

# ***Cardicola langeli* sp. n. (Digenea: Aporocotylidae) from heart of sheepshead, *Archosargus probatocephalus* (Actinopterygii: Sparidae) in the Gulf of Mexico, with an updated list of hosts, infection sites and localities for *Cardicola* spp.**

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**Abstract:** *Cardicola langeli* n. sp. (Digenea: Aporocotylidae) infects the heart of sheepshead, *Archosargus probatocephalus* (Walbaum, 1792) (Perciformes: Sparidae) in the northern Gulf of Mexico off Horn Island (type locality), Mississippi, USA. The new species is described herein using light and scanning electron microscopy of adult specimens and can be most easily distinguished from the other 24 accepted species of *Cardicola* Short, 1953 by the combination of having (i) an ovovitelline duct that extends anteriorly and that (ii) is posterior to the ootype, (iii) a male genital pore that is lateral to the oviducal seminal receptacle and (iv) a female genital pore lateral to the ootype. The new species is the only member of *Cardicola* so far reported to have tegumental spines that are distally flattened and broad, rather than pointed. The new species generally resembles the two other species of *Cardicola* that infect sparids, i.e. *Cardicola cardiocolum* (Manter, 1947) (type species) from jolthead porgy, *Calamus bajonado* (Block et Schneider), in the Gulf of Mexico and *Cardicola aurata* Holzer, Montero, Repullés, Sitja-Bobadilla, Alvarez-Pellitero, Zarza et Raga, 2008, from gilthead seabream, *Sparus aurata* Linnaeus, in the Mediterranean Sea, by having a spheroid anterior sucker with concentric rows of minute spines anterior to the mouth and by having a similar general arrangement of the vitellarium, gonads and genitalia. However, it differs from them by having the combination of the aforementioned five features plus asymmetrical posterior caeca and a dextral posterior caecum that extends beyond the posterior margin of the ovary. Probable eggs of *C. langeli* n. sp. that contain a ciliated miracidium infect gill epithelium and are spheroid. An updated list of hosts, infection sites and geographic localities for the 25 accepted species of *Cardicola* is provided.

**Keywords:** fish blood fluke, taxonomy, 'Sanguinicolidae', vascular system, parasite

Adults of the accepted species of *Cardicola* Short, 1953 (Digenea: Aporocotylidae) infect the blood vascular system (principally the lumen of the heart) of marine and euryhaline bony fishes, with records now from most ocean basins (Table 1). Similar to that of Aporocotylidae, *Cardicola* has been the subject of extensive, recent taxonomic activity: 17 of its 24 (71%) accepted species have been described since the year 2000. As a result, it is now the most species-rich marine aporocotylid genus; however, taxonomic revision subsequent to redescription of its type species [*Cardicola cardiocolum* (Manter, 1947) Short, 1953] may change that total (Bullard and Overstreet 2003, Bullard 2010a, McVay et al. 2011, Bullard et al. 2012). The genus includes what is probably now the most extensively-studied marine fish blood fluke: *Cardicola forsteri* Cribb, Daintith et Munday 2000, a blood fluke of true tunas (*Thunnus* spp., Scombridae) cultured in sea cages of South Australia and the Mediterranean Sea (Cribb et al. 2000, 2011, Colquitt et al. 2001, Bullard et

al. 2004, Aiken et al. 2006, 2008, 2009, Hayward et al. 2007, 2008). Aside from this marquee aporocotylid most published work with *Cardicola* has focused on species discovery (Cribb and Bray 2011), and our knowledge of the general biology of most other species of *Cardicola* is lacking. Herein, I describe another new species of *Cardicola* based on specimens collected from the heart of sheepshead, *Archosargus probatocephalus* (Walbaum, 1792) (Perciformes: Sparidae) in Mississippi Sound, northern Gulf of Mexico.

## **MATERIALS AND METHODS**

Sheepshead were captured on 9 July 2009 by baited hook and line. After capture, fish were maintained alive in aerated, ambient water or immediately killed by spinal severance, placed in a cooler with a small amount of ice and transported to the laboratory for necropsy. The heart of each fish was extracted, placed in a petri dish, immersed in physiologic saline, bisected to expose its lumen and examined with the aid of a dissecting

microscope. Probable eggs of the new species were photographed embedded in gill epithelium by wet mounting clipped gill filaments on coverslipped glass slides.

Living specimens were pipetted onto a glass slide and heat-killed with an EtOH burner flame before being transferred to a vial of 5% neutral buffered formalin, rinsed thoroughly with 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 in Canada balsam (Bullard and Overstreet 2004). The five specimens for scanning electron microscopy (SEM) were dehydrated, immersed in hexamethyldisilazane 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 equipped with differential interference contrast (DIC) optical components and a drawing tube. Measurements were obtained by using a calibrated ocular micrometre and are herein reported in micrometres ( $\mu\text{m}$ ) followed, in parentheses, first by the mean and then by the number of specimens measured for that feature. Common names for fishes follow Froese and Pauly (2012). Fish classification and nomenclature follow Nelson (2006). Nomenclature for Aporocotylidae follows Bullard et al. (2009). Specimens were deposited in the USNPC (holotype and a paratype) and IPCAS (a paratype).

## RESULTS

### *Cardicola langeli* sp. n.

Figs. 1–8

Diagnosis of adult (measurements and illustrations based on 12 whole-mounted adult specimens including the holotype, two paratypes and five sputter-coated specimens): Body flat, ventrally concave, elongate oval in shape, 1260–1720 (1485;  $n = 7$ ) long, 280–400 (328; 7) or 4.1–4.8 $\times$  longer than wide, having anterior and posterior ends equally rounded, lacking posterolateral body protuberance. Body-margin inconsistently crimped ventrally or straight depending on state of contraction when fixed, spined (Figs. 1–3).

Tegumental body spines minute, 2–3 (2; 7) long, approximately 500 nm wide (Figs. 4, 5), near limits of light microscopy but best visualized with 100 $\times$  oil immersion objective or SEM, not associating with pronounced tegumental peduncles or body protuberances, protruding from tegument approximately 700 nm, in transverse rows (Figs. 4, 5). Tegumental spine rows distributing along ventrolateral body surface for entire body length from mouth to extreme posterior body end, distributing in approximately 260–383 (309; 5) rows each spaced 5 (5; 7) apart per side of body or a total of 520–766 (616; 5) rows, approximately 5 (5; 7), 18–25 (22; 5), and 8–13 (10; 6) in breadth in anterior, middle and posterior portions of body, respectively, having 2–4 (4; 7), 8–10 (9; 7), 8–9 (8; 7) spines per row in anterior, middle and posterior portions of body, respectively. Fused or rosethorn-shaped spines lacking.

