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A new genus and two new species of asteroid-associated Polynoidae (Annelida: Polychaeta: Macellicephalinae) from the deep Indo-West Pacific

Cheah Hoay **Chuar**[1*], Natsumi **Hookabe**[2], Yoshihiro **Fujiwara**[3], Iffah **Iesa**[1], Itaru **Kobayashi**[4], Dongsheng **Zhang**[5,6] & Naoto **Jimi**[7,8]

Abstract. Two new species of asteroid-associated polychaete (Polynoidae: Macellicephalinae) belonging to a new genus were collected during deep-sea expeditions in the western Pacific and eastern Indian Ocean. *Ovatocirra*, new genus, is distinguished from other Macellicephalinae genera by the following combination of characters: 18–22 body segments; median antenna present; lateral antennae and frontal filament absent; pharynx with numerous papillae and lacking jaws; 9–10 pairs of elytra, smooth or with uneven texture on exposed, non-overlapping surfaces; and ovate to subovate ventral cirri from segment 3 onward. *Ovatocirra flavida*, new species, and *Ovatocirra shinkaiae*, new species, are distinguished based on morphology and molecular data from three genetic markers (COI, 16S, and 18S). In addition, *Macellicephala grimaldii* is transferred to *Ovatocirra* as *Ovatocirra grimaldii* (Fauvel, 1913), new combination. This study contributes to the knowledge of the biodiversity and biogeography of deep-water asteroid-associated polychaetes in the Indo-West Pacific, highlighting the importance of continued exploration and taxonomic research in these regions.

Key words. deep sea, commensal, scale worm, asteroids, taxonomy

INTRODUCTION

Polynoidae Kinberg, 1856 is one the most speciose polychaete families, comprising approximately 900 species (Read & Fauchald, 2026). Members of this family are widely distributed, inhabiting environments ranging from shallow intertidal waters to deep hadal trenches. They are also found in extreme marine habitats, such as anchialine caves and deep-sea chemosynthetic-based ecosystems (methane seeps, hydrothermal vents, and organic falls) (Gonzalez et al., 2025; Hiley et al., 2025). Currently, eight polynoid subfamilies are accepted (Read & Fauchald, 2026), most of which are primarily composed of shallow-water species. The exception is the Macellicephalinae, a diverse group of deep-sea scaleworms containing 146 species across 41 genera (Gonzalez et al., 2025; Read & Fauchald, 2026).

Polynoids are also the most diverse polychaete family in terms of symbiotic relationships with other invertebrates, with many species reported as symbionts, predominantly commensal or mutualistic, though a few are parasitic (Martin & Britayev, 1998, 2018). Many commensal polynoids are associated with echinoderms, most commonly asteroid sea stars, but they also interact with a wide range of hosts, including cnidarians, polychaetes, crustaceans, poriferans, molluscs, and others (Martin & Britayev, 1998, 2018; Molodtsova et al., 2016).

Commensal polynoids often exhibit morphological adaptations that facilitate their associations with hosts. These adaptations include cryptic colourations matching the body colour of their hosts (Di Camillo et al., 2011; Sugiyama et al., 2026), swollen antennae and cirri or elytra with prominent macrotubercles that mimic the body surface of their echinoderm hosts (Hanley, 1989; Ruff, 1991; Britayev & Fauchald, 2005; Jimi et al., 2025); ventral sucker-like lobes (Gibbs, 1969; Britayev & Zamishliak, 1996) or modified hooked neurochaetae (Pettibone, 1969; Ruff, 1991; Taboada et al., 2020), both hypothesised to facilitate attachment to their hosts.

Accepted by: Lim Swee Cheng

[1]St. John's Island National Marine Laboratory, Tropical Marine Science Institute, National University of Singapore, 18 Kent Ridge Road, 119227, Singapore; E-mail: tmscch@nus.edu.sg (*corresponding author)

[2]Institute for Extra-cutting-edge Science and Technology Avant-garde Research of Life (X-Star), Japan Agency for Marine-Earth Science and Technology (JAMSTEC), Yokosuka, Kanagawa 237 − 0061, Japan.

[3]Research Institute for Marine Technology & Engineering, JAMSTEC, Yokosuka, Kanagawa 237 − 0061, Japan.

[4]Research Center for Inland Seas, Kobe University, Awaji, Hyogo, 656-2401, Japan.

[5]State Key Laboratory of Submarine Geoscience, Second Institute of Oceanography, Ministry of Natural Resources, Hangzhou, China.

[6]School of Oceanography, Shanghai Jiao Tong University, Shanghai 200030, China.

[7]Sugashima Marine Biological Laboratory, Graduate School of Science, Nagoya University, 429-63 Sugashima, Toba, Mie 517-0004, Japan.

[8]Centre for Marine & Coastal Studies, Universiti Sains Malaysia 11800 USM, Penang, Malaysia.

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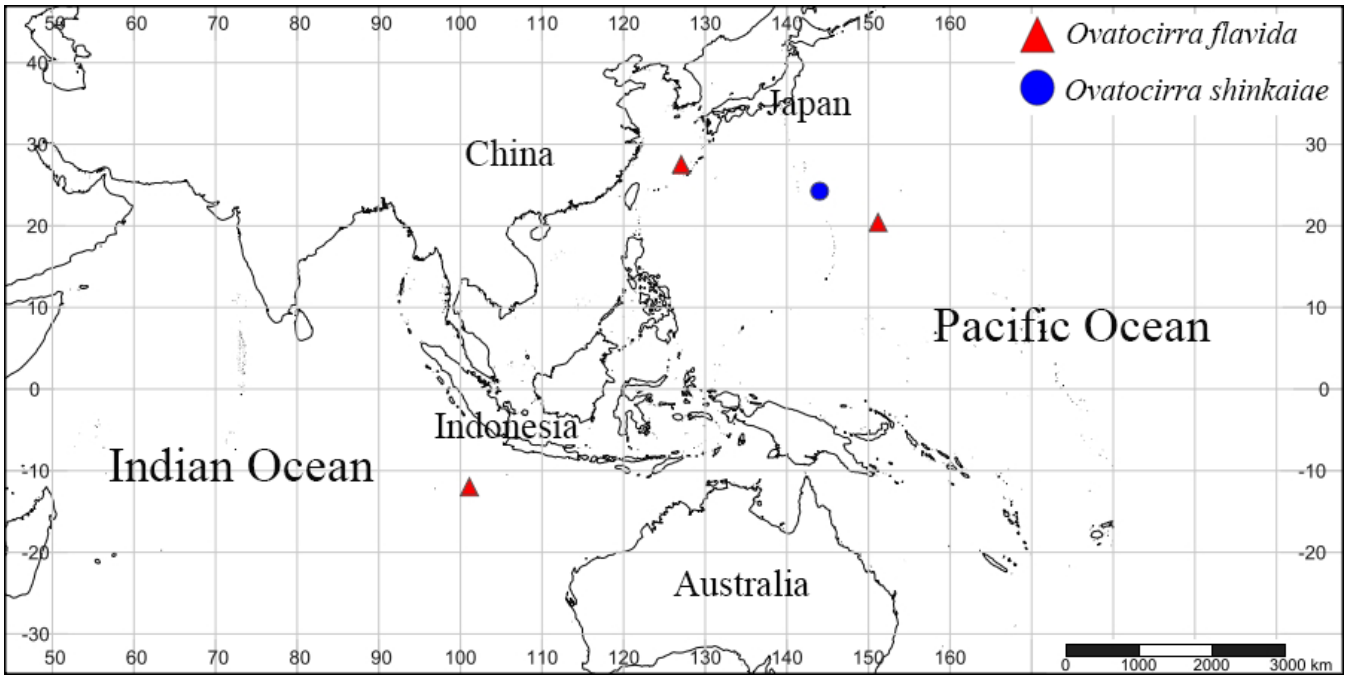

Fig. 1. Geographic distribution of *Ovatocirra flavida*, new genus and species, and *Ovatocirra shinkaiae*, new genus and species, in the Indo-west Pacific region. Map created using SimpleMappr, with modifications using Adobe Photoshop 27.4.0.

Recent deep-sea expeditions to the western Pacific and eastern Indian Ocean have collected polynoids commensal with different species of asteroid sea stars. By using advanced sampling equipment, including human-occupied vehicles (HOV) and remotely operated vehicles (ROV), these expeditions have yielded intact specimens enabling new insights into the morphology, phylogeny, and ecology of these deep-sea commensal polynoids. Integrating morphological evidence with molecular data (COI, 16S, and 18S), this study describes a new genus and two new species. Additionally, a species previously placed in *Macellicephala* M'Intosh, 1885 is re-assigned to this new genus.

MATERIAL AND METHODS

Sample collection. Samples were collected from deep-water seamounts and trench-associated habitats during four expeditions: three in the western Pacific and one in the eastern Indian Ocean (Fig. 1). Western Pacific material was obtained during Cruise YK23-16S (September 2023), the Digital Deep-sea Typical Habitats International Cruise DY86-II (August–September 2024; Digital DEPTH Programme, 2024), and Cruise YK24-15C (October 2024). Eastern Indian Ocean material was collected during the National University of Singapore–OceanX Expedition (NUS-OX; OXR20251007) (October 2025).

During Cruise YK23-16S, two specimens (NSMT-Pol P-1055 and NSMT-Pol P-1056) were collected off Iheya North Knoll, northwest of Iheya Island, Okinawa, Japan, using the HOV *Shinkai 6500* deployed from R/V *Yokosuka*. Both specimens were recovered from washings of a single individual of the stalked crinoid, *Proisocrinus ruberrimus* Clark, 1910.

During Cruise DY86-II, one specimen (ZRC.ANN.3588) was collected from O-Yatagarasu Guyot, western Pacific Ocean, using the HOV *Jiaolong* deployed from R/V *Shen Hai Yi Hao*. The specimen was recovered from the HOV biobox used to store megafauna collected with the manipulator arm.

During Cruise YK24-15C, two specimens (NSMT-Pol H-1057 and NSMT-Pol P-1058) were collected from the vicinity of the northern Mariana Trench, western Pacific Ocean, using the HOV *Shinkai 6500* deployed from R/V *Yokosuka*. Both specimens were attached to the oral surface of an asteroid sea star (*Hymenaster* sp.) and were removed for subsequent examination.

During the NUS-OX Expedition, two specimens (ZRC.ANN.3586 and ZRC.ANN.3587) were collected from an unnamed seamount in the Monsoon Rise region (hereafter "Seamount 3"), eastern Indian Ocean, using the ROV *Chimaera* deployed from R/V *OceanXplorer*. Both specimens were attached to the oral surface of an asteroid sea star (*Evoplosoma* sp.) and were removed after retrieval for subsequent examination, photography, and preservation.

