Syst Parasitol (2018) 95:807–827
https://doi.org/10.1007/s11230-018-9817-x

Tetraphyllidean and onchoproteocephalidean cestodes of elasmobranchs from Moreton Bay, Australia: description of two new species and new records for seven described species

Scott C. Cutmore · Thomas H. Cribb · Michael B. Bennett · Ian Beveridge

Received: 22 June 2018 / Accepted: 13 August 2018 / Published online: 28 August 2018

Abstract Parasitological examination of elasmobranchs of Moreton Bay, Queensland, Australia, resulted in the discovery of cestodes belonging to several armed genera of the Tetraphyllidea and Onchoproteocephalidea. Two new tetraphyllideans, *Yorkeria moretonensis* n. sp. and *Yorkeria williamsi* n. sp., are described from *Chiloscyllium* cf. *punctatum* (Hemiscylliidae). *Yorkeria moretonensis* n. sp. differs from its congeners in the possession of vitelline follicles that are discontinuous in the region of the ovary and in the length of its pedicels. *Yorkeria williamsi* n. sp. is most similar to *Y. parva* Southwell, 1927, but has larger, oval bothridia, longer pedicels and differences in the sizes of the scolex hooks. *Yorkeria longstaffae* Caira, Jensen & Rajan, 2007 is reported from Moreton Bay for the first time, and *Spiniloculus mavensis* Southwell, 1925 is re-reported from the type-locality and likely type-host (Moreton Bay and *Chiloscyllium* cf. *punctatum*, respectively), over 90 years after its original description. Six known onchoproteocephalideans, *Acanthobothrium cannoni* Campbell & Beveridge, 2002, *A. chisholmae* Campbell & Beveridge, 2002, *A. ocallaghani* Campbell & Beveridge, 2002, *A. margieae* Fyler, 2011, *Megalonchos shawae* Caira, Reyda & Mega, 2007 and *M. sumansinghai* Caira, Reyda & Mega, 2007, are reported from Moreton Bay for the first time, representing significant range extensions for all species.

This article was registered in the *Official Register of Zoological Nomenclature* (ZooBank) as urn:lsid:zoobank.org:pub:42732B3E-2FED-488E-9896-7843B7BD6004. This article was published as an Online First article on the online publication date shown on this page. The article should be cited by using the doi number. This is the Version of Record.

This article is part of the Topical Collection Cestoda.

S. C. Cutmore (✉) · T. H. Cribb
School of Biological Sciences, The University of Queensland, Brisbane, QLD 4072, Australia
e-mail: scott.cutmore@uqconnect.edu.au

M. B. Bennett
School of Biomedical Sciences, The University of Queensland, Brisbane, QLD 4072, Australia

I. Beveridge
Faculty of Veterinary and Agricultural Sciences, Veterinary Clinical Centre, The University of Melbourne, Werribee, VIC 3030, Australia

Introduction

As part of a parasitological survey of commercial fishes of Moreton Bay, in south-eastern Queensland, Australia, a range of elasmobranchs and teleosts were examined for adult and larval cestodes. From these collections, new species and new host/locality records for specimens belonging to the Phyllobothriidea Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014have been reported by Cutmore et al. (2017) and the Trypanorhyncha Diesing, 1863 by Beveridge et al. (2017) and Beveridge & Schaeffner (in press). This study reports new data for species belonging to several genera of armed cestodes, some belonging to the Tetraphyllidea and some to the Onchoproteocephalidea. In addition, two new species of *Yorkeria* Southwell, 1927 are formally described from the brownbanded bambooshark, *Chiloscyllium* cf. *punctatum* (Hemiscylliidae).

Materials and methods

Host and parasite collection

Elasmobranchs were collected from Moreton Bay, Queensland, using gill nets, seine nets or sourced from the commercial fishery. All hosts were identified to species using Last & Stevens (2009). Due to substantial changes in batoid nomenclature in recent years, that here follows Last et al. (2016), with the older name provided in brackets. Specimens of *Chiloscyllium punctatum* Müller & Henle are reported in this study as *Chiloscyllium* cf. *punctatum*, as the status of this shark species in Australian waters remains ambiguous (see Cutmore et al., 2010; Naylor et al., 2012). The status of *Maculabatis* cf. *astra* is similarly ambiguous (Naylor et al., 2012).

Sharks and rays were euthanised by neural pithing and spiral intestines were removed, opened longitudinally and examined under a dissecting microscope. Cestodes were removed, washed and subsequently killed in near-boiling saline solution (0.85% NaCl solution). Worms were fixed in 10% formalin for morphological examination and scanning electron microscopy (SEM) and in 100% ethanol for molecular analysis. Some individual worms were preserved for parallel morphological and molecular analysis (hologenophores *sensu* Pleijel et al., 2008).

Morphological samples

Specimens for morphological examination were washed in fresh water, overstained in Mayer's haematoxylin or Celestine blue, destained in a solution of 1.0% HCl, and neutralised in 0.5% ammonium hydroxide solution. Specimens were dehydrated in a graded ethanol series, cleared in methyl salicylate and mounted in Canada balsam. Measurements were made using an Olympus SC50 digital camera mounted on an Olympus BX-53 compound microscope using cellSens Standard imaging software. Measurements are in micrometres unless stated otherwise and are given as the range followed in parentheses by the mean and number of measurements taken (n). Drawings were made using an Olympus BH-2 compound microscope and drawing tube. Measurements of scolex hooks follows Campbell & Beveridge (2002) for species of *Acanthobothrium* van Beneden, 1850, Caira et al. (2007b) for species of *Megalonchos* Baer & Euzet, 1962, Caira et al. (2007a) for species of *Yorkeria* and Desjardins & Caira (2011) for species of *Spiniloculus* Southwell, 1925. Ordinal designation for cestode genera follows Caira et al. (2016). All type- and voucher specimens are deposited in the Queensland Museum (QM), Brisbane, Australia. All specimens not noted as hologenophores are paragenophores (*sensu* Pleijel et al., 2008). Comparative material of *Yorkeria* was borrowed from the South Australian Museum, Adelaide (SAM).

Specimens for SEM were dehydrated in a graded ethanol series, transferred to hexamethyldisilazane and allowed to air-dry overnight. Specimens were mounted on carbon tab pin stubs and sputter-coated with 20–30 nm of platinum (EIKO IB-5 Ion Coater, EIKO Engineering Company, Ibaraki, Japan). Specimens were examined using either a JEOL JSM 6300F or JSM-6610 scanning electron microscopes (JEOL Ltd, Tokyo, Japan).

Molecular sequencing and phylogenetic analysis

Specimens for molecular analysis were processed according to the protocols used by Cutmore et al. (2011). The partial D1-D3 28S rDNA region was amplified and sequenced using LSU5 (Littlewood, 1994), 300F (Littlewood et al., 2000), ECD2 (Littlewood et al., 1997) and 1200R (Lockyer et al., 2003).

Sequences generated in this study were aligned with related taxa (inferred from Caira et al., 2014) from GenBank using MUSCLE version 3.7 (Edgar, 2004) with ClustalW sequence weighting and UPGMA clustering for iterations 1 and 2. The resultant alignments were refined by eye using MESQUITE (Maddison & Maddison, 2018). The ends of each sequence were trimmed, and ambiguously aligned sites were identified and masked manually (those constituting more than three bases and present in two or more of the sequences in the dataset).

Bayesian inference analyses of the 28S rDNA datasets were performed using MrBayes version 3.2.6 (Ronquist et al., 2012) run on the CIPRES portal (Miller et al., 2010). The software jModelTest version 2.1.10

(Darriba et al., 2012) was used to estimate the best nucleotide substitution model for the datasets, and analyses were conducted using the closest approximation to the GTR+Γ model, predicted as the best estimator by the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) in jModelTest for both datasets. Each Bayesian inference analysis was run over 10,000,000 generations (ngen = 10,000,000) with two runs each containing four simultaneous Markov Chain Monte Carlo (MCMC) chains (nchains = 4) and every 1,000th tree saved (samplefreq = 1,000). Bayesian analyses used the following parameters: 'nst = 6', 'rates = gamma', 'ngammacat = 4', and the prior parameters of the combined dataset were set to 'ratepr = variable'. Samples of substitution model parameters, and tree and branch lengths were summarised using the parameters 'sump burnin = 3,000' and 'sumt burnin = 3,000'. Outgroup taxa were chosen based on the analyses of Caira et al. (2014).

Order Tetraphyllidea
Genus *Yorkeria* Southwell, 1927

Yorkeria williamsi n. sp.

Syn. *Yorkeria parva* Southwell, 1927 of Williams (1964)

Type-host: *Chiloscyllium* cf. *punctatum* (Orectolobiformes: Hemiscylliidae), brownbanded bambooshark.
Type-locality: Off Port of Brisbane (27°23′S, 153°11′E), Moreton Bay, Queensland, Australia.
Other localities: off Ormiston (27°30′S, 153°16′E), Moreton Bay; off Heron Island, southern Great Barrier Reef, Queensland, Australia.
Site in host: Spiral intestine.
Prevalence: 60% (6 of 10).
Type-material: Holotype (QM G232951) and 17 paratypes (QM G232952–61, G237639–45; hologenophores G232960–61).
Representative DNA sequences: 28S rDNA, three replicates (one submitted to GenBank, MH729995).
ZooBank registration: To comply with the regulations set out in article 8.5 of the amended 2012 version of the *International Code of Zoological Nomenclature* (ICZN, 2012), details of the new species have been submitted to ZooBank. The Life Science Identifier (LSID) for *Yorkeria williamsi* n. sp. is urn:lsid:zoobank.org:act:01FE4997-686B-4C1B-B33A-8D5AEB5433BD.
Etymology: This species is named after Professor H. H. Williams, who first reported this species under the name *Y. parva*.

Description (Figs. 1, 2A–F)

[Based on 10 mounted specimens and one specimen for SEM.] Worms euapolytic, mature worms 5.8–7.6 (6.9, n = 3) mm long, with up to 38 segments; maximum width at level of scolex. Scolex consisting of paired bothridia attached to each pedicel; 2 pedicels uniting posteriorly into peduncle. Bothridia 381–523 × 221–352 (439 × 281, n = 17); anterior loculus 100–200 (157, n = 10) long, posterior loculus 210–320 (259, n = 10) long. Pedicels 320–570 × 90–130 (400 × 106, n = 10). Cephalic peduncle 233–497 × 101–141 (356 × 122, n = 8). Four prominent muscle bundles extending from bothridia though pedicels to peduncle.

Hooks yellow, arcuate, with bases embedded in anterior loculus and tips oriented anteriorly; medial and lateral hooks dissimilar; medial hook 212–239 × 132–155 (225 × 143, n = 19); lateral hook 100–113 × 55–84 (105 × 66, n = 19).

