Zootaxa 3236: 1–35 (2012)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

New Australasian Zalmoxidae (Opiliones: Laniatores) and a new case of male polymorphism in Opiliones

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Abstract

Six new species of litter-inhabiting harvestmen, four from New Caledonia and two from Australia, in the genus *Zalmoxis* Sørensen, 1886 (Opiliones: Laniatores: Zalmoxidae) are described and illustrated using light microscropy and SEM. A molecular phylogeny including these and related species indicates that the New Caledonian *Zalmoxis* are monophyletic, though the morphology of one species is consistent with the apomorphies of *Metazalmoxis* Roewer, 1912. Accordingly, *Zalmoxis* Sørensen, 1886 is considered the senior synonym of *Metazalmoxis* Roewer, 1912 **new synonymy.** *Zalmoxis* therefore remains the sole zalmoxid genus outside of the Neotropics. The new species add significantly to the known morphological diversity of Zalmoxidae, specifically in the case of one species from Queensland, Australia, with polymorphic males—the first such record for the superfamily Zalmoxoidea.

Key words: Grassatores, *Zalmoxis*, *Metazalmoxis*, Southwest Pacific, intrasexual polymorphism

Introduction

Since its original description 126 years ago, Zamoxidae Sørensen, 1886 has undergone a turbulent taxonomic history, including a period of synonymy in the system Phalangodinae (Roewer 1912, 1923) and subsequent resurrection (Staręga 1989). The taxonomic history of Zalmoxidae and the nominal genus *Zalmoxis* Sørensen, 1886 is detailed in a recent catalogue of Paleotropical Zalmoxidae (Sharma *et al.* 2011) and is not repeated here. Subsequent to multiple revisions, Zalmoxidae of the Paleotropics are restricted to 50 described species of *Zalmoxis* (distributed throughout Southeast Asia and the Southwest Pacific) and the monotypic genus *Metazalmoxis* Roewer,

Accepted by A. Pérez-González: 1 Feb.2012; published: 16 Mar. 2012

1912 (restricted to the Seychelles) (reviewed in Sharma *et al*. 2011). The two genera are distinguished by the number of tarsomeres in the first and fourth walking legs: on leg I, *Zalmoxis* have three tarsomeres, whereas *Metazalmoxis* have four; on leg IV, *Zalmoxis* have six tarsomeres, whereas *Metazalmoxis* have five.

In order to broaden knowledge of Zalmoxidae in general, and to address the taxonomic validity of *Metazalmoxis* in particular, new material was examined from research expeditions to New Caledonia (made by Jerome Murienne and P.P.S. from April to May, 2007) and Australia (made by Ronald M. Clouse and P.P.S. from April to May, 2011). Type material of eight described *Zalmoxis* was examined for comparative purposes; these specimens are listed below. In this study, six new species of *Zalmoxis* are described from the research expeditions, four from New Caledonia and two from Australia. All species described were examined using scanning electron microscopy. I additionally illustrate the genitalia of *Zalmoxis darwinensis* Goodnight & Goodnight, 1948 based on material from recent collections. Finally, these and other Paleotropical Zalmoxidae were sequenced for six molecular loci in order to determine their phylogenetic relationships. One of the aims was to test the systematic validity of the genus *Metazalmoxis*. As one of the New Caledonian *Zalmoxis* described here bears four tarsomeres in the first walking leg, and another species, five tarsomeres in the fourth walking leg (the conditions occurring in *Metazalmoxis*), the validity of these characters as justification for separating the two Paleotropical genera was scrutinized.

Material and methods

Abbreviations. Examined specimens are lodged in the following repository institutions:

MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA (USA).
AMNH	American Museum of Natural History, New York, NY (USA)
MNHN	Muséum National d'Histoire naturelle, Paris (France)
QM	Queensland Museum, Brisbane (Australia)
MAGNT	Museum and Art Galleries of the Northern Territory, Darwin (Australia)
WAM	Western Australian Museum, Perth (Australia)

Taxonomy. The holotype and a female paratype were photographed in dorsal and ventral positions using a JVC KY-F70B digital camera mounted on a Leica MZ 12.5 stereomicroscope. A series of images (from 5 to 15) was taken at different focal planes and assembled with the dedicated software package Auto-Montage Pro Version 5.00.0271 by Syncroscopy. Additional specimens were examined with a Zeiss EVO 50 scanning electron microscope (SEM). The genitalia of one to two males were dissected out and also examined with the Zeiss EVO 50 SEM. Specimens used for DNA extraction are indicated as such among the type material. All measurements are given in mm unless otherwise indicated.

The following type material (much of which has been illustrated recently in Sharma *et al.* 2011) has been examined for comparison:

Zalmoxis marchei Roewer, 1912: male holotype and 5 male paratypes (MNHN) from Mariana Islands (specific locality unspecified).

Zalmoxis neocaledonicus Roewer, 1912: male holotype (MNHN) from Noumea, New Caledonia.

Zalmoxis mitobatipes (Roewer, 1926): 1 male and 3 female paratypes (MCZ) from Mt. Makeling, Philippine Islands [Mt. Makiling, Los Baños, Luzon, Philippines], collected by Baker.

Zalmoxis jewetti (Goodnight & Goodnight, 1947): male holotype (AMNH) from Mt. Dafansero, Cyclops Mountains, New Guinea, 4700 ft (1432 m) elevation, collected 22 April 1945 by G.G. Jewett.

Zalmoxis remingtoni (Goodnight & Goodnight, 1948): male holotype (AMNH) from seven miles (11.2 km) south of La Foa, New Caledonia, collected 11 March 1945 by C.L. Remington.

Zalmoxis darwinensis (Goodnight & Goodnight, 1948): male holotype (AMNH) from Darwin, Australia, collected 9–13 February 1945 by Borys Malkin.

Zalmoxis tuberculatus Goodnight & Goodnight, 1948: male holotype (AMNH) from La Foa, New Caledonia, collected 11 March 1945 by C.L. Remington; 2 male and 1 juvenile paratypes (AMNH) from La Foa, New Caledonia, collected 31 March 1945 by C.L. Remington; 1 female paratype (AMNH) from La Foa, New Caledonia, collected 7 March 1945 by C.L. Remington.

TABLE 1. List of species and gene fragments included in phylogenetic analysis, with voucher numbers, GenBank accession numbers, and collecting localities.

	Voucher #	18S rRNA	28S rRNA	COI	CytB	H3	H4
Fisiphallius chicoi Tourinho and Pérez González, 2006	MCZ DNA101551	GQ912750	GQ912832.2	JN885759		GQ912939	FR850196
Fisiphallius sp.	MCZ DNA104055-1	JF786508	JF786579			JF786367	FR850212
Fisiphallius sp.	MCZ DNA104057	JF786509	JF786592			JF786368	
Ethobunus zalmoxiformis (Roewer, 1949)	MCZ DNA101424	FJ796478	FJ796490.2	FJ796494		FJ796501	FJ475953
Pirassunungoleptes calcaratus H. Soares, 1966	MCZ DNA101114	GQ912753	GQ912834/5	GQ912897		GQ912941	HE605012
Zalmoxis cardwellensis Forster, 1955	MCZ DNA103199	JN885754	JN885733	JN885770		JN885788	HE605023
Zalmoxis cardwellensis Forster, 1955	MCZ DNA106308	JN885755	JN885734	JN885769			
Zalmoxis cuspanalis Roewer, 1927	MCZ DNA106192-1	JN885740	JN885722	JN885765	JN885778		HE605019
Zalmoxis cf. *dammermani*	MCZ DNA102500	JN885742	JN885738	JN885773		JN885790	HE605028
Zalmoxis darwinensis Goodnight & Goodnight, 1948	MCZ DNA106321	JN885751	JN885730	JN885768			HE605022
Zalmoxis falcifer **sp. nov.**	MCZ DNA105836	JN885750	JN885729	JN885771		JN885789	HE605024
Zalmoxis furcifer **sp. nov.**	MCZ DNA106311	JN885756	JN885735				HE605025
Zalmoxis furcifer **sp. nov.**	MCZ DNA106316	JN885757	JN885736				HE605026
Zalmoxis furcifer **sp. nov.**	MCZ DNA106318	JN885758	JN885737	JN885772			HE605027
Zalmoxis cf. *insularis*	MCZ DNA103581	JN885745	JN885725	JN885760	JN885776	JN885781	HE605013
Zalmoxis kaktinsae **sp. nov.**	MCZ DNA102350	JN885749	JN885728	JN885761		JN885783	HE605015
Zalmoxis mendax **sp. nov.**	MCZ DNA102246	JN885747	JN885739			JN885782	HE605014
Zalmoxis mitobatipes (Roewer, 1926)	MCZ DNA106196-2	JN885741	JN885721	JN885764			HE605018
Zalmoxis cf. *neocaledonicus*	MCZ DNA100914	GQ912754	GQ912836.2	GQ912898	JF786382	GQ912942	FR850245
Zalmoxis perditus **sp. nov.**	MCZ DNA102356	JN885748	JN885727	JN885762		JN885784	HE605016
Zalmoxis princeps **sp. nov.**	MCZ DNA102358	JN885746	JN885726	JN885763	JN885777	JN885785	HE605017
Zalmoxis pygmaeus Sørensen, 1886	MCZ DNA103579	JN885753	JN885732	JN885767		JN885787	HE605021
Zalmoxis cf. *robustus*	MCZ DNA103580	JN885752	JN885731	JN885766		JN885786	HE605020
Zalmoxis sp.	MCZ DNA102487	JN885743	JN885723	JN885774	JN885779	JN885791	HE605029
Zalmoxis sp.	MCZ DNA102528	JN885744	JN885724	JN885775	JN885780	JN885792	HE605030

continued next page

TABLE 1. (continued)

	Locality	Coordinates	Collector
Fisiphallius chicoi Tourinho and Pérez González, 2006	São José community, Gurupá municipality, Pará, Brazil	1.197ºS, 51.783ºW	C. A. Rheims, F. Rego
Fisiphallius sp.	Santuario de fauna y flora Iguaque, Boyaca, Colombia	5º42'36"S, 73º27'50"W	L.R. Benavides, Campos, C. Flórez, G.
Fisiphallius sp.	Santuario de fauna y flora Iguaque, Boyaca, Colombia	5º42'36"S, 73º27'50"W	L.R. Benavides, Campos, C. Flórez, G.
Ethobunus zalmoxiformis (Roewer, 1949)	Volcán Poás, Costa Rica	n/a	A. Pérez-González
Pirassunungoleptes calcaratus H. Soares, 1966	Cachoeira do Saltão, Brotas, Estado do São Paulo, Brazil	22º23'35"S, 47º53'11"W	L.E. Acosta
Zalmoxis cardwellensis Forster, 1955	Paluma Range N.P., Queensland, Australia	19º0'39.2"S, 146º12'19.9"E	n/a
Zalmoxis cardwellensis Forster, 1955	Paluma Range N.P., Queensland, Australia	19º0'15.7"S, 146º24'9.2"E	R.M. Clouse, P.P. Sharma
Zalmoxis cuspanalis Roewer, 1927	Mount Makiling, Los Baños, Luzon, Philippines	14º07'49.5"N, 121º12'36.0"E	P.A.C. Buenavente et al.
Zalmoxis cf. *dammermani*	Gunung Gede-Pangrango N.P., Jawa Barat, Indonesia	06º44'46"S, 106º59'48"E	R.M. Clouse, C. Rahmadi, G. Giribet
Zalmoxis darwinensis Goodnight & Goodnight, 1948	Howard Springs Reserve, N.T., Australia	12º27'27.6"S, 131º03'3.9"E	R.M. Clouse, P.P. Sharma
Zalmoxis falcifer **sp. nov.**	Bonaparte Archipelago, W.A., Australia	14°31'5.1"S, 124°55'38.7"E	M.S. Harvey
Zalmoxis furcifer **sp. nov.**	Daintree N.P., Emmagen Creek, Queensland, Australia	16°03'40.9"S, 145°27'42.2"E	R.M. Clouse, P.P. Sharma
Zalmoxis furcifer **sp. nov.**	Barron Gorge N.P., Crystal Cascades trail, Queensland,	16°57'50.6"S, 145°40'45.2"E	R.M. Clouse, P.P. Sharma
Zalmoxis furcifer **sp. nov.**	Russell River N.P., Graham Range, Queensland, Australia	17°17'30.3"S, 145°57'36.7"E	R.M. Clouse, P.P. Sharma
Zalmoxis cf. *insularis*	Colo-I-Suva, Viti Levu, Fiji	18º03'35.1"S, 178º28'14.0"E	J. Murienne, P.P. Sharma
Zalmoxis kaktinsae **sp. nov.**	Mont Mou, Province Sud, New Caledonia	22°3'36.5"S, 166°20'56.2"E	J. Murienne, P.P. Sharma
Zalmoxis mendax **sp. nov.**	Mt. Panie track, Province Nord, New Caledonia	20°33'S, 164°47'E	Bouchard, Burwell, G.B. Monteith
Zalmoxis mitobatipes (Roewer, 1926)	Cabangaan Silang Cavite, Luzon, Philippines	14º10'29.1"N, 125º01'0.5"E	P.A.C. Buenavente et al.
Zalmoxis cf. *neocaledonicus*	Ningua Res. Camp, Province Sud, New Caledonia	n/a	G.B. Monteith
Zalmoxis perditus **sp. nov.**	Baie d'Upi, Isle of Pines, Province Sud, New Caledonia	22°35'21.0"S, 167°31'20.1"E	J. Murienne, P.P. Sharma
Zalmoxis princeps **sp. nov.**	Port Boisé Bay, Province Sud, New Caledonia	22°20'31.3"S, 166°57'33.3"E	J. Murienne, P.P. Sharma
Zalmoxis pygmaeus Sørensen, 1886	Savura Park, Viti Levu, Fiji	18º04'15.0"S, 178º26'39.9"E	J. Murienne, P.P. Sharma
Zalmoxis cf. *robustus*	Serea, Viti Levu, Fiji	17º51'2.4"S, 178º17'47.1"E	J. Murienne, P.P. Sharma
Zalmoxis sp.	Bukit Linggua, near Doloduo, north Sulawesi, Indonesia	00º34'31"N, 123º53'42"E	R.M. Clouse, C. Rahmadi, G. Giribet
Zalmoxis sp.	Madang, Bitabag Reserve, Papua New Guinea	05º08'19.3"S, 145º46'28.2"E	R.M. Clouse, Ulai, Nataniel

Zalmoxis cardwellensis Forster, 1955: 3 male and 1 female paratypes (MCZ) from 40 miles (64 km) south of Mackay, Queensland, Australia, collected 21 November 1957 by P.J. Darlington; 1 male paratype (MCZ) from 40 miles (64 km) south of Mackay, Queensland, Australia, collected 21 November 1957 by P.J. Darlington; 1 male paratype (MCZ) from Lockerby, N. Cape York, Queensland, Australia, collected January 1958 by P.J. Darlington; 1 male paratype (MCZ) from 5 miles (8 km) west of Ravenshoe, Atherton Tableland, collected 20 February 1958 by P.J. Darlington.

Molecular methods. Specimens of *Zalmoxis* were collected by several individuals (mainly by Ronald M. Clouse in New Guinea, by Ronald M. Clouse and Gonzalo Giribet in Sulawesi, and by P.P.S. over three collecting expeditions in the Southwest Pacific during 2007–2011). Outgroup taxa consisted of two Neotropical exemplars of Zalmoxidae and three exemplars of Fissiphalliidae, the sister family of Zalmoxidae (Giribet *et al.* 2010, Sharma & Giribet, 2011). All specimens included in the study and their locality data are given in Table 1.

Total DNA was extracted from the legs of animals using Qiagen's DNEasy tissue kit (Valencia, CA, USA). Purified genomic DNA was used as a template for PCR amplification. Molecular markers consisted of two nuclear ribosomal genes (complete 18S rRNA and a ca. 3200-bp fragment of 28S rRNA), two nuclear protein-encoding genes (histone H3, and histone H4), and two mitochondrial protein-encoding genes (cytochrome *c* oxidase subunit I and cytochrome *b*). Primer sequences employed and fragment lengths are described in Sharma & Giribet (2011).

Polymerase chain reactions (PCR), visualization by agarose gel electrophoresis, and direct sequencing were conducted as described in Sharma & Giribet (2009a). Chromatograms obtained from the automatic sequencer were read and sequences assembled using the sequence editing software Sequencher (Gene Codes Corporation, Ann Arbor, MI, USA). Sequence data were edited in Se-Al v. 2.0a11 (Rambaut 1996).

Phylogenetic analyses. Maximum likelihood (ML) analysis was conducted on static alignments, which were inferred as follows. Sequences of ribosomal genes were aligned using MUSCLE v. 3.6 (Edgar 2004) with default parameters, and subsequently treated with GBlocks v. 0.91b (Castresana 2000) to cull positions of ambiguous homology. Sequences of protein-encoding genes were not length variable; treatment with GBlocks v. 0.91b had no effect on alignment length, but alignments were confirmed nevertheless using protein sequence translations. The size of data matrices for each gene subsequent to treatment with GBlocks v. 0.91b is provided in Table 2.

TABLE 2. Length of gene partition alignment prior and subsequent to treatment with GBlocks v. 0.91b.

Partitions	Original length of alignment (bp)	Fraction retained by GBlocks (%)	Final length of alignment (bp)
18S rRNA	1758	99	1755
28S rRNA	3237	98	3157
COI	751	100	751
CytB	421	100	421
H3	327	100	327
H4	160	100	160

ML analysis was conducted using RAxML v. 7.2.7 (Stamatakis 2006) on 12 CPUs of a cluster at Harvard University, FAS Research Computing (odyssey.fas.harvard.edu). For the maximum likelihood searches, a unique GTR model of sequence evolution with corrections for a discrete gamma distribution (GTR + G) was specified for each data partition, and 250 independent searches were conducted. Nodal support was estimated via the rapid bootstrap algorithm (1000 replicates) using the GTR-CAT model (Stamatakis *et al.* 2008).

Taxonomy

Order Opiliones Sundevall, 1833

Suborder Laniatores Thorell, 1876

Infraorder Grassatores Kury in Giribet *et al.*, 2002

Family Zalmoxidae Sørensen, 1886

Type genus. *Zalmoxis* Sørensen, 1886; type species *Zalmoxis robustus* Sørensen, 1886, by subsequent designation: Roewer (1949: 20).

Zalmoxis princeps sp. nov.