Morphological examination. Live specimens were photographed on board before fixation. Unless otherwise noted, specimens were fixed and preserved in 70–75% ethanol, then examined and photographed in the laboratory using stereomicroscopy, compound microscopy, and DSLR photography. Where applicable, chaetae were prepared for scanning electron microscopy (SEM) by mounting on brass stubs, air-drying, sputter-coating with platinum using a JEOL JEC-3000FC auto fine coater, and examining with a JEOL JSM-6010PLUS/LV SEM. Focus-stacked images were processed using Leica Application Suite X or Zerene Stacker version 1.04.

Cruise-specific imaging equipment was as follows. For YK23-16S, live specimens were photographed with a Nikon D5600 DSLR camera; preserved material was examined using a Leica Ivesta 3 Greenough stereomicroscope and KEYENCE BZ-X1000 compound microscope. For YK24-15C, live specimens were photographed using an Olympus OM-D E-M5 Mark II digital camera; preserved material was examined and photographed using a Nikon SMZ18 stereomicroscope and a Nikon ECLIPSE Ni compound microscope, both with a Nikon D7500 camera. For DY86-II, live images were taken with a Zeiss Axiocam 208 colour camera mounted on a Zeiss Stemi 305 stereomicroscope and with an Olympus Tough TG-6 digital camera. For NUS-OX, live images were taken with a Nikon Digital Sight 10 camera mounted on a Nikon SMZ25 stereomicroscope and with a Nikon D850 DSLR camera; several elytra were removed and fixed in absolute ethanol for subsequent molecular analyses, and the remaining material was fixed in 10% formalin before transfer to 75% ethanol for long-term preservation. Preserved specimens from DY86-II and NUS-OX were examined using a Nikon SMZ25 stereomicroscope, and photographed with a Leica M205 C stereomicroscope with a Leica DMC5400 camera, a Leica DM2500 compound microscope with a Leica Flexacam C3 camera, and a Canon EOS 6D DSLR camera mounted on a Visionary Digital Passport system.

All examined material is deposited in the Zoological Reference Collection (ZRC), Lee Kong Chian Natural History Museum, National University of Singapore, Singapore, and the National Museum of Nature and Science, Tsukuba, Japan (NSMT).

DNA extraction, amplification, and sequencing. Genomic DNA was extracted from tissue using the DNeasy Blood & Tissue Kit (Qiagen). Partial sequences of two mitochondrial markers (cytochrome c oxidase subunit I, COI; 16S rRNA, 16S) and one nuclear marker (18S rRNA, 18S) were amplified by PCR and Sanger-sequenced. Cruise-specific details are provided below.

For YK23-16S, DNA was extracted from parapodial tissue. PCR was performed using TaKaRa Ex Taq (Takara Bio) on a Veriti 96-Well Thermal Cycler (Thermo Fisher Scientific), with primer pairs polyLCO/polyHCO (Carr et al., 2011) for COI and 16Sar-L/16Sbr-H (Palumbi et al., 1991) for 16S. Cycling conditions were: 94°C for 2 min; 35 cycles of 94°C for 40 s, 50–52°C for 75 s, and 72°C for 60 s; final extension at 72°C for 7 min. PCR products were purified using ExoSAP-IT (Thermo Fisher Scientific) and Sanger-sequenced by FASMAC, Kanagawa, Japan.

For YK24-15C, DNA extraction, amplification, and sequencing followed Jimi et al. (2021).

For DY86-II and NUS-OX, DNA was extracted from elytra, with a final elution volume of 50 µL. PCR was performed on a ProFlex 3 × 32-well PCR System (Applied Biosystems). Each 25 µL reaction contained 5 µL template DNA, 2.5 µL of each primer (10 µM), 12.5 µL GoTaq G2 Green Master Mix (Promega), and nuclease-free water to volume. The following primer pairs and cycling conditions were used: COI (~650 bp) with polyLCO/polyHCO (Carr et al., 2011), 95°C for 4 min; 40 cycles of 94°C for 30 s, 52°C for 1 min, and 72°C for 75 s; final extension at 72°C for 8 min; 16S (~450 bp) with Ann16SF (Sjölin et al., 2005) and 16SbrH (Palumbi, 1996), 95°C for 4 min; 35 cycles of 94°C for 30 s, 52°C for 1 min, and 72°C for 75 s; final extension at 72°C for 8 min; and 18S (~1800 bp) with 18SA (Medlin et al., 1988) and 18SB (Nygren & Sundberg, 2003), 95°C for 4 min; 35 cycles of 94°C for 30 s, 52°C for 1 min, and 72°C for 3 min; final extension at 72°C for 8 min. PCR products were checked on 1% agarose gel stained with SYBR Safe (Invitrogen) in 1× TAE buffer (30 min) and visualised using a SafeBlue Illuminator System (Major Science). Amplicons were purified using the QIAquick PCR Purification Kit (Qiagen) and Sanger-sequenced using BigDye Terminator v3.1 chemistry (Applied Biosystems) on an ABI PRISM 3730xl Genetic Analyser (Applied Biosystems) by 1st BASE, Singapore.

Phylogenetic analyses. COI, 16S rRNA and 18S rRNA sequences from the collected specimens were processed following Jimi et al. (2021). The phylogenetic placement of the two new species within Polynoidae was assessed using maximum-likelihood (ML) analysis based on the dataset of Bonifácio & Menot (2018), supplemented with sequences generated in this study. *Neoleanira tetragona* (Örsted, 1845) and *Sthenelais boa* (Johnston, 1833) were selected as outgroups. The concatenated nucleotide matrix of COI, 16S rRNA and 18S rRNA was analysed using IQ-TREE 2 (Minh et al., 2020), with best-fit substitution models selected automatically using ModelFinder (Kalyaanamoorthy et al., 2017). Node support was assessed using 1000 ultrafast bootstrap (UFBoot) replicates (Hoang et al., 2018). All sequences generated in this study were deposited in GenBank (NCBI) and are listed in Table 1.

SYSTEMATICS

Family Polynoidae Kinberg, 1856

Subfamily Macellicephalinae Hartmann-Schröder, 1971

Genus *Ovatocirra*, new genus

[New Japanese name: tamago-urokomushi-zoku]

Type species. *Ovatocirra flavida*, new species.

Diagnosis. Macellicephalinae with body short, dorsoventrally flattened, with 18–22 segments. Prostomium with median antenna, without lateral antennae and frontal filaments. Pharynx with numerous distal papillae; jaws absent. Tentaculophores without chaetae. Elytra in nine to ten pairs, firmly attached on segments 2, 4, 5, 7, 9, 11, 13, 15, 17 (and 19 when 10 pairs are present), completely covering dorsum; elytra smooth or unevenly textured. Parapodia biramous; notopodia with acicular lobe elongate, tapering; neuropodia with acicular lobe elongate or rounded; tips of

Fig. 2. Maximum-likelihood (ML) phylogeny of Polynoidae inferred from the concatenated three-gene dataset (COI, 16S rRNA and 18S rRNA). The two new species are shown in bold. *Neoleanira tetragona* and *Sthenelais boa* were used as outgroups. Node labels indicate ultrafast bootstrap (UFBoot) support values (%) from 1,000 replicates.

Table 1. GenBank accession numbers for DNA sequences of *Ovatocirra flavida*, new genus and species, and *Ovatocirra shinkaiae*, new genus and species, obtained in this study.

Species	Status	Voucher	COI	16S	18S
Ovatocirra flavida	Holotype	ZRC.ANN.3586	PZ812644	PZ827277	PZ827616
Ovatocirra flavida	Paratype 1	ZRC.ANN.3587	PZ812645	PZ827278	PZ827617
Ovatocirra flavida	Paratype 2	ZRC.ANN.3588	PZ812646	PZ827279	PZ827618
Ovatocirra flavida	Paratype 4	NSMT-Pol P-1056	PZ812647	PZ827280	–
Ovatocirra shinkaiae	Holotype	NSMT-Pol H-1057	PZ812648	PZ827281	PZ827619

noto- and neuroaciculae penetrating epidermis. Ventral cirri inserted basally on neuropodia of segment 2, tapering; from segment 3 onwards inserted medially on neuropodia, styles ovate to subovate.

Remarks. Phylogenetic analyses recovered the two species of the newly proposed genus *Ovatocirra* as a clade nested within the *Macellicephala* clade; the relationship between *Ovatocirra* and *Abyssarya* was weakly supported (Fig. 2). Despite this phylogenetic placement, *Ovatocirra* can be readily distinguished from other members of the clade by a unique suite of morphological characters, including the form of pharyngeal papillae, the absence of jaws, and the shape of ventral cirri (Table 2).

Within Macellicephalinae, *Ovatocirra* resembles *Bathymacella* Pettibone, 1976, *Macelloides* Uschakov, 1957, and *Vampiropolynoe* Marcus & Hourdez, 2002 in lacking the typical stout, interlocking chitinous jaws (Table 2). Among these genera, it is most similar to *Bathymacella* and *Macelloides* in possessing numerous pharyngeal papillae, although Pettibone (1976) described these structures in *Bathymacella* as pleated folds rather than distinct papillae. However, *Ovatocirra* can be distinguished from *Bathymacella*, *Macelloides*, and *Vampiropolynoe* by the shape of its ventral cirri. It further differs from *Macelloides*, which has denticulate jaw plates and elongated neuropodia (Pettibone, 1976), and from *Vampiropolynoe*, which possesses sclerotised jaw plates and the characteristic curved acicular lobes on the tentacular segment (Marcus & Hourdez, 2002).

Among genera currently assigned to Macellicephalinae, none has been described as having ovate to subovate ventral cirri; however, *Macellicephala grimaldii* Fauvel, 1913, which was described as having similar ventral cirri, is discussed below. The only other apparent exception is *Macelloides*, for which Uschakov (1957) described the ventral cirri of the first chaetiger as spherical and those of subsequent segments as pointed. However, Pettibone (1976) later clarified that the 'spherical ventral cirri' correspond to bulbous spherical areas medial to the cirrophores of the buccal cirri. Accordingly, the combination of diagnostic characters in *Ovatocirra*, notably the presence of numerous pharyngeal papillae, the absence of jaws, and the ovate ventral cirri, is unique within Macellicephalinae and supports the erection of a new genus.

Etymology. The generic name *Ovatocirra* is derived from the Latin 'ovatus' (oval) and the suffix '-cirra' (from Latin 'cirrus'), referring to the characteristic oval ventral cirri.

