

# REDESCRIPTION AND NEW HOST RECORD OF *CAPSALA LAEVIS* (MONOGENOIDEA: CAPSALIDAE: CAPSALINAE) FROM GILL OF ROUNDSCALE SPEARFISH, *TETRAPTURUS GEORGII* (PERCIFORMES: ISTIOPHORIDAE) IN THE NORTHWESTERN ATLANTIC OCEAN

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**ABSTRACT:** Specimens of a capsalid collected from the gill arches of 2 roundscale spearfish, *Tetrapturus georgii* Lowe, 1840, (Perciformes: Istiophoridae), captured in the northwestern Atlantic Ocean were identified as *Capsala laevis* (Verrill, 1875) Johnston, 1929 by having the combination of papillae on the ventral surface of haptor, dorsomarginal body sclerites in a single column extending the entire body length, haptoral accessory sclerites, conical papillae distributing over the ventral body surface, and an anterior attachment organ with a fimbriated posterior margin. The new specimens plus the holotype were used to conduct a taxonomic redescription of *C. laevis* using light and scanning electron microscopy. We documented that the holotype (USNPC No. 7179) and the new specimens of *C. laevis* from roundscale spearfish each had papillae on the ventral surface of the anterior attachment organs and sensory papillae on the dorsal body surface. Although data are insufficient at this time to justify proposal of a new species, the new specimens differed from the holotype and published accounts of *C. laevis* by having a sinistral dorsomarginal patch comprising 27–35 sclerites whereas the holotype has a dorsomarginal patch comprising 60 sclerites. *Capsala laevis* morphologically most closely resembles *Capsala ovalis* (Goto, 1894) Price, 1938, but can be most easily differentiated from it by having dorsomarginal body sclerites. This represents the first record of any parasite from the recently taxonomically resurrected roundscale spearfish, long considered by some as a junior subjective synonym of white marlin, *Tetrapturus albidus* Poey, 1860 and, concomitantly, a new host record for Capsalidae Baird, 1853. An updated list of host records for *C. laevis* is provided. A perusal of that literature reveals that the identity of the type host for *C. laevis* is indeterminate beyond Istiophoridae species and that subsequent reports of the type host as '*T. albidus*' are presumptuous (originally reported in 1875 by Verrill as "bill-fish" only). Our results indicated that 2 records of *C. laevis* from the swordfish, *Xiphias gladius* Linnaeus, 1758, (Perciformes: Xiphiidae) are dubious, i.e., study of the museum voucher USNPC No. 8154 indicates that Linton's 1940 record from the northwestern Atlantic Ocean likely represents a new species of *Capsala* Bosc, 1811 and that the Kayaş et al. 2010 record from the Aegean Sea likely depicts a species of *Capsaloides* Price, 1938.

Billfishes (Xiphoidei) are among the most charismatic and sought after marine vertebrates, drawing considerable attention from the sport fish and seafood industries throughout their worldwide range. The billfishes are presently divided into 2 extant families comprising the monotypic Xiphiidae (for the swordfish, *Xiphias gladius* Linnaeus, 1758) and the remaining billfishes of Istiophoridae, which includes 3 genera and 9 accepted species (Collette et al., 2006). *Tetrapturus* Rafinesque, 1810 includes white marlin, *Tetrapturus albidus* Poey, 1860; striped marlin, *Tetrapturus audax* (Philippi, 1887); and all of the extant spearfishes: Mediterranean spearfish, *Tetrapturus belone* Rafinesque, 1810; longbill spearfish, *Tetrapturus pfluegeri* Robins and de Syla, 1963; shortbill spearfish, *Tetrapturus angustirostris* Tanaka, 1915; and roundscale spearfish, *Tetrapturus georgii* Lowe, 1841 (see also Robins, 1974; Nakamura, 1985; Shivji et al., 2006). According to Collette et al. (2006), spearfishes are the scarcest of istiophorids and, perhaps because of this, their ectoparasites are correspondingly less well known than the ectoparasites of congeneric marlins and other billfishes (Lawler, 1981; Williams and Bunkley-Williams, 1996; Whittington, 2004; Chisholm and Whittington, 2007). Of those spearfishes, and based on molecular sequence data, roundscale spearfish is regarded as the most phylogenetically divergent (Collette et al., 2006) and infrequently encountered species (Barse and Bullard, pers. obs.). However, it has recently come to light that the roundscale spearfish may in fact be the most commonly encountered of spearfishes, one whose identity has been overlooked for years due to its superficial resemblance to white marlin (Beerkircher et al., 2009).

We recently had the rare opportunity to collect parasites from roundscale spearfish in the northwestern Atlantic Ocean. Herein, we describe the morphological features of those parasite specimens using light and scanning electron microscopy, provide an updated list of hosts for the parasite (Table I), and comment on its type host as well as on the taxonomy of a few related capsalids infecting billfishes.

## MATERIALS AND METHODS

Two roundscale spearfish were sampled opportunistically at the weigh-in dock (38°20.4'N, 75°05.0'W) designated for the 38th Annual White Marlin Open Tournament (Ocean City, Maryland) on 11 August 2011. The exact capture location of these roundscale spearfish, like most fishes landed at recreational fishing tournaments, was not made available to us but the fish were caught within 185 km of the Ocean City Inlet sea buoy (38.19°19.6'N, 75°05.6'W). Roundscale spearfish were morphologically identified in the field by having a bill that is rounded in cross-section, and the 2 specimens were distinguished from sympatric billfishes, e.g., white marlin and longbill spearfish, in possessing a combination of lateral scales with a rounded base and 2–3 lateral points, a first dorsal fin with a high anterior lobe that is rounded rather than sharply pointed and that rapidly slopes downward to a lower height, and a relatively greater distance from the anus to origin of first anal fin (Nakamura, 1985; Beerkircher et al., 2009). A 1-cm<sup>3</sup> piece of somatic muscle from each fish was preserved in the field in 95% EtOH, and our morphological identification was confirmed genetically by applying a species-specific PCR primer test for the mitochondrial NADH dehydrogenase 4 gene to those 2 samples (M. Shivji, pers. comm.).

The gill, buccal cavity, and external body surface of the roundscale spearfish were carefully examined with the naked eye and monogenoids were removed from the fish using fine forceps, heat-killed with freshwater heated to 60 C, and immediately fixed in 10% neutral buffered formalin. Later, whole specimens were transferred to, and held in, a vial of 5% neutral buffered formalin, placed overnight in distilled water, stained overnight in Van Cleave's hematoxylin with several additional drops of Ehrlich's hematoxylin, made basic in 70% ethanol with lithium carbonate and butyl-amine, dehydrated, cleared in clove oil, and permanently mounted on over-sized glass slides using Canada balsam (Bullard et al., 2004). The 4 specimens for scanning electron microscopy (SEM) were dehydrated, immersed in hexamethyldisilazane

Received 31 January 2012; revised 9 March 2012; accepted 26 March 2012.

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DOI: 10.1645/GE-3093.1

TABLE 1. Records of *Capsala laevis* (Verrill, 1875) Johnston, 1929 (Monogeneoidea: Capsalidae: Capsalinae) showing diversity of host species and geographic localities. Footnotes clarify some conflicting identifications of specimens.

Host species	Site in host	Geographic locality	Museum no.(s)	Reference(s)
<i>Tetrapturus georgii</i> Lowe, 1840, roundscale spearfish	Gill arches	Northwestern Atlantic Ocean; landed at Ocean City, Maryland	USNPC Nos. 105628, 105629	Present study
Istiophoridae sp. (=type host) (as "bill-fish" only)	In mouth	Block Island, Rhode Island, USA (NW Atlantic Ocean)	USNPC 7179 (=holotype)	Verrill, 1875
<i>Tetrapturus albidus</i> Poey, 1860, white marlin (also as <i>Tetrapturus lessonae</i> )	Gill arches	Concarneau, France (NE Atlantic Ocean)	Not reported	Dollfus, 1949
	Body, gills, and inside mouth	La Parguera, Puerto Rico (Caribbean Sea)	USNPC 81999*	Dyer et al., 1992 (as <i>Tristomella laevis</i> )
<i>Tetrapturus audax</i> (Phillippi, 1887), striped marlin (also as <i>Tetrapturus tenuirostratus</i> )	Body surface	Gulf of Mannar, India (Indian Ocean)	CMFRI†	Devaraj, 1976
<i>Tetrapturus pfluegeri</i> (Robins and de Sylva, 1963), longbill spearfish	Body, gills, and inside mouth	Aguadilla, Puerto Rico (Caribbean Sea)	Not reported	Williams and Bunkley-Williams, 1996 (as <i>T. laevis</i> )
<i>Makaira indica</i> (Cuvier, 1832), black marlin (also as <i>Histiophorus brevirostris</i> )	Not reported	Madras, India (Bay of Bengal, Indian Ocean)	Not reported	Bell, 1891 (as <i>Tristomum histiophori</i> ; syn. of <i>Capsala laevis</i> in Goto [1894])
	Not reported	Cape Recife, South Africa (SW Indian Ocean)	HWML 44299‡	Pritchard, 1961 (as <i>T. laevis</i> )
<i>Makaira mazara</i> (Jordan and Snyder, 1901), Indo-Pacific blue marlin	Not reported	Not reported	GL 212198	Chisholm & Whittington, 2007 (originally as <i>Tristomella pricei</i> )
<i>Makaira nigricans</i> Lacepède, 1802, blue marlin		La Parguera and Desecheo Island, Puerto Rico (Caribbean Sea)	USNPC 82000–82003§	Dyer et al., 1992 (as <i>Tristomella laevis</i> )
<i>Istiophorus platypterus</i> (Shaw, 1792), sailfish (also as "Atlantic sailfish")	Body, gills and inside mouth	Arecibo, Puerto Rico (Caribbean Sea)	Not reported	Williams and Bunkley-Williams, 1996 (as <i>Tristomella laevis</i> )
<i>Xiphias gladius</i> Linnaeus, 1758, swordfish	Alcoholic material from gill	Woods Hole, Massachusetts (NW Atlantic Ocean)	USNPC 8154	Linton, 1940
	Gills	Ayvacik, Çanakkale, Turkey (Aegean Sea, Mediterranean Sea)	Not reported#	Kayış et al., 2010 (as <i>Tristomella laevis</i> )
<i>Katsuwonus pelamis</i> (Linnaeus, 1758), skipjack tuna (as <i>Gymnosarda pelamys</i> )	Gills	South of Martha's Vineyard, Massachusetts, USA (NW Atlantic Ocean)	USNPC 4878¶	Linton, 1898 (as <i>Tristomum laeve</i> )
<i>Mola mola</i> (Linnaeus, 1758), ocean sunfish	Skin	Off South Africa (SE Atlantic Ocean)	HWML 1453	Chisholm and Whittington, 2007 (originally as <i>Capsala martinieri</i> )

