

Three New Infaunal Species of *Taeniogyrus* (Echinodermata: Holothuroidea: Apodida: Chiridotidae: Taeniogyrinae) from Southern Coast of Wakayama, Japan

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Three infaunal apodid sea cucumbers collected in Kushimoto, Shirahama, and Susami, in the southern coast of Wakayama, Japan are described. They have different morphological characteristics in body color, ossicle arrangement, and internal organs, each other. First species, animal displays a large body size (approximately 70–150 mm) and pale body color (semi-transparent pink with anterior tip brownish) was found out. Second species, animal displays a small body size (approximately 20 mm) and pale body color (transparent yellow) with whitish wheel-papillae on three dorsal interradialia was found out. Third species, animal displays a moderate body size (approximately 20–35 mm) and deep red or reddish brown body color with dark yellowish wheel-papillae on three dorsal interradialia was found out. All three species having 10 tentacles, sigmoid-hook ossicles, and wheel ossicles in their body wall, turned out to be belonging to the genus *Taeniogyrus* Semper, 1867, and new to science.

Key Words: sea cucumber, Pacific Ocean, intertidal, subtidal, Kushimoto, Shirahama, Susami.

Introduction

Recently, sea cucumbers of the subfamily Taeniogyrinae (type genus *Taeniogyrus* Semper, 1867) have been actively investigated in Japan (e.g., Inoue and Kajihara 2012; Solis-Marin et al. 2014; Yamana and Tanaka 2017a; Yamana et al. 2017). Although there has been considerable debate concerning the genus *Taeniogyrus* (see O’Loughlin and VandenSpiegel 2010), it is presently well-defined morphologically and 27 species are accepted (WoRMS 2021). The principal components of the diagnosis of Taeniogyrinae are as follows: apodid sea cucumber of 10 or 12 tentacles; body wall ossicles wheels of chiridotid type and sigmoid-hooks, or sigmoid-hooks only, circular wheels or plate-like wheels (O’Loughlin and VandenSpiegel 2007), and rarely lacking ossicles in body wall (Becher 1909; Smirnov 1998; O’Loughlin and VandenSpiegel 2010). The sigmoid-hook ossicles are the only known form of four genera, i.e., *Sigmodota* Studer, 1876, *Scoliorhapis* Clark, 1946, *Taeniogyrus*, and *Rowedota* O’Loughlin and VandenSpiegel, 2010. Among them, *Sigmodota* has 12 tentacles, *Scoliorhapis* is devoid of wheel ossicles, and *Rowedota* has wheel ossicles with

teeth restricted in inter-spork part of inner rim, arranged in six separated groups. The type genus *Taeniogyrus* has both sigmoid-hooks and chiridotid type wheels, and several species show a unique arrangement of these ossicles; for example, *T. japonicus* (Marenzeller, 1882) has aggregations of sigmoid-hooks (hook-papillae), and *T. yvonnae* Moura, Campos, and Esteves, 2015 has aggregations of the wheel ossicles (wheel-papillae).

It has been clarified that the congeners of genus *Taeniogyrus* live in various environments and their lifestyles are diverse: the polar region (e.g., *T. antarcticus* Heding, 1931); abyssal environment (e.g., *T. yvonnae*); interstitial environment (e.g., *T. mijim* Yamana, Tanaka, and Nakachi, 2017); and epizoic conditions on sea-urchins (e.g., *T. cidaridis* Ohshima, 1914). The body sizes of these congeners are also diverse. For example, *T. yvonnae* reaches 190 mm in an elongated state (Moura et al. 2015), whereas *T. mijim* only reaches 11 mm in an anesthetized state (Yamana et al. 2017). However, the congeners of the shallow species usually range from 10 to 50 mm in length (Moura et al. 2015).

Here, we describe *Taeniogyrus* specimens collected from Kushimoto, Shirahama, and Susami, in the coast of Waka-

yama, Japan and compared these to all its congeners via a careful survey of the literature, resulting in the conclusion that these three species are new species.

Materials and Methods

Sea cucumbers were collected by hand picking, from sediments approximately 5–10 cm below the bottom surface, from the subtidal zone (5–13 m deep) of sandy-gravel sediments at the Sabiura Coast (33°28′46″N, 135°44′47″E) of Kushimoto Town (Fig. 1), from the lower intertidal zone of sandy-gravel shore (33°41′40″N, 135°20′58″E) at Shirahama Town (Fig. 1), the lower intertidal zone of sandy-gravel shore at the east side of the Cape Yesu-zaki (33°30′15″N, 135°35′25″E) of Susami Town (Fig. 1), Wakayama, southern end of the mainland of Japan. All examined specimens were fixed and preserved in 80% ethanol. All the specimens from Kushimoto and Susami (16 individuals), and about half the number of larger specimens from Shirahama (ca. 35 individuals) were fixed after anaesthetization; the remaining of smaller specimens from Shirahama (ca. 35 individuals) were fixed without anaesthesia. Anaesthetization was performed in a menthol solution: 0.37 g of menthol was dissolved into 100 mL of 99% ethanol, which was diluted to 3.0% with seawater. The specimens were immersed in the diluted menthol-ethanol solution for 1.0–2.0 h; then, before fixation, magnesium chloride ($\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$) was added to the solution at a ratio of 3.0 g per 100 mL for further anaesthetization. All the specimens were dissected, their tentacles and internal organs were examined under a stereoscopic dissecting microscope (SMZ, Nikon Japan Inc., Japan). Color of living specimens before fixation are noted. All

the specimens are deposited in the Invertebrate Collection of the Wakayama Prefectural Museum of Natural History (WMNH-INV), in Kainan, Wakayama, Japan.

To extract ossicles, small pieces of tissue (about 2×2 mm) from 3–5 type materials for every species were isolated using sharpened ophthalmologic scissors under the dissecting microscope, from following five body parts: dorsal anterior body-wall, dorsal posterior body-wall, ventral anterior body-wall, ventral posterior body-wall, and one or two of the tentacles, and each body parts was dissolved using a commercial bleach (Kitchen Bleach, Mitsuei Chemical Co., Ltd., Japan). Ossicles extracted from all five parts were mounted on glass slides in polyester resin (RIGOLAC, Showadenko KK., Japan) and observed under a compound microscope (Optiphot XF-NT, Nikon Japan Inc., Japan). Several ossicles from the tentacles and the anterior dorsal body-wall were rinsed with deionized water, dehydrated in 99% ethanol, mounted on aluminium stubs using conductive tape (NEM Tape, Nisshin EM Co., Ltd.), dried at room temperature, and observed using a scanning electron microscope (SEM) (JSM-6480LV, JEOL Ltd., Japan).

To observe microstructure of ciliated funnels, small pieces of tissue containing funnels were isolated from holotypes of three new species by using sharpened ophthalmologic scissors under the dissecting microscope, and rinsed with deionized water, and with a drop of deionized water the pieces were mounted on aluminium stubs using conductive tape, then dried by using a vacuum freeze-dryer (FN-500, Nishiyama-seisakusho Co., Ltd., Japan) and observed by using a SEM (JCM-7000, JEOL Ltd., Japan).

The ossicles were classified into ‘wheels’ (i.e., wheel-like ossicles with six spokes and a series of teeth on the inner margin of the rim), ‘sigmoid-hooks’ (i.e., fishhook-like os-

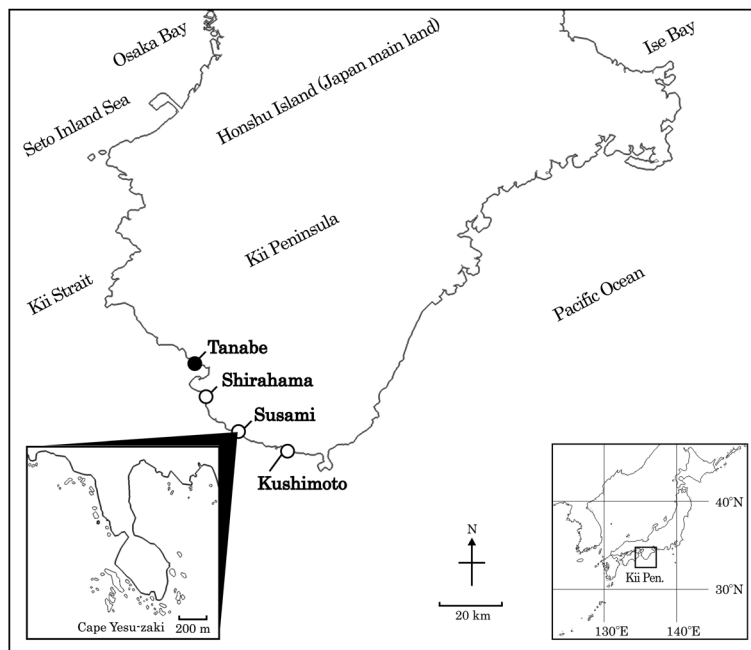


Fig. 1. Map showing the Kii Peninsula. Blank circles and a solid black circle denote the sampling sites, for the three new taeniogyrid species of the present study and the previous studies (Yamana and Tanaka 2017a; Yamana et al. 2017), respectively.

sicles, with a pointed end and open-loop end, with the point of the hook turned outward body), and 'rods' (i.e., rod-like ossicles, slightly curved, sometimes distally branching or spreading, sometimes centrally spinous). For every species, measurements of 4–48 ossicles were taken for every tissue sample to the nearest micrometer. Measured ossicles numbers were varying according to their density. To compare these measurements among individuals and among parts of the body, Kruskal–Wallis tests were performed. The dissected specimens, glass slides, and SEM materials were also deposited in WMNH-INV.

In the present study, positions of the plates of calcareous ring and internal organs are classified by Ludwig's [1889–1892 (1889): 156] naming: *RI–RV*, *IR1–IR5*, namely, the radials (*R*): *RI*, medioventral; *RII*, left ventral; *RIII*, right ventral; *RIV*, left dorsal; *RV*, right dorsal; and interradials (*IR*): *IR1*, left ventral; *IR2*, right ventral; *IR3*, left dorsolateral; *IR4*, right dorsolateral; *IR5*, mediodorsal.

The mitochondrial cytochrome *c* oxidase subunit 1 (*COI*) gene DNA extraction from small pieces of ethanol-preserved tissue (ventral body wall with longitudinal muscle) were shown in the results of each species. DNA extraction and sequencing for *COI* sequence for a paratype of *Taeniogyrus flavus* sp. nov. (WMNH-INV-2016-137) was carried out following the method of Yamana et al. (2017). On the other hand, those of the holotype and a paratype of each species, *T. albulus* sp. nov. (holotype and WMNH-2020-10) and *T. rubrus* sp. nov. (holotype and WMNH-INV-2020-29), were conducted by the methods of Ogawa et al. (2020). The newly obtained sequences have been deposited with International Nucleotide Sequence Databases (INSD) through the DNA Data Bank of Japan. A homology search of *COI* sequences was performed by BLAST (Altschul et al. 1990, 1997) with the discontinuous Mega BLAST program from the National Center for Biotechnology Information (<http://blast.ncbi.nlm.nih.gov/Blast.cgi>). We supplement this to expect to determine the potential synonyms or relatives of these species in the viewpoint of phylogeny study as well as morphological study. Also, we are expecting the development of the future phylogenetics and taxonomy based on such molecular biological method.

Taxonomy

Order **Apodida** Brandt, 1835 sensu Östergren (1907)

Family **Chiridotidae** Östergren, 1898

Subfamily **Taeniogyrinae** Smirnov, 1998

Genus **Taeniogyrus** Semper, 1867

[Japanese name: Kuruma-kagi-namako-zoku]

Taeniogyrus albulus Yamana, Hirabayashi,

Tanaka, and Ogawa, sp. nov.

[New Japanese name: Kushimoto-kuruma-kagi-namako]

(Figs 2, 3A, 4; Tables 1, 2)

Material examined. Holotype: WMNH-INV-2017-100 (length 134 mm, width 10 mm, collected from Kushimoto on 12 July 2017; INSD accession number LC655787,

433 bps). Paratypes: 7 specimens, WMNH-INV-2017-101 (length 81 mm, width 11 mm, collected from Kushimoto on 3 September 2017); WMNH-INV-2018-21 (length 69 mm, width 7 mm, collected from Kushimoto on 24 April 2018); WMNH-INV-2018-22 (length 76 mm, width 9 mm, collected from Kushimoto on 24 April 2018); WMNH-INV-2018-23 (length 151 mm, width 13 mm, collected from Kushimoto on 22 May 2018); WMNH-INV-2019-300 (length 55 mm, width 4 mm, collected from Kushimoto on 22 May 2019); WMNH-INV-2020-10 (length 55 mm, width 9 mm, collected from Kushimoto on 26 June 2019; LC655788, 628 bps); WMNH-INV-2020-11 (length 121 mm, width 13 mm, collected from Kushimoto on 30 December 2019).

