

ERUDITUNCUS N. GEN. (TETRAPHYLLIDEA: ONCHOBOTHRIIDAE) WITH A REDESCRIPTION OF *E. MUSTELI* (YAMAGUTI, 1952) N. COMB. AND COMMENTS ON ITS HOOK HOMOLOGIES

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ABSTRACT: Examination of type and new material of *Platybothrium musteli* Yamaguti, 1952, resulted in the erection of a new genus, *Erudituncus*, the new combination *Erudituncus musteli* (Yamaguti, 1952), and the redescription of the newly combined species. This species exhibits novel hook morphology. Each bothridium bears 2 pairs of hooks, the axial pair comprising 1 medial and 1 lateral bipronged hook and the abaxial pair comprising a lateral unipronged hook and a medial, simple hook element. Based on the position of the hook talons, we suggest that the inner prong of the axial hooks of *Erudituncus* is homologous to the single prong of the axial hooks of *Calliobothrium* and the axial prongs of *Dicranobothrium*, *Platybothrium*, *Phoreiobothrium*, and *Onchobothrium*; the outer prong of the axial hooks of *Erudituncus* is homologous to the abaxial prongs of *Dicranobothrium*, *Platybothrium*, *Phoreiobothrium*, and *Onchobothrium*; and the abaxial hooks of *Erudituncus* and *Calliobothrium* are homologous. *Erudituncus musteli* was lacking from 31 individuals of the type host of record, the triakid shark *Mustelus manazo* Bleeker, 1854, examined for this study, but was obtained from 2 individuals of the triakid shark *Hemitriakis japonica* (Müller and Henle, 1839). Therefore, *H. japonica* is proposed as the probable type host of *E. musteli*.

Platybothrium musteli Yamaguti, 1952, was originally described from *Mustelus manazo* Bleeker, 1854, in Japan. Close examination of Yamaguti's (1952) figures and type specimens suggests that this species may not be a typical member of *Platybothrium* Linton, 1890; each bothridium is divided into 2, rather than 3, loculi, and the lateral hooks on each bothridium seem to possess 3, rather than 2, pointed elements. Unfortunately, to our knowledge, *P. musteli* has not been reported since its original description, and the only available material are the 3 specimens constituting the type series, none of which is in sufficiently good condition and/or orientation to provide a complete picture of its morphology. Recent collections from elasmobranchs in Japan provided new material of this species, allowing for a redescription. This has prompted us to erect the new genus diagnosed here because it is clear that, among other distinctive features, this species possesses a previously unknown hook condition. An explanation of the hook terminology adopted for this species and the hook component homology assertions made in the development of this terminology are presented. These new collections also call into question the identification of the type host of this species.

MATERIALS AND METHODS

The spiral intestines of 30 individuals of the type host of record for *Platybothrium musteli*, *Mustelus manazo*, collected with bottom trawls in Japan from Tsugaru Straits near Shiriyazaki, Aomori Prefecture, Tokyo Bay near Yokohama, Kanagawa Prefecture, and Japan Sea near Tsushima, Nagasaki Prefecture, and sent to us by Atsuko Yamaguchi in January 1996, were examined for tapeworms. Twenty-six of the intestines had been frozen at -30 C for a short time and subsequently fixed in 4% formalin. Tapeworms were removed, identified, and placed in 70% ethanol for storage. Tapeworms were removed from the remaining 4 intestines, fixed in 4% formalin, and sent to the University of Connecticut, where they were identified and placed in 70% ethanol for storage. In addition, tapeworms were removed from the spiral intestines of 2 specimens of *Hemitriakis japonica* (Müller and Henle, 1839) and 1 specimen of *M. manazo* collected from a set net in Suruga Bay near Yui, Shizuoka Prefecture, Japan, in December 1996 and October 1999,

fixed in 4% formalin, identified, and placed in 70% ethanol for storage. Specimens prepared as whole mounts for light microscopy were stained with Delafield's hematoxylin or carmine, dehydrated in a graded ethanol series, cleared in xylene, clove oil, or methyl salicylate, and mounted in Canada balsam.

