GUIDUS N. GEN. (CESTODA: TETRAPHYLLIDEA), WITH DESCRIPTION OF A NEW SPECIES AND EMENDATION OF THE GENERIC DIAGNOSIS OF *MARSUPIOBOTHRIUM*

Verónica A. Ivanov*

Laboratorio de Helmintología, Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Pabellón II, piso 4, Lab. 52, C1428EHA, Buenos Aires, Argentina. *e-mail: ivanov@bg.fcen.uba.ar*

ABSTRACT: *Guidus* n. gen. (Cestoda, Tetraphyllidea) is proposed for 3 cestode species from skates (*Bathyraja* spp.: Rajiformes, Rajidae). Members of *Guidus* differ from those of all other phyllobothriid genera in possessing 4 sessile and conspicuously muscular, saclike bothridia; a bothridial aperture toward anterior end of scolex, and perpendicular to scolex axis; aperture surrounded by a continuous sphincter of circular muscles, and 1 marginal accessory sucker. A new species, *Guidus argentinense* n. sp., is described, the diagnosis of *Marsupiobothrium antarcticum* is emended, and it is transferred to the new genus along with *Marsupiobothrium awii*. These species can be easily distinguished from *G. argentinense* by the presence of lappets in the bothridial margin. In addition, the diagnosis of *Marsupiobothrium* is emended based on the redescription of the type species, *Marsupiobothrium alopias*.

Little is known about the cestode fauna of species of *Bath-yraja* Ishiyama (Rajiformes, Rajidae). Even though this skate genus is diverse, with about 51 valid species, only 3 have been reported as hosts for tetraphyllidean cestodes (Campbell, 1977; Wojciechowska, 1990a, 1990b, 1991a, 1991b; Rocka and Zdzi-towiecki, 1998). Most records are of phyllobothriids in *Eche-neibothrium* van Beneden, 1850, *Anthocephalum* Linton, 1890, *Pseudanthobothrium* Baer, 1956, *Notomegarhynchus* Ivanov and Campbell, 2002, and *Marsupiobothrium* Yamaguti, 1952, whereas onchobothriids are represented only by *Onchobothrium* De Blainville, 1828.

During a survey on the cestode fauna of elasmobranch fishes from the southwestern Atlantic Ocean, specimens of a peculiar tapeworm were collected from *Bathyraja brachyurops* (Fowler). The new cestode resembles *Marsupiobothrium antarcticum* Wojciechowska, 1991 and *Marsupiobothrium awii* Rocka and Zdzitowiecki, 1998 also from *Bathyraja* spp. Examination of type material of *Marsupiobothrium alopias* Yamaguti, 1952, revealed some features that have gone undescribed in the generic diagnosis (Yamaguti, 1952; Schmidt, 1986; Euzet, 1994) but that could shed some light on the evaluation of the systematic position of the species subsequently included in this genus.

Marsupiobothrium alopias was originally described as possessing a scolex with 4 sessile bothridia in the shape of pyriform sacs, with the opening provided with a muscular sphincter especially developed in the posterior margin, and a submarginal accessory sucker. Since the original description, 7 additional species have been assigned to *Marsupiobothrium* (Yamaguti, 1952; Deshmukh and Shinde, 1975; Shinde and Deshmukh, 1980; Wojciechowska, 1991a; Caira and Runkle, 1993; Rocka and Zdzitowiecki, 1998). However, some of these species do not precisely match the scolex configuration of the type species. As a consequence, a new genus and species are proposed, and *M. antarcticum* and *M. awii* are transferred to the new genus.

MATERIALS AND METHODS

Cestodes were recovered from the spiral intestine of a single specimen of *B. brachyurops* caught in August 1998 in coastal waters off Buenos Aires Province, Argentina ($37^{\circ}6'39''S$, $54^{\circ}20'2''W$), and fixed in 4% formalin. Specimens prepared for light microscopy were hydrated

in a graded ethanol series, stained with Harris' hematoxylin, dehydrated in a graded ethanol series, cleared in methyl salicylate, and mounted in Canada balsam. The specimen prepared for scanning electron microscopy (SEM) was hydrated in a graded ethanol series, postfixed in 1% osmium tetroxide overnight at room temperature, dehydrated in a graded ethanol series, and dried using hexamethyldisilazane. After dehydration, the specimen was mounted on a stub with carbon tape, coated with gold in a Thermo VG Scientific Polaron SC 7630, and examined in a Philips XL 30 scanning electron microscope. A gravid segment was embedded in paraffin and transverse serial sections were cut at a thickness of 10 µm. All sections were stained with Harris' hematoxylin and counterstained with eosin. Measurements include the range followed in parentheses by the mean, standard deviation, number of worms examined (n), and the total number of observations when more than 1 measurement per worm was taken (n). All measurements are in micrometers unless otherwise stated. Figures were drawn with the aid of a drawing tube on a Zeiss Axioskop microscope. Museum abbreviations used are as follows: BMNH, Natural History Museum, London, U.K.; MACN-Pa, Museo Argentino de Ciencias Naturales, Colección Parasitológica, Buenos Aires, Argentina; MPM, Meguro Parasitological Museum, Tokyo, Japan.

