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***Calliobothrium* spp. (Eucestoda: Tetraphyllidea: Onchobothriidae)
in *Mustelus schmitti* (Chondrichthyes: Carcharhiniformes) from
Argentina and Uruguay**

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CALLIOBOTHRIUM SPP. (EUCESTODA: TETRAPHYLLIDEA: ONCHOBOTHRIDAE) IN *MUSTELUS SCHMITTI* (CHONDRICHTHYES: CARCHARHINIFORMES) FROM ARGENTINA AND URUGUAY

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ABSTRACT: Three species of *Calliobothrium* inhabit the spiral intestine of *Mustelus schmitti* in Argentina and Uruguay. *Calliobothrium verticillatum australis* is redescribed and its taxonomic status modified to species as *C. australis*. *Calliobothrium barbarae* n. sp. can be distinguished from all other species of *Calliobothrium*, which are small bodied, nonlacinate, and without accessory piece between the bases of axial hook, by worm length, number of segments, cocoon morphology, and hooks shape. *Calliobothrium lunae* n. sp. is different from other *Calliobothrium* spp., which are small bodied, nonlacinate, and have an accessory piece, by the number of segments and testes, hook shape, cocoon morphology, and the presence of ciliumlike projections on the distal surface of muscular pads. *Calliobothrium australis* is clearly distinguished from other large-bodied, lacinate species of the genus by worm length, number of testes, ovary shape, cocoon morphology, hook shape, and in being hyperapolytic. The oioxenous specificity involving *Calliobothrium* spp. and *Mustelus* spp. described by previous authors is confirmed in this study.

Eucestodes of the onchobothriid tetraphyllidean *Calliobothrium* van Beneden, 1850, are common inhabitants of sharks, i.e., *Mustelus* Linck, 1790; in fact, only 1 species of the genus (*C. creveyae* Butler, 1987) inhabits a host other than *Mustelus* spp. Moreover, most of the *Calliobothrium* spp. show specificity for a single species of *Mustelus*, even when other congeneric host species are sympatric with the preferred host (Nasin et al., 1997). Ostrowski de Núñez (1973) presented a strikingly different view of host specificity patterns among *Calliobothrium* spp., when she reported *C. verticillatum australis* Ostrowski de Núñez, 1973, *C. eschrichti* van Beneden, 1850, and *C. lintoni* Euzet, 1954, in the narrownose smooth-hound shark, *M. schmitti* Springer, 1939, from Argentine waters. These species were previously reported inhabiting other species of *Mustelus* in the Mediterranean Sea, northeastern Atlantic Ocean, and Japan. The unusual nature of the report by Ostrowski de Núñez (1973) prompted us to make new collections from the same and new localities, to reexamine the taxonomic status of the *Calliobothrium* spp. inhabiting *M. schmitti*.

MATERIALS AND METHODS

A total of 52 specimens of *M. schmitti* was obtained from catches of commercial trawlers in the following localities: 7 specimens off La Paloma (Uruguay) in July 1993, 30 specimens off Mar del Plata (Provincia de Buenos Aires, Argentina) in December 1995, and 15 specimens off Puerto Quequén (Provincia de Buenos Aires, Argentina) in February 2000. The mucosal surface of some spiral intestines of hosts from Argentina was examined fresh, and the worms were removed and placed directly into fixative (10% hot formalin). Other spiral intestines were fixed in 10% formalin for later examination for worms and transferred to 70% alcohol for storage after 48 hr. Specimens prepared for light microscopy were hydrated in a graded ethanol series, stained with Harris' hematoxylin, dehydrated in a graded ethanol series, cleared in methyl salicylate, and mounted in Canada balsam. Specimens recovered from elasmobranchs off Uruguay were relaxed in seawater, killed with hot water, fixed with AFA, and stored in 70% ethanol. Whole mounts were stained with Mayer's hematoxylin.

Specimens prepared for scanning electron microscopy (SEM) were hydrated in a graded ethanol series, postfixed in 1% osmium tetroxide overnight, dehydrated in a graded ethanol series, and dried using tetramethylsilane. Specimens were then mounted on stubs with adhesive tape, coated with gold in a Balzeus SCD 40 coater, and examined in a Philips 515 scanning electron microscope. Mature segments of specimens of each different species were embedded in paraffin and serially sectioned at 10 μ m in transverse view. All sections were stained with Harris' hematoxylin and counterstained with eosin. Specimens from the personal collection of Ostrowski de Núñez were also studied.

Measurements include the range followed in parentheses by the mean, standard deviation, number of worms examined (n), and the total number of observations when more than 1 measurement per worm was taken (n). Hook terminology and hook measurements follow those of Caira (1985) and Nasin et al. (1997) (see Fig. 8). All measurements are in micrometers unless otherwise stated. Figures were drawn with the aid of a drawing tube on a Zeiss Axioskop microscope. Museum abbreviations used are as follows: MACN, Museo Argentino de Ciencias Naturales, Colección Helminológica, Buenos Aires, Argentina, and USNPC, U.S. National Parasite Collection, Beltsville, Maryland, USA.

DESCRIPTIONS

Calliobothrium australis Ostrowski de Núñez, 1973

(Figs. 1–21)

Redescription (based on 20 specimens: 15 whole mounts, 3 observed with SEM and 2 as cross sections): Worms hyperapolytic, 60.4–99.0 (74.0 $\pm$ 13.0; n = 15) mm long; maximum width 1,000–1,920 (1,302 $\pm$ 309; n = 15) at the level of last mature segment; 250–310 (293 $\pm$ 17; n = 15) segments per worm (Fig. 9). Scolex 325–435 (375 $\pm$ 29; n = 15) long, 235–310 (269 $\pm$ 24; n = 15) wide, composed of 4 trilobulate bothridia, lacking velum, each bothridium bearing apical muscular pad with 3 accessory suckers, 2 pairs of hooks (Figs. 1, 10). Bothridia 300–340 (315 $\pm$ 15; n = 21; n = 15) long, 93–140 (269 $\pm$ 24; n = 21; n = 15) wide; anterior loculus 170–215 (193 $\pm$ 14; n = 21; n = 15) long; middle loculus 40–62 (54 $\pm$ 6; n = 21; n = 15) long; posterior loculus 62–92 (75 $\pm$ 6; n = 21; n = 15) long. Ratio of locular lengths (anterior–middle–posterior) 1:0.19–0.34 (0.28 $\pm$ 0.04):0.30–0.49 (0.39 $\pm$ 0.05). Muscular pad 32–50 (39 $\pm$ 6; n = 21; n = 15) long, 107–132 (114 $\pm$ 8; n = 21; n = 15) wide; central accessory sucker 40–50 (43 $\pm$ 3; n = 10; n = 15) in diameter, lateral accessory suckers 30–37 (35 $\pm$ 3; n = 15) in diameter (Fig. 13). Hooks hollow, covered by a thin layer of tissue with the

