

## SPECIES OF *GORGODERINA* (DIGENEA: GORGODERIDAE) IN *RANA VAILLANTI* AND *RANA* CF. *FORRERI* (ANURA: RANIDAE) FROM GUANACASTE, COSTA RICA, INCLUDING A DESCRIPTION OF A NEW SPECIES

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**ABSTRACT:** *Gorgoderina parvicava*, *G. diaster*, and *G. megacetabularis* n. sp. are reported inhabiting the urinary bladders of *Rana vaillanti* and *R. cf. forreri* from northwestern Costa Rica. *Gorgoderina megacetabularis* n. sp. differs from all other species of the genus by the combination of the following characters: small body size (2.78–3.17, mean 2.92 mm), sucker ratio (1:3.1–3.7), and by the presence of 2 compact, oval, unlobed vitelline masses. Redescription of *G. diaster* including previously undescribed details on the reproductive apparatus and morphometric data is provided. This is the first record of the 3 species of *Gorgoderina* in Costa Rica and is the first record of *G. diaster* in *R. vaillanti* and *R. cf. forreri*.

The digenean *Gorgoderina* comprises 51 described species, all of which are parasites in the urinary bladder of anurans and caudates (Amphibia) throughout the world. Approximately half of them are distributed in North and South America. As part of an inventory of eukaryotic parasites of vertebrates in the Área de Conservación de Guanacaste (ACG) in Costa Rica, specimens of 3 species of *Gorgoderina* were collected including an undescribed species, inhabiting *Rana vaillanti* or *R. cf. forreri* (or both).

*Rana vaillanti* Brocchi, 1877 is distributed in low and moderate elevations from southern México (Veracruz, Oaxaca, and Chiapas states) (Meyer and Wilson, 1971) through the Pacific slope down to Colombia and Ecuador (Hillis and de Sá, 1988). Few helminthological studies of this amphibian species have been conducted, most of them in México (Razo-Mendivil et al., 1999; Guillén-Hernández et al., 2000; Pérez-Ponce de León et al., 2000; Goldberg et al., 2002; Paredes-Calderón et al., 2004) and 2 records in Costa Rica (Zelmer and Brooks, 2000; León-Règagnon et al., 2001; Rodríguez-Ortíz et al., 2003). These studies have reported 25 helminth species parasitizing *R. vaillanti*.

*Rana forreri* Boulenger, 1883 was previously considered to occur along the Pacific coastal plain and adjacent lowlands of México and Central America (Flores-Villela et al., 1995), although molecular evidence indicates (Hillis et al., 1983; Zaldivar-Riverón et al., 2004) it is a composite taxon. Specimens in Costa Rica previously considered to be *R. forreri* presumably constitute an undescribed species of this group of frogs. Only 4 parasitological studies of this amphibian species complex have been conducted; 3 in México (Pérez-Ponce de León et al., 2000; Goldberg and Bursey, 2002; Cabrera-Guzmán et al., 2004) and 1 in Costa Rica (Desser, 2001; Rodríguez-Ortíz et al., 2003). These studies have reported 23 parasite taxa. Most of them dealt with nematodes having direct life cycles that reflect the more terrestrial character of this amphibian species complex().

### MATERIALS AND METHODS

Between 1998 and 1999, specimens of *R. vaillanti* and *R. cf. forreri* were collected in various parts of the ACG, Costa Rica. Hosts were

examined for helminth parasites. Specimens of *Gorgoderina* spp. were removed from the urinary bladder and placed in saline solution (0.6%), fixed in hot 4% formaldehyde, and preserved in 70% ethanol. Some specimens were stained in Mayer's paracarmine or Gomori's trichrome, dehydrated, cleared in methyl salicylate, and whole mounted in Canada balsam. Figures were drawn with the aid of a drawing tube. Measurements are presented as range with mean in parentheses and expressed in micrometers ( $\mu\text{m}$ ). Specimens for scanning electron microscopy were dehydrated with a graded series of ethanol and critical-point dried with  $\text{CO}_2$ , then covered with gold-palladium mixture. They were examined using a Hitachi S2460N electron microscope. The following abbreviations are used: CHCR, Colección Helmintológica de Costa Rica; CNHE, Colección Nacional de Helmintos, Instituto de Biología, Universidad Nacional Autónoma de México; CHIOC, Coleção Helmintológica do Instituto Oswaldo Cruz Fundação Instituto Oswaldo Cruz, Rio de Janeiro, Brazil; HWML, Harold W. Manter Laboratory of Parasitology, Lincoln, Nebraska; NHM, Natural History Museum, London, U.K.; NBM, New Brunswick Museum, New Brunswick, Canada; USNPC, United States National Parasite Collection, Beltsville, Maryland(). The following specimens were examined for comparison: *G. alobata* NHM, 1965.6.25. 1–2; *G. attenuata* CNHE, 1178–1180, 1182, 1446, 1544–1548, 2416, 3401–3405, 3412, 3413, 3793; HWML, 740, 17079, 20121–20126, 20888, 20955, 21344, 21949, 24898, 31259, 33206; USNPC, 051644.00, 075452.00, 081464.00; NBM, 3542 and 10 not cataloged slides; *G. diaster* CHIOC, 17426, 25255, 25256; HWML, 20250; NHM, 1980.11.12.7–8 and 1 slide from the reference collection of D. R. Brooks; *G. intermedia* USNPC, 007996.00; *G. parvicava* CNHE, 1177, 2415; CHIOC, 19076, 21076, 21509–21511, 21871–21877, 25261, 25262, 25264, 25269, 25271–25279, 25284, 25288, 25290, 29043, 34171; NHM, 1988.9.15.9; *G. tenua* USNPC, 008976.00; *G. vitelliloba* NHM, 1933.7.19.22, 1937.6.8.151, 1946.5.8.182, 1975. 8.16.113–114, 1976.4.9.18–22, 1983.6.9.3, 1984.10.9.16; HWML, 34301. Prevalence and intensity are used following Margolis et al. (1982).

