

The species of *Schendylops* Cook, 1899 (Chilopoda, Geophilomorpha, Schendylidae) from Madagascar

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ABSTRACT

Four of the five species of the geophilomorph centipede genus *Schendylops* Cook, 1899 hitherto known from Madagascar, i.e. *S. insolitus* (Lawrence, 1960), *S. paucispina* (Lawrence, 1960), *S. mascarenicus* (Lawrence, 1960) and *S. silvicola* (Lawrence, 1960), are re-described based on the type material preserved in the collections of the Muséum national d'Histoire naturelle in Paris. A key is provided for the identification of all Malagasy species of the genus, which likely form a clade within *Schendylops*.

RÉSUMÉ

Les espèces de Schendylops Cook, 1899 (Chilopoda, Geophilomorpha, Schendylidae) de Madagascar.

Quatre espèces de chilopodes géophilomorphes du genre *Schendylops* Cook, 1899 parmi les cinq connues jusqu'ici de Madagascar, c'est-à-dire *S. insolitus* (Lawrence, 1960), *S. paucispina* (Lawrence, 1960), *S. mascarenicus* (Lawrence, 1960) et *S. silvicola* (Lawrence, 1960), sont redécrisées d'après le matériel type conservé dans les collections du Muséum national d'Histoire naturelle de Paris. Une clé est fournie pour l'identification de toutes les espèces de ce genre connues de Madagascar, qui forment très vraisemblablement un clade.

KEY WORDS

Chilopoda,
Geophilomorpha,
Schendylidae,
Schendylops,
Madagascar,
identification key.

MOT CLÉS

Chilopoda,
Geophilomorpha,
Schendylidae,
Schendylops,
Madagascar,
clé d'identification.

INTRODUCTION

The amphiatlantic chilopod genus *Schendylops* Cook, 1899 is distributed in the Neotropical Region, Africa and Madagascar (Pereira *et al.* 1997). Hoffman & Pereira (1997) hypothesized that its age antedates the formation of the Atlantic Ocean in the Mesozoic. It comprises 63 known species, the majority of which (51) are distributed in the Neotropical Region, while seven species are known from mainland Africa and five from Madagascar. Recent contributions to the study of the Neotropical species include Pereira & Minelli (1993, 1996) and Foddai *et al.* (2000); the African species have been revised by Pereira & Minelli (1995, 2001). Regarding the *Schendylops* species from Madagascar, Hoffman & Pereira (1997) revised *S. grandidieri* (the type of the genus) and transferred to *Schendylops* four species originally described by R. F. Lawrence (1960) under the genus *Haploschendyla*. The descriptions of this author were incorrect in respect to a key character (number of coxal organs) and incomplete as to many other important traits. As a complement to the partial treatment of these species in Hoffman & Pereira (1997), we redescribe them here on the basis of re-examination of the type material preserved in the collections of the Muséum national d'Histoire naturelle in Paris.

ABBREVIATIONS

- a.a. antennal article;
- d. dorsal;
- p.l. pair(s) of legs;
- v. ventral.

SYSTEMATICS

Family SCHENDYLIDAE Cook, 1896

Genus *Schendylops* Cook, 1899

DIAGNOSIS. — Pleurites of second maxillae not fused to the coxosternum. Apical claw of second maxillae pectinate on both d. and v. edges. Sterna with pore fields. Last pair of legs with seven podomeres; praetar-

sus in form of a small hirsute tubercle or replaced by a small spine or altogether absent. Coxopleura of the last leg-bearing segment each with two internal coxal organs of simple structure ("homogeneous coxal glands" *sensu* Brölemann & Ribaut 1912).

Schendylops insolitus (Lawrence, 1960) (Figs 1-4)

Haploschendyla insolita Lawrence, 1960: 18.

Schendylops insolita (sic) — Hoffman & Pereira 1997: 17.

Schendylops insolitus — Hoffman & Pereira 1997: 22.

TYPE MATERIAL EXAMINED. — Holotype ♂, reference "Haploschendyla insolita", 75 p.l., body length 35 mm, from Madagascar: Moramanga, forêt à Niagarakely, XII.1955, R. F. Lawrence leg. (MNHN coll. Myriapodes 127). Cephalic capsule and mouth parts in one original slide, trunk in alcohol. Lawrence stated in his original description: "Holotype ♀", but this is evidently a typographic error as his description is clearly based on a male specimen.

TYPE LOCALITY. — Madagascar: Moramanga, forêt à Niagarakely.

DISTRIBUTION. — Madagascar: Moramanga: Niagarakely.

DIAGNOSIS. — A *Schendylops* species with v. pore fields extending along the whole body length. Of the other *Schendylops* species in Madagascar, this trait is present only in *S. mascarenicus* (Lawrence, 1960) and *S. grandidieri* (De Saussure & Zehntner, 1897). Characters in Table 5 and in the key differentiate *Schendylops insolitus* from these two species and from the other Madagascar congeners.

REDESCRIPTION

Male holotype. 75 p.l., body length 35 mm; maximum body width 1.0 mm. Colour of preserved specimen pale orange.

Antennae c. 2.0 times as long as the cephalic plate, distally slightly attenuate. Setae on a.a. I-VI of different length and few in number, those of remaining articles progressively shorter and more numerous towards the tip of the appendage (Fig. 1A). Terminal a.a. with c. 21 claviform sensory setae on external border, c. six on internal border (Fig. 1B). Distal end of this a.a. with c. seven very small specialised setae, apparently not split at the apical end (Fig. 1B). Dorsal and

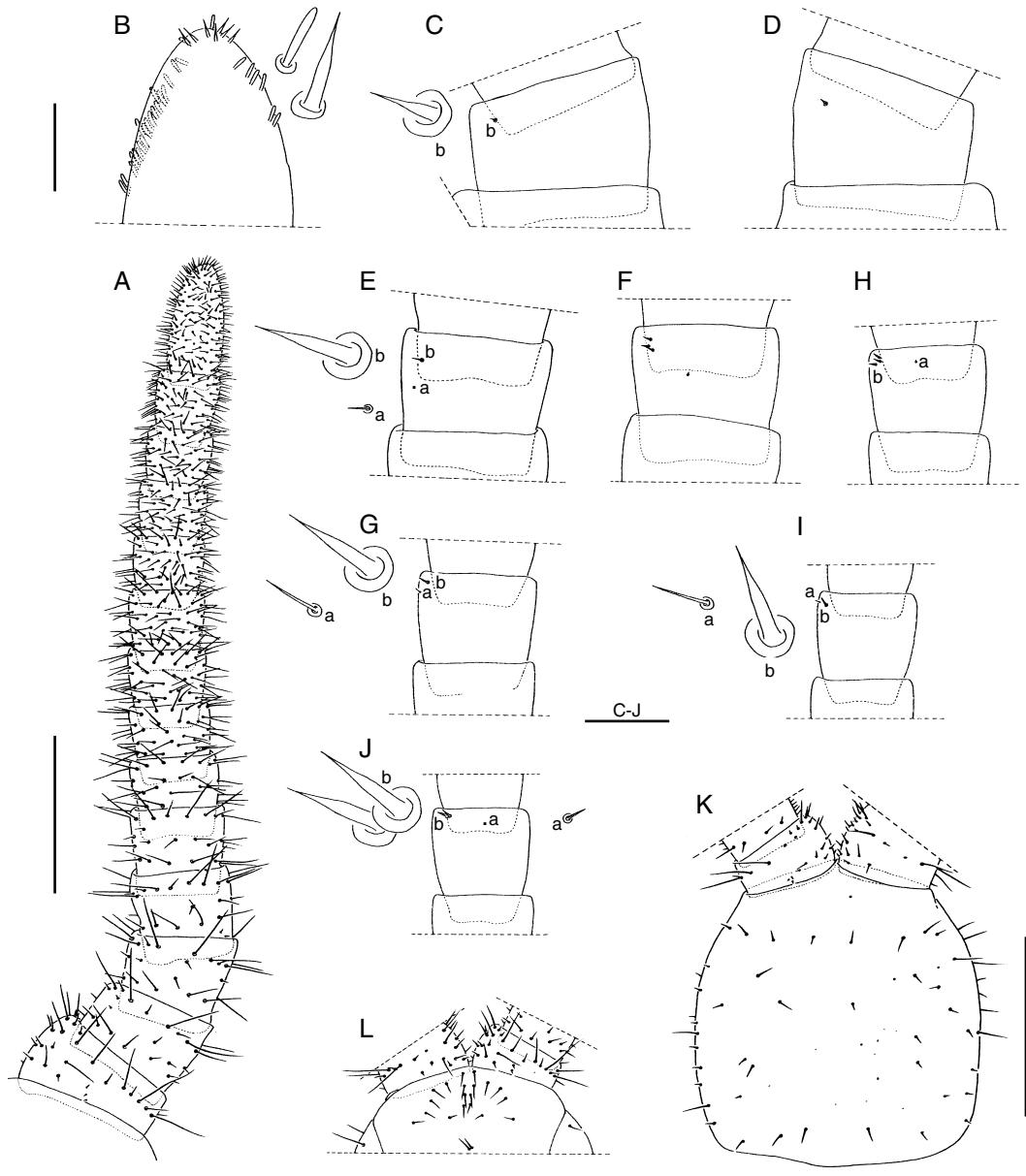


FIG. 1. — *Schendylops insolitus* (Lawrence, 1960), ♂ holotype, Madagascar, Moramanga; A, left antenna, ventral; B, left antennal article XIV, dorsal, with enlarged detail of one of the apical hyaline sensilla and one of the lateral claviform sensilla; C, left antennal article II, ventral; D, left antennal article II, dorsal; E, left antennal article V, ventral; F, left antennal article V, dorsal; G, left antennal article IX, ventral; H, left antennal article IX, dorsal; I, left antennal article XIII, ventral; J, left antennal article XIII, dorsal; K, cephalic shield; L, clypeus and bases of antennae. a, b, types of setae. Scale bars: A, 0.3 mm; B, 0.05 mm; C-J, 0.1 mm; K, 0.5 mm; L, 0.4 mm.

TABLE 1. — *Schendylops insolitus* (Lawrence, 1960), ♂ holotype, distribution of type a and b setae on antennal articles II, V, IX and XIII.

	Ventral		Dorsal			
	a	b	Fig.	a	b	Fig.
II	—	1	1C	—	1	1D
V	1	1	1E	1	3	1F
IX	1	1	1G	1	3	1H
XIII	1	1	1I	1	2	1L

v. surface of a.a. II, V, IX and XIII with very small specialised setae (Fig. 1C-J; Table 1). On the v. side these setae are restricted to an internal lateral area of the a.a. and are represented by two different types: a and b. Type a setae very thin, not divided apically; type b setae very similar to those of the apex of terminal a.a. (a, b, Fig. 1C, E, G, I). Specialised setae on the d. side restricted to an external lateral area and represented by similar type a and b setae of v. side (a, b, Fig. 1D, F, H, J). Cephalic plate nearly as long as wide (ratio 1.06:1), shape and chaetotaxy as in Figure 1K. Clypeus with 1+1 postantennal setae, 9+8 median setae and 1+1 praelabral setae (Fig. 1L).

Labrum with 23 teeth, those of central arc robust and with obtuse tip, the lateral ones less sclerotised, smaller and with a sharp medial extension (Fig. 2A).

Mandible: dentate lamellae subdivided into three distinct blocks, with 3,3,4 teeth (Fig. 2B, C); pectinate lamellae with 17-20 teeth each.

First maxillae with large lappets on both coxosternum and telopodites (Fig. 2E). Coxosternum without setae, median projections of coxosternum well developed and provided with 3+2 setae (Fig. 2D, E). Article II of telopodite with 6+4 v. setae and 5+5 d. sensilla (Fig. 2D, E).

Second maxillae (Fig. 2D, F-H) with 14+14 setae on coxosternum, arranged as in Figure 2D. Apical claw of telopodite bipectinate, v. edge with 12 teeth (Fig. 2F, G), d. with 14 teeth.

Forcipulae: telopodites, when closed, not extending beyond the anterior margin of head. Tergum of the forcipular segment with an irregular transverse median row of nine setae and few additional ones on the remaining surface (Fig. 2J). All

articles of telopodites lacking teeth (Fig. 2I, J). Calyx of poison gland cylindrical (Fig. 2K). Chaetotaxy of coxosternum and telopodites as in Fig. 2I, J.

Walking legs with chaetotaxy (Fig. 2L) uniform throughout body length. Claws ventrobasally with two spines (one anterior, one posterior); a third smaller spine occurs internally very close to the posterior one (Fig. 2M).

Sterna: pore fields present from first to penultimate sternum. Pore fields undivided on sterna I-XXIX and LXXI-LXXIV, divided in two sub-symmetrical areas on sterna XXX-LXX; fields with a small additional group of pores at each side of the anterior border. Shape and relative size of fields changing along the trunk as in Figures 2N-R and 3. Number of pores on selected sterna: on sternum I: 5+42+5 pores; II: 5+67+6; III: 0+71+6; IV: 5+84+8; X: 10+99+9; XVI: 8+123+8; XXVI: 4+131+4; XXIX: 3+128+6; XXX: 6+69+53+5; XXXI: 3+58+59+3; XXXV: 4+50+42+4; XLV: 2+24+24+2; LVI: 28+25; LXIX: 3+27+28+1; LXX: 0+35+27+1; LXXI: 69; LXXIV: 2+28+2.

