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Nagmia rodmani n. sp., *Nagmia cisloi* n. sp., and *Probolitrema richiardii* (López, 1888) (Gorgoderidae: Anaporrhutinae) from Elasmobranchs in the Gulf of California, Mexico

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ABSTRACT: The generic diagnosis of *Nagmia* Nagaty, 1930, is emended to include species having some vitelline follicles extending into the extracecal space. Two new species belonging in the genus are described from the Gulf of California: *Nagmia rodmani* n. sp. from the body cavity of the giant electric ray, *Narcine entemedor* Jordan and Starks, 1895, and *Nagmia cisloi* n. sp. from the body cavity of the smoothtail mobula, *Mobula thurstoni* (Lloyd, 1908). Both species are distinguished from each other and the 13 other known congeners by the number of testicular follicles, ratio of widths of oral sucker to ventral sucker, and position of the vitelline follicles relative to the ceca. *Nagmia rodmani* is distinct based on the combined features: 12–17 follicles per testis, sucker width ratio of 1:1.7–2.0, vitelline follicles extending into the extracecal space, and the excretory vesicle being I-shaped and lacking perpendicular lateral branches along the main stem. *Nagmia cisloi* is distinct based on the combined features: 23–26 follicles per testis, body measuring 13.4 mm long by 14.6 mm wide, eggs measuring 47–48 µm long by 43–47 µm wide, and the excretory vesicle is I-shaped and has lateral perpendicular branches along the main stem. Supplemental data are provided for the anaporrhutine species *Probolitrema richiardii* (López, 1888) collected from a variety of rays in the Gulf of California. Our specimens are indistinguishable from those described as *Probolitrema californiense* Stunkard, 1935, and *Probolitrema mexicana* Markell (1956), both of which previously had been synonymized under *P. richiardii*. Checklists of parasites reported from *N. entemedor* and *M. thurstoni* are provided.

KEY WORDS: Digenea, Gorgoderidae, Anaporrhutinae, *Nagmia rodmani* n. sp., *Nagmia cisloi* n. sp., *Probolitrema richiardii*, *Narcine entemedor*, *Mobula thurstoni*, parasites, elasmobranchs, Gulf of California, Mexico.

Gorgoderids in the subfamily Anaporrhutinae Looss, 1901, are large trematodes that live in the body cavity of elasmobranchs worldwide. There are arguably 5 anaporrhutine genera, but distinction among these is based on some ambiguous morphological features that are summarized in the discussion. Larval stages are not known for any species in the subfamily. In this paper, we conclude an investigation on the digeneans found in a total of 817 elasmobranchs representing 42 species collected from at least 7 sites along the western shore of the Gulf of California (for collection sites, see Tyler, 2001). Digeneans belonging in Azygiidae Lühe, 1909; Syncoeliidae Looss, 1899; Ptychogonimidae Dollfus, 1937; and Gorgoderidae Looss, 1901, were collected from elasmobranchs during the field study. Species in Azygiidae, Syncoeliidae, and Ptychogonimidae were reported by Curran and Overstreet (2000). A gorgoderid from the collection belonging in *Anaporrhutum* Ofenheim, 1900, was described by Curran et al. (2003). Herein, the remaining gorgoderid mate-

rial from the collection is investigated and 2 new species of *Nagmia* Nagaty, 1930, are described: 1 from the giant electric ray, *Narcine entemedor* Jordan and Starks, 1895, the second from the smoothtail mobula, *Mobula thurstoni* (Lloyd, 1908). Supplemental data are provided for the only other gorgoderid species encountered, *Probolitrema richiardii* (López, 1888), from a variety of hosts.

MATERIALS AND METHODS

Gorgoderids were collected from the body cavity of rays obtained from commercial gill-nets or collected with hand spears during a survey of the metazoan parasites of elasmobranchs in the Gulf of California (see Tyler, 2001). Specimens of *Nagmia floridensis* Markell, 1953, were collected from the Atlantic stingray, *Dasyatis sabina* (Lesueur, 1824), from the Mississippi Sound off Biloxi, Mississippi, U.S.A., for comparative purposes. Gorgoderids were removed from the body cavity and killed with near boiling water. Killed specimens collected in Mexico were placed in 10% formalin buffered in seawater, and those killed in Mississippi were placed in 10% formalin buffered with monobasic and dibasic sodium phosphate. Worms in formalin solution were washed and then stained in aqueous Van Cleave's hematoxylin and prepared following the protocol of Curran et al. (2003). Measurements are ranges

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in μm unless indicated otherwise. Taxonomic terms follow those by Manter (1970). Ecological terms follow those by Bush et al. (1997). Names of fish are from the checklist of Nelson et al. (2004) or the catalogue by Eschmeyer (1998). Illustrations were made with the aid of a drawing tube. Specimens are deposited in the Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM, CNHE), Mexico City, Mexico; at the Harold W. Manter Laboratory (HWML) of the University of Nebraska State Museum in Lincoln, Nebraska, U.S.A.; and the Santa Barbara Museum of Natural History (SBMNH) in Santa Barbara, California, U.S.A.

Nagmia

Diagnosis

Modified from diagnoses of Yamaguti (1971) and Brooks and Mattis (1978). Gorgoderidae, Anaporphutinae. Body large; subdivided into relatively small forebody and circular or subcircular hindbody; hindbody dorsoventrally flattened or concave ventrally and convex dorsally. Tegument lacking spines. Oral sucker terminal with subterminal mouth. Prepharynx absent. Pharynx prominent. Esophagus about as long as pharynx. Ventral sucker about one third of body length from anterior end. Intestine bifurcating in forebody. Ceca with irregular margins, terminating blindly in posterior fourth of body. Testes consisting of opposing, extracecal grapelike bunches of follicles in hindbody; bunches with more than 3 follicles, with each follicle associated with a single tertiary sperm duct; tertiary sperm ducts uniting, forming secondary sperm duct; secondary sperm ducts uniting as vasa efferentia on each side of body; vasa efferentia converging, forming single male duct. Seminal vesicle elongated. Pars prostatica present. Ejaculatory duct short, unarmed. Cirrus and cirrus sac absent. Genital atrium indistinct. Genital pore medial, immediately posterior to cecal bifurcation (with the exception in *Nagmia pacifica* [Caballero, 1945], which has the genital pore at level of pharynx). Ovary submedian, amphitypic. Seminal receptacle submedian, immediately preovarian, larger than ovary. Laurer's canal absent. Vitellarium consisting of opposing ventral fields of tubular or dendritic follicles, each connecting to a common reservoir through 2 opposing vitelline ducts; vitelline fields intercecal or with some tubules extending into cecal space or extracecal space; reservoir median or submedian, adjacent to and communicating with ootype. Mehlis' gland present. Uterus intercecal. Eggs with well-developed embryos, thin-shelled, with indistinct operculum. Excretory vesicle I-shaped; main stem either lacking branches or having multiple perpendicular lateral branches; excretory pore terminal or subterminal. Parasitic in

the body cavity or pericardium of marine elasmobranchs. Type species *Nagmia yorkei* Nagaty, 1930.

