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Two new genera of geoplaninid land planarians (Platyhelminthes : Tricladida : Terricola) of Brazil in the light of cephalic specialisations

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Abstract. Two new genera of geoplaninid land planarians are described. Cephalic specialisations, mainly external morphology and musculature development, partially define each genus. *Cephaloflexa*, gen. nov. shows some peculiar characteristics, such as a gradual narrowing of the anterior third of the body and an upwards roll of the anterior tip, the absence of eyes and sensory pits on the apex, and the existence of a retractor muscle derived from the ventral cutaneous longitudinal musculature. *Geoplana bergi* Graff, 1899 is allocated to *Cephaloflexa* and is designated as the type species. The ventral cutaneous longitudinal muscles of *Supramontana,* gen. nov. (monotypic), are partially sunk into the mesenchyme, thus constituting a cephalic retractor muscle. A new species of each genus is also described. The external morphology and anatomy of the cephalic region of the new genera and of *Geoplana* Stimpson, 1857, *Choeradoplana* Graff, 1896 and *Issoca* C. G. Froehlich, 1955 are analysed. Emendations to the diagnoses of *Issoca* and *Choeradoplana* are proposed based on cephalic differentiations.

Spanish abstract. Se decriben *Cephaloflexa*, gen. nov. y *Supramontana*, gen. nov., dos nuevos géneros de planarias terrrestres de la subfamilia Geoplaninae, ambos caracterizados por especializaciones cefálicas, como la morfología externa y el desarrollo muscular. Se describe una nueva especie de cada género. Se transfiere *Geoplana bergi* Graff, 1899 para el género *Cephaloflexa* y se la designa especie tipo. *Cephaloflexa*, gen. nov. presenta características peculiares, como el tercio anterior del cuerpo muy fino, región anterior enrollada hacia el dorso, ausencia de ojos y fosetas sensoriales en el ápice anterior del cuerpo, y un músculo retractor derivado de la musculatura subcutánea longitudinal ventral. *Supramontana*, gen. nov., género monotípico, tiene parte de la musculatura subcutánea longitudinal ventral hundida en el mesénquima y transformada en la región anterior en un músculo retractor cefálico. Se analiza la morfología externa y la anatomía de la región cefálica de *Geoplana* Stimpson, 1857, *Choeradoplana* Graff, 1896 e *Issoca* Froehlich, 1955 y se proponen enmiendas a las diagnosis de *Choeradoplana* e *Issoca* basadas en las diferenciaciones cefálicas.

Introduction

The land planarian subfamily Geoplaninae Stimpson, 1857 contained eight genera until Ogren and Kawakatsu (1990) subdivided *Geoplana* into six new genera: *Amaga*, *Enterosyringa*, *Gigantea*, *Notogynaphallia*, *Pasipha*, and *Pseudogeoplana* (a collective group). These new genera, together with *Geoplana* s.s., *Choeradoplana* Graff, 1896, *Geobia* Diesing, 1861, *Issoca* C. G. Froehlich, 1955, *Gusana* E. M. Froehlich, 1978, *Liana* E. M. Froehlich, 1978, *Xerapoa* C. G. Froehlich, 1955, and *Polycladus* Blanchard, 1845, constitute the 14 current genera of Geoplaninae. The systematics of the family Geoplanidae (Stimpson) is still poorly resolved and there are relatively few neotropical species described in the literature. This is illustrated by the fact, that from the type locality of the species herein described, 40 species have been registered but only seven have been described in the literature (Leal-Zanchet and Carbayo 2000, 2001; Carbayo and Leal-Zanchet 2001).

Generally, the descriptions of the species of Geoplaninae are based principally on external characteristics, the development and constitution of cutaneous and mesenchymal musculature in the pre-pharyngeal region, cephalic specialisation, and the anatomy and histology of the reproductive system. The internal anatomy of the cephalic region does not usually attract researchers' attention, unless the head shows a differentiated shape. Thus, the internal cephalic anatomy of most geoplaninid species is largely unknown.

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Eleven genera in the subfamily Geoplaninae appear to be natural groups based on exclusive characters. They are *Issoca*, *Choeradoplana*, *Xerapoa*, *Amaga*, *Gigantea*, *Gusana*, *Pasipha*, *Geobia*, *Liana*, *Enterosyringa*, and *Polycladus*. The last four genera are monospecific. In the present work, two new genera and two new species of the subfamily Geoplaninae are described, based principally on cephalic specialisation. One genus may be differentiated based on external cephalic characters; the other, not. We compare the cephalic structures of the new genera with three other genera of Geoplaninae, including *Issoca*, *Choeradoplana* and *Geoplana*, the type genus of the subfamily (Ogren and Kawakatsu 1990). We propose emendations for the definitions of *Issoca* and *Choeradoplana*. In addition, we emphasise the need for analysing the anatomy of the cephalic region of Geoplaninae and the importance of its use in classification as previously recommended by C. G. Froehlich (1955) and E. M. Froehlich (1978).

Material and methods

The national forest of São Francisco de Paula, state of Rio Grande do Sul, located in the district of Rincão dos Kroeff, between 29°23′ and 29°27′S, and 50°23′ and 50°25′W, in South Brazil is the type locality of the genera and species described here. The area (~1600 ha) lying at an altitude of ~930 m is dominated by ombrophilous forest mixed with *Araucaria angustifolia*. The type specimens of the new genera, as well as specimens of *Geoplana josefi* Carbayo & Leal-Zanchet, 2001, *Geoplana franciscana* Leal-Zanchet & Carbayo, 2001 and *Choeradoplana iheringi* Graff, 1899, were manually collected from under natural material on the soil. In the laboratory, they were measured and the external morphology and the colour pattern studied, both in live and fixed animals. Animals were killed using boiling water and fixed in 10% Lillie's neutral formaldehyde or SUSA (Romeis 1989). Tissue blocks were dehydrated in an ascending series of ethyl alcohol concentrations, treated with isopropyl alcohol and embedded in Paraplast. Sagittal, transverse or horizontal 6–12 μm serial sections of either the anterior region, the pharynx, the pre-pharyngeal region or the copulatory apparatus were stained using the Mallory/Cason and Masson/Goldner (MG) trichrome methods (Romeis 1989); the remaining body portions were preserved in 70% ethanol. A single specimen of each species was preserved in clove oil to allow better visualisation of the eyes.

The positions of the mouth and gonopore, DMI and DGI, respectively, are expressed as distances from anterior tip relative to the body length. The ratio of the height of subcutaneous musculature to the height of the body (cutaneous muscular index, CMI) was calculated by C. G. Froehlich's method (1955). Cutaneous muscle fibres were counted in transverse and saggital sections of the pre-pharyngeal and pharyngeal regions respectively. Specimens of *Issoca rezendei* (Schirch, 1929) collected in Cabo Frio, Rio de Janeiro, Brazil and *Cephaloflexa bergi* (Graff, 1899) from the state of São Paulo, from E. M. Froehlich's Land Planarians Scientific Collection (EMF, Department of Zoology, University of São Paulo), were also analysed. They were preserved in 70% ethanol and were processed as described above. The type material is deposited in the Zoological Museum of the University of São Paulo-SP (MZUSP) and in the Zoological Museum of the University of the Vale do Rio dos Sinos, São Leopoldo-RS (MZU). Winsor's (1998) nomenclature was adopted for classification of the secretory cells.

Family **GEOPLANIDAE** Stimpson

Subfamily **GEOPLANINAE** Stimpson

Genus ***Cephaloflexa***, gen. nov.

Type species: *Geoplana bergi* Graff, 1899.

Definition

Geoplaninae with elongated subcylindrical or subsemicircular body, anterior third very gradually narrowing, without constriction or widening; without grooves on ventral surface. At rest, body rolled in the form of a plane spiral, with anterior tip rolled upwards. When creeping, anterior tip rolled upwards and ventrally concave. Creeping sole wide. Eyes and sensory pits absent on apex; cephalic retractor muscle formed by a thickening of ventral longitudinal cutaneous musculature; on body margins retractor distant from epidermis; CMI, 7–21%; longitudinal mesenchymal musculature absent; penis papilla absent; transverse sub-neural mesenchymal musculature only present in cephalic region; male atrium richly folded; common glandular ovovitelline duct, dorsal to female atrium; female atrium ending in a dorso-anteriorly directed proximal diverticulum (vagina); without either sensory papillae or adenodactyls.

Localities

States of Rio de Janeiro, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul, Brazil.

Etymology

The generic epithet refers to the characteristic shape of the head, which is rolled upwards (*cephalus*, Latin form of the Greek *kephale*, + *flexus*, *-i* from the Latin). The gender is female.

Cephaloflexa bergi (Graff), comb. nov.

(Figs 1, 2)

Geoplana bergi Graff, 1899: 323, pl. 7, figs 18–19.
Choeradoplana iheringi Schirch, 1929: pl. 3, fig. 7; 37, fig. 9.
Geoplana meixneri Riester, 1938: 11, figs 7–9, pl. 1, fig. 3.
Geoplana bergi (?) Riester, 1938: 16, figs 13–15, pl. 1, fig. 5.
Geoplana bergi Marcus, 1951: 58, pl. 21, fig. 122; pl. 24, figs 155–159; pl. 39, figs 287–288.
Notogynaphallia bergi Ogren & Kawakatsu, 1990: 140.
Notogynaphallia meixneri Ogren & Kawakatsu, 1990: 142.

Material examined

São Paulo-SP, Brazil. Horto Florestal, Nr. 579B, coll. E. M. Froehlich and O. Françoso, 15.v.1985 (EMF): anterior tip, transverse section on five slides; pre-pharyngeal region, transverse sections on five slides; pharynx and copulatory apparatus, sagittal sections on 29 slides. Reserva Florestal da Cidade Universitária Armando de Sales Oliveira, Campus USP, Nr. 735, coll. C.M. Resende, 12.xi.1987 (MZUSP): anterior tip, transverse sections on 21 slides; ovaries, sagittal sections

on 18 slides; pre-pharyngeal region, transverse sections on 14 slides; pharynx and copulatory apparatus, horizontal sections on 40 slides. Região de Caboclos, Iporanga, Nr. 880, coll. P. Gnaspini, 2.x.1992 (EMF): anterior tip, transverse sections on seven slides. Parque do Jaraguá, Nr. 646, coll. M. Ramos and O. Françoso, 13.xi.1986 (EMF): anterior tip, transverse sections on eight slides; ovaries, sagittal sections on 24 slides; pre-pharyngeal region, transverse sections on six slides. Fazenda Intervales, Iporanga, Nr. 848, coll. S. Caramachi, 4.ii.1990 (EMF): copulatory apparatus, sagittal sections on 19 slides.

Diagnosis

Cephaloflexa up to 80 mm in length; dorsum orange, brownish, dark-greenish, greyish, or black, with or without a dark sagittal stripe; head black; eyes marginal; retractor muscle 1.4× thicker than ventral longitudinal cutaneous musculature in pre-pharyngeal region; CMI, 17–21%; no glandular margin; pharynx cylindrical, with dorsal insertion shifted posteriad; oesophagus : pharynx ratio, 25%; copulatory apparatus long; prostatic vesicle intrabulbar, proximal quarter paired; distal part of efferent ducts, intrabulbar; penis papilla absent; male and female atria folded; gonopore at level of middle third of female atrium; female atrium ciliated; male atrium twice as long as female atrium.

Description

External features

See Table 1 for measurements of fixed specimens. Creeping sole, 83–88% of body width (Table 2).

Head

Sensory pits: simple invagination, ~30 μm deep, absent on first 14–84 μm. *Eyes*: irregularly uniserial, absent on first 63–160 μm. *Cutaneous musculature*: different arrangement to that of pre-pharyngeal body region; ventral longitudinal cutaneous layer thickened anteriad, initially on sides, anteriorly near to sagittal plane to form retractor muscle, lenticular in cross-section, with edges separated from epidermis (Fig. 1); at maximum thickness, retractor with ~1000 fibres, weakly joined in bundles (specimen 735), 1.4× thicker than ventral cutaneous longitudinal in pre-pharyngeal region; just behind retractor (where body width twice that of region of retractor), ventral cutaneous longitudinal with ~1100 fibres (specimen 735) at level of retractor, other layers of cutaneous musculature very weak; close to anterior tip, number of retractor fibres diminishes, till extinction of retractor. *Mesenchymal musculature*: different arrangement to that of pre-pharyngeal body region; fibres of supra- and sub-intestinal mesenchymal layers scarce and obliquely placed towards ventral side; those of diagonal layer directed to body margins; some mesenchymal fibres joined in a sub-neural transverse layer; dorso-ventral fibres scarce. *Secretions*: openings of erythrophil, xanthophil and basiphil granulous secretory cells throughout entire body surface; erythrophil cell necks joined in bundles on ventral region; basiphil cells more numerous on dorsal region; numerous openings of rhabditogen cells through cutaneous surface, except on sensory border; body cells in mesenchyme, under cutaneous musculature, particularly abundant dorsally to retractor.