REDESCRIPTION

Marsupiobothrium alopias Yamaguti, 1952 (Figs. 1–3)

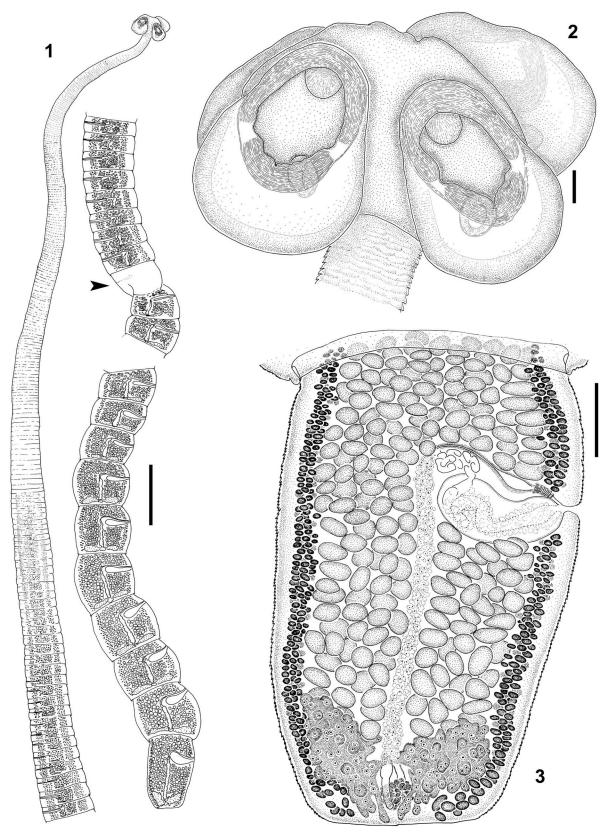
Diagnosis (based on 2 complete specimens): Worms euapolytic, 25.4-26.2 mm long; greatest width at level of mature segments; segments craspedote, 73-91 per worm (Fig. 1). Scolex composed of 4 bothridia, lacking apical organ (Figs. 1, 2), 375 long, 550-660 wide. Bothridia pyriform, saclike, conspicuously muscular, 305-345 (326 \pm 22) long, 225–265 (245 \pm 17) wide, attached to massive scolex proper, having muscular sphincter, 2 accessory suckers, and bothridial aperture oblique to scolex axis (Fig. 2). Sphincter encircling bothridial aperture formed by 2 muscular pads of circular musculature arranged in 2 semicircles, anterior and posterior, separated by a space at level of lateral notches of bothridial margin, a few muscular fibers form continuous sphincter externally to muscular pads; muscular pads 40-50 thick (Fig. 2). Accessory suckers on bothridial distal surface (inside pouch); anterior sucker underneath anterior muscular pad, 50–67 (59 \pm 5) in diameter; posterior sucker at level of mid-bothridium, 50–68 (62 \pm 5) in diameter (Fig. 2). Bothridial musculature 25–32 (30 \pm 3) thick. Cephalic peduncle undistinguished from germinative zone. Germinative zone 6.7–7.8 mm long. Surface of germinative zone and entire strobila covered by scutes (Figs. 2, 3).

Immature segments wider than long (Fig. 1). Mature segments as wide as long to longer than wide, 470-880 (666 ± 173) long, 810-1,060 (924 ± 103) wide, length-to-width ratio 0.56-0.86 (0.71):1; last mature segment 1,000-1,300 long, 600-750 wide, length-to-width ratio 1.66-1.73:1; 4-6 mature segments per strobila.

Testes oval, 43–75 (60 \pm 11) long, 32–65 (49 \pm 9) wide; 1 row deep; 155–187 (172 \pm 13) in number in mature segments, 34–47 (41) postvaginal testes; extending anteriorly from anterior margin of ovary to anterior margin of segment (Fig. 3). Cirrus sac oval, slightly curved

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^{*} Consejo Nacional de Investigaciones Científicas y Técnicas (CONI-CET), Argentina.



FIGURES 1–3. *M. alopias* Yamaguti, 1952, syntype (MPM 22698). (1) Entire worm, bar = 1 mm, arrow indicates a turn in the strobila, being all the genital pores unilateral. (2) Scolex, bar = 50 μ m. (3) Mature segment, bar = 200 μ m.

anteriorly in mature segments, $250-375 (335 \pm 39) \log_{100}$, $75-150 (107 \pm 24)$ wide, occupying 39-79% (58) of segment width (Figs. 1, 3); containing cirrus covered with short microtriches; surrounded by numerous gland cells inside cirrus sac. Vas deferens coiled, extending anteriorly from anterior margin of cirrus sac (Fig. 3).

