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Heteronchoineans (Monogenoidea) from the Gills of Crevalle Jack, *Caranx hippos* (Perciformes, Carangidae), from Everglades National Park, Florida, with a Redescription of *Protomicrocotyle mirabilis* (Gastrocotylinea, Protomicrocotylidae)

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abstract: Examination of the gills of 10 crevalle jack, *Caranx hippos* (Linnaeus) (Carangidae), from the northeastern portion of Florida Bay, Everglades National Park, Florida revealed 3 species of Heteronchoinea (Monogenoidea): *Protomicrocotyle mirabilis* (MacCallum, 1918) Johnston & Tiegs, 1922 (Gastrocotylinea, Protomicrocotylidae) (prevalence = 80%; intensity = 2–16 parasites/host; mean intensity = 7 parasites/host); *Allopyragraphorus hippos* (Hargis, 1956) Yamaguti, 1963 (Microcotylinea, Allopyragraphoridae) (80%; 1–8; 3.5); and *Cemocotyle noveboracensis* Price, 1962 (Microcotylinea, Cemocotylidae) (80%; 1–100; 35.3). Two crevalle jack (standard length 139–140 mm) were uninfected; 3 (standard length 154–183 mm) had mean intensities (all parasite species) of 14.3 (intensity = 5–20) parasites per host; 5 larger hosts (standard length = 312–395 mm) were more heavily infected with the 3 parasite species (mean intensity = 63.8 [intensity = 16–109] parasites per host). *Protomicrocotyle mirabilis* is redescribed and figured; *A. hippos* is considered a valid species and distinct from *Allopyragraphorus incomparabilis* (MacCallum, 1917) Yamaguti, 1963 (previously considered synonyms); and *C. noveboracensis* is distinguished from congenerics in part by lacking a haptoral lappet.

key words: Monogenoidea, Heteronchoinea, Protomicrocotylidae, Allopyragraphoridae, Cemocotylidae, *Protomicrocotyle mirabilis*, *Allopyragraphorus hippos*, *Cemocotyle noveboracensis*, Carangidae, *Caranx hippos*, crevalle jack, Everglades National Park, Florida.

This paper, the third in a series reporting the results of surveys of the monogenoidean fauna of Florida's marine fishes, includes the findings from examinations of the gills of 10 crevalle jack, *Caranx hippos* (Linnaeus) (Carangidae), from Florida Bay, Everglades National Park. *Rhabdosynochus rhabdosynochus* Mizelle & Blatz, 1941; *Rhabdosynochus hargisi* Kritsky, Boeger & Robaldo, 2001; and *Rhabdosynochus hudsoni* Kritsky, Boeger & Robaldo, 2001 (all Diplectanidae) had been recorded from the gills of common snook, *Centropomus undecimalis* (Bloch); the fat snook, *Centropomus parallelus* Poey; and the tarpon snook, *Centropomus pectinatus* Poey (all Centropomidae), from 9 localities in Florida (Kritsky et al., 2010). Finally, *Microcotyle archosargi* MacCallum, 1913 (Microcotylidae); *Neobenedenia* sp. (Capsalidae); *Euryhaliotrema carbunculariu*m Kritsky & Bakenhaster, 2011; *Euryhaliotrema dunlapae* Kritsky & Bakenhaster, 2011; *Euryhaliotrema amydrum* Kritsky & Bakenhaster, 2011; and *Euryhaliotrema spirulum* Kritsky & Bakenhaster, 2011 (all Dactylogyridae) were recorded or described from the sheepshead, *Archosargus probatocephalus* (Walbaum) (Sparidae), from Indian River Lagoon in Florida (Kritsky & Bakenhaster, 2011).

Caranx hippos is a subtropical species found in neritic waters of the continental shelves of the Atlantic Ocean from about 45°N to 33°S. In the western Atlantic, the fish has been recorded from Nova Scotia in the north to Uruguay in the south (Froese and Pauly, 2010). Twenty species of Monogenoidea and one unidentified species of *Axine** (Axinidae) have been reported from crevalle jack: *Ahpua piscicola* Caballero y C. & Bravo-Hollis, 1973 (Chauhaneidae); *Allopyragraphorus caballeroi** (Zerecero y D., 1960) Yamaguti, 1963 (Allopyragraphoridae); *Allopyragraphorus hippos* (Hargis, 1956) Yamaguti, 1963 (Allopyragraphoridae); *Allopyragraphorus incomparabilis* (MacCallum, 1917) Yamaguti, 1963 (Allopyragraphoridae); *Allopyragraphorus winteri* (Caballero y C. & Bravo-Hollis, 1965) Bravo-Hollis & Salgado-Maldonado, 1983 (Allopyragraphoridae); *Cemocotyle noveboracensis* Price, 1962 (Cemocotylidae); *Cemocotylella elongata* (Meserve, 1938) Price, 1962 (Cemocotylidae); *Dionchus remorae* (MacCallum, 1916) Price, 1938 (Dionchidae); *Neomicrocotyle indica** Ramalingam, 1960

