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Madagascar's living giants: discovery of five new species of endemic giant pill-millipedes from Madagascar (Diplopoda: Sphaerotheriida: Arthrosphaeridae: *Zoosphaerium*)

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ABSTRACT

Five new species of the endemic giant pill-millipede genus *Zoosphaerium* from Madagascar are described: *Z. muscorum* sp. n., *Z. bambusoides* sp. n., *Z. tigrioculatum* sp. n., *Z. darthvaderi* sp. n., and *Z. heileios* sp. n. The first three species fit into the *Z. coquerelianum* species-group, where *Z. tigrioculatum* seems to be closely related to *Z. isalo* Wesener, 2009 and *Z. bilobum* Wesener, 2009. *Z. tigrioculatum* is also the giant pill-millipede species currently known from the highest elevation, up 2000 m on Mt Andringitra. *Z. muscorum* and *Z. darthvaderi* were both collected in mossy forest at over 1000 m (albeit at distant localities), obviously a previously undersampled ecosystem. *Z. darthvaderi* and *Z. heileios* both possess very unusual characters, not permitting their placement in any existing species-group, putting them in an isolated position. The females of *Z. xerophilum* Wesener, 2009 and *Z. pseudoplatylabum* Wesener, 2009 are described for the first time, both from samples collected close to their type localities. The vulva and washboard of *Z. pseudoplatylabum* fit very well into the *Z. platylabum* species-group. Additional locality and specimen information is given for nine species of *Zoosphaerium*: *Z. neptunus* (Butler, 1872); *Z. villosum* Wesener & Sierwald, 2005; *Z. amabile* Wesener, 2009; *Z. tampolo* Wesener, 2009; *Z. smaragdinum* Wesener, 2009; *Z. viridissimum*, Wesener, 2009; *Z. pseudopitigerum* Wesener, 2009; and *Z. analavelona* Wesener, 2009.

KEY WORDS: Diplopoda, Sphaerotheriida, Afrotropical, Madagascar, giant pill-millipedes, new species.

INTRODUCTION

Madagascar, the world's fourth largest island, harbours a high number of species of plants and animals that are unique worldwide and is therefore regarded as one of the most important biodiversity hotspots (Myers *et al.* 2000) and a model region for the study of species diversification (Vences *et al.* 2009). Many of the endemic species which exist only on Madagascar are still undescribed (Vieites *et al.* 2009).

The giant pill-millipedes, whose Malagasy name is Tainkintana (star droppings), undoubtedly are among the most conspicuous mega-invertebrates of the island. All giant pill-millipedes (order Sphaerotheriida) have a relatively uniform outer appearance; a body of 12 tergites of which the first (the collum) is very small and the second (the thoracic shield) is laterally concave (Fig. 1). The posterior body end is covered with a hemispherical anal shield (Fig. 1). All Sphaerotheriida are capable of rolling into a perfect ball as a defence mechanism. The anal shield fits into the concave lateral part of the thoracic shield in order to roll up, completely covering the head and the collum. The anal shield even carries special sclerotised 'locking carinae' on its underside, which the giant pill-millipede can use to lock itself up from the inside.

The three Malagasy genera *Sphaeromimus* de Saussure & Zehntner, 1902, *Microsphaerotherium* Wesener & VandenSpiegel, 2007 and *Zoosphaerium* Pocock, 1895 are all strictly endemic and, together with the Indian genus *Arthrosphaera*, comprise the family Arthrosphaeridae (Wesener & VandenSpiegel 2009), which currently incorporates 95 species. All Arthrosphaeridae share stridulation organs as important apomorphies in



Fig. 1. *Zoosphaerium muscorum* sp. n., holotype, 36.5 mm long, watercolour drawing, habitus, natural coloration with some artistic improvisation in the shading and highlights.

both the female (the washboard) and the male sex (the harp). These stridulation organs are a unique feature for millipedes. The genera from Madagascar, however, do not form a monophylum: *Sphaeromimus* is more closely related to *Arthrosphaera* from India than to *Zoosphaerium* and *Microsphaerotherium* from Madagascar (Wesener & VandenSpiegel 2009).

Currently, 55 species of giant pill-millipedes are known from Madagascar, of which three belong to *Sphaeromimus*, two to *Microsphaerotherium* and the majority (about 50 species) to *Zoosphaerium*. The genus *Microsphaerotherium* was recently discovered in Madagascar and incorporates the smallest known giant pill-millipede species (adults of *M. ivohibiense* Wesener & VandenSpiegel, 2007 are less than 10 mm long), which are probably adapted to a life deep inside the soil (Wesener & VandenSpiegel 2007). However, some species of *Zoosphaerium* (e.g., *Z. neptunus* (Butler, 1872)) display island gigantism where rolled-up specimens can reach a size comparable to a baseball or small orange (Wesener & Wägele 2008). Therefore, both the smallest (*Microsphaerotherium ivohibiense*) as well as the largest (*Zoosphaerium neptunus*) giant pill-millipede species live only on Madagascar.

Despite their peculiarity, the Malagasy giant pill-millipedes are severely understudied. Almost no study was undertaken after a period of major groundwork done more than a century ago (de Saussure & Zehntner 1897, 1902). Their ecology, development and life history are virtually unknown. Thirty-six out of 55 species (excluding *nomina dubia* and species only known from females) were first described only within the last five years (Wesener & Wägele 2008), 31 of those in the last year alone (Wesener 2009). The inventory of giant pill-millipedes from Madagascar, however, seems to be far from complete. New samples from the California Academy of Sciences and the Field Museum of Natural History collected during general inventory programmes, mainly from previously unsampled areas, included five new species all belonging to the genus *Zoosphaerium* (Fig. 2). This brings the total number of Arthrosphaeridae species known to 100. Additional material included the first known females of *Z. xerophilum* Wesener, 2009 and *Z. pseudoplatylabum* Wesener, 2009.

MATERIAL AND METHODS

Abbreviations:

- BLF – Collection code for Madagascar sample at CASC;
- CASC – California Academy of Sciences, San Francisco, USA;
- FMNH – Field Museum of Natural History, Chicago, USA;
- FMNH-INS – Millipede collection code for samples at FMNH;
- ZMUC – Zoological Museum, University of Copenhagen, Denmark.

The material accumulated by Brian Fisher and Charles Griswold (CASC), Steve Goodman (FMNH), Miguel Vences (Braunschweig), and Jörn Köhler (Mainz), was collected using pitfall traps or hand-collecting during general inventory programmes. Specimens were dissected (see Wesener & Sierwald 2005*b* for a description), and important structures were drawn using a standard *camera lucida* mounted on an Olympus SZX12 stereomicro-

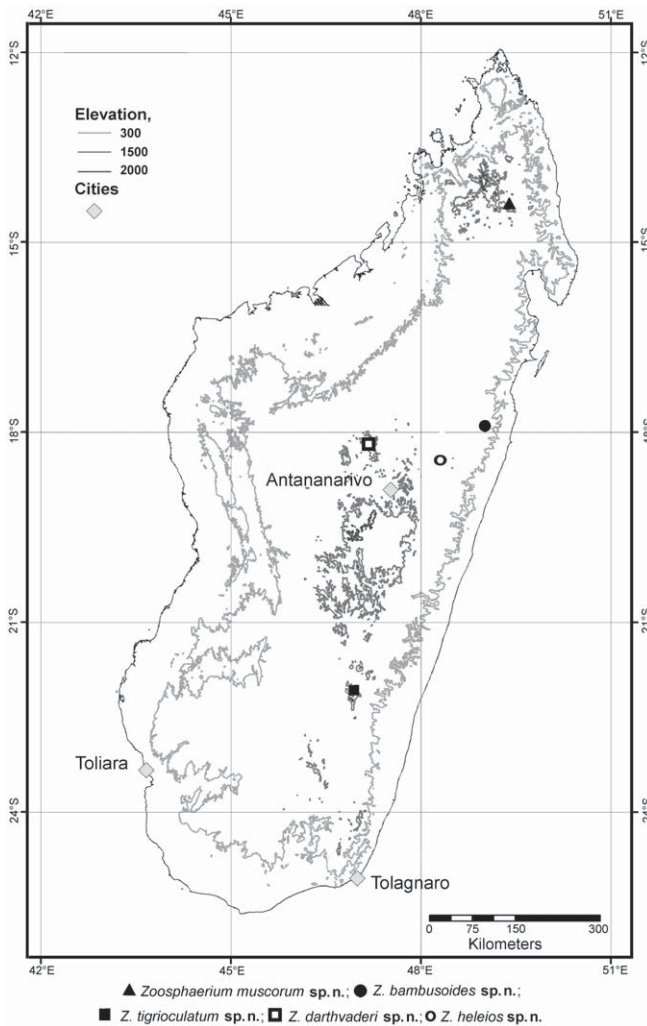


Fig. 2. Distribution map of new *Zoosphaerium* species.

scope. Watercolour illustrations were made following a method taught by Peggy Macnara, where many light washes of watercolour pigment were laid down in contrasting colours to build up tones, and then several thin washes were built up to add colour and highlights. Artistic licence was taken in the choices of highlight and shadow, though the overall colour is fairly accurate. For scanning electron microscopy, samples were cleaned and dehydrated in an ethanol series (80 %, 90 %, 95 % and twice in 100 %) and air-dried overnight. The samples were then mounted on aluminium stubs before being coated with gold in a sputter coater for 240 seconds. SEM micrographs were taken using a Zeiss Leo EVO SEM, based at the FMNH. Dry SEM material was removed from stubs and returned to alcohol. All images were later modified using Adobe Photoshop CS2 and assembled into plates using Adobe Illustrator CS2.

TAXONOMY

The terminology used in this paper has been explained extensively in other recent works (Wesener & Sierwald 2005*b*; Wesener 2009) and is strictly followed here. An assignment of *Zoosphaerium* species to species-groups was undertaken by Wesener and Wägele (2008). The grouping into species-groups is based mainly on the shape of the posterior telopods (*Z. libidinosum*, *Z. coquerelianum*, *Z. piligerum* and *Z. blandum* species-groups) or a combination of characters found on the anal shield and female vulva (*Z. platylabum* species-group). However, it is currently unclear if these species-groups indeed represent monophyletic units: a phylogenetic analysis of *Zoosphaerium* species would be necessary to confirm this hypothesis. Currently, however, the system of species-groups that is in place helps sort the species of *Zoosphaerium*.

New species assigned to the Zoosphaerium coquerelianum species-group

***Zoosphaerium muscorum* Wesener & Bespalova, sp. n.**

Figs 1, 3–5, 17A

Etymology: From Latin *muscorum* (mossy), referring to the type locality, a mossy forest, as well as to the green colour (Fig. 1) of this species.

Differential diagnosis: The thick posterior telopods of *Z. muscorum* sp. n. (Figs 4A–C) can only be confused with those of *Z. tampolo* Wesener, 2009. However, the colour (Fig. 1), shape of the first sternite (Fig. 3C), number of stridulation ribs on the male harp (Fig. 3E), and the shape of the anal shield (at least in the male) in *Z. muscorum* (Figs 3A, B) are different from those of *Z. tampolo*. *Z. muscorum* is the only known Sphaerotheriida species with only up to seven ventral spines on the walking legs (Fig. 3D).

Description:

Male.

Body length: Holotype: length 36.5 mm, width of thoracic shield 17.1 mm, height of thoracic shield 10 mm.

Habitus: Medium sized, mostly glabrous pill-millipede. Very few short and even fewer longer hairs sparsely dispersed along tergites, mostly seen at margins.

Colouration: Some discolouration may have occurred because of preservation in alcohol. Tergites shiny, dark olive-green with a very thin dark khaki rim at posterior edge of tergite (Fig. 1). Anal shield same as tergites. Upper part of legs olive-green, ending in

banana-yellow colour at tip that covers 3/4 of tarsus. Collum olive-green, with a large yellowish spot covering most of the medial area. Compared to tergites, antennae are more bluish green and head brighter green.

