

Fourteen New Species of Dicyemids (Phylum: Dicyemida) from Seven Species of Decapodiformes (Mollusca: Cephalopoda) in the Kumano Sea, Japan

Hidetaka Furuya^{1,3} and Takeya Moritaki²

¹ Department of Biology, Graduate School of Science, Osaka University, 1-1 Machikaneyama, Toyonaka, Osaka 560-0043, Japan
E-mail: hfuruya@bio.sci.osaka-u.ac.jp

² Marine Biological Laboratory, Toba Aquarium, 3-3-6 Toba, Toba, Mie 517-8517, Japan
E-mail: moritaki@aquarium.co.jp

³ Corresponding author

(Received 28 October 2021; Accepted 29 March 2022)

<http://zoobank.org/03A070DC-A02C-4FF8-A00D-FD59C7614189>

Fourteen new species of dicyemid mesozoans are described from six sepiid species (Mollusca: Cephalopoda: Sepiida) and a sepiolid species (Mollusca: Cephalopoda: Sepiolida) collected in the Kumano Sea, off the Kii Peninsula, Pacific coast of Honshu, Japan: *Dicyema bacterocephalum* sp. nov., *Dicyema gozaense* sp. nov., and *Pseudicyema anemophilum* sp. nov. from *Sepia koiensis* Hoyle, 1855; *Dicyema conocephalum* sp. nov. and *Dicyema tenuipoeceum* sp. nov. from *Sepia tenuipes* Sasaki, 1929; *Dicyema hyalocephalum* sp. nov. from *Austrosquilla bipapillata* (Sasaki, 1920); *Dicyema lorigeroeceum* sp. nov., *Dicyema tympanocephalum* sp. nov., and *Pseudicyema cuplacephalum* sp. nov. from *Sepia lorigera* Wülker, 1910; *Dicyema miense* sp. nov. and *Pseudicyema jinshoae* sp. nov. from *Sepia subtenuipes* Okutani and Horikawa, 1987; *Pseudicyema daioense* sp. nov. from *Sepia aureomaculata* Okutani and Horikawa, 1987; *Dicyema shimaense* sp. nov. and *Pseudicyema physocaudatum* sp. nov. from *Sepia madokai* Adam, 1939. The dicyemid fauna and their cooccurrence patterns of species are briefly discussed in relation to possible interaction of chromidinid ciliates.

Key Words: cephalopods, chromidinids, dicyemids, host specificity, cuttlefish, renal organ, parasites.

Introduction

Dicyemid mesozoans, Phylum Dicyemida, are the commonest and most characteristic endosymbionts in the renal sac of benthic cephalopod molluscs. The renal organs of cephalopods are composed of the renal complex (renal and pancreatic appendages) and the branchial heart complex (branchial heart and pericardial appendage). Prior to release, urine accumulates in a renal sac, the fluid-filled lumen of which is a unique environment providing living space for a diversity of endosymbionts (Hochberg 1982; Furuya et al. 2004).

To date, 135 dicyemid species have been described from cephalopod hosts distributed in a variety of geographical localities: the Okhotsk Sea, the Sea of Japan, western and eastern North Pacific Ocean, South Pacific Ocean, North Indian Ocean, the Mediterranean Sea, western and eastern North Atlantic Ocean, the Gulf of Mexico, and the Antarctic Ocean (Nouvel 1947; McConnaughey 1951; Hochberg 1990; Short 1991; Furuya 1999, 2018; Furuya and Tsuneki 2003; Catalano 2013; Castellanos-Martinez et al. 2016). Of more than 50 species recognized from 27 cephalopod hosts in Japanese waters, 50 nominal species have been described in just 18 hosts (Furuya 2016). Typically, two or three dicyemid species are found in a single specimen of the host, and most of them show high host specificity (Furuya 1999,

2018).

In the present paper, fourteen new dicyemid species are described based on specimens found in the renal sacs of six sepiid species and a sepiolid species from the Kumano Sea, off the Pacific coast. Findings of all fourteen species represent the first records of dicyemids in these host species.

Materials and Methods

A total of 228 specimens of sepiids and sepiolids

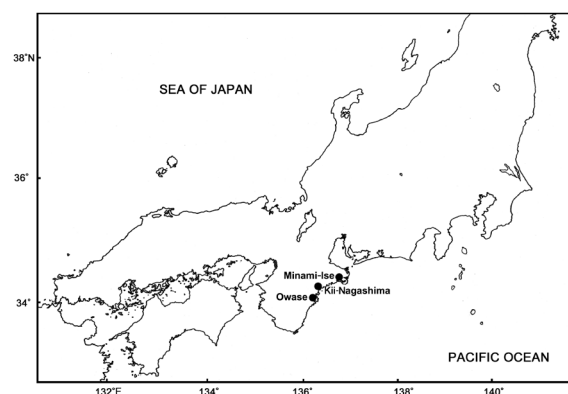


Fig. 1. Collection localities of host species obtained for this study (see Table 1 for the species of hosts and dicyemids in each locality).

Table 1. Prevalence of chrominid ciliates and dicyemid species.

Cephalopod species	Locality	Prevalence of chrominid ciliates	Prevalence of dicyemid species
<i>Austrorossia bipapillata</i>	Minamiise, Mie	None (0/42)	<i>Dicyema hyalocephalum</i> sp. nov. 100% (42/42)
<i>Sepia aureomaculata</i>	Minamiise, Mie	<i>Chromidina</i> sp. A 100% (5/5)	<i>Pseudicyema daioense</i> sp. nov. 80% (4/5)
<i>S. kobeensis</i>	Minamiise and Owase, Mie	<i>Chromidina</i> sp. B 76.7% (23/30)	<i>D. bacterocephalum</i> sp. nov. 3.3% (1/30) <i>D. gozaense</i> sp. nov. 73.3% (22/30) <i>P. anemophilum</i> sp. nov. 23.3% (7/30)
<i>S. lorigera</i>	Minamiise, Mie	<i>Chromidina</i> sp. C 100% (10/10)	<i>D. lorigeroeceum</i> sp. nov. 100% (10/10) <i>D. tympanocephalum</i> sp. nov. 10% (1/10) <i>P. cuplacephalum</i> sp. nov. 33% (3/10)
<i>S. madokai</i>	Minamiise and Owase, Mie	<i>Chromidina</i> sp. D 9.5% (2/21)	<i>D. shimaense</i> sp. nov. 23.8% (5/21) <i>P. physocaudatum</i> sp. nov. 9.5% (2/21)
<i>S. subtenuipes</i>	Kiinagashima, Mie	<i>Chromidina</i> sp. E 83.3% (25/30)	<i>D. miense</i> sp. nov. 63.3% (19/30) <i>P. jinshoae</i> sp. nov. 26.7% (8/30)
<i>S. tenuipes</i>	Minamiise, Mie	<i>Chromidina</i> sp. F 93.4% (85/91)	<i>D. conocephalum</i> sp. nov. 30.8% (28/91) <i>D. tenuipoeceum</i> sp. nov. 39.6% (36/91)

[*Austrorossia bipapillata* (Sasaki, 1920), *Sepia aureomaculata* Okutani and Horikawa, 1987, *S. kobeensis* Hoyle, 1885, *S. lorigera* Wülker, 1910, *S. madokai* Adam, 1939, *S. subtenuipes* Okutani and Horikawa, 1987, and *S. tenuipes* Sasaki, 1929] were examined for dicyemids during 2013 to 2021 (Table 1). Host specimens were collected by the fisherman in the Kumano Sea (off Minami-Ise, Kii-Nagashima, and Owase, Mie Pref.; Fig. 1). Host specimens were identified based on the morphological characters (Sasaki 1929) and comparison of mitochondrial cytochrome *c* oxidase subunit I (H. Nakajima, unpublished data).

Small pieces of the renal organ with attached dicyemids were removed and smeared on glass microscope slides. The smears were fixed immediately in Bouin's solution for 24 h and then stored in 70% ethanol. Most were later stained in Ehrlich's hematoxylin and counterstained with eosin. Stained smears were mounted in Entellan (Merck, Darmstadt, Germany). Dicyemids were observed using a light microscope (Olympus BH-2, Tokyo, Japan) at magnifications up to 2000 \times . Measurements and drawings were made with the aid of an ocular micrometer and a drawing tube (Olympus U-DA, Tokyo, Japan), respectively. In general, body lengths of dicyemids are classified as: the small (<1000 μ m), medium (1000–2500 μ m), and large-sized species (>2500 μ m).

The calotte shape is not only the major character for identification of dicyemid species, but it also represents the mode of inhabiting the renal appendage. In general, four basic types of calotte shape are recognized. Dicyemids with conical calottes (Type I) insert the anterior region of the body into crypts or folds in the renal appendages; those with cap-shaped (Type II) or disc-shaped calottes (Type III) attach to the broad, flat or gently rounded surfaces of the renal appendages; and dicyemids with irregular shaped bodies and calottes (Type IV) occur when more than three species coexist (Furuya et al. 2003a).

The terminology for cell names used in the description of infusoriform larvae follows those of Nouvel (1948), Short and Damian (1966), Furuya et al. (1992a, 1997), and Furuya

(1999). Abbreviations used in figures and tables are as follows: A, apical cell; AG, agamete (axoblast); AL, anterior lateral cell; AN, axial cell nucleus; AX, axial cell; C, couvercle cell; CA, capsule cell; CL, calotte; D, diapolar cell; DC, dorsal caudal cell; DI, dorsal internal cell; DV, developing vermiform embryo; E, enveloping cell; F, fertilized egg; G, germinal cell; I, infusorigen; IF, infusoriform embryo; L, lateral cell; LC, lateral caudal cell; M, metapolar cell; MD, median dorsal cell; NI, nucleus of infusorigen; O, oogonium; P, propolar cell; PA, parapolar cell; PD, paired dorsal cell; PO, primary oocyte; PVL, posteroventral lateral cell; R, refringent body; S, spermatogonium; SP, sperm; SS, secondary spermatocyte; U, urn cell; UC, urn cavity; UP, uropolar cell; V, vermiform embryo; VC, ventral caudal cell; VI, ventral internal cell; V1, first ventral cell; V2, second ventral cell; V3, third ventral cell.

Dicyemid specimens on single slides are deposited in the mesozoan collection (Me) of the National Museum of Nature and Science, Tsukuba (NSMT), Japan, and there are others in the first author's collection. The symbiotypes of the cuttlefish and sepiolids (host specimens) are deposited in the molluscan collection (Mo) of NSMT.

Results

Systematics

Family **Dicyemidae** van Beneden, 1882

Genus **Dicyema** von K  lliker, 1849

Dicyema bacterocephalum Furuya, sp. nov.

[New Japanese name: Marub  -nihaich  ]

(Figs 2, 3; Tables 1–3)

Diagnosis. Small sized dicyemid, body length reaching 1120 μ m. Calotte cap- or disc-shaped. Vermiform stages with 20, 22 peripheral cells: 4 propolar cells+4 metapolar cells+2 parapolar cells+10 or 12 trunk cells. Infusoriform

Table 2. Number of peripheral cells of 14 new species of dicyemids.

Dicyemids	Cell number	Number of nematogens	Number of vermiform embryos	Number of rhombogens
<i>Dicyema bacterocephalum</i> (n=30)	20	10	5	2
	21	0	0	0
	22	15	4	1
	28	7	7	5
<i>D. conocephalum</i> (n=56)	29	4	5	4
	30	5	6	2
	31	3	4	1
	32	1	1	1
<i>D. gozaense</i> (n=55)	26	1	2	1
	27	1	1	1
	28	5	5	2
	29	7	5	3
	30	5	4	2
	31	3	5	1
<i>D. hyalocephalum</i> (n=60)	22	20	20	20
<i>D. lorigeroeum</i> (n=60)	23	2	2	1
	24	2	1	1
	25	3	1	2
	26	4	3	3
	27	2	2	4
	28	8	6	4
	29	3	3	1
	30	1	1	0
<i>D. miense</i> (n=77)	26	4	3	3
	27	2	2	3
	28	5	4	4
	29	3	2	2
	30	4	4	4
	31	5	3	1
	32	3	4	2
	33	3	2	1
	34	3	2	1
<i>D. shimaense</i> (n=102)	28	22	14	12
	29	4	5	8
	30	18	11	8
<i>D. tenuipoeum</i> (n=50)	22	20	20	5
<i>D. tympanocephalum</i> (n=90)	22	50	20	20
<i>Pseudicyema anemophilum</i> (n=41)	29	6	1	1
	30	7	2	1
	31	5	3	1
	32	3	2	1
	33	3	1	0
	34	1	1	1
<i>P. cuplacephalum</i> (n=53)	29	1	1	2
	30	2	1	1
	31	3	3	2
	32	3	3	3
	33	5	5	5
	34	3	2	2
	35	2	2	1
<i>P. daioense</i> (n=63)	29	2	2	2
	30	4	2	3
	31	10	5	3
	32	9	2	2
	33	6	1	1
	34	4	1	1
	35	1	1	1
<i>P. jinshoae</i> (n=73)	30	7	3	3
	31	5	2	3
	32	12	5	6
	33	6	1	2
	34	8	3	3
	35	2	1	1
<i>P. physocaudatum</i> (n=61)	31	3	2	2
	32	6	4	2
	33	11	7	4
	34	8	6	3
	35	7	5	3

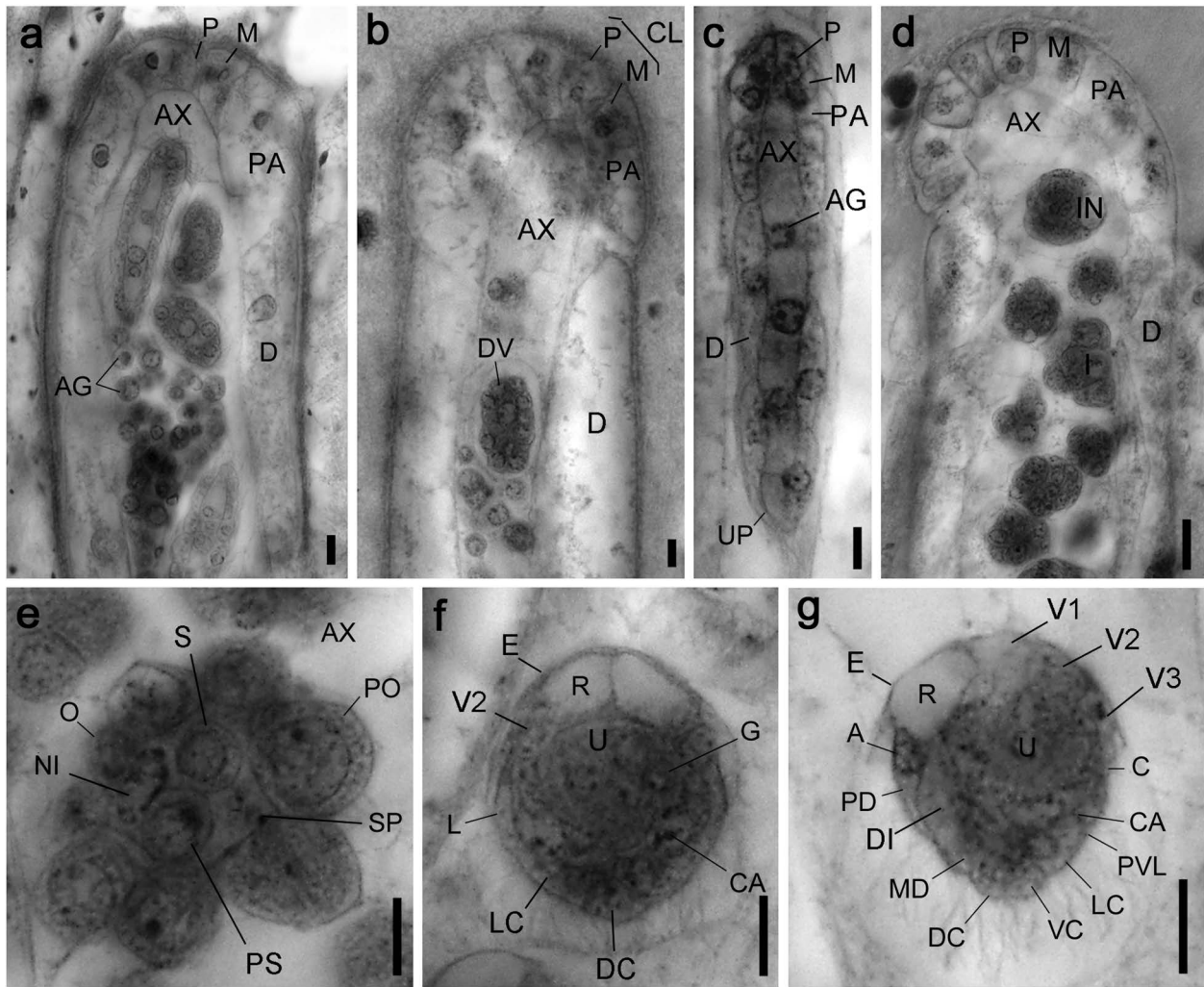


Fig. 2. *Dicyema bacterocephalum* sp. nov., photographs of syntype specimens on slide NSMT-Me-58: a, b, Nematogen, anterior region; c, vermiform embryo within axial cell; d, rhombogen, anterior region; e, infusorigen; f, g, infusoriform embryos, horizontal section (f), sagittal section (g). Scale bars: 10 µm.

embryos with 37 cells; refringent bodies solid; and 2 nuclei present in each urn cell.

Description. *Nematogens* (Figs 2a–d, 3a, c–e). Body length 510–1110 µm, width 60–75 µm; widest in region of parapolar cells; trunk width mostly uniform. Peripheral cell number 20 or 22 (Table 2): 4 propolar cells+4 metapolar cells+2 parapolar cells+8 or 10 diapolar cells+2 uropolar cells. Calotte cap- or disc-shaped, rounded anteriorly; cilia about 4 µm long, oriented anteriorly. Propolar cells equal or larger than metapolar cells, their nuclei equal to or smaller than metapolar cell nuclei. Propolar cells occupy anterior 30–40% of calotte length when viewed laterally (Fig. 2a, b). Cytoplasm of propolar cells more darkly stained by hematoxylin than that of other peripheral cells (Fig. 2a, b). Axial cell cylindrical, pointed anteriorly, extending forward to the base of propolar cells (Fig. 2a, b). About 19 vermiform embryos present per axial cell of large individuals. Accessory nuclei seen in trunk peripheral cells.

Vermiform embryos (Figs 2c, 3d, e). Full-grown vermiform embryos length 47–72 µm, and 17–20 µm in width. Peripheral cell number 20 or 22 (Table 2); trunk cells arranged in

opposed pairs. Anterior end of calotte rounded. Axial cell rounded anteriorly, extending to the base of propolar cells (Figs 2c, 3e). Axial cell of full-grown embryos with 2 agametes.

Rhombogens (Figs 2d, 3f, g). Body similar in length to nematogens, 750–1120 µm in length and 45–120 µm in width. Peripheral cell number typically 20 or 22 (Table 2). Calotte, axial cell shape and anterior extent similar to nematogens. A maximum of 9, usually 3–5 infusorigens present in the axial cell of each parent individual. About 70 infusoriform embryos present per axial cell of large individuals.

Infusorigens (Figs 2e, 3h; n=10). Mature infusorigens medium-sized; composed of 6–8 (mode 6) external cells (oogonia and primary oocytes)+3–4 (mode 3) internal cells (spermatogonia, primary spermatocytes, and secondary spermatocytes)+4–8 (mode 6) spermatozoa. Mean diameter of fertilized eggs 11.7 µm; that of spermatozoa 2.2 µm. Axial cell round or ovoid, diameter 11–12 µm.

Infusoriform embryos (Figs 2f, g, 3i–k; n=10). Full-grown embryos large, length 26.8 ± 1.8 µm (mean \pm SD, excluding cilia); length–width–height ratio 1.0:0.81:0.73; shape ovoid,

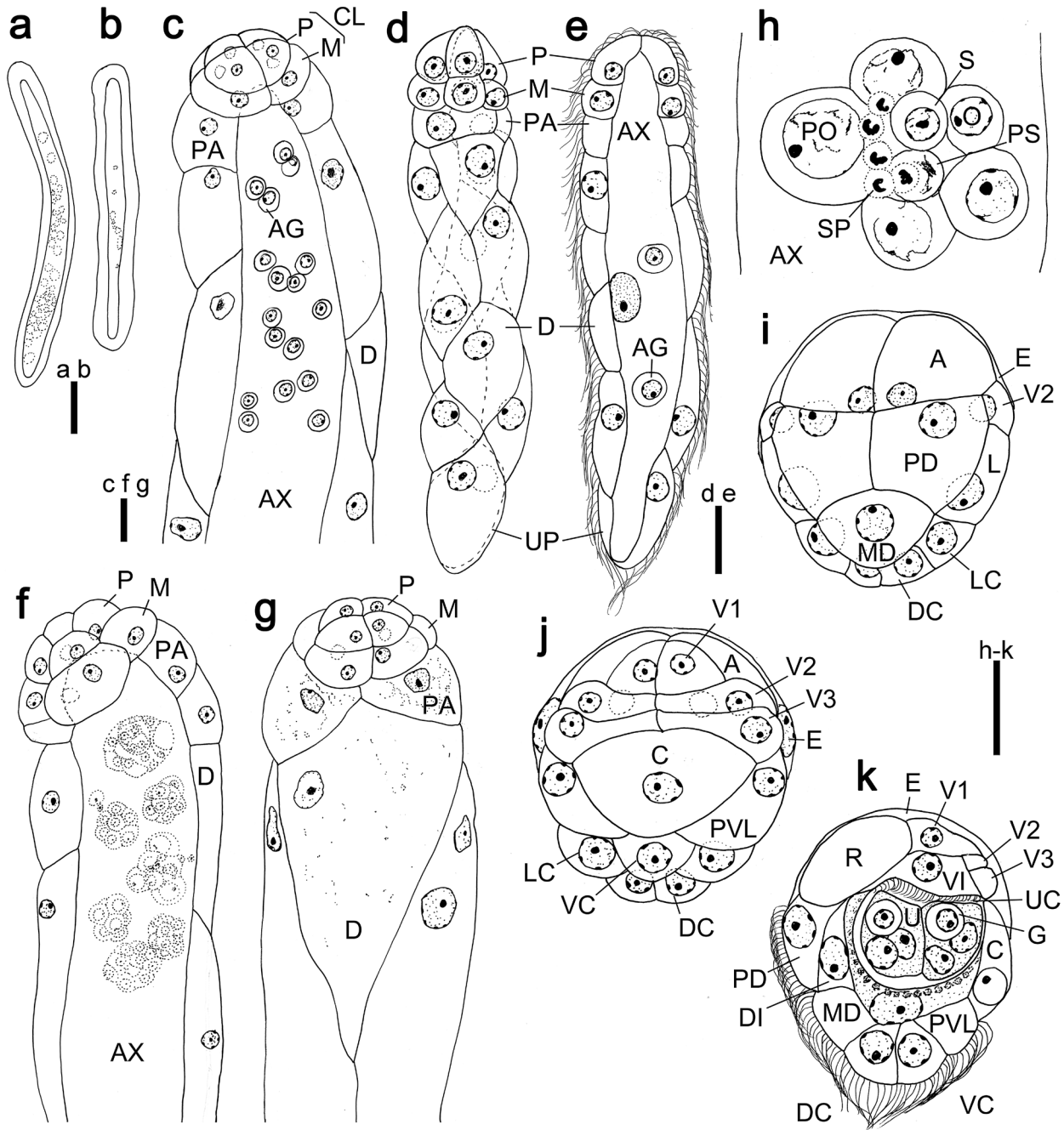


Fig. 3. *Dicyema bacterocephalum* sp. nov., drawn from syntype specimens on slide NSMT-Me-58: a, Nematogen, entire; b, rhombogen, entire; c, nematogen, anterior region; d, e, vermiform embryo within axial cell, cilia omitted (f, d), optical section (e); f, g, rhombogen, anterior region; h, infusorigen; i–k, infusoriform embryos, dorsal view (i: cilia omitted), ventral view (j: cilia omitted), sagittal section (k). Scale bars: a, b, 100 µm; c–k, 10 µm.

bluntly rounded and pointed posteriorly; cilia at posterior end 7 µm long. Refrangent bodies present, solid, occupying anterior 30–40% of embryo length when viewed laterally (Fig. 2g). Cilia project from ventral internal cells into urn cavity (Fig. 3k). Capsule cells contain small granules (Fig. 3k). Mature embryos with 37 cells: 33 somatic+4 germinal cells. Somatic cells of several types present: external cells covering large part of anterior and lateral surfaces of embryo (2 enveloping cells); external cells with cilia on external surfaces (2 pairs of dorsal cells+1 median dorsal cell+2 dorsal caudal cells+2 lateral caudal cells+1 ventral caudal

cell+2 lateral cells+2 posteroventral lateral cells), external cells with refrangent bodies (2 apical cells); external cells without cilia (1 couverte cell+2 first ventral cells+2 second ventral cells+2 third ventral cells); internal cells with cilia (2 ventral internal cells); and internal cells without cilia (2 dorsal internal cells+2 capsule cells+4 urn cells). Each urn cell contains 2 nuclei and germinal cell (Fig. 3k). All somatic nuclei pycnotic in mature infusoriform embryos.

Remarks. *Dicyema bacterocephalum* sp. nov. is the first species of the genus found in *Sepia kobeensis* and is similar to *D. balamuthi* McConnaughey, 1949, *D. clavatum* Furuya

Table 3. Three groups of new dicyemid species sharing some diagnostic characters.

<i>Sepia</i> species	Dicyemid species	Calotte type*	Shape of calotte tip in vermiform embryos	Peripheral cell number	Cell number of infusoriform embryos	Group*
<i>S. aureomaculata</i>	<i>P. daioense</i> sp. nov.	II	round	29–35	39	1
<i>S. kobeensis</i>	<i>D. bacterocephalum</i> sp. nov.	II or III	round	20, 22	37	3
	<i>D. gozaense</i> sp. nov.	I	acute	26–31	39	2
	<i>P. anemophilum</i> sp. nov.	II	round	29–34	39	1
	<i>D. oxycephalum</i>	I	acute	28–34	39	2
<i>S. longipes</i>	<i>P. cappacephalum</i> sp. nov.	II	round	32–34	39	1
<i>S. lorigera</i>	<i>D. lorigeroeceum</i> sp. nov.	I	acute	23–30	39	2
	<i>D. tympanocephalum</i> sp. nov.	III	round	22	37	3
	<i>P. cuplacephalum</i> sp. nov.	II	round	29–35	39	1
<i>S. madokai</i>	<i>D. shimaense</i> sp. nov.	I	acute	28–30	39	2
	<i>P. physocaudatum</i> sp. nov.	II	round	31–35	39	1
<i>S. subtenuipes</i>	<i>D. miense</i> sp. nov.	I	acute	26–34	39	2
	<i>P. jinshoae</i> sp. nov.	II	round	30–35	39	1
<i>S. tenuipes</i>	<i>D. conocephalum</i> sp. nov.	I	acute	28–32	37	2
	<i>D. tenuipoceum</i> sp. nov.	III	round	22	37	3

* Type I, conical; Type II, cap-shaped; Type III, disc-shaped. # See text for explanation.

and Koshida, 1992, *D. colurum* Furuya, 1999, *D. hadrum* Furuya, 1999, and *D. schulzianum* van Beneden, 1876 in the calotte shape of vermiform stages and peripheral cell numbers (Beneden 1876; McConnaughey 1949; Furuya et al. 1992b; Furuya 1999). However, *D. bacterocephalum* sp. nov. is distinguishable from *D. balamuthi*, *D. clavatum*, *D. colurum*, and *D. hadrum* in the cell number of infusoriform embryos (37 vs. 39). *Dicyema bacterocephalum* sp. nov. shares the cellular composition and cell number of infusoriform embryos with *D. schulzianum* but there is a marked difference in the number of peripheral cells; *D. bacterocephalum* sp. nov. has 20 or 22 peripheral cells, while *D. schulzianum* is consistently 22. Both individuals having 20 and 22 peripheral cells are found in a single axial cell in *D. bacterocephalum* sp. nov.

Etymology. The species name is an adjective composed of two Ancient Greek roots, *bact* and *-kephalos*, meaning “rod” and “-headed” in reference to the characteristic shape of the body of vermiform stages.

Taxonomic summary. *Type material:* a syntype slide (NSMT-Me-58) collected on 10 April 2016; additional syntypes on slide series No. SK3517 (5 slides) in the author's collection.

Type locality: off Minami-Ise (34°08'N, 136°40'E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 150 m.

Other materials examined: None.

Host: symbiotype, *Sepia kobeensis* Hoyle, 1855 (Mollusca: Cephalopoda: Sepiida), female (immature), 64 mm ML (NSMT-Mo-85901).

Collector of host: T. Moritaki.

Site: anterior ends (calottes) attach to surfaces of the renal appendages or inserted into crypts of the renal appendages within the renal sacs.

Prevalence: in 1 of 30 host specimens examined (3.3%).

Dicyema conocephalum Furuya, sp. nov.

[New Japanese name: Kono-nihaichū]

(Figs 4, 5; Tables 1–3)

Diagnosis. Medium-sized dicyemid; body length reaching 1540 µm. Calotte conical in shape. Vermiform stages with 28–32 peripheral cells: 4 propolar cells+4 metapolar cells+2 parapolar cells+18–22 trunk cells. Infusoriform embryos with 37 cells; refringent bodies solid; and two nuclei present in each urn cell.

Description. *Nematogens* (Figs 4a, b, 5a). Body length 700–1540 µm, width 45–60 µm; widest in region of parapolar cells; trunk width mostly uniform. Peripheral cell number 28–32 (Table 2): 4 propolar cells+4 metapolar cells+2 parapolar cells+16–20 diapolar cells+2 uropolar cells. Calotte conical in shape, rounded anteriorly; cilia on calotte about 4 µm long, oriented anteriorly. Propolar cells and their nuclei equal to or smaller than metapolar cells and their nuclei. Propolar cells occupy anterior 40–50% of calotte length when viewed laterally (Fig. 4a, b). Cytoplasm of propolar and parapolar cells contains fibrous structure, more darkly stained by hematoxylin than cytoplasm of other peripheral cells (Fig. 4a, b). Axial cell cylindrical, pointed anteriorly; cell extending forward to base of metapolar cells (Fig. 5a). About 30 vermiform embryos present per axial cell of large individuals. Accessory nuclei seen in trunk peripheral cells.

Vermiform embryos (Figs 4c, 5d, e). Full-grown vermiform embryos length 54–70 µm, width 13–15 µm. Peripheral cell number 28–32 (Table 2); trunk cells arranged in opposed pairs. Anterior end of calotte pointed acutely. Axial cell is pointed anteriorly, extending to the base of metapolar cells (Figs 4c, 5d, e). Axial cell of full-grown embryos with one agamete.

