by skin, and snout tip not strongly pointed or protracted; Fig. 1B, G). We have not examined material of *L. bilineatus* but suspect, based on information provided in the original description (Craig et al., 2015), that this species is also a member of our core group. Although there is some evidence from a recent molecular phylogenetic study to suggest that this core group of *Lepadichthys* (as defined herein) may not be monophyletic (because *L. misakius* and *L. trishula* were not recovered as a monophyletic group; see Conway et al., 2020), and although we have not identified any putative derived characteristics that would provide an additional line of evidence to group these nine taxa together, we tentatively consider this core group of *Lepadichthys* to be monophyletic for the time being.

We do not consider the remaining three species of *Lepadichthys* (*L. caritus*, *L. lineatus*, and *L. minor*) to belong to this core group outlined above because they do not exhibit all of the diagnostic characters of *Lepadichthys* proposed by Briggs (1955), and also lack the preopercular lateral-line canal. For example, *Lepadichthys lineatus* and *L.*

caritus do not exhibit the large circular opening between the premaxillae present in the core members of *Lepadichthys* (and also members of *Flabellicauda* and *Lepadicyathus*). As pointed out by previous authors (e.g., Hayashi and Hayashi, 1985; Craig and Randall, 2008), *L. lineatus* shares a number of features in common with the members of *Discotrema*, and is potentially more closely related to *Discotrema* than to the other members of *Lepadichthys* (as confirmed in the molecular phylogenetic study of Conway et al., 2020 in which *L. lineatus* is placed as a member of a clade that also includes *Diademichthys lineatus* and *Discotrema crinophilum*). *Lepadichthys minor* is known from relatively few specimens, but our preliminary observations of this miniature species (max recorded 21.8 mm SL) have revealed that it shares a number of characters in common with *Flabellicauda* and *Lepadicyathus* and is potentially more closely related to the members of these genera than to the members of the core group of *Lepadichthys*. Determination of the generic placement of these three 'outlier' species of *Lepadichthys* is beyond the scope of this paper but is forthcoming (K. Fujiwara, unpubl.).

MATERIAL EXAMINED

Acyrtus rubiginosus: UF 149202 (CS), 20.0 mm SL, St. Croix, US Virgin Islands.

Diademichthys lineatus: 20 specimens: AMS I. 17262-052, 33.8 mm SL, Papua New Guinea; AMS I. 19542-002, 40.1 mm SL, AMS I. 22128-031, 47.3 mm SL, Solomon Islands; AMS I. 21927-010, 42.0 mm SL, Philippines; AMS I. 21963-005, 32.7 mm SL, Northern Territory, Australia; AMS IB. 2319, 44.5 mm SL, MNHN 1883-0902, holotype, 36.6 mm SL, MNHN 1980-240, 56.0 mm SL, New Caledonia; KAUM-I. 16279, 52.7 mm SL, KAUM-I. 39315, 49.3 mm SL, KAUM-I. 47239, 44.0 mm SL, KAUM-I. 79654, 26.4 mm SL, KAUM-I. 79655, 45.7 mm SL, KAUM-I. 89579, 35.8 mm SL, KAUM-I. 89823, 39.9 mm SL, KAUM-I. 89840, 47.4 mm SL, Kyusyu, Japan; KAUM-I. 62531, 49.0 mm SL, KAUM-I. 79449, 30.8 mm SL, Ryukyu Islands, Japan; KAUM-I. 79911, 31.1 mm SL, Malaysia; ROM 65282 (CS), 35.6 mm SL, New Caledonia.

Discotrema crinophilum: 3 specimens: KAUM-I. 72122, 26.3 mm SL, YCM-P 14952 (CS), 15.8 mm SL, Ryukyu Islands, Japan; ROM 85350 (CS), 25.4 mm SL, Raja Ampat, Indonesia.

Gobiesox funebris: AMNH 5557 (CS), 46.7 mm SL, Baja California, Mexico.

