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Selachohemecus benzi n. sp. (Digenea: Sanguinicolidae) from the blacktip shark *Carcharhinus limbatus* (Carcharhinidae) in the northern Gulf of Mexico

Stephen A. Bullard[1], Robin M. Overstreet[1,*] & John K. Carlson[2]
[1]*Gulf Coast Research Laboratory, Department of Coastal Sciences, The University of Southern Mississippi, PO Box 7000, Ocean Springs, Mississippi 39566, USA*
[2]*Shark Population Assessment Group, National Marine Fisheries Service, Southeast Fisheries Science Center, 3500 Delwood Beach Road, Panama City, Florida 32408, USA*

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Abstract

Selachohemecus benzi Bullard & Overstreet n. sp. infects the heart and kidney of the blacktip shark *Carcharhinus limbatus* in the northern Gulf of Mexico off Florida and Mississippi, USA. Specimens of *S. olsoni* Short, 1954, the only congener and only other named blood fluke reported from a chondrichthyan in the Gulf of Mexico, were collected from the heart of the Atlantic sharpnose shark *Rhizoprionodon terraenovae* from two new localities, Apalachicola Bay, Florida, and Mississippi Sound, Mississippi, USA. The new species differs from *S. olsoni* by having a larger body (1.4–3.8 mm long), robust tegumental body spines numbering 51–63 along each lateral body margin, a testis extending from the posterior caeca to the ovary, and a medial ovary with lobes. We amend the diagnosis of *Selachohemecus* Short, 1954 to accommodate it and provide a diagnostic key for all named chondrichthyan blood flukes.

Introduction

Few blood flukes (Sanguinicolidae von Graff, 1907) reportedly infect chondrichthyans (Smith, 1997, 2002). A total of four nominal species, each belonging to monotypic genera, have been reported from the vascular system of each of two sharks (Short, 1954; Maillard & Ktari, 1978), a ray (Madhavi & Rao, 1970) and two chimaeras (Van der Land, 1967; Kamegai et al., 2002). Only one species, *Selachohemecus olsoni* Short, 1954, was described previously from a chondrichthyan in the Gulf of Mexico. This study treats a new species of *Selachohemecus* Short, 1954 from the heart and kidney of a carcharhinid shark from the northern Gulf of Mexico and extends the geographical range of *S. olsoni*.

*Author for correspondence (E-mail: robin.overstreet@usm.edu)

Materials and methods

Sharks were captured by gill-net, longline and hook and line in summer of 1995, 1999 and 2004, as well as by trawl in October 2002 and 2003. Sharks were pithed immediately after capture, and the heart from each shark was extracted, bisected, sprayed with 8.5 ppt sodium chloride (NaCl) solution or an anticoagulant solution of 5.0 gm NaCl and 2.0 gm NaCl-citrate/L of distilled water to dislodge the flukes, and examined with the aid of a dissecting microscope. Flukes were killed under slight coverslip pressure with heat from an ethanol-burner flame and stored in 5–10% neutral phosphate-buffered formalin. Wholemounts were stained in Van Cleave's haematoxylin with several additional drops of Ehrlich's haematoxylin, made alkaline at 70% ethanol with lithium carbonate and butyl-amine, dehydrated, cleared in clove oil and mounted in Canada balsam. Several

specimens for scanning electron microscopy (SEM) were dehydrated, immersed in hexamethyldisilazane for 15 min, dried under a vacuum for 10 min and sputter-coated with gold-palladium. Illustrations of mounted specimens were made with the aid of a drawing tube. Measurements are reported in micrometres and given as the range followed by the sample size in parentheses. The holotype and two paratypes were deposited in the United States National Parasite Collection (USNPC), and another paratype was deposited in the Natural History Museum, London (NHML).

Selachohemecus Short, 1954

Amended diagnosis

Body elongate, 4–10× longer than wide, dorsoventrally flattened, ventrally concave, with posterior end tapering more than anterior end, spined. Tegumental body spines C-shaped, directed ventrally, with each on a separate peduncle, in single ventrolateral column, not continuous posteriorly. Rosethorn-shaped spines lacking. Nervous system with paired lateral nerve cords connecting anteriorly and posteriorly. Mouth medioventral, subterminal. Oral sucker and pharynx lacking. Oesophagus medial, extending posteriorly either straight or sinuously along mid-line for 1/4–1/3 of body length. Intestine X-shaped, with four short caeca of equal length, lacking diverticula. Testis occupies middle 1/3 of body, posterior to caecal intersection. Auxiliary external seminal vesicle lacking. Cirrus-sac present or absent. Cirrus sinistral, post-gonadal. Ovary considerably post-caecal; post-ovarian space 1/4–1/3 of body length. Laurer's canal lacking. Oötype dextral, near mid-line, comprising an inconspicuous ovoid chamber posterior to ovary. Oviducal seminal receptacle present, bulbous or not depending on amount of sperm in duct. Uterus post-gonadal, not extending laterad beyond ventrolateral nerve cords; uterine eggs spheroid, thin-shelled. Vitellarium follicular, extending from nerve commissure to ovary, with asymmetrical posterior branches, with longer dextral branch flanking gonads; common collecting duct originating from dextral branch of vitellarium. Common genital pore dorsal, post-gonadal, opening near posterior end of body between mid-line and sinistral ventrolateral nerve cord. Adults infecting vascular system of carcharhinid sharks. Type-species: *S. olsoni* Short, 1954 from the heart of Atlantic sharpnose shark *Rhizoprionodon terraenovae* (Richardson) (as *Scoliodon terranovae*) (Carcharhiniformes: Carcharhinidae) from Alligator Harbor, Florida, USA.