Last leg-bearing segment with pleurites at the sides of praetergum. Praesternum not divided along sagittal plane; shape and chaetotaxy of tergum and sternum as in Figure 4A, B. Coxopleuron slightly protruding at the distal v. end, setae numerous on v. internal area, remaining surface with less numerous setae. Two single ("homogeneous") coxal organs on each coxopleuron (Fig. 4B, C). Coxal organs opening on membrane between coxopleuron and sternum, partially covered by the latter (Fig. 4B, C). Last legs inflated, with seven podomeres, shape and chaetotaxy as in Figure 4A, B. Praetarsus as a very small tubercle with one small apical spine (Fig. 4D).

Terminal segments: posterior margin of intermediate tergum convex, that of intermediate sternum slightly concave. Posterior margin of first genital sternum medially slightly convex, laterally slightly concave (Fig. 4B, E). Gonopods biarticulate, basal article with nine setae, apical article with c. five setae (Fig. 4F); penis dorsally without apical setae (Fig. 4G).

Female unknown.

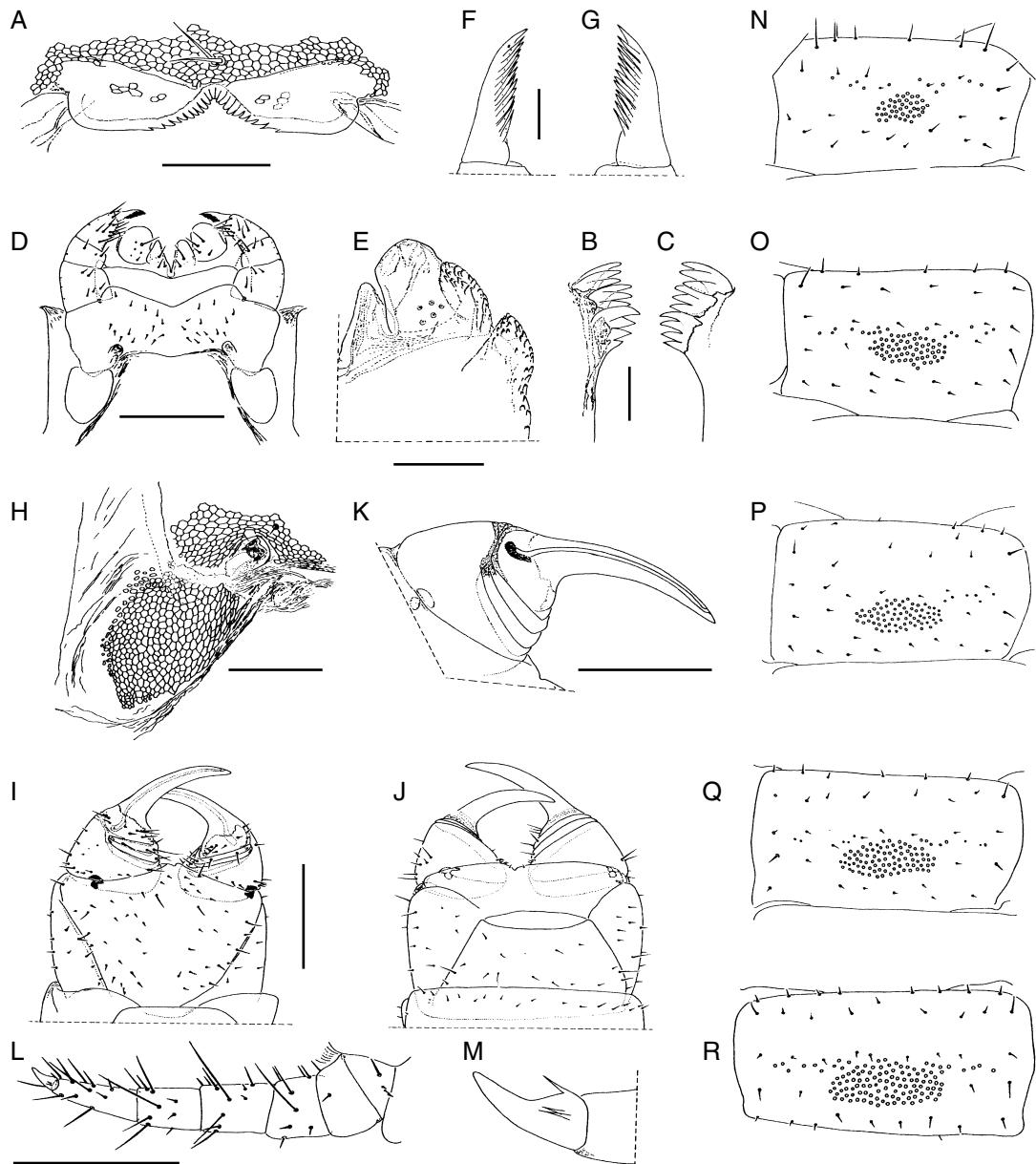


FIG. 2. — *Schendylops insolitus* (Lawrence, 1960), ♂ holotype, Madagascar, Moramanga; A, labrum; B, C, dentate lamellae of mandibles; D, first and second maxillae, ventral; E, right first maxilla, dorsal; F, detail of distal end of telopodite of right second maxilla, ventral; G, detail of distal end of telopodite of left second maxilla, ventral; H, detail of posterior external region of right second maxilla, ventral; I, forcipular segment with poison claws, ventral; J, the same, dorsal; K, detail of poison gland in right poison claw, ventral; L, right leg IV, ventral; M, claw of right leg XIII, ventral; N-R, sternite I, II, III, IV, X. Scale bars: A, H, 0.1 mm; B, C, F, G, 0.03 mm; D, K, L, 0.3 mm; E, 0.1 mm; I, J, N-R, 0.4 mm; M, 0.05 mm.

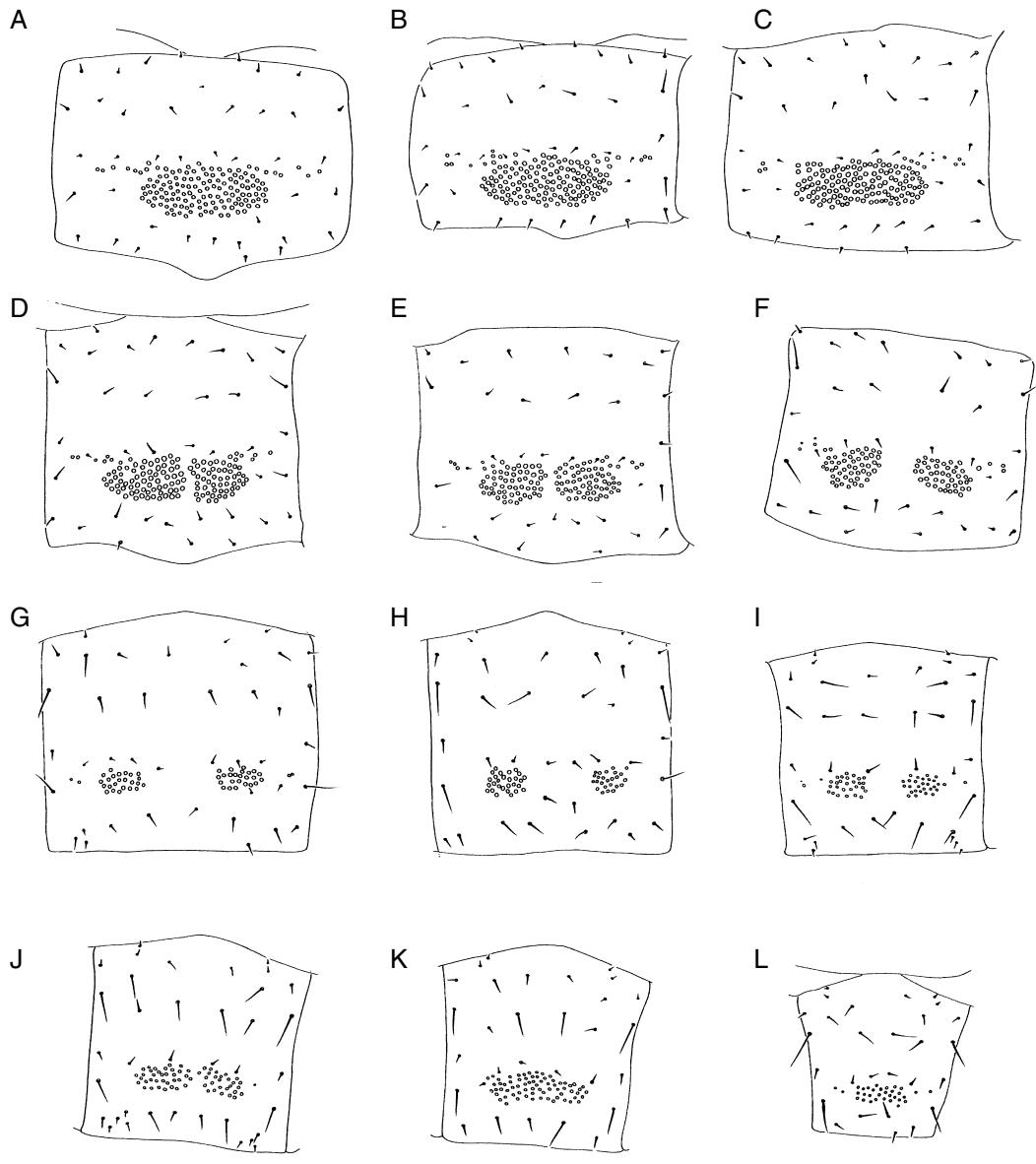


FIG. 3. — *Schendyllops insolitus* (Lawrence, 1960), ♂ holotype, Madagascar, Moramanga; A-L, sterna XVI, XXVI, XXIX, XXX, XXXI, XXXV, XLV, LVI, LXIX, LXX, LXXI, LXXIV. Scale bar: 0.4 mm.

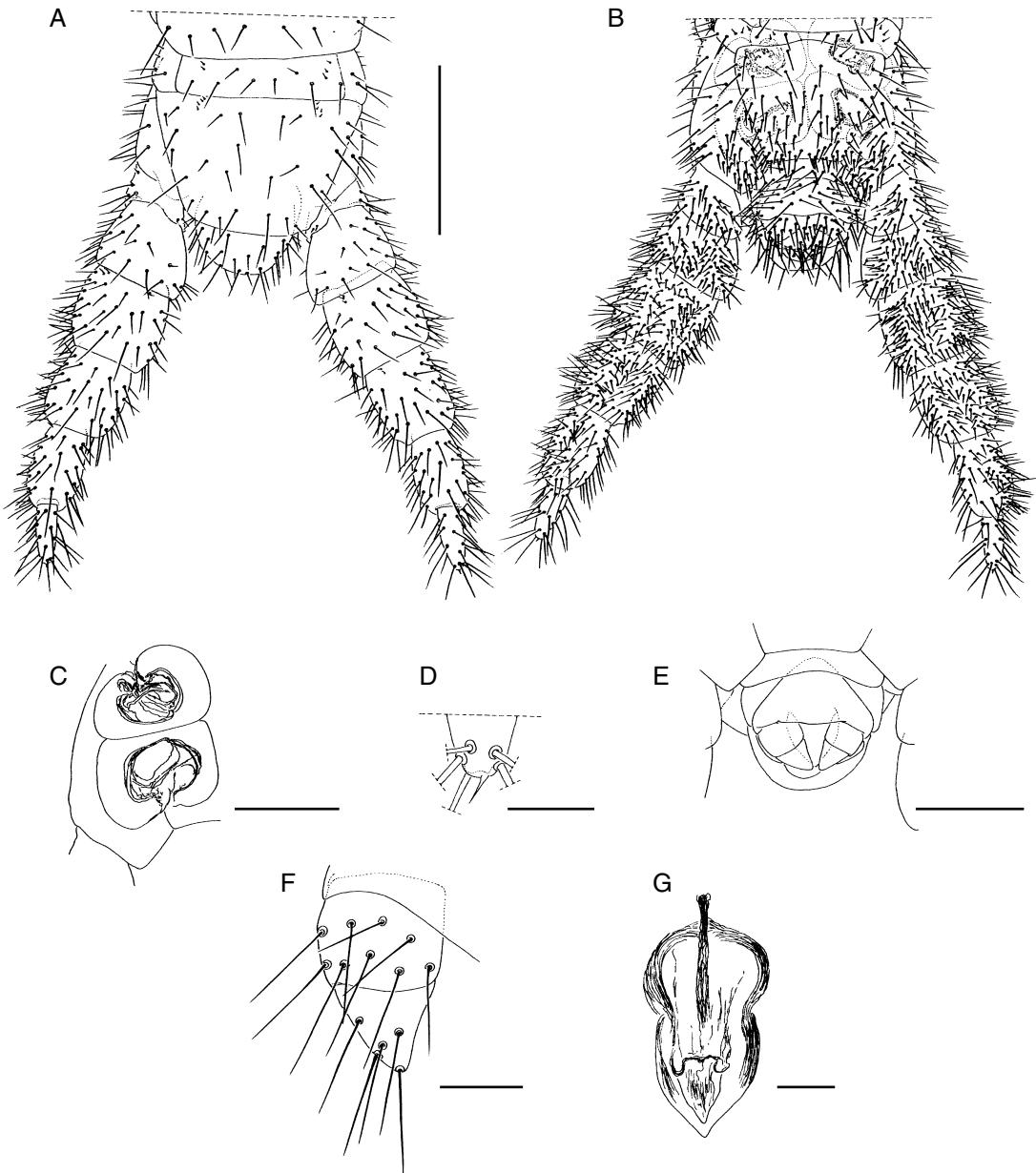


FIG. 4. — *Schendylops insolitus* (Lawrence, 1960), ♂ holotype, Madagascar, Moramanga; **A**, last leg-bearing segment and terminal segments, dorsal; **B**, the same, ventral; **C**, right coxal organs, ventral; **D**, detail of distal end of last podomere of right last leg, ventral; **E**, genital region, ventral; **F**, right gonopod, ventral; **G**, penis, dorsal. Scale bars: A, B, 0.4 mm; C, E, 0.2 mm; D, F, G, 0.05 mm.

