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Reflections on the genus *Amaga* Ogren and Kawakatsu 1990, and description of a new genus of land planarian (Platyhelminthes: Tricladida: Geoplanidae)

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Amaga amagensis, the type species of the genus *Amaga*, and *Amaga bogotensis* are re-described. Detailed analysis of the morphology of *A. amagensis* revealed important taxonomic features, such as testes located dorsally to the supraintestinal parenchymal muscular layer, and secretory accumulations opening through the lateral margins of the body. These characters, as well as other morphological features, are discussed, culminating in an emendation of the generic diagnosis of *Amaga*. *Amaga bogotensis* exhibits a characteristic set of morphological features, namely an eversible penis, a male atrium lined with large musculosecretory papillae, and independent muscular coats around both male and female atrium. Therefore, a new genus is proposed for this species.

Keywords: Platyhelminthes; Tricladida; Geoplaninae; *Amaga*; *Bogga*; Colombia.

Introduction

Many land planarian taxa are taxonomically poorly characterized because of insufficient knowledge of their anatomical features, hindering phylogenetic and evolutionary studies on this group of organisms. An example of this situation is the genus *Amaga* Ogren and Kawakatsu, 1990 of the subfamily Geoplaninae, which has been erected solely on information from the literature and not on detailed examination of specimens (cf. Ogren and Kawakatsu 1990). The type species *Amaga amagensis* (Fuhrmann, 1914) has not been studied since its original description (Fuhrmann 1914). As the current diagnosis of *Amaga* Ogren and Kawakatsu, 1990 fails to provide unique diagnostic features, it embraces a heterogeneous group of 11 species and because the diagnostic features of *Amaga* are ambiguous and inconclusive, this situation greatly hampers the elucidation of new taxa.

Geoplana bogotensis Von Graff, 1899, currently placed in the genus *Amaga*, was originally described from a single worm from Bogotá (Colombia). Von Graff (1899)

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described only the external characters and sent the single worm to the Museum für Naturkunde in Berlin. A few years later he received another seven specimens from the environs of Bogotá. This material was studied by his student Busson (1903). Two worms from the new material were sectioned and Busson considered his description of the anatomy to complement the description of *G. bogotensis* given by Von Graff and also described the new variety *G. bogotensis* var. *buergeri*, which was merely based on differences in colour pattern and body shape. Later, Fuhrmann (1914) collected 38 specimens of *Geoplana* near Bogotá. This material was identified as *Geoplana bogotensis* because the general characteristics and the copulatory organs agreed with Busson's account of the species. Fuhrmann also considered the external differences that Busson mentioned in support of his new variety to be the result of preservation or fixation artefacts.

Hyman (1955) identified one of her specimens from Tuicochchaca (Peru) as *G. bogotensis* on the basis of external features and found that the copulatory apparatus differed from that described by both Busson and Fuhrmann. Therefore, Hyman considered her animal to represent the true *G. bogotensis*, in contrast to Busson's and Fuhrmann's specimens. Du Bois-Reymond Marcus (1957) provided a succinct account of this confusing situation and, to avoid further confusion, considered Hyman's worm to represent a new species. One year later she called it *Geoplana libbieae* (Du Bois-Reymond Marcus 1958) and considered Busson's and Fuhrmann's specimens to represent the true *G. bogotensis*.

Ogren and Kawakatsu (1990) split the genus *Geoplana* into several taxa, based on the informal groups delineated by Froehlich (1967), to facilitate further taxonomic studies. The authors erected the genus *Amaga* and included *G. bogotensis* Von Graff, 1899 and *G. bogotensis* var. *buergeri sensu* Hyman (1955) as separate species, *Amaga bogotensis* and *Amaga buergeri*, respectively. Subsequently, Kawakatsu et al. (1992) transferred *G. bogotensis* Von Graff, 1899 to the collective genus *Pseudogeoplana* Ogren and Kawakatsu, 1990.

The present paper details the anatomy of two species of land planarian from Colombia. Their general characteristics and the gross morphology of their copulatory apparatuses are concordant with the current broad diagnosis of *Amaga*, albeit that they also have new structures. As any attempt to coin a new genus would be premature without first re-examining the type species, we here also provide a detailed re-description of the type material, so as to enable a re-evaluation of the generic characters of the genus *Amaga*.

Materials and methods

The type material of *A. amagensis* was received on loan from the Natural History Museum, London (NHM) as a series of histological sections on glass slides. According to Fuhrmann (1914) the material was stained in acid Haemalum and treated with a mixture of picric acid and fuchsin. The type specimen of *A. bogotensis* was obtained from the Museum für Naturkunde, Berlin (ZMB), preserved in alcohol. It was cut transversally into several pieces, according to body regions; each of these parts was dehydrated in a graded series of ethanol, treated with isopropyl alcohol and embedded into paraffin wax. The same procedures were followed in the case of one specimen from Bogotá (ZMA V.Pl. 6904.1), housed in the Zoological Museum Amsterdam (ZMA), except for the isopropyl alcohol treatment, and clove oil was used as clearing agent. Serial sections 8 μm thick were made of the various regions of the body. The sections were stained with Mallory–Cason stain. The slides of *G. bogotensis* made by Busson were studied and photographed at the Naturhistorisches Museum Wien (NHW). The subepidermal muscular index (SMI; given by the subepidermal musculature thickness: body height ratio) was calculated at the pre-pharyngeal region, after Froehlich (1955). Drawings were prepared using a camera lucida.

Abbreviations used in the figures

The following abbreviations are used in the figures: cm, circular musculature; cs, creeping sole; dep, dorsal epidermis; dm, diagonal muscle; e, eye; ed, ejaculatory duct; es, erythrophil secretion; fa, female atrium; gl, glands; go, gonopore; gr, glandular ridge; in, intestinal branch; lm, longitudinal muscle; ma, male atrium; od, oviduct; ov, ovary; ph, pharynx; pm, parenchymal muscle; pp, penis papilla; pv, prostatic vesicle; sb, subintestinal transverse muscle layer; sep, secretory papilla; sg; shell glands; sp, supraintestinal transverse muscle layer; te, testis; va, vagina; vd, vas deferens; vep, ventral epidermis; vi, vitellarium; vnp, ventral nerve plate.

Systematic account

Order **TRICLADIDA** Lang, 1884
Family **GEOPLANIDAE** Stimpson, 1857
Subfamily **GEOPLANINAE** Stimpson, 1857
Genus ***Amaga*** Ogren and Kawakatsu, 1990

Emended diagnosis

Geoplaninae of large broad and flattened body with well-developed glandular body margins. SMI: 5–7%. Testes placed above supra-intestinal parenchymal transverse muscular layer; male atrium folded, with ejaculatory duct opening through a small papilla-like fold; penis eversible; prostatic vesicle extrabulbar, bifurcate and elongate. Ovovitelline ducts approaching copulatory apparatus from anterodorsal aspect and opening at the same point into the vagina. No cephalic specializations; subepidermal musculature not insunk. Parenchymal longitudinal musculature absent. Adenodactyls or glandulo-muscular organs absent. Type species: *Geoplana amagensis* Fuhrmann, 1914.