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(Protomicrocotylidae); *Neomicrocotyle pacifica** (Meserve, 1938) Ramalingam, 1960 (Protomicrocotylidae); *Neomicrocotyle unnithani** Yamaguti, 1968 (= *Abortipedia indica* Unnithan, 1962) (Protomicrocotylidae); *Protomicrocotyle ivoriensis* Wahl, 1972 (Protomicrocotylidae); *Protomicrocotyle manteri* Bravo-Hollis, 1967 (Protomicrocotylidae); *Protomicrocotyle mirabilis* (MacCallum, 1918) Johnston & Tiegs, 1922 (Protomicrocotylidae); *Protomicrocotyle nayaritensis** Bravo-Hollis, 1979 (Protomicrocotylidae); *Pseudomazocraes monsivaisae** Caballero y C. & Bravo Hollis, 1955 (Discocotylidae); *Pseudomazocraes riojai** (Caballero C. & Bravo Hollis, 1963) Lebedev, 1970 (Discocotylidae); *Pseudomazocraes selene* Hargis, 1957 (Discocotylidae); *Salinocotyle mexicana** (Caballero C. & Bravo Hollis, 1963) Lebedev, 1984 (Chauhaneidae); and *Zeuxapta seriolae** (Meserve, 1938) Price, 1962 (Heteraxinidae) (see Price, 1938; Koratha, 1955; Unnithan, 1962; Wahl, 1972; Radha, 1975; Lamothe-Argumedo et al., 1997; Pérez-Ponce de León et al., 1999; Luque et al., 2000). Species identified above by an asterisk have been reported only from the Pacific coastal waters off North America or the Pacific Ocean. Although *Caranx hippos* has been listed in the literature as host for these species, their hosts are probably the Pacific crevalle jack, *Caranx caninus* Günther (an eastern Pacific species and possible synonym of *C. hippos* [see Froese & Pauly, 2010]) or other species of *Caranx* occurring in the Indo-Pacific Ocean.

MATERIALS AND METHODS

During 6–10 June 2009, 10 crevalle jack were collected with a 183-m bag seine from the northeastern part of Florida Bay, Everglades National Park by personnel of the Florida Fish and Wildlife Conservation Commission—Fish and Wildlife Research Institute (FWC-FWRI). After capture, fish were iced and transported to the laboratory at the Everglades National Park's Florida Bay Ranger Station and Science Center in Key Largo, Florida, where the gills were excised, doused in hot water (65–70°C), fixed in 5% phosphate-buffered formalin, and subsequently shipped to Idaho State University for study. Helminths were then removed from the gills or sediment with a fine probe and dissecting microscope, identified, and counted. Some specimens were mounted unstained in Gray and Wess medium (Humason, 1979) for study of haptoral and copulatory structures. Other specimens were stained with Gomori's trichrome (Humason, 1979) or Vancleave's hematoxylin (Bullard et al., 2004) and mounted in Canada balsam for observation of soft internal features. Measurements, in micrometers, represented the greatest straight-line distances between extreme points and were presented as the average followed by the range and number (n) of specimens measured in parentheses; body length included the haptor. Terminology of clamp sclerites was that of Boeger and Kritsky (1993), and definitions of ecological terms were those of Bush et al. (1997). Voucher specimens of helminths collected for this study and a designated neotype of *Allopyragraphorus hippos* were deposited in the United States National Parasite Collection, Beltsville, Maryland, U.S.A. (USNPC); voucher specimens of each species were also placed in the FWC-FWRI Invertebrate Specimen Collection, St. Petersburg, Florida (FSBC-I). For comparative purposes, type and voucher specimens available in the USNPC were examined as indicated in the respective species accounts.