Distal surface of anterior loculus covered in acicular filitriches. Distal surface of posterior loculus covered in acicular filitriches and lingulate spinitriches. Proximal surface of bothridia covered in acicular filitriches and gladiate spinitriches, diminishing in size and number posteriorly, not quite reaching posterior extremity of bothridium. Pedicels covered in acicular filitriches and gladiate spinitriches; spinitriches largest on medial surface of pedicel, diminishing in size towards lateral surface, arranged in parallel oblique rows. Cephalic peduncle coved in acicular filitriches and semi-elongate gladiate spinitriches. Gladiate spinitriches on pedicels noticeably larger and wider than those on cephalic peduncle.

Segments acraspedote. Terminal segment elongate, mature, 932–2,010 × 250–480 (1,122 × 341, n = 10). Genital pores alternating irregularly, 450–980 (764, n = 6), or 22–75 (55)% of segment length, from posterior margin of segment. Testes distributed in single layer, anterior to genital pore, 65–74 (69, n = 5) in number, spherical to ovoidal, 18–25 × 25–35 (23 × 29, n = 10). Cirrus-sac pyriform, 110–190 × 50–120 (144 × 82, n = 5); cirrus highly convoluted within sac, armature visible in distal region. Internal and external seminal vesicles absent.

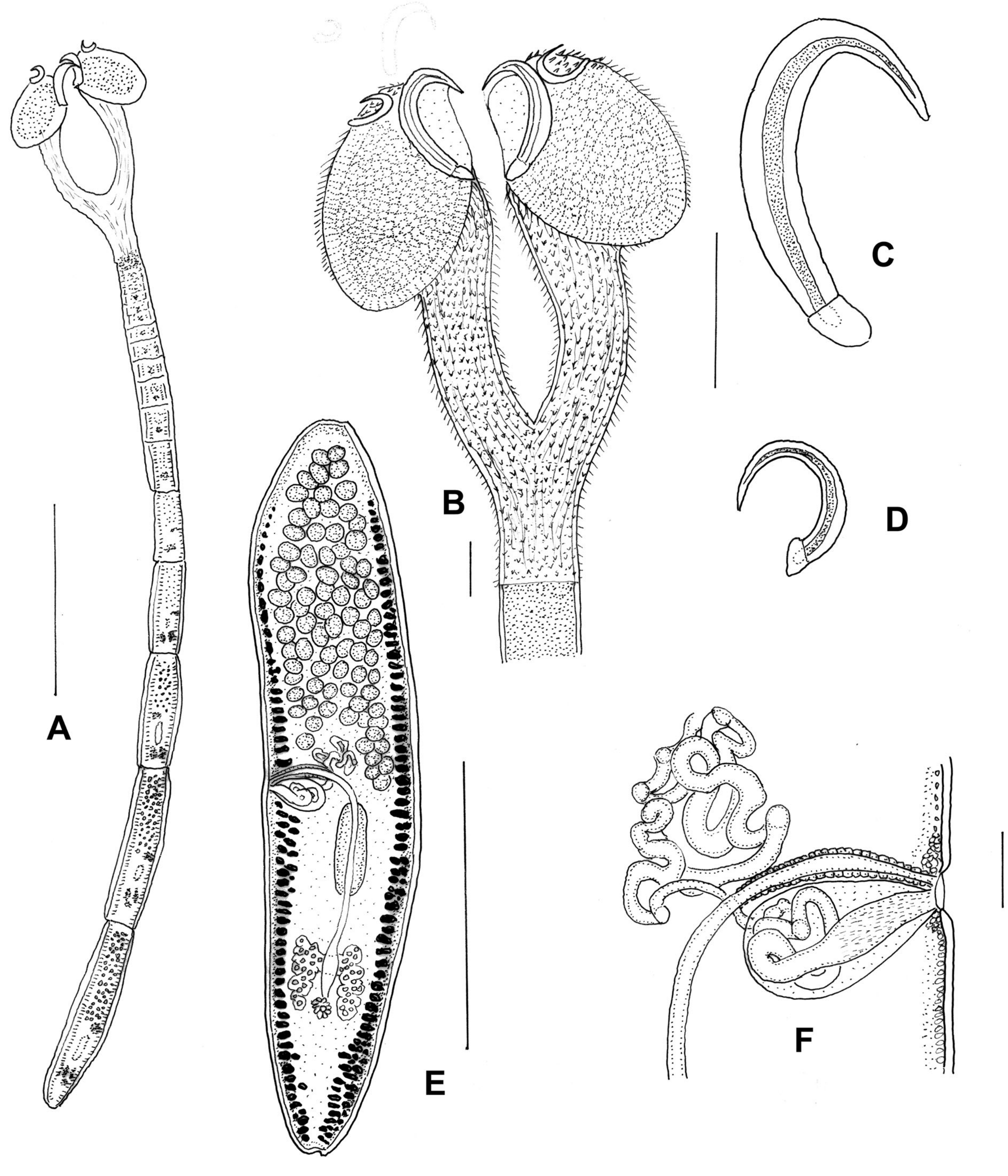


Fig. 1 *Yorkeria williamsi* n. sp. A, Entire cestode; B, Scolex; C, Medial hook; D, Lateral hook; E, Mature segment; F, Cirrus-sac and distal vagina. *Scale-bars*: A, 1 mm; B–F, 100 µm

Ovary tetra-lobed, 90–180 × 90–200 (144 × 132, n = 5); anterior margin of ovary 220–870 (516, n = 5) from posterior margin of segment. Mehlis' gland posterior to ovarian isthmus, 50–80 (58, n = 5) in diameter. Vagina enters genital atrium anterior to cirrus-sac, runs posteriorly to ovarian isthmus; wall of distal vagina thickened. Uterus thick-walled, extending in mid-region of segment from anterior to ovary to level of cirrus-sac. Eggs absent. Vitelline follicles arranged in dorsal and ventral columns laterally, follicles 13–25 × 6–12 (19 × 9, n = 10); follicle columns not interrupted in region of ovary. Osmoregulatory canals not observed.

Remarks

The features of this species do not conform with any of the described species of *Yorkeria*. Using the key of Caira et al. (2007a), they would be identified as *Y. parva* Southwell, 1927, but differ in having larger, more elongated bothridia and in the sizes of the scolex hooks. The specimens described here are, however, identical to the description of '*Y. parva*' provided by Williams (1964), based on a specimen collected from *C. punctatum* from Heron Island off the coast of Queensland. Caira et al. (2007a) re-examined this specimen (SAM V1062) and considered the possibility that it might be an undescribed species. The same specimen was re-examined, compared with present specimens and proved to be identical with the material described herein. As it differs from all known species morphologically, a new name is proposed for it.

Sequence data for this species are identical with those of *Y. izardi* Caira, Jensen & Rajan, 2007 (KF685904.1), also found in *C.* cf. *punctatum* from Queensland (Caira et al., 2014). *Yorkeria izardi* differs morphologically from the present species quite significantly in having extremely short pedicels (Caira et al., 2007a). An image of the scolex of the hologenophore of *Y. izardi*, kindly provided by Dr J. N. Caira, clearly confirms its identity with the morphological description of that species. Failure to find any possible errors in the attribution of sequence data raises the possibility of the occurrence of morphological variants of a single species. Such a phenomenon has not previously been reported in cestodes, but is well recognised among trichostrongyloid nematodes (Dróżdż, 1995). Further molecular investigations are required to resolve this issue, but in the interim, a new name recognises its morphological distinctiveness, fully cognizant of the possibility that future studies may show that it is a synonym of *Y. izardi*.

***Yorkeria moretonensis* n. sp.**

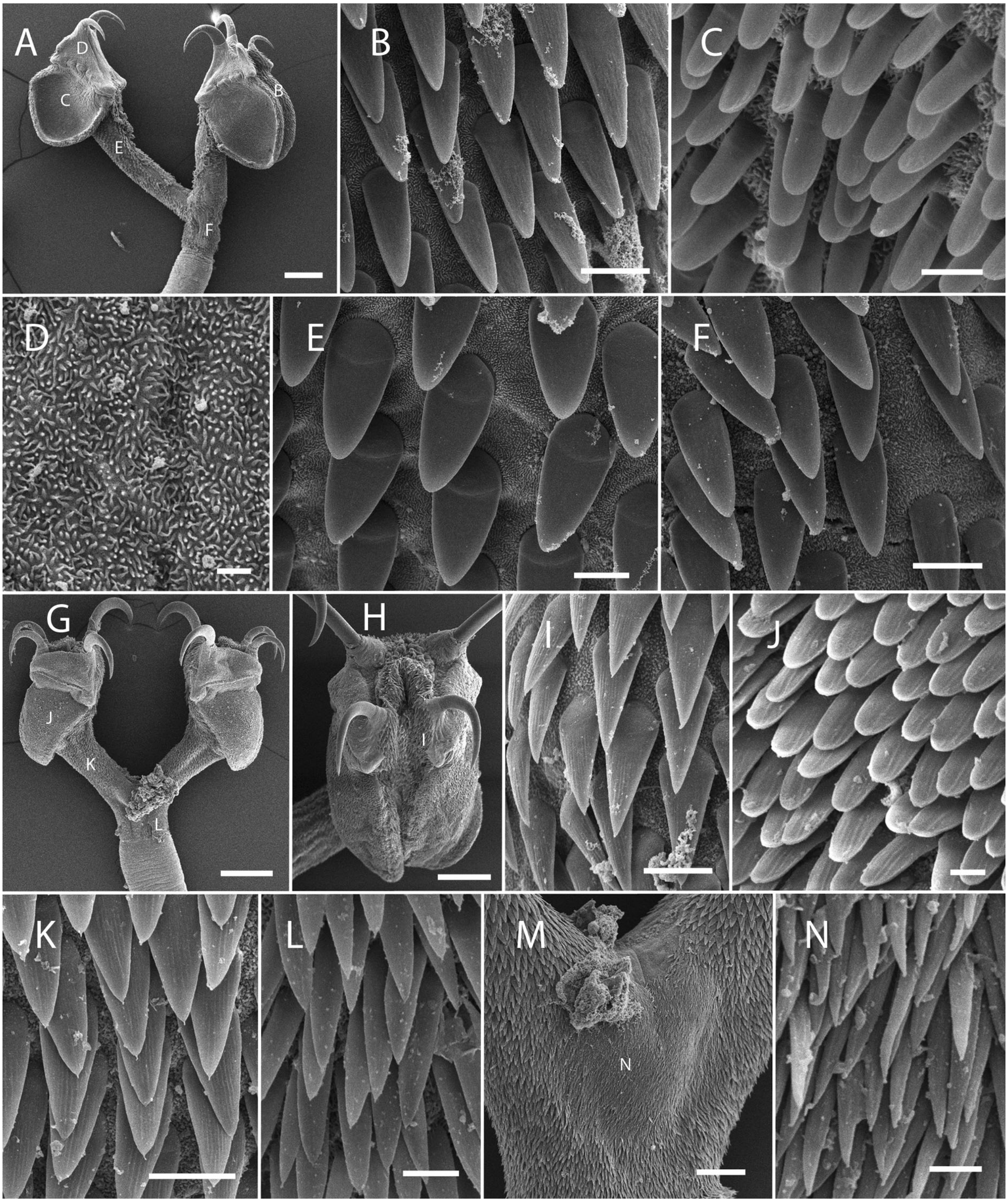
Type-host: *Chiloscyllium* cf. *punctatum* (Orectolobiformes: Hemiscylliidae), brownbanded bambooshark.
Type-locality: Off Port of Brisbane (27°23′S, 153°11′E), Moreton Bay, Queensland, Australia.
Other locality: Off Ormiston (27°30′S, 153°16′E), Moreton Bay.
Site in host: Spiral intestine.
Prevalence: 50% (5 of 10).
Type-material: Holotype (QM G232962) and 31 paratypes (QM G232963–80, G237626–38; hologenophores G232978–80).
Representative DNA sequences: 28S rDNA, three replicates (one submitted to GenBank, MH729996).
ZooBank registration: To comply with the regulations set out in article 8.5 of the amended 2012 version of the *International Code of Zoological Nomenclature* (ICZN, 2012), details of the new species have been submitted to ZooBank. The Life Science Identifier (LSID) for *Yorkeria moretonensis* n. sp. is urn:lsid:zoobank.org:act:499E36AA-828E-4792-8C17-CA2B79F5165B.
Etymology: This species is named for the location from where its hosts were collected.

