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Three new species of *Spiniloculus* (Cestoda: Tetraphyllidea) from *Chiloscyllium punctatum* (Elasmobranchii: Orectolobiformes) off Borneo with clarification of the identity of the type of the genus

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Abstract: The type species (*Spiniloculus mavensis* Southwell, 1925) of the previously monotypic tetraphyllidean genus *Spiniloculus* Southwell, 1925 is redescribed from the type material from Moreton Bay, Australia. As a consequence the identity of this species is definitively resolved. Three new species in the genus, all collected from *Chiloscyllium punctatum* Müller et Henle (brownbanded bambooshark), in Borneo, are described. *Spiniloculus calhouni* sp. n. conspicuously differs from all three of its congeners in its possession of post-poral testes. *Spiniloculus fylerae* sp. n. and *Spiniloculus paigeae* sp. n. differ from their two other congeners in that they are relatively small worms (4–6.5 and 2.2–5 mm in total length, respectively) with fewer than 30 proglottids. They can be distinguished from one another in that, while the vitelline follicles are interrupted at the level of its ovary in *S. fylerae*, this is not the case in *S. paigeae*. Furthermore, whereas the cirrus sac of the former species is pyriform, it is elongate-oval in the latter species. This brings the total number of species in the genus to four, and lends support to the suggestion that the original identity of the type host of *S. mavensis* as *Mustelus* sp. was in error. This work also extends the range of the genus to include the island of Borneo. A key to the species of *Spiniloculus* is provided. Morphological data generated here, using both light and scanning electron microscopy, support the suggested close affinities between *Spiniloculus* and *Yorkeria* Southwell, 1927, both of which parasitize bamboosharks.

Keywords: Cestoda, Tetraphyllidea, *Spiniloculus*, *Chiloscyllium*, bamboo sharks, new species, Borneo

The cestode *Spiniloculus mavensis* Southwell, 1925 has been treated on a number of occasions by a diversity of authors, perhaps in large part as a result of its unusual scolex morphology. This species was originally described by Southwell (1925) from specimens collected from a shark identified as "*Mustelus* sp.", which had been sent to him from Moreton Bay, Australia. In an addendum, Southwell (1930) expanded on his original description of *S. mavensis* based on five specimens collected from *Chiloscyllium indicum* in Ceylon (i.e., Sri Lanka). Subhapradha (1955) reported the species from *Chiloscyllium griseum* Müller et Henle taken off the Madras Coast of India. Baer and Euzet (1962) reiterated the fact that the species also parasitizes *Chiloscyllium indicum* (Gmelin). Williams (1964) further expanded on Southwell's concept of the species based on specimens taken from *Hemiscyllium punctatum* (=*Chiloscyllium punctatum*) from Heron Island, Australia. Most recently, Caira (1990) used scanning electron microscopy to clarify the nature of the bothridial loculi of specimens taken from *Chiloscyllium punctatum* near Mackay and Balgal, Australia. Thus, at present the concept of *S. mavensis* is based on specimens taken from "*Mustelus* sp." and three species of *Chiloscyllium* from Australia, India, and Sri Lanka.

Given the high degree of host specificity exhibited by the hooked tetraphyllideans in general (e.g., Caira and Jensen 2001), it seems likely that the current understanding of the morphology and host associations of *S. mavensis* is based on material of several species. Although the suggestion that *Spiniloculus* may include more than a single species was made decades ago by Williams (1964), the unknown whereabouts of the type material has inhibited progress towards resolving this issue. The situation has recently changed owing to the discovery of three of Southwell's four type slides of *S. mavensis* in a collection of Southwell's specimens left in the care of L. Euzet by Jean Baer following their revision of Southwell's material (Baer and Euzet 1962). Examination of these specimens allowed resolution of some of the ambiguities present in the original and subsequent treatments of *S. mavensis* which is herein redescribed. Furthermore, new collections from three species of *Chiloscyllium* from Malaysian and Indonesian Borneo provide insight into the host associations of *Spiniloculus*. Material from one of these host species yielded specimens that, following a more definitive circumscription of *S. mavensis*, can now be recognized as representing three new species of *Spiniloculus*, each of which is described below. As a consequence the genus is

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definitively no longer monotypic. The interesting pattern of host associations that has emerged from examination of this newly collected material is considered.

MATERIALS AND METHODS

Specimens of *Chiloscyllium* Müller et Henle were collected from a diversity of localities in Malaysian and Indonesian Borneo (i.e. Kalimantan) between May 2002 and July 2007. The sharks examined consisted of 27 specimens of *C. punctatum* (14 males ranging in size from 41.1 to 91.3 cm in total length [TL] and 13 females ranging in size from 68 to 84 cm TL), 22 specimens of *C. indicum* (8 males ranging in size from 41.1 to 58 cm in TL and 14 females ranging in size from 38.7 to 60 cm in TL), and 7 specimens of *Chiloscyllium hasselti* Bleeker (3 males ranging in size from 42 to 76 cm in TL and 4 females ranging in size from 42 to 69 cm in TL). In each case, the spiral intestine was removed and opened with a longitudinal incision. Tapeworms were fixed in 4% formalin buffered in seawater and subsequently transferred to 70% ethanol for storage. Whole mounts for light microscopy were prepared as follows. Specimens were hydrated in a graded ethanol series, stained with Delafield's haematoxylin, dehydrated in a graded ethanol series, cleared in methyl salicylate, and mounted in Canada balsam under coverslips on glass slides. Specimens prepared as serial sections were dehydrated in a graded ethanol series, lightly stained in fast green, cleared in xylene, and embedded in paraffin. Serial sections of proglottids of one species were cut at approximately 8 µm intervals, stained in Gill's haematoxylin, counterstained in eosin, cleared in xylene, and mounted on glass slides under coverslips in Canada balsam according to conventional techniques.

Illustrations were drawn with the aid of a drawing tube. Hook measurements taken consisted of total length and greatest width of the medial and lateral hooks. Terminology for elements of the scolex and strobila follows Caira et al. (1999, 2001). Microthrix terminology follows Chervy (2009). Measurements were made using a SPOT digital camera equipped with SPOT software (version 4.5) attached to a Zeiss Axioskop 2 compound microscope. All measurements are given in micrometres unless otherwise stated. For each measurement, the range is followed in parentheses by the mean, standard deviation, number of worms measured, and number of measurements taken, if more than one measurement was made per worm.

Specimens were prepared for examination with scanning electron microscopy (SEM) as follows. They were hydrated in a graded ethanol series, transferred to distilled water, post–fixed in 1% osmium tetroxide overnight, dehydrated in a graded ethanol series, transferred to hexamethyldisilizane (HMDS) (Ted Pella Inc., Redding, California) for approximately 10 min and, after removal of the bulk of hexamethyldisilizane, allowed to air dry in a fume hood. Specimens were then mounted on aluminum stubs with carbon tape, and sputter coated with approximately 35 nm of gold-palladium. Scanning electron microscopy was performed using a LEO/Zeiss DSM982 Gemini field emission scanning electron microscope.

