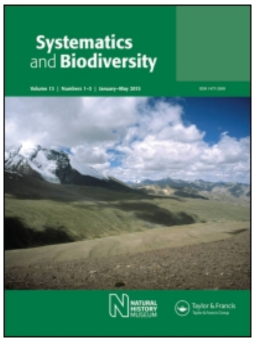

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Expanding known global biodiversity of *Yamaguticestus* (Cestoda: Phyllobothriidea) parasitizing catsharks (Pentanchidae and Scyliorhinidae)

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Research Article

Expanding known global biodiversity of *Yamaguticestus* (Cestoda: Phyllobothriidea) parasitizing catsharks (Pentanchidae and Scyliorhinidae)

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This paper aimed to test the prediction that substantial undiscovered biodiversity in the tapeworm genus *Yamaguticestus* Caira, Bueno & Jensen, 2021 exists in the 16 of 18 genera of catsharks globally that have not yet been examined for tapeworms. A total of 200 catsharks of 10 species representing eight genera were sampled opportunistically from the waters off Australia, Chile, Malaysian Borneo, South Africa, South Korea, and the UK between 1991 and 2017. Six species in four genera (i.e., *Apristurus* Garman, *Asymbolus* Whitley, *Holohalaelurus* Fowler, and *Scyliorhinus* Blainville) were found to host a total of six new species of *Yamaguticestus*, tripling the number of described species. The new species are *Yamaguticestus africanae* sp. nov. from *Scyliorhinus capensis*, *Yamaguticestus ellisi* sp. nov. from *Scyliorhinus canicula*, *Scyliorhinus fairweatherae* sp. nov. from *Holohalaelurus regani*, *Yamaguticestus kihongkimi* sp. nov. from *Scyliorhinus torazame*, and *Yamaguticestus kuchtai* sp. nov. from *Apristurus aphyodes*. The new species were characterized using a combination of light and scanning electron microscopy; sequence data for the D1–D3 region of the *28S rRNA* gene were generated for five of the species. Transfer of a species formerly assigned to *Calyptrobothrium* Monticelli, 1893 that is morphologically consistent with *Yamaguticestus* added *Cephaloscyllium* Gill to the list of catshark genera known to host this genus. Most tapeworm species exhibited a remarkably low prevalence and intensity of infection suggesting that our failure to detect infection in the four genera of sharks represented by small sample sizes may not be indicative of their unsuitability as hosts. Our results suggest that the earlier prediction that 70 species of *Yamaguticestus* remain to be discovered in catsharks across the planet may actually be an underestimate.

http://zoobank.org/urn:lsid:zoobank.org:pub:63F48CF6-ED06-44FC-839D-

Keywords: *28S rRNA* gene, biodiversity, catsharks, cestode, Eucestoda, morphology, new species, Pentanchidae, Scyliorhinidae, *Yamaguticestus*

Introduction

The tapeworm genus *Yamaguticestus* Caira, Bueno & Jensen, 2021 was erected by Caira et al. (2021) to accommodate a series of species, bearing uniloculated bothridia with apical suckers, that parasitize small squaliform sharks and catsharks. At present, the genus includes only three described species. One of these (i.e., *Yamaguticestus squali* [Yamaguti, 1952] Caira, Bueno & Jensen, 2021) parasitizes the squaliform shark *Squalus suckleyi* (Girard) and the other two (i.e., *Yamaguticestus metini* Caira, Bueno & Jensen, 2021 and *Yamaguticestus longicolle* [Molin, 1858] Caira et al., 2021) parasitize the catsharks *Halaelurus natalensis* (Regan) and *Scyliorhinus stellaris* (L.), respectively. Given the sizeable number of genera and species of squaliform sharks (Weigmann, 2016) and catsharks (Weigmann et al., 2018) globally, Caira et al. (2021) attributed the surprisingly low described diversity in this genus to the poorly sampled nature of both shark groups. In fact, these authors predicted that more than 50 species of *Yamaguticestus* remain to be discovered in

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squaliform sharks and more than 70 species in catsharks.

The primary aim of the present study was to explore the prediction that substantial undiscovered novelty of *Yamaguticestus* exists in catsharks by examining one or more species in as many of the 10 unsampled genera of Pentanchidae Smith and six unsampled genera of Scyliorhinidae Gill as possible for tapeworms. However, because of the small size, and thus low commercial value of catsharks, our sample was limited to species that could be obtained as by-catch of fisheries targeting other more commercially valuable taxa. Cognizant of the low prevalence and intensity of infection typical of species of *Yamaguticestus* (e.g., Pickering & Caira, 2014; Caira et al., 2021), we strove to necropsy as many specimens of each shark species as possible. The 200 sharks representing eight genera and 10 species necropsied yielded a total of only 30 specimens of *Yamaguticestus*. As a consequence, the descriptions of most of the six new species are based on relatively small numbers of specimens. Fortunately, interspecific morphological differences were sufficient to allow species to be distinguished despite the limited amount of material. Having confirmed the association of *Yamaguticestus* with three additional genera of catsharks, we became curious about a species originally assigned to *Calyptrobothrium* Monticelli, 1893 collected from species of the scyliorhinid genus *Cephaloscyllium* Gill by Alexander (1963) and Caira et al. (1999). Examination of specimens confirmed the affinities of both species with members of the genus, expanding the hosts of *Yamaguticestus* to include a sixth genus of catshark.

Materials and methods

Collection details

The cestodes described here resulted from the examination of 200 specimens of four species of pentanchids and six species of scyliorhinids from a variety of locations around the globe. The sharks examined are as follows: six specimens of *Haploblepharus edwardsii* (Schinz), 15 specimens of *Holohalaelurus regani* (Gilchrist), one specimen of *Poroderma pantherinum* (Müller & Henle), and 24 specimens of *Scyliorhinus capensis* (Müller & Henle) collected using a bottom trawl during a hake survey cruise of the *FRV Africana* working off the coast of South Africa in April through May of 2010; 58 specimens of *Scyliorhinus canicula* (L.) collected in collaboration with the commercial trawling vessel *FV Maximus* working in the North Sea off Lowestoft, UK, in August 2013; 68 specimens of *Scyliorhinus torazame* (Tanaka) collected from a fish market in Busan, Korea, in November 2013; 12 specimens of *Asymbolus analis* (Ogilby) – two collected in fish traps off Tuncurry, New South Wales, Australia, in September 1991 and 10 collected off Sydney, Australia and sent to us by Ken Graham; four specimens of *Atelomycterus marmoratus* (Anonymous [Bennett]) collected from fish markets in Malaysian Borneo in June and October 2002 and April 2004; four specimens of *Schroederichthys bivius* (Müller & Henle) collected off the Falkland Islands in July 2017 and provided by Francisco Concha. See Appendix, Supplementary Material Table S1 for size, sex, and detailed locality data for the 192 shark specimens examined. Of these sharks, 70 were assigned unique specimen numbers, consisting of a collection code and collection number (e.g., AF-14), and basic morphometric data and a series of digital photographs were collected. Additional data for these 70 specimens are available in the Global Cestode Database (Caira et al., 2020a) by searching by unique specimen numbers. In the cases of the accessioned sharks, a small sample of liver tissue was removed from each shark and fixed in 95% ethanol, and sequence data were generated for the NADH dehydrogenase subunit 2 (NADH2) following Naylor et al. (2012) to confirm host identities. In addition, cestodes taken from seven specimens of *Apristurus aphyodes* Nakaya & Stehmann and from one specimen of *S. canicula* collected using a bottom trawl off Scotland in September 2004 were sent to us by Roman Kuchta.

The body cavity of each shark necropsied was opened with a mid-ventral longitudinal incision. The spiral intestine was removed and opened with a mid-ventral incision. In most cases, a small portion of the middle of the strobila was removed from the first cestode specimen encountered in each host species and preserved in 95% ethanol for molecular work; the remainder of the specimen (i.e., hologenophore sensu Pleijel et al., 2008) was preserved in 10% seawater-buffered formalin (9:1) for morphological work. Additional specimens were preserved for morphological or molecular work depending on the total number of specimens of a species found.

Morphological methods

Methods for preparing and examining cestodes for descriptive work with light and scanning electron microscopy (SEM) followed Caira et al. (2021), as did the methods for preparing drawings and taking

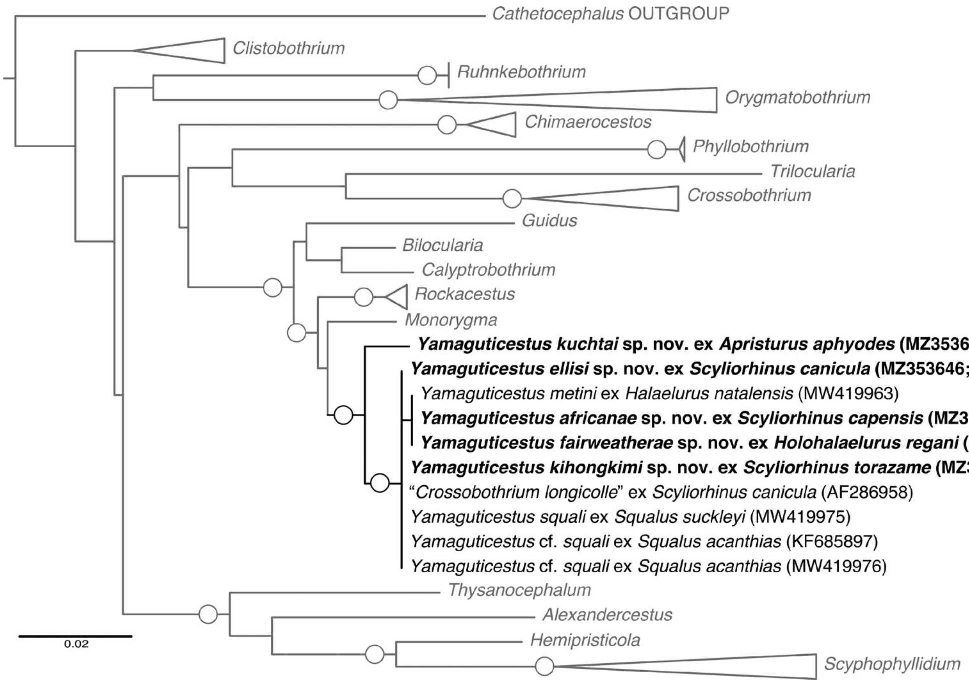


Fig. 1. Phylogeny of the Phyllobothriidea inferred from maximum likelihood analysis of the D1–D3 region of the *28S rRNA* gene. Nodes with 95% or greater bootstrap support are denoted with open circles. Clades of genera represented by more than one specimen, other than *Yamaguticestus*, are collapsed. New species described here for which data were generated *de novo* are indicated in bold. Terminal labels for the clade of *Yamaguticestus* consist of cestode species name and host species name followed by the GenBank accession number and host number for new species in parentheses. Scale bar indicates number of substitutions per site.

measurements. Measurements are given in the text as a range (in micrometres unless stated otherwise); in instances in which measurements came from more than four cestode specimens the range is followed in parentheses by mean, standard deviation, number of specimens measured, and total number of measurements in cases in which more than one measurement was made per worm. We also examined what we believe are both of Alexander's paratype specimens of *Calyptrobothrium chalarosomum* Alexander, 1963 as well as the specimens Caira et al. (1999) provisionally identified as *Calyptrobothrium* sp.