Head: Eyes with 106 or 107 ocelli. Antennae long and thin, with cylindrical joints (Fig. 5A). Length of antennomeres: 1=2>3>4=5<6. Sclerotised teeth present basally of

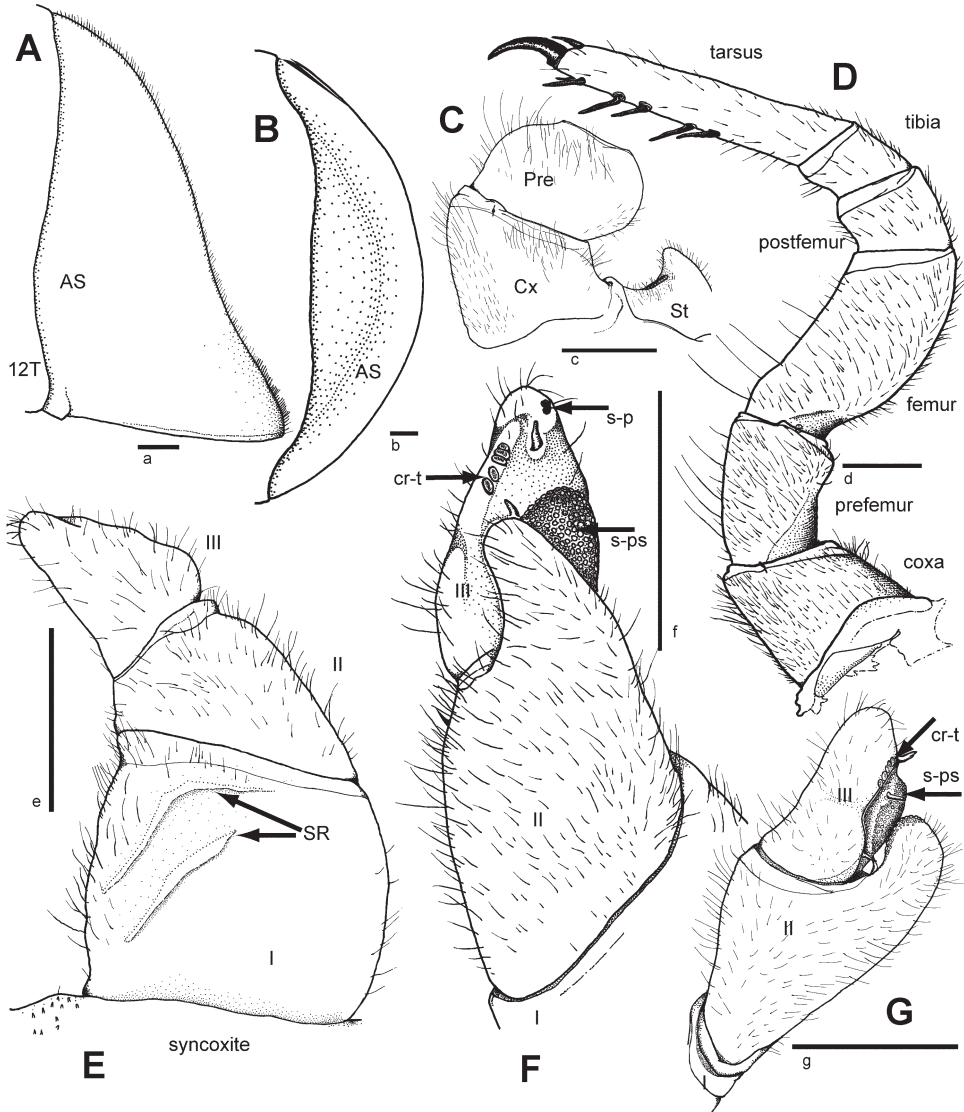


Fig. 3. *Zoosphaerium muscorum* sp. n., holotype: (A) anal shield, lateral view; (B) anal shield, dorsal view; (C) coxa and prefemur of first left leg with first stigmatic plate, posterior view; (D) 9th left leg, posterior view; (E–G) right anterior telopod: (E) anterior view, (F) posterior view, (G) lateral view. Roman numerals refer to number of podomere. Abbreviations: 12T – tergite 12, AS – anal shield, cr-t – crenulated, sclerotised teeth, Cx – coxa, Pre – prefemur, s-p – sclerotised spot, s-ps – field of sclerotised spots, SR – stridulation ribs, St – stigmatic plate. Scale bars = 1 mm.

antennomere 1–2. First antennomere with shallow groove but without sensilla basiconica. Apical disc bearing 23–25 sensory cones (Fig. 5B). Mouthparts not dissected. Collum glabrous, with very sparse setae around margins, mostly located on corners at either side of head.

Thoracic shield: Surface like tergites.

Tergites: Surface completely smooth, waxy, and shiny, with no pits and very few hairs. Alcohol seems to quickly bead up and run off of specimen. Under magnification (50×) tergites display a leather-like pattern. In SEM imaging, surface is shown to be covered in miniscule pits holding stubby spines (sensorial setae?). Specimen quickly dries once out of alcohol. Tips of paratergites projecting posteriorly and form sharp points.

Endotergum: Double row of marginal bristles reaching 2/3 of distance to edge of margin. Single row of large, elliptical cuticular impressions. Internal section with short spines and very few isolated long bristles (Fig. 17A).

Anal shield: Slight bell shape; top of bell a simple gradual slope, bottom exhibits bell-like flare. Entire surface covered by a carpet of short hairs. Underside carrying two black locking carinae, anterior one very short, about 1/5 length of posterior one. Carinae separated by a space about as long as 2 times anterior carina. Posterior carina slightly curved towards margin of anal shield.

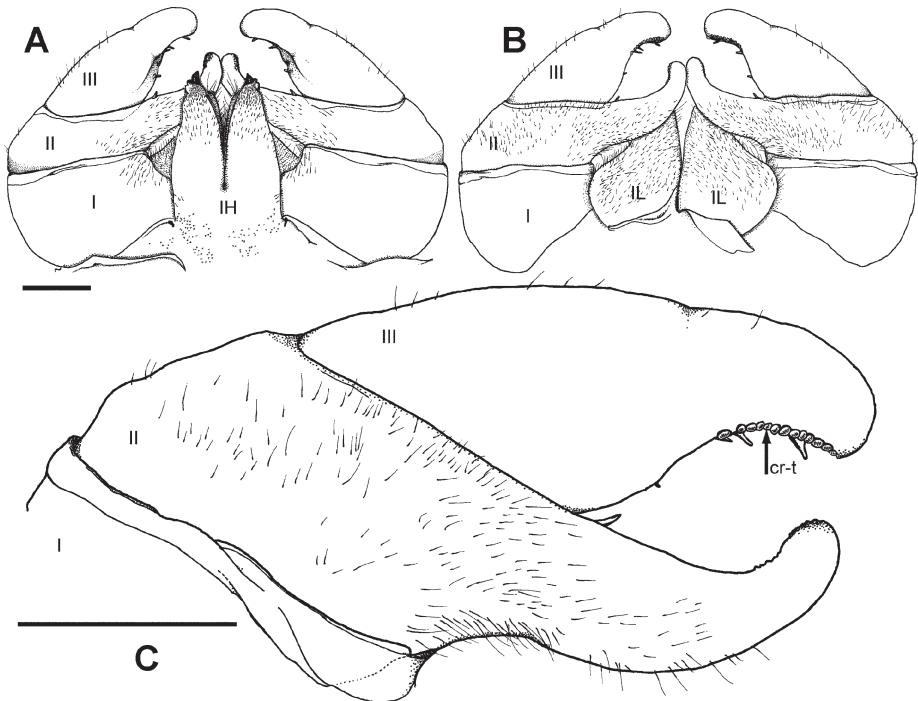


Fig. 4. *Zoosphaerium muscorum* sp. n., holotype, posterior telopods: (A) anterior view; (B) posterior view; (C) right posterior telopod, posterior view, detail. Roman numerals refer to number of podomere. Abbreviations: cr-t – crenulated, sclerotised teeth, IH – inner horns, IL – inner lobes. Scale bars = 1 mm.

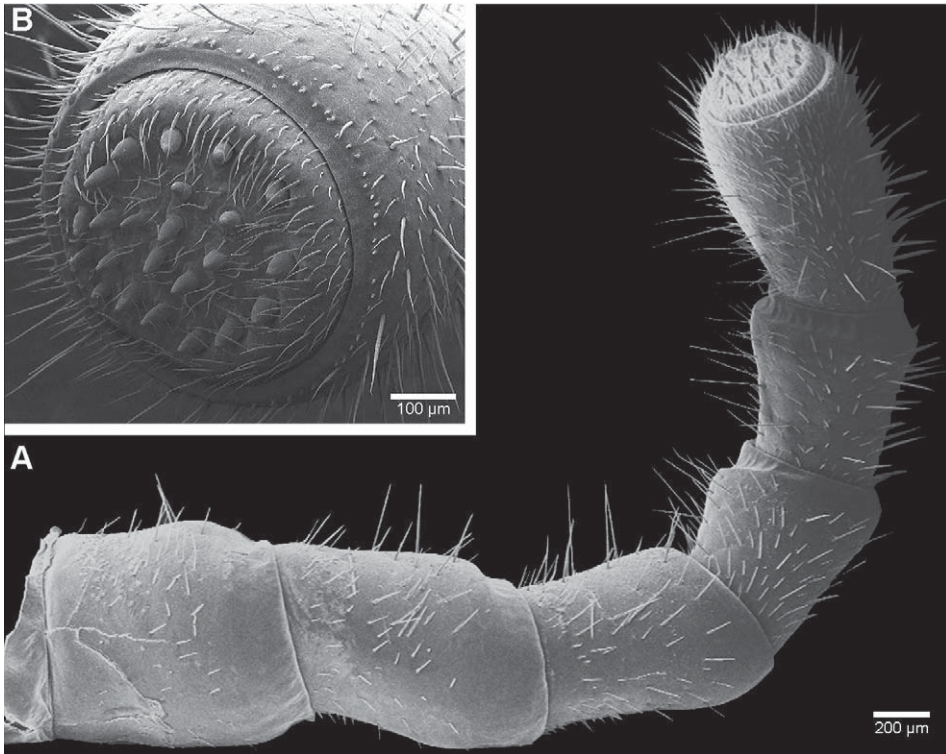


Fig. 5. *Zoosphaerium muscorum* sp. n., holotype, left antenna, SEM: (A) lateral view, (B) apical view on disc.

Legs: Tarsi 1 with 4, 2 with 5 or 6, 3 with 5 or 6, and 4–21 with 5–7 ventral spines. First 3 leg pairs with an apical spine. Tarsi of legs 4–21 with an apical spine. In leg 10, femur 1.87 \times , tarsi 5.3 \times longer than wide (Fig. 3D).

Stigmatic plates: First plate with triangular lobe, short and stout, curved towards coxa (Fig. 3C).

Female. Unknown.

Male sexual characters: Gonopore covered with a single, undivided, rounded sclerotised plate. Apical portion of plate membranous. Covers 1/2 height and 1/2 width of coxa. Anal shield forms slight bell shape and entire surface covered by a carpet of short hairs (Figs 3A, B).

Anterior telopods (Figs 3E–G): Harp with two strongly pronounced stridulation ribs—one long and well pronounced rib located mesally of a less pronounced and shorter one. On anterior side, several tiny sclerotised spines located on mesal margin of syncoxite. Process of second podomere bent laterally and hooked towards third podomere, apex covered with sclerotised spots. One large sclerotised spine located basally, juxtaposed to similar spine on third podomere. Third podomere slightly cupped towards second podomere; contains several divided and slightly lobed areas. One large lobed area on mesobasal side covered with a mound of sclerotised spots. On lateral side, two slightly lobed edges, the more apical one includes five sclerotised, crenulated teeth. Apical

lobed area includes a large forked spine below a brown sclerotised spot. A third spine located underneath forked spine next to the large lobe of sclerotised spots.

Posterior telopods (Figs 4A–C): Movable finger thick (1.97× longer than wide), weakly curved, and abruptly tapering apically giving finger a gourd-like appearance. Shallowly hollowed out inner margin with four sclerotised spines, one positioned apically, two (one positioned below the other) in middle of cavity, and one located at base of hollow. On apical posterior margin 12–14 sclerotised, crenulated teeth in a row. Fixed finger almost as long as, and hooked towards, movable finger. Sclerotised spine located on mesal side near base of fixed finger. Inner part of fixed finger tip covered with many sclerotised spots. Movable finger completely glabrous on both sides except for a few hairs on lateral portion, second podomere with numerous hairs on both sides. On anterior side of first podomere a small patch of hair present mesally. Tips of inner horns curved inward, base of inner horns covered by patches of many tiny sclerotised spines.

Holotype: ♂ (FMNH-INS 7898). MADAGASCAR: *Antsiranana* Prov.: western slope of Anjanaharibe-Sud, 13.0 km SW Belfingotra, 1600 m, mossy forest, 14°45.9'S:49°25.9'E, S.M. Goodman, 4–9.xi.1999.

Distribution & Ecology: *Z. muscorum* is currently only known from the Mountain of Anjanaharibe in north-eastern Madagascar (Fig. 2). It is possible that this species is restricted to the mossy forest on this mountain. The polished appearance of the surface might be related to the fact that this species probably lives in very wet surroundings, and the smoothness prevents water drops sticking to the cuticle.

***Zoosphaerium bambusoides* Wesener & Bespalova, sp. n.**

Figs 6–8, 17B

Etymology: The name refers to the bamboo-like colour of the species.

Differential diagnosis: The posterior telopods (Figs 7A–C) clearly mark *Z. bambusoides* as a member of the *Z. coquerelianum* species-group. The body size, colour, and shape of the posterior telopods closely resemble those of *Z. smaragdinum* Wesener, 2009. *Z. bambusoides* differs from the latter in the presence of up to 10 spines on the walking legs (Fig. 6C), a tarsal spine on leg 3, 27–29 and sensory cones on the antenna (Fig. 8B), the absence of sclerotised teeth on antennomere 4 (Fig. 8A), longer marginal bristles on the endotergum (Fig. 17B), and the absence of a membranous lobe on the posterior telopods (Fig. 7C).

Description:

Male.

Body length: Holotype: length 22.7 mm, width of thoracic shield 12.4 mm, height of thoracic shield 6.5 mm.

Habitus: Small, glabrous pill-millipede (Fig. 6A).