Rhombogens (Figs 4d, 5b, c). Body length 700–1100 µm, similar to that of nematogens, width 60–72 µm. Peripheral cell number typically 28–32 (Table 2). Calotte shape, axial cell shape, and anterior extent similar to those of nemato-

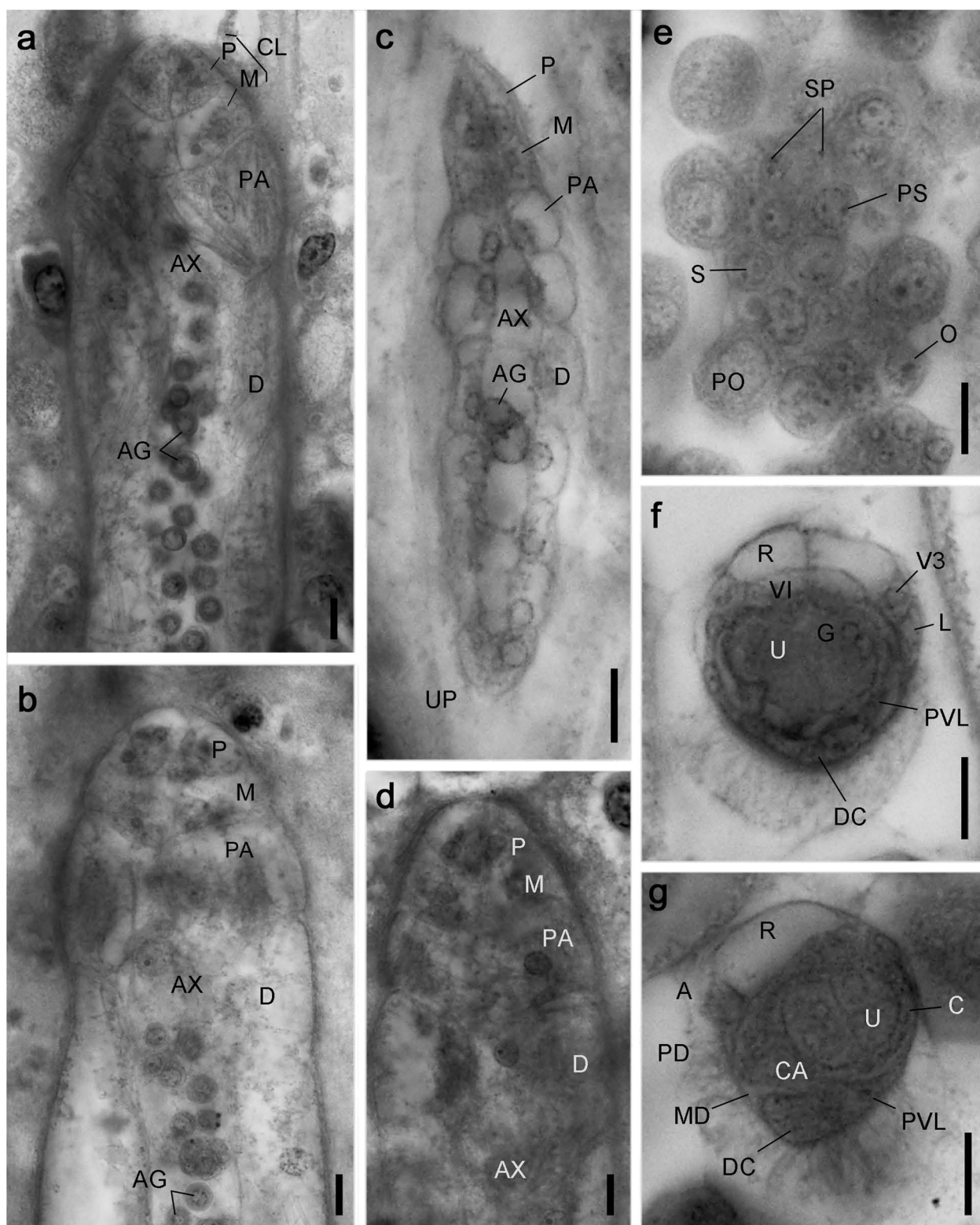


Fig. 4. *Dicyema conocephalum* sp. nov., photographs of syntype specimens on slide NSMT-Me-61: a, b, Nematogen, anterior region; c, vermiform embryo within axial cell; d, rhombogen, anterior region; e, infusorigen; f, g, infusoriform embryos, horizontal section (f), sagittal section (g). Scale bars: 10 μ m.

gens. A maximum of 2 infusorigens present in the axial cell of each parent individual. About 30 infusoriform embryos present per axial cell of large individuals.

Infusorigens (Figs 4e, 5h; $n=10$). Mature infusorigens medium-sized, composed of 6–15 (mode 7) external cells

(oogonia and primary oocytes)+3–6 (mode 4) internal cells (spermatogonia, primary spermatocytes, and secondary spermatocytes)+4–26 (mode 8) spermatozoa. Mean diameter of fertilized eggs 13.7 μ m; that of spermatozoa 2.5 μ m. Axial cell ovoid or round, diameter 12–17 μ m.

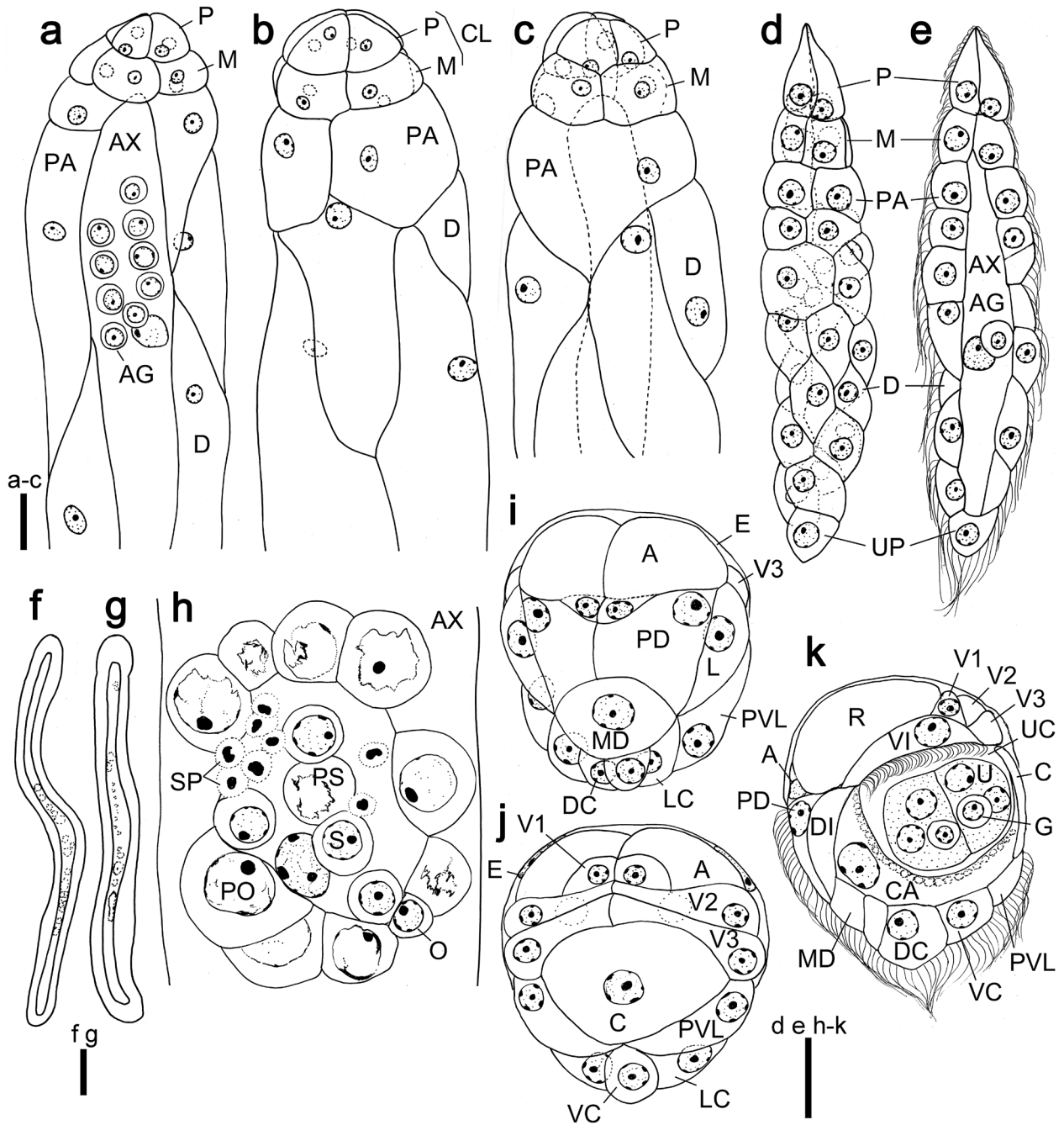


Fig. 5. *Dicyema conocephalum* sp. nov., drawn from syntype specimens on slide NSMT-Me-61: a, b, Nematogen, anterior region; c, rhombogen, anterior region; d, e, vermiform embryo within axial cell, cilia omitted (d), optical section (e); f, nematogen, entire; g, rhombogen, entire; h, infusorigen; i–k, infusoriform embryos, dorsal view (i: cilia omitted), ventral view (j: cilia omitted), sagittal section (k). Scale bars: a–e, h–k, 10 µm; f, g, 50 µm.

Infusoriform embryos (Figs 4f, g, 5i–k; $n=20$). Full-grown embryos large, length $26.7 \pm 1.8 \mu\text{m}$ (mean \pm SD, excluding cilia); length–width–height ratio 1.0:0.87:0.81; ovoid, bluntly rounded to pointed posteriorly; cilia at posterior end 7 µm long. Refracting bodies, solid, occupying anterior 30–40% of embryo length when viewed laterally (Fig. 4g). Cilia project from ventral internal cells into urn cavity (Fig. 5k). Capsule cells contain small granules (Fig. 5k). Mature embryos with 37 cells: 33 somatic+4 germinal cells. Somatic cells of several types present: external cells covering large part of anterior and lateral surfaces (2 envelop-

ing cells); external cells with cilia on external surfaces (2 paired dorsal cells+1 median dorsal cell+2 dorsal caudal cells+2 lateral caudal cells+1 ventral caudal cell+2 lateral cells+2 posteroventral lateral cells); external cells with refracting bodies (2 apical cells); external cells without cilia (1 couverte cell+2 first ventral cells+2 second ventral cells+2 third ventral cells); internal cells with cilia (2 ventral internal cells); and internal cells without cilia (2 dorsal internal cells+2 capsule cells+4 urn cells). Each urn cell contains two nuclei and a single germinal cell (Fig. 5k). All somatic nuclei pycnotic in mature infusoriform embryos.

Remarks. *Dicyema conocephalum* sp. nov. is the first species of the genus found in *Sepia kobeensis*. It is characterized by an acutely pointed calotte of vermiform embryos, a large number of peripheral cells variable number from 28 to 32 (Table 1). *Dicyema ganapatti* Kalavati, Narasimhamurti, and Suseela, 1984 and *D. oxycephalum* Furuya, 2009, are very similar to *D. conocephalum* sp. nov. in the shape of the calotte in vermiform stages and the number of peripheral cells (Kalavati et al. 1984; Furuya 2009). However, *D. conocephalum* sp. nov. differs from *D. oxycephalum* in the cell number of infusoriform embryos (37 vs. 39; cf. Furuya 2009). The axial cells of *D. conocephalum* sp. nov. extend forward to the middle of the metapolar cells, whereas those of *D. ganapatti* end forward to the middle of metapolar cells. In addition, *D. conocephalum* sp. nov. can be distinguished from *D. ganapatti* based on the typical number of agametes (1 vs. 2) in full-grown vermiform embryos (Kalavati et al. 1984).

Etymology. The species name “*conocephalum*” is an adjective composed of two Ancient Greek roots, *konikós* and *-kephalos*, meaning “conical” and “-headed” in reference to the characteristic anterior part of vermiform embryos.

Taxonomic summary. *Type material:* a slide of syntypes (NSMT-Me-61) collected on 30 November 2015; additional syntypes on slide series No. ST3303 (5 slides) in the author's collection.

Type locality: off Minami-Ise (34°08'N, 136°40'E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 260 m.

Other materials examined: slide series No. ST3505 (5 slides) collected off Minami-Ise (34°08'N, 136°40'E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 260 m, 10 April 2016, in the author's collection.

Host: symbiotype, *Sepia tenuipes* Sasaki, 1929 (Mollusca: Cephalopoda: Sepiida), male (mature), 107 mm ML (NSMT-Mo-85904).

Collector of host: T. Moritaki.

Site: anterior ends (calottes) inserted into crypts of the renal appendages within the renal sacs.

Prevalence: in 28 of 91 host specimens examined (30.8%).

Dicyema gozaense Furuya, sp. nov.

[New Japanese name: Goza-nihaichū]

(Figs 6, 7; Tables 1–3)

Diagnosis. Medium-sized dicyemid; body length reaching 3200 µm. Calotte conical in shape. Vermiform stages with 26–31 peripheral cells: 4 propolar cells+4 metapolar cells+2 parapolar cells+16–21 trunk cells. Infusoriform embryos with 39 cells; refringent bodies solid; and two nuclei present in each urn cell.

Description. *Nematogens* (Figs 6a, 7c, d). Body length 600–3020 µm, width 40–85 µm; widest in region of parapolars; trunk width mostly uniform. Peripheral cell number 26–31 (Table 2): 4 propolar cells+4 metapolar cells+2 parapolar cells+14–19 diapolar cells+2 uropolar cells. Calotte conical in shape, rounded anteriorly; cilia on calotte about 4 µm long, oriented anteriorly. Propolar cells and their nuclei equal to or smaller than metapolar cells and their nu-

clei. Propolar cells occupy anterior 40–50% of calotte length when viewed laterally (Figs 6a, 7c, d). Axial cell cylindrical, rounded anteriorly; cell extending from middle of metapolar cells to base of propolar cells (Fig. 7c, d). About 16 vermiform embryos present per axial cell of large individuals. Accessory nuclei seen in trunk peripheral cells.

Vermiform embryos (Figs 6b, 7e, f). Full-grown vermiform embryos length 53–108 µm, width 13–18 µm. Peripheral cell number 26–31 (Table 2); trunk cells arranged in opposed pairs. Anterior end of calotte pointed acutely. Axial cell tapered anteriorly, extending to the base of propolar cells (Fig 7f). Axial cell of full-grown embryos with one agamete.

Rhombogens (Figs 6c, d 7g). Body length 500–1500 µm in length, similar to that of nematogens, width 50–65 µm. Peripheral cell number typically 28–30 (Table 2). Calotte shape, axial cell shape, and anterior extent similar to those of nematogens. A maximum of 2 infusorigens present in the axial cell of each parent individual. About 25 infusoriform embryos present per axial cell of large individuals.

Infusorigens (Figs 6e, 7h; n=10). Mature infusorigens medium-sized, composed of 4–9 (mode 5) external cells (oogonia and primary oocytes)+3–6 (mode 3) internal cells (spermatogonia, primary spermatocytes, and secondary spermatocytes)+4–10 (mode 7) spermatozoa. Mean diameter of fertilized eggs 13.0 µm; that of spermatozoa 2.1 µm. Axial cell ovoid or round, diameter 12–17 µm.

Infusoriform embryos (Figs 6f, g, 7i–k; n=20). Full-grown embryos large, length 28.6 ± 1.7 µm (mean \pm SD, excluding cilia); length-width-height ratio 1.0:0.83:0.81; ovoid, bluntly rounded to pointed posteriorly; cilia at posterior end 7 µm long. Refringent bodies present, solid, occupying anterior 30–40% of embryo length when viewed laterally (Fig. 6g). Cilia projected from ventral internal cells into urn cavity (Fig. 7k). Capsule cells contain small granules (Figs 6g, 7k). Mature embryos with 39 cells: 35 somatic+4 germinal cells. Somatic cells of several types present: external cells covering large part of anterior and lateral surfaces of embryos (2 enveloping cells); external cells with cilia on external surfaces (2 paired dorsal cells+1 median dorsal cell+2 dorsal caudal cells+2 lateral caudal cells+1 ventral caudal cell+2 lateral cells+2 posteroventral lateral cells), external cells with refringent bodies (2 apical cells); external cells without cilia (1 covercle cell+2 anterior lateral cells+2 first ventral cells+2 second ventral cells+2 third ventral cells); internal cells with cilia (2 ventral internal cells); and internal cells without cilia (2 dorsal internal cells+2 capsule cells+4 urn cells). Each urn cell contains two nuclei and a single germinal cell (Fig. 7k). All somatic nuclei pycnotic in mature infusoriform embryos.

Remarks. *Dicyema gozaense* sp. nov. is characterized by an acutely pointed calotte of vermiform embryos, a large and a variable number of peripheral cells that ranges from 26 to 31 (Table 2). *Dicyema conocephalum* sp. nov. and *D. oxycephalum* are very similar to *D. gozaense* sp. nov. in the shape of the calotte in vermiform stages and the number of peripheral cells (Furuya 2009). However, *D. gozaense* sp. nov. differs from *D. conocephalum* sp. nov. in the cell number of infusoriform embryos (39 vs. 37). The number

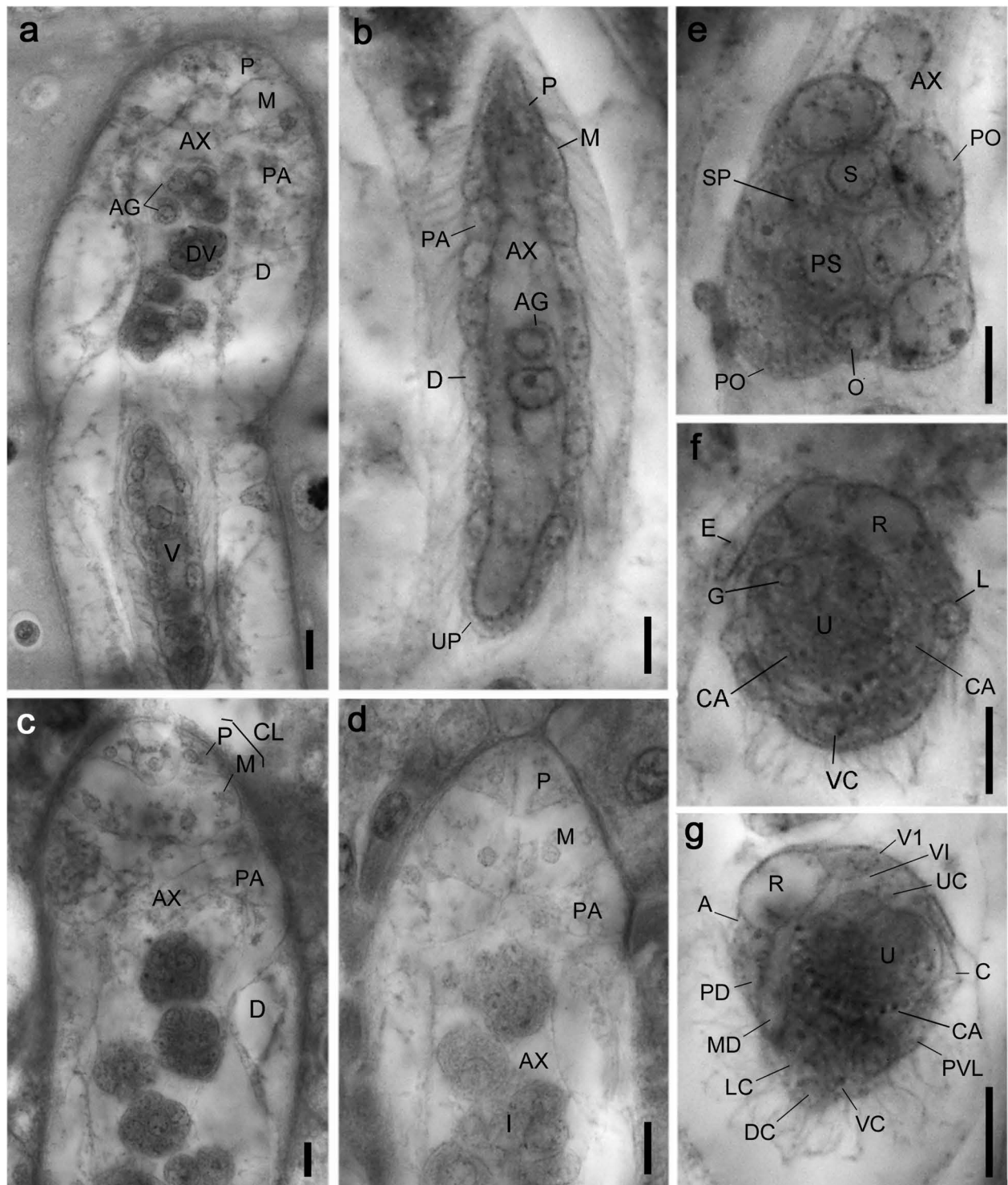


Fig. 6. *Dicyema gozaense* sp. nov., photographs of syntype specimens on slide NSMT-Me-59: a, Nematogen, anterior region; b, vermiform embryo within axial cell; c, d, rhombogen, anterior region; e, infusorigen; f, g, infusoriform embryos, horizontal section (f), sagittal section (g). Scale bars: 10 μ m.

of peripheral cells of *D. oxycephalum* ranges from 28 to 34 (Furuya 2009), which is a few more than that of *D. gozaense* sp. nov. In addition, *D. oxycephalum* has two agametes in full-grown vermiform embryos (Furuya 2009). Therefore, *D. gozaense* sp. nov. can be distinguished from *D. oxycephalum*.

Etymology. The species name “gozaense” refers to the westernmost tip of the Shima Peninsula, Mie Prefecture.

The Goza-misaki lighthouse there watches over the safety of ships across the Kumanō Sea.

Taxonomic summary. *Type material:* a syntype slide (NSMT-Me-59) collected on 10 April 2016; additional syntypes on slide series No. SK3514 (5 slides) in the author’s collection.

Type locality: off Minami-Ise (34°08’N, 136°40’E), Mie

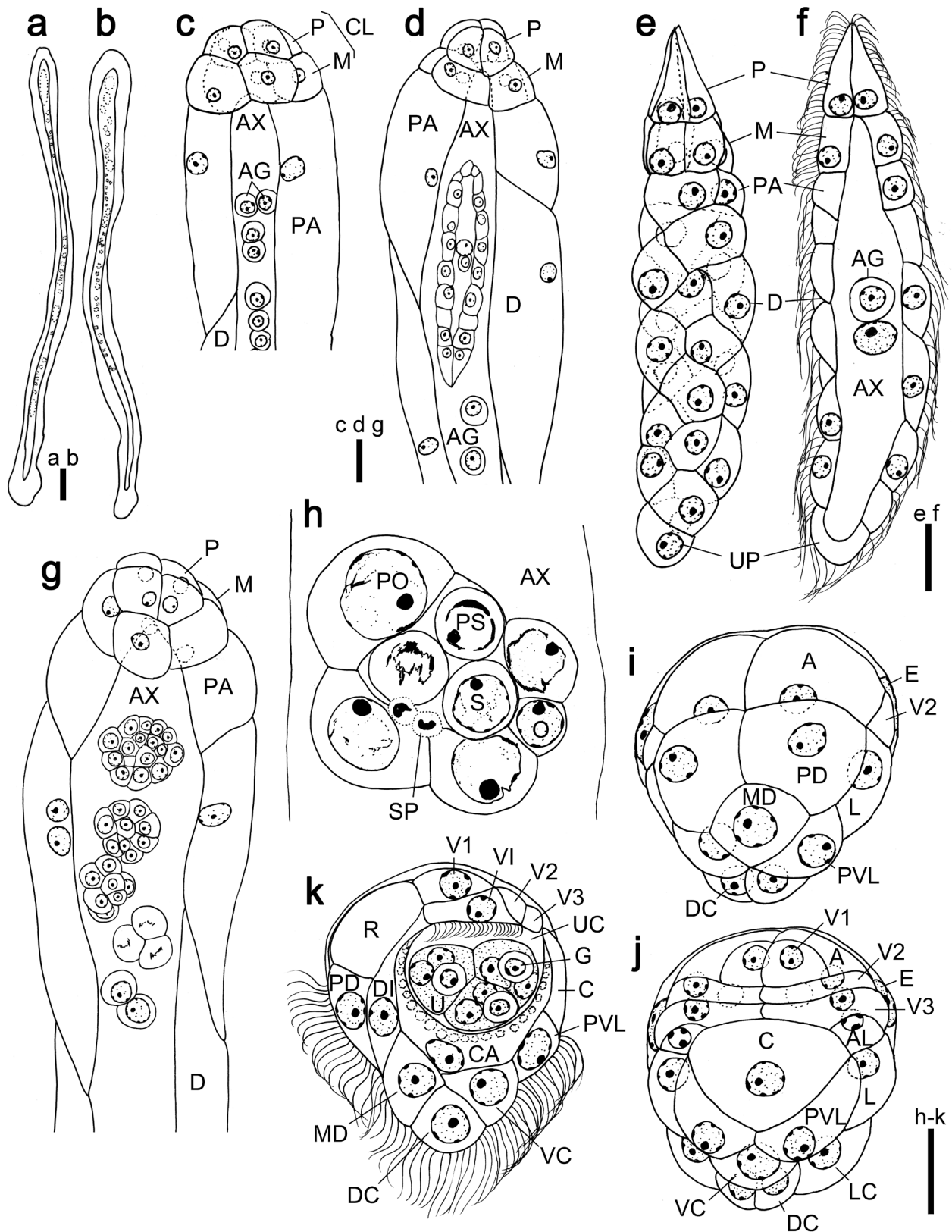


Fig. 7. *Dicyema gozaense* sp. nov., drawn from syntype specimens on slide NSMT-Me-59: a, Nematogen, entire; b, rhombogen, entire; c, d, nematogen, anterior region; e, f, vermiform embryo within axial cell, cilia omitted (e), optical section (f); g, rhombogen, anterior region; h, infusorigen; i–k, infusoriform embryos, dorsal view (i: cilia omitted), ventral view (j: cilia omitted), sagittal section (k). Scale bars: a, b, 50 μm; c–k, 10 μm.

Prefecture, Honshu, the Kumano Sea, Japan, depth 150 m.

Other materials examined: slide series No. SK3515, 3516 (each 5 slide) collected off Minami-Ise (34°08'N, 136°40'E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 150 m, in the author's collection.

Host: symbiotype, *Sepia kabiensis* Hoyle, 1855 (Mollusca: Cephalopoda: Sepiida), female (immature), 62 mm ML (NSMT-Mo-85902).

Collector of host: T. Moritaki.

Site: anterior ends (calottes) inserted into crypts of the renal appendages within the renal sacs.

Prevalence: in 22 of 30 host specimens examined (73.3%).

Dicyema hyalocephalum Furuya, sp. nov.

[New Japanese name: Yawarabōzu-nihaichū]

(Figs 8, 9; Tables 1–3)

Diagnosis. Medium-sized dicyemid; body length reaching 1720 µm. Calotte conical in shape. Vermiform stages with 22 peripheral cells: 4 propolar cells+4 metapolar cells+2 parapolar cells+12 trunk cells. Infusoriform embryos with 37 cells; refringent bodies solid; and two nuclei

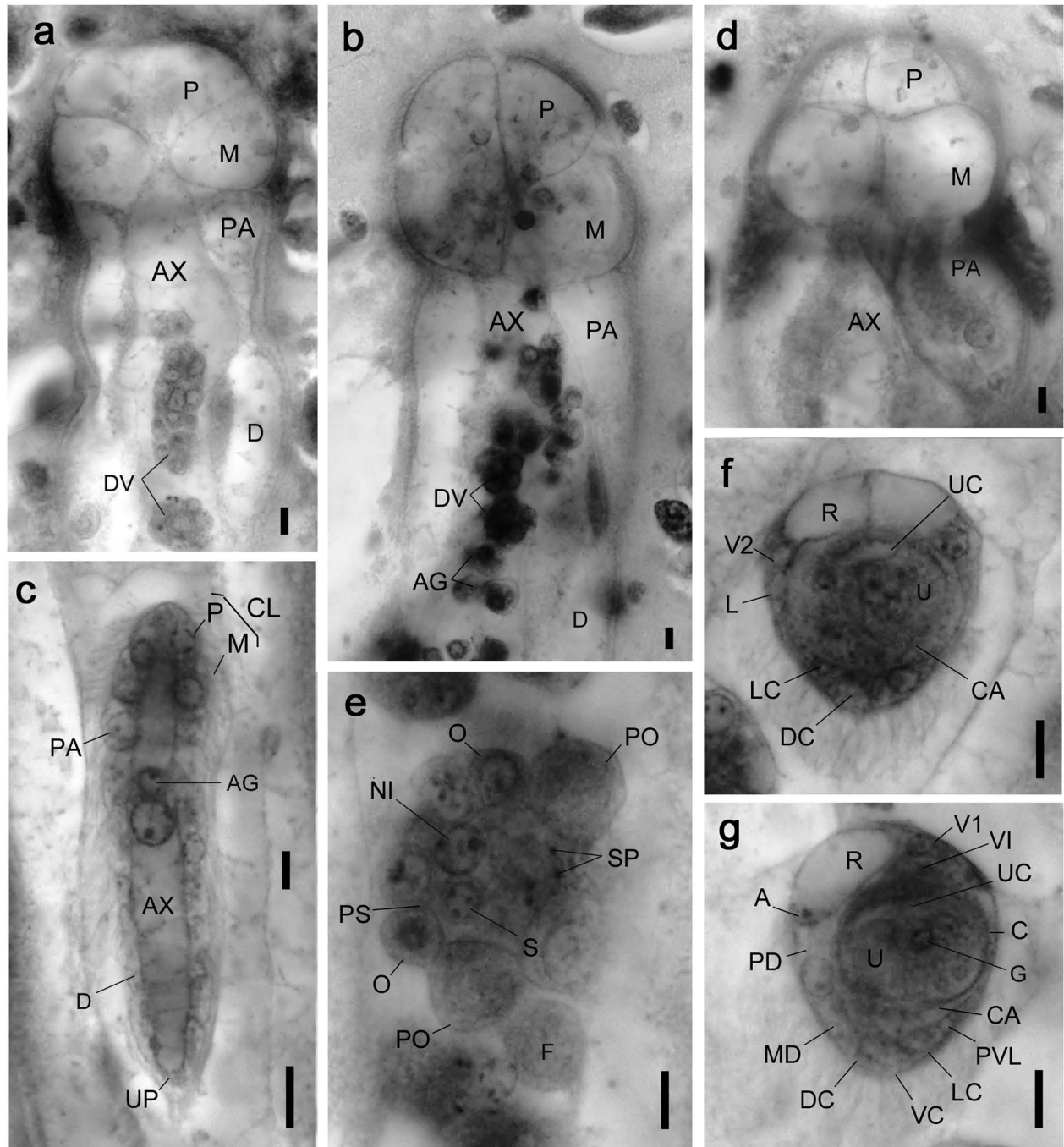


Fig. 8. *Dicyema hyalocephalum* sp. nov., photographs of syntype specimens on slide NSMT-Me-63: a, b, Nematogen, anterior region; c, vermiform embryo within axial cell; d, rhombogen, anterior region; e, infusorigen; f, g, infusoriform embryos, horizontal section (f), sagittal section (g). Scale bars: 10 µm.

present in each urn cell.

Description. *Nematogens* (Figs 8a, b, 9c, d). Body length 500–1800 µm and width 40–65 µm; widest in region of parapolar cells; trunk width mostly uniform. Peripheral cell number 20 (Table 2): 4 propolar cells+4 metapolar cells+2 parapolar cells+10 diapolar cells+2 uropolar cells. Calotte conical in shape, rounded anteriorly; cilia on calotte about 4 µm long, oriented anteriorly. Propolar cells and their nuclei equal to or smaller than metapolar cells and their nuclei.

Propolar cells occupying anterior 40–50% of calotte length when viewed laterally (Figs 8a, b, 9c, d). Axial cell cylindrical, pointed anteriorly; cell extending forward from middle of metapolar cells to base of propolar cells (Figs 8a, 9d). About 23 vermiform embryos present per axial cell of large individuals. Accessory nuclei seen in trunk peripheral cells.

Vermiform embryos (Figs 8c, 9e, f). Full-grown vermiform embryos length 50–78 µm, width 13–15 µm. Peripheral cell number 22 (Table 2); trunk cells arranged in opposed pairs.

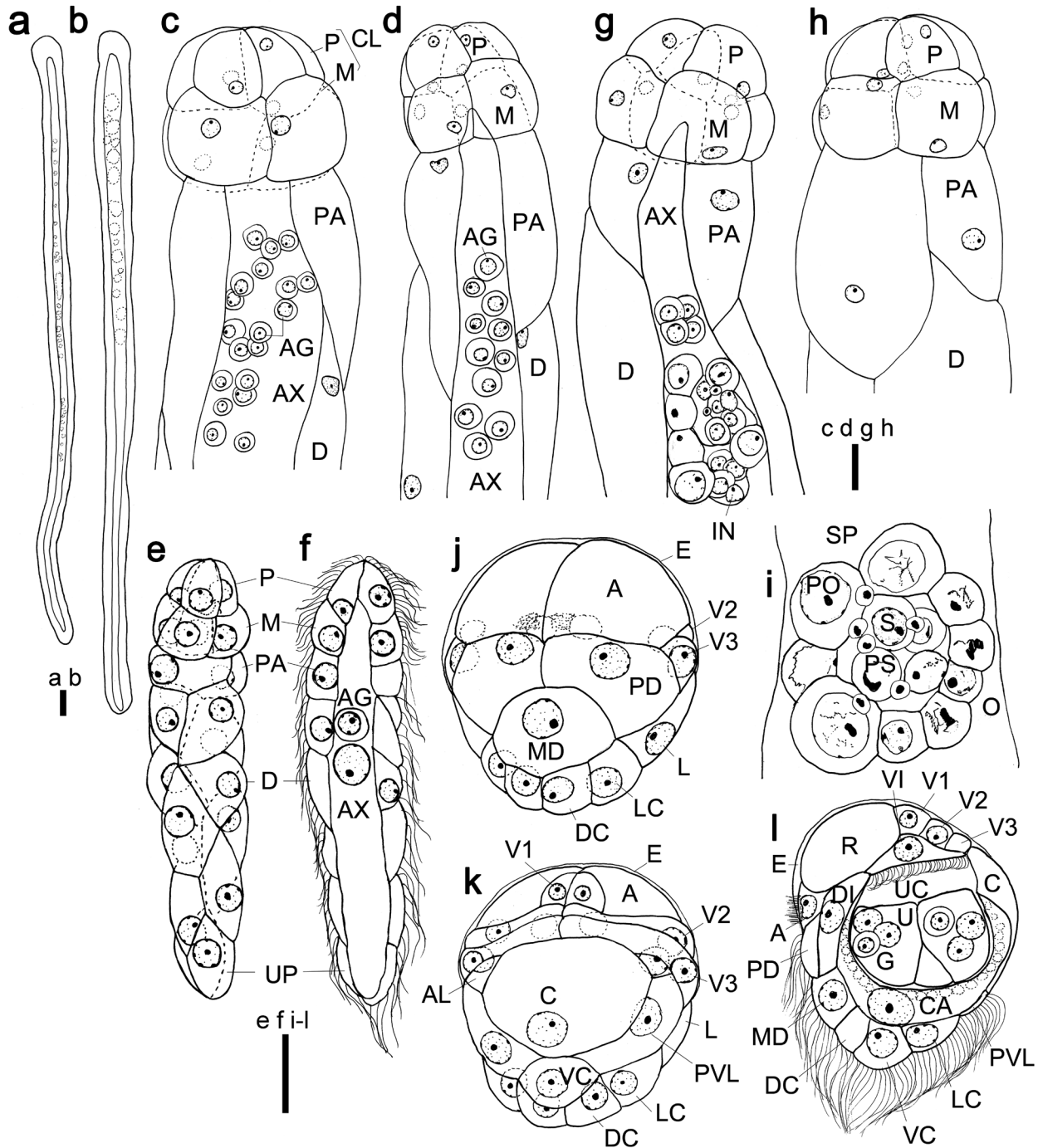


Fig. 9. *Dicyema hyalocephalum* sp. nov., drawn from syntype specimens on slide NSMT-Me-63: a, Nematogen, entire; b, rhombogen, entire; c, d, nematogen, anterior region; e, f, vermiform embryo within axial cell, cilia omitted (e), optical section (f); g, h, rhombogen, anterior region; i, infusorigen; j–l, infusoriform embryos, dorsal view (j: cilia omitted), ventral view (k: cilia omitted), sagittal section (l). Scale bars: a, b, 50 µm; c–k, 10 µm.