RESULTS

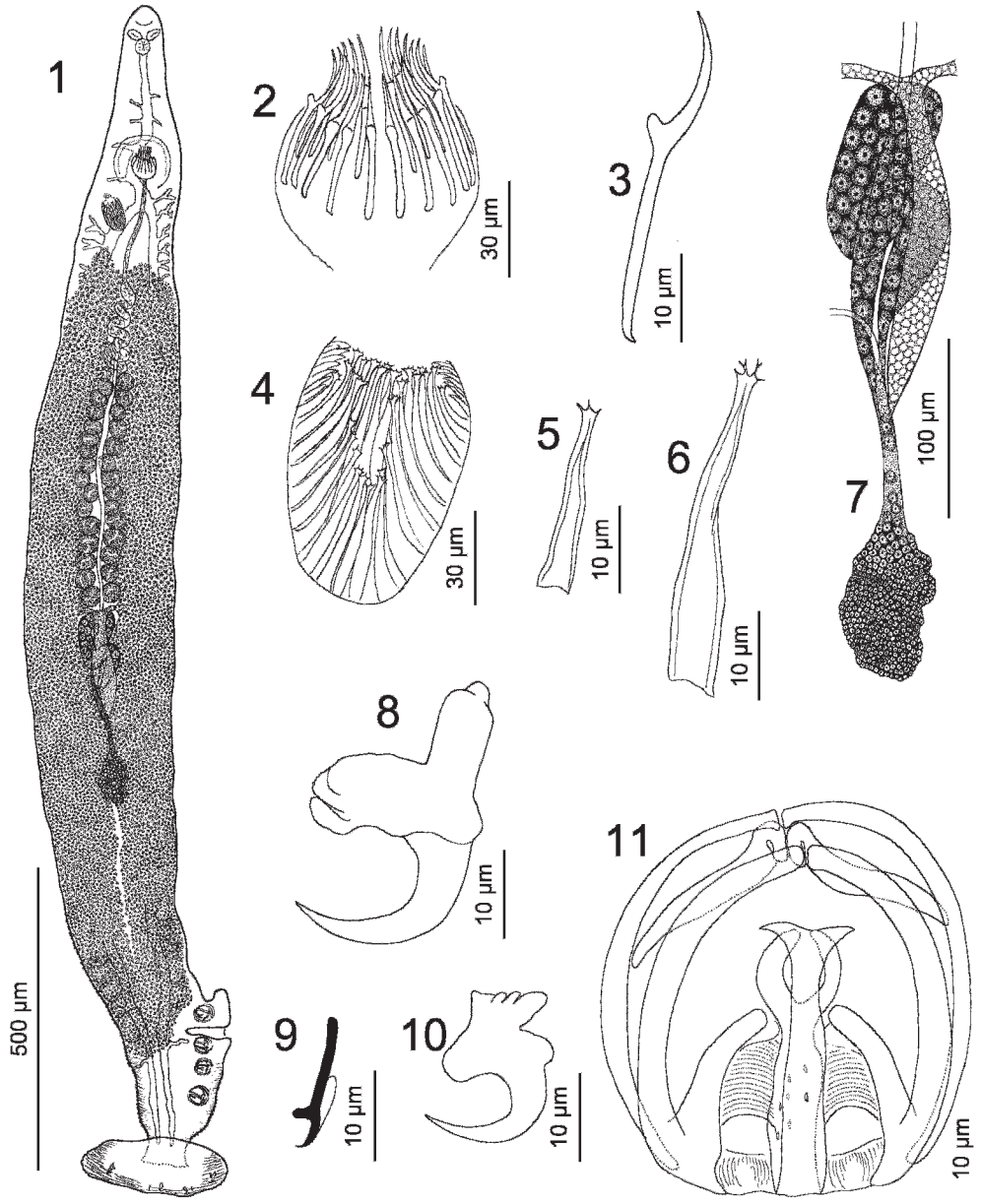
Eight of 10 crevalle jack examined for gill parasites were positive for 3 heteronchoinean species: *P. mirabilis* (Gastrocotylinea, Protomicrocotylidae), *A. hippos* (Microcotylinea, Allopyragraphoridae), and *Cemocotyle noveboracensis* (Microcotylinea, Cemocotylidae). The 2 smallest hosts (standard length [SL] = 139 and 140 mm) were not infected; 3 crevalle jack with SL = 154–183 mm were positive for the 3 helminth species (mean intensity 14.3 [range = 5–20] parasites per host); 5 larger hosts (SL = 312–395 mm) were more heavily infected (mean intensity = 63.8; range = 16–109). An account of each parasite species follows.

Class Monogenoidea Bychowsky, 1937
Subclass Heteronchoinea Boeger & Kritsky, 2001
Infrasubclass Oligonchoinea Bychowsky, 1937
Order Mazocraeidea Bychowsky, 1937
Suborder Gastrocotylinea Lebedev, 1972
Protomicrocotylidae Johnston & Tiegs, 1922
Protomicrocotyle mirabilis (MacCallum, 1918) Johnston & Tiegs, 1922
Figs. 1–11

Synonyms *Acanthodiscus mirabile* MacCallum, 1918; *Acanthodiscus mirabilis* MacCallum, 1918 (in Yamaguti, 1963); *Protomicrocotyle mirabile* (MacCallum, 1918) Johnston & Tiegs, 1922 (in Manter, 1954).

Redescription

Body 2,240 (1,470–3,080; n = 11) long, 322 (214–449; n = 15) wide at level of germarium; body proper elongate, fusiform (Fig. 1). Tegument with annular ridges from haptor to level of germarium on posterior trunk. Prohaptoral suckers 36 (29–48; n = 15) long, 55 (36–71; n = 15) wide, muscular, elongate ovate, aseptate, lying diagonally in posterolateral wall of buccal cavity. Haptor asymmetrical,



Figures 1–11. *Protomicrocotyle mirabilis* (MacCallum, 1918). **1.** Whole mount (ventral view, composite). **2.** Male copulatory organ. **3.** Spine of male copulatory organ. **4.** Vaginal vestibule. **5.** Ventral spine of vaginal vestibule. **6.** Dorsal spine of vaginal vestibule. **7.** Female reproductive system (ventral, composite). **8.** Lateral anchor. **9.** Hook. **10.** Medial anchor. **11.** Clamp (ventral view).

with 4 unilateral (dextral or sinistral) sessile clamps and large terminal lappet originating from distal haptoral constriction; transverse ventral depression present between anterior-most and adjacent posterior clamp. Clamps ventral in haptor; each 57 (49–67; $n = 7$) long, 49 (43–55; $n = 7$) wide, composed of medial sclerite and paired anterolateral, posterolateral, and accessory sclerites; medial sclerite bent as a U, with large gun-sightlike dorsal end and flared ventral end forming 2 bilateral spines; anterolateral sclerite sickle shaped, with footlike base, truncate distal end; posterolateral sclerite a simple curved rod with

truncate distal end; accessory sclerite a sigmoid rod with folded medial end (Fig. 11). Haptoral lappet transversely elongate ovate, 458 (283–691; $n = 12$) long, armed with 3 pairs of ventral sclerites (1 pair of hooks; 2 pairs of anchors): lateral anchor 33 (29–37; $n = 6$) long, usually with elongate deep root, perpendicular superficial root with keyhole tip, stout and short shaft, recurved point extending to near level of tip of superficial root (Fig. 8); medial anchor 21 (19–22; $n = 3$) long, with broadly flattened deep root, small knoblike superficial root, short shaft, recurved point extending slightly past level of tip of superficial root (Fig. 10); hook 18 (16–19; $n = 5$) long, lying between lateral and medial anchors but nearer medial anchor, with elongate deep root, perpendicular superficial root, straight shaft, short point (Fig. 9).