Microthrix terminology follows Chervy (2009). Cirrus sac shape terminology follows Clopton (2004). Museum abbreviations used are as follows: LRP, Lawrence R. Penner Parasitology Collection, University of Connecticut, Storrs, USA; NHMUK, The Natural History Museum, London, UK; NIBR, National Institute of Biological Resources, Incheon, South Korea; QM, Queensland Museum, Brisbane, Australia; SAMCTA, South African Museum Cape Town Invertebrate Collection, Cape Town, South Africa; USNM, National Museum of Natural History, Smithsonian Institution, Department of Invertebrate Zoology, Washington, D.C., USA.

Molecular methods and phylogenetic analysis

One specimen each of *Yamaguticestus africanae* sp. nov., *Yamaguticestus ellisi* sp. nov., *Yamaguticestus fairweatherae* sp. nov., *Yamaguticestus kihongkimi* sp. nov., and *Yamaguticestus kuchtai* sp. nov. were available for the generation of sequence data for the D1–D3 region of the *28S rRNA* gene (hereafter 28S) to help confirm the generic placement of these species. Extraction and Sanger sequencing protocols for generating data for all but *Y. kuchtai* sp. nov. followed Caira et al. (2021). Sequence data for the latter species were assembled by Hannah Ralicki and Elizabeth Jockusch using MITObim version 1.9.1 (Hahn et al., 2013) from Next Generation Sequencing reads generated for a related project. In all cases, hologenophores (sensu Pleijel et al., 2008) were deposited in the LRP. The sequence data for these five species were added to the matrix of Caira et al. (2021). GenBank accession numbers for these five sequences are given in the descriptions and in Fig. 1. Sequences were then aligned and a phylogenetic analysis was conducted following Caira et al. (2021). To emphasize the novel aspects of our analysis, all clades, other than *Yamaguticestus*, are represented as collapsed triangles on the tree.

Results

No specimens of *Yamaguticestus* were found in the four individuals of *Atelomycterus marmoratus*, six individuals of *Haploblepharus edwardsii*, one individual of *Poroderma pantherinum*, or four individuals of *Schroederichthys bivius* examined. In contrast, one or more individuals of *Scyliorhinus capensis*, *Scyliorhinus canicula*, *Holohalaelurus regani*, *Scyliorhinus torazame*, *Apristurus aphyodes*, and *Asymbolus analis* hosted novel species of *Yamaguticestus*. All six new species are described below.

The alignment was 1278 base pairs (bp) in length. *Yamaguticestus kuchtai* was the most divergent of the nine members of the genus included in the analysis. *Y. africanae*, *Y. metini*, and *Y. fairweatherae* were identical in sequence to one another. Similarly, *Y. ellisi*, *Y. kihongkimi*, *Y. squali*, *Y.* cf. *squali* and '*Crossobothrium longicolle*' were identical to one another. The tree resulting from the phylogenetic analysis is shown in Figure 1. Specimens of all five of the novel species for which molecular data were generated grouped robustly among the other specimens of *Yamaguticestus* in the analysis confirming our generic placement of these species.

Yamaguticestus chalarosomus (Alexander, 1963) comb. nov.

Synonym: *Calyptrobothrium chalarosomum*
Alexander, 1963

Type and only known host. *Cephaloscyllium isabellum* (Bonnaterre), draughtsboard shark (Carcharhiniformes: Scyliorhinidae).

Type locality. Pacific Ocean, Palliser Bay, Wellington, New Zealand.

Site of infection. Spiral intestine.

Specimens examined. Two paratypes, each mounted on two slides (LRP Nos. 5555–5558).

Sequence data. None.

Remarks

In 2000, Claude Alexander donated his personal collection to the Lawrence R. Penner Parasitology Collection at the University of Connecticut. Among his slides are what appear to be the paratypes of *Calyptrobothrium chalarosomum*. Not only are the label data for locality, date of collection, and host consistent with the information given in the original description, but also Alexander (1963) indicated that this species was described from 'the type and two paratype specimens' and that type specimens of species treated in that paper were deposited in the Zoology Department Collection, University of Wellington and paratype specimens were retained in his personal collection (see p. 118). These specimens are morphologically much more consistent with *Yamaguticestus* than with *Calyptrobothrium*. Most conspicuously, they possess, rather than lack, a postporal field of testes. This species is hereby transferred to *Yamaguticestus* as *Yamaguticestus chalarosomus* (Alexander, 1963) comb. nov. Not only does this action remove catsharks from the repertoire of hosts of *Calyptrobothrium* – which is otherwise known only from torpediniform rays – but it also adds *Cephaloscyllium* to the genera of scyliorhinid sharks known to host *Yamaguticestus*.

In addition, examination of specimens of the undescribed species from *Cephaloscyllium laticeps* (Duméril) off Victoria, Australia, referred to provisionally as *Calyptrobothrium* sp. by Caira et al. (1999) (LRP Nos. 2348, 2349), leads us to believe these specimens also belong to *Yamaguticestus*. They add a second species of *Cephaloscyllium* to the spectrum of hosts parasitized by members of this genus.

Yamaguticestus africanae sp. nov.
(Figs 2–9)

ZooBank number: urn:lsid:zoobank.org:act:F1564FC0-7A95-48AC-9B1B-2633F459FCE6.

Type and only known host. *Scyliorhinus capensis* (Müller & Henle), yellowspotted catshark (Carcharhiniformes: Scyliorhinidae).

Type locality. Indian Ocean off South Africa (34°28.0'S, 25°27.57'E).

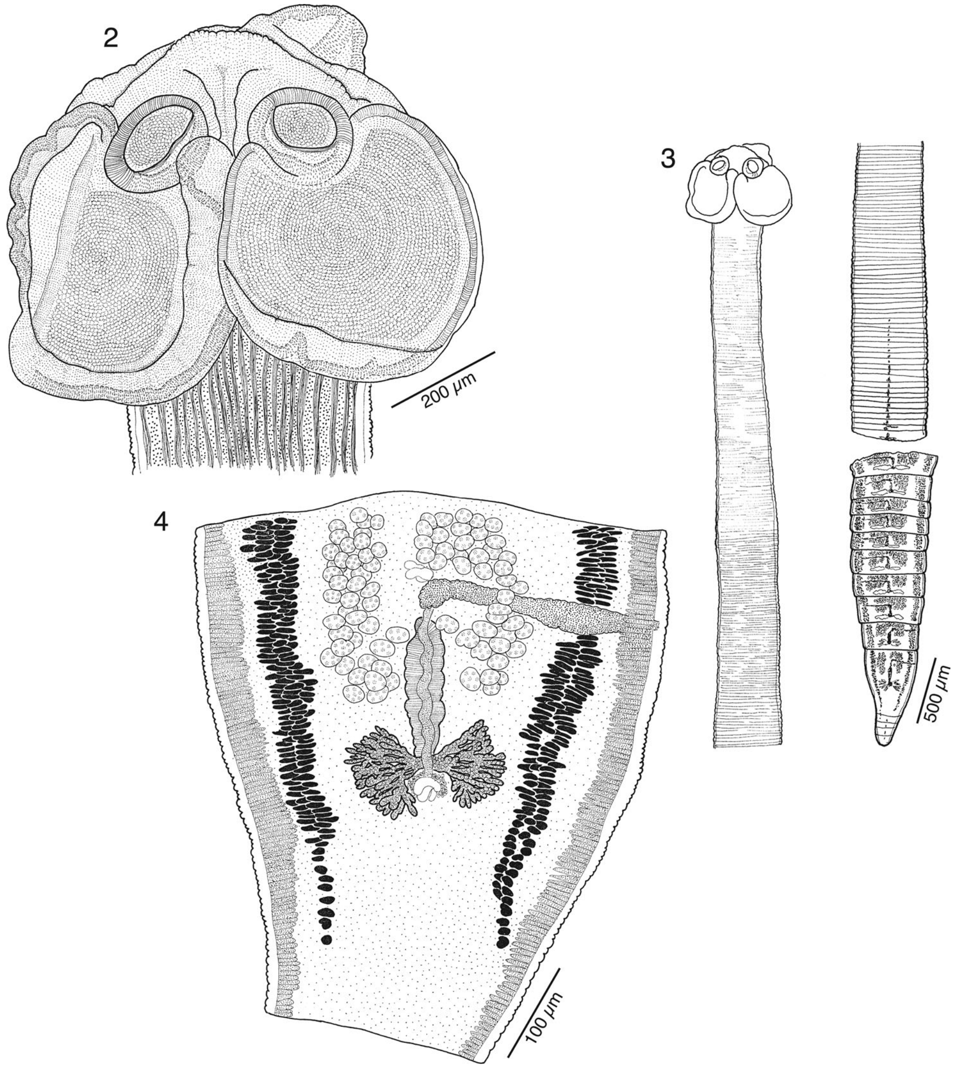
Additional localities. Indian Ocean off South Africa (34°24.38'S, 25°47.76'E).

Date of collection of holotype. 28 iv 2010.

Site of infection. Spiral intestine.

Prevalence. Two of 24 sharks examined (8%); mean intensity 2 worms per infected shark.

Type specimens deposited. Holotype (partial maturing worm, SAMCTA No. NMB P 794); 1 paratype (immature worm, USNM No. 1655916); 1 paratype (partial



Figs 2–4. Line drawings of holotype (SAMCTA No. NMB P 794) of *Yamaguticestus africanae* sp. nov. 2, scolex; 3, whole worm; 4, terminal proglottid.

immature worms [hologenophore], LRP No. 8663); scolex examined with SEM retained in personal collection of JNC.

