

RESURRECTION OF *MYCTERONASTES* (MONOGENOIDEA: MONOCOTYLIDAE), WITH DESCRIPTION OF *MYCTERONASTES CAALUSI* N. SP. FROM OLFACTORY SACS OF THE SMALLTOOTH SAWFISH, *PRISTIS PECTINATA* (PRISTIFORMES: PRISTIDAE), IN THE GULF OF MEXICO OFF FLORIDA

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21 ABSTRACT: *Mycteronastes* Kearn and Beverley-Burton, 1990 (Monogenoidea: Monocotylidae: Merizocotylinae) was resurrected from subjective synonymy with *Merizocotyle* Cerfontaine, 1894, and its diagnosis was emended to include monocotylids with a haptor lacking a central loculus and having 5 peripheral (2 bilateral pairs and an unpaired anteromedial loculus), 1 interhamular, and 17 marginal loculi. The 3 species of *Mycteronastes* accepted herein are parasitic within the olfactory sacs of rays and sawfishes: *Mycteronastes icopae* (Beverley-Burton and Williams, 1989) Kearn and Beverley-Burton, 1990 (type species) from the giant shovelnose ray, *Glaucostegus typus* (Anonymous (Bennett)) (Glaucostegidae), in the southwestern Pacific Ocean; *Mycteronastes undulatae* Kearn and Beverley-Burton, 1990 from the undulate ray, *Raja undulata* Lacepède (Rajidae), in the northeastern Atlantic Ocean; and *Mycteronastes caalusi* n. sp. from the smalltooth sawfish, *Pristis pectinata* Latham (Pristidae), in the Gulf of Mexico. *Mycteronastes caalusi* is most easily differentiated from its congeners by the combination of having 2 median cephalic papillae, an oval haptor that is wider than the body proper and lacks a deeply scalloped margin, a comparatively large anteromedial peripheral loculus, an unsclerotized male copulatory organ that is wholly anterior to the vaginal pores, a relatively small distal portion of the uterus (ootype chamber) that is mostly anterior to the vaginae, and a delicate uterus. The present study is the first report of a monocotylid from the olfactory sacs of *P. pectinata* and the first record of a species of *Mycteronastes* from the Gulf of Mexico. Notes on the taxonomy and systematics of some species assigned to *Calicotyle* Diesing, 1850 (Monocotylidae: Calicotylinae) are included.

Mycteronastes Kearn and Beverley-Burton, 1990 was proposed by Kearn and Beverley-Burton (1990) for 2 species of Monocotylidae (Monogenoidea) occurring in the olfactory sacs of rajiform rays assigned to the Rajidae and putative Rhinobatidae (see Nelson et al., 2016 and references therein for comments on the apparent paraphyly of the Rhinobatidae). The type species, *Mycteronastes icopae* (Beverley-Burton and Williams, 1989) Kearn and Beverley-Burton, 1990 (syn. *Merizocotyle icopae* Beverley-Burton and Williams, 1989), occurs in the giant shovelnose ray, *Glaucostegus typus* (Anonymous (Bennett)) (originally reported as *Rhinobatos batillum* Whitley), and the Thouin ray, *Glaucostegus thouin* (Anonymous (Lacepède)) (both Glaucostegidae, formerly “Rhinobatidae”), in the southwestern Pacific Ocean; *Mycteronastes undulatae* Kearn and Beverley-Burton, 1990 is parasitic in the undulate ray, *Raja undulata* Lacepède (Rajidae), in the northeastern Atlantic Ocean. The genus was originally based in part on monocotylid species that had a haptor with 5 peripheral loculi arranged around a central depression and 18 marginal loculi (herein considered 1 interhamular and 17 marginal), of which the largest was the unpaired interhamular loculus.

Using the results obtained from a phylogenetic analysis of the Monocotylidae based on morphological data, Chisholm et al. (1995) synonymized *Mycteronastes* and *Thaumatocotyle* Scott, 1904 with the senior *Merizocotyle* Cerfontaine, 1894. These synonymies were embraced by Chisholm and Whittington (1999) in their revision of the Merizocotylinae. Neifar et al. (2000) reinstated *Thaumatocotyle*, arguing that the numbers of peripheral and marginal loculi within the haptor were important in differentiating monocotylid genera. Marie and Justine (2006) followed Neifar et al. (2000) during their redescription of *Thaumatocotyle pseudodasybatis* Hargis, 1955, whereas Chisholm and Whittington (2012) continued to place *Thaumatocotyle*-like species in *Merizocotyle*. The subjective synonymy of *Mycteronastes* and *Merizocotyle*, however, has never been formally challenged, although Chisholm et al. (2001) suggested that *Mycteronastes* might be valid based on their preliminary analysis of 28S rDNA sequences of 26 monocotylid species.