Figs. 1–4

Types. Male holotype (MNHN [ex MCZ DNA102358]) from Port Boisé Bay (22° 20' 31.3" S, 166° 57' 33.3" E), New Caledonia, 1 m elevation, collected 29 April 2007 by J. Murienne and P.P. Sharma from sifted litter. 5 male (2 used for DNA extraction [ex MCZ DNA102358], dissected for genitalia, and mounted on SEM stub MCZ 124546; 1 mounted on SEM stubs MCZ 124547–124548; 2 in ethanol) and 4 female (4 in ethanol; 1 used for DNA extraction and leg IV mounted on SEM stub MCZ 124547) paratypes (MCZ 124549 [ex MCZ DNA102358]), same collecting data as holotype. 1 female paratype (used for DNA extraction [ex MCZ DNA102354]) from Pic du Grand Kaori (22° 16' 47.2" S, 167° 53' 41.1" E), New Caledonia, 237 m elevation, collected 17 April 2007 by J. Murienne and P.P. Sharma from sifted litter (MCZ 124550). One male paratype (used for DNA extraction [ex MCZ DNA102355]) from Forêt Nord (Kwa Neie) (22° 19' 22.5" S, 166° 54' 54.2" E), New Caledonia, 197 m elevation, collected 17 April 2007 by J. Murienne and P.P. Sharma from sifted litter (MCZ 124551).

Additional material studied. 6 juveniles, same collecting data as holotype. 1 juvenile (used for DNA extraction) from Pic du Grand Kaori (22° 16' 46.6" S, 167° 49' 40.5" E), New Caledonia, 254 m elevation, collected 17 April 2007 by J. Murienne and P.P. Sharma from sifted litter (MCZ DNA102353). 1 juvenile from Port Boisé Bay (22° 20' 26.0" S, 166° 57' 32.1" E), New Caledonia, 2 m elevation, collected 29 April 2007 by J. Murienne and P.P. Sharma from sifted litter. 1 female and 3 juveniles from Port Boisé Bay (22° 20' 31.3" S, 166° 57' 33.3" E), New Caledonia, 10 m elevation, collected 29 April 2007 by J. Murienne and P.P. Sharma from sifted litter.

Etymology. The specific epithet, an invariable noun in apposition, refers to the embellished armature of the legs and opisthosomal sternites in males of this species. From Latin, "*princeps, principis*" meaning "first, chief, sovereign".

Diagnosis. Distinguished from congeners by embellished armature of male leg IV, particularly spiny tubercles on femur and tibia; sternite 7 armed with two enlarged tubercles; anal plate armed with seven enlarged tubercles, three of these massive; rutrum with long lateral extensions; and flattened pergula with eight setae.

Description. Total length of male holotype (female paratype [MCZ 124549] in parentheses) 3.18 (2.46), greatest width of prosoma 1.05 (1.04), greatest width of opisthosoma 2.26 (1.74); length-to-width ratio 1.41 (1.41). Body campaniform, dark orange to brown (in alcohol, depending on incidence of light), almost entirely with dense microgranulate surface microstructure (sensu Murphree 1988). Eyes present on low, well-developed ocularium. Ocularium wider than long, removed from anterior margin of carapace, without spines or tubercles. Anterior margin of carapace with two pairs of pegs above coxae of leg I and single median peg. Scutal grooves of mesotergum distinctly "V" shaped. Free tergites with regular belts of setose tubercles (Fig. 1).

Ventral prosomal complex of male with coxae II and III meeting in midline, coxae I and IV not so. Anterior and posterior margins of coxae III with tubercular bridges to adjacent coxae, and coxae I–III with setose tubercles. Coxae IV of male greatly enlarged, with setose tubercles concentrated on anterior margin. Genital operculum subtriangular. Spiracles not concealed, anterior to row of tubercles. Opisthosomal sternites 3–6 and 8 with regular belts of setose tubercles, with tubercles enlarging laterally. Sternite 7 with two enlarged tubercles flanking the midline. Anal plate armed with nine tubercles: three greatly enlarged setose tubercles on transverse midline of segment, with two smaller pairs of setose tubercles flanking longitudinal midline, arranged anterior and posterior to greatly enlarged tubercles, and one small anterior-most pair (Fig. 2).

Chelicerae (Fig. 3a) sexually monomorphic, with prominent bulla on proximal article. Proximal article with denticulate granulation basally and ventrally. Second article not incrassate, free of ornamentation, with dorsal margin bearing several setae. Distal article with delicate dentition, free of ornamentation. Palpi (Fig. 3b) robust and spined ventrally and/or ventrolaterally, typical of zalmoxids. Palpal tarsus with two pairs of megaspines.

FIGURE 1. *Zalmoxis princeps* **sp. nov.** (a) Male holotype, dorsal view; (b) Male holotype, ventral view; (c) Female paratype, dorsal view; (d) Female paratype, ventral view.

Legs (I–IV; Fig. 3c–g) finely granulated. Trochanter, patella, and tibia of all legs bearing irregular rows of setose tubercles. Leg I (Fig. 3c) femur with ventral row of small tubercles. Male leg IV (Fig. 3f) sexually dimorphic, incrassate, elongated, and heavily armored. Male trochanter IV and patella IV each bearing a large ventral tubercle. Male femur IV bearing dorsal and ventral rows of prominent tubercles, with ventral row enlarging distally. Male patella IV with a row of dorsal tubercles. Male tibia IV with one dorsal, one ventral, two mesal, and two ectal rows of tubercles enlarging distally. Calcaneus of male metatarsus IV with a ventral pair of distally-directed, hook-like tubercles. Metatarsi I–IV divided distally, with calcaneus less ornamented but generally more setose. Tarsal claws I–IV smooth, unmodified. Tarsal segmentation 3: 6: 5: 6 (Fig. 3).

Appendage measurements of holotype (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.20/0.17	0.75/0.16	0.40/0.17	0.53/0.15	0.74/0.15	0.55/0.09	3.17
Leg II	0.30/0.22	1.07/0.15	0.57/0.20	0.94/0.16	1.20/0.07	1.30/0.07	5.38
Leg III	0.26/0.33	0.87/0.18	0.41/0.27	0.72/0.19	1.03/0.12	0.75/0.08	4.04
Leg IV	0.50/0.40	1.80/0.40	0.86/0.45	1.34/0.32	1.30/0.15	0.87/0.11	6.67
Palp	0.27/0.24	0.58/0.24	0.35/0.24	0.53/0.28	—	0.50/0.16	2.23
	Proximal	Second	Distal				
Chelicera	0.39/0.21	0.45/0.26	0.30/0.05				

Appendage measurements of female paratype (MCZ 124549) (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.20/0.17	0.70/0.13	0.35/0.16	0.49/0.15	0.74/0.07	0.59/0.08	3.07
Leg II	0.26/0.19	1.00/0.15	0.50/0.16	0.83/0.16	1.20/0.07	1.07/0.08	4.86
Leg III	0.24/0.25	0.87/0.16	0.38/0.23	0.64/0.16	0.91/0.09	0.65/0.10	3.69
Leg IV	0.34/0.23	1.05/0.18	0.64/0.25	0.94/0.18	1.21/0.10	0.76/0.10	4.94
Palp	0.24/0.24	0.64/0.24	0.32/0.21	0.55/0.25	—	0.47/0.16	2.22
	Proximal	Second	Distal				
Chelicera	0.54/0.31	0.80/0.27	0.21/0.03				

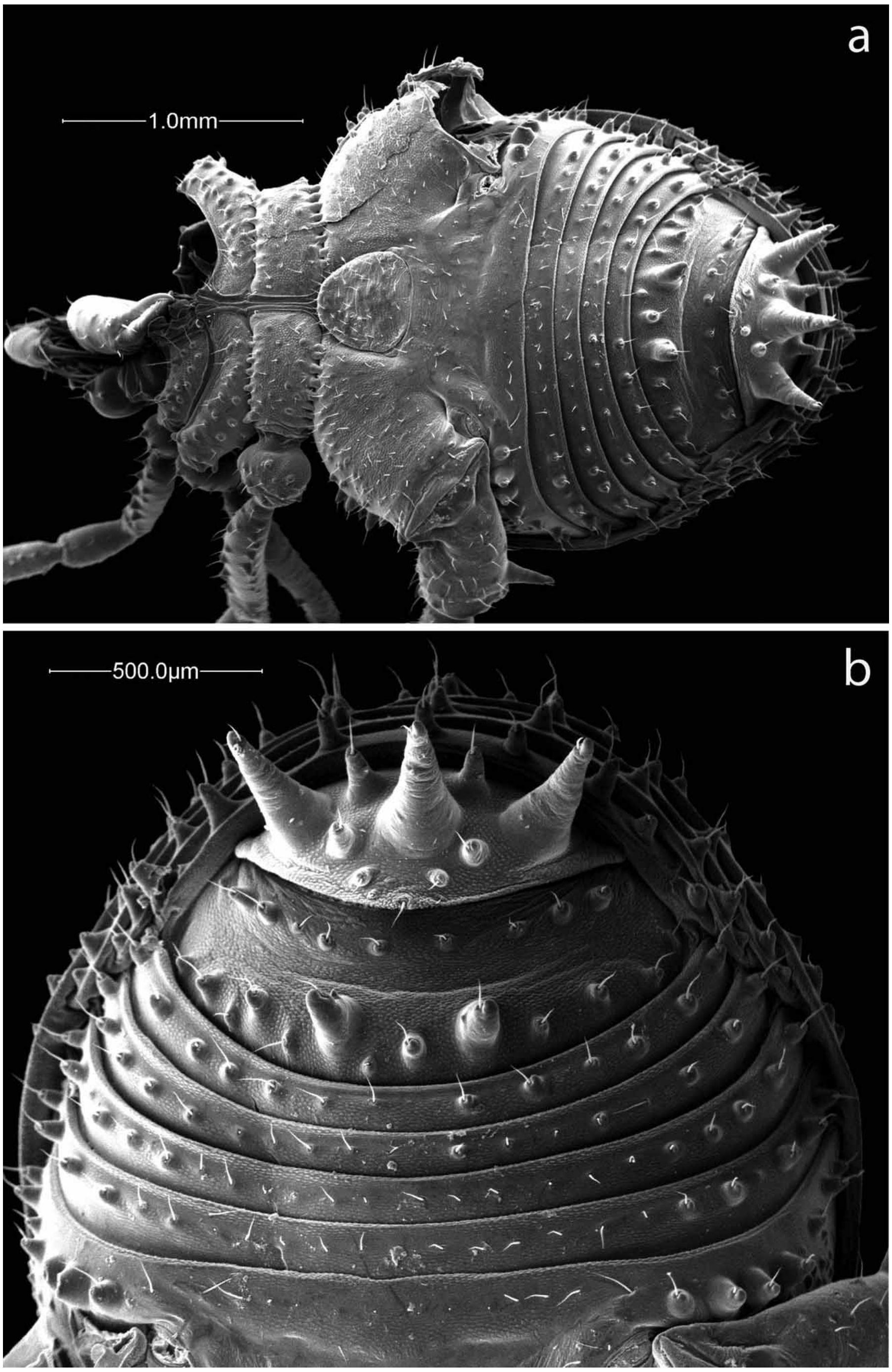

FIGURE 2. *Zalmoxis princeps* **sp. nov.** (a) Ventral view of male paratype; (b) Opisthosomal region of male paratype.

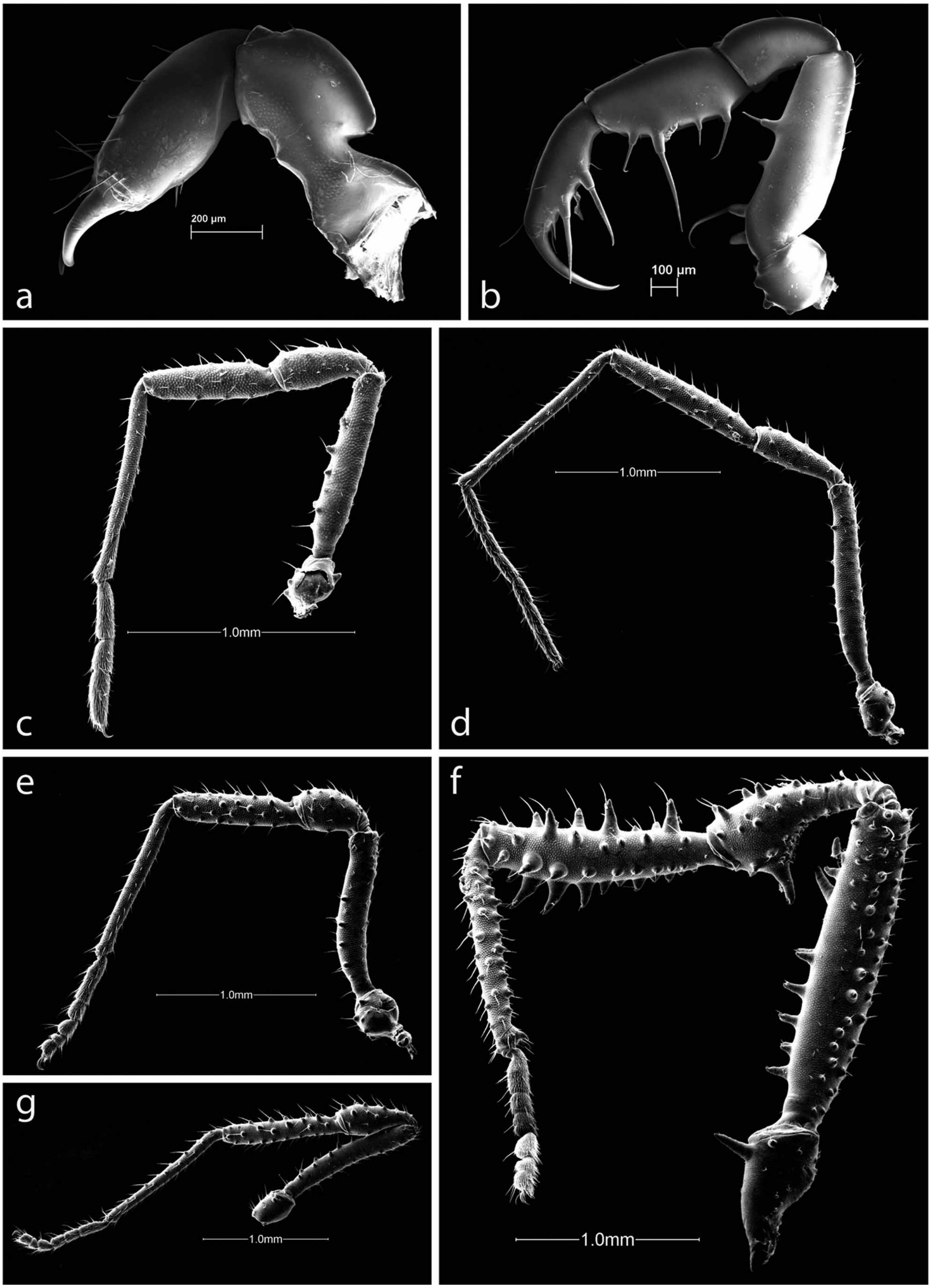

FIGURE 3. *Zalmoxis princeps* **sp. nov.** (a) Left chelicera of male paratype; (b) Left palp of male paratype; (c) Male left leg I; (d) Male left leg II; (e) Male left leg III; (f) Male left leg IV; (g) Female left leg IV.

FIGURE 4. *Zalmoxis princeps* **sp. nov.** (a) Pars distalis of male genitalia, dorsal view; (b) Pars distalis of male genitalia, ventral view.

Penis (Fig. 4) with two pairs of setae on rutrum and eight setae on pergula (one median pair, and two trios displaced laterally from midline). One pair of setae displaced from midline and posterior to pergula. Rutrum with long lateral extensions. Pergula flattened, not projecting ventrally.

Distribution. Known from three formerly contiguous forests in the southern province of New Caledonia: Pic du Grand Kaori, Forêt Nord, and Port Boisé.

Zalmoxis mendax sp. nov.

Figs. 5–8

Types. Male holotype (MNHN [ex MCZ DNA102246]) from Mt. Panie track (20° 33' S, 164° 47' E), New Caledonia, collected 18 November 2000 by Bouchard, Burwell, and G.B. Monteith. 6 male (2 in ethanol; 2 extracted for DNA, dissected for genitalia, and mounted on SEM stubs MCZ 124553–124554; 2 mounted on SEM stubs MCZ 124556–124561) and 6 female (6 in ethanol; one with leg IV mounted on SEM stub MCZ 124555) paratypes, same collecting locality as holotype (MCZ 124552).

Additional material studied. 18 females and 1 juvenile, same collecting data as holotype (MCZ).

Etymology. The specific epithet, an invariable noun in apposition, refers to the condition of the first walking leg, which bears four tarsomeres—a condition that occurs in a genus of questionable validity, *Metazalmoxis* (discussed below). From Latin, "*mendax*, *mendacis*" meaning "liar".

Diagnosis. Distinguished from congeners by its large size; unique tarsal formula (4: 7: 5: 6); stout male leg IV bearing armature only as a ventral row of tubercles enlarging distally on the femur; rounded rutrum bearing two pairs of setae; and small pergula with two pairs of ventral setae and one pair of large dorsolateral setae.

Description. Total length of male holotype (female paratype [MCZ 124552] in parentheses) 3.43 (3.28), greatest width of prosoma 1.44 (1.32), greatest width of opisthosoma 2.40 (2.24); length-to-width ratio 1.43 (1.46). Body campaniform, dark brown (in alcohol, depending on incidence of light), almost entirely with dense microgranulate surface microstructure. Eyes present on low, well-developed ocularium. Ocularium wider than long, removed from anterior margin of carapace, with low irregular tubercles. Anterior margin of carapace with two pairs of pegs above coxae of leg I and single median peg. Scutal grooves of mesotergum distinct, sinuous, and losing curvature posteriorly (not "V"-shaped). Mesotergum and free tergites with regular belts of setose tubercles (Fig. 5).