TABLE 2. — *Schendylops mascarenicus* (Lawrence, 1960), ♀ holotype, distribution of type a and b setae on antennal articles II, V, IX and XIII.

	Ventral		Dorsal			
II	a —	b 1	Fig. 5C	a —	b 1	Fig. 5D
V	1	1	5E	1	3	5F
IX	1	1	5G	1	3	5H
XIII	1	1	5I	1	6	5L

Schendylops mascarenicus (Lawrence, 1960)
(Figs 5-8)

Haploschendyla mascarenica Lawrence, 1960: 20.

Schendylops mascarenica (sic) — Hoffman & Pereira 1997: 17.

Schendylops mascarenicus — Hoffman & Pereira 1997: 22.

TYPE MATERIAL EXAMINED. — Holotype ♀, reference “*Haploschendyla mascarenica*”, 65 p.l., body length 38 mm, from Madagascar: Ambohimahosoa, VII.1948, J. Millot leg. (MNHN coll. Myriapodes 129). Head and mouth parts in one original slide, trunk in alcohol.

TYPE LOCALITY. — Madagascar: Ambohimahosoa.

DISTRIBUTION. — Madagascar: Ambohimahosoa.

DIAGNOSIS. — A *Schendylops* species with v. pore fields extending along the entire trunk. Of the other Madagascar *Schendylops* species this trait is present only in *S. insolitus* and *S. grandidieri*. Characters in Table 5 and in the key differentiate *Schendylops mascarenicus* from these two species and from the other Madagascar congeners.

REDESCRIPTION

Female holotype. 65 p.l. (not 67 as described by Lawrence [1960]), body length 38 mm; maximum body width 1.2 mm. Colour of preserved specimen pale orange.

Antennae 2.1 times as long as the cephalic plate, distally slightly attenuate. Setae on a.a. I to IV-V of different length, few in number; those of remaining articles progressively shorter and more numerous towards the tip of the appendage (Fig. 5A). Terminal a.a. with 11 claviform sensory setae on the external border and eight on the internal border (Fig. 5B). Distal end of this a.a. with five very small specialised setae, split into two very

diminutive apical branches (Fig. 5B). Dorsal and v. surface of a.a. II, V, IX and XIII with very small specialised setae (Fig. 5C-J; Table 2). On the v. side these setae are restricted to an internal lateral area of the a.a. and are represented by two different types: a and b. Type a setae very thin, not divided apically; type b setae very similar to those of the apex of the terminal a.a. (a, b, Fig. 5C, E, G, I). Specialised setae on the d. side restricted to an external lateral area, similar to type a and b setae of v. side, but some of type b setae apparently do not split apically (a, b, Fig. 5D, F, H, J).

Cephalic plate slightly longer than wide (ratio 1.2:1), shape and chaetotaxy as in Figure 5K.

Clypeus with 18 median setae and 1+1 praelabral setae (Fig. 5L).

Labrum with 30 teeth, those of central arc dark, robust, with obtuse tip, those of lateral pieces less sclerotised, smaller, with a sharp medial extension (Fig. 6A).

Mandible: dentate lamellae subdivided into three distinct blocks, with 3,3,6 teeth (Fig. 6B); pectinate lamellae with 19 teeth each.

First maxillae with lappets on both coxosternum and telopodites (Fig. 6D). Coxosternum with 1+1 setae, median projections of coxosternum well developed, provided with 3+3 setae (Fig. 6C). Article II of telopodite with 4+4 v. setae and 7+7 d. sensilla (Fig. 6C, D).

Second maxillae (Fig. 6C, E-I) with 11+12 setae on coxosternum arranged as in Fig. 6C. Apical claw of telopodite bipectinate, v. edge with c. 10-13 teeth (Fig. 6F, G), d. with 10 teeth (Fig. 6H).

Forcipulae: telopodites, when closed, not extending beyond anterior margin of head. Basal plate with 9+9 setae (Fig. 6K). All articles of telopodites lacking teeth (Fig. 6J, K). Calyx of poison gland cylindrical (Fig. 6L). Chaetotaxy of coxosternum and telopodites as in Figure 6J, K. Walking legs with chaetotaxy (Fig. 6M) uniform throughout body length. Claws ventrobasally with two spines (one anterior, one posterior); a third smaller spine occurs internally very close to the posterior one (Fig. 6N).

Sterna: pore fields present from the first to antepenultimate sternum. Pore fields undivided on sterna I-XXIV and LXI-LXIII, divided in two

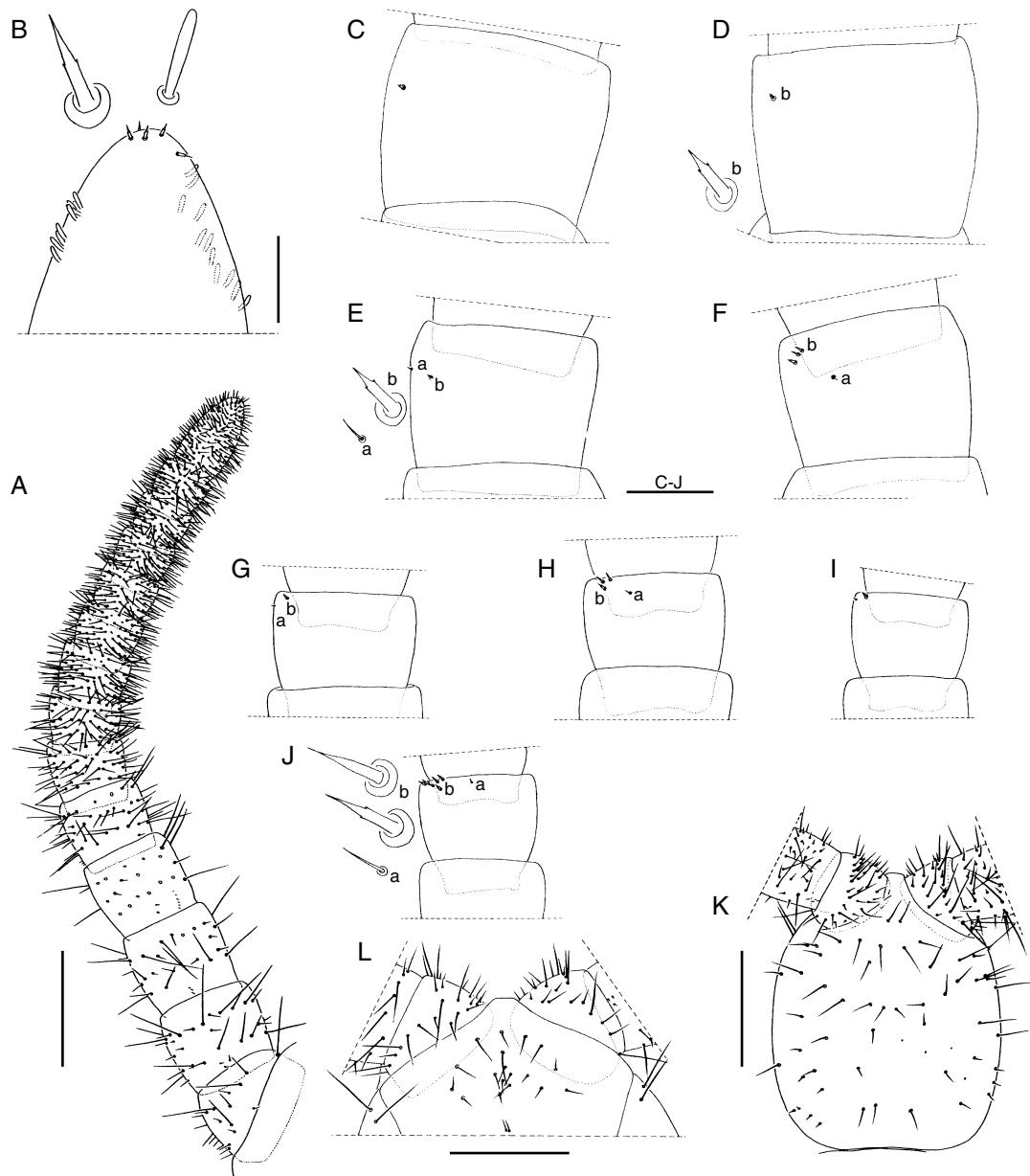


FIG. 5. — *Schendylops mascarenicus* (Lawrence, 1960), ♀ holotype, Madagascar, Ambohimahosoa; A, left antenna, ventral; B, left antennal article XIV, ventral, with enlarged detail of one of the apical hyaline sensilla and one of the lateral claviform sensilla; C, left antennal article II, ventral; D, left antennal article II, dorsal; E, left antennal article V, ventral; F, left antennal article V, dorsal; G, left antennal article IX, ventral; H, left antennal article IX, dorsal; I, left antennal article XIII, ventral; J, left antennal article XIII, dorsal; K, cephalic shield; L, clypeus and bases of antennae. a, b, types of setae. Scale bars: A, L, 0.3 mm; B, 0.05 mm; C-J, 0.1 mm; K, 0.4 mm.

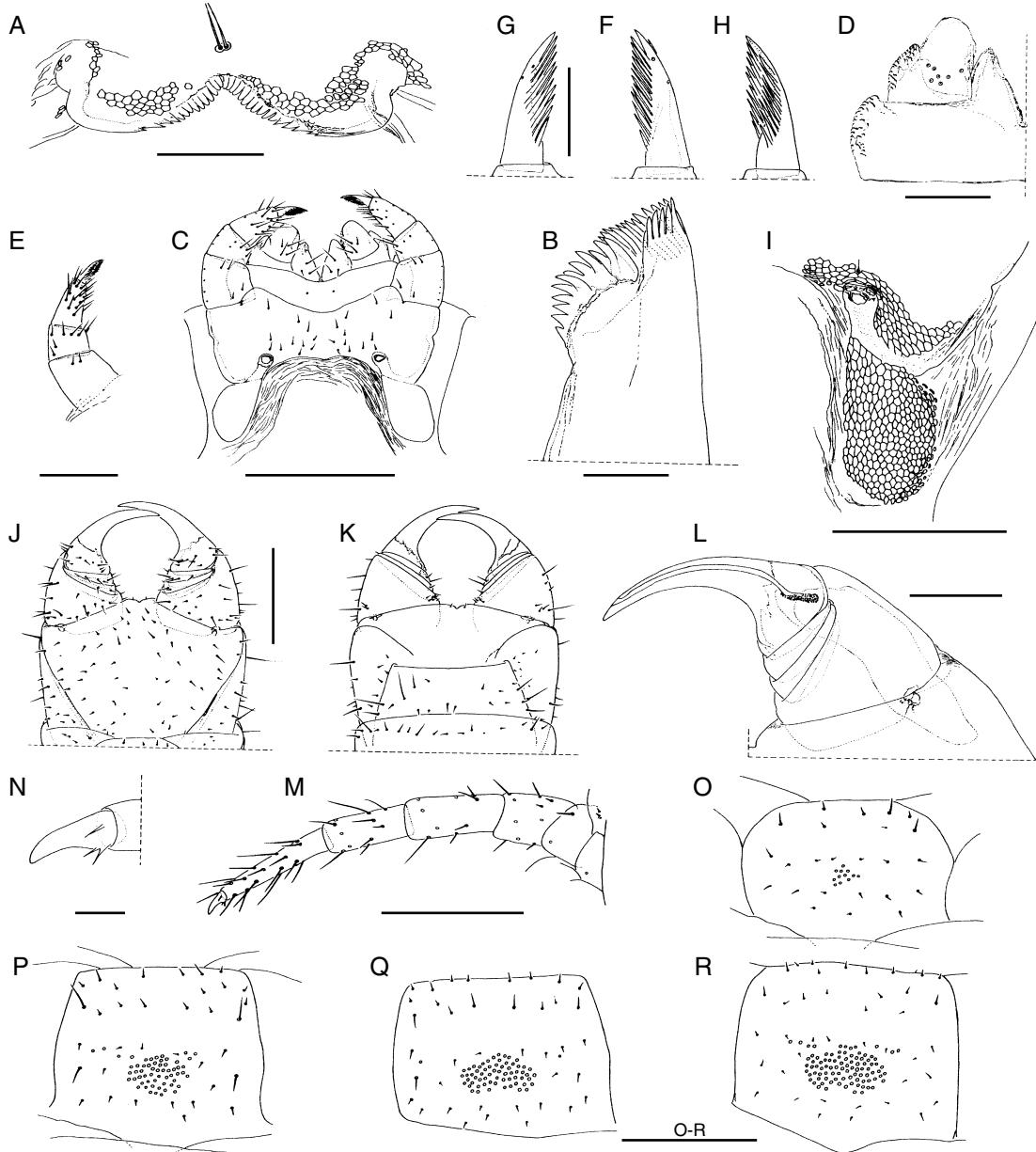


FIG. 6. — *Schendylops mascarenicus* (Lawrence, 1960), ♀ holotype, Madagascar, Ambohimahosoa; **A**, labrum; **B**, apical part of mandible; **C**, first and second maxillae, ventral; **D**, left first maxilla, dorsal; **E**, telopodite of left second maxilla, dorsal; **F**, detail of distal end of telopodite of left second maxilla, ventral; **G**, detail of distal end of telopodite of right second maxilla, ventral; **H**, the same, dorsal; **I**, detail of posterior external region of left second maxilla, ventral; **J**, forcepsular segment with poison claws, ventral; **K**, the same, dorsal; **L**, detail of poison gland in left poison claw, ventral; **M**, right leg LVIII, antero-ventral; **N**, claw of right leg LVIII, antero-ventral; **O-R**, sterna I, II, III, IV. Scale bars: A, D, 0.1 mm; B, F-H, 0.05 mm; C, J, K, 0.4 mm; E, I, L, 0.2 mm; M, O-R, 0.3 mm; N, 0.03 mm.