Ovary lobulated, H-shaped in dorsoventral view (Fig. 3), 125–250 (178 \pm 56) long, 237–675 (487 \pm 159) wide at ovarian isthmus. Mehlis gland conspicuous, posterior to ovarian isthmus. Vagina thick-walled, anterior to cirrus sac, with muscular sphincter (Fig. 3), running anteriorly to vas deferens bulk, descending posteriorly, reaching ootype region posterior to ovarian isthmus (Fig. 3). Vagina and cirrus sac join into genital atrium, marginal genital pores unilateral (Fig. 1), 59–73% (65 \pm 4) from posterior margin of segment. Vitelline follicles lateral, 2–3 dorsal and 2–3 ventral columns (Fig. 3), 18–30 (25 \pm 4) long, 13–20 (16 \pm 2) wide, interrupted at level of cirrus sac and vagina dorsal and ventrally, extending throughout the entire segment length (Fig. 3). Uterus extending anteriorly along median line of segment from ovarian isthmus to anterior margin of cirrus sac.

Taxonomic summary

Type host: Alopias vulpinus (Bonnaterre, 1788), thin-tail thresher shark (Lamniformes, Alopiidae).

Site of infection: Spiral intestine.

Type locality: Japan, Pacific Ocean. *Specimens examined:* Syntypes, MPM 22698.

Remarks

The aforementioned information emends the description of Yamaguti (1952) of M. alopias. Even if Yamaguti did not indicate the accession numbers of the type specimens, Jun Araki from the MPM confirmed the existence of a single slide with 2 complete specimens, a fragment of strobila, and a detached segment as syntypes of *M. alopias*. Yamaguti (1952) described the morphology of the scolex of M. alopias as having 4 sessile bothridia, pear-shaped, with obliquely truncated opening and provided with sphincterlike circular muscles, which forms on the posterior margin an arcuate cylindrical pad separated from the lateral margin by a distinct notch, and a small accessory sucker at the anterior end of the pouch. Examination of type specimens allowed a detailed description of these structures and the discovery of new features. The unusual sphincter encircling the bothridial aperture of M. alopias is formed by 2 muscular pads of circular muscles, 1 anterior and 1 posterior, separated by a space lacking musculature at the level of the marginal notches of the bothridial opening. Both pads are of equal thickness, with the anterior pad more developed than the posterior. A group of a few fibers of circular muscles form a continuous sphincter surrounding the muscular pads. Yamaguti (1952) described a submarginal accessory sucker; however, there are 2 suckers per bothridium in the type specimens. Both suckers are situated on the distal bothridial surface (inside the pouch in these saclike bothridia), 1 anterior sucker just beneath the anterior muscular pad, and an additional sucker approximately in the center of the bothridium. Some of the features of the segment morphology observed in the original description could not be corroborated in the type material. Yamaguti (1952) presented a drawing of a detached segment (plate VIII, Fig. 41) that might not belong to M. alopias. In his drawing, which is consistent with the detached segment mounted in the slide with the syntypes, the vitelline follicles are interrupted at the level of the ovarian lobes, whereas they are distributed throughout the entire segment in the segments that are attached to the strobila. The presence of a seminal receptacle could not be confirmed in the type specimens, maybe because the details of the ootype region described and drawn by Yamaguti (plate VIII, Fig. 42) also were based on the same detached segment. It is likely that the segments of M. alopias detach from the strobila and grow larger, but it is rather unusual for such a change in vitelline distribution to occur after detachment.

After revision of the type species of *Marsupiobothrium*, its generic diagnosis is emended as follows: scolex with 4 sessile saclike bothridia, lacking apical organ. Bothridia conspicuously muscular with muscular sphincter and 2 accessory suckers. Bothridial aperture oblique to scolex axis; muscular sphincter formed by 2 muscular pads, 1 anterior and 1 posterior; accessory suckers on distal bothridial surface. Strobila scutellate. Testes numerous, evenly distributed in preovarian field in mature segments, postvaginal testes present. Genital pores lateral. Ovary lob-

ulated, H-shaped in dorsoventral view. Vagina opening anterior to cirrus sac, vaginal sphincter present. Vitellaria follicular, lateral, extending full length of segment. Uterus extending anteriorly to level of cirrus sac.

DESCRIPTION

Guidus n. gen.

Diagnosis: Tetraphyllidea, Phyllobothriidae, Phyllobothriinae. Scolex with 4 sessile globular, saclike bothridia, lacking apical organ. Bothridia conspicuously muscular, bothridial aperture toward anterior end of scolex, perpendicular to scolex axis, surrounded by continuous sphincter of circular muscles, and 1 marginal accessory sucker. Cephalic peduncle undistinguished from germinative zone. Testes numerous, medullarly, evenly distributed in preovarian field in mature segments, in several layers in cross sections; postvaginal testes present. Cirrus sac containing armed cirrus. Ovary lobulated, H-shaped in dorsoventral view, tetralobed in cross section. Vagina opening anterior to cirrus sac, not crossing cirrus sac, vaginal sphincter present. Genital pores lateral, irregularly alternating, vagina and male duct join conspicuous genital atrium. Uterus saccate, ventral uterine pore may be present. Vitellaria follicular, lateral, extending full length of segment. Eggs fusiform. Parasites of Rajiformes, Rajidae.

