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Revision of the millipede subfamily Spiromiminae, a Malagasy group with Indian connections? (Diplopoda Spirobolida Pachybolidae)

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Recent inventory work on Madagascar has led to the discovery of several undescribed species of the millipede order Spirobolida. All three known species belonging to the endemic Malagasy subfamily Spiromiminae Brölemann 1914 are redescribed here, and 10 new species are added. The genus *Pygodon* de Saussure & Zehntner 1901 is synonymized under *Spiromimus* de Saussure & Zehntner 1901, rendering the Spiromiminae monotypic and including *Spiromimus voeltzkowi* de Saussure & Zehntner 1901, *S. univirgatus* de Saussure & Zehntner 1901, *S. dorsovittatum* (de Saussure & Zehntner 1901) n. comb., *S. triaureus* n. sp., *S. electricus* n. sp., *S. litoralis* n. sp., *S. scapularis* n. sp., *S. albipes* n. sp., *S. laticoxalis* n. sp., *S. simplicicoxalis* n. sp., *S. grallator* n. sp., *S. namoroka* n. sp., and *S. simplex* n. sp. Antennae, gnathochilarium, mandible and female copulatory organs were compared using scanning electron microscopy. In order to find apomorphies of the Spiromiminae and to construct a species-level phylogeny of *Spiromimus*, members of the other described spirobolidan genera from Madagascar, *Aphistogoniulus* Silvestri 1897 and *Madabolus* Wesener & Enghoff 2008, as well as the Indian genus *Xenobolus* Carl 1918 and the SE Asian genus *Aulacobolus* Pocock 1903, were added as outgroups to the data matrix. The phylogenetic analysis resulted in an (albeit weakly supported) strict consensus tree with the following structure: *Aulacobolus*, *Madabolus*, *Aphistogoniulus*, (*Xenobolus* (*Spiromimus simplicicoxalis* (*S. laticoxalis* (*S. voeltzkowi* ((*S. litoralis* (*S. electricus* (*S. dorsovittatus*, *S. triaureus*))) (*S. scapularis* (*S. univirgatus*, *S. albipes*)))))))). Distribution and habitat (in dry forest *vs.* rainforest) were mapped on the tree.

KEY WORDS: Madagascar, endemism, vicariance, phylogeny, ecological niche.

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INTRODUCTION

Madagascar has always attracted the curiosity of researchers. Its fauna and flora is mostly endemic, species rich and highly endangered, leading to Madagascar's status as one of the world's eight 'hottest' biodiversity hotspots (Myers et al. 2000). One explanation for the worldwide uniquely large amount of endemic species can be found in the geographical isolation of this fourth largest island from other land masses since the Mesozoic (Rabinowitz et al. 1983, Metcalfe 1998, Krause 2003). Recently, there has been a lively discussion, whether the endemic fauna of the island is the result of vicariance or dispersal events (Yoder & Nowak 2006).

Despite the importance of the fauna of Madagascar from a biogeographical and conservation point of view, only few recent studies deal with its millipedes (see species list in Enghoff 2003). Even by this standard, the order Spirobolida has received little attention. Ignoring widespread tramp species, only four spirobolidan genera, *Aphistogoniulus* Silvestri 1897, *Spiromimus* de Saussure & Zehntner 1901, *Pygodon* de Saussure & Zehntner 1901, and *Madabolus* Wesener & Enghoff 2008, are known from Madagascar, all of them strict endemics.

The genera *Spiromimus* and *Pygodon* were both described by de Saussure & Zehntner (1901), who even in their first description noted the very unusual, almost Spirostreptida-like appearance of their members: long legs

and antennae combined with a slender and elongated body. The classification of Spirobolida, especially of the suborder Trigoniulidea, is still based on the system developed by BRÖLEMANN (1914), who erected the family Spiromimidae exclusively for the genera *Spiromimus* and *Pygodon*. VERHOEFF (1936) included the Indian genus *Xenobolus* Carl 1918 in the Spiromimidae. HOFFMAN (1962) rejected this placement, based on his assumption that *Xenobolus* "[...] appears to be closely related to *Stenobolus* and *Mystalides* [now a synonym of *Aphistogoniulus*]". Later, he reduced the family Spiromimidae to subfamily rank, now including, again, only the genera *Spiromimus* and *Pygodon* (HOFFMAN 1980). A recent phylogenetic analysis based on 37 morphological characters and including numerous genera of Trigoniulidea (WESENER et al. 2008) supported, albeit weakly, the close relationship of the Indian *Xenobolus* to the Malagasy Spiromiminae. The subfamily is therefore of special interest because it may represent a Madagascar-Indian link, supporting a vicariance origin of the Spiromiminae. The genus *Spiromimus* is also remarkable because its members occur in rainforest as well as in dry forest, so far an unusual distribution pattern for Malagasy Spirobolida.

The aims of this study are:

(1) to revise the genera *Spiromimus* and *Pygodon*,
(2) to conduct a phylogenetic analysis of the species inside these genera,
(3) to determine whether this remarkable genus originated from dry forest or rainforest,
(4) to reassess the possible relationship between *Spiromimus, Pygodon* and *Xenobolus*.

MATERIAL AND METHODS

Abbreviations

BLF	Collection code for Madagascar sample at CAS
CAS	California Academy of Sciences, San Francisco, USA
FMMC	Collection code for millipede samples at the FMNH
FMNH	Field Museum of Natural History, Chicago, USA
MHNG	Muséum d'Histoire Naturelle, Genève, Switzerland
MNHN	Muséum National d'Histoire Naturelle, Paris, France
ZFMK	Zoologisches Forschungsmuseum Koenig, Bonn, Germany
ZMUC	Natural History Museum (Zoological Museum), University of Copenhagen, Denmark

Taxonomic sampling

The available type material of the genera *Spiromimus* and *Pygodon* was borrowed from MHNG. A specimen of *Spiromimus voeltzkowi* belonging to the original type series was studied at MNHN. Undetermined specimens were sorted from the backlog of the large Madagascar millipede collection (mainly collected by Brian L.

Fisher [BLF] and Steven M. Goodman) at the Field Museum of Natural History, Chicago (FMNH), California Academy of Sciences, San Francisco (CAS), Muséum National d'Histoire Naturelle, Paris (MNHN) and the Natural History Museum Copenhagen (ZMUC). The undetermined material included specimens of *S. univirgatus* as well as ten undescribed species of the genus *Spiromimus*. For the phylogenetic analysis, the following material was examined: *Madabolus maximus* Wesener & Enghoff 2008, 1 M, 1 F (FMMC 5466); *Aulacobolus* cf. *rubropunctatus* Attems 1938, 1 M, 1 F (FMMC); *Aphistogoniulus erythrocephalus* (Pocock 1893), 1 M, 1 F (CAS BLF 8874); *Xenobolus carnifex* (Fabricius 1775), 1 M, 1 F (ZMUC).

Dissections and illustrations

Pencil drawings were produced using a camera lucida. Images were taken using a Microptics®-Imaging-System (based at the FMNH). Additional images were taken with a Leica® Z6 imaging system. The Syncroscopy software Auto-Montage package was used to assemble 6-20 source images taken at different focal lengths into the final image. For scanning electron microscopy, samples were cleaned and dehydrated in an ethanol series (80%, 90%, 95% and twice in 100%) and air-dried overnight. The samples were then mounted on aluminum stubs before being coated with gold in a sputter coater for 240 sec. SEM micrographs were taken using a Zeiss (Leo) EVO SEM, also based at the FMNH. Dry SEM material was removed from stubs and returned back into alcohol. All images were later modified using Adobe Photoshop version 6.0 and assembled into plates using Adobe Illustrator version CS2.

Phylogenetic analysis

A character matrix of 23 binary and 10 multistate morphological characters (Table 1) was prepared in Mesquite 1.06 (Maddison & Maddison 2005). Outgroup comparison was made with *Xenobolus carnifex* since Verhoeff (1936) suggested a close relationship between *Xenobolus* and the Spiromiminae. *Aphistogoniulus erythrocephalus*, *Madabolus maximus* and *Aulacobolus* cf. *rubropunctatus* were selected as further outgroup taxa. Besides *Madabolus*, which forms a monophyletic group together with African genera (Wesener et al. 2008), *Aphistogoniulus* Silvestri 1897 is so far the only spirobolidan genus described from Madagascar which does not belong to the Spiromiminae, and Hoffman (1962) suggested a close relationship between *Xenobolus* and *Aphistogoniulus*. The phylogenetic analysis was undertaken with PAUP v4.0b (Swofford 2002). All multistate characters were treated as unordered. Heuristic searches were undertaken under the tbr setting. A bootstrap analysis was run using 2000 replicates. The decay values for our dataset were calculated on a Windows PC with the program PRAP 1.21 (Müller 2004) under the following heuristic settings: random addition circles, activated; nreps, 10,000; maxTrees, 10,000,000.

Taxonomic characters

One of the difficulties surrounding the class Diplopoda is the shortage of suitable morphological characters for phylogeny. The last comprehensive morphological treatment of all major millipede groups dates back to Verhoeff (1928, 1932) and is often the only source for a description of various structures. In the Spirobolida, as in most other millipede orders, the classification is chiefly based on male gono-

Table 1.

Character matrix. See Appendix 1 for a character list and discussion.

Species	Characters			
	0000000001	1111111112	2222222223	333
	1234567890	1234567890	1234567890	123
Madabolus maximus	0010000000	0000000000	0-01-0000-	--0
Aulacobolus rubropunctatus	1010000000	0000000000	0-01-0000-	--0
Aphistogoniulus erythrocephalus	0000000000	0000000000	000000000-	--0
Xenobolus carnifex	1011100111	0000010010	1011100021	001
Spiromimus simplicicoxalis n. sp.	00000-1011	0000010010	1011110032	010
Spiromimus laticoxalis n. sp.	0000011012	2100110010	1011102032	000
Spiromimus voeltzkowi	00000-1022	0111111011	1111101112	200
Spiromimus litoralis n. sp.	0000011022	0101111211	1011122110	000
Spiromimus electricus n. sp.	0000011022	1101111111	1011122020	000
Spiromimus dorsovittatus	01000-1012	1101111011	1011122021	000
Spiromimus triaureus n. sp.	0000011022	1111121211	1011102121	000
Spiromimus scapularis n. sp.	0000011022	2101211211	1111121012	100
Spiromimus univirgatus	0000011022	2111211111	1011121012	100
Spiromimus albipes n. sp.	0000011022	2101211111	1011121022	100

pods (modified 8th and 9th legs). Recent studies (Enghoff 1991, Wesener et al. 2008) show, however, that other organ systems can be successfully employed. In this study, we examined the female vulva, anterior gonopods and posterior gonopods, modified male leg-pairs 3-7 as well as mandible, gnathochilarium and antenna.

Female copulatory organ (vulva). The study of Keeton (1960) on the family Spirobolidae, as well as a recent study (Wesener et al. 2008) on Pachybolini demonstrated the importance of the vulvae for spirobolidan taxonomy. Usually, the vulvae in Spirobolida are simple, bivalve-like structures located in membranous pouches attached to the second coxae. However, in some groups, they may show a variety of forms, composition of sclerites, or the occurrence or position of setae. Generally, three separate elements can be distinguished in the spirobolid vulva: the anterior valve and posterior valve (two plates of usually the same size and with sensilla), and a third small, poorly sclerotized sclerite at the proximal juncture of both valves, traditionally called operculum (Keeton 1960). The function of the operculum is still unclear, it is unlikely to function as a lid since the vulva opening is usually located between the anterior and posterior valves (Fig. 23A-D).

Mandible and gnathochilarium. Mandibular characters have been proven useful for classification and/or phylogenetic analysis of several millipede orders: Julida (Enghoff 1991), Polyxenida (Ishii & Tamura 1995), and Polydesmida (Ishii & Tamura 1996). The mandibles of *Aphistogoniulus*, *Spiromimus* and *Xenobolus* were studied (Figs 4A, 8C, 13D, 27A), but the general structure seems to be quite conservative in the whole order Spirobolida. Only the length and structure of the molar plate as well as the number of pectinate lamellae seem to vary. Morphological constancy is also characteristic

of the pachybolid gnathochilarium (Figs 3D-F, 26C), although WESENER et al. (2008) used the number and position of setae on the lamellae linguales in their analysis.

Antenna and sensory cones. The species studied in this work show great variation in the length of the antenna (Figs 2A, 7A, 11A, 16A, 17A), but the differences were even larger between males and females of the same species. All sensilla on antennomeres five and six of *Aphistogoniulus*, *Spiromimus* and *Xenobolus* (Figs 3B-C, 8A-B, 13B-C, 26B) are quite similar to those illustrated in the literature (family Rhinocricidae, *Rhinocricus*, FONTANETTI & CAMARGO-MATHIAS 2004).

Male leg-pairs 3-7. One of the most remarkable features displayed by members of the genera *Spiromimus* and *Pygodon* are the male coxae 3-7, which are often strongly modified, featuring very long processes or species-specific modifications at least on the third and fourth coxae (Figs 2B-C, 7B, 10A, 11B, 15B, 16B, 17B, 18B). In *Xenobolus*, the third and fourth coxae also feature short processes, but the prefemur, femur and postfemur are flattened and medio-apically extended into a short process. The function of these processes is unknown, but might give the male additional support on top of the female during copulation.

Gonopods. The anterior gonopods (modified 8th leg-pair, coleopods of some authors) consist of sternite, coxite, and telopodite (Fig. 14A). The anterior gonopods form a cover for the posterior gonopods (Figs 14A-B). The posterior gonopods (modified 9th leg-pair, phallopods of some authors) can be divided into coxite and telopodite (Fig. 14C). Beside these basal divisions, no homology hypotheses about gonopodal parts exist for Spirobolida. We here offer homology hypothesis of the following gonopod structures:

- anterior gonopod coxite, mesal process (Fig. 2E, *MP*): homologous within suborder Trigoniulidea;
- anterior gonopod telopodite, lateral triangular projection (Fig. 2E, *TE*): homologous within *Spiromimus;*
- anterior gonopod telopodite, raised tip (Fig. 2E): homologous within *Spiromimus* and *Xenobolus;*
- posterior gonopod telopodite bent mesad (Fig. 7D) with a mesal branch parallel to main part of gonopod and harboring part of the sperm duct (Figs 14C-E): homologous within *Spiromimus* and *Xenobolus*.

RESULTS

Taxonomy

Family Pachybolidae Brölemann 1914
Subfamily Spiromiminae Brölemann 1914

Originally proposed as a family, this taxon was regarded as a subfamily of Pachybolidae by HOFFMAN (1980). Spiromiminae are characterized only by gonopod characters: the anterior gonopod sternite, coxite and telopodite are all elongated into slender processes, a unique feature within the Spirobolida (Fig. 2E). Other features shared by all members of Spiromiminae are: tips of main branches of posterior gonopod telopodite bent towards one another (Fig. 7D), a mesal branch on posterior gonopod telopodite present (reduced in *S. simplex* n. sp.), carrying part of the sperm canal and only weakly scler-

otized (Fig 14D-E), coxae of leg-pairs three and four with unusually wide and rod-shaped (absent in *S. simplicicoxalis* n. sp. and *S. grallator* n. sp.) modified processes (Fig. 2B).

Included genus: *Spiromimus*.

Genus ***Spiromimus*** de Saussure & Zehntner 1901

Spiromimus de Saussure & Zehntner 1901: 443.
Pygodon de Saussure & Zehntner 1901: 446, new synonym.

Type species of *Spiromimus*: *Spiromimus univirgatus* de Saussure & Zehntner 1901, by original designation. Type species of *Pygodon: Pygodon dorsovittatus* de Saussure & Zehntner 1901, by monotypy.

Diagnosis. Small to medium-sized pachybolids: males 40-60, females up to 75 mm long. Females always longer and thicker than males. Mature individuals with 42-48 body rings, no apodous rings in front of telson. Antennae strongly sexually dimorphic, being much longer in males. Body ring 6 in males ventrally greatly enlarged, protecting the gonopod pouch (Figs 7A, 15A). Anterior gonopods strongly elongated (Figs 2D, 14A), not completely retractable into pouch; sternite with a slender median process, coxite anteriorly with a slender mesal process, telopodite elongated into long process. Posterior gonopods always connected by a medium-sized sternite; coxite always with a single groove and a conical process; telopodite consisting of two branches, main branch bent mesad, tip of each gonopod facing its counterpart, both gonopods forming a rotated 'C' (Fig. 7D); telopodite with a mesal branch running parallel to main axis (Fig. 6C); space between mesal branch and main branch in some species filled with membranous folds (Fig. 2E). Main branch in some species with membranous fringe apically, towards mesal branch, this fringe sometimes elongated into membranous process (Fig. 14C).

Distribution. Endemic to Madagascar. Members are distributed in dry forest and rainforest ecosystems all over the island, with most species being confined to the northern half of Madagascar (Fig. 1). At some localities, two species can be found sympatrically.

Description

Color. Species-specific, but all known species dorsally at least with a brightly colored, continuous mid-dorsal stripe (Fig. 7A). Antennae and legs often red (Fig. 2A).

Head. Number of ocelli species-specific, circa 40 (Figs 2A, 7A, 10A, 11A, 15A, 16A, 17A, 18A). Labrum with 3 or 4 irregular teeth and a row of 8+8 stout, marginal setae. Length of antenna sexually dimorphic. Female antenna short, reaching back to third body ring. Male antenna long, reaching back to seventh body ring; relative length of antennomeres:

1<2=3=4=5=6; terminal antennomere with four large sensory cones located in a shared membranous area (Figs 3A, 8A, 13B). Antennomere six latero-apically with a field of 1-4 rows of sensilla basiconica, antennomere five latero-apically with 4-6 rows (Figs 3B-C, 8A-B, 13B-C).

