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Emerging global novelty in phyllobothriidean tapeworms (Cestoda: Phyllobothriidea) from sharks and skates (Elasmobranchii)

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New genera are erected for three clades of tapeworms originally discovered using molecular sequence data. The morphological features of each are characterized after examination of specimens with light and scanning electron microscopy. ***Rockacestus* gen. nov.** parasitizes skates. ***Ruhnkebothrium* gen. nov.** parasitizes hammerhead sharks. ***Yamaguticestus* gen. nov.** parasitizes small squaliform sharks and catsharks. The novelty of these genera is supported by a taxonomically comprehensive molecular phylogenetic analysis of the D1–D3 region of the 28S rDNA gene, which, with the addition of newly generated sequence data, is the first to include representation of 15 of the 18 genera of phyllobothriideans plus the three new genera. Five new species are described from elasmobranchs in the western Atlantic Ocean, the Gulf of California, Chile, the Falkland Islands and South Africa to help circumscribe the new genera. Two of the genera provide appropriate generic homes for ten species of phyllobothriideans from catsharks and skates with uncertain generic affinities and thus resolve longstanding taxonomic issues. Given that these genera parasitize some of the most poorly sampled groups of elasmobranchs (i.e. hammerhead sharks, squaliform sharks, catsharks and skates), based on the strict degree of host specificity observed, we predict that further work on other members of these groups will yield as many as 200 additional species in these three genera of tapeworms globally. This brings the total number of genera in the Phyllobothriidea to 21.

ADDITIONAL KEYWORDS: 28S ribosomal DNA – catsharks – hammerhead sharks – new genera – phylogenetic analysis – *Rockacestus* – *Ruhnkebothrium* – *Yamaguticestus*.

INTRODUCTION

Molecular phylogenetic analyses conducted over the last decade have done much to help inform our understanding of the systematics and phylogenetic diversity represented by the tapeworms hosted by sharks, skates and stingrays (i.e. elasmobranchs). One of the unexpected outcomes of that work was the discovery of the key role that tapeworms of elasmobranchs appear to have played in the evolution

of tapeworms of vertebrates overall (Caira & Jensen, 2014; Caira *et al.*, 2014). However, a full appreciation of these host–parasite systems, in terms of both morphological diversity and host associations, awaits more detailed investigation of some of the more poorly known groups of elasmobranch tapeworms. In the recently established order Phyllobothriidea (see Caira *et al.*, 2014) alone, three potentially novel clades constituting novel genera have emerged from molecular phylogenetic work (Ruhnke *et al.*, 2017). Previously, these taxa have been referred to merely with provisional numerical assignments: New genus 10 of Caira *et al.* (2014) and New genus 18 and New genus 20 of Ruhnke *et al.* (2017). Furthermore, their morphologies have not been described.

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This study has two primary aims. The first is to confirm the novelty of these three genera by conducting the most taxonomically comprehensive phylogenetic analysis of Phyllobothriidea to date, based on a combination of newly generated data and existing data available in GenBank, that includes representation of all but three of the 18 genera in the order. The second is to establish these genera formally, based on the description of five new species and the transfer of ten described species of uncertain status to two of the genera. In addition to expanding our knowledge of the morphological heterogeneity and complexity of the host associations of this order, this work signals the existence of substantial undiscovered diversity in these three genera of tapeworms in unexplored sharks and skates. This work resolves a series of issues of generic identity in the order, paving the way for a more comprehensive assessment of its phylogenetic relationships and host associations.

MATERIAL AND METHODS

NEW COLLECTIONS AND SPECIMEN PREPARATION

The elasmobranchs from which the tapeworms examined here were collected consisted of 22 specimens representing 11 species collected from nine countries over several decades of fieldwork. In most cases, a series of digital photographs and basic morphometric data were collected for each specimen. In each case, the unique specimen number (e.g. FA-75), which consists of a collection code and collection number, and basic size and locality data are provided in Table 1. Additional data are available in the Global Cestode Database (Caira *et al.*, 2020a) using the unique specimen number.

The body cavity of each elasmobranch was opened with a longitudinal ventral incision, and the spiral intestine was removed and opened with a mid-ventral incision. In the case of each elasmobranch species, a subset of the tapeworms found was preserved in 10% seawater-buffered formalin (9:1) for morphological work and a subset was preserved in 95% ethanol for molecular work. Also examined were two slides of tapeworms collected from the hammerhead shark *Sphyrna lewini* (Griffith & Smith, 1834) 1 (*sensu* Naylor *et al.*, 2012) sent to us several years ago by the late Tom Mattis; the collection data in Table 1 for those host specimens (TM-100 through TM-107) were obtained from the slide labels.

Methods for preparing tapeworms as whole mounts on glass slides for descriptive work using light microscopy and scanning electron microscopy (SEM) followed Caira *et al.* (2020b), as did the methods for preparing drawings and taking measurements. Measurements are given in the text as ranges, followed in parentheses by the mean, standard deviation, number of specimens measured and number of measurements made when it was possible to make more than one measurement

per specimen. All measurements are in micrometres unless otherwise noted.

Microthrix terminology follows Chervy (2009). Museum abbreviations used are as follows: CNHE, Colección Nacional de Helmintos del Instituto de Biología, Universidad Nacional Autónoma de México, Mexico; LRP, Lawrence R. Penner Parasitology Collection, University of Connecticut, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MNHNCL, Museo Nacional de Historia Natural, Santiago, Chile; NHMUK, The Natural History Museum, London, UK; NMB, National Museum Bloemfontein, Bloemfontein, South Africa; and USNM, National Museum of Natural History, Smithsonian Institution, Department of Invertebrate Zoology, Washington, DC, USA.

Sequence data were generated *de novo* here from a portion of each of ten specimens (see Molecular Methods and Phylogenetic Analysis). The remainder of each of these hologenophores and the paragenophore (*sensu* Pleijel *et al.*, 2008) was prepared as a whole mount, following Caira *et al.* (2020b).

MOLECULAR METHODS AND PHYLOGENETIC ANALYSIS

Data for the D1–D3 region of the 28S rDNA gene are presented for ten specimens of nine species for the first time. A Sanger sequencing protocol was used to generate sequence data for the following five specimens: *Yamaguticestus squali* (Yamaguti, 1952) comb. nov. ex *Squalus suckleyi* (Girard, 1855) (BAM5-wP9), *Yamaguticestus* cf. *squali* ex *Squalus acanthias* Linnaeus, 1758 (BL2P2), *Rockacestus carvajali* sp. nov. ex *Dipturus chilensis* (Guichenot, 1848) (CHL76-5), *Rockacestus* sp. nov. 6 ex *Dipturus lamillai* Concha, Caira, Ebert & Pompert, 2019 (FA8-13) and *Bilocularia hyperapolytica* Obersteiner, 1914 ex *Dalatias licha* (Bonaterre, 1788) (AZ163-7W). In these cases, DNA extraction, amplification and sequencing followed Caira *et al.* (2020b). The primer pair used for amplification was LSU-5 (5'-TAGGTCGACCCGCTGAAYTTA-3') (Littlewood *et al.*, 2000) and LSU-1500R (5'-GCTATCCTGGAGGGAACTTCG-3') (Tkach *et al.*, 2003). The primer pair used for sequencing was LSU-55F (5'-AACCAGGATTCCCCTAGTAA CGGC-3') (Bueno & Caira, 2017) and LSU-1200R (5'-GCATAGTTCCACCATCTTTTCGG-3') (Littlewood *et al.*, 2000). Data for the D1–D3 region of the 28S rDNA gene for *Yamaguticestus metini* sp. nov. ex *Halaelurus natalensis* (Regan, 1904) (JW423; AF-179), *Ruhnkebothrium bajaense* sp. nov. ex *Sphyrna lewini* 2 (JW504; BJ-323), *Rockacestus conchali* sp. nov. ex *Bathyrhaja albomaculata* (Norman, 1937) (KW1011; FA-70), *Rockacestus* sp. nov. 4 ex *Dipturus batis* (Linnaeus, 1758) (JW632; RO-21) and *Rockacestus* sp. nov. 5 ex *Amblyrhaja doellojuradoi* (Pozzi, 1935) (KW1004; FA-75) were assembled by Hannah Ralicki and Elizabeth

Table 1. Source of cestode material examined

Host species	Unique host specimen number	Host order: host family	Sex	Total length (cm)	Locality	Date collected	Collection method	Cestode data collected
<i>Amblyraja doellojuradoi</i>	FA-75	Rajiformes: Rajidae	Male	48	Atlantic Ocean, off Falkland Islands, UK (49°03'24"S, 60°46'30"W)	July 2017	Bottom trawl (Research Cruise ZDLT1-07-2017, Station 2544)	DNA
<i>Bathyraja albomaculata</i>	FA-70	Rajiformes: Arhynchobatidae	Female	36.2	Atlantic Ocean, off Falkland Islands, UK (49°38'49.8"S, 59°50'43.2"W)	July 2017	Bottom trawl (Research Cruise ZDLT1-07-2017, Station 2544)	DNA
<i>Bathyraja albomaculata</i>	FA-72	Rajiformes: Arhynchobatidae	Male	67.3	Atlantic Ocean, off Falkland Islands, UK (48°39'10.8"S, 60°44'42.6"W)	July 2017	Bottom trawl (Research Cruise ZDLT1-07-2017, Station 2540)	LM; SEM
<i>Dalatias licha</i>	AZ-163	Squaliformes: Dalatiidae	Male	119	Atlantic Ocean, off Faial, Azores, Portugal (38°31'24"N, 28°59'30"W)	October 2012	Long-line (Research Cruise <i>RV Arguipelago</i>)	DNA
<i>Dipturus batis</i>	RO-21	Rajiformes: Rajidae	Unknown	Unknown	Atlantic Ocean, off Scotland, UK (55°50'N, 09°17'W)	September 2004	Bottom trawl	DNA
<i>Dipturus chilensis</i>	CHL-18	Rajiformes: Rajidae	Male	62	Pacific Ocean, off Pūnihuīl, Chiloé Island, Chile (41°55'43"S, 74°02'16"W)	January 2008	Long-line (local fishermen)	LM; SEM
<i>Dipturus chilensis</i>	CHL-19	Rajiformes: Rajidae	Male	72	Pacific Ocean, off Pūnihuīl, Chiloé Island, Chile (41°55'43"S, 74°02'16"W)	January 2008	Long-line (local fishermen)	LM; SEM
<i>Dipturus chilensis</i>	CHL-76	Rajiformes: Rajidae	Male	85	Pacific Ocean, off Niebla, Chile (39°51'S, 73°24'W)	January 2013	Long-line (local fishermen)	DNA
<i>Dipturus lamillai</i>	FA-8	Rajiformes: Rajidae	Male	92	Atlantic Ocean, off Falkland Islands, UK (52°57'54"S, 59°45'36"W)	November 2013	Bottom trawl	DNA
<i>Halaelurus natalensis</i>	AF-161	Carcharhiniformes: Scyliorhinidae	Female	46.5	Indian Ocean, South Africa (33°47'40.2"S, 26°05'7.2"E)	May 2010	Bottom trawl (<i>FV Africana</i>)	LM
<i>Halaelurus natalensis</i>	AF-179	Carcharhiniformes: Scyliorhinidae	Female	44.5	Indian Ocean, South Africa (33°59'24"S, 25°12'1.2"E)	May 2010	Bottom trawl (<i>FV Africana</i>)	LM; DNA
<i>Halaelurus natalensis</i>	AF-180	Carcharhiniformes: Scyliorhinidae	Female	47	Indian Ocean, South Africa (33°59'24"S, 25°12'1.2"E)	May 2010	Bottom trawl (<i>FV Africana</i>)	LM
<i>Halaelurus natalensis</i>	AF-184	Carcharhiniformes: Scyliorhinidae	Male	41	Indian Ocean, South Africa (34°10'7.2"S, 24°54'55.2"E)	May 2010	Bottom trawl (<i>FV Africana</i>)	LM; SEM
<i>Sphyrna lewini</i> 2 (sensu Naylor et al., 2012)	BJ-323	Carcharhiniformes: Sphyrnidae	Unknown	Unknown	Gulf of California, Loreto, Mexico (25°49'52"N, 111°19'38"W)	August 1993	Long-line (local fishermen)	SEM; DNA
<i>Sphyrna lewini</i> 2 (sensu Naylor et al., 2012)	BJ-419	Carcharhiniformes: Sphyrnidae	Male	128	Gulf of California, San Jose del Cabo, Mexico (23°02'45"N, 109°41'33"W)	September 1993	Long-line (local fishermen)	LM
<i>Sphyrna lewini</i> 1 (sensu Naylor et al., 2012)	DEL-6	Carcharhiniformes: Sphyrnidae	Male	269.3	Atlantic Ocean, off Florida, USA (28°00'18"N, 80°04'18"W)	May 2001	Long-line (<i>RV Delaware II</i>)	LM; SEM; DNA

Table 1. Continued

Host species	Unique host specimen number	Host order: host family	Sex	Total length (cm)	Locality	Date collected	Collection method	Cestode data collected
<i>Sphyrna lewini</i> 1 (<i>sensu</i> Naylor et al., 2012)	TM-100, TM-102*	Carcharhiniformes: Sphyrnidae	Unknown	Unknown	Gulf of Mexico, Pensacola, FL, USA (30°03'25.26"N, 87°00'13.01"W)	July 1973	Hook and line	LM
<i>Sphyrna lewini</i> 1 (<i>sensu</i> Naylor et al., 2012)	TM-101	Carcharhiniformes: Sphyrnidae	Unknown	Unknown	Gulf of Mexico, Pensacola, FL, USA (30°03'25.26"N, 87°00'13.01"W)	July 1973	Hook and line	LM
<i>Sphyrna lewini</i> 1 (<i>sensu</i> Naylor et al., 2012)	TM-103–TM-107*	Carcharhiniformes: Sphyrnidae	Unknown	Unknown	Gulf of Mexico, Horn Island, MS, USA (30°13'59.37"N, 88°40'10.79"W)	August 1975	Hook and line	LM
<i>Squalus acanthias</i>	BL-2	Squaliformes: Squalidae	Female	141	Black Sea, off Balchik, Bulgaria (43°24'8.55"N, 28°09'35.66"E)	April 2010	Unknown	DNA
<i>Squalus suckleyi</i>	JN-67	Squaliformes: Squalidae	Female	60	Sea of Japan, off Oga City, Japan (39°46'55.8"N, 139°51'49.2"E)	October 1999	Drift net	SEM
<i>Squalus suckleyi</i>	BAM-5	Squaliformes: Squalidae	Male	86	Pacific Ocean, off Vancouver Island, Canada (48°50'7.9152"N, 125°08'7.7208"W)	July 2009	Hook and line	DNA

Abbreviations: DNA, sequence data; LM, light microscopy; SEM, scanning electron microscopy.
*Proglottids only.

Jockusch using MITOBIM v.1.9.1 (Hahn *et al.*, 2013) from next generation sequencing reads generated for a related project.