Type species: Guidus argentinense n. sp.

Other species: Guidus antarcticus (Wojciechowska, 1991) n. comb., Guidus awii (Rocka and Zdzitowiecki, 1998) n. comb.

Etymology: Guidus (masculine) is the Latin translation of Guido. This genus was named in honor of Guido Pastorino from the Museo Argentino de Ciencias Naturales, for his invaluable companionship and continuous encouragement of my work.

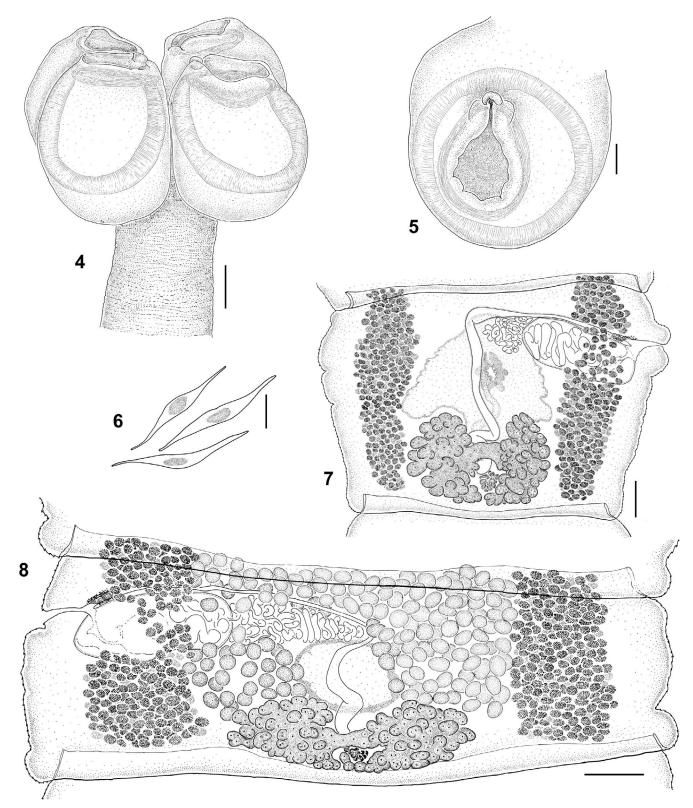
DESCRIPTION

Guidus argentinense n. sp. (Figs. 4–19)

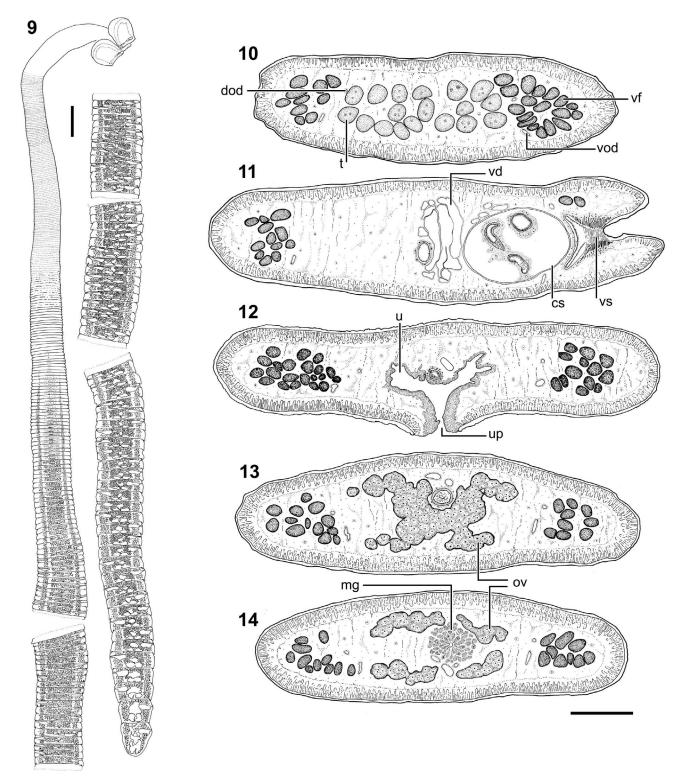
Diagnosis (based on 4 complete specimens and 1 specimen without scolex: 5 whole mounts, 1 scolex observed with SEM, and 1 gravid segment sectioned): Worms anapolytic, 75.8–116.4 mm (97.1 \pm 16.7, n = 4) long; greatest width at level of scolex or gravid segments; segments craspedote, 269-383 (341 ± 49 ; n = 5) per worm (Fig. 9). Scolex composed of 4 sessile bothridia, lacking apical organ (Figs. 4, 15, 16), 1,400–1,800 (1,550 \pm 191, n = 4) long, 2,074–2,800 (2,393 \pm 324, n = 4) wide. Bothridia globular, saclike, conspicuously muscular, 1,196- $1,640 (1,459 \pm 147, n = 4, n = 10) \log_{10}, 1,040-1,280 (1,129 \pm 96, n)$ = 4, n = 10) wide, having muscular sphincter and 1 accessory sucker; bothridial aperture toward anterior end of scolex (Figs. 4, 5, 15-17). Bothridial internal cavity 800–1,060 (954 \pm 112, n = 4, n = 10) long, 700–900 (772 \pm 74, n = 4, n = 10) wide, diameter in apical view 900; bothridial musculature 160–220 (192 \pm 32, n = 4, n = 10) thick. Accessory sucker on anterior margin of bothridium 80-151 (120 ± 17 , n = 4, n = 16) in diameter (Figs. 15–17). Muscular sphincter encircling bothridial aperture, 160-220 (192 ± 32, n = 4, n = 10) wide, at a distance of 100–130 (116 \pm 13, n = 4, n = 10) from anterior margin of bothridia. Cephalic peduncle undistinguished from germinative zone. Germinative zone 3,800-11,600 ($8,650 \pm 3,403$, n = 4) long. Surface of germinative zone and entire strobila covered by scutes (Fig. 18); surface of scutes covered by densely packed filiform (round pointed) microtriches, 2 long (Fig. 19). No microtriches were observed on different surfaces of scolex.

