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A New Brazilian Schendylid Centipede (Chilopoda: Geophilomorpha) with Unusually Structured Antennae

Luis Alberto Pereira[1], Donatella Foddai[2] and Alessandro Minelli[2]

[1]Museo de La Plata, Argentina
[2]Dipartimento di Biologia, Università di Padova, Italia

Abstract. In *Schendylops schubarti* n. sp. from Brazil: Pernambuco: Tupi the fourth antennal article is characterised by unusual chaetotaxy and by elongation. Oddly, the more proximal as well as the more distal articles are not modified. This morphological condition is quite rare in arthropods and thus far unique in centipedes.

Key words. Myriapoda, Schendylidae, new species, Brazil, antennal pattern, segment differentiation.

1. INTRODUCTION

The antennae of geophilomorph centipedes are generally characterised by a singular uniformity of structure. These appendages are always comprised of 14 articles, possibly the outcome of a stereotyped pattern of segmentation (Minelli et al. 2000). Their overall shape exhibits some variation, from setiform to slightly moniliform, but it is distinctly clavate in Ballophilidae and apically attenuate in Himantariidae. Within a given family, however, the shape of the antennae is usually quite uniform, although their length may vary in relation to body length or to the size of the cephalic plate, even among close relatives. For example, the antennae are unusually elongate in the recently described *Geophilus persephones* Foddai & Minelli, 1999, a subterranean species from a Pyrenean cave (Foddai & Minelli 1999). Within the Schendylidae, however, the antennae seem to be more plastic than in all other geophilomorph families. In particular, some species of the genera *Schendylops* Cook, 1899 and *Pectiniunguis* Bollman, 1889 have sexually dimorphic antennae (Pereira & Minelli 1996; Pereira 1999), as summarised in Tab. 1.

In all these species, however, both sexual and species-specific variation involve the whole appendage, by affecting its size or the number or distribution of sensory setae on the individual articles. But these differences are relatively trivial in respect to the singularly structured antenna of the new *Schendylops* species we describe in this paper. (This taxon was listed as *Schendylops* n.sp. in Foddai et al. 2000: 148.) In this case, a single antennal article is distinctly modified, in respect to the remaining articles of the same antenna as well as in comparison to the corresponding (fourth) article in the antenna of the other *Schendylops* species (and of schendylids in general). The most striking feature of this unusually structured antenna is the fact that the modification does not affect either the most proximal or

Tab. 1. Antennal traits showing (+) sexual dimorphism in some species of schendylid geophilomorphs (modified from Pereira 1999).

	density of setae	relative length of the antennae	relative width of the antennal articles
Schendylops pampeanus (Pereira & Coscarón, 1976)	+		
Schendylops perditus (Chamberlin, 1914)	+	+	+
Schendylops virgingordae (Crabill, 1960)	+	+	+
Schendylops coscaroni (Pereira & Minelli, 1996)	+		+
Pectiniunguis argentiniensis Pereira & Coscarón, 1976	+		+

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Tab. 2. Synopsis of diagnostic characters for *S. schubarti* n. sp., *S. paolettii* and *S. perditus*.