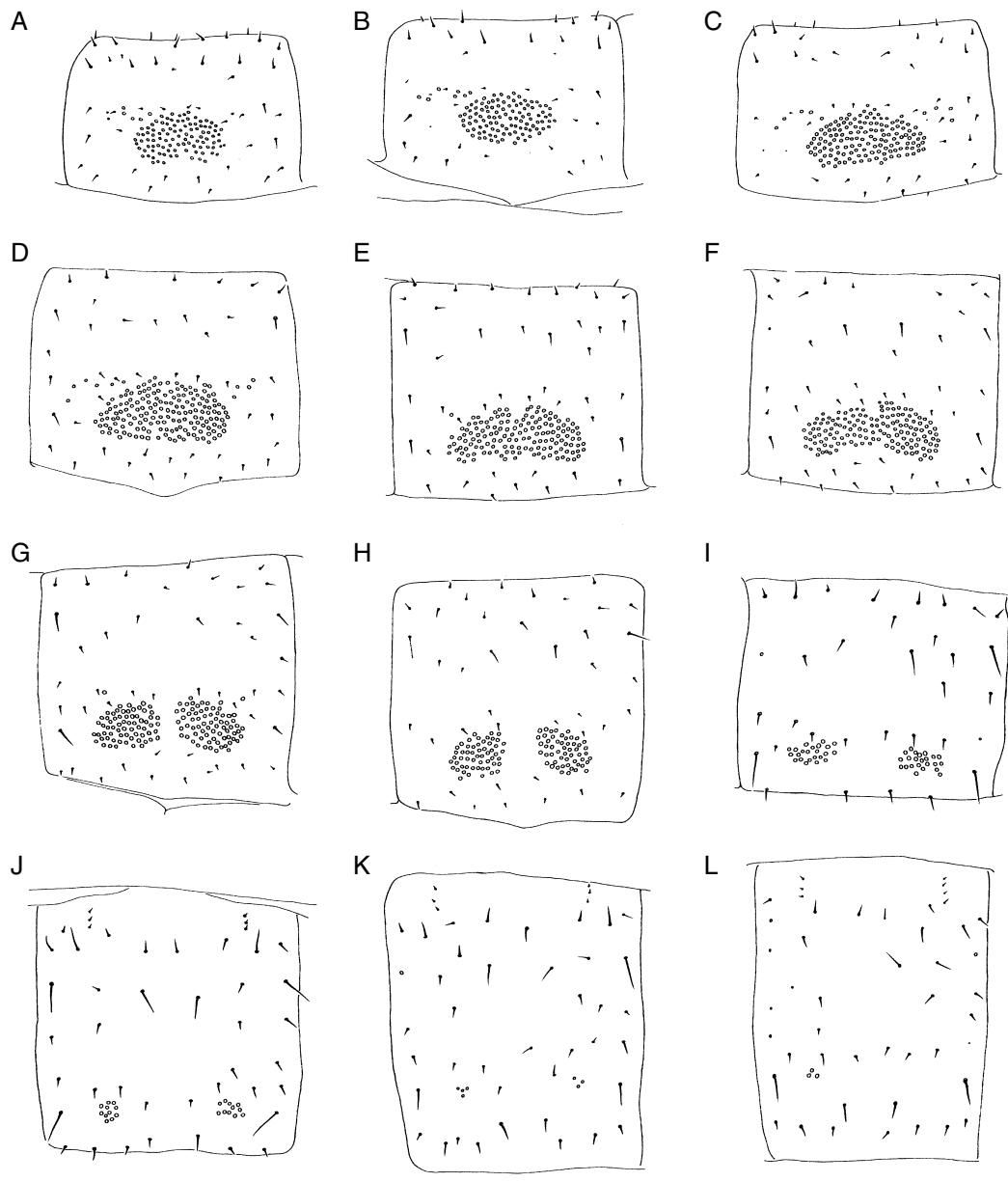


FIG. 7. — *Schendylops mascarenicus* (Lawrence, 1960), ♀ holotype, Madagascar, Ambohimahosoa; A-L, sterna V, VI, X, XVI, XXIII, XXIV, XXV, XXVI, XXXI, XXXVI, XLVI, LIII. Scale bar: 0.3 mm.

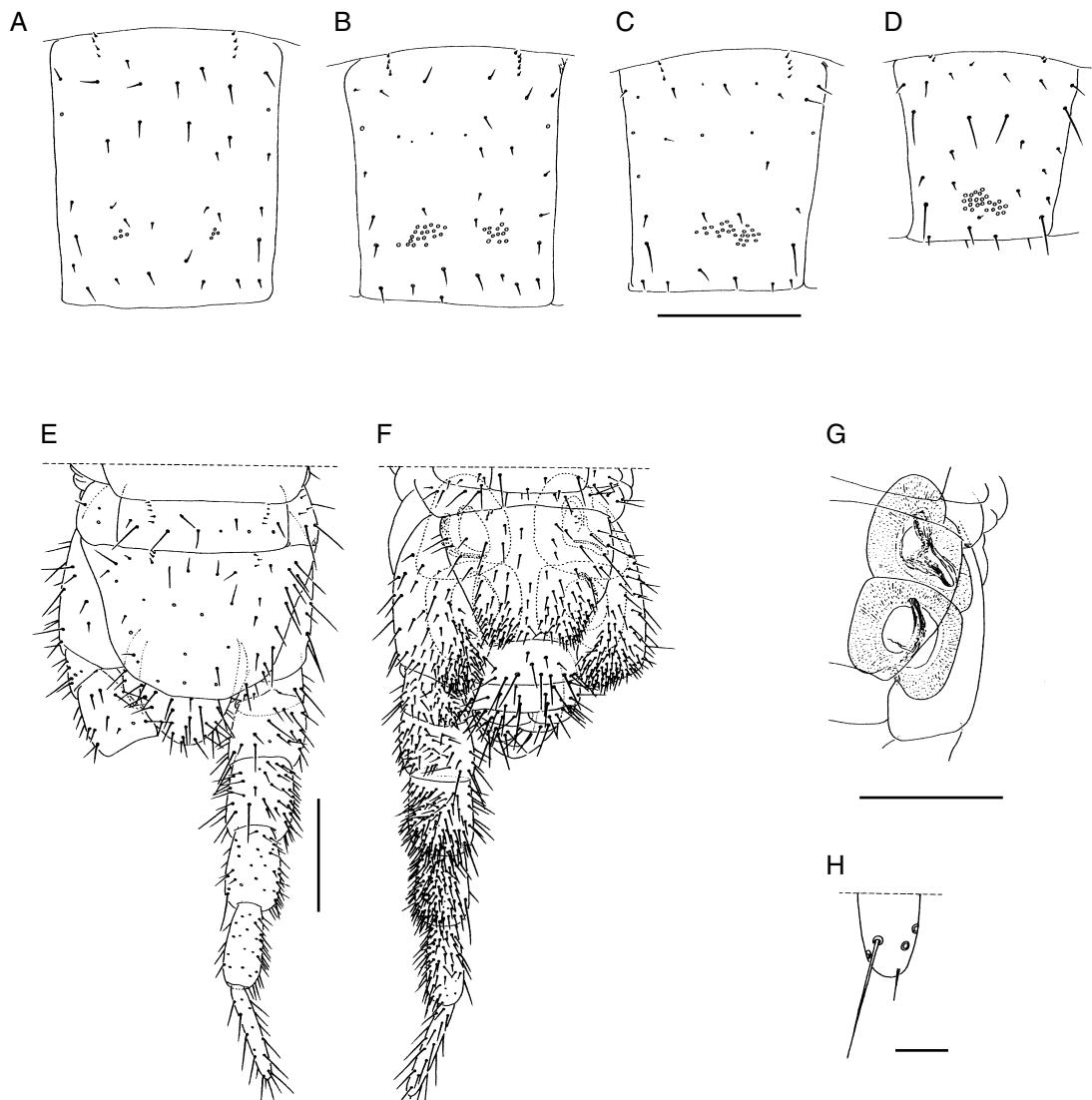


FIG. 8. — *Schendylops mascarenicus* (Lawrence, 1960), ♀ holotype, Madagascar, Ambohimahosoa; A-D, sterna LVII, LX, LXI, LXIII; E, last leg-bearing segment and terminal segments, dorsal; F, the same, ventral; G, left coxal organs, ventral; H, detail of distal end of last podomere of right last leg, ventral. Scale bars: A-G, 0.3 mm; H, 0.03 mm.

subsymmetrical areas on sterna XXV-LX (Lawrence [1960] wrote instead: "Pores se séparant sur les segments XXIV ou XXV et disparaissant sur le segment XXXII"). Sterna II to XXV with a small group of pores at both sides of the anterior border. Shape and relative size of fields changing along the trunk as in Figures 6O-R, 7 and 8A-D.

Number of pores on selected sterna: on sternum I: 12 pores; II: 4+51+3; III: 0+63+1; IV: 4+86+3; V: 7+102+1; VI: 7+105+0; X: 5+139+4; XVI: 6+164+4; XXIII: 1+143+0; XXIV: 144; XXV: 1+66+71+1; XXVI: 55+53; XXXI: 23+23; XXXVI: 11+11; XLVI: 4+3; LIII: 3+0; LVII: 4+4; LX: 19+12; LXI: 25; LXIII: 24.

Last leg-bearing segment with pleurites at the sides of praetergum. Praesternum not divided along sagittal plane; shape and chaetotaxy of tergum and sternum as in Figure 8E, F. Coxopleuron slightly protruding at the distal v. end, setae numerous on v. internal area, remaining surface with less numerous setae. Two single ("homogeneous") coxal organs on each coxopleuron (Fig. 8F, G). Coxal organs opening on membrane between coxopleuron and sternum, partially covered by the latter (Figure 8F, G). Last legs moderately inflated, with seven podomeres, shape and chaetotaxy as in Figure 8E, F. Praetarsus represented by a small subapical spine (Fig. 8H).

Terminal segments: posterior margin of intermediate tergum convex, that of intermediate sternum slightly convex. Posterior margin of first genital sternum medially slightly convex, laterally slightly concave (Fig. 8E, F). Gonopods uniarticulate (Fig. 8F).

Male unknown.

Schendylops paucispina (Lawrence, 1960) (Figs 9-11)

Haploschendyla paucispina Lawrence, 1960: 16.

Schendylops paucispina – Hoffman & Pereira 1997: 17.

Schendylops paucispinus (sic) – Hoffman & Pereira 1997: 22.

TYPE MATERIAL EXAMINED. — Holotype ♀, reference "Haploschendyla paucispina", 51 p.l., body length 26 mm from Madagascar: Ankaratra, col du Tsiafajavona, 2000 m, September (year?), R. Paulian leg. (MNHN coll. Myriapodes 130). Cephalic capsule and mouth parts in one original slide, trunk missing.

OTHER MATERIAL EXAMINED. — ♂, reference "Haploschendyla paucispina", 49 p.l., body length 24 mm, from Madagascar: Ankaratra, col du Tsiafajavona, 2550 m, VI.1948, J. Millot leg. (MNHN coll. Myriapodes 130). Cephalic capsule and mouth parts in one original slide, trunk in alcohol.

TYPE LOCALITY. — Madagascar: Ankaratra, col du Tsiafajavona, 2000 m.

DISTRIBUTION. — Madagascar: Ankaratra, col du Tsiafajavona, 2000 m and 2550 m.

DIAGNOSIS. — A *Schendylops* species with v. pore fields present only on the anterior sterna. Of the other

TABLE 3. — *Schendylops paucispina* (Lawrence, 1960), ♂ holotype, distribution of type a, b and c setae on antennal articles II, V, IX and XIII.

	Ventral			Dorsal			Fig.	
	a	b	c	Fig.	a	b	c	
II	—	1	—	9C	1	1	—	9D
V	1	1	—	9E	1	1	—	9F
IX	1	1	—	9G	1	1	2	9H
XIII	1	1	—	9I	1	1	1	9L

Madagascar *Schendylops* species this trait is present only in *S. silvicola* (Lawrence). Characters in Table 5 and in the key differentiate *S. paucispina* from this species and from all the other Madagascar congeners.