In early July 2016, a thorough necropsy was conducted on a smalltooth sawfish, *Pristis pectinata* Latham, an endangered species, soon after it had died on the Gulf of Mexico shore near Naples, Florida. In addition to members of other parasite taxa collected from various sites on or within this sawfish (M. D. Bakenhaster et al., unpubl. data), an undescribed species of Monocotylidae was discovered inhabiting the olfactory sacs of the fish. In addition, specimens of *My. icopae* were collected from 2 giant shovelnose rays in a study on parasite diversity in fishes of Moreton Bay off Queensland, Australia, in January 2016. Preliminary examination of these helminth specimens and 2 paratypes of *My. undulatae* revealed that *Mycteronastes* formed an apparently valid taxon based primarily on haptoral morphology. In the present study, *Mycteronastes* was reinstated for *My.*

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icopae, *My. undulatae*, and the undescribed species discovered in the olfactory sacs of the smalltooth sawfish.

MATERIALS AND METHODS

Parasite specimens used for this study were collected from wild hosts captured during targeted parasitological sampling or were taken as samples of opportunity from wild hosts collected for other projects. On 2 July 2016, a report to the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute (FWRI) Sawfish Hotline identified the location of a moribund smalltooth sawfish (2,835-mm stretch total length) on the Gulf of Mexico shore near Naples, Florida. When on-site monitoring of the sawfish by FWRI personnel began, the sawfish was alive but progressively weakening, and it eventually died. Within 1.5 hr postmortem the fish was packed in ice and shipped to the FWRI Charlotte Harbor Field Laboratory in Port Charlotte, Florida, where it was kept on ice until necropsy the following morning. Along with other organs, the olfactory sacs were excised and transported to FWRI headquarters in St. Petersburg, Florida, for parasitological evaluation. There, helminths were flushed from between the olfactory lamellae with a jet of artificial sea water dispensed from a standard laboratory wash bottle. The parasites were dead and uniformly flaccid when they were isolated from the rinsing under a stereomicroscope; as a result, attempts were not made to relax them with hot water before fixation. Fine-tipped probes or forceps were used to carefully lift the helminths and place them into vials containing either 5% phosphate-buffered formalin or 95% ethanol.

In addition, 2 giant shovelnose rays, *Glaucostegus typus*, were collected with barrage trap nets from Moreton Bay off Wynnum, Queensland, Australia, in January 2016. The rays were transported alive to the Moreton Bay Research Station located in Dunwich, North Stradbroke Island, Queensland, where they were euthanized by neural pithing and their olfactory sacs flushed with hot (60 C) sea water. The freshly killed helminths were then generally treated as described above.

Vials containing formalin-fixed specimens were shipped to Idaho State University, where the helminths were individually mounted unstained on microscope slides in Gray and Wess medium for study of haptor and copulatory sclerites. Other helminth specimens were stained with Gomori's trichrome, astra blue, Gill's formulation #2 hematoxylin, Mayer's hematoxylin, or VanCleave's hematoxylin (Humason, 1979; Pritchard and Kruse, 1982); dehydrated through a graded ethanol series; cleared in beechwood creosote; and mounted in Canada balsam for study of soft anatomy. Illustrations were prepared with the aid of a microprojector or a camera lucida mounted on a phase contrast microscope. Measurements (all in micrometers) were obtained with the aid of a calibrated filar micrometer mounted on a compound microscope, were represented by straight-line distances between extreme points, and they were expressed as the mean followed in parentheses by the range and number (n) of structures measured; body length included that of the haptor.

Terminology for the haptor loculi of monocotyliids followed that of Chisholm et al. (1995), except that the term "marginal loculus" was reserved for those loculi occurring external to the peripheral loculi and lateral or anterolateral to the haptor anchors; the loculus (occasionally 2, 3, or 4) that occurs between the anchors was termed the "interhamular loculus." Determining the direction of the