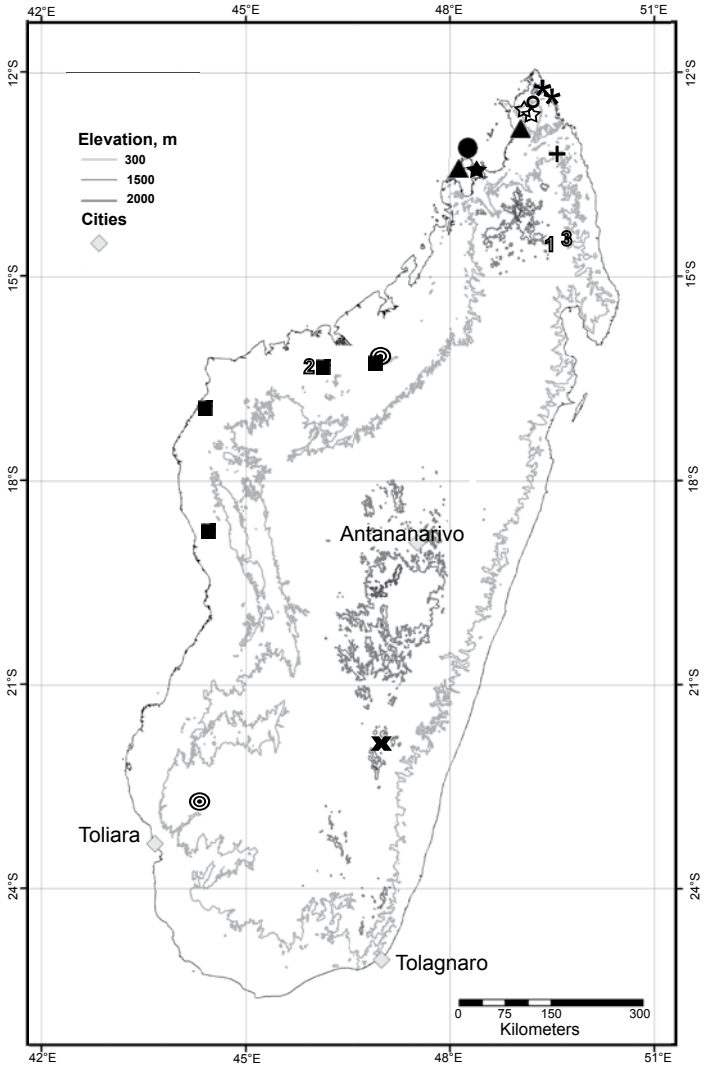

Fig. 01: Distribution of *Spiromimus* species: ▲ *S. univirgatus,* ● *S. voeltzkowi,* ★ *S. dorsovittatus,* ■ *S. triaureus* n. sp., ☆ *S. electricus* n. sp., ✱ *S. littoralis* n. sp., + *S. scapularis* n. sp., **o** *S. albipes* **n. sp.**, ◎ *S. laticoxalis* n. sp., ✖ *S. simplicicoxalis* n. sp., **1** *S. grallator* **n. sp.**, **2** *S. namoroka* n. sp., **3** *S. simplex* n. sp.

Fig. 1. — Distribution map, legends included in Figure.

Gnathochilarium shape typical of spirobolidans (Fig. 3D). Lamellae linguales each with two setae, one behind the other. Stipites laterally slightly excavated, each with three apical setae. Mentum with several transverse ridges in basal half. Palpi of gnathochilarium with numerous sensilla. Hypopharyngeal crest with a field of spine-like structures (Fig. 3F). Central pads of endochilarium separated into two levels: an apical lower level with a circular arrangement of 4-10 sensilla (Fig. 3E) and a basal higher level (medial palps) with a large group of sensilla, located towards hypopharyngeal crest (Fig. 3E).

Mandible (Figs 4A, 8C, 13D, terminology after ENGHOFF 1979). External tooth simple, rounded; inner tooth with three cusps, laterally an additional, isolated, simple tooth. Number of pectinate lamellae 6-10, species-specific. Mesal margin of pectinate area with circa two rows of small, slender spines, spine-row continued along mesal margin of otherwise smooth intermediate area. Molar plate small and short, with 3-6 shallow transverse furrows.

Collum. Lateral margins rounded, lateral lobes not extending ventrally as far as second body ring, surface smooth (Fig. 2A). Body rings divided by sutures into three transverse zones: prozona, mesozona and metazona. Ozopores starting on ring 6, located closely in front of, but not touching suture between, mesozona and metazona (Figs 4E-F, 9A). Ozopore with cone-shaped closure mechanism (Fig. 9B). Surface of ventral half on meso- and metazona with weak longitudinal impressions (Fig. 4E). Anal valves with neither lips nor micropunctation, nor grooves, nor hair (Fig. 2D), but in one species (*Spiromimus dorsovittatus*) each with a single spine (Fig. 6A). Preanal ring not protruding above anal valves. Subanal scale inconspicuous.

First and second leg pairs: coxa elongated and fused with sternite (Fig. 12A, C), ventral margin of podomeres from prefemur to tarsus each with 2-5 setae (Figs 12B, D). Leg-pair three and beyond: cylindrical coxa (Fig. 4C), each podomere ventroapically with a single pair of setae (Figs 4B, 8D). Tarsi with four pairs of ventral setae and a single apical seta, ventral margin apically with two setae on each side (Fig. 4B). Claw large, curved. Stigma inconspicuous, on a small bump (Fig. 4D).

Male sexual characters. Coxae three and four (often 3-7) modified, with species-specific, in most cases very large, rod-shaped processes. Sixth and seventh body rings conspicuously enlarged, tips of gonopods visible in ventral view. Antennae elongated, reaching back to body ring 8. Legs without tarsal pads (Figs 4B, 8D).

Anterior gonopods. Sternite basally wide, with slender median process, process as long as or even longer than rest of sternite (Fig. 2D). Coxite in oral view elongated into slender, mesal process, running parallel to sternal process. Telopodite in oral view basally surrounded by coxite; mesal margin of telopodite always with slender tip projecting distad, parallel to sternal and coxal processes (Fig. 2D).

Posterior gonopods. Almost entirely concealed by anterior gonopods *in situ* but apical part visible in oral view (Fig. 14A-B). Posterior gonopods connected with one another by a sclerotized, triangular sternite (Fig. 7D). Suture between coxite and telopodite well visible. Coxite with a single groove and a finger-shaped process at its base. Telopodite bent mesad, facing telopodite of opposite side. Telopodite with a mesal branch, running parallel

to main branch; mesal branch not strongly sclerotized. Sperm canal running along mesal margin of telopodite, often divergent into two branches, openings located on tip of gonopod main branch and on mesal branch.

Female characters. Legs somewhat shorter in relation to body diameter than in males, antennae much shorter. Vulvae (Fig. 23A-C) located in pouches behind coxosternite of second legs, consisting of two valves plus a small, poorly sclerotized operculum at its base. Valves simple, smooth, dimensions sometimes species-specific, area closest to operculum with a dense cover of long setae (Fig. 23A); a few additional setae on lateral parts of valves (Fig. 24A).

KEY TO THE *SPIROMIMUS* SPECIES

1 Male coxa 6 cylindrical (Fig. 17B). Mesal coxite process of anterior gonopods wide, triangular retrorse projection of telopodite absent (Fig. 17D). Posterior gonopod mesal branch of triangular shape, extending beyond telopodite main branch (Figs 17E, 18E). **2**

— Male coxa 6 rectangular (Fig. 10A). Mesal coxite process of anterior gonopods slender, telopodite tip with minute triangular retrorse projection (Fig. 2D). Posterior gonopod mesal branch neither triangular, nor sharp-edged, as long as or shorter than main branch (Fig. 2F), or mesal branch even completely absent (Fig. 22F). **3**

2 Head conspicuously red (Fig. 17A). Coxa 4 in males with strongly developed, rod-shaped process which protrudes posteriorly back to coxa 7, coxa 5 rectangular (Fig. 17B). .....*Spiromimus laticoxalis* n. sp.

— Head grey or brown (Fig. 17A). Coxae three and four only with short, cone-shaped process, remaining coxae cylindrical (Fig. 18B). .... *S. simplicicoxalis* n. sp.

3 Posterior gonopod mesal branch completely reduced (Fig. 22E). ....*S. simplex* n. sp.

— Posterior gonopod always with mesal branch. **4**

4 Posterior gonopod telopodite, area between main and mesal branches completely filled with membranous folds (Fig. 5B). Main branch very wide and well-rounded. **5**

— Posterior gonopod telopodite, area between main and mesal branches not or only partly filled with membranous folds (Figs 2F, 6B, 7D). **6**

5 Anterior gonopod sternite with 'shoulders' (Fig. 5A). Posterior gonopod main branch not conspicuously curved (Fig. 5B). ....*S. voeltzkowi* de Saussure & Zehntner 1901

— Anterior gonopod sternite without 'shoulders' (Fig. 21A). Posterior gonopod main branch conspicuously curved upwards (Fig. 21C). ....*S. namoroka* n. sp.

6 Posterior gonopod mesal branch basally thin (Figs 6C, 7D, 10D, 14C). Area between mesal and main branch not filled with any membranous folds. ... **7**

— Posterior gonopod mesal branch basally wide (Figs 2F, 15E, 16E). Area between mesal and main branch at least in basal half completely filled with membranous folds. **10**

7 Posterior gonopod main branch apically slim, basally of tip with slender membranous process at circa 2/3 of its length (Figs 6C, 10D). **8**

— Posterior gonopod apically wide, no membranous processes (Figs 7D, 14C). **9**

8 Medium-sized, 55-70 mm long. Anal valves with conspicuous, triangular spine (Fig. 6A). Anterior gonopod coxite processes strongly extending beyond sternite, lateral triangular excavation absent (Fig. 6B). .... *S. dorsovittatus* (de Saussure & Zehntner 1901) n. comb.

— Small, 30-42 mm long. Anal valves without spine (Fig. 10B). Anterior gonopod coxite process shorter than sternite, telopodite with lateral triangular excavation (Fig. 10C). ..... *S. electricus* n. sp.

9 Body black, laterally and dorsally with three golden stripes (Fig. 7A, C). Posterior gonopod mesal branch basally of medium width, apically diverging into two wide tips. Main branch apically also diverging into two wide tips, basal part membranous (Fig. 7D, G). ..... *S. triaureus* n. sp.

— Body black, dorsally with single orange or yellow stripe (Fig. 11A). Posterior gonopod mesal branch very thin, apically not diverging (Figs 14C, E). Main branch apically rectangular (Fig. 14C-D). .*S. litoralis* n. sp.

10 Anterior gonopod coxite process as long as or even slightly extending beyond sternite (Fig. 16D). Posterior gonopod, area between mesal and main branch only filled in basal half with membranous folds (Fig. 16E). . **11**

— Anterior gonopod coxite process at least slightly shorter than sternite (Figs 2E, 15D). Posterior gonopod, area between mesal and main branch filled at basal 3/4 with membranous folds, only tip is not in direct contact with main branch (Figs 2F, 15E). **12**

11 Male < 50 mm long and < 3.5 mm wide. Body rings cylindrical, not moniliform (Fig. 16A). Male coxae three and four with large processes (Fig. 16B). Anterior gonopod with triangular excavation (Fig. 16D). Posterior gonopod mesal branch basally extremely wide, of greater width than main branch (Fig. 16F). ..... *S. albipes* n. sp.

— Male > 60mm long and > 4.0 mm wide. Body rings moniliform (Fig. 19A-B). Male coxae three and four with tiny processes (Fig. 19D). Anterior gonopod without triangular excavation (Fig. 20A). Posterior gonopod mesal branch basally wide, (Fig. 20B). .....*S. grallator* n. sp.

12 Head black (Fig. 2A). Anterior gonopod sternite without 'shoulders' (Fig. 2E). ..... *S. univirgatus* de Saussure & Zehntner 1901

— Head orange-reddish (Fig. 15A). Anterior gonopod sternite with 'shoulders' (Fig. 15D). .....*S. scapularis* n. sp.

Spiromimus univirgatus de Saussure & Zehntner 1901 (Figs 2-4)

Spiromimus univirgatus de Saussure & Zehntner 1901: 444, figs 16-19, 56-58. Type presumably lost. Type locality: "Insula Nossibé, Madagascar".

Spiromimus univirgatus – de Saussure & Zehntner 1902: 160, plate XI, fig. 47; plate XIII, fig. 4. – Enghoff 2003: 624 (lists species name).

Material examined. 2 M, 8 F, FMMC 3928, Madagascar: Province d'Antsiranana, Réserve Spéciale de l'Ankarana, 22.9 km 224° SW Anivorano Nord, tropical dry forest, 80 m, 12°54'32"S, 49°6'35"E, coll. Fisher, Griswold et al., 10-16.ii.2001, pitfall trap.

Diagnosis. 42-61 mm long with 45 or 46 podous rings. Anterior gonopod coxite mesally with slender process (Fig. 2D), slightly shorter than sternal lobe (Fig. 2D). Telopodite laterally with small triangular excavation (Fig. 2D). Tip of telopodite slender, laterally without retrorse process (Fig.

2D). Posterior gonopod main branch apically bent backwards, forming well-rounded 'hook' (Fig. 2E). Mesal branch very thick, tapering apically (Fig. 2F). Area between mesal branch and telopodite almost completely filled with membranous folds (Fig. 2E). Male coxa 3 elongated into long and slender process extending back towards coxa 5 (Fig. 2B-C). Coxa 4 with long and wide process extending back to coxa 6. Coxae 5 and 6 rectangular, mesal margins elongated into short and slender processes. Coxa 7 with large, conical process (Fig. 2B-C). Pro- and mesozonite greyish-black (Fig. 2A). Metazonites black, body rings dorsally with slender, orange-golden stripe. Anal valves red, anteriorly with large, dark spot (Fig. 2D).

S. univirgatus is, in the general shape of the posterior gonopods, most similar to *S. scapularis* n. sp., it differs from the latter in the black color of the head (red in *S. scapularis*) and the absence of 'shoulders' on the anterior gonopod sternite.

Description. Specimens agree with the description of de Saussure & Zehntner (1901, 1902). Studied male and female specimens from Ankarana possess the same ring number (45 or 46) as those described in the literature. However, the studied specimens are significantly larger. Male specimens are 42 mm long and 3.05-3.3 mm wide; females 52-61 mm long and 4.9-5.2 mm wide.

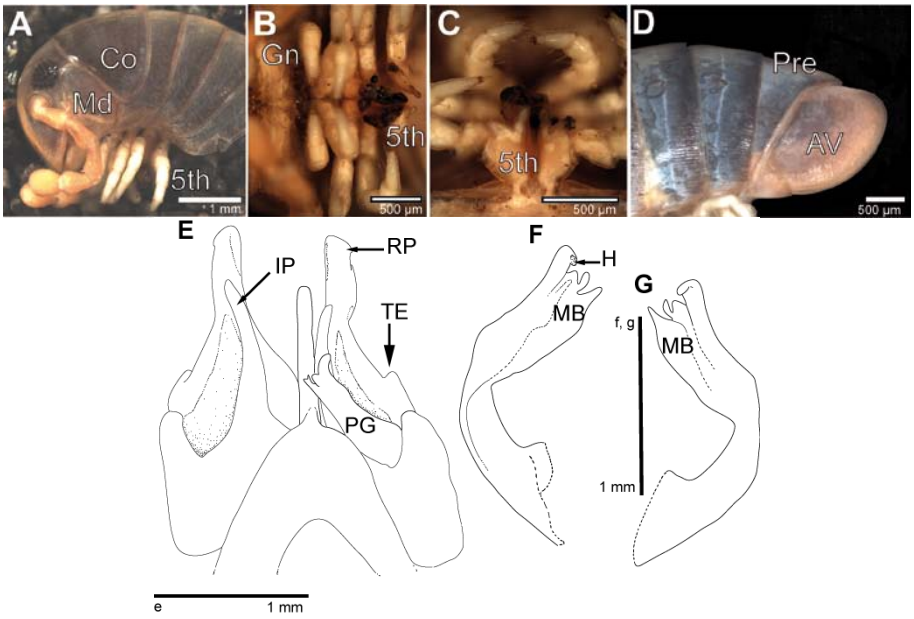

Fig. 2. — *Spiromimus univirgatus*, FMMC 3928, male: A: head and anterior trunk segments, lateral view; B: legs 1-5, ventral view; C: leg 5, posterior view; D: telson, lateral view; E: anterior gonopods, oral view; F: posterior gonopod, oral view; G: posterior gonopod, anal view. Abbreviations: 5th = 5th pair of legs; AV = anal valves; Co = collum; Gn = gnathochilarium; H = hook; IP = mesal coxite process; MB = mesal branch; Md = mandible; PG = posterior gonopod; Pre = preanal ring; RP = retrorse process; TE = triangular excavation. Scale bars = 1 mm.

Antenna with five rows of sensilla basiconica lateroapically on antennomere 5 (Fig. 3B), three rows on antennomere 6 (Fig. 3C). The four apical sensorial cones are located in membranous area (Fig. 3A). *Gnathochilarium* shaped typical for Spirobolida (Fig. 3D-F).

Mandible with eight rows of pectinate lamellae, number of teeth declining proximad (Fig. 4A). Molar plate with three transverse furrows (Fig. 4A).

Anterior valve of vulva slightly extending beyond and protruding above posterior valve (Fig. 23A). Few, long setae located at margins where operculum, anterior and posterior valves touch each other (Fig. 23A).

Distribution. The species was recorded in NW-Madagascar, the island of Nosy Bé and the Ankarana dry forest (Fig. 1).

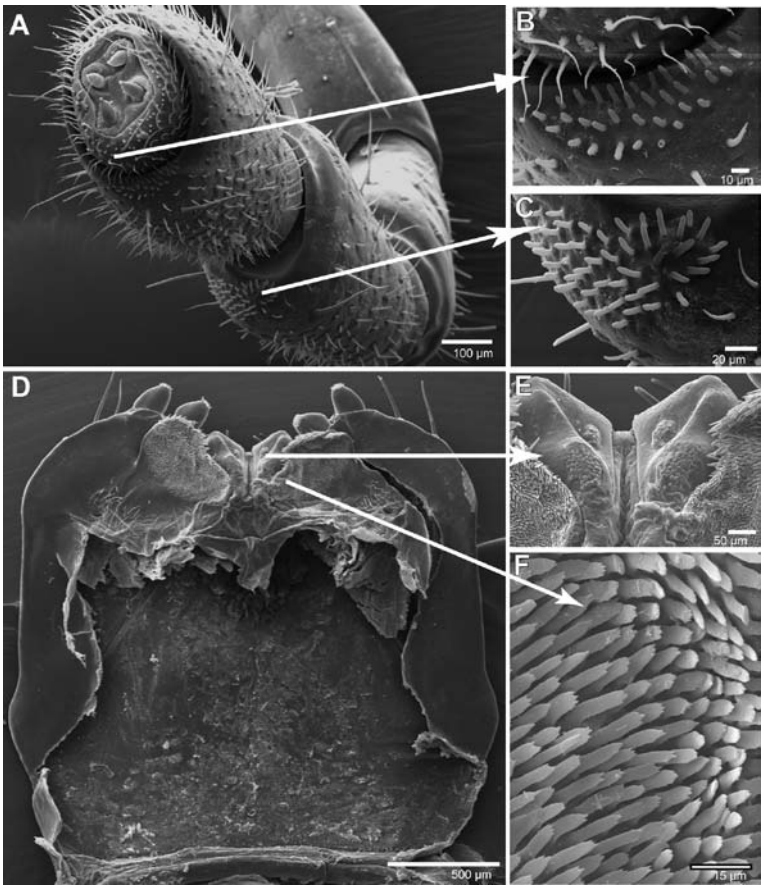

Fig. 3. — *Spiromimus univirgatus*, FMMC 3928, male, SEM: A-C, left antenna, A: apical view; B: margin between antennomere 6 and disc; C: margin between antennomere 5 and 6; D-F: gnathochilarium, underside, D: overview; E: central pads and medial palps, detail; F: spine-like structures on hypopharyngeal crest. Scale bars: A = 100 µm; B = 10 µm; C = 20 µm; D = 500 µm; E = 15 µm; F = 50 µm.