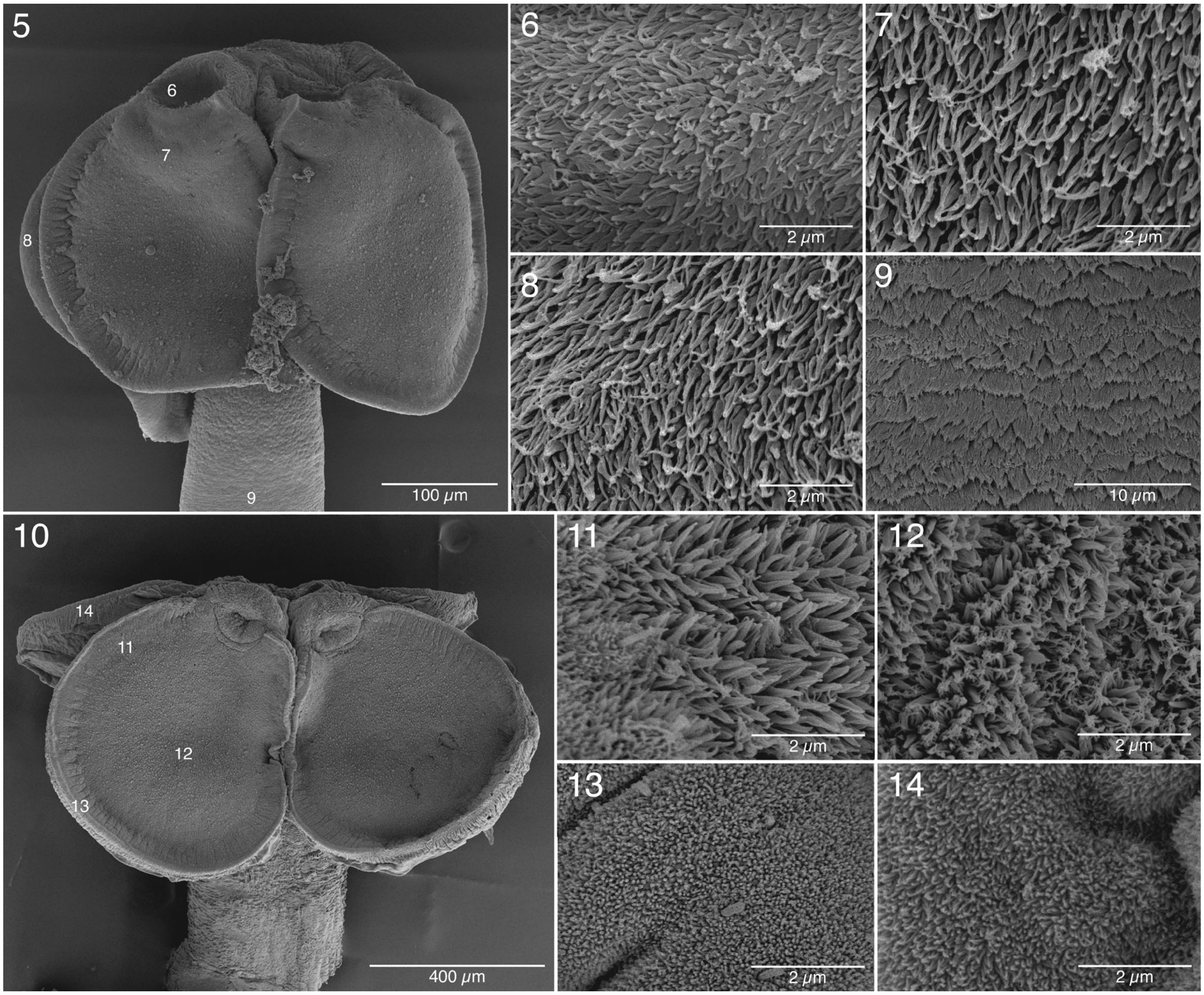
Sequence data. GenBank accession MZ353645 (hologenophore, paratype, AF-118-1V, LRP No. 8663).

Etymology. The name of this species recognizes the crew of South African Fisheries Research Vessel (FRV) *Africana* (Department of Agriculture, Forestry and Fisheries, Cape Town) for the key role they played in the collection of specimens of the type host of this species.

Description

(Based on 1 partial maturing worm, 1 immature worm, 1 partial immature worm [hologenophore], and 1 scolex examined with SEM): Worms euapolytic, weakly craspedote (Fig. 3), greater than 8.5 mm in length; proglottids at least 72 in total number; maximum width at level of scolex. Scolex 637 long, 819 wide, bearing 4 bothridia. Bothridia 583–589 long, 422 wide, sessile anteriorly, free posteriorly, with anterior sucker and single, undivided loculus (Figs 2, 5); apical sucker 171–190 long, 159–179 wide; apical sucker length as per cent of bothridial length 29–33%. Cephalic peduncle lacking. Neck 2946 long.

Distal surface of apical sucker (Fig. 6) and loculus (Fig. 7) densely covered with gladiate spinitriches and capilliform filitriches; proximal bothridial surface



Figs 5–14. Scanning electron micrographs of *Yamaguticestus africanae* sp. nov. (5–9) and *Yamaguticestus ellisi* sp. nov. (10–14). 5, scolex of *Y. africanae* sp. nov., small numbers indicate locations of 6–9; 6, distal surface of sucker of *Y. africanae* sp. nov.; 7, distal surface of bothridium of *Y. africanae* sp. nov.; 8, proximal surface of bothridium of *Y. africanae* sp. nov.; 9, surface of cephalic peduncle of *Y. africanae* sp. nov.; 10, scolex of *Y. ellisi* sp. nov., small letters indicate locations of 11–14; 11, distal surface of bothridium near rim of *Y. ellisi* sp. nov; 12, distal surface of centre of bothridium of *Y. ellisi* sp. nov; 13, distal surface of bothridium near rim of *Y. ellisi* sp. nov; 14, proximal surface of bothridium of *Y. ellisi* sp. nov.

densely covered with gladiate spinitriches and capilliform filitriches (Fig. 8); neck and strobila scutellate; scutes comprised of capilliform filitriches (Fig. 9).

Immature proglottids at least 203 in number, wider than long, becoming longer than wide with maturity. Terminal immature proglottid 511 long, 488 wide; length to width ratio 1.4:1. Testes 82 in total number, 17 in number in post-poral field. Genital pores irregularly alternating, 80% of proglottid length from posterior end. Vagina 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 (Fig. 4), H-shaped in frontal view, tetralobed in cross-section, strongly digitiform. Vitellarium follicular; follicles elongate oval, arranged in 2 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 median, ventral, sacciform, extending from ovarian isthmus to cirrus sac; uterine duct not observed. Excretory vessels 4, arranged in 1 dorsal and 1 ventral pair on each lateral margin of proglottid. Measurements of testes, cirrus sac, and ovary not made as data were available only from immature worms.

Remarks

Despite the limited nature of the available material, *Yamaguticestus africanae* sp. nov. can be distinguish from all four valid members of the genus. It is a smaller worm than *Yamaguticestus chalarosomus*, *Y. metini* Caira et al., 2021, *Y. squali* (Yamaguti, 1952) Caira et al., 2021 as redescribed from the holotype specimen of Yamaguti (1952) by Vasileva et al. (2002), and *Yamaguticestus longicolle* (Molin, 1858) Caira et al., 2021 as redescribed by Euzet (1959) (greater than 8.5 vs. over 300, 80, 141, and 150–300 mm in total length [TL], respectively). While it could be argued that the partial and immature nature of the specimen measured here might undermine these differences, *Y. africanae* sp. nov. also possesses conspicuously fewer testes than all four species (82 vs. 312–362, 158–184, 237–301, and 170–230, respectively). In terms of its two congeners that have been examined with SEM, *Y. africanae* sp. nov. conspicuously differs from both *Y. metini* and *Y. squali* in bearing spinitriches on its distal bothridial surfaces that are gladiate, rather than gongylate, in form.

***Yamaguticestus ellisi* sp. nov.**

(Figs 10–17)

ZooBank number: urn:lsid:zoobank.org:act:1E4ACAF1-19E2-4206-855F-389913CD2F4F.

Type and only known host. *Scyliorhinus canicula* (L.), lesser spotted dogfish (Carcharhiniformes: Scyliorhinidae).

Type locality. North Sea off Lowestoft (52°28'36.26"N, 01°45'27.69"E), UK.

Additional locality. North Atlantic Ocean, off Scotland (56°47'N, 09°2'W).

Date of collection of holotype. 12 iix 2013.

Site of infection. Spiral intestine.

Prevalence. Two of 58 sharks examined off Lowestoft (3%); mean intensity 1.5 worms per infected shark.

Type specimens deposited. Holotype (partial gravid worm [hologenophore], NHMUK No. 2021.5.25.1); 1 paratype (partial mature worm, USNM No. 1655921); SEM voucher (LRP No. 10282); scolex examined with SEM retained in personal collection of JNC.

Sequence data. GenBank accession MZ353646 (hologenophore, holotype, UK2-1V, NHMUK No. 2021.5.25.1).

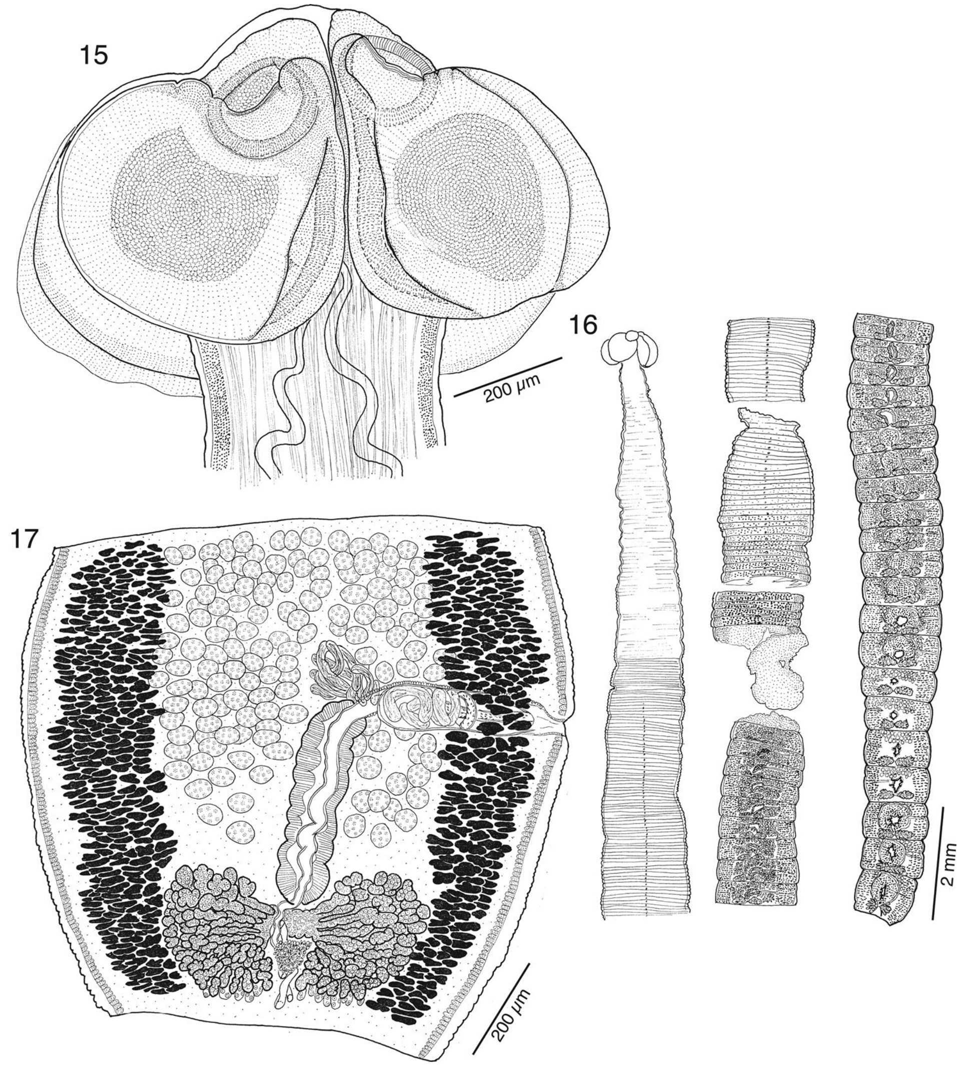
Etymology. This species honours Jim Ellis, Senior Researcher, Centre for Environment, Fisheries and Aquaculture Science, Lowestoft, UK, for the time, energy, and expert assistance he provided to JNC and KJ to ensure the successful collection of sharks from local fishers.

