ZOOTAXA

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New giant pill-millipede species from the littoral forest of Madagascar (Diplopoda, Sphaerotheriida, *Zoosphaerium*)

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Abstract

Two new species of the Malagasy sphaerotheriid genus *Zoosphaerium*, *Z. villosum* **sp. nov.**, and *Z. arborealis* **sp. nov**., are described. Characters of a shiny black new putative species of the genus *Zoosphaerium* are described and illustrated. Z*oosphaerium alluaudi* DeSaussure & Zehntner is redescribed. The characters defining the genus *Zoosphaerium* are summarized: three jointed anterior telopods, first joint with a stridulation organ termed 'harp' composed out of 1–2 stridulation ribs. Females with stridulation ribs on the subanal plate, termed 'washboard'. Operculum of female vulva constricted in the middle ('subreniform'). 6th joint of antennae of cylindrical shape. The nomenclatural history of the genus name is discussed. The intraspecific variability of many characters commonly used to delineate species within the genus *Zoosphaerium* and other members of the order Sphaerotheriida is analyzed in detail. Ontogenetic changes in the female vulva and the male telopods are discussed and illustrated.

Zwei neue Arten der Madagassischen Gattung *Zoosphaerium*, *Z. villosum* **sp. nov.** und *Z. arborealis* **sp. nov**., werden beschrieben. Merkmale einer wahrscheinlich neuen, aber hier nicht benannten Art der Gattung werden beschrieben und illustriert. Die Art Z*oosphaerium alluaudi* DeSaussure & Zehntner, 1902 wird wiederbeschrieben. Die nomenklatorische Geschichte und die Merkmale der Gattung *Zoosphaerium* werden zusammengefasst. Mitglieder der Gattung zeichnen sich durch folgende Merkmale aus: Dreigliedrige anteriore Telopoden mit einem Stridulationsorgan auf dem ersten Glied, welches aus 1–2 Stridulationsrippen besteht und als Harfe bezeichnet wird. Weibchen mit mehreren Stridulationsrippen auf der Subanalplatte, „washboard" genannt. Operculum der weiblichen Vulva am Oberrand in der Mitte eingebuchtet (subreniform). 6. Antennenglied zylindrisch geformt. Die intraspezifische Variabilität mehrerer in der Gattung *Zoosphaerium* häufig benutzter Artmerkmale wurde untersucht. Formenwandel der weiblichen Vulven und männlicher Telopoden während der Ontogenie werden beschrieben und abgebildet.

Key words: *Zoosphaerium*, Sphaerotheriida, giant pill-millipedes, Madagascar, Diplopoda, Conservation; SEM, characters, intraspecific variation

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Introduction

Completion of species discovery was identified as the first step in the endeavor to chart the biosphere on our planet in Systematics Agenda 2000 (1994). Organism groups vary greatly in their ratio of known and described species to yet-to-be-discovered species diversity. The historical bias against invertebrates and among them the millipedes is certainly in part due to technical difficulties and amount of effort required to assess their morphological characters, tasks that attracted few researchers in the past as well as in the present. Current estimates of millipede species diversity assume the existence of approximately 80,000 millipede species (Hoffman 1980). Currently described are roughly 10,000 nominal species, and since no species catalog is available, even this figure remains uncertain.

The discovery of new millipede species is thus not surprising, especially from less well-collected regions of the world. Below, we describe two new species of the Malagasy genus *Zoosphaerium* and report on the characters of a third putative new species. The specimens were acquired through extensive inventory program conducted by the Field Museum of Natural History (Dr. Steven M. Goodman) and through fieldwork by the first author during a four-week expedition to the southern littoral forest fragments around Tolagnaro (Fort Dauphin). The two newly described species are endemic to the eastern Madagascar littoral forest, one of the most threatened ecosystems of the world (Lowry *et al.* 2001; deGouvenain & Srilander 2003; Vincelette *et al.* 2003).

The Malagasy sphaerotheriid genus *Zoosphaerium* was proposed by Pocock (1895) for *Sphaerotherium neptunus*, Butler, itself based on an incompletely described specimen. Authors like DeSaussure & Zehntner (1897/1902; 1901) and Brolemann (1922), being unaware of this genus, placed Malagasy sphaerotheriid species they described either in the genus *Sphaerotherium* (e.g., *Zoosphaerium alluaudi*) or in the new subgenus *Globotherium* as Brolemann did in 1922. Brolemann designated *Sphaerotherium digitale* DeSaussure & Zehntner, 1897 as the type species of the subgenus.

In the original description of *Zoosphaerium* two attributes were mentioned as identifying characters, the cylindrical apical joints of the antennae and the special form of the operculum of the female vulva (Figs 2b, 20a). Brolemann based his genus *Globotherium* on one of these characters, the special form of the operculum. Jeekel (1999: 9) concluded that '… it seems best to use *Zoosphaerium* preliminarily for the cohesive group of Sphaerotheriidae from Madagascar," but he felt that it did not seem '…necessary at present to formally synonymize the two generic names.' However, he listed the type species of *Globotherium* under *Zoosphaerium*. For all practical purposes, this was interpreted as a formal synonymy by Enghoff (2003). One other endemic sphaerotheriid genus is known from Madagascar, the genus *Sphaeromimus*, containing currently three valid species (Wesener & Sierwald in press).

Material and Methods

Material & preparations

Specimens were preserved in 70% ethanol. All measurements are given in mm.

Dissections, illustrations. Dissections were made with a scalpel to remove the following body parts: right antennae, gnathochilarium, epipharynx, anterior telopod (paratelopod *sensu* Mauriès, 2001) and posterior telopod, 9th left leg pair in males, 2nd leg pair in females, 1st leg pair with 1st sternite, subanal plate and washboard in females. A section of the endotergum (underside of posterior margin of tergites) of the 9th segment was removed using scissors.

Drawings were made using a camera lucida mounted on a dissecting scope. Specimens were held in position using clean sand at the bottom of dissecting dishes.

SEM preparations. Specimens were dehydrated through a series of alcohols to 100% ethanol, mounted on stubs using sticky tabs and air-dried overnight. Stubs were sputter-coated with gold and observed with an AMRAY 1810 SEM. *Zoosphaerium alluaudi* was observed using a Zeiss DSM 950. Digital photos were made using a Nikon D70 digital camera mounted on a dissecting scope.

Type material of all available *Zoosphaerium* species (deposited in the collections of BM, MNHN, ZMB) was examined by the first author prior to the completion of this manuscript.

Terms

Millipedes fall squarely into the category of neglected organisms in many different aspects, beginning with extensive under-collected geographic regions around the world (Bueno-Villegas *et al.* 2004), scientific collection development (low level of identification and computerization, Sierwald & Reft 2004), lack of identification tools and non-standardized nomenclature of morphological features. Thorough comparative morphological investigations, culminating in the works by Verhoeff (e.g., 1928, 1932) and Attems (e.g., 1930), became rare in the past decades (with some noteworthy exceptions, e.g., Köhler & Alberti 1990) and were largely replaced by an alpha-taxonomic research focus. Consequently, morphological terminology in millipedes can be ambiguous and is sometimes insufficiently explained. Morphological terms relevant to the species description below are discussed in more detail by Wesener & Sierwald (in press).

Abbreviations

3 aT	three anterior teeth on mandible
12T	12th tergite
As	anal shield
aT	apical tooth
cP	central pads at the tip of the lingual lamella on gnathochilarium

cT	comb teeth
EP	exterior plate of vulva
f.	female
iL ?	intermediate lobe
IP	inner plate of vulva
LL	lingual lamella
m.	male
mp	molar plate
mpp	molar plate process
O	operculum of vulva
P	palpi of gnathochilarium
PM	locking carinae of anal shield
PL	Pleurite
S	Sternite

Museum acronyms

BM	British Museum, London
CAS	California Academy of Sciences, San Francisco
FMNH	Field Museum of Natural History, Chicago
MNHN	Muséum National d'Histoire Naturelle, Paris
SMNG	Naturkundemuseum, Görlitz
ZMB	Museum für Naturkunde der Humboldt-Universität, Berlin
ZSMC	Zoologische Staatssammlung, München

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Ramilijaona and D. Rakotondravony is gratefully acknowledged. During fieldwork QIT Madagascar provided logistics support (arranged by J. B. Ramanamanjato). Collecting permits were arranged by Dr. O.Ramilijaona (Department de Biologie Animale, Université díAntananarivo). Special thanks go to the Direction des Eaux et Forêts, Antananarivo for arranging collecting and export permits. The first author conducted the fieldwork on an expedition organized by Prof. Dr. J.U. Ganzhorn (University of Hamburg). A 20-day visit of the first author at the Muséum National díHistoire Naturelle to study the type collection and millipede undetermined material was supported by Synthesys grant FR-TAF-186. Special thanks go to Dr. J.-J. Geoffroy and L.E. Leoz for the organisation of this visit.

Results

Genus *Zoosphaerium* Pocock, 1895
Figures 1–23

Zoosphaerium Pocock, 1895: 410,
Zoosphaerium, —Chamberlin 1921, Jeekel 1971, 1974, 1999, Enghoff 2003
Globotherium Brolemann, 1922: 230, tentatively synonymized by Jeekel 1999: 9; Enghoff 2003, Table 8–19 (all *Globotherium* species assigned to *Zoosphaerium*)
Zoosphaerium: —Jeekel 1971: 29, 1974, 1999; Enghoff 2003
Type species: *Sphaerotherium neptunus* Butler, 1872. BM

DeSaussure & Zehntner (1902) mentioned that this species might represent a juvenile of *Z. hippocastanum* (Gervais, 1847; sub *Zephronia*). A study of holotypes of both species shows clearly that both are separate species (redescription in prep.). Furthermore, additional material of *Z. neptunus* is present in the recent collections from Madagascar in the California Academy of Sciences and the Field Museum of Natural History.

Other species included: 33 nominal species, see Jeekel (1999) and Enghoff (2003) for complete listing. This genus is endemic to Madagascar, the one species, *Z. insulans* (Karsch, 1881), reported from Mauritius, represents possibly an introduced species of the South African genus *Sphaerotherium* (description in prep.).

Diagnosis: Known members of the genus range from 15 to over 100 mm in body length and are the biggest known Sphaerotheriida and even the heaviest known Diplopoda. Members of the genus *Zoosphaerium* can be distinguished from other sphaerotheriids by the following combination of characters: antennae long, apical antennomere cylindrical (rounded in *Sphaeromimus*) with a variable number (4 – >60) of sensorial cones (always >35 in *Sphaeromimus*), number of cones species-specific. Tarsi in *Zoosphaerium* long (up to 4.5 times longer than wider, 2.5–3.0 times longer than wide in *Sphaeromimus*), tarsi covered with ventral spines. Anterior telopods with three joints (four in *Sphaeromimus*) distally of syncoxite (fused coxites). Males with 1–2 (3 or more in *Sphaeromimus*) more or less strong stridulatory ridges on a plate termed 'harp' located on the first joint of the anterior telopods. Females with more or less well-developed, stridulatory ridges on the

subanal plate (=hypoproct) called 'washboard' by Jeekel (1999). Operculum of vulvae in *Zoosphaerium* with a central depression (subreniform) (round and smooth in *Sphaeromimus*). This high number of characters allows easy differentiation between the two Malagasy sphaerotheriid genera, *Zoosphaerium* and *Sphaeromimus.*

Zoosphaerium alluaudi species-group

A group of Malagasy pill-millipede species shares a number of characters, identifying them as a species-group. These species are *Zoosphaerium alluaudi* (DeSaussure & Zehntner, 1897), *Z. coquerelianum* (DeSaussure & Zehntner, 1897), *Z. globulus* (DeSaussure & Zehntner, 1897), *Z. imbecillum* (DeSaussure & Zehntner, 1897), *Z. voeltzkowianum* (DeSaussure & Zehntner, 1897) and *Z. villosum* **sp. nov.** Furthermore, at least three more species awaiting description. Species of this group can be identified by a striking similarity of the shape of posterior telopods (Figs 3e, 12e). The movable finger (2nd joint) of the posterior telopods is very broad (at least 2 times longer than broad) and the concavity inside of movable finger reaches only half the length of the finger (Figs 3f, 12e). Additional shared characters are found in the endotergum (underside of the tergites) and the locking carinae of the anal shield, which are very similar in all these species (Figs 7b, 14d). Nevertheless, the species are clearly distinguishable by numerous characters: shape of anterior pair of telopods, number of sensory cones on antennae, sensory cones on gnathochilarium, shape of operculum of female vulva, body size, bristle patterns on collum and different structures on the surface of tergites (see table 1 for a summary of similar and distinctive characters). A phylogenetic analysis will be necessary to confirm if the *alluaudi*-group represents a monophyletic group among Malagasy sphaerotheriids, which will may deserve genus status. Such phylogenetic analysis is not part of this revision of species.

Zoosphaerium alluaudi (DeSaussure and Zehntner, 1897)

Figs 1–8

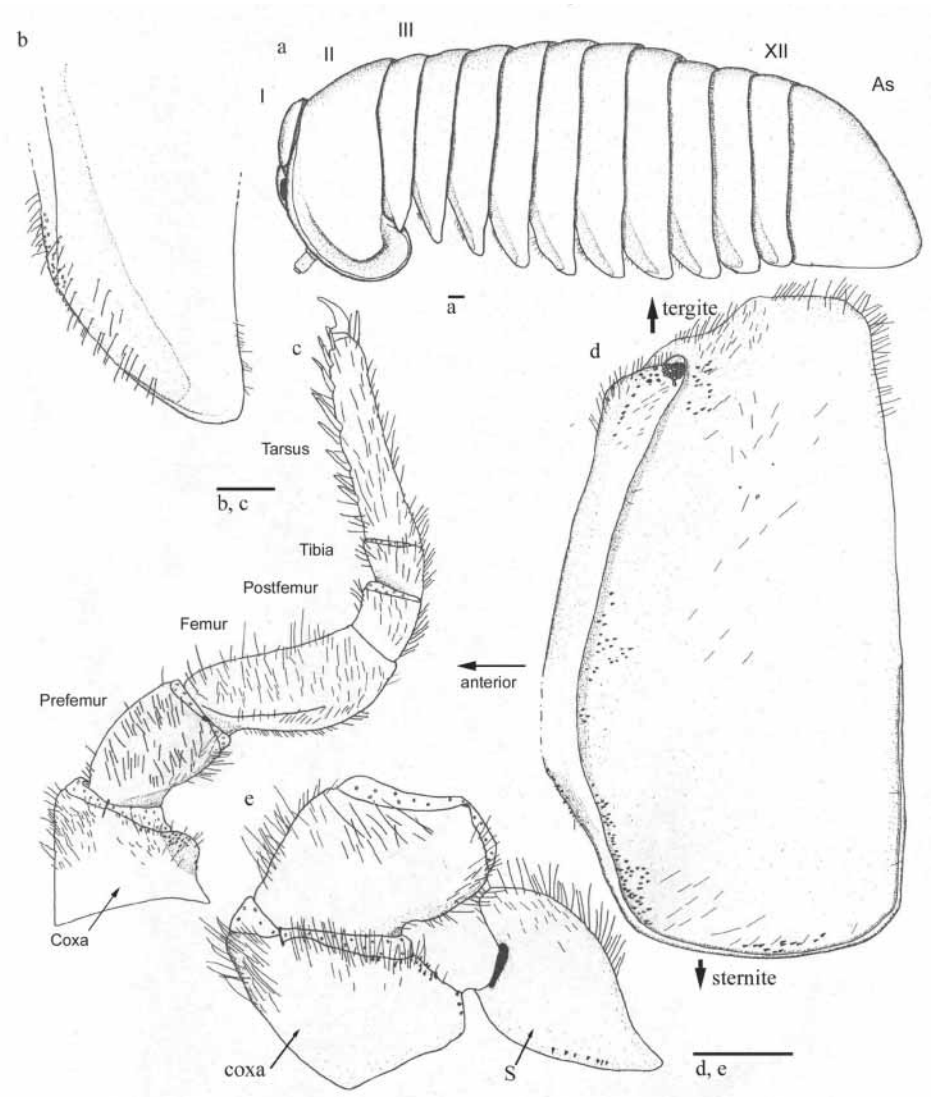
Zoosphaerium alluaudi DeSaussure and Zehntner, 1897, publication of figure
Zoosphaerium alluaudi,—DeSaussure and Zehntner 1902, publication of description
Zoosphaerium alluaudi,—Jeekel 1999 (lists species name)
Zoosphaerium alluaudi,—Enghoff 2003 (lists species name)

Lectotype: 1 m. (designated herewith), MNHN CB006. *Locus typicus*: Madagascar; Province Toliara; Fort Dauphin; leg. Ch. Alluaud.

Lectoparatypes: 2 f. (designated herewith), MNHN CB006, same data as lectotype.

Other Material: 1 m., 2 f., FMNH; 1 m., 1 f., CAS; 1 m., 1 f., ZSMC. Locality:

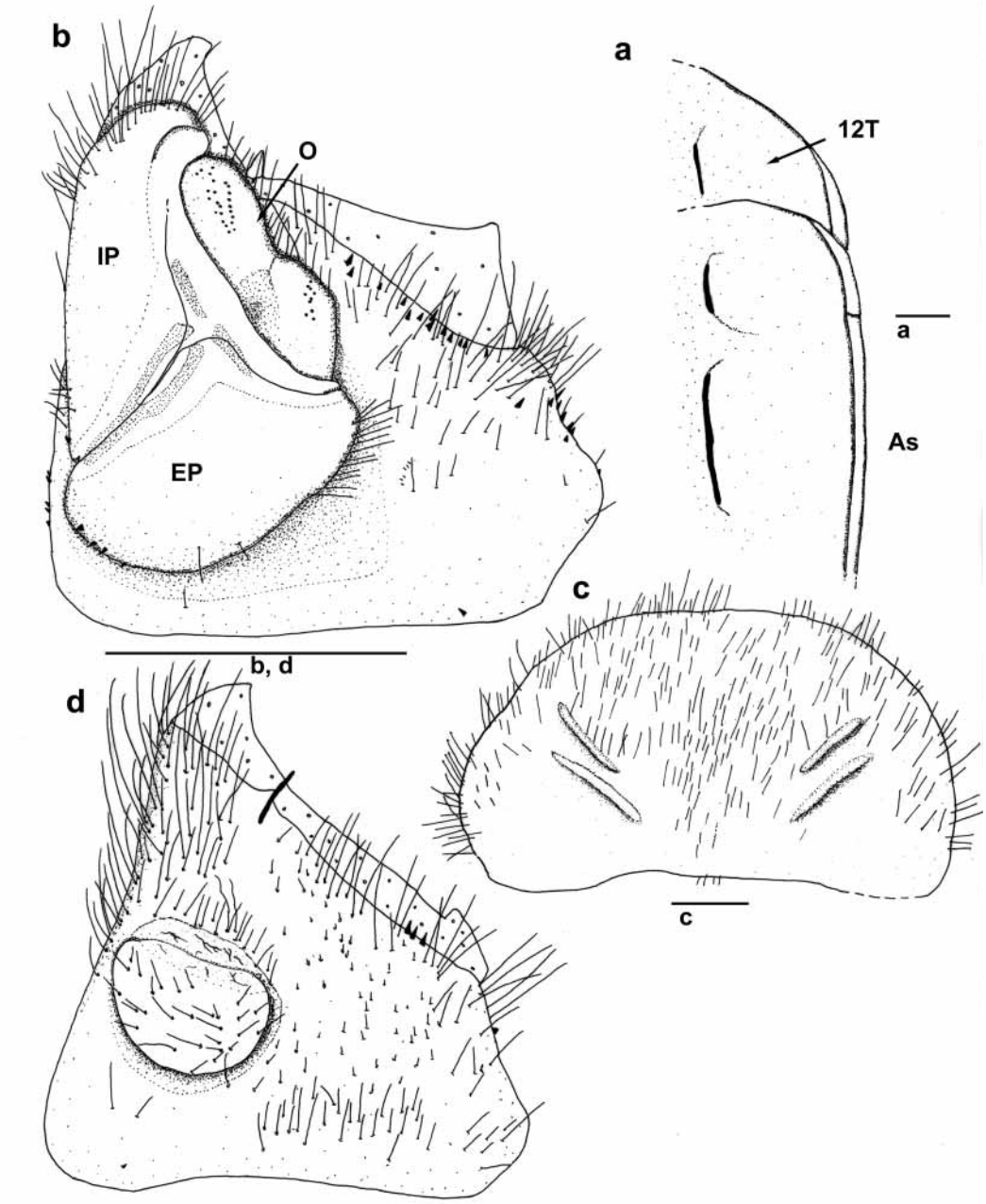
Madagascar; Province Toliara; Foret Petriky; littoral forest with dry forest elements; collected from wet leaf litter; 25°03'S 046°53'E; 17.IV.2003; leg. T. Wesener. 1 m., 3 w. same collection data. These specimens were sent to the Université de Antananarivo/ Madagascar. 1 f. (immature); Foret Petriky; littoral forest with dry forest elements; 10m NN; 25°3.72' S, 046°52.16' E; leg. 22.IX.1998; FMNH 4063



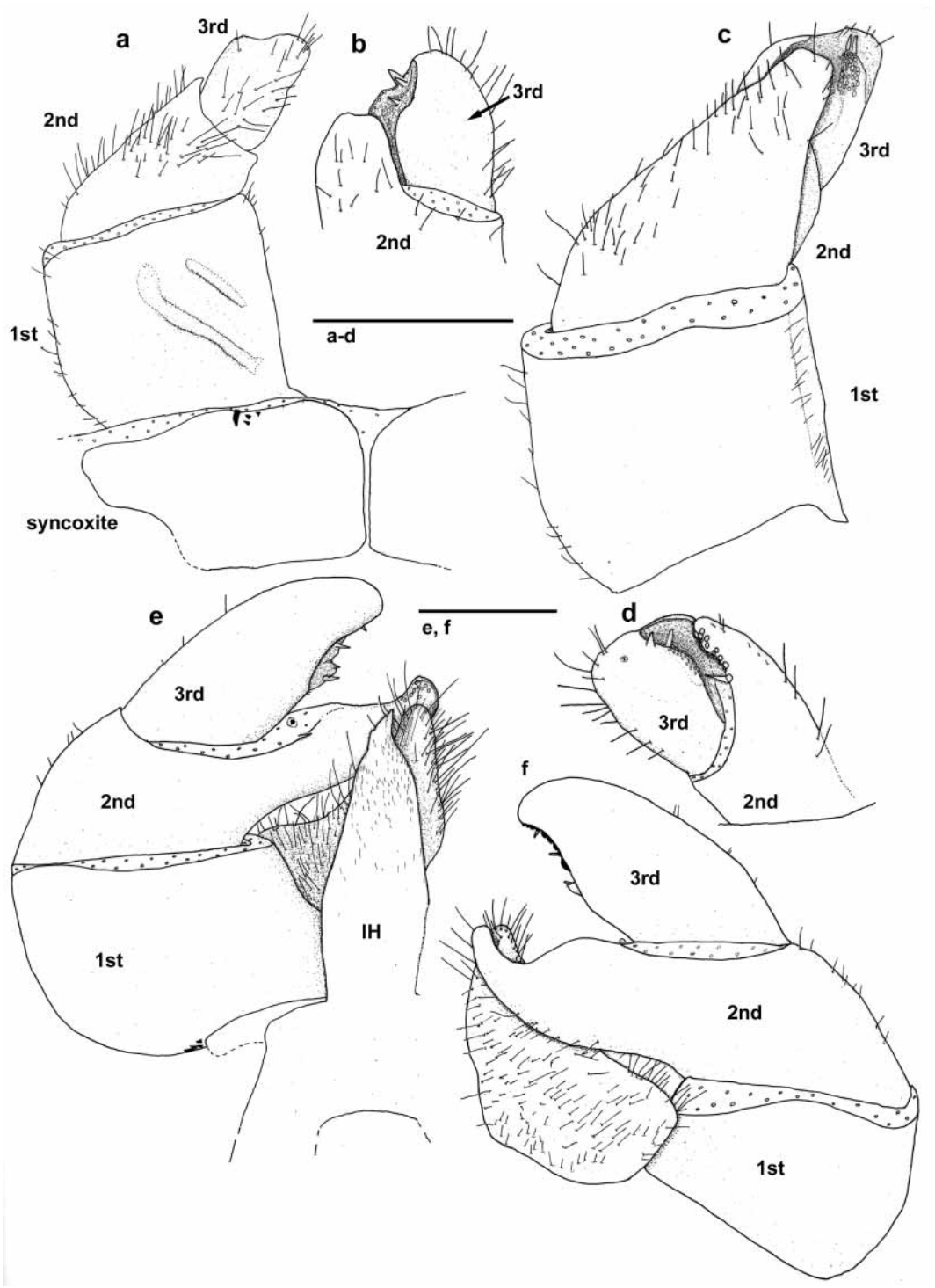
FIGURES 1 A–E: *Z. alluaudi*, male FMNH, a: habitus, b: 7th paratergite; c: 9th left leg, posterior view; d: 5th left pleurite; e: coxa and prefemur of 1st left leg with 1st left sternite, posterior view. S = sternite. Scale bars = 1 mm.

