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A new species of *Parapinnanema* (Nematoda, Chromadoridae) from Dr Theodor Mortensen's Pacific Expedition 1914–16 with an identification key to the genus

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Abstract

A new species from the family Chromadoridae is described from samples collected during Dr Mortensen's Pacific Expedition 1914–16 to Honolulu, Hawaii. *Parapinnanema hawaiiensis* **sp. nov.** is characterized by a low *c'* ratio and especially by a peculiar complex morphology of the median part of the gubernaculum. An updated and modified key to all the valid species of *Parapinnanema* is proposed.

Key words: Chromadorida, Euchromadorinae, Hawaii, taxonomy, marine nematodes

Introduction

The family Chromadoridae, generally marine and represented by about 410 species (Tchesunov 2014), has been recorded worldwide, and their abundance appears to be positively correlated with an increase in sediment grain size (Heip *et al.* 1985).

Chromadoridae are currently divided into five subfamilies: Chromadorinae, Euchromadorinae, Harpagonchinae, Hypodontolaiminae and Spilipherinae. Euchromadorinae accommodates 12 genera and more than 60 species (Tchesunov 2014). They are characterized by having a cuticle with a complex heterogeneous ornamentation, often with lateral differentiation. The six outer labial and four setiform cephalic sensilla may be arranged in a single circle. The amphideal transverse fovea is slit-like or oval, and located posterior to the cephalic setae. The buccal cavity is characterized by a large dorsal tooth, with or without denticles or smaller ventrosublateral teeth. The pharynx has or lacks a defined terminal bulb, and the gubernaculum is usually with hammer- or L-shaped lateral pieces (incorrectly indicated as formed from the cloacal lining, *i.e.* with the term telamon) (Decraemer & Smol, 2006). The precloacal supplements are missing, but a precloacal differentiation of the body cuticle may be present (Tchesunov 2014).

The genus *Parapinnanema* (sub-family: Euchromadorinae) was established by Inglis (1969) together with the genus *Austranema* Inglis, 1969, which Warwick & Coles (1975) subsequently synonymized with the first genus. This synonymization appears to be correct, since both genera have similar modifications of the lining of the oesophastome, lack an oesophageal bulb, and have a pronounced precloacal modification in the males. The distinction that *Parapinnanema* had two circles of six and four cephalic setae, whereas *Austranema* had a single circle of ten, cannot be maintained, since *A. pectinata* (Wieser & Hopper, 1967) and *A. colesi* (Inglis, 1968) both have two circles. Furthermore, the characteristic thickness of the battlement-like cuticle of *Parapinnanema* in the oesophageal region is clearly only a matter of the degree of cuticular thickness, since a slight thickening can be seen also in *Parapinnanema harveyi* Warwick & Coles, 1975 and other species.

Currently, *Parapinnanema* comprises 11 species (Gourbault & Vincx, 1994).

Among the unidentified material that was collected during Dr Mortensen's Pacific Expedition 1914–1916, and

deposited at the Natural History Museum of Copenhagen, some specimens belonging to *Parapinnanema* were found from the Hawaii samples. The samples of this expedition comprise material collected from Auckland and Campbell Islands, New Zealand, New South Wales, Philippine Islands, Japan, Hawaii, California and other localities of the Pacific coast of North America, Panama and the West Indies, and have been studied by some of the greatest pioneers of nematology, including Ditlevsen (1922, 1930), Kreis (1932), and Allgén (1947a,b; 1951). Ditlevsen (1922) wrote: “It is to be expected that the study of this material – besides enriching science with a great number of unknown forms – will contrive to throw light upon the geographical distribution of this group of animals”. In particular, there is little information on the composition of the assemblages of free-living marine nematodes from Hawaii, mainly documented by Allgén (1951). He studied the material collected from Honolulu and Hilo, and reported several species belonging to the family Chromadoridae (Table 1). However, no species of *Parapinnanema* have been reported so far from Hawaii. Almost a century after Dr Mortensen's Pacific Expedition, unknown species are still to be discovered from these samples.

In the present paper a new species of *Parapinnanema* is described and its systematic position is discussed. This has been also an occasion to propose an updated identification key to the species of the genus *Parapinnanema*.

TABLE 1. List of species belonging to Chromadoridae documented by Allgén (1951) and their current taxonomic position. The validity of the species is in accordance with Gerlach & Riemann (1973).