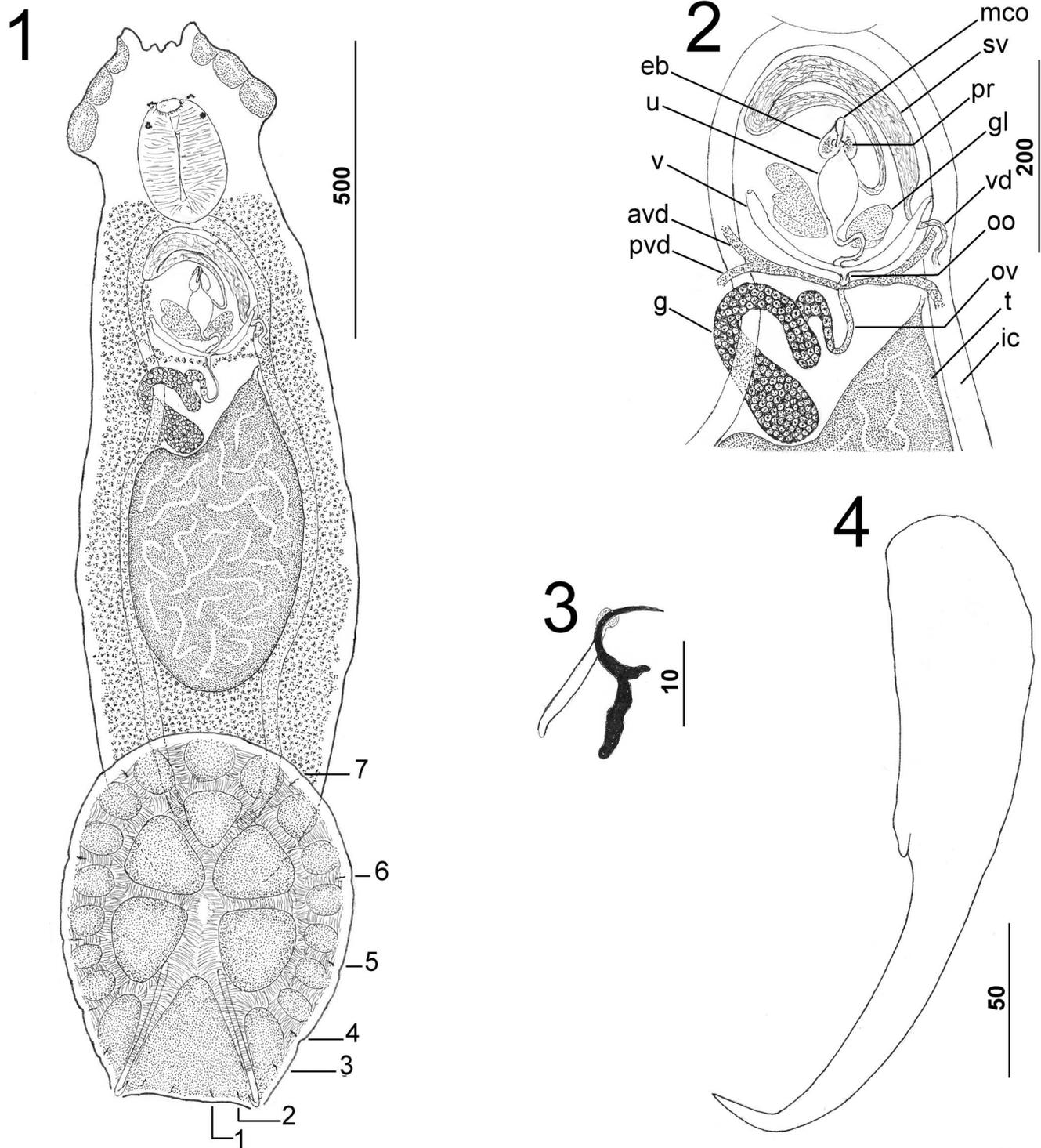
coil of the germarium followed the method described for the male copulatory organ (MCO) by Kritsky et al. (1985). Numbering of haptor hook pairs was as shown in Figure 1.

Fish classification followed Nelson et al. (2016) and family group names, specific nomenclature, and common names of fishes followed Van der Laan et al. (2014), Eschmeyer et al. (2016), and Froese and Pauly (2016), respectively. Type and voucher specimens of the helminths were deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.; the University of Nebraska State Museum, Harold W. Manter Laboratory (HWML), Lincoln, Nebraska; and the Invertebrate Specimen Collection (FSBC-I) of the Florida Fish and Wildlife Conservation Commission's Florida Wildlife Research Institute, St. Petersburg, Florida, as indicated in the respective species accounts. In addition, 2 paratypes of *My. undulatae* (HWML 31693) were examined.

DESCRIPTION

Mycteronastes Kearn and Beverley-Burton, 1990

Emended diagnosis: Monocotyliidae, Merizocotylineae. Body comprising body proper (cephalic region, trunk, and peduncle) and haptor. Tegument lacking scales. Two bilateral diagonal cephalic lobes, each with 3 head organs; 1 or 2 small terminal lobes between distal ends of bilateral lobes. Two pairs of eyespots. Mouth midventral at level of anterior end of muscular pharynx. Two intestinal ceca; each lacking diverticula and ending blindly posterior to testis. Trunk fusiform, flattened dorsoventrally. Peduncle short, delicate, uniting with dorsal surface of haptor above central haptor depression. Haptor plate like, having 5 peripheral, 1 interhamular, and 17 marginal loculi; central loculus absent or represented by slight depression on ventral haptor surface. Peripheral loculi comprising 2 bilateral pairs and a single unpaired anteromedial loculus. Pair of ventral anchors; each with bilaterally flattened base as long as or longer than smoothly arcing shaft. Seven pairs of hooks ventral in haptor; hook pairs 1 and 2 interhamular near posterior haptor margin, 5 pairs of hooks extrahamular with members of pair 3 situated within posterior-most marginal loculus; remaining extrahamular pairs at or near ends of alternating septa of marginal loculi beginning with anterior septum of posterior-most marginal loculus; 2 anterior-most marginal septa lacking hooks (see Fig. 1). Each haptor hook with elongate sweeping point and slightly inflated shaft comprising 2 subunits. Genital pore midventral, posterior to pharynx. Testis single, intercecal; seminal vesicle forming transverse arc anterior to genital pore, then folding back on itself before narrowing into ejaculatory duct; MCO sclerotized or not, directed posteriorly from anterior end of ejaculatory bulb; ejaculatory bulb containing 2 prostatic reservoirs. Germarium lying to right of anterior end of testis, forming a counterclockwise coil with right intestinal cecum extending through proximal ring of coil; oviduct delicate; ootype receiving vitelline ducts, common vaginal duct; uterus (ootype chamber of Kearn and Beverley-Burton, 1990) directed anteriorly, opening into genital atrium. Two vaginae; bilateral vaginal pores submarginal on anteroventral surface of trunk. Vitellarium distributed throughout trunk, except absent in regions of other reproductive organs. Parasites of the olfactory sacs of rajiform (skates and rays) and pristiform (sawfishes) fishes.