\* Chisholm and Whittington (2007) re-identified M1579-4 as *Capsaloides nairagi* and M1579-5, -6, and -8 as *Capsaloides cornutus*.

† Central Marine Fisheries Research Institute, Mandapam Camp, India.

‡ Chisholm and Whittington (2007) reported as "cannot ID."

§ Chisholm and Whittington [2007] re-identified USNPC 82001 as *Capsala pricei*.

|| Likely a new species of *Capsala* (see Discussion).

# Likely *Capsaloides* sp. (see Discussion).

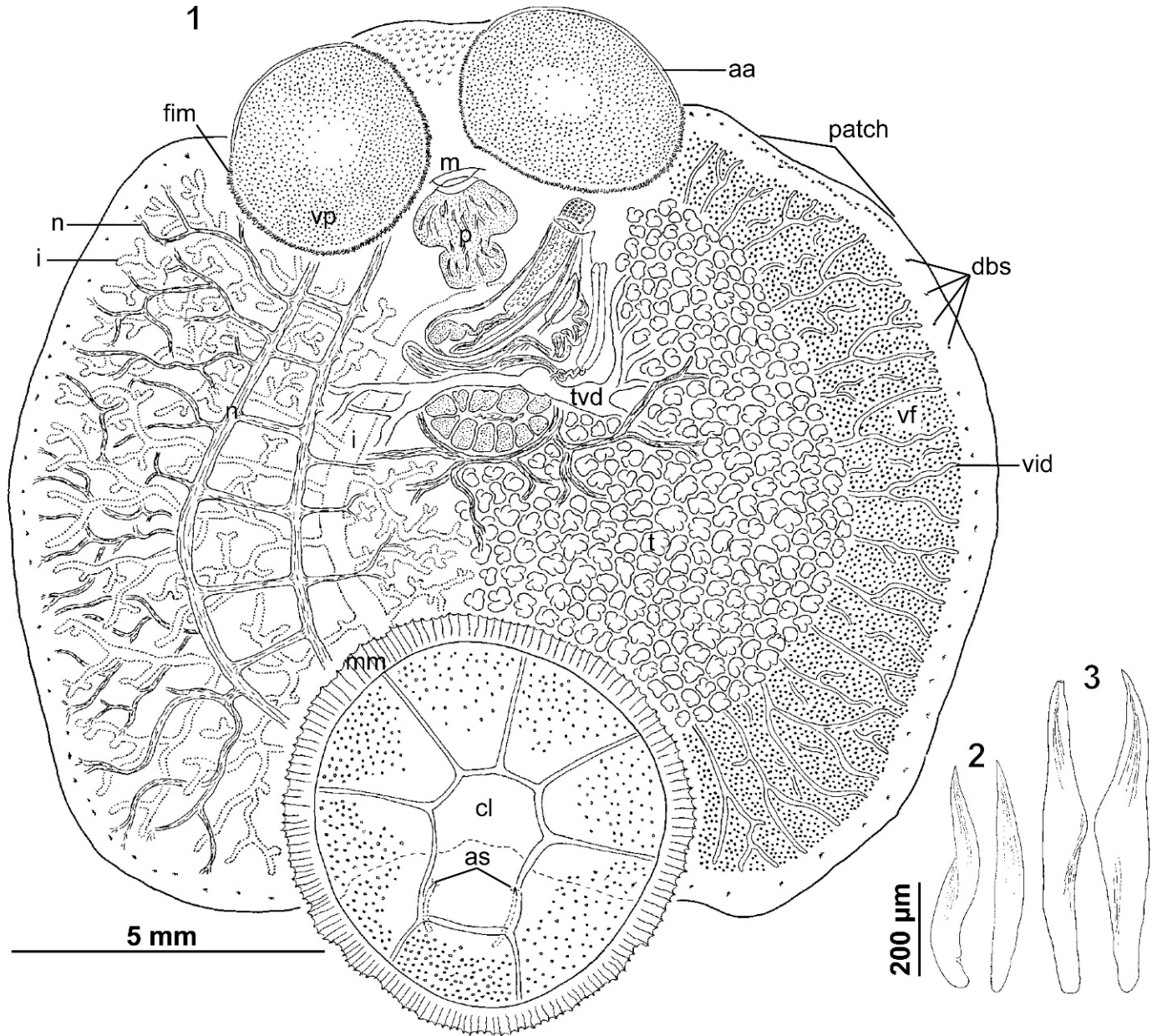
¶ Re-identified as *Capsala lintoni* by Price (1939).

for 30 min, air dried for 45 min, and sputter-coated with 15 nm gold palladium. Illustrations of stained, whole-mounted specimens were made with the aid of a Leica DM-2500 (Leica, Wetzlar, Germany) equipped with differential interference contrast (DIC) optical components and a drawing tube (Bullard and Jensen, 2008; Bullard, 2010). Photographs of whole-mounted specimens were made on that microscope using a digital, single-lens reflex camera. Parasite measurements are herein reported in micrometers ( $\mu\text{m}$ ) followed by their mean and the number measured in parentheses. Counts and measurements of structures in the holotype of *C. laevis* (Verrill, 1875) Johnston, 1929 (USNPC No. 7179), when visible, are reported in square brackets immediately following those measurements. Scientific names, taxonomic authorities, and dates for fish taxa follow Eschmeyer (2010). Higher-level fish classification and nomenclature follows Nelson (2006) and Collette et al. (2006). Classification and anatomical terms for the parasites were crafted in light of those used by Chisholm and Whittington (2006; 2007).