REDESCRIPTION

Male with 49 p.l., body length 24 mm. Colour of preserved specimen in alcohol pale ochre. Antennae 2.5 times as long as the cephalic plate, distally slightly attenuate. Setae on a.a. I-V of different length, few in number; those of remaining articles progressively shorter, more numerous towards the tip of the appendage (Fig. 9A).

Terminal a.a. with 23 claviform sensory setae on the external border and 11 on the internal border (Fig. 9B). Distal end of this a.a. with five very small specialised setae with two very small apical branches (Fig. 9B). Dorsal and v. surface of a.a. II, V, IX and XIII with very small specialised setae (Fig. 9C-J; Table 3). On the v. side these setae are restricted to an internal lateral area of the a.a. and are represented by two different types: a and b. Type a setae very thin, not divided apically; type b setae very similar to those of the apex of the terminal a.a. (a, b, Fig. 9C, E, G, I). Specialised setae on d. side restricted to an external lateral area and represented by three different types: a and b similar to a and b of v. side, type c setae similar in size to type b, but apparently not divided apically and darker (ochreous) in colour (a, b, c, Fig. 9D, F, H, J).

Cephalic plate slightly longer than wide (ratio 1.1:1), shape and chaetotaxy as in Figure 9K.

Clypeus with 1+1 postantennal setae, 5+6 median setae and 1+1 praelabral setae (Figs 9L; 10A, B).

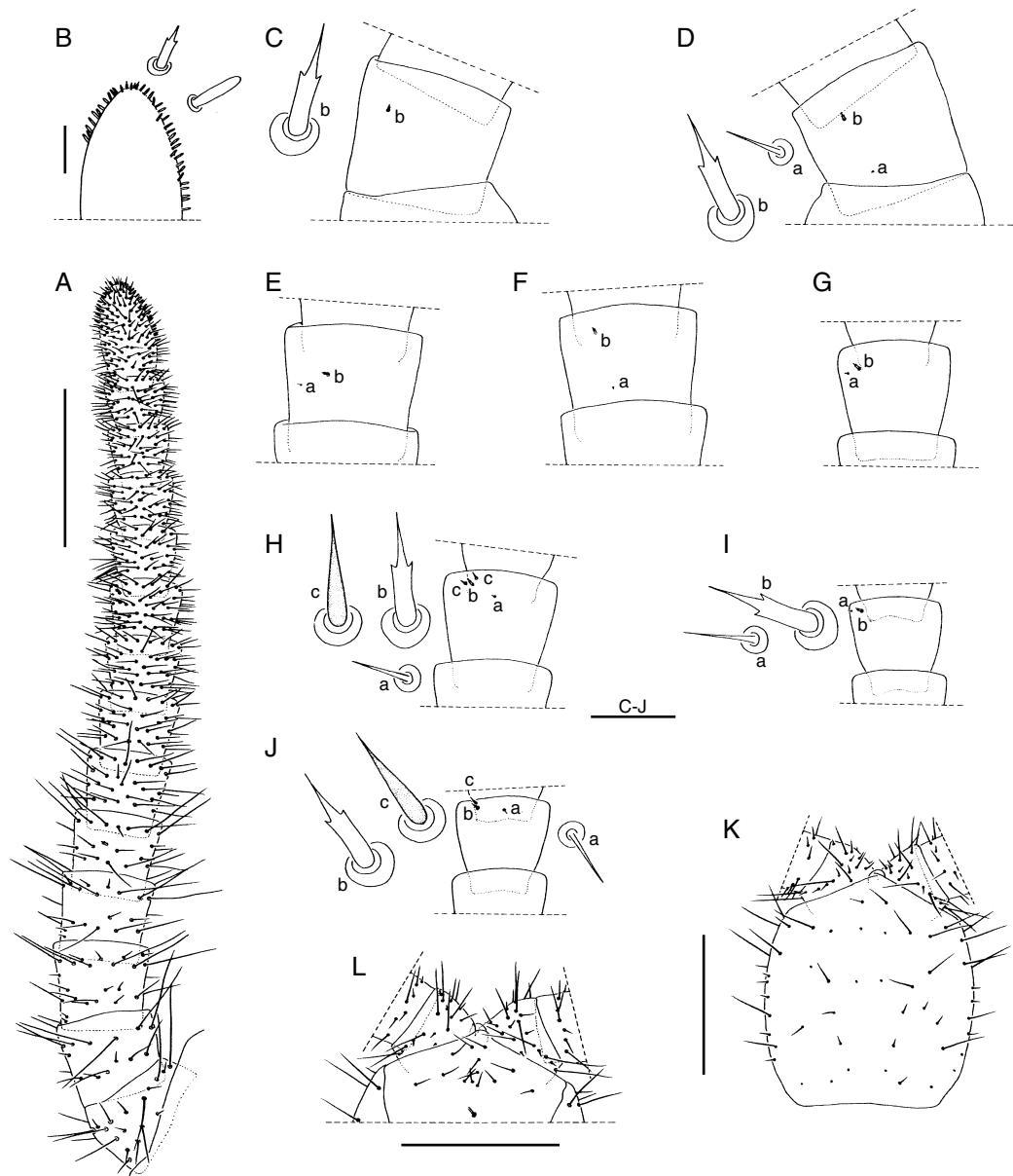


FIG. 9. — *Schendylops paucispina* (Lawrence, 1960), ♂, Madagascar, Ankaratra; **A**, left antenna, ventral; **B**, left antennal article XIV, ventral, with enlarged detail of one of the apical hyaline sensilla and one of the lateral claviform sensilla; **C**, left antennal article II, ventral; **D**, left antennal article II, dorsal; **E**, left antennal article V, ventral; **F**, left antennal article V, dorsal; **G**, left antennal article IX, ventral; **H**, left antennal article IX, dorsal; **I**, left antennal article XIII, ventral; **J**, left antennal article XIII, dorsal; **K**, cephalic shield; **L**, clypeus and bases of antennae. **a**, **b**, **c**, types of setae. Scale bars: A, 0.3 mm; B, 0.05 mm; C-K, 0.1 mm; L, 0.4 mm.

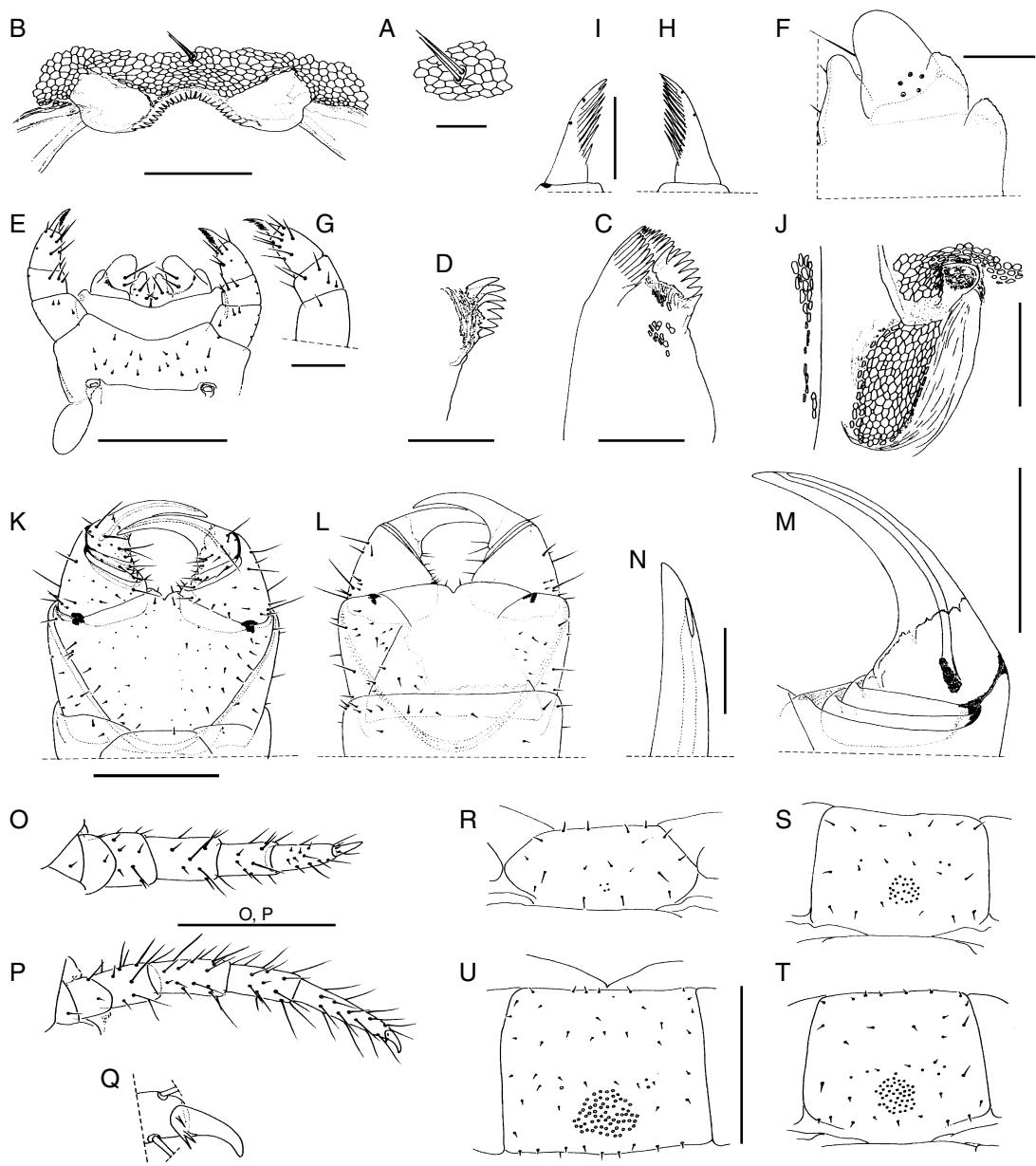


FIG. 10. — *Schendylops paucispina* (Lawrence, 1960), ♂, Madagascar, Ankaratra; A, detail of paelabral setae; B, labrum; C, apical part of mandible; D, dentine lamellae of mandible; E, first and second maxillae, ventral; F, right first maxilla, dorsal; G, telopodite of right second maxilla, ventral; H, detail of distal end of telopodite of left second maxilla, ventral; I, detail of distal end of telopodite of right second maxilla, ventral; J, detail of posterior external region of right second maxilla, ventral; K, forcipular segment with poison claws, ventral; L, the same, dorsal; M, detail of poison gland in left poison claw, ventral; N, detail of apical part of right poison claw, dorsal; O, left leg XVI, ventral; P, left leg L, ventral; Q, claw of left leg L, antero-ventral; R-U, sterna I, II, III, VIII. Scale bars: A, Q, 0.03 mm; B, F, G, J, 0.1 mm; C, D, H, I, N, 0.05 mm; E, O, P, R-U, 0.3 mm; K, L, 0.4 mm; M, 0.2 mm.