Gender. Feminine.

Ovatocirra flavida, new species

[New Japanese name: yamabuki-urokomushi]

(Figs. 3–8; Tables 1–2)

Material examined.

Holotype (ZRC.ANN.3586; NUS-OX; chaetae used for SEM) and **paratype 1** (ZRC.ANN.3587; NUS-OX; 12.4 mm long, 8 mm wide), Seamount 3-Station 2 (SM3-2), Monsoon Rise, Christmas Island Seamount Province, eastern Indian Ocean (11.981380° S, 101.097887° E), collected by ROV *Chimaera* (Station CHR10; Dive CHR0594), 1,200 m, 14 October 2025; fixed in 10% formalin and preserved in 75% ethanol (several elytra fixed in absolute ethanol).

Paratype 2 (ZRC.ANN.3588; DY86-II), 9.5 mm long, 7 mm wide, O-Yatagarasu Guyot, western Pacific Ocean (start 20.4157° N, 151.1762° E, end 20.4499° N, 151.1891° E), collected by HOV *Jiaolong* (Dive DY86II-OY-JL307), 1,336–1,676 m, 26–27 August 2024; fixed and preserved in 75% ethanol.

Paratype 3 (NSMT-Pol P-1055; YK23-16S; 8.5 mm long, 5.1 mm wide) and **paratype 4** (NSMT-Pol P-1056; YK23-16S; 5.0 mm long, 3.6 mm wide), off Iheya North Knoll, northwest of Iheya Island, Okinawa, Japan (27.506893° N, 127.061005° E), collected by HOV *Shinkai 6500* (Dive 1730), 1,572 m, 26 September 2023; fixed and preserved in 70% ethanol.

Description (based on holotype). Holotype (ZRC.ANN.3586) 11 mm long, 7 mm wide (including chaetae), 22 segments (including tentacular segment). Body robust, compact, dorsoventrally flattened; surface smooth (Figs. 3, 4). Live specimen with large, overlapping, bright yellow elytra, body slightly translucent (blood vessels observed through body wall, especially on parapodia) (Fig. 3); ethanol-preserved specimen pale yellow to light brown (Fig. 4).

Prostomium slightly bilobed, wider than long; lobes not pronounced, with very shallow median notch (Fig. 4C). Eyes absent. Median antenna present; ceratophore prominent, inserted anterodorsally on prostomium (Fig. 4A, C, D). Style

Table 2. Diagnostic morphological characters of *Ovatocirra*, new genus and selected other genera within the subfamily Macellicephalinae.

Character/Genus	*Abyssarya* Bonifácio & Menot, 2018	*Ovatocirra*, new genus	*Bathymacella* Pettibone, 1976	*Macellicephala* M'Intosh, 1885	*Macelloides* Uschakov, 1957	*Vampiropolynoe* Marcus & Hourdez, 2002
Frontal filament	Present	Absent	Absent	Absent or Present	Absent	Present
Segments	18	18–22	18	18	30	up to 45
Elytral pairs	9	9–10	9	9	15	10
Ventral cirri	Tapering	Oval to suboval	Tapering	Tapering	Tapering	Tapering
Pharyngeal papillae	Could not be counted	Numerous	Pleated folds*	9 pairs	Numerous	Several pairs
Jaws	2 pairs	Absent	Absent	2 pairs	Absent (with slender, denticled, chitinous plates)	Absent (with small sclerotinised plates)
Reference	Bonifácio & Menot (2018)	This study	Averincev (1972), Pettibone (1976)	Pettibone (1976)	Uschakov (1957), Pettibone (1976)	Marcus & Hourdez (2002), Hourdez (2022)

*Pettibone (1976) described the distal pharynx as encircled by "pleated folds" rather than distinct papillae.

of median antenna tapering, basally swollen (Fig. 4C, D). Lateral antennae absent. Frontal filaments absent. Facial tubercle absent. Palps smooth, short, tongue-shaped, wide and thick basally, about 1.5 times as long as prostomium (Fig. 4B–D, F). Pharynx not everted in holotype, dissected in paratypes (ZRC.ANN.3587 and NSMT-Pol P-1056); numerous terminal pharyngeal papillae present; jaws absent (Fig. 4G, H).

Tentacular segment with tentaculophores inserted laterally and slightly ventral to prostomium, without chaetae. Tentacular styles smooth, distally tapering, short, slightly longer than median antenna, reaching segment 2 (Fig. 4C, D). Dorsal style slightly longer than ventral tentacular style.

Second segment with elytrophores, biramous parapodia with chaetae (Fig. 4C, D). Ventral cirri inserted basally on neuropodia, tapering, basally swollen, about 3 times as long as following cirri, differing in shape (Fig. 4B, D, F).

Body with 10 pairs of elytra. Elytra oval to subreniform, firmly attached on prominent, bulbous elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, and 19; elytra completely cover dorsum (Figs. 3, 4). On living specimen, elytra bright, vivid yellow, and non-overlapping surfaces with distinctive mounds (Figs. 3, 5C). Elytral pigmentation lost in ethanol (Figs. 4E, 5A, B), but numerous small yellow pigment spots visible on some, particularly along outer and inner non-overlapping elytra surfaces (Fig. 5D).

Parapodia biramous, with notopodia slightly shorter than neuropodia (Fig. 6). Notopodia cylindrical, acicular lobe elongate, tapering (Fig. 6A, D). Tip of notoacicula penetrating epidermis. Neuropodia large, fan-shaped, pre-chaetal (acicular) lobe elongate, tapering (Fig. 6A, D). Tip of neuroacicula penetrating epidermis. Neuropodial post-chaetal lobe rounded to slightly truncate (Fig. 6B, E).

Cirrigerous segments with prominent, bulbous dorsal cirrophores, inserted on notopodial posterodorsal sides (Fig. 6D–F). Dorsal cirri style smooth, tapering, reaching neurochaetae tips. Dorsal tubercles distinct, conical to subconical, slightly smaller than elytrophores (Figs. 4A, E, 6D–F).

Ventral cirri present from segment 2 (buccal segment) to last segment; inserted basally on neuropodia of segment 2, style smooth, tapering, about 3 times as long as following ventral cirri (Fig. 4B, D, F). Ventral cirri from segment 3 onward inserted medially on neuropodia, with prominent cirrophores; styles short, ovate to subovate (Figs. 4B, D, F, 6A, B, E).

Notochaetae slender, moderate in number (about 10–20 per ramus), distally straight to slightly curved, with spinous rows on convex margins, with pointed tips (Figs. 6A, D, 7A, 8A). Neurochaetae longer and stouter than notochaetae, more abundant (about 40 per ramus) (Fig. 6A, D). Upper neurochaetae mainly with pointed tips, with faint transverse serrations along the convex margin (Figs. 7B, 8B). Middle

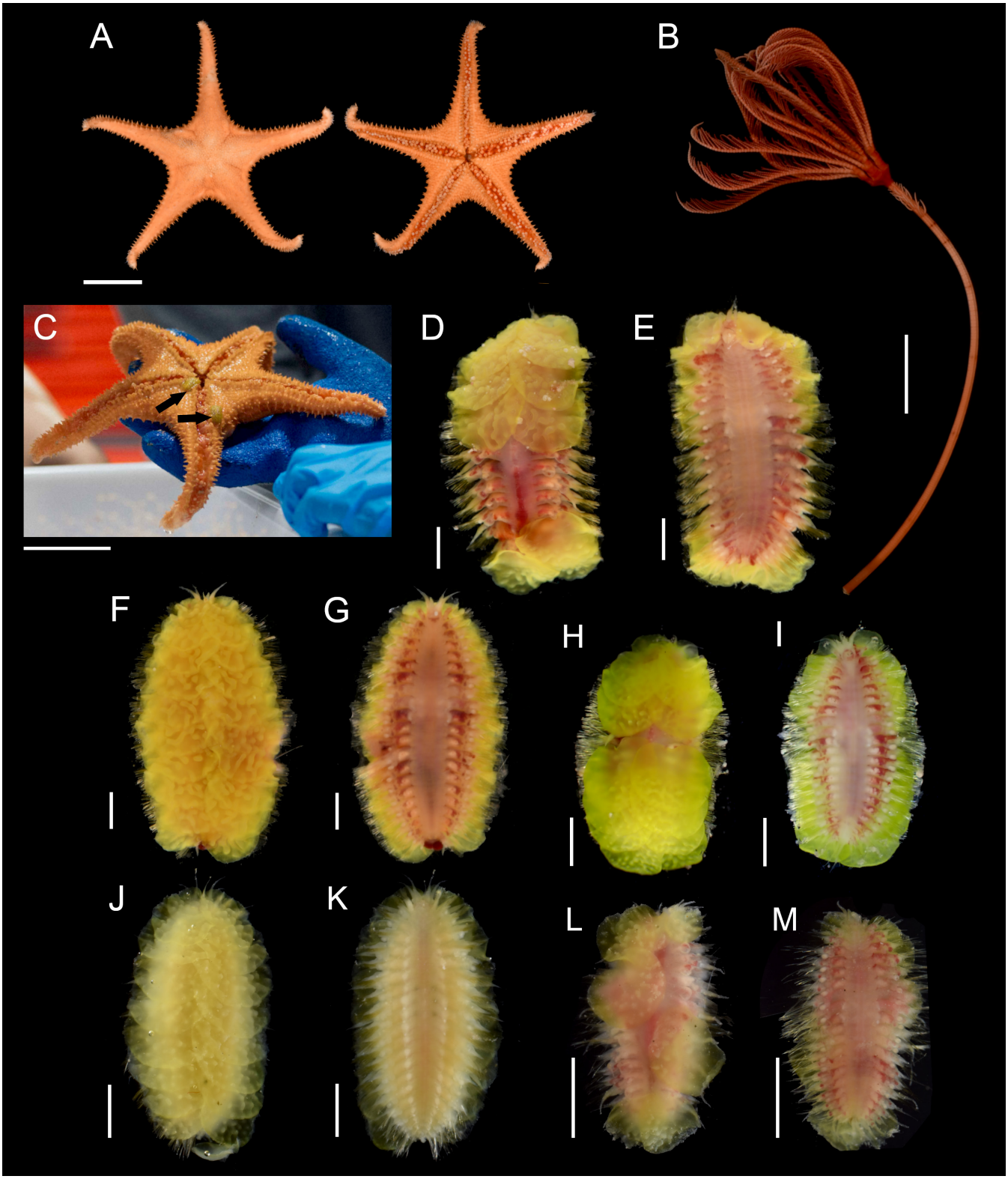

Fig. 3. Live specimens of *Ovatocirra flavida*, new genus and species, D, E, holotype (ZRC.ANN.3586); F, G, paratype 1 (ZRC.ANN.3587); H, I, paratype 2 (ZRC.ANN.3588); J, K, paratype 3 (NSMT-Pol P-1055); L, M, paratype 4 (NSMT-Pol P-1056). A, asteroid host (*Evoplosoma* sp.) for holotype and paratype 1. B, crinoid host (*Proisocrinus ruberrimus*) for paratypes 3 and 4. C, *Ovatocirra flavida* (black arrows) attached to the oral surface of the asteroid host. D, F, H, J, L, whole body, dorsal view. E, G, I, K, M, whole body, ventral view. Scale bars: A–C, 50 mm; D–M, 2 mm.