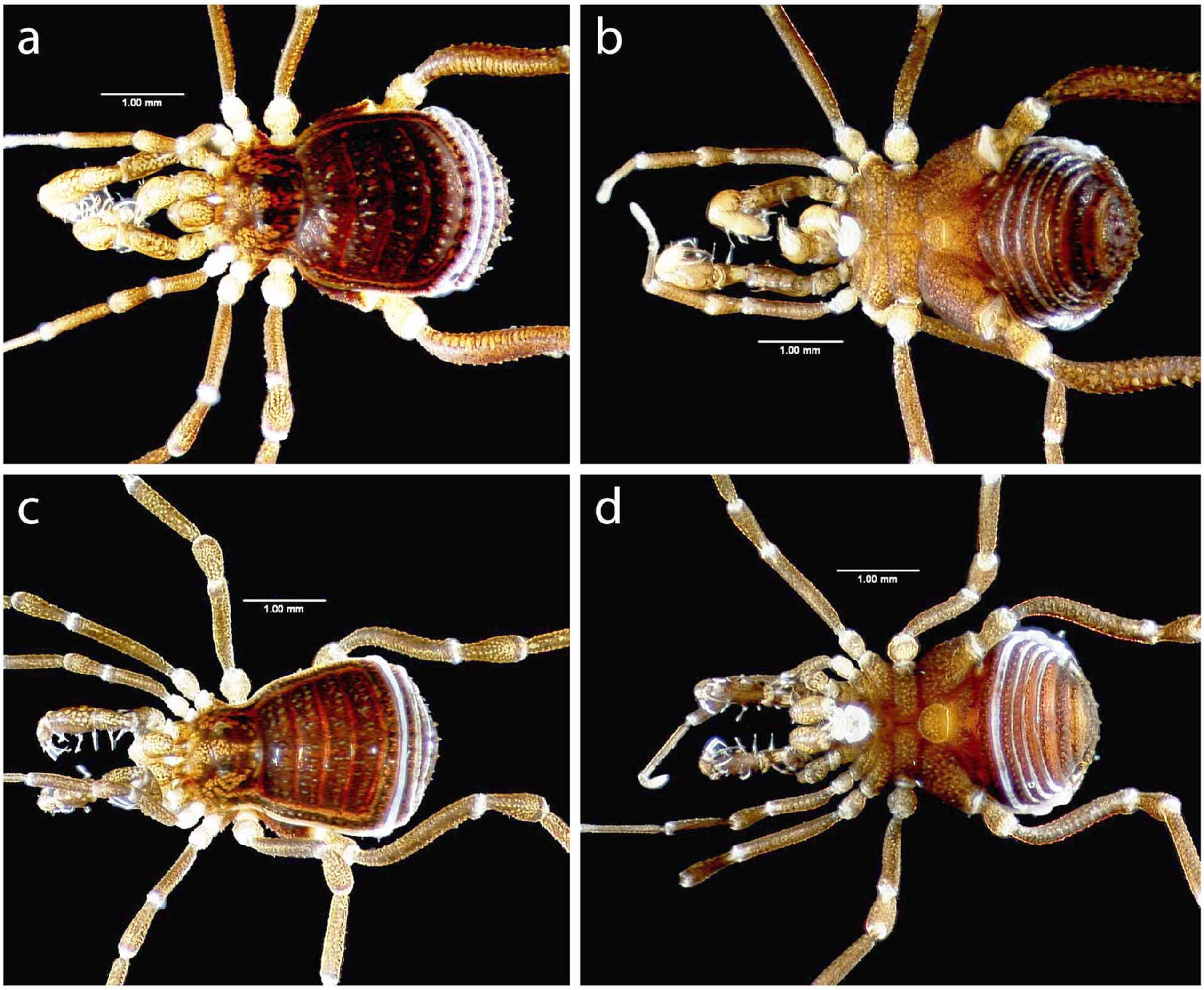

FIGURE 5. *Zalmoxis mendax* **sp. nov.** (a) Male holotype, dorsal view; (b) Male holotype, ventral view; (c) Female paratype, dorsal view; (d) Female paratype, ventral view.

Ventral prosomal complex of male with coxae II and III meeting in midline, coxae I and IV not so (Fig. 6a). Anterior and posterior margins of coxae III with tubercular bridges to adjacent coxae, and coxae I–IV with low setose tubercles. Coxae IV of male greatly enlarged, with setose tubercles uniformly distributed. Genital operculum sub-triangular. Spiracles not concealed, anterior to row of tubercles. Opisthosomal sternites with regular belts of low setose tubercles. Anal plate armed with three tubercles slightly larger than others (Fig. 6a).

Chelicerae (Fig. 6b) sexually monomorphic, with prominent bulla on proximal article. Proximal article with denticulate granulation basally and ventrally. Second article not incrassate, free of ornamentation, with dorsal margin bearing several setae. Distal article with delicate dentition, free of ornamentation. Palpi (Fig. 6c) robust and spined ventrally and/or ventrolaterally, typical of zalmoxids. Palpal tarsus with two pairs of megaspines.

Legs (I–IV; Fig. 7) finely granulated. Leg I trochanter with two ventral tubercles, femur with ventral row of small tubercles (Fig. 7a). Leg IV sexually dimorphic, male leg IV incrassate, elongated, and lightly armored (Fig. 7d). Male femur IV bearing ventral row of prominent tubercles enlarging distally. Male patella IV with a row of dorsal tubercles. Male tibia IV with one dorsal, one ventral, two mesal, and two ectal rows of tubercles enlarging distally. Calcaneus of male metatarsus IV with a ventral pair of distally-directed, hook-like tubercles. Metatarsi I–IV divided distally, with calcaneus less ornamented but generally more setose. Tarsal claws I–IV smooth, unmodified. Tarsal segmentation 4: 7: 5: 6 (Fig. 7).

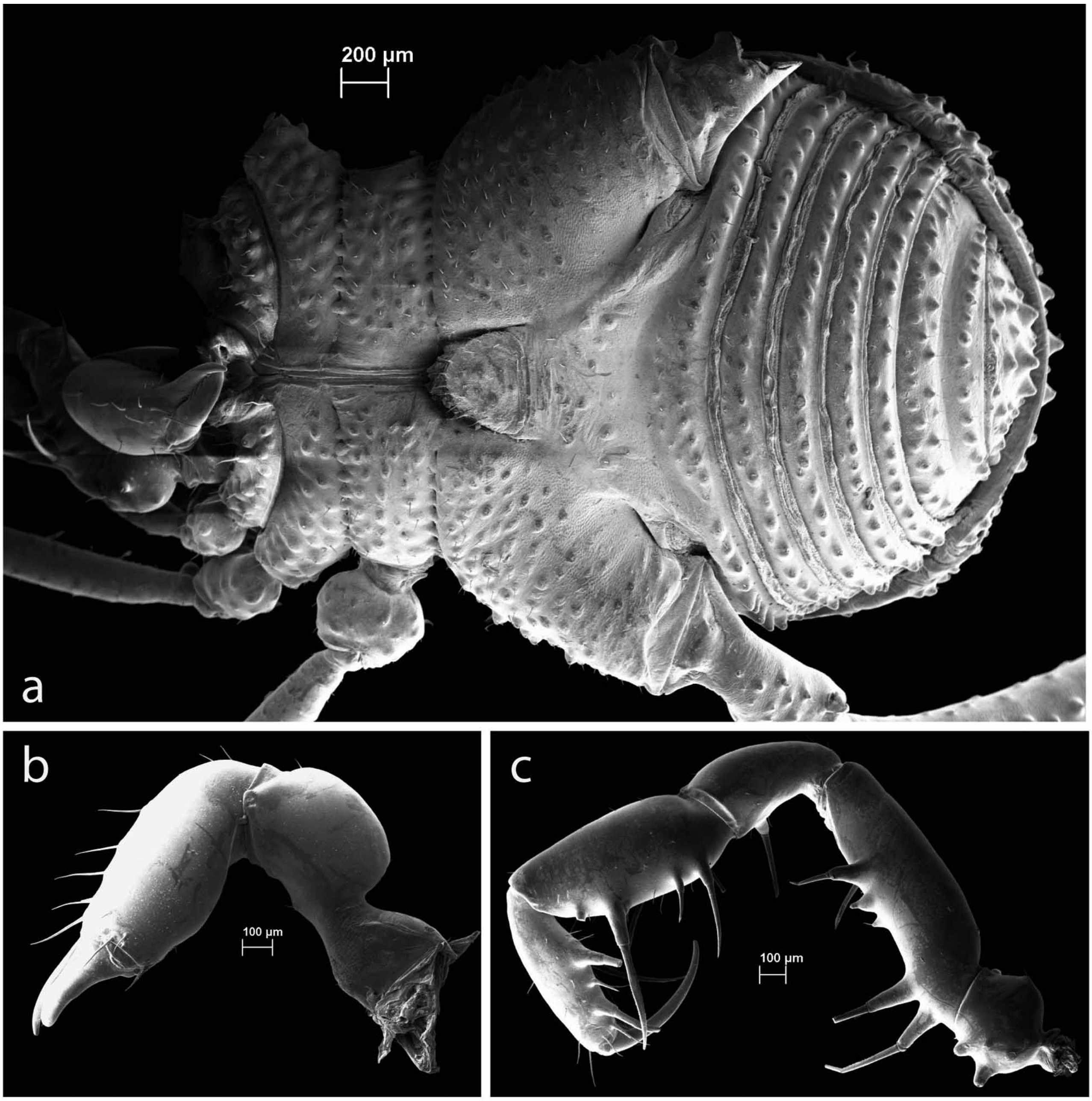

FIGURE 6. *Zalmoxis mendax* **sp. nov.** (a) Ventral view of male paratype; (b) Left chelicera of male paratype; (c) Left palp of male paratype.

Appendage measurements of holotype (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.29/0.24	1.29/0.16	0.55/0.23	0.84/0.16	1.44/0.07	0.80/0.10	5.21
Leg II	0.43/0.24	2.14/0.24	0.84/0.25	1.76/0.19	2.18/0.08	1.64/0.10	8.99
Leg III	0.42/0.43	1.62/0.24	0.65/0.34	1.22/0.25	1.92/0.13	1.04/0.11	6.87
Leg IV	0.60/0.42	2.66/0.40	1.28/0.50	2.04/0.36	2.38/0.28	1.18/0.13	10.14
Palp	0.27/0.33	0.92/0.28	0.45/0.29	0.69/0.37	—	0.73/0.20	3.06
	Proximal	Second	Distal				
Chelicera	0.63/0.35	1.02/0.31	0.43/0.09				

Appendage measurements of female paratype (MCZ 124552) (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.26/0.23	1.09/0.16	0.50/0.20	0.78/0.16	1.24/0.06	0.75/0.11	4.62
Leg II	0.29/0.25	1.80/0.20	0.75/0.24	1.54/0.17	1.80/0.09	1.68/0.08	7.86
Leg III	0.36/0.36	1.50/0.20	0.60/0.30	1.10/0.21	1.70/0.12	0.93/0.10	6.19
Leg IV	0.52/0.30	2.00/0.22	0.74/0.32	1.60/0.24	2.13/0.14	1.26/0.11	8.25
Palp	0.25/0.30	0.85/0.27	0.49/0.25	0.63/0.34	—	0.64/0.19	2.86
	Proximal	Second	Distal				
Chelicera	0.63/0.35	1.02/0.31	0.43/0.09				

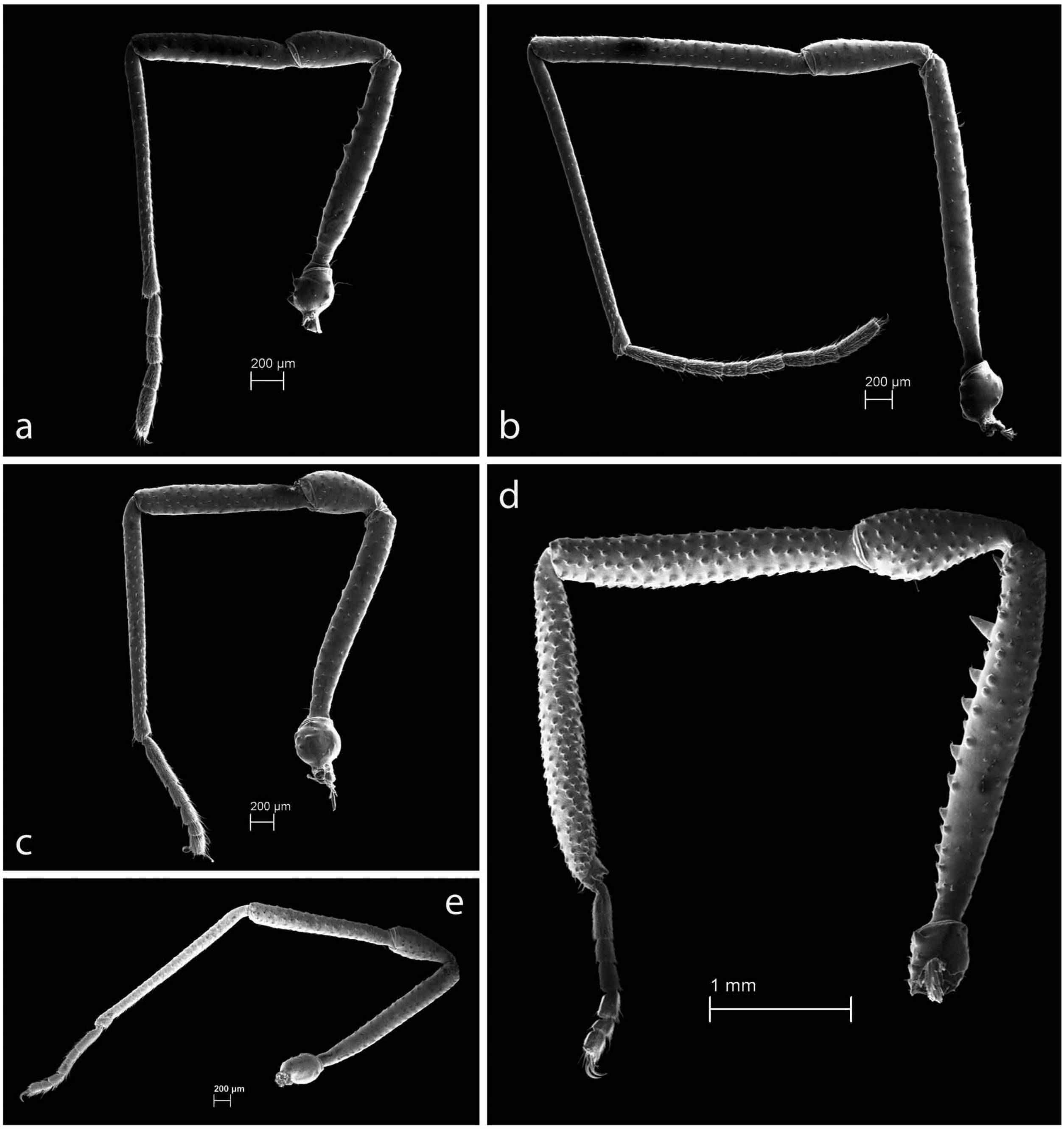

FIGURE 7. *Zalmoxis mendax* **sp. nov.** (a) Male left leg I; (b) Male left leg II; (c) Male left leg III; (d) Male left leg IV; (e) Female left leg IV.

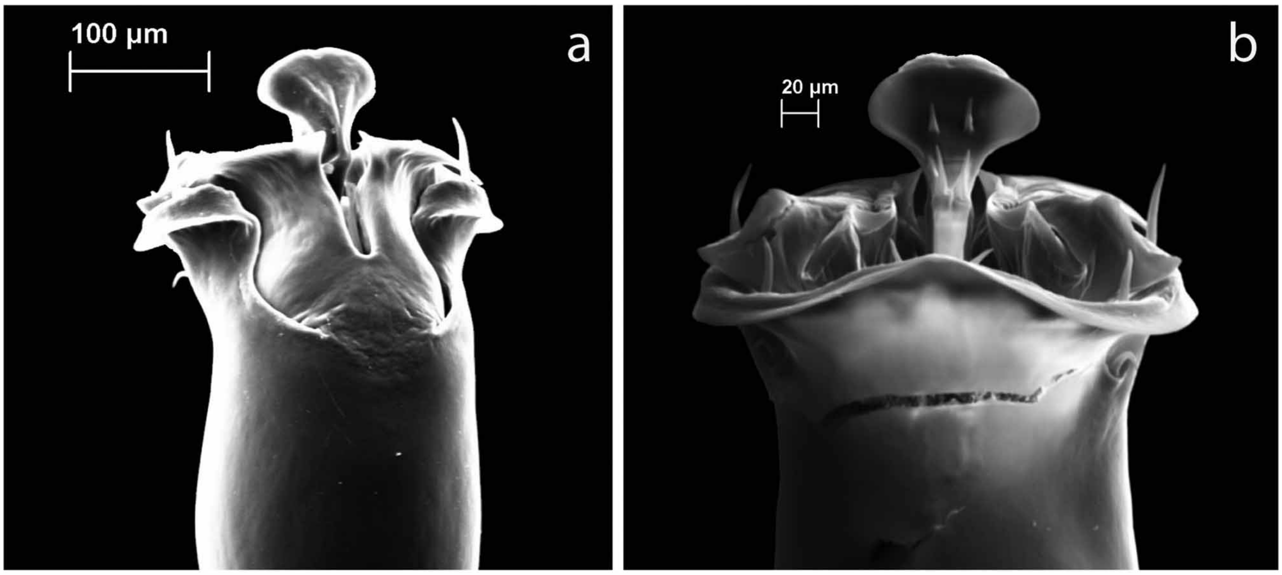

FIGURE 8. *Zalmoxis mendax* **sp. nov.** (a) Pars distalis of male genitalia, dorsal view; (b) Pars distalis of male genitalia, ventral view.

Penis (Fig. 8) with two pairs of setae on rutrum and three pairs setae on pergula (one median, one ventrolateral, and one dorsolateral). One pair of setae displaced from midline and posterior to pergula. Rutrum small with rounded edges, wider than long, without lateral arrowhead-like extensions. Pergula slightly projecting ventrally.

Distribution. Known only from type locality.

Zalmoxis kaktinsae sp. nov.

Figs. 9–11

Types. Male holotype (MNHN [ex MCZ DNA102350]) from Mt. Mou, summit (22° 3' 36.5" S, 166° 20' 56.2" E), New Caledonia, 1227 m elevation, collected 12 April 2007 by J. Murienne and P.P. Sharma from sifted litter. 1 male paratype (used for DNA extraction, dissected for genitalia, and mounted on SEM stubs MCZ 124562–124563]), same collecting data as holotype.

Etymology. The name honors Natalia Kaktins, a secondary school teacher of Latin and the classics who introduced the author to the mythology of Zalmoxis and other Thracian deities.

Diagnosis. Distinguished from congeners by the belt of large tubercles on sternite 7; the large tubercle on the lateral-most part of each opisthosomal sternite, forming a row on each side; armature of tibia IV in males, which bears a ventral row of tubercles with a single large tubercle in the center, and three smaller tubercles distally and five proximally; rutrum subrectangular in shape, longer than wide, tapering proximally; and a “double” pergula fused medially, bearing eight setae set equidistant from each other.

Description. Total length of male holotype 2.04, greatest width of prosoma 0.86, greatest width of opisthosoma 1.36; length-to-width ratio 1.50. Body campaniform, dark orange to brown (in alcohol, depending on incidence of light), almost entirely with dense microgranulate surface microstructure. Eyes present on low, well-developed ocularium. Ocularium wider than long, removed from anterior margin of carapace, without spines or tubercles. Anterior margin of carapace with two pairs of pegs above coxae of leg I and single median peg. Mesotergum generally smooth, mesotergal grooves distinctly “V”-shaped. Free tergites armed with regular belts of pointed setose tubercles (Fig. 9).

