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The sea cucumber order Apodida (Echinodermata: Holothuroidea) from Indonesia: description of a new species and species checklist

Ana **Setyastuti**[1*] & Carsten **Lüter**[2]

Abstract. Apodida is an order of sea cucumbers, distributed worldwide from shallow to deep waters, comprising approximately 320 extant species in 41 genera and three families. The inventory of apodid species in Indonesia is limited, and a list of species identified or recorded in this region is not available. This study provides a list of Indonesian apodid species which includes material from several locations that were not previously explored, together with a new species *Polycheira nusalaut* that is described here. Of the 69 apodid species listed here, 35 have their type localities in Indonesia.

Key words. Holothuroid, *Polycheira nusalaut*, new species

INTRODUCTION

Apodids are unique among holothuroids in lacking podia (tube feet and papillae) and radial water canals. They are vermiform with a thin, usually transparent, body wall. With lengths ranging from a few millimeters to more than 3 m, apodids include some of the world's largest extant echinoderms (Kerr, 2001). These sea cucumbers inhabit shallow waters to deep-sea habitats and are distributed worldwide, with approximately 320 extant species in 41 genera, comprising three families (WoRMS Editorial Board, 2025). Over the past three decades, systematic revisions have been made with three genera being invalid, i.e., *Trochodota* Ludwig, 1891 (accepted as *Taenogyrus* Semper, 1867), *Lepidotrochus* Belyaev & Mironov, 1980 (accepted as *Neolepidotrochus* Bohn, 2005), and *Pendekaplectana* Heding, 1931 (accepted as *Polyplectana* H.L. Clark, 1907). At the same time, some 50 new apodid species and 12 new genera were described (Rowe & Gates, 1995; Smirnov, 1998; Kerr, 2001; Bohn, 2005; O'Loughlin & Vandenspiegel, 2010; WoRMS Editorial Board, 2025).

To date, there is only a limited inventory of the apodid species in Indonesia. Several papers have been published describing collections of holothuroids that include apodids from Indonesia (formerly known as the East Indies), most notably Ludwig (1875), Théel (1886), Sluiter (1881, 1887, 1894, 1901), Clark (1907), and Heding (1928). More than half a century later, Clark & Rowe (1971) provided a detailed distribution of shallow-water species of each echinoderm class occurring throughout the Indo-West Pacific region, listing all references known up to that time. Further, Rowe (1983) specifically described holothuroids collected from Java Island, whilst Massin (1996, 1999) described collections from Ambon Island and the Spermonde archipelago, South Sulawesi. Massin & Tomascik (1996) described collections from an anchialine lagoon on Kakaban Island. Other publications that involved apodid collections from elsewhere in Indonesia include those from Timor Island, East Nusa Tenggara (Purwati & Wirawati, 2008); Seram Island, Maluku (Setyastuti, 2009); Sanur Beach, Bali (Setyastuti, 2014); Ambon Bay, Maluku (Setyastuti, 2016); the Banda Islands (Setyastuti & Wirawati, 2018); Tikus Island and Pari Island, Seribu archipelago (Setyastuti, 2011; Setyastuti & Vimono, 2020). More recently, Wirawati et al. (2019) provided diagnoses and distributions of shallow-water holothuroids (including apodids) in Indonesia. However, a listing of all Apodida species described, recorded, and distributed in Indonesia is not available. Thus, this study aims to provide a list of apodid species from Indonesia, based on historical records and re-descriptions of species collected from several locations that have not been explored previously, and the description of a new species.

MATERIAL AND METHODS

Morphological analyses. Specimens were collected by hand while snorkelling during low tide at four locations in Indonesia (Fig. 1). Three specimens were collected by the first author during fieldwork on Simeulue Island (2017),

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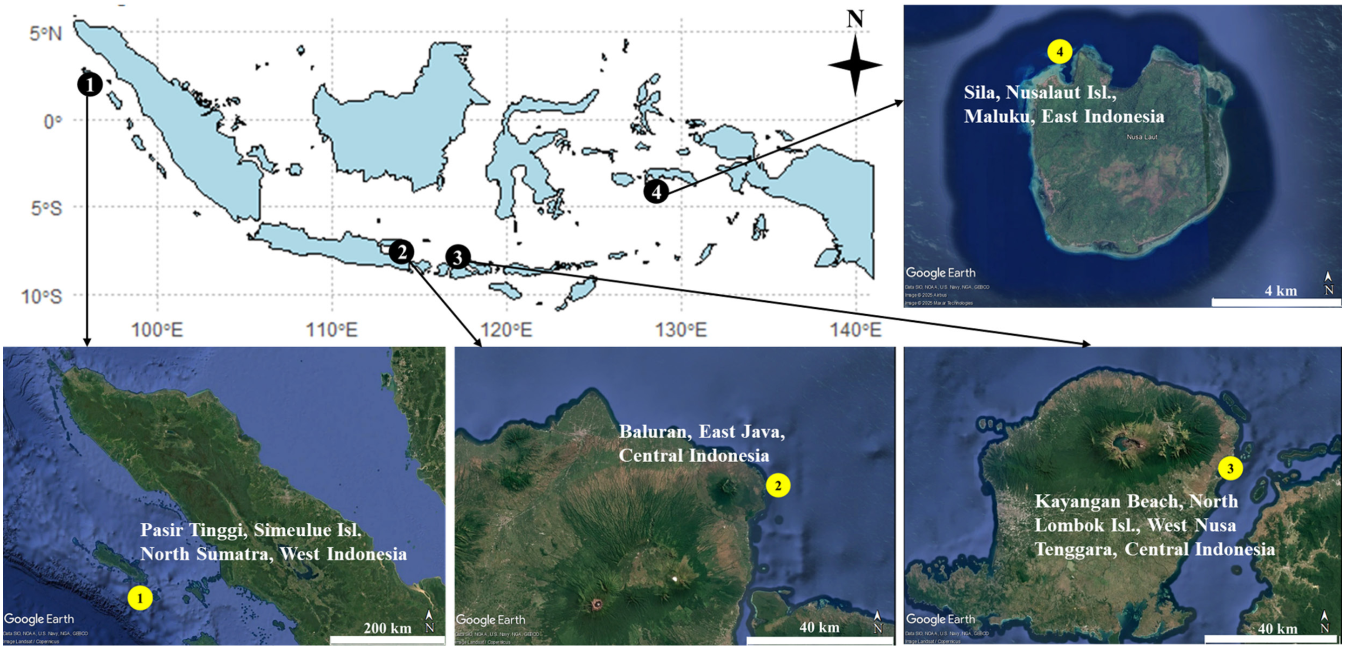


Fig. 1. Apodid collection sites: (1) Simeulue Island, Aceh, North Sumatra (MZB.Hol.254, *Polycheira rufescens*); (2) Baluran, Situbondo Regency, East Java (MZB.Hol.421, *Chiridota smirnovi*); (3) Kayangan Beach, North Lombok Regency, West Nusa Tenggara (MZB. Hol.267, *Opheodesoma grisea* and MZB.Hol.266, *Synaptula denticulata*); (4) Nusa Laut Island, Maluku (MZB.Hol.310, *Polycheira nusalaut*, new species).

Nusa Laut Island (2009), and Kayangan Beach, Lombok (2019). Another sample from Baluran (2015) was obtained from the reference collection of the Research Center for Oceanography, National Research and Innovation Agency (BRIN) in Jakarta. Specimens were labelled and fixed with 70% ethanol. All specimens were registered and deposited in the Museum Zoologicum Bogoriense (MZB) in Bogor, Indonesia.

Ossicle preparations, observations, and image photographs using a scanning electron microscope (SEM) were conducted in the morphology laboratory of Museum für Naturkunde (MFN), Berlin, Germany. Ossicles were extracted from the body wall, tentacle, and longitudinal muscle. Tissues were dissolved in fresh household bleach (sodium hypochlorite 5–7%) in centrifuge tubes. After centrifugation at 1,000 rpm for 10–15 min, the bleach was pipetted off, and the ossicles were rinsed and centrifuged with distilled water, which was then pipetted off afterward. To preserve the ossicles, 70% ethanol was added to the tubes. Finally, ossicles were mounted directly on aluminium stubs (without double-sided conducting tape) and dried at room temperature. The ossicles were then sputter-coated with gold using a QUORUM Q150R S sputter coater machine and photographed using a scanning electron microscope (ZEISS EVO LS 10). The procedure for ossicle isolation is provided in Fig. 2, and all the aluminium stubs were stored in the invertebrate laboratory at MFN in Berlin, Germany.

In the present study, comprehensive ossicle measurements were conducted, particularly for *Polycheira rufescens,* which was collected from Aceh, North Sumatra, West Indonesia, and *P. nusalaut*, new species, that was collected from Nusa Laut Island, Maluku, East Indonesia, to determine whether each variable that was measured (Table 1) is significantly different between the two species. SEM images of ossicles were measured (length and width) using the ImageJ 1.54p software (http://imagej.org). A total of 20 variables (10 SEM images per variable) were measured and analysed using different statistical tests based on the normality of the indicator data for each group. Definitions of variables and measurements are presented in Table 1 and Fig. 16. Initially, a Shapiro-Wilk normality test was performed for each specimen data group. When both groups are normally distributed and have equal variances, the unpaired t-test was used for further analysis. If some data were normal but had unequal variance, Welch's test was performed. Otherwise, if some data were skewed, the Wilcoxon rank-sum test was used. Principal component analysis (PCA) was conducted to identify the variables driving specimen differences and to visualise whether ossicle sizes clustered by specimen. Discriminant function analysis (DFA) was conducted to evaluate how well the ossicle morphometric variables distinguished the specimens, yielding classification accuracy (%). All statistical analyses were performed in R.

List of apodid species from Indonesia. The apodid species list from Indonesia (Table 4) was compiled from reliable publications and results from this study. The current status of each species (name validity) was determined from the World Register of Marine Species (WoRMS: https://www.marinespecies.org/).

RESULTS

The present study morphologically identified five species of Apodida (*Chiridota smirnovi*, *Polycheira*

Table 1. Description of morphometric variables for wheels and rods from anterior and posterior body walls, as well as the tentacles and longitudinal muscles, together with their abbreviations used in the text.

Abbreviation	Variable description	Variable measurement or derivation
AWD	Anterior wheel diameter	Only complete wheels with six spokes and teeth were measured
AASW	Anterior apex spoke width	Percentage ratio of apex spoke width to diameter
AMSW	Anterior middle spoke width	Percentage ratio of middle spoke width to diameter
ABSW	Anterior basal spoke width	Percentage ratio of basal spoke width to diameter
ACWD	Anterior centre disc wheel diameter	Percentage ratio of centre disc wheel diameter to diameter
ASL	Anterior spoke length	Percentage ratio of spoke length to diameter
PWD	Posterior wheel diameter	Only complete wheels with six spokes and teeth were measured
PASW	Posterior apex spoke width	Percentage ratio of apex spoke width to diameter
PMSW	Posterior middle spoke width	Percentage ratio of middle spoke width to diameter
PBSW	Posterior basal spoke width	Percentage ratio of basal spoke width to diameter
PCWD	Posterior centre disc wheel diameter	Percentage ratio of the centre disc wheel diameter to the diameter
PSL	Posterior spoke length	Percentage ratio of the spoke length to the diameter
ACRL	Anterior curved rod length	Only curved rods (C-shaped) were measured
ACRW	Anterior curved rod width	Only curved rods (C-shaped) were measured
PCRL	Posterior curved rod length	Only curved rods (C-shaped) were measured
PCRW	Posterior curved rod width	Only curved rods (C-shaped) were measured
TRL	Tentacle rod length	Length measured from end to end
TRW	Tentacle rod width	Width measured at the middle part of the rod
LMRL	Longitudinal muscle rod length	Length measured from end to end
LMRW	Longitudinal muscle rod width	Width measured at the middle part of the rod

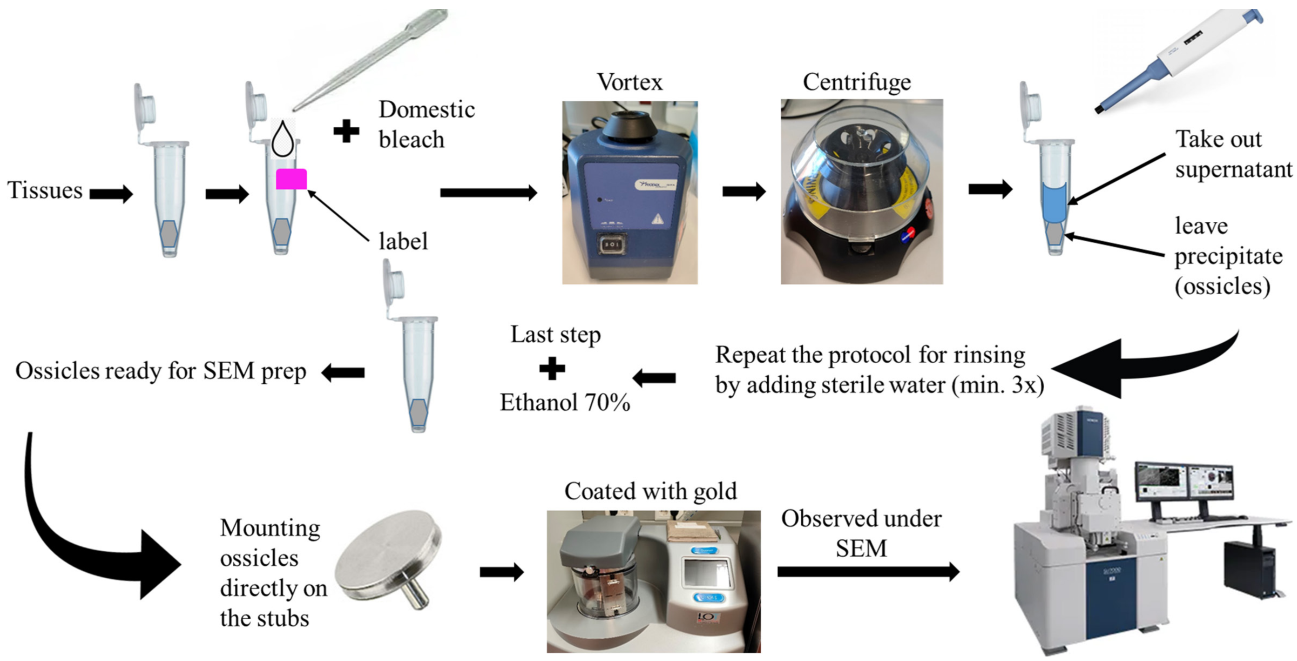


Fig. 2. Procedure of sea cucumber ossicle isolation for observation under the scanning electron microscope (SEM).

Fig. 3. *Chiridota smirnovi* Massin, 1996. A: specimen photograph; B: calcareous ring.

rufescens, *Opheodesoma grisea*, *Synaptula denticulata*), including a species new to science; *Polycheira nusalaut*, new species. A key to the Apodida species treated in the present study, along with updated systematics and nomenclature for each species, is presented below.

A total of 69 apodid species and one subspecies, *Synapta maculata sundaensis* (Heding, 1928), have been recorded from Indonesian waters (Table 4). The species list was compiled based on the results of the present study and data from 27 relevant publications.

KEY TO APODIDA SPECIES FROM INDONESIA DURING THE PRESENT STUDY (*indicates new species)

1. Tentacles peltato-digitate. Body wall ossicle wheels............... .... Family Chiridotidae (2)
– Tentacles pinnate or digitate. Body wall ossicle anchors and anchor-plates... Family Synaptidae (4)
2. Tentacles 8, typically 10-14 tentacles (*Chiridota*). C-shaped rods thick, strongly curved to O-shaped, and smooth extremities .. ..*Chiridota smirnovi*
– Tentacles 18 (typically 16-20).......................... *Polycheira* (3)
3. Tentacle rods longer (126.2±28.5 µm long), 29-33% area at each rod-end is covered by small spines. Wheel in the body wall has an inner rim with regular circling, wheel-spoke has a rather straight shape, and wheel center disc is less convex with a shorter diameter ....*Polycheira rufescens*
– Tentacle rods shorter (91.4±12.1 µm long), 13-20% area at each rod-end is covered by small spines. Wheel at the body wall has an inner rim with rather irregular/bumpy circling, wheel spokes always have a wide center shape and taper at the ends, and wheel center disc is more convex with longer diameter .. .. *Polycheira nusalaut*, new species*
4. Ossicles of anchor stock irregularly branched ....*Opheodesoma grisea*
– Ossicles of anchor stock unbranched ... *Synaptula denticulata*

SYSTEMATICS

Subclass Paractinopoda Ludwig, 1891

Order Apodida Brandt, 1835

Family Chiridotidae Östergren, 1898

Genus *Chiridota* Eschscholtz, 1829

Chiridota smirnovi Massin, 1996
(Figs. 3, 4)

Chiridota smirnovi Massin, 1996: 49, fig. 35A–F. – Siddiq et al., 2016: 57, tab 1.