Anterior end of calotte bluntly pointed. Axial cell pointed anteriorly, extending to the base of propolar cells (Fig. 9f). Axial cell of full-grown embryos with one agamete.

Rhombogens (Figs 8d, 9g, h). Body length 500–1720 µm similar to nematogens, width 50–85 µm. Peripheral cell number typically 22 (Table 2). Calotte shape, axial cell shape, and anterior extent are similar to those of nematogens. A maximum of 3 infusorigens present in the axial cell of each parent individual. About 50 infusoriform embryos present per axial cell of large individuals.

Infusorigens (Figs 8e, 9i; $n=20$). Mature infusorigens medium-sized, composed of 8–23 (mode 10) external cells (oogonia and primary oocytes)+4–11 (mode 6) internal cells (spermatogonia, primary spermatocytes, and secondary spermatocytes)+7–24 (mode 7) spermatozoa. Mean diameter of fertilized eggs 12.1 µm; that of spermatozoa 2.0 µm. Axial cell ovoid or round, diameter 13–26 µm.

Infusoriform embryos (Figs 8f, g, 9j–k; $n=20$). Full-grown embryos large, length 26.9 ± 1.7 µm (mean \pm SD, excluding cilia); length–width–height ratio 1.0:0.87:0.84; ovoid, bluntly rounded to pointed posteriorly; cilia at posterior end 7 µm long. Refracting bodies present, solid, occupying anterior 30–40% of embryo length when viewed laterally (Fig. 8g). Cilia project from ventral internal cells into urn cavity (Fig. 9l). Capsule cells contain small granules (Figs 8g, 9l). Mature embryos 39 cells: 35 somatic+4 germinal cells. Somatic cells of several types present: external cells covering large part of anterior and lateral surfaces of embryos (2 enveloping cells); external cells with cilia on external surfaces (2 paired dorsal cells+1 median dorsal cell+2 dorsal caudal cells+2 lateral caudal cells+1 ventral caudal cell+2 lateral cells+2 posteroventral lateral cells); external cells with refracting bodies (2 apical cells); external cells without cilia (1 couverte cell+2 anterior lateral cells+2 first ventral cells+2 second ventral cells+2 third ventral cells); internal cells with cilia (2 ventral internal cells); and internal cells without cilia (2 dorsal internal cells+2 capsule cells+4 urn cells). Each urn cell contains two nuclei and a single germinal cell (Fig. 9l). All somatic nuclei pycnotic in mature infusoriform embryos.

Remarks. *Dicyema hyalocephalum* sp. nov. is the first species of the genus described from *Austrorossia bipapillata*. This species is very similar to *D. apollyoni* Nouvel, 1947, *D. awajiense* Furuya, 2006, *D. guaycurensis* Castellanos-Martinez, Gomez, Hochberg, Gestal, and Furuya, 2011, *D. misakiense* Nouvel and Nakao, 1938 and *D. shimantoense* Furuya, 2008 in the calotte shape of vermiform stages, peripheral cell numbers (Nouvel and Nakao 1938; Nouvel 1947; Furuya 2006a, 2008; Castellanos-Martinez et al. 2011). However, *D. hyalocephalum* sp. nov. is distinguishable from *D. awajiense*, *D. misakiense*, and *D. shimantoense* in the cell number of infusoriform embryos (39 vs. 37) (Nouvel and Nakao 1938; Furuya 2006a, 2008). *Dicyema hyalocephalum* sp. nov. is also distinguishable from *D. guaycurensis* in the maximum agamete number of vermiform embryos (4 vs. 1) (Castellanos-Martinez et al. 2011). *Dicyema hyalocephalum* sp. nov. is the most similar species to *D. apollyoni* but these two species can be distinguishable by the maximum num-

ber of infusorigens per rhombogen (3 vs. 2) and maximum length of adult vermiform stages (1720 vs. 3000 µm).

Etymology. The species name “*hyalocephalum*” is an adjective composed of two Ancient Greek roots, *hualos* and *-kephalos*, meaning “transparent” and “-headed” in reference to the characteristic anterior part of adult vermiform stages.

Taxonomic summary. *Type material:* a syntype slide (NSMT-Me-63) collected on 14 March 2018; additional syntypes on slide series No. AB5788 (5 slides) in the author’s collection.

Type locality: off Minami-Ise (34°08’N, 136°40’E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 180 m.

Other material examined: None.

Host: symbiotype, *Austrorossia bipapillata* (Sasaki, 1920) (Mollusca: Cephalopoda: Sepiolida), male (mature), 45 mm ML (NSMT-Mo-85906).

Collector of host: T. Moritaki.

Site: anterior ends (calottes) inserted into crypts of the renal appendages within the renal sacs.

Prevalence: in 42 of 42 host specimens examined (100%).

Dicyema lorigeroeceum Furuya, sp. nov.

[New Japanese name: Usubeni-nihaichū]

(Figs 10, 11; Tables 1–3)

Diagnosis. Medium-sized dicyemid; body length reaching 1590 µm. Calotte conical in shape. Vermiform stages with 23–30 peripheral cells: 4 propolar cells+4 metapolar cells+2 parapolar cells+13–20 trunk cells. Infusoriform embryos with 39 cells; refracting bodies solid; and two nuclei present in each urn cell.

Description. *Nematogens* (Figs 10a, b, 11a, c, d). Body length 500–1100 µm, width 40–52 µm; widest in region of parapolars; trunk width mostly uniform. Peripheral cell number 23–30 (Table 2): 4 propolar cells+4 metapolar cells+2 parapolar cells+11–18 diapolar cells+2 uropolar cells. Calotte conical in shape, rounded anteriorly; cilia on calotte about 4 µm long, oriented anteriorly. Propolar cells and their nuclei equal to or smaller than metapolar cells and their nuclei. Propolar cells occupying anterior 30–40% of calotte length when viewed laterally (Fig. 10a, b). Cytoplasm of propolar and metapolar cells contain small granules, more darkly stained by hematoxylin than cytoplasm of other peripheral cells (Fig. 10a, b). Axial cell cylindrical, pointed anteriorly; cell extending forward to base of metapolar cells (Fig. 11d). About 10 vermiform embryos present per axial cell of large individuals. Accessory nuclei seen in trunk peripheral cells.

Vermiform embryos (Figs 10c, d, 11f, g). Full-grown vermiform embryos length 45–68 µm, width 10–13 µm. Peripheral cell number 23–30 (Table 2); trunk cells arranged in opposed pairs. Anterior end of calotte acutely pointed. Axial cell pointed anteriorly, extending to the base of propolar cells (Figs 10d, 11f, g). Axial cell of full-grown embryos with one agamete.

Rhombogens (Figs 10e, f, 11b, e). Body length 500–1590 µm, similar to that of nematogens, width 50–70 µm.

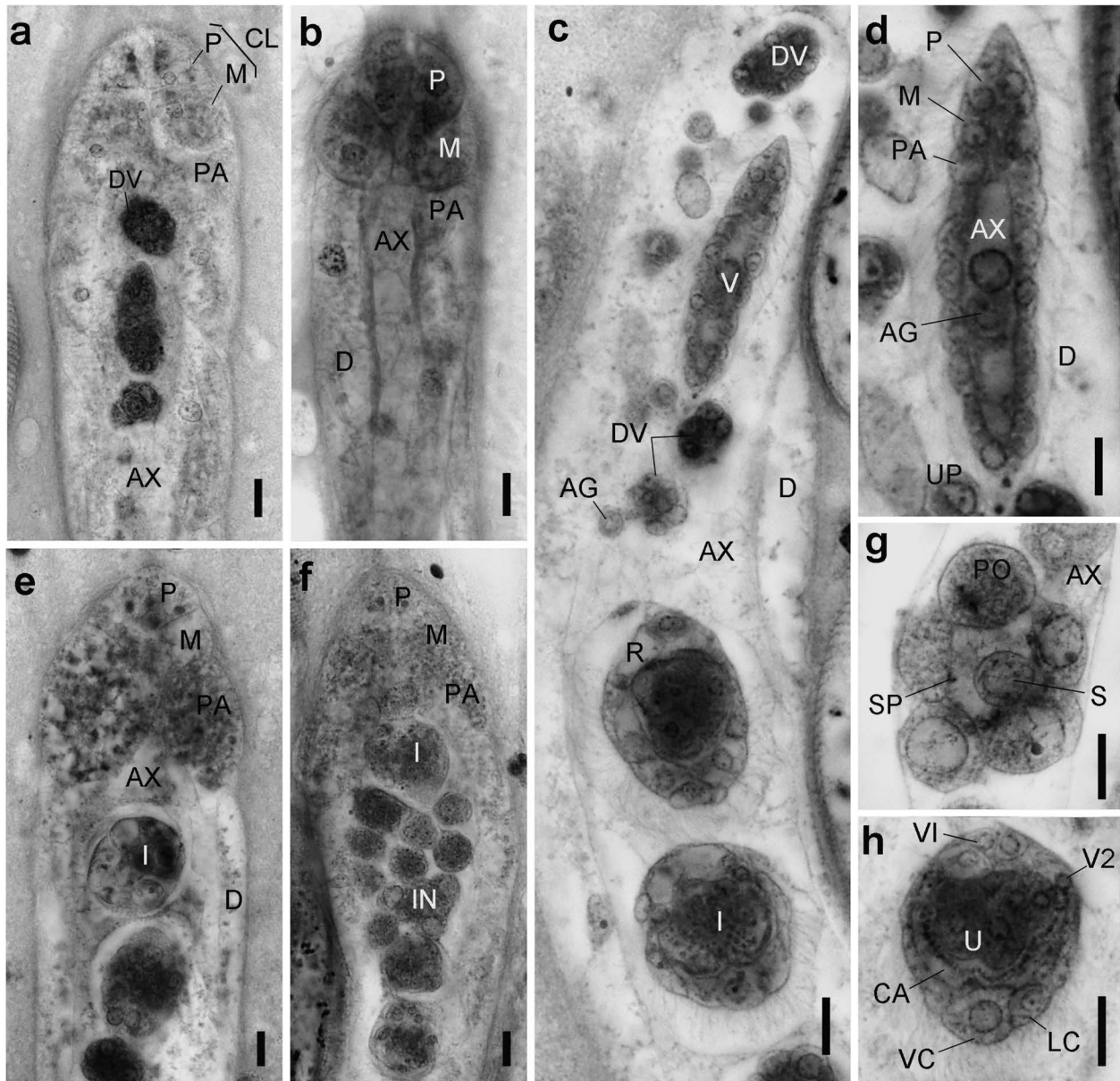


Fig. 10. *Dicyema lorigeroeceum* sp. nov., photographs of syntype specimens on slide NSMT-Me-64: a, b, Nematogen, anterior region; c, body part of transitional stage from nematogen to rhombogen, note that both vermiform embryos and infusoriform embryos present within axial cell; d, vermiform embryos within axial cell; e, f, rhombogen, anterior region; g, infusorigen; h, infusoriform embryo, horizontal section. Scale bars: 10 μ m.

Peripheral cell number typically 23–29 (Table 2). Calotte shape, axial cell shape, and anterior extent similar to those of nematogens. Cytoplasm of propodeal and metapodeal cells contain small granules (Fig. 10e, f). A maximum of 2 infusorigens present in the axial cell of each parent individual. About 30 infusoriform embryos present per axial cell of large individuals.

Infusorigens (Figs 10g, 11h; $n=20$). Mature infusorigens medium-sized, composed of 6–14 (mode 8) external cells (oogonia and primary oocytes)+3–5 (mode 4) internal cells (spermatogonia, primary spermatocytes, and secondary spermatocytes)+4–12 (mode 8) spermatozoa. Mean diameter of fertilized eggs 12.7 μ m; that of spermatozoa 2.4 μ m. Axial cell ovoid or round, diameter 13–17 μ m.

Infusoriform embryos (Figs 10c, h, 11i–k; $n=50$). Full-

grown embryos large, length $28.3 \pm 2.1 \mu$ m (mean \pm SD, excluding cilia); length–width–height ratio 1.0:0.84:0.83; ovoid, bluntly rounded to pointed posteriorly; cilia at posterior end 7 μ m long. Refrigent bodies present, solid, occupying anterior 30–35% of embryo length when viewed laterally (Fig. 11k). Cilia project from ventral internal cells into urn cavity (Fig. 11k). Capsule cells contain small granules (Fig. 11k). Mature embryos with 39 cells: 35 somatic+4 germinal cells. Somatic cells of several types present: external cells covering large part of anterior and lateral surfaces of embryos (2 enveloping cells); external cells with cilia on external surfaces (2 paired dorsal cells+1 median dorsal cell+2 dorsal caudal cells+2 lateral caudal cells+1 ventral caudal cell+2 lateral cells+2 posteroventral lateral cells); external cells with refrigent bodies (2 apical cells); external

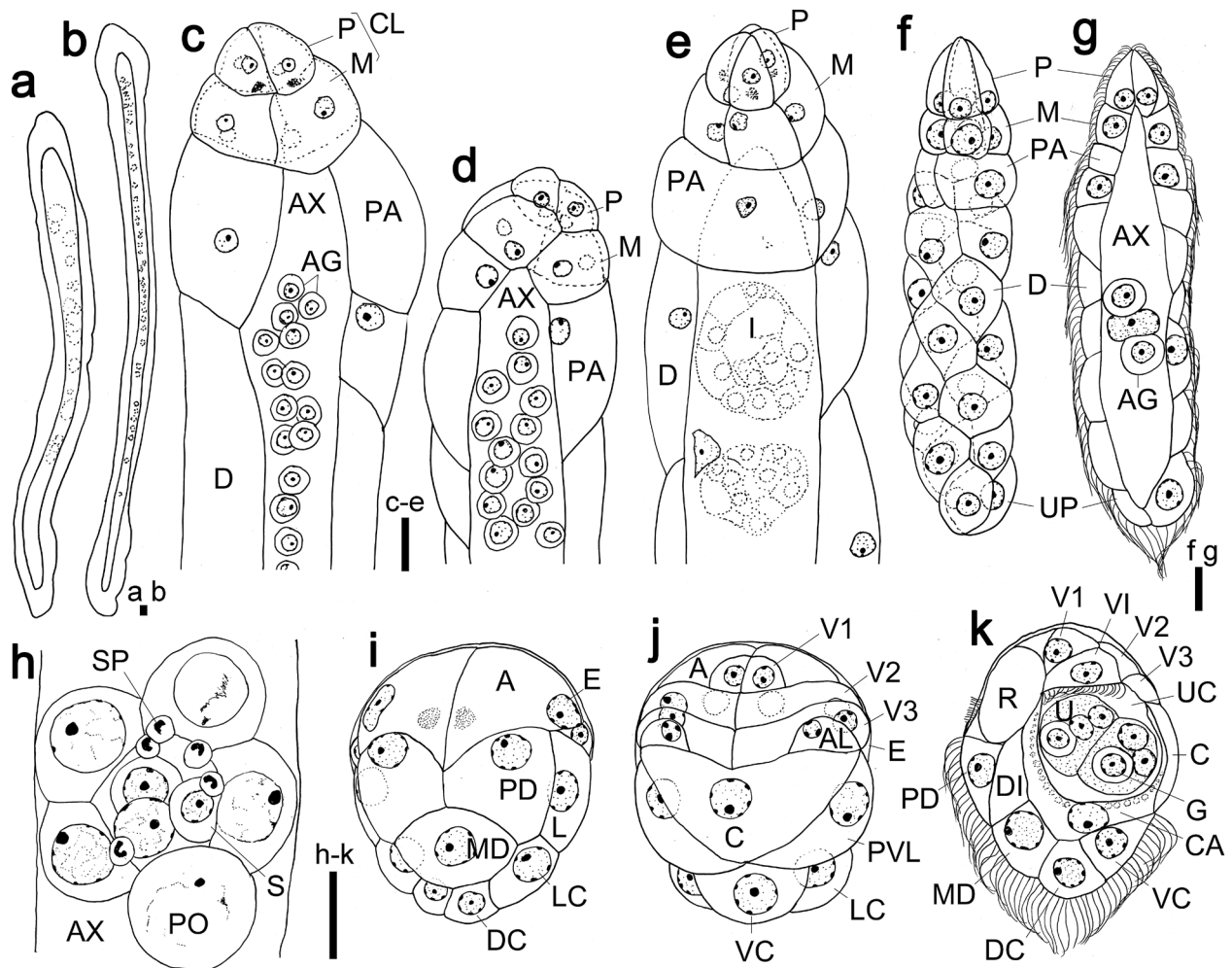


Fig. 11. *Dicyema lorigeroeum* sp. nov., drawn from syntype specimens on slide NSMT-Me-64: a, Nematogen, entire; b, rhombogen, entire; c, d, nematogen, anterior region; e, rhombogen, anterior region; f, g, vermiform embryo within axial cell, cilia omitted (f), optical section (g); h, infusorigen; i–k, infusoriform embryos, dorsal view (i: cilia omitted), ventral view (j: cilia omitted), sagittal section (k). Scale bars: 10 μ m.

cells without cilia (1 couvercle cell + 2 anterior lateral cells + 2 first ventral cells + 2 second ventral cells + 2 third ventral cells); internal cells with cilia (2 ventral internal cells); and internal cells without cilia (2 dorsal internal cells + 2 capsule cells + 4 urn cells). Each urn cell contains two nuclei and single germinal cell (Fig. 11k). All somatic nuclei pycnotic in mature infusoriform embryos.

Remarks. *Dicyema lorigeroeum* sp. nov. is the first species of the genus found in *Sepia lorigera*. This new species is characterized by an acutely pointed calotte of vermiform embryos, numbers of peripheral cells, and a variable number of peripheral cells that ranges from 23 to 30 (Table 2). This new species is very similar to *D. conocephalum* sp. nov., *D. gozaense* sp. nov. and *D. oxycephalum*, in the shape of the calotte in vermiform stages and the number of peripheral cells (Furuya 2009). However, *D. lorigeroeum* sp. nov. differs from *D. conocephalum* sp. nov. in the cell number of infusoriform embryos (39 vs. 37). *Dicyema lorigeroeum* sp. nov. can be distinguished from *D. oxycephalum* in the number of agamete in full-grown vermiform embryos (1 vs. 2) and a smaller number of peripheral cells (28 vs. 30,

32) (Furuya 2009), and is very similar to *D. gozaense* sp. nov., from which it differs in the number of peripheral cells (28 vs. 29) and in the anterior extent of adult vermiform stages (metapolar cells vs. propolar cells).

Etymology. The species name “*lorigeroeum*” is composed of the epithet of the host, *Sepia lorigera*, and the Ancient Greek word *oiceon*, meaning “inhabiting”.

Taxonomic summary. *Type material:* a syntype slide (NSMT-Me-64) collected on 14 February 2018; additional syntypes on slide series No. SL5779 (5 slides) in the author’s collection.

Type locality: off Minami-Ise (34°08’N, 136°04’E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 180 m.

Other materials examined: None.

Host: symbiotype, *Sepia lorigera* Wülker, 1910 (Mollusca: Cephalopoda: Sepiida), male (mature), 157 mm ML (NSMT-Mo-85907).

Collector of host: T. Moritaki.

Site: anterior ends (calottes) inserted into crypts of the renal appendages within the renal sacs.

Prevalence: in 10 of 10 host specimens examined (100%).

Dicyema miense sp. nov.

[New Japanese name: Mie-nihaichū]

(Figs 12, 13; Tables 1–3)

Diagnosis. Medium-sized dicyemid; body length

reaching 1210 µm. Calotte conical in shape. Vermiform stages with 26–34 peripheral cells: 4 propolar cells+4 metapolar cells+2 parapolar cells+16–24 trunk cells. Infusoriform embryos with 39 cells; refringent bodies solid; and two nuclei present in each urn cell.

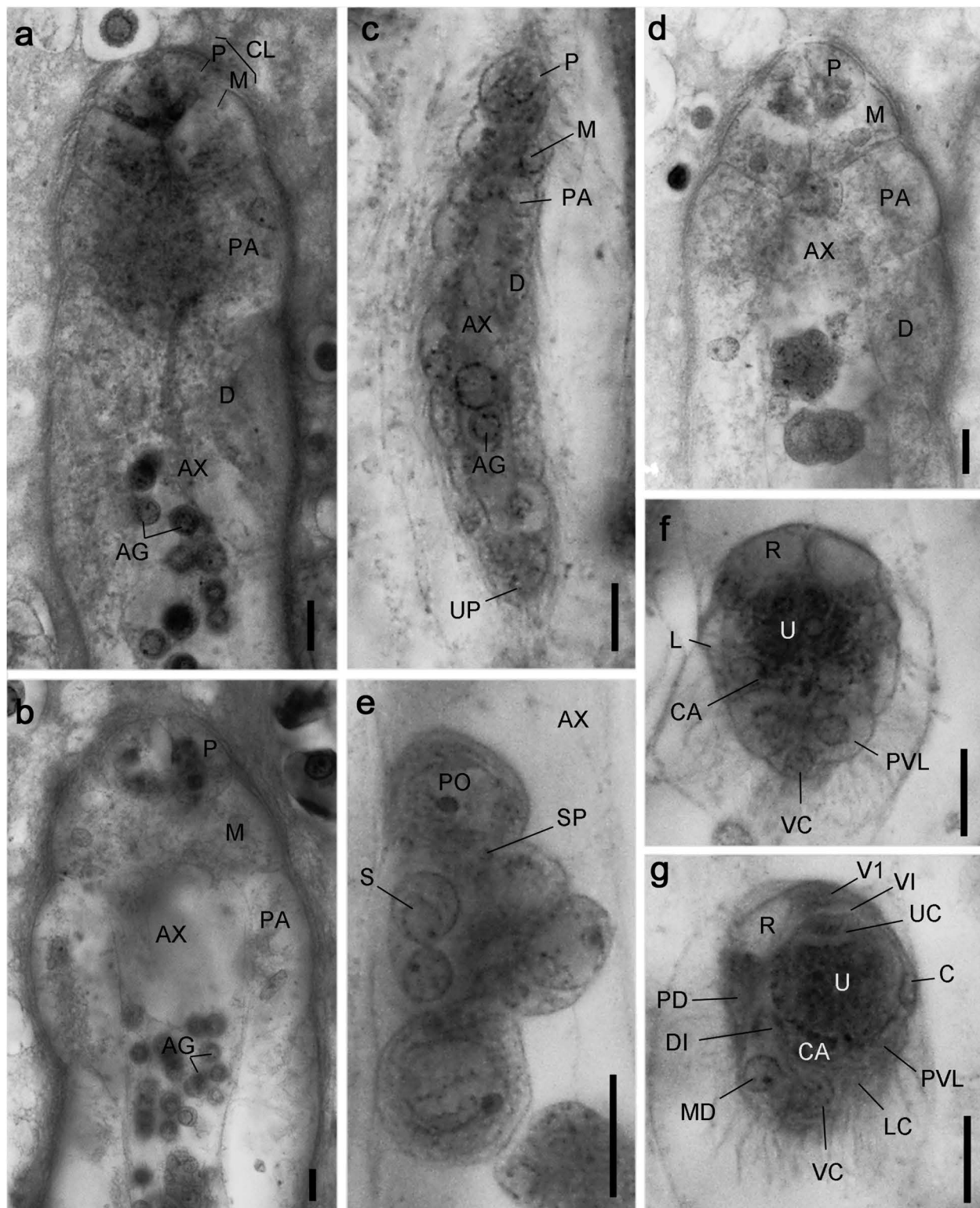


Fig. 12. *Dicyema miense* sp. nov., photographs of syntype specimens on slide NSMT-Me-68: a, b, Nematogen, anterior region; c, vermiform embryo within axial cell; d, rhombogen, anterior region; e, infusorigen; f, g, infusoriform embryos, horizontal section (f), sagittal section (g). Scale bars: 10 µm.

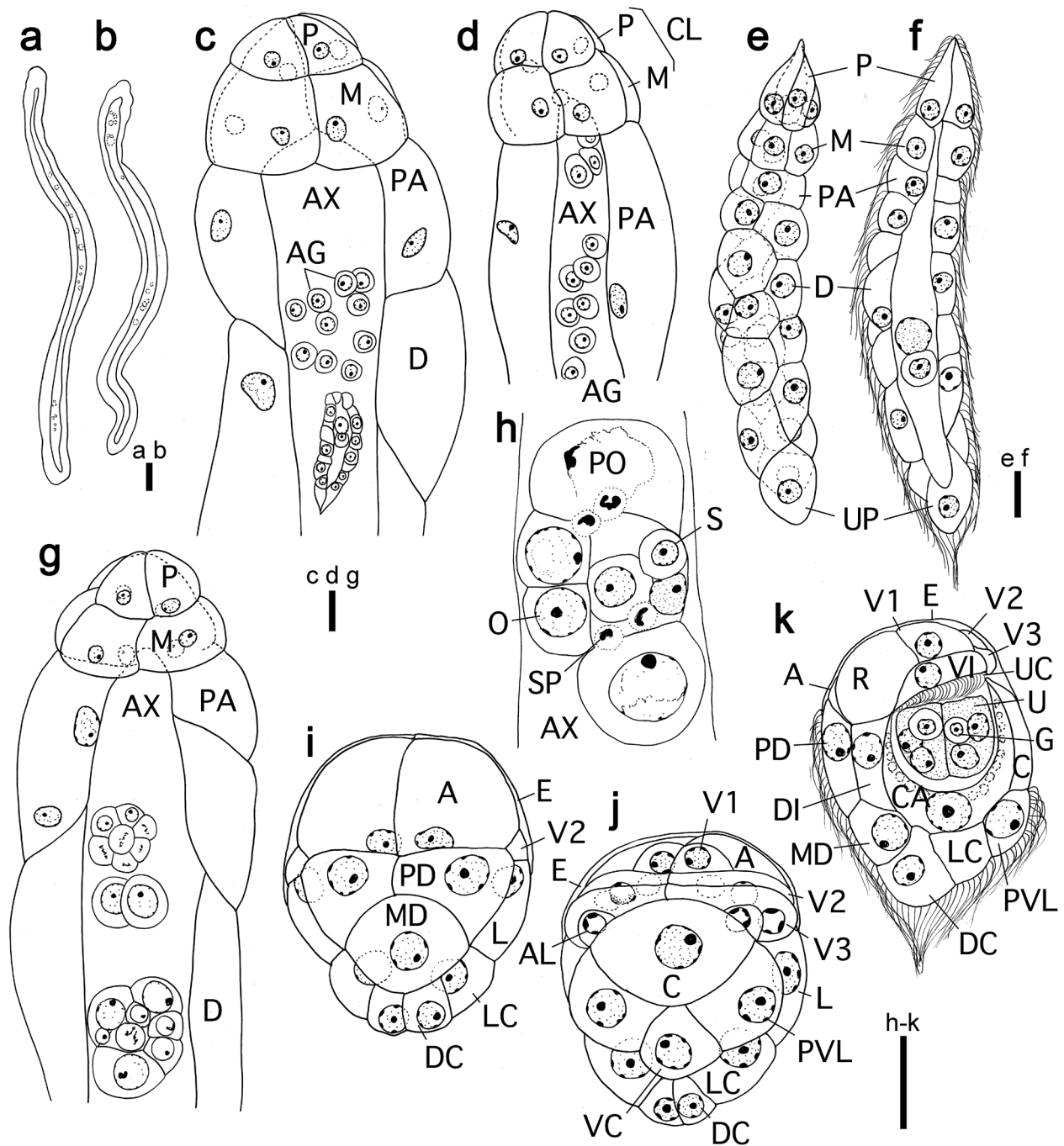


Fig. 13. *Dicyema miense* sp. nov., drawn from syntype specimens on slide NSMT-Me-68: a, nematogen, entire; b, rhombogen, entire; c, d, nematogen, anterior region; e, f, vermiform embryo within axial cell, cilia omitted (e), optical section (f); g, rhombogen, anterior region; h, infusorigen; i–k, infusoriform embryos, dorsal view (i: cilia omitted), ventral view (j: cilia omitted), sagittal section (k). Scale bars: a, b, 50 μ m; c–k, 10 μ m.

Description. *Nematogens* (Figs 12a, b, 13a, c, d). Body length 800–1180 μ m, width 32–40 μ m; widest in region of parapolar cells; trunk width mostly uniform. Peripheral cell number 26–34 (Table 2): 4 propolar cells+4 metapolar cells+2 parapolar cells+14–22 diapolar cells+2 uropolar cells. Calotte conical in shape, rounded anteriorly; cilia on calotte about 4 μ m long, oriented anteriorly. Propolar cells and their nuclei equal to or smaller than metapolar cells and their nuclei. Propolar cells occupy anterior 30–40% of calotte length when viewed laterally (Fig. 13c, d). Axial cell

cylindrical, rounded anteriorly; cell extending forward to middle of metapolar cells (Fig. 13d). About 10 vermiform embryos present per axial cell of large individuals. Accessory nuclei present in trunk peripheral cells.

Vermiform embryos (Figs 12c, d, 13e, f). Full-grown vermiform embryos length 40–57 μ m, width 12–14 μ m. Peripheral cell number 26–34 (Table 2); trunk cells arranged in opposed pairs. Anterior end of calotte acutely pointed. Axial cell pointed anteriorly, extending to the base of propolar cells (Fig. 13f). Axial cell of full-grown embryos with

one agamete.

Rhombogens (Figs 12d, 13g). Body length 900–1210 µm, similar to that of nematogens, in length, width 60–75 µm. Peripheral cell number typically 26–34 (Table 2). Calotte shape, axial cell shape, and anterior extent similar to those of nematogens. A maximum of 3 infusorigens present in the axial cell of each parent individual. About 30 infusoriform embryos present per axial cell of large individuals.

Infusorigens (Figs 12e, 13h; $n=10$). Mature infusorigens medium-sized, composed of 5–8 (mode 6) external cells (oogonia and primary oocytes)+2–4 (mode 2) internal cells (spermatogonia, primary spermatocytes, and secondary spermatocytes)+4–8 (mode 4) spermatozoa. Mean diameter of fertilized eggs 13.3 µm; that of spermatozoa 2.5 µm. Axial cell ovoid or round, diameter 13–15 µm.

Infusoriform embryos (Figs 12f, g, 13i–k; $n=20$). Full-grown embryos large, length 28.3 ± 2.1 µm (mean \pm SD, excluding cilia); length–width–height ratio 1.0:0.84:0.81; ovoid, bluntly rounded to pointed posteriorly; cilia at posterior end 7 µm long. Refracting bodies present, solid, occupying anterior 35–40% of embryo length when viewed laterally (Fig. 13k). Cilia project from ventral internal cells into urn cavity (Fig. 13k). Capsule cells contain small granules (Fig. 13k). Mature embryos with 39 cells: 35 somatic+4 germinal cells. Somatic cells of several types present: external cells covering large part of anterior and lateral surfaces of embryos (2 enveloping cells); external cells with cilia on external surfaces (2 paired dorsal cells+1 median dorsal cell+2 dorsal caudal cells+2 lateral caudal cells+1 ventral caudal cell+2 lateral cells+2 posteroventral lateral cells); external cells with refracting bodies (2 apical cells); external cells without cilia (1 couverte cell+2 anterior lateral cells+2 first ventral cells+2 second ventral cells+2 third ventral cells); internal cells with cilia (2 ventral internal cells); and internal cells without cilia (2 dorsal internal cells+2 capsule cells+4 urn cells). Each urn cell contains two nuclei and a single germinal cell (Fig. 13k). All somatic nuclei pycnotic in mature infusoriform embryos.