Table 1. Measurements (mm) of fixed specimens of *Cephaloflexa bergi*

DM: distance of mouth from anterior end; DMI: DM/body length; DG: distance of gonopore from anterior end; DGI: DG/body length.

	Specimen				
	579B	735	880	646	848
Length	53	57	30	55	51
Width	4.5	6	4	5	4.5
DM	35	43	24	35	31
DMI	66%	75%	80%	64%	61%
DG	44	50	Absent	45	40.5
DGI	83%	88%	–	82%	79%

Pre-pharyngeal region

Cutaneous musculature: circular subcutaneous layer, under which is a diagonal layer comprising decussate bundles, and under the diagonal layer, a longitudinal layer, also arranged in bundles; dorsal longitudinal cutaneous muscle, on average, ~1.5× thicker than ventral cutaneous muscle (Table 2). *Mesenchymal musculature*: muscle fibres arranged in all directions, but part of them united in three layers: a dorsal diagonal layer with decussate fibres, a supra-intestinal transverse layer, and a sub-intestinal transverse layer; sub-intestinal layer slightly more developed than supra-intestinal layer. *Secretions*: openings of basiphil and xanthophil secretory cells onto body surface of pre-

Table 2. Thickness of cutaneous musculature in the pre-pharyngeal region of *Cephaloflexa bergi*

Total thickness is given in μm and the lowest and highest numbers of muscle fibres in parentheses. CMI: cutaneous muscular index.

	Specimen		
	579B	735	646
Dorsal circular	4.3 (1–3)	4.3 (1–3)	2.2 (1–2)
Dorsal diagonal	15.2 (2–4)	15.2 (4–6)	6.5 (1–4)
Dorsal longitudinal	69.6 (59–83)	89.1 (70–86)	65.2 (70–82)
Dorsal total	86.9	108.7	73.9
Ventral circular	3.2 (2–4)	4.3 (1–3)	5.4 (1–3)
Ventral diagonal	18.5 (4–5)	21.7 (3–5)	18.5 (4–5)
Ventral longitudinal	54.3 (35–49)	54.3 (40–47)	41.3 (45–48)
Ventral total	76.1	76.1	65.2
CMI	17%	20%	21%
Creeping sole width : body width	86%	83%	88%

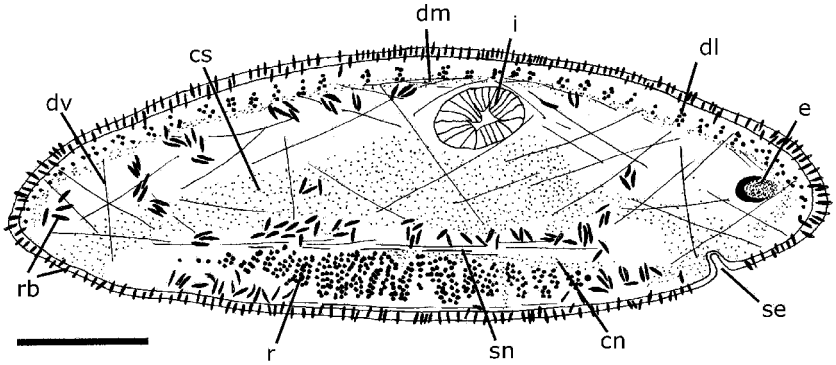


Fig. 1. *Cephaloflexa bergi*, comb. nov. Diagrammatic transverse section of the head region (specimen 909A). Scale bar: 0.1 mm. (cn, cutaneous nerve net; cs, central nervous system; dl, dorsal cutaneous longitudinal muscles; dm, diagonal mesenchymal muscles; dv, dorso-ventral mesenchymal muscles; e, eyes; i, instestine; r, retractory muscles; rb, rhabdoids; se, sensory pit; sn, sub-neural transverse mesenchymal muscles.)

pharyngeal region, former less frequent on dorsal surface than on margins and ventral surface; openings of erythrophil and rhabditogen cells throughout dorsal and lateral body regions, scarce on creeping sole. Cell glands not concentrated into glandular margin.

Digestive system

Mouth: DMI, 61–80% (Table 1), at end of middle third of pharyngeal cavity. *Pharynx*: cylindrical, with dorsal insertion posteriorly displaced, distally folded, 2.8 mm long (specimen 579B) or ~5% of body length. External and internal epithelia densely ciliated. Basiphil, xanthophil and erythrophil secretory cells open through distal region of pharynx. Outer musculature consists of longitudinal sub-epithelial layer (~6 μm), under which is another layer with crossed longitudinal and circular fibres (~100 μm thick). Inner musculature consists of thick subepithelial layer (~100 μm) with fibres circularly and longitudinally placed, with some inserted radial fibres. *Oesophagus*: folded walls; 0.25× pharynx length. Epithelium cubic ciliated. Musculature of a circular layer (70 μm thick), interposed with longitudinal fibres.

Male reproductive system

Testes: dorsal, pre-pharyngeal, between ovaries and root of pharynx; most anterior and posterior ones situated, in relation to anterior tip, at a distance equivalent to 37% and 67% of body length respectively (specimen 735). *Efferent ducts*: dorsal to nerve plate; increased in diameter near prostatic vesicle, thus forming spermiducal vesicles; at the level of prostatic vesicle, they extend anteriad and to sagittal plane, continue into common muscle coat, then open into paired branches of prostatic vesicle (Fig. 2). Epithelium ciliated. Muscularis of spermiducal vesicles with a layer of circular muscle fibres (15 μm thick). *Prostatic vesicle*: proximal region of the paired branches directed anteriorly, then curved postero-dorsally and subsequently joined to form an unpaired branch; the latter downwards directed, except for distal part, which is postero-dorsally curved. Epithelium columnar ciliated, higher in unpaired branch (~90 μm). Paired branches and proximal quarter of unpaired branch with xanthophil and basiphil granulous secretory cells. Distal three quarters of unpaired branch with openings of erythrophil and xanthophil granulous secretory cells,

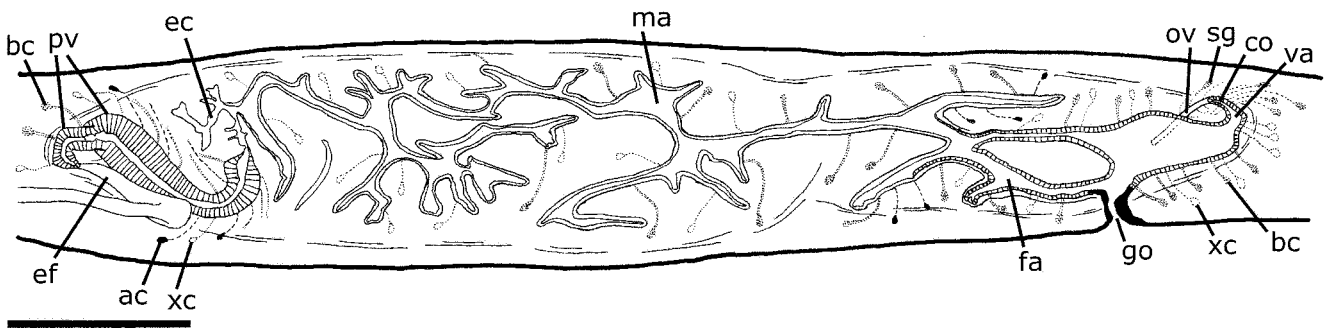


Fig. 2. *Cephaloflexa bergi*, comb. nov. Sagittal reconstruction of the copulatory apparatus (specimen 911). Scale bar: 1 mm. (ac, erythrophil secretory cells; bc, basiphil secretory cells; co, common glandular ovovitelline duct; ec, ejaculatory cavity; ef, efferent duct; fa, female atrium; go, gonopore; ma, male atrium; ov, ovovitelline duct; pv, prostatic vesicle; sg, shell glands; va, vagina; xc, xanthophil secretory cells.)

ventrally, and erythrophil and basiphil secretory cells, dorsally. Cell bodies of secretory cells mainly anterior to copulatory apparatus. Muscularis consists of circular fibres (maximum thickness ~80 μm). *Ejaculatory cavity*: large, with pleated walls, anterior to male atrium and dorsal to distal portion of prostatic vesicle. Epithelium columnar ciliated, with openings of scarce secretory cells with short necks and ill-defined staining properties, possibly xanthophil. Muscularis consists of circular fibres (~80 μm thick). *Male atrium*: long, divided into two regions, proximal half with abundant small folds and openings of xanthophil secretory cells, and distal half with large folds and openings of xanthophil and basiphil secretory cells; towards female atrium, openings of basiphil cells more abundant, xanthophil cells scarcer. Epithelium cubic non-ciliated. Muscularis consists of dense circular subepithelial layer (~8 μm thick) and subjacent longitudinal layer (~32 μm).

Female reproductive system

Ovaries: 160 μm long and 25 μm high, dorsally to nerve plate and at a distance from anterior end equivalent to 34% of body length. *Ovovitelline ducts*: dorsal to nerve plate and ventral to efferent ducts; emerge dorsally from median third of each ovary; at level of gonopore, curve dorso-medially. Last ascending third with openings of shell glands. *Common glandular ovovitelline duct*: short (Fig. 2), posteriad directed, dorsal to female atrium, with openings of shell glands. *Vagina*: short and wide, dorso-anteriorly directed and communicating with proximal region of female atrium. Epithelium pseudo-stratified, non-ciliated, with openings of xanthophil granular secretory cells. *Female atrium*: elongated, with gonopore in mid third (Fig. 2); anterior to gonopore, rather spacious but narrower posteriorly. Epithelium columnar (~20 μm) ciliated, xanthophil on its apical half. Openings of xanthophil and basiphil secretory cells, the latter more numerous on ventral epithelium and towards male atrium. Openings of erythrophil secretory cells through epithelium of transition region of male-female atria. Muscularis of circular subepithelial coat (6 μm) and a subjacent longitudinal (11 μm). Female atrium length, half that of male.

Common muscle coat

Distal portion of efferent ducts, prostatic vesicle, male and female atria and vagina enveloped by muscle coat. Layer of longitudinal and circular fibres, 10 μm thick in proximal region of male atrium; at female atrium, fibres scarcer.

Remarks

In general, the description of *Cephaloflexa bergi* presented here agrees with accounts by other authors. This species was originally described as *Geoplana bergi* Graff (1899). Riester (1938), Marcus (1951), and C. G. Froehlich (1955, 1956) all redescribed the species, and the latter two authors included *Geoplana meixneri* and *G. bergi* (?) sensu Riester in the synonym list of *Geoplana bergi*. *Geoplana meixneri* and *G. bergi* were later transferred by Ogren and Kawakatsu (1990) to the genus *Notogynaphallia*. Although, in the original description of *Cephaloflexa bergi*, there is no mention of the rolling up of the cephalic region, the animals present a narrow form of the cephalic region and an absence of eyes in the apex, which are diagnostic characteristics of *Cephaloflexa*. Besides this, the pharynx and the copulatory apparatus are very similar to those of *Cephaloflexa bergi*, varying only in details. Therefore, we maintain the synonymy proposed by Marcus (1951).

In contrast, the two specimens of *G. bergi* (?) analysed by Riester (1938) had an unpaired prostatic vesicle, differing from the material analysed by Marcus (1951), as well as that studied here. A possible explanation is the fact that one of Riester's specimens (790/1914) was in an initial phase of maturation, and the second specimen (67/1929), apparently mature, was perhaps not completely mature. In two species of *Geoplana*, *G. polyophthalma* Graff, 1899 and *G. josefi*, the paired portion of the prostatic vesicle is considerably smaller in incompletely mature specimens than in mature animals (Froehlich 1956; F. Carbayo, personal observation). Riester (1938) compared the external morphology of his specimens with those of Graff. In relation to the character of the prostatic vesicle, *G. meixneri* is similar to the material examined here in that the proximal seminal vesicle is paired.

Cephaloflexa araucariana, sp. nov.

