Zootaxa 3280: 29–55 (2012)
www.mapress.com/zootaxa/

Article

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

Forgotten gods: Zalmoxidae of the Philippines and Borneo (Opiliones: Laniatores)

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Abstract

The limits of zalmoxid distribution in Southeast Asia are poorly understood, but a focus of recent research. Here we describe six new species of litter-inhabiting harvestmen in the genus *Zalmoxis* Sørensen, 1886 (Opiliones: Laniatores: Zalmoxidae) using light microscopy and SEM. Three of these species are from the Philippine Islands (*Zalmoxis gebeleizis* **sp. nov.**, *Zalmoxis derzelas* **sp. nov.**, and *Zalmoxis sabazios* **sp. nov.**) and the other three from Borneo (*Zalmoxis zibelthiurdos* **sp. nov.**, *Zalmoxis bendis* **sp. nov.**, and *Zalmoxis kotys* **sp. nov.**). The collecting localities of these species add to the known range of Zalmoxidae, which have not previously been reported from Borneo. The new species add to known morphological variation of *Zalmoxis*, specifically with respect to sexually dimorphic tarsomeres, body size, and armature of the anal plate.

Key words: Grassatores, *Zalmoxis*, Zalmoxoidea, Southeast Asia

Introduction

> "The belief of the Getae in respect of immortality is the following. They think that they do not really die, but that when they depart this life they go to Zalmoxis, who is called also Gebeleizis by some among them. To this god every five years they sacrifice a messenger, who is chosen by lot out of the whole nation, and charge to bear him their several requests [to Zalmoxis]." —Herodotus, *Histories*, Book IV, 94–96.

The opiliofauna of the Philippine Islands is remarkably diverse, harboring lineages with disparate evolutionary histories that are only beginning to be understood. These include an ancient lineage of Cyphophthalmi recently discovered in Mindanao (Clouse *et al.* 2011); the recently described family Petrobunidae, the nominal genus of which is endemic to the Philippines (Sharma & Giribet 2011); the elusive and strictly Southeast Asian family Sandokanidae, with the genus *Biantoncopus* Martens & Schwendinger endemic to Leyte (Martens & Schwendinger 1998; Schwendinger 2007; Sharma & Giribet 2009); and the curious lineage Zalmoxidae, which is notable for its disjunct, amphi-Pacific distribution (Kury & Pérez-González 2007; Giribet *et al.* 2010; Sharma *et al.* 2011).

Subsequent to an extensive revision of Zalmoxidae—made necessary by a turbulent taxonomic history (Staręga 1989; Kury 2003; Sharma *et al.* 2011; Sharma 2012)—the nominal genus *Zalmoxis* Sørensen, 1886 is presently known to occur in the Indian Ocean (Mauritius, the Seychelles Islands), several Pacific island groups (Fiji, Micronesia, New Caledonia, the Solomon Islands), as well as the tropics of Australia, New Guinea, the Molucca Islands, Sulawesi, Java, and the Philippine Islands. The zalmoxids of the Philippines are known from two islands: four species are described from Luzon (*Zalmoxis soerenseni* Simon, 1892, *Zalmoxis mitobatipes* (Roewer, 1926), *Zalmoxis cuspanalis* Roewer, 1927 and *Zalmoxis luzonicus* Roewer, 1949) and two from Mindanao (*Zalmoxis heynemani* Suzuki, 1977 and *Zalmoxis mindanaonicus* Suzuki, 1977). The only reported collections of zal-

Accepted by A. Pérez-González: 14 Mar. 2012; published: 26 Apr. 2012

moxids from these islands (in fact, the type material of these six species) occurred over half a century ago. No zalmoxids have been recorded from other islands in the Philippines or from Borneo, which most probably is a sampling artifact, given the presence of suitable forest habitat on these islands, and the occurrence elsewhere of Zalmoxidae on numerous islands of smaller size and poorer habitat quality (*e.g.*, *Zalmoxis bonka* (Forster, 1949) from Savo Island; Sharma *et al.* 2011).

In order to broaden knowledge of Zalmoxidae and address the limits of the range of *Zalmoxis* in Southeast Asia, new material was obtained from researchers from the National Museum of the Philippines. Additionally, we examined older museum collections of Opiliones from the Philippines and Borneo. In this study, six new species of *Zalmoxis* are described: one from Panay, one from Mindoro, one from Palawan, and three from Borneo. We additionally illustrate the genitalia and anal plate armature of *Zalmoxis mitobatipes* and *Zalmoxis cuspanalis* from material collected in a 2010 expedition to Luzon (*Zalmoxis soerenseni* and *Zalmoxis luzonicus* were not found on this trip), as we obtained recent collections of these two species more than 80 years after they were last reported.

Materials 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)
MHNG—Muséum d'Histoire naturelle, Ville de Genève (Switzerland)
MNHN—Muséum National d'Histoire naturelle, Paris (France)
NMP—National Museum of the Philippines, Manila (Philippines)

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 male paratypes were also examined using SEM. Specimens used for DNA extraction are indicated as such among the type material. All measurements are given in mm unless otherwise indicated. Nomenclature of body ornamentation follows Murphree (1988).

The following type material has been examined for comparison:

Zalmoxis marchei Roewer, 1912: male holotype and 5 male paratypes (MNHN) from Mariana Islands (without specific locality).

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.

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.

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 gebeleizis sp. nov.

Figs. 1–4, 22b

Types. Male holotype (PNM [ex MCZ DNA104059]) from the research station of the Philippine Endemic Species Conservation Program (PESCP), Sibaliw, Municipality of Buruanga, Province of Aklan, Panay Island (11º 49’ 11” N, 121º 58’ 0” E), Philippines, 450 m elevation, collected October 2008 by Cichosz & Einhaupl. 2 female paratypes (in ethanol), same collecting data as holotype (PNM [ex MCZ DNA104059]). 2 male (1 dissected for genitalia, mounted on SEM stub MCZ 124579; 1 mounted on SEM stubs 124576–124577) and 4 female (1 used for DNA extraction [ex MCZ DNA104060]; 1 mounted on SEM stubs MCZ 124576, 124578; 2 in ethanol) paratypes, same collecting data as holotype (MCZ 124575). 1 male paratype (in ethanol) (MNHG [ex MCZ DNA104058]) and 2 female paratypes (in ethanol) (MHNG [ex MCZ DNA104060]), same collecting data as holotype.

Etymology. Like the genus name, the specific epithet, a noun in apposition, refers to a god of the Getae (or Thracians, an ancient civilization of Indo-Europeans that inhabited the territory to the north and east of the Aegean Sea, and had extensive contact with the Greeks and Romans). Gebeleizis was the bearded god of thunderstorms and possibly a synonym or reincarnation of Zalmoxis.