Ventral prosomal complex with coxae II and III meeting in midline, coxae I and IV not so (Fig. 10a). Anterior and posterior margins of coxae III with tubercular bridges to adjacent coxae, and coxae I–II with low setose tubercles. Coxae IV greatly enlarged, with setose tubercles concentrated on anterior surface. Genital operculum semicircular. Spiracles not concealed, anterior to row of tubercles. Single large tubercle on the lateral-most part of each opisthosomal sternite, forming an anteroposterior row of large tubercles along lateral edges of sternites. Opisthosomal sternites additionally armed with low tubercles tapering medially, except sternite 7, which bears six large tubercles medially and two larger tubercles laterally. Anal plate armed with five tubercles approximating the size of median tubercles of sternite 7 (Fig. 10b).

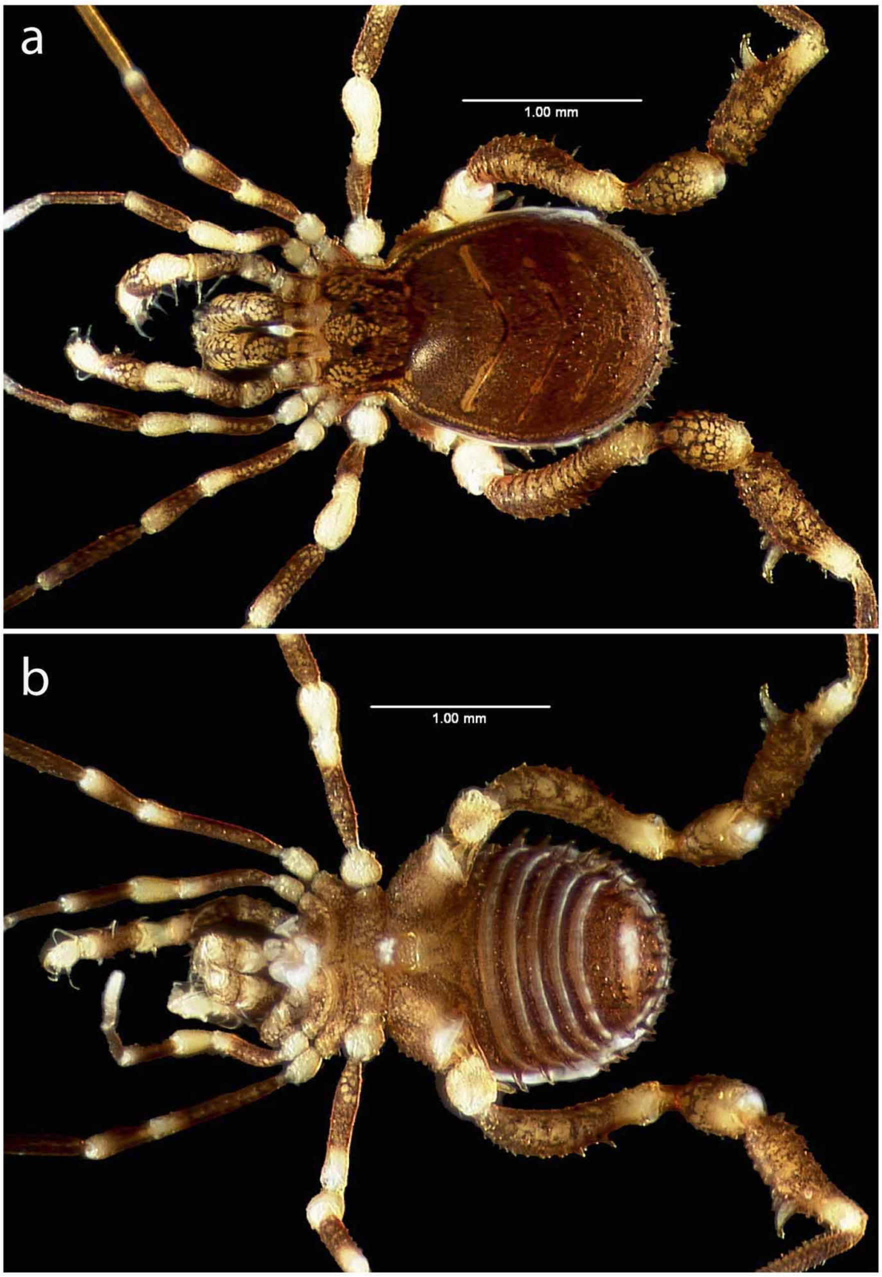

FIGURE 9. *Zalmoxis kaktinsae* **sp. nov.** (a) Male holotype, dorsal view; (b) Male holotype, ventral view.

Chelicerae (Fig. 11a) sexually monomorphic, with prominent bulla on proximal article. Proximal article with denticulate granulation basally and ventrally. Second article not incrassate, free of ornamentation, with dorsal margin bearing several setae. Distal article with delicate dentition, smooth, free of ornamentation. Palpi (Fig. 11b) robust and spined ventrally and/or ventrolaterally, typical of zalmoxids. Palpal tarsus with two pairs of megaspines.

Legs (I–IV) finely granulated, of striated appearance due to de-pigmented regions on leg joints (Fig. 11c–f). Leg I trochanter with one ventral and one dorsal tubercle, femur with ventral row of small tubercles (Fig. 11c). Leg IV incrassate, elongated, and heavily armored (Fig. 11f). Trochanter IV with one large ventral tubercle; femur IV bearing ventral row of four prominent tubercles with intermittent small tubercles. Femur, patella, and tibia IV dorsally and laterally covered with low setose tubercles. Male tibia IV with one dorsal row of tubercles enlarging proximally; and one ventral row of nine tubercles, with the largest, distally-directed, hook-like tubercle flanked by three smaller tubercles distally and five proximally. Metatarsus IV with a ventral row of setose tubercles and a lateral row of bulbous setose tubercles. Metatarsi I–IV divided distally, with calcaneus less ornamented but generally more setose. Tarsal claws I–IV smooth, unmodified. Tarsal segmentation 3: 4: 5: 5 (Fig. 11).

Appendage measurements of holotype (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.16/0.14	0.54/0.10	0.28/0.14	0.40/0.12	0.55/0.06	0.43/0.06	2.36
Leg II	0.19/0.14	0.81/0.10	0.39/0.25	0.65/0.13	0.71/0.06	0.84/0.07	3.59
Leg III	0.19/0.23	0.66/0.15	0.33/0.20	0.54/0.15	0.64/0.08	0.40/0.06	2.76
Leg IV	0.35/0.27	1.20/0.27	0.54/0.33	0.88/0.27	0.95/0.11	0.44/0.07	4.36
Palp	0.19/0.15	0.35/0.16	0.23/0.16	0.35/0.18	—	0.28/0.13	1.40
	Proximal	Second	Distal				
Chelicera	0.39/0.19	0.45/0.20	0.17/0.04				

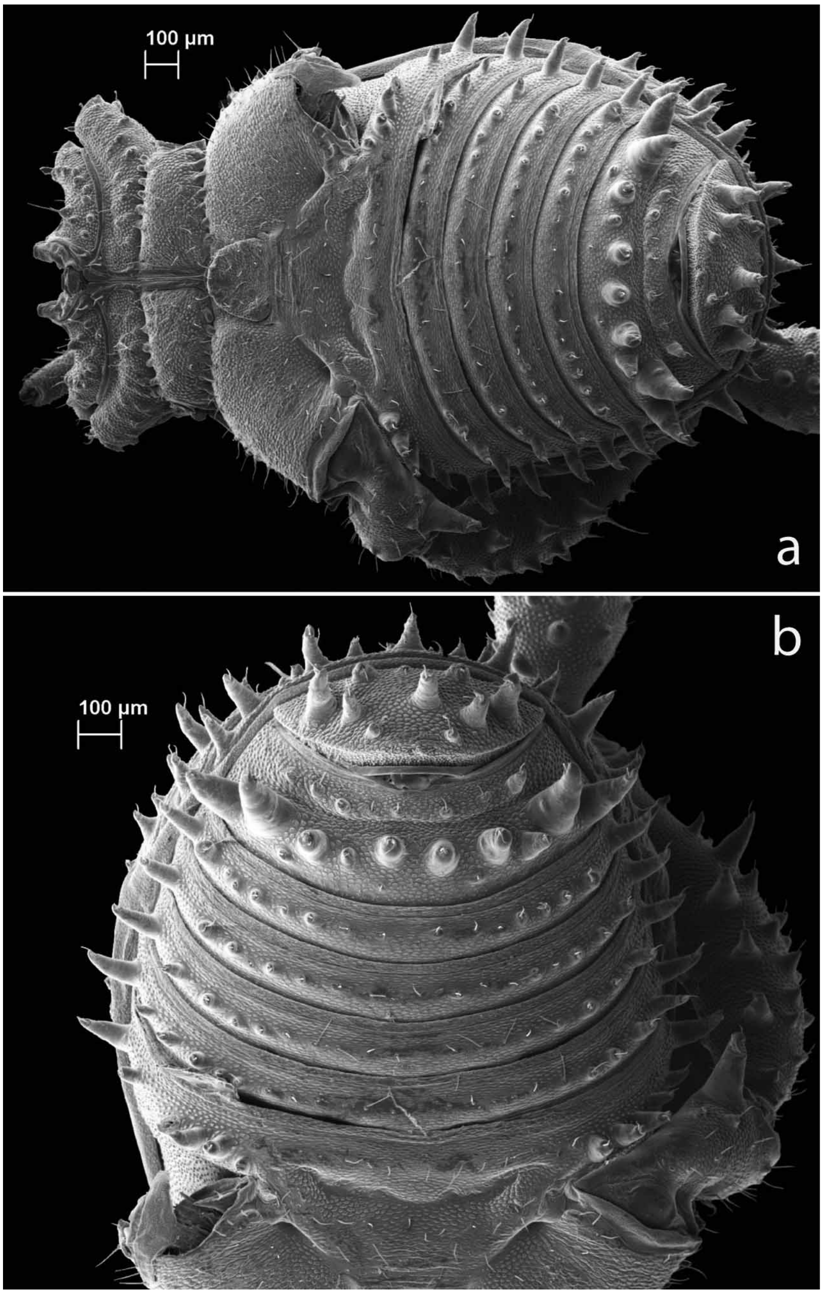

FIGURE 10. *Zalmoxis kaktinsae* **sp. nov.** (a) Ventral view of male paratype; (b) Opisthosomal region of male paratype.

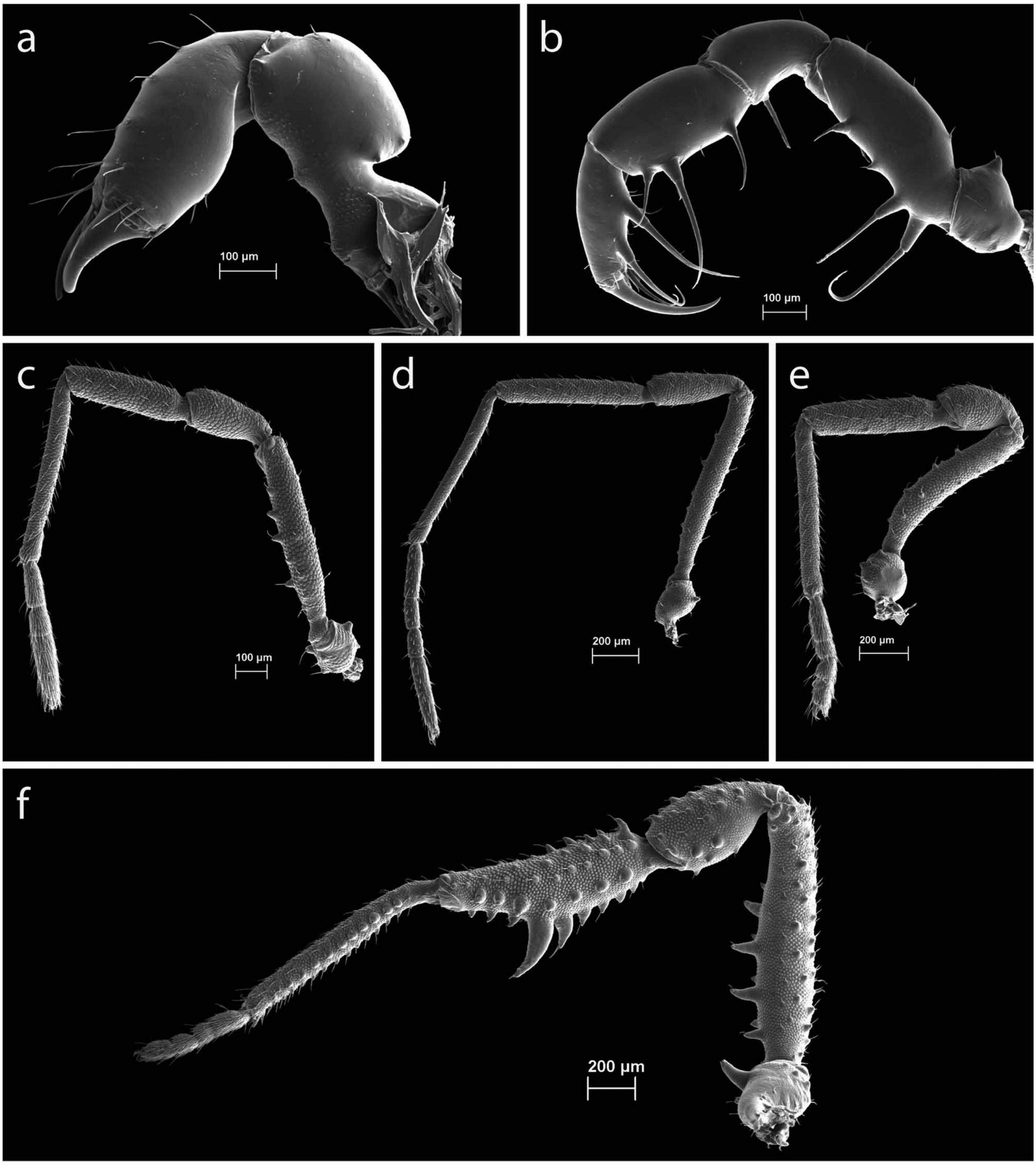

FIGURE 11. *Zalmoxis kaktinsae* **sp. nov.** (a) Left chelicera of male paratype; (b) Left palp of male paratype; (c) Male left leg I; (d) Male left leg II; (e) Male left leg III; (f) Male left leg IV.

Penis (Fig. 12) with two pairs of setae on diminutive rutrum and a “double” pergula fused medially. Eight setae on pergula (set approximately equidistant from each other). One pair of setae displaced from midline and slightly posterior to pergula. Rutrum small and subrectangular, longer than wide, without lateral arrowhead-like extensions or rounded edges, and tapering proximally. Pergula slightly projecting ventrally. Female unknown.

Distribution. Known only from type locality.

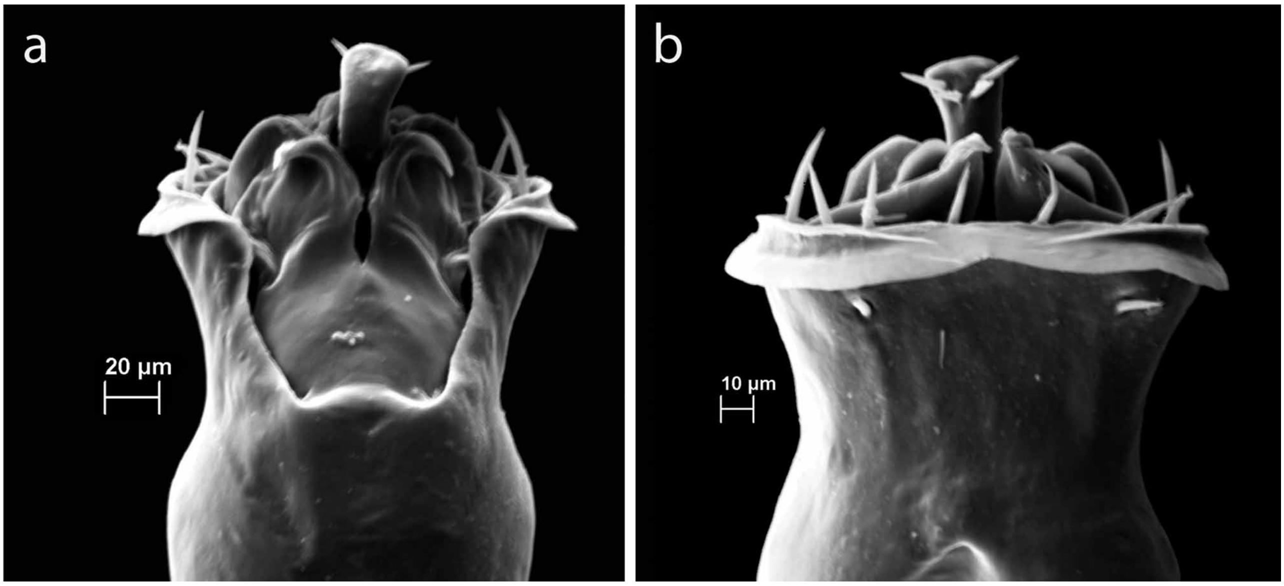

FIGURE 12. *Zalmoxis kaktinsae* **sp. nov.** (a) Pars distalis of male genitalia, dorsal view; (b) Pars distalis of male genitalia, ventral view.

Zalmoxis perditus **sp. nov.**
Figs. 13–14

Types. Male holotype (MNHN [ex MCZ DNA102356]) from Baie d'Upi, Isle of Pines (22° 35' 21.0" S, 167° 31' 20.1"E), New Caledonia, 4 m elevation, collected 20 April 2007 by J. Murienne and P.P. Sharma from sifted litter. 1 female (in ethanol, used for DNA extraction [ex MCZ DNA102356]) paratype, same collecting data as holotype (MCZ 124564).

Additional material studied. One juvenile, same collecting data as holotype.

Etymology. The name refers to the collecting locality of this species, the Isle of Pines, which is located to the south of the main island of New Caledonia (Grande Terre). From Latin, "*perditus, -a, -um*" meaning "lost" or "abandoned".

Diagnosis. Distinguished from congeners by the coloration pattern, forming a pigment-free "U" shape on the opisthosomal sternites; a single lateral peg on the ectal surface of coxae II of both sexes; two ventroectal tubercles on femur IV of males; five tubercles, enlarging distally, on tibia IV of males; rutrum of arrowhead shape; and a "double" pergula not fused medially, bearing eight setae set equidistant from each other.

Description. Total length of male holotype (female paratype [MCZ 124564] in parentheses) 1.96 (1.50), greatest width of prosoma 0.76 (0.66), greatest width of opisthosoma 1.34 (1.26); length-to-width ratio 1.46 (1.19). Body campaniform, dark orange to brown (in alcohol, depending on incidence of light), almost entirely with dense microgranulate surface microstructure. Eyes present on low, well-developed ocularium. Ocularium wider than long, removed from anterior margin of carapace, without spines or tubercles. Anterior margin of carapace with two pairs of pegs above coxae of leg I and single median peg. Scutal grooves of mesotergum distinctly "V"-shaped. Free tergites with regular belts of small setose tubercles (Fig. 13).