Diagnosis: Up to 43 mm long. Both sexes of equal size. Color olive-green, tergites at posterior margin brown. Surface of tergites smooth and glabrous. Joints 1–5 of antennae with sclerotized teeth. Apical joint with 4 sensorial cones. All antennal joints without a groove (Figs. 4 a–c). 3rd joint of posterior telopods (leg pair 23) remarkably thick (Figs

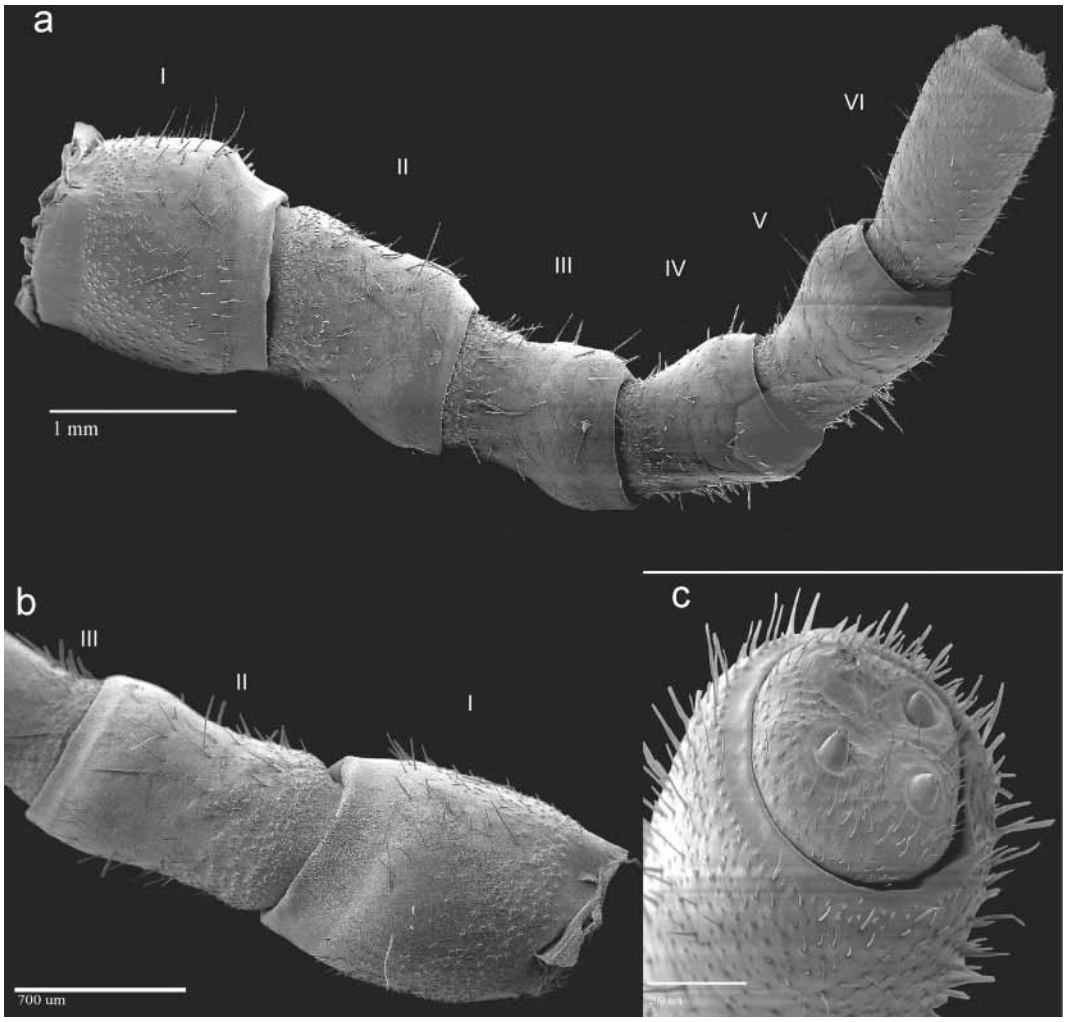
3e–f). Two stridulation ribs on each male harp and each side of female washboard (Figs 2c, 3a). Two well-developed black locking carinae on each side of the anal shield, posterior carina 2-times longer than anterior carina (Fig. 2a).



FIGURES 2 A–D: *Z. alluaudi*, a: female FMNH, left side of the anal shield (As); b: female FMNH, coxa of 2nd left leg with vulva, posterior view; c: female FMNH, subanal plate with washboard; d: male FMNH, coxa of 2nd left leg with male gonopore. As = Anal shield; O = Operculum; IP = inner plate; EP = exterior plate; 12T = 12th tergite.
Scale bars = 1 mm



FIGURES3 A–F: *Z. alluaudi*, male FMNH. a: left anterior telopod, anterior view; b: right anterior telopod, 3rd joint, inner view; c: right anterior telopod, joint 1–3, posterior view; d: right anterior telopod, joint 2–3, inner view from above; e: left posterior telopod, anterior view; f: left posterior telopod joint 1–3 with left inner horn and inner lobe, posterior view. IH = inner horn. Scale bars = 1 mm



FIGURES4 A–C: *Z. alluaudi*, female FMNH, SEM, right antennae. a: lateral view; b: joints 1 and 2; c: apical view on sensorial cones.

Similar species: Some species of the *alluaudi*-group are very similar to *Z. alluaudi*. See Table 1 for separation of these species.

Description: Body length: males (4 specimens): length up to 42.5 mm, width of thoracic shield up to 21.5, height of thoracic shield up to 11.6. Females (7 specimens): length up to 43.0, width up to 23.1, height up to 11.6. Both sexes of equal size.

Habitus: the thoracic shield is remarkably high (Fig. 1a). Tergites very smooth and hairless.

Coloration: tergites olive-green, posterior margin with a thin brown line. Head, antennae and legs also olive-greenish. Preserved specimens darken in alcohol.

Head: with numerous hairs and hair-pits especially around the labrum and lateral of eyes. Some single, long hairs around the eyes and distributed on the entire head. Posterior margin of head towards the collum with a patch of small hairs.

Antennae: shape as in the description of the genus. Length of antennomeres: 1>2>3=4=5<6; sixth antennomere longest, of cylindrical shape (Figs. 4a) with four sensory cones (Fig. 4c). First antennomere remarkably broader than the others (Fig. 4b). Sclerotized teeth at the base of antennomere 1–5, reaching apical border only on first antennomere.

Mandible: with seven rows of pectinate lamellae; number of teeth declining from apical to proximal (Figs. 8a–b). Condylus with two ridge-like impressions and one strong developed step near the apical margin (Fig. 8c).

Gnathochilarium: ventral side with many bristles, only few on the lingual lamella (Fig. 5a) (homology of gnathochilarial sclerites with those found in the helminthomorph millipedes uncertain, see Hoffman, 1976: 125). Lateral of palpi a field with four sensory cones, all four located together (Figs 5b–c). Two different types of sensory cells on central pads: long, cylinder-shaped ones with a pit in their middle and more plain ones without a pit (Figs. 6a–b). *Epipharynx:* similar shape in all known species of giant pill-millipedes (Figs 6c, 7a) (see Verhoeff, 1928, p. 841; Wesener & Sierwald, in press).

Collum: anterior margin with long, isolated hairs, standing in two rows, posterior margin with 2–4 hairs, edges with up to five long hairs. Remaining parts of collum bald.

Thoracic shield (enlarged 2nd tergite, =Brustschild *sensu* Verhoeff, 1928: 473): with few hairs in the concave lateral extension of the thoracic shield („Brustschildgruben"), especially located near the margins. Anterior marginal brim only little broader than the rest of the brim (Fig. 1a).

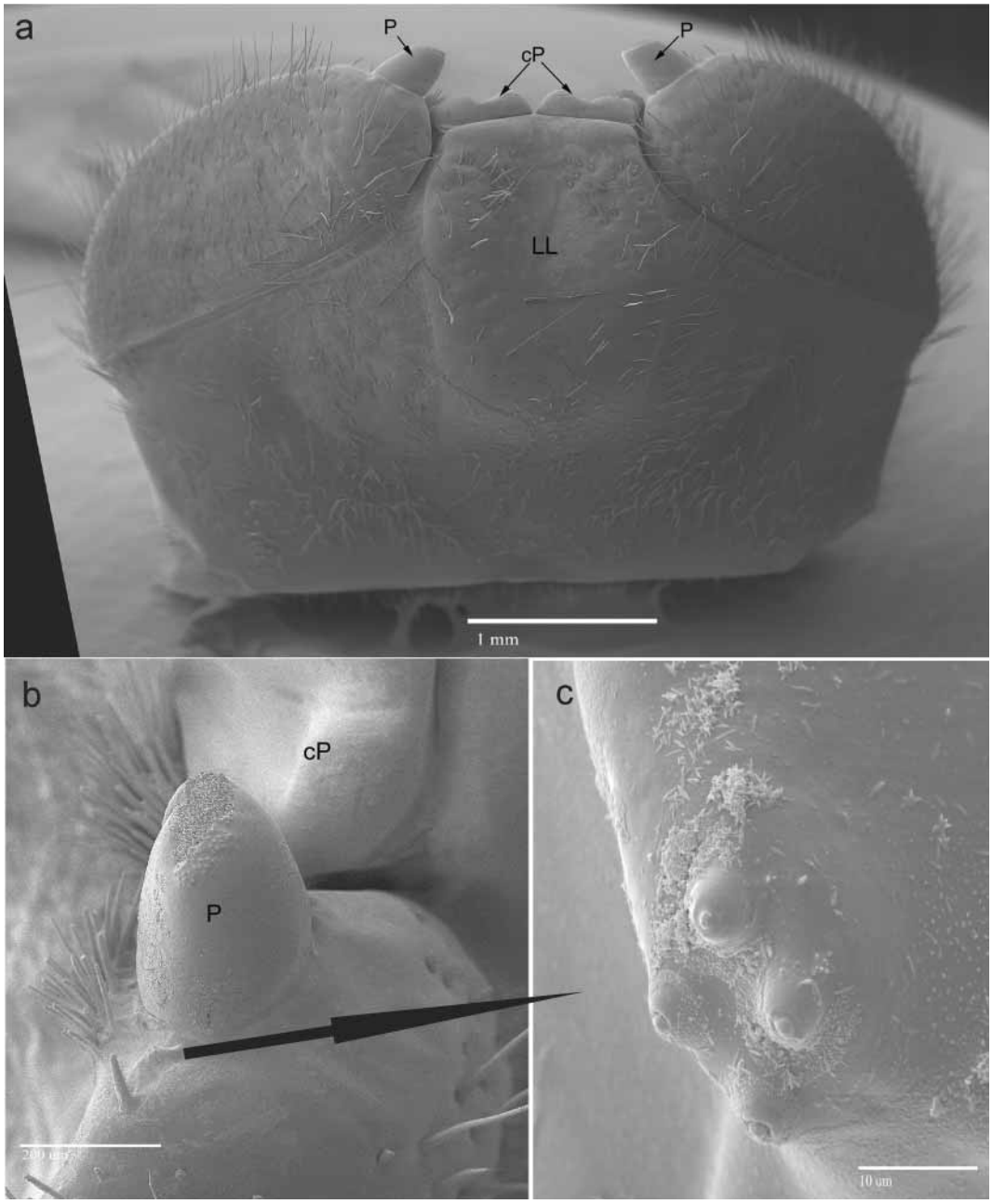
Tergites: anterior paratergite depressions (called ëSeitenlappení by Verhoeff, 1928: 385) of tergites 3–12 with few, isolated hairs, on the anterior margin a few ribs and some sclerotized spots (Fig. 1b). Tips of the posterior margins of paratergites slightly projecting posteriorly. Tergites smooth and glabrous, except for the anterior paratergite depression.

Endotergum: with one, rarely two rows of marginal bristles. Internal section with short spines and very few, isolated bristles. Between marginal ridge and internal area one row of rounded nodules. Marginal ridge lightly undulating towards the nodules (Fig. 7b). Bristles scaly (Fig. 7c).

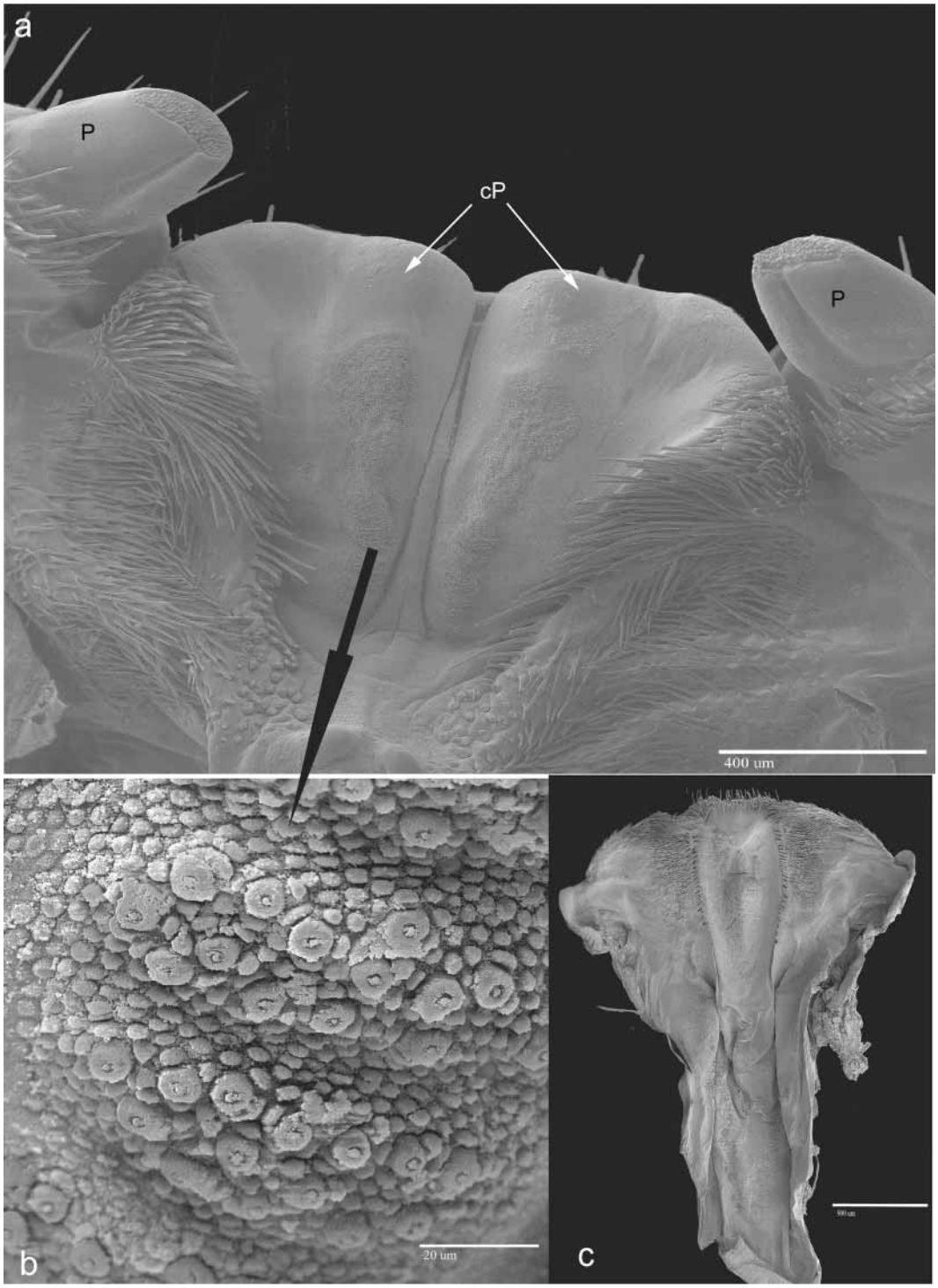
Anal shield: rounded, neither bell-shaped nor tapered (Fig. 1a). In contrast to the glabrous tergites in both sexes, covered with many small (sensory?) hairs. Ventral side carries two black locking carinae on both sides, anterior one similar to those of tergites, posterior carinae three times longer than anterior one, posteriorly closer to the margin than anteriorly. Locking carinae separated from each other by a distance equal to the length of the shorter carina. Distinct suture present in the space between both carinae representing the border of a 13th tergite fused with the anal shield. Where the suture reaches the margin of the anal shield, a small, distinct triangular invagination is visible (Fig. 2a).

Legs: tarsi of first and second pair of legs with only seven ventral spines, weakly curved claws and without apical spine. Tarsi of legs 3–21 with curved claws, 11–13 ventral spines and one apical spine. 9th leg pair with no coxal lobe, but a small, well-

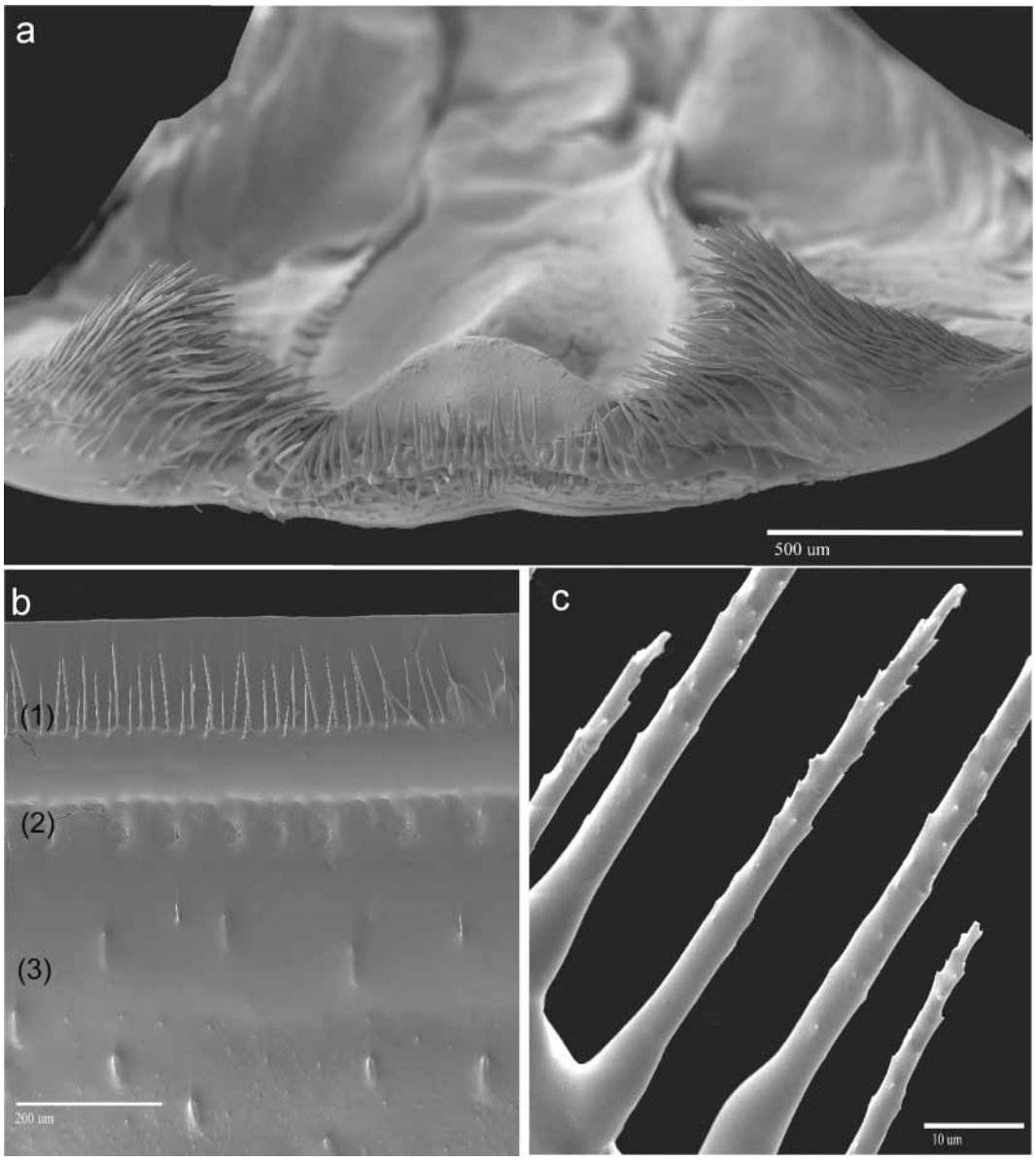
rounded outer rim covered with many small, black triangular spines (Fig. 1c) on coxa. Coxae of all legs at the inside margin covered with a patch of long hairs, the following leg joints with some isolated, long hairs at the inner margin. Femora of all legs with a crenulated ridge (Fig. 1c).



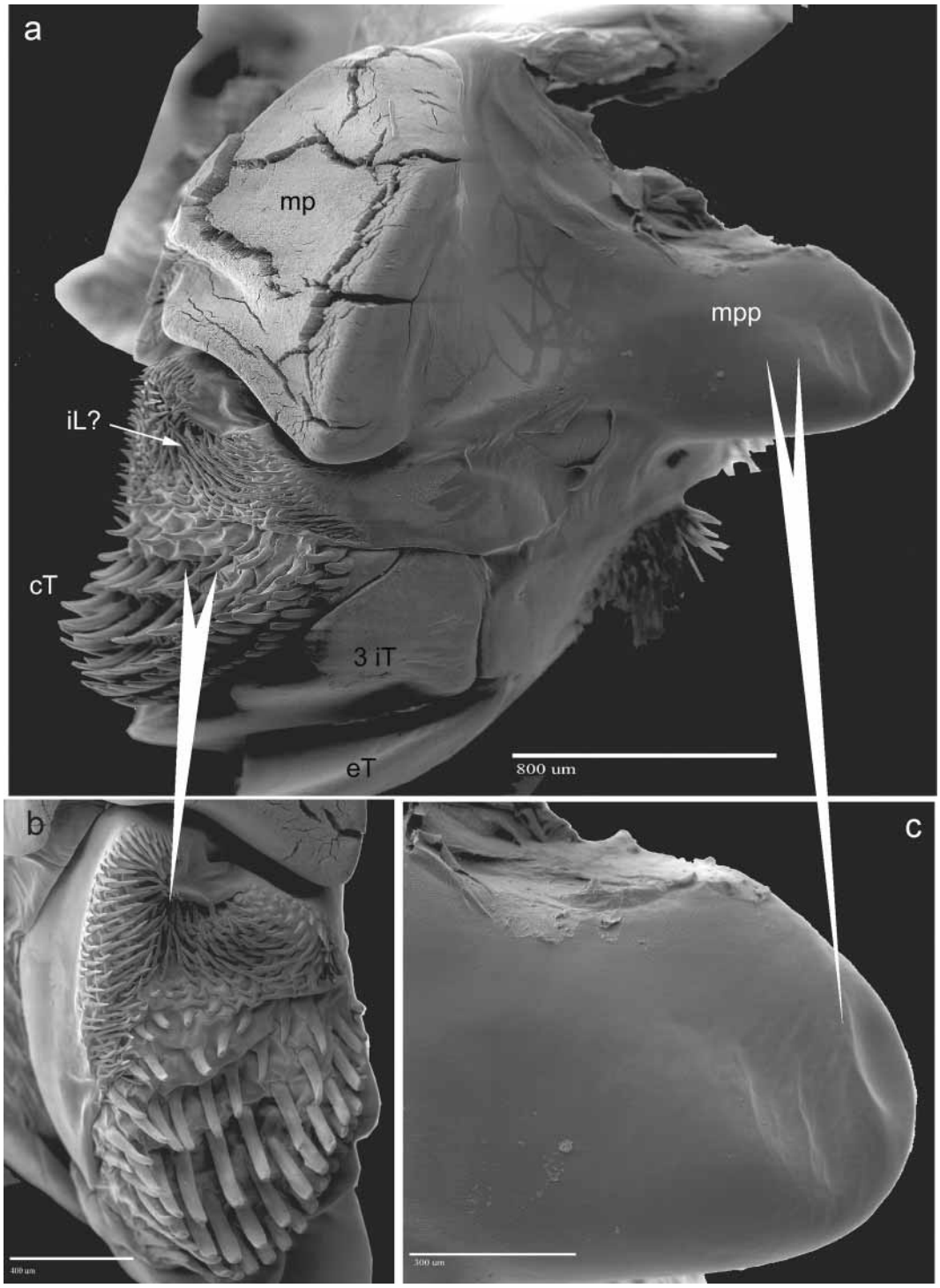
FIGURES 5 A–C: *Z. alluaudi*, female FMNH, SEM, gnathochilarium. a: ventral view; b: right palpi, arrow = field of sensorial cones; c: field of sensorial cones. cP = central pads, LL = lingual lamella, P = palpus.