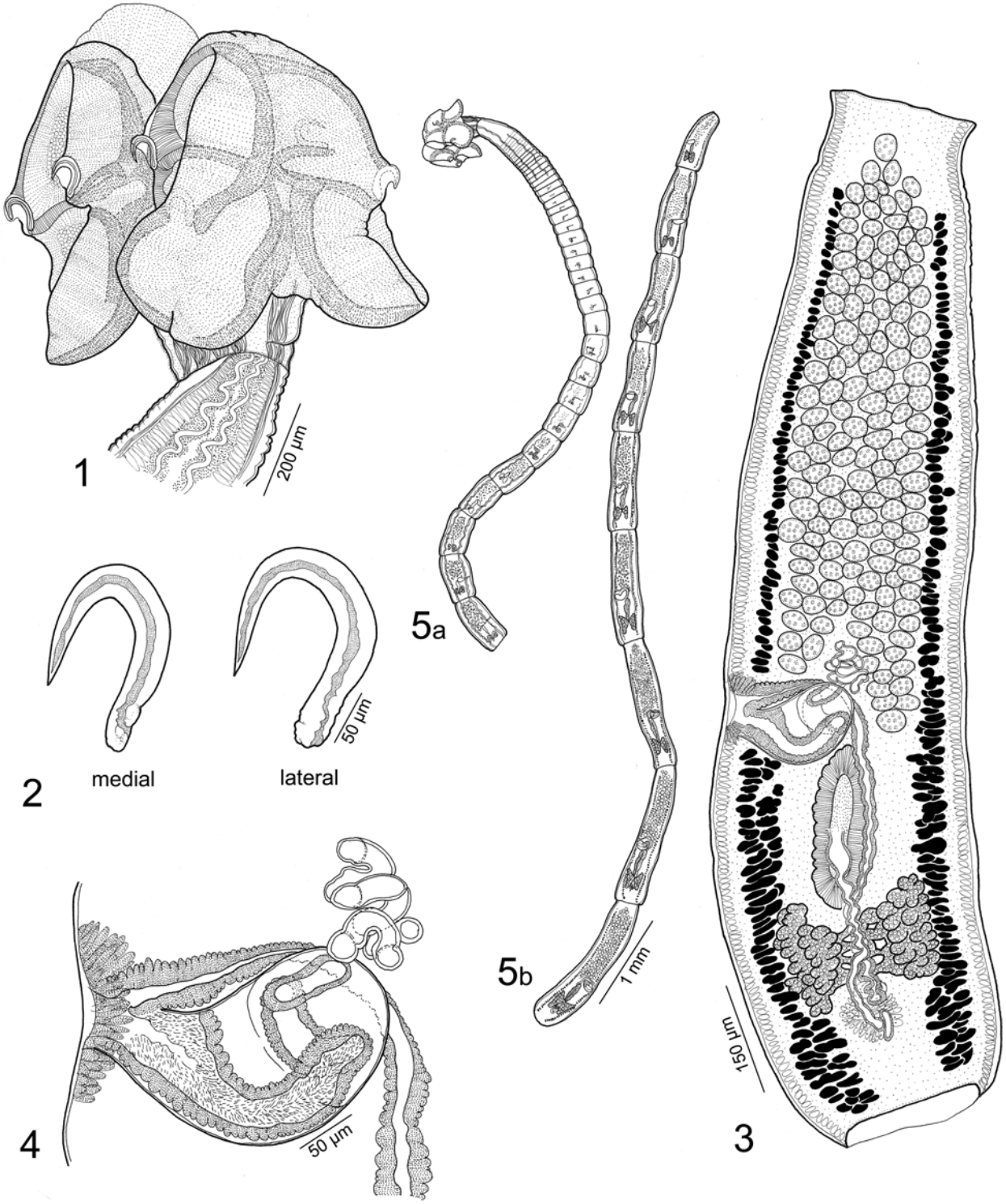
Museum abbreviations are as follows: BMNH, The Natural History Museum of London, London, England; IPCAS, Institute of Parasitology, Academy of Sciences of the Czech Republic, České Budějovice, Czech Republic; LRP, Lawrence R. Penner Parasitology Collection, Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut, USA; MZB, Museum Zoologicum Bogoriense, Zoological Division, Research Center for Biology, Indonesian Institute of Science, Cibinong, Indonesia; MZUM(P) Muzium Zoologi, Universiti Malaya, Kuala Lumpur, Malaysia; SBC, Sarawak Biodiversity Center, Kuching, Sarawak, Malaysia; and USNPC, U.S. National Parasite Collection, Beltsville, Maryland, USA. Inquiry at a diversity of public and private collections globally resulted in the location of three of Southwell's four type specimens of *Spiniloculus mavensis* in the personal collection of L. Euzet. These specimens have been deposited at the Natural History Museum of London (BMNH Nos. 2011.1.4.1–3).

RESULTS

Spiniloculus mavensis Southwell, 1925 Figs. 1–5

Redescription (based on whole mounts of 1 specimen labelled type and 2 specimens labelled cotypes): Worms euapolytic, 11.6–34.2 mm (24 ± 11; 3) long, greatest width 730–914 (802 ± 98; 3) at scolex; 37–57 (46 ± 10; 3) proglottids per worm. Scolex consisting of cephalic peduncle and 2 pairs of bothridia. Bothridia fused in back-to-back pairs; each bothridial pair borne on a pedicel; bothridia 499–659 (587 ± 49; 3; 7) long, 317–408 (375 ± 35; 2; 5) wide, with 1 pre-hook loculus, 1 pair of uni-pronged hooks, and 1 post-hook loculus; post-hook loculus with transverse muscle bundles at midlevel. Pre-hook loculus) 198–334 (267 ± 42; 3; 8) long, 287–372 (345 ± 39; 1; 4) wide. Post-hook loculus 281–355 (316 ± 23; 3; 8) long, 317–408 (375 ± 35; 2; 5) wide. Pedicels 253–376 (327 ± 56; 2; 4) long, 245–294 (269 ± 35; 1; 2) wide. Cephalic peduncle 393 (393 ± 0; 1) long, 242 (242 ± 0; 1) wide, with 4 coiled muscle bundles extending from posterior margin of scolex proper to anterior margin of strobila, 2 muscle bundles extending through each pedicel to attach to proximal surface of each bothridium in a pair. Lateral and medial hooks yellow, hollow, C-shaped, of approximate equal curvature, inconspicuously dissimilar in size, oriented anteriorly, with prongs rather than bases adjacent to one another. Medial hook 79–83 (82 ± 2; 3; 6) long, 53–60 (56 ± 3; 3; 4) wide at base; prong maximum width 15–20 (18 ± 2; 3; 6). Lateral hook 84–87 (85 ± 1; 3; 6) long, 52–64 (59 ± 5; 3; 6) wide at base, prong width at middle of length 17–18 (17 ± 1; 3; 7). Scolex surfaces not examined with SEM; minute spinitriches visible on surfaces of pedicels and cephalic peduncle with light microscopy.

Proglottids acraspedote. Immature proglottids wider than long, becoming longer than wide with maturity. Mature proglottids 3–8 (5 ± 2; 3) in number, 1,954–2,889 (2,353 ± 483; 3) long, 480–702 (562 ± 122; 3) wide, length to width ratio 4–5:1 (4:1 ± 0.4; 3). Testes 122–150 (137 ± 14; 3) in total number, 30–71 (49 ± 14; 3; 9) long, 44–75 (56 ± 9; 3; 9) wide, 1 layer deep, in multiple irregular pre-poral columns; post-poral testes absent. Cirrus sac pyriform, 248–324 (281 ± 39; 3) long, 156–196 (178 ± 21; 3) wide, containing coiled cirrus; cirrus cov-



Figs. 1–5. Line drawings of *Spiniloculus mavensis* (BMNH No. 2011.1.4.1–3). **Fig. 1.** Scolex. **Fig. 2.** Hooks. **Fig. 3.** Terminal proglottid. **Fig. 4.** Detail of terminal genitalia. **Fig. 5a, b.** Whole worm.

ered with small spinitriches. Vas deferens minimal, arranged in relatively few small coils at anteromedial margin of cirrus sac, entering cirrus sac at anterior margin. Internal and external seminal vesicles lacking.

Ovary in posterior third of proglottid, 236–308 (272 ± 50; 2) long, 279–302 (291 ± 16; 2) wide, H-shaped in frontal view, tetralobed in cross-section, ovarian margins lobulated. Genital pores lateral, irregularly alternat-

ing along length of strobila, 42–48% (45 ± 4; 2) from posterior margin of proglottid. Vagina weakly sinuous, extending anteriorly from ootype region along midline of proglottid, then laterally along anterior margin of cirrus sac, opening into common genital atrium. Vitelline follicles in 2 lateral bands; each band consisting of 1 dorsal and 1 ventral column anterior to genital pore, and 2–3 columns of follicles posterior to genital pore; columns extending from approximately 3rd row of testes to posterior margin of proglottid, interrupted on poral side by vagina and cirrus sac, uninterrupted by ovary. Mehlis' gland posterior to ovarian isthmus. Uterus extending from ootype to cirrus sac, ventral to vagina. Gravid proglottids not seen.

Type host of record: "'Ground-shark' (*Mustelus* sp.)".

Likely actual type host: *Chiloscyllium* cf. *punctatum* (Müller et Henle), brownbanded bambooshark.

Type locality: Moreton Bay, Brisbane, Queensland, Australia.

Additional locality: Balgal Beach, Queensland, Australia.

Site of infection: Spiral intestine.

Specimens deposited: Type and 2 cotypes: BMNH 2011.1.4.1–3.

Etymology: Not given by Southwell (1925).

Remarks. The material examined here consists of a slide labelled "type", which bears the proglottid and hooks, and possibly also the scolex, figured by Southwell (1925) in the original description of *S. mavensis*, and two slides labelled "cotype". As a consequence, several of the inconsistencies surrounding the identity of *S. mavensis*, noted by Williams (1964), can now be resolved. This species should be considered to possess 122–150 testes. Southwell's (1925; fig. 244) illustration of the proglottid should be considered to be schematic only because examination of the actual specimen reveals that particular proglottid actually bears 139 testes, rather than the 100 testes figured. Southwell's (1930) report of 180 testes in his material from *C. indicum* suggests he may have been dealing with a different species of *Spiniloculus*. In addition, while Southwell (1925) did not mention the presence of minute spines (=spinitriches sensu Chervy 2009) on the scolex of *S. mavensis*, they are clearly visible with a light microscope on the pedicels and cephalic peduncles of all three type specimens. In addition, it appears that Southwell's illustration of the terminal genitalia of the proglottid includes the cirrus, but not the cirrus sac. For clarification, a detail of the terminal genitalia has been provided here (Fig. 4). We have also presented a drawing of the complete type specimen (Fig. 5a, b) so as to allow *S. mavensis* to be more readily compared to its congeners.