Remarks. *Dicyema miense* sp. nov. is the first species of the genus found in *Sepia subtenuipes* and is characterized by an acutely pointed calotte of vermiform embryos and numbers of peripheral cells, and a variable number of peripheral cells that ranges from 26 to 34 (Table 2). It is very similar to *D. gozaense* sp. nov., *D. lorigeroeceum* sp. nov. and *D. oxycephalum* in the shape of the calotte in vermiform stages, the number of peripheral cells, and the number of infusoriform embryos (Furuya 2009). However, *D. miense* sp. nov. can be distinguished from *D. gozaense* sp. nov. and *D. oxycephalum* in an anterior extent of adult vermiform stages (metapolar cells vs. propolar cells). *Dicyema miense* sp. nov. can also be distinguished from *D. lorigeroeceum* sp. nov. by the maximum number of peripheral cells (34 vs. 30): it has no clear maximum in its distribution of peripheral cells, while *D. lorigeroeceum* sp. nov. has a maximum of 28 peripheral cells.

Etymology. The species name “*miense*” refers to the location of the Mie-Island off Minami-Ise, Mie Prefecture, in Kumano Sea.

Taxonomic summary. *Type material*: a syntype slide

(NSMT-Me-68) collected on 25 October 2016; additional syntypes on slide series No. SS3618 (5 slides) in the author's collection.

Type locality: off Kii-Nagashima (34°01'N, 136°39'E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 150 m.

Other materials examined: slide series No. SS3614–3617 (each 5 slide) collected off Kii-Nagashima (34°01'N, 136°39'E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 150 m, 25 October 2016, in the author's collection.

Host: symbiotype, *Sepia subtenuipes* Okutani and Hori-kawa, 1987 (Mollusca: Cephalopoda: Sepiida), female (immature), 68 mm ML (NSMT-Mo-85910).

Collector of host: T. Moritaki.

Site: anterior ends (calottes) inserted into crypts of the renal appendages within the renal sacs.

Prevalence: in 19 of 30 host specimens examined (63.3%).

Dicyema shimaense sp. nov.

[New Japanese name: Shima-nihaichū]

(Figs 14, 15; Tables 1–3)

Diagnosis. Medium-sized dicyemid; body length reaching 1190 µm. Calotte conical in shape. Vermiform stages with 28–30 peripheral cells: 4 propolar cells+4 metapolar cells+2 parapolar cells+18–20 trunk cells. Infusoriform embryos with 39 cells; refracting bodies solid; and two nuclei present in each urn cell.

Description. *Nematogens* (Figs 14a, b, 15a, c, d). Body length 640–1190 µm, width 38–48 µm; widest in region of parapolars; trunk width mostly uniform. Peripheral cell number 28–30 (Table 2): 4 propolar cells+4 metapolar cells+2 parapolar cells+16–18 diapolar cells+2 uropolar cells. Calotte conical in shape, rounded anteriorly; cilia on calotte about 4 µm long, oriented anteriorly. Propolar cells and their nuclei equal to or smaller than metapolar cells and their nuclei. Propolar cells occupy anterior 30–40% of calotte length when viewed laterally (Fig. 15c, d). Cytoplasm of propolar, metapolar, and parapolar cells contain small granules, more darkly stained by hematoxylin than cytoplasm of other peripheral cells (Fig. 14a). Axial cell cylindrical, rounded anteriorly; cell extending forward to base of metapolar cells (Fig. 15d). About 15 vermiform embryos present per axial cell of large individuals. Accessory nuclei seen in trunk peripheral cells.

Vermiform embryos (Figs 14c, 15f, g). Full-grown vermiform embryos length 56–105 µm, width 12–16 µm. Peripheral cell number 28–30 (Table 2); trunk cells arranged in opposed pairs. Anterior end of calotte acutely pointed. Axial cell pointed anteriorly, extending to the base of propolar cells (Figs 14c, 15f, g). Axial cell of full-grown embryos with one agamete.

Rhombogens (Figs 14d–f, 15e). Body length similar 285–650 µm, similar that of nematogens, in length, and width 41–51 µm. Peripheral cell number typically 28–29 (Table 2). Calotte shape, axial cell shape, and anterior extent similar to those of nematogens. Cytoplasm of propolar cells, metapolar cells, and parapolar cells contains small granules (Fig. 14d–f). A maximum of 2 infusorigens present in the axial

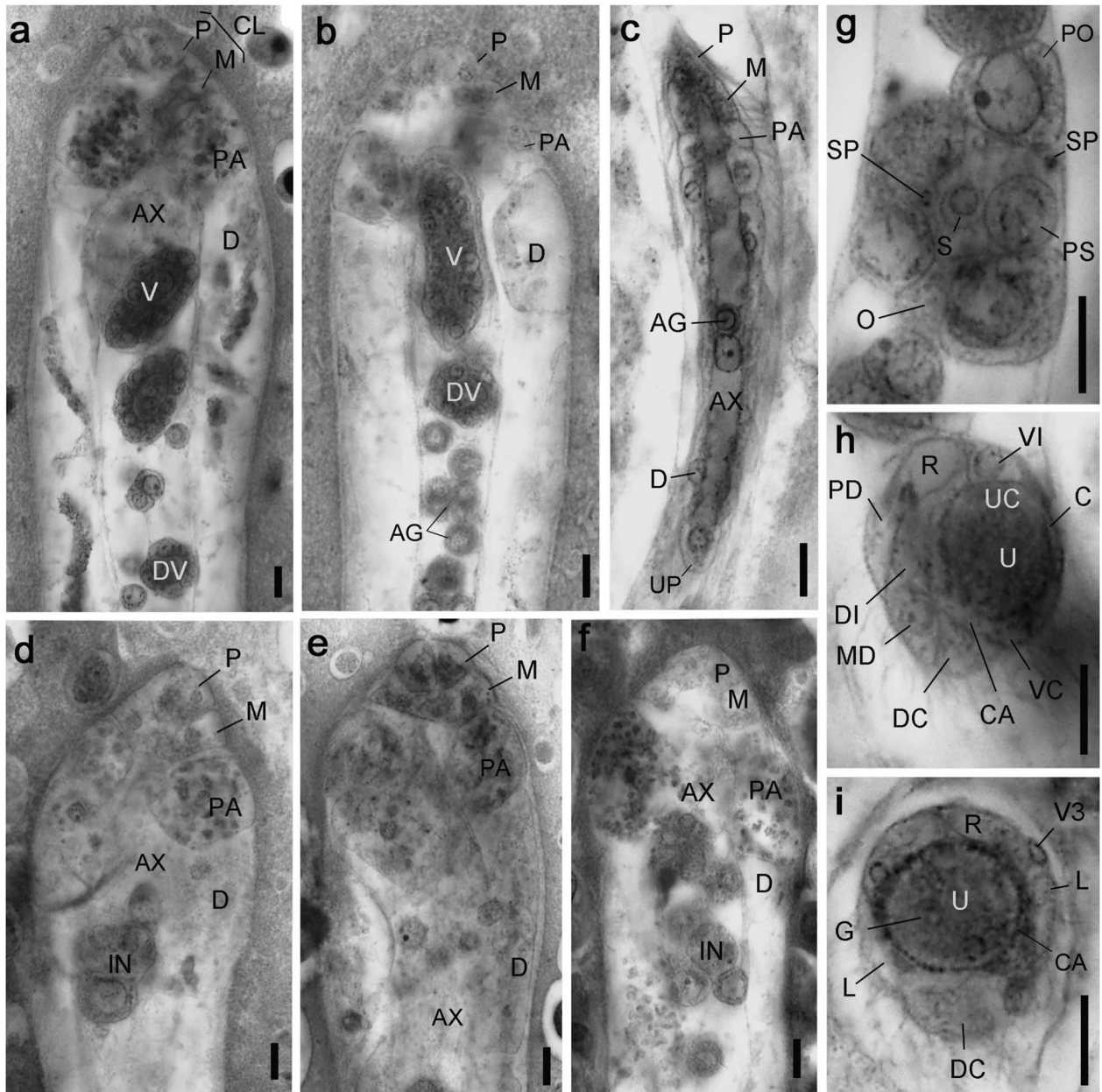


Fig. 14. *Dicyema shimaense* sp. nov., photographs of syntype specimens on slide NSMT-Me-70: a, b, Nematogen, anterior region; c, vermiform embryo within axial cell; d-f, rhombogen, anterior region; g, infusorigen; h, i, infusoriform embryos, sagittal section (h), horizontal section (i). Scale bars: 10 µm.

cell of each parent individual. About 10 infusoriform embryos present per axial cell of large individuals.

Infusorigens (Figs 14g, 15h; $n=20$). Mature infusorigens medium-sized, composed of 5–12 (mode 7) external cells (oogonia and primary oocytes)+3–4 (mode 4) internal cells (spermatogonia, primary spermatocytes, and secondary spermatocytes)+2–12 (mode 6) spermatozoa. Mean diameter of fertilized eggs 12.0 µm; that of spermatozoa 2.1 µm. Axial cell ovoid or round, diameter 13–17 µm.

Infusoriform embryos (Figs 14h, i, 15i–k; $n=12$). Full-grown embryos large, length 26.5 ± 2.5 µm (mean \pm SD, excluding cilia); length–width–height ratio 1.0:0.79:0.85; ovoid, bluntly rounded to pointed posteriorly; cilia at posterior end 7 µm long. Refractive bodies present, solid, occu-

pying anterior 30–35% of embryo length when viewed laterally (Fig. 15k). Cilia project from ventral internal cells into urn cavity (Fig. 15k). Capsule cells contain small granules (Figs 14i, 15k). Mature embryos with 39 cells: 35 somatic+4 germinal cells. Somatic cells of several types present: external cells covering large part of anterior and lateral surfaces of embryos (2 enveloping cells); external cells with cilia on external surfaces (2 paired dorsal cells+1 median dorsal cell+2 dorsal caudal cells+2 lateral caudal cells+1 ventral caudal cell+2 lateral cells+2 posteroventral lateral cells); external cells with refringent bodies (2 apical cells); external cells without cilia (1 couvercle cell+2 anterior lateral cells+2 first ventral cells+2 second ventral cells+2 third ventral cells); internal cells with cilia (2 ventral internal cells); and

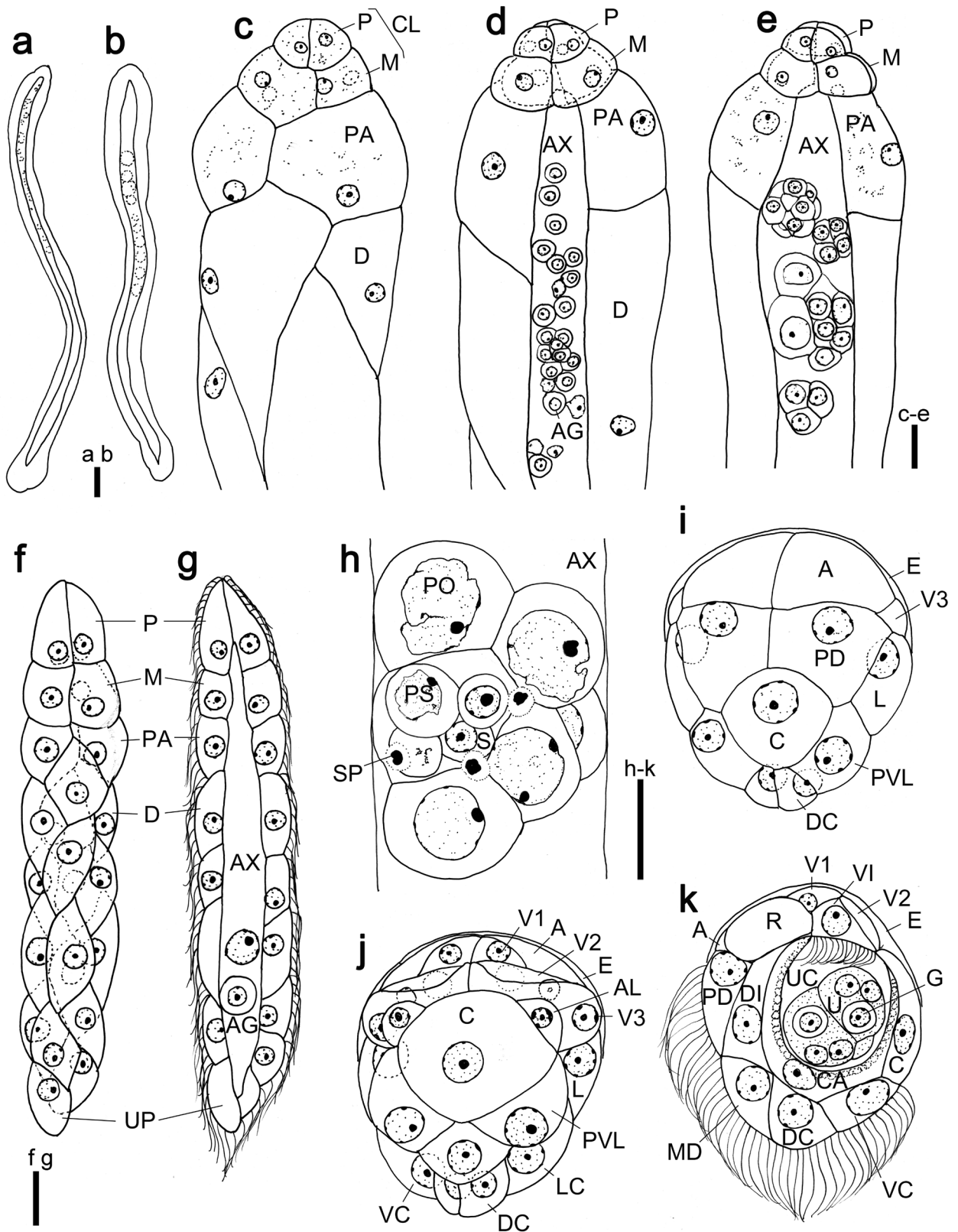


Fig. 15. *Dicyema shimaense* sp. nov., drawn from syntype specimens on slide NSMT-Me-70: a, Nematogen, entire; b, rhombogen, entire; c, d, nematogen, anterior region; e, rhombogen, anterior region; f, g, vermiform embryo within axial cell, cilia omitted (f), optical section (g); h, infusorigen; i–k, infusoriform embryos, dorsal view (i: cilia omitted), ventral view (j: cilia omitted), sagittal section (k). Scale bars: a, b, 50 μm; c–k, 10 μm.

internal cells without cilia (2 dorsal internal cells+2 capsule cells+4 urn cells). Each urn cell contains two nuclei and a single germinal cell (Fig. 15k). All somatic nuclei pycnotic

in mature infusoriform embryos.

Remarks. *Dicyema shimaense* sp. nov. is the first species of the genus found in *Sepia madokai*. It is very similar

to *D. gozaense* sp. nov., *D. lorigeroeceum* sp. nov., and *D. oxycephalum* in the shape of the calotte in vermiform stages, an acutely pointed calotte of vermiform embryos, and the cell number of infusoriform embryos (Furuya 2009). However, *D. shimaense* sp. nov. differs from *D. gozaense* sp. nov. and *D. oxycephalum* in the anterior extent of adult vermiform stages (metapolar cells vs. propolar cells). *Dicyema shimaense* sp. nov. has 28–29 peripheral cells, while *D. lorigeroeceum* sp. nov. has a variable number of peripheral cells ranging from 26 to 34 (Table 2).

Etymology. The species name “*shimaense*” refers to the Shima Peninsula type locality, famous for its beautiful landscape in the Ise-Shima National Park at the northern end of the Kumano Sea.

Taxonomic summary. *Type material:* a syntype slide (NSMT-Me-70) collected on 8 March 2019; additional syntypes on slide series No. SM4024 (5 slides) in the author’s collection.

Type locality: off Kii-Nagashima (34°01’N, 136°37’E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 180 m.

Other materials examined: slide series No. SM3312 (5 slides) collected off Minami-Ise (34°12’N, 136°40’E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 200 m, 30 November 2015, in the author’s collection.

Host: symbiotype, *Sepia madokai* Adam, 1939 (Mollusca: Cephalopoda: Sepiida), female (immature), 54 mm ML (NSMT-Mo-85912).

Collector of host: T. Moritaki.

Site: anterior ends (calottes) inserted into crypts of the renal appendages within the renal sacs.

Prevalence: in 5 of 21 host specimens examined (23.8%).

***Dicyema tenuipoeceum* Furuya, sp. nov.**

[New Japanese name: Udeboso-nihaichū]

(Figs 16, 17; Tables 1–3)

Diagnosis. Small-sized dicyemid, body length reaching 1540 µm. Calotte cap- or disc-shaped. Vermiform stages with 22 peripheral cells: 4 propolar cells+4 metapolar cells+2 parapolar cells+12 trunk cells. Infusoriform embryos with 37 cells; refringent bodies solid; and 2 nuclei present in each urn cell.

Description. *Nematogens* (Figs 16a, c, d, 17a, b). Body length 550–1540 µm, width 50–83 µm; widest in region of parapolars; trunk width mostly uniform. Peripheral cell number 22 (Table 2): 4 propolar cells+4 metapolar cells+2 parapolar cells+10 diapolar cells+2 uropolar cells. Calotte cap- or disc-shaped, rounded anteriorly; cilia about 4 µm long, oriented anteriorly. Propolar cells equal to or larger than metapolar cells, their nuclei equal to or smaller than metapolar cell nuclei. Propolar cells occupy anterior 50% of calotte length when viewed laterally (Fig. 17d). Axial cell cylindrical, pointed anteriorly, extending forward to base of propolar cells (Fig. 17c, d). About 15 vermiform embryos present per axial cell of large individuals. Accessory nuclei seen in trunk peripheral cells.

Vermiform embryos (Figs 16c, 17e, f). Full-grown vermiform embryos length 60–80 µm, 15–16 µm in width. Pe-

ripheral cell number 22 (Table 2); trunk cells arranged in opposed pairs. Anterior end of calotte rounded. Axial cell pointed anteriorly, extending to the base of propolar cells (Fig. 17f). Axial cell of full-grown embryos with 2 agametes.

Rhombogens (Figs 16d, 17g). Body length 950–1450 µm, similar to that of nematogens, in length and 70–90 µm in width. Peripheral cell number typically 22 (Table 2). Calotte, axial cell shape and anterior extent similar to nematogens. Maximum of 4 infusorigens present in the axial cell of each parent individual. About 40 infusoriform embryos present per axial cell of large individuals.

Infusorigens (Figs 16f, 17h; n=10). Mature infusorigens medium-sized; composed of 6–14 (mode 8) external cells (oogonia and primary oocytes)+3–6 (mode 3) internal cells (spermatogonia, primary spermatocytes, and secondary spermatocytes)+4–15 (mode 6) spermatozoa. Mean diameter of fertilized eggs 12.8 µm; that of spermatozoa 3.0 µm. Axial cell round or ovoid, diameter 12–15 µm.

Infusoriform embryos (Figs 16g, h, 17i–k; n=20). Full-grown embryos large, length 26.2 ± 1.5 µm (mean \pm SD, excluding cilia); length–width–height ratio 1.0:0.90:0.88; shape ovoid, and pointed posteriorly; cilia at posterior end 7 µm long. Refringent bodies present, solid, occupying anterior 50–60% of embryo length when viewed laterally (Fig. 16h). Cilia project from ventral internal cells into urn cavity (Fig. 17k). Capsule cells contain small granules (Figs 16h, 17k). Mature embryos with 37 cells: 33 somatic+4 germinal cells. Somatic cells of several types present: external cells covering large part of anterior and lateral surfaces of embryo (2 enveloping cells); external cells with cilia on external surfaces (2 pairs of dorsal cells+1 median dorsal cell+2 dorsal caudal cells+2 lateral caudal cells+1 ventral caudal cell+2 lateral cells+2 posteroventral lateral cells); external cells with refringent bodies (2 apical cells); external cells without cilia (1 couverte cell+2 first ventral cells+2 second ventral cells+2 third ventral cells); internal cells with cilia (2 ventral internal cells); and internal cells without cilia (2 dorsal internal cells+2 capsule cells+4 urn cells). Each urn cell containing 2 nuclei and a germinal cell (Fig. 17k). All somatic nuclei pycnotic in mature infusoriform embryos.

Remarks. *Dicyema tenuipoeceum* sp. nov. is similar to *D. balamuthi*, *D. clavatum*, *D. colurum*, *D. hadrum*, *D. japonicum* Furuya and Tsuneki, 1992, and *D. schulzianum* in the calotte shape of vermiform stages and peripheral cell numbers (Beneden 1876; McConnaughey 1949; Furuya et al. 1992b; Furuya 1999). However, *D. tenuipoeceum* sp. nov. is distinguishable from *D. balamuthi*, *D. clavatum*, *D. colurum*, and *D. hadrum* in the cell number of infusoriform embryos (37 vs. 39). It also shares the same cell number of infusoriform embryos with *D. japonicum* and *D. schulzianum*. However, *D. tenuipoeceum* sp. nov. infusoriform embryos lack anterior lateral cells, which distinguished this species from *D. japonicum*. *Dicyema schulzianum* was recorded from *Sepia elegans* Blainville, 1827, and *Rondeletiola minor* (Naef, 1912) in the western Mediterranean (Beneden 1876; Nouvel 1947). Rhombogens of *D. schulzianum* have at most two infusorigens, while those of *D. tenuipoeceum* sp. nov. have four. Thus, *D. tenuipoeceum* sp. nov. can be distin-

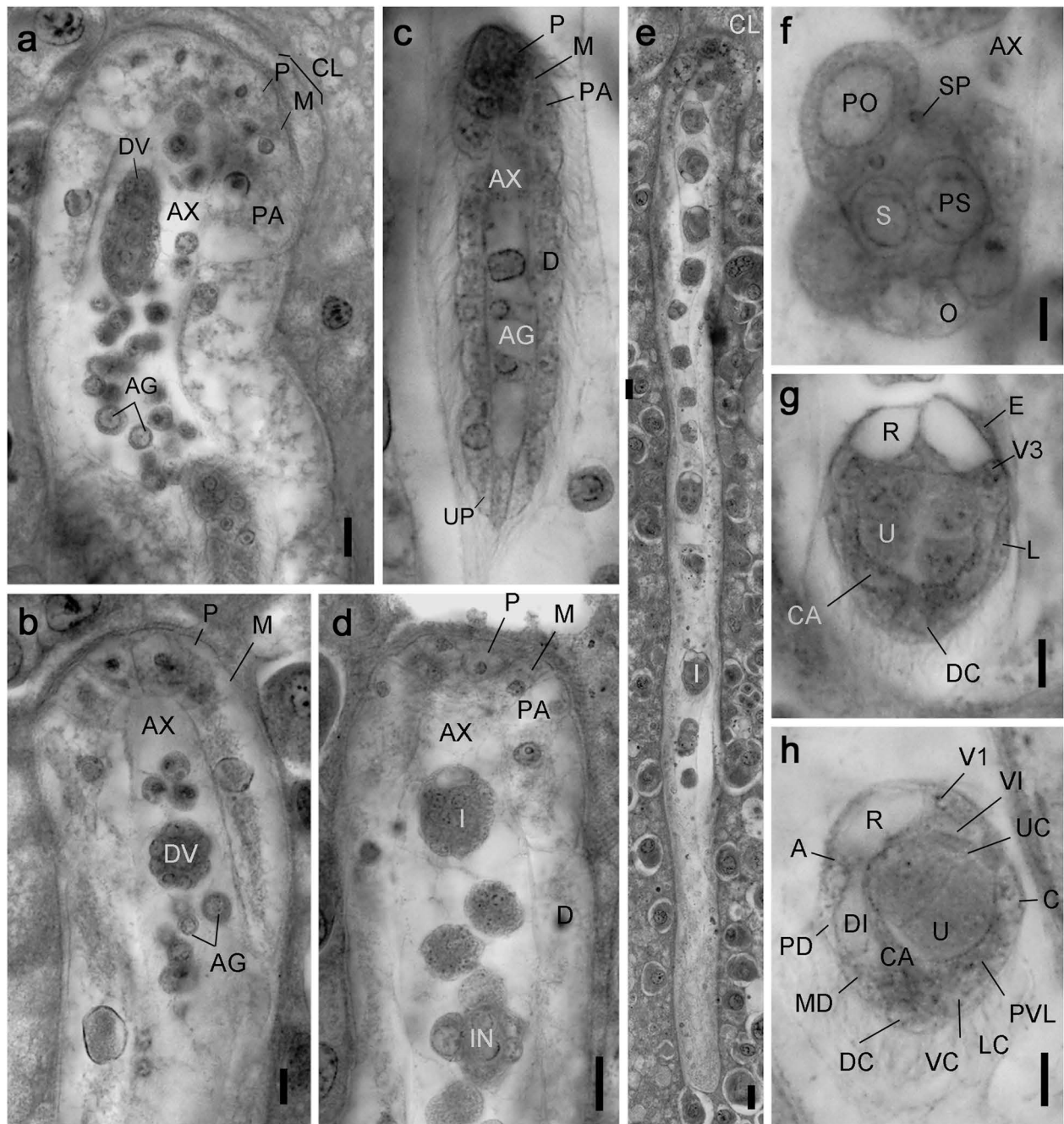


Fig. 16. *Dicyema tenuipoeceum* sp. nov., photographs of syntype specimens on slide NSMT-Me-62: a, b, Nematogen, anterior region; c, vermiform embryo within axial cell; d, rhombogen, anterior region; e, rhombogen, entire; f, infusorigen; g, h, infusoriform embryos, horizontal section (g), sagittal section (h). Scale bars: 10 µm.

guished from *D. schulzianum* in the maximum number of infusorigens and geographical distribution.

Etymology. The species name “*tenuipoeceum*” is composed of the epithet of the host, *tenuipes*, and the Ancient Greek word *oiceon*, meaning “inhabiting” in reference to its host.

Taxonomic summary. *Type material:* a syntype slide (NSMT-Me-62) collected on 10 April 2016; additional syntypes on slide series No. ST3503 (5 slides) in the author’s collection.

Type locality: off Minami-Ise (34°04’N, 136°36’E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 260 m.

Other materials examined: slide series No. ST3763 (5 slide) collected off Owase (34°04’N, 136°33’E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 300 m, 22 January 2018, in the author’s collection.

Host: symbiotype, *Sepia tenuipes* Sasaki, 1929 (Mollusca: Cephalopoda: Sepiida), female (mature), 85 mm ML (NSMT-Mo-85905).

Collector of host: T. Moritaki.

Site: anterior ends (calottes) attach to surfaces of the renal appendages within the renal sacs.

Prevalence: in 36 of 91 host specimens examined (39.6%).

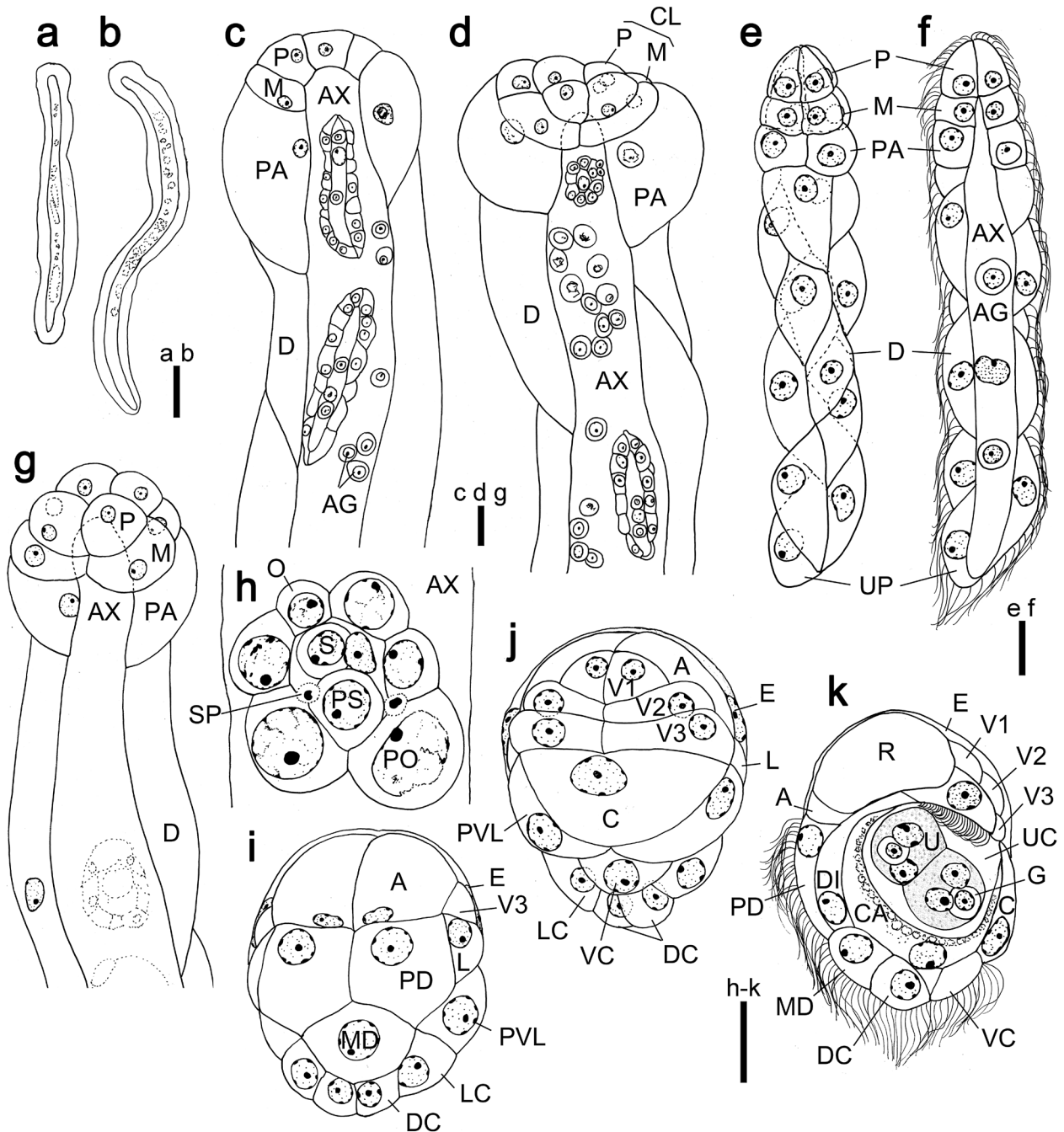


Fig. 17. *Dicyema tenuipoeceum* sp. nov., drawn from syntype specimens on slide NSMT-Me-62: a, Nematogen, entire; b, rhombogen, entire; c, d, nematogen, anterior region; e, f, vermiform embryo within axial cell, cilia omitted (e), optical section (f); g, rhombogen, anterior region; h, infusorigen; i-k, infusoriform embryos, dorsal view (i: cilia omitted), ventral view (j: cilia omitted), sagittal section (k). Scale bars: a, b, 100 μ m; c-k, 10 μ m.

Dicyema tympanocephalum Furuya, sp. nov.

[New Japanese name: Taiko-nihaichū]

(Figs 18, 19; Tables 1–3)

Diagnosis. Small-sized dicyemid, body length reaching 1540 μ m. Calotte disc-shaped. Vermiform stages with 22 peripheral cells: 4 propolar cells+4 metapolar cells+2 parapolar cells+12 trunk cells. Infusoriform embryos with 37 cells; refringent bodies solid; and 2 nuclei present in each urn cell.

