ELAPHROBATES EUZETI GEN. AND SP. N. (DIGENEA: SANGUINICOLIDAE) FROM SNAPPERS (LUTJANIDAE) IN THE GULF OF MEXICO

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Summary « Elaphrobates euzeiti gen. and sp. n. (Digenea: Sanguinicolidae) from snappers (Lutjanidae) in the Gulf of Mexico »

Elaphrobates euzeiti gen. and sp. n. (Digenea: Sanguinicolidae) infects the heart and branchial vessels of the red snapper (Lutjanus campechanus) and the heart of the gray snapper (Lutjanus griseus) in the Gulf of Mexico. It has ventrolateral tegumental spine rows each consisting of 4-7 spines, an oral sucker with 6-7 concentric spine rows, sinuous posterior ceca extending to the ovary and 2-4 times longer than the anterior ceca, a single mostly intercelcal testis not extending beyond the lateral nerve cords, a post-testicular ovary, a dextral ootype at or immediately anterior to level of the female pore, and a post-cecal and mostly post-ovarian uterus. It lacks both rosethorn-shaped spines and an auxiliary seminal vesicle. Elaphrobates euzeiti achieves locomotion by reversible, wave-like undulations of the lateral body margins in conjunction with traction provided by the tegumental spines in tread-like rows. The digenean can attach by creating suction with its flat, ventrally concave body on smooth surfaces or by pinching tissue between adjacent tegumental spine rows. The eggs of this fluke are spheroid

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to elongate, apparently depending on the stage of miracidial development; they lodge within the afferent branchial arteries or embed within the gill epithelium. This is the first report of a blood fluke from a lutjanid and the fifth adult sanguinicolid described from fishes of the Gulf of Mexico.

**Key words**

Blood Fluke - Sanguinicolidae - *Elaphrobates euzeti* - New Genus and Species - Lutjanidae - Gulf of Mexico - Host-Parasite Association

**Résumé** « *Elaphrobates euzeti* gen. et sp. n. (Digenea : Sanguinicolidae) parasite de lutjanides (Lutjanidae) dans le Golfe du Mexique »

*Elaphrobates euzeti* gen. et sp. n. (Digenea : Sanguinicolidae) infeste le cœur et les vaisseaux branchiaux du red snapper (*Lutjanus campechanus*) et le cœur du gray snapper (*Lutjanus griseus*) dans le Golfe du Mexique. Il possède des rangées d’ épines tégumentaires ventro-latérales comprenant 4 à 7 épines, une ventouse orale pourvue de 6 à 7 rangées concentriques d’épines, des caecums postérieurs sinueux s’étendant jusqu’à l’ovaire et 2 à 4 fois plus longs que les caecums antérieurs, un testicule unique intercaecal ne dépassant pas les cordons nerveux latéraux, un ovaire post-testiculaire, un ootype dextre au niveau du pore femelle ou immédiatement antérieur à lui, et un utérus post-caecal et principalement post-ovarien. Il n’y a ni épines en forme de pomme épineuse, ni vésicule séminale accessoire. *Elaphrobates euzeti* se déplace grâce à des ondulations réversibles, en forme de vagues, des bords du corps, associées à des tractions sur des épines tégumentaires disposées en rangées ressemblant à des semelles. Ce digène peut s’attacher sur des surfaces lisses par une succion de son corps plat et concave ou bien en pinçant les tissus entre des rangées adjacentes d’épines tégumentaires. Les œufs sont sphériques à allongés, suivant, semblable-t-il, le stade de développement du miracidium ; ils se logent à l’intérieur des artères branchiales ou bien sont trouvés enrobés dans l’épithélium branchial. Il s’agit de la première mention d’un parasite sanguin chez un Lutjanid et le 5ème Sanguinicolidae décrit chez des poissons au Mexique.