(Figs 3–8)

Material examined

Holotype. National forest of São Francisco de Paula-RS, Brazil, 930 m, under a fallen log. Nr. 238, coll. A.M. Leal-Zanchet, 3.iv.1998 (MZUSP): anterior tip, transverse sections on 18 slides; sub-anterior tip, sagittal sections on 20 slides; pre-pharyngeal region, transverse sections on seven slides; pharynx, sagittal sections on 13 slides; copulatory apparatus, sagittal sections on 18 slides.

Paratypes. For all paratypes, same locality as holotype. Nr. 218, coll. F. Carbayo, 3.iii. 1998 (MZU): anterior tip, transverse sections on five slides; pre-pharyngeal region, transverse sections on five slides; pharynx and copulatory apparatus, horizontal sections on 12 slides. Nr. 437, coll. F. Carbayo, 25.ix.1998 (MZUSP): preserved in 70% ethanol. Nr. 443, coll. F. Carbayo, 9.x.1998 (MZU): anterior body half, horizontal sections on 10 slides; posterior body half, horizontal sections on 21 slides. Nr. 505, coll. F. Carbayo, 25.xi.1998 (MZU): preserved in clove oil. Nr. 521, coll. F. Carbayo, 16.xii.1998 (MZU): whole specimen, sagittal sections on nine slides. Nr. 529, coll. F. Carbayo, 21.xii.1998 (MZU): anterior tip, sagittal sections on 17 slides; sub-anterior tip, sagittal sections on five slides; pre-pharyngeal region, transverse sections on 13 slides; pharynx, sagittal sections on 20 slides; copulatory apparatus, sagittal sections on 17 slides. Nr. 530, coll. F. Carbayo, 21.xii.1998 (MZU): whole specimen, horizontal sections on 14 slides. Nr. 619, coll. F. Carbayo, 23.ii.1999 (MZU): pre-pharyngeal region, transverse sections on three slides; pharynx and copulatory apparatus, sagittal sections on 11 slides. Nr. 651, coll. M. Cardoso, 23.iii.1999 (MZUSP): pre-pharyngeal region, transverse

sections on five slides; pharynx and copulatory apparatus, sagittal sections on 16 slides. Nr. 701, coll. F. Carbayo, 30.v.1999 (MZU): pre-pharyngeal region, transverse sections on eight slides; pharynx and copulatory apparatus, sagittal sections on 16 slides.

Diagnosis

Cephaloflexa of a small–medium size, 40–45 mm long; back bluish-grey with two black lateral bands; retractor muscle twice as thick as ventral longitudinal cutaneous musculature in pre-pharyngeal region; CMI, 7–14%; no glandular margin; pharynx cylindrical, with dorsal insertion posteriorly displaced; oesophagus:pharynx ratio variable, 33–66%; distal portion of intrabulbar efferent ducts receiving erythrophil secretions; intrabulbar prostatic vesicle with paired branches and one unpaired branch of approximately the same length; paired branches with erythrophil secretions; penis papilla absent; male atrium folded; female atrium short, non-ciliated; gonopore between female and male atria; male atrium eight times as long as female atrium.

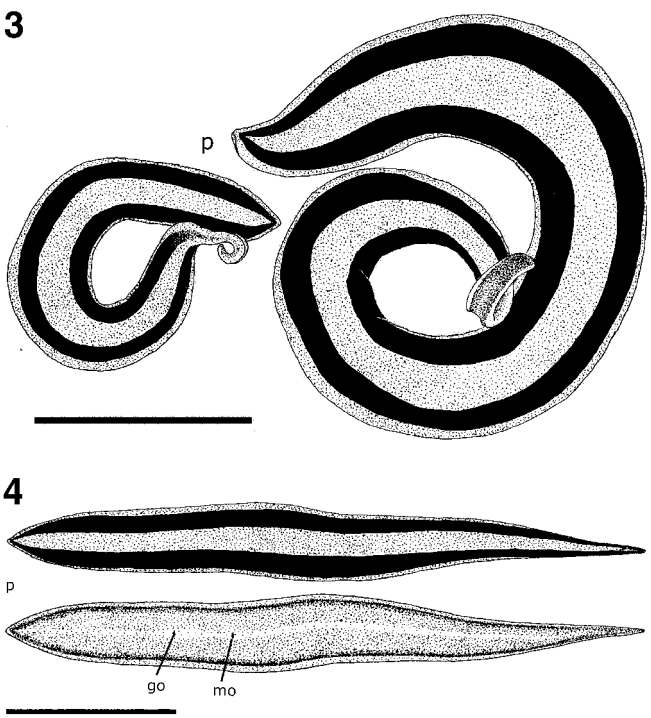
Description

External features

Shape: up to 45 mm in maximum extension (Table 3). Body sub-cylindrical, wider in pharynx region; posterior end obtuse, anterior pointed (Figs 3,4). In life, anterior tip permanently rolled towards dorsal surface (Fig. 3), ventral side slightly concave. *Colour pattern*: Back bluish-grey, with two black lateral bands (~1/4 of body width) separated by a light grey stripe of about same width as bands. Ventral surface dark grey, becoming black near margins and on anterior 1/8 of body (Fig. 4). Thin, pale median stripe (1/9 of body width), a little wider in mouth and gonopore regions, and absent on anterior 1/8 of body. In animals fixed with neutral formaldehyde, bluish-grey colour becomes grey, ventral surface flat in anterior region. *Eyes*: monolobated, 20–30 μm in diameter and without halos; all along body margin, except for apex, where absent; number of eyes gradually diminishes towards posterior end. *Creeping sole*: 73–84% of body width in pre-pharyngeal region (Table 4); anteriad narrower than body, disappearing before reaching apex (Fig. 14*e*).

Head

Sensory pits: simple invagination, ~20 μm deep, on anterior quarter of body, but absent on first 60 μm (holotype) or 72 μm (paratype 218). *Eyes*: absent in first ~260 μm of body (holotype and paratype 218). *Cutaneous musculature*: as in *Cephaloflexa bergi*, but more developed (Fig. 5); thickness of retractor muscle twice that of ventral longitudinal cutaneous musculature in pre-pharyngeal



Figs 3–4. *Cephaloflexa araucariana*, sp. nov. *3*, Dorsal view of two living specimens. Scale bar: 5 mm. *4*, Dorsal and ventral views of the holotype. Scale bar: 10 mm. (go, gonopore; mo, mouth; p, posterior end of the body.)

Table 3. Measurements (mm) of type specimens of *Cephaloflexa araucariana*

?: not measured; *: after fixation; DG: distance of gonopore from anterior end; DGI: DG/body length; DM: distance of mouth from anterior end; DMI: DM/body length.

	Specimen										
	218	Holotype	437	443	505	521	529	530	619	651	701
Maximum length in extension	40	45	?	41	40	27	45	30	40	40	40
Length at rest	23	30	14	14	25	13	20	14	18	17	20
Maximum width in extension	1.5	3–4	?	2	3.5	1.75	2.5	2.5	2	2	2.5
Maximum width at rest	3	6	?	4.5	4	2.5	5	4	4	4.5	3.5
Length*	25	38	21	28	31	15	31	16	24	23	27
Width*	1.5	4.5	3	2	3	2.75	3.5	3.5	4	3.5	4
DM*	19	23	12	17	20	11	19	11.5	15	14	17
DMI*	76%	60%	57%	61%	64%	73%	62%	72%	62%	61%	63%
DG*	22	27	15	21	25	12.5	22.5	13	18	16.5	20.5
DGI *	88%	71%	72%	75%	81%	83%	72%	81%	75%	72%	76%

Table 4. Thickness of cutaneous musculature in the pre-pharyngeal region of *Cephaloflexa araucariana*
Total thickness is given in μm and the lowest and highest numbers of muscle fibres in parentheses. ?: not visible on sections; CMI: cutaneous muscular index.

	Specimen					
	218	Holotype	529	619	651	701
Dorsal circular	2.2	4.3	4.3	2.2	4.3	4.3
	(?)	(1–3)	(2–3)	(1–2)	1–3)	(1–2)
Dorsal diagonal	6.5	6.5	6.5	10.9	10.9	10.9
	(?)	(3–5)	3–4)	(4–6)	(3–5)	(6–8)
Dorsal longitudinal	26.1	32.6	47.8	47.8	50	56.5
	(25–30)	(26–42)	(52–85)	(49–66)	(30–54)	(42–68)
Dorsal total	34.8	43.5	58.7	60.9	65.2	69.6
Ventral circular	2.2	4.3	4.3	4.3	6.5	2.2
	(?)	(1–3)	(2–4)	(2–4)	(1–3)	(1–3)
Ventral diagonal	6.5	6.5	6.5	10.9	15.2	6.5
	(?)	(3–5)	(3–5)	(4–8)	(4–6)	(3–4)
Ventral longitudinal	21.8	34.8	39.1	34.8	32.6	34.8
	(26–28)	(26–34)	(31–69)	(30–36)	(36–42)	(46–66)
Ventral total	30.4	45.6	50	50	54.3	43.5
CMI	11%	7%	12%	14%	14%	12%
Creeping sole width : body width	84%	?	78%	73%	78%	83%

region; retractor muscle consists of muscle bundles, each bundle with 45–60 fibres. *Mesenchymal musculature*: similar to that of *C. bergi*. *Secretions*: openings of erythrophil secretory cells onto dorsal and ventro-lateral surface; openings of basiphil secretory cells most abundant onto ventral surface through bundles of parallel cell necks.

Pre-pharyngeal region

Cutaneous musculature (Table 4): as in *Cephaloflexa bergi*; dorsal longitudinal layer, on an average, 1.3 times thicker than ventral; CMI, 11–14% (but 7% in holotype, which may be a result of contraction at the time of fixation) (Table 4). *Mesenchymal musculature*: muscle fibres in all directions, but some grouped together in a dorsal diagonal layer, with crossed fibres, and two transverse supra- and sub-intestinal layers, the latter more developed (Fig. 6). *Secretions*: xanthophil and basiphil secretory cells with openings onto dorsal and ventral body surfaces, xanthophil more abundant dorsally, basiphil ventrally; erythrophil and rhabditogen cells with openings onto dorsal surface and body margins, the latter more abundant dorsally. Gland cells not concentrated into glandular margin.

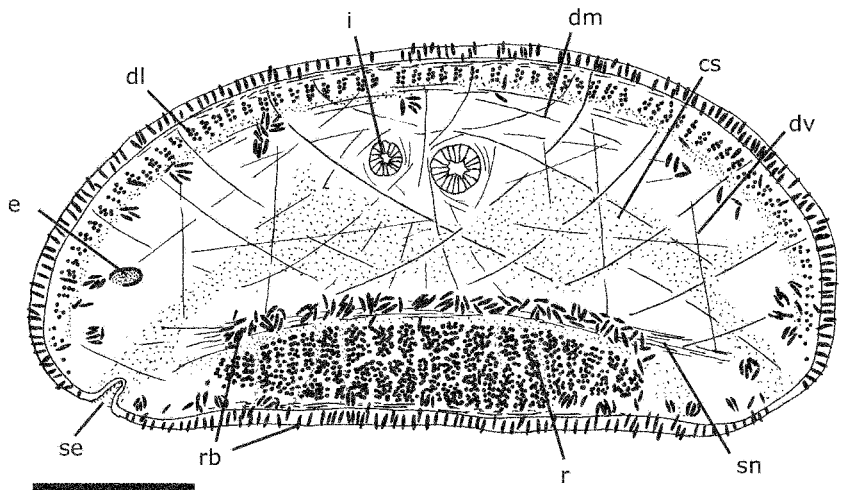


Fig. 5. *Cephaloflexa araucariana*, sp. nov. Diagrammatic transverse section of head region (holotype). Scale bar: 0.1 mm. (cs, central nervous system; dl, dorsal cutaneous longitudinal muscles; dm, diagonal mesenchymal muscles; dv, dorso-ventral mesenchymal muscles; e, eyes; i, intestine; r, retractor muscles; rb, rhabdoids; se, sensory pit; sn, sub-neural transvers mesenchymal muscles.)

