

Research Article

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Some nematodes of the genus *Rhabdias* Stiles et Hassall, 1905 (Nematoda: Rhabdiasidae) parasitising amphibians in French Guiana

Yuriy Kuzmin¹, Louis H. du Preez² and Kerstin Junker³

¹Department of Parasitology, Institute of Zoology, Kyiv, Ukraine;

²Unit for Environmental Sciences and Management, North-West University, Potchefstroom, South Africa;

³Agricultural Research Council-Onderstepoort Veterinary Institute, Onderstepoort, South Africa

Abstract: Based on material collected from *Rhinella* cf. *margaritifera* (Laurenti) and *Rhi. marina* (Linnaeus) (Anura: Bufonidae) during a parasite survey of the herpetofauna of French Guiana, updated descriptions of *Rhabdias androgyna* Kloss, 1971 and *R. fuelleborni* Travassos, 1926 are presented. In addition to metrical data, which may overlap in closely related species, emphasis is placed on qualitative characters. *Rhabdias androgyna* is distinguished by the unique presence of an outer and inner cephalic cuticular inflation, a shoulder-like broadening of the body at the anterior end, a wide and shallow buccal capsule (average buccal ratio 0.36) with serrated lumen in apical view, a prominent anterior dilatation of the oesophagus, and the presence of an additional posterior dilatation anterior to the oesophageal bulb. Characters that may help to differentiate *R. fuelleborni* from closely related species parasitising the *Rhi. marina* species group are the presence of six relatively uniform lips, and the division of the buccal capsule into an anterior and posterior segment, with differently structured walls. Both the presence of *R. androgyna* and *R. fuelleborni* in French Guiana constitute new geographic records. A single specimen of *Rhabdias* sp. is described from *Pristimantis chiastonotus* (Lynch et Hoegmoed) (Anura: Craugastoridae). This species differs from all its Neotropical congeners by the distinct globular swelling of its head, similar to that seen in only one Palearctic and one Afrotropical *Rhabdias* species. A list of species of *Rhabdias* parasitising amphibians in the Neotropical Realm is also provided.

Keywords: *Rhabdias androgyna*, *Rhabdias fuelleborni*, *Rhinella*, *Pristimantis*, morphology, Neotropical Realm, new geographical records

Nematodes of the genus *Rhabdias* Stiles et Hassall, 1905 are lung-dwelling parasites of amphibians and, to some extent, reptiles. The genus has a world-wide distribution and comprises more than 70 nominal species (Kuzmin and Tkach 2014). Together with most other rhabdiasids, members of this genus share a heterogonic life cycle, in which a parasitic hermaphroditic generation and a free-living generation of males and females alternate (Anderson 2000, Kuzmin 2013, Tkach et al. 2014). No less than 18 species of *Rhabdias* occur in the Neotropical Realm, 15 of which are parasitic in amphibians. Most species are known from their first descriptions only, and their exact geographic distribution and host range are still to be investigated. Especially descriptions dating back into the 20th century often lack morphological detail, rendering comparison with more recently collected materials difficult. However, in order to be able to study the phylogenetic relationships between the Neotropical species of *Rhabdias* themselves as well as with their congeners worldwide, detailed knowledge about their host spectrum, geographic range as well as morphology is imperative.

Of the 15 nominal species parasitising amphibians in the Neotropical Realm, two of which are considered *species inquirendae*, nine species have been reported from the northern parts of the Neotropics (Mexico and Central America) and six species occur in South America only (see below). During a brief herpetological and helminthological survey of amphibians and reptiles in French Guiana in April 2012, the lungs and other organs of collected hosts were screened for parasites. Three distinct nematode species belonging to *Rhabdias* were found in the lungs of the three anurans, *Rhinella* cf. *margaritifera* (Laurenti), *Rhi. marina* (Linnaeus) (Bufonidae), and *Pristimantis chiastonotus* (Lynch et Hoogmoed) (Craugastoridae). The specimens from *Rhi. cf. margaritifera* were identified as *R. androgyna* Kloss, 1971. This species was originally described based on three specimens from Brazil (Kloss 1971), and no further descriptions of the species have been published since. In order to augment the somewhat perfunctory original description, we examined the recently collected material and give a detailed description of their

Address for correspondence: K. Junker, Agricultural Research Council-Onderstepoort Veterinary Institute, Private Bag X05, Onderstepoort 0110, South Africa. Phone: +27 12 529 9215; Fax: +27 12 529 9434; E-mail: junkerk@arc.agric.za

morphology. The nematodes from *Rhi. marina* were identified as *R. fuelleborni* Travassos, 1926, though by some characters they were closer to *R. elegans* Gutiérrez, 1945, emphasising the need for updated morphological studies. The description of the gravid individuals recovered from *Rhi. marina* is presented below. One nematode found in the lungs of *P. chiastonotus* clearly differed from all *Rhabdias* spp. known in the Neotropics. As it further illustrates the diversity of *Rhabdias* in the Neotropical Realm, we present the description of this single specimen, concluding that it belongs to a new species of *Rhabdias* that may be named and formally described in future, once additional material is available.

MATERIALS AND METHODS

In April 2012, nine *Rhinella cf margaritifera* and a single specimen each of *Rhi. marina* and *Pr. chiastonotus* were collected in French Guiana as part of an unrelated study and examined for parasites by one of the authors (L.H.duP.). Hosts are stored in the collection of L.H.duP., North-West University: *Rhi. cf margaritifera* (field no. AL120416A1, AL120418D1-2, AL120419A1-3); *Rhi. marina* (field no. AL120410D1); *Pr. chiastonotus* (field no. AL120417I1). In future, it may thus be possible to ascertain the precise identity of hosts currently assigned to the *Rhi. cf margaritifera* species complex.

Helminths collected from the lungs were fixed in hot 70% ethanol and subsequently stored in 70% ethanol. For identification and morphological studies, specimens were temporarily mounted in lactophenol and examined under a Zeiss Axio Imager M1 microscope with differential interference contrast and equipped with a digital camera. Measurements were taken with the aid of digital imaging software (Zeiss AxioVision40 version 4.6.3), and line drawings were made based on single or series of digital images. All measurements are given in micrometres unless otherwise stated. Body widths were measured excluding the cuticular inflation. The classification of amphibian hosts follows that of Frost (2014) and Fouquet et al. (2007), that of reptilian hosts Uetz and Hošek (2015).