Nagmia rodmani n. sp. (Figs. 1–3)

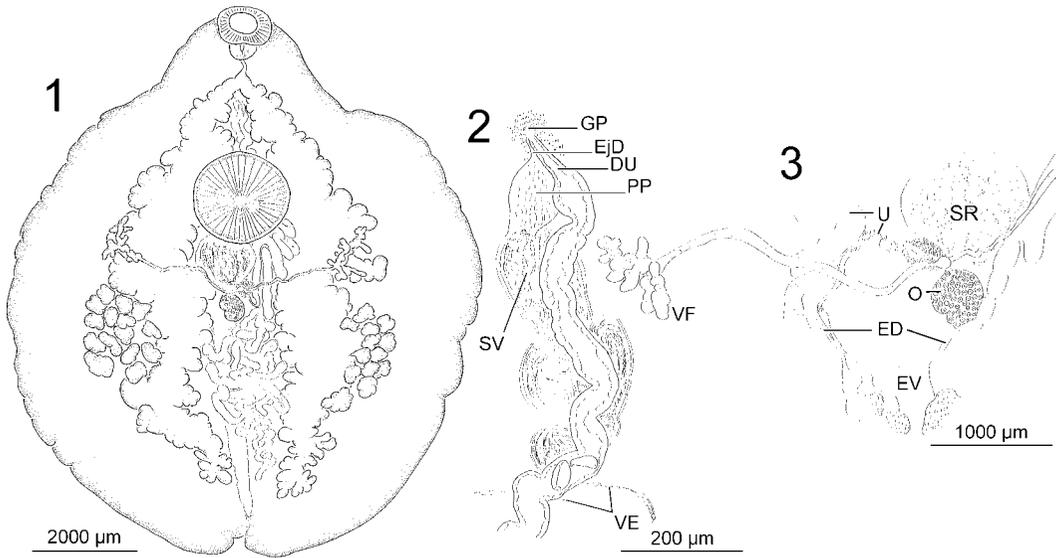
Description

Based on 10 adult specimens. Body flat, pyriform, 4.6–11.0 mm long, 4.4–9.3 mm wide. Oral sucker 470–802 long, 619–1,062 wide. Pharynx 219–407 long, 313–583 wide. Esophagus sinuous, 250–400 long. Ventral sucker 897–1,699 long, 1,027–2,195 wide. Ratio of oral sucker width to ventral sucker width 1:1.7–2.0. Forebody 1,179–2,807 long, representing 22–33% of body length. Hindbody 2,554–6,933 long, representing 47–61% of body length.

Testes follicular, in posterior half of body; left testicular field comprising 12–17 follicles, with entire field measuring 991–2,761 long, representing 17–26% of body length; right testicular field comprising 14–17 follicles, with entire field measuring 1,109–2,690 long, representing 16–26% of body length (1 exceptional specimen had both fields measuring 32% of body length). Seminal vesicle elongated, looping, intercecal, preacetabular or partially overlapping ventral sucker dorsally; proximal end 59–66 wide, distal end 121–250 wide. Pars prostatica 156–274 long, 85–152 wide. Ejaculatory duct 59–117 long, opening into small genital atrium; genital atrium surrounded by gland cells. Genital pore opening medial, immediately posterior to cecal bifurcation.

Ovary irregular or subspherical, 258–548 long, 376–642 wide. Seminal receptacle thin walled, 517–1,086 long, 587–1,154 wide. Vitelline follicles tubular; tubules in 2 ventrolateral fields; fields 375–1,487 long, 401–920 wide, with most tubules straddling ceca but some extending into extracecal space; direct distance between left and right vitelline fields 2,891–3,481, representing 38–44% of body width in 8 individuals greater than 8 mm long and 33–34% of body width in 2 individuals less than 8 mm long. Vitelline reservoir immediately preovarian. Mehlis' gland dorsal to vitelline reservoir. Uterus confined to intercecal space; distal portion extending into forebody, with walls forming short metraterm; metraterm lying ventral to male duct, opening into genital atrium. Eggs 39–62 long, 25–47 wide in metraterm.

Excretory vesicle I-shaped, extending nearly to level of ovary, lacking perpendicular lateral branches; excretory pore opening into groove at terminal end of body.



Figures 1–3. *Nagmia rodmani* n. sp. **1.** Ventral view of holotype from body cavity of *Narcine entemedor* (Narcinidae) from off Loreto, Gulf of California, Mexico. **2.** Ventral view of terminal genitalia from a paratype specimen from *N. entemedor* from the type locality. **3.** Dorsal view of ovarian complex of paratype from separate specimen of *N. entemedor* from the type locality. (DU, distal portion of uterus, or metraterm; ED, collecting ducts of excretory system; EJD, ejaculatory duct obscured by distal portion of ventral metraterm; EV, excretory vesicle; GP, genital pore; O, ovary; PP, pars prostatica; SR, seminal receptacle; SV, seminal vesicle; U, uterus; VE, vasa efferentia; VF, vitelline follicles.)

Taxonomic Summary

Type host: Giant electric ray, *N. entemedor* (Narcinidae).

Type locality: Gulf of California, near Loreto, Mexico (26°04'04"N, 111°12'31"W).

Site of infection: Body cavity.

Prevalence of infection: 100% (3 fish examined).

Mean intensity of infection: 6.7 worms per infection (ranging from 3 to 10 worms per infection).

Specimens deposited: Holotype IBUNAM, CNHE No. 6199; 1 Paratype HWML No. 48889; 1 Paratype SBMNH 423115.

Etymology: The specific name *rodmani* refers to James Rodman (National Science Foundation) in recognition of his appreciation of, and dedication to, taxonomic research.