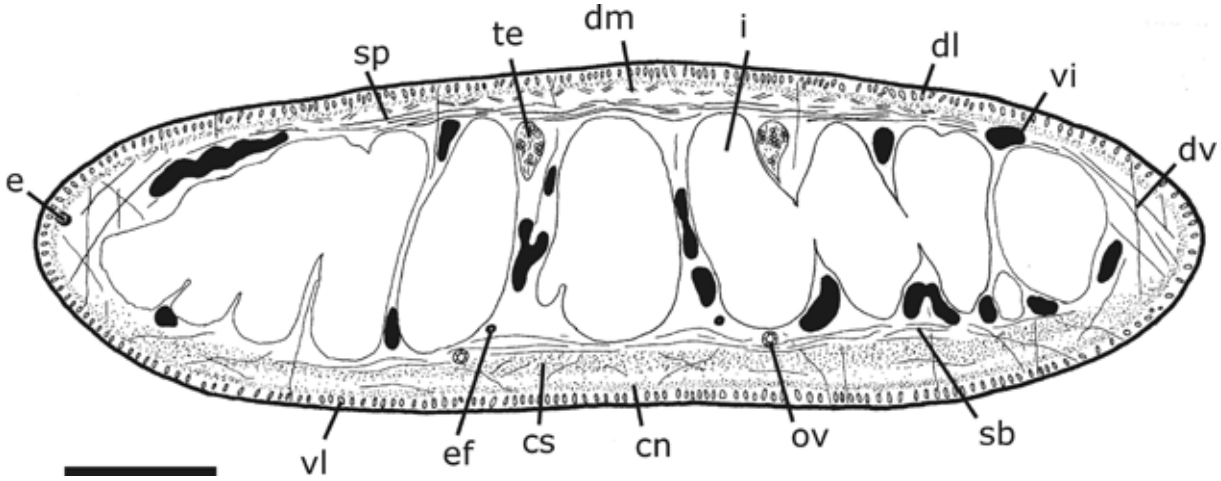


Fig. 6. *Cephaloflexa araucariana*, sp. nov. Diagrammatic transverse section of the pre-pharyngeal region (holotype). Circular and diagonal cutaneous muscle layers are omitted. Scale bar: 0.5 mm. (cs, central nervous system; cn, cutaneous nerve net; dl, dorsal cutaneous longitudinal muscles; dm, diagonal mesenchymal muscles; dv, dorso-ventral mesenchymal muscles; e, eyes; ef, efferent duct; i, intestine; ov, ovovitelline duct; sb, sub-intestinal transverse mesenchymal muscles; sp, supra-intestinal transverse mesenchymal muscles; te, testes; vi, vitellaria; vl, ventral cutaneous longitudinal muscles.)

Digestive system

Mouth: DMI, 57–76% (Table 3); approximately located in middle third of pharyngeal cavity (Fig. 7). Epithelium of mouth canal apically erythrophil. *Pharyngeal cavity*: epithelium squamous to cubic, ciliated near dorsal insertion of pharynx. Muscularis of three layers, thin longitudinal subepithelial, followed by a circular and a diagonal. *Pharynx*: cylindrical, with dorsal insertion posteriorly displaced; ~l.5 mm long, or 4–5% of body length (Fig. 7); distally with numerous folds, lumen wall strongly pleated. External and internal epithelia cubic ciliated. Xanthophil, erythrophil and basiphil granular secretory cells, with cell bodies external to pharynx and openings onto apical surface. Outer musculature consists of thin longitudinal subepithelial layer under which is a thicker circular layer with crossed longitudinal fibres. Inner musculature of thick circular layer (~90 μm), with sparse crossed longitudinal fibres. Oesophagus : pharynx ratio, 33–66%. In two specimens, posterior branches of intestine connected by fine diverticulum behind copulatory apparatus.

Male reproductive system

Testes: dorsal, pre-pharyngeal, in an irregular row on each side of body (Fig. 6), between ovaries and esophagus; most anterior and posterior testes are located, in relation to anterior end, at 34% and 63% of body length, respectively

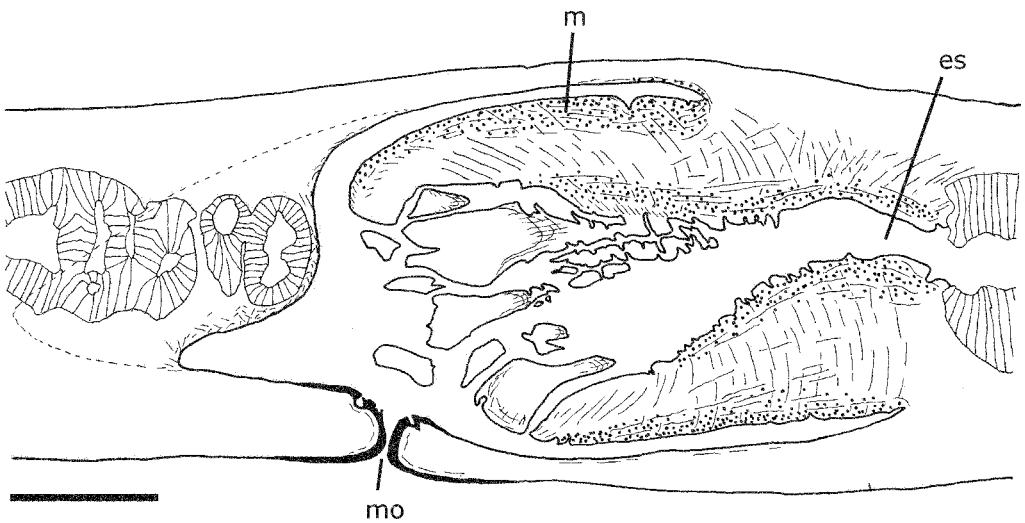


Fig. 7. *Cephaloflexa araucariana*, sp. nov. Sagittal reconstruction of the pharynx (holotype). Scale bar: 0.5 mm. (es, oesophagus; i, intestine; m, muscles; mo, mouth.)

(holotype) or 28% and 57%, respectively (paratype 529). *Efferent ducts*: dorsal to nerve plate; at prostatic vesicle level, curved anteriad and to sagittal plane, penetrating lateroventrally into penis bulb (Fig. 8). Epithelium cubic; intrabulbar portion with openings of erythrophil secretory cells. Muscularis of circular fibres (~8 μm thick). *Prostatic*

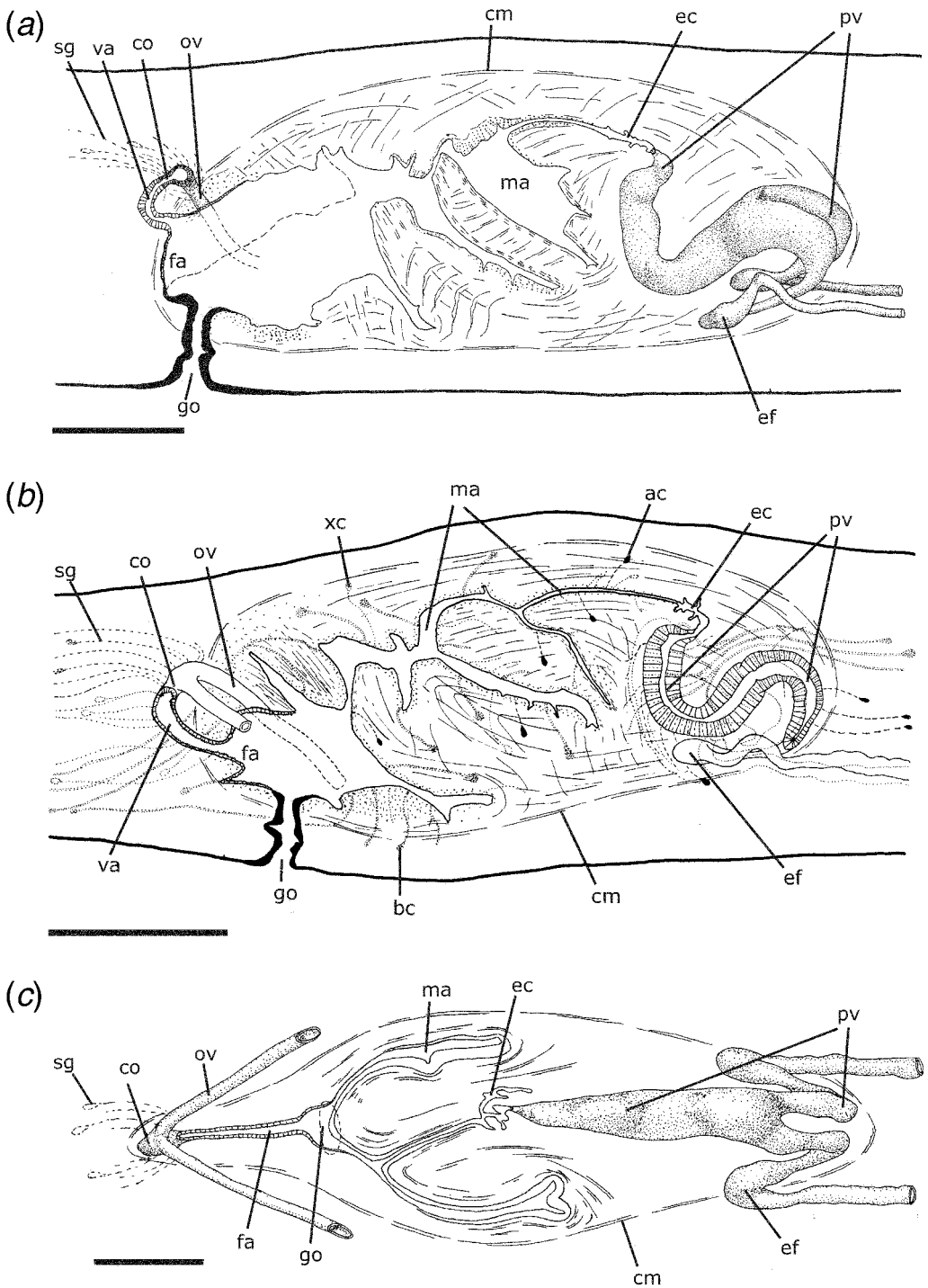


Fig. 8. Copulatory apparatus of *Cephaloflexa araucariana*, sp. nov. Sagittal reconstruction from (*a*) the holotype; and (*b*) paratype (429). Scale bar: 0.5 mm. (*c*) Horizontal reconstruction (paratype 443). Scale bar: 0.25 mm. (ac, erythrophil secretory cells; bc, basiphil secretory cells; cm, common muscle coat; co, common glandular ovovitelline duct; ec, ejaculatory cavity; ef, efferent duct; fa, female atrium; go, gonopore; ma, male atrium; ov, ovovitelline duct; pp, penis papilla; pv, prostatic vesicle; sg, shell glands; va, vagina; xc, xanthophil secretory cells.)

vesicle: intrabulbar, sinuous on sagittal plane; paired proximal branches, each one with shape of inverted U; unpaired distal half U-shaped. Epithelium tall columnar ciliated, with the maximum height in unpaired portion (~30–55 μm). Erythrophil secretory cells open into prostatic vesicle, more abundant on paired branches; ventral wall of unpaired part also with openings of xanthophil secretory cells, dorsal wall with openings of basiphil secretory cells; cell bodies of secretory cells of efferent ducts and vesicle situated anteriorly to penis bulb. Muscularis: circular layer (~45 μm thick). *Ejaculatory cavity*: pleated, opening into dorsal proximal part of male atrium. Epithelium cubic ciliated with openings of abundant secretory cells with ill-defined staining properties. Muscularis of crossed longitudinal and circular fibres (~15 μm thick). *Male atrium*: male and female atria come together at gonopore (Fig. 8*a*, *b*); lengthened cavity with folded wall; proximal half with large ventral folds occupying greater part of cavity, distal half with smaller folds (Fig. 8*a*, *b*); proximal half presents the function of eversible penis papilla, which is more apparent in horizontal sections (Fig. 8*c*). Epithelium cubic non-ciliated. Proximal half with abundant openings of amorphous xanthophil and granulous erythrophil secretory cells. Distal half with abundant openings of basiphil secretory cells, and less frequent, xanthophil and erythrophil cells. Muscularis of subepithelial circular layer (10–22 μm), followed by a longitudinal layer (20–45 μm).

Female reproductive system

Ovaries: elongated (0.1 × 0.6 mm); placed ventrally to sub-intestinal transverse mesenchymatic muscle layer and dorsally to nerve plate; in relation to anterior body end, at 34% (holotype) or 26% (paratype 529) of body length. *Ovovitelline ducts*: dorsal to nerve plate; emerge laterally from middle third of ovaries; anterior to gonopore, dorso-medially curved. Epithelium columnar ciliated. Distal portion with shell glands. *Common glandular ovovitelline duct*: short; dorsal to female atrium (Fig. 8). Epithelium columnar ciliated, with openings of shell glands. *Vagina*: dorso-anteriorly directed until posterior wall of female atrium. Epithelium columnar non-ciliated with irregular surface and openings of xanthophil secretory cells. *Female atrium*: small, laterally narrow (Fig. 8*c*), anatomically indistinguishable from distal portion of male atrium. Epithelium columnar non-ciliated with irregular surface. Xanthophil and abundant basiphil secretory cells. Muscularis (~10 μm thick) of a circular subepithelial layer, followed by a longitudinal layer. Female atrium length, 1/8 that of male.