Colouration: Some discolouration may have occurred because of preservation in alcohol. When observed in alcohol, tergites reminiscent of bamboo leaves. Tergites vibrant dark green with thin sand-coloured strip at posterior margin. Dorsal side of anal shield same colour as tergites, while ventral side of anal shield, as well as ventral side of thoracic shield under light has a bright teal tint. Legs close to colour of tergite, though with teal-tinted tarsi. Head and collum also close to colour of tergite, though with a more yellow tint, and brown area around the mandibles. Antennae olive-green.

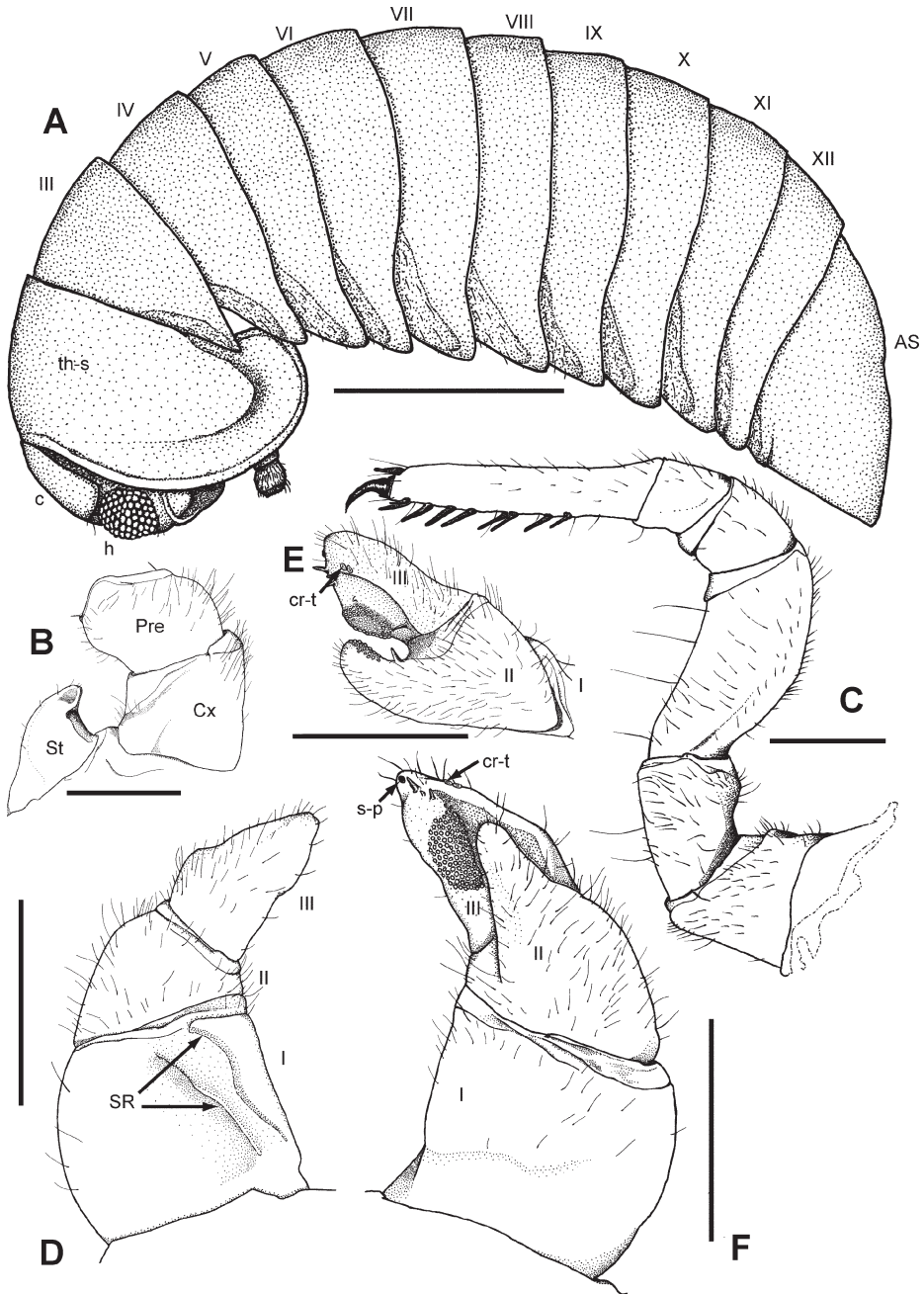


Fig. 6. *Zoosphaerium bambusoides* sp. n., holotype: (A) habitus, lateral view; (B) coxa and prefemur of first right leg with first stigmatic plate, posterior view; (C) 9th left leg, posterior view; (D–F) left anterior telopod: (D) anterior view, (E) lateral view, (F) posterior view. Roman numerals refer to number of podomere or tergite. Abbreviations: c – collum (tergite 1), h – head, AS – anal shield, cr-t – crenulated, sclerotised teeth, Cx – coxa, Pre – prefemur, s-p – sclerotised spot, SR – stridulation ribs, St – stigmatic plate, th-s – thoracic shield (tergite 2). Scale bars: (A) = 10 mm, (B–F) = 1 mm.

Head: Eyes with *ca* 92 ocelli. Antennae long and thin, with cylindrical joints (Fig. 8A). First antennomere with groove but without sensilla basiconica. Sclerotised teeth at base of antennomere 1–3. Length of antennomeres: $1 > 2 = 3 > 4 > 5 < 6$. Apical disc bearing 27–29 sensory cones (Fig. 8B). Mouthparts not dissected. Collum glabrous, with 1–3 setae at corners on either side of head.

Thoracic shield: Surface like tergites.

Tergites: Surface glabrous, shiny, covered with minute depressions like orange peel (50×). Tips of paratergites project posteriorly, forming sharp points (Fig. 6A).

Endotergum: Single row of marginal bristles reaching 2/3 of distance to edge of margin. Single row of elliptical cuticular impressions. Internal section with short spines and very few isolated long bristles (Fig. 17B).

Anal shield: Fairly well-rounded with a very slight indication of a bell shape because of a small bulge toward dorsal side (Fig. 6A). Surface like tergites. Underside carrying two brown locking carinae, anterior one very short, about 1/6 the length of posterior one. Carinae separated by a space about as long as 2× the anterior carina. Posterior carina slightly curved towards margin of anal shield.

Legs: Tarsi 1 with 5, 2 with 6, 3 with *ca* 7, and 4–21 with 8–10 ventral spines. First two leg pairs with an apical spine. Tarsi of legs 4–21 with an apical spine. In leg 10 femur 1.89×, tarsi 5.4× longer than wide (Fig. 6C).

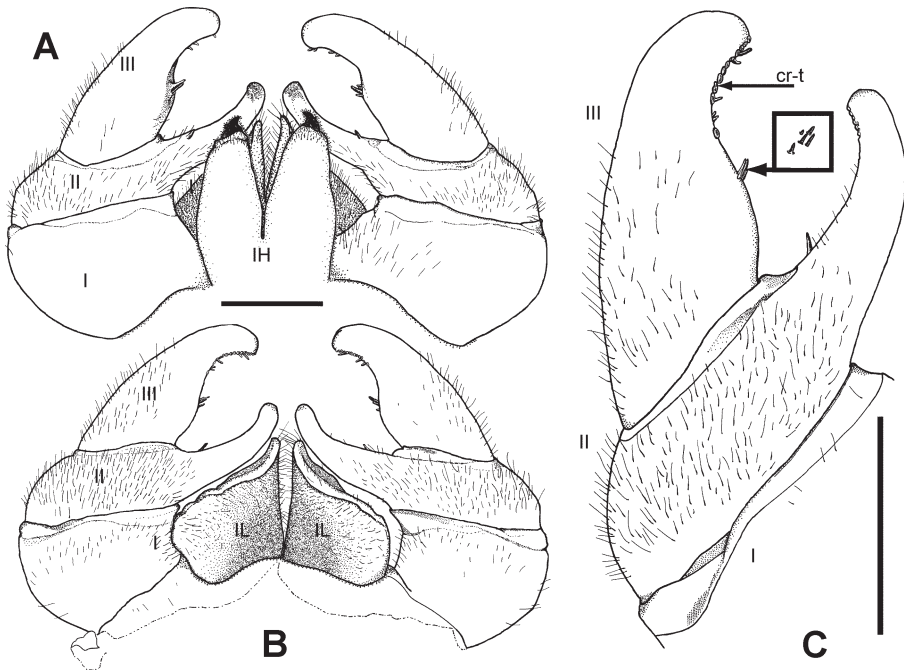


Fig. 7. *Zoosphaerium bambusoides* sp. n., holotype, posterior telopods: (A) anterior view; (B) posterior view; (C) right posterior telopod, posterior view, detail. Roman numerals refer to number of podomere. Abbreviations: cr-t – crenulated, sclerotised teeth, IH – inner horns, IL – inner lobes. Scale bars = 1 mm.

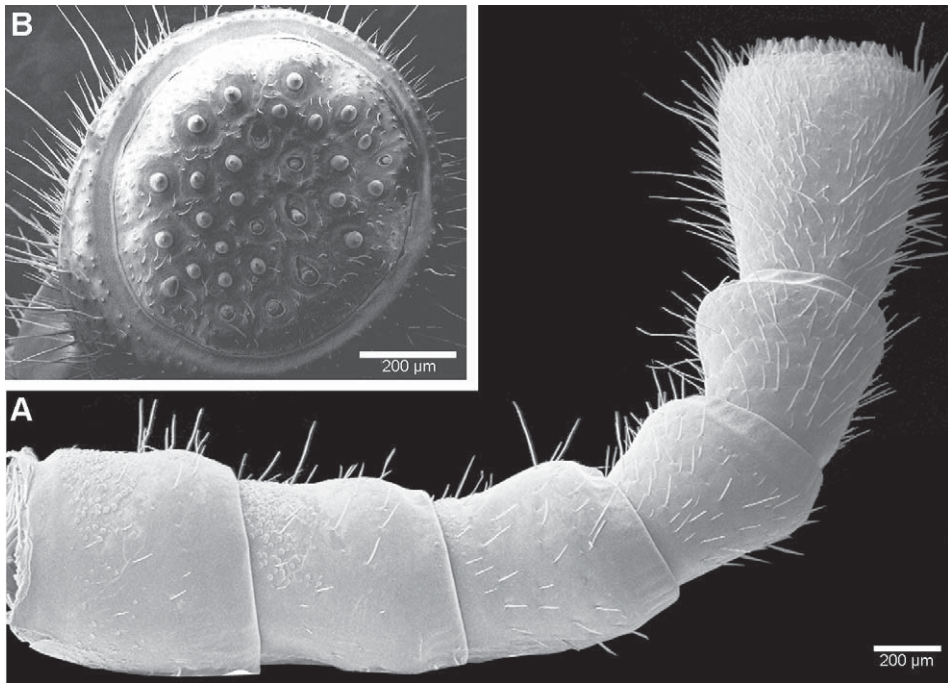


Fig. 8. *Zoosphaerium bambusoides* sp. n., holotype, left antenna, SEM: (A) lateral view, (B) apical view on disc.

Stigmatic plates: First plate with triangular lobe. Lobe short and stout, with a thin, pinched, triangular area at apex projecting towards coxa (Fig. 6B).

Female. Unknown.

Male sexual characters: Gonopore covered with a single undivided, elliptical sclerotised plate. Small apical portion of plate membranous. Covers 1/2 height and 2/3 width of coxa. Anal shield with slight bell shape, glabrous.

Anterior telopods (Figs 6D–F): Harp with 2 strongly pronounced stridulation ribs – one long and well pronounced rib lying mesally to a less pronounced and shorter one. Top rib steep and step-like. Process of second podomere slightly hooking towards third podomere; apical portion facing third podomere covered with sclerotised spots. Below spots at base of projection lies a sclerotised spine. Third podomere basally also includes sclerotised spine. Large lobe covered by a mound of sclerotised spots located on mesal half of process. Deep concavity located on lateral half. Vertical row of three spines lying at apex following a brown sclerotised spot. Two sclerotised, crenulated teeth sitting on apicolateral margin of concavity. Small fifth sclerotised spine lying close to lateral margin of mound of sclerotised spots. Anterior telopods curve gently towards each other, creating a circular laurel wreath shape more than a horseshoe shape.

Posterior telopods (Figs 7A–C): Movable finger moderately thick (2.46× longer than wide), weakly hooking towards fixed finger. In total, there are 10 sclerotised spines located mesally on movable finger; 5 in a clump on a raised mound located in middle of process (4 arranged in a square, with a tiny fifth spine located basally), 2 apically, and

3 laterally of medial area in a triangular formation. On apical posterior margin are 14 sclerotised, crenulated teeth. Fixed finger slightly shorter than movable finger, curving towards latter. Sclerotised spine located basally. Tip of fixed finger flat, inner part containing a slightly squared off depression. Area above depression covered by a few sclerotised spots. Some sparse hair located on movable finger on upper half of posterior side, and on lateral margin of anterior side. Second podomere covered by numerous hairs on anterior and posterior sides. First podomere with some hairs on upper portion of posterior side as well as mesal portion of anterior side. Inner lobes quite thin and flat, curving steeply inwards to create deep bowl shape. Tips of inner horns curving slightly inward.