FIGURES 6 A–C: *Z. alluaudi*, female FMNH, SEM. a: gnathochilarium, central pads; b: gnathochilarium, sensorial cones on central pads; c: epipharynx, ventral view. cP = central pads, P = palpus.



FIGURES 7 A–C: *Z. alluaudi*, female FMNH, SEM. a: epipharynx, distal; b: endotergum, (1) = marginal ridge with external row of marginal bristles, (2) = band of flattened nodules , (3) = internal area; c: marginal bristle of endotergum.



FIGURES 8 A–C: *Z. alluaudi*, female FMNH, SEM, left mandible. a: overview; b: pectinate lamella; c: condylus. 3 aT = three anterior teeth, aT = apical tooth, cT = comb teeth, iL ? = intermediate lobe, mp = molar plate, mpp = molar plate process.

Sternite: First sternite lobe long, reaching above the apical edge of the coxae of first leg pair, covered sparsely with hairs and curved towards the coxa (Fig. 1e). Anterior smooth covered with some isolated, long hairs. Posterior margin hairless, but with one row of small, triangular black spines (Fig. 1e). Sternites three and beyond with a spine-like process which reaches almost the stigma opening of the more anterior sternite.

Female sexual characters: second leg pair without coxal lobe, but on exterior margin with some short, triangular black spines. Subanal plate with washboard, consisting of well-developed stridulation ribs, two ribs on each side. Stridulation ribs symmetrical and short, ending just above the middle line of the subanal plate (Fig. 2c).

Vulvae large, covering more than 2/3 of the coxa. Operculum short, ending before the apical edge of coxae. Apical margin of operculum constricted in the middle (subreniform) with two rounded lateral tips. Space between the tips invaginated. Invagination dividing operculum in two nearly same-sized parts; operculum without a median suture. Interior tip of operculum reaching higher than the exterior tip. Basal margin of operculum straight.

Exterior and inner plates (EP, IP) of vulva below the operculum surrounding the basal margin of the operculum. Inner plate long and broad, reaching almost as high as the operculum. Exterior plate not as long as the inner one, reaching only to first quarter of the operculum. Posterior margins of both inner and exterior plate with short, triangular black spines (Fig. 2b). Cyphopod sclerites consisting of two triangular apical sclerites and a much larger third sclerite formed like a tuning-fork, all visible as dark structures near the suture of the vulva between inner and exterior plate (Fig. 2b).

Male sexual characters: second leg pair without coxal lobe, but on exterior margin with some short, triangular black spines and covered with many hairs. Male gonopore (located at inside margin of 2nd coxae, called penes and pseudopenes by other authors, see Wesener & Sierwald in press) covered with a big, sclerotized, undivided and rounded plate. Apical part of plate membranous (Fig. 2d). Anal shield without any invagination or other sexual dimorphism.

Anterior telopods: syncoxite of anterior telopods on both sides without hairs. First joint with a stridulation harp and two stridulation ribs. Inner ridge short, reaching only 1/3 of the length of the lateral one. Lateral ridge long, beginning at the basal margin of the first joint and ending just at its apical margin (Fig. 3a). Posterior side of the first joint inside with a longitudinal depression (Fig. 3c). Margins of depression laterally with one row of hairs, otherwise surface hairless. Second joint on posterior side rectangular with rounded edges (Figs 3b–d). Point of process reaching 2/3 of the height of third joint. Towards the third joint with sclerotized spots and one spine (Fig. 3d). Apical margin of third joint well rounded, reaching inside higher than outside. Inner side arched strongly towards the process of the second joint, on the inner margin of the invagination with numerous sclerotized spots and three spines, juxtaposed the sclerotized structures of the second joints process (Figs 3b, 3d).

Posterior telopods: movable finger (3rd joint) of chela enlarged. Invagination towards the immovable process of the second joint with three non-sclerotized spines, on posterior side with one short row of crenulated teeth. Immovable digit (process of 2nd joint) with slightly curved tip. Anterior side basally with one spine, apically with sclerotized spots juxtaposed the invagination of the third joint. Chelae only at margins with a few isolated hairs, on rest of surface hairs absent. First joint basally with some small, black triangular spines (Figs 3e–f). Inner horns (IH) of syncoxite (=coxal horn sensu Van Den Spiegel, 2002 = "Hörner des Syncoxits" Verhoeff) with a pointed tip (Fig. 3e).

Distribution & Ecology: This species appears to be endemic in the littoral forest fragment of Petriky. This forest shows a transition between southern spiny forest and the more northern hylaea-forest, making the ecological condition unique; its plant species composition is unique when compared to other Malagasy littoral forests (Dumetz 1999). *Zoosphaerium alluaudi* was the only sphaerotheriid species collected in this area. At the beginning of the dry season, the leaf litter was rather thick (30 cm) and dry. Moist leaf litter accumulated under a few isolated trees. *Zoosphaerium alluaudi* was collected only from the moist leaf litter. No juveniles were collected. One female contained bright orange to yellowish eggs, measuring about 1 mm in diameter. After dissection of female, 1539 eggs were counted, a few eggs (not counted) were lost during dissection.

Conservation: The conservation of this species is directly linked to the future of the forest Petriky. This forest is the largest still existing fragment of the southern littoral forest in Madagascar. Unfortunately, this forest is still damaged, patches of trees are separated from each other, sometimes even single trees are separated from each other by sandy areas without vegetation. Moist leaf litter was found only under trees. The forest is under significant human pressure through wood removal and grazing animals from surrounding fishing villages. The anticipated, extensive mining project in this area (Vincelette *et al.* 2003) will result in a complete destruction of the remaining forest of Petriky, preserving only a very small area of 60 ha of indigenous forest. Hence, *Z. alluaudi* is a highly endangered species, which will not survive the next ten years, if current human activities continue and no conservation efforts are made.

Intraspecific variation: Body length of females is not significant higher than those of males. The number of stridulation ribs on the female washboard correlates with the size of female, but is constant in mature ones. Surprisingly, even very small males (20 mm body length) show fully developed telopods.

***Zoosphaerium villosum* sp. nov**
Figs 9–16

Holotype: 1 m, coll. Madagascar, Province Toamasina, Toamasina, Station Forestiére de Tampolo; 3.–16.IV.1996; relatively undisturbed littoral forest; 17°17.2' S 49°24.5' E; 10 m NN; leg. S. Goodman; FMMC 3958.

Paratypes: 1 m. FMMC 8247; 1 f. FMMC 8248, 1 m. CAS, same coll. data.

Additional material: 1m. FMMC 7828; 4 m. FMMC 7827, same collection data as type-material. 1 m., 3f. coll. Côte Sud-Ouest, leg. Grandidier, MNHN CB016

Diagnosis: The shape of the posterior telopods easily identifies this species as another member of the *alluaudi*-species group. *Zoosphaerium villosum* **sp. nov.** features unique characters**,** which separate this species unambiguously from others in the group. Tergites and anal shield are densely covered with short hairs, each hair inserting in a small pit (Fig. 9b). Harp on male telopods with two stridulation ridges and the tips of the 3rd joint of anterior telopods rounded (Figs. 12a–d). Furthermore, the shape of the first sternite and shape of the male gonopore differs in *Z. villosum* from other species of the genus (Figs. 10a, 13a).

Similar species: See Table 1 for a comparison with closely related species.

Description: Males (4 specimens): length: 43.2–64.6, width of thoracic shield: 21.1–33.6, height of thoracic shield 12.2–17.4. Females (4 specimens): length: 43.3–57.9, width: 24.25–30.25, height: 12.2–16.1. Body length of males is not significantly greater than those of females.

Coloration: The body is dirty blackish green. Posterior margin of the tergites with a thin dark-brown line. Collum and head dark green. Head, ocelli, antennae and legs green. In alcohol-preserved animals, pieces of the dark green pigment layer break off and brown body tissues become visible.

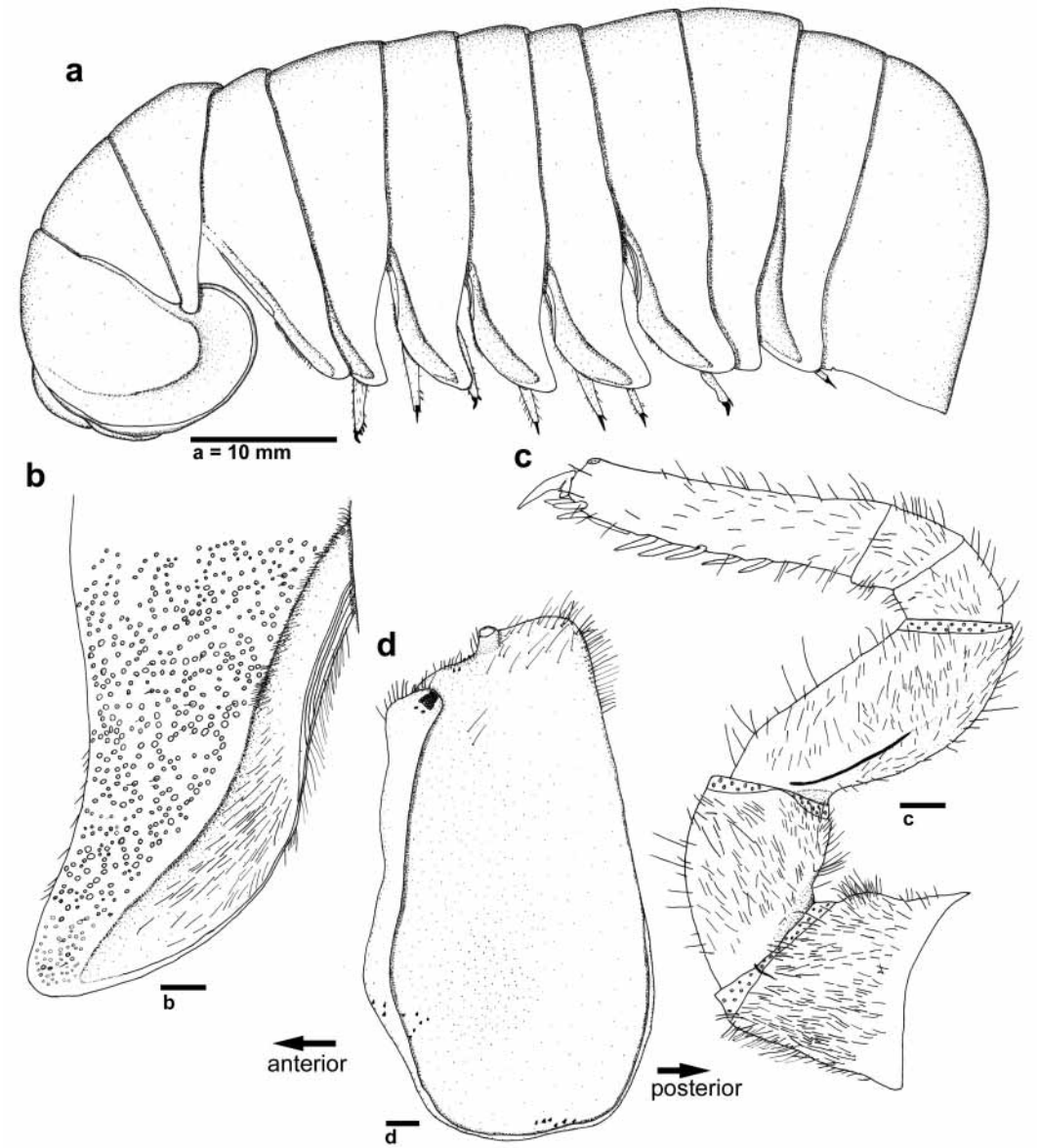
Head: with some long hairs and numerous setiferous pits mostly around the clypeus and lateral of the eyes. Some long, isolated hairs around the eyes and more distributed on the entire head. Posterior margin of head towards collum with a patch of very short hairs. Edges of antennal socket each with little crenulated teeth and a single short spine.

Antennae: overall shape as in genus description. Very long, with thin, long, cylindrical joints; length of antennomeres: 1>2>3>4=5<6. 6th antennomere long (Fig. 14a), with 35 (25) to 45 sensory cones (Fig. 14c). 1st and 2nd joints with small crenulated teeth and one invagination each; 3rd joint with some small crenulated teeth at base (Fig. 14b).

Mandible: molar plate process of mandible with a single, sharp furrow near the apical end (Fig. 16a); 7 pectinate lamellae with long and thin teeth, number of teeth declining proximally (Fig. 16b).

Gnathochilarium: posterior surface with many hairs but fewer hairs on the lingual lamella (Fig. 15a). Lateral of palpi is a pit with three sensorial cones (Fig. 15c). *Epipharynx* shaped like in other sphaerotheriid species (Fig. 15b).

Collum: anterior margin with three rows of isolated hairs; rest of collum, especially posterior margin with only few isolated hairs. *Thoracic shield:* A few hairs in the concave lateral extension of the thoracic shield, which are remarkably large in this species. Marginal brim very thin, only anteriorly a little broader (Fig. 9a). Underside of thoracic shield with two rounded impressions at the posterior edges.

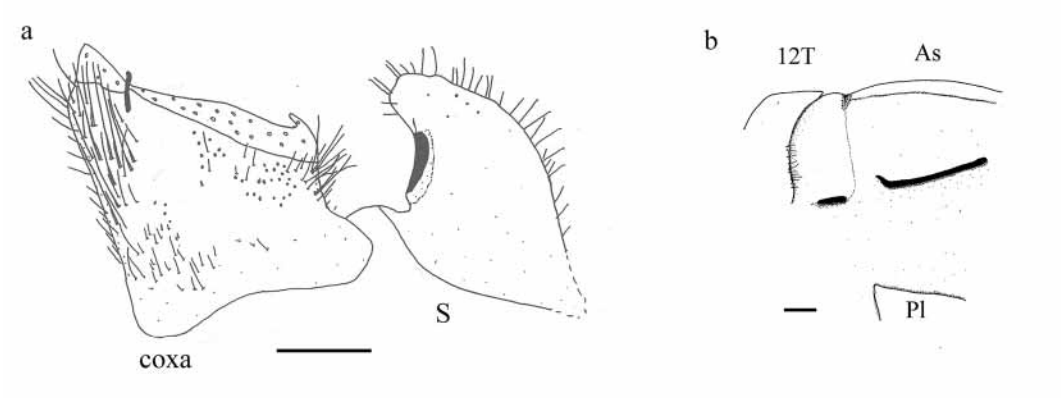


FIGURES 9 A–D *Z. villosum* **sp. nov.**, male holotype. a: habitus; b: 7th paratergite, detail; c: left 9th leg, posterior view; d: 5th left pleurite. Scale bars = 1 mm

Tergites: anterior paratergite depression densely covered with hairs and several ridges. Tips of paratergites project posteriorly. Tergites covered with numerous small pits (Fig. 9b), some of them with a single hair inserting at the center, giving the body in some specimens a furry look. Posterior margins of tergites with a visible fringe of short hairs, originating from the underside of posterior margin of tergites, the endotergum.

Endotergum: features two rows of marginal bristles. Marginal ridge regularly rounded; proximal of marginal ridge with a distinct band of cuticular patterns (Fig. 14d). Inner area covered with numerous hairs and spines. Bristles of endotergum scaly.

Anal shield: rounded, neither bell-shaped nor tapered. Anal shield more densely covered with hairs than tergites. Ventral surface carries two black locking carinae on each side, locking carinae sloping weakly towards the posterior end of the anal shield (Fig. 10b: 12T = 12th tergite; As = anal shield; PL = pleurite), posterior one up to three times longer than the anterior one. Locking carinae separated from each other by a distance equal to the length of the shorter carina. Distinct suture present between both carinae. Where the suture reaches the margin of the anal shield, a small, distinct triangular invagination is visible



FIGURES 10 A–B: *Z. villosum* **sp. nov.**, male holotype. a: coxa of 1st pair of legs with 1st left sternite, posterior view; b: left closing margins of anal shield. 12T = 12th tergite, As = anal shield, PL = pleurite, S = sternite, Scale bars = 1 mm

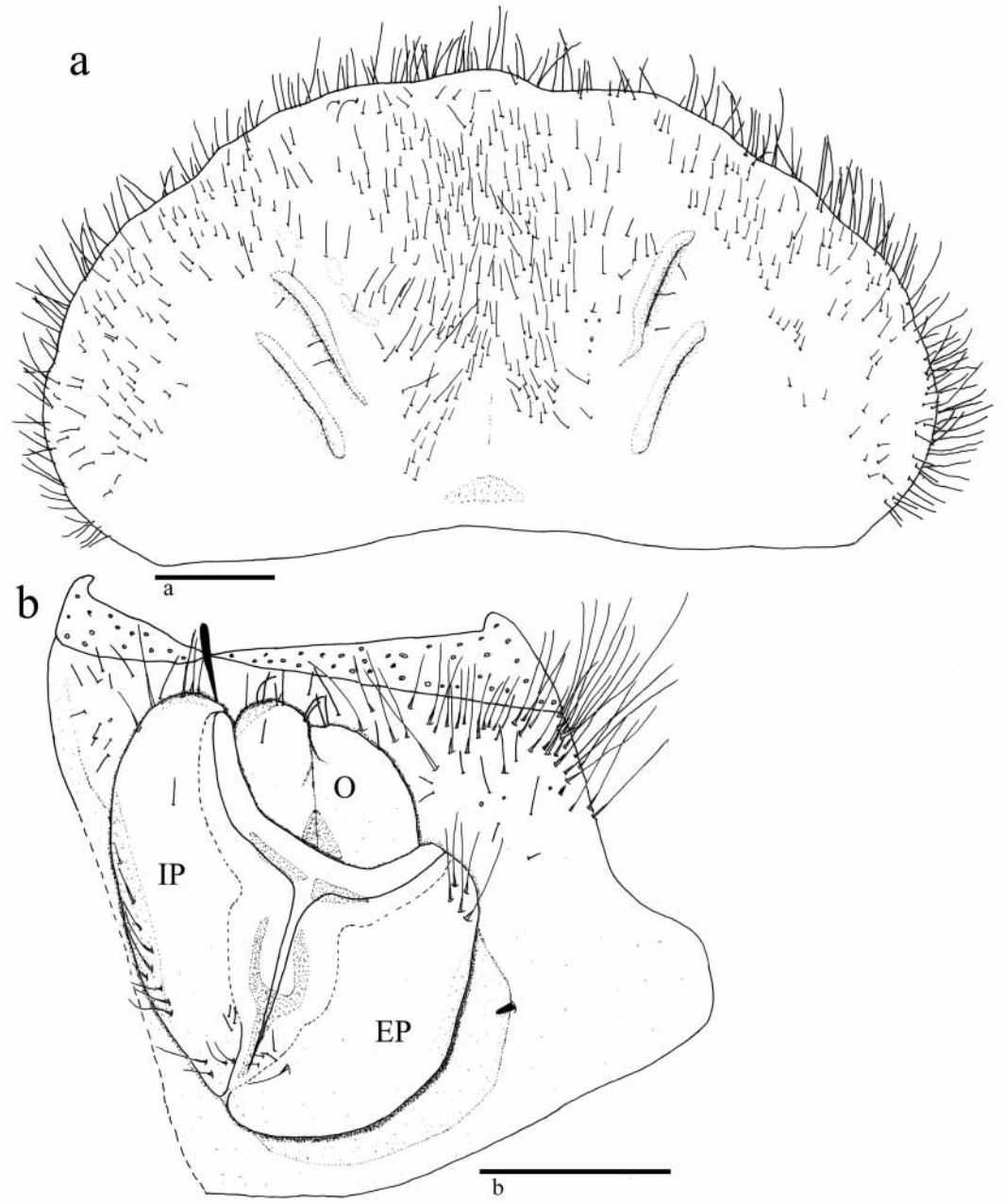
Legs: tarsi of first leg pair with only three to six, second pair with only five to eight ventral spines, claws only weakly curved and without an apical spine. Tarsi of the following legs with 8–11 ventral spines, curved claws and one apical spine. Coxae of all legs covered at the inside margin with a patch of long hairs, the following leg joints with some isolated, long hairs as well. 9th pair of legs without coxal lobes and spines. All legs feature a crenulated ridge on the femora (Fig. 9c).

Sternite: First sternite with a sclerotized ledge (Fig. 10a) and long lobe, the latter reaching towards the beginning of prefemur and curved towards the leg pair. Anterior margin irregularly rounded with one small invagination near the tip, covered with long, isolated hairs. Posterior part of the sternite bald (Fig. 10a: S = sternite). Sternites three and beyond with a spine like process which reaches almost the stigma opening of the next anterior sternite.

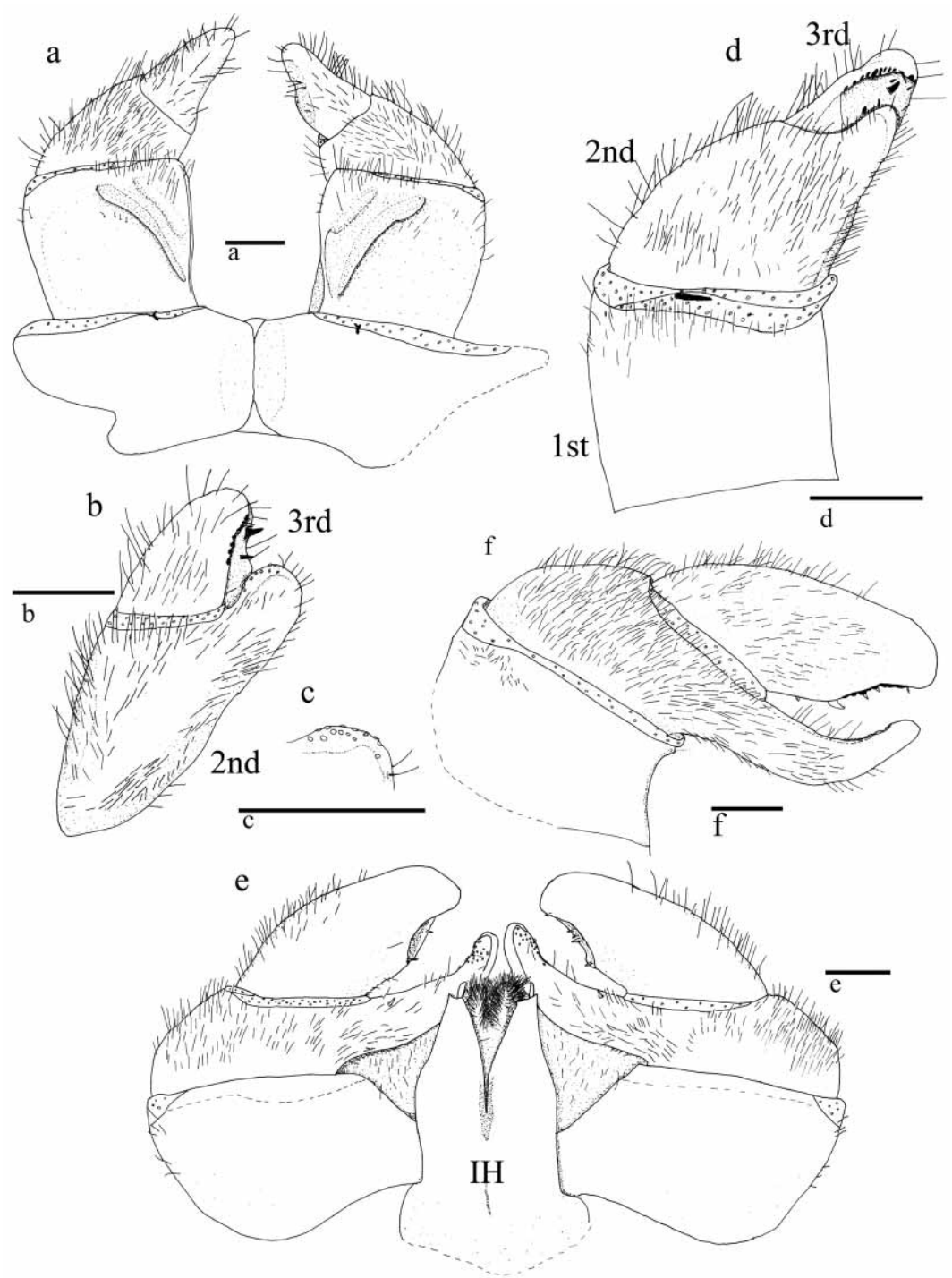
Female sexual characters: 2nd pair of legs without coxal lobe. Operculum (Fig. 11b: O) of vulvae small, not reaching upper margin of coxa. Apical margin constricted in the middle (= subreniform), lower margin straight. Exterior and interior plate (Fig. 11b: EP, IP) of vulvae long and broad, its anterior margin reaching around the base of the operculum; interior plate about 2/3 the size of the operculum, exterior plate only 1/3 the

size of the operculum. Cyphopod sclerites consisting of two triangular apical sclerites and a much larger third sclerite shaped like a tuning-fork; all visible as dark structures near the suture of the vulva between inner and exterior plates (Fig. 11b).