FIGURES 1–4. *Mycteronastes caalusi* sp. n. from olfactory sacs of smalltooth sawfish, *Pristis pectinata*. (1) Whole mount (composite, ventral view). (2) Terminal portions of reproductive systems (ventral view). (3) Hook. (4) Anchor. Small numbers on Fig. 1 refer to the positions of respective hook pairs in the haptor. Abbreviations: avd = anterior vitelline duct; eb = ejaculatory bulb; g = germarium; gl = prostate gland; ic = intestinal cecum; mco = male copulatory organ; oo = ootype; ov = oviduct; pr = prostatic reservoir; pvd = posterior vitelline duct; sv = seminal vesicle; t = testis; u = uterus; v = vagina; vd = vas deferens.

Taxonomic summary

Type species: *Mycteronastes icopae* (Beverley-Burton and Williams, 1989) Kearns and Beverley-Burton, 1990 from olfactory sacs of giant shovelnose ray, *Rhinobatos batillum* Whitley [now *Glaucostegus typus* (Anonymous (Bennett))], and Thouin ray, *Glaucostegus thouin* (Anonymous (Lacepède)) (both Rajiformes: Glaucostegidae).

Other species: *Mycteronastes undulatae* Kearns and Beverley-Burton, 1990 from olfactory sacs of undulate ray *Raja undulata* (Lacepède) (Rajiformes: Rajidae). *Mycteronastes caalusi* n. sp. from olfactory sacs of smalltooth sawfish, *Pristis pectinata* Latham (Pristiformes: Pristidae).

Mycteronastes icopae (Beverley-Burton and Williams, 1989) Kearns and Beverley-Burton, 1990

Syn. *Merizocotyle icopae* Beverley-Burton and Williams, 1989.

Taxonomic summary

Type host: Giant shovelnose ray, *Rhinobatos batillum* Whitley [now *Glaucostegus typus* (Anonymous (Bennett))] (Rajiformes: Glaucostegidae).

Type locality: Heron Island, Great Barrier Reef, Queensland, Australia (23°27'S, 151°55'E).

Current records: *Glaucostegus typus*: Moreton Bay off Wynnum, Queensland, Australia, 18 January 2016.

Infection site: Olfactory sacs.

Previous records (all as Me. icopae): *Glaucostegus typus*: Shark Bay, Heron Island, Great Barrier Reef, Queensland, Australia (23°27'S, 151°55'E) (Beverley-Burton and Williams, 1989; Chisholm and Whittington, 1996, 1999, 2000, 2002, 2003; Chisholm et al., 2001 [locality listed only as "Heron Island"]; Hamwood et al., 2002; Cribb et al., 2003, 2004; Whittington et al., 2004); Moreton Bay off Dunwich, Stradbroke Island, Queensland, Australia (27°30'S, 153°25'E) (Cribb et al., 2004; Whittington et al., 2004); Makassar Strait, Muara Pasir, Manggar, East Kalimantan, Indonesia (01°14'58.92"S, 116°13'23.80"E) (Chisholm and Whittington, 2012). Thouin ray, *Glaucostegus thouin* (Anonymous (Lacepède)): Makassar Strait, Pagatan, South Kalimantan, Indonesia (03°14'44.80"S, 115°54'59.40"E) (Chisholm and Whittington, 2012).

Specimens studied: 7 voucher specimens, USNM 1422259–1422265.

Remarks

Mycteronastes icopae was originally assigned to *Merizocotyle* by Beverley-Burton and Williams (1989), who nevertheless recognized that its haptor differed from that of all described species of *Merizocotyle* by having 5 peripheral loculi (2 bilateral pairs and 1 anteromedial loculus) arranged around a central depression and 18 marginal loculi (herein 17 marginal and 1 interhamular). Taking what they considered a conservative approach, Beverley-Burton and Williams (1989) chose not to propose a new genus to accommodate the species, while recognizing that *Me. icopae* was morphologically similar to the undescribed *Merizocotyle* sp. of Kearns (1968). The following year, Kearns and Beverley-Burton (1990) transferred *Me. icopae* to their new genus *Mycteronastes* as its type species. *Merizocotyle* sp. of Kearns (1968) was described and named *My. undulatae* and was

considered the only congener by Kearns and Beverley-Burton (1990).

The original description of *My. icopae* is satisfactory, except that 2 small bilateral prostatic reservoirs were observed within the ejaculatory bulbs of the available voucher specimens. *Mycteronastes icopae* is easily distinguished from *My. undulatae* and *My. caalusi* by having a sclerotized tubular MCO (sclerotization of the MCO lacking in the latter 2 species).