Description

(Based on 1 partial gravid worm [hologenophore], 1 partial mature worm, and 1 scolex examined with SEM and its strobilar voucher): Worms apolytic, acraspedote (Fig. 16); mature worm greater than 20.7 mm in length with at least 253 proglottids; gravid worm greater than 32.7 mm in length with at least 292 proglottids; maximum width 1365–1655 at level of immature proglottids. Scolex 679–697 long, 945–955 wide, bearing 4 bothridia. Bothridia 562–674 long, 504–592 wide, sessile anteriorly, free posteriorly, with anterior sucker and single, undivided loculus (Figs 10, 15); apical sucker 166–207 long, 144–198 wide; apical sucker length as per cent of bothridial length 25–35%. Cephalic peduncle lacking. Neck 1562–2682 long.

Distal surface of loculus densely covered with gladiate spinitriches and capilliform filitriches (Fig. 12), capilliform filitriches becoming less dense near rim (Fig. 11); distal surface of bothridial rim with band of acicular filitriches (Fig. 13); proximal bothridial surface densely covered with small gladiate spinitriches (Fig. 14), filitriches not observed; neck and strobila weakly scutellate; scutes comprised of capilliform filitriches.

Immature proglottids at least 259 in number, wider than long, becoming less so with maturity. Mature proglottids 6–12 in number; terminal mature proglottid on mature worm 958 long by 1005 wide, length to width ratio 0.26:1; genital pore 67% of proglottid length from posterior end. Posterior-most mature proglottid on gravid worm 405 long, 1543 wide, length to width ratio 0.95:1; genital pore 62% of proglottid length from posterior end. Terminal dehisced proglottid 858 long, 1077 wide, length to width ratio 0.8:1; genital pore 73% from posterior end. Testes 137–145 in total number, 14–20 in post-poral field, 28–36 long, 40–53 wide. Cirrus sac narrowly oblong, 209–243 long, 68–78 wide, thin-walled, containing coiled cirrus; cirrus armed with spinitriches. Vas deferens minimal, coiled medial and slightly anterior to cirrus sac. Genital pores irregularly alternating. Vagina surrounded by gland cells for distal half, 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



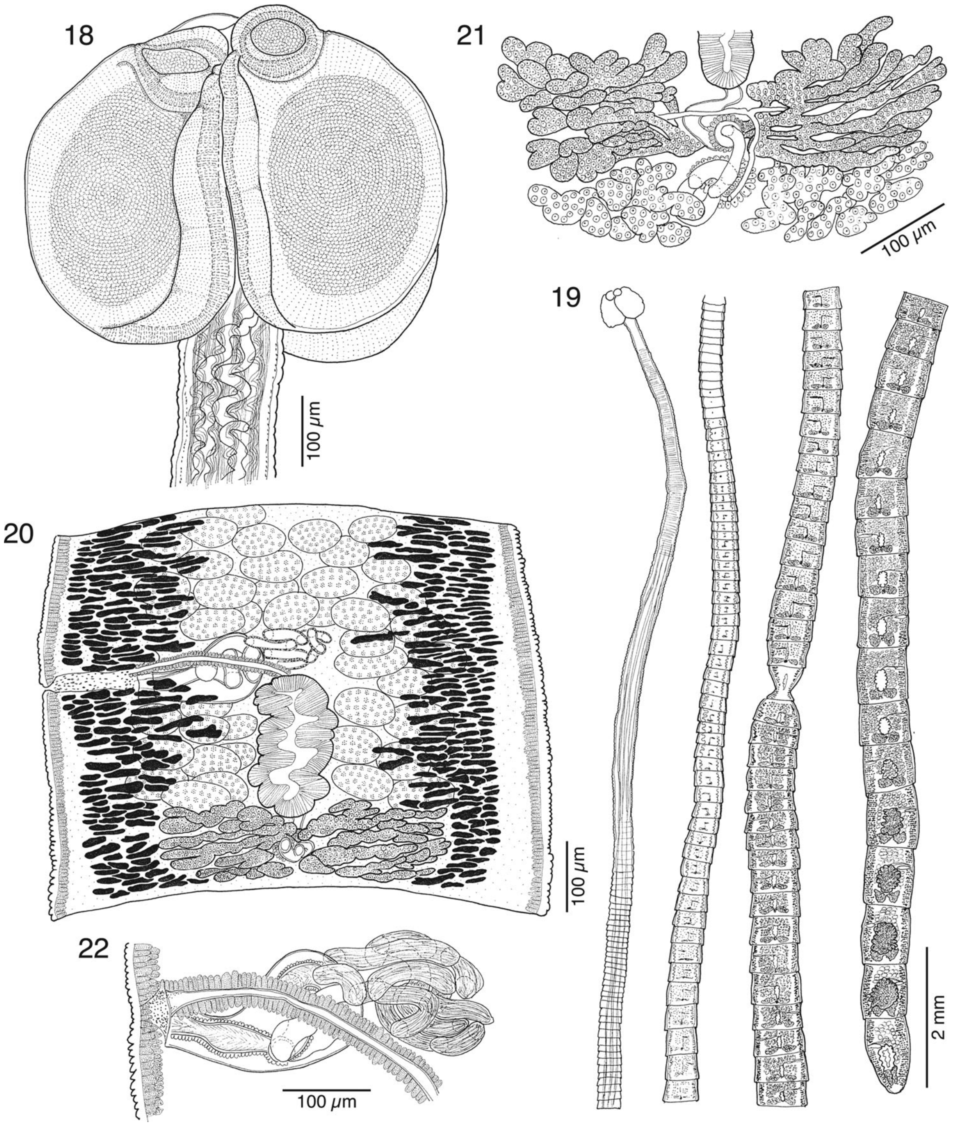
Figs 15–17. Line drawings of *Yamaguticestus ellisi* sp. nov. 15, scolex (paratype, USNM No. 1655921); 16, whole worm (holotype, NHMUK No. 2021.5.25.1); 17, terminal proglottid (paratype, USNM No. 1655921).

genital atrium anterior to cirrus sac. Ovary near posterior margin of proglottid (Fig. 17), H-shaped in frontal view, tetralobed in cross section, strongly digitiform, 235 long, 497 wide in terminal mature proglottid of mature worm, 124 long, 722 wide in posterior-most mature proglottid of gravid worm, 331 long, 471 wide in terminal dehisced proglottid on gravid worm. Vitellarium follicular; follicles irregular in shape, arranged in 2 lateral bands; each band consisting of multiple columns of follicles, extending throughout length of proglottid, not interrupted by terminal genitalia or ovary. Uterus median, ventral, sacciform, extending from ovarian isthmus to cirrus sac; uterine duct not observed. Excretory vessels 4, arranged in 1 dorsal and 1 ventral pair on each lateral margin of proglottid. Eggs too densely packed for shape to be characterized.

Remarks

Yamaguticestus ellisi sp. nov. is a longer worm (greater than 20.7–32.7 vs. greater than 8.5 mm in TL) with a greater number of testes (137–145 vs. 82) than *Y. africanae*. It is a smaller worm (greater than 20.7–32.7 vs. over 300, 150–300, 80, 141 mm) with fewer testes (137–145 vs. 312–362, 170–230, 158–184, and 237–301) than *Y. chalarosomus*, *Y. longicolle*, *Y. metini*, and *Y. squali*, respectively. As in the case of *Y. africanae*, *Y. ellisi* sp. nov. differs from *Y. metini* and *Y. squali* in possessing gladiate, rather than gongylate, spinitriches on its distal bothridial surfaces.

We believe the specimen included in the molecular phylogenetic analysis of Olson et al. (2001) as *Crossobothrium longicolle* (Molin, 1858) Euzet, 1959 (GenBank accession AF286958) is actually *Y. ellisi* sp. nov. Not only was this specimen collected from the type



Figs 18–22. Line drawings of *Yamaguticestus fairweatherae* sp. nov. 18, scolex (holotype, SAMCTA No. NMB P 795); 19, whole worm (paratype, USNM No. 1655917); 20, subterminal mature proglottid (paratype, USNM No. 1655917); 21, detail of ovary (paratype, LRP No. 10333); 22, detail of terminal genitalia (paratype, USNM No. 1655917).

host and locality of *Y. ellisi* sp. nov., but also the series of proglottids that constitute the voucher of the specimen (LRP No. 2113) are generally consistent with those of *Y. ellisi* sp. nov.

Yamaguticestus fairweatherae sp. nov.

(Figs 18–28)

ZooBank number: urn:lsid:zoobank.org:act:2CA66FBC-283D-4438-8093-7BA16A39F3F6.

Type and only known host. *Holohalaelurus regani* (Gilchrist), Izak catshark (Carcharhiniformes: Pentanchidae).