### DESCRIPTION

#### *Gorgoderina megacetabularis* n. sp.

(Figs. 1–4)

**Description (based on 46 specimens):** Measurements based on 13 mature specimens. Body spindle shaped, blunt anterior end, pointed posterior end; body length (BL) 2,780–3,170 (2,920) (n = 7). Forebody 340–680 (520) long (12.2–21.4% [17.8%] of BL) (n = 7), 160–220 (190) (n = 7) wide at level of cecal bifurcation. Hindbody 1,110–1,770 (1,580) long (39.9–55.8% [51.1%] of BL) (n = 7), 240–290 (270) (n = 7) wide at level of anterior testis (Fig. 1). Tegumental surface aspinose, with numerous regular ridges surrounding body, covered with knoblike protuberances. Numerous large papillae present on tegument, concentrating on oral sucker and on the region between both suckers (Figs. 2, 3A, B).

Received 13 January 2004; revised 7 April 2004; 24 June 2004; accepted 9 July 2004.

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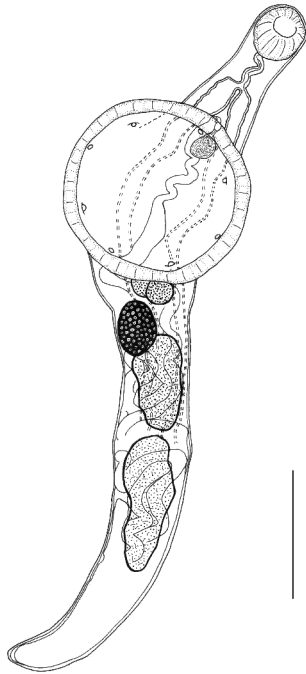


FIGURE 1. *Gorgoderina megacetabularis* n. sp. ventral view. Bar = 50  $\mu$ m.

Oral sucker subterminal, spherical (Fig. 2), 180–250 (210) long, 170–220 (200) wide ( $n = 9$ ); 5 pairs of papillae surrounding oral opening (Fig. 2a–e). Four additional pairs of papillae flanking the stylet pit on apical region of body (Fig. 3C); 1 pair of papillae on dorsal border of oral opening (Figs. 2f; 3A), and 1 pair on lateral borders of oral aperture (Fig. 2g); 2 extra pairs are located on the oral cavity (Fig. 2h, i). Small papillae on the oral sucker surface, arrangement varying among examined specimens (Fig. 3A). Pharynx absent. Esophagus curved, thick walled, 140–230 (190) long (5–7.25% [6.5%] of BL) ( $n = 10$ ). Intestinal bifurcation 250–360 (330) (8.99–11.35% [11.3%] of BL) ( $n = 10$ ) from anterior end of body. Ceca simple, initial portion wider and lobed; ceca ending at 170–400 (260) (6.1–12.6% [8.9%] of BL) ( $n = 8$ ) from posterior extremity (Fig. 1).

Ventral sucker in anterior third of body; 380–740 (560) long, 510–730 (600) wide ( $n = 6$ ). Eight papillae on internal surface of acetabulum (Fig. 1); 2 pairs lateral to longitudinal axis, covered with flattened scales (Fig. 3D); 1 pair of simple papillae located on middle line of longitudinal axis of sucker and 1 additional pair on transversal axis (Fig. 3E). Sucker ratio 1:3.1–3.7 (3.43).

Testes 2, elongate, borders irregular, sometimes bilobed, in tandem, intercecal, postequatorial, at 84–570 (215) (3–18% [7.36%] of BL) ( $n = 10$ ) from posterior margin of ventral sucker. Anterior testis smaller than posterior testis, sometimes partially overlapping one another. Anterior end of anterior testis overlapping posterior end of ovary; 200–430 (340) long, 90–250 (170) wide, 150–220 (180) deep ( $n = 12$ ). Posterior testis 330–730 (530) long, 140–270 (180) wide, 130–220 (170) deep ( $n = 11$ ). Vas deferens runs anteriorly. Seminal vesicle oval or spherical, dorsal to the anterior edge of acetabulum; 57–210 (130) long, 70–140 (110) wide, 90–210 (140) deep ( $n = 10$ ). Distal end of seminal vesicle surrounded by prostatic cells;