Remarks

Nagaty (1930) erected *Nagmia* for species of Anaporrhutinae with large numbers of testicular follicles in opposing extracecal clusters and with vitelline

fields in the intercecal space. Yamaguti (1971) considered the ceca to be diverticulate, but we consider the ceca to have irregular margins instead. Yamaguti (1971) described the excretory vesicle as being tubular, with or without side branches. We, like Brooks and Mattis (1978), prefer to call the excretory vesicle I-shaped, and we called the side branches of Yamaguti (1971) perpendicular lateral branches associated with the bladder. Brooks and Mattis (1978) refined the diagnosis of *Nagmia* to include species with vitelline follicles that extend at least partially into the extracecal space. While no single feature serves to differentiate *Nagmia* from other anaporrhutine genera, collectively, the number of testicular follicles, location of the vitelline fields, irregular cecal margins, and the type of excretory vesicle effectively distinguish the genus (Nagaty, 1930; Markell, 1953a; Brooks and Mattis, 1978; Curran et al., 2003).

Nagmia rodmani n. sp. differs from the 13 recognized species in *Nagmia*. These are *N. yorkei*, *Nagmia larga* (Lühe, 1906), and *Nagmia yamagutia* Tandon, 1969, from the Indian Ocean; *Nagmia concolori* (Nagaty and Abdel-Aal, 1961), *Nagmia nebrii* Nagaty and Abdel-Aal, 1961, and *Nagmia stegostomatis* (Nagaty and Abdel-Aal, 1961) from the Red

Sea; *Nagmia rosettensis* Melouk, 1940, from the Mediterranean Sea off northern Egypt; *Nagmia africana* Fischthal and Thomas, 1972, *Nagmia senegalensis* Fischthal and Thomas, 1972, and *Nagmia trygonis* (Dollfus, 1971) from the eastern tropical Atlantic Ocean off Senegal; *N. pacifica* and *Nagmia peruviana* Tantalean and Rodriguez, 1990, from the eastern Pacific Ocean; and *N. floridensis* from the Gulf of Mexico. Given the rarity, poor fixation of specimens, and low number of specimens examined in most records concerning these species (i.e., Lühe, 1906; Nagaty, 1930; Melouk, 1940; Markell, 1953a; Nagaty and Abdel-Aal, 1961; Tandon, 1969; Dollfus, 1971; Fischthal and Thomas, 1972; Tantalean and Rodriguez, 1990), additional material and/or molecular evaluation could modify this list.

We differentiated *N. rodmani* from most of its 13 congeners on the basis of the location of the vitelline tubules. In some species the vitelline tubules are entirely intercecal (e.g., *N. yorkei*, *N. larga*, *N. pacifica*, *N. concolori*, *N. nebrii*, *N. stegostomatis*, and *N. peruviana*); in some they are largely intercecal with some follicles ventrally overlapping the ceca (e.g., *N. rosettensis*, *N. africana*, *N. senegalensis*, and *N. yamagutia*). Only specimens of *N. floridensis*, *N. trygonis*, and *N. rodmani* have at least some vitelline tubules that extend into the extracecal space. Essentially, these 3 species have relatively longer vitelline ducts compared with other species in *Nagmia*. *Nagmia rodmani* is very similar to *N. floridensis* in size and overall body shape, and the range in length of the testicular field relative to overall body length is identical for both species (16–26% in *N. rodmani* and in all 10 specimens of *N. floridensis* we collected from *D. sabina* in the Mississippi Sound). *Nagmia rodmani* differs from *N. floridensis* by having 12–17 testicular follicles per field compared with 13–30 reported by Brooks and Mattis (1978) and 17–27 in our specimens of *N. floridensis*. The ratio of the oral sucker width to ventral sucker width is 1:1.7–2.0 in *N. rodmani* compared with 1:1.2–1.7 in *N. floridensis* (Markell, 1953a; Brooks and Mattis, 1978). *Nagmia rodmani* and *N. floridensis* also differ slightly by the configuration of the vitellarium. The right and left vitelline foci, the points of divergence of vitelline tubules from the primary ducts, in *N. rodmani* are 2,891–3,481 μm apart, ranging from 38–44% of the body width. The vitelline foci in our 10 specimens of *N. floridensis* are 1,628–2,470 μm apart, representing 22–34% of the body width. Consequently, the relatively longer distance between the vitelline fields in

N. rodmani provides a good differentiating feature. *Nagmia floridensis* has been reported from a variety of coastal rays in the Gulf of Mexico (Markell, 1953a; Brooks and Mattis, 1978; present study). We have also collected *N. floridensis* from the cownose ray, *Rhinoptera bonasus* (Mitchill, 1815), off Mississippi, U.S.A. (Olson et al., 2003). The distribution of *N. rodmani* and *N. floridensis* on opposite sides of Central America suggests to us that the 2 species may be sister taxa whose ancestral population may have become isolated by closing of the Panamanian Isthmus approximately 3.5–3.1 million years ago (Coates and Obando, 1996).

Nagmia rodmani differs from *N. trygonis* by having a smaller body (4.6–11.0 mm long, 4.4–9.3 mm wide compared with 13–18.5 mm long, 12.5–17.0 mm wide) and a lower sucker width ratio (1:1.7–2.0 compared with 1:2.0–3.6). Dollfus (1971) had only 2 specimens of *N. trygonis*, which he originally described as *Nagmioides trygonis* Dollfus, 1971, from the marbled stingray, *Trygon marmorata* Steindachner, 1892 (= *Dasyatis marmorata* [Steindachner, 1892]), off Senegal in western Africa. Brooks and Mattis (1978) declared *Nagmioides* Dollfus, 1971, a junior synonym of *Nagmia*, a decision with which we agree. Fischthal and Thomas (1972) described *N. senegalensis* based on specimens collected from the same host, *D. marmorata*, off Senegal, and did not compare their specimens with *N. trygonis*. A thorough comparison between *N. trygonis* and *N. senegalensis* requires an investigation of more specimens. *Nagmia rodmani* differs from *N. senegalensis* by lacking 5 anterior lobes on the pharynx and because the vitelline follicles extend into the extracecal space rather than being intercecal and overlapping the ceca.