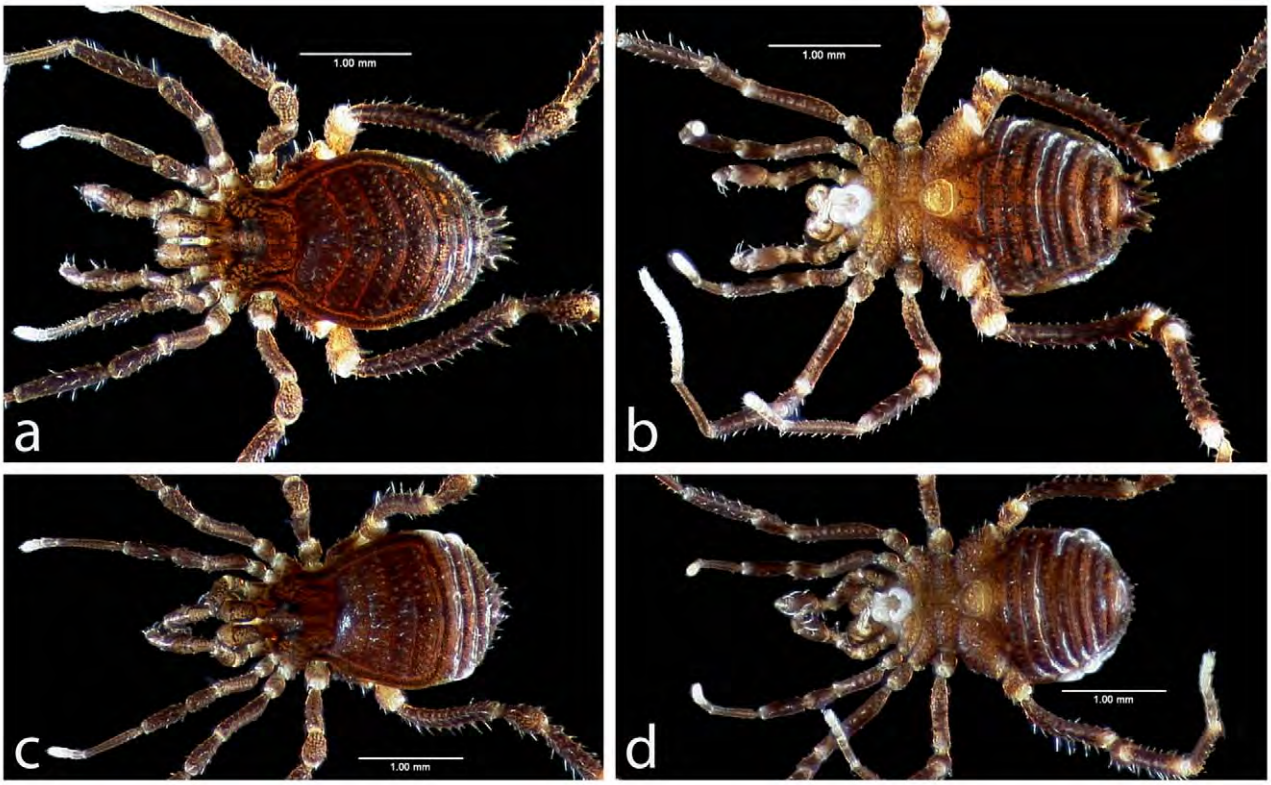

FIGURE 1. *Zalmoxis gebeleizis* **sp. nov.** (a) Male holotype, dorsal view; (b) Male holotype, ventral view; (c) Female paratype, dorsal view; (d) Female paratype, ventral view.

Diagnosis. Distinguished from congeners in the armature of the anal plate, which bears a pair of large bifurcating, setose tubercles; and in the male genitalia, wherein the rutrum bears three pairs of setae, and the pergula is medially jointed and bears two ventrolateral pairs of setae.

Description. Total length of male holotype (female paratype [MCZ 124575] in parentheses) 2.55 (2.34), greatest width of prosoma 0.96 (0.88), greatest width of opisthosoma 1.68 (1.60); length-to-width ratio 1.52 (1.46). Body campaniform, reddish brown to dark brown (in ethanol, depending on incidence of light), lighter in color in the trochanters and distal tips of all legs, 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 forming obtuse "V" shape anteriorly in male, grooves less arcuate in female. Mesotergum and 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 anteriorly. 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 two rows of tubercles: posterior row with four setose tubercles, middle pair more prominent than flanking pair; anterior row with three large setose tubercles, flanking pair of tubercles bifurcating and with broad bases (Figs. 2, 22b).

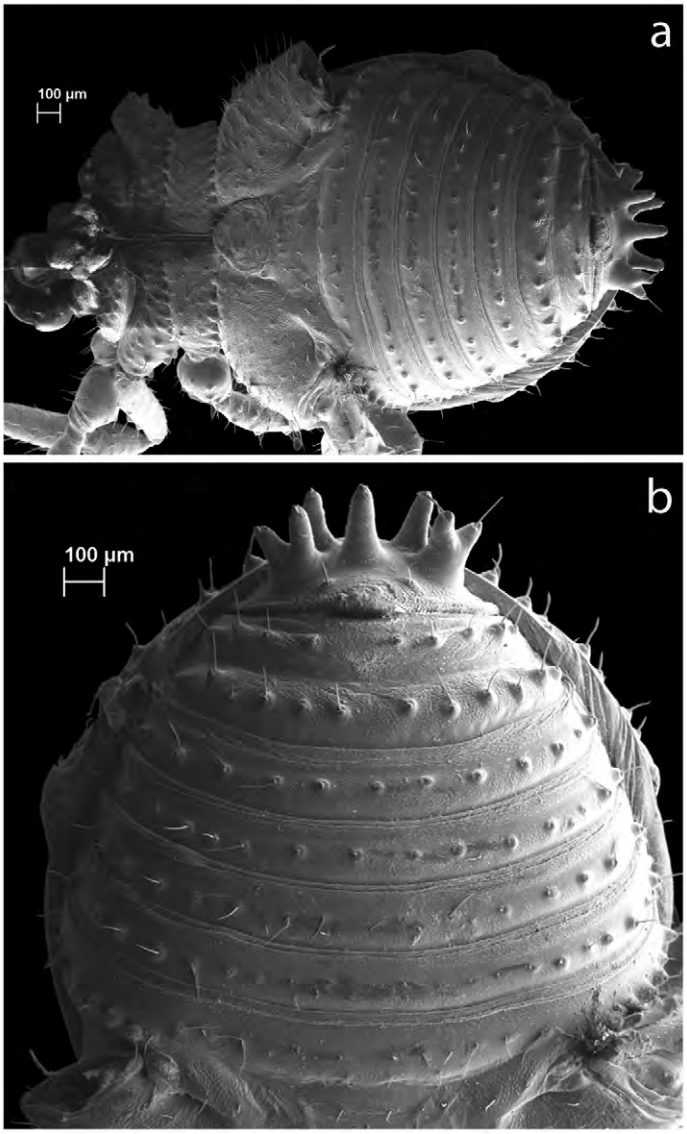

FIGURE 2. *Zalmoxis gebeleizis* **sp. nov.** (a) Ventral view of male paratype; (b) Opisthosomal region of male paratype.

Chelicerae (Fig. 3a) sexually monomorphic, with prominent bulla on proximal article. Proximal article with denticulate granulation basally and ventrally. Second article not incrassate, smooth, 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.