Species
<i>Chromadorella filiformis</i> (Bastian, 1865) Filipjev, 1918
= <i>Chromadora filiformis</i> Bastian, 1865
= <i>Dichromadora tenuicauda</i> Schuurmans Stekhoven, 1950
= <i>Chromadorella filiformoides</i> Chitwood, 1951
= <i>Chromadorella filiformoides membranata</i> (Micoletzki, 1922)
<i>Chromadorina pacifica</i> (Allgén, 1947) Wieser, 1954
= <i>Chromadora pacifica</i> (Allgén, 1947) Wieser, 1954
<i>Euchromadora vulgaris</i> (Bastian, 1865) de Man 1886
= <i>Chromadora vulgaris</i> Bastian, 1865
<i>Graphonema amokuræ</i> (Ditlevsen, 1921) Inglis, 1921
= <i>Euchromadora amokuræ</i> (Ditlevsen, 1921)
= <i>Spiliphæra amokuræ</i> Ditlevsen, 1921
<i>Spiliphæra gracilicauda</i> de Man, 1893
= <i>Spiliphæra gracilicauda breviseta</i> Allgén, 1959
= <i>Spiliphæra gracilicauda dolichura</i> Allgén, 1951
<i>Spiliphæra longiseta</i> (Allgén, 1951) Wieser, 1954
sp incertae sedis
<i>Spiliphæra tenuicauda</i> (Allgén, 1951) Wieser, 1954
sp inquirenda, ? to <i>Prochromadorella</i>
<i>Spilophorella campbelli</i> Allgén, 1928
<i>Steineridora loricata</i> (Steiner, 1916) Inglis, 1969
= <i>Euchromadora loricata</i> (Steiner, 1916)
= <i>Spiliphæra loricata</i> Steiner, 1916

Material and methods

The specimens were mounted as permanent glycerine slides and deposited at the Natural History Museum of Denmark. The coverslip was supported by tiny glass beads to avoid squeezing the specimens, and sealed with Glyceel. Specimens were studied and measured using an Optiphot-2 Nikon equipped with DIC Nomarski

illumination. Drawings were made using a camera lucida mounted on a Zeiss Universal microscope. All measurements are in micrometers and curved structures were measured along the arc.

Abbreviations

a = total body length divided by maximum body diameter

abd = anal body diameter

b = total body length divided by pharyngeal length

c = total body length divided by tail length

c' = tail length divided by anal body diameter

cbd = corresponding body diameter

hd = head diameter

L = body length

mbd = maximum body diameter

s' = spicule length divided by abd

spic = spicule

TL = tail length

Results

Systematics

Order CHROMADORIDA Chitwood, 1933

Superfamily CHROMADOROIDEA Filipjev, 1917

Family CHROMADORIDAE Filipjev, 1917

Subfamily EUCHROMADORINAE Gerlach & Riemann, 1973

Genus *Parapinnanema* Inglis, 1969

Emended diagnosis (Gourbault & Vincx, 1994): Thick cuticle on the pharyngeal region; amphids with surrounding fringe of cuticle; buccal cavity conical with one dorsal and two subventral plates; one large pointed tooth on the dorsal plate and three denticles plus a ventral tooth on each subventral plate; tail conico-cylindrical; raised precloacal and caudal modifications of the cuticle in males; elongated vulva, vagina opening wide, an internal double sphincter around the uterine chamber.

Number of species: 11

Type species: *Parapinnanema wilsoni* Inglis, 1969

List of valid species: The present list of valid species is in accordance with Gourbault & Vincx (1994). For each species taxonomical notes and geographical distribution are provided.

P. alii (Murphy, 1965); Murphy, 1965:154, Fig. 155 a–b [*Nygmatonchus alii*]; Inglis, 1969: p 187 (*Austranema alii* n. comb.), 195–197, Figs 38–40; Warwick & Coles, 1975: p 405 (*Parapinnanema alii* n. comb.); Gourbault & Vincx, 1994: 153–155, Figs 8,9; Tchesunov (2014): 377 (erroneously reported as valid *Austranema alii*); Maldives, New Caledonia, Australia, Chile.

P. bableti Gourbault & Vincx, 1994; Gourbault & Vincx, 1994:142–147, Figs. 1–4; Polynesia.

P. colesi (Inglis, 1968); Inglis, 1968:36–37, Figs 6–13 [*Euchromadora colesi*]; Inglis, 1969: p 187 (*Austranema colesi* n. comb.); Warwick & Coles, 1975: p 405 (*Parapinnanema colesi* n. comb.); Tchesunov (2014): 377 (erroneously reported as valid *Austranema colesi*); New Caledonia.

P. harveyi Warwick & Coles, 1975; Warwick & Coles, 1975: 409–411, Fig. 3a–f; Isles of Scilly.

P. imbricata Belogurov, Belogurova & Smolyanko, 1985; Belogurov *et al.*, 1985:50–54, Fig. 1; Sea of Japan.

P. mexicanum (Jensen, 1986); Jensen, 1986: Fig. 4 [*Austranema mexicanum*]; Gourbault & Vincx, 1994: p 155

(*Parapinnanema mexicanum* n. comb.); Tchesunov (2014): 377 (erroneously reported as valid *Austranema mexicanum*); Gulf of Mexico.

P. pectinatum (Wieser & Hopper, 1967); Wieser & Hopper, 1967:286, Figs 53a–d [*Euchromadora pectinatum*]; Inglis, 1969: p 187 (*Austranema pectinatum* n. comb.); Warwick & Coles, 1975: p 405 (*Parapinnanema pectinatum* n. comb.); Tchesunov (2014): 377 (erroneously reported as valid *Austranema pectinatum*); Florida.

