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Research article

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Seven new giant pill-millipede species and numerous new records of the genus *Zoosphaerium* from Madagascar (Diplopoda, Sphaerotheriida, Arthrosphaeridae)

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Abstract. Seven new species of the giant pill-millipede genus *Zoosphaerium* Pocock, 1895 are described from Madagascar: *Z. nigrum* sp. nov., *Z. silens* sp. nov., *Z. ambatovaky* sp. nov., *Z. beanka* sp. nov., *Z. voahangy* sp. nov., *Z. masoala* sp. nov. and *Z. spinopiligerum* sp. nov. All species are described based on drawings and scanning electron microscopy, while genetic barcoding of the COI gene was successful for six of the seven new species. Additional COI barcode information is provided for the first time for *Z. album* Wesener, 2009 and *Z. libidinosum* (de Saussure & Zehntner, 1897). *Zoosphaerium nigrum* sp. nov. and *Z. silens* sp. nov. belong to the *Z. libidinosum* species-group, *Z. ambatovaky* sp. nov. to the *Z. coquerelianum* species-group, *Z. beanka* sp. nov., *Z. voahangy* sp. nov. and *Z. masoala* sp. nov. to the *Z. platylabum* species-group and *Z. spinopiligerum* sp. nov. to the *Z. piligerum* species-group. Updated identification keys are provided for each species-group. Two western dry forest species, *Z. silens* sp. nov. and *Z. voahangy* sp. nov. are recorded from two localities, while the other five species are currently only known from their type localities. Of special conservation concern might be *Z. ambatovaky* sp. nov. from the lowland rainforest fragment of Ambatovaky, a nowadays isolated lowland rainforest, rapidly shrinking due to slash and burn agriculture. In addition to the new species, new locality data is provided for 11 species and numerous unidentifiable species of *Zoosphaerium*: *Z. neptunus* (Butler, 1872), *Z. platylabum* (de Saussure & Zehntner, 1902) and *Z. piligerum* (de Saussure & Zehntner, 1897) from the central eastern montane forests, as well as *Z. ambrense* Wesener, 2009, *Z. aureum* Wesener, 2009, *Z. libidinosum*, *Z. corystoides* Wesener, 2009, *Z. discolor* Wesener, 2009, *Z. smaragdinum* Wesener, 2009, *Z. villosum* Wesener & Sierwald, 2005 and *Microsphaerotherium anjzorobe* Wesener, 2009.

Keywords. Microendemism, Tsingy, dry forest, forest fragments, soil arthropod.

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Introduction

Madagascar, located off the eastern coast of Africa, has been isolated from other continents for more than 120 my. Its separation from India took place ca 90 my ago (Krause 2003; Ali & Aitchison 2008). As a result of this long period of isolation, many Malagasy plant and animal groups have a high percentage of endemics, making the island an important biodiversity hotspot (Myers *et al.* 2000). Around 86% of the occurring invertebrate species solely live on Madagascar (Goodman & Benstead 2005). Some of the most striking members of this endemic mega-invertebrate fauna belong to the millipedes, order Diplopoda. The so-called fire millipedes of the order Spirobolida have a conspicuous red and black coloration (Wesener *et al.* 2009a, 2009b, 2011a), whereas giant pill-millipedes of the order Sphaerotheriida possess stridulation organs in both sexes (Wesener & VandenSpiegel 2009; Wesener *et al.* 2011b) and (only on Madagascar) can reach the size of a small orange when rolled-up (Enghoff 2003). During the last 12 years, numerous new species and genera of both groups have been described from the island (Wesener *et al.* 2008, 2011a, 2014; Wesener 2009, 2011; Wesener & Enghoff 2009).

All Malagasy giant pill-millipedes belong to the family Arthrosphaeridae, which comprises four genera. Three genera are strictly endemic to Madagascar, while a fourth genus is found in southern India and Sri Lanka (Wesener & VandenSpiegel 2009; Wesener *et al.* 2010a). This peculiar biogeographic pattern represents the shared connection between Madagascar and India until 90 my ago. Species of the geographically closest family, Sphaerotheriidae, are found in South Africa. The strictly endemic Malagasy giant pill-millipedes belong to the genera *Sphaeromimus* de Saussure & Zehntner, 1902, *Microsphaerotherium* Wesener & VandenSpiegel, 2007 and *Zoosphaerium* Pocock, 1895. In the genus *Zoosphaerium*, comprising the vast majority of species, 42 new species have been described since 2005. Many of these species are endemic to very restricted geographical areas and are therefore listed as critically endangered on the IUCN Red List (e.g., Rudolf & Wesener 2017a, 2017b).

In an effort to understand Madagascar's role as a major biodiversity hotspot, two general inventory programs have recently been undertaken: one organized by the Field Museum, Chicago and headed by Steve Goodman and his team, and a second organized by the California Academy of Sciences, headed by Brian Fisher and his team. Both programs yielded numerous samples of Malagasy giant pill-millipedes. In total, these samples contained specimens of 11 already described species as well as seven new species which are described here.

Material & methods

Abbreviations

CAS	= California Academy of Sciences, San Francisco, CA, USA
CASENT	= Entomology Collection, California Academia of Sciences
FMNH	= Field Museum, Chicago, IL, USA
FMNH-INS	= Insect and Myriapoda Collection voucher numbers for the Field Museum
MBI	= Madagascar Biodiversity Inventory
NHMD	= Natural History Museum of Denmark, University of Copenhagen, Denmark
ZFMK	= Zoological Research Museum A. Koenig, Leibniz Institute for Animal Biodiversity, Bonn, Germany
ZFMK-MYR	= collection number of the Myriapoda Collection at the ZFMK

Dissection and illustrations

Structures were dissected and drawn using a camera lucida mounted on an Olympus SZX12 stereo microscope. Pencil drawings were transferred to ink using Pigma Micron pens with widths 005 and 04 and later edited in Adobe Photoshop CS2. The naming of morphological structures follows the terms established in previous papers (Wesener & Sierwald 2005a; Wesener 2009).

Photography and scanning electron microscopy

Habitus photographs were taken at multiple focal planes with a DUN (Palmyra, Virginia) BK-Plus imaging system based at the ZFMK. Images were stacked using the software Auto-Montage (Syncroscopy). For scanning electron microscopy (SEM), the endotergum was dissected. The samples were cleaned and dehydrated via an ethanol series (2 × at 96%, 3 × at 100%) before being mounted on aluminum stubs. The samples were coated with gold for 240 seconds in a sputter coater. SEM images were taken using a Supra VR 300VP (Carl Zeiss AG) scanning electron microscope utilizing the Software SmartSEM ver. 5.00, based at the ZFMK. After the study, dry coated SEM material was removed from stubs and returned to alcohol. All images were later edited using Adobe Photoshop CS2 and assembled into plates in Adobe Illustrator CS2.

DNA extraction and molecular barcoding

In order to match males to females, investigate the intraspecific and interspecific genetic distances of the species described here, as well as elucidate phylogenetic relationships a molecular genetic barcoding study (Hebert *et al.* 2003) was conducted. Genomic DNA was extracted from the muscle tissue of the legs of 12 specimens of *Zoosphaerium* (see Table 1). In order to barcode the specimens, the cytochrome *c* oxidase subunit I was amplified. Information on DNA extraction, PCR and sequencing procedures can be obtained from a previous study (Sagorny & Wesener 2017). BLAST searches (Altschul *et al.* 1997) were performed to confirm sequence identities. Sequences were concatenated by hand or utilizing the software Seqman (DNASTAR Inc.). The entire dataset was translated into amino acids to rule out the accidental amplification of pseudogenes. Fifteen additional COI sequences representing seven different species of *Zoosphaerium* described in previous studies (Wesener *et al.* 2010a; Sagorny & Wesener 2017; Wesener & Anilkumar 2020) were downloaded from GenBank. Moreover, two sequences of the closely related Malagasy genus *Sphaeromimus* (Wesener & Sierwald 2005b; Wesener *et al.* 2014; Moritz & Wesener 2017) as a near outgroup and one sequence of the basal (Wesener & VandenSpiegel 2009; Wesener 2014) Sphaerotheriida family Procyliosomatidae as a far outgroup were added to the dataset.

All sequences were aligned in Bioedit (Hall 1999). The final dataset included 30 sequences from 22 morphospecies with 674 positions (12 newly sequenced, 18 from Genbank). Sequences of newly sequenced specimens were uploaded to Genbank and their accession codes (MW633250–MW633261) are provided here (Table 1).

A phylogenetic tree was reconstructed in the IQ-TREE web server (Trifinopoulos *et al.* 2016) using a maximum likelihood (ML) as the optimality criterion. General Time Reversible (GTR) (Tavaré 1986) and a gamma distribution with a proportion of invariant sites was selected as the best fitting model by IQ-TREE. Branch support was estimated based on an ultrafast bootstrap analysis using 1000 bootstrap replicates. The resulting tree (Fig. 1) was edited in Adobe Illustrator CS2.

Using the p-distances approach, a pairwise distance analysis was conducted in MEGA6 (Tamura *et al.* 2013). A table listing all calculated distances is provided (Table 2).

Results

Barcoding analysis

Intraspecific distances are between 0 and 2.5%, if female specimens whose identity is unknown are excluded (Table 2). In contrast to this, interspecific distances between the 15 identified species of the genus *Zoosphaerium* vary between 9.1 and 20%. The lowest interspecific distance (9.1%) is observed between *Z. minutus* Sagorny & Wesener, 2017 and *Z. mangabe* Wesener, 2017, but a similarly low p-distance (9.8%) is present between *Z. ambatovaky* sp. nov. and *Z. villosum*. All other interspecific distances are above 10%.

Table 1. Material examined for molecular data. CAS = California Academy of Sciences, San Francisco; FMNH = Field Museum of Natural History, Chicago; MZUF = Museum “La Specola”, Florence, Italy; ZFMK = Zoological Research Museum Alexander Koenig, Bonn, Germany. Specimens marked by an asterisk (12) were newly sequenced for this study. M = Madagascar.

Species	Voucher number	Genbank #	Locality
<i>Procyliosoma leae</i> (Silvestri, 1917)	QVMAG 23:45801	FJ409910.1	Australia, Tasmania
<i>Sphaeromimus musicus</i> (de Saussure & Zehntner, 1897)	ZFMK MYR 2273	KJ713244.1	M, Tsimelahy
<i>Sphaeromimus musicus</i> (de Saussure & Zehntner, 1897)	ZFMK MYR 2276	KJ713245.1	M, Tsimelahy
<i>Zoosphaerium album</i> Wesener, 2009 *	ZFMK MYR 7202	MW633250	M, Makay
<i>Zoosphaerium alluaudi</i> (de Saussure & Zehntner, 1897)	FMNH-INS 56000	FJ409926.1	M, Petriky
<i>Zoosphaerium alluaudi</i> (de Saussure & Zehntner, 1897)	FMNH-INS	FJ409927.1	M, Petit Lavasoa
<i>Zoosphaerium ambatovaky</i> sp. nov. (holotype) *	CASENT 9068294/1	MW633257	M, Ambatovaky
<i>Zoosphaerium bartolozzii</i> Wesener & Anilkumar, 2020	MZUF	MN783351	M, Ambalamanakana
<i>Zoosphaerium beanka</i> sp. nov. (holotype) *	FMNH-INS 3119897	MW633258	M, Beanka
<i>Zoosphaerium bemanevika</i> Sagorny & Wesener, 2017	FMNH-INS 2858678	KY399019.1	M, Bemanevika, Matsaborimena
<i>Zoosphaerium bemanevika</i> Sagorny & Wesener, 2017	FMNH-INS 3196510	KY399020.1	M, Bemanevika, Amberivery
<i>Zoosphaerium bemanevika</i> Sagorny & Wesener, 2017	FMNH-INS 2858686C	KY399021.1	M, Bemanevika, Amberivery
<i>Zoosphaerium libidinosum</i> (de Saussure & Zehntner, 1897) *	ZFMK MYR35/ Mangatsiaka	MW633251	M, Mangatsiaka
<i>Zoosphaerium mangabe</i> Wesener, 2020	FMNH-INS 2858681B	KY399026.1	M, Marojejy
<i>Zoosphaerium minutus</i> Sagorny & Wesener, 2017	FMNH-INS 2858676	KY399022.1	M, Bemanevika, Matsaborimena
<i>Zoosphaerium minutus</i> Sagorny & Wesener, 2017	FMNH-INS 2858686A	KY399023.1	M, Bemanevika, Amberivery
<i>Zoosphaerium nigrum</i> sp. nov. (holotype) *	CASENT9068289	MW633254	M, Midongy
<i>Zoosphaerium neptunus</i> (Butler, 1872)	FMNH-INS 56005	FJ409929.1	M, Perinet
<i>Zoosphaerium silens</i> sp. nov. (holotype) *	FMNH-INS 3119887	MW633252	M, Kirindy-Mite
<i>Zoosphaerium silens</i> sp. nov. *	FMNH-INS 3119875	MW633253	M, Andranomena
<i>Zoosphaerium spinopiligerum</i> sp. nov. (holotype) *	FMNH-INS 3119885	MW633255	M, Midongy-Befotaka
<i>Zoosphaerium cf. spinopiligerum</i> sp. nov. (♀) *	FMNH-INS 3119888/ ZFMK	MW633256	M, Midongy-Befotaka
<i>Zoosphaerium villosum</i> (Wesener & Sierwald, 2005)	ZFMK-MYR 00330	KY399028.1	M, Ambodivohangy
<i>Zoosphaerium voahangy</i> sp. nov. (holotype) *	FMNH-INS 3119921	MW633260	M, Analava
<i>Zoosphaerium voahangy</i> sp. nov. (paratype) *	FMNH-INS 3119919/ (ZFMK)	MW633261	M, Ambinda
<i>Zoosphaerium</i> sp. Brown	FMNH-INS 56072	FJ409931.1	M, Ivorona
<i>Zoosphaerium</i> sp. Green	FMNH-INS 3119870	KY399027.1	M, Brickaville
<i>Zoosphaerium</i> sp. Ma	FMNH-INS 3195649	KY399024.1	M, Masoala, Ambohitsito
<i>Zoosphaerium</i> sp. Ma	FMNH-INS 3195650	KY399025.1	M, Masoala, Sarahandrano
<i>Zoosphaerium</i> sp. Anjiamangirina *	FMNH-INS 3119906	MW633259	M, Anjiamangirina

The maximum likelihood analysis of the COI barcoding gene does not support the monophyly of *Zoosphaerium* (Fig. 1), as *Sphaeromimus musicus* is nested within the *Zoosphaerium* clade. All individual species of *Zoosphaerium* comprising more than one sequence are well-supported (>99%), but interspecific relationships mostly lack sufficient statistical support (Fig. 1). One well-supported clade comprises *Zoosphaerium silens* sp. nov., *Z. album* and *Z. libidinosum* (95%). Furthermore, the clade comprising *Zoosphaerium ambatovaky* sp. nov., *Z. bemanevika*, and *Z. villosum* as well as two unidentified species of *Zoosphaerium* from Brickaville and Masoala, respectively, receives good support (98%). A third, well-supported sister group relation is visible between an unnamed female *Zoosphaerium* from Anjiamangirina and *Zoosphaerium voahangy* sp. nov.

Table 2. Estimates of evolutionary divergence between sequences. The number of base differences per site between sequences are shown. The analysis involved 30 nucleotide sequences. Codon positions included were 1st + 2nd + 3rd. All ambiguous positions were removed for each sequence pair. There were a total of 674 positions in the final dataset. Evolutionary analyses were conducted in MEGA6.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29		
1. <i>Procyliosoma</i> sp.																															
2. <i>Sphaeromimus muscius</i> 1	0.233																														
3. <i>Sphaeromimus muscius</i> 2	0.233	0.000																													
4. <i>Zoosphaerium villosum</i>	0.227	0.180	0.180																												
5. <i>Zoosphaerium</i> sp. Breckaville	0.233	0.189	0.189	0.113																											
6. <i>Zoosphaerium nangabe</i>	0.204	0.198	0.198	0.132	0.134																										
7. <i>Zoosphaerium</i> sp. Ma	0.233	0.195	0.195	0.045	0.110	0.136																									
8. <i>Zoosphaerium</i> sp. Ma	0.234	0.196	0.196	0.043	0.111	0.135	0.001																								
9. <i>Zoosphaerium minutus</i> 1	0.196	0.193	0.193	0.126	0.132	0.091	0.122	0.120																							
10. <i>Zoosphaerium minutus</i> 2	0.203	0.190	0.190	0.128	0.134	0.095	0.123	0.122	0.012																						
11. <i>Zoosphaerium bemanevika</i> 1	0.222	0.167	0.167	0.106	0.122	0.141	0.117	0.119	0.131	0.131																					
12. <i>Zoosphaerium bemanevika</i> 2	0.227	0.170	0.170	0.107	0.119	0.144	0.114	0.116	0.131	0.134	0.010																				
13. <i>Zoosphaerium bemanevika</i> 3	0.222	0.167	0.167	0.106	0.122	0.141	0.117	0.119	0.131	0.131	0.000	0.010																			
14. <i>Zoosphaerium</i> sp. brown	0.197	0.191	0.191	0.159	0.160	0.149	0.165	0.163	0.128	0.128	0.149	0.152	0.149																		
15. <i>Zoosphaerium neptunus</i>	0.203	0.192	0.192	0.149	0.154	0.148	0.154	0.153	0.139	0.145	0.150	0.156	0.150	0.150																	
16. <i>Zoosphaerium alluaudi</i> PL	0.197	0.168	0.168	0.146	0.145	0.131	0.151	0.153	0.120	0.120	0.151	0.156	0.151	0.113	0.148																
17. <i>Zoosphaerium alluaudi</i> Petriky	0.200	0.172	0.172	0.145	0.145	0.132	0.151	0.153	0.120	0.120	0.151	0.156	0.151	0.113	0.148	0.003															
18. <i>Zoosphaerium bartolozzi</i>	0.210	0.196	0.196	0.141	0.141	0.131	0.139	0.141	0.122	0.119	0.150	0.151	0.150	0.132	0.147	0.113	0.112														
19. <i>Zoosphaerium nigrum</i>	0.219	0.189	0.189	0.156	0.145	0.155	0.161	0.160	0.136	0.140	0.155	0.158	0.155	0.143	0.160	0.139	0.136														
20. <i>Zoosphaerium silens</i> 1	0.222	0.195	0.195	0.155	0.166	0.163	0.166	0.165	0.159	0.153	0.163	0.168	0.163	0.158	0.171	0.160	0.162	0.151	0.167												
21. <i>Zoosphaerium silens</i> 2	0.226	0.205	0.205	0.160	0.173	0.166	0.166	0.164	0.160	0.155	0.167	0.172	0.167	0.168	0.172	0.161	0.163	0.155	0.175	0.025											
22. <i>Zoosphaerium ambatosaky</i>	0.217	0.183	0.183	0.098	0.107	0.107	0.103	0.104	0.104	0.103	0.113	0.111	0.113	0.129	0.144	0.120	0.120	0.125	0.138	0.150	0.157										
23. <i>Zoosphaerium beanka</i>	0.216	0.180	0.180	0.134	0.145	0.148	0.141	0.139	0.138	0.136	0.144	0.141	0.144	0.147	0.159	0.135	0.135	0.145	0.148	0.142	0.146	0.134									
24. <i>Zoosphaerium voahangy</i> 1	0.228	0.186	0.186	0.163	0.155	0.163	0.165	0.166	0.161	0.161	0.178	0.175	0.178	0.161	0.176	0.148	0.148	0.163	0.144	0.149	0.200	0.137	0.163								
25. <i>Zoosphaerium voahangy</i> 2	0.225	0.182	0.182	0.164	0.154	0.162	0.163	0.165	0.163	0.153	0.150	0.175	0.172	0.175	0.147	0.144	0.150	0.142	0.184	0.190	0.132	0.160	0.008								
26. <i>Zoosphaerium spinophiligerum</i> 1	0.219	0.167	0.167	0.128	0.132	0.131	0.138	0.139	0.129	0.129	0.154	0.154	0.154	0.140	0.153	0.111	0.112	0.117	0.143	0.159	0.158	0.119	0.142	0.160	0.148						
27. <i>Zoosphaerium spinophiligerum</i> 2	0.218	0.162	0.162	0.119	0.114	0.132	0.128	0.129	0.128	0.129	0.144	0.142	0.144	0.122	0.144	0.107	0.108	0.116	0.139	0.148	0.158	0.113	0.135	0.153	0.144	0.064					
28. <i>Zoosphaerium</i> sp. Aujiamangirina	0.233	0.182	0.182	0.174	0.169	0.178	0.178	0.180	0.160	0.163	0.177	0.180	0.177	0.168	0.177	0.166	0.169	0.153	0.161	0.190	0.169	0.132	0.150	0.153	0.158	0.148	0.086	0.148	0.150		
29. <i>Zoosphaerium album</i>	0.231	0.198	0.198	0.132	0.141	0.152	0.146	0.147	0.134	0.134	0.155	0.152	0.155	0.144	0.167	0.149	0.148	0.147	0.148	0.126	0.128	0.132	0.150	0.153	0.158	0.137	0.131	0.173			
30. <i>Zoosphaerium libidinosum</i>	0.213	0.187	0.187	0.166	0.170	0.160	0.181	0.182	0.158	0.157	0.160	0.162	0.160	0.158	0.181	0.158	0.158	0.152	0.153	0.123	0.133	0.154	0.160	0.178	0.179	0.157	0.142	0.195	0.144		

Taxonomy

Class Diplopoda de Blainville in Gervais, 1844

Order Sphaerotheriida Brandt, 1833

Family Arthrosphaeridae Jeekel, 1974

Genus *Zoosphaerium* Pocock, 1895

Zoosphaerium Pocock, 1895: 410.

Globotharium Brolemann, 1922: 230 (formal synonymization in Wesener & Wägele 2008: 9).

Heligmasoma Chamberlin, 1921: 58 (formal synonymization in Wesener & Wägele 2008: 9).

See Wesener (2016) for a summary; five additional species have been described since then (Sagorny & Wesener 2017; Wesener & Anilkumar 2020).

Type species

Sphaerotherium neptunus Butler, 1872.

Other species included

66 and 11 nomina dubia (including the species described below).