Description. *Nematogens* (Figs 18a, b, 19a, c, d). Body length 450–1420 μ m, width 42–105 μ m; widest in region

of parapolars; trunk width mostly uniform. Peripheral cell number 22 (Table 2): 4 propolar cells+4 metapolar cells+2 parapolar cells+10 diapolar cells+2 uropolar cells. Calotte disc-shaped, rounded anteriorly; cilia about 4 μ m long, oriented anteriorly. Propolar cells equal to or larger than metapolar cells, their nuclei equal to or smaller than metapolar cell nuclei. Propolar cells occupy anterior 40–50% of calotte length when viewed laterally (Fig. 19c). Axial cell cylindrical, pointed anteriorly, extending forward to base of propolar cells (Figs 18b, 19c). About 20 vermiform embryos present per axial cell of large individuals. Accessory nuclei seen

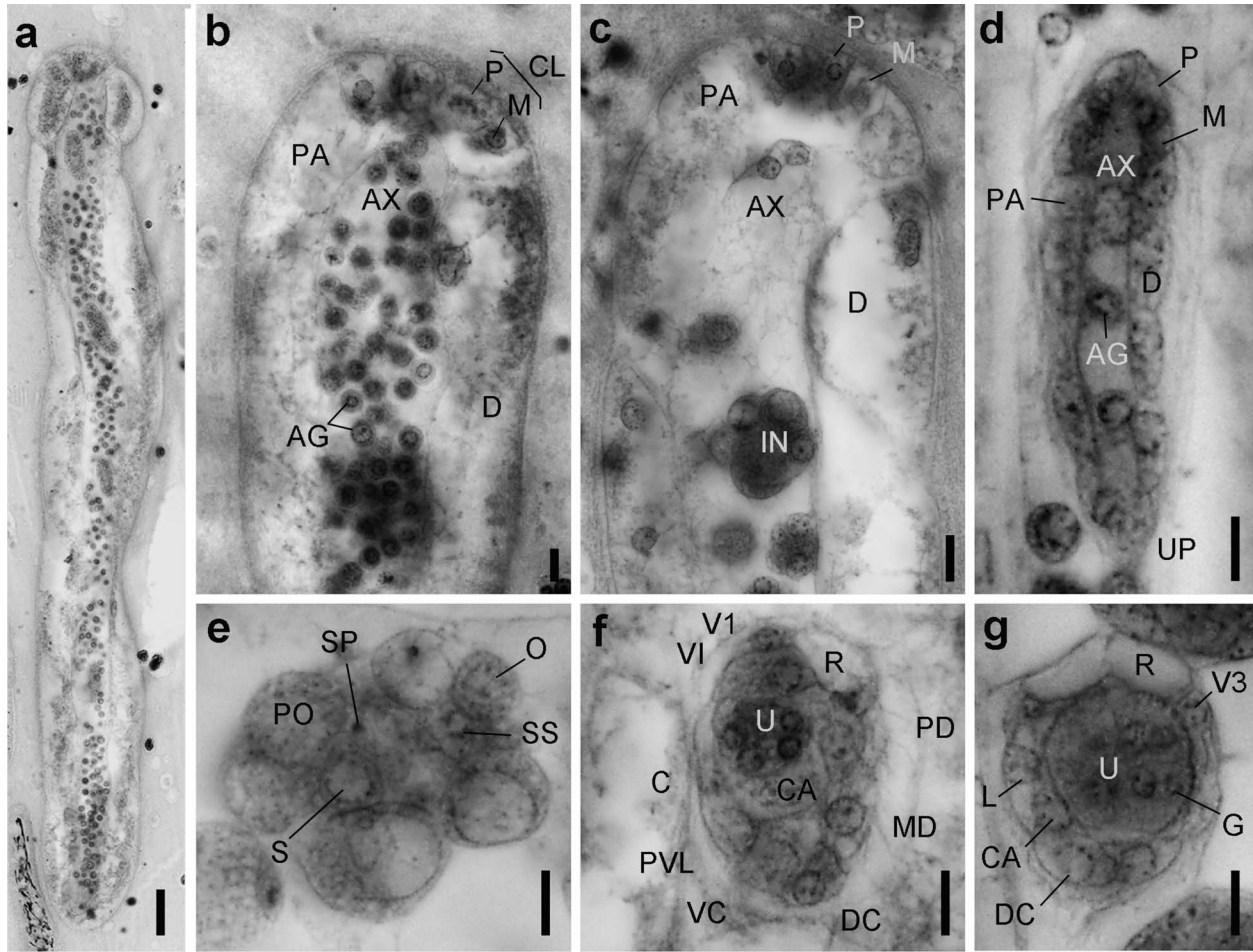


Fig. 18. *Dicyema tympanocephalum* sp. nov., photographs of syntype specimens on slide NSMT-Me-65: a, Nematogen, entire; b, nematogen, anterior region; c, nematogen, anterior region; d, vermiform embryo within axial cell; e, infusorigen; f, g, infusoriform embryos, sagittal section (f), horizontal section (g). Scale bars: a, 50 μ m; b–g, 10 μ m.

in trunk peripheral cells.

Vermiform embryos (Figs 18d, 19e, f). Full-grown vermiform embryos length 51–79 μ m, 12–20 μ m in width. Peripheral cell number 22 (Table 2); trunk cells arranged in opposed pairs. Anterior end of calotte rounded. Axial cell pointed anteriorly, extending to the base of propolar cells (Fig. 19f). Axial cell of full-grown embryos with 2 agametes.

Rhombogens (Figs 18c, 19g). Body length 550–1380 μ m, similar to that of nematogens, in length and 50–95 μ m in width. Peripheral cell number typically 22 (Table 2). Calotte, axial cell shape and anterior extent similar to nematogens. Maximum of 2 infusorigens present in the axial cell of each parent individual. About 25 infusoriform embryos present per axial cell of large individuals.

Infusorigens (Figs 18e, 19h; $n=20$). Mature infusorigens medium-sized; composed of 10–20 (mode 12) external cells (oogonia and primary oocytes)+3–6 (mode 4) internal cells (spermatogonia, primary spermatocytes, and secondary spermatocytes)+3–7 (mode 4) spermatozoa. Mean diameter of fertilized eggs 12.7 μ m; that of spermatozoa 2.6 μ m. Axial cell round or ovoid, diameter 12–20 μ m.

Infusoriform embryos (Figs 18f, g, 19i–k; $n=20$). Full-grown embryos large, length 26.7 ± 2.3 μ m (mean \pm SD, excluding cilia); length–width–height ratio 1.0:0.87:0.84;

shape ovoid, pointed posteriorly; cilia at posterior end 7 μ m long. Refrangent bodies present, solid, occupying anterior 50–60% of embryo length when viewed laterally (Figs 18f, 19k). Cilia project from ventral internal cells into urn cavity (Fig. 19k). Capsule cells contain small granules (Figs 18g, 19k). Mature embryos with 37 cells: 33 somatic+4 germinal cells. Somatic cells of several types present: external cells covering large part of anterior and lateral surfaces of embryo (2 enveloping cells); external cells with cilia on external surfaces (2 pairs of dorsal cells+1 median dorsal cell+2 dorsal caudal cells+2 lateral caudal cells+1 ventral caudal cell+2 lateral cells+2 posteroventral lateral cells), external cells with refringent bodies (2 apical cells); external cells without cilia (1 couvercle cell+2 first ventral cells+2 second ventral cells+2 third ventral cells); internal cells with cilia (2 ventral internal cells); and internal cells without cilia (2 dorsal internal cells+2 capsule cells+4 urn cells). Each urn cell containing 2 nuclei and a germinal cell (Fig. 19k). All somatic nuclei pycnotic in mature infusoriform embryos.

Remarks. *Dicyema tympanocephalum* sp. nov. is similar to *D. balamuthi*, *D. clavatum*, *D. colurum*, *D. hadrum*, *D. japonicum*, and *D. schulzianum*, and *D. tenuipoeceum* sp. nov. in the calotte shape of vermiform stages and peripheral cell numbers (Beneden 1876; McConnaughey 1949; Furuya et

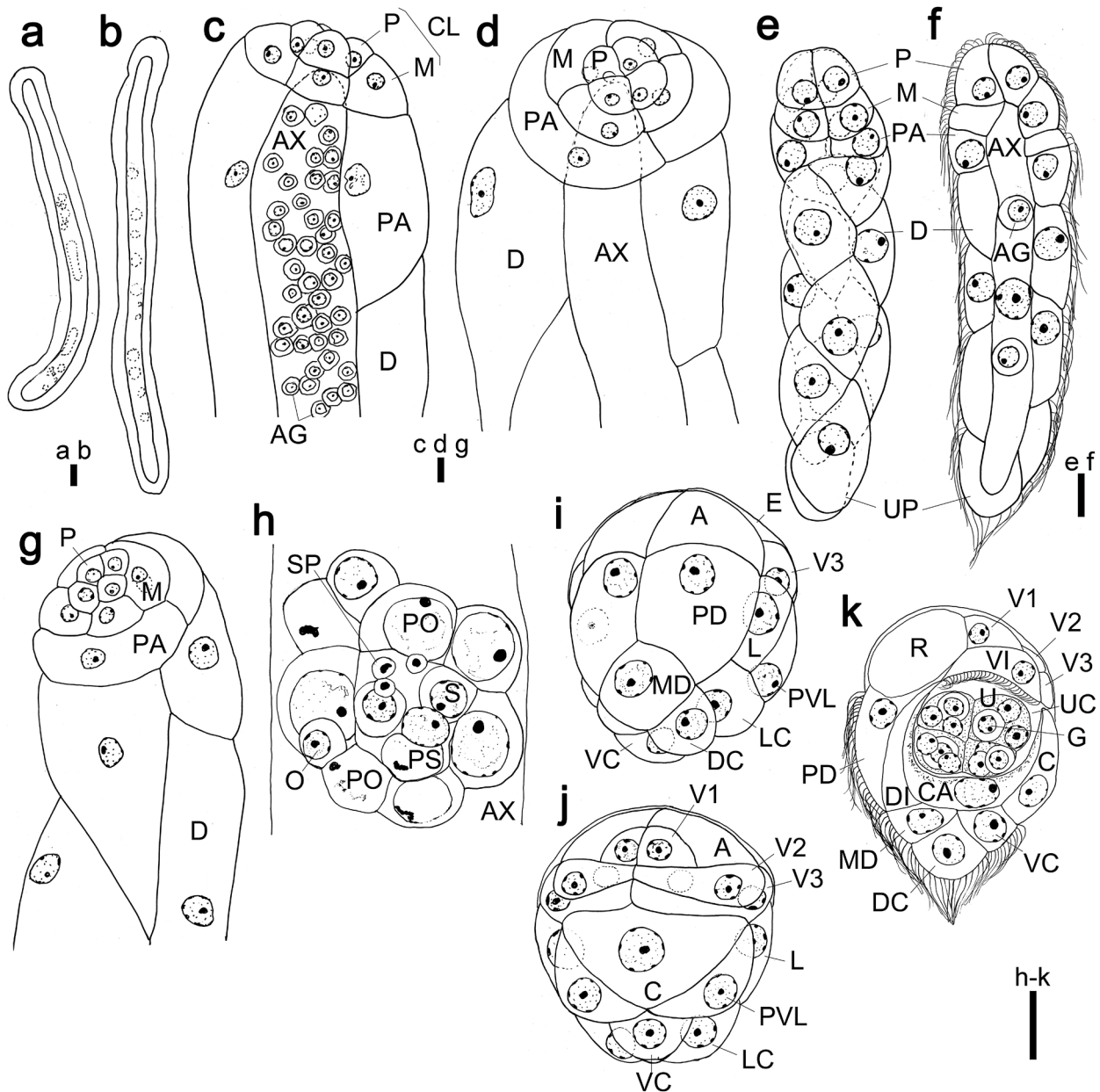


Fig. 19. *Dicyema tympanocephalum* sp. nov., drawn from syntype specimens on slide NSMT-Me-65: a, Nematogen, entire; b, rhombogen, entire; c, d, nematogen, anterior region; e, f, vermiform embryo within axial cell, cilia omitted (e), optical section (f); g, rhombogen, anterior region; h, infusorigen; i–k, infusoriform embryos, dorsal view (i: cilia omitted), ventral view (j: cilia omitted), sagittal section (k). Scale bars: a, b, 50 μ m; c–k, 10 μ m.

al. 1992a; Furuya 1999). However, *D. tympanocephalum* sp. nov. is distinguishable from *D. balamuthi*, *D. clavatum*, *D. colurum*, and *D. hadrum* in the cell number of infusoriform embryos (37 vs. 39).

Dicyema tympanocephalum sp. nov. shares the same cell number of infusoriform embryos with *D. japonicum*, *D. schulzianum*, and *D. tenuipoeceum* sp. nov., but *D. tympanocephalum* sp. nov. infusoriform embryos have third ventral cells instead of the anterior lateral cells. The rhombogens of *D. tympanocephalum* sp. nov. have at most two infusorigens, while those of *D. tenuipoeceum* sp. nov. have four. Therefore, *D. tympanocephalum* sp. nov. can be distinguishable from *D. japonicum* and *D. tenuipoeceum* sp. nov.

Dicyema tympanocephalum sp. nov. is very similar to *D.*

schulzianum in morphological characters except in the maximum size of adult vermiform stages. Large adult individuals of *D. tympanocephalum* sp. nov. reach nearly 1500 μ m in length, while those of *D. schulzianum* are at most 1000 μ m. *Dicyema schulzianum* is recorded from *S. elegans* and *R. minor* in the western Mediterranean (Beneden 1876; Nouvel 1947). In dicyemids, differences found in host species and geographical distribution represent empirically distinct species. Thus, *D. tympanocephalum* sp. nov. can be separated confidently from *D. schulzianum* by differences in the maximum size of adult vermiform stages, host species and geographical distribution.

Etymology. The species name “*tympanocephalum*” is an adjective composed of two Ancient Greek roots, *tympano*

and *-kephalos*, meaning “drum” and “-headed” in reference to the characteristic anterior part of adult vermiform stages.

Taxonomic summary. *Type material*: a syntype slide (NSMT-Me-65) collected on 14 February 2018; additional syntypes on slide series No. SL5779 (5 slides) in the author's collection.

Type locality: off Minami-Ise (34°08'N, 136°04'E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 180 m.

Other materials examined: None.

Host: symbiotype, *Sepia lorigera* Wülker, 1910 (Mollusca: Cephalopoda: Sepiida), male (mature), 157 mm ML (NSMT-Mo-85907).

Collector of host: T. Moritaki.

Site: anterior ends (calottes) attach to surfaces of the renal appendages within the renal sacs.

Prevalence: in 1 of 10 host specimens examined (10.0%).

Genus *Pseudicyema* Nouvel, 1933

Pseudicyema anemophilum sp. nov.

[New Japanese name: Kazeno-nihaichū]

(Figs 20, 21; Tables 1–3)

Diagnosis. Small-sized dicyemid, body length reaching 1250 µm. Calotte cap-shaped. Vermiform stages with 29–34 peripheral cells: 4 propolar cells+4 metapolar cells+2 parapolar cells+19–24 trunk cells. Infusoriform embryos with 39 cells; refringent bodies solid; and 2 nuclei present in each urn cell.

Description. *Nematogens* (Figs 20a, b, 21a, c). Body length 650–1250 µm, width 65–75 µm; widest in region of parapolars; trunk width mostly uniform. Peripheral cell number 29–34 (Table 2): 4 propolar cells+4 metapolar cells+2 parapolar cells+17–22 diapolar cells+2 uropolar cells. Calotte cap-shaped, rounded anteriorly; cilia about 4 µm long, oriented anteriorly. Propolar cells equal to or larger than metapolar cells, their nuclei equal to or smaller than metapolar cell nuclei. Propolar cells occupy anterior 50% of calotte length when viewed laterally (Figs 20a, b, 21c). Cytoplasm of propolar cells more darkly stained by hematoxylin than that of other peripheral cells (Fig. 20a, b). Axial cell cylindrical, rounded anteriorly, extending forward to base of propolar cells (Fig. 20a, b). About 6 vermiform embryos present per axial cell of large individuals. Accessory nuclei seen in trunk peripheral cells.

Vermiform embryos (Figs 20c, 21d, e). Full-grown vermiform embryos length 52–77 µm, 17–19 µm in width. Peripheral cell number 29–34 (Table 2); trunk cells arranged in opposed pairs. Anterior end of calotte rounded. Axial cell pointed anteriorly, extending to the base of propolar cells (Figs 20c, 21d, e). Axial cell of full-grown embryos with 2 agametes.

Rhombogens (Figs 20d, 21f, g). Body length similar 480–1100 µm, similar to that of nematogens, in length and 40–52 µm in width. Peripheral cell number typically 29–34 (Table 2). Calotte, axial cell shape and anterior extent similar to nematogens. Maximum of 2 infusorigens present in the axial cell of each parent individual. About 15 infusoriform embryos present per axial cell of large individuals.

Infusorigens (Figs 20g, 21h; n=20). Mature infusorigens medium-sized; composed of 5–12 (mode 5) external cells (oogonia and primary oocytes)+2–4 (mode 4) internal cells (spermatogonia, primary spermatocytes, and secondary spermatocytes)+3–9 (mode 6) spermatozoa. Mean diameter of fertilized eggs 11.7 µm; that of spermatozoa 2.5 µm. Axial cell round or ovoid, diameter 11–18 µm.

Infusoriform embryos (Figs 20e, f, 21i–k; n=20). Full-grown embryos large, length 22.6 ± 1.4 µm (mean \pm SD, excluding cilia); length–width–height ratio 1.0:0.84:0.78; shape ovoid, pointed posteriorly; cilia at posterior end 7 µm long. Refringent bodies present, solid, occupying anterior 30–40% of embryo length when viewed laterally (Fig. 20f). Cilia project from ventral internal cells into urn cavity (Fig. 21k). Capsule cells contain small granules (Fig. 21k). Mature embryos with 39 cells: 35 somatic+4 germinal cells. Somatic cells of several types present: external cells covering large part of anterior and lateral surfaces of embryo (2 enveloping cells); external cells with cilia on external surfaces (2 pairs of dorsal cells+1 median dorsal cell+2 dorsal caudal cells+2 lateral caudal cells+1 ventral caudal cell+2 lateral cells+2 posteroventral lateral cells); external cells with refringent bodies (2 apical cells); external cells without cilia (1 covercle cell+2 anterior lateral cells+2 first ventral cells+2 second ventral cells+2 third ventral cells); internal cells with cilia (2 ventral internal cells); and internal cells without cilia (2 dorsal internal cells+2 capsule cells+4 urn cells). Each urn cell containing 2 nuclei and a germinal cell (Fig. 21k). All somatic nuclei pycnotic in mature infusoriform embryos.

Remarks. *Pseudicyema anemophilum* sp. nov. is the first species of the genus found in *Sepia kobeensis* and only the fourth species to be described in the genus. It is distinguishable from other 2 species, *P. truncatum* (Whitman, 1883) and *P. nakaoi* Furuya, 1999, in the calotte shape (cap-shaped vs. disc-shaped) and the number of peripheral cells of vermiform stages (29–34 vs. 22) (Nouvel 1947; Furuya 1999). *Pseudicyema anemophilum* sp. nov. is very similar to *P. capacephalum* Furuya, 2009 in the calotte shape and the number of infusoriform embryos but the new species is clearly distinguished by the maximum number of infusorigens (2 vs. 3) and the range of peripheral cells of vermiform stages (29–34 vs. 32–34) (Furuya 2009).

Etymology. The species name is an adjective composed of two Ancient Greek roots, *anemos* and *-philos* meaning “wind” and “like”, because host specimens were all collected under windy conditions.

Taxonomic summary. *Type material*: a syntype slide (NSMT-Me-60) collected on 14 April 2018; additional syntypes on slide series No. SK5792 (5 slides) in the author's collection.

Type locality: off Owase (34°01'N, 136°35'E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 150 m.

Other materials examined: slide series No. SK3515, 3516 (each 5 slide) collected off Minami-Ise (34°08'N, 136°35'E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 150 m, in the author's collection.

Host: symbiotype, *Sepia kobeensis* Hoyle, 1855 (Mollus-

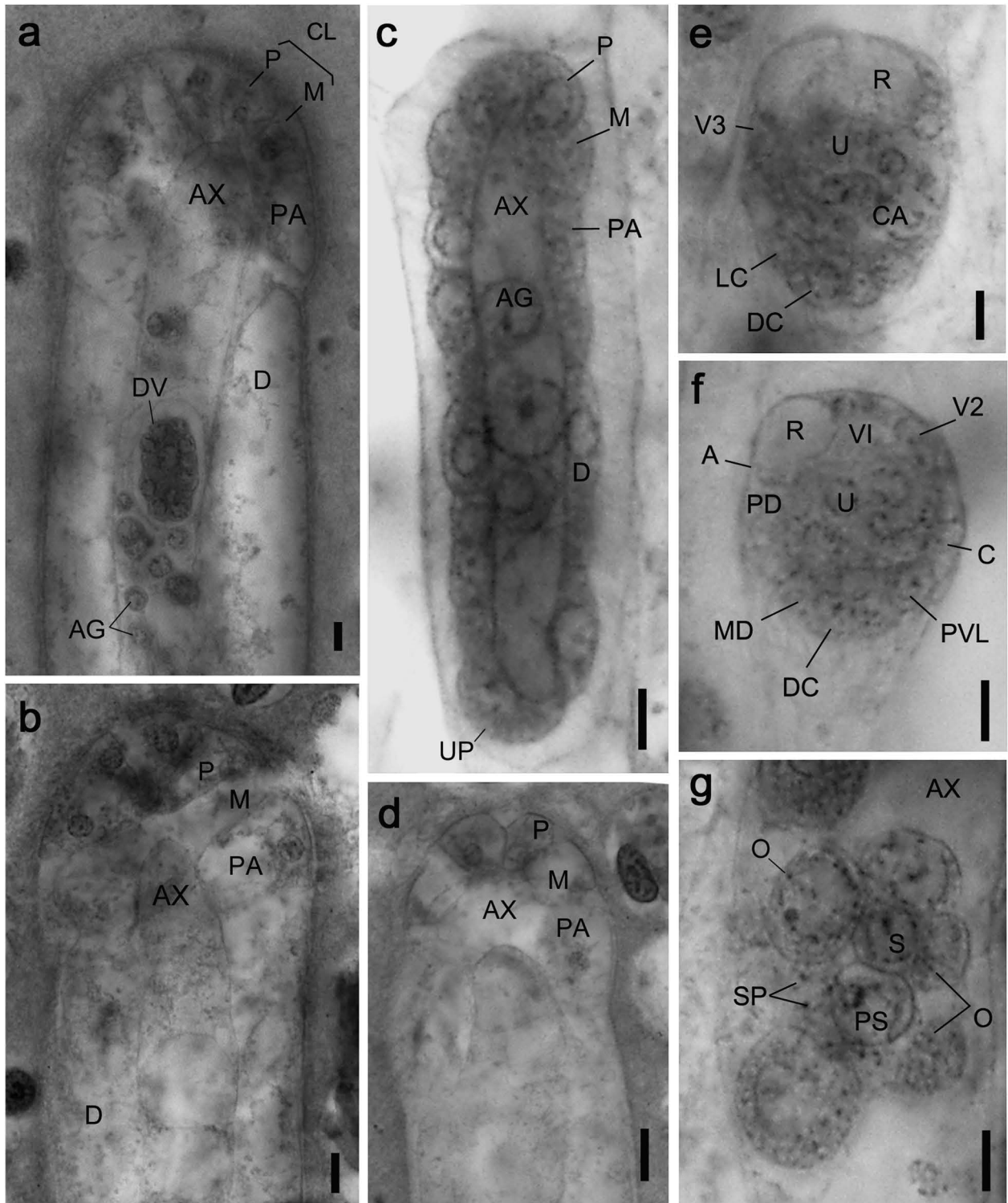


Fig. 20. *Pseudicyema anomophilum* sp. nov., photographs of syntype specimens on slide NSMT-Me-60: a, b, Nematogen, anterior region; c, vermiform embryos within axial cell; d, rhombogen, anterior region; e, f, infusoriform embryos, horizontal section (e), sagittal section (f); g, infusorigen. Scale bars: 10 μ m.

ca: Cephalopoda: Sepiida), female (immature), 79 mm ML (NSMT-Mo-85903).

Collector of host: T. Moritaki.

Site: anterior ends (calottes) attach to surfaces of the renal appendages or inserted into crypts of the renal appendages within the renal sacs.

Prevalence: in 7 of 30 host specimens examined (23.3%).

Pseudicyema cupulacephalum sp. nov.

[New Japanese name: Kupura-nihaichū]

(Figs 22, 23; Tables 1–3)

Diagnosis. Small-sized dicyemid, body length reaching 1150 μ m. Calotte cap-shaped. Vermiform stages with 29–35 peripheral cells: 4 propolar cells+4 metapolar cells+

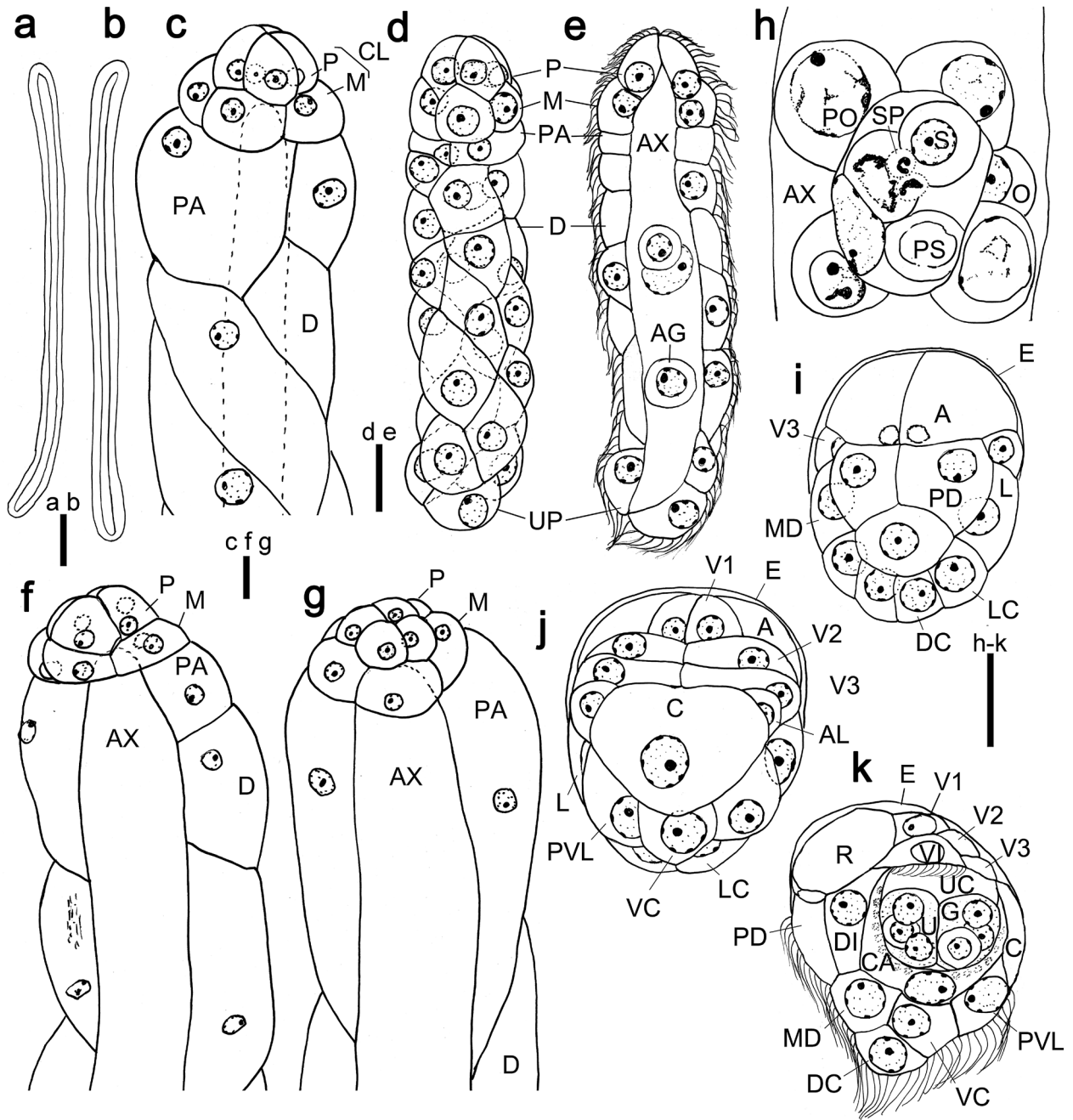


Fig. 21. *Pseudicyema anemophilum* sp. nov., drawn from syntype specimens on slide NSMT-Me-60: a, Nematogen, entire; b, rhombogen, entire; c, nematogen, anterior region; d, e, vermiform embryo within axial cell, cilia omitted (d), optical section (e); f, g, rhombogen, anterior region; h, infusorigen; i–k, infusoriform embryos, dorsal view (i: cilia omitted), ventral view (j: cilia omitted), sagittal section (k). Scale bars: a, b, 100 μ m; c–k, 10 μ m.

2 parapolar cells+19–25 trunk cells. Infusoriform embryos with 39 cells; refringent bodies solid; and 2 nuclei present in each urn cell.

Description. *Nematogens* (Figs 22a–c, 23a, c). Body length 450–980 μ m, width 40–60 μ m; widest in region of parapolars; trunk width mostly uniform. Peripheral cell number 29–35 (Table 2): 4 propolar cells+4 metapolar cells+2 parapolar cells+17–23 diapolar cells+2 uropolar cells. Calotte cap-shaped, rounded anteriorly; cilia about 4 μ m long, oriented anteriorly. Propolar cells equal to or larger than metapolar cells, their nuclei equal to or smaller than metapolar cell nuclei. Propolar cells occupy anterior

40–50% of calotte length when viewed laterally (Figs 22b, 23c). Cytoplasm of propolar cells more darkly stained by hematoxylin than that of other peripheral cells (Fig. 22a–c). Axial cell cylindrical, rounded anteriorly, extending forward to the base of metapolar cells (Fig. 22a, b). About 6 vermiform embryos present per axial cell of large individuals. Accessory nuclei seen in trunk peripheral cells.

Vermiform embryos (Figs 22d, 23d, e). Full-grown vermiform embryos length 57–105 μ m, 14–20 μ m in width. Peripheral cell number 29–35 (Table 2); trunk cells arranged in opposed pairs. Anterior end of calotte rounded. Axial cell pointed anteriorly, extending to the base of propolar cells

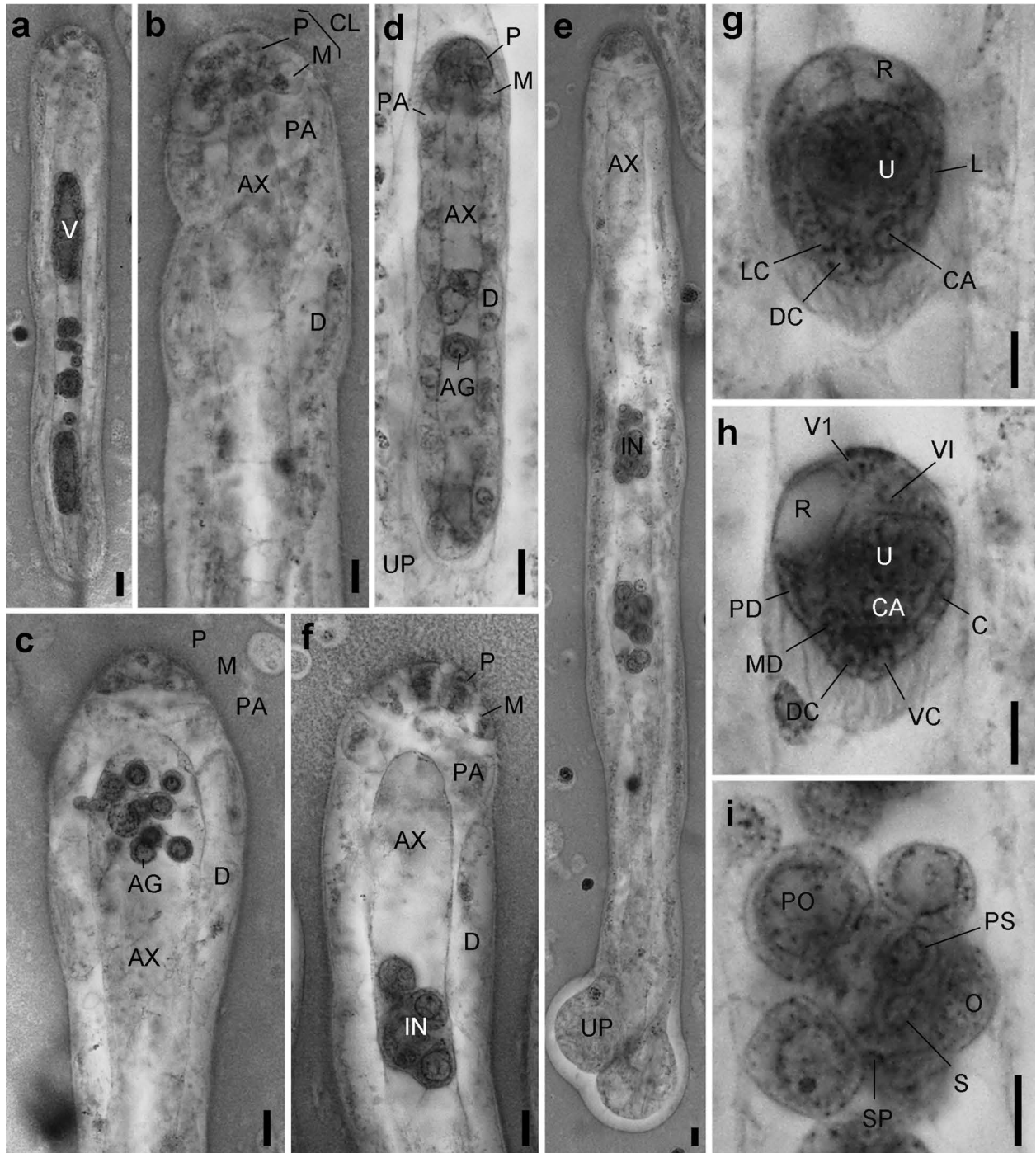


Fig. 22. *Pseudicyema cupulacephalum* sp. nov., photographs of syntype specimens on slide NSMT-Me-66: a, Nematogen, entire; b, c, nematogen, anterior region; d, vermiform embryos within axial cell; e, rhombogen, entire; f, rhombogen, anterior region; g, h, infusoriform embryos, horizontal section (g), sagittal section (h); i, infusorigen. Scale bars: 10 μ m.