Mouth subterminal, ventral. Pharynx 47 (39–57; $n = 15$) wide, subovate, muscular, lying medial and immediately posterior to prohaptoral suckers. Esophagus elongate, with lateral diverticula, looped dextrally around genital atrium, bifurcating to 2 intestinal ceca slightly posterior to genital atrium; intestinal cecum in each lateral field of body proper, extending into haptor as 2 blind sacs; lateral intestinal diverticula numerous, usually branched distally; diverticula absent in distal portion of haptor.

Genital atrium unarmed, subspherical, near posterior limit of cephalic area. Testes 27 (23–33; $n = 12$) in number; pregermarial, intercecal, lying in 2 bilateral rows along body midline; each 43 (28–54; $n = 39$) in diameter, subspherical. Vas deferens expanded and coiled immediately anterior to testicular zone, then narrowing to a straight tube and extending to male copulatory organ (MCO); vas efferentia, prostate not observed. MCO 50 (42–56; $n = 14$) wide, bulbous, armed with 19 (16–21; $n = 18$) spines arranged in a tight circle on distal half of MCO bulb, with tips directed outward and extending into genital atrium (Fig. 2); spines hooklike, each with elongate basal root, submedial erect thumb and distal sicklelike end (Fig. 3). Germarium intercecal, comprising proximal germarial bulb with narrow canal extending anteriorly where it expands and forms the distal twisted M-shaped portion of germarium near midlength of trunk (Fig. 7); oviduct elongate; genitointestinal canal extending to right intestinal cecum (observed in single specimen) (Fig. 7); ootype, origin of uterus not observed; uterus a delicate straight tube extending anteriorly along body midline to genital atrium, usually containing 1–3 eggs. Vaginal pore ventral on either side of body midline but opposite that of haptoral clamps, immediately anterior to vaginal vestibule; vaginal vestibule 82 (66–99; $n = 12$) long, 59 (41–75; $n = 12$) wide (when not flared distally), armed with numerous flattened spines (Fig. 4); ventral spines short (Fig. 5), dorsal spines elongate (Fig. 6); each spine distally spinulose; vaginal canal not observed. Vitellarium dense, coextensive with intestine; vitelline reservoir usually shifted to left of body midline, receiving pair of bilateral vitelline ducts immediately anterior to germarium (Fig. 7). Egg elongate ovate, 180 (167–193; $n = 2$) long (not including polar filaments), 68 (66–70; $n = 2$) wide, with long anterior and posterior polar filaments.

Taxonomic summary

Locality: Florida Bay, Everglades National Park, Florida (25.102–25.226°N, 80.452–80.680°W), 6–10 June 2009.

Site: Gill lamellae.

Prevalence: 8 of 10 hosts infected.

Mean intensity: 7.0 (range = 2–16).

Specimens deposited: 23 voucher specimens, USNPC 103314, 103315, 103316, 103317, 103318, FSBC-I 070094.

Museum specimens examined: Paratype, *P. manteri* (USNPC 75514); type, *Protomicrocotyle pacifica* Meserve, 1938 (USNPC 9166); 3 voucher specimens, *P. pacifica* from *Xurel marginatus* (USNPC 100122); "type" and 3 "paratypes," *Acanthodiscus mirabile* (USNPC 35628); 2 voucher specimens, *Protomicrocotyle mirabilis* from *Caranx latus* (USNPC 37110); 8 voucher specimens, *P. mirabilis* from *C. hippos* (USNPC 82534, 82663, 99974); voucher specimen, *P. mirabilis* from *Caranx crysos* (USNPC 99973); 3 voucher specimens, *P. mirabilis* from *Carangoides ruber* (USNPC 85298); 2 voucher specimens, *Protomicrocotyle celebensis* (sic) from *Caranx ignobilis* (USNPC 101567); voucher specimen, *Protomicrocotyle mannarensis* Ramalingam, 1960 from *Caranx melampygus* (USNPC 74798); holotype, *Lethacotyle fijiensis* Manter & Prince, 1953 (USNPC 48718).