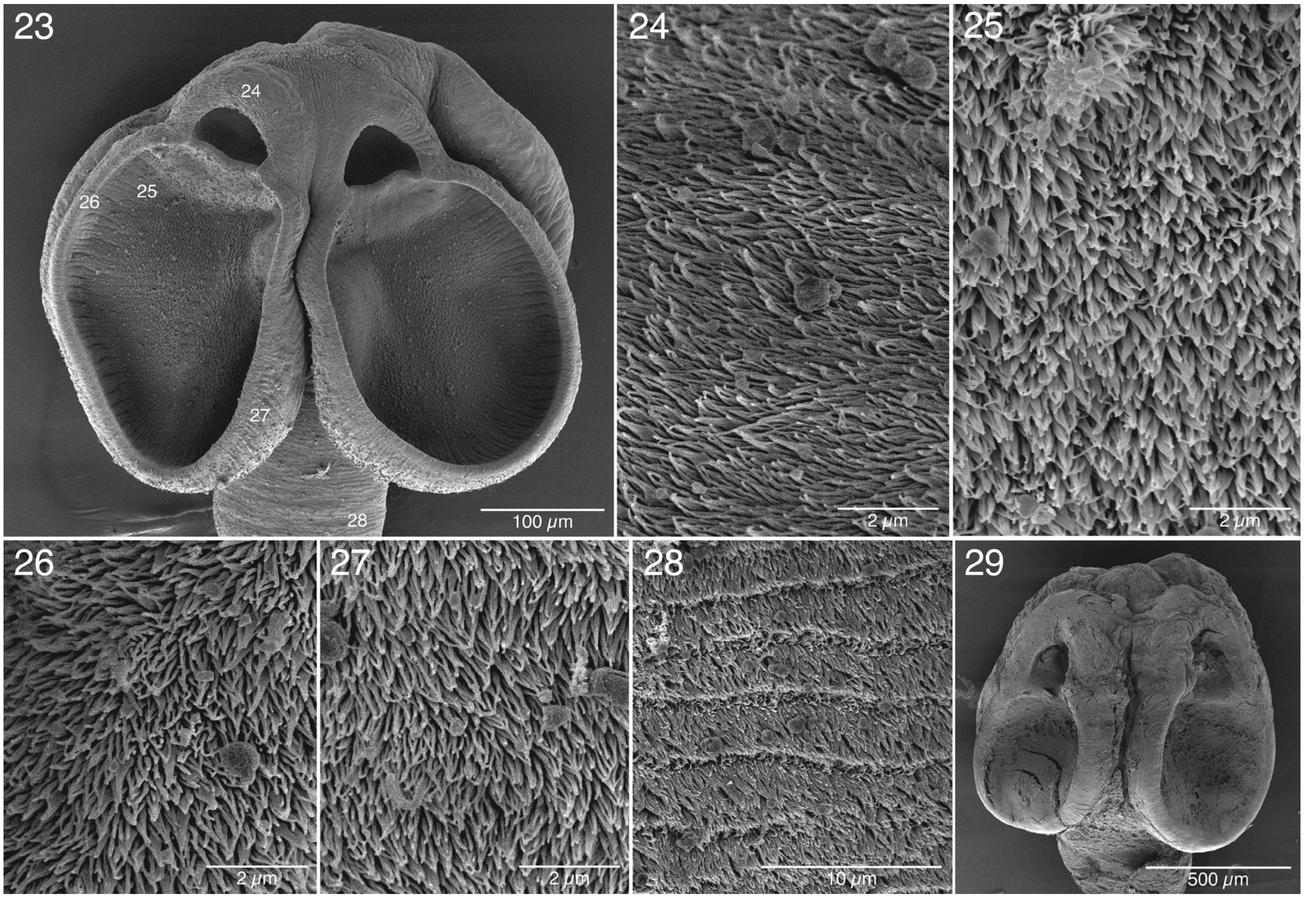
Type locality. Indian Ocean off South Africa (36°31.08'S, 21°12.16'E).

Additional localities. Indian Ocean off South Africa (36°17.60'S, 20°06.6'E; 36°34.27'S, 21°40.11'E; 34°23.83'S, 26°2.44'E).

Date of collection of holotype. 19 iv 2010.

Site of infection. Spiral intestine.

Prevalence. Five of 15 sharks examined (33%); mean intensity 4 worms per infected shark.



Figs 23–29. Scanning electron micrographs of *Yamaguticestus fairweatherae* sp. nov. (23–28) and *Yamaguticestus kuchtai* sp. nov. (29). 23, scolex of *Y. fairweatherae* sp. nov., small numbers indicate locations of 24–28; 24, distal surface of bothridium of *Y. fairweatherae* sp. nov. anterior to sucker; 25, distal surface of bothridium of *Y. fairweatherae* sp. nov. away from rim; 26, distal surface of bothridium of *Y. fairweatherae* sp. nov. near rim; 27, proximal surface of bothridium of *Y. fairweatherae* sp. nov.; 28, surface of cephalic peduncle of *Y. fairweatherae* sp. nov.; 29, scolex of *Y. kuchtai* sp. nov.

Type specimens deposited. Holotype (gravid worm, SAMCTA No. NMB P 795), 1 paratype (mature worm, SAMCTA No. NMB P 796), 1 paratype (gravid worm without scolex, SAMCTA No. NMB P 797); 1 paratype (gravid worm, USNM No. 1655917), 1 paratype (partial mature worm, USNM No. 1655918), 2 paratypes (gravid worms without scolices, USNM Nos. 1655219, 1655920); 1 paratype (mature worm, LRP No. 10333), 1 paratype (gravid worm without scolex, LRP No. 10334), 1 paratype (hologenophore, LRP No. 8665); scolex examined with SEM retained in personal collection of JNC.

Sequence data. GenBank accession MZ353647 (hologenophore, paratype, AF-24-1V, LRP No. 8665).

Etymology. This species is named for Tracey Fairweather, lead scientist during the research cruise of the *FRV Africana* that led to the discovery of this species, not only for providing JNC and KJ with the opportunity to participate in the cruise, but also for facilitating their work during the cruise.

Description

(Based on 2 gravid worms with scolices, 4 gravid worms without scolices, 2 complete mature worms, 1 partial mature worm, 1 hologenophore, and 1 scolex examined with SEM): Worms apolytic, weakly craspedote (Fig. 19), 29.9–48.9 mm (40.4 ± 8; 4) long; proglottids 159–318 (234 ± 75; 4) in total number; maximum width at level of mature proglottids. Scolex 465–644 (543 ± 61; 6) long, 580–624 (603 ± 16; 5) wide, bearing 4 bothridia. Bothridia 453–537 (494 ± 26; 5; 15) long, 302–436 (346 ± 43; 5; 13) wide, sessile anteriorly, free posteriorly, with anterior sucker and single, undivided loculus (Figs 18, 23); apical sucker 109–127 (117 ± 7; 6; 14) long, 105–147 (124 ± 11; 6; 17) wide; apical sucker length as per cent of bothridial length 22–25% (23 ± 1;

4; 7). Cephalic peduncle lacking. Neck 2.7–7.9 (4.5 ± 2.1; 4) long.

Distal bothridial surface anterior to apical sucker (Fig. 24) and loculus (Fig. 25) densely covered with gladiate spinitriches and capilliform filitriches; filitriches becoming less dense near rim (Fig. 26); proximal bothridial surface densely covered with gladiate spinitriches and capilliform filitriches (Fig. 27); neck and strobila scutellate; scutes comprised of capilliform filitriches (Fig. 28).

Immature proglottids 140–293 (219 ± 65; 5) in number, wider than long, becoming longer than wide with maturity. Mature proglottids 10–23 (13 ± 6; 5) in number; terminal mature proglottid 569–937 (708 ± 115; 10) long, 535–1041 (790 ± 159; 10) wide, length to width ratio 0.6–1.3:1 (0.9 ± 0.2; 10); genital pore 50–59% (55 ± 3; 10) of proglottid length from posterior end. Gravid and dehisced proglottids 3–16 (7 ± 5; 6) in number; terminal gravid or dehisced proglottid 681–1927 (1196 ± 397; 8) long, 657–1038 (866 ± 149; 8) wide, length to width ratio 2.5–8.0:1 (1.4 ± 0.5; 8); genital pore 53–71% (63 ± 7; 8) of proglottid length from posterior end. Testes 57–100 (81 ± 18; 7) in total number, 9–21 (14 ± 4; 9) in post-poral field, 20–50 (39 ± 8; 10; 39) long, 32–91 (63 ± 14; 10; 39) wide. Cirrus sac pyriform (Fig. 22), 180–293 (250 ± 36; 8) long, 64–102 (77 ± 12; 8) wide, thin-walled, containing weakly coiled cirrus; cirrus armed with spinitriches. Vas deferens minimal, coiled medial to cirrus sac. Genital pores irregularly alternating. Vagina surrounded by gland 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 near or near posterior margin of proglottid (Fig. 20), H-shaped in frontal view (Fig. 21), tetralobed in cross-section, strongly digitiform, 144–238 (184 ± 35; 8) long, 307–611 (446 ± 112; 8) wide. Vitellarium follicular; follicles generally wider than long, arranged in 2 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 median, ventral, sacciform, extending from ovarian isthmus to cirrus sac; uterine duct entering uterus at mid-level. Excretory vessels 4, arranged in 1 dorsal and 1 ventral pair on each lateral margin of proglottid. Eggs too densely packed to be characterized.

Remarks

With a TL of 29.9–48.9 mm, *Yamaguticestus fairweatherae* sp. nov. is a larger worm than *Y. africanae* (8.5 mm) and a smaller worm than *Y. chalarosomus*, *Y. longicolle*, *Y. metini*, and *Y. squali* (over 300, 150–300, 80, and 141 mm in TL, respectively). It bears a scolex that is shorter (465–644 vs. 679–697) and much narrower (580–624 vs. 945–955) than that of *Y. ellisi*. It further differs from *Y. metini* in that its ovary is terminal, rather than subterminal, in position, from *Y. africanae* in possessing a greater number of proglottids (159–318 vs. at least 72), and from *Y. chalarosomus*, *Y. ellisi*, and *Y. longicolle* in possessing fewer testes (57–100 vs. 312–362, 137–145, and 170–230, respectively). Unlike *Y. squali* and *Y. metini*, the distal surfaces of its bothridia bear gladiate, rather than gongylate, spinitriches.

***Yamaguticestus kihongkimi* sp. nov.**
(Figs 30–32)

ZooBank number: urn:lsid:zoobank.org:act:FC6F9017-0E64-417B-BC7F-3C809DACB2A4.

Type and only known host. *Scyliorhinus torazame* (Tanaka), cloudy catshark (Carcharhiniformes: Scyliorhinidae).

Type locality. Sea of Japan off Busan (35°09'16.2"N, 129°07'39.8"E), South Korea.

Date of collection of holotype. 18 xi 2013.

Site of infection. Spiral intestine.

Prevalence. One of 68 sharks examined (2%); mean intensity 1 worm per infected shark.

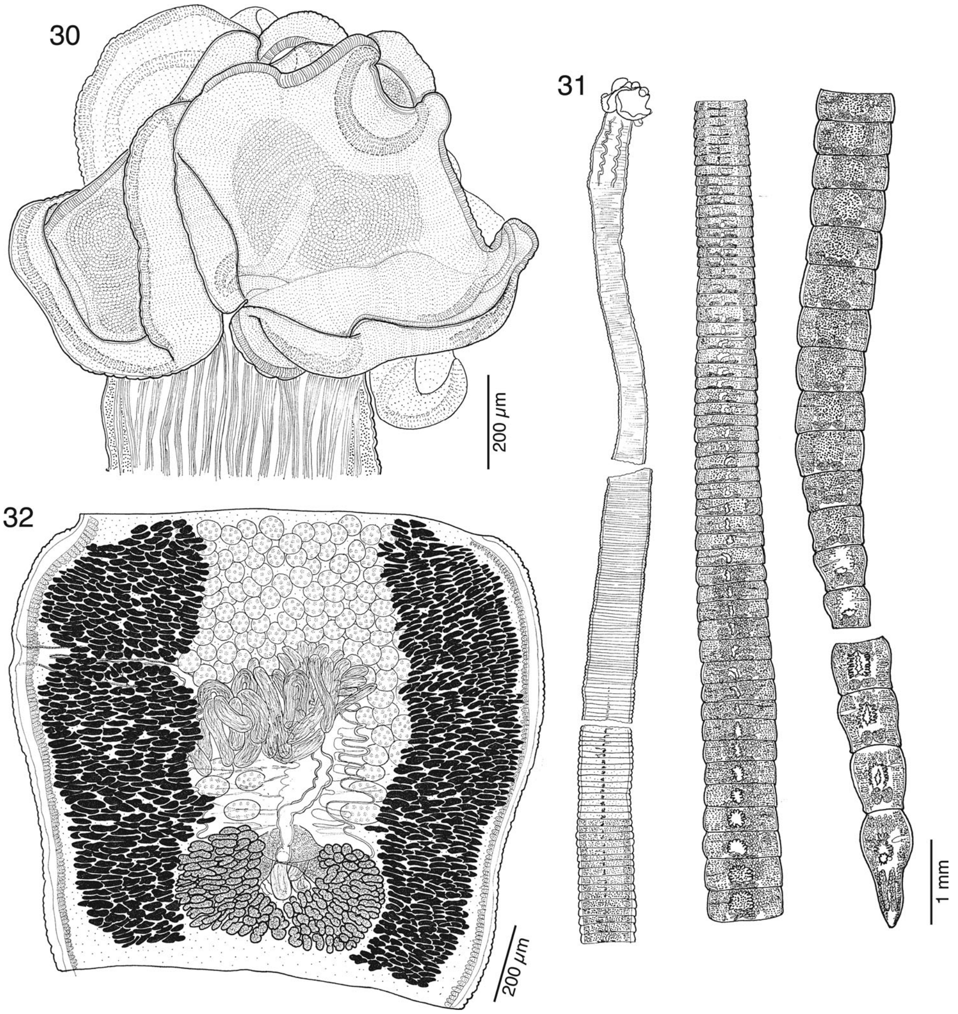
Type specimens deposited. Holotype (partial gravid worm, NIBRIV No. 0000886084).