Common muscular coat

Distal portion of efferent ducts, prostatic vesicle, vagina and male and female atria enveloped by coat consisting of a compact muscle layer. Layer, 10–20 μm thick (in proximal region of male atrium), of crossed diagonal fibres, followed by a thin circular layer; in distal region of female atrium, with fibres scattered.

Habitat and biology

The animals were collected from beneath fallen logs and amongst leaf litter in the National Forest of São Fransisco de Paula, RS, Brazil. Habitats included areas of native ombrophilous forest with and without *Araucaria angustifolia*, and reforested areas with *A. angustifolia*. Specimen 529 was found feeding on an individual of Gonyleptidae (Opiliones : Laniatores).

Remarks

Cephaloflexa araucariana is externally distinguished from *Cephaloflexa bergi* by its smaller size (30–45 mm of maximum length) and characteristic colour pattern. In addition, the retractor is proportionally more developed; the copulatory apparatus is more compact in relation to that of *Cephaloflexa bergi*, the female atrium being very short; the paired and unpaired branches of the prostatic vesicle are approximately of the same length; erythrophil secretory cells open into the paired portions of the prostatic vesicle; erythrophil and xanthophil secretory cells open into the male atrium throughout its surface, as well as basiphil cells into the distal 2/3; the female atrium is not ciliated; the vagina has a cylindrical epithelium; and the male and female atria come together at the level of the gonopore.

Etymology

The specific epithet refers to *Araucaria angustifolia* (Bert.) Kuntze, the most common tree of the region.

Genus ***Supramontana***, gen. nov.

Type species: *Supramontana irritata*, sp. nov.

Definition

Long and wide-bodied Geoplaninae, with parallel margins. Back and ventral side flat-convex; creeping sole wide; eyes and sensory pits surround entire cephalic region; without glandular cushions; cephalic region with ventral longitudinal cutaneous musculature modified into a retractor muscle, sunk into mesenchyme, dissipating at anterior end in bundles running towards margins of body; throughout body length. Ventral longitudinal cutaneous musculature in two layers; one at usual position and another sunk into mesenchyme, internal to cutaneous nerve plexus; CMI, 16–21%. Longitudinal mesenchymal musculature absent. Penis papilla present; male atrium poorly folded; common glandular ovovitelline duct, dorsal to female atrium. Female canal (vagina) as a dorso-anteriorly directed diverticulum of female atrium. Sensory papillae and adenodactyls absent.

Locality

State of Rio Grande do Sul, Brazil.

Etymology

The generic name (from the Latin, *supra* + *montanus*) is a reference to the former name of the city (São Francisco de Cima da Serra). The gender is female.

Supramontana irritata, sp. nov.

(Figs 9–14)

Material examined

Holotype. National forest of São Francisco de Paula-RS, Brazil, 930 m, under a fallen log. Nr. 164, coll. A.M. Leal-Zanchet, 11.xii.1997 (MZUSP): pharyngeal region, transverse sections on six slides; pharynx, sagittal sections on 17 slides; copulatory apparatus, sagittal sections on 21 slides.

Paratypes. For all paratypes, same locality as holotype. Nr. 119, coll. L. Dornelles, 1.ix.1997 (MZU): anterior tip, transverse sections on five slides; copulatory apparatus, sagittal sections on 11 slides. Nr. 190, coll. A.M. Leal-Zanchet, 14.i.1998 (MZU): pre-pharyngeal region, transverse sections on nine slides; copulatory apparatus, horizontal sections on 15 slides. Nr. 197, coll. F. Carbayo, 14.i.1998 (MZU): preserved in 70% ethanol. Nr. 486, coll. T. Fleck, 25.xi.1998 (MZUSP): Anterior tip, transverse sections on 10 slides. Nr. 575, coll. A.L. Seitenfus, 26.i.1999 (MZUSP): preserved in 70% ethanol. Nr. 586, coll. I.A. Fick, 11.ii.1999 (MZU): pre-pharyngeal region, transverse sections on five slides; pharynx and copulatory apparatus, sagittal sections on 51 slides. Nr. 652, coll. M. Cardoso, 23.iii.1999 (MZU): anterior tip, sagittal sections on 52 slides; pre-pharyngeal region, transverse sections on 6 slides; pharynx, sagittal sections on 25 slides; copulatory apparatus, sagittal sections on 24 slides. Nr. 733, coll. I.A. Fick, 11.ii.1999 (MZU): preserved in clove oil. Nr. 893, coll. F. Carbayo, 14.ix.1999 (MZU): pre-pharyngeal region, transverse sections on five slides; pharynx and copulatory apparatus, sagittal sections on 29 slides. Nr. 906, coll. F. Carbayo, 14.x.1999 (MZU): anterior tip, sagittal sections on four slides.

Diagnosis

Supramontana up to 11 cm long; back and ventral side plane-convex; CMI, 16–21%; no glandular margin; pharynx bell-shaped; efferent ducts open laterally into proximal region of prostatic vesicle; prostatic vesicle horizontal, extrabulbar, with erythrophil secretions; common glandular ovovitelline duct long, dorsal to female atrium and posteriad directed; vagina with ciliated epithelium; female atrium with pluristratified epithelium; male atrium twice as long as female.

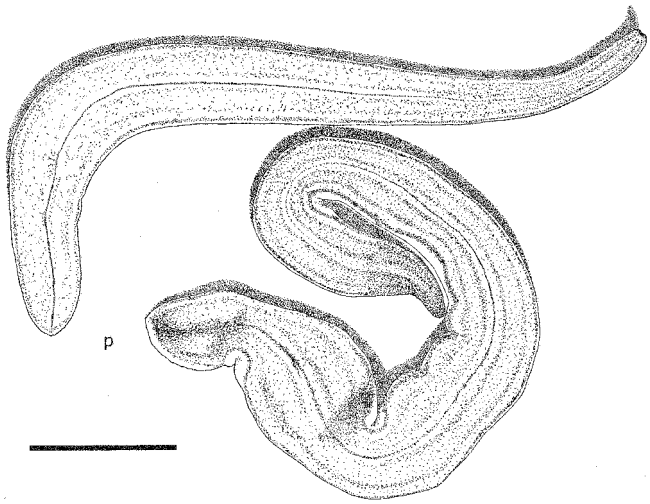


Fig. 9. *Supramontana irritata*, sp. nov. Dorsal view of a living specimen. Scale bar: 10 mm. (p, posterior end of body.)

Description

External features

Shape: body elongated, up to 11 cm (maximum length on extension) (Table 5), with parallel margins, back and ventral side plane-convex; body wider in pharyngeal region, narrowing towards ends, anterior tip rounded and posterior obtuse (Fig. 9); when creeping, anterior end with inverted 'U' shape in cross-section; for locomotion, they stretch body forwards, fix anterior tip onto substratum and contract posterior region, to complete the cycle. When stimulated, they advance nervously and quickly, more so than usual in

Table 5. Measurements (in mm) of type specimens of *Supramontana irritata*

*: After fixation; DG: distance of gonopore from anterior end; DGI: DG/body length; DM: distance of mouth from anterior end; DMI: DM/body length.

	Specimen										
	190	486	652	586	893	575	733	Holotype	197	906	119
Maximum length in extension	105	85	110	55	60	85	90	90	75	56	37
Maximum width in extension	4.5	6	4	4.5	2.5	4	5	3.5	3	3	2
Length at rest	59	45	43	–	30	60	45	65	34	28	?
Width at rest	7	10	6	–	6	6	7	6	5	5	?
Length*	70	58	55	54	54	53	52	52	38	34	21
Width*	6.5	6	6	6.5	4	7	7	4	5	4	3.25
DM*	39	32	34	30	36	29	32	34	23	23.5	13
DMI*	56%	55%	62%	56%	67%	55%	62%	65%	61%	69%	62%
DG*	51	44	44	41	45	40	42	43	29	28.5	16
DGI*	73%	76%	80%	76%	83%	75%	81%	83%	76%	84%	76%

Geoplanidae. *Colour pattern*: dorsal side (Fig. 9) of straw-yellow background, brownish on anterior 1/8; with distinct narrow dark brown stripe (1/20 of body width) that dissolves on 1/5 anterior of body and continues until posterior end. Spots dark brown dispersed onto dorsum, progressively scarcer towards posterior end, besides spots gathered together to form three pairs of irregular bands (1/10 of body width), para-median, lateral and para-marginal, varying in intensity among specimens. Para-median and para-marginal bands usually more visible than lateral. In some specimens lateral bands sparser, whereas in others particularly dense. Ventral side of whitish-yellow colour, ochre on edges of anterior body third. *Eyes*: without light halos; anteriorly (1/15 of body length) irregularly uniserial and marginal; further back, spread to both sides of dorsal surface, over an area equal to 2/5 body width; scarcer towards posterior end, but maintaining this same position. Biggest (~43 μm in diameter) at anterior end of body; in pre-pharyngeal region, some ventral, at a distance from margin equal to 1/16 body width. *Creeping sole*: 86–88% of body width in pre-pharyngeal region (Table 6); towards anterior end, tapers more rapidly than body width, until disappearing at approximately 0.5 mm before tip (Fig. 14*a*).

Head

Sensory pits: simple invagination, 13 μm deep, surrounding whole cephalic region. *Eyes*: contouring anterior tip. *Cutaneous musculature*: position different from that of pre-pharyngeal region; ventral longitudinal cutaneous subdivided in two portions, one at usual position and another internal sunk in mesenchyme, transformed in a retractor muscle, irregularly lenticulate in cross-section (Fig. 10). Towards anterior tip, both portions of ventral longitudinal layers concentrate in median region, with external portion of ventral longitudinal layer more outstanding. Musculature progressively occupies less width in relation to that of body and near apex, with fibres gradually detached from epidermis but keeping position in relation to cutaneous nerve plexus. Further anteriorly, bundles of this musculature extend to body margins, disappearing a little before anterior end. Layers of diagonal and circular cutaneous musculature diminish in thickness towards anterior tip. *Mesenchymal musculature*: as intestine becomes less apparent, fibres of transverse and diagonal mesenchymal muscle layers become dorso-ventral. Fibres of sub-neural transverse layer direct to dorsal edges on transverse plane, disappearing at anterior tip. Dorso-ventral fibres scarce. *Secretions*: openings of basiphil secretory cells onto all body surface, more abundant dorsally; openings of xanthophil cells onto dorsal epidermis, abundant towards margins and scarce onto creeping sole; openings of rhabditogen cells scarce onto dorsal epidermis and abundant onto creeping sole. In retractor region, cell bodies between retractor muscle and sub-neural transverse mesenchymal musculature.

Pre-pharyngeal region

Cutaneous musculature (Table 6): circular subepithelial, followed by a diagonal layer with decussate bundles, and

Table 6. Thickness of cutaneous musculature in the pre-pharyngeal region of *Supramontana irritata*
Total thickness is given in μm and the lowest and highest numbers of muscle fibres in parentheses. ?: not visible on sections; *muscle bundles not defined; CMI: ratio of the height of subcutaneous musculature to the height of the body; NSVL: not sunk ventral longitudinal; SVL: sunk ventral longitudinal.

	Specimen			
	Holotype	586	652	893
Dorsal circular	2.2	2.2	2.1	2.2
	(1–2)	(1–2)	(1–2)	(1–2)
Dorsal diagonal	15.2	8.7	13.0	13.0
	(3–6)	(2–4)	(2–3)	(2–3)
Dorsal longitudinal	58.7	45.6	52.0	45.6
	(45–66)	(23–43)	(38–64)	(25–56)
Dorsal total	76.1	56.5	67.4	58.7
Ventral circular	4.3	2.2	4.3	2.2
	(2–3)	(1–2)	(1–2)	(1–2)
Ventral diagonal	15.2	13.0	32.6	13.0
	(5–7)	(2–6)	(3–6)	(2–5)
SVL	102.2	65.2	84.5	43.5
	(20–40)	(*)	(73–75)	(24–48)
NSVL	32.6	23.9	63.0	17.4
	(14–25)	(*)	(26–38)	(18–30)
SVL + NSVL	150.0	97.8	156.5	73.9
Ventral total	170.0	115.2	189.1	89.1
CMI	18%	21%	20%	16%
Creeping sole width : body width	88%	86%	86%	?