Subanal plate rounded, center of anterior margin slightly excavated. The washboard with two small, weakly developed, symmetrical stridulation ribs, ending well in front of anterior margin (Fig. 11a).



FIGURES 11 A–B: *Z. villosum* **sp. nov.**, female paratype. a: subanal plate with washboard; b:coxa of 2nd left leg pair with vulva. EP = exterior plate, IP = inner plate, O = operculum. Scale bars = 1 mm



FIGURES 12 A–F: *Z. villosum* **sp. nov.**, male holotype. a: anterior telopods, anterior view; b: inner view of 2–3 joint of right anterior telopod; c: detail of tip of process of 2nd joint of right anterior telopod, inner view; d: right anterior telopod, posterior view; e: posterior pair of telopods, anterior view; f: right posterior telopod, posterior view. IH = inner horns.
Scale bars = 1 mm

Male sexual characters: male gonopore covered by a single large, broad plate. Sclerotized part of plate with a few long hairs. Second pair of legs without coxal lobe (Fig. 13a).

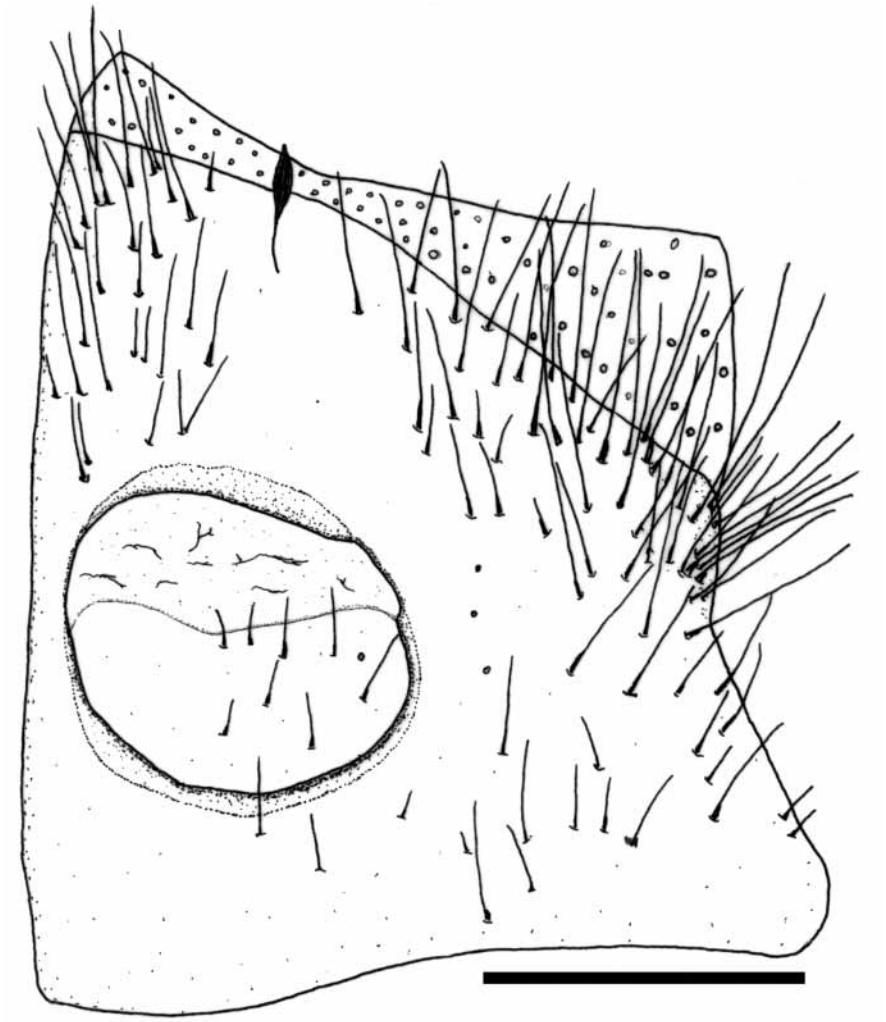
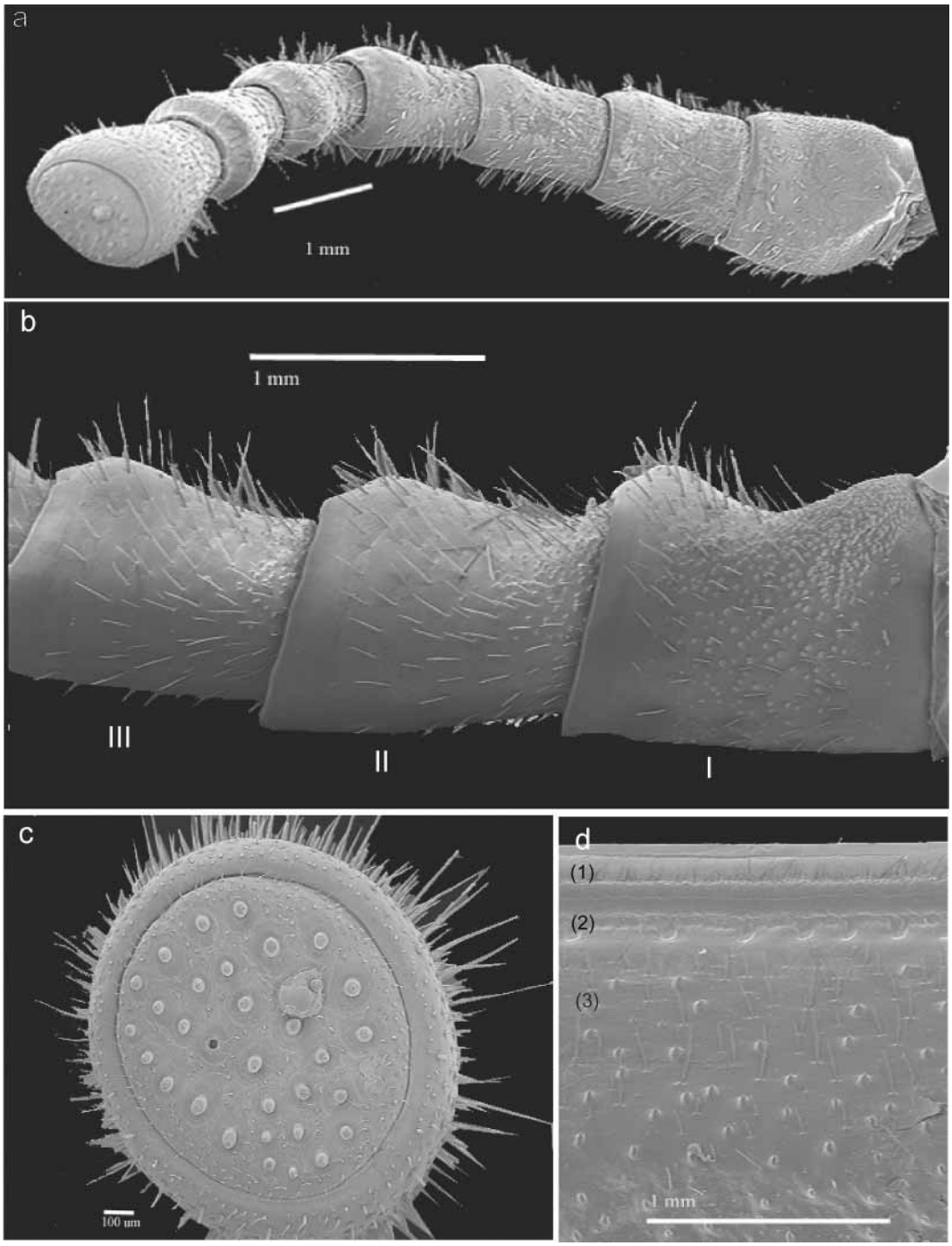


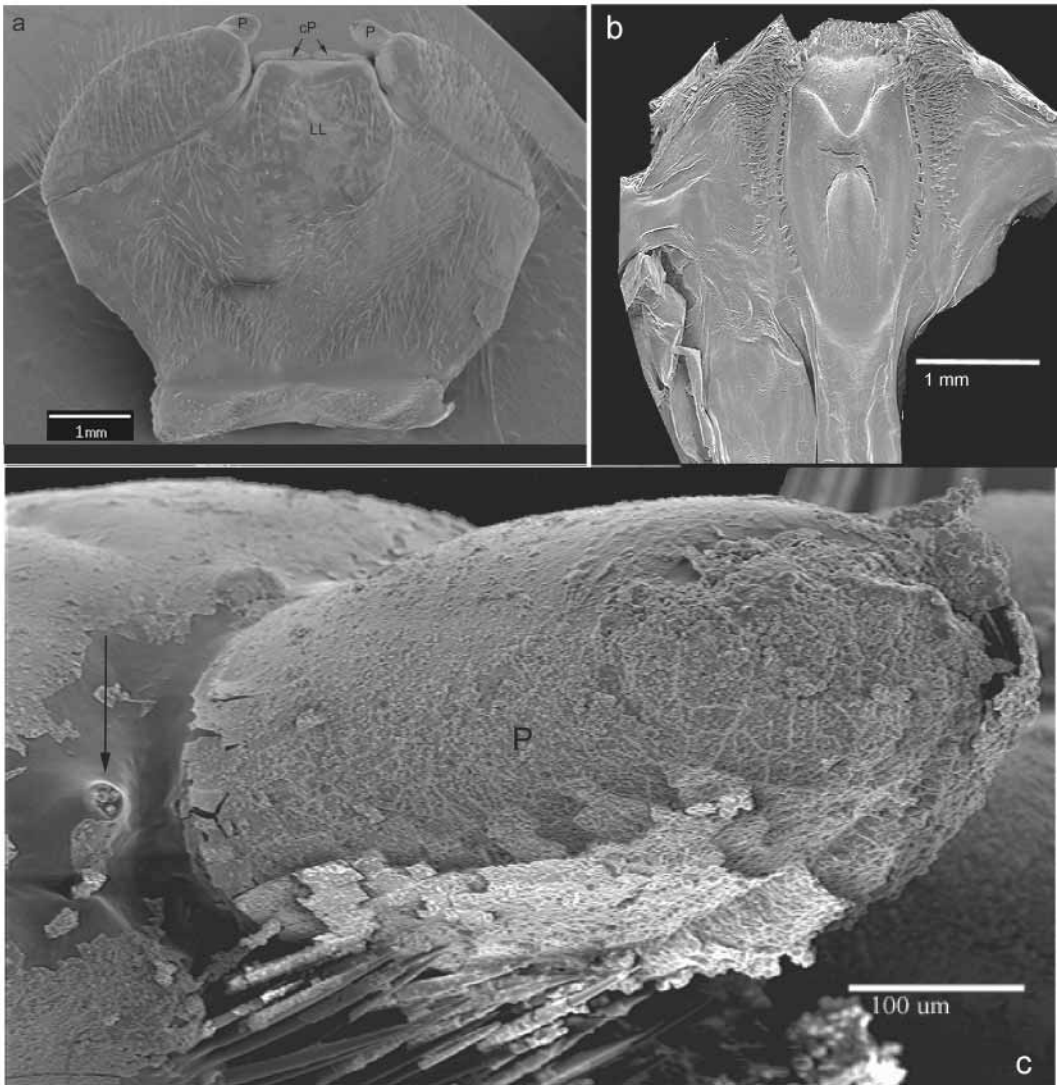
FIGURE 13 a. *villosum* **sp. nov.**, male holotype. a: left coxa of 2nd pair of legs with male gonopore, posterior view. Scale bars = 1 mm

Anterior telopods: with three joints distally of syncoxite, inner margin of first joint with 'harp' consisting of one long and one short stridulation ridge, long ridge very strong and regular, curved centrally towards middle of the body, beginning on the posterior margin and ending just in front of the anterior margin of first joint (Fig. 12a). Posterior side of second telopod joint at the inside with a projection, which reaches up to half the length of the third joint (Fig. 12b). The apical part features round sclerotized spots (Fig. 12c). The third joint long and well-rounded, tapering distally, posterior side with large membranous invagination covered with few sclerotized spines, one of them

extraordinarily big. Border of invagination with up to 11 sclerotized black teeth positioned juxtaposed the round sclerotized spots of the second joint (Figs 12b–d).



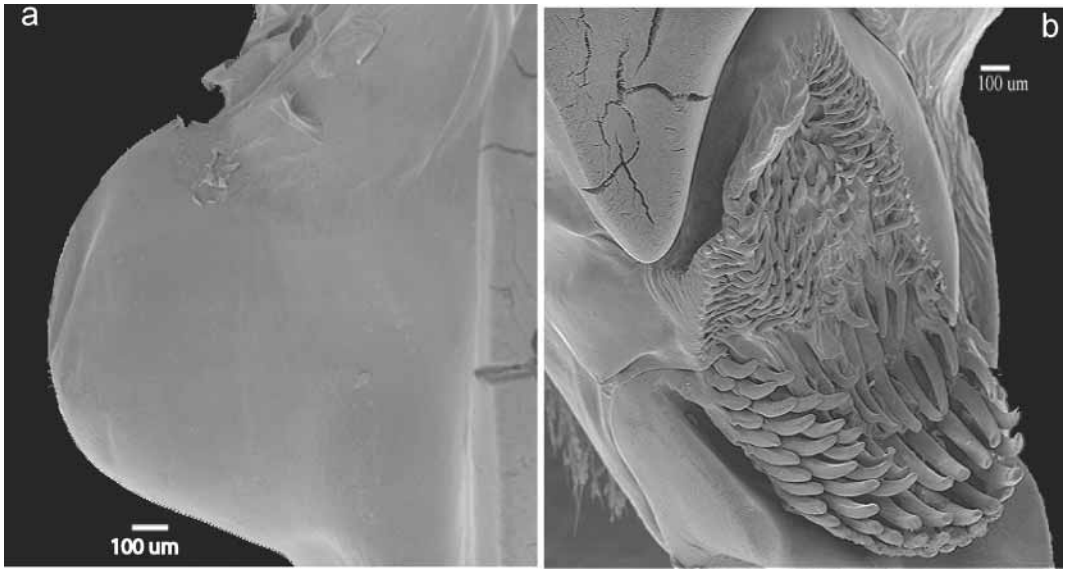
FIGURES 14 A–D: *Z. villosum* **sp. nov.**, male paratype, SEM. a: lateral view on antennae; b: lateral view on antennae joints 1–3; c: apical view on sensorial cones of antennae; d: endotergum, (1) = marginal ridge with external row of marginal bristles, (2) = band of flattened nodules , (3) = internal area.



FIGURES 15 A–C: *Z. villosum* **sp. nov.**, male paratype, SEM. a: ventral view of gnathochilarium; b: ventral view of epipharynx; c: right palp of gnathochilarium with sensorial cones, dorsal view, arrow = field of sensorial cones, cP = central pads, LL = lingual lamella, P = palpus.

Posterior telopods: chela of very specific shape. Third joint very broad, the membranous concavity extending over only a part of the anterior margin. Four non-sclerotized spines, basal spine big, two smaller spines in the middle and a fourth spine on the distal end of the membranous invagination. Posterior side of third joint with oblique sclerotized teeth restricted to the membranous invagination. Immovable finger of second joint thin, but as long as movable finger. Inside of immovable finger invaginated, with round sclerotized knobs juxtaposed the tip of the membranous field of the movable finger (third joint). Remarkable is one short spine on the anterior side near the base of the

immovable digit. Base of second and third joint densely covered with hairs, apically almost hairless. Syncoxite and first joint almost hairless. Tips of inner horns of telopod coxa with terminal portion of inner lobe bent posteriorly more than 25 degree. Subanal lobe densely covered with hairs (Figs 12e–f).



FIGURES 16 A–B: *Z. villosum* **sp. nov.**, male paratype, SEM. a: left mandible, condylus; b: left mandible, pectinate lamellae.

Distribution & Ecology: This species, belonging to the six largest sphaerotheriid species of the world, is only known from the small littoral forest of Toamasina, and may be endemic in this area. Ecological data, not yet available, may shed light on the function of the dense hair coverage on the tergites of this species. The hairs may have sensorial functions or may keep dirt particles away from the body of the animal. Such suggestions may indicate euedaphic and burrowing habits of this species. Behavioral observations can elucidate the function of the extraordinarily big movable finger of the posterior telopods. The dissected female, collected in the middle of April 1996, did not contain eggs.

Conservation: The fate of this species is dependent on the future of the littoral forest fragment near Toamasina, where the specimens were collected. No other collecting sites have been recorded for this species thus far. All recently published records indicate a very fast destruction of the scattered remaining patches of littoral forest on the east coast of Madagascar (Dumetz 1999, deGouvenain & Srilander 2003). These large-bodied millipedes play an important, albeit understudied role in the decomposition cycle (Ashwini & Sridhar 2003) and millipede populations will have to be carefully monitored if planned reforestation with endemic plants is to be successful.

Intraspecific variation: The lack of material precludes examination of intraspecific variability. The three males show identical formed telopods. The paratype selected for

SEM shows a unique feature in sphaerotheriids, his antennae has seven joints before the small disc carrying the sensory cones.

TABLE 1: Differences between members of the *Zoosphaerium alluaudi* species-group. Abbreviations: ant. = anterior; post = posterior; tsh = thoracic shield; SR = stridulation ribs; AS = sensory cones on antennae; aT = anterior telopods; pT = posterior telopods; O = operculum of vulva; St = sternite, md = mandible; gn = gnathochilarium, n°. = number.

Character	*Z. alluaudi*	*Z. villosum sp. nov.*	*Z. coquerelianum*	*Z. globulus*	*Z. imbecillum*	*Z. voeltzkowianum*
body length (maximum)	43	64.6	62.4	?	19.9	30
width tsh	23.1	33.6	32.4	14.9	11	15.5
tergite surface	glabrous	with numerous, big rounded pits and hairs	with numerous small pits, glabrous	glabrous	glabrous	glabrous
anal shield surface	densely covered with hairs	densely covered with hairs	with numerous small pits, bald	glabrous	glabrous	glabrous
N° of AS-cones	4	25–45	18–28	4	4	4
coloration	olive-greenish	blackish-green	brown-dark brown	brown	brown	brown, with traces of greenish
Hairs on collum	only on borders	few hairs	few hairs	only on borders	only on borders	only on borders
Shape of 1st St	tip of lobe blunt	tip of lobe narrow, but blunt	tip of lobe blunt	tip of lobe pointed	tip of lobe very broad, blunt	tip of lobe very broad, blunt
marginal bristles, # of rows	1	2	2	1–2	1	1
ant. locking carinae	1st short, straight,	1st short, straight	1st short, tilted	1st short, one section tilted	1st short tilted	1st short, tilted
post. locking carinae	2nd 2.2 x 1st, straight	2nd 3 x 1st, straight	2nd 2.5 x 1st, straight	2nd 3.5 x 1st, straight	2nd 4.5 x 1st, straight	2nd 3.5 x 1st, straight
paratergites, posterior tips	slightly projecting posteriorly	projecting posteriorly	projecting posteriorly	not or only slightly projecting posteriorly	not or only slightly projecting posteriorly	slightly projecting posteriorly
O (size)	low but broad, ending slightly before apical margin of coxa	big, ending before apical margin	very big, almost reaching the apical margin of coxa	female unknown	female unknown	very small (immature!)
O (form)	with two low, blunt lobes	with two high blunt lobes, no division	divided on 1/4th of height in two well-rounded lobes	female unknown	female unknown	shallow invagination on apical margin (immature!)

.....continued on the next page

TABLE 1 (continued)

Character	*Z. alluaudi*	*Z. villosum sp. nov.*	*Z. coquerelianum*	*Z. globulus*	*Z. imbecillum*	*Z. voeltzkowianum*
washboard, SR #	2	2	2–3	female unknown	female unknown	2
Male gonopore plate	plate 1/3th of coxa height	plate almost 1/2th of coxa height	plate small, 1/4th of coxa height	plate 1/3th of coxa height	plate small, 1/4th of coxa height	plate 1/3th of coxa height
harp, SR #	2	2	1	2	2	2
3rd joint of aT, invagination	deep	deep	deep	no invagination	no invagination	shallow
2nd joint pT, ant. surface	glabrous	with numerous hairs	with hairs	glabrous	glabrous	few hairs on borders
2nd joint pT, post. surface	glabrous	with numerous hairs	with numerous hairs	with numerous hairs	with few hairs	with numerous hairs
3rd joint pT Width-Length ratio	1 : 2.2	1 : 2.4	1 : 2.2	1 : 2.4	1 : 3	1 : 2.4
Sensorial cones lateral of gn-palpi	4, grouped together	3, grouped together in one pit	no dissection	no dissection	no dissection	no dissection
Molar plate process of md	with 2 ridges and 1 step	1 sharp ridge	no dissection	no dissection	no dissection	no dissection