	schubarti	*paolettii*	*perditus*	*janauarius*	*lomanus*
body length (mm)	17	16	13	21	17
pairs of legs (♂,♀)	37, ?	35-37, 37-39-41	35, 37	43, ?	?, 43
antennae of the ♂ longer than those of the ♀	?	no	yes	?	?
a.a. XIV: claviform sensilla: internal, external	2, 7	2, 18	?, ?	3, 17	1, 9
a.a. XIV: tip of apical sensilla	tripartite	undivided	tripartite	undivided	undivided
number of apical sensilla	4-5	5	5	5	5
standard sensilla[1]	tripartite	undivided	tripartite	undivided	undivided
dorsal standard sensilla[1] on a.a. II, V, IX, XIII	1, 2, 1, 1	1, 1, 1, 1	1, 2, 2, 2	1, 1, 2, 2	0, 0, 1, 1
dorsal extra sensilla[2] on a.a. II, V, IX, XIII (fig. 3a)	1, 1, 1, 1	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0
dorsal extra sensilla[3] on a.a. II, V, IX, XIII (fig. 4c)	0, 0, 2, 3	0, 0, 1, 1	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0
ventral standard sensilla[1] on a.a. II, V, IX, XIII	1, 1, 1, 1,	1, 1, 1, 1	1, 1, 1, 1	1, 1, 1, 1	1, 1, 1, 1
extra sensilla[4] on a.a. II, V, IX, XIII, ventral (fig. 3a)	0, 1, 1, 1	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0
extra sensilla[5] on a.a. II, V, IX, XIII, ventral	0, 0, 0, 0	0, 0, 1, 1	0, 0, 0, 0	0, 0, 0, 0	0, 0, 0, 0
a.a. IV much longer than a.a. I–III and V–XIII and provided with numerous small setae (fig. $1S_{IV}$)	yes	no	no	no	no
a.a. I and II and lateral margins of clypeus with numerous, distally very thin setae	no	no	yes	no	no
clypeal setae: postantennal, medial, prelabral	1+1, 6+6, 1+1	1+1, 2+2, 1+1	1+1, 6+8, 1+1	1+1, 5+5, 1+1	1+1, 4+4, 1+1
teeth of labrum: central arc, lateral pieces	10, 7+7	15, 3+4	11, 6+5	10, 6+5	13, 4+4
dentate lamella of mandible: teeth per block	3, 2, 4	3, 3, 2	3, 3, 2 or 3, 3, 3	4, 3, 2 or 3, 3, 2	3, 3, 2
number of hyaline teeth, pectinate lamella	22	20	18	16	?
I maxillae: setae on coxosternum	1+1	absent	1+1	absent	absent
I maxillae: setae on median projection, ventral	2+2 (large), 1+1 (small)	1+1	2+2	1+1	1+1
I maxillae: setae on II article of telopodite, ventral	3+3	1+1	3+3	1+2	1+1
I maxillae: sensilla on II article of telopodite, dorsal	5+5	3+3	4+4	3+3	3+3
II maxillae: setae on coxosternum	ca. 12+11	ca. 6+6	ca. 7+6	ca. 8+8	ca. 7+6
II maxillae: teeth (v., d.) on internal edge of claw	12, 18	10, 10	11, 17–18	7, 10	12–14, 17–18
a blunt but not sclerotized prominence on medial edge of forcipular trochanteropraefemur	yes	no	no	no	no
basal internal edge of forcipular tarsungulum	smooth	with a small pale tooth	smooth	with a small tooth	with a small tooth
poison calyx length (length to width ratio)	3:1	2:1	1.5:1	1:1	2:1
poison calyx symmetric (in dorsal or ventral view)	yes	no	no	yes	no
poison ducts[6] on the external side of the calyx	yes	no	no	no	yes
last sternum with pore fields	♂: XIX of 37 ♀: unknown	♂: XIV of 37 ♀: XIV of 39	♂: XIV of 35 ♀: XV of 37	♂: XV of 43 ♀: unknown	♂: unknown ♀: XVIII of 43
apical spines on the praetarsus of last pair of legs	1	2	1	3-4	2
metatarsus vs. tarsus of last pair of legs	much longer	same length	much longer	same length	much longer
pleurites at the side of last praetergum	absent	absent	present	absent	present
sternum of last leg-bearing segment of ♂	trapeziform	subtriangular	trapeziform	trapeziform	trapeziform

[1] standard sensilla: sensilla of the same kind as those at the apex of a.a. XIV present on an internal lateral area (ventral) and on an external lateral area (dorsal) of a.a. II, V, IX and XIV.
[2] extra sensilla: sensilla accompanying the standard sensilla, but different in shape (with undivided tip) and size (smaller).
[3] extra sensilla: sensilla accompanying the standard sensilla, but different in size (smaller) and colour (darker).
[4] extra sensilla: sensilla accompanying the standard sensilla, but with different shape and size.
[5] extra sensilla: sensilla accompanying the standard sensilla, but different in size (smaller) and colour (darker).
[6] poison ducts: the whole of minute ducts forming the poison calyx.

the most distal articles, which are usually the most plastic elements of the antenna in arthropods. Instead, the fourth, modified article of the new species lies between normal articles I–III and V–XIV. As we discuss below, corresponding modifications of an intermediate portion of an arthropod antenna, not affecting the proximal and distal parts of the same, are extremely unusual.

2. TAXONOMY

2.1. Genus *Schendylops* Cook, 1899 (Family Schendylidae)

Diagnosis. Pleurites of second maxillae not fused to coxosternum. Apical claw of second maxillae pectinate on both dorsal and ventral edges. Sterna with pore fields. Last pair of legs with seven podomeres; praetarsus in form of a small hirsute tubercle or replaced by a small spine or altogether absent. Coxopleura of last leg-bearing segment each with two internal coxal organs of simple structure ('homogeneous coxal glands' sensu Brölemann & Ribaut 1912).

2.2. *Schendylops schubarti* n.sp.

Diagnosis. A *Schendylops* species without pore field on the first sternum and with pore fields present on some anterior sterna only. Other Neotropical species of the same genus share these traits (i.e., *S. anamariae* (Pereira, 1981), *S. andesicola* (Chamberlin, 1957), *S. dentifer* (Chamberlin, 1957), *S. edentatus* (Kraus, 1957), *S. interfluvius* (Pereira, 1984), *S. janauarius* (Pereira, Minelli & Barbieri, 1995), *S. lomanus* (Chamberlin, 1957), *S. oligopus* (Pereira, Minelli & Barbieri, 1995), *S. pallidus* (Kraus, 1955), *S. paolettii* (Pereira & Minelli, 1993), *S. perditus* (Chamberlin, 1914), *S. peruanus* (Turk, 1955), *S. potosius* (Chamberlin, 1956), *S. titicacaensis* (Kraus, 1954) and *S. virgingordae* (Crabill, 1960)), but the new species can be differentiated very easily from all of them (and from all remaining schendylids) by the very unusual elongation of the forth antennal article, which is much longer than antennal articles I–III and V–XIII (at least in the male; the female is unknown). In addition, several species among those listed above differ from *S. schubarti*, either in the shape of the sternal pore fields (in that they have two small additional anterolateral clusters of pores, separated from the main field), or in the extremely low (*S. oligopus*, with 27–29 in the male) or quite high (at least 51 in the female) number of pairs of legs. Therefore, for a confident identification of the new species, it is only necessary to compare it to those with the same form and distribution of ventral pores and similar range of pairs of legs, i.e. *S. perditus*, *S. paolettii*, *S. janauarius* and *S. lomanus* (see Tab. 2).

