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(Nematoda: Cystidicolidae) from the Skipjack Tuna *Katsuwonus
pelamis***

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CTENASCAROPHIS LESTERI N. SP. AND PROSPINITECTUS EXIGUUS N. SP. (NEMATODA: CYSTIDICOLIDAE) FROM THE SKIPJACK TUNA, KATSUWONUS PELAMIS

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ABSTRACT: Two cystidicolid nematodes, *Ctenascarophis lesteri* n. sp. and *Prospinitectus exiguus* n. sp., are described from the skipjack tuna, *Katsuwonus pelamis*, from Fiji, New Caledonia, Marquesas Islands, New Zealand, Papua New Guinea, and Puerto Rico. The former species differs from *Ctenascarophis gastricus*, the only other member of the genus, by having comb rows extending farther posterior than two-thirds the body length, to the anus in the female; it also has differently distributed spines on each comb, with a maximum of 32 rather than 8. The male has 7 rows of precloacal longitudinal crests; 3 pairs of precloacal, 1 pair adanal, and 6 pairs postcloacal papillae; and a spicule ratio of 1:3.4–1:5.0. The latter species differs from *Prospinitectus mollis*, the only other species in the genus, by being less than one-half as long, 3.5–5.9 mm long; with a proportionally longer esophagus; fewer spines per spine ring, a maximum of 49 compared with 100; deirids that lack spinules; males with an unornamented precloacal cuticle as well as a different number and distribution of caudal papillae, 2 precloacal and 7 postcloacal; and a smaller spicule ratio, 1:4 rather than 1:5–1:7.

This study describes 2 new nematodes found in the skipjack tuna, *Katsuwonus pelamis*. The specimens used for this study were collected throughout the host's geographic range for a study using these and other parasites to delineate worldwide stocks of the skipjack tuna for management purposes (Lester et al., 1985). As stated by Lester et al. (1985), the nematodes "*Ctenascarophis* type and *Spinitectus* type were found in the gut of virtually every fish in which they were sought, from every area." Specimens from several regions were sent to the Gulf Coast Research Laboratory for further study and identification.

MATERIALS AND METHODS

Fish viscera were frozen and flown to Brisbane, Queensland, Australia, for dissection as reported by Lester et al. (1985). All nematodes were fixed and preserved in 70% ethyl alcohol. Some were subsequently cleared by evaporating the alcohol from a 5-part glycerine:95-part alcohol solution. Specimens for study using scanning electron microscopy (SEM) were sonicated, hydrated, buffered in 0.1 M sodium cacodylate (NaCaC), postfixed in OsO₄, rinsed in 0.1 M NaCaC, dehydrated, critical point dried, and sputter-coated with gold. These worms were examined in a JEOL JSM-

T330 scanning electron microscope. Because of the poor quality of photographs of some dirty, previously frozen material, some were retouched to hide debris and charging. A few specimens were sectioned in paraffin and stained with hematoxylin and eosin. Most line drawings were prepared with the aid of a drawing tube. All nematodes used for measurements were sexually mature, and measurements are given in micrometers unless otherwise indicated. Measurements of holotype specimens are enclosed in parentheses and follow ranges of all specimens.

DESCRIPTION

***Ctenascarophis lesteri* n. sp.**

(Figs. 1–21)

General: Body slender, increasing in width gradually from anterior end to preanal region then narrowing to tip of tail, with cuticular annulations and cuticular combs. Cuticular annulations narrow, unornamented, extending posteriorly from pseudolips to short distance beyond excretory pore. Cuticular combs transverse, raised, each bearing 3 or more posteriorly directed sharp spines. Combs arranged in series, equally spaced, forming 4 sublateral longitudinal rows; longitudinal comb rows beginning slightly posterior to end of muscular esophagus extending posteriorly to level of ejaculatory duct in males, extending beyond anus in females. Comb spines largest and uniform in size in anterior one-third of body, posteriorly becoming progressively smaller but increasing in number per comb, with maximum number reaching 32 on narrow transversely spread combs (Figs. 1, 7, 8, 20). Lateral alae narrow, reaching from level of muscular esophagus to level beyond mid-body. Mouth elongated dorsoventrally, flanked by small lateral pseudolips; pseudolips 2, with each bearing 1 rounded tooth near stomal margin, with each having median dorsoventral projections thickening at tips, forming small teeth before fusing with sclerotized walls of V-shaped buccal capsule. Vestibule (pharynx of CIH Keys [Chabaud, 1975]) with tubular lumen and sclerotized lining. Circumstomal area with 2 subventral papillae, with 2 subdorsal papillae, with 2 lateral am-

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FIGURES 1-6. *Ctenascaphis lesteri* n. sp. 1. Anterior end, lateral view. Scale bar = 50 μ m. 2. En face view, composite scanning electron microscopy (SEM) and Nomarski optics. 3. Anterior extremity, lateral view, composite SEM and Nomarski optics. 4. Anterior extremity ventral view, composite SEM and Nomarski optics. Scale bar = 10 μ m for Figures 2-4. 5. Posterior end of male, ventral view, composite of SEM and Nomarski optics, showing disposition of caudal papillae in relationship to alae, cloacal vent, and longitudinal tessellated ridges. Scale bar = 50 μ m. 6. Posterior end of male showing spicules and papillae, lateral view. Scale bar = 50 μ m.

phids. Nerve ring bulbous, surrounding anterior end of muscular esophagus (Fig. 1). Excretory pore opposite posterior one-fourth of muscular esophagus.