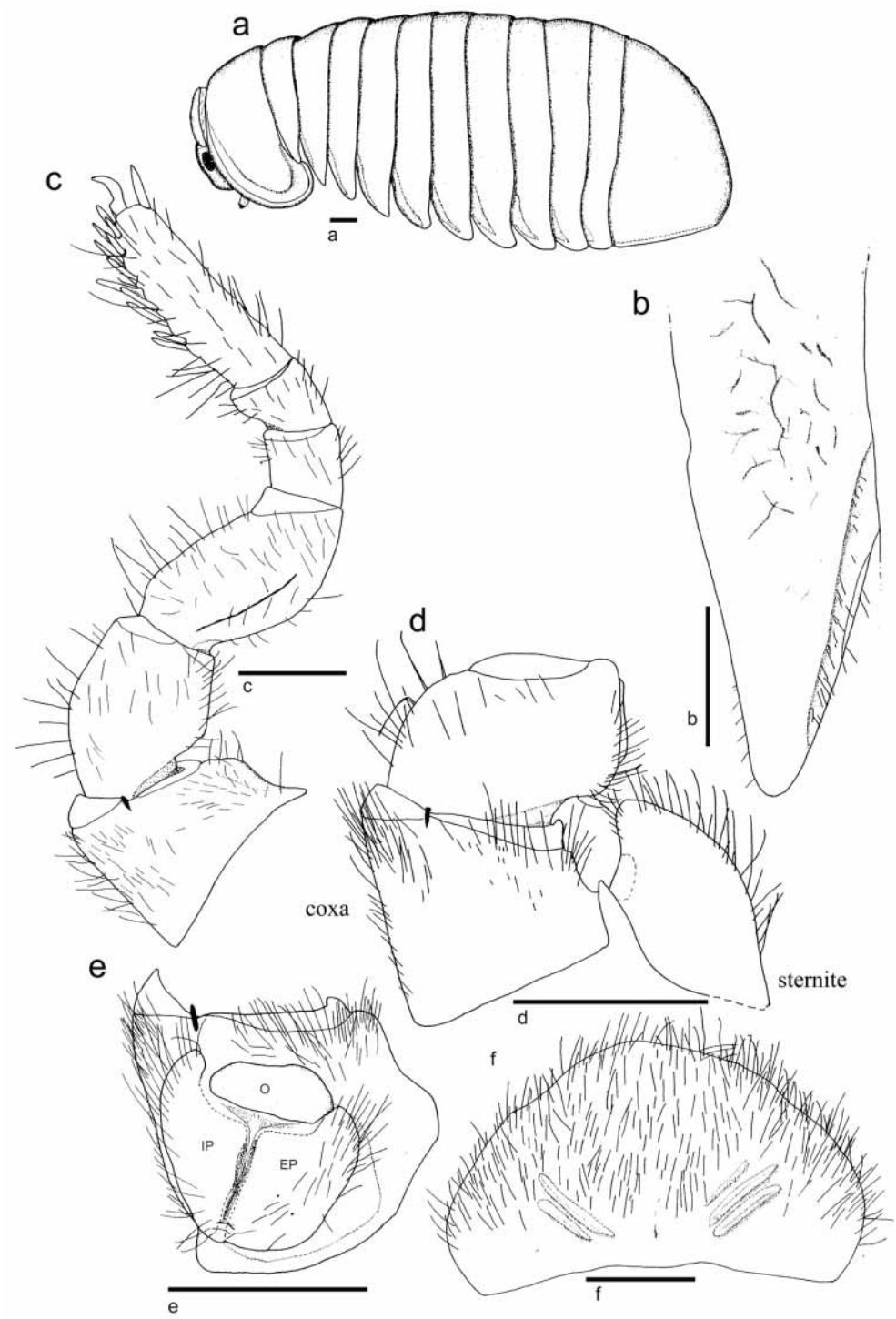
Zoosphaerium sp. from Sainte Luce

Figs 17–18

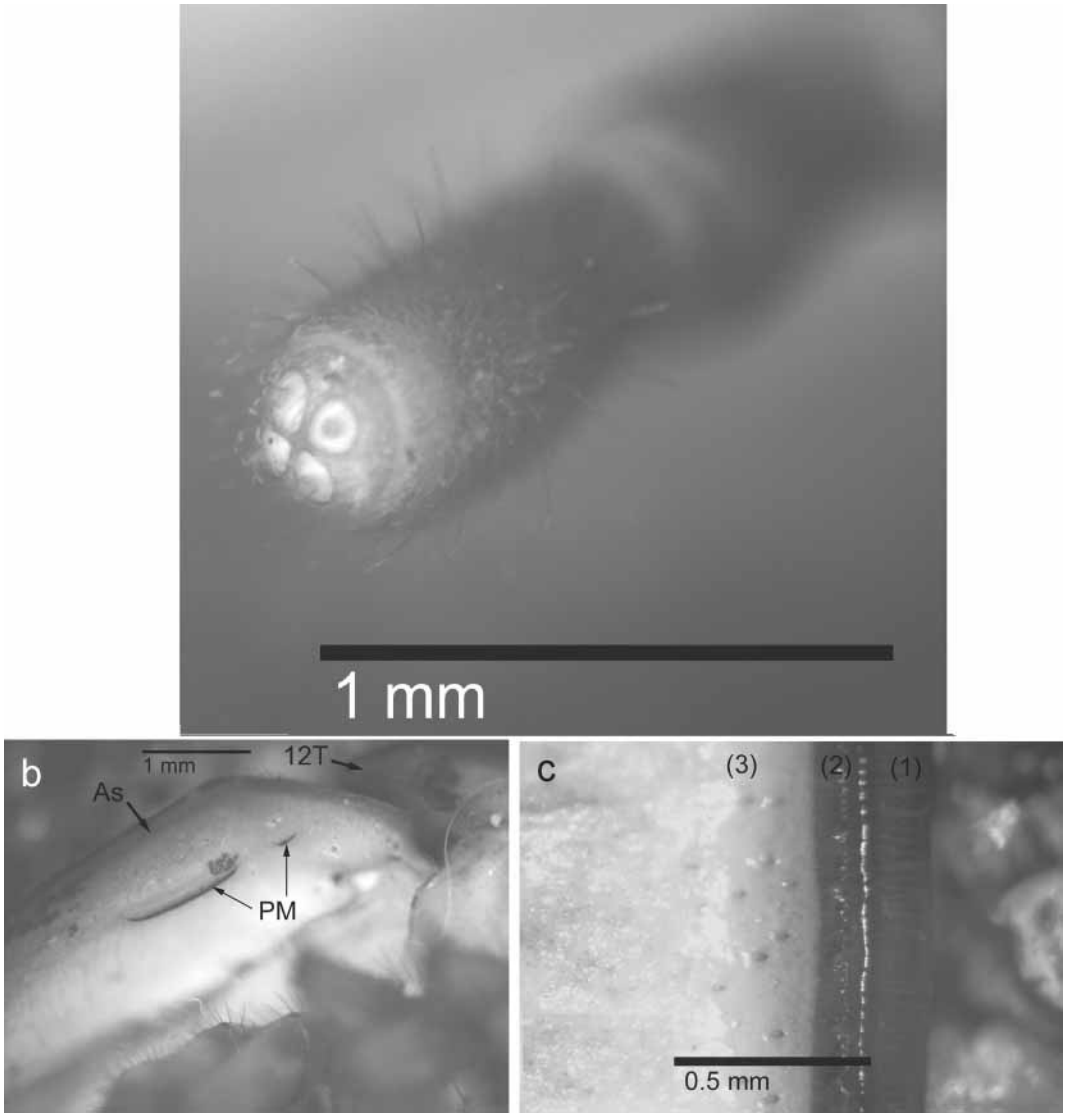
Material: 1f. (mature), 1f. (immature) coll. Madagascar, Province Toliara: Sainte Luce, littoral forest, 24°47'S 47°10'E; 08.IV.2003, leg. T. Wesener

Diagnosis: Splendid, black-colored pill millipede. Surface tergites 2–6 with a pattern of irregular, rounded sulci resembling roughened leather (Fig. 16b). Antennae with four sensory cones (Fig. 17a). Anal shield with two locking carinae, first punctiform, second 6 times longer (Fig. 17b). Concave lateral extension of the thoracic shield small, but marginal brim remarkably broad (Fig. 16a). Lateral extension and the depressions of paratergites white to yellowish. Vulvae small, covering only up to 2/3 of the coxa. Operculum of vulvae small, ending far before the apical edge of coxa (Fig. 16e). Males unknown.

Similar species: A comparison of this species with other Malagasy Sphaerotheriida species is very difficult, because males are missing. For this reason, no new species is described at this point. Drawings of the female are given for the comparison with other unsorted material, which may contain males of this undescribed species.



FIGURES 17 A–F: *Zoosphaerium sp.* Sainte Luce, female. a: habitus; b: 5th paratergite; c: 9th left leg, posterior view; d: coxa and prefemur of 1st left leg with 1st left sternite; e: coxa of 2nd left leg with vulva, posterior view; f: subanal plate. EP = exterior plate, IP = inner plate, O = operculum, S = sternite. Scale bars = 1 mm.



FIGURES 18 A–C: *Zoosphaerium sp.* Sainte Luce, female; digital photo. a: tip of right antennae, b: left closing margins of anal shield, As = anal shield, 12T = 12th tergite, PM = locking carinae; c: endotergum, (1) = marginal ridge with external row of marginal bristles, (2) = band of flattened nodules , (3) = internal area. Scale bars = 1 mm

Description: *Body length*: 22.5 mm (mature female); width of thoracic shield: 11.2 mm (mature female); height of thoracic shield: 5.8 (mature female).

Habitus: posterior tergites higher than anterior ones (Fig. 16a).

Coloration: tergites shiny-black, smaller specimen blackish-white. Lateral extensions of thoracic shield and anterior paratergite depressions lighter, whitish to yellow in color. Antennae olive-green, legs and head light-brown.

Head: with numerous hairs and hair-pits especially around the labrum and laterally around the eyes. A few long hairs around the eyes and distributed on the entire head. Posterior margin of head towards the collum without a patch of short hairs. Head with up to 60 ocelli on each side.

A*ntennae:* shaped like in description of genus. Sixth antennomere longest, with 4 sensory cones (Fig. 17a). First antennomere much broader than the others.

Collum: Anterior margin with some isolated hairs arranged in a single row. Posterior margin with 4 hairs. Rest of collum hairless. *Thoracic shield:* marginal brim very broad (Fig. 16a). A few long hairs in the concave lateral extension of the thoracic shield. Concave lateral extensions small. Anterior paratergite depression of *tergites* 3–12 with some hairs, on the anterior margin of posterior tergites 1–2 ribs. Tips of the posterior margins of paratergites 8–12 projecting posterior. Tergites outside of the anterior paratergite depression bald, surface chagrined resembling roughened leather (Fig. 16b)

Endotergum with one dense row of marginal bristles. Internal part with short spines and isolated bristles. Marginal ridge straight. Interior of marginal ridge one row of flat round cuticular impressions, each nodule isolated, far away from the next (Fig. 17c).

Anal shield: well-rounded, neither bell-shaped nor tapered (Fig. 16a). A few short, isolated (sensory?) hairs sparsely distributed over the entire surface of the anal shield. Ventral side carries two black locking carinae on both sides, anterior punctiform, posterior one more than six times longer than anterior one, at posterior end closer to the margin of the anal shield than at the anterior. Locking carinae separated from each other by a distance equal to the double length of the shorter anterior carina. Suture visible between locking carinae.

Legs: tarsi of first pair of legs with two, those of second with up to four ventral spines, weakly curved claws and without apical spine. Tarsi of legs 3–21 with curved claws, 10–12 ventral spines and one apical spine. 9th leg pair without coxal lobe (Fig. 16c). Coxae of all legs at the margins covered with many long hairs, the following leg joints with a few isolated, long hairs mostly around the margins. Femur with a black crenulated ridge (Fig. 16c).

Sternite: first sternite lobe broad and short, reaching above apical edge of the coxae of the first leg pair (Fig. 16d). Apical margin rounded regularly and covered with many long hairs. Inner margin of sternite curved. Sternites three and beyond with a spine-like process which reaches about the stigma opening of the anterior sternite.

Female sexual characters: second leg pair without coxal lobe (Fig. 16e). Vulvae small, covering up to 2/3 of the coxa. Operculum small, ending far before the apical edge of coxae. Apical margin of operculum slightly constricted in the middle (subreniform). Invagination dividing operculum irregular in two same sized parts, but no suture between the parts is visible. Both parts of operculum almost of same height. Basal margin straight. Exterior and inner plates (EP, IP) of vulva both surrounding the basal margin of the operculum. Inner plate very long and broad, reaching above the height of operculum. E xterior plate not as long as the inner one, reaching only the basal 1/3 part of the operculum.

Cyphopod sclerites consisting of two triangular apical sclerites and a much larger third sclerite formed as a tuning-fork; all visible as dark structures near the suture of the vulva between inner and exterior plate (Fig. 16e). *Subanal plate* with washboard, consisting of regular symmetrical stridulation ribs. On each side 2–3 stridulation ribs, which are short, ending just above the middle of the subanal plate (Fig. 16f).

Ecology: This species was collected in wet leaf litter in the littoral forest fragment of Sainte Luce together with two other Sphaerotheriida, *Zoosphaerium arborealis* **sp. nov.** and *Sphaeromimus splendidus* Wesener & Sierwald (in press). The niche separation of these three species is still unknown.

Conservation: This species was found only in the littoral forest fragment of Sainte Luce. Its survival is directly connected to the existence of the Sainte Luce littoral forest.

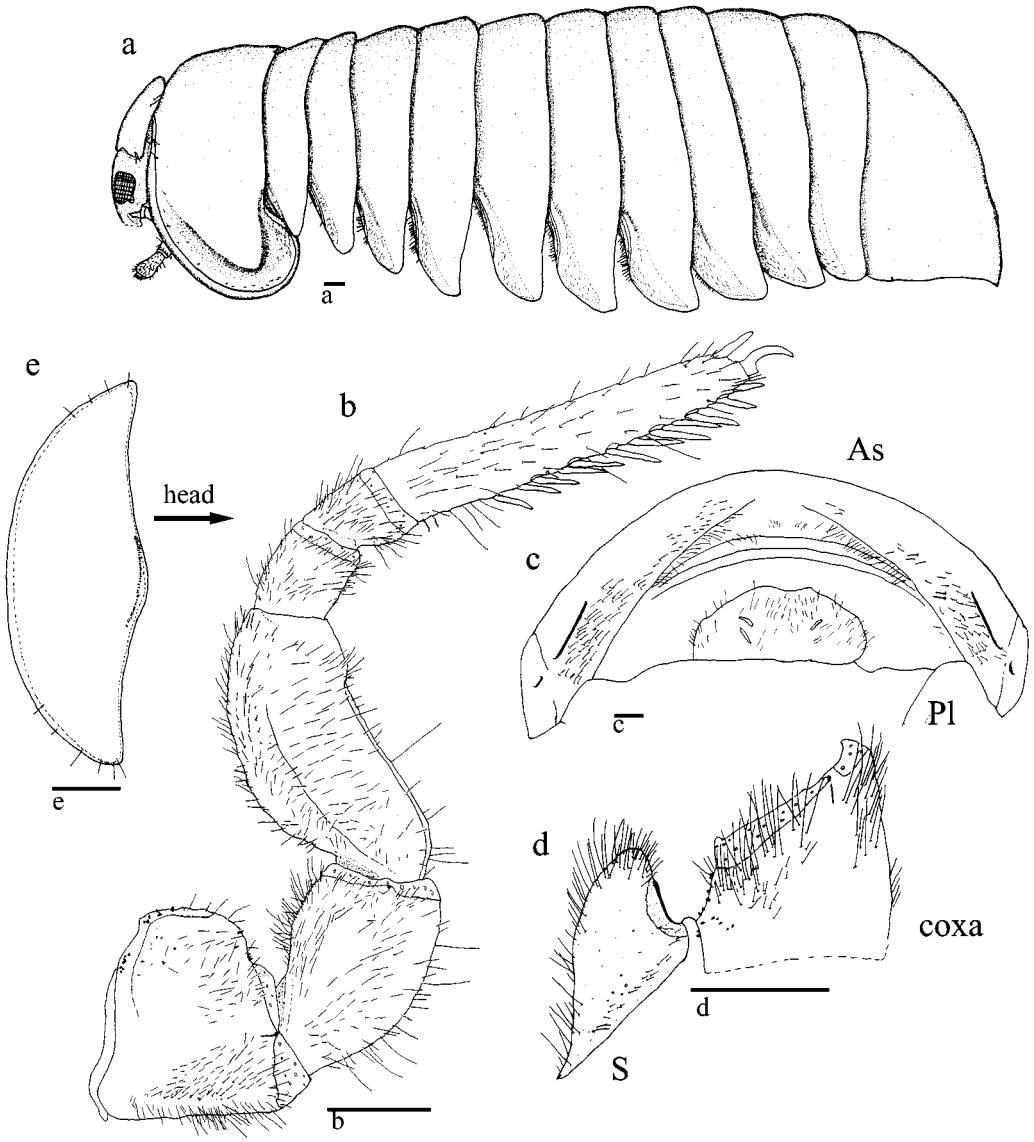
***Zoosphaerium arborealis* sp. nov.**
Figs 19–29

Material: Holotype: 1 m., FMNH. L*ocus typicus*: Madagascar; Province Toliara; Mandena; littoral forest; in leaf litter; 24°56.51'S, 046°59.70'E; IV.2003; leg. T. Wesener.

Paratypes: 2 m., 8 f. (mature) FMNH; 1 m., 2 f. (mature) CAS; 1 m., 2 f. (mature) ZSMC; 3 f. SMNG VNR 13554; Madagascar; Province Toliara; Mandena; littoral forest; in leaf litter and on trees; 24°56.51'S, 046°59.70'E; IV.2003; leg. T. Wesener. 2 m., 2 f. FMNH. Madagascar; Province Toliara; Sainte Luce; littoral forest; in leaf litter; 24°46.77'S, 047°10.28'E; 07.IV.2003; leg. T. Wesener.

Other Material: 29 f. (mature) Université de Antananarivo. Madagascar; Province Toliara; Mandena; littoral forest; in leaf litter; on trees; many inside of dead stems of *Pandanus sp.*; 24°56.51'S, 046°59.70'E; IV.2003; leg. T. Wesener. 7 m., 11 w. (immature), FMNH. Madagascar; Province Toliara; Mandena; littoral forest; in leaf litter; on trees; many inside of dead stems of *Pandanus sp.*; 24°56.51'S, 046°59.70'E; IV.2003; leg. T. Wesener. 1 m., 2 w. (immature), FMNH. Madagascar; Province Toliara; Sainte Luce; littoral forest; in leaf litter;; 24°46.77'S, 047°10.28'E; 07.IV.2003; leg. T. Wesener. 3 m., 13 w. (mature) FMNH. Locality: Province Fianarantsoa; Parc National de Andringitra, Forêt d'Ravaro, 12.5 km SW Antanifotsy, 22°12.7'S, 46°50.7'E, 1500 m, 9–16.i.2000, undisturbed mid-elevation forest /w Acanthaceae, leg. S. Goodman.

Diagnosis: Medium-sized pill-millipede up to 40 mm in body length. Males distinctly smaller than females. Tergites brown, legs and antennae red (Fig. 29a). Body smooth or with a few hairs, anal shield slightly tapered (Fig. 19a). Antennae with 7–24 sensory cones (Fig. 22b), first and second joint with invagination, all joints at least basal with sclerotized teeth (Fig. 22a). First sternite at inner margin straight (Fig.19d). Anal shield ventrally on each side with two well-developed black locking carinae. Anterior locking carinae short, posterior one 3–4 times longer than anterior carina (Fig. 19c). Anterior telopods with two stridulation ribs, number of ribs on female washboard variable (Figs. 20b, 21a).



FIGURES19 a–e: *Z. arborealis* **sp. nov.**, female paratype. a: habitus; b: right 9th legpair, posterior view; c: posterior view on anal shield; d: coxa of 1st right leg with 1st right sternite, posterior view; e: collum (1st tergite). As = anal shield, Pl = pleurite, S = sternite. Scale bars = 1 mm

Similar species: *Z. arborealis* is closely related with *Z. lambertoni* (Brolemann, 1922). Nevertheless, *Z. arborealis* the inner horns and inner lobes of the posterior telopods are unique in shape (Figs 21e, f). Additionally, the locking carinae of the anal shield are strongly developed in *Z. arborealis*, but weakly developed in *Z. lambertoni* (Brolemann, 1922: 235–236, "*font défaut en tant quíarêtes pigmentées* [...]"). The type specimen of *Z. lambertoni* (Brolemann, 1922), deposited at the L`Académie Malgache in Antananarivo/Madagascar, cannot be located. Thus, the species cannot be compared to *Z.*

arborealis. All other species of *Zoosphaerium* with similar posterior telopods like *Z. anomalum* (DeSaussure & Zehntner, 1897) have a differently formed anal shield. The lower margin at the posterior end of the anal shield is never tapered in *Z. arborealis*.

Description: Males (14 specimens): length: 19.0–26.45, width of thoracic shield: 9.65–13.15, height of thoracic shield 5.5–7.2. Females (45 specimens): length: 21.0–40.0, width: 10.75–20.0, height: 6.75–11.35.

Habitus: tergites more posterior higher than anterior (Fig. 19a). Tergites very smooth, sometimes with a broad patch of hairs at the anterior and posterior margin.

Coloration: tergites brown, posterior margin darker (Figs. 29a–b), smaller specimen olive-brown. Antennae and legs dark-orange to red. Red color fades in alcohol.

Head: with numerous hairs and hair-pits especially around the labrum and lateral of eyes. A few single, long hairs around the eyes and distributed on the entire head. Posterior margin of head towards the collum with a patch of short hairs (Fig. 23d). Edges of antennal groove with 5–6 small spines and sclerotized teeth (Fig. 23b). Head with up to 90 ocelli on each side (Fig. 23c). Tömösváry organ inside with a coral-like structure (Fig. 23e).

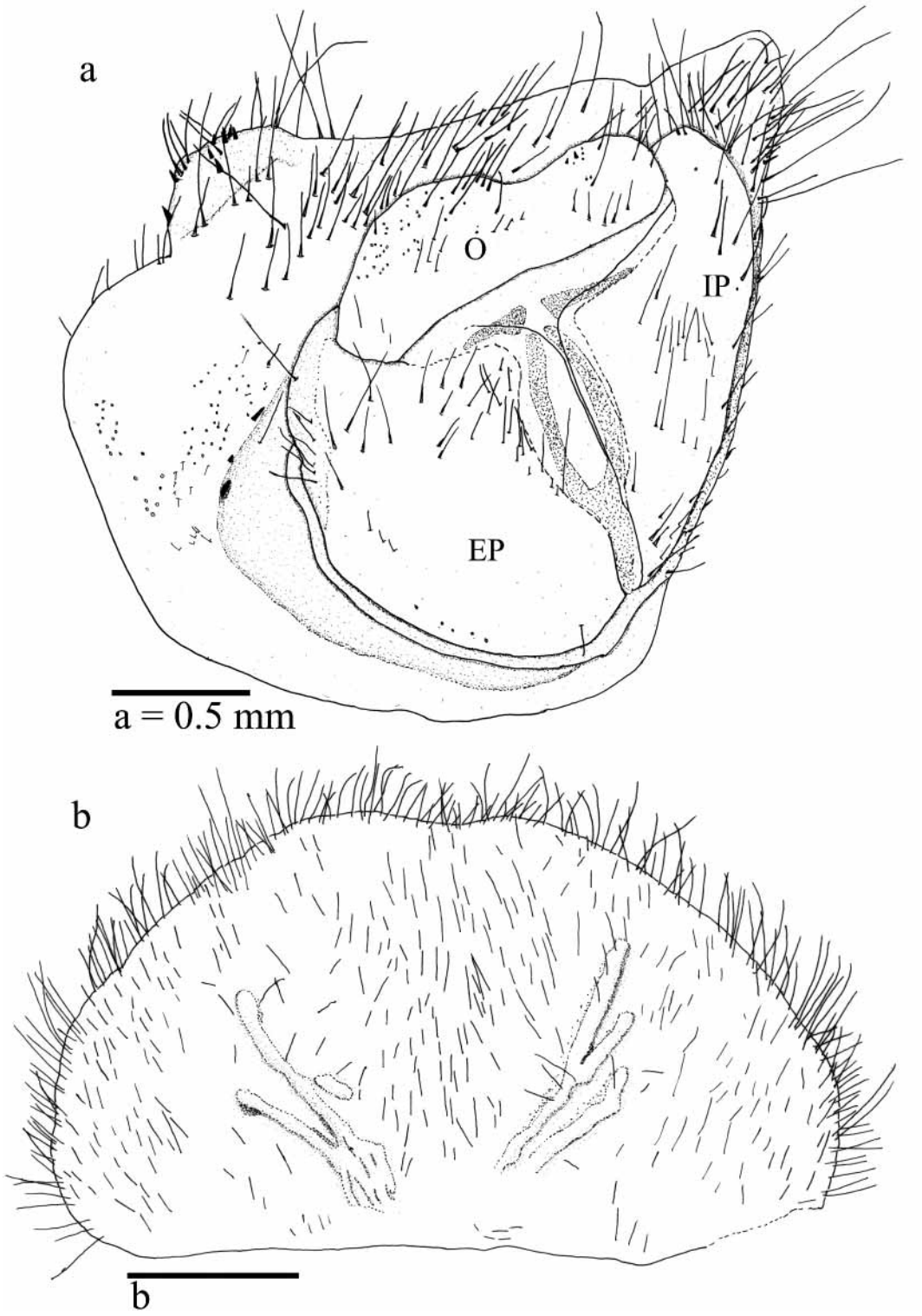
Antennae: shaped as described for the genus. Length of antennomeres: 1>2>3=4=5<6; sixth antennomere longest, of cylindrical shape (Figs. 22a) with 7–24 sensory cones (Fig. 22b). First antennomere much broader than the others (Fig. 22c). Sclerotized teeth at the base of antennomeres one through six, reaching the apical border at first antennomere. First and second joint with invaginations (Fig. 22c).

Mandible: with seven rows of pectinate lamellae; number of teeth declining proximally (Fig. 27b). Condylus with two strongly developed steps near the apical margin (Fig. 27c). *Gnathochilarium:* ventral side with bristles, only few on the lingual lamella (Fig. 24a). With a field with three sensory cones lateral to the palpi (Fig. 24b). Two different types of sensory cells on the central pads: long ones without a pit and smaller, cylinder-shaped ones with a central pit (Fig. 25a). Sensory cones on palpi distributed regularly over the tip (Fig. 25b). *Epipharynx:* shaped as in other members of this genus (Figs. 26b, 27a).