RESULTS

Rhabdiasidae Railliet, 1915

Genus *Rhabdias* Stiles et Hassal, 1905

Rhabdias androgyna Kloss, 1971

Figs. 1, 2

Morphological description (based on 29 gravid specimens; measurements are given as the range followed by the mean in parentheses): Medium sized, slender worms, 7.9–15.4 mm (11.9 mm) long, 200–294 (250) wide at oesophago-intestinal junction, 269–473 (371) wide at vulva. Body of relatively uniform width throughout most of its length, but tapering anteriorly from level of oesophago-intestinal junction onwards; posterior end tapering slightly at short distance anterior to anus, but with rapidly narrowing tail (Fig. 2A).

Body cuticle irregularly inflated along entire body, inflation more pronounced in cephalic and tail regions (Figs. 1A,G, 2A,D). Cephalic inflation divided into usu-

ally distinctly rounded outer and inner layers (Figs. 1A, 2D). Maximum width of outer cephalic inflation 273–706 (473), of inner inflation 214–335 (269). Inner cephalic inflation terminated at its connection to body wall on level of shoulder-like broadening of body outline. Usually distinct narrowing of outer cephalic inflation seen at this point as well, followed by gradual narrowing of inflation to level of oesophago-intestinal junction from whereon inflation retains more or less constant width with irregular, pronounced folds in some specimens. Caudal cuticular inflation with one large transverse fold prior to anus, and second large fold posterior to anus, reaching midlength of tail and followed by a series of smaller folds, rapidly decreasing in size (Fig. 1G). Posterior portion of tail tip without cuticular inflation. Lateral pores in body wall present, arranged in two lines, one on each side of body. Each pore connected to straight duct crossing inflated part of body cuticle (Fig. 2B).

Prominent dilatation of body present in anterior part at 40–89 (58) from anterior end, shoulder-like in lateral view (Figs. 1A,F). At this point, body 157–225 (194) wide; body width anterior to shoulder-like broadening 141–203 (170). Body wall anterior to shoulder-like broadening with 4 longitudinal elevations on dorsal, ventral and both lateral sides (Fig. 1B); elevations decreasing posteriorly and disappearing at level of shoulder-like broadening.

Oral opening small, round, in most specimens situated at bottom of apical depression of body wall (Figs. 1A, 2D). Depression depth possibly related to fixation. Four larger submedian lips and two smaller lateral lips present (Fig. 1B). Submedian lips projecting slightly into oral opening, narrow and elongate, with one internal labial papilla and two external labial papillae each. On each lip, thin cuticular 'M'-shaped fold present, separating external labial papillae from internal part of lip. Lateral lips situated at larger distance from oral opening, each bearing one internal labial and one minute external labial papilla. Amphidial openings small, rounded, situated at base of lateral lips.

Vestibulum funnel-shaped anteriorly and cylindrical with cuticularised wall posteriorly (Fig. 1C,F). In lateral view this subdivision not always visible, anterior part absent in some specimens; posterior cylindrical part measured in 10 specimens, 9–15 (11) long. Velum absent. Buccal capsule 7–9 (8) long and 19–27 (23) wide, length to width ratio 0.29–0.47 (0.36), round in apical view, a flattened oval in lateral view, thick-walled with cylindrical lumen; in apical view, inner wall serrated along its length excepting its bottom (Fig. 1D,E); posterior segment absent.

Oesophagus 598–751 (684) long, occupying 4.7–8.0% (5.9%) of total body length, generally club-shaped, its shoulders reaching anterior level of buccal capsule (Fig. 1F). Distinct rounded dilatation present in anterior, muscular part; smaller dilatation halfway between nerve ring and posterior bulb (Figs. 1A, 2D). Width of oesophagus 62–77 (69) at anterior end, 88–111 (100) at muscular dilatation, 54–69 (60) at level of nerve ring. Maximum width of oesophagus at posterior bulb, 108–159 (135).

Nerve ring at 210–300 (254) from anterior end, just posterior to anterior dilatation of oesophagus (Fig. 1A). Excre-