Holotype: ♂ (BLF 13126-B (CASENT 9032797)). MADAGASCAR: *Toamasina Prov.*: Reserve Betampona, Camp Rendrirendry 34.1 km, 332° Toamasina, 390 m, rainforest, 17°55'26"S:49°11'59"E, B.L. Fisher *et al.*, general collecting in camp, 28.xi.2005.

Distribution & Ecology: *Z. bambusoides* is currently only known from the lowland rainforest of Betampona (Fig. 2). The lowland rainforests of Madagascar are impacted severely by human development (Moat & Smith 2007).

Zoosphaerium tigriculatum Wesener & Bespalova, sp. n.

Figs 9, 10, 17C

Etymology: From Latin *tigris* (tiger) and *oculus* (ornament).

Differential diagnosis: The shape of the posterior telopods (Figs 9E–G) of *Z. tigriculatum* clearly identifies this species as a member of the *Z. coquerelianum* species-group. The presence of one large triangular membranous lobe on the fixed finger and two large membranous lobes on the movable finger (Fig. 9G) is a character shared only with *Z. isalo* Wesener, 2009 and *Z. bilobum* Wesener, 2009. *Z. tigriculatum* has a unique combination of characters, like crenulated teeth on the third podomere of the anterior telopods (Fig. 9C), separating it clearly from the latter two (Table 1).

Description:

Male.

Body length: Holotype: length 20.7 mm, width of thoracic shield 11.8 mm, height of thoracic shield 6.3 mm.

Habitus: Small, glabrous pill-millipede.

Colouration: Some discolouration may have occurred because of preservation in alcohol. Tergites anteriorly khaki coloured, followed by seaweed-green stripe, followed by dark brown margin at posterior. Dorsal side of anal shield same colour as tergites, ventral side of anal shield has light green tint. Legs bright teal under light. Head, collum and antennae dark olive-green.

Head: Eyes with *ca* 65 ocelli. Antennae long and thin, with cylindrical joints (Fig. 10A). Length of antennomeres: 1=2>3>4=5<6. Small shallow concavity at base of first antennomere (Fig. 10B). Many sclerotised teeth at base of antennomere 1–3. Two rows of sensilla basiconica present on first antennomere (Fig. 10B), isolated sensilla also present on second antennomere (Fig. 10C). Apical disc bearing 4 sensory cones (Fig. 10D). Mouthparts not dissected. Collum glabrous with few setae at corners on either side of head.

TABLE 1

Comparison of *Z. isalo* Wesener, 2009, *Z. bilobum* Wesener, 2009 and *Z. tigriloculatum* sp. n.
Abbreviations: ANT – antenna, aT – anterior telopod, bas. – basiconica, Endo – endotergum.

Character	<i>Z. isalo</i>	<i>Z. bilobum</i>	<i>Z. tigriloculatum</i> sp. n.
shape of anal shield	tapering	tapering	weakly bell-shaped
locking carinae	2 nd 3× 1 st	2 nd 2.5× 1 st	2 nd 4× 1 st
1 st leg, no. of ventral spines	3 or 4	6 or 7	4 or 5
2 nd leg, no. of ventral spines	4 or 5	8 or 9	6 or 7
aT, 2 nd podomere in av	visible	not visible	visible
aT, 3 rd podomere	w.o. crenulated teeth	w.o. crenulated teeth	w. crenulated teeth
ANT, sclerotised teeth	on antennomere 1–4	on antennomere 1–5	on antennomere 1–3
ANT, sensilla bas.	only on 1 st	on 1 st and 5 th	on 1 st and 2 nd
Endo, marginal bristle	protruding to margin	extending beyond margin	extending beyond
Endo, cuticular patterns	single row	two rows	two rows

Thoracic shield: Surface like tergites.

Tergites: Surface glabrous, shiny and smooth. Under magnification (50×) tergites display leathery pattern. Under SEM, surface covered by miniscule pits holding stubby sensory hair. Tips of paratergites projecting posteriorly and fairly rounded.

Endotergum: Double row of marginal bristles of varying lengths, some extending far past edge of margin. Two rows of regularly distributed cuticular impressions between marginal ridge and inner area. Internal section with short spines and very few isolated long bristles (Fig. 17C).

Anal shield: Fairly well-rounded with very slight indication of bell shape because of some bulge toward dorsal side. Surface like tergites. Underside carrying 2 black locking carinae, anterior one short, about 1/4 length of posterior one. Carinae separated by a space about as long as 1/2 anterior carina. Anterior carina slightly curving towards margin of anal shield.

Legs: Tarsi 1 with 4 or 5, 2 with 6 or 7, 3 with 8 or 9, and 4–21 with 8–10 ventral spines. First 2 leg pairs with an apical spine. Tarsi of legs 4–21 with an apical spine. In leg 10 femur 1.89×, tarsi 4.70× longer than wide (Fig. 9A).

Stigmatic plates: First plate with triangular lobe. Lobe short and thin, pinched, triangular area at apex projecting towards coxa.

Female. Unknown.

Male sexual characters: Gonopore covered with a single, medially divided, elliptical sclerotised plate. Small apical portion of plate membranous. Covers 1/2 height and 2/3 width of coxa. Anal shield with slight bell shape, covered with very short setae.

Anterior telopods (Figs 9B–D): Harp with one strongly pronounced stridulation rib. Process of second podomere only slightly bent towards third podomere; apical portion facing third podomere covered with sclerotised spots. Below spots at base of projection with a sclerotised spine. Third podomere basally also including sclerotised spine. Large lobe covered by a mound of sclerotised spots located on mesal half of process, concavity

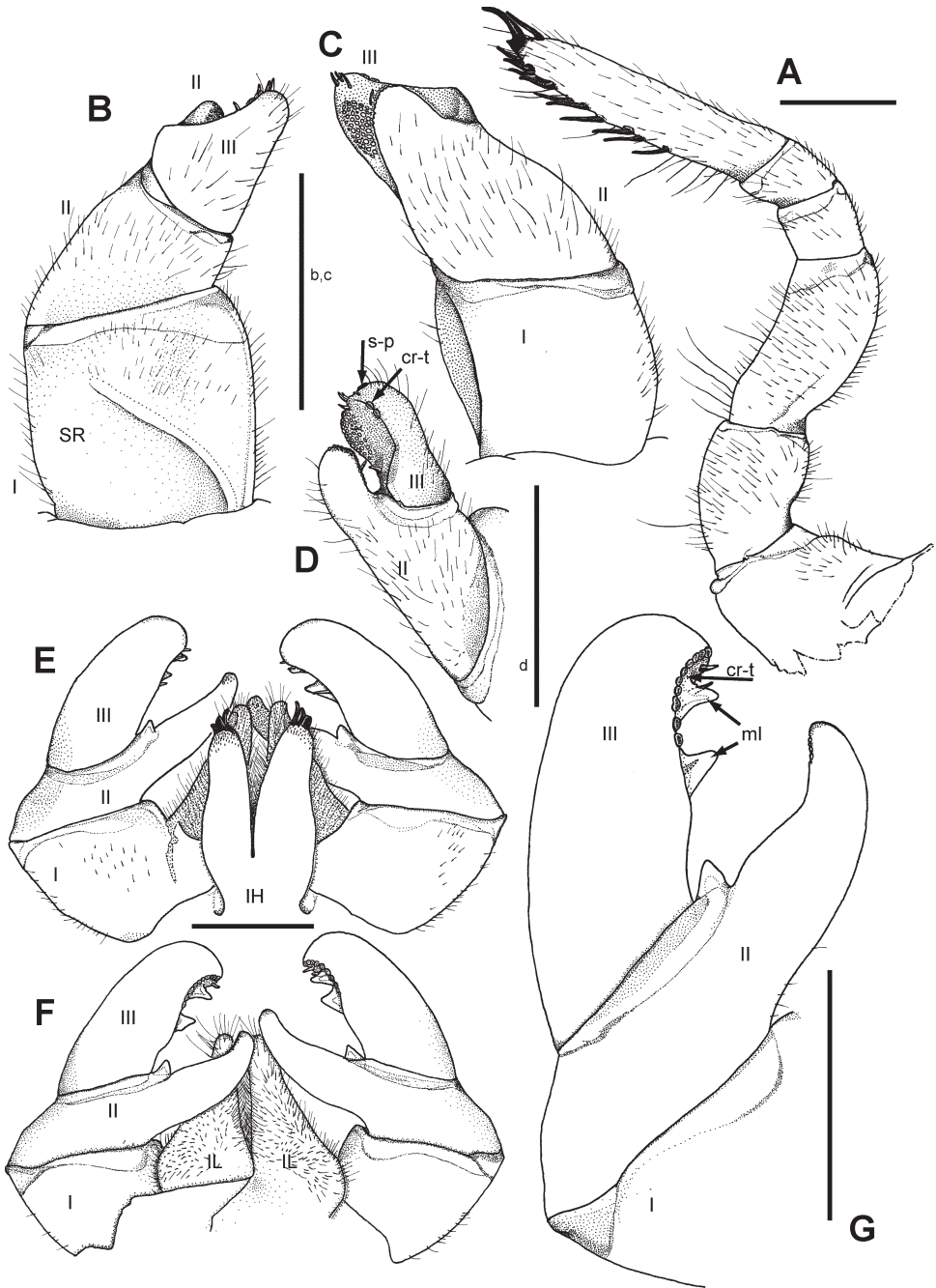


Fig. 9. *Zoosphaerium tigrioculatum* sp. n., holotype: (A) 9th left leg; (B–D) left anterior telopod: (B) anterior view, (C) posterior view, (D) lateral view; (E–G) posterior telopods: (E) anterior view, (F) posterior view, (G) right posterior telopod, posterior view, detail. Roman numerals refer to number of podomere. Abbreviations: cr-t – crenulated, sclerotised teeth, ml – membranous lobe, IH – inner horns, IL – inner lobes, s-p – sclerotised spot, SR – stridulation rib. Scale bars = 1 mm.

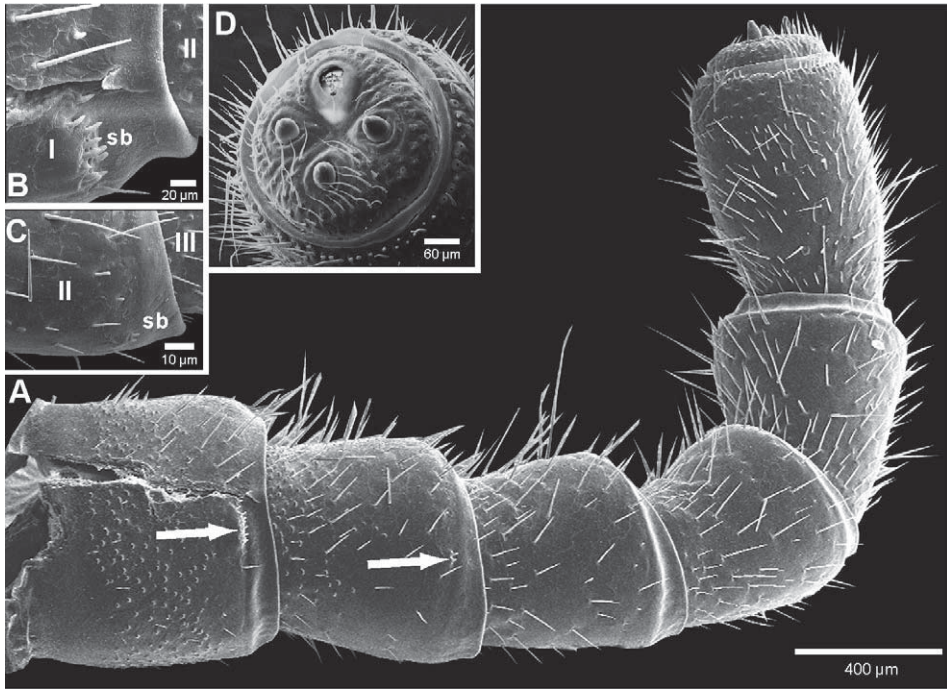


Fig. 10. *Zoosphaerium tigrioculatum* sp. n., holotype, left antenna, SEM: (A) lateral view; (B) *sensilla basiconica* on first antennomere; (C) *sensilla basiconica* on second antennomere (apomorphy of the species); (D) apical view on disc. Arrows point to *sensilla*. Abbreviation: sb – *sensilla basiconica*.

on lateral half. A brown sclerotised spot located at very apex of podomere. Tiny sclerotised spine lateral to brown sclerotised spot, 3 or 4 sclerotised spines meso-apically, small sclerotised spine close to lateral margin of mound of sclerotised spots. Two sclerotised, crenulated teeth on apicolateral margin of concavity.

Posterior telopods (Figs 9E–G): Movable finger moderately thick (2.32× longer than wide), weakly hooking towards fixed finger. One spine located apically, second slightly below first, third at midpoint of finger. Two membranous lobes present, one at midpoint, posteriorly to spine, second between midpoint and apex. On apical posterior margin are 11 sclerotised, crenulated teeth. Fixed finger slightly shorter than movable finger, curving towards latter. Membranous lobe located basally. Tip of fixed finger covered by some sclerotised spots. Telopods shiny and glabrous except for a small patch anteriorly and laterally on first podomere. Inner lobes fairly thin. Tips of inner horns slightly curving inward.