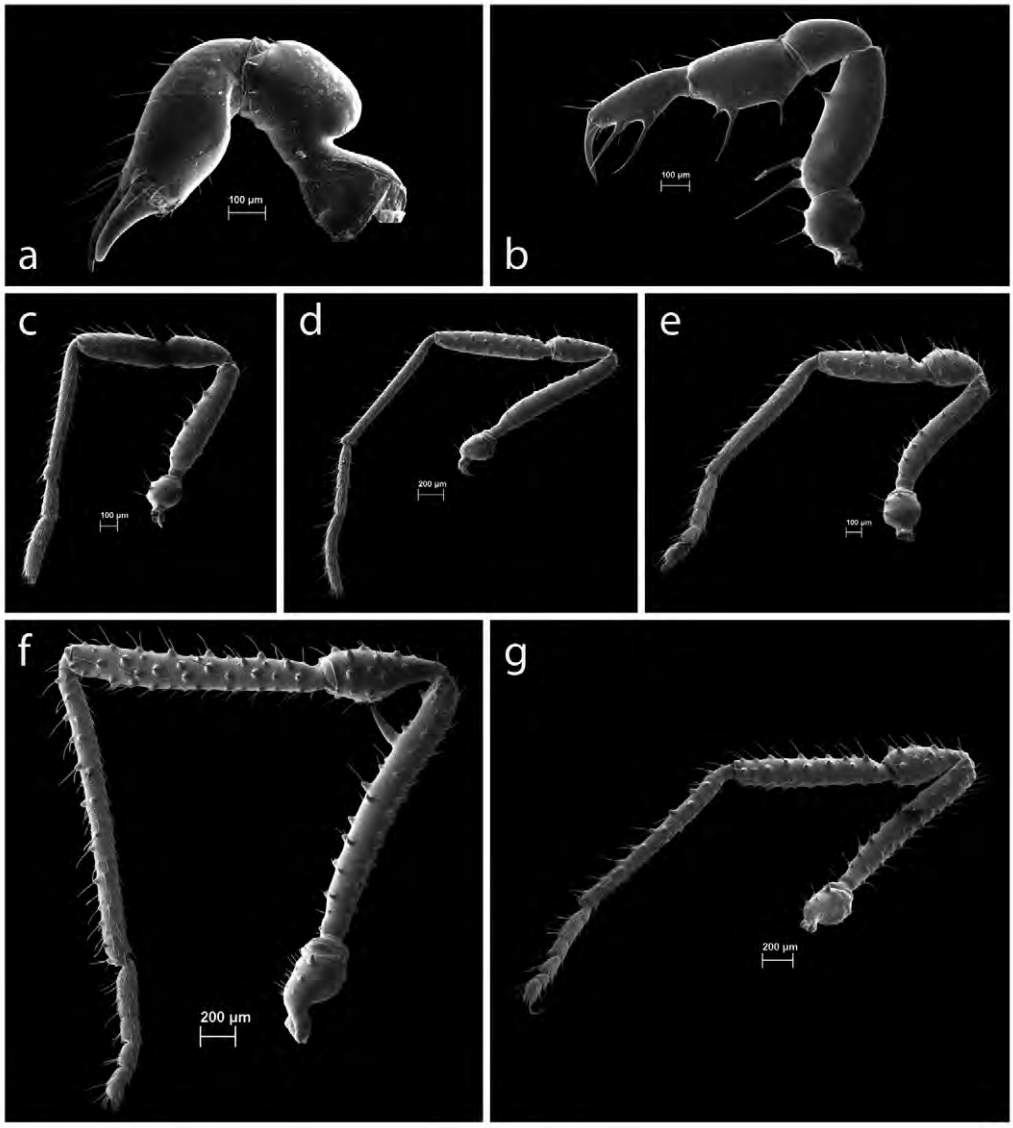

FIGURE 3. *Zalmoxis gebeleizis* **sp. nov.** (a) Left chelicer of male paratype; (b) Left palp of male paratype; (c) Male left leg I; (d) Male left leg II; (e) Male left leg III; (f) Male left leg IV; (g) Female left leg IV.

Legs (Figs. 3c–g) finely granulated. Trochanters, patellae, and tibiae of all legs bearing irregular rows of setose tubercles. Leg I (Fig. 3c) trochanter with one small tubercle dorsally and two tubercles ventrally. Male leg IV (Fig. 3f) sexually dimorphic, elongated, and armed. Male trochanter IV with mesal row of three small tubercles enlarging distally, one prominent posterior tubercle. Male femur IV slightly arcuate, bearing ventral and ventrolateral row of tubercles, with single large ventral tubercle on subdistal portion. Male patella and tibia IV with 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: 6: 5: 5.

Appendage measurements of holotype (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.21/0.19	0.74/0.16	0.41/0.17	0.52/0.17	0.83/0.09	0.60/0.10	3.31
Leg II	0.22/0.21	1.00/0.14	0.42/0.16	0.78/0.16	0.97/0.08	1.08/0.08	4.47
Leg III	0.26/0.25	0.87/0.17	0.44/0.23	0.67/0.20	1.04/0.12	0.68/0.10	3.96
Leg IV	0.26/0.15	0.82/0.10	0.37/0.16	0.73/0.10	0.91/0.06	0.40/0.06	3.49
Palp	0.21/0.21	0.52/0.21	0.33/0.18	0.34/0.22	—	0.39/0.15	1.79
	Proximal	Second	Distal				
Chelicera	0.56/0.27	0.75/0.24	0.24/0.05				

Appendage measurements of female paratype (MCZ 124575) (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.19/0.16	0.61/0.15	0.33/0.17	0.45/0.15	0.71/0.08	0.54/0.10	2.83
Leg II	0.23/0.20	0.95/0.15	0.48/0.18	0.74/0.16	0.92/0.08	1.06/0.09	4.38
Leg III	0.22/0.22	0.77/0.15	0.36/0.23	0.57/0.17	0.84/0.12	0.60/0.11	3.36
Leg IV	0.24/0.17	0.86/0.15	0.42/0.20	0.75/0.16	0.98/0.10	0.73/0.10	3.98
Palp	0.19/0.18	0.47/0.18	0.26/0.17	0.33/0.22	—	0.36/0.14	1.61
	Proximal	Second	Distal				
Chelicera	0.45/0.24	0.67/0.23	0.22/0.04				

Penis (Fig. 4) with three pairs of setae on rutrum and two ventrolateral pairs of long setae on pergula. One small ventrolateral pair of setae posterior to pergula. Rutrum of arrowhead shape, apical/distal portion with lateral extensions. Pergula flattened, not projecting ventrally, and disjointed medially.

Distribution. Known only from type locality.

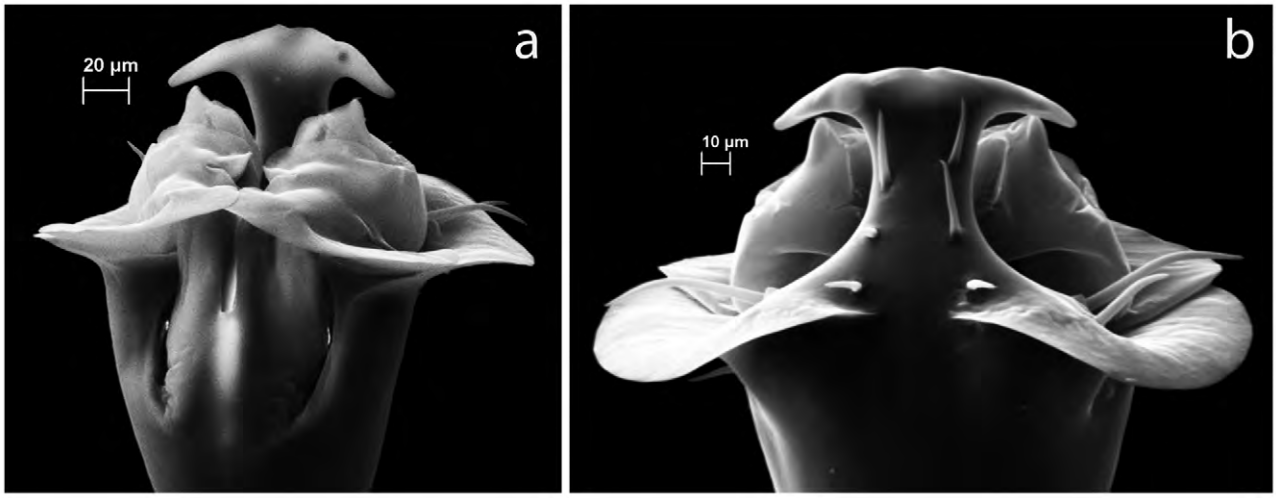

FIGURE 4. *Zalmoxis gebeleizis* **sp. nov.** (a) Pars distalis of male genitalia, dorsal view; (b) Pars distalis of male genitalia, ventral view.

Zalmoxis derzelas sp. nov.

Figs. 5–8, 22e

Types. Male holotype (NMP [ex MHNG PHI-79/117]) from moss and roots on a small cliff along a riverbank, in primary forest, Puerto Galera, Province of Orienal Mindoro, Mindoro Island, Philippines, 0–300 m elevation, collected 27–29 December 1979 by L. Deharveng and J. Crousset. 1 male paratype (MHNG), same collected data as

holotype. 2 male paratypes (1 dissected for genitalia and mounted on SEM stub MCZ 124585; 1 mounted on SEM stubs 124583–124584), same collecting data as holotype (MCZ 124582).

Additional material studied. 1 subadult female, same collecting data as holotype.

Etymology. The specific epithet, a noun in apposition, refers to a god of the Getae (or Thracians). Derzelas was the chthonic god of the afterlife.

Diagnosis. Distinguished from congeners in the slightly incrassate metatarsus III; and the male femur IV with a prominent ventrodistal tubercle, flanked distally by three small conical tubercles of equal size.

Description. Total length of male holotype 2.48, greatest width of prosoma 0.92, greatest width of opisthosoma 1.66; length-to-width ratio 1.49. Body campaniform, light brown (in ethanol, depending on incidence of light, and due to depigmentation over time), 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 arcuate, not forming "V" shape. Mesotergum and free tergites without regular belts of setose tubercles (Fig. 5).