## REDESCRIPTION

### *Capsala laevis* (Verrill, 1875) Johnston, 1929 (Figs. 1–30)

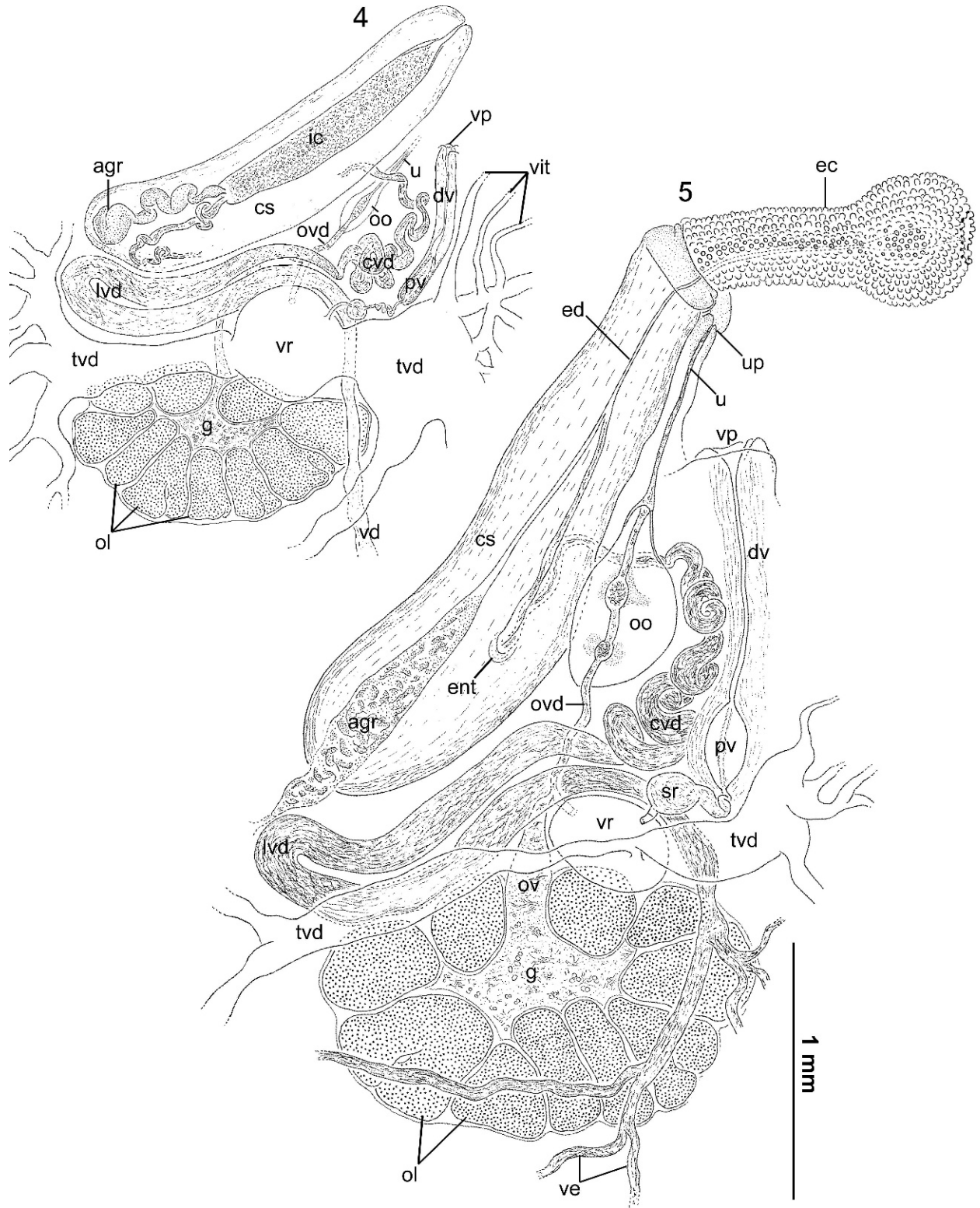
*Diagnosis* (based on the holotype of *Capsala laevis* [USNPC No. 7179] plus 3 stained, whole-mounted voucher specimens [USNPC Nos. 105628–105629] and 4 sputter-coated specimens from the gill arches of 2 roundscale spearfish, *Tetrapturus georgii*): Body opaque in life, lacking pinkish or reddish coloration, approximately discoid, having smooth-surfaced and equally-rounded edges lacking scalloped margins, 12,360–17,300 (14,306; 3) [8,010] long including haptor or 10,950–15,860 (12,836; 3) [7,350] excluding haptor, 11,120–14,000 (12,606; 3) [6,500] in maximum width or 1.04–1.24 [1.13]  $\times$  longer than wide, with 2 pairs of eyespots dorsal to mouth, surface bearing papillae dorsally and ventrally (Figs. 1, 6–8, 17–23). Dorsal papillae covered by hair-like probable sensilla (Figs. 22, 23),



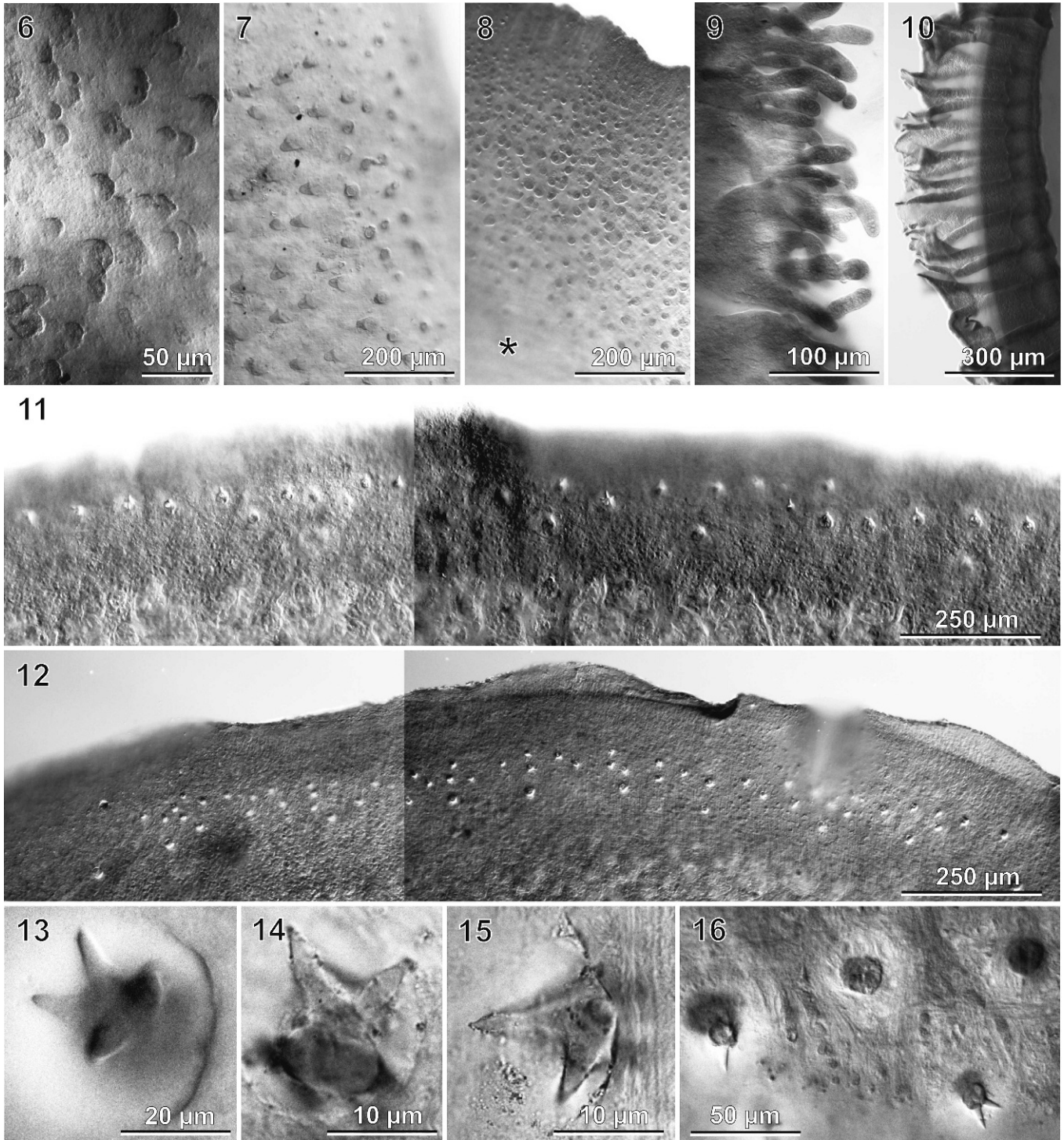
FIGURES 1-3. *Capsala laevis* (Verrill, 1875) Johnston, 1929 (Monogeneoidea: Capsalidae: Capsalinae) from the northwestern Atlantic Ocean. Scale values beside each bar. (1) Body of adult specimen (RSS-3; USNPC No. 105629) from gill of roundscale spearfish, *Tetrapturus georgii* Lowe, 1841 (Perciformes: Istiophoridae). Sinistral anterior attachment organ (aa), fimbria (fim) of dextral anterior attachment organ, mouth (m), ventral papillae of anterior attachment organ (vp; note that center lacks papillae), anterior and posterior extent of the patch of small dorsolateral body sclerites (patch), pharynx (p), nerve (n), intestine (i), dorsomarginal body sclerites (dbs), transverse vitelline duct (tvd), vitelline follicles (vf), vitelline duct (vid), testes (t), haptoral marginal membrane (mm), haptoral central loculus (cl), haptoral accessory sclerites (as). (2) Accessory sclerites of holotype (USNPC No. 7179) from gill of Istiophoridae sp. (3) Accessory sclerites of voucher specimen (RSS-3; USNPC No. 105629).

distributing sporadically but most obvious about the anterior attachment organs and haptoral peduncle (Fig. 22), 10–20 (15; 30) [25] wide at base, 22–40 (25; 30) [25] long (Figs. 6, 23); ventral papillae lacking comparable hair-like surface of dorsal papillae (Figs. 18–20), conical or knob-like, 20–100 wide at base; no ventral papillae between haptor and ventral body surface and absent from region immediately anterior to haptor (Figs. 7, 17–20). Anterior attachment organs bilaterally symmetrical, 2,250–3,060 (2,682; 6) [1,680] in diameter, connecting with body in center of attachment organ, circular or oblong, strongly ventrally concave, bearing numerous ventral papillae (Figs. 1, 8, 21); ventral papillae of anterior attachment organ distributing primarily lateral to strongly concave central portion of sucker, each having a nearly indistinct pore at apex of papilla, 10–20 (15; 10) [15] in maximum width; rim of anterior attachment organ

