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Neotropical Monogenoidea. 49. Four new species of the Diplectanidae (Dactylogyrinea) from the gills of some pachyurines (Teleostei: Sciaenidae) from the Rio Tocantins and Rio Doce Basins, with the proposal of *Anoplectanum* n. g. and *Spinomatrix* n. g.

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Abstract

Four new species of the Diplectanidae from the gills of freshwater sciaenid species (Pachyurinae) in Brazil are described and two new genera, *Anoplectanum* n. g. and *Spinomatrix* n. g., are proposed. These are: *Diplectanum copiosum* n. sp. from *Pachyurus junki* and *Petilipinnis grunniens*; *Anoplectanum haptorodynatum* n. g., n. sp. from *Pachyurus junki* and *Petilipinnis grunniens*, and *A. microsoma* n. g., n. sp. from *Petilipinnis grunniens*, all in the Tocantins Basin; and *Spinomatrix penteormos* n. g., n. sp. from *Pachyurus adspersus* in the Rio Doce Basin. *Anoplectanum* is proposed to accommodate diplectanids lacking squamodiscs and having a superficial root of the ventral anchor as long or longer than the deep root. *Spinomatrix* is proposed for species having a haptoral and peduncular armature composed of spines, hooks, anchors, squamodiscs and armed muscular pads.

Introduction

The Diplectanidae Monticelli, 1903 is composed of about 220 species of gill parasites of Perciformes, Cyprinodontiformes, Siluriformes, Anguiliformes, Pleuronectiformes, Scorpaeniformes, Beloniformes, Cypriniformes and Clupeiformes (Domingues, 2004). Most are marine species, but a few are reported from freshwater fishes. In the rivers of South America, six species of diplectanids are known from *Plagioscion* spp. (Sciaenidae), all members of *Diplectanum* Diesing 1858. These are: *Diplectanum cayennense* Euzet & Durette-Desset 1974, a parasite of *Plagioscion auratus* Castelnau; *D. decorum* Kritsky & Thatcher 1984, *D. gymnopeus* Kritsky & Thatcher 1984 and *D. piscinarius* Kritsky & Thatcher 1984, all parasites of *Plagioscion squamosissimus* Heckel; *D. hilum* Kritsky & Thatcher 1984, a parasite of *Plagioscion* sp.; and *D. pescadae* Kritsky & Thatcher 1984, a parasite of *P. squamosissimus* and *Plagioscion* sp. No diplectanid has previously been recorded from a species of the Pachyurinae, another lineage of continental South American sciaenids.

During a study on the historical biogeography of freshwater sciaenids in the Neotropics, four new species of the Diplectanidae were collected from the gills of species of some pachyurines caught in the Rio Tocantins and its tributaries, and in the

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Rio Piranga, a tributary of the Rio Doce. These species are described herein. Two new genera are proposed to accommodate three of these species.

Materials and methods

Specimens of *Pachyurus junki* Soares & Casatti and *Petilipinnis grunniens* Casatti were collected using gill-nets from the Rio Tocantins (in the municipalities of Lajeado, Peixe, Santa Helena, Ipueiras and Porto Nacional), Rio São Valério (municipality of Santa Rosa), Rio Areia, Rio Santa Tereza (municipality of Peixe) and Rio Crixas (municipality of Brejinho de Nazaré), State of Tocantins, Brazil, during November and December of 2002 and July of 2003. Specimens of *Pachyurus adspersus* Steindachner were collected with gill-nets and hook-and-line in the locality of Cachoeirinha da Brecha, Rio Piranga, municipality of Vau-Açu, Rio Doce Basin, State of Minas Gerais, Brazil, during January of 2003. Gills were removed, submersed in hot water (65°C) and vigorously shaken, then formalin was added to obtain a final concentration of 3–5%. Some specimens were stained with Gomori's trichrome and mounted in Canada balsam for a study of their internal organs according to Kritsky et al. (1986); other specimens were cleared and mounted in Hoyer's mounting medium (see Humason, 1979) in order to study their sclerotised parts. Illustrations were prepared with the aid of an Olympus BX51 microscope, with phase contrast and a camera lucida. Measurements, presented in micrometres, were made following the procedure of Mizelle & Klucka (1953); the mean is followed by the range and the number of structures measured (n). The numbering of the hook pairs follows that recommended by Mizelle & Price (1963). Type-specimens are deposited in the helminthological collections of the Instituto Nacional de Pesquisas da Amazônia (INPA) - Brazil, the Coleção Helmintológica do Museu de Zoologia de São Paulo (MZUSP) - Brazil, the Coleção Helmintológica do Instituto Oswaldo Cruz (IOC) - Brazil, the United States National Parasite Collection (USNPC) - USA, the Musée National d'Histoire Naturelle, Paris (MNHN) – France, and the Harold W. Manter Laboratory of Parasitology (HWML) - USA, as presented in the respective descriptions.

Subclass Polyonchoinea Bychowsky, 1937
Order Dactylogyridea Bychowsky, 1937
Diplectanidae Monticelli, 1903

Diplectanum copiosum n. sp.