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FIGURES 1–8. *Calliobothrium australis*. 1. Scolex. Bar = 50 μm . 2. Detail of hooks. Bar = 25 μm . 3. Detail of hooks. Bar = 25 μm . 4. Mature segment. Bar = 200 μm . 5. Detail of terminal genitalia. Bar = 40 μm . 6. Detail of cocoons. Bar = 100 μm . 7. Detail of ootype region. Bar = 100 μm . 8. Hook measurements. Abbreviations: mg, Mehlis' gland; o, ovary; oc, oocapt; od, oviduct; sr, seminal receptacle; u, uterus; ud, uteroduct; vg, vagina.

FIGURE 9. *Calliobothrium australis*. Entire worm. Bar = 1 mm.

exception of tips, extending posteriorly into 40–60% of anterior loculus length. Axial hooks more recurved than abaxial hooks (Figs. 2, 3). Lateral medial axial hooks of equal shape and size; hook measurements: A, 52–82 (69 ± 7 ; $n = 40$; $n = 15$); B, 105–142 (121 ± 9 ; $n = 40$; $n = 15$); C, 42–62 (51 ± 4 ; $n = 40$; $n = 15$). Accessory piece absent. Lateral, medial abaxial hooks of equal curvature, size; hook measurements: D, 62–91 (80 ± 7 ; $n = 40$; $n = 15$); E, 95–136 (121 ± 9 ; $n = 40$; $n = 15$); F, 35–47 (42 ± 3 ; $n = 40$; $n = 15$).

Proximal surfaces of bothridia covered with densely packed bladelike microtriches, 2.5 long, 0.8 wide at base, 6 microtriches/ μm^2 approximately, no filiform microtriches observed (Fig. 11). Distal surfaces of bothridia covered with small and short filiform microtriches, 25 microtriches/ μm^2 approximately (Fig. 12). Distal surfaces of apical suckers and muscular pads covered with small and short filiform microtriches, 27 microtriches/ μm^2 approximately (Fig. 15). Proximal surface of muscular pads covered with bladelike microtriches, 1.4 long, 0.6 wide at base, 5 microtriches/ μm^2 approximately (Fig. 14). Segments covered with filiform microtriches, 1.3 long, 0.2 wide at base, 12 microtriches/ μm^2 approximately (Figs. 16, 17), flaps covered with elongate bladelike microtriches, 2.3 long, 0.6 wide at base, 9 microtriches/ μm^2 approximately (Fig. 18).

Segments lacinate (Figs. 4, 9). First 3 segments with 4 posterior triangular flaps (2 ventrally and 2 dorsally), third flap growing in between ventral and dorsal flaps from segment 3 to 46–56 (43–53 segments having 6 flaps, 3 ventrally and 3 dorsally), central notch in middle flap from segment 46–56 to 255–264 (205–209 segments having 8 flaps, 4 dorsally and 4 ventrally), submedian flaps fused with lateral of its own side from segment 255–264 to 292–307 (32–52 segments having 4 flaps, 2 dorsally and 2 ventrally). Immature segments 246–303 (284 ± 16 ; $n = 15$) in number, wider than long to quadrangular. Mature segments 4–15 (9 ± 3 ; $n = 15$) in number, 1,240–5,120 ($2,546 \pm 920$; $n = 40$; $n = 15$) long, 780–1,920 ($1,205 \pm 231$; $n = 40$; $n = 15$) wide; length to width ratio 1–5.1 (2.2):1 (Fig. 4). Detached gravid segments up to 7,200 long, 1,920 wide. Testes spherical, 52–100 (73 ± 9 ; $n = 80$; $n = 15$) in diameter; distributed in 2 lateral fields separated by uterus and vas deferens bulk, from anterior margin of ovary to anterior margin of segment; total number of testes per mature segment 129–208 (171 ± 23 ; $n = 40$; $n = 15$), 23–43 (30 ± 5 ; $n = 40$; $n = 15$) preporally, 36–59 (49 ± 6 ; $n = 40$; $n = 15$) postporally, 67–121 (92 ± 15 ; $n = 40$; $n = 15$) antiporally (Fig. 4); 1 or 2 layers in cross section, anterior to cirrus sac (Fig. 19). Vas deferens well developed, highly coiled, bulk extending anteriorly, in anterior one-third of segment, approximately 45–85 (66) in diameter to 15–22 (17) when entering cirrus sac posteriorly. Cirrus sac spherical, 87–125 (104 ± 12 ; $n = 30$; $n = 15$) long, 75–100 (88 ± 6 ; $n = 30$; $n = 15$) wide; extending 12–18% ($15 \pm 1\%$; $n = 25$; $n = 5$) of segment width, containing coiled cirrus; cirrus covered with small microtriches (Figs. 4, 5, 20). Ovary branched, divided into numerous elongated digitiform lobules, located at posterior end of segment, occupying 32–44% (38%) of total segment length; 640–1,660 ($1,045 \pm 283$; $n = 30$; $n = 15$) long, 640–1,400 (930 ± 196 ; $n = 30$; $n = 15$) wide (Fig. 4), 2 lobed in cross sections (Fig. 21). Vagina parallels anterior margin of cirrus sac, not crossing it, distally wider (approximately 42–62 [55]) and surrounded by large glandular cells (Fig. 5), then thinner (17–27 [21]), curving in midline, descending straight to ovarian isthmus, forming seminal receptacle, 45–70 (56) wide at junction with oviduct (Fig. 7). Oocapt conspicuous, 55–87 (73 ± 4 ; $n = 20$; $n = 13$) in diameter. Mehli's gland posterior to ovarian isthmus, 92–180 (124 ± 27 ; $n = 20$; $n = 15$). Genital pores lateral, irregularly alternating, 65–87% ($74 \pm 5\%$; $n = 30$; $n = 15$) of segment length from posterior margin; vagina and male duct join in genital atrium (Fig. 5). Vitellaria extending from 4 to 8% (6%) of total segment length anteriorly to 6–10% (8%) of total segment