Lepadichthys caritus: 2 specimens: ANSP 111853, paratype, 20.0 mm SL, USNM 247380, paratype, 14.6 mm SL, Seychelles.

Lepadichthys coccinotaenia: 60 specimens (including holotype) listed in Fujiwara et al. (2020).

Lepadichthys conwayi: 42 specimens (including holotype) listed in Fujiwara and Motomura (2020a).

Lepadichthys ctenion: 3 specimens: SMF 5431, holotype, 33.7 mm SL, SMF 5824, paratype, 37.2 mm SL, USNM 424446, 34.9 mm SL, Pakistan.

Lepadichthys erythraeus: 80 specimens: BMNH 1975.4.5.148, 20.1 mm SL, BPBM 18235, 2, 29.6–30.9 mm SL, BPBM 18362, 1 of 2, 34.4 mm SL, USNM 424443, 9, 25.2–40.1 mm SL, USNM 424445, 26 of 27, 14.9–29.5 mm SL, USNM 424447, 10, 19.7–30.7 mm SL, USNM 424450, 14, 16.4–28.4 mm SL, USNM 424451, 17, 17.0–31.1 mm SL, Red Sea.

Lepadichthys frenatus: 37 specimens (including lectotype and paralectotype) listed in Fujiwara and Motomura (2019a) plus AMS I. 27134-018 (CS), 30.3 mm SL, Middleton Reef, Australia.

Lepadichthys lineatus: 4 specimens: CAS 162701, holotype, 21.2 mm SL, Red Sea; KAUM-I. 128500, 22.0 mm SL, Kyusyu, Japan; SAIAB 9319, 2 (CS), 24.3–25.2 mm SL, South Africa.

Lepadichthys minor: 6 specimens: AMS IA. 832, paratype, 19.1 mm SL, Vanuatu; ANSP 51054, 2 paratypes, 17.0–20.8 mm SL, Samoa; BPBM 33610, 1 of 3, 21.8 mm SL, New Caledonia; KAUM-I. 70995, 18.2 mm SL, Ryukyu Islands, Japan; ROM 73449, 1 of 2 (CS), 13.4 mm SL, Vietnam.

Lepadichthys misakius: 83 specimens (including holotype) listed in Fujiwara and Motomura (2019a).

Lepadichthys sandaracatus: 18 specimens: AMS IB. 307, holotype, 33.2 mm SL, WAM P. 2136-001, 35.6 mm SL, WAM P. 26662-020, 4, 29.7–37.4 mm SL, WAM P. 27590-025, 2, 32.9–33.2 mm SL, WAM P. 27965-004, 2, 32.4–34.2 mm SL, WAM P. 28428-002, 6, 31.8–43.5 mm SL, WAM P. 31812-032, 12.5 mm SL, WAM P. 34441-001, 27.9 mm SL, Western Australia, Australia.

Lepadichthys trishula: 24 specimens (including holotype) listed in Fujiwara et al. (2020).

Lepadicyathus mendeleevi: 2 specimens: ZIN 53413, holotype, 13.5 mm SL, ZIN 53413a, paratype, 15.0 mm SL, Papua New Guinea.

Unguitrema nigrum: MNHN 2015-0142, paratype, 10.0 mm SL, Papua New Guinea.

DATA ACCESSIBILITY

 ZooBank publication urn:lsid:zoobank.org:pub:75772C30-CA0A-44D4-A619-2D2C0484CBC9.

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LITERATURE CITED

Allen, G. R., and M. V. Erdmann. 2012. Reef Fishes of the East Indies. Volumes I–III. Tropical Reef Research, Perth, Australia.

Briggs, J. C. 1955. A monograph of the clingfishes (order Xenopterygii). Stanford Ichthyological Bulletin 6:1–224.

Briggs, J. C. 1962. A new clingfish of the genus *Lepadichthys* from the New Hebrides. Copeia 1962:424–425.

Briggs, J. C. 1966. A new clingfish of the genus *Lepadichthys* from the Red Sea. Contribution to the Knowledge of the Red Sea 35:37–40.