*Holotype, type-host and type-locality:*MZUSP 5946-a, from *Pachyurus junki*, Rio Tocantins, municipality of Santa Helena, State of Tocantins, Brazil, IV/2002.
Other specimens: Paratypes (30), Rio Tocantins, municipality of Santa Helena, State of Tocantins, IV/2002 (5 in INPA 341a-e; 13 in IOC 36501a-m; 12 in MZUSP 5946b-m); paratypes (2), Rio Tocantins, municipality of Ipueiras, State of Tocantins, 21/XI/2002, 11°18′50″S, 48°27′26″W (2 in INPA 342a,b); paratypes (3), Rio Tocantins, municipality of Peixe, State of Tocantins, 01/XII/2002, 11°46′19″S, 48°37′15″W (3 in INPA 343a-c); paratypes (2), Rio São Valério, municipality of Santa Rosa, State of Tocantins, 18/XI/2002, 11°21′57″S, 48°28′35″W (2 in INPA 344a,b); paratype (1), Rio Crixas, municipality of Brejinho de Nazaré, State of Tocantins, 01/XII/2002, 11°02′31″S, 48°34′10″W (USNPC 95411); paratype (1), Rio Areia, State of Tocantins, 07/VII/2003 (UNSPC 95412); paratype (1), Rio Tocantins, municipality of Porto Nacional, State of Tocantins, 09/VII/2003, 10°41′45″S, 48°25′54″W (USNPC 95413); vouchers (20), host: *Petilipinnis grunniens*, Rio Tocantins, municipality of Santa Helena, State of Tocantins, IV/2002 (11 in MNHN 249HG no. Ti126, Ti126 bis, Ti127, Ti127 bis, Ti128, Ti128 bis, Ti129, Ti129bis, Ti130, Ti130 bis, Ti131; 9 in USNPC 95414); vouchers (5) host: *P. grunniens*, Rio Tocantins, municipality of Peixe, State of Tocantins, 01/XII/2002, 11°46′19″S, 48°37′15″W (5 in HWML 48086); voucher (1), host: *P. grunniens*, Rio São Valério, municipality of Santa Rosa, State of Tocantins, 18/XI/2002, 11°21′57″S, 48°28′35″W (HWML 48087); voucher (1), host: *P. grunniens*, Rio Santa Tereza, municipality of Peixe, State of Tocantins, 08/VII/2003 (HWML 48088); voucher (1), host: *P. grunniens*, Rio Tocantins, municipality of Ipueiras, State of Tocantins, 21/XI/2002, 11°18′50″S, 48°27′26″W (HWML 48089); voucher (1), host: *P. grunniens*, Rio Tocantins, municipality of Porto Nacional, State of Tocantins, 01/XII/2002, 10°41′45″S, 48°25′54″W (HWML 48090).

Site of infection: Gills.
Etymology: The specific epithet is Latin and refers to the fact that the species is abundant (*copiosus* = plentiful).

Description (Figures 1–9)

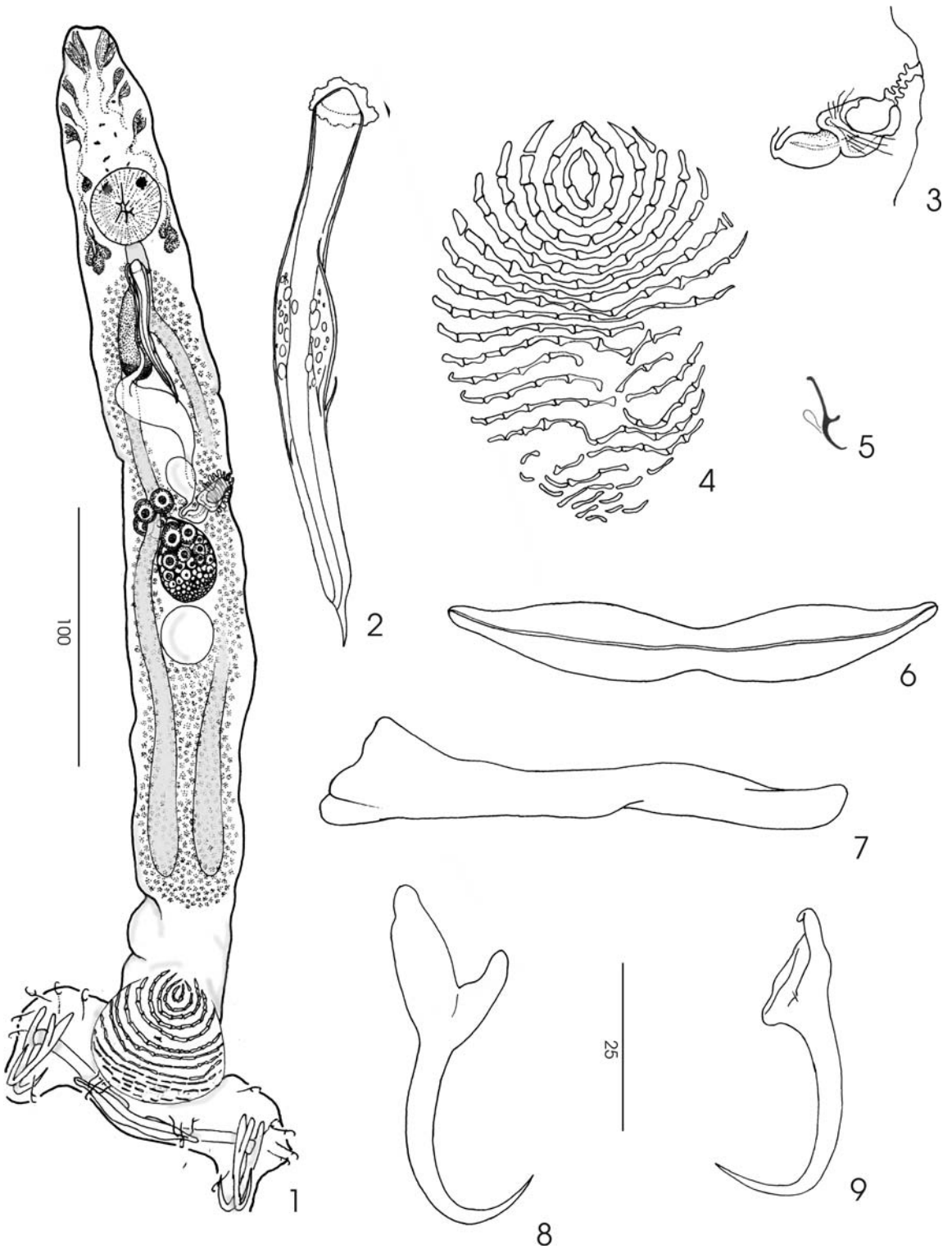
[Based on 70 specimens.] Body elongate, fusiform, with smooth tegument; length 571 (440–760; n = 9), greatest width 76 (55–90; n = 10) at level of testis. Four cephalic lobes poorly developed. Four groups of head organs moderately developed in cephalic lobes, adjacent cephalic areas. Cephalic glands posterolateral to pharynx. Eye-spots 2, with oval granules; accessory granules common in cephalic area and anterior trunk. Mouth subterminal, midventral; pharynx bulbous, 38 (33–50; n = 9) in diameter; oesophagus long; intestinal caeca 2, not confluent, extending to posterior trunk. Peduncle as long as wide. Haptor laterally expanded, approximately 3 times wider than long. Squamodiscs oval, ventral and dorsal; each formed by approximately 22 rings of phalangiform sclerites; anterior rings concentric, progressively tending to form straight line posteriorly; squamodisc, 73 (56–98; n = 14) long, 58 (52–75; n = 14) wide. Anchors 2 pairs, ventral and dorsal. Ventral anchor 42 (38–45; n = 11) long, 17 (16–19; n = 4) wide, with wide deep root longer than superficial root; shaft slightly curved continuous with point. Dorsal anchor with short deep root, strongly truncated superficial root, 39 (35–42; n = 11) long, 15 (14–16; n = 8) wide. Ventral bar with tapering extremities, mid-ventral longitudinal groove and medial constriction, 75 (68–82; n = 15) long. Dorsal bars 2, similar, 59 (53–71; n = 16) long; proximal extremity expanded. Hooks 10 (9–11; n = 38) long, similar, with depressed thumb, straight shaft, short point and uniform shank; filamentous hook loop (FH loop) shorter than shank length; hook pair 1 inconspicuous, with ventral, bilateral lobes at level of extremities of ventral bar. Male copulatory organ (MCO) elongate, 70 (56–80; n = 18) long, composed of 2 nested tubes (tube within a tube); external tube with mid-length expansions (1 flap-like, 1 pointed), distally acute; aperture of internal tube subterminal, not extending from external tube; small sclerites of irregular size in medial area of MCO between external and internal tubes; delicate fringe-like sclerotisation around MCO base; accessory piece absent. Testis spherical, posterior to germarium ('ovary'). Vas deferens apparently looping left intestinal caecum. Seminal vesicle sigmoid, a simple dilation of vas deferens; prostatic reservoir pyriform, divided in two bands, dorsal to MCO. Germarium ovoid, loops right intestinal caecum; oviduct, oötype, uterus and eggs not observed. Genital pore ventral. Vaginal tube sclerotised, dilate distally; aperture sinistral; pre-atrium tubular, slightly sclerotised; atrium scoop-shaped, heavily sclerotised. Seminal receptacle pyriform. Vitelline follicles dense, coextensive with intestinal caeca.