Male (based on 11 mature specimens): Body 3.5-4.5 mm (4.1 mm) long by 48-78 (69) at greatest width; posterior portion coiled at least twice. Transverse comb rows 71-95 (87) in number, beginning 241-261 (253) from anterior end, spaced apart 19-24 (22) for leading 3-4 rows, spaced 23-31 (28) throughout remainder of body length; comb spines measuring 7-10 (9) in esophageal region, gradually decreasing in size posteriorly. Vestibule 67-69 (69) long. Esophagus 1.47-2.00 mm (1.94 mm) in total length, 42-44% of body length; muscular portion 97-360 (349) long, 13-19% of total esophageal length; glandular portion 1.27-1.64 mm (1.51 mm) long, ending posteriorly between transverse comb rows numbered 66-73. Nerve ring 88-101 (94) from anterior end. Deirids not observed. Excretory pore 163-181 (170) from anterior end. Testis reflexed, with anterior bend located 37-52% of body length from cephalic end. Vas deferens 1.05-1.20 mm (1.18 mm) long, having distinct junction with ejaculatory duct (Fig. 17). Spicules dissimilar in shape, unequal in length; left spicule longest, 242-376 (314) in length, with proximal end capitate, with distal end having thin walls

appearing as 2 pointed projections; right spicule arcuate, relatively short, 70-80 (77) long, with proximal end capitate, with distal end sharply pointed. Spicule ratio (right:left) 1:3.4-1:5.0. Caudal alae approximately 2.8 times length of tail, slightly expanded laterally, with margins not united anteriorly. Caudal papillae comprise 10 symmetrical pairs (Figs. 5, 6, 12-15); anterior 8 pairs of papillae pedunculate, coursing through caudal alae, terminating distally as distinct circular sensilla on ventral alar surface; posterior 2 pairs of papillae nonpedunculate, sessile, parallel, with laterally located member greater in diameter (Fig. 15); precloacal papillae 3 pairs, having equal size and appearance, arranged in 2 groups (1 pair anteriorly and 2 pairs posteriorly); adanal papillae 1 pair; postcloacal papillae 6 pairs, arranged as 3 sets (3 pairs, 1 pair, and 2 pairs). Phasmids circular porelike openings immediately posterior to sessile papillae (Figs. 5, 6, 15). Cloacal vent appearing as transverse opening between alae. Longitudinal ridges located along ventral cuticle for more than 15% of body length anterior to cloacal vent, tessellated, numbering 7 full rows, each consisting of oblong cuticular plates (Figs. 5, 11). Posterior end coiled ventrally 2 or more times; tail flexed, 45-67 (61) long (Fig. 10).

FIGURES 7–11. *Ctenascarophis lesteri* n. sp., scanning electron micrographs. 7. Anterior end, with lateral alae beginning anterior to 4 longitudinal rows of transverse cuticular combs. Scale bar = 50 μ m. 8. Lateral alae and combs bearing spines. Scale bar = 4.0 μ m. 9. Excretory pore. Scale bar = 1.0 μ m. 10. Coiled male posterior end with left spicule protruding (arrowhead) and indication of the anterior extent of the ventral tessellated ridges (arrow). Scale bar = 50 μ m. 11. Oblong, truncated, cuticular laminae that form the longitudinal tessellated ridges. Scale bar = 3.0 μ m.

FIGURES 12–16. *Ctenascaphis lesteri* n. sp. 12. Photomicrograph of male posterior end, lateral view, focused to show short, arcuate, right spicule (arrow indicates proximal end, sheath extends farther anteriorly). Scale bar = 20 μ m. 13. Photomicrograph of male posterior end, lateral view, focused to show longer, left spicule. Scale bar = 20 μ m. 14. Scanning electron micrograph (SEM) of circular sensilla on ventral alar surface of male. Scale bar = 2.0 μ m. 15. SEM of right side members of parallel pairs of small, sessile, posterior papillae and porelike phasmid of male. Scale bar = 1.0 μ m. 16. Embryonated egg with polar filaments from dissected female. Scale bar = 10 μ m.