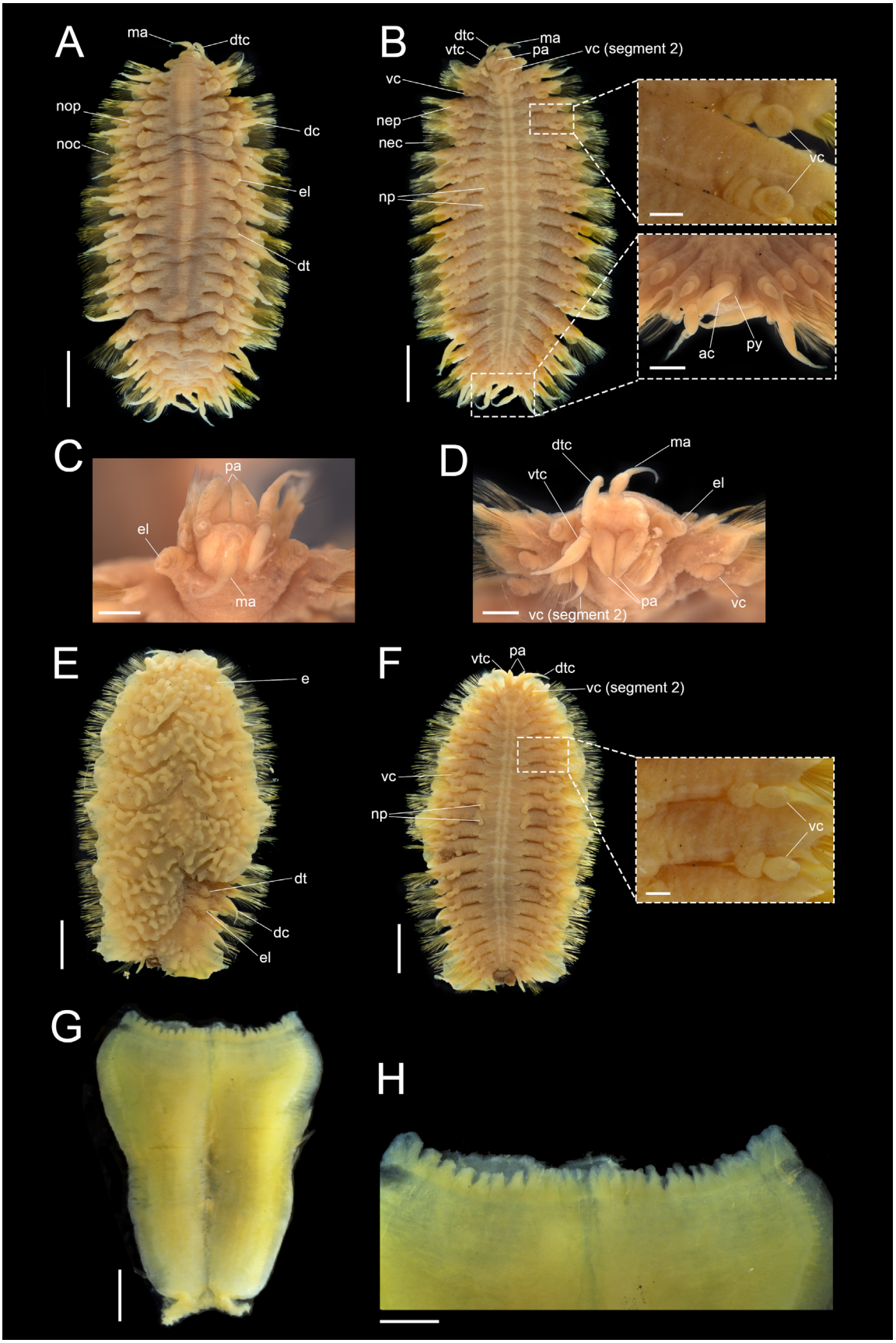

Fig. 4. Preserved specimens of *Ovatocirra flavida*, new genus and species, A–D, holotype (ZRC.ANN.3586); E–H, paratype 1 (ZRC.ANN.3587). A, whole body, dorsal view. B, whole body, ventral view (upper inset: ventral cirri; lower inset: pygidial end). C, anterior, dorsal view. D, anterior, frontal view. E, whole body, dorsal view. F, whole body, ventral view (inset: ventral cirri). G, pharynx opened to show internal surface. H, distal end of pharynx, showing short pharyngeal papillae. Abbreviations: ac, anal cirrus; dc, dorsal cirrus; dt, dorsal tubercle; dtc, dorsal tentacular cirrus; e, elytron; el, elytrophore; ma, median antenna; nec, neurochaetae; nep, neuropodium; noc, notochaetae; nop, notopodium; np, nephridial papillae; pa, palp; py, pygidium; vc, ventral cirrus; vtc, ventral tentacular cirrus. Scale bars: A, B, E, F, 2 mm; C, D, G and lower inset in B, 0.5 mm; H, upper inset in B and inset in F, 0.25 mm.

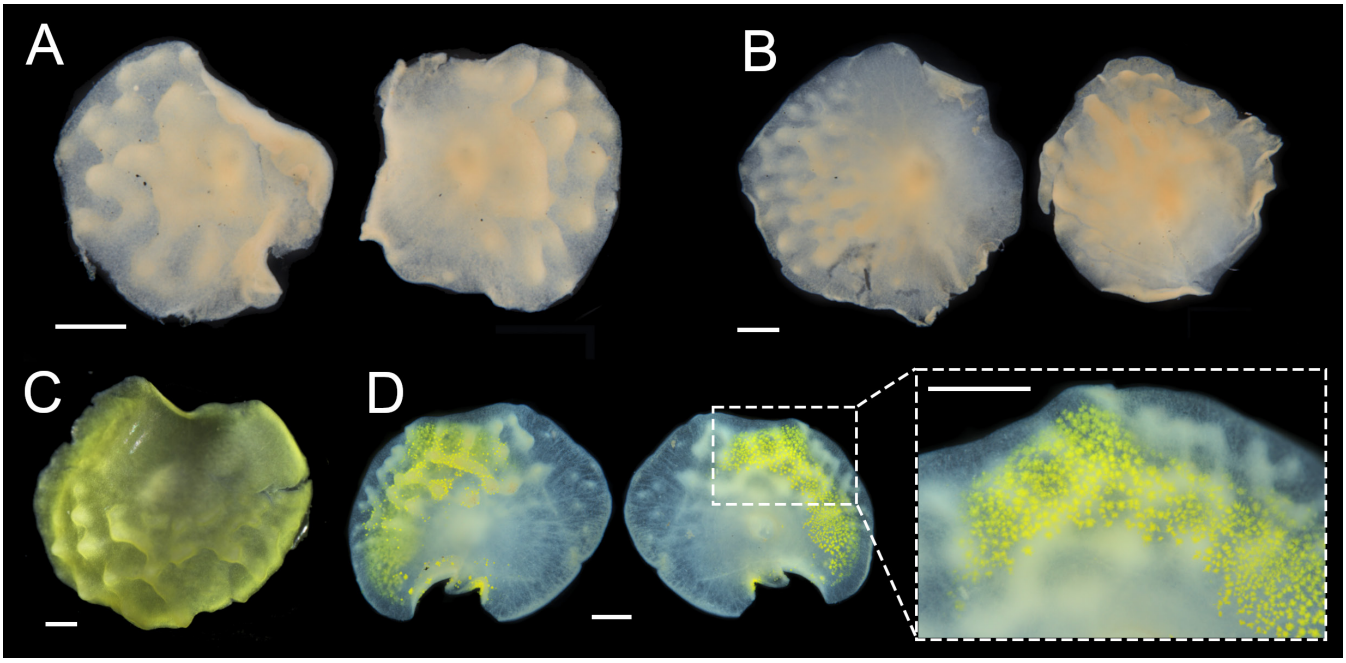

Fig. 5. Elytra of *Ovatocirra flavida*, new genus and species, A–C, holotype (ZRC.ANN.3586); D, paratype 2 (ZRC.ANN.3588). A, preserved elytra from an anterior segment. B, preserved elytra from a posterior segment. C, elytron from a mid-body segment in life. D, residual pigmentation on the dorsal (left) and ventral (right) surfaces after fixation and preservation in 75% ethanol. Scale bar: 0.5 mm.

to lower neurochaetae with hooked tips, with faint transverse serrations on convex margin (Figs. 7C, D, 8C).

Nephridial papillae present from segment 5; prominent and tuberculate on segments 10 and 11, inconspicuous on other segments (Fig. 4B, F).

Pygidium with a pair of anal cirri (one lost in holotype), tapering, as long as dorsal cirri of preceding segment (Fig. 4B).

Morphological variation. In life, the elytra of paratype 2 appear neon yellow (Fig. 3H), whereas paratypes 3 and 4 have light lemon-yellow elytra (Fig. 3J, L). Preserved paratypes 3 and 4 are olive-brown and markedly darker than the other specimens. Paratype 3 with nephridial papillae only slightly enlarged on segments 10–12.

Etymology. The specific epithet *flavida* is derived from the Latin 'flavidus' (yellowish) and refers to the yellow colouration of the elytra in this species.

Distribution. Western Pacific Ocean and eastern Indian Ocean.

Ecology. The holotype and paratype 1 were attached to the oral surface of a goniasterid asteroid (*Evoplosoma* sp.), suggesting a commensal association (Fig. 3C). The host asteroid was observed in situ perched on the stalk of an unbranched bamboo coral, likely feeding on the coral. Paratypes 3 and 4 were recovered from washings of the stalked crinoid *Proisocrinus ruberrimus* (colloquially "Moulin Rouge", after the iconic red windmill of the Parisian cabaret; Fig. 3B), suggesting that this crinoid may also serve as a host for this species. Paratype 2 was recovered from the HOV biobox together with other megafauna, including antipatharians, asteroids, holothuroids, octocorals, and ophiuroids. All specimens were collected from deep-water seamount habitats at depths of 1,200–1,676 m, where bottom-water temperatures ranged from 2 to 4°C.