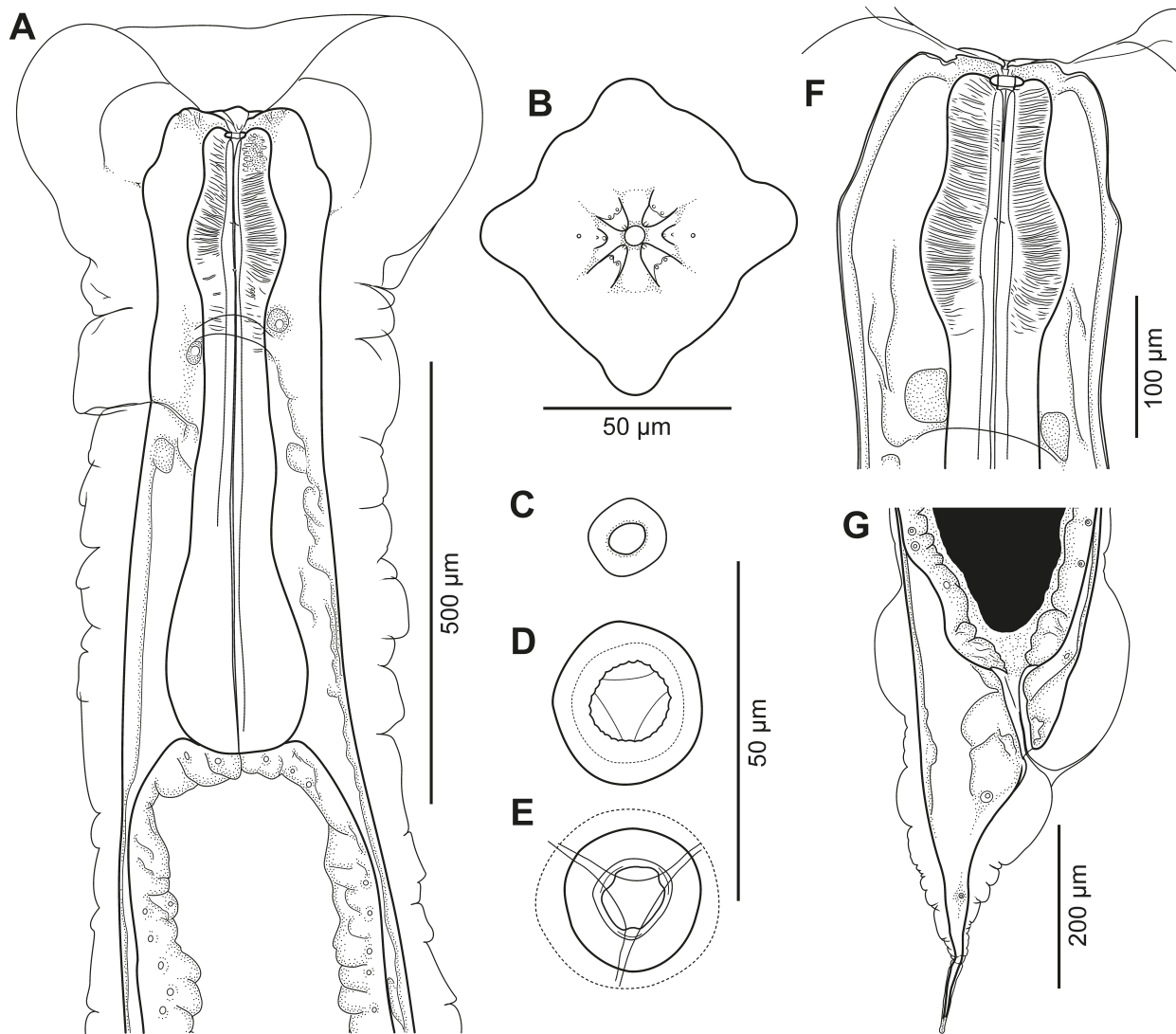


Fig. 1. *Rhabdias androgyna* Kloss, 1971 from *Rhinella* cf. *margaritifera*, line drawings. **A** – anterior part of body, lateral view; **B** – anterior extremity, *en face* view; **C** – optical section through vestibulum; **D** – optical section through mid-region of buccal capsule; **E** – optical section through bottom of buccal capsule; **F** – anterior end, dorsoventral view; **G** – caudal part, lateral view.

tory pore situated between level of nerve ring and second slight dilatation of oesophagus (Fig. 1A), at 293–356 (321) from anterior end. Excretory glands not observed in gravid specimens. Intestine thick-walled, in some specimens apex of intestine wider than base of oesophageal bulb, with shallow depression accommodating bulb (Fig. 2D); in other specimens base of oesophageal bulb and apex of intestine equal in size, but intestine widening abruptly at short distance from oesophago-intestinal junction to same width as in former specimens. Contents of intestine reddish to brown in anterior part, darkening to black posteriorly. Rectum straight, slightly dilated anteriorly, with weakly cuticularised walls (Fig. 1G).

Vulva usually just pre-equatorial, in some specimens at mid-length of body, slit-like and slightly salient; situated at 3.7–7.2 mm (5.7 mm) from anterior end, i.e. 44.5–50.8% (47.6%) of body length. Vagina transverse, short, straight, cuticularised. Uteri amphidelphic, approximately equal, thin-walled, tubular, with eggs arranged in 2–3 rows; majority of eggs near vulva containing first-stage larvae.

Eggs 101–113 × 47–51 (five eggs measured outside uterus in a specimen damaged in region of vulva). Anterior and posterior distal flexure of female genital system at some distance from oesophago-intestinal junction and anus, respectively, situated in oviduct. Distal parts of ovaries and oviducts usually looped and often folded upon themselves. Proximal ends of ovaries overlapping slightly at level of vulva. Testis zone in ovaries (Fig. 2C) observed in some specimens, usually seen in posterior ovary (n = 6), but also identified in anterior ovaries (n = 2).

Tail 304–455 (373) long, i.e. 2.4–4.4% (3.1%) of body length. A distinct elevation of body wall posterior to anus followed by an abrupt narrowing of tail (Fig. 1G), especially pronounced in larger specimens. Phasmids at 131–180 (163) from tail tip, tip of tail filled with granular material.

Description of one immature specimen from host lungs (Fig. 2E,F). Body smaller and comparatively narrower than in gravid worms; body length 4.2 mm, width at oesophago-intestinal junction 132, width at vulva 150. Body cuticle less inflated and cephalic inflation less pro-