Description (Figs. 2G–N, 3)

[Based on 12 mounted specimens and three specimens for SEM.] Worms euapolytic, largest worm 8.1 mm with 18 segments; maximum width at level of scolex. Scolex consisting of paired bothridia attached to each pedicel; 2 pedicels uniting posteriorly into peduncle. Bothridia 291–406 × 152–232 (350 × 192, n = 18); anterior loculus 103–156 (115, n = 18) long; posterior loculus 190–276 (227, n = 18) long. Pedicels 157–336 × 63–100 (230 × 81, n = 22). Cephalic peduncle 135–189 × 87–133 (155 × 117, n = 11). Four prominent muscle bundles extending from bothridia though pedicels to peduncle.

Hooks yellow, arcuate, with bases embedded in anterior loculus and tips oriented anteriorly; medial and lateral hooks dissimilar; medial hook 158–188 × 80–133 (174 × 118, n = 22); lateral hook 85–107 × 51–80 (101 × 71, n = 21).

Distal surface of anterior loculus covered in acicular filitriches. Distal surface of posterior loculus covered in acicular filitriches and lingulate spinitriches. Proximal surface of bothridia covered in papilliform filitriches and aristate, gladiate spinitriches, diminishing in size and number posteriorly, not quite reaching posterior extremity of bothridium. Pedicels covered in papilliform filitriches and aristate,



gladiate spinitriches; spinitriches largest on medial surface of pedicel, diminishing in size towards lateral surface, arranged in parallel oblique rows. Cephalic peduncle coved in acicular filitriches and elongate gladiate spinitriches. Noticeable patch of very elongate, gladiate spinitriches present at most-anterior

◀**Fig. 2** New species of *Yorkeria* from Moreton Bay, scanning electron micrographs. A–F, *Yorkeria williamsi* n. sp. ex *Chiloscyllium* cf. *punctatum*. A, Scolex, letters indicates where B–F were taken; B, Proximal bothridial surface; C, Distal surface of posterior loculus; D, Distal surface of anterior loculus; E, Peduncle surface; F, Cephalic peduncle surface. G–N, *Yorkeria moretonensis* n. sp. ex *Chiloscyllium* cf. *punctatum*. G, Scolex, letters indicates where J–L were taken; H, Proximal fusion of paired bothridia, letter indicates where I was taken; I, Proximal bothridial surface; J, Distal surface of posterior loculus; K, Peduncle surface; L, Cephalic peduncle surface; M, Junction of pedicels uniting into peduncle, letter indicates where N was taken; N, Surface at most-anterior portion of cephalic peduncle. *Scale-bars*: A, G, 100 µm; H, 50 µm; M, 20 µm; B, E, F, I, K, 5 µm; C, L, 2 µm; D, J, N, 1 µm

portion of cephalic peduncle. Gladiate spinitriches on pedicels noticeably larger and wider than those on cephalic peduncle.

Segments acraspedote. Terminal segment elongate, mature, 1,237–2,286 × 264–326 (1,797 × 284, n = 7). Genital pores alternating irregularly, in posterior half of segment, 584–1,117 (853, n = 7), or 44–51 (47)% of segment length, from posterior margin of segment. Testes distributed in single layer, anterior to genital pore, 75–88 (80, n = 5) in number, spherical to ovoid, 37–77 × 45–74 (53 × 58, n = 21). Cirrus-sac pyriform, 108–146 × 61–102 (127 × 75, n = 7); cirrus highly convoluted within sac, armature not visible, not fully developed. Internal and external seminal vesicles absent.

Ovary tetra-lobed, H-shaped in dorso-ventral view, 114–241 × 125–178 (179 × 147, n = 7); anterior margin of ovary 315–656 (477, n = 7), or 25–30 (27)% of segment length, from posterior margin of segment. Mehlis' gland posterior to ovarian isthmus, 40–50 (46, n = 5) in diameter. Vagina enters genital atrium anterior to cirrus-sac, runs posteriorly to ovarian isthmus; wall of distal vagina thickened. Uterus thick-walled, extending in mid-region of segment from anterior to ovary to level of cirrus-sac. Eggs absent. Vitelline follicles arranged in dorsal and ventral columns laterally, follicles 24–46 × 12–23 (34 × 16, n = 21) wide; follicle columns interrupted irregularly in region of ovary; either with occasional follicle in ovarian region or with no follicles in ovarian region on one side and continuous follicles on alternate side. Osmoregulatory canals not observed.

Remarks

The species described here is immediately distinguishable from all species described thus far, apart from *Y. kelleyae* Caira & Tracey, 2002, in the possession of vitelline follicles that are discontinuous in the region of the ovary. However, in *Y. moretonensis* n. sp., the discontinuity is variable with occasional follicles being present in the region of the ovary, or, more extremely, vitelline follicles being continuous on one side of the segment and completely absent in the ovarian region on the other side; in *Y. kelleyae* the vitelline follicles terminate anterior to the ovary and recommence posterior to it. *Yorkeria moretonensis* n. sp. is immediately distinguishable from *Y. kelleyae* in pedicel length; *Y. kelleyae* effectively lacks pedicels (Caira & Tracy, 2002, Fig. 13). For these reasons, the species described here is considered to be new.

***Yorkeria longstaffae* Caira, Jensen & Rajan, 2007**

Type-host: *Chiloscyllium* cf. *punctatum* (Orectolobiformes: Hemiscylliidae), brownbanded bambooshark.
Type-locality: Yorkey's Knob, Queensland, Australia.
New material
Host: *Chiloscyllium* cf. *punctatum*.
New locality: Off Mud Island, (27°20′S, 153°14′E); off Port of Brisbane (27°23′S, 153°11′E), Moreton Bay, Queensland, Australia.
Site in host: Spiral intestine.
Prevalence: 20% (2 of 10).
Voucher material: Three fragmented specimens (QM G237646–48).

Description (Fig. 4F–H)

Bothridia 160–280 × 110–150 (220 × 130, n = 2). Lateral hook 100–135 × 75–80 (118 × 78, n = 2); medial hook 75–80 × 40–50 (78 × 45, n = 2). Pedicels 200–350 (275, n = 2) long. Peduncle 50–120 (85, n = 2) long. Mature segment 1,700 × 510. Genital pore 850 from posterior end. Testes mainly anterior to genital pore *c.*55 in number, ovoid and up to 80 in diameter, to elongate and up to 210 × 60. Ovary tetra-lobed, each lobe *c.*210 long, 60 wide. Mehlis' gland posterior to ovary, 70 in diameter. Vagina enters genital atrium anterior to cirrus-sac. Vitelline follicles uninterrupted in region of ovary. Uterine primordium

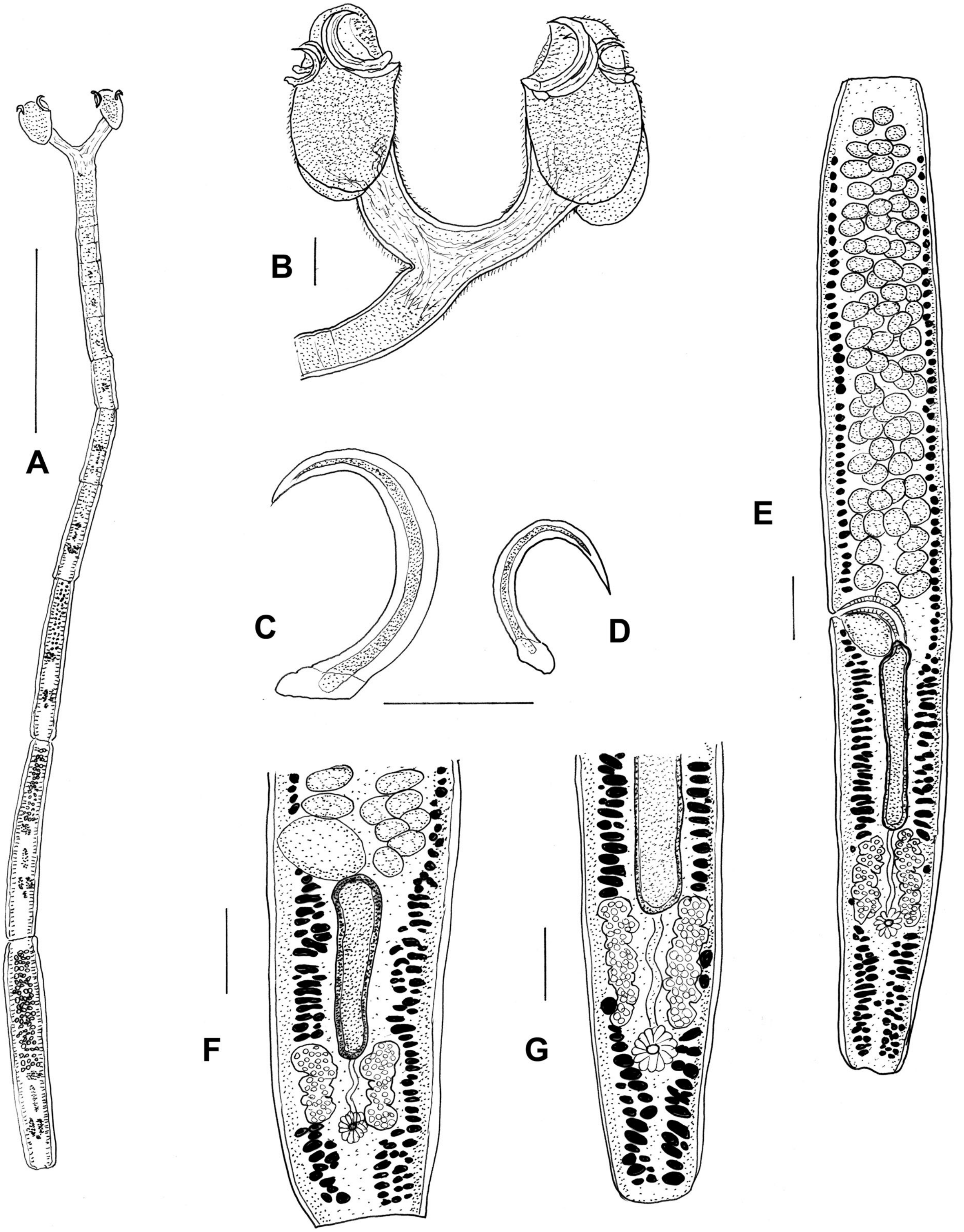


Fig. 3 *Yorkeria moretonensis* n. sp. A, Entire cestode; B, Scolex; C, Medial hook; D, Lateral hook; E, Mature segment; F, G, Posterior ends of mature segments showing variation in distribution of vitelline follicles. *Scale-bars*: A, 1 mm; B–G, 100 µm

extends from anterior to ovary to level of genital atrium, 280 long.