Remarks

Diplectanum copiosum n. sp. is distinguished from other species in the genus by presenting the following combined characteristics: (1) a heavily sclerotised, cup-shaped vaginal atrium (Figure 3); (2) irregular sclerites and mid-lateral expansions in the external tube of the male copulatory organ (Figure 2); and (3) the aperture of the internal tube of the MCO subterminal and not extending from the external tube (Figure 2).

Anoplectanum **n. g.**

Diagnosis
Body fusiform, divided into cephalic area, trunk, peduncle and haptor. Tegument thin, smooth. Eye-spots 2. Mouth mid-ventral, sub-terminal; pharynx bulbous; intestinal caeca 2, non-confluent. Haptor laterally expanded. Adhesive accessory organs (AAO) absent. Anchors 2 pairs, ventral and dorsal; ventral anchor with superficial root longer than deep root; dorsal anchor with superficial root truncate. Ventral bar with mid-ventral, longitudinal groove. Dorsal bar 2, similar. Hooks 14, with typical diplectanid distribution (5 pairs ventral; 2 pairs dorsal), similar. Copulatory complex lacking accessory piece; male copulatory organ (MCO) composed of 2 nested tubes, directed posteriorly, with enlarged base, tapered and coiled or sinuous distally; slightly sclerotised cone at distal portion of vas deferens; internal tube not extending



Figures 1–9. *Diplectanum copiosum* n. sp. 1. Holotype (ventral); 2. Male copulatory organ. 3. Vagina. 4. Squamodisc. 5. Hook. 6. Ventral bar. 7. Dorsal bar. 8. Ventral anchor. 9. Dorsal anchor. *Scale-bars*: 1, 100 μm; 2–9, 25 μm.

beyond external tube; MCO. Testis posterior to germarium; seminal vesicle an expansion of vas deferens; vas deferens apparently loops left caecum. Vagina sclerotised, with sinistro-ventral aperture; pre-atrium muscular; vaginal atrium heavily sclerotised. Germarium loops right intestinal caecum. Genital pore ventral. Vitelline follicles dense, coextensive with intestinal caeca. Parasites of Pachyurinae (Sciaenidae). Type-species: *A. haptorodynatum* n. sp.
Other species: A. microsoma n. sp.
Etymology: The generic epithet derives from Greek and refers to the absence of accessory adhesive organs on the haptor in species of this genus.

Remarks

Anoplectanum n. g. is proposed to accommodate species of the Diplectanidae with a unique combination of characteristics: (1) the lack of accessory adhesive organs (AAO); (2) the MCO composed of nested tubes with a funnel-shaped base; (3) a slightly sclerotised cone in the distal region of the vas deferens; (4) a vaginal aperture which is sinistro-ventral, with a conspicuous, muscular pre-atrium and a heavily sclerotised vaginal atrium; and, most distinctively (5) the ventral anchor with a superficial root as long or longer than the deep root.

Other diplectanid genera also have species in which the AAO are absent: *Lobotrema* Tripathi, 1959, *Rhabdosynochus* Mizelle & Blatz, 1941, *Murraytrema* Price, 1937, *Murraytrematoides* Yamaguti, 1958, *Rhamnocercus*, Monaco, Wood & Mizelle, 1954, *Rhamnocercoides* Luque & Iannacone, 1991 and *Nasobranchitrema* Yamaguti, 1965. The absence of an AAO within the Diplectanidae is, however, likely to be secondary for many of these species and represents many independent events within the evolutionary history of the family.