To allow us to assess the hypothesized novelty of the proposed new genera as robustly as possible, in addition to data generated *de novo*, the matrix on which our phylogenetic analysis was based included comparable data from GenBank for voucher adult specimens of 56 species representing 15 of the 18 established phyllobothriidean genera recognized as valid by Ruhnke *et al.* (2017) as modified by Caira *et al.* (2020b). With respect to our new genera, also included from GenBank were data for a specimen from *Squalus acanthias* originally identified by Caira *et al.* (2014) as *Phyllobothrium squali* Yamaguti, 1952 (KF685897), a specimen from *Scyliorhinus canicula* (Linnaeus, 1758) originally identified as *Crossobothrium longicollis* (Molin, 1858) Euzet, 1959 (AF286958) by Olson *et al.* (2001) and a specimen from *Sphyrna lewini* 1 originally identified as New genus 10 sp. 1 (KF685889) by Caira *et al.* (2014). The three genera of phyllobothriideans that were not represented in our molecular analysis (i.e. *Bibursibothrium* McKenzie & Caira, 1998, *Cardiobothrium* McKenzie & Caira, 1998 and *Flexibothrium* McKenzie & Caira, 1998) are monotypic and difficult to collect given that all three parasitize sawsharks of the genus *Pristiophorus* Müller & Henle, 1837 (see McKenzie & Caira, 1998). However, inclusion of these three genera is unlikely to alter the results of our analyses, given their dramatically different morphologies.

Sequences were initially aligned using the default parameter settings of MAFFT v.7.388 (Katoh & Standley, 2013) and trimmed using GENEIOUS PRIME 2019.1.3 (Biomatters, Newark, NJ, USA). They were then re-aligned using PRANK (Löytynoja & Goldman, 2010) on the webPRANK Server (<https://www.ebi.ac.uk/goldman-srv/webprank/>) using the default settings, but with the '+F flag' removed. GTR+I+G was selected as the best-ranked model of molecular evolution according to the corrected Akaike information criterion (AICc) implemented in PARTITIONFINDER v.2.1.1 (Lanfear *et al.*, 2017).

A maximum likelihood (ML) analysis was conducted in GARLI v.2.01 (Zwickl, 2006) on the 51-node Xanadu computer cluster of the Computational Biology Core (CBC) within the Institute for Systems Genomics at the University of Connecticut. Tree searches were conducted with default GARLI settings over 50 independent search replicates. Nodal support for inferred ML clades was estimated using bootstrap analysis [ten search replicates, 100 bootstrap (BS) replicates each]. The program SUMTREES v.4.0.0 (Sukumaran & Holder, 2015) implemented in the software package DENDROPY v.4.0.3 (Sukumaran & Holder, 2010) was used to map bootstrap values onto the tree with the best ML score.

RESULTS

PHYLOGENETIC ANALYSIS

Sequence data for the D1–D3 region of the 28S rDNA gene of the ten specimens newly presented here have been deposited in GenBank; in each case, their hologenophore or paragenophore has been deposited in LRP. Accession numbers for the five specimens representing species described or treated below are given in the taxonomic summaries. Accession numbers for the additional five specimens are as follows: *Yamaguticestus* cf. *squali*, GenBank accession MW419976, hologenophore (BL2P2) LRP no. 8683; *Rockacestus* sp. nov. 6, GenBank accession MW419974, hologenophore (VB119; FA-8-13) LRP no. 8910; *Rockacestus* sp. nov. 5, GenBank accession MW419961, hologenophore (KW1004; FA-75) LRP no. 10325; *Rockacestus* sp. nov. 4, GenBank accession MW419960 (JW632; RO-21); *Bilocularia hyperapolytica*, GenBank accession MW419972, paragenophore (AZ-163-7W) LRP no. 8139.

The tree resulting from our phylogenetic analysis is shown in Figure 1. Specimens of each of the putative new genera grouped together independently from specimens of all other genera included in the analysis. All three genera were highly supported, with BS values of 100%. In combination with the unique morphological features outlined below, these results support erection of the three new genera. The tree also shows the relatively low amount of sequence divergence in the D1–D3 region of the 28S rDNA gene among some of the specimens collected from different host species in all three new genera.

RUHNEBOTHRIUM GEN. NOV.

ZooBank registration: 9518EC43-EC41-4B3B-AF5C-C0C03F180D9F.

Diagnosis: Worms euapolytic, acraspedote. Scolex with four bothridia; cephalic peduncle and myzorhynchus lacking; neck present. Bothridia consisting of small, simple anterior loculus and expansive, highly folded posterior loculus. Scolex with slender gladiate or cyrillionate spinitriches and capilliform filitriches; slender band of papilliform filitriches on distal surface of bothridial rim. Neck and strobila scutellate. Immature proglottids wider than long; mature proglottids longer than wide. Testes numerous, extending throughout most of proglottid; post-ovarian field absent. Vas deferens minimal. Genital pores lateral, irregularly alternating; genital atrium shallow. Cirrus sac narrowly oblong or pyriform, containing coiled cirrus; cirrus armed with spinitriches. Vagina weakly sinuous, extending from ootype along midline of proglottid to

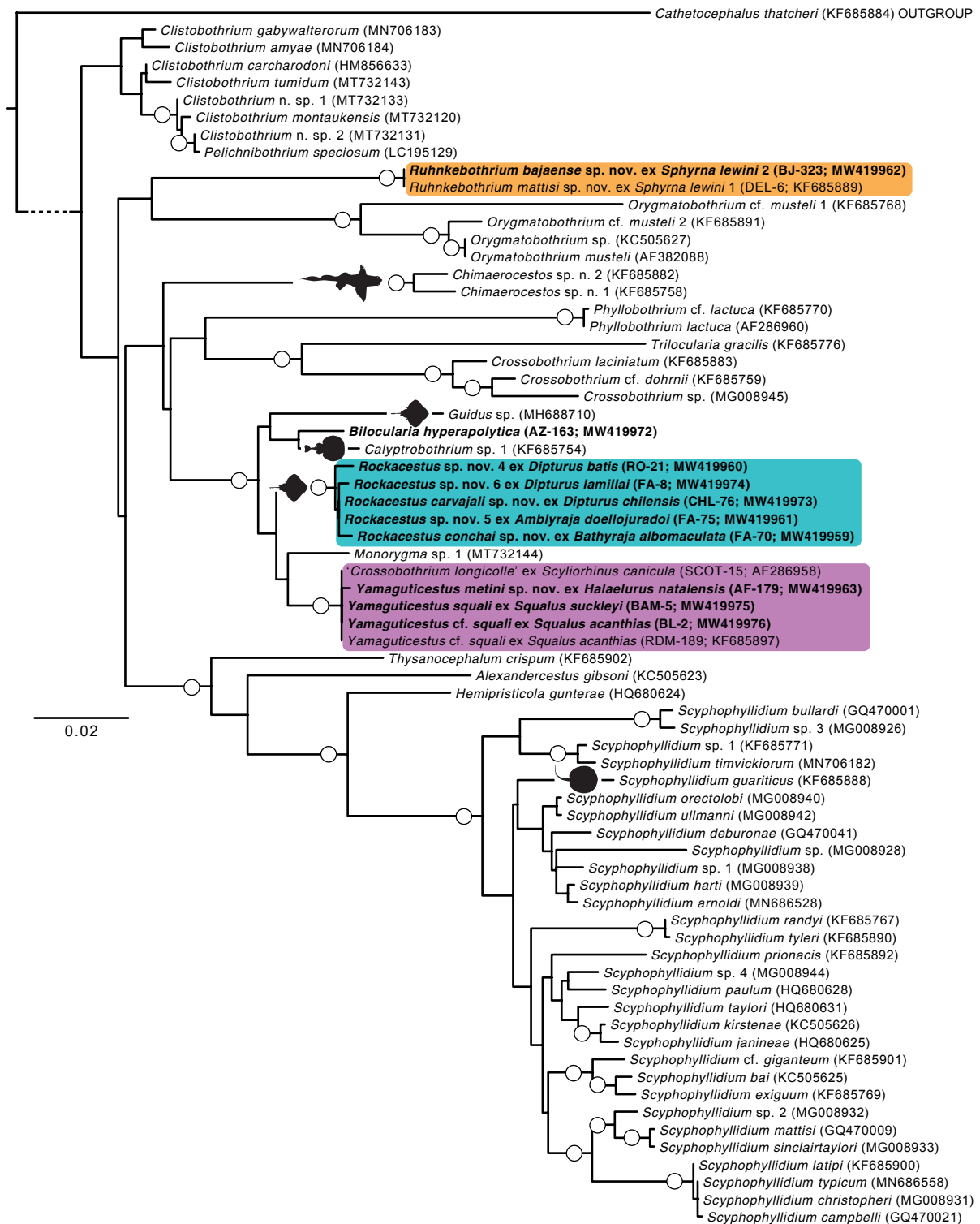


Figure 1. Phylogenetic tree resulting from maximum likelihood analysis of the D1–D3 region of the 28S rDNA gene for new genera and all but three valid genera of Phyllobothriidea. Scale bar indicates number of nucleotide substitutions per site. Nodes with bootstrap support values $\geq 90\%$ are indicated with open circles. Labels of tips of taxa in new genera are presented as cestode name, host name and unique host specimen number and GenBank accession number in parentheses. Labels of tips of other taxa are presented as cestode name, as modified by [Caira et al. \(2020b\)](#), and GenBank accession number in parentheses. New sequences are indicated in bold. New genera are indicated with coloured rectangles. Taxa parasitizing non-shark chondrichthyans are indicated with black host icons on their branches.

anterior margin of cirrus sac, then laterally to open into genital atrium anterior to cirrus; vaginal sphincter absent; seminal receptacle present. Ovary H-shaped in frontal view, tetralobed in cross-section; ovarian margins lobulate or digitiform. Vitellarium follicular; follicles in two lateral bands; each band consisting of multiple columns of follicles, extending length of proglottid, usually interrupted dorsally and ventrally by terminal genitalia, not interrupted by ovary. Uterus medial, ventral, sacciform, extending from anterior margin of ovary to level of cirrus sac. Excretory vessels 4, arranged in one dorsal and one ventral pair on each lateral margin of proglottid. Parasites of hammerhead sharks (Sphyrnidae Gill). Cosmopolitan.

Type species: *Ruhnkebothrium mattisi* sp. nov.

Additional species: *Ruhnkebothrium bajaense* sp. nov.

Etymology: This genus honours Dr Tim Ruhnke, whose keen insight into the taxonomic complexity of the Phyllobothriidea has led to key advancements in the systematics of the members of this order. *Bothrium* is derived from the Greek βοθρίων, a well or pit. The gender is neuter.

Provisional name: New genus 10 of Caira *et al.* (2014) and Ruhnke *et al.* (2017).

Remarks: Among the 18 genera of Phyllobothriidea considered valid (see Ruhnke *et al.*, 2017; Caira *et al.*, 2020b), *Ruhnkebothrium* differs from all but one in that, rather than bearing bothridia that are essentially oval in form, it bears bothridia that are narrow anteriorly and extensive and highly folded posteriorly. In addition, rather than an apical sucker, each bothridium bears an anterior locusus. In both respects, the bothridia of *Ruhnkebothrium* resemble those of *Thysanocephalum* Linton, 1890. The scolex of *Thysanocephalum* was considered historically to consist of four small bothridia followed by an elaborately folded structure referred to variously as a 'pseudoscolex' (e.g. Linton, 1892: p. 544) or a 'metascolex' (e.g. Euzet, 1959: p. 136). However, Caira *et al.* (1999) determined that the entire structure constitutes the scolex, which bears four extensive bothridia, each of which consists of a narrow anterior locusus and a broad, highly folded posterior locusus. *Ruhnkebothrium* is easily distinguished from *Thysanocephalum*, in that its uterus extends only to the cirrus sac, rather than to the anterior margin of the proglottid and in that the surface of its neck bears scutes rather than elaborate leaf-like folds (Caira *et al.*, 1999). In addition, unlike *Thysanocephalum*, the proximal and distal bothridial surfaces of *Ruhnkebothrium* bear slender, simple

gladiate or cyrillionate spinitriches rather than serrate gladiate spinitriches.

RUHNKEBOTHRIUM MATTISI SP. NOV.

(Figs 2A–C, 3)

ZooBank registration: 79276324-95ED-41AC-8B82-544744F596AB.

Description: [Based on two whole mature worms, one partial mature worm (hologenophore), one detached mature proglottid, three detached gravid proglottids, three detached dehisced proglottids, and two scolices examined with SEM.] Worms euapolytic, acraspedote, 33.6–36.2 mm long; proglottids 127–145 in total number; maximum width at level of scolex or terminal proglottid. Scolex consisting of four bothridia, 1043–1223 long, 1121–1743 wide. Bothridia consisting of small, simple anterior locusus (Fig. 3B) and expansive, highly folded posterior locusus (Figs 2A, 3A), 1043–1223 (1111 ± 98 ; 2; 3) long, 509–878 (692 ± 179 ; 2; 4) wide, sessile anteriorly, free posteriorly; anterior locusus 69–94 (78 ± 10 ; 2; 5) long, 74–96 (87 ± 8 ; 2; 6) wide. Cephalic peduncle lacking. Neck 2255–3245 long. Distal surface of anterior locusus with slender gladiate spinitriches and capilliform filitriches (Fig. 3D); distal surface of anterior, narrow portion of posterior locusus with slender gladiate spinitriches and capilliform filitriches (Fig. 3E, F); distal surface of posterior locusus with dispersed slender gladiate spinitriches and densely arranged capilliform filitriches (Fig. 3G); capilliform filitriches becoming less dense near margins of distal surfaces of posterior locusus; rim of distal surface of posterior locusus with small band of papilliform filitriches only (Fig. 3C). Proximal bothridial surface with extremely slender gladiate spinitriches and capilliform filitriches (Fig. 3H). Neck (Fig. 3I) and strobila with capilliform filitriches arranged in narrow, convex scutes. Immature proglottids wider than long, becoming longer than wide with maturity (Fig. 2B), 120–142 in number. Mature proglottids three to seven in number. Terminal proglottid 1326–2448 long, 1420–1585 wide; length-to-width ratio 0.9–1.5:1 (Fig. 2C). Testes 211–306 (256 ± 44 ; 3; 5) in total number, 43–78 (59 ± 16 ; 3; 5) in number in post-poral field, 47–70 (56 ± 8 ; 2; 8) long, 58–86 (73 ± 8 ; 2; 8) wide. Vas deferens minimal, coiled medial to cirrus sac. Cirrus sac narrowly oblong (*sensu* Clopton, 2004), slightly curved anteriorly, 588–623 long, 118–155 wide, thin walled, containing coiled cirrus; cirrus armed with spinitriches. Genital pores irregularly alternating, 62–68% of proglottid length from posterior end; genital atrium shallow. Vagina surrounded by glandular cells, weakly sinuous, extending from ootype along