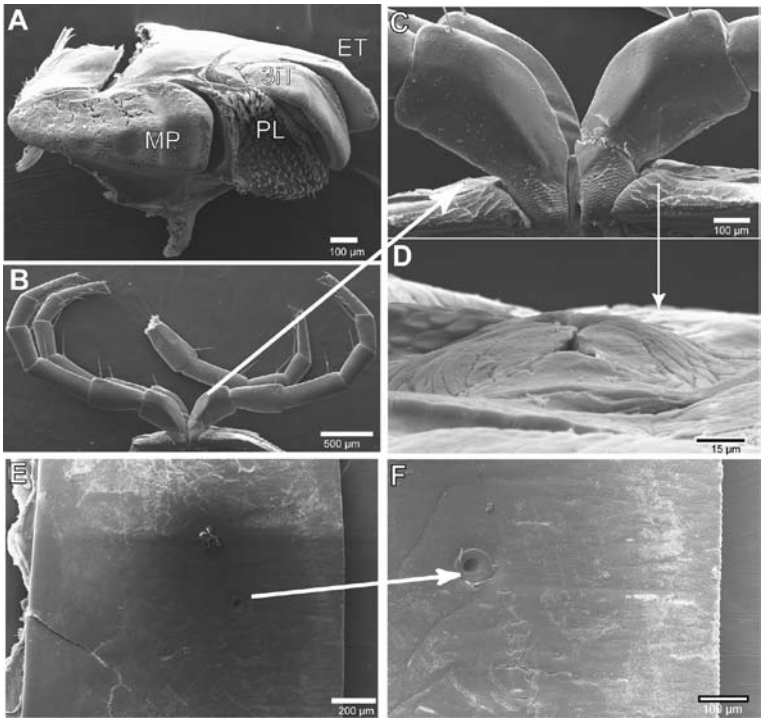

Fig. 4. — *Spiromimus univirgatus*, FMMC 3928, male, SEM: A: left mandible, mesal view; B: legs, anal view; C: coxae, anal view; D: spiracle; E: midbody ring, lateral view; F: detail of ozopore. Abbreviations: 3iT = 3-combed inner tooth; ET = external tooth; MP = molar plate; PL = pectinate lamellae. Scale bars: A, C, F = 100 µm; B = 500 µm; D = 15 µm; E = 200 µm.

Spiromimus voeltzkowi de Saussure & Zehntner 1901 (Fig. 5)

Spiromimus voeltzkowi de Saussure & Zehntner 1901: 445, figs 20-26.
Spiromimus voeltzkowi – de Saussure & Zehntner 1902: 164, plate XII, fig. 5. – Enghoff 2003: 624 (lists species name).

Material examined

Lectotype (designated herewith). 1 M, MHNG, Madagascar, Province Antsiranana, Island of Nosy Bé, collected by A. Voeltzkow.

Paralectotype (designated herewith). 1 immature male, MNHN CB055, same data as lectotype.

Other material examined. 1 M, CAS, Madagascar, Nossi-Be, Hellville, coll. E.S. Ross, 20.xi.1959, det. R.L. Hoffman, 1969.

Diagnosis. 28-38 mm long, with 40-42 podous rings (data from de Saussure & Zehntner 1901). Anterior gonopod coxite mesally with slender process (Fig. 5A), extending only up to half length of slender sternal lobe (Fig. 5A). Sternite with strongly developed 'shoulders' (Fig. 7A). Telopodite without excavation (Fig. 5A). Tip of telopodite slender, with short retrorse pro-

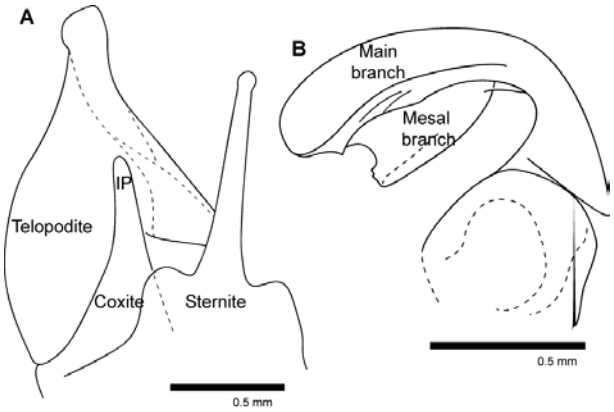

Fig. 5. — *Spiromimus voeltzkowi*, lectotype, MHNG, male: A: anterior gonopods, oral view; B: posterior gonopod, anal view. Abbreviations: IP = mesal coxite process. Scale bars = 0.5 mm.

cess (Fig. 5A). Tip of main branch of posterior gonopod well-rounded, without 'hook' (Fig. 5B). Mesal branch very thick, at tip as wide as basally (Fig. 5B). Area between mesal and main branch completely filled with membranous folds (Fig. 5B). Male coxa 3 with small, knob-like process. Coxa 4 with long and very thick process extending back to coxa 6. Coxa 5 with thick process extending to coxa 6. Coxa 6 rectangular, mesal margin elongated into short and slender process. Coxa 7 with small, knob-like process. Body rings blackish with dirty-whitish spots (due to preservation in alcohol?), dorsally with slender orange-golden stripe. Anal valves red.

S. voeltzkowi shares the special shape of the posterior gonopods, where the mesal and main branch are well-rounded and almost completely fused with membranous folds (Fig. 5B), only with *S. namoroka* n. sp. In the latter, however, is the anterior gonopod sternite without shoulders and the posterior gonopod is apically strongly bended upwards.

Description. See DE SAUSSURE & ZEHNTNER (1902).

Remarks. This species was not present in freshly collected material.

Distribution. Only known from the island of Nosy Bé (Fig. 1).

Spiromimus dorsovittatus (de Saussure & Zehntner 1901), new comb. (Fig. 6)

Pygodon dorsovittatum DE SAUSSURE & ZEHNTNER 1901: 446 figs 28-32. Type locality: "Insula Nossibé, Madagascar".

Pygodon dorsovittatum – DE SAUSSURE & ZEHNTNER 1902: 167, plate XIII, fig. 7. – ENGHOFF 2003: 623 (lists species name).

Material examined

Lectotype (designated herewith). Male, MHNG, Madagascar, Island of Nosy Bé, collected by A. Voeltzkow.

Paralectotype. 1 F, MHNG, same data as lectotype.

Diagnosis. Males 57 mm, females up to 70 mm long, with 47 or 48 body rings. Anterior gonopod coxite mesally with slender process (Fig. 6B), strongly extending beyond sternal lobe (Fig. 6B). Telopodite without excavation (Fig. 6B). Tip of main branch of posterior gonopod bent backwards, forming well-rounded 'hook' (Fig. 6C). Mesal branch thin (Fig. 6C). No membranous folds between mesal and main branch. Male coxa 3 elongated into long and slender process extending back towards coxa 5. Coxa 4 with long and slender process extending back to coxa 6. Coxa 5 with short knob,

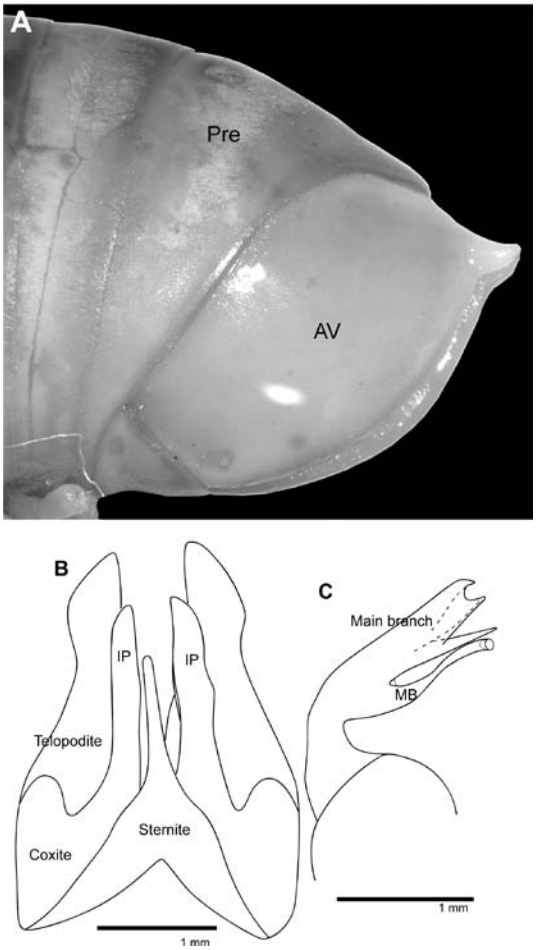

Fig. 6. — *Spiromimus dorsovittatus*, A female paratype, B-C male lectotype, MHNG: A: telson; B: anterior gonopods, oral view; C: posterior gonopod, oral view. Abbreviations: AV = anal valves; IP = mesal coxite process; MB = mesal branch; Pre = preanal ring. Scale bars = 1 mm.

located at mesal margin. Coxae 6 and 7 unmodified. Coloration dark, dorsally with large stripe. Anal valves with a spine (Fig. 6A).

S. dorsovittatus shares the large body size and the relatively wide anterior gonopod telopodite processes (Fig. 6B) only with *S. grallator* n. sp. *S. dorsovittatus* differs from all other *Spiromimus* species (also from all other Spirobolida known from Madagascar) in the presence of a triangular spine on the anal valves (Fig. 6A).

Description. See DE SAUSSURE & ZEHNTNER (1902).

Remarks. The presence of a spine on the anal valves in *S. dorsovittatus* prompted DE SAUSSURE and ZEHNTNER to describe the new monotypic genus *Pygodon* to encompass this species (DE SAUSSURE & ZEHNTNER 1901). Such a spine is indeed a unique feature within the suborder Trigoniulidea. As for the gonopods, however, *S. dorsovittatus* falls well in with the genus *Spiromimus*. *Pygodon dorsovittatum* is here transferred into the genus *Spiromimus*; *Pygodon* is therefore regarded as a junior subjective synonym of *Spiromimus*.

Distribution: only known from the island of Nosy Bé (Fig. 1). No specimens of this species were found in samples collected during recent inventory programs undertaken by the CAS and FMNH. Furthermore, no additional specimens of *S. dorsovittatus* could be located in the vast backlog of the MNHN.

Spiromimus triaureus new species (Figs 7-9)

Material examined

Holotype. M, FMMC 7870, Madagascar, Province Mahajanga, Reserve Forestière de l'Ankarafantsika, 5 km SSW Ampijoroa, slightly disturbed deciduous forest, 16°20.3'S, 46°47.6'E, 160 m, coll. S. Goodman, 4-7.ii.1997, pitfall trap.

Paratypes. 3 F, FMMC 7870, same data as holotype; 1 M, 1 F, ZMUC, same data as holotype.

Other material examined. 1 M, 1 F, 2 immatures, CAS BLF 4511, Province Mahajanga, Forêt de Tsimembo, 8.7 km 336° NNW Soatana, tropical dry forest, 20 m, 19°1'17"S, 44°26'26"E, coll. Fisher, Griswold et al., 21-25.xi.2001; 1 M, 1 F, CAS BLF 6587, Province Mahajanga, Parc National de Namoroka, 16.9 km 317° NW Vilanandro, tropical dry forest, 100 m, 16°24'24"S, 045°18'36"E, coll. Fisher, Griswold et al. 12-16.xi.2002; 1 M, CAS BLF 6694, Province Mahajanga, Réserve Spéciale de Bemarivo, 23.8 km 223° SW Besalampy, tropical dry forest, 30 m, 16°55'30"S, 044°22'06"E, coll. Fisher, Griswold et al., 19-23.xi.2002.

Diagnosis. 43-54 mm long, 44 body rings. Coxite process of anterior gonopod extending up to 2/3 of sternal lobe length (Fig. 7F). Telopodite laterally with large triangular excavation (Fig. 7E-F), tip slender, with strongly developed retrorse process (Fig. 7E-F). Tip of main branch of posterior gonopod wide and well-rounded, without 'hook' (Fig. 7D), basally with widely projecting membranous fold (Fig. 7G). Mesal branch well-developed, constricted in proximal half, expanding at tip into two lobes (Fig. 7G). Male coxa 3 elongated into long and slender process extending back to coxa 5. Coxa 4 with long and wide process, extending back to coxa 7. Coxae 5 and

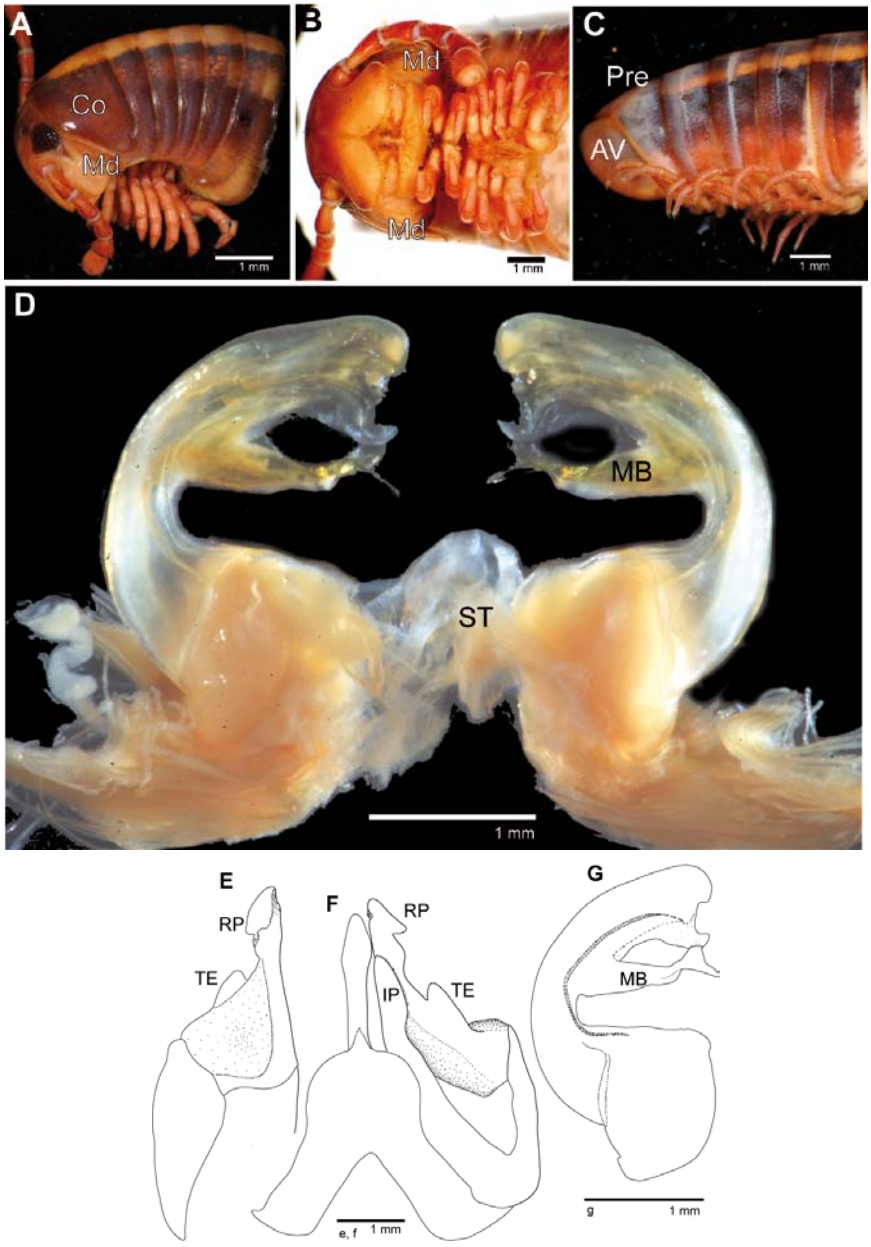

Fig. 7. — *Spiromimus triaureus* n. sp., holotype, male, FMMC 7870. A: head and anterior trunk segments, lateral view; B: legs 1-7, ventral view; C: telson; D: posterior gonopods, anal view; E: anterior gonopod, anal view; F: anterior gonopod, oral view; G: posterior gonopod, oral view. Abbreviations: AV = anal valves; IP = mesal coxite process; MB = mesal branch; Pre = preanal ring; RP = retrorse process; ST = sternite; TE = triangular excavation. Scale bars = 1 mm.

6 very flat and rectangular, mesally with short conical process. Coxa 7 elongated into short cone (Fig. 7B). Coloration black, dorsally and laterally with three broad, golden stripes (Fig. 7A). Head, antenna, legs, anal valves and ventral part of body rings red (Fig. 7A, C).

Spiromimus triaureus shares a 'hookless' posterior gonopod with a well-rounded tip (Fig. 7D, G) only with *S. voeltzkowi* and *S. namoroka* n. sp.

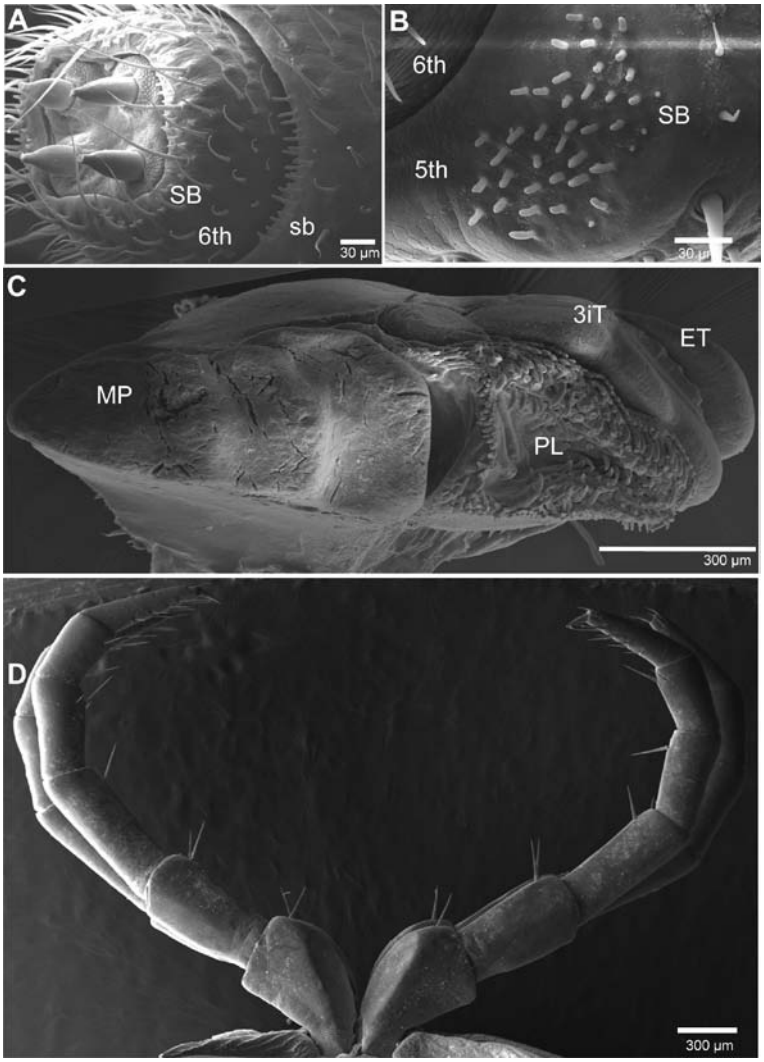

Fig. 8. — *Spiromimus triaureus* n. sp., paratype, male, FMMC 7870, SEM. A: antenna, apical view; B: margin between antennomere 5 and 6; C: left mandible; D: legs, anal view. Abbreviations: 3iT = 3-combed inner tooth; ET = external tooth; MP = molar plate; PL = pectinate lamellae; SB = sensilla basiconica. Scale bars: A-B = 30 µm; C-D = 300 µm.