Sequence data. GenBank accession MZ353648 (hologenophore, holotype, KO-24-1V, NIBRIV No. 0000886084).

Etymology. This species is named for Ki-Hong Kim of Pukyong National University in South Korea for graciously hosting and providing exceptional logistical support to JNC and KJ during their fieldwork in Busan, South Korea.

Description

(Based on 1 partial gravid worm): Worm apolytic, acraspedote (Fig. 31), greater than 48.2 mm in length; proglottids at least 179 in total number; maximum width 1528 at level of mature proglottids. Scolex 932 long, 1062 wide, bearing 4 bothridia. Bothridia 754–846 long,



Figs 30–32. Line drawings of holotype (NIBRIV No. 0000886084) of *Yamaguticestus kihongkimi* sp. nov. 30, scolex; 31, whole worm; 32, subterminal mature proglottid.

789–815 wide, sessile anteriorly, free posteriorly, with anterior sucker and single, undivided loculus (Fig. 30); apical sucker 216–236 long, 150–171 wide; apical sucker length as per cent of bothridial length 26–31%. Cephalic peduncle lacking. Neck 6675 long; neck and strobila scutellate. Microtriches not observed.

Immature proglottids more than 132 in number, wider than long, Mature proglottids at least 27 in number; posterior-most mature proglottid 492 long, 1468 wide, length to width ratio 0.34:1; genital pore 57% from posterior end. Gravid proglottids as least 12 in number; dehisced proglottids at least 8 in number; terminal dehisced proglottid 2359 long, 1141 wide, length to width ratio 2:1; genital pore 75% from posterior end. Testes 132–135 in total number, 23–25 in number in post-poral field, 21–28 long, 44–54 wide in posterior-most mature proglottid, 45–62 long, 54–61 wide in terminal dehisced proglottid. Cirrus sac narrowly oblong, 303 long, 55 wide in posterior-most mature proglottid, 310 long, 65 wide in terminal dehisced proglottid, thin-walled, containing weakly coiled cirrus; cirrus armed with spinitriches. Vas deferens extensively coiled, medial and posterior to cirrus sac. Genital pores irregularly alternating. Vagina surrounded by gland cells, weakly sinuous, extending from ootype essentially 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 near posterior margin of proglottid (Fig. 32), H-shaped in frontal view, tetralobed in cross-section, strongly digitiform, 159 long, 693 wide in posterior-most mature proglottid, 294 long, 566 wide in terminal dehisced proglottid. Vitellarium follicular; follicles irregular in shape, arranged in 2 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 median, ventral, sacciform, extending from ovarian isthmus to cirrus sac; uterine duct entering uterus at mid-level. Excretory vessels 4, arranged in 1 dorsal and 1 ventral pair on each lateral margin of proglottid. Eggs too densely packed to be characterized.

Remarks

Yamaguticestus kihongkimi sp. nov. exibits a scolex that is both longer (932 vs. 472–596, 637, 465–644, 600–800, and 679–697) and wider (1062 vs. 529–704, 819, 580–624, 300–400, and 945–955) than that of *Y. metini*, *Y. africanae*, *Y. fairweatherae*, *Y. longicolle*, and *Y. ellisi*, respectively, and shorter (932 vs. 2900) and narrower (1062 vs. 2900) than that of *Y. squali*. In addition, it is larger in TL than *Y. africanae* and *Y. ellisi* (48.2 vs. 8.5 and 20.7–32.7 mm, respectively) and shorter in TL than *Y. metini*, *Y. squali*, and *Y. longicolle* (48.2 vs. 80, 141, and 150–300, respectively). It further differs from *Y. fairweatherae* in its possession of an apical sucker that is longer (216–236 vs. 109–127) and slightly wider (150–171 vs. 105–147). This new species is a much smaller worm (48.2 vs. over 300 mm in TL) with many fewer testes (132–135 vs. 312–362) than *Y. chalarosomus*. Given only a single specimen of this species was found in the 68 specimens of *S. torazame* examined, we were not able to characterize the microtriches of this species with SEM.

***Yamaguticestus kuchtai* sp. nov.**

(Figs 29, 33–37)

ZooBank number: urn:lsid:zoobank.org:act:DD8966B1-CE0A-4CED-AEA2-7314566DC15D.

Type and only known host. *Apristurus aphyodes* Nakaya & Stehmann, white ghost catshark (Carcharhiniformes: Pentanchidae).

Type locality. North Atlantic Ocean off Scotland (57°38'N, 09°52'W).

Date of collection of holotype. 2 ix 2004.

Site of infection. Spiral intestine.

Prevalence. Prevalence and intensity not calculated.

Type specimens deposited. Holotype (mature worm, NHMUK No. 2021.5.25.2), 1 paratype (mature worm, NHMUK No. 2021.5.25.3), 1 paratype (detached mature proglottid, NHMUK No. 2021.5.25.4), 1 paratype (detached gravid proglottid, NHMUK No. 2021.5.25.5); 3 paratypes (mature worms, USNM Nos. 1655922–1655924), 1 paratype (detached gravid proglottid, USNM No. 1655925); 2 paratypes (mature worms, LRP Nos. 10328 and 10329), 1 paratype (detached mature proglottid, LRP No. 10330), 1 paratype (detached gravid proglottid, LRP No. 10331), 2 SEM vouchers (LRP Nos. 10283 and 10284); scolices examined with SEM retained in personal collection of JNC.

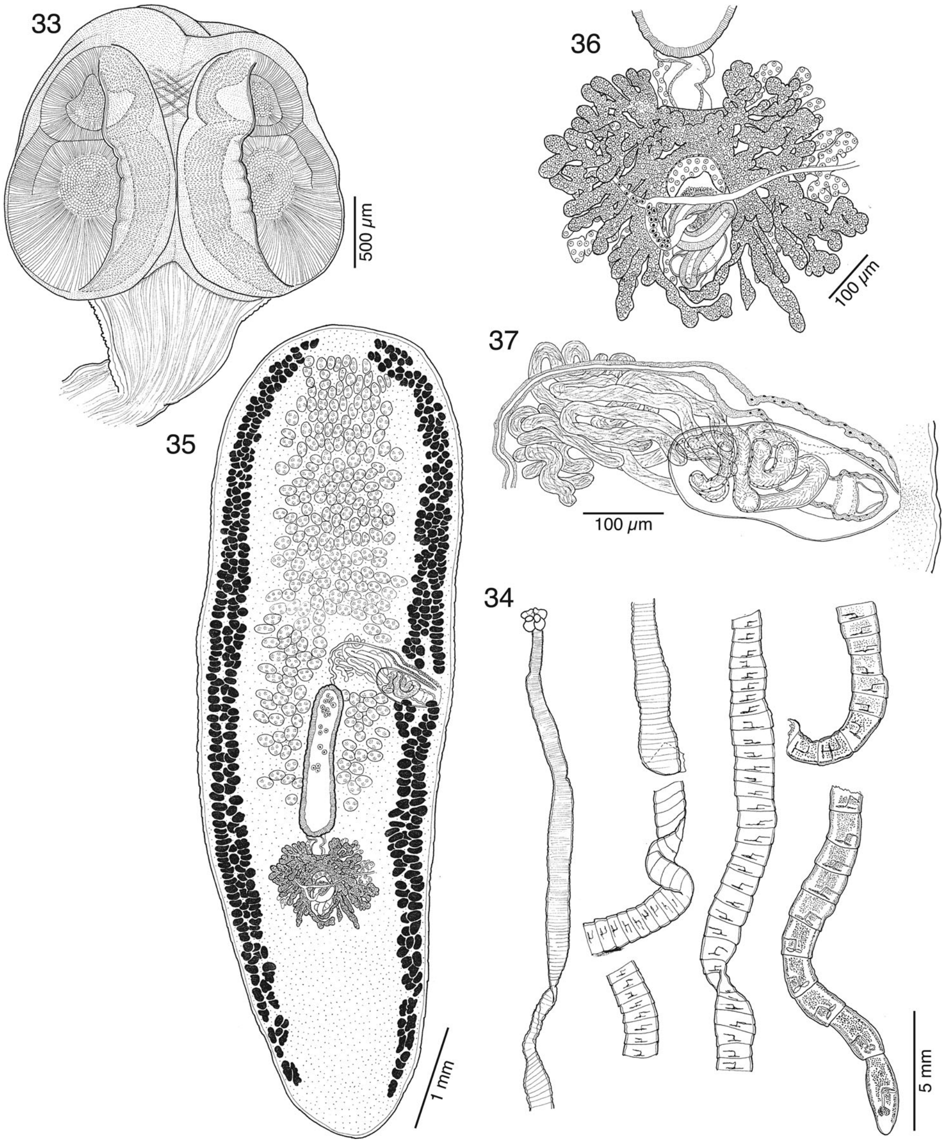
Sequence data. GenBank accession MZ353679 (hologenophore, JW418, RO-14, LRP No. 10368).

Etymology. This species honours Roman Kuchta of the Czech Academy of Sciences for his extensive work on the taxonomy and systematics of cestodes as well as for collecting the type material of this species.

Description

(Based on 7 mature worms, 2 detached mature proglottids, 3 detached gravid proglottids, and 2 scolices examined with SEM): Worms euapolytic, acraspedote (Fig. 34), 89–164 mm (113 ± 33; 7) long; proglottids 181–246 (205 ± 21; 7) in total number; maximum width at level of posterior-most immature proglottids. Scolex 717–1125 long, 975–1235 wide, bearing 4 bothridia. Bothridia 695–957 (839 ± 82; 7; 13) long, 546–746 (630 ± 65; 7; 13) wide, sessile anteriorly, free posteriorly, highly muscular, with anterior sucker and single, undivided loculus (Fig. 33); apical sucker 280–406 (345 ± 36; 7; 17) long, 332–512 (399 ± 49; 7; 18) wide; apical sucker length as per cent of bothridial length 36–48% (43 ± 4; 6; 13). Cephalic peduncle lacking. Neck 5.1–14 (9.7 ± 3.6; 7) long. Microtriches not observed.