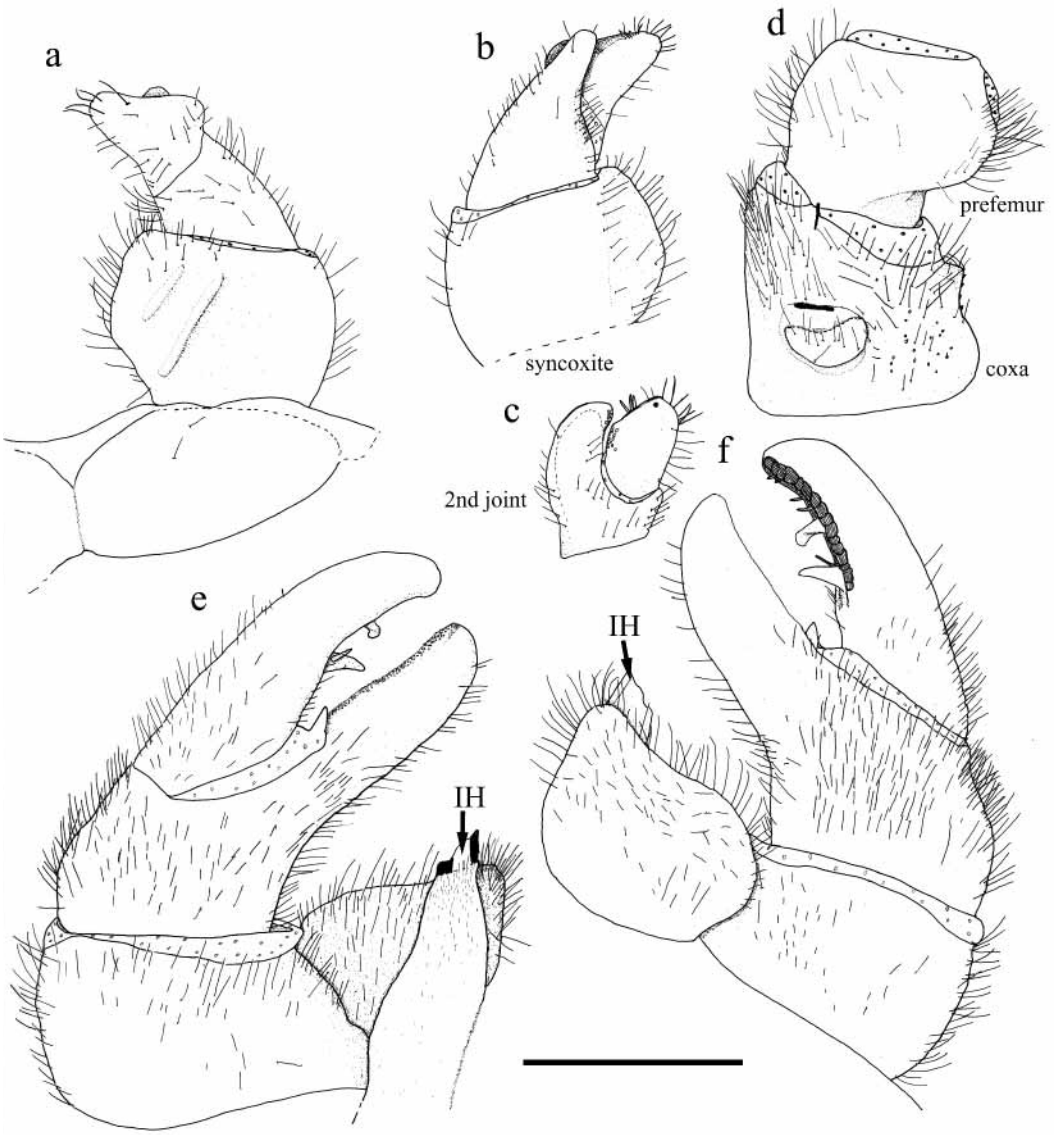
Collum: Anterior margin bald, in the middle with a row of very small, dark-brown sclerotized teeth. Posterior margin on each half with 4–6 hairs, inserting lateral and at the edges. Rest of collum hairless. *Thoracic shield:* A few hairs in the concave lateral extension of the thoracic shield, especially near the margins. Anterior marginal brim broader than the rest of the brim (Fig. 19a).

Anterior paratergite depression of *tergites* 3–12 with many hairs, on the anterior margin with a few ribs (Fig. 19a), otherwise tergites are almost hairless and smooth. Tips of the posterior margins of paratergites 8–12 projecting posteriorly.

Endotergum with two or more rows of marginal bristles. Internal part with short spines and few, isolated bristles. Bristles scaly (Fig. 25c). Marginal ridge straight. Interior of marginal ridge one row of round flat nodules (Fig. 26a).

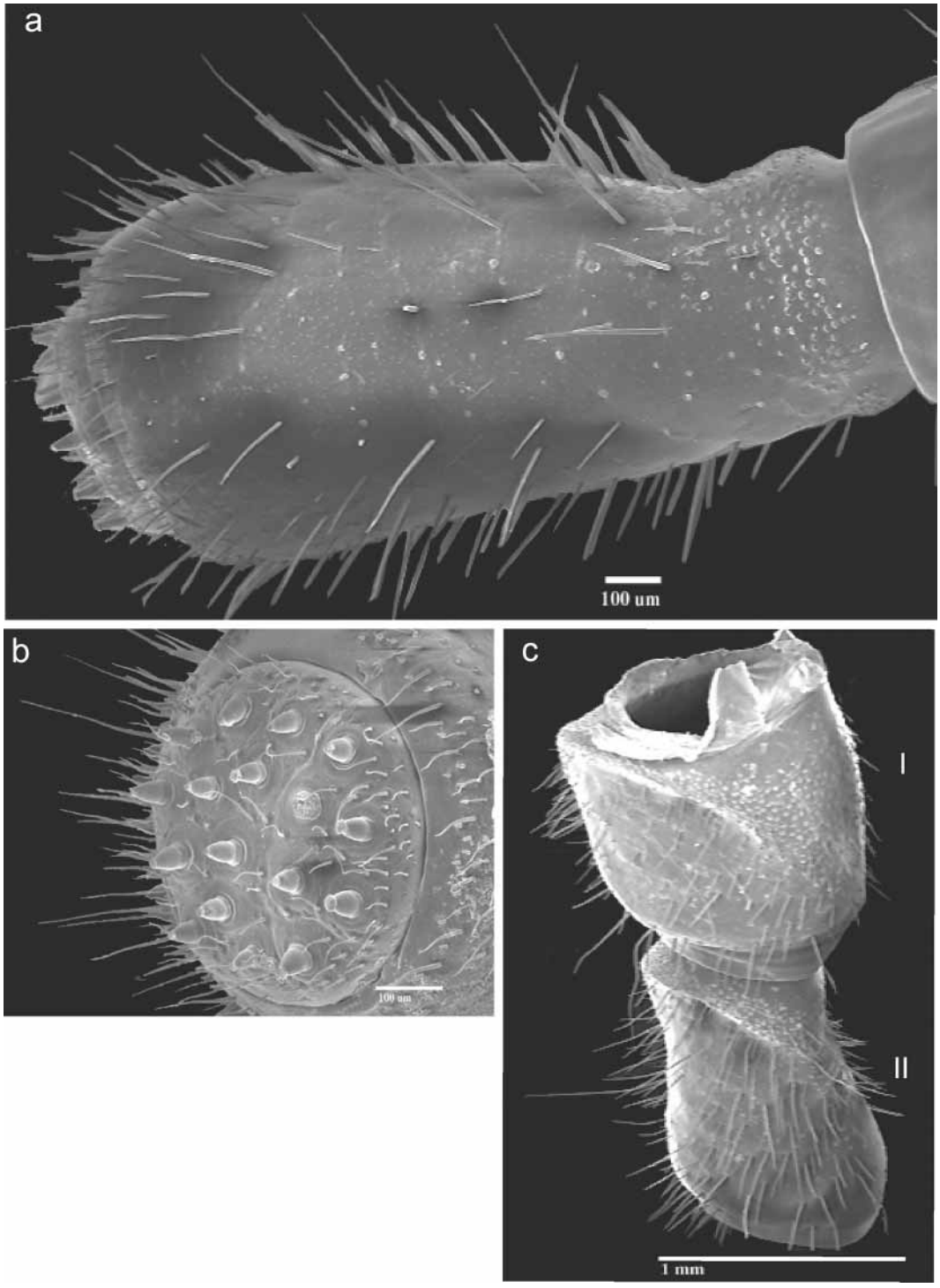


FIGURES20 a–b: *Z. arborealis* **sp. nov.**, female paratype. a: coxa of 2nd right leg with vulva, posterior view; b: subanal plate with washboard. EP = exterior plate, IP = inner plate, O = operculum. Scale bars = 1 mm

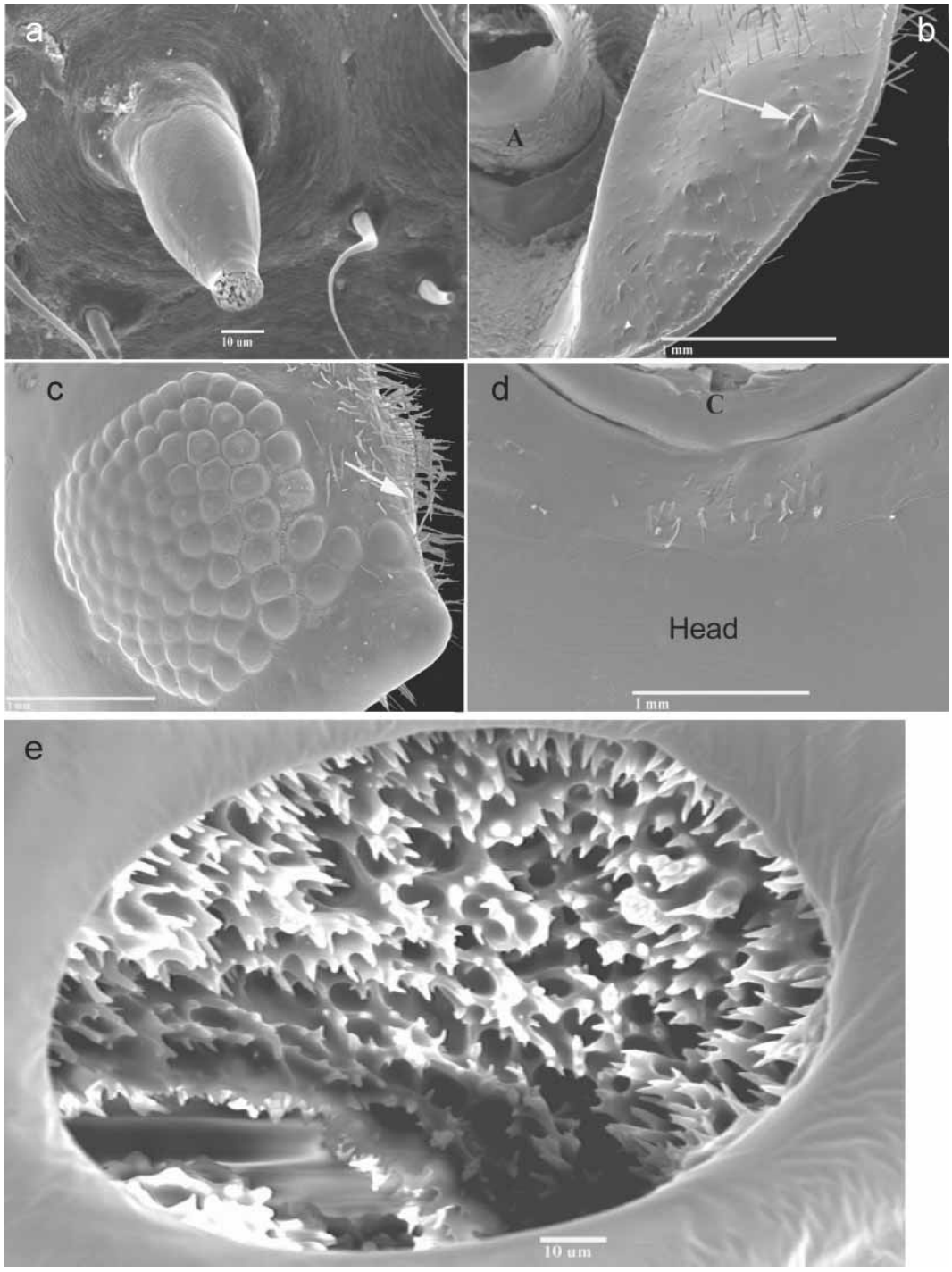


FIGURES 21 a–f: *Z. arborealis* **sp. nov.**, male holotype. a: right anterior telopod, anterior view; b: right anterior telopod, joint 1–3, posterior view; c: right anterior telopod, joint 2–3, inner view; d: 2nd left leg coxa and prefemur with male gonopore, posterior view; e: left posterior telopod, anterior view; f: left posterior telopod, posterior view. IH = inner horns.
Scale bars = 1 mm

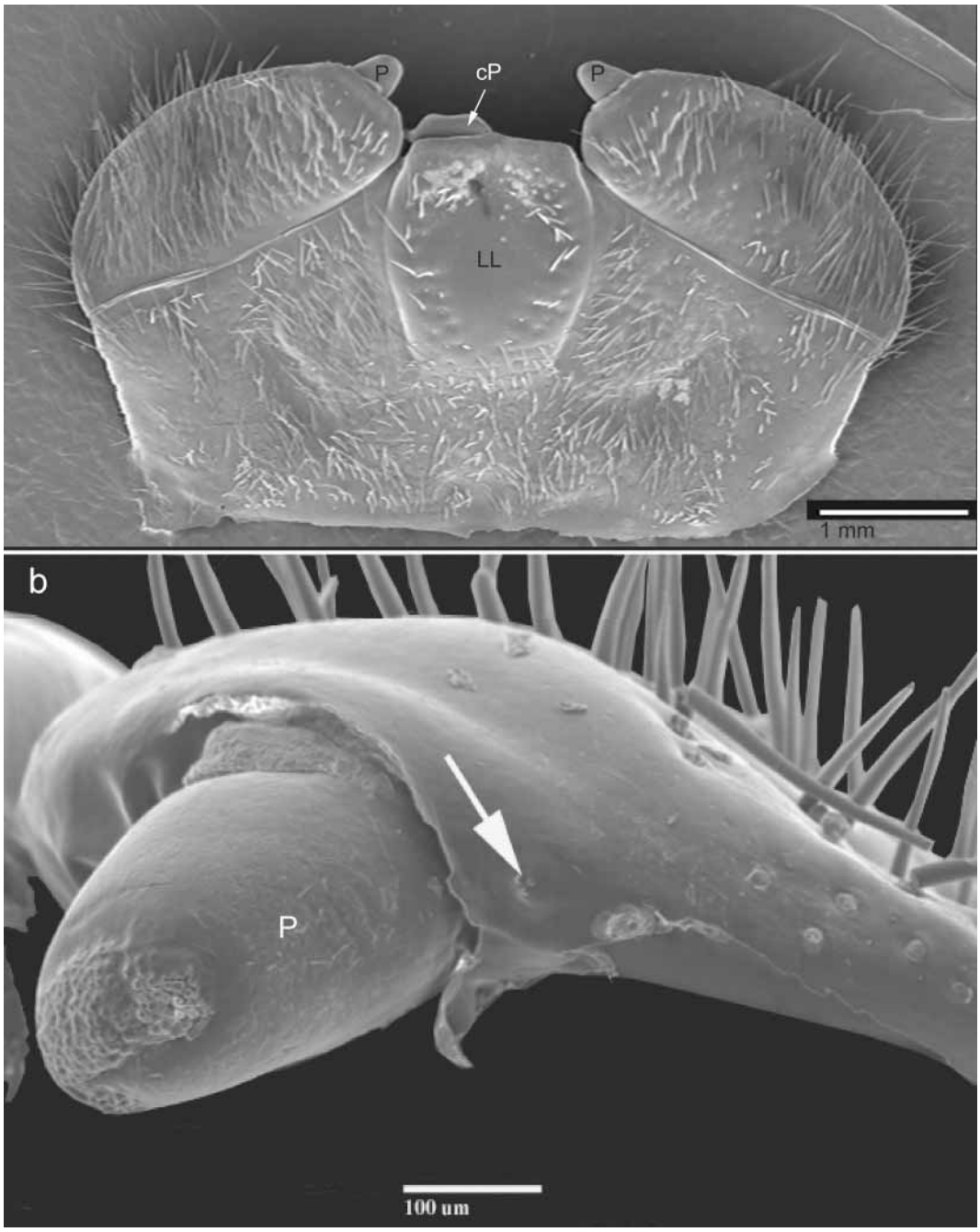
Anal shield: lower margin at posterior end tapered (Fig. 19a). Only in some males near posterior margin with many short (sensory?) hairs. Ventral side carries two black locking carinae on both sides, anterior one similar to those of tergites, posterior one more than three and a half times longer than anterior one, at posterior end nearer to the margin than anteriorly. Locking carinae separated from each other by a distance equal to the double length of the shorter carina. Distinct suture present between both carinae. Where the suture reaches the margin of the anal shield, a small, distinct triangular invagination is visible (Fig. 19c).



FIGURES 22 a–c: *Z. arborealis* **sp. nov.**, female paratype, SEM: right antennae. a:, 6th joint lateral; b: apical view on sensorial cones; c: 1st and 2nd joint.



FIGURES 23 a–e: *Z. arborealis* **sp. nov.**, female paratype, SEM. a: right antennae, sensorial cone, detail; b: edges of the antennal grove, A = insertion of antennae, arrow = spines; c: right field of ocelli, arrow = aberrant ocellus; d: posterior border of the head towards the collum with patch of small hairs, C = collum; e: Inner view of the thömösvary-organ.



FIGURES 24 a–b: *Z. arborealis* **sp. nov.**, female paratype, SEM, gnathochilarium. a: ventral view; b: apical view on right palp, arrow = field of sensorial cones, cP = central pads, LL = lingual lamella, P = palpus.

Legs: tarsi of first pair of legs with 4–6, those of second with 6–9 ventral spines, weakly curved claws and without apical spine. Tarsi of legs 3–21 with curved claws, 10–14 ventral spines and one apical spine. 9th leg pair without coxal lobe but with a few

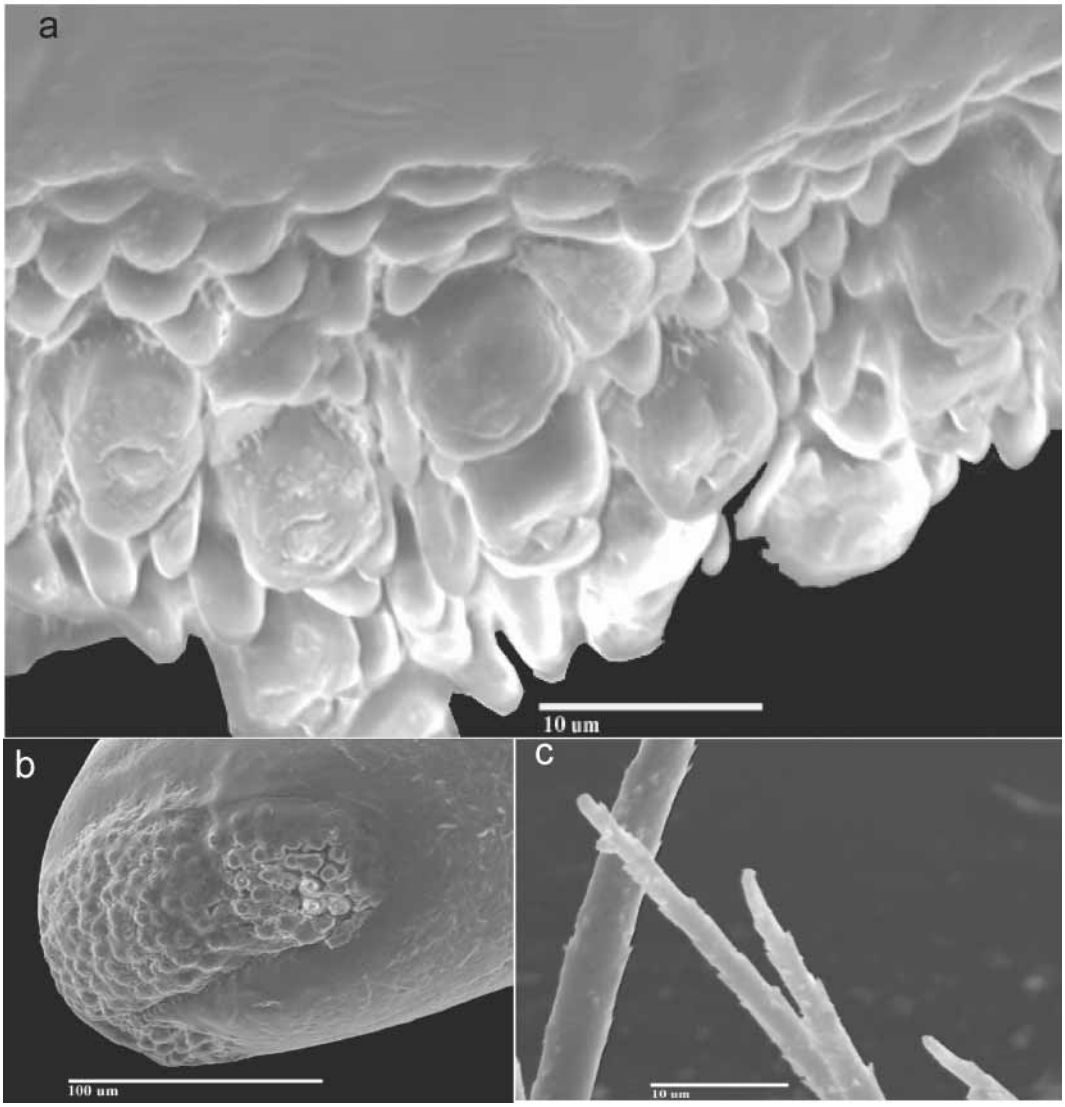
small, black triangular spines (Fig. 19b). Coxae of all legs at the inside margin covered with many long hairs, the following leg joints with a few isolated, long hairs at the inner margin. Femur with a dark crenulated ridge (Fig. 19b).

Sternite: first sternite lobe broad and short, reaching the apical edge of the coxae of first leg pair, covered sparsely with hairs (Fig. 19d). Apical margin rounded regularly and covered with many long hairs. Basal margin with few hairs (Fig. 19d). Inner margin of sternite remarkably straight. Sternites three and beyond with a spine like process which reaches about the stigma opening of the anterior sternite.

Female sexual characters: second leg pair without coxal lobe, but on exterior margin with some short, triangular black spines (Fig. 20a). *Vulvae* well-developed, covering more than 2/3 of the coxa (Fig. 20a). Operculum small, ending before the apical edge of coxae. Apical margin of operculum constricted in the middle (subreniform) with two broadly rounded equally sized lateral tips. Both parts of operculum of same height. Basal margin almost straight. Exterior and inner plates (EP, IP) of vulva below the operculum surrounding the basal margin of the operculum. Inner plate very long and broad, reaching almost 2/3 of height of operculum. Exterior plate not as long as the inner one, reaching only the basal 1/2 part of the operculum. Cyphopod sclerites consisting of two triangular apical sclerites and a much larger third sclerite formed like a tuning-fork; all visible as dark structures near the suture of the vulva between inner and exterior plate (Fig. 20a). *Subanal plate* with washboard, consisting of irregular, asymmetrical 1–4 stridulation ribs. Length of ribs very variable (Fig. 20b).

Male sexual characters: second leg pair without coxal lobe, but on exterior margin with some short, triangular black spines and covered with many hairs (Fig. 21d). *Male gonopore* covered half with a sclerotized, undivided, rounded plate, which is slightly excavated at apical margin. Gonopore plate covered with hairs. Apical part of plate membranous (Fig. 21d). Anal shield without any invagination or other sexual dimorphism, but in some cases with patch of (sensory?) hairs at posterior margin.