Distribution

Peru, Colombia and Amazonian Brazil.

Amaga amagensis (Fuhrmann, 1914)

Material examined

Type material: NHM 1928.1.4.83–88 + 1928.1.4.90–91 + 1928.1.4.112 + 1928.1.4.92–95, sagittal sections of the pharynx and copulatory organs; 1928.1.4.110–111 + 1928.1.4.113 + 1928.1.4.89 + 1928.1.4.114–115, sagittal sections of the posterior end of a second animal; 1928.1.4.96–109, transversal section of pre-pharyngeal region; 1928.1.4.116–120, horizontal sections of the anterior end; Cafetal la Camelia, south of the Amagá river valley, Colombia, altitude 1600–1800 m (note that there is a mix up in the numbering and assignment of slides to specimens concerning the two sagittally sectioned animals; the order given above represents the original, continuous series of sections).

Description

Body height 1800 μm. Creeping sole wide and ciliated, up to 90% of the body width in transverse sections (Figure 1A).

Eye cups distributed anteriorly in a single row; diameter of the pigment cup ranging from 40 to 60 μm. In the pre-pharyngeal region the eyes extend marginally in irregular rows. Sensory pits inconspicuous in anterior part, absent in pre-pharyngeal region. Nervous system arranged in a flat nerve plexus.

Xanthophil secretions open to the exterior at the margins of the body, forming a glandular ridge or margin (Figure 1A,C). Rhabdite-forming cells are distributed in the dorsal parenchyma. Epidermal cells of the dorsal body surface densely packed with rhabdites; ventral epidermis sparsely provided with small rhabdites. The dorsal epidermis (30 μm) is thicker than the ventral epidermis (20 μm).

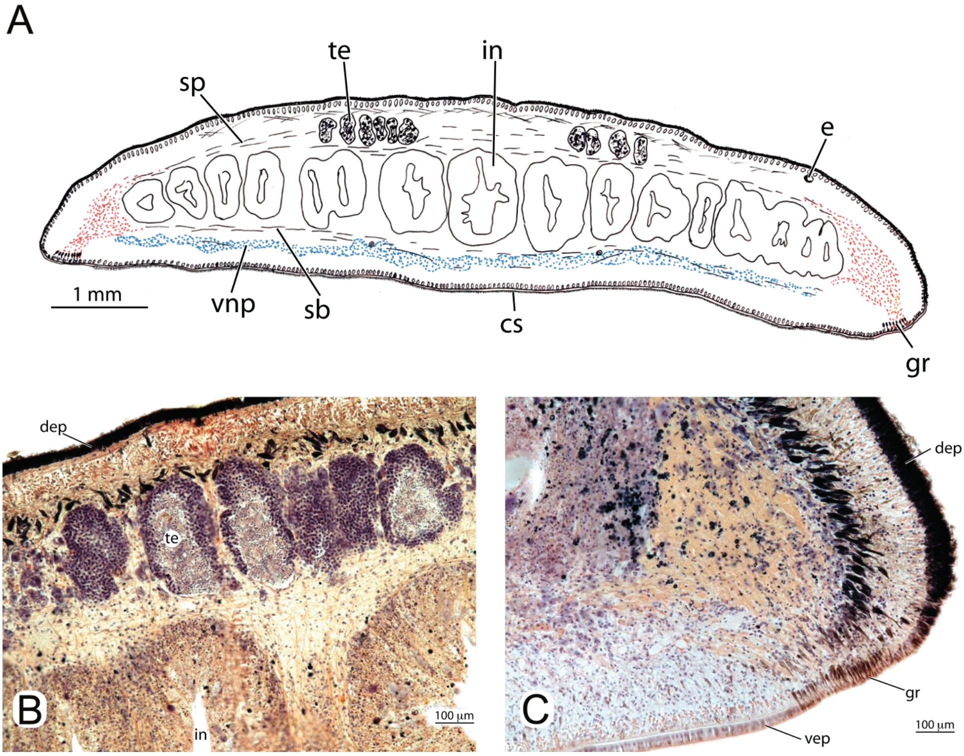

Figure 1. *Amaga amagensis.* NHM 1928. (A) Transverse reconstruction of pre-pharyngeal region. (B) Transverse section of pre-pharyngeal region, showing dorsal position of testes. (C) Transverse section of glandular ridge. See text for abbreviations.

Subepidermal musculature tripartite, composed of circular, double diagonal and longitudinal layers. Longitudinal layer packed in small, separate bundles, stronger dorsally (60–75 μm high) than ventrally (40–50 μm high). In the anterior region the subepidermal musculature has the same arrangement as in the rest of the body, so does not exhibit any specialization. Parenchymal musculature weak, composed of a few thin, obliquely running fibres, and other fibres arranged in three layers: supra-intestinal and subintestinal transversal layers, and a dorsal double layer of diagonal fibres. Longitudinal parenchymal muscle fibres absent.

Pharynx incompletely present in the type material. Mouth located at least 5.6 mm from the posterior end of the pharyngeal pouch. Pharynx of the collar-type, long and flat and highly folded. Oesophagus not observed, as the root of the pharynx was not present in the slides of the type material. Pharyngeal pouch mainly surrounded by circular muscle fibres, with a few interspersed longitudinal fibres. Outer pharynx epithelium ciliated. Outer pharyngeal musculature composed of thin layers of intermingled longitudinal and circular muscles. Inner pharyngeal musculature not observed, as only the external pharynx layers were sectioned.

The globular testes measure about 200 × 320 μm. The testes are located dorsally and placed above the parenchymal supra-intestinal transversal muscle layer (Figure 1A,B). The follicles are arranged in multiple irregular rows on each side of the pre-pharyngeal region of the body. Vasa deferentia densely filled with spermatozoa. Each vas deferens communicates terminally with one of the branches of the bifurcated prostatic vesicle (Figure 2A,B). Prostatic vesicle anteriorly bifurcated with two long branches (about 2.1 mm long) (Figure 2A,B). From the point where the two branches unite, the prostatic vesicle curves anteriad and subsequently posteriad and penetrates the common muscular coat of the copulatory apparatus. The tubular prostatic vesicle is lined with a cuboidal, nucleated and ciliated epithelium. It is surrounded by a thick (20–25 μm) layer of intermingled longitudinal and circular muscle fibres (Figure 6B). The prostatic vesicle is surrounded also by brownish, granular secretions, which are discharged into its proximal section. Upon penetrating the muscular coat of the copulatory apparatus, the prostatic vesicle communicates with the ejaculatory duct. The latter is lined with cuboidal, nucleated and ciliated cells and is surrounded by a thin layer of circular muscles. The penis is of the eversible type, consisting of an irregular fold traversed by the ejaculatory duct and is covered by a cuboidal, nucleated epithelium, which is underlain by a layer of circular muscle. In one specimen the penis is everted (Figure 2B) and has a globular shape. In the other specimen the penis is not everted and has a small penial fold (Figure 2A).