Illustrations were drawn using a drawing tube. Hook terminology and measurements were adapted from Caira (1985a, 1985b). Measurements for medial and lateral axial hooks (Fig. 1) are: A' and A, distance from tip of outer prong to junction between outer and inner prongs; B' and B, distance from tip of inner prong to junction between inner and outer prongs; C' and C, distance from axial tip of base to junction between inner prongs; D' and D, distance from axial tip of base to tip of inner prongs; F' and F, length of talon (not illustrated); G' and G, hook total length measured from anteriormost to posteriormost extremities of hooks. Measurements for the lateral abaxial hook (Fig. 1) are: H, distance from axial tip of base to tip of prong; I, distance from tip of prong to anteriormost extremity of base; J, distance from anteriormost extremity of base to axial tip of base. The length and width of the medial abaxial hook and accessory piece were measured (Fig. 1, measurements not illustrated). Other morphological terminology follows Caira et al. (1999) or Caira et al. (2001). All measurements are given in micrometers unless otherwise stated. For each measurement, the range is followed by the mean, standard deviation, number of worms measured (n), and number of measurements taken (n) if more than 1 measurement was made per worm.

The following museum abbreviations were used: Institute of Parasitology, Academy of Sciences of the Czech Republic, České Budejovice, Czech Republic (IPCAS), Meguro Parasitological Museum, Tokyo, Japan (MPM), and U.S. National Parasite Collection, Beltsville, Maryland (USNPC).