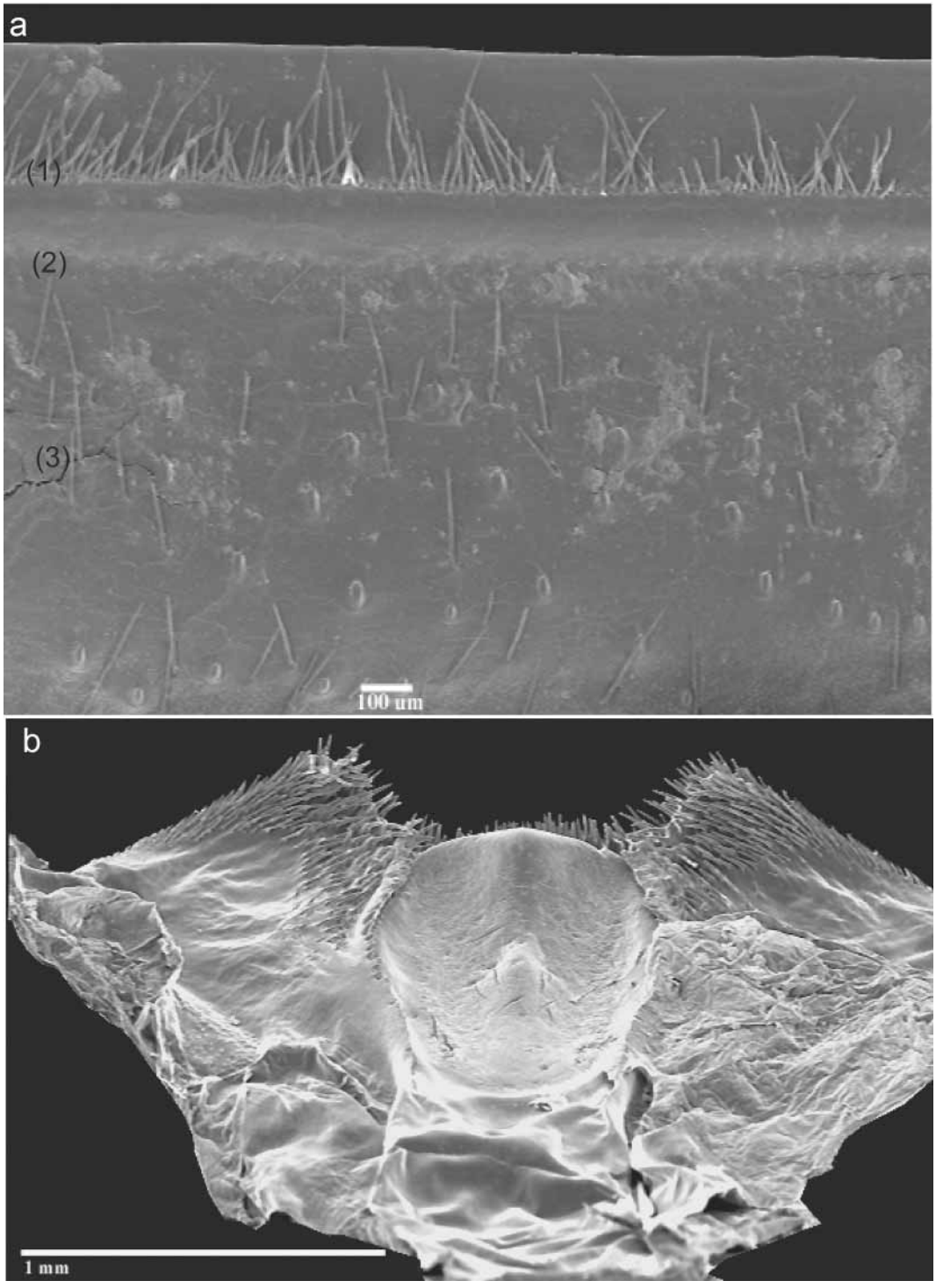
Anterior telopods: syncoxite of anterior telopods with few isolated hairs. First joint with a stridulation harp and two stridulation ribs. Inner ridge short, reaching only 1/2 of the length of the more laterally ridge. Lateral ridge long, beginning at the basal margin of the first joint and ending just at its apical margin (Fig. 21a). Posterior side of the first joint inside with an impression. Margins of impression laterally with one row of hairs. First joint with exception of margins on both sides bold. Second joint on posterior side with a lobe-like apically stout process (Figs. 21b). Tip of process reaching only slightly above the third joint. Towards the third joint with sclerotized spots (Fig. 21c). Third joint inner margin drawn out, at apical margin broad. Apical margin almost straight, only slightly excavated near the middle, tip of second joint process visible. Inner margin of third joint towards second joint process with some spines and sclerotized spots, juxtaposed to the spots on the second joint (Fig. 21c). Third joint apically with some thick bristles (Figs 21a–b).



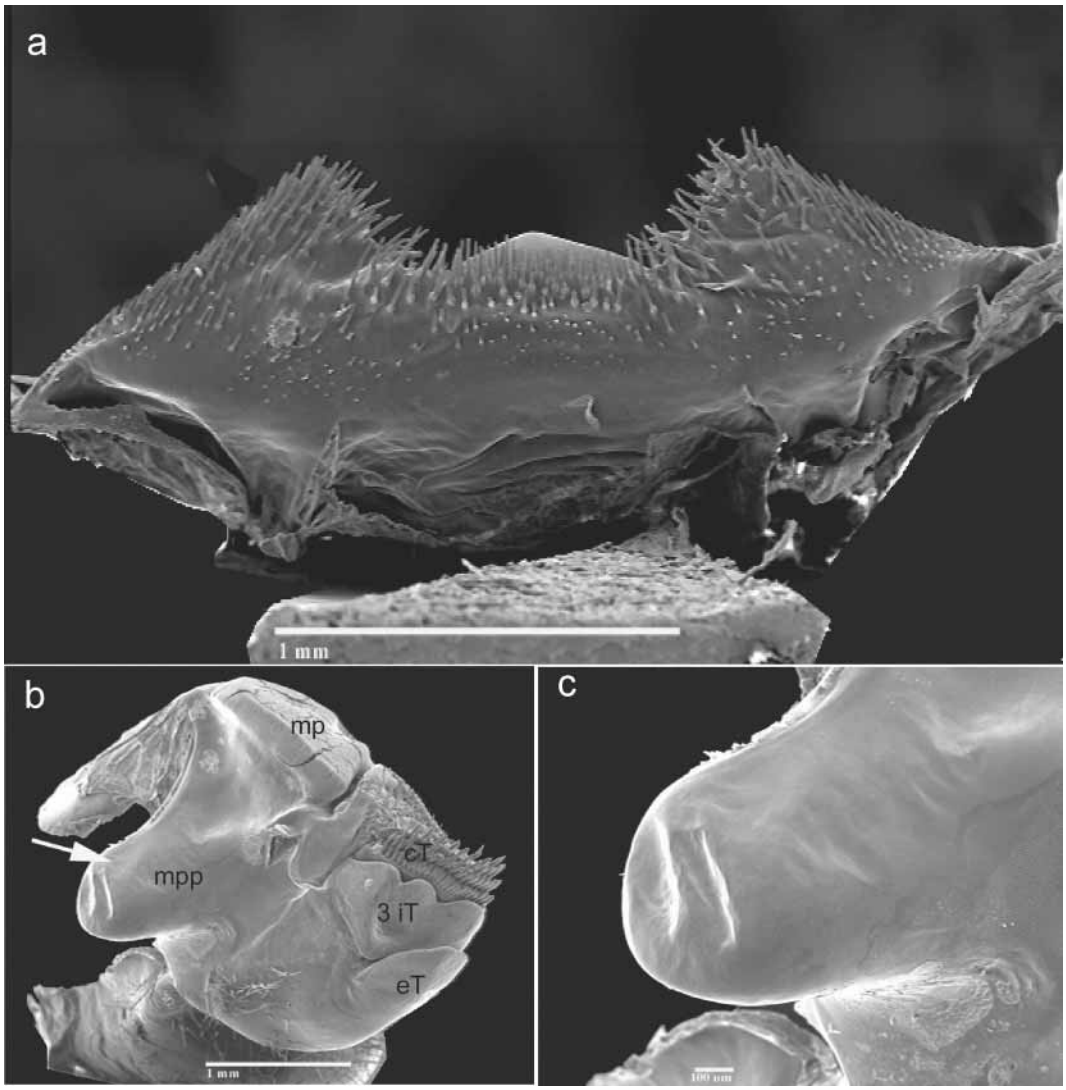
FIGURES 25 a–c: *Z. arborealis* **sp. nov.**, female paratype, SEM. a: gnathochilarium, two types of sensorial cones on the central pads; b: detail of palpus tip; c: bristle of endotergum

Posterior telopods: movable finger (third joint) of chela long and slightly curved towards the immovable finger (process of second joint, Fig. 21e). Invagination towards the immovable process of the second joint with 4–5 small, non-sclerotized spines, after one third of length of third joint with one big spine, after half of length with one finger-shaped process. Third joint on posterior side with 17th sclerotized teeth, size of teeth declining basally (Fig. 21f).

Immovable digit (process of second joint) almost straight with slightly curved tip. Anterior side basally with one spine, apically with numerous sclerotized spots juxtaposed the invagination of the third joint. Chelae only basally with hairs, on rest of surface hairs absent (Figs. 21f). Inner horns (IH) of syncoxite with a pointed tip (Figs 21e–f).



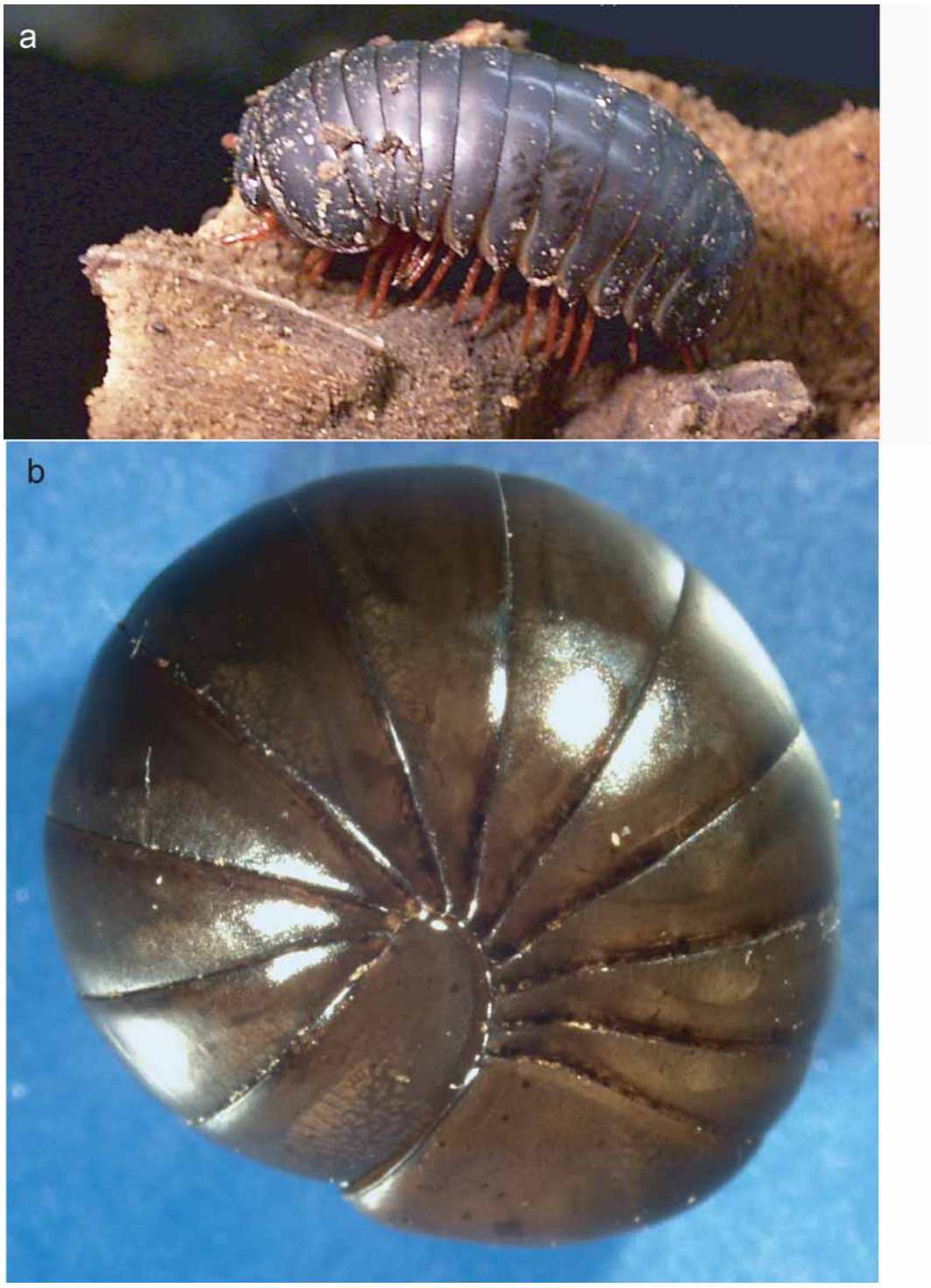
FIGURES 26 a–b: *Z. arborealis* **sp. nov.**, female paratype, SEM. a: endotergum, (1) = marginal ridge with external row of marginal bristles, (2) = band of flattened nodules , (3) = internal area.; b: basal view on ventral side of epipharynx.



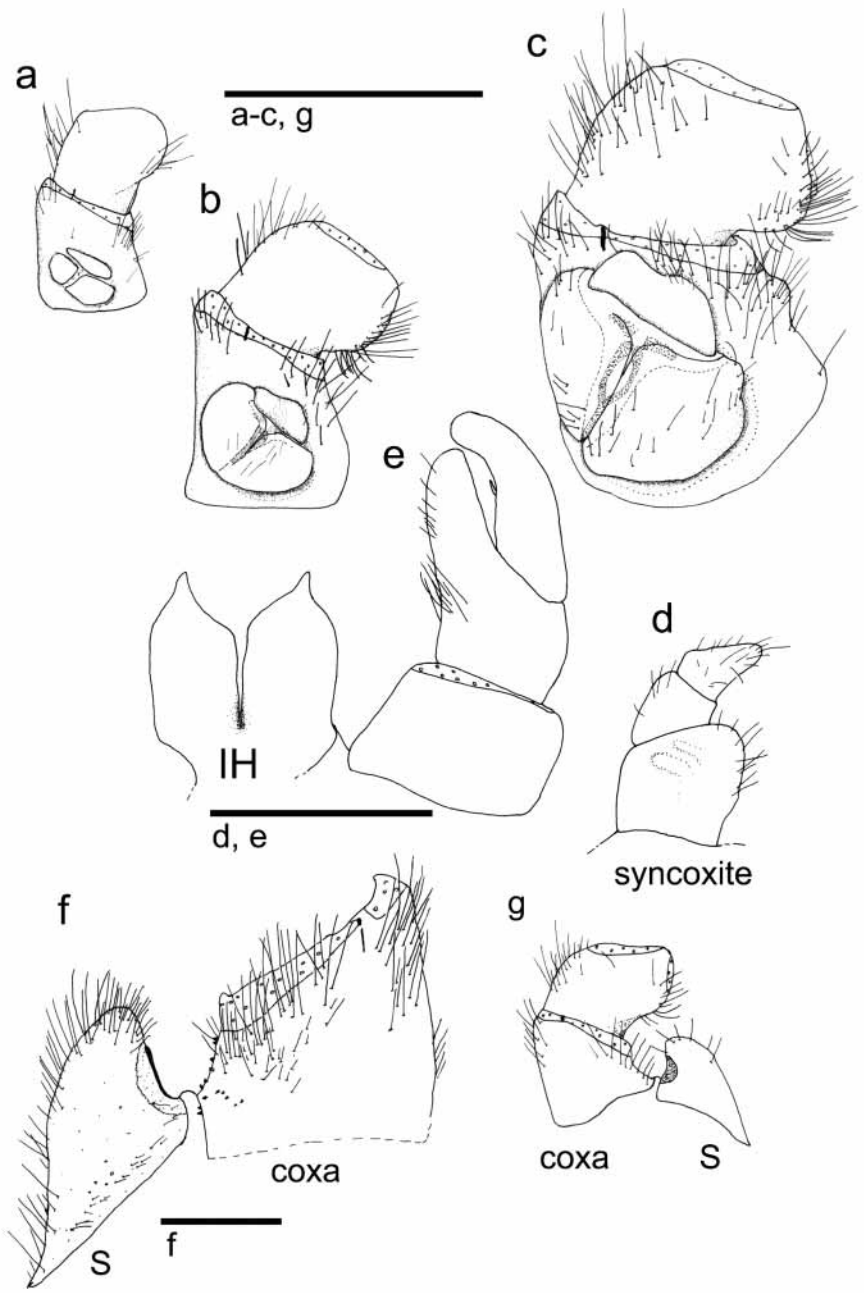
FIGURES 27 a–c: *Z. arborealis* **sp. nov.**, female paratype, SEM. a: epipharynx, distal view; b: right mandible, distolateral view, arrow = condylus; c: right mandible, view on condylus, aT = apical tooth, cT = comb teeth, mp = molar plate, mpp = molar plate process,.

Distribution & Ecology: This species has an extraordinarily wide distribution. It is the only species described from littoral forests, which is not restricted to one forest site. *Zoosphaerium arborealis* was also discovered in another ecosystem, in the montane forest of PN Andringitra at over 1200 m elevation.

In the littoral forests this species was collected in the fragments of Mandena and Sainte Luce. In both forests *Z. arborealis* is associated with a species of the giant pill-millipede genus *Sphaeromimus splendidus* Wesener & Sierwald (in press) and it also occurs in Sainte Luce sympatrically with *Zoosphaerium sp. Sainte Luce*.



FIGURES 28 a–b: *Z. arborealis* **sp. nov.**, female paratype, digital photo. a: living animal, climbing on small branch; b: living animal, rolled in a ball.



FIGURES 29 a–g : *Z. arborealis* **sp. nov.**, paratypes. a: left female coxa and prefemur with vulva, immature female of 10,5 mm body length, posterior view; b: left female coxa and prefemur of immature female of 14,15 mm body length, posterior view; c: left female coxa and prefemur of mature female of 21,75 mm body length, posterior view; d: left anterior telopod, joint 1–3, immature male of 14,3 mm body length; e: right posterior telopod joint 1–3 with inner horns of syncoxite of immature male of 14.3 mm body length; f: 1st leg right coxa with 1st sternite of mature specimen (female paratype); g: 1st leg right coxa with 1st sternite of immature female of 14,15mm body length. Abbreviations: IH = inner horns; S = sternite
Scale bars = 1 mm

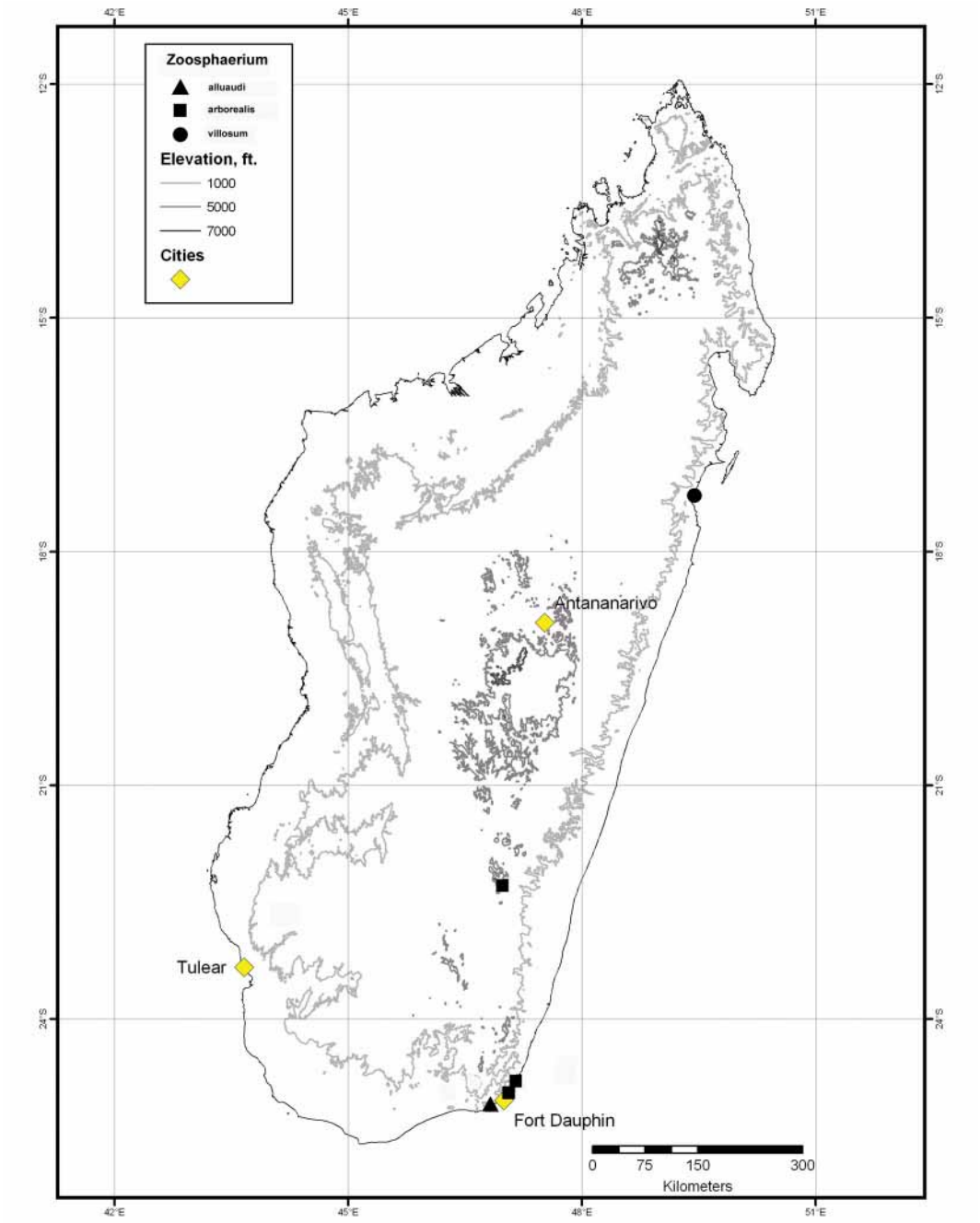


FIGURE30: Distribution map.

To date, all 33 species of Malagasy pill millipede genus *Zoosphaerium* were known from museum material only. Observation of living specimens are presented here for the first time. During an expedition in beginning of April 2003 to the Malagasy southern littoral forests, the first author observed the activity, diversity, behavior and habitats of *Zoosphaerium arborealis* in the littoral forest fragment near Mandena (Fig. 30).

This species was common in the littoral forest of Mandena. On 18 collection days >300 specimens were observed. Smaller individuals were often found in dead, rotten wood, especially in dead, excavated stems of *Pandanus sp*. (Pandanaceae), normally 5–15 specimen of almost the same size in a single stem. These stems were hollow, filled with numerous fecal pellets, indicating that the species feeds on the soft and stringy contents of the stems. Numerous smaller specimens were discovered in piles of dead wood, which were common in this forest, especially near the tracks. In these piles of dead wood, the giant pill-millipedes occurred together with larvae of *Scarabaeidae* and *Cestonidae* (Insecta: Coleoptera) and spirostreptids (Diplopoda), the most common arthropods.

The leaf litter was thin in the littoral forest of Mandena, after 1–2 cm the soil was strongly riddled with fine roots of trees. Below 20 cm the soil is sandy. After a few dry days, the soil and root layer and leaf litter dry out. Apparently, the sandy ground cannot hold the water and the layer of leaf litter is too thin to prevent moisture loss of the layers below. Only a few animals could be detected in this dry leaf litter, in some places Blattodea (Insecta) were found.

More leaf litter accumulates in some dips and under special trees (*Phyllexylon xyophylloides*, Fabaceae*; Homalium albiflorum*, Flavouriaceae*; Ophiocolea delphinensis*, Bigoniaceae).

Adult specimens of *Z. arborealis* were collected in such places or under wood during drier days. Numerous pellets show that the animals use these moist microhabitats as retreats and for feeding. In the moist patches some Isopoda and Amphipoda (both Crustacea) could be found as well.

Adults of *Z. arborealis* were collected at dawn after rainfall during the night and also after heavy rainfalls in the thin leaf litter. A day earlier, before the rain, no specimens were observed at these sites. Numerous specimens of all sizes could be observed after heavy rainfalls walking on the tracks. It must be noted that adult specimen were observed climbing tree trunks more than 150 cm high, feeding on the stem (Fig. 29a). While climbing on trees, members of this species do not roll into a ball after mechanical disturbance, only the head is tucked under the thoracic shield. Such arboreal behavior was previously reported only from South-African giant pill-millipedes of the genus *Sphaerotherium* (Haacker & Fuchs 1972).

No eggs were found in dissected females. The smallest juvenile stadium had 19 leg pairs. No matings were observed.

