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***Gaharitrema droneni* n. gen., n. sp. (Digenea: Zoogonidae: Lepidophyllinae) from the Pudgy Cuskeel, *Spectrunculus grandis* (Ophidiiformes: Ophidiidae), from Deep Waters off Oregon, with Updates Keys to Zoogonid Subfamilies and Genera**

Charles K. Blend

Corpus Christi, Texas, ilovethesea@att.net

Gábor R. Rácz

University of Nebraska - Lincoln, grac2@unl.edu

Scott Gardner

University of Nebraska - Lincoln, slg@unl.edu

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## **GAHARITREMA DRONENI** N. GEN., N. SP. (DIGENEA: ZOOGONIDAE) FROM THE PUDGY CUSKEEL, **SPECTRUNCULUS GRANDIS** (OPHIDIIFORMES: OPHIDIIDAE), FROM DEEP WATERS OFF OREGON, WITH UPDATED KEYS TO ZOOGONID SUBFAMILIES AND GENERA

Charles K. Blend<sup>1</sup>, Gabor R. Racz<sup>2</sup>, and Scott L. Gardner<sup>2</sup>

<sup>1</sup> Corpus Christi Museum of Science and History, 1900 N. Chaparral Street, Corpus Christi, Texas 78401.

<sup>2</sup> Harold W. Manter Laboratory of Parasitology, W529 Nebraska Hall, University of Nebraska–Lincoln, Lincoln, Nebraska 68588-0514. Correspondence should be sent to Charles K. Blend at: [ilovethesea@att.net](mailto:ilovethesea@att.net)

### KEY WORDS ABSTRACT

Deep-Sea  
Digenea  
*Gaharitrema droneni*  
Keys  
Lepidophyllinae  
Northeastern Pacific Ocean  
Ophidiidae  
Ophidiiformes  
Oregon  
Pudgy Cuskeel  
*Spectrunculus grandis*  
Zoogonidae

*Gaharitrema droneni* n. gen., n. sp. (Digenea: Zoogonidae: Lepidophyllinae) is described from the intestine of the pudgy cuskeel, *Spectrunculus grandis* (Günther, 1877) (Ophidiiformes: Ophidiidae), collected at 2,800 m depth from the northeastern Pacific Ocean off Oregon. The new genus is distinguished from *Brachyenteron* Manter, 1934 and *Steganoderma* Stafford, 1904, the 2 closest lepidophylline genera, and from 4 other zoogonid genera erected since 2007, the last major revision of the family, by a combination of diagnostic features including a pyriform or spindle-shaped body, smooth testes and ovary, narrow ceca that reach with the vitellarium into the hindbody, an unspecialized ventral sucker, non-filamented eggs, a claviform cirrus pouch, and an unpocketed ejaculatory duct and metraterm, and the new genus lacks circumoral spines. We present updated keys to the 3 subfamilies of the Zoogonidae Odhner, 1902, as well as to the genera of the Cephaloporinae Yamaguti, 1934 and the Lepidophyllinae Stossich, 1903. A listing of the parasites known from *S. grandis* also is presented. This study documents the third family of digeneans (Zoogonidae) known to parasitize *S. grandis*, and it is a new host record (i.e., the first zoogonid reported from this host species). We discuss the relatively impressive presence of the Zoogonidae and their hosts within the deep sea. Specifically, of the 35 genera we recognize within this digenean family, 14 (40%) have deep-sea representatives. At least 37 species within 27 genera and 19 families within 11 orders of deep-sea fish are known to harbor zoogonids. Furthermore, of the 37 known deep-sea fish species parasitized by zoogonids, only 5 (13.5%) harbor 2 or more zoogonid species; the remaining 32 (86.5%) harbor only 1 parasite species each, indicating strong host specificity. Finally, the dietary ecology of *S. grandis* is presented, allowing us to speculate that *Gaharitrema droneni* may be utilizing gastropods and polychaetes as well as *S. grandis* to complete its life cycle in the deep sea.

The Zoogonidae Odhner, 1902 is a cosmopolitan family of digenetic trematodes that parasitize the alimentary tract, gall bladder, bile duct, or urinary bladder of teleosts and elasmobranchs (Bray, 2008b), and it is composed of 3 subfamilies containing 34 genera. The Zoogoninae Odhner, 1902 contains 10 genera, and members all possess a vitellarium that forms 1 or 2 compact masses, or several follicles, in an undivided median field, as well as egg capsules that are weakly tanned or membranous (Bray, 2008b; WoRMS, 2019). The Lepidophylli-

nae Stossich, 1903 contains 21 genera, and members all possess a vitellarium that forms paired fields of follicles as well as an egg capsule that is strongly tanned and develops an operculate shell (Bray, 2008b; WoRMS, 2019). The Cephaloporinae Yamaguti, 1934 contains 3 genera; *Cephaloporus* Yamaguti, 1934 and *Yamagutiplectognathotrema* Parukhin, 1977 were considered lepidophyllines, while *Plectognathotrema* was considered an aberrant member of the Fellodistomidae Nicoll, 1909 (Bray, 2002, 2008b; Cutmore et al., 2014; WoRMS, 2019). Cephaloporines possess an unusually posterior ventral sucker, paired fields of vitelline follicles, and a lateral genital pore close to the level of the oral sucker, and they exclusively parasitize teleosts of

Version of record, first published online with fixed content and layout, in compliance with ICZN Arts. 8.1.3.2, 8.5, and 21.8.2 as amended, 2012. Zoobank publication registration: [urn:lsid:zoobank.org:pub:urn:lsid:zoobank.org:pub:1DEA77CC-B281-451C-9AE3-CED07517F216](https://zoobank.org/pub:urn:lsid:zoobank.org:pub:urn:lsid:zoobank.org:pub:1DEA77CC-B281-451C-9AE3-CED07517F216).

the family Monacanthidae (filefish and leatherjackets) (Cutmore et al., 2014).

The purpose of this study was to add to our knowledge of the Zoogonidae with the description of a new species representing a new genus of lepidophylline from the intestine of the pudgy cuskeel, *Spectrunculus grandis* (Günther, 1877) (Ophidiidae), collected from deep waters off Oregon over 50 yr ago (see Fontaine et al., 2012). We present updated keys to the 3 subfamilies of the Zoogonidae as well as to the genera of the Lepidophyllinae and the Cephaloporinae. A list of the parasites known from *S. grandis* (Table I) is given, new host and parasite records presented, and we discuss the presence of the Zoogonidae within the deep sea.

## MATERIALS AND METHODS

An unknown number of pudgy cuskeel, *S. grandis*, were collected aboard ship and examined for parasites by the late Dr. James E. McCauley, Dept. of Oceanography, Oregon State University, Corvallis, Oregon. Fish were collected by otter trawl from 2,800 m depth within the northeastern Pacific Ocean approximately 137 km west of Newport, Lincoln County, Oregon. Specimens of *S. grandis* were immediately fixed at sea by injecting the body cavity, mouth, and anus with AFA or 4% seawater formaldehyde and preserved in 10% neutral seawater-formalin before being transferred back to the laboratory for necropsy (see Eagle and McCauley, 1964, 1965; McCauley, 1964, 1968). Digeneans were stained with either Mayer's carmalum or Van Cleave's hematoxylin combination and mounted in Canada balsam (see McCauley and Pequegnat, 1968). Drawings were done with the aid of an Olympus CH30 compound microscope (Olympus Corporation, Center Valley, Pennsylvania) using a drawing tube and a Nikon Superhigh-Performance 3 Zoom Coolpix 990 digital camera (Nikon Corporation, Melville, New York) and image software system. Measurements are in micrometers ( $\mu\text{m}$ ) with the holotype followed by the range and mean in parentheses; the number [n] of measurements is also noted where needed. Two-dimensional measurements are given with the length before the width. Comparative measurements were taken from the original species descriptions or re-descriptions unless otherwise stated. If needed, some critical measurements that were not available or were obviously in error in the original descriptions were calculated from original illustrations and are identified herein. Fish classification and authorities follow FishBase (Froese and Pauly, 2019), while digenean authorities follow Bray (2008b) and WoRMS (2019). Digenean identification was based on Bray (2008a, 2008b), and ecological terms followed Bush et al. (1997).