Female (26 specimens): Body 3.75–5.74 mm (4.92 mm) long; width increasing posteriorly from 29 to 43 (39) at level of first transverse comb row to greatest width of 63–99 (83) at 78–89% of body length from anterior end; transverse comb rows 176–277 (233) in number, beginning 196–266 (243) from anterior end, spaced 19–24 (22) apart for leading 3 or 4 rows and 24–31 (27) apart throughout remainder of body length. Comb spines 7–12 long in esophageal region, decreasing in size posteriorly, becoming flush with annulated body cuticle. Vestibule 74–93 (85) long. Esophagus 1.28–2.05 mm in total length, 35–45% of body length; anterior muscular portion 147–253 (200) long; glandular portion 1.13–1.75 mm (1.54 mm) long; esophageal–intestinal junction between transverse comb rows

57–84 (71). Nerve ring 93–111 (97) from cephalic end. Deirids not observed. Excretory pore 170–181 (174) from anterior end. Vulva (Fig. 19) either slightly salient or flush with body, occasionally with fertilization plug, situated 0.93–1.10 mm (1.01 mm) from posterior end, opening internally into ovjector, narrowing to muscular vagina; vagina usually directed posteriorly, 135–172 (152) long. Uterus didelphic, amphidelphic, reflexed, with each uterine sac associated with single ovary. Gonoducts reflexed, extending to 1.68–2.30 mm (1.91 mm) of anterior end of body, 44–59 (51) from posterior end. Eggs containing vermiform embryos, 31–39 (36) long by 17–19 (18) wide, with smooth shell; shell thick, with several polar filaments at each end; filaments up to 54 long. Rectum 58–76 long; rectal

FIGURES 17–21. *Ctenascarophis lesteri* n. sp. 17. Male reproductive tract showing seminal vesicle containing spermatozoa (arrow), followed by vas deferens (arrowhead). Scale bar = 20 μ m. 18. Photomicrograph showing junction (arrow) of the glandular esophagus and the intestine as well as the anterior tip (arrowhead) of the male gonoduct. Scale bar = 20 μ m. 19. Lateral view of ventrally located vulva (arrowhead showing lip), ovijector, anteriorly directed vagina vera and eggs in the uterus. Scale bar = 23 μ m. 20. Scanning electron micrograph of female posterior end showing the posterior reach of the transversely spread, flattened, multispined cuticular combs, the transverse anus, and lateral phasmids (arrows) near mucro at the tip of the tail. Scale bar = 4.0 μ m. 21. Female posterior end, lateral view, demonstrating the posterior extent of the longitudinal rows of combs and the female gonoduct, the position of the anus, and single mucro at tip of the tail (arrow shows phasmid). Scale bar = 20 μ m.

glands not observed. Tail tapered, 36–44 (39) long, with distinct mucro at tip. Phasmids 8–9 from tip of tail (Figs. 20, 21).

Taxonomic summary

Type host: *Katsuwonus pelamis* (Linnaeus, 1758) (Pisces: Scombridae) skipjack tuna.

Site of infection: Stomach.

Prevalence: Common throughout range of host where examined.

Type locality: Seas off Fiji; other localities: New Caledonia, Marquesas Islands, New Zealand, Papua New Guinea, and Puerto Rico.

Specimens deposited: Holotype (male) National Museum Parasite Collection, USNM Helm. Coll. No. 82900; allotype USNM Helm. Coll. no. 82901; paratypes USNM Helm. Coll. no. 82902 (2 males and 2 females), H. W. Manter Laboratory, University of Nebraska State Museum, HWML no. 36610 (2 males and 2 females), and Gulf Coast Research Laboratory Museum no. 1143 (2 males and 2 females).

Etymology: This species is named in honor of R. J. G. Lester, who originally collected the material and who has contributed greatly toward advancing marine parasitology.

Remarks

Mamaev (1968) described the genus *Ctenascarophis* Mamaev, 1968, establishing *Ctenascarophis gastricus* Mamaev, 1968 as the type species. *Ctenascarophis gastricus* was found in the stomach of *Auxis thazard* (Lacépède, 1800), the frigate mackerel, collected in the South China Sea. *Ctenascarophis lesteri* differs from *C. gastricus*, the only other species in the genus, primarily in the details of cuticular ornamentation, the number and distribution of caudal papillae, and the size and shape of spicules. The 4 sublateral longitudinal rows of combs of *C. lesteri* extend posteriorly to the region of the ejaculatory duct in males and to the anus in females (Figs. 20, 21), farther posteriorly than the comb rows of *C. gastricus*, which occur in the anterior two-thirds of the bodies of both sexes. The combs of *C. lesteri* begin just posterior to the junction of the muscular and glandular esophagus (Fig. 1), compared to beginning anterior to this junction near the excretory pore in *C. gastricus*. Posteriorly, the number of comb spines of *C. lesteri* increases and the spine size decreases; the combs narrow and spread transversely (Figs. 8, 20). Mamaev (1968) stated that in *C. gastricus* the number of spines increases posteriorly to a maximum of 8 and then decreases until the last combs may bear only 1 spine. The female tail of *C. lesteri* is more tapered than that of *C. gastricus* and has a distinct mucro at its tip (Figs. 20, 21). Mamaev (1968) described "numerous wave-like longitudinal crests" covering the entire ventral cuticle anterior to the cloacal opening of the male *C. gastricus*; only 7 longitudinal rows of such crests are present in male *C. lesteri* (Figs. 5, 11). The consistent 3 preanal, 1 adanal, and 6 postanal pairs of papillae (1–2, 1, 3, 2), with the posterior 2 pairs sessile and arranged in parallel order (Figs. 5, 6) in *C. lesteri* differs from the 4 preanal and 6 postanal pairs of papillae (1–1–3–1) of *C. gastricus*, all of which are pedunculate and arranged in a longitudinal series. The right spicule of *C. lesteri* is more arcuate with a more recurved,