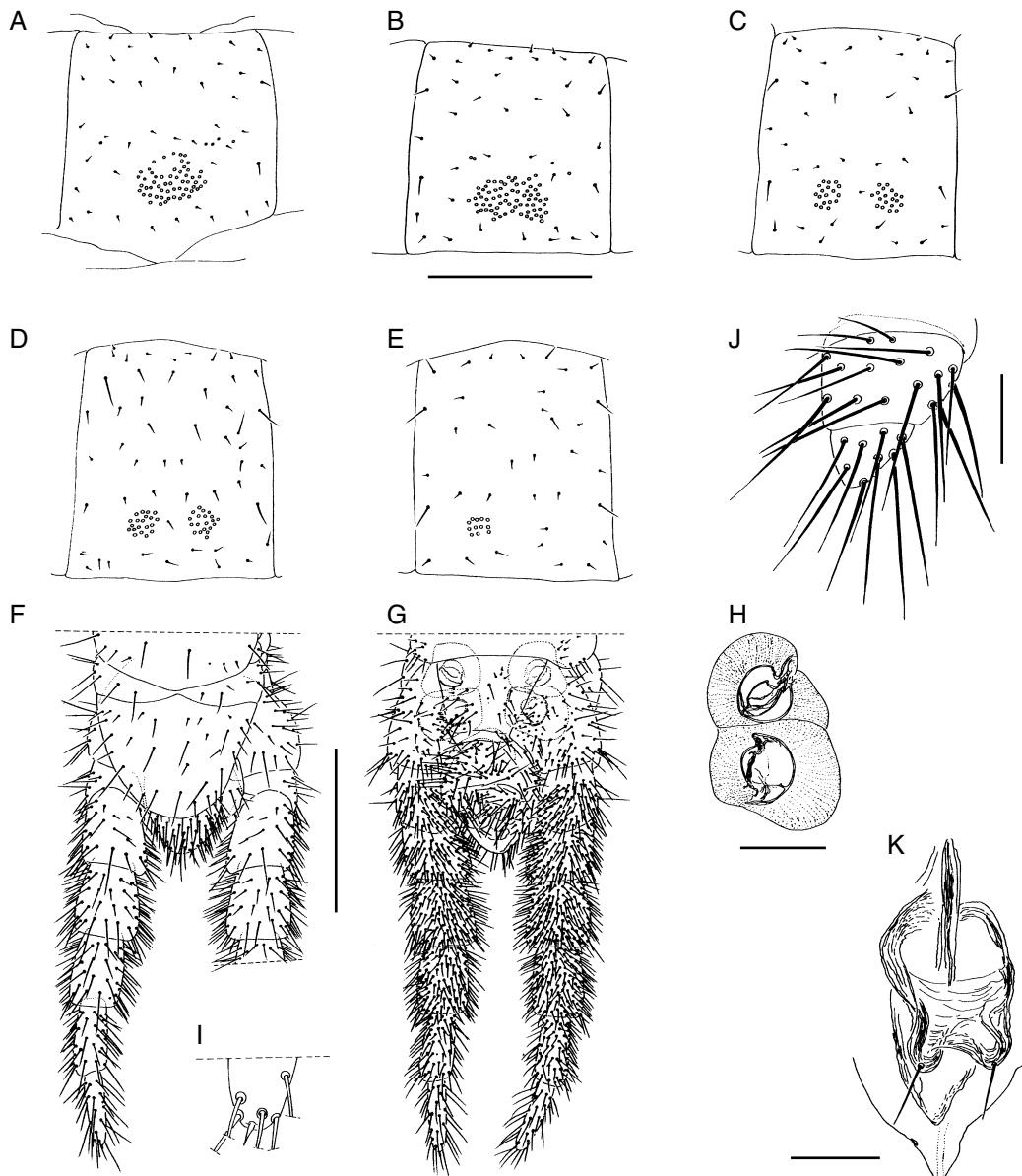


FIG. 11. — *Schendylops paucispina* (Lawrence, 1960), ♂, Madagascar, Ankaratra; A-E, sterna XIV, XIX, XX, XXI, XXII; F, last leg-bearing segment and terminal segments, dorsal; G, the same, ventral; H, left coxal organs, ventral; I, detail of distal end of last podomere of left last leg, ventral; J, left gonopod, ventral; K, penis, dorsal. Scale bars: A-E, 0.3 mm; F, G, 0.4 mm; H, 0.1 mm; I, 0.03 mm; J, K, 0.05 mm.

Labrum with 26 teeth, those of central arc dark, with obtuse tip; lateral teeth less sclerotized, each with a relatively long, very sharp medial extension (Fig. 10B).

Mandible: dentate lamellae with seven or eight teeth, not subdivided into blocks (Fig. 10C, D); pectinate lamellae with 18 teeth each (Fig. 10C) (Lawrence [1960] described the mandible as formed by “un bloc de trois dents suivi d'une rangée de cinq dents”).

First maxillae with lappets on both coxosternum and telopodites (Fig. 10F). Coxosternum without setae, median projections of coxosternum well developed, provided with 2+2 large setae (Fig. 10E). Article II of telopodite with 2+2 v. setae and 4+5 d. sensilla (Fig. 10E, F).

Second maxillae (Fig. 10E, G-J) with 9+9 setae on coxosternum, arranged as in Figure 10E. Apical claw of telopodite bipectinate, v. edge with c. 7-11 teeth (Fig. 10H, I), d. with 10 teeth.

Forcipulae: telopodites, when closed, not extending beyond anterior margin of head. All articles of telopodites lacking teeth (Fig. 10K, L). Calyx of poison gland cylindrical (Fig. 10M). Chaetotaxy of coxosternum and telopodites as in Figure 10K, L.

Walking legs with chaetotaxy (Fig. 10O, P) uniform throughout body length. Claws ventrobasally with two spines (one anterior, one posterior); a third spine, similar in size, occurring internally very close to the posterior one (Fig. 10Q).

Sterna: pore fields present on sterna I to XXII only; undivided on sterna I to XIX, divided in two subsymmetrical areas on sterna XX-XXI and excentrically single on sternum XXII (12+0 pores, Fig. 11E). Sterna II-XIX with a small group of pores at both sides of the anterior border of pore fields. Shape and relative size of fields changing along the trunk as in Figures 10R-U and 11A-E. Number of pores on selected sterna: on sternum I: 4 pores; II: 1+27+2; III: 2+46+3; VIII: 1+66+2; XIV: 1+57+4; XIX: 2+70+2; XX: 18+19; XXI: 20+20; XXII: 12+0. We cannot detect the pores described by Lawrence (1960) as occurring on the sterna posterior to segment XXII close to the posterior sternal border.

Last leg-bearing segment without pleurites at sides of praetergum. Praetergum with posterior border conspicuously “clubbed” on the middle (Fig. 11F). Praesternum not divided along sagittal plane; shape and chaetotaxy of tergum and sternum as in Figure 11F, G. Coxopleuron not protruding at the distal v. end, setae numerous on v. internal area, remaining surface with less numerous setae. Two single (“homogeneous”) coxal organs on each coxopleuron (Fig. 11G, H). Coxal organs opening on membrane between coxopleuron and sternum, partially covered by latter (Fig. 11G, H). Last legs inflated, with seven podomeres, shape and chaetotaxy as in Figure 11G, H. Praetarsus as a very small tubercle with one small apical spine (Fig. 11I).

Terminal segments: posterior margin of intermediate tergum strongly convex, that of intermediate sternum slightly concave. Posterior margin of first genital sternum slightly concave (Fig. 11F, G). Gonopods biarticulate, basal article with 16 setae, apical article with eight setae (Fig. 11J); penis dorsally with 1+1 apical setae (Fig. 11K). The adult condition of the specimen is proved by the presence of reproductive organs full of mature sperm. Female with 51 p.l., body length 26 mm. Cephalic capsule and mouth parts similar to the male. Trunk missing, making it impossible to describe and illustrate the last leg-bearing segment and terminal segments. The only data Lawrence (1960) gives about these parts are the following: “Pattes : 51 paires ; la dernière épaisse, à dernier article à peine plus long que le pénultième et moitié de sa largeur”.

Schendylops silvicola (Lawrence, 1960) (Figs 12-14; 15A-D)

Haploschendyla silvicola Lawrence, 1960: 13.

Haploschendyla major Lawrence, 1960: 15.

Schendylops silvicola — Hoffman & Pereira 1997: 17, 22.

TYPE MATERIAL EXAMINED. — Holotype ♀, reference “*Haploschendyla silvicola*”, 61 pairs of legs, body length 42 mm, from Madagascar: Ankaratra, forêt de Manjakatombo, 1800-2000 m, I.1956, R. F. Lawrence leg. (MNHN coll. Myriapodes 131). Holotype ♀,

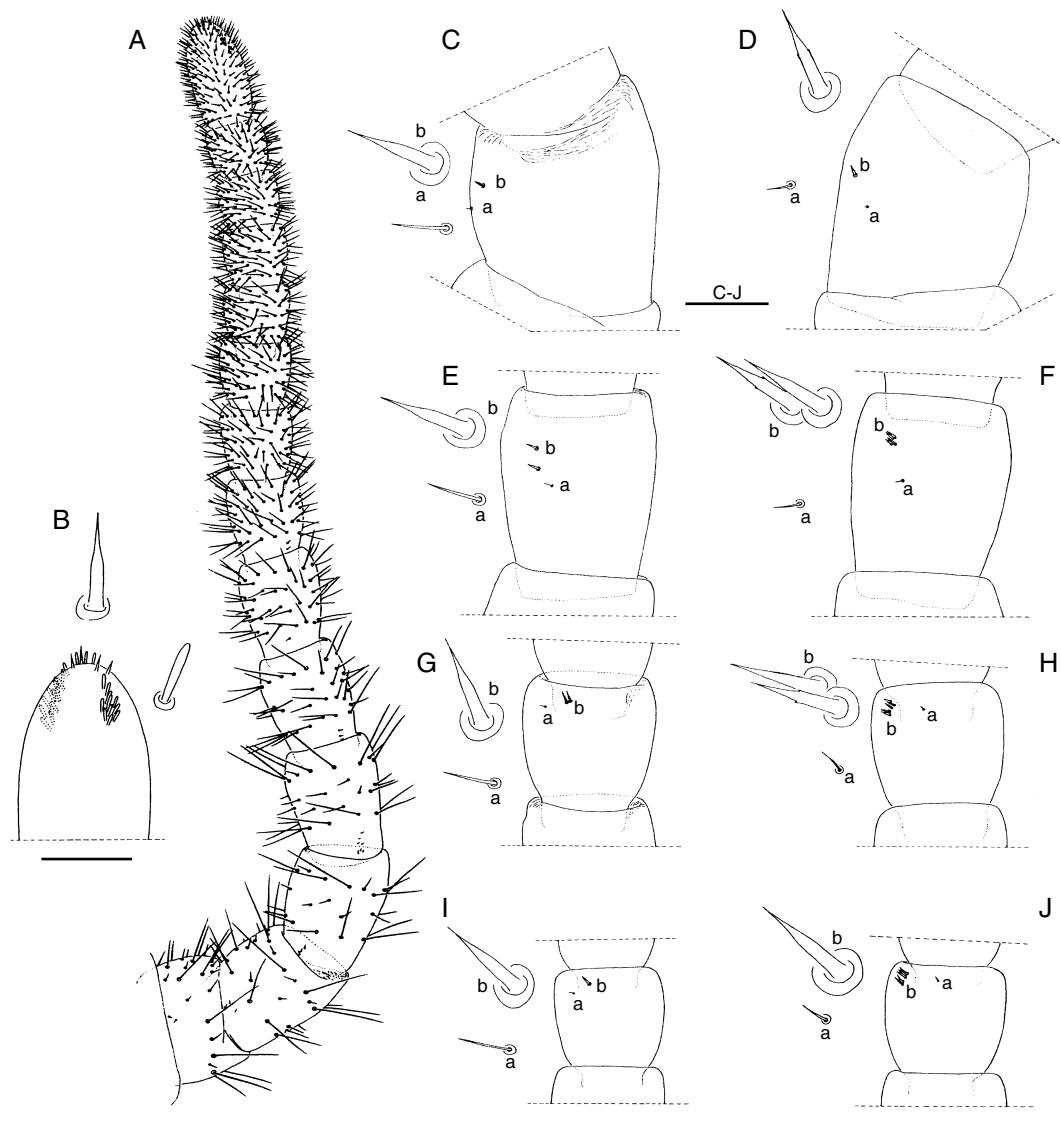


FIG. 12. — *Schendyllops silvicola* (Lawrence, 1960), ♀ holotype, Madagascar, Ankaratra; **A**, left antenna, ventral; **B**, left antennal article XIV, dorsal, with enlarged detail of one of the apical hyaline sensilla and one of the lateral claviform sensilla; **C**, left antennal article II, ventral; **D**, left antennal article II, dorsal; **E**, left antennal article V, ventral; **F**, left antennal article V, dorsal; **G**, left antennal article IX, ventral; **H**, left antennal article IX, dorsal; **I**, left antennal article XIII, ventral; **J**, left antennal article XIII, dorsal. **a**, **b**, types of setae. Scale bars: A, 0.03 mm; B, 0.05 mm; C-J, 0.1 mm.

reference “*Haploschendyla major*”, 61 p.l., body length 43 mm; paratype ♀, reference “*Haploschendyla major*”, 59 p.l., body length 38 mm, both from Madagascar: Mont d’Ambre, XII.1948, R. Paulian leg. (MNHN coll. Myriapodes 128). All three specimens with cephalic capsule and mouth parts on their original slides, trunks in alcohol.

TYPE LOCALITY. — Madagascar: Ankaratra: forêt de Manjakatompo.

DISTRIBUTION. — Madagascar: Ankaratra: Manjakatompo; Mont d’Ambre.

DIAGNOSIS. — A *Schendylops* species with v. pore fields present only on anterior sterna. Among the other Madagascar *Schendylops* species, this trait is present only in *S. paucispina*. Characters in Table 5 and in the key differentiate *S. silvicola* from this species and from all other Madagascar congeners.

REDESCRIPTION

Female holotype (of *S. silvicola*). 61 p.l., body length 43 mm; maximum body width 1.4 mm. Colour of preserved specimen in alcohol pale orange. (The original description, referring to freshly preserved specimens, states: “Couleur : corps et pattes jaunes, plaque céphalique antennes et tergite I un peu plus foncés, orange”). Antennae 2.7 times as long as the cephalic plate, distally slightly attenuate. Setae on a.a. I-V of different length, few in number; those of remaining articles progressively shorter and more numerous towards the tip of the appendage (Fig. 12A). Terminal a.a. with 14 claviform sensory setae on external border, c. 11 on internal border and three on the tip (Fig. 12B). Distal end of this a.a. with four very small specialised setae, apparently not split at the apical end (Fig. 12B). Dorsal and v. surface of a.a. II, V, IX and XIII with very small specialised setae (Fig. 12C-J; Table 4). On the v. side these setae are restricted to an internal lateral area of the a.a. and represented by two different types: a and b. Type a setae very thin, not divided apically; type b setae very similar to those of apex of terminal a.a. (a, b, Fig. 12C, E, G, I). Specialised setae on d. side restricted to an external lateral area, similar to type a and b setae of v. side, but some of type b setae apparently with two diminutive apical branches (a, b, Fig. 12D, F, H, J).

Cephalic plate slightly longer than wide (ratio 1.14:1), shape and chaetotaxy as in Figure 13A.