While we understand that in situ fixation of digeneans is not ideal, specimens measured herein appeared in good condition upon close examination. Furthermore, we felt that because of the inherent rarity of this material (i.e., from the deep sea), the benefits to our limited knowledge of deep-sea helminth communities afforded by this study justified the completion of this work.

Digenean specimens used in this study are housed in the Harold W. Manter Laboratory of Parasitology (HWML), University of Nebraska–Lincoln, Lincoln, Nebraska (Original HWML No. 42859).

## DESCRIPTION

### *Gaharitrema* n. gen.

*Diagnosis:* Zoogonidae, Lepidophyllinae. Body pyriform or spindle-shaped. Tegument spined; spines more numerous and larger anteriorly. Oral sucker subspherical, large. Ventral sucker subspherical, larger than oral sucker, equatorial. Pre-pharynx absent. Pharynx round to oval, smaller than oral sucker. Esophagus straight or sigmoid. Intestinal bifurcation in forebody. Ceca extend either to level of posterior margin of ventral sucker or to level of ovary, terminate blindly. Testes 2, opposite, smooth, round to oval, post-equatorial. Cirrus pouch clavate or comma-shaped, large, conspicuous, extends posterior to ventral sucker. Seminal vesicle bipartite. Pars prostatica cylindrical, conspicuous. Ejaculatory duct tubular, conspicuous. Cirrus present. Genital atrium voluminous. Genital pore submedian, sinistral, anterior to ventral sucker at level of esophagus. Ovary submedian, dextral, smooth, oval to globular, pre-testicular, equatorial to just post-equatorial. Seminal receptacle canalicular, near ovary in inter-testicular space. Laurer's canal present. Oötype median; Mehlis' gland cells inconspicuous. Uterus extensive, occupies most of hindbody, extends from genital pore to near posterior extremity. Metratrem conspicuous. Vitellarium follicular, in 2 symmetric lateral fields, restricted to hindbody. Eggs numerous, operculate. Excretory vesicle I-shaped, extends at least to level of testes. Excretory pore terminal. Parasitic in intestine of deep-sea teleosts.

### Taxonomic summary

*Type species:* *Gaharitrema droneni* n. sp.

*ZooBank registration:* urn:lsid:zoobank.org:act:9B0E55D2-46AC-490B-B3B6-EF95F5D41B08.

*Etymology:* The generic designation comes from a combination of "Gahari," the Hindi word for "deep," and the Greek "trema" for trematode; therefore, a genus of "deep-sea trematode."

### *Gaharitrema droneni* n. sp.

(Figs. 1–7)

*Description:* Measurements based on 6 adult, whole-mounted specimens in darkened mounting media with additional observations from 2 immature specimens; 1 adult specimen with left margin slightly torn at level of ventral sucker. With the characteristics of the genus. Body pyriform to spindle-shaped, widest at level of ventral sucker or just posterior, 1,920 (1,520–2,200; 1,863) long  $\times$  672 (424–712; 614) wide at level of pharynx, 1,064 (760–1,280; 1,028) wide at level of ventral sucker, 720 (560–1,060; 785) wide at level of testes; body width at ventral sucker 55.4% (48.0–59.5%; 55.3%) of body length. Forebody attenuated to rounded extremity, 740 (616–880; 729) long; 38.5% (35.5–43.4%; 39.3%) of body length. Hindbody attenuated to curved extremity and broadly rounded, 1,180 (860–1,380; 1,134) long. Tegument spined, spines easily dislodged, larger and denser anteriorly, extend to level of posterior margin of ventral sucker or testes where they become smaller and more sporadic, spines 12 (12–20; 15) [n = 5] long in forebody. Pre-oral lobe absent. Oral sucker large, subspherical, subterminal, 368 (312–416; 365)  $\times$  384 (288–424; 367); oral sucker length 19.2% (18.2–21.1%; 19.7%) of body length. Ventral sucker large, median, slightly protuberant, circular to subcircular, larger than oral sucker, in middle third of

**Table 1.** Parasites reported from the pudgy cuskeel, *Spectrunculus grandis*\* (Günther, 1877) (Ophidiiformes: Ophidiidae), including infection site, locality, and references.

Species†	Infection site	Locality	References
C – <i>Philobythos</i> sp.	Intestine	NE Atlantic Ocean	A. Jones and R. A. Bray, unpubl. data
CO – <i>Naobranchia maxima</i> Ho, 1975	Gill filaments	Off Galapagos Islands	Ho (1975)
D – <i>Gonocerca oregonensis</i> McCauley, Pequegnat and Brownell, 1970	Stomach	Coast of Oregon	McCauley et al. (1970); Yamaguti (1971); Love and Moser (1983)‡
D – <i>Steringophorus haedrichi</i> Bray and Campbell, 1995	Intestine	Porcupine Seabight and western coast of British Isles, NE Atlantic Ocean	Bray and Gibson (1998); Bray et al. (1999); Klimpel et al. (2001, 2009)‡
D – <i>Steringophorus margolisi</i> Bray, 1995	Intestine	Rockall Trough and western coast of British Isles, NE Atlantic Ocean	Bray (1995); Bray et al. (1999); Klimpel et al. (2001, 2009)‡; Bray and Kuchta (2006)
D – <i>Steringophorus</i> sp.	Intestine§	—	NHM Collections (Access. # 1992.3.24.10–14)

\* Based on Froese and Pauly (2019), the following host synonymies were also searched for *S. grandis*: *Bassogigas grandis* (Günther, 1877), *Neobythites grandis* (Günther, 1877), *Sirembo grandis* Günther, 1877, and *Spectrunculus radcliffei* Jordan and Thompson, 1914.

† C, Cestoda; CO, Copepoda; D, Digenea. We used the taxonomic designation and authority for each species provided by the World Register of Marine Species ([www.marinespecies.org](http://www.marinespecies.org)).

‡ These references are host–parasite checklists and should not be considered original records.

§ Record for this parasite species had no information for this characteristic, so the most likely infection site is given.

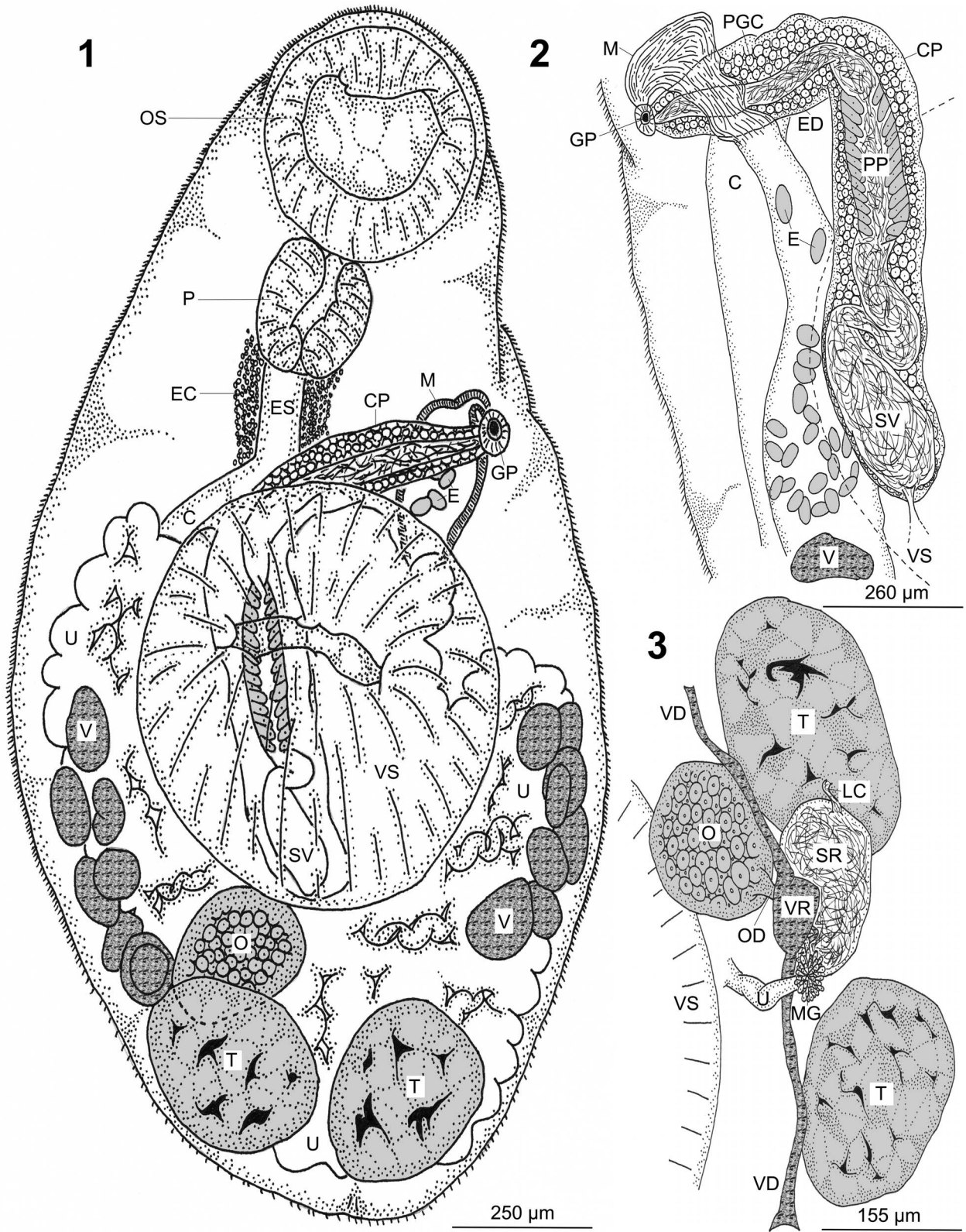
|| Specimens of this parasite species collected from this host species are currently housed in the Natural History Museum (NHM) Collections, London, U.K. (Accession numbers also given).