Ventral prosomal complex with coxae II and III meeting in midline, coxae I and IV not so. Anterior and posterior margins of coxae III with tubercular bridges to adjacent coxae, and coxae I–II with low setose tubercles. Coxae II with lateral peg on ectal surface in both sexes. Coxae IV greatly enlarged. Genital operculum sub-triangular. Spiracles not concealed, anterior to row of tubercles. Coloration pattern of opisthosomal sternites forming a pigment-free "U" shape in both sexes. Opisthosomal sternites armed with low tubercles tapering medially, except sternite 8, which bears six larger tubercles. Anal plate armed with five tubercles, two of these large (Fig. 13).

Chelicerae sexually monomorphic, with prominent bulla on proximal article. Proximal article with denticulate granulation basally and ventrally. Second article not incrassate, free of ornamentation, with dorsal margin bearing several setae. Distal article with delicate dentition, free of ornamentation. Palpi robust and spined ventrally and/or ventrolaterally, typical of zalmoxids. Palpal tarsus with two pairs of megaspines.

Legs (I–IV) finely granulated, of slightly striated appearance due to de-pigmented regions on leg joints. Femora of legs I–II with ventral row of small tubercles. Male leg IV incrassate, elongated, and armored. Femur of male leg IV with two large ventroectal tubercles flanked by row of smaller ventromesal tubercles; tibia IV bearing ventral row of seven tubercles tapering proximally. Femur, patella, and tibia IV dorsally and laterally covered with low setose tubercles. Metatarsi I–IV divided distally, with calcaneus less ornamented but generally more setose. Tarsal claws I–IV smooth, unmodified. Tarsal segmentation 3: 5: 5: 6.

FIGURE 13. *Zalmoxis perditus* **sp. nov.** (a) Male holotype, dorsal view; (b) Male holotype, ventral view; (c) Female paratype, dorsal view; (d) Female paratype, ventral view.

Appendage measurements of holotype (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.15/0.12	0.42/0.10	0.24/0.13	0.34/0.10	0.47/0.06	0.31/0.06	1.93
Leg II	0.17/0.13	0.56/0.09	0.33/0.13	0.53/0.11	0.49/0.05	0.59/0.05	2.67
Leg III	0.17/0.18	0.51/0.10	0.27/0.16	0.42/0.14	0.52/0.07	0.35/0.06	2.24
Leg IV	0.23/0.23	0.89/0.22	0.44/0.25	0.67/0.19	0.70/0.10	0.40/0.06	3.33
Palp	0.14/0.12	0.32/0.12	0.21/0.13	0.28/0.16	—	0.29/0.13	1.24
	Proximal	Second	Distal				
Chelicera	0.22/0.16	0.52/0.15	0.12/0.03				

Appendage measurements of female paratype (MCZ 124564) (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.15/0.12	0.44/0.11	0.24/0.12	0.29/0.10	0.40/0.06	0.35/0.06	1.87
Leg II	0.15/0.13	0.49/0.10	0.30/0.12	0.45/0.10	0.44/0.06	0.60/0.06	2.43
Leg III	0.16/0.14	0.45/0.11	0.25/0.15	0.34/0.13	0.47/0.06	0.40/0.06	2.07
Leg IV	0.17/0.15	0.69/0.12	0.34/0.16	0.52/0.13	0.64/0.07	0.42/0.06	2.78
Palp	0.12/0.14	0.34/0.12	0.17/0.13	0.27/0.15	—	0.27/0.08	1.17
	Proximal	Second	Distal				
Chelicera	0.22/0.15	0.51/0.17	0.14/0.03				

Penis (Fig. 14) with two unpaired setae on right margin of rutrum (possible anomaly) and a “double” pergula with unfused, slightly projecting margins. Eight setae on distal pergula (set approximately equidistant from each other). One pair of setae displaced from midline and slightly posterior to proximal pergula. Rutrum with lateral arrowhead-like extensions.

Distribution. Known only from type locality.

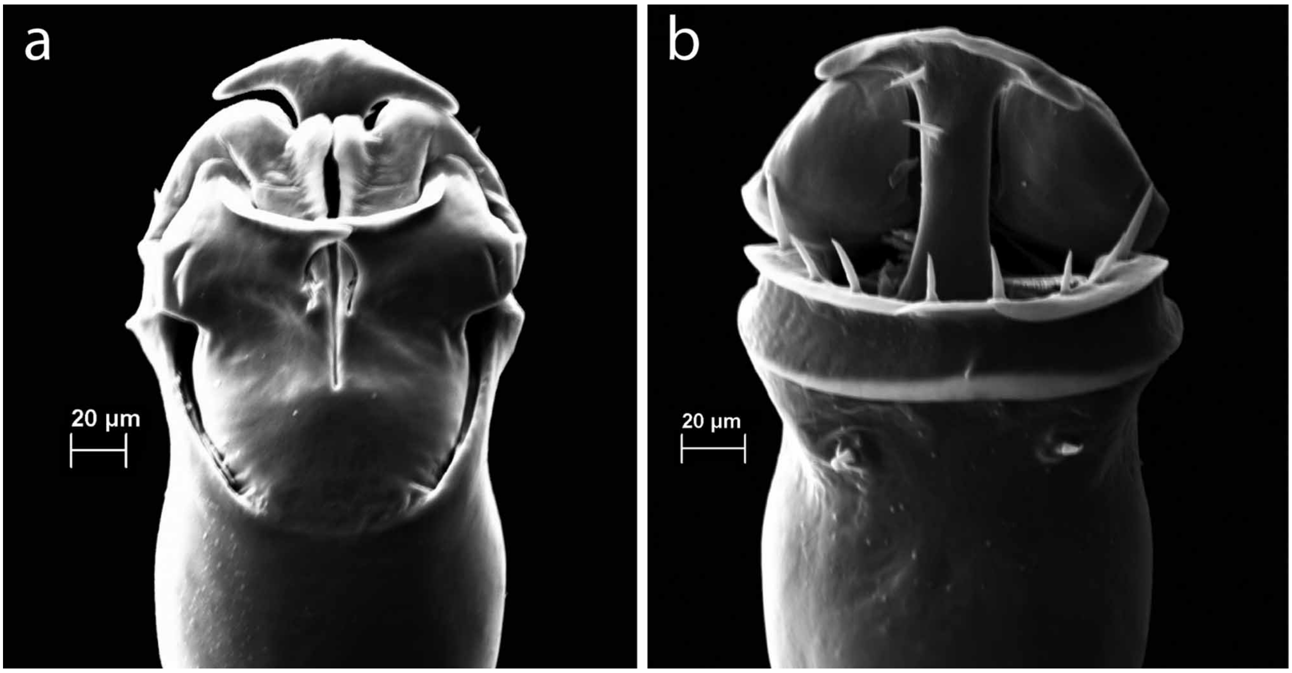

FIGURE 14. *Zalmoxis perditus* **sp. nov.** (a) Pars distalis of male genitalia, dorsal view; (b) Pars distalis of male genitalia, ventral view.

Zalmoxis falcifer sp. nov.

Figs. 15–18

Types. Male holotype (WAM [ex MCZ DNA105836]) from Bonaparte Archipelago, W.A. (14° 31' S 124° 55' E), Australia, collected August 2002 by M.S. Harvey. 1 male (used for DNA extraction [ex MCZ DNA105836], dissected for genitalia, and mounted on SEM stubs MCZ 124565–124566) and 1 female (in ethanol; legs mounted on SEM stub MCZ 124574) paratype, same collecting data as holotype (MCZ 124567).

Etymology. The specific epithet, an invariable noun in apposition, refers to the gargantuan curved spine on tibia IV of males of the species. From Latin, “*falcifer*, *-era*, *-erum*, itself from “*falx*, *falcis*” meaning “sickle” or alternatively a curved pole-arm historically used in combat by the Thracians and Dacians; and “*ferre*” meaning “to carry” or “to bear”.

Diagnosis. Distinguished from congeners by greatly incrassate tibia IV with a massively enlarged apophysis in males. Apophysis curved into a semicircle, ornamented with setose tubercles, and bearing four smaller tubercles on concave edge. Rutrum enlarged, rhomboid in dorsal aspect, with lateral extensions and bearing two pairs of setae.

Description. Total length of male holotype (female paratype [MCZ 124567] in parentheses) 2.28 (2.12), greatest width of prosoma 1.00 (0.85), greatest width of opisthosoma 1.74 (1.68); length-to-width ratio 1.31 (1.26). Body campaniform, dark orange to light brown (in alcohol, depending on incidence of light), almost entirely with dense microgranulate surface microstructure. Eyes present on low, well-developed ocularium. Ocularium wider than long, removed from anterior margin of carapace, without spines or tubercles. Anterior margin of carapace with two pairs of pegs above coxae of leg I and single median peg. Scutal grooves of mesotergum forming obtuse "V" shape. Area IV and margin of area V of mesotergum, and free tergites with belts of prominent setose tubercles (Fig. 15).

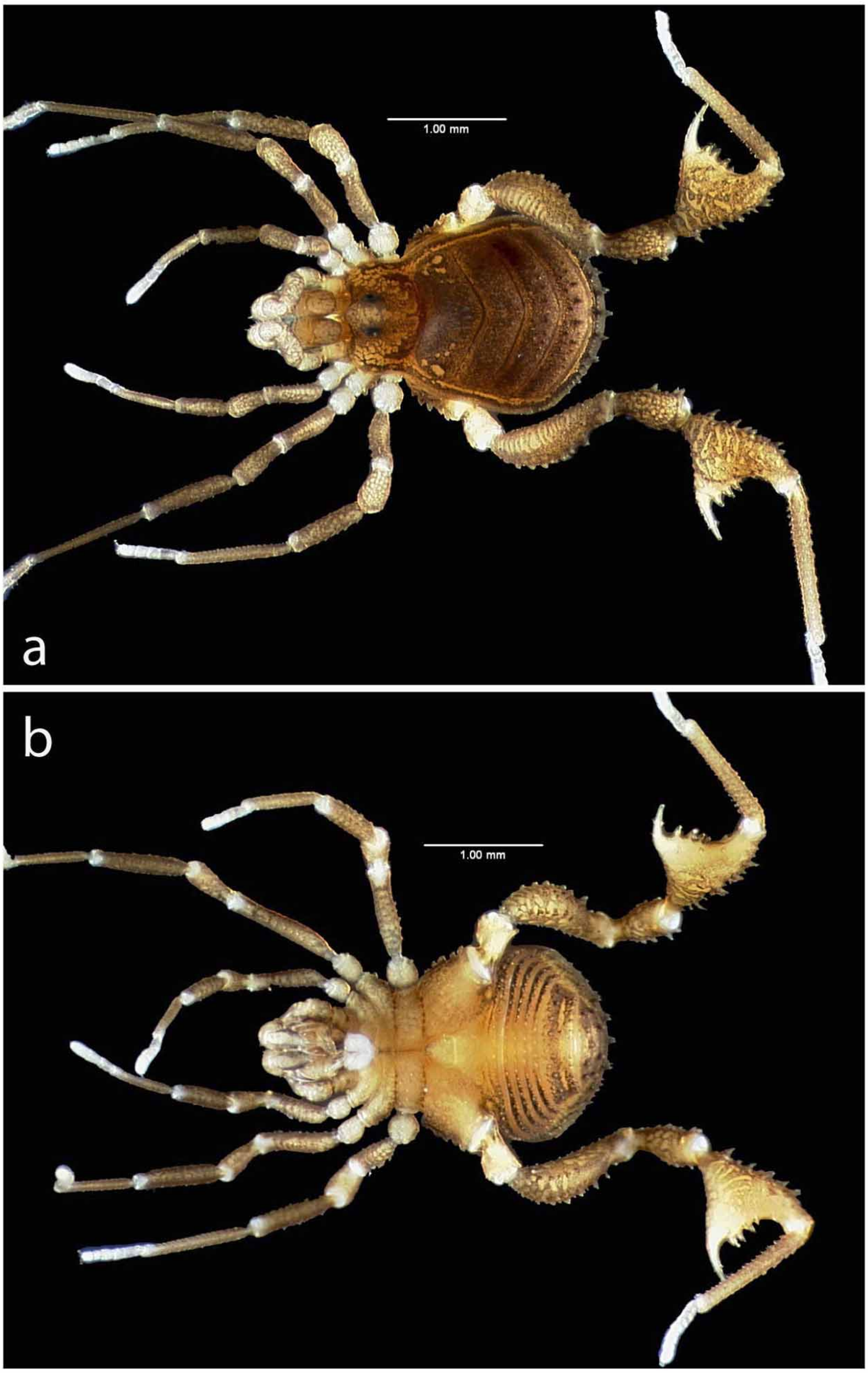

FIGURE 15. *Zalmoxis falcifer* **sp. nov.** (a) Male holotype, dorsal view; (b) Male holotype, ventral view.

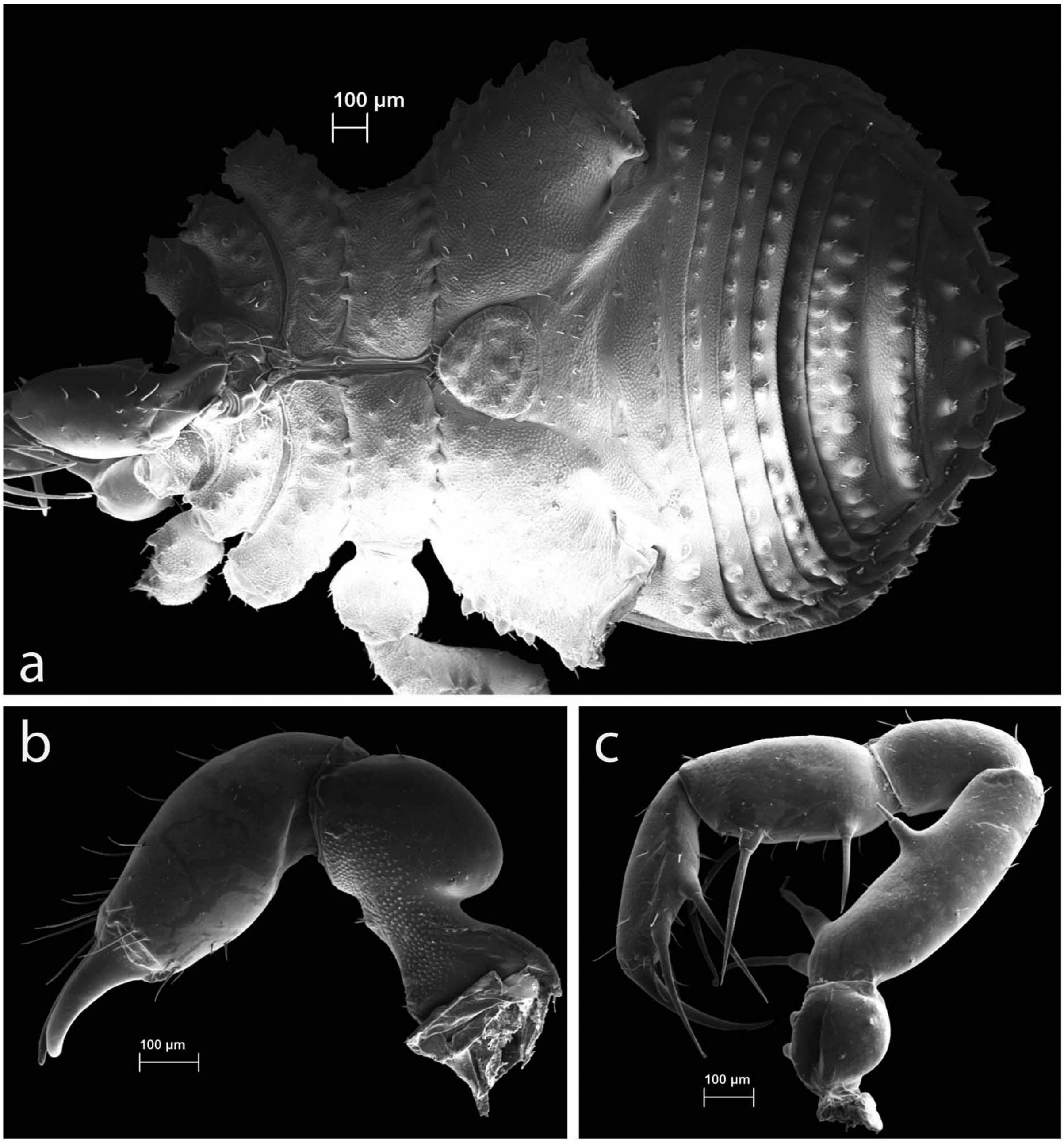

FIGURE 16. *Zalmoxis falcifer* **sp. nov.** (a) Ventral view of male paratype; (b) Left chelicera of male paratype; (c) Left palp of male paratype.

Ventral prosomal complex with coxae II and III meeting in midline, coxae I and IV not so (Fig. 16a). Anterior and posterior margins of coxae III with tubercular bridges to adjacent coxae, and coxae I–III with low setose tubercles. Coxae IV greatly enlarged, with larger setose tubercles on anterior margin. Genital operculum sub-triangular. Spiracles not concealed, anterior to row of tubercles. Opisthosomal sternites armed with belts of low tubercles, except sternite 7, which bears one anterior and one posterior belt, with posterior belt of tubercles larger than anterior. Anal plate armed with eight prominent setose tubercles (Fig. 16a).

Chelicerae (Fig. 16b) sexually monomorphic, with prominent bulla on proximal article. Proximal article with denticulate granulation basally and ventrally. Second article not incrassate, smooth, free of ornamentation, with dorsal margin bearing several setae. Distal article with delicate dentition, free of ornamentation. Palpi (Fig. 16c) robust and spined ventrally and/or ventrolaterally, typical of zalmoxids. Palpal tarsus with two pairs of megaspines.

Legs (I–IV) finely granulated (Fig. 17). Femora of legs I–II with ventral row of small tubercles (Fig. 17a, b). Male leg IV incrassate, elongated, and heavily armored (Fig. 17d, e). Coxa IV of male with single tubercle on mesal surface. Femur IV of male incrassate and bearing multiple rows of prominent tubercles on ventral and ventrolateral surfaces. Tibia IV of male greatly incrassate with a massively enlarged apophysis. Apophysis curved into a semicircle, ornamented with setose tubercles on both mesal and ectal surfaces, and bearing four smaller tubercles on concave edge. Metatarsus IV of male with ventral row of tubercles tapering distally. Calcaneus of male metatarsus IV with a small ventral pair of distally-directed, hook-like tubercles. Metatarsi I–IV divided distally, with calcaneus less ornamented but generally more setose. Tarsal claws I–IV smooth, unmodified. Tarsal segmentation 3: 5: 5: 6 (Fig. 15).