Remarks

The genera of blood flukes infecting sharks and chimaeras, *Selachohemecus* Short, 1954, *Chimaerohemecus* Van der Land, 1967 and *Hyperandrotrema* Maillard & Ktari, 1978, differ from all other blood fluke genera by having one or two ventrolateral columns of C-shaped tegumental body spines (Short, 1954; Van der Land, 1967; Maillard & Ktari, 1978). Teleost blood flukes typically have several ventrolateral rows of straight, spike-like tegumental body spines, each with a slightly recurved distal tip, e.g. *Elaphrobates euzeti* Bullard & Overstreet, 2003 (see Bullard & Overstreet, 2003) and *Cardicola* spp. (see Bullard & Overstreet, 2004). *Paradeontacylix* McIntosh, 1934, another genus comprised of species that reportedly infect teleosts only, have rosethorn-shaped spines at the posterior body end in addition to spike-like lateral tegumental body spines (McIntosh, 1934; Ogawa & Egusa, 1986). *Selachohemecus* differs from the other genera of chondrichthyan blood flukes by having an intestine that is X-shaped, consisting of short anterior and posterior caeca of approximate equal length, rather than an intestine that is U-shaped, consisting of long posterior caeca only. In addition to that feature, a combination of lacking Laurer's canal and having a single ventrolateral column of tegumental body spines, a post-caecal ovary and a common genital pore further separates *Selachohemecus* from the other genera of chondrichthyan blood flukes. *Chimaerohemecus* has inter-caecal gonads, two ventrolateral columns of tegumental body spines and separate genital pores. *Hyperandrotrema* has posterior caeca that extend to near the posterior end of the body, a common genital pore and Laurer's canal present. *Orchispirium* Madhavi & Rao, 1970, a monotypic genus whose only known species infects the mesenteric vessels of a stingray (Madhavi & Rao, 1970), is unusual because it apparently lacks tegumental body spines and has a testis with 9–11 transverse coils that fill the inter-caecal space.

***Selachohemecus benzi* n. sp.**

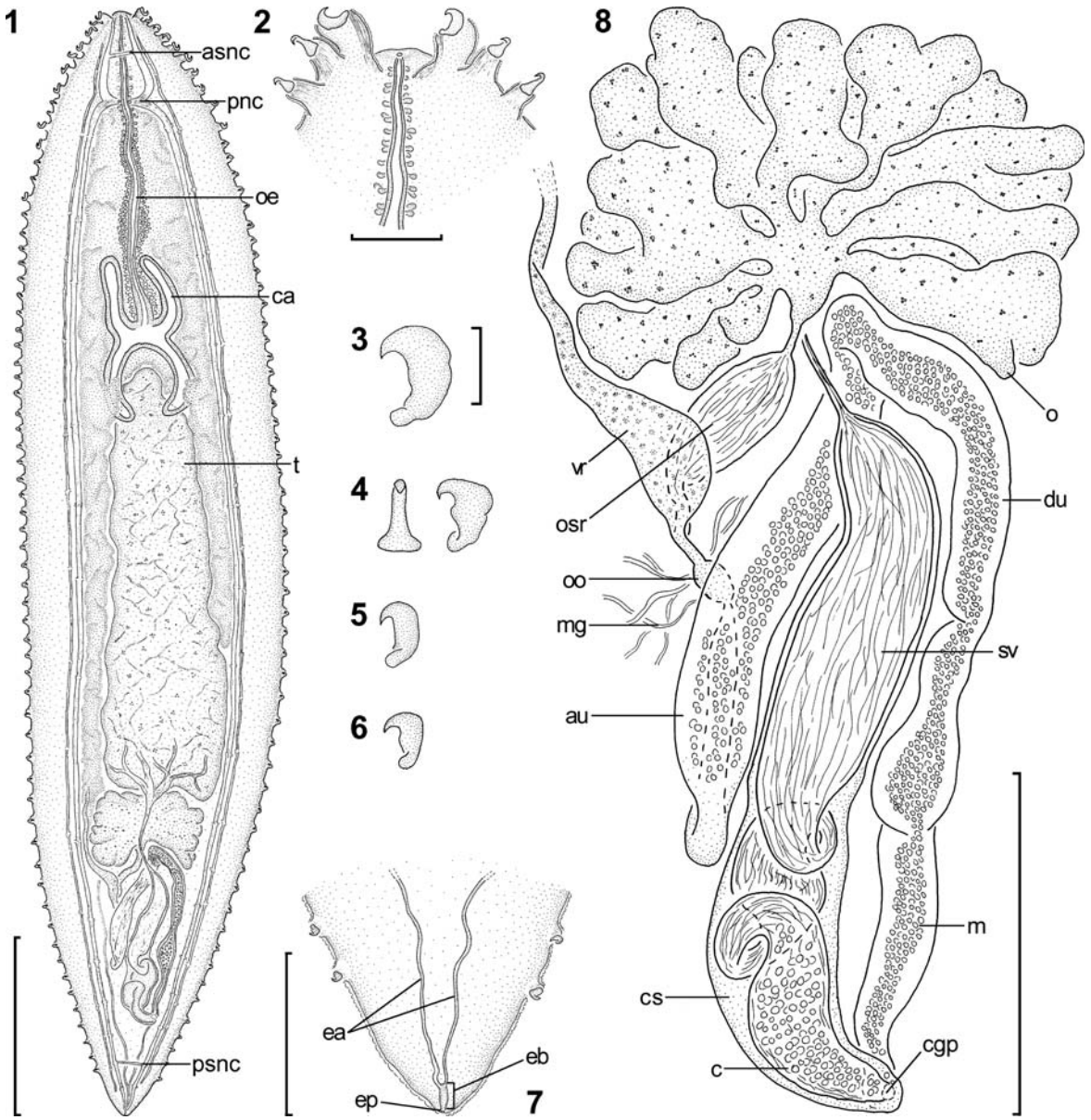
Type-host: *Carcharhinus limbatus* (Valenciennes) blacktip shark (Carcharhiniformes: Carcharhinidae).
Primary site of adult: Attached to luminal surface of atrium and ventricle; other site: kidney (one adult specimen).
Type-locality: Northern Gulf of Mexico, Apalachicola Bay, Florida, USA (29 ° 39′N, 85° 11′W); other localities: Eastern Gulf of Mexico, Tampa Bay, Florida, USA and Northern Gulf of Mexico, off Mississippi, USA (30° 14′N, 88° 43′W).
Prevalence and intensity of infection: 14 of 51 (27%) blacktip sharks off Florida were infected: 6 had 1 worm; 6 had 3–8; and 2 had 15 and 20; 1 of 30 (3%) blacktip sharks from off Mississippi and Louisiana was infected with 1 adult specimen.
Type-material: Holotype, USNPC (Beltsville, Maryland) No. 95846, Paratypes, USNPC Nos 95847, 95848; BMNH (London) Reg. No. 2005.6.6.1.
Etymology: The name *benzi* is for Dr George William Benz (Middle Tennessee State University, Murfreesboro, Tennessee, USA) in recognition of his contributions to elasmobranch parasitology.