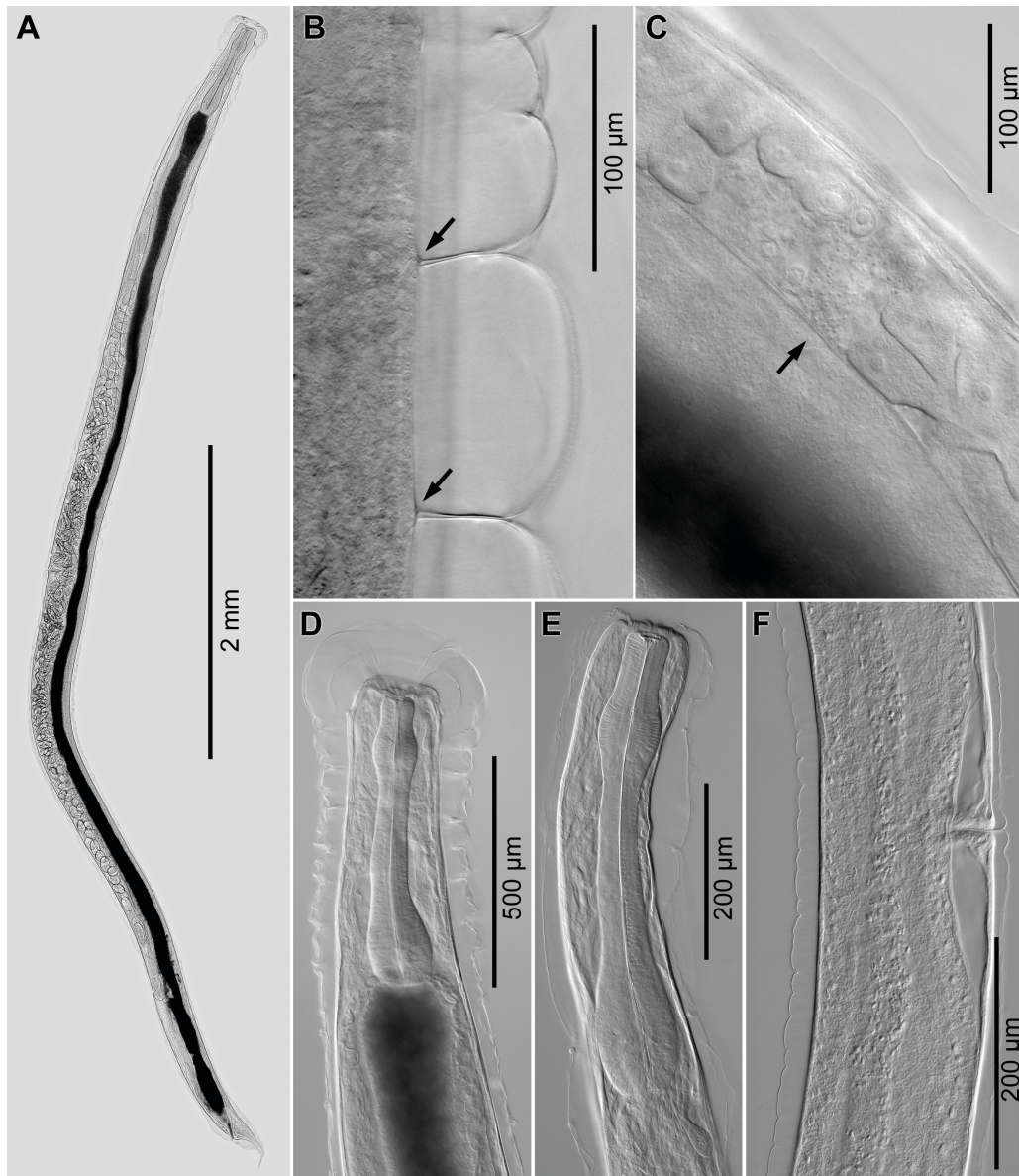


Fig. 2. *Rhabdias androgyna* Kloss, 1971 from *Rhinella* cf. *margaritifera*, photomicrographs. **A** – general view of gravid specimen; **B** – section of body wall at level of oesophagus, showing lateral pores (arrows) and ducts; **C** – testis zone (arrow) in posterior syngonium; **D** – anterior part of body, dorsoventral view; **E**, **F** – immature specimen: **E** – anterior part of body, lateral view; **F** – region of vulva, lateral view.

nounced, though division into inner and outer inflations obvious (Fig. 2E); inflations 142 and 164 wide, correspondingly. Shoulder-like broadening of body outline indistinct, anterior part of body wide, truncated (Fig. 2E). Apical depression of body wall absent. Vestibulum 9 deep. Buccal capsule 8 long and 24 wide (ratio 0.33). Oesophagus of same shape as that in gravid individuals, 530 long (12.6% of body length). Width of oesophagus 49 at apex, 71 at anterior dilatation, 42 at nerve ring; bulb 92 wide. Nerve ring at 184, and excretory pore at 260 from anterior end. Excretory glands present, their posterior parts pyriform, situated posterior to oesophago-intestinal junction (Fig. 2E). Intestine wide, occupying almost whole inner space of body in anterior and posterior part, with ventral narrowing in region of vagina (Fig. 2F). Contents of intestine granulated, not coloured. Rectum short, conical. Vulva slightly sali-

ent, postequatorial, situated at 2.3 mm from anterior end (54.3% of body length). Uteri short, empty (Fig. 2F). Other parts of genital system narrow, lacking germinal cells. Tail of same shape as that in gravid individuals, slightly narrower and more elongated, 232 long (5.5% of body length).

Host: *Rhinella* cf. *margaritifera* (Laurenti) (Bufonidae); collected during 9–23 April 2012.

Locality: Nouragues National Reserve, French Guiana, 04°02'23.5"N; 52°40'29.2"W.

Site of infection: Lungs.

Prevalence and intensity of infection: Six of nine hosts infected (67%), with a mean intensity of infection of 13 (2–25).

Deposition of specimens: Seventy-one specimens (S/2014/4–S/2014/8; S/2014/18) deposited in the National Collection of Animal Helminths (NCAH), Agricultural Re-

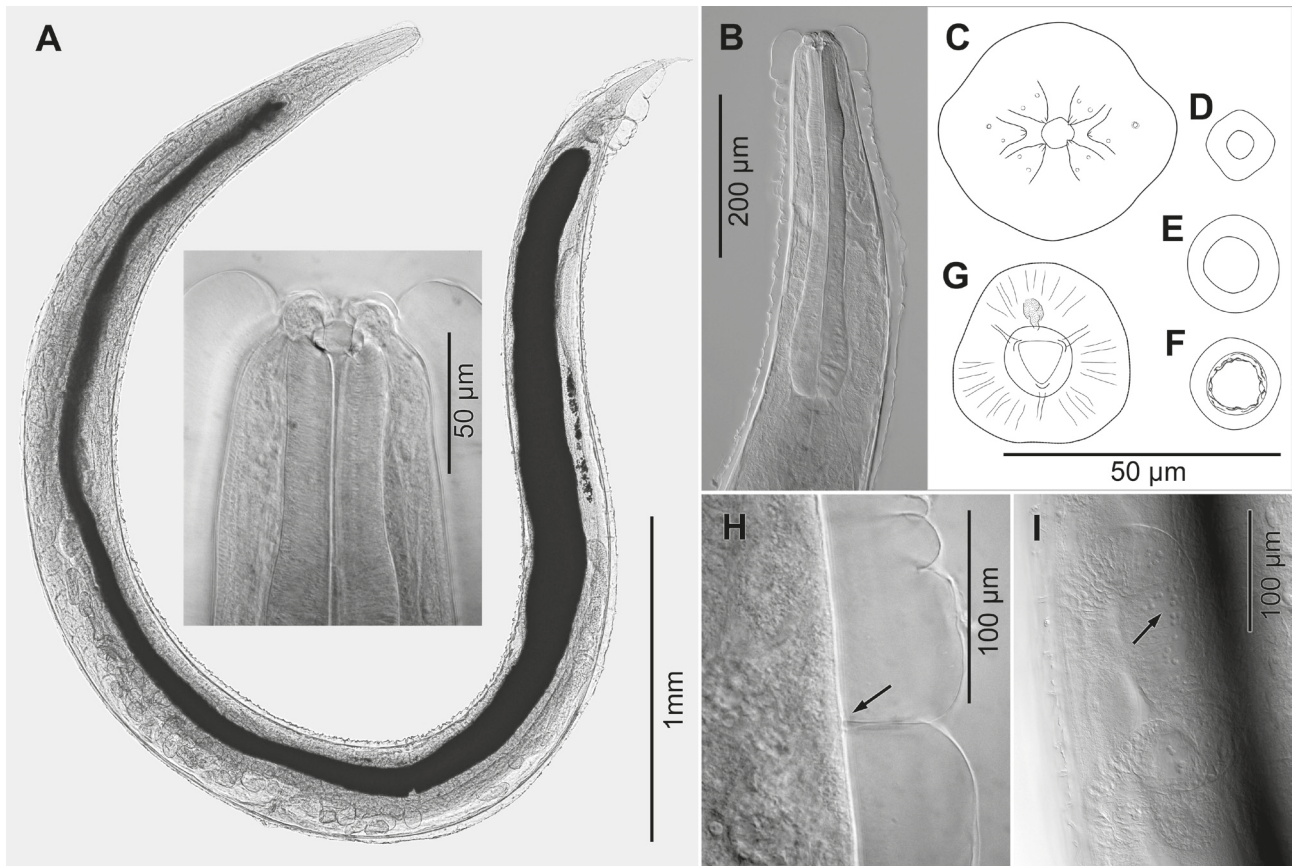


Fig. 3. *Rhabdias fueleborni* Travassos, 1926 from *Rhinella marina*. **A** – general view and anterior end (inset); **B** – anterior part of body, lateral view; **C** – anterior extremity, *en face* view; **D** – optical section through vestibulum; **E** – optical section through anterior segment of buccal capsule; **F** – optical section through posterior segment of buccal capsule; **G** – optical section through bottom of buccal capsule and apex of oesophagus; **H** – section of body wall showing lateral pore (arrow) and duct; **I** – oviduct with sperm cells inside (arrow).