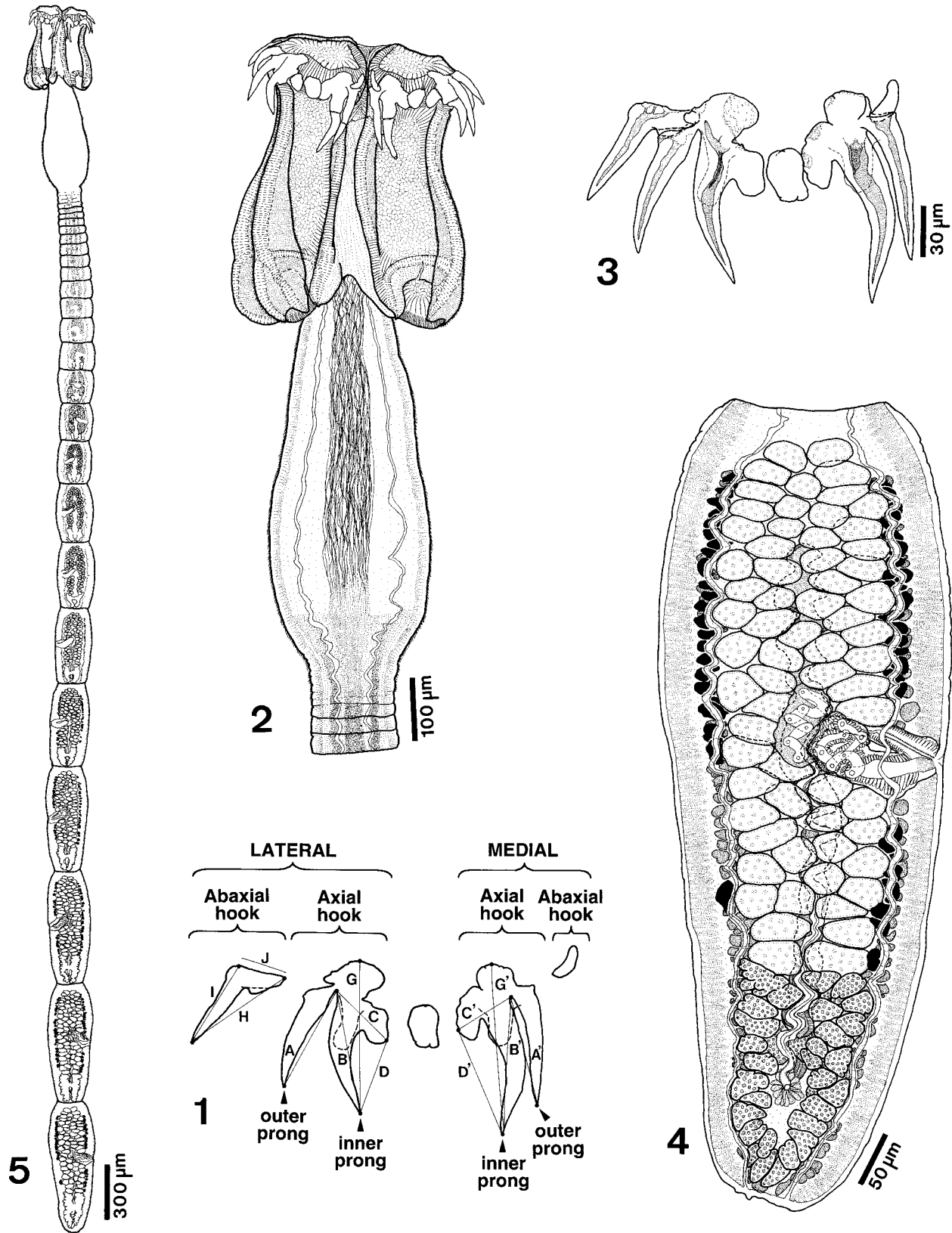
DESCRIPTION

Erudituncus n. gen.

Diagnosis: Scolex with 4 bothridia and cephalic peduncle. Each bothridium with specialized anterior region in form of loculus and 2 pairs of articulated hooks; each bothridium divided into 2 loculi by 1 transverse septum. Lateral and medial axial hooks each hollow, with 2 prongs, 1 talon, and medially extended base. Lateral abaxial hook hollow, with 1 prong and medially extended base; medial abaxial hook solid, in form of simple oblong element, lacking prongs and base. Segments acraspedote, eupolytic. Genital pores lateral, irregularly alternating. Testes numerous, in primary field, lateral and anterior to vagina, and postvaginal field. Vagina anterior to cirrus sac. Ovary posterior, H-shaped in dorsoventral view, tetralobed in cross section. Vitelline follicles lateral, in 1 dorsal and 1 ventral column on each margin of the segment; dorsal and ventral columns interrupted at genital atrium; dorsal columns also interrupted by ovary. Uterus medial, extending beyond

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FIGURES 1–5. Line drawings of *Erudituncus musteli* n. comb. 1. Hook components drawn disarticulated to more clearly illustrate hook terminology and hook measurements. 2. Scolex of voucher (MPM 19764). 3. Hooks of holotype (MPM 22777). 4. Dorsal view of segment of voucher (MPM 19764). 5. Whole worm drawing of voucher (MPM 19764).

cirrus sac, not reaching anterior margin of segment. Eggs not known. Parasites of Triakidae in waters near Japan.

Type and only known species: Erudituncus musteli (Yamaguti, 1952) n. comb.

Etymology: This name comes from the Latin “eruditus” (instructed, educated) and “uncus” (hook), which were chosen because we find the hook morphology of this taxon to be very illuminating with respect to hook morphologies in this family.

Remarks

Erudituncus is a member of the Onchobothriidae (Tetraphyllidea), whose species possess bothridial hooks. *Erudituncus* is distinguished from all other onchobothriid genera by its hook morphology. Whereas most onchobothriids possess a single pair of hooks, *Biloculuncus* Nasin, Caira, and Euzet, 1997, *Calliobothrium* Van Beneden, 1850 and *Erudituncus* possess 2 pairs of hooks. However, unlike *Biloculuncus* and *Calliobothrium*, the axial hooks of *Erudituncus* are bipronged rather than unipronged. *Erudituncus* also differs from all other onchobothriid genera recognized by Caira et al. (2001) except *Biloculuncus*, *Phoreiobothrium* Linton, 1889, and *Uncibilocularis* Southwell, 1925, in its possession of 2 rather than 1 or 3 bothridial loculi. It is distinguished from *Phoreiobothrium* and *Uncibilocularis* in its possession of 2 pairs rather than 1 pair of hooks. *Erudituncus* is most similar to *Biloculuncus*. In addition to differences in hook morphology, they can be distinguished from each other by the shape of the ovary in dorsoventral view and cross section (H-shaped and tetralobed in *Erudituncus* and inverted A-shaped and bilobed in *Biloculuncus*).