Type material. Holotype ♂ with 37 pairs of legs, body length 17 mm, from Brazil: Pernambuco: Tupi, close to Ipojuca, 17.II.1935, Otto Schubart legit.

Depository of type. Museu de Zoologia da Universidade de São Paulo, Brazil.

Description. Holotype ♂ with 37 pairs of legs, body length 17 mm, maximum body width 0.9 mm. Colour (of preserved specimen in alcohol) pale ochre with forcipular segment darker.

Antennae ca. 2.7 times as long as cephalic plate, distally slightly attenuate. Fourth antennal article (a.a.) unusually elongate, ca. 1.9 times as long as wide (Figs. 1, 8). Setae on a.a. I to V–VI (except IV) of different lengths and relatively few in number, setae on a.a. VII to XIV progressively shorter and more numerous towards tip of appendage (Fig. 1); a.a. IV with numerous small setae characterised by their extremely thin, hyaline apical portion, visible only at high magnification, and occupying distal half of each seta (Fig. 1 s_{IV}). Terminal antennal article with ca. 7 claviform sensory setae on external border and ca. 2 on internal border (Fig. 2). Distal end of this a.a. with ca. 4–5 very small specialised setae ending in three small apical branches (Fig. 2). Dorsal and ventral surface of a.a. II, V, IX and XIII with very small specialised setae (Figs. 3–6; Tab. 3). On the ventral side these setae restricted to internal lateral area and represented by two different types: a and b. Type a setae very thin and not divided apically, type b setae very similar to those of apex of terminal antennal article (a, b, Fig. 3). Specialised setae on the dorsal side restricted to external lateral area and represented by three different types: a and b similar to a and b of ventral side and type c setae similar in size to type b, but much darker (ochreous) in colour (a, b, c, Fig. 4).

Cephalic plate slightly longer than wide (ratio 1.2: 1), shape and chaetotaxy as in Figs. 7–8.

Clypeus with 1+1 postantennal setae, 6+6 median setae and 1+1 praelabral setae (Fig. 9).

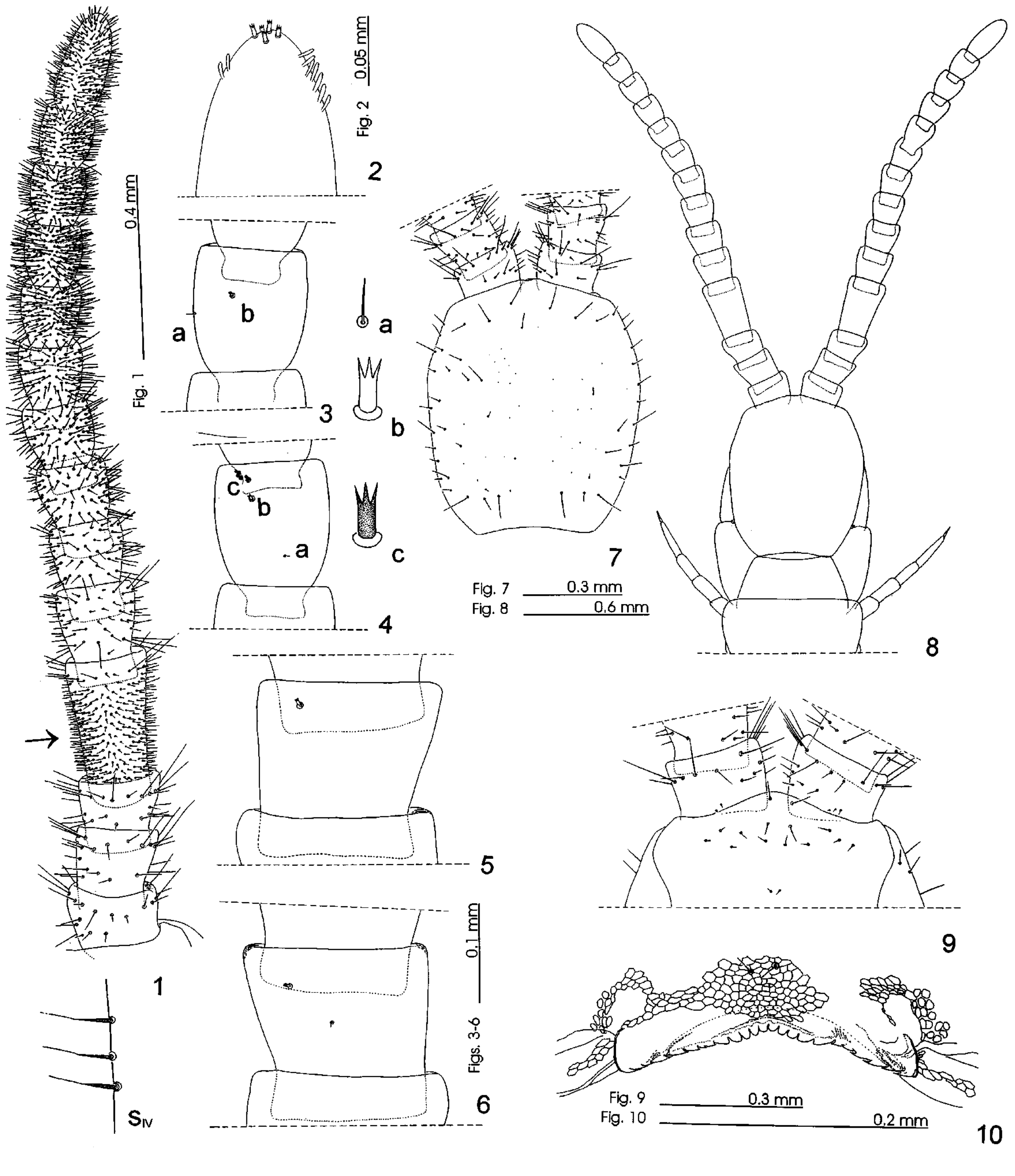
Labrum with 24 teeth, those of central arc dark, with round tip, lateral ones less sclerotized, but relatively long and sharply pointed (Fig. 10).