P. rhipsoides Gourbault & Vincx, 1994; Gourbault & Vincx, 1994:150–152, Fig. 7–8; Guadeloupe.

P. ritae Gourbault & Vincx, 1994; Gourbault & Vincx, 1994:147–149, Fig. 5–6; Guadeloupe.

P. shirleyae (Coles, 1965); Coles, 1965:182–184 fig 2, 8, 19–21, 34 [*Euchromadora shirleyae*]; Inglis, 1969: p 187 (*Austranema shirleyae* n. comb.), 172 Figs 44–4–6, 85–90; Grimaldi-De Zio, 1968 p 347; Warwick & Coles, 1975: p 405 (*Parapinnanema shirleyae* n. comb.); Tchesunov (2014): 377 (erroneously reported as valid *Austranema shirleyae*); South Africa, Mediterranean Sea.

P. wilsoni Inglis, 1969; Inglis, 1969:194, Figs 51–55, 66–75, 97–98; Australia.

***Parapinnanema hawaiiensis* sp. nov.**

(Figs. 1, 2, 3; Table 2)

Specimens. 3 adult males; 1 adult female.

Type material. Holotype, adult male, collected by Dr Theodor Mortensen on May 5, 1915, during the Pacific Expedition 1914–1916, at 10 m depth in an unspecified coastal area of Honolulu, Hawaii, mounted for light microscopy and deposited at the Natural History Museum of Denmark (NHMD) under accession number ZMUC NEM-5338. Paratypes, one adult female and two adult males, collected together with holotype, mounted together on the same slide for light microscopy and deposited at the NHMD under accession number ZMUC NEM-5329.

Etymology: The species name refers to the geographical origin.

Description of Male: Body cylindrical with blunt head and conico-cylindrical tail (Fig. 1A). Six internal labial sensillae in form of papillae. Six outer labial and four cephalic sensillae in a single circle, and in form of setiform papillae. Cuticle annulated and complex, battlement-like and heterogeneous, as typical for the genus (Fig. 1C). Annulation starts about 7 μm from the anterior end (at the level of the dorsal tooth), and is generally 3 μm thick, but thickens to 4 μm in the pharyngeal region. The cuticular annulation consists of two concentric layers of heavily sclerotized annules that are anteriorly directed on the anterior half of the body and posteriorly directed on the posterior body half. Four fields devoid of ornamentation are present in the posterior body part (two laterally, one dorsally and ventrally) (Fig. 1D). The non-ornamented zones are narrower anteriorly (6 μm wide) and larger in the median (14 μm) and caudal body regions (16 μm).

The cuticular sheath of the anterior end of the buccal cavity is supported by the usual twelve buccal rugae (Fig. 1B). The dorsal tooth is shallowly set into the wall of the buccal cavity, and is relatively large (Figs 1B and 3A). There are two small pointed ventral teeth and a lateral one. Amphideal fovea transverse, 12 μm wide, slit-like, located 6 μm from anterior body end (Fig. 1C). Diameter of amphidial fovea 0.5 of the cbd. Pharynx cylindrical, slightly enlarged posteriorly. Nerve ring at about 47% of the PL. Cardia cells not visible. Reproductive system monorchic. Male spicules arcuate (63 μm , 1.0 abd) with a small capitulum. Lateral pieces of the gubernaculum L-shaped, with the sharp flexure forming an almost exact right-angle (Figs 1E and 3C). The L-shaped pieces are about one-fifth the length of the spicules (41 μm). The proximal parts of the L-shaped pieces are about 1.7 the length of the distal one (Fig. 1E). The median piece of the gubernaculum is complex and consists of a plate with swollen distal end and is characterized by a distinct tooth (Figs 1E and 3C, D). It is laterally expanded and reaches the L-shaped pieces. Two differently oriented tips are also present in its distal part.

Cloacal opening surrounded by about 8 incomplete annules with a thick, protruding border (Fig. 1G). A cuticular elevation, 3 μm high, rises just anterior to the cloacal opening (Figs 1D and 3C). Anterior to the cloaca, at about 88 μm , the ventral body cuticle is modified into a distinctive raised area that comprised about 11 annules (8 μm high) (Figs. 1D and 3B). A morphologically similar area is present on the ventral side of the tail, but this is smaller and sometimes difficult to discern. Tail conico-cylindrical, spinneret present; non-annulated asymmetrical tail tip 18 μm long (Fig. 1D). No terminal setae observed.