Erudituncus musteli (Yamaguti, 1952) n. comb.

(Figs. 1–5)

Synonym: Platybothrium musteli Yamaguti, 1952.

Redescription (based on 6 complete worms): Worms euapolytic, 3.64–6.76 mm (4.72 ± 1.14 , $n = 6$) long, with greatest width 330–420 (371 ± 37 , $n = 4$) at scolex; 12–28 (16.7 ± 6 , $n = 6$) segments per worm. Scolex 650–1,150 (910.8 ± 208.2 , $n = 6$) long, with 4 bothridia and cephalic peduncle. Cephalic peduncle 380–840 (647.9 ± 177.7 , $n = 6$) long, gradually wider posteriorly, extending beyond posterior margin of bothridia. Bothridia 310–460 (404.1 ± 59 , $n = 6$, $n = 11$) long by 140–195 (170.6 ± 17.8 , $n = 6$, $n = 9$) wide, each with specialized anterior region in form of loculus, 2 pairs of articulated hooks, and 1 accessory piece; each divided into 2 loculi by 1 transverse septum. Specialized anterior region loculus 62–75 (68.4 ± 4.2 , $n = 4$, $n = 7$) long by 135–175 (149.2 ± 14.6 , $n = 4$, $n = 6$) wide. Anterior loculus 192–280 (250.9 ± 31.5 , $n = 6$, $n = 11$) long by 140–195 (170.6 ± 17.8 , $n = 6$, $n = 9$) wide. Posterior loculus 88–130 (108.3 ± 12.5 , $n = 6$, $n = 12$) long by 108.8–150 (132 ± 13.1 , $n = 5$, $n = 8$) wide.

Lateral and medial axial hooks each with 1 anteriorly and axially extended base, 1 inner prong, 1 outer prong, and 1 talon; talon extending from proximal surface of base and lying under inner prong. Axial prongs and talons hollow; internal channel of prongs unconnected, with separate openings on each prong. Lateral abaxial hook hollow, with 1 prong and medially extended base; base articulating with and lying under proximal surface of lateral axial hook. Medial abaxial hook solid, crescent-shaped, lacking prong and base, articulating with and lying on anterodistal surface of outer prong of medial axial hook. Lateral hook measurements (Fig. 1): A, 74–100 (85.3 ± 8.1 , $n = 6$, $n = 9$); B, 76–95 (86.8 ± 6.8 , $n = 6$, $n = 9$); C, 42–55 (48 ± 5.3 , $n = 6$, $n = 7$); D, 48–65 (55.9 ± 6.2 , $n = 6$, $n = 7$); E, 25–32 (28.8 ± 2.5 , $n = 6$, $n = 7$); G, 92–115 (105.6 ± 6.7 , $n = 6$, $n = 9$); H, 60–82 (71.4 ± 7.8 , $n = 6$, $n = 7$); I, 40–70 (60 ± 10.6 , $n = 6$, $n = 7$); J, 19–65 (36.4 ± 14.7 , $n = 6$, $n = 7$). Medial hook measurements (Fig. 1): A', 78–92 (84.2 ± 5 , $n = 4$, $n = 8$); B', 91–126 (103.8 ± 10.9 , $n = 4$, $n = 8$); C', 42–50 (45.6 ± 2.7 , $n = 4$, $n = 8$); D', 75–95 (85.8 ± 7.2 , $n = 4$, $n = 8$); F', 30–36 (33 ± 2.7 , $n = 4$, $n = 8$); G', 115–138 (126.6 ± 8.2 , $n = 4$, $n = 7$); abaxial hook length, 25–35 (29.5 ± 4 , $n = 5$, $n = 8$); abaxial hook width, 8–11 (9.1 ± 1.2 , $n = 4$, $n = 7$). Accessory piece rounded, 22–35 (29.8 ± 3.9 , $n = 6$, $n = 9$) long by 24–32 (28.3 ± 3.1 , $n = 6$, $n = 9$) wide, between axial hook bases.