Immature segments wider than long; 247–349 (306 ± 44 , n = 5) in number (Fig. 9). Mature segments wider than long, 640-750 (710 ± 43 , n = 5, n = 36) long, 2,210–2,610 (2,349 \pm 109, n = 5, n = 36) wide, length-to-width ratio 0.27–0.32 (0.30):1; 11–18 (13 ± 3 , n = 5) mature segments per strobila (Figs. 8, 9). Gravid segments wider than long to longer than wide, 640-2,160 ($1,062 \pm 418$, n = 5, n = 30) long, 1,500–2,680 (2,114 \pm 320, n = 5, n = 30) wide, length-to-width ratio 0.27–1.44 (0.54):1; 10–35 (22 ± 10 , n = 5) gravid segments per strobila (Figs. 7, 9).

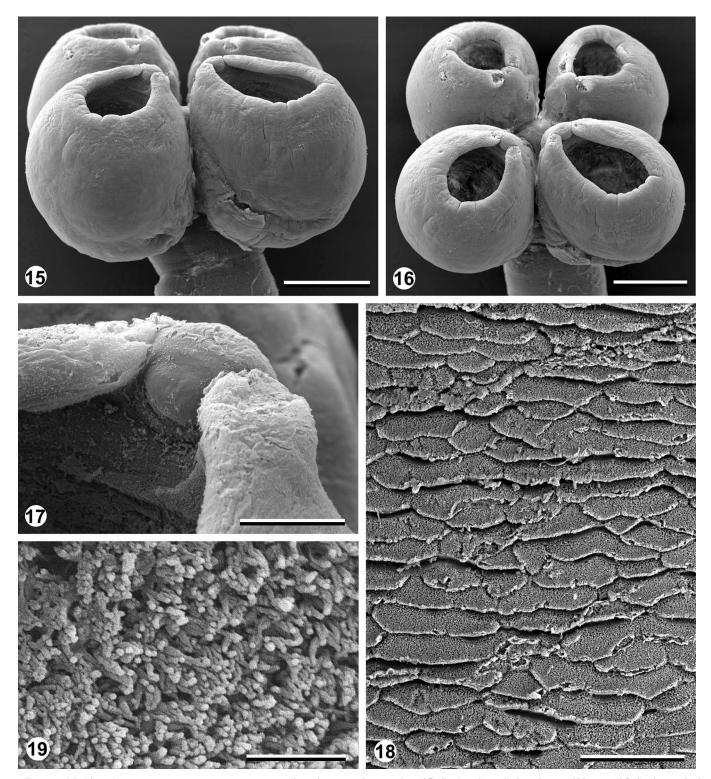
Testes oval, 50–85 (71 ± 10, n = 5, n = 50) long, 30–80 (51 ± 14, n = 5, n = 50) wide, 2–3 rows deep in cross section (Fig. 10); 89–153 (119 ± 19, n = 5, n = 30) in number in mature segment, 18–33 (25 ± 5, n = 5, n = 30) postvaginal testes; up to 200 testes per immature segment; extending anteriorly from anterior margin of ovary to anterior



FIGURES 4–8. *G. argentinense* n. gen. et n. sp. (4) Scolex, bar = 400 μ m. (5) Detail of bothridium in apical view, bar = 200 μ m. (6) Eggs, bar = 25 μ m. (7) Gravid segment, bar = 200 μ m. (8) Mature segment, bar = 200 μ m.