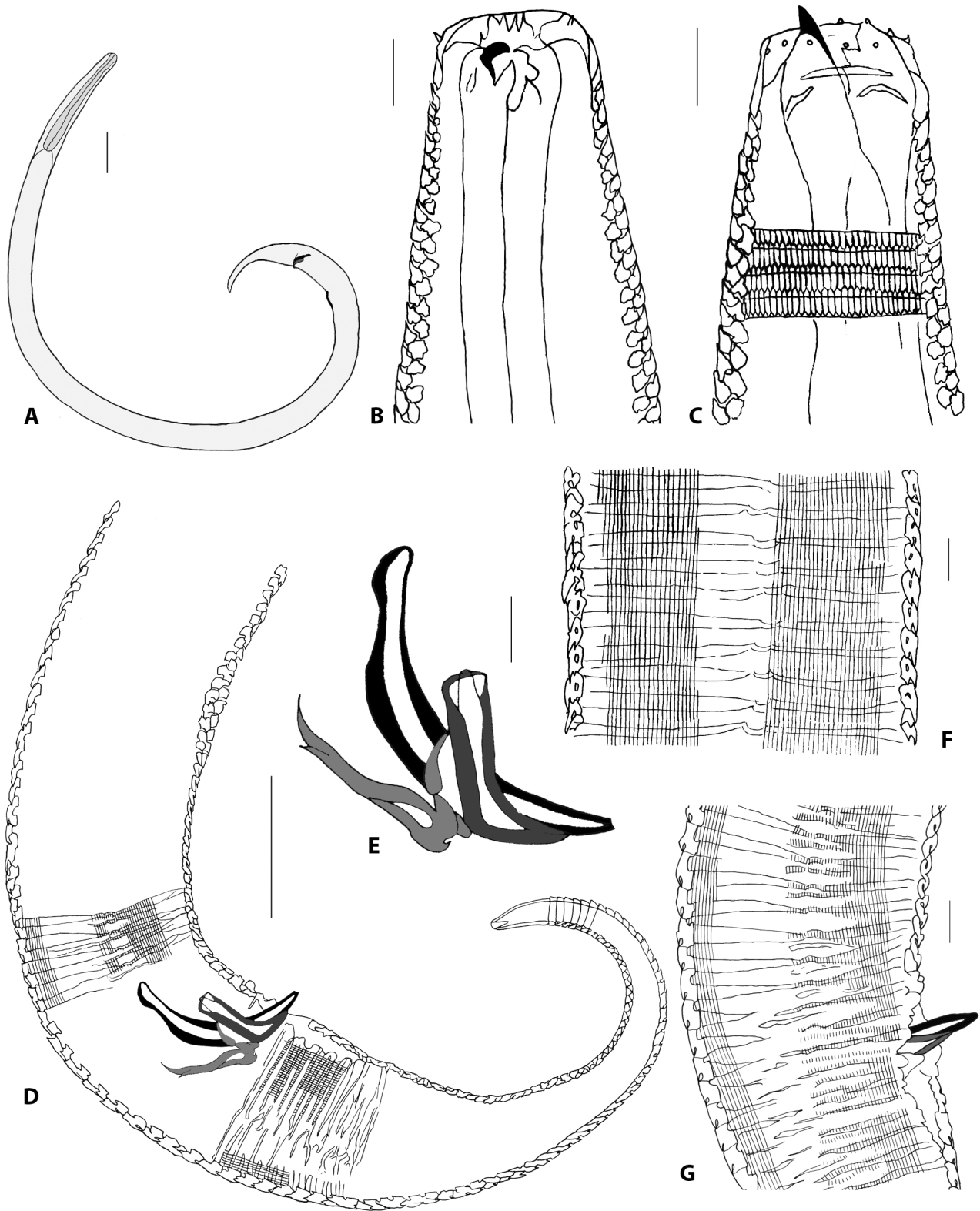


FIGURE 1. *Parapinnanema hawaiiensis* sp. nov. A) holotype habitus; B) detail of the buccal cavity of the holotype; C) detail of the cuticular ornamentation in the cervical region of a male paratype; D) cuticular ornamentation in the middle body of the holotype; E) caudal region of the holotype; F) detail of the copulatory apparatus of the holotype; G) pattern of the cuticular ornamentation in the cloacal region of a male paratype. Scale bars: A, 100µm; B, C, E, F, G 10 µm; D, 50 µm.