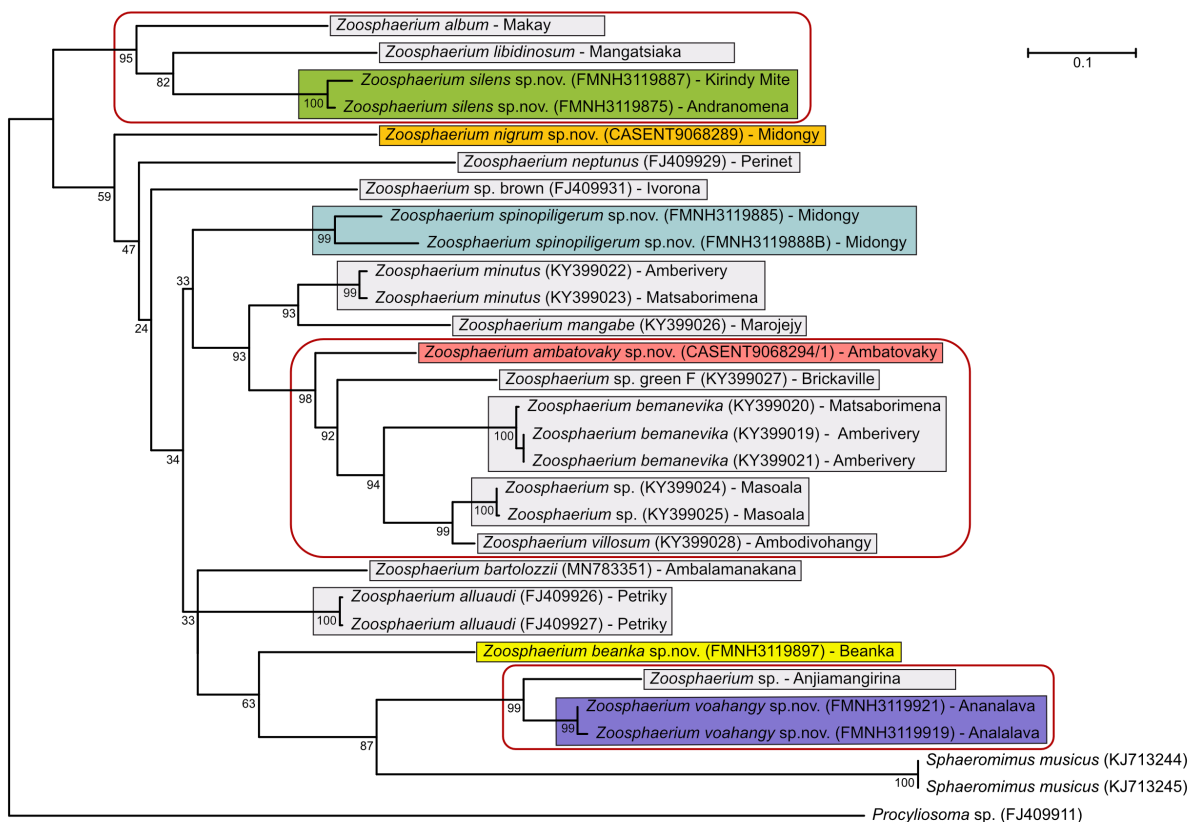


Fig. 1. Maximum likelihood tree inferred from the COI dataset with 1000 bootstrap pseudoreplicates implementing the GTR+I+G model. Colors representing newly described species of *Zoosphaerium*: orange = *Z. nigrum* sp. nov.; green = *Z. silens* sp. nov.; red = *Z. ambatovaky* sp. nov.; yellow = *Z. beanka* sp. nov.; purple = *Z. voahangy* sp. nov.; blue = *Z. masoala* sp. nov. Round-cornered rectangles indicate well-supported sister group relationships.

Distribution

Endemic to Madagascar.

Remarks

The diverse genus *Zoosphaerium* has been divided into six species-groups (Wesener & Wägele 2008; Wesener 2009). Six additional species are currently not assignable to any group (Sagorny & Wesener 2017). Four species are only known from females and an additional 11 species are nomina dubia. A key to the species-groups has been published elsewhere (Wesener 2009).

***Zoosphaerium libidinosum* species-group**

Remarks

Species can be identified as members of the *Z. libidinosum* species-group based on morphological characters of the posterior telopods, in which the third telopoditomere carries more than 15 large crenulated teeth as well as two large membranous lobes (Wesener & Wägele 2008). The species-group now contains 16 described species distributed in all types of forests all over Madagascar, including the arid spiny bush (Wesener 2009).

Key to species of the *Zoosphaerium libidinosum* species-group

1. Anal shield without locking carinae (in small, immature individuals sometimes traces of carinae are visible)2
 - Anal shield with two obvious locking carinae7
2. Operculum of vulva at least weakly notched apically. Fifth antennomere with field of sensilla basiconica apically3
 - Operculum of vulva well-rounded apically. No sensilla basiconica present on fifth antennomere4
3. Tergites dark green, in alcohol almost blackish, posterior margin light brown to yellow. Tarsus of walking legs broad, only 3.0 times as long as wide. Third podomere of anterior telopods with four large, sclerotized teeth. Endotergal marginal bristles strongly extending beyond tergite*Z. haackeri* Wesener, 2009
 - Tergites almost white, with light, shiny-green field dorso-laterally on each side. Tarsus of walking legs of usual size, 3.8 times as long as wide. Third podomere of anterior telopods with single large, sclerotized tooth. Endotergal marginal bristles slightly extending beyond tergite*Z. album* Wesener, 2009
4. Anterior telopod second podomere process slightly extending beyond third podomere. Third podomere laterally with plateau and mesally with a sharp, prominent process. Tergites light green with distinct, light brown posterior margin. Male harp with two weakly-developed stridulation ribs*Z. discolor* Wesener, 2009
 - Anterior telopod second podomere process shorter than third podomere. Third podomere of anterior telopods only laterally with plateau5
5. Tergites dark, almost blackish green, posteriorly with distinct and wide light brown margin. Anal shield covered with numerous short hairs. Endotergum with a single row of marginal bristles, slightly extending beyond tergite*Z. mitoho* Wesener, 2009
 - Tergites with dark green, light green pattern, posteriorly with distinct, thin light brown margin. Anal shield glabrous. Endotergum with two or more rows of marginal bristles, clearly extending beyond apical margin6

6. Endotergum with ≥ 3 rows of marginal bristles, strongly extending beyond tergite. Third podomere of anterior telopods laterally with a triangular projection. Tarsi of walking legs >3.7 times as long as wide. Male harp with two strongly developed stridulation ribs
**Z. libidiosum** (de Saussure & Zehntner, 1897)
- Endotergum with two rows of marginal bristles, strongly extending beyond tergite. Third podomere of anterior telopods laterally without triangular projection. Tarsi of walking legs 3.5 times as long as wide. Male harp with two weakly developed stridulation ribs**Z. silens** sp. nov.
7. Second and third podomeres of posterior telopods covered with numerous minute hairs. Antennae with four apical cones; tergites glossy, glabrous8
- Second and third podomeres of posterior telopods glabrous or covered with long setae10
8. Tergites black. Anterior telopod with one stridulation rib**Z. nigrum** sp. nov.
- Tergites jade-like green. Anterior telopod at least apically with 2 stridulation ribs9
9. Tergites glossy, completely jade-like green. Male harp with two basally fused stridulation ribs. Third podomere of anterior telopods mesally with sharp, prominent process. Endotergum with one row of rounded cuticular impressions. Fixed finger of posterior telopod basally without membranous lobe**Z. anomalum** (de Saussure & Zehntner, 1902)
- Tergites glossy, jade-like green, with shiny dark green pattern. Male harp with two fully separate stridulation ribs. Third podomere of anterior telopods without process. Endotergum without cuticular impressions. Fixed finger of posterior telopod with basal membranous lobe
**Z. pulchellum** Wesener, 2009
10. Posterior end of anal shield in both sexes excavated11
- Posterior end of anal shield well-rounded14
11. Tergites glossy, green. Male harp with two weakly-developed stridulation ribs. Third podomere of anterior telopods with a single large sclerotized tooth**Z. endemicum** Wesener, 2009
- Tergites matte, brownish. Male harp with two well-developed stridulation ribs12
12. Locking carinae on anal shield of similar length. Third podomere of posterior telopods with ca 28 large sclerotized teeth. Antenna with more than 40 apical cones
**Z. xerophilum** Wesener, 2009
- Posterior locking carina at least two times as long as anterior carina. Third podomere of posterior telopods with less than 25 large sclerotized teeth. Antenna with less than 30 apical cones
13
13. Posterior locking carina of anal shield more than three times as long as anterior carina
**Z. arborealis** Wesener & Sierwald, 2005
- Posterior locking carina ca twice as long as anterior one**Z. lambertoni** (Brolemann, 1922)
14. Anal shield glabrous, golden. Tergites with unique pitch-black/reddish-brown pattern. Third podomere of anterior telopods without large sclerotized teeth. First antennomere without sensilla basiconica. Sclerotized teeth present on antennomeres 1–4. Endotergal marginal bristles not extending beyond tergite margin**Z. aureum** Wesener, 2009
- Anal shield covered with few, minute hairs of dirty brownish color. Tergites with light brown, blackish coloration pattern. Third podomere of anterior telopods laterally with at least a single large sclerotized tooth. First antennomere with sensilla basiconica. Sclerotized teeth present on antennomeres 1–5. Endotergal marginal bristles slightly extending beyond tergite margin15

15. Legs short, femur 1.45 times as long as wide, tarsus 3.2 times as long as wide. Third pair of legs without apical spine. Third podomere of posterior telopods with ca 18 large sclerotized teeth. Endotergum with two rows of marginal bristles. Posterior locking carina 4 times as long as anterior carina. Antenna with 25 or fewer apical cones*Z. priapus* (de Saussure & Zehntner, 1897)
- Legs of usual size, femur 1.9 times as long as wide, tarsus 4.2 times as long as wide. Third pair of legs with apical spine. Third podomere of posterior telopods with ca 22 large sclerotized teeth. Endotergum with three rows of marginal bristles. Locking carinae of equal size. Antenna with 35–86 apical cones*Z. pseudopriapus* Wesener, 2009

Zoosphaerium nigrum sp. nov.

[urn:lsid:zoobank.org:act:4F170F43-C7A9-44A4-A004-47FD58FD8A2F](https://doi.org/10.21203/rs.3.rs-170743-v1)

Figs 2A, 3–4, 5A

Diagnosis

Posterior telopods (Fig. 4H–I) identify this species as a member of the *Z. libidinosum* species-group. Within this group, *Zoosphaerium nigrum* sp. nov. shares a number of characters with only *Z. anomalum* (de Saussure & Zehntner, 1902) and *Z. pulchellum* Wesener, 2009. These include the presence of two locking carinae, four apical cones on each antenna, and shiny, glossy tergites. Moreover, the second and third podomeres of the posterior telopods are covered with numerous minute hairs. *Zoosphaerium nigrum* sp. nov. differs from these two species in the black coloration (jade-like green in the others), the presence of only a single weak stridulation rib on the anterior telopod and differently shaped podomeres.

Etymology

‘Nigrum’, adjective, after the dark colour of the species.

Material examined

Holotype

MADAGASCAR – Fianarantosa • ♂; Parc National Befotaka-Midongy, Papango, 28.5 km S of Midongy-Sud, Mount Papango; 23°50'27" S, 46°57'27" E; alt. 1250 m; montane rainforest; 17 Nov. 2006; B.L. Fisher *et al.* leg.; coll. no. BLF14945; CASENT 9068289.

Description

Male

BODY LENGTH. Holotype male: length ca 28 mm, width of thoracic shield 13.1 mm, of tergite 7 13.5 mm (widest), height of thoracic shield 7.1 mm, of tergite 7 7.4 mm (highest).

COLORATION. Some discoloration may have occurred because of preservation in ethanol. Tergites, head, anal shield and appendages dark green to black (Fig. 2A). Posterior margin of tergites with a thin brown margin.

HEAD. Wide and short. Eyes with >120 ommatidia. Aberrant ocellus located in antennal groove. Antennae short, with cylindrical joints, reaching posteriorly to leg pair 3. Length of antennomeres 1=2=3=4=5<6. A shallow groove present on antennomere 1. Male apical disc with four apical sensory cones. Organ of Tömösváry located in antennal groove.

GNATHOCHILARIUM AND MANDIBLE. Not dissected.

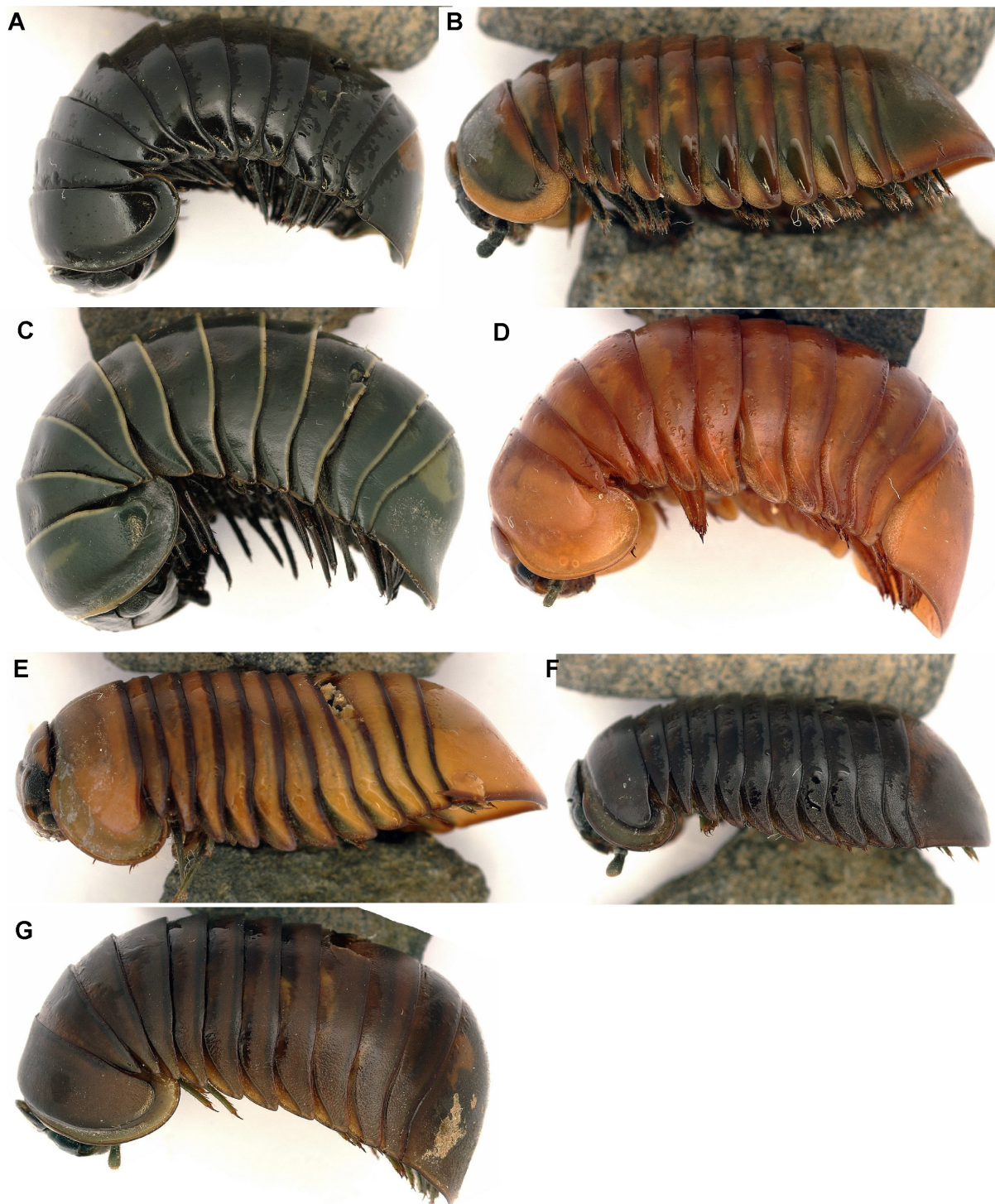


Fig. 2. Habitus photographs of the seven new species of *Zoosphaerium*, lateral view. **A.** *Zoosphaerium nigrum* sp. nov., holotype (CASENT 9068289). **B.** *Z. silens* sp. nov., holotype (FMNH-INS 3119887). **C.** *Z. ambatovaky* sp. nov., holotype (CASENT 9068294/1). **D.** *Z. beanka* sp. nov., holotype (FMNH-INS 3119897). **E.** *Z. voahangy* sp. nov., holotype (FMNH-INS 3119921). **F.** *Z. masoala* sp. nov., holotype (FMNH-INS 3195651). **G.** *Z. spinopiligerum* sp. nov., holotype (FMNH-INS 3119885). Not to scale.

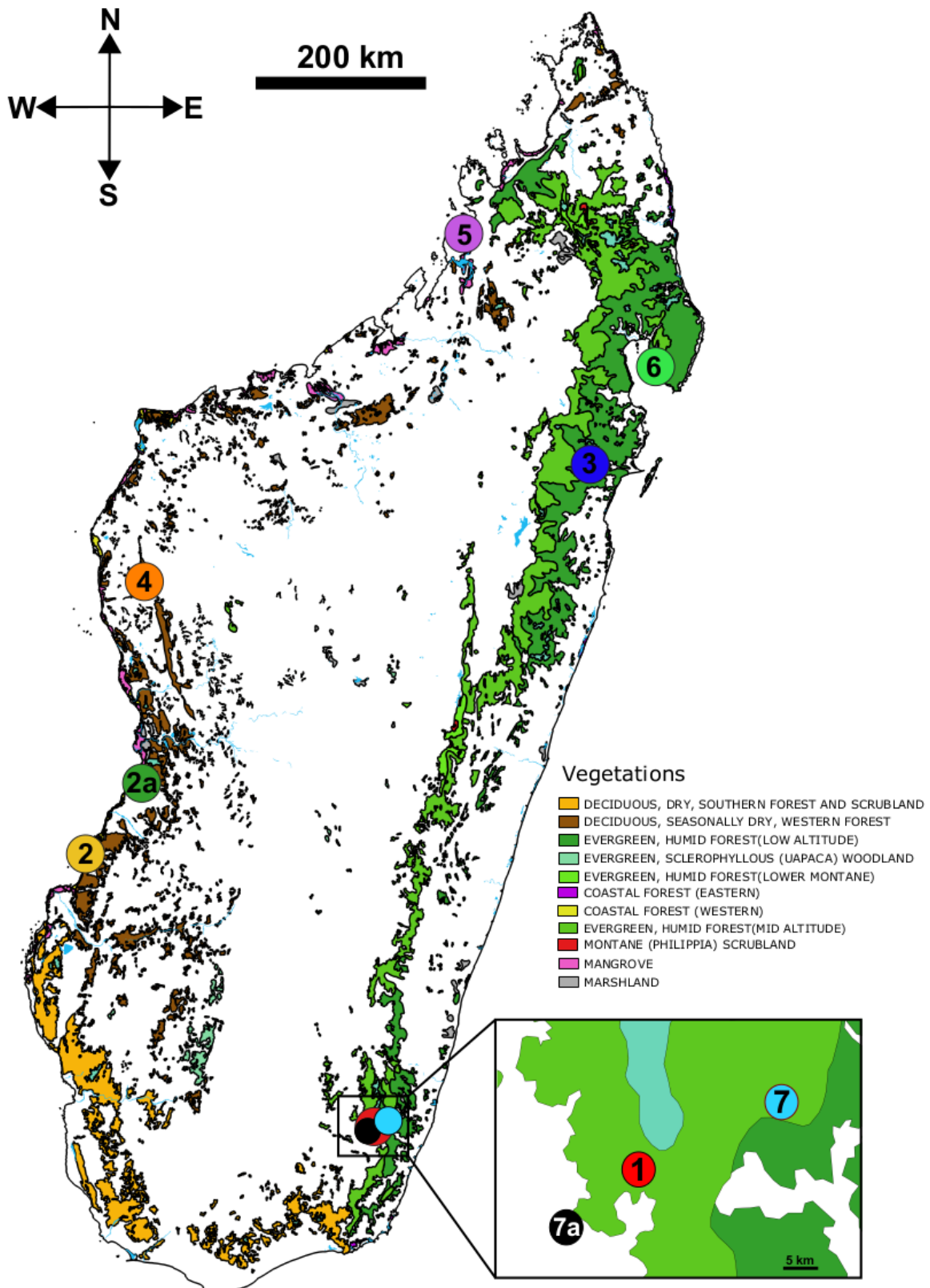


Fig. 3. Distribution map of the newly described species of *Zoosphaerium*. Vegetation color marks modified from Moat & Smith 2007. 1 = *Z. nigrum* sp. nov.; 2 = *Z. silens* sp. nov.; 3 = *Z. ambatovaky* sp. nov.; 4 = *Z. beanka* sp. nov.; 5 = *Z. voahangy* sp. nov.; 6 = *Z. masoala* sp. nov.; 7 = *Z. spinopiligerum* sp. nov. Numbers followed by 'a' mark additional, non-type localities.