**Mots clés**

Parasite sanguin - Sanguinicolidae - *Elaphrobates euzeti* - Nouveau genre et espèce - Lutjanidae - Golfe du Mexique - Association hôte-parasite
Introduction

Sanguinicolidae von Graff, 1907, a family of fish digeneans, presently includes approximately 51 marine species allocated to 18 genera, 12 of which are monotypic. It also includes approximately 26 freshwater species, and all these have been assigned to either Sanguincola Plehn, 1905 or the monotypic Paracardicoloides Martin, 1974 (e.g., Smith, 1997). We suspect the 77 species represent a small proportion of the total because the sites that adult blood flukes commonly infect (e.g., heart, branchial vessels, and mesenteric vessels) are not always examined during routine fish necropsies. In addition, some blood flukes occur seasonally and others are difficult to see in vivo because they are flat, slender, opaque, or nearly transparent, and both collecting and fixing intact specimens can present a challenge because of the worms’ delicate, easily damaged tegument. In the Gulf of Mexico (GOM), only four adult sanguinicolidis in three genera have been described from five fishes; all these species occurred off Florida (Manter, 1947; Short, 1953, 1954). Herein, we describe a new genus and species based on light and scanning electron microscopy of specimens collected from Lutjanus campechanus and Lutjanus griseus caught in the GOM off Mississippi and Florida, respectively.

Materials and Methods

Most of 215 specimens of the red snapper, L. campechanus, examined for this study were caught by rod and reel, trawl, or longline from various localities in the GOM off Mississippi, Alabama, and Florida from May 1999 through November 2001. Of those 215 red snapper, at least the hearts of 24 were opportunistically sampled at fishing tournaments held in Dauphin Island, Alabama, and Gulfport, Mississippi, during July 1999; their exact locations of capture were not released, but they were from the northern GOM as were seven lane snapper (Lutjanus synagris), three gray snapper (Lutjanus griseus), several cubera snapper (Lutjanus cyanopterus), five vermilion snapper (Rhomboptilus aurorubens), and four wenchman (Pristipomoides aquilonaris). The hearts of two additional gray snapper examined for this study were caught by longline off Tampa, Florida, in October 2001. Hearts of other lutjanids that were collected from Little or Grand Cayman islands were examined. They were obtained from a beachside fishstand in Grand Cayman Island, British West Indies, during the same period: seven gray snapper, six mutton snapper (Lutjanus analis), two dogtooth snapper (Lutjanus joco), one schoolmaster (Lutjanus apodus), and one yellowtail snapper (Ocyurus chrysurus). Live fishes were killed by severing the spinal cord. Hearts were then extracted and placed in a petri dish partially filled with either an 8.5 ppt sodium chloride (NaCl) solution or a solution of 5 grams NaCl and 2 grams sodium citrate per liter of distilled water, bisected,
probed gently, sprayed with one of the salt solutions, and examined with a dissecting microscope. Portions of gill were removed, placed on a slide with seawater, cover-slipped, examined with the aid of a compound microscope equipped with Nomarski optics, and photographed with a digital camera. Flukes were examined live in a salt solution, relaxed before killing them under slight coverslip pressure with the flame from an ethanol-burner, and transferred to a vial of 5% neutral buffered formalin.

Whole mounts were stained in Van Cleave’s hematoxylin with several additional drops of Ehrlich’s hematoxylin, made basic at 70% ethanol with lithium carbonate and butyl-amine, dehydrated, cleared in clove oil, and mounted in Canada balsam. Three specimens were embedded in paraffin, sectioned at 4 μm, and stained with Gill’s hematoxylin and eosin. To elucidate fine structure of the esophageal gland and the gonads, a specimen was embedded in methyl methacrylate/butyl methacrylate, serially sectioned at 1 μm, and stained with azure blue, hematoxylin, and eosin. Four specimens were prepared for scanning electron microscopy (SEM) by immersion in hexamethyldisilazane for 15 min, dried under a vacuum for 10 min, sputter-coated with gold-palladium, and examined with a JOEL 6300V scanning electron microscope.

Drawings were made with the aid of a drawing tube. Measurements are reported in μm and given as ranges followed by the sample size in parentheses.

**Description**

*Elaphrobates* gen. n.