FIGURES 10–18. *Calliobothrium australis*, scanning electron micrographs. **10.** Scolex. Bar = 50 μm . **11.** Microtriches on proximal bothridial surface. Bar = 2.5 μm . **12.** Microtriches on distal bothridial surface. Bar = 2.5 μm . **13.** Detail of muscular pad showing apical suckers. Bar = 10 μm . **14.** Microtriches on proximal surface of muscular pad. Bar = 2.5 μm . **15.** Microtriches on distal surface of muscular pad. Bar = 1 μm . **16.** Immature segment. Bar = 10 μm . **17.** Detail of microtriches on anterior half of immature segment. Bar = 1 μm . **18.** Detail of microtriches on flaps of immature segment. Bar = 2.5 μm .

length posteriorly, on poral and aporal sides of segments; arranged in 2 lateral bands of follicles; interrupted dorsally at cirrus sac and vagina level on poral side; each band consisting of 2 or 3 dorsal rows and 2 or 3 ventral rows of oval follicles (Figs. 19–21); individual follicles, 37–65 (45 ± 8 ; $n = 30$; $n = 15$) long, 22–42 (34 ± 5 ; $n = 30$; $n = 15$) wide. Uterus saccate with irregular margins, reaching 10–19% (13%) of total segment length from anterior margin; visible in immature segments. Excretory ducts lateral, ventral excretory ducts 17–27 (18 ± 5 ; $n = 10$; $n = 5$) in diameter, joined by transverse duct at posterior margin of segment. Onchospheres 22–25 (25 ± 1 ; $n = 23$) in diameter, packaged in groups of 6–8 (7 ± 1 ; $n = 20$; $n = 3$) within elongate, filamentous cocoons 500–535 (53 ± 16 ; $n = 20$; $n = 3$) long, 47–65 (61 ± 5 ; $n = 20$; $n = 3$) wide (Fig. 6).

Taxonomic summary

Type host: *Mustelus schmitti* Springer, 1939, narrownose smooth-hound shark, Chondrichthyes, Carcharhiniformes, Triakidae.

Site of infection: Spiral intestine.

Type locality: Mar del Plata, Buenos Aires Province, Argentina ($38^{\circ}00'S$, $57^{\circ}33'W$).

Other localities: Puerto Quequén, Provincia de Buenos Aires, Argentina ($38^{\circ}32'S$, $58^{\circ}42'W$); La Paloma, Departamento de Rocha, Uruguay ($34^{\circ}40'S$, $54^{\circ}10'W$).

Specimens deposited: Holotype MACN no. 409/1; 4 voucher specimens MACN no. 405/1–4; 2 voucher specimens USNPC no. 92398.

Remarks

Ostrowski de Núñez (1973) described *C. australis* as a new subspecies of *C. verticillatum* (Rudolphi, 1819) on the basis of differences in the number of testes per segment, ovary shape, and the mode of detachment of segments, observations that were based on examination of a single mature specimen. In the present study, new material was collected from the type host and locality, and additional localities, and ranges for all measurements, sectioning of mature segments, and details of the surfaces observed with SEM are presented for the first time. Detailed examination of the type and of the new specimens collected in this study convinced us that all represent a species distinct from *C. verticillatum*, hence, our designation of *C. australis*. In this study, *C. australis* is compared with the descriptions of *C. verticillatum* made by Euzet (1954, 1959) because this is the most detailed description available at present.

Calliobothrium australis can be distinguished from *C. verticillatum* by the following combination of characters: maximum worm length (99 mm in *C. australis*, 120 mm in *C. verticillatum*); number of testes (129–208 in *C. australis*, 110–130 in *C. verticillatum*); ovary shape (ovary highly branched, formed by numerous elongated acini in *C. australis*, ovary lobulated in *C. verticillatum*); ovary shape in cross section (2 lobed in *C. australis*, 4 lobed in *C. verticillatum*); number of onchospheres per cocoon (6 or 7 in *C. australis*, 10–12 in *C. verticillatum*); cocoon shape (elongate in *C. australis*, fusiform with polar filaments in *C. verticillatum*); distribution of vitellaria (uninterrupted by cirrus sac in *C. australis*, interrupted by cirrus sac in *C. verticillatum*); strobilae hyperapolytic in *C. australis*,

FIGURES 19–21. *Calliobothrium australis*, cross sections of mature segment. **19.** Cross section at the level of testes anterior to cirrus sac. **20.** Cross section at the level of cirrus sac. **21.** Cross section at the level of ovarian isthmus. Bar = 100 μ m. Abbreviations: cs, cirrus sac; mg, Mehlis' gland; nc, nerve cord; o, ovary; t, testis; u, uterus; vf, vitelline follicle; vg, vagina; vod, ventral osmoregulatory duct.

apolytic in *C. verticillatum* and by differences in the number of segments in different stages of lappets development.

