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Two new species of Syllidae (Annelida) from Misaki Bay and Sugashima Island, Japan

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Abstract

The shorelines of Japan host diverse ecosystems, particularly in the shallow coastal waters, which are rich in syllid species. This study describes two new Syllidae species: *Virchowia christophi* **sp. nov.**, discovered at Misaki and Sugashima Island, and *Paraopisthosyllis rufa* **sp. nov.**, found at Misaki. Additionally, we provide a redescription of *Syllis okadai* Fauvel, 1913, based on specimens collected from Misaki. *Virchowia christophi* **sp. nov.** shows a unique combination of characters, such as branched nuchal epaulettes together with a complex colouration pattern featuring white, beige, and brown transverse lines, along with white refringent dots, and chaetae with long distal teeth. The second new species, *Paraopisthosyllis rufa* **sp. nov.**, is distinguished from similar species by its vivid red colouration and segments secondarily triannulated. *Paraopisthosyllis rufa* **sp. nov.** is able to generate a secondary ventral tail while the developing stolon (reproductive unit) is still attached to the parental stock. This trait has previously been observed in species of *Megasyllis* San Martín *et al.* 2008 and *Alcyonosyllis* Glasby & Watson, 2001, two genera that are phylogenetically closely related to *Paraopisthosyllis* Hartmann-Schröder, 1991. This is the first report of the genus *Paraopisthosyllis* from Japan. Dense ciliation around eyes is identified as a new characteristic of *Syllis okadai* and its stolons are described in detail. The phylogenetic position of all three species is investigated using maximum likelihood, combining three genes (18S, 16S, COI). *Paraopisthosyllis rufa* **sp. nov.** forms a monophyletic clade with other *Paraopisthosyllis* species. *Syllis okadai* from Misaki is sister to the already investigated *Syllis okadai* from Manazuru, Japan. *Virchowia christophi* **sp. nov.** has an ambiguous phylogenetic position within Autolytinae since current molecular data suggests that *Virchowia* Langerhans, 1879 might be paraphyletic.

Key words: *Virchowia*, *Paraopisthosyllis*, taxonomy, phylogeny, systematics

Introduction

Syllidae Grube, 1850 is a monophyletic family of free living, marine, small- to medium sized worms belonging to the Annelida (Aguado & San Martín 2009; San Martín & Worsfold 2015; San Martín & Aguado 2022). The family is divided into five subfamilies Anoplosyllinae Aguado & San Martín, 2009; Autolytinae Langerhans, 1879; Eusyllinae Malaquin, 1893; Exogoninae Langerhans, 1879 and Syllinae Grube, 1850 (Aguado & San Martín 2009) and currently, approximately 1,100 species across more than 70 genera have been described. Among these, *Syllis* Lamarck, 1818, stands out as the most diverse genus, with nearly 200 extant species (Read & Fauchald 2024), though it remains in need of revision (San Martín & Aguado 2022). Syllids have a cosmopolitan distribution in marine waters and occur in high abundances between the intertidal and the deep sea (San Martín & Aguado 2022).

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Syllids exhibit remarkable diversity in their morphology and ecology, occupying habitats ranging from interstitial spaces to reef ecosystems and hydrothermal vents (Nygren 2004; San Martín & Aguado 2022; Jimi *et al.* 2024). Their body organization mostly follows the typical annelid, however, exceptions with branching body plans are known (Aguado *et al.* 2022). Whilst most syllids are free-living organisms, both exo- and endosymbiotic species have been found, with poriferans, cnidarians, bryozoans, echinoderms, and tunicates representing the most common hosts (Martin & Britayev 2018). Despite their high diversity and often cryptic appearance, syllids can be recognized by their proventricle, an anterior differentiation of their digestive tube (Glasby 2000; Aguado *et al.* 2012; Rouse *et al.* 2022). Species identification can be difficult within the family, however, characters such as pattern of cirri alternation, chaetal morphology and number of segments allow to identify many genera and, in many cases, even species. Syllids have been known to science for a long time, though new species continue to be discovered (e.g., Jimi *et al.* 2024) as marine ecosystems are further explored and survey techniques improve. The shallow waters along Japan's coastline are particularly noteworthy, exhibiting high syllid diversity across the islands, as documented by Imajima and Hartman in 1964 and Imajima in 1966. Several taxonomic studies on Syllidae have been conducted along the Japanese coast (Imajima 1997; San Martín and Nishi 2003; Aguado *et al*. 2006, 2008, 2022; Cejp *et al*. 2023; Jimi *et al*. 2024; Fourreau *et al.* 2024), though the immense biodiversity of the group remains far from fully documented, presenting many challenges yet to be tackled. In this study we describe two new species of Syllidae from Misaki Bay, Japan: *Paraopisthosyllis rufa* **sp. nov.** (Syllinae) and *Virchowia christophi* **sp. nov.** (Autolytinae), the latter also found in Sugashima Island. Their phylogenetic relationships within the family and their respective subfamilies are analysed and detailed descriptions and iconography provided. Additionally, a new report of *Syllis okadai* from Misaki and photographs of live specimens, complementary to previous descriptions, are included.

Material and Methods

All specimens were collected in Misaki, Japan in 2019 and 2022, and Sugashima Island in 2024, in intermediate depths between 2–10 m on rocky shorelines. After collection, specimens were anesthetized by menthol or 7% MgCl2 (w/v in distilled water) solution and photographed using a stereoscopic microscope (SZX-16, Olympus, Tokyo, Japan) equipped with a CCD camera (DP74, Olympus). Specimens were fixed in 100% EtOH. Specimens were examined and drawings were made with the Leica S APO stereomicroscope and Leica DM 2500 microscope, pictures were taken using a KEYENCE VHX-7000 digital microscope. For scanning electron microscopy (SEM), the specimens were treated with OsO4 for 20 min, rinsed with ddH2O, dehydrated in a graded ethanol series (20%, 50%, 70%, 90%, 100%, 20 min each), critical point dried using a BALZERS CPD 030 and placed on stubs. They were then coated with gold twice using a BALZERS SCD 050 and SEM photographed in a JSM-IT500. The figures were prepared in Adobe Photoshop C3 (Adobe) and Adobe Illustrator (Adobe). Types and voucher specimens have been deposited at the National Museum of Nature and Science of Tokyo (NSMT) and the Biodiversitätsmuseum Georg-August-Universität Göttingen (ZMUG). Comparative material of *Virchowia pectinans* (Hartmann-Schröder, 1983) from the Australian Museum (AM) was examined by MA in 2012 thanks to a 'Geddes visiting fellowship'.

Phylogenetic analyses were conducted using two mitochondrial markers (16S, COI) and one nuclear marker (18S), which have previously been shown to be effective and remain suitable for phylogenetic research in syllids (Aguado & Bleidorn 2010; Aguado *et al.* 2022, Jimi *et al*. 2024). DNA was extracted following the DNeasy Blood and Tissue Protocol of QIAGEN. The library was sequenced as 150 bp paired-end run, on an Illumina NovaSeq 6000 S4 PE150. Base calling was performed with freeIbis (Renaud *et al.* 2013), adaptor and primer sequences were removed using lee-Hom (Renaud *et al.* 2014) and reads with low complexity and false paired indices were discarded. Quality checking was done using FASTQC v0.11.9. Raw data of all libraries were trimmed excluding low-quality reads; adaptors and primer sequences were removed using Trim Galore v0.6.7 (Krueger 2015). All trimmed reads were broken down into *k*-mers and reassembled into contigs in a de novo assembly using SPAdesv3.13.0 (Prjibelski *et al*. 2020). SPAdes was used with default settings and a minimum *k*-mer size of 31 (*Paraopisthosyllis rufa* **sp. nov.**), and 91 for the other syllids. The *k*-mers were chosen based on the quality assessment of the assemblies done by QUAST v5.1 (Gurevich *et al.* 2013) and altered if necessary. COI and 16S gene were obtained from the assembled mitochondrial genomes annotated by MITOS (Bernt *et al.* 2013). The nuclear 18S gene sequence was identified using BLASTN (Altschul *et al.* 1990; Zhang *et al.* 2000) against the assemblies with the sequences of 18S of *Virchowia clavata* Langerhans, 1879 (GQ856171), *Paraopisthosyllis alternocirra* San Martín & Hutchings, 2006 (JF903786) and *Syllis okadai* (EF123857-8), respectively, as queries. Alignments were made using the online tool

TABLE 1. Comparative list of key characters, reproductive mode and distribution for *Virchowia* species. *Virchowia christophi* **sp. nov.** in bold. S: scissipary, AS: anterior scissiparity.

Virchowia	Pharynx sinuation	Trepan teeth	Proventricle in chaetiger	Reproductive mode	Chaetae Morphology (Compound)	Distribution	References
V. branchiata (Averincev, 1972)	1-several	20 uneq 1L+(1–3)S	6–8(2–3)	S; AS	two large teeth at top, serrations along edge, short + thick	Antarctic Ocean	Averincev 1972; Nygren 2004
V. clavata (Langerhans, 1879)	Several	24 eq	5(1)	S; AS	two large teeth at top, serrations along edge, long+ slender	Northeast Australia	Nygren 2004
V. japonica (Imajima & Hartman, 1964)	?	?	?	S; AS?	two large teeth at top, serrations half way, long+ slender	Pacific Ocean (Japan)	Imajima & Hartmann 1964
V. longipharyngia (Hartmann-Schröder, 1989)	Several	20 eq	4–5(1)	?	no large teeth at top, serrations along edge, long+thick	Southwest Pacific	Nygren 2004
V. pectinans (Hartmann-Schröder, 1983)	1	17 uneq 1L+(1–2)S	5–6(2)	S; AS	second tooth very large, serrations along edge, shorter + slender	East Indian Ocean	Nygren 2004
V. spirifer (Augener, 1913)	1	28 uneq 1L+(1–3)S	3(1)	S; AS	second tooth very large, no serrations, one small tooth on the edge, long+slender	Southwest Pacific, East Indian Ocean	Hartmann-Schröder 1989; Nygren 2004
***V. christophi* sp. nov.**	2 sinuations	25 uneq 1L+(1–2)S	3–6	S; AS	two teeth at top, second larger, no serrations	Pacific Ocean (Japan)	This study

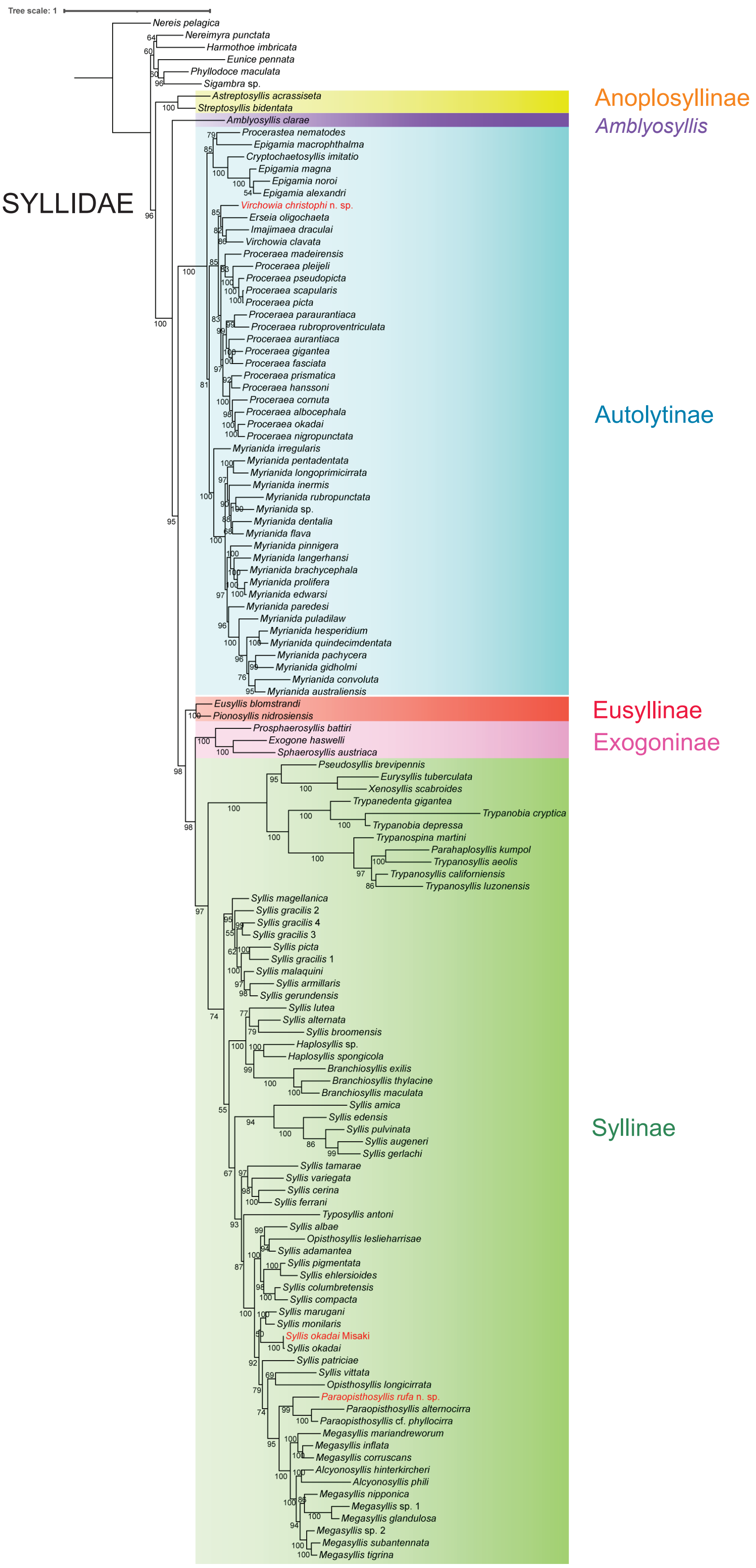

FIGURE 1. Maximum likelihood tree of Syllidae. Bootstrap values are shown. The newly described species *Virchowia christophi* **sp. nov.**, *Paraopisthosyllis rufa* **sp. nov.** and the redescribed *Syllis okadai* from Misaki are in red. Yellow = Anoplosyllinae; purple = *Amblyosyllis clarae*; blue = Autolytinae; red = Eusyllinae; pink = Exogoninae; green = Syllinae.