**Diagnosis:** With characters of Sanguinicolidae von Graff, 1907. Body of adult elongate, less than 8 X longer than wide, dorsoventrally flattened, ventrally concave, spined. Tegmental spines in ventrolateral transverse rows. Rosethorn-shaped spines lacking. Oral sucker spherical, at anterior extremity of body, spined; spines on oral sucker spike-like, arranged in concentric rows. Mouth ventral, near equator of oral sucker, immediately posterior to concentric spine rows. Pharynx lacking. Intestine X-shaped, lacking diverticula, with intersection medial, connecting to esophagus ventrally, with posterior branches conspicuously longer than anterior ones. Testis single, roughly rectangular in shape, dorsal to posterior ceca, not extending laterally beyond lateral nerve cords. Auxiliary seminal vesicle lacking. Cirrus sac present; cirrus sinistral, post-gonadal. Male pore dorsal, lateral to sinistral lateral nerve cord. Ovary medial, dorsal to lateral nerve cords, post-testicular or slightly overlapping posterior testicular border, irregular. Oviduct with medial portion swollen with sperm and functioning as seminal receptacle. Uterus not extending anterior to ovary. Female pore dorsal, sinistral, anteromedial to cirrus and nerve cord, near level of ootype. Excretory ves-
ciple ovoid. Adult and juvenile infecting vascular system of marine teleosts.


Etymology: The Greek, masculine 'Elaphrobates' refers to 'elaphros,' meaning light in weight and 'bates,' meaning one that treads.

Type species: Elaphrobates euzeti sp. n.

Elaphrobates euzeti sp. n. (Figs 1-15)

Adult (Based on 24 specimens): Body 835-1596 (20) long, 172-467 (20) wide, 3.4-4.9 X longer than wide, with anterior and posterior ends tapered equally (Figs 1, 4, 5). Tegumental body spines 9-16 (14) long, 1-3 (14) wide at base, protruding from tegument as ≤ 0.5 X total spine length, with recurved distal tip, not fused at base, with lateral-most spine in each row 3-14 (13) from body margin (Figs 1, 2, 6-9, 11). Tegumental spine rows extending along entire body length, with 183-267 (18) rows per side or total of 368-532 (18) rows; each row 16-25 (19) long, with number of spines per row increasing from anterior end to middle of body and then decreasing posteriorly, generally following pattern of 4-5-6-7-6-5-4 spines per row (Figs 1, 2, 6-9, 11). Nervous system with commissure joining lateral cords 89-154 (19) or 7-12% of body length from anterior end of body, extending perpendicular to midline, 25-67 (20) long, 7-22 (20) wide (Figs 1, 2); ventrolateral nerve cords paired, 801-1522 (20) long, 7-12 (20) wide, 40-89 (20) from body margin, parallel to lateral body margins, contiguous anteriorly and posteriorly, located 24-58 (14) or 2-5% of body length from posterior end of body, with secondary branches extending laterally and medially (Fig. 1); dorsolateral nerve cords apparently lacking.

Oral sucker delicate, 12-28 (19) long, 15-27 (19) wide (Figs 1, 2, 10, 11); sucker spines approximately 1 long or 6-11% of lateral tegumental spine length, approximately 0.3 wide (Fig. 2); oral sucker spine rows 6-7 in number (16), located between distal end and slightly anterior to equator of oral sucker, equally spaced (Fig. 2); mouth 2-4 (18) in diameter or 7-21% of oral sucker width (Fig. 2). Esophagus 378-692 (20) long or 40-46% of body length, 15-37 (19) in maximum width, extending sinuously posteriad along midline, curving 6-12 times, widening posteriorly (Fig. 1); esophageal wall thickening from 2-3 (20) near mouth to 3-10 (20) in posterior half of esophagus (Fig. 1). Esophageal glands surrounding esophagus; anterior gland concentrated between nerve commissure and oral sucker, mostly between lateral
Figures 1-3: *Elaphrobates euzeti* gen. and sp. n. from *Lutjanus campechanus*, holotype, ventral view.

Figure 1. Whole mount, scale bar = 300 μm.

Figure 2. Oral sucker, oral sucker spines, mouth, anterior portions of esophagus and lateral nerve cords, and lateral tegumental spines, scale bar = 25 μm.