Diagnosis. Body large, up to 150 mm. Living body color semi-transparent pink, anterior tip and tentacles pale brown. Fixed body color yellowish white, anterior tip and tentacles ochre yellow. Tentacles ten, with thick, palmate, bumpy skin, with up to 12 digits. Single Polian vesicle in *RI*. Body wall containing wheel, curved rod, sigmoid-hook ossicles. Sigmoid-hook ossicles large and outer bend edge with paired rows of spinelets, each row 3–5 spinelets, between 2 rows forming depression. Curved rod ossicles, with spinous ends, centrally with sparse teeth, sometimes teeth along entire length, rods only found sparsely from the anterior body surface. A band of ciliated funnels situated near right side of midventral longitudinal muscle. Funnels long (about 0.3–0.5 mm), curved like French horn, wide opening (about 0.2 mm).

Holotype description. Body cylindrical, large; length of holotype specimen (WMNH-INV-2017-100) 134 mm; width 10 mm (Fig. 2A; Table 1). Living body color semi-transparent pink, anterior tip and tentacles pale brown (Fig. 2B); preserved body color yellowish white, anterior tip and tentacles ochre yellow (Fig. 2A). Mouth anterior; anus posterior; oral disc strongly inclined toward ventral side. Dorsal skin smooth, ventral skin rough.

Ten tentacles, non-retractile; thick, palmate, bumpy skin; each tentacle with maximum 12 digits (Table 1); sensory cups absent (Fig. 2C). Tentacle digitations more frequent on ventral side than dorsal side (Table 1).

Single Polian vesicle in *RI*, vesicle shaped fusiform (in 2.9 mm, width about 1/3 of length) (Fig. 2H). Stone canal single, thin, coiled and short (about 0.9 mm), madreporite small, worm-like, twisted (about 0.7 mm in length), situated left side of the anterior end of dorsal mesentery (Fig. 2H). A band of ciliated funnels situated near right side of medioventral longitudinal muscle *RI*, not clustered, lacking in anterior or posterior ends (Fig. 2D). Funnels long (approximately 0.4 mm), strongly curved (> about 90°), like a French horn, laterally depressed narrow opening (approximately 0.7 mm in width; 0.2 mm in height), slit along proximal side to the funnel base, and with short stalk (Fig. 3A). Intestine with no loop, situated along *IR5*. Hermaphrodite; having two ovaries and two testes; ovary in two clusters in anterior body, one each side of dorsal mesentery, tubules well-branched; testis in 2 tubules in middle body, both adhered to abdominal canal, one in mid-dorsal region of left

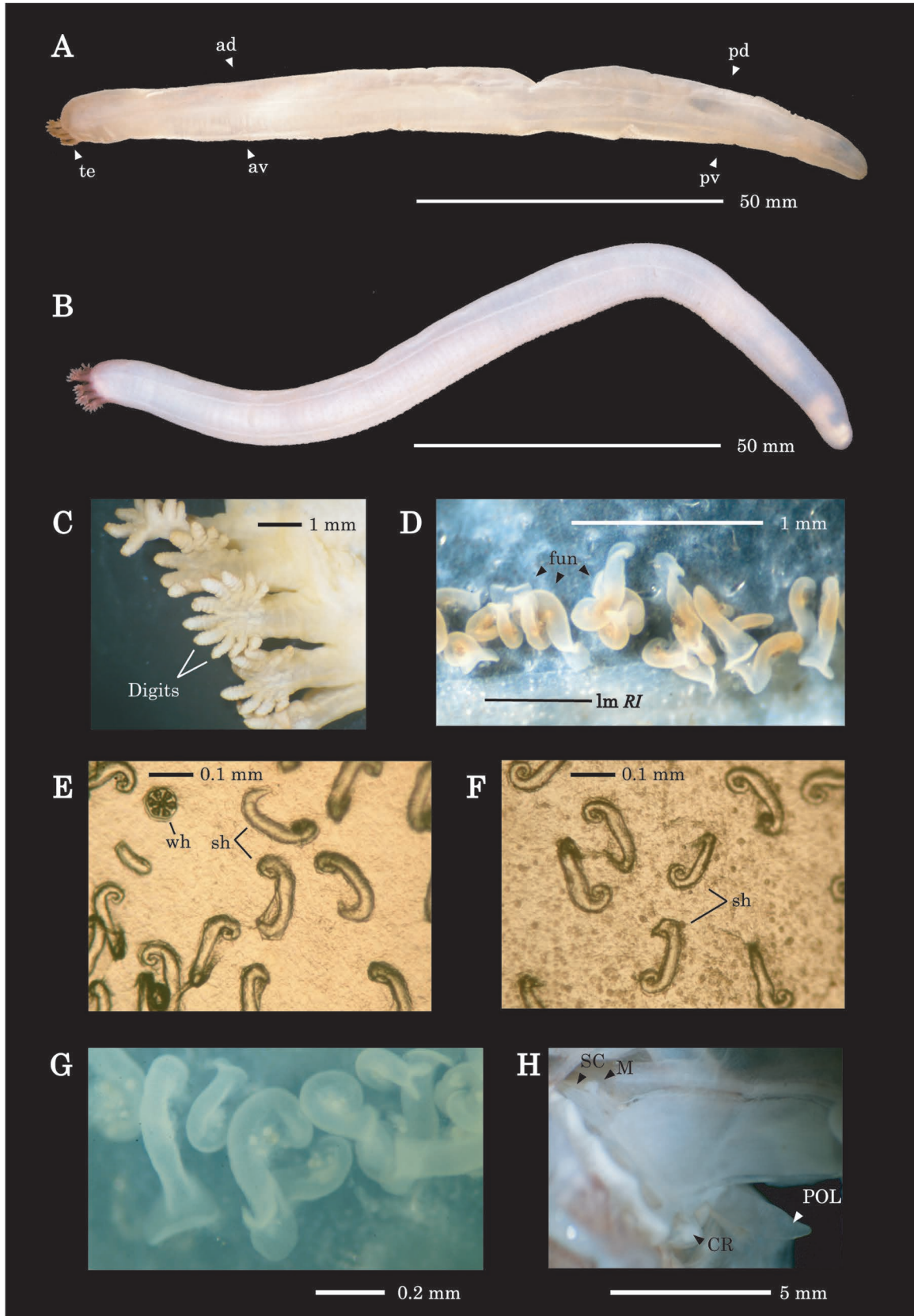


Fig. 2. External and internal morphologies of *Taeniogyrus albulus* sp. nov. A–G: holotype (WMNH-INV-2017-100); H: paratype (WMNH-INV-2018-23). A, B, Lateral views of preserved state and anaesthetized state, respectively; C, tentacles of left side (viewed from left side, dorsal upper); D, ciliated funnels along with *lm RI* (anterior left); E–G, microphotograph of anterior dorsal skin containing ossicles (E), anterior ventral skin containing ossicles (F), and ciliated funnels (G); H, left internal view of preserved states (anterior left). Abbreviations: ad, anterior dorsal; av, anterior ventral; CR, calcareous ring; fun: ciliated funnels; lm: longitudinal muscle; M, madreporite; pd, posterior dorsal; POL, Polian vesicle; pv, posterior ventral; SC, stone canal; sh, sigmoid-hook ossicle; te, tentacle; wh, wheel ossicle.

Table 1. Measurements of body size, counts of tentacles and Polian vesicles, and gonad type for type specimens of *Taeniogyrus albulus* sp. nov.

Registration No. of WMNH-INV-	Type status	Body size (mm)		Counts			Gonad type
		Length	Width	Tentacles	Tentacle digits	Polian vesicles	
2017-100	Holotype	134	10	10	8–11	1	hermaphroditic
2017-101	Paratype	81	11	10	8–11	1	immature
2018-21	Paratype	69	7	10	8–11	1	immature
2018-22	Paratype	76	9	10	7–11	1	hermaphroditic
2018-23	Paratype	151	13	10	6–8	1	hermaphroditic
2019-300	Paratype	55	4	10	5–8	1	immature
2020-10	Paratype	55	9	10	8–11	1	hermaphroditic
2020-11	Paratype	121	13	10	10–12	1	hermaphroditic

WMNH-INV: Invertebrate Collection of the Wakayama Prefectural Museum of Natural History.

side of dorsal mesentery, one on midventral side, tubules unbranched.

Calcareous ring with 5 thick radial, 5 thick inter-radial plates; distally flattened ends (Fig. 4A); all with deep posterior depression and shallow anterior depression, *RI* with wide anterior notch, others without notch or perforation.

Body wall thin (less than 0.5 mm in thickness), containing wheel, curved rod, sigmoid-hook ossicles (Figs 2E, F, 4B–D; Table 2), wheel ossicles scattered sparsely in anterior to middle body surface, occasionally lacking posteriorly (Table 2). Wheel ossicle aggregations (wheel-papillae) absent; wheel ossicles scattered sparsely in anterior to middle body surface, occasionally lacking posteriorly (Table 2). Wheel ossicle diameter 33–82 μm (means 59–68 μm in different tissues) (Table 2), rounded-hexagonal, 6 spokes (Fig. 4B). Inner margin of rim parallel to outer margin. Teeth triangular-shaped, tip gradually blunted, 8–19 per inter-spokes area (means 13–15 in different tissues) (Table 2); often reduced in number and size at corners, but no discontinuities in tooth series. Spokes broad, breadth 15–25% of wheel ossicle diameter (means 19–22%) (Table 2).

Curved rod ossicles, length 107–120 μm (Table 2), very rarely present, spinous ends, centrally with sparse teeth, sometimes teeth along entire length (Fig. 4C), rods only found from the anterior body surface (Table 2).

Sigmoid-hook ossicles scattered densely throughout body surface (Fig. 2E, F), scattered even on longitudinal muscles, not in clear rows or circles. Sigmoid-hook ossicles thick, large, outer bend edge with paired rows of spinelets, each row with 3–5 spinelets, internal space between 2 rows forming depression (Fig. 4D). Open-loop end bending strongly, few teeth in shank tip; length 144–185 μm (means 165–173 μm in four different tissues) (Table 2).

Tentacles containing small rods (Fig. 4E; Table 2), spinous, curved, mostly branching distally, weakly expanding centrally. Rod ossicles length 37–77 μm , breadth 3–10 μm (Table 2).

Variation including paratypes. Length of largest paratype specimen (WMNH-INV-2018-23) 151 mm; width 13 mm (Fig. 2A; Table 1). Tentacle digitations more frequent in medium-sized specimens than large- and small-sized specimens (Table 1). In all eight type specimens with single Polian vesicle, vesicle shaped fusiform. Wheel teeth triangular-shaped, tip gradually blunted, 7–19 per radiant (means

12–16 in measured five type specimens) (Table 2). Spokes breadth 15–27% of wheel ossicle diameter (individual means 19–25% in measured five type specimens) (Table 2). Occasionally spokes bifurcate at close to rim and forming Y-shaped spokes observed at very low frequencies. Wheel diameter 33–86 μm (means 53–72 μm in different tissues and in measured five type specimens) (Table 2), differed significantly among individuals in all body parts (Kruskal–Wallis test, $P < 0.01$) and differed significantly among parts of the body in three specimens (WMNH-INV-2017-101, 2018-21, and 2018-23) among the present measured five type specimens (Kruskal–Wallis test, $P < 0.05$). Curved rod length 88–120 μm (Table 2), rods only found from the anterior body surface (Table 2). Occasionally, rods with 1 short central branch. Sigmoid-hook length 137–208 μm (means 162–189 μm in four different tissues and in measured five type specimens) (Table 2), length of posterior body parts significantly larger than anterior parts in two of five measured specimens (WMNH-INV-2018-21 and 2018-23). Tentacles rod length 28–106 μm (means 49–68 μm in measured five type specimens) (Table 2).

Remarks. *Taeniogyrus albulus* sp. nov. has curved rod ossicles in the skin of the anterior body. Among all the taeniogyrid genera, although this feature has been reported in two *Rowedota* species [*R. mira* (Cherbonnier, 1988) and *R. chippiru* Yamana, Tanaka, and Nakachi, 2017], *T. albulus* sp. nov. is easily distinguishable from these two species based on the shape of the wheel ossicle. However, the presence of body wall rods has not been reported in the genus *Taeniogyrus* at present. Therefore, *T. albulus* sp. nov. is also easily distinguishable from other nominal *Taeniogyrus* species.