Remarks

Although only three fragmented specimens were found, their features were essentially those of *Y. longstaffae* originally described from the same host species in the Cairns region. The tiny peduncle is a characteristic feature of this species.

Genus *Spiniloculus* Southwell, 1925

Spiniloculus mavensis Southwell, 1925

Type-host of record: "Ground-shark (*Mustelus* sp.)".
Likely type-host: *Chiloscyllium* cf. *punctatum* (Orectolobiformes: Hemiscylliidae), brownbanded bambooshark.
Type-locality: Moreton Bay, Queensland, Australia.
New material
Host: *Chiloscyllium* cf. *punctatum*.
Localities: Off Green Island (27°25′S, 153°14′E); off Wellington Point (27°27′S, 153°14′E); off Wynnum (27°24′S, 153°10′E); off Mud Island, (27°20′S, 153°14′E); off Port of Brisbane (27°23′S, 153°11′E); off Ormiston (27°30′S, 153°16′E), Moreton Bay, Queensland, Australia.
Site in host: Spiral intestine.
Prevalence: 60% (6 of 10).
Voucher material: 47 voucher specimens (QM G232749–77, G237007–22, G237660–61; hologenophores QM G232757–59).
Representative DNA sequences: 28S rDNA, four replicates (one submitted to GenBank, MH729994).

Description (Figs. 4E, 5)

[Based on nine mounted specimens and six specimens for SEM.] Worms 17–32.9 (23.9, n = 7) mm long, with 47–83 (65, n = 7) segments. Bothridia 440–630 × 334–461 (563 × 382, n = 18); pre-hook loculus 174–306 (230, n = 18) long; post-hook loculus 268–374 (334, n = 18) long. Lateral hook 76–97 × 48–69 (87 × 60, n = 18 length, 11 width); medial hook 69–96 × 51–66 (83 × 58, n = 18 length, 11 width). Pedicels 140–243 × 137–252 (196 × 187, n = 18). Cephalic peduncle 297–512 × 153–263 (386 × 196, n = 9).

Distal surface of posterior loculus covered in papilliform filitriches and lingulate spinitriches. Proximal surface of bothridia covered in acicular filitriches and aristate, elongate, gladiate spinitriches; spinitriches absent anterior to level of hooks. Pedicels covered in acicular filitriches and elongate, gladiate spinitriches; spinitriches largest close to bothridia, diminishing in size, breadth and becoming more densely arranged towards cephalic peduncle. Cephalic peduncle coved in acicular filitriches and elongate, aristate, gladiate spinitriches; spinitriches largest posteriorly, diminishing in size and becoming more densely arranged anteriorly. Spinitriches on pedicels larger and wider than those on cephalic peduncle. Most anterior portion of cephalic peduncle, between pedicels, covered in papilliform filitriches, lacking spinitriches.

Terminal segment 1,463–2,146 × 342–430 (1,844 × 377, n = 9). Genital pore 690–1,017 (870, n = 9), or 42–54 (47)% of segment length, from posterior margin of segment. Testes anterior to genital pore, 104–144 (124, n = 9) in number, 34–70 × 33–57 (46 × 48, n = 27). Cirrus-sac 168–204 × 138–216 (179 × 159, n = 9). Ovary tetra-lobed, 182–257 × 183–270 (217 × 226, n = 9); anterior margin of ovary 307–561 (447, n = 9), or 19–30 (24)% of segment length, from posterior margin of segment. Vitelline follicles in lateral fields, uninterrupted in region of ovary, follicles 12–31 × 24–44 (18 × 34, n = 27).

Remarks

We here re-report *S. mavensis* from the type-locality (Moreton Bay), over 90 years after its original description by Southwell (1925). As discussed by Caira (1990) and Desjardins & Caira (2011), the likely actual type-host of *S. mavensis* is *C.* cf. *punctatum*. The prevalence of *S. mavensis* in six of the ten *C.* cf. *punctatum* examined during this study, and absence of infections in 101 individuals of 15 other shark species examined in the region (see Cutmore et al., 2017; Beveridge & Schaeffner, in press), supports the proposal that the true type-host is *C. punctatum*. Measurements of the new specimens agree with those given in the re-description of the type-material by Desjardins & Caira (2011). Details of the types of microthrix present on the scolex of this species were not provided by Southwell (1925), Caira (1990) or Desjardins & Caira (2011); these data are provided

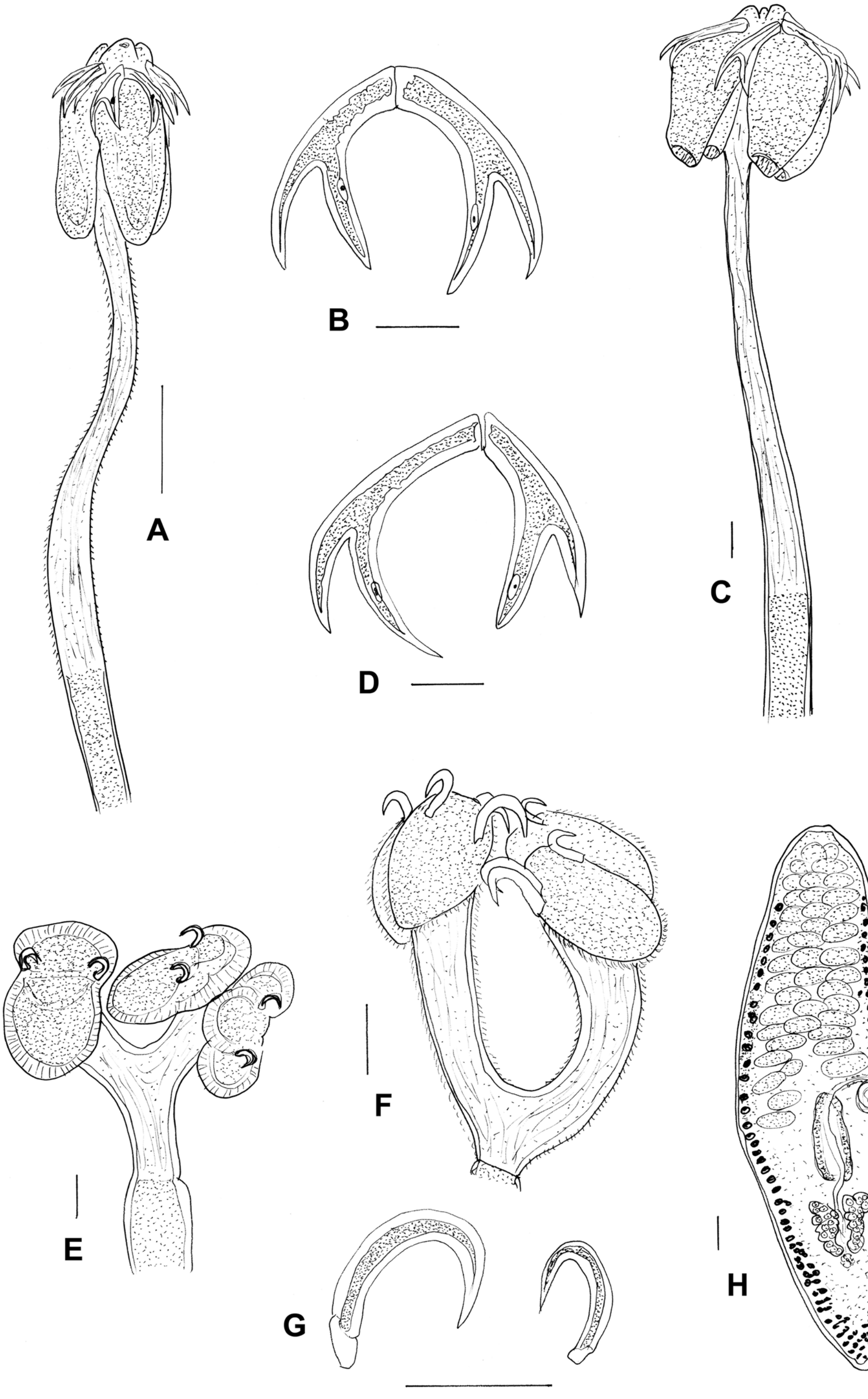


Fig. 4 *Megalonchos* spp., *Spiniloculus mavensis* Southwell, 1925 and *Yorkeria longstaffae* Caira, Jensen & Rajan, 2007 from Moreton Bay. A, *Megalonchos shawae* Caira, Reyda & Mega, 2007, scolex; B, *M. shawae*, bothridial hooks; C, *Megalonchos sumansinghai* Caira, Reyda & Mega, 2007, scolex; D, *M. sumansinghai*, bothridial hooks; E, *Spiniloculus mavensis*, scolex; F, *Yorkeria longstaffae* Caira, Jensen & Rajan, 2007, scolex; G, *Y. longstaffae*, lateral and medial hooks; H, *Y. longstaffae*, mature segment. *Scale-bars*: 100 μm

based on SEM of the new specimens. The size of the terminal segment and ovary are larger in the type-material; however, we do not consider these differences significant, with some overlap in the ranges of the terminal segment and ovary lengths. Notably, the cirrus-sac length does differ between the two collections, but we think these differences may be attributable to differences in the way this variably-shaped feature was measured. Novel 28S rDNA sequence data of *S. mavensis* differs from the only other *Spiniloculus* sequence (that of *Spiniloculus* n. sp. 1 infecting *C. punctatum* from Bangsaray, Thailand) by 25 bases.