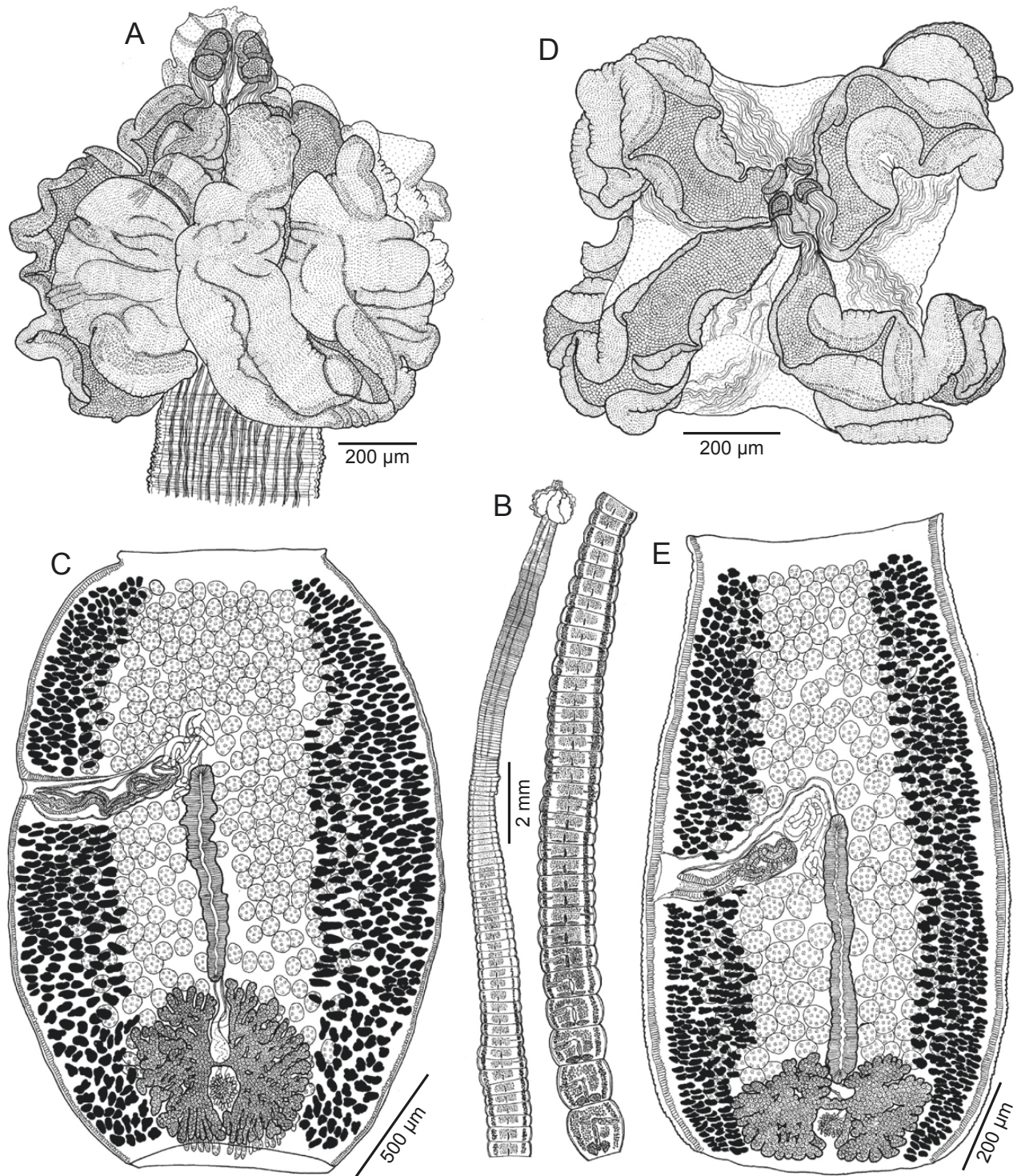


Figure 2. Line drawings of adults of *Ruhnkebothrium* (specimen accession numbers in parentheses). A, scolex of *Ruhnkebothrium mattisi* (LRP no. 10295). B, whole worm of *Ru. mattisi* (LRP no. 10295). C, mature proglottid of *Ru. mattisi* (USNM no. 1638656). D, scolex of *Ruhnkebothrium bajaense* (CNHE no. 10662). E, mature proglottid of *Ru. bajaense* (CNHE no. 10662).

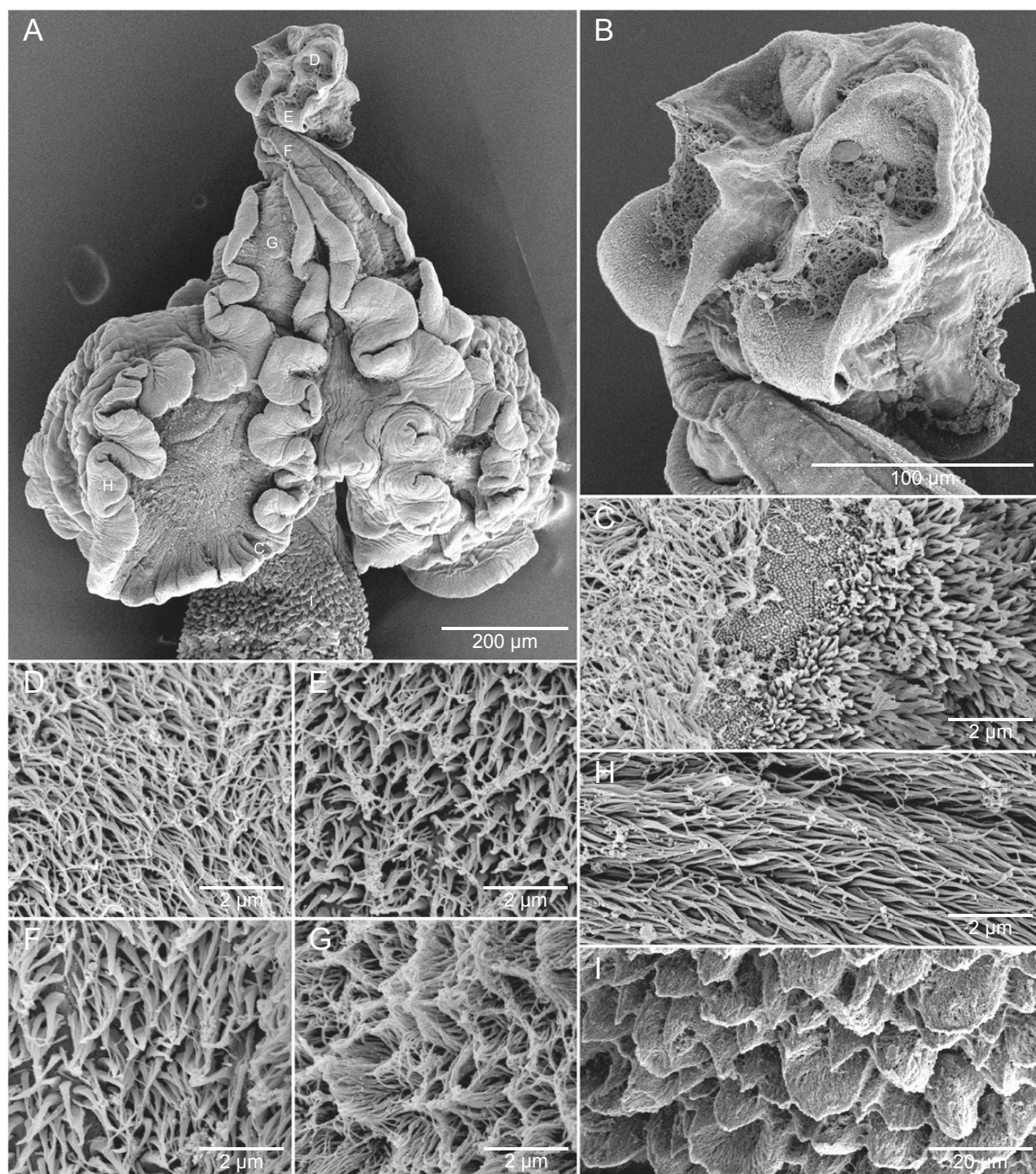


Figure 3. Scanning electron micrographs of *Ruhnkebothrium mattisi*. A, scolex. B, detail of anterior loculi. C, distal surface of rim of posterior loculus. D, distal surface of anterior loculus. E, distal surface of anterior-most region of posterior loculus adjacent to anterior loculus. F, distal surface of posterior loculus as it expands. G, distal surface of expanded region of posterior loculus. H, proximal surface of posterior loculus. I, scutes on surface of neck.

midline of proglottid to anterior margin of cirrus sac, then laterally along anterior margin of cirrus sac to open into common genital atrium anterior to cirrus. Ovary at posterior of proglottid, H-shaped in frontal view, 421–808 long, 737–810 wide, tetralobed in cross-section; ovarian margins digitiform. Vitellarium follicular; follicles somewhat irregular in shape, arranged in two lateral bands; each band consisting of multiple columns of follicles, extending throughout length of proglottid, interrupted dorsally and ventrally by terminal genitalia, not interrupted by ovary. Uterus medial, ventral, sacciform, extending from ovarian isthmus to cirrus sac; uterine duct entering uterus at mid-level. Excretory vessels 4, arranged in one dorsal and one ventral pair on each lateral margin of proglottid. Detached mature proglottids 2477 long, 1782 wide, length-to-width ratio 1.4:1; genital pore 63% of proglottid length from posterior end; testes 229 in total number, 66 in post-poral field, 77–93 (87 ± 7 ; 1; 4) long, 77–87 (82 ± 4 ; 1; 4) wide; cirrus sac 562 long, 124 wide; ovary 615–701 long, 578–606 wide. Detached gravid proglottids (two from same host) 3514–5395 long, 1773–2001 wide, length-to-width ratio 2.0–2.7:1; genital pore 51–60% of proglottid length from posterior end; testes degenerated; cirrus sac 627–740 long, 191–203 wide; ovary 766–807 long, 807–869 wide; oncospheres spherical, 22–26 (24 ± 1 ; 2; 8) long, 21–26 (25 ± 2 ; 2; 8) wide, too densely packed to assess whether packaged in cocoons. Detached dehiscent proglottids (four from three different hosts) 2938–3947 (3407 ± 416 ; 4) long, 1096–1394 (1228 ± 150 ; 4) wide, length-to-width ratio 2.5–3.1 (2.8 ± 0.2 ; 4):1; genital pore 50–53% (50 ± 2 ; 4) of proglottid length from posterior end; testes degenerated; cirrus sac 554–689 (623 ± 68 ; 3) long, 162–217 (194 ± 29 ; 3) wide; ovary 638–721 (690 ± 36 ; 4) long, 477–894 (689 ± 175 ; 4) wide.

Type host: *Sphyrna lewini* 1 of the scalloped hammerhead complex (*sensu* Naylor *et al.*, 2012) (Carcharhiniformes: Sphyrnidae).

Type locality: Gulf of Mexico off Pensacola, FL, USA (30°03'25.26"N, 87°00'13.01"W).

Additional localities: Gulf of Mexico off Horn Island, MS, USA (30°13'59.37"N, 88°40'10.79"W); Atlantic Ocean, FL, USA (28°00'18"N, 80°04'18"W).

Site of infection: Spiral intestine.

Type material: Holotype (mature worm, USNM no. 1638656), four paratype detached proglottids (one mature, USNM no. 1638657; one gravid, USNM no. 1638658; two dehiscent, USNM nos 1638659 and 1638660); two paratypes [one complete mature

worm, LRP no. 10295; one partial mature worm (hologenophore) LRP no. 8304]; three paratype detached proglottids (two gravid, LRP nos 10296 and 10297; one dehiscent, LRP no. 10298); two paratypes (immature worm SEM vouchers, LRP nos 10274 and 10299).

Sequence data: GenBank accession KF865889, hologenophore LRP no. 8304 (TE-86; DEL-6).

Etymology: This species is named after the late Dr Tom Mattis, not only for providing some of the type material, but also for his life-long interest in cestode taxonomy.

Provisional name: New genus 10 n. sp. 1 of Caira *et al.* (2014).

RUHNKEBOTHRIUM BAJAENSE SP. NOV.

(Figs 2D, E, 4)

ZooBank registration: B2A2E247-2A00-4599-AA76-ABA973D3349E.

Description: [Based on one whole mature worm, one partial mature worm (hologenophore), and two scolices examined with SEM.] Worms euapolytic, acraspedote, 31.7 mm long; proglottids 185 in total number; maximum width at level of terminal proglottid. Scolex consisting of four bothridia, 722 long, 749–858 wide. Bothridia consisting of small, simple anterior loculus (Fig. 4B) and expansive, highly folded posterior loculus (Figs 2D, 4A), 636–753 (695 ± 52 ; 2; 4) long, 366–391 (384 ± 10 ; 2; 5) wide, sessile anteriorly, free posteriorly; anterior loculus 43–50 ($N = 1$) long, 58–85 (73 ± 15 ; 2; 4) wide. Cephalic peduncle lacking. Neck 845 long. Distal surface of anterior loculus with extremely slender gladiate spinitriches and capilliform filitriches (Fig. 4D); distal surface of anterior, narrow portion of posterior loculus with slender gladiate spinitriches and capilliform filitriches (Fig. 4E, F); distal surface of posterior loculus with slender gladiate spinitriches and capilliform filitriches (Fig. 4G); capilliform filitriches becoming less dense near margins of distal surfaces of posterior loculus; rim of distal surface of posterior loculus with small band of papilliform filitriches only (Fig. 4C). Proximal bothridial surface near rim with cyrillionate spinitriches and capilliform filitriches (Fig. 4H), replaced by extremely slender gladiate spinitriches and capilliform filitriches away from rim. Neck (Fig. 4I) and strobila with capilliform filitriches arranged in wide, flat scutes. Immature proglottids wider than long, becoming longer than wide with maturity, 180 in number. Mature proglottids five in