Remarks. *Ovatocirra flavida*, new species, closely resembles *Macellicephala grimaldii* Fauvel, 1913, described from the Josephine Bank (west of the southern coast of Iberian Peninsula, North Atlantic Ocean); it was collected at a relatively shallow depth of 204 m, and the holotype was a small (6 mm by 4 mm), incomplete specimen (20 segments on one side; a rudimentary chaetiger on the other), with the median antenna, tentacular cirri, palps, and most elytra missing or broken off. Despite this, Fauvel's description indicates clear similarities with *O. flavida* including 10 pairs of elytra, comparable noto- and neurochaetal types, enlarged nephridial papillae on segment 10 and 11, and most notably, the oval (or globular as described by Fauvel) ventral cirri (Fauvel, 1913, 1914).

The type material of *M. grimaldii* was not available for study, as our loan request was not answered. We have therefore relied on Fauvel's original description and illustrations (Fauvel, 1913, 1914), which indicate that *M. grimaldii* differs from *O. flavida* in several characters: (1) elytral surface texture (few granulations in *M. grimaldii* vs. distinct mounds in *O. flavida*); (2) ventral cirri of segment 2 (short, as long as following ones in *M. grimaldii* vs. about 3 times longer than the subsequent cirri in *O. flavida*); and (3) parapodial morphology, including the position and shape of acicular lobes (notoacicular lobe dorsally placed in *M. grimaldii* vs. ventrally placed in *O. flavida*; neuroacicular lobe nearly lanceolate and distally much elongated, with a much shorter neuropodial post-chaetal lobe in *M. grimaldii* vs. fan-shaped

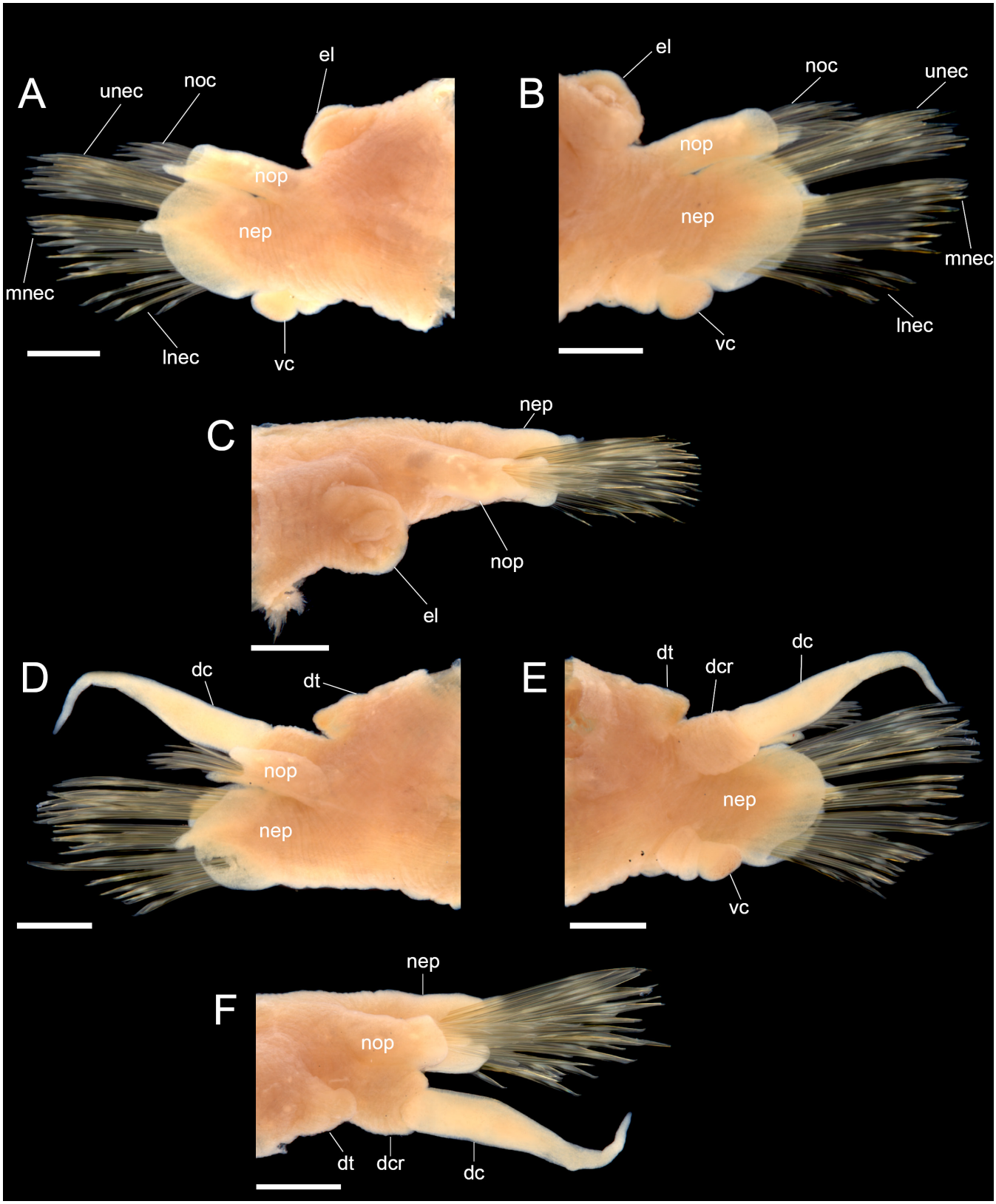

Fig. 6. Parapodia of *Ovatocirra flavida*, new genus and species, holotype (ZRC.ANN.3586). A–C, right parapodia from segment 13 and D–F, segment 14. A, D, anterior view. B, E, posterior view. C, F, dorsal view. Abbreviations: dc, dorsal cirrus; dcr, dorsal cirrophore; dt, dorsal tubercle; el, elytrophore; lnec, lower neurochaetae; mnec, middle neurochaetae; nep, neuropodium; noc, notochaetae; nop, notopodium; unec, upper neurochaetae; vc, ventral cirrus. Scale bar: 0.5 mm.

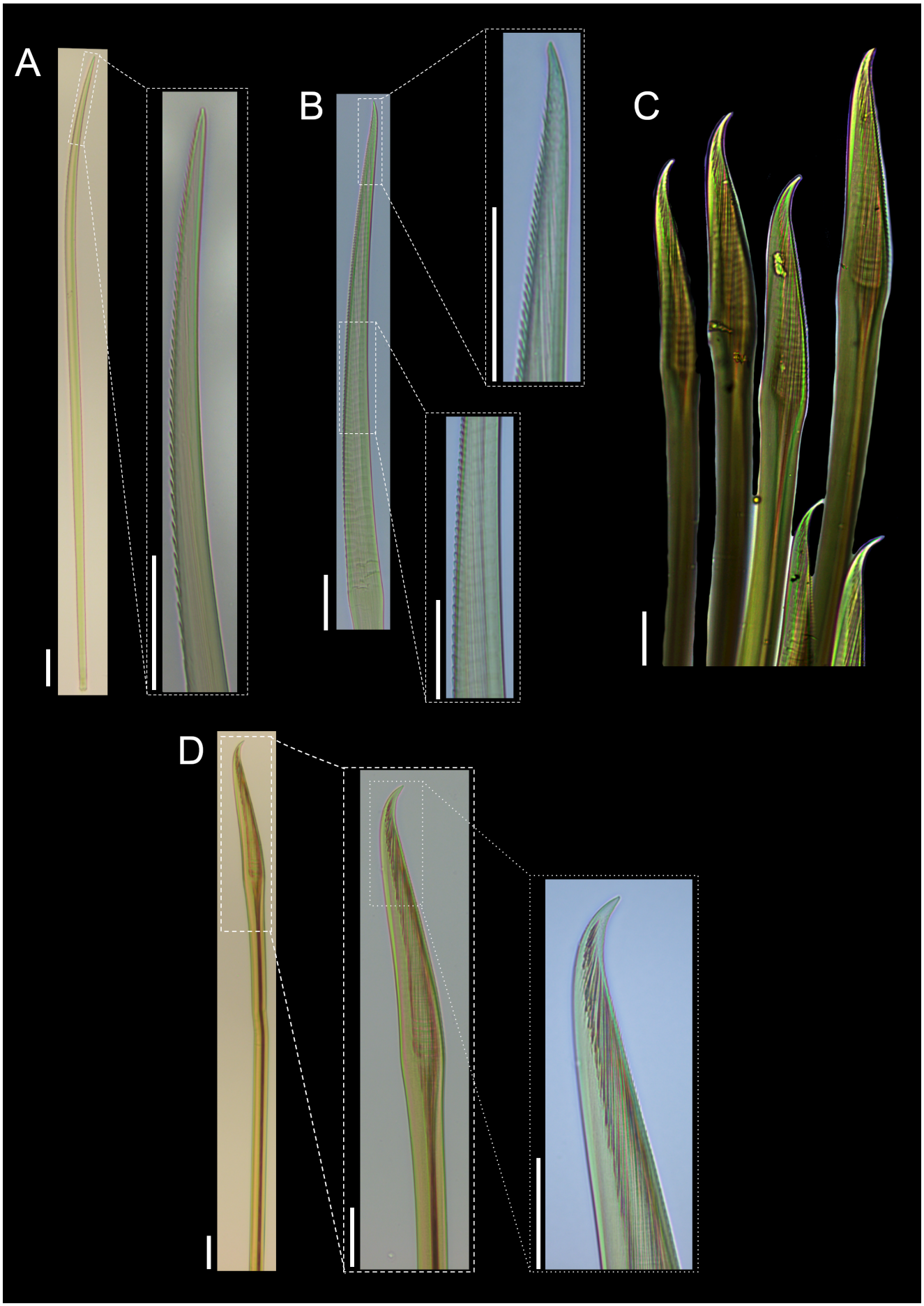

Fig. 7. Chaetae of *Ovatocirra flavida*, new genus and species, holotype (ZRC.ANN.3586), all from segment 15. A, notochaeta. B, upper neurochaeta. C, middle to lower neurochaetae. D, middle to lower neurochaeta. Scale bar: 50 µm.