Nervous system difficult to trace in most specimens, comprising at least a ventrolateral nerve cord plus associ-

ated anterior commissures (Figs. 1–3). Ventrolateral nerve cords paired and extending posteriad in parallel with body margin, showing secondary branches extending laterad and mediad, 10–15 (12; 6) wide near midbody at widest level, appearing widest in anterior region of body in some specimens and narrowing somewhat posteriorly, 43–50 (48; 6) from body margin at midbody, contiguous at body ends, becoming confluent with paired cord in posterior body end (Fig. 1). Dorsolateral nerve cord not clearly evident but trace of its commissure evident at level midway between ventrolateral nerve commissure and anterior body end. Commissure of ventrolateral nerve cord 88–138 (112; 6) or 7–8% (8%; 6) of body length from anterior body end, 38–50 (45; 6) across width of worm, 8–15 (11; 6) in diameter, perpendicular to long axis of body, coursing dorsal to oesophagus. Ventral and dorsal tegumental sensory papillae not evident with SEM.

Anterior sucker spinous, comprising a spheroid structure centring on mouth, 23–28 (25; 6) long, 25–30 (28; 6) wide or 6–10% (9%; 6) of body width, consistently wider than long, directing ventrally (Figs. 1–3). Anterior sucker spines distributing in concentric rows anterior to mouth, each spine <1 long, numbering approximately 80 in posteriormost row at equator of anterior sucker, decreasing in number as diameter of sucker lessens anteriorly. Mouth a minute pore, 3 (3; 7) in diameter, medioventral, 12–14 (13; 4) from anterior end (Figs. 2, 3).

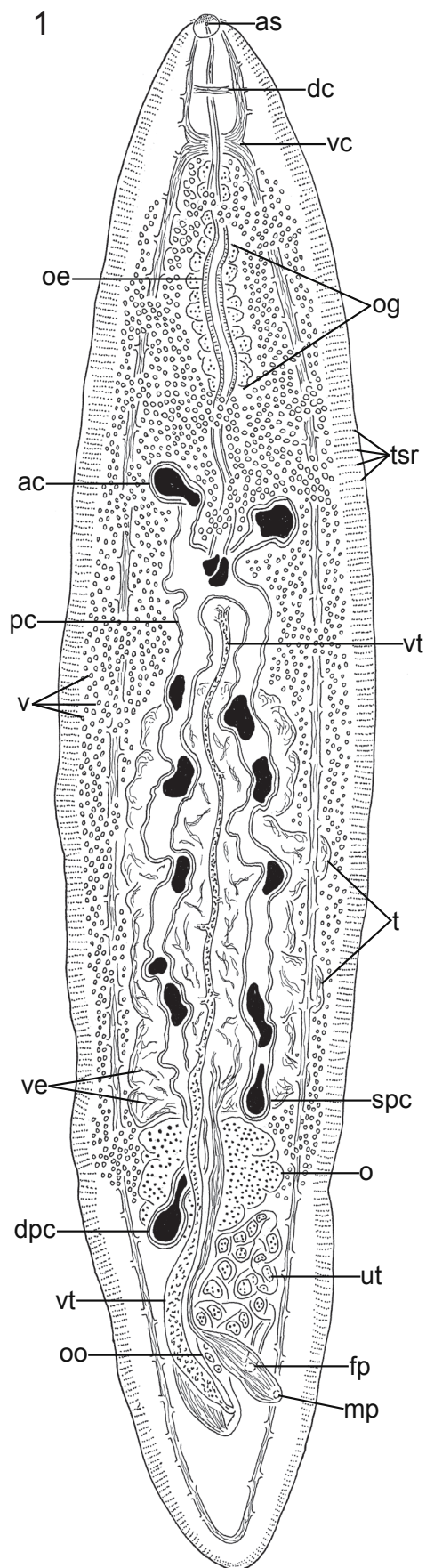
Terminal preoral lobe not evident with light microscopy or SEM. Spines associated with oesophagus or mouth not evident with light microscopy or SEM. Pharynx absent. Oesophagus 415–650 (497; 6) long or 29–38% of body length, 10–25 (20; 7) wide, widest at level midway between nerve commissure and end of oesophagus, slightly sinuous in posterior portion but more or less straight anteriorly, widening slightly posteriorly before connecting with caecal bifurcation anteroventrally; oesophageal wall 3–8 (5; 7) thick or 20–53% (28%; 6) of oesophagus width (Fig. 1). Oesophageal gland extremely diffuse and difficult to distinguish from surrounding parenchyma in stained whole-mounted specimens, appearing to envelop oesophagus in middle portion of oesophagus midway between caecal intersection and ventrolateral nerve commissure, 225–250 (238; 2) long or 41–60% (51%; 2) of oesophagus length, concentrating in area approximately 25–100 (60; 3) wide or 7–25% (17%; 3) of body width, not clearly differentiated into anterior and posterior portions (Fig. 1).

Intestine X- or H-shaped, with paired anterior and posterior caeca intersecting medially (Fig. 1). Intersection of anterior and posterior caeca 415–650 (522; 4) or 32–38% (35%; 4) of body length from anterior end. Anterior caeca equal or not equal in length, 75–138 (93; 6) long or 5–9% (6%; 6) of body length, 16–19% (18%; 6) of oesophagus length, 26–50 (42; 6) wide or 9–18% (13%; 6) of body width, not extending lateral to ventrolateral nerve cord,

smooth, rounded anteriorly, lacking diverticula (Fig. 1). Posterior caeca not extensively convoluted but extending posteriad sinuously, with dextral caecum longer in all specimens studied. Dextral posterior caecum extending beyond posterior margin of ovary, 580–780 (670; 6) long or 43–48% (45%; 6) of body length, 6.4–10.3× (7.8×; 6) length of anterior caeca, 13–25 (17; 5) wide before expanding distally to 25–48 (33; 5) or 1.8–2.3× (2.0×; 5) its width before expanding; sinistral posterior caecum shorter in all specimens, extending to level of posterior margin of testis only, preovarian, 420–610 (488; 6) long or 26–38% (33%; 6) of body length, 5.7–8.1% (7.3%; 6) of dextral posterior caecum length, 5.7–6.3× (6.0×; 4) length of anterior caeca, 20–30 (26; 5) wide before expanding distally to 25–38 (33; 4) or 0.8–1.9× (1.3×; 4) its width before expanding (Fig. 1).