FIGURES 9–14. *G. argentinense* n. gen. et n. sp. (9) Entire worm, bar = 400 μ m. (10–14) Cross sections of gravid segment, bar = 200 μ m. (10) At level of testes anterior to cirrus sac. (11) At level of genital pore. (12) At level of uterine pore. (13) At level of ovarian isthmus. (14) At level of Mehlis' gland. Abbreviations: cs, cirrus sac; dod, dorsal osmoregulatory duct; mg, Mehlis' gland; ov, ovary; t, testis; u, uterus; up, uterine pore; vd, vas deferens; vf, vitelline follicle; vs, vaginal sphincter; vod, ventral osmoregulatory duct.



FIGURES 15–19. *G. argentinense* n. gen. et n. sp., scanning electron micrographs. (15) Scolex, lateral view, bar = 500 μ m. (16) Scolex, apical view, bar = 500 μ m. (17) Detail of accessory sucker, bar = 100 μ m. (18) Detail of scutes on the surface of germinative zone, bar = 50 μ m. (19) Detail of microtriches on scutes, bar = 2 μ m.

margin of segment (Fig. 8), degenerating in gravid segments (Figs. 7, 11, 16). Cirrus sac oval, 560–700 (620 ± 42 , n = 5, n = 30) long, 200–260 (234 ± 18 , n = 5, n = 30) wide in mature segments, occupying 29–38% (33) of segment width (Fig. 8); 550–700 (628 ± 54 , n = 5, n = 25) long, 180–400 (292 ± 54 , n = 5, n = 25) wide in gravid

segments, occupying 31–44% (36) of segment width (Figs. 7, 11) containing cirrus covered with slender, short microtriches. Vas deferens extensive, highly coiled, extending from proximal margin of cirrus sac to mid-segment (Figs. 7, 8, 11).

Ovary lobulated, H-shaped in dorsoventral view (Figs. 7, 8), X-

shaped in cross section at level of isthmus (Fig. 13), 210–320 (281 \pm 29, n = 5, n = 30) long, 780–950 (870 \pm 53, n = 5, n = 30) wide at ovarian isthmus in mature segments; 270–530 (395 \pm 79, n = 5, n = 30) long, 680–940 (840 \pm 67, n = 5, n = 25) wide at ovarian isthmus in gravid segments, occupying 33–48% (38) of segment width (Fig. 7).

Vagina thick-walled, anterior to cirrus sac, having conspicuous muscular sphincter (Fig. 11), running anteriorly to vas deferens bulk, descending posteriorly, reaching ootype region posterior to ovarian isthmus (Figs. 7, 8). Vagina and cirrus sac join into conspicuous genital atrium 180–250 (219 \pm 23, n = 5, n = 20) deep, marginal genital pores alternate irregularly, 59–88% (71 \pm 6, n = 5, n = 50) from posterior margin of segment.

Vitelline follicles in lateral columns, several follicles deep not distributed in dorsal or ventral columns (Figs. 10–14), 30–60 (47 \pm 6, n = 5, n = 50) long, 25–40 (33 \pm 5, n = 5, n = 50) wide, not interrupted at level of cirrus sac and vagina, extending throughout the entire segment length (Figs. 7, 8, 10–14). Uterus saccate, having small lateral branches in older gravid segments, conspicuous uterine pore present ventrally at 37–53% (47) from anterior margin of segment, uterine duct running anteriorly from ootype region, joining uterus at level of posterior margin of cirrus sac (Figs. 7, 12). Unembryonated eggs fusiform, 95–105 long (n = 5), 11–12 (n = 5) wide (Fig. 6).

Taxonomic summary

Type host: Bathyraja brachyurops (Fowler, 1910), broadnose skate (Rajiformes, Rajidae).

Site of infection: Spiral intestine.

Type locality: Southwestern Atlantic Ocean, coastal waters off Buenos Aires Province, Argentina (37°6'39"S, 54°20'2"W).

Specimens deposited: holotype and 2 paratypes, MACN-Pa No. 432/ 1–7; 1 paratype, USNPC No. 98040.

Etymology: This species is named after the type locality, since the host was captured in waters under Argentine jurisdiction.

Remarks

Guidus n. gen. is placed in the Phyllobothriidae Braun, 1900 (Tetraphyllidea Carus, 1863) based on the morphology of the scolex consisting on 4 hookless bothridia. The new genus lacks the strong metascolex present in the Thysanocephalinae Euzet, 1953, the bothridial loculi as in the Triloculariinae Yamaguti, 1959 and the Rhinebothriinae Euzet, 1953, and the conspicuous myzorhynchus that is present in the Echeneibothriinae de Beauchamp, 1905. *Guidus* n. gen. is consistent in all respects with the diagnosis of Phyllobothriinae de Beauchamp, 1905 given by Euzet (1994) and emended by McKenzie and Caira (1998).