Figure 3. Genitalia, scale bar = 150 μm.
nerve cords, with spherical cells; posterior gland 87-409 (13) in maximum length or 18-36% (12) of esophageal length, 62-186 (13) in maximum width or 25-42% (13) of body width, lacking surrounding membrane (Fig. 1), with associated ducts; ducts 2 (10) in diameter, with extremely thin walls, refractive, containing basophilic material in sectioned material, extending laterally, piercing through esophageal wall. Cecal intersection of anterior and posterior ceca 40-46% of body length from anterior end of body (Fig. 1); anterior ceca 67-244 (20) long or 7-15% of body length, 14-61 (20) wide or 0.6-2.2 X esophageal width, usually between nerve cords, with each cecum extending slightly anterolaterally, with short gastrodermal cells, containing granular material within lumen; material refractive, dense, brownish-yellow in both live and whole-mounted specimens, usually concentrated in distal portion (Fig. 1); posterior ceca 211-524 (20) long or 23-34% of body length, 1.9-4.3 X length of anterior ceca, usually unequal in length (dextral posterior cecum 5-99 longer than sinistral one in 12 of 20 specimens), 7-50 (15) wide or 23-135% of anterior ceca width, not extending laterally beyond nerve cords, sinuous, extending posteriorly roughly in parallel with lateral body margin, with each cecum having swollen distal end; distal swelling 32-77 (20) wide or 1-6 X width of mid-level of posterior ceca, a blind-ending sac, with some specimens having same granular material as in anterior ceca (Figs. 1, 3).

Testis irregular in shape, 174-196 (19) long or 18-25% of body length, 67-248 (18) wide or 37-53% of body width, 1.3-2.6 X longer than wide, occupying region between cecal intersection and ends of posterior ceca, enclosing clearly defined refractive processes (Fig. 1); processes extending dorsoventrally, roughly 1-3 (10) in diameter. Vasa efferentia difficult to trace in fixed specimens, a meshwork of fine ducts entwined throughout testicular tissue, containing spermatozoa in all examined specimens; ducts 3-7 (5) in diameter, extending primarily dorsoventrally; vas deferens 140-388 (17) long, 7-27 (14) wide, slightly sinistral, extending ventromedially from testis and posteriad between ends of posterior ceca, sinuous, roughly consistent in width for entire length, containing spermatozoa in all specimens (Figs. 1, 3). Seminal vesicle 43-151 (20) long or 5-11% of body length, 12-45 (20) wide or 5-16% of body width, directed slightly sinistrad, constricted distally at level of sinistral nerve cord, containing sperm in 15 of 20 specimens, relatively narrow if without sperm (Figs 1, 3); wall of vesicle 2-4 (20) thick (Figs 1, 3). Cirrus (non-extruded) 15-42 (14) long or 18-52% of seminal vesicle length, 10-21 (20) wide or 33-107% of seminal vesicle width, 1-3 X longer than wide, located 50-174 (19) or 4-11% of body length from posterior end of body, evertting dorsally through male pore between nerve cord and sinistral lateral body margin, surrounded by sac; sac with thin walls (Figs 1, 3, 15). Post-testicular space 268-552 (20) long or 28-35% of body length (Fig. 3).
Ovary with relatively thin outer wall (indistinct in Figs 1, 3), 69-198 (19) long or 7-15% of body length, 82-244 (19) wide or 33-83% of body width, mostly occupying region between lateral nerve cord, medial, anterior to seminal vesicle, dorsal to distal swellings of posterior ceca, containing refractive dorsoventral processes similar to those through testis (Figs 1, 3). Oviduct 51-196 (18) long, 12-56 (19) wide, extending posteriad and slightly dextrad, leaving ovary medioventrally, conspicuously crooked as much as