The anterior gonopods are different in the latter. The three golden stripes of *S. triaureus* n. sp. identify this species unambiguously.

Description

Male

Measurements. 44 podous rings. Body length circa 43 mm, midbody width 3.8 mm.

Color. Frontal part of head, antennae and legs red (Fig. 7A). Body rings laterally and dorsally black, ventrally red. Anal valves and subanal scale red. Anal valves anteriorly with round dark spot (Fig. 7C). Rings dorsally and laterally with three broad, golden stripes.

Anterior gonopods mesal process of coxite slender and elongated (Fig. 7E), extending up to basal 2/3 of sternite. Telopodite laterally with small, sharp, triangular excavation (Fig. 7E). Tip of telopodite slender and elongated, apically with short but sharp triangular, retrorse process (Fig. 7F).

Posterior gonopod tip of main branch slender and well-rounded, (Fig. 7G). No hook present (Fig. 7G). Main branch with slender membranous process originating from mesal side of posterior gonopod; membranous process extending as far as main branch (Fig. 7G). Mesal branch wide at base, constricted at middle, apically dilated into two wide, membranous folds (Fig. 7G). Area between mesal and main branch of telopodite without any connecting membranous folds (Fig. 7D, G).

Female

Measurements. 44 podous rings. Body length 51-54 mm, midbody width 5.2-5.3 mm.

Vulva anterior and posterior valves of similar size (Fig. 23B). 3-4 rows of long setae around the area where operculum, anterior and posterior valves meet (Fig. 23B).

Distribution. Widespread in Western Malagasy dry forests (Fig. 1).

Derivatio nominis. *"triaureus"*, adjective, consisting out of tri = three and aureus = golden, referring to the three golden stripes along the body.

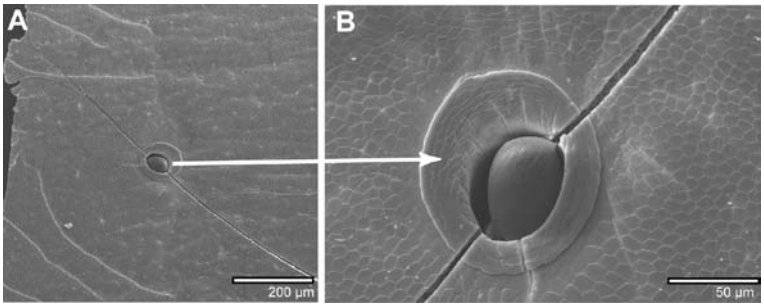

Fig. 9. — *Spiromimus triaureus* n. sp., paratype, male, FMMC 7870, SEM, midbody ring. A: lateral view; B: lateral view, detail of ozopore. Scale bars: A = 200 µm; B = 50 µm.

Spiromimus electricus new species (Fig. 10)

Material examined

Holotype. M, ZMUC 00101018, Madagascar, Province Antsiranana, Montagne d'Ambre, montane rainforest, 1000 m, coll. Scharff et al.

Paratypes. 2 M, 2 F, ZMUC 00101019, same data as holotype; 2 M, 1 F, ZMUC 00101020, same data as holotype, but collected at 1100 m; 3 M, MNHN, Montagne d'Ambre, coll. Roussette, 14.xii.1965.

Other material examined. 1 M, FMMC, same collection data as holotype; 2 M, MNHN, Province Antsiranana, Joffreville, 12°31'15.59"S, 49°10'39.52"E, coll. A. Treha, Janvier 1961.

Diagnosis. 30 to 42 mm long, with 43 or 44 body rings. Mesal coxal process of anterior gonopod extending up to 2/3 of sternal lobe length (Fig. 10C). Telopodite laterally with small triangular excavation (Fig. 10C), tip slender, with small retrorse process (Fig. 10C). Tip of main branch of pos-

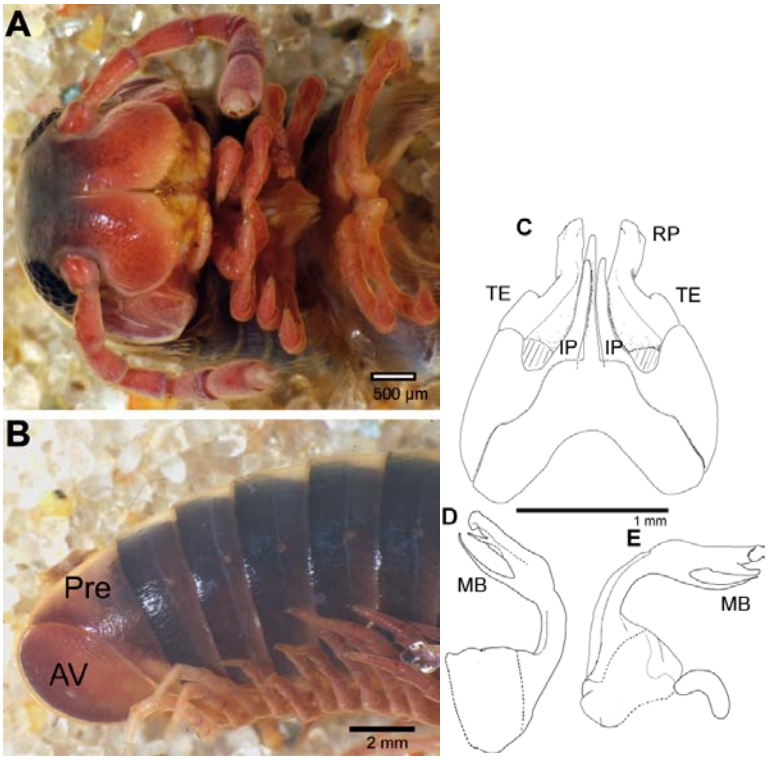

Fig. 10. — *Spiromimus electricus* n. sp., paratype, male, ZMUC. A: head and legs 1-7, ventral view; B: telson; C: anterior gonopods, oral view; D: posterior gonopod, oral view; E: posterior gonopod, anal view. Abbreviations: AV = anal valves; IP = mesal coxite process; MB = mesal branch; Pre = preanal ring; RP = retrorse process; TE = triangular excavation. Scale bars: A = 0.5 mm; B = 2 mm; C-E = 1 mm.

terior gonopod well-rounded, bent backwards, forming well-rounded 'hook' (Fig. 10D). Mesal branch thin (Fig. 10E). Large gap between mesal and main branch; gap without membranous folds. Male coxa 3 elongated into long and slender process extending back to coxa 5. Coxa 4 with long and wide process, extending back to coxa 6. Coxa 5 with short conical process, very flat and rectangular. Coxa 6 unmodified. Coxa 7 at mesal margin ventrally with swollen knob (Fig. 10A). Coloration black, with red anal valves and appendages (Fig. 10A-B). Body rings dorsally with orange stripe.

Spiromimus electricus n. sp. shares a very slender mesal branch of the posterior gonopods with *S. dorsovittatus* and *S. litoralis* n. sp. Furthermore, it shares with *S. dorsovittatus* the slender membranous process located near the tip. However, it can be easily distinguished from both species by the far slimmer posterior gonopod tip (Fig. 10D-E) and the longer mesal process of the anterior gonopod coxite (Fig. 10C).

Description

Male

Measurements. 43 or 44 podous rings. Body length 31-33 mm long, midbody width 2.7-3.4 mm.

Color. Frontal part of head, antennae and legs red (Fig. 10A). Body rings black. Anal valves and subanal scale red. Anal valves anteriorly with round dark spot (Fig. 10B). Obligatory dorsal yellow stripe.

Anterior gonopods sternite rising into slender process (Fig. 10C). Mesal coxite process slender and elongated, extending up to 2/3 of sternite length. Telopodite laterally with large, sharp triangular excavation. Tip of telopodite slender and pointed, apically with large, sharp, triangular retrorse process (Fig. 10C).

Posterior gonopod main branch slender and well-rounded (Fig. 10D), forming well-rounded hook (Fig. 10E). Main branch basally of tip with slender membranous process, as long as main branch (Fig. 10E). Mesal branch very slender, protruding up to telopodite tip (Fig. 10E). Area between mesal and main branch without any connecting membranous folds.

Female

Measurements. 43 podous rings. Body lengh 38-42 mm, midbody width 4.0-4.1 mm.

Distribution. Currently only recorded from the rainforest area around Montagne d'Ambre, North Madagascar (Fig. 1).

Derivatio nominis. "*electricus*", adjective, refers to the type locality, Montagne d'Ambre.

Spiromimus litoralis new species (Figs 11-14)

Material examined

Holotype. M, FMMC 3912, Madagascar, Province Antsiranana, Forêt d'Orangea, 3.6 km 128°SE Remena, littoral rainforest, 90 m, 12°15'32"S, 49°22'29"E, coll. Fisher, Griswold et al., pitfall trap, 22-28.ii.2001.

Paratypes. 206 males and females, FMMC 3912, same data as holotype; 1 M, 1 F, FMMC 8206, same data as holotype, but general collecting.

Other material examined. 1 M, MNHN, Madagascar, Province Antsiranana, St. Fo. d'Andranomanitra, coll. A. Treha, 01.1961. Probably close to Andranomanitra Nord, 12°24'0"S, 49°19'0"E; 1 M, 1 F, CAS BLF 3200, Province d'Antsiranana, Forêt d'Orangea, 3.6 km 128° SE Ramena, littoral rainforest, 90 m, 12°15'32"S, 49°22'29"E, coll. Fisher, Griswold et al. 22-28.ii.2001.

Diagnosis. 40-50 mm long, with 43-45 body rings. Anterior gonopod coxite mesally with slender process (Fig. 11D), extending only up to basal half of sternal lobe (Fig. 11E). Telopodite laterally with strongly developed triangular excavation (Figs 11F, 14A-B), tip slender, with strongly developed retrorse process (Figs 11D, 14A-B). Posterior gonopod tip well-rounded, almost rectangular, slightly bent backwards, forming well-rounded 'hook' (Fig. 14C). Mesal branch thin (Fig. 14E). Large gap between mesal and main branch and telopodite, this gap without membranous folds. Male coxa 3 elongated into long and slender process extending back to coxa 4. Coxa 4 with long and wide process, extending back to coxa 6. Coxa 5 without process, but very flat and rectangular. Coxa 5 unmodified. Coxa 7 at mesal margin ventrally with swollen knob (Fig. 11B). Coloration greyish, dorsally with

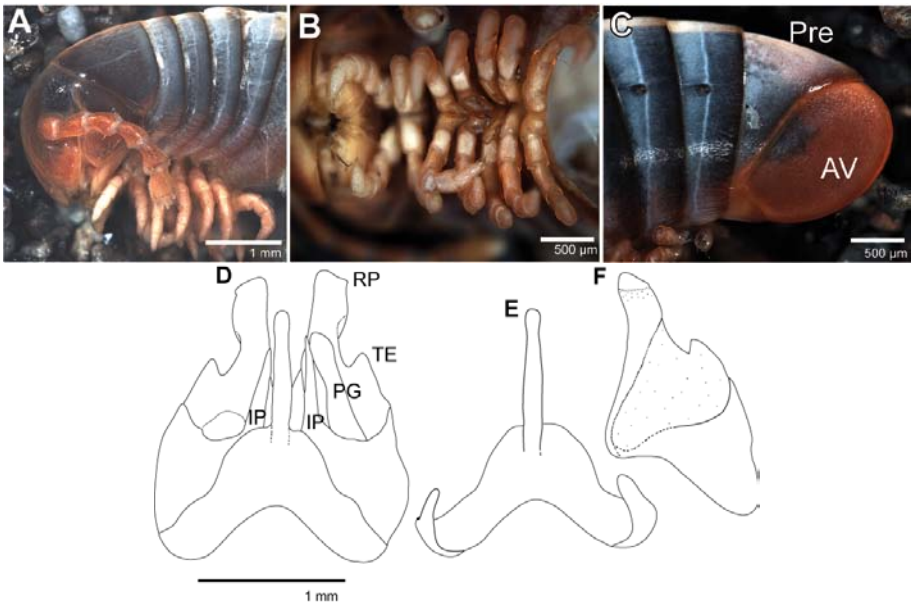

Fig. 11. — *Spiromimus litoralis*, n. sp., A-C, male paratype, FMMC 8206, D-F male holotype. A: head and anterior trunk segments, lateral view; B: legs 1-7, ventral view; C: telson; D: anterior gonopods, oral view; E: anterior gonopod, separated sternite, anal view; F: left half of anterior gonopod, anal view. Abbreviations: AV = anal valves; IP = mesal coxite process; PG = posterior gonopod; Pre = preanal ring; RP = retrorse process; TE = triangular excavation. Scale bars: A, D-F = 1 mm; B, C = 0.5 mm.

orange stripe. Posterior margin of body rings black, ventral side and legs red (Fig. 11A-C).

Spiromimus litoralis n. sp. shares a very slender mesal branch of the posterior gonopods with *S. dorsovittatus* (de Saussure & Zehntner 1901) and *S. electricus* n. sp. (Fig. 14E). It can be easily distinguished from both species by the shorter mesal process of the anterior gonopod coxite (Fig. 14A-B). Furthermore, the posterior gonopod tip is in *S. litoralis* of almost rectangular shape (Fig. 14C), while it is far slimmer in the other two species. *S. dorsovittatus* and *S. electricus* both feature a membranous process basally to the posterior gonopod tip, which is completely absent in *S. litoralis*.

Description

Male

Measurements. 43-45 podous rings. Body length 39-46 mm, midbody width 2.8-3.1 mm.

Color. Head, antennae and legs red (Fig. 11A). Ventral parts of metazonites, anal valves and subanal scale red. Anal valves anteriorly with round dark spot (Fig. 11C). Obligatory dorsal orange-reddish stripe, thicker

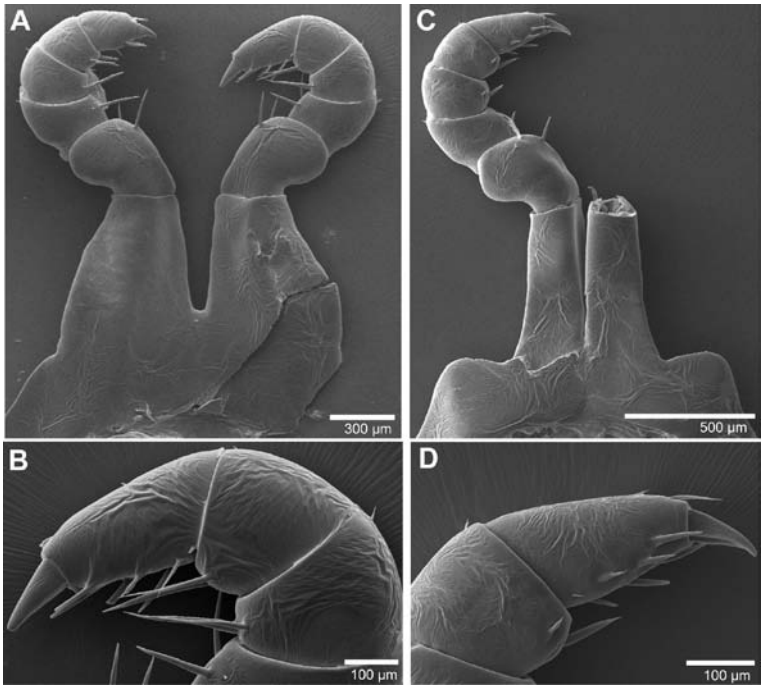

Fig. 12. — *Spiromimus litoralis* n. sp., male paratype, FMMC 8206, SEM. A: first leg pair, anal view; B: apical part of first leg, anal view; C: second leg pair, anal view; D: apical part of second leg, anal view. Scale bars: A = 300 µm; B = 500 µm; C-D = 100 µm.

than in other members. Prozonites and preanal ring grey, metazonites laterally and dorsally black (Fig. 11C).

Anterior gonopods elongated. Sternite rising into slender process (Fig. 11E). Coxite mesal process reaching only up to basal half of sternite (Fig. 11D). Telopodite laterally with strongly developed, sharp triangular excavation (Figs 11D, F; 14A-B). Tip of telopodite slender and elongated, apically with short but sharp triangular retrorse process (Figs 11D, 14A-B).

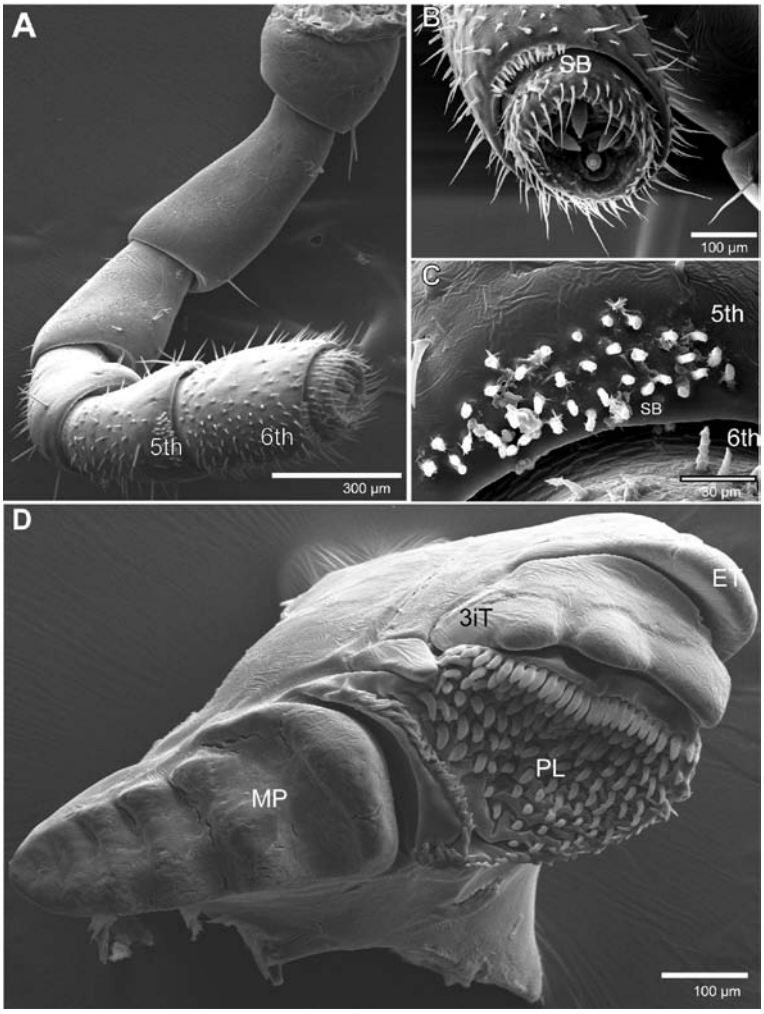

Fig. 13. — *Spiromimus litoralis* n. sp., male paratype, FMMC 8206, SEM. A: antenna, overview; B: antenna, antennomere 6 and disc; C: antenna, margin between antennomeres 5 and 6; D: left mandible. Abbreviations: 3iT = 3-combed inner tooth; ET = external tooth; MP = molar plate; PL = pectinate lamellae; SB = sensilla basiconica. Scale bars: A = 300 µm; B, D = 100 µm; C = 30 µm.