Obvious morphological differences exist among the 3 species from the eastern Pacific Ocean: *N. rodmani*, *N. pacifica*, and *N. peruviana*. *Nagmia rodmani* differs from both species with which it is sympatric by having the vitelline tubules extending into the extracecal space rather than being entirely intercecal. *Nagmia rodmani* differs from *N. pacifica* by having the genital pore opening immediately posterior to the intestinal bifurcation rather than at the pharyngeal level. Tantalean and Rodriguez (1990) described *N. peruviana* from the smoothtail mobula, *Mobula lucasana* Beebe and Tee-Van, 1938 (= *M. thurstoni*), off Peru; *N. rodmani* differs from it by having fewer testicular follicles per field (12–17 compared with 21–35) and a smaller testicular field length (17–26% of body length compared with 42–44% of body length).

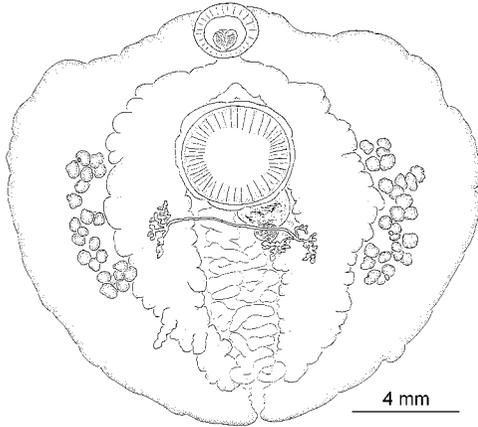


Figure 4. *Nagmia cisloi* n. sp., ventral view of holotype from body cavity of *Mobula thurstoni* (Myliobatidae) from the Gulf of California, Mexico. Ventral sucker obscures observation of terminal genitalia.

***Nagmia cisloi* n. sp.
(Fig. 4)**

Description

Based on 1 adult specimen with anterior end slightly curled ventrally. Body flat, pyriform, 13.4 mm long (estimated due to curl), 14.6 mm wide. Oral sucker 1,935 long, 2,313 wide. Pharynx 873 wide. Esophagus sinuous, approximately 400 long. Ventral sucker 3,729 long, 4,012 wide. Ratio of oral sucker width to ventral sucker width 1:1.7. Forebody 3,511 long, representing approximately 26% of body length. Hindbody 8,556 long, representing approximately 64% of body length.

Testes follicular in middle third of body; left testicular field comprising 26 follicles with field measuring 5,074 long, representing 38% of body length; right testicular field comprising 23 follicles with field measuring 5,192 long, representing 39% of body length; follicles lobed or entire, 235–556 wide. Seminal vesicle obscured, 786 wide at widest observable part. Pars prostatica roughly spindle shaped, 371 wide (length not clearly measurable). Ejaculatory duct (length not clearly measurable), emptying into genital atrium. Genital pore medial, opening immediately anterior to ventral sucker.

Ovary subspherical, submedian on left side, 556 long, 767 wide. Seminal receptacle thin walled 1,416 long, 1,581 wide. Vitelline follicles tubular; tubules in 2 opposing ventral fields at ovarian level; left field 1,982 long, 755 wide; right field 1,369 long, 2,006 wide. Vitelline tubules overlapping ceca but not extending into extracecal space. Direct distance

between left and right vitelline fields 4.4 mm, representing 30% of body width. Vitelline reservoir occurring lateral to ovary on left side. Uterus confined to intercecal space; distal portion extending dorsal to ventral sucker and into forebody, with walls forming a metraterm; metraterm lying ventral to male duct, opening into genital atrium. Eggs 47–48 long, 43–47 wide in metraterm.

Excretory vesicle presumably I-shaped, anterior extent not observed. Posterior region of main stem with perpendicular lateral branches on both sides; excretory pore slightly subterminal, dorsal.

Taxonomic Summary

Type host: Smoothtail mobula, *M. thurstoni* (Myliobatidae).

Type locality: Gulf of California, off La Paz, Baja California Sur, Mexico (24°12'24"N, 110°25'04"W).

Site of infection: Body cavity.

Prevalence of infection: 50% (2 fish examined).

Mean intensity of infection: 1 worm per infection.

Specimen deposited: Holotype IBUNAM, CNHE No. 6198.

Etymology: The name *cisloi* honors Paul R. Cislo (Yale University), an exceptional teacher and biologist who played a major role in the collection of the material used in this work.

Remarks

Nagmia cisloi n. sp. is described from a single specimen that was slightly curled ventrally at the level of the oral sucker. Despite this, we consider the specimen to differ so dramatically from other species of *Nagmia* that we are comfortable naming the new species. *Nagmia cisloi* may be distinguished from the congeners found in the Indian Ocean, Red Sea, and Mediterranean Sea based on differences in 1 or more important specific features: testicular follicle number, sucker width ratio, body size, and egg size. *Nagmia cisloi* and *N. rosettensis* from the Mediterranean Sea have only a slightly different number of testicular follicles per lateral field (23–26 compared with 18–22 for *N. rosettensis*) but *N. cisloi* has a larger body (13.4 mm long by 14.6 mm wide compared with 7–9 mm long by 6–8 mm wide), and smaller eggs (47–48 μ m long by 43–47 μ m wide compared with 66 μ m long by 62 μ m wide) (Melouk, 1940). *Nagmia cisloi* has fewer testicular follicles per field (23–26) and smaller eggs (47–48 μ m long by 43–47 μ m wide)

than *N. yorkei* from the Indian Ocean, which has 29–35 testicular follicles per field and eggs measuring 96 μm long by 48 μm wide (Nagaty, 1930). *Nagmia cisloi* has more testicular follicles per field (23–26) and a smaller sucker width ratio (1:1.7) than *N. larga* from the Indian Ocean, where the species has 14–16 testicular follicles per field and a sucker width ratio of 1:2.8 (see Baylis, 1927) and smaller eggs than *N. yamagutia*, the other species from the Indian Ocean, where the species has eggs measuring 60–75 μm long by 48–55 μm wide (Tandon, 1969). *Nagmia cisloi* differs from the 3 species found in the Red Sea (*N. concolori*, *N. nebrii*, and *N. stegostomatis*) by having smaller, rounder eggs measuring 47–48 μm long by 43–47 μm wide compared with 60 μm long by 30 μm wide for these 3 species (Nagaty and Abdel-Aal, 1961).

