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Large populations of two new species of *Ophiambix* (Echinodermata, Ophiuroidea) discovered on Japanese hot vents and cold seeps

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Abstract. Two new species and two new occurrence records of the genus *Ophiambix* Lyman, 1880 (Echinodermata: Ophiuroidea), were found on hydrothermal vents at the Pacific coast of Japan. *Ophiambix kagutsuchi*, new species, is distinguished from other congeners in having small granules separated from each other on aboral surface of disc, flat teeth, second from oral-most arm spines being cylindrical and spiniform in shape, and one small and spiniform tentacle scale on each tentacle pore. *Ophiambix macrodonta*, new species, is distinguished from the other congeners in having small granules circularly arranged surrounding the periphery of disc scales on aboral surface of disc, flat teeth, second from oral-most arm spines being flat and leaf-like in shape, and one small and spiniform tentacle scale on each tentacle pore. Furthermore, *Ophiambix epicopus* Paterson & Baker, 1988, was recorded from Japan for the first time and another congener, *Ophiambix aculeatus* Lyman, 1880, was also collected. *Ophiambix kagutsuchi*, new species, and *Ophiambix macrodonta*, new species, were collected from deep-sea chemosynthetic environments. A tabular key to all six species of the genus *Ophiambix* is provided.

Key words. brittle star, endemism, new species, hydrothermal vent, Pacific Ocean

INTRODUCTION

Ophiuroidea (Echinodermata) contains the largest number of species within the Echinodermata and occurs in a great variety of marine habitats, such as muddy substrates, living infaunally in sediments, under rocks, in the interstices of sponges and hard corals, and on surfaces of various animals such as soft corals (Stöhr et al., 2012; Okanishi, 2016). They are globally one of the dominant deep-sea megafauna (Gage & Tyler, 1991), but diversity in chemosynthetic ecosystems such as hydrothermal vents and hydrocarbon seeps remains poorly understood. Since reports of ophiuroids from cold seeps by Hecker (1985), 10 species including *Ophiacantha longispina* Stöhr & Segonzac, 2005, *Ophiactis tyleri* Stöhr & Segonzac, 2005, *Ophienigma spinilimbatum* Stöhr & Segonzac, 2005, *Ophiocten centobi* Paterson, Tyler & Gage, 1982, *Ophioctenella acies* Tyler, Paterson, Sibuet, Guille, Murton & Segonzac, 1995, *Ophiolamina epraewas* Stöhr & Segonzac, 2006, *Ophiomitra spinea* Verrill, 1885, *Ophioplinthaca chelys* (Thomson, 1877), *Ophiotreta valenciennesi rufescens* (Koehler, 1896), and *Spinophiura jolliveti* Stöhr & Segonzac, 2006, have been collected from chemosynthetic ecosystems to date (Hecker, 1985; Stöhr & Segonzac, 2005, 2006). As our knowledge grows, we have gained better understanding of ophiuroids within these settings, and it appears ophiuroid diversity has likely been underestimated (Stöhr & Segonzac, 2005). In Japanese waters, surveys of ophiuroids recorded 346 species, which represent approximately three-quarters of the North Pacific Ocean ophiuroid fauna (Okanishi, 2016; Okanishi & Fujita, 2018a, 2018b). However, no ophiuroid species have been recorded from chemosynthetic habitats around Japan.

The enigmatic ophiuroid genus *Ophiambix* was originally erected by Lyman (1880) for the monotypic *Ophiambix aculeatus* Lyman, 1880, and was known from deep waters (146–5,315 m) of the Pacific and Atlantic Oceans (Lyman, 1880; H. L. Clark, 1911; Bartsch, 1983; Paterson, 1985; Paterson & Baker, 1988; Borrero-Perez et al., 2008). Out of the four species of *Ophiambix* currently considered to be valid, *O. aculeatus* Lyman, 1880, *O. devaneyi* Paterson, 1985, *O. epicopus* Paterson & Baker, 1988, and *O. meteoris* Bartsch, 1983, only *O. aculeatus* has been recorded from Japanese waters (Lyman, 1880).

Ophiambix has a characteristically flat body and their arms are well differentiated from the disc in a manner superficially similar to that of asteroids. The genus has been assigned to four families, Ophiomyxidae (see Lyman, 1880), Ophiactidae (see Meissner, 1901), Ophiacanthidae (see Matsumoto, 1917; Bartsch, 1983; Paterson, 1985), and Ophiuridae (see Paterson, 1985; Paterson & Baker, 1988; Borrero-Pérez et al.,

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2008). Recent phylogenomic studies show that *Ophiambix epicopus* forms a clade with *Ophiophrura* H. L. Clark, 1911, *Ophioplexa* Martynov, 2010, *Ophiomyces* Lyman, 1869, *Ophiotholia* Lyman, 1880, and *Ophiuroconis* Matsumoto, 1915, and the genus *Ophiambix* was suggested to be assigned to the newly re-established family Ophioscolecidae Lütken, 1869, but further data is required to confirm its exact systematic position (O'Hara et al., 2017).

In this study, we present new occurrence records of *O. epicopus* in Japanese waters and formally describe two new species of *Ophiambix* from chemosynthetic ecosystems in Japanese waters.

MATERIAL AND METHODS

Specimens used in this study were collected by the manned deep submergence vehicles (DSVs) SHINKAI 2000 and SHINKAI 6500, and the remotely operated vehicles (ROVs) DOLPHIN 3K and HYPER-DOLPHIN on-board R/Vs NATSUSHIMA and YOKOSUKA, or by beam trawling on R/V HAKUHO MARU and T/S TOYOSHIO MARU. Of the 453 specimens used in this study, 175 specimens of *Ophiambix kagutsuchi*, new species, were collected from hydrothermal vents (51 from Tarama Knoll, 64 from the Iheya North Original Site, Iheya North field, one from Izena Hole field, 24 from Hatoma Knoll field, and 4 from Dai-yon Yonaguni Knoll field) or from the surface of sunken woods (31 specimens from Ryukyu Trench), and 272 specimens of *Ophiambix macrodonta*, new species, were collected from a hydrocarbon seep (Kuroshima Knoll). Five specimens of *Ophiambix aculeatus* and one specimen of *Ophiambix epicopus* were collected by beam trawls and their microhabitats are thus unknown. All examined specimens were deposited in the National Museum of Nature and Science, Tsukuba, Japan (NSMT).

The holotypes and paratypes of the two new species were fixed in 99% ethanol. Two paratypes (NSMT E-13070 and NSMT E-13050) of *Ophiambix kagutsuchi*, new species, and the holotype (NSMT E-13059) and four paratypes (NSMT E-13060, NSMT E-13061, NSMT E-13064 and NSMT E-13068B) of *Ophiambix macrodonta*, new species, were partly dissected to observe their internal ossicles. For observation by scanning electron microscopy (SEM), the ossicles were isolated using domestic bleach (approximately 5% sodium hypochlorite solution), washed in deionised water, dried in air, and mounted on SEM stubs using double-sided conductive tape. The specimens prepared were examined with a Keyence VHX D510 (National Museum of Nature and Science) using the SEM mode, and a JEOL JSM-5510LV (Misaki Marine Biological Station, the University of Tokyo).

Morphological terminology used herein follows Hotchkiss & Glass (2012), Stöhr et al. (2012), and Okanishi & Fujita (2018a), and systematics follows O'Hara et al. (2018). Collection locality names for vents and seeps surveyed during deep-sea expeditions of Japan Agency for Marine-Earth Science and Technology (JAMSTEC) follow Nakajima et al. (2014).

TAXONOMY

Class Ophiuroidea Gray, 1840

Order Ophiacanthida incertae sedis

Genus *Ophiambix* Lyman, 1880
(New Japanese name: Kaede-kumohitode-zoku)

Type species. *Ophiambix aculeatus* Lyman, 1880

Ophiambix aculeatus Lyman, 1880
(New Japanese name: Togari-kaede-kumohitode)

Ophiambix aculeatus Lyman, 1880: 11, pl. 2(29–30); 1882: 235, pl. 27(10–12); H. L. Clark, 1911: 114; 1915: 222; Matsumoto, 1917: 101; Paterson & Baker, 1988: 1583–1584, figs. 1g–i, 2g, 4.
Ophiambyx aculeatus – Meissner, 1901: 927 (misspelling).

Material examined. NSMT E-9834, 1 specimen, ethanol, collected with ORE beam trawl of 4 m span by the R/V HAKUHO MARU, KH-88-04, St. SR75, east off Hachinohe, Aomori Prefecture, northeast of Japan, 40°45.70′N, 144°50.00′E–40°46.70′N, 144°50.60′E, 4,870–5,030 m, 4 October 1988. NSMT E-11906A (2 specimens, ethanol), NSMT E-11906B (1 specimen, ethanol), and NSMT E-11906C (1 specimen, dry), collected with ORE beam trawl of 4 m span by the R/V HAKUHO MARU, KH-05-01, St. RT-04, north slope of Ryukyu Trench, Okinawa Prefecture, southwest of Japan, 24°52.46′N, 127°25.90′E–24°51.73′N, 127°25.13′E, 4,466–4,634 m, 18 May 2005 (Fig. 1).

Distribution. Japan: east off Yakushima Island, north slope of Ryukyu Trench, east off Hachinohe (Lyman, 1880; H. L. Clark, 1911; present study); Republic of Fiji: Fiji Islands (Lyman, 1880); United States: off Puruawa Point, Hawaiian Islands (Lyman, 1880); New Zealand: off White Island (Paterson & Baker, 1988). Depth range 430–4,634 m.

Ophiambix epicopus Paterson & Baker, 1988
(New Japanese name: Sharin-kaede-kumohitode)

Ophiambix epicopus Paterson & Baker, 1988: 1589–1590, figs. 2a–d, h, i, 3g–i, 4.

Material examined. NSMT E-13035, 1 specimen, ethanol, collected with beam trawl by the T/S TOYOSHIO MARU, To-03, St. 11, north of Kuroshima Island, Kerama Island Group, Ryukyu Islands, Okinawa Prefecture, southwest of Japan, 26°19.18′N, 127°25.56′E, 596–606 m, 24 May 2003 (Fig. 1).

Distribution. Japan: north of Kuroshima Island, Kerama Islands (present study); New Zealand: northwest of Napier Island, Kermadec Islands (Paterson & Baker, 1988). Depth range 530–606 m. This is a new record of the present species from Japanese waters.