Although a detailed description of the position of reproductive organs has not been made in most studies of *Taeniogyrus* congeners, there have been limited studies regarding hermaphroditism (e.g., Heding 1928). Among the *Taeniogyrus* congeners in Japanese waters, *T. mijim* has been reported as hermaphroditic, having two long tubules of ovaries and testis, which are unbranched and isolated from the intestine (Yamana et al. 2017). On the other hand, *T. albulus* sp. nov. is also hermaphroditic. However, the position of its reproductive organs is unique in *T. albulus* sp. nov.: the ovary is in two clusters of well-branched tubules in the anterior body, one on each side of the dorsal mesentery; the testis is in two tubules in the middle body, adhered to the intestine, one in the

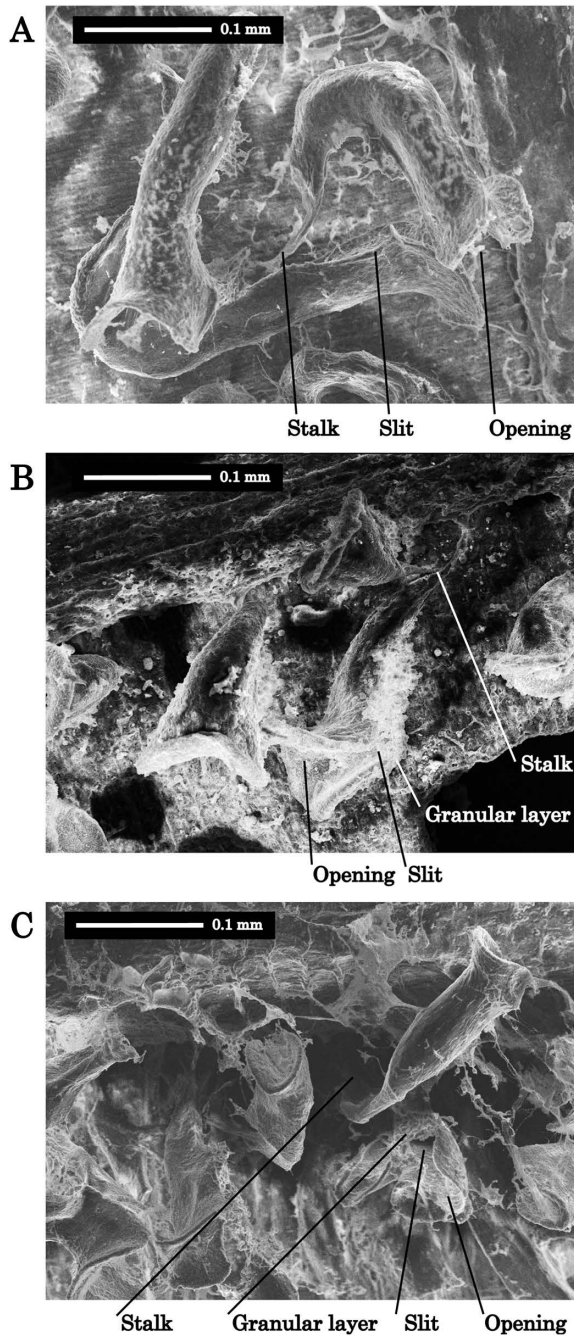


Fig. 3. SEM images of ciliated funnels of holotypes of three new *Taeniogyrus* species. A, *T. albulus* sp. nov. (WMNH-INV-2017-100); B, *T. flavus* sp. nov. (WMNH-INV-2016-135); C, *T. rubrus* sp. nov. (WMNH-INV-2019-299).

mid-dorsal of the left side of the dorsal mesentery and one in the midventral side. There is a possibility that *T. albulus* sp. nov. will also be distinguishable from the other congeners by the position of its reproductive organs, but which must be studied in more *Taeniogyrus* species.

Distribution. Known only from the type locality, in shallow water (9–13 m deep) at Kushimoto, Wakayama, southern end of the mainland of Japan.

Etymology. The specific name is derived from the Latin adjective *albulus* (meaning whitish), based on its body color.

DNA barcode sequences. Two specimens of sequence

of the mitochondrial *COI* gene, 433 bps and 628 bps were obtained from the holotype (WMNH-INV-2017-100: INSD accession number LC655787, base frequency A=19.9%, C=14.6%, G=20.1%, T=45.4%) and a paratype specimen (WMNH-INV-2020-10: LC655788, base frequency A=19.1%, C=14.8%, G=21.8%, T=44.3%), respectively. In BLAST searches, the closest hits to the partial *COI* sequence are from *Leptosynapta clarki* Hedding, 1928 (HM542244–HM542248 and HM542251–HM542253, with 83.8–84.0% similarity in 98–100% coverage).

***Taeniogyrus flavus* Yamana and Tanaka, sp. nov.**

[New Japanese name: Shirahama-kuruma-kagi-namako]

(Figs 3B, 5, 6; Tables 3, 4)

Material examined. Holotype: WMNH-INV-2016-135 (length 17.3 mm, width 2.0 mm, collected from Shirahama on 23 June 2016). Paratypes: 5 specimens, WMNH-INV-2016-136 (length 16.8 mm, width 1.9 mm, collected from Shirahama on 23 June 2016); WMNH-INV-2016-137 (length 14.1 mm, width 1.6 mm, collected from Shirahama on 23 June 2016; INSD accession number LC637701, 819 bps); WMNH-INV-2016-138 (length 13.1 mm, width 1.8 mm, collected from Shirahama on 24 June 2016); WMNH-INV-2016-139 (length 3.8 mm, width 0.9 mm, collected from Shirahama on 24 June 2016); WMNH-INV-2016-140 (length 8.3 mm, width 0.9 mm, collected from Shirahama on 24 June 2016). Other materials: 64 specimens, WMNH-INV-2016-141–204 (length 1.2–16.1 mm breadth 0.8–2.1 mm, collected from Shirahama on 24 June 2016).

Diagnosis. Body color translucent pale yellow, with whitish spots of wheel-papillae along three dorsal inter-radii. Tentacles ten, with 3–5 pairs of digits. Polian vesicles 1–3 in *RI*. Ciliated funnels solitary arranged along with inter-radius of near right of medioventral longitudinal muscle *RI*, and near left side of left lateral longitudinal muscle *RII*. Funnels curved at middle about 90 degrees, with bugle horn like opening. Outer bend edge of sigmoid hook ossicles frequently having very minute spinelets.

Holotype description. Body small, anaesthetized length of largest specimen (holotype, WMNH-INV-2016-135) 17.3 mm (after preservation), cylindrical, straight, or weakly bend downward, slightly tapered toward posterior end (Fig. 5A; Table 3). Body color (of living and preserved specimens) translucent pale yellow. Mouth anterior; anus posterior. Oral disc inclined toward ventral side.

Tentacles ten, non-retractile, slender, with smooth or rarely bumpy skin. Each tentacle with 3–5 pairs of digits; sensory cups absent (Fig. 5C). Color of tentacles (of living and preserved specimens) pale yellow.

Polian vesicles two in *RI* (1.3 mm and 1.7 mm in length), branched in basal part (Table 3). Stone canal single, thin, coiled and short (about 0.2 mm), with a small coffee bean-like madreporite (about 0.15 mm in diameter) just behind of *IR5* calcareous plate (Fig. 5C). One ambiguous row of ciliated funnels situated in inter-radius of near right of medioventral longitudinal muscle *RI* (Fig. 5F), and another am-

Table 2. Measurements (Mean \pm sd μ m) of ossicles from five specimens of *Taeniogyrus albulus* sp. nov.

No. ^a	Skin ^b	n	Rod		n	Sigmoid-hook		n	Wheel ^c		
			Length	Breadth		Length	Breadth		Diameter ^d	Teeth ^e	Spoke width ^f
2017-100	T	49	56 \pm 9.7	5.6 \pm 1.6	0			0			
	Range		37–77	3–10							
	AD	3	113 \pm 6.6	19 \pm 5.5	23	169 \pm 8.1	27 \pm 3.1	4	59 \pm 18	13 \pm 3.3	19 \pm 2.8
	Range		107–120	13–23		147–185	21–37		33–72	8–15	15–21
	PD	0			28	173 \pm 9.5	26 \pm 2.1	15	68 \pm 13	15 \pm 2.6	21 \pm 2.3
	Range					150–187	22–30		34–82	8–19	17–25
	AV	0			22	168 \pm 6.3	27 \pm 2.0	2	62	14	22
	Range					154–179	24–32		58, 66	13, 15	21, 23
PV	0			44	165 \pm 7.4	25 \pm 1.6	0				
Range					144–179	22–30					
2017-101	T	50	49 \pm 9.4	4.1 \pm 1.0	0			0			
	Range		34–77	3–6							
	AD	4	99 \pm 7.4	14 \pm 0.8	11	165 \pm 8.3	26 \pm 2.2	15	62 \pm 7.2	14 \pm 2.3	25 \pm 1.6
	Range		89–105	13–15		153–177	22–29		40–71	9–19	22–27
	PD	0			44	162 \pm 6.9	25 \pm 1.5	5	54 \pm 5.7	12 \pm 1.5	21 \pm 2.4
	Range					148–175	22–28		45–61	11–15	18–24
	AV	4	99 \pm 8.4	15 \pm 0.8	21	169 \pm 4.1	27 \pm 2.0	10	65 \pm 2.9	14 \pm 1.5	24 \pm 1.8
	Range		91–107	14–16		161–175	22–31		61–70	11–16	21–26
PV	0			31	172 \pm 5.6	27 \pm 1.8	17	64 \pm 7.3	14 \pm 2.1	23 \pm 1.6	
Range					161–184	24–30		43–74	9–18	20–26	
2018-21	T	46	68 \pm 13	5.8 \pm 2.1	0			0			
	Range		38–106	3–11							
	AD	0			21	171 \pm 10	26 \pm 1.9	24	60 \pm 5.4	13 \pm 1.3	22 \pm 2.5
	Range					146–190	23–29		52–74	10–16	17–27
	PD	0			25	184 \pm 10	28 \pm 2.8	11	58 \pm 6.7	14 \pm 2.2	20 \pm 2.9
	Range					159–198	24–34		42–66	10–17	16–23
	AV	6	106 \pm 11	20 \pm 3.6	34	170 \pm 10	26 \pm 1.9	5	53 \pm 7.0	12 \pm 1.8	24 \pm 2.1
	Range		88–119	16–27		150–191	22–30		47–64	10–14	21–26
PV	0			17	180 \pm 11	27 \pm 1.4	14	63 \pm 6.7	14 \pm 1.9	22 \pm 1.7	
Range					166–201	24–30		51–75	9–16	19–24	
2018-22	T	45	60 \pm 14	4.7 \pm 1.3	0			0			
	Range		28–89	3–8							
	AD	1	116	15	17	175 \pm 7.4	25 \pm 2.1	8	68 \pm 4.1	14 \pm 0.9	22 \pm 1.1
	Range		116	15		159–188	22–31		63–75	13–15	20–23
	PD	0			29	175 \pm 6.5	26 \pm 1.9	17	71 \pm 11	13 \pm 2.4	20 \pm 2.0
	Range					163–189	23–32		44–84	7–16	16–25
	AV	6			20	163 \pm 9.1	24 \pm 1.5	7	67 \pm 5.1	13 \pm 1.5	22 \pm 1.0
	Range					137–175	21–28		61–76	11–15	21–23
PV	0			43	171 \pm 7.7	25 \pm 1.7	0				
Range					148–184	23–29					
2018-23	T	46	65 \pm 11	5.3 \pm 1.5	0			0			
	Range		41–83	3–10							
	AD	0			21	177 \pm 5	28 \pm 1.8	16	65 \pm 10	13 \pm 2.2	23 \pm 1.6
	Range					167–185	26–32		44–78	9–16	20–27
	PD	0			30	189 \pm 7.2	28 \pm 2.0	13	72 \pm 8.3	15 \pm 1.8	22 \pm 1.8
	Range					169–200	24–32		50–86	12–18	20–26
	AV	1	111	17	9	171 \pm 12	27 \pm 3.1	12	71 \pm 5.3	15 \pm 1.4	22 \pm 1.9
	Range		111	17		150–185	25–35		64–80	12–17	20–25
PV	0			34	181 \pm 8.8	28 \pm 2.6	6	65 \pm 5.9	16 \pm 1.2	21 \pm 2.0	
Range					161–208	24–33		59–76	15–18	19–24	

^a Registration No. of WMNH-INV: Invertebrate Collection of the Wakayama Prefectural Museum of Natural History. ^b Body skin: T, tentacle; AD, anterior dorsal; PD, posterior dorsal; AV, anterior ventral; PV, posterior ventral. ^c Only wheels with six spokes were measured. ^d Values were measured across opposite vertices of a hexagon. ^e Values were counted for individual radii of a hexagon. ^f Values are reported as the percentage of spoke breadth in a diameter.