sharper distal point than that in *C. gastricus* (Figs. 6, 12). The longer left spicule of *C. lesteri* has a swollen proximal end and very thin lateral walls that give the appearance of 2 pointed projections near the distal tip (Fig. 13), different in both respects from the left spicule of *C. gastricus*. Also, the ratio of right : left spicules in *C. lesteri* is greater than that for *C. gastricus* (1:3.4–1:5.0 vs. 1:3.1). Morphological characteristics of *C. lesteri* are consistent in specimens regardless of the geographic origin of the collection.

Prospinitectus exiguus n. sp.

(Figs. 22–38)

General: Body relatively small compared with other member of genus, with dome-shaped anterior end, relatively slender, gradually widening posteriorly for 70–80% of body length. Tail relatively short, conical. Cuticle with smooth narrow annulations; transverse spine rings beginning within 1.8% of body length from anterior end, in series, spaced approximately equal distance apart, elevated, complete, extending posteriorly to 17–21% of body length from posterior end; each ring giving rise to posteriorly directed pointed spines, bearing 24 or more spines in anterior rings, with number and size of spines per ring gradually decreasing posteriorly (Figs. 22, 30, 31, 34). Mouth dorsoventrally elongate, with 2 reduced lateral pseudolips; pseudolips each with well developed pointed apical tooth. Cephalic papillae 8, with external circle of 4 submedian papillae plus 2 amphids, with internal circle of 4 submedian labial papillae. Vestibule (pharynx of CIH Keys) absent. Esophagus making direct contact with buccal capsule (Fig. 22), divided into 2 regions; muscular esophagus anterior, comparatively short; glandular esophagus posterior, relatively long. Nerve ring located near middle of muscular esophagus, between spine rows 4 and 6. Deirids 2, nonspinous, lateral, located directly anterior to first spine ring (Fig. 33). Excretory pore slightly anterior to junction of muscular and glandular portions of esophagus. Tail conical.

Male (based on 5 mature specimens): Body 3.55–4.05 mm (3.87 mm) long by 28–42 (35) wide at anterior end, increasing in width posteriorly to 72–78 (76) at greatest width, 52 times longer than greatest width, narrowing abruptly posterior to cloaca; posterior portion coiled 2 or 3 times (Fig. 34). Transverse spine rings 46–56 (52) in number, beginning 66–74 (71) from anterior end, extending posterior beyond level of esophageal–intestinal junction, with 24–49 (33) spines per ring. Esophagus 1.98–2.55 mm (2.29 mm) in total length, 46–60% (51%) of body length; muscular portion 306–356 (340) long, 13–15.5% (14.3%) of total esophageal length; glandular portion extending farther posterior than anterior reflex of gonoduct, 1.82–1.93 mm (1.9 mm) long, with weak esophageal–intestinal valve. Nerve ring 156–175 (166) from anterior end. Deirids 64–70 (68) from cephalic end. Excretory pore 292–313 (304) from anterior end. Gonoduct reflexed, with bend 1.59–1.81 mm (1.64 mm) or 44–47% (46%) of body length from anterior end, with distal tip of reflexed testis extending posterior to esophageal–intestinal valve. Spicules dissimilar in shape, unequal in length; left spicule 362–366 (364) long, narrow, without ventral spur or membranous ala, tapering to a fine point distally; right spicule 88–96 (94) long, thicker than left