The male atrium consists of an irregularly and elaborately folded cavity, with most folds located at the dorsal side of the atrium. Male atrium about 1.5 times longer than female atrium and surrounded by orange–brown granular secretions that are discharged through its epithelium. Male atrium lined with a squamous, non-ciliated and nucleated epithelium, which is underlain by a weak layer of circular muscles. Glands that are stained dark purple discharge their secretion through the epithelial lining of the gonopore. The common muscular coat that envelopes the male and female copulatory apparatus is composed of loosely arranged fibres

The vitellarian follicles are located dorsally and ventrally to the intestinal branches. Ovaries are placed 1.1 mm from the anterior tip, measuring about 500 μm in dorsoventral direction and 250 μm in width. Ovaries embedded in the transversal subintestinal parenchymatic muscle layer. Oviducal tubes not conspicuous. Ovovitelline duct

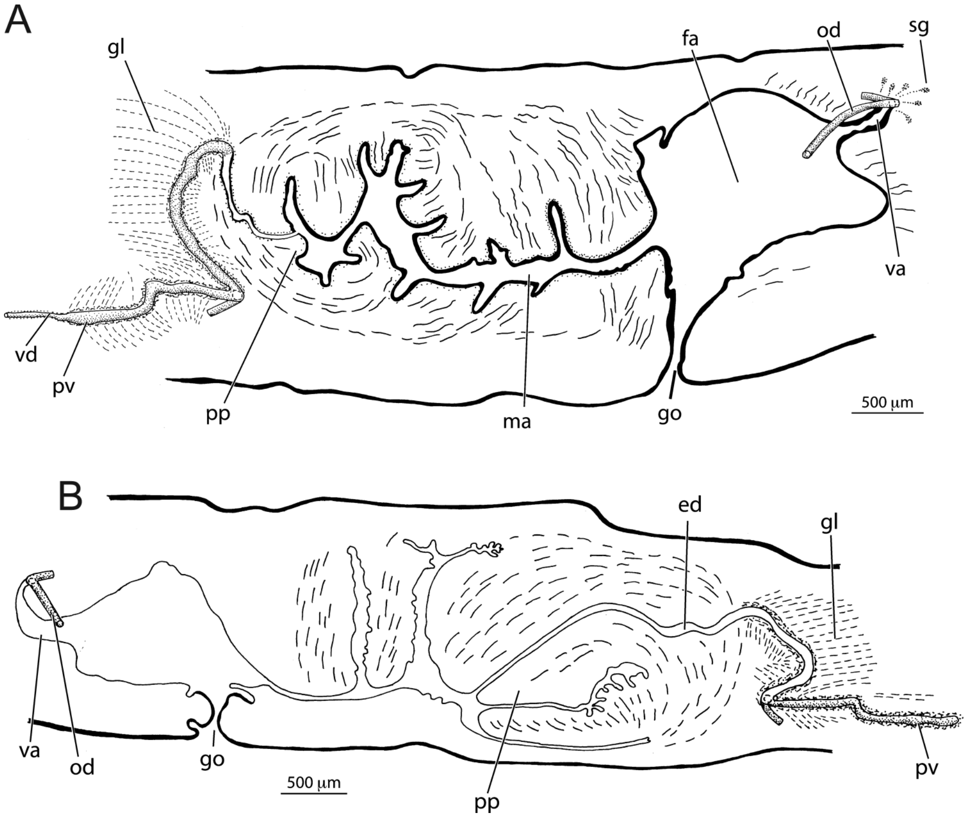

Figure 2. *Amaga amagensis.* NHM 1928. (A) Sagittal reconstruction of copulatory apparatus of specimen B. (B) Sagittal reconstruction of copulatory apparatus of specimen A. See text for abbreviations.

emerges from the ventrolateral part of each ovary. At the level of the gonopore the ovovitelline ducts ascend at a 45° angle towards the dorsal body surface and eventually open separately into the vagina. Just before communicating with the vagina, the oviducts receive the secretion of shell glands. The nucleated epithelium of the oviducts is surrounded by a thin layer of circular muscles. The female atrium consists of a cavity lined with a nucleated, non-ciliated epithelium. The vagina emerges from the posterodorsal section of the female atrium and curves anterodorsally, attaining a somewhat horizontal orientation.

Discussion

The histological sections of the type material were in good condition but, unfortunately, the animal was incompletely sectioned. Sections from the pre-pharyngeal region, anterior part of the pharynx and the region posterior to the copulatory apparatus are not available. Our observations on the type material are basically concordant with those of Fuhrmann (1914). A few detailed measurements made by Fuhrmann, such as the size of the ovaries, are different from ours but may simply result from the precision of our modern equipment. Furthermore, Fuhrmann did not describe that the prostatic vesicle extends anteriorly for a considerable distance. He considered both the branched and unbranched sections of the prostatic vesicle to be part of the vasa deferentia. He described these presumed vasa deferentia as being surrounded by a strong musculature and receiving the secretion of numerous glands. But our examination revealed that there are no histological differences between the muscular prostatic vesicle and its anterior muscularized branches, and that they actually belong to the same organ, namely the prostatic vesicle. It is only at a still farther anterior position, on the sides of the pharyngeal pouch, that each of the branches communicates with the vas deferens (Figure 2A). The latter is narrower than the prostatic vesicle branches, does not receive any secretions and is surrounded by a weak layer of circular muscles.

Genus **Bogga** Grau and Sluys, gen. nov.

Diagnosis

Geoplaninae with large, broad, and flattened body; anterior third gradually narrowing; posterior end rounded or obtuse. Eyes and sensory pits encircle the anterior end of the body. Sensory pits distributed in a single row. SMI: 9–10%. Subepidermal and parenchymal musculature without cephalic specializations. Parenchymal longitudinal muscles absent. Male copulatory apparatus with eversible penis. Male atrium lined with multiple, large musculo-secretory papillae. Vagina emerging from the posterodorsal section of the female atrium; ovovitelline ducts approaching female canal from the anterodorsal side. Shell glands opening into the distal region of the oviducts. Common glandular duct very reduced or absent. Adenodactyls absent. Type species: *Geoplana bogotensis* Von Graff, 1899.

Distribution

Bogotá, Colombia.

Etymology

The generic epithet refers to a combination of the names Bogotá and Amaga. Gender: feminine.

Bogga bogotensis (Von Graff, 1899), comb. nov.

Diagnosis

Broad leaf-like body; grey–black dorsal surface with a dark yellow marginal stripe that encircles the body and a dark yellow mid-dorsal stripe; both stripes about the same width; eyes located marginally; SMI: 9–10%; pharynx of the collar type; oesophagus small; globular prostatic vesicle located immediately posterior to pharyngeal pouch; small eversible penis; male atrium twice as long as female atrium; shell glands opening into the distal region of the oviducts. Oviducts ascending laterally to the gonopore. Vagina emerging from the posterodorsal wall of the genital atrium, with dorsal or anterodorsal orientation.