Type material. Holotype RMNH Ech. 06030 (RMNH: Nationaal Natuurhistorisch Museum (Naturalis), Leiden, Netherlands).

Type locality. Ambon, Indonesia (Massin, 1996).

Material examined. MZB. Hol. 421 (one specimen), 50 × 35 mm in ethanol, collected in Bilik Beach, Baluran National Park, East Java; during low tide, under rocks, on seagrass bed; 0–0.5 m depth; coll. AM Siddiq, 30 July 2015.

External morphology. Small species, body cylindrical, tapering toward both anterior and posterior. Colour in ethanol is the same as in life, whitish translucent (Fig. 3A). Body covered with numerous small warts. Mouth and anus terminal. Eight digitate tentacles.

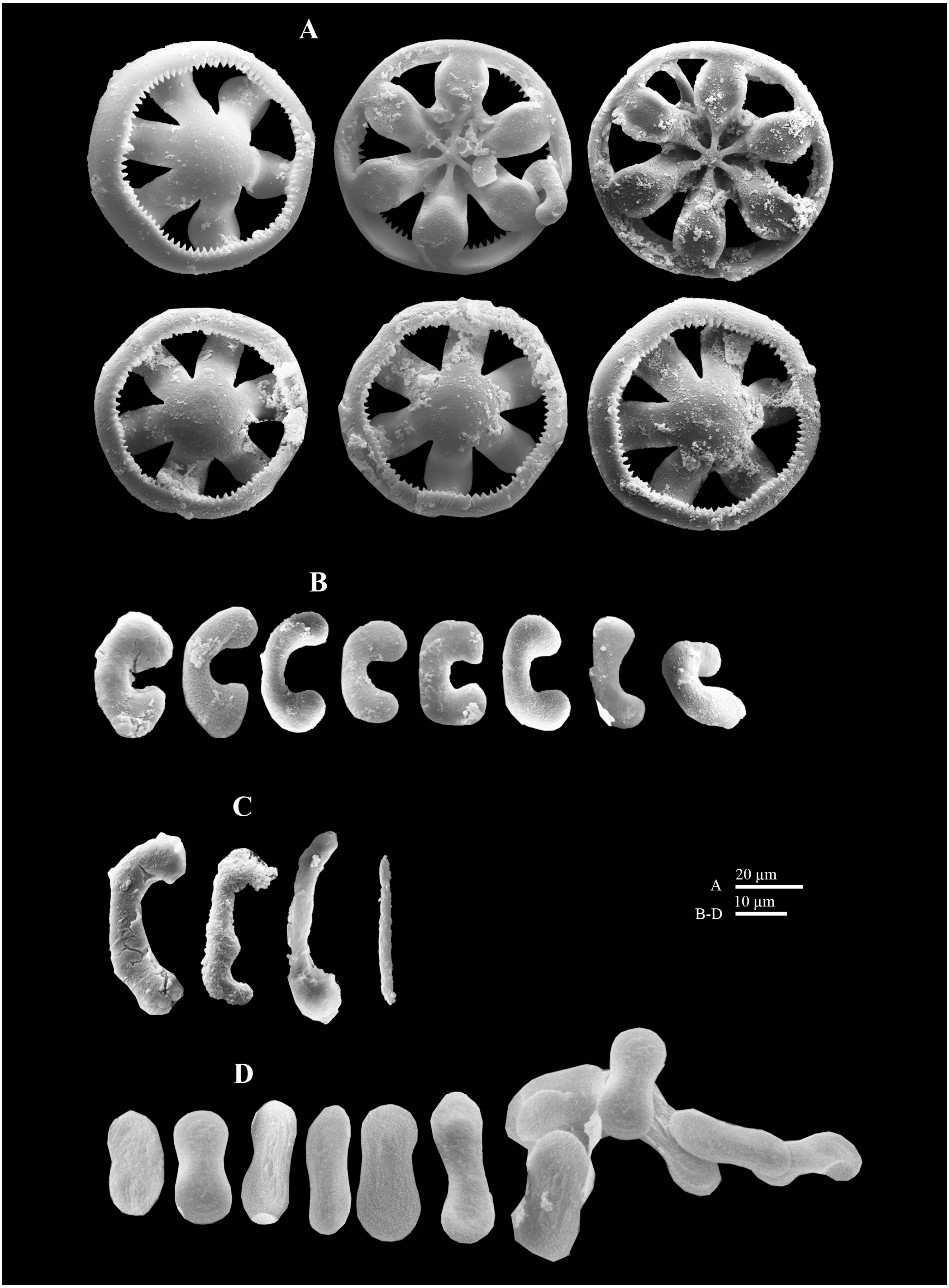
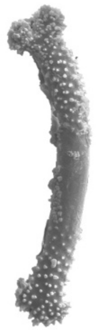
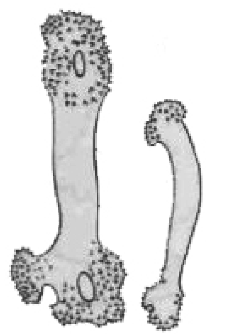
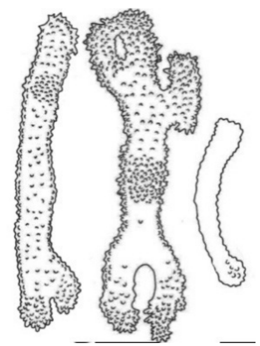


Fig. 4. *Chiridota smirnovi* Massin, 1996. Ossicles of the body wall. A: wheels; B: C-shaped rods. C: tentacle rods. D: longitudinal muscles ossicles.

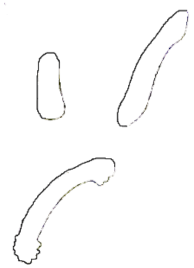
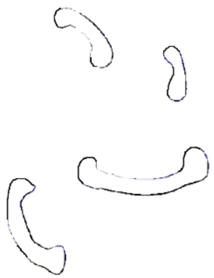
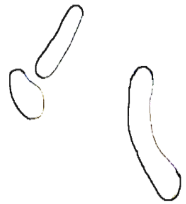
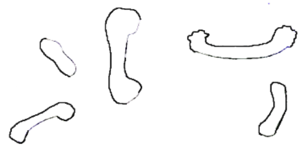
Table 2a. Character comparison between *Polycheira nusalaut,* new species, and its congeners (NA: information not available/not mentioned in the original description/reference(s)).

Character	***Polycheira nusalaut*, new species**	***Polycheira rufescens* (Brandt, 1835) of this study (MZB.Hol. 254)**	***Polycheira echinata* Heding, 1928 (original description): 309**	***Polycheira fusca* (Quoy & Gaimard, 1833) (original description): 126-127**	***Polycheira fusca* (Quoy & Gaimard, 1833) by Cherbonnier, 1952: 16, fig. 5, a-h (re-description of the holotype)**	***Polycheira fusca* (Quoy & Gaimard, 1833) of Cherbonnier, 1988: 269, fig. 12a-l.**
	Holotype MZB.Hol.310	MZB.Hol. 254; holotype unknown (Rowe & Gates, 1995)	Holotype unknown	Holotype in the Muséum National d'Histoire Naturelle, Paris, Laboratoire Malacologie (Cherbonnier, 1988)	Redescription of type specimen deposited in the Muséum National d'Histoire Naturelle, Paris, Laboratoire Malacologie	Madagascar: Tanikely islet (near Nosy Be), Cherbonnier collection, 1960: 14 specimens; Tuléar, Galenon collection, 1972: 6 specimens; Thomassin collection, 1972: 80 specimens. Comoros Islands: Grande Comore, Anthony collection, 1972: 1 specimen. Glorieuses Islands, Millot collection, 1958: 1 specimen (Cherbonnier, 1988)
Geographical records	Desa Sila, Nusalaut Island, Maluku, Indonesia	Simeulue, Aceh. Type locality Bonin Ils (as 'in insulis Bononsimensibus').	Type locality: Koh Lom, Gulf of Siam	Type locality: not mentioned specifically in the description, rather stated as "Cette espèce habite le havre Carteret à la Nouvelle-Irlande" (translation: This species inhabits Carteret Harbour in New Ireland).		Madagascar, Comoros, and Glorieuses Islands
Body colour	Uniform dark brown in living animal, light brown in preserved specimen (pers. obs.)	Variable, ranging from dark violet through clear reddish to almost colorless (Clark, 1907); pale greyish, blackish-purple (Heding, 1928); reddish brown (Samyn et al., 2006); dark brown to almost black with numerous creamy brown circles (this study)	Colorless (original description of *Polycheira echinata*)	Body slender, elongated, smooth body, violet, becoming brownish (original description of *Fistularia fusca*).	Preserved specimen is uniformly yellowish-white (Cherbonnier, 1952)	Uniformly reddish-brown. Their tegument is rather thick and very densely transversely wrinkled, and is dotted with numerous small warts (this is comparable to the description of *P. rufescens* of this study)

Character	***Polycheira nusalaut*, new species**	***Polycheira rufescens* (Brandt, 1835) of this study (MZB.Hol. 254)**	***Polycheira echinata* Heding, 1928 (original description): 309**	***Polycheira fusca* (Quoy & Gaimard, 1833) (original description): 126-127**	***Polycheira fusca* (Quoy & Gaimard, 1833) by Cherbonnier, 1952: 16, fig. 5, a-h (re-description of the holotype)**	***Polycheira fusca* (Quoy & Gaimard, 1833) of Cherbonnier, 1988: 269, fig. 12a-l.**
Number of tentacles	18	18	17	16	17	18
Rods of body wall	Elongated C-shaped, spiny at the whole edge; size 82.9±6.9 µm anterior, 74.3±10.6 µm posterior	Curved or C-shaped, with spines (blunt) at the ends; 40–60 µm long (Heding, 1928: 306–309); 80.4±19.8 µm anterior, 70.9±13.0 µm posterior (this study)	According to the original description, "Slightly curved with distinctly spiny ends/massive spines at ends; size larger than the corresponding rods in large specimen of *P. rufescens*"	NA	Smooth rods found in the radii and mesenteries, rods with denticulated ends, and some are slightly nodular, found in the interadii	Rods curved, with a finely undulating edge, with extremities ornamented or not with nodules; some of these rods are provided with one or two pointed ends
Tentacle rods	Stout, straight/slightly bent, without perforations and unbranched; dense blunt-spines at the ends; mean size 91.4±12.1 µm (n=10)	Stout, large, straight/ slightly bent, the ends are distinctly swollen and full of blunt spines, with/ without perforations and branched at ends; size >150 µm (Heding, 1928), mean length 126.2±28.5 µm (n=10; this study)	Thin, straight/slightly bent, without perforations and unbranched at the ends; spiny at the ends; size <110 µm	NA	Rods, perforated or not, but always strongly spiny at the extremities, some rods have their entire surface covered with spines.	Very large (> 5000 µm), extremely rough due to the presence of many asperities, but there are also rods that are short and almost smooth (2800 µm)
Tentacle rod area with small spines (see also figures in the row below)	13–20% area at each end is covered by small spines	29–33% area at each end is covered by small spines	7–10% area at each end is covered by small spines	NA	26–31% (perforated rod/ left fig.) and 21–27% (unperforated rod/right fig.) area at each end covered by small spines	100% (left), 30–50% (middle)
Tentacle rod shape				NA		

Character	*Polycheira nusalaut*, new species	*Polycheira rufescens* (Brandt, 1835) of this study (MZB.Hol. 254)	*Polycheira echinata* Heding, 1928 (original description): 309	*Polycheira fusca* (Quoy & Gaimard, 1833) (original description): 126-127	*Polycheira fusca* (Quoy & Gaimard, 1833) by Cherbonnier, 1952: 16, fig. 5, a-h (re-description of the holotype)	*Polycheira fusca* (Quoy & Gaimard, 1833) of Cherbonnier, 1988: 269, fig. 12a-l.
Wheel of body wall	Wheels mostly with six spokes, several with 4-5-spoked; diameter 30–90 µm (anterior part), 40–100 µm (posterior part)	Wheels always with six spokes; diameter 80–140 µm (Heding, 1928), 40–120 µm (this study)	According to the original description, "The arrangement of the wheels is as in *P. rufescens*, but the wheels are smaller"; size only 40–90 µm in diameter"	NA	Wheels with six spokes; diameter 50-110 µm	Wheels with six spokes, unequal size; diameter 2.5 mm
Wheel inner rim	Circling rather irregular/ bumpy	Circling regularly	NA	NA	NA	NA
Wheel spoke shape			NA	NA		
Wheel center disc	More convex with longer diameter (34.8±2.9 µm anterior, 35.5±3.8 µm posterior)	Less convex with shorter diameter (32.5±3.0 µm anterior, 31.3±1.4 µm posterior)	NA	NA	NA	NA
Oval bodies of longitudinal muscles	Present, numerous	Present, numerous	Present, wanting	NA	Present, unknown amount	Present, unknown amount

Table 2b. (Continued from Table 2a) Character comparison between *Polycheira nusalaut,* new species and its congeners (NA: information not available/not mentioned in the original description/reference(s)).

Character	***Chiridota dubia*** **Semper, 1867: 21, tab. 5, fig. 4; tab. 8, fig. 16.**	***Chiridota incongrua*** **Semper, 1867: 22, tab. 5, fig. 5, 25; tab. 8, fig. 12.**	***Chiridota panaensis*** **Semper, 1867: 19, tab. 5, fig. 1, 15, 21, 27.**	***Chiridota variabilis*** **Semper, 1868: 20-21; tab. 5, fig. 6, 7, 9–11; tab. 6, fig. 11; tab. 8, fig. 5, 6.**	***Chiridota vitiensis*** **Gräffe in Semper, 1867: 19, tab. 5, fig. 8, 20; tab. 6, f. 12; tab. 8, fig. 7.**
Number of specimens examined	1	1	3	5	1
Geographical records	Type locality: Camiquin, Northern Luzon (Norden von Luzon), Philippines	Type locality: Camiquin, Northern Luzon (Norden von Luzon), Philippines	Type locality: Panaon near Surigao (Panaon bei Surigao), Philippines	Type locality: Mariveles, Manila Bay (Bai von Manila), Philippines	Type locality:Viti Island (Viti-Inseln), Fiji
Body colour	NA	NA	Colour in life: ark violet-black	NA	Pale reddish
Number of tentacles	18	16	19	17 or 18	18
Rods of the body wall (figures based on original description)					
Tentacle rods	NA	NA	NA	NA	NA
Tentacle rod area with small spines	NA	NA	NA	NA	NA
Tentacle rod shape	NA	NA	NA	NA	NA
Wheel of body wall	Wheels with six spokes; diameter not mentioned in original description.	Wheels with six spokes; diameter not mentioned in original description.	Wheels with six spokes; diameter not mentioned in original description.	Wheels with six spokes; diameter not mentioned in original description.	Wheels with six spokes; diameter not mentioned in original description.
Wheel inner rim	NA	NA	NA	NA	NA

Character	*Chiridota dubia* Semper, 1867: 21, tab. 5, fig. 4; tab. 8, fig. 16.	*Chiridota incongrua* Semper, 1867: 22, tab. 5, fig. 5, 25; tab. 8, fig. 12.	*Chiridota panaensis* Semper, 1867: 19, tab. 5, fig. 1, 15, 21, 27.	*Chiridota variabilis* Semper, 1868: 20-21; tab. 5, fig. 6, 7, 9–11; tab. 6, fig. 11; tab. 8, fig. 5, 6.	*Chiridota vitiensis* Gräffe in Semper, 1867: 19, tab. 5, fig. 8, 20; tab. 6, f. 12; tab. 8, fig. 7.
Wheel spoke shape (figures based on original description)					
Wheel center disc	NA	NA	NA	NA	NA
Oval bodies of longitudinal muscles	Figured in the original description, but not specifically noted as oval bodies of longitudinal muscle	Figured in the original description, but not specifically noted as oval bodies of longitudinal muscle	Figured in the original description, but not specifically noted as oval bodies of longitudinal muscle	Figured in the original description, but not specifically noted as oval bodies of longitudinal muscle	NA

Internal morphology. Radial and interradial pieces of calcareous ring are of the same size: 1 mm wide and high (Fig. 3B). The internal organs of the present material were not available due to evisceration during the preservation process. Longitudinal muscles completely attached.