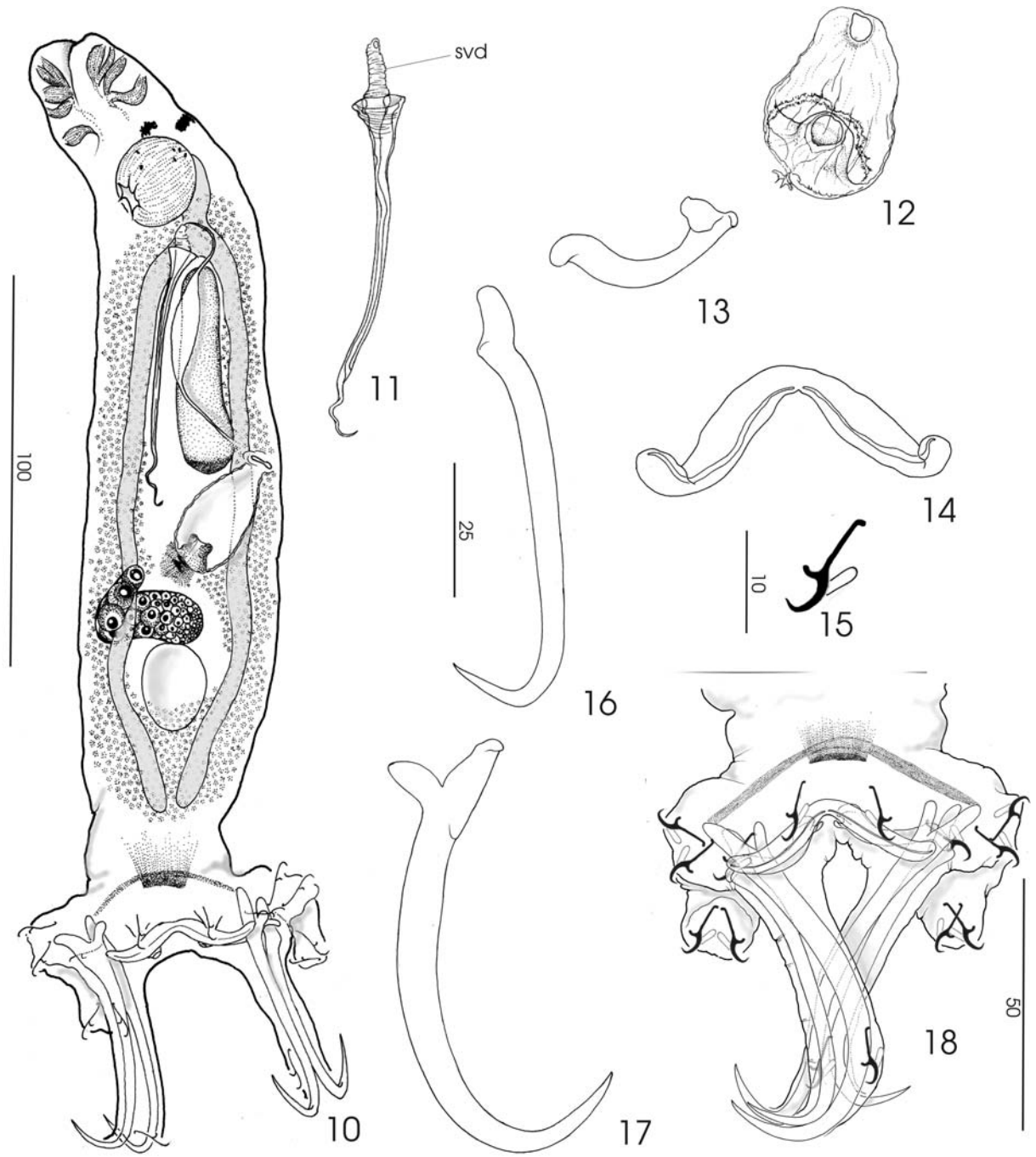
Among these genera, species of *Lobotrema*, *Murraytrema*, *Rhamnocercus* and *Rhamnocercoides* also possess an MCO composed of nested tubes, as in *Anoplectanum* spp. However, none of them depict the distal portion of the vas deferens as slightly sclerotised, or the superficial root of the ventral anchor as long or longer than the deep root, as observed in species of the new genus.

***Anoplectanum haptorodynatum* n. sp.**

Holotype, type-host and type-locality: MZUSP 5949a, *Petilipinnis grunniens*, Rio Tocantins, municipality of Porto Nacional, State of Tocantins, Brazil, 30/XII/2002, 10°41′45″S, 48°25′54″W. *Other specimens:* Paratypes (2), Rio Tocantins, municipality of Porto Nacional, State of Tocantins, 30/XII/2002, 10°41′45″S, 48°25′54″W (2 in MZUSP 5949b-c); paratypes (6), Rio Tocantins, municipality of Santa Helena, State of Tocantins, IV/2002 (2 in HWML 48094; 2 in INPA 347a,b; 2 in IOC 36504a-b); paratypes (2), Rio São Valério, municipality of Santa Rosa, State of Tocantins, 18/XI/2002, 11°21′57″S, 48°28′35″W (1 in MNHN 240 HG no. Ti 113; 1 in USNPC 95418); paratype (1), Rio Tocantins, municipality of Lajeado, State of Tocantins, 01/XII/2002, 09°42′55″S, 48°21′43″ W (MNHN 241HG no. Ti114); paratype (1), Rio Tocantins, municipality of Ipueiras, State of Tocantins, 21/XI/2002, 11°18′50″S, 48°27′26″W (INPA 348); paratype (1); Rio Tocantins, municipality of Peixe, State of Tocantins, 01/XII/2002, 11°46′19″S, 48°37′15″W (USNPC 95419).
Site of infection: Gills.
Etymology: The specific epithet comes from the greek (*dynatos* = powerful) and refers to the presence of elongate anchors in the haptor.