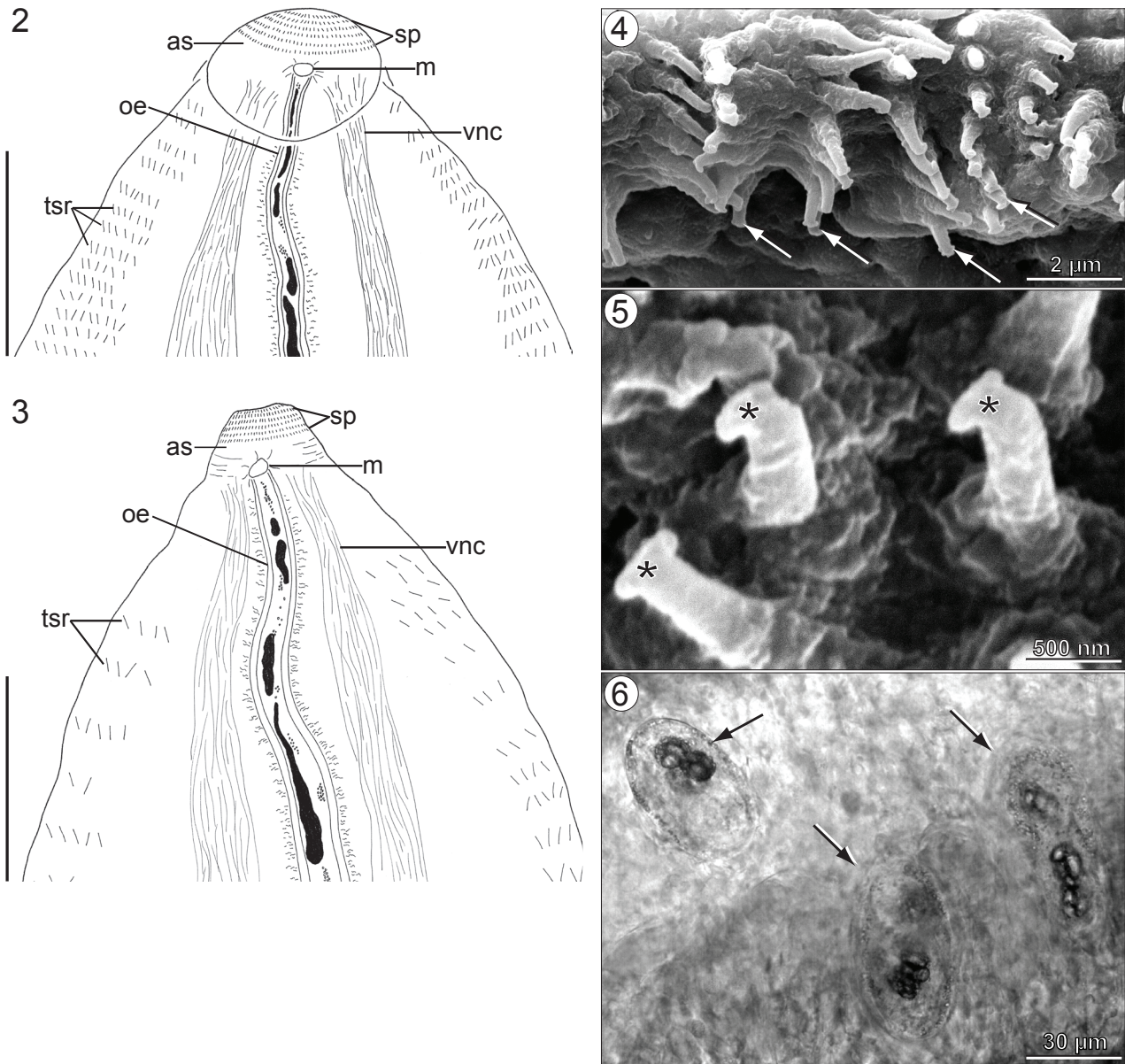
Genitalia mostly delimited laterally by ventrolateral nerve cord (Figs. 1, 7, 8). Testis having irregular margins, poorly staining in most specimens, lateral lobes present in some specimens, 350–550 (440; 6) long or 27–34% (30%; 6) of body length, 150–210 (178; 6) in maximum width or 40–62% (55%; 6) of body width at level of posterior 1/3 of body, 2.2–3.4× (2.5×; 6) wider than long, extending laterad beyond limits of posterior caeca and in some specimens slightly lateral to ventrolateral nerve cord, not extending anteriorad to level of caecal intersection; post-testicular space 370–530 (442; 6) long or 28–32% (30%; 6) of body length, accommodating male and female reproductive tracts.

Vasa efferentia difficult to trace in fixed specimens, an interconnecting meshwork of fine ducts entwining throughout testicular tissue, containing spermatozoa, extending primarily along ventral surface of testis, uniting in posterior region of testis to form vas deferens; vas deferens 175–225 (198; 4) long, 10–25 (16; 3) wide at level of ovary, extending posteriad from posterior margin of testis, passing ventral to and in sinistral portion of ovary, curving mediad and crossing midline before curving and directing sinistrally, extremely thin-walled, containing sperm in all specimens, 8–13 (10; 4) wide before connecting with seminal vesicle (Figs. 7, 8). Seminal vesicle oblong, 50–125 (84; 6) long, 10–30 (16; 6) wide or 4.2–6.8× (5.5×; 6) longer than wide, orienting diagonally posteriad or nearly transverse. Gland surrounding seminal vesicle indistinct. Everted cirrus small, nipple-like, unarmed, ap-



**Fig. 1.** *Cardicola langeli* sp. n. from heart of sheephead, *Archosargus probatocephalus* in the northern Gulf of Mexico (holotype, USNPC No. 106126). **Abbreviations:** ac – anterior caecum; as – sucker; dc – dorsolateral nerve commissure; dpc – dextral posterior caecum; fp – female genital pore; mp – male genital pore; o – ovary; oe – oesophagus; og – oesophageal gland; oo – ootype; pc – posterior caecum; spc – sinistral posterior caecum; t – testis; tsr – transverse spine rows; ut – uterus; v – vitelline follicles; vc – ventrolateral nerve commissure; ve – vasa efferentia; vt – primary vitelline duct. Ventral view. Scale bar = 500  $\mu$ m.





**Figs. 2–6.** *Cardicola langeli* sp. n. from heart of sheephead, *Archosargus probatocephalus*, in the northern Gulf of Mexico. **Fig. 2.** Anterior end of adult specimen showing spines (sp) of anterior sucker (as) arranged in concentric rows anterior to the mouth (m) as well as the anterior portion of the oesophagus (oe), ventrolateral nerve cord (vnc) and transverse spine rows (tsr). Ventral view. Scale bar = 40  $\mu$ m. **Fig. 3.** Anterior end of juvenile specimen showing comparable features as in Fig. 2. Note that the anterior sucker is less spheroid and resembles a proboscis-like structure (cf. penetration organ of the cercaria of *Cardicola forsteri* Cribb, Daintith et Munday, 2000 – see Cribb et al. 2011). Ventral view. Scale bar = 40  $\mu$ m. **Fig. 4.** Tegumental spine rows (arrows). **Fig. 5.** High magnification view of three spines (\*) depicted in Fig. 4. Note that tips of spines appear flattened and broad, rather than sharply pointed. Scanning electron micrographs. **Fig. 6.** Eggs (arrowheads) embedded in epithelium. Light microscopy of wet-mounted live specimens.

proximately 8 long and 5 wide, everting dorsally at level of sinistral ventrolateral nerve cord.