FIGURES 22–29. *Prospinitectus exiguus* n. sp. 22. Anterior end, lateral view, showing relationship of muscular esophagus to the stomal area, spine rings, nerve cord, excretory pore, and glandular esophagus. Scale bar = 50 μ m. 23. En face view, composite using scanning electron microscopy (SEM) and Nomarski optics, shows the relationship of papillae, amphids, and terminal teeth on the pseudolips. 24. Anterior extremity, lateral view, composite SEM and Nomarski optics. Scale bar for Figures 23–25 = 20 μ m. 26. Male posterior end, lateral view, showing pedunculate papillae in domelike inflations of the caudal alae, posterior sessile papillae, the relationship of the right and left spicules, and the position of the cloacal vent. Scale bar = 57 μ m. 27. Male posterior end, ventral view, composite of SEM and Nomarski optics, illustrating the circular sensilla in lobes of the caudal alae and 3 posterior pairs of sessile papillae, and the shape and position of the cloacal vent. Scale bar = 50 μ m. 28. Female lateral view, demonstrating the relationship of the vulva, ovjector, and posteriorly directed vagina vera. Scale bar = 10 μ m. 29. Female posterior end, lateral view. Scale bar = 50 μ m.

spicule, arcuate, slightly recurved with distal end rounded. Spicule ratio 1:3.7–1:4.2 (1:3.9). Gubernaculum absent (Figs. 26, 27). Caudal alae approximately 3 times length of tail, slightly expanded laterally, with margins not united anteriorly. Caudal alae with 9 symmetrical pairs of papillae (Figs. 26, 27); anterior pedunculate pairs 6, coursing through domelike lobes of caudal alae, terminating as circular sensilla on ventral alar surface (Fig. 35); posterior sessile papillae 3, relatively small. Precloacal papillae 2, pedunculate, of equal length; postcloacal papillae 7 pairs, with 4 pedunculate pairs (arranged 1, 1, 1, 1), with 3 sessile pairs (arranged 2 parallel, 1). Phasmids not observed. Cloacal vent appearing as transverse opening between alae. Precloacal area without ventral cuticular crests or other

modifications. Posterior end coiled ventrally; tail flexed, 60–65 (64) long.

Female (based on 15 mature specimens): body 3.55–5.89 mm (4.9 mm) long by 31–43 (39) wide at cephalic end, increasing in width posteriorly to 88–126 (110) at greatest width, narrowing abruptly posterior to anus, 45 times longer than wide. Transverse spine rings 71–150 in number, beginning 51–70 (62) from anterior end, extending posteriorly beyond level of esophageal–intestinal junction, with 20–40 (34) spines per ring. Esophagus 1.91–2.04 mm (2.02 mm) in total length, 40–53% (43%) of body length; junction of muscular and glandular esophagus between spine rings 9 and 11; muscular portion 294–361 (310) long, 15–17.7% (15.2%) of total esophageal length; glandular portion

FIGURES 30–33. *Prospinitectus exiguus* n. sp. 30. Scanning electron micrograph (SEM) of female anterior end showing complete spine rings. Scale bar = 10 μ m. 31. Photomicrograph illustrating the length, shape, proportions, and attachment of the spines. Scale bar = 13 μ m. 32. SEM, teeth at tips of pseudolips. Scale bar = 1.5 μ m. 33. Nonspinous deirid. Scale bar = 1.0 μ m.

1.68–1.80 mm (1.73 mm) long, usually extending farther posterior than tip or reflex of anterior gonad; esophageal–intestinal valve weak. Nerve ring 163–178 (167) from anterior end. Deirids 52–164 (61) from cephalic end. Excretory pore 284–321 (310) from anterior end. Vulva usually not salient, 3.65–3.84 mm (3.74 mm) or 73–80% (76%) of body length from anterior end, opening into rounded muscular ovijector, narrowing into vagina; vagina elongate, muscular, directed anteriorly, with ovijector plus vagina 279–325 (302) in length (Fig. 28). Uterus didelphic, amphidelphic, with posterior member always reflexed, with anterior member usually reflexed, extending anterior to esophageal–intestinal junction, 1.89–1.92 mm (1.90 mm) from anterior end. Eggs containing vermiform embryos, 30–35 (33) by 17–20 (19); shell smooth, without filaments, 3–4 thick (Figs. 37, 38). Rectum 54–62 (59) long; rectal glands 4, surrounding rectum. Tail tapered, bluntly rounded, 43–61 (47) long. Phasmids 21 from tip of tail (Figs. 29, 36).

Taxonomic summary

Type host: *Katsuwonus pelamis* (Linnaeus, 1758) (Pisces: Scombridae) skipjack tuna.

Sites of infection: Intestine, especially near pyloric ceca, and occasionally stomach.

Prevalence: Common throughout host range.

Type locality: Seas off New Zealand; other localities: Fiji, Papua New Guinea, Marquesas Islands, and Puerto Rico.

Specimens deposited: Holotype (male) National Parasite Collection, USNM Helm. Coll. no. 82903; allotype USNM Helm. Coll. no. 82904; paratypes USNM Helm. Coll. no. 82905 (1 male and 2 females), H. W. Manter Laboratory, University of Nebraska State Museum, HWML no. 36611 (1 male and 2 females), Gulf Coast Research Laboratory Museum no. 1144 (1 male and 2 females).