body, 680 (544–808; 688) × 648 (552–816; 675); length of ventral sucker 35.4% (33.8–42.6%; 37.0%) of body length. Ratio of ventral sucker:oral sucker length 1:1.85 (1:1.74–1:2.06; 1:1.88); ratio of ventral sucker:oral sucker width 1:1.69 (1:1.69–1:2.04; 1:1.84). Pre-pharynx absent. Pharynx large, muscular, round or oval, 232 (168–264; 223) × 200 (136–224; 191); length of pharynx 12.1% (10.7–14.2%; 12.0%) of body length. Ratio of oral sucker:pharynx width 1:1.92 (1:1.68–1:2.28; 1:1.96). Esophagus straight or sigmoid, surrounded by conspicuous cells along outer wall, 292 (80–292; 184) long; 15.2% (5.3–15.2%; 9.8%) of body length. Intestinal bifurcation in forebody, anterior to ventral sucker by 100 (80–120; 92) long. Ceca moderately wide, thick-walled, inconspicuous, extend posteriorly near lateral margins either to level of posterior margin of ventral sucker or to level of ovary, terminate blindly and at times arcuate posteriorly, (104–160; 133) [n = 5] wide; post-cecal distance (320–552; 436) [n = 2]. Ceca width and post-cecal distance not observed in holotype; in 2 immature specimens, ceca width 104–116 ( $\bar{x}$  = 110), post-cecal distance 240–384 ( $\bar{x}$  = 312).

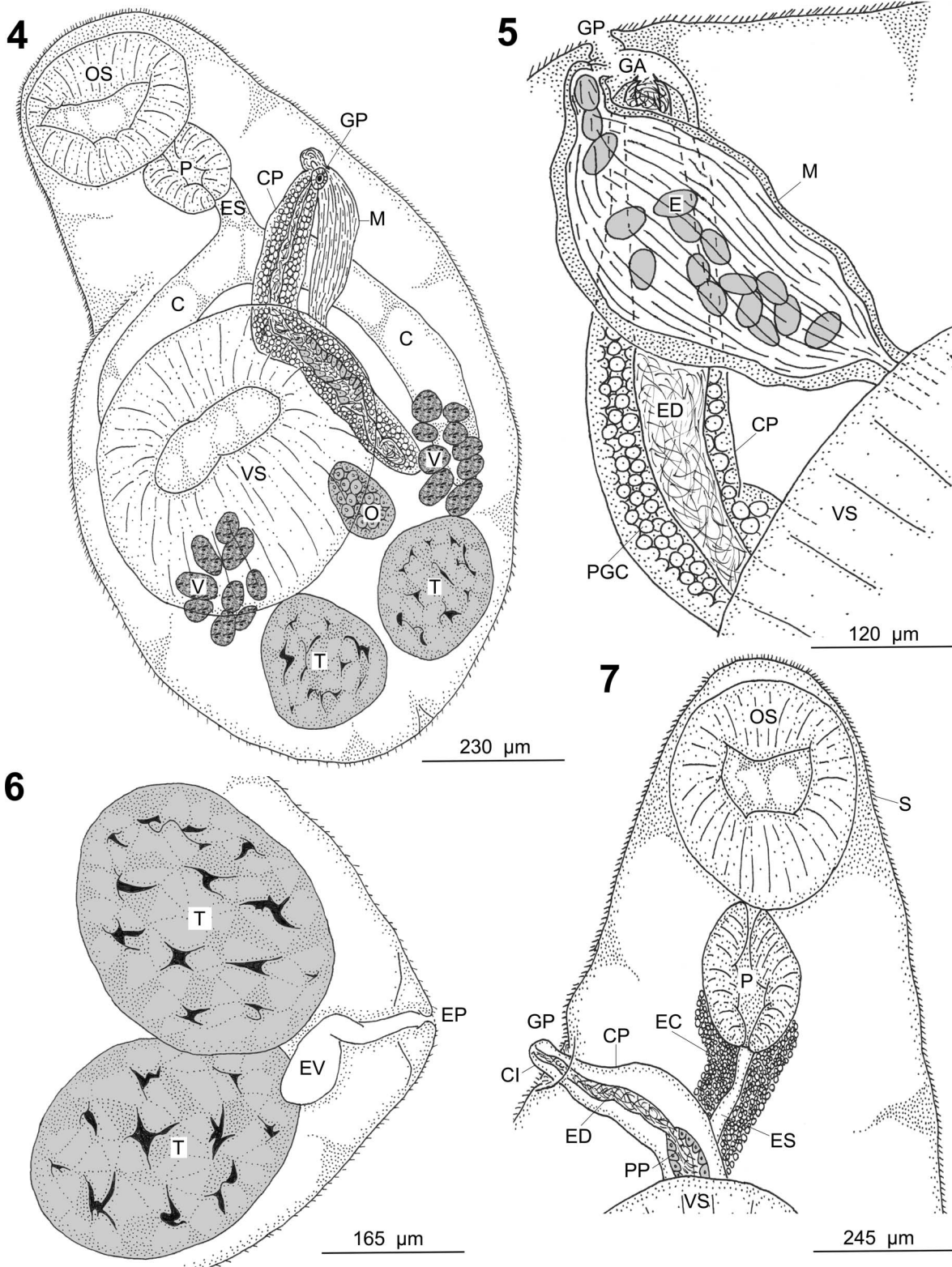
Testes 2, smooth, round to oval, opposite, near posterior extremity; left testis 340 (280–340; 295) × 220 (176–288; 229), left testis length 17.7% (12.7–18.4%; 16.1%) of body length; right testis 352 (288–380; 335) × 272 (212–296; 253), right testis length 18.3% (16.1–21.6%; 18.2%) of body length; body width at testes 37.5% (35.6–49.1%; 42.1%) of body length; inter-testicular space 56 (56–148; 123) [n = 5] wide; post-testicular space 144 (108–344; 203) × 504 (232–792; 459) and 7.5% (7.1–15.9%; 10.5%) of body length. Cirrus pouch large, conspicuous, clavate to comma-shaped, filled with prostatic gland cells, extends postero-dextrally along transverse course from genital pore to anterior margin of ventral sucker, turns due posterior to run along midline to either terminate at level of posterior half of ventral sucker or turns postero-sinistrally at or near level of posterior margin of ventral sucker to terminate short distance posterior to sucker or at level of anterior margin of testes, 1,064 (788–1,296; 1,017) × 168 (104–216; 164); length of cirrus pouch 55.4% (51.8–58.9%; 54.5%) of body length. Seminal vesicle bipartite, occupies posterior third of cirrus pouch, from posterior end of cirrus pouch it passes