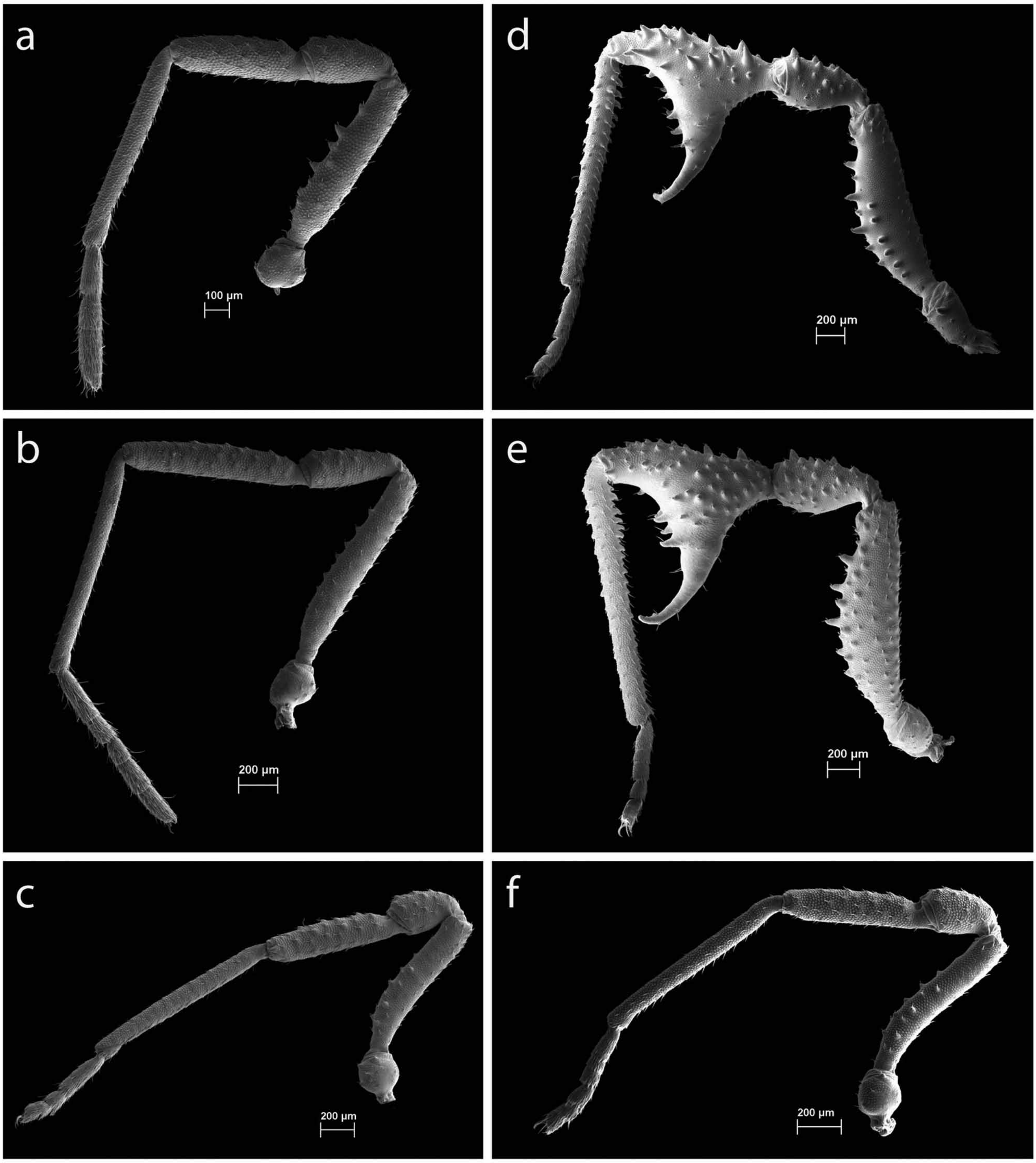

FIGURE 17. *Zalmoxis falcifer* **sp. nov.** (a) Male left leg I; (b) Male left leg II; (c) Male left leg III; (d) Male left leg IV, mesal view; (e) Male right leg IV, ectal view; (f) Female left leg IV.

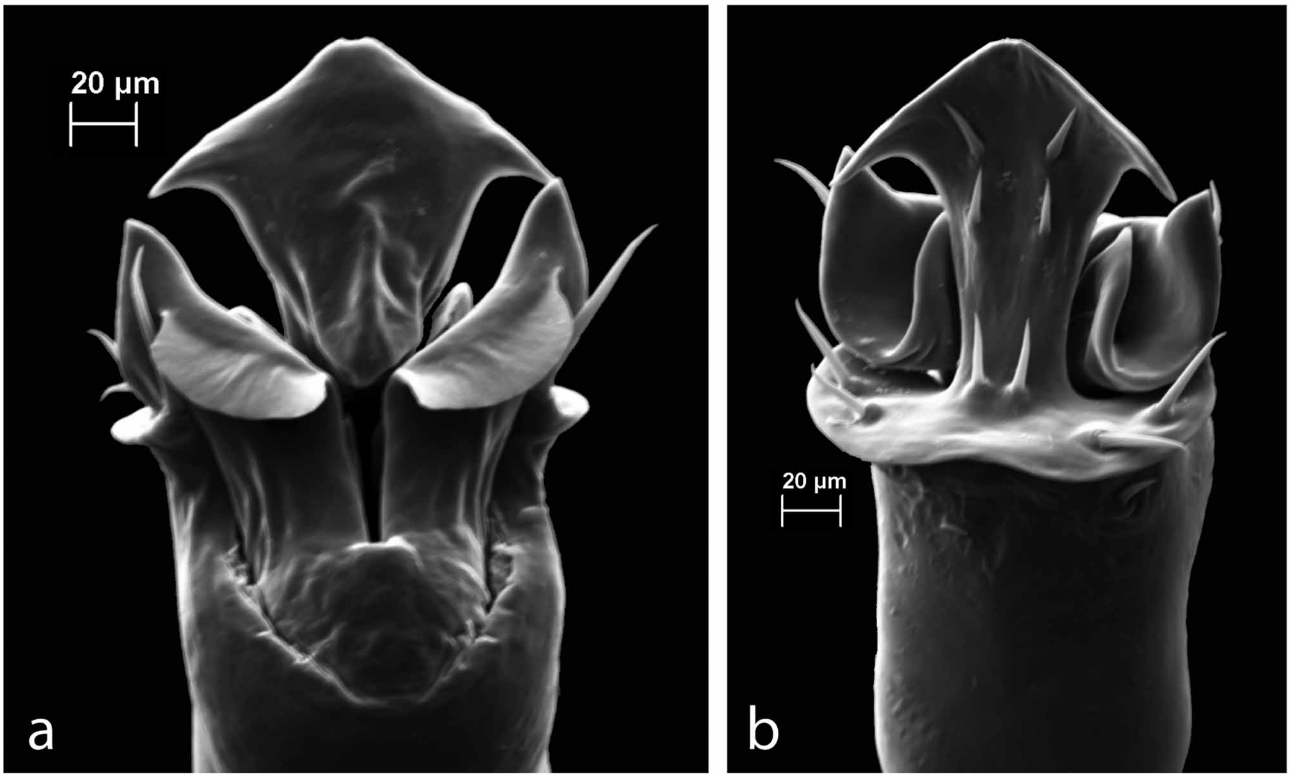

FIGURE 18. *Zalmoxis falcifer* **sp. nov.** (a) Pars distalis of male genitalia, dorsal view; (b) Pars distalis of male genitalia, ventral view.

Appendage measurements of holotype (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.16/0.17	0.72/0.15	0.36/0.17	0.47/0.16	0.74/0.09	0.52/0.10	2.97
Leg II	0.22/0.20	1.00/0.16	0.48/0.20	0.85/0.17	1.09/0.09	0.87/0.10	4.51
Leg III	0.25/0.25	0.80/0.18	0.40/0.25	0.71/0.19	1.07/0.11	0.60/0.10	3.83
Leg IV	0.33/0.30	1.30/0.36	0.55/0.32	1.05/1.04	1.60/0.14	0.62/0.11	5.45
Palp	0.15/0.15	0.44/0.16	0.26/0.15	0.35/0.21	—	0.37/0.16	1.57
	Proximal	Second	Distal				
Chelicera	0.45/0.23	0.66/0.20	0.19/0.04				

Appendage measurements of female paratype (MCZ 124574) (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.20/0.17	0.69/0.13	0.36/0.16	0.46/0.14	0.78/0.08	0.53/0.08	3.02
Leg II	0.21/0.19	0.92/0.14	0.48/0.16	0.75/0.14	0.97/0.08	0.88/0.09	4.21
Leg III	0.23/0.19	0.82/0.14	0.38/0.20	0.62/0.16	0.98/0.09	0.57/0.09	3.60
Leg IV	0.25/0.20	1.06/0.16	0.40/0.17	0.74/0.15	1.22/0.11	0.61/0.08	4.28
Palp	0.16/0.15	0.44/0.15	0.25/0.15	0.35/0.18	—	0.37/0.14	1.57
	Proximal	Second	Distal				
Chelicera	0.46/0.24	0.65/0.21	0.20/0.04				

Penis (Fig. 18) with two pairs of setae on rutrum and three pairs setae on pergula (one median pair at base of rutrum, and two pairs displaced laterally from midline). One pair of setae displaced from midline and posterior to pergula. Rutrum enlarged, rhomboid in dorsal aspect, with lateral extensions. Pergula projecting ventrally.

Distribution. Known only from type locality.

Zalmoxis furcifer sp. nov.
Figs. 19–22, 25

Types. Male holotype (QM [ex MCZ DNA106311]) from Daintree National Park, Cape Tribulation Road, Emmagen Creek, adjacent to "4WD track", Cape Tribulation section, Queensland (16° 3' 40.9" S, 145° 27' 42.2" E), Australia, 30 m elevation, collected 26 April 2011 by R.M. Clouse and P.P. Sharma from sifted litter. 6 male (3 in ethanol; 1 dissected for genitalia and mounted on SEM stub MCZ 124568; 1 dissected for genitalia and mounted on SEM stubs MCZ 124568, MCZ 124571; 1 mounted on SEM stubs 124572–124573) and 5 female (3 in ethanol; 1 used for DNA extraction [ex MCZ DNA106311]; 1 mounted on SEM stub MCZ 124570) paratypes, same collecting locality as holotype (MCZ 124569). 2 male and 3 female paratypes (MAGNT) from Daintree National Park, Mossman Gorge, on trail at end of road, Cape Tribulation section, Queensland (16° 28' 19.5" S, 145° 19' 49.7" E), Australia, 69 m elevation, collected 28–IV–2011 by R.M. Clouse and P.P. Sharma from sifted litter. 3 male and 3 female paratypes (WAM) from Barron Gorge National Park, Crystal Cascades trail, Queensland (16° 57' 50.6" S, 145° 40' 45.2" E), Australia, 75 m elevation, collected 29–IV–2011 by R.M. Clouse and P.P. Sharma from sifted litter. 2 male and 2 female paratypes (MHNG) from vicinity of Russell River National Park, Graham Range, Queensland (17° 17' 30.3" S, 145° 57' 36.7" E), Australia, 44 m elevation, collected 30–IV–2011 by R.M. Clouse and P.P. Sharma from sifted litter.

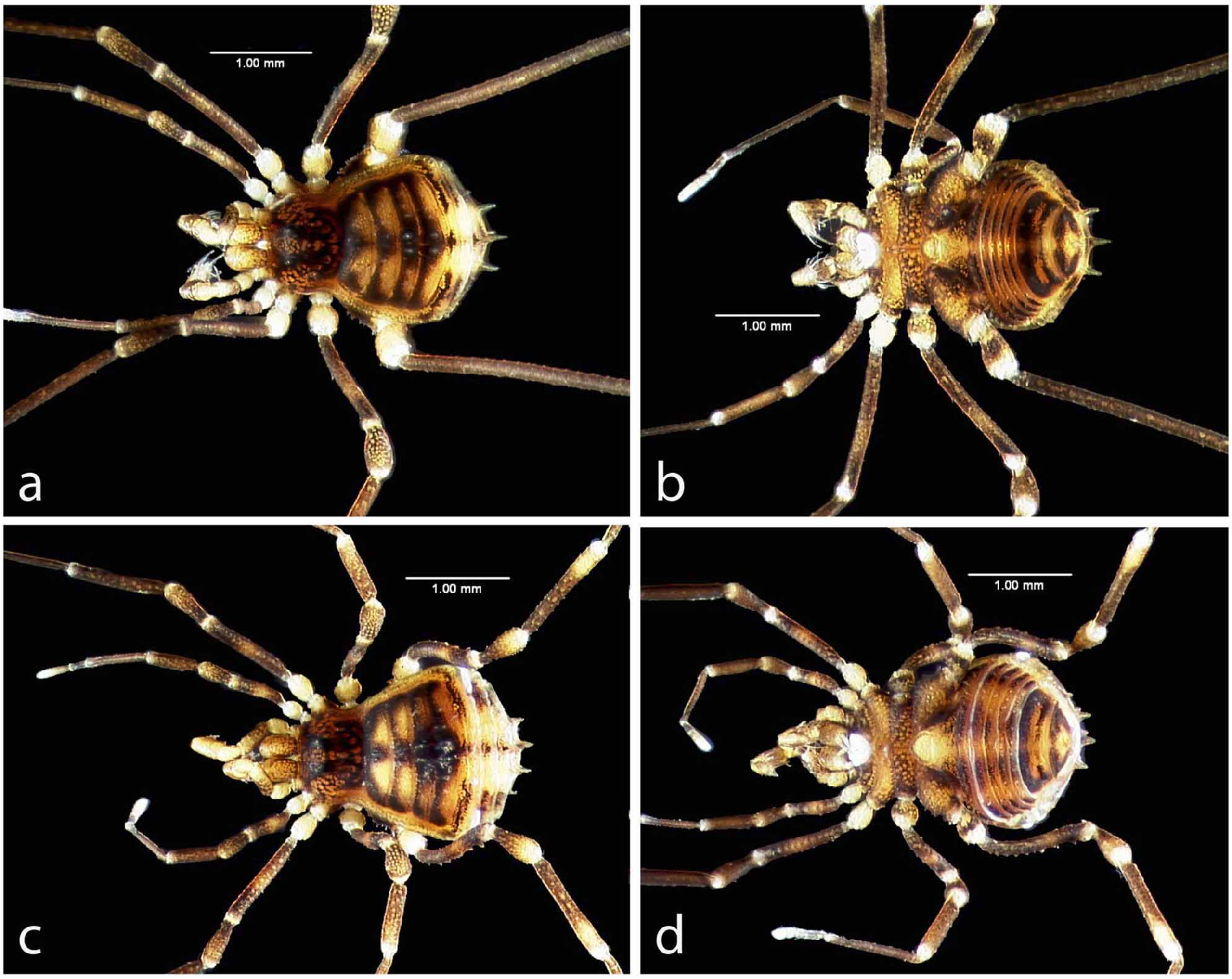

FIGURE 19. *Zalmoxis furcifer* **sp. nov.** (a) Male holotype, dorsal view; (b) Male holotype, ventral view; (c) Female paratype, dorsal view; (d) Female paratype, ventral view.

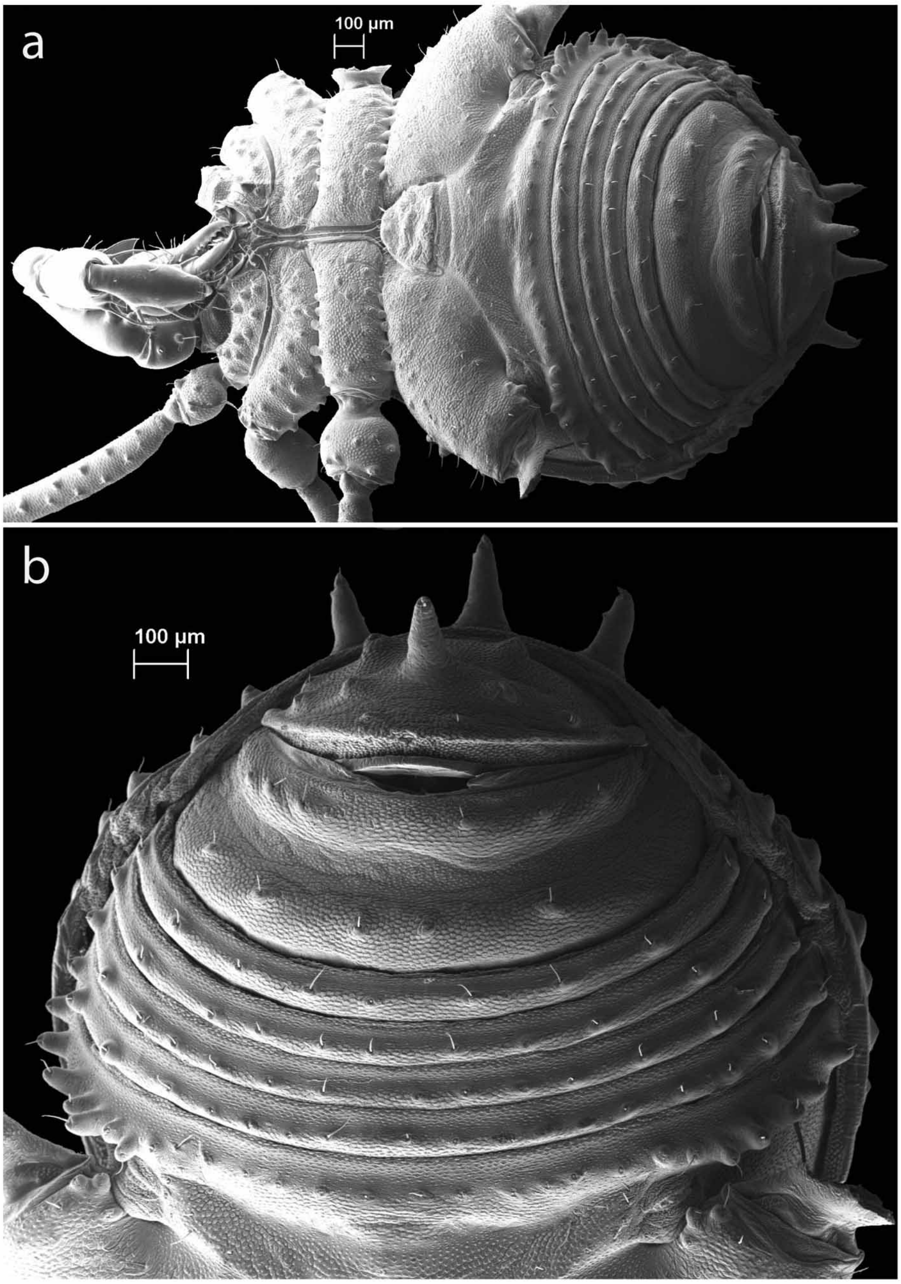

FIGURE 20. *Zalmoxis furcifer* **sp. nov.** (a) Ventral view of male paratype; (b) Opisthosomal region of male paratype.