TABLE 4. — *Schendylops silvicola* (Lawrence, 1960), ♀ holotype, distribution of type a and b setae on antennal articles II, V, IX and XIII.

	Ventral			Dorsal		
	a	b	Fig.	a	b	Fig.
II	1	1	12C	1	1	12D
V	1	2	12E	1	4	12F
IX	1	2	12G	1	5	12H
XIII	1	1	12I	1	5	12L

Clypeus with 1+1 postantennal setae, 8+7 median setae and 1+1 praelabral setae (Fig. 13B).

Labrum with 25 teeth, those of central arc dark, robust, with obtuse tip; those of lateral pieces less sclerotised, smaller, with a sharp medial extension (Fig. 13C).

Mandible: dentate lamellae with eight teeth, not subdivided into blocks (Fig. 13D); pectinate lamellae with 18-20 teeth each.

First maxillae with large lappets on both coxosternum and telopodites (Fig. 13F). Coxosternum without setae, median projections of coxosternum well developed, provided with 2+3 setae (Fig. 13E). Article II of telopodite with 4+4 v. setae and 7+7 d. sensilla (Fig. 13E, F) (in the original description of *H. silvicola* Lawrence [1960] mentioned a “telopodite apparemment à trois articles”, but this was due to an artefact in the original slide).

Second maxillae (Fig. 13E, G) with 9+12 setae on coxosternum, arranged as in Figure 13E. Apical claw of telopodite bipectinate, v. edge with 10 teeth (Fig. 13G), d. with 12 teeth.

Forcipulae: telopodites, when closed, not extending beyond anterior margin of head. Tergum of the forcipular segment with 13+15 setae distributed as in Figure 13I. All articles of telopodites lacking teeth (Fig. 13H, I). Calyx of poison gland cylindrical (Fig. 13J). Chaetotaxy of coxosternum and telopodites as in Figure 13H, I.

Walking legs with chaetotaxy (Fig. 13K, L) uniform throughout body length. Claws ventrobasally with two spines (one anterior, one posterior); a third smaller spine occurring internally very close to the posterior one (Fig. 13M).

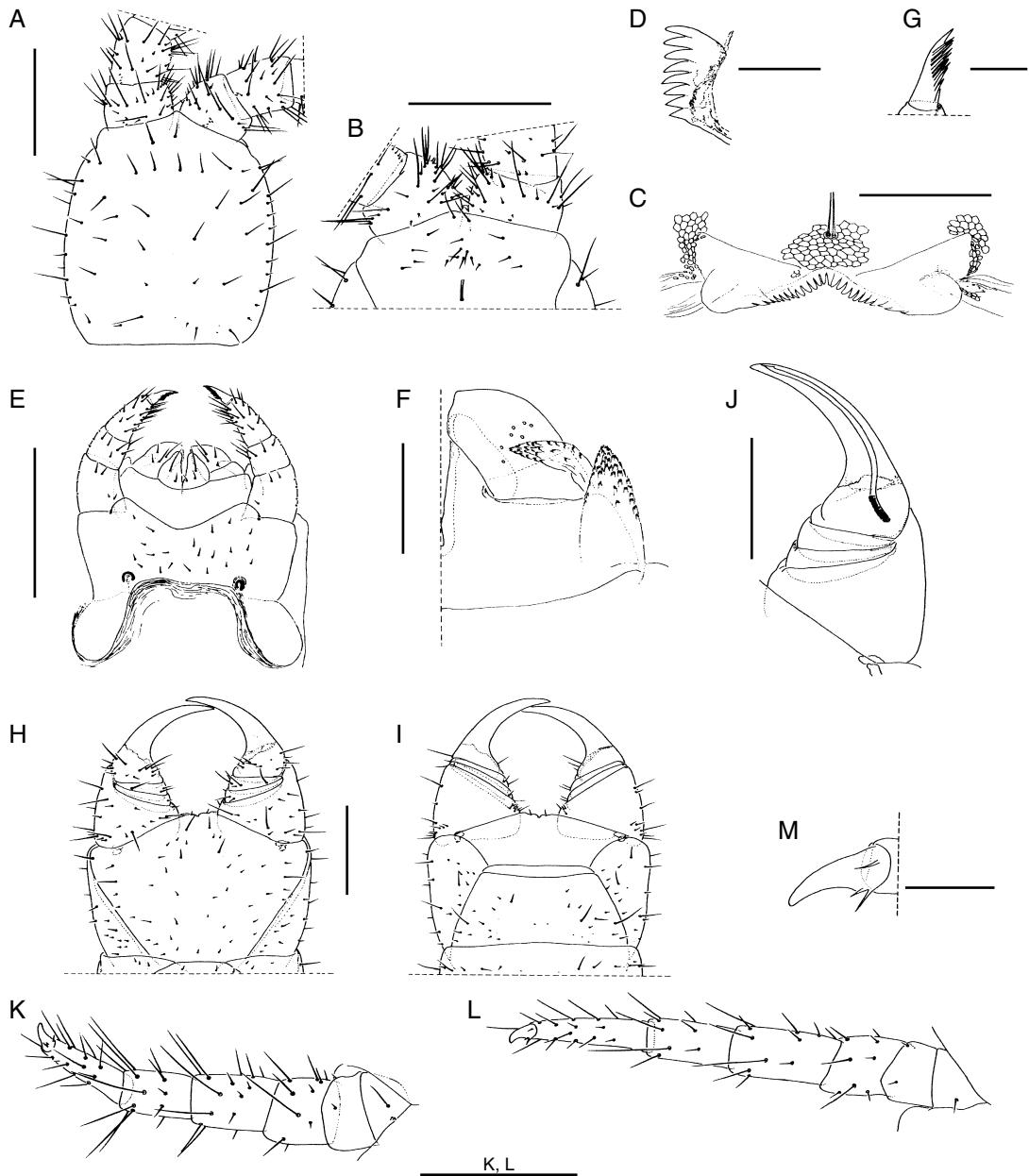


FIG. 13. — *Schendyllops silvicola* (Lawrence, 1960), ♀ holotype, Madagascar, Ankaratra; **A**, cephalic shield; **B**, clypeus and bases of antennae; **C**, labrum; **D**, denticulate lamella of right mandible; **E**, first and second maxillae, ventral; **F**, right first maxilla, dorsal; **G**, detail of distal end of telopodite of right second maxilla, ventral; **H**, forcipular segment with poison claws, ventral; **I**, the same, dorsal; **J**, detail of poison gland in left poison claw, ventral; **K**, right leg II, ventral; **L**, right leg LIII, ventral; **M**, claw of right leg LIII, ventral. Scale bars: A, B, E, H, I, 0.4 mm; C, F, 0.1 mm; D, G, M, 0.05 mm; J-L, 0.3 mm.

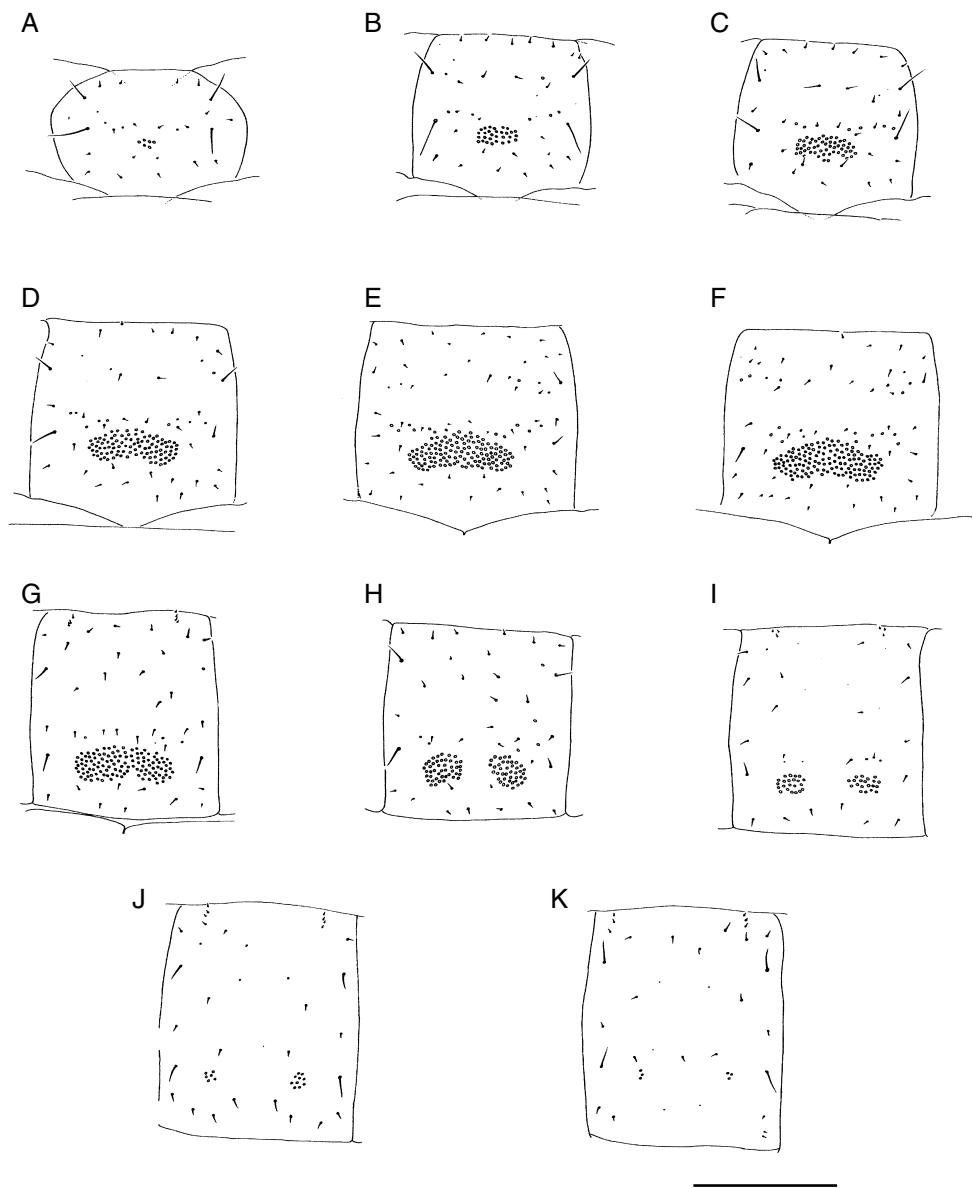


FIG. 14. — *Schendylops silvicola* (Lawrence, 1960), ♀ holotype, Madagascar, Ankaratra; A-K, sterna I, II, III, VII, XII, XV, XXII, XXIII, XXVI, XXIX, XXXII. Scale bar: 0.4 mm.

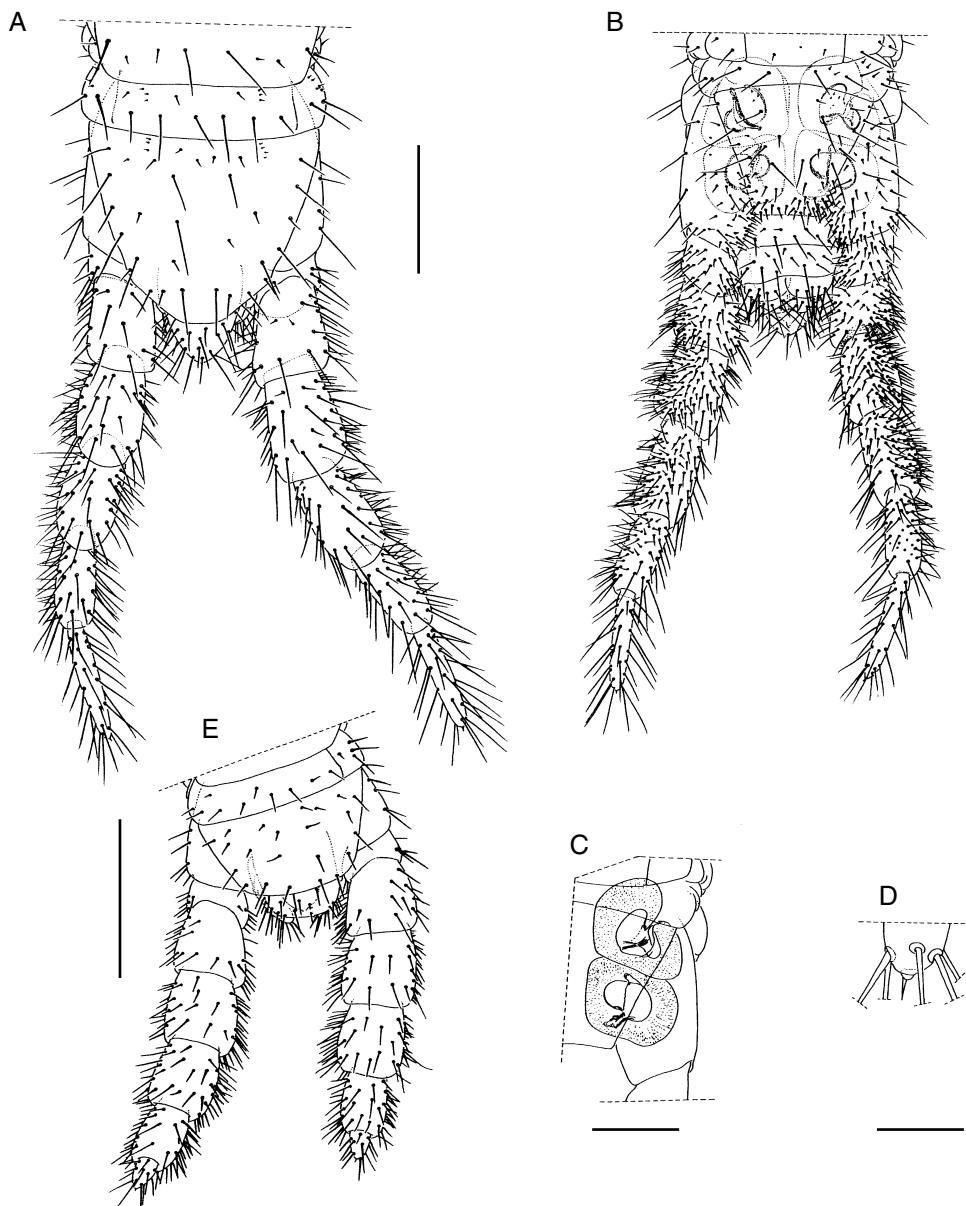


FIG. 15. — **A-D**, *Schendylops silvicola* (Lawrence, 1960), ♀ holotype, Madagascar, Ankaratra; **A**, last leg-bearing segment and terminal segments, dorsal; **B**, the same, ventral; **C**, left coxal organs, ventral; **D**, detail of distal end of last podomere of left last leg, dorsal; **E**, *Schendylops grandidieri* (De Saussure & Zehntner, 1897) (♂ lectotype, Madagascar, Sikora), last leg-bearing segment and terminal segments, dorsal. Scale bars: A, B, 0.3 mm; C, 0.2 mm; D, 0.05 mm; E, 0.4 mm.