anteriorly, loops back on itself, and turns again to run anteriorly; proximal portion large, saccate to sausage-shaped; distal portion tubular, sinuous; 420 (268–760; 475) × 80 (48–104; 83); length of seminal vesicle 20.0% (20.0–43.2%; 30.4%) of cirrus pouch length. Pars prostatica cylindrical, conspicuous, occupies middle third of cirrus pouch, surrounded by prostatic cells, filled with bleb-like cells, 392 (204–416; 303) × 64 (64–120; 80); 36.8% (20.7–37.6%; 29.7%) of cirrus pouch length. Ejaculatory duct distinct, long, narrow to moderately wide, tubular, occupies anterior third of cirrus pouch and often longer, runs mostly straight and tapers at distal end, 524 (228–540; 404) × 52 (24–60; 43); 49.2% (28.9–49.2%; 39.3%) of cirrus pouch length; cirrus present, occasionally everted. Genital atrium voluminous, deep, with distinct border; genital pore submedian, sinistral near left margin (appears marginal or just submarginal when worm rolled), anterior to ventral sucker and pre-bifurcal at level of esophagus, (28–88; 55) [n = 3] from left margin (genital pore appeared marginal in holotype, which is slightly rolled), 624 (252–768; 602) from anterior extremity.

Ovary smooth, globular to oval, submedian, dextral, either partially overlapped by ventral sucker or anterior margin contiguous with sucker, immediately pre-testicular and posterior margin contiguous with or overlaps anterior margin of right testis (1 specimen with ovary anterior to right testis by 28 long or 1.8% of body length; 1 specimen with inter-testicular ovary that is contiguous with medial margins of both testes), 264 (192–264; 229) × 168 (152–280; 191); length of ovary 13.8% (9.8–14.0%; 12.5%) of body length; pre-ovarian space 1,472 (1,008–1,576; 1,332) long. Seminal receptacle canalicular, large, globular to oval, in inter-testicular space immediately posterior to and contiguous with ovary, dorsally overlaps left or anterior margin of right testis (1 specimen with inter-testicular ovary has seminal receptacle located short distance posterior to ovary and between testes), 232 (140–232; 190) [n = 5] × 216 (120–216; 167) [n = 5]. Laurer's canal present, opening not observed but expected to be dorsal. Mehlis' gland inconspicuous, medial, inter-testicular, proximate to vitelline reservoir, seminal receptacle, oviduct, and ovary. Uterus extensive, conspicuous, coiled, occupies most of



**Figures 1–3.** *Gaharitrema droneni* n. gen., n. sp. (Digenea: Zoogonidae: Lepidophyllinae) from the intestine of the pudgy cuskeel, *Spectrunculus grandis* (Günther, 1877) (Ophidiiformes: Ophidiidae). (1) Composite of adult, ventral view. Note: Gonads and vitellarium illustrated entirely ventral to uterus for ease of observation. (2) Male terminal genitalia of paratype, dorsal view. (3) Composite of proximal female system, dorsal view. Note: Image rotated 90° (anterior to left, posterior to right). Abbreviations: C, cecum; CP, cirrus pouch; E, egg; EC, esophageal cells; ED, ejaculatory duct; ES, esophagus; GP, genital pore; LC, Laurer's canal; M, metraterm; MG, Mehlis' gland; O, ovary; OD, oviduct; OS, oral sucker; P, pharynx; PGC, prostatic gland cells; PP, pars prostatica; SR, seminal receptacle; SV, seminal vesicle; T, testis; U, uterus; V, vitellarium; VD, vitelline duct; VR, vitelline reservoir; VS, ventral sucker.



**Figures 4–7.** *Gaharitrema droneni* n. gen., n. sp. (Digenea: Zoogonidae: Lepidophyllinae) from the intestine of the pudgy cuskeel, *Spectrunculus grandis* (Günther, 1877) (Ophidiiformes: Ophidiidae). (4) Immature individual exhibiting posterior extent of cecum and cirrus pouch, voucher specimen, ventral view. (5) Metraterm and distal end of cirrus pouch of paratype, ventral view. Note: Specimen is slightly rolled so genital pore appears marginal, and metraterm is illustrated ventral to cirrus pouch for ease of observation. (6) Excretory vesicle of paratype, ventro-lateral view. (7) Esophageal cells and everted cirrus of paratype, ventral view. Abbreviations: C, cecum; CI, cirrus; CP, cirrus pouch; E, egg; EC, esophageal cells; ED, ejaculatory duct; EP, excretory pore; ES, esophagus; EV, excretory vesicle; GA, genital atrium; GP, genital pore; M, metraterm; O, ovary; OS, oral sucker; P, pharynx; PGC, prostatic gland cells; PP, pars prostatica; S, spines; T, testis; V, vitellarium; VS, ventral sucker.

hindbody, loops extend anterior to near anterior margin of ventral sucker and then narrow to genital pore; in midbody, loops widen laterally to reach near body margin and dorsally overlap vitelline fields before they narrow somewhat at level of testes to pass through inter-testicular space to near posterior extremity, 1,320 (968–1,640; 1,315) × 872 (520–976; 837) wide at level of vitelline fields; post-uterine space 92 (28–284; 122) long and 4.8% (1.3–18.7%; 7.0%) of body length. Metraterm thick-walled with striated musculature, voluminous, long, passes dorsally over distal end of cirrus pouch, conspicuously dilated at anterior end to appear like an ampulla, 344 (168–520; 307) × 180 (88–192; 147). Vitellaria in 2 symmetrical fields of follicles along lateral margins, restricted to hindbody, extend anteriorly from level of testes to near midlevel of ventral sucker; left/poral vitelline field composed of 8 (7–10; 8) [n = 5] follicles, and right/aporal vitelline field composed of 8 (8–9; 8) [n = 5] follicles; follicles oblong to subcircular to irregular in shape, large; follicles in holotype (120–132; 126) [n = 4] × (76–92; 84) [n = 4] in left field, (92–160; 133) [n = 5] × (60–108; 80) [n = 5] in right field; follicles in all measured specimens (80–148; 109) [n = 26] × (48–120; 70) [n = 26] in left field, (72–160; 112) [n = 29] × (48–108; 71) [n = 29] in right field; left vitelline field 416 (264–480; 392) long and 21.7% (17.4–25.8%; 21.0%) of body length; right vitelline field 520 (280–560; 411) long and 27.1% (12.7–36.8%; 22.8%) of body length; pre-vitelline space 1,060 (912–1,420; 1,151) long and 55.2% (55.2–64.8%; 61.6%) of body length; post-vitelline space 420 (280–500; 364) long and 21.9% (16.7–22.7%; 19.5%) of body length. Vitelline reservoir circular to subtriangular, medial, inconspicuous, near to or overlaps left margin of seminal receptacle, (72–112; 91) [n = 3] × (40–52; 48) [n = 3] (vitelline reservoir not observed in holotype). Paired vitelline ducts proceed medially between vitelline fields at or near level of ovary to join vitelline reservoir; right duct passes between ovary and right testis (1 specimen with ducts that pass medially from vitelline fields to midline, turn posterior, and run to level near posterior margin of ventral sucker to join vitelline reservoir). Eggs numerous, oval, either smooth or crenulated, operculate, amber, non-filamented, non-embryonated; eggs in holotype (34–40; 36.4) [n = 5] × (24–28; 26) [n = 5]; eggs in all measured specimens (34–44; 39.2) [n = 31] × (18–28; 22.7) [n = 35].

Excretory vesicle I-shaped, extends to at least level of testes, inconspicuous and often occluded by eggs, 156 [n = 1] × 132 [n = 1] (excretory vesicle not observed in holotype). Excretory pore terminal.

### Taxonomic summary

*Type host:* *Spectrunculus grandis* (Günther, 1877) (syn. *Parabassogigas grandis* [Günther, 1877]) (Ophidiiformes: Ophidiidae); pudgy cuskeel.

*Type locality/collection date:* Northeastern Pacific Ocean, approx. 137 km off Newport, Oregon, 44°40'06.6"N, 125°52'46.4"W; depth = 2,800 m; 12 January 1965.