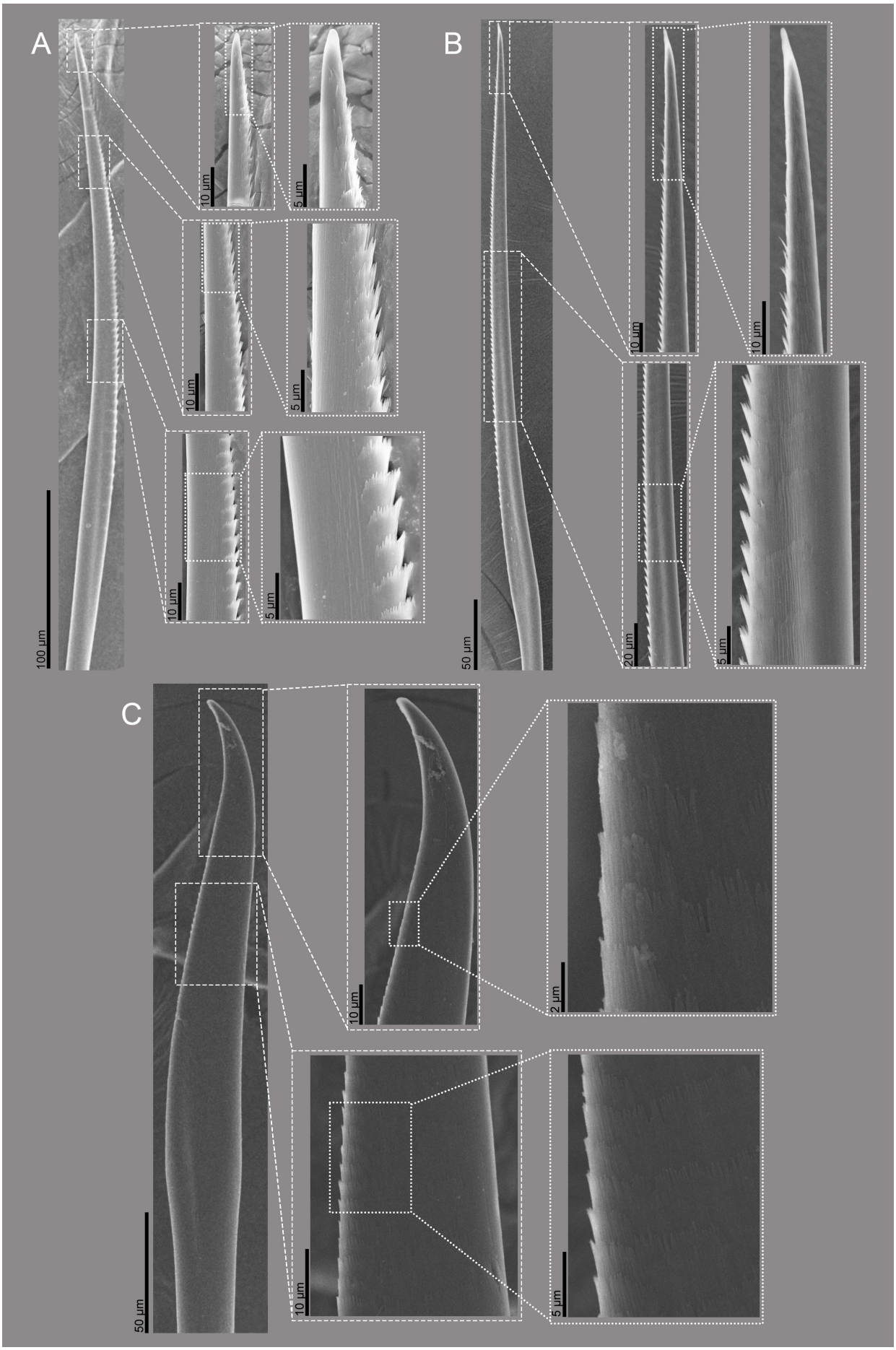

Fig. 8. SEM micrographs showing serration of chaetae in *Ovatocirra flavida*, new genus and species, holotype (ZRC.ANN.3586). A, notochaeta (segment 13). B, upper neurochaeta (segment 15). C, middle neurochaeta (segment 15).

neuroacicular lobe, distally only slightly elongated, and with a subequal neuropodial post-chaetal lobe in *O. flavida*). Pharyngeal characters cannot be assessed for *M. grimaldii*, as Fauvel did not report the details (Fauvel, 1913, 1914); the pharynx was likely neither everted nor dissected.

Knox (1959) reviewed *Macellicephala* and highlighted the globular ventral cirri of *M. grimaldii* as unique among congeners. He also noted that variation in key characters (e.g., segment number and chaetae) suggested that *Macellicephala*-like taxa might not form a natural group, and that additional material would be necessary to resolve relationships. Hartmann-Schröder (1974) subsequently modified and expanded Knox's diagnostic character list for *Macellicephala* and likewise listed the globular ventral cirri for *M. grimaldii*. Pettibone (1976) then conducted a major revision of *Macellicephala* and the subfamily Macellicephalinae, resulting in several new combinations and the establishment of several new genera and subfamilies to accommodate various deep-water forms. In that revision, however, *M. grimaldii* was regarded as an indeterminable polynoid because the specimen was incomplete, and with over 20 segments, does not conform to the emended diagnosis of *Macellicephala* (18 segments; Pettibone, 1976). The distinctive globular ventral cirri were not mentioned or discussed. Consistent with this uncertainty, recent deep-water polynoid studies involving *Macellicephala* have not included *M. grimaldii* as a member of the genus (Bonifácio & Menot, 2018; Neal et al., 2018), and the genus diagnosis has remained stable (18 segments, 9 pairs of elytra, pharynx with 2 pairs of jaws and 9 pairs of papillae) (Pettibone, 1976; Bonifácio & Menot, 2018; Neal et al., 2018; Murray et al., 2025).

On the basis of Fauvel's (1913, 1914) original description, especially the distinctive ventral cirri, together with additional characters aligning with the diagnosis of the newly proposed genus *Ovatocirra*, we conclude that *M. grimaldii* is congeneric and consequently propose the new combination *Ovatocirra grimaldii* (Fauvel, 1913).

***Ovatocirra shinkaiae*, new species**

[New Japanese name: kyokuhi-yadori-urokomushi]
(Figs. 9–11; Tables 1–2)

Material examined.
Holotype (NSMT-Pol H-1057; Cruise YK24-15C) and **paratype** (NSMT-Pol P-1058; Cruise YK24-15C; 12 mm long, 7 mm wide), in the vicinity of the northern Mariana Trench, western Pacific Ocean (24.253648° N, 144.015378° E), collected by HOV *Shinkai 6500* (Dive #1816), 4,461 m, 2 October 2024; fixed and preserved in 70% ethanol (several elytra fixed in absolute ethanol).

Description (based on holotype). Holotype (NSMT-Pol H-1057) 14 mm long, 8 mm wide (including chaetae), 18 segments (including tentacular segment). Body robust, compact, dorsoventrally flattened; surface smooth (Fig. 9D–G). Live specimen with large, overlapping, white elytra, body whitish (Fig. 9); ethanol preserved specimen whitish (Fig. 10).

Prostomium slightly bilobed, wider than long; lobes not pronounced, with very shallow median notch (Fig. 10A). Eyes absent. Median antenna present; ceratophore prominent, inserted anterodorsally on prostomium (Fig. 10A, B). Style of median antenna tapering, basally swollen (Fig. 10A, B). Lateral antennae absent. Frontal filaments absent. Facial tubercles present, two subconical lobes ventral to median antennal ceratophore (Fig. 10B). Palps smooth, short, tongue-shaped, wide and thick basally, about half as long as prostomium (Fig. 10B). Pharynx not everted in holotype, dissected in paratype; numerous terminal pharyngeal papillae present; jaws absent.

Tentacular segment with tentaculophores inserted laterally and slightly ventral to prostomium, without chaetae. Tentacular styles smooth, distally tapering, short, slightly longer than median antenna, reaching segment 2 (Fig. 10A, B). Dorsal style slightly longer than ventral tentacular style.

Second segment with elytrophores, biramous parapodia with chaetae (Fig. 10A). Ventral cirri inserted basally on neuropodia, tapering, basally swollen, longer than following cirri, differing in shape (Fig. 10B).

Body with 9 pairs of elytra. Elytra oval to subreniform, firmly attached on prominent, bulbous elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, and 17; elytra completely cover dorsum (Figs. 9, 10A). Elytra white in live specimens (Fig. 9). Ethanol preserved elytra whitish; elytral surface smooth, margins smooth (Fig. 10A, E, F).

Parapodia biramous, with notopodia slightly shorter than neuropodia (Fig. 11A–C). Notopodia short, acicular lobe elongate, tapering (Fig. 11A, C). Tip of notoacicula penetrating epidermis. Neuropodia large, fan-shaped, pre-chaetal (acicular) lobe rounded (Fig. 11A, C). Tip of neuroacicula penetrating epidermis. Neuropodial post-chaetal lobe rounded to slightly truncate (Fig. 11B), occasionally appearing weakly bilobed (Fig. 11D). Lobe shape not consistent across parapodia within a single specimen.

Cirrigerous segments with prominent, bulbous dorsal cirrophores, inserted on notopodial posterodorsal sides (Fig. 11C, D). Dorsal cirri style smooth, tapering, reaching neurochaetae tips. Dorsal tubercles distinct, conical to subconical, slightly smaller than elytrophores (Fig. 11C, D).

Ventral cirri present from segment 2 (buccal segment) to last segment; inserted basally on neuropodia of segment 2, style smooth, tapering, about 2 times as long as following ventral cirri (Fig. 10B). Ventral cirri from segment 3 onwards inserted medially on neuropodia, with prominent cirrophores, styles short, ovate to subovate (Figs. 10B, C, 11A–D).