Ovary not strongly dendritic or branched, lacking deep lobes, having small lateral lobes (Figs. 7, 8), 80–163 (118; 6) long or 6–9% (8%; 5) of body length, 150–200 (174; 7) wide or 38–67% (53%; 5) of body width, 1.1–1.9 $\times$  (1.5 $\times$ ; 6) wider than long, medial, occupying space immediately posterior to testis, dorsal to vas deferens, not

extending laterad beyond ventrolateral nerve cords, with posterior margin of ovary being straight across breadth of body or having slightly pointed end extending posterior before connecting with oviduct (Figs. 1, 7, 8). Post-ovarian space 305–390 (337; 6) long or 20–25% (23%; 6) of body length (Fig. 1). Oviduct extending 75–113 (96; 6) directly posteriad from posteromedial margin of ovary, straight (Fig. 7) or slightly convoluted (Fig. 8), 5–8 (6; 6)

wide, connecting with oviducal seminal receptacle well posterior to ovary and at level approximately equal to that of junction of vas deferens and seminal vesicle. Oviducal seminal receptacle comprising distal portion of oviduct, 88–145 (123; 6) long, 23–48 (34; 6) wide or 2.5–6.3× longer than wide, extending posteriorly in parallel with and medial to ventrolateral nerve cord, residing at level of male genital pore, narrowing posteriorly before curving sharply dorsally, giving rise to a short duct that extends anteriorly a short distance before joining with vitelline duct, filled with sperm in all specimens, primarily posterior to level of genitalia and gonads (Figs. 7, 8).

Vitellarium follicular, distributing from level of ventrolateral nerve commissure posteriorly to posterior margin of ovary, symmetrical (lacking dextral or sinistral extensions), extending lateral to ventrolateral nerve cords along length (Fig. 1); secondary collecting ducts indistinct; common collecting duct medial, a sinuous duct extending posteriorly at least from level of caecal intersection before passing ventral to ovary and lateral to oviducal seminal receptacle, extending ventrally along track of oviduct and medial to vas deferens before uniting with oviduct and forming ovovitelline duct (Fig. 1). Ovovitelline duct 23–25 (24; 6) long, 5 (5; 6) wide, extending anteriorly a short distance before connecting with ootype (Figs. 7, 8). Ootype 50–55 (53; 2) long, 20–25 (23; 2) wide, oblong, directing slightly medially, wholly anterior to level of junction of oviduct and vitelline duct, at level of or slightly anterior to male and female genital pores; post-ootype distance 133–198 (162; 5) or 10–13% (11%; 5) of body length (Figs. 7, 8).

Uterus extending anteriorly from ootype, highly convoluted for entire length, comprising ascending and descending portions (Figs. 7, 8). Ascending uterus extending anteriorly in a straight line distance (not including all turns of duct) 138–213 (162; 5) or 9–13% (11%; 6) of body length, 30–48 (34; 4) in maximum width, primarily occupying space between ootype and ovary as well as space immediately lateral to vas deferens, continuing anteriorly and reaching level of distal tip of dextral posterior caecum, post-testicular, primarily postovarian (Figs. 7, 8). Transition from ascending to descending uterus slightly sinistral to posterior margin of ovary or abutting posterior margin of ovary. Descending uterus a convoluted tube connecting with metraterm, 113–138 (125; 2) long or 75–81% (78%; 2) of ascending uterus length, 18–25 (22; 2) in maximum width, connecting with proximal portion of metraterm immediately anterior to, or at level of, oviducal seminal receptacle and ootype (Figs. 7, 8). Metraterm 50–63 (57; 2) long, 36–40 (38; 2) wide, occupying space between ascending uterus and ventrolateral nerve cord, with wall 4–8 (6; 2) thick, directing medially and crisscrossing (dorsal to) with seminal vesicle (Figs. 7, 8). Uterine eggs seemingly amassed in irregularly-shaped clusters 20–25 (23; 3) in diameter, filling uterus lumen (Figs. 7, 8). Female genital pore dorsal, sinistral, postovarian, anteromedial to male

genital pore, dorsal to seminal vesicle (Fig. 7) or slightly lateral to it (Fig. 8), 158–238 (185; 5) or 10–14% (12%; 5) from posterior body end (Figs. 1, 7, 8). Excretory system indistinct in fixed, whole-mounted specimens.

Probable eggs infecting gill epithelium, spheroid (not spindle-shaped as in *Cardicola laruei* Short, 1953 – see McVay et al. 2011), lacking polar extensions, containing ciliated miracidium (Fig. 6).

Type and only host: Sheepshead, *Archosargus probatocephalus* Walbaum, 1792 (Perciformes: Sparidae).

Type locality: Off Horn Island (30°15'18"N; 88°35'28"W), Mississippi, Mississippi Sound, Northern Gulf of Mexico, USA.

Site in host: Lumen of heart.

Prevalence of infection: Twelve of 16 (75%) sheepshead had 1–4 flukes each (mean intensity 1.4).