Ossicles. Body wall with wheels and C-shaped rods. Wheels six-spoked, diameter 60–70 µm, internal rim spinous with number of spines between spokes varies between 8–10 (Fig. 4A). C-shaped rods present throughout body wall, numerous, thick, strongly curved, with slightly enlarged smooth extremities, 25–30 µm long (Fig. 4B). Tentacles with irregular rods, 30–35 µm long, straight or slightly curved (Fig. 4C). Longitudinal muscles are thin, straight or hourglass shaped, 20–30 µm long (Fig. 4D).

Remarks. Rarely reported species. This study represents only the second recorded instance of this species both globally and in Indonesia.

Ecology. Deposit feeder, living in the seagrass bed.

Depth range. 0–2 m depth.

Geographic distribution. Ambon (Massin, 1996) and Baluran National Park, East Java (present study).

Genus *Polycheira* H. L. Clark, 1907

Polycheira rufescens (Brandt, 1835)
(Figs. 5–7)

Chiridota rufescens Brandt, 1835: 59. – Ludwig, 1881: p. 579.
Chiridota dubia Semper, 1867: 21, tab. 5, fig. 4; tab. 8, fig. 16.
Chiridota incongrua Semper, 1867: 22, tab. 5, fig. 5, 25; tab. 8, fig. 12.
Chiridota panaensis Semper, 1867: 19, tab. 5, fig. 1, 15, 21, 27.
Chiridota variabilis Semper, 1868: p. 20-21; tab. 5, fig. 6, 7, 9–11; tab. 6, fig. 11; tab. 8, fig. 5, 6.
Chiridota vitiensis Gräffe in Semper, 1867: 19, tab. 5, fig. 8, 20; tab. 6, f. 12; tab. 8, fig. 7.
Fistularia fusca Quoy & Gaimard, 1834: 126, plate 8, fig. 1-4.
Polycheira fusca–Cherbonnier, 1952: 16, fig. 5, a-h. – Cherbonnier, 1988: 269, fig. 12a-l.
Polycheira vitiensis (Gräffe in Semper, 1867): 19, tab. 5, fig. 8, 20; tab. 6, f. 12; tab. 8, fig. 7.
Polycheira rufescens–Clark, 1907: 120, pl. VII, figs. 14–18. – Clark & Rowe, 1971: 188, fig. 100b. – Thandar, 1989: 451, figs. 1a, 2. – Rowe & Gates, 1995: 334. – Massin, 1996: 172, fig. 14. – Samyn et al., 2006: 42, fig. 46A–E. – Purwati & Wirawati, 2012: 245, figs. 14, 15A–F. – Wirawati et al., 2019: 77.

Type material. Type status and whereabouts unknown (Rowe & Gates, 1995).

Type locality. Bonin Islands (as 'in insulin Bononsimensibus') (Brandt, 1835).

Material examined. MZB. Hol. 254 (one specimen); 30 × 20 mm in ethanol; collected in Desa Pasir Tinggi, Simeulue, Aceh; during low tide under rocks, on a rocky shore; 0–1 m depth; coll. A. Setyastuti, 27 July 2017.

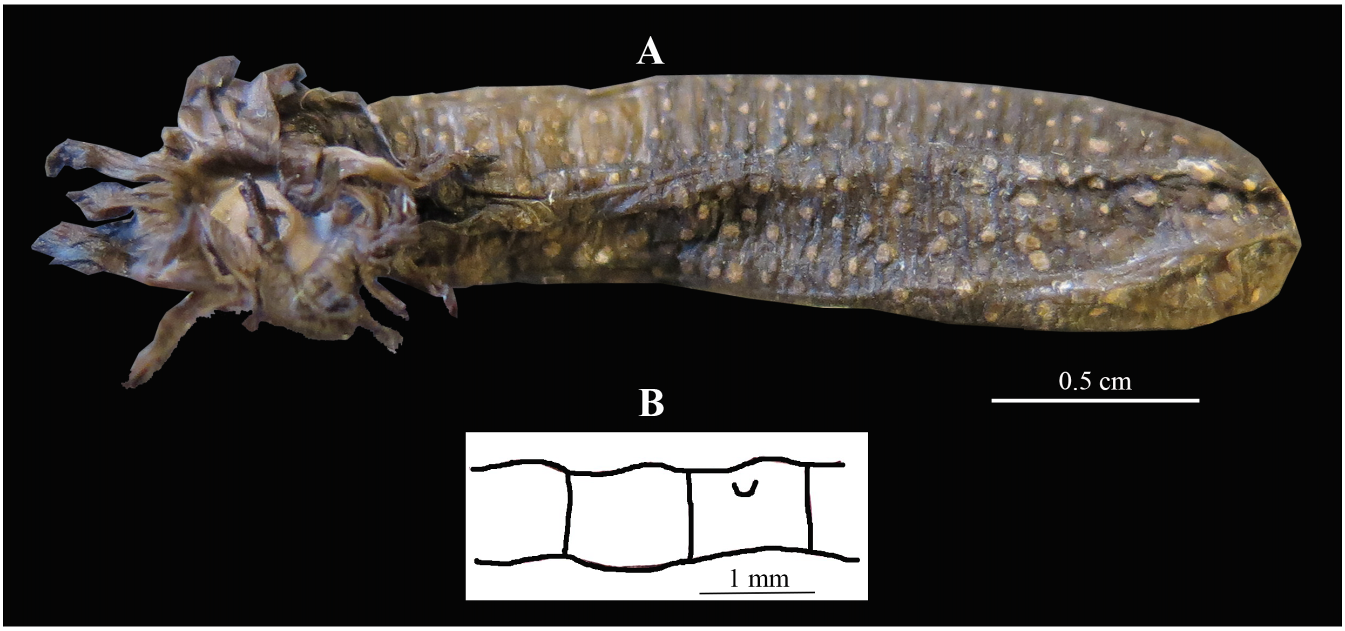


Fig. 5. *Polycheira rufescens* (Brandt, 1835). A: specimen photograph, showing the integument with numerous whitish circular patches; B: calcareous ring.

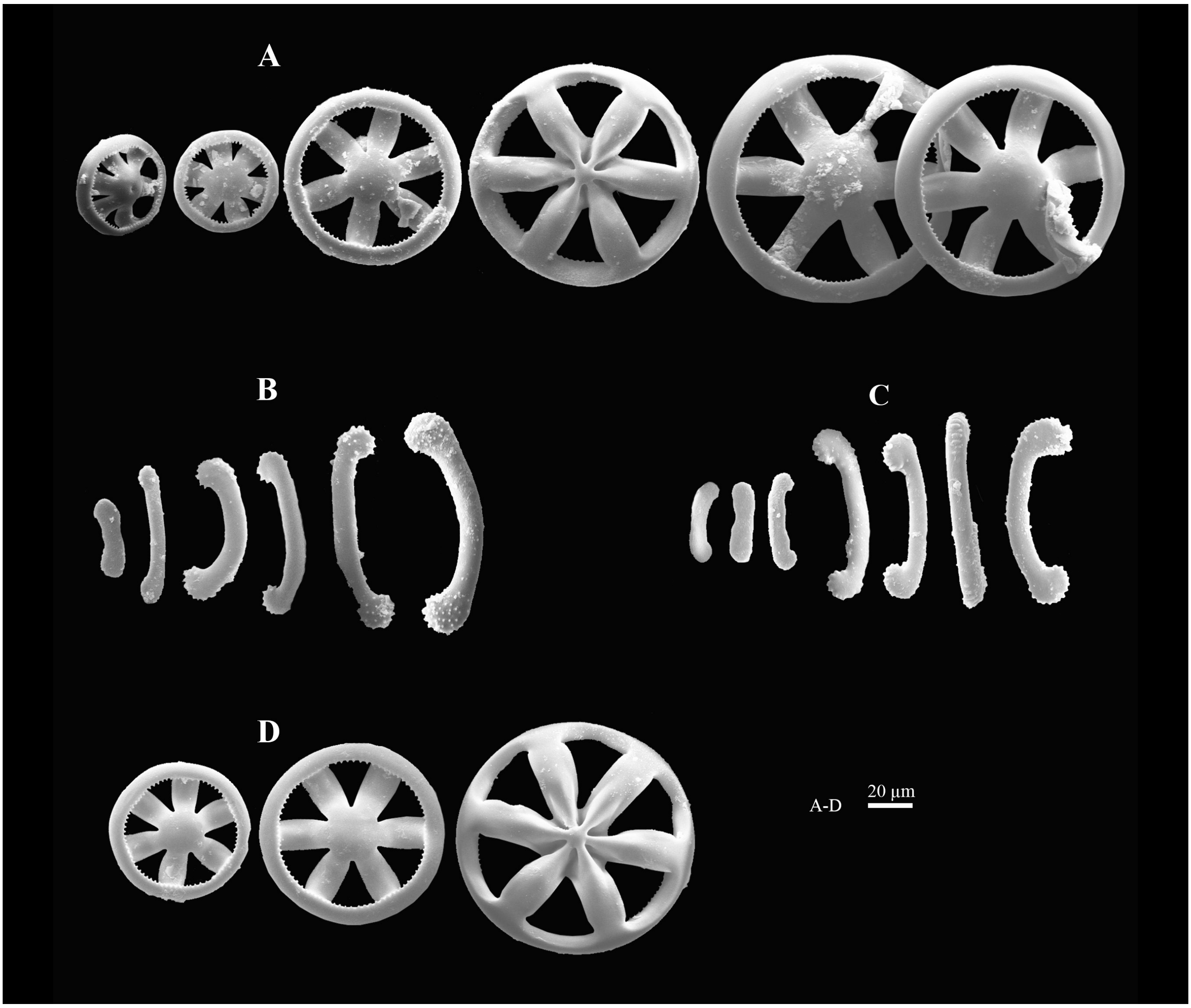


Fig. 6. *Polycheira rufescens* (Brandt, 1835). A: wheels from the anterior body wall; B: curved rods from the anterior body wall; C: curved rods from the posterior body wall; D: wheels from the posterior body wall.

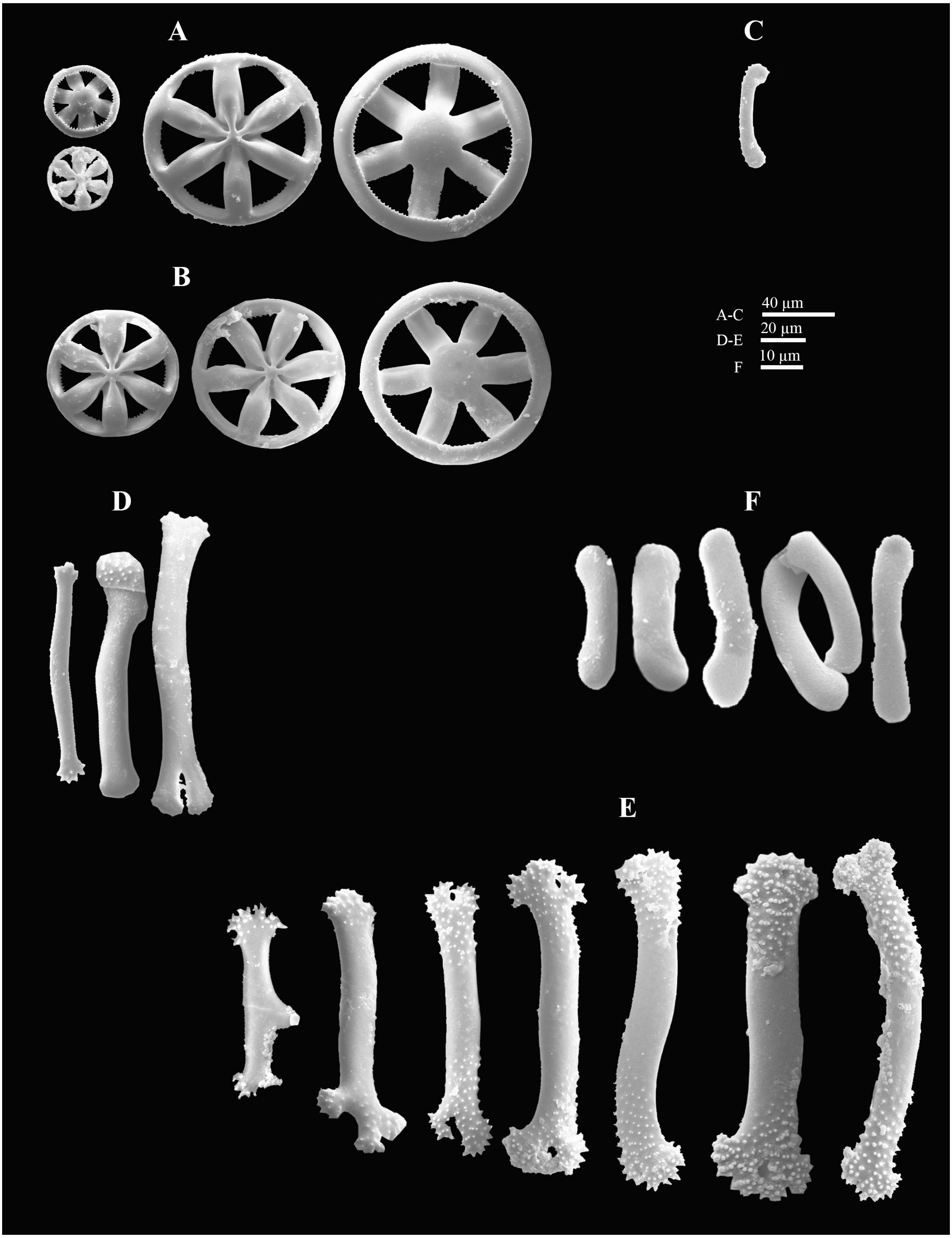


Fig. 7. *Polycheira rufescens* (Brandt, 1835) ossicles. A: wheels from a circular patch on the anterior wall; B: wheels from a circular patch on the posterior wall; C: curved rod from the a circular patch on the posterior wall; D, E: tentacle rods; F: ossicles of longitudinal muscles.

Table 3. Wheel and rod ossicle measurements (µm) of *Polycheira rufescens* and *Polycheira nusalaut,* new species. The number of ossicles measured is limited to n = 10 SEM images per variable. See Table 1 for abbreviations.