Tab. 3. Number of different kind of sensilla on each antennal article in the holotype of *Schendylops schubarti* n.sp.

	ventral				dorsal			
	a	b	c	Figs.	a	b	c	Figs.
II		1		5	1	1		6
V	1	1			1	2		
IX	1	1			1	1	2	
XIII	1	1		3	1	1	3	4

Mandible: dentate lamellae subdivided into three distinct blocks, with 3, 2, 4 teeth on right (Fig. 11) and 3, 3, 3 teeth on left mandible (Fig. 12), pectinate lamella with ca. 22 hyaline teeth.

First maxillae with large lappets on both coxosternum and telopodites (Fig. 15). Coxosternum with 1+1 very small setae, median projections of coxosternum well developed and provided with 2+2 large setae and 1+1 small setae (Figs. 13, 15). Article II of telopodite with 3+3 ventral setae and 5+5 dorsal sensilla (Figs. 14–15). Second maxillae (Figs. 13, 16–17) with 12+11 setae on coxosternum, arranged as in Fig. 13. Apical claw of telopodite bipectinate, ventral edge with ca. 12 teeth, dorsal with ca. 18 teeth (Fig. 16).



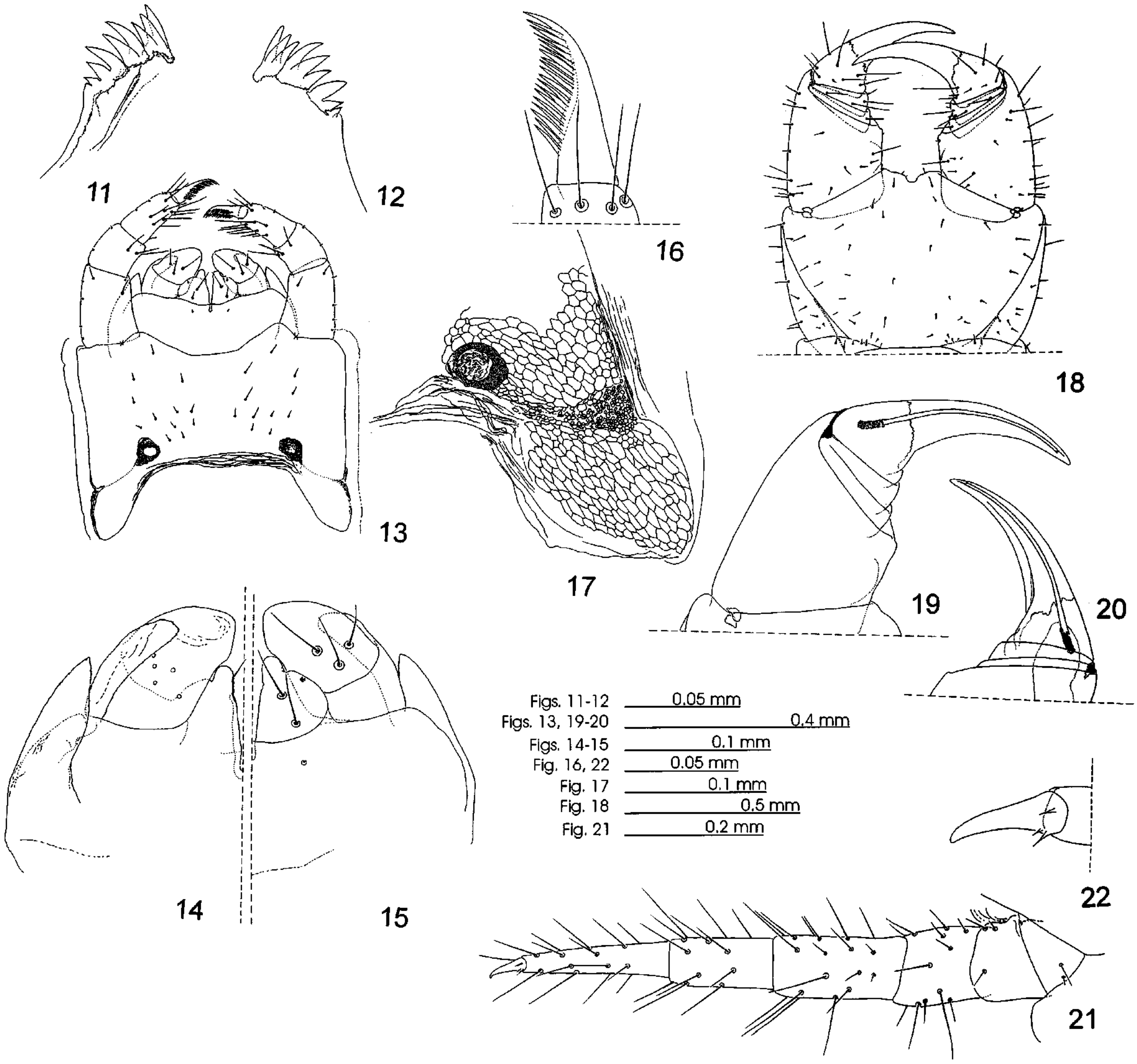
Figs. 1–10. *Schendylops schubarti* n. sp. (♂ holotype; Brazil: Pernambuco: Tupi). **1.** Left antenna, ventral, arrow points to the area from where few setae are drawn at a higher magnification (s_{IV}: setae a.a. IV). **2.