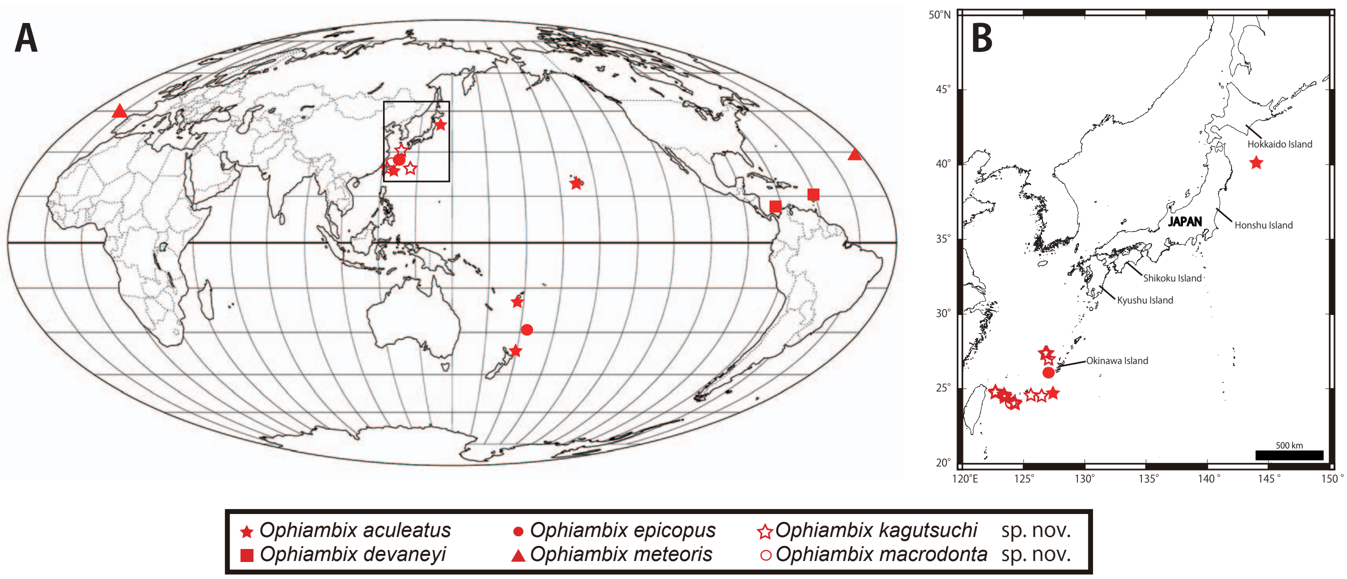

Fig. 1. A, known distribution of *Ophiambix aculeatus*, *O. devaneyi*, *O. epicopus*, *O. kagutsuchi*, new species, *O. macrodonta*, new species, and *O. meteoris*; B, enlarged area, sampling localities of examined specimens of *Ophiambix aculeatus*, *O. epicopus*, *O. kagutsuchi*, new species, and *O. macrodonta*, new species, in this study.

***Ophiambix kagutsuchi*, new species**
(New Japanese name: Kagutsuchi-kaede-kumohitode)
(Figs. 2–5)

Holotype. R/V YOKOSUKA, DSV SHINKAI 6500: NSMT E-13071, ethanol, collected with slurp gun, cruise YK17-17, Dive #1508, hydrothermal vent at Tarama Knoll (Yamanaka et al., 2015), Okinawa Trough, off Sakishima Island, Okinawa Prefecture, southwest of Japan, 25°05.4573′N, 124°32.7256′E, 1,730 m, 3 August 2017.

Paratypes. NSMT E-13072 (40 specimens, ethanol), NSMT E-13073 (2 specimens, ethanol), collected in the same locality as the holotype. NSMT E-13070 (1 specimen, ethanol), and NSMT E-13069 (7 specimens, ethanol), collected with slurp gun, cruise YK17-17, Dive #1509, hydrothermal vent at Tarama Knoll, Okinawa Trough, off Sakishima Island, Okinawa Prefecture, southwest of Japan, 25°05.4734′N, 124°32.6917′E, 1,979 m, 4 August 2017.

R/V NATSUSHIMA, ROV HYPER DOLPHIN: NSMT E-13036 (2 specimens, ethanol), collected with slurp gun, cruise NT11-20, Dive #1331, Hatoma Knoll field, Okinawa Trough, Sakishima Islands, Okinawa Prefecture, southwest of Japan, 24°51.477′N, 123°50.507′E, 1,477 m, 9 October 2011. NSMT E-13037 (1 specimen, ethanol), collected with slurp gun, cruise NT11-20, Dive #1329, Izena Hole field, off Okinawa Island, Okinawa Prefecture, southwest of Japan, 27°14.815′N, 127°04.089′E, 1,617 m, 5 October 2011. NSMT E-13038 (5 specimens, ethanol) and NSMT E-13039 (5 specimens, ethanol), collected with slurp gun, cruise NT10-07, Dive #1118, sunken wood at Ryukyu Trench, Sakishima Islands, Okinawa Prefecture, southwest of Japan, 24°57.186′N, 125°57.294′E, 276 m, 27 April 2010. NSMT E-13040 (3 specimens, ethanol), collected with slurp gun, cruise NT10-07, Dive #1114, sunken wood at Ryukyu Trench, Sakishima Islands, Okinawa Prefecture, southwest of Japan, 24°45.000′N, 126°44.982′E, 499 m, 22 April 2010. NSMT E-13041 (15 specimens, ethanol) and NSMT E-13042 (3 specimens, ethanol), collected with slurp gun, cruise NT09-10, Dive #1031, sunken wood at Ryukyu Trench, Sakishima Islands, Okinawa Prefecture, southwest of Japan, 24°57.186′N, 125°57.294′E, 276 m, 12 July 2009.

R/V NATSUSHIMA, DSV SHINKAI 2000: NSMT E-13043 (1 specimen, ethanol), collected with slurp gun, cruise NT02-07, Dive #1359, Hatoma Knoll field, Okinawa Trough, Sakishima Islands, Okinawa Prefecture, southwest of Japan, 24°51.596′N, 123°50.376′E, 1,469 m, 6 June 2002. NSMT E-13044 (6 specimens, ethanol), cruise NT02-07, Dive #1354, Hatoma Knoll field, Okinawa Trough, Sakishima Islands, Sakishima Islands, Okinawa Prefecture, southwest of Japan, 24°51.468′N, 123°50.497′E, 1,473 m, 29 May 2002. NSMT E-13045 (13 specimens, ethanol), collected with slurp gun, cruise NT01-05, Dive #1277, Hatoma Knoll field, Okinawa Trough, Sakishima Islands, Okinawa Prefecture, southwest of Japan, 24°51.649′N, 122°50.292′E, 1,497 m, 29 May 2001. NSMT E-13046 (3 specimens, ethanol), collected with manipulator, cruise NT01-05, Dive #1276, Dai-yon Yonaguni Knoll field, Okinawa Trough, Sakishima Islands, Okinawa Prefecture, southwest of Japan, 24°50.790′N, 122°42.090′E, 1,384 m, 28 May 2001. NSMT E-13047 (1 specimen, ethanol), collected with manipulator, cruise NT01-05, Dive #1276, Dai-yon Yonaguni Knoll field, Okinawa Trough, Sakishima Islands, Okinawa Prefecture, southwest of Japan, 24°50.666′N, 122°42.047′E, 1,386 m, 28 May 2001. NSMT E-13048 (1 specimen, ethanol), NT00-06, cruise Dive #1189, Hatoma Knoll field, Okinawa Trough, Sakishima Islands, Okinawa Prefecture, southwest of Japan, 24°51.402′N, 123°50.646′E, 1,468 m, 29 May 2000. NSMT E-13049 (1 specimen, ethanol), cruise NT00-06, Dive #1184, Hatoma Knoll field, Okinawa Trough, Sakishima Islands, Okinawa Prefecture, southwest of Japan, 24°51.229′N, 123°50.458′E, 1,523 m, 21 May 2000. NSMT E-13050 (1 specimen, ethanol), collected with slurp gun, cruise NT99-07, Dive #1094, Iheya North Original Site, Iheya North