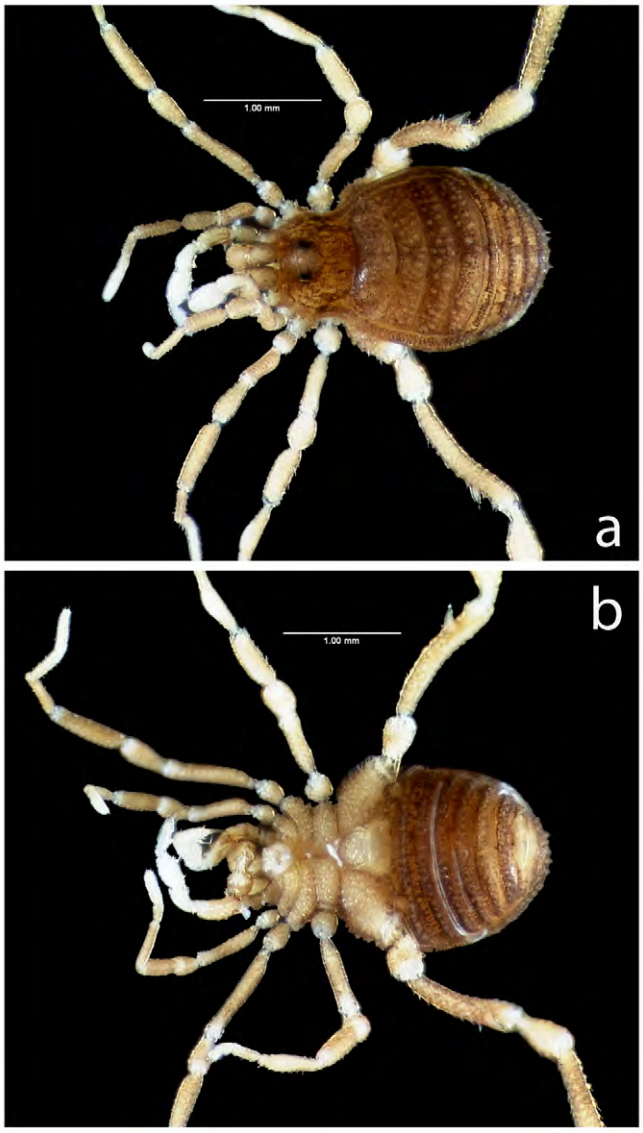

FIGURE 5. *Zalmoxis derzelas* **sp. nov.** (a) Male holotype, dorsal view; (b) Male holotype, ventral view.

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 anteriorly. Genital operculum sub-triangular.

Spiracles not concealed, anterior to row of tubercles. Opisthosomal sternites with regular belts of low setose tubercles enlarging laterally. Anal plate armed with two rows of blunt setose tubercles: posterior row with three setose tubercles, flanking more prominent; anterior row with five setose tubercles, enlarging medially (Figs. 6, 22e).

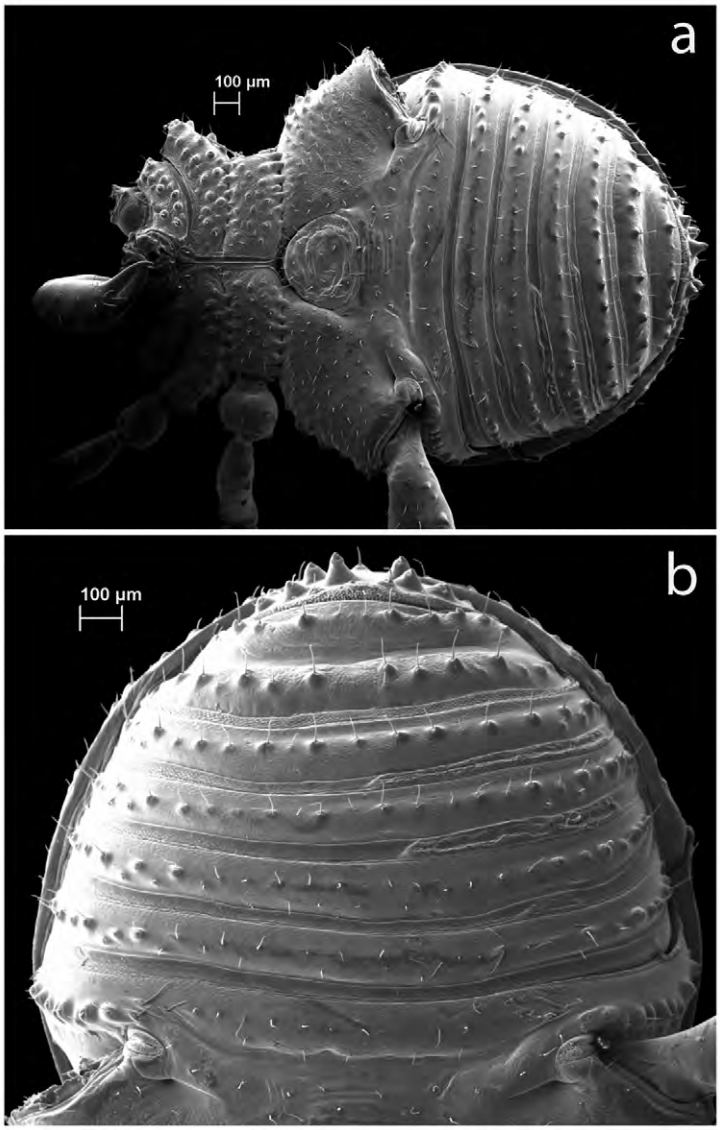

FIGURE 6. *Zalmoxis derzelas* **sp. nov.** (a) Ventral view of male paratype; (b) Opisthosomal region of male paratype.

Chelicerae (Fig. 7a) 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. 7b) robust and spined ventrally and/or ventrolaterally, typical of zalmoxids. Palpal tarsus with two pairs of megaspines.

Legs (Figs. 7c–f) finely granulated. Trochanters, patellae, and tibiae of all legs bearing irregular rows of setose tubercles. Leg I (Fig. 7c) trochanter with one small tubercle dorsally and two small tubercles ventrally. Male metatarsus III (Fig. 7e) slightly incrassate along transverse axis. Male leg IV (Fig. 7f) elongated and armed; trochanter with two small tubercles enlarging distally on mesal surface; femur slightly arcuate with a prominent ventrodistal tubercle, flanked distally by three small conical tubercles of equal size; patella and tibia with 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: 6: 5: 5.

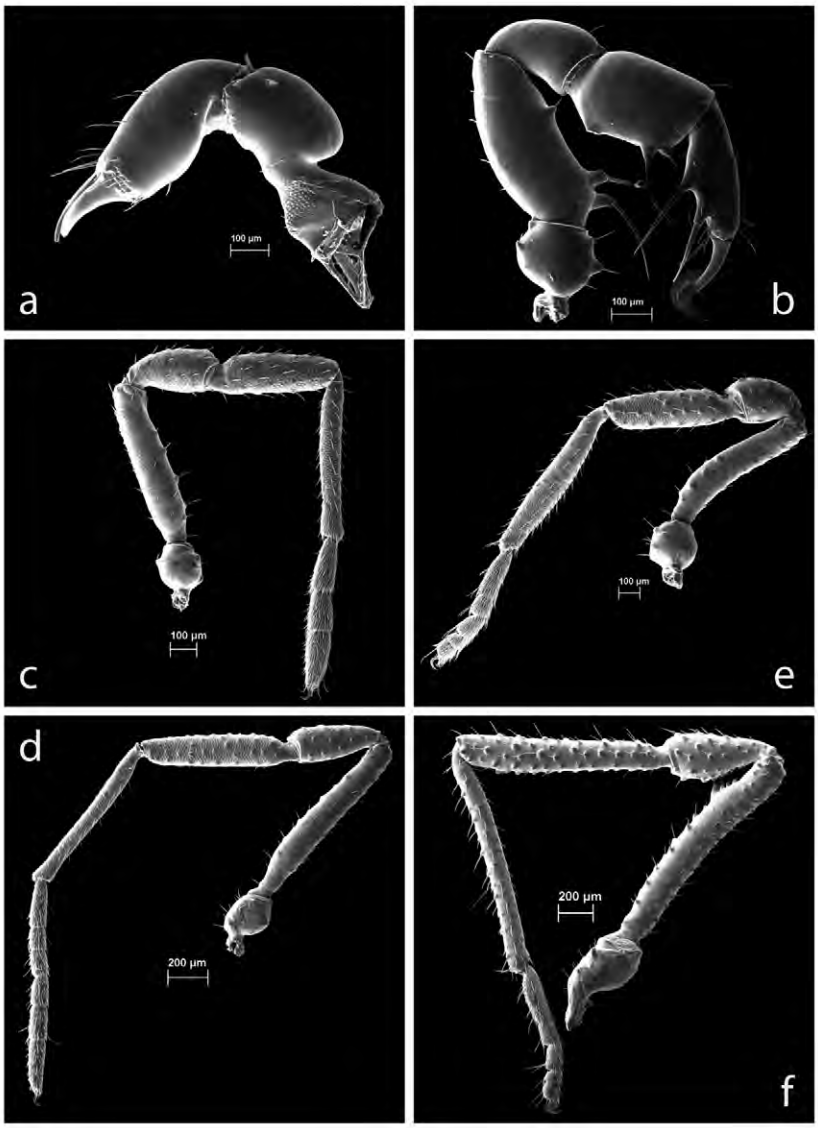

FIGURE 7. *Zalmoxis derzelas* **sp. nov.** (a) Left chelicer of male paratype; (b) Right palp of male paratype; (c) Male right leg I; (d) Male left leg II; (e) Male left leg III; (f) Male left leg IV.