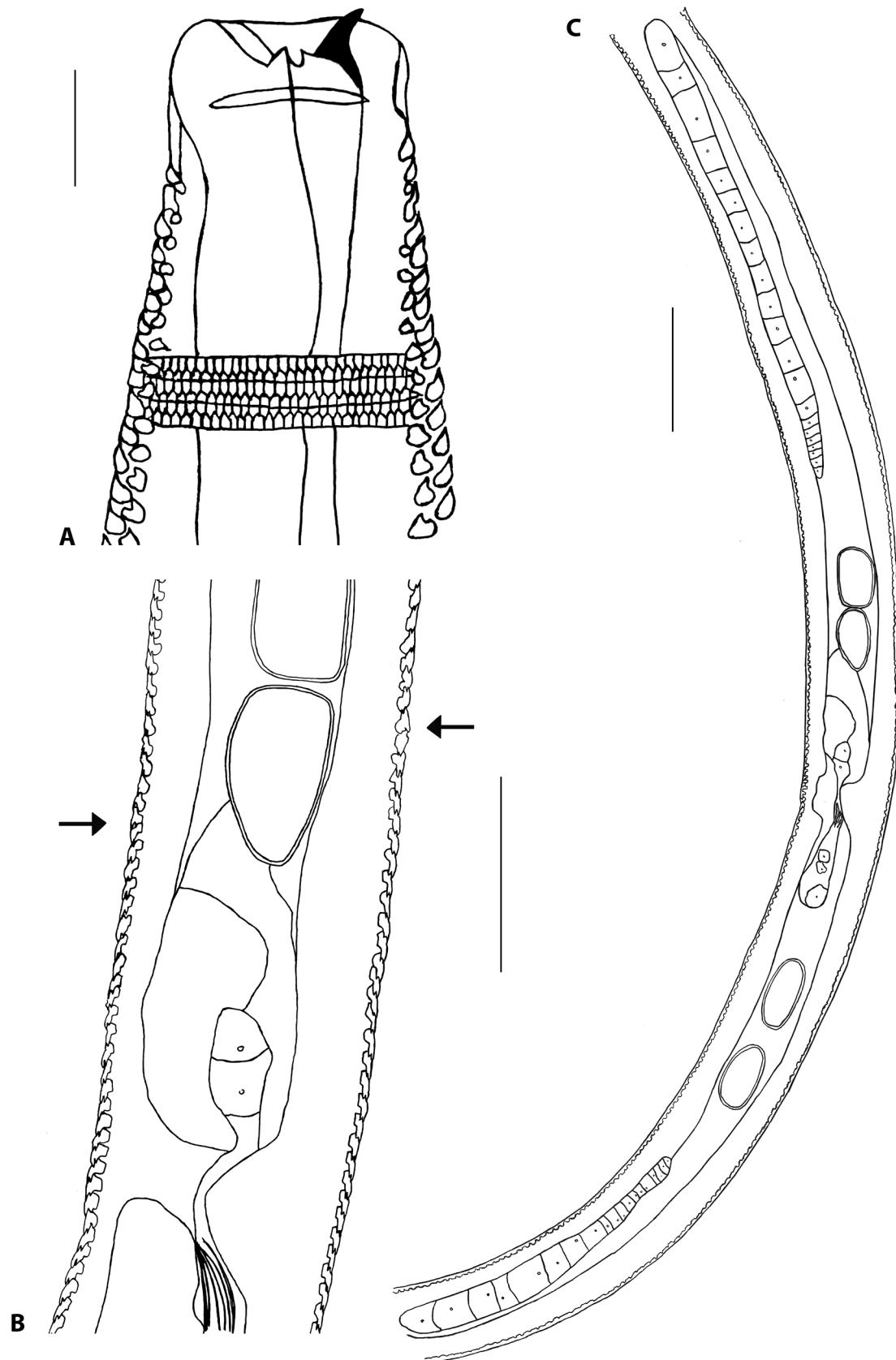


FIGURE 2. *Parapinnanema hawaiiensis* sp. nov., female paratype A) buccal cavity; B) detail of the change of direction (indicated by the arrows) of the epicuticle sculpture in the vulvar region; C) detail of the ovaries, eggs and vulva. Scale bars: A, 10 μ m; B, 50 μ m; C, 100 μ m.