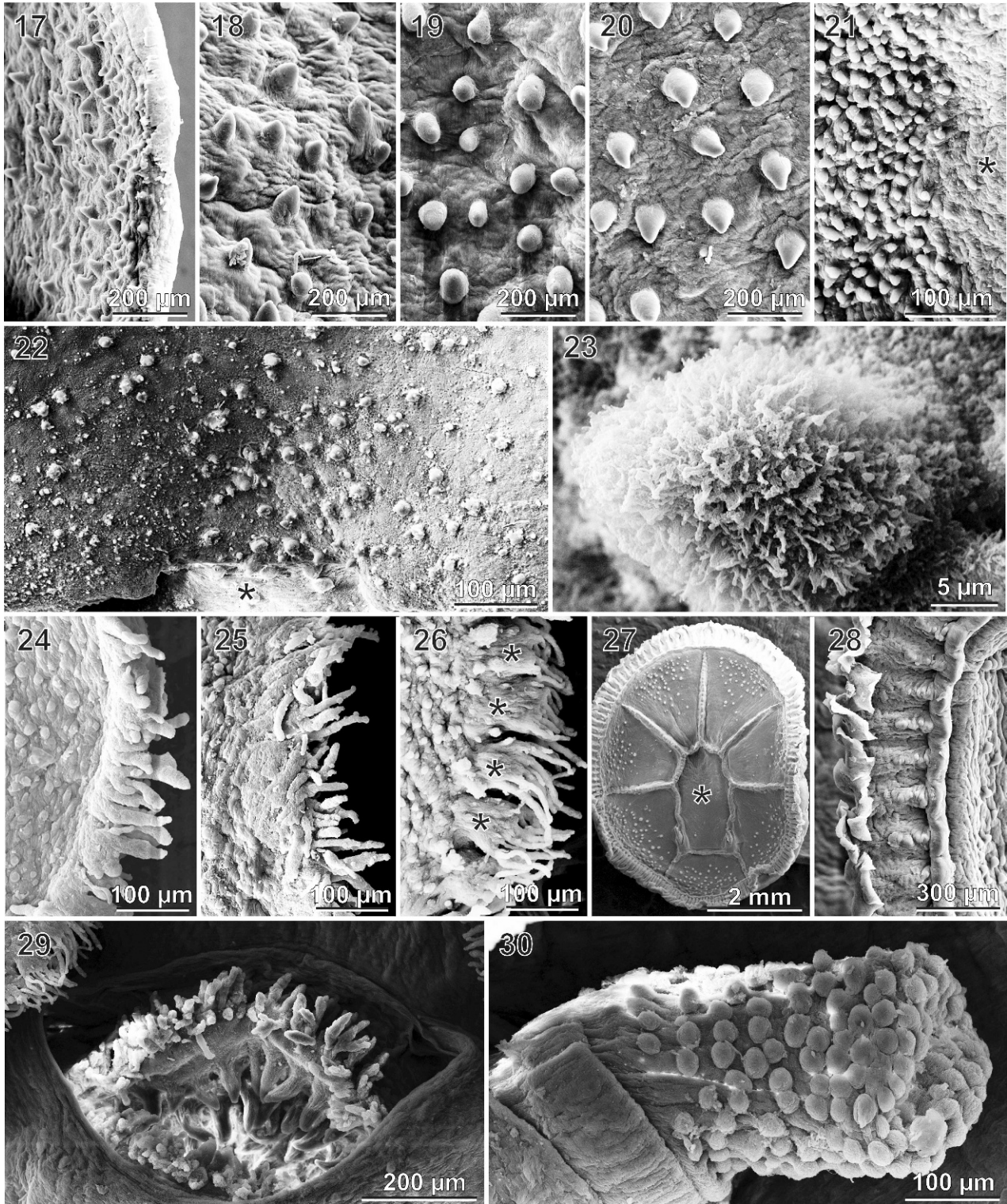
fimbriated around posteromedial 270° or two-thirds of sucker rim (Figs. 1, 9, 24–26); slender processes of fimbria each 85–220 (110; 6) [105] long, 13–15 (13; 30) wide at base, connecting to rim of anterior attachment organ directly in anterior portion (Figs. 24, 25) or by a peduncle in posterior portion (Fig. 26). Haptor circular, 4,520–5,400 (4,940; 3) [2,800] long (excluding marginal membrane) or 34–42% [38%] body length, extending beyond posterior body margin 1,410–1,560 (1,470; 3) [1,400] or 9–13% (12%; 3) [19%] of body length, having 4 anterior loculi, 3 posterior loculi, and 1 keyhole-shaped central loculus, having marginal membrane, with ventral papillae, including 1 pair of accessory sclerites (Figs. 1–3, 27). Marginal membrane scalloped, of uniform width around haptor rim, 290–340 (320; 3) [200] wide, having approximately 168–230 (193; 3) scallops total, comprising a series of overlapping lamellar



FIGURES 4-5. Genitalia of *Capsala laevis* (Verrill, 1875) Johnston, 1929 (Monogeneoidea: Capsalidae: Capsalinae) from the northwestern Atlantic Ocean, ventral views, both illustrations are same scale. Vasa efferentia (ve), vas deferens (vd), dextral loop of vas deferens (lvd), tightly coiled ascending portion of vas deferens (cvd), entry point of vas deferens to cirrus sac (ent), cirrus sac (cs), ejaculatory duct (ed), inverted cirrus (ic), everted cirrus (ec), vaginal pore (vp), distal vagina (dv), proximal vagina (pv), seminal receptacle (sr), vitelline ducts (vit), vitelline reservoir (vr), transverse vitelline duct (tvd), ovary lobes (ol), germarium (g), oviduct (ov), ovo-vitelline duct (ovd), ootype (oo), uterus (u), uterine pore (up). (4) Holotype (USNPC No. 7179) from gill of Istiophoridae sp. (5) Voucher specimen (RSS-1; USNPC No. 105628) from gill of roundscale spearfish, *Tetrapturus georgii* Lowe, 1841 (Perciformes: Istiophoridae).



FIGURES 6–16. *Capsala laevis* (Verrill, 1875) Johnston, 1929 (Monogenoidea: Capsalidae: Capsalinae) from gill of roundscale spearfish, *Tetrapturus georgii* Lowe, 1841 (Perciformes: Istiophoridae) (RSS-1, 2, 3; USNPC Nos. 105628–29) and Istiophoridae sp. (holotype, USNPC No. 7179) from the northwestern Atlantic Ocean; light micrographs of whole-mounted specimens. Scale values beside each bar. (6) Papillae of dorsal body surface of holotype, dorsal view. (7) Papillae of ventral body surface (at level of genitalia) of holotype, ventral view. (8) Papillae on ventral surface of sinistral anterior attachment organ showing field of peripheral papillae and central region of sucker (\*slightly out of focus) that has many fewer papillae, voucher RSS-2; ventral view. (9) Slender processes of fimbria of posterior margin of anterior attachment organ, voucher RSS-1, ventral view. (10) Haptoral marginal membrane, voucher RSS-2, ventral view. (11) Dense patch of dorsomarginal body sclerites just posterior to sinistral anterior attachment organ, holotype, dorsal view. (12) Dense patch of dorsomarginal body sclerites just posterior to sinistral anterior attachment organ, holotype, dorsal view. (13) Antero-dextral dorsomarginal body sclerite, voucher RSS-2; note that the sclerite resides within a tegumental pocket, dorsal view. (14) Antero-dextral dorsomarginal body sclerite from holotype, dorsal view. (15) Postero-sinistral dorsomarginal body sclerite from holotype, dorsal view. (16) Higher magnification view of dorsomarginal body sclerites from Figure 11, dorsal view.



FIGURES 17–30. *Capsala laevis* (Verrill, 1875) Johnston, 1929 (Monogeneoidea: Capsalidae: Capsalinae) from roundscale spearfish, *Tetrapturus georgii* Lowe, 1841 (Perciformes: Istiophoridae); scanning electron micrographs. Scale values beside each bar. (17) Papillae on ventral body surface between anterior attachment organs (extreme anterior end of worm at right). (18) Papillae on ventral body surface immediately posterior to anterior attachment organ. (19) Papillae on ventral body surface at level posterior to cirrus sac. (20) Papillae on ventral body surface anterior to haptor. (21) Papillae on ventral surface of anterior attachment organ (\*right side of image is the central, apapillate portion of the sucker). (22) Dorsum of posterior region of body showing numerous large papillae. (23) Higher magnification view of a papilla from Figure 22. Note that the surface of the papilla is covered by hair-like projections that may comprise ‘sensilla.’ (24) Anterior-most slender processes of fimbria on sinistral anterior attachment organ. (25) Medial slender processes of fimbria on sinistral anterior attachment organ. (26) Posterior-most slender processes of fimbria on sinistral anterior attachment organ; note presence of peduncle-like connections (\*) between processes and sucker rim. (27) Haptor showing marginal membrane, haptoral