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Remarks. *Rhabdias androgyna* was described by Kloss (1971) based on three specimens from Belém (Pará, Brazil; see below). The diagnosis of the species was rather brief, merely postulating its resemblance to *R. pseudosphaerocephala* Kuzmin, Tkach et Brooks, 2007 (cited as *R. sphaerocephala* Goodey, 1924) in possessing a prominent cuticular swelling at the anterior end, and differentiating it from *R. fueleborni* by its more slender oesophagus and shorter tail. On the other hand, the division of the cephalic cuticular inflation into an inner and outer layer, and the characteristic shape of the anterior end (presence of shoulder-like broadening) in *R. androgyna* are clearly illustrated in figs. 4a and 12 in Kloss (1971).

By these characters, the present specimens corresponded to those described by Kloss (1971) as *R. androgyna*. The type specimens in Kloss (1971) were characterised by the following measurements: body 9.4–13.4 mm long, oesophagus 577–618 long (4.3–6.6% of body length), tail 330–412 long (2.8–3.7% of body length), and vulva at 5.0–6.4 mm from anterior end, or at 48–56% of body length. The specimens examined in the present study correspond well to those studied by Kloss (1971), but have a slightly longer oesophagus, occupying 4.7–8.0% of the body length.

The conspicuous structure of the cephalic cuticular inflation, the shape of the anterior part of the body, as well as the wide and shallow buccal capsule (average buccal ratio 0.36) with serrated lumen in apical view, the rounded and very prominent anterior dilatation of the oesophagus, and the presence of an additional posterior dilatation anterior to the oesophageal bulb are distinctive morphological characters of *R. androgyna*. Kloss (1971) did not illustrate an apical view nor described the lip structure of *R. androgyna*. In the present paper, we provide detail on this important morphological character for the first time.

The occurrence of *R. androgyna* in French Guiana is a new locality record.

Rhabdias fueleborni Travassos, 1926

Fig. 3

Description [based on 4 specimens; measurements are given as the range for 3 complete and 1 incomplete (anterior part only) specimens]: Body elongated, wider in mid-region, gradually tapering toward extremities (Fig. 3A). Anterior end rounded, posterior end pointed. Body length 6.2–7.0 mm, body width 150–160 at oesophago-intestinal junction, 283–302 at vulva. Cuticle inflated along entire body, inflation more pronounced in anterior and posterior parts. Cephalic inflation short, 99–144 wide, not distinctly separated from cuticular inflation along body (Fig. 3B). In

caudal region, inflation reaching level of phasmids posteriorly. Lateral pores and ducts present (Fig. 3H).

Anterior extremity with slight constriction at level of oesophageal apex (Fig. 3A, inset), and 4 low, rounded subapical elevations of body wall (Fig. 3C). Oral opening rounded. Six lips present. Submedian lips close to edge of oral opening, lateral lips somewhat smaller, situated at some distance from oral opening (Fig. 3C). Each submedian lip bearing one prominent internal labial papilla and two minute external labial papillae. Lateral lips with one internal and one external labial papilla each. Amphidial openings round, situated at base of lateral lips, each surrounded by circular elevation of body wall. Vestibulum 9–10 deep, prominent, cylindrical, with narrow lumen (Fig. 3A, inset, D). Buccal capsule doliiform, 9 deep and 18–19 wide, depth to width ratio 0.47–0.50. Lumen of buccal capsule almost cylindrical, 9 wide and 9 long. Buccal capsule walls consisting of anterior segment 4–5 long, with smooth internal surface, and posterior segment 4–5 long, with rough internal surface (Fig. 3E,F). Entrance to oesophageal lumen funnel-shaped in lateral view, triangular with rounded sclerotised corners in apical view (Fig. 3G).

Oesophageal apex rounded, encircling posterior half of buccal capsule (Fig. 3A, inset). Oesophagus club-shaped, with dilatation in anterior half and oval posterior bulb (Fig. 3B). Length of oesophagus 431–441 or 6.2–7.0% of body length. Oesophagus width 33–36 at apex, 44–47 at anterior dilatation, 35–37 at nerve ring; bulb 71–73 wide. Nerve ring encircling oesophagus posterior to anterior dilatation, at 163–177 from anterior end. Excretory pore at 203 from anterior end (measured in 1 specimen). Excretory glands indistinct.

Anterior end of intestine narrower than oesophageal bulb, then abruptly widening posteriorly. Contents of intestine brownish to black. Rectum narrow, prominently cuticularised, wider in anterior part.

Vulva slightly pre-equatorial; distance from anterior end to vulva 3.1–3.4 mm or 49.4–49.9% of total length. Vulvar lips slightly salient. Uteri amphidelphic. Eggs numerous, most eggs containing fully developed larvae, 100–116 × 42–53 (n = 10, measured in uteri). Both distal flexures of genital system at posterior part of oviducts. Proximal parts of ovaries far overlapping level of vulva. Testis zones not observed in studied specimens, however, sperm cells present in oviduct of one specimen (Fig. 3I).

Tail conical, gradually tapering, 313–345 long (4.7–5.4% of body length), tail tip pointed and lacking cuticular inflation (Fig. 3A)

Host: *Rhinella marina* (Linnaeus) (Bufonidae); collected during 10 April 2012.

Locality: Wetland in the capital city Cayenne, French Guiana, 04°53'55.7"N; 52°20'15.2"W.

Site of infection: Lungs.

Prevalence and intensity of infection: Five specimens from a single host examined.

Deposition of specimens: Four specimens (S/2014/9) deposited in the NCAH.