** apical region of left a.a. XIV, ventral. **3.** left a.a. XIII, ventral (**a, b:** a, b type setae). **4.** left a.a. XIII, dorsal (**a, b, c:** a, b, c type setae). **5.** left a.a. II, ventral. **6.** left a.a. II, dorsal. **7.** cephalic shield and bases of antennae. **8.** cephalic shield, antennae, forcipular segment and first leg-bearing segment. **9.** clypeus and bases of antennae. **10.** labrum.

Forcipulae: when closed, telopodites do not extend beyond anterior margin of head. Basal plate with irregular transverse median row of ca. 11 setae and few additional smaller ones scattered on remaining surface. All articles of telopodites lack dark sclerotized teeth. Internal edge of trochanteropraefemur with apical very small, blunt and not sclerotized prominence (Figs. 18–19). Calyx of poison gland cylindrical (Figs. 19–20). Chaetotaxy of coxosternum and telopodites as in Fig. 18.

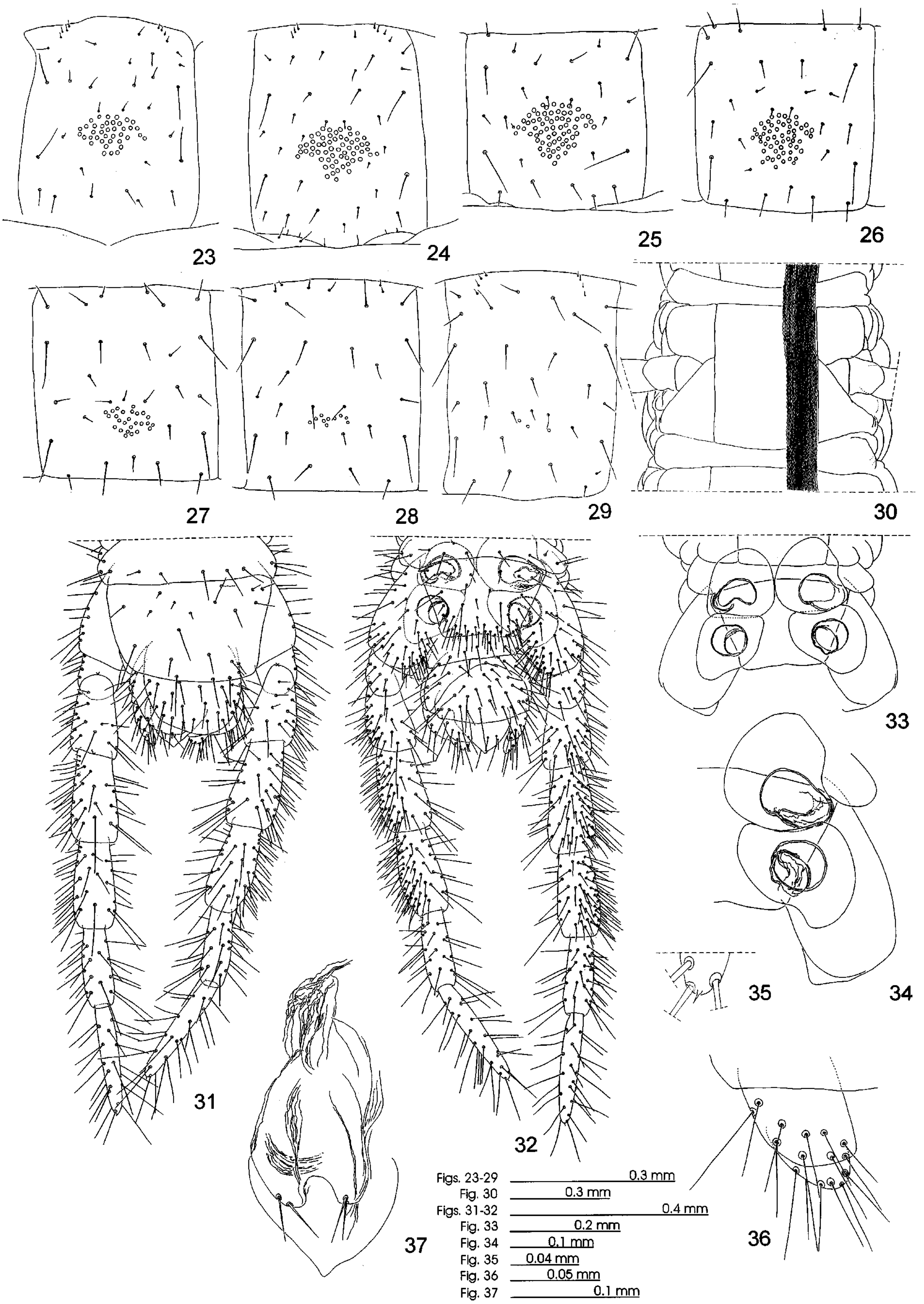
Walking legs with chaetotaxy (Fig. 21) uniform throughout body length. Claws ventrobasally with two spines (one anterior, one posterior); a third smaller spine occurs internally very close to posterior one (Fig. 22).