Mycteronastes undulatae Kearns and Beverley-Burton, 1990

Syns. *Merizocotyle* sp. of Kearns (1968) and Kearns and Vasconcelos (1979); *Me. undulatae* (Kearns and Beverley-Burton, 1990)

Chisholm, Wheeler, and Beverley-Burton, 1995; *Me. undulata* of Chisholm and Whittington (1999) and Álvarez et al. (2006).

Taxonomic summary

Type host: Undulate ray, *Raja undulata* (Lacepède) (Rajiformes: Rajidae).

Type locality: Eastern Atlantic Ocean off Arcachon, France.

Infection site: Olfactory sacs.

Previous records: *Raja undulata*: Eastern Atlantic Ocean off Arcachon, France (Kearns, 1968 as *Merizocotyle* sp., Kearns and Beverley-Burton, 1990); eastern Atlantic Ocean off Lisbon (Tagus estuary) and Sines, Portugal (Kearns and Vasconcelos, 1979 as *Merizocotyle* sp.; Kearns and Beverley-Burton, 1990); Atlantic continental shelf off the mouth of the Muros-Noia estuary, northwest coast of Spain (42°35'–42°41'N, 09°02'–09°10'W) (Álvarez et al., 2006 as *Me. undulata*). Small-eyed ray, *Raja microocellata* Montagu: Atlantic continental shelf off the mouth of the Muros-Noia estuary, northwest coast of Spain (42°35'–42°41'N, 09°02'–09°10'W) (Álvarez et al., 2006 as *Me. undulata*).

Specimens studied: 2 paratypes, HWML 31693.

Remarks

The 2 paratypes of *My. undulatae* had been slightly damaged, probably from flattening during preparation for mounting. Kearns and Beverley-Burton (1990) distinguished *My. undulatae* from *My. icopae* (the only congener at the time) in part by *My. undulatae* lacking a sclerotized MCO and an ejaculatory bulb. However, figure 1C of the terminal male copulatory apparatus of *My. undulatae* in Kearns and Beverley-Burton (1990) could not be reconciled with the terminal male structures observed in the 2 paratypes. In both specimens, a short unsclerotized MCO originated from the anterior end of a small ejaculatory bulb and extended posteroventrally toward the genital pore. The ejaculatory bulb contained 2 small prostatic reservoirs, each with anteriorly directed ducts that entered the unsclerotized MCO. In *My. icopae*, the sclerotized MCO also is directed posteroventrally from its origin on the anterior end of the ejaculatory bulb. Thus, the same basic organization of the terminal male genitalia (see Fig. 2) is present in all 3 species herein assigned to *Mycteronastes*.

Mycteronastes caalusi n. sp.

(Figs. 1–4)

Description: Body 2,040 (1,640–2,430; n = 40) long. Cephalic region with well-developed bilateral cephalic lobes and head organs and having 2 small terminal lobes. Eyespots dorsal at level

of mouth; members of anterior pair infrequently dissociated, smaller, closer together than those of posterior pair; eye granules minute. Pharynx ovate, 216 (174–252; n = 39) long, 193 (146–217; n = 39) wide; esophagus short to indistinct; intestinal ceca narrow. Trunk 539 (337–670; n = 39) wide at level of testis. Haptor 791 (633–1,090; n = 41) long; 646 (510–851; n = 40) wide, oval in outline, with straight posterior border; marginal membrane delicate, uniform in width, lacking deeply scalloped margins at level of each of 14 haptoral hooks (7 pairs). Anchor 322 (203–405; n = 48) long, with short straight point, evenly curved shaft, bilaterally flattened base. Each hook lying just internal to marginal membrane of haptor; hook distribution as shown in Figure 1. Hook 21 (19–23; n = 15) long, with elongate sickle-like point, protruding thumb having terminal constriction, and shank comprising 2 subunits; proximal subunit of shank reniform, distal subunit forming short arc; filamentous hook (FH) loop extending to near level of proximal end of shank. Common genital pore and atrium midventral in anterior portion of trunk. Testis 593 (487–728; n = 36) long, 341 (264–405; n = 36) wide, ovate, dorsoventrally flattened, with sinistral lobe giving rise to vas deferens; proximal portion of vas deferens not observed, distal portion extending anteriorly and arcing dextrally to form seminal vesicle. MCO lacking sclerotization, directed posteriorly from anterior end of ejaculatory bulb; ejaculatory bulb with 2 small prostatic reservoirs containing fine granular secretion. Basophilic follicular glands within intercecal space anterior to vaginae near level of terminal male and female genitalia; the organ in which the ducts of these glands empty was not determined. Germarium 77 (50–107; n = 35) wide at proximal end, gently tapered distally, dorsoventrally looping right intestinal cecum, becoming coiled to form 2 complete counterclockwise rings before giving rise to elongate oviduct and ootype. Mehlis' gland not observed. Uterus delicate, anterior to vaginae. Bilateral vaginal pores ventral at level of uterus, posterior to level of MCO and common genital pore; vaginae delicate, often slightly expanded but lacking obvious proximal constriction, directed posteromedially and diagonally from vaginal pores to empty into female duct on body midline near or ootype. Vitellarium dense; bilateral anterior and posterior vitelline ducts merge to form common vitelline duct that empties into female duct near ootype; vitelline ducts draining 4 zones of vitellarium within trunk (antero- and postero-dextral and antero- and postero-sinistral zones). Uterus usually empty or containing single collapsed egg; egg with indeterminate shape; proximal filament very long, delicate, convoluted.