Etymology: The specific Latin adjectival epithet for the masculine gender *exiguus*, meaning small or short,

FIGURES 34–38. *Prospinitectus exiguus* n. sp. 34. Scanning electron microscopy (SEM), tightly coiled male posterior end. Scale bar = 30 μ m. 35. SEM, paired sensilla (arrowheads) on domelike lobes of the ventral surface of the caudal alae. Scale bar = 5.0 μ m. 36. SEM, tip of female tail showing lateral phasmids (arrowheads) and anus (arrow). Scale bar = 5.0 μ m. 37. Eggs in the uterus embedded in a gel matrix. Scale bar = 20 μ m. 38. Eggs freed from gel matrix. Scale bar = 20 μ m.

refers to the relatively small size of individuals of the species.

Remarks

Mamaev (1968) described *Spinitectus mollis* Mamaev, 1968 from the stomach of *A. thazard*, the frigate mackerel, from the South China Sea. He assigned that species tentatively to the genus *Spinitectus* Fourment, 1883. Petter (1979), working with 2 male specimens from the intestine of *Euthynnus affinis* (Cantor, 1849), the kawakawa, or eastern little tuna, from Kuala Lumpur, Malaysia, exhibiting characteristics of *S. mollis*, recognized that the cephalic structures of the species did not fit those diagnostic for *Spinitectus*. She there-

fore described the new genus *Prospinitectus* Petter, 1979, with *Prospinitectus mollis* (Mamaev, 1968) as the type species. Schmidt and Kuntz (1969), unaware of Mamaev's publication, described *Spinitectus palawanensis* Schmidt and Kuntz, 1969 from *Euthynnus yaito* Kishinouye, 1915, considered a synonym of *E. affinis* (see Collette and Nauen, 1983). Petter (1979) then placed the name *S. palawanensis* in synonymy with *Prospinitectus mollis*. The cephalic features of *P. exiguus* compare closely with those used as diagnostic characters of *Prospinitectus* and other diagnostic features generally conform. There is no vestibule (pharynx). *Prospinitectus exiguus* differs in several respects from *P. mollis*, the only other species in the genus. *Prospini-*

tectus exiguus is a much smaller nematode, neither the mature males (3.5–4.1 versus 8.2–13.1 mm) nor females (3.5–5.9 versus 11.0–15.4 mm) reach one-half the length of mature *P. mollis*. The esophageal length in *P. exiguus* is 43–60% of the body length, but in *P. mollis* the esophagus extends posteriorly only 19–20% of the body length. The number of spines on the anterior spine ring of *P. exiguus* is 28–49 (Figs. 22, 30) compared to 70–100 for *P. mollis*. The spines of *P. mollis* are interrupted in the lateral fields, but those of *P. exiguus* are continuous throughout the circumference of the anterior spine rings and have no regular breaks. Both Mamaev (1968) and Petter (1979) described the deirids of *P. mollis* with a minute circlet of spinules, a feature that is lacking in *P. exiguus* (Fig. 33). The long spicule of the male of *P. mollis* is alate and has a ventral spur, but the long spicule of *P. exiguus* is devoid of alae and has no ventral spur; the spicule ratio of *P. mollis* is greater (1:5–1:7 rather than 1:4). There are differences in the number and distribution of caudal papillae, and the precloacal cuticle of the male *P. exiguus* is not ornamented with longitudinal rows of rectangular thickenings typical of *P. mollis*. The females of *P. exiguus* have detectable phasmids. The morphological characteristics of *P. exiguus* were consistent among species, regardless of their geographic origin.

DISCUSSION

The apical end of *C. gastricus* was not illustrated in en face view by Mamaev (1968). We used both Nomarski microscopy and SEM to study the apical structures of *C. lesteri*. We deemed the SEM photographs showing apical views of uncleaned specimens as unpublishable, but we used them for interpretations and to make composite illustrations (Figs. 2–4). Within the family Cystidicolidae, the apical features of *C. lesteri* relate most closely to those of *Caballeronema* Margolis, 1977. The dorsoventral projections of the pseudolips of *C. lesteri* are similar to structures of *Caballeronema wardlei* (Smedley, 1934) as described by Margolis (1977). We consider the projections in *C. lesteri* as extensions of the pseudolips because no distinct suture or division from the pseudolips could be discerned using SEM. Margolis (1977: fig. 9) considered the projections dorsal and ventral to the pseudolips of *C. wardlei* to be 2-pronged, horn-like extensions of the buccal cavity wall. Petter (1984) illustrated 2 groups of cystidicolids, 1 with fish hosts inhabiting fresh water and a second with fish hosts inhabiting salt water; she illustrated corresponding differences and similarities in apical characteristics. As would be expected, these features for *C. lesteri* place the species most closely with marine species of Cystidicolidae.