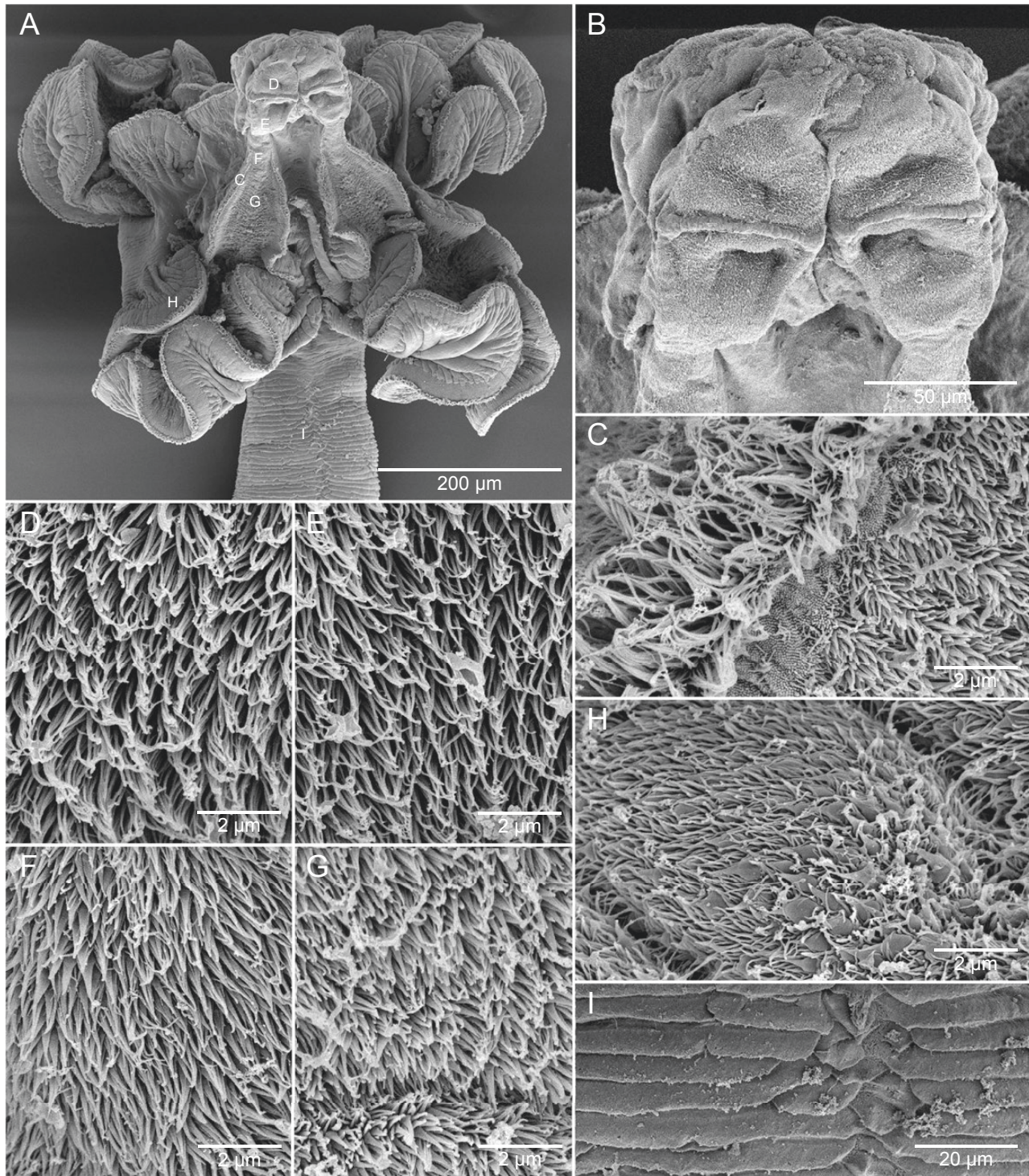


Figure 4. Scanning electron micrographs of *Ruhnkebothrium bajaense*. A, scolex. B, detail of anterior loculi. C, distal surface of rim of posterior loculus. D, distal surface of anterior loculus. E, distal surface of anterior-most region of posterior loculus adjacent to anterior loculus. F, distal surface of posterior loculus as it expands. G, distal surface of expanded region of posterior loculus. H, proximal surface of posterior loculus. I, scutes on surface of neck.

number. Terminal proglottid 1362 long, 760 wide; length-to-width ratio 1.8:1 (Fig. 2E). Testes 234–257 in total number, 49–53 in number in post-poral field, 31–49 (39 ± 8 ; 2; 8) long, 34–53 (43 ± 7 ; 2; 8) wide. Vas deferens minimal, coiled medial to cirrus sac. Cirrus sac narrowly oblong (*sensu* Clopton, 2004), slightly curved anteriorly, 311–388 long, 76–113 wide, thin walled, containing coiled cirrus; cirrus armed with spinitriches. Genital pores irregularly alternating, 47% of proglottid length from posterior end; genital atrium shallow. Vagina weakly sinuous, extending from ootype along midline of proglottid to anterior margin of cirrus sac, then laterally along anterior margin of cirrus sac to open into common genital atrium anterior to cirrus sac. Ovary at posterior of proglottid, H-shaped in frontal view, 273 long, 408 wide, tetralobed in cross-section; ovarian margins lobulate. Vitellarium follicular; follicles somewhat irregular in shape, arranged in two lateral bands; each band consisting of multiple columns of follicles, extending throughout length of proglottid, interrupted dorsally and ventrally by terminal genitalia, not interrupted by ovary. Uterus medial, ventral, sacciform, extending from ovarian isthmus to cirrus sac; uterine duct not observed. Excretory vessels 4, arranged in one dorsal and one ventral pair on each lateral margin of proglottid.

Type host: *Sphyrna lewini* 2 of the scalloped hammerhead complex (*sensu* Naylor *et al.*, 2012) (Carcharhiniformes: Sphyrnidae).

Type locality: Gulf of California off San Jose del Cabo, Baja California Sur, Mexico (23°02'45"N, 109°41'33"W).

Additional locality: Gulf of California off Loreto, Baja California Sur, Mexico (25°49'52"N, 111°19'38"W).

Site of infection: Spiral intestine.

Type material: Holotype (mature worm, CNHE no. 10662); one paratype (partial mature worm hologenophore, LRP no. 10278), two paratypes (immature worm SEM vouchers, LRP nos 10276 and 10277).

Sequence data: GenBank accession MW419962 (BJ-323; JW504), hologenophore LRP no. 10278.

Etymology: This species is named for its type locality in the waters off the Baja Peninsula in Mexico; the name also serves as a reminder that this species parasitizes the Pacific form of the scalloped hammerhead.

Remarks: This new species differs from its only known congener, *Ru. mattisi*, as follows. The genital

pore of *Ru. bajaense* is more posterior in position in the proglottid (47% vs. 62–68% from posterior end), and its bothridia are much less folded than those of *Ru. mattisi*. Furthermore, it possesses cyrillionate rather than slender gladiate spinitriches near the rims of its proximal bothridial surfaces, and the scutes of its neck and strobila are wide and flat (Fig. 4I), rather than narrow and convex (Fig. 3I).

YAMAGUTICESTUS GEN. NOV.

ZooBank registration: B380C792-EF6D-47B5-A28C-91AE303CE3F2.

Diagnosis: Worms euapolytic, apolytic or anapolytic, acraspedote or weakly craspedote. Scolex with four bothridia; cephalic peduncle and myzorhynchus lacking; neck present. Bothridia round to oval in form, with apical sucker and single, undivided loculus. Scolex spinitriches gongylate columnar or gladiate; filitriches capilliform. Neck and strobila scutellate. Immature proglottids wider than long; mature proglottids square or longer than wide. Testes numerous, extending throughout most of proglottid; post-ovarian field absent. Vas deferens minimal. Genital pores lateral, irregularly alternating; genital atrium shallow. Cirrus sac narrowly oblong or pyriform, containing coiled cirrus; cirrus armed with spinitriches. Vagina straight or weakly sinuous, extending from ootype along midline of proglottid to anterior margin of cirrus sac, then laterally to open into genital atrium anterior to cirrus; vaginal sphincter present or absent; seminal receptacle absent. Ovary terminal or subterminal, H-shaped in frontal view, tetralobed in cross-section; ovarian margins digitiform. Vitellarium follicular; follicles in two lateral bands; each band consisting of multiple columns of follicles, extending length of proglottid, can be interrupted ventrally by terminal genitalia, not interrupted by ovary. Uterus medial, ventral, sacciform, extending from ovarian isthmus to level of cirrus sac. Excretory vessels 4, arranged in one dorsal and one ventral pair on each lateral margin of proglottid. Parasites of catsharks (Scyliorhinidae Gill and Pentanchidae Smith) and small squaliform sharks. Cosmopolitan.

Type species: *Yamaguticestus metini* sp. nov.

Additional species: *Yamaguticestus longicollis* (Molin, 1858) comb. nov. and *Yamaguticestus squali* (Yamaguti, 1952) comb. nov.

Etymology: This genus honours Professor Satyu Yamaguti for his extensive contributions to cestode systematics,

which included description of the first member of this lineage known to parasitize a squaliform shark. *Cestus* is Latin for 'girdle'. The gender is masculine.

Provisional name: New genus 18 of [Ruhnke et al. \(2017\)](#).

Remarks: *Yamaguticestus* differs from the 19 valid genera of the Phyllobothriidea (i.e. including *Ruhnkebothrium*) as follows. Its possession of bothridia that lack facial and marginal loculi distinguishes it from *Cardiobothrium*, *Chimaerocestos* Williams & Bray, 1984 and *Trilocularia* Olsson, 1867. It differs from *Thysanocephalum* and *Ruhnkebothrium* in that its bothridia are flat and oval, rather than triangular and highly folded. Its flat, oval bothridia also distinguish it from *Alexandercestus* Ruhnke & Workman, 2013, *Bibursibothrium*, *Clistobothrium* Dailey & Vogelbein, 1990, *Flexibothrium*, *Guidus* Ivanov, 2006, *Hemipristicola* Cutmore, Theiss, Bennett & Cribb, 2011 and *Phyllobothrium* Van Beneden, 1850, which bear bothridia that are stalked, highly folded, recurved anteriorly to form open grooves, bear a deep central cavity or are pouch-like in form. *Yamaguticestus* differs from *Orygmatobothrium* Diesing, 1863 in that its bothridia lack, rather than bear, a unique central glandulomuscular organ. Unlike those of *Monorygma* Diesing, 1863 and *Pelichnobothrium* Monticelli, 1889, the vitelline follicles of *Yamaguticestus* are arranged in two lateral fields, rather than in a circumcortical band. The new genus differs from *Bilocularia* Obersteiner, 1914 in its possession of a testicular field that extends to the anterior margin of the ovary in post-poral and anti-poral regions, rather than being limited to the region anterior to the cirrus sac. It differs from *Calyptrbothrium* Monticelli, 1893 in possessing, rather than lacking, a post-poral field of testes. Unlike *Crossobothrium* Linton, 1889, the proglottids of *Yamaguticestus* bear, rather than lack, posterior laciniations. This new genus most closely resembles *Scyphophyllidium* Woodland, 1927 but differs in its possession of an ovary with digitiform, rather than lobulated, margins and a uterus that occupies no more than half the length of the mature proglottid, rather than extending two-thirds or more of the length of the proglottid.

YAMAGUTICESTUS SQUALI (YAMAGUTI, 1952)

COMB. NOV.

BASIONYM: *PHYLLOBOTHRIMUM SQUALI* YAMAGUTI, 1952

(FIG. 5A–E)

The following details of the surface features on the scolex of this species, based on examination of a specimen with SEM collected from the type host near the type locality, expand the original description of this species by [Yamaguti \(1952\)](#) and the redescription

based on the holotype by [Vasileva et al. \(2002\)](#).

Anterior-most regions of bothridia densely covered with capilliform filitriches (Fig. 5B). Distal surfaces of loculus densely covered with gongylate columnar spinitriches and capilliform spinitriches (Fig. 5C); distal surfaces of apical sucker not observed. Proximal bothridial surfaces densely covered with capilliform filitriches (Fig. 5D). Cephalic peduncle lacking. Neck (Fig. 5E) and strobila with capilliform filitriches arranged in wide scutes.

Synonyms: *Phyllobothrium squali* Yamaguti, 1952; *Crossobothrium squali* (Yamaguti, 1952) Williams, 1968.

Type host: Pacific spiny dogfish, *Squalus suckleyi* (Girard, 1855), (Squaliformes: Squalidae de Blainville).

Additional hosts: None.

Type locality: Pacific Ocean, off Onahama, Hukusima Prefecture, Japan.

Additional localities: Sea of Japan, off Oga City, Akita Prefecture, Japan (39°46'55.8"N, 139°51'49.2"E) (JN-67); eastern Pacific Ocean, off Bamfield, Vancouver Island, Canada (48°50'7.9152"N, 125°08'7.7208"W).

Site of infection: Spiral intestine.

Material examined: One specimen examined with SEM collected from a shark collected off the west coast of Japan.

Sequence data: GenBank accession MW419975, hologenophore (BAM5-wP9) LRP no. 8674.

Remarks: By erecting the genus *Yamaguticestus*, we have established a more appropriate home for the species formerly referred to as *Phyllobothrium squali*. The transfer of this species from *Phyllobothrium*, as *Yamaguticestus squali*, resolves the issue of the non-monophyly of *Phyllobothrium* that has been raised by a number of previous authors (e.g. [Ruhnke, 2011](#); [Caira et al., 2014](#)). However, issues surrounding the identity of *Y. squali* remain. It was originally described by [Yamaguti \(1952\)](#) from a host identified as the Pacific spiny dogfish (*Squalus suckleyi* as *Squalus suckleyii*) off the eastern coast of Japan. [Vasileva et al. \(2002\)](#) subsequently provided a thorough redescription of this species based on examination of the holotype, in which they included illustrations of the scolex and details of the terminal genitalia for the first time. However, this species has also been reported from sharks identified as the piked dogfish (*Squalus acanthias*) from a variety of other localities globally, including the north-eastern Atlantic Ocean