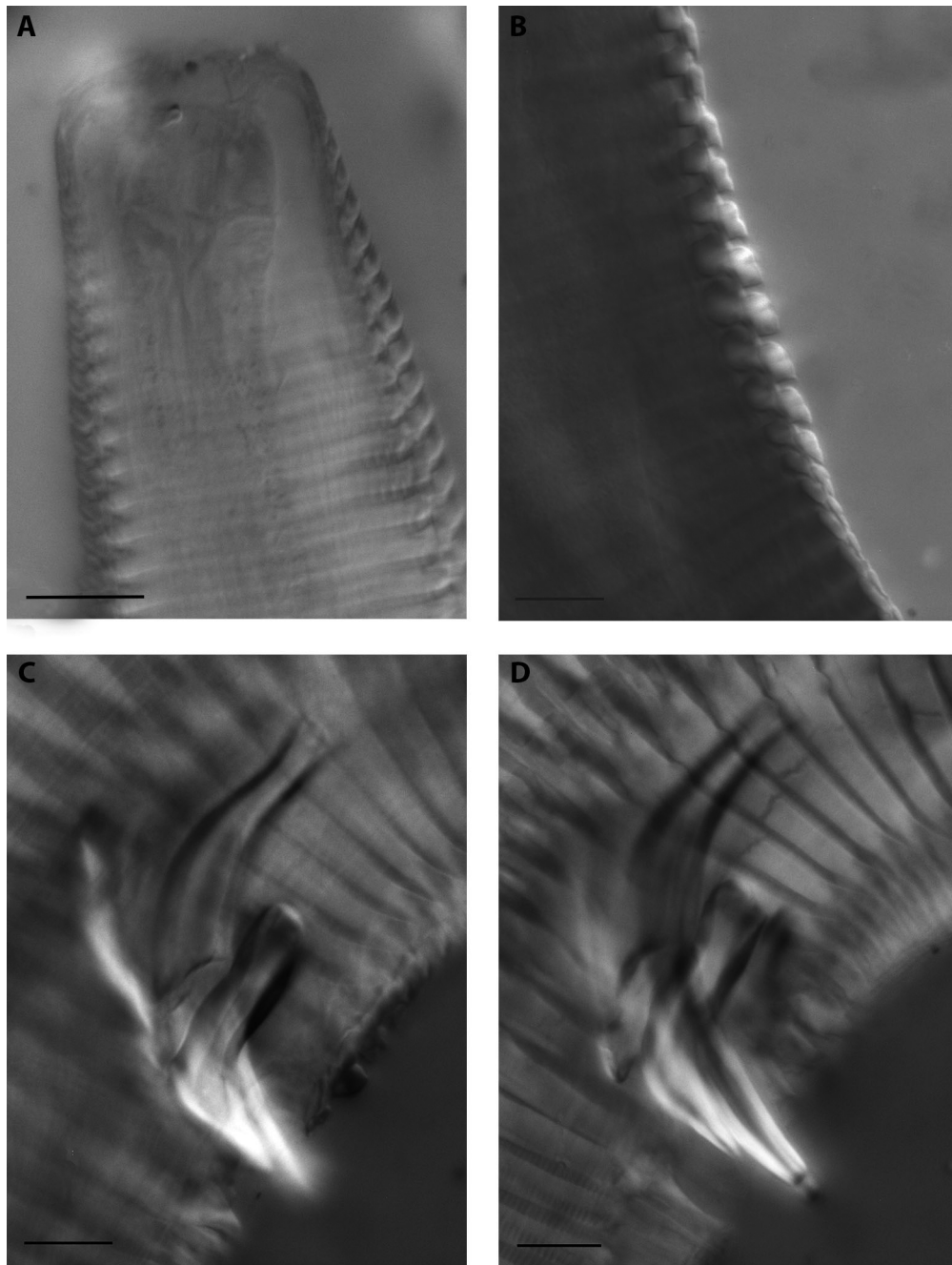


FIGURE 3. Light micrographs of *Parapinnanema hawaiiensis* sp. nov. A) buccal cavity of the holotype; B) detail of the precloacal modification of the cuticle of a male paratype; C) and D) details of the copulatory apparatus of the holotype. Scale bars: A, B, C, D, 10 μ m.

Description of female: General appearance similar to the male. Genital system didelphic, amphidelphic with reflexed ovaries (Fig. 2C). Four eggs present in each branch of uterus. Musculature developed as a sphincter around the uterine chamber, with paired spermathecae. Vulva elongated extending over 11 annules; vagina open. A change of the direction of the epicuticle sculpture is observed in the vulvar region of the female (Fig. 2B).

Diagnosis. *Parapinnanema hawaiiensis* sp. nov. is a relatively slender animal ($L = 2184\text{--}2250$ μ m, $a = 33\text{--}36$) with a buccal cavity which does not have a massive dorsal tooth and does have small subventral teeth, and a complex copulatory apparatus with the spicules (63–74 μ m long) partially covered by the gubernaculum structure. Proximal part of L-shaped piece is about 1.7 the length its distal part. Gubernaculum very complex, with its median part forming a plate with swollen distal end and a distinct tooth. A lateral expansion starting from the distal part reaches the L-shaped pieces giving them a hump-like perception. Two tips, differently orientated, present in the proximal part of the median piece.

Differential diagnosis. *Parapinnanema hawaiiensis* **sp. nov.** is in morphologically similar to *P. alii*, *P. bableti* and *P. ritae* having similar total body length of the male and the De Man ratio values *a*, *b* and *c* (Tab. 3). However, the new species differs by its lower ratios *c'* and is distinguished by the presence of a lateral expansion of the median gubernaculum piece which is absent in the other species of the genus.

TABLE 2. Morphometric measurements for *Parapinnanema hawaiiensis* **sp. nov.** (all measurements in μm , except ratios; minimum and maximum values are provided for male paratypes).

Character	Holotype	Paratype 1-male	Paratype 2-male	Paratype 1-female
Slide number	NEM-5338	NEM-5329	NEM-5329	NEM-5329
Total length	2184	2223	2250	2259
Head diameter	22	20	21	20
Inner labial sensilla	Papillate	Papillate	Papillate	Papillate
Outer labial sensilla	2	2	n.v.	2
Cephalic sensilla	2	2	n.v.	2
Dorsal tooth	4	4	4	4
Subventral teeth	2	2	2	2
Distance from anterior to anterior edge of amphid	6	6	6	6
Amphid diameter	12	12	nv	14
Distance from anterior edge to nerve ring	139	134	138	105
Nerve ring cbd	55	47	51	46
Pharynx Length	294	295	282	310
Pharynx cbd	59	57	56	60
Maximum body diameter	66	66	63	75
Distance from anterior edge to vulva	n/a	n/a	n/a	1092
Vulva cbd	n/a	n/a	n/a	75
Distance from anterior to anus	1964	2009	2034	1994
abd	63	59	56	38
Spicules	63	65	74	n/a
Gubernaculum	33	34	31	n/a
Distance from anus to most anterior supplement	88	91	104	n/a
Tail length	220	214	216	264
a	33	34	36	30
b	7.4	7.5	8.0	7.3
c	9.9	10.4	10.4	8.5
c'	3.5	3.6	3.9	7.0
Distance from anterior edge to vulva divided by total body length	n/a	n/a	n/a	0.48
s'	1.0	1.1	1.3	n/a

TABLE 3. Morphometrics of all the valid species of *Parapinnanema*, together with their distribution.