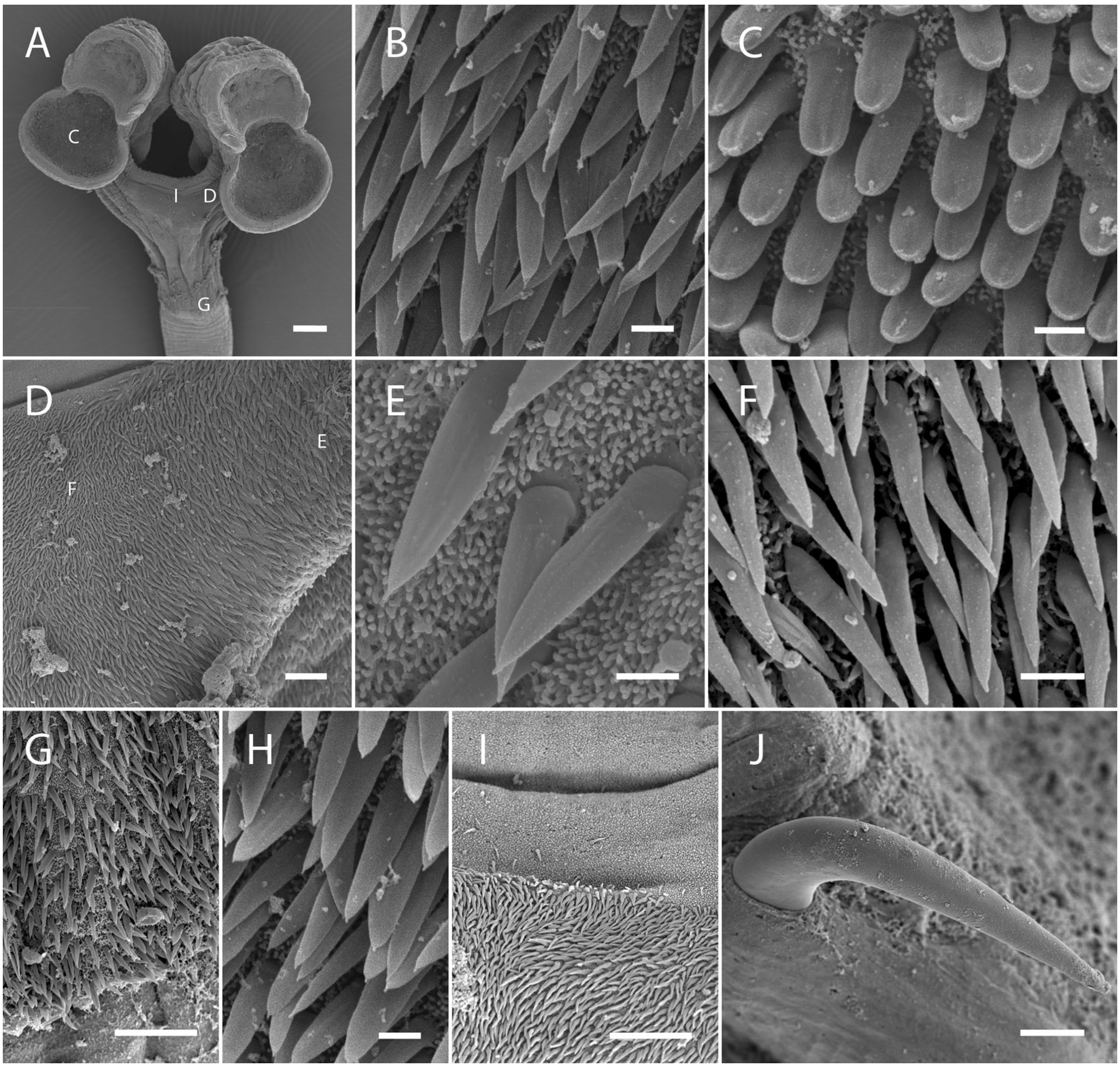


Fig. 5 *Spiniloculus mavensis* ex *Chiloscyllium* cf. *punctatum* from Moreton Bay, scanning electron micrographs. A, Scolex, letters indicates where C, D, G and I were taken; B, Proximal bothridial surface; C, Distal surface of posterior loculus; D, Peduncle, letters indicates where E and F were taken; E, Peduncle surface at bothridial end; F, Peduncle surface at bothridial end; G, Cephalic peduncle; H, Cephalic peduncle surface; I, Most anterior portion of cephalic peduncle; J, Hook. *Scale-bars*: A, 100 μm; D, G, I, J, 10 μm; B, C, E, F, H, 1 μm

Order Onchoproteocephalidea
Genus *Acanthobothrium* van Beneden, 1850

Acanthobothrium cannoni Campbell & Beveridge, 2002

Type-host: *Himantura australis* Last, Naylor & Manjaji-Matsumoto [as *Himantura uarnak* (Gmelin)] (Myliobatiformes: Dasyatidae), honeycomb stingray.
Type-locality: Fog Bay, Northern Territory, Australia.
New material
New host: *Maculabatis* cf. *astra* (Myliobatiformes: Dasyatidae), blackspotted whipray.
New locality: Garden Island (27°36′S, 153°20′E), Moreton Bay, Queensland, Australia.
Site in host: Spiral intestine.
Prevalence: 100% (1 of 1).
Voucher material: Two voucher specimens (QM G 237005–06).

Description (Fig. 6A, B)

[Based on two mounted specimens. Hook measurements in Table 1.] Specimens 55, 67 mm long. Scolex 700 × 620, 850 × 900. Bothridia 710 × 270, 720 long. Anterior bothridial loculus 310 long; middle loculus 160 long; posterior loculus 140 long. Lateral and medial hooks similar; abaxial prong more slender, shorter and terminating in blunt tip; axial prong longer, terminating in sharp tip, with cuticular expansion at origin. Origin of hooks embedded in broad sclerotised plate. Cephalic peduncle *c.*10 mm long. Fully mature segments not present.

Remarks

The specimens described here are attributed to *A. cannoni*. Similar species present in the Australian region are *A. jonesi* Campbell & Beveridge, 2002 and *A. pichelinae* Campbell & Beveridge, 2002. However, the new specimens lack the external spurs present on the hooks of *A. pichelinae* and the sclerotised plate joining the hooks does not extend to the axial and abaxial prongs as it does in *A. jonesi*. In addition, the abaxial prongs of both medial and lateral hooks of *A. cannoni* terminate bluntly, shown in the original figures of the species (figure 47 in Campbell & Beveridge, 2002), but not mentioned in the original description. For these reasons, the present specimens appear to belong to *A. cannoni*. The species was originally described from another dasyatid, *Himantura uarnak* (now *Himantura australis*).

Acanthobothrium chisholmae Campbell & Beveridge, 2002

Type-host: *Pastinachus ater* (Macleay) [as *Pastinachus sephen* (Forsskål)] (Myliobatiformes: Dasyatidae), cowtail stingray.
Type-locality: Nickol Bay, Western Australia, Australia.
New material
Host: *Pastinachus ater*.
New locality: Off Peel Island, Moreton Bay (27°30′S, 153°20′E), Queensland, Australia.
Site in host: Spiral intestine.
Prevalence: 100% (1 of 1).
Voucher material: Two scoleces (QM G237004).

Description (Figs. 6C, D)

[Based on two mounted specimens. Hook measurements in Table 1.] Scolex 200 × 160, 230 × 190. Bothridia 180 × 50, 190 × 70. Anterior bothridial loculus 310 long; middle loculus 50 long; posterior loculus 30 long. Cephalic peduncle 250 long, surface smooth. Hooks sub-symmetrical. Hook prongs elongate, slender; tubercle present on medial aspect of medial hook immediately anterior to bifurcation; irregular surface on medial aspect of lateral hook, almost at level of bifurcation.

Remarks

The specimens described here are attributed to *A. chisholmae*, originally described from the same host species, *P. ater* (Macleay) [as *P. sephen* (Forsskål)], but from Western Australia. There are some minor differences in the hook measurements, but the original description was based on two specimens only and therefore the differences observed are attributed to intraspecific variation.

Acanthobothrium margieae Fyler, 2011

Type-host: *Orectolobus japonicus* Regan (Orectolobiformes: Orectolobidae), Japanese wobbegong.