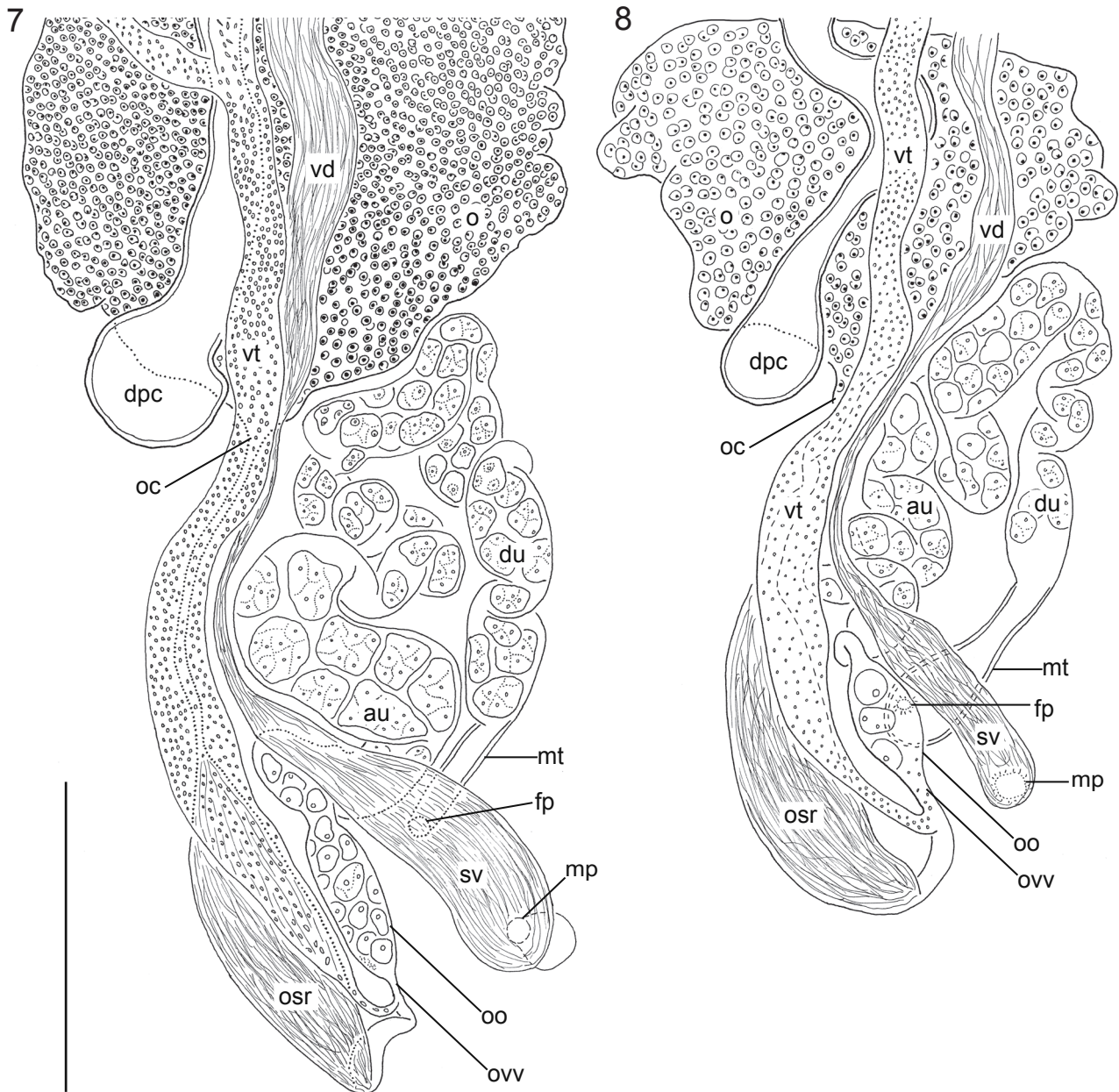
Specimens deposited: Holotype and one paratype in the United States National Parasite Collection (USNPC No. 106126=USNPC holotype, 106127=USNPC paratype); one paratype in the Institute of Parasitology, Academy of Sciences of the Czech Republic, České Budějovice (IPCAS D-692).

Etymology: The specific epithet *langeli* honours my former ichthyology student Christopher Adam Langel (Kaukauna, Wisconsin, USA; 8 April 1986–10 March 2012) for his inspiring ‘beginner’s mind’ about the sea and its biology.

**Remarks.** *Cardicola langeli* sp. n. can be most easily distinguished from its congeners (Table 1) by the combination of having (i) an ovovitelline duct that extends anteriorly (Figs. 1, 7, 8) and that (ii) is posterior to the ootype (Figs. 7, 8), (iii) a male genital pore that is lateral to the oviducal seminal receptacle (Figs. 1, 7, 8) and (iv) a female genital pore that is lateral to the ootype (Figs. 7, 8). All species of *Cardicola* except *C. langeli*; *C. cardiocolum* (Manter, 1947) Short, 1953 (type species); *C. whitteni* Manter, 1954; *C. forsteri* Cribb, Daintith et Munday, 2000; *C. palmeri* Bullard et Overstreet, 2004; *C. aurata* Holzer, Montero, Repullés, Sitjà-Bobadilla, Alvarez-Pellitero, Zarza et Raga, 2008; and *C. opisthorchis* Ogawa, Ishimaru, Shirakashi, Takami et Grabner, 2011 have an ovovitelline duct that is anterior to the ootype and that extends posteriorly, rather than anteriorly, from the junction of the oviduct and vitelline duct.

Among the species of *Cardicola* having an ovovitelline duct in that orientation, only the new species and *C. whitteni* possess a male genital pore that is lateral to the oviducal seminal receptacle. The remaining aforementioned species have a male genital pore that is markedly posterior to the level of the oviducal seminal receptacle. *Cardicola langeli* has a female pore that is dorsolateral to the ootype but that of *C. whitteni* is far anterior to the level of the ootype. The new species somewhat, but not uncannily, resembles *C. cardiocolum* and *C. aurata*, i.e. the other species of *Cardicola* infecting porgies (Sparidae), by having a spheroid anterior sucker with concentric rows of minute spines anterior to the mouth and by having a similar general arrangement of the vitellarium, gonads and genitalia.





**Figs. 7, 8.** *Cardicola langeli* sp. n. from heart of sheephead, *Archosargus probatocephalus*, in the northern Gulf of Mexico. **Fig. 7.** Genitalia (holotype, USNPC No. 106126). **Abbreviations:** au – ascending uterus; dpc – distal posterior caecum; du – descending uterus; fp – female genital pore; mp – male genital pore; mt – metraterm; o – ovary; oc – oviduct connection with ovary; oo – ootype; osr – oviducal seminal receptacle; ovv – ovovitelline duct; sv – seminal vesicle; vd – vas deferens; vt – vitelline duct. Ventral view. Scale bar = 100  $\mu$ m. **Fig. 8.** Genitalia (paratype USNPC No. 106127) showing comparable features as illustrated in Fig. 7. Ventral view at same scale as Fig. 7.

However, the new species is most easily differentiated from *C. cardiocolum* and *C. aurata* at least by having the aforementioned combination of four diagnostic features plus asymmetrical posterior caeca, including a long dextral posterior caecum that extends beyond the posterior margin of the ovary.

The literature holds no example of an aporocotylid having flattened, broad tips of the lateral tegumental spines as were observed in *C. langeli*. Ultrastructure study can

be timely, expensive and logistically prohibitive, so this feature is likely not altogether practical for the taxonomy of aporocotylids, and certainly it is probable that other described aporocotylid species have unique spines that simply have not been described in adequate detail. However, these spines, being minute and at the limit of resolution for light microscopy, do not appear different from those of other aporocotylids having tegumental spines with distally recurved, sharply pointed tips unless viewed with SEM.