*Site of infection:* Intestine.

*Specimens deposited:* Holotype HWML 216075 (1 slide); paratypes HWML 216076 (5 specimens on 5 slides); vouchers HWML 42859 (20 specimens on 19 slides).

*ZooBank registration:* urn:lsid:zoobank.org:act:CD345089-E712-4D0F-8878-5D5DCE77C97E.

*Etymology:* The species is named in honor of Dr. Norman O. Dronen, Department of Wildlife & Fisheries Sciences, Texas

A&M University, for his numerous contributions to the field of parasitology and for his lifetime of service and teaching to his many students.

### Remarks

*Gaharitrema* belongs in the Zoogonidae based on the following diagnostic combination of features: a genital pore in the forebody that is neither median nor close to the anterior extremity or lateral edge of the ventral sucker; a cirrus pouch with proximal extremity oriented posteriorly; an ovary that is entire and in the hindbody; a distinct alimentary tract as opposed to absent or greatly reduced; an ejaculatory duct and metraterm that are unarmed; testes in the hindbody; and a fish host (Bray, 2008a). Unlike members of the Cephaloporinae, *Gaharitrema* lacks an unusually posterior ventral sucker, a lateral genital pore close to the level of the oral sucker, and a monacanthid host, yet it possesses an operculate egg and vitellaria in paired fields of follicles and not in 1 or 2 compact masses (i.e., Zoogoninae); therefore, the new genus is placed in the Lepidophyllinae (Bray, 2008b; Cutmore et al., 2014).

In the key by Bray (2008b), *Gaharitrema* most closely resembles 2 lepidophylline genera, *Brachyenteron* Manter, 1934 and *Steganoderma* Stafford, 1904. *Brachyenteron* was erected by Manter (1934) with the description of *Brachyenteron peristedioni* Manter, 1934 from the intestine of the flathead searobin, *Peristedion brevirostre* (Günther, 1860) (Scorpaeniformes: Peristediidae) (syn. *Peristedion platycephalum* [Goode and Bean, 1886]), collected from 247–285 m depth off Tortugas, Florida. While several species of *Brachyenteron* are known from deep waters (e.g., *Brachyenteron campbelli* Bray and Gibson, 1986; *Brachyenteron dextroporus* Kuramochi, 2005; *Brachyenteron helicoleni* Bray and Kuchta, 2006; *B. peristedioni*; *Brachyenteron rissoanum* Bray and Campbell, 1995), the new genus differs from *Brachyenteron* in a combination of several diagnostic morphological features (Manter, 1934; Bray, 2008b). Most noticeable is the relatively much larger hindbody in members of *Brachyenteron* compared to *Gaharitrema*, resulting in the relatively more anterior position of the gonads, vitellaria, and ventral sucker in *Brachyenteron* (i.e., larger post-acetabular, post-testicular [PTS] and post-vitelline space [PVS] as well as post-testicular portion of the uterus in relation to body length). *Gaharitrema droneni* has a PTS of only 7.1–15.9% of body length, a PVS of only 16.7–22.7% of body length, and the post-acetabular space and post-testicular portion of the uterus are clearly smaller. Two species, *B. helicoleni* and *Brachyenteron japonicum* Machida and Kuramochi, 2000, have a small PTS of 12.5% and 11–19% of body length, resulting in a comparably small post-testicular portion of the uterus (Machida and Kuramochi, 2000; Bray and Kuchta, 2006). Species of *Brachyenteron* can lack tegumental spines (e.g., *B. helicoleni*) and have considerably smaller oral and ventral suckers in relation to body size (*G. droneni* has an oral and ventral sucker length of 19.7% and 37.0% of body length, respectively; *B. rissoanum* is closest in oral sucker length [17.5% of body length], while *Brachyenteron parexocoeti* Manter, 1947 is closest in ventral sucker length [26.8% of body length] (see Manter, 1947; Bray and Campbell, 1995)). *Brachyenteron* species may have a tegumental pit on the posterior lip of the ventral sucker (e.g., *Brachyenteron pyncorganum* [Rees, 1953] Overstreet and Pritchard, 1977), and all have a distinct pre-pharynx, a noticeably smaller pharynx in relation to body size (*G. droneni* has a pharynx length of 12.0% of

body length; *B. rissoanum* is closest in pharynx length at 11.1% of body length), and short ceca that can end either in the forebody or at the level of the ventral sucker (*G. droneni* possesses longer ceca that extend either to the level of the posterior margin of the ventral sucker or to the level of the ovary, which itself is in the post-acetabular region). The cirrus pouch of species of *Brachyenteron* is clavate to elongate claviform and can be either entirely anterior to the ventral sucker or extend to the midlevel of it, whereas in the new genus, the cirrus pouch is noticeably larger (length of cirrus pouch 51.8–58.9% of body length) and clavate to comma-shaped, and it extends to the posterior half of the ventral sucker, a short distance posterior to the sucker, or to the level of the anterior margin of the testes. The cirrus pouch of *B. pycnorganum* (syn. *Steganoderma pycnorganum* Rees, 1953) as originally described and illustrated by Rees (1953, fig. 1) extends in a broad curve from the genital atrium to the midline of the worm and only overlaps the anterior half of the ventral sucker (i.e.,  $\neq$  *G. droneni*); however, the illustration of the cirrus pouch of this species given by Bray (1987, fig. 6b) appears more comparable in length to this feature within *G. droneni*, although it is more retroflexed in this specimen. The ovary and vitellarium of species of *Brachyenteron* can be found in the forebody (e.g., *Brachyenteron doederleiniae* Yamaguti, 1938); however, neither feature in *Gaharitrema* is found there.

*Gaharitrema* also resembles the lepidophylline genus *Steganoderma*, which was established by Stafford (1904) for *Steganoderma formosum* Stafford, 1904, found in the ceca and intestine of the Atlantic halibut, *Hippoglossus hippoglossus* (Linnaeus, 1758) (Pleuronectiformes: Pleuronectidae), from the western Atlantic Ocean off Canada. Of the 7 known species of *Steganoderma*, *S. formosum* is the only species reported from the deep sea (see Sekerak and Arai, 1977; Scott, 1987; Klimpel et al., 2001, 2009); however, unlike *Gaharitrema*, species of *Steganoderma* also have been found in freshwater teleosts from South America (e.g., *Steganoderma macrophallus* Szidat and Nani, 1951; *Steganoderma oviformis* Szidat, 1962; *Steganoderma szidati* Viozzi, Flores and Núñez, 2000; *Steganoderma valchetensis* Etchegoin, Cremonte and Escalante, 2002). The new genus further differs from *Steganoderma* in a combination of several diagnostic morphological features (Stafford, 1904; Bray, 1987, 2008b). Most noticeable again is the relatively much larger hindbody in members of *Steganoderma* than in *Gaharitrema*, resulting in the gonads, vitellarium, and ventral sucker positioned conspicuously further anterior from the posterior extremity in the former genus (i.e., larger post-acetabular, PTS, and PVS, as well as post-testicular portion of the uterus in relation to body length). *Gaharitrema droneni* has a relatively small PTS of <16% of body length, a PVS of <23% of body length, and the post-acetabular space and post-testicular portion of the uterus are clearly smaller. Some species of *Steganoderma* (i.e., *Steganoderma atherinae* [Price, 1934] Manter, 1947; *S. macrophallus*; *S. valchetensis*) have a relatively large oral sucker relative to body size (cf. *Gaharitrema*); however, the remaining species of this genus have a much smaller oral sucker (i.e., *S. formosum*; *S. oviformis*; *Steganoderma rhipidium* Wang, 1986; *S. szidati*). The ventral sucker relative to body size is considerably larger in the new genus (*G. droneni* has a ventral sucker length 37.0% of body length; the 2 closest *Steganoderma* species for this feature are *S. oviformis* = 28.9% and *S. valchetensis* = 22.5–30.9%; see Szidat, 1962; Etchegoin et al., 2002). Furthermore, the ventral sucker is either equal in size to the