Records: Caranx hippos (type host): New York Aquarium (type locality) (MacCallum, 1918); off Port Aransas, Texas (Koratha, 1955); Gulf of Mexico, Sound of Campeche, Campeche, Mexico (Caballero y C. and Bravo-Hollis, 1967); Ebrié Lagoon, Ivory Coast (Africa) (Wahl, 1972); Sontecomapan, Veracruz, Mexico (Bravo-Hollis, 1988); Cumaná (fishermen's catch), Venezuela (Bashirullah

and Rodriguez, 1992); Puerto Rico (Bunkley-Williams and Williams, 1994, 1995; Williams and Bunkley-Williams, 1996); coast of Rio de Janeiro, Brazil (Luque et al., 2000; Luque and Alves, 2001). *Caranx crysos:* Islas Mujeres, Quintana Roo, Mexico (Bravo-Hollis, 1988). *Caranx latus:* Dry Tortugas, Key West, Florida (Manter, 1954); Tuxpan, Veracruz, Mexico (Caballero y C. and Bravo-Hollis, 1965); Bahía de Chetumal, Quintana Roo, Mexico (Bravo-Hollis, 1988); Puerto Rico (Bunkley-Williams and Williams, 1994, 1995; Williams and Bunkley-Williams, 1996); Laguna Madre, San Fernando, Tamaulipas, Mexico (Iruegas-Buentello, 1999). *Caranx* sp.: Isla Cozumel, Quintana Roo, Mexico (Bravo-Hollis, 1988). *Carangoides ruber:* Puerto Rico (Williams and Bunkley-Williams, 1996). *Trachinotus carolinus:* Jicacal, Veracruz, Mexico (Bravo-Hollis, 1988).

Remarks

This species was described originally as *Acanthodiscus mirabile* by MacCallum (1918), who proposed the genus with *A. mirabile* as its type species. Johnston & Tiegs (1922) pointed out that the generic name was preoccupied and renamed it *Protomicrocotyle* Johnston & Tiegs, 1922. Three species of *Protomicrocotyle* have been reported from crevalle jack in the Atlantic Ocean: the type species from the western and eastern Atlantic (Koratha, 1955; Caballero y C. and Bravo-Hollis, 1967; Wahl, 1972 among others); *P. manteri* from the western Atlantic (Lamothe-Argumedo, 1970; Bravo-Hollis, 1988); and *P. ivoriensis* from the eastern Atlantic (Wahl, 1972). Bravo-Hollis (1979) described *P. nayaritensis* from the Pacific crevalle jack, *C. hippos caninus* Günther (= *C. caninus* Günther), from the Pacific Ocean off Mexico. Although currently considered distinct, Froese & Pauly (2010) indicated that *C. caninus* may be a junior synonym of *C. hippos*.

Protomicrocotyle mirabilis differs from *P. manteri* by possessing fewer spines on the MCO (16–21 in *P. mirabilis*; 33–38 in *P. manteri*) and numerous spines with spinulose tips in the vaginal vestibule (spines few and papillae like in *P. manteri*) (see Bravo-Hollis, 1967; USNPC 75514). *Protomicrocotyle mirabilis* is also distinquished from *P. ivoriensis* and *P. nayaritensis* by the number of spines on the MCO (25–26 in *P. ivoriensis*; 48–54 in *P. nayaritensis*) and number and morphology of the spines of the vaginal vestibule (vaginal vestibule an elongate tube densely armed with small, morphologically variable spines in *P. ivoriensis*; spines of vaginal vestibule few and papillate in *P. nayaritensis*) (see Wahl, 1972; Bravo-Hollis, 1979).

Museum specimens of *P. mirabilis* from the horse-eye jack, *C. latus* Agassiz (USNPC 37110, apparently representing the record of Manter [1954]), the blue runner, *C. crysos* (Mitchill) (USNPC 99973, identified by Salgado-Maldonado), and the bar jack, *Carangoides ruber* (Bloch) (USNPC 85298, representing the record of Williams and Bunkley-Williams [1996]) were limited in number and quality. Additional specimens from these hosts will be required to determine whether they represent *P. mirabilis* or closely related species specific to the respective hosts. Available specimens of *P. pacifica* (USNPC 9166, 100122) from the bigeye trevally, *X. marginatus* (Gill) (now *Caranx sexfasciatus* Quoy & Gaimard), lack accessory sclerites in the haptoral clamps (present in *P. mirabilis*), justifying Ramalingam's (1960) transfer of the species to *Neomicrocotyle* Ramalingam, 1960.

Yamaguti (1953) stated in the description of *P. celebesensis* Yamaguti, 1953 that the vagina opens "ventrally near the lateral (right or left) margin of the body" and that "a longitudinal row of 4 chitinous suctorial valves (clamps) on the right or left margin" of the haptor was present (latter parentheses ours). However, Yamaguti (1953) did not indicate any relationship of the position of the clamps with that of the vaginal pore in *P. celebesensis*. Although the clamps and distal components of the vagina also occurred on either the right or the left side of the body in *P. mirabilis*, their respective positions were not independent. In this species, distal components of the vagina always occurred on the side of the body opposite that of the haptoral clamps, suggesting that specimens of *P. mirabilis* form 2 groups of mirror images. These groups, however, are not absolute mirror images because the proximal components of the female reproductive system (germarium and vitelline reservoir) always occurred as shown in Figs. 1 and 7, with the vitelline reservoir and the distal loop of the germarium always lying slightly to the left of the body midline. The different positions of the vaginal components and corresponding positions of the clamps, along with the constant orientation of the germarium and vitelline reservoir, suggest that individual specimens of *P. mirabilis* might be adapted for specific positions on the gill arches, a hypothesis that could not be tested with the collection methods used in this study.

The present finding of *P. mirabilis* in Florida Bay of the Everglades National Park represents the first record of the species in Florida.