Ossicle type	Ossicle location	Ossicle dimension	*Polycheira nusalaut* n. sp. (MZB. Hol.310) Mean ± SD (range)	*Polycheira rufescens* (MZB.Hol.254) Mean ± SD (range)
Wheel	Anterior body wall	AWD	85.3±17.4 (53–106)	94.7±25.4 (42–117)
Wheel	Anterior body wall	AASW	17.7±2.3 (13–22)	17.5±2.6 (14–24)
Wheel	Anterior body wall	AMSW	21.4±2.3 (19–26)	17.4±2.3 (15–23)
Wheel	Anterior body wall	ABSW	15.6±1.8 (13–19)	15.3±2.0 (12–19)
Wheel	Anterior body wall	ACWD	34.8±2.9 (31–42)	32.5±3.0 (26–39)
Wheel	Anterior body wall	ASL	24.3±2.3 (19–29)	24.2±1.4 (21–25)
Wheel	Posterior body wall	PWD	87.8±26.1 (49–121)	93.5±16.7 (64–113)
Wheel	Posterior body wall	PASW	15.4±2.4 (12–20)	16.6±1.8 (14–20)
Wheel	Posterior body wall	PMSW	20.1±2.8 (15–25)	17.2±1.3 (15–19)
Wheel	Posterior body wall	PBSW	15.6±1.7 (12–18)	14.3±1.1 (11–16)
Wheel	Posterior body wall	PCWD	35.5±3.8 (32–45)	31.3±1.4 (29–34)
Wheel	Posterior body wall	PSL	24.3±2.1 (19–27)	24.3±2.1 (19–27)
Rod	Anterior body wall	ACRL	82.9±6.9 (71–97)	80.4±19.8 (52–120)
Rod	Anterior body wall	ACRW	11.6±0.9 (10–13)	10.8±1.7 (8–14)
Rod	Posterior body wall	PCRL	74.3±10.6 (56–93)	70.9±13.0 (49–89)
Rod	Posterior body wall	PCRW	9.9±1.5 (7–12)	9.2±1.2 (7–11)
Rod	Tentacles	TRL	91.4±12.1 (74–107)	126.2±28.5 (83–163)
Rod	Tentacles	TRW	9.9±3.0 (8–18)	15.9±3.3 (11–22)
Rod	Longitudinal muscles	LMRL	49.6±5.9 (39–58)	38.8±5.3 (32–52)
Rod	Longitudinal muscles	LMRW	6.5±1.9 (4–10)	8.3±1.5 (6–11)

External morphology. Small sized, body cylindrical. In living animals and in ethanol, the body colour is the same, dark brown to almost black, with numerous creamy-brown circular patterns (Fig. 5A). Body wall firm, rough to the touch, less than 1 mm thick. Mouth and anus terminal. Tentacles 18, the length of the stalks 4 mm, peltato-digitate.

Internal morphology. Radial pieces of calcareous ring as large as interradial pieces (1 mm wide and high). Radial pieces with lightly concave posterior margin and central anterior notch, interradial pieces with small anterior tooth (Fig. 5B). Cuvierian tubules, stone canal, madreporite, and gonad were not available for observation. Tentacle ampullae present, 1.5 mm. Five Polian vesicles, sac-like, 3–5 mm long. Longitudinal muscles flat and thick, medially attached, and lateral margins free. Inner body wall dark-greyish. Intestine filled with fine white sand.

Ossicles. Body wall with wheels and curved rods. Wheels from anterior body wall 42–117 (94.7±25.4) µm across (Fig. 6A); curved rods 52–120 (80.4±19.8) µm long (Fig. 6B, Tables 3, 4), smaller rods usually with smoother surface, but generally the curved rods have warty or many blunt spines at the distal part/extremities. Posterior body wall composed of ossicles that are similar to those in the anterior body wall, wheels 64–113 (93.5±16.7) µm and curved rods 49–89 (70.9±13.0) µm long (Fig. 6C, D, Tables 3, 4). Spokes of the wheels are always straight (Table 2a, Fig. 16); the wheel centre disc is less convex (Table 2a, Fig. 16) with a shorter diameter 26–39 (32.5±3.0) µm than *Polycheira nusalaut*, new species (ZMB Hol. 310). Anterior circular pattern consists only of wheels, size varies from 40–120 µm across (Fig. 7A). Posterior circular pattern with wheels, 80–120 µm across (Fig. 7B), and a few curved rods, 50–60 µm long (Fig. 7C).

Tentacle rods are generally straight with two variant shapes, smooth surface (Fig. 7D) and warty surface (Fig. 7E), size 83–163 (126.2±28.5) µm long (Table 3). Longitudinal muscles consist of numerous smooth rods, 32–52 (38.8±5.3) µm long (Fig. 7F; Table 3).

Ecology. Benthic, deposit feeder, detritus feeder, inshore, tropical.

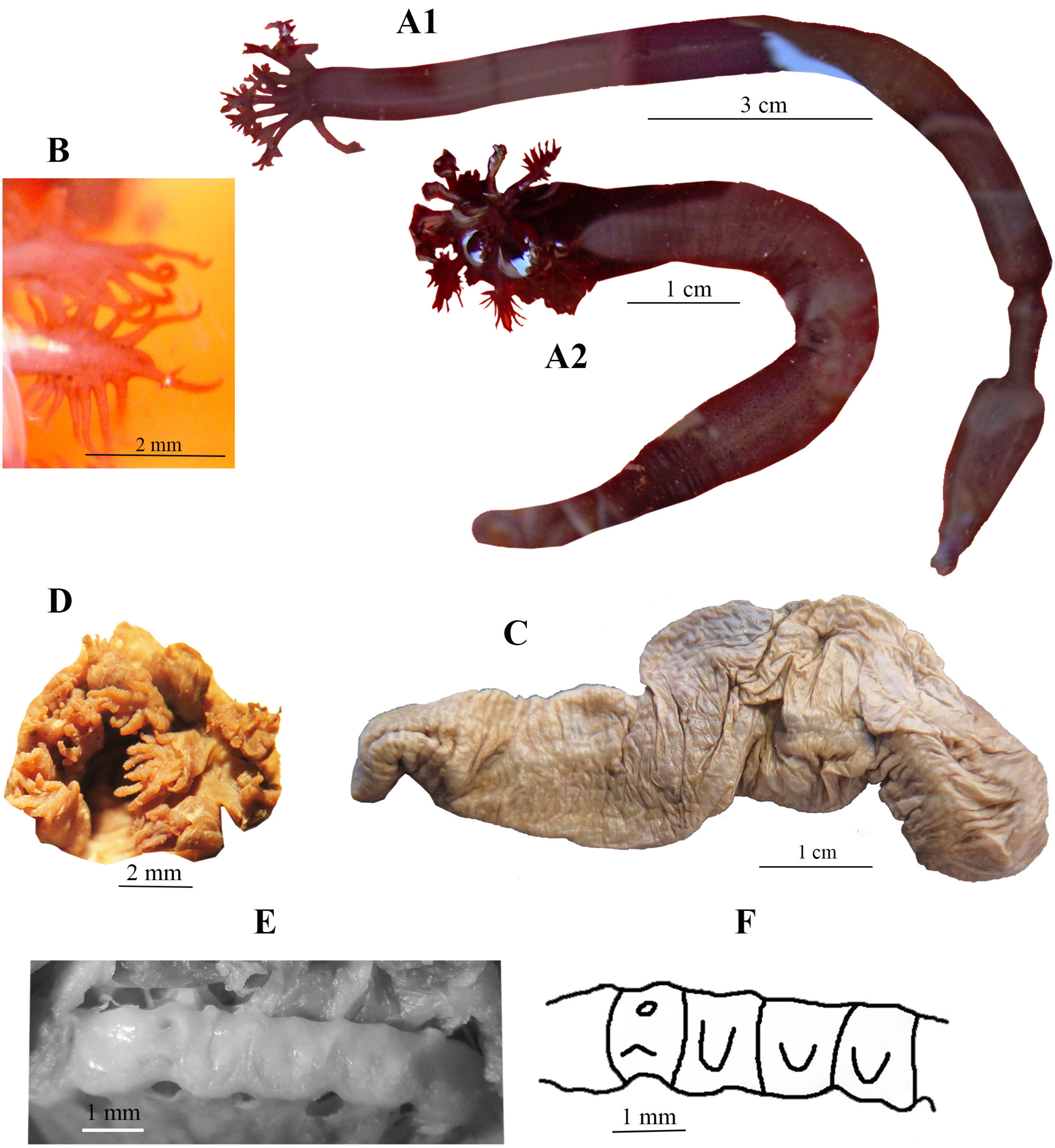


Fig. 8. *Polycheira nusalaut*, new species. Living animal (A1: relaxed, A2: contracted), B: detail of digitate tentacle in living animal, C: preserved specimen, D: preserved tentacle, E: calcareous ring, F: line drawing of calcareous ring.

Depth range. 0–1 m depth (present study).

Geographic distribution. Africa, Indonesia, Philippines, North Australia, China, Pacific Ocean (Samyn et al., 2006).

***Polycheira nusalaut*, new species**
(Figs. 8–9)

Etymology. Named after its type locality, Nusa Laut Island, Indonesia.

Type material. Holotype MZB. Hol. 310 (one specimen); 70 × 30 mm in ethanol; specimen collected during low tide in a rocky shore area with patchy seagrass, 0.5–2 m depth; coll. A. Setyastuti, 6 October 2009.

Type locality. Desa Sila, Nusa Laut Island, Maluku, Indonesia.

External morphology. Body cylindrical, worm-like. Body colour of living animal uniformly dark brown (Fig. 8A). In ethanol, body uniformly light brown (Fig. 8C). Body wall

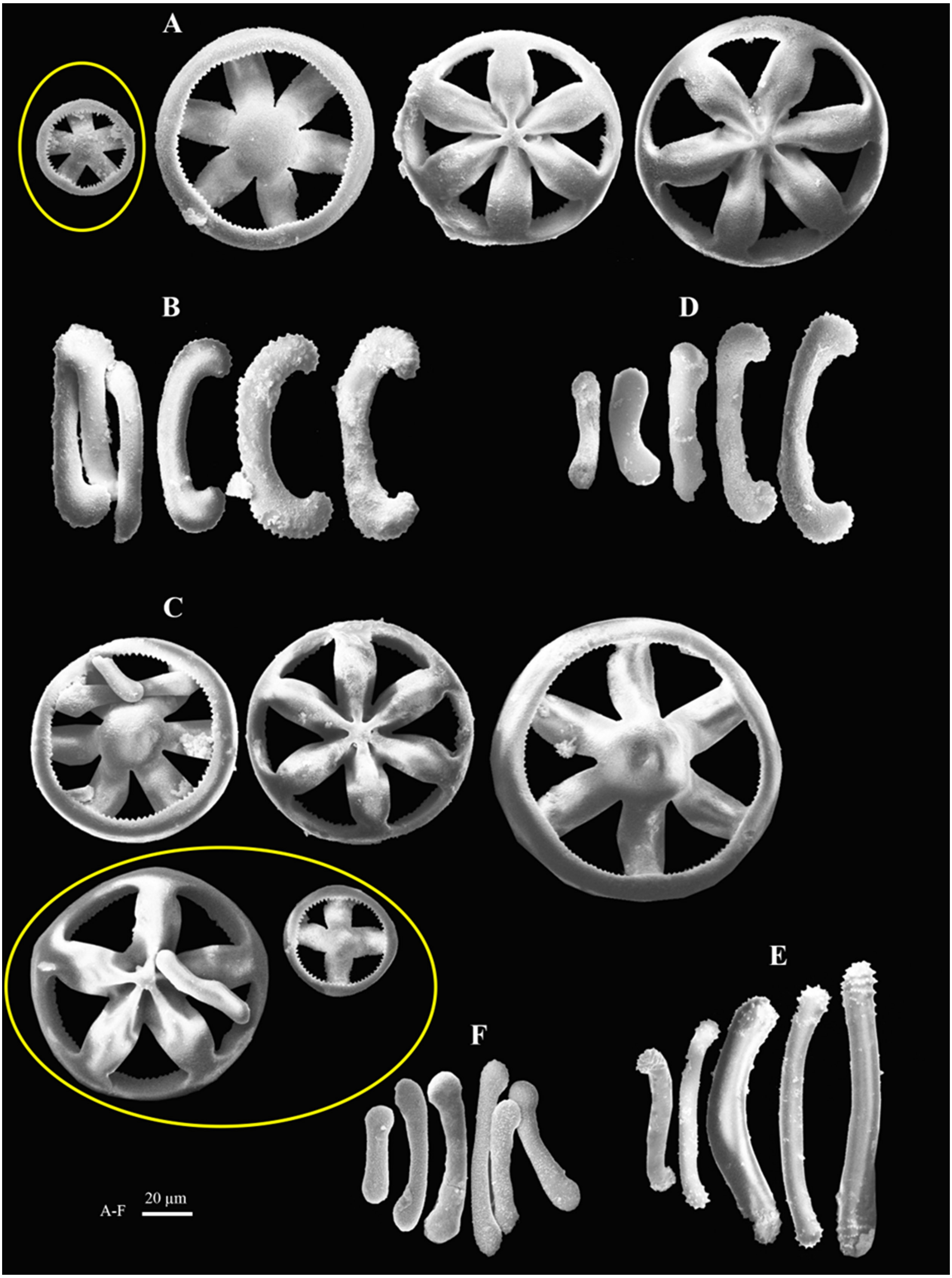


Fig. 9. *Polycheira nusalaut*, new species. A, B: Ossicles of anterior body wall, A: wheels; B: C-shaped rods. C, D: Ossicles of posterior body wall, C: wheels; D: C-shaped rods. E: tentacle rods. F: ossicles of longitudinal muscles. The yellow line delineates wheels with less than six spokes.

slightly rough to the touch, less than 1 mm thick. Mouth and anus terminal. Mouth surrounded by 18 small tentacles, each with 16 digitations (Fig. 8B, D); the base of the tentacle with numerous small circular warts. Dorsal papillae and ventral tube feet are absent.

Internal morphology. Calcareous ring stout, thick, radial and interradial pieces with the same width and height, and both with small anterior teeth. Radial pieces with anterior perforation (Fig. 8E, F). Cuvierian tubules, Polian vesicle, stone canal, and madreporite were not available for observation. Tentacle ampullae present. Gonad in two tufts and branched. Longitudinal muscles flat, medially attached and lateral margins free, dark grey. Inner body wall light brown.

Ossicles. Body wall with wheels and C-shaped rods; ossicles size slightly bigger posteriorly than anterior. Wheels six-spoked, internal rim spinous with number of spines between spokes 6–14, depending on the wheel sizes, diameter 53–106 (85.3±17.4) µm anteriorly (Fig. 9A; Table 3) and 49–121 (87.8±26.1) µm posteriorly (Fig. 9C, Table 3). Spokes of the wheels always have a wide middle and are tapered at the ends (Table 2a; Fig. 16); the wheel center disc is more convex (Table 2a; Fig. 16) with a longer diameter 31–42 (34.8±2.9) µm than *Polycheira rufescens* (Hol. 254) described in this study. C-shaped rods more curved but elongated, enlarged end, spiny at the whole edge, 71–97 (82.9±6.9) µm long anteriorly (Fig. 9B; Table 3) and 56–93 (74.3±10.6) µm long posteriorly (Fig. 9D; Table 3). Tentacles hold rods, 74–107 (91.4±12.1) µm long (Fig. 9E; Table 3), with numerous small spines at the end; the proportion of the area with spines is about 13–20% at each end (Table 2a). Longitudinal muscles with numerous stout rods with smooth surfaces, always with enlarged and rounded rods 39–58 (49.6±5.9) µm long (Fig. 9F; Table 3).

Remarks. Previously, only two species were placed in the genus *Polycheira*, i.e., *P. rufescens* and *P. echinata* (WoRMS Editorial Board, 2025). With the description of *P. nusalaut*, new species, now three species belong to the genus.

In living animals, *P. nusalaut*, new species, has dark brown body colour, while *P. rufescens* can occur in various colours (dark violet, clear reddish to almost colourless, pale greyish, blackish-purple, dark brown to almost black with numerous creamy brown circles), and *P. echinata* is known to be colourless. Both *P. nusalaut* and *P. rufescens* have 18 tentacles, while *P. echinata* has 17 tentacles. Tentacle rods of *P. nusalaut* are shorter (91.4±12.1 µm) compared to *P. rufescens* (126.2±28.5 µm) and *P. echinata* (<110 µm). The area at each end of the tentacle rods that is covered by small spines is narrowest in *P. echinata* (7–10%), while in *P. nusalaut*, it is 13–20% and in *P. rufescens* is the largest (29–33%). Wheels in the body wall in *P. nusalaut*, has an inner rim with an irregular/bumpy circular shape and centre disc wheel is more convex and longer diameter (34.8±2.9 µm anterior, 35.5±3.8 µm posterior). In the case of *P. rufescens*, the inner rim wheel is of a regular circular shape and center disc wheel is less convex with a shorter diameter (32.5±3.0 µm anterior, 31.3±1.4 µm posterior). Unfortunately, no information is available for *P. echinata*. Numerous oval bodies of longitudinal muscles are present in both *P. nusalaut* and *P. rufescens*, but are wanting in *P. echinata*. Distinctive morphological characteristics that can be used to separate the new species from its congeners are presented in Table 2.