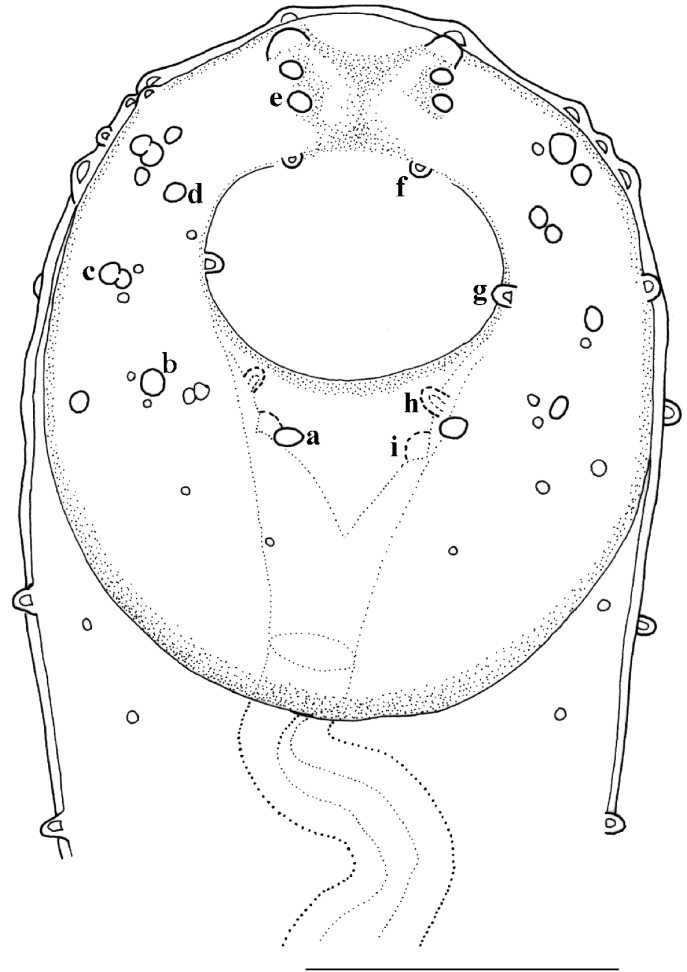


FIGURE 2. *Gorgoderina megacetabularis* n. sp. Oral sucker. (a–e) 5 pairs of papillae surrounding oral opening; (f–i) 4 pairs of papillae in the oral opening. Bar = 20  $\mu$ m.

opening into genital atrium. Genital pore anterior to ventral sucker, medially, at 400–520 (570) (14.4–16.4% [19.5%] of BL) ( $n = 5$ ) from anterior extremity of body (Fig. 1). Ovary oval, dextral (in 39 of the 46 specimens), posterior to vitellaria, at 50–160 (100) (1.8–5.0% [3.42%] of BL) ( $n = 3$ ) from posterior end of acetabulum, 180–250 (220) long, 130–170 (140) wide, 130–160 (140) deep ( $n = 11$ ). Vitellaria 2, compact oval masses, immediately posterior to acetabulum on middle line of body (Fig. 4A). Dextral vitelline gland 81–130 (110) long, 79–120 (90) wide, 80–130 (110) deep ( $n = 12$ ); left vitelline gland 80–140 (110) long, 70–130 (100) wide, 60–120 (90) deep ( $n = 12$ ). Mehlis' gland and Laurer's canal not observed. Uterine loops filling postacetabular region and overlapping dorsally and ventrally with testes, partially overlapping ovary and vitelline glands, opening to genital atrium (Fig. 4B). Eggs thin shelled, embryonated, 25–32 (28) long, 15–20 (17) wide. Excretory vesicle could not be observed. Excretory pore terminal (Fig. 3F).

#### Taxonomic summary

*Type host:* *Rana vaillanti* Brocchi, 1877 (Anura: Ranidae).

*Site of infection:* Urinary bladder.

*Prevalence, intensity:* See Table II.

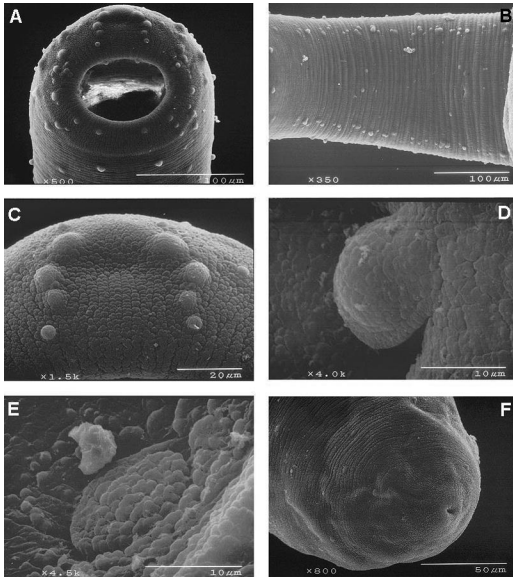


FIGURE 3. SEM photomicrographs of *Gorgoderina megacetabularis* n. sp. **A.** Oral sucker. **B.** Preacetabular region. **C.** Stylet pit. **D.** Acetabular papilla covered with flattened scales. **E.** Acetabular simple papilla. **F.** Body posterior extremity.

**Co-occurrence:** *Gorgoderina megacetabularis* n. sp. co-occurred with *G. parvicava* in 2 hosts and with *G. diaster* in 2 hosts.

**Type locality:** Río Pizote between Brasilia and Dos Ríos, sector San Gerardo (San Cristóbal), ACG, Costa Rica.

**Other localities:** Río Pizote, sector Santa Rosa and Sector Caribe, ACG, Costa Rica.

**Type specimens:** Holotype, CNHE 5000; paratypes, CNHE 5001, USNPC 94751, 94752, CHCR 115; vouchers, CNHE 5002, USNPC 94793, 94754.