Description (Figures 10–18)

[Based on 14 specimens.] Body 343 (260–420; n = 7) long, greatest width 62 (46–91; n = 8), usually at level of testis. Four pairs of head organs well developed, located in cephalic lobes and adjacent cephalic areas. Pharynx 29 (22–34; n = 10) in diameter; oesophagus short. Haptor *c*.3 times wider than long. Ventral 74 (68–79; n = 6) long, 18 (14–21; n = 5) wide, with well developed superficial and deep roots of similar length, elongate shaft and recurved point. Dorsal anchor 71 (65–74; n = 7) long, 12 (10–14; n = 5) wide, with conspicuous deep root, inconspicuous superficial root, straight shaft and recurved point. Ventral bar with blunt extremities, 49 (46–54; n = 4) long. Dorsal bar 27 (25–36; n = 7) long, with blunt, depressed distal end and expanded proximal end. Hooks 12 (11–12; n = 17) long, similar, with erect thumb, shaft and recurved point; shaft with proximal point recurved. Male copulatory organ (MCO) 59 (48–68; n = 10) long, with distal portion



Figures 10–18. *Anoplectanum haptorodynatum* n. sp. 10. Holotype (ventral). 11. Male copulatory organ. 12. Vagina. 13. Dorsal bar. 14. Ventral bar. 15. Hook. 16. Dorsal anchor. 17. Ventral anchor. 18. Haptor (ventral). Figs 11–14, 16 are to the 25 μm scale. Fig 15 is to the 10 μm scale. *Abbreviation*: svd, sclerotised distal portion of vas deferens. *Scale-bars*: 10, 100 μm; 11–14,16, 25 μm; 15, 10 μm; 18, 50 μm.

of external tube sinuous and aperture of internal tube subterminal. Prostatic reservoir elongate. Germarium pyriform; oviduct, oötype, uterus and eggs not observed. Vaginal atrium wide, urn-shaped; proximal floor heavily sclerotised with projecting central aperture.

Remarks

Anoplectanum haptorodynatum n. sp. is characterised by the presence of: (1) ventral and dorsal anchors with an elongate shaft (Figures 16–18); (2) a vaginal atrium which is wide and urn-shaped, with a heavily sclerotised floor and a projecting central aperture (Figure 12); and (3) the external tube of the MCO is sinuous distally (Figure 11).

Anoplectanum microsoma n. sp.

Holotype, type-host and type-locality: MZUSP 5948a, *Pachyurus junki*, Rio Tocantins, municipality of Santa Helena, State of Tocantins, Brazil, IV/2002.
Other specimens: Paratypes (2), Rio Tocantins, municipality of Peixe, State of Tocantins, 01/XII/2002, 11°46′19″S, 48°37′15″W (2 in MZUSP 5948b-c); paratypes (5), Rio Tocantins, municipality of Santa Helena, State of Tocantins, IV/2002 (2 in INPA 346a,b; 2 in IOC 36503a-b; 1 in USNPC 95416); paratypes (2), Rio Tocantins, municipality of Ipueiras, State of Tocantins, 21/XI/2002, 11°18′50″S, 48°27′26″W (1 in MNHN 242HG no. Ti115; 1 in USNPC 95417); paratype (1), Rio Santa Tereza, State of Tocantins, 08/VII/2003 (MNHN 243HG no. Ti 116); voucher (1), host: *Petilipinnis grunniens*, Rio Tocantins, municipality of Peixe, State of Tocantins, 01/XII/2002, 11°46′19″S, 48°37′15″W (HWML 48092); vouchers (1), *P. grunniens*, Rio Tocantins, municipality of Porto Nacional, State of Tocantins, 30/XII/2002, 10°41′45″S, 48°25′54″W (HWML 48093).
Site of infection: Gills.
Etymology: The specific epithet derives from the Greek (mikros = small; soma = body) and alludes to the small size of this species: it is treated as a noun.

Description (Figures 19–27)

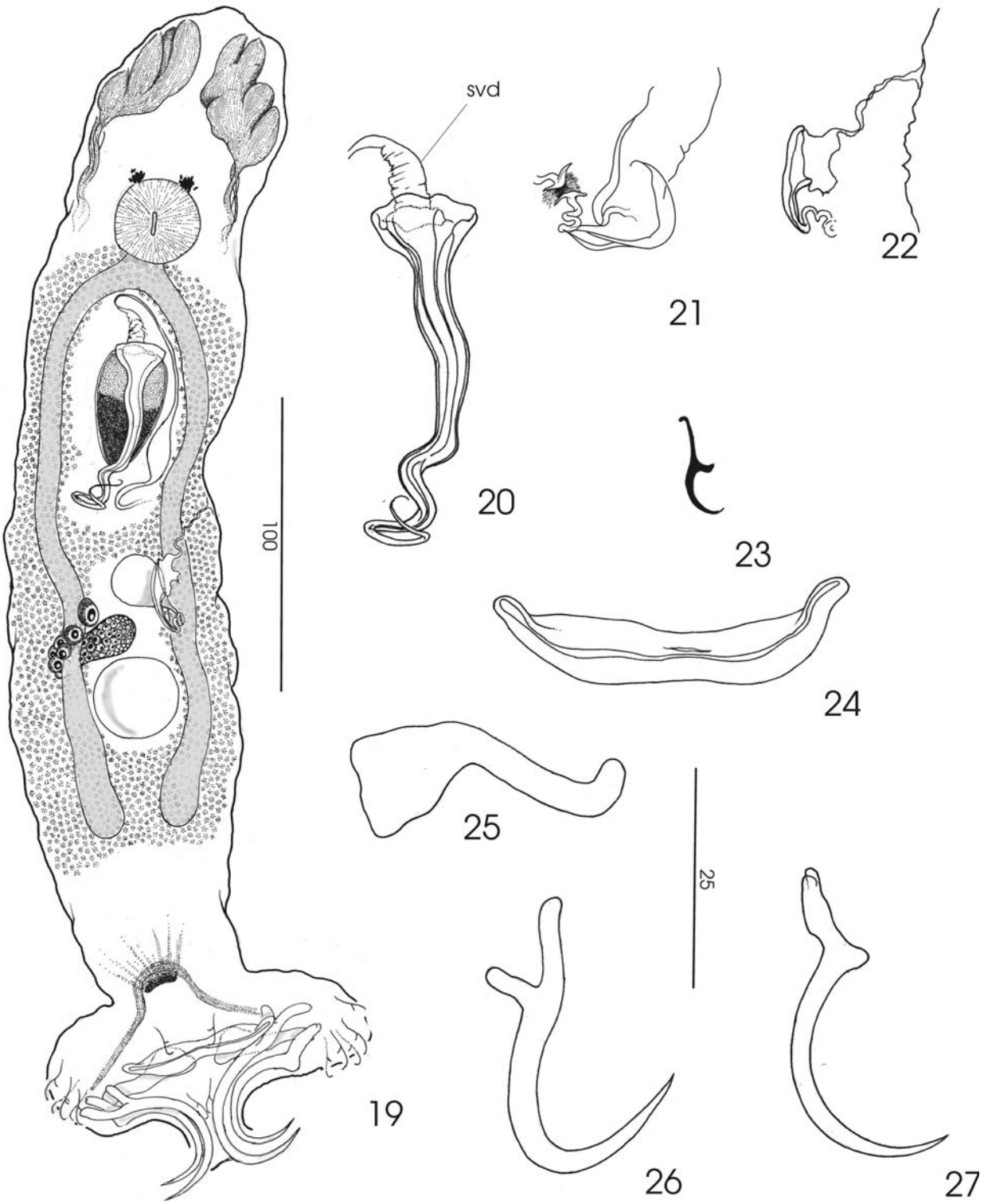
[Based on 13 specimens.] Body 275 (270–280; n = 2) long, greatest width 46 (36–53; n = 8), usually at level of testis. Head organs well developed; 3 pairs, located in cephalic lobes and adjacent cephalic areas. Pharynx 23 (19–26; n = 6) in diameter; oesophagus short or inconspicuous. Haptor, *c*.3 times wider than long. Ventral anchor 31 (26–35; n = 4) long, 11 (10–12; n = 2) wide, with superficial root longer than deep root, superficial root continuous with shaft, and shaft and point about equal in length. Dorsal anchor 28 (22–32; n = 5) long, 10 (9–12; n = 7) wide, with long, conspicuous deep root, inconspicuous superficial root, shaft and point evenly curved. Ventral bar 37 (36–38; n = 5) long, with tapered extremities. Dorsal bar 25 (23–27; n = 4) long, spatulate proximally, bent distally. Hooks similar, with proximally recurved shank, depressed thumb and short recurved point; each 11 (10–12; n = 28) long. Male copulatory organ (MCO) coiled distally, 40 (36–43; n = 11) long. Prostatic reservoir ovoid, divided into 2 bands, dorsal to MCO. Germarium pyriform, loops right intestinal caecum; oviduct, oötype uterus and eggs not observed. Vaginal atrium muscular with funnel-shaped proximal sclerotisation; vaginal duct sclerotised.