Notochaetae slender, moderate in number (about 10–20 per ramus), distally straight to slightly curved, with spinous

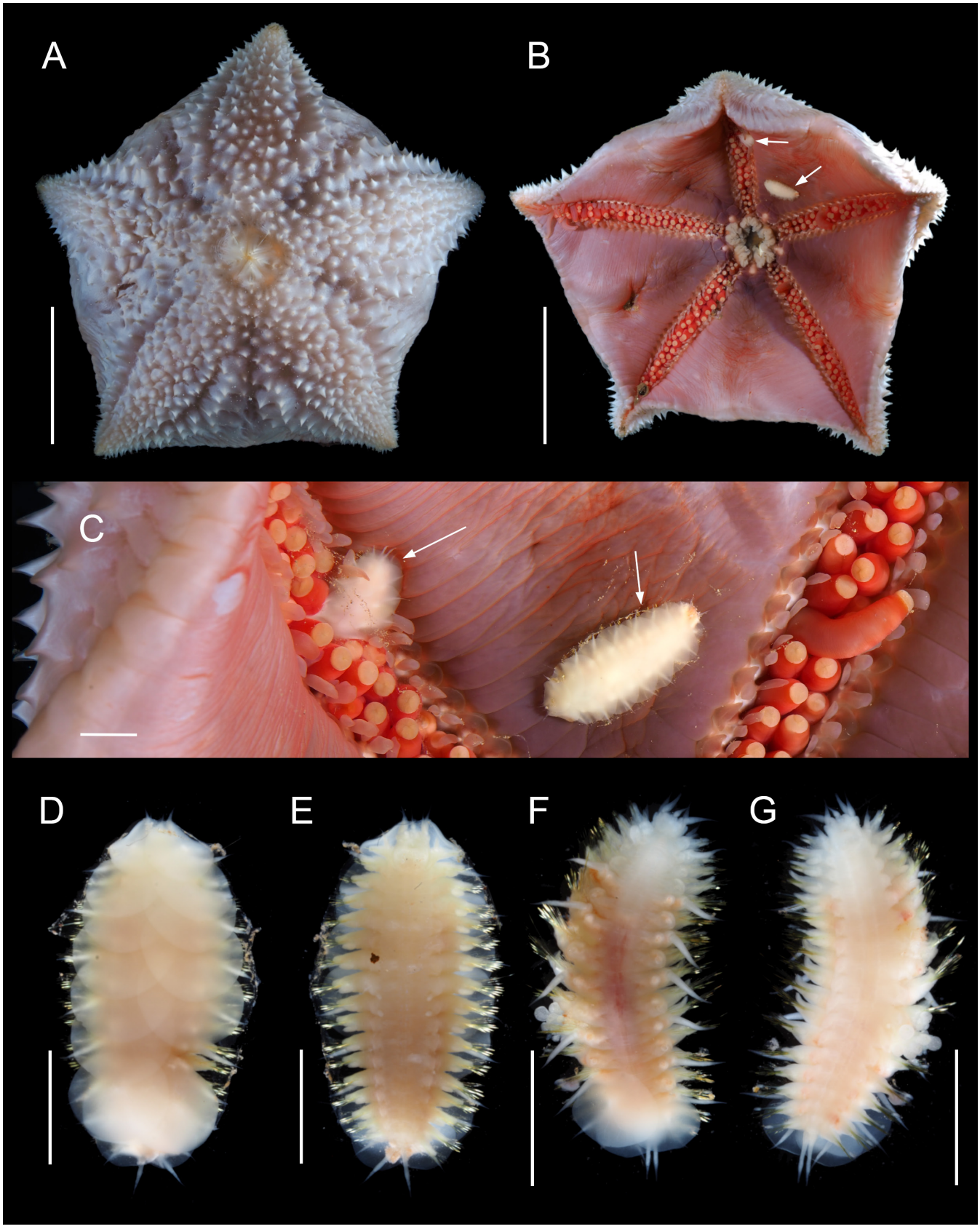

Fig. 9. Live specimens of *Ovatocirra shinkaiae*, new genus and species, D, E, holotype (NSMT-Pol H-1057); F, G, paratype (NSMT-Pol P-1058). A, aboral surface of asteroid host (*Hymenaster* sp.). B, *Ovatocirra shinkaiae* (white arrows) attached to the oral surface of the host. C, close-up of *Ovatocirra shinkaiae* (white arrows). D, F, whole body, dorsal view. E, G, whole body, ventral view. Scale bars: A, B, 50 mm; C–G, 5 mm.

rows on convex margins, with pointed tips (Fig. 11E). Neurochaetae longer and stouter than notochaetae, more abundant (about 30 per ramus). Upper neurochaetae mainly with pointed tips, with faint transverse serrations along the convex margin. Middle to lower neurochaetae with hooked tips with faint transverse serrations on convex margin (Fig. 11F); some newly emerged chaetae with sigmoid tips (Fig. 11G).

Nephridial papillae present from segment 5; prominent and tuberculate on segments 9 and 10, inconspicuous on other segments (Fig. 10C).

Pygidium with a pair of anal cirri, tapering, as long as dorsal cirri of preceding segment (Fig. 10D).

Etymology. The specific epithet *shinkaiae* is derived from the name of the HOV *Shinkai 6500*, treated here as feminine, and refers to the submersible used to collect the type material of this species.

Distribution. North of the Mariana Trench, western Pacific Ocean.

Ecology. This species was found attached to the oral surface of an asteroid (*Hymenaster* sp.), suggesting a commensal association (Fig. 9B). One specimen was observed partially buried in the host's ambulacral groove (Fig. 9C).

Remarks. As discussed by Murray et al. (2025), the term 'facial tubercle' has been used inconsistently in the literature and can be confusing. Here, we follow Murray et al. (2025) in applying this term to the structure located between the upper lip and the anteroventral part of the prostomium. Structures present in the same region have been described using different terminology. For example, in *Macelloides* and *Abyssarya*, the rounded lobes or oval projections situated ventral to the median antenna have been referred as anteroventrally extended prostomial lobes (Pettibone, 1976; Bonifácio & Menot, 2018). In *Bathymacella*, two small protrusions in this position were originally described as "lateral prostomial horns" (Averincev, 1972) but were later interpreted by Pettibone (1976) as the ceratophores of the lateral antennae. As noted by Bonifácio & Menot (2018), further investigation of polynoid anatomy is needed to resolve the sometimes confusing terminology applied to prostomial morphological characters.

Phylogeny. In the ML tree (Fig. 2), *Ovatocirra flavida* was recovered as sister to *O. shinkaiae* with 100% bootstrap support, and together they formed a well-supported clade consistent with the newly proposed genus *Ovatocirra*. This clade was placed within the *Macellicephala* species clade.

DISCUSSION

Polynoids are generally predatory, with a muscular pharynx typically armed with jaws (Hourdez, 2022). However, some taxa show dietary modifications, including the ingestion of algal fragments (Jumars et al., 2015). Marcus & Hourdez (2002) suggested that the hydrothermal vent species with modified feeding structures (jaws absent and replaced by small sclerotinised plates) may instead graze on bacterial mats. In addition, some commensal polynoids feed kleptoparasitically or coprophagically (Jumars et al., 2015). A similar strategy may apply to *Ovatocirra*, new genus, which also lacks jaws (Fig. 4G). Members of this genus may therefore take advantage of their host's diet, reducing the need to actively capture prey. Alternatively, they may feed on epibionts, or on mucus and detritus on the asteroid host's surface, as observed and hypothesised for shallow water commensal species by Wagner et al. (1979). Direct feeding on host tissues appears unlikely, as no obvious discolouration or damage was visible on the oral surface of the asteroids (Figs. 3A, 9B), although this should be validated by a specialist in Asteroidea. Within Macellicephalinae, the number of distal pharyngeal papillae is typically consistent within genera, as also noted by Murray et al. (2025). Consistent with this pattern, both new species described here show a similar distal pharyngeal morphology. Like many other commensal polynoids, these new species also bear hooked neurochaetae (Figs. 7C, D, 8C, 11F); although their tips point dorsally or upward, they are presumed to aid attachment to the host (Hanley, 1989; Ruff, 1991; Molodtsova et al., 2016).

In polynoids, ventral cirri are typically short, digitiform, and distally tapering (Pettibone, 1982; Hourdez, 2022; Rouse et al., 2022) and are thought to have sensory and secretory functions (Lawry, 1967). However, several genera within Arctonoinae, a subfamily that largely comprises commensal polynoids, show reduced, absent or otherwise modified ventral cirri. For example, the shallow water species *Arctonoe fragilis* (Baird, 1863), a commensal inhabiting the ambulacral grooves of asteroids, is characterised by having vestigial, button-like ventral cirri (Hanley, 1989; Ruff, 1995). Although its original description was inadequate and subsequent workers were unable to locate the type material, specimens have continued to be identified as *A. fragilis* primarily on the basis of the distinctive reduced ventral cirri and consistent association with asteroids (Hanley, 1989). Similar patterns occur among deep-water genera, *Bathynoe* Ditlevsen, 1917 and *Parabathynoe* Pettibone, 1990, both containing species commensal with asteroids and are lacking ventral cirri on all segments except segment 2. Ditlevsen (1917) noted this as a "peculiar feature", but it was not discussed further by him, or by subsequent authors describing additional species in the genus. In contrast to reduction or loss, modified ventral cirri also occur in some deep-water commensals. *Brychionoe karenae* Hanley & Burke, 1991 (Polynoinae), a commensal of antipatharians, is characterised by large ventral cirri with numerous long papillae on the ventral surface (Hanley & Burke, 1991). Likewise, *Phyllosheila wigleyi* Pettibone, 1961 (Polynoidae incertae sedis), collected from the ambulacral groove of a brisingid sea star, possesses large, leaf-like ventral cirri resembling those of phyllodocids (Pettibone, 1961).