(Figs 22d, 23e). Axial cell of full-grown embryos with 2 agametes.

Rhombogens (Figs 22d, 23f, g). Body length 680–1150 μ m, similar to that of nematogens, in length and 35–60 μ m in width. Peripheral cell number typically 29–35 (Table 2). Calotte, axial cell shape and anterior extent similar to nematogens. Maximum of 3 infusorigens present in the axial cell of each parent individual. About 35 infusoriform embryos present per axial cell of large individuals.

Infusorigens (Figs 22i, 23h; $n=20$). Mature infusorigens

medium-sized; composed of 3–9 (mode 6) external cells (oogonia and primary oocytes)+2–4 (mode 3) internal cells (spermatogonia, primary spermatocytes, and secondary spermatocytes)+2–11 (mode 4) spermatozoa. Mean diameter of fertilized eggs 11.2 μ m; that of spermatozoa 2.0 μ m. Axial cell round or ovoid, diameter 11–16 μ m.

Infusoriform embryos (Figs 22e, f, 23i–k; $n=20$). Full-grown embryos large, length $21.6 \pm 1.2 \mu$ m (mean \pm SD, excluding cilia); length–width–height ratio 1.0:0.85:0.83; shape ovoid, pointed posteriorly; cilia at posterior end 7 μ m

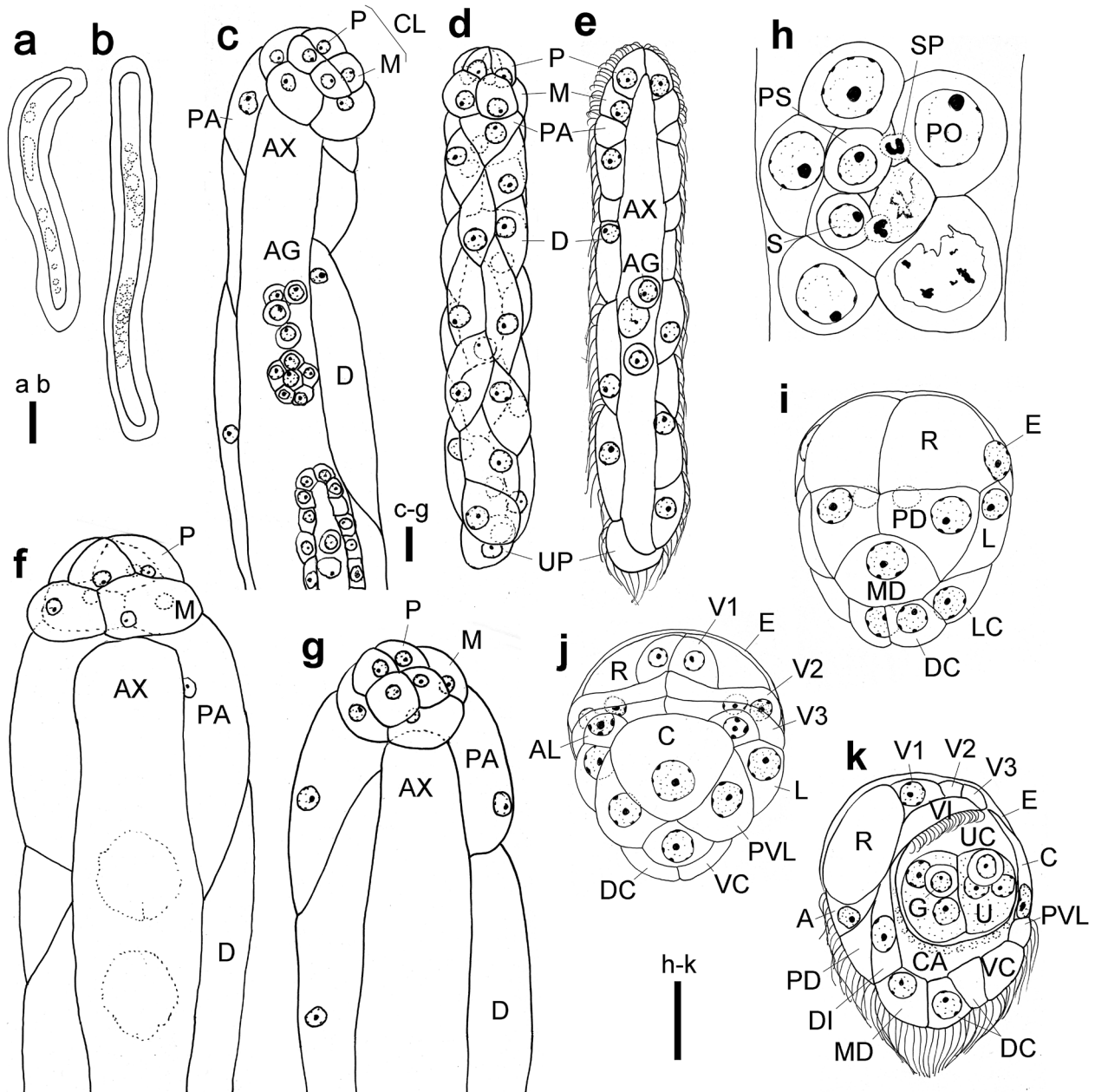


Fig. 23. *Pseudicyema cupulacephalum* sp. nov., drawn from syntype specimens on slide NSMT-Me-66: a, Nematogen, entire; b, rhombogen, entire; c, nematogen, anterior region; d, e, vermiform embryo within axial cell, cilia omitted (d), optical section (e); f, g, rhombogen, anterior region; h, infusorigen; i–k, infusoriform embryos, dorsal view (i: cilia omitted), ventral view (j: cilia omitted), sagittal section (k). Scale bars: a, b, 50 µm; c–k, 10 µm.

long. Refrangent bodies present, solid, occupying anterior 30–40% of embryo length when viewed laterally (Figs 22h, 23k). Cilia project from ventral internal cells into urn cavity (Fig. 23k). Capsule cells contain small granules (Fig. 23k). Mature embryos with 39 cells: 35 somatic+4 germinal cells. Somatic cells of several types present: external cells covering large part of anterior and lateral surfaces of embryo (2 enveloping cells); external cells with cilia on external surfaces (2 pairs of dorsal cells+1 median dorsal cell+2 dorsal caudal cells+2 lateral caudal cells+1 ventral caudal cell+2 lateral cells+2 posteroventral lateral cells); external cells with refrangent bodies (2 apical cells); external cells without cilia (1 couvercle cell+2 anterior lateral cells+2 first ventral

cells+2 second ventral cells+2 third ventral cells); internal cells with cilia (2 ventral internal cells); and internal cells without cilia (2 dorsal internal cells+2 capsule cells+4 urn cells). Each urn cell containing 2 nuclei and a germinal cell (Fig. 23k). All somatic nuclei pycnotic in mature infusoriform embryos.

Remarks. *Pseudicyema cupulacephalum* sp. nov. is the first species of the genus found in *S. lorigera* and is the fifth species to be described in this genus. It is distinguishable from two other species, *P. truncatum* and *P. nakaoi*, in the calotte shape (cap-shaped vs. disc-shaped) and the number of peripheral cells of vermiform stages (29–35 vs. 22) (Whitman 1883; Nouvel 1947; Furuya 1999). *Pseudicyema cupula-*

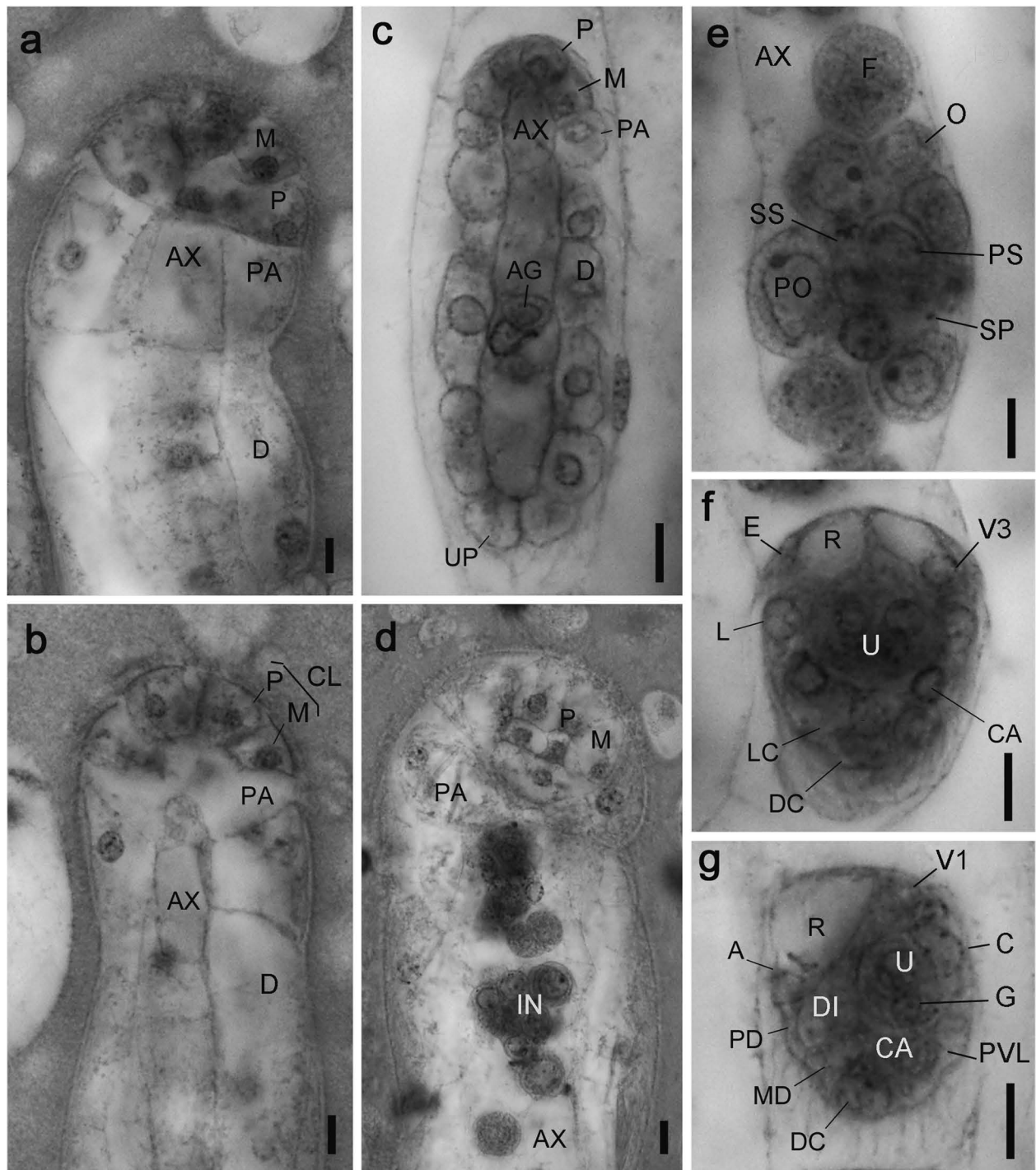


Fig. 24. *Pseudicyema daioense* sp. nov., photographs of syntype specimens on slide NSMT-Me-67: a, b, Nematogen, anterior region; c, vermiform embryos within axial cell; d, rhombogen, anterior region; e, infusorigen; f, g, infusoriform embryos, horizontal section (f), sagittal section (g). Scale bars: 10 μ m.

cephalum sp. nov. is very similar to *P. cappacephalum*, and *P. anemophilum* sp. nov. in the calotte shape and the number of infusoriform embryos, but is distinguished by the maximum number of infusorigens (2 vs. 3) and the range of peripheral cells of vermiform stages (29–35 vs. 32–34 and 29–34) (Furuya 2009).

Etymology. The species name “*cupulacephalum*” is an adjective composed of two Ancient Greek roots, *kýpello* and *-kephalos*, meaning “cup” and “-headed” in reference to the

characteristic anterior part of vermiform embryos.

Taxonomic summary. *Type material:* a syntype slide (NSMT-Me-66) collected on 14 December 2018; additional syntypes on slide series No. SL3920 (5 slides) in the author’s collection.

Type locality: off Minami-Ise (34°04’N, 136°33’E), Mie Prefecture, Honshu, the Kuman Sea, Japan, depth 250 m.

Other materials examined: slide series No. SL4118 (5 slides) collected off Minami-Ise (34°09’N, 136°36’E), Mie

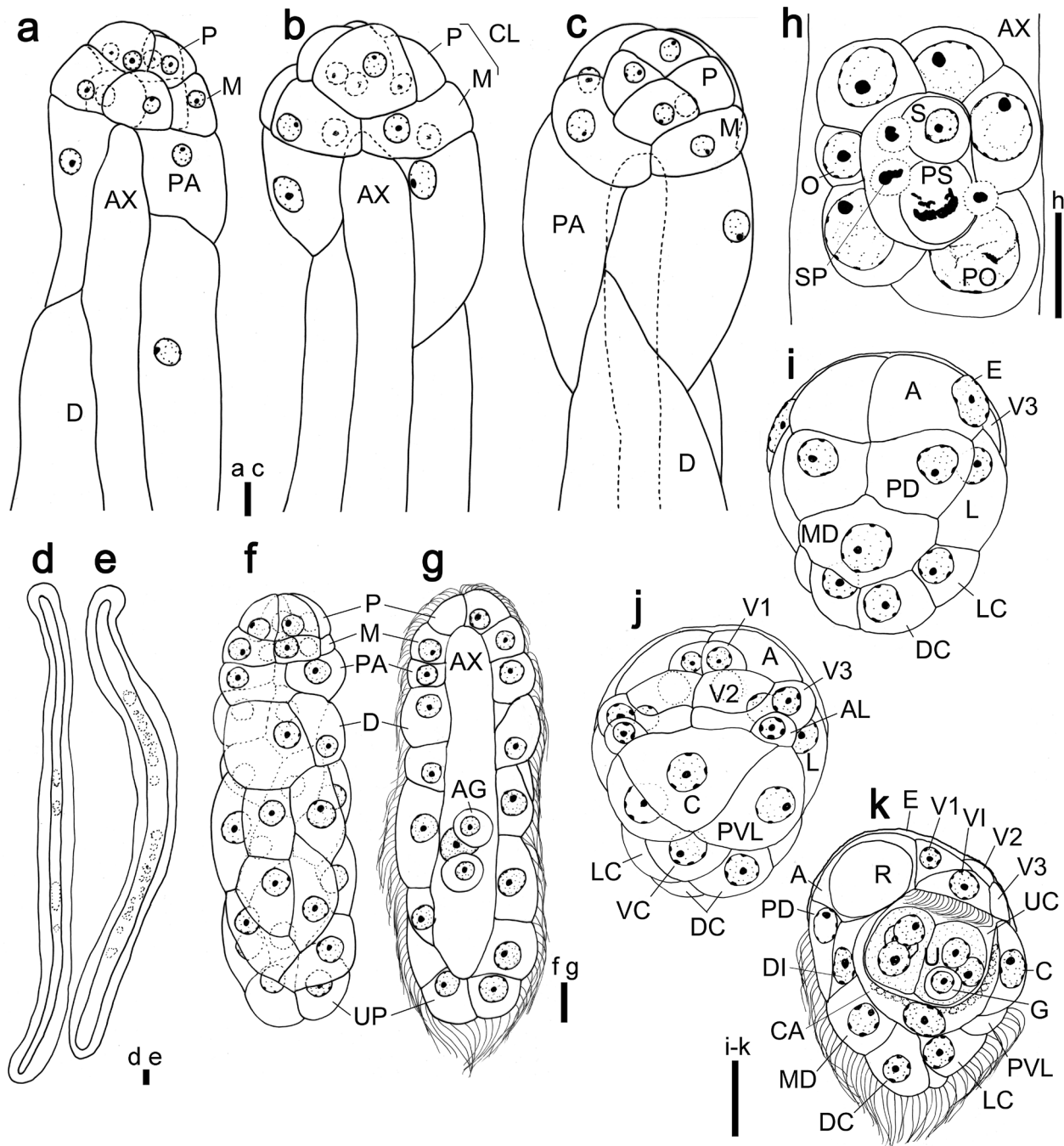


Fig. 25. *Pseudicyema daioense* sp. nov., drawn from syntype specimens on slide NSMT-Me-67: a, b, Nematogen, anterior region; c, rhombogen, anterior region; d, nematogen, entire; e, rhombogen, entire; f, g, vermiform embryo within axial cell, cilia omitted (f), optical section (g); h, infusorigen; i–k, infusoriiform embryos, dorsal view (i: cilia omitted), ventral view (j: cilia omitted), sagittal section (k). Scale bars: 10 μ m.

Prefecture, Honshu, the Kumano Sea, Japan, depth 180 m, 5 December 2019, in the author's collection.

Host: symbiotype, *Sepia lorigero* Wülker, 1910 (Mollusca: Cephalopoda: Sepiida), female (mature), 211 mm ML (NSMT-Mo-85908).

Collector of host: T. Moritaki.

Site: anterior ends (calottes) attach to surfaces of the renal appendages or inserted into crypts of the renal appendages within the renal sacs.

Prevalence: in 3 of 10 host specimens examined (33.3%).

***Pseudicyema daioense* sp. nov.**

[New Japanese name: Daiō-nihaichū]

(Figs 24, 25; Tables 1–3)

Diagnosis. Small- to medium- sized dicyemid, body length reaching 1550 μ m. Calotte cap-shaped. Vermiform stages with 29–35 peripheral cells: 4 propolar cells+4 metapolar cells+2 parapolar cells+19–25 trunk cells. Infusoriiform embryos with 39 cells; refringent bodies solid; and 2 nuclei present in each urn cell.

Description. *Nematogens* (Figs 24a–c, d, 25a, c). Body length 850–1550 µm, width 50–81 µm; widest in region of parapolar cells; trunk width mostly uniform. Peripheral cell number 29–35 (Table 2): 4 propolar cells+4 metapolar cells+2 parapolar cells+17–23 diapolar cells+2 uropolar cells. Calotte cap-shaped, rounded anteriorly; cilia about 4 µm long, oriented anteriorly. Propolar cells equal to or larger than metapolar cells, their nuclei equal to or smaller than metapolar cell nuclei. Propolar cells occupy anterior 50–60% of calotte length when viewed laterally (Figs 24a, b, 25a, b). Cytoplasm of propolar cells more darkly stained by hematoxylin than that of other peripheral cells (Fig. 24a, b). Axial cell cylindrical, rounded anteriorly, extending forward to base of metapolar cells (Figs 24a, b, 25a, b). About 10 vermiform embryos present per axial cell of large individuals. Accessory nuclei seen in trunk peripheral cells.

Vermiform embryos (Figs 24c, 25f, g). Full-grown vermiform embryos length 52–88 µm, 15–21 µm in width. Peripheral cell number 29–35 (Table 2); trunk cells arranged in opposed pairs. Anterior end of calotte rounded. Axial cell rounded anteriorly, extending to the base of propolar cells (Figs 24c, 25g). Axial cell of full-grown embryos with 2 agametes.

Rhombogens (Figs 24d, e, 25c, e). Body length 750–1580 µm, similar to that of nematogens, in length and 42–75 µm in width. Peripheral cell number typically 29–35 (Table 2). Calotte, axial cell shape and anterior extent similar to nematogens. Maximum of 2 infusorigens present in the axial cell of each parent individual. About 60 infusoriform embryos present per axial cell of large individuals.

Infusorigens (Figs 24e, 25h; $n=10$). Mature infusorigens medium-sized; composed of 7–12 (mode 8) external cells (oogonia and primary oocytes)+3–5 (mode 4) internal cells (spermatogonia, primary spermatocytes, and secondary spermatocytes)+4–13 (mode 4) spermatozoa. Mean diameter of fertilized eggs 11.0 µm; that of spermatozoa 3.1 µm. Axial cell round or ovoid, diameter 12–15 µm.

Infusoriform embryos (Figs 24f, g, 25i–k; $n=27$). Full-grown embryos large, length 22.6 ± 2.2 µm (mean \pm SD, excluding cilia); length–width–height ratio 1.0:0.86:0.86; shape ovoid, pointed posteriorly; cilia at posterior end 7 µm long. Refracting bodies present, solid, occupying anterior 40–50% of embryo length when viewed laterally (Figs 24f, 25k). Cilia project from ventral internal cells into urn cavity (Fig. 25k). Capsule cells contain small granules (Fig. 25k). Mature embryos with 39 cells: 35 somatic+4 germinal cells. Somatic cells of several types present: external cells covering large part of anterior and lateral surfaces of embryo (2 enveloping cells); external cells with cilia on external surfaces (2 pairs of dorsal cells+1 median dorsal cell+2 dorsal caudal cells+2 lateral caudal cells+1 ventral caudal cell+2 lateral cells+2 posteroventral lateral cells); external cells with refracting bodies (2 apical cells); external cells without cilia (1 couverte cell+2 anterior lateral cells+2 first ventral cells+2 second ventral cells+2 third ventral cells); internal cells with cilia (2 ventral internal cells); and internal cells without cilia (2 dorsal internal cells+2 capsule cells+4 urn cells). Each urn cell containing 2 nuclei and a germinal cell

(Fig. 25k). All somatic nuclei pycnotic in mature infusoriform embryos.

Remarks. *Pseudicyema daioense* sp. nov. is the first species of the genus found in *S. lorigera* and is very similar to *P. cappacephalum*, *P. anemophilum* sp. nov., and *P. cupulacephalum* sp. nov. in the calotte shape and the number of infusoriform embryos. However, *P. daioense* sp. nov. is distinguished from *P. cappacephalum* and *P. anemophilum* sp. nov. in the anterior extent of adult vermiform stages (metapolar cells vs. propolar cells) (Furuya 2009), and from *P. cupulacephalum* sp. nov. by the shape of anterior axial cell of vermiform embryos (rounded vs. pointed) and the external shape of second ventral cells of infusoriform embryos (extended laterally vs. located ventrally).

Etymology. The species name “*daioense*” refers to the type locality, near Cape Daio in the picturesque Ise-Shima National Park at the northern end of Kumano Sea.

Taxonomic summary. *Type material:* a syntype slide (NSMT-Me-67) collected on 26 February 2016; additional syntypes on slide series No. OL3383 (5 slides) in the author’s collection.

Type locality: off Minami-Ise (34°08’N, 136°34’E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 360 m.

Other materials examined: slide series No. SA3382 (each 5 slide) collected off Minami-Ise (34°08’N, 136°34’E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 360 m, 26 February 2016, in the author’s collection.

Host: symbiotype, *Sepia aureomaculata* Okutani and Horikawa, 1987 (Mollusca: Cephalopoda: Sepiida), male (mature), 82 mm ML (NSMT-Mo-85909).

Site: anterior ends (calottes) attach to surfaces of the renal appendages or inserted into crypts of the renal appendages within the renal sacs.

Prevalence: in 4 of 5 host specimens examined (80%).

Pseudicyema jinshoae sp. nov.

[New Japanese name: Jinsho-nihaichū]

(Figs 26, 27; Tables 1–3)

Diagnosis. Small-sized dicyemid, body length reaching 1210 µm. Calotte cap-shaped. Vermiform stages with 30–35 peripheral cells: 4 propolar cells+4 metapolar cells+2 parapolar cells+20–25 trunk cells. Infusoriform embryos with 39 cells; refracting bodies solid; and 2 nuclei present in each urn cell.

Description. *Nematogens* (Figs 26a, b, 27a, c, d). Body length 800–1210 µm, width 38–50 µm; widest in region of parapolar cells; trunk width mostly uniform. Peripheral cell number 30–35 (Table 2): 4 propolar cells+4 metapolar cells+2 parapolar cells+18–23 diapolar cells+2 uropolar cells. Calotte cap-shaped, rounded anteriorly; cilia about 4 µm long, oriented anteriorly. Propolar cells equal to or larger than metapolar cells, their nuclei equal to or smaller than metapolar cell nuclei. Propolar cells occupy anterior 50–60% of calotte length when viewed laterally (Figs 26a, b, 27c, d). Cytoplasm of propolar cells more darkly stained by hematoxylin than that of other peripheral cells (Fig. 26a, b). Axial cell cylindrical, rounded anteriorly, extending from

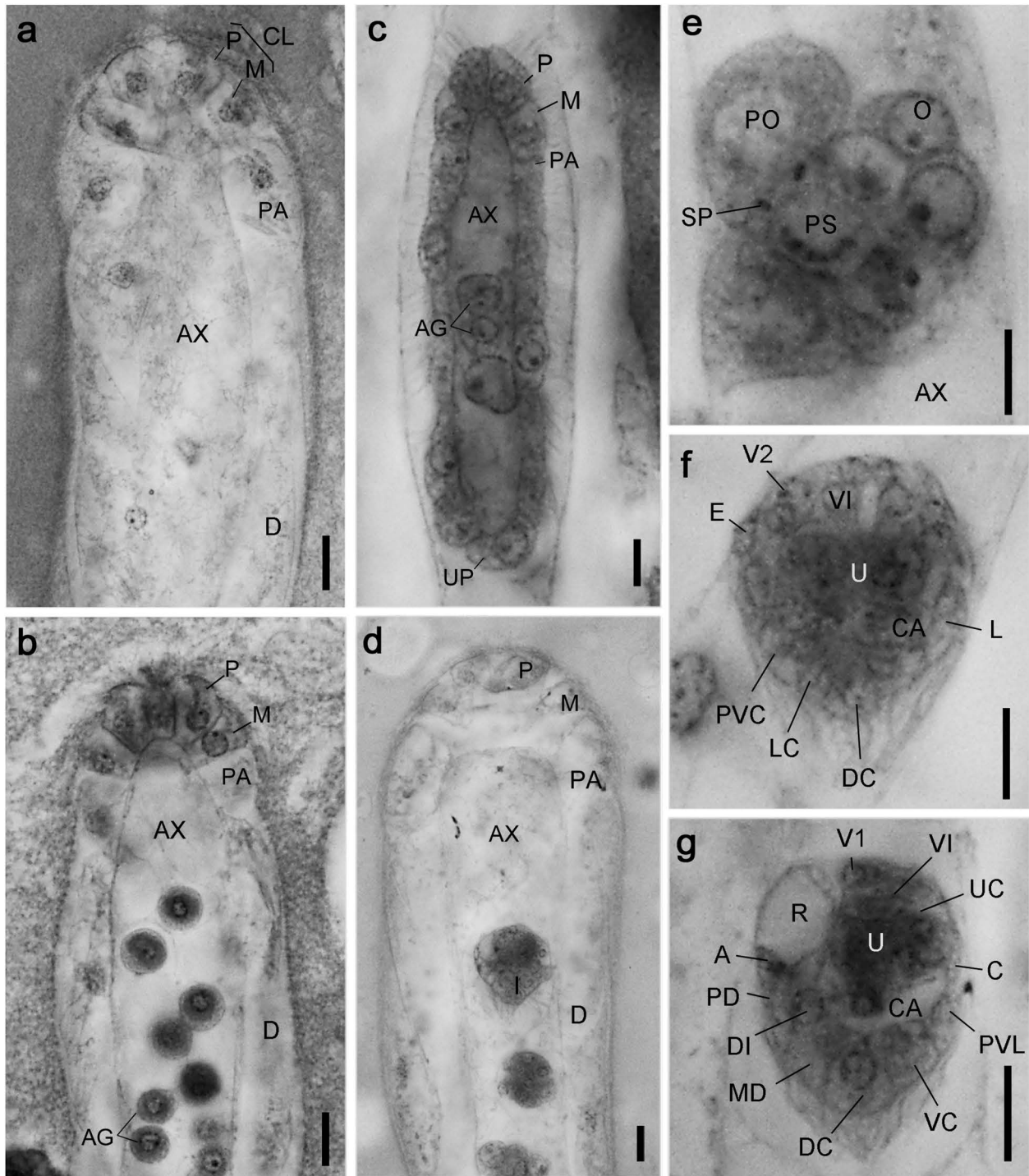


Fig. 26. *Pseudicyema jinshoae* sp. nov., photographs of syntype specimens on slide NSMT-Me-69: a, b, Nematogen, anterior region; c, vermiform embryos within axial cell; d, rhombogen, anterior region; e, infusorigen; f, g, infusoriform embryos, horizontal section (f), sagittal section (g). Scale bars: 10 μ m.

middle of parapolar cells to base of propolar cells (Figs 26a, b, 27c, d). About 10 vermiform embryos present per axial cell of large individuals. Accessory nuclei seen in trunk peripheral cells.

Vermiform embryos (Figs 26c, 27f, g). Full-grown vermiform embryos length 73–97 μ m, 15–20 μ m in width. Peripheral cell number 30–35 (Table 2); trunk cells arranged in opposed pairs. Anterior end of calotte rounded. Axial cell pointed anteriorly, extending to the base of propolar cells

(Figs 26c, 27g). Axial cell of full-grown embryos with 2 agametes.

Rhombogens (Figs 26d, 27e). Body length 820–1260 μ m, similar to that of nematogens, in length and 40–60 μ m in width. Peripheral cell number typically 30–35 (Table 2). Calotte, axial cell shape and anterior extent similar to nematogens. Maximum of 5 infusorigens present in the axial cell of each parent individual. About 40 infusoriform embryos present per axial cell of large individuals.

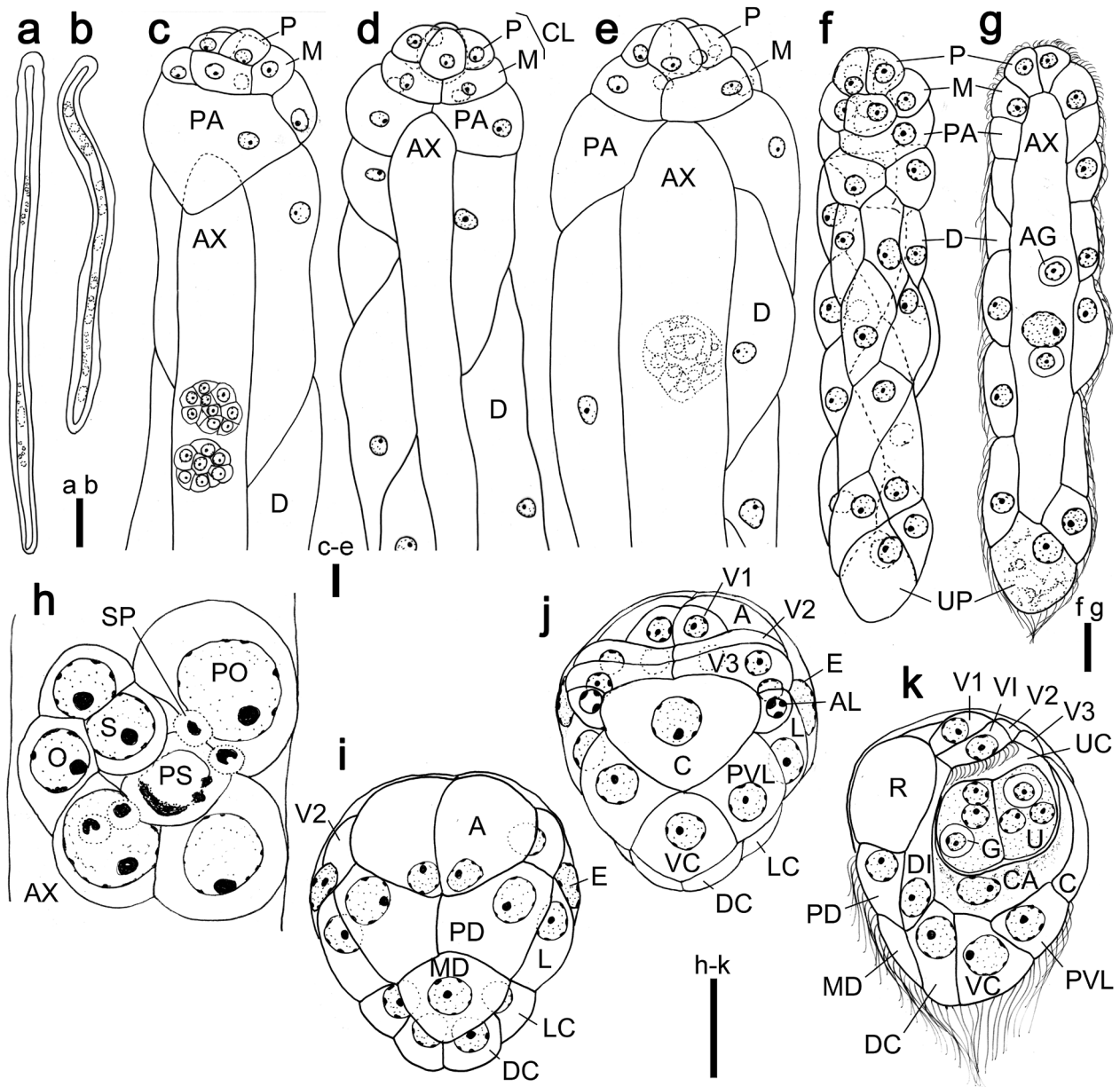


Fig. 27. *Pseudicyema jinshoae* sp. nov., drawn from syntype specimens on slide NSMT-Me-69: a, Nematogen, entire; b, rhombogen, entire; c, d, nematogen, anterior region; e, rhombogen, anterior region; f, g, vermiform embryo within axial cell, cilia omitted (f), optical section (g); h, infusorigen; i-k, infusoriform embryos, dorsal view (i: cilia omitted), ventral view (j: cilia omitted), sagittal section (k). Scale bars: a, b, 50 μ m; c-k, 10 μ m.