Species	Sex	n	L	a	b	c	c'	spic / V	Distribution/Habitat
<i>P. alii</i> (Murphy, 1965)	♂	3	1600–2000	37.6–41.0	6.2–8.5	8.2–10.3		58	Maldives, Ari Atoll; subtidal; sand; Murphy 1965
			1800	39.5	7.2	9.5	5.1		
	♀	4	1900–2050	27.2–31.5	7.1–7.9	8.5–9.8		45.3–50.7	
			1980	29.4	7.5	8.9	6	48.1	
	♂	3	1700–2100	32.7–38.7	7.4–8.0	8.9–9.8	4.5–5.7	38–52	Western Australia, Shark Bay; sublittoral, 12 m; Inglis 1969
			1930	36.4	7.7	9.3	5	45	
	♀	2	1900–2310	37–40.5	7–7.2	10–11	5.7	45.9–47.3	
	♂	10+2	1465–2010/3325	31.2–37.6	6.8–8.4	8.7–9.5	4.3–4.9	55–63/92	New Caledonia, South-western Lagoon; 9–13 m; mud, fine sand; Gourtbault & Vincx 1994
		10	1847±169	35.2±2.1	7.5±0.3	9.0±0.6	4.7±0.3	66±2.6	
	♀	9	1825–2260	32.1–34.9	7.1–7.8	8.1–8.9	6.9–7.3	47.3–48.5	
			1989±133	32.8±2.0	7.4±0.2	8.5±0.3	7.1±0.4	47.8±1.5	
	♂	15	1735–2245	36.1–44.9	7.1–7.7	8.4–9.9	4.4–5.3	70–77	
<i>P. bableri</i> Gourtbault & Vincx, 1994	♀	16	1906±123	39.5±2.6	7.3±0.2	9.1±0.2	4.8±0.2	72.4±2.3	Tuamotu Archipelago, Fangataufa Atoll; lagoon habitat, 6–38 m; fine to medium sand; Gourtbault & Vincx 1994
			1780–2185	27.4–32.1	6.8–7.8	7.9–8.9	7.4–8.7	46.3–47.7	
			2062±150	30.7±1.7	7.3±0.4	8.4±0.3	8±0.5	46.9±0.5	
	♂	5	2270–3430	39.7–47.3	8.8–9.6	10–11.5	4.6–6	39–61	
<i>P. colesi</i> (Inglis, 1968)	♀	4	2954±576	43.7±3.2	9.3±3.1	11±0.6	5.2±0.6	49.6±9.4	New Caledonia, St Vincent's Bay; sublittoral, 4–14 m; fine to coarse sand; Inglis 1968
			3240–3580	32.8–38.2	8.8–9.7	10.1–11.4		48.7–49.5	
			3422.5±141	34.8±2.3	9.2±0.3	10.7±0.6		49±0.3	
<i>P. harveyi</i> Warwick & Coles, 1975	♂	3	3810–3860					53–58	Isles of Scilly; intertidal; coarse sand; Warwick & Coles 1975
	♀	1	3570	56.6	8.3	11.9	6.5	47.8	
<i>P. hawaiiensis</i> sp. nov.	♂		2184–2250	33–36	7.4–8.0	9.9–10.4	3.5–3.9	63–74	Hawaii, Honolulu; coastal area, 10 m; present study
	♀		2219±33	34.3±1.5	7.6±0.3	10.2±0.3	3.7±0.2	67±6	
	♀		30		7.3	8.5	7.0	48	

.....continued on the next page

TABLE 3. (Continued)