Briggs, J. C. 1969a. A new species of *Lepadichthys* (Gobiesocidae) from the Seychelles, Indian Ocean. Copeia 1969: 464–466.

Briggs, J. C. 1969b. A new genus and species of clingfish (family Gobiesocidae) from the Bahama Islands. Copeia 1969:332–334.

Briggs, J. C. 1976. A new genus and species of clingfish from the western Pacific. Copeia 1976:339–341.

Briggs, J. C. 2001. New species of *Lepadichthys* from the Philippine Islands. Copeia 2001:499–500.

Briggs, J. C., and G. Link. 1963. New clingfishes of the genus *Lepadichthys* from the northern Indian Ocean and Red Sea (Pisces, Gobiesocidae). Senckenbergiana Biologica 44:101–105.

Conway, K. W., C. D. King, A. P. Summers, D. Kim, P. A. Hastings, G. I. Moore, S. P. Iglésias, M. V. Erdmann, C. C. Baldwin, G. Short, K. Fujiwara, T. Trnski, G. Voelker, and L. Rüber. 2020. Molecular phylogenetics of the clingfishes (Teleostei: Gobiesocidae)—implications for classification. Copeia 108:886–906.

Conway, K. W., G. I. Moore, and A. P. Summers. 2017b. A new genus and species of clingfish (Teleostei: Gobiesocidae) from Western Australia. Copeia 105:128–140.

Conway, K. W., G. I. Moore, and A. P. Summers. 2019. A new genus and two new species of miniature clingfishes from temperate southern Australia (Teleostei, Gobiesocidae). ZooKeys 864:35–65.

Conway, K. W., A. L. Stewart, and C. D. King. 2017a. A new species of the clingfish genus *Trachelochismus* from bay and estuarine areas of New Zealand (Teleostei: Gobiesocidae). Zootaxa 4319:531–549.

Conway, K. W., A. L. Stewart, and A. P. Summers. 2018a. A new genus and species of clingfish from the Rangitāhua Kermadec Islands of New Zealand (Teleostei, Gobiesocidae). ZooKeys 786:75–104.

Conway, K. W., A. L. Stewart, and A. P. Summers. 2018b. A new species of sea urchin associating clingfish of the genus *Dellichthys* from New Zealand (Teleostei, Gobiesocidae). ZooKeys 740:77–95.

Costa, W. J. E. M. 2012. The caudal skeleton of extant and fossil cyprinodontiform fishes (Teleostei: Atherinomorpha): comparative morphology and delimitation of phylogenetic characters. Vertebrate Zoology 62:161–180.

Craig, M. T., S. V. Bogorodsky, J. E. Randall, and A. O. Mal. 2015. *Lepadichthys bilineatus*, a new species of clingfish from Oman (Teleostei: Gobiesocidae), with a redescription of *Lepadichthys erythraeus* Briggs and Link from the Red Sea. Zootaxa 3990:113–122.

Craig, M. T., and J. E. Randall. 2008. Two new species of the Indo-Pacific clingfish genus *Discotrema* (Gobiesocidae). Copeia 2008:68–74.

Fraser, T. H. 1970. Two new species of the clingfish genus *Derilissus* (Gobiesocidae) from the western Atlantic. Copeia 1970:38–42.

Fricke, R. 2014. *Unguitrema nigrum*, a new genus and species of clingfish (Teleostei: Gobiesocidae) from Madang, Papua New Guinea. Journal of the Ocean Science Foundation 13:35–42.

Fricke, R., J. N. Chen, and W.-J. Chen. 2016. New case of lateral asymmetry in fishes: a new subfamily, genus and species of deep water clingfishes from Papua New Guinea, western Pacific Ocean. Comptes Rendus Biologies 340:47–62.

Fricke, R., W. N. Eschmeyer, and R. Van der Laan (Eds.). 2021. Eschmeyer's Catalog of Fishes: Genera, Species, References. https://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp. Electronic version accessed on 4 February 2021.