Material examined

Holotype: ZMB 743. Preserved in 70% ethanol. Sections were prepared as follows: anterior region 1: transverse sections on seven slides; anterior region 2: sagittal sections on 11 slides; pre-pharyngeal region: transverse sections on four slides; pharynx: sagittal sections on 14 slides; copulatory apparatus: sagittal sections on 24 slides.

NHW 2741. Original material of *G. bogotensis* var. *buergeri* studied by Busson. Sagittal sections of the copulatory apparatus on 167 slides.

ZMA V.Pl. 6904.1. National Park, Bogotá, Colombia, 15 August 1975, coll. J. Tamsitt; front end: horizontal sections on 37 slides; pre-pharyngeal region: transverse sections on 13 slides; pharynx and copulatory apparatus: sagittal sections on 78 slides.

Description

Both ZMA V.Pl. 6904.1 and the holotype specimen have a broad, leaf-like body, with gradually tapering front end and the hind end rounded or obtuse. The holotype measured 33 mm in length, excluding the anterior body tip, which was absent (Figure 3C). Judging from the shape of the body, the missing region may have measured 0.5–1 mm in length. The ZMA V.Pl. 6904.1 specimen measured 42 mm in length and 8 mm in width (Figure 3B). The body reached its maximum width, 6–8 mm, at its median region. The mouth is at a distance from the anterior tip equivalent to 76% of body length, while the gonopore is located at 88% in the holotype (Table 1). In both specimens the creeping sole comprises over 90% of the body width. The ground colour

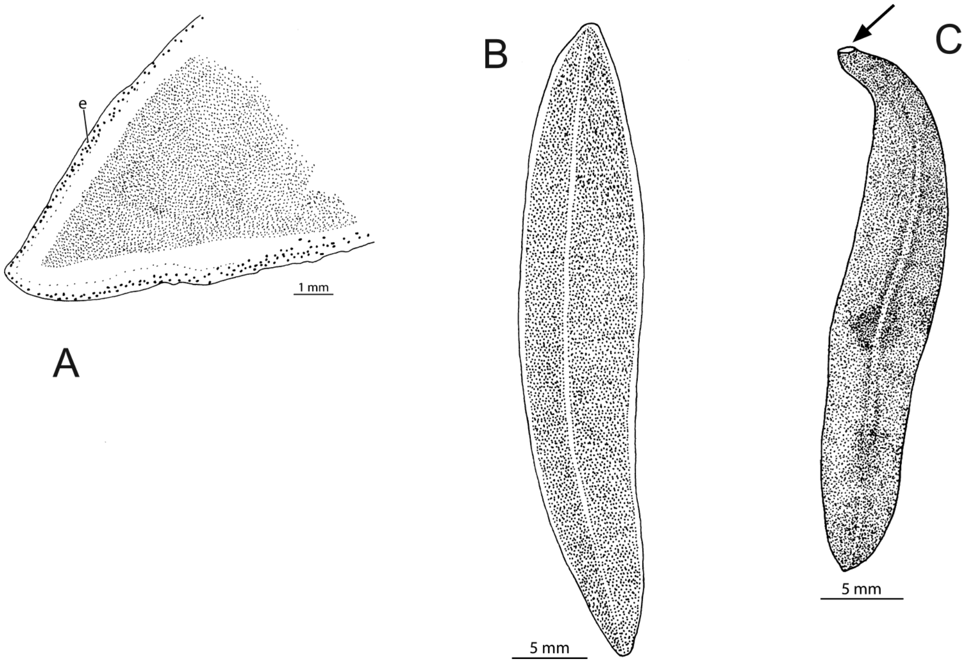

Figure 3. *Bogga bogotensis*. (A) ZMA V.Pl. 6904.1, anterior region showing eye distribution. (B) ZMA V.Pl. 6904.1, external features of preserved specimen. (C) Holotype ZMB 743, external features of preserved specimen. See text for abbreviations.

Table 1. Measurements (in mm) of fixed specimens of *Bogga bogotensis*.

	Length	Width	Height	DMI	DGI
ZMA V.Pl. 6904.1	42	8	2	68%	86%
Holotype	33	6	1.3	76%	88%

DMI, distance of mouth from anterior end relative to body length; DGI, distance of gonopore from anterior end relative to body length.

of the dorsal surface is grey–black in the ZMA V.Pl. 6904.1 animal; ventral surface whitish. A prominent dark yellow mid-dorsal stripe runs from the anterior tip to the posterior body margin. Dorsal surface also provided with a dark yellow marginal stripe that encircles the body (Figure 3B).

Eye cups multicellular, with the pigment cups measuring 38–40 μm in diameter. In the V.Pl. 6904.1 animal eyes are present in a single row at the anterior end (Figure 3A), while from 1 or 2 mm behind the anterior margin the eye cups extend further backwards along the body margin in rows of three or four eyes on either side of the body. Sensory pits were only observed in the holotype, in which they are located ventrolaterally in a single row that encircles the anterior region of the body. The central nervous system consists of a ventral nerve plate (Figure 4A).

In both specimens the epidermis of the body margins is penetrated by granular xanthophil and fine erythrophil secretions. Rhabdite-forming cells are abundant in the dorsal parenchyma. Rhabditogen cells are also present ventrally, but only very scarcely. Cells with granular erythrophil and xanthophil secretions discharge their secretions through the ventral epidermis. Erythrophil cells discharge their granular secretion through the entire epidermis of the pre-pharyngeal region, i.e. through both ventral and dorsal regions. In the holotype, the creeping sole is clearly ciliated; this was not evident in the V.Pl. 6904.1 specimen, which may result from a fixation artefact.

Both V.Pl. 6904.1 and the holotype specimen show the three subepidermal muscle layers characteristic of the Geoplaninae (Table 2): a subepidermal circular layer, followed by a double diagonal layer with decussate fibres, and then a longitudinal layer arranged in bundles. Thickness of subepidermal musculature relative to body height: SMI: 10.2% (holotype). In the anterior end of the body there are no glandular nor muscular specializations. In the pre-pharyngeal region of the holotype the ventral longitudinal muscle layer is thicker than the dorsal one (68 μm and 45 μm, respectively). In the V.Pl. 6904.1 specimen the dorsal subepidermal musculature (90 μm in thickness) is only slightly thicker than the ventral one (86 μm in thickness).

In both specimens the parenchymal musculature consists of fibres arranged in various directions, but mainly orientated vertically (especially between the intestinal diverticles). Other parenchymal muscle fibres are arranged in three layers, namely a subintestinal transversal layer, a supra-intestinal transversal layer, and a dorsal double diagonal layer with decussate fibres (Figure 4A,B). The parenchymal musculature does not form any specializations in the cephalic region.

The mouth is located in the middle of the pharyngeal pouch, the latter being surrounded by a single, subepithelial circular muscle layer. The collar-shaped pharynx (Figure 4C) is highly folded on its free margin, filling the pouch almost completely.