Among the genera currently included in Phyllobothriinae, Guidus n. gen. is similar to Pithophorus Southwell, 1925, Scyphophyllidium Woodland, 1927, Carpobothrium Shipley and Hornell, 1906, Bibursibothrium McKenzie and Caira, 1998, and Marsupiobothrium in the possession of saclike bothridia. Species in the new genus have bothridia with only anterior opening instead of bothridia open anterior and posteriorly as in Pithophorus. They also differ from Scyphophyllidium in their possession of a muscular sphincter encircling the bothridial aperture. Guidus n. gen. can be distinguished from Carpobothrium by the presence of a marginal accessory sucker and muscular sphincter rather than flaps with muscular pads. The muscular sphincter around the bothridial opening and the bothridia not subdivided internally into 2 compartments distinguish the new genus from Bibursibothrium guidus n. gen. is most similar to Marsupiobothrium by the possession of a muscular sphincter and accessory sucker, but they differ in the morphology of the sphincter being a single ring of circular muscle in Guidus n. gen. and a more complex structure formed by a combination of unconnected muscular pads and a thin ring of circular musculature in Marsupiobothrium. In addition, there is a single marginal accessory sucker per bothridium in Guidus n. gen., whereas 2 accessory suckers placed inside the bothridium are present in Marsupiobothrium. Both genera also differ in the disposition of bothridial aperture, which is anterior and perpendicular to the scolex axis in species of the new genus and obliquely truncated in Marsupiobothrium, and in the relative size of the scolex proper respect to the bothridia (massive in Marsupiobothrium and reduced in Guidus n. gen.). Guidus n. gen. also can be distinguished from all these phyllobothriid genera in the possession of a preformed uterine pore, which is at least present in G. argentinense n. sp.

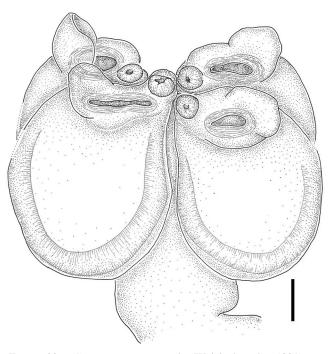


FIGURE 20. *G. antarcticus* n. comb. (Wojciechowska, 1991), paratype (BMNH 1992.1.6.31). Scolex, bar = $200 \mu m$.

REDESCRIPTION

Guidus antarcticus (Wojciechowska, 1991) n. comb.

(Fig. 20)

Diagnosis (amended description of the scolex based on a single immature specimen): Scolex composed of 4 sessile bothridia, lacking apical organ, 1,150 long, 1,450 wide. Bothridia globular, saclike, conspicuously muscular, 830–950 long, 650–700 wide, having muscular sphincter and 1 accessory sucker. Bothridial aperture toward anterior end of scolex, perpendicular to scolex axis; apical margin of bothridium projecting anteriorly in outgrowth of tissue in form of a lappet, opposite to accessory sucker (Fig. 20). Bothridial internal cavity 600–750 long, 500 wide, bothridial musculature 100–120 thick. Accessory sucker on anterior margin of bothridium, 120–130 in diameter. Muscular sphincter encircling bothridial aperture, 50–60 wide, formed by uninterrupted ring of circular muscles.

Taxonomic summary

Type host: Bathyraja maccaini Springer, 1971, McCain's skate (Rajiformes, Rajidae).

Additional host: Bathyraja eatonii (Günther, 1876), Eaton's skate (Rajiformes, Rajidae).

Site of infection: Spiral intestine.

Type locality: Shelf around Joinville Island, off tip of Antarctica Peninsula.

Synonym: Marsupiobothrium antarcticum Wojciechowska, 1991.

Specimens examined: Paratype, BMNH 1992.1.6.31 (immature specimen from *B. eatonii*).

Remarks

Wojciechowska (1991b) described the scolex of M. antarcticum as having "4 jarlike bothridia, open at one side. On the top of each bothridium a bilobed process and a sucker are present" (p. 69). This species was placed in *Marsupiobothrium* based on the broad diagnosis of the genus available at that time. The study of a paratype specimen revealed that the anterior margin of the bothridia forms a lappet that projects anteriorly, in opposite position to the accessory sucker. The accessory sucker is marginal, and there exists a continuous muscular sphincter around the bothridial aperture. These features are also shared by M. awii from the same host species (Rocka and Zdzitowiecki, 1998;