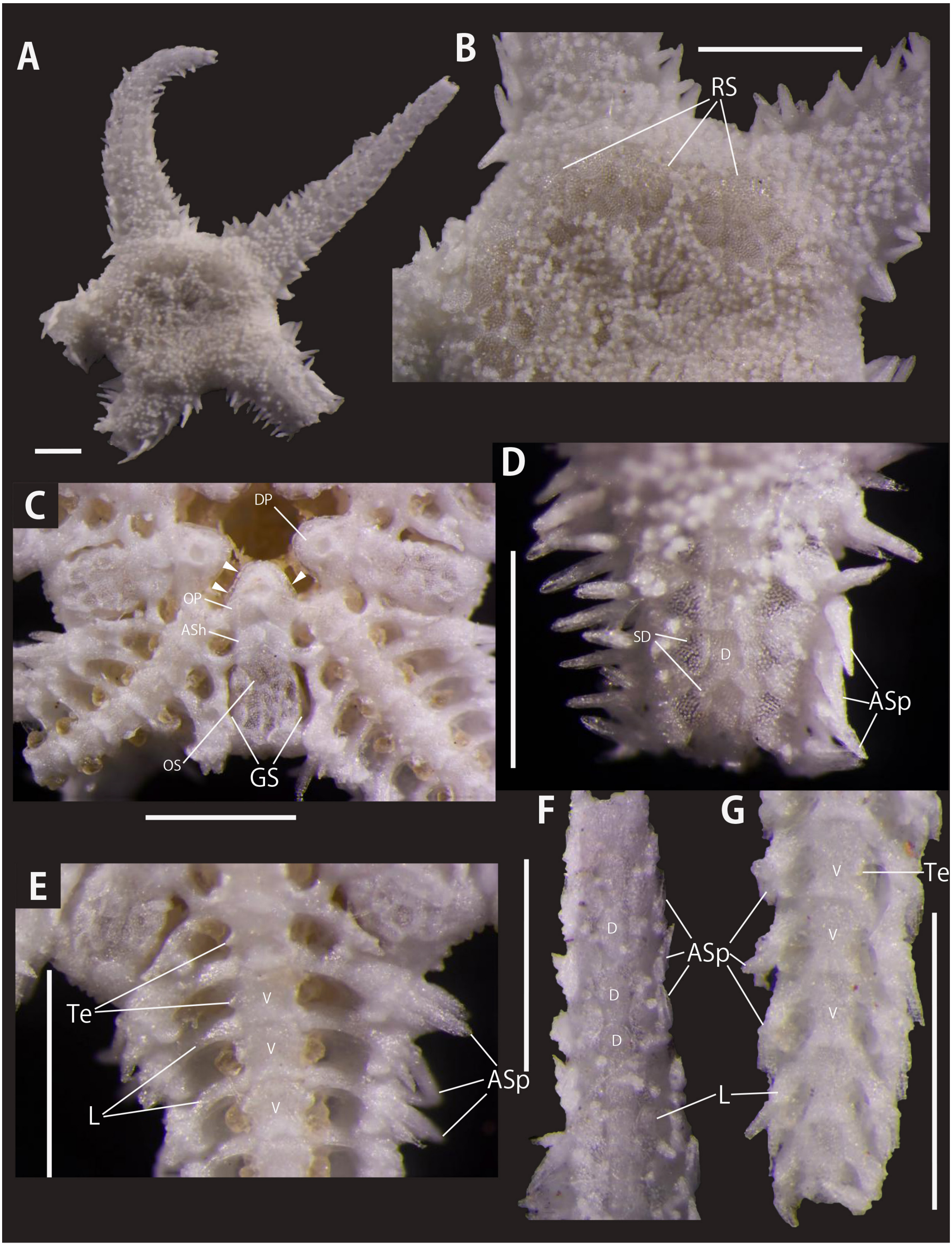

Fig. 2. *Ophiambix kagutsuchi*, new species, holotype (NSMT E-13071). A, aboral body; B, aboral disc and proximal portion of arm; C, oral disc and proximal portion of arms, arrow heads indicate oral papillae; D, proximal portion of aboral surface of arm; E, proximal portion of oral surface of arm; F, distal portion of aboral surface of arm; G, distal portion of oral surface of arm. Abbreviations: ASh, adoral shield; ASp, arm spine; D, dorsal arm plate; GS, genital slit; L, lateral arm plate; OP, oral plate; OS, oral shield; RS, radial shield; SD, supplementary dorsal plate; Te, tentacle scale; V, ventral arm plate. Scale bars = 1 mm.

field, Okinawa Trough, Okinawa Prefecture, southwest of Japan, 27°47.022′N, 126°54.000′E, 1,000 m, 8 May 1999. NSMT E-13051 (2 specimens, ethanol), NSMT E-13052 (1 specimen, ethanol), collected with slurp gun, cruise NT99-07, Dive #1094, Iheya North Original Site, Iheya North field, Okinawa Trough, Okinawa Prefecture, southwest of Japan, 27°47.262′N, 126°53.921′E, 990 m, 8 May 1999. NSMT E-13053 (2 specimens, ethanol), collected with manipulator, cruise NT99-07, Dive #1093, Iheya North Original Site, Iheya North field, Okinawa Trough, Okinawa Prefecture, southwest of Japan, 27°47.190′N, 126°54.133′E, 1,058 m, 7 May 1999. NSMT E-13054 (6 specimens, ethanol), cruise NT99-07, Dive #1092, Iheya North Original Site, Iheya North field, Okinawa Trough, Okinawa Prefecture, southwest of Japan, 27°47.220′N, 126°53.913′E, 968 m, 6 May 1999. NSMT E-13055 (46 specimens, ethanol), cruise N96-07, Dive No. #0863, Iheya North Original Site, Iheya North field, Okinawa Trough, Okinawa Prefecture, southwest of Japan, 27°47.178′N, 126°54.149′E, 1,049 m, 7 May 1996.

R/V NATSUSHIMA, ROV DOLPHIN 3K: NSMT E-13056 (6 specimens, ethanol), cruise NT98-08, Dive #0376, Iheya North Original Site, Iheya North field, Okinawa Trough, Okinawa Prefecture, southwest of Japan, 27°47.502′N, 126°54.000′E, 21 June 1998.

Diagnosis. Aboral disc as well as arms covered by small granules separated from each other. Second from oral-most arm spines on proximal portion of arm flattened and long. Teeth flattened and forming a horizontal row on oral-most edge of dental plate. Tentacle scales on each tentacle pore two in number, spiniform (width/length: 1/3–1/4), smaller than tentacle pore on proximal portion of the arm (Table 1).

Etymology. The species epithet "kagutsuchi" is named for Kagutsuchi, the Japanese god of fire in an ancient Japanese mythology, referring to the hot-vent habit of the new species. Noun held in apposition.

Description of holotype (NSMT E-13071). Disc. Pentagonal, 4 mm in diameter (Fig. 2A). Aboral surface covered by small granules of almost uniform size, separated from each other, approximately 50–70 μm in diameter (Fig. 2B). Removal of granules shows underlying plates are scalar, circular in outline, and imbricating, each approximately 250–350 μm in diameter (Fig. 2B). Radial shields triangular, distally wider, 350 μm in width, 350 μm in length and sharpen to centre (Fig. 2B), and completely concealed by the granules (Fig. 2B). On oral surface, adoral shields parallelogram-shaped, wider than long, approximately 250 μm in width, 120 μm in length (Fig. 2C), one overlapping the other. Oral plates trapezoidal, approximately 250 μm in width, 180 μm in length at radial edge, 250 μm in length at abradial edge, in contact with each other (Fig. 2C). Oral shields pentagonal, slightly rounded, with convex distal edge, approximately 360 μm in width, 60–260 μm in length (Fig. 2C). Interradial oral disc area narrow, covered by scales under thick skin, approximately 200–300 μm in length (Fig. 2C). Genital slits narrow, almost extending from edge of oral shield to two-thirds height of oral interradial disc, 0.1 mm width (Fig. 2C). Oral papillae and teeth rudimentary, very thin, narrow and flat ossicles, approximately 10 μm in length, forming a continuous horizontal row on oral edge of dental and oral plates (Fig. 2C). Teeth and oral papillae quite similar in shape but in this study and for descriptive purposes, the ossicles on top of the dental plate are called teeth and ossicles on oral edge of oral plate are called oral papillae. With the exception of the oral-most row of papillae, 6 to 7 thin and fan-shaped teeth forming vertical row on the dental plate. Second tentacle pore inside the mouth slit.

Arms. Five, one complete arm 5 mm long and other four arms have lost tips (Fig. 2A). 1.0 mm width and 0.5 mm height in proximal portion, elliptical in section. Arms tapering gradually toward the arm tip (Fig. 2A).

On proximally arm, aboral surface covered by small granules as those on aboral disc (Fig. 2D) decreasing in number and disappearing on arm tip (Fig. 2F). After removal of the granules, exposed dorsal arm plates oblong, longer than wide, proximal edge slightly wider than distal edge (Fig. 2D). A pair of fan-shaped supplementary dorsal arm plates on both lateral sides of each dorsal arm plate (Fig. 2D) and irregularly shaped smaller supplementary plates on distal side of dorsal arm plates separating them from each other (Fig. 2D). On middle portion of the arm, these supplementary plates disappear and dorsal arm plates are in contact, gradually decreasing in size toward the arm tip (Fig. 2F). Lateral arm plates thin, widely separated from each other throughout the arm (Fig. 2C, E, G). Tentacle pore forming large hole (Fig. 2C, E, G). On proximal portion of the arm, ventral arm plates almost square with concave distal edge (Fig. 2C, E) and toward the arm tip, becoming oblong, longer than wide with distal concave edge (Fig. 2G), contiguous throughout the arms (Fig. 2G). Three flat and pointed arm spines on proximal portion of arms, middle one longest, same length as corresponding arm segment, aboral-most half length of the middle spine, and the oral-most spine shortest, approximately one-fifth length of the middle spine (Fig. 2D). Arm spines decreasing in number to one toward arm tip, transforming into hook-shape, approximately the same length as the corresponding arm segment (Fig. 2F, G) (see detailed descriptions of each ossicle in next section). One small, rudimentary tentacle scale at each tentacle pore (Fig. 2E) although small, tentacle scales present on distal portion of arm (Fig. 2G).

Description of ossicle morphology (paratypes, NSMT E-13070 and NSMT E-13050). Vertebrae streptospondylous-like articulation with zagapophyses framing the water vascular canal on proximal side (Fig. 3B); large wing-like muscle flanges on oral-distal side (Fig. 3A, C); longitudinal groove on oral side (Fig. 3C); a pair of lateral ambulacral canals opening inside the oral groove (Fig. 3C); "T"-shaped groove on aboral side (Fig. 3D); narrow and thick, long "lateral shield" covering lateral-oral side (Fig. 3B, C), forming a large depression on oral fossae on proximal side (Fig. 3B).

Lateral arm plates longer than high, oblong (Fig. 3G) with thin leaf-like projection to inner side (Fig. 3E–G). On inner

Table 1. Tabular key to the species of the genus *Ophiambix*. Characters of *O. aculeatus*, *O. devaneyi*, *O. epicopus*, and *O. meteoris* are referred to Paterson & Baker (1988; Figs. 1–4). Abbreviations: lc, length of the corresponding arm segment; w/l, width/length.

Species	**Armaments of aboral disc**	**Armaments of proximal portion of aboral surface of arm**	**Shape and arrangement of teeth**	**Shape of the second from oral most arm spine**	**Number, size, and shape of tentacle scale**	**References and figures**
O. kagutsuchi, new species	Small granules, separated	Small granules, in contact	Flat, forming a horizontal row on the oral-most edge of dental plate	Slightly flat and long	One small (1/4–1/5 lc) and spiniform (w/l: 1/3–1/4)	This study, Figs. 2–5
O. macrodonta, new species	Small granules, arranged in a circle bordering each disc scale	No granules nor spines	Flat, forming a horizontal row on the oral-most edge of dental plate	Flat and leaf like	One small (1/4–1/5 lc) and spiniform (w/l: 1/3–1/4)	This study, Figs. 6–10
O. aculeatus Lyman, 1880	Spines	Small granules	Scattered on dental plate without forming a regular row	Cylindrical and spiniform	Three small (1/8 lc) and spiniform (w/l: 1/1)	Paterson & Baker (1988), figs. 1g–i, 2g, 4
O. devaneyi Paterson, 1985	Small granules, in contact	Small granules	Scattered on dental plate without forming a regular row	Flat and leaf like	Two large (2/3–1/2 lc) and spiniform (w/l: 1/3)	Paterson & Baker (1988), figs. 1a–c, 2e, 4
O. epicopus Paterson & Baker, 1988	Small granules, in contact	Small granules	Scattered on dental plate without forming a regular row	Flat and leaf like	One small (1/3 lc) and spiniform (w/l: 1/4)	Paterson & Baker (1988), figs. 2a–d, h, i, 3g–i, 4
O. meteoris Bartsch, 1983	Spines	Spines	Scattered on dental plate without forming a regular row	Cylindrical and spiniform	Four or five, large 1/2–1/3 lc and spiniform (w/l: 1/3–1/5)	Paterson & Baker (1988), figs. 1d–f, 2f, 4

side, one well-defined elevated structure, consisting of open meshed stereom, on aboral-proximal side (Fig. 3G). A single perforation opening on aboral-distal side (Fig. 3G). On external side, three spine articulations on oral-distal edge (Fig. 3E–G), composed of horizontal dorsal and ventral lobes, basically parallel but opening toward external side (Fig. 3E). Middle articulation the largest, aboral and oral ones slightly smaller than middle one (Fig. 3E). Ventral lobes slightly larger than dorsal lobes (Fig. 3E, F). Nerve and muscle openings between the lobes, separated by a bridge (Fig. 3E). Ventral arm plates basically oblong, longer than wide, concave on both lateral sides and distal side (Fig. 3H).