Figures 4-9: *Elaphrobates euzeti* gen. and sp. n. from *Lutjanus campechanus*. 4-8. Scanning electron micrographs (SEM).
Figure 4. Body, adult, dorsal view, scale bar = 200 µm.
Figure 5. Body, adult, ventral view, scale bar = 200 µm.
Figure 6. Lateral body margin, adult, ventral view showing rows of lateral tegumental spines, scale bar = 50 µm.
Figure 7. Rows of lateral tegumental spines, ventral view, scale bar = 5 µm.
Figure 8. Lateral tegumental spines, dorsal view, scale bar = 5 µm.
Figure 9. Lateral tegumental spines, ventral view, wet-mount, Nomarski illumination, scale bar = 20 µm.
90° at distal end (Figs 1, 3) ; medial portion distended with sperm, 33-175 (16) long or 47-98% of oviduct length, 12-56 (17) wide, containing ova in 3 of 20 specimens (Fig. 3) ; ova within oviduct 1-2 per specimen, 7 in diameter (Fig. 3). Vitellarium consisting of vitelline follicles compacted in elongated and lobed bands, dorsal to nerve cords, occupying space from level of nerve commissure to level just anterior to proximal region of seminal vesicle (Fig. 1) ; collecting ducts with numerous laterally directed branches in anterior half of body ; common vitelline duct 140-372 (19) long, 12-32 (19) wide, traceable from level just posterior to nerve commissure to distal portion of oviduct, sinuous, extending posteriorly roughly parallel and ventral to esophagus, passing ventral to ceca and gonads and vas deferens, widening just posterior to ovary before connecting with oviduct dorsally, with distal portion containing separated large vitelline cells. Female duct between common vitelline duct and ootype short, extending directly posterior (Fig. 3) ; ootype 14-74 (15) long, 10-34 (15) wide, posterior to oviduct, spherical or ovoid, dextral (Figs 1, 3). Mehlis’ gland a loose aggregation of few cells surrounding ootype. Uterus 159-613 (9) long, 16-40 (20) wide, not extending laterally beyond nerve cords, recurving dorsad and anteriad immediately from ootype and following sinuous course diagonally across midline of body, passing dorsal to vas deferens, recurving second time ventral to posterior margin of ovary before extending short distance posteriorly, recurving third time immediately before connecting to metraterm (Figs 1, 3) ; metraterm 37-136 (19) long or 17-55% of uterine length, 7-40 (19) wide or 23-143% of uterine width, not extending beyond sinistral nerve cord, with wall 2-7 (19) thick. Female genital pore 5-19 (19) in diameter, 23-114 (19) in straight line distance from male pore, about midway between nerve cord and seminal vesicle (Figs 1, 3, 15). Uterine eggs 7-12 (14) long, 7-10 (14) in diameter, thin-shelled, spherical or ovoid when isolated, pliable and therefore compressed when tightly packed (Figs 1, 3) ; released eggs in branchial arterioles or clustered in branchial artery typically with fibrotic encapsulation, 30-50 (11) long, 25-40 wide, with some undergoing degeneration (Fig. 14) ; released eggs in branchial epithelium or abutting lamellae (not in lamellar epithelium) without fibrotic encapsulation, thin-shelled, attenuated and rounded at both ends, arcuate, with each containing developed or developing miracidium, 134-174 (14) long, 25-30 (14) wide (Fig. 13).

Excretory vesicle 9-22 (13) long, 5-11 (13) wide, 1-3 X longer than wide, located between posterior confluence of nerve cords and posterior end of body (Figs 1, 3), with cellular wall 2-4 (12) thick ; collecting ducts connected at mid-line and dorsal to posterior nerve confluence, sinuous, extending anteriorly internal to nerve cords, 161-223 (2) long or 13-17% of body length ; excretory pore 2-3 (7) wide, terminal, sphincter indistinct (Figs 1, 3).
Figures 10-15: *Elaphrobates euzeti* gen. and sp. n. from *Lutjanus campechanus*.
Figure 10. Oral sucker, adult, ventral view, SEM, scale bar = 10 μm.
Figure 11. Oral sucker and anterior rows of lateral tegumental spines, adult, ventral view, whole mount, Nomarski illumination, scale bar = 50 μm.
Figures 12-14: Wet-mount, Nomarski illumination.
Figure 12. Spheroid eggs embedded within gill epithelium containing early stage developing miracidia, scale bar = 25 μm.
Figure 13. Elongate eggs embedded within gill epithelium containing developed miracidia with cilia, scale bar = 25 μm.
Figure 14. Spheroid eggs containing developing miracidia lodged within afferent branchial artery, scale bar = 50 μm.
Figure 15. Dorsal surface showing female genital pore and everted cirrus, SEM, scale bar = 10 μm.
Juvenile (Based on 1 specimen): Body 455 long, 47 wide. Tegmental body spines 8 long, 1 wide at base, recurved tip lacking. Tegmental spine rows 7 long, with roughly 182 rows per side of body, consisting of 4 separated spines in anterior and posterior regions of body, consisting of 5 spines in middle region of body. Nerve cords not apparent. Oral sucker 20 in diameter; oral sucker spine rows 7 in number, between mouth and anterior end, concentric, with minute spines; mouth 3 in diameter, opening ventrally near equator of oral sucker. Digestive and reproductive systems not apparent. Excretory vesicle 5 in diameter, medial, near posterior end of body, with cellular wall 1 thick; excretory pore and collecting ducts not apparent.