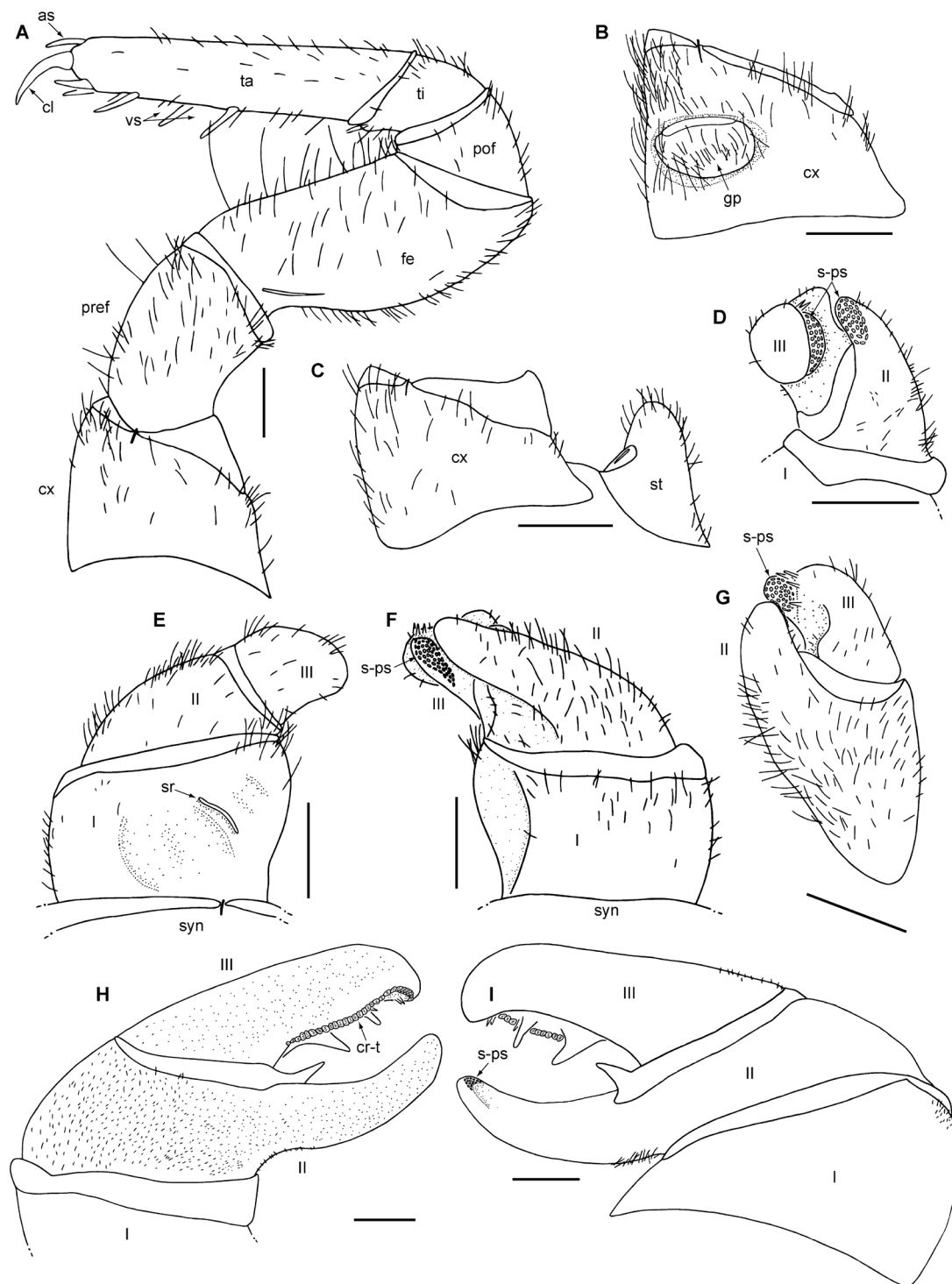


Fig. 4. *Zoosphaerium nigrum* sp. nov., holotype (CASENT 9068289). **A.** Left leg 9, posterior view. **B.** Left coxa 2 with gonopore, posterior view. **C.** Left coxa 1 with stigmatic plate, posterior view. **D.** Left anterior gonopod, mesal view. **E.** Left anterior gonopod, anterior view. **F.** Left anterior gonopod, posterior view. **G.** Left anterior gonopod, lateral view. **H.** Right posterior telopod, posterior view. **I.** Right posterior telopod, anterior view. Abbreviations: as = apical spine; cl = claw; cr-t = crenulated teeth; cx = coxa; fe = femur; gp = gonopore; pof = postfemur; pref = prefemur; s-ps = sclerotized spots; sr = stridulation rib; st = stigmatic plate; syn = syncoxite; ta = tarsus; ti = tibia; vs = ventral spines. Roman numerals indicate telopoditomerites. Scale bars = 1 mm.

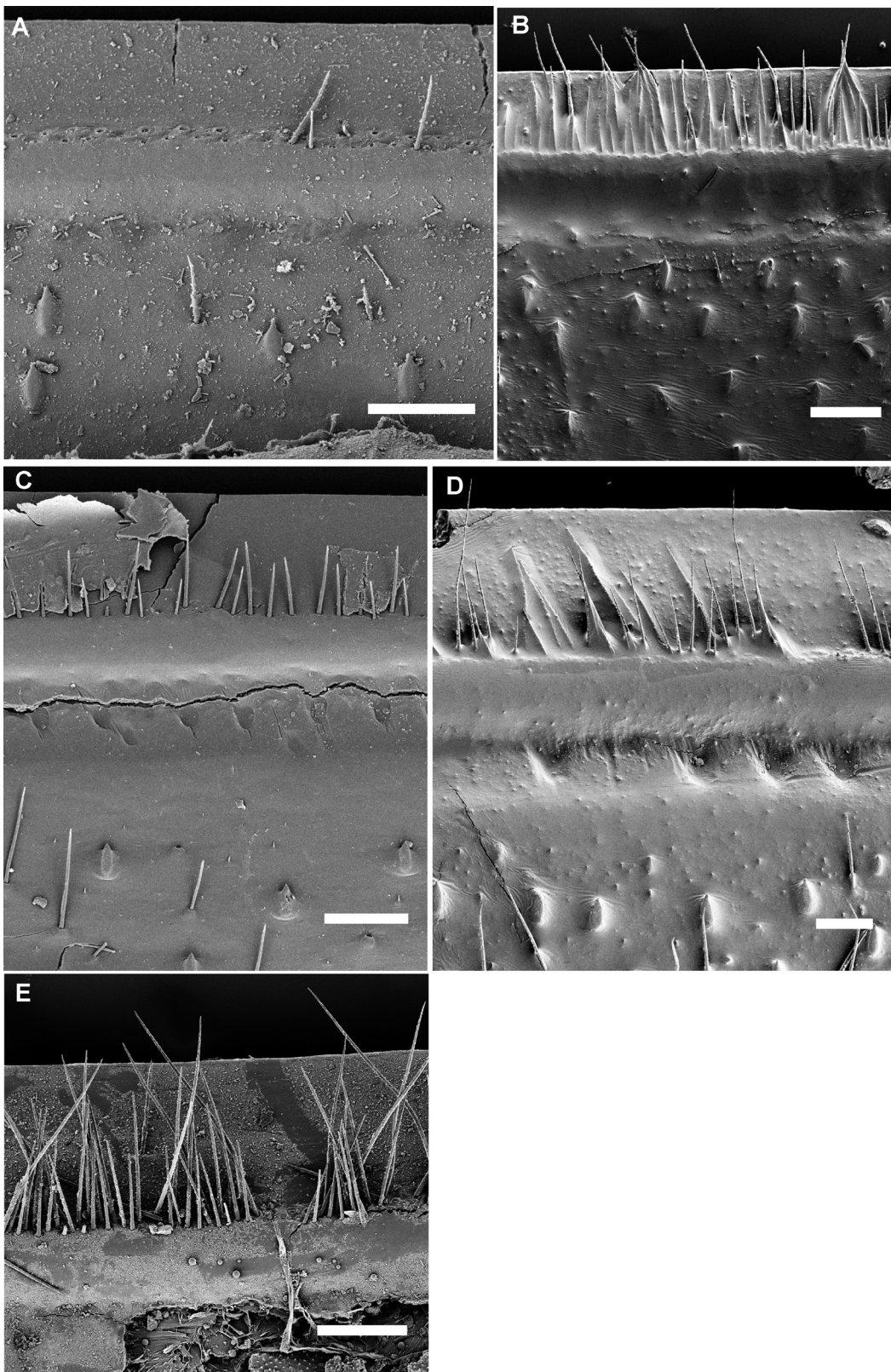


Fig. 5. Scanning electron micrographs of the endoterga of midbody rings. **A.** *Zoosphaerium nigrum* sp. nov., holotype (CASENT 9068289). **B.** *Z. silens* sp. nov., holotype (FMNH-INS 3119887). **C.** *Z. ambatovaky* sp. nov., holotype (CASENT 9068294/1). **D.** *Z. beanka* sp. nov., holotype (FMNH-INS 3119897). **E.** *Z. voahangy* sp. nov., holotype (FMNH-INS 3119921). Scale bars = 100 μ m.

STIGMATIC PLATES. First stigmatic plate triangular, apex well rounded, nearly as wide as at base. Mesal margin straight, not curved towards coxa. Hair most abundant on apical margin, very few hairs on basal and lateral margins (Fig. 4C).

PLEURITES. First pleurite laterally modified and extending backwards with a broad, apically rounded process. Other pleurites well-rounded.

COLLUM. Glabrous with very sparse setae around margins, mostly located at corners on either side of head.

THORACIC SHIELD. Smooth and glabrous, without protuberances.

TERGITES. Surface glabrous and shiny, lacking small pits. Tips of paratergites of midbody tergites projecting posteriorly.

ENDOTERGUM. Inner section with numerous short triangular spines and very few longer setae. Middle area above spines with single row of sparse, circular cuticular impressions slightly varying in size. Apically a single row of short marginal bristles, protruding to $\frac{2}{3}$ distance to tergite margin. Bristles with numerous small spines (Fig. 5A).

ANAL SHIELD. Large and slightly bell-shaped. Several tiny setae present in posterior part. Underside with two black locking carinae, posterior one 2 times as long as anterior one, both located close to anal shield margin.

LEGS. Leg 1 with 5 ventral spines, leg 2 with 3, leg 3 with 3–5. First two leg pairs without an apical spine, spine present on leg 3. Leg pairs 4–21 with 5–7 ventral spines and an apical spine. On leg 9, femur 1.8 and tarsus 4.6 times as long as wide. All podomeres with setae (Fig. 4A).

Male sexual characters

GONOPORE. Covered with a single undivided, rounded membranous plate (Fig. 4B).

ANTERIOR TELOPODS. Harp with a single weak stridulation rib (Fig. 4E). First podomere with only a few setae, restricted to apical parts of lateral margins, 1.5 times wider than long. Process of second podomere as long as $\frac{2}{3}$ of third podomere, not visible in anterior view, with apical mound of a few sclerotized spots juxtaposed to third podomere. Third podomere without sclerotized teeth, but with a conspicuous process carrying sclerotized spots (Fig. 4F–G); base of process with four spines (Fig. 4G). Second and third podomeres sparsely setose.

POSTERIOR TELOPODS. Movable finger weakly curved; hollowed-out inner margin with two non-sclerotized lobes and ca three smaller sclerotized spines, posterior aspect with ca 29 crenulated teeth. Fixed finger thinner than movable finger, with slightly curved tip; basally with single membranous lobe, on inner margin covered with numerous sclerotized spots. Second and third podomeres without any long hair, but on both sides densely covered with very small pits, one very small seta standing in each pit. First podomere without those pits but with some isolated, standard longer hairs.

Female

Unknown.

Distribution and ecology

Zoosphaerium nigrum sp. nov. is currently known only from the montane rainforests of Midongy-Befotaka (Fig. 3) where it coexists with another species of the genus, *Z. spinopiligerum* sp. nov. (see below), as well as with a species of the genus *Sphaeromimus* (Moritz & Wesener 2017).

Zoosphaerium silens sp. nov.

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Figs 2B, 3, 5B, 6

Diagnosis

The posterior telopods (Fig. 6H–I) identify *Z. silens* sp. nov. as a member of the *Z. libidinosum* species-group. *Zoosphaerium silens* sp. nov. shares the absence of locking carinae with a number of spiny forest species. It differs from all other species except *Z. libidinosum* in the color of the tergites, the glabrous anal shield and the presence of at least two rows of very long endotergal bristles. *Zoosphaerium silens* sp. nov. differs from *Z. libidinosum* in the wider tarsus (3.5 versus 3.8 times as long as wide), the presence of only two rows of endotergal bristles (three rows in *Z. libidinosum*) and the absence of a lateral triangular projection on the third podomere of the anterior telopods (present in *Z. libidinosum*).

Z. silens sp. nov. differs by more than 14% uncorrected p-distance in the COI gene from *Z. album* and *Z. libidinosum*.

Etymology

‘Silens’ (= ‘quiet’), noun in apposition, after the reduced stridulation ribs in the male.

Material examined

Holotype

MADAGASCAR – **Toliara** • ♂; Parc National de Kirindy Mite, 25.6 km SW of Belo sur Mer; 20°56.6' S, 43°52.3' E; alt. 10 m; dry deciduous forest; 9 Mar. 2007; V. Soarimalala leg.; coll. no. VS-1348; FMNH-INS 3119887.

Paratype

MADAGASCAR – **Toliara** • ♀; same collection data as for holotype; FMNH-INS 3119887.

Other material

MADAGASCAR – **Toliara** • 4 ♂♂; Réserve Spéciale d'Andranomena; 20°10'31" S, 44°28'25" E; alt. 18 m; dry deciduous forest; 12 Mar. 2010; V. Soarimalala leg.; coll. no. VS-1815; FMNH-INS 3119875 • 1 ♂; same collection data as for preceding; ZFMK MYR11137.

Description

BODY LENGTH. Largest female (paratype): length ca 27.2 mm, width of thoracic shield 14.3 mm, of tergite 8 14.8 mm (widest), height of thoracic shield 8.2 mm, of tergite 8 10.1 mm (highest).

COLORATION. Some discoloration may have occurred because of preservation in ethanol. Tergites dorsally orange to brown, especially at posterior margin, laterally green except for paratergite depressions which are yellow. Anal shield light brown to yellowish dorsally as well as posteriorly, laterally green. Thoracic shield green, but grooves and margins yellow-brownish (Fig. 2B). Head and antennae green, legs basally light brown, apically green.

HEAD. Wide and short. Eyes with >75 ommatidia. Aberrant ocellus located in antennal groove. Antennae short, with cylindrical joints, protruding posteriorly to leg pair 3. Length of antennomeres 1=2=3=4=5<6. A shallow groove present on antennomere 1. Male apical disc with 11 or 12 apical sensory cones. Organ of Tömösváry located in antennal groove.

GNATHOCHILARIUM AND MANDIBLE. Not dissected.

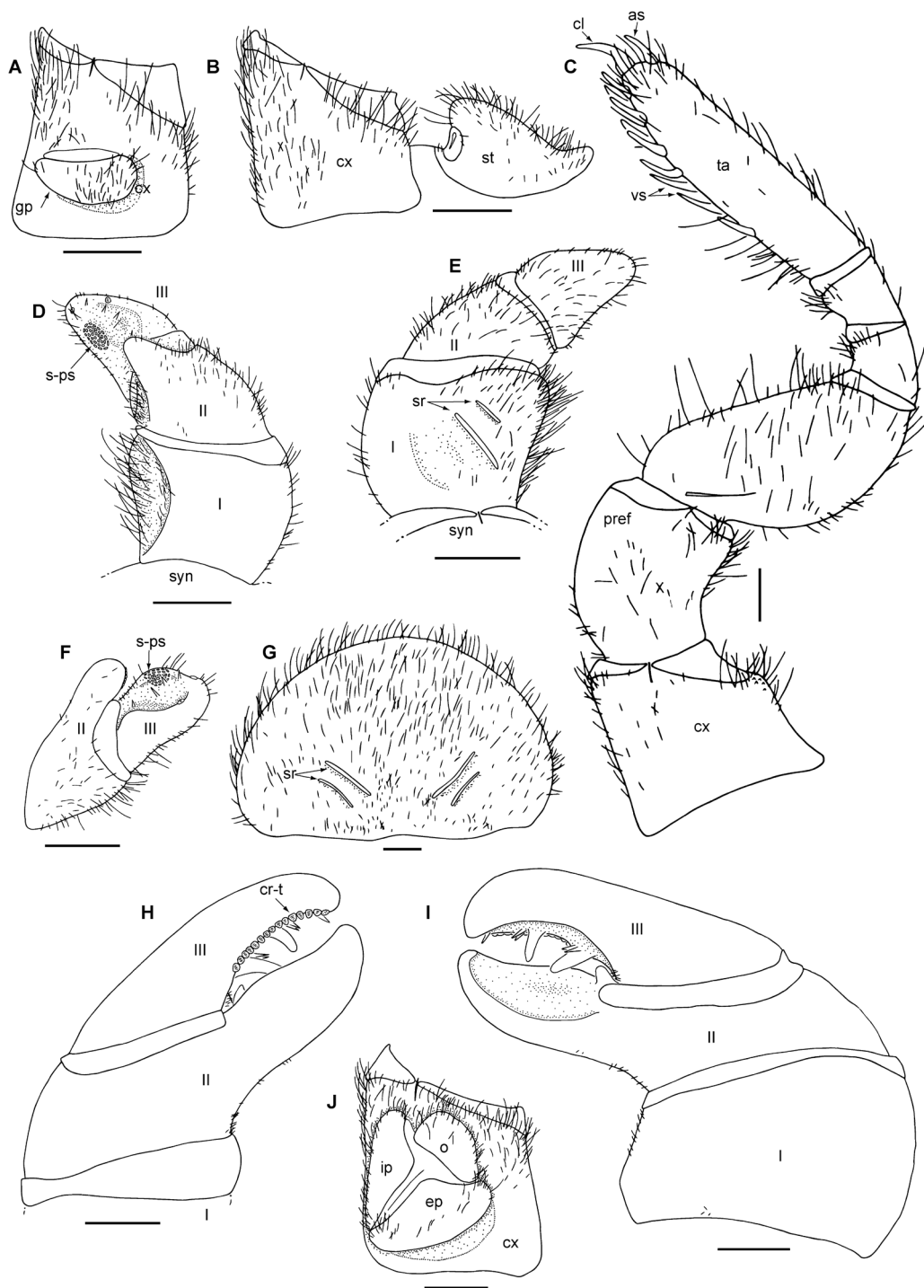


Fig. 6. *Zoosphaerium silens* sp. nov., holotype (FMNH-INS 3119887). **A.** Left coxa 2 with gonopore, posterior view. **B.** Left coxa 1 with stigmatic plate, posterior view. **C.** Left leg 9, posterior view. **D.** Left anterior gonopod, posterior view. **E.** Left anterior gonopod, anterior view. **F.** Left anterior gonopod, lateral view. **G.** Female subanal plate with washboard. **H.** Right posterior telopod, posterior view. **I.** Right posterior telopod, anterior view. **J.** Left female coxa 2 with vulva, posterior view. Abbreviations: as = apical spine; cl = claw; cr-t = crenulated teeth; cx = coxa; ep = external plate; gp = gonopore; ip = inner plate; o = operculum; pref = prefemur; s-ps = sclerotized spots; sr = stridulation rib; st = stigmatic plate; syn = syncoxite; ta = tarsus; vs = ventral spines. Roman numerals indicate telopoditomerites. Scale bars = 1 mm.

STIGMATIC PLATES. First plate triangular, apex well rounded, nearly as wide as at base. Mesal margin slightly curved towards coxa. Hairs most abundant on apical margin, very few hairs on basal and lateral margins (Fig. 6B).

PLEURITES. First pleurite weakly modified, slightly extending posteriorly. Other pleurites well-rounded.

COLLUM. Glabrous with very sparse setae around margins, mostly located at corners on either side of head.

THORACIC SHIELD. Smooth and glabrous, without protuberances.

TERGITES. Surface glabrous and matte, lacking small pits. Tips of paratergites of midbody tergites projecting posteriorly.

ENDOTERGUM. Inner section with numerous short triangular spines and very few longer setae. Middle area above spines with a single row of sparse elliptical cuticular impressions slightly varying in size. Apically two rows of dense marginal bristles, every second bristle strongly protruding above tergite margin (Fig. 5B). Bristles with numerous small spines.

ANAL SHIELD. Large and well-rounded. In both sexes glabrous. Underside lacking locking carinae.

LEGS. Leg 1 with 1 ventral spine, leg 2 with 1, leg 3 with 5 or 6. First two leg pairs without an apical spine, spine present on leg 3. Leg pairs 4–21 with 8–10 ventral spines and an apical spine. On leg 9, femur 1.7 and tarsus 3.5 times as long as wide. All podomeres with setae (Fig. 6C).

Male sexual characters

GONOPORE. Covered with a single undivided, rounded membranous plate, very wide, located on basal half of coxa (Fig. 6A).

ANTERIOR TELOPODS. Harp with two weak stridulation ribs (Fig. 6E). First podomere with numerous setae mainly at lateral margin, as wide as long. Process of second podomere as long as basal fifth of third podomere, not visible in anterior view, with apical mound of a few sclerotized spots juxtaposed to third podomere. Third podomere with an apical sclerotized spot and a lateral crenulated tooth, mesally with an elevated area carrying sclerotized spots (Fig. 6D, F); lower area carrying 4 spines (Fig. 6D, F). Second and third podomeres sparsely setose.

POSTERIOR TELOPODS. Movable finger weakly curved; hollowed-out inner margin with two non-sclerotized lobes and ca five smaller sclerotized spines, posterior aspect with ca 15 large crenulated teeth. Fixed finger wider than movable finger, with slightly curved tip; basally with single membranous lobe, on inner margin covered with a few sclerotized spots. Second and third podomeres lacking long hair, almost completely glabrous. First podomere glabrous except for a few setae at mesal margin.

Female sexual characters

Washboard with two short interrupted stridulation ribs on each half (Fig. 6G). Vulva covering more than $\frac{2}{3}$ of coxa surface. Operculum large, ending before coxal margin. Apical margin of operculum well-rounded, reaching apicalmost point medially. Mesal plate reaching up to half of operculum's height (Fig. 6J).

Distribution and ecology

Zoosphaerium silens sp. nov. is currently known from the western dry forest of Kirindy-Mite as well as from the dry forest of Andranomena further north (Fig. 3). These populations differ by an uncorrected p-distance of 2.8% (Table 2).

Zoosphaerium coquerelianum species-group

Remarks

Species can be identified as members of the *Zoosphaerium coquerelianum* species-group based on morphological characters of the posterior telopods (Wesener & Wägele 2008; Wesener 2009). Telopoditomere 3 only carries small sclerotized teeth and is always slightly longer and >1.5 times as wide as the immovable finger. Similar telopod characters occur in some members of the *Z. platylabum* species-group, but the locking carinae in this group are located close to the last pleurites, while they are positioned close to the anal shield margin in species of the *Z. coquerelianum* group. The species-group now contains 23 described species distributed in humid to subhumid forests all over Madagascar. Species of this group are conspicuously absent from the spiny forest ecosystem and the western dry forest (Wesener 2009; Wesener *et al.* 2010b; Sagorny & Wesener 2017; Wesener & Anilkumar 2020).