## DISCUSSION

The presence/absence of, and morphological features related to, the sucker associated with the mouth of aporocotyliids is probably best informed by the study of conspecific cercaria, juveniles and adults, but this is seldom possible and most species are described from adults only. This has been discussed fairly extensively (Bullard and Overstreet 2003, Nolan and Cribb 2006, Bullard et al. 2008, 2012, Bullard 2010a, b, 2012, McVay et al. 2011) and it is thought that juveniles or small adults of a given species can have a sucker whereas larger adults can lack that sucker. For example, McVay et al. (2011) showed that the holotype of *C. laruei* lacks an evident sucker but that newly-collected materials comprising smaller adult specimens had a spinous anterior sucker with concentric rows of spines anterior to the mouth. The same seems true for small and large adult specimens of *Cardicola parvus* Bullard, Baker et de Buron, 2012 (Bullard, personal observations). Regarding observations of the sucker in cercaria of *Cardicola* spp., the only cercaria that has been illustrated is that of *C. forsteri*.

Cribb et al. (2011) treated this type of sucker (oral sucker) as a specialized penetration organ, and that structure strongly resembles the thimble-shaped, spinous sucker (Fig. 3) we observed in a specimen of *C. langeli* that measured 1 260 µm in length and 280 µm in width. In adult specimens of *C. langeli* the sucker apparently becomes spheroid, directed ventrally and with posterior constrictions where it connects with the body (Fig. 2). Conversely, despite being present in the cercaria of *C. forsteri*, the sucker is absent in the adult of *C. forsteri* (see Cribb et al. 2000) and in the adults of at least a few other species of *Cardicola*, e.g. *C. currani* and *C. nonamo* Bullard, 2010 (see Bullard and Overstreet 2004, Bullard 2010a). These results together reinforce the notion that adults of some species of *Cardicola* 'lose' the sucker and that in others it may be retained but paedomorphic and homologous to the penetration organ.

Egg morphology might be underutilized as a means of differentiating species of *Cardicola* and aporocotyliid genera. The egg for the vast majority of aporocotyliid species has not been described, but that for several members of *Cardicola* has been well-documented from both wild and aquacultured fishes wherein intense infections of eggs in the gill can be associated with disease (see Bullard and Overstreet 2002, 2004, 2008, Braicovich et al. 2006, Holzer et al. 2008, Ogawa et al. 2010, McVay et al. 2011). Shirakashi et al. (2012) used ITS2 sequence data to ascribe 'crescent' eggs infecting the afferent filament artery and 'oval' eggs infecting the gill lamellae of Pacific bluefin tuna (*Thunnus orientalis*) to *Cardicola opisthorchis* and *Cardicola orientalis*, respectively.

Eggs presumed to be *C. laruei* from the gill of seatrouts (*Cynoscion* spp.) are spindle-shaped (McVay et al. 2011), even before a fully-developed, ciliated miracidium is evident within the egg. In contrast, *C. langeli*, *C. currani*,

*C. aurata* and *C. ambrosioi* reportedly each have an oval egg. The egg of no other species of *Cardicola* has been described to date, but future species descriptions that include details of the fully-developed egg could help elucidate if egg shape is principally the result of fluke ancestry or the site of infection in the host. Such details could also contribute to a revised generic diagnosis for *Cardicola*. Noteworthy in this regard, however, is that no data are available on the shape of the egg of *C. cardiocolum* (type species). It should also be noted that aporocotyliid eggs undergo considerable *ex-utero* development and that morphologically dissimilar eggs may represent conspecific, different-aged eggs. Hence, eggs that contain fully-developed, ciliated miracidia should be used for interspecific comparisons whenever possible.

The present study brings the total number of species assigned to *Cardicola* to 25 (Table 1). The genus presently accommodates flukes that mature in the blood vascular system (none reported from body cavity) of 'higher bony fishes' (subdivision Euteleostei) (see Johnson and Patterson 1996, Nelson 2006). Among euteleosteans, *Cardicola* spp. infect mullets (Mugiliformes: Mugilidae) plus ten host families of Perciformes and thus, remarkably, no record of any nominal, accepted species of *Cardicola* exists from any fish species assigned to the remaining 26 euteleostean orders. Of course, other blood fluke genera include species that infect those orders, but whether or not '*Cardicola*' is a group containing perciform blood flukes plus a few atypical species that infect euryhaline fishes is not convincing. A few species, i.e. *C. mugilis* Yamaguti, 1970, *C. brasiliensis* Knoff et Amato, 1992, *C. currani* Bullard et Overstreet, 2004, *C. palmeri* and *C. parvus*, mature in euryhaline mugilids and drums (Sciaenidae), show strong associations with estuaries and may presumptively include freshwater-origin or brackish-water intermediate hosts. However, the vast majority of species assigned to *Cardicola* infect obligate, stenohaline marine euteleosteans. The life cycle of only *C. forsteri* has been determined with molecular markers (Cribb et al. 2011).

A total of 14 fish blood flukes currently assigned to nine genera are known to range in the Gulf of Mexico (Table 1; Linton 1910, McIntosh 1934, Short 1954, Bullard and Overstreet 2003, 2006, Bullard et al. 2006, Bullard and Jensen 2008, Bullard 2010b, 2012): *Deontacylix ovalis* Linton, 1910, *Paradeontacylix sanguinicoloides* McIntosh, 1934, *C. cardiocolum*, *C. laruei*, *C. palmeri*, *C. currani*, *C. langeli*, *Elaphrobates euzeti* Bullard et Overstreet, 2003, *Psettarium anthicum* Bullard et Overstreet, 2006, *Selachohemecus olsoni* Short, 1954, *Selachohemecus benzi* Bullard, Overstreet et Carlson, 2006, *Myliobaticola richardheardi* Bullard et Jensen, 2008, *Littorellicola billhawkinsi* Bullard, 2010 and *Pearsonellum lemusi* Bullard, 2012. The diversity of host lineages exploited by these flukes as well as the genus-level and species-level diversity of aporocotyliids seemingly indicates that Gulf of Mexico fish blood flukes remain worthy of exploration

**Table 1.** Records of adult infections of accepted nominal species of *Cardicola* Short, 1953<sup>1</sup> in chronological order of species descriptions.