Posterior gonopod main branch well-rounded, but of almost rectangular shape (Fig. 14C). Part of tip bending backwards, forming short and well-rounded hook (Fig. 14D). Main branch basally with slender membranous fringe (Fig. 14D). Mesal branch very slender, protruding up to telopodite tip (Fig. 14E). Area between mesal and main branch without any connecting membranous folds (Figs 14C-E).

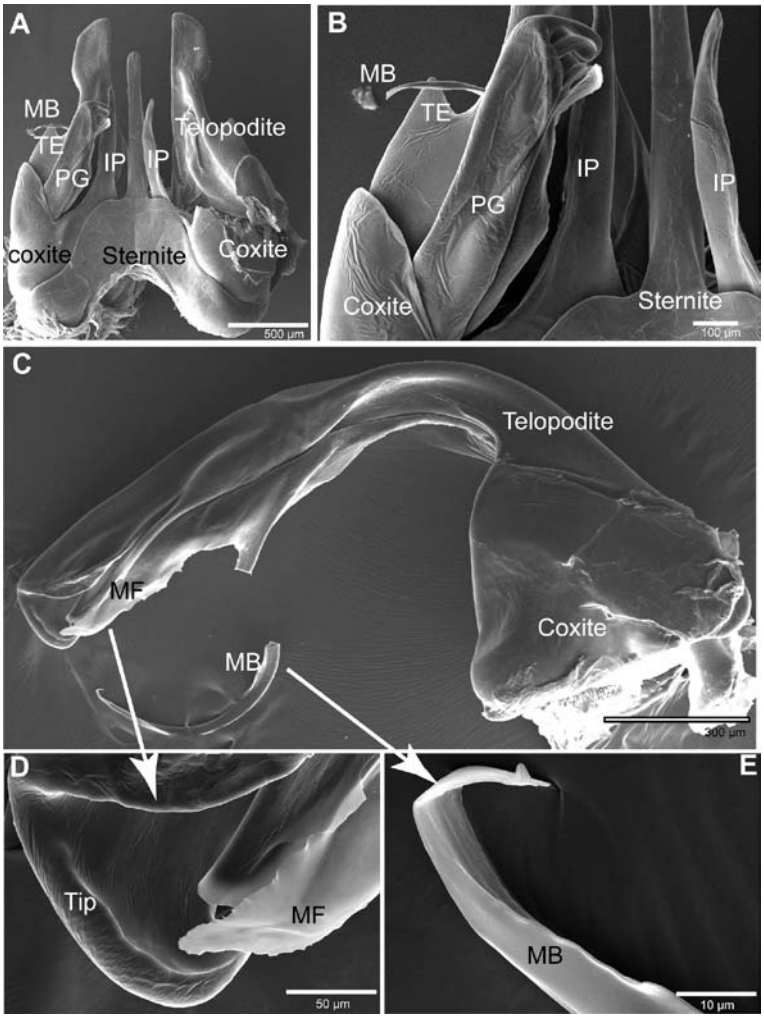

Fig. 14. — *Spiromimus litoralis* n. sp., male paratype, FMMC 8206, SEM. A: gonopod block, oral view; B: gonopod block, detail, mesal branch of posterior gonopod broken; C: posterior gonopod, anal view; D: detail of tip with membranous fringe; E: detail of mesal branch. Abbreviations: IP = mesal coxite process; MB = mesal branch of posterior gonopod telopodite (here broken off!); MF = membranous fringe; PG = posterior gonopod; TE = triangular excavation. Scale bars: A = 500 µm; B = 100 µm; C = 300 µm; D = 50 µm; E = 10 µm.

Female

Measurements. 44 podous rings. Body length 46-50 mm, midbody width 4.0-4.2 mm.

Vulva. Anterior and posterior valves of similar size (Fig. 23C). Three or four rows of long setae surrounding the area where operculum, anterior and posterior valves touch each other (Fig. 23C). Anterior valve with a special-shaped seta standing inside a large pit (Fig. 24A).

Distribution. Known from the littoral forest Forêt d'Orangea and a second locality close to Antsiranana in NE Madagascar (Fig. 1).

Derivatio nominis. *"litoralis"*, adjective, refers to the type locality, a littoral forest.

Spiromimus scapularis new species (Fig. 15)

Material examined

Holotype. M, CAS BLF 9558, Madagascar, Province d'Antsiranana, Forêt de Binara, 7.5 km 230° SW Daraina, tropical dry forest, 375 m, 13°15'18"S, 049°37'00"E, coll. B.L. Fisher, pitfall trap, 1.xii.2003.

Paratypes. 1 F, 1 imm., CAS BLF 9558, same data as holotype.

Other material examined. 3 M, 5 imm., CAS BLF 9656, Forêt de Binara, 9.1 km 233° SW Daraina, rainforest, 650-800 m, 13°15'48" S, 049°36'12" E, coll. B.L. Fisher, 3.xii.2003.

Diagnosis. Circa 43 mm long. Coxite process of anterior gonopod slender (Fig. 15D), slightly shorter than sternal lobe (Fig. 15D). Sternite with pronounced shoulders (Fig. 15D). Telopodite laterally with large triangular excavation (Fig. 15D), tip slender, laterally with strongly developed, sharp retrorse process (Fig. 15D). Tip of main branch of posterior gonopod bent backwards, forming well-rounded 'hook' (Fig. 15E). Mesal branch very wide, tapering apically (Fig. 15E). Area between mesal and main branch at basal 2/3 filled by membranous folds (Fig. 15F). Male coxa 3 elongated into long and slender process extending back to coxa 5. Coxa 4 with long and wide process, extending back to coxa 6. Coxa 5 rectangular, mesal margin elongated into short and slender process. Coxa 6 slightly rectangular, without a process. Coxa 7 with large, conical process (Fig. 15B). Pro- and mesozonite greyish-black (Fig. 15A). Posterior margin of metazonites black, body rings dorsally with slender orange-golden stripe. Anal valves, legs and antenna orange (Fig. 15C).

Spiromimus scapularis n. sp. seems to be closely related to *S. univirgatus*. Both species share very similar posterior gonopods. *S. scapularis* differs from *S. univirgatus* in the presence of well-developed 'shoulders' on the anterior gonopod sternite (Fig. 15D), a feature only shared with *S. voeltzkowi*.

Description

Male

Measurements. 39 podous rings. Body length circa 43 mm, midbody width 2.95 mm.

Color. Altered by alcohol. Apical part of head, antennae, and legs orange (Fig. 15A). Body rings faded, greyish, posterior margin darker. Anal valves and subanal scale orange (Fig. 15C). Rings dorsally with single, slender, orange stripe.

Anterior gonopod sternite rising into slender process, with pronounced shoulders (Fig. 15D). Coxite mesal process slender and elongated (Fig. 15D), extending up to basal 2/3 of sternite. Telopodite laterally with large, sharp triangular excavation (Fig. 15D). Tip of telopodite slender and elongated, apically with well-developed, sharp triangular retrorse process (Fig. 15D).

Posterior gonopod main branch slender and well-rounded (Fig. 15E). Part of tip bending backwards, forming short and well-rounded hook (Fig. 15F). Main branch basally of tip with sharp, membranous process, extending beyond tip (Fig. 15F). Mesal branch protruding up to telopodite tip. Process starting wide, tapering apically (Fig. 15E). Area between mesal and main branch only apically without any connecting membranous folds (Fig. 15E-F).

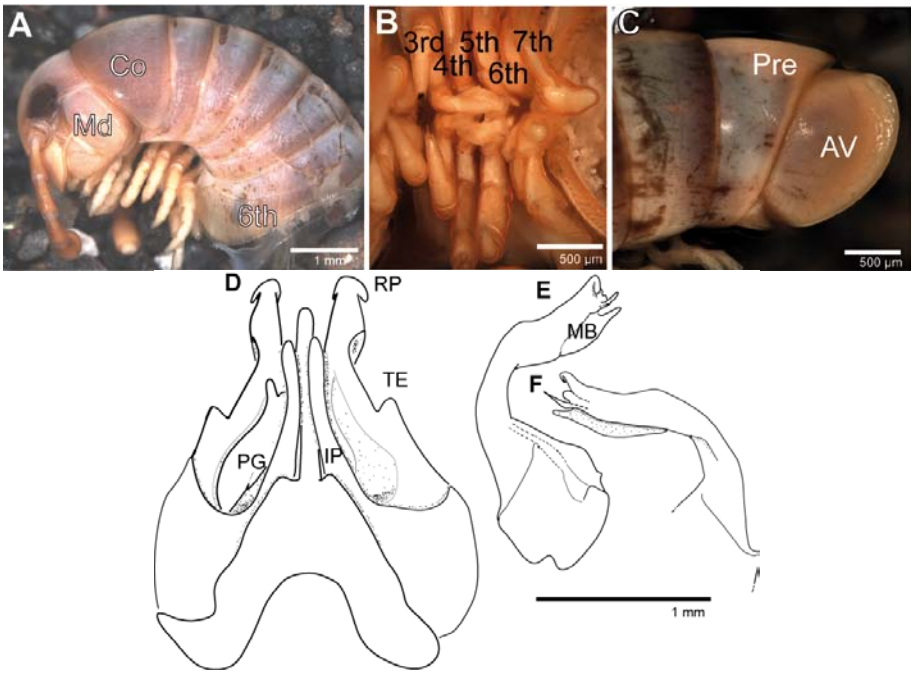

Fig. 15. — *Spiromimus scapularis* n. sp., male holotype, CAS BLF 9558. A: head and anterior trunk segments, lateral view; B: legs 1-7, ventral view; C: telson; D: anterior gonopods, oral view; E: posterior gonopod, anal view; F: posterior gonopod, oral view. Abbreviations: AV = anal valves; Co = collum; IP = mesal coxite process; MB = mesal branch; Md = mandible; Pre = preanal ring; RP = retrorse process; TE = triangular excavation. Scale bars: A, D-F = 1 mm; B-C = 500 µm.

Female

Measurements. Specimen broken into several pieces, some of which definitely missing. Midbody width 4.7 mm.

Distribution. Known only from the dry forest of Binara, North Madagascar (Fig. 1).

Derivatio nominis. "s*capularis*", adjective, refers to shoulders on the anterior gonopods.

Spiromimus albipes new species (Fig. 16)

Material examined

Holotype. M, FMMC 3927, Madagascar, Province d'Antsiranana, Réserve Spéciale d'Ambre, 3.5 km, 235° SW Sakaramy, 325 m, 12°28'8"S, 49°14'32"E, tropical dry forest, coll. Fisher, Griswold et al., 26-31.i.2001, pitfall trap.

Paratypes. 2 M, 1 F, FMMC 3927, same data as holotype.

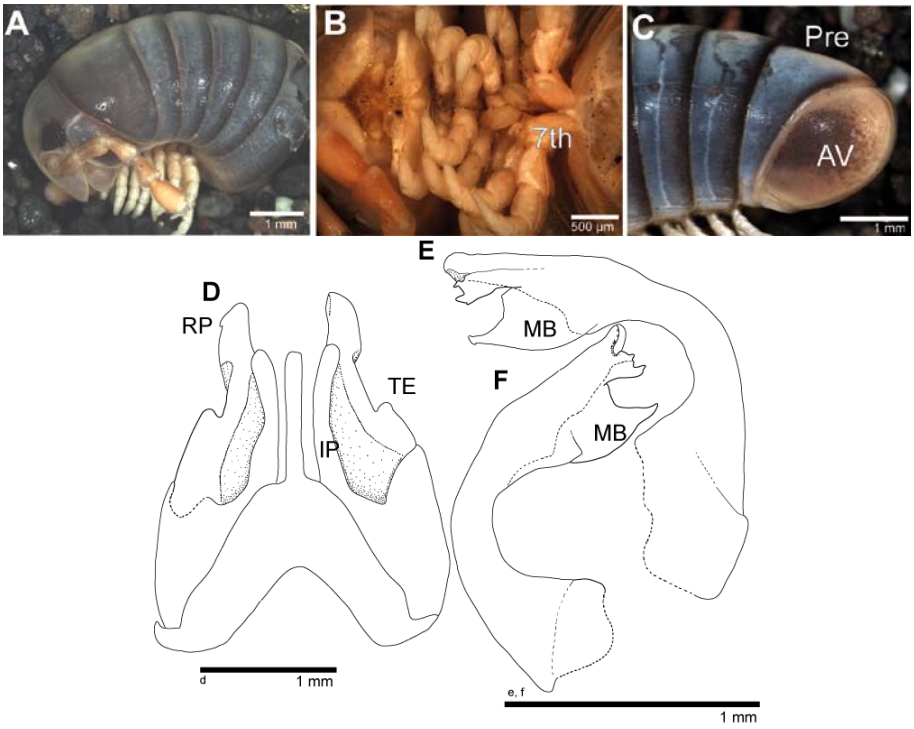

Fig. 16. — *Spiromimus albipes* n. sp., male holotype, FMMC 3927, A. head and anterior trunk segments, lateral view; B: legs 1-7, ventral view; C: telson; D: anterior gonopods, oral view; E: posterior gonopod, oral view; F: posterior gonopod, anal view. Abbreviations: AV = anal valves; IP = mesal coxite process; MB = mesal branch; Pre = preanal ring; RP = retrorse process; TE = triangular excavation. Scale bars: A, C-F = 1 mm; B = 500 µm.

Diagnosis. 41-61 mm long, with 44 or 45 podous rings. Mesal coxal process of anterior gonopod slender (Fig. 16D), slightly longer than sternal lobe (Fig. 16D). Sternite without shoulders (Fig. 16D). Telopodite laterally with small triangular excavation (Fig. 16D). Tip of telopodite slender, laterally with small but sharp, retrorse process (Fig. 16D). Tip of main branch of posterior gonopod bent backwards, forming well-rounded 'hook' (Fig. 16F). Mesal branch very wide, tapering apically (Fig. 16E). Area between mesal and main branch only basally filled with membranous folds (Fig. 16E). Male coxa 3 elongated into long and slender process extending back to coxa 5. Coxa 4 with long and wide process, protruding ventrally (Fig. 16B). Coxa 5 rectangular, mesal margin elongated into short and slender process. Coxa 6 slightly rectangular, without process. Coxa 7 with large, conical process (Fig. 16B). Pro- and mesozonite greyish-black (Fig. 16C). Posterior margin of metazonites black, body rings dorsally with slender golden stripe. Anal valves and legs white (Fig. 16A).

Spiromimus albipes n. sp. differs from all congeneric species by the presence of an extraordinary wide, triangular, mesal branch on the posterior gonopods (Fig. 16E-F). Only in *S. albipes* is the process of the male coxa 4 bent ventrally instead of posteriorly (Fig. 16B). This character state, however, should be evaluated again when more specimens of *S. albipes* become available.

Description

Male

Measurements. 44 or 45 podous rings. Body length 41-49 mm long, midbody width 3.3-3.5 mm.

Color. Altered by alcohol. Apical part of head and antennae orange. Legs and anal valves whitish. Anal valves anteriorly with round dark spot (Fig. 16C). Body rings faded, greyish, posterior margin darker (Fig. 16A). Rings dorsally with single, slender, golden stripe.

Anterior gonopod sternite rising into slender process, without shoulders (Fig. 16D). Coxite mesal process slender and elongated (Fig. 16D), extending beyond sternite. Telopodite laterally with small sharp triangular excavation (Fig. 16D). Tip of telopodite slender and elongated, apically with small sharp triangular retrorse process (Fig. 16D).

Posterior gonopod main branch slender and well-rounded (Fig. 16F). Part of main branch tip bending backwards, forming short and well-rounded hook (Fig. 16F). Main branch basally of tip with wide, membranous fringe ending in two irregularly rounded processes, as long as tip (Fig. 16E). Mesal branch strongly triangular, protruding up to telopodite tip, very wide, tapering apically (Fig. 16E). Area between mesal and main branch without connecting membranous folds (Fig. 16F-G).

Female

Measurements. 45 podous rings. Body length 61 mm, midbody width 4.85 mm.

Distribution. Known only from the dry forest north of Montagne d'Ambre, North Madagascar (Fig. 1).

Derivatio nominis. *"albipes"*, adjective, refers to the white legs of this species.

Spiromimus laticoxalis new species (Fig. 17)

Material examined

Holotype. M, FMMC 3952, Madagascar, Province de Mahajanga, Parc National d'Ankarafantsika, Ampijoroa Station Forestière, 40 km 306°NW Andranofasika, 130 m, tropical dry forest, 16°19'15"S, 46°48'38"E, coll. Fisher, Griswold et al., pitfall trap, 26.iii.-1.iv.2001.

Paratypes. 4 F, 13 imm., FMMC 3952, same data as holotype.

Other material examined. 1 M, 3 F, MNHN. Madagascar, Forêt Sakaraha, coll. 31/12/1961, CD. Probably 22°56'0.00"S, 44°32'60.00"E,

Diagnosis. 32-48 mm long, with 45 podous rings. Mesal process of anterior gonopod coxite wide, long (Fig. 17D) extending up to basal 2/3 of sternal lobe (Fig. 17D). Sternite without shoulders (Fig. 17D). Telopodite without triangular excavation (Fig. 17D), tip slender, without retrorse process (Fig. 17D). Posterior gonopod tip well-rounded, without 'hook' (Fig. 17F). Mesal branch triangular, elongated, extending beyond main branch

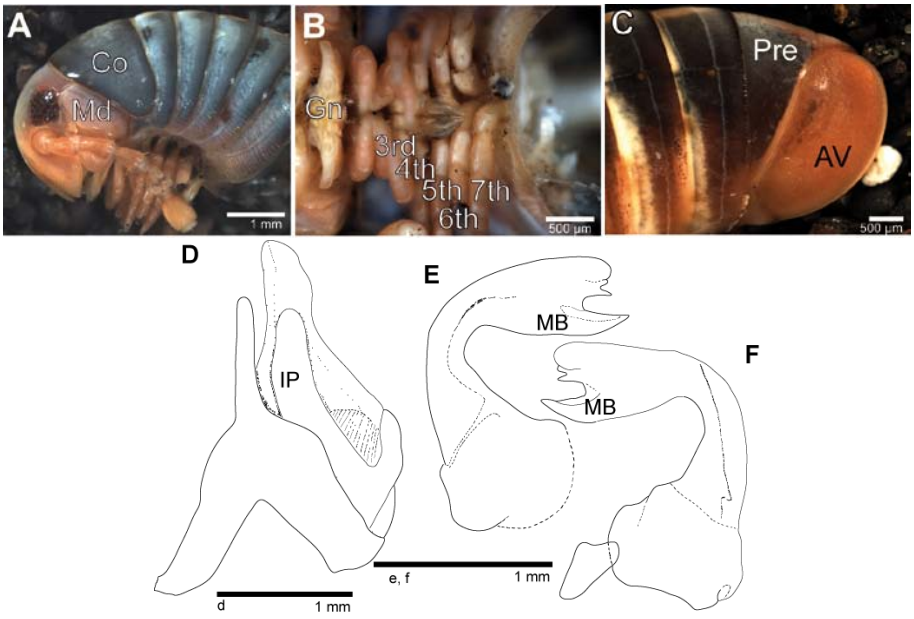

Fig. 17. — *Spiromimus laticoxalis* n. sp., male holotype, FMMC 3952. A: head and anterior trunk segments, lateral view; B: legs 1-7, ventral view; C: telson; D: anterior gonopods, oral view; E: posterior gonopod, oral view; F: posterior gonopod, anal view. Abbreviations: AV = anal valves; Gn = gnathochilarium; IP = mesal coxite process; MB = mesal branch; Md = mandible; Pre = preanal ring. Scale bars: A, C-F = 1 mm; B = 500 µm.