As described here, *Ovatocirra* possesses ovate to subovate ventral cirri (Figs. 4B, F, 6A, B, E, 10B, C, 11A–D) and is currently hypothesised to be commensal with deep-water

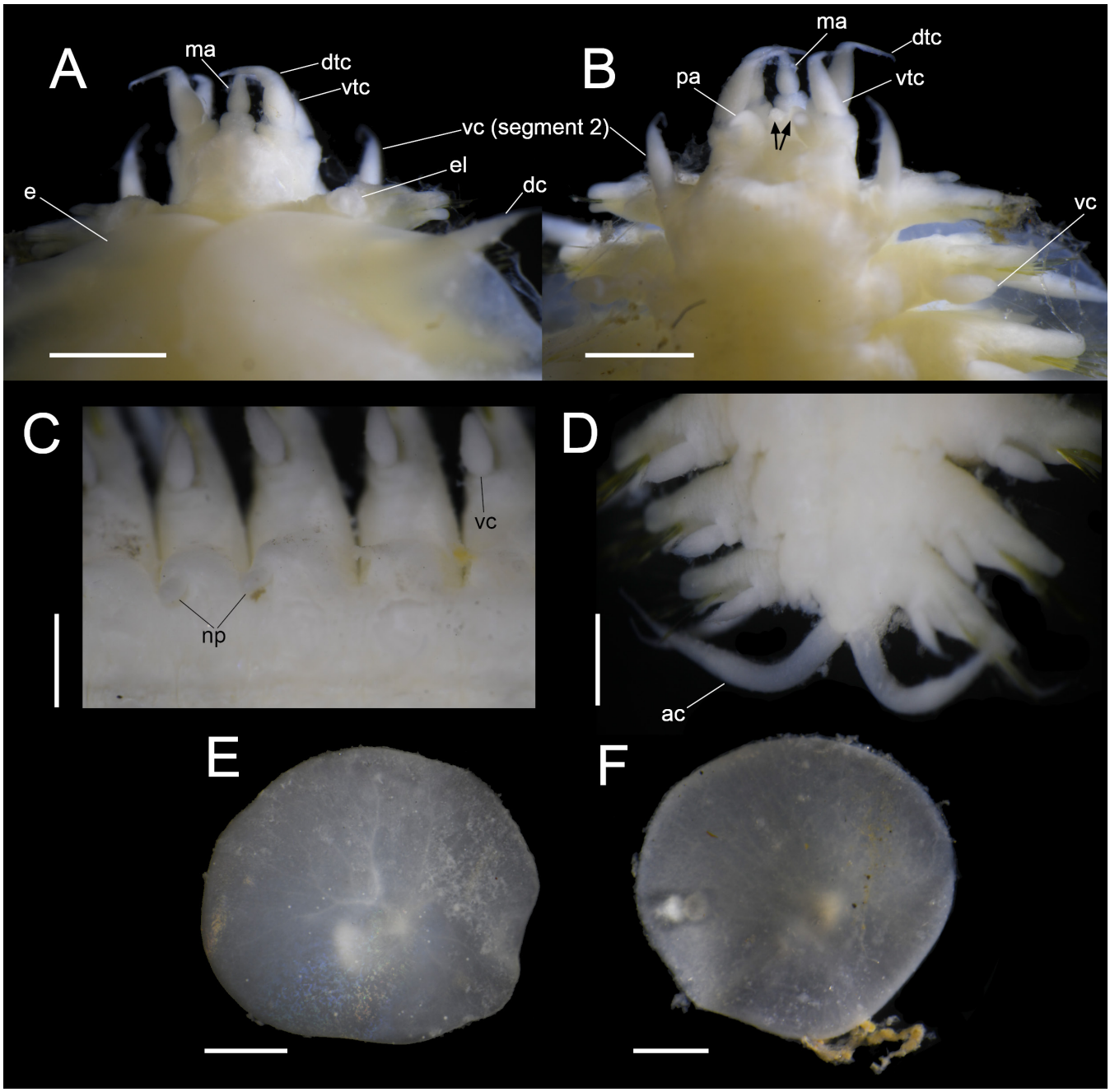

Fig. 10. Preserved specimen of *Ovatocirra shinkaiae*, new genus and species, holotype (NSMT-Pol H-1057). A, anterior end, dorsal view. B, anterior end, ventral view; black arrows indicate facial tubercles. C, mid-body segments, ventral view (horizontal). D, posterior end, ventral view. E, elytron from a mid-body segment, dorsal view. F, elytron from a mid-body segment, ventral view. Abbreviations: ac, anal cirrus; dc, dorsal cirrus; dtc, dorsal tentacular cirrus; e, elytron; el, elytrophore; ma, median antenna; np, nephridial papillae; pa, palp; vc, ventral cirrus; vtc, ventral tentacular cirrus. Scale bar: 1 mm.

asteroids, and also possibly with crinoids, as the new species were found in association with these groups. Additional material will be required to determine whether members of this genus are restricted to these two groups or also associate with other echinoderms. Nevertheless, the modified ventral cirri likely reflect adaptation to a commensal lifestyle on their hosts. At present, *Ovatocirra* appears to be the only genus in Macellicephalinae with modified ventral cirri.

Commensal polynoids often display colour patterns that mimic their hosts (Britayev & Zamishliak, 1996; Martin & Britayev, 1998; Sugiyama et al., 2026). In contrast, *Ovatocirra flavida*, new species, has bright yellow elytra, and *Ovatocirra shinkaiae*, new species, has white elytra that appear conspicuously different from the colour of the hosts' oral surfaces (Figs. 3, 9). A similar pattern occurs in *Asterophilia carlae* Hanley, 1989, a shallow water commensal associated with asteroids and other echinoderms (Hanley, 1989; Sugiyama et al., 2020). They have been reported as consistently reddish or whitish regardless of host colour (Sugiyama et al., 2020). The type specimen was attached to a blue asteroid, and Hanley (1989) noted the flesh-coloured polynoid as incongruous with its host. Despite this colour mismatch, Hanley (1989) highlighted the three raised mounds

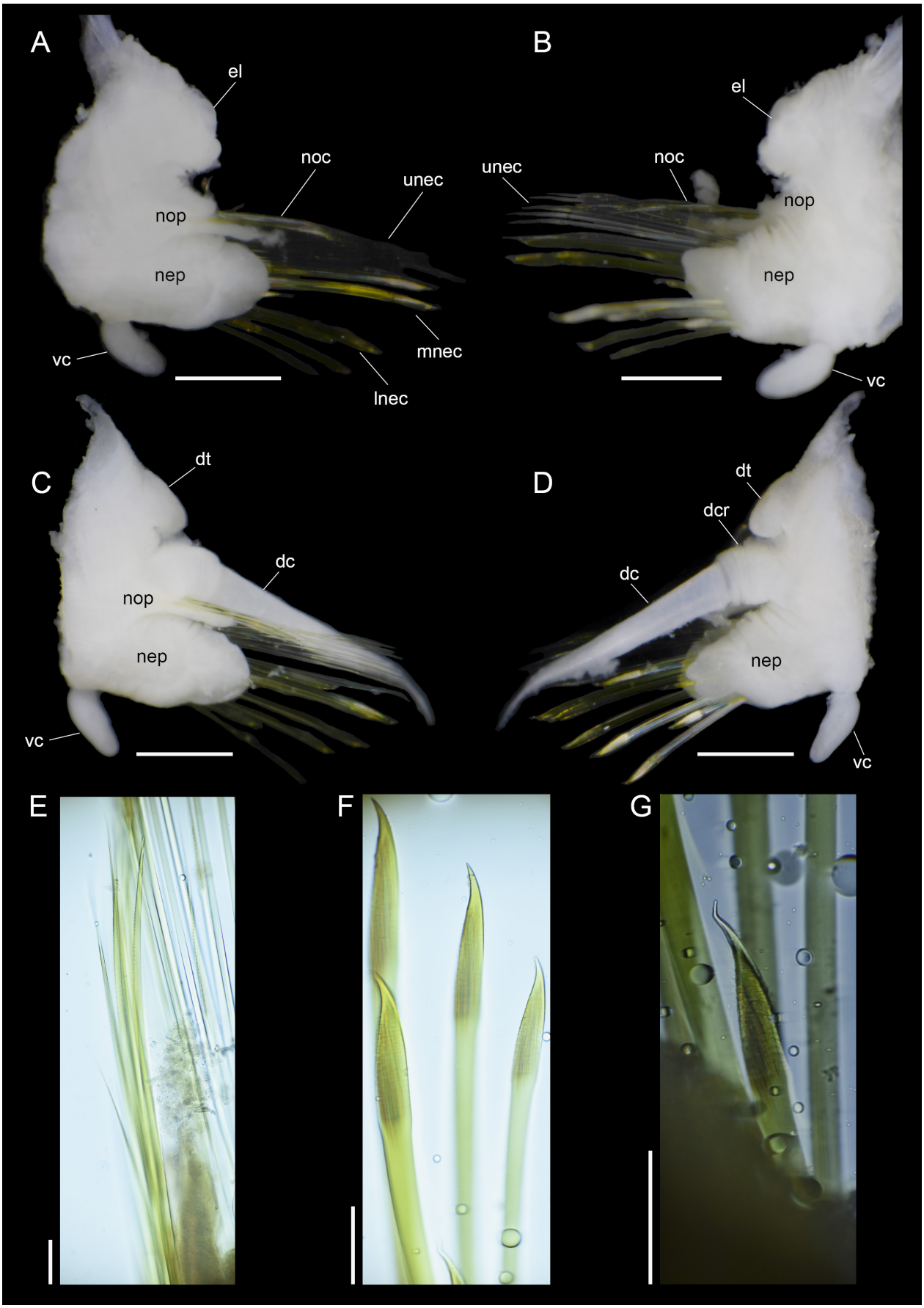

Fig. 11. Parapodia and chaetae of *Ovatocirra shinkaiae*, new genus and species, holotype (NSMT-Pol H-1057). A, B, left parapodia from segment 13 and C, D, segment 14. A, C, anterior view. B, D, posterior view. E, notochaetae. F, lower neurochaetae. G, neurochaeta with sigmoid tip. Abbreviations: dc, dorsal cirrus; dcr, dorsal cirrophore; dt, dorsal tubercle; el, elytrophore; lnec, lower neurochaetae; mnec, middle neurochaetae; nep, neuropodium; noc, notochaetae; nop, notopodium; unec, upper neurochaetae; vc, ventral cirrus. Scale bars: A–D, 0.5 mm; E–G, 0.1 mm.

on the edge of each elytron as an example of morphological mimicry, resembling the tube feet of the host. Likewise, in the abyssal asteroid-commensal polynoid *Bathynoe cascadiensis* Ruff, 1991, the characteristic elongated macrotubercles on the elytra were suggested to mimic the spines and tube feet of the asteroids, potentially reducing the likelihood of attack or rejection by the host (Ruff, 1991).

In *Ovatocirra flavida*, new species, the elytral mound-like protrusions are less pronounced than those in *A. carlae* or *B. cascadiensis*. However, the overall rugose dorsal surface of the elytra seemingly closely matches the tuberculate oral surface of the host asteroid (Fig. 3C). Conversely, the smooth elytra of *O. shinkaiae*, new species, correspond closely to the smooth oral surface of its host (Fig. 9B, C). In addition, because the worms were attached to the host's oral surface, which is considered one of the most protected sites (Martin & Britayev, 1998), the yellow or whitish colouration may be less likely to increase exposure to predators. Although not tested here, the vivid yellow pigmentation in *O. flavida*, new species (Fig. 5D), could also suggest the potential for fluorescence. In polynoids, luminescent elytra have most often been interpreted as a mechanism to deter or distract predators (Verdes & Gruber, 2017; Livermore et al., 2018). However, Taboada et al. (2021) hypothesised that a deep-sea polynoid may have a mutualistic relationship with its carnivorous sponge host, using bioluminescent elytra to attract zooplankton and thereby benefiting both parties. Fresh material will be needed to determine whether this newly described species is bioluminescent.

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