Immature proglottids 107–242 (189 ± 42; 7) in number, wider than long, becoming longer than wide with maturity. Mature proglottids 1–5 (3 ± 1.5; 7) in number; terminal mature proglottid 2527–3484 (2861 ± 417; 7) long, 1007–1515 (1301 ± 189; 7) wide; length to width ratio 1.8–3.4:1 (2.3 ± 0.6; 7). Testes 186–361 (269 ± 69; 7) in total number, 16–39 (24 ± 8; 7) in number in postporal field, 31–59 (44 ± 4; 7; 28) long, 40–76 (55 ± 11; 7; 28) wide. Cirrus sac narrowly oblong (Fig. 37), 299–432 (373 ± 43; 7) long, 101–151 (122 ± 16; 7) wide, thin-walled, tilted slightly anteriorly, containing weakly coiled cirrus; cirrus armed with spinitriches. Vas deferens minimal, coiled medial to cirrus sac. Genital pores irregularly alternating, 40–69% (55 ± 9; 7) of proglottid length from posterior end. Vagina surrounded by gland cells, weakly sinuous, extending from ootype along midline of proglottid to anterior margin of cirrus sac, then



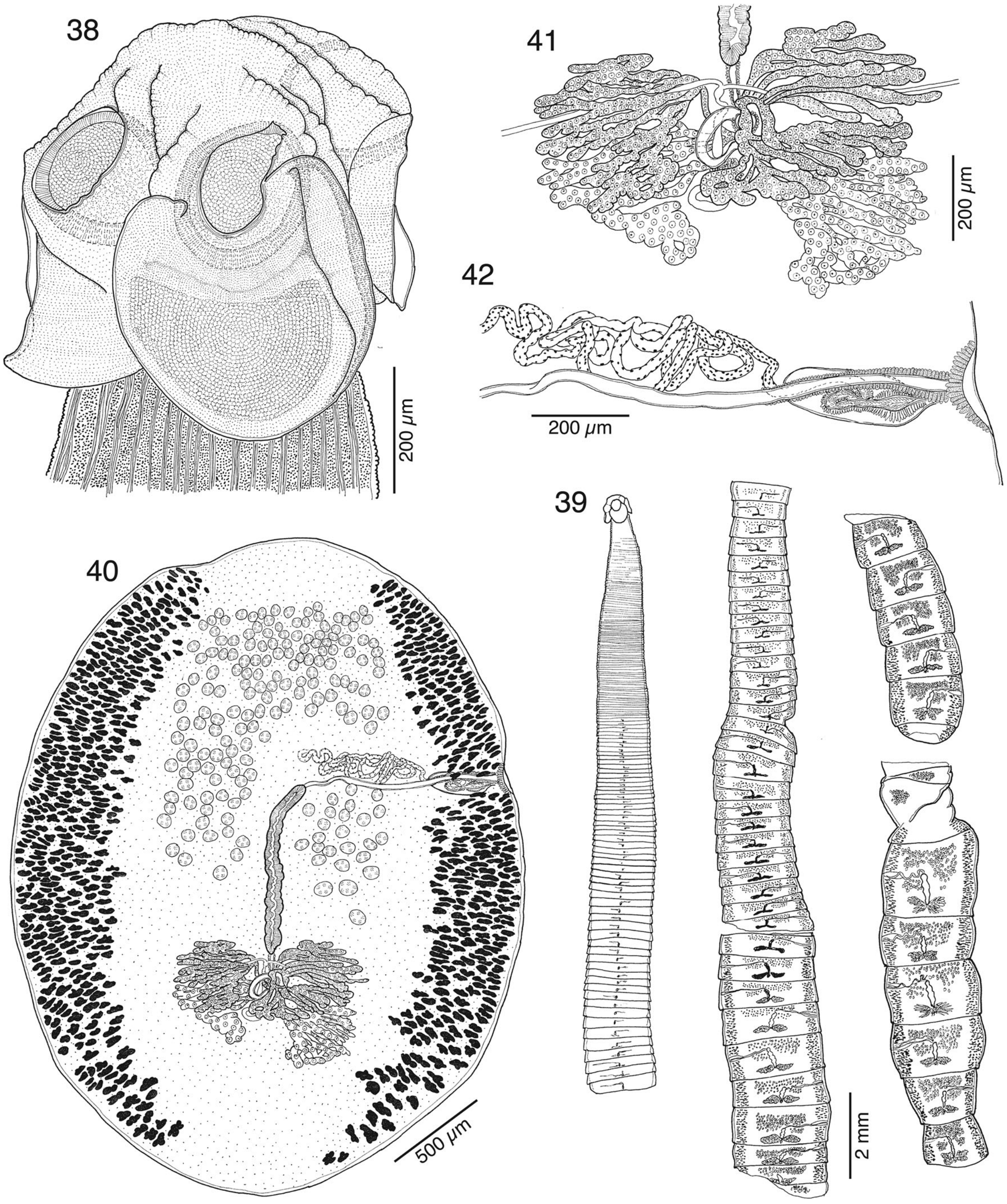
Figs 33–37. Line drawings of *Yamaguticestus kuchtai* sp. nov. 33, scolex (holotype, NHMUK No. 2021.5.25.2); 34, whole worm (paratype, USNM No. 1655922); 35, detached mature proglottid (paratype, NHMUK No. 2021.5.25.4); 36, detail of ovary (paratype, NHMUK No. 2021.5.25.5); 37, detail of terminal genitalia (paratype, NHMUK No. 2021.5.25.5).

laterally along anterior margin of cirrus sac to open into common genital atrium anterior to cirrus sac. Ovary subterminal in position (Fig. 35), H-shaped in frontal view (Fig. 36), tetralobed in cross-section, strongly digitiform, 297–565 (444 ± 198; 7) long, 390–670 (510 ± 97; 7) wide. Vitellarium follicular; follicles oval in shape, arranged in 2 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 median, ventral, sacciform, extending from ovarian isthmus to cirrus sac; uterine duct entering uterus at mid-level. Excretory vessels 4, arranged in 1 dorsal and 1 ventral pair on each lateral margin of proglottid.

Detached mature proglottids 3833–5589 long, 1186–1385 wide, length to width ratio 3.2–4:1; genital pore 52–56% of proglottid length from posterior end. Detached gravid proglottids 5917–6507 long, 978–1514 wide, length to width ratio 3.9–6.4:1; genital pore 47–58% proglottid length from posterior end. Eggs too collapsed to be characterized.

Remarks

This new species is greater in TL than *Y. africanae*, *Y. ellisi*, *Y. fairweatherae*, *Y. kihongkimi*, and *Y. metini* (89–164 vs. 8.5, 20.7–32.7, 29.9–48.9, 48.2, and 80 mm, respectively). It possesses fewer



Figs 38–42. Line drawings of *Yamaguticestus tuncurryensis* sp. nov. 38, scolex (holotype, QM No. G239135); 39, whole worm (holotype, QM No. G239135); 40, detached mature proglottid (holotype, USNM No. 1655927); 41, detail of ovary (holotype, USNM No. 1655927); 42, detail of terminal genitalia (holotype, USNM No. 1655927).

proglottids than *Y. longicolle* and *Y. metini* (181–246 vs. 400–600 and 400, respectively). Its scolex is conspicuously shorter (717–1125 vs. 2900) and narrower (975–1235 vs. 2900) than that of *Y. squali*. It further differs from *Y. africanae*, *Y. ellisi*, and *Y. kihongkimi* in its possession of a greater number of testes (186–361 vs. 82, 137–145, and 132–135, respectively) and further differs from *Y. fairweatherae* in possessing a longer scolex (717–1125 vs. 465–644). *Yamaguticestus kuchtai* sp. nov. further differs from

Y. squali and *Y. longicolle* in that its ovary is conspicuously subterminal, rather than terminal, in position. It is a substantially smaller worm (89–164 vs. over 300 mm in TL) with fewer proglottids (181–246 vs. 414–461) than *Y. chalarosomus*.

The surfaces of the scolex of all specimens of *Y. kuchtai* appeared to be disrupted. This was confirmed in the specimens prepared for and examined with SEM (Fig. 29). As a consequence, characterization of the microtriches of the surfaces of the scolex was not possible.

Yamaguticestus tuncurryensis sp. nov.

(Figs 38–42)

ZooBank number: urn:lsid:zoobank.org:act:169C5164-D902-4CD6-AE70-6393AEC8D040.

Type and only known host. *Asymbolus analis* (Ogilby), grey spotted catshark (Carcharhiniformes: Scyliorhinidae).

Type locality. Pacific Ocean off Tuncurry (32°10'23.49"S, 152°30'38.66E), New South Wales, Australia.

Date of collection of holotype. 26 ix 1991.

Site of infection. Spiral intestine.

Prevalence. One of 12 sharks examined (8%); mean intensity 1 worm per infected shark.

Type specimens deposited. Holotype mounted on 5 slides: 2 slides (1 partial worm including scolex and 2 gravid proglottids, QM No. G239135), 1 slide (portion of strobila, USNM No. 1655926), 1 slide (5 detached mature proglottids, USNM No. 1655927), 1 slide (2 detached mature and 2 detached pre-gravid proglottids, LRP No. 10332).

Sequence data. None.

Etymology. This species is named for its type locality, the fishing town of Tuncurry in New South Wales, Australia.

Description

(Based on 1 partial mature worm and what we assume are its 5 detached mature proglottids, 2 detached pre-gravid proglottids, and 2 detached gravid proglottids): Worms euapolytic, acraspedote (Fig. 39), greater than 58.1 mm in length; proglottids at least 200 in total number; maximum width at level of mature proglottids. Scolex 649 long, 641 wide, bearing 4 bothridia. Bothridia 474–534 long, 388 wide, sessile anteriorly, free posteriorly, with anterior sucker and single, undivided loculus (Fig. 38); apical sucker 206–232 long, 222–234 wide; apical sucker length as per cent of bothridial length 41–44%. Cephalic peduncle lacking. Neck 332 long; neck and strobila weakly scutellate. Microtriches not observed.

Immature proglottids wider than long, becoming longer than wide with maturity. Mature proglottids 1104–2274 long, 1703–2277 wide, length to width ratio 0.5–1.2:1. Testes 134–174 in total number, 19–23 in number in post-poral field, 36–50 long, 36–50 wide. Cirrus sac narrowly oblong (Fig. 42), 293–332 long, 79–84 wide, thin-walled, containing weakly coiled cirrus; cirrus armed with spinitriches. Vas deferens minimal, coiled medial to cirrus sac. Genital pores irregularly alternating, 56–60% of proglottid length from posterior end. Vagina surrounded by gland 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 (Fig. 40), H-shaped in frontal view (Fig. 41), tetralobed in cross-section, strongly digitiform, 170–182 long, 691–910 wide. Vitellarium follicular; follicles irregular in shape, arranged in 2 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 median, ventral, sacciform, extending from ovarian isthmus to cirrus sac; uterine duct entering uterus at mid-level. Excretory vessels 4, arranged in 1 dorsal and 1 ventral pair on each lateral margin of proglottid.