oral sucker or smaller in species of *Steganoderma* (see Bray, 2008b), whereas it is considerably larger in the new genus (544–808  $\times$  552–816 vs. 312–416  $\times$  288–424, sucker length ratio = 1:1.74–1:2.06, sucker width ratio = 1:1.69–1:2.04). We note that in *S. oviformis* and *S. valchetensis*, however, the ventral sucker is larger than the oral sucker (550  $\times$  610 vs. 200 wide in *S. oviformis* and 90–199  $\times$  88–210 vs. 90–147  $\times$  80–155 with a sucker width ratio = 1:0.99–1:1.64 in *S. valchetensis*; see Szidat, 1962; Etchegoin et al., 2002). *Steganoderma* species have a short pre-pharynx, but we did not observe this feature in *Gaharitrema*. We note that the type descriptions of *S. oviformis*, *S. szidati*, and *S. valchetensis* either failed to illustrate this feature and/or stated that the pre-pharynx was “apparently absent” (see Szidat, 1962; Viozzi et al., 2000; Etchegoin et al., 2002). *Steganoderma* species possess a noticeably smaller pharynx in relation to body size (*G. droneni* has pharynx length = 12.0% of body length; the 2 closest *Steganoderma* species for this feature are *S. macrophallus* = 7.5–8.6% and *S. valchetensis* = 8.3–10.1%; see Szidat and Nani, 1951; Etchegoin et al., 2002), can lack an esophagus (e.g., *S. atherinae*), and possess ceca noticeably longer (extending to the testes) than the new genus (ceca of *G. droneni* extend either to the level of the posterior margin of the ventral sucker or to the level of the ovary, which is pre-testicular). The cirrus pouch of species of *Steganoderma* contains a saccular seminal vesicle, is claviform, is straight or curved, and can be either entirely anterior to the ventral sucker or extend to the midlevel of it. In the new genus, the cirrus pouch contains a bipartite seminal vesicle, is noticeably larger (length of cirrus pouch 51.8–58.9% of body length), and is clavate to comma-shaped, and it extends to the posterior half of the ventral sucker, a short distance posterior to the sucker, or to the level of the anterior margin of the testes. We note that the cirrus pouch of *S. macrophallus* as illustrated by Szidat and Nani (1951, fig. 5b) appears most comparable in length to that of *G. droneni*, although, like its congeners, it, too, only extends to the midlevel of the ventral sucker. *Steganoderma* has vitellaria that are similar in number and distribution to *Gaharitrema*; however, the vitelline follicles of members of the former genus can extend into the forebody (e.g., *S. valchetensis*, wherein the vitelline follicles were described as “in lateral fields extending posteriorly from intestinal bifurcation [which is pre-acetabular] to about posterior half of ventral sucker”; see Etchegoin et al., 2002, p. 150); the vitellarium is restricted to the hindbody in *Gaharitrema*. Finally, the excretory vesicle is saccular and short in *Steganoderma* (see Bray, 2008b; fig. 5 of Szidat and Nani, 1951; fig. 1 of Etchegoin et al., 2002; where the excretory vesicle of *S. macrophallus* and *S. valchetensis* extends anteriorly only to the midlevel of the PTS); this feature in *G. droneni* is tubular/I-shaped and extends to at least the level of the testes. We note that the excretory vesicle of *S. rhipidium* appears to be tubular and extends to the testes (see fig. 6 of Wang, 1986).

Prior to this study, the Lepidophyllinae contained 21 genera; however, 4 of these genera were established after the comprehensive work by Bray (2008b). *Oesophagotrema* Chaari, Derbel, and Neifar, 2011 was erected by Chaari et al. (2011) with the description of *Oesophagotrema mediterranea* Chaari, Derbel and Neifar, 2011 from the esophagus and vomerine teeth of a needlefish, *Tylosurus acus imperialis* (Rafinesque, 1810) (Beloniformes: Belonidae), collected off Sfax, Tunisia. *Porangatus* Fernandes, Malta and Morias, 2013 was erected by Fernandes et al. (2013) with the description of *Porangatus ceteyus* Fernandes, Malta and Morias, 2013 from the intestine of the atipa,



*Hoplosternum littorale* (Hancock, 1828) (Siluriformes: Callichthyidae), collected from Lake Catalão, Amazonas State, Brazil. *Prosteganoderma* Hassanine, 2007 was established by Hassanine (2007) with the description of *Prosteganoderma brayi* Hassanine, 2007 from the middle intestine of the blue-barred parrotfish, *Scarus ghobban* (Forsskål, 1775) (Perciformes: Scaridae), from the Red Sea off Sharm El-Sheikh, South Sinai, Egypt; while mentioned as an addendum in Bray (2008b, p. 628), this genus was not included in Bray’s key to the lepidophylline genera. *Whitegonimus* Jezewski, Zdzitowiecki and Laskowski, 2009 was erected by Jezewski et al. (2009) with the description of *Whitegonimus ozoufae* Jezewski, Zdzitowiecki and Laskowski, 2009 from the stomach of the black southern cod, *Patagonotothen tessellata* (Richardson, 1845) (Perciformes: Nototheniidae), collected off Tierra del Fuego, Argentina.

All 4 genera differ from *Gaharitrema* in their overall appearance (i.e., fusiform, oval elongate, or plump and stout body vs. pyriform or spindle-shaped body); smaller suckers and pharynx relative to overall body size; possessing a pre-pharynx (it is lacking in *Porangatus*); longer ceca (reach to mid-hindbody, anterior edge or midlevel of posterior testis, midtesticular level or near posterior extremity vs. extend either to level of posterior margin of ventral sucker or to level of ovary); tandem, oblique, or contiguous vs. opposite and non-contiguous testes; a cirrus pouch that is entirely anterior to, slightly overlaps the anterior margin of, or reaches the midlevel of the ventral sucker vs. one that is noticeably larger (length of cirrus pouch 51.8–58.9% of body length) and extends to the posterior half of the ventral sucker, a short distance posterior to the sucker, or to the level of the anterior margin of the testes; a genital pore either at the level of the pharynx or the intestinal bifurcation vs. the level of the esophagus (it is at the level between the pharynx and intestinal bifurcation in *Whitegonimus*); an ovary that appears submedian sinistral or median vs. submedian dextral (see fig. 1 of Chaari et al., 2011; ovary is submedian dextral in *Porangatus* and *Whitegonimus*); and the hindbody is more extensive in these 4 genera with the gonads, ventral sucker, and/or vitellarium positioned further anterior from the posterior extremity, producing a larger post-testicular portion of the uterus (uterus is pre-testicular in *Prosteganoderma*, and gonads are post-acetabular and distributed in tandem along the longitudinal axis in *Whitegonimus*).

*Oesophagotrema* further differs from *Gaharitrema* in the site of infection (esophagus and vomerine teeth vs. intestine), small papillae on the lips of the ventral sucker, an undivided seminal vesicle, and more longitudinally restricted vitelline fields (between anterior testis and ovary, which is entirely post-acetabular vs. from level of testes to near midlevel of ventral sucker). *Porangatus* additionally differs from *Gaharitrema* in its freshwater host, sinuous grooves and spines on the tegument of the inner surface of the ventral sucker, no esophagus, a seminal receptacle that may be lacking (i.e., “[t]rue seminal receptacle not observed”; see Fernandes et al., 2013), vitellarium that is composed of numerous large and small follicles distributed from as far anterior as the level of the intestinal bifurcation to near the posterior end of the body and that may or may not be confluent anteriorly and almost confluent in the PTS, no metraterm (i.e., “[m]etraterm not differentiated”; see Fernandes et al., 2013), and a Y-shaped excretory vesicle instead of an I-shaped one as seen in *Gaharitrema*. *Prosteganoderma* differs from *Gaharitrema* in possessing a large prominent, subglobular to subrectangular fleshy fold of the body

wall surrounding the ventral sucker (supplementary attachment organ?), a pre-testicular uterus (winds between ovary and testes), and entirely post-acetabular vitellarium. *Whitegonimus* differs from *Gaharitrema* in the site of infection (stomach), more longitudinally dispersed vitelline follicles that extend from the anterior part of the ventral sucker to the posterior margin of the anterior testis, a possibly non-operculate egg (i.e., “operculum not observed”; see Jezewski et al., 2009), and a Y-shaped excretory vesicle with short arms at the level of the anterior testis.