(Fig. 17E). Area between mesal and main branch not filled with membranous folds (Fig. 17F). Male coxa 3 with short, wide knob. Coxa 4 with long and wide process, protruding to coxa 7 (Fig. 17B). Coxa 5 rectangular, mesal margin elongated into short and slender process. Coxa 6 rectangular, without process. Coxa 7 with small, conical process (Fig. 17B). Pro- and mesozonite laterally and dorsally greyish-black, ventrally red (Fig. 17A). Posterior margin of metazonites black, body rings dorsally with slender golden stripe. (Fig. 17C). Head, antenna, legs and anal valves red (Fig. 17A-C).

Spiromimus laticoxalis n. sp. differs from all congeneric species except *S. simplicicoxalis* by the fact that the mesal coxite process on the anterior gonopods is wide instead of slim (Fig. 17D). Furthermore, only in *S. laticoxalis* and *S. simplicicoxalis* n. sp. is the mesal branch of the posterior gonopods of unique shape: triangular, sharp-edged and overreaching the main branch (Fig. 17E-F). *S. laticoxalis* differs from *S. simplicicoxalis* n. sp. in the presence of a long, rod-shaped coxal process on the coxa 4, a slender mesal process on the coxa 5 and a small cone on coxa 7 (Fig. 17B).

Description

Male

Measurements. 45 podous rings. Body length circa 32 mm, midbody width 3.55 mm.

Color. Legs, antennae, ventral side of body rings and apical part of head red (Fig. 17A). Subanal scale and anal valves red, anteriorly with round dark spot (Fig. 17C). Body rings faded greyish, posterior margin darker (Fig. 17C). Rings dorsally with single, slender red stripe.

Anterior gonopod sternite rising into slender process, without shoulders (Fig. 17D). Mesal coxite process wide and elongated (Fig. 17D), extending up to basal 2/3 of sternite. Telopodite without triangular excavation (Fig. 17D), tip slender and elongated, without retrorse process (Fig. 17D).

Posterior gonopod main branch slender and well-rounded (Fig. 17E), without hook (Fig. 17F). Main branch basally with slender membranous fringe, extended apically into two irregularly rounded processes, which are as long as tip (Fig. 17E). Mesal branch strongly triangular, with sharp, elongated tip, extending beyond main branch. Mesal branch basally wide, tapering apically (Fig. 17E). Area between mesal and main branch without any connecting membranous folds (Fig. 17E-F).

Female

Measurements. 45 podous rings. Body length 48 mm, midbody width 4.4-4.9 mm.

Intraspecific variation. Specimens from Sakaraha are larger than those from the type locality Anakarafantsika. Males from Sakaraha are 41 mm long and 3.3 mm wide, while females are 52 mm long and 5.25 mm wide.

Distribution. Widely distributed over Madagascar. The two localities Anakarafantsika and Sakaraha are more than 700 km distant from one another (Fig. 1).

Derivatio nominis. *"laticoxalis"*, adjective, refers to the wide anterior gonopod coxal process.

Spiromimus simplicicoxalis new species (Fig. 18)

Material examined

Holotype. M, FMMC 3994, Madagascar, Province Fianarantsoa, Reserve Andringitra, 8.5 km SE Antanitotsy, montane rainforest, 1990 m, 22°10'S, 46°58'E, coll. Sylvian, B.L. Fisher, Winkler extraction, 6.iii.1997.

Diagnosis. 32 mm long with 45 podous rings. Mesal process of anterior gonopod coxite wide (Fig. 18D) extending up to basal 1/2 of sternal lobe (Fig. 18D). Sternite without shoulders (Fig. 18D). Telopodite without triangular excavation (Fig. 18D), tip slender, without retrorse process (Fig. 18D). Tip of main branch of posterior gonopod well-rounded, basally with sharp 'hook' (Fig. 18F). Mesal branch triangular, elongated, distinctly longer than

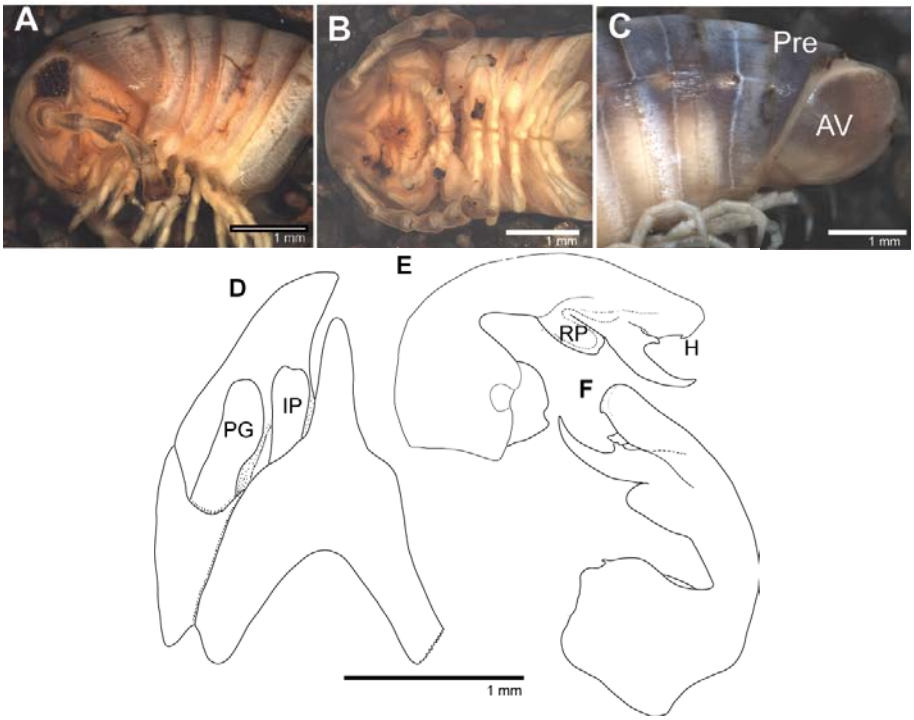

Fig. 18. — *Spiromimus simplicicoxalis* n. sp., male holotype, FMMC 3994. A: head and anterior trunk segments, lateral view; B: legs 1-7, ventral view; C: telson; D: anterior gonopods, oral view; E: posterior gonopod, anal view; F: posterior gonopod, oral view. Abbreviations: AV = anal valves; H = hook; IP = mesal coxite process; MB = mesal branch; Pre = preanal ring; RP = rectangular process. Scale bars = 1 mm.

tip of main branch (Fig. 18E). Basally of mesal branch with rectangular process (Fig. 18F). Area between mesal and main branch not filled with membranous folds (Fig. 18E). Male coxa 3 with short, wide knob. Coxa 4 with short conical process (Fig. 18B). Coxae 5, 6 and 7 cylindrical and unmodified (Fig. 18B). Coloration strongly altered by alcohol (Fig. 18A). Legs whitish, head and antenna brown, anal valves with orange color (Fig. 18A-C).

Spiromimus simplicicoxalis n. sp. differs from all congeneric species except *S. laticoxalis* in the presence of a wide mesal coxite process on the anterior gonopods (Fig. 18D). Furthermore, only those two species feature, on the posterior gonopods, a sharp-edged mesal branch of triangular shape which extends beyond the main branch (Fig. 18E-F). *S. simplicicoxalis* is the only *Spiromimus* species without strongly elongated male coxal processes (Fig. 18B). A rectangular process basally of the mesal branch on the posterior gonopods is only present in *S. simplicicoxalis* (Fig. 18F).

Description

Male

Measurements. 45 podous rings. Body length circa 32 mm, midbody width 3.55 mm.

Color. Head, antennae, subanal scale and anal valves with traces of orange (Fig. 18C). Legs whitish. Body rings faded greyish, posterior margin darker, ventrally light brown (Fig. 18A). Rings dorsally with single, slender, yellow stripe.

Anterior gonopod sternite rising into slender process, without shoulders (Fig. 18D). Mesal coxite process wide and elongated (Fig. 18D), extending up to basal half of sternite. Telopodite without triangular excavation (Fig. 18D).

Posterior gonopod main branch slender and elongated, with sharp-edged hook (Fig. 18F), without membranous area (Fig. 18E). Mesal branch strongly triangular, with sharp, elongated apex which strongly overreaches main branch (Fig. 18E). Basally of mesal branch with large rectangular process (Fig. 18F). Area between mesal and main branch without any connecting membranous folds (Fig. 18E-F).

Distribution. Known only from montane rainforest of Andringitra, southeastern Madagascar (Fig. 6).

Derivatio nominis. "*simplicicoxalis*", adjective, refers to the near absence of coxal processes in the male of this species.

Spiromimus grallator new species (Figs 19-20)

Material examined

Holotype. M, ZMUC 00101021, Madagascar, Province Antsiranana, Reserve Anjanaharibe-Sud, 12.2 km WSW Befingotra, 1985 m, montane rainforest, 14°45'S, 49°26'E, coll. B.L. Fisher, 25.xi.1994.

Paratypes. 1 M, 1 F, ZMUC 00101022, same data as holotype.

Diagnosis. 63-74 mm long, only 4.5-6.1 wide, 41 moniliform body rings. Male antenna reaching back to eight body ring (Fig. 19C). Legs in

males 1.3 times as long as body ring width (Fig. 19A). Anterior gonopod coxite process longer than sternal lobe (Fig. 20A). Telopodite without excavation (Fig. 20A), tip slender, with weakly developed retrorse process (Fig. 20A). Tip of main branch of posterior gonopod bent backwards, forming well-rounded 'hook' (Fig. 20C). Mesal branch slightly more slender and shorter than main branch, apically strongly tapering into sharp-edged tip (Fig. 20B). Mesal and main branch only basally connected with membranous folds (Fig. 20B). Main branch before well-rounded apex with large membranous lobe which slightly overlaps the mesal branch (Fig. 20C). Male coxae 3, 4 and 5 elongated into short and slender processes reaching back to following coxa. Coxa 6 rectangular. Coxa 7 with tiny cone. Coloration laterally and ventrally dark, dorsally with wide red stripe.

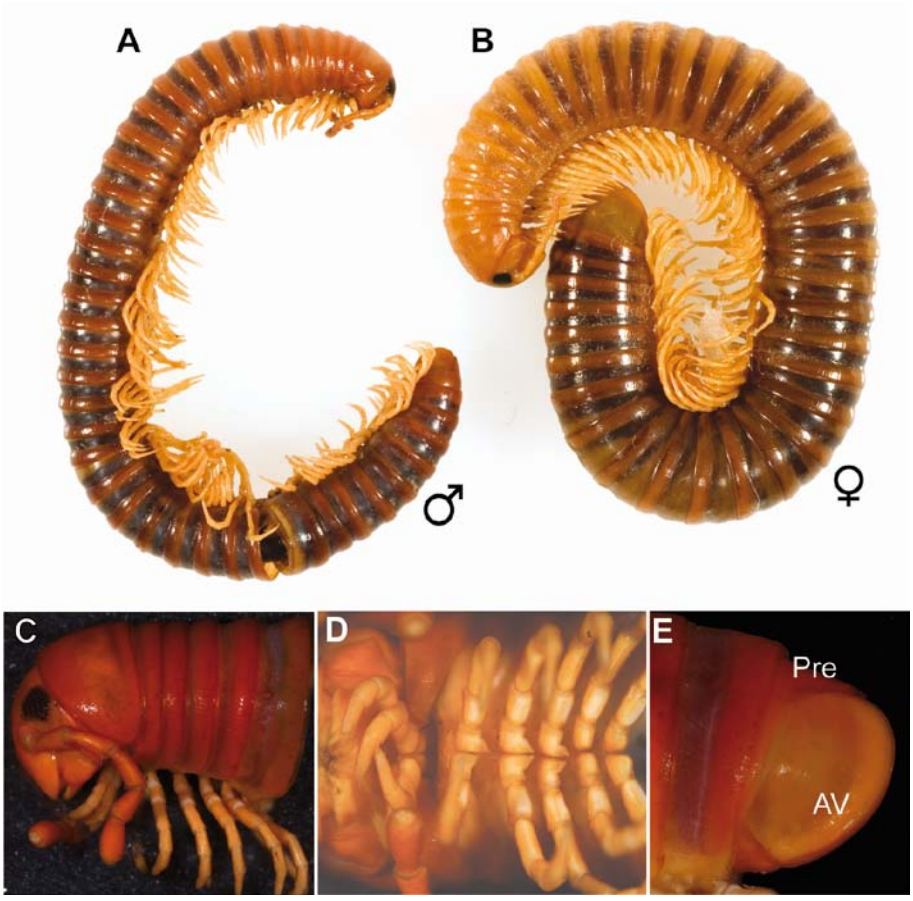

Fig. 19. — *Spiromimus grallator* n. sp., A male paratype; C-E male holotype; B female paratype, ZMUC. A: male habitus; B: female habitus; C: head and anterior trunk segments, lateral view; D: legs 1-7, ventral view; E: telson. Abbreviations: AV = anal valves; Pre = preanal ring. Not to scale, but A and B of equal size.

Spiromimus grallator n. sp. shares a large body size and the general shape of the anterior gonopods (compare Fig. 20A with Fig. 6B) only with *Spiromimus dorsovittatus* (de Saussure & Zehntner 1901). *S. grallator* n. sp. differs from the latter in the absence of a spine on the anal valves (Fig. 19E), presence of moniliform body rings (Fig. 19A-B), the only short male coxal processes (Fig. 19C) and differently shaped posterior gonopods (compare Fig. 20B-C with Fig. 6B).

Description

Male

Measurements. 40 or 41 rings. Body length circa 65 mm, midbody width 4.5 mm.

Color. Strongly faded in alcohol, only part of holotype (shielded by label) shows potential natural color. Head, antennae and legs orange (Fig. 19A). Body rings laterally and ventrally black, dorsally red. Anal valves and subanal scale red. Anal valves anteriorly with round dark spot (Fig. 19E). Rings dorsally with wide, red stripe.

Anterior gonopods coxite process slender and elongated, longer than sternite (Fig. 20A). Telopodite without triangular excavation (Fig. 20A). Tip of telopodite relatively wide and elongated, apically with short but sharp triangular, retrorse process (Fig. 20A).

Posterior gonopod tip of main branch slender and well-rounded (Fig. 20B). Part of tip bending backwards, forming short and well-rounded hook (Fig. 20C). Main branch with lobe-like, membranous process originating from mesal side. Membranous process extending as far as and even slightly overlapping mesal branch (Fig. 20B). Mesal branch wide at base, apically strongly tapering into sharp-edged apex (Fig. 20C). Area between mesal and

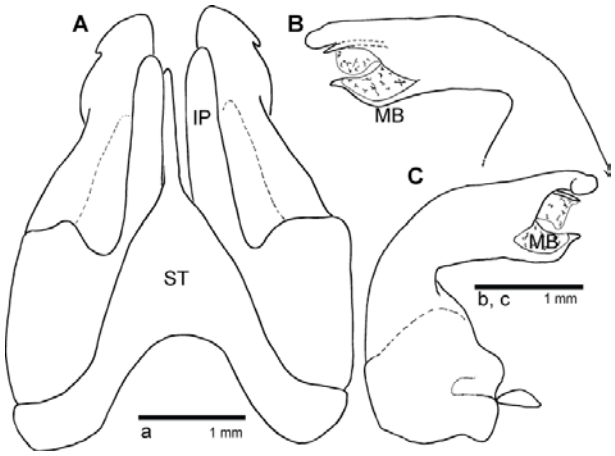

Fig. 20. — *Spiromimus grallator* n. sp., male holotype, ZMUC. A: anterior gonopods, oral view; B: posterior gonopod, oral view; C: posterior gonopod, anal view. Abbreviations: IP = mesal coxite process; MB = mesal branch; ST = sternite. Scale bars = 1 mm.

main branch of telopodite only basally connected with membranous folds (Fig. 20B-C). Mesal branch slightly shorter than main branch.

Female
Measurements. 41 rings. Body length 74 mm, midbody width 6.1 mm.

Distribution. Only recorded from the montane rainforest at Anjanaharibe (Fig. 1). *Spiromimus grallator* is currently the Malagasy millipede species known from the highest elevation, 1985 m.

Derivatio nominis. "*grallator*", noun in apposition, meaning 'stilt-walker' and referring to the extraordinary long legs.

Spiromimus namoroka new species (Fig. 21)

Material examined
Holotype. M, CAS BLF 6586, Madagascar, Province Mahajanga, PN Namoroka, 16.9 km 317° NW Vilanandro, tropical dry forest, 100 m, 16°24'24"S, 45°18'36"E, coll. C. Griswold, B. Fisher et al., 12-16.xi.2003.
Paratypes. 1 M, 1 F, CAS BLF 6586, same data as holotype.

Diagnosis. Males 40 mm long, 42 body rings. Male antenna reaching to body ring 7. Anterior gonopod coxite process reaching to 3/4 of sternal lobe length (Fig. 21A). Telopodite laterally with large triangular excavation (Fig. 21A), tip slender, with strongly developed retrorse process (Fig. 21A). Posterior gonopod tip wide, well-rounded, curved upwards, without 'hook' (Fig. 21C), basally with spine-like, projecting membranous fold (Fig. 21B). Mesal branch thin, first tapering towards tip, but at tip expanding into two lobes (Fig. 21C). Area between main and mesal branches except for tip

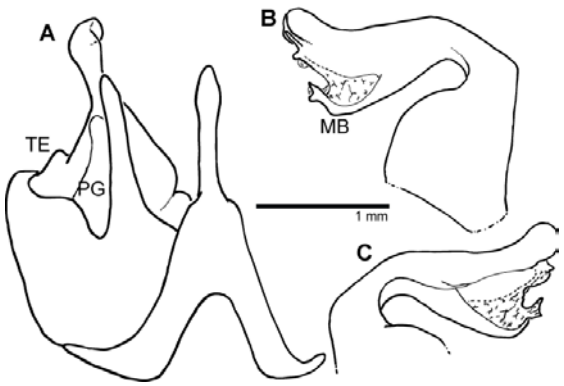

Fig. 21. — *Spiromimus namoroka* n. sp., male holotype, CAS BLF 6586. A: anterior gonopods, oral view; B: posterior gonopod, oral view; C: posterior gonopod, anal view. Abbreviations: MB = mesal branch; PG = posterior gonopod; TE = triangular excavation. Scale bars = 1 mm.

completely filled with membranous folds (Fig. 21B-C). Male coxa 3 elongated into long and slender process reaching to coxa 5. Coxa 4 with long and wide process, reaching to coxa 6. Coxae 5 and 6 flat and rectangular, without any processes. Coxa 7 elongated into large cone. Coloration dark, dorsally with single lighter stripe. Antenna, legs, anal valves and ventral part of body rings reddish.