**Etymology:** The specific epithet refers to the size of the ventral sucker, which is relatively much larger than that for any other known species in the genus.

## Remarks

The new species differs from all the described species of *Gorgoderina* in having a sucker ratio of 1:3.1–3.7; *G. insularis* Richard, Chabaud and Brygoo, 1968, which occurs in *Ptychadena mascareniensis* in Madagascar has a sucker ratio averaging 1:2.4 and is most similar in this regard (Table I).

Fully ovigerous specimens of *G. megacetabularis* n. sp. are small, thus resembling *G. alobata* Lees and Mitchell, 1966, *G. attenuata* (Stafford, 1902) Stafford, 1905, *G. carli* Baer, 1930, *G. chilensis* Dioni, 1947, *G. darwini* Mañé-Garzón and González, 1978, *G. intermedia* Holl, 1928, *G. insularis*, *G. gracilis* Wongsawad et al., 1999, *G. tenua* Rankin, 1937, *G. symmetriorchis* Dwivedi, 1968, and *G. vitelliloba* Olsson, 1876. In addition to the sucker ratio, the new species differs from *G. attenuata*, *G. chilensis*, *G. darwini*, *G. intermedia*, *G. insularis*, *G. tenua*, and *G. vitelliloba* by having vitelline glands arranged in 2 compact, unlobed oval masses, whereas the vitellaria are lobed in all other small species of *Gorgoderina*.

The new species most closely resembles *G. alobata*, which occurs in *Bombina variegata* in Europe, by having small body

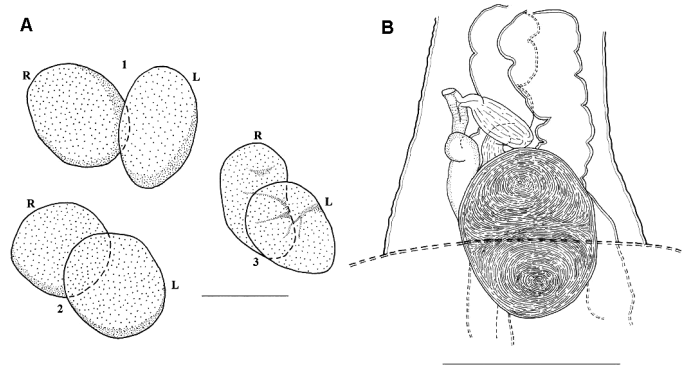


FIGURE 4. *Gorgoderina megacetabularis* n. sp. **A.** Vitellaria from 3 specimens; 1 and 2 ventral view, 3 lateral view (L left vitellaria, R right vitellaria). **B.** Ventral view of seminal vesicle and genital atrium. Bar = 100  $\mu$ m.

size and unlobed vitellaria. However, *G. alobata* has a sucker ratio of 1:1 and intestinal ceca extending only to the level of the posterior end of the posterior testis, whereas in the new species they reach two thirds the way between the posterior testis and the posterior end of the body.

## REDESCRIPTION

### *Gorgoderina diaster* Lutz, 1926

(Fig. 5)

Six specimens were collected in 2 hosts. Measurements are based on 3 mature specimens. Body length 7,820–7,910 (7,860), maximum wide at level of posterior testis 930 (11.8% of BL). Forebody 810–1,020 (915) long (10.35–12.89% [11.64%] of BL), 750 wide at level of cecal bifurcation; hind-body 6,311 long (80.3% of BL), 930 maximum wide. Oral sucker subterminal, spherical, 480 in diameter. Pharynx absent. Esophagus long and curved. Intestinal bifurcation 740 (9.35–9.5% of BL) from anterior end of body. Ceca simple and lobed; right cecum ending at 350–850 (620) (4.5–10.7% [7.9%] of BL) from posterior extremity; left cecum at 350–550 (460) (4.5–6.95% [5.85%] of BL) (Fig. 5A). Four penetration glands on each side of the oral sucker, opening dorsally, anterior to this structure. Ventral sucker at 3,200 (41% of BL) from anterior end, 700–780 (730) long, 740–750 wide. Sucker ratio 1: 1.25–1.59 (1.49). Testes 2, oval, in tandem. Anterior testis at 800 (10.2% of BL) to posterior margin of ventral sucker, 640–730 long, 450–570 wide; posterior testis 710–750 long, 410–500 wide. Seminal vesicle bipartite, anterior to acetabulum; proximal portion 130–250 long, 150–160 wide, distal portion 170 long, 190 wide. Genital pore at 890 (11.32% of BL) from anterior end of body. Ovary pretesticular, sinistral, at 450 (5.72% of BL) to posterior margin of ventral sucker, 450–520 (470) long, 300–390 (350) wide. Vitellaria 2 clusters of pre-ovarian follicles, at 100–370 (1.3–4.7% of BL) to posterior margin of ventral sucker, right vitellarium with 12 follicles, left vitellarium with 7–8 follicles (Fig. 5B). Mehlis' gland dorsal at junction of vitelline duct. Laurer's canal opening dorsally between vitellarium, ovary, and anterior testis (Fig. 5C). Uterine loops filling postacetabular region. Eggs 27–32 (29) long, 17 wide. Excretory vesicle Y-shaped, bifurcation at level of vitellaria. Excretory pore terminal.