Remarks. Two species that are morphologically close have been reported from Bufonidae and some Leptodactylidae in South America: *R. fuelleborni* and *R. elegans* (see Kloss 1974, González and Hamann 2008). According to Kloss (1974), *R. elegans* is generally smaller than *R. fuelleborni* and has a smaller buccal capsule (inside measurements): 7 × 9 μm vs 9 × 9 μm, correspondingly. The original descriptions of both *R. fuelleborni* and *R. elegans* offer no information on lip structure. However, González and Hamann (2008) mentioned the presence of 6 small lips in *R. fuelleborni* compared to the absence of distinct lips in *R. elegans*. *Rhabdias elegans* has a body length of 4.6–9.5 mm (after Gutiérrez 1945) or 4.7–10.3 mm (after Kloss 1971). Judging by this character, the current specimens, 6.2–7.0 mm long, are closer to *R. elegans* than to *R. fuelleborni*, with a body length of 10–12 mm (after Travassos 1926) or 6.6–16.3 mm (after Kloss 1971).

However, based on the dimension of the buccal capsule lumen (9 × 9 μm) and the presence of 6 distinct lips, we assign them to *R. fuelleborni*. Furthermore, similar to the present specimens, the position of the vulva is slightly pre-equatorial in *R. fuelleborni* (see Travassos 1926). *Rhabdias elegans* has been reported mostly from the southern parts of South America, i.e. from southern Brazil, Paraguay, Uruguay and Argentina (Gutiérrez 1945, Kloss 1974, González and Hamann 2008). The only record of this species from Mexico (Goldberg et al. 2002) may be a misidentification (Martínez-Salazar and León-Règagnon 2007) and needs confirmation. *Rhabdias fuelleborni* has a wider distribution and has been recorded from a vast area, including the aforementioned countries and northern Brazil (Kloss 1974, Vicente et al. 1990, Martínez-Salazar and León-Règagnon, 2007, González and Hamann 2008). These differences in the distribution range of the two species were also taken into consideration in the identification of the present specimens from French Guiana.

Rhabdias sp.

Fig. 4

Description (based on a single specimen): Body slender, elongated (Fig. 4A), 6.2 mm long. Body cuticle almost evenly inflated along entire body, narrow, except for anterior end bearing prominent spherical cephalic inflation. Cephalic cuticular inflation 165 wide, distinctly separated from inflated cuticle of body (Fig. 4B). Anterior end with rounded dilatation at level of anterior part of oesophagus, posterior to level of buccal capsule (Fig. 4B). Body width 82 at anterior end (including dilatation), 156 at oesophago-intestinal junction, 222 at vulva. Apparently, 6 lips present around oral opening (head structures not examined in apical view). Vestibulum 10 deep. Buccal capsule 11 deep and 18 wide (depth to width ratio 0.61), doliiform, with cylindrical lumen. Buccal capsule walls consisting of anterior and posterior segments 6 and 5 long, correspondingly.

Oesophagus with rounded apex, distinct dilatation in anterior part and egg-shaped, elongated bulb. Length of oesophagus 534, or 8.6% of body length. Width of



Fig. 4. *Rhabdias* sp. from *Pristimantis chiastonotus*. **A** – general view; **B** – anterior end, lateral view; **C** – caudal region, lateral view; **D** – region of vulva, lateral view; **E** – posterior syngonium with testis zone (arrow).

oesophagus 40 at apex, 54 at anterior dilatation, 41 at nerve ring; bulb 87 wide. Anterior end of intestine wider than oesophageal bulb and surrounding its posterior end (Fig. 4A). Nerve ring situated at 180, excretory pore at 226 from anterior extremity.

Vulva postequatorial, situated at 3.4 mm from anterior end (55% of body length). Vulval lips slightly salient (Fig. 4D). Uteri amphidelphic, tubular, containing eggs arranged in 2–3 rows, some eggs near vagina with fully developed embryos. Egg size 93–112 × 42–58 (n = 10; measured in uteri). Ovaries overlapping level of vulva. Testis zone observed in posterior ovary, somewhat posterior to level of vulva (Fig. 4E).

Tail 208 long (3.3% of body length), abruptly narrowing in anterior part, gradually tapering in posterior part (Fig. 4C). Phasmids situated at 58 from tail tip.

Host: *Pristimantis chiastonotus* (Lynch et Hoogmoed) (Craugastoridae); collected during 17 April 2014.

Locality: Parare camp site, Nouragues National Reserve, French Guiana, 04°02'16.7"N; 52°40'22.6"W.

Site of infection: Lungs.

Prevalence and intensity of infection: One specimen from a single host examined.

Deposition of specimens: One specimen (S/2014/3) deposited in the NCAH.

Remarks. The present specimen of *Rhabdias* sp. appears to differ from all known species of the genus in Neotropical amphibians. In possessing a globular cephalic cuticular inflation, it is close to *R. pseudosphaerocephala* and *R. androgyna* (see Kloss 1971, present study). *Rhabdias pseudosphaerocephala* differs, however, from *Rhab-*

dias sp. by having a comparatively shorter oesophagus (4.4–6.5% vs 8.6% of body length), a less pronounced anterior dilatation of the oesophagus, a narrower oesophageal bulb, and a longer tail (3.7–5.0% vs 3.3% of body length) (Kuzmin et al. 2007). *Rhabdias androgyna* can be distinguished from *Rhabdias* sp. by the shape of its buccal capsule, the absence of a posterior segment of the buccal capsule, a smaller buccal capsule ratio, and a cephalic inflation that is not simple but divided into an outer and inner layer.

In two species of *Rhabdias* the body itself shows a pronounced globular swelling in the head region, similar to that seen in the present specimen: *R. sphaerocephala* from *Bufo bufo* (Linnaeus) (syn. *B. vulgaris* Laurenti) (Bufonidae) in England, and *R. ohlerae* Junker, Lhermitte-Vallarino et Bain, 2010 from *Leptopelis brevirostris* (Werner) (Arthroleptidae) in Cameroon. However, in both these species the constriction that sets off the bulbous cephalic swelling from the remainder of the body is more pronounced and the oesophagus is shorter [6.6–7.5% of body length, calculations based on maximum and minimum values given by Goodey (1924), for *R. sphaerocephala*, and 6.9% of body length for *R. ohlerae*]; in addition, the tail is shorter in *R. ohlerae* (4.2% of body length) (Goodey 1924, Junker et al. 2010).