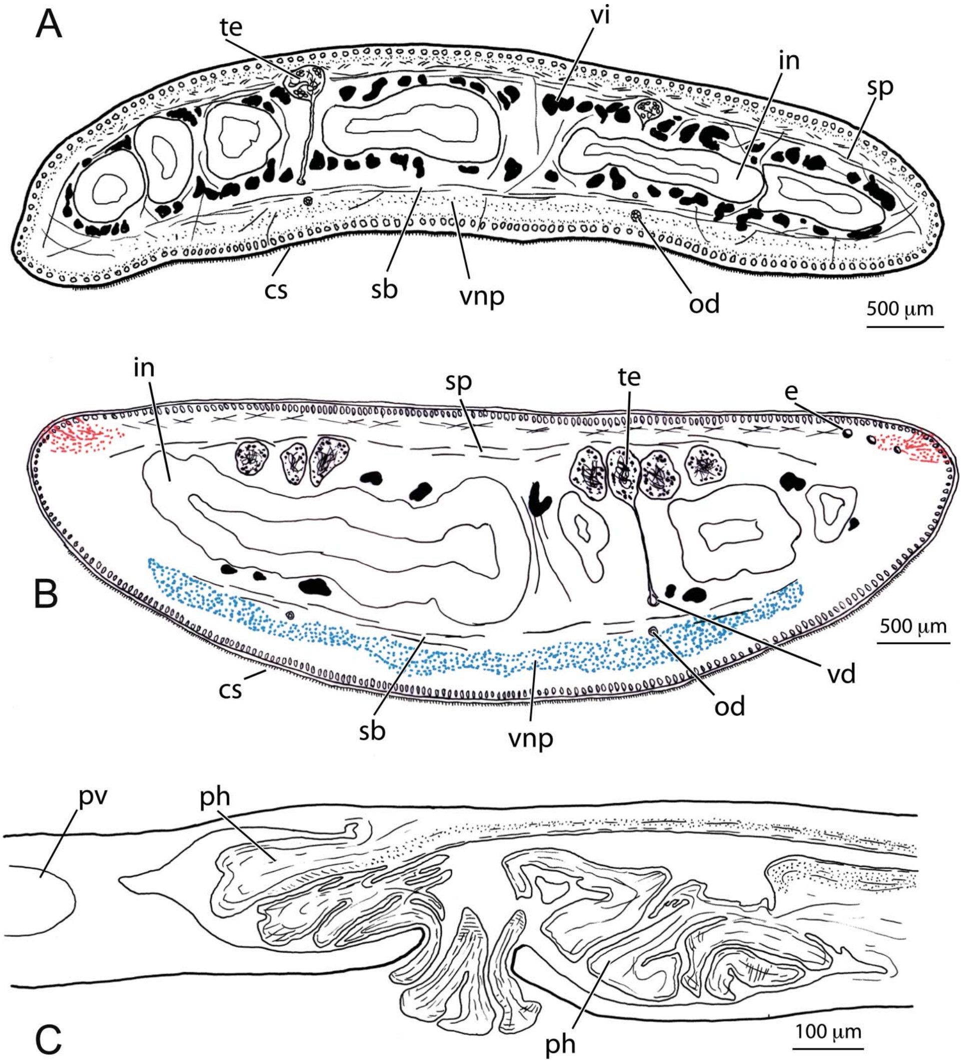

Figure 4. *Bogga bogotensis*. (A) Holotype ZMB 743. Transverse section of the pre-pharyngeal region. (B) ZMA V.Pl. 6904.1, transverse section of the pre-pharyngeal region. (C) Holotype ZMB 743, sagittal reconstruction of pharynx. See text for abbreviations.

An oesophagus is present, but it was not completely observable in either of the specimens because it was not completely sectioned. The outer pharyngeal lining consists of a flat, cuboidal epithelium. The outer pharynx musculature is composed of a layer of intermingled longitudinal and circular fibres (about 5 μm in thickness). The outer epithelium of the distal region of the pharynx is penetrated by two types of secretory cells, producing erythrophil and xanthophil granules, respectively. The inner pharyngeal and oesophageal epithelia are underlain by a thin layer of longitudinal muscles (6 μm in thickness), followed by a much thicker layer of circular fibres (60 μm in thickness).

Table 2. *Bogga bogotensis*: thickness (in μm) of the subepidermal musculature at the prepharyngeal region of the holotype and ZMA V.Pl. 6904.1.

Muscle layer/SMI/ Creeping sole	Holotype	V.Pl. 6904.1
Dorsal circular	4.5 (1–2)	3.7 (1–2)
Dorsal diagonal	17 (1–3)	12 (2–4)
Dorsal longitudinal	24 (16–24)	81 (35–40)
Dorsal total	45	90
Ventral circular	5.7 (1–2)	5 (1–2)
Ventral diagonal	11.4 (1–3)	11.4 (2–4)
Ventral longitudinal	51.4 (20–33)	65 (30–45)
Ventral total	68	86
SMI	10%	9%
Creeping sole width	92%	95%

Maximum and minimum values of fibres per bundle are given in parentheses. Width of creeping sole is also given. SMI, subepidermal muscular index.

The globular testes measure about 200–250 μm in diameter. The follicles are located dorsally, arranged in five to seven rows on either side of the body. The testes are located between the intestinal branches, just beneath the supra-intestinal transversal muscle layer and extend from the level of the ovaries in the anterior region of the body to the root of the pharynx. In the holotype the most anterior and posterior testes are located, in relation to the anterior end, at 17% and 50% of body length, respectively.

The vasa deferentia run above the subintestinal transverse muscle layer and are located dorsally to the ovovitelline ducts (Figure 4B). At the level of the prostatic vesicle the vasa deferentia bend dorsomedially and, subsequently, open separately into the anterolateral part of the prostatic vesicle. Posterior to the pharynx, the vasa deferentia are dilated to spermiducal vesicles that are full of spermatozoa. The vasa deferentia are lined with a squamous to cuboidal epithelium and are surrounded by a layer of circular muscle fibres (4 μm in diameter).

The ellipsoid prostatic vesicle is located directly behind the posterior wall of the pharyngeal pouch, at 0.2 mm and 0.6 mm in holotype and specimen V.Pl. 6904.1, respectively. The vesicle is lined with a flat, non-ciliated epithelium and is surrounded by a subepithelial layer of intermingled muscle fibres (45 μm in thickness). Numerous erythrophil finely granular secretions are discharged into the prostatic vesicle.

In the holotype, the prostatic vesicle does not have any open connection with the rest of the copulatory apparatus. In the region between the prostatic vesicle and the gonopore there are scattered fragments of muscle fibres roughly delimiting an elongated region that should be occupied by the penial bulb and the male atrium. This region contains tissue without cells or nuclei, without any signs of wall or cavity. Furthermore, there is no communication between this region and the female atrium, i.e. it is an isolated cavity that is continuous with the ample gonopore channel (Figure 5D). Gonopore completely open.