The ossicle measurements of *P. nusalaut*, new species, and *P. rufescens* in this study are shown in Table 3, and statistical analyses based on these measurements are presented in Figs. 17 and 18. The two species differed significantly in their anterior middle spoke width (AMSW), posterior center disc wheel diameter (PCWD), posterior middle spoke width (PMSW), tentacle rod length (TRL), tentacle rod width (TRW), longitudinal rod length (LMRL), and longitudinal rod width (LMRW). The PCA plot (Fig. 18a) showed that variable measurements such as TRL, TRW, LMRW, posterior spoke length (PSL), and posterior wheel diameter (PWD) influenced the separation of *P. rufescens*, while AMSW, PCWD, PMSW, LMRL, posterior basal spoke width (PBSW), and posterior curved rod width (PCRW) were strongly associated with the separation of *P. nusalaut*. Additionally, a discriminant function analysis (DFA; Fig. 18b) showed the classification accuracy was 100%, indicating a clear distinction, with no overlap between *P. rufescens* and *P. nusalaut*, based on ossicle measurements.

Ecology. Benthic, deposit feeder.

Depth range. 0.5–2 m depth.

Geographic distribution. Currently, it is only known from the type locality.

Family Synaptidae Burmeister, 1837

Genus *Opheodesoma* Fisher, 1907

Opheodesoma grisea (Semper, 1868)

(Figs. 10–12)

Synapta grisea Semper, 1868: 11, pl. 4, figs. 6–7.
Opheodesoma mauritiae Heding, 1928: 130, fig. 4 (1), 6 (14–17), 7 (5, 10).
Opheodesoma africana Heding, 1931: 645, fig. 2 (2–3, 6–11).
Opheodesoma grisea–Heding, 1928: 129, fig. 6(7–9), fig. 7(3, 9). –Clark & Rowe, 1971: 186, pl. 30, fig. 11.– Rowe & Doty, 1977: 235, figs. 5a, 8g. – Cherbonnier, 1988: 244, fig. 109A–F. – Kerr, 1994: 171, fig. 4e–f.– Rowe & Gates, 1995: 340.– Massin, 1999: 102, figs. 86a–j, 87 (synonymy and records before 1999). – Purwati & Wirawati, 2008: 375, fig. 3a–b. – Wirawati et al., 2019: 78. – Wirawati, 2020: 99, tab. 13. – Setyastuti & Vimono, 2020: 88, tab. 12.

Type material. Type status and whereabouts are unknown (Rowe & Gates, 1995).

Type locality. Bohol, Philippines (Semper, 1868).

Fig. 10. Preserved specimen of *Opheodesoma grisea* (Semper, 1868).

Material examined. MZB. Hol. 267 (one specimen); 72 × 20 mm in ethanol; collected in Kayangan Beach, Lombok; during low tide, in an area with patches of seagrass, 0.5–1.5 m depth; coll. A. Setyastuti, 19 April 2019.

External morphology. Body cylindrical, worm-like, anterior-half of specimen damaged. In ethanol, body uniformly black (Fig. 10). Body wall rough to the touch, less than 1 mm thick. Mouth and anus terminal. Tentacles were not available for observation.

Internal morphology. Calcareous ring and internal organs were not available for observation.

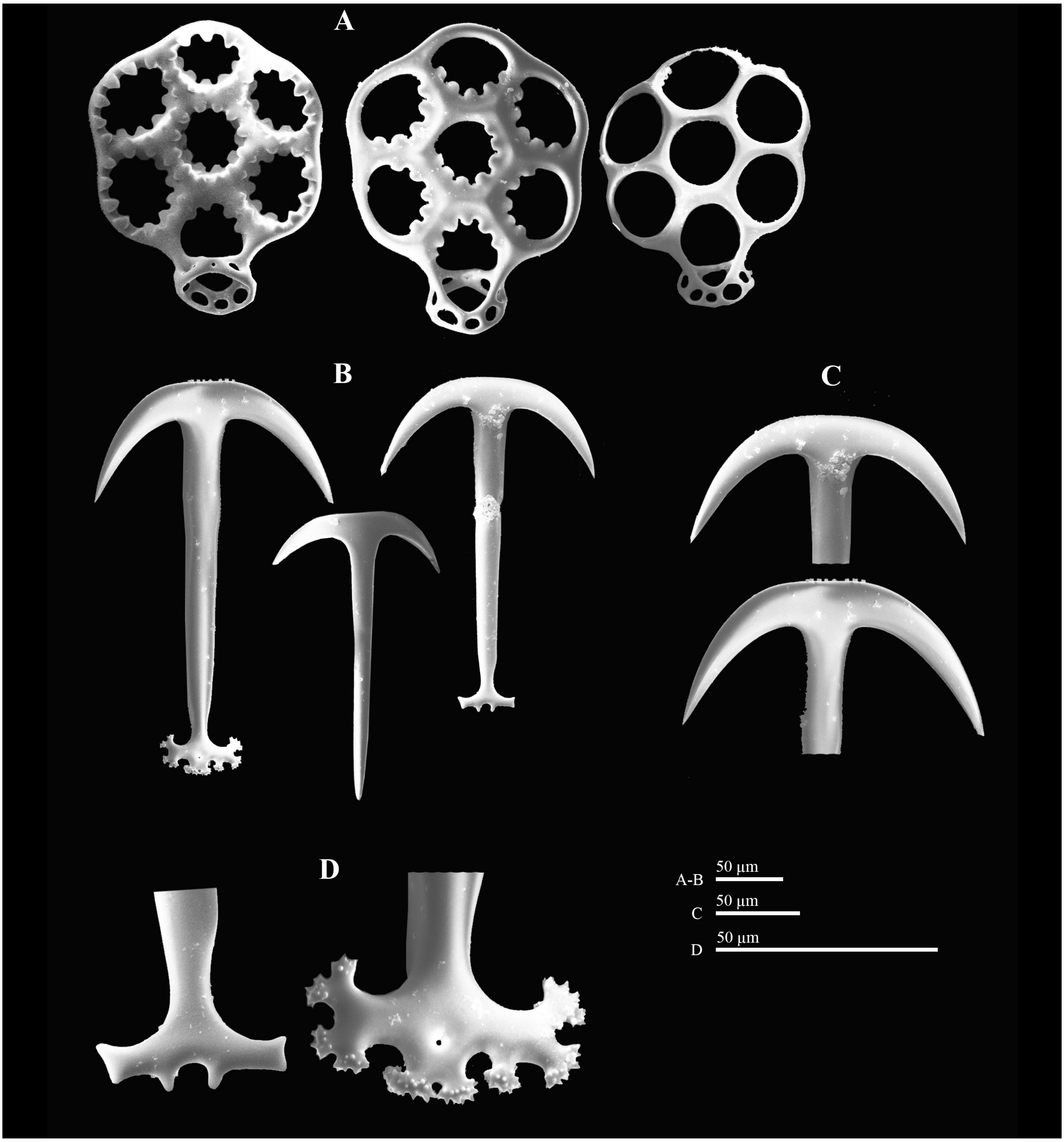


Fig. 11. *Opheodesoma grisea* (Semper, 1868). Ossicles of the anterior body wall. A: anchor-plates; B: anchor; C: anchor vertex; D: anchor stock.

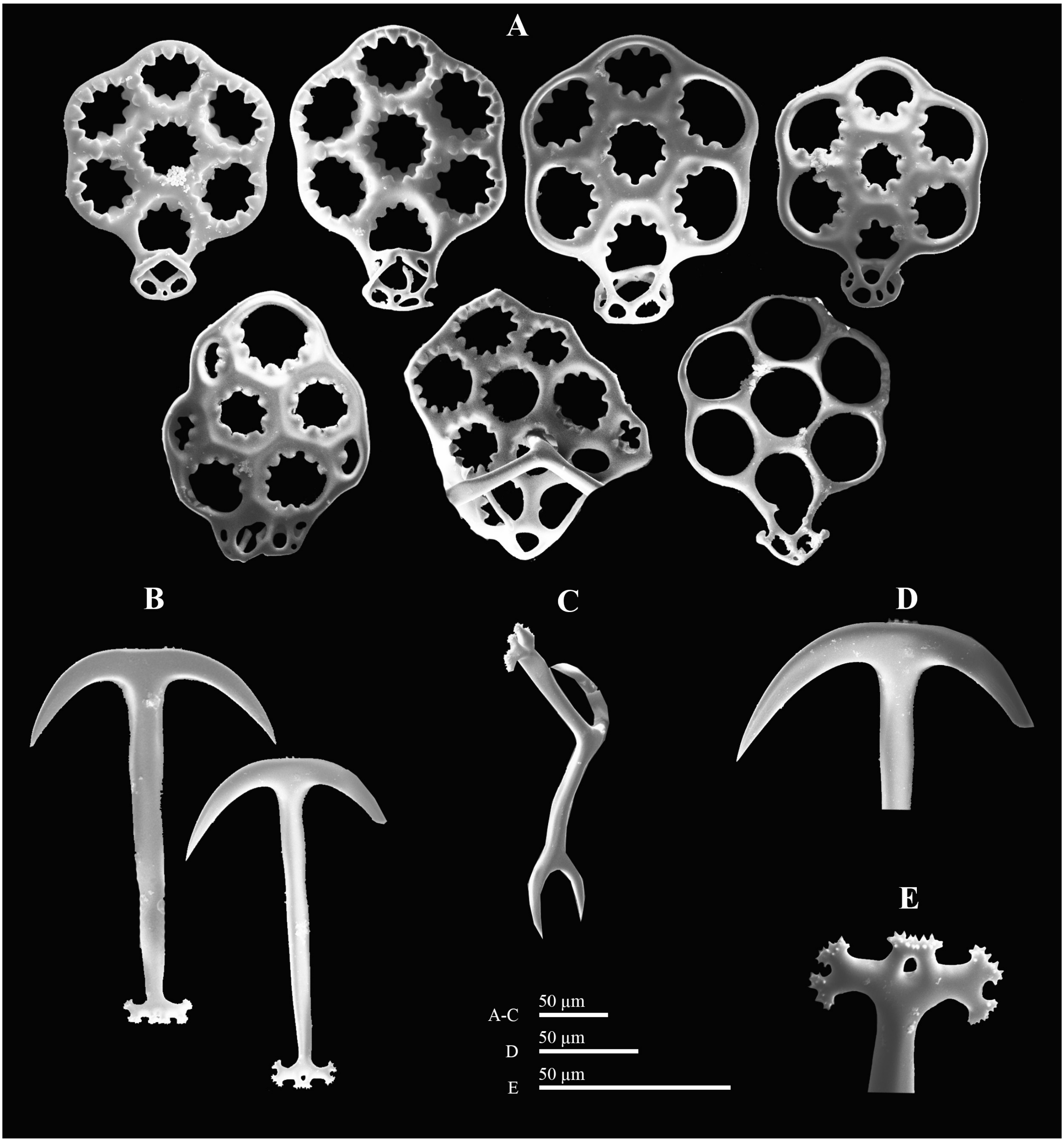


Fig. 12. *Opheodesoma grisea* (Semper, 1868). Ossicles of the posterior body wall. A: anchor-plates; B: anchor; C: rod; D: anchor vertex; E: anchor stock.

Ossicles. Anterior body wall holds anchor, anchor plates, and miliary granules. Anchor with smooth arms, length x wide: 200–280 × 125–175 µm (Fig. 11B), vertex with 0-8 small knobs (quadrangular teeth) (Fig. 11C), stock branched and granulous (Fig. 11D). Anchor-plates quadrangular, 175 µm length, 250 µm wide, seven serrated holes with a double row of teeth on one side of each hole; posterior part very narrow with 5–7 small smooth holes; bridges smooth or knobbed, centrally attached to a bar horizontally dividing the large posterior serrated hole (Fig. 11A). Miliary granules very abundant.

Posterior body wall holds anchors that are slightly smaller than those in the anterior wall, 250–275 × 150–175 µm (Fig. 12B, D, E). Anchor plates with regular or irregular-square shapes; regular square shape has similar characteristics to anterior body wall; irregular square shapes with 8–9 serrated holes, posterior part with 3–5 small smooth holes (Fig. 12A). Rods only a few (Fig. 12C).

Ecology. Benthic, deposit feeder, detritus feeder, inshore, tropical (Rowe & Gates, 1995).

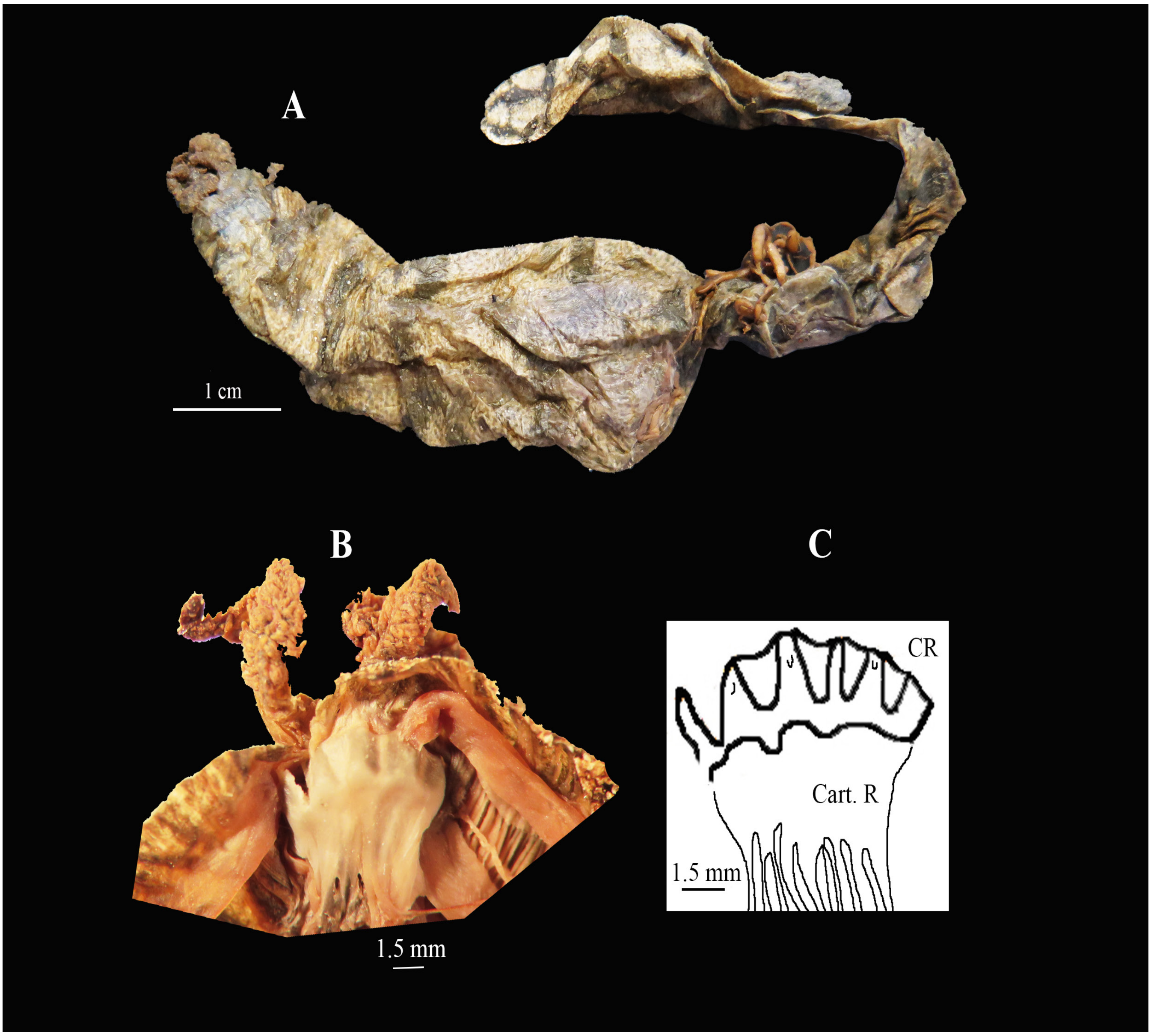


Fig. 13. *Synaptula denticulata* Heding, 1928. A: specimen photograph, B: calcareous ring (CR) photograph, C: CR illustration; Cart. R (cartilagenous ring).