Holotype: ♂ (CASC BLF 13757 (CASENT 9032798)). MADAGASCAR: *Fianarantsoa Prov.*: Parc National d'Andringitra, Plateau d'Andohariana, 35.9 km 205° Ambalavao, ericoid thicket, 2000 m, 22°09'08"S: 46°53'57"E, B.L. Fisher *et al.*, 15.iv.2006.

Distribution & Ecology: *Z. tigrioculatum* is a giant pill-millipede species found at the highest elevation (2000 m) on Madagascar. It seems to live in the ericoid shrub above the tree line. This species has only been recorded from the summit of Andringitra (Fig. 2).

New species not assigned to any existing Zoosphaerium species-groups

Currently, there are only three species, *Z. subreflexum* Jeekel, 1999, *Z. fisheri* Wesener, 2009 and *Z. analavelona* Wesener, 2009, which could not be assigned to a species-group. The two newly described species do not share any special characters with each other or with the three species mentioned above. They feature unusual characters which place them in an isolated position inside *Zoosphaerium*.

***Zoosphaerium darthvaderi* Wesener & Bepalova, sp. n.**

Figs 11–13, 17D

Etymology: From the “Star Wars” character Darth Vader, whose helmet strongly resembles the anal shield of this species (Fig. 11D).

Differential diagnosis: Differs (at least in the male) from all other Malagasy Sphaerotheriida in the presence of a strongly bell-shaped anal shield (Figs 11A, D). Male gonopore large, strongly sclerotised and protruding from the coxa (Fig. 11F), a unique character within the Sphaerotheriida. The posterior telopods of *Z. darthvaderi* resemble those of members of the *Z. coquerelianum* species-group (Wesener 2009), but the fixed finger, as well as the inner lobes, are more slender than in any other member of the group (Figs 12D–F). The anterior telopods are elongated (Figs 12A–C), resembling those of members of the *Z. neptunus* species-group (Wesener & Wägele 2008). The male stridulation rib is strongly reduced, almost invisible (Fig. 12A).

Description:

Male.

Body length: Holotype: length 20.8 mm, width of thoracic shield 9.4 mm, height of thoracic shield 5.2 mm.

Habitus: Small, mostly glabrous pill-millipede. Tergites on posterior margin with conspicuous rows of longer hair (Fig. 11A).

Colouration: Some discolouration may have occurred because of preservation in alcohol. Tergites are green-brown with an ochre rim at posterior edge of tergite. Anal shield one solid colour, browner than tergites. Legs and antennae jade-green, legs with yellow tips. Head and collum are dark leafy green.

Head: Eyes with 65–70 ocelli (Fig. 11A). Antennae long and thin, with cylindrical joints (Fig. 13A). Length of antennomeres: 1>2>3=4>5<6. First antennomere without groove or sensilla basiconica. Sclerotised teeth present on antennomeres 1–3. Apical disc bearing around 20 sensory cones (Fig. 13B). Mouthparts not dissected. Collum with just a few hairs around perimeter, median part glabrous.

Thoracic shield: Surface like tergites.

Tergites: Surface of tergites covered with numerous minute pits. Paratergites not projecting posteriorly.

Endotergum: Single, sparse row of marginal bristles reaching edge, or a little past edge, of margin. Cuticular impressions absent. Internal section with short triangular spines and few isolated long bristles (Fig. 17D).

Anal shield: Pronounced bell shape (Figs 11D, E); top of bell featuring a prominent hump densely covered in very short hairs. Underside with 2 black locking carinae,

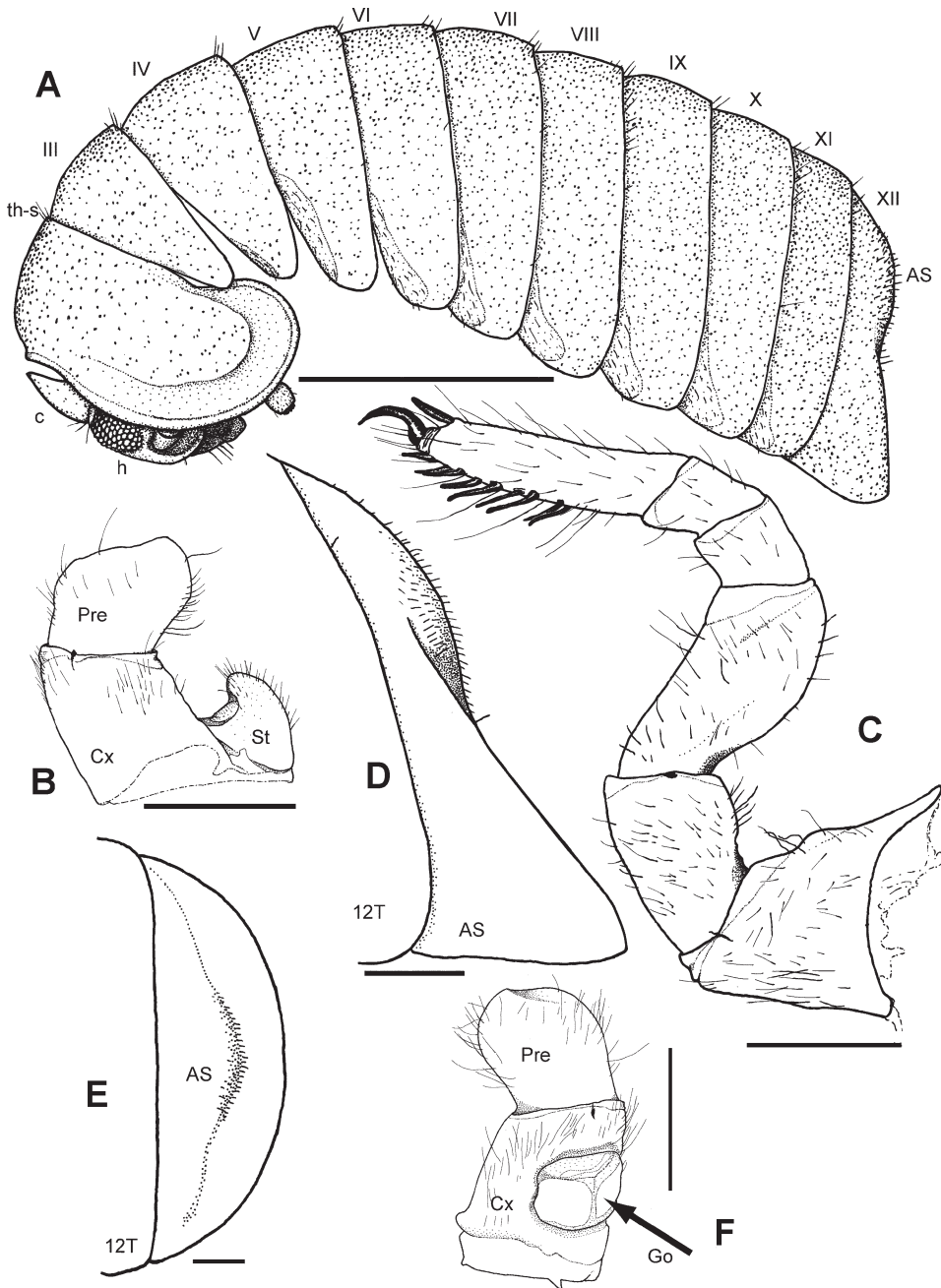


Fig. 11. *Zoosphaerium darthvaderi* sp. n., holotype: (A) habitus, lateral view; (B) coxa and prefemur of first left leg with first stigmatic plate, posterior view; (C) 9th left leg, posterior view; (D) anal shield, lateral view; (E) anal shield, dorsal view; (F) male second right coxa and prefemur with strongly sclerotised gonopore, posterior view. Roman numerals refer to number of tergite. Abbreviations: c – collum (tergite 1), h – head, AS – anal shield, Cx – coxa, Go – gonopore, Pre – prefemur, St – stigmatic plate, th-s – thoracic shield (tergite 2). Scale bars: (A) = 10 mm, (B–F) = 1 mm.

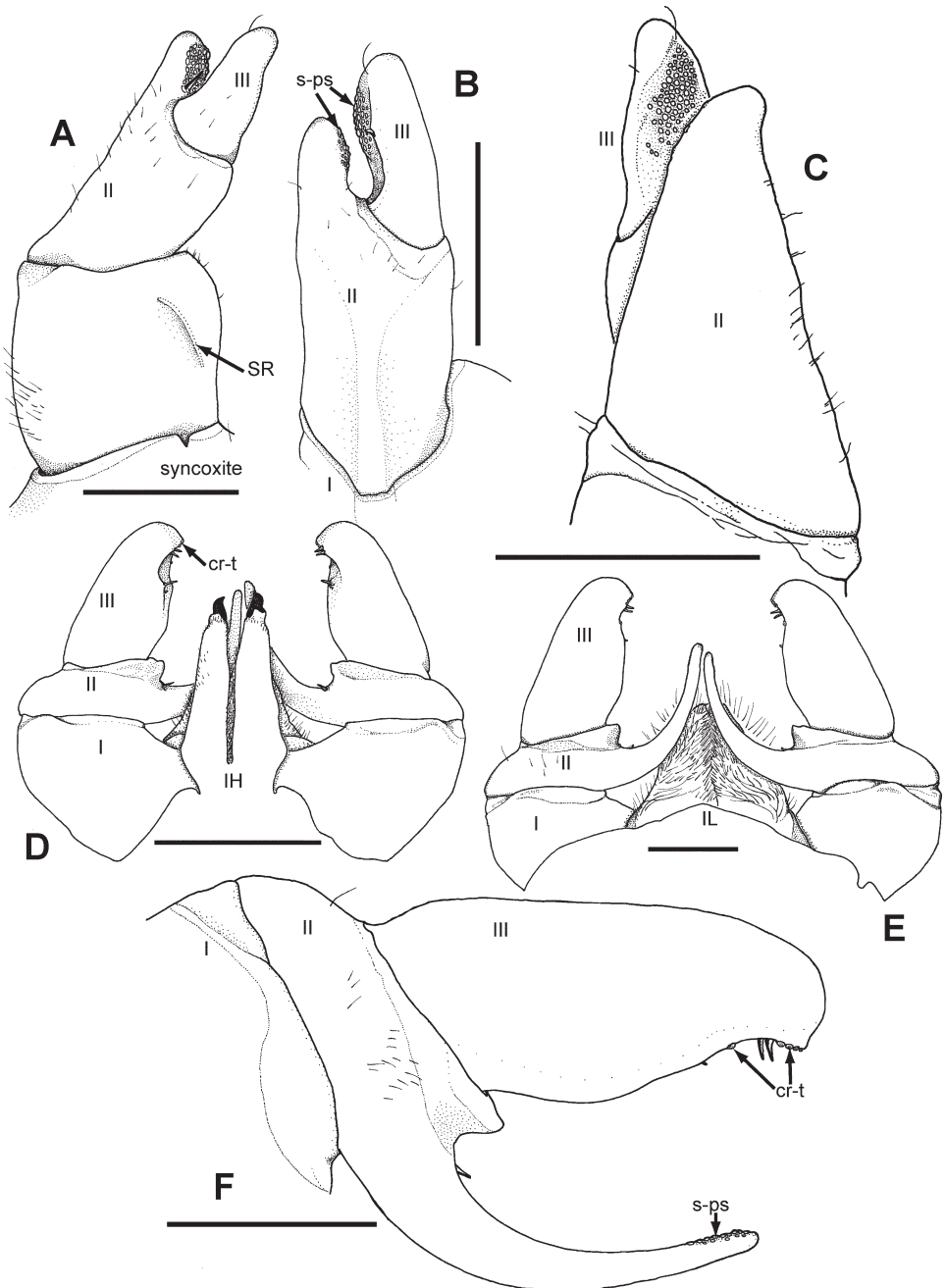


Fig. 12. *Zoosphaerium darthvaderi* sp. n., holotype: (A–C) left anterior telopod: (A) anterior view, (B) lateral view, (C) posterior view; (D–F) posterior telopods: (D) anterior view, (E) posterior view, (F) right chela, posterior view. Roman numerals refer to number of podomere. Abbreviations: cr-t – crenulated, sclerotised teeth, IH – inner horns, IL – inner lobes, s-ps – sclerotised spots, SR – stridulation rib. Scale bars = 1 mm.

posterior one twice as long as anterior one, latter slightly curving posteriorly towards margin of anal shield. Carinae separated by a space about as long as 0.5 length of anterior carina.

Legs: Tarsi 1 with 4, 2 with 6, 3 with *ca* 7 ventral spines. First 2 leg pairs without an apical spine. Tarsi of legs 3–21 with an apical spine and 8–10 ventral spines. In leg 10, femur 1.87×, tarsi 3.87× longer than wide (Fig. 11C).

Stigmatic plates: First plate with triangular lobe. Lobe short and stout, and slightly curving towards coxa (Fig. 11B).

Female. Unknown.