Description (Figures 1–25)

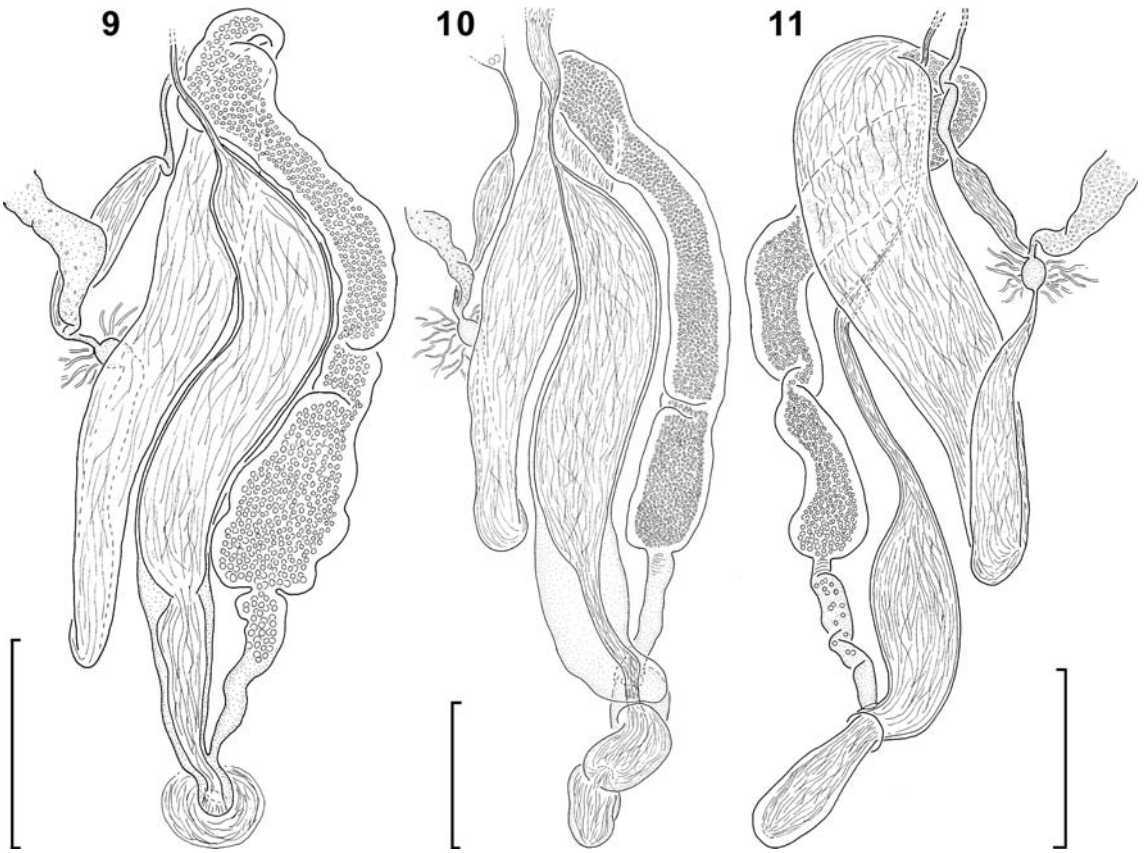
[Based on 16 wholemounts, several sputter-coated specimens, and 2 serially sectioned adult specimens.] Body 1,449–3,831 (16) long, 408–597 (16) wide, 3–7 × longer than wide (Figure 1). Tegumental body spines 51–63 (16) per side of body or a total of 102–126 (16), ending about 100–208 (8) or 4–7% of body length from posterior end of body; spines in anterior region of body conspicuous; longest spine 20–30 (16) long, 5–12 (16) wide (Figures 3,12,14,15); spines in mid-body and posterior region of body 12–20 (16) long, 5–12 (16) wide (Figures 4–6); base knob-like (Figures 3–6,15). Peduncles in anterior region of body 30–50 (16) long, 15–37 (16) wide (Figures 12,15); peduncles in mid-body and posterior region of body 15–30 (13) long, 7–22 (14) wide; peduncular muscle fibers connecting to base of spine. Ventrolateral nerve-cord 1,449–3,831 (15) long, 7–22 (14) wide near midbody at widest level, 77–189 (14) from body margin, confluent in posterior end of body, with secondary branches extending laterally and medially; dorsolateral nerve-cord paired, extending parallel with ventrolateral nerve-cord between that nerve-cord and body margin, *c*.5 wide, with secondary branches extending laterally and medially. Primary commissure perpendicular to mid-line of body, connecting ventrolateral nerve-cords, 149–263 (13) or 6–10% of body length from anterior end of body, 52–136 (13) across width of worm, 15–32 (13) in diameter; secondary commissures connecting ventrolateral nerve-cords anteriorly and posteriorly; anterior secondary commissure between primary commissure and anterior end of body; posterior secondary commissure just anterior to level of posterior-most lateral tegumental body spines (Figure 1). Sensory papillae abundant in posterior region of body, ventral; some with sensory cilium; sensory cilium 4 long (Figure 13).

Mouth 2–5 (10) in diameter, 10–12 (6) from anterior end of body (Figures 1, 2, 12). Oesophagus 544–1,105 (14) long or 26–38% of body length, 25–60 (12) in maximum width, ventral to primary nerve-commissure, dorsal to secondary nerve-commissure (Figure 1); oesophageal wall thickening from 1–3 (5) near mouth to 5–22 (5) posteriorly. Oesophageal gland enveloping oesophagus for entire length, with gland-cells most abundant in area 283–472 (5) long or 34–52% of oesophageal length and 50–85 (5) wide or up to 2 × width of oesophagus. Caecal intersection 29–31% of body length from anterior end of body; anterior caeca 136–338 (13) long or 7–9% of body length, 17–80 (12) wide; posterior caeca 104–308 (14) long or 6–10% of body length, 10–75 (13) wide, containing granular material within lumen of some individuals (Figure 18); granular material dense, brownish-yellow in stained wholemounted specimens.