TABLE I. Species of *Gorgoderina* Looss, 1902. BL = body length (mm); OS = oral sucker; Ac = acetabulum.

Species	Distribution	Host	Vitelline glands	BL	OS/Ac
<i>G. africana</i> Meskal, 1970	Africa	<i>Rana angolensis</i>	Unlobed	4.02–5.85	1:1.59–2
<i>G. alobata</i> Lees & Mitchell, 1966	Austria; Yugoslavia; Czech Republic; Greece; Poland	<i>Bombina variegata</i>	Unlobed	2.24–3.2	1:1
<i>G. attenuata</i> (Stafford, 1902) Stafford, 1905	Canada; United States; México; Guatemala	<i>R. catesbeiana</i> <i>R. virescens</i> <i>Bufo</i> sp. <i>Triturus viridescens</i> <i>Ambystoma lermaensis</i> <i>A. dumerilii</i> <i>R. dunni</i> <i>R. montezumae</i> <i>R. megapoda</i> <i>R. vaillanti</i> <i>R. pipiens</i> <i>R. blairi</i> <i>Leptodactylus melanonotus</i>	Lobed	3.3–7.2	1:2.1
<i>G. aurora</i> Ingles, 1936	United States	<i>R. aurora</i> <i>B. boreas</i>	Lobed	5–8	1:2–2.4
<i>G. beninensis</i> Bourgat, Dossou & Gasc, 1976	Africa	<i>Dicroglossus occipitalis</i>	Unlobed	7.5	1:1.76
<i>G. bilobata</i> Rankin, 1937	United States	<i>A. opacum</i> <i>Desmognathus fuscus</i> <i>Pseudotriton montanus</i> <i>P. ruber</i> <i>T. viridescens</i>	Lobed	3.49–8.16	1:1.26
<i>G. bombinae</i> Yu & Lee, 1983	Korea	<i>Bombina orientalis</i>	Unlobed	1.79–4.84	1:1.2–1.5
<i>G. bufonis</i> (Frandsen, 1957) Yamaguti, 1971	United States	<i>B. boreas</i>	Lobed	7.5–9	1:1.2
<i>G. capsensis</i> Joyeux & Baer, 1934	Tunisia	<i>R. esculenta ridibunda</i>	Lobed	6.0	1:2
<i>G. carangis</i> (MacCallum, 1913) Yamaguti, 1971	United States	<i>Caranx crysos</i>	Unlobed	13	1:0.6
<i>G. carioca</i> Fernandes, 1958	Brazil	<i>L. ocellatus</i>	Clusters of follicles	6–11.95	1:1.5
<i>G. carli</i> Baer, 1930	India	<i>Uraeotyplus oxyurus</i> <i>Ichthyophis orthoplicatus</i>	Unlobed	3	1:0.65–1.66
<i>G. cedroi</i> Travassos, 1924	Brazil	<i>Elosia nasus</i>	Unlobed	4.3–6	1:1.6
<i>G. chauhani</i> Prasad & Prasad, 1990*					
<i>G. chilensis</i> Dioni, 1947	Uruguay; Chile.	<i>Rhinoderma darwini</i>	Lobed	2.76–3.63	1:2.1
<i>G. cryptorchis</i> Travassos, 1924	Ecuador; Brazil; Para- guay	<i>B. crucifer</i> <i>L. ocellatus</i> <i>B. d'orbignyi</i>	Lobed	4–4.7	1:1.35
<i>G. darwini</i> Mañe-Garzón & González, 1978	Chile	<i>Melanophryniscus stelzneri</i>	Lobed	2.85–3.99	1:0.73
<i>G. diaster</i> Lutz, 1926	Venezuela; Colombia; Costa Rica	<i>Pseudis paradoxus</i> <i>R. palmipes</i> <i>Hyla goughi</i> <i>Rana</i> sp. <i>B. marinus</i> <i>R. cf. forreri</i> <i>R. vaillanti</i>	Clusters of follicles	5.39	1:1.3
<i>G. ellipticum</i> Dwivedi, 1968	India	<i>R. cyanophlyctis</i> <i>Haplobatrachus tigerinus</i> <i>Euphlyctis cyanophlyctis</i>	Unlobed	4.69–5.72	1:1.5
<i>G. gracilis</i> Wongsawad et al., 1999	Thailand	<i>Ichthyophis supachaii</i>	Unlobed	2.25–2.4	1:0.75–1
<i>G. guptai</i> Jahan, 1973	India	<i>Bufo</i> sp.	Lobed	3.58	1:0.7
<i>G. indica</i> Gupta & Jehan, 1971	India	<i>Bufo</i> sp.	Lobed	3.58	1:0.7
<i>G. infundibulata</i> Dwivedi, 1968	India	<i>B. melanostictus</i>	Unlobed	5.58–6.01	1:1.6–1.8
<i>G. insularis</i> Richard, Chabaud & Brygoo, 1968	Madagascar	<i>Ptychadaena mascareniensis</i>	Lobed	1.99–2.2	1:2.3–2.4



TABLE I. Continued.