Taxonomic summary

Type host: Smalltooth sawfish, *Pristis pectinata* Latham (Pristiformes: Pristidae).

Type locality: Gulf-side beach near Clam Pass, Collier County, near Naples, Florida (26°13'00"N, 81°49'04"W), 2 July 2016.

Infection site: Olfactory sacs.

Specimens studied: Holotype, USNM 1422225; 51 paratypes, USNM 1422226–1422258, HWML 139001, FSBC-I 133253.

Etymology: The species was named for Caalus, a chief of the vanished Calusa Tribe at the onset of the 16th century Spanish invasion of southwest Florida (Granberry, 2011), with hope that this time-spanning connection to a newly discovered species from his homeland evokes reflection on the toll and permanence of

extinction and the importance of protecting Florida's natural and cultural heritage.

Remarks

Mycteronastes caalusi n. sp. differs from its congeners by having (1) 2 medial terminal cephalic papillae (1 in *My. undulatae*), (2) an oval haptor that is wider than the body proper and lacks a deeply scalloped haptoral margin (haptor circular in outline, with scalloped margins, and narrower than body proper in *My. undulatae*; circular, scalloped, and wider than body proper in *My. icopae*), (3) a comparatively large anteromedial peripheral loculus (corresponding loculus comparatively small in *My. undulatae* and *My. icopae*), (4) an unsclerotized MCO that is wholly anterior to the vaginal pores (MCO sclerotized and extending to level of vaginal pores in *My. icopae*), (5) a relatively small distal portion of the uterus that is mostly anterior to the vaginae (uterus massive, extending well posterior to vaginae in *My. undulatae*; uterus posterior to vaginal pores and wholly inter-vaginal in *My. icopae*), and (6) a delicate uterus (uterus well developed, with thick walls in both congeners).

The figures of the haptoral hooks presented in the original descriptions of *My. undulatae* and *My. icopae* (see fig. 1E in Kearn and Beverley-Burton, 1990 and fig. 4 in Beverley-Burton and Williams, 1989) suggested that the hooks of *My. caalusi*, with their long, sweeping point, would also be diagnostic. However, the respective drawings in the original descriptions of both *My. undulatae* and *My. icopae* are inaccurate. As seen in the available type and voucher specimens, the hooks of all 3 species possessed the same basic morphology as depicted in Figure 3; thus, hook morphology was of little value in differentiating the species of *Mycteronastes*.

DISCUSSION

Species of *Mycteronastes*, as defined herein, differed from other merizocotyline by having 5 peripheral (an unpaired anteromedial loculus and 2 bilateral posterior pairs), 1 interhamular, and 17 marginal loculi; the central loculus is absent or replaced by a slight central depression in the haptor. This configuration resembles that seen in species of *Empruthotrema* Johnston & Tiegs, 1922 in which 5 peripheral, 1–3 interhamular (based on the respective locations of haptoral hook pairs 1 and 2), and 12 marginal loculi are present. *Mycteronastes* is further differentiated from *Empruthotrema* by its species possessing a pair of anchors and having the unpaired peripheral loculus anteromedial to the paired peripheral loculi (species of *Empruthotrema* lack anchors and have the unpaired peripheral loculus posteromedial in the haptor). The presence or absence of the central loculus was less useful in differentiating the 2 genera. Although some species of *Empruthotrema* have been described with a well-developed central loculus (see Whittington, 1990; Whittington and Kearn, 1992; Chisholm and Whittington, 1999; Hernández-Orts et al., 2010, among others), the central loculus may be replaced by a shallow depression in others, as observed in an undescribed species of *Empruthotrema* recently collected from the smooth butterfly ray, *Gymnura micrura* (Bloch and Schneider), in the Gulf of Mexico (D. C. Kritsky and S. A. Bullard, unpubl. data).

In their phylogenetic analysis of the Monocotylidae, Chisholm et al. (1995) could not demonstrate synapomorphies for

TABLE I. Positions of hooks within the haptors of monocotylids assigned to the Merizocotylineae based on original descriptions.