Sterna: pore fields present on sterna I to XXXII only, undivided on sterna I-XXII, divided in two subsymmetrical areas on sterna XXIII-XXXII; on sterna I to XXVI with a small group of pores at both sides of the anterior border of pore fields.

Shape and relative size of fields changing along the trunk as in Figure 14. Number of pores on selected sterna: on sternum I: 2+6+1; II: 2+30+3; III: 2+53+4; VII: 5+96+4; XII: 5+127+5; XV: 5+136+5; XXII: 1+117+2; XXIII: 2+45+41+2; XXVI: 2+22+20+2; XXIX: 6+10; XXXII: 3+3.

Last leg-bearing segment with pleurites at sides of praetergum. Praesternum not divided along the sagittal plane; shape and chaetotaxy of tergum and sternum as in Figure 15A, B. Coxopleuron slightly protruding at the distal v. end, setae numerous on v. internal margin, the remaining surface with few larger setae. Two single ("homogeneous") coxal organs on each coxopleuron (Fig. 15B, C). Coxal organs opening on the membrane between coxopleuron and sternum, partially covered by latter (Fig. 15B, C). Last legs moderately inflated, with seven podomeres, shape and chaetotaxy as in Figure 15A, B. Praetarsus as a very small tubercle with one small apical spine (Fig. 15D).

Terminal segments: posterior margin of intermediate tergum strongly convex, that of intermedi-

ate sternum slightly concave. Posterior margin of first genital sternum medially slightly convex, laterally slightly concave (Fig. 15A, B). Gonopods uniarticulated (Fig. 15B).

Male unknown.

Variation

59 or 61 p.l. (females); 55 p.l. (sex?). Body length 40-45 mm.

Schendylops grandidieri

(De Saussure & Zehntner, 1897)
(Fig. 15E)

Schendyla Grandidieri De Saussure & Zehntner, 1897: pl. XII, figs 8a-8g; 1902: 332.

Schendylops grandidieri — Cook 1899: 305. — Brölemann & Ribaut 1912: 169. — Hoffman & Pereira 1997: 13.

TYPE LOCALITY. — Madagascar: Sikora.

DISTRIBUTION. — Madagascar: Sikora.

DIAGNOSIS. — A *Schendylops* species with v. pore fields extending along the whole body length. Of the other Madagascar *Schendylops* species this trait is present only in *S. mascarenicus* and *S. insolitus*. Characters in Table 5 and in the key differentiate *Schendylops grandidieri* from these two species and from the other Madagascar congeners.

KEY TO THE MADAGASCAR SPECIES OF *SCHENDYLOPS* (updating the previous key in Hoffman & Pereira 1997)

1. Ventral pore fields on both anterior and posterior sterna 2
- Ventral pore fields on anterior sterna only 4
2. Pore fields ending on antepenultimate sternum; 1+1 setae on the coxosternum of the first maxillae; 65 p.l. (♀) *S. mascarenicus*
- Pore fields ending on penultimate sternum; no setae on the coxosternum of the first maxillae; either 55 or 75 p.l. 3
3. Coxosternum of the second maxillae with c. 28 setae; 75 p.l. (♂); basal internal edge of forcipular tarsungulum unarmed; ratio of length of tarsus to length of metatarsus of ♂ terminal legs c. 1.25:1 (Fig. 4A) *S. insolitus*
- Coxosternum of the second maxillae with c. 19 setae; 55 p.l. (♂); basal internal edge of forcipular tarsungulum with a small tubercle; ratio of length of tarsus to length of metatarsus of ♂ terminal legs c. 2.0:1 (Fig. 15E) *S. grandidieri*

4. Specialised ochraceous setae on the d. surface of the antennae (on a.a. IX and XIII); 49 (♂), 51 (♀) p.l.; pore fields on sterna I to XXII; last pedal segment without pleurites at the sides of praetergum; posterior border of praetergum of last leg-bearing segment conspicuously “clubbed” medially (Fig. 11F) *S. paucispina*
- No specialised ochraceous setae on the d. surface of the antennae; 55 (sex?), 59, 61 (♀) p.l.; pore fields on sterna I to XXXII; last pedal segment with pleurites at the sides of praetergum; posterior border of praetergum of last leg-bearing segment not “clubbed” medially (Fig. 15A) *S. silvicola*

TABLE 5. — Synopsis of external features of the Madagascar species of the genus *Schendylops* Cook, 1899.

	<i>S. grandidieri</i>	<i>S. insolitus</i>	<i>S. mascarenicus</i>	<i>S. paucispina</i>	<i>S. silvicola</i>
Pairs of legs	♂: 55; ♀: ?	♂: 75; ♀: ?	♂: ?; ♀: 65	♂: 49; ♀: 51	♀: 59, 61; sex?: 55
Maximum body length (mm)	23	35	38	26	45
Length of antennae to length of cephalic shield	2.1	2.0	2.1	2.5	2.7
Specialised ochraceous setae on the dorsal surface of antennae	none	none	none	on antennal article IX and XIII	none
Clypeal setae: postantennal, middle, paelabral	2, c. 13, 0	2, c. 17, 2	0, c. 18, 2	2, c. 11, 2	2, c. 15, 2
Dentate lamellae of mandibles divided into blocks	yes	yes	yes	no	no
Setae of coxosternum of maxillae I	none	none	1+1	none	none
Setae on the coxosternum of maxillae II	c. 19	c. 28	c. 23	c. 18	c. 21
Tubercle on the basal internal edge of forcipular tarsungulum	very small	none	none	none	none
Sterna with pore fields	I to penultimate	I to penultimate	I to antepenultimate	I to mid-body (XXII)	I to mid-body (XXXII)
Last praetergum completely fused to the pleurites	no	no	no	yes	no
Dorsal apical setae of penis	0+0	0+0	?	1+1	?
Posterior border of praetergum of last leg-bearing segment conspicuously “clubbed” medially	no	no	no	yes	no
Length of tarsus to length of metatarsus of ♂ last legs	2.0	1.25	?	1.0	?

DISCUSSION

It remains to be seen whether all the numerous species of geophilomorph centipedes currently referred to the genus *Schendylops* really form a monophyletic unit. Their geographical distribution, with a majority of Neotropical species accompanied by a few species in the African

mainland (from Morocco to South Africa) and Madagascar, invites closer investigation. But this is not an easy task, as the whole generic classification of schendylid geophilomorphs is still grounded on characters of uncertain phylogenetic value.

The Madagascar *Schendylops* species, on the other hand, are likely to form a monophyletic lineage

characterized by a very short trochanteropraefemur of the forcipular telopodites, with the ratio between the width and the length of the external border between 0.95:1 (*S. paucispina*, *S. mascarenicus*) to 1.30:1 (*S. insolitus*). This putative clade will anyway deserve to be placed in *Schendyllops*, as the type species of this genus is one of the Malagasy species, i.e. *Schendyllops grandidieri*.

None of the five Madagascar species have setae on a tubercle-like base on the podomeres of the terminal legs, such as present in two of the seven species living on the African mainland, i.e. *Schendyllops australis* (Silvestri, 1907) and *S. pumicosus* (Demange, 1963).

A map of the localities where species of *Schendyllops* have been collected in Madagascar is given in Figure 16.

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REFERENCES

- BRÖLEMMANN H. W. & RIBAUT H. 1912. — Essai d'une monographie des Schendylina (Myriapodes Geophilomorphes). *Nouvelles Archives du Muséum d'Histoire naturelle, Paris* sér. 5, 4: 53-183.
- COOK O. F. 1899. — The Geophiloidea of the Florida Keys. *Proceedings of the Entomological Society of Washington* 4: 302-312.
- DE SAUSSURE H. & ZEHNTNER L. 1897. — Myriapodes, in GRANDIDIER A. (ed.), *Histoire physique, naturelle et politique de Madagascar*. Imprimerie nationale, Paris, 28 p., Atlas, pls I-XII.
- DE SAUSSURE H. & ZEHNTNER L. 1902. — Histoire naturelle des Myriapodes, in GRANDIDIER A. (ed.), *Histoire physique naturelle et politique de Madagascar. Mémoires du Muséum national d'Histoire naturelle, Paris* 37 (53): i-viii +1-356.
- FODDAI D., PEREIRA L. A. & MINELLI A. 2000. — A catalogue of the geophilomorph centipedes (Chilopoda) from Central and South America including Mexico. *Amazoniana* 16 (1/2): 59-185.
- HOFFMAN R. L. & PEREIRA L. A. 1997. — The identity and taxonomic status of the generic names *Schendyllops* Cook, 1899, and *Schendylurus* Silvestri, 1907, and the proposal of *Orygmadyla*, a new related genus from Peru (Chilopoda: Geophilomorpha: Schendylidae). *Myriopodologica* 5 (2): 9-32.
- LAWRENCE R. F. 1960. — Myriapodes-Chilopodes. *Faune de Madagascar. XII. Institut de la Recherche scientifique, Tananarive-Tsimbazaza*, 123 p.
- PEREIRA L. A. & MINELLI A. 1993. — On two new species of *Schendylurus* Silvestri, 1907 from Venezuela, with redescription of *S. colombianus* Chamberlin, 1921 and *S. virgingordae* Crabbill 1960 (Chilopoda: Geophilomorpha: Schendylidae). *Tropical Zoology* special issue 1: 105-123.

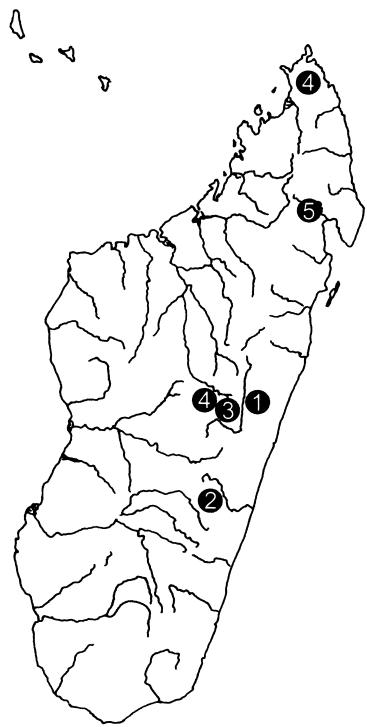


FIG. 16. — Collection locality of *Schendyllops insolitus* (Lawrence, 1960) (1), *S. mascarenicus* (Lawrence, 1960) (2), *S. paucispina* (Lawrence, 1960) (3), *S. silvicola* (Lawrence, 1960) (4), *S. grandidieri* (De Saussure & Zehntner, 1897) (5) (position of the type locality of this species tentative, after latitude and longitude of Alan'i Sikiory = ? "Sikora").

- PEREIRA L. A. & MINELLI A. 1995. — The African species of the genus *Schendylurus* Silvestri, 1907 (Chilopoda Geophilomorpha Schendylidae). *Memorie della Società entomologica Italiana* 73 (1994): 29-58.
- PEREIRA L. A. & MINELLI A. 1996. — The species of the genus *Schendylurus* Silvestri, 1907 of Argentina, Brazil and Paraguay (Chilopoda: Geophilomorpha: Schendylidae). *Tropical Zoology* 9: 225-295.
- PEREIRA L. A. & MINELLI A. 2001. — A re-description of the South African centipede *Schendylops caledonicus* (Chilopoda Geophilomorpha Schendylidae). *Bollettino della Società entomologica Italiana* 133 (1): 13-25.
- PEREIRA L. A., FODDAI D. & MINELLI A. 1997. — Zoogeographical aspects of Neotropical Geophilomorpha. *Entomologica Scandinavica Supplementum* 51: 77-86.

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