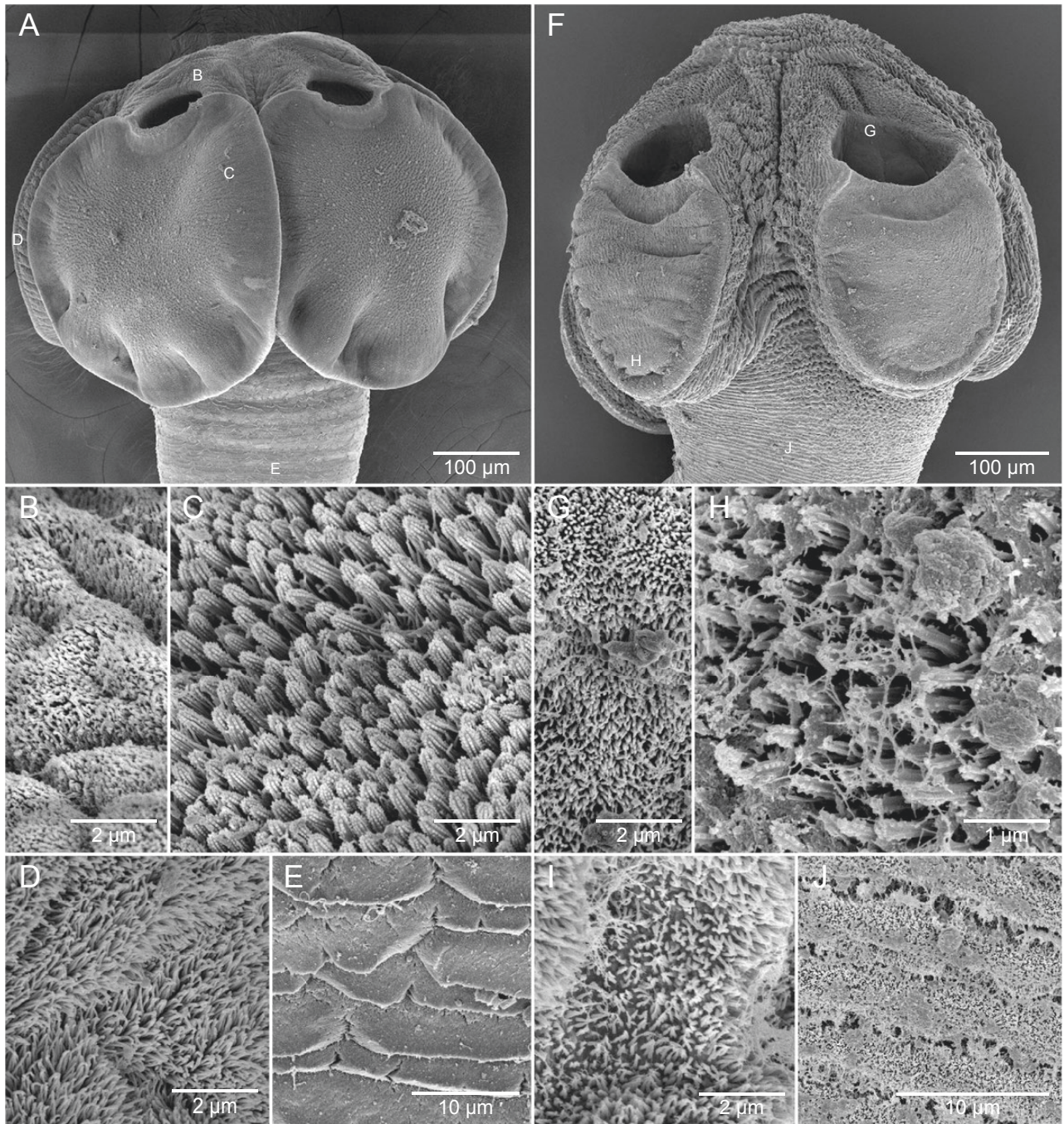


Figure 5. Scanning electron micrographs of *Yamaguticestus*. A, scolex of *Yamaguticestus squali*. B, surface of bothridium of *Y. squali* anterior to apical sucker. C, distal surface of bothridium of *Y. squali*. D, proximal surface of bothridium of *Y. squali*. E, scutes on surface of neck of *Y. squali*. F, scolex of *Yamaguticestus metini*. G, surface of apical sucker of *Y. metini*. H, distal surface of bothridium of *Y. metini*. I, proximal surface of bothridium of *Y. metini*. J, scutes on surface of neck of *Y. metini*.

in the Bay of Biscay off Concarneau, France (Euzet, 1959) and the Irish Sea (McCullough & Fairweather, 1983; McCullough *et al.*, 1986), the western Atlantic Ocean off Rhode Island, USA (Pickering & Cairá, 2012; Ruhnke & Workman, 2013; Cairá *et al.*, 2014) and the

Black Sea (Vasileva *et al.*, 2002). Given the relatively strict degree of host specificity seen in most groups of elasmobranch-hosted cestodes (Cairá & Jensen, 2014), reports from two different host species would normally have warranted closer scrutiny. However,

the situation was confounded by the fact that *Squalus suckleyi* has been considered a junior synonym of *Squalus acanthias* for decades (see [Compagno, 1984](#)), and this synonymy has been embraced by many of those working with *P. squali* previously. For example, [Vasileva et al. \(2002\)](#) listed *Squalus acanthias* as the type host of *P. squali*, and [Pickering & Caira \(2012\)](#) referred to the cestodes of *Squalus acanthias* off Rhode Island as *P. squali* because *Squalus acanthias* was the accepted identity of the type host of this cestode species at that time. The relatively recent application of molecular methods to help inform elasmobranch identifications has led to a more careful assessment of the identities and distributions of species of *Squalus* Linnaeus, 1758 globally ([Ebert et al., 2010](#)). One of the results of that work was the resurrection of the name *Squalus suckleyi* for the species that occurs in the northern Pacific Ocean and is both molecularly and morphologically distinct from *Squalus acanthias*, which is now considered to be restricted to the Atlantic Ocean and the southern portions of the Pacific Ocean.

This revised host taxonomy has profound implications for the taxonomy of *P. squali*. The type host of *P. squali* is *Squalus suckleyi*, but the shark specimens reported to host this cestode species off Rhode Island, France and Ireland and in the Mediterranean and Black Seas are *Squalus acanthias*. This causes us to revisit the question of the conspecificity of the cestodes reported from *Squalus suckleyi* and *Squalus acanthias*. Although [Vasileva et al. \(2002\)](#) found their worms from the Black Sea (and thus from *Squalus acanthias*) generally to be consistent with the morphology of the holotype of *P. squali* (from *Squalus suckleyi*), they reported the worms from the Black Sea to be substantially larger than the holotype from *Squalus suckleyi* off Japan (i.e. 214–603 vs. 141 mm). Also interesting is the fact that the bothridia of the worm identified as *P. squali* taken from *Squalus acanthias* in the Irish Sea and examined with SEM by McCullough & Fairweather (1983: fig. 9) are more folded than those of the specimen of *P. squali* from *Squalus suckleyi* off Japan examined here ([Fig. 5A](#)). These differences led us to begin to question the conspecificity of material from these two host species and thus to advocate that the concept of *P. squali* be limited to information taken from specimens parasitizing *Squalus suckleyi* in the northern Pacific Ocean. More detailed comparisons between that material and specimens collected from *Squalus acanthias* in localities throughout the Atlantic Ocean and its adjacent water bodies are required to assess whether specimens from the two host species and their associated localities are conspecific. Until that time, specimens from *Squalus acanthias*, including those of [Ruhnke & Workman \(2013\)](#) and [Caira et al. \(2014\)](#) for which sequence data were generated, should be referred to as *Yamaguticestus* cf. *squali*.

As noted by [Vasileva et al. \(2002\)](#), the material from the velvet belly shark *Etmopterus spinax* (Linnaeus, 1758), which [Euzet \(1959\)](#) identified as *Crossobothrium squali*, differs from *Y. squali* in a number of respects. We believe this material is likely to represent an undescribed species of *Yamaguticestus*, the formal description of which requires examination of additional material.

YAMAGUTICESTUS LONGICOLLIS (MOLIN, 1858) COMB. NOV.

BASIONYM: *TETRABOTHRUM LONGICOLLIS* MOLIN, 1858, AS '*LONGICOLLE*'

A detailed account of the taxonomic history of *Y. longicollis* was provided by [Ruhnke \(2011\)](#) in his monograph on the Phyllobothriidae. Given the lack of figures and the brevity of the original description by Molin (1858), [Ruhnke \(2011\)](#) discussed the redescription and associated specimens of [Euzet \(1959\)](#) from the type host, *Scyliorhinus stellaris* (Linnaeus, 1758), and included photomicrographs of one of Euzet's specimens (MNHN HEL 138). In that work, [Ruhnke \(2011\)](#) treated this species as *incertae sedis* under the name *Crossobothrium longicolle* (Molin, 1858) Euzet, 1959, noting that, although it failed to conform to the diagnosis of *Crossobothrium* and in fact resembled *P. squali*, a more appropriate generic home was unavailable at that time. This species as redescribed by [Euzet \(1959\)](#) and characterized by [Ruhnke \(2011\)](#) is fully consistent with the concept of *Yamaguticestus* advanced here. We hereby transfer this species to the new genus as *Yamaguticestus longicollis*. It differs conspicuously from *Y. squali* in its possession of a smaller scolex that is much longer than wide (600–800 by 300–400 vs. 2900 in diameter).

Our results help to resolve a puzzling issue surrounding the identity of a specimen collected from the catshark *Scyliorhinus canicula* off the UK, for which sequence data for the D1–D3 region of the 28S rDNA gene (AF286958; LRP no. 2113) were generated by [Olson et al. \(2001\)](#). These authors referred to this specimen as *Crossobothrium longicolle*. However, [Ruhnke & Workman \(2013\)](#) found this specimen to be morphologically consistent with, and identical in sequence to, a specimen they identified as *Phyllobothrium squali* (KC543441; LRP no. 7967) collected from the dogfish *Squalus acanthias* off Rhode Island. In the absence of reports of *Y. squali* or any of its relatives from catsharks, [Ruhnke & Workman \(2013\)](#) suggested that this cestode and the host from which it came might have been misidentified by [Olson et al. \(2001\)](#). In the tree resulting from our analysis, [Olson et al.'s \(2001\)](#) specimen of '*Crossobothrium longicolle*' groups

robustly among species of *Yamaguticestus*, members of which we now know can be hosted by either squaliform sharks or catsharks. This suggests that the original identification of the host of this specimen as *Scyliorhinus canicula* was probably correct. However, the specific identity of this specimen as '*C. longicollis*' is doubtful given that the type host of *Y. longicollis* is *Scyliorhinus stellaris*. The fact that the sequences are identical is insufficient to reject this hypothesis given the low amount of sequence divergence seen among members of this genus in this region of the 28S rDNA gene. As a consequence, we believe this species is likely to represent an undescribed member of the genus, the description of which will require examination of additional material.

***YAMAGUTICESTUS METINI* SP. NOV.**

(FIGS 5F–J, 6)

ZooBank registration: 54904E20-1BBD-4F54-AE02-EA093DE8E5DE.

Description: (Based on one whole mature worm, one partial mature worm, one immature worm, two detached mature proglottids, two detached gravid proglottids, four detached dehiscent proglottids, and one scolex examined with SEM.) Worms euapolytic, acraspedote, 80 mm long; proglottids 400 in total number; maximum width at level of mature proglottids. Scolex consisting of four bothridia, 472–596 long, 529–704 wide. Bothridia oval, with apical sucker and single, undivided locus (Figs 5F, 6A), 409–435 (478 ± 60 ; 2; 4) long, 280–315 (302 ± 15 ; 2; 4) wide, sessile anteriorly, free posteriorly; apical sucker 201–281 (231 ± 28 ; 3; 8) long, 176–253 (224 ± 27 ; 3; 6) wide; apical sucker length as percentage of bothridial length 46–57% (50 ± 4 ; 3; 6). Cephalic peduncle lacking. Neck 1016 long. Distal surface of apical sucker (Fig. 5G) and anterior-most regions of locus densely covered with acicular filitriches; distal surface of remainder of locus densely covered with gongylate columnar spinitriches and capiliform filitriches (Fig. 5H). Proximal bothridial surface densely covered with acicular filitriches (Fig. 5I). Neck and strobila with capilliform filitriches arranged in wide scutes (Fig. 5J). Immature proglottids wider than long, becoming longer than wide with maturity (Fig. 6B), 397 in number. Mature proglottids three in number. Terminal proglottid 2138 long, 1567 wide; length-to-width ratio 1.4:1 (Fig. 6C). Testes 158–184 in total number, 13–20 in number in post-poral field, 30–42 (34 ± 4 ; 2; 8) long, 33–50 (42 ± 6 ; 2; 8) wide. Vas deferens minimal, coiled medial to cirrus sac. Cirrus sac narrowly oblong (*sensu* Clopton, 2004), 451 long, 79 wide, thin walled,

containing weakly coiled cirrus (Fig. 6E); cirrus armed with spinitriches. Genital pores irregularly alternating, 73% of proglottid length from posterior end; genital atrium shallow. Vagina surrounded by glandular cells, weakly sinuous, extending from ootype along midline of proglottid to anterior margin of cirrus sac, then laterally along anterior margin of cirrus sac to open into common genital atrium anterior to cirrus sac. Ovary subterminal in position, H-shaped in frontal view, 577 long, 554 wide, tetralobed in cross-section; ovarian margins strongly digitiform (Fig. 6D). Vitellarium follicular; follicles irregular in shape, arranged in two lateral bands; each band consisting of multiple columns of follicles, extending throughout length of proglottid, interrupted ventrally by terminal genitalia, not interrupted by ovary. Uterus medial, ventral, sacciform, extending from ovarian isthmus to cirrus sac; uterine duct entering uterus at mid-level. Excretory vessels 4, arranged in one dorsal and one ventral pair on each lateral margin of proglottid. Detached mature proglottids (two, each from different host) 1977–2814 long, 1521–2019 wide, length-to-width ratio 1.3–1.4:1; genital pore 67–68% of proglottid length from posterior end; testes 169–186 in total number, 17 in post-poral field, 29–43 (36 ± 4 ; 2; 8) long, 37–60 (49 ± 8 ; 2; 8) wide; cirrus sac 389–417 long, 68–84 wide; ovary 435–591 long, 578–606 wide. Detached gravid proglottids (two from same host) 4065–5318 long, 1781–3097 wide, length-to-width ratio 1.7–2.3:1; genital pore 57–58% of proglottid length from posterior end; testes 187–203 in total number, 22–24 in post-poral field, 45–57 (50 ± 5 ; 2; 8) long, 61–72 (67 ± 4 ; 2; 8) wide; cirrus sac 422–429 long, 87–92 wide; ovary 652–938 long, 615–711 wide; oncospheres spherical, 23–26 (24 ± 1 ; 2; 8) long, 20–25 (23 ± 2 ; 2; 8) wide, too densely packed to assess whether packaged in cocoons. Detached dehiscent proglottids (four from same host) 6145–8028 (6971 ± 882 ; 4) long, 1974–2552 (2269 ± 236 ; 4) wide, length-to-width ratio 1.8–2.2 (2 ± 0.2 ; 4):1; genital pore 45–56% (50 ± 5 ; 4) of proglottid length from posterior end; testes 159–172 (167 ± 7 ; 3) in total number, seven to 14 in post-poral field, 54–104 (81 ± 14 ; 4; 16) long, 70–104 (82 ± 9 ; 4; 16) wide; cirrus sac 499–586 (540 ± 37 ; 4) long, 85–129 (109 ± 18 ; 4) wide; ovary 827–1323 (1045 ± 218 ; 4) long, 749–1092 (866 ± 154 ; 4) wide.

Type host: Tiger catshark, *Haelaelurus natalensis* (Regan, 1904) (Carcharhiniformes: Pentanchidae).

Type locality: Indian Ocean off South Africa (33°47'40.2"S, 26°05'7.2"E).

Additional localities: Indian Ocean off South Africa (33°59'24"S, 25°12'1.2"E; 34°10'7.2"S, 24°54'55.2"E).