Appendage measurements of holotype (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.13/0.12	0.48/0.10	0.28/0.12	0.33/0.11	0.49/0.06	0.44/0.007	2.15
Leg II	0.21/0.22	0.96/0.15	0.51/0.17	0.72/0.16	0.84/0.09	1.06/0.09	4.30
Leg III	0.16/0.16	0.52/0.11	0.28/0.15	0.41/0.12	0.59/0.10	0.44/0.07	2.40
Leg IV	0.25/0.14	0.68/0.10	0.34/0.13	0.59/0.10	0.68/0.06	0.39/0.05	2.93
Palp	0.17/0.19	0.44/0.19	0.29/0.16	0.29/0.21	—	0.35/0.13	1.54
	Proximal	Second	Distal				
Chelicera	0.47/0.24	0.67/0.22	0.19/0.05				

Penis (Fig. 8) with two pairs of setae on rutrum and one pair of setae at the boundary with the pergula. Pergula with one pair of ventrolateral setae and one pair of dorsolateral setae projecting ventrally. One small ventrolateral pair of setae posterior to pergula. Rutrum of arrowhead shape, apical/distal portion with lateral extensions.

Distribution. Known only from type locality.

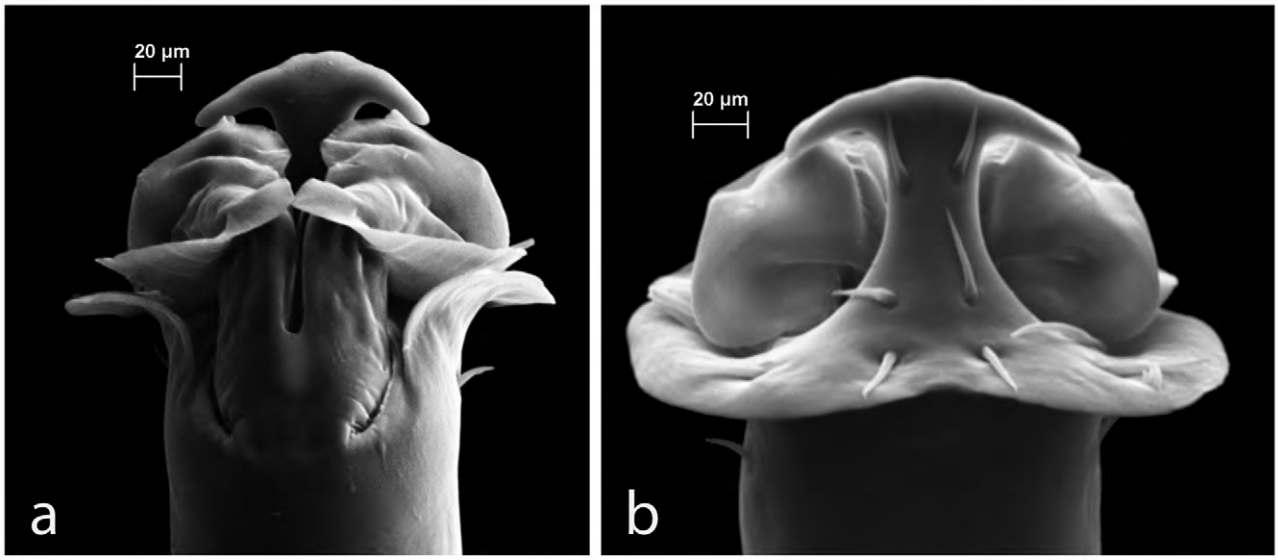

FIGURE 8. *Zalmoxis derzelas* **sp. nov.** (a) Pars distalis of male genitalia, dorsal view; (b) Pars distalis of male genitalia, ventral view.

Zalmoxis sabazios sp. nov.
Fig. 9–10

Types. Male holotype (NMP [ex MCZ DNA105635, ex MHNG PHI-09/07]) from Sabang Underground National Park, Daylight Hole and Lions Cave, in primary forest, Puerto Princesa Region, Palawan (10º 9’ 6” N, 118º 53’ 10” E), Philippine Islands, 100–200 m elevation, collected 6–8 December 2009 by A. Schulz. 1 female (used for DNA extraction [ex MCZ DNA106535]) paratype (MHNG), same collecting data as holotype.

Etymology. The specific epithet, a noun in apposition, refers to a god of the Getae (or Thracians). Sabazios was the god of the sky, often represented as a nomadic horseman.

Diagnosis. Distinguished from congeners by the single conical tubercle in the center of the anal plate; the belts of conical tubercles on the last two free tergites; the armature of the male femur IV, which bears irregular rows tubercles, the largest and most distal tubercle directed posterolaterally; and the armature of the male tibia IV, which bears a posterolateral row of five tubercles restricted to proximal half of segment and a ventral row of three tubercles, with the largest distal-most.

Description. Total length of male holotype (female paratype in parentheses) 2.60 (2.14), greatest width of prosoma 0.94 (0.88), greatest width of opisthosoma 1.72 (1.66); length-to-width ratio 1.51 (1.29). Body campaniform, dark orange to brown (in ethanol, 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 forming obtuse “V” shape anteriorly. Mesotergum and free tergites with regular belts of setose tubercles. Last two free tergites bearing rows of pointed setose tubercles (Fig. 9).

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 anteriorly. 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 two rows of tubercles: posterior row with four low tubercles; anterior row with three tubercles, median tubercle larger and prominent (Fig. 9).

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.

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

Legs finely granulated. Trochanters, patellae, and tibiae of all legs bearing irregular rows of setose tubercles. Femur of leg I with minute ventral row of tubercles. Male leg IV incrassate and armed. Trochanter IV with one prominent posterior tubercle. Femur IV of male arcuate with irregular rows of tubercles and one larger subdistal tubercle directed posterolaterally. Tibia IV of male incrassate with two rows tubercles: posterolateral row consisting of 5 tubercles extending to middle of podomere's length and enlarging distally; ventral row irregular, with two tubercles in middle of podomere's length and a large distal tubercle projecting distally. 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.

Penis (Fig. 10) with two pairs of setae on rutrum with bases in close proximity, and three pairs of setae on pergula (one medial, two ventrolateral) with bases in close proximity. One small dorsolateral pair of setae posterior to pergula. Rutrum shaped as an anchor, lateral extensions with fimbriate margins. Pergula protruding slightly.

Distribution. Known only from type locality.

Appendage measurements of holotype (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.17/0.17	0.58/0.15	0.35/0.17	0.46/0.16	0.57/0.07	0.52/0.10	2.65
Leg II	0.24/0.21	0.95/0.16	0.50/0.21	0.83/0.17	0.94/0.08	1.15/0.10	4.61
Leg III	0.25/0.27	0.75/0.16	0.38/0.26	0.63/0.20	0.80/0.13	0.58/0.11	3.39
Leg IV	0.40/0.30	1.50/0.20	0.65/0.34	1.13/0.33	0.98/0.16	0.75/0.12	5.41
Palp	0.20/0.16	0.40/0.16	0.27/0.17	0.43/0.24	—	0.27/0.15	1.57
	Proximal	Second	Distal				
Chelicera	0.32/0.20	0.55/0.21	0.20/0.05				

Appendage measurements of female paratype (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.19/0.15	0.54/0.14	0.30/0.16	0.39/0.15	0.59/0.08	0.47/0.09	2.48
Leg II	0.22/0.17	0.83/0.16	0.36/0.20	0.66/0.18	0.80/0.08	1.04/0.10	3.91
Leg III	0.24/0.25	0.68/0.17	0.35/0.24	0.55/0.17	0.79/0.10	0.61/0.11	3.22
Leg IV	0.34/0.24	1.02/0.17	0.50/0.25	0.83/0.21	1.04/0.13	0.77/0.10	4.50
Palp	0.19/0.16	0.48/0.15	0.23/0.16	0.30/0.19	—	0.31/0.14	1.51
	Proximal	Second	Distal				
Chelicera	0.31/0.20	0.56/0.21	0.19/0.05				

***Zalmoxis zibelthiurdos* sp. nov.**
Figs. 11–14

Types. Male holotype (MHNG [ex MCZ DNA104061]) from East Kalimantan Province, Sungai Wain Protection Forest, ca. 15 km north of Balikpapan, Borneo, (1º 8’ 36” N, 116º 50’ 59” E) Indonesia, 80 m elevation, collected 5 October 2008 by P.J. Schwendinger. 2 male and 4 female paratypes (MHNG), same collecting data as holotype. 2 male and 4 female paratypes (NMP), same collecting data as holotype. 4 male (1 in ethanol; 2 dissected for genitalia and mounted on SEM stub MCZ 124590; 1 mounted on SEM stubs MCZ 124587–124588) and 4 female (1 mounted on SEM stubs MCZ 124587, 124589) paratypes, same collecting data as holotype (MCZ 124586).