Testis 408–1,399 (16) long or 28–40% of body length, 164–442 (16) wide or 40–77% of body width, 2.2–5.7× longer than wide, dorsal to posterior caeca (Figure 1), enclosing rod-like refractive processes; processes extending dorsoventrally, *c*.4 in diameter. Post-testicular space 487–1,154 (16) long or 27–35% of body length. Vasa efferentia comprising interconnecting meshwork of fine ducts entwined throughout testicular tissue, containing spermatozoa in all examined specimens, 10–13 (5) in diameter, extending primarily dorsoventrally and along ventral surface of testis, coalescing in posterior region of testis; vas deferens 99–323 (14) long, 12–45 (14) wide,



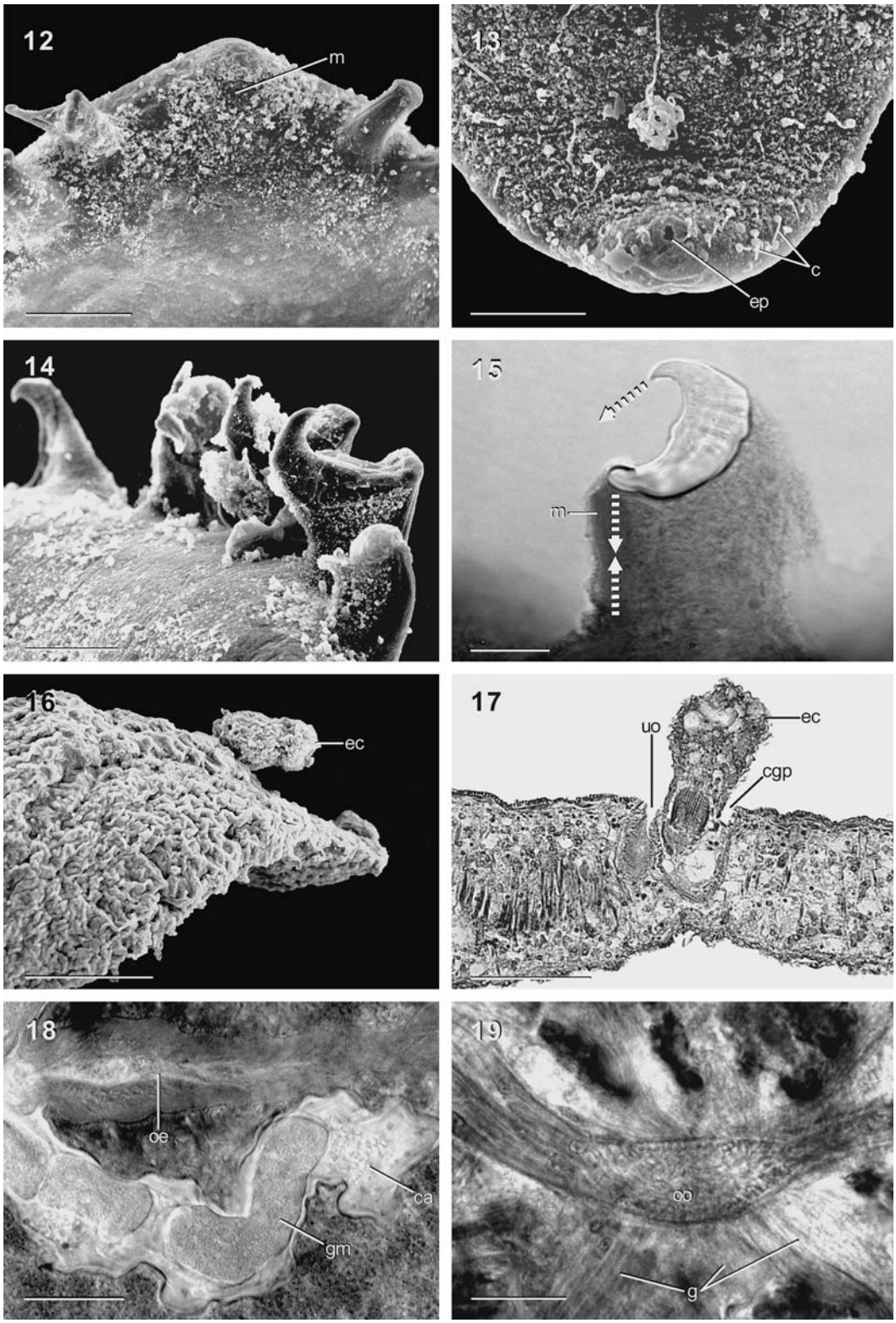
Figures 1–8. *Selachohemecus benzi* n. sp. from the heart of the blacktip shark *Carcharhinus limbatus*. 1. Body of holotype, proximal portion of uterus filled with sperm, ventral view, holotype. 2. Anterior end of different adult showing mouth, flanking tegumental body spines, distal region of oesophagus and scant oesophageal gland-cells abutting oesophagus, ventral view. 3–6. Tegumental body spines. 3. Spine from anterior body region, lateral view; 4. Spines from between caecal intersection and mouth, frontal (at left) and lateral (at right) views; 5. Spine from between genital pore and posterior end of body, lateral view; 6. Spine from near excretory pore, lateral view. 7. Posterior end of body showing excretory bladder and arms, terminal excretory pore and position of posterior-most tegumental body spines, ventral view (nerve not illustrated). 8. Genitalia, oviducal seminal receptacle with sperm, ascending and descending portions of uterus and metraterm with eggs, ventral view. Eggs in the distal portion of the inverted cirrus represent artifact, but their presence demonstrates that eggs can be drawn into this portion of sac. *Scale-bars*: 1, 500 μm; 2, 150 μm; 3–6, 20 μm; 7, 200 μm; 8, 150 μm. *Abbreviations*: asnc, anterior secondary nerve commissure; au, ascending uterus; c, cirrus; ca, caecum; cgp, common genital pore; cs, cirrus-sac; du, descending uterus; ea, excretory arms; eb, excretory bladder; ep, excretory pore; m, metraterm; mg, mehlis gland ducts; o, ovary; oe, oesophagus; oo, oötype; osr, oviducal seminal receptacle; pnc, primary nerve commissure; psnc, posterior secondary nerve commissure; sv, seminal vesicle; t, testis; vr, vitelline reservoir.