In addition, *C. australis* differs from *C. lintoni*, *C. riseri* Nasin, Caira et Euzet, 1997, *C. violae* Nasin, Caira et Euzet, 1997, *C. pellucidum* Riser, 1955, and *C. evani* Caira, 1985 in the lack of an accessory piece between the bases of axial hooks. Whereas *C. eschrichti*, *C. hayhowi* Nasin, Caira et Euzet, 1997, and *C. leuckarti* van Beneden, 1850, have acraspedote or slightly craspedote segments, *C. australis* has laciniate strobilae. *Calliobothrium creeveyae* is smaller than *C. australis* (14–19 mm and 60–99 mm, respectively); also, the posterior margin of the bothridia is 3 lobed in *C. creeveyae* and entire in *C. australis*. There are conspicuous differences between *C. australis* and *C. nodosum* Yoshida, 1917; *C. australis* is smaller (*C. australis* 60–100 mm, *C. nodosum* 160 mm), has elongated hooks (thorn-like in *C. nodosum*), lacks cephalic peduncle (1,300–1,500 long

in *C. nodosum*), and it is hyperapolytic, whereas *C. nodosum* has numerous gravid segments attached to the strobilae. Finally, *C. australis* can be easily distinguished from *C. tylotocephalum* Alexander, 1963, in worm length (up to 99 mm in *C. australis*, 286 mm in *C. tylotocephalum*), mature segments shape (longer than wide in *C. australis*, wider than long in *C. tylotocephalum*), and *C. australis* has slender scolex and hooks and is hyperapolytic, whereas *C. tylotocephalum* has a markedly robust scolex and hooks and is apolytic.

***Calliobothrium barbarae* n. sp.**

(Figs. 22–42)

Diagnosis (based on 32 specimens: 27 whole mounts, 3 observed with SEM and 2 as cross sections): Worms apolytic, 3.9–22.0 (8.6 ± 3.9 ; $n = 25$) mm long; maximum width 215–375 (304 ± 39 ; $n = 25$) at the level of scolex; 10–31 (20 ± 6 ; $n = 25$) segments per worm (Fig. 22). Scolex 360–525 (431 ± 42 ; $n = 20$) long, 245–375 (304 ± 39 ; $n = 20$) wide, composed of 4 bothridia, carried on cephalic peduncle (Figs. 23, 32); cephalic peduncle 425–5,300 ($1,226 \pm 1,108$; $n = 21$). Bothridia 280–410 (325 ± 32 ; $n = 34$; $n = 20$) long, 105–155 (130 ± 14 ; $n = 34$; $n = 20$) wide; subdivided in 3 loculi, anterior loculus 125–230 (183 ± 24 ; $n = 34$; $n = 20$) long; middle loculus 47–110 (64 ± 13 ; $n = 34$; $n = 20$) long; posterior loculus 50–100 (76 ± 13 ; $n = 34$; $n = 20$) long. Ratio of locular lengths (anterior–middle–posterior) 1:0.24–0.59 (0.35 ± 0.09); 0.25–0.69 (0.42 ± 0.10). Each bothridia bearing 2 pairs of hooks and anterior muscular pad having 1 conspicuous sucker, muscular pad 55–75 (63 ± 6 ; $n = 34$; $n = 20$) long, 100–137 (116 ± 11 ; $n = 34$; $n = 20$) wide (Fig. 35); accessory sucker 57–62 (59 ± 3 ; $n = 34$; $n = 20$) in diameter. Hooks hollow, covered by a thin layer of tissue with the exception of tips, extending posteriorly into 29–50% (39%) of anterior loculus length. Axial hooks more recurved than abaxial hooks (Figs. 24, 25). Lateral and medial axial hooks of equal shape and size; hook measurements: A, 37–64 (55 ± 8 ; $n = 40$; $n = 20$); B, 67–91 (81 ± 6 ; $n = 40$; $n = 20$); C, 42–55 (46 ± 3 ; $n = 40$; $n = 20$). Accessory piece absent. Lateral and medial abaxial hooks of equal curvature and size; hook measurements: D, 75–100 (87 ± 6 ; $n = 40$; $n = 20$); E, 112–140 (126 ± 8 ; $n = 40$; $n = 20$); F, 37–55 (47 ± 4 ; $n = 40$; $n = 20$).

Proximal surfaces of bothridia covered with densely packed bladelike microtriches, 3 long, 0.7 wide at base, 5 or 6 microtriches/ μm^2 approximately, no filiform microtriches observed (Fig. 33). Distal surfaces of bothridia covered with small and short filiform microtriches (Fig. 34). Distal surfaces of apical suckers and muscular pads covered with small and short filiform microtriches. Proximal surface of muscular pads covered with bladelike microtriches, 1 long, 0.2 wide at base, 9 or 10 microtriches/ μm^2 approximately (Fig. 36). Cephalic peduncle surface covered with densely packed bladelike microtriches, 3.5–4.0 long, 1 wide at base, 3 microtriches/ μm^2 approximately, uniformly distributed throughout its entire length (Fig. 38). Strobila covered with filiform microtriches, 1 long, 35 microtriches/ μm^2 approximately (Figs. 37, 39).

Segments slightly craspedote, immature segments 7–20 (12 ± 4 ; $n = 25$) in number, longer than wide. Mature segments 2–5 (3 ± 1 ; $n = 25$) in number, 370–800 (556 ± 119 ; $n = 20$; $n = 20$) long, 165–340 (221 ± 43 ; $n = 20$; $n = 20$) wide;