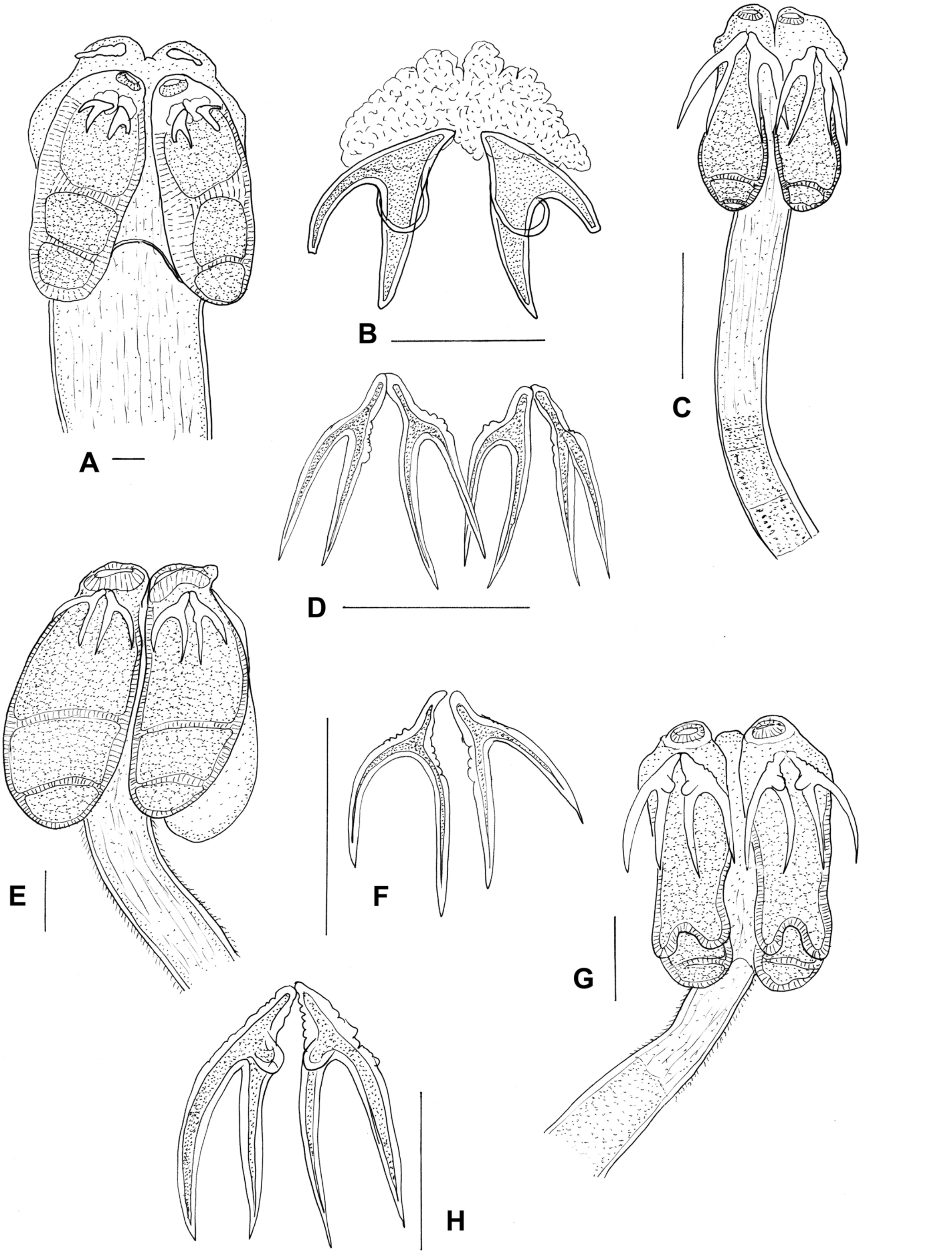


Fig. 6 *Acanthobothrium* species from Moreton Bay. A, *Acanthobothrium cannoni* Campbell & Beveridge, 2002, scolex; B, *A. cannoni*, bothridial hooks; C, *Acanthobothrium chisholmae* Campbell & Beveridge, 2002, scolex; D, *A. chisholmae*, bothridial hooks; E, *Acanthobothrium margiae* Fyler, 2011, scolex; F, *A. margiae*, bothridial hooks; G, *Acanthobothrium ocallaghani* Campbell & Beveridge, 2002, scolex; H, *A. ocallaghani*, bothridial hooks. *Scale-bars*: 100 µm

Table 1 Measurements of hooks of *Acanthobothrium* species from Moreton Bay, Queensland

Species	*A. cannoni*		*A. chisholmae*		*A. margiae*		*A. ocallaghani*	
Source	Campbell & Beveridge (2002) (n = 13)	This study (n = 2)	Campbell & Beveridge (2002) (n = 4)	This study (n = 1)	Fyler (2011) (n = 10)	This study (n = 4)	Campbell & Beveridge (2002) (n = 10)	This study (n = 3)
Lateral, handle (A)	59–80 (67)	60, 70	49–52 (50)	30	70–84 (78)	61–79 (70)	27–42 (32)	25–35 (30)
Lateral axial prong (B)	75–100 (88)	70, 70	80–92 (86)	75	141–167 (155)	123–168 (143)	76–84 (78)	60–70 (63)
Lateral abaxial prong (C)	42–60 (47)	45, 60	74–80 (77)	80	144–173 (157)	123–166 (139)	61–65 (64)	60–70 (64)
Lateral, total axial length (D)	130–155 (142)	120, 120	123–132 (127)	110	205–239 (222)	191–239 (209)	103–112 (108)	90–105 (103)
Lateral, total abaxial length	100–125 (116)	105, 110	125–130 (127)	130	–	–	91–106 (97)	95–105 (97)
Lateral, width	80–95 (83)	65, 70	62–65 (64)	35		60–85 (69)	40–65 (48)	50–70 (62)
Medial, handle (A’)	50–87 (67)	60, 70	45–51 (49)	30	62–78 (71)	54–75 (63)	30–36 (32)	30–35 (33)
Medial axial prong (B’)	70–100 (90)	75, 75	99–105 (101)	75	144–173 (157)	122–175 (146)	72–91(93)	70–80 (73)
Medial abaxial prong (C’)	35–62 (48)	40, 45	77–81 (79)	85	123–156 (137)	119–140 (127)	49–65 (59)	60–70 (63)
Medial, total axial length (D’)	120–155 (143)	115, 125	140–145 (143)	110	205–237 (220)	172–242 (203)	95–118 (112)	95–110 (100)
Medial, total abaxial length	105–130 (114)	95, 110	124–130 (128)	120	–	–	80–103 (93)	90–100 (95)
Medial, width	70–90 (83)	70, 70	46–47 (46)	30	–	50–80 (60)	42–61 (48)	45–55 (50)

Type-locality: Off Penghu Island, East China Sea, Taiwan.

New material

New hosts: *Orectolobus maculatus* (Bonnaterre), spotted wobbegong; *Orectolobus ornatus* (De Vis), ornate wobbegong (Orectolobiformes: Orectolobidae).

New localities: Off Wynnum (27°24′S, 153°10′E); off Port of Brisbane (27°23′S, 153°11′E); off Wellington Point (27°27′S, 153°14′E), Moreton Bay, Queensland, Australia.

Site in host: Spiral intestine.

Prevalence: *O. maculatus*: 22% (2 of 9); *O. ornatus*: 13% (1 of 8).

Voucher material: Five voucher specimens (QM G232739–43; hologenophores QM G232739–41).

Representative DNA sequences: 28S rDNA, three replicates (two submitted to GenBank MH72-9997–98).

Description (Fig. 6E, F)

[Based on four mounted specimens. Hook measurements in Table 1.] Scolex 350–480 × 250–380 (423 × 315, n = 4). Bothridia 372–499 × 120–170 (444 × 140, n = 4). Anterior bothridial loculus 300–400 (350, n = 4) long, posterior extremity bi-lobed, overhanging subsequent loculi; middle loculus 60 long; terminal loculus 50 long. Medial and lateral hooks sub-symmetrical, with elongated prongs. Peduncle *c.*150 long, with prominent, spiniform microtriches. Largest specimen with 175 segments, terminal segments immature.

Remarks

All specimens of *Acanthobothrium* collected from orectolobids during this survey were broken, lacking terminal segments. However, the new specimens were identifiable based on possessing the distinctive concave posterior margin and lateral lappets of the first loculus, which is described for just two species, *A. brayi* Campbell & Beveridge, 2002 and *A. margieae* (see Campbell & Beveridge, 2002; Fyler, 2011). Both species were described from orectolobids; *A. brayi* from *Sutorectus tentaculatus* (Peters) off South Australia, and *A. margieae* from *Orectolobus japonicus* Regan off Taiwan. Three of the features used to differentiate *A. margieae* from *A. brayi* (the extreme hyperapolysis of *A. margieae*, the number of testes and the number of segments) were not observable in the new specimens as the Moreton Bay material lacked the posterior portion of the strobila. However, it is clear in one of the specimens that there were at least 175 segments, indicative of it being *A. margieae* rather than *A. brayi*. The other feature used to differentiate these two species was the length of the cephalic peduncle (75–130 in *A. margieae vs* 200–580 in *A. brayi*). In the new material, the cephalic peduncle was 150 µm long, consistent with that of *A. margieae*. In addition, 28S rDNA sequence data of the new material are identical to those of *A. margieae* from the type-host and type-locality (HQ437682–83) (Fyler, 2011). This record represents the first report of *A. margieae* from Australian waters (previously being only known from off Taiwan), and the first from *O. maculatus* (Bonnaterre) and *O. ornatus* (De Vis).

Acanthobothrium ocallaghani Campbell & Beveridge, 2002

Type-host: *Aptychotrema vincentiana* (Haacke) (Rhinopristiformes: Rhinobatidae), western shovelnose ray.
Type-locality: Musgrave Shoal, South Australia, Australia.
New material
New host: *Aptychotrema rostrata* (Shaw) (Rhinopristiformes: Rhinobatidae), eastern shovelnose ray.
New locality: Off Port of Brisbane (27°23′S, 153°11′E), Moreton Bay, Queensland, Australia.
Site in host: Spiral intestine.
Prevalence: 14% (1 of 7).
Voucher material: Six voucher specimens (QM G237654–59).

Description (Fig. 6G, H)

[Based on three mounted specimens. Hook measurements in Table 1.] Largest specimen 2.75 mm long, with 19 segments; terminal segments pre-mature. Scolex 300–380 × 290–330 (350 × 310, n = 3). Bothridia 270–330 × 120–170 (290 × 140, n = 3). Apical pads well developed, 90–110 (103, n = 3). Anterior bothridial loculus 120–140 (130, n = 3) long; middle loculus 80–90 (80, n = 3) long; posterior loculus 50–70 (60, n = 3) long. Hooks sub-symmetrical. Cephalic peduncle with prominent microtriches.

Pre-mature segments 310–670 × 110–190 (440 × 130, n = 5). Terminal segment most mature, 930 × 200. Genital pore alternating irregularly, posterior to mid-point of segment. Testis 32–46 (36, n = 5) in number, with 12 (10–15, n = 5) pre-poral, 5–6 (5, n = 5) post-poral and 17–25 (20, n = 5) aporal. Cirrus-sac globular, *c.*80 in diameter; distal cirrus armed with prominent microtriches. Genital atrium *c.*40 × 30. Vagina enters atrium anterior to cirrus-sac.

Remarks

The cestodes described here most closely resemble *A. ocallaghani* as described from the congener of the host of the present specimens, *Ap. vincentiana*, from South Australia (Campbell & Beveridge, 2002). Most measurements are comparable, although the ratio of lengths of the bothridial loculi are slightly different. Hook measurements are similar to those of the original description. The major difference appears to be in the number of segments, with 5–11 in the type series (Campbell & Beveridge, 2002), and more than 19 being found in the present specimens. Whether this is due to intraspecific variation, or whether two closely related species occur in *Ap. rostrata* and *Ap. vincentiana* cannot be determined based on the material available. Consequently, the present specimens from *Ap. rostrata* have been identified as *A. ocallaghani*.

Genus *Megalonchos* Baer & Euzet, 1962

Megalonchos shawae Caira, Reyda & Mega, 2007

Type-host: *Hemipristis elongata* (Klunzinger) (Carcharhiniformes: Hemigaleidae), snaggletooth shark.
Type-locality: Arafura Sea, northeast of the Wessel Islands, Australia.
New material
Host: *Hemipristis elongata*.
New locality: Off Wynnum (27°24′S, 153°10′E), Moreton Bay, Queensland, Australia.
Site in host: Spiral intestine.
Prevalence: 100% (2 of 2).
Voucher material: Six voucher specimens deposited in the Queensland Museum, Brisbane, Australia (QM G 232728–33, G237649–53; hologenophores QM G 232728–30).
Representative DNA sequences: 28S rDNA, three replicates (one submitted to GenBank, MH729992).

Description (Fig. 4A, B)

[Based on six mounted specimens. Hook measurements in Table 2.] Largest specimen 9 mm, with premature segments. Scolex 600–780 × 450–550 (660 × 500, n = 5). Bothridia 580–750 × 180–280 (640 × 240, n = 5). Cephalic peduncle 1,250–1,750 (1,510, n = 4) long, with prominent microtriches. Pre-mature segments with 87, 97 (n = 2) testes.