MAFFT v7 (Katoh & Standley 2013) with default gap opening and gap extension penalties and inspected using BioEdit v7.2 (Hall 1999). Single genes were concatenated with FASconCAT-G (Kück & Meusemann 2010; Kück & Longo 2014). The maximum likelihood analyses were performed using IQ-Tree v2.2.0 (Nguyen *et al.* 2015; Chernomor *et al.* 2016), and best-fitting models were selected with the IQ-TREE embedded instance of modelfinder (Kalyaanamoorthy *et al.* 2017). Support values were estimated based on bootstrapping protocol with 1000 pseudoreplicates (BP). Analyses were made for each marker separately as well as for the concatenated gene matrix (COI+16S+18S). *Eunice pennata* Müller, 1776 (Eunicidae); *Harmothoe imbricata* Linnaeus, 1767 (Polynoidae); *Nereis pelagica* Linnaeus, 1758 (Nereididae); *Phyllodoce maculata* Linnaeus, 1767 (Phyllodocidae); *Nereimyra punctata* Müller, 1788 (Hesionidae) and *Sigambra* sp. Müller, 1858 (Pilargidae) were selected as outgroups. GenBank Accession numbers for the sequences of the new species are: *Virchowia christophi* **sp. nov.** (18S: PV288372, 16S: PV275265, COI: PV285284); *Paraopisthosyllis rufa* **sp. nov.** (18S: PV288371, 16S: PV275264). GenBank accession numbers for all terminals are provided in Sup. Table 1.

Three different analyses were run independently, the first one containing all Syllidae (Fig. 1), the second one including only Autolytinae species (Fig. 2) and outgroups, and the third one included only the Syllinae (Fig. 3) and outgroups. The second and third analyses were conducted to more accurately determine the position of the new species within the groups to which they were found to belong in the first analysis (Fig. 1).

Results

Phylogenetic results

In the analysis containing all terminals, Syllidae is monophyletic and well supported (BP 96) (Fig. 1). Within Syllidae, Anoplosyllinae is the sister group to a large clade containing the rest of all other syllids (BP 100). Within this large clade, *Amblyosyllis clarae* Aguado *et al.* 2019 is sister to the rest, which are grouped in a large clade (BP 95). Within this latter clade, the classical subfamilies: Autolytinae, Eusyllinae, Exogoninae and Syllinae (as defined by Aguado *et al*. 2012) are monophyletic (BPs 100, 100, 100, 97, respectively). Within Autolytinae, the genus *Virchowia* is paraphyletic. *Virchowia christophi* **sp. nov.** is nested within a clade with *Erseia oligochaeta* Nygren *et al.,* 2010 (BP 82), *V. clavata* and *Imajimaea draculai* San Martín & López, 2002 (BP 85). The genus *Epigamia* Nygren, 2004 is paraphyletic, with *Procerastea nematodes* Langerhans, 1884 (BP 79) and the recently described species *Cryptochaetosyllis imitatio* Jimi *et. al.* 2024 (BP 100) placed inside. Within Syllinae, *Syllis okadai* from Misaki is joined to *S. okadai* from Manazuru, Japan; and the new species *Paraopisthosyllis rufa* **sp. nov.** is nested within *Paraopisthosyllis* species (BP 99) and sister to *Megasyllis*-*Alcyonosyllis* species (BP 100).

In the second analysis, focused on Autolytinae relationships (Fig. 2), Autolytinae is monophyletic, well supported (BP 100) and split into two lineages, all *Myrianida* Milne Edwards, 1845 (BP 88) and all other Autolytinae (BP 91), respectively. The second group is split further into two lineages, one with all *Epigamia* and *Cryptochaetosyllis* (BP 93); and a second one (BP 93) comprising *Erseia oligochaeta* sister to a clade with all *Proceraea* Ehlers, 1864 species (BP 58) and a clade including *Virchowia christophi* **sp. nov.** *Virchowia clavata*, *Procerastea nematodes* and *Imajimaea draculai*. Bootstrap support for *Virchowia, Procerastea* Langerhans, 1884 and *Imajimaea* clade is not high (BP 77). *Procerastea nematodes* and *Imajimaea draculai* appear as sister taxa (BP 90), with *Virchowia clavata* as the sister to these two (BP 86). *Virchowia christophi* **sp. nov.** is the sister species to all three latter species, rendering *Virchowia* paraphyletic, though this clade is not well supported (BP 77).

In the third analysis, focused on Syllinae relationships (Fig. 3), Syllinae is monophyletic and well supported (BP 99). Syllinae splits into two major groups, one clade (BP 100) consisting of *Pseudosyllis brevipennis* Grube, 1863; *Xenosyllis scabroides* San Martín *et al.* 2008; *Eurysyllis tuberculata* Ehlers, 1864; *Parahaplosyllis kumpol* Álvarez-Campos *et al.* 2013; *Trypanospina martini* Álvarez-Campos *et al.* 2018; *Trypanedenta gigantea* McIntosh, 1885; *Trypanobia depressa* Augener, 1913 *Trypanobia cryptica* Aguado, Murray & Hutchings, 2015 and several species of the genus *Trypanosyllis* Claparède, 1864, which is paraphyletic. This clade has been previously informally named "the Ribbon Clade" (Aguado *et al.* 2015; Ribeiro *et al.* 2020; Ponz-Segrelles *et al.* 2021). The second clade includes the remaining Syllinae (BP 82) (Fig. 3) and was previously referred to informally as "Clade 2" by Ribeiro *et al.* (2020). The redescribed *S. okadai* from Misaki (Japan) groups together with *S. okadai* from Manazuru (Japan) and are both the same species (BP 100). They are nested within the paraphyletic genus *Syllis* (BP 91). The new species

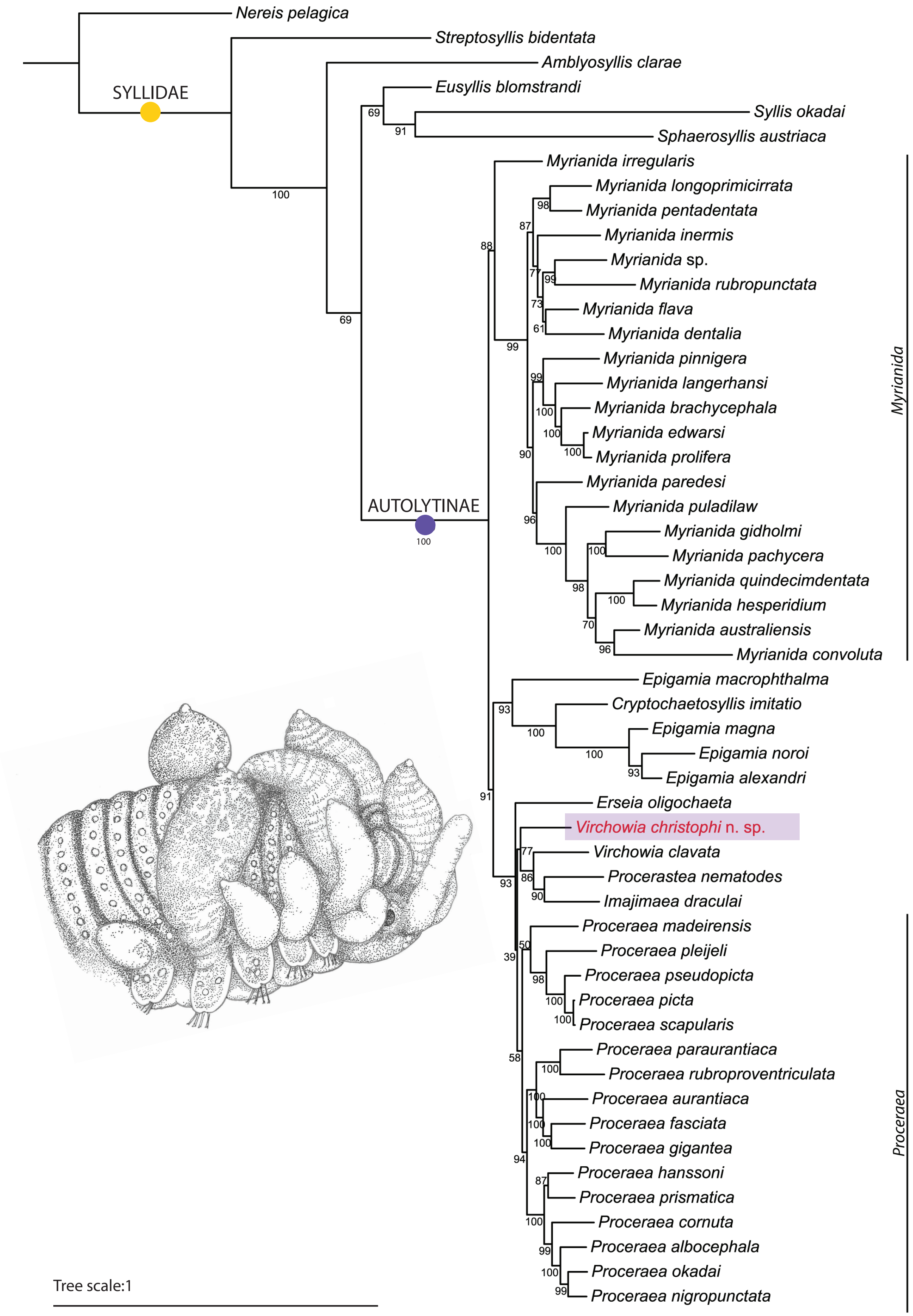

FIGURE 2. Maximum likelihood tree of Autolytinae. Bootstrap values are shown. The newly described species *Virchowia christophi* **sp. nov.** is in red.

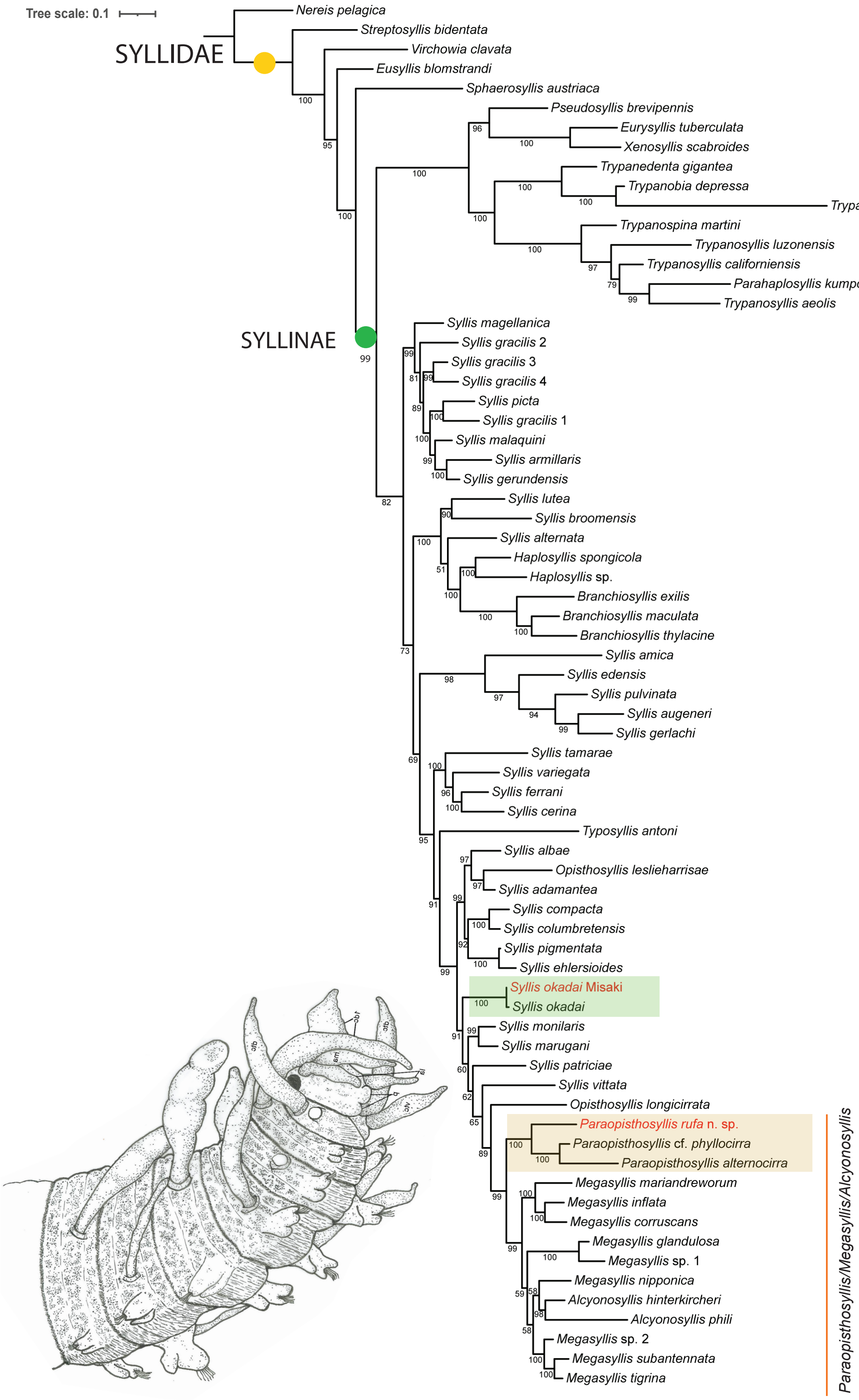

FIGURE 3. Maximum likelihood tree of Syllinae. Bootstrap values are shown. The newly described species *Paraopisthosyllis rufa* **sp. nov.** and the redescribed *Syllis okadai* from Misaki are in red.

Paraopisthosyllis rufa **sp. nov.** clusters with other species of *Paraopisthosyllis* (BP 100), together forming the monophyletic genus *Paraopisthosyllis*, which is the sister taxon to the *Megasyllis* and *Alcyonosyllis* group (BP 99). Their positions did not change in comparison with the topology obtained from analysing all Syllidae together (Fig. 1), while their bootstrap support values are slightly modified (Figs 1, 3).