Key to the species of the *Zoosphaerium coquerelianum* group

1. Male harp with two to three stridulation ribs2
 - Male harp with a single stridulation rib11
2. Tergites glossy, anteriorly shiny light green, posteriorly dark green. Specimen more than 50 mm long. Anal shield not well-rounded, with steep slope. Movable finger of posterior telopods 1.6 times as long as wide, apically with groove*Z. amabile* Wesener, 2009
 - Coloration pattern different, or if similar then specimens less than 35 mm long. Anal shield well-rounded or bell-shaped. Movable finger of posterior telopods 1.9–2.5 times as long as wide, without apical groove3
3. Antenna with four apical cones4
 - Antenna with >10 apical cones5
4. Anal shield surface covered with short hairs. Posterior locking carina of anal shield 2.5–3 times as long as anterior carina*Z. alluaudi* (de Saussure & Zehntner, 1902)
 - Anal shield surface glabrous. Posterior locking carina of anal shield more than 3.5 times as long as anterior carina*Z. voeltzkowianum* (de Saussure & Zehntner, 1897)
5. Male harp with three stridulation ribs. Endotergum with three rows of marginal bristles, bristles slightly extending beyond tergite. Sclerotized teeth present on antennomeres 1–5. Movable finger of posterior telopods 2 times as long as wide. Posterior locking carina of anal shield four times as long as anterior carina. Male anal shield bell-shaped*Z. trichordum* Wesener, 2009
 - Male harp with two stridulation ribs. Endotergum with one up to two rows of marginal bristles, bristles not reaching tergite margin. Sclerotized teeth only present up to antennomere 3 or 46
6. Only up to eight ventral spines on walking legs7
 - At least nine ventral spines on walking legs8
7. Movable finger of posterior telopod thick, 2.5 times as long as wide. Leg 3 with an apical spine. On anal shield, second locking carina 2–3 times as long as first*Z. ambatovaky* sp. nov.
 - Movable finger of posterior telopod very thick, 2 times as long as wide. Leg 3 without an apical spine. On anal shield, second locking carina 4–5 times as long as first*Z. muscorum* Wesener & Bespalova, 2010

8. Male anal shield well-rounded, with slight bell shape. Posterior locking carina of anal shield six times as long as anterior carina. Up to 10 ventral spines on walking legs*Z. bambusoides* Wesener & Bespalova, 2010
 – Male anal shield well-rounded. Posterior locking carina of anal shield three to four times as long as anterior carina. Usually more than 10 ventral spines on walking legs9
9. Leg 3 without an apical spine. Specimens only slightly more than 30 mm long. Tergites jade-like green with thin brown posterior margin, texture glossy. Operculum of vulva deeply notched, strongly extending beyond coxa. Apical disc with ca 14 apical cones*Z. smaragdinum* Wesener, 2009
 – Leg 3 with an apical spine. Specimens more than 50 mm long. Tergites never jade-like, not glossy. Operculum of vulva not protruding above coxal margin. Apical disc with more than 20 apical cones10
10. Specimens more than 60 mm long. Tergites dark-green, covered with numerous large pits and short setae. Sclerotized teeth present on antennomeres 1–3, disc with ca 45 apical cones. Endotergum with two rows of marginal bristles*Z. villosum* Wesener & Sierwald, 2005
 – Specimens less than 60 mm long. Tergites light-brown, glabrous. Sclerotized teeth present on antennomeres 1–4, disc with 20–30 apical cones. Endotergum with a single row of marginal bristles*Z. bemanevika* Sagorny & Wesener, 2017
11. Movable finger 3 times as long as wide*Z. ambrense* Wesener, 2009
 – Movable finger <2.5 times as long as wide12
12. Antenna with four apical cones. Movable finger of posterior telopods at inner margin with two membranous lobes13
 – Antenna with >10 apical cones. Movable finger of posterior telopods at inner margin with a single membranous lobe17
13. Process of second podomere of anterior telopod not visible in anterior view. Fifth antennomere with a field of sensilla basiconica. Collum with isolated, long setae. Endotergum with one row of large cuticular impressions and a second row of much smaller impressions; bristles long, strongly protruding above tergite*Z. bilobum* Wesener, 2009
 – Process of second podomere of anterior telopod visible in anterior view14
14. Podomere 3 of anterior telopod with crenulated teeth15
 – Podomere 3 of anterior telopod without crenulated teeth16
15. Collum glabrous, with a few setae at corners on either side of head. Endotergum with two rows of regularly distributed circular impressions, marginal bristles strongly protruding above tergite. Sensilla basiconica present on antennomeres 1 and 2. Anal shield weakly bell-shaped*Z. trigrioculatum* Wesener & Bespalova, 2010
 – Collum glabrous, anterior margin with two rows of setae. Endotergum with a single row of elliptical cuticular impression, marginal bristles protruding to margin. Sensilla basiconica absent. Anal shield well rounded*Z. bartolozzi* Anilkumar & Wesener, 2020
16. Collum glabrous. Endotergum with a single row of large cuticular impressions, marginal bristles slightly protruding above tergite margin. Second leg with 4 or 5 ventral spines. Anal shield tapering*Z. isalo* Wesener, 2009

- Collum glabrous. Endotergum with a single row of slightly rounded elliptical cuticular impressions, marginal bristles protruding to margin. Second leg with 6 or 7 ventral spines. Anal shield well rounded*Z. taiti* Anilkumar & Wesener, 2020

- 17. First pair of stigmatic plates greatly enlarged, with a well-rounded tip18
 - First pair of stigmatic plates triangular, tapering towards tip19

- 18. Operculum of vulva ending clearly before coxal margin, deeply notched, divided into two large, well-rounded, similar-sized lobes. Third podomere of anterior telopod laterally with ca five large sclerotized teeth. Sensilla basiconica on first antennomere absent. Posterior locking carina of anal shield two times as long as anterior carina. Endotergal marginal bristles protruding up to tergite margin. Movable finger of posterior telopods thick, 1.9 times as long as wide*Z. tampolo* Wesener, 2009
 - Operculum of vulva ending before coxal margin, elongated into a single median lobe, lobe only shallowly notched at tip. Third podomere of anterior telopod without any large sclerotized teeth. Sensilla basiconica on first antennomere present. Locking carinae of anal shield of equal length. Endotergal marginal bristles very short, ending far before tergite margin. Movable finger of posterior telopods thick, 2.1 times as long as wide*Z. ignotum* Wesener, 2009

- 19. Tergite texture orange-peel like. Collum covered with isolated, long hairs. Body size of adult female >50 mm. Endotergum with two rows of marginal bristles and a single row of large circular cuticular impressions20
 - Tergite texture glossy or smooth. Collum glabrous. Body size of adults <35 mm. Endotergum with a single row of marginal bristles and either without or with two rows of cuticular impressions22

- 20. Posterior locking carina on anal shield 2.5 times as long as anterior carina. Third podomere of anterior telopods without large sclerotized teeth. Anal shield glabrous*Z. coquerelianum* (de Saussure & Zehntner, 1897)
 - Posterior locking carina on anal shield >4 times as long as anterior carina. Third podomere of anterior telopods with at least three large sclerotized teeth. Anal shield covered with short hair21

- 21. Third podomere on anterior telopods with 3 or 4 crenulated teeth. Endotergal marginal bristles very short, protruding up to 1/3 of distance to tergite margin. Tips of vulvar operculum widely separated*Z. mangabe* Wesener, 2020
 - Third podomere on anterior telopods with ca seven large sclerotized teeth. Endotergal marginal bristles protruding up to tergite margin. Tips of vulvar operculum fused*Z. tainkintana* Wesener, 2009

- 22. Tergites glossy. Female anal shield bell-shaped, in male with steep slope. Fixed finger of posterior telopods wide, only slightly curved towards movable finger. Movable finger 1.8 times as long as wide, on posterior side with ten small sclerotized teeth. Sclerotized teeth on antenna only present on first antennomere. Endotergum without cuticular impressions*Z. viridissimum* Wesener, 2009
 - Tergites matte. Anal shield well-rounded. Fixed finger of posterior telopods slender, strongly curved towards movable finger. Movable finger 2.4 times as long as wide, on posterior side with ca 25 small sclerotized teeth. Sclerotized teeth present on antennomeres 1–3. Endotergum with a single row of large and a second row of smaller circular cuticular impressions*Z. denticulatum* Wesener, 2009

Zoosphaerium ambatovaky sp. nov.

[urn:lsid:zoobank.org:act:42C1A931-D533-4FF6-B76A-CAB8F7E1461D](https://doi.org/10.21203/rs.3.rs-1111111/v1)

Figs 2C, 3, 5C, 7

Diagnosis

The presence of only 7 or 8 ventral spines on the walking legs in *Z. ambatovaky* sp. nov., especially in combination with a glossy green color, two stridulation ribs on the male harp and more than 10 apical cones on the antenna, is only shared with *Z. muscorum* Wesener & Bespalova, 2010. The new species differs from *Z. muscorum* in the presence of an apical spine on the third leg pair (absent in *Z. muscorum*), the movable finger of the posterior telopod being 2.5 times as long as wide (2 times as long as wide in *Z. muscorum*) and the second locking carina of the anal shield being 2–3 times as long as the first (4–5 times as long as the first in *Z. muscorum*).

Etymology

‘Ambatovaky’, noun in apposition, after the forest of Ambatovaky, the only known locality for this species (Fig. 3).

Material examined

Holotype

MADAGASCAR – **Toamasina** • ♂; Rés. Speciale Ambatovaky, Sandrangato River; 16°46'22" S, 49°15'56" E; alt. 450 m; rainforest; 20 Feb. 2010; B.L. Fisher *et al.* leg.; coll. no. BLF24311; CASENT 9068294/1.

Description

Male

BODY LENGTH. Holotype male: length ca 44 mm, width of thoracic shield 23.1 mm, of tergite 5 24.4 mm (widest), height of thoracic shield 14.1 mm (highest).

COLORATION. Some discoloration may have occurred because of preservation in ethanol. Head, collum, thoracic shield and tergites shiny green with a conspicuous narrow light posterior margin (Fig. 2C). Anal shield of a different color, jade-like green. Antennae green, legs basally dark green, apically brownish.

HEAD. Eyes with >95 ommatidia. Antennae long, with cylindrical joints, protruding posteriorly to leg pair 4. Length of antennomeres 1>2>3=4=5<6. A shallow groove present on antennomere 1. Male apical disc with 45/35 apical sensory cones. Organ of Tömösváry located in antennal groove.

GNATHOCHILARIUM AND MANDIBLE. Not dissected.

STIGMATIC PLATES. First stigmatic plate triangular, apex well rounded, nearly as wide as at base, slightly turned towards coxa. Hair most abundant on apical margin, very few hairs on basal and lateral margins (Fig. 7C).

PLEURITES. First pleurite well-rounded, not projecting.

COLLUM. Glabrous.

THORACIC SHIELD. Smooth and glabrous, without protuberances.

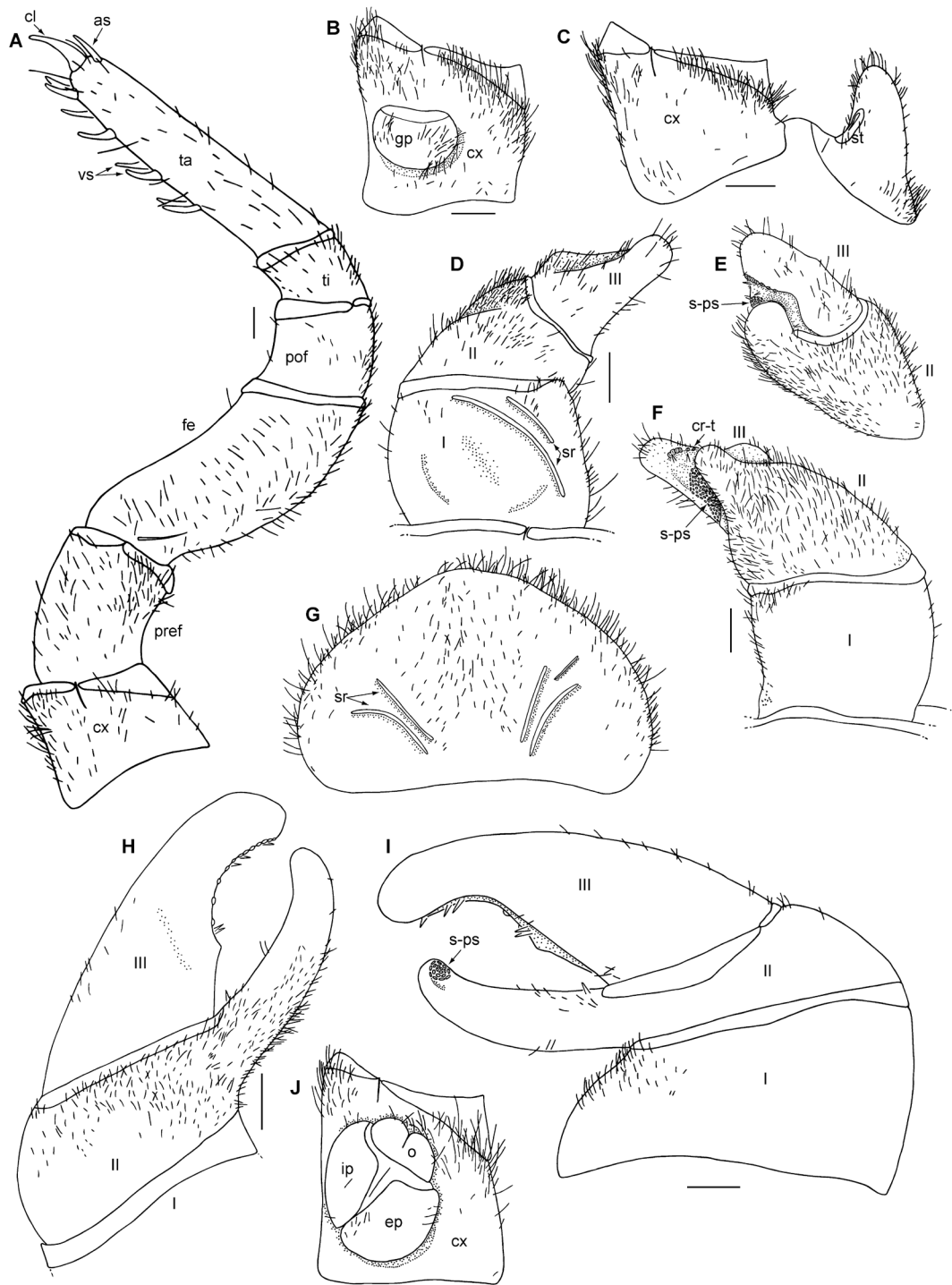


Fig. 7. *Zoosphaerium ambatovaky* sp. nov., holotype (CASENT 9068291). **A.** Left leg 9, posterior view. **B.** Left coxa 2 with gonopore, posterior view. **C.** Left coxa 1 with stigmatic plate, posterior view. **D.** Left anterior gonopod, anterior view. **E.** Left anterior gonopod, posterior view. **F.** Left anterior gonopod, lateral view. **G.** Left female coxa 2 with vulva, posterior view. **H.** Female subanal plate with washboard. **I.** Right posterior telopod, posterior view. **J.** Right posterior telopod, anterior view. Abbreviations: as = apical spine; cl = claw; cr-t = crenulated teeth; cx = coxa; ep = external plate; fe = femur; gp = gonopore; ip = inner plate; o = operculum; pof = postfemur; pref = prefemur; s-ps = sclerotized spots; sr = stridulation rib; st = stigmatic plate; ta = tarsus; ti = tibia; vs = ventral spines. Roman numerals indicate telopoditomer. Scale bars = 1 mm.

TERGITES. Surface glabrous and shiny, lacking small pits. Tips of paratergites of midbody tergites projecting posteriorly.

ENDOTERGUM. Inner section with numerous short triangular spines and longer setae. Middle area above spines with a single row of sparse circular cuticular impressions slightly varying in size. Apically with 1–2 rows of short marginal bristles, protruding to $\frac{2}{3}$ of distance of tergite margin (Fig. 5C). Bristles with numerous small spines.

ANAL SHIELD. Male anal shield bell-shaped, without hairs, glabrous. Underside with two black locking carinae, posterior one 2–3 times as long as anterior one, both located close to anal shield margin.

LEGS. Leg 1 with 4 ventral spines, leg 2 with 6 or 7, leg 3 with 6. First two leg pairs without an apical spine, spine present on leg 3. Leg pairs 4–21 with 7 or 8 ventral spines and an apical spine. On leg 9, femur 2 and tarsus 4.5 times as long as wide. All podomeres with setae (Fig.).

Male sexual characters

GONOPORE. Covered with a single undivided, rounded membranous plate, covering $\frac{1}{4}$ of surface of coxa. Gonopore located on basal half of joint (Fig. 7B).

ANTERIOR TELOPODS. Harp with two stridulation ribs, one long and well pronounced rib located laterally of a less pronounced and shorter mesal rib (Fig. 7D). First podomere with only a few setae, restricted to apical parts of lateral margins, 1.5 times as wide as long. Process of second podomere nearly as long as basal $\frac{2}{3}$ of third podomere, not visible in anterior view, and with an apical mound of a few sclerotized spots juxtaposed to third podomere (Fig. 7E–F). Third podomere with an apical brown sclerotized spot and a field of elevated sclerotized spots at inner margin below brown spot; two small spines located below sclerotized spot (Fig. 7F); depression lateral to field of spots with one small sclerotized spine, lateral margin with up to 6 crenulated teeth (Fig. 7E–F). Second podomere densely setose, third podomere with setae mainly apically and laterally.

POSTERIOR TELOPODS. Movable finger (podomere 3) 2.5 times as long as wide, weakly curved towards immovable finger (process of podomere 2). Shallowly hollowed-out inner margin with five sclerotized spines, three positioned apically and two in middle of cavity next to small membranous lobe. Additional sclerotized spine at base of movable finger. Posterior aspect with ca 12 small crenulated teeth (Fig. 7H). Immobile finger thinner and shorter than movable finger, curved towards the latter. Sclerotized spine located on anterior side near base of immovable finger. Inner part of immovable finger apically covered with a few sclerotized spots (Fig. 7I). Movable finger glabrous on both sides except for a few hairs basolaterally. Second podomere in posterior view setose, in anterior view with a few setae on finger.

Female

Unknown.

Distribution and ecology

Zoosphaerium ambatovaky sp. nov. is currently known only from the type locality, a lowland rainforest close to the Ille Sainte Marie (Fig. 3). This species seems to be closely related to *Z. muscorum* from the montane forest of Anjanaharibe-Sud, the only species with which it shares the presence of only 7 or 8 ventral spines on the walking legs, as well as a glossy green color, two stridulation ribs on the male harp and more than 10 apical cones on the antenna. A female *Zoosphaerium* from the same forest (CASENT 9068291B) belongs to a different species. The forest of Ambatovaky is isolated and shrinking rapidly (Rakotondrasoa *et al.* 2017).

Zoosphaerium platylabum species-group

Remarks

Species can be identified as members of the *Zoosphaerium platylabum* species-group based on the number of locking carinae (always 2) of the anal shield that are located close to the last pleurite, as well as on morphological characters of the female vulva, whose apical processes are usually sharp-edged (with the exception of those in *Z. tsingy* Wesener, 2009). The posterior telopods (Wesener & Wägele 2008) show two vastly different modifications: the movable finger is either very thick, or quite elongated and slender. The species-group now contains 6+3 described species distributed in humid as well as western dry forests all over Madagascar. Species of this group are conspicuously absent from the southern spiny forest ecosystem (Wesener 2009).

Key to species of the *Zoosphaerium platylabum* species-group

1. Movable finger of posterior telopods very thick, <2 times as long as wide, width strongly decreasing towards tip; apically with minute sclerotized nubs on posterior as well as on anterior side2
 - Movable finger slender, at least 3 times as long as wide, width not decreasing towards tip; apically sclerotized structures only present on posterior side3
2. Movable finger 1.2 times as long as wide, at inner margin with a small membranous lobe. First stigmatic plate greatly enlarged, lobe not triangular or tapering towards tip. Antenna with more than 35 apical cones*Z. platylabum* (de Saussure & Zehntner, 1902)
 - Movable finger 1.6 times as long as wide, at inner margin without lobe. First stigmatic plate large, lobe triangular and tapering towards well-rounded tip. Antenna with 23–35 apical cones ..
.....*Z. pseudoplatylabum* Wesener, 2009
3. Anterior edges of thoracic shield slightly projecting towards head. Movable finger shorter than fixed finger*Z. solitarium* Wesener, 2009
 - Anterior edges of thoracic shield well-rounded. Movable finger at least slightly longer than fixed finger4
4. Male harp with two stridulation ribs. Movable finger 3 times as long as wide5
 - Male harp with a single stridulation rib. Movable finger >4 times as long as wide7
5. Movable finger on posterior telopods with five spines and no membranous lobes. Immobile finger of posterior telopod slender, 4 times as long as wide, apical part tapering and curved towards movable finger. Only 7 or 8 ventral spines on legs. Found in eastern rainforests, Masoala Peninsula*Z. masoala* sp. nov.
 - Movable finger on posterior telopods with spines and at least one large, triangular membranous lobe. Immobile finger of posterior telopod wide, 2.7 times as long as wide, not curved, parallel to movable finger, apically only weakly tapering. 10 or more ventral spines on legs. Found in western dry forests6
6. Light brown. Antennae with four apical cones. Third podomere of anterior telopods lacking crenulated teeth*Z. beanka* sp. nov.
 - Olive green. Antennae with >15 apical cones. Third podomere of anterior telopods laterally with 2 or 3 crenulated teeth*Z. tsingy* Wesener, 2009
7. Tergites shiny black, appendages red. Anal shield strongly developed, shaped like a helmet. Fixed finger of posterior telopod slightly curved towards movable finger. Operculum of vulva

- deeply notched, divided into two sharp ‘horns’. Female washboard on each side with a single stridulation rib*Z. corystoides* Wesener, 2009
- Tergites light brown or olive-brownish, appendages brown or green. Anal shield well-rounded. Fixed finger of posterior telopod parallel to movable finger8
8. Up to 30 mm long. Movable finger of posterior telopod with 25 teeth, three spines located at apex. Endotergum with two dense rows of long marginal bristles, protruding above tergite margin. (Female unknown)*Z. voahangy* sp. nov.
- Up to 55 mm long. Movable finger of posterior telopod with ca 15 teeth, three spines located at regular intervals along entire margin. Endotergum with a single row of short, dense marginal bristles, protruding up to $\frac{2}{3}$ of distance towards tergite margin. Operculum of vulva only very shallowly notched, forming two sharp horns. Female washboard with four stridulation ribs
.....*Z. broelemanni* Wesener, 2009

Zoosphaerium beanka sp. nov.

urn:lsid:zoobank.org:act:7F9589AA-AD5D-473F-A7C1-FB94F30FF8AD

Figs 2D, 3, 5D, 8

Diagnosis

The shape and position of the locking carinae place *Z. beanka* sp. nov. in the *Z. platylabum* species-group, but the telopods of *Z. beanka* sp. nov. have almost no similarities to those of any other described giant pill-millipede species except *Z. tsingy*. Both species share characters of the posterior telopods, namely the presence of spines and at least one large membranous lobe on the movable finger, and an uncurved, wide immovable finger (2.7 times as long as wide) that is parallel to the movable finger. *Zoosphaerium beanka* sp. nov. differs from the latter in the light brown color (olive in *Z. tsingy*), the presence of only four apical cones on the antenna (> 15 in *Z. tsingy*) and the differently shaped anterior telopods, in which telopoditomere 3 lacks crenulated teeth (present in *Z. tsingy*).