Remarks

The new specimens are missing the terminal region of the strobila. However, they possess the feature distinctive for *Megalonchos shawae*, having posteriorly located pores on the axial prongs (Table 2), which differentiates it from the other species from *Hemipristis elongata*, *Megalonchos sumansinghai* Caira, Reyda & Mega, 2007 (see Caira et al., 2007b). The new specimens possess pores that are 31–40 (35)% and 30–47 (41)% from the posterior tip of the axial prong on the lateral and medial hooks, respectively; these data overlap and agree with the measurements of the type material [35–41 (38)% and 36–46 (42)% for the

Table 2 Hook measurements for new specimens of *Megalonchos* compared to those from original descriptions. Two measurements of each character were taken from each specimen for the new material

Species	*Megalonchos shawae*		*Megalonchos sumansinghai*	
Source	Caira et al. (2007)	This study (n = 6)	Caira et al. (2007)	This study (n = 7)
Lateral hook handle (A)	225–270 (241)	249–306 (273)	180–200 (190)	162–239 (198)
Lateral hook, medial prong (B)	190–230 (209)	198–241 (223)	160–185 (172.3)	153–195 (175)
Lateral hook, to pore (B1)	120–145 (128)	127–155 (144)	50–65 (57.9)	47–68 (58)
Lateral hook, pore to tip (B2)	70–95 (81)	64–86 (79)	100–125 (112.9)	103–127 (117)
Lateral hook, lateral prong (C)	110–140 (122)	115–147 (137)	120–145 (133.7)	118–163 (139)
Lateral hook, total length (D)	305–405 (350)	315–421 (386)	245–345 (307.3)	277–370 (323)
Lateral pore %	35–41 (38)%	31–40 (35)%	62–70 (65)%	64–72 (67)%
Medial hook handle (A)	150–205 (171)	148–215 (190)	140–170 (156.7)	129–190 (164)
Medial hook, medial prong (B)	150–185 (165)	152–195 (177)	130–165 (152)	142–181 (158)
Medial hook, to pore (B1)	90–110 (97)	101–109 (104)	40–55 (46.7)	30–58 (44)
Medial hook, pore to tip (B2)	60–85 (81)	46–89 (73)	80–120 (105.7)	100–131 (114)
Medial hook, lateral prong (C)	130–155 (142)	132–171 (153)	145–175 (160)	141–190 (162)
Medial hook, total length (D)	275–340 (306)	304–355 (327)	245–295 (276.4)	250–327 (288)
Medial pore %	36–46 (42)%	30–47 (41)%	72–73 (69.4)%[a]	67–79 (72)%

[a]Either range or mean incorrect in original description

lateral and medial hooks, respectively]. In addition, all other hook measurements of the new specimens overlap those from the original description (Table 2). The 28S rDNA sequence data of the new specimens are identical to those of *M. shawae* infecting the type-host and type-locality (KF685764.1) (Caira et al., 2014).

Megalonchos sumansinghai Caira, Reyda & Mega, 2007

Type-host: *Hemipristis elongata* (Klunzinger) (Carcharhiniformes: Hemigaleidae), snaggletooth shark.
Type-locality: Arafura Sea, northeast of the Wessel Islands, Australia.
New material
Host: *Hemipristis elongata*.
New locality: Off Wynnum (27°24′S, 153°10′E), Moreton Bay, Queensland, Australia.
Site in host: Spiral intestine.
Prevalence: 100% (2 of 2).
Voucher material: Seven voucher specimens deposited in the Queensland Museum, Brisbane, Australia (QM G 232721–7; hologenophores QM G 232721–2).
Representative DNA sequences: 28S rDNA, two replicates (one submitted to GenBank, MH729993).

Description (Fig. 4C, D)

[Based on seven mounted specimens. Hook measurements in Table 2.] Largest specimen 16 mm with pre-mature segments. Scolex 550–830 × 340–500 (664 × 420, n = 5). Bothridia 450–770 × 190–230 (590 × 212, n = 5). Cephalic peduncle 2.15, 2.55 (n = 2), with prominent microtriches. Pre-mature segments with *c.*90 testes.

Remarks

The new specimens collected during this study broadly agree with the original description of *Megalonchos sumansinghai*, possessing the anteriorly positioned pores on the axial prongs (Table 2), which distinguishes this species from *M. mandleyi* and *M. shawae* (see Caira et al., 2007b). The new specimens of possess pores that are 64–72 (67)% and 67–79 (72)% from the posterior tip of axial prong on the lateral and medial hooks, respectively; these data overlap and agree with the measurements of the type-material of *M. sumansinghai* [62–70 (65)% and 72–73 (69.4)% for the lateral and medial hooks, respectively]. It should be noted that in the original description, the pore position in the medial hook was reported incorrectly, with a mean less than the range. However, the position in the new specimens broadly correlates to the mean provided. In addition, all other hook measurements of the new specimens overlapped those from the original description (Table 2).

Molecular results

Genetic data were generated for six species in this study: *Acanthobothrium margieae*, *Megalonchos sumansinghai*, *M. shawae*, *Spiniloculus mavensis*, *Yorkeria williamsi* n. sp. and *Y. moretonensis* n. sp. The phylogenetic relationships of *Acanthobothrium margieae*, relative to other *Acanthobothrium* species for which molecular data are available, was defined by Fyler (2011); the new molecular data are identical to that of Fyler (2011), thus phylogenetic analysis was not conducted for this species. Sequences for the two species of *Megalonchos* were aligned with those for species of *Anthobothrium* van Beneden, 1850, *Dioecotaenia* Schmidt, 1969 and *Duplicibothrium* Williams & Campbell, 1978 (Table 3). Alignment of this dataset yielded 1,232 characters for analysis, and Bayesian inference analysis showed that the *M. sumansinghai* and *M. shawae* formed a strongly supported clade, sister to *Dioecotaenia cancellata* (Linton, 1890) Schmidt, 1969 (Fig. 7A). Sequences for species of *Spiniloculus* and *Yorkeria* were aligned with those for species of *Balanobothrium* Hornell, 1911, *Pachybothrium* Baer & Euzet, 1962 and *Pedibothrium* Linton, 1908 (Table 3). Alignment of this dataset yielded 1,279 characters for analysis. Bayesian inference analysis resulted in a phylogram in which *Spiniloculus* spp. and *Yorkeria* spp. formed a strongly

Table 3 Collection data and GenBank accession numbers for species included in phylogenetic analyses

Species	Host species	GenBank ID	Reference
Onchoproteocephalidea			
Acanthobothrium margieae Fyler, 2011	*Orectolobus maculatus* (Bonnaterre)	MH729997	This study
	Orectolobus ornatus (De Vis)	MH729998	This study
Megalonchos shawae Caira, Reyda & Mega, 2007	*Hemipristis elongata* (Klunzinger)	MH729992	This study
Megalonchos sumansinghai Caira, Reyda & Mega, 2007	*Hemipristis elongata*	MH729993	This study
Platybothrium auriculatum Yamaguti, 1952	*Prionace glauca* (Linnaeus)	KF685898	Caira et al. (2014)
Triloculatum andersonorum Caira & Jensen, 2009	*Negaprion acutidens* (Rüppell)	KF685895	Caira et al. (2014)
Tetraphyllidea			
Anthobothrium caseyi Ruhnke & Caira, 2009	*Prionace glauca*	KF685879	Caira et al. (2014)
Anthobothrium sp. 1	*Carcharhinus tilstoni* (Whitley)	KF685752	Caira et al. (2014)
Anthobothrium sp. 2	*Carcharhinus isodon* (Müller & Henle)	GQ470169	Jensen & Bullard (2010)
Balanobothrium sp.	*Stegostoma fasciatum* (Hermann)	KF685880	Caira et al. (2014)
Ceratobothrium xanthocephalum Monticelli, 1892	*Isurus oxyrinchus* Rafinesque	KF685756	Caira et al. (2014)
Dinobothrium planum Linton, 1922	*Cetorhinus maximus* (Gunnerus)	KF685886	Caira et al. (2014)
Dioecotaenia cancellata (Linton, 1890)	*Rhinoptera* cf. *steindachneri*	KF685760	Caira et al. (2014)
Duplicibothrium minutum Williams & Campbell, 1978	*Rhinoptera* cf. *steindachneri*	KF685885	Caira et al. (2014)
Duplicibothrium sp. 1	*Rhinoptera* cf. *steindachneri*	KF685763	Caira et al. (2014)
Duplicibothrium sp. 2	*Neverita duplicate* (Say)	GQ470151	Jensen & Bullard (2010)
Pachybothrium hutsoni (Southwell, 1911)	*Nebrius ferrugineus* (Lesson)	EF095260	Waeschenbach et al. (2007)
Pedibothrium mounseyi Caira, Tracy & Euzet, 2004	*Nebrius ferrugineus*	KF685893	Caira et al. (2014)
Pedibothrium veravalensis Shinde, Jadhav & Deshmukh, 1980	*Stegostoma fasciatum*	KF685894	Caira et al. (2014)
Spiniloculus mavensis Southwell, 1925	*Chiloscyllium* cf. *punctatum*	MH729994	This study
Spiniloculus sp.	*Chiloscyllium punctatum* Müller & Henle	KF685775	Caira et al. (2014)
Yorkeria hilli Caira & Tracy, 2002	*Chiloscyllium punctatum*	KF685903	Caira et al. (2014)
Yorkeria izardi Caira, Jensen & Rajan, 2007	*Chiloscyllium* cf. *punctatum*	KF685904	Caira et al. (2014)
Yorkeria moretonensis n. sp.	*Chiloscyllium* cf. *punctatum*	MH729996	This study
Yorkeria williamsi n. sp.	*Chiloscyllium* cf. *punctatum*	MH729995	This study

supported clade (Fig. 7B); within this clade the two *Spiniloculus* species formed a monophyletic clade. Conversely, the three *Yorkeria* species were paraphyletic relative to species of *Spiniloculus*; *Yorkeria hilli* Caira & Tracy, 2002 and *Y. williamsi* n. sp. formed a strongly-supported clade, sister to a strongly-supported clade of *Y. moretonensis* n. sp., *S. mavensis* and *Spiniloculus* sp.