Additional material studied. 1 male, 3 females and 2 juveniles from Daintree National Park, Mossman Gorge, on trail at end of road, Cape Tribulation section, Queensland (16° 28' 19.5" S, 145° 19' 49.7" E), Australia, 69 m elevation, collected 28–IV–2011 by R.M. Clouse and P.P. Sharma from sifted litter. 3 males, 4 females (1 used for DNA extraction [MCZ DNA106316]), and 2 juveniles from Barron Gorge National Park, Crystal Cascades trail, Queensland (16° 57' 50.6" S, 145° 40' 45.2" E), Australia, 75 m elevation, collected 29–IV–2011 by R.M. Clouse and P.P. Sharma from sifted litter. 2 males, 2 females (1 used for DNA extraction [MCZ DNA106318]) and 1 juvenile from vicinity of Russell River National Park, Graham Range, Queensland (17° 17' 30.3" S, 145° 57' 36.7" E), Australia, 44 m elevation, collected 30–IV–2011 by R.M. Clouse and P.P. Sharma from sifted litter. 2 females and 2 juveniles from vicinity of Russell River National Park, Graham Range, Queensland (17° 17' 23.5" S, 145° 57' 38.4" E), Australia, 38 m elevation, collected 30–IV–2011 by R.M. Clouse and P.P. Sharma from sifted litter. 2 females from Emmagen Creek, Daintree National Park, Cape Tribulation section, Queensland (16° 3' 41" S, 145° 27' 43" E), Australia, 22 m elevation, collected 18–II–2003 by C. D'Haese and G. Giribet.

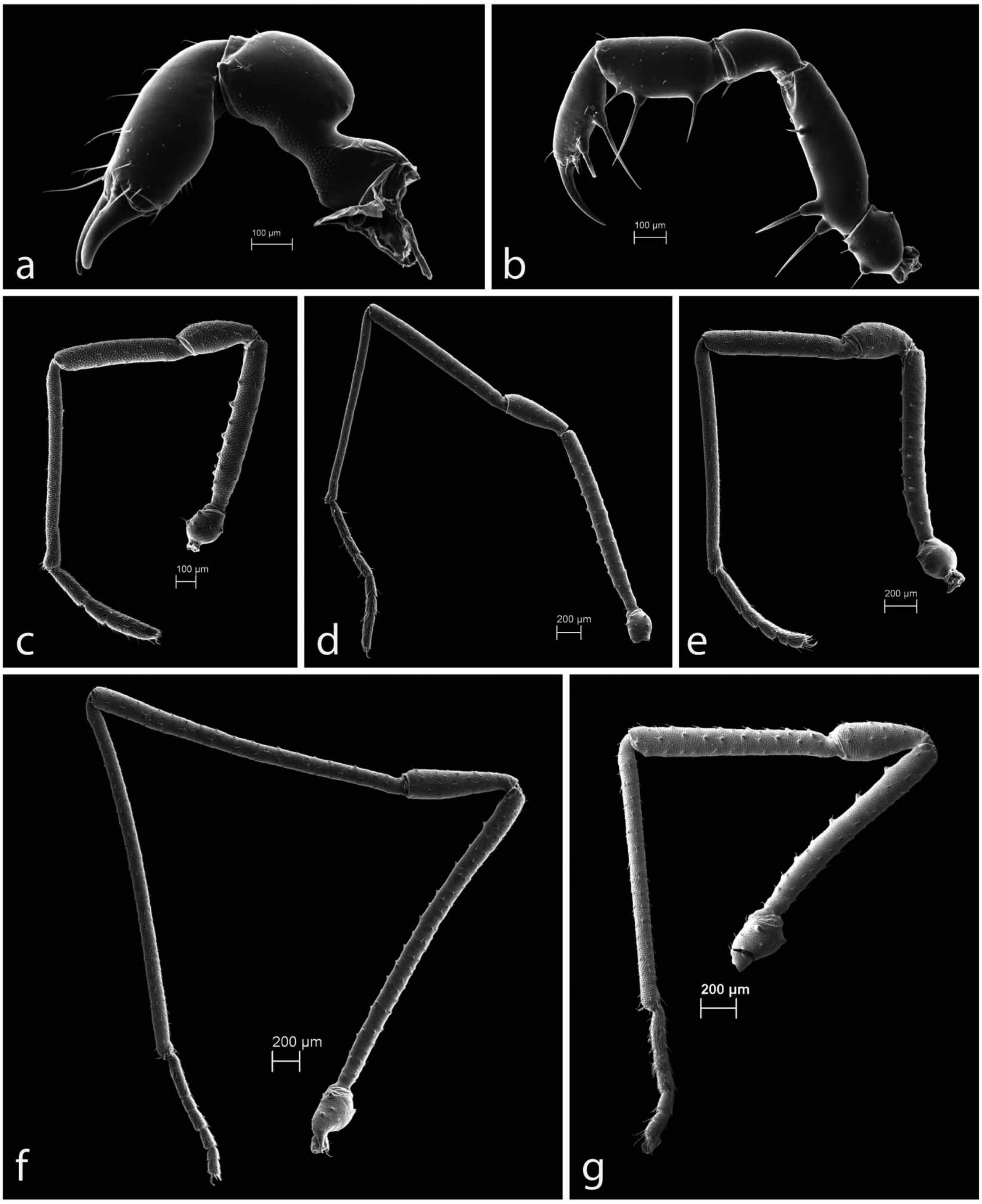

FIGURE 21. *Zalmoxis furcifer* **sp. nov.** (a) Left chelicera of male paratype; (b) Left palp of male paratype; (c) Male left leg I; (d) Male left leg II; (e) Male left leg III; (f) Male left leg IV; (g) Female left leg IV.

Etymology. The specific epithet, an invariable noun in apposition, refers to the incidence of polymorphism in males of this species, likely indicative of alternative mating strategies. Derived from Latin, "*furcifer*" meaning "rascal" or "scoundrel".

Diagnosis. Distinguished from congeners by coloration pattern; armature of free tergites (three large tubercles at posterior margin of last tergite) and anal plate (single large median tubercle); and greatly elongate walking leg IV in males.

Description. Total length of male holotype (female paratype [MCZ 124569] in parentheses) 2.26 (2.26), greatest width of prosoma 1.04 (0.94), greatest width of opisthosoma 1.74 (1.82); length-to-width ratio 1.30 (1.24). Body campaniform, colored yellow and black or brown (in alcohol, depending on incidence of light), almost entirely with dense microgranulate surface microstructure. Eyes present on low, well-developed ocularium. Ocularium wider than long, removed from anterior margin of carapace, without spines or tubercles. Anterior margin of carapace with two pairs of pegs above coxae of leg I and single median peg. Scutal grooves of mesotergum slightly curved, not "V"-shaped. Areas III–IV of mesotergum bearing medial pair of minute tubercles. Opisthosomal tergite VI with belt of small setose tubercles, tergite VII with median tubercle prominently enlarged, and tergite VIII with three large median tubercles. Dorsum mottled, with pigmentation concentrated on margins and midline of mesotergal areas (Fig. 19).

Ventral prosomal complex with coxae II and III meeting in midline, coxae I and IV not so (Fig. 20a). Anterior and posterior margins of coxae III with tubercular bridges to adjacent coxae, and coxae I–III with low setose tubercles. Coxae IV greatly enlarged. Genital operculum sub-triangular. Spiracles not concealed, anterior to row of tubercles. Opisthosomal sternites armed with belts of flattened tubercles. Anal plate armed with one prominent median tubercle, flanked by four smaller tubercles, in turn adjacent to even smaller and very low tubercles. Venter mottled, with pigmentation concentrated around spiracles, sternites 7–8, and margins of anal plate. (Fig. 19).

Chelicerae (Fig. 21a) sexually monomorphic, with prominent bulla on proximal article. Proximal article with denticulate granulation basally and ventrally. Second article not incrassate, free of ornamentation, with dorsal margin bearing several setae. Distal article with delicate dentition, free of ornamentation. Palpi (Fig. 21b) robust and spined ventrally and/or ventrolaterally, typical of zalmoxids. Palpal tarsus with two pairs of megaspines.

Legs (I–IV) finely granulated (Fig. 21c–g). Femora of legs I–IV with ventral row of fine tubercles. Male leg IV greatly elongated but neither armored nor incrassate (Fig. 21f). Coxae of all legs with few tubercles on mesal surface. Metatarsi I–IV divided distally, with calcaneus less ornamented but generally more setose. Tarsal claws I–IV smooth, unmodified. Tarsal segmentation 3: 6: 5: 6 (Fig. 21c–f).

Appendage measurements of holotype (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.21/0.18	1.02/0.16	0.44/0.18	0.78/0.14	1.40/0.07	0.67/0.10	4.52
Leg II	0.29/0.25	1.85/0.16	0.69/0.21	1.76/0.15	1.13/0.06	1.29/0.10	7.01
Leg III	0.25/0.27	1.40/0.15	0.53/0.27	1.19/0.16	1.88/0.10	0.80/0.09	6.05
Leg IV	0.25/0.33	4.70/0.15	1.74/0.28	5.30/0.14	4.80/0.13	1.05/0.10	17.84
Palp	0.18/0.18	0.50/0.17	0.27/0.15	0.37/0.19	—	0.38/0.13	1.70
	Proximal	Second	Distal				
Chelicera	0.51/0.13	0.68/0.22	0.20/0.07				

Appendage measurements of female paratype (MCZ 124574) (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.20/0.17	0.74/0.14	0.35/0.16	0.53/0.15	0.85/0.06	0.56/0.08	3.23
Leg II	0.24/0.23	1.17/0.15	0.53/0.19	0.96/0.16	1.22/0.07	1.12/0.10	5.24
Leg III	0.25/0.24	0.87/0.15	0.41/0.24	0.67/0.17	1.10/0.10	0.63/0.09	3.93
Leg IV	0.26/0.24	1.32/0.16	0.51/0.25	1.14/0.18	1.57/0.10	0.76/0.10	5.56
Palp	0.16/0.17	0.48/0.16	0.25/0.15	0.35/0.19	—	0.35/0.14	1.59
	Proximal	Second	Distal				
Chelicera	0.54/0.25	0.67/0.22	0.25/0.05				

Penis (Fig. 22) with two pairs of setae on rutrum and four pairs setae on pergula (one median pair, two ventrolateral pairs with bases in close proximity, and one lateral pair). One pair of setae displaced from midline and posterior to pergula. Rutrum arrowhead-like with lateral extensions. Pergula projecting ventrally, typical of zalmoxids.

Variation. Manifested in the size of the body and the fourth walking legs of males. Male body length 2.00–2.48 (n=20); male leg IV length 9.20–18.30 mm (n = 20).

Distribution. Known from multiple sites in the northern part of the Wet Tropics Range of Queensland, Australia. The range likely extends from Daintree National Park in the north to Russell River National Park in the south.

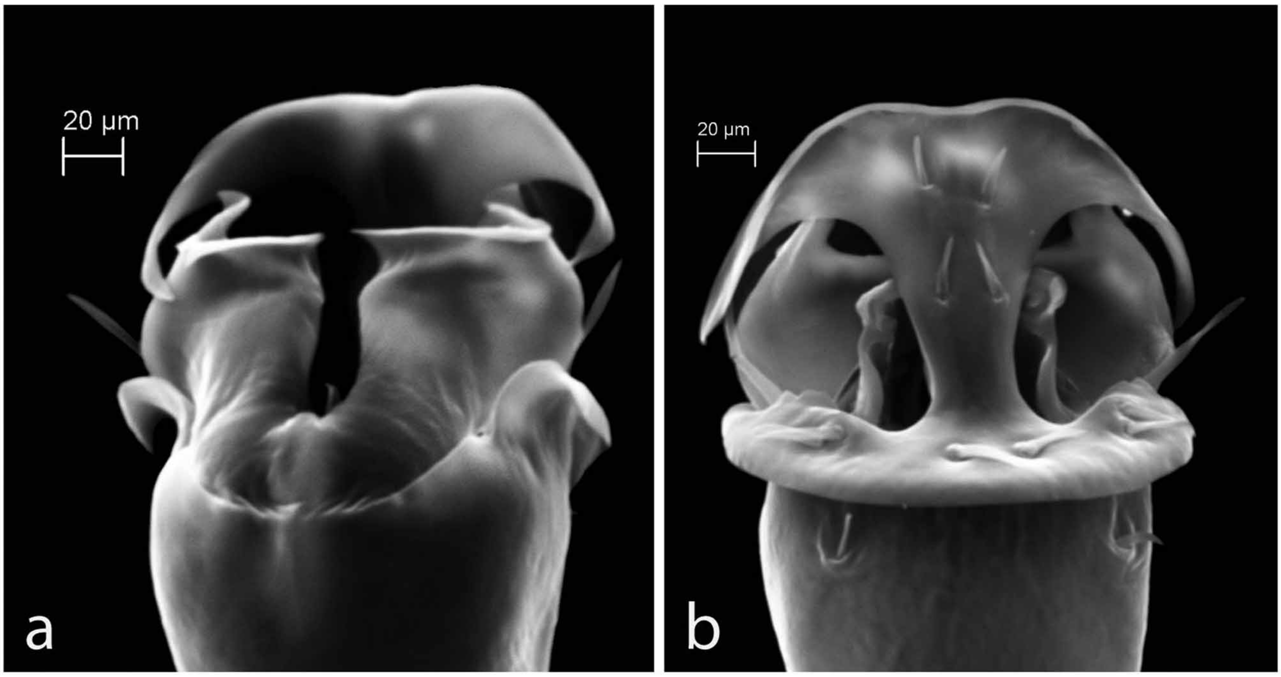

FIGURE 22. *Zalmoxis furcifer* **sp. nov.** (a) Pars distalis of male genitalia, dorsal view; (b) Pars distalis of male genitalia, ventral view.

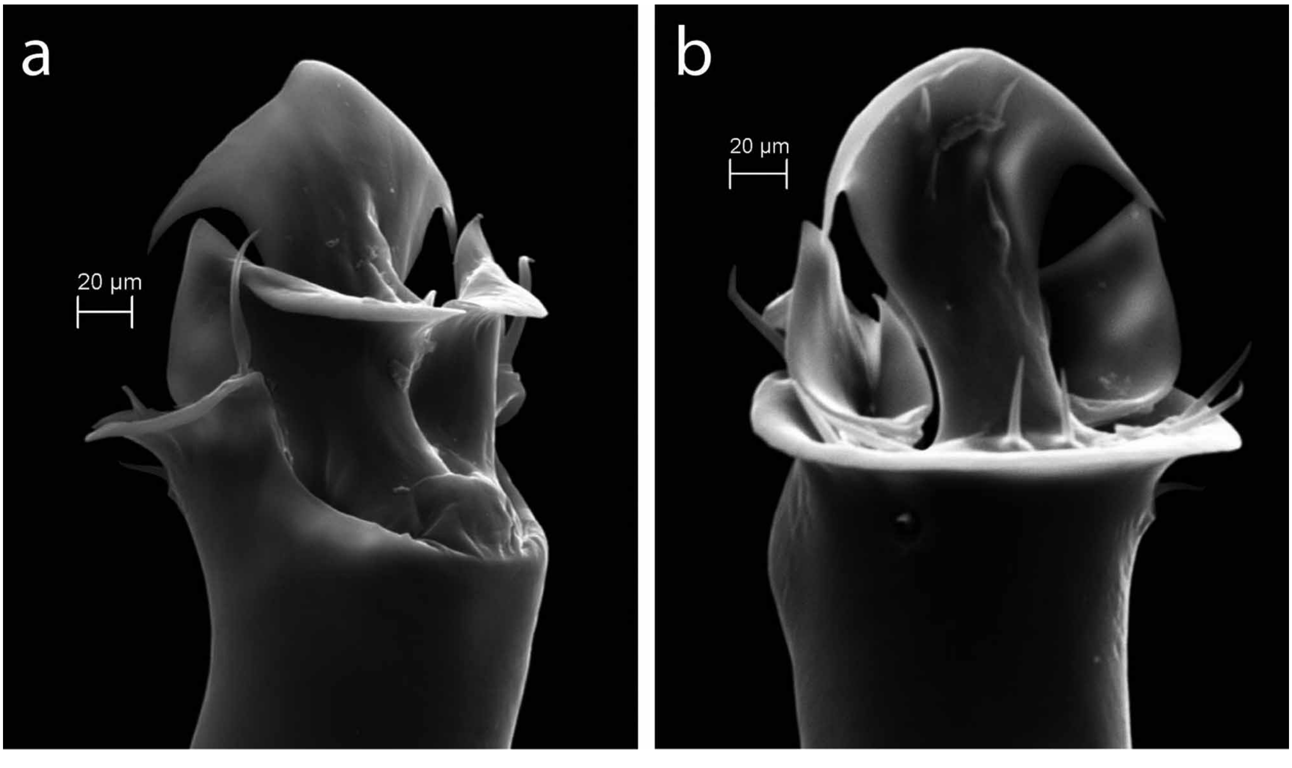

FIGURE 23. *Zalmoxis darwinensis* Goodnight & Goodnight, 1948. (a) Pars distalis of male genitalia, dorsolateral view; (b) Pars distalis of male genitalia, ventrolateral view.

Results

Maximum likelihood analysis of the six-gene dataset resulted in a tree topology with ln*L* = -20363.67 (Fig. 24). Monophyly of Zalmoxidae, when rooted with the three specimens of *Fissiphallius*, is supported (BS = 95%), as is the monophyly of the Indo-Pacific Zalmoxidae (BS = 100%), all in the genus *Zalmoxis*. While nodal support for internal relationships within the Indo-Pacific clade is limited, there is moderate support for the monophyly of the New Caledonian species (BS = 70%) and the sister relationship of this group to the Fijian *Zalmoxis* cf. *insularis* (BS = 60%). The placement of *Zalmoxis mendax* **sp. nov.** as sister group to the remaining New Caledonian *Zalmoxis* is also moderately supported (BS = 61%).