Segments acraspedote. Immature segments 11–26 (14.8 ± 5.8 , $n = 6$) in number, 75–174 (114.9 ± 28.7 , $n = 6$, $n = 12$) long by 122–228 (178.5 ± 44.9 , $n = 3$, $n = 6$) wide, becoming longer than wide with maturity. Mature segments 1–2 (1.8 ± 0.4 , $n = 6$) in number, 442–

1,360 (818 ± 259.2 , $n = 6$, $n = 11$) long by 185–260 (223.8 ± 36.8 , $n = 2$, $n = 4$) wide. Testes 53–76 (66.1 ± 8.2 , $n = 4$, $n = 7$) in number, 29–55 (37.4 ± 10.5 , $n = 5$, $n = 11$) long by 30–89 (49.1 ± 18 , $n = 5$, $n = 11$) wide, 1 layer deep, in 3–4 preopercular columns, extending from near anterior margin of segment to anterior margin of ovary; postvaginal testes 11–15 (12 ± 1.7 , $n = 3$, $n = 6$) in number. Cirrus sac bent anteriorly, 125–135 (127.5 ± 4.3 , $n = 3$, $n = 5$) long by 29–65 (49.8 ± 13.2 , $n = 3$, $n = 5$) wide, containing coiled cirrus; cirrus 10–20 (15.8 ± 4.8 , $n = 3$, $n = 5$) wide; no cirrus microtriches seen. Vas deferens medial, coiled lateral and anterior to cirrus sac, entering proximal end of cirrus sac. No internal or external seminal vesicle seen.

Ovary posterior, 105–438 (245.4 ± 121.3 , $n = 4$, $n = 6$) long by 75–144 (113.2 ± 28.4 , $n = 3$, $n = 5$) wide, H-shaped in dorsoventral view, tetralobed in cross section, ovarian margins follicular. Genital pores lateral, irregularly alternating, 51–60% (54.6 ± 3 , $n = 6$, $n = 11$) from posterior margin of segment. Vagina sinuous, extending anteriorly from ootype region along midline of segment, then laterally along anterior margin of cirrus sac, joining cirrus at genital pore. Vitelline follicles lateral, in 2 dorsal and 2 ventral columns; each column 1 follicle wide, interrupted by vagina and cirrus sac on oral side; dorsal columns extending from near anterior extent of testes to anterior margin of ovary; ventral columns extending from near anterior margin of testes to posterior margin of segment. Uterus extending from ootype region to approximately anterior $\frac{1}{4}$ of segment, ventral to vagina. No gravid segments or eggs seen.

Taxonomic summary

Type host of record: Mustelus manazo Bleeker, 1854, starspotted smooth-hound.

Probable type host: Hemitriakis japonica (Müller and Henle, 1839), Japanese tope shark.

Type locality: Sea of Japan.

Additional localities: Suruga Bay near Yui, Shizuoka Prefecture, Japan ($35^{\circ}04'N$, $138^{\circ}33'E$).

Site of infection: Spiral intestine.

Material examined: Holotype and 2 paratypes (MPM 22777), 1 voucher (MPM 19764), 1 voucher (IPCAS C-334), 1 voucher (USNPC 90909).

Remarks

The above information emends Yamaguti's (1952) description of *Platybothrium musteli*, now as *Erudituncus musteli* (Yamaguti, 1952). Yamaguti (1952) did not indicate the number of type specimens of *E. musteli*, but correspondence with Shunya Kamegai at the MPM confirmed the existence of only 1 slide of *E. musteli* in that collection. That slide includes 3 specimens of *E. musteli*; 1 specimen is circled and labeled as the type, and the other 2 are considered paratypes. To our knowledge, these 3 specimens constitute the entire type series of *E. musteli*. Close comparison of the type material with the newly collected voucher material indicates that these specimens are conspecific.