In specimen V.Pl. 6904.1 the prostatic vesicle penetrates the common muscle coat of the copulatory apparatus and continues inside the penial bulb as a sinuous to slightly helicoidal ejaculatory duct. The latter opens into the male atrium through

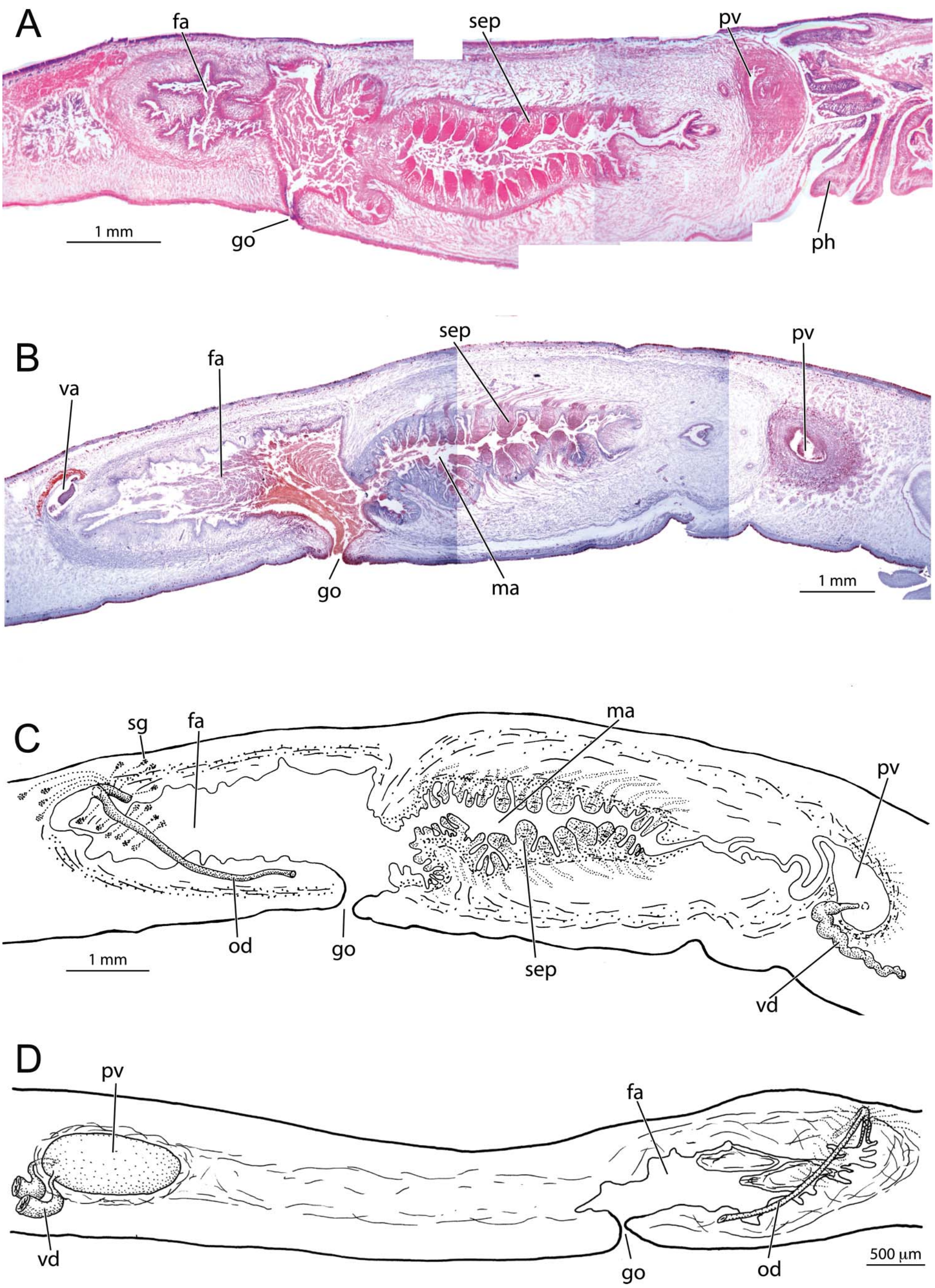

Figure 5. *Bogga bogotensis*. (A) NHW 2741, sagittal section of copulatory apparatus. Gaps in dorsal and ventral epidermis due to composite nature of the photograph. (B) ZMA V.Pl. 6904.1, sagittal section of copulatory apparatus. (C) ZMA V.Pl. 6904.1, sagittal reconstruction of copulatory apparatus. (D) Holotype ZMB 743, sagittal reconstruction of copulatory apparatus. See text for abbreviations.

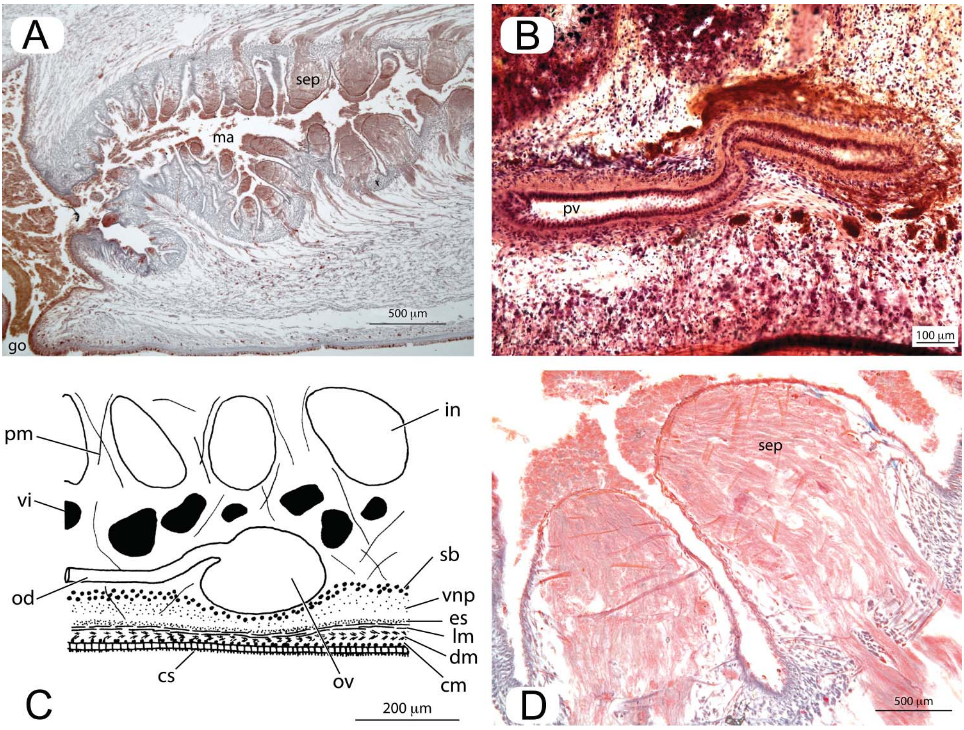

Figure 6. (A) *Bogga bogotensis*. ZMA V.Pl. 6904.1, sagittal section of secretory papillae. (B) *Amaga amagensis.* NHM 1928, sagittal section of branch of prostatic vesicle. (C) *Bogga bogotensis*. Holotype, sagittal reconstruction drawing of position of the ovaries. (D) *Bogga bogotensis*, ZMA V.Pl. 6904.1, sagittal section of secretory papillae. See text for abbreviations.

a small papilla. The ejaculatory duct is lined with tall, ciliated and nucleated cells, and is surrounded by a circular muscle layer; it does not receive any conspicuous secretions.