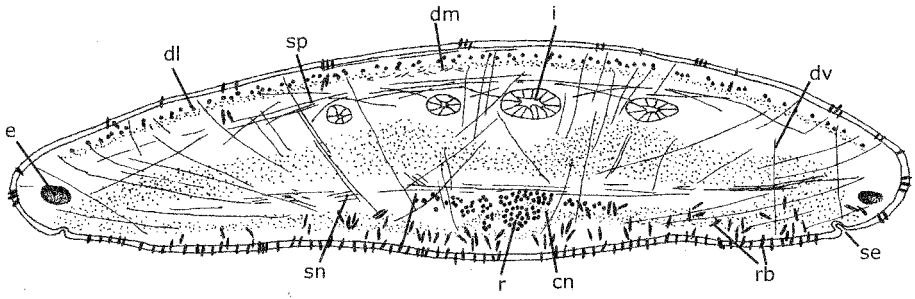


Fig. 10. *Supramontana irritata*, sp. nov. Diagrammatic transverse section of head region (paratype 486). Scale bar: 0.25 mm. (cn, cutaneous nerve net; dl, dorsal cutaneous longitudinal muscles; dm, diagonal mesenchymal muscles; dv, dorso-ventral mesenchymal muscles; e, eyes; i, intestine; r, retractor muscles; rb, rhabdoids; se, sensory pit; sn, sub-neural transverse mesenchymal muscles; sp, supra-intestinal transverse mesenchymal muscles.)

another internal longitudinal layer with fibres in bundles; the latter, well developed in ventral region and subdivided into two portions, one dorsal to cutaneous nerve plate. Towards body margins, cutaneous musculature diminishes in thickness to extinction. Ventral longitudinal layer ~2.3× thicker than dorsal (probably responsible for the quick movement of animal when excited). CMI, 16–21% (Table 6). *Mesenchymal musculature*: diagonal dorsal layer, with decussate fibres, between cutaneous nerve plate and supra-intestinal layer; three transverse layers, namely, supra-intestinal, sub-intestinal and sub-neural (Fig. 11). *Secretions*: openings of basiphil and xanthophil secretory cells onto all body surface, the latter more abundant on body margins. Openings of rhabditogen cells onto dorsal epidermis and, more abundantly, on body margins. Without a typical glandular margin.

Digestive system

Mouth: DMI, 55–69% (Table 5), approximately located in anterior third of pharyngeal cavity (Fig. 12). *Pharyngeal cavity*: epithelium non-ciliated, cubic to squamous. Muscularis (15μm thick) of thin longitudinal subepithelial layer, followed by a circular layer and another of crossed diagonal fibres. *Pharynx*: bell-shaped (Fig. 12), ~1.5 mm long, dorsal insertion posterior to mouth; distally with many folds. External and internal epithelia cubic and densely ciliated. Openings of xanthophil, erythrophil and basiphil granulous secretory cells, with cell bodies external to pharynx, onto apical surface of pharynx. Outer musculature (25 μm thick), thin subepithelial longitudinal layer followed by thicker circular layer, interposed with longitudinal fibres. Inner musculature, subepithelial circular layer (40 μm maximum thickness), followed by longitudinal layer (5 μm).

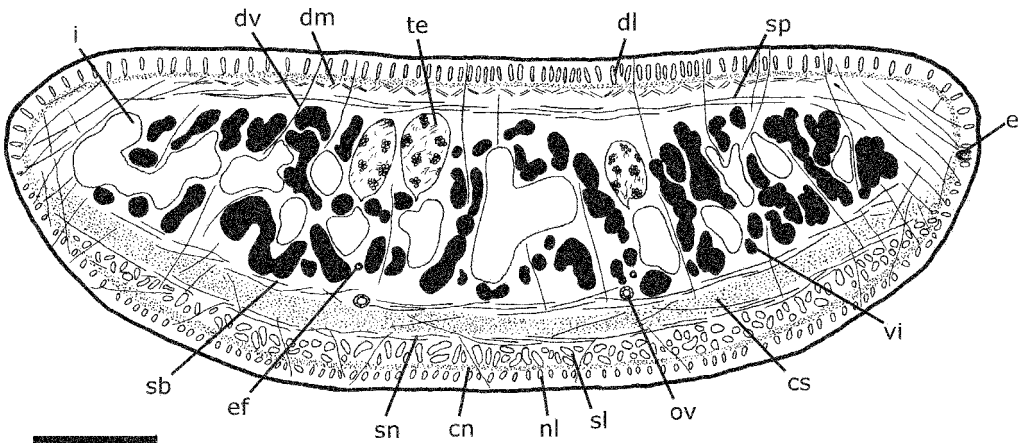


Fig. 11. *Supramontana irritata*, sp. nov. Diagrammatic transverse section of the pre-pharyngeal region (holotype). Circular and diagonal cutaneous muscle layers are omitted. Scale bar: 0.5 mm. (cn, cutaneous nerve net; cs, central nervous system; dl, dorsal cutaneous longitudinal muscles; dm, diagonal mesenchymal muscles; dv, dorso-ventral mesenchymal muscles; e, eyes; ef, efferent duct; i, intestine; nl, normal cutaneous longitudinal muscles; ov, ovovitelline duct; sb, sub-intestinal transverse mesenchymal muscles; sl, sunk longitudinal cutaneous muscles; sn, sub-neural transverse mesenchymal muscles; sp, supra-intestinal transverse mesenchymal muscles; te, testes; vi, vitellaria.)

Without oesophagus, pharynx lumen directly communicates with intestine.

Male reproductive system

Testes: pre-pharyngeal, dorsal or dorso-interstitial to intestine (Fig. 11). Most anterior and posterior testes positioned 18% and 58%, respectively, of body length, from anterior end. Posterior-most testes located approximately 1 mm before ventral insertion of pharynx. *Efferent ducts*: open laterally onto proximal region of prostatic vesicle (Fig. 13). *Prostatic vesicle*: extrabulbar, unpaired, straight and dilated in proximal region, sinuous and canalicular distally. Distal portion penetrates penis bulb and continues as ejaculatory duct on entering penis papilla. Epithelium columnar ciliated (10 μm thick) with openings of erythrophil secretory cells. Muscularis of subepithelial layer (25 μm maximum thickness) with crossed diagonal fibres, followed by longitudinal layer (6 μm thick), both distally decreased in thickness. *Ejaculatory duct*: epithelium columnar ciliated (10 μm thick) without openings of secretory cells, surrounded by thin layer of circular muscles. *Penis papilla*: conical, with dorsal insertion slightly displaced posteriorly (Fig. 13 *a*,*b*). Xanthophil cells open onto proximal two-thirds of papilla, and erythrophil cells all over surface, particularly abundant near to ventral insertion of papilla; cell bodies of both types external to penis bulb. Muscularis of 10 μm-thick circular layer, followed by longitudinal layer. Mesenchyme of papilla with longitudinal and radial muscle fibres. *Male atrium*: only partially occupied by penis papilla. Epithelium columnar non-ciliated, apically xanthophil, with openings of xanthophil cells with short necks and basiphil cells with longer necks; the latter more abundant on distal portion of atrium. Muscularis of circular layer (15 μm thick).

Female reproductive system

Ovaries: elongated (0.5 × 0.06 mm in paratype 652); dorsal to nerve plate; in relation to anterior end, at 16% of body length (paratype 652). *Ovovitelline ducts*: dorsal to nerve plate, emerge dorsally from middle third of ovaries; at level of gonopore, dorso-medially curved (Fig. 13). Openings of shell glands onto distal quarter of ascending course. *Common ovovitelline duct*: very long (~1 mm), posteriad directed, dorsal to female atrium, with distal portion curved ventrally. Epithelium cubic ciliated with openings of shell glands. Muscularis a layer of crossed diagonal fibres. *Vagina*: short, slightly curved dorso-anteriorly, communicating with proximal region of female atrium. Epithelium ciliated, cubic in proximal region and columnar in distal, with openings of xanthophil and numerous basiphil secretory cells. Muscularis a layer of circular fibres (6 μm). *Female atrium*: epithelium pluristratified, with openings of xanthophil and numerous basiphil secretory cells. Muscularis a circular muscle layer. Female atrium length half that of male.

Common muscular coat

Encompassing distal portion of prostatic vesicle, male and female atria and vagina. Layer of crossed diagonal fibres, 10 μm thick in proximal region of male atrium, 15 μm at level of female atrium.

Habitat and locality

The animals were collected in the national forest of São Francisco de Paula-RS, Brazil, from on the ground under fallen logs and amongst fallen leaves, in areas with ombrophilous forest, with and without *Araucaria angustifolia*, as well as in areas being reforested with *Pinus elliottii*.

Etymology

The specific name is derived from its characteristically quick movement (from the Latin, *irritatus*, -a) when stimulated; more so than in other geoplanids.

Significance of cephalic specialisations in the systematics of Geoplaninae

As can be seen in the above descriptions, structures of the cephalic region are important in the systematics of Geoplaninae. These specialisations are of heightened importance in a taxonomic group in which the genera are

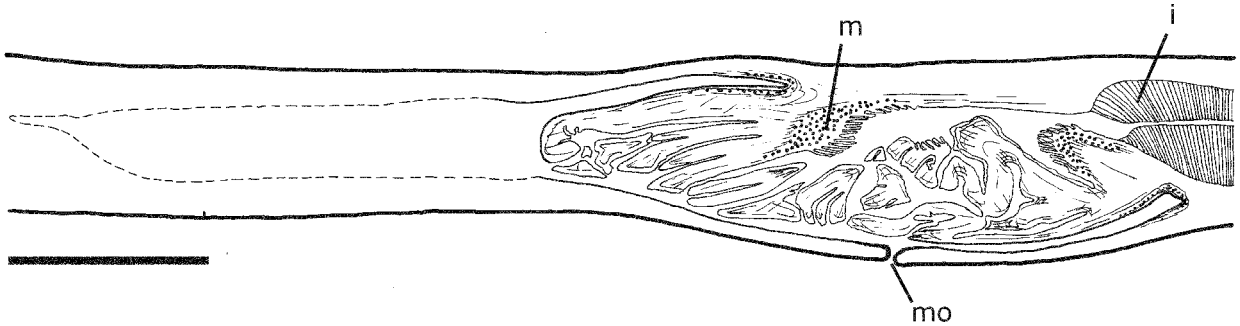


Fig. 12. *Supramontana irritata*, sp. nov. Sagittal reconstruction of the pharynx (paratype 893). Scale bar: 1 mm. (i, intestine; m, muscles; mo, mouth.)

defined by a combination of characters rather than unique characters. *Geoplana*, the type genus of the subfamily Geoplaninae, is characterised by a lack of cephalic specialisation, for example glandulo-muscular organs (Ogren and Kawakatsu 1990). In some groups, internal specialisations of the cephalic region (organisation of the cutaneous and mesenchymatic musculature, presence and type of secretory cells) are to be found together with external specialisations of the cephalic region (form and distribution of eyes and sensory pits). This occurs in the genera *Choeradoplana*, *Issoca* and *Cephaloflexa*. In other genera (e.g. *Supramontana* and *Geobia*), there are no external