Infusorigens (Figs 26e, 27h; $n=10$). Mature infusorigens medium-sized; composed of 4–9 (mode 5) external cells (oogonia and primary oocytes) + 2, 3 (mode 2) internal cells (spermatogonia, primary spermatocytes, and secondary spermatocytes) + 5–14 (mode 8) spermatozoa. Mean diameter of fertilized eggs 11.9 μ m; that of spermatozoa 2.5 μ m. Axial cell round or ovoid, diameter 12–14 μ m.

Infusoriform embryos (Figs 26f, g, 27i–k; $n=20$). Full-grown embryos large, length $22.8 \pm 1.5 \mu$ m (mean \pm SD, excluding cilia); length–width–height ratio 1.0:0.87:0.85; shape ovoid, pointed posteriorly; cilia at posterior end 7 μ m long. Refrigrant bodies present, solid, occupying anterior 30–40% of embryo length when viewed laterally (Figs 26g, 27k). Cilia project from ventral internal cells into urn cav-

ity (Fig. 27k). Capsule cells contain tiny granules (Fig. 27k). Mature embryos with 39 cells: 35 somatic + 4 germinal cells. Somatic cells of several types present: external cells covering large part of anterior and lateral surfaces of embryo (2 enveloping cells); external cells with cilia on external surfaces (2 pairs of dorsal cells + 1 median dorsal cell + 2 dorsal caudal cells + 2 lateral caudal cells + 1 ventral caudal cell + 2 lateral cells + 2 posteroventral lateral cells); external cells with refrigrant bodies (2 apical cells); external cells without cilia (1 couvercle cell + 2 anterior lateral cells + 2 first ventral cells + 2 second ventral cells + 2 third ventral cells); internal cells with cilia (2 ventral internal cells); and internal cells without cilia (2 dorsal internal cells + 2 capsule cells + 4 urn cells). Each urn cell containing 2 nuclei and a germinal cell

(Fig. 27k). All somatic nuclei pycnotic in mature infusoriform embryos.

Remarks. *Pseudicyema jinshoae* sp. nov. is the first species of the genus found in *S. subtenuipes*. It is very similar to *P. anemophilum* sp. nov., *P. cappacephalum*, *P. cupulacephalum* sp. nov. and *P. daioense* sp. nov. in the calotte shape and the number of infusoriform embryos (Furuya 2009). However, *P. jinshoae* sp. nov. is distinguished from *P. anemophilum* sp. nov. by the anterior extent of adult vermiform stages (metapolar cells vs. propolar cells). *Pseudicyema jinshoae* sp. nov. differs from *P. cappacephalum* and *P. cupulacephalum* sp. nov. in the maximum number of infusorigens (5 vs. 3). In addition, *P. jinshoae* sp. nov. can be separated from *P. daioense* sp. nov. by the external shape of second ventral cells of infusoriform embryos (extended laterally vs. located ventrally).

Etymology. The species name “*jinshoae*” refers to name of the bottom trawl fishing boat “Jinsho-maru” which caught the host cephalopods.

Taxonomic summary. *Type material:* a syntype slide (NSMT-Me-69) collected on 25 June 2018; additional syntypes on slide series No. SS3864 (5 slides) in the author's

collection.

Type locality: off Kii-Nagashima (34°01'N, 136°40'E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 160 m.

Other materials examined: slide series No. SS3869 (5 slides) collected off Kii-Nagashima (34°01'N, 136°40'E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 160 m, 25 June 2018, in the author's collection.

Host: symbiotype, *Sepia subtenuipes* Okutani and Horikawa, 1987 (Mollusca: Cephalopoda: Sepiida), female (submature), 116 mm ML (NSMT-Mo-85911).

Collector of host: T. Moritaki.

Site: anterior ends (calottes) attach to surfaces of the renal appendages or inserted into crypts of the renal appendages within the renal sacs.

Prevalence: in 8 of 30 host specimens examined (26.7%).

***Pseudicyema physocaudatum* sp. nov.**

[New Japanese name: Shiribukure-nihaichū]

(Figs 28, 29; Tables 1–3)

Diagnosis. Medium-sized dicyemid, body length reaching 2050 µm. Calotte cap-shaped. Vermiform stages

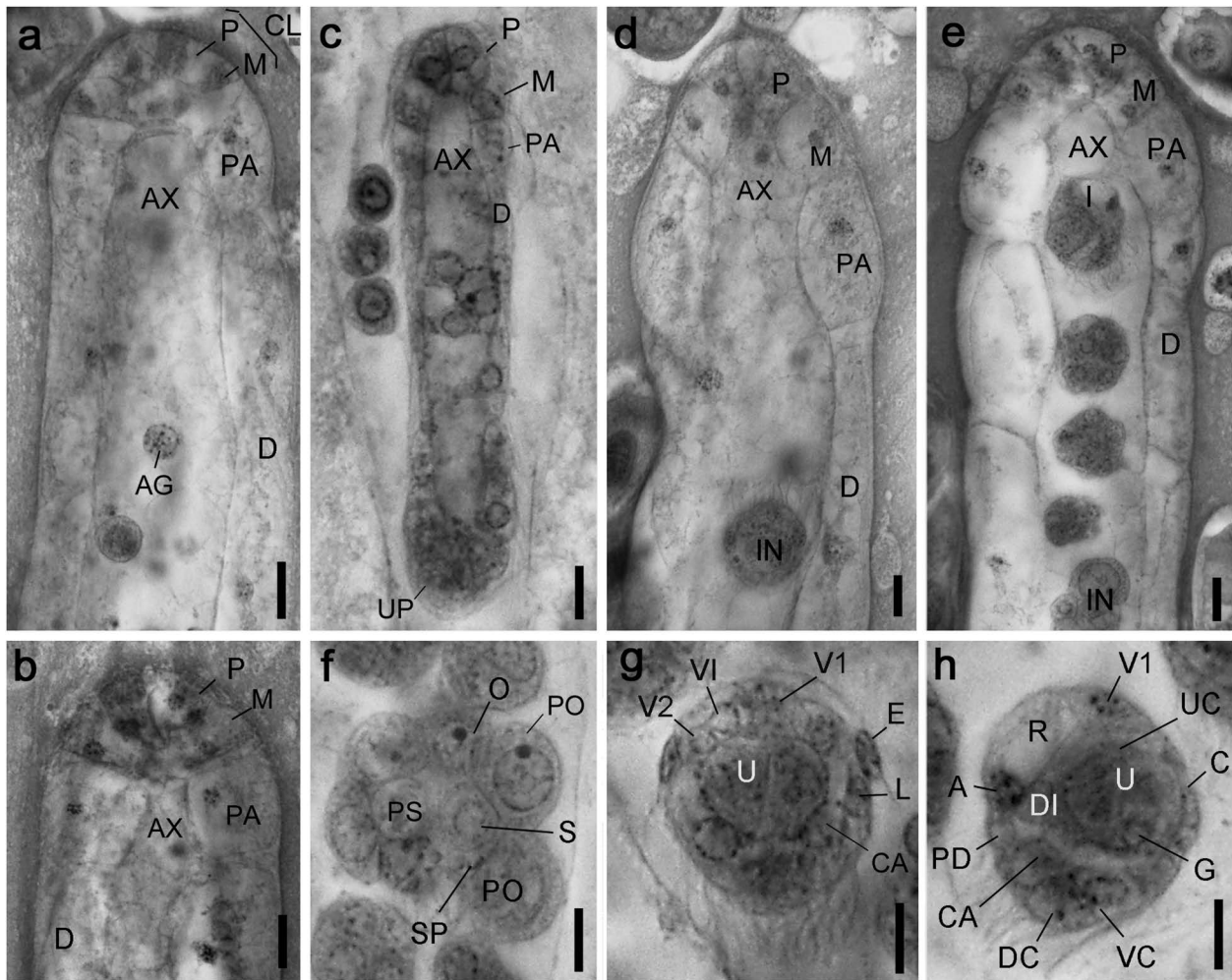


Fig. 28. *Pseudicyema physocaudatum* sp. nov., photographs of syntype specimens on slide NSMT-Me-71: a, b, Nematogen, anterior region; c, vermiform embryos within axial cell; d, e, rhombogen, anterior region; f, infusorigen; g, h, infusoriform embryos, horizontal section (g), sagittal section (h). Scale bars: 10 µm.

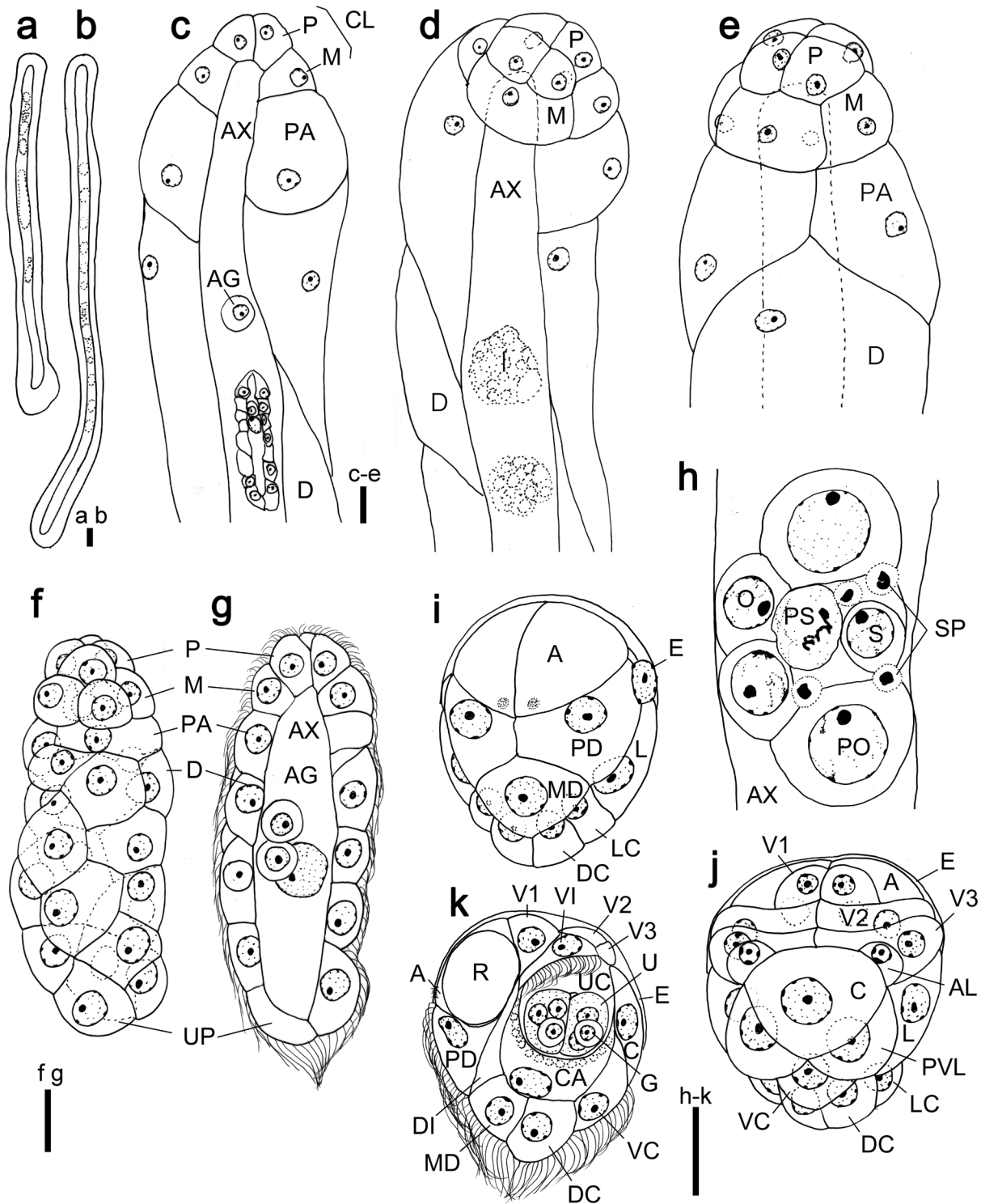


Fig. 29. *Pseudicyema physocaudatum* sp. nov., drawn from syntype specimens on slide NSMT-Me-71: a, Nematogen, entire; b, rhombogen, entire; c, nematogen, anterior region; d, e, rhombogen, anterior region; f, g, vermiform embryo within axial cell, cilia omitted (f), optical section (g); h, infusorigen; i–k, infusoriform embryos, dorsal view (i: cilia omitted), ventral view (j: cilia omitted), sagittal section (k). Scale bars: a, b, 20 μm; c–k, 10 μm.

with 31–35 peripheral cells: 4 propolar cells+4 metapolar cells+2 parapolar cells+21–25 trunk cells. Infusoriform embryos with 39 cells; refringent bodies solid; and 2 nuclei present in each urn cell.

Description. *Nematogens* (Figs 28a, b, 29a, c). Body length 1100–2050 μm, width 40–55 μm; widest in region

of parapolars; trunk width mostly uniform. Peripheral cell number 31–35 (Table 2): 4 propolar cells+4 metapolar cells+2 parapolar cells+19–23 diapolar cells+2 uropolar cells. Calotte cap-shaped, rounded anteriorly; cilia about 4 μm long, oriented anteriorly. Propolar cells equal to or larger than metapolar cells, their nuclei equal to or smaller

than metapolar cell nuclei. Propolar cells occupy anterior 40% of calotte length when viewed laterally (Figs 28a, b, 29c). Cytoplasm of propolar cells more darkly stained by hematoxylin than that of other peripheral cells (Fig. 28a, b). Axial cell cylindrical, rounded anteriorly, extending forward to base of propolar cells (Fig. 29c). About 10 vermiform embryos present per axial cell of large individuals. Accessory nuclei seen in trunk peripheral cells.

Vermiform embryos (Figs 28c, 29f, g). Full-grown vermiform embryos length 71–106 µm, 14–22 µm in width. Peripheral cell number 31–35 (Table 2); trunk cells arranged in opposed pairs. Anterior end of calotte rounded. Axial cell tapered anteriorly, extending to the base of propolar cells (Fig. 29g). Axial cell of full-grown embryos with 3 agametes.

Rhombogens (Figs 28d, e, 29d, e). Body length 1140–1650 µm, similar to that of nematogens, in length and 50–70 µm in width. Peripheral cell number typically 31–35 (Table 2). Calotte, axial cell shape and anterior extent similar to nematogens. Maximum of 5 infusorigens present in the axial cell of each parent individual. About 50 infusoriform embryos present per axial cell of large individuals.

Infusorigens (Figs 28f, 29h; $n=20$). Mature infusorigens medium-sized; composed of 4–11 (mode 5) external cells (oogonia and primary oocytes)+2–6 (mode 3) internal cells (spermatogonia, primary spermatocytes, and secondary spermatocytes)+3–11 (mode 5) spermatozoa. Mean diameter of fertilized eggs 11.9 µm; that of spermatozoa 2.2 µm. Axial cell round or ovoid, diameter 11–16 µm.

Infusoriform embryos (Figs 28g, h, 29i–k; $n=50$). Full-grown embryos large, length 21.2 ± 1.3 µm (mean \pm SD, excluding cilia); length–width–height ratio 1.0:0.89:0.84; shape ovoid, pointed posteriorly; cilia at posterior end 7 µm long. Refracting bodies present, solid, occupying anterior 30–40% of embryo length when viewed laterally (Figs 28h, 29k). Cilia project from ventral internal cells into urn cavity (Fig. 29k). Capsule cells contain small granules (Fig. 29k). Mature embryos with 39 cells: 33 somatic+4 germinal cells. Somatic cells of several types present: external cells covering large part of anterior and lateral surfaces of embryo (2 enveloping cells); external cells with cilia on external surfaces (2 pairs of dorsal cells+1 median dorsal cell+2 dorsal caudal cells+2 lateral caudal cells+1 ventral caudal cell+2 lateral cells+2 posteroventral lateral cells); external cells with refracting bodies (2 apical cells); external cells without cilia (1 couverte cell+2 anterior lateral cells+2 first ventral cells+2 second ventral cells+2 third ventral cells); internal cells with cilia (2 ventral internal cells); and internal cells without cilia (2 dorsal internal cells+2 capsule cells+4 urn cells). Each urn cell containing 2 nuclei and a germinal cell (Fig. 29k). All somatic nuclei pycnotic in mature infusoriform embryos.

Remarks. *Pseudicyema physocaudatum* sp. nov. is the first species of the genus found in *S. lorigera* and is very similar to *P. anemophilum* sp. nov., *P. cappacephalum*, *P. cupulacephalum* sp. nov., *P. daioense* sp. nov., and *P. jinshoae* in the calotte shape and the number of infusoriform embryos (Furuya 2009). However, *P. physocaudatum* sp. nov. is distinguished from *P. anemophilum* sp. nov., *P. cappacephalum*,

and *P. cupulacephalum* sp. nov. by the maximum number of infusorigens (5 vs. 2, 3) (Furuya 2009). It differs from *P. daioense* sp. nov., and *P. jinshoae* in the anterior extent of axial cell of adult vermiform stages (propolars vs. metapolars).

Etymology. The species name “*physocaudatum*” is an adjective composed of two Ancient Greek roots, *physa* and *kerkos*, meaning “swelling” and “tail” in reference to the characteristic anterior part of vermiform embryos.

Taxonomic summary. *Type material:* a syntype slide (NSMT-Me-71) collected on 5 December 2019; additional syntypes on slide series No. SM4117 (5 slides) in the author’s collection.

Type locality: off Owase (34°09′N, 136°36′E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 180 m.

Other materials examined: slide series No. SM3312 (5 slides) collected off Minami-Ise (34°12′N, 136°40′E), Mie Prefecture, Honshu, the Kumano Sea, Japan, depth 200 m, 30 November 2015, in the author’s collection.

Host: symbiotype, *Sepia madokai* Adam, 1939 (Mollusca: Cephalopoda: Sepiida), female (mature), 92 mm ML (NSMT-Mo-85913).

Collector of host: T. Moritaki.

Site: anterior ends (calottes) attach to surfaces of the renal appendages or inserted into crypts of the renal appendages within the renal sacs.

Prevalence: in 2 of 21 host specimens examined (9.5%).

Occurrence and Diversity

Occurrence patterns of dicyemids and chromidinid ciliates. In this study fourteen species of dicyemids were found in the renal sacs of six sepiid species and a sepiolid species from the Kumano Sea, off the Pacific coast of Honshu (Table 1). One to three species of dicyemids were found in each cephalopod species: a single species in *A. bipapillata* and *S. aureomaculata*, two species in *S. madokai*, *S. subtenuipes*, and *S. tenuipes*, and three species in *S. kubiensis* and *S. lorigera* (Table 1). The prevalence of dicyemids ranged widely from 3.3% to 100% (Table 1). *Dicyema hyalocephalum* sp. nov., *D. lorigeroeceum* sp. nov., and *P. daioense* sp. nov. were detected in all host individuals, while *D. bacterocephalum* sp. nov. and *D. tympanocephalum* sp. nov. were found in only one host individual. Three dicyemid species were found in each *S. kubiensis* and *S. lorigera* but they were never co-occurred; one or two species were typically found together in a renal sac or a single host individual (Table 4).

Chromidinid ciliates, *Chromidina* spp., were found in all the sepiid species but not in the sepiolid, *A. bipapillata* (Tables 1, 4, 5). These ciliates occur predominantly in *S. aureomaculata*, *S. kubiensis*, *S. lorigera*, *S. subtenuipes* and *S. tenuipes* but not *S. madokai*. There were various cooccurrence patterns involving ciliates (Table 4). The combination of a single species of chromidinid with a single dicyemid species occurred with relatively high prevalence in each sepiid host, while that of two dicyemid species with a single species of chromidinid was less frequent. In these sepiid species, there-

Table 4. Combination of dicyemid and chromidinid species found in renal organs of individual cuttlefish specimens.

Cephalopod species	Parasite species	Occurrence
<i>Sepia aureomaculata</i> (n=5)	<i>Chromidina</i> sp. A	1
	C. sp. A + <i>Dicyema daioense</i> sp. nov.	4
<i>S. kobeensis</i> (n=29)	C. sp. B	4
	C. sp. B + <i>D. gozaense</i> sp. nov.	14
	C. sp. B + <i>Pseudicyema anemophilum</i> sp. nov.	3
	C. sp. B + <i>D. gozaense</i> sp. nov. + <i>D. bacterocephalum</i> sp. nov.	1
	C. sp. B + <i>D. gozaense</i> sp. nov. + <i>P. anemophilum</i> sp. nov.	2
	<i>D. gozaense</i> sp. nov.	3
	<i>D. gozaense</i> sp. nov. + <i>P. anemophilum</i> sp. nov.	2
	None	1
<i>S. lorigera</i> (n=10)	C. sp. C + <i>D. lorigeroeum</i> sp. nov.	7
	C. sp. C + <i>D. lorigeroeum</i> sp. nov. + <i>P. cuplacephalum</i> sp. nov.	3
<i>S. madokai</i> (n=21)	C. sp. D + <i>D. shimaense</i> sp. nov.	1
	C. sp. D + <i>D. shimaense</i> sp. nov. + <i>P. physocaudatum</i> sp. nov.	1
	<i>D. shimaense</i> sp. nov.	2
	<i>D. shimaense</i> sp. nov. + <i>P. physocaudatum</i> sp. nov.	1
	None	16
<i>S. subtenuipes</i> (n=30)	C. sp. E	4
	C. sp. E + <i>D. miense</i> sp. nov.	12
	C. sp. E + <i>D. miense</i> sp. nov. + <i>P. jinshoae</i> sp. nov.	3
	C. sp. E + <i>P. jinshoae</i> sp. nov.	5
	<i>D. miense</i> sp. nov.	3
<i>S. tenuipes</i> (n=91)	None	2
	C. sp. F	26
	C. sp. F + <i>D. conocephalum</i> sp. nov.	23
	C. sp. F + <i>D. tenuipoeum</i> sp. nov.	33
	C. sp. F + <i>D. conocephalum</i> sp. nov. + <i>D. tenuipoeum</i> sp. nov.	3
	<i>D. conocephalum</i> sp. nov.	2
	None	4

fore, chromidinids are as common as, or more common than, dicyemids.

Morphological diversity of dicyemid species. The new species reported here have three types of calotte shape: conical, cap-shaped or disc-shaped (Table 3). According to the criterion of calotte shape (see Materials and Methods), the new dicyemid species are classified as follows: Type I, *D. hyalocephalum* sp. nov., *D. gozaense* sp. nov., *D. lorigeroeum* sp. nov., *D. shimaense* sp. nov., *D. miense* sp. nov., and *D. conocephalum* sp. nov.; Type II, *D. bacterocephalum* sp. nov., *Pseudicyema daioense* sp. nov., *P. anemophilum* sp. nov., *P. cuplacephalum* sp. nov., *P. physocaudatum* sp. nov., and *P. jinshoae* sp. nov.; Type III, *D. bacterocephalum* sp. nov., *D. tympanocephalum* sp. nov. and *D. tenuipoeum* sp. nov.

Both the total cell number and cellular composition of infusoriform embryos are species-specific and thus represent significant features that can be used in the identification and classification of dicyemids (Furuya 1999; Furuya et al. 2004). In present study, two variations of embryonic cell numbers were observed: 37 and 39. Infusoriform embryos with 37 cells occurs in five species of *Dicyema*: *D. bacterocephalum* sp. nov., *D. conocephalum* sp. nov., *D. hyalocephalum* sp. nov., *D. tenuipoeum* sp. nov., *D. tympanocephalum* sp. nov. Those with 39 cells were found in four species of *Dicyema* (*D. gozaense* sp. nov., *D. lorigeroeum* sp.

nov., *D. shimaense* sp. nov., and *D. miense* sp. nov.) and all five species of *Pseudicyema* (i.e., *P. daioense* sp. nov., *P. anemophilum* sp. nov., *P. cuplacephalum* sp. nov., *P. physocaudatum* sp. nov., *P. jinshoae* sp. nov.). This is all infusoriform embryos of *Pseudicyema* have 39 cells and the common cellular composition.

In addition to the calotte shape, based on the cell arrangement with the calottes and embryonic characters, the new dicyemids are divided into three groups: (1) *Pseudicyema* species that have infusoriform embryos with 39 cells and 29–35 peripheral cells (*P. daioense* sp. nov., *P. anemophilum* sp. nov., *P. cuplacephalum* sp. nov., *P. physocaudatum* sp. nov., and *P. jinshoae* sp. nov.); (2) *Dicyema* species that have vermiform embryos with an acutely shaped calotte and around 30 peripheral cells (*D. gozaense* sp. nov., *D. lorigeroeum* sp. nov., *D. shimaense* sp. nov., *D. miense* sp. nov., and *D. conocephalum* sp. nov.); and (3) *Dicyema* species that have 22 peripheral cells and disc-shaped calottes in adult vermiform stages (*D. bacterocephalum* sp. nov., *D. tympanocephalum* sp. nov. and *D. tenuipoeum* sp. nov.).

Discussion

Benthic cephalopod species on the continental shelf

Table 5. Chrominid ciliates and dicyemid species in Japanese sepiid cephalopods.

Cephalopod species	Chromidinids	Dicyemid species*	References
<i>Sepia aureomaculata</i>	Present	<i>P. daioense</i> sp. nov.	This study
<i>S. esculenta</i>	None	<i>D. hadrum</i> Furuya, 1999 <i>D. rhadinum</i> Furuya, 1999 <i>Dn. mastigoides</i> Furuya, 1999 <i>Dn. minabense</i> Furuya, 1999 <i>P. nakaoi</i> Furuya, 1999	Furuya (1999)
<i>S. kubiensis</i>	Present	<i>D. bacterocephalum</i> sp. nov. <i>D. gozaense</i> sp. nov. <i>P. anemophilum</i> sp. nov.	This study
<i>S. latimanus</i>	None	<i>Dn. ryukyuense</i> Furuya, 2006	Furuya (2006)
<i>S. longipes</i>	Present	<i>D. oxycephalum</i> Furuya, 2009 <i>P. cappacephalum</i> Furuya, 2009	Furuya (2009)
<i>S. lorigera</i>	Present	<i>D. lorigeroeum</i> sp. nov. <i>D. tympanocephalum</i> sp. nov. <i>P. cuplacephalum</i> sp. nov.	This study
<i>S. lysidus</i>	None	<i>D. lycidoeeum</i> Furuya, 1999	Furuya (1999)
<i>S. madokai</i>	Present	<i>D. shimaense</i> sp. nov. <i>P. physocaudatum</i> sp. nov.	This study
<i>S. subtenuipes</i>	Present	<i>D. miense</i> sp. nov. <i>P. jinshoae</i> sp. nov.	This study
<i>S. tenuipes</i>	Present	<i>D. conocephalum</i> sp. nov. <i>D. tenuipoeum</i> sp. nov.	This study
<i>Sepiella japonica</i>	Present	<i>D. sepiellae</i> Furuya, 2008	Furuya (2008)

* *D*: *Dicyema*; *Dn*: *Dicyemene*; *P*: *Pseudicyema*.

in the Kumano Sea. The host cephalopods were obtained from catches taken by the bottom-trawl fishing boat “Jinsho-maru” operating in the Kumano Sea. The catch is mainly the sea cucumber *Parastichopus nigropunctatus* (Augustin, 1908) which inhabits in sandy seabed environments down to a depth of 600 m, from Hokkaido to Kyushu and is processed to be sold as dried product, which is in high demand to China, South Korea, Japan and the United States. Several species of benthic cephalopods are caught together with *P. nigropunctatus* as by-catch, so they clearly occupy the same environment in the Kumano Sea.

There is a rich diversity of octopods in this area. Two large octopod species, *Octopus tenuicirrus* (Sasaki, 1929) and *Opisthoteuthis depressa* Ijima and Ikeda, 1895, are frequently collected from 200–300 m deep in the Kumano Sea. The collected individuals vary in size regardless of the catch season, suggesting the lack of a distinct breeding season in these octopus species. The small to medium-sized octopuses, *Scaevargus patagiatus* Berry, 1913, *Amphioctopus kagoshimensis* (Ortmann, 1888), and *Callistoctopus minor* (Sasaki, 1920) are occasionally found at depths of 150–200 m. In addition, two unknown species, *Enteroctopus* sp. and *Octopus* sp., have also been found at similar depth. More research is needed to clarify the systematics of octopods in the Kumano Sea region.

The octopod fauna in the Kumano Sea appears to be close to that of the Suruga Bay in terms of predominance of *O. tenuicirrus* and *Opisthoteuthis depressa*. Neither species is

found east of the Boso Peninsula, off which two other large species, *O. hongkongensis* Hoyle, 1885, and *O. conispadiceus* (Sasaki, 1917), are present (Okutani et al. 1987; Gleadall 1993). In Japanese waters, the octopod fauna on the continental shelf is probably common from the Kumano Sea to the Boso Peninsula, with a slightly different species composition north of the Boso Peninsula. *Octopus hongkongensis* and *O. conispadiceus* probably occupy a benthic niche East of the Boso Peninsula, while *O. tenuicirrus*, *Enteroctopus* sp., and *O. depressa* occupy the western areas.

Among benthic Decapodiformes, *A. bipapillata*, *Euprymna morsei* (Verrill, 1881), *Euprymna berryi* Sasaki, 1929, *Sepia kubiensis*, *S. longipes* Sasaki, 1913, *S. lorigera*, *S. madokai*, *S. subtenuipes*, *S. tenuipes*, and *Sepiolina nipponensis* (Verrill, 1911) have been found in the Kumano Sea (H. Furuya, unpublished data). Overall, the species collected in the Kumano Sea indicate a rich diversity of benthic cephalopods.

Dicyemids were found in all the octopod and sepiid species, but not in the sepiolids *E. morsei*, *E. berryi*, or *Sepiolina nipponensis*, despite the fact that all these cephalopods are found in the same area and habitat. The difference between the sepiolids and the other host cephalopods is the body size. The sepiolid is a cephalopod group consisting of small-sized species. Cephalopod species eat different crustaceans and shellfish depending on their body size, even in the species having the same habitat. It suggests the presence of an intermediate host, although it is known that infection can occur without the intermediate host (Lapan and Morowitz

1975).

Dicyemid species in the Rossiinae. *Austrorossia bipapillata* is the second species of Rossiinae in which dicyemids are known. Host to only one dicyemid species, apparently, it is common in deeper parts of the continental shelf in the Japanese western Pacific Ocean (from Suruga Bay to Tosa Bay), and has been recorded also from the Philippines (Okutani et al. 1987). The only other species in this family investigated for dicyemids, *Rossia pacifica* Berry, 1911, is host to ten dicyemid species, and is found across a relatively wide range of localities across the northern Pacific Ocean, from Japan to Southern California, and a wide range of depth habitats, from the lower intertidal region down to 300 m (Bogolepova-Dobrokhotova 1962; Hoffman 1965; Hochberg 1990; Furuya 2007).