Detached mature proglottids 2797–5522 (3956 ± 1288; 5; 5) long, 2017–2575 (2302 ± 261; 5; 5) wide, length to width ratio 1.2–2.7:1 (1.8 ± 0.8; 5; 5); genital pore 59–66% (62 ± 3; 5; 5) from posterior end. Detached pre-gravid proglottids 7406–8059 long, 2502–2525 wide, length to width ratio 2.9–3.2:1; genital pore 58–63% from posterior end. Detached fully gravid proglottids 8097–9028 long, 5058–5341 wide, length to width ratio 1.6–1.7:1. Eggs too densely packed to be characterized.

Remarks

Yamaguticestus tuncurryensis sp. nov. differs from *Y. ellisi*, *Y. fairweatherae*, *Y. kihongkimi*, and *Y. squali* in that it is euapolytic, rather than apolytic. In addition, it has a narrower scolex than *Y. ellisi* (641 vs. 945–955), a greater number of testes than *Y. fairweatherae* (134–174 vs. 57–100), and an ovary that is subterminal, rather than terminal as it is in *Y. kihongkimi* and *Y. squali*. Its detached mature proglottids are conspicuously wider (2017–2575 vs. 1186–1385) and more oval as assessed by length to width ratio (1.2–2.7:1 vs. 3.2–4.4:1) than those of *Y. kuchtai*. This new species is a conspicuously larger worm (greater than 58.1 vs. 8.5 mm in TL) with a greater number of testes (134–174 vs. 82) than *Y. africanae*. *Yamaguticestus tuncurryensis* sp. nov. differs from *Y. longicolle* in that it is a smaller worm (greater than 58.1 vs. 150–300 mm in TL) with an ovary that is subterminal rather than terminal. This new species differs from *Y. metini* in possessing longer bothridia (388 vs. 280–315) and a shorter cirrus sac (330–417 vs. 451) and in that the apical suckers of its bothridia are shorter relative to the length of the bothridia than those of *Y. metini* (41–44% vs. 46–57%). As a result of the limited available material, this species was not characterized with SEM nor were sequence data generated.

Discussion

All seven species treated here are fully consistent with the original diagnosis of *Yamaguticestus* presented by Caira et al. (2021). Our work brings the total number of described species in the genus to 10. Evidence of several undescribed species in the squaliforms *Squalus acanthias* L. and *Etmopterus spinax* L. (see Vasileva et al., 2002) and the scyliorhinid *Cephaloscyllium laticeps* (see Caira et al., 1999) expands the diversity of the genus even further. But even without the latter taxa, with 10 valid species, *Yamaguticestus* ranks third among the 22 other phyllobothriidean genera with respect to total number of species; it is exceeded only by *Rockacestus* Caira et al., 2021 and *Scyphophyllidium* Woodland, 1927 with 10 and 43 valid species, respectively (Caira et al., 2020b, 2021).

At this point, five of the 10 described species of *Yamaguticestus* have been examined with SEM. Both species examined by Caira et al. (2021) were found to possess gongylate columnar spinitriches on their distal bothridial surfaces. In contrast, all three species examined here possessed gladiate spinitriches on these surfaces. This type of intrageneric variation is unusual among the Phyllobothriidea and in fact has been observed only on the proximal bothridial surfaces across species of *Scyphophyllidium* (see Table 1 of Caira et al., 2020b) and *Orygmatobothrium* Diesing, 1863 (see Ivanov, 2008). However, to our knowledge, it has not been observed on the distal bothridial surfaces of either of these other genera.

Our results expand the pattern of low, or even no, sequence divergence seen among species of *Yamaguticestus* in the D1–D3 region of the *28S rRNA* gene reported by Caira et al. (2021) to include five additional members of the genus. This is especially puzzling given the substantial differences in size and morphology, as observed with both light and scanning electron microscopy, that exist across species of *Yamaguticestus* – not to mention their differences in geographic distribution and host associations. It would be extremely interesting to explore interspecific variation further using additional molecular markers (e.g., COI; see Ruhnke et al., 2020) across members of this genus.

One of the most striking aspects of the biology of *Yamaguticestus* is the remarkably low intensity of infection seen in many of its members. The five species described here for which intensity was assessed occurred in intensities of only 1–4 worms per host. These numbers are consistent with those seen previously in other members of the genus. Caira et al. (2021) reported finding only a single specimen of *Y. metini* in each of the four of 50 specimens of the tiger catshark *Halaelurus natalensis* they found infected. Similarly low intensities have been observed in *Y.* cf. *squali* (as *Phyllobothrium squali* Yamaguti, 1952) in the squaliform shark *Squalus acanthias*. Vasileva et al. (2002) reported a mean intensity of 2.4 worms in the 9 of 17 individuals they found infected in the Black Sea. Pickering and Caira (2014) reported mean seasonal intensities of infection that ranged from 1–2.3 worms in the 25 of 217 sharks they found infected off the coast of Rhode Island. However, *Y. chalarosomus* appears to be an exception given Alexander (1963) reported finding as many as eight worms in one of the catsharks he examined.

The fact that several species of *Yamaguticestus* also appear to exhibit an exceptionally low prevalence of infection leads one to wonder how it is possible these species can maintain sufficiently high population sizes to survive in a marine ecosystem. Of particular note are *Y. kihongkimi* and *Y. ellisi* each of which had an intensity of infection of only one worm per host and a prevalence of infection of 2% and 3%, respectively in the 68 and 58 sharks examined. One thing to consider is that these results represent only snapshots in time and thus it is possible that these low numbers are not representative of infection prevalences and intensities over the full year. In fact, Pickering and Caira (2014) found some evidence for seasonal variation in prevalence and intensity in *Y.* cf. *squali* across the 33 months of their study. They found prevalence to be uniformly low in winter (5%), spring (5%), and summer (7%), and to peak in autumn (17%). Intensity was one worm per host in winter and spring, 1–2 worms per host in summer, but

Table 1. Key distinguishing features of species of *Yamaguticestus*.

Species of *Yamaguticestus*	***Y. squali* (Yamaguti, 1952) Caira et al., 2021**	***Y. longicolle* (Euzet, 1959) Caira et al., 2021**	***Y. metini* Caira et al., 2021**	***Y. chalarosomus* (Alexander, 1963) n. comb.**	***Y. africanae* sp. nov.**	***Y. ellisi* sp. nov.**	***Y. fairweatherae* sp. nov.**	***Y. kihongkimi* sp. nov.**	***Y. kuchtai* sp. nov.**	***Y. tuncurryensis* sp. nov.**
Source	Yamaguti (1952); Vasileva et al. (2002)	Euzet (1959)	Caira et al. (2021)	Alexander (1963)	this study	this study	this study	this study	this study	this study
Apolysis	apolytic	apolytic†	euapolytic	apolytic	euapolytic	apolytic	apolytic	apolytic	euapolytic	euapolytic
Total length (mm)	140; 141	150–300	80	over 300	>8.5	>20.7–32.7	29.9–48.9	>48.2	89–164	>58.1
Total no. proglottids.	300	400–600	400	414–461	at least 72	>253–292	159–318	at least 179	181–246	at least 200
Scolex length	2850; 2900	600–800	472–596		637	679–697	465–644	932	717–1125	649
Scolex width	2850; 2900	300–400	529–704	1196–1650	819	945–955	580–624	1062	975–1235	641
Bothridial length	not given; 1500–1800		409–435	949–1105	583–589	562–647	453–537	754–846	695–957	474–534
Bothridial width			280–315		422	504–592	302–436	789–815	546–746	388
Apical sucker length	300–350; 289–360	150	201–281	598–650	171–190	166–207	109–127	216–236	280–406	206–232
Apical sucker width	300–350; 289–360	150	176–253	598–650	159–179	144–198	105–147	150–171	332–512	222–234
Spinithrix shape on distal bothridial surface	gongylate*		gongylate		gladiate	gladiate	gladiate			
Total no. testes	80–100; 237–301	170–230	158–184	312–362	82	137–145	57–100	132–135	186–361	134–174
Cirrus sac length	500; 354–495	350	451			209–243	180–293	303	299–432	293–332
Cirrus sac width	150–200; 96–161	200	79			68–78	64–102	55	101–151	79–84
Ovary position			subterminal		subterminal	near post. margin	near post. margin	near post. margin	subterminal	subterminal
Ovary length			577			235	144–238	159	297–565	170–182
Ovary width			554			497	307–611	623	390–670	691–910

*Caira et al. (2021).

†Following terminology of Caira et al. (1999).

increased to 1–12 worms per host for a mean intensity of 2.3 in autumn.

Given these data, the importance of sample size when evaluating the presence of *Yamaguticestus* in a species of catshark cannot be understated. Furthermore, if the prevalences observed in the two infected scyliorhinid species and four infected pentanchid species are an indication of prevalences across their respective families in general, larger sample sizes may be required to detect infections in scyliorhinids than in pentanchids. Prevalence in the scyliorhinids examined here ranged from 2–13%, whereas in the pentanchids it ranged from 8–50%. In this context, given the small sample size necropsied (i.e., 1–6 individuals per species), neither the pentanchid species *Haploblepharus edwardsii*, the scyliorhinid species *Atelomycterus marmoratus*, *Poroderma pantherinum*, and *Schroederichthys bivius*, nor their respective genera should be eliminated as possible hosts for *Yamaguticestus* until a larger number of individuals has been examined.

Our results lead us to believe that the prediction of Caira et al. (2021) that the species of pentanchids and scyliorhinids not yet examined for *Yamaguticestus* will be found to host 70 additional species globally is actually a relatively conservative estimate. Beyond three additional species of *Scyliorhinus* Blainville, the new species described here expand the catshark hosts of *Yamaguticestus* to include species in the pentanchid genera *Apristurus* Garman, *Asymbolus* Whitley, and *Holohalaelurus* Fowler. Transfer of *Y. chalarosomus* expands the hosts of *Yamaguticestus* even further to include a species of *Cephaloscyllium* and thus also a second genus of scyliorhinid shark. In total, the seven species of catsharks considered here alone yielded 10% of the biodiversity predicted by Caira et al. (2021). The vast majority of the 160 species of pentanchids and scyliorhinids (Weigmann et al., 2018; Soares et al., 2019; White et al., 2019) remain to be examined. Given that more than 50% of these belong to the six genera now known to host *Yamaguticestus*, even if none of the other 10 genera of catsharks are found to host *Yamaguticestus* – which seems unlikely given the non-selective nature of our sampling of host genera – what is now 63 additional species is likely to be an underestimate of global biodiversity.

Disclosure statement

The authors declare no conflicts of interest.

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Supplementary material

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