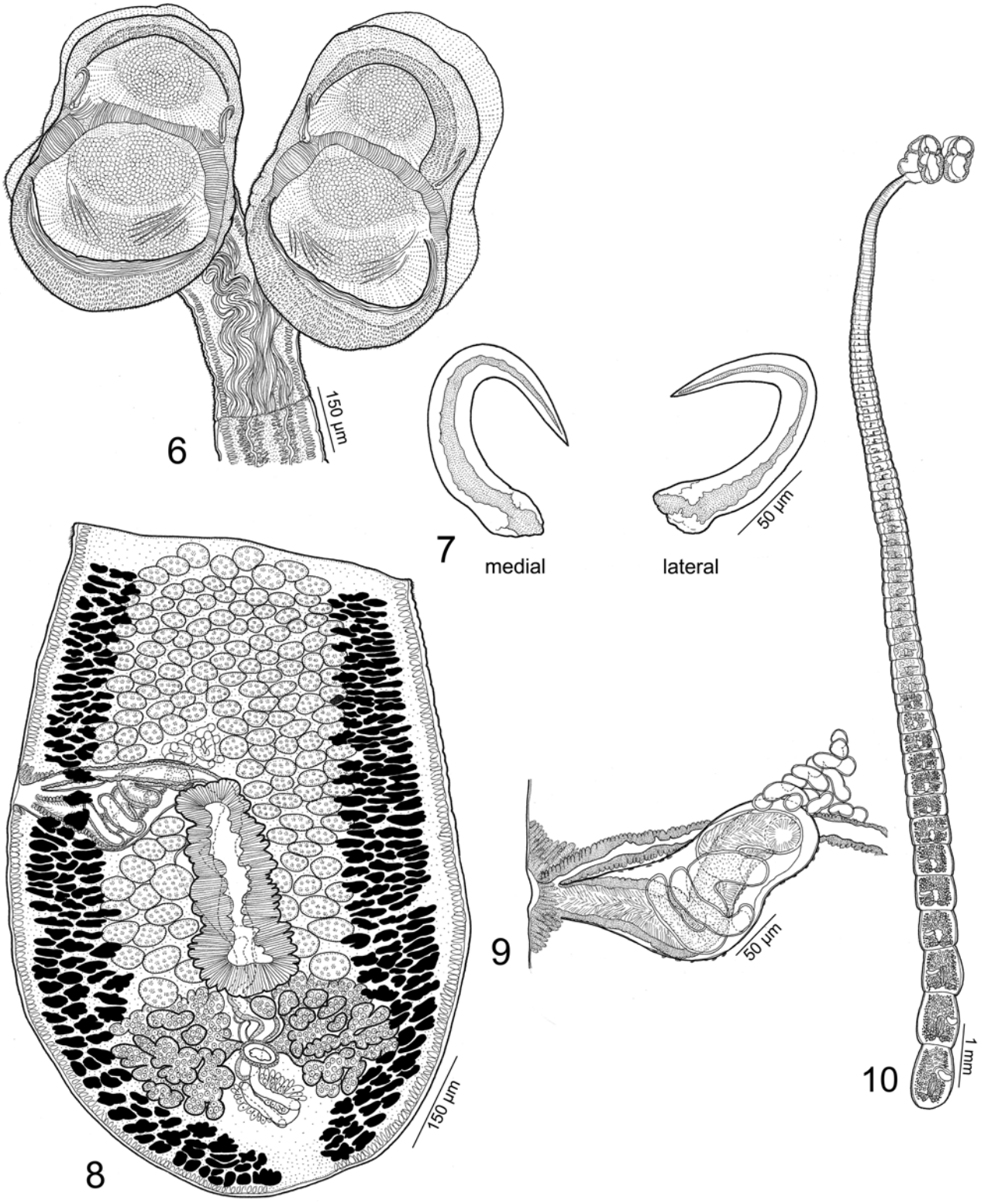
We have restricted our redescription of *S. mavensis* to observations made on the type material taken from Moreton Bay, Australia. The Australian specimens identified as *S. mavensis* by both Williams (1964) and Caira (1990) have been intentionally excluded because both authors were working from a very small number of specimens and, given that Australia may also be found to be home to more than a single species of *Spiniloculus*, we believe this material is more appropriately considered in the context of a broader study focused specifically on the Australian member(s) of this genus.

Spiniloculus calhouni sp. n. Figs. 6–16

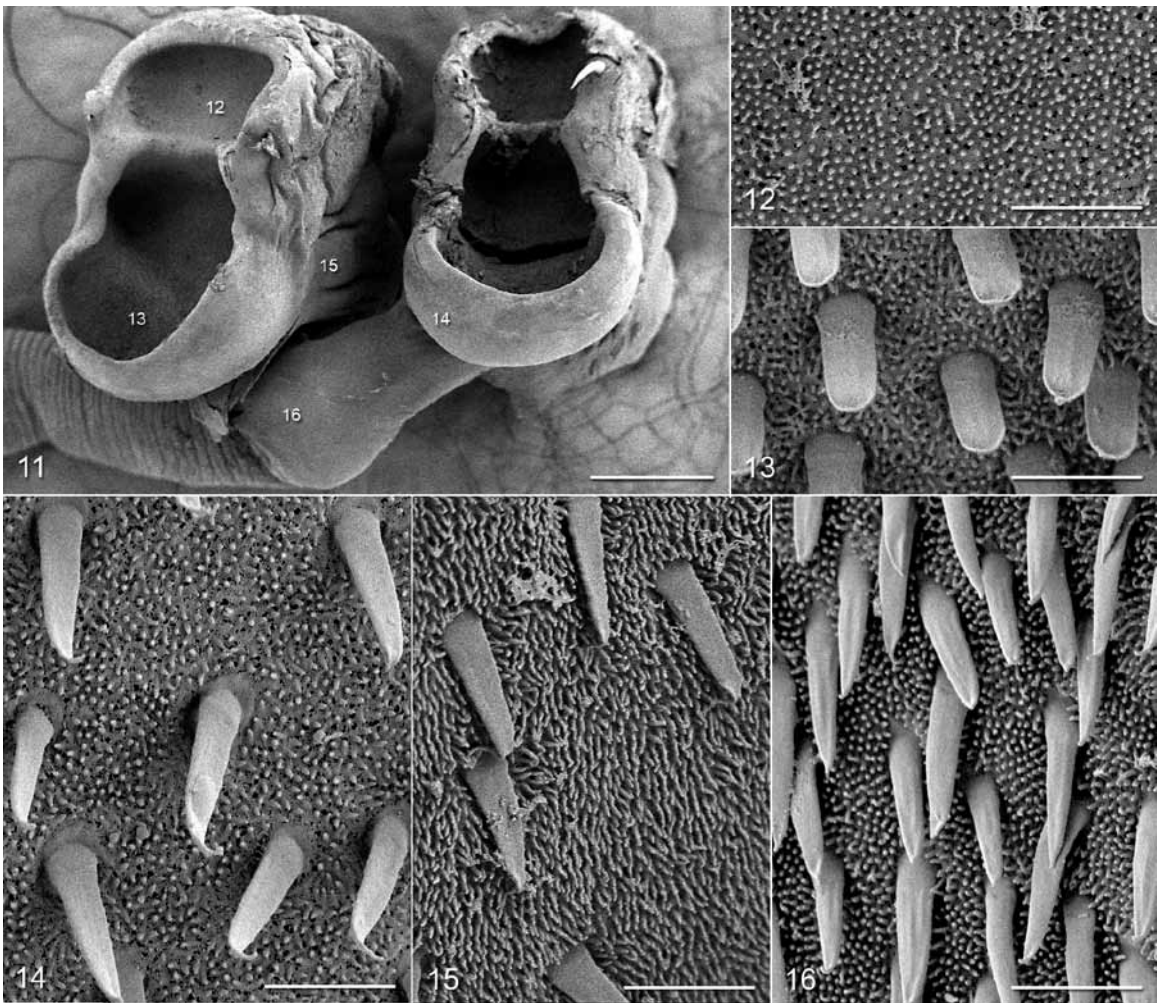
Description (based on whole mounts of 6 complete worms and 2 scolices prepared for SEM): Worms euapolytic, 11.1–18.8 mm (14.1 ± 2.7; 6) long, greatest width 760–1,803 (1,156 ± 396; 5) at scolex; 71–106 (88 ± 12; 6) proglottids per worm. Scolex consisting of cephalic peduncle and 2 pairs of bothridia. Bothridia fused in back-to-back pairs; each bothridial pair borne on a pedicel; bothridia 627–803 (701 ± 52; 5; 13) long, 312–506 (424 ± 77; 4; 10) wide, with 1 pre-hook loculus, 1 pair of uni-pronged hooks, and 1 post-hook loculus; post-hook loculus with transverse muscle bundles at midlevel. Pre-hook loculus 230–329 (273 ± 36; 5; 14) long, 323–482 (398 ± 51; 4; 11) wide. Post-hook loculus 365–475 (427 ± 36; 5; 12) long, 326–506 (433 ± 68; 4; 9) wide. Pedicels 196–480 (306 ± 105; 5; 9) long, 99–212 (150 ± 43; 5; 8) wide. Cephalic peduncle 237–421 (335 ± 81; 5) long, 140–300 (208 ± 59; 5) wide, with 4 coiled muscle bundles extending from posterior margin of scolex proper to anterior margin of strobila, 2 muscle bundles extending through each pedicel to attach to proximal surface of each bothridium in a pair. Lateral and medial hooks yellow, hollow, C-shaped, of approximate equal curvature, inconspicuously dissimilar in size, oriented anteriorly, with prongs rather than bases adjacent to one another. Medial hook 95–129 (115 ± 11; 6; 19) long, 73–99 (88 ± 9; 5; 12) wide at base; prong maximum width 24–30 (27 ± 2; 5; 15). Lateral hook 95–130 (115 ± 10; 6; 16) long, 78–98 (91 ± 7; 5; 9) wide at base, prong width at middle of length 18–30 (25 ± 3; 6; 15).