Suborder Microcotylinea Lebedev, 1972
Allopyragraphoridae Yamaguti, 1963
Allopyragraphorus hippos (Hargis, 1956) Yamaguti, 1963

Synonyms *Pyragraphorus hippos* Hargis, 1956; *Pyragraphorus incomparabilis* of Koratha (1955) nec MacCallum (1917); *Hargisiella hippos* (Hargis, 1956) Unnithan, 1971; *A. incomparabilis* of Williams and Bunkley-Williams (1996) (part).

Measurements

Body 2,420 (1,530–3,250; $n = 15$) long; width at germarium 624 (334–836; $n = 16$). Prohaptoral sucker 41 (31–53; $n = 17$) long, 50 (36–61; $n = 17$) wide. Pharynx 51 (41–62; $n = 16$) wide. Testis 48 (30–70; $n = 24$) wide. Clamp 47 (39–58; $n = 17$) long, 31 (27–36; $n = 15$) wide; clamp number 138 (92–172; $n = 15$).

Taxonomic summary

Locality: Florida Bay, Everglades National Park, Florida (25.102–25.226°N; 80.452–80.680°W), 6–10 June 2009.

Site: Gill lamellae.

Prevalence: 8 of 10 hosts infected.

Mean intensity: 3.5 (range = 1–8).

Specimens deposited: Neotype, USNPC 103319; 16 voucher specimens, USNPC 103320, 103321, 103322, 103323, FSBC-I 070092.

Museum specimens examined: 2 voucher specimens, *A. hippos* from *C. hippos* (USNPC 82580); 3 cotypes, *Microcotyle incomparabilis* MacCallum, 1917 (USNPC 36528); 3 voucher specimens, *A. incomparabilis* from *Carangoides ruber* (USNPC 85297, 85299); voucher specimen, *A. incomparabilis* from *Caranx crysos* (USNPC 85942); 4 voucher specimens, *Pyragraphorus pyragraphorus* (MacCallum & MacCallum, 1913) Sproston, 1946 from *Trachinotus carolinus* (USNPC 36559).

Records: C. hippos (type host): Port Aransas, Texas (as *P. incomparabilis*) (Koratha, 1955); Alligator Harbor, Florida (type locality) (Hargis, 1956a); Cumaná (fishermen's catch), Venezuela (Bashirullah and Rodriguez, 1992); Puerto Rico ([Bunkley-Williams and Williams, 1994, 1995] and as *A. incomparabilis* by Williams and Bunkley-Williams, [1996]); coast of Rio de Janeiro, Brazil (Luque et al., 2000; Luque & Alves, 2001). *Caranx latus:* Puerto Rico (Bunkley-Williams and Williams, 1994, 1995).

Remarks

Hargis (1956a) adequately described this species as *P. hippos* from the gills of crevalle jack off Florida. Although a specific locality within the Gulf of Mexico was apparently inadvertently omitted with the description, original museum records for the holotype in the USNPC indicate Alligator Harbor, Florida as type locality. The holotype was placed on loan in 1959 but never returned to the USNPC and is now considered lost (Hoberg and Pilitt, personal communication). A neotype for the species (USNPC 103319) was therefore designated from collections of this study to define the species and differentiate it from the similar *A. incomparabilis*.

Hargis (1956a) differentiated *P. hippos* from *P. incomparabilis* by the following: "1) dorsal loop elements of clamp longer, 2) vaginal tube simple, not sculptured, 3) body shorter, even though relaxed, 4) vitellaria not in dorsal lobe of haptor, 5) host." Yamaguti (1963) transferred the species, along with *P. incomparabilis* and *P. caballeroi* Zerecero y D., 1960, to *Allopyragraphorus*. Williams and Bunkley-Williams (1996) considered *A. hippos* and *A. incomparabilis* to be synonyms, stating that Hargis' (1956a) smaller worms were "probably less mature and had less developed vitellaria." However, examination of specimens for this study from Florida and the 2 voucher specimens of *A. hippos* in the USNPC (82580) revealed that fully mature worms (specimens lacking developing haptoral clamps and with eggs or egg material in utero) were consistently smaller than fully mature specimens of *A. incomparabilis* from *Carangoides ruber* and *Caranx crysos* and that vitelline follicles were absent or only minimal numbers were present in the basal portions of the haptor of *A. hippos*, whereas they were densely distributed throughout the dorsal lobe of the haptor in specimens of *A. incomparabilis* (USNPC 85297, 85299, 85942). Finally, figure 12 in Koratha (1955), reported to be of *P. incomparabilis* from *C. hippos* at Port Aransas, Texas, shows that this specimen also lacked vitelline follicles in the haptor, indicating that the record in Koratha (1955) represented *A. hippos* as previously suggested in Hargis (1956a). The consistent differences between the distribution of vitelline follicles in specimens taken from crevalle jack and that in specimens from other carangid hosts indicates that *A. hippos* is a distinct species and that the synonomy proposed by Williams and Bunkley-

Williams (1996) is unjustified. Finally, specimens of *A. hippos* on *C. latus* (reported in Bunkley-Williams and Williams, 1994, 1995) were not available for study; this record requires confirmation.

Cemocotylidae Price, 1962
Cemocotyle noveboracensis Price, 1962

Synonyms *Axine carangis* MacCallum 1918; *A.* (*Heteraxine*) *carangis* (MacCallum, 1918) Yamaguti, 1938; *H. carangis* (MacCallum, 1918) Yamaguti, 1938.