Male sexual characters: Gonopore unusual, covered by an extremely large plate of 3 sclerotised sections with membranous parts between them (Fig. 11F). Two sections large and equal in size, located next to each other (one mesally, one laterally) and together covering width of gonopore. Above them, a small apical sclerotised section covered by a large membranous region gives gonopore a flat top. Gonopore plate protruding prominently above coxa (Fig. 11F). Anal shield featuring a prominent hump covered in a carpet of very short hairs (Fig. 11D).

Anterior telopods (Figs 12A–C): Harp secondarily (?) reduced, with one barely visible stridulation rib. Second podomere process short, portion facing third podomere mostly covered with a mound of sclerotised spots. Below, spots at base of projection with a sclerotised spine. Third podomere possessing cavity which faces second podomere. Cavity basally deep, apically containing a large mound of sclerotised spots, laterally of cavity one small sclerotised spine. No sclerotised, crenulated teeth anywhere on anterior telopods, nor brown sclerotised spot.

Posterior telopods (Figs 12D–F): Movable finger thick (2.0× longer than wide), apically weakly curved and barely tapering. Shallow meso-apical cavity with 4 sclerotised spines, 2 positioned apically, 2 (1 short one positioned below 1 long one) in middle of cavity.

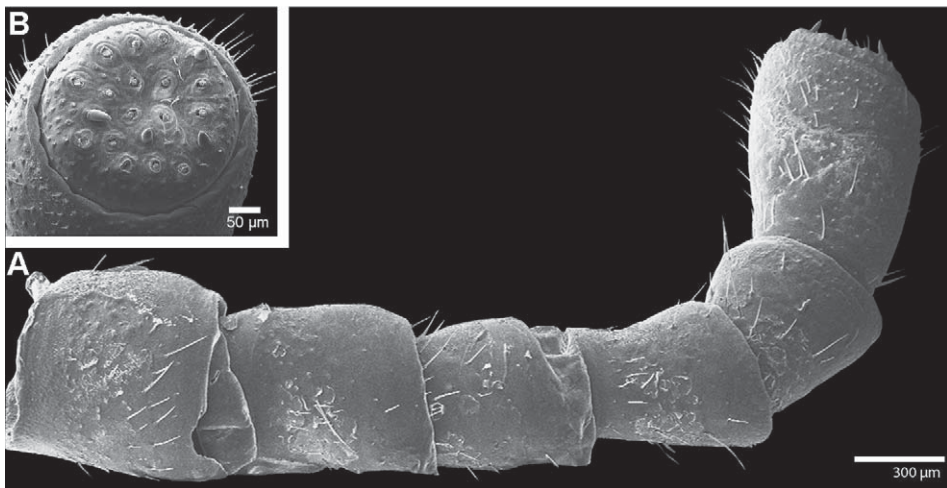


Fig. 13. *Zoosphaerium darthvaderi* sp. n., holotype, left antenna, SEM: (A) lateral view, (B) apical view on disc.

On apical posterior margin are 5 or 6 large, sclerotised, crenulated teeth, 1 isolated and located much more basally than others. Fixed finger almost as long as movable finger, curved, very slender (9.2× longer than wide, when length measured from base of projecting second podomere to tip). Sharp lobe and long sclerotised spine located laterally at base of fixed finger. Tip of fixed finger latero-apically covered with a mound of sclerotised spots. Chelae almost completely glabrous, except for a few isolated setae on lateral area of posterior side of second podomere. Inner lobes of syncoxite very slender. Tips of inner horns curving inward.

Holotype: ♂ (FMNH-INS 7884). MADAGASCAR: *Antananarivo Prov.*: R.S d'Ambohitantely, 24 km NE Ankazobe, disturbed transitional mossy forest, 1450 m, 18°10.1'S:47°16.6'E, S.M. Goodman, pitfall traps, 7–12.xii.1997.

Paratypes: immature 3♂ (FMNH-INS 7884, 8185, 8187) same data as holotype.

Distribution & Ecology: *Z. darthvaderi* is currently only known from mossy forests of Ambohitantely (Fig. 2).

***Zoosphaerium heleios* Wesener & Bepalova, sp. n.**

Figs 14–16, 17E

Etymology: From Greek *helos* (marsh), meaning “of a marsh”, referring to the unusual type locality of this species.

Differential diagnosis: *Z. heleios* cannot be assigned to any of the existing species-groups, neither does it share any similarity in the posterior telopods (Figs 15A–C) with those species currently not assigned to any group (*Z. fisheri* Wesener, 2009 and *Z. anavelona* Wesener, 2009). There are some similarities in the general shape of the posterior telopods to those of *Z. corystoides* Wesener, 2009 and *Z. ambrense* Wesener, 2009, with a strongly elongated, slender movable finger and a much shorter fixed finger (Figs 15A–C), but *Z. heleios* differs from those two species in almost all other aspects, like the shape of the anterior telopods, endotergum, female vulva and antenna. *Z. heleios* differs from all other *Zoosphaerium* species in the presence of a (reduced?) very narrow operculum (Fig. 14D) of the female vulva.

Description:

Male.

Body length: Holotype: length 25.0 mm, width of thoracic shield 13.5 mm, height of thoracic shield 7.2 mm.

Habitus: Small sized, mostly glabrous pill-millipede.

Colouration: Some discolouration may have occurred because of preservation in alcohol. Tergites dark chestnut, with dark olive-green on indent of paratergites, on concave lateral extension of thoracic shield, on ventral side of tergites, and on legs (olive-green colour only seen well under bright light). Head and antennae dark olive-green, with yellow undertones. Collum dark chestnut fading to dark olive-green towards head. Anal shield as tergites.

Head: Eyes with 83–87 ocelli. Antennae long and thin, with cylindrical joints (Fig. 16A). Length of antennomeres: 1=2=3>4<5<6. First antennomere with groove and two rows of sensilla basiconica (Fig. 16A). Sclerotised teeth prominently present on antennomeres

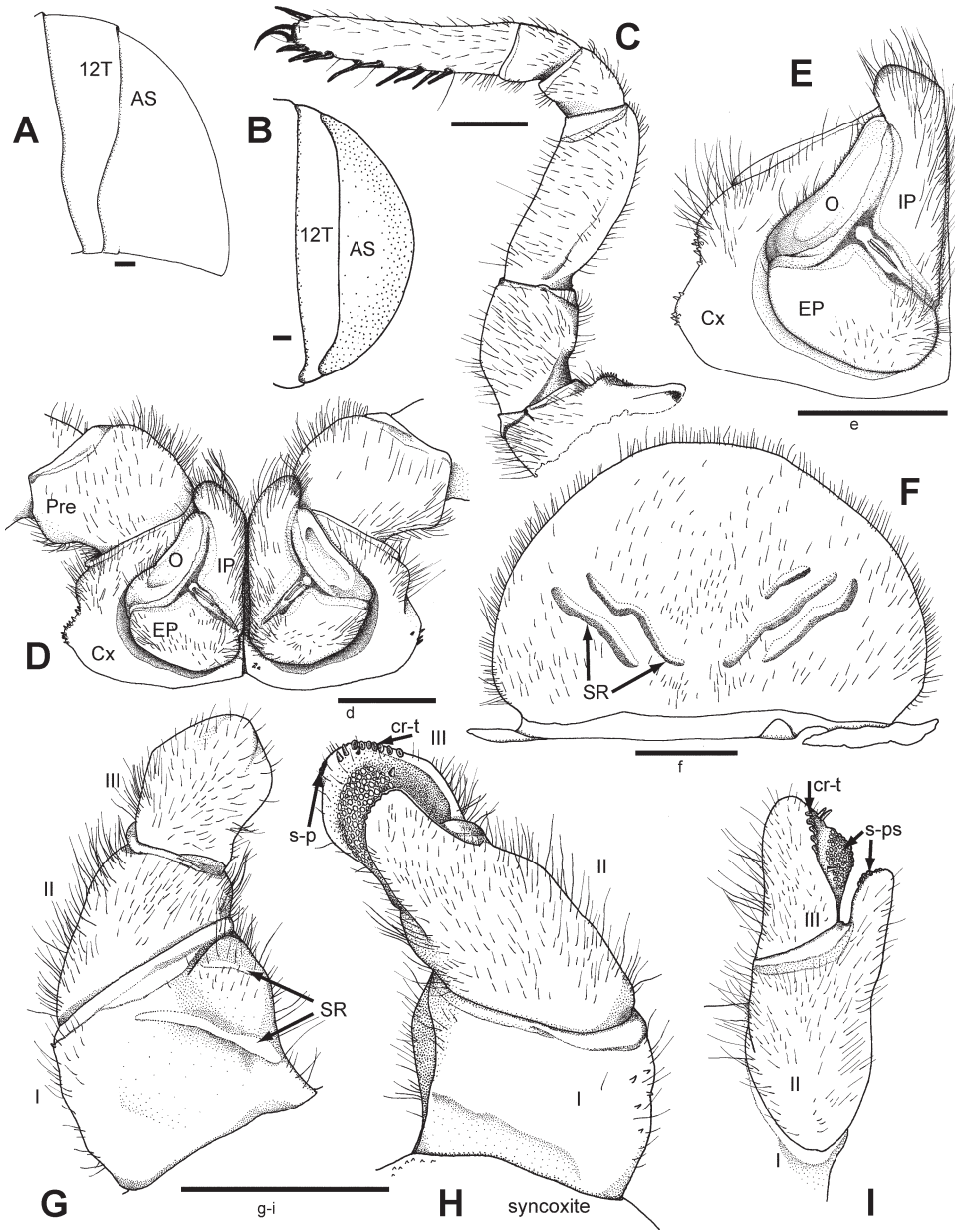


Fig. 14. *Zoosphaerium heleios* sp. n., (A–C, G–I) holotype; (D–F) female paratype: (A) anal shield, lateral view; (B) anal shield, dorsal view; (C) 9th left leg, posterior view; (D) coxae and prefemora of second leg pair with vulvae, posterior view; (E) second right coxa with vulva, detail; (F) female subanal plate with washboard and stridulation ribs; (G–I) left anterior telopod: (G) anterior view, (H) posterior view, (I) lateral view. Roman numerals refer to number of podomere. Abbreviations: 12T – tergite 12, AS – anal shield, cr-t – crenulated, sclerotised teeth, Cx – coxa, EP – external, lateral plate of vulva, IP – inner, mesal plate of vulva, ml – membranous lobe, Pre – prefemur, s-p – sclerotised spot, s-ps – sclerotised spots, SR – stridulation rib. Scale bars = 1 mm.

1–5. Apical disc bearing 31–42 sensory cones (Fig. 16B). Mouthparts not dissected. Sparse field of isolated setae all over collum, mostly located at margin closest to head.

Thoracic shield: Surface like tergites, except for a field of short hairs at margin nearest to head.

Tergites: Surface appears to have small depressions like an orange peel (50×). Very few short isolated setae found on posterior margin of paratergites. Tips of paratergites projecting posteriorly, forming blunt points.

Endotergum: Double row of marginal bristles reaching past edge of margin. Single row of irregular, circular cuticular patterns. Internal section with short spines and very few isolated long bristles (Fig. 17E).

Anal shield: Glabrous, top well rounded, lower margin slightly tapering downwards posteriorly (Figs 14A, B). Underside with 2 black locking carinae; anterior one short, about 1/3 length of posterior one. Carinae separated by a space about as long as 1/2 anterior carina. Posterior carina slightly rounded towards margin of anal shield.

Legs: Tarsi 1 with 4 or 5, 2 with 7 or 8, 3 with eight, and 4–21 with 9–11 ventral spines. First two leg pairs without an apical spine. Tarsi of legs 3–21 with an apical spine. In leg 10, femur 2.08×, tarsi 4.8× longer than wide (Fig. 14C).

Stigmatic plates: First plate with triangular lobe. Lobe short and stout, apex very thin and strongly curving towards coxa.

Male sexual characters: Gonopore covered with a single undivided, elliptical sclerotised plate. Apical portion of plate membranous. Covers 2/3 height and 2/3 width of coxa.

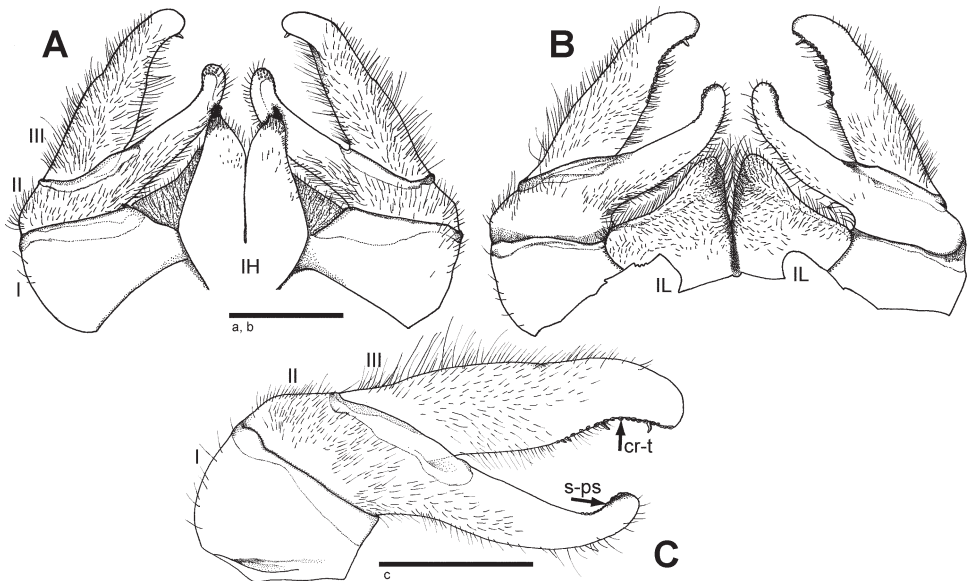


Fig. 15. *Zoosphaerium heleios* sp. n., holotype, posterior telopods: (A) anterior view; (B) posterior view; (C) right posterior telopod, posterior view. Roman numerals refer to number of podomere. Abbreviations: cr-t – crenulated, sclerotised teeth, IH – inner horns, IL – inner lobes, s-ps – sclerotised spots. Scale bars = 1 mm.