Taxonomic results

Virchowia christophi **sp. nov. Aguado, Springer, Oguchi, Sato, Jimi & Miura Figs 4–10, Table 1**

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Material examined. Holotype (NSMT-Pol H-975) and two paratypes (NSMT-Pol P-976): Japan, Misaki: Arahaima Beach, Sagami Bay, Misaki, 35°09'34"N 139°36'40"E, 2–5 m, coll. Oguchi, 2022. Three paratypes (ZMUG 32498) and additional material (NSMT-Pol 113615): Japan, Misaki: Sagami Bay, Misaki Marine Biological Station, 35°09'36.1"N 139°36'40.1"E, 2–5 m, coll. Aguado & Oguchi 2019, Sato & Aguado 2024. Additional material (ZMUG 32500): Japan, Sugashima Island: Kamekobana, 34°28'40"N 136°53'00"E, 5 m, coll. Jimi, Tsuyuki & Ishibashi 2024.

Comparative material. *Virchowia pectinans* (Hartmann-Schröder, 1983) (AM-W41620): New South Wales: S. of Grasshopper Is., 2004.

Description. Length between 8.7–12.8 mm for 37–39 segments, width 0.35–4 mm. Adult specimens with developing stolons. Body consists of prostomium, 13 segments, stolon head, 37–39 stolon segments (depending on the stolon's developmental stage) and pygidium. Adult specimens without stolon consist of prostomium, 50 segments and pygidium. Body slender, tubular, ventrally flattened and thickest in segments 5–7 (Fig. 4A). Body and appendages contracted in fixed material (Fig. 4A), longer and slender in live specimens (Fig. 5A, B). Prostomium with four red eyes in trapezoidal arrangement. Nuchal epaulettes sand coloured in both live and fixed specimens, originating dorsally on prostomium (Figs 4A, 5B), bifurcated (Fig. 6A–C, E), and highly ciliated (7C). One band of cilia around the eyes (Fig. 7D). Median antenna thick (Fig. 4A), sand coloured, as long as three segments (Fig. 5A–B). Lateral antennae slim, sand coloured, length 2/3 of median antenna (Figs 4A, 5A–B). Palps ventrally located, basally fused to the prostomium, free distal ends (Fig. 6D). Peristomium fused with prostomium, not distinguishable. Dorsal tentacular cirri 2/3 length of median antenna, ventral pair long, thinner than dorsal pair (Figs 4A, 5A–B). Median antenna, lateral antennae, tentacular cirri cylindrical, distally pointed (Figs 4A, 5A–B, 6A–B, E). First dorsal cirri reaching chaetiger 3, longer than lateral antennae, fourth dorsal cirri as long as first pair (Figs. 4A, 5A–B). Second and third dorsal cirri smaller, as long as ventral tentacular cirri (Figs 4A, 5A–B). Ventral cirri fused to parapodia (Figs 4A, 7A). Dorsal cirri follow consistent pattern of alternation (pointing up: U; down: D): adult head, U, D, D, U, D, U, D, D, U, D, U, D, U, stolon head, D, U, D, U, D, U, D, D, D, U, D, U, D, U, D, D, U, U, D, D, D, U, D, D, U, U, D, D, D, U, D, D, U, D, D, U, D, stolon pygidium (Fig. 5A–B). Same alternation pattern in all specimens. No alternation in cirri placement (Fig. 8A). Upwards oriented dorsal cirri clavate, thick, sandy colouration, distally pointed (Figs 4A, 5A–B). Downwards oriented dorsal cirri short, slim, whitish, distally pointed (Figs 4A, 5A–B).

Segments faintly secondarily annulated, more pronounced in anterior region (Figs 4A, 6A, 8B). All dorsal surface, dorsal cirri and antennae with glandular openings (Figs 8B, 9D, E). Bunch of cilia in antennae and first dorsal cirri (Figs 7A, B, 9A–D) and "star-shaped" filament extensions (Fig. 9B, F). Striking colour pattern (Figs 5, 6), consistent in all specimens, only slight deviations in the stolons. Colouration identical in both live and fixed specimens with no fading observed after five years of storage. Segment colours vary between sandy/beige and dark brown. Thin, dark brown bands mark the end/the beginning of each segment (Fig. 5A, B). Two dark-brown, rounded spots located laterally between segments 3/4; 8/9 and 12/13 of the adult holotype. Spots can vary in size; but placement is consistent in all specimens. Most segments with at least one line of small white refringent dots spanning across the width of the segment, some segments with up to four lines of white dots. Dotted lines may continue onto the downwards oriented dorsal cirri, but never onto the upwards oriented dorsal cirri. Most segments do not vary in colour within themselves, but the number of white dots per annulation may vary within a segment. Segments 10 and 11 of the adult holotype appear almost white and shining due to high number of white dots. Segments 4, 9 and 13 of the adult holotype appear dark brown. Parapodia with 7–10 chaetae (Fig. 10A). Parapodia rounded, bilobed (Fig. 10A). Chaetae bidentate, without blade serration (Figs 4B–C, 10B–D), and simple (shafts

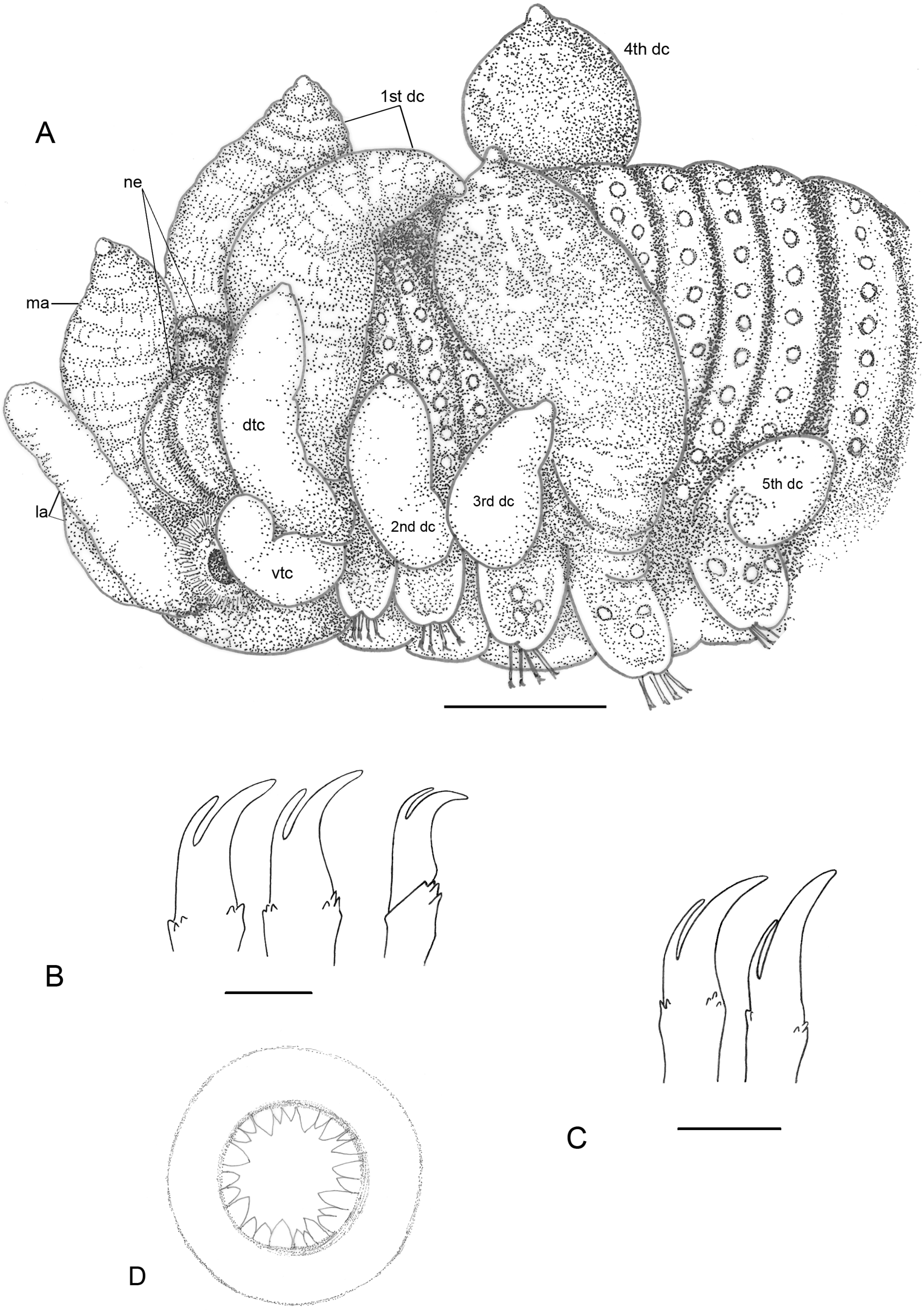

FIGURE 4. *Virchowia christophi* **sp. nov.** NSMT-Pol P-976; A Anterior end, lateral view, ma = median antenna, la= lateral antenna, ne = nuchal epaulettes, dtc = dorsal tentacular cirri, vtc = ventral tentacular cirri, dc = dorsal cirri; B midbody chaetae; C posterior chaetae, dorsal most in the fascicle (ventral compound chaetae as in midbody segments); D trepan. Scale bars: A = 400 µm; B, C = 5 µm.

FIGURE 5. *Virchowia christophi* **sp. nov.** A whole specimen, dorsal view. B whole specimen, dorsal view, arrows pointing at stolon head. Detail in B shows anterior end, ma = median antenna; la = lateral antenna; ne = nuchal epaulettes; dtc = dorsal tentacular cirri; vtc = ventral tentacular cirri; 1dc = first dorsal cirrus. Scale bars: A, B = 1000 µm.

and blades fused, Figs 10 B, C), 1–2 most-ventral ones within the chaetae fascicle remain compound (Fig. 10D). Proximal tooth larger than distal one (Figs 4C, 10C, D). Chaetae from anterior and posterior-most segments with elongated distal teeth, especially the proximal one. No simple chaetae or bayonet chaetae present. Two pointed aciculae. Long and twice-sinuated pharynx reaching segments 1–3. Trepan provided with 25 unequal teeth, alternating 1 large and 1–2 small teeth, arranged in 1 ring (Fig. 4D). Proventricle cylindrical, occupying segments 3–6 (not clearly seen by transparency) in both live and fixed specimens. Pygidium with two small, opaque and cylindrical anal cirri (Fig. 5A–B, 6F).

FIGURE 6. *Virchowia christophi* **sp. nov.** A anterior end, lateral view. B anterior end detail, dorsal view. C anterior end, dorsal view. D anterior end, ventral view. E anterior end, lateral view. F posterior end, dorsal view. 1dc = first dorsal cirrus; ne = nuchal epaulettes; e = eyes; ma = median antenna; la = lateral antenna; vtc = ventral tentacular cirrus; dtc = dorsal tentacular cirrus; pa = palps; ac = annal cirri. Scale bars: A–D, F = 200 µm; E = 500 µm.

Reproduction. Schizogamy by anterior scissiparity. Developing stolon behind segment 13 (Fig. 5A–B). Stolon with four red eyes in trapezoidal arrangement, anterior pair larger (Fig. 5B). Median and lateral antennae developed, small, white opaque. Cirri, at this point of development (Figs 5A, B, 8C–D), with same colour and shape as anterior adult cirri. Pattern of alternation consistent across all stolon specimens. Pygidium with pair of small, rounded, white opaque anal cirri. Segment colours vary between sandy/beige and dark brown. Colouration pattern as described for the atoke specimens. Two dark-brown, rounded spots located laterally between segments 4/5; 8/9; 9/10; 10/11; 14/15; 15/16; 22/23; 30/31 of the stolon. Segments 6, 7, 13, 17, 18, 24–26, 29, 30 and 33–36 of the stolon appear almost white and shining due to high number of white dots. Segments 5, 8–11, 15, 16, 20, 24, 28 and 32 dark brown. Parapodia with 7–10 chaetae. Chaetae with slim shafts, no blade serration. Bayonet chaetae not seen. No notochaetae present at the described development stage.

Habitat. Rocky shorelines, shallow waters 2–5 m deep, on algae and below rocks.