extensions of haptor tegument that form a contiguous gasket, lacking fimbria (Figs. 1, 10, 27, 28). Haptoral septa relatively narrow, bearing small papillae along ridge, none appearing bifid where connecting to haptoral rim (Figs. 1, 27). Papillae of loculi relatively small, distributing along periphery of haptor medial to marginal membrane (Fig. 27), lacking from within, or lateral to, central loculus, variable in size, 15–40 (20; 10) [30] wide at base. Accessory sclerites with sharp, exposed point directing anteriorly, slightly bent laterad, juxtaposed, approximately equal in total length and thickness, 710–840 (793; 6) [500, 475] long or 15–17% (16%; 6) [18%] of haptor diameter, 80–100 (93; 6) [50, 50] thick, protruding from haptor ventral surface at posterior corners of central loculus (Figs. 2, 3); marginal hooklets not evident. Irregularly-spaced dorsomarginal body sclerites distributing in uneven dextral and sinistral columns extending entire body length, approximately 200–250 (225; 2) [135] from body margin (Figs. 1, 11–16); dorsomarginal sclerites each residing within a tegumental pocket (Figs. 13–15); dextral column having a total of 28–35 (34; 3) [36] sclerites having 3 or 4 cusps (with some dorsomarginal sclerites appearing broken and falsely giving a count of 1 or 2 cusps), extending posterior and dorsal to haptor, with at least 2 sclerites dorsal to haptor; sinistral column having a total of 53–61 (57; 3) [90] sclerites, including dense patch of sclerites (Figs. 1, 11, 12); body margin anterior to dense patch of sclerites having 2–5 (4; 3) [3] sclerites each having 3 or 4 cusps; region of dense patch having 27–35 (30; 3) [60] sclerites approximately half the size of other dorsomarginal sclerites outside patch and having 2–3 [2–4] cusps, extending 1,975–2,250 (2,108; 3) [1,720] or 14–18% (17%; 3) [22%] of body length along margin from level of posterior margin of sinistral anterior attachment organ to level of ootype (Figs. 1, 11, 12); body margin posterior to region of dense patch having 21–25 (23; 3) [28] sclerites having 3 or 4 cusps, with 2 [4] sclerites dorsal to haptor (Fig. 1).

Mouth 700 [600] wide (Figs. 1, 29). Pharynx 1,290–1,600 (1,430; 3) [700] long, 1,400–1,760 (1,560; 3) [970] wide, extensively papillate around rim of pharynx plus and within opening to esophagus (Fig. 29), connecting with esophagus posteromedially; papillae of pharynx approximately 100 long, 45 wide (Fig. 29). Intestine thin-walled, approximately 5 thick, with highly dendritic secondary branches extending laterad and mediad from 2 primary crura 140–200 (150; 3) in maximum width; secondary branches terminating approximately 300–400 (350; 3) from lateral body margin.

Nerve system comprising 2 sets of paired cords and myriad secondary branches entwining with intestinal branches (Fig. 1); paired cords 100 in maximum width, extending nearly entire length of body; secondary branches 25 in maximum width, extending laterally and medially, running dorsal and ventral to intestine; nerve tissue non-staining with hematoxylin, appearing highly refractory and wispy with DIC.

Testes extensive, tightly packed, dorsal to nerve, numbering approximately 453–477 (465; 3), having approximately 4–6 lobes each, 100–300 (217; 30) in diameter (Fig. 1); testicular field terminating approximately 1,400–1,700 (1,650; 3) from lateral body margin, 5,690–6,700 (6,130; 3) long or 42–55% body length, 8,220–9,700 (9,006; 3) wide or 69–74% (72%; 3) of body width, extending to level of anterior attachment organs, extending posterior to level of haptor, coextensive with intestine, nerve, and vitelline ducts. Vasa efferentia ventral to testicular field, extensively branched, collecting anteriorly and forming common duct overlapping sinistral portion of ovary (Figs. 1, 4, 5). Vas deferens ventral to ovary, extending anterior from sinistral portion of ovary, traversing midline immediately anterior to ovary, looping in the dextral portion of body; loop is 1,500–2,100 (1,827; 3) [930] long or 13–17% (14%; 3) [14%] of maximum body width, 150–200 (173; 3) [100] in maximum width, extending anterior as a tightly coiled tube in sinistral portion of body before curving medially and dorsal to cirrus sac, entering posterior half (proximal portion) of cirrus sac (Figs. 1, 4, 5). Cirrus sac 2,350–3,080 (2,826; 3) [1,600] long or 21–24% (22%; 3) [25%] of body width, 550–720 (640; 3) [225] in maximum width, enveloping accessory gland reservoir and cirrus, having wall 25–30 (28; 3) [25] thick; male accessory gland reservoir straight (if cirrus everted; Figs. 5, 30) or convoluted (if cirrus not everted; Fig. 4), 650–900 (775) long or 30–80% of cirrus sac length, 150–195 (168; 3) in maximum width; cirrus extensively papillate for entire length, having

shaft and bulb; shaft 550 long, 270 wide; bulb spheroid, 450 in diameter (Figs. 5, 30); cirrus papillae each approximately 30 wide (Fig. 30). Male genital pore lateral to pharynx, immediately posterior to sinistral anterior attachment organ, 2,600–2,700 (2,650; 2) [2,240] or approximately 24% [30%] of body length from anterior body end (Figs. 1, 4, 5).

Ovary medial, lobed, immediately posterior to transverse loop of vas deferens, 1,000–1,900 (1,366; 3) [1,100] long or 8–16% (11%; 3) [15%] of body length, 1,030–1,950 (1,527; 3) [600] wide or 8–14% (12%; 3) [9%] of body width, enclosing a germarium 300 (2) long and 600–900 (750; 2) wide (Figs. 1, 4, 5). Oviduct extending directly anterior from germarium, curving sinistral and connecting with the short duct 55–100 (76; 3) long and 20–35 (27; 3) wide and extending from vitelline reservoir dorsal to vas deferens (Figs. 4, 5). Vitellarium comprising vitelline follicles and corresponding collecting ducts that coalesce to form transverse vitelline duct and accompanying vitelline reservoir; vitelline follicles extensive, forming a continuous layer principally dorsal to all other internal anatomy but occupying spaces between testes, gut, and nerve, each 40–60 (50; 10) in diameter, containing gold-colored granular material, most obvious in lateral regions of body (Fig. 1); vitelline ducts extremely thin-walled with smaller ducts approximately 20 wide, terminating near distal tips of intestine in lateral body margin, combining to form larger ducts medially and anterior to ovary; transverse vitelline duct extending 2,000–2,350 (2,150; 3) across width of body or 15–19% (17%; 3) of body width, 100–500 (290; 3) wide; vitelline reservoir sinistral, a distinct chamber not a simple expansion of transverse vitelline duct, variable in size depending on volume of vitelline material it contains, 320–550 (420; 3) [350] in diameter, dorsal to transverse vitelline duct (Figs. 1, 4, 5). Vaginal pore sinistral, at level of esophagus, posterior to male genital pore (Figs. 4, 5). Vagina 1,100–1,400 (1,267; 3) long, comprising distal and proximal portions plus a seminal receptacle; distal portion of vagina a narrow tube communicating with vaginal pore, 800–1,000 (867; 3) long or 62–73% (69%; 3) of total vagina length, 20 wide, with glandular wall 50–70 (60; 3) thick; proximal vagina 300–500 (400; 3) long or 27–38% (31%; 3) of total vagina length, 300–500 (400; 3) wide; seminal receptacle extending 255–450 (352; 3) posterior from proximal portion of vagina, beginning as a narrow and convoluted tube 25 wide, expanding with sperm and becoming 175–185 (183; 3) in maximum width, constricting to a narrow tube 15 wide that lacks darkly staining aggregates of sperm and connects with vitelline reservoir ventrally. Ovo-vitelline duct extending 450–500 (475; 3) before connecting with ootype, 35–60 (45; 3) wide (Figs. 4, 5). Ootype 700–740 (717; 3) [420] long, 350–400 (367; 3) [155] wide, occupying space between cirrus sac and tightly coiled ascending portion of vas deferens, distal portion of ootype having a flap demarcating it from uterus; uterus a simple tube extending 640–735 (675; 3) anterior from ootype and opening immediately posterior to male genital pore (Figs. 4, 5).

### Taxonomic summary

*Type host:* Istiophoridae sp. (originally reported by Verrill [1875] as “bill-fish” only).

*Type locality:* Northwestern Atlantic Ocean; Block Island Sound between Point Judith (Narragansett, Rhode Island) and Race Point (Fisher’s Island, New York).

*Sites of infection and other host species:* Table I.

### Remarks

*Capsala laevis* is currently defined as having a single longitudinal row (=column) of dorsomarginal body sclerites, each with 3–4 cusps, a small patch of multicuspoid sclerites on the sinistral body margin posterior to the genital pore, irregularly distributed ventral body surface papillae that are conical, and “finger-like projections” (=slender processes of fimbria) on the posterior margin of the anterior attachment organs (Chisholm and

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septa and loculi, and papillae distributing laterally to central loculus (\*). (28) Marginal membrane. (29) Mouth and papillate pharynx, showing smaller papillae extending from rim of pharynx as well as larger papillae within pharynx. (30) Partially everted cirrus, showing papillae on shaft.

Whittington, 2007). Our specimens from roundscale spearfish have each of these diagnostic features (see Redescription). Despite a focused attempt to detect a significant morphological difference between our specimens from roundscale spearfish and the holotype of *C. laevis* (USNPC 7179) from Istiophoridae sp., we found only a few seemingly slight differences, none of which currently justifies the proposal of a new species, despite roundscale spearfish comprising a new host record for capsalid monogenoids. The newly collected specimens of *C. laevis* differed from the holotype by having a sinistral dense patch of dorsomarginal body sclerites comprising 27–35 sclerites (Figs. 1, 11) rather than comprising the 60 sclerites (Fig. 12) in the holotype, which is a much smaller specimen. We think that the other morphometric differences are simply related to the small size of the holotype, as indicated by the fact that most ratios or proportions for the holotype are within or near the range of the newly collected specimens.