length to width ratio 1.6–3.7 (2.5):1 (Fig. 29). Gravid segments 1–10 (6 ± 2 ; $n = 20$) in number, 530–1,220 (850 ± 139 ; $n = 20$; $n = 20$) long, 200–400 (286 ± 60 ; $n = 20$; $n = 20$) wide; length to width ratio 1.7–5.8 (3.1):1 (Fig. 30). Detached gravid segments up to 2,100 long, 640 wide. Testes spherical to oval, 50–107 (72 ± 12 ; $n = 30$; $n = 20$) long, 40–67 (56 ± 6 ; $n = 30$; $n = 20$) wide; distributed in 2 columns; total number of testes per mature segment 8–13 (10 ± 1 ; $n = 60$; $n = 25$), 3–4 (3 ± 1 ; $n = 60$; $n = 25$) preporally, 1–2 (1 ± 1 ; $n = 60$; $n = 25$) postporally, 4–7 (5 ± 1 ; $n = 60$; $n = 25$) antiporally (Figs. 29, 30); 1 layer in cross section anterior to cirrus sac (Fig. 40). Vas deferens well developed, highly coiled, bulk extending well anteriorly of cirrus sac, approximately 20–25 (21) in diameter. Cirrus sac oval in shape, curved anteriorly, 87–150 (120 ± 14 ; $n = 30$; $n = 20$) long, 37–62 (46 ± 6 ; $n = 30$; $n = 20$) wide; extending 49–60% ($55 \pm 4\%$; $n = 13$; $n = 6$) of segment width (Fig. 41), containing coiled cirrus; cirrus 175–225 (198 ± 19 ; $n = 7$; $n = 3$) long, covered with small microtriches. Ovary inverted V shaped in dorsoventral view, bilobed in cross section (Fig. 42), located at posterior end of segment; 137–240 (202 ± 29 ; $n = 25$; $n = 20$) long, 137–250 (175 ± 39 ; $n = 25$; $n = 20$) wide; ovarian lobe on aporal side slightly longer than lobe on poral side. Vagina anterior to cirrus sac, crossing it in posterior half, covered with ciliate epithelium distally (Fig. 28), descending straight to ovarian isthmus, forming small seminal receptacle, 20–30 (22) wide at junction with oviduct (Fig. 31). Mehli's gland in posterior one-third of ovary, 37–75 (49 ± 9 ; $n = 20$; $n = 15$); uteroduct expanded at base (Fig. 31). Genital pores lateral, irregularly alternating, 37–65% ($46 \pm 5\%$; $n = 60$; $n = 25$) of segment length from posterior margin; vagina and male duct join in genital atrium (Fig. 28). Vitellaria extending from 10 to 21% (16%) of total segment length anteriorly to 20–22% (21%) of total segment length posteriorly, on poral and aporal sides of segments; arranged in 2 lateral bands of follicles; uninterrupted at cirrus sac and vagina level on poral side; each band consisting of 1 follicle deep in cross section (Figs. 40–42); individual follicles, 25–55 (41 ± 11 ; $n = 30$; $n = 15$) long, 25–32 (29 ± 3 ; $n = 30$; $n = 15$) wide. Uterus saccate, reaching anteriormost margin of segment; visible in mature and gravid segments. Excretory ducts lateral, ventral excretory ducts 5–17 (10 ± 6 ; $n = 5$; $n = 5$) in diameter, joined by transverse duct at posterior margin of segment. Onchospheres 22–25 (23 ± 1 ; $n = 35$) in diameter, packaged in groups of 8–10 (9 ± 1 ; $n = 45$; $n = 4$) within oval cocoons with polar filaments (Figs. 26, 27); cocoons 125–137 (129 ± 7 ; $n = 40$; $n = 4$) long, 75–82 (79 ± 4 ; $n = 40$; $n = 4$) wide; filaments 375–405 (390 ± 21 ; $n = 10$; $n = 2$) long.

Taxonomic summary

Type host: *Mustelus schmitti* Springer, 1939, narrownose smooth-hound shark, Chondrichthyes, Carcharhiniformes, Triakidae.

Site of infection: Spiral intestine.

Type locality: Puerto Quequén, Provincia de Buenos, Argentina ($38^{\circ}32'S$, $58^{\circ}42'W$).

Other localities: Mar del Plata, Provincia de Buenos Aires, Argentina ($38^{\circ}00'S$, $57^{\circ}33'W$); La Paloma, Departamento de Rocha, Uruguay ($34^{\circ}40'S$, $54^{\circ}10'W$).

FIGURES 22–31. *Calliobothrium barbarae* n. sp. 22. Entire worm. Bar = 0.5 mm. 23. Scolex. Bar = 100 μ m. 24. Detail of hooks. Bar = 15 μ m. 25. Detail of hooks. Bar = 15 μ m. 26. Detail of cocoon. Bar = 25 μ m. 27. Cocoon. Bar = 50 μ m. 28. Detail of terminal genitalia. Bar = 50 μ m. 29. Mature segment. Bar = 100 μ m. 30. Gravid segment. Bar = 100 μ m. 31. Detail of ootype region. Bar = 20 μ m. Abbreviations: mg, Mehlis' gland; o, ovary; od, oviduct; sr, seminal receptacle; u, uterus; ud, uteroduct; vg, vagina.

FIGURES 32–39. *Calliobothrium barbarae* n. sp., scanning electron micrographs. 32. Scolex. Bar = 50 μ m. 33. Microtriches on proximal bothridial surface. Bar = 2.5 μ m. 34. Microtriches on distal bothridial surface. Bar = 2 μ m. 35. Detail of muscular pad showing apical sucker. Bar = 50 μ m. 36. Microtriches on proximal surface of muscular pad. Bar = 2 μ m. 37. Microtriches on immature segment surface. Bar = 2 μ m. 38. Microtriches on cephalic peduncle surface. Bar = 2.5 μ m. 39. Microtriches on mature segment surface. Bar = 2.5 μ m.

FIGURES 40–42. *Calliobothrium barbarae* n. sp., cross sections of mature segment. **40.** Cross section at the level of testes anterior to cirrus sac. **41.** Cross section at the level of cirrus sac. **42.** Cross section at the level of ovarian isthmus. Bar = 50 μ m. Abbreviations: cs, cirrus sac; o, ovary; t, testis; u, uterus; vd, vas deferens; vf, vitelline follicle; vg, vagina; vod, ventral osmoregulatory duct.

Specimens deposited: Holotype and 4 paratypes, MACN no. 410/1-3; 2 paratypes, USNPC no. 92399.

Etymology: This species is named after the senior author's niece Bárbara Lazo Ivanov for her enthusiastic interest in zoology.