The male atrium of V.Pl. 6904.1 is a long and relatively narrow cavity, with its wall projecting into this cavity as numerous large, muscular and secretory papillae (Figure 5B,C). These papillae are 300–400 µm tall and 150–250 µm wide at their base. A thick layer of circular muscle fibres, underlain by a longitudinal one, surrounds the male atrium in which the papillae are embedded. Each papilla also has its own circular musculature, as well as radial fibres running from one side of the papilla to the other. Two-thirds of each papilla is filled with a fine erythrophil secretion, originating from secretory cells located in the parenchyme anterior to the male atrium, albeit still located within the common muscular coat (Figure 6A). The papillae have no lumen or cavity and the erythrophil secretion is discharged through the epithelium of each papillae (Figure 6D).

The male atrium is almost completely filled with erythrophil secretions originating from these secretory papillae. It is lined with a low, ciliated epithelium, and is surrounded by intermingled longitudinal and circular muscle fibres. Male and female atria are clearly separated by a dorsal fold located on the male side, just above the gonopore (Figure 5C). The opening of the male atrium is narrowed by a dorsal and ventral fold, slightly anterior to the gonopore. A muscular coat separately covers each atrium, as suggested by a clear muscular division at the level of the dorsal atrial fold that separates male and female atria.

In both animals the vitellarian follicles are relatively small, located dorsally and ventrally to the intestine in the parenchymal space delimited by the supra-intestinal and subintestinal parenchymal muscle layers, without invading the space between the intestinal branches.

The ovaries are large and elongate, up to 500 μm long by 200 μm wide. They are ventrally located above the subintestinal parenchymal muscle layer (Figure 6C) at 5.6 mm from the anterior tip in the holotype. The ovovitelline ducts arise from the posterodorsal surface of the ovaries.

The oviducts run between the subintestinal muscle layer and the ventral nerve plate. At the level of the female atrium the ducts run dorsomedially and, subsequently, open into the vagina; common oviduct very small or absent. Ovovitelline ducts lined by a ciliated epithelium and surrounded by a layer of interwoven muscle fibres. Shell glands, producing a granular xanthophil secretion, open into the distal half of the ascending sections of the oviducts. After it has received the openings of the oviducts, the vagina dilates to form a cavity that is three to four times as wide as the oviducts. The female atrium is lined with a secretory epithelium. Granular xanthophil secretions fill the lumen of the female atrium, which is principally surrounded by longitudinal and circular muscle fibres.

Discussion

We agree with Fuhrman (1914) that *G. bogotensis* and *G. bogotensis* var. *buergeri* concern one and the same species, a conclusion that is supported by the fact that the V.Pl. 6904.1 and the holotype specimen examined by us conform to the published descriptions of both of these taxa.

The copulatory apparatus of the holotype was never described in the literature. Furthermore, the copulatory complex is only partly present in the holotype because the section between the prostatic vesicle and the female atrium is fully disintegrated, hence complicating taxonomic assignment of this specimen (Figure 5D). However, the V.Pl. 6904.1 animal and the holotype share two rare characteristics that strongly suggest their conspecificity: (1) the internal pharynx epithelium being underlain by a thin layer of longitudinal muscles, followed by a much thicker layer of circular fibres; (2) the ovaries being located above the subintestinal transversal parenchymal muscle layer (Figure 6C). Such a pharyngeal muscle arrangement is presently only known from one other Andean species, *Notogynaphallia andina* (Hyman, 1961) (Carbayo 2003), while such a location of the ovaries is only known from *Notogynaphallia sexstriata* (Von Graff, 1899) (Carbayo 2003). Furthermore, another suite of features also points to their conspecificity: (1) similar size, body shape and colour pattern; (2) xanthophil and erythrophil glands opening through the body margins; (3) collar-shaped pharynx; (4) close proximity between the pharyngeal pouch and the prostatic vesicle; (5) elliptical, extra-bulbar prostatic vesicle; (6) similar size ratio of male–female atria; (7) vagina located in posterodorsal section of female atrium; (8) ovovitelline ducts ascending posterior to the gonopore; (9) direct communication between the oviducts and the vagina. Additionally, the animals were collected from the same locality (Bogotá, Colombia). Differences in ratio of dorsal versus ventral subepidermal longitudinal musculature between the two animals may be the result of the more contracted state of the V.Pl. 6904.1 specimen.

The NHW 2741 animal described by Busson (1903) is most probably also conspecific with the holotype. First, the copulatory apparatus of this animal is morphologically identical to the V.Pl. 6904.1 specimen (Figure 5A). Second, a series of other similarities between V.Pl. 6904.1 and the animal described by Busson (1903) as the variety *buergeri* support our conclusion that the latter should be considered as a member of that species. These features do not only concern the gross morphology but also characters such as: (1) secretory muscular papillae projecting into the male atrium, (2) zone of circular muscles at the bases of these papillae surrounding the male atrium, (3) location of the ovaries above the subintestinal muscle layer, (4) direct communication between the oviducts and the vagina.

In contrast to Busson (1903), we do not consider the penis-like fold at the end of the ejaculatory duct to be a true penis papilla, because it is not morphologically differentiated from the rest of the male atrium by the presence, for example, of associated muscle layers or glandular secretions. Earlier, it was already noted that the " . . . presumed intra-antral papilla of *Amaga*, which appears more like folds of the atrial wall, is not homologous with the penis papilla of the genus *Geoplana* . . . " (E.M. Froehlich, in Ogren and Kawakatsu 1990, p. 87).

General discussion

Re-evaluation of the diagnostic features of Amaga

The diagnostic features of many genera in the Geoplaninae need to be re-evaluated, preferably in the context of a phylogenetic analysis of the entire group of land planarians. However, it is not our intention to present in this paper a complete revision of the genus *Amaga* but rather to discuss the morphological features of its type species and to propose an emendation of the generic diagnosis.

The type species *Amaga amagensis* has a rather simple and conventional anatomy as it has few or no anatomical novelties that can easily be used to distinguish it from other species of Geoplaninae. The main diagnostic feature, originally proposed, albeit tentatively, by Froehlich (1967) and subsequently formalized by Ogren and Kawakatsu (1990) is the presence of a small intra-antral penis papilla. This papilla is actually a projection from the anterior wall of the male atrium. Other characters mentioned by Ogren and Kawakatsu (1990), such as body shape and size, and absence of musculoglandular organs, are features to be found in many other taxa and therefore unable to uniquely define the genus *Amaga*. On the basis of our study of the type species as well as other species of Geoplaninae, we do not consider the intra-antral penis papilla as forming a good diagnostic character for generic rank because the presumed papilla does not show any independent structural features, such as the presence of its own muscle layers or the openings of special kinds of secretory cells. This presumed papilla is not even a permanent structure, as is evident from Fuhrmann's figures of the copulatory apparatus of both his worms. For example, his fig. 24 shows a worm with its intromittent organ clearly formed by a fold of the male atrial wall. Therefore, the current diagnosis, mentioning the presence of an intra-antral papilla, leads to confusion in cases of other animals in which the male atrium exhibits a highly folded wall, so resulting in a poorly defined papilla. In view of the above, we interpret the presumed intra-penial papilla of *Amaga* actually to be the tip of an eversible penis, housed in a folded male atrium.