Nagmia cisloi is larger in body size (13.4 mm long, 14.6 mm wide) than either *N. africana* (3.7–5.6 mm long by 3.0–5.0 mm wide) or *N. senegalensis* (4.9–12.0 mm long by 2.5–10.5 mm wide), both from the eastern Atlantic Ocean (see Fischthal and Thomas, 1972), and differs from *N. trygonis*, a third eastern Atlantic species, by having smaller rounder eggs measuring 47–48 μm long by 43–47 μm wide compared with 49–70 μm long by 30–40 μm wide, and having the vitelline fields farther apart in *N. trygonis*, measuring 6.6 mm, representing 39% of body width compared with 4.4 mm, representing 30% of body width in *N. cisloi* (see Dollfus, 1971). Also, the vitelline tubules extend at least partially into the extracecal space in *N. trygonis*, compared with overlapping the ceca in *N. cisloi*.

Nagmia cisloi most closely resembles the 3 species in the eastern Pacific Ocean: *N. pacifica*, *N. rodmani*, and *N. peruviana*; and *N. floridensis* from the western Atlantic Ocean. *Nagmia cisloi* and *N. pacifica* are about the same size, but *N. cisloi* has about twice as many testicular follicles per field (23–26 compared with 9–13) and the genital pore is located immediately posterior to the intestinal bifurcation rather than at pharynx level (Lamothe-Argumedo, 1969). *Nagmia pacifica* is the only species in the genus that has the genital pore located so far anteriorly. Additionally, the 2 species have approximately the same sucker width ratio (1:1.7), but *N. cisloi* has larger suckers with the oral sucker measuring 1,935 μm long by 2,313 μm wide and the ventral sucker measuring 3,729 μm long by 4,012 μm wide compared with an oral sucker measuring 510–983 μm long by 907–945 μm wide and a ventral sucker measuring 1,021–1,644 μm long by 1,134–1,758 μm wide (Caballero, 1945). Since our specimen was heat fixed without pressure, fixation artifact does not

explain the relatively larger sucker sizes in *N. cisloi*. *Nagmia cisloi* differs from *N. rodmani* by having about twice as many testicular follicles per field (23–26 compared with 12–17) and a relatively shorter distance between the vitelline fields (30% of body width compared with 38–44% in *N. rodmani*). *Nagmia cisloi* has about the same number of testicular follicles per field (23–26 compared with 13–30) as *N. floridensis* from the Gulf of Mexico, and about the same distance between vitelline fields (30% compared with 22–34% of body width), but specimens of *N. cisloi* have relatively longer testicular follicle fields relative to body length (38–39% compared with 16–26% of body length in *N. floridensis*). In addition, the sucker width ratio is 1:1.7 in *N. cisloi* compared with 1:1.2–1.7 in *N. floridensis*. *Nagmia cisloi* occurs in the same host, *M. thurstoni*, and shares the same number of testicular follicles per field as the remaining species, *N. peruviana*, but relative testicular field length appears to be greater in *N. peruviana* (42–44% compared with 38–39% of body length). Additionally, the hindbody is broadly circular and the sucker width ratio is 1:1.7 in *N. cisloi*, whereas the hindbody is oval and the sucker width ratio is 1:1.3 in *N. peruviana*. Tantalean and Rodriguez (1990) fixed their specimens of *N. peruviana* with unheated 10% formalin with pressure; consequently, the features that distinguish *N. cisloi* from *N. peruviana* may be distorted. Specimens of *N. peruviana* killed in hot water or hot formalin with no pressure are required for more adequate comparison between the species.

Probolitrema richiardii (Fig. 5)

Synonyms: *Distoma richiardii* López, 1888; *Anaporphutum richiardii* Looss, 1900; *Probolitrema californiense* Stunkard, 1935; *Probolitrema mexicana* Markell (1956).

Supplemental Data

Based on 7 adult specimens. Body 5.3–9.5 mm long, 4.0–7.5 mm wide. Tegument smooth. Oral sucker terminal, 548–779 long, 658–1,003 wide. Mouth subterminal. Prepharynx absent. Pharynx 282–470 long, 376–525 wide. Esophagus sinuous, lacking minute diverticula, 250–455 long. Ceca ending blindly near posterior end of body; margins irregular. Ventral sucker in anterior half of body, lacking peduncle, 1,015–1,770 long, 991–1,746 wide. Ratio of oral sucker width to ventral sucker width 1:1.5–1.6. Forebody conical, 1,694–2,381

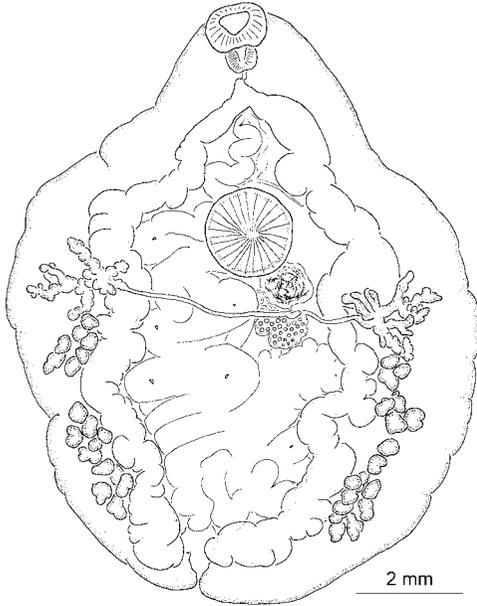


Figure 5. *Probolitrema richiardii*, ventral view of specimen from the body cavity of *Urobatis* sp. (Urolophidae) from off Isla San Esteban, Gulf of California, Mexico.

long, representing 23–38% of body length. Hindbody flat, oval, 2,419–5,546 long, representing 40–62% of body length.

Testicular follicles extracecal, distributed in 2 opposing elongated fields in hindbody; left testicular field comprising 15–25 follicles, entire field measuring 1,534–3,304 long, representing 26–41% of body length; right testicular field with 18–25 follicles, entire field measuring 1,510–3,304 long, representing 25–46% of body length; testicular follicles lobed to entire, 172–415 wide. Vasa efferentia joining at level dorsal to ventral sucker, forming looping elongated seminal vesicle; seminal vesicle 86–101 wide at proximal end, 149–235 wide at greatest width near distal end. Pars prostatica 172–227 long, 117–172 wide. Ejaculatory duct 45–59 long, opening into shallow genital atrium. Genital pore medial, opening immediately posterior to intestinal bifurcation.