We identified a few taxonomically important morphological features previously not ascribed to *C. laevis*. First, the anterior attachment organs have papillae on the ventral surface between the central concavity of the sucker and the margin of the sucker (Figs. 1, 8, 21). These papillae could be sensory in nature because each one has a pore-like structure at its apex. Some monogenoids have such sensory papillae associated with the ventral surface of the haptor or anterior attachment organs (Lyons, 1972), and we suspect that SEM would reveal that other *Capsala* spp. have such sense papillae associated with their anterior attachment organs. Alternatively, however, it seems just as likely that these pores could facilitate exudation of an adhesive. Second, well-developed papillae are indeed present on the dorsum of *C. laevis* (Figs. 6, 22, 23). These papillae give us the impression that they, too, are sensory in nature because they are covered with abundant hair-like structures which perhaps function as “sensory sensilla” (Lyons, 1972). The structures are somewhat variable in shape, and no clear pattern or arrangement of these probable sensory papillae was detectable in the specimens we studied. The condition of the holotype makes it easily understandable as to why these features have been previously overlooked. Based on these results, it is clear to us that *C. laevis* has several morphologically and functionally distinct, i.e., not homologous, papillae on the body. Hence, we have described distinctive ‘papillae’ having a probable sensory function associated with both the dorsum as well as the ventral surface of the anterior attachment organs. Transmission electron microscopy of those sites might shed light on the fine-scale anatomy of these structures, which are likely to represent important taxonomic characters for capsalids. Importantly, and regarding phylogenetic studies of *Capsala* spp., morphology (present study) indicates that the ‘dorsal body papillae’ are not homologous to the ‘ventral body papillae.’

*Capsala laevis* is morphologically most similar to *C. ovalis* (Goto, 1894) Price, 1938, and it is noteworthy that the distinctness of *C. laevis* and *C. ovalis* has been questioned in the taxonomic literature. Chisholm and Whittington (2007) provided a useful description of the taxonomic status of *C. ovalis* (Goto, 1894) Johnston, 1929 (originally *Tristomum ovale* Goto, 1894), which was originally reported from the mouth cavity of Indo-Pacific sailfish, *Istiophorus platypterus* (Shaw, 1792) (as *Histiophorous orientalis*), “*Histiophorus* sp.,” and “perhaps a species of *Cybbium*” off Misaki (western Pacific Ocean off Japan). Goto’s (1894) description of *C. ovalis* is detailed, but apparently no type material exists, which has caused problems. Goto (1899) states

that Verrill and Bell (Table I) loaned their type materials of *C. laevis* and *Tristomum histiophori* Bell, 1891 (respectively) to him and, after comparing those materials to his own specimens, he effectively considered *C. ovalis* and *T. histiophori* as junior subjective synonyms of *C. laevis* (as *Tristomum leve* Verrill) (see also Setti, 1899). Yamaguti (1968) illustrated specimens that he took to be *C. ovalis* but, according to Chisholm and Whittington (2007), may have been *C. laevis* because they had ventral body surface papillae, 2 columns of dorsomarginal sclerites, and a sinistral patch of dorsomarginal sclerites. Chisholm and Whittington (2007) distinguished *C. ovalis* from *C. laevis* by the fact that Goto (1894) detailed papillae on the ventral surface of the anterior attachment organ of *C. ovalis*. However, and as already described by Price (1938), the holotype of *C. laevis*, as well as our specimens of *C. laevis* from roundscale spearfish, both have papillae on the ventral surface of the anterior attachment organ, indicating that this feature is not unique to *C. ovalis*. Goto’s (1894) illustration of these papillae, if not stylized, shows that they are proportionally much larger than the ones we observed in the holotype of *C. laevis* and our specimens from roundscale spearfish. Moreover, the distribution of the papillae in *C. ovalis* seems markedly distinct from *C. laevis*; Goto’s (1894) illustration of *C. ovalis* shows that the papillae are evenly distributed across the ventral surface of the anterior attachment organ whereas, in the holotype and our specimens of *C. laevis*, the papillae are absent from the central portion of the sucker and relegated to its periphery (Figs. 1, 21). Further differentiating these species is the presence–absence of a fimbria on the trailing edge of the anterior attachment organ, which is present in *C. laevis* and reportedly absent in *C. ovalis*. Given the results of the present study and the highly detailed nature of Goto’s illustrations, we are now curious if the size and distribution of the ventral papillae of the anterior attachment organ in *Capsala* spp. might be useful diagnostic features.

As a seemingly minor point, we have observed that previous authors have mistaken the nerve system of capsalids for the intestine or vice versa. Not infrequently, the intestine is stylized as having 2 sets of paired cords, but this is incorrect. In other instances, the nerve system is not illustrated completely but is meshed with the stylized depiction of the intestine. The intestine and nerve system are quite distinct, i.e., the intestine being extremely thin-walled, appearing hollow (non-staining) in some portions or filled with ingested contents in others; whereas the nerve is a solid structure that lacks a lumen, appears wispy or striated when viewed with DIC microscopy, and is ventral to the intestine. Those features in *C. laevis*, as we have illustrated them herein, seemingly fit the general pattern in the *Capsala* spp. familiar to us. The stacking of nerve, intestine, vitelline ducts, vitelline follicles, and testes in species of *Capsala* makes the differentiation of these various systems challenging; however, perhaps some of these features eventually could be used to differentiate genera or species, e.g., these features in digeneans are used variously to diagnose families, genera, and species. Hence, we think that it is important to illustrate them, describe them, and not confuse them.

## DISCUSSION

At first glance of the literature, one could have the impression that *C. laevis* has been well characterized morphologically;



however, perusal of these works reveals that a detailed anatomic study of this species, one that includes critical study of the holotype, is lacking. The subsequent problems with, results of, and recommendations about the taxonomy of *C. laevis* and congeners have been detailed by Goto (1894; 1899), Setti (1899), Johnston (1929), Price (1938), Linton (1940), Dollfus (1949), Devaraj (1976), Lamothe-Argumedo (1997), and Chisholm and Whittington (2007). Originally, as part of a large taxonomic survey of invertebrate marine life found off the coast of the northeastern United States, Verrill (1875) included the monogenoids *Tristoma laeve* (syn. *C. laevis*) from “mouth of bill-fish,” *Tristoma cornutum* (syn. *Capsaloides cornutus* [Verrill, 1875] Price, 1938) “on gills of bill-fish (*Tetrapturus albidus*),” and a species of *Nitzschia* Baer, 1826 (probably *Nitzschia superba* MacCallum, 1921 but reported as *Nitzschia elegans* Baer, 1826) “on gills of sturgeon (*Acipenser oxyrinchus* Mitchell).” In this remarkable publication (including descriptions of hundreds of primarily free-living invertebrates), Verrill did not provide a figure of a monogenoid nor did his narrative describe the anatomy of these species in enough detail to help distinguish them from the tens of additional species of *Capsala* Bosc, 1811 described since 1875. Verrill (1885) provided a figure of *C. laevis* and *C. cornutus* (page 689; figures 1943 and 1944, respectively), but these figures do not show morphological characteristics unique for either species and, moreover, the figure for *C. laevis* is dubious, based on the relative size of the haptor and body. Clearly, it was not drawn from the holotype (USNPC No. 7179). Subsequently, perhaps because of its large size, ectoparasitic lifestyle, and the fact that it infects large, charismatic, epipelagic billfishes hunted worldwide, several parasitologists have reported infections of *C. laevis* (Table I) and described the specimens. Seldom have these worms been regarded as conspecific with *C. laevis* upon collection, and considerable museum-based taxonomic work has been required to resolve the identities of these worms, usually resulting in synonymies (Goto, 1899; Chisholm and Whittington, 2007) rather than in delineation of cryptic species.

Subsequent to Verrill’s (1875, 1885) work, Goto (1894; 1899), Price (1938), Dollfus (1949), Devaraj (1976), Lamothe-Argumedo (1997), and Chisholm and Whittington (2007) provided original morphological information about specimens thought to be *C. laevis*. However, there was often doubt that their specimens were conspecific with the holotype of *C. laevis*. The first author following Goto (1894, 1899, see below) to publish observations of the holotype of *C. laevis* was Price (1938). He studied the holotype plus, unfortunately, specimens collected from “dorado” (presumed to be dolphin, *Coryphaena hippurus* Linnaeus, 1758, [Perciformes: Coryphaenidae]) which were actually *Capsala poeyi* (Pérez-Vigueras, 1935) Price, 1938 (present study of voucher USNPC No. 18874; Chisholm and Whittington, 2007). Price’s (1938) redescription does not mention papillae on the dorsum nor does it mention the sinistral patch of dorsomarginal sclerites diagnostic for *C. laevis*, but he did record papillae on the ventral surface of the anterior attachment organs. Dollfus (1949) provided a description of specimens from the gill arches of “white marlin” in the northeast Atlantic Ocean off France, emphasizing details of the haptor accessory sclerites and dorsomarginal body sclerites. He compared Price’s (1938) specimens of *C. poeyi*, which he took to represent *C. laevis*, with his own specimens of *C. laevis*. Devaraj (1976) studied specimens collected from striped marlin captured in the Indian Ocean; that report includes a few

diagnostic characteristics for *C. laevis*, i.e., haptor with ventral papillae, marginal membrane present, 1 column of dorsomarginal body sclerites having 3 cusps, and cirrus with papillae. The voucher specimens from this study were not available to us, but those specimens should be examined to confirm if they represent *C. laevis* or a closely related species. Lamothe-Argumedo (1997) revised the generic diagnoses for Capsalinae, providing illustrations for some species of the genera treated therein. The illustration provided for *C. laevis* (Lamothe-Argumedo, 1997) either represents a new species of *Capsala* or it is highly stylized. If the latter, it lacks some key features that define *C. laevis*, e.g., the drawing lacks a dense patch of dorsomarginal body sclerites while exaggerating the sizes of other structures, e.g., slender processes of the fimbria of anterior attachment organ, haptor marginal membrane, testicular field and testes; or misinterpreting them, e.g., position of mouth, differentiating nerve from intestine, number of dorsomarginal body sclerites, number of scallops in haptor marginal membrane, lateral extent of testicular field. We do not have access to the specimen(s) upon which this drawing was based, but the features drawn for *C. laevis* therein are dubious.