Distal surfaces of pre-hook loculus with papilliform filitriches (Fig. 12). Distal surfaces of post-hook loculus with lingulate spinitriches interspersed with papilliform filitriches (Fig. 13). Proximal bothridial surfaces with gladiate spinitriches interspersed with papilliform filitriches (Fig. 14). Surfaces of pedicels (Fig. 15) and cephalic peduncle (Fig. 16) with gladiate, slightly aristate spinitriches interspersed with acicular filitriches.

Proglottids acraspedote. Immature proglottids wider than long, becoming longer than wide with maturity. Mature proglottids 5–10 (6 ± 3; 6) in number, 588–1,145 (923 ± 187; 6) long, 478–748 (623 ± 111; 6) wide, length to width ratio 1–2:1 (2:1 ± 0.4; 6). Testes 127–177 (146 ± 19; 6) in number, 14–37 (28 ± 6; 6; 18) long, 24–62 (45 ± 12; 6; 18) wide, in multiple irregular pre-poral and post-poral columns; post-poral testes 10–20 (15 ± 2; 10; 20) in number. Cirrus sac elongate-oval, slightly bent up, 276–345 (312 ± 29; 4) long, 61–108 (83 ± 21; 5) wide,



Figs. 6–10. Line drawings of *Spiniloculus calhouni* sp. n. **Fig. 6.** Scolex (MZUM[P] No. 2010.46(H)). **Fig. 7.** Hooks (LRP No. 7567). **Fig. 8.** Terminal proglottid (USNPC No. 104132). **Fig. 9.** Detail of terminal genitalia (USNPC No. 104132). **Fig. 10.** Whole worm (LRP No. 7567).



Figs. 11–16. Scanning electron micrographs of *Spiniloculus calhouni* sp. n. **Fig. 11.** Scolex. Note: small numbers correspond to the figures showing higher magnification images of these surfaces. **Fig. 12.** Distal surface of pre-hook bothridial loculus. **Fig. 13.** Distal surface of post-hook bothridial loculus. **Fig. 14.** Proximal surface of bothridium. **Fig. 15.** Surface of pedicel. **Fig. 16.** Surface of cephalic peduncle. Scale bars: Fig. 11 = 200 µm; Figs. 12–16 = 2 µm.

containing coiled cirrus; cirrus covered with small spinitriches. Vas deferens minimal, arranged in relatively few small coils at anteromedial margin of cirrus sac, entering cirrus sac at anteromedial margin. Internal and external seminal vesicles lacking.

Ovary in posterior third of proglottid, 105–194 (155 ± 34; 6) long, 223–453 (349 ± 91; 6) wide, H-shaped in frontal view, tetralobed in cross-section, ovarian margins lobulated. Genital pores lateral, irregularly alternating along length of strobila, 53–61% (57 ± 3; 6) from posterior margin of proglottid. Vagina sinuous, extending anteriorly from ootype region along midline of proglottid, then laterally along anterior margin of cirrus sac, opening into common genital atrium. Vitelline follicles in 2 lateral bands, each band consisting of multiple follicles; bands extending from approximately 3rd row of testes to posterior margin of proglottid, interrupted on poral side by vagina and dorsally by cirrus sac, uninterrupted by ovary. Mehlis' gland posterior to ovarian isthmus. Uterus extending from ovarian isthmus to anterior margin of cirrus sac, ventral to vagina. Gravid proglottids not seen.

Type and only host: *Chiloscyllium punctatum* Müller et Henle, brownbanded bambooshark.

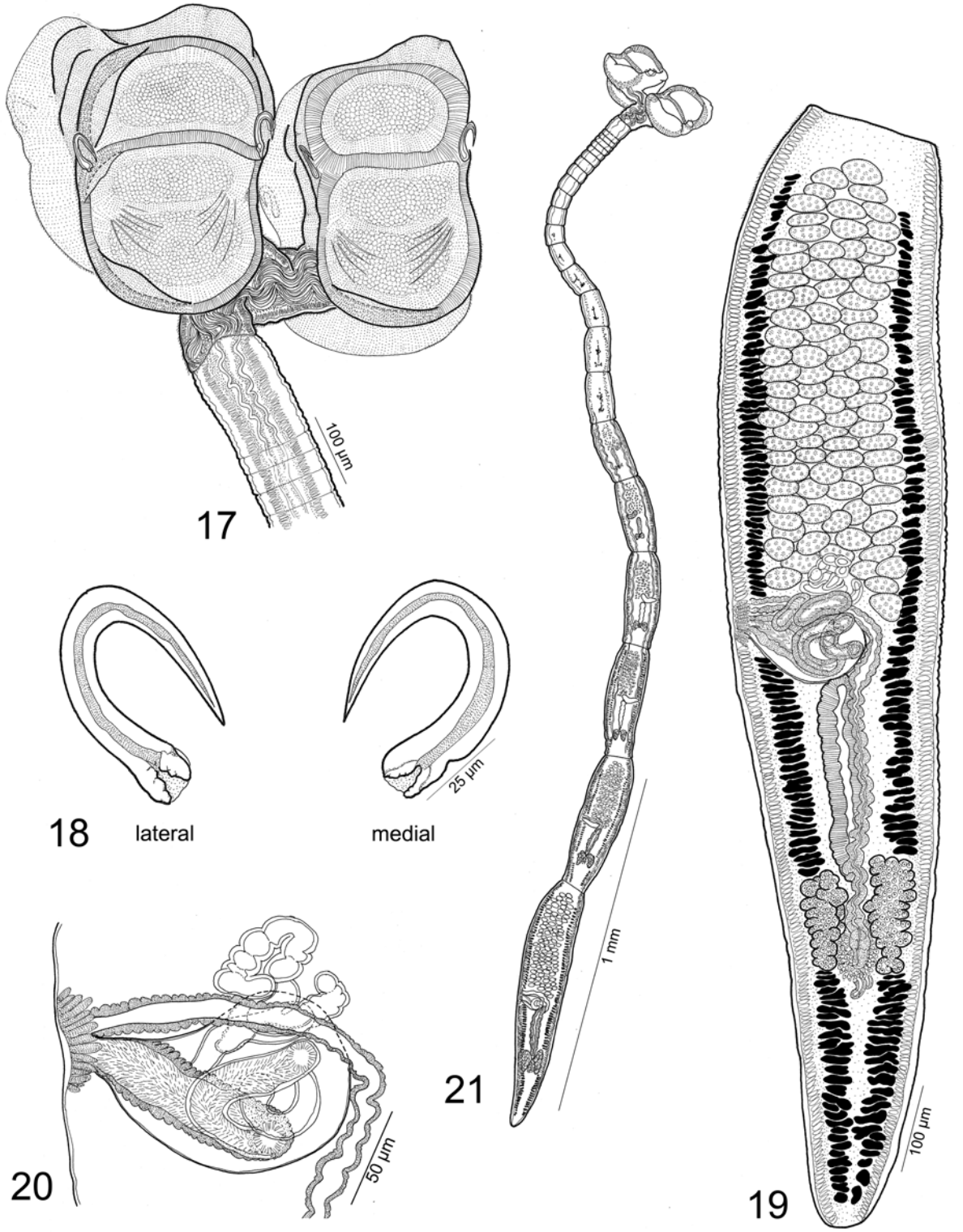
Type locality: Off Mukah, Sarawak, Malaysia (2°54′0″N, 112°5′59″E).

Site of infection: Spiral intestine.