Remarks

Anoplectanum microsoma n. sp. is characterised by presenting the following characteristics: (1) a sclerotised, funnel-shaped vaginal atrium (Figure 22); (2) the proximal extremity of the dorsal bar strongly expanded (Figure 25); (3) the distal extremity of the MCO coiled (Figure 20); and (4) the ventral and dorsal anchors with a relatively short shaft (Figures 26, 27). The new species can be easily distinguished from the type-species of the genus, *A. haptorodynatum* n. sp., by the comparative morphology of the anchors, vaginal atrium and MCO.

Spinomatrix n. g.

Diagnosis
Body fusiform, divided into cephalic area, trunk, peduncle and haptor. Tegument thin, smooth. Four groups of cephalic lobes with head organs. Eye-spots present, 4. Pharynx spherical, bulbous; mouth mid-ventral, subterminal. Intestinal caeca 2, non-confluent. Peduncular spines present, with superficial and deep roots. Haptor laterally expanded; ventral and dorsal squamodiscs present. Ventral and dorsal pairs of anchors, dissimilar. Ventral bar with antero-medium constriction, 2 short postero-submedian, projections for articulation with dorsal bar and longitudinal groove.



Figures 19–27. Anoplectanum microsoma n. sp. 19. Holotype (ventral). 20. Male copulatory organ. 21–22. Vagina. 23. Hook. 24. Ventral bar. 25. Dorsal bar. 26. Ventral anchor. 27. Dorsal anchor. *Abbreviation*: svd, sclerotised distal portion of vas deferens. *Scale-bars*: 19, 100 μm; 20–27, 25 μm.

Hooks 7 pairs, with typical distribution of family (five pairs ventral and two dorsal), similar; dorsal and ventral sub-globose, muscular structures present bearing spines disposed in rosette. Male copulatory organ (MCO) straight, oriented posteriorly, formed by 2 nested tubes; external tube twisted; accessory piece absent. Prostatic reservoir single. Vas deferens apparently loops left intestinal caecum. Two seminal vesicles tandem, piriform, simple expansions of vas deferens. Vagina muscular, with sinistro-ventral aperture. Germarium loops right intestinal caecum. Common genital pore ventral. Vitelline follicles dense, co-extensive with intestinal caeca. Parasites of species of Pachyurinae. Type-species: *S. penteormos* n. sp.
Etymology: The generic epithet is derived from the Greek and refers to the extensive presence of spines on the peduncle and haptor of the species of the genus (*spina* = thorn; *matrix* = where something originates).

***Spinomatrix penteormos* n. sp.**

Holotype, type-host and type-locality: MZUSP 5947, *Pachyurus adspersus*, Jusante Cachoeirinha da brecha, Rio Piranga, municipality of Vau-Açú, State of Minas Gerais, Brazil (20°32′S,42°57′W); 20/Jan/2003.
Other specimens: Paratypes (6) (IOC 36502a-f), (6) (INPA 345a-f), (6) MZUSP (5947b-g), (5) (USNPC 95415), (3) (HWML 48091), (6) (MNHN 248 HG no. Ti 122, Ti122 bis, Ti123, Ti 124, Ti 125, Ti 125bis).
Site of infection: Gills.
Etymology: The specific name is derived from the Greek and refers to the presence of five types of anchoring structures on the haptor and peduncle of the species of the genus: ventral and dorsal anchors, peduncular spines, hooks, haptoral spines, and squamodiscs (*pente* = five; *ormos* = anchorage).