As there have been considerable taxonomic changes within the Zoogonidae over the last decade or so, we present updated keys to the 3 subfamilies of the Zoogonidae, based on the comprehensive work by Bray (2008b) (see also Bray and Justine, 2014), as well as new and/or modified keys to the 3 genera of the Cephaloporinae and the 22 genera now within the Lepidophyllinae.

**Key to the Subfamilies of the Zoogonidae Odhner, 1902 (Based in Part on Bray, 2008b)**

- 1a. Vitellarium forms 1 or 2 compact masses, or several follicles, in undivided median field .....  
 ... Zoogoninae Odhner, 1902\* (Syns. Dipterostominae Stossich, 1903; Parvipyrinae Yamaguti, 1970)
- 1b. Vitellarium forms paired fields of follicles ..... 2
- 2a. Ventral sucker located far posterior; parasitizes teleosts within the Monacanthidae (filefish and leatherjackets) ..... Cephaloporinae Yamaguti, 1934 (Syn. Plectognathotrematinae Kamegai, 1970)
- 2b. Ventral sucker located in midbody or further anterior; parasitizes non-monacanthid teleosts. ....  
 .... Lepidophyllinae Stossich, 1903 (Syns. Hudsoniinae Campbell, 1975; Lecithostaphylinae Odhner, 1911; Pseudopalaeorchiinae Yamaguti, 1971; Steganodermatinae Yamaguti, 1934; Steganoderminae Yamaguti, 1934)

\*No new genera have been erected within the Zoogoninae since Bray (2008b), which provides a key to the 10 recognized zoogonine genera.

**Key to the Genera of the Cephaloporinae Yamaguti, 1934 (Based in Part on Bray, 2002, 2008b)**

- 1a. Transverse rows of rosette-shaped adhesive organs in ventral sucker; ovary entire .....  
 ..... *Plectognathotrema* Layman, 1930 (Syn. *Plectognathotrema (Alloplectognathotrema)* Kamegai, 1970)
- 1b. Ventral sucker unspecialized (no rosette-shaped adhesive organs); ovary lobed ..... 2
- 2a. Body fusiform or oval; testes in forebody; ceca terminate in forebody. .... *Cephaloporus* Yamaguti, 1934
- 2b. Body pyriform; testes lateral to ventral sucker; ceca reach posterior part of ventral sucker .....  
 ..... *Yamagutiplectognathotrema* Parukhin, 1977 (Syn. *Plectognathotrematoides* Yamaguti, 1971 nec Parukhin, 1971)

**Key to the Genera of the Lepidophyllinae Stossich, 1903 (Based in Part on Bray, 2008b)**

- 1a. Body flattened spatulate; testes deeply lobed; in urinary bladder of marine teleosts. .... 2

- 1b. Body more or less oval or rounded in cross-section, oval to pyriform or fusiform in ventral view; testes more or less entire; not usually found in urinary bladder..... 3
- 2a. Ceca narrow, reach level of testes; ovary subglobular to slightly lobed; vitellarium entirely in hindbody ..... *Lepidophyllum* Odhner, 1902 (Syn. *Paralepidophyllum* Yamaguti, 1934)
- 2b. Ceca dilate or diverticulate, almost reach posterior extremity; ovary deeply lobed; vitellarium in posterior forebody, lateral to ventral sucker and in hindbody; in *Hexagrammos* spp..... *Urinatrema* Yamaguti, 1934
- 3a. Ceca short, saccular, divergent, or, if narrow, not reaching into hindbody ..... 4
- 3b. Ceca narrow, reach well into hindbody or to testes or beyond..... 7
- 4a. Genital pore at level of oral sucker or pharynx; in freshwater teleosts ..... *Limoderetrema* Bray, 1987
- 4b. Genital pore usually in mid- to posterior forebody; in marine teleosts ..... 5
- 5a. Excretory vesicle Y-shaped; testes close to posterior extremity..... *Koiea* Bray and Campbell, 1995
- 5b. Excretory vesicle I-shaped; testes well separated from posterior extremity ..... 6
- 6a. Ovary pre-testicular (occasionally inter-testicular) ....  
.. *Brachyenteron* Manter, 1934 (Syns. *Cypseluritrematoides* Yamaguti, 1970; *Prolateroporus* Yamaguti, 1971)
- 6b. Ovary post-testicular.....  
..... *Panopula* Overstreet and Pritchard, 1977
- 7a. Ventral sucker not divided..... 8
- 7b. Ventral sucker divided equatorially or longitudinally by ridge or row of papillae ..... 20
- 8a. Vitellarium in hindbody ..... 9
- 8b. Vitellarium extends into forebody..... 18
- 9a. Eggs filamented; ovary multilobate.....  
..... *Anarhichotrema* Shimazu, 1973 (Syn. *Neolissorhis* Machida, 1985)
- 9b. Eggs not filamented; ovary entire or irregular ..... 10
- 10a. Two to 6 rows of enlarged circumoral spines present ..... *Overstreetia* Bray, 1985
- 10b. No enlarged circumoral spines present..... 11
- 11a. Body elongate, narrow; cirrus pouch elongate, undulating; pockets in ejaculatory duct and metratrum ..... *Pseudopalaeorchis* Kamegai, 1970
- 11b. Body squat to oval to fusiform; cirrus pouch claviform; unpocketed ejaculatory duct and metratrum ..... 12
- 12a. Ceca extend as far as level of ovary but do not reach testes..... *Gaharitrema*
- 12b. Ceca reach at least to level of testes ..... 13
- 13a. Ventral sucker shaped like inflated balloon, with narrow aperture surrounded by strong sphincter ..  
..... *Saculoacetabulum* Machida and Kuramochi, 1999
- 13b. Ventral sucker rounded, with midventral aperture.. 14
- 14a. Seminal vesicle bipartite ..... 15
- 14b. Seminal vesicle saccular to elongate..... 16
- 15a. Ventral sucker surrounded by prominent fleshy fold of body wall; uterus pre-testicular .....  
..... *Prosteganoderma* Hassanine, 2007
- 15b. Ventral sucker unspecialized with no fleshy fold; uterus extends beyond testes to posterior extremity.....  
..... *Whitegonimus* Jezewski, Zdzitowiecki and Laskowski, 2009
- 16a. Parasitizes esophagus and vomerine teeth of teleosts; testes tandem ..... *Oesophagotrema* Chaari, Derbel and Neifar, 2011
- 16b. Parasitizes intestine of teleosts; testes symmetrical or oblique..... 17
- 17a. Ventral sucker sessile; ceca reach testes .....  
..... *Steganoderma* Stafford, 1904 (Syn. *Nordostrema* Issaitschikow, 1928)
- 17b. Ventral sucker pedunculate; ceca extend beyond testes.....  
..... *Lecithostaphylus* Odhner, 1911 (Syns. *Cypseluritrema* Yamaguti, 1970; *Manteroderma* Skrjabin, 1957; *Steganoderma* (*Lecithostaphylus*) Odhner, 1911; *Steganoderma* (*Opisthoarchiotrema*) Gupta and Sharma, 1974)
- 18a. Vitellarium distributed in forebody and extends to near posterior end of body; excretory vesicle Y-shaped; esophagus lacking .....  
..... *Porangatus* Fernandes, Malta and Morias, 2013
- 18b. Vitellarium distributed in forebody and extends to level of ventral sucker in anterior hindbody; excretory vesicle saccular; esophagus present..... 19
- 19a. Excretory vesicle long; in marine teleosts.....  
.. *Deretrema* Linton, 1901 (Syns. *Deretrema* (*Deretrema*) Linton, 1910; *Deretrema* (*Luxitrema*) Bray, 1987; *Deretrema* (*Spinoderetrema*) Bray, 1987)
- 19b. Excretory vesicle short; in freshwater teleosts .....  
..... *Pseudochetosoma* Dollfus, 1951 (Syn. *Ochetosoma* (*Pseudochetosoma*) Dollfus, 1951)
- 20a. Ventral sucker divided longitudinally; oral sucker infundibuliform with several anterior lobes; eggshell with 2 raised bands.....  
.. *Dupliciporia* Reimer, 1985 (Syns. *Liliaoralis* Korotaeva, 1994; *Parasteganoderma* Machida and Araki, 1990)
- 20b. Ventral sucker divided equatorially; oral sucker subglobular to infundibuliform, unlobed; eggshell smooth..... 21
- 21a. Ventral sucker divided equatorially by internal ridge and external cleft..... *Proctophantastes* Odhner, 1911 (Syn. *Neosteganoderma* Byrd, 1964)
- 21b. Ventral sucker divided equatorially by internal row of large papillae.....  
..... *Steganodermatoides* Parukhin and Lyadov, 1979 (Syns. *Allosteganoderma* Campbell, 1983; *Hudsonia* Campbell, 1975 nec Edwards, 1923 or Leroux, 1940)