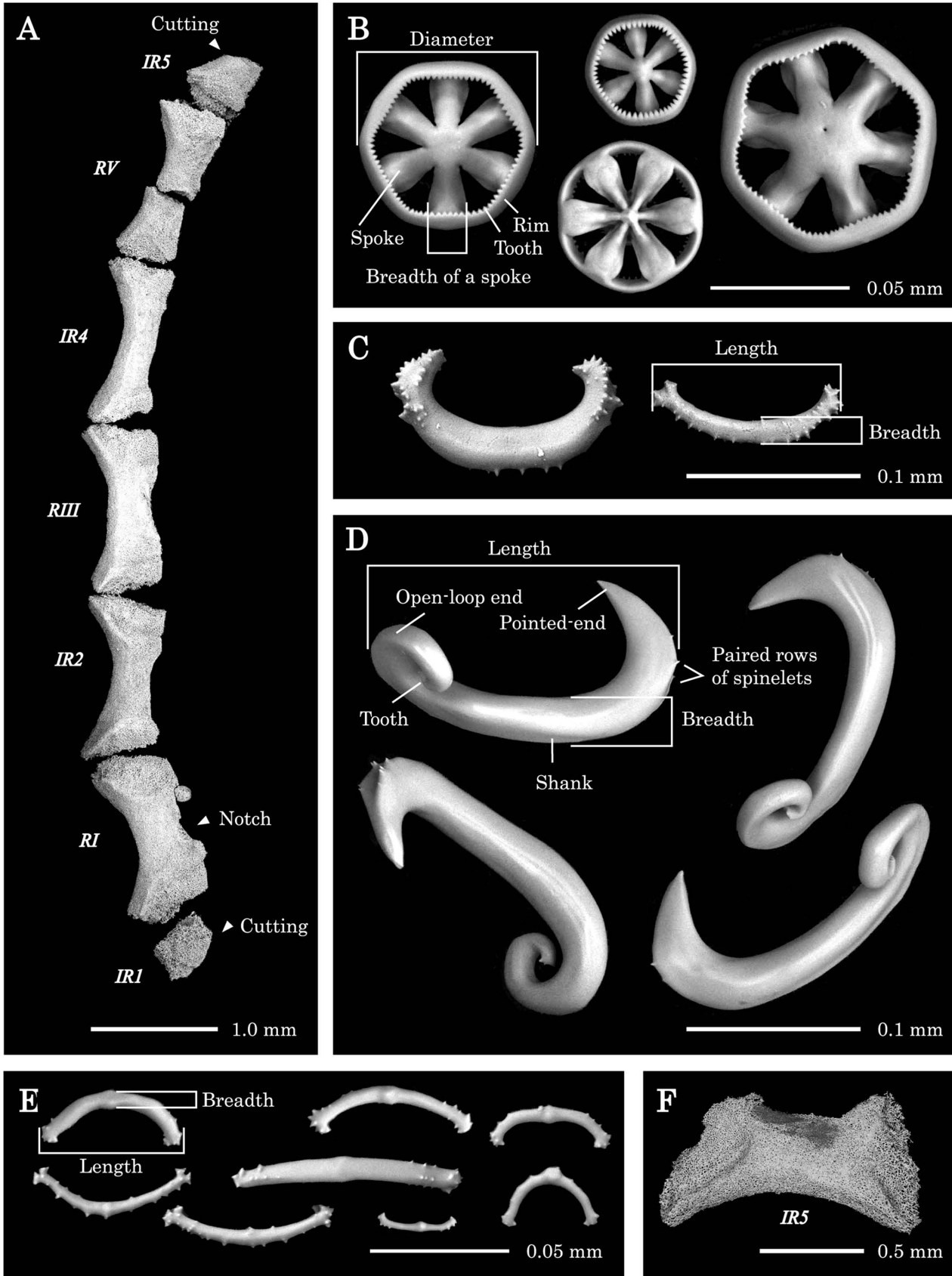


Fig. 4. SEM images of calcareous ring parts and body ossicles of *Taeniogyrus albulus* sp. nov. A-E: holotype (WMNH-INV-2017-100); F: paratype (WMNH-INV-2017-101). A, Right parts of calcareous ring (viewed from right side, dorsal upper); B-D, wheel ossicles from a wheel papilla of anterior dorsal (B), curved rod ossicles (C) and sigmoid-hook ossicles (D) from anterior dorsal skin; E, rod ossicles from a lateral tentacle; F, calcareous plate IR5 of a paratype.

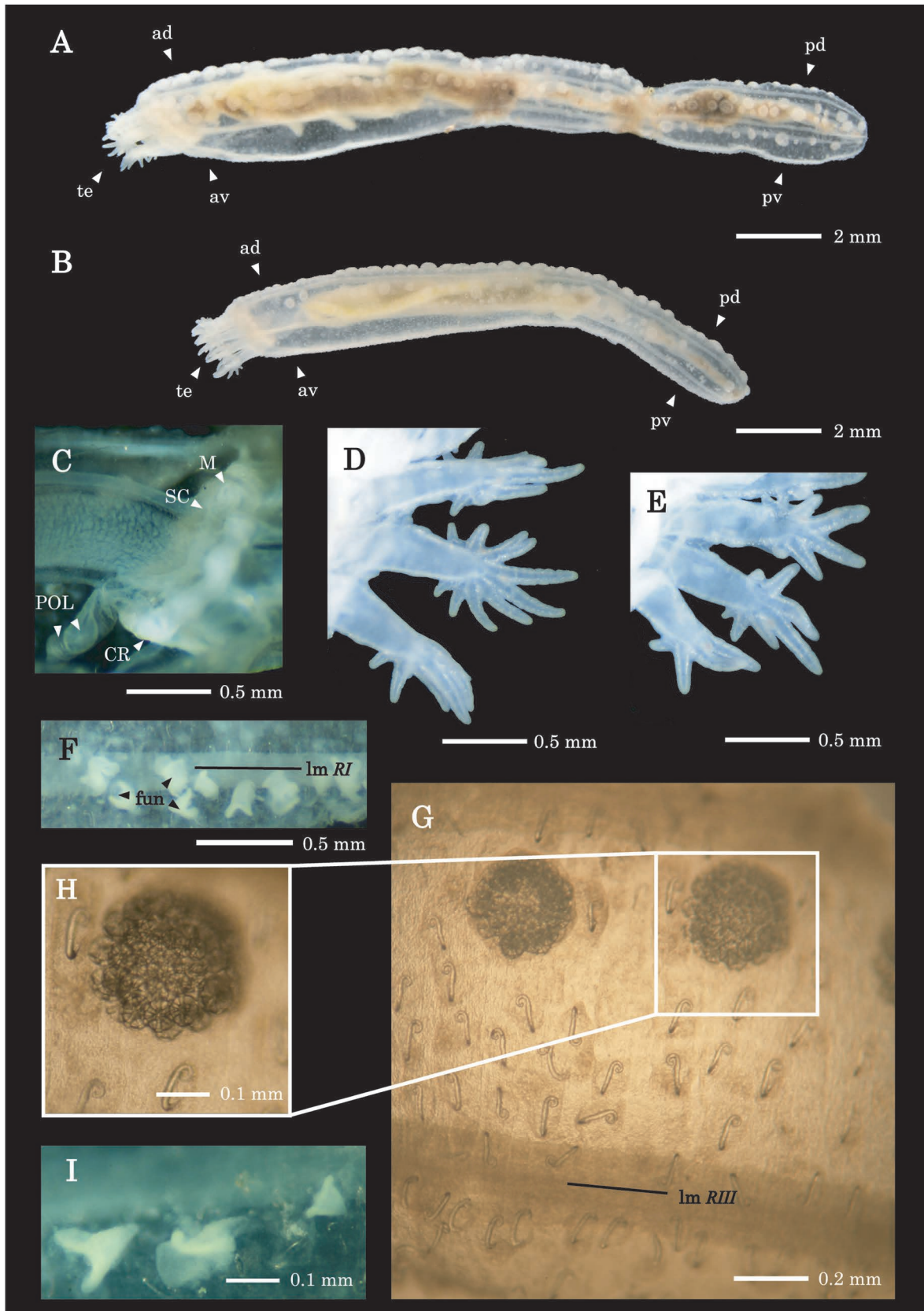


Fig. 5. External and internal morphologies of *Taeniogyrus flavus* sp. nov. A, D, G–I: holotype (WMNH-INV-2016-135); B, E: paratype (WMNH-INV-2016-138); C, F: paratype (WMNH-INV-2016-137). A, B, Lateral views of preserved states of the holotype and paratype, respectively; C, F, Right internal views of preserved states of a paratype (WMNH-INV-2016-137); D, E, tentacles of left side (viewed from oral disc) of the holotype and paratype, respectively; G, H, microphotograph of anterior dorsal skin of the holotype containing ossicles; I, microphotograph of ciliated funnels of the holotype. Abbreviations: ad, anterior dorsal; av, anterior ventral; CR, calcareous ring; fun: ciliated funnels; lm: longitudinal muscle; M, madreporite; pd, posterior dorsal; POL, Polian vesicle; pv, posterior ventral; SC, stone canal; te, tentacle.

Table 3. Measurements of body size, counts of tentacles and Polian vesicles, and gonad type for type specimens of *Taeniogyrus flavus* sp. nov.

Registration No. of WMNH-INV-	Type status	Body size (mm)		Counts			Gonad type
		Length	Width	Tentacles	Tentacle digits	Polian vesicles	
2016-135	Holotype	17.3	2.0	10	8–10	2	testis
2016-136	Paratype	16.8	1.9	10	6–9	3	ovary
2016-137	Paratype	14.1	1.6	10	6–9	2	ovary
2016-138	Paratype	13.1	1.8	10	6–8	2	testis
2016-139	Paratype	3.8	0.9	10	6–8	1	immature
2016-140	Paratype	8.3	0.9	10	6–7	2	ovary

WMNH-INV: Invertebrate Collection of the Wakayama Prefectural Museum of Natural History.

biguous row situated interradiar zone *IR3*, near left side of left lateral longitudinal muscle *RII*, both running through anterior to posterior body cavity, dense in anterior to middle. Each funnel moderately curved (= about 90°), with deep notch at upper ends of opening, and slit with granular layer along proximal side to the funnel base (Fig. 3B). Funnels separately standing, small (about 0.05–0.2 mm), with short stalk. Intestine with no loop, situated along mediodorsal with mesentery *IR5*. Each 2–4 tubules of ovaries or testis present in both sides of dorsal mesentery, branched in basal part, rarely branched in other part.

Calcareous ring composed of five radial and five inter-radial plates, these all being thick and broad, all with low anterior projection and shallow posterior depression (Fig. 6A), with distally spread and flattened. Low trapezoid anterior projection in *RI* (Fig. 6F), and low triangle anterior projection in *IR5* (Fig. 6A), both symmetrical designs.

Body-wall thin (less than 0.5 mm in thickness), containing wheel and sigmoid-hook ossicles (Figs 4, 5; Table 4). Wheel ossicles only present in wheel-papillae (Fig. 5F), which scattered only in three dorsal inter-radial body-wall, ranging from tentacle base to body posterior end. Wheel ossicles rounded-hexagonal with six spokes. Inner margin of rim approximately parallel to outer margin. Teeth sharp, with 9–16 per inter-spokes area. Spokes narrow, their breadth amounting to 20–26% of wheel ossicle diameter (Fig. 6C; Table 4). Wheel ossicle diameter 46–75 µm in anterior dorsal side and 43–74 µm in posterior dorsal side.

Sigmoid-hook ossicles in body-wall scattered in inter-radii. Along both sides of longitudinal muscles, with pointed end facing toward inter-radius, and open-loop end facing toward longitudinal muscles (Fig. 5E). Outer bend edge frequently having minute teeth (Fig. 6D), but mostly blunt and not easy to detect. Breadth of shank almost constant, sometimes broadest at bend. Length 91–104 µm in anterior dorsal side, 84–111 µm in posterior dorsal side, 85–96 µm in anterior ventral side, and 74–94 µm in posterior ventral side.