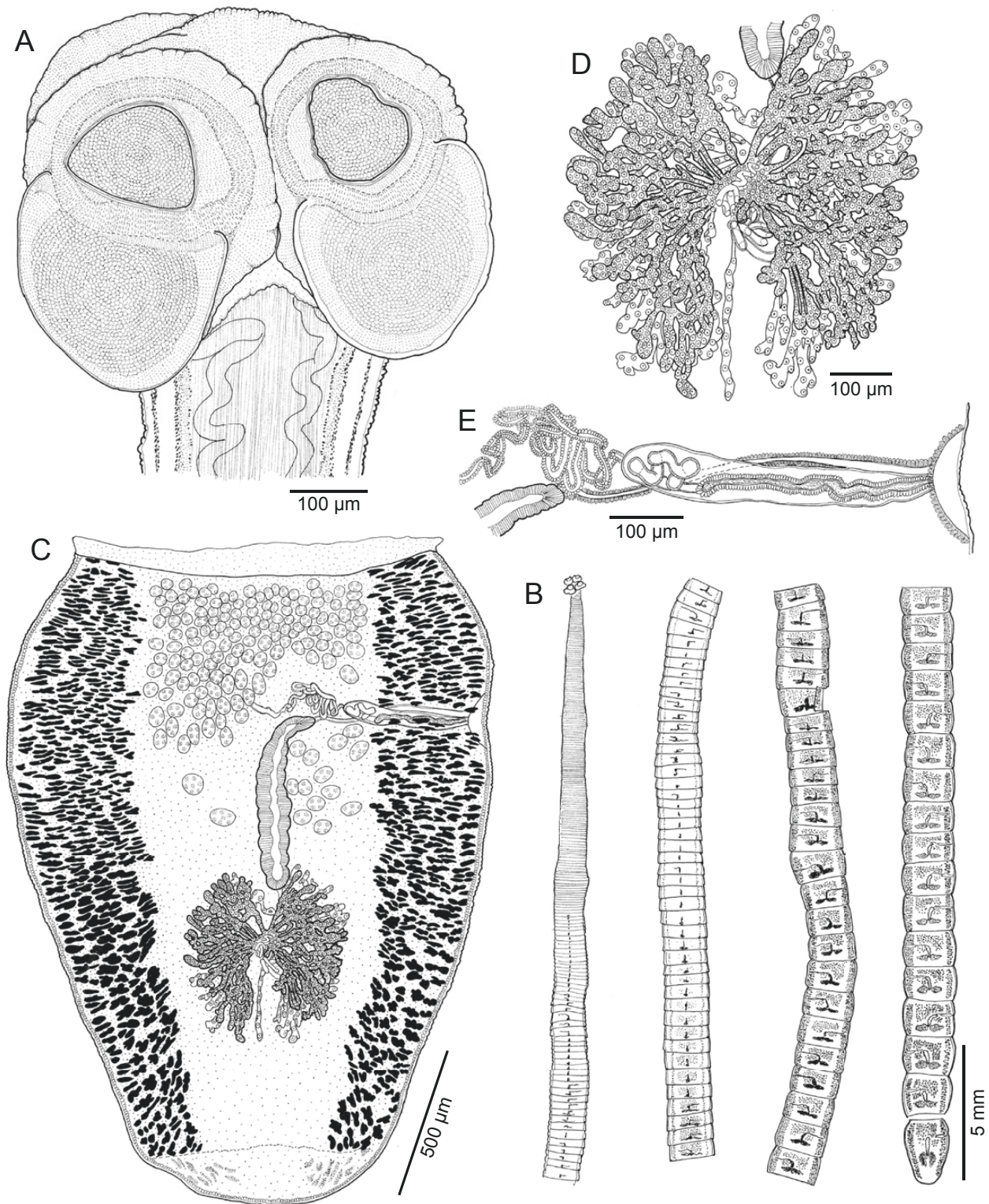


Figure 6. Line drawings of adult of *Yamaguticestus metini* (specimen accession numbers in parentheses). A, scolex (NMB P no. 734). B, whole worm (USNM no. 1638648). C, mature proglottid (USNM no. 1638648). D, detail of ovary (USNM no. 1638648). E, detail of terminal genitalia (USNM no. 1638648).

Site of infection: Spiral intestine.

Type material: Holotype [mature worm (on three slides), NMB P no. 734], two paratype detached proglottids (both dehiscent, NMB P nos 735 and 736); one paratype (mature worm, USNM no. 1638648), three paratype detached proglottids (one mature, USNM no. 1638649; one gravid, USNM no. 1638650; one dehiscent, USNM no. 1638651); one paratype (immature worm, LRP no. 10288), five paratype detached proglottids (one mature, LRP no. 10289; one gravid, LRP no. 10290; three dehiscent, LRP nos 10291, 10331, and 10332), one paratype (immature worm SEM voucher, LRP no. 10292).

Sequence data: GenBank accession MW419963, hologenophore (AF-179; JW423) LRP no. 10326.

Etymology: This species is named for Dr Metin Coşgel, Professor of Economics at the University of Connecticut, in recognition of his dedication, advocacy and enthusiasm for ecology and evolutionary biology as interim Head of the Department of Ecology & Evolutionary Biology.

Remarks: *Yamaguticestus* differs from both *Y. squali* and *Y. longicollis* in the remarkably large size of its apical sucker, which, rather than being restricted to the anterior margin of the bothridium as in *Y. longicollis* and *Y. squali* as redescribed by [Euzet \(1959\)](#) and [Vasileva et al. \(2002\)](#), occupies nearly half of the length of the bothridium. Furthermore, unlike both previously described species, the ovary of *Y. metini* is subterminal, rather than terminal, in position in the proglottid.

ROKACESTUS GEN. NOV.

ZooBank registration: E44B4965-FD5A-4B87-8813-AA9CE2244938.

Diagnosis: Worms euapolytic, acraspedote or craspedote. Scolex with four bothridia; cephalic peduncle and myzorhynchus lacking; neck present. Bothridia moderately to highly folded, with apical sucker and marginal loculi. Scolex spinitriches gladiate; filitriches papilliform or acicular. Neck and strobila scutellate. Immature proglottids wider than long; mature proglottids longer than wide. Testes numerous, extending throughout most of proglottid; post-ovarian field of testes absent. Vas deferens minimal or extensive. Genital pores lateral, irregularly alternating; genital atrium shallow. Cirrus sac pyriform to elongate oval, containing coiled

cirrus; cirrus armed with spinitriches. Vagina weakly sinuous, extending from ootype along midline of proglottid to anterior margin of cirrus sac, following anterior margin of cirrus to open into genital atrium anterior to cirrus; vaginal sphincter present or absent; seminal receptacle absent. Ovary terminal to subterminal in proglottid, H-shaped in frontal view, tetralobed in cross-section; ovarian margins lobulated or rarely digitiform. Vitellarium follicular; follicles in two extensive lateral bands usually converging on midline in mature proglottids; each band consisting of multiple columns of follicles, extending length of proglottid, interrupted or not by terminal genitalia; uninterrupted by ovary. Uterus medial, ventral, sacciform, extending from ovarian isthmus to cirrus sac. Excretory vessels 4, arranged in one dorsal and one ventral pair on each lateral margin of proglottid. Parasites of skates (Rajiformes). Cosmopolitan.

Type species: *Rockacestus carvajali* sp. nov.

Additional species: *Rockacestus arctowskii* (Wojciechowska, 1991) comb. nov., *Rockacestus brittanicus* (Williams, 1968) comb. nov., *Rockacestus conchali* sp. nov., *Rockacestus georgiensis* (Wojciechowska, 1991) comb. nov., *Rockacestus piriei* (Williams, 1968) comb. nov., *Rockacestus radioductus* (Kay, 1942) comb. nov., *Rockacestus rakusai* (Wojciechowska, 1991) comb. nov., *Rockacestus siedleckii* (Wojciechowska, 1991) comb. nov. and *Rockacestus williamsi* (Schmidt, 1986) comb. nov.

Provisional species: *Rockacestus* sp. nov. 4 ex *Dipturus batis*; *Rockacestus* sp. nov. 5 ex *Amblyraja doellojuradoi*; *Rockacestus* sp. nov. 6 ex *Dipturus lamillai*.

Etymology: The name *Rajicestus* Rocka & Laskowski, 2017 was originally established for cestodes from skates with the features of this genus. Unfortunately, Rocka & Laskowski in [Rocka \(2017\)](#) neither provided text differentiating the genus nor designated a type species and thus, based on the International Code of Zoological Nomenclature ([ICZN, 1999](#); Articles 13.1 and 13.3), the name *Rajicestus* is unavailable. The name *Rockacestus* honours both Dr Anna Rocka's earlier work on the cestodes of skates and the fact that she and her colleague were the first to recognize the distinctive nature of these skate cestodes. *Cestus* is Latin for 'girdle'. The gender is masculine.

Provisional name: New genus 20 of [Ruhnke et al. \(2017\)](#) and [Bueno \(2018\)](#).

Remarks: *Rockacestus* differs conspicuously from all but four of the 20 valid genera of phyllobothriideans

(i.e. including *Ruhnkebothrium* and *Yamaguticestus*) in its possession of marginal loculi on its bothridia. With respect to the four other genera with marginal loculi, it differs from *Cardiobothrium* in lacking, rather than possessing, distinct facial loculi. Unlike *Chimaerocestos*, the vitelline follicles of *Rockacestus* are distributed throughout the length of the proglottid, rather than being restricted to the posterior regions of the proglottid. It is readily distinguished from *Crossobothrium* in that its proglottids lack laciniations, and its neck and strobila bear, rather than lack, scutes. *Rockacestus* differs from the subset of species of *Scyphophyllidium* with marginal loculi in that its bothridia are moderately to highly folded, rather than essentially flat, and in that the spinitriches on its scolex are simple gladiate rather than serrate gladiate or gongylate columnar.

Beyond providing an appropriate generic home for the two new species described here, erection of this genus provides an appropriate generic placement for all eight species of *Phyllobothrium* from skates considered *incertae sedis* by Ruhnke *et al.* (2017) in the most recent revision of the Phyllobothriidea, and we hereby transfer these eight species to *Rockacestus*. These species parasitize a variety of skate taxa. Wojciechowska (1991) described *Ro. arctowskii*, *Ro. georgiensis*, *Ro. rakusai* and *Ro. siedleckii* from *Bathyraja* sp. 2, *Amblyraja georgiana* (Norman, 1938), *Bathyraja maccaini* Springer, 1971 and *Bathyraja eatonii* (Günther, 1876), respectively. Williams (1968) described *Ro. brittanicus*, *Ro. piriei* and *Ro. williamsi* (as *Phyllobothrium minutum* Williams, 1968) from *Raja montagui* Fowler, 1910, *Leucoraja naevus* (Müller & Henle, 1841) (as *Raja naevus*) and *Leucoraja fullonica* (Linnaeus, 1758) (as *Raja fullonica*), respectively. *Rockacestus radioductus* was described from *Beringraja binoculara* (Girard, 1855) (as *Raja binoculara*) by Kay (1942). Sequence data were generated here for three additional, putatively novel species of *Rockacestus*, which we have referred to provisionally as *Rockacestus* sp. nov. 4, *Rockacestus* sp. nov. 5 and *Rockacestus* sp. nov. 6.

ROKACESTUS CARVAJALI SP. NOV.

(Figs 7, 8A–E)

ZooBank registration: C1BE31F7-1E16-4A24-920B-E42B5796066E.

Description (Based on two whole mature worms, three whole immature worms, and three scolices examined with SEM.) Worms euapolytic, craspedote, 13.1–14.5 mm long; proglottids 75–81 in total number; maximum width at level of scolex. Scolex consisting

of four bothridia, 546–903 (774 ± 165 ; 4) long, 900–1146 (1049 ± 104 ; 5) wide. Bothridia folded (Figs 7A, 8A), with apical sucker and single loculus, 406–648 (509 ± 104 ; 4; 7) long, 378–753 (552 ± 134 ; 4; 7) wide when folded, sessile anteriorly, free posteriorly; loculus with marginal loculi and posterior depression bounded by circular band of muscle fibres (Fig. 7B); apical sucker 84–155 (118 ± 21 ; 5; 15) long, 85–154 (116 ± 21 ; 5; 16) wide; posterior depression 126–214 (156 ± 36 ; 3; 7) long, 132–199 (165 ± 30 ; 3; 7) wide. Cephalic peduncle lacking. Neck 5.2–6.7 mm long. Distal surface of apical sucker and anterior portions of loculus with papilliform filitriches (Fig. 8B); distal surface of posterior depression with lingulate spinitriches and papilliform filitriches (Fig. 8C). Proximal bothridial surface with papilliform filitriches (Fig. 8D). Neck (Fig. 8E) and strobila with capilliform filitriches arranged in wide scutes. Immature proglottids wider than long, becoming longer than wide with maturity, 71–76 in number (Fig. 7C). Mature proglottids wider than long (Fig. 7D), becoming longer than wide posteriorly (Fig. 7E), four or five in number. Terminal proglottid 1143–1424 long, 537–540 wide, length-to-width ratio 2.1–2.6:1. Testes 46–55 (50 ± 4 ; 4; 4) in total number, nine to 12 (10 ± 1 ; 4; 4) in number in post-poral field, 38–53 (47 ± 5 ; 2; 6) long, 64–83 (74 ± 8 ; 2; 6) wide. Vas deferens coiled medial to cirrus sac. Cirrus sac oval, 302 long, 132 wide, thin walled, containing coiled cirrus; cirrus armed with spinitriches. Genital pores irregularly alternating, 73–79% of proglottid length from posterior end; genital atrium shallow. Vagina weakly sinuous, extending from ootype along midline of proglottid to anterior margin of cirrus sac, then laterally along anterior margin of cirrus sac to open into common genital atrium anterior to cirrus. Ovary at or near posterior margin of proglottid, H-shaped in frontal view, 344–406 long, 182–252 (217 ± 50 ; 4) wide, tetralobed in cross-section; ovarian margins lobulate. Vitellarium follicular; follicles arranged in two lateral bands that converge medially; each band consisting of multiple columns of follicles, extending throughout length of proglottid, partly or fully interrupted by terminal genitalia, uninterrupted by ovary; follicles highly variable in form. Excretory vessels 4, arranged in one dorsal and one ventral pair on each lateral margin of proglottid. Gravid proglottids not observed.

Type host: Yellownose skate, *Dipturus chilensis* (Guichenot, 1848) (Rajiformes: Rajidae de Blainville).

Type locality: Pacific Ocean off Puñihuil on the island of Chiloé, Chile (41°55'43"S, 74°02'16"W).

Additional locality: Pacific Ocean off Niebla, Los Rios, Chile (39°51'S, 73°24'W).