Species	Distribution	Host	Vitelline glands	BL	OS/Ac
<i>G. intermedia</i> Holl, 1928	United States	<i>T. viridescens</i>	Lobed	1.44–2.76	1:1.56 1:1.87
<i>G. kajika</i> (Ozaki, 1926) Ozaki, 1935	Japan	<i>Polypedates buergeri</i>	Unlobed	4.55	1:1.42
<i>G. malaysiensis</i> Fichtal & Kuntz, 1965	Borneo	<i>R. kuhli</i>	Lobed	3.574	1:1.02–1.14
<i>G. megacysta</i> Mañé-Garzón & González, 1978	Uruguay	<i>L. ocellatus</i>	Unlobed	3.97–4.84	1:0.6
<i>G. megalorchis</i> Bravo, 1949	México; Costa Rica	<i>B. marinus</i>	Lobed	6.33–8.88	1:1.6
<i>G. multilobata</i> Ingles & Langston, 1933	United States	<i>R. boylii</i> <i>R. pretiosa</i> <i>R. aurora</i>	Clusters of follicles	7.1–11.7	1:1.69
<i>G. opaca</i> (Stafford, 1902) Stafford, 1905	Canada	<i>B. lentiginosus</i>	Lobed	6.58–7.59	1:1.5
<i>G. orientalis</i> Strom, 1940	Kirghizia	<i>R. esculenta</i>	Lobed	5.54–8.0	1:1.92
<i>G. parvicava</i> Travassos, 1922	México; Guatemala; Brazil; Uruguay; Costa Rica	<i>L. ocellatus</i> <i>L. pentadactylus</i> <i>R. vaillanti</i> <i>Pseudis</i> sp. <i>Rana</i> sp.	Unlobed	11–14	1:0.9
<i>G. permagna</i> Lutz, 1926	Venezuela	<i>L. pentadactylus</i>	Lobed	8.4–21.1	1:0.82–1.42
<i>G. pigulevskyi</i> Fernandes, 1958	Brazil	<i>L. ocellatus</i>	Clusters of follicles	10.5–14.7	1:1.2
<i>G. rhyacosiredonis</i> (Bravo, 1943)	México	<i>Rhyacosiredon altamirani</i>	Lobed	3.22–3.94	1:2.1
<i>G. rochalimai</i> Pereira & Cuocolo, 1940	Brazil	<i>B. paracnemys</i>	Clusters of follicles	10.3–16.6	1:1.6
<i>G. schistorchis</i> Steelman, 1938	United States	<i>Necturus maculosus</i>	Lobed	1.58–3.28	1:1.27
<i>G. simplex</i> Looss, 1902	Canada; United States	<i>R. catesbeiana</i> <i>R. clamitans</i> <i>R. pipiens</i> <i>B. americanus</i>	Lobed	7–12	1:1.3 1:1.5
<i>G. skarvilovitschi</i> Pigulevsky, 1953	México	<i>R. montezumae</i>	Lobed	3–10	1:2–2.3
<i>G. sphincterostoma</i> Fischthal, 1977	Africa	<i>Phrynobatrachus</i> sp.	Unlobed	2.96–3.02	1:1.46–2.13
<i>G. skrjabini</i> Pigulevsky, 1953	Russia	<i>R. temporaria</i>	Clusters of follicles	9–10	1:1.5–2.3
<i>G. stricta</i> (Oshmarin, 1965) Yamaguti, 1975*	Russia	<i>Formio niger</i>		2.8–5.35	
<i>G. symmetriorchis</i> Dwivedi, 1968	India	<i>R. limnocharis</i>	Unlobed	2.81–3.39	1:1.6
<i>G. tanagawaensis</i> Uchida & Itagaki, 1974	Japan	<i>B. japonicus</i>	Lobed	6.5–8.5	1:1.28–1.33
<i>G. tanneri</i> Olsen, 1937	United States	<i>R. pretiosa</i>	Lobed	2.07–7.67	1:2.25
<i>G. tenua</i> Rankin, 1937	United States	<i>Eurycea guttolineata</i>	Lobed	3.06–3.32	1:1.3
<i>G. translucida</i> (Stafford, 1902) Stafford, 1905	Canada; United States	<i>T. americanus</i> <i>Rana</i> <i>Bufo</i>	Lobed	8.06–9.45	1:1.5
<i>G. valdiviensis</i> Puga, 1979	Chile	<i>Caudiverbera caudiverbera</i>	Unlobed	4.63–9.86	1:1.6
<i>G. vitelliloba</i> (Olsson, 1876) Ssinizin, 1905	Spain; Turkey; Russia	<i>R. temporaria</i> <i>R. ridibunda</i> <i>R. arvalis</i> <i>R. macronemmis</i> <i>B. vulgaris</i> <i>B. bufo</i> <i>Bombinatus igneus</i>	Lobed	3–3.45	1:1.09
<i>G. zigzagorchis</i> Chin, 1963	China	<i>R. boulengeri</i> <i>R. adenopleura</i>	Lobed	5.6–6.2	1:1.45
<i>G. megacetabularis</i> n. sp.	Costa Rica	<i>R. vaillanti</i>	Unlobed	2.78–3.17	1:3.1–3.7

\* Cited in reviewed literature; original descriptions were unavailable.