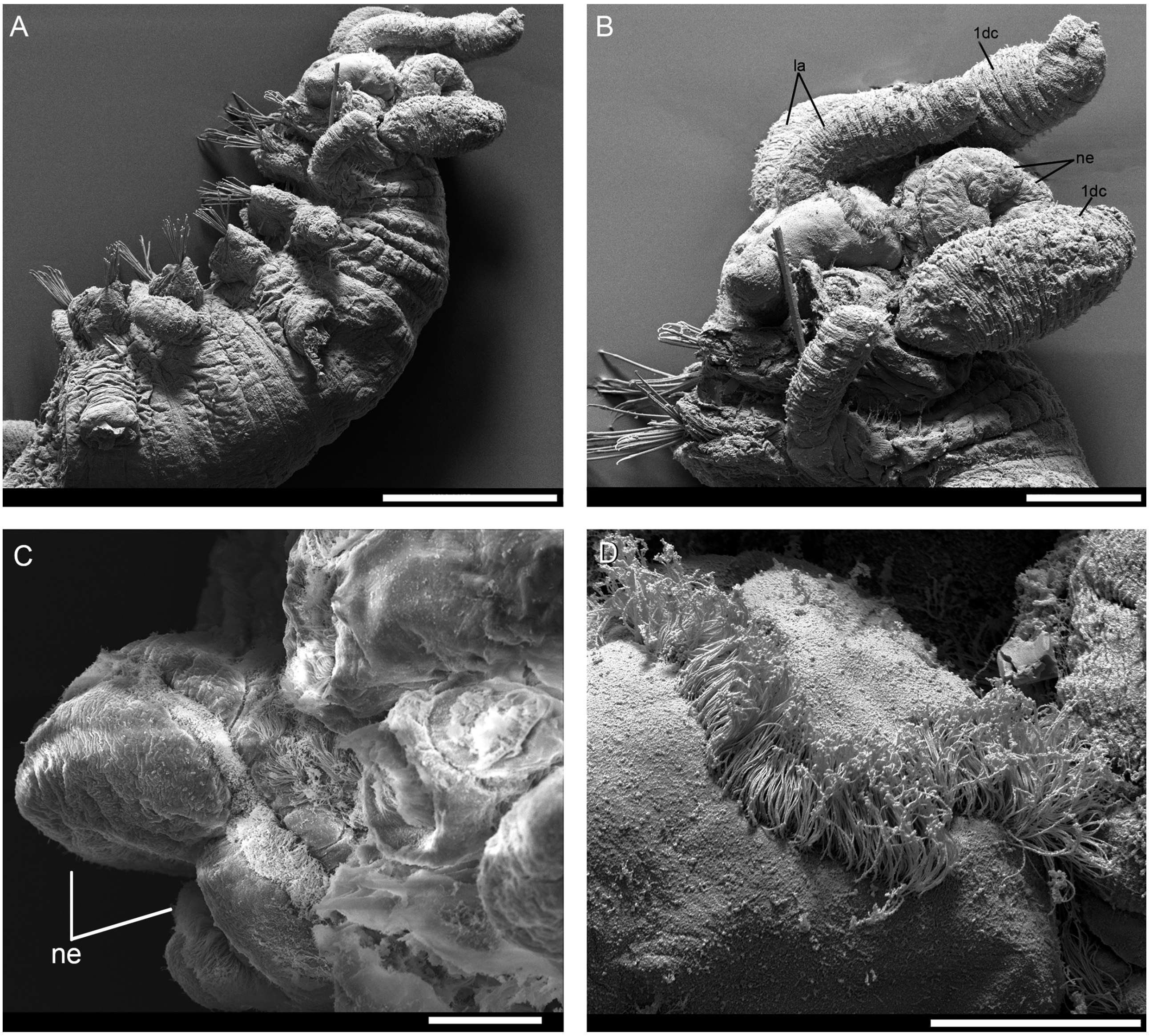

FIGURE 7. *Virchowia christophi* **sp. nov.** ZMUG 32498, A anterior end, lateral view. B anterior end detail, lateral view. C detail of ciliation in nuchal epaulettes. D detail of ciliation around the eye. la = lateral antenna; ma = median antenna; ne = nuchal epaulettes; 1dc = first dorsal cirrus; dc = tentacular cirri. Scale bars: A = 300 µm; B = 100 µm; C = 50 µm; D = 30 µm.

Remarks. *Virchowia christophi* **sp. nov.** is characterized by the unique combination of bifurcated nuchal epaulettes, a striking colour pattern, the distinctly shaped chaetae (with long distal teeth and absence of serration on verge), and the alternation pattern of dorsal cirri in colour, shape and size. Its diagnostic characters fit well with those from the genus *Virchowia* (Nygren, 2004) (Table 1). The palps in *Virchowia christophi* **sp. nov.** are not completely fused to the prostomium. *Virchowia branchiata* Averincev, 1972, from the Antarctic, is the only other Autolytinae with nuchal epaulettes as bifurcated outgrowths (Nygren 2004). However, this species has chaetae with fine spinulation on verge, bayonet chaetae and less teeth on the trepan ring. *Virchowia pectinans* from Australia has a complex colour pattern, whose colours are similar to those of *V. christophi* **sp. nov.** (pers. obs. from AM fixed material). However, the colour pattern is different and it has chaetae with more curved distal teeth and long spinulation on verge. The number of trepan teeth and convolutions of the pharynx are also different to those of *V. christophi* **sp. nov.** In Japan, the only known species of the genus is *V. japonica* Imajima & Hartman, 1964, which

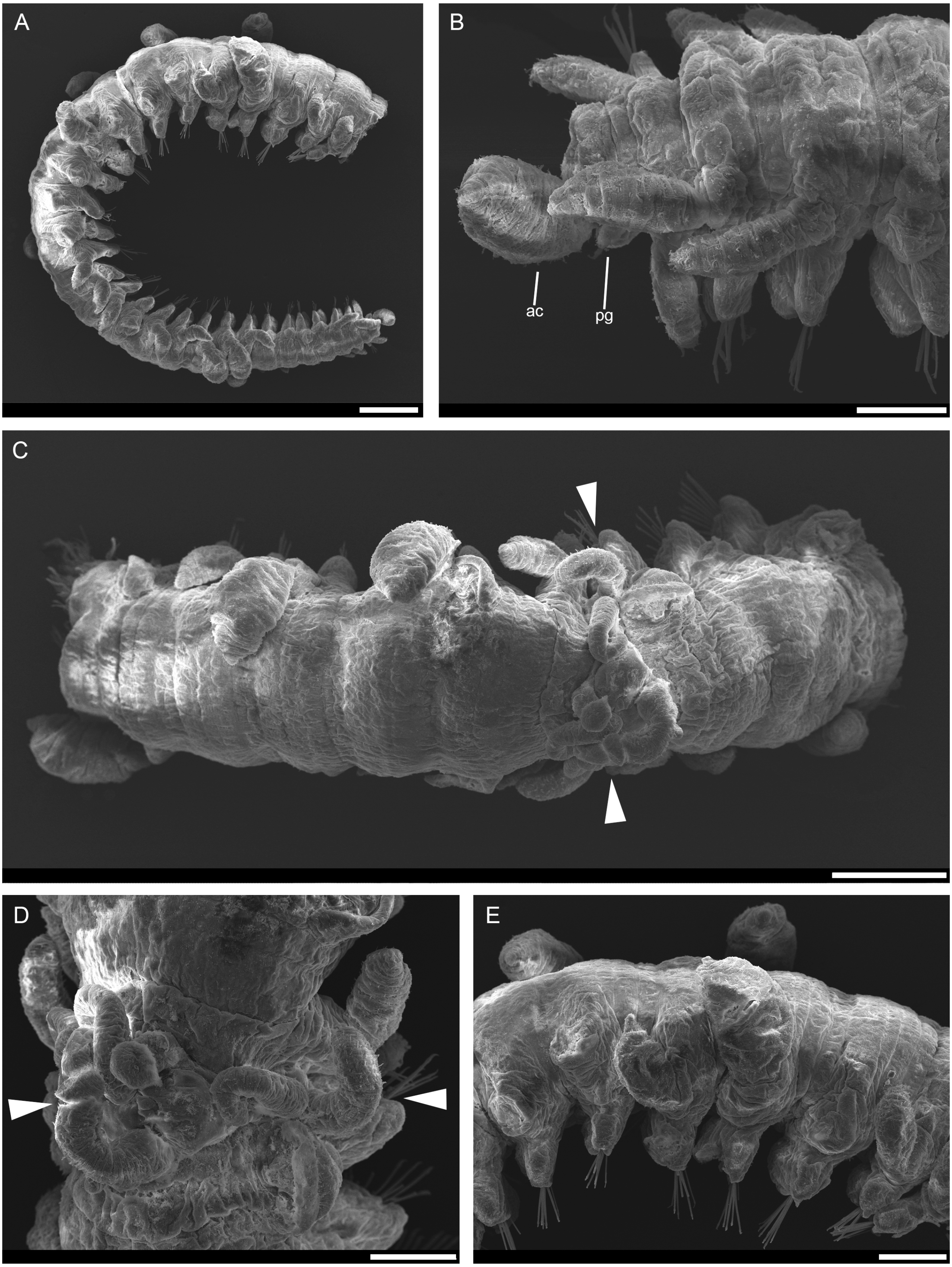

FIGURE 8. *Virchowia christophi* **sp. nov.** ZMUG 32498, A posterior end, lateral view. B posterior end detail, dorsolateral view; pg = pygidium; ac = anal cirri; second anal cirrus lost. C midbody section, dorsal view; arrows pointing at developing stolon head. D midbody section detail, dorsal view; arrows pointing at developing stolon head. E midbody section detail, lateral view. Scale bars: A, C = 200 µm; B = 50 µm; D, E = 100 µm.

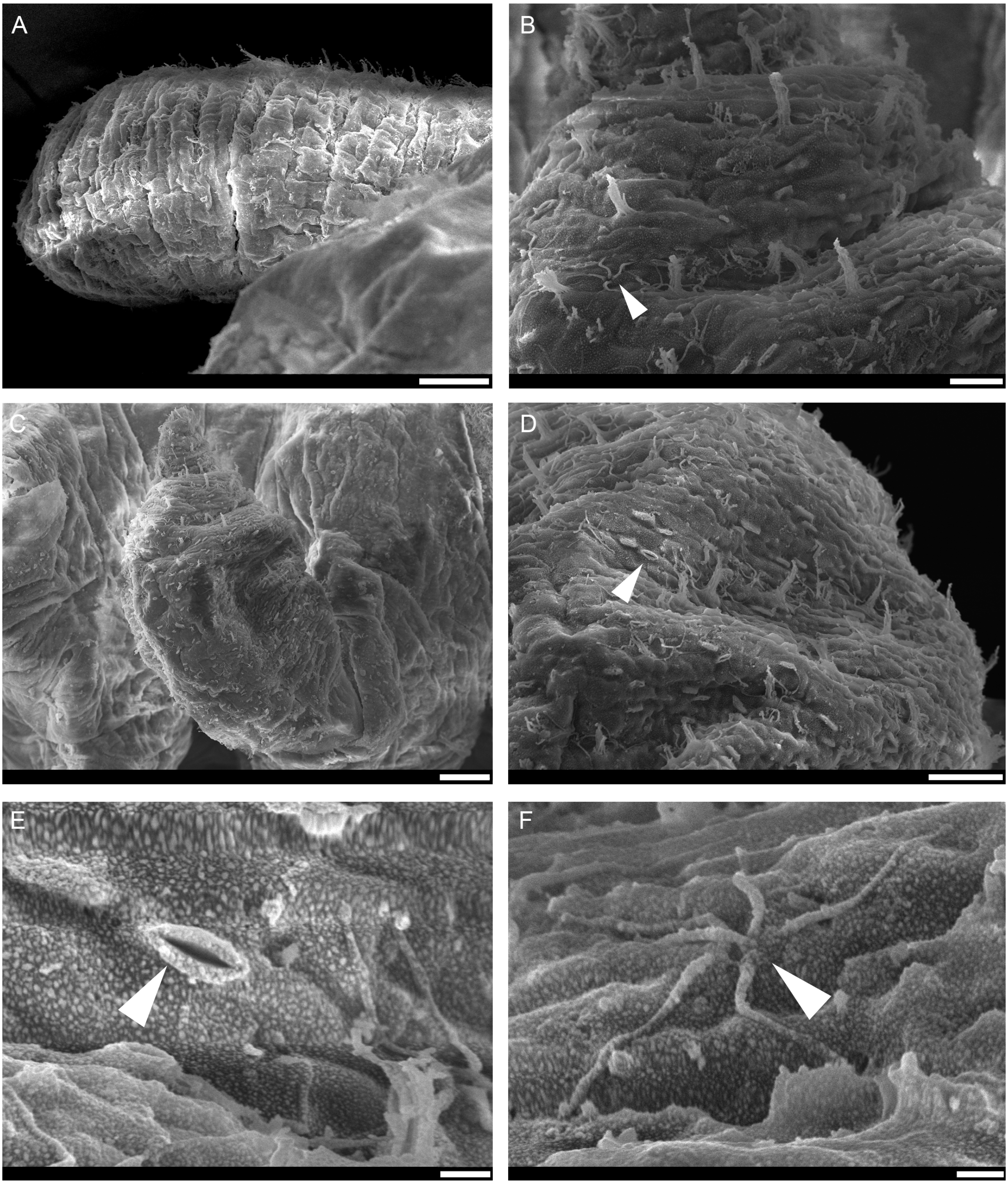

FIGURE 9. *Virchowia christophi* **sp. nov.** ZMUG 32498, A, C dorsal cirri detail. B, F dorsal cirri detail; arrows pointing at star-shaped extensions. D, E dorsal cirri detail; arrows pointing at glandular openings. Scale bars: A, C = 20 µm; B = 5 µm; D = 10 µm; E, F = 1 µm.

was described from a single male stolon (Nygren 2004). This species possesses compound chaetae with serrations on the verge and includes bayonet chaetae. In contrast, *V. christophi* **sp. nov.** mostly has simple chaetae with shafts and fangs fully fused, (excepting those located most ventrally in the chaetiger), long distal teeth, serrations on the verge completely missing, and absence of bayonet chaetae. Additionally, *V. japonica* exhibits only DU-groups of alternating cirri, while the dorsal cirri alternation pattern in *V. christophi* **sp. nov.** is different. Regarding the shape of compound chaetae, *V. spirifer* Augener, 1913 is the only other species of *Virchowia* without serrations or spines along the cutting margin of the chaetae. Similarly, *Imajimaea draculai* also lacks blade serration along the blades of compound chaetae. However, *V. christophi* **sp. nov.** can be distinguished from *V. spirifer* and *I. draculai*, in addition to the bifurcated nuchal epaulettes, by its chaetae shape, trepan structure, absence of bayonet chaetae, and distinct dorsal cirri pattern.