Fig. 1). The configuration of the scolex of M. antarcticum and M. awii is similar to G. argentinense in the shape of bothridia, orientation of bothridial aperture, 1 accessory sucker in the margin of the bothridium, and the presence of a single muscular sphincter in the shape of a ring of circular muscles around the bothridial aperture, rather than the features described for M. alopias in this study. Therefore, M. antarcticum and M. awii are transferred to the new genus as Guidus antarcticus n. comb. and Guidus awii n. comb., respectively. Both species can be easily distinguished from G. argentinense by the presence of lappets in the bothridial margins. In addition, specimens of G. argentinense have craspedote segments, mature segments wider than long, are smaller than G. antarcticus (75.8-116.4 vs. 140 mm), but they have twice the number of segments (269-383 vs. 190) and are anapolytic instead of apolytic-like G. awii. The original figures of G. antarcticus (Fig. 1b) show that the lateral bands of vitelline follicles are interrupted at level of vagina and cirrus sac, whereas the vitellaria are continuous throughout the entire segment length in G. argentinense. Even if no scutes were observed on the tegument of the strobila of the immature paratype of G. antarcticus, neither were mentioned in the original descriptions of G. antarcticus and G. awii, this feature should be verified on properly preserved specimens.

DISCUSSION

The original description of *Marsupiobothrium* led to the inclusion of several species in this genus that do not precisely agree with the morphology of *M. alopias*. The creation of *Guidus* allows the transfer of *M. antarcticum* and *M. awii* to this new genus, leaving a total of 5 species in *Marsupiobothrium in* addition to *M. alopias*, i.e., *Marsupiobothrium forte* (Linton, 1924), *Marsupiobothrium gobelinus* Caira and Runkle, 1993, *Marsupiobothrium karbharii* Deshmukh and Shinde, 1975, *Marsupiobothrium rhinobati* Shinde and Deshmukh, 1980, and *Marsupiobothrium rhynchobati* Shinde and Deshmukh, 1980.

The species collected from rhinobatids, i.e., M. rhinobati, M. rhynchobati, and M. karbharii, agree with M. alopias in having saclike bothridia, a lateral bothridial opening rather than apical, and bounded by 2 muscular pads. However, they differ in the number and position of the accessory suckers. Only 1 sucker per bothridium at the anterior end of each bothridium is described and drawn for these species. Unfortunately, the descriptions are very brief and the drawings are somewhat unclear, making it difficult to confirm whether they share a different arrangement of the structures on the scolex. The apical accessory sucker described in an eccentric position in relation to the bothridial opening by Deshmukh and Shinde (1975) and Shinde and Deshmukh (1980) might be in fact the internal sucker observed in *M. alopias*. If this is the case, the presence of the other sucker could have remained unnoticed because it overlaps with the anterior muscular pad and it could be somewhat difficult to distinguish if not studied carefully. All these 3 species require redescription based on new collections from type hosts and localities to warrant inclusion in Marsupiobothrium.

Marsupiobothrium forte was described by Linton (1924) from immature specimens from *Sphyrna zygaena* (L.) (Carcharhiniformes) as *Orygmatobothrium forte* and transferred to *Marsupiobothrium* by Yamaguti (1952). Its possession of cup-shaped bothridia with anterior accessory sucker described as "enclosed in the bothridial cup" (Linton, 1924), muscular sphincter at the margins of the bothridia, and a scutellate strobila described as "crossed by fine transverse lines, which make a serrate outline on the lateral margins", concur with *M. alopias*. However, collections of new specimens should be required

to verify the number of suckers per bothridium, the features of the sphincter, and morphology of the adult worms.

Marsupiobothrium gobelinus from *Mitsukurina owstoni* Jordan (Lamniformes) has shallow cup-shaped stalked bothridia with marginal accessory suckers, and even if a muscular sphincter was not described, its presence was confirmed by J. N. Caira (pers. comm.). Caira and Runkle (1993) acknowledged that the placement of this species in *Marsupiobothrium* was somewhat questionable. Based on the emended diagnosis of *Marsupiobothrium*, it is apparent that this species should be transferred from the genus. Indeed, it is more similar to *Guidus* in having marginal accessory suckers and a muscular sphincter, but that *M. gobelinus* bears bothridia with delicate muscular walls, conspicuously stalked, vagina crossing cirrus sac, and parasitizes a laminform shark prevents the transfer of this species to the new genus.

Guidus argentinense is a peculiar tapeworm in several aspects of its morphology. The presence of a uterine pore is rather unusual for tetraphyllidean cestodes; it has only been described previously in *Chimaerocestos prudhoei* Williams and Bray, 1984. In addition, the vitelline follicles are distributed in lateral bands that are formed by several deep follicles instead of arranged in dorsal and ventral columns as in most tetraphyllideans.

Some of the species in the genera with saclike bothridia also have scutellate strobila, which could suggest that these taxa share a common evolutionary origin. This feature also has been observed in species of *Paraorygmatobothrium* Ruhnke, 1994. However, in the latter genus, the scutes seem to be restricted to the neck (Ruhnke, 1994), whereas they cover all the segments along the strobila in the species possessing saclike bothridia, i.e., *M. alopias, G. argentinense*, and *Scyphophyllidium uruguayense* Brooks, Marques, Perroni and Sidagis, 1999.

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