Etymology

‘Beanka’, noun in apposition, after the type and only known locality for this species, the dry forest of Beanka (Fig. 3).

Material examined

Holotype

MADAGASCAR – Mahajanga • ♂; Forêt de Beanka; 18°01'25" S, 44°30'08" E; alt. 220 m; slightly disturbed dry deciduous forest; 14 Jan. 2010; Z.H. Harimpitia leg.; coll. no. Z.H.H-031; FMNH-INS 3119897.

Description

BODY LENGTH. Male (holotype): length 36.7 mm, width of thoracic shield up 22.1 mm (widest), height of thoracic shield 11.8 mm (highest).

COLORATION. Head, collum, thoracic shield, tergites and anal shield light brown (Fig. 2D). Antennae green, legs light brown.

HEAD. Eyes with more than 75 ommatidia. Antennae short, protruding back to leg 3. Length of antennomeres 1 > 2 = 3 = 4 = 5 < 6. A shallow groove present on antennomere 1, disc with 4 apical cones.

GNATHOCHILARIUM AND MANDIBLE. Not dissected.

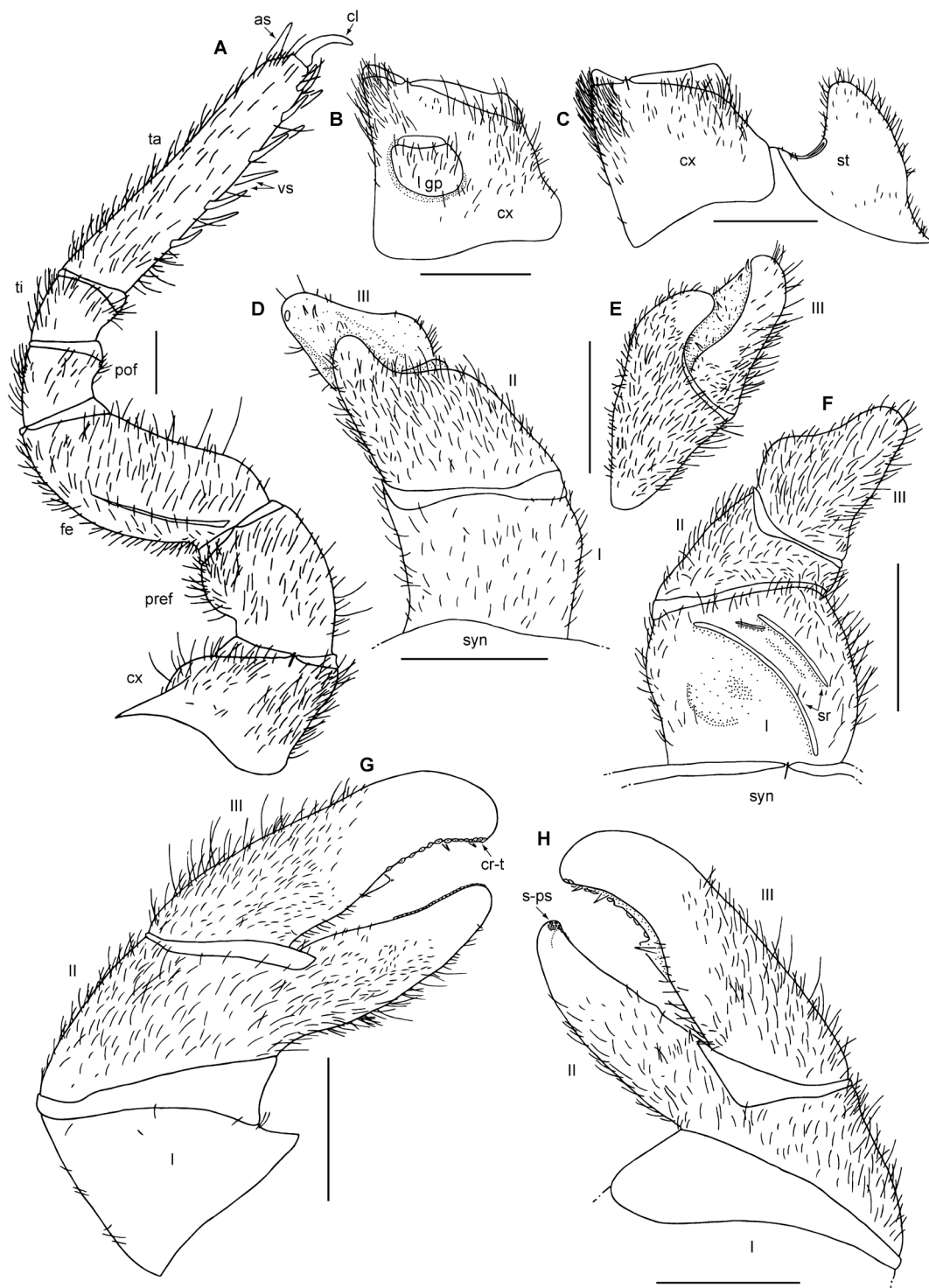


Fig. 8. *Zoosphaerium beanka* sp. nov., holotype (FMNH-INS 3119906). **A.** right leg 9, posterior view. **B.** Left coxa 2 with gonopore, posterior view. **C.** Left coxa 1 with stigmatic plate, posterior view. **D.** Left anterior gonopod, posterior view. **E.** Left anterior gonopod, lateral view. **F.** Left anterior gonopod, anterior view. **G.** Right posterior telopod, posterior view. **H.** Right posterior telopod, anterior view. Abbreviations: as = apical spine; cl = claw; cr-t = crenulated teeth; cx = coxa; fe = femur; gp = gonopore; pof = postfemur; pref = prefemur; s-ps = sclerotized spots; sr = stridulation rib; st = stigmatic plate; syn = syncoxite; ta = tarsus; ti = tibia; vs = ventral spines. Roman numerals indicate telopoditomeres. Scale bars = 1 mm.

STIGMATIC PLATES. First stigmatic plate triangular, apex well rounded, nearly as wide as at base, slightly turned towards coxa. Hairs most abundant on apical margin, very few hairs on basal and lateral margins (Fig. 8C).

PLEURITES. First pleurite slightly extending posteriorly in a well-rounded process.

COLLUM. Margins covered with a few short hairs, central part glabrous.

THORACIC SHIELD. Surface like those of tergites, glabrous.

TERGITES. Smooth and glabrous, no small pits present. Paratergites projecting slightly posteriorly.

ENDOTERGUM. Inner section with numerous short spines and isolated bristles. Between marginal ridge and inner area, a single row of sparse large, circular cuticular impressions. Externally one or two rows of marginal bristles, standing irregularly to each other. Bristles scaly, of medium length, longest reaching slightly above tergite margin (Fig. 5D).

ANAL SHIELD. Rounded, neither bell-shaped nor tapered, glabrous. Ventral side of anal shield with two black locking carinae, located close to laterotergites. Anterior carina small, posterior carina 2–3 times as long as anterior carina.

LEGS. Leg 1 with 6 or 7 ventral spines, leg 2 with 8, leg 3 with 10. First two leg pairs without an apical spine, spine present on leg 3. Leg pairs 4–21 with 9 or 10 ventral spines and an apical spine. On leg 9, femur 2 and tarsus 4.9 times as long as wide. All podomeres with setae (Fig. 8A).

Male sexual characters

GONOPORE. Covered with a single undivided, rounded membranous plate, covering $\frac{1}{4}$ of surface of coxa. Gonopore located centrally on joint (Fig. 8B).

ANTERIOR TELOPODS. Harp with two stridulation ribs, mesal rib smaller than lateral one, both ribs well developed (Fig. 8F). First podomere 1.2 times as wide as long. Second podomere process lobe-like and slightly curved, with rounded edges, protruding up to half of third podomere height, apically with sclerotized spots. Third podomere long, as long as first; cavity mesally with numerous sclerotized spots and three thin, sclerotized spines; one sclerotized spot located close to tip. Podomeres 1–3 covered on both sides with numerous long, isolated hairs.

POSTERIOR TELOPODS. Movable finger with a well-rounded tip, not tapering towards tip; hollowed-out inner margin with one non-sclerotized lobe and 3 or 4 sclerotized spines, posterior aspect with ca 14 small sclerotized teeth. Movable finger slightly longer than fixed finger, the latter straight, as wide as third podomere. Fixed finger at margin with numerous sclerotized spots. All podomeres covered on both sides with numerous, long isolated hairs, only tips of chela glabrous (Fig. 8G–H).

Female

Unknown.

Distribution and ecology

Zoosphaerium beanka sp. nov. is currently known only from the dry forest of Beanka (Fig. 3). With most known dry forest giant pill-millipede species being widespread (Wesener & Wägele 2008; Wesener 2009), this species can be expected in surrounding dry forest fragments.

Zoosphaerium voahangy sp. nov.

urn:lsid:zoobank.org:act:11B9C806-A111-48FC-AC36-035385125232

Figs 2E, 3, 5E, 9

Diagnosis

The position of the locking carinae close to the last pleurite identifies *Z. voahangy* sp. nov. as a member of the *Z. platylabum* species-group. The uniquely slender and elongated posterior telopods in combination with the presence of a single stridulation rib on the male harp and more than 35 apical cones on the antennae, are characters only shared with *Z. broelemanni* Wesener, 2009. *Zoosphaerium voahangy* sp. nov. differs from *Z. broelemanni* in the differently shaped anterior telopods, spination and teeth number of the movable finger of the posterior telopod (see key), as well as in characters of the endotergum, which has two dense rows of long marginal bristles in the former, but a single row of short bristles in the latter.

Etymology

‘Voahangy’, noun in apposition, to honor the great collector and Malagasy scientist Voahangy Soarimalala.

Material examined

Holotype

MADAGASCAR – Mahajanga • ♂; Analalava, 5.5 km NNE of Ambinda Village; 14°18.6′ S, 47°54.9′ E; alt. 120 m; dry deciduous forest; 8 Dec. 2004; V. Soarimalala leg.; coll. no. VS-508; FMNH-INS 3119921.

Paratype

MADAGASCAR – Mahajanga • ♂; same collection data as for holotype; FMNH-INS 3119919.

Description

BODY LENGTH. Male (holotype): length 26.3 mm, width of thoracic shield 16.1 mm, of tergite 7 16.7 mm (widest), height of thoracic shield 8.9 mm, of tergite 7 9.3 mm (highest).

COLORATION. Head, collum, thoracic shield and tergites light brown with dark posterior margins. Anal shield entirely light brown (Fig. 2E). Antennae dark green, legs basally light brown, apically green.

HEAD. Eyes with more than 65 ommatidia. Antennae short, protruding back to leg 5. Length of antennomeres 1=2=3=4=5<6. A shallow groove present on antennomere 1, disc with 48/49 apical cones.

GNATHOCHILARIUM AND MANDIBLE. Not dissected.

STIGMATIC PLATES. First stigmatic plate triangular, apex sharply edged, pointed, turned towards coxa. Hairs most abundant on apical margin (Fig. 9C).

PLEURITES. First pleurite extending posteriorly in a well-rounded process. Second pleurite also with a well-rounded process, but not projecting. Remaining pleurites broadly rounded.

COLLUM. Margins with a few short hairs, central part glabrous.

THORACIC SHIELD. Surface like those of tergites, glabrous.

TERGITES. Smooth and glabrous, no small pits present. Paratergites projecting slightly posteriorly.

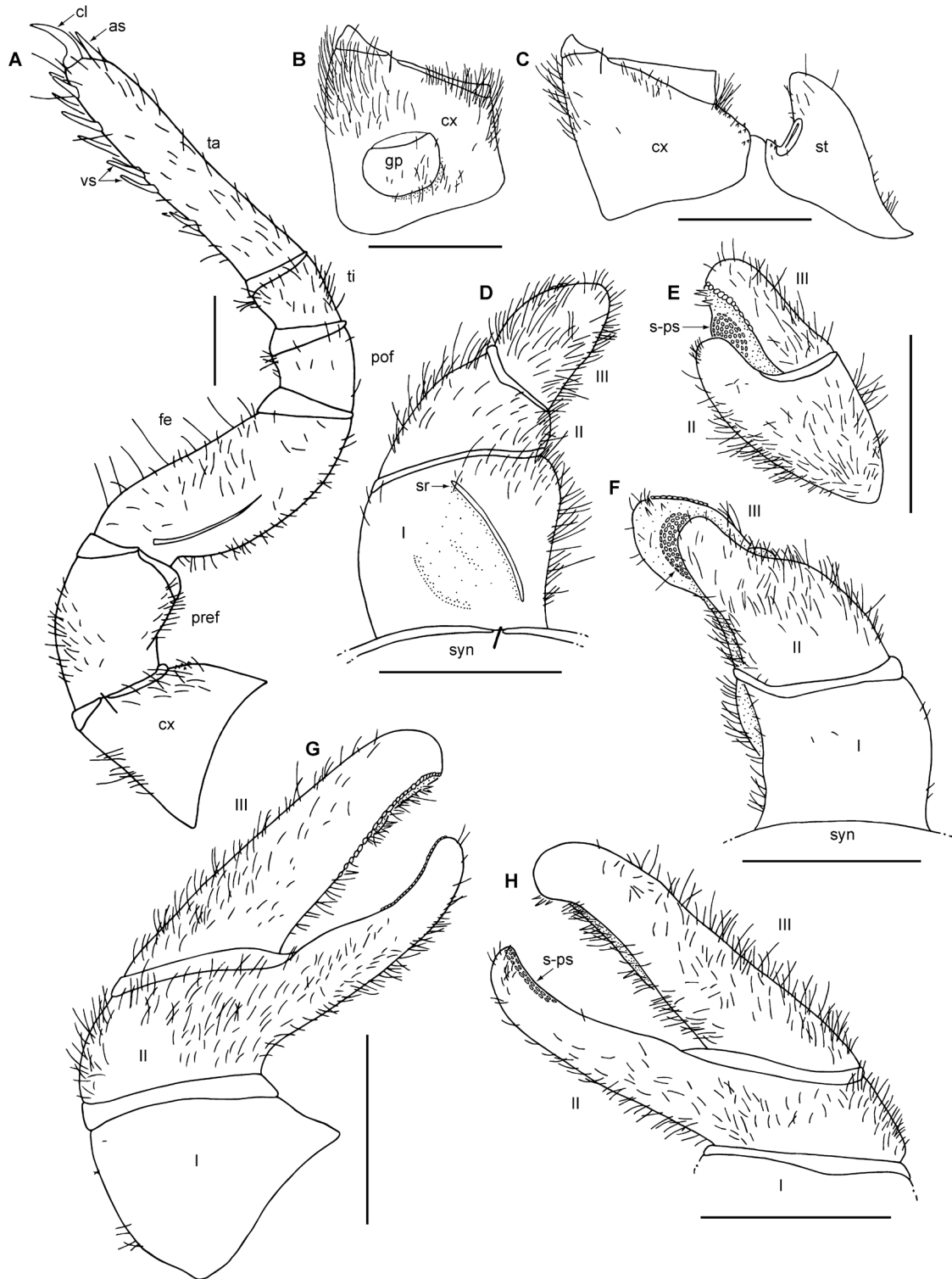


Fig. 9. *Zoosphaerium voahangy* sp. nov., holotype (FMNH-INS 3119921). **A.** left leg 9, posterior view. **B.** Left coxa 2 with gonopore, posterior view. **C.** Left coxa 1 with stigmatic plate, posterior view. **D.** Left anterior gonopod, anterior view. **E.** Left anterior gonopod, lateral view. **F.** Left anterior gonopod, posterior view. **G.** Right posterior telopod, posterior view. **H.** Right posterior telopod, anterior view. Abbreviations: as = apical spine; cl = claw; cx = coxa; fe = femur; gp = gonopore; pof = postfemur; pref = prefemur; s-ps = sclerotized spots; sr = stridulation rib; st = stigmatic plate; syn = syncoxite; ta = tarsus; ti = tibia; vs = ventral spines. Roman numerals indicate telopoditomeres. Scale bars = 1 mm.

ENDOTERGUM. Inner section with numerous short spines and isolated bristles. Between marginal ridge and inner area a single row of sparse, circular cuticular impressions. Externally two dense rows of marginal bristles. Bristles scaly, the longest reaching above tergite margin (Fig. 5E).

ANAL SHIELD. Rounded, neither bell-shaped nor tapered, glabrous. Ventral side with two black locking carinae, located closely to laterotergites. Anterior carina small and posterior carina 2–3 times as long as anterior carina.

LEGS. Leg 1 with 4 ventral spines, leg 2 with 5 or 6, leg 3 with 7. First two leg pairs without an apical spine, spine present on leg 3. Leg pairs 4–21 with 9 or 10 ventral spines and an apical spine. On leg 9, femur 2.1 and tarsus 5.1 times as long as wide. All podomeres with setae (Fig. 9A).

Male sexual characters

GONOPORE. Covered with a single undivided, apically rounded, membranous, basally sclerotized plate covering $\frac{1}{4}$ of surface of coxa. Gonopore located basally on joint (Fig. 9B).

ANTERIOR TELOPODS. Harp with single stridulation rib located mesally, long and well developed (Fig. 9D). First podomere 1.1 times as wide as long. Second podomere process lobe-like and slightly curved with rounded edges, protruding up to half of third podomere height, apically with sclerotized spots (Fig. 9F). Third podomere long, almost as long as first; cavity mesally with numerous sclerotized spots and three thin, sclerotized spines located apically (Fig. 9E–F); one sclerotized spot located close to tip, laterally with a row of ca 11 crenulated teeth (Fig. 9E). Podomeres 1–3 covered on both sides with numerous long, isolated hairs.

POSTERIOR TELOPODS. Movable finger slender and long, with a well-rounded tip, not tapering towards tip; hollowed-out inner margin with 3 or 4 sclerotized spines located apically, posterior aspect with ca 25 small sclerotized teeth (Fig. 9G). Movable finger 4 times as long as wide, slightly longer than fixed finger. Fixed finger straight, only apically curved towards movable finger, not tapering, more slender than third podomere. Fixed finger at margin with numerous sclerotized spots (Fig. 9H). First podomere in posterior view almost glabrous, podomeres 2 and 3 covered on both sides with numerous long, isolated hairs.

Female

Unknown.

Distribution and ecology

The only known habitat of *Z. voahangy* sp. nov., the forest of Analalava (Fig. 3), is a small (2 km south to north, 750 m east to west) fragment of disturbed and partly degraded lowland rainforest, isolated by 30 km from Betampona, the only other remaining lowland rainforest fragment in a 100 km radius.

Zoosphaerium masoala sp. nov.

[urn:lsid:zoobank.org:act:F62E0E9E-172D-4076-BD01-509AD42BAE89](https://doi.org/10.3896/EBL.758.1-48)

Figs 2F, 3, 10A, 11

Diagnosis

The shape and position of the locking carinae, as well as the slender posterior telopods place *Z. masoala* sp. nov. in the *Z. platylabum* species-group. *Zoosphaerium masoala* sp. nov. differs from all other species of the group in the combination of the presence of two stridulation ribs on the male harp, slender posterior telopods in which both fingers reach almost the same length and >10 apical cones on the antenna.

Etymology

‘Masoala’, noun in apposition, after the forest and peninsula of Masoala, the largest remaining area of lowland rainforest on Madagascar, for which the species described here is the first recorded giant pill-millipede species (Fig. 3).

Material examined

Holotype

MADAGASCAR – **Toamasina** • ♂; Région Sava, Parc National de Masoala, Forêt de Tampolo, 1.2 km S of Ambodiforaha village; 15°43'45.6" S, 49°57'49.4" E; alt. 15 m; pitfall buckets, littoral forest; 11 Dec. 2015; V. Soarimalala leg.; coll. no. VS-2582; FMNH-INS 3195651.

Description

Male

BODY LENGTH. Length 23.9 mm, width of thoracic shield 14.2 mm (widest), height of thoracic shield 7.2 mm (highest).

COLORATION. Head, collum, thoracic shield and tergites dark brown to black. Grooves of thoracic shield greenish, anal shield lighter brown (Fig. 2F). Antennae and legs green.

HEAD. Eyes with more than 50 ommatidia. Antennae short, protruding back to leg 4. Length of antennomeres $1 > 2 > 3 = 4 = 5 < 6$. A shallow groove present on antennomere 1, disc with 33/12 apical cones.

GNATHOCHILARIUM AND MANDIBLE. Not dissected.

STIGMATIC PLATES. First stigmatic plate triangular, apex well-rounded, slender, curved towards coxa. Hair most abundant on apical margin (Fig. 11C).