Figures 9–11. Selachohemecus benzi n. sp. from *Carcharhinus limbatus*, genitalia of adults demonstrating morphological variability. 9. Ventral view of genitalia (cirrus everted) showing sperm in seminal vesicle, oviducal seminal receptacle and ascending uterus, as well as eggs in the descending uterus and metraterm. 10. Ventral view of genitalia (swollen cirrus everted) showing obvious cirrus-sac surrounding distal portion of seminal vesicle and no egg in the ascending uterus. 11. Dorsal view of genitalia (cirrus everted) showing constricted proximal portion of seminal vesicle and a few eggs in metraterm. *Scale-bars*: 150 μm.

extends posteriorly along mid-line and curves slightly sinistrally before joining cirrus-sac. Cirrus-sac with wall 3–7 (9) thick (Figures 8–11). Seminal vesicle 244–497 (14) long, 30–109 (14) wide, containing sperm in 12 of 16 specimens, runs parallel to sinistral ventrolateral nerve-cord before narrowing and looping dorsally. Cirrus 74–223 (11) long or 26–53% of seminal vesicle length (non-extruded), 25–90 (11) wide or 28–187% of seminal vesicle width (non-extruded), 87–209 (7) long (extruded) (Figures 8–11, 16, 17). Common genital pore 164–319 (16) or 6–11% of body length from posterior end of body, 62–149 (16) from sinistral body margin, 119–211 (16) from dextral body margin; sperm with cylindrical head and long whip-like tail (Figure 23).

Ovary medial, lobed, 109–308 (16) long or 5–9% of body length, 159–452 (16) wide or 37–79% of body width, 110–170% wider than long, occupies space immediately posterior to testis and between ventrolateral nerve-cords, anterior to seminal vesicle and dorsal to vas deferens, contains refractive dorsoventral rod-like processes (Figures 1, 8, 20). Oviduct including oviducal seminal receptacle 99–249 (14) long, 17–37 (14) wide; oviducal seminal receptacle 62–149 (11) long, 20–37 (11) wide. Oötype 17–60 (9) long, 12–30 (9) wide, at level of seminal vesicle (Figures 1, 8–11, 19). Vitellarium with vitelline follicles compacted in dense lobules, occupies space dorsolateral to testis and alimentary tract; common collecting duct 149–348 (11) long, 17–57 (11) wide. Mehlis' gland comprising a loosely-aggregated field of weakly staining cells surrounding lumen of oötype. Uterus extends posteriorly from oötype short distance before curving ventrally and connecting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Figures 12–19. *Selachohemecus benzi* n. sp. from *Carcharhinus limbatus*. 12. Mouth (m) and flanking peduncles and tegumental body spines, ventral view, scanning electron micrograph (SEM). 13. Excretory pore (ep) and sensory papillae, some of which exhibit a cilium (c), ventral view, SEM. 14. Spines and peduncles in anterior region of body, dorsal view, SEM. 15. Dextral anterior-most spine and peduncle with muscle fibres (m) connected to knob-like proximal end of spine, ventral view, light micrograph (LM) of wholemount. 16. Everted cirrus (ec), lateral view, SEM. 17. Everted cirrus (ec) extruding from common genital pore (cgp), LM of histological section. Note that uterine opening (uo) is just lateral to base of everted cirrus. 18. Granular material (gm) within caecum (ca) near oesophagus (oe), LM of wholemount. 19. Oötype (oo) and glandular ducts (g) connecting laterally, LM of whole mount. *Scale-bars*: 12–14, 20 μm; 15, 10 μm; 16, 100 μm; 17, 50 μm; 18, 100 μm; 19, 15 μm.

to ascending portion; ascending portion extends anteriorly and diagonally across mid-line, occasionally filled with eggs (Figure 8) or sperm and thereby superficially resembling seminal vesicle (Figures 9–11), curves ventrally near posterior margin before connecting with descending portion; descending portion extends posteriorly; metraterm weakly muscular, comprising distal-most portion of female reproductive tract, demarcated from descending uterus by obvious constriction (Figures 9–11) or not (Figure 8), with eggs (Figures 8, 9, 11) or not (Figure 10), 119–273 (13) long or 9–29% of uterine length, 15–65 (13) wide, with wall 3–10 (9) thick. Uterine eggs 5–7 (12) in diameter or 5–13% of uterus width at widest level (Figure 21); ejected eggs 11–14 (10) in diameter (presumably much larger when lodged in host tissue [e.g. Bullard & Overstreet, 2003, 2004]), containing 1 large spheroid and darkly-staining body as well as several smaller dense lipid-like bodies, with thin shell (Figure 22).

Excretory bladder appears *c*.70 long, oblong, medial, between posterior confluence of nerve-cord and posterior end of body, with arms; arms *c*.5 wide, paired, uniting just anterior to excretory pore, visible in region posterior to genitalia in one specimen; excretory pore medial, terminal, *c*.2 wide (Figures 7, 13).