Remarks

Calliobothrium barbarae n. sp. differs from *C. lintoni*, *C. riseri*, *C. pellucidum*, *C. violae*, and *C. evani* in the absence of an accessory piece between the bases of the axial hooks. *Calliobothrium verticillatum*, *C. australis*, *C. nodosum*, *C. tylotocephalum*, and *C. creveyae* have laciniate strobilae different from the slightly craspedote strobilae of *C. barbarae*. *Calliob-*

othrium barbarae is most similar to *C. eschrichti* and *C. hayhowi*. *Calliobothrium barbarae* has been reported erroneously as *C. eschrichti* by Ostrowski de Núñez (1973). But there exist many differences between *C. barbarae* and *C. eschrichti*: worm length (3.9–22.0 mm in *C. barbarae*, 1.9–2.6 mm in *C. eschrichti*); number of segments (10–31 in *C. barbarae*, 8–10 in *C. eschrichti*); number of onchospheres per cocoon (8–10 in *C. barbarae*, 16–20 in *C. eschrichti*); distribution of vitelline follicles (uninterrupted in *C. barbarae*, interrupted by cirrus sac in *C. eschrichti*); abaxial hook shape (triangular axial articulation process on the abaxial hooks in *C. barbarae*, rectangular axial articulation process on the abaxial hooks in *C. eschrichti*); and type of microtriches on distal bothridial surface (lacking small bladelike microtriches in *C. barbarae*). In addition, *C. barbarae* is larger and has more segments than *C. hayhowi* (up to 22 mm and 31 segments in *C. barbarae*, up to 5 mm and 10 segments in *C. hayhowi*); ovary shape (inverted V shape in *C. barbarae*, H shape in *C. hayhowi*); microthrix pattern on distal bothridial surface (*C. barbarae* lacks the small bladelike microtriches present in *C. hayhowi*). Finally, whereas the onchospheres of *C. barbarae* are released in groups of 8–10 within bifilamented cocoons, they are retained individually within hexagonal compartments of the uterine wall in *C. hayhowi*.

Calliobothrium lunae n. sp.

(Figs. 43–56)

Diagnosis (based on 18 specimens: 11 whole mounts, 5 observed with SEM and 2 as cross sections): Worms apolytic, 2.2–5.0 (3.6 ± 0.8 ; $n = 11$) mm long; maximum width 260–450 (316 ± 70 ; $n = 11$) at the level of scolex; 7–10 (9 ± 1 ; $n = 11$) segments per worm (Fig. 43). Scolex 300–490 (387 ± 65 ; $n = 11$) long, 260–450 (316 ± 70 ; $n = 11$) wide, composed of 4 bothridia carried on cephalic peduncle (Figs. 44, 51); cephalic peduncle 275–525 (429 ± 71 ; $n = 11$). Bothridia, 225–360 (282 ± 47 ; $n = 20$; $n = 11$) long, 107–140 (121 ± 11 ; $n = 20$; $n = 11$) wide, subdivided in 3 loculi; anterior loculus 130–207 (160 ± 24 ; $n = 20$; $n = 11$) long; middle loculus 57–87 (69 ± 11 ; $n = 20$; $n = 11$) long; posterior loculus 37–72 (55 ± 12 ; $n = 20$; $n = 11$) long. Ratio of locular lengths (anterior–middle–posterior) 1:0.38–0.52 (0.43 ± 0.03):0.27–0.40 (0.33 ± 0.04). Each bothridium bearing anterior muscular pad and 2 pairs of hooks. Muscular pad 130–200 (155 ± 19 ; $n = 15$; $n = 11$) long, 57–90 (69 ± 12 ; $n = 15$; $n = 11$) wide, with crenulated margins, 1 pair of posterolateral muscular flaps and 1 conspicuous accessory sucker, accessory sucker 60–87 (72 ± 11 ; $n = 15$; $n = 11$) in diameter (Fig. 55). Hooks hollow, covered by a thin layer of tissue with the exception of tips, extending posteriorly into 60–86% (77%) of anterior loculus length. Axial hooks more recurved than abaxial hooks (Figs. 45, 46). Lateral and medial axial hooks of equal shape and size; hook measurements: A, 82–117 (103 ± 9 ; $n = 20$; $n = 11$); B, 115–135 (125 ± 6 ; $n = 20$; $n = 11$); C, 47–60 (53 ± 4 ; $n = 20$; $n = 11$). Axial hook bases articulate with a triangular accessory piece, accessory piece solid, 15–24 (19 ± 3 ; $n = 20$; $n = 11$) long, 17–30 (20 ± 3 ; $n = 20$; $n = 11$) wide, wider at anterior end, anterior margin having 1 or 2 notches (Fig. 46). Lateral and medial abaxial hooks of equal curvature and size; hook measurements: D, 102–135 (113 ± 9 ; $n = 20$; $n = 11$);

FIGURES 43–50. *Calliobothrium lunae* n. sp. **43.** Entire worm. Bar = 200 μ m. **44.** Scolex. Bar = 100 μ m. **45.** Detail of hooks. Bar = 20 μ m. **46.** Detail of hooks. Bar = 20 μ m, arrow shows the notch in anterior margin of axial hooks. **47.** Cross section of mature segment at the level of testes. Bar = 25 μ m. **48.** Cross section of mature segment at the level of ovary posterior to ovarian isthmus. Bar = 25 μ m. **49.** Mature segment. Bar = 100 μ m. **50.** Gravid segment. Bar = 100 μ m. Abbreviations: o, ovary; od, oviduct; t, testis; vd, vas deferens; vf, vitelline follicle; vod, ventral osmoregulatory duct.

FIGURES 51–56. *Calliobothrium lunae* n. sp., scanning electron micrographs. **51.** Scolex. Bar = 100 μm . **52.** Microtriches on proximal bothridial surface. Bar = 2.5 μm . **53.** Microtriches on mature segment. Bar = 1 μm . **54.** Microtriches on cephalic peduncle. Bar = 1 μm . **55.** Detail of muscular pad showing sucker. Bar = 25 μm . **56.** Microtriches on distal surface of muscular pad. Bar = 2.5 μm .

E, 112–137 (125 ± 8 ; $n = 20$; $n = 11$); F, 22–30 (25 ± 2 ; $n = 20$; $n = 11$).