Sterna: pore fields on sterna II–XIX only. All fields undivided, shape changing along trunk as in Figs. 23–29. Number of pores on selected sterna: on sternum II, 39 pores; on IV, 60; on VIII, 66; on XIII, 56; on XVI, 26; on XVIII, 10; on XIX, 3.

Last leg-bearing segment apparently without pleurites at sides of praetergum. Praesternum not divided along sagittal plane; shape and chaetotaxy of tergum and sternum as in Figs. 31–32. Coxopleura slightly protruding at their distal ventral ends, setae numerous on



Figs. 11–21. *Schendylops schubarti* n. sp. (♂ holotype; Brazil: Pernambuco: Tupi). **11.** dentate lamella of right mandible. **12.** dentate lamella of left mandible. **13.** first and second maxillae, ventral. **14.** left first maxilla, dorsal. **15.** left first maxilla, ventral. **16.** claw of right second maxilla, dorsal. **17.** detail of posterior external region of left second maxilla, ventral. **18.** forcipular segment with poison claws, ventral. **19.** detail of poison gland in right forcipular telopodite, ventral. **20.** detail of poison gland in right poison claw, dorsal. **21.** right leg IV, ventral. **22.** claw of right leg IV, antero-ventral.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Figs. 23-29 0.3 mm
Fig. 30 0.3 mm
Figs. 31-32 0.4 mm
Fig. 33 0.2 mm
Fig. 34 0.1 mm
Fig. 35 0.04 mm
Fig. 36 0.05 mm
Fig. 37 0.1 mm

ventral internal margin, the remaining surface with few larger setae. Two single ('homogeneous') coxal organs on each coxopleuron (Figs. 32–34). Coxal organs open on membrane between coxopleuron and sternum, partially covered by latter (Figs. 32–34). Last legs moderately inflated, with seven podomeres, shape and chaetotaxy as in Figs. 31–32. Praetarsus as a very small tubercle with 1 small apical spine (Fig. 35).

Terminal segments: intermediate tergum with posterior border convex, intermediate sternum with posterior margin slightly concave; first genital sternum with posterior margin convex (Figs. 31–32). Gonopods biarticulate, basal article with ca. 10 setae, apical article with ca. 6 setae (Fig. 36), penis dorsally with 2+2 apical setae (Fig. 37). Adult condition proved by abundant presence of spermatozoa (Fig. 30).

Female. Unknown.

Etymology. The species is named after its collector, the distinguished myriapodologist Otto Schubart (17.ii.1900–8.xi.1962).

3. DISCUSSION

The comparison of the new species with other species of *Schendylops* in terms of metric profiles of the antennae (Fig. 38) invites the following considerations. The exceptional length of the fourth antennal article of *S. schubarti* is remarkable both in comparison with the remaining articles of the same antenna (Fig. 38A) and with the length of the fourth antennal article in the other species. As to the width, all profiles, those of *S. schubarti* included, follow the same trend, i.e. a regular decrease from the base towards the tip of the antenna (Fig. 38B). The fourth article, with its remarkable length to width ratio (Fig. 38C) stands out also after normalising the ratios with respect to the length of the cephalic shield (Fig. 38D) or the total body length (Fig. 38E).