Fricke, R., and P. Wirtz. 2017. *Lecanogaster gorgoniphila*, a new species of clingfish (Teleostei: Gobiesocidae) from São Tomé and Principe, eastern Atlantic Ocean. Archipélago, Life and Marine Sciences 35:1–10.

Fricke, R., P. Wirtz, and A. Brito. 2015. *Diplecogaster tonstricula*, a new species of cleaning clingfish (Teleostei: Gobiesocidae) from the Canary Islands and Senegal, eastern Atlantic Ocean, with a review of the *Diplecogaster-ctenocrypta* species-group. Journal of Natural History 50:731–748.

Fujita, K. 1990. The Caudal Skeleton of Teleostean Fishes. Tokai University Press, Tokyo.

Fujiwara, K. 2019. Gobiesocidae, p. 327–329. *In*: Identification Guide to Fishes of the Amami Islands in the Ryukyu Archipelago, Japan. H. Motomura, K. Hagiwara, H. Senou, and M. Nakae (eds.). The Minaminippon Shimbun Kaihatsu Center, Kagoshima.

Fujiwara, K., K. Hagiwara, and H. Motomura. 2020. Redescription of *Lepadichthys coccinotaenia* Regan 1921 and description of *Lepadichthys trishula* sp. nov. from southern Japan (Gobiesocidae: Diademichthyinae). Ichthyological Research 67:422–438.

Fujiwara, K., and H. Motomura. 2018. Revised diagnosis and first Northern Hemisphere records of the rare clingfish *Lepadichthys akiko* (Gobiesocidae: Diademichthyinae). Species Diversity 23:87–93.

Fujiwara, K., and H. Motomura. 2019a. Validity of *Lepadichthys misakius* (Tanaka 1908) and redescription of *Lepadichthys frenatus* Waite 1904 (Gobiesocidae: Diademichthyinae). Zootaxa 4551:275–298.

Fujiwara, K., and H. Motomura. 2019b. A new species, *Propherallodus longipterus*, from the Philippines and redescription of *P. briggsi* Shiogaki and Dotsu 1983 (Gobiesocidae: Diplocrepinae). Ichthyological Research 66:35–48.

Fujiwara, K., and H. Motomura. 2020a. A new species of *Lepadichthys* from the Central South Pacific and comments on taxonomic status of *Lepadichthys springeri* Briggs, 2001 (Gobiesocidae). Copeia 108:833–846.

Fujiwara, K., and H. Motomura. 2020b. *Kopua minima* (Döderlein 1887), a senior synonym of *K. japonica* Moore, Hutchins and Okamoto 2012, and description of a new species of *Aspasma* (Gobiesocidae). Ichthyological Research 67:50–67.

Fujiwara, K., M. Okamoto, and H. Motomura. 2018. Review of the clingfish genus *Kopua* (Gobiesocidae: Trachelochisminae) in Japan, with description of a new species. Ichthyological Research 65:433–453.

Ghedotti, M. J. 2000. Phylogenetic analysis and taxonomy of the poecilioid fishes (Teleostei: Cyprinodontiformes). Zoological Journal of the Linnean Society 130:1–53.

Hanken, J., and D. B. Wake. 1993. Miniaturization of body size: organismal consequences and evolutionary significance. Annual Review of Ecology and Systematics 24:501–519.

Hastings, P. A., and K. W. Conway. 2017. *Gobiesox lanceolatus*, a new species of clingfish (Teleostei: Gobiesocidae) from Los Frailes submarine canyon, Gulf of California, Mexico. Zootaxa 4221:393–400.

Hayashi, M., K. Hagiwara, and H. Hayashi. 1986. Osteology of the cling fishes in Japan (family: Gobiesocidae). Science Report of the Yokosuka City Museum 34:39–66.

Hayashi, M., and H. Hayashi. 1985. Two new records of gobiesocid fishes from Japan, and the morphological study of their key characters. Science Report of the Yokosuka City Museum 33:49–67.