Depth range. 0–36 m depth (Rowe & Gates, 1995).

Geographic distribution. Australia (Great Barrier Reef, N coast, NE coast, Ashmore Reef, Torres Strait, Whitsunday Islands); west-central Pacific Ocean; Indonesia (Spermonde, Lombok (present study)).

Genus *Synaptula* Örsted, 1849

Synaptula denticulata Heding, 1928
(Figs. 13–15)

Synaptula denticulata Heding, 1928: 177, fig. 22(1–4);
Synaptula denticulata–Clark & Rowe, 1971: 186; Setyastuti, 2009: 383, figs. 18, 19a–e; Setyastuti, 2016: 17, tab. 3; Wirawati et al., 2019: 80.

Type material. Type status and whereabouts unknown. Heding examined 14 specimens for this species (Heding, 1928).

Type locality. Tual (as "Toeal"), Maluku (Heding, 1928).

Material examined. MZB. Hol. 266 (one specimen); 110 × 15 mm in ethanol; collected in Kayangan beach, Lombok; coll. during low tide, in an area with patchy seagrass, 0.5–1.5 m depth; coll. A. Setyastuti, 19 April 2019.

External morphology. Body cylindrical, worm-like. In ethanol, body colour uniformly greenish with many dark green transverse bands and numerous dark spots over the surface (Fig. 13A). Body wall rough to the touch, less than 1 mm thick. Mouth and anus terminal. Mouth surrounded by 10 tentacles, small, peltato-dendritic, with light green stalks and light brown crowns. Dorsal body wall and ventral tube feet absent.

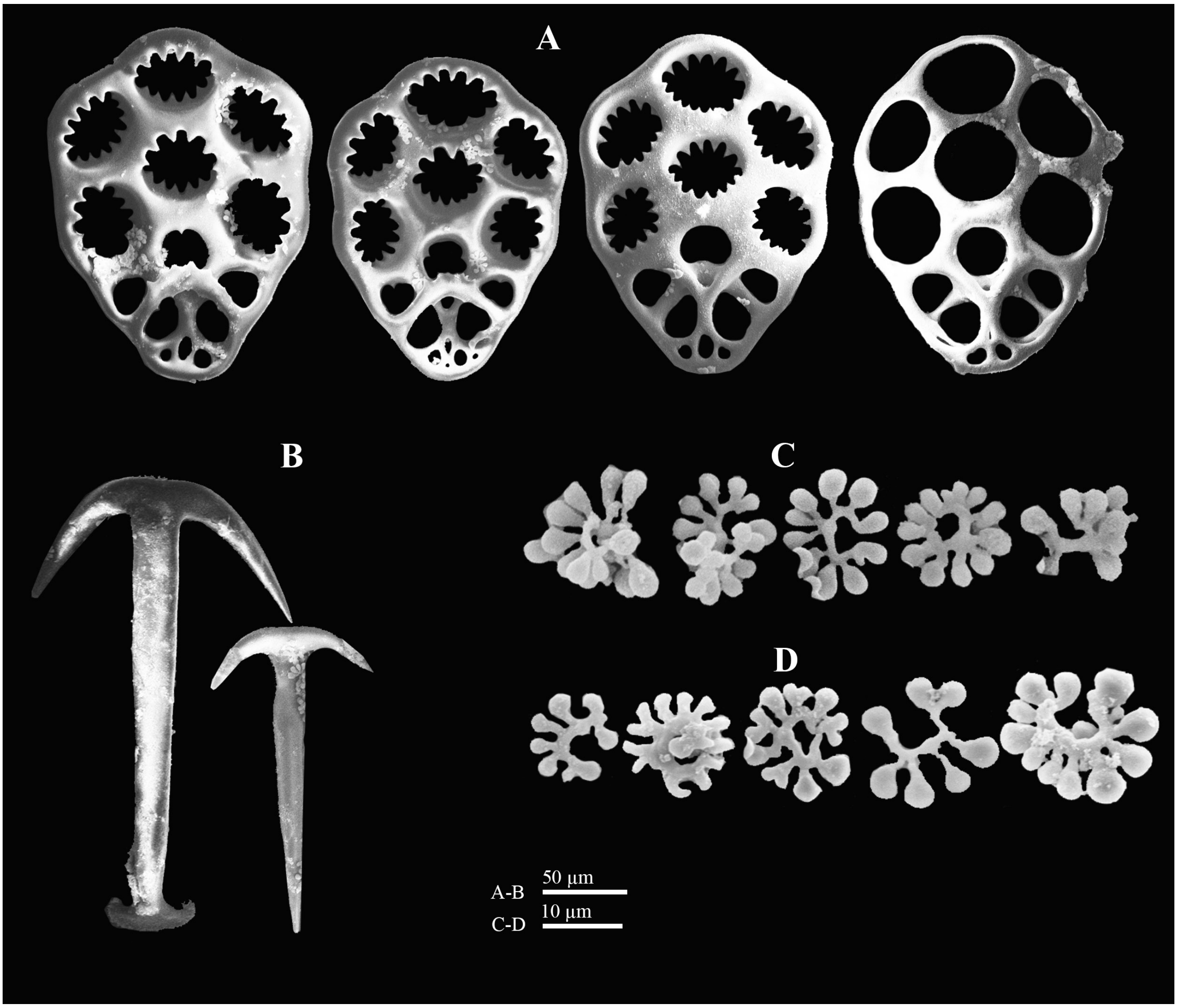


Fig. 14. *Synaptula denticulata* Heding, 1928. A: anchor-plates of anterior body wall; B: anchors of anterior body wall; C: miliary granules of anterior body wall; D: miliary granules of tentacles.

Internal morphology. Calcareous ring calcified, completely embedded in a large cartilaginous ring (Fig. 13B, C). Tentacle ampullae present. Many Polian vesicles. Cuvierian tubules, stone canal, madreporite and gonads were not available for observation. Longitudinal muscles flat and completely attached to the body wall.

Ossicles. Anterior and posterior body wall hold anchor, anchor plates, and miliary granules of the same size and similar shape (Figs. 14, 15). Anchors 175–275 µm long and 100–160 µm wide; arms smooth, a few knobs on the vertex; stock finely dented (Figs. 14B, 15B). Anchor-plates ovate; 180–220 µm long and 125–150 µm wide; with six serrated holes; 3 articular holes, central one nearly always serrated, lateral ones always smooth; bridge spiny; posterior part with 3–5 small holes (Figs. 14A, B; 15A, C, D). Miliary granules 12–15 µm across (Figs. 14C, 15E). Tentacles hold only miliary granules, 10-20 µm across (Fig. 14D).

Remarks. The morphological colour pattern and ossicles of the present material resemble *Synaptula denticulata*. However, the present material has ten tentacles, while the holotype in the original description noted 13 tentacles.

Ecology. Deposit feeder, detritus feeder, shallow water.

Depth range. 0–2 m depth (Heding, 1928 and present material).

Geographic distribution. Tual (Kai Islands) and Lombok (present study).

DISCUSSION

The family Chiridotidae, while resolved as a monophyletic group in recent molecular analyses (Miller et al., 2017), does not include the genus *Polycheira*. The genus was created by H. L. Clark (1907) to accommodate the previously described *Chiridota rufescens* Brandt, 1835. After examining numerous specimens from many localities, Clark proposed *Polycheira* based on the number of tentacles, which is 18

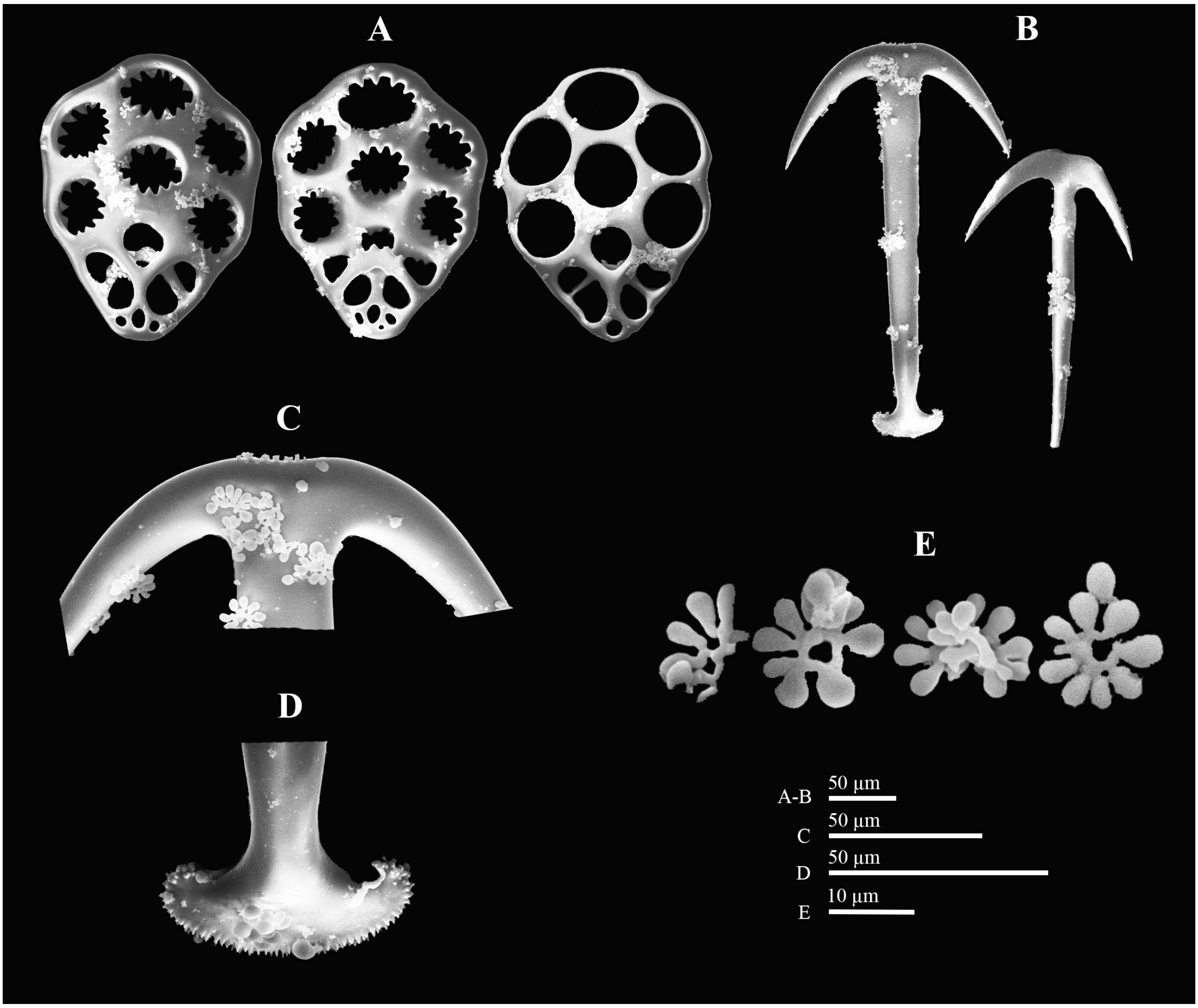


Fig. 15. *Synaptula denticulata* Heding, 1928. Ossicles of the posterior body wall. A: anchor-plates; B: anchors; C: anchor vertex; D: anchor stock; E: miliary granules.

(or exceptionally 17 or 19), with digits 9–16 on each side and numerous Polian vesicles. Two decades later, Heding (1928) described a new species, *Polycheira echinata*, thereby refuting Clark's argument that this genus is monotypic.

Polycheira nusalaut, new species, and *Polycheira rufescens* (Brandt, 1835), described in this study, are additional evidence that contradicts the statement by Clark (1907): page 121 which stated "The collection and examination of such a large amount of material as is indicated by the above list of localities where this species occurs leaves little room for doubt that all of the Indo-Pacific Chiridotas with 16–19 tentacles must be referred to this one species" [referring to *Polycheira rufescens*].

Polycheira nusalaut, new species, is certainly distinct from *P. rufescens* and its synonymous species as presented in Table 2. The PCA results (Fig. 18a) indicated that ossicle measurements provide meaningful morphological differentiation between *P. nusalaut* and *P. rufescens*, particularly along PC1, even though there is a partial overlap, suggesting that the species share a degree of morphometric similarity. On the other hand, the DFA analysis (Fig. 18b) maximised between-group differences and confirmed the complete separation of the two species. This suggests that ossicle morphometrics carry diagnostic features that can reliably differentiate the two species. Meanwhile, *P. echinata* differs from *P. rufescens* and *P. nusalaut* based on the number of tentacles (17), the tentacle rod area with small spines being the narrowest (7–10%), and only a few/absent oval bodies of longitudinal muscles (Heding, 1928; Thandar, 1989). However, due to the unknown deposition of the holotype of *P. echinata*, the character comparison relies solely on the original description that only provides an incomplete description of the ossicles.

Hence, the genus is now represented by three nominal species: *Polycheira rufescens* (Brandt, 1835); *Polycheira echinata* Heding, 1928; and *Polycheira nusalaut,* new species, which is described here. Our findings suggest that the diversity of the apodid *Polycheira* is still underestimated. We strongly advocate an integrative taxonomic approach, including

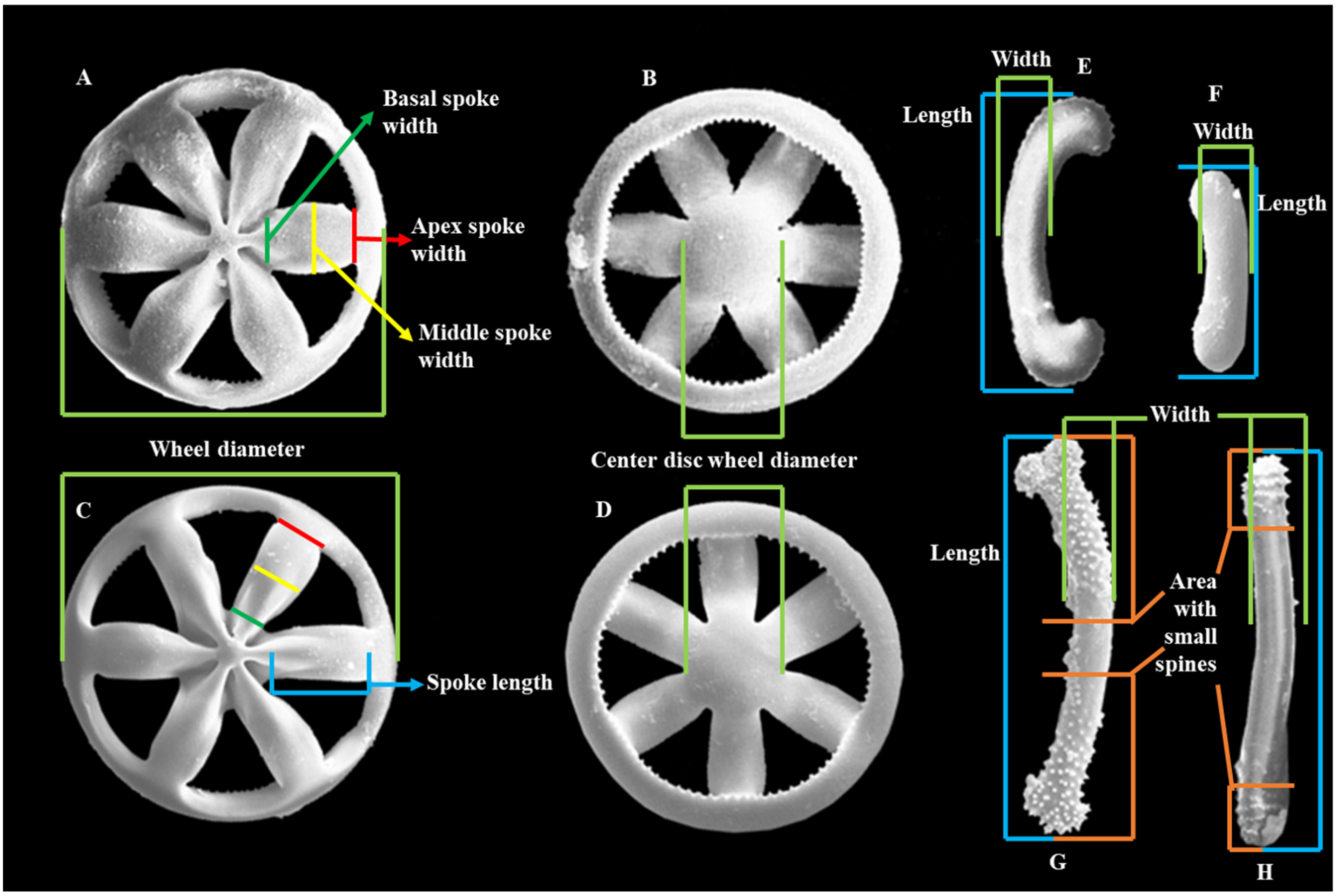


Fig. 16. Definition of morphometric variables utilised for ossicles of *Polycheira rufescens* and *Polycheira nusalaut*, new species (without scale). A, B, F, H: ossicles of *Polycheira nusalaut*, new species (MZB. Hol. 310). C, D, E, G: ossicles of *Polycheira rufescens* (MZB. Hol. 254).

ossicle morphometric and molecular analyses, which will help to further uncover the cryptic diversity of *Polycheira* in Indonesia.