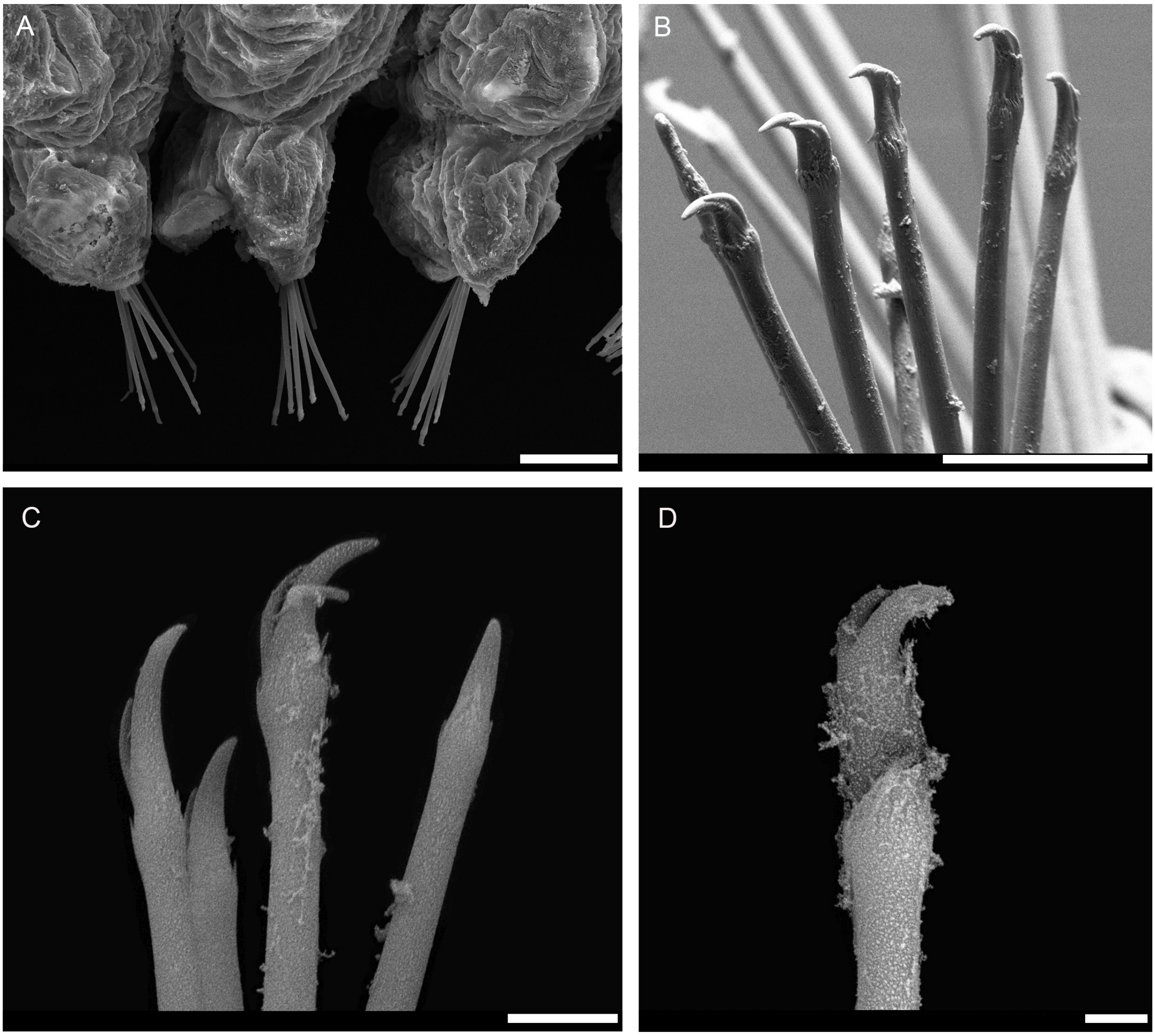

FIGURE 10. *Virchowia christophi* **sp. nov.** ZMUG 32498, A Parapodia with chaetae, lateral view. B, midbody chaetae. C posterior chaetae, D compound chaetae, most ventral in the fascicle. Scale bars: A = 50 µm; B = 20 µm; C = 5 µm; D = 2 µm.

SEM images revealed glandular structures covering the entire body of *V. christophi* **sp. nov.** While similar structures have been observed in other syllids (San Martín & Aguado 2012; Jimi *et al*. 2024), their function remains unclear.

Distribution. Misaki Sagami, Bay; Sugashima Island; Japan; NW Pacific.

Etymology. This species is dedicated to Professor Dr. Christoph Bleidorn, for all his important contributions to systematics, and specifically to the phylogenetic relationships of Annelida.

Paraopisthosyllis rufa **sp. nov. Springer, Aguado, Sato, Oguchi, Jimi & Miura Figs 11–17, Table 2**

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Material examined. Holotype (NSMT-Pol H-977) and seven paratypes (NSMT-Pol P-978): Japan, Misaki: Arahaima Beach, Sagami Bay, Misaki, 35°09'34"N 139°36'40"E, 2–5 m, coll. Sato, 2022. Paratypes (NSMT-Pol P-1006, ZMUG 32499) and additional material. (NSMT-Pol 113616): Japan, Misaki: Araihama Beach, Sagami Bay, Misaki Marine Biological Station, 35°09'36.1"N 139°36'40.1"E, 2–5 m, coll. Oguchi & Aguado 2019, Sato & Aguado 2024.

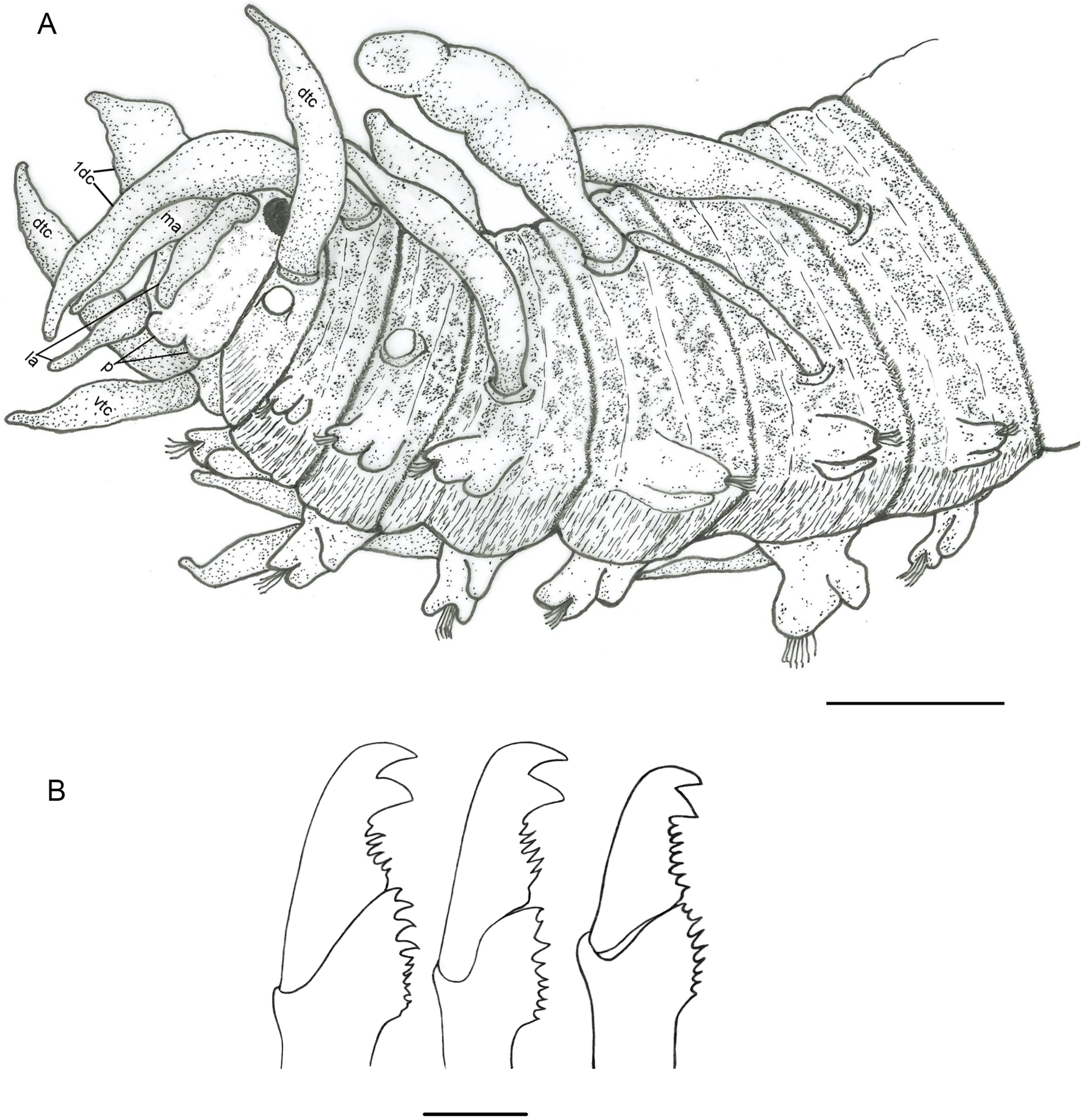

FIGURE 11. *Paraopisthosyllis rufa* **sp. nov.** NSMT-Pol P-978, A anterior end, ventrolateral view; ma = median antenna; la = lateral antenna; p = palps; dtc = dorsal tentacular cirri; vtc = ventral tentacular cirri; 1dc = first dorsal cirrus. B midbody chaetae. Scale bars: A = 500 µm; B = 5 µm.

FIGURE 12. *Paraopisthosyllis rufa* **sp. nov.** A complete specimen, lateral view. B complete specimen, dorsal view; arrow pointing at proventricle. Scale bars: A, B = 1000 µm.

FIGURE 13. *Paraopisthosyllis rufa* **sp. nov.** A anterior region, lateral view; e = eyes; p = palps; la = lateral antenna; ma = median antenna. B anterior region, ventral view. C Anterior region detail, ventral view; p = palps. D anterior region detail, lateral view. E midbody section. Scale bars: A, B = 500 µm; C = 100 µm; D, E = 200 µm.

FIGURE 14. *Paraopisthosyllis rufa* **sp. nov.** A posterior end with anal cirri folded over midbody region, dorsal view; pg = pygidium. B posterior region with developing female stolon attached, dorsal view. C, D detail of developing female stolon; arrows pointing at stolon eyes. E detail of developing female stolon and secondary tail, ventrolateral view; st = developing secondary tail. F Detail of developing female stolon, arrow pointing at developing secondary tail, ventral view. G Regenerating posterior end, ventral view; ac = anal cirri. H mature female stolon, dorsal view. Scale bars: A, C = 200 µm; B = 2000 µm; D, E, F, G = 500 µm; H = 1000 µm.

Description. Large-sized body, largest specimen examined (holotype) 19.5 mm long, 0.8 mm wide, prostomium, 94 body segments and pygidium. Paratypes vary significantly in number of segments and body length. Body length ranges between 7.75–19.5 mm, number of segments between 58–94. Body cylindrical, broad (Figs 11A, 12A–B), flattened ventrally (Fig. 13 A, D). Main body colour red, anterior end reddish/pink, midbody section dark red, posterior region light red to white/opaque (Figs 12–14) (in live and fixed specimens). Appendages in anterior region faintly orange/red coloured (Fig. 12B), in midbody and posterior section white/opaque (Fig. 12A–B). Segments secondarily triannulated (Figs 11A, 12A, 13D, E). Segments thickest in anterior region, segments 1–8 enlarged (Figs 12A–B, 13A, 15A). Body surface, including cirri, covered by small papillae (Figs 15C–E, 16G). Prostomium with 4 lensed eyes arranged in trapezoidal shape, one thick and short median antenna and two lateral antennae (Figs 11A, 12A, 13A, D). Ciliation around the eyes present (Fig. 15C). Median antenna similar to prostomium length, lateral antennae longer than prostomium (Figs 13D, 15A, B). Palps broad, elongated, rounded, reddish in colour, basally fused (Fig. 13B, C). Peristomium with elongated, forward-pointing, cylindrical dorsal and ventral tentacular cirri (Figs 13D, 15A–B). Dorsal one longer than ventral one (Fig. 13D). Nuchal organs in ciliated grooves (Fig. 15B, E). Dorsal cirri digitiform (Fig. 12A, B), in a consistent pattern in their arrangement and length (Figs 12A, B, 13E). The dorsal cirri pointing upwards (U) arranged on a high position (closer to the dorsum) are double the length and thickness than those downwards (D) directed, whose arrangement is closer to the ventral side (Fig. 12A). The pattern of the first nine dorsal cirri is: U, D, D, U, D, U, D, D, U. Following ones alternate in a D, U, D, U, D, U pattern until they shift to the same position and continue at same arrangement height along the rest of the body. The shift from alternating to non-alternating dorsal cirri is consistent across all specimens, but the segment at which the alternation stops varies between individuals and ranges from segment 32–37. In some specimens, fourth dorsal cirri thickened compared to rest of upwards oriented dorsal cirri (Figs 11A, 15A). Ventral cirri of same length as parapodia, ovate, covered in small papillae (Figs 16A–E, 17A, C). Parapodia short, thick, distally bilobed, each with 12 compound chaetae (Fig. 17A–C). Compound chaetae bidentate with small serrations along the inner margin of the blade (5µm) (Figs. 11B, 17C, D). Shafts smooth and slender. Longest chaetae article ~43 µm, shortest ~18 µm. Simple chaetae not seen. Pygidium short and triangular, with two club-shaped and short anal cirri (Fig. 14A, 16F). Pharynx straight, occupying segments 1–6, followed by a cylindrical proventricle present in segments 7–11 in both live and fixed specimens (Fig. 12B). One single pharyngeal tooth located retarded on posterior dorsal outer side of the pharynx.

Reproduction. Schizogamy by scissiparity. Paratypes adult specimens developing mature dicerous female stolons (Fig. 14B–H). The stolon head with two pairs of red eyes (Fig. 14E–F, H). Lateral antennae opaque, smaller than cirri, observed in developing and mature stolons (Fig. 14H). Female stolons with ovules visible by transparency, red/purple in colour (Fig. 14B–D, H). Dorsal cirri and ventral cirri present, elongated. Parapodia and compound chaetae present, notoaciculae present in mature stolons (Fig. 14H). Pygidium with two club-shaped anal cirri, similar to adult specimens (Fig. 14B, D). Stock forming a secondary tail ventrally while the stolon is still attached to the parental stock observed in paratype (Fig. 14F). Regenerating posterior end after detachment of stolon (Fig. 14G).

Habitat. Rocky shorelines, shallow waters 2–5 m deep, on algae and coral rubble.