Measurements

Body 4,950 (3,680–5,790; $n = 30$) long; width at germarium 617 (319–845; $n = 37$). Prohaptoral sucker 40 (30–50; $n = 35$) long, 47 (38–56; $n = 35$) wide. Pharynx 43 (34–51; $n = 35$) wide. Genital atrium 198 (155–223; $n = 31$) wide. Testes 63 (46–83; $n = 33$) in number; each 53 (25–89; $n = 108$) wide. Terminal (posterior-most) clamp 42 (37–47; $n = 30$) long, 53 (47–66; $n = 34$) wide; clamp number (short row) 21 (9–28; $n = 36$), long row 49 (30–63; $n = 32$). Egg 131 (110–159; $n = 23$) long (not including polar filaments), 55 (40–74; $n = 23$) wide.

Taxonomic summary

Locality: Florida Bay, Everglades National Park, Florida (25.102–25.226°N; 80.452–80.680°W), 6–10 June 2009.

Site: Gill lamellae.

Prevalence: 8 of 10 hosts infected.

Mean intensity: 35.3 (range = 1–100).

Specimens deposited: 52 voucher specimens, USNPC 103324, 103325, 103326, 103327, FSBC-I 070093.

Museum specimens examined: 2 syntypes, *Microcotyle carangis* MacCallum, 1913 (USNPC 35170) [erroneously designated holotype and paratype by Price (1962)]; 19 voucher specimens + fragments, *Cemocotyle carangis* (MacCallum, 1913) Sproston, 1946 from *Caranx crysos* (USNPC 37735, 37736, 37737, 99965); 6 voucher specimens, *Cemocotyle carangis* from *Caranx hippos* (USNPC 85935, 99966); voucher specimen, *Cemocotyle carangis* from *T. carolinus* (USNPC 37742); holotype, *Cemocotyle borinquenensis* Price, 1962 (USNPC 37734); holotype, 10 paratypes, *Cemocotyle noveboracensis* Price, 1962 (USNPC 37738, 37739); 1 voucher specimen, *C. noveboracensis*, 3 voucher specimens, *C. carangis* (on 1 slide) from *Carangoides ruber* (USNPC 37740); 11 voucher specimens, *Cemocotyle noveboracensis*, 1 voucher specimen, *C. carangis* (on 2 slides) from *Carangoides ruber* (USNPC 37741); 7 voucher specimens, *Cemocotyle noveboracensis* (redetermined) from *Caranx hippos* (USNPC 82581); 3 voucher specimens, *Cemocotyle noveboracensis* from *Caranx latus* (USNPC 84688); holotype, *Cemocotyle saqae* Manter & Prince, 1953 (USNPC 48719); holotype, paratype, *Cemocotyle trachuri* Dillon & Hargis, 1965 (USNPC 61087); holotype, 32 specimens (not identified as either types or voucher specimens) on 1 slide, *Cemocotylella carangis* Yamaguti, 1968 (USNPC 63680).

Records: Caranx hippos (type host): New York Aquarium (type locality) (as *A. carangis*) (MacCallum, 1918; Price, 1962); Alligator Harbor, Florida (as *H. carangis*) (Hargis, 1956b); Gulf of Mexico, Campeche, Mexico (Caballero y C. and Bravo-Hollis, 1967); City of Carmen, Campeche, Mexico (Bravo-Hollis and Salgado-Maldonado, 1983); Cumaná (fishermen's catch), Venezuela (Bashirullah and Rodriguez, 1992); Puerto Rico (Bunkley-Williams and Williams, 1994, 1995; Williams and Bunkley-Williams, 1996); coastal zone of the State of Rio de Janeiro, Brazil (Luque et al., 2000; Luque and Alves, 2001). *Caranx latus:* Puerto Rico (Williams and Bunkley-Williams, 1996); Laguna Madre, San Fernando, Tamaulipas, Mexico (Iruegas-Buentello, 1999). *Carangoides ruber:* United States (New York) (Price, 1962).

Remarks

Price (1962) described *Cemocotyle noveboracensis* on the basis of a holotype and 10 paratypes (USNPC 37738, 37739) from the gills of *Caranx hippos* and apparently some voucher specimens (USNPC 37740, 37741) from the gills of *Carangoides ruber*, all collected by G. A. MacCallum from the New York Aquarium. The original description of *Cemocotyle noveboracensis* is adequate, except that Price (1962) records and depicts in his plate II, figure 10 a terminal anchor-bearing lappet that he states was present in only 1 specimen of the species. Our examination of the type specimens, however, revealed that none of the 11 specimens had a haptoral lappet. Although USNPC 37740 and 37741 include worms that Price (1962) identified as *C. noveboracensis* and *Cemocotyle carangis*, none of specimens of *C. noveboracensis* had an armed lappet and none of those of *C. carangis* (all with armed lappets) had the orientation of the clamps and lappet as shown in Price's (1962) plate II, figure 10. Thus, it is uncertain what specimen might

have been used to develop this figure. The absence of an armed lappet in all type and voucher specimens of *C. noveboracensis*, including the 52 specimens collected from Everglades National Park for this study, suggests that the absence of a lappet is diagnostic for *C. noveboracensis*. All other congeners possess armed haptoral lappets and morphological characteristics of the genital atrium and male copulatory organ that differentiate them from *C. noveboracensis*.