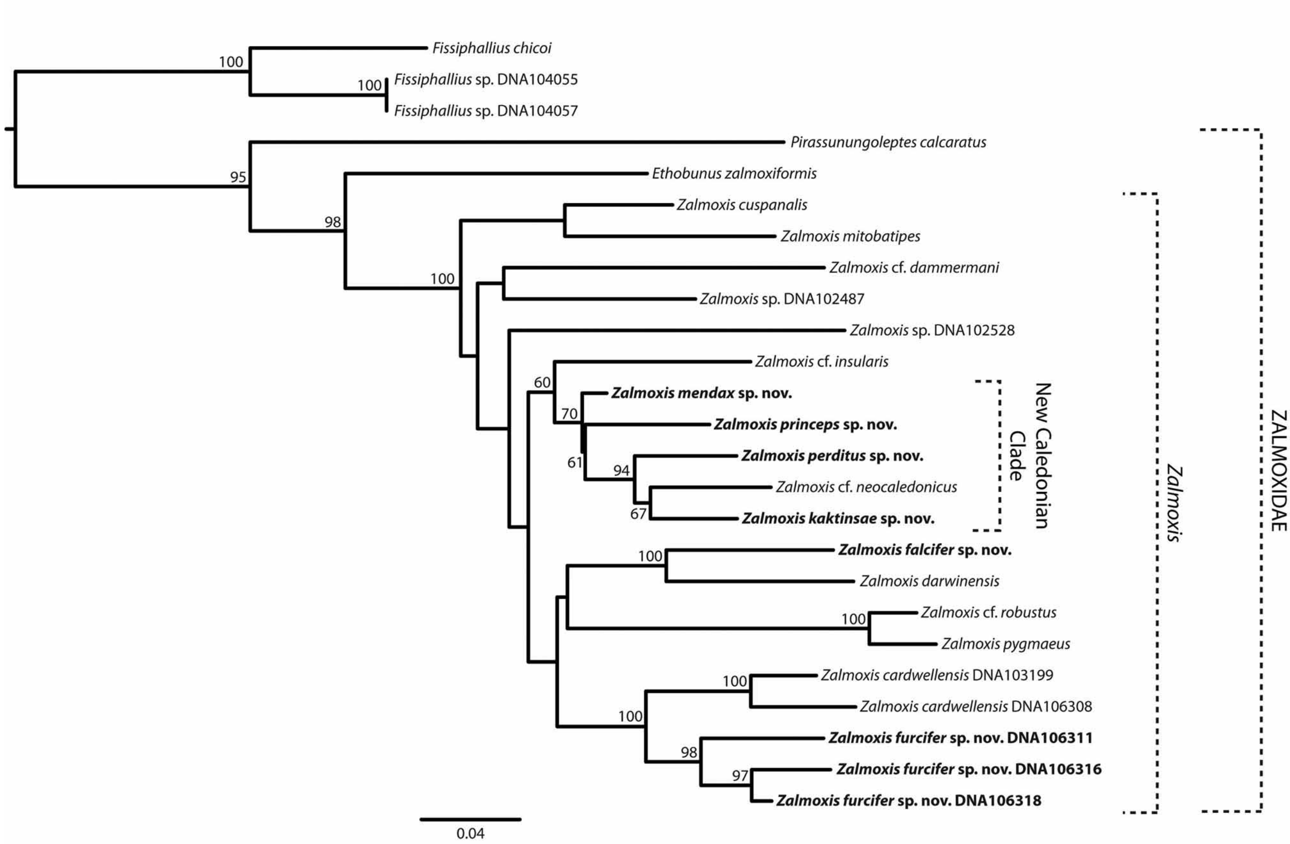

FIGURE 24. Phylogenetic relationships of *Zalmoxis* inferred from maximum likelihood analysis of six molecular loci (ln*L* = -20363.67). Numbers on nodes indicate bootstrap resampling frequencies. Newly described species are in boldface.

Discussion

During their complex taxonomic history, the Indo-Pacific Zalmoxidae have been divided into approximately 20 genera, many of these monotypic and erected arbitrarily (*e.g.*, Roewer, 1915, 1949). Even subsequent to the swath of synonymies proposed by Goodnight & Goodnight (1957), a number of genera persisted until a recent revision reduced these to two: *Zalmoxis* and *Metazalmoxis* (Sharma *et al*. 2011). The latter, a monotypic genus known only from the Seychelles (Roewer, 1912), was examined and re-described over 70 years after its original description (Rambla, 1983). The genitalic structures illustrated by Rambla (1983) did not suggest a clear distinction between the two genera. However, owing to the unusual tarsal formula of *Metazalmoxis* (4: 8: 5: 5) with respect to that of *Zalmoxis* (3: 5–9: 5: 6), and given the unavailability of fresh *Metazalmoxis* specimens for extraction of genetic material and molecular sequence data, the two were maintained as separate genera (Sharma *et al.* 2011).

In the present study, I describe six new species of *Zalmoxis* from the Southwest Pacific. One of the New Caledonian species, *Zalmoxis kaktinsae* **sp. nov.**, bears the tarsal formula (3: 4: 5: 5). Another, *Zalmoxis mendax* **sp. nov.**, bears the tarsal formula (4: 7: 5: 6). These two unique tarsal formulae would, according to earlier criteria, justify novel generic assignment to these species. However, phylogenetic analysis of molecular sequence data of the new species place all six squarely within the genus *Zalmoxis*, with the New Caledonian species constituting a monophyletic group with variable tarsal formulae (3–4: 4–7: 5: 5–6) (BS = 70%; Figure 24). The inclusion and phylogenetic placement of new species in *Zalmoxis* that bear four tarsomeres on leg I and five tarsomeres on leg

IV—the putative apomorphies of *Metazalmoxis*—obviates taxonomic justification for *Metazalmoxis*. I therefore synonymize *Metazalmoxis* **new synonymy** with *Zalmoxis*. The type species of *Metazalmoxis* therefore becomes *Zalmoxis ferrugineus* (Roewer, 1912) **new combination**.

I additionally sequenced individuals from multiple populations of *Zalmoxis furcifer* **sp. nov.** (Fig. 24; three terminals retained for phylogenetic purposes). These specimens constitute a monophyletic species (BS = 98%) wherein the morphology is basically unchanged, but the lengths of the body and fourth walking leg differ in the males (Fig. 25). I also observe that the lengths of the legs do not vary discretely, but continuously throughout the three populations of *Zalmoxis furcifer* **sp. nov.** (20 males observed), such that each population has males with legs of variable length. This morphology is consistent with male polymorphism in *Zalmoxis furcifer* **sp. nov.** and constitutes the first report of this phenomenon in Zalmoxoidea.

Male polymorphism is taxonomically widespread in arthropods and associated with variation in male reproductive success (Shuster & Wade 2003; Taborsky *et al.* 2008). Known cases in Opiliones include supposedly extreme cases of chelicera, body size and pigmentation in the sexually dimorphic eupnoid family Monoscutidae (Forster 1944; Taylor 2011). Among Laniatores, male di- or polymorphism occurs in many Gonyleptoidea and is associated with alternative mating strategies (large males, or majors, are territorial and combative; small males, or minors, sneak copulations) (Buzatto *et al.* 2011). Recent studies testing behavioral predictions arising from the allometry of the appendages in Gonyleptidae found the morphology consistent with these alternative mating strategies even when the elongate leg (used for male-male competition) varied in length continuously (Buzatto *et al.* 2011; Zatz *et al.* 2011), a putative case of male polyphenism (West-Eberhard 2003)—although typically, the term "polyphenism" is restricted to the case in which two or more distinct phenotypes are elicited by the environmental cue without intermediate phenotypes (Fusco & Minelli 2010). Such cases of polyphenic males are postulated to result from genetic variation in the distribution of the switch points that determine which morphotype is expressed under each value of the environmental cue (Tomkins & Hazel 2007; Fusco & Minelli 2010). Among insects, the mechanism of polyphenism involves environmental stimuli altering patterns of endocrine interactions, resulting in the execution of alternative developmental pathways (Emlen & Nijhout 2001; Nijhout 2003).

As with the gonyleptids investigated previously (Buzatto *et al.* 2011; Zatz *et al.* 2011), I am unable to categorize the variation in males of *Zalmoxis furcifer* **sp. nov.** into discrete morphs in the absence of a statistical arbiter (*e.g.*, Knell 2009), owing to the continuous variation in leg length. The occurrence of this phenomenon in multiple species of Gonyleptoidea and its association with alternative mating strategies suggests that male polymorphism in *Zalmoxis furcifer* **sp. nov.** may be similarly attributable to alternative mating strategies. However, this remains entirely speculative insofar as no data exists to our knowledge on the behavior or life cycle of any Zalmoxidae, and large sample sizes are required to pursue such behavioral studies. However, the accessibility of this species' multiple collecting localities, as well as its hardiness in captivity for at least 3–4 weeks (Ronald M. Clouse and I kept 16 individuals of *Zalmoxis furcifer* **sp. nov.** alive in Australia during this period for observation, but had to desist upon the end of the collecting trip; unpublished observation), could make testing this hypothesis relatively facile in future.

Though male polymorphism had not been reported in Zalmoxoidea heretofore, there does exist circumstantial evidence that this phenomenon occurs more broadly within the superfamily. Some other species of Zalmoxidae exhibit a sexually dimorphic leg IV that is unarmed and elongate, the superlative exemplars including the Philippine species *Zalmoxis cuspanalis* Roewer, 1927 and *Zalmoxis mitobatipes*, and multiple constituents of the Neotropical genera *Pachylicus* Roewer, 1923 (Goodnight & Goodnight, 1983) and *Traiania* Soares & Avram, 1981 (González-Sponga, 1987). In some cases, previous workers observed males of one species with variably sized legs (*e.g.*, *Pachylicus hirsutus* Goodnight & Goodnight, 1983), but did not have a sufficiently large sample size to attribute the observation to male polymorphism (*e.g.*, *Pachylicus hirsutus* was known from six males, only one of which had shortened fourth legs; Goodnight & Goodnight, 1983). Taken to an extreme, overlooking the possibility of male polymorphism in Zalmoxidae could engender multiple spurious descriptions of the same species. For example, species of *Traiania* are distributed in close proximity to each other, and several have remarkably similar genitalia (González-Sponga, 1987), which is suggestive of polymorphic males. However, one of the diagnostic characters utilized by González-Sponga was the length of the male leg IV, which is bound to result in multiple synonymous species if male polymorphism occurs in one or more *Traiania* (González-Sponga, 1987). The documentation of polymorphic males in *Zalmoxis furcifer* **sp. nov.** is therefore advocative of reexamination of previously described species that differ only in the lengths of sexually dimorphic legs.

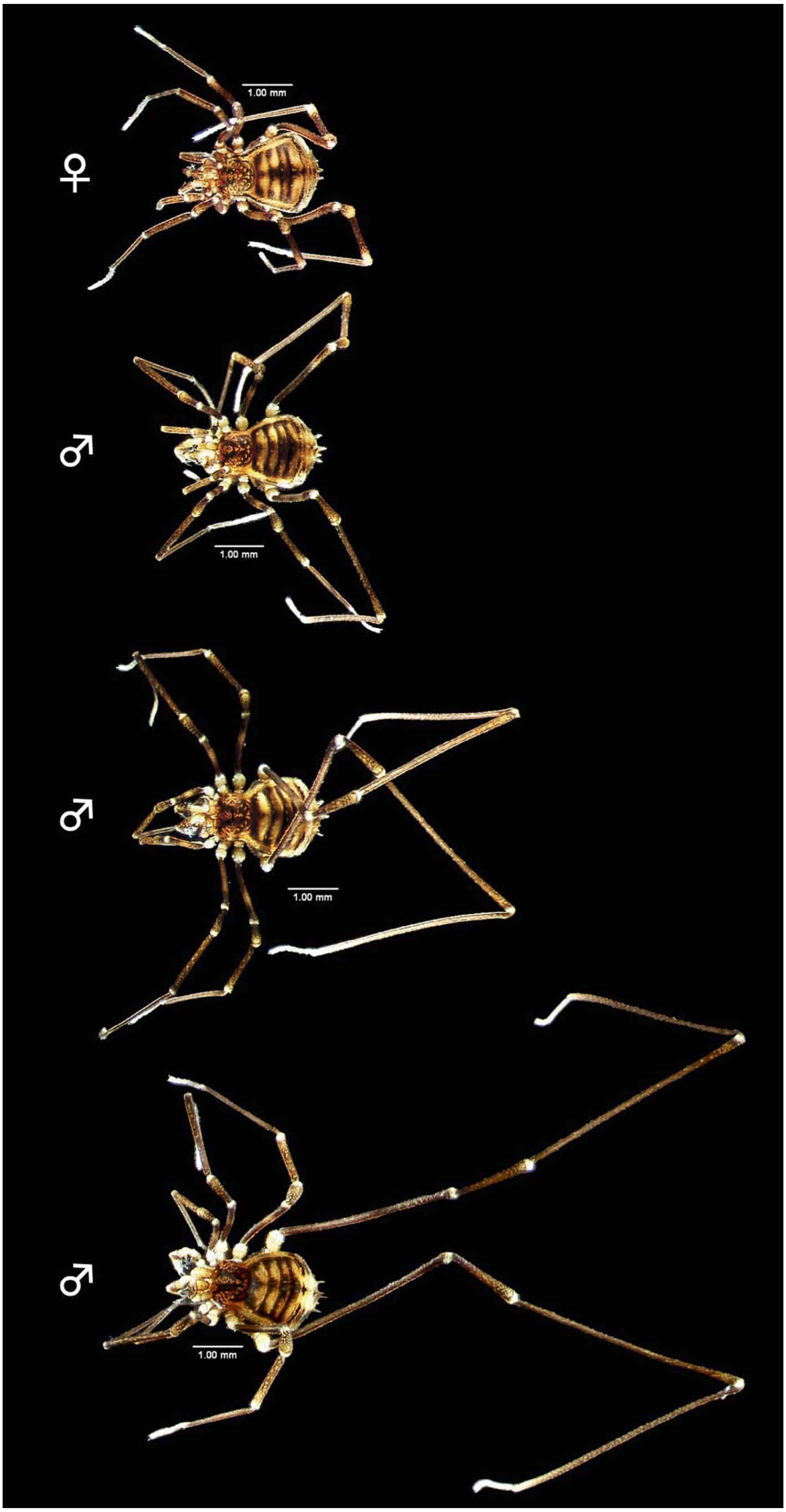

FIGURE 25. Male polymorphism in *Zalmoxis furcifer* **sp. nov.** Paratype specimens photographed are from the same collecting locality (Daintree National Park, Mossman Gorge, on trail at end of road, Cape Tribulation section, Queensland [16° 28' 19.5" S, 145° 19' 49.7" E], Australia, 69 m elevation).

The description of these six species doubles the number of New Caledonian *Zalmoxis* and nearly doubles that of Australian *Zalmoxis*. A significant addition to known morphological modifications in Opiliones is the spectacular tibial embellishment of *Zalmoxis falcifer* **sp. nov.** The addition of genitalic illustrations for the six new species, as well as for *Zalmoxis darwinensis* (Fig. 23) also contributes generally to known morphological diversity of pergula shape and setation, an important set of characters for zalmoxid taxonomy. Variation in genitalic morphology has been insufficiently investigated in Paleotropical Zalmoxidae, making it difficult at present to infer homology of structures or propose genitalic synapomorphies for derived clades. However, the fragmentary data available for some *Zalmoxis* corroborates the potential utility of male genitalia as a source of phylogenetically informative characters. For example, the genitalia of two northern Australian sister species, *Zalmoxis darwinensis* and *Zalmoxis falcifer* **sp. nov.** (BS = 100%), are very similar with respect to setation and rutrum shape, as well as stragulum shape (Figs. 18, 23). Similarly, the "double" pergula morphology occurs only in a derived clade among the New Caledonian species, which includes *Zalmoxis kaktinsae* **sp. nov.** and *Zalmoxis perditus* **sp. nov.** (BS = 94%) (Figs. 12, 14). The genitalic morphology of the third member of this clade, *Zalmoxis neocaledonicus*, is presently unknown. Redoubled efforts to assess the variation and phylogenetic informativeness of genitalic morphology are anticipated to inform identification of synapomorphies for derived species groups in future.

On a biogeographical note, I also observe that *Zalmoxis princeps* **sp. nov.** is distributed throughout several formerly contiguous forests in southern New Caledonia, similar to the distantly related cyphophthalmid harvestman *Troglosiro juberthiei* Shear, 1993 (Shear, 1993; Sharma & Giribet, 2009b), another New Caledonian endemic. Paleotropical zalmoxid diversity and distribution remains greatly underestimated and potentially dozens of undiscovered species await formal description. For example, the limits of zalmoxid range in the Philippine islands (beyond Luzon and Mindanao; Sharma *et al.* 2011) are unclear. Similarly, it remains unknown whether Zalmoxidae even occur in Borneo. The origins of the Indian Ocean *Zalmoxis* are also unknown, though it is likely that these species colonized Mauritius and the Seychelles from Southeast Asia by way of the South Equatorial Current (the distribution of the unrelated family Podoctidae, whose origin is reconstructed to Southeast Asia (Sharma & Giribet 2011), similarly includes the Seychelles, Reunion, Madagascar, and parts of East Africa). I anticipate that future systematic efforts will elucidate the biogeography of this curious South Pacific genus.

Acknowledgements

I am indebted to Jerome Murienne and Ronald M. Clouse for their indefatigable efforts, awareness, and invaluable wisdom in the field. Gonzalo Giribet supervised the research and greatly improved an earlier version of this manuscript. Collecting efforts in New Caledonia were greatly facilitated by the guidance of Hervé Jourdan (Institut de recherché pour de developpement, Noumea) and his team members. Collecting efforts in Fiji were made possible by Marika Tuiwawa (University of the South Pacific, Suva) and his team members Hilda Waqa and Tokasaya "Tox" Cakacaka (who contributed to fieldwork). Suzie Yee Shaw provided invaluable logistical support in Fiji, and her sons Colin and Joshua Yee Shaw assisted with sorting Fijian material. Collections from the Philippines were made available thanks to Arvin C. Diesmos, Perry A.C. Buenavente, and Rafe Brown. Collecting efforts in Australia were generously aided by Sarah L. Boyer, Alan Andersen, Ben Hoffmann, and Graham Brown. Discussions with Abel Pérez-González refined the taxonomic action and ideas presented here. Laura Leibensperger sorted and accessioned Zalmoxidae collections from the Southwest Pacific, and assisted with designation and distribution of type specimens. Adam Graham and the Center for Nanoscale Studies at Harvard University provided support for SEM work. Fieldwork in New Caledonia was supported by the Goelet award, the Kalathia Family Trust, and the Explorers Club, awarded to P.P.S. in 2006. Fieldwork in Fiji and the Philippines was supported by two MCZ Putnam Expedition Grants, awarded to P.P.S. (2008), and to Ronald M. Clouse and P.P.S (2009), respectively. Fieldwork in Australia was supported by a Deakin-Royce Fellowship, awarded to P.P.S. (2011). Molecular study was facilitated by the Life Sciences DNA Sequencing Facility (Harvard University) and supported by the BioNeoCal grant. Adriano Kury, Abel Pérez-González, and an anonymous referee reviewed this work for publication.

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