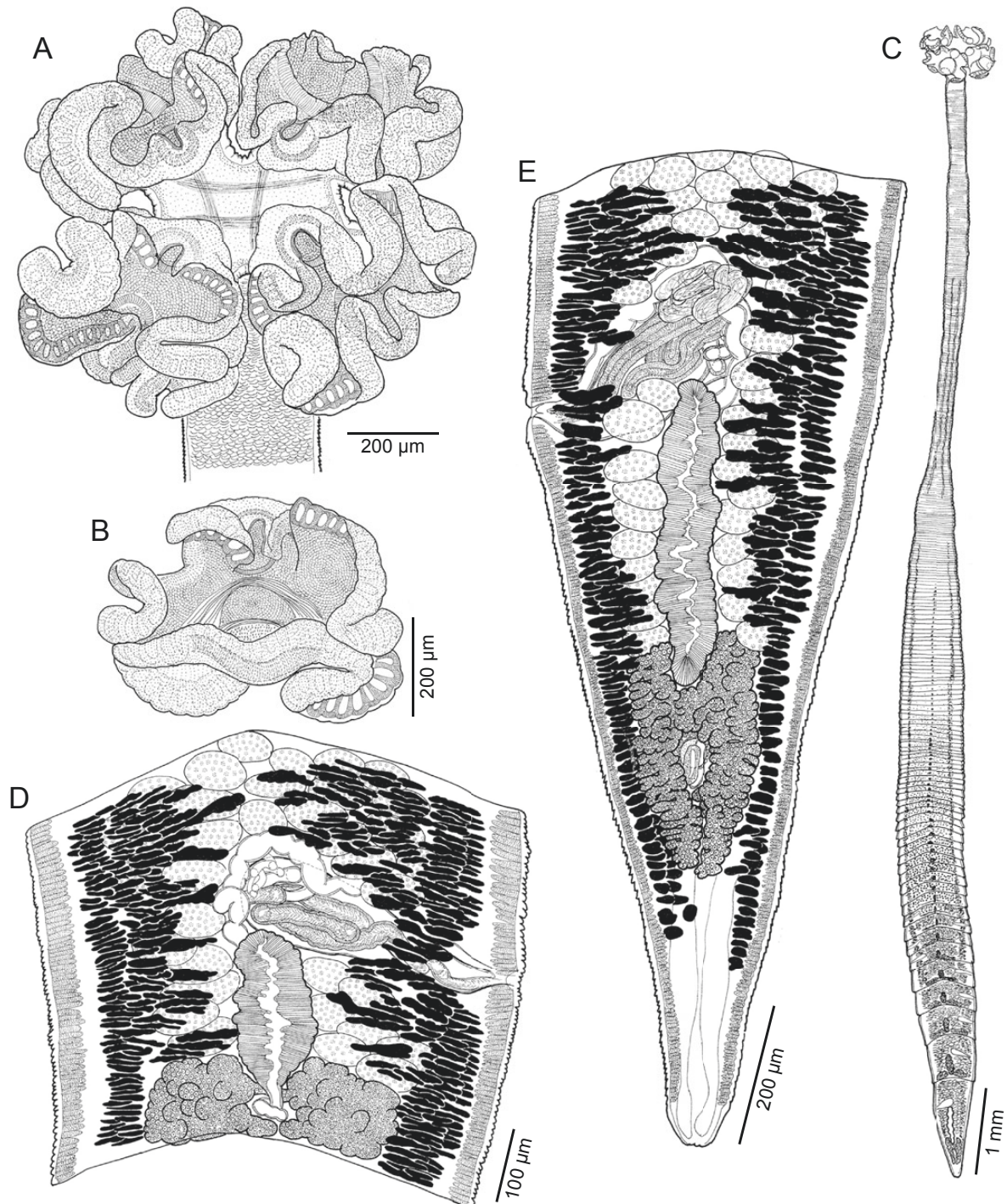


Figure 7. Line drawings of adult of *Rockacestus carvajali* (specimen accession numbers in parentheses). A, scolex (LRP no. 9770). B, detail of single bothridium (MNHNCL no. PLAT-15023). C, whole worm (MNHNCL no. PLAT-15023). D, subterminal mature proglottid (MNHNCL no. PLAT-15023). E, terminal mature proglottid (MNHNCL no. PLAT-15023).

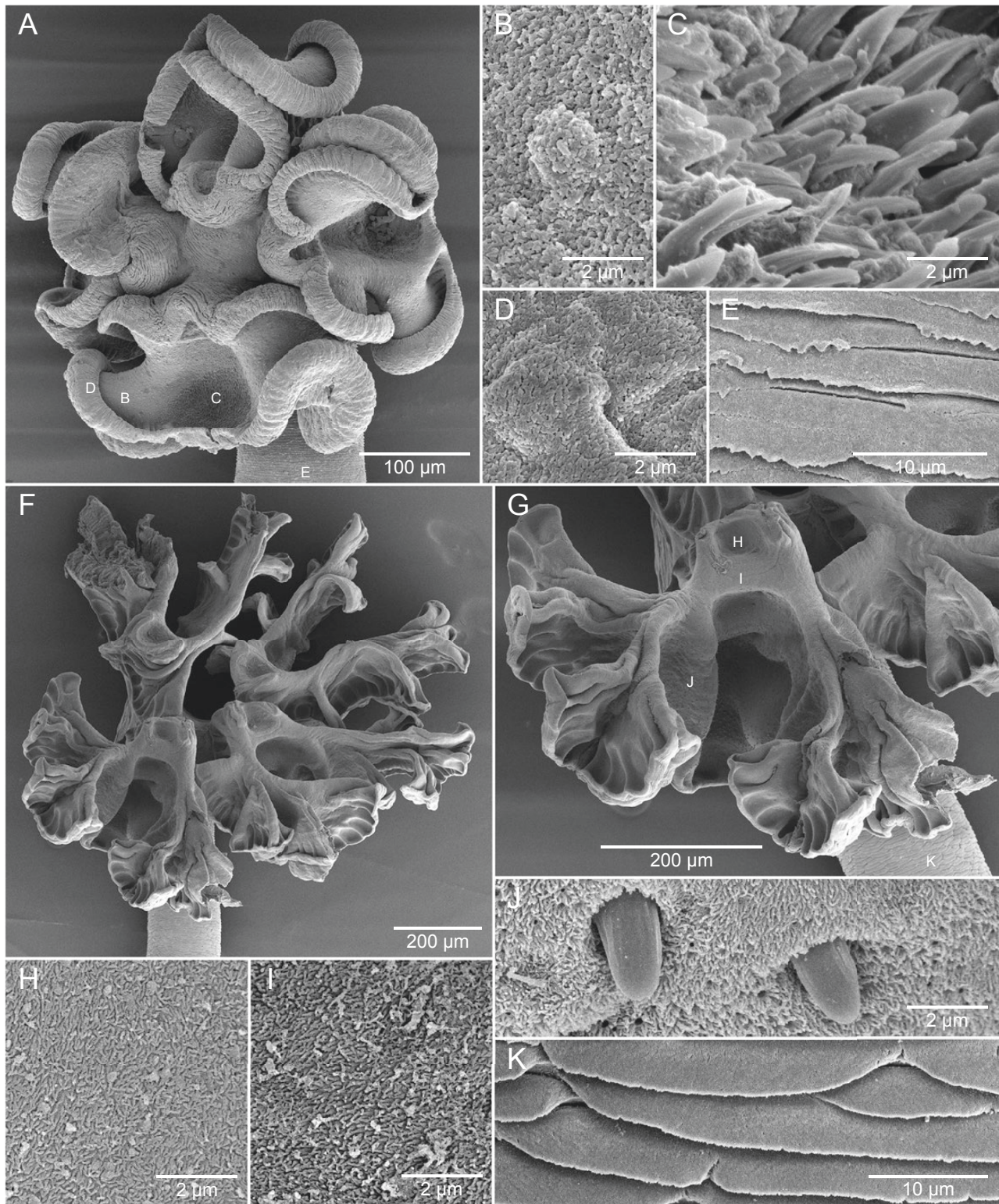


Figure 8. Scanning electron micrographs of *Rockacestus*. A, scolex of *Rockacestus carvajali*. B, distal surface of bothridium of *Ro. carvajali*. C, distal surface of posterior depression of bothridium of *Ro. carvajali*. D, proximal surface of bothridium of *Ro. carvajali*. E, scutes on surface of neck of *Ro. carvajali*. F, scolex of *Rockacestus conchai*. G, bothridium of *Ro. conchai*. H, distal surface of apical sucker of *Ro. conchai*. I, distal surface of anterior region of loculus of *Ro. conchai*. J, distal surface of remainder of bothridium of *Ro. conchai*. K, scutes on surface of neck of *Ro. conchai*.

Site of infection: Spiral intestine.

Type material: Holotype (mature worm, MNHNCL no. PLAT-15023); two paratypes (one mature worm, USNM no. 1638652; one immature worm, USNM no. 1638653); two paratypes (immature worms, LRP nos 9770 and 9771), three paratypes (mature worm SEM vouchers, LRP nos 9773–9775).

Sequence data: GenBank accession MW419973, hologenophore (CHL-76-5; VB136) LRP no. 8913.

Etymology: This species is named for Chilean parasitologist Dr Juan Carvajal, without whose assistance with the logistics, our fieldwork in Chile, which led to collection of the type material of this species, would not have been possible.

Remarks: *Rockacestus carvajali* is the smallest member of the genus, with a total length of 13.1–14.5 (vs. 15–33, 170, 60–170, 50, 26–58, 50–140, 36–62 and 90 mm in *Ro. arctowskii*, *Ro. brittanicus*, *Ro. georgiensis*, *Ro. piriei*, *Ro. radioductus*, *Ro. rakusai*, *Ro. siedleckii* and *Ro. williamsi*, respectively). It further differs from all of these species except *Ro. georgiensis* and *Ro. piriei* in possessing bothridia that are highly, rather than moderately, folded. It possesses fewer testes per proglottid than both of the latter species (47 vs. 140–190 and 150, respectively).

ROCKACESTUS CONCHAI SP. NOV.

(FIGS 8F–K, 9)

ZooBank registration: A1AA7903-EA81-4CEB-BE94-1F1A1B8D713B.

Description (Based on five whole mature worms, and three scolices examined with SEM.) Worms euapolytic, craspedote, 9.9–16.9 (12.9 ± 3 ; 5) mm long; proglottids 64–105 (81 ± 17 ; 5) in total number; maximum width at level of scolex. Scolex consisting of four bothridia (Figs 8F, 9A), 1122–1775 (1306 ± 265 ; 5) wide. Bothridia highly folded (Fig. 8G), with apical sucker and single loculus, 478–624 (559 ± 76 ; 3; 4) long, 600–830 (699 ± 96 ; 3; 4) wide when folded, sessile anteriorly, free posteriorly; loculus with marginal loculi; apical sucker 81–135 (111 ± 18 ; 4; 12) long, 96–140 (121 ± 12 ; 5; 13) wide. Cephalic peduncle lacking. Neck 5.1–7.4 (5.8 ± 1 ; 5) mm long. Distal surface of apical sucker (Fig. 8H) and anterior portions of loculus (Fig. 8I) with acicular filitriches; distal surface of loculus with sparsely arranged lingulate spinitriches and acicular

filitriches (Fig. 8J). Proximal bothridial surface with acicular filitriches. Neck (Fig. 8K) and strobila with capilliform filitriches arranged in wide scutes. Immature proglottids wider than long, becoming longer than wide with maturity (Fig. 9B), 63–101 (78 ± 16 ; 5) in number. Mature proglottids becoming longer than wide posteriorly (Fig. 9C, D), one to three (2.4 ± 0.9 ; 5) in number. Terminal proglottid 987–1580 (1270 ± 275 ; 5) long, 368–540 (462 ± 77 ; 5) wide, length-to-width ratio 2.3–3 (2.7 ± 0.3 ; 5):1. Testes 51–73 (61 ± 9 ; 4; 4) in total number, ten to 14 (12 ± 2 ; 4; 4) in number in post-poral field, 35–55 (43 ± 5 ; 5; 20) long, 60–90 (76 ± 8 ; 5; 20) wide. Vas deferens extensive, coiled medial to cirrus sac. Cirrus sac oval, 209–358 (281 ± 57 ; 5) long, 113–164 (143 ± 21 ; 5) wide, thin walled, containing coiled cirrus; cirrus armed with spinitriches. Genital pores irregularly alternating, 66–75% (69 ± 3 ; 5) of proglottid length from posterior end; genital atrium shallow. Vagina weakly sinuous, extending from ootype along midline of proglottid to anterior margin of cirrus sac, then laterally along anterior margin of cirrus sac to open into common genital atrium anterior to cirrus. Ovary at or near posterior margin of proglottid, H-shaped in frontal view, 252–445 (325 ± 77 ; 5) long, 167–266 (214 ± 49 ; 4) wide, tetralobed in cross-section; ovarian margins lobulated. Vitellarium follicular; follicles arranged in two lateral bands that converge medially; each band consisting of multiple columns of follicles, extending throughout length of proglottid, interrupted partly or completely by terminal genitalia, uninterrupted by ovary; follicles highly variable in form. Excretory vessels 4, arranged in one dorsal and one ventral pair on each lateral margin of proglottid. Gravid proglottids not observed.

Type host: White-dotted skate, *Bathyraja albomaculata* (Norman, 1937) (Rajiformes: Arhynchobatidae Fowler).

Type locality: Atlantic Ocean off the Falkland Islands ($48^{\circ}39'10.8''\text{S}$, $60^{\circ}44'42.6''\text{W}$).

Additional localities: Atlantic Ocean off the Falkland Islands ($49^{\circ}38'49.8''\text{S}$, $59^{\circ}50'43.2''\text{W}$).

Site of infection: Spiral intestine.

Type material: Holotype (mature worm, NHMUK no. 2020.12.17.1); two paratypes (mature worms, USNM nos 1638654 and 1638655); two paratypes (mature worms, LRP nos 10293 and 10294), three paratypes (immature worm SEM vouchers, LRP nos 10279–10281).