Two other species recorded in this study, *Opheodesoma grisea* and *Synaptula denticulata*, are commonly found in seagrass habitats (Setyastuti, 2016); and have been reported in many previous publications (Massin, 1999; Purwati & Wirawati, 2008; Setyastuti, 2009; Wirawati et al., 2019; Wirawati, 2020; Setyastuti & Vimono, 2020). On the other hand, this is only the second report of *Chirodota smirnovi* both in Indonesia and globally. Its first description was in 1996, based on the specimen collected from Ambon, Maluku (Massin, 1996), representing East Indonesia, and the current study recorded the species from East Java (representing West Indonesia), indicating that this species has a large distribution area. The limited number of reports for this species may be the result of its cryptic behaviour, which non-taxonomic studies may have overlooked during the collection and identification process.

Among 69 apodid species listed in Table 4, four out of 14 genera of Chiridotidae, two out of 10 genera of Myriothrochidae, and 10 out of 17 genera of Synaptidae were recorded in Indonesia; this shows that about 22% (almost a quarter) of the world's extant apodid species—about 320 species (WoRMS Editorial Board, 2025)—are distributed in the region. However, these results are unexpectedly low when considered with regards to the vast area of Indonesia, which possesses more than 17,000 islands (BIG, 2021), with a wide variety of microhabitats and ecosystems from shallow water to the deep sea, even though this number is higher than in the Southern Ocean (O'Loughlin et al., 2015; Martins & Souto, 2020; Mackenzie et al., 2021) or Malaysia (Kamarudin et al., 2010).

Furthermore, the discovery of new Apodida in Indonesia within the last decade has been relatively slow compared to the previous decades. The type locality data for species collected in Indonesia (Table 4) showed that about half of the 69 species discovered in the region were described before 2000. This illustrates the paucity of recent taxonomic studies in Indonesia. The challenges may be due to (1) the small number of Indonesian researchers consistently working on the taxonomy of this taxon group; (2) the difficulty in accessing the area or locations that are 'scientifically interesting' because of limited public transportation; (3) establishing a marine biodiversity inventory (in general) requires specialised equipment (e.g., a research vessel) that is very costly, and (4) lack of national funding for marine biodiversity studies or when these avenues exist, are relatively small.

Even so, to date, Indonesian waters have contributed 35 apodid species new to science out of the approximately

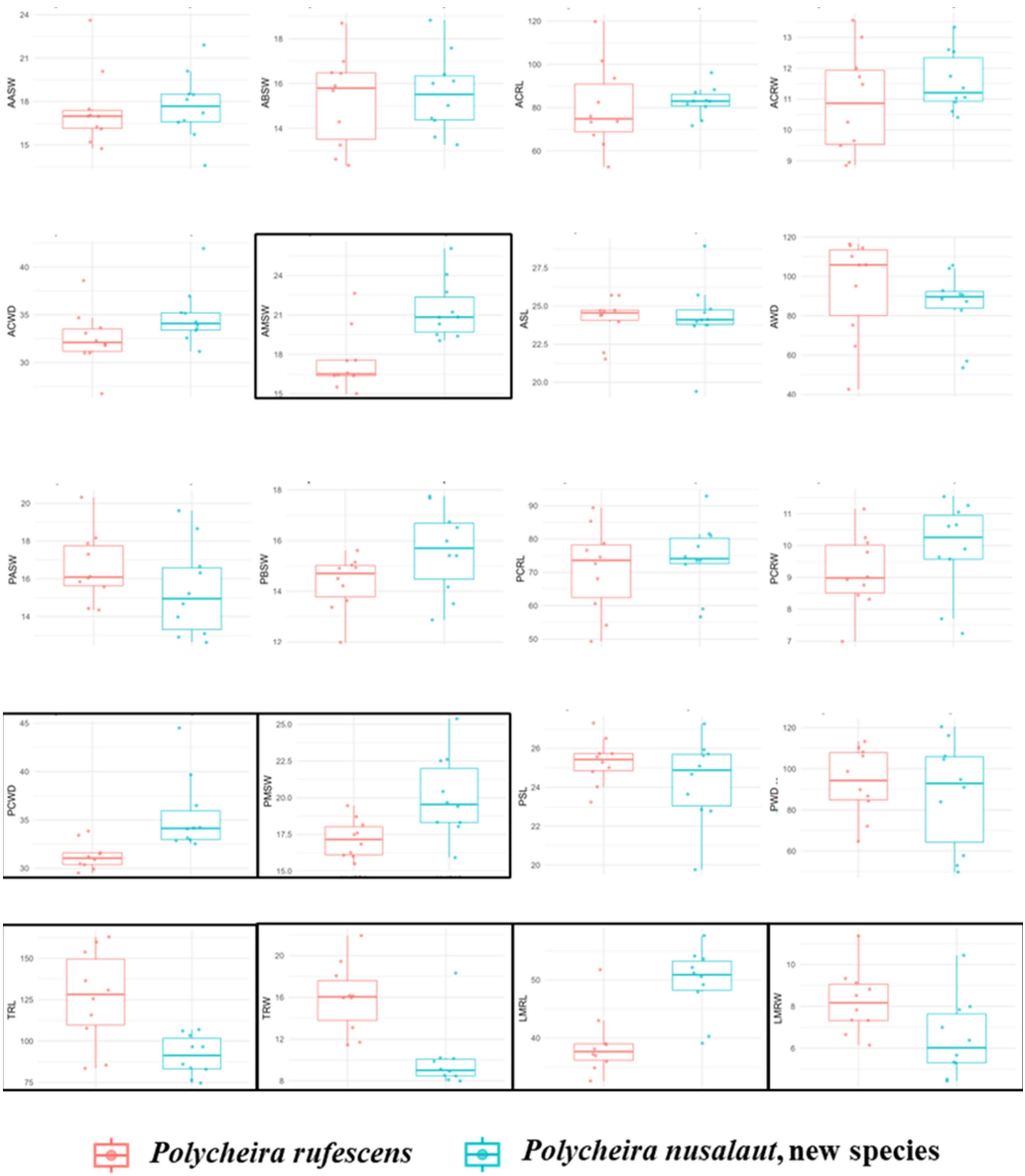


Fig. 17. Box plots of ossicle measurements comparing *Polycheira rufescens* (MZB. Hol. 254) and *P. nusalaut*, new species (MZB. Hol. 310). Each box plot corresponds to the variables listed in Table 1. The horizontal line inside the box indicates the median value; and the box boundaries represent the lower and upper quartiles; whiskers extend to the value within 1.5 times the interquartile range; points outside the plot represent outliers. The plots with black outlines (AMSW, PCWD, PMSW, TRL, TRW, LMRL, LMRW) indicate variables with significant p-values (< 0.05) that point to differences between the two species.

320 species known worldwide. This gives us a sense of optimism, and we expect that future research will lead to more discoveries of holothuroids new to science and apodids in particular, from Indonesian waters. There are still many locations to investigate in order to uncover their species diversity before it is too late, given the rapid habitat degradation and/or anthropogenic effects that are outpacing our capacity to find what is present. Scientific collaboration and joint research are urgently needed to uncover their diversity that still largely remains poorly known in this region.

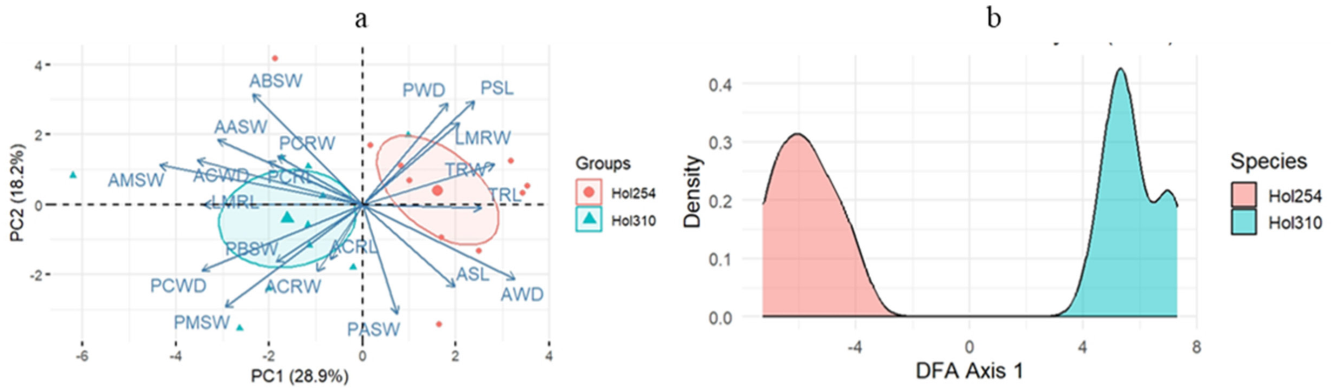


Fig. 18. (a) The PCA of ossicle morphometrics shows that the first two components, PC1 and PC2, explained 28.9% and 18.2% of the total variance, respectively accounting for 47.1% overall. Along PC1, variable measurements of Polycheira rufescens (MZB. Hol. 254) and Polycheira nusalaut, new species (MZB. Hol. 310), showed partial separation. Variable measurements, such as TRL, TRW, PSL, and PWD, were strongly associated with the positive side of PC1, while PC2 was mainly influenced by ABSW, AASW, PCRW, and AMSW, reflecting additional within-species variation. (b) The DFA plot shows DFA axis 1 is the discriminant function (a linear combination of the morphometric variables) that best separates P. rufescens and P. nusalaut, new species; while density (y-axis) is the probability density estimate of the relative frequency of morphometric measurements samples along DFA1 to understand how concentrated the data is at each point. The density distribution along DFA1 showed a clear distinction, with no overlap between the two species. The classification accuracy was 100%, indicating that all specimens were correctly assigned to their respective groups based on ossicle measurements.

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Table 4. Species list of Indonesian Apodida during the present survey and according to the literature. New species indicated by (*), and species type localities from Indonesia are indicated by (†), rvw=review.

Species (present status)	Cited as	Locations recorded	References
Chiridotidae Östergren, 1898			
Chiridota rigida Semper, 1867	*Chiridota liberata* Sluiter, 1887	Jakarta Bay (cited as Batavia Bay); East Indies	Sluiter, 1887; Clark & Rowe, 1971
	Chiridota rigida Semper, 1867	Ambon, Maluku; Kur Island (Tual); Jakarta Bay (cited as Batavia Bay); Lucipara; Binangka; Edam Island; Ambon; East Indies	Ludwig, 1888; Sluiter, 1901; Clark, 1907; Clark & Rowe, 1971; Massin, 1996
	Chiridota amboinensis Ludwig, 1888	Ambon, Maluku; East Indies	Ludwig, 1888; Clark & Rowe, 1971; Massin, 1996
Chiridota smirnovi Massin, 1996†	*Chiridota smirnovi* Massin, 1996	Ambon, Maluku	Massin, 1996; Setyastuti, 2016
Chiridota stuhlmanni Lampert, 1896	*Chiridota stuhlmanni* Lampert, 1896	Spermonde, South Sulawesi	Massin, 1999
Chiridota violacea (J. Müller, 1849)	*Chiridota violacea* (J. Müller, 1849)	Banda, Maluku	Heding, 1928
Polycheira rufescens (Brandt, 1835)	*Chiridota rufescens* Brandt, 1835	Jakarta Bay (cited as Batavia Bay); Dongala, Labuan Pandan (Lombok), Sarasa Island	Sluiter, 1887, 1901; Wirawati et al., 2019
	Chiridota panaensis Semper, 1867	Jakarta Bay (cited as Batavia Bay)	Sluiter, 1887
	Chiridota variabilis Semper, 1867	Sunda Strait, Java; Jakarta Bay (cited as Batavia Bay)	Sluiter, 1881; Théel, 1886
	Polycheira rufescens (Brandt, 1835)	Sebesi, Sunda Strait; Timor; Ambon; Ternate; Saparua Bay; East Indies	Clark, 1907; Heding, 1928; Clark & Rowe, 1971
Polycheira echinata Heding, 1928	*Polycheira echinata* Heding, 1928	East Indies	Clark & Rowe, 1971
***Polycherira nusalaut*, new species*†**		Nusa Laut Island, Maluku	This study
Sigmodota contorta (Ludwig, 1875)	*Chiridota contorta* Ludwig, 1875	Bangka-Belitung Island, East Sumatera	Ludwig, 1875
	Sigmodota contorta (Ludwig, 1875)	Java Sea (Stat. 319)	Sluiter, 1901
Taeniogyrus clavus Heding, 1928†	*Taeniogyrus clavus* Heding, 1928	Kei Island, Maluku	Heding, 1928
Taeniogyrus keiensis Heding, 1928†	*Taeniogyrus keiensis* Heding, 1928	Kei Island, Maluku	Heding, 1928
Myriotrochidae Théel, 1877			
Myriotrochus rinkii Steenstrup, 1851	*Myriotrochus rinkii* Steenstrup, 1851	Jakarta Bay (cited as Batavia Bay)	Sluiter, 1887
Trochoderma elegans Théel, 1877	*Trochoderma elegans* Théel, 1877	Jakarta Bay (cited as Batavia Bay)	Sluiter, 1887
Synaptidae Burmeister, 1837			
Anapta gracilis Semper, 1867	*Anapta gracilis* Semper, 1867	East Indies	Clark & Rowe, 1971