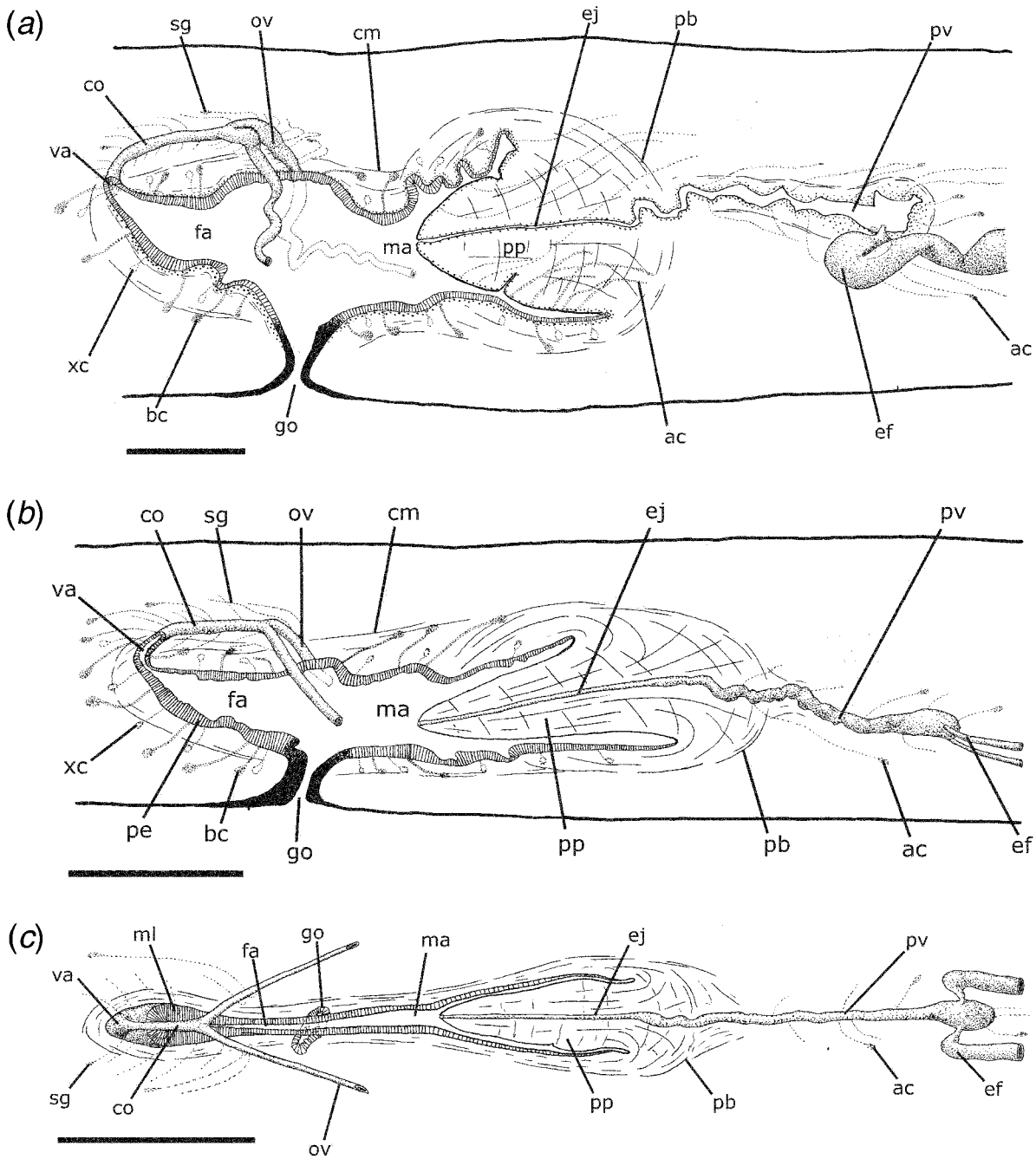


Fig. 13. Copulatory apparatus of S*upramontana irritata*, sp. nov. Sagittal reconstruction from (*a*) the holotype; and (*b*) paratype (893). Scale bar: 0.5 mm. (*c*) Horizontal reconstruction (paratype 190). Scale bar: 1 mm. (ac, erythrophil secretory cells; bc, basiphil secretory cells; cm, common muscle coat; co, common glandular ovovitelline duct; ef, efferent duct; ej, ejaculatory duct; fa, female atrium; go, gonopore; ma, male atrium; ml, multilayered lining of the female atrium; ov, ovovitelline duct; pb, penis bulb; pe, pluristratified epithelium; pp, penis papilla; pv, prostatic vesicle; sg, shell glands; va, vagina; xc, xanthophil secretory cells.)

differences evident, but there are internal specialisations (C. G. Froehlich 1955; F. Carbayo, personal observation).

In this section, we compare the new genera with the type species of the two other genera of Geoplaninae with external cephalic specialisations, i.e. *Choeradoplana* and *Issoca*. Their type species are *Choeradoplana iheringi* and *Issoca rezendei* respectively. For further comparison with a genus lacking cephalic specialisations, we analysed *Geoplana josefi* and *G. franciscana*, chosen as examples because we lacked the type species of the Geoplaninae subfamily – *Geoplana vaginuloides* (Darwin, 1844). We also compared these species with the original description of *G. vaginuloides*.

Genus ***Geoplana*** Stimpson

Geoplana josefi Carbayo & Leal-Zanchet

(Figs 14*b*, 15)

Material examined

Paratype. National forest of São Francisco de Paula-RS, Brazil, 930 m, under a fallen log. Nr. 259, coll. A.M. Leal-Zanchet, 4.v.1998 (MZU): anterior region, transverse sections on 28 slides.

Remarks

Besides the more or less conical form of the head, there are no external morphological distinguishing characters, such as expansions or grooves. Eyes and sensory pits surround the anterior tip of the body, including the apex (Fig. 14*b*). C. G. Froehlich (1955) described the musculature of the head of the type species, *Geoplana vaginuloides* Darwin, 1844 as possessing no muscular specialisation. In *Geoplana josefi* there are some fibres of the diagonal layer directed to the ventral side, and some mesenchymal fibres combined into a loose sub-neural mesenchymal layer (Fig. 15). The rhabditogen cells, which are not very abundant, are more common on the dorsal than on the ventral side, and their cell bodies are subjacent to the cutaneous nerve plate.

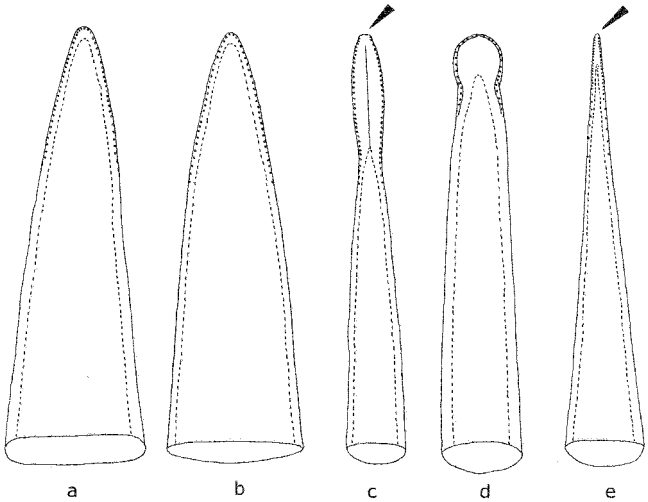


Fig. 14. Diagrammatic reconstruction of the anterior third of the body in ventral view. (*a*) *Supramontana irritata*, sp. nov., (*b*) *Geoplana josefi*, (*c*) *Choeradoplana iheringi*, (*d*) *Issoca rezendei*, and (*e*) *Cephaloflexa araucariana*, sp. nov. Arrowheads show anterior tip of the body without eyes. Dashed lines show the border of the creeping sole. In different scales.

Geoplana franciscana Leal-Zanchet & Carbayo

Material examined

Holotype. National forest of São Francisco de Paula-RS, Brazil, 930 m, under a fallen log. Nr. 110C, coll. M. Cardoso, 27.v.1997 (MZUSP): anterior region, sagittal sections on 12 slides.

Remarks

The musculature arrangement and rhabditogen cell distribution is similar to that of *G. josefi* (see above).

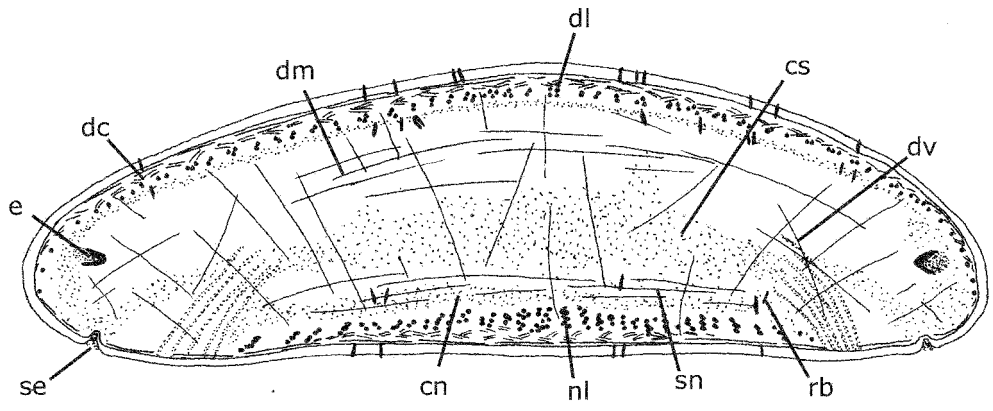


Fig. 15. *Geoplana josefi*. Diagrammatic transverse section of head region (paratype Nr. 259). Scale bar: 0.25 mm. (cn, cutaneous nerve net; cs, central nervous system; dc, diagonal cutaneous muscles; dl, dorsal cutaneous longitudinal muscles; dm, diagonal mesenchymal muscles; dv, dorso-ventral mesenchymal muscles; e, eyes; nl, normal cutaneous longitudinal muscles; rb, rhabdoids; se, sensory pit; sn, sub-neural transverse mesenchymal muscles.)

Genus ***Choeradoplana*** Graff

Choeradoplana iheringi Graff

Material examined

National forest of São Francisco de Paula-RS, Brazil: Nr. 120, 930 m, under a fallen log, coll. F. Carbayo, 1.ix.1997 (MZU): transverse sections on eight slides.

Remarks

Our observations of the head coincide, in general, with the description by C. G. Froehlich (1955). The anterior tip is dilated and rolled towards the back; ventrally it possesses two glandular cushions, separated by a median groove (Fig. 14*c*). Sensory pits are in the shape of simple invaginations and eyes skirt the anterior region, except for the apex.

The genus is characterised by possessing part of the cutaneous longitudinal muscle partially sunk into the mesenchyme (internal to the cutaneous nerve system). Anteriorly, the retractor muscle fibres (derived from that layer) are concentrated in the median ventral region. The normal longitudinal cutaneous layer also sinks into the mesenchyme and weakens, becoming thinner than the internal layer (sunk). Thus, the retractor presents a triangular shape in cross section (Fig. 16). Further ahead, the retractor disappears, together with the other cutaneous layers. Some fibres of the dorsal longitudinal cutaneous musculature are arranged dorso-ventrally.

A large number of fibres of the dorso-ventral mesenchymal muscle layer are fixed to the epidermis. The sub-intestinal mesenchymal muscle layer is weak, but the supra-intestinal layer is highly developed. This layer, together with dorso-ventral mesenchymal fibres, constitute the interwoven muscle (or *Muskelgeflecht* (Graff 1899)). Some mesenchymal fibres are arranged sub-neurally, thus forming a sub-neural transverse layer, which does not, however, occur posterior to the cephalic region.

Rhabditogen cells are very abundant, opening all over the cutaneous surface. Dorsally, the cell bodies of these are placed between the dorsal diagonal and supra-intestinal transverse mesenchymal muscle layers, whereas ventrally they are placed between the retractor and the epidermis.

Genus ***Issoca*** C. G. Froehlich

Issoca rezendei (Schirch)

Material examined

Cabo Frio-RJ, Brazil: Nr. 913 (EMF): anterior tip: transverse sections on five slides; Nr. 914: 6.ix.1976 (EMF): anterior tip: sagittal sections on two slides.

Remarks

Our analysis of *Issoca rezendei* is, in general, in agreement with that of C. G. Froehlich (1955). The cephalic region characteristically has the shape of a spoon, being laterally widened and ventrally concave (Fig. 14*d*). Sensory pits are in the shape of simple invaginations, with the eyes surrounding the anterior end, including the apex.

The ventral longitudinal cutaneous musculature is concentrated in the median region (Fig. 17) forming the retractor, which is circular-shaped in cross-section. Further anteriorly, the retractor dissolves owing to the successive separation into bundles towards the body margins and the back. The layers of circular and diagonal cutaneous musculature are inconspicuous.

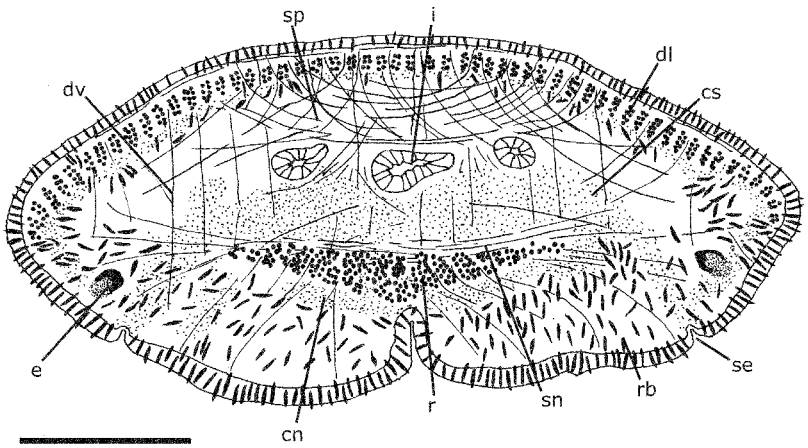


Fig. 16. *Choeradoplana iheringi*. Diagrammatic transverse section of head region (specimen Nr. 120). Scale bar: 0.25 mm. (cn, cutaneous nerve net; cs, central nervous system; dl, dorsal cutaneous longitudinal muscles; dv, dorso-ventral mesenchymal muscles; e, eyes; i, intestine; r, retractor muscles; rb, rhabdoids; se, sensory pit; sn, sub-neural transverse mesenchymal muscles; sp, supra-intestinal transverse mesenchymal muscles.)