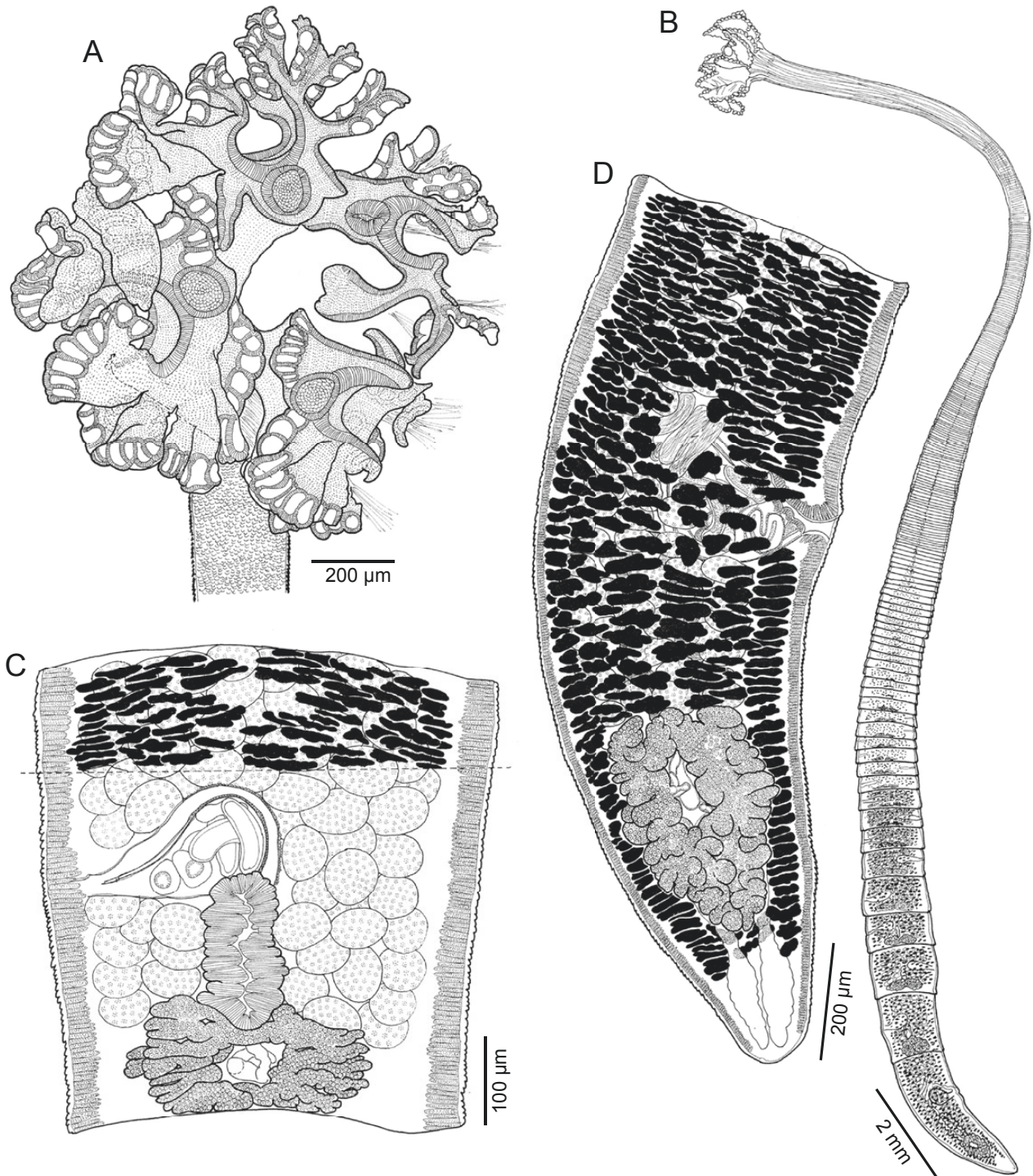


Figure 9. Line drawings of adult of *Rockacestus conchali* (specimen accession numbers in parentheses). A, scolex (USNM no. 1638654), posterior portions of right two bothridia incomplete. B, whole worm (NHMUK no. 2020.12.17.1). C, subterminal mature proglottid (NHMUK no. 2020.12.17.1), with vitelline follicles not shown posterior to dashed line. D, terminal mature proglottid (NHMUK no. 2020.12.17.1).

Sequence data: GenBank accession MW419959, hologenophore (FA-70, KW1011) LRP no. 10324.

Etymology: This species is named for elasmobranch biologist Francisco Concha, in recognition of his appreciation of cestode taxonomy as evidenced by his collection of the type material of this species from the Falkland Islands.

Remarks: *Rockacestus conchai* is smaller in total length (9.9–16.9 vs. 170, 70–170, 50, 26–58, 50–140, 36–62 and 90 mm) and has fewer testes (73 vs. 100, 140–190, 150, 100 or more, 120–165, 85–105 and 80–100) than *Ro. brittanicus*, *Ro. georgiensis*, *Ro. piriei*, *Ro. radioductus*, *Ro. rakusai*, *Ro. siedleckii* and *Ro. williamsi*, respectively. The bothridia of *Ro. conchai* are conspicuously more delicate and folded than those of the remaining two species (i.e. *Ro. arctowskii* and *Ro. carvajali*). It can be distinguished further from *Ro. arctowskii* in possessing a smaller apical sucker (81–135 long by 96–140 vs. 212–250 in diameter) and from *Ro. carvajali* in lacking, rather than possessing, a posterior depression bounded by circular band of muscle fibres.

DISCUSSION

The tree resulting from our molecular phylogenetic analysis, which includes additional representation of *Rockacestus*, *Ruhnkebothrium* and *Yamaguticestus*, is consistent with those of previous studies (e.g. [Ruhnke & Workman, 2013](#); [Caira et al., 2014, 2020b](#); [Bueno, 2018](#)) in supporting the novel taxonomic status of these taxa. This result is not unexpected given the ubiquitous use of 28S rDNA sequence data, but confirmation in a broader taxonomic context lends additional support for erecting these new genera. Furthermore, each genus exhibits a suite of morphological features that distinguishes it from the other phyllobothriidean genera. However, a subset of these features also expands the potential number of instances of homoplasy in several key morphological and ultrastructural features previously identified as homoplasious by [Caira et al. \(2020b\)](#) across phyllobothriidean phylogenetic tree space. For example, *Rockacestus* can be added to the list of genera (including *Chimaerocestos*, *Cardiobothrium*, at least some species of *Crossobothrium* and *Scyphophyllidium*) with bothridial marginal loculi. The three new genera join *Orygmatobothrium* and the clade consisting of *Alexandercestus* + *Hemipristicola* + *Scyphophyllidium* in bearing scutes consisting of densely arranged capilliform filitriches on the neck and strobila. *Yamaguticestus* joins *Orygmatobothrium* and the clade consisting of *Alexandercestus* + *Hemipristicola* +

Scyphophyllidium, in which the spinitriches on one or more of the bothridial surfaces are gongylate columnar in shape. The triangular, highly folded bothridia of *Ruhnkebothrium* bear some striking similarities to those of *Thysanocephalum*. More formal evaluation of the evolution of these features would be interesting to pursue in the context of a phylogenetic tree based on additional molecular data.

In all three new genera, at least one instance of congeners that are morphologically distinct but identical in sequence for the D1–D3 region of the 28S rDNA gene was observed. In such cases, morphological features were considered sufficient to recognize the species as distinct. In the case of *Ru. bajaense* and *Ru. mattisi*, the morphological differences are presented in the Remarks section of the description of the latter. In the case of *Yamaguticestus*, as noted above, further work comparing specimens of *Y. squali* and *Y. cf. squali* is required to address the question of the conspecificity of these specimens. *Rockacestus carvajali* is identical in sequence to a species (i.e. *Rockacestus* sp. nov. 5) that has not yet been described, and thus the differences are not presented here, but preliminary observation shows the apical suckers of the bothridia of the latter to be conspicuously larger than those of the former. Although the low level of interspecific sequence divergence is somewhat unusual for this gene, it has been observed in other phyllobothriideans (e.g. [Cutmore et al., 2017](#); [Ruhnke et al., 2020](#)). Nonetheless, it would be interesting to determine whether the genetic similarities seen here for a portion of one gene are reflected in sequence data for other molecular markers.

Beyond expanding the diversity of elasmobranchs known to host phyllobothriideans, the host associations of all three genera are interesting in other respects. The hosts of *Ruhnkebothrium* provide further support for the contention of [Naylor et al. \(2012\)](#) that the scalloped hammerhead *Sphyrna lewini* consists of a pair of essentially allopatric species, one that occurs primarily in the Atlantic and Indian Oceans (i.e. *Sphyrna lewini* 1) and one that occurs in the Pacific Ocean (i.e. *Sphyrna lewini* 2). In addition to genetic differences that [Naylor et al. \(2012\)](#) found between sharks from the two regions, which were consistent with earlier work by others ([Abercrombie et al., 2005](#); [Duncan et al., 2006](#); [Quattro et al., 2006](#); [Zemlak et al., 2009](#)), scalloped hammerheads in the Atlantic Ocean and the Gulf of California were each found to host their own species of *Ruhnkebothrium*.

The fact that all ten species of *Rockacestus* are parasites of skates is interesting given that by far the majority of the 70 other species of phyllobothriideans parasitize sharks (see, e.g. [Ruhnke et al., 2017](#)). However, there are exceptions in the cases of a handful of other phyllobothriidean species. Both known species

of *Chimaerocestos* parasitize holocephalans rather than elasmobranchs (Williams & Bray, 1984; Caira *et al.*, 2014). *Scyphophyllidium guariticum* (Marques, Brooks & Lasso, 2001) Caira, Jensen & Ruhnke, 2020 parasitizes a freshwater stingray (Potamotrygonidae Garman) (see Marques *et al.*, 2001). All three species of *Calypotrobothrium* parasitize members of the batoid order Torpediniformes (i.e. electric rays) (Ruhnke *et al.*, 2017). All three species of *Guidus* parasitize Rajiformes (i.e. skates) (Ivanov, 2006). Thus, *Rockacestus* is not the first genus whose members parasitize batoids or Rajiformes. Our results (Fig. 1) are consistent with those of previous phylogenetic analyses (Caira *et al.*, 2014) in that *Chimaerocestos* and *Scyphophyllidium guariticum* were found to be nested deeply among different shark-parasitizing genera in the order, suggesting that their associations with non-selachian hosts are likely to be the result of independent host-switching events in each case. However, with the addition of *Rockacestus* to the analysis, a reasonably well-supported group has emerged that includes three of the four batoid-parasitizing genera (i.e. *Calypotrobothrium*, *Guidus* and *Rockacestus*). Given that these genera are interspersed among three genera that include species that parasitize sharks (i.e. *Monorygma*, *Bilocularia* and *Yamaguticestus*) and the intergeneric relationships within the clade are not well supported, this result requires further investigation, ideally using additional molecular markers.

The disparate nature of the host associations of *Yamaguticestus* is also intriguing given the high degree of host specificity at various taxonomic levels exhibited by most other phyllobothriideans. All but two of the 20 other genera parasitize a single order, family or even genus of sharks (Ruhnke *et al.*, 2017). In contrast, *Yamaguticestus* parasitizes two distantly related orders of sharks: one in the Squalomorphi and one in the Galeomorphi. The two other genera with comparably broad host associations are *Crossobothrium*, which also parasitizes species in an order in the Squalomorphi and one in the Galeomorphi, and *Scyphophyllidium*, which parasitizes several orders of galeomorph sharks and a stingray. Given that tapeworms are transmitted trophically between the sequence of hosts in their complex life cycles, similarities in host diet and habitat might account for such disparate host associations. All six host species of *Yamaguticestus* (i.e. *E. spinax*, *H. natalensis*, *Squalus acanthias*, *Scyliorhinus canicula*, *Squalus suckleyi* and *Scyliorhinus stellaris*) are relatively small sharks; none reaches a total length of > 2 m, and most are < 1.2 m in total length (Ebert *et al.*, 2013; Froese & Pauly, 2019). All six are also demersal or epibenthopelagic, occurring in continental shelf waters at depths of < 200 m, although *E. spinax*, *Squalus acanthias* and *Squalus suckleyi* are also known from deeper waters

(Ebert *et al.*, 2013; Froese & Pauly, 2019). All six species generally feed on a variety of invertebrates and small fish (Compagno *et al.*, 1989; Hanchet, 1991; Cortés, 1999; Koen Alonso *et al.*, 2002; Kousteni *et al.*, 2017; Tribuzio *et al.*, 2017). As a consequence, the association of *Yamaguticestus* with small squaliform sharks (i.e. Squalidae and Etmopteridae) and pentanchid and scyliorhinid sharks might be attributable to ecological commonalities, such as dietary overlap (e.g. Barria *et al.*, 2018; Bengil *et al.*, 2019), and thus is a result of host-switching events, rather than shared evolutionary histories. However, data on the types of intermediate hosts used by larvae of species of *Yamaguticestus* are required to examine this explanation further. Given definitive host diet, benthic invertebrates and small fishes should be prioritized as possible hosts of the larval forms of these tapeworms.

In light of the surprisingly small number of species of hammerhead sharks, catsharks, squaliform sharks and skates that have been examined for phyllobothriideans to date, substantial novelty in all three new genera is likely to remain to be discovered and described. Insight with respect to the potential magnitude of that novelty can be obtained from the predictions of global phyllobothriidean diversity of Ruhnke *et al.* (2017), which were based on the number of species in each elasmobranch group and the assumption of strict (i.e. oioxenous *sensu* Euzet & Combes, 1980) host specificity of phyllobothriidean species. The dearth of other phyllobothriidean genera in the subset of the 13 species of hammerheads (Sphyrnidae) that have been examined leads us to believe that the majority of the estimated ten additional phyllobothriidean species in hammerhead sharks will belong to *Ruhnkebothrium*. The subset of the 43 species of Squalidae that have been examined host the phyllobothriidean genus *Trilocularia* in addition to *Yamaguticestus*. We anticipate that ~50% of the 50 or so species of phyllobothriideans predicted by Ruhnke *et al.* (2017) to be hosted by squalids will belong to *Yamaguticestus*. The Etmopteridae, which were not predicted to host phyllobothriideans by Ruhnke *et al.* (2017), are now known to host at least one species of *Yamaguticestus* (see Euzet, 1959). As a consequence, at least a subset of the 48 species in the family seems likely to add modest diversity to this number. To our knowledge, *Yamaguticestus* is the only genus of phyllobothriidean known to parasitize catsharks (Pentanchidae and Scyliorhinidae). As a consequence, all of the ~40 or more additional species of cestodes predicted by Ruhnke *et al.* (2017) to be hosted by the Pentanchidae (with 11 genera and 110 species) and all of the ~30 or more additional species predicted to be hosted by the Scyliorhinidae (with six genera and 48 species) are likely to be species of *Yamaguticestus*. With respect to *Rockacestus*, existing records indicate that this genus

is widespread in skates of the families Rajidae and Arhynchobatidae. The only other phyllobothriidean genus known to parasitize skates is *Guidus*, and all three known species parasitize the genus *Bathyraja*. This leads us to believe that the majority of the > 130 novel species of phyllobothriideans predicted by Ruhnke *et al.* (2017) to parasitize skates in these two families will belong to the genus *Rockacestus*. Thus, the combined species diversity in these three new genera will easily exceed 150 species.

We believe the skate cestodes referred to by Beer *et al.* (2019) as Phyllobothriidea New Genus, for which sequence data for the 28S rDNA gene were deposited in GenBank as Phyllobothriidea gen. n. sp. 1, Phyllobothriidea gen. n. sp. 2 and Phyllobothriidea gen. n. sp. 3, also belong to *Rockacestus*. Sequence data for these taxa and the specimen referred to by Beer *et al.* (2019) as *Phyllobothrium piriei* were not included in our analyses because their specific identities are somewhat problematic. Vouchers are not available in a public collection. The specimen identified as *Phyllobothrium piriei* came from a different genus of skate than the type host of *P. piriei* (now *Ro. piriei*). Most importantly, specimens of this genus assigned the same species designation do not all form monophyletic groups relative to those of other species. Nonetheless, that work adds *Psammobatis* Günther to the list of genera of Arhynchobatidae known to host *Rockacestus*. We would also note that the relaxed degree of host specificity reported by Beer *et al.* (2019) for these cestodes, if verified, could appreciably reduce the global estimates of undiscovered diversity in this genus. However, the conflicts we found between morphology and 28S rDNA sequence data suggest that additional molecular data are required to confirm species boundaries.

Moving forward with survey work, it is important to note that one of the greatest challenges of the present study was the relatively rare nature of essentially all of the species described here. In many cases, a substantial amount of collecting effort was required to obtain even a small number of specimens. For example, *Y. metini* had a prevalence of 8% and an intensity of one worm per infected shark; in other words, we examined 50 individuals of *H. natalensis*, only four of which were infected, and each infected shark hosted only a single worm. We would therefore caution against eliminating an elasmobranch species from consideration as a viable host until a considerable number of individuals of that host species have been examined.

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