Species	Sex	n	L	a	b	c	c'	spic / V	Distribution/Habitat
<i>P. imbricatum</i> Belogurov, Belogurova & Smolyanko, 1985	♂	5	3700–4200	44.9–54	8.9–10.8	10.7–12.7		84.4–91.2	Sea of Japan; Moneron I., sublittoral, 40–80 m; coarse sand
	♀	6	3100–3800	43.2–46.1	7.4–8.3	9.1–10.6		48.7–58.1	
<i>P. mexicanum</i> (Jensen, 1986)	♂	2	1320–1428	38–43	6.1–6.6	8.2–8.8	6	50	Gulf of Mexico; sublittoral; medium to coarse sand; Jensen 1986
	♀	1	1710	40	6.9	7.5	9.1	49	
<i>P. pectinatum</i> (Wieser & Hopper, 1967)	♂	2	1650–1970				4.6–5.1	37–40	Florida, Biscayne Bay; sublittoral, 4 m; sand; Wieser & Hopper 1967
	♀	1				7.4	48		
<i>P. ritae</i> Gourtbault & Vinex, 1994	♂	7	2020–2160	36.3–45.6	7.5–8.4	9.2–10.0	4.8–5.9	67–70	Guadeloupe; mangroves; Gourtbault & Vinex 1994
			2099±42	41.9±2.8	8.0±0.5	9.4±0.3	5.6±0.4	68.4±0.9	
	♀	7	2185–2400	31.8–38.8	7.7–8.3	8.7–9.2	6.0–8.7	44.4–46.2	
			2266±73	36.3±2.4	8.0±0.2	8.9±0.1	7.4±0.8	45.4±0.6	
<i>P. rhipsoides</i> Gourtbault & Vinex, 1994	♂	1	1670	37.1	7.4	8.8	4.5	70	Guadeloupe; mangroves; Gourtbault & Vinex 1994
	♀	2	1650–1670	33.0–39.8	6.7–6.9	8.3–8.5	6.5–6.7	49.7–50.3	
<i>P. shirleyae</i> (Coles, 1965)	♂	12	3120–4120	46.4–57.8	7.4–9.6	11.8–13.1	4.1–5.2	57–73	South Africa; sublittoral, 27 m; coarse sand; Coles 1965
			3489±340	52.4±3.5	8.2±0.6	12.3±0.5	4.4±0.3	65.9±4	
	♀	12	3020–3800	32–40	07–8	07–9	6.6–8.8	46–48	
			3370±238	41.7±3.5	7.5±0.3	8.8±0.6	7.9±0.6	46.8±1.2	
<i>P. wilsoni</i> (Inglis, 1969)	♂	4	1340–1780	34.1–43.2	5.8–6.6	9.4–11.7	3.2–3.7	39–46	Western Australia, Cape Leeuwin; subtidal; sand, algae; Inglis 1969
	♀	2	1522.5±185 2340–2760	37.6±4.3 32–40	5.9±0.6 5.6–6	10.2±1 9.1–10.6	3.5±0.2 5.3–5.4	41.5±3	

Key to the adult males of the genus *Parapinnanema*

A previous key to the genus was proposed by Warwick & Coles (1975). An updated and modified key to the species is provided below.

1. Buccal cavity with a series of comb-like teeth 2
- Buccal cavity without comb-like teeth 3
2. Male body length > 3000 μm *P. imbricatum*
- Male body length < 3000 μm *P. pectinatum*
3. L-shaped pieces of gubernaculum with proximal and distal limbs about equal length (ratio < 2) 4
- L-shaped pieces of gubernaculum with lengths of the proximal limbs > distal ones (ratio > 2) 10
4. Male body length < 1450 μm *P. mexicanum*
- Male body length > 1450 μm 5
5. Sharp flexure of the L-shaped pieces at more than right angle 6
- Sharp flexure of the L-shaped pieces at ~ right angle 7
6. Spicules with a protuberance at the ventral side of the proximal part and capitulum clearly ventrally curved *P. bableti*
- Spicules without a protuberance at the ventral side of the proximal part and capitulum *P. ritae*
7. Median piece laterally expanded up to the L-shaped piece *P. hawaiiensis*
- Median piece without lateral expansions 8
8. Double-jointed spicules present *P. rhipsoides*
- Double-jointed spicules absent 9
9. L-shaped pieces of gubernaculum notched distally *P. alii*
- L-shaped pieces of gubernaculum not notched *P. colesi*
10. Sharp flexure of the L-shaped pieces at a > right angle *P. shirleyae*
- Sharp flexure of the L-shaped pieces at ~ right angle 11
11. L-shaped pieces of gubernaculum with proximal limb about 2.6 times as long as the distal one and with a bulge on the inner surface *P. wilsoni*
- L-shaped pieces with proximal limb being 2.1 times as long as distal limb, and without bulge *P. harveyi*

Discussion

Wieser & Hopper (1967) and Gourbault & Vincx (1994) emphasised that the species of *Parapinnanema* are distinguished by subtle characters. Warwick & Coles (1975) suggested the structure of the buccal cavity and the male copulatory apparatus as the most useful characters to identify species of the genus. In particular, the relative lengths of the proximal and distal parts of the L-shaped pieces of the gubernaculum were used by the authors to distinguish most species. However, these show some variability making use of this character somewhat ambiguous. This variability is reported, for instance, in the original description of *P. colesi* (Inglis 1968), as well as when comparing the descriptions of *P. alii*, the most widespread species of this genus (Murphy 1965; Gourbault & Vincx 1994).

The exact position of the precloacal modifications of the cuticle could be a useful character, but information on this particular feature was poorly reported in some of the original descriptions. Also the location of the post-cloacal modifications is visible only when the mounted specimen is orientated in a certain way, and is therefore poorly documented. Accordingly, the male copulatory apparatus remains the most useful character to distinguish the species of the genus.

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