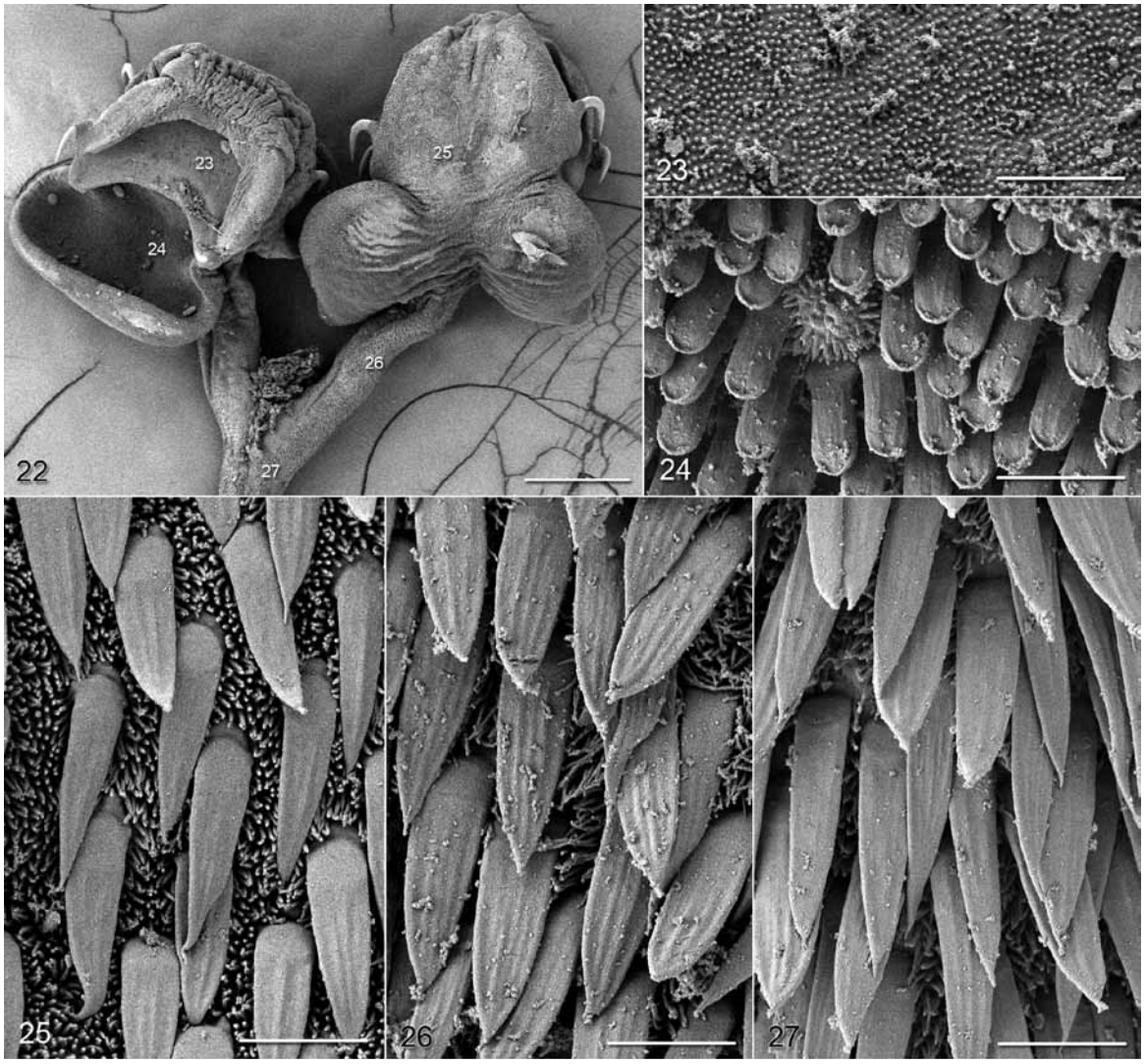
Prevalence: 2 of 27 (7%) of sharks examined; neither shark infected with other *Spiniloculus* or *Yorkeria* species.

Specimens deposited: Holotype (MZUM[P] No. 2010.46(H)), 1 paratype (IPCAS No. C-592), 1 paratype (LRP No. 7567), 2 SEM vouchers (LRP Nos. 7568–7569), 1 paratype (SBC No. P-00042), 2 paratypes (USNPC No. 104132).

Etymology: This distinctive worm is named in honour of coach Jim Calhoun in recognition of his unwavering dedication to excellence, remarkable ability to recognize and culture talent, and for his contributions towards transforming the University of Connecticut into an institution of distinction.



Figs. 17–21. Line drawings of *Spiniloculus fylerae* sp. n. **Fig. 17.** Scolex (MZUM[P] No. 2010.47(H)). **Fig. 18.** Hooks (LRP No. 7570). **Fig. 19.** Terminal proglottid (USNPC No. 104134). **Fig. 20.** Detail of terminal genitalia (USNPC No. 104134). **Fig. 21.** Whole worm (USNPC No. 104134).

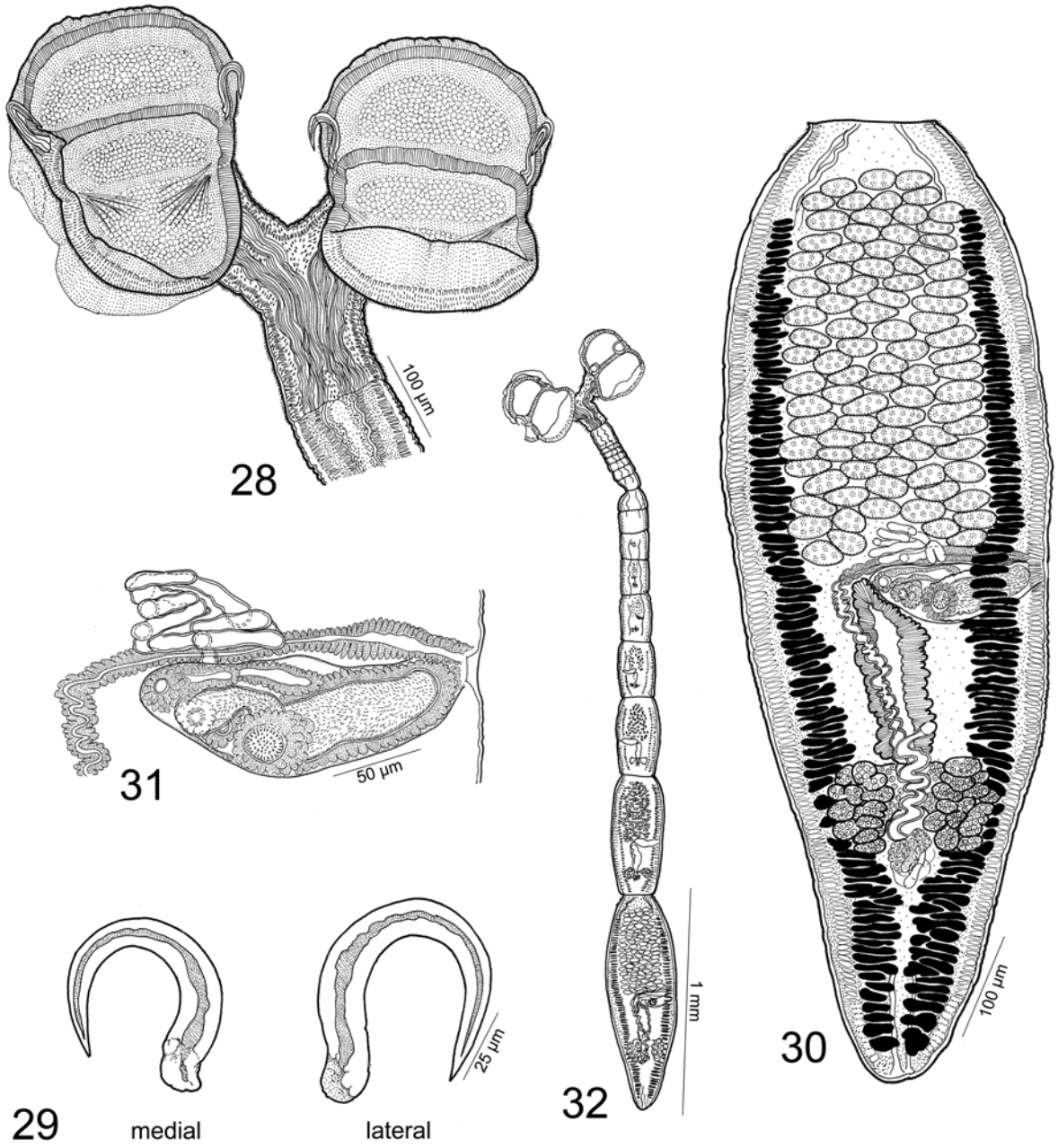


Figs. 22–27. Scanning electron micrographs of *Spiniloculus fylerae* sp. n. **Fig. 22.** Scolex. Note: small numbers correspond to the figures showing higher magnification images of these surfaces. **Fig. 23.** Distal surface of pre-hook bothridial loculus. **Fig. 24.** Distal surface of post-hook bothridial loculus. **Fig. 25.** Proximal surface of bothridium. **Fig. 26.** Surface of pedicel. **Fig. 27.** Surface of cephalic peduncle. Scale bars: Fig. 22 = 100 μm; Figs. 23–27 = 2 μm.

Remarks. This species conspicuously differs from *S. mavensis* in its possession of post-poral testes. It further differs from *S. mavensis* in its possession of a greater number of proglottids (71–106 vs. 37–57) and multiple vitelline follicles per lateral band, rather than 1–2 columns of follicles in each band.