Tentacles containing rod ossicles (Fig. 6B; Table 4), these mostly bifurcate distally, rarely bifurcate twice or more and with another branch at centrally. Distal ends spinous. Rod ossicle length 45–69 µm, breadth 4–9 µm.

Variation including paratypes. Two Polian vesicles in the holotype, but 1–3 Polian vesicles in five paratype specimens (Table 3). In individuals with single Polian vesicle (width about 1/2 of length), vesicle shaped fusiform, and in individuals with 2 or 3 Polian vesicles, vesicle shaped

globular. Calcareous ring plate with low trapezoid anterior projection in *RI*, and low triangle anterior projection in *IR5*, in small specimen (WMNH-INV-2016-140) (Fig. 6E), each projection slightly higher than that of large specimens (WMNH-INV-2016-135 and 2016-137) (Fig. 6F, G).

Wheel diameter means of 53–62 µm in anterior dorsal side and means of 62–67 µm in posterior dorsal side, differing significantly among specimens in anterior part (Kruskal–Wallis test, $P < 0.05$), but not in posterior part (Kruskal–Wallis test, $P > 0.05$). Wheel diameters in four specimens (WMNH-INV-2016-136–139) significantly different between anterior and posterior parts (Kruskal–Wallis test, $P_s < 0.05$), but not in the largest specimen (WMNH-INV-2016-135). Sigmoid-hook length 77–114 µm (individual means of 90–107 µm in measured five type specimens) in anterior dorsal side, 78–111 µm (individual means 83–95 µm in measured five type specimens) in posterior dorsal side, 76–112 µm (individual means 80–97 µm in measured five type specimens) in anterior ventral side, and 65–102 µm (individual means 78–90 µm in measured five type specimens) in posterior ventral side. Length significantly different among specimens in all four body parts (Kruskal–Wallis test, $P_s < 0.05$), but not significantly different between anterior and posterior parts of five specimens (Kruskal–Wallis test, $P_s > 0.05$). Length of sigmoid-hooks also significantly different among four body parts in all five specimens (Kruskal–Wallis test, $P_s < 0.05$), and in four specimens (WMNH-INV-2016-135, 137–139) hook in dorsal parts significantly larger than that of ventral parts (Kruskal–Wallis test, $P_s < 0.05$). Tentacles rod length 43–77 µm, means of 57–63 µm in different five specimens, significantly different among them (Kruskal–Wallis test, $P < 0.05$).

Remarks. Up to date, seven species of *Taeniogyrus* with wheel-papillae have been reported (Table 5): 1) *T. bamberi* O’Loughlin, 2015; 2) *T. cidaridis*; 3) *T. clavus* Heding, 1928; 4) *T. dayi* Cherbonnier, 1952; 5) *T. heterosigmus* Heding, 1931; 6) *T. prydzii* O’Loughlin and VandenSpiegel, 2010; and 7) *T. yvonnae*. Since *T. flavus* sp. nov. has 1–3 Polian vesicles, and ciliated funnels along with medioventral and left dorsal, and such features are not reported in these seven species and most of the other congeners (Table 5), but arrangement of ciliated funnels of *T. bamberi* have not been reported. Although ciliated funnels have not been reported, sigmoid hooks of this species apparently larger (means 247 µm in anterior and 273 µm in posterior) than that of *T. flavus* sp. nov. (ranged in 77–114 µm) (Table 5), and body color of this

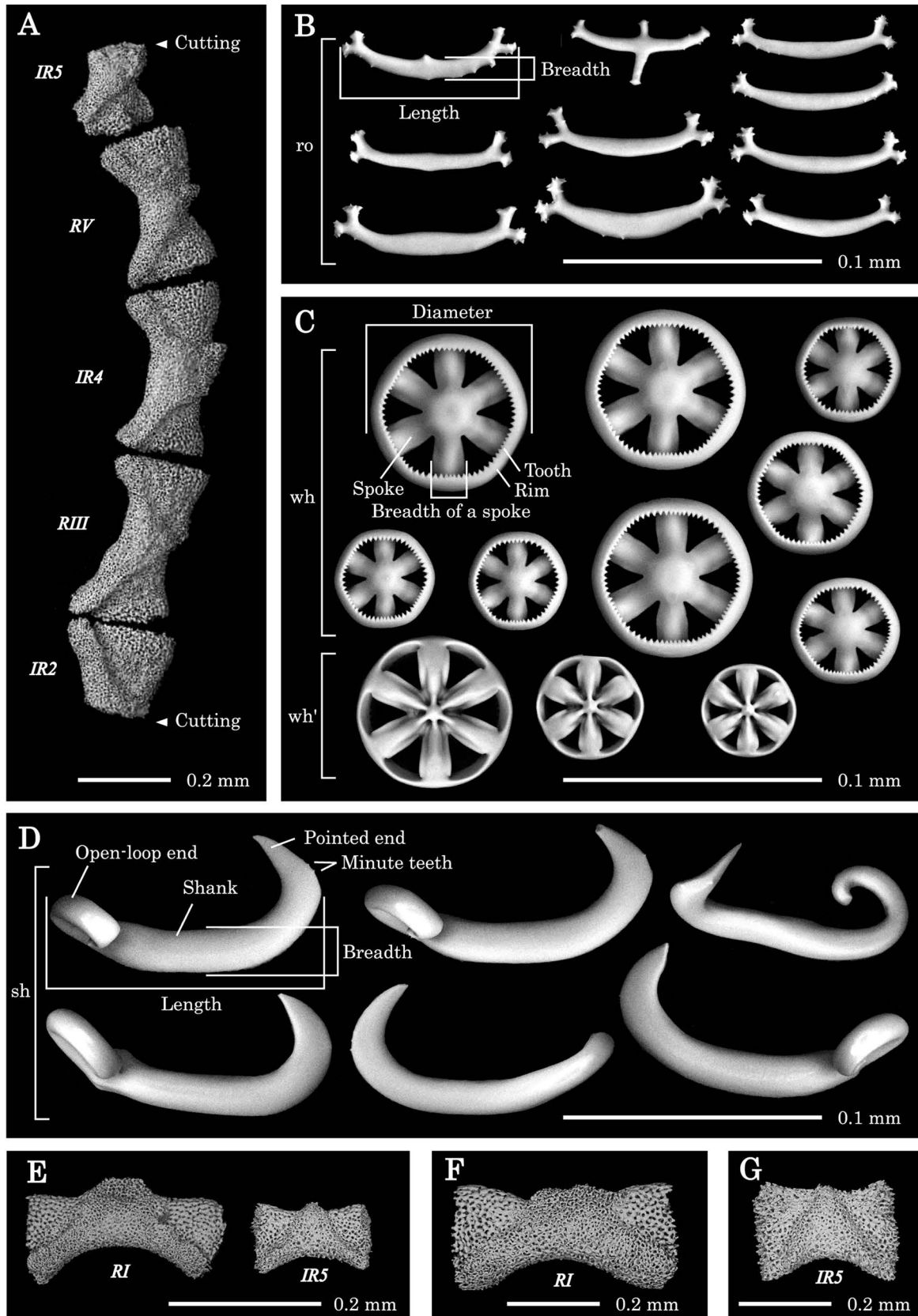


Fig. 6. SEM image of calcareous ring parts and body ossicles of *Taeniogyrus flavus* sp. nov. A–D, F: holotype (WMNH-INV-2016-135); E: small-sized paratype (WMNH-INV-2016-140); G: middle sized paratype (WMNH-INV-2016-137). A, Right parts of calcareous ring (viewed from right side, dorsal upper); B–D, rod ossicles from a lateral tentacle (B), wheel ossicles from a wheel papilla of anterior dorsal (C), and sigmoid-hook ossicles from anterior dorsal skin (D); E–G, calcareous plate *RI* and *IR5* of a small-sized paratype (E), *RI* of holotype (F), and *IR5* of a middle-sized paratype (G) (anterior upper). Abbreviations: ro, rod ossicles; sh, sigmoid-hook ossicles; wh, wheel ossicles; wh', internal side of wheel ossicles.

Table 4. Measurements (Mean \pm sd μ m) of ossicles from five specimens of *Taeniogyrus flavus* sp. nov.

No. ^a	Skin ^b	n	Rod		n	Sigmoid-hook		n	Wheel ^c		
			Length	Breadth		Length	Breadth		Diameter ^d	Teeth ^e	Spoke width ^f
2016-135	T	54	59 \pm 5.5	6.9 \pm 1.2	0			0			
	Range		45–69	4–9							
	AD	0			13	95.9 \pm 4.4	13.7 \pm 0.9	17	62.3 \pm 9.6	11.8 \pm 1.5	22.4 \pm 1.6
	Range					91–104	12–15		46–75	10–14	20–26
	PD	0			19	95.2 \pm 7.5	13.3 \pm 1.4	21	62.3 \pm 8.4	12.6 \pm 1.9	22.1 \pm 1.1
	Range					84–111	11–16		43–74	9–16	21–25
	AV	0			10	90.5 \pm 3.8	13.2 \pm 0.8	0			
	Range					85–96	12–14				
2016-136	PV	0			22	90.5 \pm 7.2	12.5 \pm 1.2	0			
	Range					74–97	10–14				
	T	43	62.5 \pm 7.1	7.3 \pm 1.6	0			0			
	Range		47–76	4–10							
	AD	0			12	107 \pm 6.4		21	58.6 \pm 7.6	12.2 \pm 1.2	22.0 \pm 1.5
	Range					96–114			43–68	10–14	20–25
	PD	0			17	92.5 \pm 7.9		21	61.8 \pm 10.4	12.8 \pm 2.0	21.5 \pm 1.4
	Range					79–106			39–75	8–16	20–26
2016-137	AV	0			27	97.2 \pm 6.0		0			
	Range					87–112					
	PV	0			24	87.8 \pm 8.2		0			
	Range					71–102					
	T	48	59.2 \pm 6.2	7.0 \pm 1.3	0			0			
	Range		45–74	5–11							
	AD	0			14	104 \pm 5.0	15.3 \pm 1.2	14	56.7 \pm 10.3	11.5 \pm 2.1	22.2 \pm 1.7
	Range					96–114	13–17		41–72	8–15	19–25
2016-138	PD	0			17	93.2 \pm 6.5	13.5 \pm 1.7	18	66.9 \pm 12.8	13.1 \pm 1.9	22.2 \pm 2.0
	Range					81–104	11–16		44–84	9–17	20–27
	AV	0			25	92.8 \pm 5.3	13.5 \pm 0.9	0			
	Range					84–104	12–15				
	PV	0			30	87.7 \pm 6.0	12.2 \pm 1.3	0			
	Range					73–97	10–14				
	T	42	57.1 \pm 6.2	6.8 \pm 1.2	0			0			
	Range		44–74	4–10							
2016-139	AD	0			6	104 \pm 3.9	14.7 \pm 0.8	12	54.9 \pm 8.1	11.5 \pm 1.3	23.6 \pm 2.4
	Range					97–108	14–16		41–64	10–15	21–29
	PD	0			11	91.3 \pm 3.9	13.2 \pm 0.9	11	64.6 \pm 9.4	13.2 \pm 2.4	22.0 \pm 1.0
	Range					84–97	12–15		47–76	9–16	20–24
	AV	0			15	90.8 \pm 6.7	14.1 \pm 0.7	0			
	Range					77–107	13–16				
	PV	0			22	83.2 \pm 5.6	12.2 \pm 1.1	0			
	Range					65–92	11–14				
2016-139	T	35	59.3 \pm 7.1	6.5 \pm 1.5	0			0			
	Range		43–77	3–10							
	AD	0			19	89.6 \pm 5.9	12.6 \pm 1.1	12	53.1 \pm 7.7	11.9 \pm 1.2	22.4 \pm 1.6
	Range					77–98	11–15		39–67	10–13	19–25
	PD	0			9	82.7 \pm 3.4	11.4 \pm 1.0	14	60.8 \pm 11.1	12.3 \pm 1.9	21.4 \pm 2.2
	Range					78–87	10–13		41–76	9–15	17–26
	AV	0			17	80.0 \pm 2.7	11.4 \pm 0.9	0			
	Range					76–85	10–13				
2016-139	PV	0			15	77.9 \pm 2.2	10.5 \pm 0.6	0			
	Range					73–81	10–12				

^a Registration No. of WMNH-INV: Invertebrate Collection of the Wakayama Prefectural Museum of Natural History. ^b Body skin: T, tentacle; AD, anterior dorsal; PD, posterior dorsal; AV, anterior ventral; PV, posterior ventral. ^c Only wheels with six spokes were measured. ^d Values were measured across opposite vertices of a hexagon. ^e Values were counted for individual radii of a hexagon. ^f Values are reported as the percentage of spoke breadth in a diameter.