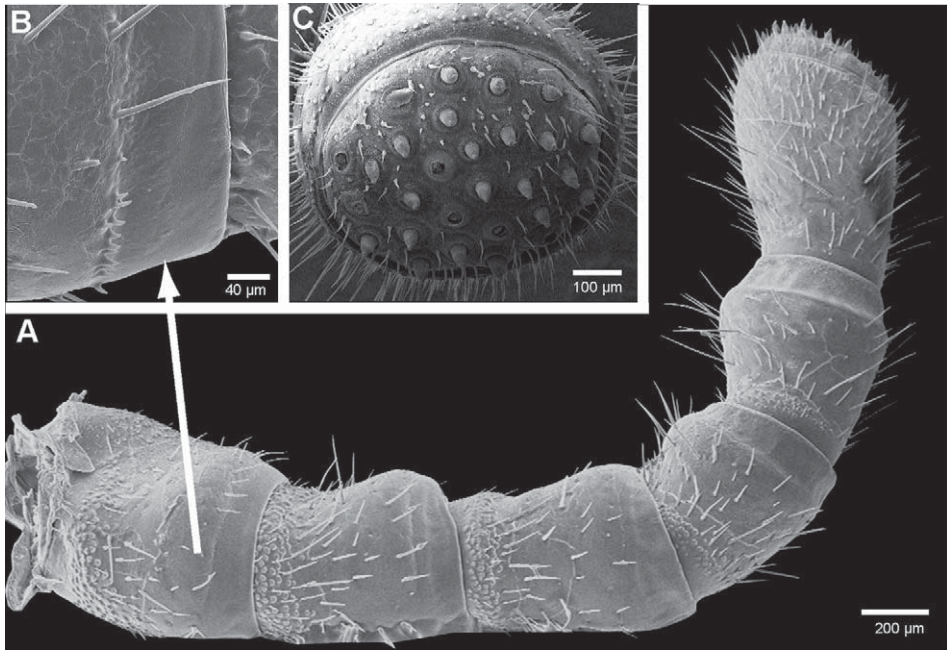


Fig. 16. *Zoosphaerium heleioides* sp. n., holotype, left antenna, SEM: (A) lateral view, (B) *sensilla basiconica* on 1st antennomere, (C) apical view on disc.

Top of anal shield fairly well rounded, a little humped, lower margin at posterior end tapering downwards (Fig. 14A). Upper surface covered by a sparse carpet of very short setae, lower surface glabrous.

Anterior telopods (Figs 14G–I): Harp with two strongly pronounced stridulation ribs – upper rib protrudes robustly, creating a sort of triangular plateau. A few tiny sclerotised spines located basally on lateral part of first podomere. Lateral edge of syncoxite near first podomere also with many tiny sclerotised spines. Second podomere process has rectangular mound of sclerotised spots apically, directly juxtaposed to large mound of sclerotised spots on third podomere. Third podomere's sclerotised mound takes up 2/3 of process, and laterally a fairly deep concavity rimmed by podomere's lateral margin takes up 1/3. Sclerotised spine located on lateral rim of mound, and another at base of mound. Lateral apical margin has 5–7 sclerotised, crenulated teeth, 2 or 3 sclerotised spines at apex, and 2 brown sclerotised spots mesally of spines.

Posterior telopods (Figs 15A–C): Movable finger rather elongated (3.19× longer than wide), weakly curving towards fixed finger. Four sclerotised spines on mesal side in shallow cavity; 1 apically, 1 at median of cavity, and 2 (one positioned below the other) at base of cavity. On meso-apical posterior margin are 16 or 17 sclerotised teeth. Fixed finger slightly shorter than movable finger, hooking towards latter. Sclerotised spots on apicolateral part of fixed finger. Movable finger anteriorly and posteriorly except for area around apex densely covered in long hairs. Second podomere anteriorly, as well as mesal portion of fixed finger, covered in hairs. First podomere mostly glabrous except for a small patch on mesal margin facing inner horns.

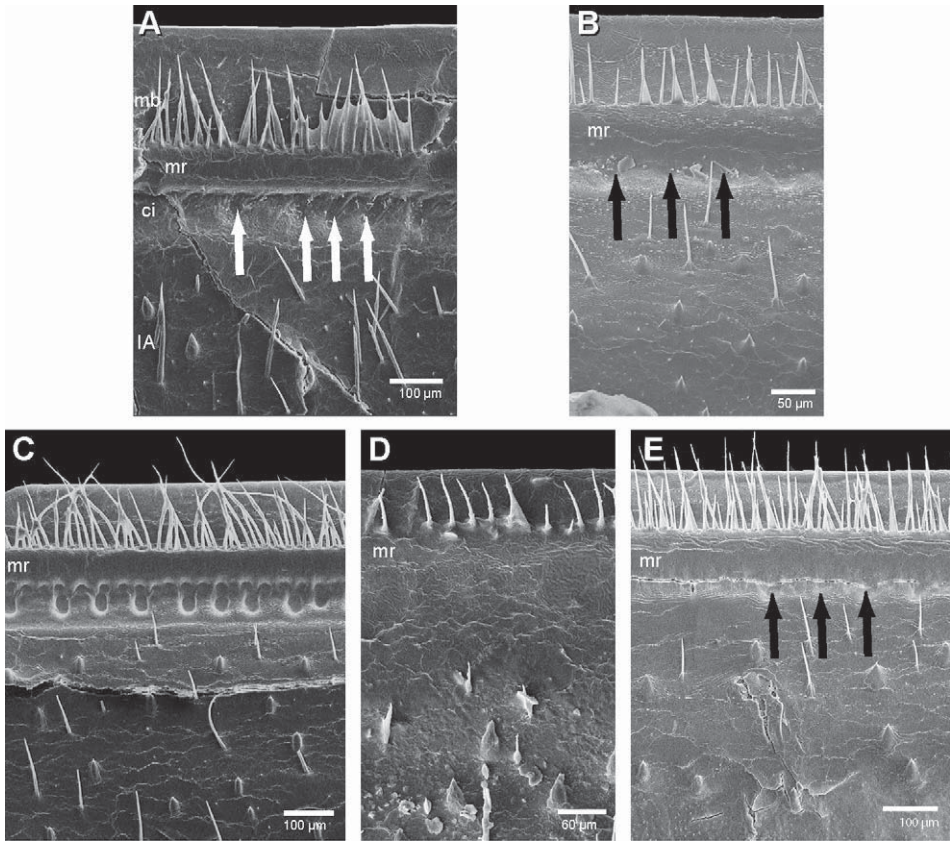


Fig. 17. Endoterga of tergites 10, arrows point to cuticular impressions: (A) holotype of *Zoosphaerium muscorum* sp. n., (B) holotype of *Z. bambusoides* sp. n., (C) holotype of *Z. tigioculatum* sp. n., (D) holotype of *Z. darthvaderi* sp. n., (E) holotype of *Z. heleioides* sp. n. Abbreviations: ci – cuticular impressions, IA – inner area with spines and long setae, mr – marginal ridge, mb – marginal bristles.

Female.

Body length: Paratypes: length up to 32.6 mm, width of thoracic shield up to 16.3 mm, height of thoracic shield up to 9.4 mm.

Female sexual characters: Vulva large, covering more than 3/4 of coxa (Fig. 14D). Operculum short, flat and disc-shaped, with shallowly indented middle. Mesal plate long and fairly thin, extending beyond coxa and operculum, and hooking towards prefemur, covered apically in long hairs. Suture between inner and outer plates containing some sort of structure under membrane of which two parallel strips poke up and out of membrane (Fig. 14E). Subanal plate with washboard possessing up to 3 stridulation ribs on each half; 2 long and well-developed, a third short rib sometimes present mesally (Fig. 14F).

Holotype: ♂ (CASC BLF 10673 (CASENT 9032796)). MADAGASCAR: *Toamasina* Prov.: Torotorofotsy, on low vegetation, marsh edge, montane rainforest, 1070 m, 18°52'15"S:48°20'51"E, leg. Malagasy ant team, 28.iii.2004.

Paratypes: 1♂ 2♀ 2 immatures (CASC BLF 10673), same data as holotype.

Distribution & Ecology: *Z. heleios* is currently only known from the marshes of Torotorofotsy (Fig. 2). This species is the only Malagasy giant pill-millipede species ever recorded from marshes.

Description of new females

Zoosphaerium xerophilum Wesener, 2009

Fig. 18

Zoosphaerium xerophilum: Wesener 2009: 40.

Description:

Anal shield shape: Top well rounded, bottom sharply tapering downward. From apical view, shield looks slightly but sharply pointed posteriorly like bottom half of a hazelnut.

Female sexual characters: Subanal plate with washboard possessing up to 5 stridulation ribs on each half, some long, some shorter. Vulva large, covering more than 3/4 of coxa (Fig. 18). Operculum large, reaching past apical edge of coxa, with indent at apex halving it into two small same-sized mounds. Meso-apical region of operculum shallowly indented. Mesal plate long and broad, protruding to 0.5 of operculum height, but not past apical edge of coxa.

Material examined: MADAGASCAR: *Antsiranana* Prov.: 1 ♀ (FMNH-INS 55897) Forêt d' Ambre, tropical dry forest, J. Köhler *et al.*, iii.2008.

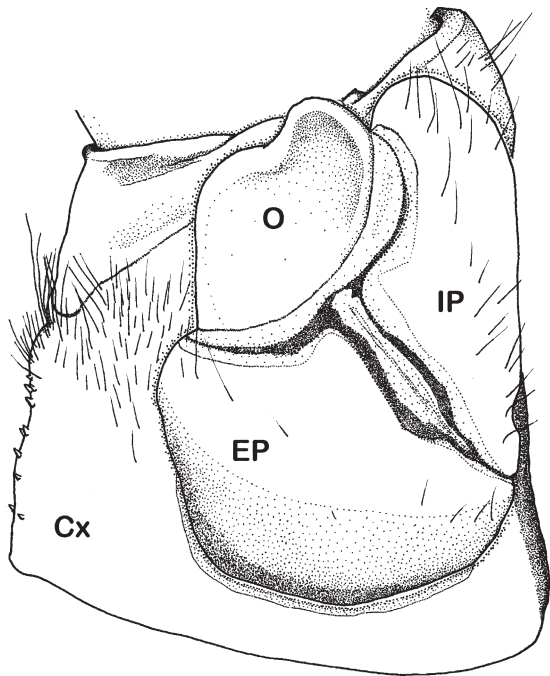


Fig. 18. *Zoosphaerium xerophilum* Wesener, 2009 (FMNH-INS 55897), right second coxa with vulva, posterior view. Abbreviations: Cx – coxite, EP – external, lateral plate, IP – inner, mesal plate, O – operculum. Scale bar = 1 mm.

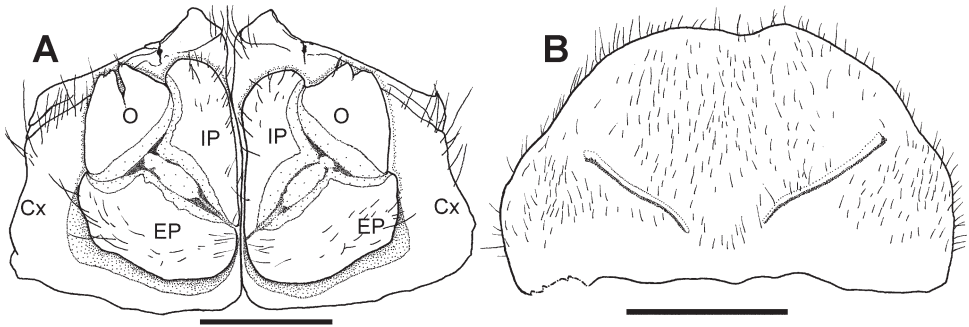


Fig. 19. *Zoosphaerium pseudoplatylabum* Wesener, 2009 (FMNH-INS 7801): (A) female 2nd coxae with vulvae, posterior view; (B) subanal plate with washboard. Abbreviations: Cx – coxite, EP – external, lateral plate, IP – inner, mesal plate, O – operculum. Scale bars = 1 mm.

Zoosphaerium pseudoplatylabum Wesener, 2009

Fig. 19

Zoosphaerium pseudoplatylabum: Wesener 2009: 54.