Etymology. The specific epithet, a noun in apposition, refers to a god of the Getae (or Thracians). Zibelthiurdos was the god of storms and wielder of lightning—possibly a manifestation of Gebeleizis and/or the Greek god Zeus.

Diagnosis. Distinguished from congeners by the incrassate male metatarsus IV, more torose than the elongate metatarsus IV of *Zalmoxis dammermani* (Roewer, 1927); the prominent setose dorsal protuberance on the calcaneus of metatarsus IV in both sexes; and the male genitalia, wherein the pergula protrudes slightly and the rutrum bears two distal pairs of setae with the bases in close proximity.

Description. Total length of male holotype (female paratype [MCZ 124586] in parentheses) 1.50 (1.50), greatest width of prosoma 0.66 (0.65), greatest width of opisthosoma 1.04 (1.09); length-to-width ratio 1.44 (1.38). Body campaniform, yellow-orange to dark orange (in ethanol, 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 indistinct, not forming obtuse “V” shape. Mesotergum and free tergites with seven regular belts of minute setose tubercles (Fig. 11).

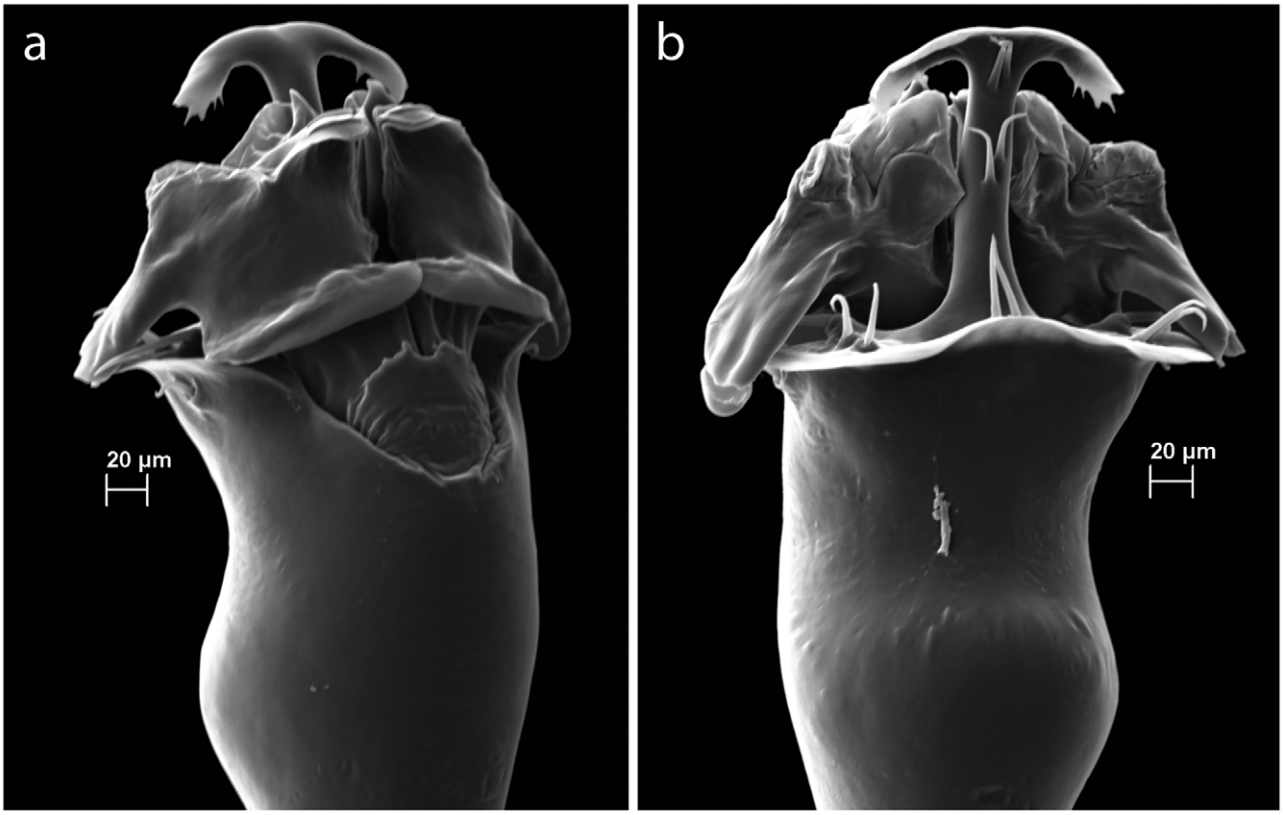

FIGURE 10. *Zalmoxis sabazios* **sp. nov.** (a) Pars distalis of male genitalia, dorsolateral view; (b) Pars distalis of male genitalia, ventral view.