In parasitising a host from the genus *Pristimantis* Jiménez de la Espada, *Rhabdias* sp. is close to *R. tobagoensis* Moravec et Kaiser, 1995, described from *Pristimantis* cf. *terraebolivaris* (Rivero) (syn. *Eleutherodactylus* cf. *terraebolivaris* Rivero) on Tobago Island (Moravec and Kaiser 1995). This species differs from *Rhabdias* sp. in the absence of a distinct cephalic cuticular inflation, a shorter buccal capsule (6–9 µm vs 11 µm), a wider body (maximum body width 408–476 µm vs 222 µm), longer tail and shorter oesophagus.

We conclude that the current specimen belongs to an as yet undescribed species of *Rhabdias*. It would, however, not be reasonable to describe a new taxon based on a single specimen only, and we thus prefer to leave the specimen unnamed until additional material for a comprehensive description becomes available.

DISCUSSION

The two nominal *Rhabdias* species, *R. androgyna* and *R. fuelleborni*, whose descriptions were updated in the present study, belong to a group of *Rhabdias* occurring in bufonid hosts in South America, mainly Brazil (Kloss 1971, 1974). *Rhabdias androgyna* was originally described from a host in Belém (Pará, Brazil) recorded as '*Bufo typhonius*' Schneider, but likely belonging to *Rhi. margaritifera* (Laurenti). We found this species in a related host, *Rhi.* cf. *margaritifera*, in French Guiana. Presumably, *R. androgyna* is a specific parasite of at least a part of the *Rhi. margaritifera* complex of species. Presently, the latter is considered as comprising at least 15 species belonging to several phylogenetic lineages (Ávila et al. 2010); of these, *Rhi. lescurei* Fouquet, Gaucher, Blanc et Velez-Rodriguez, *Rhi. margaritifera* and *Rhi. martyi* Fouquet, Gaucher, Blanc et Velez-Rodriguez have been recorded from French Guiana (Fouquet et al. 2007). According to our unpublished data, some

species of this group may harbour *Rhabdias* parasites other than *R. androgyna*. The relationships of *Rhabdias* parasites with their hosts from the *Rhi. margaritifera* group may be a subject of separate studies in future.

The following is a list of *Rhabdias* species parasitising amphibians in the Neotropical Realm, including updated data on their host and geographic range. It is noteworthy that not all parasite records were accompanied by detailed morphological studies. Especially with regard to species of *Rhabdias* whose original descriptions were somewhat perfunctory, their presence in new hosts and localities might need confirmation, once updated descriptions are available.

- ***R. alabialis*** Kuzmin, Tkach et Brooks, 2007 from *Rhinella marina* (Linnaeus) [syn. *Bufo marinus* (Linnaeus)] (type host), *Scinax boulengeri* (Cope) and *Smilisca baudinii* (Duméril et Bibron) (Hylidae) in Costa Rica (Kuzmin et al. 2007, Bursey and Brooks 2010).
- ***R. androgyna*** Kloss, 1971 from hosts identified as '*Bufo typhonius* (Linnaeus)' (type host), but most likely representing what is currently considered the *Rhinella margaritifera* species group (Fouquet et al. 2007, Frost 2014), in Brazil (type locality) (Kloss 1971); from *Proceratophrys appendiculata* (Günther) (Odontophrynidae) in Brazil (Boquimpani-Freitas et al. 2001); from *Rhi. margaritifera* in Guyana (McAllister et al. 2010); from *Rhi.* cf. *margaritifera* in French Guiana (present paper).
- ***R. breviensis*** Nascimento, Gonçalves, Melo, Giese, Furtado et Santos, 2013 from *Leptodactylus petersii* (Steindachner) (type host) and *L. macrosternum* Miranda-Ribeiro (Leptodactylidae) in Brazil (Nascimento et al. 2013).
- ***R. elegans*** Gutiérrez, 1945 from *Rhinella arenarum* (Hensel) (syn. *Bufo arenarum* Hensel) (type host) in Argentina (type locality), Paraguay and Uruguay (Gutiérrez 1945, Kloss 1971); from *Rhi. rubescens* (Lutz) (syn. *B. rufus* Garman) in Brazil (Kloss 1971); from *Odontophrynus americanus* (Duméril et Bibron) (Odontophrynidae) in Argentina (González and Hamann 2009); from *Leptodactylus melanonotus* (Hallowell) in Mexico (Goldberg et al. 2002), however, the identity of this *Rhabdias* species might need confirmation (Martínez-Salazar et al. 2009); from the lizard *Anolis chrysolepis* Duméril et Bibron (syn. *Anolis nitens* Wagler) (Dactyloidae) in Guyana (McAllister et al. 2010); however, this is an unusual host association and the identification might need confirmation. Lists of additional hosts were compiled by González and Hamann (2009) and McAllister et al. (2010).
- ***R. fuelleborni*** Travassos, 1926 from *Rhinella marina* (type host), *Rhi. ictérica* (Spix) (syn. *Bufo marinus ictericus* Müller) and *Rhi. schneideri* (Werner) (syn. *B. m. paracnemis* Müller et Hellmich) in Brazil (type locality) (Travassos 1926, Kloss 1971); from *Rhi. ma-*

rina, *Smilisca cyanosticta* (Smith) and *Lithobates vaillanti* (Brocchi) (syn. *Rana vaillanti* Brocchi) (Ranidae) in Mexico (Goldberg et al. 2002); from *Rhi. marina* in French Guiana (present paper).