Discussion

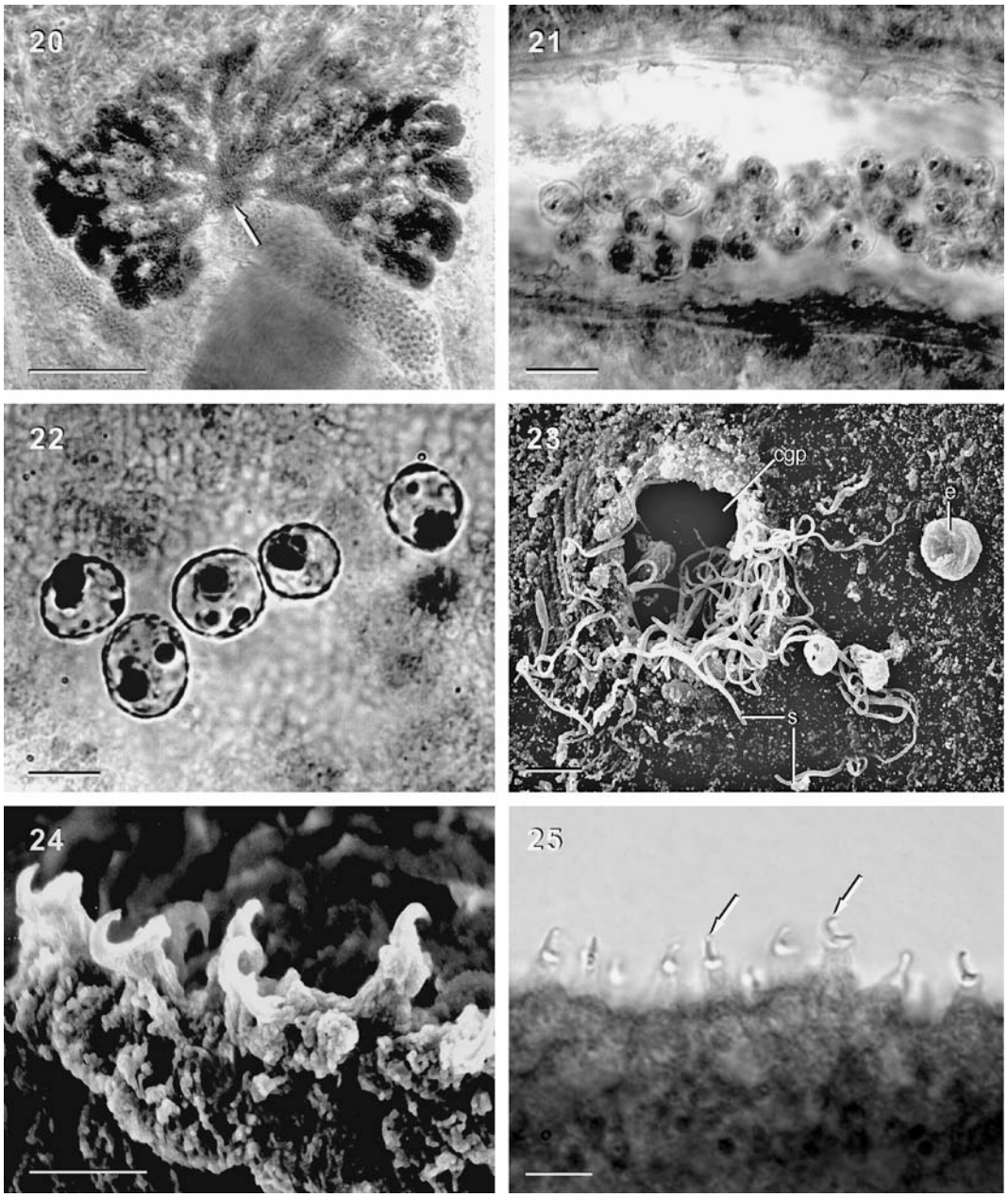
Selachohemecus benzi n. sp. differs most notably from *S. olsoni*, the only other known species of this genus, by the combination of having a 1.4–3.8 mm long body, robust tegumental body spines numbering 51–63 on each side of the body, a testis extending from the posterior caeca to the ovary, and a medial ovary with lobes. *S. olsoni* has a smaller body (982–1,374 × 172–196 μm), minute, sickle-like tegumental body spines numbering 180–310 per each side of the body (Figures 24, 25), a sinistral testis not extending to the posterior caeca, and an ovoid, sinistral ovary overlapping the posterior portion of the testis.

We consider *S. benzi* congeneric with *S. olsoni* even though *S. olsoni* apparently lacks a cirrus-sac. We also consider the terminal genitalia in *S. olsoni* to be a simple version of the more complex genitalia in *S. benzi*. Based on our interpretation of the genitalia in *S. benzi*, we consider the structure labeled as the vas deferens by Short (1954) to comprise a seminal vesicle and a short, indistinct cirrus. Furthermore, adults of *S. olsoni* are minute compared to those of *S. benzi*, and perhaps components of the genitalia, namely the cirrus-sac, of *S. olsoni* are difficult to distinguish simply because they are much smaller than those of *S. benzi*.

The single specimen of *S. benzi* that infected the kidney of a 74 cm TL blacktip shark from Tampa Bay demonstrated that the adult of this species can occur in a site other than the heart. This specimen, not included in the description, was small (1,459 × 309 μm) but had sperm in the seminal vesicle as well as poorly developed eggs (*c*. 5 μm wide) in the uterus.

We did not make detailed live observations of a specimen of *S. benzi* or *S. olsoni*, but based on the presence of prominent muscles in each of the lateral peduncles, the tegumental body spines of these sanguinicolids probably pinch host tissue. Upon contracting the peduncular muscle, the flukes may pivot each tegumental body spine at the base, and the distal tip of the spine may arc ventrally and toward the heart tissue (Figure 15). We suspect that the C-shaped tegumental body spines of *Hyperandrotrema cetorhini* Maillard & Ktari, 1978 and *Chimaerohemecus trondheimensis* Van der Land, 1967 function similarly.