Spiniloculus fylerae sp. n. Figs. 17–27

Description (based on whole mounts of 10 complete worms, and 1 specimen prepared for SEM): Worms euapolytic, 4–6.5 mm (5.2 ± 1; 10) long, greatest width 559–782 (674 ± 71; 8) at scolex; 17–23 (20 ± 2; 10) proglottids per worm. Scolex consisting of cephalic peduncle and 2 pairs of bothridial. Bothridia fused in back-to-back pairs; each bothridial pair borne on a pedicel; bothridia 225–421 (341 ± 54; 10; 23) long, 204–333 (270 ± 34; 9; 29) wide, with 1 pre-hook loculus, 1 pair of uni-pronged hooks, and 1 post-hook loculus; post-hook loculus with transverse muscle bundles at midlevel. Pre-hook loculus 96–177 (140 ± 22; 9; 27) long, 206–332 (264 ± 38; 9; 27) wide. Post-hook loculus 149–261 (201 ± 35; 8; 22) long, 204–333 (275 ± 32; 9; 31) wide. Pedicels 90–207 (134 ± 34; 6; 12) long, 66–129 (99 ± 16; 6; 11) wide. Cephalic peduncle 218–337 (273 ± 46; 5) long, 66–119 (103 ± 17; 7) wide, with 4 coiled muscle bundles extending from posterior margin of scolex proper to anterior margin of strobila, 2 muscle bundles extending through each pedicel to attach to proximal surface of each bothridium in a pair. Lateral and medial hooks yellow, hollow, C-shaped, of approximate equal curvature and size, oriented anteriorly, with prongs rather than bases adjacent



Figs. 28–32. Line drawings of *Spiniloculus paigeae* sp. n. **Fig. 28.** Scolex (USNPC No. 104129). **Fig. 29.** Hooks (MZUM[P] No. 2010.41(H)). **Fig. 30.** Terminal proglottid (MZUM[P] No. 2010.41(H)). **Fig. 31.** Detail of terminal genitalia (MZUM[P] No. 2010.41(H)). **Fig. 32.** Whole worm (MZUM[P] No. 2010.41(H)).

to one another. Medial hook 54–70 (63 ± 5; 9; 18) long, 31–50 (45 ± 6; 7; 11) wide at base; prong width at middle of length 11–16 (13 ± 2; 9; 17). Lateral hook 62–76 (69 ± 4; 8; 14) long, 41–54 (48 ± 4; 8; 14) wide at base, prong maximum width 12–16 (14 ± 1; 8; 21).

Distal surfaces of pre-hook loculus with papilliform filitriches (Fig. 23). Distal surfaces of post-hook loculus with lingulate spinitriches interspersed with acicular filitriches (Fig. 24). Proximal bothridial surfaces with weakly aristate gladiate spinitriches interspersed with acicular filitriches (Fig. 25). Surfaces of pedicels (Fig. 26) and cephalic peduncle (Fig. 27) with weakly aristate gladiate spinitriches interspersed with capilliform filitriches.

Proglottids acraspedote. Immature proglottids wider than long, becoming longer than wide with maturity. Mature proglottids 1–2 (1.1 ± 0.4; 12) in number, 765–1,011 (871 ± 102; 9) long, 230–291 (275 ± 17; 9) wide, length to width ratio 2–4:1 (3:1 ± 0.7; 9). Testes 87–102 (94 ± 6; 7) in number, 13–28 (19 ± 4; 7; 24) long, 22–53 (39 ± 7; 7; 24) wide, in multiple irregular pre-poral columns; post-poral testes absent. Cirrus sac pyriform, 111–163 (142 ± 15; 8) long, 33–48 (41 ± 6; 8) wide, containing

coiled cirrus; cirrus covered with small spinitriches. Vas deferens minimal, arranged in relatively few small coils at anteromedial margin of cirrus sac, entering cirrus sac near anteromedial margin. Internal and external seminal vesicles lacking.

Ovary in posterior third of proglottid, 75–120 (100 ± 16; 8) long, 106–150 (135 ± 17; 8) wide, H-shaped in frontal view, tetralobed in cross-section, ovarian margins lobulated. Genital pores lateral, irregularly alternating along length of strobila, 43–55% (50 ± 4; 10) from posterior margin of proglottid. Vagina sinuous, extending anteriorly from ootype region along midline of proglottid, then laterally along anterior margin of cirrus sac, opening into common genital atrium. Vitelline follicles in 2 lateral bands; each band consisting of 1 dorsal and 1 ventral column of follicles, extending from approximately 3rd row of testes to posterior margin of proglottid, interrupted dorsally on poral side by vagina and cirrus sac, interrupted by ovary; Mehlis' gland posterior to ovarian isthmus. Uterus extending from ovarian isthmus to cirrus sac, ventral to vagina. Gravid proglottids not seen.

Type and only known host: *Chiloscyllium punctatum* (Müller et Henle), brownbanded bambooshark.

Type locality: Off Mukah, Sarawak, Malaysia (2°54′0″N, 112°5′59″E).

Additional locality: Off Kelapseban, Central Kalimantan, Indonesia (3°14′29.6″S, 112°54′52″E).

Site of infection: Spiral intestine.

Prevalence: 5 of 27 (18.5%) of sharks examined; 1 of 9 from Kelapseban; 4 of 18 from Mukah; 1 shark also with *S. paigeae*, 3 sharks also with *S. paigeae* and *Yorkeria yubodoensis*, and 1 shark also with *S. paigeae*, *Yorkeria saliputium*, and *Yorkeria yubodoensis*.

Specimens deposited: Holotype (MZUM[P] No. 2010.47(H)), 1 paratype (MZUM[P] No. 2010.48(P)), 1 paratype (IPCAS No. C-593), 2 paratypes (LRP Nos. 7570–7571), 1 SEM voucher (LRP 7572), 1 paratype (MZB No. Ca 141), 1 paratype (SBC No. P-00043), 3 paratypes (USNPC Nos. 104133–104134).

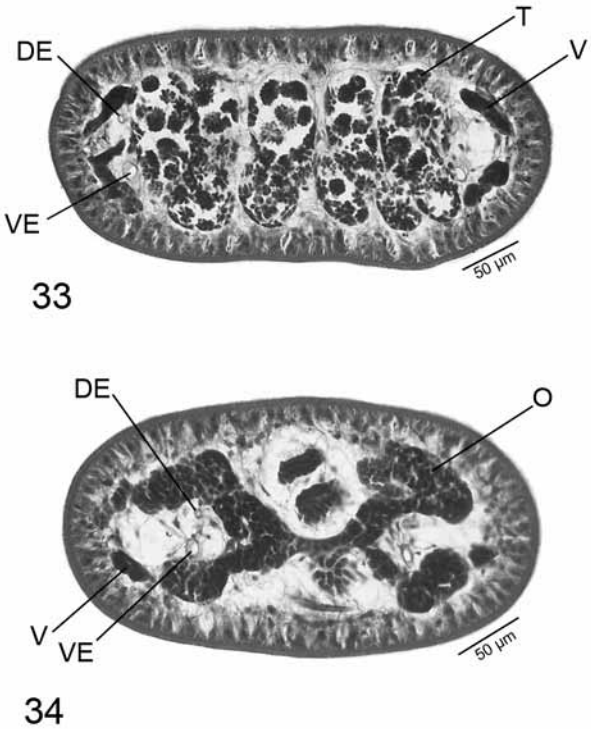
Etymology: This species is named in honour of Dr. Carrie Fyler in recognition of her support and encouragement of the first author.

Remarks. This species conspicuously differs from *S. calhouni* in that it lacks post-poral testes. It is a substantially smaller worm than both *S. calhouni* and *S. mavensis* (4–6.5 mm TL vs. 11.1–18.8 and 11.6–34.2, respectively). It also possesses fewer testes than both species (87–102 vs. 127–177 and 122–150, respectively) and, unlike both species, exhibits vitelline follicles that are interrupted by the ovary.