Remarks. *Paraopisthosyllis rufa* **sp. nov.** is characterized by the distinctive alternation pattern of dorsal cirri and the distinct shape of the compound chaetae, together with its prominent colour in both live and fixed specimens (5 years storage). It is the first record of the genus *Paraopisthosyllis* in Japan (Jimi 2024). Chaetae of *P. rufa* **sp. nov.** are most similar to those of *P. correiae* Paresque *et al.* 2016*, P. fusigera* Augener, 1913*, P. ornaticirra* San Martín & Hutchings, 2006 and *P. phyllocirra* Hartmann-Schröder, 1991. They all have bidentate compound chaetae with serrations along the blade and spinulations on the chaetae shafts. Additionally, *P. brevicirra* Hartmann-Schröder, 1979*, P. fusigera* and *P. phyllocirra* all lack simple chaetae as *P. rufa*. **sp. nov.** Like in most *Paraopisthosyllis* species (except for *P. fusigera* and *P. victoriae* San Martín, López & Aguado, 2009) the body surface of *P. rufa* **sp. nov.** is covered with small papillae. *P. rufa* **sp. nov.** is further differentiated from *P. victoriae* by the continuous prominence of the intersegmental furrows and from *P. fusigera* by a longer pharynx and proventricle, as well as the red colouration. The regeneration of the pygidium, while the stolon is still attached, firstly reported herein for *Paraopisthosyllis*, is a feature in common with *Megasyllis* and *Alcyonosyllis* (Aguado & Glasby 2015; Nakamura *et al.* 2023; Sato *et al.* 2024). The three genera form a monophyletic group, potentially inheriting this ability from their common ancestor. Convergently, other genera within Syllinae regenerate the pygidium while the stolons are still attached, such as *Ramisyllis kingghidorahi* Aguado *et al*. 2022, *R. multicaudata* Glasby, Schroeder & Aguado, 2012, *Parahaplosyllis kumpol* and some species of *Trypanobia* Imajima & Hartmann, 1964, *Trypanosyllis* and *Myrianida* (Okada 1937; Glasby *et al.* 2012; Álvarez-Campos *et al.* 2013; Aguado *et al.* 2022). However, a detailed morphological comparison of this process in different groups has never been performed.

Distribution. Misaki, Sagami Bay; Japan; NW Pacific.

Etymology. This species is the first known species of *Paraopisthosyllis* with a striking red colouration and is therefore named "*rufa*" from Latin "rufus" meaning red.

TABLE 2. Comparative list of key characters, habitats and distributions for *Paraopisthosyllis* species. *Paraopisthosyllis rufa* **sp. nov.** in bold. Aus: Australia; WA: Western Australia; NSW: New South Wales; QLD: Queensland; SA: South Australia; NT: Northern Territory; VC: Victoria.

Species	Dorsal cirri at different levels	Chaetae	Habitat	Distribution	References
P. alternocirra (San Martín & Hutchings, 2006)	Smooth, club-shaped	Compound, bidentate and unidentate falcigers	Algae, seagrasses, and sponges, from intertidal to shallow depths	Australia (WA)	San Martín & Hutchings 2006
P. brevicirra (Hartmann-Schröder, 1979)	Smooth, club-shaped	Compound; unidentate falcigers	Sand and debris, intertidal	Australia (WA)	Hartmann-Schröder 1979; San Martín & Hutchings 2006
P. correiae (Paresque *et al.*, 2016)	With papillae, club-shaped	Compound, bidentate	Intertidal	Brazil (Pernambuco)	Paresque *et al.* 2016
P. fusigera (Augener, 1913)	Smooth, club-shaped	Compound, bidentate	Coralline sand, from intertidal to shallow depths	Australia (WA)	Augener 1913; San Martín & Hutchings 2006
P. kalimna (San Martín & Hutchings, 2006)	Smooth, fusiform	Compound, bidentate	Rocky rubble, sediment, brown algae with epiphytes, shallow depths	Australia (WA)	San Martín & Hutchings 2006
P. kuluguhin (Paresque *et al.*, 2016)	Smooth, club-shaped	Compound, bidentate	Coral rubble, shallow depths	Phillippines (Luzon)	Paresque *et al.* 2016
P. ornaticirra (San Martín & Hutchings, 2006)	Smooth, club-shaped	Compound, bidentate falcigers	Caulerpa, in shallow depths	Australia (WA)	Hartmann-Schröder 1991b; San Martín & Hutchings 2006
P. pardus (Aguado & Glasby, 2015)	Smooth, club-shaped. Clear alternation in size and length	Compound, long bidentate falcigers	Coral rubble, shallow depths	Australia (QLD)	Aguado & Glasby 2015
P. phyllocirra (Hartman-Schröder, 1991)	Smooth, leaf-shaped. Clear alternation in size and length	Compound, long bidentate falcigers	Coralline sand, intertidal	Australia (QLD)	Hartmann-Schröder 1991b; San Martín & Hutchings 2006
***P. rufa* sp. nov.**	With papillae, cylindrical. Clear alternation in size and length	Compound, long bidentate falcigers	Coral rubble, algae, intertidal	Japan (Misaki)	This publication
P. victoriae (San Martín *et al.* 2009)	Smooth, club-shaped	Compound, bidentate	Coral rubble, algae	Barbados	San Martín *et al.* 2009

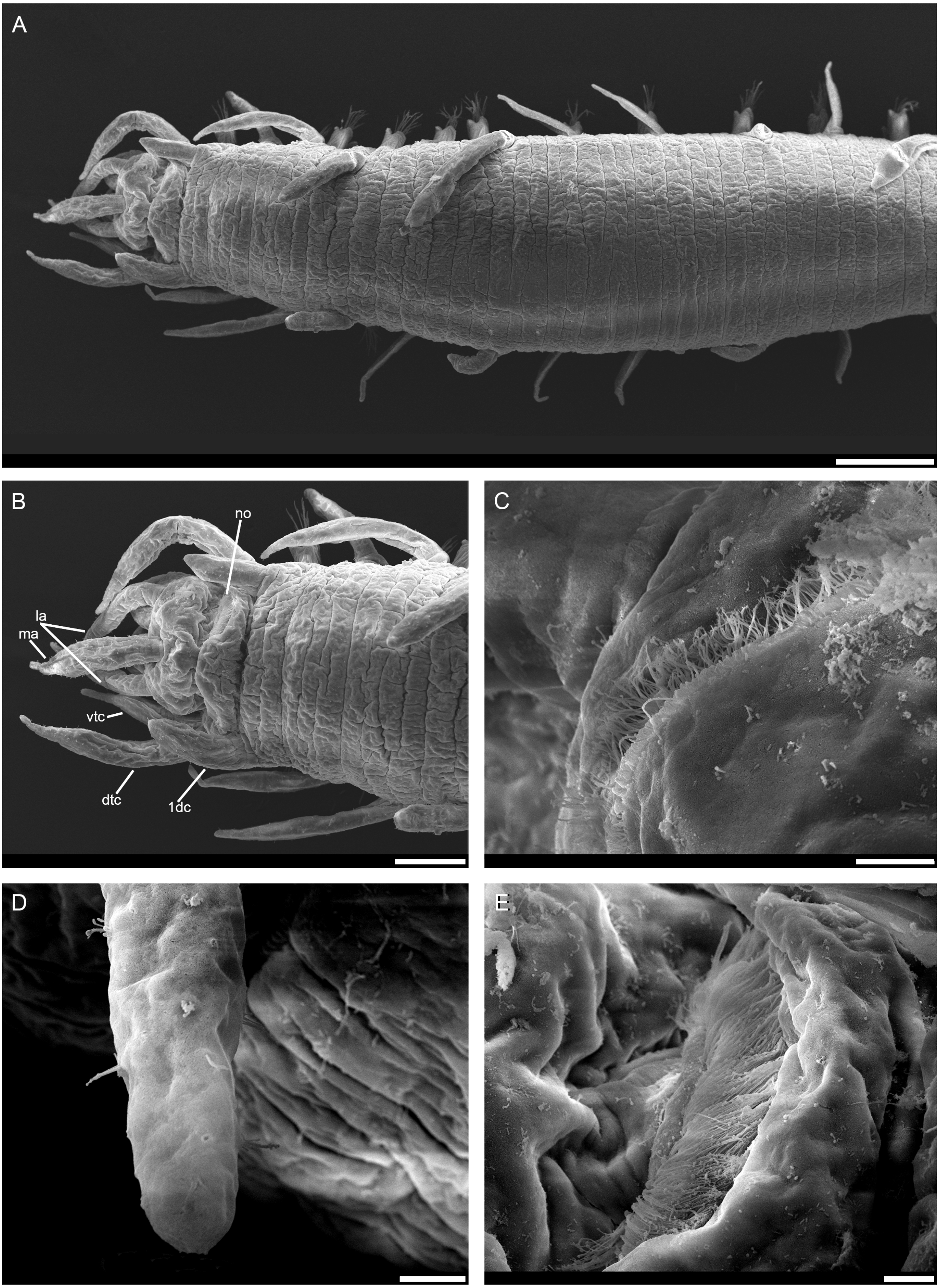

FIGURE 15. *Paraopisthosyllis rufa* **sp. nov.** ZMUG 32499, A anterior end, dorsal view. B anterior end, dorsal view; ma = median antenna; la= lateral antenna; vtc = ventral tentacular cirri; dtc = dorsal tentacular cirri; 1dc = first dorsal cirrus; no = nuchal organ. C, E detail of nuchal organ, dorsal view. D detail of dorsal cirrus with papillae, dorsal view. Scale bars: A = 200 µm; B = 100 µm; C, D, E = 10 µm.

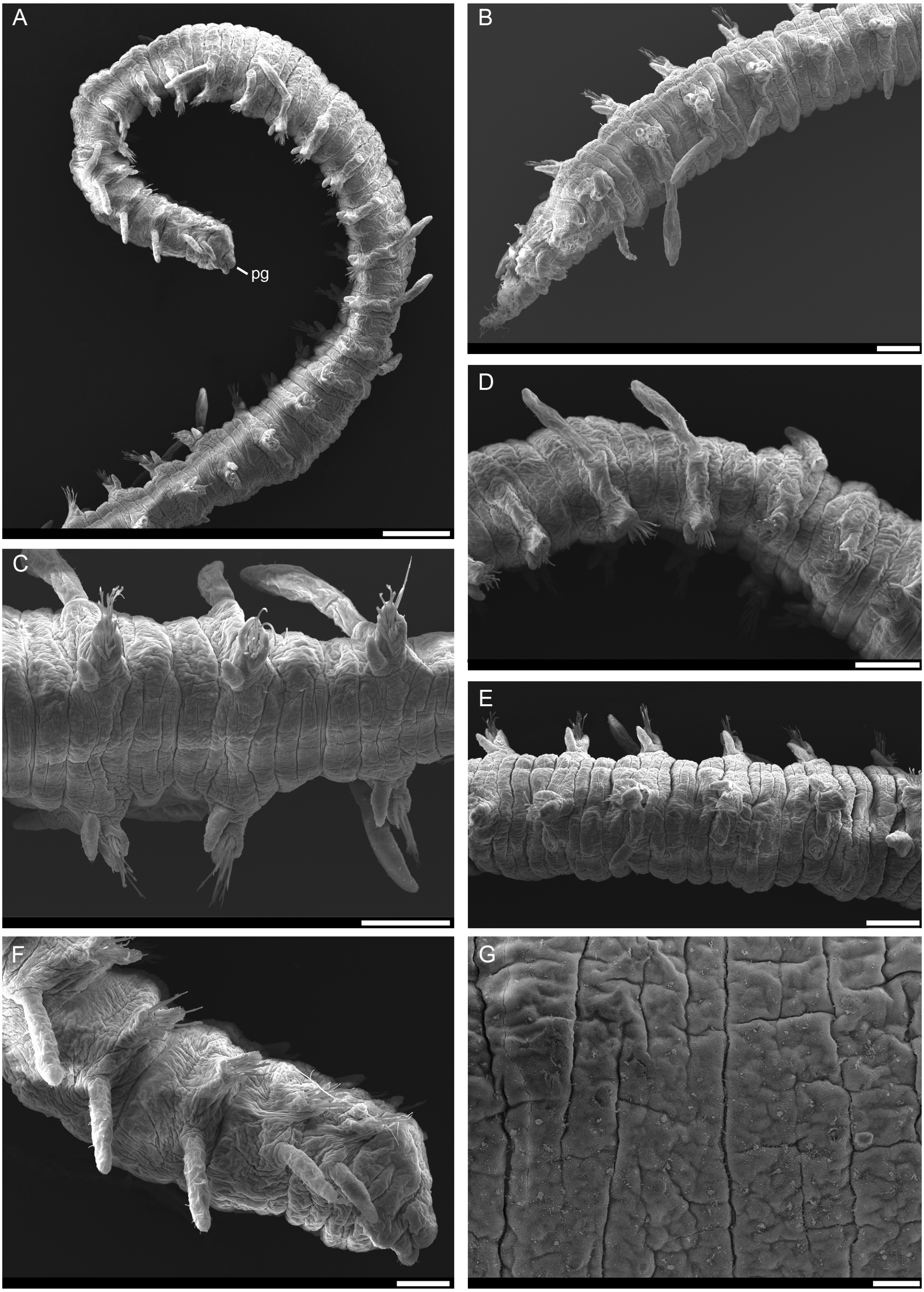

FIGURE 16. *Paraopisthosyllis rufa* **sp. nov.** ZMUG 32499, A posterior region, lateral view; pg = pygidium. B midbody region detail, ventrolateral view. C midbody region detail, ventral view. D midbody region detail, lateral view. E midbody region detail, ventrolateral view. F posterior end detail, lateral view. G segment detail, body surface covered in papillae, lateral view. Scale bars: A = 200 µm; B, C, D, E = 100 µm; F = 50 µm; G = 20 µm.