Proximal surfaces of bothridia covered with bladelike microtriches, 3.5–4.0 long, 0.7–1.0 wide at base, 1.6 microtriches/ μm^2 approximately, no filiform microtriches observed (Fig. 52). Distal surfaces of bothridia covered with small and short filiform microtriches. Distal surfaces of apical suckers and mus-

cular pads covered with small and short filiform microtriches, 60 microtriches/ μm^2 approximately, interspersed by ciliumlike projections (Fig. 56). Proximal surface of muscular pads covered with bladelike microtriches. Cephalic peduncle surface covered with densely packed bladelike microtriches, 2 long, 0.7 wide at base, 5 microtriches/ μm^2 approximately, uniformly distributed throughout its entire length (Fig. 54). Strobila covered

with filiform microtriches, 1.7 long, 7 microtriches/ μm^2 approximately (Fig. 53).

Segments acraspedote. Immature segments 5–8 (7 ± 1 ; $n = 11$) in number, longer than wide. Mature segments 1–2 (1 ± 0 ; $n = 11$) in number, 600–1,150 (841 ± 177 ; $n = 15$; $n = 11$) long, 130–210 (171 ± 22 ; $n = 15$; $n = 11$) wide; length to width ratio 3.7–6.8 (4.9):1 (Fig. 49). Gravid segments 0–2 (0.7 ± 0.6 ; $n = 11$) in number, 640–1,450 ($1,166 \pm 321$; $n = 9$; $n = 9$) long, 100–240 (190 ± 55 ; $n = 9$; $n = 9$) wide; length to width ratio 5.2–7.6 (6.2):1 (Fig. 50). Testes oval, 40–67 (53 ± 7 ; $n = 55$; $n = 11$) long, 50–85 (66 ± 9 ; $n = 55$; $n = 11$) wide; distributed in 2 columns; total number of testes per mature segment 20–34 (26 ± 4 ; $n = 21$; $n = 11$), 8–15 (12 ± 2 ; $n = 21$; $n = 11$) preporally, 1 or 2 (1 ± 0 ; $n = 21$; $n = 11$) postporally, 10–18 (13 ± 2 ; $n = 21$; $n = 11$) antiporally; 1 layer in cross section anterior to cirrus sac (Fig. 47). Vas deferens well developed, highly coiled, bulk extending well anteriorly of cirrus sac, approximately up to 25 in diameter. Cirrus sac oval in shape, 75–112 (97 ± 12 ; $n = 15$; $n = 11$) long, 42–65 (53 ± 8 ; $n = 15$; $n = 11$) wide; extending 57–67% ($62 \pm 4\%$; $n = 10$; $n = 8$) of segment width, containing coiled cirrus covered with small microtriches. Ovary inverted A shaped in dorsoventral view (Fig. 49), bilobed in cross section (Fig. 48), located at posterior end of segment; 200–375 (293 ± 67 ; $n = 15$; $n = 11$) long, 105–145 (124 ± 13 ; $n = 15$; $n = 11$) wide. Vagina anterior to cirrus sac, crossing it in posterior half, descending straight to ovarian isthmus. Mehli's gland posterior to ovarian isthmus, 42–57 (47 ± 8 ; $n = 6$; $n = 3$) in diameter. Genital pores lateral, irregularly alternating, 28–39% ($33 \pm 3\%$; $n = 15$; $n = 11$) of mature segment length from posterior margin; vagina and male duct join in genital atrium. Vitellaria extending from 8 to 18% (12%) of total segment length anteriorly to 20–25% (23%) of total segment length posteriorly, on poral and aporal sides of segments; arranged in 2 lateral bands of follicles; interrupted at cirrus sac and vagina level on poral side; each band consisting of 1 follicle deep in cross section; individual follicles, 27–55 (37 ± 13 ; $n = 25$; $n = 9$) long, 17–30 (21 ± 6 ; $n = 25$; $n = 9$) wide. Uterus saccate, reaching almost anteriormost margin of segment, visible in gravid segments. Onchospheres packaged in groups of several (more than 20) within oval cocoons.

Taxonomic summary

Type host: *Mustelus schmitti* Springer, 1939, narrownose smooth-hound shark, Chondrichthyes, Carcharhiniformes, Triakidae.

Site of infection: Spiral intestine.

Type locality: La Paloma, Departamento de Rocha, Uruguay ($34^{\circ}40'S$, $54^{\circ}10'W$).

Other locality: Mar del Plata, Provincia de Buenos Aires, Argentina ($38^{\circ}00'S$, $57^{\circ}33'W$).

Specimens deposited: Holotype and 4 paratypes, MACN no. 411/1-5; 2 paratypes, USNPC no. 92400.

Etymology: This species is named in honor of Dr. Gabriela Luna, University of Irvine, California, for her special friendship with the senior author (V.A.I.).

Remarks

Calliobothrium lunae n. sp. differs from *C. barbarae*, *C. eschrichti*, *C. hayhowi*, *C. leuckarti*, *C. verticillatum*, *C. australis*,

C. nodosum, *C. tylocephalum*, and *C. creeveyae* in its possession of an accessory piece between the bases of the axial hooks. *Calliobothrium lunae* can be differentiated from *C. violae* in having bothridia with margins undivided posteriorly rather than bilobed as in *C. violae*. In *C. evani*, the bothridia are attached in pairs, with each pair being mounted on a distinct pedicel, whereas all 4 bothridia of *C. lunae* are attached to the mesoscolex (Ivanov and Campbell, 2002). In addition, the hooks of *C. evani* are asymmetrical rather than symmetrical. *Calliobothrium lunae* is most similar to *C. riseri*, *C. lintoni*, and *C. pellucidum* in possessing bothridial muscular pads with crenulated margins that extend as distinct muscular flaps above the bases of the hooks. But *C. lunae* differs from *C. riseri* in the morphology of the cocoons (oval with several onchospheres in *C. lunae*, elongate, filamentous with 8 onchospheres in *C. riseri*) and in shape of gravid segments (length to width ratio 5.2–7.6:1 in *C. lunae*, 2–4:1 in *C. riseri*). In addition, the hooks of *C. riseri* are more robust than they are in *C. lunae*, and the abaxial hooks lack the anterior notch present in *C. lunae* between the bases and the blades (Fig. 46, arrow). *Calliobothrium lunae* differs from *C. pellucidum* in its possession of an accessory piece that is broader anteriorly than posteriorly rather than approximately square, fewer number of testes (averaging 26 in *C. lunae*, 35 in *C. pellucidum*), and fewer number of segments (7–10 in *C. lunae*, 10–14 in *C. pellucidum*). Finally, *C. lunae* can be distinguished from *C. lintoni* in that its axial hooks are more recurved than the abaxial hooks, whereas in *C. lintoni* the axial and abaxial hooks are equally recurved and in its possession of abaxial hook bases with axial extensions that are single rather than bifid. In addition, *C. lunae* has ciliumlike projections on the distal surface of the muscular pad, which were not observed in *C. lintoni*.