Examination of the type specimens suggests that the figures in Yamaguti (1952) illustrate the scolex of the holotype and the terminal segment of the holotype or 1 of the paratype specimens. These figures are supplemented here by illustrations of the hooks of the holotype and scolex, segment, and whole worm of a voucher specimen. Examination of the type specimens indicates that the segment drawn in Yamaguti (1952) is oriented laterally, not ventrally, as Yamaguti's figure caption states. This explains some of the differences between Yamaguti's (1952) segment drawing and interpretations of aspects of the ovary, vitelline follicles, and genital pore and the segment, drawn here in dorsal view, and interpretations presented here.

The limited amount of available material precluded the use of scanning electron microscopy and histological sectioning in our investigation of *E. musteli*. However, we have reported that the ovary is tetralobed in cross section, having determined this from dorsoventral and lateral views of whole mounts as opposed to cross sections. Also, we can make some statements about the microtrich patterns in this species. What appear to be spiniform microtriches can be seen on the proximal bothridial surfaces of whole-mounted specimens; larger spiniform microtriches can be seen on the cephalic peduncle; and the strobila appears to lack spiniform microtriches, despite Yamaguti's (1952) statement that the “proglottides (sic) are finely spined all over.” These character as-

assessments should be confirmed using the appropriate techniques as additional material of this species is available.

DISCUSSION

The hook morphology of *Erudituncus musteli* is sufficiently distinct to justify erection of a new genus. *Erudituncus* most closely resembles *Biloculuncus* and *Calliobothrium*. Members of these 3 genera are unique among onchobothriids in their possession of bothridia bearing 2 pairs rather than 1 pair of hooks. In *Calliobothrium* and *Biloculuncus*, all 4 hooks are unipronged. However, in *Erudituncus*, if our interpretation is correct, the lateral and medial axial hooks are bipronged, the lateral abaxial hook is unipronged and quite typical, and the medial abaxial hook lacks a prong and is very reduced. This novel hook morphology allows certain assertions of homology to be made between taxa with a single pair of bipronged or tripronged hooks and taxa with 2 pairs of hooks.

Identifying hook component homologs is crucial in order to properly compare hook morphologies and develop characters for use in systematic analyses including onchobothriid taxa. Initial examination of the hooks of *Erudituncus* indicated that several different interpretations of hook component homologies might be possible. Our assertions of homology were based on the position of a hook component called a talon. Talons are present in some taxa with 2 pairs of hooks (*Erudituncus* and some *Calliobothrium* species), as well as in some taxa with 1 pair of bipronged or tripronged hooks (*Dicranobothrium* Euzet, 1953, *Platybothrium*, *Phoreiobothrium*, and *Onchobothrium* de Blainville, 1828), but are unknown in taxa with 1 pair of unipronged hooks such as *Pachybothrium* Baer and Euzet, 1962, and *Yorkeria* Southwell, 1927. Thus, we were unable to include the latter hook morphology in our homology proposals.

A talon is a blunt, proximal, hook base extension, which can be hollow or solid. Hollow talons are found in *Erudituncus*, *Dicranobothrium*, *Platybothrium*, and *Phoreiobothrium*; solid talons are found in *Onchobothrium*; and solid, talonlike extensions are seen in some *Calliobothrium* species (e.g., *C. evani* Caira, 1985, *C. riseri* Nasin, Caira, and Euzet, 1997, and *C. violae* Nasin, Caira, and Euzet, 1997). In all cases, the talons are present on both medial and lateral hooks and are closest in position to a particular hook prong. Based on the position of the talons in these taxa, the following hook prongs are likely to be homologous: the inner prong of the axial hooks of *Erudituncus*, the single prong of the axial hooks of *Calliobothrium*, and the axial prongs of *Dicranobothrium*, *Platybothrium*, *Phoreiobothrium*, and *Onchobothrium*. Prongs attached to these homologs are also likely to be homologous as follows: the outer prong of the axial hooks of *Erudituncus* and the abaxial prongs of *Dicranobothrium*, *Platybothrium*, *Phoreiobothrium*, and *Onchobothrium* (*Calliobothrium* lacks this hook component). Finally, the abaxial hooks of *Erudituncus* and *Calliobothrium* are likely homologs (*Dicranobothrium*, *Platybothrium*, *Phoreiobothrium*, and *Onchobothrium* lack this hook component). The terminology chosen for the hooks of *Erudituncus* resulted from these homology proposals and is summarized in Figure 1.