Spiromimus namoroka n. sp. shares a 'hookless' posterior gonopod with a well-rounded tip (Fig. 21B-C) only with *S. voeltzkowi* de Saussure & Zehntner 1901 and *S. triaureus* n. sp. A wide posterior gonopod main branch with a dilating mesal branch is also shared with *S. triaureus*. The very wide main branch with its strongly curved tip (Fig. 21C) is a unique character inside *Spiromimus*.

Description

Male

Measurements. 42 rings. Body length circa 42 mm, midbody width 3.2 mm.

Color strongly faded in alcohol, brownish, dorsally with lighter stripe.

Anterior gonopods process of coxite slender and elongated, reaching up to basal 3/4 of sternite. Telopodite laterally with small sharp triangular excavation (Fig. 21A). Tip of telopodite slender and elongated, on tip with short, but sharp retrorse process.

Posterior gonopod tip well-rounded and conspicuously curved upwards (Fig. 21B-C). Main branch wide and well-rounded, no hook present (Fig. 21C). Slender, spine like membranous process originating from mesal side of posterior gonopod, protruding up to main gonopod tip (Fig. 21B). Mesal branch wide at base, then narrowing, but apically dilated into two wide membranous folds (Fig. 21C). Area between mesal and main branch connected with membranous folds, only apically free.

Female

Measurements. Specimen broken in several pieces, some of which definitely missing, midbody width 4.7 mm.

Distribution. Known only from the dry forest Namoroka, West Madagascar (Fig. 1).

Derivatio nominis. "*namoroka*", noun in apposition, referring to the type locality.

Spiromimus simplex new species (Figs 22-23)

Material examined

Holotype. M, ZMUC 00101023, Madagascar, Province Antsiranana, Reserve Marojejy, 8.4 km NNW of Manantenina, rainforest, 700 m, 14°26"S, 49°45'E, coll. Coddington, Larcher, Scharff, Griswold & Andriamasimanana, 10-17.xi.1993.

Other material examined. 1 immature M, ZMUC 00101024, same data as holotype; 1 immature M, 2 F, CAS BLF 8726, Parc National de Marojejy, Manantenina

River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, rainforest, 450 m, 14°26'12"S, 049°46'30"E, coll. B.L. Fisher et al., 12-15.xi.2003.

Diagnosis. Male 36 mm long, 43 body rings. Male antenna reaching backwards to body ring 7 (Fig. 22A). Coxite process of anterior gonopod slightly longer than sternal lobe (Fig. 23A). Telopodite laterally with extraordinary large triangular excavation (Fig. 23A), tip slender, with weakly developed retrorse process (Fig. 23A). Posterior gonopod tip slender, well-rounded, tip curved upwards forming well-rounded 'hook' (Fig. 23C). Tip basally with wide membranous lobe and visible projection of the sperm canal (Fig. 23B). Mesal branch completely reduced (Fig. 23B-C). Male coxa 3 elongated into long and slender process reaching to coxa 5. Coxa 4 with long and wide process, reaching to coxa 5. Coxa 5 flat and rectangular, mesally with slender process reaching back to coxa 6. Coxa 6 rectangular, without any process. Coxa 7 elongated into large cone (Fig. 22B). Coloration dark, dorsally with

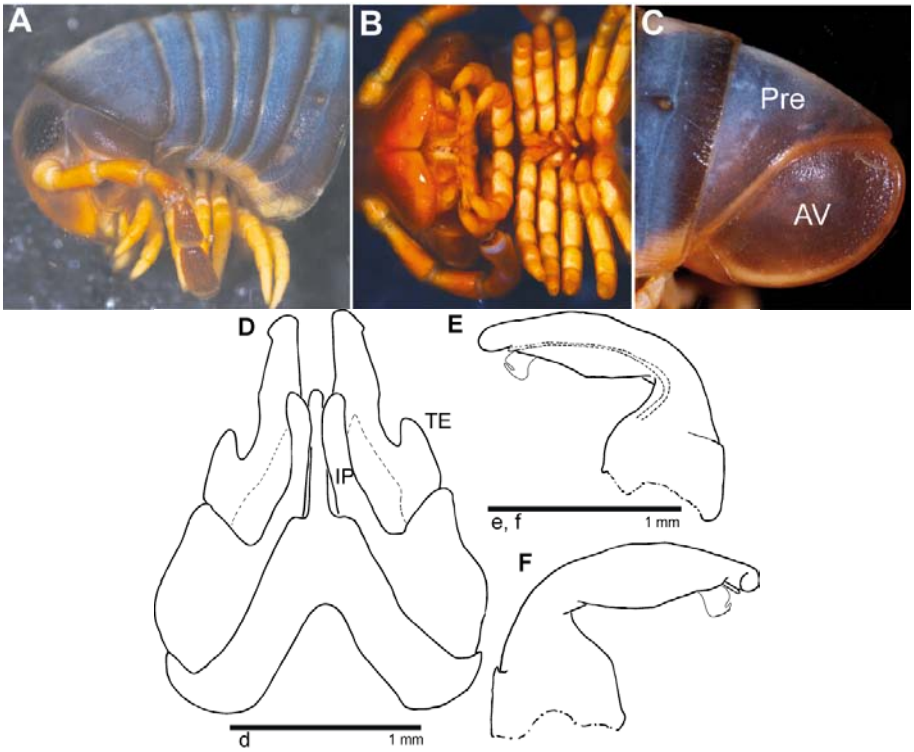

Fig. 22. — *Spiromimus simplex* n. sp., male holotype, ZMUC. A: head and anterior trunk segments, lateral view; B: legs 1-7, ventral view; C: telson; D: anterior gonopods, oral view; E: posterior gonopod, oral view; F: posterior gonopod, anal view. Abbreviations: AV = anal valves; IP = mesal coxite process; Pre = preanal ring; TE = triangular excavation. A-C not to scale. Scale bars = 1 mm.

single lighter stripes (Fig. 22A). Antenna, legs, and poster part of anal valves reddish (Fig. 22C).

Spiromimus simplex n. sp. shares a strongly elongated anterior gonopod coxite process and a large triangular excavation with *Spiromimus albipes* n. sp. The complete reduction of posterior gonopod mesal branch is unique.

Description

Male

Measurements. 43 rings. Body length circa 36 mm, midbody width 3.1 mm.

Color strongly faded in alcohol, body rings on mesozona light grey, on

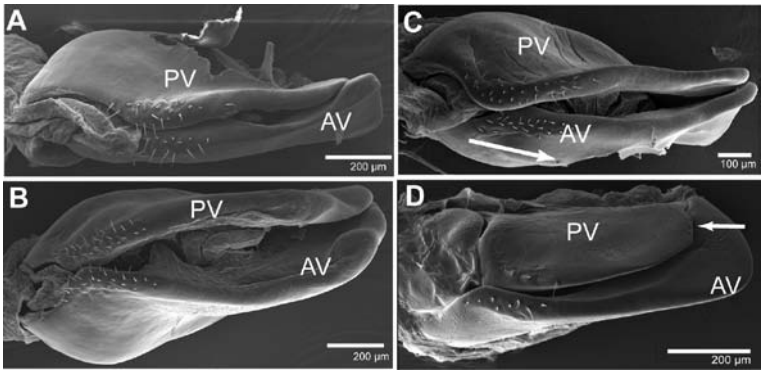

Fig. 23. — Left vulva. A: *Spiromimus univirgatus*; B: *S. triaureus* n. sp.; C: *S. litoralis* n. sp.; D: *Xenobolus carnifex*. Abbreviations: AV = anterior valve; PV = posterior valve. Arrows point to sensorial cells. Scale bars: A-B, D = 200 µm; C = 100 µm.

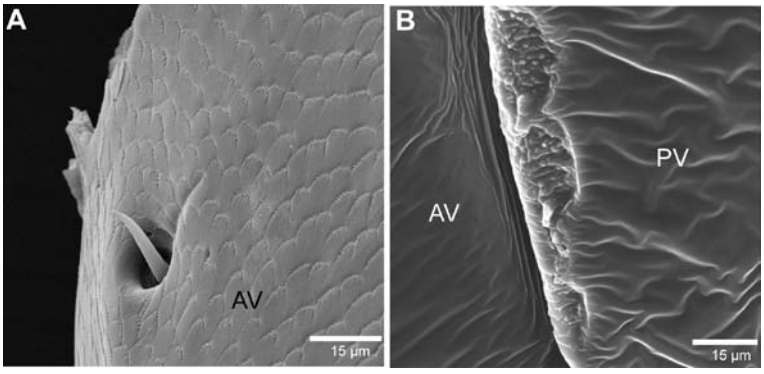

Fig. 24. — Sensory cells on vulva. A: *Spiromimus litoralis* n. sp., special setae; B: *Xenobolus carnifex*, sensory cones. Abbreviations: AV = anterior valve; PV = posterior valve. Scale bars = 15 µm.

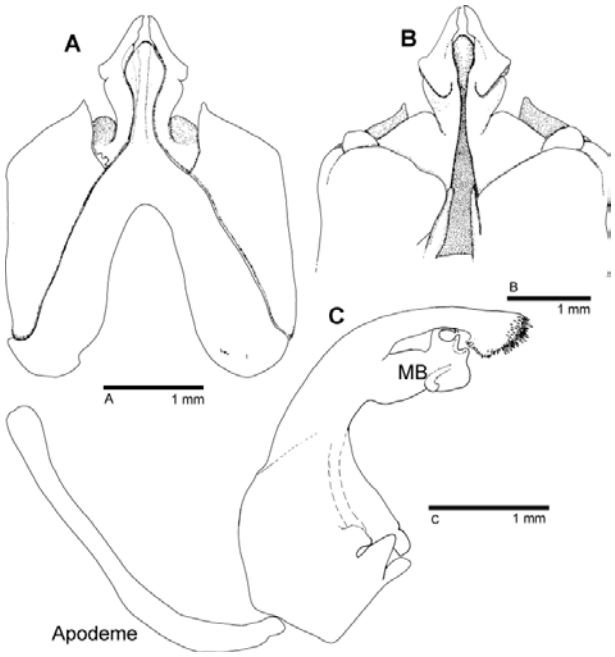

Fig. 25. — *Xenobolus carnifex*, ZMUC. A: anterior gonopods, oral view; B: anterior gonopods, anal view; C: posterior gonopod, anal view. Abbreviations: MB = mesal branch. Scale bars = 1 mm.

metazona dark grey to black. All rings ventrally with a thin orange stripe (Fig. 22A). Head, legs, antenna and posterior part of anal valves orange-reddish (Fig. 22A-C).

Anterior gonopod mesal process of coxite slender and elongated (Fig. 23A), slightly longer than sternite. Telopodite laterally with large sharp triangular excavation (Fig. 23A). Tip of telopodite slender and elongated, on tip with short retrorse process (Fig. 23A).

Posterior gonopod tip well-rounded and relatively slender (Fig. 23B-C), well-rounded hook present (Fig. 23C). Sperm canal projecting as slender, spine like process. basally of sperm canal with membranous lobe of medium size (Fig. 23B). Mesal branch completely reduced.

Distribution. Only recorded from Marojejy, NE Madagascar (Fig. 1).

Derivatio nominis. "*simplex*", adjective, referring to the complete reduction of the posterior gonopod mesal branch.

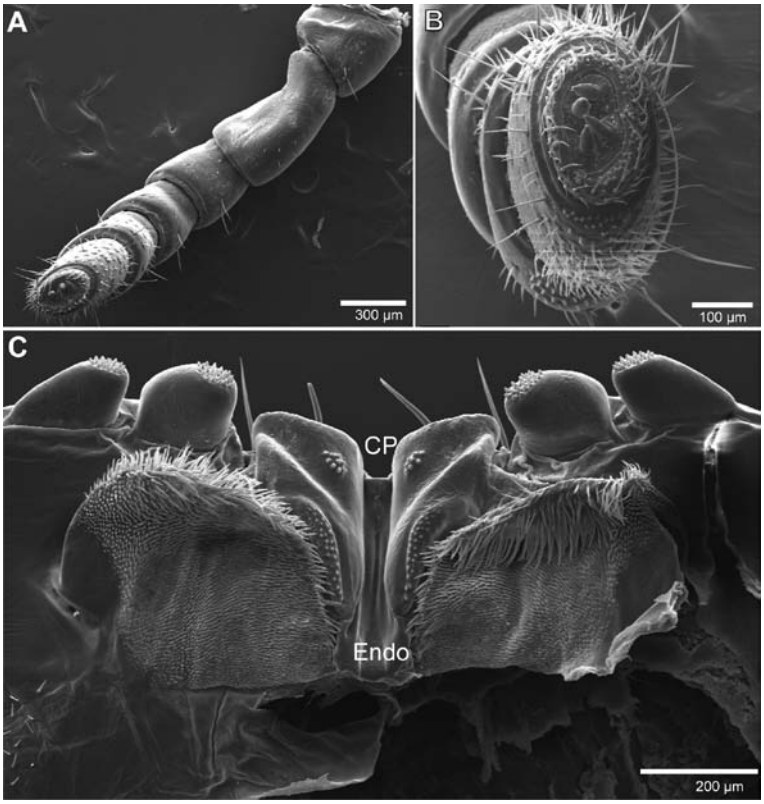

Fig. 26. — *Xenobolus carnifex*, male, ZMUC, SEM. A: antenna, overview; B: antenna, apical view; C: underside of gnathochilarium. Abbreviations: CP = central pads; Endo = endochilarium. Scale bars: A = 300 µm; B = 100 µm; C = 200 µm.

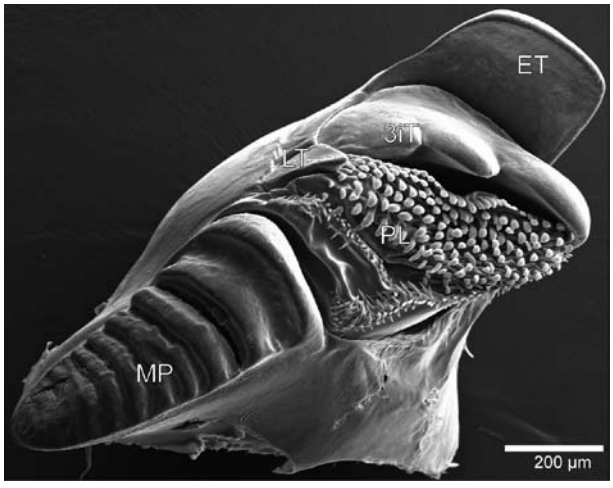

Fig. 27. — *Xenobolus carnifex*, ZMUC, male, SEM, left mandible, inner view. Abbreviations: 3iT = 3-combed inner tooth; ET = external tooth; LT = lateral tooth; MP = molar plate; PL = pectinate lamellae. Scale bar = 200 µm.

DISCUSSION

Phylogenetic analysis of Spiromimus and Xenobolus

Spiromimus now includes 13 species, five distributed in rainforests, six in dry forests and two living in unknown habitats. We examined characters in all species of the genus, except for *S. grallator* n. sp., *S. namoroka* n. sp. and *S. simplex* n. sp., which were discovered after the analysis was completed. Furthermore, we studied specimens of *Aulacobolus rubropunctatus*, *Madabolus maximus*, *Xenobolus carnifex* and *Aphistogoniulus erythrocephalus*. Therefore, our analysis includes members of all currently described Malagasy genera of Spirobolida (Table 1). The PAUP analysis resulted in three most parsimonious trees (strict consensus tree shown in Fig. 28) with 61 steps. Eight characters are parsimony uninformative (because they are autapomorphies of single taxa).

Phylogenetic position of the subfamily Spiromiminae

The presence of a sclerotized sternite connecting the posterior gonopods and the reduction of anterior gonopod apodemes identify the Spiromiminae as members of the suborder Trigoniulidea, family Pachybolidae. Within the Pachybolidae, the Spiromiminae represents one of four currently valid subfamilies (HOFFMAN 1980). Spiromiminae are now a monotypic subfamily, since *Pygodon* is here synonymized under *Spiromimus*.

Tree description

Clade A, *Xenobolus* and *Spiromimus* (Spiromimidae sensu VERHOEFF 1936), is present and well-supported in all trees. Six characters support Clade A with the exception of male coxal processes, all are gonopod characters of uncertain homology. The genus *Spiromimus* is also, not surprisingly, recovered in all trees (Fig. 28, clade B). Only a single character supports this clade, the absence of tarsal pads in male *Spiromimus*. This character is most likely homoplastic, since males without tarsal pads appear in several spirobolidan groups.

The species level phylogeny inside *Spiromimus* (Fig. 28, clades D-J) is surprisingly well-resolved. The strict consensus tree shows a full resolution of intrageneric relationships, and at least a single unique character state supports each node (Fig. 28). However, the statistical support for many nodes is quite weak.

Origins of Spiromimus

Within *Spiromimus*, the species branching off first is *S. simplicicoxalis* which is distributed in the montane rainforests around Andringitra (Table 2, Fig. 6). Since the near outgroups of *Spiromimus* are also rainforest animals,

the roots of the genus *Spiromimus* seem to be in the rainforest, with the dry forest having been colonized several times by its members (Fig. 28). Species of *Spiromimus* which live in close proximity to one another are surprisingly not closely related to one another. *Spiromimus albipes* can be found just 10 km distant from *S. electricus* in North Madagascar (Fig. 6): however, those two species are not closely related (Fig. 28). *S. albipes* is more closely related to *S. univirgatus* (50 km distance) and *S. scapularis* (100 km distance) than to *S. electricus*. The two almost sympatric species *S. laticoxalis* and *S. triaureus* (3 km distance) do not form a monophyletic group (Fig. 28). The radiation of the genus *Spiromimus* might not be a recent event. Different expansion and speciation events could have contributed to the now widespread distribution of *Spiromimus* species on Madagascar. While most species were only recorded from a single locality, two species (*S. triaureus* and *S. laticoxalis*) show a very wide distribution in the dry forest ecosystem of Western Madagascar (Fig. 1).

The subfamily Spiromiminae

In our tree, *Xenobolus* is the sister taxon to *Spiromimus,* supporting the Spiromimidae sensu VERHOEFF (1936). However, this grouping was only obtained by scoring gonopod characters of unclear homology, viz., that we regarded the elongation of the anterior gonopod telopodite and sternite in *Xenobolus* and *Spiromimus* as homologous (Figs 2D, 25A). Additionally, we treated the mesal branch carrying part of the sperm channel on the posterior gonopods as homologous in *Xenobolus* and *Spiromimus* (Figs 2E, 25C). The homology of such structures, however, remains dubious, at best. An elongation of the anterior gonopod telopodite and sternite is, for example,

Table 2.