We cannot offer an explanation for the unusual plasticity within the geophilomorph centipedes of the antennae of some schendylid genera, and of *Schendylops* in particular. In the present context, however, it may be apt to cite some further examples of otherwise stable traits that only become variable, but then in very conspicuous way, in just one or a few scattered instances. For example, the flagellar axoneme with its 9+2 pattern of microtubules shared by most eukaryotes provided with cilia or flagella, but for a small number of exceptions, which are mostly concentrated in a few taxa, e.g. in the sperm cells of Diptera (DALLAI 1979). Eleven antennal articles are found in most Coleoptera, irrespective of the moniliform, setate, clavate or pectinate shape of the appendage and although beetle antennae with a reduced number of articles are far from rare, those with more than 12 are rare exceptions. However, more than 30 articles can be counted in some Rhipiceridae (LAWRENCE & BRITTON 1991) and even more in some Cerambycidae.

As we said in the introduction, arthropods with singularities occurring at mid-length without affecting the more proximal and the more distal articles of a relatively uniform appendage are far from frequent (MINELLI 1996). The most conspicuous examples are provided by copepods and by blister beetles. In most copepods, the male antennulae exhibit a singularity (geniculation) at mid-length (HUYS & BOXSHALL 1991). In the males of some species of blister beetles (Coleoptera Meloidae), articles 6 and 7 (of 11) of the antenna are conspicuously modified, whereas those more proximal or distal to them follow the usual pattern. A most interesting feature of these animals is, that the occurrence of modified appendages is accompanied by unusually complex post-embryonic development (in the hypermetamorphic blister beetles) or by the occurrence of modifications along the main body axis (body flexure in copepods) (MINELLI 1996). As to myriapods, a potential candidate for inclusion in this small collection of antennae with nonterminal modification is *Choneiulus subterraneus* (Silvestri, 1903): the females of some populations of this species have a curious a.a. II with a very narrow proximal 'stalk' and a wider apical portion, dorsad displaced in respect to the stalk (ENGHOFF 1984). In the case of *S. schubarti* (whose development is completely unknown) no species-specific singularity is found along the main body axis, but a 'mid-body anomaly' along the main body axis belongs to the ground-plan of Chilopoda (MINELLI et al. 2000). One is tempted to ask whether there is a topological equivalence between the mid-body anomaly and the modified fourth antennal article of *S. schubarti* within their respective axis. To be sure, only adequate studies of expression patterns of relevant position-specifying genes would provide convincing evidence.

In the case of *Schendylops schubarti*, the peculiar antennal structure is quite probably independent from and subsequent to the segmentation of the appendage.

Figs. 23–37. *Schendylops schubarti* n. sp. (♂ holotype; Brazil: Pernambuco: Tupi). **23–29.** sterna II, IV, VIII, XIII, XVI, XVIII, XIX. **30.** bundles of sperm cells at the level of the leg-bearing segment XXIV. **31.** last leg-bearing segment and terminal segments, dorsal. **32.** the same, ventral. **33.** detail of right and left coxal organs, ventral. **34.** detail of left coxal organs, ventral. **35.** detail of distal end of last podomere of right last leg, ventral. **36.** right gonopod, ventral. **37.** penis, dorsal.

According to the model developed by MINELLI et al. (2000), the fourth antennal article of geophilomorph centipedes would be the middle one of the triplet derived from the meromeric (secondary) segmentation of the second element of a primary set of five holosegments (primary segments; cf. MINELLI 2000).

The chaetotaxy of the elongate fourth antennal article of *S. schubarti* is characterised by unusually high density of sensory setae, coupled with the disruption of the usual (although not absolutely strict) regularity of their distribution on the article's surface. These two features (increased density and loss of pattern) are often coupled. For instance, in earthworms the setae are regularly arranged when their number is small, but as soon as their number becomes larger than 8, they become distributed around the whole ring (perichaetinae distribution, as in many Megascolecidae; SIMS 1982). Another example are those families of actinedidan mites (e.g., Trombidiidae and Erythraeidae) which are hypertrichous, i.e. covered by a very large number of unpatterned setae, at variance with the usual constant pattern found in the remaining majority of actinedids.

Increased density is sometimes due to miniaturisation. For instance, in the very tiny spider *Comaroma simonii* Bertkau, 1878 (Araneae: Anapidae), just 1.6 mm body length, the slit sense organs on the prosomal appendages have lost their usual patterned and symmetrical distribution (KROPF 1997). However, a similar