Species (present status)	Cited as	Locations recorded	References
Anapta subtilis Sluiter, 1887†	*Anapta subtilis* Sluiter, 1887	Jakarta Bay (cited as Batavia Bay); East Indies	Sluiter, 1887; Clark, 1907; Clark & Rowe, 1971
Euapta godeffroyi (Semper, 1868)	*Euapta godeffroyi* (Semper, 1868)	Taruna Bay, Gross-Sangir Island; Spermonde, South Sulawesi; East Indies	Sluiter, 1901; Clark & Rowe, 1971; Massin, 1999
Euapta magna Heding, 1928	*Labidoplax magna* Heding, 1928	East Indies	Clark & Rowe, 1971
Oestergrenia dubia (Semper, 1867)	*Synapta dubia* Semper, 1867	Jakarta Bay (cited as Batavia Bay)	Sluiter, 1887
	Labidoplax dubia (Semper, 1867)	Dutch East Indies	Clark, 1907; Clark & Rowe, 1971
Oestergrenia incerta (Ludwig, 1875)†	*Synapta incerta* Ludwig, 1875	Bangka-Belitung Island, East Sumatera	Ludwig, 1875; Théel, 1886
	Labidoplax incerta Ludwig, 1875	Java Sea (Stat. 319)	Sluiter, 1901
Oestergrenia variabilis (Théel, 1886)	*Labidoplax variabilis* (Théel, 1886)	Kei Island; East Indies	Heding, 1928; Clark & Rowe, 1971
Opheodesoma glabra (Semper, 1868)	*Synapta glabra* Semper, 1868	Ambon, Maluku	Sluiter, 1894; Massin, 1996
	Euapta glabra Semper, 1868	Selayar, Bima	Sluiter, 1901
	Opheodesoma glabra (Semper, 1868)	Ambon, Maluku; Selayar; East Indies	Clark, 1907; Heding, 1928; Clark & Rowe, 1971
Opheodesoma grisea (Semper, 1867)	*Synapta grisea* Semper, 1867	Jakarta Bay (cited as Batavia Bay); Ambon, Maluku	Sluiter, 1887; Sluiter, 1894; Massin, 1996
	Opheodesoma grisea (Semper, 1867)	Jakarta Bay (cited as Batavia Bay); Timor; Bima; Saleh Bay; East Indies; Spermonde, South Sulawesi; Nusa Tenggara Timur; Lombok; Sanur, Bali; Ambon, Maluku; Pari Island, Seribu Archipelago; Java Sea	Clark, 1907; Heding, 1928; Clark & Rowe, 1971; Massin, 1999; Purwati & Wirawati, 2008; Setyastuti, 2014, 2016; Wirawati et al., 2019; Setyastuti & Vimono, 2020; this study
	Euapta grisea Semper, 1867	Semau Island; Timor; South Sulawesi (Sailus kecil, Paternoster); Bima Bay; Siau Island (North Sulawesi); Saleh Bay (Dangar Besar, Sumbawa)	Sluiter, 1901
Opheodesoma cf. *grisea* (Semper, 1867)†	*Opheodesoma* cf. *grisea* (Semper, 1867)	Ambon, Maluku	Massin, 1996
Opheodesoma radiosa (Lesson, 1830)	*Opheodesoma radiosa* (Lesson, 1830)	East Indies	Clark & Rowe, 1971
Opheodesoma serpentina (J. Müller, 1850)†	*Synapta serpentina* J. Müller, 1850	Jakarta Bay (cited as Batavia Bay); Ambon, Maluku	Sluiter, 1887; Ludwig, 1888; Massin, 1996
	Euapta serpentina J. Muller, 1850	Bima Bay (Sumbawa); Kur (Maluku)	Sluiter, 1901
	Opheodesoma serpentina (J. Müller, 1850)	Jakarta Bay (cited as Batavia Bay); Bima; Kur; Ambon; Ternate; Edam Island; East Indies	Clark, 1907; Heding, 1928; Clark & Rowe, 1971
Patinapta laevis (Bedford, 1899)	*Patinapta laevis* (Bedford, 1899)	Saparua Bay; East Indies	Heding, 1928; Clark & Rowe, 1971

Species (present status)	Cited as	Locations recorded	References
Patinapta ooplax (von Marenzeller, 1882)	*Patinapta ooplax* (von Marenzeller, 1882)	East Indies	Clark & Rowe, 1971
	Synapta ooplax von Marenzeller, 1882	Arafura Sea (Stat. 274)	Sluiter, 1901
	Leptosynapta ooplax von Marenzeller, 1882	Dutch East Indies	Clark, 1907
Polyplectana kafersteini (Selenka, 1867)	*Synapta kafersteini* Selenka, 1867	Ambon, Maluku; Spermonde, South Sulawesi	Ludwig, 1888; Massin, 1999
	Polyplectana kafersteini (Selenka, 1867)	Ambon; Jakarta Bay (cited as Batavia Bay); Ternate	Clark, 1907; Clark & Rowe, 1971
Polyplectana kallipeplos (Sluiter, 1887)†	*Synapta kallipeplos* Sluiter, 1887	Jakarta Bay (cited as Batavia Bay); Spermonde, South Sulawesi	Sluiter, 1887; Massin, 1999
Polyplectana nigra (Semper, 1867)	*Chondrocloea nigra* Semper, 1867	Kaniungan kecil (East Kalimantan)	Sluiter, 1901
	Pendekaplectana nigra (Semper, 1867)	East Indies	Clark & Rowe, 1971
Protankyra assymmetrica (Ludwig, 1875)†	*Synapta assymetrica* Ludwig, 1875	Bangka-Belitung Island, East Sumatera	Ludwig, 1875; Théel, 1886
	Protankyra assymmetrica Ludwig, 1875	Selayar; Java Sea (Stat. 319); Bangka; Sunda; near Madura; East Indies	Sluiter, 1901; Clark, 1907; Clark & Rowe, 1971
Protankyra buitendijki Rowe, 1983†	*Protankyra buitendijki* Rowe, 1983	Semarang, Java	Rowe, 1983
Protankyra bankensis (Ludwig, 1875)†	*Synapta bankensis* Ludwig, 1875	Bangka-Belitung Island, East Sumatera	Ludwig, 1875; Théel, 1886
	Protankyra bankensis (Ludwig, 1875)	Bangka Island; Sunda; East Indies	Clark, 1907; Clark & Rowe, 1971
Protankyra errata Koehler & Vaney, 1905	*Protankyra errata* Koehler & Vaney, 1905	Andaman	Clark, 1907
Protankyra insolens (Théel, 1886)	*Protankyra insolens* (Théel, 1886)	Arafura Sea (Stat. 274); Aru Island	Sluiter, 1901; Clark, 1907
Protankyra javaensis Heding, 1928†	*Protankyra javaensis* Heding, 1928	Java Sea	Heding, 1928
Protankyra ludwigii (Sluiter, 1890)†	*Protankyra ludwigii* Sluiter, 1890	Nusa Tenggara Timur; Timor Sea (Stat. 294); Jakarta Bay (cited as Batavia Bay); Flores	Sluiter, 1901; Clark, 1907
Protankyra petersi (Semper, 1868)†	*Synapta petersi* Semper, 1868	Ambon, Maluku	Semper, 1868; Théel, 1886; Clark, 1907; Massin, 1996
	Protankyra petersi (Semper, 1868)	Ambon, Maluku; East Indies	Heding, 1928; Clark & Rowe, 1971
Protankyra pseudodigitata (Semper, 1867)	*Protankyra innominata* Ludwig, 1875	Makassar	Sluiter, 1901
	Protankyra pseudodigitata (Semper, 1867)	Samalona, Makassar; East Indies	Clark, 1907; Heding, 1928; Clark & Rowe, 1971
Protankyra rodea (Sluiter, 1890)†	*Protankyra rodea* Sluiter, 1890	Lombok (Labuan Bajo), Nomini Bay (Timor); Jakarta Bay (cited as Batavia Bay), Lombok, Timor, Madura; East Indies	Sluiter, 1901; Clark, 1907; Clark & Rowe, 1971

Species (present status)	Cited as	Locations recorded	References
Protankyra cf. *similis* (Semper, 1868)	*Protankyra* cf. *similis* (Semper, 1868)	Ambon, Maluku	Massin, 1996; Setyastuti, 2016
Protankyra suspecta Sluiter, 1901†	*Protankyra suspecta* Sluiter, 1901	Buton Strait	Sluiter, 1901; Clark, 1907
Rynkatorpa challengeri (Théel, 1886)	*Protankyra challengeri* Théel, 1886	Arafura Sea (Stat. 271); Aru Island; Andaman Island	Sluiter, 1901; Clark, 1907
Rynkatorpa bicornis (Sluiter, 1901)	*Protankyra bicornis* Sluiter, 1901	Timor (Banda Sea, Stat. 284)	Sluiter, 1901; Clark, 1907
Rynkatorpa sluiteri (Fisher, 1907)†	*Protankyra sibogae* Sluiter, 1901	Flores Sea (Stat. 45)	Sluiter, 1901
	Protankyra sluiteri Fisher, 1907	North Sumbawa	Clark, 1907
Synapta maculata (Chamisso & Eysenhardt, 1821)	*Synapta maculata* (Chamisso & Eysenhardt, 1821)	Celebes; Lucipara; Ternate; East Indies; Timor Island, Nusa Tenggara Timur; Spermonde, South Sulawesi; Ambon, Maluku; Sanur, Bali; Papua Barat; Rote; Seram; Halmahera; Makassar Strait; Sumba; Sumbawa; Sawu; Lombok; Sumatera; Jawa; Selayar; Pari Island, Seribu Archipelago	Clark, 1907; Heding, 1928; Clark & Rowe, 1971; Massin, 1996, 1999; Purwati & Wirawati, 2008; Setyastuti, 2014, 2016; Wirawati et al., 2019; Setyastuti & Vimono, 2020
	Synapta beselii Jaeger, 1833	Celebes; Ambon, Maluku	Semper, 1868; Théel, 1886
	Chondrocloea baselii Jaeger, 1833	Selayar; Saleh Bay; Lucipara Island; Sebangkatan Island; Timor; Lombok; Rote; Seram Island; Sawu; Karangkelang Island	Sluiter, 1901
Subspecies: *Synapta maculata sundaensis* (Heding, 1928)†	*Synapta maculata* var. *sundaensis* Heding, 1928	Sebesi, Sunda Strait	Heding, 1928
Synaptula alba Heding, 1928†	*Synaptula alba* Heding, 1928	Banda, Maluku; East Indies	Heding, 1928; Clark & Rowe, 1971
Synaptula albolineata Heding, 1928†	*Synaptula albolineata* Heding, 1928	Banda, Maluku; East Indies	Heding, 1928; Clark & Rowe, 1971
Synaptula ater Heding, 1928†	*Synaptula ater* Heding, 1928	Tual, Maluku; East Indies	Heding, 1928; Clark & Rowe, 1971
Synaptula bandae Heding, 1928†	*Synaptula bandae* Heding, 1928	Banda, Maluku; Ambon, Maluku; East Indies	Heding, 1928; Clark & Rowe, 1971; Massin, 1996; Setyastuti, 2016
Synaptula denticulata Heding, 1928†	*Synaptula denticulata* Heding, 1928	Seram Island; Tual, Maluku; East Indies	Heding, 1928; Clark & Rowe, 1971; Setyastuti, 2009, 2016; Wirawati et al., 2019; this study
Synaptula cf. *denticulata* Heding, 1928	*Synapta* cf. *denticulata* Heding, 1928	Spermonde, South Sulawesi; Timor Island, Nusa Tenggara Timur; Osi Island, Maluku; Tikus Island, Seribu Archipelago; Kei Island	Massin, 1999; Purwati & Wirawati, 2008; Setyastuti, 2009, 2011; Wirawati et al., 2019
Synaptula indivisa (Semper, 1868)	*Synapta indivisa* Semper, 1868	Ambon, Maluku	Sluiter, 1894; Massin, 1996
	Synaptula indivisa (Semper, 1868)	Rote Island, East Indies	Clark, 1907; Clark & Rowe, 1971

Species (present status)	Cited as	Locations recorded	References
	Condrocloea indivisa Semper, 1868	Rote Island	Sluiter, 1901
Synaptula lactea (Sluiter, 1887)†	*Synapta lactea* Sluiter, 1887	Jakarta Bay (cited as Batavia Bay)	Sluiter, 1887; Rowe & Gates, 1995
	Synaptula lactea (Sluiter, 1887)	Jakarta Bay (cited as Batavia Bay), Banda, Jedan (Dobo); Kei Island; East Indies	Clark, 1907; Heding, 1928; Clark & Rowe, 1971
	Condrocloea lactea Sluiter, 1887	Banda; Pulau Jedan	Sluiter, 1901; Setyastuti & Wirawati, 2018
Synaptula lamperti Heding, 1928†	*Synaptula lamperti* Heding, 1928	Banda, Maluku	Heding, 1928; Rowe & Gates, 1995; Wirawati et al., 2019
	Synaptula membrana Heding (1928)†	Banda, Maluku	Heding, 1928; Rowe & Gates, 1995
	Synaptula purpurea Heding (1928)†	Banda, Maluku; East Indies	Heding, 1928; Clark & Rowe, 1971; Rowe & Gates, 1995
Synaptula cf. *lamperti* Heding, 1928	*Synaptula* cf. *lamperti* Heding, 1928	Spermonde, South Sulawesi	Massin, 1999
Synaptula macra (H.L. Clark, 1938)	*Synaptula macra* (H.L. Clark, 1938)	Ambon, Maluku	Jangoux & Sukarno, 1974
Synaptula maculata (Sluiter, 1887)†	*Synaptula reticulata* (Semper, 1867) var. maculata (Sluiter, 1887)	Jakarta Bay (cited as Batavia Bay)	Sluiter, 1887
	Synaptula maculata (Sluiter, 1887)	East Indies	Clark & Rowe, 1971
Synaptula media Cherbonnier & Feral, 1984	*Synaptula media* Cherbonnier & Feral, 1984	Spermonde, South Sulawesi	Massin, 1999
Synaptula minima Heding, 1928†	*Synaptula minima* Heding, 1928	Kei Island, Maluku	Heding, 1928
Synaptula neirensis Heding, 1928†	*Synaptula neirensis* Heding, 1928	Banda Neira, Maluku; East Indies	Heding, 1928; Clark & Rowe, 1971
Synaptula psara (Sluiter, 1887)†	*Synapta psara* Sluiter, 1887	Jakarta Bay (cited as Batavia Bay)	Sluiter, 1887
	Synaptula psara (Sluiter, 1887)	Jakarta Bay (cited as Batavia Bay); Selayar; Tual; East Indies; Spermonde, South Sulawesi	Clark, 1907; Heding, 1928; Clark & Rowe, 1971; Massin, 1999
	Condrocloea psara Sluiter, 1887	Selayar	Sluiter, 1901
Synaptula recta (Semper, 1867)	*Synapta striata* Sluiter, 1887	Jakarta Bay (cited as Batavia Bay); East Indies	Sluiter, 1887; Clark & Rowe, 1971
	Synaptula recta (Semper, 1867)	Jakarta Bay (cited as Batavia Bay); Timor; Selayar; Dutch East Indies; Spermonde, South Sulawesi; Kai Island; Lombok; Tual	Clark, 1907; Heding, 1928; Clark & Rowe, 1971; Massin, 1999; Wirawati et al., 2019
	Chondrocloea recta (Semper, 1867)	Banda sea (Stat. 282)	Sluiter, 1901
	Chondrocloea albo-punctata Sluiter, 1901	Selayar	Sluiter, 1901
Synaptula reticulata (Semper, 1867)	*Synapta reticulata* Semper, 1867	Jakarta Bay (cited as Batavia Bay); Ambon, Maluku	Sluiter, 1887; Koehler, 1895; Massin, 1996

Species (present status)	Cited as	Locations recorded	References
	Synaptula reticulata (Semper, 1867)	Dutch East Indies; Spermonde, South Sulawesi; Tual	Clark, 1907; Heding, 1928; Clark & Rowe, 1971; Massin, 1999
	Chondrocloea reticulata Semper, 1867	Salawatti Island (West Papua); Jedan Island; Tual; Taam Island; Banda; Biaru Island; Saleh Bay; Selayar; Labuan Bajo; Banda	Sluiter, 1901; Setyastuti & Wirawati, 2018
	Synaptula striata (Sluiter, 1887)	Tual, Maluku	Heding, 1928
Synaptula cf. *reticulata* (Semper, 1867)	*Synaptula* cf. *reticulata* (Semper, 1867)	Spermonde, South Sulawesi	Massin, 1999
Synaptula spinifera Massin & Tomascik, 1996†	*Synaptula spinifera* Massin & Tomascik, 1996	Kakaban Island, East Kalimantan	Massin & Tomascik, 1996
Synaptula spec.	*Synaptula* spec.	Spermonde, South Sulawesi	Massin, 1999
Synaptula tualensis Heding, 1928†	*Synaptula tualensis* Heding, 1928	Tual, Maluku; East Indies	Heding, 1928; Clark & Rowe, 1971
Synaptula virgata (Sluiter, 1901)†	*Chondrocloea virgata* Sluiter, 1901	Salawatti Island, West Papua; Ambon, Maluku	Sluiter, 1901; Heding, 1928; Massin, 1996
	Chondrocloea aspera Sluiter, 1901	Gebe Island (Halmahera)	Sluiter, 1901
	Synaptula virgata (Sluiter, 1901)	Salawati Island, West Papua; Gebe, Ternate; Ambon; Kei Island; Java Sea; East Indies	Clark, 1907; Heding, 1928; Clark & Rowe, 1971
	Synaptula aspera (Sluiter, 1901)	Tual, Maluku; East Indies	Heding, 1928; Clark & Rowe, 197
Synaptula violacea Heding, 1928	*Synaptula violacea* Heding, 1928	East Indies	Clark & Rowe, 1971

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