Taxonomic summary

Type host: Lutjanus campechanus (Poey, 1860) (Perciformes: Lutjanidae), red snapper; other host: Lutjanus griseus (Linnaeus, 1758), gray snapper.

Sites: Lutjanus campechanus: adults in atrium, ventricle, and bulbous arteriosus of heart; juvenile in branchial vessel; eggs in gill epithelium and lumen of afferent branchial arteries; L. griseus: heart.

Type locality: Northern Gulf of Mexico, approximately 50 km south of Ocean Springs, Mississippi, USA (N 30° 02' 0.596, W 88° 36' 0.748); other localities: northern Gulf of Mexico, area between N 29° 55' 0.596 to N 30° 01' 0.884 and W 88° 28' 0.748 to W 88° 31' 0.466 (red snapper); off Tampa, Florida, N 28° 58.1, W 84° 26.3 (gray snapper).

Prevalence and intensity of infection: Thirty-nine of 215 red snapper (18%) were infected with 1 specimen in 24 fish; 2 in 4; 3 in 6; and 5, 7, 8, 12, or 40 in 5; 1 in 12 gray snapper (8%).

Specimens deposited: Holotype, United States National Parasite Collection, Beltsville, Maryland, USNPC No. 92256; paratypes, USNPC No. 92257; H. W. Manter Laboratory, University of Nebraska State Museum, Lincoln, Nebraska, HWML Coll. No. 16703 (2 slides); and Gulf Coast Research Laboratory Museum, The University of Southern Mississippi, Ocean Springs, Mississippi, GCRL 2039-2040 (2 slides).

Etymology: The species was named to honor Professor Louis Euzet for his numerous contributions to helminthology.

Remarks

Elaphrobates gen. n. appears similar to monotypic Pearsonellum Overstreet and Køie, 1989, monotypic Metoplehniella Lebedev & Parukhin, 1972, and Cardicola Short, 1953 by possessing an elongate body with rounded ends, an esophagus roughly 30-50% of body length, anterior and posterior cecal branches, a single medial testis anterior to a medial ovary, testis not extending to lateral body margin, and male genital pore at level of
or posterior to female genital pore. It also possesses tegumental spines in rows, as do *Cardiola* and *Pearsonellum*, and possibly *Metaplehninia*. It is unclear from the illustration and description of *Metaplehninia lethyrini* Lebedev and Parukhin, 1972 whether there is more than one marginal spine per row (Lebedev and Parukhin, 1972). *Elaphro Bates* differs from *Cardiola* and *Metaplehninia* by possessing an oral sucker and from *Pearsonellum* by lacking an auxiliary seminal vesicle and possessing an oral sucker with spines. Furthermore, *Metaplehninia* possesses a highly lobed ovary and testis, with the testis being mostly post-cecal. The gonads of the new genus are irregular in shape but lack lobes.

*Elaphro Bates euzeti* sp. n. appears most similar to *Pearsonellum con ventum* Overstreet and Køie, 1989 by the shared generic morphological features, but differs from it in addition to the above mentioned features by possessing a uterus not extending or coiling anterior to the ovary.

Live specimens of *E. euzeti* were easier to collect than fixed or dead ones. Although nearly transparent and difficult to distinguish from associated heart tissue, when sprayed with a salt solution and illuminated by an overhead light source, crawling individuals glistened, making them readily apparent. In hosts that had been on ice $\geq 4$ hours, blood coagulated, encasing some specimens and making their collection a challenge. However, blood did not coagulate as readily when diluted with the citrate solution. Also, the flukes remained active in that solution for $> 4$ hours. When kept on ice for $> 4$ hours, specimens exhibited a degenerating tegument and vacuolated parenchyma, features that precluded distinct staining. These iced specimens often deteriorated during collection.

Activity of *E. euzeti* was determined by examining about 30 live specimens collected throughout the year. Locomotion of the worm over the surface of a dissected heart immersed in a salt solution was achieved by repeated, coordinated wave-like undulations of the lateral body margins. When removed from tissue, the worm continued to exhibit these undulatory waves, which traveled anterior to posterior during forward movement and posterior to anterior during reverse movement. The slightly recurved distal tip of the lateral tegumental spines hooked into heart tissue, and we suspect that the insertion of select rows of spines in conjunction with the undulations provided the necessary traction for crawling. Locomotion over a smooth glass surface did not provide this traction and resulted in a much slower movement than when on tissues of the dissected heart.