Another feature proposed by Ogren and Kawakatsu (1990) for *Amaga* concerns the situation that the female canal opens into the dorsal section of the female atrium and that the oviducts approach the canal from an anterodorsal direction. Besides being common to *Geoplana*, this condition applies to species of other genera of the Geoplaninae, such as *Notogynaphallia* Ogren and Kawakatsu, 1990, and *Polycladus* Blanchard, 1845. It is worth noting that the ovovitelline ducts open directly into the vagina and do not fuse to form a common glandular duct, as in most other genera of the Geoplaninae, such as *Cephaloflexa* Carbayo and Leal-Zanchet, 2003, *Choeradoplana* Von Graff, 1896, *Issoca* Froehlich, 1955, *Supramontana* Carbayo and Leal-Zanchet, 2003, and in some species of *Geoplana.* Therefore, we propose this feature as a diagnostic character for the genus *Amaga*.

One taxonomic character we wish to emphasize is the position of the testes in relation to the parenchymal muscle layers. In most members of the Geoplaninae the testes are placed underneath the supra-intestinal transversal muscle layer. The fact that in *Amaga* the testes are located above the supra-intestinal layer of transverse muscles deserves special attention. The testes occur dorsally to this muscle layer as well as at the level of this layer or shortly underneath the layer in some Andean species, such as *Notogynaphallia andina* (Hyman, 1962), *Gigantea urubambensis* Negrete et al., 2010, and in *Polycladus gayi* Blanchard, 1845 (personal observation J.H.G.).

Systematic position of Bogga *Grau and Sluys, gen. nov.*

Dorsal testes, broad creeping sole and subepidermal longitudinal muscles arranged in bundles provide substantial evidence that the animals from Bogotá belong to the subfamily Geoplaninae. Currently, the Geoplaninae comprises 17 genera, plus a collective group, *Pseudogeoplana* Ogren and Kawakatsu, 1990, which was specifically created to include all species for which morphological knowledge is insufficient to place them in one of the other genera of the subfamily.

Within this subfamily there are no genera into which we could comfortably fit our specimens from Bogotá and therefore the new genus *Bogga* was created to taxonomically accommodate the animals. The genus *Bogga* is characterized by a unique feature, i.e. a male atrium lined with secretory papillae, a feature not known from other genera of the Geoplaninae. Musculo-glandular accessory organs are not common in the Geoplaninae. Currently there is only one genus that is known for its glandular structures in the male copulatory organs, namely *Gigantea* Ogren and Kawakatsu, 1990. Carbayo (2008) suggested that the secretory structures in *Gigantea* are not homologous between the different species in the genus. Furthermore, the author divided these structures into two types, muscularized and non-muscularized, and also discussed their position inside the copulatory apparatus. However, the monophyletic status of *Gigantea* has been questioned, based on the fine morphology of these glandular structures (cf. Carbayo 2008). Nonetheless, *Bogga* and *Gigantea* are different in their morphological aspects. The male atrium of *Gigantea* is filled with a large penis papilla from which the embedded secretory papillae project outwards. In *Bogga*, however, the secretory papillae are embedded in the wall of the male atrium and project towards its lumen. Furthermore, a permanent penial structure is absent in *Bogga* because the penis is merely represented by a very small papilla at the proximal region of the male atrium. Additionally, the genus *Gigantea* is characterized by a posterior approach of the female canal, whereas in *Bogga* the female canal approaches the female atrium from an anterior direction.

The secretory papillae of *Bogga* appear be to unique among the known glandulo-muscular organs. Many different types of muscularized glandular organs are known to occur in other taxa of Geoplanidae, but these are different from the papillae in *Bogga* because the latter lack a duct or small canal.

The presence of secretory papillae projecting into the male atrium is not part of any of the current generic diagnoses within the Geoplaninae. On the basis of other characters, either separately or combined (e.g. subepidermal and parenchymal muscle layers, distribution of eyes and sensory pits), we were unable to comfortably fit the specimens from Bogotá into any of the present genera of the Geoplaninae and therefore a new genus was erected.

Presently, the phylogenetic relationships within the Geoplaninae, and land planarians in general, have not been analysed in any detail, and the type species of many South American genera await detailed taxonomic re-description. From that perspective, one should remain reluctant to propose monotypic genera. Nevertheless, we felt compelled to propose a new genus to accommodate the specimens from Bogotá, thus avoiding the unnatural groupings of species in very large genera that have so much troubled land planarian taxonomy – see for example, the several genera that have been split off from the large genus *Geoplana* (cf. Ogren and Kawakatsu 1990). In this way we hope to provide future explorations of the Colombian land planarian fauna with a stable and natural taxonomic basis.

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References

Busson B. 1903. Ueber einige Landplanarien. Sitzungsber Akad Wien. 112(1):375–429.

Carbayo F. 2003. Revisión de *Notogynaphallia* (Ogren & Kawakatsu, 1990). PhD thesis. Departamento de Biología Animal. Parasitología, Ecología, Edafología y Química Agrícola. Universidad de Salamanca.

Carbayo F, Leal-Zanchet AM. 2003. Two new genera of geoplaninid land planarians (Platyhelminthes: Tricladida: Terricola) of Brazil in the light of cephalic specializations. Invertbr Syst. 17(3):449–468.

Du Bois-Reymond Marcus E. 1957. On Turbellaria. Acad Brasil Ciênc. 29(1):153–159.

Froehlich C.G. 1967. A contribution to the zoogeography of neotropical land planarians. Acta Zool Lill. 23:153–162.

Fuhrmann O. 1914. Planaires terrestres de Colombie. In: Fuhrmann O, Mayor E. editors. “Voyage d’Exploration Scientifique en Colombie”. Mém Soc Sci Natur de Neuchatel. 5 (2):748–792 + 3 pls.

Froehlich CG. 1955. Sôbre morfologia e taxonomia das Geoplanidae. Bol Fac Filos Cienc Letr Univ Sao Paulo, Ser. Zool. 19:195–279.

Hyman LH. 1955. Miscellaneous marine and terrestrial flatworms from South America. Am Mus Novit. 1742:1–33.

Ogren RE, Kawakatsu M. 1990. Index to the species of the Geoplanidae (Turbellaria, Tricladida, Terricola). Part I: Geoplaninae. Bull Fuji Women's Coll, Ser. II. 28:79–166.

Von Graff L. 1899. Monographie der Turbellarien. II. Tricladida Terricola (Landplanarien). I–XII+574 pp. Atlas von Achtundfünfzig Tafeln zur Monographie der Turbellarien II. Tricladida Terricola (Landplanarien). Pls I–LVIII. Leipzig (Germany): Wilhelm Engelmann.