The type host for *C. laevis* probably will not ever be known for certain, because Verrill (1875, 1885) did not provide a specific epithet or binomial for the host nor, to our knowledge, is the infected individual billfish in existence as a museum voucher. Verrill’s (1875) designation of “bill-fish” could have been one of the several billfishes that were already known, described, and named in 1875, including *Tetrapturus georgii* Lowe, 1840, but Verrill did not specify any one of them. Perhaps contributing to the confusion was that Verrill (1875) reported specimens of *C. cornutus* from white marlin, perhaps leading subsequent authors (e.g., Linton, 1898; Price, 1938) to assume that the host for *C. laevis* was also *T. albidus*. Such would be unequivocal if these capsalids were collected from the same individual host, but that detail was not reported either. We think it possible, or more likely, that Verrill (1875) did not positively identify the host as white marlin because he did not attach a binomial name to the type host. Verrill’s later publication (1885) is awkward in that it provides a figure of *C. laevis* and *C. cornutus* but does not apparently provide any accompanying text explaining the origin(s) of the specimen(s) illustrated. The first author to ascribe white marlin as the type host for *C. laevis* was Linton (1898) who, without justification, specified “gills of *Tetrapturus albidus*” and cited Verrill (1885); however, Verrill (1885) does not report a host(s) for any capsalid. Interestingly, in a footnote on page 503 of Verrill (1885), Verrill states that, “The naturalists associated with the writer in this work in 1883 were: . . . Prof. Edwin Linton . . .” This made us wonder if perhaps Linton may have had first-hand knowledge of the type host for *C. laevis*, but nowhere is that stated in either of Verrill’s publications (1875; 1885) or in Linton (1898). Price (1938), perhaps influenced by Linton (1898), also listed the type host as “white marlin, *Tetrapturus imperator*” without justification, and subsequent authors have followed suit in listing white marlin as the type host. We find no justification for this. Regardless of the ambiguity of the type host for *C. laevis*, capsalid records from “white marlin” must now be reconsidered, as some of those may have, in fact, been roundscale spearfish. In any event, all of this underscores the need to base capsaline taxonomy on character-

istics of the worms themselves rather than on their host affiliation(s).

The 2 records of *C. laevis* from swordfish, *Xiphias gladius* Linnaeus, 1758, (Perciformes: Xiphidae), are dubious. First, Linton (1940) reported a single specimen (USNPC No. 8154) from the alcohol wash of the gill of a swordfish presumably captured from the northwestern Atlantic Ocean before being landed and necropsied by Linton at Woods Hole, Massachusetts in June 1911 (accessioned as "*Placunella lata*"; with original slide label reading, "in vial with *T. coccineum* from gills of swordfish"). We borrowed this specimen and believe it represents a new species of *Capsala* by having the following combination of morphological features: (1) papillae on ventral surface of haptor present (including on ventral surface of central loculus); (2) dorsomarginal body sclerites not crown-like, having cusps, distributing in a single column per side of body (not in transverse rows) and including a dense patch of smaller spines at level of cirrus sac and interrupting sinistral column of dorsomarginal sclerites (having a total of 39 dextral sclerites plus 54 sinistral sclerites comprising 6 sclerites anterior to patch, 19 within patch, and 29 posterior to patch); (3) haptoral accessory sclerites approximately 500  $\mu$ m long and 150  $\mu$ m in maximum width with a medial flange; (4) ventral surface of anterior attachment organs bearing papillae; and (5) anterior attachment organ lacking fimbria. Two other genera of Capsalinae include species reported from swordfish, i.e., *Capsaloides* Price, 1938 (see Chisholm and Whittington, 2006) and *Tristoma* Cuvier, 1817 (see Chisholm and Whittington, 2007), but USNPC No. 8154 cannot represent a species of either genus. *Capsaloides* spp. have crown-like dorsomarginal body sclerites rather than sclerites having cusps as in species of *Capsala*. *Tristoma* spp. have transverse rows of dorsomarginal body sclerites rather than a single or double column of sclerites per side of the body as in species of *Capsala*. The collection of heat-killed specimens from *X. gladius* is in progress and, given the condition of the voucher we studied, we think better quality specimens are required for an adequate description of this species, including with both light and scanning electron microscopy. There are other inaccuracies in the narrative of Linton (1940) that will be corrected when this species is described, e.g., the voucher specimen has many testes, not 2 in tandem, posterior to the genital atrium. Second, Kayış et al. (2010) reported *C. laevis* (as *Tristomella laevis*) from the gill of swordfish captured in the Aegean Sea off Turkey. The photograph provided by these authors shows the body of 2 worms as side-by-side dorsal and ventral views, but neither represents *C. laevis* because the haptor does not extend past the posterior body margin. We can only hazard a guess as to the identity of these specimens, but it seems likely they could represent a species of *Capsaloides*. Another unusual record of *C. laevis* (HWML 1453) comprises that of the ocean sunfish, *Mola mola* (Linnaeus, 1758), (Tetraodontiformes: Molidae) (Chisholm and Whittington, 2007, appendix 1). On the other hand, it is not unbelievable from an ecological perspective because ocean sunfishes seemingly are massive, slow-swimming platforms for colonization of ectoparasites in the epipelagic zone.

The record of *C. laevis* from roundscale spearfish reported herein represents the first record of any symbiont from roundscale spearfish, and it seems likely that many new parasite records from this epipelagic fish will be forthcoming. Broadly, additional information on the identity of pelagic fish capsalids, in concert with molecular data (e.g., Whittington et al., 2004; Perkins et al.,

2009; Bullard et al., 2011), could provide the baseline information needed for testing hypotheses concerning the ecology and coevolution of platyhelminths and fishes in pelagic ecosystems as well as the utility of using these parasites as "tags" or stock identifiers for highly migratory fishes like tunas and billfishes. Although our present morphological results failed to identify a capsalid species unique to roundscale spearfish, the potential remains for finding other metazoan parasites that do, indeed, exhibit specificity for particular istiophorids. In this way, parasite taxonomy remains applicable and relevant to fisheries and fish biology as our understanding of the phylogenetic relationships and biodiversity of billfishes continues to grow and as we seek new tools for assessing their populations and defining management units (Beerkircher et al., 2009). Fascinatingly, new istiophorids remain to be described and, probably, new parasites infect them. For example, Pristas (1980) reported morphological differences between a species of *Tetrapturus*, which he called "hatchet marlin," and both white marlin and longbill spearfish in the Gulf of Mexico. Collette et al.'s (2006) molecular results did not reject the possibility that the so-called 'hatchet marlin' may be an additional valid species of spearfish. As molecular techniques continue to advance, our knowledge of the population dynamics and species boundaries of capsalids infecting these majestic pelagic fishes will also be enhanced.

#### ACKNOWLEDGMENTS

We thank Jim Motsko (Director and President, White Marlin Open Tournament [WMOT], Ocean City, Maryland), for facilitating access to roundscale spearfish at WMOT; Jason Boos, Katherine Fingles, and Meredith Murray (Salisbury University, Salisbury, Maryland) plus Christina Patten (Virginia Tech University, Blacksburg, Virginia) for helping collect billfish capsalids at WMOT; Andrew McElwain (Aquatic Parasitology Laboratory, Auburn University, Auburn, Alabama) for taking the SEM micrographs; and Eric Hoberg and Pat Piltitt (both United States National Parasite Collection, Beltsville, Maryland) plus Scott Gardner (Harold W. Manter Laboratory of Parasitology, Lincoln, Nebraska) for ensuring the safe deposition of our voucher materials and for loaning relevant capsalid specimens. We thank Mahmood Shivji (Nova Southeastern University, Dania Beach, Florida) for providing molecular confirmation of our field identifications of the 2 roundscale spearfish sampled. The bulk of this work was conducted during A.M.B.'s sabbatical stay in S.A.B.'s laboratory, which was supported by a grant from Maryland SeaGrant. This is a contribution of the Southeastern Cooperative Fish Parasite and Disease Project (Department of Fisheries and Allied Aquacultures, Auburn University) and was supported in part by NSF-DEB grant numbers 1112729, 1051106, and 1048523 to SAB.