The level of host specificity exhibited by the chondrichthyan blood flukes *C. trondheimensis*, *S. olsoni*, *S. benzi*, *Orchispirium heterovitellatum* Madhavi & Rao, 1970 and *H. cetorhini* is indeterminate because the vascular system of few sharks, rays and chimaeras has been examined critically



Figures 20–25. *Selachohemecus* spp. 20–23. *S. benzi* n. sp. from *Carcharhinus limbatus*. 20. Ovary showing central junction of lobes (arrow) that ultimately gives rise to proximal portion of oviduct (not in focal plane), LM of wholemount. 21. Uterine eggs, LM of wholemount. 22. Released eggs, same magnification as those of Figure 21, LM of wholemount. 23. Sperm (s) and ovoid egg (e) associated with common genital pore (cgp), dorsal view, SEM. 24–25. *S. olsoni* Short, 1954 from the heart of the Atlantic sharpnose shark *Rhizoprionodon terraenovae*. 24. Tegumental body spines from mid-body, SEM, lateral view. 25. Tegumental body spines, two of which are indicated by arrows, from mid-body, lateral view, LM of wholemount. *Scale-bars*: 20, 100 μm; 21–23, 10 μm; 24–25, 4 μm.

for the presence of blood flukes (Tables 1, 2). However, based on our limited data, *S. olsoni* and *S. benzi* are apparently highly host-specific, each infecting a single host species, even though infected individuals of both shark species were captured simultaneously from Apalachicola Bay, the type-

Table 1. Sanguinicolids reported from chondrichthyans

Parasite	Host		Site	Locality	Reference
Selachohemecus olsoni	*Rhizoprionodon terraenovae*	Atlantic sharpnose shark	heart	Alligator Harbor, Florida, USA	Short, 1954
				Apalachicola Bay, Florida, USA	Present study
				Mississippi Sound, Mississippi, USA	Present study
Selachohemecus benzi n. sp.	*Carcharhinus limbatus*	blacktip shark	heart	Apalachicola Bay, Florida, USA	Present study
				Northern Gulf of Mexico, off Mississippi, USA	Present study
			kidney	Tampa Bay, Florida, USA	Present study
Orchispirium heterovitellatum	*Himantura imbricata*	scaly whipray	mesenteric vessels	Bay of Bengal, off Waltair Coast, India	Madhavi & Rao, 1970
Hyperandrotrema cetorhini[1]	*Cetorhinus maximus*	basking shark	circulatory system	Mediterranean Sea off Tunisia	Maillard & Ktari, 1978
			not reported	Oslofjorden, Norway	Smith, 1972[2]
			heart	North Sea off Montrose, Scotland	Smith, 1972[2]
Chimaerohemecus trondheimensis	*Chimaera monstrosa*	rabbit fish	dorsal aorta	Trondheimsfjorden, Norway	Van der Land, 1967
			not reported	Korsfjorden (*sic.*), Norway	Lockyer et al., 2003
	Hydrolagus mitsukurii	spookfish	dorsal aorta and postcardinal vein around kidney	Suruga Bay, Japan	Kamegai et al., 2002
Chimaerohemecus sp.[3]	*Hydrolagus affinis*	smalleyed rabbitfish	heart	North Atlantic Ocean, off Southwest Greenland	Karlsbakk et al., 2002

[1]Sproston (1948) stated that, "...two specimens only, of a blood fluke belonging to the family Spirorchiidae (*sic.*), were recovered from the branchial blood vessels" of a basking shark caught "just west of Plymouth Sound," England. These specimens probably are *H. cetorhini* because this blood fluke infects the basking shark in the region. However, we did not examine Sproston's (1948) specimens, we do not know where these specimens are now and we do not know of another report that includes a further observation of any of Sproston's (1948) blood flukes.
[2]Bray & Cribb (2003) confirmed the identity of a specimen from Smith's (1971) collections as *H. cetorhini* (BMNH 1988.11.24.16).
[3]We attempted to borrow these specimens to identify them, but they were no longer in existence.

Table 2. Sharks examined for blood flukes in the present study.

Host		n	Prevalence (%)	Locality
SQUALIFORMES				
Dalatiidae - Sleeper sharks				
Etmopterus gracilispinis	broadbanded lanternshark	3	0	Northern Gulf of Mexico
Etmopterus hillianus	Caribbean lantershark	1	0	Northern Gulf of Mexico
Etmopterus pusillus	smooth lanternshark	1	0	Northern Gulf of Mexico
Squalus cubensis	Cuban dogfish	76	0	Northern Gulf of Mexico
SQUATINIFORMES				
Squatinidae - Angel sharks				
Squatina dumeril	sand devil	27	0	Northern Gulf of Mexico
HEXANCHIFORMES				
Hexanchidae - Cow sharks				
Heptranchias perlo	sharpnose sevengill shark	1	0	Northern Gulf of Mexico
CARCHARHINIFORMES				
Carcharhinidae - Requiem sharks				
Carcharhinus leucas	bull shark	4	0	Northern Gulf of Mexico, off Mississippi
Carcharhinus limbatus	blacktip shark	17	0	Northern Gulf of Mexico, off Louisiana
		13	8	Northern Gulf of Mexico, off Mississippi
		15	27	Tampa Bay, Florida
		36	28	Northern Gulf of Mexico, off Florida
Carcharhinus brevipinna	spinner shark	5	0	Northern Gulf of Mexico, off Louisiana
		1	0	Northern Gulf of Mexico, off Mississippi
		1	0	Northern Gulf of Mexico, off Florida
Carcharhinus plumbeus	sandbar shark	1	0	Northern Gulf of Mexico
Carcharhinus isodon	finetooth shark	1	0	Northern Gulf of Mexico, off Louisiana
		3	0	Northern Gulf of Mexico, off Florida
Carcharhinus acronatus	blacknose shark	2	0	Northern Gulf of Mexico, off Mississippi
		1	0	Northern Gulf of Mexico, off Florida
		5	0	Eastern Gulf of Mexico, off Florida
Carcharhinus signatus	night shark	1	0	Northern Gulf of Mexico
Rhizoprionodon terraenovae	Atlantic sharpnose shark	6	33	Northern Gulf of Mexico, off Mississippi
		12	17	Northern Gulf of Mexico, off Florida
Triakidae - Houndsharks				
Mustelus canis	smooth dogfish	1	0	Northern Gulf of Mexico, off Florida
Sphyrinidae - Hammerhead sharks				
Sphyrna zygaena	scalloped hammerhead shark	9	0	Northern Gulf of Mexico, off Florida
		1	0	Eastern Gulf of Mexico, off Florida
Sphyrna tiburo	bonnethead shark	3	0	Eastern Gulf of Mexico, off Florida

locality for *S. benzi*. In addition, we examined the hearts of several other shark species from the Northern Gulf of Mexico as well as from Apalachicola Bay, but none was infected (Table 2). We find it particularly noteworthy that an infection was not observed in nine specimens of the spinner shark *Carcharhinus brevipinna* (Müller & Henle) because it and the blacktip shark are sympatric species that are morphologically similar and closely related (Compagno, 1988).