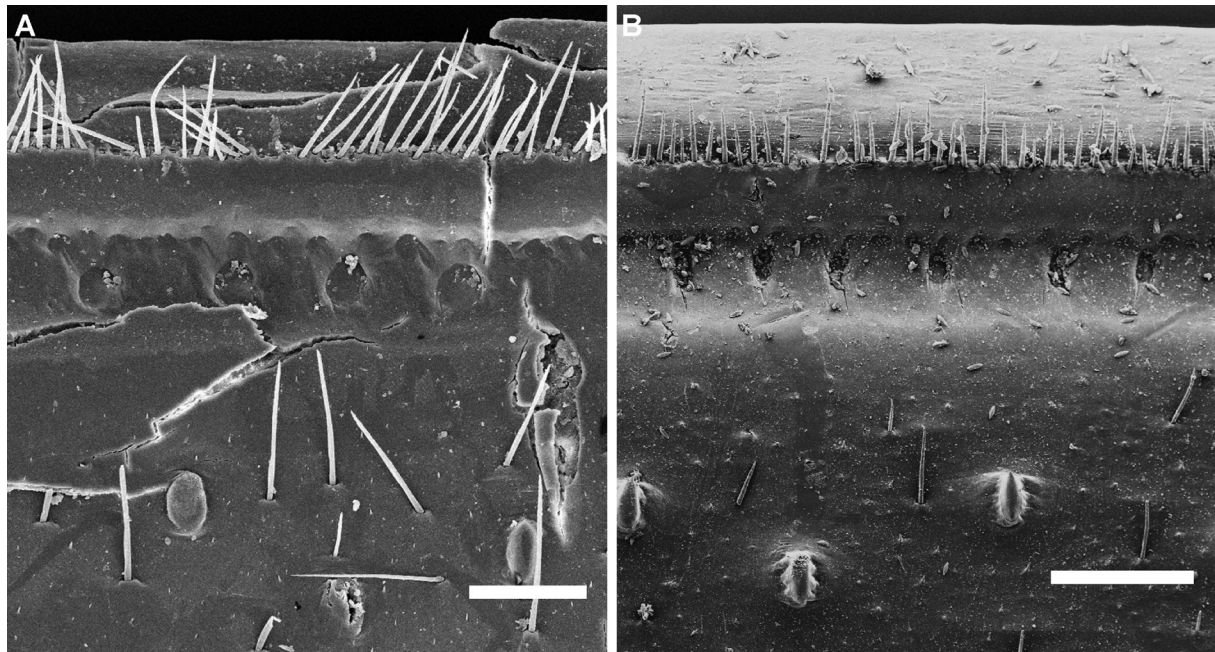


Fig. 10. Scanning electron micrographs of the endoterga of midbody rings. **A.** *Zoosphaerium masoala* sp. nov., holotype (FMNH-INS 3195651). **B.** *Z. spinopiligerum* sp. nov., holotype (FMNH-INS 3119885). Scale bars = 100 μ m.

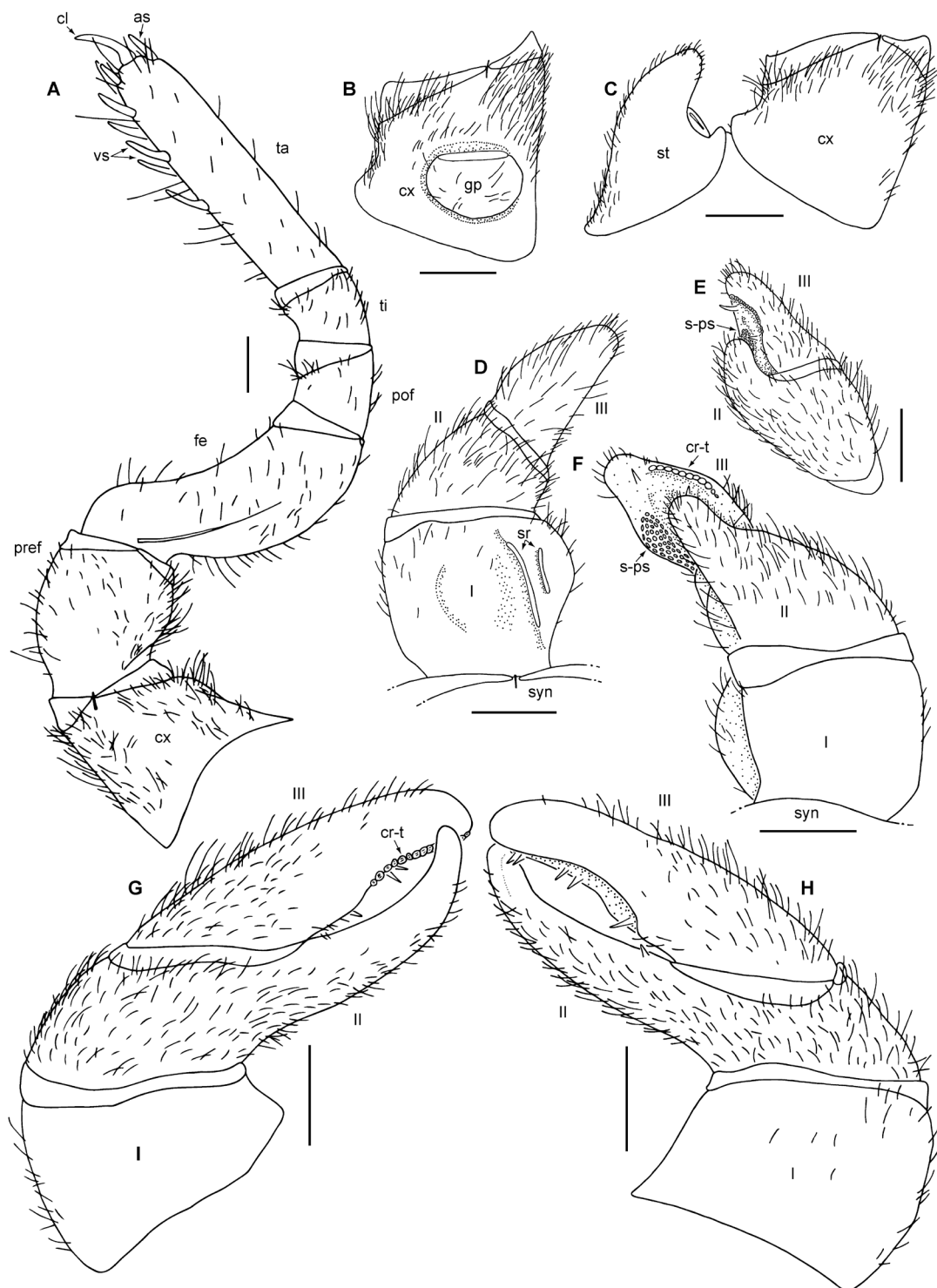


Fig. 11. *Zoosphaerium masoala* sp. nov., holotype (FMNH-INS 3195651). **A.** Left leg 9, posterior view. **B.** Right coxa 2 with gonopore, posterior view. **C.** Right coxa 1 with stigmatic plate, posterior view. **D.** Left anterior gonopod, anterior view. **E.** Left anterior gonopod, lateral view. **F.** Left anterior gonopod, posterior view. **G.** Right posterior telopod, posterior view. **H.** Right posterior telopod, anterior view. Abbreviations: as = apical spine; cl = claw; cr-t = crenulated teeth; cx = coxa; fe = femur; gp = gonopore; pof = postfemur; pref = prefemur; s-ps = sclerotized spots; sr = stridulation rib; st = stigmatic plate; syn = syncoxite; ta = tarsus; ti = tibia; vs = ventral spines. Roman numerals indicate telopoditomer segments. Scale bars = 1 mm.

PLEURITES. First pleurite extending slightly posteriorly in a long, thin process.

COLLUM. Margins covered with a few short hairs, central part glabrous.

THORACIC SHIELD. Surface like those of tergites, glabrous.

TERGITES. Smooth and glabrous, no small pits. Paratergites projecting slightly posteriorly.

ENDOTERGUM. Inner section with numerous short spines and isolated bristles. Between marginal ridge and inner area a single row of sparse large, circular cuticular impressions, distance between impressions larger than their diameter. Marginal brim wavy towards inner area. Externally 1 or 2 rows of marginal bristles. Bristles scaly, of medium length, longest reaching slightly above tergite margin (Fig. 10A).

ANAL SHIELD. Rounded, neither bell-shaped nor tapered, covered with numerous short setae. Ventral side of anal shield with two black locking carinae, located close to laterotergites. Anterior carina small and posterior carina 3 times as long as anterior carina.

LEGS. Leg 1 with 1 ventral spine, leg 2 with 2–4, leg 3 with 3 or 4. First two leg pairs without an apical spine, spine present on leg 3. Leg pairs 4–21 with 7 or 8 ventral spines and an apical spine. On leg 9, femur 2.4 and tarsus 4.2 times as long as wide. All podomeres with setae (Fig. 11A).

Male sexual characters

GONOPORE. Covered with a single undivided, rounded, apically membranous, basally sclerotized plate, covering $\frac{1}{4}$ of surface of coxa. Gonopore located basally on joint (Fig. 11B).

ANTERIOR TELOPODS. Harp with two stridulation ribs, mesal rib smaller than lateral one, both ribs well developed, located in mesal corner (Fig. 11D). First podomere 1.1 times as wide as long. Second podomere process lobe-like and slightly curved, with rounded edges, protruding up to half of third podomere height, apically with sclerotized spots. Third podomere long, as long as first; cavity mesally with numerous sclerotized spots and three thin, sclerotized spines; one sclerotized spot located close to tip; laterally with up to 12 crenulated teeth. Podomeres 1–3 covered on both sides with numerous long, isolated hairs.

POSTERIOR TELOPODS. Movable finger with a well-rounded tip, tapering towards tip; hollowed-out inner margin without lobes but with 5 sclerotized spines, 2 located apically, 2 at midpoint and 1 basally (Fig. 11H). Posterior aspect of movable finger with ca 14 small sclerotized teeth (Fig. 11G). Movable finger slightly longer than fixed finger, the latter slender (4 times as long as wide), apically curved towards former. Fixed finger basally with a single spine, at margin with numerous sclerotized spots. First podomeres almost glabrous, movable and immovable finger covered on both sides with numerous long, isolated hairs, only tips of chela glabrous.

Female

Unknown.

Distribution and ecology

This species is currently known only from the vast lowland rainforests of the Masoala Peninsula on the east coast (Fig. 3).

Remarks

Despite several attempts, no DNA could be extracted from the male holotype. Therefore, its degree of similarity to the two much larger females known and sequenced from the Masoala area (KY399024 and KY399025) could not be assessed (see Fig. 1).

Zoosphaerium piligerum species-group

Remarks

Species can be identified as members of the *Z. piligerum* species-group based on morphological characters of the posterior telopods (Wesener & Wägele 2008), which are slender and greatly elongated. The species-group now contains four described species distributed in the eastern rainforests at higher elevations (Wesener 2009).

Key to species of the *Zoosphaerium piligerum* species-group

1. Antenna with four apical cones. Endotergum without cuticular impressions. Third podomere of anterior telopods lateral of cavity without sclerotized teeth. Body length <20 mm. Movable finger of posterior telopods >4.5 times as long as wide*Z. micropiligerum* Wesener, 2009
– Antenna with >10 apical cones. Endotergum with a single row of circular cuticular impressions. Third podomere of anterior telopods with at least two large, sclerotized teeth. Body length of mature females >35 mm. Movable finger of posterior telopods ≤3.5 times as long as wide2
2. Anal shield bell-shaped. Posterior telopod fixed finger strongly curved, ca 25% shorter than movable finger. Operculum of vulva protruding above coxal margin. Endotergum with two rows of marginal bristles, slightly extending beyond tergite margin*Z. piligerum* (de Saussure & Zehntner, 1897)
– Anal shield well rounded. Posterior telopod fixed finger slightly curved, only slightly shorter than movable finger. Operculum of vulva not reaching coxal margin. Endotergum with a single row of marginal bristles, not reaching tergite margin3
3. Tergites matte, covered with short setae, dark brown. Third podomere of anterior telopods laterally with 3 or 4 crenulated teeth. Legs with 10–12 ventral spines*Z. spinopiligerum* sp. nov.
– Tergites glossy, black. Third podomere of anterior telopods laterally with 1 or 2 crenulated teeth. Legs with 8 or 9 ventral spines*Z. pseudopiligerum* Wesener, 2009

Zoosphaerium spinopiligerum sp. nov.

[urn:lsid:zoobank.org:act:B5E6A6B0-F750-4227-8F0B-4F6417FDF88D](https://zoobank.org/urn:lsid:zoobank.org:act:B5E6A6B0-F750-4227-8F0B-4F6417FDF88D)

Figs 2G, 3, 10B, 12

Diagnosis

The greatly elongated posterior telopods identify *Zoosphaerium spinopiligerum* sp. nov. as a member of the *Z. piligerum* species-group. *Zoosphaerium spinopiligerum* sp. nov. shares the shape of the vulva and the anal shield, as well as a similar posterior telopod with *Z. pseudopiligerum*. *Zoosphaerium spinopiligerum* sp. nov. differs from the latter in the non-glossy tergites, differences in the shape of the anterior telopods, as well as the higher number of ventral spines on the legs (see key above).

Etymology

‘Spinopiligerum’, noun in apposition, as a reference to the higher number of ventral spines on the legs compared to related species.

Material examined

Holotype

MADAGASCAR – **Fianarantsoa** • ♂; Parc National de Midongy-Befotaka, 6 km N of Befotaka village; 23°46.7' S, 47°06.4' E; alt. 815 m; dense humid transitional lowland and montane forest; 8 Feb. 2008; V. Soarimalala leg.; coll. no. VS-1442; FMNH-INS 3119885.

Other material

MADAGASCAR – **Fianarantsoa** • 1 ♀; Parc National de Midongy-Befotaka, 11.5 km SW of Befotaka village; 23°53.3' S, 46°53.3' E; alt. 1053 m; dense humid transitional lowland and montane forest; 27 Feb. 2008; V. Soarimalala leg.; coll. no. VS-1536; FMNH-INS 3119888.

Description

BODY LENGTH. Male: length 37.1 mm, width of thoracic shield 22.3 mm (widest), height of thoracic shield 11.1 mm (highest). Female (paratype): length 28.8 mm, width of thoracic shield 16.8 mm, height of thoracic shield up to 8.7 mm.

COLORATION. Tergites brown with dark brown posterior margin (Fig. 2G). Collum dark brown to green. Head dark green with yellow-brown markings. Anal shield brown. Antennae dark green, legs basally light brown, apically dark green.

HEAD. Eyes with more than 80 ommatidia. Antennae long and slender, protruding back to leg 3. Length of antennomeres 1=2=3=4=5<6. A shallow groove present on antennomere 1, disc with 22/18 apical cones.

GNATHOCHILARIUM AND MANDIBLE. Not dissected.

STIGMATIC PLATES. First stigmatic plate lobular, apex well rounded, very slightly curved towards coxa. Hairs most abundant on apical margin (Fig. 12C).

PLEURITES. First pleurite slightly extending posteriorly in a long, thin process.

COLLUM. Median part of collum glabrous.

THORACIC SHIELD. Surface similar to that of tergites.

TERGITES. Paratergites slightly projecting posteriorly. Tergites covered with small pits and hairs.

ENDOTERGUM. Inner section with numerous short spines and isolated bristles. Between marginal ridge and inner area a single row of sparse large, elliptical cuticular impressions, distance between impressions 2–3 times as large as their diameter. Marginal brim wavy towards inner area. Externally with 1 row of sparse marginal bristles. Bristles scaly, short, the longest reaching $\frac{1}{3}$ of distance towards tergite margin (Fig. 10B).

ANAL SHIELD. Rounded, slightly flattened in male, covered with numerous short setae. Ventral side of anal shield with two black locking carinae, located close to laterotergites. Anterior carina small, posterior carina 6 or 7 times as long as anterior carina.

LEGS. Leg 1 with 5 ventral spines, leg 2 with 6, leg 3 with 8. First two leg pairs without an apical spine, spine present on leg 3. Leg pairs 4–21 with 10–12 ventral spines and an apical spine. On leg 9, femur 2.1 and tarsus 5.2 times as long as wide. All podomeres with setae (Fig. 12A).

Male sexual characters

GONOPORE. Covered with a single undivided, rounded, apically membranous, basally sclerotized plate, covering $\frac{1}{4}$ of surface of coxa. Gonopore located basally on joint (Fig. 12B).

ANTERIOR TELOPODS. Harp with two stridulation ribs, both ribs of same size and well developed, located in mesal corner (Fig. 12D). First podomere 1.3 times as wide as long. Second podomere process lobe-

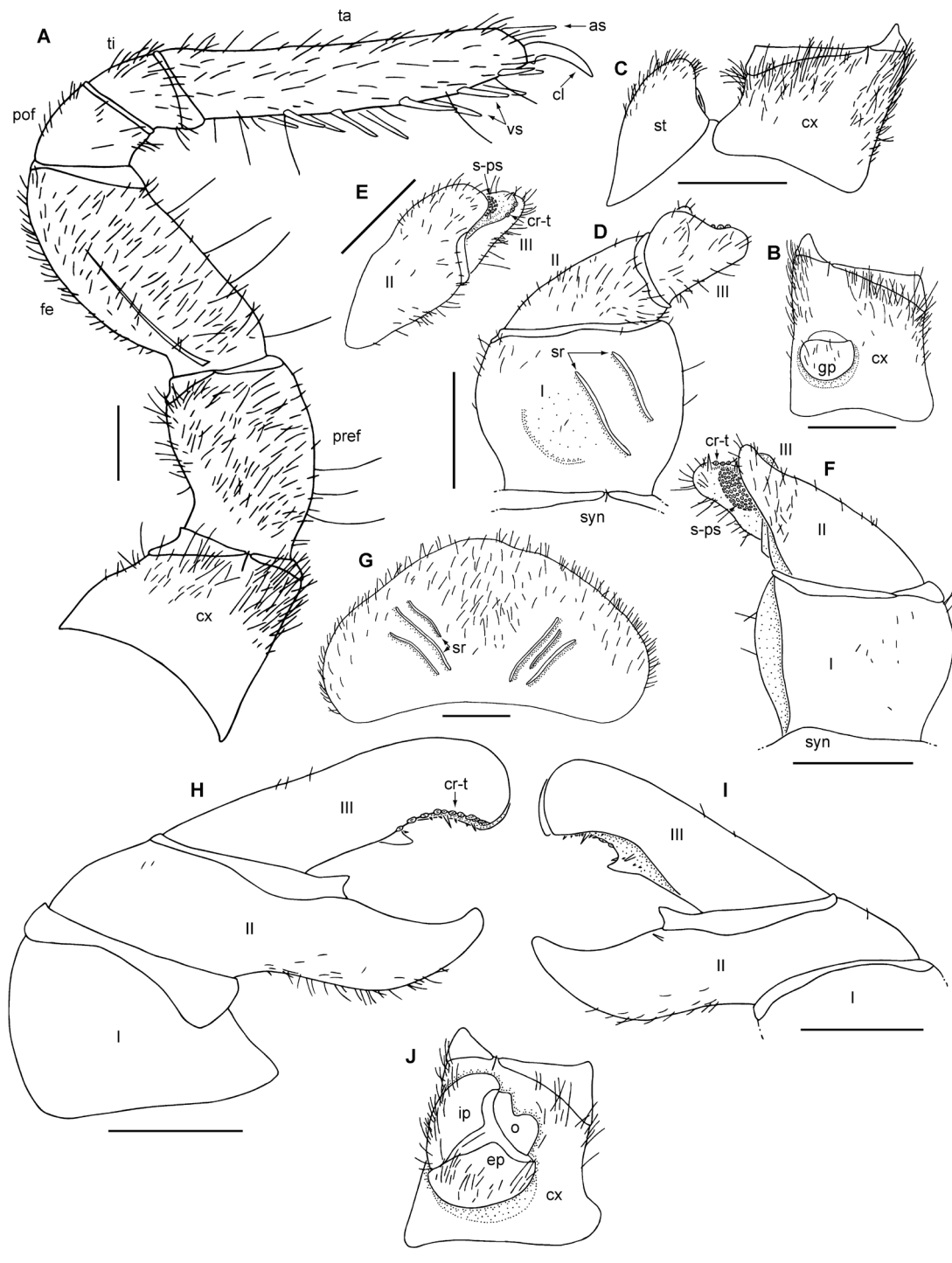


Fig. 12. *Zoosphaerium spinopiligerum* sp. nov., holotype (FMNH-INS 3119885). **A.** Right leg 9, posterior view. **B.** Left coxa 2 with gonopore, posterior view. **C.** Right coxa 1 with stigmatic plate, posterior view. **D.** Left anterior gonopod, anterior view. **E.** Left anterior gonopod, lateral view. **F.** Left anterior gonopod, posterior view. **G.** Female subanal plate with washboard. **H.** Right posterior telopod, posterior view. **I.** Right posterior telopod, anterior view. **J.** Left female coxa 2 with vulva, posterior view. Abbreviations: as = apical spine; cl = claw; cr-t = crenulated teeth; cx = coxa; ep = external plate; fe = femur; gp = gonopore; ip = inner plate; o = operculum; pof = postfemur; pref = prefemur; s-ps = sclerotized spots; sr = stridulation rib; st = stigmatic plate; syn = syncoxite; ta = tarsus; ti = tibia; vs = ventral spines. Roman numerals indicate telopoditomeres. Scale bars = 1 mm.

like and slightly curved, with rounded edges, protruding up to $\frac{2}{3}$ of third podomere height, apically with sclerotized spots, visible in anterior view (Fig. 12D–F). Third podomere narrow, half as long as first; cavity mesally with numerous sclerotized spots and three thin, sclerotized spines (Fig. 12E–F); one sclerotized spot located close to tip; laterally with up to 4 crenulated teeth. Podomeres 1–3 on both sides with numerous long, isolated hairs.

POSTERIOR TELOPODS (FIGS). Movable finger strongly curved, apically with invagination. Hollowed-out inner margin with one large triangular membranous lobe and 3–5 smaller sclerotized spines (Fig. 12H). Posterior aspect of movable finger with ca 11 small, sclerotized teeth (Fig. 12I). Immobile finger slender, with weakly curved tip, slightly shorter than movable finger. Anterior side of immobile finger basally with a membranous lobe and a sclerotized spine, at tip with numerous small sclerotized spots (Fig. 12I). All three podomeres of posterior telopods on both sides glabrous. Inner horns of syncoxite apically curved posteriorly. Tips sharp, entire horns covered with numerous short hairs.

Female sexual characters

Subanal plate wide, slightly triangular. Washboard with well-developed stridulation ribs, with 3 ribs on each half (Fig. 12G). Vulva large, covering more than $\frac{2}{3}$ of coxa (Fig. 12J). Operculum small and low, ending far before coxal margin. Apical margin of operculum medially notched, lateral tip twice as high as mesal one, well rounded. Mesal plate long, extending beyond operculum.

Distribution and ecology

Zoosphaerium spinopiligerum sp. nov. occurs in sympatry with *Z. nigrum* sp. nov. and *Sphaeromimus midongy* Moritz & Wesener, 2017 in the remote mountainous forests of Midongy in the southeast of Madagascar (Fig. 3).