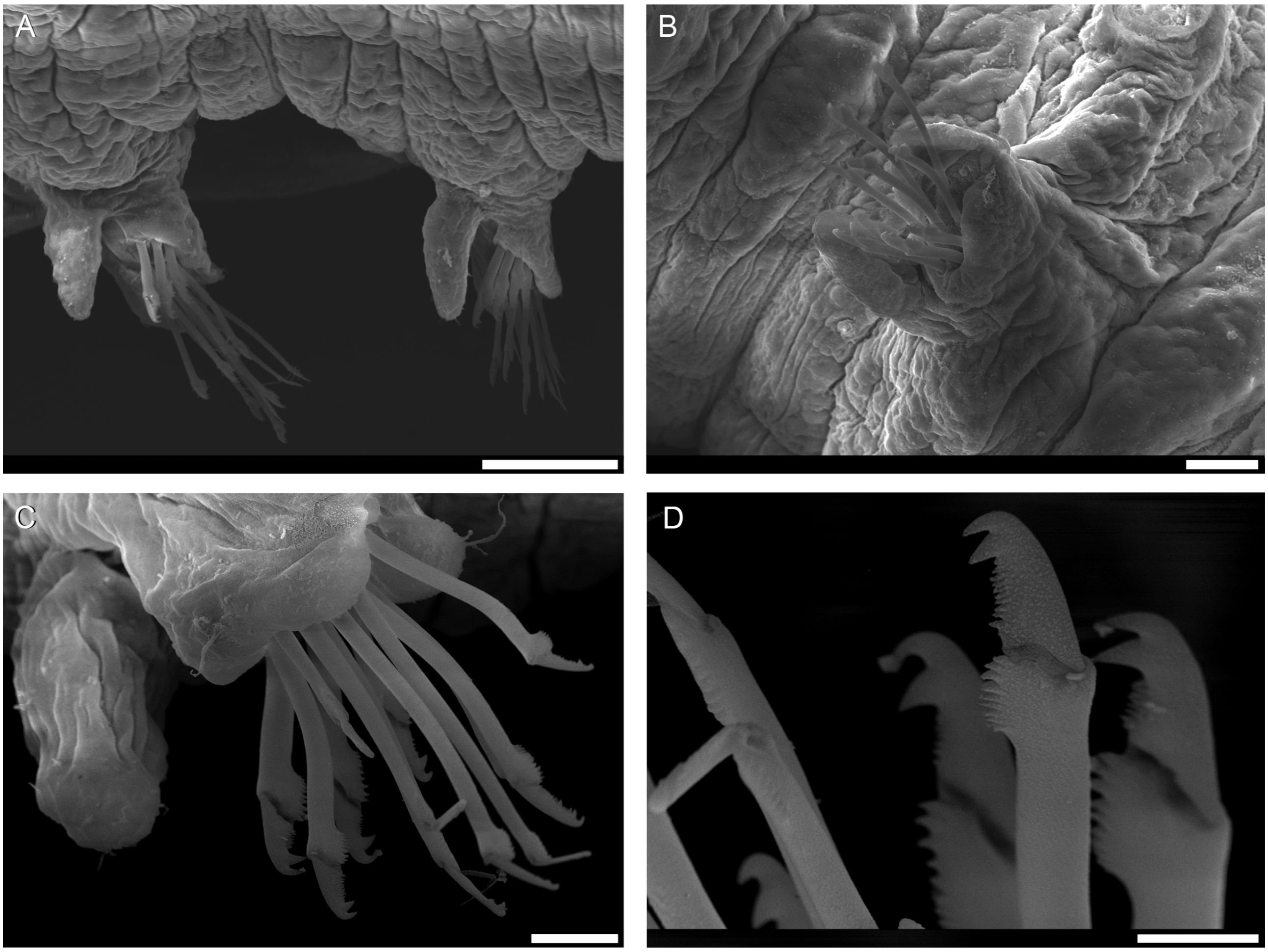

FIGURE 17. *Paraopisthosyllis rufa* **sp. nov.** ZMUG 32499, A parapodia, lateral view. B parapodium detail, ventral view. C parapodium with chaetae detail, ventrolateral view. D chaetae detail, ventrolateral view. Scale bars: A = 50 µm; B = 20 µm; C = 10 µm; D = 5 µm.

Syllis okadai Fauvel, 1934 Figs 18–20

Syllis okadai Fauvel, 1934; pp. 307–309, text-figs. 1, 2.
Syllis okadai Fauvel, 1953; pp. 152–153, fig. 76.
Typosyllis okadai Imajima and Hartman, 1964; p. 137.
Typosyllis okadai Imajima, 1966; pp. 268–270, text-fig. 56.
Syllis okadai Aguado, Nygren and Siddall, 2007; pp. 556, fig. 1.

Material examined. Two specimens (NSMT-Pol 113617), Japan, Misaki: Araihama Beach, Sagami Bay, Misaki Marine Biological Station, 35°09'36.1"N 139°36'40.1"E, 2–5 m, coll. Oguchi & Aguado, 2019. Additional material (ZMUG 32501): Japan, Misaki: Sagami Bay, Misaki Marine Biological Station, 35°09'36.1"N 139°36'40.1"E, 2–5 m, coll. Aguado & Sato 2024.

Description. Largest specimen complete, 11.8 mm long and 0.5 mm wide without chaetae. 82 chaetigers, prostomium and pygidium. Body subcylindrical, broad, ventrally flattened (Fig. 18). Segments 1–2 dark brown, segments 3–6 white, segments 7–9 dark brown, rest is dark red, segments ventrally white (Fig. 18A–E). Dorsal side with four rows of white spots, two spots per row and segment, rows located more ventrally fade out posteriorly (Fig. 18A–E). Head appendages (except palps), pygidium and cirri white (Fig. 18A, D–E). Prostomium with one median antenna located at the posterior end, two pairs of orange/red eyes and a pair of lateral antennae (Figs 18A, D–E, 19B). Two brown palpi form the anterior part of the prostomium (Fig. 18A, D–E). Grooves of cilia around the eyes, nuchal organs located at the posterior end of the prostomium, between prostomium and first segment (Fig. 20B, E).

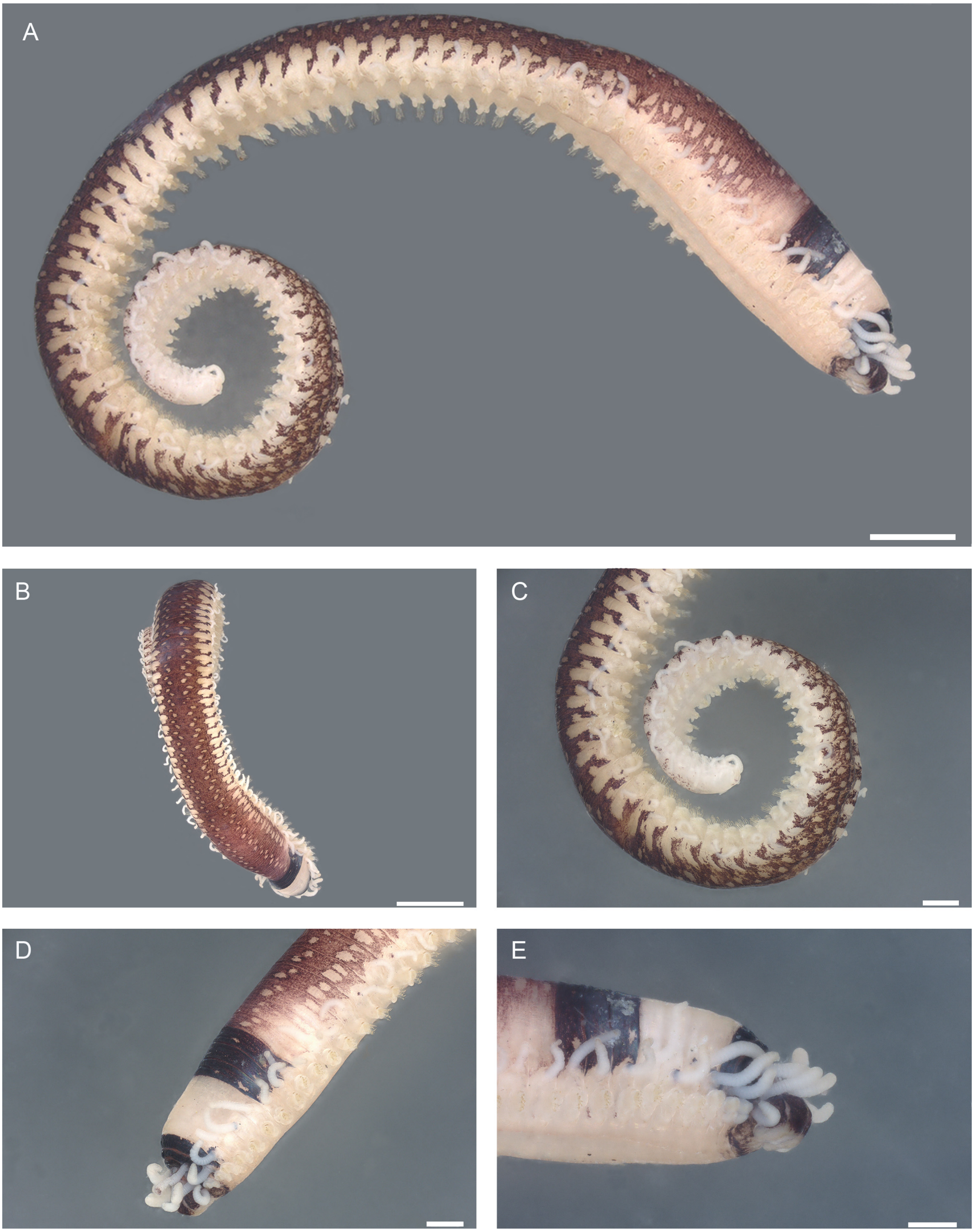

FIGURE 18. *Syllis okadai*, A complete specimen, lateral view. B anterior and midbody region, dorsal view. C Posterior region with pygidium, lateral view. D anterior end, lateral view. E anterior end detail, lateral view. Scale bars: A = 500 µm; B = 1000 µm; C, D, E = 200 µm.

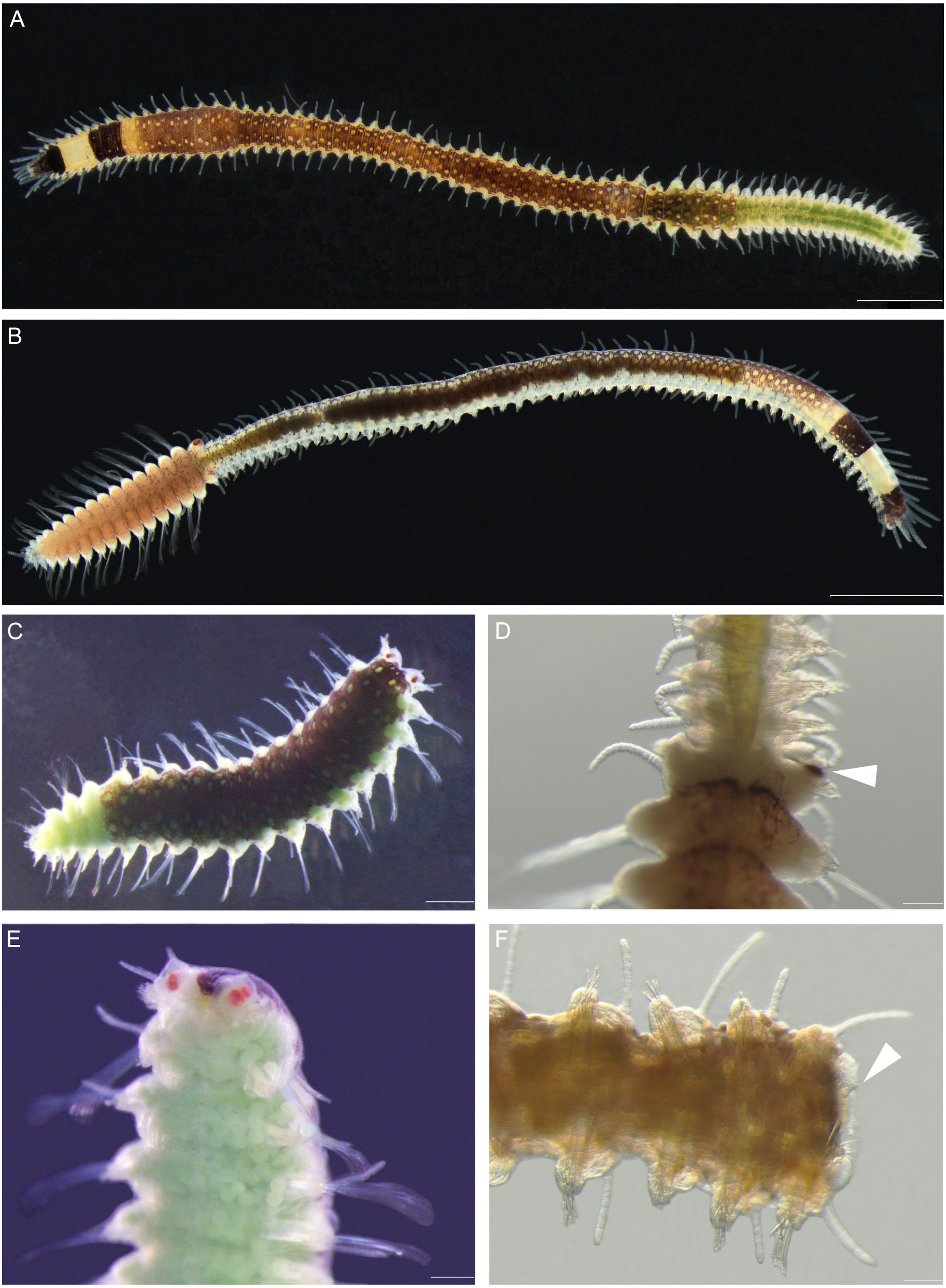

FIGURE 19. *Syllis okadai,* A complete specimen with female stolon attached, dorsal view. B complete specimen with male stolon attached, dorsal view. C female stolon, dorsal view. D formation of tail primordia before stolon detachment, dorsal view. E female stolon, ventral view. F regenerating pygidium after stolon detachment, dorsal view. Scale bars: A, B, C, E = 2000 µm; D, F = 200 µm.