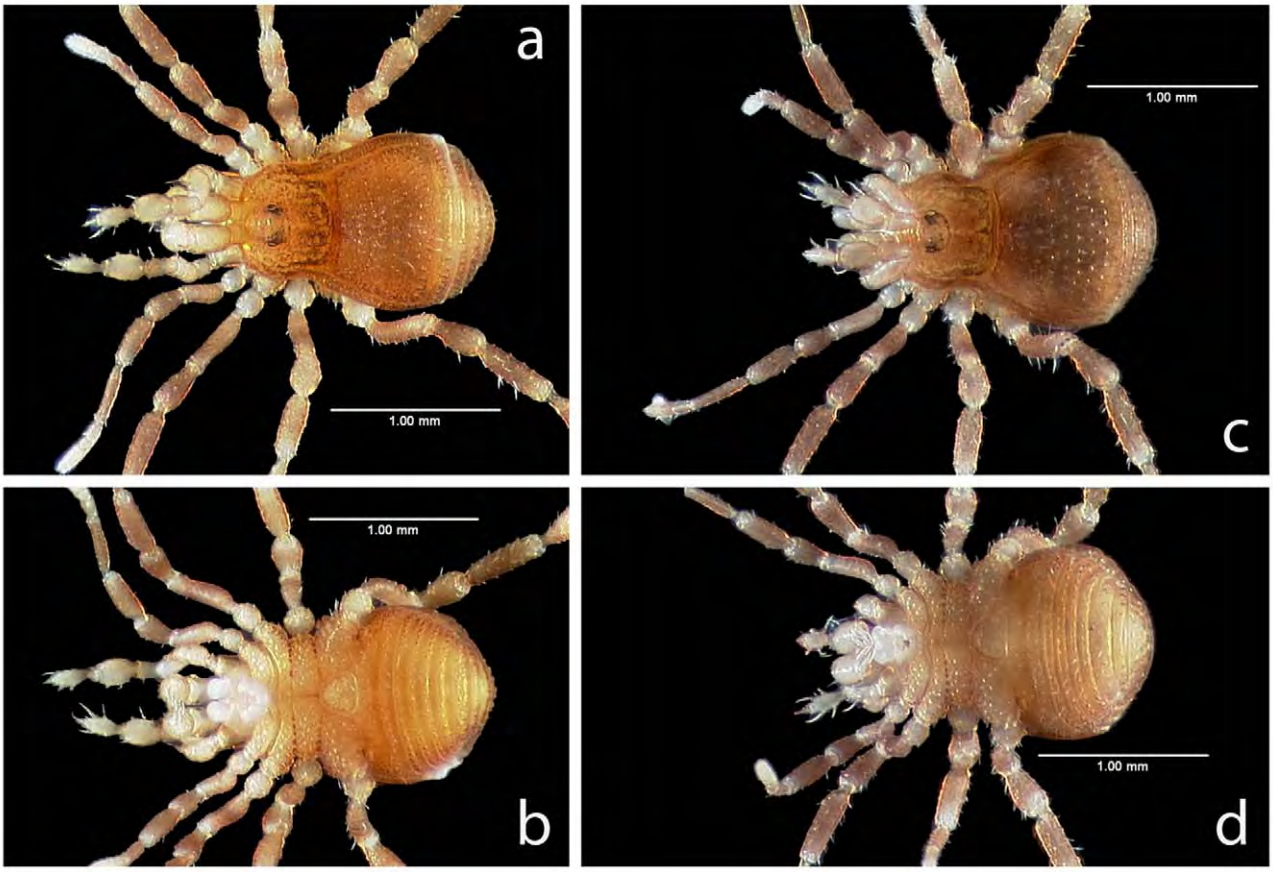

FIGURE 11. *Zalmoxis zibelthiurdos* **sp. nov.** (a) Male holotype, dorsal view; (b) Male holotype, ventral view; (c) Female paratype, dorsal view; (d) Female paratype, ventral view.

Ventral prosomal complex of male with coxae II and III meeting in midline, coxae I and IV not so. Anterior and posterior margins of coxae III with tubercular bridges to adjacent coxae, and coxae I–III with setose tubercles. Coxae IV of male not greatly enlarged. Genital operculum sub-triangular. Spiracles not concealed, anterior to row of tubercles. Opisthosomal sternites with regular belts of low setose tubercles tapering medially. Anal plate without prominent tubercles (Fig. 12).

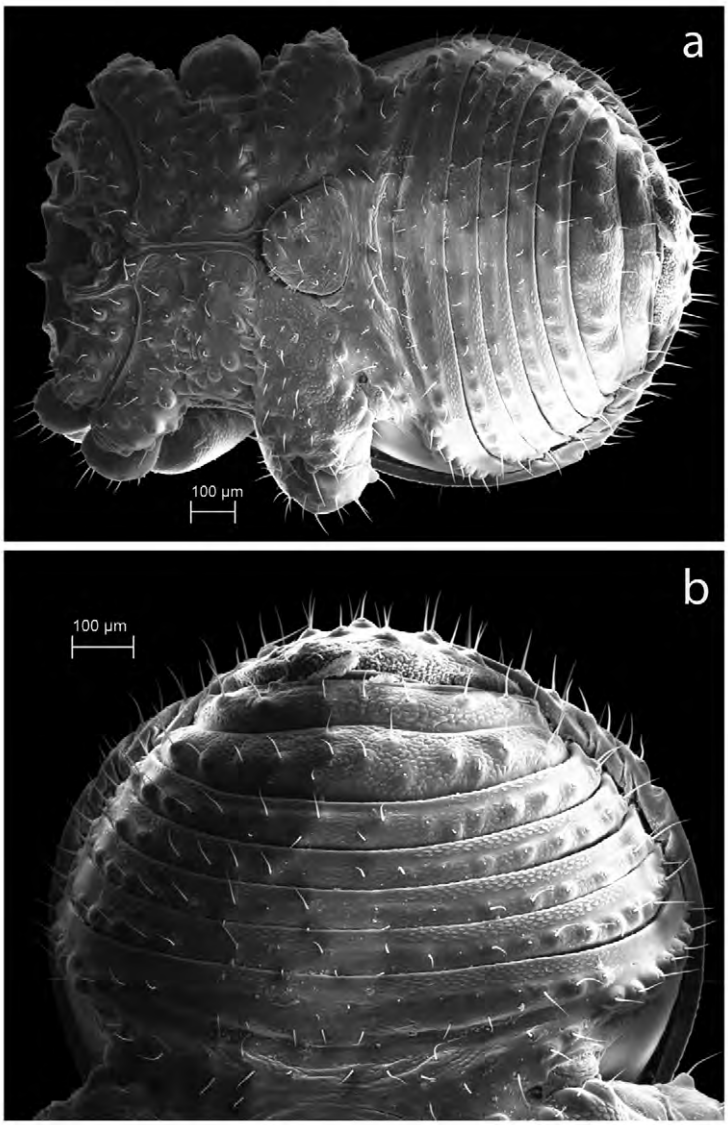

FIGURE 12. *Zalmoxis zibelthiurdos* **sp. nov.** (a) Ventral view of male paratype; (b) Opisthosomal region of male paratype.

Chelicerae (Fig. 13a) 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. 13b) robust and spined ventrally and/or ventrolaterally, typical of zalmoxids. Palpal tarsus with two pairs of megaspines.
Legs (Figs. 13c–g) finely granulated. Trochanters, patellae, and tibiae of all legs bearing irregular rows of setose tubercles. Leg I (Fig. 13c) trochanter with one small tubercle dorsally. Femur IV of both sexes (Figs. 13f–g) with ventral row of tubercles. Male leg IV (Fig. 13f) sexually dimorphic, but not elongated or armed. Male metatarsus IV stocky, incrassate. Metatarsi I–IV divided distally, with calcaneus less ornamented but generally more setose. Calcaneus of metatarsus IV in both sexes with single large dorsal tubercle. Tarsal claws I–IV smooth, unmodified. Tarsal segmentation 3: 5: 5: 6.

Appendage measurements of holotype (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.14/0.13	0.44/0.11	0.27/0.14	0.33/0.12	0.42/0.07	0.44/0.09	2.04
Leg II	0.15/0.16	0.66/0.13	0.35/0.15	0.47/0.13	0.48/0.07	0.81/0.07	2.92
Leg III	0.17/0.17	0.51/0.12	0.27/0.17	0.41/0.14	0.51/0.10	0.48/0.07	2.35
Leg IV	0.17/0.18	0.64/0.11	0.37/0.17	0.50/0.14	0.66/0.19	0.59/0.09	2.93
Palp	0.15/0.15	0.38/0.14	0.20/0.12	0.23/0.16	—	0.27/0.09	1.23
	Proximal	Second	Distal				
Chelicera	0.42/0.20	0.56/0.19	0.16/0.04				