Four completely separate rows of transverse,

tooth-bearing combs (Figs. 7, 8) are unique to members of *Ctenascaphis*, and this cuticular characteristic is used to separate them from members of *Spinitectus* in the CIH Keys (Chabaud, 1975). The spine rings of *Spinitectus beaveri* Overstreet, 1970 may divide into 1, 2, or 3 longitudinal rows at the level of the glandular esophagus (Overstreet, 1970), but the spines of *S. beaveri* are thicker, are much longer, and do not occur on distinct combs (Jilek and Crites, 1982).

The males of Spirurida from fishes sometimes have precloacal, cuticular ornamentation in the form of tessellated ridges, or waves of small rectangular crests (Crites and Overstreet, 1991). These waves of rectangular crests are especially prevalent in various species of *Spinitectus* (Overstreet, 1970; Petter 1979, 1984; Petter and Morand, 1988). Mamaev (1968) described waves of crests ornamenting the entire ventral, precloacal cuticle of *C. gastricus*, and precloacal ridges are also present in *C. lesteri*. The medial, ventral cuticle anterior to the cloacal vent in *C. lesteri* is modified, forming 7 complete rows and sometimes 1 low, depressed row of oblong truncated cuticular laminae that comprise the longitudinal tessellated ridges (Figs. 5, 11).

As demonstrated by Crites and Overstreet (1991) for *Heliconema brooksi* Crites and Overstreet, 1991, the caudal sensory sensilla of *C. lesteri* are the circular tips of pedunculate papillae that traverse the caudal alae and appear on their ventral surfaces (Figs. 5, 13). In the adults of *C. lesteri*, the anterior 8 pairs of surface sensilla mark the distributional pattern of internal pedunculatelike structures, 3 preanal, 1 adanal, and 4 postanal pairs. The posteriormost 2 pairs of parallel sensilla have no internal pedunclelike structure. This morphological feature with similar relationships of both sensilla and pedunculate papillae to caudal alae may well be the anatomical state for all members of Habronematoidea, and particularly Cystidicolidae. One could speculate that this is a pattern common to all of the genera of the order Spirurida having caudally alate males.

The vestibule passes from the buccal capsule to the muscular esophagus in members of *Ctenascaphis*. Cross-sections of *C. lesteri* show that the vestibule lumen is circular. The nerve ring surrounds the anterior end of the muscular esophagus almost immediately following its junction with the vestibule (Fig. 1). The nerve ring for *C. lesteri* is unusually long, and, in optical

section, it appears almost bulbular in outline, with the edges and lumen of the muscular esophagus passing through it. Mamaev (1968) illustrated the nerve ring of *C. gastricus* as a large rounded organ. The nerve ring of *Spinitectus* is often illustrated as a large organ positioned near the anterior end of the muscular esophagus (Overstreet, 1970; Petter, 1984). When redescribing *Spinitectus jamundensis* Thatcher and Padilha, 1977, Petter and Morand (1988) reported the presence of a ring of large gland cells immediately posterior to the nerve ring surrounding the muscular esophagus. This report led us to suspect that such a ring of gland cells might also encircle the muscular esophagus of *C. lesteri*. Study of the large nerve ring of *C. lesteri* utilizing both interference microscopy and stained cross-sections of paraffin-embedded specimens revealed only nerve cells; no gland cell was found.

Members of several nematode genera have eggs with polar filaments. *Rhabdochona* Railliet, 1916 (members of subgenus *Filochona* Saidov, 1953) of Thelazioidea and *Metabronema* York and Maplestone, 1926; *Ascarophis* van Beneden, 1871; *Ctenascarophis*; *Cystidicola* Fischer, 1798; *Spinitectoides* Petter, 1969; and *Spinitectus* of the family Cystidicolidae (Habronematoidea) all have species with polar filaments. *Ctenascarophis gastricus* and *C. lesteri* (Fig. 16) have numerous, long, slender polar filaments. Among the Cystidicolidae, most of the species having eggs with polar filaments occur in fish hosts that may spend all or part of their life cycle in marine habitats. These filaments, useful in species identification and taxonomy, may be an evolutionary adaptation reflecting the ecological adaptations for entanglement, floating, or some other function that expedites transmission to the intermediate hosts.