Remarks

The female specimen examined here is only tentatively placed in *Z. spinopiligerum* sp. nov. as its COI barcode shows quite a p-distance to the male holotype (Table 2). Such a distance is far higher than usually present in millipedes.

New locality data for Zoosphaerium species in Madagascar

Zoosphaerium neptunus (Butler, 1872)

Sphaerotherium digitale de Saussure & Zehntner, 1897: pl. 5 fig. 16.

Sphaerotherium pygidiale de Saussure & Zehntner, 1902: 42.

See Wesener & Wägele (2008) for a revision and Wesener (2016) for a complete bibliography.

Material examined

MADAGASCAR – **Antsiranana** • 3 ♂♂; SAVA, Parc National de Marojejy, 6.5 km NW of Manantenina village; 14°27'21.2" S, 49°46'29.8" E; alt. 780 m; disturbed lowland humid forest, pitfalls; 31 May 2016; V. Soarimalala leg.; FMNH-INS 2858681 • >30 juvs; Marojejy; 14°26' S, 49°45' E; alt. 700 m; 10–17 Nov. 1993; NHMD. – **Toamasina** • 1 ♀; Reserve Betampona, Camp Rendriendry, 34.1 km 332° from Toamasina; 17°55.26" S, 049°11.59" E; alt. 390 m; general collecting in camp, rainforest; 28 Nov. 2005; Brian L. Fisher *et al.* leg.; coll. no. BLF 13126; CASENT 9032818 • 1 ♀; Reserve Nationale Integrale Betampona, Betampona, 35.1 km NW of Toamasina; 17°55.05" S, 49°12.03" E; alt. 500 m; rainforest, general collecting; 15–17 Dec. 2007; Brian L. Fisher *et al.* leg.; coll. no. BLF 19514; CASENT 9068298 • 1 ♀; Region Atsinanana, Reserve Naturelle Integrale, along Piste Principale

(PP); 17°54.8' S, 49°11.6' E; alt. 400–500 m; in relatively intact lowland humid forest, pitfall 2, bucket 6; 10 Nov. 2015; Steven M. Goodman leg.; FMNH-INS SMG-19237 • 1 ♀; same collection data as for preceding; by hand; coll. no. SMG-19235; FMNH-INS 2858602 • 1 ♀; same collection data as for preceding; pitfall 3, bucket 5; 11 Nov. 2015; coll. no. SMG-19246; FMNH-INS 2858597 • 1 ♀; same collection data as for preceding; coll. no. SMG-19247; FMNH-INS 2858600 • 1 ♀; same collection data as for preceding; pitfall 1; 12 Nov. 2015; coll. no. SMG-19255; FMNH-INS 2858599 • 1 ♀; same collection data as for preceding; pitfall 3; coll. no. SMG-19256; FMNH-INS 2858604 • 1 ♂; same collection data as for preceding; pitfall 2; coll. no. SMG-19254; FMNH-INS 2858593 • 1 ♂; same collection data as for preceding; pitfall 1; 13 Nov. 2015; coll. no. SMG-19263; FMNH-INS 2858594 • 1 ♂; same collection data as for preceding; coll. no. SMG-19264; FMNH-INS 2858591 • 1 ♀; same collection data as for preceding; pitfall 3; 15 Nov. 2015; coll. no. SMG-19271; FMNH-INS 2858603 • 1 ♀; Region Atsinanana, Reserve Naturelle Integrale, along Piste Principale (PP) between 1650 and 2550 m; 17°54.62' S, 49°11.70' E; alt. 460–520 m; in undisturbed lowland humid forest, pitfall 4, bucket 8; 17 Nov. 2015; Steven M. Goodman leg.; coll. no. SMG-19289; FMNH-INS 2858598 • 1 ♂; same collection data as for preceding; bucket 11; coll. no. SMG-19291; FMNH-INS 2858590 • 1 ♀; same collection data as for preceding; pitfall 5, bucket 3; coll. no. SMG-19290; FMNH-INS 2858596 • 1 ♂; same collection data as for preceding; pitfall 4, bucket 1; 21 Nov. 2015; coll. no. SMG-19313; FMNH-INS 2858592.

Remarks

We provide further locality information including the lowland forest of Betampona and lowland forests in Marojejy for this relatively widespread species of *Zoosphaerium* (Fig. 13A). The gigantic females of *Z. neptunus* are currently the largest Sphaerotheriida known, reaching the size of a tennis ball or small orange when rolled up. The juveniles of this species show swarming behavior around Andasibe (Wesener & Schütte 2010), a so far unique behavior for giant pill-millipedes.

Zoosphaerium platylabum (de Saussure & Zehntner, 1897)

See Wesener & Wägele (2008) for a revision and Wesener (2016) for a complete bibliography.

Material examined

MADAGASCAR – **Toamasina** • 1 ♂; Forêt d'Analamay, 9 km NE of Ambohimanarivo village; 18°47'55.4" S, 48°19'23.6" E; alt. 1100 m; degraded montane forest, pitfall buckets; 14 Jan. 2009; V. Soarimalala leg.; coll. no. VS-1635; FMNH-INS 3195652 • 1 ♂; Forêt d'Analamay, 10 km E of Ambohimanarivo village; 18°48'29.4" S, 48°20'13.8" E; alt. 1060 m; dense humid transitional lowland and montane forest; 31 Jan. 2009; V. Soarimalala leg.; FMNH-INS 3119883 • 1 ♂; Parc National de Zahamena, Onibe River; 17°45'33" S, 48°51'17" E; alt. 780 m; rainforest, general collecting in camp; 21 Feb. 2009; B.L. Fisher *et al.* leg.; coll. no. BLF 22169; CASENT 9068304 • 1 ♂, 1 ♀; Corridor Forestier Analamay-Mantadia, Ambohibolakely; 18°46'39" S, 48°21'45" E; alt. 971 m; rainforest, general collection; 23–28 Nov. 2012; B.L. Fisher *et al.* leg.; coll. no. BLF 29952; CASENT 9068293 • 2 specs; Alaotra-Mangoro, about 4.7 km NE of Andasibe village; 18°54'4.2" S, 48°27'00.0" E; alt. 985 m; degraded lower montane forest, pitfalls; Jan. 2014; Toky Randriamora leg.; FMNH-INS 2858672 • 1 ♂; Alaotra-Mangoro, 1.5 km N of Sahavarina village, about 4.5 km NW of Antaniditra village and 7 km SE of Ambatovy mine site; 18°51'48.3" S, 48°21'23.9" E; alt. 925 m; open anthropogenic habitat and degraded lower montane forest, pitfalls; Mar. 2014; Toky Randriamora leg.; FMNH-INS 2858673 • 2 specs; same collection data as for preceding; coll. no. VS-1676; FMNH-INS 2858674 • 1 spec.; same collection data as for preceding; FMNH-INS 3196509 • 1 spec.; Alaotra-Mangoro, about 1 km S of Ambodiriana village; 19°02'00.4" S, 48°20'20.3" E; alt. 980 m; degraded lower montane forest, pitfalls; Mar. 2014; Toky Randriamora leg.; FMNH-INS 2858675.

Remarks

Zoosphaerium platylabum was previously known only from a few specimens collected near Andasibe (Wesener & Wägele 2008; Wesener *et al.* 2010b). Now, the species has been found at several additional montane rainforest sites north of Andasibe, all at elevation levels of 780–1100 m (Fig. 13B).

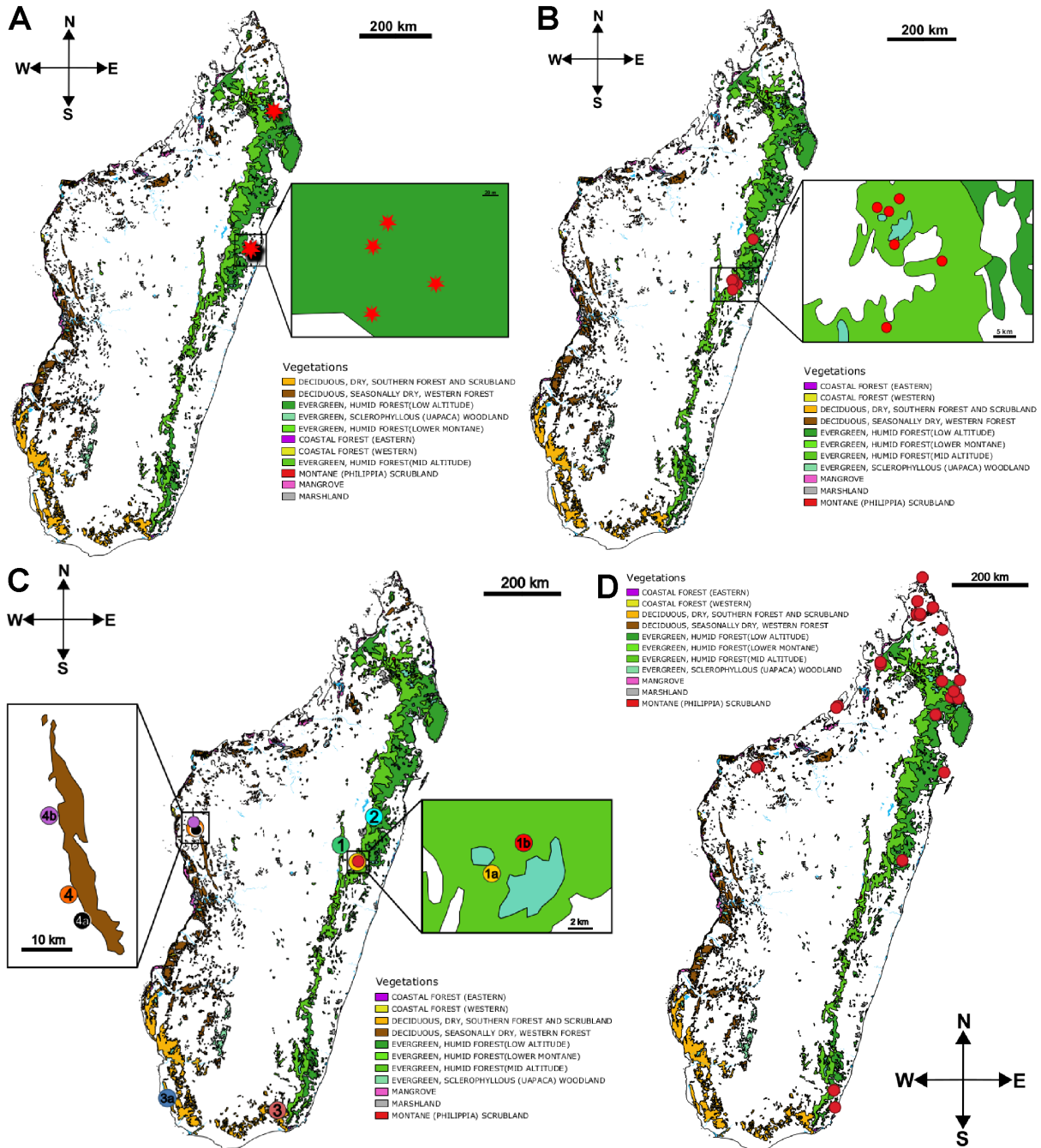


Fig. 13. Distribution maps marking new localities for known species of *Zoosphaerium*. Vegetation color marks modified from Moat & Smith 2007. **A.** *Z. neptunus* (Butler, 1872). **B.** *Z. platylabum* (de Saussure & Zehntner, 1897). **C.** 1 = *Z. piligerum* (de Saussure & Zehntner, 1897); 2 = *Z. villosum* Wesener & Sierwald, 2015; 3 = *Z. libidinosum* (de Saussure & Zehntner, 1897); 4 = *Zoosphaerium discolor* Wesener, 2009. **D.** Unidentifiable juvenile *Zoosphaerium* samples.

Zoosphaerium piligerum (de Saussure & Zehntner, 1897)

See Wesener & Wägele (2008) for a revision and Wesener (2016) for a complete bibliography.

Material examined

MADAGASCAR – **Antananarivo** • 1 spec.; Forêt d’Antsahabe, 6 km SE of Anjozorobe; 18°25.3' S, 47°56.6' E; alt. 1250 m; dense humid montane forest; 4 Dec. 2005; V. Soarimalala leg.; coll. no. VS-667; FMNH-INS 3119912. – **Toamasina** • 1 spec.; Forêt d’Analamay, 12.5 km E of Ambohimananarivo village; 18°48'20.8" S, 48°21'38.1" E; alt. 1060 m; dense humid transitional lowland and montane forest; 10 Feb. 2009; V. Soarimalala leg.; coll. no. VS-1706; FMNH-INS 3119891 • 1 ♂; Forêt d’Analamay, 10 km E of Ambohimananarivo village; 18°49'25.9" S, 48°20'1.8" E; alt. 1050 m; dense humid transitional lowland and montane forest; 20 Feb. 2009; V. Soarimalala leg.; coll. no. VS-1741; FMNH-INS 3119882.

Remarks

Currently listed as critically endangered in the IUCN Red List (Rudolf & Wesener 2017a), *Z. piligerum* seems to be more widespread in the eastern montane forests (Fig. 13C) than when the species was assessed as critically endangered in the IUCN Red List (Wesener & Wägele 2008).

Zoosphaerium villosum Wesener & Sierwald, 2005

Material examined

MADAGASCAR – **Toamasina** • 1 ♂; Parc National de Zahamena, Tetezambatana forest, near jct of Nosivola and Manakambahiny Rivers; 17°44'35" S, 48°43'46" E; alt. 860 m; general collecting in camp, rainforest; 18–19 Feb. 2009; B.L. Fisher *et al.* leg.; coll. no. BLF 21973; CASENT 9068292.

Remarks

Another locality for this species (Fig. 13C), which appears to be common in northeastern Malagasy lowland rainforests, is added (cf Wesener *et al.* 2010b).

Zoosphaerium libidinosum (de Saussure & Zehntner, 1897)

See Wesener & Wägele (2008) for a revision and Wesener (2016) for a complete bibliography.

Material examined

MADAGASCAR – **Toliara** • 1 ♂; Mahafaly Plateau, Atsimo-Anrefena, 4 km NE of Vohombe village; 24°23.9' S, 43°50.8' E; alt. 80 m; in spiny bush, pitfalls; 27 Feb. 2003; Voahangy Soarimalala leg.; coll. no. VS-540; FMNH-INS 3196503 • 1 spec.; 10.0 km SSW of Tranomaro, along Vohondava River; 24°41.2' S, 46°27.2' E; alt. 225 m; spiny bush; 18 Mar. 2005; V. Soarimalala leg.; coll. no. VS-572; FMNH-INS 3177004.

Remarks

Additional locality data for this very widespread species, occurring almost everywhere in the southern spiny forest ecosystem, is provided (Fig. 13C).

Zoosphaerium discolor Wesener, 2009

Material examined

MADAGASCAR – **Mahajanga** • 1 ♀; Forêt de Beanka, 4.9 km S of Ambinda; 18°03.7' S, 44°31.5' E; alt. 320 m; slightly disturbed dry deciduous tsingy forest; 27 Oct. 2009; V. Soarimalala leg.; coll. no. VS-1783; FMNH-INS 3119880 • 1 ♀; Majunga, Reserve forestière Beanka, 50.7 km E of Maintirano;

17°52'49" S, 44°28'08" E; alt. 140 m; tropical dry forest on tsingy, general collecting; 28–31 Oct. 2009; B.L. Fisher *et al.* leg.; coll. no. BLF23002; CASENT9068288 • 1 ♂; Forêt de Beanka; 18°01.25' S, 44°30.08' E; alt. 220 m; slightly disturbed dry deciduous forest; 14 Jan. 2010; Z.H. Harimpiria leg.; FMNH-INS 3119897B.

Remarks

This species, previously known from the western dry forests of Bemaraha and Kirindy (Wesener 2009), has now also been recorded from Beanka (Fig. 13C).

Zoosphaerium aureum Wesener, 2009

Material examined

MADAGASCAR – Antsiranana • 1 ♂; Montagne d'Ambre; 12°32' S, 49°10' E; alt. 1100 m; 23–28 Nov. 1993; NHMD.

Remarks

We provide collection information for one additional specimen from the type locality. *Zoosphaerium aureum* is currently classified as Least Concern (Rudolf & Wesener 2017b) on the IUCN Red List.

Zoosphaerium smaragdinum Wesener, 2009

Material examined

MADAGASCAR – Antsiranana • 3 juvs; Marojejy; 14°26' S, 49°45' E; alt. 700 m; 10–17 Nov. 1993; NHMD.

Remarks

Three more specimens have been collected from the type locality. *Zoosphaerium smaragdinum* is currently classified as Near Threatened (Rudolf & Wesener 2017c) on the IUCN Red List.

Zoosphaerium ambrense Wesener, 2009

Material examined

MADAGASCAR – Antsiranana • 1 ♀; Montagne d'Ambre, 2 km away from park entrance; 12°32' S, 49°10' E; alt. 1000 m; 23–28 Nov. 1993; J. Coddington, N. Scharff, S. Larcher, C. Griswold and R. Andriamasimanana leg.; NHMD • 1 ♂, 2 ♀♀; same collection data as for preceding; alt. 1100 m; NHMD • 1 ♂; same collection data as for preceding; NHMD • 1 ♂; same collection data as for preceding; NHMD • 1 ♂; same collection data as for preceding; NHMD • 1 ♂; same collection data as for preceding; NHMD.

Remarks

We provide collection information for several more specimens of *Z. ambrense* that were sampled at the type locality.

Zoosphaerium corystoides Wesener, 2009

Material examined

MADAGASCAR – Antsiranana • 2 ♂♂, 2 specs; Montagne d'Ambre; 12°32' S, 49°10' E; alt. 1100 m; 23–28 Nov. 1993; J. Coddington, N. Scharff, S. Larcher, C. Griswold and R. Andriamasimanana leg.; NHMD • 1 ♂; same collection data as for preceding; NHMD.

Remarks

Additional specimens were collected at the type locality, Montagne d'Ambre. *Zoosphaerium corystoides* is currently classified as Least Concern (Rudolf & Wesener 2017d) on the IUCN Red List.

Unidentifiable *Zoosphaerium* spp. (mainly immatures)

Material examined

MADAGASCAR – **Antsiranana** • 1 spec.; Marojejy Res.; 4 km NNW of Manantenina; 14°26' S, 49°45' E; alt. 700 m; 10–16 Nov. 1993; J. Coddington, N. Scharff, S. Larcher, C. Griswold and R. Andriamasimanana leg.; NHMD • 1 ♀; Montagne d'Ambre; 12°32' S, 49°10' E; alt. 1100 m; 23–28 Nov. 1993; J. Coddington, N. Scharff, S. Larcher, C. Griswold and R. Andriamasimanana leg.; NHMD • 1 spec.; same collection data as for preceding; NHMD • 2 specs; N Ankarana Reserve, base of tsingy summit; 12.8461° S, 49.15° E; alt. 284 m; dry deciduous forest on limestone; 8 Apr. 2007; Ken Emberton leg.; coll. no. MBI-2038; FMNH-INS 000 103 908 • 1 spec.; N Ankarana Reserve, local tsingy, summit; 12.8465° S, 49.1503° E; alt. 294 m; dry deciduous forest on limestone; 8 Apr. 2007; Ken Emberton leg.; coll. no. MBI-2037; FMNH-INS 000 103 909 • 1 spec.; NE Ankarana Reserve, roadside; 12.8329° S, 49.2286° E; alt. 331 m; dry deciduous forest on lava; 14 Apr. 2007; Ken Emberton leg.; coll. no. MBI-2066; FMNH-INS 000 103 904 • 2 specs; E Ankarana Reserve, talus and rocks below 20 m tsingy cliff; 12.8609° S, 49.2267° E; alt. 294 m; dry deciduous forest on limestone; 14 Apr. 2007; Ken Emberton leg.; coll. no. MBI-2068; FMNH-INS 000 103 911 • 1 spec.; NE Ankarana Reserve, local limestone summit; 12.8738° S, 49.2249° E; alt. 315 m; dry deciduous forest on limestone; 14 Apr. 2007; Ken Emberton leg.; coll. no. MBI-2064; FMNH-INS 000 103 920 • 4 specs; NE Ankarana Reserve, talus below tsingy visible from road; 12.8617° S, 49.2266° E; alt. 266 m; dry deciduous forest on limestone; 14 Apr. 2007; Ken Emberton leg.; coll. no. MBI-2062; FMNH-INS 000 103 922 • 2 spec.; NE Analamerana, near summit; 12.6833° S, 49.5333° E; alt. 36 m; litter-loam pockets in limestone brocks, dry deciduous forest on limestone; 23 Apr. 2007; Ken Emberton leg.; coll. no. MBI-2072; FMNH-INS 000 103 929 • 3 specs; NE Analamerana, 160 m downslope E from summit; 12.6833° S, 49.5333° E; limestone outcrop, dry deciduous forest on limestone; 25 Apr. 2007; Ken Emberton leg.; coll. no. MBI-2086; FMNH-INS 000 103 921 • 1 spec.; NE Analamerana, on W bank of Antafiamantsina River, at waterfall, 3rd rapid up; 12.6833° S, 49.5333° E; dry deciduous forest on limestone; 26 Apr. 2007; Ken Emberton leg.; coll. no. MBI-2099; FMNH-INS 000 103 903 • 7 specs; NE Analamerana, small tsingy 180 m above river, ca 30 minute walk; 12.6833° S, 49.5333° E; dry deciduous forest on limestone; 26 Apr. 2007; Ken Emberton leg.; coll. no. MBI-2094; FMNH-INS 000 103 917 • 2 specs; N Cap d'Ambre, Pointe du Phoque; 11.9698° S, 49.2845° E; alt. 11 m; spring-bottle tree stand, dry deciduous forest on limestone; 4 May 2007; Ken Emberton leg.; coll. no. MBI-2108; FMNH-INS 000 103 910 • 2 specs; NW of Antalaha, S of Mahadera, Mt. Ambohodrapaka; 14.6805° S, 50.0325° E; alt. 270 m; partially cut rainforest on granite; 29 Jul. 2007; Ken Emberton leg.; coll. no. MBI-2403; FMNH-INS 000 103 906 • 2 specs; same collection data as for preceding; coll. no. MBI-2404; FMNH-INS 000 103 907 • 1 spec.; NW of Antalaha, S of Mahadera, Mt Ambohodrapaka; 14.6836° S, 50.031° E; alt. 369 m; partially cut rainforest on granite; 29 Jul. 2007; Ken Emberton leg.; coll. no. MBI-2417; FMNH-INS 000 103 924 • 1 spec.; NW of Antalaha; 14.4123° S, 50.1755° E; alt. 1790 m; 30 Jul. 2007; Ken Emberton leg.; coll. no. MBI-2439; FMNH-INS 000 103 905 • 2 specs; NW of Antalaha, S of Mahadera, Mt Ambohodrapaka; 14.6873° S, 50.0301° E; alt. 499 m; rainforest, on quartzite; 30 Jul. 2007; Ken Emberton leg.; coll. no. MBI-2430; FMNH-INS 000 103 915 • 1 spec.; NW of Antalaha, S of Mahadera, Mt. Ambohodrapaka; 14.6872° S, 50.0293° E; alt. 545 m; 30 Jul. 2007; Ken Emberton leg.; coll. no. MBI-2434; FMNH-INS 000 103 918 • 1 spec.; NW of Antalaha, SW of Andranofotsy, Mt Ambodivohitra; 14.8157° S, 49.9634° E; alt. 487 m; rainforest on quartzite; 10 Aug. 2007; Ken Emberton leg.; coll. no. MBI-2459; FMNH-INS 000 103 913 • 2 specs; NW of Antalaha, SW of Andranofotsy, Mt Ambodivohitra;