Another example of a host species infected by a wide diversity of dicyemids on both sides of the northern Pacific Ocean is the giant octopus *E. dofleini* (Hochberg 1990; Furuya 2007). The wide distribution of both *E. dofleini* and *R. pacifica* is possibly correlated to their dicyemid species diversity. However, Furuya (2018) has recently reported a single host species, *O. longispadiceus*, with as many as seven dicyemid species collected from hosts captured in a relatively restricted geographical range of localities. It seems unlikely that these two extreme patterns of dicyemid occurrence are solely a property of host habitat and distribution, so further research is necessary to investigate the differences in cephalopod life history traits and their possible effects on dicyemid distribution.

The dicyemid fauna in Sepia. Around 120 species of *Sepia* Linnaeus, 1758 have been described from the world's oceans. Those known to contain dicyemids include: (in the Mediterranean Sea) *S. elegans* (Beneden 1876; Whitman 1883; Nouvel 1947) and *S. orbignyana* Férssac, 1826 (Whitman 1883; Nouvel 1933, 1937, 1947); *S. officinalis* Linnaeus, 1758 from the eastern North Atlantic Ocean, English Channel, Mediterranean Sea (Beneden 1882; Whitman 1883; Nouvel 1933, 1947; Furuya and Hochberg 1999); *S. elliptica* Hoyle, 1885 from Western Bay of Bengal (Kalavati et al. 1978, 1984); *S. papuensis* Hoyle, 1885 from Australia (Catalano 2013); and from Japan, *S. latimanus* Quoy and Gaimard, 1832, *S. lycidas* Gray, 1849, *S. esculenta* Hoyle, 1885, *S. kobeensis*, *S. longipes*, *S. peterseni* Appellöf, 1886, and *S. madokai* (Furuya 1999, 2006c, 2009; Furuya and Tsuneki 2003).

According to these descriptions, *Sepia* species are hosts of 4 dicyemid genera, *Dicyema*, *Dicyemene* Whitman, 1883, *Microcyema* van Beneden, 1882, and *Pseudicyema*. *Microcyema* is a rare genus reported in only *S. officinalis* (Beneden 1876; Nouvel 1947). *Dicyema* and *Dicyemene* are commonly reported among benthic species of cephalopods and include more than 90% of dicyemid species. *Dicyema* species are predominantly found in shallow-water cephalopods distributed on the continental shelf at the depth of less than 300 m, have never been described from deep-water cephalopods, and are only rarely recorded in mid-depth hosts (Furuya and Hochberg 2002). This pattern suggests that ancestral *Dicyema* species first occurred in the shallow-water

cephalopods and subsequently spread throughout the shallow-water cephalopods by co-evolution and host-switching.

Pseudicyema is known from shallow-water cephalopod species in Europe and Japan (Whitman 1883; Nouvel 1947; Furuya 1999, 2009), mainly in *Sepia* species and *Rossia macrosoma* (Chiaie, 1830) (Nouvel 1947). *Pseudicyema* was erected by Nouvel (1933) to include a single species, *D. truncatum* Whitman, 1883, which is distinguishable from species in *Dicyema* principally by the orientation of cells in the calotte. In *Pseudicyema* the cells in the propolar tier alternate with cells in the metapolar tier whereas the tiers typically are opposite each other in *Dicyema* to which the terms plagiotropal (alternate or bilaterally symmetrical) and orthotropal (opposite or radially symmetrical), respectively, have been applied (McConnaughey 1949). McConnaughey (1949) and Hochberg (1990), identified *Pseudicyema* as a junior synonym of *Dicyema*.

The differences in the orientation of the propolar and metapolar cells are evident in the vermiform stages of a given species and appear to be genus specific (Furuya 1999, 2009). The characteristic orientation patterns are easily observed shortly after the vermiform embryos begin to develop in both genera. In *P. nakaoi* and *P. truncatum* the cells of the propolar tier consistently alternate with those of the metapolar tier whereas they are always opposite in *D. acuticephalum* Nouvel, 1947 and *D. japonicum* (Furuya et al. 1994, 2001). In several other species of *Dicyema*, the orientation of the calotte cells has been reported to present a mixture of both patterns although the opposite or orthotropal arrangement is dominant. In at least one other species, *D. typoides* Short, 1964 from *Octopus vulgaris* Cuvier, 1797 in Florida [now known to be probably *O. insularis* Leit and Haimovich, 2008 in Leite et al. (2008), or *O. americanus* Froriep, 1806 in Avendaño et al. (2020)], the orientation pattern has been described as being predominantly alternate or plagiotropal (Short 1964). The calotte shape of *Pseudicyema* species is restricted in either cap-shaped or disc-shaped calotte (Nouvel 1947; Furuya 1999), so species with a conical calotte are unlikely to belong to genus *Pseudicyema*. Further critical study of *D. typoides* is necessary to confirm its generic identification. In the present study, based on the consistent and characteristic difference in the orientation of cells in each tier of the calotte, *Pseudicyema* is herein considered to be a valid genus distinct and separate from *Dicyema*.

Co-occurrence pattern of dicyemids and chromidinid ciliates. In cephalopods, chromidinids are the most frequently encountered parasites after dicyemids. To date, a total of 31 species of cephalopods representing 22 genera harbor chromidinids (Hochberg 1982, 1983, 1990; Furuya et al. 2004; Furuya 2009). In contrast to dicyemids, chromidinids characteristically infect oceanic cephalopods (epi- and meso-pelagic squids and octopods). Infection of benthonic or epi-benthonic hosts has been reported occasionally, but in all instances chromidinids were found only in octopods that produce planktonic larvae [i.e., *Octopus salutii* Verrany, 1839, *O. vulgaris*, *Scaevargus unicirrhus* (Delle Chiaie, 1841), and *Eledone cirrhosa* (Lamarck, 1798)] or in Sepioidea whose young feed in surface waters (i.e., *Sepia elegans*,

S. orbignyana and *Sepiola rondeleti* Leach, 1817) (Hochberg 1983). It is possible that the planktonic larvae are infected with chromidinids before they settle to the bottom and pick up dicyemids (Furuya et al. 2004). Although the paralarvae of small- to medium-sized sepiids examined in this study are unknown, they are possibly planktonic. Planktonic paralarvae are not produced in the large-sized sepiid species laying large eggs, such as *Sepia esculenta*, *S. pharaonis* Eherenberg, 1881, *S. latimanus*, and *S. lycidas*.

Cephalopods are infected with chromidinids following consumption of the crustaceans on which they prey. In the squid *Pterygioteuthis giardi* Fischer, 1896, a small crustacean species, *Nematoscelis* G. O. Sars, 1883, is considered to be the intermediate host of chromidinids (Hochberg 1982). The large-sized sepiid species with non-planktonic larvae have no chance to be in contact with pelagic crustaceans. They feed on different prey, such as epibenthic fish and benthic crustaceans, which are not infected with chromidinids. This explains why chromidinids are generally found in small- to medium-sized sepiid species (Hochberg 1990), never in large species (Furuya et al. 2004).

The body shape and diphasic life cycle of chromidinids are very similar to those of dicyemids and well-adapted to the requirements of their endoparasitic environment (Hochberg 1982). The infection site of both dicyemids and chromidinids is almost identical. According to previous studies (Nouvel 1945; Furuya et al. 2004), it is rather rare that both dicyemids and chromidinids co-exist in the renal organ; there appeared to be no competition between these two organisms. However, the present study revealed both dicyemids and chromidinids occupying the same renal organs. Chromidinids occupy folds of the renal appendage as well as dicyemids, so their niche is apparently identical and there might be some competition between dicyemids and chromidinids in cuttlefish renal sacs.

Species differences have not been investigated at the molecular level but chromidinid species can be distinguishable based on the shape of the anterior region and ciliation patterns. Therefore, chromidinids may also be host specific. Small- to medium-sized sepiid species are infected with a single chromidinid species and there are two co-occurrence patterns in the renal organs, with either one or two dicyemid species. Chromidinids exhibit configurations of the attachment end in the anterior region (head) that mirror shapes observed in dicyemids (Hochberg 1990), and the heads of *Chromidina elegans* (Foettinger, 1881) and *C. coronata* (Foettinger, 1881) are comparable to the conical and disc-type calotte in the dicyemids, respectively. In both organisms, a variety of head shapes is probably the result of interaction between phylogenetically unrelated organisms.

Morphological characters in dicyemids appears to result from adaptation to the structure of the host's renal tissues and helps to facilitate niche separation of coexisting species. Similar adaptation is seen in the life cycle and morphology of chromidinids. The site of infection by both dicyemids and chromidinids is almost identical. In octopuses, their niche is basically separated because it is rather rare that dicyemids and chromidinids coexist in the renal organ (Nouvel 1937;

Furuya and Hochberg 1999; Furuya et al. 2004). There appears to be no competition between these two organisms. In the *Sepia*, however, there must be competition and niche separation between dicyemids and chromidinids due to their co-occurrence patterns. The symbiont fauna in the renal sac of *Sepia* is distinct and likely complicated configuration due to the additional of chromidinids. In contrast to the large number of chromidinid species with a conical anterior region, dicyemid species with the cap- and disc-shaped anterior region (calotte) are found in all species of the *Sepia*. This suggests competition between dicyemids and chromidinids likely occur and competitive exclusion may select for character displacement in the anterior region and habitat segregation.

Reproductive strategy on hermaphroditic gonads.

Reproductive traits (the size and number of hermaphroditic gonads, and infusorigens) are diagnostic characteristics of the dicyemid species (Furuya et al. 1993, 2007). There is a negative curvilinear relationship between the number of infusorigens per rhombogen and the number of gametes (egg-line and sperm-line cells) per infusorigen (Furuya et al. 2003b; Furuya 2005, 2006a–c). Irrespective of genera, the condition of the rhombogens can be categorized into four distinct groups with respects to reproductive strategies: (1) forming a relatively small number of medium- to large-sized infusorigens (less than 5) and producing a relatively large number of gametes (more than 20) per infusorigen; (2) producing a large number of infusorigens (more than 5), each of which has at most 20 gametes; (3) producing large numbers of large-sized infusorigens with a large number of gametes; and (4) forming a relatively small number of small-sized infusorigens with a few gametes (at most 10). Rhombogens of all dicyemid species have a small number of medium-sized infusorigens, and thus these species belong to group (1).

The mean total number of hermaphroditic gonads (infusorigens) found in a rhombogen parent ranges from 1 to 30, but most species produce only 1 (Furuya et al. 2003b). The number of infusorigens is positively correlated with the adult body size but the maximum number per parent individual is species specific. Therefore, the size and number of infusorigens are diagnostic characteristics of dicyemids (Furuya et al. 1993; Furuya and Tsuneki 2007). In the present study, except for *D. bacterocephalum* sp. nov., the rhombogens of all species belong to Type 1, which have a small number of medium- to large-sized infusorigens. *Dicyema bacterocephalum* sp. nov. has usually 3–5, occasionally 9 infusorigens, so it belongs to Type 2, which produces more than 5 infusorigens.

Most of the new dicyemid species in the present study have a small number of medium- to large-sized infusorigens, which is a general characteristic of species with a small- to medium-sized body (Furuya et al. 2003a). These new species mostly have a body length of around 1000 µm, which is the boundary between a small and a medium in body size. All the new species have a similar reproductive performance and presumably a similar reproductive strategy.

Three groups of dicyemids in sepiids. Except for *D. hyalocephalum* from *A. bipapillata*, the new species de-

scribed in the present study were found in only *Sepia* species living in a similar habitat. Three groups of new dicyemid species are recognized based on the sharing of some diagnostic characters: calotte shapes, the peripheral cell numbers of vermiform stages, and the total cell number of infusoriform embryos (Table 3).

In infusoriform embryos, two types of embryonic cell numbers, 37 and 39, were found in the new species. Embryos with 37 cells occurs in five species of *Dicyema*, while those with 39 cells occur in four species of *Dicyema* and all five species of *Pseudicyema*. The cellular constitution of infusoriform embryos is a common feature of the *Pseudicyema* species. Previously described species of *Pseudicyema* also have the same cell number of infusoriform embryos, that is, *P. cappacephalum* from *S. longipes*, *P. nakaoi* from *S. esculenta*, and *P. truncatum* from *S. officinalis*. In other genera, a common total cell number is not necessarily a genus-specific character. There are some variations in the total cell numbers of infusoriform embryos: 35, 37, plus 39 cells in *Dicyema*, 37, 39, or 41 in *Dicyemennea*, and 35 or 43 in *Dicyemodoca* Wheeler, 1897 (Furuya 1999, 2018; Furuya et al. 2004). It is notable that *Pseudicyema* species show no variation in characters of infusoriform embryos. In addition, the new *Pseudicyema* species reported here have a species-specific range in their peripheral cell number, which overlaps among species, although species show differences in the range and the peak of peripheral cell numbers (Tables 2, 3).

In vermiform embryos, *D. gozaense* sp. nov., *D. lorigeroeceum* sp. nov., *D. shimaense* sp. nov., *D. miense* sp. nov., and *D. conocephalum* sp. nov. have an acutely pointed calotte. This calotte type in *Dicyema* was first found in *D. oxycephalum* from *S. longipes* (Furuya 2009). Such vermiform embryos appear frequently in each host species (Table 3). An acutely pointed calotte seems to be much more advantageous for inserting the body into the narrow gaps or folds of renal epidermis than a rounded calotte. In addition, these species show some overlap in peripheral cell number (Table 3). Thus, a group is formed by collecting the *Dicyema* species with acutely pointed vermiform embryos with around 30 peripheral cells.

The disc-shaped calotte is found in three dicyemid species: *D. bacterocephalum* sp. nov., *D. tympanocephalum* sp. nov., and *D. tenuipoeceum* sp. nov. They also have 22 peripheral cells in their vermiform stages and 37 cells in their infusoriform embryos. As a rule, different species of dicyemids appear to be able to coexist in the renal sac without competition when their calottes are different in shape (Furuya et al. 2003a). In dicyemids from *Sepia*, species with disc-shaped calottes are typically found together with a species having a conical or cap-shaped calotte.

In conclusion, the dicyemids can be categorized into three groups as follows, (1) *Pseudicyema* species that have infusoriform embryos with 39 cells and 29–35 peripheral cells; (2) *Dicyema* species that have vermiform embryos with the acutely pointed calotte and around 30 peripheral cells; and (3) *Dicyema* species with 22 peripheral cells and a disc-shaped calotte in adult vermiform stages. However, two or three dicyemid species belonging to the same group

are never found in the same cephalopod species. In other words, dicyemid species sharing the same calotte shape or the same number of cells never co-occur in a renal organ. In these dicyemids, the variation of calotte shapes is probably the result of interaction among species perhaps also involving chromidinids. This suggests that niche separation occurs in the renal organs of *Sepia* species, as reported for other dicyemid species (Furuya et al. 2003a; Furuya 2018).

Preliminary molecular analyses suggest the occurrence of the occasional host switching by dicyemids and cospeciation between the dicyemid species and the host cephalopods (Nakajima and Furuya 2019). Although the phylogenetic relationship among new dicyemid species found in *Sepia* have not been analysed, a close relationship among species is suggested due to shared diagnostic characteristics, such as the peripheral cell number in vermiform stages and the cell number in infusoriform embryos. Yoshida et al. (2006) indicated the monophyly of *Doratosepion* Rochebrune, 1884 subgeneric group, suggesting a close affinity among these host *Sepia* species. It is plausible that the cospecification occurred from an ancestor in the course of sepiid speciation, especially in small- to medium-sized *Doratosepion* species including *S. aureomaculata*, *S. kobeensis*, *S. lorigera*, *S. longipes*, and *S. subtenuipes*.

The dicyemid fauna in Japanese waters. In the present study, the number of dicyemid species described from Japanese waters has been increased from 50 to 64. The largest number of species have been described in the genus *Dicyema* (37 species), followed by *Dicyemennea* (18 species), *Pseudicyema* (7 species), and *Dicyemodoca* (2 species). The genus *Dicyema* is predominant in hosts in Japanese waters. The number of *Pseudicyema* species has been increased from two to seven, which accounts for 11% of Japanese dicyemid species. Recently, a species of *Conocyema* sp. (Dicyemida: Conocyemidae) has been found in *Octopus* spp. in the North Pacific Ocean (Tosa Bay and the Kumano Sea) (H. Furuya, unpublished data), which is the fifth dicyemid genus encountered in Japan. Regarding dicyemid genera found within European hosts, *Microcyema* (recorded only in the European cuttlefish, *Sepia officinalis*) has not been reported from hosts in Japanese waters. However, since there are many species of *Sepia* that exist in Japanese waters, perhaps in the future Japanese species of *Microcyema* may be eventually found. In contrast, only the three genera *Dicyema*, *Dicyemennea*, and *Dicyemodoca* have been recorded in the seas around North America (McConnaughey 1949; Hochberg 1990; Short 1991), which is a feature of host habitat distribution since Sepiidae are absent from the Americas (Khromov 1998). Regional differences in distribution of the cephalopod fauna are expected to be linked directly to that of the dicyemid fauna due to narrow host specificity (Furuya 2018).

Host specificity of dicyemid species. Dicyemid species described recently are host-specific, which is of use in the reliable identification of host cephalopod species. Previously *O. vulgaris* was considered to be a cosmopolitan species, although it was known to harbor different dicyemid species in different waters, such as the western North, eastern Atlantic

Ocean, the Mediterranean Sea, the Gulf of Mexico and the northwest Pacific. This corroborates the presence of some cryptic species forming the *O. vulgaris* species complex, as recently reported (Leite et al. 2008; Gleadall 2016; Amor et al. 2017; Avendaño et al. 2020). Among the species complex, the cryptic species in the Japanese water has been recently classified as *Octopus sinensis* d'Orbigny, 1834 by Gleadall (2016). *Octopus sinensis* harbors three dicyemid species, which have never been found in other *O. vulgaris* species complex (Nouvel and Nakao 1938; Nouvel 1947; Furuya et al. 1992a). The other species within this complex also harbor distinct dicyemid species (Beneden 1876; Nouvel 1934, 1947; McConaughy and Kritzler 1952; Couch and Short 1964; Short 1964; Hochberg 1990). Therefore, dicyemid species are available as markers for host species identification. In Sepiid species, especially those of the *Doratosepion* species complex, juveniles cannot be easily distinguished due to the paucity of distinctive morphological features. Therefore, combined with molecular sequence analysis, host specificity of parasites can be useful tool for the systematics of host organisms.

There are a number of dicyemids having a relatively wide host range, infecting different host genera (Nouvel 1947; Hochberg 1990; Furuya 1999). For instance, *Dicyema macrocephalum* van Beneden, 1876 was reported to infect, at most, five sepiolids in three different genera, i.e., *Sepia*, *Sepietta* Naef, 1912, and *Sepiola* Leach, 1817 (Beneden 1876; Nouvel 1947). Dicyemids that infect more than two host species in different genera have been so far only from Europe, and especially the Mediterranean Sea (Nouvel 1947; Hochberg 1990; Furuya 1999). In view of the closer dicyemid-cephalopod host specificity observed within the Japanese fauna, it may be that further dicyemid species distinctions are possible in other regions, too, so it may prove fruitful to re-investigate the dicyemid fauna of Mediterranean cephalopods.

Acknowledgments

We thank Hiroaki Nakajima and Yuki Ito for preparing smears, and Fuko Onoda for her assistance with data processing. We also thank Ian Gleadall for the valuable advice on current cephalopod systematics. This study was supported by Grants-in-Aid for Scientific Research from the Japan Society for the Promotion of Science (research grant no. JP21K06303).

References

- Amor, M. D., Norman, M. D., Roura, A., Leite, T. S., Gleadall, I. G., Reid, A., Perales-Raya, C., Lu, C. C., Silvey, C. J., Vidal, E. A. G., Hochberg, F. G., Zheng, X., and Strugnell, J. M. 2017. Morphological assessment of the *Octopus vulgaris* species complex evaluated in light of molecular-based phylogenetic inferences. *Zoologica Scripta* 46: 275–288.
- Avendaño, O., Roura, Á., Cedillo-Robles, C. E., González, Á. F., Rodríguez-Canul, R., Velázquez-Abunader, I., and Guerra, Á. 2020. *Octopus americanus*: a cryptic species of the *O. vulgaris* species complex redescribed from the Caribbean. *Aquatic Ecology* 54: 909–925.
- Beneden, É. van. 1876. Recherches sur les Dicyémides, survivants actuels d'un embranchement des Mésozoaires. *Bulletins de l'Académie Royale de Belgique* 42: 3–111.
- Beneden, É. van. 1882. Contribution à l'histoire des Dicyémides. *Archives de Biologie* 3: 195–228.
- Bogolepova-Dobrokhotova, I. I. 1962. Dicyemidae of the Far-Eastern seas. II. New species of the genus *Dicyemene*. *Zoologicheskii Zhurnal* 41: 503–518.
- Catalano, S. R. 2013. First descriptions of dicyemid mesozoans (Dicyemida: Dicyemidae) from Australian octopus (Octopodidae) and cuttlefish (Sepiidae) species, including a new record of *Dicyemene* in Australian waters. *Folia Parasitologica* 60: 306–320.
- Castellanos-Martinez, S., Gomez, M. C., Hochberg, F. G., Gestal, C., and Furuya, H. 2011. A new dicyemid from *Octopus hubbsorum* (Mollusca: Cephalopoda: Octopoda). *Journal of Parasitology* 97: 265–269.
- Castellanos-Martinez, S., Aguirre-Macedo, M. L., and Furuya, H. 2016. Two new species of dicyemid mesozoans (Dicyemida: Dicyemidae) from *Octopus maya* Voss and Solis-Ramirez (Octopodidae) off Yucatan, Mexico. *Systematic Parasitology* 93: 551–564.
- Couch, J. A. and Short, R. B. 1964. *Dicyema bilobum* sp. n. (Meso-zoa: Dicyemidae) from the northern Gulf of Mexico. *Journal of Parasitology* 50: 641–645.
- Furuya, H. 1999. Fourteen new species of dicyemid mesozoans from six Japanese cephalopods, with comments on host specificity. *Species Diversity* 4: 257–319.
- Furuya, H. 2005. Three new species of *Dicyema* (Phylum Dicyemida) from *Amphioctopus kagoshimensis* (Mollusca: Cephalopoda: Octopodidae). *Species Diversity* 10: 231–147.
- Furuya, H. 2006a. Three new species of dicyemid mesozoans (Phylum Dicyemida) from *Amphioctopus fangsiao* (Mollusca: Cephalopoda), with comments on the occurrence patterns of dicyemids. *Zoological Science* 23: 105–119.
- Furuya, H. 2006b. Two new species of *Dicyema* (Dicyemida: Dicyemidae) from *Amphioctopus areolatus* (Mollusca: Cephalopoda: Octopodidae). *Species Diversity* 11: 257–269.
- Furuya, H. 2006c. A new species of *Dicyemene* Whitman, 1883 (Phylum Dicyemida) from *Sepia latimanus* (Mollusca: Cephalopoda: Decapodidae) off Okinawa, Japan. *Systematic Parasitology* 65: 205–213.
- Furuya, H. 2007. Redescription of two *Dicyemene* (Phylum: Dicyemida) from *Rossia pacifica* (Mollusca: Cephalopoda: Decapoda). *Journal of Parasitology* 93: 841–849.
- Furuya, H. 2008. Three new dicyemids from *Octopus sasaki* (Mollusca: Cephalopoda: Octopoda). *Journal of Parasitology* 94: 1071–1081.
- Furuya, H. 2009. Two new dicyemids from *Sepia longipes* (Mollusca: Cephalopoda: Decapoda). *Journal of Parasitology* 95: 681–689.
- Furuya, H. 2016. Diversity and morphological adaptation of dicyemids in Japan. Pp. 401–418. In: Motokawa, M. and Kajihara, H. (Eds) *Species Diversity of Animals in Japan*. Springer Japan, Tokyo.
- Furuya, H. 2018. Eleven new species of dicyemid (Phylum Dicyemida) from *Octopus longispadiceus* and *O. tenuicirrus* (Mollusca: Cephalopoda: Octopoda) in Japanese waters. *Species Diversity* 23: 143–179.
- Furuya, H. and Hochberg, F. G. 1999. Three new species of *Dicyema* (Phylum Dicyemida) from cephalopods in the Western Mediterranean. *Vie et Milieu* 49: 117–128.
- Furuya, H. and Hochberg, F. G. 2002. New species of *Dicyemene* (Phylum: Dicyemida) in deep-water *Graneledone* (Mollusca: Cephalopoda: Octopoda) from the Antarctic. *Journal of Parasitology* 88: 330–336.

- Furuya, H. and Tsuneki, K. 2003. Biology of dicyemid mesozoans. *Zoological Science* 20: 519–532.
- Furuya, H. and Tsuneki, K. 2007. Developmental patterns of the hermaphroditic gonad in dicyemid mesozoans (Phylum Dicyemida). *Invertebrate Biology* 126: 295–306.
- Furuya, H., Tsuneki, K., and Koshida, Y. 1992a. Two new species of the genus *Dicyema* (Mesozoa) from octopuses of Japan with notes on *D. misakiense* and *D. acuticephalum*. *Zoological Science* 9: 423–437.
- Furuya, H., Tsuneki, K., and Koshida, Y. 1992b. Development of the infusoriform embryo of *Dicyema japonicum* (Mesozoa: Dicyemidae). *Biological Bulletin* 183: 248–257.
- Furuya, H., Tsuneki, K., and Koshida, Y. 1993. The development of the hermaphroditic gonad in four species of dicyemid mesozoans. *Zoological Science* 10: 455–466.
- Furuya, H., Tsuneki, K., and Koshida, Y. 1994. The development of the vermiform embryos of two mesozoans, *Dicyema acuticephalum* and *Dicyema japonicum*. *Zoological Science* 11: 235–246.
- Furuya, H., Tsuneki, K., and Koshida, Y. 1997. Fine structure of a dicyemid mesozoan, *Dicyema acuticephalum*, with special reference to cell junctions. *Journal of Morphology* 231: 297–305.
- Furuya, H., Hochberg, F. G., and Tsuneki, K. 2001. Developmental patterns and cell lineages of vermiform embryos in dicyemid mesozoans. *Biological Bulletin* 201: 405–416.
- Furuya, H., Hochberg, F. G., and Tsuneki, K. 2003a. Calotte morphology in the phylum Dicyemida: niche separation and convergence. *Journal of Zoology* 259: 361–373.
- Furuya, H., Hochberg, F. G., and Tsuneki, K. 2003b. Reproductive traits of dicyemids. *Marine Biology* 142: 693–706.
- Furuya, H., Hochberg, F. G., and Tsuneki, K. 2004. Cell number and cellular composition in infusoriform larvae of dicyemid mesozoans (Phylum Dicyemida). *Zoological Science* 21: 877–889.
- Furuya, H., Hochberg, F. G., and Tsuneki, K. 2007. Cell number and cellular composition in vermiform larvae of dicyemid mesozoans (Phylum Dicyemida). *Journal of Zoology* 272: 284–292.
- Gleadall, I. G. 1993. Identification of the long-ligula octopuses of Japan. Pp. 145–158. In: Okutani, T., O'Dor, R. K., and Kubodera, T. (Eds) *A Status Report. In "Recent Advances in Fisheries Biology."* Tokai University Press, Hadano.
- Gleadall, I. G. 2016. *Octopus sinensis* d'Orbigny, 1841 (Cephalopoda: Octopodidae): valid species name for the commercially valuable East Asian common octopus. *Species Diversity* 21: 31–42.
- Hochberg, F. G. 1982. The "kidneys" of cephalopods: a unique habitat for parasites. *Malacologia* 23: 121–134.
- Hochberg, F. G. 1983. The parasites of cephalopods: a review. *Memoirs of the National Museum Victoria* 44: 109–145.
- Hochberg, F. G. 1990. Diseases of Cephalopoda. Diseases caused by protists and mesozoans. Pp. 47–202. In: Kinne, O. (Ed.) *Diseases of Marine Animals. Vol. III.* Biologische Anstalt Helgoland, Hamburg.
- Hoffman, E. G. 1965. Mesozoa of the sepiolid, *Rossia pacifica* (Berry). *Journal of Parasitology* 51: 313–320.
- Kalavati, C., Narasimhamurti, C. C., and Suseela, T. 1978. A new species of *Dicyemene*, *D. coromandelensis* n. sp. from *Sepia elliptica* Hoyle. *Proceedings Indian Academy of Sciences (Animal Sciences)* 87: 161–167.
- Kalavati, C., Narasimhamurti, C. C., and Suseela, T. 1984. Four new species of mesozoan parasites (Mesozoa: Dicyemidae) from cephalopods of Bay of Bengal. *Proceedings of the Indian Academy of Sciences (Animal Sciences)* 93: 639–654.
- Khromov, D. N. 1998. Distribution patterns of Sepiidae. *Smithsonian Contributions to Zoology* 586: 191–206.
- Kölliker, A. von. 1849. Über *Dicyema paradoxum*, den Schmarotzer der Venenanhänge der Cephalopoden. *Berichte von der Königlichen Zootomischen Anstalt zu Würzburg* 2: 53–58.
- Lapan E. A. and Morowitz, H. J. 1975. The dicyemid Mesozoa as an integrated system for morphogenetic studies. 1. Description, isolation and maintenance. *Journal of Experimental Zoology* 193: 147–160.
- Leite, T. S., Haimovici, M., Molina, W., and Warnke, K. 2008. Morphological and genetic description of *Octopus insularis*, a new cryptic species in the *Octopus vulgaris* complex (Cephalopoda: Octopodidae) from the tropical southwestern Atlantic. *Journal of Molluscan Studies* 74: 63–74.
- McConnaughey, B. H. 1949. Mesozoa of the family Dicyemidae from California. *University of California Publications in Zoology* 55: 1–34.
- McConnaughey, B. H. 1951. The life cycle of the dicyemid Mesozoa. *University of California Publications in Zoology* 55: 295–336.
- McConnaughey, B. H. and Kritzler H. 1952. Mesozoan parasites of *Octopus vulgaris* Lam. from Florida. *Journal of Parasitology* 38: 59–64.
- Nakajima, H. and Furuya, H. 2019. Coevolution and host switching in dicyemids. P. 51. In: Terakita, A. (Ed.) *Abstract of the 90th Annual Meeting of the Zoological Society of Japan.* Kyorinsha, Tokyo. [In Japanese]
- Nouvel, H. 1933. Recherches sur la cytologie, la physiologie et la biologie des Dicyémides. *Annales de l'Institut Océanographique* 13: 165–255.
- Nouvel, H. 1934. Observations sur les Dicyémides provenant d'un poulpe de Mauritanie, description de deux espèces nouvelles. *Bulletin Societe Zoologique de France* 59: 176–186.
- Nouvel, H. 1937. Recherches sur les nématogènes fondateurs des Dicyémides. *Bulletin Biologique de la France et de la Belgique* 71: 374–392.
- Nouvel H. 1945. Les Dicyémides de quelque Céphalopodes côtes françaises avec indication de la presence de Chromidinides. *Bulletin de l'Institut Océanographique* 887: 1–8.
- Nouvel, H. 1947. Les Dicyémides. 1^{re} partie: systématique, générations, vermiformes, infusorigène et sexualité. *Archives de Biologie* 58: 59–220.
- Nouvel, H. 1948. Les Dicyémides. 2^e partie: infusoriforme, tératologie, spécificité du parasitisme, affinités. *Archives de Biologie* 59: 147–223.
- Nouvel, H. and Nakao, Y. 1938. Dicyémides du Japon. *Bulletin de la Société Zoologique de France* 63: 72–80.
- Okutani, T., Tagawa, M., and Horikawa, H. 1987. *Cephalopods from Continental Shelf and Slope Around Japan.* Japan Fisheries Resource Conservation Association, Tokyo, 194 pp.
- Sasaki, M. 1929. A monograph of the dibranchiate cephalopods of the Japanese and the adjacent waters. *Journal of the College of Agriculture, Hokkaido Imperial University* 20: 1–357.
- Short, R. B. 1964. *Dicyema typoides* sp. n. (Mesozoa: Dicyemidae) from the northern Gulf of Mexico. *Journal Parasitology* 50: 646–651.
- Short, R. B. 1991. Marine flora and fauna of the eastern United States, Dicyemida. NOAA Technical Reports NMFS 100: 1–16.
- Short, R. B. and Damian, R. T. 1966. Morphology of the infusoriform larva of *Dicyema aegira* (Mesozoa: Dicyemidae). *Journal of Parasitology* 52: 746–751.
- Yoshida, M., Tsuneki, K., and Furuya, H. 2006. Phylogeny of selected Sepiidae (Mollusca, Cephalopoda) based on 12S, 16S, and COI sequences, with comments on the taxonomic reliability of several morphological characters. *Zoological Science* 23: 342–351.
- Whitman, C. O. 1883. A contribution to the embryology, life history, and classification of the dicyemids. *Mittheilungen aus der Zoologischen Station zu Neapel* 4: 1–89.