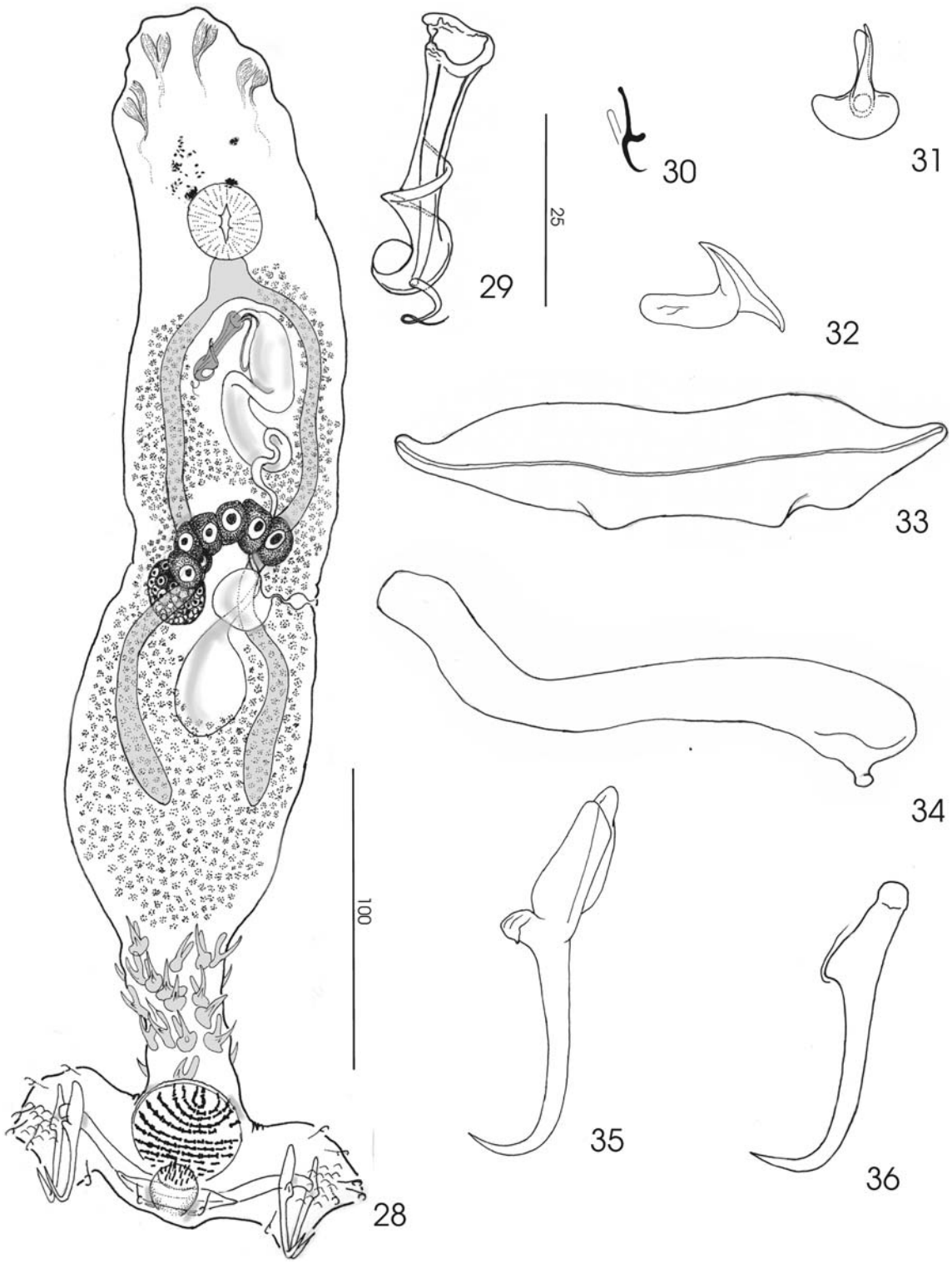
Description (Figures 28–38)

[Based on 33 specimens.] Body 439 (385–475; n = 5) long, 76 (45–95; n = 5) wide at level of testis. Eye-spots 4; those of posterior pair closer together; accessory granules often scattered in cephalic area and anterior trunk. Head organs organised in 4 groups which are associated with each cephalic lobe. Pharynx 34 (30–40; n = 13) in diameter; oesophagus short. Peduncle conspicuous, as long as haptor. Peduncular spines 13 (10–15; n = 8) long, 15 (12–18; n = 8) wide, with wide deep root. Haptor 47 (35–65; n = 5) long, 148 (115–170; n = 5) wide. Tegumental scales on ventro- and dorsolateral surfaces of haptor (at level of anchor base). Squamodisc with *c*.11 concentric rows of sclerites, 38 (30–47; n = 9) long, 47 (40–58; n = 8) wide. Ventral anchor 49 (45–53; n = 7) long, 22 (17–25; n = 7) wide, with short superficial root, elongate, complex deep root, long, straight shaft and evenly curved point. Dorsal anchor 43 (40–44; n = 5) long, 18 (17–19; n = 5) wide, with truncate superficial root, long deep root, long, straight shaft and short, recurved point. Ventral bar 64 (53–77; n = 14) long. Dorsal bars 62 (55–74; n = 11) long. Hooks with proximal extremity of shank slightly bulbous, depressed thumb, straight shaft and recurved point; each hook 11 (10–12; n = 11) long. Dorsal and ventral haptoral bulbous structure 19 (12–26; n = 10) in diameter, bears spines with wide base, arranged in rosette. Male copulatory organ (MCO) 38 (30–48; n = 14) long; distal half of external tube twisted; internal tube well separated from external tube, exposed sub-terminally and coiled distally. Testis sub-ovate, post-ovarian; 23 (14–30; n = 4) long, 14 (12–15; n = 4) wide. Prostatic reservoir elongate. Vagina with subterminal atrium. ovate Seminal receptacle ovate. Oötype, uterus and eggs not observed.