Arm spines flattened and pointed on proximal to middle portion of arms and on distal portion of the arm, transforming into hook with up to four secondary teeth (Fig. 3I, J).

Oral plates irregularly oblong, with notches for water ring canals and oral tentacles on aboral periphery part and oral central part, respectively (Fig. 4A, B). Depression for aboral tentacle located just below the notch for water ring canal (Fig. 4B). Abradial and adradial muscular attached area on middle portion of abradial side (Fig. 4A) and aboral central portion (Fig. 4B) of adradial side, respectively. A presumable depression for water ring canal on aboral central part of abradial side (Fig. 4A). Adradial genital plate “T”-shaped, distally wider, the length approximately two times longer than width (Fig. 4C, D). No distinctive articulation for radial shield (Fig. 4C, D). Radial shield triangular with round apexes, slightly pointing to centre part of the disc, with two slight depressions, indicating articulations for adradial genital plates at periphery of disc on inner side (Fig. 4E). Dental plate pyramid-shaped, facing its flat aspect to oral surface (Fig. 4F). No distinctive articulation for teeth recognisable for the dental plate (Fig. 4F).

Colour. Uniformly creamy white in alcohol. Living colour is unknown.

Distribution. Japan: hydrothermal vents in Okinawa Trough and sunken wood found in Ryukyu Trench, southwest of Japan. Depth range 276–1,979 m (Fig. 1).

Remarks. *Ophiambix kagutsuchi*, new species, can be distinguished from the other four congeners and *Ophiambix macrodonta*, new species, by: 1) armament of aboral body; 2) shape and arrangement of teeth; 3) shape of arm spine; 4) aboral disc covered by small granules arranged in circles surrounding the periphery of the disc scales, and absence of granules on the aboral arm surface; 5) teeth are flat, minute, forming a horizontal row on the oral-most edge of the dental plate; 6) second oral-most arm spines are flat and leaf-like; 7) number, size, and shape of tentacle scales (see also Table 1 and Remarks of *O. macrodonta*, new species, below).

The 175 examined specimens showed various developmental stages (0.8 to 3.2 mm in disc diameter), probably from juvenile to adult, but the diagnostic characters could be observed for all specimens.

Ophiambix macrodonta, new species

(New Japanese name: Ōba-kaede-kumohitode)
(Figs. 5–10)

Holotype. R/V NATSUSHIMA, ROV HYPER-DOLPHIN: NSMT E-13059 (1 specimen, dry), cruise NT04-03, Dive #0300, Kuroshima Knoll seep site, Ryukyu Islands, Sakishima Islands, Okinawa Prefecture, southwest of Japan, 24°07.822′N, 124°11.538′E, 638 m, 25 April 2004.

Paratypes. NSMT E-13060 (1 specimen, dry), NSMT E-13061 (1 specimen, dry), NSMT E-13062 (1 specimen, dry), NSMT E-13063 (1 specimen, dry), NSMT E-13064 (1 specimen, dry), NSMT E-13065 (1 specimen, ethanol), NSMT E-13058 (131 specimens, ethanol), NSMT E-13057 (108 specimens, ethanol), same locality as the holotype. NSMT E-13066 (6 specimens, ethanol), cruise NT04-03, Dive #0299, Kuroshima Knoll seep site, Ryukyu Islands, Sakishima Islands, Okinawa Prefecture, southwest of Japan, 24°07.833′N, 124°11.558′E, 641 m, 24 April 2004. NSMT E-13067 (12 specimens, ethanol), cruise NT04-03, Dive #290, Kuroshima Knoll seep site, Ryukyu Islands, Sakishima Islands, Okinawa Prefecture, southwest of Japan, 24°07.828′N, 124°11.56′E, 641 m, 13 April 2004.

R/V NATSUSHIMA, DOLPHIN 3K: NSMT E-13068A (7 specimens, ethanol), NSMT E-13068B (1 specimen, ethanol), collected with slurp gun, cruise NT02-07, Dive #0558, Kuroshima Knoll seep site, Ryukyu Islands, Sakishima Islands, Okinawa Prefecture, southwest of Japan, 24°07.812′N, 124°11.366′E, 644 m, 22 May 2002.

Diagnosis. Aboral disc covered by small granules in a circular arrangement around periphery of disc scales, but arms not covered by such granules. Arm spines on proximal portion of the arms flattened and leaf-like. Teeth flattened, plate-shaped and forming a horizontal row on oral-most edge of dental plate. Two tentacle scales on each tentacle pore, spiniform, conspicuously smaller than tentacle pore (width/length: 1/3–1/4) on proximal portion of arm (Table 1).

Etymology. The specific epithet “macrodonta” is a Latin adjective which means to have large teeth, referring to the flat, wide teeth of the new species.

Description of holotype (NSMT E-13059). Disc. Pentagonal, 6 mm in diameter (Figs. 5A, B, 6A). Aboral surface covered by polygonal scales, approximately 250–350 μm in diameter, arranged in mosaic (Figs. 5D, 6B). Each scale covered by small granules of uniform size, approximately 40–60 μm in diameter, in contact with each other and forming two or three circular rows on the periphery of each scale (Figs. 5D, 6B, C). Radial shields oval, 850 μm in length and 500 μm in width, almost completely concealed by granules except on the margins (Figs. 5D, 6B). Adoral shields curved, bar-like, wider than long, approximately 500 μm in length and 150 μm in width (Fig. 5F, G), separated from each other. Visible part of jaws trapezoid, approximately 500 μm in length and 250 μm in width, contiguous (Fig. 5G). Oral shields elliptical in shape, longer than wide, slightly acute on both adradial edges,

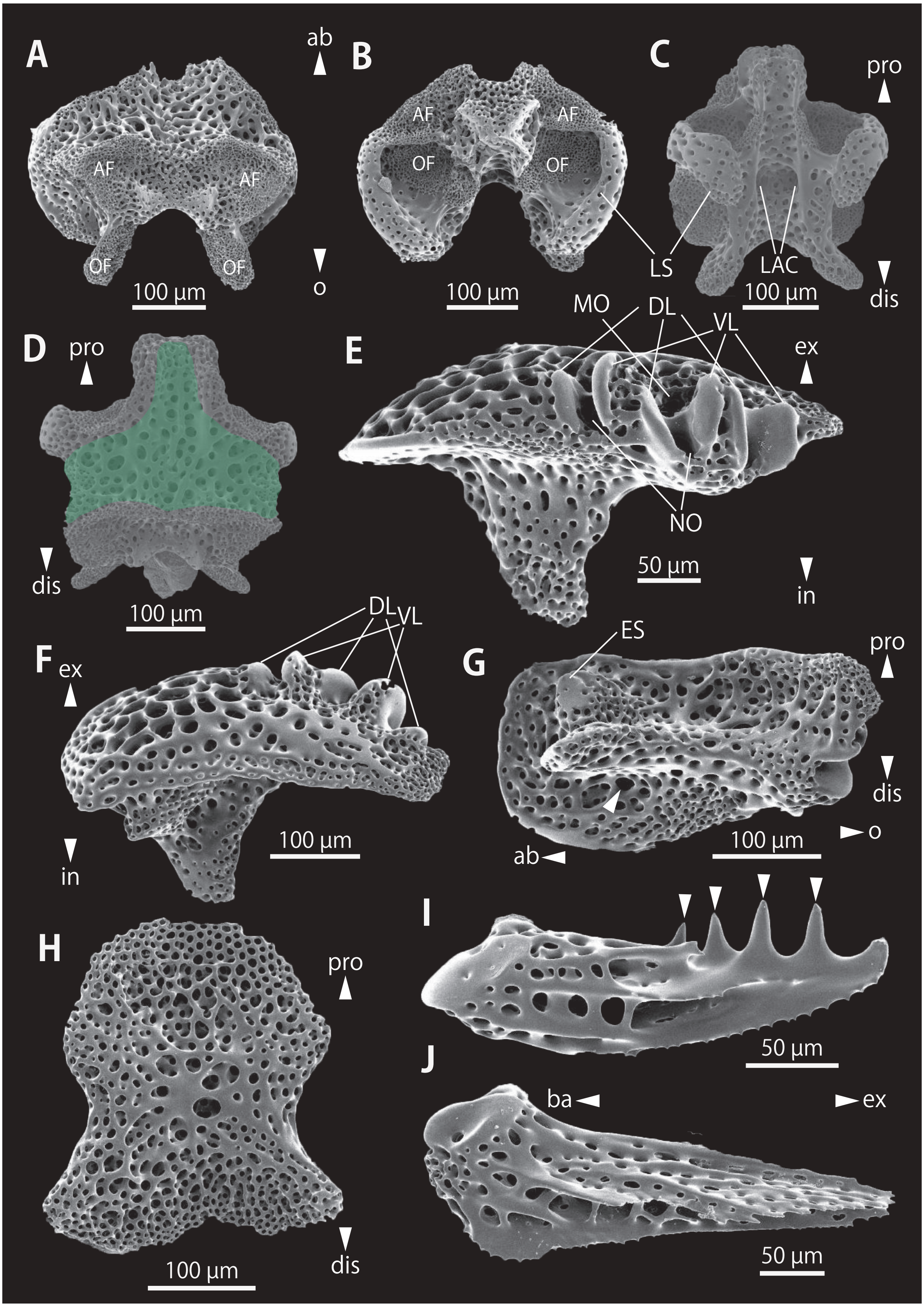

Fig. 3. *Ophiambix kagutsuchi*, new species, a paratype (NSMT E-13070), SEM images of ossicles. A–D, vertebrae from proximal portion of arm, distal view (A), proximal view (B), oral view (C), aboral view, green illustration indicates "T"-shaped groove (D); E–G, lateral arm plates from proximal portion of arms, oral view (E), adoral view (F), inner view (G) an arrow head indicates a perforation; H, ventral arm plates from proximal portion of arm, inner view; I, J, arm spines from distal (I) and proximal (J) portion of arm, arrow heads indicate secondary teeth. Orientations: ab, aboral side; ba, basal side; dis, distal side; ex, external side; in, inner side; o, oral side; pro, proximal side. Abbreviations: AF, aboral muscle fossae; DL, dorsal lobe; ES, elongated structure; LAC, lateral ambulacral canal; MO, muscle opening; NO, nerve opening; OF, oral muscle fossae; VL, ventral lobe.