Description:

Anal shield shape: Well rounded until bottom, where slightly flared and very slightly tapered downward.

Female sexual characters: Vulva large, covering more than 3/4 of coxa (Fig. 19A). Operculum large, reaching almost to apical edge of coxa, with deep notch apically, sometimes with second tiny notch on lateral half. Mesal plate long and broad, protruding to 1/4 operculum height (Fig. 19A). Subanal plate with washboard possessing one weakly developed stridulation rib on each half (Fig. 19B).

Material examined: MADAGASCAR: *Fianarantsoa* Prov.: 1♂ 1♀ (FMNH-INS 7801), 13♂ (FMNH-INS 7913) extreme northern limit of R.S. de Ivohibe, along Hefitany R., ca 7.5 km ENE Ivohibe, montane rainforest, 1200 m, 22°28.2'S:46°57.6'E, S.M. Goodman, pitfall traps, 3.ix.1997.

Additional material and locality information

Zoosphaerium amabile Wesener, 2009

Zoosphaerium amabile: Wesener 2009: 74.

Material examined: MADAGASCAR: *Toamasina* Prov.: 1♂ 1♀ (immature) (CASC BLF 8256) Montagne d'Akirindro, 7.6 km 341° NNW Ambinanitelo, rainforest, 600 m, 15°17'18"S:49°32'54"E, B.L. Fisher, C. Griswold *et al.*, general collecting, 17–21.iii.2003.

Distribution: Previously only know from a single male (Wesener 2009), this is another record from the type locality.

Zoosphaerium ambrense Wesener, 2009

Zoosphaerium ambrense: Wesener 2009: 84.

Material examined: MADAGASCAR: *Antsiranana* Prov.: 2♂ 1♀ (immature) (FMNH-INS 55898) Forêt d'Ambre, Fontenay Nature Parc, Köhler & Franzen, 26.ii.2008; 1♂ (immature) (FMNH-INS 55899) Forêt d'Ambre, Lac Mahery, Köhler & Franzen, 27.ii.2008.

Distribution: Other specimens collected close to the type locality. Unfortunately, a precise description and coordinates of the locality are still unavailable.

Zoosphaerium analavelona Wesener, 2009

Zoosphaerium analavelona: Wesener 2009: 122.

Material examined: MADAGASCAR: 1 ♀ (FMNH-INS 7886) Forêt de Analavelona, nr source of Manasy R., 16 km NW d'Andranoheza, rainforest, 1250 m, 22°38.5'S:44°10.3'E, S.M. Goodman, pitfall traps, 2–10.xi.2000.

Distribution: Another record from the type locality (Wesener 2009).

Zoosphaerium neptunus (Butler, 1872)

Zoosphaerium neptunus (Butler): Pocock 1895: 410; Wesener & Wägele 2008: 10.

Material examined: MADAGASCAR: *Toamasina Prov.*: 1 ♀ (CASC BLF 13126) Reserve Betampona, Camp Rendrirendry 34.1 km 332° Toamasina, 390 m, rainforest, 17°55'26"S:49°11'59"E, B.L. Fisher *et al.*, general collecting in camp, 28.xi.2005. *Antsiranana Prov.*: 1 ♀ (FMNH-INS 7917) RNI d'Marojejy, along tributary of Mananatenina R., 8 km NW Mananatenina, rainforest, 450 m, 14°26.2'S:49°46.5'E, S.M. Goodman, pitfall traps, 4–13.x.1996. *Mahajanga Prov.*: 1 ♂ 1 ♀ (ZCMV 11314) nr Hevirina, Makira Plateau, M. Vences, 23.vi.2009, in group migration.

Distribution: The new localities fit very well into the known distribution of this species (Wesener & Wägele 2008). One of the few widespread Malagasy giant pill-millipede species.

Zoosphaerium platylabum (de Saussure & Zehntner, 1897)

Zoosphaerium platylabum (de Saussure & Zehntner): Wesener & Wägele 2008: 50.

Material examined: MADAGASCAR: 1 ♂ (FMNH-INS 55900) Andasibe-Perinet, 18°57.609'S:48°25.728'E, T. Wesener & K. Schütte, 18.vi.2007.

Distribution: Another specimen known from the type locality.

Remarks: The male seems to be not fully mature. Living colour was light brown, with dark brown posterior margins and dark green legs and antennae.

Zoosphaerium pseudopiligerum Wesener, 2009

Zoosphaerium pseudopiligerum: Wesener 2009: 118.

Material examined: MADAGASCAR: 1 ♂ (FMNH-INS 13914) Res. Andohohela, 11 km NW Enakara, 940 m, rainforest, 24°34' S:49°49'E, B.L. Fisher, #489, 16.xi.1992.

Distribution: Another record from the type locality (Wesener 2009).

Zoosphaerium pseudopriapus Wesener, 2009

Zoosphaerium pseudopriapus: Wesener 2009: 46.

Material examined: MADAGASCAR: *Antsiranana Prov.*: 2 ♂ 2 ♀ (CASC BLF 10877) Forêt de Binara, 9.1 km 233° SW Daraina, rainforest, 650–800 m, 13°15'48"S:49°36'12"E, B.L. Fisher, general collecting in camp, 19.xi.2004.

Distribution: The new locality is only a few kilometres from the type locality.

Zoosphaerium smaragdinum Wesener, 2009

Zoosphaerium smaragdinum: Wesener 2009: 80.

Material examined: MADAGASCAR: *Antsiranana Prov.*: 1 ♀ (FMNH-INS 7920) RNI d'Marojejy, montane rainforest, 1875 m, 14°26.8'S:49°44.1'E, S.M. Goodman, pitfall traps, 13–20.xi.1996.

Distribution: Another record from the type locality (Wesener 2009).

Zoosphaerium tampolo Wesener, 2009

Zoosphaerium tampolo: Wesener 2009: 94.

Material examined: MADAGASCAR: *Antsiranana Prov.*: 4♂ (FMNH-INS 7029) Station Forestiere de Tampolo, littoral rainforest, 10 m, 17°17.2'S:49°24.5'E, S.M. Goodman, 3–16.iv.1997; >25♂ (FMNH-INS 7879) same data as previous, but pitfall traps; 4♂ (FMNH-INS 7881), 11♂ (FMNH-INS 7882) same data as previous.

Distribution: This species is still only known from Tampolo (Wesener 2009).

Zoosphaerium villosum Wesener & Sierwald, 2005

Zoosphaerium villosum: Wesener & Sierwald 2005: 19; Wesener & Wägele 2008: 42.

Material examined: MADAGASCAR: *Toamasina Prov.*: 3♀ (CASC BLF 13126) Reserve Betampona, Camp Rendriendry 34.1 km 332° Toamasina, 390 m, rainforest, 17°55'26"S:49°11'59"E, B.L. Fisher *et al.*, general collecting in camp, 28.xi.2005; 1♀ (CASC BLF 13243) Reserve Betampona Camp Vohitsivalana, 37.1 km 338° Toamasina, rainforest, 520 m, 17°53'12"S:49°12'09"E, B.L. Fisher *et al.*, general collecting in camp, 1–3.xii. 2005. *Antsiranana Prov.*: 1♂ (FMNH-INS 7819) Forêt de Betaolana, 11.0 km NW Ambogiangezoka, Befnolana camp #2, rainforest, 1200 m, 14°36.6'S:49°25.5'E, S.M. Goodman, 18.x.1999; 4♂ (FMNH-INS 7827), 1♂ (FMNH-INS 0000) Station Forestiere de Tampolo, littoral rainforest, 10 m, 17°17.2'S:49°24.5'E, S.M. Goodman, pitfall traps, 3–16.iv.1997.

Distribution: This species is obviously relatively widely distributed in rainforests in north-eastern Madagascar.

Zoosphaerium viridissimum Wesener, 2009

Zoosphaerium viridissimum: Wesener 2009: 104.

Material examined: MADAGASCAR: *Antsiranana Prov.*: 1♂ (FMNH-INS 7895) RNI d'Marojejy, rainforest, camp 3, 14°26.8'S:49°44.1'E, S.M. Goodman, pitfall traps, 13–20.xi.1996.

Distribution: Another record from the type locality (Wesener 2009).

DISCUSSION

Four of the five species come from ecosystems whence no pill-millipedes have heretofore been recorded. *Z. muscorum* and *Z. darthvaderi* are recorded from very humid mossy forest, *Z. tigrioculatum* from an ericoid thicket above the tree line, and *Z. heleios* from a swampy marsh (Fig. 2). Otherwise, all new collection data was added to nine previously described species from their known areas of distribution (Wesener & Wägele 2008; Wesener 2009). This finding highlights how successfully giant pill-millipedes have adapted to the different natural ecosystems in Madagascar, being present in arid shrubland as well as in extremely wet mossy forest, from marsh edges and littoral forests on the coast up to the mountain summits. However, a single species is most often restricted to a single ecosystem; more than 30 % of the species even being microendemic to a single forested area (Wesener 2009). Giant pill-millipedes are surprisingly absent from all anthropogenically modified habitats, like rice fields or eucalyptus plantations (Wesener & Sierwald 2005a).

The discovery of five new species, including two with such unusual combinations of characters that they cannot be associated with any species-group, highlights how little we know about the giant pill-millipede fauna of Madagascar. The phylogeny of the genus *Zoosphaerium* on Madagascar is also insufficiently known: it is unclear whether the existing species-groups are monophyletic (Wesener 2009). This is exemplified by the newly described *Z. darthvaderi*, which shares similarities in the posterior telopods with the *coquerelianum* species-group, but the anterior telopods are characteristic of the *neptunus* species-group. A recent phylogenetic study, focusing on the family level, only recovered some of the *Zoosphaerium* species-groups as monophyletic (Wesener

& VandenSpiegel 2009). A species-level phylogeny of the genus *Zoosphaerium* is not available because of the character richness of this genus (more than 200 morphological characters need to be keyed), but would be very useful in clarifying the relationships of microendemic species which sometimes exhibit island gigantism. The evolution of invertebrate island gigantism is still unknown.

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REFERENCES

- BUTLER, A.G. 1872. Descriptions of new Myriopoda of the family Glomeridae. *The Annals and Magazine of Natural History, including Zoology, Botany, and Geology, Series 4* **10**: 354–359.
- MOAT, J. & SMITH, P. 2007. *Atlas of the vegetation of Madagascar*. Richmond, Surrey, UK: Kew Publishing.
- MYERS, N., MITTERMEIER, R.A., MITTERMEIER, C.G., FONSECA, G.A.B. & KENT, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.
- POCOCK, R.I. 1895. Descriptions of new genera of Zephronidae, with brief preliminary diagnoses of some new species. *The Annals and Magazine of Natural History, including Zoology, Botany, and Geology, Series 6* **16**: 409–415.
- SAUSSURE, H., DE & ZEHNTNER, L. 1897. Atlas de l'histoire naturelle des Myriapodes. In: Grandidier, A., ed., *Histoire physique, naturelle et politique de Madagascar*. Paris: Imprimerie nationale.
- 1902. Myriapodes de Madagascar. In: Grandidier, A., ed., *Histoire physique, naturelle et politique de Madagascar. Mémoires du Muséum national d'Histoire naturelle* **27** (53): i–viii + 1–356, pls 13–15.
- VENCES, M., WOLLENBERG, K.C., VIEITES, D.R. & LEES, D.C. 2009. Madagascar as a model region of species diversification. *Trends in Ecology and Evolution* **24** (8): 456–465.
- VIEITES, D.R., WOLLENBERG, K.C., ANDREONE, F., KÖHLER, J., GLAW, F. & VENCES, M. 2009. Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proceedings of the National Academy of Sciences of the USA* **106**: 8267–8272.
- WESENER, T. 2009. Unexplored richness: discovery of 31 new species of giant pill-millipedes endemic to Madagascar, with a special emphasis on microendemism (Diplopoda, Sphaerotheriida). *Zootaxa* **2097**: 1–134.
- WESENER, T. & SIERWALD, P. 2005a. New giant pill-millipede species from the littoral forest of Madagascar (Diplopoda, Sphaerotheriida, *Zoosphaerium*). *Zootaxa* **1097**: 1–60.
- 2005b. The giant pill-millipedes of Madagascar: Revision of the genus *Sphaeromimus*, with a review of the morphological terminology (Diplopoda, Sphaerotheriida, Sphaerotheriidae). *Proceedings of the California Academy of Sciences, Fourth Series* **56** (29): 557–599.
- WESENER, T. & VANDENSPIEGEL, D. 2007. *Microsphaerotherium ivohibiense*, a new genus and species of giant-pill millipedes from Madagascar (Diplopoda, Sphaerotheriida, Arthrospheerinae). *Journal of Afro-tropical Zoology* **3**: 153–160.
- 2009. A first phylogenetic analysis of giant pill-millipedes (Diplopoda: Sphaerotheriida), a new model Gondwanan taxon, with special emphasis on island gigantism. *Cladistics* **25**: 545–573.
- WESENER, T. & WÄGELE, J.-W. 2008. The giant pill-millipedes of Madagascar: revision of the genus *Zoosphaerium* (Myriapoda, Diplopoda, Sphaerotheriida). *Zoosystema* **30** (1): 5–85.