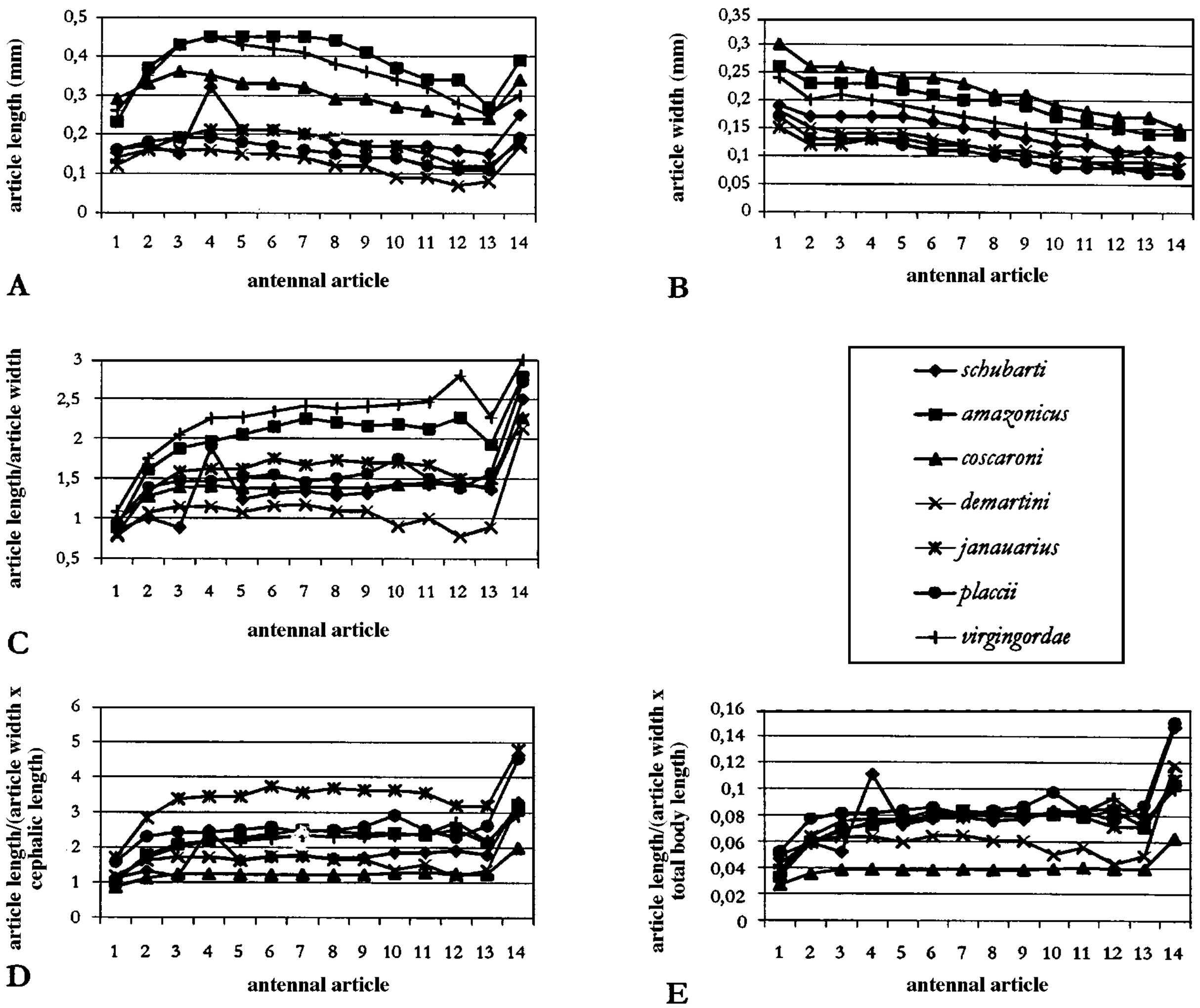

Fig. 38. Metric profiles of antennae in some *Schendylops* species, *S. amazonicus* (Pereira, Minelli and Barbieri, 1994), *S. coscaroni* (Pereira and Minelli, 1996), *S. demartini* (Pereira and Minelli, 1996), *S. janauarius* (Pereira, Minelli and Barbieri, 1995), *S. placcii* (Pereira and Minelli, 1996), *S. schubarti* n.sp., *S. virgingordae* (Crabill, 1960). The individual profiles have been drawn for one male specimen for each species: a species from Martinique for *S. virgingordae*, the allotype for *S. coscaroni* and the holotypes for the remaining species.

behaviour has never been found in the tiniest of geophilomorphs. For instance, in *Dinogeophilus oligopodus* Pereira, 1984 (Geophilidae), 5 mm total length and 0.2 mm maximum body width, the number of antennal setae is very small, but the whole basic pattern is filled and no perturbation is observed (Pereira 1984).

In the case of the fourth antennal article of *S. schubarti* the increased number of sensory setae is coupled with loss of the usual regularity in distribution, but miniaturisation cannot be advocated to explain this loss of order in the chaetotaxy. As this fourth article is approximately 1.5 times as long as expected from its position along the appendage (Fig. 38), we can estimate than, on average, one in two of the prospective epidermal cells of this article have undergone one extra mitosis. One may wonder whether this happened before each cell was committed to default epithelial, or to specialised sensory fate, or after that. In the first case, the extra mitoses might have disrupted some control events in cell specification.

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Corresponding address: Alessandro Minelli, Department of Biology, University of Padova, Via Ugo Bassi 58 B, 35131 Padova, Italy; Fax: +39 (049) 827-6300,
e-mail: almin@civ.bio.unipd.it

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