	Host	Site(s)	Locality	Reference(s)
<b><i>Cardicola cardiocolum</i></b> (Manter, 1947) Short, 1953 (type species) (as <i>Psettarium</i> )	<i>Calamus bajonado</i> (Bloch et Schneider) (Perciformes: Sparidae), jolthead porgy (type host)	heart	Gulf of Mexico, off Tortugas, Florida, USA (type locality)	Manter (1947), Short (1953)
<b><i>Cardicola laruei</i></b> Short, 1953	<i>Cynoscion arenarius</i> Ginsburg (Perciformes: Sciaenidae), sand seatrout (type host)	heart	Northern Gulf of Mexico, off Franklin and Wakulla Counties, Florida, USA (type locality)	Short (1952, 1953)
			Eastern Gulf of Mexico, Tampa Bay, Florida, USA	McVay et al. (2011)
	<i>Cynoscion nebulosus</i> (Cuvier) (Perciformes: Sciaenidae), spotted seatrout	‘washings of gut’ heart	Northern Gulf of Mexico, off Franklin and Wakulla Counties, Florida, USA Eastern Gulf of Mexico, Tampa Bay, Florida, USA	Short (1953) McVay et al. (2011)
		heart	Northwestern Atlantic Ocean, St. John’s River Estuary, Florida, USA	McVay et al. (2011)
<b><i>Cardicola coriododacis</i></b> Manter, 1954	<i>Odax pullus</i> (Forster) (Perciformes: Odacidae), greenbone (type host) (as <i>Coriododax pullus</i> )	gill <sup>2</sup>	Southwest Pacific Ocean, off Wellington, New Zealand (type locality)	Manter (1954)
<b><i>Cardicola whitteni</i></b> Manter, 1954	<i>Nemadactylus macropterus</i> (Forster) (Perciformes: Cheilodactylidae), tarakihi (type host) (as <i>Dactylopagrus macropterus</i> )	gill <sup>2</sup>	Southwest Pacific Ocean, off Wellington, New Zealand (type locality)	Manter (1954)
<b><i>Cardicola chaetodontis</i></b> Yamaguti, 1970	<i>Chaetodon miliaris</i> Quoy et Gaimard (Perciformes: Chaetodontidae), millet butterflyfish (type host)	gill, heart	Central Pacific Ocean, off Hawaii, USA (type locality)	Yamaguti (1970)
	<i>Chaetodon aureofasciatus</i> Macleay, golden butterflyfish	blood <sup>3</sup>	Southwestern Pacific Ocean, Lizard Island, Australia	Nolan and Cribb (2006)
	<i>Chaetodon citrinellus</i> Cuvier, speckled butterflyfish	blood <sup>3</sup>	Southwestern Pacific Ocean, Moorea, French Polynesia	Nolan and Cribb (2006)
	<i>Chaetodon flavirostris</i> Günther, black butterflyfish	blood <sup>3</sup>	Southwestern Pacific Ocean, Heron Island, Australia	Nolan and Cribb (2006)
	<i>Chaetodon lineolatus</i> Cuvier, lined butterflyfish	blood <sup>3</sup>	Southwestern Pacific Ocean, New Caledonia	Nolan and Cribb (2006)
	<i>Chaetodon reticulatus</i> Cuvier, mailed butterflyfish	blood <sup>3</sup>	Southwestern Pacific Ocean, Moorea, French Polynesia	Nolan and Cribb (2006)
	<i>Chaetodon ulietensis</i> Cuvier, Pacific double-saddle butterflyfish	blood <sup>3</sup>	Southwestern Pacific Ocean, Heron Island, Australia	Nolan and Cribb (2006)
	<i>Chaetodon unimaculatus</i> Bloch, teardrop butterflyfish	blood <sup>3</sup>	Southwestern Pacific Ocean, Palau	Nolan and Cribb (2006)
			blood <sup>3</sup>	Southwestern Pacific Ocean, Heron Island, Australia
<b><i>Cardicola mugilis</i></b> Yamaguti, 1970	<i>Mugil cephalus</i> Linnaeus (Mugiliformes: Mugilidae), flathead mullet (type host)	heart, blood vessels	Central Pacific Ocean, off Hawaii, USA (type locality)	Yamaguti (1970)
<b><i>Cardicola brasiliensis</i></b> Knoff et Amato, 1992	<i>Mugil platanus</i> Günther Brazil mullet (type host)	heart, kidney, liver, gill	Southwestern Atlantic Ocean, off Rio de Janeiro, Brazil (type locality)	Knoff and Amato (1992)
<b><i>Cardicola forsteri</i></b> Cribb, Daintith et Munday, 2000	<i>Thunnus maccoyii</i> (Castelnau) (Perciformes: Scombridae), southern bluefin tuna (type host)	heart	Southwestern Pacific Ocean, off Rabbit Island (type locality) and Louth Island, South Australia	Cribb et al. (2000), see also Aiken et al. (2007)
		heart	Northwestern Atlantic Ocean, off Cape Lookout, North Carolina, USA	Bullard et al. (2004)
	<i>Thunnus thynnus</i> (Linnaeus), northern bluefin tuna	heart	Mediterranean Sea, Puerto de Mazarron, Spain	Aiken et al. (2007)
		heart, kidney, gill <sup>4</sup>	Adriatic Sea, Island of Brač, Croatia	Mladineo and Tudor (2004)
<b><i>Cardicola palmeri</i></b> Bullard et Overstreet, 2004	<i>Pogonias cromis</i> (Linnaeus) (Perciformes: Sciaenidae), black drum	heart	Northern Gulf of Mexico, Mississippi Sound, USA (type locality)	Bullard and Overstreet (2004)
<b><i>Cardicola currani</i></b> Bullard et Overstreet, 2004	<i>Sciaenops ocellatus</i> Linnaeus) (Perciformes: Sciaenidae), red drum	heart	Northern Gulf of Mexico, Mississippi Sound, USA (type locality)	Bullard and Overstreet (2004), see also Overstreet (1983)
<b><i>Cardicola coeptus</i></b> Nolan et Cribb, 2006	<i>Siganus punctatus</i> (Schneider et Forster) (Perciformes: Siganidae), gold-spotted spinefoot (type host)	heart, gill	Southwestern Pacific Ocean, Heron Island, Australia (type locality)	Nolan and Cribb (2006)
	<i>Siganus vulpinus</i> (Schlegel et Müller), foxface	heart, gill	Southwestern Pacific Ocean, Heron Island, Australia	Nolan and Cribb (2006)
<b><i>Cardicola covacinae</i></b> Nolan et Cribb, 2006	<i>Siganus punctatus</i> (type host)	heart	Southwestern Pacific Ocean, Heron Island, Australia (type locality)	Nolan and Cribb (2006)
<b><i>Cardicola bartolii</i></b> Nolan et Cribb, 2006	<i>Siganus lineatus</i> (Valenciennes), golden-lined spinefoot (type host)	heart, gill	Southwestern Pacific Ocean, Heron Island, Australia (type locality)	Nolan and Cribb (2006)
	<i>Siganus corallinus</i> (Valenciennes), blue-spotted spinefoot	heart, gill	Southwestern Pacific Ocean, Heron Island, Australia	Nolan and Cribb (2006)

(continued)



Table 1. Continued.