Table 5. Morphological comparison of all the congeners of *Taeniogyrus* Semper, 1867.

Species name	Information source	Habitat ^a	Body size (mm)	Body color	PV ^b	SC ^c	TDP ^d	Ciliated funnels ^e	Wheel ossicle	Wheel-papilla	Hook-papilla	Ossicle size (µm)	
												Wheel	Hook
<i>T. albulus</i> sp. nov.	Present study	NWP	151×13	Pink with anterior body tip brown (living), yellowish white (preserving)	1	1	2-6	MV	+	-	-	33-84	137-208
<i>T. antarcticus</i>	Heding (1931); O'Loughlin and VandenSpiegel (2007)	AO	Up to 15	Pale yellow-brown (preserving)	3-9	1	5	Few long, thin ciliated funnels present (nr for arrangements)	+	-	-	64-80	64-208
<i>T. australianus</i>	Stimpson (1855); Heding (1928); O'Loughlin and VandenSpiegel (2010)	SWP	Up to 95	Yellowish white to pale orange (living and preserving)	1	nr	6-7	MV and LD	+	-	+	48-88	120-136
<i>T. bambergi</i>	O'Loughlin et al. (2015)	WS	32×3	Off-white to grey with faint orange to purple tinge (preserving)	1	nr	4	nr	+	+	-	80-88	ca. 247 (anterior); ca. 273 (posterior)
<i>T. cidaridis</i>	Ohshima (1914, 1915)	NWP	36×3.5	White (preserving)	1	1	4-5	nf	+	+	-	30-135	120-185
<i>T. clavus</i>	Heding (1928)	SWP	nr	White (preserving)	1	1	5	nf	+	+	-	35-140	ca. 175
<i>T. dayi</i>	Cherbonnier (1952)	SAO	50×4	Reddish brown to pale purple (living and preserving)	1	3	3-4	MD	+	+	-	ca. 100	ca. 100
<i>T. dendyr*</i>	Mortensen (1925); Pawson (1970)	SWP	133×9	White or faint purple (living), white to orange (preserving)	1	1	4-6	MD and LD*	+	-	+	86-105	94-134
<i>T. diasemus</i> ^f	Parker (1881); Dendy (1909); Clark (1921); Pawson (1970)	SWP	Up to 50	Reddish brown (living), yellowish (preserving)	nr	nr	5	nr	-	-	-	ca. 160	ca. 110
<i>T. flavus</i> sp. nov.	Present study	NWP	17.3×2.0	Translucent pale yellow (living and preserving)	1-3	1	3-5	MV and LD	+	+	-	39-75	77-114
<i>T. furecipraeditus</i>	Salvini-Plawen (1972)	NAO	Up to 5	Semi-transparent pale red (preserving)	1	1	nr	nr	+	-	-	ca. 80	ca. 70-90
<i>T. havelockensis</i>	Rao (1975)	IO	3.0×0.5	Transparent with pinkish tinge (living)	1	1	1	nr	+	-	-	38-48	40-56
<i>T. heterosignus</i>	Heding (1931); O'Loughlin and VandenSpiegel (2007)	IO	Up to 3	nr	1	1	nr	2 rows (not MD)	+	+	-	ca. 50-90	ca. 80
<i>T. inexpectatus</i>	Smirnov (1989)	OS	Up to 12	nr	1	nf	1-3	nf	+	-	-	67-112	67-100
<i>T. japonicus*</i>	Marenzeller (1882); Ohshima (1913)	NWP	149×7	Deep red (living), faded red (preserving)	1	1	7-8	MD* and LD*	+	+	-	46-63	41-117
<i>T. kenensis</i>	Heding (1928)	SWP	30×3	Yellowish grey (preserving)	12	1	3-4	nr	+	-	-	30-120	180-220
<i>T. maculatus</i>	Clark (1921); O'Loughlin and VandenSpiegel (2010)	SWP	Up to 26	Pink with minute dark spots (living), pale to dark reddish-brown (preserving)	1	nr	3-5	MD	+	-	-	66-77	ca. 60-180
<i>T. nijini</i>	Yamana et al. (2017)	NWP	11.2×1.0	White to pink (preserving)	1	nf	1	MV	+	-	-	50-79	54-85
<i>T. misakiensis</i>	Ohshima (1914, 1919) (see Yamana et al. 2017)	NWP	30×3	White (preserving)	nr	nr	4	nf	+	-	-	75-130	95-130
<i>T. neocaledonicus</i>	Smirnov (1997)	SWP	9×1	Yellowish (preserving)	nr	nr	2	nr	+	-	-	38-40	40-90
<i>T. papillis</i>	O'Loughlin and VandenSpiegel (2007)	IO	Up to 60	Semi-transparent with close cover of dark red papillae (living), translucent with red flecking of internal organs (preserving)	1	1	5	MD	+	-	-	64-96	64-80
<i>T. prydzii</i>	O'Loughlin and VandenSpiegel (2010)	SWP	Up to 50	nr	1	nr	6	MV	+	+	-	Up to 90	232-272
<i>T. purpureus</i>	Lesson (1830); Theil (1886); O'Loughlin and VandenSpiegel (2010)	SAO	Up to 100	Pale to dark purplish-red (living and preserving)	8-16	1	2-6	nr	+	-	-	120-160	80-144
<i>T. roebucki</i>	Joshua (1914)	IO	75×6	Red (living and preserving)	1	1	2	nr	+	-	-	ca. 80	ca. 130
<i>T. roseus</i>	Ohshima (1914)	NWP	30×4	Red (living)	1	nf	3	MD and LD	+	-	-	37-105	80-95
<i>T. rubrus</i> sp. nov.	Present study	NWP	37.1×2.2	Red or reddish brown (living and preserving)	2 or 3	1	4-6	MV and LV	+	+	-	35-152	132-154
<i>T. tantulus</i>	O'Loughlin and VandenSpiegel (2007)	SWP	Up to 11	Translucent white (preserving)	1	1	4-5	MD	+	-	-	40-104	60-80
<i>T. venustus</i>	Semon (1887)	MS	27×4	Semi-transparent brown (preserving)	1	1	2-3	nr	+	-	-	ca. 90	ca. 90
<i>T. verrucosus</i>	Yamana and Tanaka (2017a)	NWP	27.8×2.7	Semi-transparent yellowish white (living), white (preserving)	1	1	2-4	MD and LD	+	-	-	28-75	36-71
<i>T. yvonnae</i>	Moura et al. (2015)	SAO	Up to 190	Semi-transparent (living and preserving)	15-21	1	3-4	MV and LV	+	+	-	86-169	336-405

^a Habitat: AO, Antarctic Ocean; IO, Indian Ocean; MS, Mediterranean Sea; NAO, North Atlantic Ocean; NWP, North-West Pacific Ocean; OS, Okhotsk Sea; SAO, South Atlantic Ocean; SWP, South-West Pacific Ocean; WS, Weddell Sea. ^b PV: Numbers of the Polian vesicles. ^c SC: Numbers of the Stone canal. ^d TDP: Numbers of the Tentacle Digits Pairs. ^e Arrangement of the ciliated funnels lines: MV: mid-ventral; MD: mid-dorsal; LD: left-dorsal; LV: left-ventral. ^f The species was mostly referred as *T. dumediniensis*. * Yamana con-tributing. Abbreviations: nf: not found; nr: not reported; +: exist; -: absent. * Species presently belonging to *Taeniogyrus* Semper, 1867, but it will be removed to *Scotiodota* Clark, 1908 in near future (Yamana et al. accepted).

species (off-white to grey with faint orange to purple tinge in preserving status) also different from that of *T. flavus* sp. nov. (translucent pale yellow) (Table 5). Thus, *T. flavus* sp. nov. is distinguishable from most of the nominated species, by the number of Polian vesicles, the arrangements of two rows of the ciliated funnels, size range of sigmoid hooks, and its body color. Additionally, another new species described below *T. rubrus* sp. nov. also possess wheel-papillae, but body color of *T. rubrus* sp. nov. (red or reddish brown in living and preserving status) apparently different from this new species (Table 5).

Although the body size of *T. australianus* (Stimpson, 1855) has been reported as at least twice as large as that of *T. flavus* sp. nov. (Table 5), ossicle shapes and body appearances of *T. australianus* previously reported (O'Loughlin and VandenSpiegel 2010) are similar to those of *T. flavus* sp. nov. However, according to Heding (1928) and O'Loughlin and VandenSpiegel (2010), the sigmoid-hook ossicles are not scattered but gathered in small papillae in *T. australianus*, and this feature is quite different from those of *T. flavus* sp. nov. The measurements of the ossicles of *T. australianus* are reported to be larger than those of *T. flavus* sp. nov., with the length of the sigmoid-hook ossicles of *T. australianus* ranging within 120–136 µm (O'Loughlin and VandenSpiegel 2010). The original evaluation of *T. australianus* was quite simple and without figures (Stimpson 1855); but, detailed descriptions and figures have been reported by Heding (1928) and O'Loughlin and VandenSpiegel (2010). According to these reports, there are five pairs of digits on the tentacles (Heding 1928) or up to seven pairs (O'Loughlin and VandenSpiegel 2010). There are two-series of ciliated funnels in an inter-radius of near right of the mid-ventral longitudinal muscle *RI* and near left of the left lateral longitudinal muscle *RII* (O'Loughlin and VandenSpiegel 2010). These features conform well to *T. flavus* sp. nov. Furthermore, in the photograph provided by O'Loughlin and VandenSpiegel (2010), the wheel-papillae are confined to only three dorsal inter-radial zones, identical to *T. flavus* sp. nov. On the other hand, a single Polian vesicle occurs in the descriptions of *T. australianus* provided by both Heding's (1928) and O'Loughlin and VandenSpiegel's (2010), which differs from *T. flavus* sp. nov. having mostly two (or sometimes more) Polian vesicles (Table 5).

Distribution. Known only from the type locality at Shirahama, in sandy-gravel shore, Wakayama, southern end of the mainland of Japan.

Etymology. The specific name is derived from the Latin adjective *flavus* (meaning yellow), based on its body color.

DNA barcode sequence. A 819bps sequence of the mitochondrial *COI* gene was obtained from a paratype specimen (WMNH-INV-2016-137: INSD accession number LC637701). Base frequency was A=21.2%, C=13.1%, G=22.8%, T=42.9%. In BLAST searches, the closest hit to the partial COI sequence is from *Taeniogyrus verruculosus* Yamana and Tanaka, 2017 (LC203483, with 83.0% similarity in 100% coverage). The results of BLAST search are correspond to the morphological identification that the present species belongs to *Taeniogyrus*, but it is shown that present

genus includes great genetic diversity at the same time.

Taeniogyrus rubrus Yamana, Hirabayashi,
Hirai, Dan, and Ogawa, sp. nov.

[New Japanese name: Yesuzaki-kuruma-kagi-namako]
(Figs 3C, 7, 8; Tables 6, 7)

Material examined. Holotype: WMNH-INV-2019-299 (length 34.2 mm, width 3.5 mm, collected from Kushimoto on 15 June 2019; INSD accession number LC655785, 615 bps). Paratypes: 7 specimens, WMNH-INV-2020-29 (length 23.7 mm, width 2.2 mm, collected from Susami on 4 August 2020; LC655786, 622 bps), WMNH-INV-2020-33 (length 33.2 mm, width 3.1 mm, collected from Kushimoto on 1 November 2020), WMNH-INV-2021-49 (length 19.7 mm, width 2.0 mm, collected from Kushimoto on 6 August 2021), WMNH-INV-2021-50 (length 30.4 mm, width 2.7 mm, collected from Kushimoto on 6 August 2021), WMNH-INV-2021-51 (length 24.5 mm, width 2.3 mm, collected from Kushimoto on 6 August 2021), WMNH-INV-2021-52 (length 37.1 mm, width 2.2 mm, collected from Kushimoto on 6 August 2021), WMNH-INV-2021-53 (length 28.5 mm, width 2.6 mm, collected from Kushimoto on 6 August 2021).

Diagnosis. Body color red or reddish brown with dark yellowish spots of wheel-papillae along three dorsal interradial. Tentacles ten, with 4–6 digit pairs. With up to 3 Polian vesicles in *RI*. A band of ciliated funnels situated along with inter-radius near right side midventral longitudinal muscle *RI*, and a sparse row of ciliated funnels situated along with left side of left ventral longitudinal muscle *RII*. Funnels strongly curved, like French horn, and with wide opening. Sigmoid-hook ossicles large (all exceed 100 µm in adult animals), without minute spinelet or gap.