The apical features of *P. exiguus* agree fairly well with the redescription of the male of *P. mollis* by Petter (1979). Using both SEM and Nomarski optics, we found the pseudolips to be small but not reduced to the extent of those illustrated by Petter (1979) for *P. mollis*. Each pseudolip has an apical tooth and 2 cephalic papillae (Figs. 22–25, 32). Four sublateral papillae and 2 lateral amphids are located in defined areas lateral to the pseudolips. The oral opening has a distinct dorsoventral orientation. SEM reveals the pseudolabial teeth to be more apical and more sharply pointed (Fig. 32) than those illustrated for *P. mollis*. The pseudolips do not overhang the buccal cavity in the same manner as those

of the North American species of *Spinitectus* from freshwater fishes as demonstrated by Jilek and Crites (1982) and for South American species from fishes by Petter (1984) and by Petter and Morand (1988). The apical features of *Prospinitectus* are quite different from those of *Spinitectus*. We agree with the assessment of Petter (1979) that the cephalic features of species of *Prospinitectus* and their lack of a vestibule places that genus among the more primitive members of Cystidicolidae. On the other hand, cuticular spines and their arrangement on transverse rings are much like those of species of *Spinitectus*. The spine rings of *P. exiguus* (Figs. 22, 30) are complete and not interrupted laterally as are those of *P. mollis* as indicated by Mamaev (1968) and Petter (1979). The spine rings of *P. exiguus* are most like those of *Spinitectus carolini* Holl, 1928, but the rings are not broken and grouped into quads or triplets of spines near the midbody level as they are in *S. carolini* (see Jilek and Crites, 1982).

The deirids of *P. exiguus* are situated laterally immediately anterior to the first spine ring. Each deirid protrudes from a longitudinally oriented pore with defined lateral lips (Fig. 33) similar to the deirid pores demonstrated for *Spinitectus* by Jilek and Crites (1982). The deirids of *P. exiguus* are devoid of spines whereas those of *P. mollis* may have 2 or 3 fine, terminal spines. A variety of spinous and nonspinous deirids is found in members of Habronematoidea. The phasmids of the female of *P. exiguus* occur laterally near the tip of the tail (Figs. 29, 36). The phasmids of the males were not discerned, yet what we describe as a small, sessile pair of posterior papillae actually may be phasmids, but we could not ascertain openings in these structures using interference microscopy or SEM. The phasmids of the female of *P. exiguus* appear as definite openings in the cuticle.

The male tail of *P. exiguus* is very tightly coiled (Fig. 34) and difficult to orient in ventral view. The ventral view presented as Figure 27 is a composite, but the lateral view is drawn from the holotype specimen with the aid of a drawing tube (Fig. 26). In *C. lesteri*, the circular sensilla are the tips of the pedunculate papillae that traverse the caudal alae. However, in *P. exiguus*, the sensilla of the pedunculatelike papillae appear on the surface at the apex of domelike expansions of the caudal alae (Figs. 26, 27, 35). These domelike expansions, or inflations, were not noted or illustrated by Mamaev (1968). Pet-

ter (1979) did not describe these inflations with their apical sensilla, but her illustrations of ventral and lateral views of the male posterior end of *P. mollis* suggest that they may be present. These domelike expansions can best be observed using SEM (Fig. 35). They have not been observed for any other cystidicolid. The males of *P. exiguus* are notable in 2 other respects. First, most members of the family Cystidicolidae have some degree of preanal ornamentation, as present in *P. mollis*, species of *Ctenascaphis*, and many species of *Spinitectus*, but we could not ascertain any preanal ornamentation in *P. exiguus*. Secondly, the vast majority of cystidicolids have 4 pairs of pedunculate preanal papillae, as does *P. mollis*, and almost all the cystidicolids have 3 or more pairs, but *P. exiguus* has only 2 pairs. The posterior 3 pairs of caudal papillae are not found at the tip of inflations (Figs. 26, 27). Posterior sessile papillae (nonpedunculate papillae) seldom are noted in the descriptions of nematodes of the family Cystidicolidae, but illustrations of many species in several genera, particularly *Spinitectus*, indicate that these papillae may not be uncommon near the posterior end of the male tail. Two pairs of sessile papillae arranged in tandem as found in *P. exiguus* (Fig. 27) and in *C. lesteri* are not commonly reported, but they are seen and confirmed most easily using SEM.

Mamaev (1968) made no mention of the muscular ovijector and vagina vera of *P. mollis*, and their directional orientation is not known, even though it is probably directed anteriorly, similar to that in *P. exiguus* (Fig. 28). Mamaev described and figured small, conical protuberances at the ends of the eggs of *P. mollis*. The eggs of *P. exiguus* have a smooth shell (Figs. 37, 38) and no true protuberance, but the eggs in the uterus of fixed specimens of *P. exiguus* were embedded in a gelatinous matrix (Fig. 37). When these were released by dissection from the uterus, they often had gelatinous material adhering to their shells, particularly near the ends. De (1988) described and illustrated the eggs of *Spinitectus minor* (Stewart, 1914) as having "transparent polar formations, low polar caps in some, while irregular polar flocks in others . . ." Overstreet (1970) described the surface of the eggshells of *S. beaveri* as being covered with minute granules. Eggs from species of several genera of Cystidicolidae and the genus *Rhabdochona* of the family Rhabdochonidae have gelatinous materials attached to or covering the eggs; all are parasites of fishes.

This phenomenon may be more common than has been demonstrated, and, as with egg filaments, it may be ecologically correlated with successful transmission to the intermediate host.

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