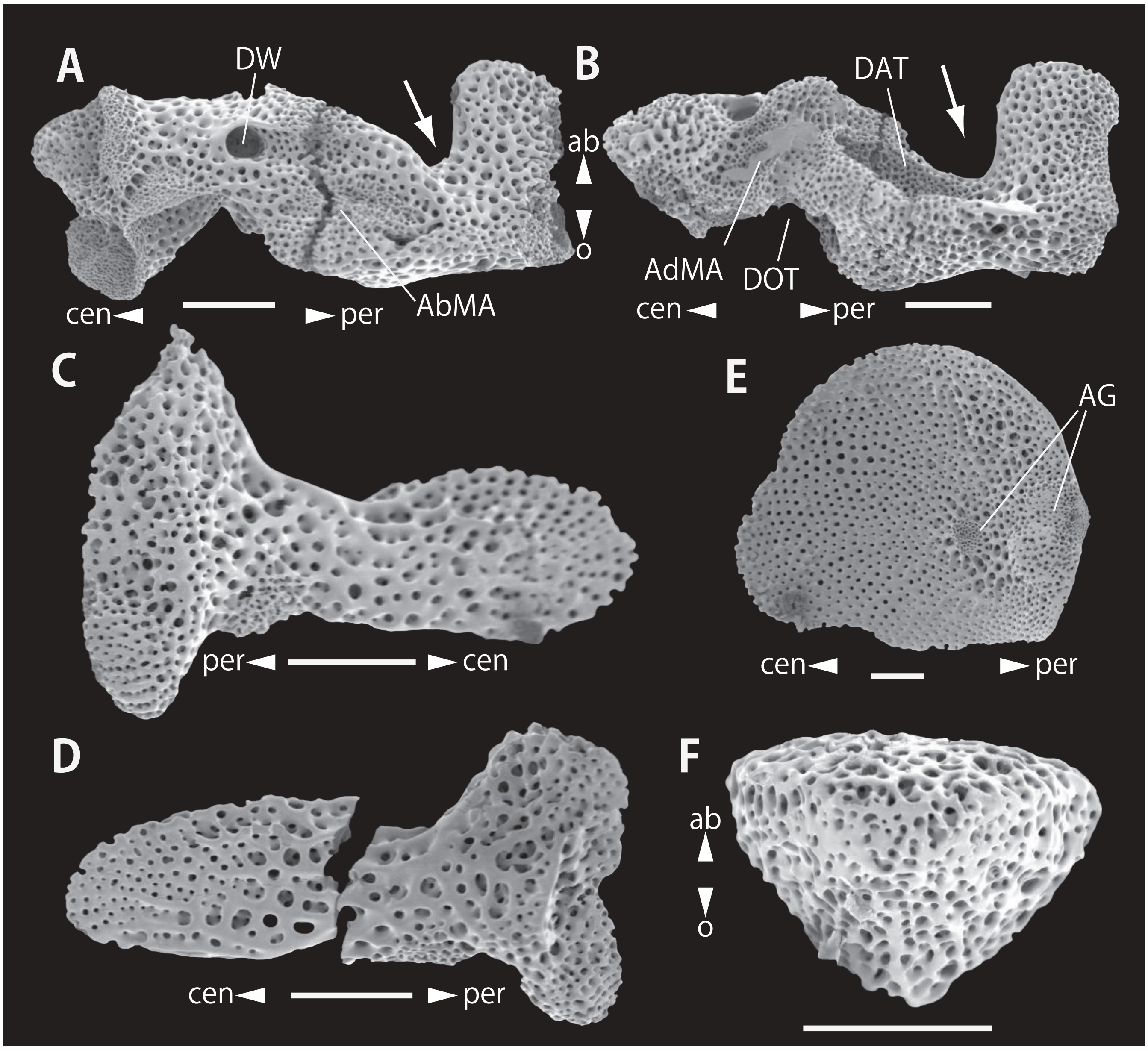

Fig. 4. *Ophiambix kagutsuchi*, new species, a paratype (NSMT E-13050), SEM images of ossicles. A, B, oral plates of abradial side (A) and adradial side (B), partly cracking, arrows indicate neural grooves; C, D, adradial genital plates, aboral view (C) and oral view, partly cracking (D); E, inner view of a radial shield; F, external view of a dental plate. Orientations: ab, aboral side; cen, centre of disc; o, oral side; per, periphery of disc. Abbreviations: AbMA, abradial muscle attachment area; AdMA, adradial muscle attachment area; AG, articulation for genital plate; DAT, depression for aboral tentacle; DOT, depression for oral tentacle; DW, presumable depression for water ring canal. Scale bars = 100 µm.

approximately 300 µm in length and 650 µm in width (Fig. 5G). Interradial oral disc area narrow, covered by polygonal and mosaic scales, approximately 200–300 µm in length as those on aboral disc (Figs. 5G, 6E). Genital slits long and wide, almost extending to the disc edge from distal edge of oral shield, 0.3 mm in width (Figs. 5F, G, 6E). Oral papillae and teeth rudimentary, very thin, narrow and flat ossicles, approximately 10 µm in width, forming a horizontal row on oral edge of dental plate and oral plate (Figs. 5H, 6E). Second tentacle pore inside the mouth slit (Figs. 5H, 6E).

Arms. Five, two complete arms 25 mm and 26 mm, while the other three arms have lost their tips. In proximal portion, 1.5 mm wide and 1 mm high, shape of section elliptical. Arms tapering gradually toward the arm tip.

Aboral surface covered by dorsal arm plates and supplementary dorsal arm plates, no granules (Figs. 6G, 7A). On proximal portion of the arm, dorsal arm plates semicircular, wider than long, proximal edge straight (Figs. 6G, 7A, B). One large, fan-shaped supplementary dorsal arm plate on both lateral sides of the dorsal arm plate (Figs. 6G, 7B). Three smaller, polygonal plates at distal edges of the dorsal arm plates and the two larger supplementary dorsal plates (Figs. 6G, 7A). Toward the arm tip, these supplementary plates decrease in size and gradually disappear with dorsal arm plates becoming contiguous (Fig. 7C). Lateral arm plates thin, widely separated throughout the arm (Figs. 5F, 7D, E). On proximal portion of the arm, ventral arm plates almost square, slightly concave lateral edges (Figs. 5E, 6H, 7D) and oblong. On distal portion of the arm, ventral arm plates longer than wide,

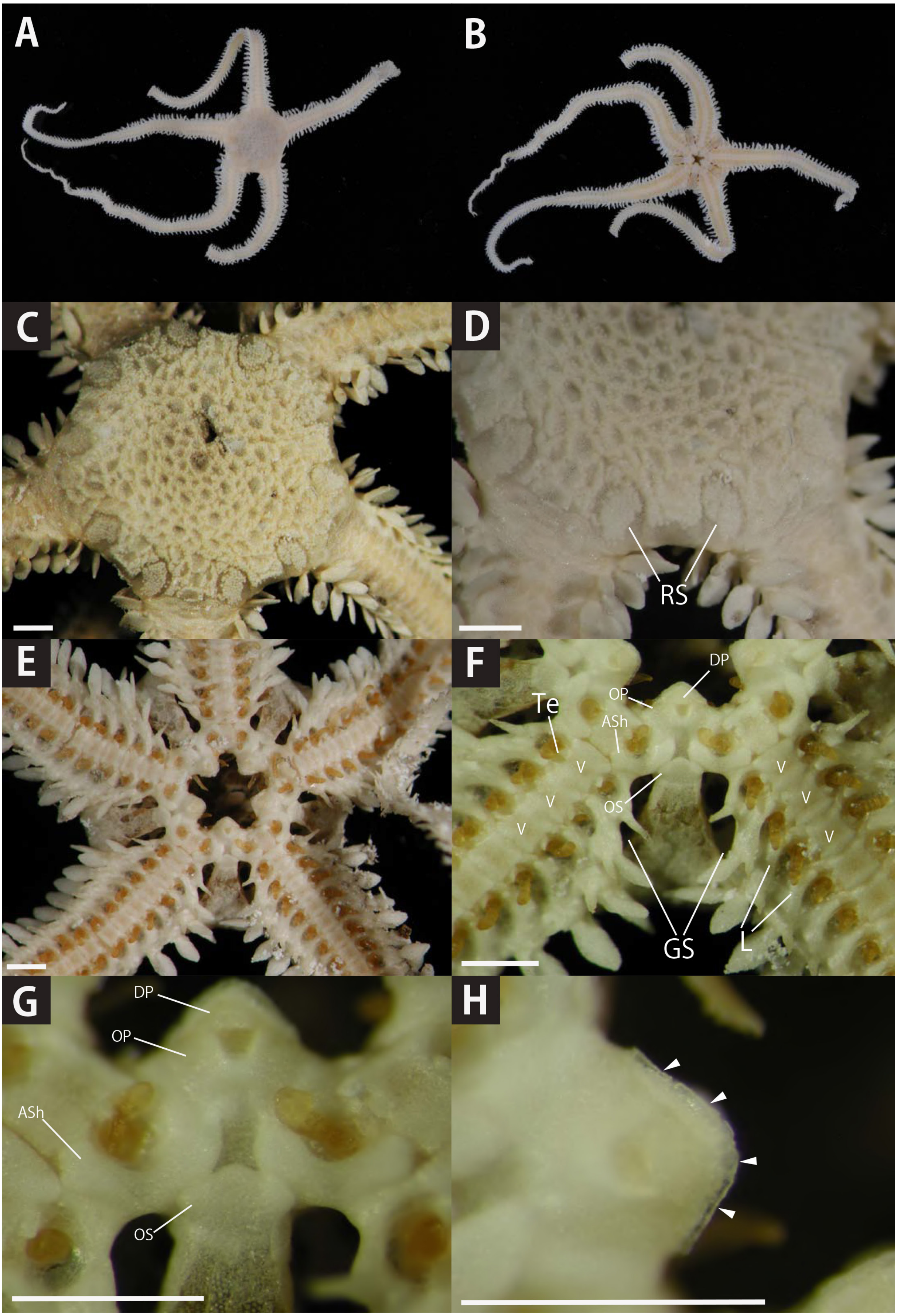

Fig. 5. *Ophiambix macrodonta*, new species, holotype (NSMT E-13059). A, aboral body; B, oral body; C, aboral disc and proximal portion of arm; D, aboral periphery of disc and proximal portion of arm; E, oral disc and proximal portion of arms; F, oral periphery of disc and proximal portion of arm; G, a jaw; H, top of a jaw, arrow heads indicate teeth and oral papillae. Abbreviations: ASh, adoral shield; DP, dental plate; GS, genital slit; L, lateral arm plate; OP, oral plate; OS, oral shield; RS, radial shield; Te, tentacle scale; V, ventral arm plate. Scale bars = 1 mm.

concave lateral edges more pronounced (Fig. 7E). Ventral arm plates contiguous throughout the arms. Three flat arm spines on proximal portion of arms, aboral-most and middle spines flat and leaf-like, and the oral-most spine cylindrical, narrow, and pointed (Figs. 6G, H, 7A, D). All three spines equal in length to corresponding arm segment (Figs. 6G, H, 7A, D). Toward the tip, the aboral-most and middle arm spines transforming into cylindrical and pointed shape, and oral-most one transforming into hook, approximately same length as corresponding arm segment (Fig. 7C, E, F) (see detailed descriptions of each ossicle in next section). One small, triangular tentacle scale at each tentacle pore (Fig. 7D), although small, tentacle scales present on distal portion of the arm (Fig. 7E).