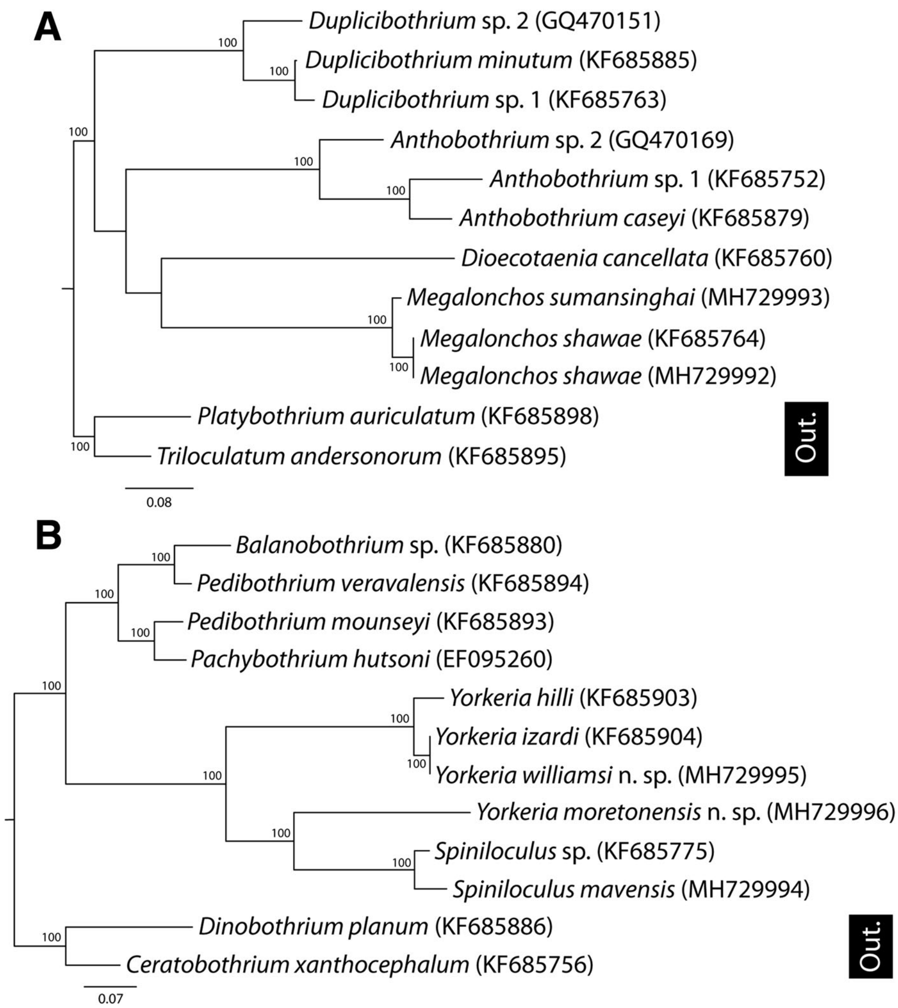


Fig. 7 Phylograms based on Bayesian inference analyses of the partial 28S rDNA dataset. A, Relationships between *Megalonchos* spp. and related taxa; B, Relationships between *Spiniloculus mavensis*, *Yorkeria* spp. and related taxa. Posterior probabilities are shown at the nodes; support values < 80 not shown. *Abbreviation*: Out., Outgroup

Acknowledgements We thank John Page, Dave Thompson and Joanna Stead for their assistance in the collection of elasmobranch specimens, Dr Susan Theiss for help in the production of SEM images, Dr Janine Caira for the image of the hologenophore of *Y. izardi* and Dr L. Chisholm for access to material in the South Australian Museum.

Funding We acknowledge the Australian Biological Resources Study (ABRS) for their ongoing support. This study was funded by the ABRS National Taxonomy Research Grant RF215-40.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional, national and international guidelines for the care and use of animals were followed.

References

Beveridge, I., Cribb, T. H., & Cutmore, S. C. (2017). Larval trypanorhynch cestodes in teleost fish from Moreton Bay, Queensland. *Marine and Freshwater Research, 68,* 2123–2133.

Beveridge, I., & Schaeffner, B. C. Trypanorhynch cestodes (Platyhelminthes) parasitic in elasmobranchs and crustaceans in Moreton Bay, Queensland. *Memoirs of the Queensland Museum* (In press).

Caira, J. N. (1990). The tapeworm *Spiniloculus mavensis* (Tetraphyllidea: Onchobothriidae) from the brownbanded bambooshark in Australia. *Australian Journal of Zoology, 37,* 705–710.

Caira, J. N., & Tracy, R. (2002). Two new species of *Yorkeria* (Tetraphyllidea: Onchobothriidae) from *Chiloscyllium punctatum* (Elasmobranchii: Hemiscylliidae) in Thailand. *Journal of Parasitology*, *88*, 1172–1180.

Caira, J. N., Jensen, K., & Barbeau, E. (2016). Global Cestode Database. World Wide Web electronic publication. www.tapewormdb.uconn.edu. Accessed April 25, 2018.

Caira, J. N., Jensen, K., & Rajan, C. (2007a). Seven new *Yorkeria* species (Cestoda: Tetraphyllidea) from Borneo and Australia and their implications for identification of *Chiloscyllium* (Elasmobranchii: Orectolobiformes) species. *Journal of Parasitology, 93,* 357–376.

Caira, J. N., Jensen, K., Waeschenbach, A., Olson, P. D., & Littlewood, D. T. J. (2014). Orders out of chaos - molecular phylogenetics reveals the complexity of shark and stingray tapeworm relationships. *International Journal for Parasitology, 44,* 55–73.

Caira, J. N., Reyda, F. B., & Mega, J. D. (2007b). A revision of *Megalonchos* Baer & Euzet, 1962 (Tetraphyllidea: Onchobothriidae), with the description of two new species and transfer of two species to *Biloculuncus* Nasin, Caira & Euzet, 1997. *Systematic Parasitology, 67,* 211–223.

Campbell, R. A., & Beveridge, I. (2002). The genus *Acanthobothrium* (Cestoda: Tetraphyllidea: Onchobothriidae) parasitic in Australian elasmobranch fishes. *Invertebrate Systematics, 16,* 237–344.

Cutmore, S. C., Bennett, M. B., & Cribb, T. H. (2010). A new tetraphyllidean genus and species, *Caulopatera pagei* n. g., n. sp. (Tetraphyllidea: Phyllobothriidae), from the grey carpetshark *Chiloscyllium punctatum* Müller & Henle (Orectolobiformes: Hemiscylliidae). *Systematic Parasitology, 77,* 13–21.

Cutmore, S. C., Bennett, M. B., Miller, T. L., & Cribb, T. H. (2017). Patterns of specificity and diversity in species of *Paraorygmatobothrium* Ruhnke, 1994 (Cestoda: Phyllobothriidae) in Moreton Bay, Queensland, Australia, with the description of four new species. *Systematic Parasitology, 94,* 941–970.

Cutmore, S. C., Theiss, S. M., Bennett, M. B., & Cribb, T. H. (2011). A new phyllobothriid genus and species from the snaggletooth shark, *Hemipristis elongata* (Carcharhiniformes: Hemigaleidae), from Moreton Bay, Australia. *Folia Parasitologica, 58,* 187–196.

Darriba, D., Taboada, G. L., Doallo, R., & Posada, D. (2012). jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods, 9,* 772.

Desjardins, L., & Caira, J. N. (2011). 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. *Folia Parasitologica, 58,* 55–68.

Dróżdż, J. (1995). Polymorphism in the Ostertagiinae Lopez-Neyra, 1947 and comments on the systematics of these nematodes. *Systematic Parasitology, 32,* 91–99.

Edgar, R. C. (2004). MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research, 32,* 1792–1797.

Fyler, C. A. (2011). An extremely hyperapolytic *Acanthobothrium* species (Cestoda: Tetraphyllidea) from the Japanese wobbegong, *Orectolobus japonicus* (Elasmobranchii: Orectolobiformes) in Taiwan. *Comparative Parasitology, 78,* 4–14.

ICZN (2012). *International Commission on Zoological Nomenclature*: Amendment of articles 8, 9, 10, 21 and 78 of the International Code of Zoological Nomenclature to expand and refine methods of publication. *Bulletin of Zoological Nomenclature, 69,* 161–169.

Jensen, K., & Bullard, S. A. (2010). Characterization of a diversity of tetraphyllidean and rhinebothriidean cestode larval types, with comments on host associations and life-cycles. *International Journal for Parasitology, 40,* 889–910.

Last, P. R., & Stevens, J. D. (2009). *Sharks and rays of Australia* (2nd ed). Collingwood: CSIRO Publishing, 644 pp.

Last, P. R., White, W. T., Carvalho, M. R., Séret, B., Stehmann, M. F. W., & Naylor, G. J. P. (2016). *Rays of the world*. Melbourne: CSIRO Publishing.

Littlewood, D. T. J. (1994). Molecular phylogenetics of cupped oysters based on partial 28S rRNA gene sequences. *Molecular Phylogenetics and Evolution, 3,* 221–229.

Littlewood, D. T. J., Curini-Galletti, M., & Herniou, E. A. (2000). The interrelationships of Proseriata (Platyhelminthes: Seriata) tested with molecules and morphology. *Molecular Phylogenetics and Evolution, 16,* 449–466.

Littlewood, D. T. J., Rohde, K., & Clough, K. A. (1997). Parasite speciation within or between host species? Phylogenetic evidence from site-specific polystome monogeneans. *International Journal for Parasitology, 27,* 1289–1297.

Lockyer, A. E., Olson, P. D., & Littlewood, D. T. J. (2003). Utility of complete large and small subunit rRNA genes in resolving the phylogeny of the Neodermata (Platyhelminthes): implications and a review of the cercomer theory. *Biological Journal of the Linnean Society, 78,* 155–171.

Maddison, W. P., & Maddison, D. R. (2018). Mesquite: a modular system for evolutionary analysis. Version 3.01. http://mesquiteproject.org.

Miller, M. A., Pfeiler, E., & Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the gateway computing environments workshop (GCE), 14 Nov. 2010, New Orleans, LA, USA, pp. 1–8.

Naylor, G. J. P., Caira, J. N., Jensen, K., Rosana, K. A. M., White, W. T., & Last, P. R. (2012). A DNA sequence-based approach to the identification of shark and ray species and its implications for global elasmobranch diversity and parasitology. *Bulletin of the American Museum of Natural History, 367,* 1–262.

Pleijel, F., Jondelius, U., Norlinder, E., Nygren, A., Oxelman, B., Schander, C., et al. (2008). Phylogenies without roots? A plea for the use of vouchers in molecular phylogenetic studies. *Molecular Phylogenetics and Evolution, 48,* 369–371.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., et al. (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology, 61,* 539–542.

Southwell, T. (1925). A monograph on the Tetraphyllidea with notes on related cestodes. *Memoirs of the Liverpool School of Tropical Medicine (New Series), 2,* 1–368.

Waeschenbach, A., Webster, B. L., Bray, R. A., & Littlewood, D. T. J. (2007). Added resolution among ordinal level relationships of tapeworms (Platyhelminthes: Cestoda) with complete small and large subunit nuclear ribosomal RNA genes. *Molecular Phylogenetics and Evolution, 45,* 311–325.

Williams, H. H. (1964). Some new and little known cestodes from Australian elasmobranchs with a brief discussion on their possible use in problems of host taxonomy. *Parasitology, 54,* 737–748.