Holotype description. Medium-sized body, anesthetized length of holotype specimen (WMNH-INV-2019-299) 34.2 mm (after preservation); cylindrical, straight, or weakly bent downward; slightly tapered toward posterior end (Table 6). Body color (living and preserved specimens) red or reddish brown. Dark yellowish spots of wheel-papillae locally observed on dorsal inter-radial skin. Mouth anterior; anus posterior; oral disk inclined toward ventral side.

Tentacles ten, non-retractile, with 4–6 pairs digits; sensory cups absent (Fig. 7C; Table 6). Tentacles color translucent red in living, pink to whitish in preserving.

Polian vesicles in *RI*, branched in basal part. In the holotype with 2 Polian vesicles (2.7 mm and 0.9 mm in length) (Table 6), vesicles shaped globular. Stone canal single, short (0.25 mm long), with a coffee bean-like madreporite (0.15 mm diameter) just behind of *IR5* calcareous plate (Fig. 7I). Ciliated funnels (1 band) in inter-radius near right side medioventral longitudinal muscle *RI* (Fig. 7D; Table 6); 1 sparse row of ciliated funnels situated along with left side of left ventral longitudinal muscle *RII* (Fig. 7D). Funnels short (0.15 mm), weakly curved (< about 90°), with narrow opening (0.05 mm wide), with very short stalk, and slit with granular layer along proximal side to the funnel base (Fig. 3C). Intestine situated along *IR5* through anterior to middle

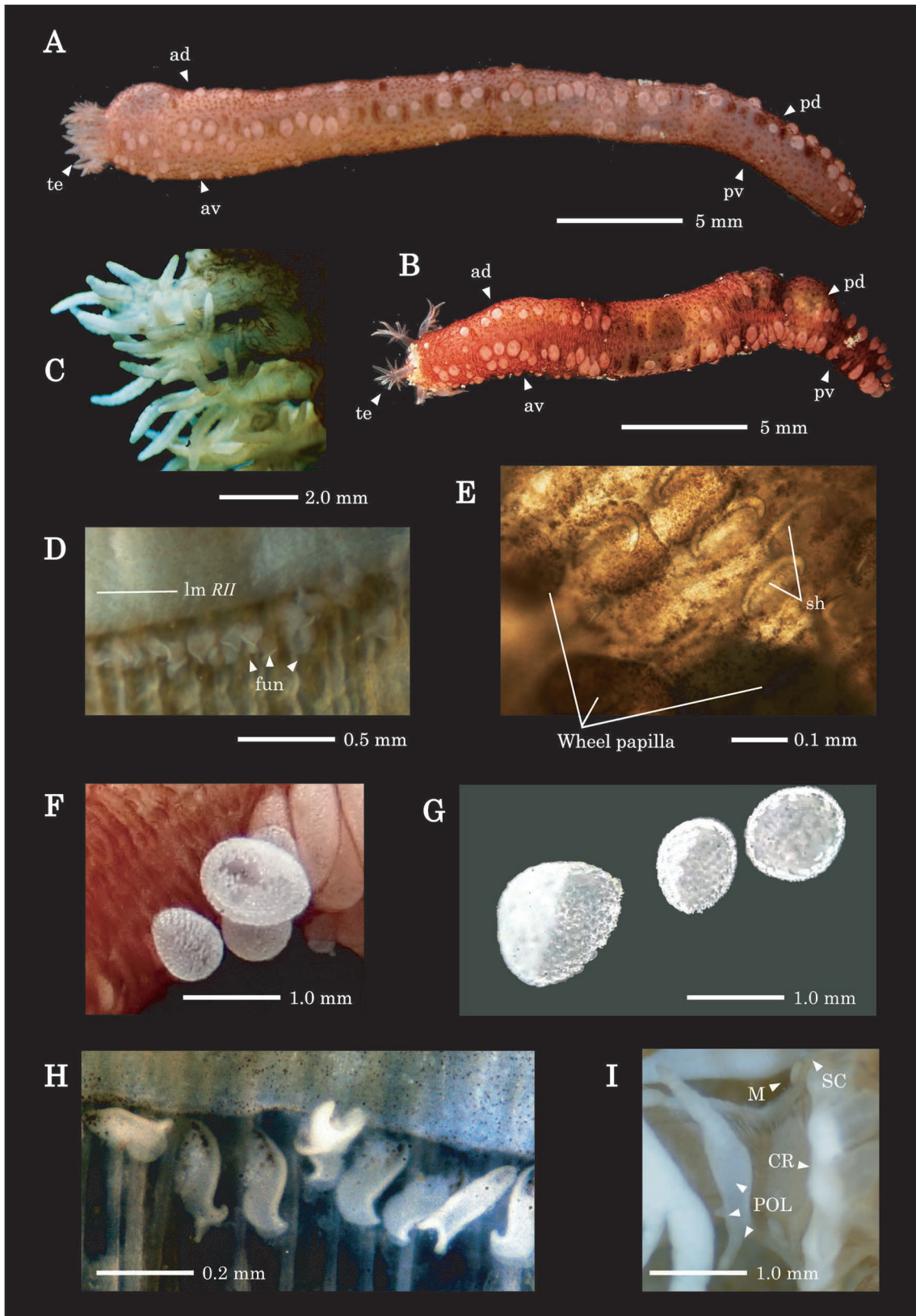


Fig. 7. External and internal morphologies of *Taeniogyrus rubrus* sp. nov. A–E: paratype (WMNH-INV-2020-33); F–I: paratype (WMNH-INV-2021-50). A, B, Dorsal views of preserved state with anaesthetization and active state without anaesthetization, respectively; C–E, microphotographs of tentacles of left side (viewed from oral disc) (C), ciliated funnels situated along with *lm RII* (D) (anterior left), and anterior dorsal skin containing ossicles (E); F–I, microphotographs of discharging phase of wheel-papillae (F), discharged wheel-papillae (G), ciliated funnels (H), right internal view of preserved states (I) (anterior right). Abbreviations: ad, anterior dorsal; av, anterior ventral; CR: calcareous ring; fun: ciliated funnels; *lm*: longitudinal muscle; M: madreporite; pd, posterior dorsal; POL: Polian vesicle; pv, posterior ventral; SC: stone canal; sh, sigmoid-hook ossicle; te, tentacle.

Table 6. Measurements of body size, counts of tentacles and Polian vesicles, and gonad type for type specimens of *Taeniogyrus rubrus* sp. nov.

Registration No. of WMNH-INV-	Type status	Body size (mm)		Counts			Gonad type
		Length	Width	Tentacles	Tentacle digits	Polian vesicles	
2019-299	Holotype	34.2	3.5	10	8–10	2	testis
2020-29	Paratype	23.7	2.2	10	6–9	3	ovary
2020-33	Paratype	33.2	3.2	10	6–9	2	ovary
2021-49	Paratype	19.7	2.0	10	8–10	1	ovary
2021-50	Paratype	30.4	2.7	10	8–10	2	ovary
2021-51	Paratype	24.5	2.3	10	6–9	1	ovary
2021-52	Paratype	37.1	2.2	10	8–10	2	immature
2021-53	Paratype	28.5	2.6	10	7–10	1	ovary

WMNH-INV: Invertebrate Collection of the Wakayama Prefectural Museum of Natural History.

body, over left dorsal longitudinal muscle *RIV* in middle body, straight in *IR3* along under side of *RIV*, no refraction until end of body, turning to anterior side about 1/5 of posterior body, then returning straight to the end in *IR3* along upper side of *RII*. Ovaries or testis in two tubules in middle body, tubules branched in basal part, two tubules present on both sides.

Calcereous ring with 5 thick radial, 5 thick inter-radial plates; distally flattened ends (Fig. 8A); except *IR5* all with shallow posterior depression and anterior projection, *IR1* and *IR2* with a blunt projection. *IR3* and *IR4* with a sharp projection, and low trapezoid anterior projection with slight central notch in *RI*, and low triangle anterior projection in *IR5* (Fig. 8E, F).

Body-wall thick (more than 1.5 mm in thickness), containing wheel and sigmoid-hook ossicles (Fig. 8A–D; Table 7). Wheel ossicles in dorsal skin present in wheel-papillae, only lined in 3 dorsal inter-radial body walls, range from tentacle base to posterior end (Fig. 7; Table 7). Wheel ossicles small, diameter less than 100 µm (mean 52–68 µm) (Table 4). Wheel ossicles larger in posterior body than anterior body (Table 4). Wheel ossicles rounded-hexagonal, 6 thick spokes; narrow rim, inner rim margin approximately parallel to outer margin. Teeth sharp and massive (5 µm in height in a wheel of 45 µm diameter), 7–15 per inter-spoke area (Table 7). Spokes widen, widest prior to rim, breadth 17–27% of wheel ossicle diameters (Fig. 8C; Table 7). Wheel ossicles small, means 56 µm and 60 µm in anterior and posterior dorsal, respectively (Table 7).

Sigmoid-hook ossicles in body wall scattered in inter-radii from anterior to posterior; both sides of longitudinal muscles, pointed end toward inter-radius, open-loop end toward longitudinal muscles (Fig. 7E), except tentacles and oral disk. Sigmoid-hook ossicles large, all the hooks exceed 130 µm (Fig. 8D; Table 7); thickened, smooth; shank breadths exceed 10–20 µm (Table 7), pointed end sharpened, no minute tooth or gap on surface (Fig. 8D).

Tentacles contain rod ossicles (Fig. 8B; Table 7); mostly bifurcate distally, first branches usually 4 or 5, second and third branches developed; distal ends spinous. Rod ossicle length 45–69 µm, rod breadth 3–10 µm in stem central.

Variation including paratypes. Largest paratype specimen (WMNH-INV-2021-52) length 37.1 mm (after preservation) (Table 6). Body color (living and preserved speci-

mens) red or reddish brown with dark yellowish spots of wheel-papillae locally observed on dorsal inter-radii skin (Fig. 7A, B). In the holotype with 2 Polian vesicles, but 1–3 Polian vesicles in seven paratypes (Table 6). In individuals with single Polian vesicle, vesicle shaped fusiform (width about 1/4 of length), and in types with 2 or 3 Polian vesicles, vesicles shaped globular. Wheel teeth, 7–18 per radiant (individual means 9–14 in measured three type specimens). Spoke breadth 21–23% of wheel ossicle diameters (Fig. 8C; Table 7). Wheel ossicles are small and all the diameter less than 100 µm (individual means 52–68 µm in measured three type specimens) (Table 7). Wheel ossicles larger in posterior body than anterior body, and significantly different (Kruskal–Wallis test, $P < 0.05$) in one of large specimens (WMNH-INV-2020-33) (Table 7). However, diameters in anterior and posterior parts are not significantly different in holotype (Kruskal–Wallis test, $P > 0.05$). Wheel-papillae easily discharged to outside by stimulus and become hemispherical sucks (Fig. 7F, G). Sigmoid-hook large, all the hooks exceed 100 µm (individual means 132–148 µm in measured three type specimens) in the present type series (Fig. 8D; Table 7). Sigmoid-hook length significantly different among all measured specimens in anterior ventral, anterior dorsal, and posterior ventral body parts (Kruskal–Wallis test, $P_s < 0.05$), not significantly different in posterior dorsal part or between anterior and posterior parts in all measured specimens (Kruskal–Wallis test, $P_s > 0.05$). Tentacle rod 56–101 µm in length (means 59–78 µm in different specimens); rod breadth 3–10 µm in stem central; ossicle length independent of body size (Tables 6, 7).

Remarks. As noted above, *Taeniogyrus* species with wheel-papillae, presently seven *Taeniogyrus* species and one new species *T. flavus* which described above, have been reported (Table 5). Among these congeners, *T. yvonnae* possess the arrangement of two rows of ciliated funnels which agrees with that of *T. rubrus* sp. nov. However, *T. yvonnae* also possess huge hook ossicles mostly exceed 300 µm (Table 5). Thus, *T. flavus* sp. nov. is distinguishable from these congeners and described above by the arrangement of two rows of ciliated funnels and its body color (Table 5). Additionally, *T. rubrus* sp. nov. has shown a habit of discharging wheel-papillae, which have been reported in partial congeners of Chiridotidae (Kubota and Inada 2003; Yamana and Tanaka 2017b); but, the adaptive significance of this habit

Table 7. Measurements (Mean \pm sd μ m) of ossicles from three specimens of *Taeniogyrus rubrus* sp. nov.