	Host	Site(s)	Locality	Reference(s)
<i>Cardicola watsonensis</i> Nolan et Cribb, 2006	<i>Siganus corallinus</i> (type host)	heart	Southwestern Pacific Ocean, Lizard Island, Australia (type locality)	Nolan and Cribb (2006)
<i>Cardicola lafii</i> Nolan et Cribb, 2006	<i>Siganus fuscescens</i> (Houttuyn), mottled spinefoot (type host)	heart	Southwestern Pacific Ocean, Lizard Island, Australia (type locality)	Nolan and Cribb (2006)
<i>Cardicola milleri</i> Nolan et Cribb, 2006	<i>Lutjanus bohar</i> (Forsskål) (Perciformes: Lutjanidae), two-spot red snapper (type host)	heart	Southwestern Pacific Ocean, Lizard Island, Australia (type locality)	Nolan and Cribb (2006)
<i>Cardicola parilus</i> Nolan et Cribb, 2006	<i>Siganus fuscescens</i> (type host)	heart	Indian Ocean, Ningaloo Reef off Western Australia (type locality)	Nolan and Cribb (2006)
<i>Cardicola tantabiddii</i> Nolan et Cribb, 2006	<i>Siganus fuscescens</i> (type host)	heart	Indian Ocean, Ningaloo Reef off Western Australia (type locality)	Nolan and Cribb (2006)
<i>Cardicola ambrosioi</i> Braicovich, Etchegoin, Timi et Sardella, 2006	<i>Percophis brasiliensis</i> Quoy et Gaimard (Perciformes: Percophidae), Brazilian flathead (type host)	liver, gill	Southwestern Atlantic Ocean, off Mar del Plata, Argentina (type locality)	Braicovich et al. (2006)
<i>Cardicola aurata</i> Holzer, Montero, Repullés, Sitjà-Bobadilla, Alvarez-Pellitero, Zarza et Raga, 2008	<i>Sparus aurata</i> Linnaeus (Perciformes: Sparidae), gilthead seabream (type host)	gill	Mediterranean Sea, off Valencia, Spain (type locality)	Holzer et al. (2008)
<i>Cardicola orientalis</i> Ogawa, Tanaka, Sugi-hara et Takami, 2010	<i>Thunnus orientalis</i> (Temminck et Schlegel) (Perciformes: Scombridae), Pacific bluefin tuna (type host)	gill	Western Pacific Ocean, off Japan (type locality)	Ogawa et al. (2010)
<i>Cardicola nonamo</i> Bullard, 2010	<i>Phanerodon furcatus</i> Girard (Perciformes: Embiotocidae), white seaperch (type host)	heart	Eastern Pacific Ocean, Monterey Bay, California, USA (type locality)	Bullard (2010a)
	<i>Rhacochilus toxotes</i> Agassiz (Embiotocidae), rubberlip seaperch	gill	Eastern Pacific Ocean, Naples Reef, California, USA	Bullard (2010a)
<i>Cardicola opisthorchis</i> Ogawa, Ishimaru, Shirakashi, Takami et Grabner, 2011	<i>Thunnus orientalis</i> (type host)	heart	Western Pacific Ocean, off Japan (type locality)	Ogawa et al. (2011)
<i>Cardicola parvus</i> Bullard, Baker et de Buron, 2012	<i>Micropogonias undulatus</i> (Linnaeus) (Perciformes: Sciaenidae), Atlantic croaker (type host)	heart	Northwestern Atlantic Ocean, South Atlantic Bight (type locality)	Bullard et al. (2012)
<i>Cardicola langeli</i> n. sp.	<i>Archosargus probatocephalus</i> (Perciformes: Sparidae), sheepshead (type host)	heart	Northern Gulf of Mexico, off Horn Island, USA (type locality)	present study

<sup>1</sup>Bullard (2010a) treated *Cardicola congruenta* Lebedev et Mamaev, 1968, *Cardicola grandis* Lebedev et Mamaev, 1968 (see Lebedev and Mamaev 1968, Bullard and Overstreet 2006), *Cardicola ahi* Yamaguti, 1970 (see Yamaguti 1970) and *Cardicola kurochkini* (Parukhin, 1976) Bullard et Overstreet, 2006 (see Parukhin 1976) as *species incertae sedis*. <sup>2</sup>Manter (1954) specified “gills and coelom probably from blood vessels”. <sup>3</sup>Nolan and Cribb (2006) reported heart, gill, and blood vessels of intestine. <sup>4</sup>Eggs only, not adults.

and taxonomic discovery. For example, new aporocotylid species continue to be collected from commonly-occurring and easily-captured fishes in the Gulf of Mexico, e.g. *C. langeli* from sheepshead.

Although fish blood fluke genera seemingly include species that infect particular orders or related orders of definitive hosts, within a fish family congeneric aporocotylids, including *Cardicola* spp., do not seemingly show obvious morphological similarities. For example, the new species (*C. langeli*), *C. cardiocolum* and *C. aurata* all infect porgies (Sparidae) (Table 1); however, none is remarkably similar to another. Although in an unusual site of infection, *Skoulekia meningialis* Alama-Bermejo, Montero, Raga et Holzer, 2011 also infects a sparid and clearly does not belong within *Cardicola*: it has a posterolateral body protuberance (absent in *Cardicola* spp.) and a uterus that is lateral to the ovary and extends anterior to it (uterus is postovarian in *Cardicola* spp.) (Alma-Bermejo et al. 2011). Likewise, even congeneric, sympatric blood flukes that infect confamilial fishes are not obviously morphologically similar. For example, *C. palmeri* and *C. currani* infect sciaenids of Mississippi Sound (Bullard and Overstreet 2004) but, relative to other spe-

cies of *Cardicola*, these flukes are not morphologically similar: *C. palmeri* has an ovoid body outline, anterior and posterior caeca that are sinuous and approximately equal in length, a large, transverse, seminal vesicle and large cirrus. In contrast, *C. currani* has an elongate body, long posterior caeca, short anterior caeca, a small seminal vesicle and tiny cirrus. *Cardicola* spp. that infect tunas (*Thunnus* spp.: Scombridae) provide another example (Cribb et al. 2000, Ogawa et al. 2010, 2011). Collectively, this morphological diversity is interesting regarding the natural history of aporocotylids, especially within *Cardicola*, since it may indicate a rapid rate of speciation within biodiverse vertebrate groups like Perciformes.

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