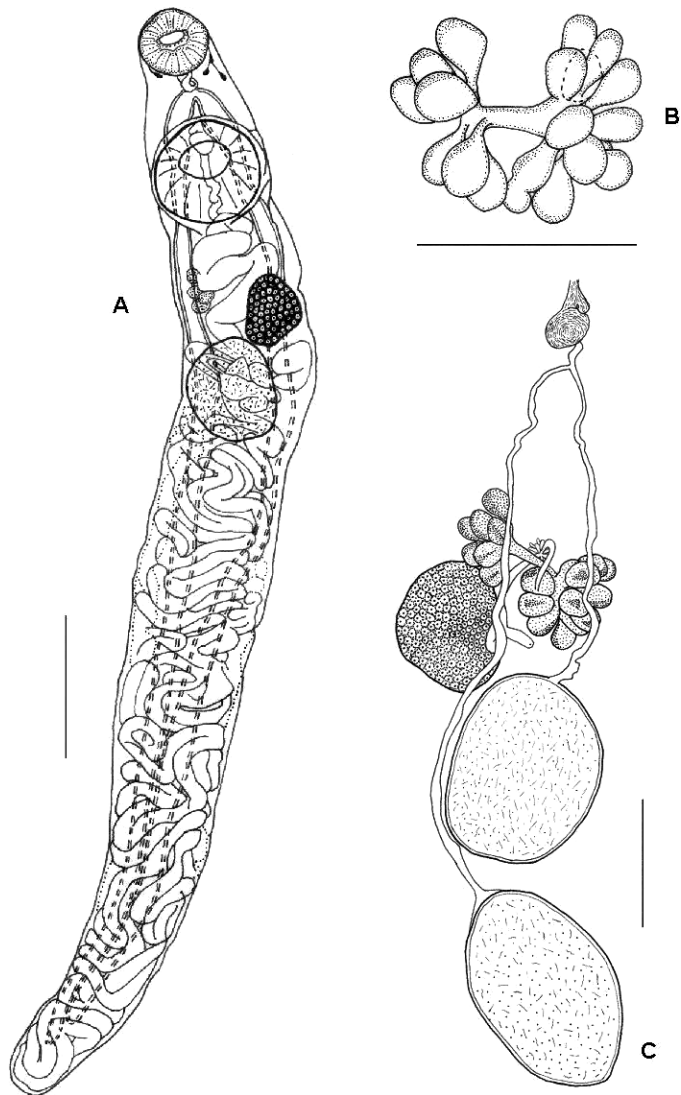


FIGURE 5. *Gorgoderina diaster*. A. Ventral view. Bar = 1,000  $\mu$ m. B. Vitelline glands. Bar = 300  $\mu$ m. C. Mehlis' gland, Laurer's canal, ovary, and testes. Bar = 500  $\mu$ m.

**Taxonomic summary**

*Host:* *Rana vaillanti* Brocchi, 1877; *R. cf. forreri* Boulenger, 1883 (Anura: Ranidae), new host, new record.

*Site of infection:* Urinary bladder.

*Prevalence, intensity:* See Table II.

*Co-occurrence:* With *G. megacetabularis* n. sp. in 2 specimens of *R. vaillanti*.

*Locality:* Río Pizote between Brasilia and Dos Ríos, sector San Gerardo, ACG, Costa Rica (*R. vaillanti*).

*Other localities:* Laguna Los Jicaros, sector Santa Elena; Camino a Playa Naranjo, sector Santa Rosa, ACG, Costa Rica (*R. cf. forreri*).

*Vouchers:* CNHE 4984

*Previous records:* *Rana palmipes* and *Pseudis paradoxa* from Maracay, Venezuela (Lutz, 1928; Fernandes, 1958); *Bufo marinus* from 15 km west of Neiva, Huila, Colombia (Brooks, 1976), and from King Rhom, Jamaica (voucher NHM-1980.11.12.7-8); new record.

**Remarks**

The original description of *G. diaster* (Lutz, 1926) is inadequate. Fernandes (1958) redescribed this species adding some morphometric information, but he based his observations on 1 single specimen. In this study, previously undescribed details about the male and female reproductive apparatus, penetration glands, and additional morphometric data are provided, based on the study of the material collected by Lutz—CHIOC17426, 25255, 25256—and on the material collected in Guanacaste.

**ADDITIONAL OBSERVATIONS**

***Gorgoderina parvicava* Travassos, 1922**

**Taxonomic summary**

*Host:* *Rana vaillanti* Brocchi, 1877 (Anura: Ranidae).

*Site of infection:* Urinary bladder.

*Prevalence, intensity:* See Table II.

*Co-occurrence:* With *G. megacetabularis* n. sp. in 2 specimens of *R. vaillanti*.

*Locality:* Río Pizote between Dos Ríos and Brasilia, sector San Cristobal, ACG, Costa Rica, new locality.

*Vouchers:* CNHE 4985, 4986.

*Previous records:* *Leptodactyllus ocellatus* from Provincia do Manguinhos, Angra dos Reis, São Paulo, Brazil (Travassos, 1922), Recife (Chacon, Cordeiro, Engenho do Meio, Tejipió,

TABLE II. Prevalence (P) and intensity (I) of *Gorgoderina diaster*, *G. parvicava*, and *G. megacetabularis* n. sp. in *Rana vaillanti* (Rv) and *R. cf. forreri* (Rf) of Guanacaste, Costa Rica.