We extend the geographical range of *S. olsoni* to the northern Gulf of Mexico off Mississippi (Tables 1, 2). Previously, *S. olsoni* was known from off Florida only (Short, 1954). We collected a total of three specimens of *S. olsoni* from the hearts of two of six Atlantic sharpnose sharks from Mississippi Sound as well as >20 and >40 specimens from 2 of 12 Atlantic sharpnose sharks *Rhizoprionodon terraenovae* from Apalachicola Bay, Florida.

Key to chondrichthyan blood flukes

1. Intestine X-shaped 2
   Intestine U-shaped 3
2. Testis entirely post-caecal; ovary sinistral .....*Selachohemecus olsoni*
   Testis ventral to posterior caeca; ovary medial ..... *Selachohemecus benzi*
3. Testis not coiled 4
   Testis coiled ..... *Orchispirium heterovitellatum*
4. Genital pore common, medial ....*Hyperandrotrema cetorhini*
   Genital pores separate, sinistral .... *Chimaerohemecus trondheimensis*

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References

Bray, R.A. & Cribb, T.H. (2003) The digeneans of elasmobranchs - distribution and evolutionary signficance. *In*: Combes, C. & Jourdane, J. (Eds.) *Taxonomy, ecology and evolution of metazoan parasites - Livre hommage au Professeur Louis Euzet*. Perpignan: Les Presses Universitaires de Perpignan, pp. 67–96.

Bullard, S.A. & Overstreet, R.M. (2003) *Elaphrobates euzeti* gen. and sp. n. (Digenea: Sanguinicolidae) from snappers (Lutjanidae) in the Gulf of Mexico. *In*: Combes, C. & Jourdane, J. (Eds.) *Taxonomy, ecology and evolution of metazoan parasites - Livre hommage au Professeur Louis Euzet*. Perpignan: Les Presses Universitaires de Perpignan, pp. 97–113.

Bullard, S.A. & Overstreet, R.M. (2004) Two new species of *Cardicola* (Digenea: Sanguinicolidae) in drums (Sciaenidae) from Mississippi and Louisiana. *Journal of Parasitology*, **90**, 128–136.

Compagno, L.J.V. (1988) *Sharks of the Order Carcharhiniformes*. Princeton, New Jersey: Princeton University Press, 486 pp.

Kamegai, S., Machida, M. & Kuramochi, T. (2002) Two blood flukes from deep-sea fishes of Suruga Bay, Japan. *Bulletin of the National Science Museum Series A (Zoology)*, **28**, 29–34.

Karlsbakk, E., Aspholm, P.E., Berg, V., Hareide, N.R. & Berland, B. (2002) Some parasites of the small-eyed rabbitfish, *Hydrolagus affinis* (Capello, 1867) (Holocephali), caught in the deep waters off SW Greenland. *Sarsia*, **87**, 179–184.

Lockyer, A.E., Olson, P.D., Østergaard, P., Rollinson, D., Johnston, D.A., Attwood, S.A., Southgate, V.R., Horak, P., Snyder, S.D., Le, T.H., Agatsuma, T., McManus, D.P., Carmichael, A.C., Naem, S. & Littlewood, D.T.J. (2003) The phylogeny of the Schistosomatidae based on three genes with emphasis on the interrelationships of *Schistosoma* Weinland, 1858. *Parasitology*, **126**, 203–224.

Madhavi, R. & Rao, K.H. (1970) *Orchispirium heterovitellatum* gen. et sp. nov. (Trematoda: Sanguinicolidae) from the ray fish, *Dasyatis imbricatus* Day, from Bay of Bengal. *Journal of Parasitology*, **56**, 41–43.

Maillard, C. & Ktari, M.H. (1978) *Hyperandrotrema cetorhini* n. g., n. sp. (Trematoda, Sanguinicolidae) parasite du système circulatoire de *Cetorhinus maximus* (Selacii). *Annales de Parasitologie Humane et Comparée*, **53**, 359–365.

McIntosh, A. (1934) A new blood trematode, *Paradeontacylix sanguinicoloides* n. g., n. sp., from *Seriola lalandi* with a key to the species of the family Aporocotylidae. *Parasitology*, **26**, 463–467.

Ogawa, K. & Egusa, S. (1986) Two new species of *Paradeontacylix* McIntosh, 1934 (Trematoda: Sanguinicolidae) from the vascular system of a cultured marine fish, *Seriola purpurascens*. *Fish Pathology*, **21**, 15–19.

Short, R.B. (1954) A new blood fluke, *Selachohemecus olsoni*, n. g., n. sp. (Aporocotylidae) from the sharp-nosed shark, *Scoliodon terra-novae*. *Proceedings of the Helminthological Society of Washington*, **21**, 78–82.

Smith, J.W. (1972) The blood flukes of cold-blooded vertebrates and some comparison with the schistosomes. *Helminthological Abstracts*, **41**, 161–204.

Smith, J.W. (1997) The blood flukes (Digenea: Sanguinicolidae and Spirorchidae) of cold-blooded vertebrates: Part 2. Appendix I: Comprehensive parasite-host list; Appendix II: Comprehensive host-parasite list. *Helminthological Abstracts*, **66**, 329–344.

Smith, J.W. (2002) Family Sanguinicolidae von Graff, 1907. *In*: Gibson, D.I., Jones, A. & Bray, R.A. (Eds.) *Keys to the Trematoda* . Vol. 1. Wallingford: CAB International and The Natural History Museum, pp. 433–452.

Sproston, N.G. (1948) On the genus *Dinobothrium* van Beneden (Cestoda), with a description of two new species from sharks, and a note on *Monorygma* sp. from the electric ray. *Parasitology*, **39**, 73–90.

Van der Land, J. (1967) A new blood fluke (Trematoda) from *Chimaera monstrosa* L. *Proceedings. Koninklijke Nederlandse Akademie van Wetenschappen, Section C, Biological and Medical Sciences*, **70**, 110–120.