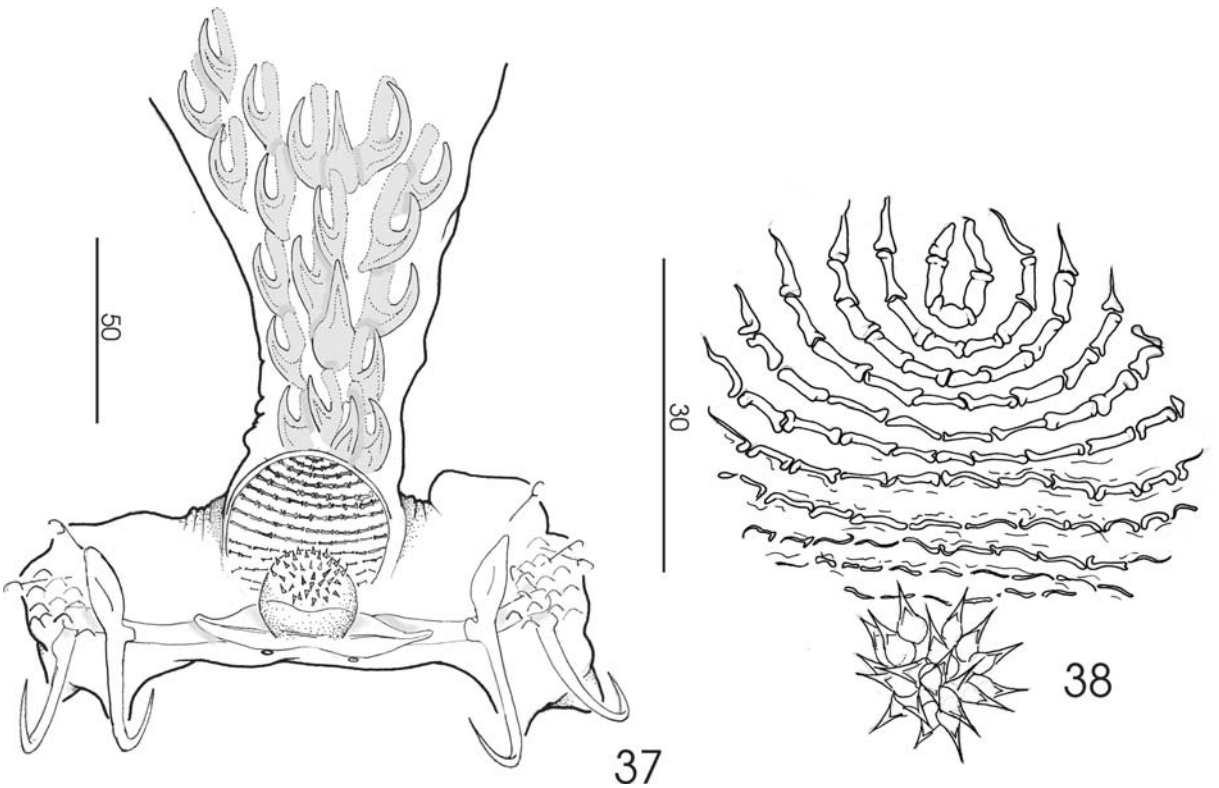
Remarks

Several putative synapomorphies suggest that *Spinomatrix* n. g. is phylogenetically close to genera traditionally allocated to the Rhamnocercinae Monaco, Wood & Mizelle, 1954, i.e. *Rhamnocercus* Monaco, Wood & Mizelle, 1954 and *Rhamnocercoides* Luque & Iannacone, 1991. Species of these taxa share the presence of accessory haptoral spines and peduncular spines which bear both superficial and deep roots. Although species of the new genus may appear similar to species of *Diplectanocotyla* Yamaguti, 1953 in terms of sharing peduncular spines, these are not provided with roots in the later taxon (see Mendoza-Franco et al., 2004) and are likely not homologous structures.

Some fundamental morphological differences among the representatives of the ''Rhamnocerci-



Figures 28–36. *Spinomatrix penteormos* n. sp. 28. Holotype (ventral view). 29. Male copulatory organ. 30. Hook. 31. Peduncular spine, ventral view. 32. Peduncular spine, lateral view. 33. Ventral bar. 34. Dorsal bar. 35. Ventral anchor. 36. Dorsal anchor. *Scale-bars*: 28, 100 μm; 29–36, 25 μm.



Figures 37–38. *Spinomatrix penteormos* n. sp. 37. Detail of the haptor (ventral). 38. Squamodisc and spines located on the bulbous muscular structure of the haptor. *Scale-bars*: 38, 50 μm; 39, 30 μm;

nae'' and *Spinomatrix*, however, support the taxonomic and evolutionary validity of the new genus proposed herein. In contrast to the species of the ''Rhamnocercinae'', the only species of *Spinomatrix* exhibits both ventral and dorsal squamodiscs (Figures 28, 37), and ventral and dorsal bulbous muscular pads on the haptor (Figures 28, 37) armed with spines arranged in a rosette (Figs. 37, 38). Furthermore, the single species of *Spinomatrix* has scales located ventro- and dorso-laterally on the haptor (Figure 37). In species of *Rhamnocercoides* and *Rhamnocercus*, the ventral and dorsal haptoral spines, in multiples of three, are perpendicular to the bars and not associated with a bulbous structure. The peduncular spines of the species of *Spinomatrix* also differ from those of species of *Rhamnocercoides* and *Rhamnocercus* by having a superficial root which is much longer than the deep root.

Spinomatrix penteormos n. sp. is the only diplectanid to possess both squamodiscs and peduncular spines (with deep and superficial roots) simultaneously. The concurrent presence of these structures in a single species provides evidence for the resolution of the argument on the homology of the echinodisc (*sensu* Hargis, 1955). The echinodisc, i.e. the cluster of peduncular spines of the rhamocercines, is considered by Hargis (1955) homologous to the squamodisc, based on their comparable function and position. Seamster & Monaco (1956), however, rejected Hargis' (1955) proposal based on their belief that the origin of the peduncular and haptoral spines is parenchymal, whereas the squamodisc is of epidermal origin. The discovery of the new species thus supports Seamster & Monaco's (1956) opinion. Not only are these structures concurrent, but they also occur in distinct positions on the peduncle (spines) and haptor (squamodics) of *S. penteormos*, and thus rejecting the hypothesis for their homology is justifiable.

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