Spiromimus species and their habitat.

Species	Ecosystem
Spiromimus univirgatus de Saussure & Zehntner 1901	dry forest
Spiromimus voeltzkowi de Saussure & Zehntner 1901	?
Spiromimus dorsovittatus (de Saussure & Zehntner 1901)	?
Spiromimus triaureus n. sp.	dry forest
Spiromimus electricus n. sp.	rain forest
Spiromimus litoralis n. sp.	rain forest/dry forest
Spiromimus scapularis n. sp.	dry forest
Spiromimus albipes n. sp.	dry forest
Spiromimus laticoxalis n. sp.	dry forest
Spiromimus simplicicoxalis n. sp.	rain forest

also visible in the Australian genus *Austrostrophus* (HOFFMAN 2003). An additional character uniting *Spiromimus* and *Xenobolus* are the male coxal processes on legs three and four. Such processes are present in numerous millipede genera, and it is just a coincidence that none of our other outgroup genera features such processes. The special shape and spectacular length of the processes in most *Spiromimus* species is indeed unique for the whole

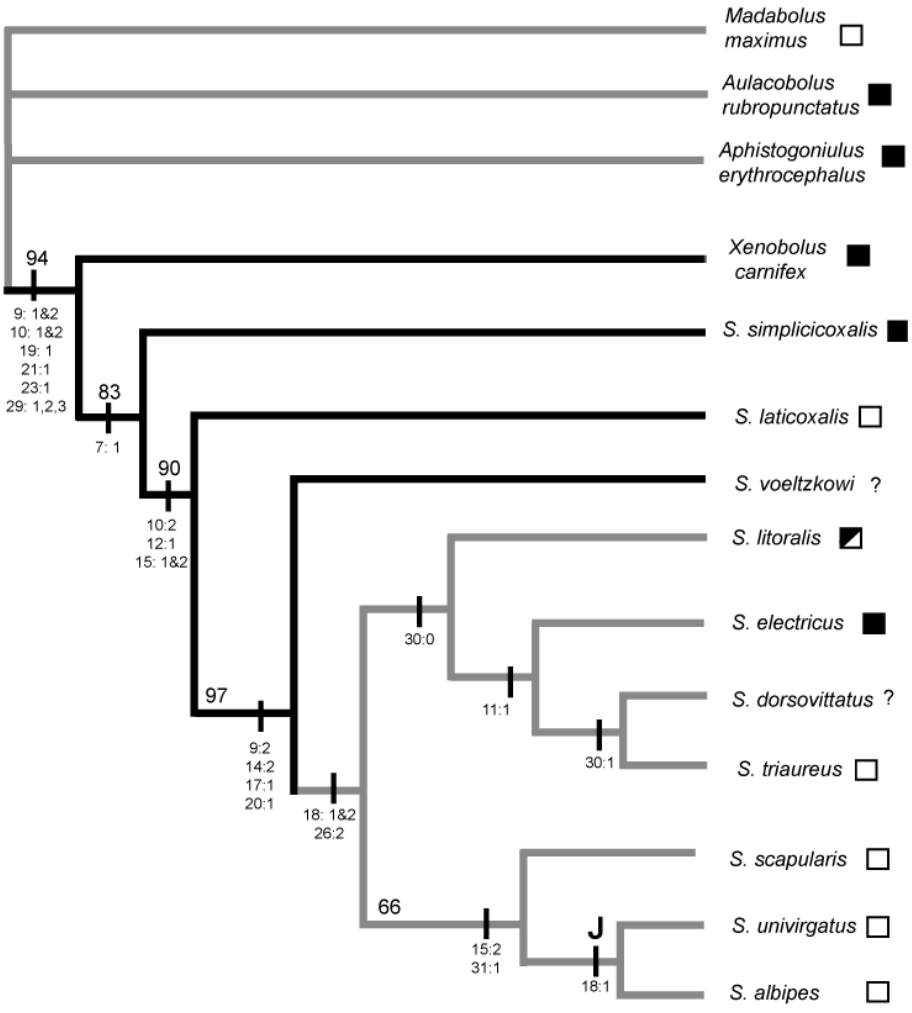

Fig. 28. — Cladistic analysis of *Spiromimus* species, strict consensus tree. Numbers above nodes show the bootstrap support of each node (bootstrap values < 50% are not shown). Numbers below branches refer to the character states supporting the branch. Black boxes = rainforest taxa; empty boxes = dry forest taxa. Habitats of *S. voeltzkowi* and *S. dorsovittatus* are unknown.

order Spirobolida. *Xenobolus* and the basalmost *Spiromimus* species, *S. simplicicoxalis*, however, show only a more common conical extension of the coxa. It is likely that the strongly modified coxal processes in most *Spiromimus* species evolved inside the genus. No single non-gonopod character was identified which convincingly supports a close relationship of *Xenobolus* and *Spiromimus*. The mandible (Figs 4A, 27), gnathochilarium (Figs 3D-F, 26C) and antenna (Figs 3A-C, 26A-B) of both genera fit very well in with the general pattern observed inside the order Spirobolida. The molar plate is surprisingly short in *Spiromimus* (Fig. 4A).

Therefore, we do not place *Xenobolus* inside the Spiromiminae but tentatively maintain the Spiromiminae sensu Hoffman 1980. With the synonymization of *Pygodon* the subfamily now includes only a single genus, *Spiromimus*. A more thorough revision of the family Pachybolidae will be necessary to get better insights in the justification and relationships of the subfamily Spiromiminae.

Contrary to HOFFMAN's (1962) view, we were unable to find any character supporting a close relationship between *Xenobolus* and *Aphistogoniulus*.

The limited amount of variation in available morphological characters currently hampers phylogenetic work inside Spirobolida. Possibly a molecular approach will be necessary to solve the tricky internal relationships of the family Pachybolidae.

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REFERENCES

BRÖLEMANN H.W. 1914. Étude sur les Spirobolides (Myriapodes). *Annales de la Société Entomologique de France* 83: 1-38.

DE SAUSSURE H. & ZEHNTNER L. 1901. Myriopoden aus Madagaskar und Zansibar. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 26: 429-460.

DE SAUSSURE H. & ZEHNTNER L. 1902. Myriapodes de Madagascar. In: Grandidier A. *Histoire Physique, Naturelle et Politique de Madagascar* 27 (53): i-viii, 1-356, pls 13-15.

ENGHOFF H. 1979. Taxonomic significance of the mandibles in the order Julida, pp. 27-38. In: Camatini M., Edit. Myriapod biology. *London, UK: Academic Press*, 456 pp.

ENGHOFF H. 1991. A revised cladistic analysis and classification of the millipede order Julida. With establishment of four new families and description of a new nemasomatoid genus from Japan. *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 29: 241-263.

ENGHOFF H. 2003. Diplopoda, Millipedes, pp. 617-627. In: Goodman S.M. & Benstead J.P., Edits. The Natural History of Madagascar. *University of Chicago Press*, 1709 pp.

FONTANETTI C.S. & CAMARGO-MATHIAS M.I. 2004. External morphology of the antennae of *Rhinocricus padbergi* Verhoeff 1938 (Diplopoda, Spirobolida). *Brazilian Journal of Morphological Sciences* 21 (2): 73-79.

HOFFMAN R.L. 1962. Studies on spiroboloid millipeds IV. Systematic and nomenclatorial notes on the family Pachybolidae. *Revue Suisse de Zoologie* 69: 759-783.

HOFFMAN R.L. 1980. Classification of the Diplopoda. *Genève, Switzerland: Muséum d'Histoire Naturelle Genève*, 237 pp.

HOFFMAN R.L. 2003. A new genus and species of trigoniuline milliped from Western Australia (Spirobolida: Pachybolidae: Trigoniulinae). *Records of the Western Australian Museum* 22: 17-22.

ISHII K. & TAMURA H. 1995. The mandibular structure as a diagnostic character in taxonomy of diplopods. *Acta Zoologica Fennica* 196: 232-235.

ISHII K. & TAMURA H. 1996. A taxonomic study of polydesmoid millipedes (Diplopoda) based on their mandibular structures, pp. 101-111. In: Geoffroy J.-J. et al., Edits. Acta Myriapodologica (*Mémoirs de Muséum National d'Historie Naturelle*) 169.

KEETON W.T. 1960. A taxonomic study of the milliped family Spirobolidae (Diplopoda: Spirobolida). *Memoirs of the American Entomological Society* 17: 1-146.

KRAUSE D.W. 2003. Late Cretaceous vertebrates of Madagascar: A window into Gondwanan biogeography at the end of the age of dinosaurs, pp. 40-47. In: Goodman S.M. & Benstead J.P., Edits. The Natural History of Madagascar. *University of Chicago Press*, 1709 pp.

MADDISON W.P. & MADDISON D.R. 2005. Mesquite: A modular system for evolutionary analysis.' Version 1.06. Available at http://mesquiteproject.org [Accessed on 2 September 2006].

METCALFE I. 1998. Palaeozoic and Mesozoic geological evolution of the SE Asian region: multidisciplinary constraints and implications from biogeography, pp. 25-42. In: Hall R. & Holloway J.D., Edits. Biogeography and Geological Evolution of SE Asia. *Leiden: Backhuys Publishers*, II + 417 pp.

MÜLLER K. 2004. PRAP — calculation of Bremer support for large data sets. *Molecular Phylogenetics and Evolution* 31: 780-782.

MYERS N., MITTERMEIER R.A., MITTERMEIER C.G., FONSECA G.A.B. & KENT J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.

RABINOWITZ P.D., COFFIN M.F. & FALVEY D. 1983. The separation of Madagascar and Africa. *Science* 220: 67-69.

SWOFFORD D. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0 (Sinauer Associates: Sunderland, MA, USA).

VERHOEFF K.W. 1928. Diplopoda I. In: *Bronn's Klassen und Ordnungen des Tierreiches* 5 (2.I): 1-1071.

VERHOEFF K.W. 1932. Diplopoda II. In: *Bronn's Klassen und Ordnungen des Tierreiches* 5 (2.II): 1073-2084.

VERHOEFF K.W. 1936. Ueber einige Myriapoden und Isopoden aus Dekan, gesammelt von Herrn S. Jones, Madras. *Records of the Indian Museum* 37: 503-508.

WESENER T., ENGHOFF H. & WÄGELE J.-W. 2008. Pachybolini — a tribe of giant Afrotropical millipedes: arguments for monophyly and the description of a new genus from Madagascar (Diplopoda: Spirobolida: Pachybolidae). *Invertebrate Systematics* 22: 37-53.

YODER A.D. & NOWAK M.D. 2006. Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. *Annual Review of Ecology, Evolution, and Systematics* 37: 405-431.

APPENDIX 1
CHARACTER DISCUSSION

Character 1. *Telson, preanal ring*, 0: not protruding above anal valves; 1: protruding above anal valves. The preanal rings in *Aphistogoniulus*, *Madabolus* and *Spiromimus* do not protrude, while the rings in *Xenobolus* and *Aulacobolus* strongly surmount the anal valves. A protruding preanal ring occurs in several Spirobolida families.

Character 2. *Telson, anal valves*, 0: without a spine; 1: with a single spine. Only the anal valves of *Spiromimus dorsovittatus* carry a single spine, unique within Pachybolidae.

Character 3. *Telson, anal valves*, 0: no 'lips' present; 1: well-visible 'lips' at posterior margin. Lips are absent in *Aphistogoniulus* and all *Spiromimus* species, but prominent in *Xenobolus* and *Aulacobolus*.

Character 4. *Vulva, anterior valve*, 0: circa as large as posterior valve; 1: much larger than posterior valve. Both valves are of equal size except for *Xenobolus* (Fig. 19D).

Character 5. *Vulva, special sensorial cells apically on posterior valve*, 0: absent; 1: present. Special cells are only present in *Xenobolus* (Fig. 24B).

Character 6. *Male antenna*, 0: same length as in female; 1: much longer than in female. Of the investigated genera, only in *Spiromimus* the male antennae are much longer than the female antennae. However, also other Spirobolida genera show this character.

Character 7. *Male legs (Ml), tarsal pads*, 0: present; 1: absent. Tarsal pads are present in *Madabolus*, *Aulacobolus*, *Aphistogoniulus* and *Xenobolus*, absent in all *Spiromimus* species.

Character 8. *Ml 1-7, prefemur, femur and postfemur*, 0: unmodified; 1: flat, laterally extended, projecting medially. These podomeres are laterally extended only in *Xenobolus*, so far a unique character within Pachybolidae.

Character 9. *Ml, coxal process on 3rd leg*, 0: absent; 1: present, small knob; 2: present, protruding back to 5th leg. A process is absent in *Madabolus*, *Aulacobolus*, and *Aphistogoniulus*, but a small process is present in *Xenobolus*. In *Spiromimus*, at least a small knob is always present.

Character 10. *Ml, coxal process on 4th leg*, 0: absent; 1: present, small knob; 2: present, protruding back to 6th or 7th leg. See character 9 for a discussion.

Character 11. *Ml, coxal process on 5th leg*, 0: absent; 1: present, small knob; 2: present, slender. A coxal process is absent in *Madabolus*, *Aulacobolus*, *Aphistogoniulus* and *Xenobolus*.

Character 12. *Ml, coxal of 5th leg, shape*, 0: cylindrical; 1: rectangular, flat. 5th coxa is cylindrical in *Madabolus*, *Aulacobolus*, *Aphistogoniulus* and *Xenobolus*.

Character 13. *Ml, coxal process on 6th leg*, 0: absent; 1: present, slender. A coxal process is absent in *Aphistogoniulus* and *Xenobolus*.

Character 14. *Ml, coxa of 6th leg, shape*, 0: cylindrical; 1: rectangular, flat. 6th coxa is cylindrical in *Madabolus*, *Aulacobolus*, *Aphistogoniulus* and *Xenobolus*.

Character 15. *Ml, coxal process on 7th leg*, 0: absent; 1: present, small knob; 2: present, large cone. A coxal process is absent in *Madabolus*, *Aulacobolus*, *Aphistogoniulus* and *Xenobolus*.

Character 16. *Coloration, stripes*, 0: no stripe, 1: single dorsal stripe; 2: three dorsal stripes. *Madabolus*, *Aulacobolus*, *Aphistogoniulus* are without a stripe, while *Xenobolus* has a single stripe.

Character 17. *Anterior gonopods (aG), coxite, mesal process in oral view*, 0: wide; 1: slender. Only in *Spiromimus* is the coxite process slender (Fig. 25A).

Character 18. *aG, telopodite, lateral triangular projection*, 0: absent; 1: small; 2: strongly developed. A lateral projection is only present in *Spiromimus* (Fig. 25A-B).

Character 19. *aG, telopodite, apically*, 0: well-rounded or with a thick process; 1: strongly elongated and slender. The telopodite is well-rounded in *Madabolus*, *Aulacobolus*, *Aphistogoniulus* while it is strongly elongated in *Xenobolus* (Fig. 25A-B).

Character 20. *aG telopodite, tip, lateral triangular retrorse projection*, 0: absent; 1 present. A retrorse projection is absent in *Madabolus*, *Aulacobolus*, *Aphistogoniulus* and *Xenobolus* (Fig. 25B).

Character 21. *aG sternal lobe*, 0: not elongated; 1: elongated, slender. The lobe is not elongated in *Madabolus*, *Aulacobolus*, *Aphistogoniulus* but slender in *Xenobolus* (Fig. 25A).

Character 22. *aG sternite, basis, oral view*, 0: without 'shoulders'; 1: forming shoulders. The sternite is without shoulders in *Aphistogoniulus* and *Xenobolus* (Fig. 25A) Shoulders are, however, present in *Madabolus* and *Aulacobolus*. Since those shoulders are distinct of similar shoulders observed in *Spiromimus*, this character is coded as non-applicable (-) in *Madabolus* and *Aulacobolus*.

Character 23. *posterior gonopods (pG)*, 0: pair shaped like a 'U'; 1: pair shaped like a turned 'C'. The pair of posterior gonopods are shaped like a U in *Madabolus*, *Aulacobolus* and *Aphistogoniulus*, like a turned C in *Xenobolus* and *Spiromimus* (Fig. 25C).

Character 24. *pG, coxite and telopodite*, 0: telopodite connected with the coxite only via membranous folds and the sperm canal; 1: telopodite fused with the coxite, but a suture is well-visible. The telopodite is only connected via membrane in *Aphistogoniulus*, fused in all other species (Fig. 25C).

Character 25. *pG, telopodite*, 0: divided into two branches, forming almost a circle; 1: divided into two branches, both branches running parallel. Both branches of posterior gonopods form a circle in *Aphistogoniulus*, and are parallel in *Xenobolus* (Fig. 25C). Since the telopodite is of a different shape in *Madabolus* and *Aulacobolus*, this character is scored as non-applicable (-).

Character 26. *pG, tip, hook*, 0: absent; 1: present, sharp; 2: present, well-rounded. A hook is absent in *Madabolus*, *Aulacobolus*, *Aphistogoniulus* and *Xenobolus*.

Character 27. *pG, basal membranous area at tip of main branch*, 0: absent; 1: present, wide projecting; 2: present, slender. A membranous area is absent in *Madabolus*, *Aulacobolus*, *Aphistogoniulus* and *Xenobolus*.

Character 28. *pG, sperm canal, discharging at*, 0: tip; 1: basal membranous area. A branch of the sperm canals discharges into the gonopod tip in *Madabolus*, *Aulacobolus*, *Aphistogoniulus* and *Xenobolus*.

Character 29. *pG, mesal branch, length*, 0: absent; 1: shorter than main branch; 2: as long as main branch; 3: longer than main branch. A mesal branch is absent in *Madabolus*, *Aulacobolus*, *Aphistogoniulus* but present and as long as the tip in *Xenobolus* (Fig. 25C).

Character 30. *pG, mesal branch, width*, 0: slender; 1: medium; 2: large. Since a mesal branch is absent, this character is non-applicable in *Madabolus*, *Aulacobolus*, *Aphistogoniulus*, medium in *Xenobolus* (Fig. 25C).

Character 31. *pG, area between mesal and main branch*, 0: empty; 1: partially filled with membranous folds; 2: completely filled with membranous folds. Since a mesal branch is absent, this character is non-applicable in *Madabolus*, *Aulacobolus*, *Aphistogoniulus*, empty in *Xenobolus* (Fig. 25C).

Character 32. *pG, area at basis of mesal branch*, 0: unmodified; 1: with rectangular segment. Because of the absence of a mesal branch is this character non-applicable in *Madabolus*, *Aulacobolus*, *Aphistogoniulus*, unmodified in *Xenobolus* (Fig. 25C).

Character 33. *pG, tip*, 0: without spines; 1: spines present. The tip is without spines in *Madabolus*, *Aulacobolus*, *Aphistogoniulus*, *Spiromimus*, but covered with numerous ones in *Xenobolus* (Fig. 25C).