No. ^a	Skin ^b	n	Rod			n	Sigmoid-hook			n	Wheel ^d		
			Length	Breadth	DB ^c		Length	Breadth	Diameter ^e		Teeth ^f	Spoke width ^g	
2019-299	T	23	59 \pm 5.5	6.9 \pm 1.2	5.7 \pm 1.9	0				0			
	Range		45–69	4–9	3–10								
	AD	0				3	141 \pm 6.8	17.3 \pm 4.6	9	55.7 \pm 8.3	9.2 \pm 1.4	21.5 \pm 2.3	
	Range						136–149	12–20		43–68	7–11	18–25	
	PD	0				9	142 \pm 8.3	19.0 \pm 2.4	5	60.0 \pm 11.5	11.6 \pm 3.3	22.3 \pm 3.7	
	Range						131–152	15–22		48–74	8–15	17–27	
	AV	0				5	138 \pm 3.6	14.4 \pm 2.4	0				
	Range						133–142	12–17					
PV	0				4	148 \pm 9.1	20.5 \pm 1.7	0					
Range						140–160	19–23						
2020-29	T	41	78.1 \pm 12	7.5 \pm 2.5	7.1 \pm 1.3	0				0			
	Range		57–100	3–13	5–10								
	AD	0				11	137.4 \pm 6.6	19.8 \pm 1.7	18	51.5 \pm 3.0	10.3 \pm 2.3	20.7 \pm 2.8	
	Range						129–153	18–22		47–59	7–15	16–26	
	PD	0				7	136.1 \pm 14	18.9 \pm 2.1	12	59.2 \pm 4.6	12.3 \pm 1.3	23.2 \pm 3.1	
	Range						115–152	16–21		53–66	11–15	16–27	
	AV	0				6	135.8 \pm 3.9	19.2 \pm 0.8	0				
	Range						130–141	18–20					
PV	0				12	131.5 \pm 12	18.4 \pm 2.1	0					
Range						104–151	15–23						
2020-33	T	23	67.4 \pm 12	4.8 \pm 0.9	4.6 \pm 0.8	0				0			
	Range		56–101	3–7	4–6								
	AD	0				15	146.5 \pm 7.2	17.3 \pm 4.6	22	59.2 \pm 7.6	12.2 \pm 2.9	22.3 \pm 1.8	
	Range						134–158	12–20		35–70	8–17	20–26	
	PD	0				20	142.1 \pm 8.3	19.0 \pm 2.4	22	68.1 \pm 6.9	13.5 \pm 2.7	21.8 \pm 1.9	
	Range						131–152	15–22		56–84	9–18	18–25	
	AV	0				19	142.2 \pm 5.1	21.9 \pm 1.8	0				
	Range						132–151	17–25					
PV	0				27	135.5 \pm 8.8	19.0 \pm 1.8	0					
Range						112–152	14–23						

^a Registration No. of WMNH-INV: Invertebrate Collection of the Wakayama Prefectural Museum of Natural History. ^b Body skin: T, tentacle; AD, anterior dorsal; PD, posterior dorsal; AV, anterior ventral; PV, posterior ventral. ^c Total number of the distal branches were counted. ^d Only wheels with six spokes were measured. ^e Values were measured across opposite vertices of a hexagon. ^f Values were counted for individual radians of a hexagon. ^g Values are reported as the percentage of spoke breadth in a diameter.

has not been revealed to date. One paratype of this species was found by one of the present authors (Ichinosuke Dan), of the 6th grade student at Kobe-Shimohatadai Elementary School (as at August 2020), during the nature observation meeting held by WMNH and Susami Crustacean Aquarium. At first, it was misidentified as *Chiridota rigida* Semper, 1867, which was recently reported from the same site of the Cape Yesu-zaki as new to Japan (Yamana and Tanaka 2017b). After that, it was also turned out that the holotype specimen had been misidentified as *C. rigida* too. Although there is a striking resemblance in their external appearances, the anatomical characteristics are obviously different between *C. rigida* and *T. rubrus* sp. nov.: the ciliated funnels are situated along the mid-dorsal and left lateral mesentery in *C. rigida*, moreover *C. rigida* has 12 tentacles (see Yamana and Tanaka 2017b).

Distribution. Known only from two type localities, in the sandy-gravel sediment at Cape Yesu-zaki (lower intertidal zone) and Kushimoto (5–13 m deep) (where, the speci-

men numbers were larger than that of Yesu-zaki, but this was not reflected the actual circumstances because of a new law named “Revised Fisheries Act” was enforced from 1 December 2020, which made all the holothurians in Japanese waters must not be able to catch, with an exception of the area Kushimoto, where we applied for a license), Wakayama, southern end of the mainland of Japan.

Etymology. The specific name is derived from the Latin adjective *rubrus* (meaning red), based on its body color.

DNA barcode sequences. Two specimens of sequence of the mitochondrial *COI* gene, 615bps and 622bps were obtained from the holotype (WMNH-INV-2019-299: INSD accession number LC655785, base frequency A=21.0%, C=13.8%, G=20.3%, T=44.9%) and a paratype specimen (WMNH-INV-2020-29: LC655786, base frequency A=21.1%, C=13.7%, G=20.6%, T=44.7%), respectively. In BLAST searches, the closest hits to the partial *COI* sequence are from *Chiridota albatrossii* Edwards, 1907 (KX874398 and KX874397, with 84.9–85.1% similarity in 98–100% cov-

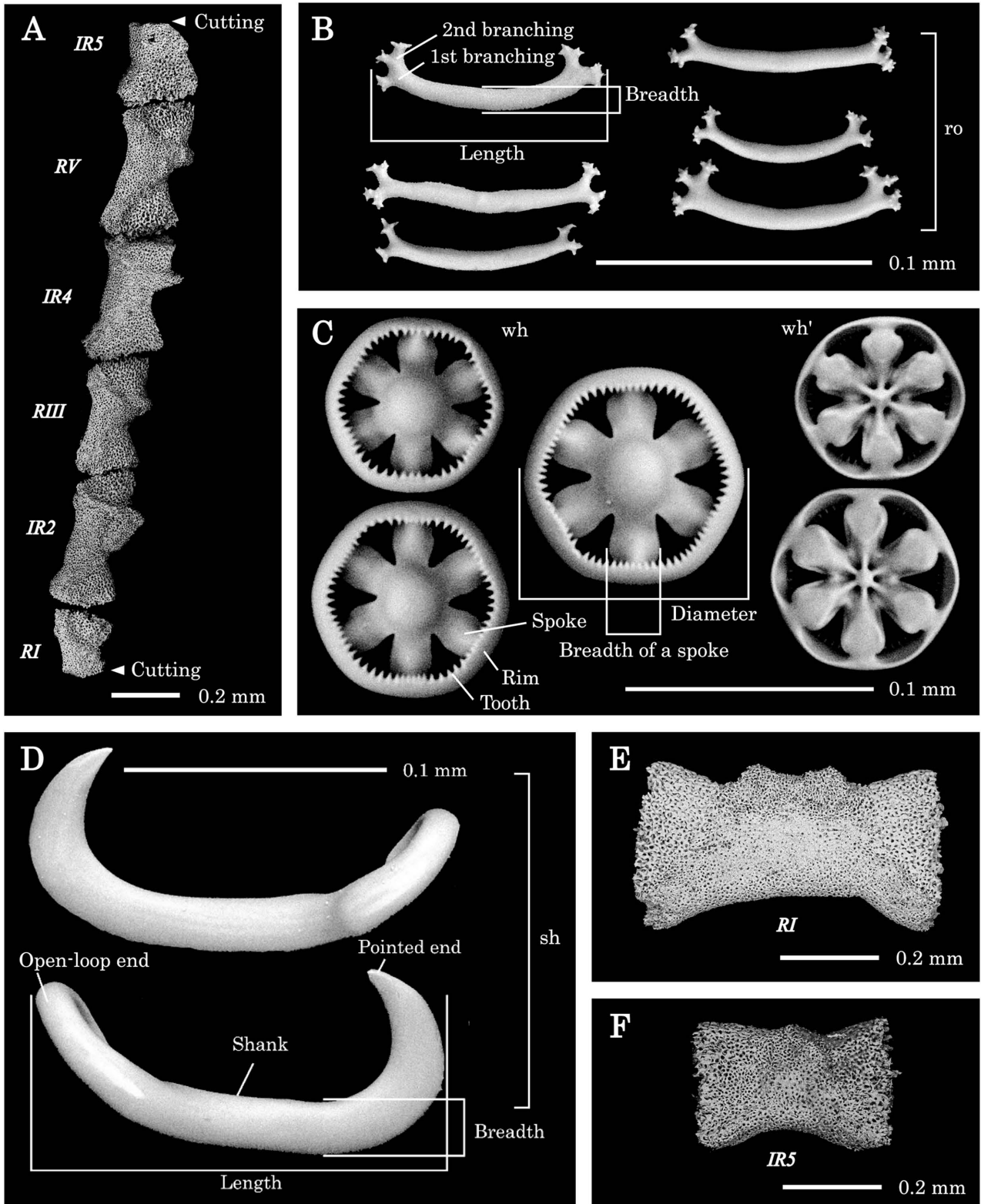


Fig. 8. SEM image of calcareous ring parts and body ossicles of *Taeniogyrus rubrus* sp. nov. A–D: holotype (WMNH-INV-2019-299); E, F: paratype (WMNH-INV-2021-50). A, Right parts of calcareous ring (viewed from right side, dorsal upper); B–D, rod ossicles from a lateral tentacle (B), wheel ossicles from a wheel papilla of anterior dorsal skin (C), and sigmoid-hook ossicles from anterior dorsal skin (D); E, F, calcareous plates of medioventral *RI* (E) and mediodorsal *IR5* (F) (anterior upper). Abbreviations: ro, rod ossicles; sh, sigmoid-hook ossicles; wh, wheel ossicles; wh', internal side of wheel ossicles.

erage) and *Taeniogyrus verruculosus* (LC203483, with 84.1–84.33% similarity in 99 or 100% coverage). The results of BLAST searches shows that there is a great genetic diversity in present genus. It is suggested that the genus *Taeniogyrus* containing large diversity both genetically and morphologically, requires for comprehensive taxonomic revision involving the other apodid holothurians in the future.

Discussion

In Japan, six species of *Taeniogyrus* have been reported to date: *T. cidaridis* from the Goto Islands, at a depth of 55 fathoms (101 m) off Sagami Bay and 120 fathoms (220 m) in the Uraga Strait (Ohshima 1914, 1915); *T. japonicus* from the shallow water of Sagami Bay (Marenzeller 1882; Ohshima 1914); *T. mijim* from the intertidal and subtidal areas at several sites in southern Japan (Yamana et al. 2017); *T. misakiensis* (Ohshima, 1919) (see Yamana et al. 2017) at a depth of 60 fathoms (110 m) off Sagami Bay (Ohshima 1914, 1919); *T. roseus* (Ohshima, 1914) from the shallow water of Okinawa (Ohshima 1914); and *T. verruculosus* from the intertidal shore of Wakayama (Yamana and Tanaka 2017a). None of these agreed morphologically with the present three new species *T. albulus* sp. nov., *T. flavus* sp. nov., and *T. rubrus* sp. nov. (Table 3).

In the present study, three new species were described from a small area that included three localities (Shirahama, Susami, and Kushimoto) at a distance approximately 20 km apart (Fig. 1). In a previous study (Yamana et al. 2017; Yamana and Tanaka 2017a), two new species were described from an adjacent locality (Tanabe) only 10 km away from the Shirahama locality (Fig. 1). Thus, we infer that the diversity of the infaunal *Taeniogyrus* species has been underestimated in Japanese waters, and future studies are required.

Key to Japanese species of *Taeniogyrus*

1. Wheel-papillae present, but hook-papillae absent 2
 - Neither hook-papillae nor wheel-papillae lacking 3
 - Hook papillae present, but wheel papillae absent
 - *T. japonicus*
2. Body color white, Polian vesicle single *T. cidaridis*
 - Body color pale yellow, Polian vesicles 1–3, ciliated funnels present *T. flavus* sp. nov.
 - Body color red or reddish brown, Polian vesicles 2–3
 - *T. rubrus* sp. nov.
3. Head brown, live body pink, fixed body yellowish white *T. albulus* sp. nov.
 - Body color white to pink, tentacle digits only one pair
 - *T. mijim*
 - Body color red, tentacle digits three pairs *T. roseus*
 - Body white, covered with numerous minute papillae, hooks small (<75 µm) *T. verruculosus*

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