Yamaguti (1952) originally reported *Erudituncus musteli* (as *Platybothrium musteli*) from *Mustelus manazo* in the Sea of Japan. We believe it is very likely that this host record is in error. We have examined more than 30 specimens of *M. manazo* from several localities in Japan, and although numerous speci-

mens of *Calliobothrium* were discovered as a result of these collections, not a single specimen of *E. musteli* has been encountered in these hosts. Yet, both specimens of *Hemitriakis japonica* examined in the present study hosted at least 1 specimen of *E. musteli*. *Hemitriakis japonica* and *M. manazo* are both members of the family Triakidae and are morphologically similar to one another in a number of respects. Given the nascent state of carcharhiniform systematics and taxonomy at the time Yamaguti conducted this work, it seems likely that his identification of the host individual from which his material came was incorrect.

According to Compagno (1984), the Triakidae (Carcharhiniformes) consists of 5 currently monotypic genera, *Furgaleus* Whitley, 1951, *Galeorhinus* Blainville, 1816, *Gogolia* Compagno, 1973, *Hypogaleus* Smith, 1957, and *Scylliogaleus* Boulenger, 1902; 2 ditypic genera, *Hemitriakis* Herre, 1923, and *Iago* Compagno and Springer, 1971; and 2 more speciose genera, *Triakis* Müller and Henle, 1838, and *Mustelus* Linck, 1790, with 5 and 20 species, each. To date, no tapeworm records exist for *Gogolia*, *Hypogaleus*, *Scylliogaleus*, or *Iago*. Tapeworms have been reported from 2 species of *Triakis*, but these records suggest that, although these taxa host a diversity of tapeworms (e.g., see Young, 1954; Riser, 1955; Heinz and Dailey, 1974; Ruhnke, 1994, 1996), only *T. scyllium* Müller and Henle, 1839, hosts an onchobothriid, *Onchobothrium triacis* (Yamaguti, 1952) Caira and Machida, 1986. *Galeorhinus galeus* (Linnaeus, 1758) hosts at least 1 *Calliobothrium* species, and species of *Mustelus* typically host 1 or more species of *Calliobothrium* (see Euzet, 1959; Butler, 1987; Nasin et al., 1997, respectively), *Acanthobothrium* Van Beneden, 1849, and *Onchobothrium*. *Furgaleus macki* (Whitley, 1943) hosts *Biloculuncus* (see Caira and Ruhnke, 1990; Nasin et al., 1997), and, as demonstrated here, *Hemitriakis japonica* hosts a species of *Erudituncus*. *Acanthobothrium* and *Onchobothrium* species, recorded from at least 14 and 4 families of elasmobranchs, respectively, are fairly widely distributed, so we do not consider these tapeworm genera sufficiently host specific to have predictive value at this time. However, *Biloculuncus*, *Calliobothrium*, and *Erudituncus* have never been reported from any host genera other than the 4 cited above. In fact, these 3 genera of onchobothriids seem to be restricted to particular genera of triakid sharks. Based on these data, the following predictions about onchobothriids resulting from future collections of triakids can be made. (1) Because the only known species of *Biloculuncus* was described from the only known species of *Furgaleus*, *Biloculuncus* is likely a monotypic genus with no additional species remaining to be discovered. (2) *Erudituncus* is known from *Hemitriakis*. At least 1 species of *Hemitriakis* remains to be examined for tapeworms; thus, there is a possibility that at least 1 more species of *Erudituncus* remains to be discovered. (3) *Gogolia*, *Hypogaleus*, *Scylliogaleus*, and *Iago* are likely to host onchobothriid taxa (possibly new genera) exhibiting variations on the theme of 2 pairs of hooks per bothridium. (4) The 10 or more species of *Mustelus* that have not yet been examined for tapeworms are likely to host new species of *Calliobothrium*.

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