DISCUSSION

In their revision of the small-bodied, nonlacinate species of *Calliobothrium*, Nasin et al. (1997) discussed the specificity of *Calliobothrium* spp. for a single host and predicted that each species of *Mustelus* would host at least 1 endemic species of *Calliobothrium*. The present study corroborates this prediction and is consistent with the concept of oioxenous specificity described by Euzet and Combes (1980). *Mustelus schmitti* has its own species of *Calliobothrium* (*C. australis*, *C. barbarae*, and *C. lunae*) different from other species of *Mustelus*. Nasin et al. (1997) also noted that species of *Calliobothrium* commonly occur in pairs in species of the smooth-hound sharks (*Mustelus* spp.). Moreover, the congeners parasitizing each host species appear to belong to identifiable morphological groups, a species that is small-bodied and nonlacinate and one that is large-bodied and lacinate (Nasin et al., 1997). In *M. schmitti*, there are 3 species of *Calliobothrium*, at least 1 of which belongs to each of these different morphological groups, *C. australis* (large bodied and lacinate), *C. barbarae*, and *C. lunae* (small bodied and nonlacinate). In addition, within the small-bodied group, *C. barbarae* and *C. lunae* belong to 2 subgroups: small bodied, lacking accessory piece (*C. barbarae*) and small bodied, having accessory piece (*C. lunae*). A similar combination of species has been found by Euzet (1959) in *M. mustelus* (Linnaeus, 1758) and *M. canis* (Mitchill, 1815) (see Nasin et al., 1997 for discussion on host identity). They were also parasitized by 3

species of *Calliobothrium*, *C. verticillatum* (large bodied and laciniate), *C. eschrichti* (small bodied, nonlaciniate, lacking accessory piece), and *C. lintoni* (small bodied, nonlaciniate, having accessory piece). But Alexander (1963) noted a different assemblage of species of *Calliobothrium* in *M. lenticulatus* Phillipps, 1932; *C. verticillatum*, *C. tylotocephalum* (both large bodied and laciniate), and *C. eschrichti* (small bodied, nonlaciniate, and lacking accessory piece), assuming that the identity of *C. verticillatum* and *C. eschrichti* can be confirmed. Considering these data, it appears that the assemblages of species of *Calliobothrium* parasitizing the same host species are more variable than expected, although they are certainly composed of representatives of the different morphological types. In view of the cladistic analyses made by Nasin et al. (1997) and Caira et al. (2001), none of the congeners inhabiting the same host species seems to be the closest relative of the other, as noted by Caira and Jensen (2001). They suggested that a diversity of explanations involving colonization is possible in this system. Similar patterns have been documented for the co-occurrence of pairs of species of *Gyrocotyle* Diesing, 1850, in holocephalan fishes (Bandoni and Brooks, 1987) and for multiple species of *Telorchis* Lühe, 1899, co-occurring in North American freshwater turtles (Macdonald and Brooks, 1989).

Predictions made by Nasin et al. (1997) about the attachment sites of the different morphological types of species of *Calliobothrium* within the spiral intestine of the host were also corroborated for *M. schmitti*; the small-bodied, nonlacinate species (*C. barbarae* and *C. lunae*) were found in chambers 1–3 of the spiral intestine, whereas the large-bodied, laciniate species (*C. australis*) were attached in chambers 3–5 (Ivanov, 1996; A. J. Alarcos, pers. comm.).

Euzet (1954) described a transformation in the shape of cocoons in *C. verticillatum* from inside to outside the uterus. Within the uterus the onchospheres are grouped, lined up in slightly arched cylindrical cocoons. Once in contact with seawater, the envelop of the cocoon swells, the onchospheres regroup in the center, and the cocoons become fusiform with 2 polar filaments. The elongate, filamentous cocoons described in *C. australis* were observed inside and outside the uterus. Even though there exist some subtle differences between these 2 stages of development, cocoons are always elongate and filamentous. Whereas the cocoons inside the uterus are shorter with rounded ends, and the onchospheres are lined up very close to each other, the cocoons in contact with seawater swell longitudinally, and as a consequence, they are longer, elongated, with pointed ends, and the onchospheres are lined up more scattered within the cocoon.

The microtriche pattern observed on bothridial, apical muscular pads, cephalic peduncle, and segment surfaces of *C. australis*, *C. barbarae*, and *C. lunae* is generally consistent with the patterns described for other species of *Calliobothrium* (Butler, 1987; Caira and Ruhnke, 1991; Nasin et al., 1997). Even though bladellike and short filiform microtriches have been described on proximal bothridial surfaces for most species, only the bladellike microtriches could be observed in the species described above. It might be that the short filiform microtriches are also present in these taxa, but the densely packed arrangement of the bladellike microtriches cover them. The ciliumlike projections on the distal surface of muscular pads in *C. lunae* have not been seen previously in *Callioboth-*

rium spp. Similar structures have been reported for another onchobothriid *Phoreiobothrium manirei* Caira, Healy et Swanson, 1996, on the protrusions on the posterior margin of the second loculus and on the distal bothridial surface and lateral region of the scolex of the diphyllidean *Echinobothrium hoffmanorum* Tyler, 2001.

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