The 5 slides (USNPC 85935), recorded in museum records as *C. carangis* from *Caranx hippos* from Puerto Rico, included 5 fragments of worms, only 2 of which had a complete haptor and all of which lacked the genital atrium and male copulatory organ. In fragments with complete haptors, an anchor-bearing lappet was absent, suggesting that these specimens also are *Cemocotyle noveboracensis*.

The haptor of *C. noveboracensis* is asymmetrical, having a short and a long row of clamps, with the short row occurring either on the right (26 of 49 specimens) or left (23 of 49 specimens) side of the body. As with *Protomicrocotyle mirabilis*, where "right and left" asymmetrical worms were observed, association of the position of the 2 clamp rows with site of infection on the host's gill was not determined because sites of infections on respective gill arches were not recorded during this study.

DISCUSSION

Although the present collection of crevalle jack was small (only 10 specimens examined), we observed that the prevalence and intensity of *P. mirabilis*, *Allopyragraphorus hippos*, and *C. noveboracensis* increased as host size increased. Similarly, Bashirullah and Rodriguez (1992) reported finding no monogenoids in 78 juvenile crevalle jack, whereas infections increased in subadult and adult jack examined from Venezuela. In that study, *P. mirabilis* was the most commonly encountered species in adult jack (mean intensity = 25.02, range = 1–111), whereas *C. noveboracensis* had the lowest levels (mean intensity = 2.42; range = 1–5). Williams and Bunkley-Williams (1996) indicated that *A. hippos* (*A. incomparabilis* in their report) was absent in 22 immature crevalle jack from Dauphin Island, Alabama. These recorded parasite loads in the different age (size) classes of crevalle jack suggest that infection by these worms is dependent at least in part on the probability of the host encountering infective stages rather than on the oncomiracidium actively seeking a susceptible host, i.e., the older the fish host, the greater the prevalence and intensity of infection by these monogenoids.

That ectoparasites of fishes show distinct latitudinal gradients in species diversity within the world's oceans is well documented, with species diversity and abundance of Monogenoidea significantly increasing from high to low latitudes (see Rohde, 1980, 1999; Rohde & Heap, 1998). This pattern is reflected somewhat in the monogenoidean fauna of crevalle jack in the western Atlantic region, where, as determined from published records, the diversity of monogenoidean species on the fish is greatest in the Gulf of Mexico off eastern Mexico to Venezuela while diminishing in higher northern and southern latitudes of the host's range. Eight species, *Ahpua piscicola*, *Allopyragraphorus hippos*, *A. winteri*, *C. noveboracensis*, *Cemocotylella elongata*, *Protomicrocotyle manteri*, *P. mirabilis*, and *Pseudomazocraes selene*, have been reported from crevalle jack off Venezuela and within the Gulf of Mexico off Mexico (see Bashirullah and Rodriguez, 1992; Lamothe-Argumedo et al., 1997). Apparently only 3 species (*A. hippos*, *Cemocotyle noveboracensis*, and *Protomicrocotyle mirabilis*) occur in the northern Gulf of Mexico, off Puerto Rico and along the East Coast of the United States (MacCallum, 1918; Hargis, 1956a, b; Price, 1962; Williams and Bunkley-Williams, 1996, nobis), and up to 4 species (*A. hippos*, *C. noveboracensis*, *Cemocotylella elongata*, and *P. mirabilis*) off Brazil (Luque et al., 2000; Luque and Alves, 2001). Crevalle jack has been sufficiently surveyed throughout much of its range to suggest that these diversity gradients are not the results of investigation bias but rather the outcomes of environmental or historical factors (see Rohde, 1999).

Asymmetry of the haptor in monogenoids has been correlated with water flow over the host's gill and the specific position on the gill where the worm is attached (Ogawa and Egusa, 1981). A similar correlation probably exists with *P. mirabilis* and *Cemocotyle noveboracensis*, both of which possess asymmetrical haptors. However, in *P. mirabilis* the vaginal pore occurs on the side of the body opposite that of the haptoral clamps, which suggests that copulation in *P. mirabilis* also is restricted by water flow and by the position and orientation of the worm on the gill. This is the first report of a putative correlation between copulation and the location and position of the worm on the host.

Nomenclatural notes: In this paper, authorship of the Protomicrocotylidae is assigned to Johnston and Tiegs (1922), who proposed the taxon as a subfamily within the Gyrodactyloidea. Although Poche (1926)

was the first to raise the taxon to family status, credits to Poche for the Protomicrocotylidae by Caballero y C. and Bravo-Hollis (1965, 1967) and Yamaguti (1963) are in error. According to the principle of coordination of the International Code of Zoological Nomenclature, the proposal of Johnston and Tiegs (1922) of the subfamily also meant that they established the family as well. Similarly, authorship of the Cemocotylidae is herein assigned to Price (1962), who proposed the taxon as a subfamily of the Heteraxinidae Price, 1962. Although Yamaguti (1963) was the first to raise the taxon to family status while labeling his action "Cemocotylidae n. fam.", credit to Yamaguti (1963) for the Cemocotylidae as indicated by Mamaev and Lebedev (1977, 1979) and subsequent authors is also erroneous.

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