Konstantinidis, P., and K. W. Conway. 2010. The median-fin skeleton of the Eastern Atlantic and Mediterranean clingfishes *Lepadogaster lepadogaster* (Bonnaterre) and *Gouania wildenowi* (Risso) (Teleostei: Gobiesocidae). Journal of Morphology 271:215–224.

Loya, Y., K. A. Puglise, and T. Bridge (Eds.). 2019. Mesophotic Coral Ecosystems. Springer International Publishing AG, Cham.

Monod, T. 1968. Le complèxe urophore des poissons téléostéens. Mémoires de l'Institut Français d'Afrique Noire 81:1–705.

Parenti, L. R. 1981. A phylogenetic and biogeographic analysis of cyprinodontiform fishes (Teleostei, Atherinomorpha). Bulletin of the American Museum of Natural History 168:335–557.

Randall, J. E. 1995. Coastal Fishes of Oman. Crawford House Publishing Pty Ltd, Bathurst.

Randall, J. E. 2005. Reef and Shore Fishes of the South Pacific. New Caledonia to Tahiti and the Pitcairn Islands. University of Hawaii Press, Honolulu.

Randall, J. E., G. R. Allen, and R. C. Steene. 1990. Fishes of the Great Barrier Reef and Coral Sea. First edition. Crawford House Press, Bathurst.

Regan, C. T. 1921. Three new fishes from South Africa, collected by Mr. H. W. Bell Marley. Annals of the Durban Museum 3:1–2.

Sabaj, M. H. 2020. Codes for natural history collections in ichthyology and herpetology. Copeia 108:593–669.

Sakashita, H. 1992. Sexual dimorphism and food habits of the clingfish, *Diademichthys lineatus*, and its dependence on host sea urchin. Environmental Biology of Fishes 34:95–101.

Saruwatari, T., J. A. Lopez, and T. W. Pietsch. 1997. Cyanine Blue: a versatile and harmless stain for specimen observation. Copeia 1997:840–841.

Shiogaki, M., and Y. Dotsu. 1983. Two new genera and two new species of clingfishes from Japan, with comments on head sensory canals of the Gobiesocidae. Japanese Journal of Ichthyology 30:111–121.

Smith-Vaniz, W. F. 1971. Another new species of the clingfish genus *Derilissus* from the western Atlantic (Pisces: Gobiesocidae). Copeia 1971:291–294.

Sparks, J. S., and D. F. Gruber. 2012. A new mesophotic clingfish (Teleostei: Gobiesocidae) from the Bahamas. Copeia 2012:251–256.

Springer, V. G., and T. H. Fraser. 1976. Synonymy of the fish families Cheilobranchidae (Alabetidae) and Gobiesocidae, with descriptions of two new species of *Alabes*. Smithsonian Contributions to Zoology 234:1–23.

Taylor, W. R., and G. G. Van Dyke. 1985. Revised procedure for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium 9:107–119.

Thieme, P., P. Warth, and T. Moritz. 2021. Development of the caudal-fin skeleton reveals multiple convergent fusions within Atherinomorpha. Frontiers in Zoology 18:20.

Waite, E. R. 1904. Additions to the fish fauna of Lord Howe Island, no 4. Records of the Australian Museum 5:135–186.

Weitzman, S. H., and R. P. Vari. 1988. Miniaturization in South American freshwater fishes; an overview and discussion. Proceedings of the Biological Society of Washington 101:444–465.

Wessel, P., and W. H. F. Smith. 1996. A global, self-consistent, hierarchical, high-resolution shoreline database. Journal of Geophysical Research 101:8741–8743.

Whitley, G. P. 1943. Ichthyological descriptions and notes. Proceedings of the Linnean Society of New South Wales 68: 114–144.

Whitley, G. P. 1950. Clingfishes. Australian Museum Magazine 10:124–128.

Winterbottom, R., A. R. Emery, and E. Holm. 1989. An annotated checklist of the fishes of the Chagos Archipelago, central Indian Ocean. Royal Ontario Museum Life Science Contributions 145:1–226.