#### LITERATURE CITED

- BEERKIRCHER, L., F. AROCHA, A. BARSE, E. PRINCE, V. RESTREPO, J. SERAFY, AND M. SHIVJI. 2009. Effects of species misidentification on population assessment of overfished white marlin *Tetrapturus albidus* and roundscale spearfish, *T. georgii*. *Endangered Species Research* 9: 81–90.
- BELL, F. J. 1891. Description of a new species of *Tristomum* from *Histiophorus brevirostris*. *Annals and Magazine of Natural History* 7: 534–535.
- BULLARD, S. A. 2010. *Littorellicola billhawkinsi* n. gen., n. sp. (Digenea: Aporocotylidae) from the myocardial lacunae of Florida pompano, *Trachinotus carolinus* (Carangidae) in the Gulf of Mexico, with a comment on the interrelationships and functional morphology of intertrabecular aporocotylids. *Parasitology International* 59: 587–598.
- , AND K. JENSEN. 2008. Blood flukes (Digenea: Aporocotylidae) of stingrays (Myliobatiformes: Dasyatidae): *Orchispirium heterovitellatum* from *Himantura imbricata* in the Bay of Bengal and a new genus

- and species from *Dasyatis sabina* in the Northern Gulf of Mexico. *Journal of Parasitology* **94**: 1311–1321.
- , O. OLIVARES-FUSTER, G. W. BENZ, AND C. R. ARIAS. 2011. Molecules infer origins of ectoparasite infracommunities on tunas. *Parasitology International* **60**: 447–451.
- , R. PAYNE, AND J. S. BRASWELL. 2004. New genus with two new species of capsalid monogeneans from dasyatids in the Gulf of California. *Journal of Parasitology* **90**: 1412–1427.
- CHISHOLM, L. A., AND I. D. WHITTINGTON. 2006. Revision of *Capsaloides* (Monogenea: Capsalidae) with a redescription of *C. magnaspinosus* Price, 1939 from the nasal tissue of *Tetrapturus audax* (Istiophoridae) collected off Nelson Bay, New South Wales, Australia. *Zootaxa* **1160**: 1–20.
- , AND ———. 2007. Review of the Capsalinae (Monogenea: Capsalidae). *Zootaxa* **1559**: 1–30.
- COLLETTE, B. B., J. R. MCDOWELL, AND J. E. GRAVES. 2006. Phylogeny of recent billfishes (Xiphoidei). *Bulletin of Marine Science* **79**: 455–468.
- DEVARAJ, M. 1976. *Capsala laevis* (Verrill, 1874) on *Makaira tenuirostratus* (Deraniyagala, 1951) with a discussion on host identity. *Journal of the Marine Biological Association India* **18**: 310–317.
- DOLLFUS, R. P. 1949. Présence de *Capsala laevis* (A. E. Verrill 1875) (Trematoda Monogenea) chez un *Tetrapturus* (Poisson Xiphiiforme) au large de la cote de Bretagne. *Bulletin de la Société Zoologique de France* **74**: 317–319.
- DYER, W. G., E. H. WILLIAMS JR., AND L. BUNKLEY-WILLIAMS. 1992. *Tristomella laevis* (Verrill, 1875) Guiart, 1938 (Monogenea: Capsalidae) on white and blue marlins from the southwestern coast of Puerto Rico and Desecheo Island. *Transactions of the Illinois State Academy of Science* **85**: 183–185.
- ESCHMEYER, W. N. (ed.) 2010. *Catalog of Fishes*. Available at: <http://research.calacademy.org/ichthyology/catalog>. Accessed 9 November 2010.
- GOTO, S. 1894. Studies on the ectoparasitic trematodes of Japan. *Journal of the College of Science Tokyo* **8**: 1–273.
- . 1899. Notes on some exotic species of ectoparasitic trematodes. *Journal of the Science College, Imperial University, Tokyo, Japan* **12**: 263–295.
- JOHNSTON, T. H. 1929. Remarks on the synonymy of certain tristomatid trematode genera. *Transactions and Proceedings of the Royal Academy of South Australia* **53**: 71–78.
- KAYIS, S., İ. ALTINOK, F. BALTA, AND H. B. İMRE. 2010. First report of *Tristomella laevis* (Monogenea, Capsalidae) from Aegean Sea in Turkey. *Kafkas University Vet Fak Derg* **16**(Suppl. B): S373–S375.
- LAMOTHE-ARGUMEDO, R. 1997. Nuevo arreglo taxonómico de la subfamilia Capsalinae (Monogenea: Capsalinae), clave para los géneros y dos combinaciones nuevas. *Anales Instituto Biología Universidad Nacional Autónoma México, Series Zoology* **68**: 207–223.
- LAWLER, A. R. 1981. Zoogeography and host-specificity of the superfamily Capsaloidea Price, 1936 (Monogenea: Monopisthocotylea). *Special Papers in Marine Science No. 6*, Virginia Institute of Marine Science and College of William and Mary, Gloucester Point, Virginia, 650 p.
- LINTON, E. 1898. Notes on trematode parasites of fishes. *Proceedings of the United States National Museum* **20**: 507–548.
- . 1940. Trematodes from fishes mainly from the Woods Hole region Massachusetts. *Proceedings of the United States National Museum* **88**: 1–172.
- LYONS, K. M. 1972. Sense organs of monogeneans. Behavioural aspects of parasite transmission, E. U. Canning and C. A. Wright (eds.). *Zoological Journal of the Linnaean Society* **51**(Suppl. 1): 181–199.
- NAKAMURA, I. 1985. Billfishes of the world. *FAO species catalogue, FAO fish synopsis no. 125*, vol. 5, 65 p.
- NELSON, J. S. 2006. *Fishes of the world*, 4th ed. John Wiley and Sons, Inc., New York, New York, 601 p.
- PERKINS, E. M., S. C. DONNELLAN, T. BERTOZZI, L. A. CHISHOLM, AND I. D. WHITTINGTON. 2009. Looks can deceive: Molecular phylogeny of a family of flatworm ectoparasites (Monogenea: Capsalidae) does not reflect current morphological classification. *Molecular Phylogenetics and Evolution* **52**: 705–714.
- PRICE, E. W. 1938. The monogenetic trematodes of Latin America. *Livro Jubilar Prof. Travassos. Rio de Janeiro, Brasil*, p. 407–413.
- . 1939. North American monogenetic trematodes. III. The family Capsalidae (Capsaloidea). *Journal of the Washington Academy of Sciences* **29**: 64–92.
- PRISTAS, P. J. 1980. A possible hatchet marlin (*Tetrapturus* sp.) from the Gulf of Mexico. *North-east Gulf Science* **4**: 51–56.
- PRITCHARD, M. H. 1961. Notes on two species of *Tristomella* Guiart, 1938 (Monogenea: Capsalidae), from a South African black marlin. *Journal of Parasitology* **47**: 976–977.
- ROBINS, C. R. 1974. The validity and status of the roundscale spearfish, *Tetrapturus georgii*. *NOAA technical report NMFS SSRF-675*, part **2**: 54–61.
- SETTI, E. 1899. Contributo per una revisione dei tristomi. *Atti della Società Ligure di Scienze Naturalisti e Geografici* **10**: 71–84.
- SHIVJI, M. S., J. E. MAGNUSSEN, L. R. BEERKIRCHER, G. HINTEGGER, D. W. LEE, J. E. SERFAY, AND E. D. PRINCE. 2006. Validity, identification, and distribution of the roundscale spearfish, *Tetrapturus georgii*: Morphological and molecular evidence. *Bulletin of Marine Science* **79**: 483–491.
- VERRILL, A. E. 1875. Art. X. Brief contributions to zoology from the Museum of Yale College. no. XXXIII.—Results of dredging expeditions off the New England Coast in 1874. *American Journal of Science and Arts* **10**(55–60, July to December, 1875): 36–43.
- . 1885. XVI.—Results of the explorations made by the steamer “Albatross,” off the northern coast of the United States, in 1883. *United States Commission of Fish and Fisheries Part XI, Report of the Commissioner for 1883*. Government Printing Office, Washington, D.C., 1885, p. 503–699.
- WHITTINGTON, I. D. 2004. The Capsalidae (Monogenea: Monopisthocotylea): A review of diversity, classification and phylogeny with a note about species complexes. *Folia Parasitologica* **51**: 109–122.
- , M. R. DEVENNEY, J. A. T. MORGAN, L. A. CHISHOLM, AND R. D. ADLARD. 2004. A preliminary phylogenetic analysis of the Capsalidae (Platyhelminthes: Monogenea: Monopisthocotylea) inferred from large subunit rDNA sequences. *Parasitology* **128**: 511–519.
- WILLIAMS JR., E. H., AND L. BUNKLEY-WILLIAMS. 1996. Parasites of offshore big game fishes of Puerto Rico and the western Atlantic. *Sportfish Disease Project, Department of Marine Science and Department of Biology, University of Puerto Rico, San Juan, Puerto Rico*, 382 p.
- YAMAGUTI, S. 1968. Monogenetic trematodes of Hawaiian fishes. *University of Hawaii Press, Honolulu, Hawaii*, 287 p.