The worm could attach to smooth glass by suction. It adhered by lifting all its body except the peripheral margins of the ventral surface, creating negative pressure. Suction could be destroyed by sliding a sharp needle beneath the body; however, once touched by a dissection tool, the worm usually curled and ceased activity for several minutes. The worm also could
attach by pinching heart tissue between adjacent spine rows. It could attach by the ventral surface only; when artificially detached and flipped ventral side up, although capable of righting itself, an individual rarely turned over and reattached. The worm could use its oral sucker to attach to glass; however, no individual was observed attached solely by the oral sucker. Apparently such attachment is related to feeding only.

No individual could maintain its position or swim within the salt solutions. If pipetted into a container of solution, an individual usually made rapid, repeated, flapping-like movements by folding its body in half for approximately 1 min prior to settling on the bottom of the container.

Eggs lodged in afferent branchial vessels or embedded within the gill epithelium were of different shapes, possibly due to age or level of development of the miracidium. Spheroid eggs (Fig. 14) typically possessed lipid and incompletely developed or degenerating miracidia. The elongated egg typically contained a well-developed, ciliated miracidium (Fig. 13) and was embedded within the gill, but not lamellar, epithelium.

Discussion

The dorsoventrally flat body, tread-like rows of lateral tegumental spines, and robust nervous system in *E. euzeti* probably constitute primary features enabling this fluke to relocate or to attach to the heart and blood vessel walls. Those activities in both the juvenile and adult of this species appear much more pronounced than most detached intestinal digeneans and several other blood flukes (unpublished observations). That potential presumably allows the worm to inhabit the relatively laminar, high fluid-flow vascular system. Without a means to move while remaining attached, the heart-dwelling worm could detach and be passively flushed into the branchial arterial system. Regarding attachment of the blood fluke to the wall of the blood vessel, the flat body probably allowed it to reduce drag by residing within a ‘boundary layer.’ This layer, a physical zone of reduced and unsteady fluid-flow near a surface, is created by friction as blood flows over the endothelium. Consequently, even though the blood passes through the system at a relatively high velocity, the flat specimens along the endothelium reside in a space with little or no flowing blood. Perhaps *E. euzeti* and other sanguinicolids lost a ventral sucker as they developed alternate means of attaching to their hosts such as the tegumental spines and the flat, ventrally concave body. Furthermore, that body surface may permit attachment of a few specimens to the inner walls of vessels without restricting blood flow.

The high level of activity we observed in *E. euzeti* and other blood flukes (unpublished observations) may be related to their life history. Some sanguinicolids migrate from one site to another, depending on season or life
history stage; the schistosomulum-like juvenile stage seems to develop in a different site than the adult. For example, the juvenile of *Aporocotyle simplex* Odhner, 1900 inhabits the lymphatic system of flatfishes and the egg-producing adult inhabits that site but also the branchial vessels (Køie, 1982). The juvenile of *Sanguinicola inermis* Plehn, 1905 migrates through connective tissue and muscle before entering the blood system, maturing, and producing eggs (Kirk & Lewis, 1996). In addition, Hine (1978) commonly observed adult specimens of *Paracardicoloides yamagutii* Martin, 1974 in the eel *Anguilla reinhardtii* only when they moved into the gills to lay eggs during spring and autumn.

Based on 37 specimens of eight lutjanids other than the red snapper, only 1 specimen of *E. euzeti* was collected, and it was from a single specimen of *L. griseus* caught off Tampa, Florida. This finding demonstrates that red snapper is not the only host; however, it is apparently the common one. Lane snapper (*Lutjanus synagris*), cubera snapper (*Lutjanus cyanopterus*), and other snappers that co-occurred with infected red snapper in the northern Gulf of Mexico did not exhibit infections; however, additional species and specimens of snappers from the GOM should be examined to determine the host range of this fluke and the existence of possible undescribed congeneric species of *Elaphroblates*.