Haptoral hook pairs						
1	2	3	4	5	6	7
<i>Mycteronastes</i> , including <i>My. icopae</i> (type species), <i>My. caalusi</i> , and <i>My. undulatae</i> .						
IHL	IHL	L1	S1	S3	S5	S7
<i>Merizocotyle</i> (s.s.), including <i>Me. diaphana</i> (type species) and <i>Me. euzeti</i> .						
IHL	IHL	AS	S1	S3	S5	S7
<i>Merizocotyle</i> (s.l.), including <i>Me. amplidiscata</i> , <i>Me. pugetensis</i> , and <i>Me. sinensis</i> , respectively.						
IHL	IHL	L1	L2	S3	S5	S7
IHL	IHL	L1	S1	S3	S5	S7
IHL	IHL	L1	L2	L4	L6	L8
<i>Thaumatocotyle</i> , including <i>T. concinna</i> Scott, 1904 (type species); <i>T. australiensis</i> ; <i>T. dasybatis</i> ; <i>T. longicirrus</i> Hargis, 1955; <i>T. pseudodasybatis</i> ; <i>T. retorta</i> Hargis, 1955; <i>T. roumillati</i> de Buron & Euzet, 2005; <i>T. tunisiensis</i> Neifar, Euzet, & Ben Hassine, 2000; <i>Me. macrostrobos</i> Chisholm & Whittington, 2012; <i>Me. papillae</i> Chisholm & Whittington, 2012; <i>Me. rhadinopeos</i> Chisholm & Whittington, 2012; and <i>Me. urolophi</i> .						
IHL	IHL	L1	L2	L2	L4	L5
<i>Empruthotrema</i> (s.s.), including <i>E. raiae</i> (MacCallum, 1916) Johnston & Tiegs, 1922 (type species); <i>E. chisholmae</i> Hernandez-Orts, Ahuir-Baraja, Rago, & Montero, 2010; <i>E. dasyatidis</i> ; <i>E. stenophallus</i> Chisholm & Whittington, 2005; and <i>E. tasmaniensis</i> Chisholm & Whittington, 1999.						
IHL	AS	L1	L2	L3	L4	L5
<i>Empruthotrema</i> (s.l.), including <i>E. kearni</i> Whittington, 1990 and <i>E. torpedensis</i> Kearns, 1976; and <i>E. quindecima</i> , respectively.						
IHL	IHL	L1	L2	L3	L4	L5
IHS	AS	L1	L2	L3	L4	L5
<i>Cathariotrema selachii</i> (MacCallum, 1916) Johnston & Tiegs, 1922.						
IHL	IHL	S1	S2	S3	S4	S5

Abbreviations: IHL, interhamular loculus; IHS, interhamular septum; AS, anchor septum; S, marginal septum; L, marginal loculus; the numbers refer to the marginal septa or loculi beginning with those posterior-most in haptor and lateral to the anchor or anchor septa and progressing anteriorly. Anchor septa (AS) form the lateral limits of the interhamular region of the haptor in merizocotylineae. In species of *Empruthotrema*, which lack anchors, the anchor septa are presumed to be those lying immediately lateral to or associated with hook pair 2. *Triloculotrema* Kearns, 1993 (with 3 species) and the monotypic *Squalotrema* Kearns and Green, 1983 (both Merizocotylineae according to Chisholm and Whittington, 1999) were not included in the table because it was not possible to determine homology of the haptoral loculi with those of other merizocotyline species; marginal loculi are absent in species of the 2 genera (see Kearns and Green, 1983; Kearns, 1993; Justine, 2009; Boudaya and Neifar, 2016).

Mycteronastes and *Thaumatocotyle*; thus, they synonymized the 2 genera with the senior *Merizocotyle*. However, a review of their character analysis of the patterns of loculi in the haptor (character 8) suggested that potential synapomorphies for some monocotylid genera, including *Mycteronastes* and *Thaumatocotyle*, may have been masked when Chisholm et al. (1995) combined potentially informative features into more generalized states. For example, Chisholm et al. (1995) failed to recognize the pattern (character state) of haptoral loculi present in and restricted to *My. icopae*, *My. undulatae*, and now *My. caalusi* (Table I), which likely would have provided a synapomorphy for *Mycteronastes*. Similarly, the pattern of haptoral loculi (1 central, 4 peripheral, 1 interhamular, and 12 marginal) present in the 5 species of the terminal unresolved clade in their cladogram, which included *Merizocotyle australiensis* (Beverley-Burton and Williams, 1989) Chisholm, Wheeler, and Beverley-Burton, 1995; *Merizocotyle concinna* (Scott, 1904) Chisholm, Wheeler, and Beverley-Burton, 1995 (the species on which the type of *Thaumatocotyle* is based); *Merizocotyle longicirrus* (Hargis, 1955) Chisholm, Wheeler, and Beverley-Burton, 1995; *Merizocotyle pseudodasybatis* (Hargis, 1955) Chisholm, Wheeler, and Beverley-Burton, 1995; and *Merizocotyle retorta* (Hargis, 1955) Chisholm, Wheeler, and Beverley-Burton, 1995, was not identified as a character state in their analysis, although it might have provided the needed synapomorphy for *Thaumatocotyle*.

Furthermore, Chisholm et al. (1995) did not include the type species of *Merizocotyle* (*Merizocotyle diaphana* Cerfontaine, 1894) in their ingroup or represent its pattern of haptoral loculi (1 central, 6 peripheral [1 member of anterior pair reduced], 1 interhamular, and 17 marginal; see Cerfontaine, 1894) in their character analysis. As a result, the phylogenetic and taxonomic positions of *Merizocotyle* (s.s.) within the Monocotylidae were not determined. Only *Merizocotyle euzeti* Irigoitia, Canatore, Delpiani, Incorvaia, Lanfranchi, and Timi, 2014 possesses the pattern of loculi found in *Me. diaphana* (see Cerfontaine, 1894; Irigoitia et al., 2014), which suggests that the 2 species may be sister species and the only members at present of *Merizocotyle* (s.s.).