14.8157° S, 49.9634° E; alt. 487 m; rainforest on quartzite; 10 Aug. 2007; Ken Emberton leg.; coll. no. MBI-2459; FMNH-INS 000 103 919 • 2 specs; NW of Antalaha, SW of Andranofotsy, Mt Ambodivohitra; 14.8166° S, 49.9622° E; alt. 575 m; rainforest, pandanus, palms, sphagnum on quartzite; 11 Aug. 2007; Ken Emberton leg.; coll. no. MBI-2472; FMNH-INS 000 103 912 • 1 spec.; NW of Antalaha, S of Antsahanoro, riverside hill rainforest; 14.8434° S, 50.1372° E; alt. 82 m; on quartzite; 15 Aug. 2007; Ken Emberton leg.; coll. no. MBI-2498; FMNH-INS 000 103 916 • 1 spec.; NW of Antalaha, S of Antsahanoro; 14.8445° S, 50.1359° E; alt. 131 m; riverside hill rainforest on quartzite; 15 Aug. 2007; Ken Emberton leg.; coll. no. MBI-2512; FMNH-INS 000 103 934 • 2 specs; Mt Bobanora, about 40 km W of Vohemar; 13.2141° S, 49.7574° E; alt. 320 m; viny rainforest on basalt talus; 26 Aug. 2007; Ken Emberton leg.; coll. no. MBI-2550; FMNH-INS 000 103 914 • 1 spec.; Manongorivo Reserve, slope high above Berato; 14.0366° S, 48.2882° E; alt. 897 m; rainforest on metamorphic boulders; 17 Oct. 2007; Ken Emberton leg.; coll. no. MBI-2611; FMNH-INS 000 103 933 • 2 specs; Manongorivo Reserve, Monongorivo River junction with small tributary; 13.9846° S, 48.2891° E; alt. 321 m; rainforest on granite; 20 Oct. 2007; Ken Emberton leg.; coll. no. MBI-2619; FMNH-INS 000 103 941 • 5 specs; Manongorivo Reserve, riverside flat area below cliffs, Monongorivo River; 13.9818° S, 48.2858° E; alt. 281 m; rainforest on granite; 20 Oct. 2007; Ken Emberton leg.; coll. no. MBI-2620; FMNH-INS 000 103 943. – **Mahajanga** • 1 spec.; Namoroka Reserve, southern valley on NE side of tsingy; 16.469° S, 45.3647° E; alt. 142 m; dry deciduous forest on limestone; 25 Sep. 2007; Ken Emberton leg.; coll. no. MBI-2567; FMNH-INS 000 103 936 • 2 specs; Namoroka Reserve, southern isolated tsingy canyon; 16.4674° S, 45.3806° E; alt. 432 feet; dry deciduous forest on limestone; 27 Sep. 2007; Ken Emberton leg.; coll. no. MBI-2574; FMNH-INS 000 103 928 • 2 specs; Namaroka Reserve, southern isolated tsingy; 16.4871° S, 45.3371° E; alt. 435 m; dry deciduous forest on limestone; 27 Sep. 2007; Ken Emberton leg.; coll. no. MBI-2572; FMNH-INS 000 103 927 • 9 spec.; S Namaroka National Park, low tsingy baobobs; 16.4565° S, 45.4011° E; alt. 115 m; dry deciduous forest on limestone; 29 Sep. 2007; Ken Emberton leg.; coll. no. MBI-2578; FMNH-INS 000 103 923 • 1 spec.; Anjajavy, isolated steep limestone hill near Antsangabe; 15.0643° S, 47.2373° E; alt. 30 m; dry deciduous forest on limestone; 8 Oct. 2007; Ken Emberton leg.; coll. no. MBI-2592; FMNH-INS 000 104 000 • 1 spec.; Anjajavi, side of long tsingy hill near dry mudflat; 15.026° S, 47.2712° E; alt. 22 m; dry deciduous forest on limestone; 11 Oct. 2007; Ken Emberton leg.; coll. no. MBI-2595; FMNH-INS 000 103 940. – **Toamasina** • 1 spec.; Andriantanelly Massif; 18.6907° S, 48.8063° E; alt. 589 m; rainforest; 19 May 2008; Ken Emberton leg.; coll. no. MBI-2665; FMNH-INS 000 103 932 • 1 spec.; Andriantanelly Massif, streamside cliff base; 18.6997° S, 48.806° E; alt. 301 m; in rainforest, on granite; 22 May 2008; Ken Emberton leg.; coll. no. MBI-2693; FMNH-INS 000 103 930 • 1 spec.; Makira Reserve, W of Andaparaty; 15.2302° S, 49.5975° E; alt. 430 m; rainforest; 23 Nov. 2008; Ken Emberton leg.; coll. no. MBI-3152; FMNH-INS 000 103 939 • 2 specs; N of Manona littoral forest; 16.6028° S, 49.8037° E; alt. 23 m; 2 Dec. 2008; Ken Emberton leg.; coll. no. MBI-3158; FMNH-INS 000 103 937. – **Toliara** • 2 specs; W of Ehasity; 24.154° S, 47.1821° E; alt. 347 m; rainforest; 18 Aug. 2008; Ken Emberton leg.; coll. no. MBI-2966; FMNH-INS 000 103 938 • 1 spec.; Mount Ivohibe; 24.5607° S, 47.2065° E; alt. 457 m; rainforest; 31 Aug. 2008; Ken Emberton leg.; coll. no. MBI-2900; FMNH-INS 000 103 931 • 1 spec.; W of Ehasity rainforest; 24.1514° S, 47.178° E; alt. 479 m; 18 Sep. 2008; Ken Emberton leg.; coll. no. MBI-2964; FMNH-INS 000 103 942.

Microsphaerotherium anjozorobe Wesener, 2009

Material examined

MADAGASCAR – **Antananarivo** • 1 ♀; Analamanga, 6.7 km SE of Anjozorobe village, Andasin'i Jaonera; 18°25.3' S, 47°56.6' E; alt. 1250 m; in disturbed montane forest, pitfalls 1–3; 19–23 Feb. 2016; Steven M. Goodman leg.; FMNH-INS 2858679.

Remarks

This is another record of this rare miniaturized species (Wesener 2009), previously known only from the type series collected near Andranomay. This species is currently classified as Critically Endangered (Rudolf & Wesener 2017e) on the IUCN Red List.

Discussion

Interspecific distances

The lowest interspecific distances of the COI barcoding gene in the genus *Zoosphaerium* were observed between *Z. beanka* sp. nov. and an unidentified female from Anjiamangirina with 8.6% (Table 2). Generally, interspecific distances vary between 9.1 and 20% in the genus *Zoosphaerium*. However, this genus remains poorly represented by genetic data, with only 15 of the 77 species being genetically sampled. In contrast to this, sequence data for the Malagasy giant pill-millipede genus *Sphaeromimus* is available for 11 of the 12 known species. In *Sphaeromimus*, whose species have a distribution restricted to southern Madagascar, interspecific distances vary between 8.3 and 20.8%, with a single outlier at 5.4% (Wesener *et al.* 2014; Moritz & Wesener 2017), the same range that is observed in *Zoosphaerium*. While intraspecific distances are generally below 2.5% in our dataset, at most three sequences are available for a single species. Unidentifiable females show genetic distances between 4.3 and 8.6% from identifiable male specimens, but any meaningful discussion of these specimens is difficult without the availability of male specimens and the inclusion of nuclear markers in future studies. Low intraspecific distances are also visible in the maximum likelihood tree, where species represented by more than one specimen are well-supported. This shows the usefulness of COI barcoding as a basis for species identification. However, the poor resolution within the genus *Zoosphaerium* and its non-monophyly provide clear evidence that the mitochondrial COI gene – containing little resolution at deeper evolutionary splits – does not allow a reconstruction of the phylogeny.

Giant pill-millipede diversity and endemism in Madagascar

Most of the known species of *Zoosphaerium* are highly endemic to small scattered areas in Madagascar, which are rarely visited by scientists collecting soil arthropods, so that occurrence data is still sparse for many species. Numerous species in Madagascar, including giant pill-millipedes, are severely threatened by habitat fragmentation and destruction (Harper *et al.* 2007). As of today, 19 of 70 assessed giant pill-millipede species from Madagascar are in one of the top three categories of the IUCN Red List (e.g., Rudolf & Wesener 2017a, 2017b, 2017c, 2017d). Therefore, further locality data for all species in this group is greatly needed in order to protect them. Although giant pill-millipedes have adapted to different ecosystems, several species show a striking microendemism. This microendemism is especially prevalent in rainforest and montane rainforest ecosystems of the island, with samples from forests never studied before often yielding undescribed species. In contrast to humid forests, species of *Zoosphaerium* from the spiny and western dry forest ecosystems appear to be more widespread, something that is not known for other millipede groups such as Spirobolida (Wesener *et al.* 2009a; Wesener 2020a, 2020b).

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References

- Ali J.R. & Aitchison J.C. 2008. Gondwana to Asia: plate tectonics, paleogeography and the biological connectivity of the Indian sub-continent from the Middle Jurassic through latest Eocene (166–35 Ma). *Earth-Science Reviews* 88 (3): 145–166.
- Altschul S.F., Madden T.L., Schäffner A.A., Zhang J., Zhang Z., Miller W. & Lipman D.J. 1997. Gapped BLAST and PSIBLAST: a new generation of protein database search programs. *Nucleic Acids Research* 25 (17): 3389–3402. <https://doi.org/10.1093/nar/25.17.3389>
- Brolemann H.W. 1922. Liste des myriapodes de l'Academie Malagache de Tananarive. *Bulletin de la Société zoologique de France* 47: 223–278. <https://doi.org/10.5962/bhl.part.3470>
- Chamberlin R.V. 1921. New Chilopoda and Diplopoda from the East Indian region. *Annals and Magazine of Natural History, Series 9* 7 (37): 50–87. <https://doi.org/10.1080/00222932108632489>
- Enghoff H. 2003. Diplopoda, Millipedes. In: S.G. Goodman & J.P. Benstead (eds) *The Natural History of Madagascar*: 617–627. The University of Chicago Press, Chicago.
- Goodman S.M. & Benstead J.P. 2005. Updated estimates of biotic diversity and endemism for Madagascar. *Oryx* 39 (1): 73–77. <https://doi.org/10.1017/S0030605305000128>
- Hall T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- Harper G.J., Steininger M.K., Tucker C.J., Juhn D. & Hawkins F. 2007. Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation* 34 (4): 325–333.
- Hebert P.D., Cywinska A., Ball S.L. & Dewaard J.R. 2003. Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London B* 270 (1512): 313–321. <https://doi.org/10.1098/rspb.2002.2218>
- Krause D.W. 2003. Late Cretaceous vertebrates of Madagascar: a window into Gondwanan biogeography at the end of the age of dinosaurs. In: Goodman S.M. & Benstead J.P. (eds) *The Natural History of Madagascar*: 40–47. The University of Chicago Press, Chicago.
- Moat J. & Smith P. 2007. *Atlas of the Vegetation of Madagascar Vegetation/Atlas de la Vegetation de Madagascar*. Royal Botanic Gardens, Kew (bilingual edition).
- Moritz L. & Wesener T. 2017. Integrative description of two new species of Malagasy chirping giant pill-millipedes, genus *Sphaeromimus* (Diplopoda, Sphaerotheriida, Arthrosphaeridae). *European Journal of Taxonomy* 381: 1–25. <https://doi.org/10.5852/ejt.2017.381>
- Myers N., Mittermeier R.A., Mittermeier C.G., Da Fonseca G.A. & Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403 (6772): 853–858. <https://doi.org/10.1038/35002501>
- Pocock R.I. 1895. Description of new genera of Zephronidae, with brief preliminary diagnoses of some new species. *Annals and Magazine of Natural History, Series 6* 16 (95): 409–415. <https://doi.org/10.1080/00222939508680293>
- Rakotondrasoa L.O., Malaisse F. & Bogaert J. 2017. Modélisation de la dynamique du paysage forestier de la Réserve Spéciale d'Ambatovaky (Nord-Est de Madagascar). *Tropicicultura* 35 (4): 312–324.
- Rudolf E. & Wesener T. 2017a. *Zoosphaerium piligerum*. *The IUCN Red List of Threatened Species* 2017: e.T65525146A65527960. Available from <https://doi.org/10.2305/IUCN.UK.2017-1.RLTS.T65525146A65527960.en> [accessed 7 Apr. 2020].

- Rudolf E. & Wesener T. 2017b. *Zoosphaerium aureum*. *The IUCN Red List of Threatened Species* 2017: e.T65524362A65527855. Available from <https://doi.org/10.2305/IUCN.UK.2017-1.RLTS.T65524362A65527855.en> [accessed 7 Apr. 2020].
- Rudolf E. & Wesener T. 2017c. *Zoosphaerium smaragdinum*. *The IUCN Red List of Threatened Species* 2017: e.T65525770A65528000. Available from <https://doi.org/10.2305/IUCN.UK.2017-1.RLTS.T65525770A65528000.en> [accessed 7 Apr. 2020].
- Rudolf E. & Wesener T. 2017d. *Zoosphaerium corystoides*. *The IUCN Red List of Threatened Species* 2017: e.T65524417A65527885. Available from <https://doi.org/10.2305/IUCN.UK.2017-1.RLTS.T65524417A65527885.en> [accessed 7 Apr. 2020].
- Rudolf E. & Wesener T. 2017e. *Microsphaerotherium anjzorobe*. *The IUCN Red List of Threatened Species* 2017: e.T65524228A65527805. Available from <https://doi.org/10.2305/IUCN.UK.2017-1.RLTS.T65524228A65527805.en> [accessed 7 Apr. 2020].
- Sagorny C. & Wesener T. 2017. Two new giant pill-millipede species of the genus *Zoosphaerium* endemic to the Bemanevika area in northern Madagascar (Diplopoda, Sphaerotheriida, Arthrosphaeridae). *Zootaxa* 4263 (2): 273–294. <https://doi.org/10.11646/zootaxa.4263.2.4>
- Saussure H. de & Zehntner L. 1897. Atlas de l'histoire naturelle des Myriapodes. *Histoire physique, naturelle et politique de Madagascar* 27 (53): 1–12.
- Saussure H. de & Zehntner L. 1902. Myriapodes de Madagascar. In: Grandidier A. (ed.) *Histoire physique, naturelle et politique de Madagascar* 27 (53): i–viii, 1–356.
- Tamura K., Stecher G., Peterson D., Filipski A. & Kumar S. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution* 30 (12): 2725–2729. <https://doi.org/10.1093/molbev/mst197>
- Tavaré S. 1986. Some probabilistic and statistical problems in the analysis of DNA sequences. *Lectures on Mathematics in the Life Sciences* 17 (2): 57–86.
- Trifinopoulos J., Nguyen L.T., von Haeseler A. & Minh B.Q. 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research* 44 (W1): W232–W235. <https://doi.org/10.1093/nar/gkw256>
- Wesener T. 2009. Unexplored richness: discovery of 31 new species of giant pill-millipedes endemic to Madagascar, with a special emphasis on micro-endemism (Diplopoda, Sphaerotheriida). *Zootaxa* 2097 (1): 1–131. <https://doi.org/10.11646/zootaxa.2097.1.1>
- Wesener T. 2011. Re-discovery after more than a century: a redefinition of the Malagasy endemic millipede genus *Zehntnerobolus*, with a description of a new species (Diplopoda, Spirobolida, Pachybolidae). *Zootaxa* 3018 (1): 21–26. <https://doi.org/10.11646/zootaxa.3018.1.3>
- Wesener T. 2014. A new phylogenetic analysis of the Sphaerotheriida (Diplopoda) with a revision of the Australian giant pill millipedes. *Invertebrate Systematics* 28 (2): 196–213. <https://doi.org/10.1071/IS13048>
- Wesener T. 2016. The giant pill-millipedes, order Sphaerotheriida – an annotated species catalogue with morphological atlas and list of apomorphies (Arthropoda: Diplopoda). *Bonn Zoological Bulletin – Supplementum* 63: 1–104.
- Wesener T. 2020a. Ecotone shifts in southern Madagascar: first barcoding data and six new species of the endemic millipede genus *Riotintobolus* (Spirobolida, Pachybolidae). *Zookeys* 953: 1–29. <https://doi.org/10.3897/zookeys.953.53977>

- Wesener T. 2020b. *Dichromatobolus*, a new genus of spirobolidan millipedes from Madagascar (Spirobolida, Pachybolidae). *European Journal of Taxonomy* 720: 107–120. <https://doi.org/10.5852/ejt.2020.720.1119>
- Wesener T. & Anilkumar P.A. 2020. The millipedes collected by the Museum “La Specola” on Madagascar 1989/1991, with the description of three new species of giant pill-millipedes (Diplopoda, Sphaerotheriida, Arthrosphaeridae). In: Korsós Z. & Dányi L. (eds) *Proceedings of the 18th International Congress of Myriapodology, Budapest, Hungary*. *ZooKeys* 930: 3–35. <https://doi.org/10.3897/zookeys.930.47620>
- Wesener T. & Enghoff H. 2009. Revision of the millipede subfamily Spiromiminae, a Malagasy group with Indian connections? (Diplopoda Spirobolida Pachybolidae). *Tropical Zoology* 22 (1): 71–120.
- Wesener T. & Schütte K. 2010. Swarming behaviour and mass occurrences in the world’s largest giant pill-millipede species, *Zoosphaerium neptunus*, on Madagascar and its implication for conservation efforts (Diplopoda: Sphaerotheriida). *Madagascar Conservation and Development* 5 (2): 89–94.
- Wesener T. & Sierwald P. 2005a. 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. & Sierwald P. 2005b. New giant pill-millipede species from the littoral forest of Madagascar (Diplopoda, Sphaerotheriida, *Zoosphaerium*). *Zootaxa* 1097 (1): 1–60. <https://doi.org/10.11646/zootaxa.1097.1.1>
- Wesener T. & vandenSpiegel D. 2009. A first phylogenetic analysis of giant pill-millipedes (Diplopoda: Sphaerotheriida), a new model Gondwanan taxon, with special emphasis on island gigantism. *Cladistics* 25 (6): 545–573. <https://doi.org/10.1111/j.1096-0031.2009.00267.x>
- Wesener T. & Wägele J.W. 2008. The giant pill-millipedes of Madagascar: revision of the genus *Zoosphaerium* (Myriapoda, Diplopoda, Sphaerotheriida). *Zoosystema* 30 (1): 5–82.
- Wesener T., Enghoff H. & Wägele J.W. 2008. Pachybolini – a tribe of giant Afrotropical millipedes: arguments for monophyly and the description of a new genus from Madagascar (Diplopoda: Spirobolida: Pachybolidae). *Invertebrate Systematics* 22: 37–53. <https://doi.org/10.1071/IS07008>
- Wesener T., Enghoff H., Hoffman R.L., Wägele J.-W. & Sierwald P. 2009a. Revision of the endemic giant fire millipedes of Madagascar, genus *Aphistogoniulus* (Diplopoda, Spirobolida, Pachybolidae). *International Journal of Myriapodology* 3: 15–52. <https://doi.org/10.1163/187525409X462403>
- Wesener T., Enghoff H. & Sierwald P. 2009b. Review of the Spirobolida on Madagascar, with descriptions of twelve new genera, including three genera of ‘fire millipedes’ (Diplopoda). *ZooKeys* 19: 1–128. <https://doi.org/10.3897/zookeys.19.221>
- Wesener T., Raupach M.J. & Sierwald P. 2010a. The origins of the giant pill-millipedes from Madagascar (Diplopoda: Sphaerotheriida: Arthrosphaeridae). *Molecular Phylogenetics and Evolution* 57 (3): 1184–1193. <https://doi.org/10.1016/j.ympev.2010.08.023>
- Wesener T., Bespalova I. & Sierwald P. 2010b. Madagascar’s living giants: discovery of five new species of endemic giant pill-millipedes from Madagascar (Diplopoda: Sphaerotheriida: Arthrosphaeridae: *Zoosphaerium*). *African Invertebrates* 51 (1): 133–161.
- Wesener T., Raupach M.J. & Decker P. 2011a. Mountain refugia play a role in soil arthropod speciation on Madagascar: a case study of the endemic giant fire-millipede genus *Aphistogoniulus*. *PLoS One* 6 (12): e28035. <https://doi.org/10.1371/journal.pone.0028035>

Wesener T., Köhler J., Fuchs S. & vandenSpiegel D. 2011b. How to uncoil your partner – “mating songs” in giant pill-millipedes (Diplopoda: Sphaerotheriida). *Naturwissenschaften* 98 (11): 967–975. <https://doi.org/10.1007/s00114-011-0850-8>

Wesener T., Minh-Tu Le D. & Loria S.F. 2014. Integrative revision of the giant pill-millipede genus *Sphaeromimus*, with the description of seven new species (Diplopoda, Sphaerotheriida, Arthrosphaeridae). *ZooKeys* 414: 67–104. <https://doi.org/10.3897/zookeys.414.7730>

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