Description of ossicle morphology of holotype (NSMT E-13059) and a paratype (NSMT E-13060, NSMT E-13061, NSMT E-13064, NSMT E-13068B). Vertebrae streptospondylous-like articulation with zagapophyses framing the water vascular canal on proximal side (Fig. 8A); with wing-like muscle flanges on oral-distal side (Fig. 8A–D); longitudinal groove on oral side and a pair of lateral ambulacral canals opening inside the groove (Fig. 8D); "T"-shaped groove on aboral side (Fig. 8C); narrow and thick, long lateral shield covering lateral-oral side (Fig. 8A–D), forming a large depression around oral fossae on proximal side (Fig. 8A). Adoral shield bar-like, boomerang-shaped, flaring to distal side (Fig. 8E, F). Adradial genital plates long and bar-like, slightly thinner on inner side, approximately five times longer than wide (Fig. 8G), having slit like articulation on external edge (Fig. 8H).

The first lateral arm plate oblong, wing-like, inner side wider than external side, tentacle notch distinctively concave on inner distal position (Fig. 9A). Excluding first lateral arm plate, lateral arm plates on proximal portion of arm oblong, but inner side thinner than external side (Fig. 9B). A perforation on centre of inner side (Fig. 9B). Three equally sized spine articulations on distal edge (Fig. 9C, D), composed of equally sized dorsal and ventral lobes that are horizontally parallel (Fig. 9C, D). Nerve and muscle openings between the lobes, separated by thin bridge (Fig. 9C). On middle portion of arm, lateral arm plates oblong (Fig. 8E) with thin leaf-like projection to proximal side (Fig. 9F, H). On oral side, one well-defined elevated structure on external side (Fig. 9E). The elevated structure with finer meshed stereom than surrounding area (Fig. 9E). No distinct perforation observed on inner side (Fig. 9E). Three spine articulations on distal edge (Fig. 9G, H), composed of horizontal dorsal and ventral lobes, generally parallel but opening toward external side (Fig. 9G). Aboral-most articulation largest, decreasing in size orally (Fig. 9G). Dorsal lobes basically larger than ventral lobes (Fig. 9G, H). Nerve and muscle openings between the lobes, separated by bridge (Fig. 9G, H). Granules on aboral side of the disc cone-shaped, having some dozen thorns on aboral side (Fig. 10A, B). On proximal portion of arm, aboral-most and middle arm spines flattened while oral-most spine cylindrical (Fig. 10C, D). On distal portion of arm, arm spines transforming into hook with maximum of three secondary teeth (Fig. 10E). Ventral arm plates oblong, longer than wide, slightly concave on both lateral and distal edges (Fig. 10F).

Oral plates irregularly oblong, with notches for water ring canals and oral tentacles on aboral periphery and oral central part, respectively (Fig. 10G, H). A depression for an aboral tentacle located just below the notch for water ring canal (Fig. 10H). Abradial and adradial muscular attached area on middle portion of abradial side (Fig. 10G) and central portion (Fig. 10H) of adradial side, respectively. A presumable depression for water ring canal on aboral central part of abradial side (Fig. 10G). Radial shield circular, slightly pointing to periphery of the disc, with two small and large depressions, indicating articulations for adradial genital plates at periphery of disc on inner side (Fig. 10I). Dental plate oval, stereom mesh more dense on aboral side than on oral side, without distinctive articulations for teeth (Fig. 10J).

Colour in life. Uniform creamy white colour, with brown tentacles (Fig. 6D).

Distribution. Japan: Only known from the hydrocarbon seep site on Kuroshima Knoll, southeast of Yaeyama Islands, Ryukyu Islands, southwest of Japan. Depth range 638–644 m (Fig. 1).

Remarks. *Ophiambix macrodonta*, new species, can be distinguished from the other four congeners and *Ophiambix kagutsuchi*, new species, described above, by the following four features (see also Table 1):

(1) Armament of aboral body. Aboral disc of *Ophiambix kagutsuchi*, new species, *O. devaneyi*, and *O. epicopus* are covered by small granules which are in contact with each other, whereas those of *O. aculeatus* and *O. meteoris* are covered by spines. *Ophiambix macrodonta*, new species, also possesses small granules circularly arranged to surround periphery of disc scales on aboral surface of disc. Aboral arms of *Ophiambix kagutsuchi*, new species, *O. aculeatus*, *O. devaneyi*, and *O. epicopus* are covered by small granules, whereas those of *O. meteoris* are covered by spines, and those of *O. macrodonta*, new species, are not covered by any granules or spines.

(2) Shape and arrangement of teeth. Teeth of *Ophiambix macrodonta*, new species, and *O. kagutsuchi*, new species, are flat, forming a horizontal row on the oral-most edge of the dental plate, but those of *O. aculeatus*, *O. devaneyi*, *O. epicopus*, and *O. meteoris* are spiniform, scattered on dental plate without forming a regular row.

(3) Shape of arm spine. The second from oral-most arm spines are flat and leaf-like in *Ophiambix devaneyi*, *O. epicopus*, and *O. macrodonta*, new species, slightly flat, but not leaf-like, and relatively long in *O. kagutsuchi*, new species, and cylindrical and spiniform in *O. aculeatus* and *O. meteoris*.

(4) Number, size, and shape of tentacle scales. *Ophiambix macrodonta*, new species, and *O. kagutsuchi*, new species, have one small (1/4–1/5 length of the corresponding arm

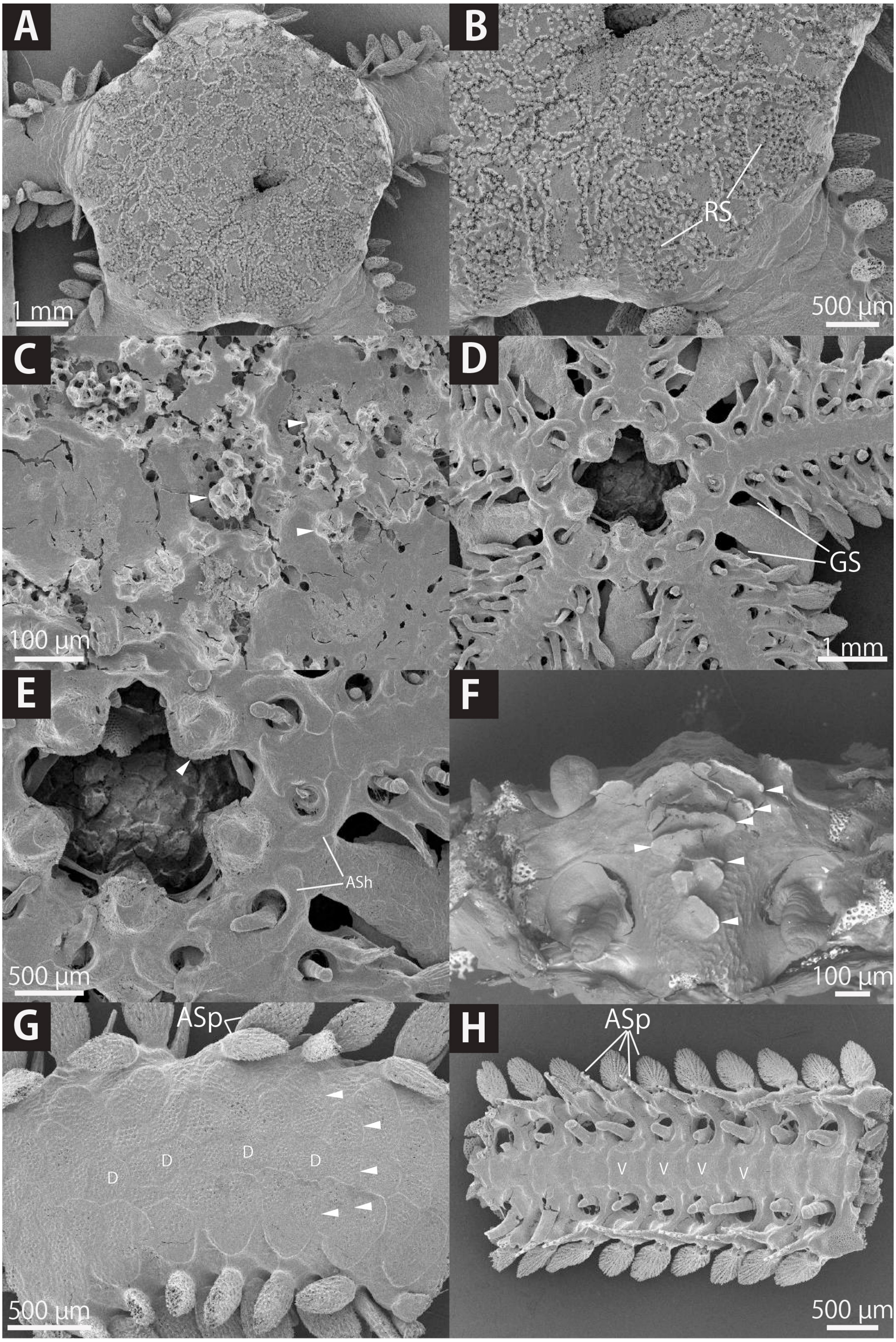

Fig. 6. *Ophiambix macrodonta*, new species, holotype (NSMT E-13059) (A–E, G, H) and a paratype (NSMT E-13060) (F), SEM images. A, aboral disc and proximal portion of arm; B, aboral periphery of disc and proximal portion of arm; C, granules (arrow heads) on aboral disc; D, oral disc and proximal portion of arms; E, jaws, an arrow head indicates teeth or oral papillae; F, a jaw from lateral view, arrow heads indicate teeth and oral papillae; G, proximal portion of aboral surface of arm, arrow heads indicate supplementary plates; H, proximal portion of oral surface of arm. Abbreviations: ASh, adoral shield; ASp, arm spine; D, dorsal arm plate; GS, genital slit; RS, radial shield; V, ventral arm plate.