Merizocotyle amplidiscata Dillon and Hargis, 1965; *Merizocotyle pugetensis* Kay, 1942; and *Merizocotyle sinensis* Timofeeva, 1984 were the only other species of *Merizocotyle* (s.l.) included in the phylogenetic analysis of Chisholm et al. (1995). These 3 species had an indeterminate relationship with the unresolved clade that included the species of *Mycteronastes* and *Thaumatocotyle*. *Merizocotyle amplidiscata* and *Me. pugetensis* have the same pattern of haptoral loculi (1 central, 7 peripheral, 1 interhamular, 17 marginal), whereas the pattern in *Me. sinensis* is unique among the Merizocotylineae (1 central, 7 peripheral, 4 interhamular, 17 marginal) (see Kay, 1942; Bonham, 1950; Dillon and Hargis, 1965; Timofeeva, 1984). These patterns suggested

that 2 additional genera may exist in the group of species composing *Merizocotyle* sensu Chisholm et al. (1995) and indicated the morphological distinctiveness of *Mycteronastes* and *Merizocotyle*.

Although not included in the phylogenetic analysis of Chisholm et al. (1995), another character with potential in determining the taxonomy and phylogenetic history of the Merizocotylineae may be the positions of the 7 pairs of hooks relative to the haptoral septa and loculi. In the 3 species of *Mycteronastes*, members of hook pairs 1 and 2 occur within the interhamular loculus, pair 3 occurs within the posterior-most marginal loculi, and the remaining pairs 4–7 occur near the ends of alternating septa beginning with the anterior septum of the posterior-most marginal loculus; the 2 anterior-most septa are not associated with members of a hook pair. With the possible exception of the hook pattern in *Me. pugetensis*, this pattern is unique to the 3 species of *Mycteronastes* (see Table I). The pattern in *Me. pugetensis* could not be definitively determined from the original description and figures of the species by Kay (1942), although the redescription of *Me. pugetensis* by Bonham (1950) indicates the same pattern present in species of *Mycteronastes*. Nonetheless, *Me. pugetensis* was excluded from *Mycteronastes* by having a different number (6) and pattern of peripheral loculi. Thus, the putative characters associated with the pattern of haptoral loculi and the distribution of hooks within the haptor of *Mycteronastes* spp. provided further evidence for the validity of the genus within the Merizocotylineae.

Chisholm et al. (2001) provided another hypothesis for the evolutionary history of the Monocotyliidae inferred from an analysis of 28S rDNA sequences sourced from 26 species representing 12 monocotyliid genera. Five merizocotyline taxa were analyzed but *My. icopae* (as *Me. icopae*) was the sole representative of *Mycteronastes* as diagnosed herein. Within their clade of merizocotyline species, *Me. icopae* was depicted to be the sister species to an unresolved clade that included the remaining merizocotyline taxa: *Empruhotrema dasyatidis* Whittington and Kearns, 1982 (as *E. dasyatis*); *Empruhotrema quindecima* Chisholm and Whittington, 1999; *Me. australiensis*; and *Merizocotyle urolophi* Chisholm and Whittington, 1999; *E. dasyatidis* and *E. quindecima* formed a terminal clade that was unresolved with the latter 3 species (see fig. 1 in Chisholm et al., 2001). Hence, within the recovered merizocotyline clade and accepting *Empruhotrema* as valid, *Merizocotyle* was paraphyletic, which led Chisholm et al. (2001) to suggest that *Mycteronastes* might be valid.

Our observations of the morphology of the three species of *Mycteronastes* (see above) support this suggestion. Furthermore, *Me. australiensis* has the haptoral pattern characteristic of *Thaumatocotyle* spp., the haptoral pattern for *Me. dasyatidis* is unique among the subfamily, and the phylogenetic analysis of Chisholm et al. (2001) excluded a species of *Merizocotyle* (s.s.). Thus, their results essentially rejected the synonymies proposed by Chisholm et al. (1995), while providing support for the validity of *Mycteronastes*.

Although unrelated to merizocotyline interrelationships, marked molecular phylogenetic differences among *Calicotyle* spp. (Calicotylineae) were observed in the phylogeny provided by Chisholm et al. (2001). *Calicotyle palombi* Euzet and Williams, 1960 and *Calicotyle stossichi* Braun, 1899 from houndsharks, *Mustelus* spp., formed the sister to the apparently monophyletic clade comprised of *Calicotyle kroyeri* Diesing, 1850; *Calicotyle*

spp.; and *Calicotyle urolophi* Chisholm, Beverley-Burton, and Last, 1991, the latter 3 species of which are found in the cloacae of rays. Their phylogenetic hypothesis supported the resurrection of *Paracalicotyle* Szidat, 1970 for calicotylineae infecting houndsharks. *Paracalicotyle* was originally based on body shape and haptoral size by Szidat (1970) and subsequently by the features and fine details of the female genitalia by Bullard and Overstreet (2000). The analysis of Chisholm et al. (2001) also supported the phylogenetic distinctiveness of the body cavity-dwelling *Dictyocotyle coeliaca* Nybelin, 1941 apart from the calicotylineae occurring in the cloacae of their hosts.

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