Ovary entire or irregular, submedian, amphitypic, 235–603 long, 415–1,002 wide. Seminal receptacle thin walled, preovarian, 564–814 long, 548–940 wide. Mehlis' gland submedian, preovarian. Laurer's canal absent. Vitelline follicles tubular, tubules in 2 ventrolateral fields in middle third of body; fields largely extracecal, 579–1,392 long, 548–1,652 wide. Vitelline reservoir submedian, ventral at posterior

margin of seminal receptacle. Uterus intercecal, thin walled, looping; loops descending from ovary and Mehlis' gland to posterior end of body then ascending and extending to genital atrium; distal uterus relatively thick walled, comprising a muscular metraterm. Eggs operculate, thin-shelled, 35–59 long, 23–50 wide in metraterm.

Excretory vesicle not fully observed; longitudinal secondary collecting ducts present lateral to vitelline fields and testes on either side of body; excretory pore opening into small groove at posterior end of body.

Taxonomic Summary

Hosts: *Urobatis* sp. (Urolophidae); whiptail stingray, *Dasyatis brevis* (Garman, 1880), and longtail stingray, *Dasyatis longa* (Garman, 1880) (Dasyatidae); whitesnout guitarfish; *Rhinobatos leucorhynchus* Günther, 1867 (Rhinobatidae); bat ray, *Myliobatis californica* Gill, 1865, and longnose eagle ray, *Myliobatis longirostris* Applegate and Fitch, 1964 (Myliobatidae).

Localities: Gulf of California, Mexico, off Isla San Esteban (28°44'05"N, 112°38'12"W); off Bahía de Los Angeles (29°02'10"N, 113°31'30"W); off Loreto (26°03'14"N, 111°11'46"W); and off Santa Rosalia (27°17'23"N, 112°08'13"W).

Site of infection: Body cavity.

Prevalence of infection: *Urobatis* sp. = 100% [$n = 2$]; *D. brevis* = 43% [$n = 7$]; *M. californica* = 6% [$n = 15$]; *M. longirostris* = 33% [$n = 3$]; *D. longa* = 50% [$n = 2$]; *R. leucorhynchus* = 100% [$n = 2$].

Mean intensity of infection: *Urobatis* sp. = 1.5 worms per infection; *D. brevis* = 1.33 worms per infection; *M. californica* = 2 worms per infection; *M. longirostris* = 1 worm per infection; *D. longa* = 1 worm per infection; *R. leucorhynchus* = 2 worms per infection.

Specimens deposited: Voucher specimen HWML No. 48890; voucher specimen SBMNH 423116; voucher specimen IBUNAM, CNHE No. 6200.

Specimens examined: *Probolitrema californiense*, holotype from the American Museum of Natural History (AMNH) No. 179; *P. californiense*, 2 paratypes (AMNH) Nos. 1487.1, 1487.2; *P. californiense*, 1 voucher specimen (USNPC) No. 82777; *P. mexicana*, holotype (USNPC) No. 49354.

Notes: The type host for *P. richiardii* is the piked dogfish, *Squalus acanthias* Linnaeus, 1758, according to López (1888) and Looss (1902). The type locality is the Mediterranean Sea, where the species

was also reported in *Mustelus vulgaris* (an invalid name) and the common eagle ray, *Myliobatis aquila* (Linnaeus, 1758) (see Ofenheim, 1900). *Probolitrema richiardii* was also reported from the body cavity of a cat shark (*Scyllium* sp.) from the Atlantic Ocean off Cape Town, South Africa (Ofenheim, 1900). Ofenheim (1900) stated that the species is recorded from the body cavity of its host.

Remarks

Probolitrema richiardii was originally described as *Distoma richiardii*. Ofenheim (1900) erected *Anaporrhutum* Brandes in Ofenheim, 1900, for *Anaporrhutum albidum* Brandes in Ofenheim, 1900, and made the new combination *Anaporrhutum richiardii* (López, 1888) for *D. richiardii*. Looss (1902) erected *Probolitrema* Looss, 1902, and created the new combination *P. richiardii* for *A. richiardii*. Diagnostic features traditionally used to characterize species in *Probolitrema* include body size, number of testicular follicles, ratio of oral to ventral sucker width, and egg size; however, Gibson (1976) found these features inadequate for distinguishing species. Furthermore, Gibson (1976) pointed out that many of the species were described before the first adequate description of the type species, *P. richiardii*, was made available by Dollfus (1937) for comparison. Consequently, Gibson (1976) considered all 10 named species in *Probolitrema* to be junior synonyms of *P. richiardii*. We tentatively agree with Gibson's (1976) decision until comparisons of life history or molecular data from the various forms are conducted.

Prior to Gibson's (1976) amalgamation of the species assigned to *Probolitrema*, 2 species from the eastern Pacific Ocean were given names: *P. californiense* and *P. mexicana* Markell, 1956. Stunkard (1935) reported *P. californiense* from *M. californica* in Monterey Bay, California, U.S.A., and Markell (1953b) reported *P. californiense* from the thornback, *Platyrhinoidis triseriata* (Jordan and Gilbert, 1880), and the shovelnose guitarfish, *Rhinobatos productus* Ayres, 1854, from off La Jolla, California, U.S.A. Stunkard (1935) contended that the main differentiating feature for *P. californiense* was a bipartite seminal vesicle, but Markell (1953b) refuted the presence of a bipartite seminal vesicle in his redescription of *P. californiense*, but he still accepted the species as valid. We examined the holotype (AMNH 179) and 2 paratypes (AMNH 1487.1, 1487.2) of *P. californiense* plus 1 voucher specimen (USNPC No. 82777) and did not observe a bipartite seminal vesicle in any of the material examined.

Instead, we found an elongated looping seminal vesicle and a large amount of sperm in the pars prostatica in 2 of the specimens. We suspect Stunkard (1935) considered the pars prostatica to be part of the seminal vesicle. Gibson (1976) noted that the measurements reported for egg size, sucker ratio, and testicular follicle number for *P. californiense* overlapped those reported for *P. richiardii*. Measurements of these 3 features from the specimens examined in the present study were also consistent with those of *P. richiardii*. Markell (1956) reported *P. mexicana* from the sicklefin smoothhound, *Mustelus lunulatus* Jordan and Gilbert, 1882, *Urobatis maculatus* Garman, 1913, and *D. brevis*, in Santa Inez Bay, Baja California, Mexico. He characterized it by the presence of diverticulate to grossly saccate intestinal ceca. We examined the holotype of *P. mexicana* (USNPC 49354) and determined that the cecal margins were irregular and prefer that term to "diverticulate or grossly saccate" since not all diverticula that emerge from the cecal margins are longer than they are wide. Specimens of *P. richiardii* from this study all had ceca with irregular margins like in the holotype for *P. mexicana*. Looss (1902) and Dollfus (1971) reported that the ceca were saccate and/or diverticulate (which we again refer to as having an irregular margin) in *P. richiardii* and Johnston (1934) also used the term saccate to describe the ceca of *Probolitrema rotundatum* Johnston, 1934. We conclude from these works and our own observations, as earlier researchers did, that the ceca are normally irregular and may appear smooth in certain individuals presumably due to fixation artifact (i.e., Ofenheim, 1900; Looss, 1902; Johnston, 1934; Woolcock, 1935). We advocate that the condition of the ceca should not be used as a specific-level feature for species of *Probolitrema*. Furthermore, we agree with Gibson (1976) and consider *P. californiense* and *P. mexicana* as junior synonyms of *P. richiardii*.