Dorso-ventrally arranged mesenchymal fibres are abundant. Fibres of the transverse and diagonal mesenchymal muscle systems are placed on the dorso-ventral plane. Fibres of the sub-neural transverse layer cross with those of the retractor. Some fibres of the sub-neural transverse layer join with bundles of the retractor that proceed to the margins. Towards the anterior end, the fibres of the sub-intestinal mesenchymatic layer dwindle, the same occurring, near to the apex, with those of the supra-intestinal and diagonal layers.

Cell bodies of rhabditogen cells are to be found near to the dorsal epidermis, just below the cutaneous musculature. These were not observed in the ventral region.

Comparative discussion

In the family Geoplanidae, six genera, including the two new genera described herein, have been described with a cephalic retractor muscle: *Cephaloflexa*, *Choeradoplana*, *Issoca*, *Supramontana*, *Pimea* Winsor, 1990, and *Coleocephalus* Fyfe, 1953. The first four belong to the same subfamily, Geoplaninae. *Pimea* and *Coleocephalus* belong to the subfamily Caenoplaninae Ogren & Kawakatsu, 1991, which includes the Geoplanidae of Australasia (with testes ventrally situated; subepithelial longitudinal musculature in large bundles; mouth in third quarter; eyes often in single row around anterior, continuing posteriorly but not usually extending dorsally). In the following discussion, we compare those genera of Geoplaninae with cephalic specialisations.

Defining features of the genus Cephaloflexa

E. M. Froehlich (1955) and C. G. Froehlich (1967) have noted that it is difficult to allocate *Cephaloflexa bergi* to any of the currently known genera, owing to its aberrant characteristics. Effectively, species with the characteristics described for *Cephaloflexa*, particularly in regard to body form and the absence of eyes and sensory pits in the apex, cannot be fitted into *Notogynaphallia*, as tentatively proposed by Ogren and Kawakatsu (1990), or into any other extant genus of Geoplaninae. The definition of *Notogynaphallia* makes no mention of the arrangement of the eyes, but the dichotomous key of Ogren and Kawakatsu (1990) indicates that this genus and the rest of the Geoplaninae have contouring eyes. Descriptions of species included in *Notogynaphallia* permit one to verify that the eyes surround the anterior region (Riester 1938; Marcus 1951; C. G. Froehlich 1955; E. M. Froehlich 1955). However, *N. andina* (Hyman, 1962), from Colombia, does not have eyes around the apex, but its external morphology differs from that of *Cephaloflexa*. The anatomy of the head remains unknown, making it impossible to discuss here its taxonomic status.

Besides the described generic characteristics, *C. bergi* and *C. araucariana* both possess different types of secretory cells opening into the prostatic vesicle, with a specific distribution in the unpaired portion of this organ: openings of erythrophil and basiphil secretions in the dorsal epithelium, and xanthophil secretions in the ventral epithelium. The presence of different types of secretions in the vesicle, as well as the form of the prostatic vesicle and the copulatory organ, should be used as additional characters for the genus.

Cephaloflexa and *Choeradoplana* share two taxonomic characters: the cephalic extremity rolled upwards and a lack of eyes (Fig. 14c, e) and sensory pits in the apex. They can be differentiated, however, because *Choeradoplana* presents (*1*) part of the longitudinal cutaneous musculature sunk, (*2*) Muskelgeflecht, (*3*) an expanded cephalic region, with two glandular cushions separated by a median groove, and (*4*) cellular bodies of rhabditogen cells that discharge through the epidermis and are ventral to the retractor muscle.

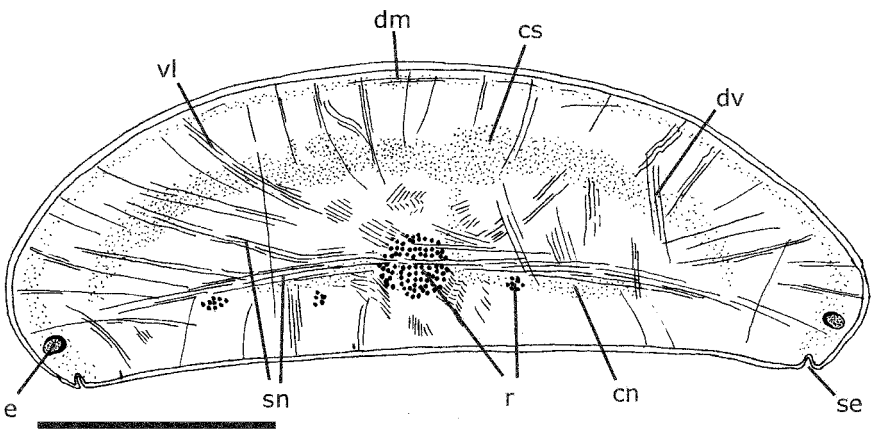


Fig. 17. *Issoca rezendei.* Diagrammatic transverse section of head region (specimen Nr. 913). Scale bar: 0.25 mm. (cn, cutaneous nerve net; cs, central nervous system; dm, diagonal mesenchymal muscles; dv, dorso-ventral mesenchymal muscles; e, eyes; r, retractor muscles; se, sensory pit; sn, sub-neural transverse mesenchymal muscles; vl, ventral cutaneous longitudinal muscles.)

Similar to *Cephaloflexa*, *Issoca* presents a retractor muscle in the anterior region of the body and has no ventral cutaneous longitudinal musculature sunk into the mesenchyme. The two genera are different in that in *Issoca* (*1*) the creeping sole is narrow (~2/3 the width of the body), (*2*) the cephalic region is expanded and spoon-shaped, and (*3*) the eyes and sensory pits contour the apex.

Supramontana also possesses a retractor muscle. This genus differs from *Cephaloflexa* in that (*1*) the body is not very narrow in the anterior region, (*2*) the fibres of the retractor muscle are partially sunk into the mesenchyme, (*3*) the eyes and sensory pits contour the apex (Fig. 14*a*), (*4*) there is a sub-neural, transverse mesenchymal muscle layer along the entire body, and (*5*) part of the longitudinal cutaneous musculature posterior to the cephalic region is sunk into the mesenchyme.

Defining features of the genus Supramontana

Supramontana presents, in common with *Choeradoplana*, the existence of a ventral longitudinal cutaneous musculature partially sunk into the mesenchyme, and the distribution of bodies of rhabditogen cells between the retractor and the ventral epidermis. The genera are different: in *Choeradoplana* (*1*) the cephalic region is rolled toward the back, expanded laterally and with a median ventral groove, (*2*) the eyes and sensory pits are absent in the anterior apex, (*3*) the fibres of the retractor muscle do not change direction (they simply become extinguished in the anterior direction), and (*4*) the transverse sub-neural mesenchymal muscle layer only occurs in the cephalic region.

Besides the presence of the retractor muscle, *Supramontana* and *Issoca* have three other characteristics in common: eyes and sensory pits contouring the entire anterior tip, the retractor muscle divided anteriorly into bundles, and a transverse sub-neural mesenchymal muscle layer along the entire body. *Supramontana* differs from *Issoca* in that in the latter: (*1*) the cephalic extremity is characteristically spoon-shaped, (*2*) the creeping sole is narrower (~2/3 the body width), and (*3*) the retractor muscle bundles are dispersed in the direction of the margins and to the dorsal body surface.

Besides these genera in Geoplaninae, *Gusana* E. M. Froehlich, 1978 and *Liana* E. M. Froehlich, 1978, from Chile, also have an insunk longitudinal cutaneous musculature. In *Gusana*: (*1*) the body abruptly becomes narrow in the anterior region, thus presenting a triangular form, (*2*) the sensory pits are branched and arranged on both sides of the body, in various series, (*3*) the longitudinal cutaneous musculature is dorsally and ventrally insunk, and (*4*) there is no retractor muscle. *Liana* has part of the ventral longitudinal cutaneous musculature sunk into the mesenchyme. In this genus the fibres of the ventral longitudinal cutaneous musculature in the cephalic region simply disappear in the direction of the extremity, without any specialisation.

Emendations to the diagnoses of Choeradoplana *and* Issoca *based on cephalic structures*

C. G. Froehlich (1955) redefined *Choeradoplana* as Geoplanidae of elongated body; creeping sole broad, more than a third of the body width; strong cutaneous longitudinal musculature, which is partially internal to the cutaneous nerve plate; mesenchymal longitudinal musculature, weak or absent; dorsal testes; cephalic region with a glandulo-muscular organ constituted of two sucker-like cushions; retractor of that organ constituted of insunk bundles of the ventral cutaneous longitudinal musculature; sensory papillae absent; copulatory apparatus without adenodactyls. This diagnosis should be complemented with the following additional cephalic characters: eyes and sensory pits absent in the anterior apex; ventral longitudinal cutaneous muscle layer completely sunk into the mesenchyme in the cephalic region; on the ventral side of the cephalic region, bodies of rhabditogen cells located between the retractor and the epidermis; part of the dorsal longitudinal cutaneous muscle fibres oriented dorso-ventrally in the cephalic region. These characteristics were observed by C. G. Froehlich (1955), but were not included in the definition of the genus.

Issoca has been defined (C. G. Froehlich 1955) as Geoplaninae with elongated body; large creeping sole, having a width greater than a third of the body width; cutaneous longitudinal musculature strong; longitudinal mesenchymal musculature very weak or absent; cephalic extremity provided with a musculo-glandular organ, whose retractor originates from the ventral longitudinal cutaneous musculature and whose adhesive surface, concave in general, is simple or incompletely bipartite; sensory papillae absent; copulatory apparatus lacking adenodactyls. This definition should be complemented with the following cephalic characters: eyes and sensory pits contouring the entire cephalic region; sub-neural transverse mesenchymatic muscle layer interspersed with muscle fibres of the retractor.

State of knowledge of Geoplaninae systematics

To select characters, polarise their states and construct a phylogeny for the Geoplaninae, still forms an extremely speculative exercise, owing to various factors: the topographic homogeneity of the anatomical structures, particularly those of the reproductive system (although they continue to be key features for species identification); insufficient knowledge of the characteristics of the more primitive Terricola (E. M. Froehlich, 1978); limited knowledge of Terricola diversity; and the likely polyphyletic nature of some of the current genera.

The degree of development of the cutaneous and mesenchymal musculatures and their arrangement in bundles along the body are of great importance to the present systematics of the three subfamilies of Geoplanidae. Within the subfamily Geoplaninae, there are four genera

characterised by cephalic specialisations of these muscle systems and of the secretory cells of the region (the set constitutes the so-called 'glandulo-muscular organ' or *Drüsenpolster*, first used for *Choeradoplana* by Graff (1899) and also used in the definitions of *Issoca*, *Coleocephalus* and *Pimea*): *Cephaloflexa*, *Choeradoplana*, *Issoca* and *Supramontana*. The genera *Amaga*, *Geobia*, *Geoplana*, *Gusana*, *Liana*, *Polycladus*, *Xerapoa* do not have such specialisations. There are also five genera (*Enterosyringa*, *Gigantea*, *Notogynaphallia*, *Pasipha* and *Pseudogeoplana*), whose diagnoses do not include those features. It is important not to treat the glandulo-muscular organ as a single character because the term cephalic glandulo-muscular organ alludes to a set of heterogeneous structures that are therefore not suitable as comparable characters for phylogenetic analysis, although all species within a genus may have a homogeneous arrangement of cutaneous and mesenchymal musculatures and secretory cells within the cephalic region.

In conclusion, to construct a solid phylogeny for the Geoplanidae, the currently employed generic characters need to be re-evaluated, with special attention paid to the cutaneous and mesenchymal muscles in the pre-pharyngeal region, and their cephalic differentiation. Secondly, the type species of the genera need to be analysed in greater depth. Ultrastructural characters of the epidermis and sensory organs must also be taken into consideration. Besides this, it is necessary to amplify knowledge of geoplanid diversity, including Geoplaninae, by extending the areas of collection to less explored regions and increasing the collection effort. Increased morphological knowledge and the contribution of molecular data should make a solid phylogenetic classification of the Geoplanidae ultimately possible.

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