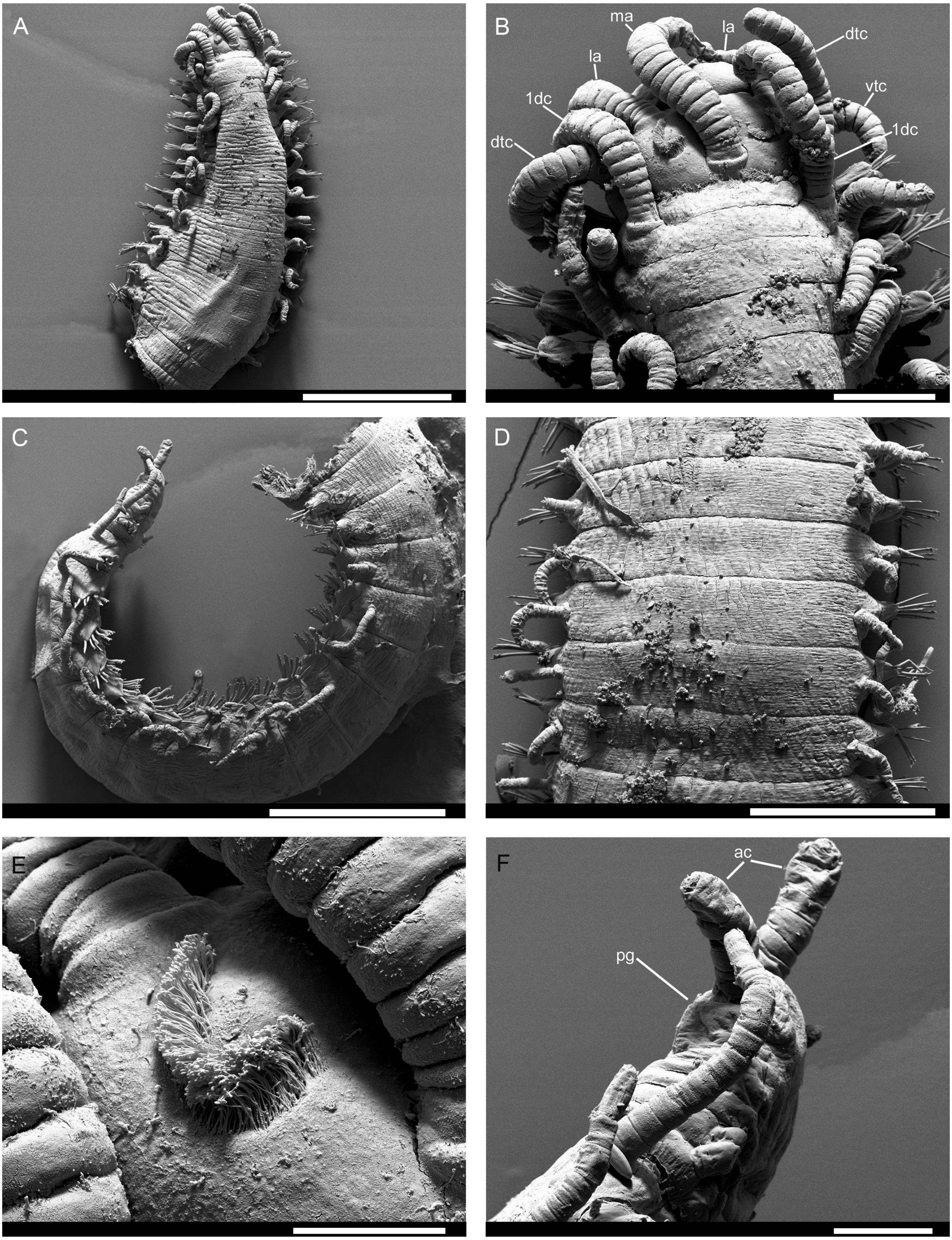

FIGURE 20. *Syllis okadai* NSMT-Pol 113617, A anterior region, dorsal view. B anterior region detail, dorsal view; ma = median antenna; la = lateral antenna; dtc = dorsal tentacular cirri; vtc = ventral tentacular cirri; 1dc = first dorsal cirrus. C posterior region, lateral view. D midbody section, dorsal view. E ciliation around eyes detail, dorsal view. F posterior end detail, lateral view; pg = pygidium; ac = anal cirri. Scale bars: A = 500 μm; B = 100; C = 400 μm; D = 300 μm; E = 30 μm; F = 50.

Two pairs of tentacular cirri (Fig. 20B). Dorsal cirri longer in anterior region, become gradually shorter towards posterior end (Fig. 18A–E). Annulated dorsal cirri (Figs 19B, F, 20A–D, F) with around 9 annulations. Pygidium with two short, white anal cirri (Fig. 20C, F). Anterior chaetae compound, 10–14 per parapodium (Fig. 21B–G). Anterior chaetae with long and slender shafts, denticles at the distal end of the shaft, large blades with serrations along the cutting margin and two distal teeth, proximal one slightly larger than distal one (Fig. 21C–D). Posterior parapodia with eight compound chaetae with short and broad shafts, bidentate (Fig. 21E–G). Additionally, posterior parapodia with two short and broad simple chaetae, one dorsal with a subdistal secondary tooth and one unidentate, distally curved ventral (Fig. 21A, E–G). Last chaetiger with only eight chaetae (six compound, two simple).

Reproduction. Schizogamy by scissiparity. Adult specimens developing each a dicerous stolon (Fig. 19A–E). Stolon with 14–21 body segments and pygidium. Stolon with two pairs of orange/red eyes, located laterally, one pair more dorsally, one more ventrally (Fig. 19A–E). Two lateral antennae developed, small (Fig. 19C, E). Female stolons with green ovules visible by transparency (Fig. 19E). Male stolons with beige sperm visible by transparency (Fig. 19B). Pygidium with pair of small and conical anal cirri. Compound chaetae present. Notoaciculae present in developing and mature stolons (Fig. 19A–E). Stock forming a pair of tail primordia ventrally while the stolon is still attached to the parental stock (Fig. 19D). The tail primordia (Fig. 19F) fuse to form a new pygidium after the detachment of stolon.

Habitat. Rocky shorelines, shallow waters 2–5 m deep, on algae and coral rubble.

Remarks. *Syllis okadai* is distinguished by a unique colour pattern (live and preserved specimens) and specially shaped compound chaetae in both the anterior and posterior regions. Additionally, the ciliated grooves around the eyes, a newly identified feature, were not mentioned in the original description. Apart from the newly identified features, the examined specimens closely match the original description.

Distribution. Cambodia, Andaman Islands; Gulf of Siam; Seto, Manazuru and Misaki, Japan.

Discussion

Both *Paraopisthosyllis* and *Virchowia* are low-diversity genera within the Syllidae family (Nygren 2004; Nygren *et al*. 2010; Aguado & Glasby 2015). As a result, species delimitation for *Virchowia christophi* **sp. nov.** and *Paraopisthosyllis rufa* **sp. nov.** is more straightforward than for many other syllid species. While these new species share similarities with their close relatives, they can be clearly distinguished by their unique combination of morphological features. The striking colouration of *Virchowia christophi* **sp. nov.**, combined with its branched nuchal epaulettes, represents a unique characteristic within the genus. Additionally, the absence of serrations along the blades of its chaetae differentiates it from species such as *V. branchiata*, *V. japonica*, and *V. pectinans* (Imajima & Hartman, 1964; Nygren, 2004). The phylogenetic position of *V. christophi* **sp. nov.** remains uncertain. It consistently clusters (though with low support value) with *V. clavata* and *I. draculai*, making the genus *Virchowia* paraphyletic in both the Autolytinae and the broader Syllidae analyses. The placements of *E. oligochaeta*, *P. nematodes* and *Cryptochaetosyllis imitatio* are inconsistent, shifting when Syllinae species are included in the analysis (Figs 1, 2). Previously, *Virchowia* was considered monophyletic, and *C. imitatio* was identified as the sister taxon to *Epigamia* (Nygren, 2004; Jimi *et al.* 2024). However, the lack of molecular data for other *Virchowia* species, as well as additional gene sequences for *I. draculai*, *P. nematodes*, and *E. oligochaeta*, leaves these phylogenetic uncertainties unresolved, necessitating further investigation. Despite these ambiguities, *V. christophi* **sp. nov.** shares key morphological features with other *Virchowia* species and aligns with the current genus diagnosis, warranting its classification within *Virchowia*.

Paraopisthosyllis rufa **sp. nov.** has a characteristic pattern of alternation in its dorsal cirri and is the only species of the genus that is, except for its appendages, brightly red in colour (both live and fixed material) (San Martín & Hutchings 2006; San Martín *et al.* 2009; Aguado & Glasby 2015; Paresque *et al.* 2016). Compared to other *Paraopisthosyllis* species, *Paraopisthosyllis rufa* **sp. nov.** lacks simple chaetae and the anterior segments are significantly enlarged. Its phylogenetic position is well supported within the genus *Paraopisthosyllis*. *Paraopisthosyllis, Alcyonosyllis* and *Megasyllis* species form a monophyletic clade and share a common ancestor, from which they may have inherited the ability to regenerate their pygidium (secondary tail) while the stolon is still attached (Aguado & Glasby 2015; Nakamura *et al.* 2023; Sato *et al.* 2024). This is the first record of the genus from Japan and the second species described from the northern hemisphere (Aguado & Glasby 2015; Paresque *et al.* 2016).

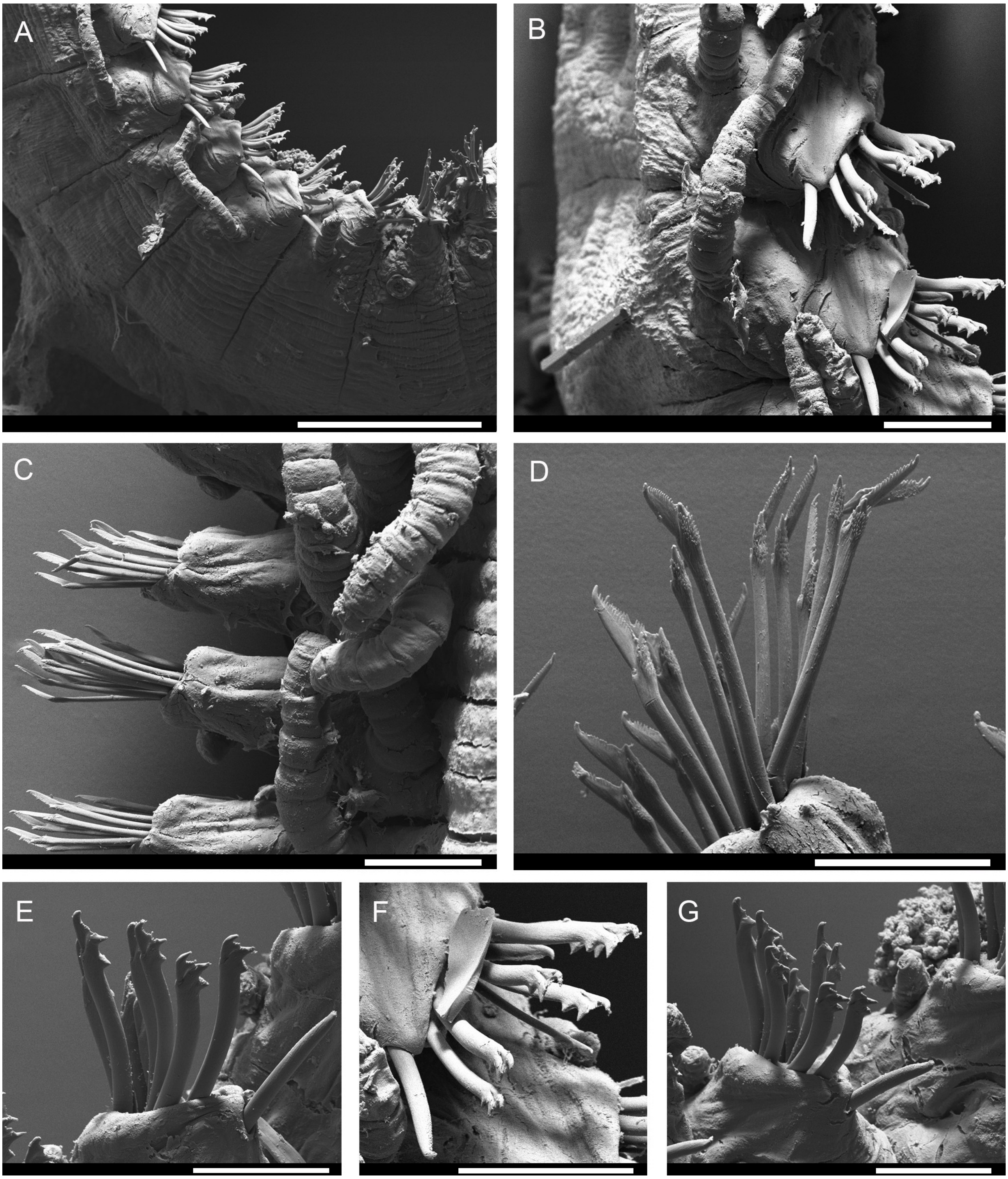

FIGURE 21. *Syllis okadai* NSMT-Pol 113617, A posterior region detail, dorsolateral view. B posterior region detail, lateral view. C anterior parapodia detail, lateral view. D anterior chaetae, lateral view. E–G posterior chaetae detail, lateral view. Scale bars: A = 200 µm; B, C, F = 50 µm; D = 30 µm; E, G= 40 µm.

Both *Paraopisthosyllis rufa* **sp. nov.** and *Virchowia christophi* **sp. nov.** reproduce sexually, their posterior region is transformed into a stolon, which detaches from the parental stock once it is mature and then releases its sperm/egg cells into the water (San Martín & Aguado 2022). In both species, young developing stolons have been observed, as well as an almost mature stolon in *V. christophi* **sp. nov.** and a mature, detached female stolon in *P. rufa* **sp. nov.** Scissiparity via stolonization, as a form of sexual reproduction, is a common reproductive mode for syllids (Franke

1999; Nygren & Sundberg 2003). While there are species capable of asexual reproduction within *Virchowia*, there is no evidence for that in *Paraopisthosyllis rufa* **sp. nov.** or *Virchowia christophi* **sp. nov.** (Imajima & Hartman 1964; Hartman-Schröder 1991; Nygren 2004; San Martín & Hutchings 2006).

The redescribed specimen of *Syllis okadai* from Misaki, Japan formed a monophyletic clade with the available *Syllis okadai* sequence from Manazuru, Japan (Aguado *et al.* 2007). They are part of the paraphyletic genus *Syllis* and are most closely related to other *Syllis* species such as *S. monilaris* Lamarck 1818, also present in Misaki, Japan. The examined specimens perfectly agreed with the original description of the holotype (Fauvel 1934; Imajima & Hartman 1964), with small differences in size and the newly found character of ciliated grooves around the eyes.

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper.

TABLE 1. Collecting data and GenBank Accession numbers for taxa included in the phylogenetic analyses. Newly added sequences written in bold.