DISCUSSION

Narcine entemedor, the type host for *N. rodmani*, is a coastal ray that occurs in the eastern Pacific Ocean from Mexico to Peru, and *M. thurstoni*, the type host for *N. cisloii*, is a ray with a circumtropical distribution between 38°N and 34°S (Froese and Pauly, 2007). Anaporrhutine species have been reported from both rays, but notably, no anaporrhutine species has been reported from *M. thurstoni* outside the eastern Pacific Ocean. Checklists are included below for parasites reported from both ray species.

Anaporrhutinae comprises the 5 genera *Anaporrhutum*, *Nagmia*, *Petalodistomum* Johnston, 1913, *Probolitrema*, and *Staphylorchis* Travassos, 1922. Stunkard (1935) and Gibson (1976) each summarized the taxonomic history of Anaporrhutinae. Members of the subfamily are all relatively large flattened gorgoderids that as adults live in the body cavity or pericardium of elasmobranchs. They all have a pharynx, 2 opposing bunches of testicular follicles, a uterus confined to the intercecal region of the hindbody, a vitellarium consisting of 2 opposing fields comprising digitiform or acinous follicles, and the main stem of the excretory vesicle extends to the level immediately posterior to the ovary. There are few features useful for differentiating genera in the subfamily. Species in *Anaporrhutum* differ from other anaporrhutines by having testicular follicles ventrally straddling the ceca (Looss, 1902; Curran et al., 2003). Species in *Nagmia* have extracecal testes, vitelline fields ventrally straddling the ceca or entirely intercecal, and ceca with irregular margins. The single species in *Petalodistomum*, *Petalodistomum polycladum* Johnston, 1913, has irregular cecal margins and extracecal testes like in species of *Nagmia* but differs from all other anaporrhutines by having each testis comprising 1 to 3 large masses rather than multiple follicles (Johnston, 1913; Johnston, 1934). Arguably, *P. polycladum* differs from members of *Nagmia* only by the number and size of the follicles that make up each testis. Consequently, *Nagmia* might possibly represent a junior synonym of *Petalodistomum*, but we hesitated to dwell on this problem here because we lacked material of *P. polycladum* for comparison. The single species in *Probolitrema*, *P. richiardii*, usually has ceca with irregular margins, and the testicular follicles and vitelline fields are extracecal (Gibson, 1976). Species in *Staphylorchis* have sinuous ceca, extracecal testes, and intercecal vitelline fields (Johnston, 1934; Markell, 1953a).

Depending on one's interpretation, the shape of the excretory vesicle may be useful or confounding when differentiating genera in Anaporrhutinae. *Anaporrhutum albidum*, *Anaporrhutum euzeti* Curran, Blend, and Overstreet, 2003, and probably all species in *Anaporrhutum* have an H-shaped excretory vesicle (Ofenheim, 1900; Curran et al., 2003). Likewise, species in *Staphylorchis* have an H-shaped excretory vesicle (Johnston, 1934; Samuel, 1952; Mehra, 1960). The shape of the excretory vesicle is more ambiguous in *P. richiardii*. Offenheim (1900) reported and clearly illustrated a Y-shaped excretory vesicle for *P. richiardii*, similar to one typically

found in species in Cryptogonimidae Ward, 1917, or Atractotrematidae Yamaguti, 1939. Gibson (1976) considered *P. richiardii* to have an H-shaped excretory vesicle. Markell (1953b) observed a sectioned specimen of *P. richiardii* and described an elongated excretory vesicle that bifurcates slightly posterior to the ovary, noting that the bifurcated arm on the ovarian side subdivided at least once more, suggesting to us that the excretory vesicle is H-shaped. We agree with Gibson (1976) and consider the excretory vesicle H-shaped in *P. richiardii* with the bifurcating arms being slightly more diagonal in orientation than those in species of *Anaporrhutum* or *Staphylorchis*. *Petalodistomum polycladum* has an I-shaped excretory vesicle equipped with numerous short perpendicular lateral branches emanating from the main stem (Johnston, 1913; Nagaty, 1930). Great variability in the configuration of the excretory vesicle has been reported among species of *Nagmia*. *Nagmia yorkei*, like *P. polycladum*, has an I-shaped excretory vesicle with numerous perpendicular lateral branches that extend as far as the inner margin of the ceca (Nagaty, 1930). Similarly, *N. senegalensis* has an I-shaped excretory vesicle with prominent perpendicular lateral branches, and *N. rosettensis* has an I-shaped excretory vesicle with some indistinct perpendicular lateral branches (Melouk, 1940; Fischthal and Thomas, 1972). *Nagmia pacifica* has an I-shaped excretory vesicle with smooth walls that lack perpendicular branches (Caballero, 1945). *Nagmia africana* and *N. floridensis* have an I-shaped excretory vesicle that lacks perpendicular branches (Fischthal and Thomas, 1972; Brooks and Mattis, 1978); *N. larga* purportedly has a Y-shaped excretory vesicle (Lühe, 1906). Observations of the excretory vesicle were not reported in the descriptions of *N. nebrii*, *N. stegostomatis*, *N. concolori*, *N. yamagutia*, *N. trygonis*, and *N. peruviana*. *Nagmia rodmani* clearly has an I-shaped excretory vesicle that lacks perpendicular lateral branches, similar to the configuration reported for *N. africana* and *N. floridensis*. *Nagmia cisloi* has several perpendicular lateral branches visible in the posterior end of the main stem, thus resembling *P. polycladum*, *N. yorkei*, *N. senegalensis*, and *N. rosettensis*.