Predation: Tergites of smaller specimen of *Z. arborealis* were found in a layer of arthropod remains around ant holes of a big, red ant species in Mandena. This layer contained mostly seeds of plants and body rings of "juliform"-diplopods. Living rolled-up specimens of *Z. arborealis* were placed near ants and ant holes, but the ants did not attack the millipedes. One big (–35 mm body length) specimen of *Z. arborealis* was placed in a cage with a small mongoose (Viveriidae, *Galidia elegans*) from the forest of Mandena. The rolled-up pill millipede was detected immediately, broken with lateral teeth and eaten

by the mongoose, except for the intestines and tergites. It is quite possible that *Galidia elegans* is a natural predator of pill millipedes. One female collected in the littoral forest of Sainte Luce had fungi on the antennae. Specimens of all three localities were strongly covered with mites (Arachnida: Acari), it is unknown if this mites are commensals or parasites.

Conservation: This species has a wide distribution. One of the sites where *Z. arborealis* was collected is already protected. Nevertheless, the distribution of this species is scattered due to the vast destruction of natural forests on Madagascar.

TABLE 2: Differences between *Z. arborealis* **sp. nov.** and species with similar formed posterior telopods or anal shield. Abbreviations: tsh = thoracic shield; SR = stridulation ribs; aT = anterior telopods; pT = posterior telopods; O = operculum of vulva; # = number.
No material of *Z. lambertoni* (Brolemann, 1922) was studied, data taken from the literature.

Characters	***Zoosphaerium arborealis* sp. nov**	***Zoosphaerium anomalum***	***Zoosphaerium lambertoni***
body length	–40	20.25	–30
width of tsh	–20	10.5	15.0
surface of tergites	few hairs	polished	polished
SR females	irregular, 1–4	?	female unknown
SR males	2	1	2
last joint aT	2>3, 3rd broad, 2nd pointed	2>3, 3rd broad, oblong, 2nd pointed	2>3, 3rd broad, almost with two tips, 2nd pointed
O (size)	ending before apical edge of coxa	female unknown	female unknown
O (form)	Apical margin of operculum slightly constricted in the middle, inner part = exterior part	female unknown	female unknown
antennal cones	7–24	4	?
1st sternite	inner margin straight	inner margin almost straight, only near tip curved	inner margin straight
anal shield	sharp-edged	well-rounded	sharp-edged
locking carinae	2; 2nd 3–4x longer 1st	2; 2nd 2x longer 1st	2, medium-sized
coloration	brown	shining green	brown
pT 2nd joint sclerotized spots	present	small, present	absent
pT 3rd joint # spines	two lobe-like, 3–5 spines	two lobe-like, two spines	two lobe-like, 2–4 spines

Characters: Species delineation must rest on unique, species-specific characters or a combination of several such characters. Ideally, intraspecific variation of characters should be assessed. Intraspecific variation [with few exceptions (Holloway 1956)] of taxonomic characters of giant pill-millipedes was unknown, since most pill-millipede species were described on the basis of few specimens, mostly of one sex only. Below, we present data on the intraspecific variability of some of the characters used in the description.

Body length: The body length is very variable within the order Sphaerotheriida. Giant pill-millipedes molt (and grow) even when they are sexually mature (DeSaussure & Zehntner 1902). In *Z. arborealis* mature females have a body length between 21 and 40 mm. Conspicuous is the distinctly smaller size of males in comparison to females (diagrams 1,2) in *Zoosphaerium arborealis.* Males of *Zoosphaerium arborealis* have an average body length of 15 mm, the females of 25 mm. This sexual dimorphism is much more pronounced when comparing the width of the specimens (diagram 1). Males of this species also have a much lower weight than females.

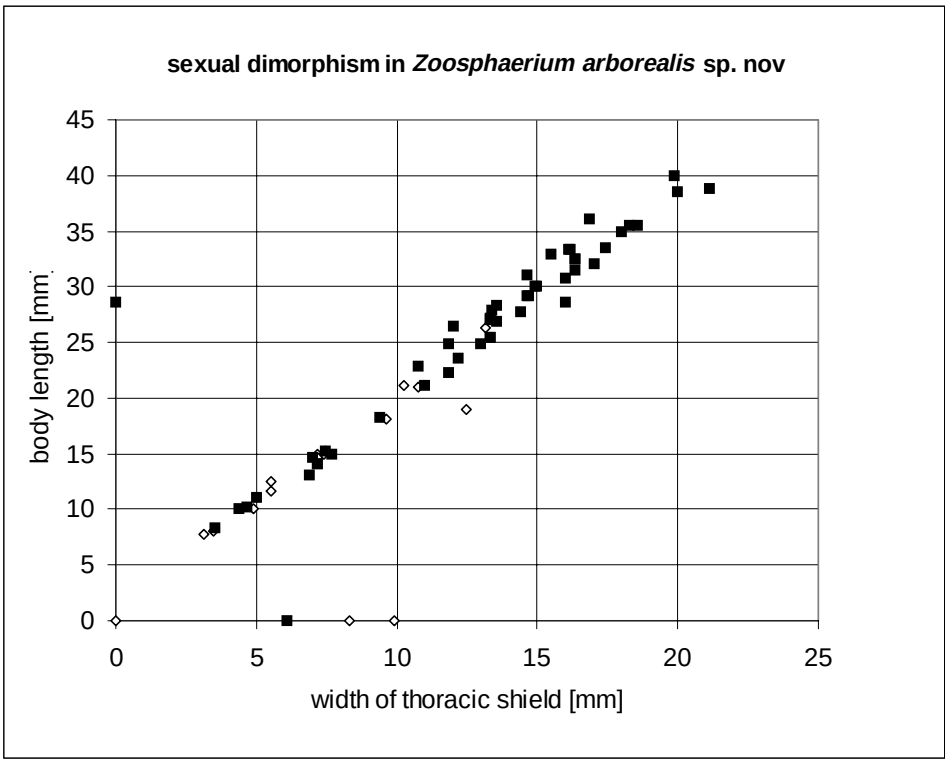


DIAGRAM 1: diamonds = males; squares = females

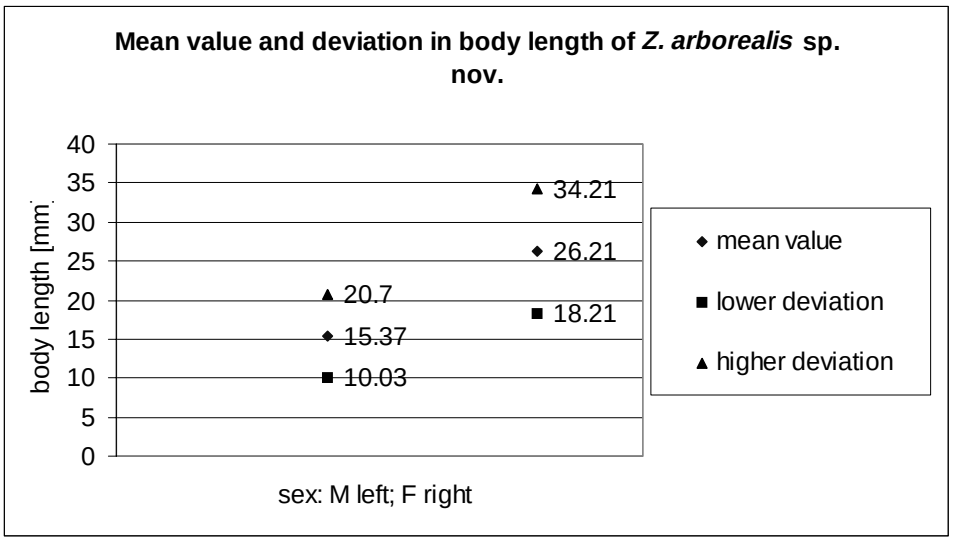


DIAGRAM 2.

Female washboard: DeSaussure & Zehntner (1902) indicated an apparent positive correlation between female body size and number of stridulation ribs on the female washboard. Here, this correlation was found in only a few numbers of specimens. In *Z. arborealis* the number of stridulation ribs varies substantially between 1 and 7.5, and does not correlate directly with the size of the specimens (diagram 3).

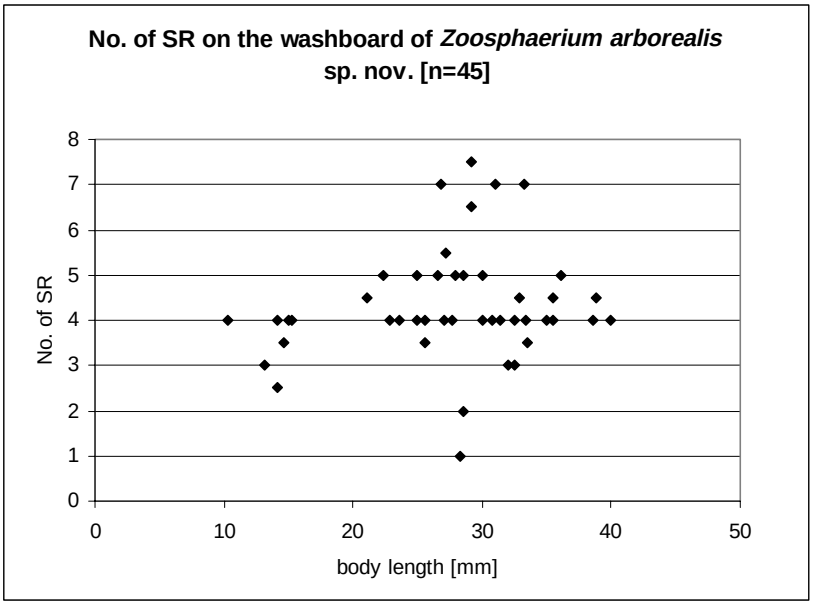


DIAGRAMM 3.

Female vulvae: The vulva of immature specimens is distinctly smaller than those of mature ones (Figs 29a–c), and simpler in structure, but the three plates of the vulva can be observed even in the smallest female (Fig. 29a). The size ratio of vulvae and coxae remains constant in mature females of different sizes; there is little or no variability in the form of the operculum and shape of cyphopod sclerites. Species-specific characteristics of the operculum shape are already present in immature individuals (Fig. 29b). Apparently, the millipede vulvae at least in Sphaerotheriidae, develop gradually over a number of molts, similar to the ontogenetic pattern observed in the female copulatory organs in spiders (Sierwald 1987).

Male telopods: DeSaussure & Zehntner (1897/1902), who illustrated the telopods of several Malagasy species in the order Sphaerotheriida, noticed the lack of variability in telopods in differently sized mature males. This study found no variation in the structure of telopods of mature males, not even in males of different populations.

During ontogeny, the male telopods develop their species-specific form over several molts. Already Verhoeff (1928: 683) commented that even very young (and small) Sphaerotheriida possess highly developed telopods, as soon as the animal possesses 19 segments: „*Es geht das noch weiter, als was Saussure (1902) von den Sphaerotheriiden angibt, daß nämlich die jungen Exemplare, die aber schon die volle Segmentzahl erreicht haben, vollkommen entwickelte Kopulationsfüße besitzen*.“ Telopods of immature males are of different shape. The anterior telopods are elongated and of very unusual shape. However, even the smallest males of *Z. arborealis* possess a chela at their posterior telopods. Almost mature males show blunt ending inner horns; the characteristic shape of the inner horns is present only in fully adult males (Figs 21e, 29e).

Male harp: The number of stridulation ribs on the harp in males of *Zoosphaerium arborealis* is intraspecificly constant, as opposed to the variable number of ribs on the washboard of females. All examined males with fully developed telopods carry two stridulation ribs on each harp. There was no variation in shape and trajectory of the ribs. Furthermore, even immature males feature two ribs on the harp (Fig. 29d).

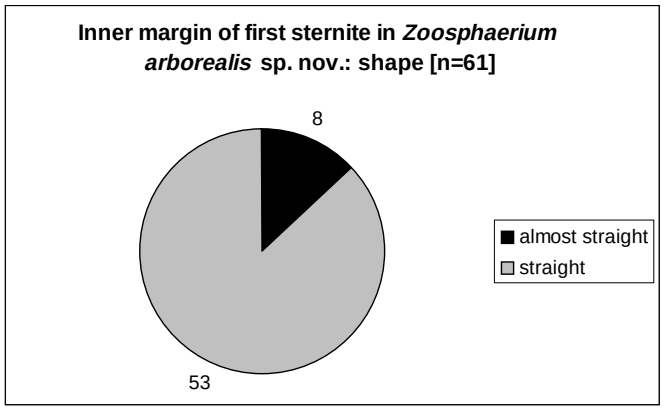


DIAGRAM 4.

First sternite: Brolemann was the first and only investigator who used the first sternite as a diagnostic character in his descriptions of sphaerotheriids (1922). Unfortunately, Brolemann had only four species with a few individuals each available for study. Consequently, he did not mentioned intraspecific variability for this character. The shape of first sternites in *Z. arborealis* varies to some extent. The inner margin of the first sternite is straight in mature and immature individuals (Fig. 29f). In only a few specimens we observed a slightly curved inner margin (Fig. 29g).

Hair coverage of tergites: Absence, presence and density of hair coverage of tergites were used as the most important taxonomic character in many species descriptions in the 19th century (Butler 1872, 1873, DeSaussure & Zehntner 1897/1902). More recently, investigations by Holloway (1956) and Van den Spiegel *et al.* (2002) demonstrated intraspecific variation of the hair coverage in New Zealand and South-African sphaerotheriid species. Likewise, we found strong individual variation in the species examined here. Almost bald specimens and individuals with patches of hairs on the anterior and posterior margin of tergites were found in the same populations.

Hair coverage of anal shield: Males of some giant pill-millipede species feature a patch of short (sensory?) hairs on the posterior margin of the anal shield (Van den Spiegel *et al.* 2002, Jeekel 1986). Some males of *Z. arborealis* possess such a patch of hairs, but this feature is not constant within populations. From 17 males only five feature such a patch of hairs, the other 12 show no trace of it.

Locking carinae of the anal shield: Already DeSaussure & Zehntner (1902: *carinules prémarginales*) used the closing ledges as characters for species differentiation. During volvation, these ledges fit over the brim of the thoracic shield (Verhoeff 1928), closing the body sphere tightly. The absence and presence, shape, length, position and number of ledges are useful for species determinations of Malagasy sphaerotheriids (DeSaussure & Zehntner, 1897/1902, 1901, Brolemann 1922). All 67 studied, non-juvenile specimens of *Z. arborealis* feature similarity formed closing ledges (Fig. 19c). The anterior carina is always short, the posterior ones are up to three times longer. The gap between the anterior and posterior carinae equals the length of the anterior carina. Juvenile specimen with only 19 pairs of legs and before reaching the full number of body rings feature locking carinae of a different shape; only one short ledge is present.

Shape of anal shield: The shape of the anal shield was also used in species descriptions by former authors (DeSaussure & Zehntner, 1897/1902, 1901, Brolemann 1922). A sexual dimorphism in shape of the anal shield was discovered recently in South-African and Australian giant pill-millipedes (Jeekel 1986, Van den Spiegel *et al.* 2003). All studied 68 specimens of both sexes of *Z. arborealis* lack such dimnorphios, instead the posterior margin of the anal shield is tapered in both males and females (Fig. 19a).

Number of sensory cones on antennae: In the past (Verhoeff 1928) the number of antennal sensory cones was employed for the delineation of families and genera within the order Sphaerotheriida. However, Silvestri (1917) and Jeekel (1974) rejected these as

apomorphic characters at the genus and family level. The almost ubiquitous presence of four sensory cones on the antennae appears to indicate such as the plesiomorphic condition within Diplopoda. Species with four or more than seven sensory cones appear in several tribes of sphaerotheriids, for example in South African, Malagasy and Australian representatives. The number of antennal cones proved useful for species diagnoses (Silvestri 1917, Van den Spiegel *et al.* 2003). Verhoeff (1928) described a remarkable sexual dimorphism in one species of the family Sphaeropoeidae. In this species, males feature about 100 sensory cones, whereas females possess around 40 antennal cones. The here studied species Z. *arborealis* shows a high variation in the number of sensory cones; the variation is not correlated with sex or body length of individuals (diagrams 5, 6).

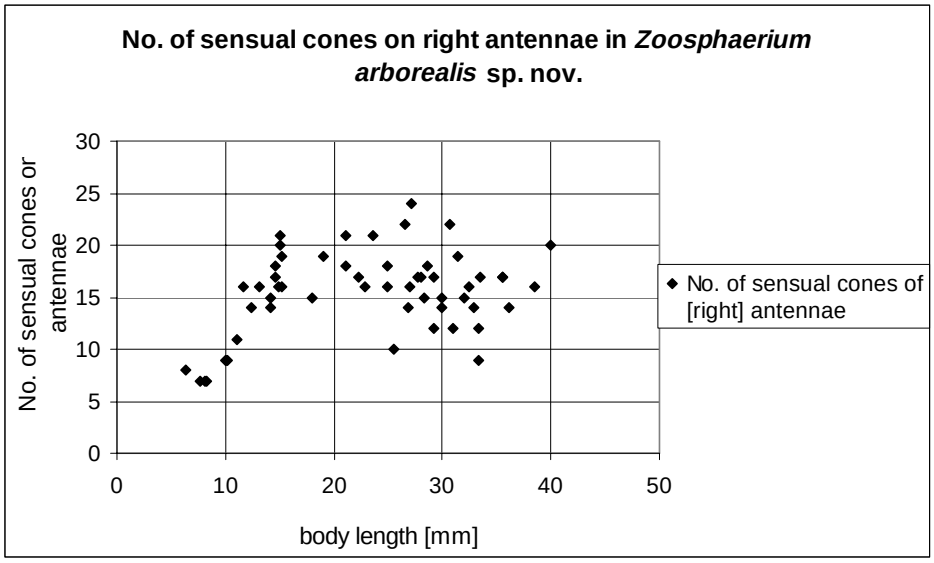


DIAGRAM 5.

Tooth on labrum: This character was used in some species descriptions, e.g., by Chamberlin (1921). Such a tooth is present in all studied Malagasy giant pill-millipedes and furthermore present in South-African and Indian material, and in members of the family Sphaeropoeidae. Possibly, the labrum tooth is present in all members of the order Sphaerotheriida and one of the many characters demonstrating the homogeneity inside this diplopod order. Form and shape of the labrum tooth vary due to abrasion (and viewing angle under the microscope). Thus, this character is not useful for species delineations within sphaerotheriids.

Hairs on clypeus and around the labrum: All specimens examined featured pits with hairs, or at least pits with missing hairs around the labrum. No species- or genus-specific patterns were observed.

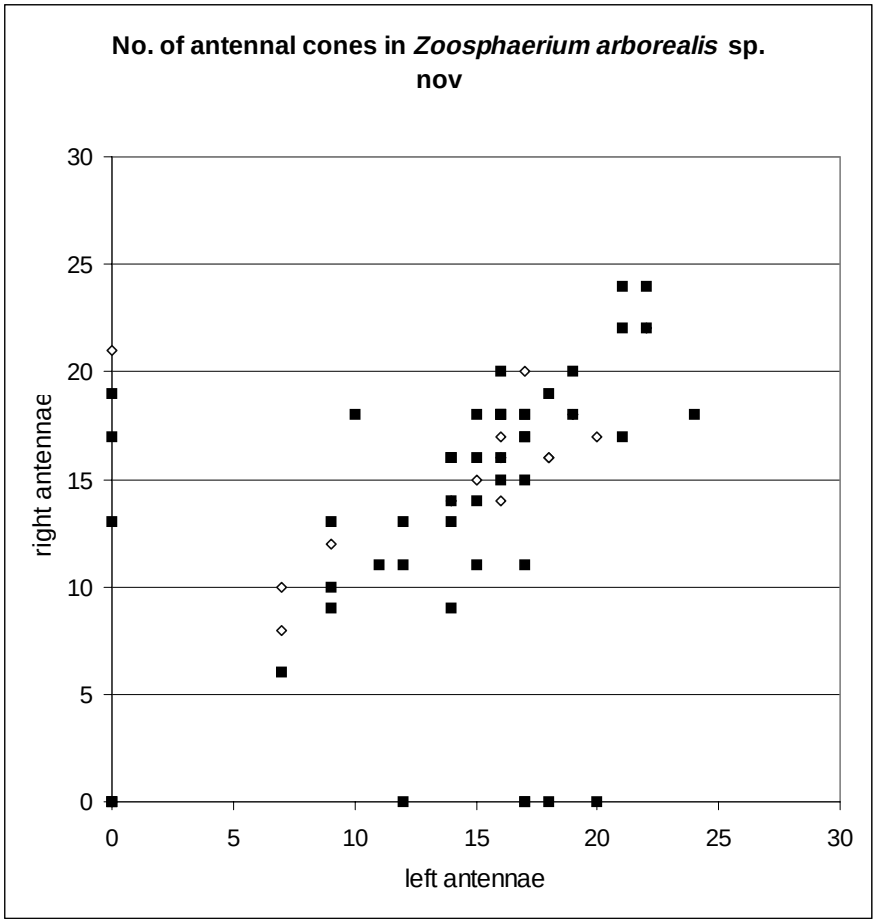


DIAGRAM 6: diamonds = males; squares = females.

Number of ocelli: All Sphaerotheriida possess a high number of ocelli, located in two lateral clusters on the head (Verhoeff 1928). On either side one ocellus is displaced laterally of the ocelli cluster (Fig. 23c). With 80–100 ocelli per cluster, the Sphaerotheriida may feature the highest number of ocelli within the Diplopoda. However, species with much fewer ocelli occur. Smaller, younger individuals possess almost the same number of ocelli as fully grown animals, but the ocelli are smaller than in adults. Juvenile specimens examined here have much fewer ocelli, arranged not in a cluster, but in a crescent-shaped patch.

Shape and position of the Tömösváry-organ: Shape and position of the Tömösváry organ are constant within the order Sphaerotheriida (Verhoeff 1928) (Fig. 23b). Possibly, morphological differences can be discerned, however, these require scanning electron microscopy (Fig. 23 e). Currently, scarcity of specimen material hampers the full investigation of this feature.

Epipharynx: The epipharynx is large and prominent in the order Sphaerotheriida. Comparison with literature data (Verhoeff 1928) and our own observation (Figs 6c, 7a, 15b, 26b, 27a) demonstrate that the epipharynx is rather uniform within this millipede group. Despite intensive search, neither species- nor genus-specific characters were detected.

Gnathochilarium: The gnathochilarium sclerites appear to be rather uniform in the order. Only the Rajasphaerinae (family Sphaeropoeidae, Hoffman 1976) feature a distinct gnathochilarium shape. Slight differences in hair density occur within the group.

The central pads and lateral sensory cones of palpi present a few useful characters, at least for species delineations. Different species feature varying numbers and types of sensory cells on the central pads (Figs 6b, 25a). Lateral of palpi are also some sensory cells, whose number and location are species-specific characters. Verhoeff (1928) was the first to mentioned these structures and interpreted them as rudimentary external palpi. The location of sensorial cones on the tip of gnathochilaria palpi may also be a taxonomic character, but in all four *Zoosphaerium* members the sensorial cones were distributed regularly (Fig. 25b). Additional material is needed to investigate the variability of these features.

Mandible: New studies indicate, that the mandible of diplopods bears several taxonomic relevant characters (Ishii & Tamura 1995; 1996). The mandibles of Sphaerotheriida were never used before as characters, no SEM-photos were ever published. Thus, taxonomic characters present in sphaerotheriid mandibles were unknown. There is indeed a striking uniformity of the mandible inside the order Sphaerotheriida. The sphaerotheriid mandible has a unique feature, the prominent molar plate process (mpp), which may function as a condylus (Figs 8a, 8c). On the tip of the molar plate process some species-specific furrows and steps are present.

Discussion

The authors are aware of the fact that most Malagasy Sphaerotheriida are in urgent need of revision. The genus *Sphaeromimus* was redescribed recently (Wesener & Sierwald, in press). Status and species composition of the second Malagasy genus *Zoosphaerium* Pocock, 1895 remains unresolved. A revision of all 34 nominal species of this genus, most of them insufficiently described, is in preparation. The most important (and in many descriptions only illustrated) taxonomic characters, the male telopods and female vulvae, are identical in clearly distinct species. Examination of new character suites to identify new species- and species-group-specific characters is required. Monophyletic species-groups will need to be identified to accommodate the already described species as well as the estimated 70 to-be-described species belonging to the *Zoosphaerium* species complex.

The species described here are all from the east Malagasy littoral forest, one of the most threatened ecosystems of the world (Lowry *et al.* 2001, deGouvenain & Srilander

2003); mining is proposed to start in Mandena, Petriky and Sainte Luce in 2006. This fact was the main reason to described these species at this time. Furthermore, three of the species are endemic to one isolated forest fragment only. The authors hope that this work provides an argument to improve the protection of the Malagasy littoral forest ecosystem.

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