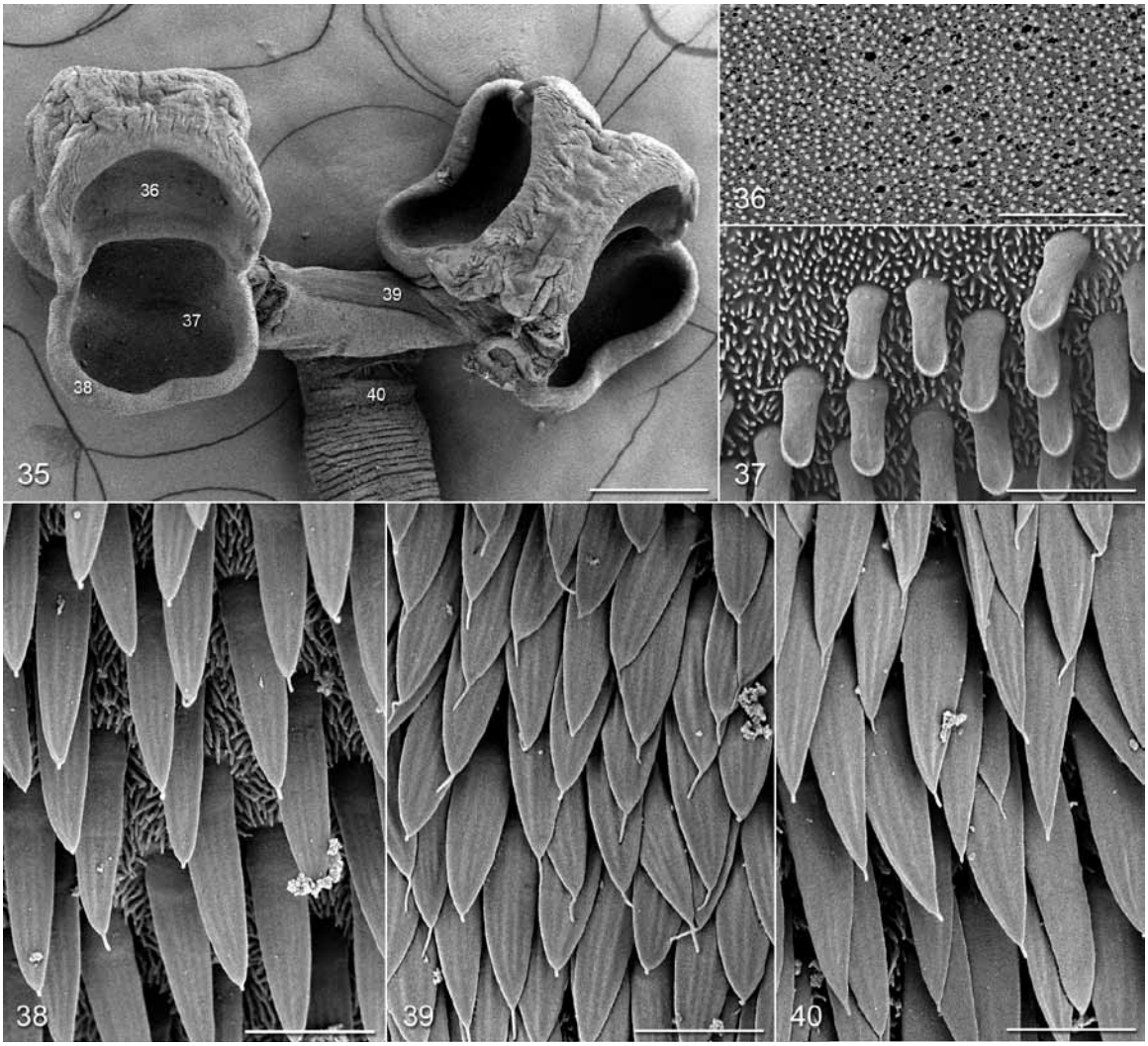
Spiniloculus paigeae sp. n. Figs. 28–40

Description (based on whole mounts of 16 complete worms, cross-sections of 2 proglottids and 2 specimens prepared for SEM): Worms euapolytic, 2.5–5 mm (3.3 ± 0.6; 16) long, greatest width 530–815 (660 ± 86; 12) at scolex; 10–21 (14 ± 3; 16) proglottids per worm. Scolex consisting of cephalic peduncle and 2 pairs of bothridia. Bothridia fused in back-to-back pairs; each bothridial pair borne on a pedicel; bothridia 277–460 (365 ± 42; 17; 33) long, 230–370 (289 ± 37; 17; 40) wide, with 1 pre-hook loculus, 1 pair of uni-pronged hooks, and 1 post-hook loculus; post-hook loculus with transverse muscle bundles at midlevel. Pre-hook loculus 97–198 (152 ± 21; 17; 39) long, 221–325 (264 ± 27; 17; 41) wide. Post-hook loculus 135–318 (218 ± 38; 17; 33) long, 195–370 (285 ± 41; 17; 38) wide. Pedicels 172–240 (204 ± 29; 5; 4) long, 60–125 (89 ± 16; 17; 24) wide. Cephalic peduncle 103–194 (149 ± 36; 7) long, 85–116 (100 ± 9; 11) wide, with 4 coiled muscle bundles extending from posterior margin of scolex proper to anterior margin of strobila, 2 muscle bundles extending through each pedicel to attach to proximal surface of each bothridium in a pair.

Lateral and medial hooks yellow, hollow, C-shaped, of approximate equal curvature, lateral hook slightly larger than medial hook, oriented anteriorly, with prongs rather than bases adjacent to one another. Medial hook 52–72 (63 ± 5; 18; 33) long, 29–50 (39 ± 6; 18; 26) wide at base; prong width at middle of length 9–15 (11 ± 2; 18; 36). Lateral hook 61–84 (70 ± 5; 18; 38) long, 32–53 (46 ± 6; 18; 24) wide at base, prong maximum width 8–17 (12 ± 2; 18; 36).



Figs. 33, 34. Cross-sections through mature proglottid of *Spiniloculus paigeae* sp. n. **Fig. 33.** Section through testes above terminal genitalia. **Fig. 34.** Section through ovary. *Abbreviations*: DE – dorsal excretory duct; O – ovary; T – testis; V – vitelline follicle; VE – ventral excretory duct.



Figs. 35–40. Scanning electron micrographs of *Spiniloculus paigeae* sp. n. **Fig. 35.** Scolex. Note: small numbers correspond to the figures showing higher magnification images of these surfaces. **Fig. 36.** Distal surface of pre-hook bothridial loculus. **Fig. 37.** Distal surface of post-hook bothridial loculus. **Fig. 38.** Proximal surface of bothridium. **Fig. 39.** Surface of pedicel. **Fig. 40.** Surface of cephalic peduncle. Scale bars: Fig. 35 = 100 µm; Figs. 36–40 = 2 µm.

Distal surfaces of pre-hook loculus with papilliform filitriches (Fig. 36). Distal surfaces of post-hook loculus with lingulate spinitriches interspersed with acicular filitriches (Fig. 37). Proximal bothridial surfaces with aristate gladiate spinitriches interspersed with acicular filitriches (Fig. 38). Surfaces of pedicels (Fig. 39) and cephalic peduncle (Fig. 40) with aristate gladiate spinitriches interspersed with acicular filitriches.

Proglottids acraspedote. Immature proglottids wider than long, becoming longer than wide with maturity. Mature proglottids 1 (n = 15) in number, 665–1,110 (843 ± 147; 15) long, 209–351 (253 ± 37; 15) wide, length to width ratio 3–5:1 (3:1 ± 0.5; 14). Testes 74–98 (88 ± 6; 12) in number, 10–23 (16 ± 3; 14; 36) long, 22–50 (35 ± 7; 14; 36) wide, 1 layer deep (Fig. 33), arranged in multiple irregular pre-poral columns; post-poral testes absent. Cirrus sac elongate-oval, 120–193 (153 ± 26; 8) long, 30–52 (38 ± 7; 8) wide, containing coiled cirrus; cirrus covered with small spinitriches. Vas deferens minimal, arranged in relatively few small coils at anteromedial margin of cirrus sac, entering cirrus sac near anteromedial margin. Internal and external seminal vesicles lacking.

Ovary in posterior third of proglottid, 56–113 (82 ± 19; 9) long, 53–170 (114 ± 34; 9) wide, H-shaped in frontal view, tetralobed in cross-section (Fig. 34), ovarian margins lobulated. Genital pores lateral, irregularly alternating along length of strobila, 52–64% (56 ± 3; 14) from posterior margin of proglottid. Vagina sinuous, extending anteriorly from ootype region along midline of proglottid, then laterally along anterior margin of cirrus sac, opening into common genital atrium. Vitelline follicles in 2 lateral bands; each band consisting of 1 dorsal and 1 ventral column, bands extending from approximately 3rd row of testes to posterior margin of proglottid, uninterrupted

by vagina, cirrus sac or ovary; Mehlis' gland posterior to ovarian isthmus. Uterine duct entering uterus posterior to midlevel. Uterus extending from ovarian isthmus to anterior margin of cirrus sac, ventral to vagina. Gravid proglottids not seen.

Type and only known host: *Chiloscyllium punctatum* (Müller et Henle), brownbanded bambooshark.

Type locality: Off Mukah, Sarawak, Malaysia (2°54′0″N, 112°5′59″E).

Additional locality: Off Kelapseban, Central Kalimantan, Indonesia (3°14′29.6″S, 112°54′52″E).

Site of infection: Spiral intestine.

Prevalence: 7 of 27 (26%) of sharks examined; 7 of 18 from Mukah; 1 of 9 from Kelapseban; 2 sharks with no other species of *Spiniloculus* or *Yorkeria*, 1 shark also with *Yorkeria pusillulus*, 4 sharks also with *S. fylerae* and *Yorkeria yubodoensis*, and 1 shark also with *S. fylerae*, *S. saliputium*, and *Yorkeria yubodoensis*.

Specimens deposited: Holotype (MZUM[P] No. 2010.41(H)), 4 paratypes (MZUM[P] Nos. 2010.42(P)–2010.45(P)), 1 paratype (SBC No. P-00041), 5 paratypes (USNPC Nos. 104129–104130), cross-sections of 1 paratype and corresponding voucher (USNPC No. 104131), 1 paratype (IPCAS No. C-594), 4 paratypes (LRP Nos. 7556–7559), cross-sections of 1 paratype and corresponding voucher (LRP Nos. 7562–7566), 2 SEM vouchers (LRP Nos. 7560–7561).

Etymology: This species was named after Paige Desjardins, the younger sister of the first author.

Remarks. This species is readily distinguished from *S. calhouni* in that it lacks post-poral testes. It further differs from *S. calhouni* and differs from *S. mavensis* in that it is conspicuously shorter in total length (2.5–5 mm vs. 11.1–18.8 and 11.6–34.2, respectively). It also possesses fewer proglottids (10–21 vs. 71–106 and 37–57, respectively) and fewer testes (74–98 vs. 127–177 and 122–150, respectively) than both species. *Spiniloculus paigeae* most closely resembles *S. fylerae*, but differs in the form of its cirrus sac, which is elongate-oval in *S. paigeae*, but pyriform in *S. fylerae*. Furthermore, whereas the vitelline follicles are interrupted by the ovary in *S. fylerae*, this is not the case in *S. paigeae*.