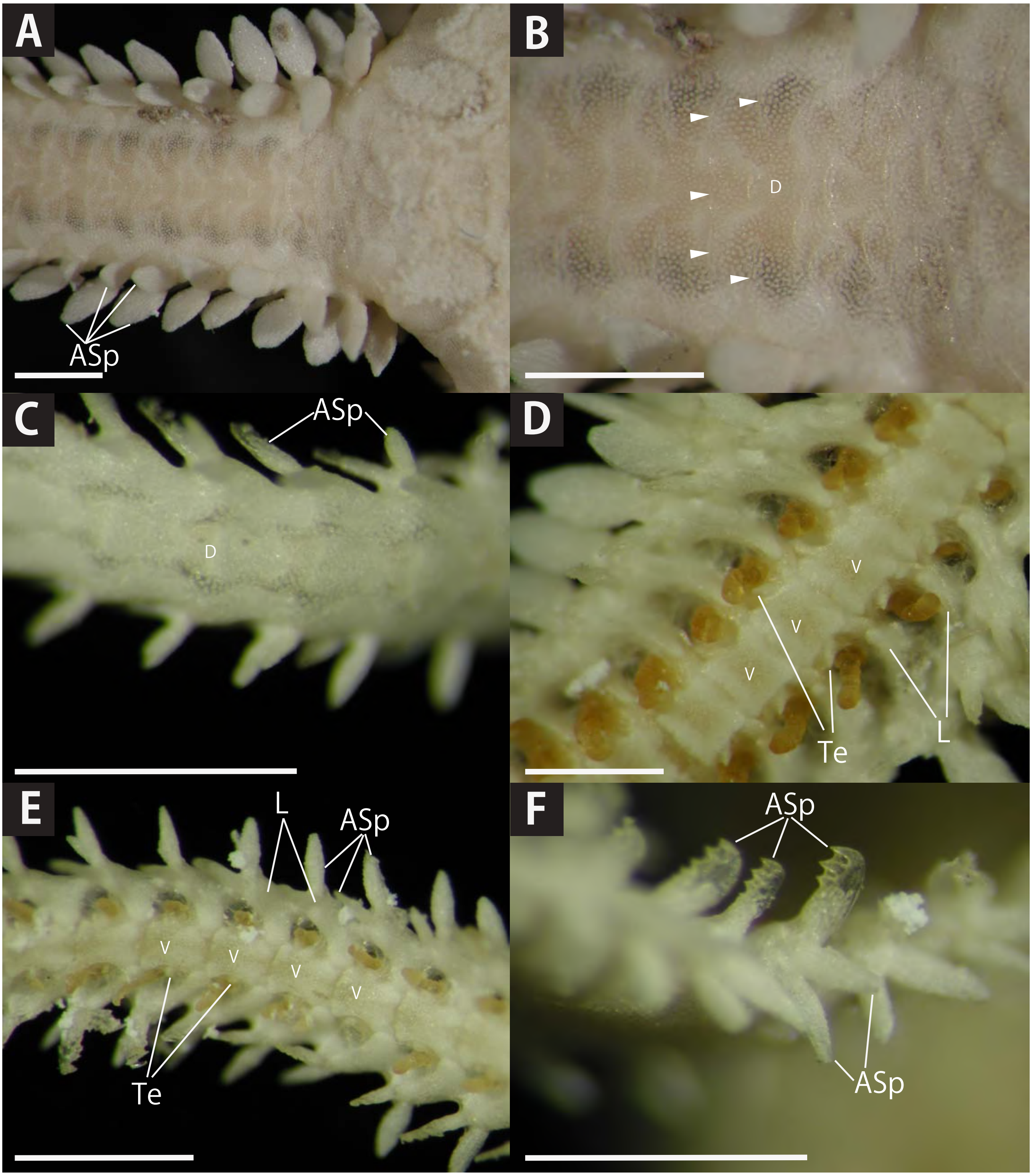

Fig. 7. *Ophiambix macrodonta*, new species, holotype (NSMT E-13059). A, proximal portion of aboral surface of arm, a part enlarged in (B), arrow heads indicate supplementary plates; C, distal portion of aboral surface of arm; D, proximal portion of oral surface of arm; E, distal portion of oral surface of arm; F, distal portion of lateral surface of arm. Abbreviations: ASp, arm spine; D, dorsal arm plate; L, lateral arm plate; Te, tentacle scale; V, ventral arm plate. Scale bars = 1 mm.

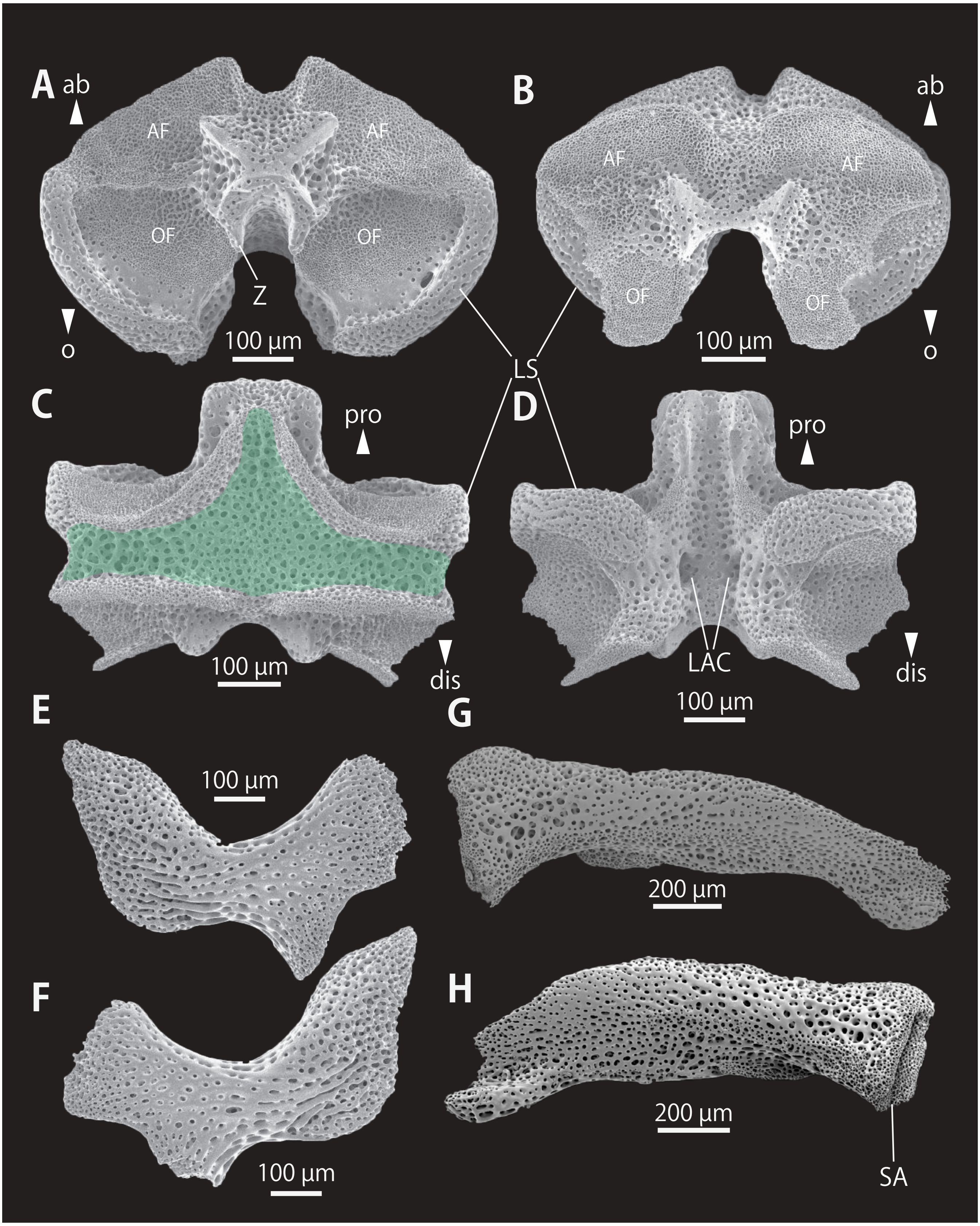

Fig. 8. *Ophiambix macrodonta*, new species, holotype (NSMT E-13059) (A–D), a paratype (NSMT E-13061) (E, F), and a paratype (NSMT E-13064) (G, H), SEM images of ossicles. A–D, vertebrae from proximal portion of arm, proximal view (A), distal view (B), aboral view, green indicates "T" shaped groove (C), oral view (D); E, F, a pair of adoral shields, oral views; G, H, adradial genital plate, aboral (G) and oral (H) views. Orientations: ab, aboral side; dis, distal side; o, oral side; pro, proximal side. Abbreviations: AF, aboral muscle fossae; LAC, lateral ambulacral canal; LS, lateral shield; OF, oral muscle fossae; SA, slit-like articulation; Z, zygapophyses.