		1998		1999	
		Rv	Rf	Rv	Rf
Number of Examined specimens		44	26	13	13
<i>Gorgoderina diaster</i>	P	1/44 (2.3%)	0	0	1/13 (7.69%)
	I	2/1	0	0	4/1
<i>Gorgoderina parvicava</i>	P	0	0	3/13 (23.1%)	0
	I	0	0	16/3	0
<i>Gorgoderina megacetabularis</i> n. sp.	P	23/44 (52.3%)	0	3/13 (23.1%)	0
	I	163/23	0	19/3	0

Tórre) and Cavaleiro (Município de Jaboatão), Estado de Pernambuco, Brazil (Dobbin, 1957); Volta Redonda, Rio de Janeiro, Brazil (Vicente and dos Santos, 1976; Faria, 1978) and Lake Diario, Maldonado, Uruguay (Mañe-Garzón and González, 1978); *L. pentadactylus labyrinthicus* from Recife (Chacon, Cordeiro, Engenho do Meio, Tejipló, Tórre) and Cavaleiro (Município de Jaboatão), Estado de Pernambuco, Brazil (Dobbin, 1957), Belo Horizonte, and Minas Gerais, Brazil (Fernandes, 1958); *Rana* sp. from La Guardianía de Macá, Município de Santa Bárbara, Suchitpeque, Guatemala (Caballero, 1946); *R. vaillanti* from Los Tuxtlas, Veracruz, México (Guillén-Hernández et al., 2000; Paredes-Calderón et al., 2004).

## DISCUSSION

Pereira and Cuocolo (1940), Pigulevsky (1953), and Fernandes (1958) separately proposed subgeneric divisions within *Gorgoderina*, mainly based on the structure and position of vitelline glands. However, the characters they used are variable among the genera in the Gorgoderidae. Therefore, we do not consider any subgeneric divisions in this study.

This is the second report of *Gorgoderina* in Costa Rica. Caballero et al. (1957) reported *G. megalorchis* Bravo-Hollis, 1948 in *Rana* sp. from Piedades de Santa Ana, Provincia de San José (Rodríguez-Ortíz et al., 2003). This study expands our knowledge of the distribution of some trematodes of *Rana* hosts through new parts of its range. These new records of *Gorgoderina* spp. in Costa Rica suggest historical affinities with the host groups.

*Gorgoderina diaster* has been reported previously in Venezuela in *R. palmipes*, *Pseudis paradoxus*, and *Hyla goughi* and in Colombia in *B. marinus*. In a phylogenetic study of the *R. palmipes* complex based on morphological and molecular characters, Hillis and de Sá (1988) suggest that *R. vaillanti* and *R. palmipes* are sister species. According to their proposal, the Andes of South America are the primary geographical barrier between these 2 species. *Rana vaillanti* is distributed in the lowland tropical forests west of the Andes and north into Central America, whereas *R. palmipes* is restricted to the lowland tropical forests east of the Andes. The presence of this digenean species in both host species may suggest an ancestral association between the parasite and the ancestor of *R. vaillanti* and *R. palmipes*. It also suggests that both host species share similar environmental conditions and feeding habits.

*Gorgoderina parvicava* occurs in México in *R. vaillanti*, in Guatemala in *Rana* sp., and in Brazil in *Leptodactylus* spp. and *Bufo* spp. These records indicate an extensive neotropical distribution, probably reflecting the distribution of their preferred hosts.

Whether *G. megacetabularis* n. sp. originated with the speciation of *R. vaillanti* or as a host-switching event from other amphibians in the region can only be tested with a phylogenetic hypothesis for species of *Gorgoderina*. *Rana vaillanti* has also been recorded as host of *G. attenuata* and *G. parvicava* in Los Tuxtlas, Veracruz, México, with a total of 4 species of *Gorgoderina* recorded in this host species. *Rana vaillanti* has predominantly aquatic habits that favor the completion of the life cycle of *Gorgoderina* and many other digeneans. This characteristic, together with its wide geographic range probably also favors speciation events by host switching of parasites that typ-

ically infect other amphibians. A similar case occurs with *G. attenuata*, known in green frogs (*R. clamitans*), bull frogs (*R. catesbeiana*), and leopard frogs (of which *R. forreri* is a member) in North America.

## ACKNOWLEDGMENTS

We are grateful to the scientific and technical staff of the ACG for support of this study, in particular: Elda Araya, Roger Blanco, Carolina Cano, Maria Marta Chavarría, Felipe Chavarría, Roberto Espinoza, Dunia Garcia, Guillermo Jiménez, Elba López, Sigifredo Marín, Alejandro Masis, Calixto Moraga, Fredy Quesada, and Petrona Rios. Thanks also to Dan Janzen and Winnie Hallwachs, scientific advisers to the ACG, for their support. We are grateful to Luis García Prieto (CNHE), Dely Noronha de Bragaça and Luis Muñiz (CHIOC), Scott Gardner (HWML), Donald McAlpine (NBM), Eileen Harris (NHM), and Pat Pilit (USNPC) for the loan of specimens. Special thanks to Berenit Mendoza Garfias for her help in scanning electron microscopy (SEM), and Gerardo Pérez-Ponce de León and Adrián Nieto Montes de Oca for revising a preliminary version of the manuscript. This study was funded by a research grant from the Natural Sciences and Engineering Research Council (NSERC) of Canada to D.R.B.

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