Other *Chiloscyllium* species examined

In Borneo, species of *Spiniloculus* were found parasitizing only *Chiloscyllium punctatum*. The prevalences of each of the three new species of this genus in this host species are given above. No shark was found to host all three species of *Spiniloculus*. However, all five of the specimens of *C. punctatum* that hosted *Spiniloculus fylerae* also hosted *S. paigeae.* Both of the sharks infected with *S. calhouni* hosted no other species of *Spiniloculus*.

No specimens of *Spiniloculus* were found in any of the 22 specimens of *Chiloscyllium indicum* necropsied from any of the localities in Malaysian or Indonesian Borneo. Similarly, none of the seven specimens of *Chiloscyllium hasselti* collected from Malaysian Borneo, was found to host any of the species of *Spiniloculus.*

DISCUSSION

This brings the total number of species of *Spiniloculus* to four and extends the range of the genus to include both Malaysian and Indonesian Borneo. In addition, this work provides some insight into the host associations of members of this genus. First, it lends support to Caira's (1990) suggestion that the identification of the original host of *Spiniloculus mavensis* may have been in error. Evidence includes: (1) The remarkably high host fidelity generally exhibited by the Onchobothriidae (see Caira and Jensen 2001), which calls into question reports of a genus parasitizing hosts belonging to two different orders. Whereas Southwell's (1925) report is from *Mustelus* (family Triakidae; order Carcharhiniformes), Southwell (1930), Subhapradha (1955), Baer and Euzet (1962), Williams (1964), and Caira (1990) all reported *Spiniloculus* from species of *Chiloscyllium* (family Hemiscylliidae; Orectolobiformes). (2) Despite work on a diversity of *Mustelus* species in or around the original locality of *S. mavensis* (e.g., Robinson 1959, Alexander 1963, Nasin et al. 1997, Pickering and Caira 2008), *Spiniloculus* has not since been reported from a species of *Mustelus*. (3) All three of the new species described here were also found to parasitize species of *Chiloscyllium*. As a consequence, we believe the genus should be considered to parasitize only *Chiloscyllium*.

As noted above, previous reports suggest that *Spiniloculus mavensis* parasitizes a diversity of species of *Chiloscyllium*; for example, Southwell (1930) reported it from *Chiloscyllium indicum* in Sri Lanka and Subhapradha (1955) reported it from *Chiloscyllium griseum* in India. Although our sample sizes were not particularly high, our failure to find *Spiniloculus* in *C. indicum* and *C. hasselti* in Borneo is interesting and bears further investigation. Also worth more detailed study would be specimens of *Spiniloculus* taken from *C. indicum* and *C. griseum* in Sri Lanka and India. For, given our results, we believe it likely that, assuming the original host identities of Southwell (1930) and Subhapradha (1955) were correct, both species of *Chiloscyllium* will be found to host species distinct from *S. mavensis*. Also of further interest would be the faunas of the following species of *Chiloscyllium*, which have not yet been examined for *Spiniloculus*: *C. arabicum* Gubanov, *C. burmensis* Dingerkus et DeFino, *C. caeruleopunctatum* Pellegrin and *C. plagiosum* Bennett.

At least nominally, all four described species of *Spiniloculus* have been reported from *Chiloscyllium punctatum*. While we are confident that the three species described here came from that host species, as noted by Caira et al. (2007), ongoing morphological and molecular work suggests that the bamboo shark species occurring in Australia, which has tentatively been identified as

Chiloscyllium punctatum by some authors (e.g., Last and Stevens 2009), is not conspecific with the species in Borneo. Given the type locality of *C. punctatum* is Java, until such time as the taxonomy of this host genus has been addressed formally, the hosts of *S. mavensis* from Australia would more appropriately be referred to as *Chiloscyllium* cf. *punctatum*.

Spiniloculus now joins the ranks of the onchobothriid genera that include multiple species parasitizing the same host species such as, for example, *Acanthobothrium* (see Ghoshroy and Caira 2001, Fyler and Caira 2006, Fyler et al. 2009), *Calliobothrium* (see Nasin et al. 1997), and *Pedibothrium* (see Caira 1992, Caira et al. 2004). In fact, this is the second such onchobothriid genus reported from *Chiloscyllium*; Caira et al. (2007) reported two or more species of *Yorkeria* parasitizing three different species of *Chiloscyllium*. Given the close relationship between *Yorkeria* and *Spiniloculus* (see Caira et al. 1999, 2001) and the fact that a number of the host specimens examined by Caira et al. (2007) were among those examined here, it is interesting that, as reported in the taxonomic summaries above, several individual sharks were found to host both two species of *Spiniloculus* and two species of *Yorkeria*.

We concur with Euzet (1994) that *Spinibiloculus* Deshmukh et Shinde, 1980, with its type *Spinibiloculus ratnagiriensis* Deshmukh et Shinde, 1980, reported from *Ginglymostoma concolor* (Rüppell) (=*Nebrius ferrugineus* [Lesson]?) at Ratnagiri on the west coast of India, should be considered a junior synonym of *Spiniloculus*. We hereby formally transfer *Spinibiloculus ratnagiriensis* to this genus as *Spiniloculus ratnagiriensis* comb. n. As noted by Euzet (1994), essentially all of the features used by Deshmukh & Shinde (1980) to distinguish *Spinibiloculus* from *Spiniloculus* do not appear to be valid. The bothridia, as illustrated, are not stalked, rather they are borne in back-to-back pairs on pedicels, as is the case in *Spiniloculus*. The post-hook loculus is undivided, a condition that has been discussed in a fair amount of detail (e.g., Williams 1964, Caira 1990), such that the post-hook loculus of *Spiniloculus* is now considered to lack an external costa. Most of the other articulated differences, such as testis number, must surely be considered of interspecific, rather than of intergeneric, importance. While the report that the vagina opens posterior to the cirrus sac is interesting, given that the vagina is invariably anterior to the cirrus sac in all other members of the order Tetraphyllidea, this observation requires confirmation. Overall, both the description and illustrations are superficial and thus, even with these irregularities aside, the validity of *Spiniloculus ratnagiriensis* remains to be confirmed. Unfortunately, Deshmukh and Shinde (1980) make no mention of the disposition of type material of their species. Furthermore, the identity of the type host of *S. ratnagiriensis* (i.e., *Ginglymostoma concolor*) is problematic. Not only is the published name a junior synonym of *Nebrius ferrugineus* Lesson, but examination of multiple specimens of *Nebrius ferrugineus* by several authors (e.g., Southwell 1925, Caira et al. 2004) has failed to yield a single specimen of *Spiniloculus*. This leads us to question the accuracy of the identification provided for the type host. In combination, all of these questions lead us to consider *S. ratnagiriensis* a *species inquirenda* until such time as it can be recollected, and/or the type specimens can be located and examined.

Finally, a comparison of the morphologies of *Yorkeria* Southwell, 1927 and *Spiniloculus* is in order. These genera share a number of unusual features that have led a diversity of authors to suggest they are closely related (e.g., Euzet 1994, Caira et al. 1999, 2001). For example, both bear C-shaped, yellow hooks that are oriented anteriorly. Both also bear four bothridia arranged in two back-to-back pairs, each pair borne on a pedicel. In both genera the bothridia are composed of only two loculi, with the hooks located at the posterior margin of the first loculus. In both genera the uterus extends only to the midlevel of the proglottid. The SEM work conducted here shows that both genera also share lingulate spinitriches on the distal surfaces of their post-hook loculus. The close affinities of these two genera are interesting given that both groups have been confirmed to parasitize only species of *Chiloscyllium* (i.e., bamboo sharks).

However, the genera differ conspicuously in that, whereas the pre-hook loculus (i.e., the specialized anterior region of the bothridium) is inconspicuous and essentially apical in its orientation in *Yorkeria*, in *Spiniloculus* it is oriented parallel to the post-hook loculus, and thus comprises a major component of the face of the bothridium. Furthermore, whereas the hooks of *Yorkeria* are large relative to the size of the pre-hook loculus, extending throughout much of the area of the pre-hook loculus, in *Spiniloculus* the hooks are small, and often inconspicuous and are restricted to the lateral margins of this loculus. It is of note that among the 16 members of these two genera, *S. calhouni* is unique in its possession of post-poral testes.

Key to species of *Spiniloculus*

1 Post-poral testes present .... *Spiniloculus calhouni* sp. n.
– Post-poral testes absent 2

2 Worms >10 mm in total length; with >30 proglottids per worm ..... *Spiniloculus mavensis*
– Worms ≤10 mm in total length; with ≤30 proglottids per worm 3

3 Cirrus sac pyriform; vitelline follicles interrupted by ovary ..... *Spiniloculus fylerae* sp. n.
– Cirrus sac elongate-oval; vitelline follicles not interrupted by ovary ..... *Spiniloculus paigeae* sp. n.

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