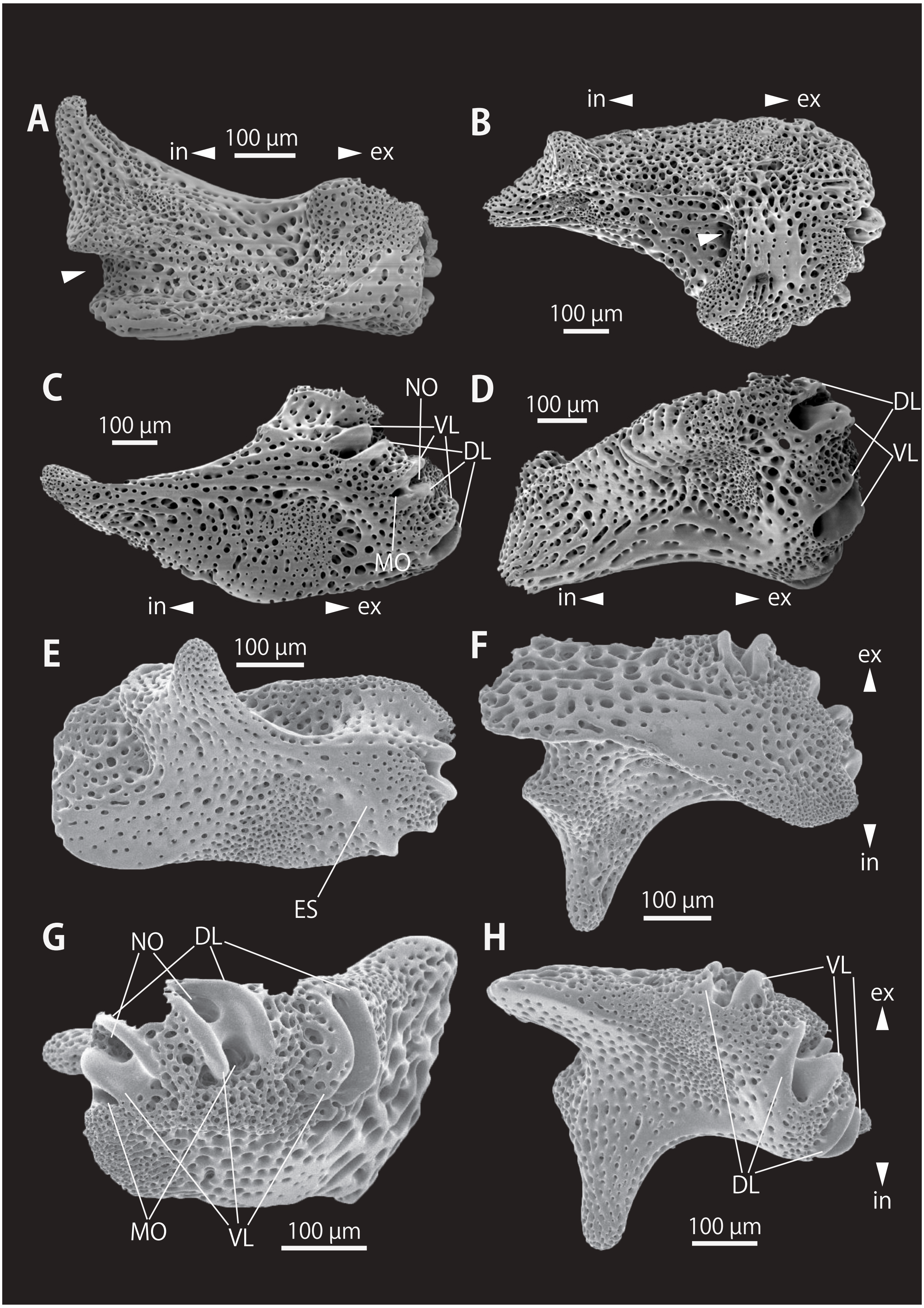

Fig. 9. *Ophiambix macrodonta*, new species, a paratype (NSMT E-13064) (A–D) and holotype (NSMT E-13059) (E–H), SEM images of ossicles. A, the first lateral arm plate, an arrow head indicates a tentacle notch; B–D, lateral arm plates from proximal portion of arms, inner view (B), an arrow head indicates a perforation (B), external view (C), and oral view (D); E–H, lateral arm plates from middle portion of arm, inner view (E), aboral view (F), external view (G), and oral view (H). Orientations: ex, external side; in, inner side. Abbreviations: DL, dorsal lobe; ES, elevated structure; MO, muscle opening; NO, nerve opening; VL, ventral lobe.

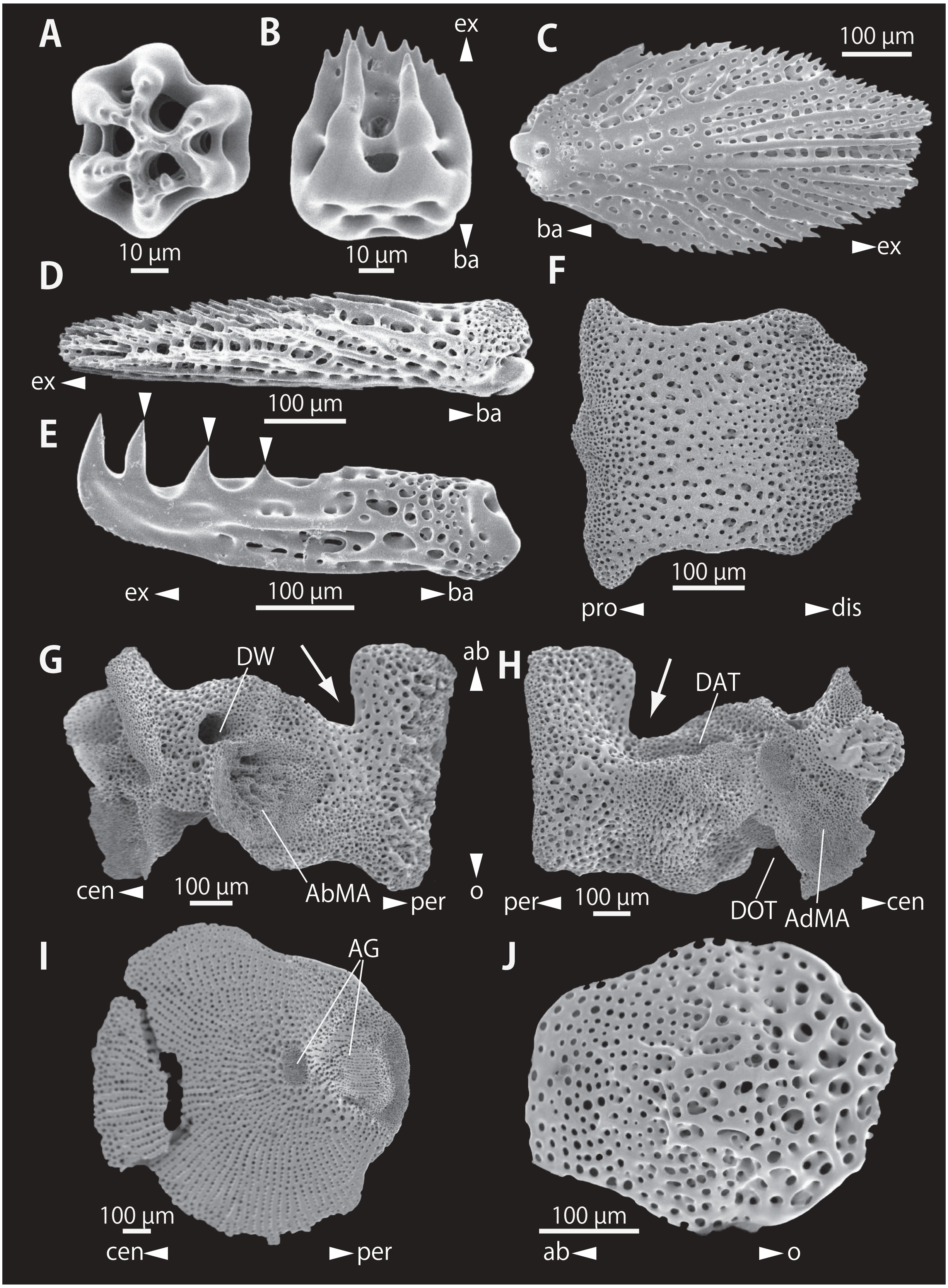

Fig. 10. *Ophiambix macrodonta*, new species, a paratype (NSMT E-13060) (A, B), holotype (NSMT E-13059) (C–F), and a paratype (NSMT E-13068B) (G–J), SEM images of ossicles. A, B, granules on aboral disc, external view (A) and lateral view (B); C–E, arm spines from proximal portion (C), middle portion (D), and distal portion of arm (E), arrow heads indicate secondary teeth; F, a ventral arm plate from proximal portion of arm, external side; G, H, oral plates of abradial side (G) and adradial side (H), arrows indicate neural grooves; I, inner view of a radial shield, partly broken; J, external view of a dental plate. Orientations: ab, aboral side; ba, basal side; cen, centre of disc; dis, distal side; ex, external side; per, periphery of disc; pro, proximal side. Abbreviations: AbMA, abradial muscle attachment area; AdMA, adradial muscle attachment area; AG, articulation for genital plate; DAT, depression for aboral tentacle; DOT, depression for oral tentacle; DW, presumable depression for water ring canal.

segment), spiniform (width/length: 1/3–1/4) tentacle scale, *O. epicopus* has one small (1/3 length of the corresponding arm segment), spiniform (width/length: 1/4) tentacle scale, *O. devaneyi* has two large (2/3–1/2 length of the arm segment), spiniform (width/length: 1/3) tentacle scales, *O. meteoris* has four or five, large (1/2–1/3 length of the arm segment), spiniform (width/length: 1/3–1/5) tentacle scales, and *O. aculeatus* has three small (approximately 1/8 length of the arm segment), spiniform (width/length: 1/1) tentacle scales on each tentacle pore on proximal portion of arm.

DISCUSSION

The difference in body size of the two new species *Ophiambix macrodonta* (3.3 to 7.0 mm in disc diameter) and *O. kagutsuchi* (0.8 to 3.2 mm in disc diameter) suggests that these could be interpreted as different sizes of the same species. However, the smallest specimen of *O. macrodonta*, new species (3.3 mm in disc diameter), and the largest specimen of *O. kagutsuchi*, new species (3.2 mm in disc diameter), were similar in size but exhibited the full set of respective diagnostic characters. All examined specimens of *O. kagutsuchi*, new species, were collected from hydrothermal vents or sunken wood environments, whereas those of *O. macrodonta*, new species, were collected only from hydrocarbon seeps. Therefore, we consider that these two taxa are indeed separate new species that can be distinguished from each other by morphological characters and by different environmental preferences.

The two new species are clearly distinguished morphologically from the previously described congeners. *Ophiambix kagutsuchi*, new species, and *O. macrodonta*, new species, have flat and wide teeth on the oral-most edge of the dental plates (Figs. 2C, 4H), whereas *O. aculeatus*, *O. devaneyi*, *O. epicopus*, and *O. meteoris* have spiniform teeth which are scattered on top of the oral plates (see Paterson & Baker, 1988). This distinct morphological difference suggests that species of *Ophiambix* may be divided into two species groups based on the shape of the teeth.

Since all specimens of the new species were collected from chemosynthetic environments, we consider them to be endemics of such environments. Although the exact habitat preferences of the other four species are unknown (Lyman, 1880; H. L. Clark, 1911; Bartsch, 1983; Paterson, 1985; Paterson & Baker, 1988; Borrero-Perez et al., 2008), the previous collection localities of *Ophiambix* were close to the highest parts of major submarine ridges in the world, where geothermal activities facilitating chemosynthetic ecosystems are likely to occur (Fig. 1). This geographical and ecological evidence suggests that *Ophiambix* may be a genus endemic to chemosynthetic environments. To ascertain this and better understand the habitat preferences of *Ophiambix*, however, further sampling is required.

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