Historically, several other genera have been included in Anaporrhutinae. In addition to the 5 genera we recognize, Dollfus (1971) and Gibson (1976) included *Pernagmia* Nagaty and Abdel-Aal, 1961, and *Nagmioides*. Nagaty and Abdel-Aal (1961) erected *Pernagmia* for specimens similar to *Nagmia*, differing only in the shape of the vitelline follicles and their position relative to the seminal receptacle

and ovary. Yamaguti (1971) considered this action untenable and referred to *Pernagmia* as a junior synonym of *Nagmia*, and we agree. Dollfus (1971) distinguished the genus *Nagmioides* from *Nagmia*, as referred to in the remarks above, on the basis that the vitelline fields ventrally straddled the ceca in the former genus but were entirely intercecal in the latter genus; however, Brooks and Mattis (1978) considered *Nagmioides* a junior synonym of *Nagmia* because they observed that the vitelline fields ventrally straddled the ceca in *N. floridensis*. We observed that the vitelline fields ventrally straddled the ceca in our specimens of *N. floridensis* as well as in both new species described herein and support the opinion of Brooks and Mattis (1978) that *Nagmioides* is a junior synonym of *Nagmia*. Markell (1953a) considered *Petalodistomum pacificum* Caballero, 1945, to be indistinguishable from species in *Nagmia* and created the new combination *N. pacifica* for the species. Despite this, Lamothe-Argumedo (1969) erected *Winteria* Lamothe-Argumedo, 1969, for *P. pacificum* on the basis that the testes and vitelline follicles were shaped differently, the testicular follicles were more numerous, the genital pore opened at the level of the pharynx rather than immediately posterior to the intestinal bifurcation, and the parasite infected a carcharhinid shark and not a skate or ray. As Lamothe-Argumedo (1969) pointed out, the numerous testicular follicles of *W. pacifica* exclude the species from *Petalodistomum*, and the position of the genital pore is unprecedented for Anaporrhutinae. We acknowledge that the position of the genital pore is aberrant in *N. pacifica*, and testicular follicle number is not a strong feature for differentiating genera in Anaporrhutinae; however, until the position of the genital pore is confirmed from more specimens of *N. pacifica*, and molecular techniques are used to compare specimens of *P. polycladum*, *N. pacifica*, and other species of *Nagmia*, controversy will surround this issue. We agree with Markell (1953a) for the present and consider this species to belong in *Nagmia* as *N. pacifica*.

CHECKLIST OF PARASITES PREVIOUSLY REPORTED FROM *NARCINE ENTEMEDOR*

Cestoda

***Acanthobothrium franus* Marques, Centritto, and Stewart, 1997**

Site of infection: Spiral valve.

Distribution: Costa Rica.

Reports: Marques et al., 1997; Ghoshroy and Caira, 2001; Campbell and Beveridge, 2002.

***Acanthobothrium inbitorium* Marques, Centritto, and Stewart, 1997**

Site of infection: Spiral valve.

Distribution: Costa Rica.

Reports: Marques et al., 1997; Ghoshroy and Caira, 2001; Campbell and Beveridge, 2002.

Copepoda

***Taeniacanthodes dojirii* Braswell, Benz, and Deets, 2002**

Sites of infection: Dorsal and ventral body surfaces.

Distribution: Gulf of California.

Report: Braswell et al., 2002.

Digenea

Anaporrhutum euzeti

Sites of infection: Body cavity, pericardial cavity.

Distribution: Gulf of California.

Report: Curran et al., 2003.

***Nagmia rodmani* n. sp.**

Site of infection: Body cavity.

Distribution: Gulf of California.

Report: Present study.

CHECKLIST OF PARASITES PREVIOUSLY REPORTED FROM *MOBULA THURSTONI*

Cestoda

***Hemionchos striatus* Campbell and Beveridge, 2006**

Site of infection: Spiral valve.

Distribution: Gulf of California.

Report: Campbell and Beveridge, 2006.

***Mobulocestus lepidoscolex* Campbell and Beveridge, 2006**

Site of infection: Nephridial system.

Distribution: Gulf of California.

Report: Campbell and Beveridge, 2006.

***Mobulocestus mollis* Campbell and Beveridge, 2006**

Site of infection: Cloaca.

Distribution: Gulf of California.

Report: Campbell and Beveridge, 2006.

***Mobulocestus nephritides* Campbell and Beveridge, 2006**

Site of infection: Nephridial system.

Distribution: Gulf of California.

Report: Campbell and Beveridge, 2006.

Copepoda

***Echthrogaleus disciarai* Benz and Deets, 1987**

Site of infection: Dorsal surface of pectoral fin.

Distribution: Gulf of California.

Report: Benz and Deets, 1987.

***Entepherus laminipes* Bere, 1936**

Site of infection: Brachial filters.

Distribution: Gulf of California.

Report: Benz and Deets, 1988.

***Kroeyerina mobulae* Deets, 1987**

Site of infection: Nasa lamellae.

Distribution: Gulf of California.

Report: Deets, 1987.

***Pupulina brevicauda* Wilson, 1952**

Sites of infection: Around mouth, anterior end.

Distribution: California.

Reports: MacGinitie, 1947; Wilson, 1952; Yamaguti, 1963.

Notes: MacGinitie (1947, p. 278) reported that *P. brevicauda* (see Wilson, 1952), parasitic on *M. thurstoni*, was itself parasitized by a "tiny trematode" mainly on the carapace of the copepod.

***Pupulina minor* Wilson, 1952**

Site of infection: Around mouth.

Distribution: California.

Reports: MacGinitie, 1947; Wilson, 1952; Yamaguti, 1963.

Notes: Wilson (1952, p. 254–258) did not give an infection site for specimens collected from *Mobula lucasana* (= *M. thurstoni*); however, she mentioned (p. 255) that conspecific specimens were collected by Bere (1936) from "around the mouth of a devilfish (probably *Mobula hypostoma* [Bancroft, 1831])."

Digenea

Nagmia peruviana

Site of infection: Visceral cavity.

Distribution: Peru.

Reports: Tantalean and Rodriguez, 1990; Tantalean et al., 1992; Luque and Oliva, 1993.

***Syncoelium vermilionensis* Curran and Overstreet, 2000**

Sites of infection: Gills, gill arches.

Distribution: Gulf of California.

Report: Curran and Overstreet, 2000.

***Nagmia cisloi* n. sp.**

Site of infection: Body cavity.

Distribution: Gulf of California.

Report: Present study.

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