## DISCUSSION

Table I provides a list of the handful of parasites reported from *S. grandis*. To date, only 1 cestode, 1 copepod, and 3 nominal digenean species are known from the pudgy cuskeel. Among the digenetic trematodes, representatives of 2 families were known from this host prior to this study: *Gonocerca oregonensis* McCauley, Pequegnat and Brownell, 1970 from the Gonoceridae Skrjabin and Guschanskaja, 1955 and *Steringophorus haedrichi* Bray and Campbell, 1995, *Steringophorus margolisi* Bray, 1995,

and an unknown species of *Steringophorus* Odhner, 1905, all from the Fellodistomidae. This study documents the third family of digeneans (Zoogonidae) known to parasitize *S. grandis*, and while this is a new host record (i.e., first zoogonid reported from this host species), it is not a new locality record, because *G. oregonensis* was reported by McCauley et al. (1970) from *S. grandis* collected off Oregon (Table I) (see also Yamaguti, 1971; Love and Moser, 1983).

The Zoogonidae family is well represented in the deep sea. Of the 35 genera within this family, 14 or 2/5 (14 of 35 or 40%) have deep-sea representatives (Bray, 2008b; Klimpel et al., 2009). At least 9 of 22 (41%) genera and 23 species within the Lepidophyllinae are known to infect deep-sea teleosts: *Anarhichotrema* (1 sp.); *Brachyenteron* (7 spp.); *Gaharitrema* (1 sp.); *Koiea* (1 sp.); *Lepidophyllum* (1 sp.); *Panopula* (3 spp.); *Proctophantastes* (4 spp.); *Steganoderma* (1 sp.); and *Steganodermatoides* (4 spp.) (see Manter, 1934; Klimpel et al., 2009; this study). At least 5 of 10 (50%) genera and 6 species within the Zoogoninae are known from deep-sea fishes: *Brevicreadium* Manter, 1954 (1 sp.); *Diptherostomum* Stossich, 1903 (1 sp.); *Pseudozoogonoides* Zhukov, 1957 (1 sp.); *Zoogonoides* Odhner, 1902 (1 sp.); and *Zoogonus* Looss, 1901 (2 spp.) (see Klimpel et al., 2009). No genera within the Cephaloporinae are known from the deep; this subfamily of zoogonids only infects monacanthids (filefish and leatherjackets), which are generally shallow-water fish.

It is no surprise that, as zoogonids are well represented in the deep sea, their piscine hosts are also strikingly diverse. At least 37 species within 27 genera and 19 families within 11 orders of deep-sea fish are known to harbor zoogonids (see Manter, 1934; Klimpel et al., 2009; this study). Among lepidophyllines, at least 11 orders, 16 families, 23 genera, and 32 species of deep-water fish hosts are known; zoogonines are found in at least 4 orders, 5 families, 6 genera, and 7 species of fish in the deep-sea. Both lepidophyllines and zoogonines infect deep-sea piscine hosts from at least 4 orders (Anguilliformes; Gadiformes; Perciformes; Pleuronectiformes), 2 families (Anarhichadidae [wolffishes]; Zoarcidae [eelpouts]), 2 genera (*Anarhichas* Linnaeus, 1758 [wolffishes]; *Lycodes* Reinhardt, 1831 [eelpouts]), and 2 species of fish, both wolffishes (the Atlantic wolffish, *Anarhichas lupus* Linnaeus, 1758, and the spotted wolffish, *Anarhichas minor* Olafsen, 1772 [Perciformes: Anarhichadidae]). We also note that among the 9 lepidophylline and 5 zoogonine genera known in the deep sea, the type species for each of these 9 genera in the former subfamily and for 4 of the 5 genera in the latter subfamily parasitize at least 1 species of fish from deep water.

Deep-sea zoogonids exhibit strong host specificity. Of the 37 known piscine species from the deep sea parasitized by zoogonids, only 5 (13.5%) host species harbor 2 or more zoogonid species (Klimpel et al., 2009). The Atlantic wolffish, *A. lupus*, leads the pack, harboring 5 species, including 2 lepidophyllines (*Brachyenteron pycnorganum* and *Lepidophyllum steenstrupi* Odhner, 1902) and 3 zoogonines (*Pseudozoogonoides subaequiporus* [Odhner, 1911] Bray and Gibson, 1986; *Zoogonoides viviparus* [Olsson, 1868] Odhner, 1902; and *Zoogonus rubellus* [Olsson, 1868] Odhner, 1902). The spotted wolffish, *A. minor*, is parasitized by 3 species, the 2 lepidophyllines *B. pycnorganum* and *L. steenstrupi* and the zoogonine *P. subaequiporus*. Finally, 3 host species harbor 2 zoogonid species each. The northern wolffish, *Anarhichas denticulatus* Krøyer, 1845 (Perciformes: Anarhichadidae), is infected with the lepidophyllines *B. pycnorganum* and *L.*

*steenstrupi*. The snubnosed spiny eel, *Notacanthus chemnitzii* Bloch, 1788 (Notacanthiformes: Notacanthidae), harbors the lepidophyllines *Koiea notacanthi* Bray and Campbell, 1995 and *Panopula spinosa* (Zubchenko, 1978) Bray and Gibson, 1986, while the smallmouth spiny eel, *Polyacanthonotus rissoanus* (De Filippi and Verany, 1857) (Notacanthiformes: Notacanthidae), is parasitized by the lepidophyllines *Brachyenteron rissoanum* and *Panopula bridgeri* Bray and Gibson, 1986. The remaining 32 (86.5%) deep-sea host species reported with zoogonids harbor 1 parasite species each, which includes 27 lepidophylline and 5 zoogonine species.

Limited molecular work has been done with members of the Zoogonidae. There are 33 DNA gene sequences currently in GenBank from 8 (8 of 35 genera = 23%) zoogonid genera representing all 3 subfamilies. Of these, 6 genera are found in the deep sea, and 4 species inhabiting deeper waters (see Klimpel et al., 2009) have sequence data available: *Lepidophyllum steenstrupi*; *Proctophantastes gillissi* (Overstreet and Pritchard, 1977) Bray and Gibson, 1986; *Zoogonoides viviparus*; and *Zoogonus rubellus*. The remaining 27 genera, or over 3/4 (77%) of the 35 known zoogonid genera, lack any DNA sequence data. Indeed, the molecular work of Cutmore et al. (2014) suggests that the Zoogoninae and Cephaloporinae may be monophyletic, but the Lepidophyllinae is paraphyletic; the latter perhaps requires subfamilial division. Clearly, more molecular work is needed.

The pudgy cuskeel, *S. grandis*, is a bathydemersal ophiidiid found at depths of 800–4,300 m in the North and South Atlantic and Pacific Oceans. Its diet is varied and is composed of crustaceans (*Paramblyops rostratus* Holt and Tattersall, 1905 [mysid]; *Eusergestes arcticus* [Krøyer, 1855] [= *Sergestes arcticus* Krøyer, 1855] [shrimps/prawns]; and unidentified amphipods, ostracods, benthic decapods, and tanaids), gastropods (3-spine cavoline, *Diacria trispinosa* [Blainville, 1821]), polychaetes, echinoderms (heart urchins), sipunculids, chaetognaths, cephalopods, finfish, and detritus (Froese and Pauly, 2019). Bray et al. (1999) stated that zoogonids utilize gastropods as a first intermediate host, while brittle stars, polychaetes, bivalves, and gastropods are second or subsequent intermediate hosts. As the diet of *S. grandis* overlaps some of these groups of organisms, it is possible that *G. droneni* may be utilizing some (e.g., gastropods, polychaetes) or all of these intermediate host groups as well as *S. grandis* to complete its life cycle in the deep sea.

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