- ***R. hermaphrodita*** Kloss, 1971 from *Rhinella crucifer* (Wied-Neuwied) (syn. *Bufo crucifer* Wied) in Brazil (Kloss 1971).
- ***R. kuzmini*** Martínez-Salazar et León-Règagnon, 2007 from *Incilius occidentalis* (Camerano) (syn. *Bufo occidentalis* Camerano) (Bufonidae) in Mexico (Martínez-Salazar and León-Règagnon 2007).
- ***R. manantlanensis*** Martínez-Salazar, 2008 from *Craugastor occidentalis* (Taylor) (Craugastoridae) in Mexico (Martínez-Salazar 2008).
- ***R. mucronata*** Schuurmans-Stekhoven, 1952 in *Leptodactylus bolivianus* (Boulenger) (syn. *L. ocellatus* Girard) in Argentina (Schuurmans-Stekhoven 1952); adults unknown and considered a *species inquirenda* (Burse et al. 2003, Martínez-Salazar et al. 2009, 2013).
- ***R. paraensis*** Santos, Melo, Nascimento, Nascimento, Giese et Furtado, 2011 from *Rhinella marina* in Brazil (Santos et al. 2011).
- ***R. peninsularis*** Martínez-Salazar, Falcón-Ordaz, González-Bernal, Parra-Olea et Pérez-Ponce de León, 2013 from *Pseudacris hypochondriaca* (Hallowell) (Hylidae) in Mexico (Martínez-Salazar et al. 2013).
- ***R. pseudosphaerocephala*** Kuzmin, Tkach et Brooks, 2007 from *Rhinella marina* (type host) in Nicaragua (type locality) and Costa Rica; from *Engystompos pustulosus* (Cope) (Leptodactylidae) and *Litobates vaillanti* in Mexico (Kuzmin et al. 2007, Bursey et Brooks 2010). Specimens originally identified as “*Rhabdias sphaerocephala* Goodey, 1924” were listed from *Rhi. marina* in Mexico, Costa Rica, Bermuda islands and Amazonia, and from *Rhi. schneideri* in Brazil (see Kloss 1971, 1974, Kuzmin et al. 2007).
- ***R. savagei*** Bursey et Goldberg, 2005 from *Rana* sp., *Litobates forreri* (Boulenger), *L. vaillanti*, *L. warszewitschii* (Schmidt), *Craugastor crassidigitus* (Taylor), *C. gollmeri* (Peters), *C. melanostictus* (Cope), *C. taurus* (Taylor), *Pristimantis caryophyllaceus* (Barbour) (syn. *Eleutherodactylus caryophyllaceus* Dunn) (Craugastoridae), *Engystompos pustulosus* and *Leptodactylus fragilis* (Brocchi) in Costa Rica (Bursey and Goldberg 2005, Bursey and Brooks 2010).
- ***R. tobagoensis*** Moravec et Kaiser, 1995 from *Pristimantis* cf. *terraebolivaris* on Tobago (Moravec and Kaiser 1995); from *Dendropsophus microcephalus* (Cope) (syn. *Hyla microcephala* Cope) (Hylidae) in Mexico (Goldberg et al. 2002), but the identity of this *Rhabdias*

species might need confirmation (Martínez-Salazar et al. 2009); from the lizard *Anolis uniformis* (Cope) (Dactyloidae) in southern Mexico (Cabrera-Guzmán and Garrido-Olvera 2014), however, this is an unusual host association and the identification might need confirmation.

- ***R. truncata*** Schuurmans Stekhoven, 1952 from *Telmatobius schreiteri* Vellard (Telmatobiidae) in Argentina (Schuurmans Stekhoven 1952); adults unknown and considered a *species inquirenda* (Burse et al. 2003, Martínez-Salazar et al. 2009, 2013).
- ***Rhabdias*** sp. from *Scinax staufferi* (Cope) in Mexico (Martínez-Salazar et al. 2009).
- ***Rhabdias*** sp. from *Pristimantis chiastonotus* in Guyana (present paper).

In the present description of *R. androgyna*, we emphasise the specific structure of its cephalic cuticular inflation consisting of two layers, the shape and structure of the buccal capsule being much wider than long, and not separated into anterior and posterior segments, as well as the specific shape of the oesophagus, with a very distinct anterior dilatation and an additional dilatation anterior to the bulb. It is important to note that these features were also observed in an immature individual of *R. androgyna*. Moreover, the size of the buccal capsule was similar in the immature individual (8 μm \times 24 μm) and gravid specimens (7–9 μm \times 19–27 μm), and may thus be used as a metrical diagnostic character.

Rhabdias fuelleborni is one of five species parasitic in toads from the *Rhi. marina* group of species, the remaining four being *R. elegans*, *R. hermaphrodita*, *R. pseudosphaerocephala* and *R. paraensis* (see Kloss 1971, 1974, Santos et al. 2011). These nematodes are rather similar morphologically and were differentiated primarily based on metrical characters related to their body length (Kloss 1974). Such characters, however, may overlap in related species, and their validity as diagnostic characters is doubtful (Baker 1978). Therefore, additional qualitative characters seem to be important for the adequate differentiation among the *Rhabdias* species within the *Rhi. marina* group. In the present study, we give a detailed account of the morphology of the anterior end of *R. fuelleborni*, which may help in the reliable identification of this species: the presence of six lips that are almost equal in shape and size, the division of the buccal capsule into anterior and posterior segments with differently structured walls. In future, similar studies of the remaining species of this group may add differential characters to their diagnoses.

The presence of two segments in the buccal capsule, observed in *R. fuelleborni* and *Rhabdias* sp. in the present study, has previously been reported in a number of species of *Rhabdias*, mostly parasites of reptiles (Lhermitte-Vallarino et al. 2009a,b, 2010, Tkach et al. 2011), but also in some species from amphibians (Junker et al. 2010). On the other hand, *R. androgyna* obviously lacks such a divi-

sion of the buccal capsule wall, and the fine structure of the buccal capsule in other Neotropical *Rhabdias* spp. is still to be investigated.

The lateral pores and ducts were studied in detail in *R. paraensis* by Santos et al. (2011), using SEM and histological methods. Lateral ducts in *R. androgyna* and *R. fuelleborni* could be observed under the light microscope in specimens with a dorsoventral orientation on the slide (Figs. 2B, 3H). These or similar structures were reported in some species of *Rhabdias* outside the Neotropical Realm (Baker 1987, Junker et al. 2010, Tkach et al. 2011), as well as in some species from other rhabdiasid genera: *Kurilonema* Szczerbak et Sharpilo, 1969 and *Pneumonema* Johnston, 1916 (Ballantyne 1986, Kuzmin and Tkach 2011). Presumably, the presence of lateral pores in Rhabdiasidae has a wider distribution than is presently known.

The hermaphroditism of all three *Rhabdias* species observed in the present study is evidenced by the presence of regions of spermatogenesis in the ovaries (syngonia), and sperm cells in the oviducts. Regions of spermatogenesis, testis zones after Runey et al. (1978), are usually located between the ovarian synapsis and growth zones, where the smaller and loosely arranged male gametes interrupt the regular pattern formed by the densely packed oocytes. Tes-

tis zones have been reported in a number of *Rhabdias* species, suggesting that hermaphroditism is characteristic for this genus. In some species, however, testis zones were not found and this led to conclusions on their parthenogenesis (Lhermitte-Vallarino and Bain 2004). In *R. androgyna*, we observed testis zones in some of the specimens only and always in one syngonium (more often in the posterior one), but not in both. We, therefore, consider that the absence of testis zones in some specimens of *Rhabdias* spp. does not constitute unambiguous evidence of their parthenogenesis.

The Neotropical Realm is the region with the highest amphibian species richness worldwide (Duellman 1999). This said, a comparatively small amount of *Rhabdias* species are currently known from the Neotropics (16 out of more than 70 comprising the world fauna), indicating that far more species are yet to be discovered.

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