The oral sucker of sanguinicolids and the arrangement of spines surrounding the mouth may not be homologous across taxa, and in some species, the shape and location of spines may be related to the site inhabited. This notion is based on the fact that *E. euzeti* exhibits similarities to other blood flukes that lack an oral sucker, such as *M. lethrini* and species of *Cardicola*, but it is dissimilar in regard to shape of body, intestine, and lateral tegumental spines as well as gonad position when compared with those species having an oral sucker, such as *P. yamagutii*. Several forms of oral suckers have been described in other adult sanguinicolids. For example, Martin (1974) described a raised oral disc armed with spine-like tegumental projections in *P. yamagutii*, a species that infects the dorsal aorta of the Australian eel. However, *P. yamagutii* differs from *E. euzeti* by possessing a U-shaped intestine without anterior ceca, two clearly distinct testes, and a pre-ovarian uterus. Overstreet and Køie (1989) provided a photograph of the oral sucker (oral disc) of *P. corventum* that lacks spines. That species clearly differs from *E. euzeti* as indicated in the remarks section. Thulin (1980) illustrated a protrusile snout with six whorls of minute spines capable of attaching to glass for *A. simplex* which contrasts with *E. euzeti*, with its spined, relatively fixed, non-protrusile, spherical oral sucker. Regarding *Deontacylix ovalis* Linton, 1910 from the body cavity of chubs in the Dry Tortugas, Linton (1910) illustrated spines encircling the mouth that continued
dorsally and laterally throughout the entire tegument. Our observations of specimens from Biscayne Bay, Florida, (Overstreet, 1969) confirmed the lack of a restricted concentric pattern of 'oral sucker type' spines surrounding the mouth, even though body spines were more dense anteriorly. There is no specific oral sucker, but the mouth opens into a distinct weakly muscular small structure. We observed a lower density of spines along both dorsal and ventral body surfaces compared with those seen marginally at the ends. In any event, we distinguish the pattern of anterior spination in D. ovalis from that in E. euzeti, which involves straight, spike-like, oral sucker-type spines clearly restricted to the oral sucker and no body spines other than the marginal recurved ones. As another example, Schell (1974) showed that the anterior end of Sanguinicola idahoensis Schell, 1974 lacked a spherical oral sucker, but it had a distinct anterior end termed a 'snout' or 'apical papilla' by various authors that was armed with 6-7 rows of concentric minute spines, presumably those found on the corresponding cercaria. That and other species of Sanguinicola infect freshwater fishes as well as possess an X-shaped intestine and a strongly lobed medial testis or multiple testes, features suggesting a distant relationship with Elaphrobates. Examinations of a series of cercariae and juvenile specimens of those species may help elucidate the development and phylogeny of both the sucker and the arrangement of spines. On the other hand, those features may represent adaptations necessary to accommodate specific sites in the host. Overstreet and Köie (1989) suggested that the oral sucker of P. corventum may be more likely to develop in species inhabiting relatively spacious areas of the heart rather than in species that lodge passively in vessels. The well-developed, spined oral sucker of E. euzeti, which is restricted to the heart, supports this suggestion; moreover, the same features occur in its juvenile even before it locates in the heart. Furthermore, the dispersed tegumental body spines of D. ovalis may be homologous to the lateral tegumental spines and not the oral sucker spines; however, D. ovalis probably possesses such an arrangement of spines because it inhabits the body cavity of its host.

Including E. euzeti, there are five sanguinicolid species in four genera reported from eight fishes in the GOM: Selachohemecus olsoni Short, 1954 from the Atlantic sharpnose shark, Rhizoprionodon terraenovae, (Carcharhinidae) by Short (1954); C. cardiocola (Manter, 1947) (as Psettaurium cardiolum) from the jolthead porgy, Calamus bajonado, (Sparidae) by Manter (1947); C. laruei Short, 1953 from the sand seatrout, Cynoscion arenarius, and the spotted seatrout, Cynoscion nebulosus, (Sciaenidae) by Short (1953); and D. ovalis from the yellow chub, Kyphosus incisor, and the Bermuda chub, Kyphosus sectatrix, (Kyphosidae) by Manter (1947). McIntosh (1934) described Paradeontaclyix sanguinicolooides McIntosh,
1934 from the yellowtail, *Seriola lalandi*, (Carangidae) from off Florida from the Atlantic Ocean bordering the GOM. However, most fishes in the GOM probably have not been examined critically for blood flukes; consequently, the biodiversity of blood flukes and the effects of those blood flukes on their hosts in that region is poorly known (Bullard & Overstreet, 2002).

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