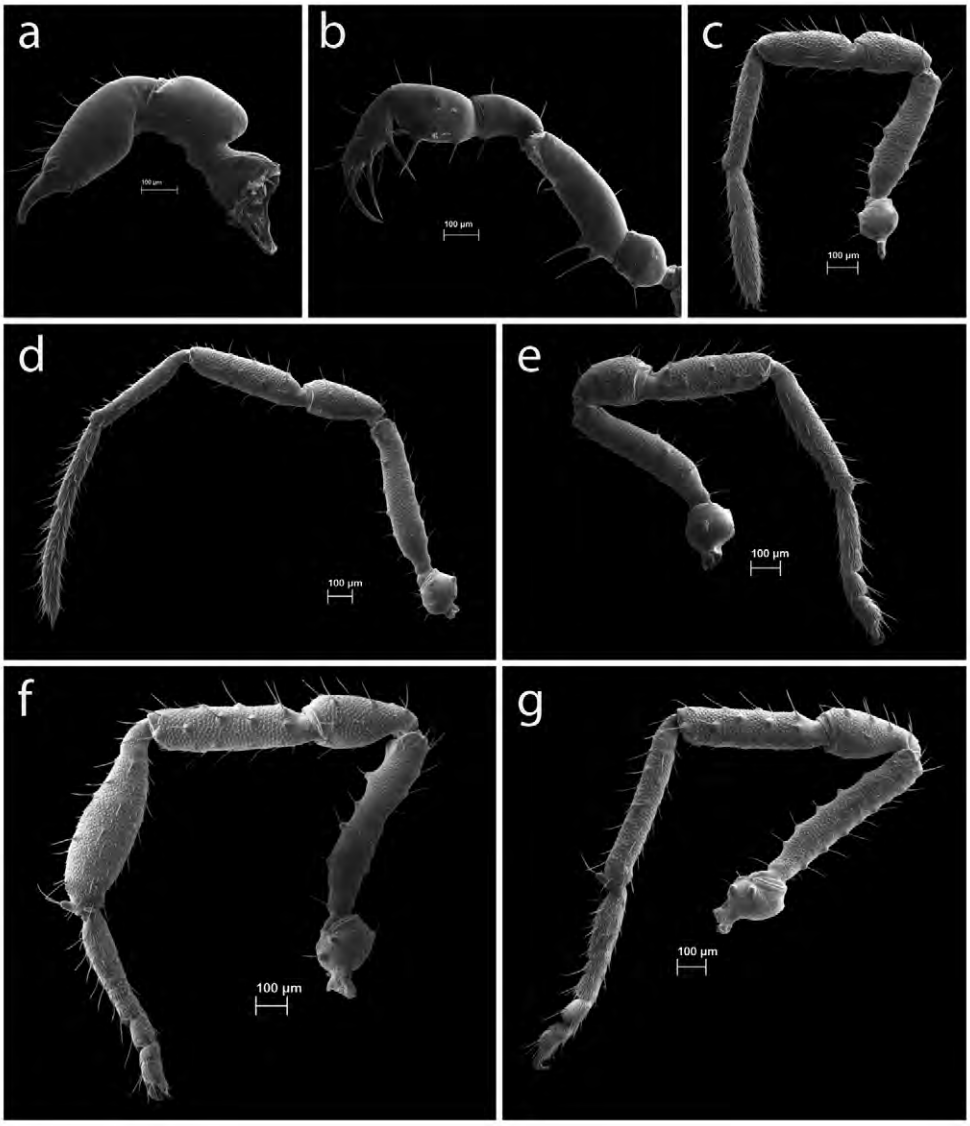

FIGURE 13. *Zalmoxis zibelthiurdos* **sp. nov.** (a) Left chelicer of male paratype; (b) Left palp of male paratype; (c) Male left leg I; (d) Male left leg II; (e) Male right leg III; (f) Male left leg IV; (g) Female left leg IV.

Appendage measurements of female paratype (MCZ 124586) (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.14/0.14	0.42/0.12	0.25/0.14	0.29/0.13	0.39/0.06	0.42/0.08	1.91
Leg II	0.16/0.15	0.59/0.13	0.34/0.15	0.43/0.14	0.45/0.06	0.80/0.06	2.77
Leg III	0.14/0.17	0.51/0.13	0.25/0.16	0.37/0.15	0.50/0.07	0.46/0.06	2.23
Leg IV	0.18/0.16	0.59/0.14	0.35/0.16	0.44/0.14	0.61/0.10	0.64/0.07	2.81
Palp	0.12/0.13	0.36/0.13	0.21/0.13	0.23/0.14	—	0.24/0.08	1.16
	Proximal	Second	Distal				
Chelicera	0.40/0.20	0.50/0.17	0.20/0.04				

Penis (Fig. 14) with two pairs of setae on distal part of rutrum with bases in close proximity, and three pairs of setae on pergula (one ventral, slightly displaced from midline; one lateral, one dorsolateral). One small ventrolateral pair of setae posterior to pergula. Rutrum of arrowhead shape, with lateral extensions. Pergula protruding slightly ventrally.

Distribution. Known only from type locality.

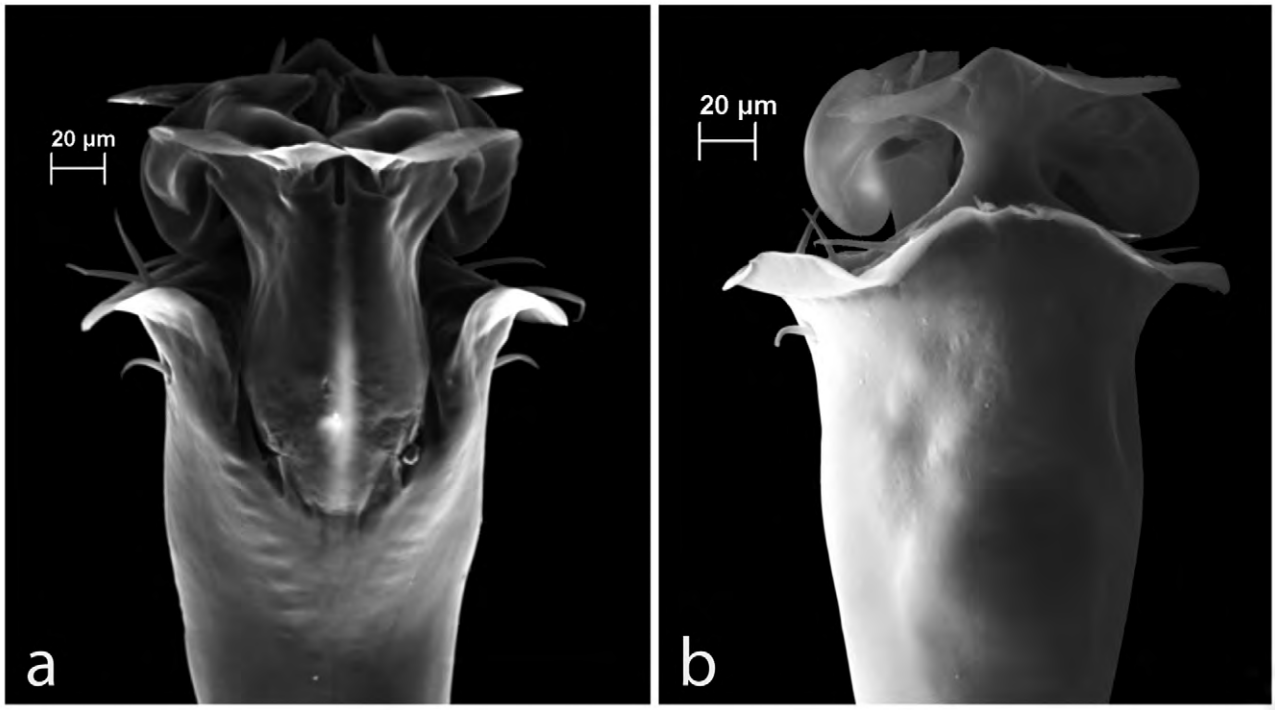

FIGURE 14. *Zalmoxis zibelthiurdos* **sp. nov.** (a) Pars distalis of male genitalia, dorsal view; (b) Pars distalis of male genitalia, ventral view.

Zalmoxis bendis sp. nov.

Figs. 15–17

Types. Male holotype (MHNG) from East Kalimantan Province, Berau District, near Kampung Suaran, ca. 40 km north of Tanjungredeb, Borneo (2º 4’ 46” N, 117º 24’ 36” E), Indonesia, 50 m elevation, collected 1 October 2008 by P.J. Schwendinger. 1 female paratype (MHNG), same collecting data as holotype. 1 male (dissected for genitalia and mounted on SEM stub MCZ 124592) and 1 female (used for DNA extraction [ex MCZ DNA104063-2]), same collecting data as holotype (MCZ 124591). 2 male (1 used for DNA extraction [ex MCZ DNA104065-1]; 1

mounted on SEM stubs MCZ 124594–124595) and 1 female (mounted on SEM stubs MCZ 124594, 124596) paratype (MCZ 124593) from East Kalimantan Province, Berau District, Hutan Mayang Mangurai, ca. 15 km southwest of Tanjungredeb, Borneo (2º 6’ 13” N, 117º 24’ 5” E), Indonesia, 20 m elevation, collected 30 September 2008 by P.J. Schwendinger. 2 female paratypes (NMP) from East Kalimantan Province, Berau District, Hutan Mayang Mangurai, ca. 15 km southwest of Tanjungredeb, Borneo (2º 6’ 13” N, 117º 24’ 5” E), Indonesia, 20 m elevation, collected 30 September 2008 by P.J. Schwendinger.

Etymology. The specific epithet, a noun in apposition, refers to a goddess of the Getae (or Thracians). Bendis was the goddess of the moon, the hunt, and healing.

Diagnosis. Distinguished from congeners in the sexually dimorphic tarsus III, which bears five tarsomeres in females, and four tarsomeres in males with the most proximal article greatly incrassate.

Description. Total length of male holotype (female paratype [MCZ 124591] in parentheses) 1.38 (1.37), greatest width of prosoma 0.68 (0.65), greatest width of opisthosoma 1.04 (1.06); length-to-width ratio 1.32 (1.29). Body campaniform, yellow-orange to dark orange (in ethanol, 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 indistinct, not forming “V” shape. Mesotergum and free tergites without regular belts of setose tubercles (Fig. 15).

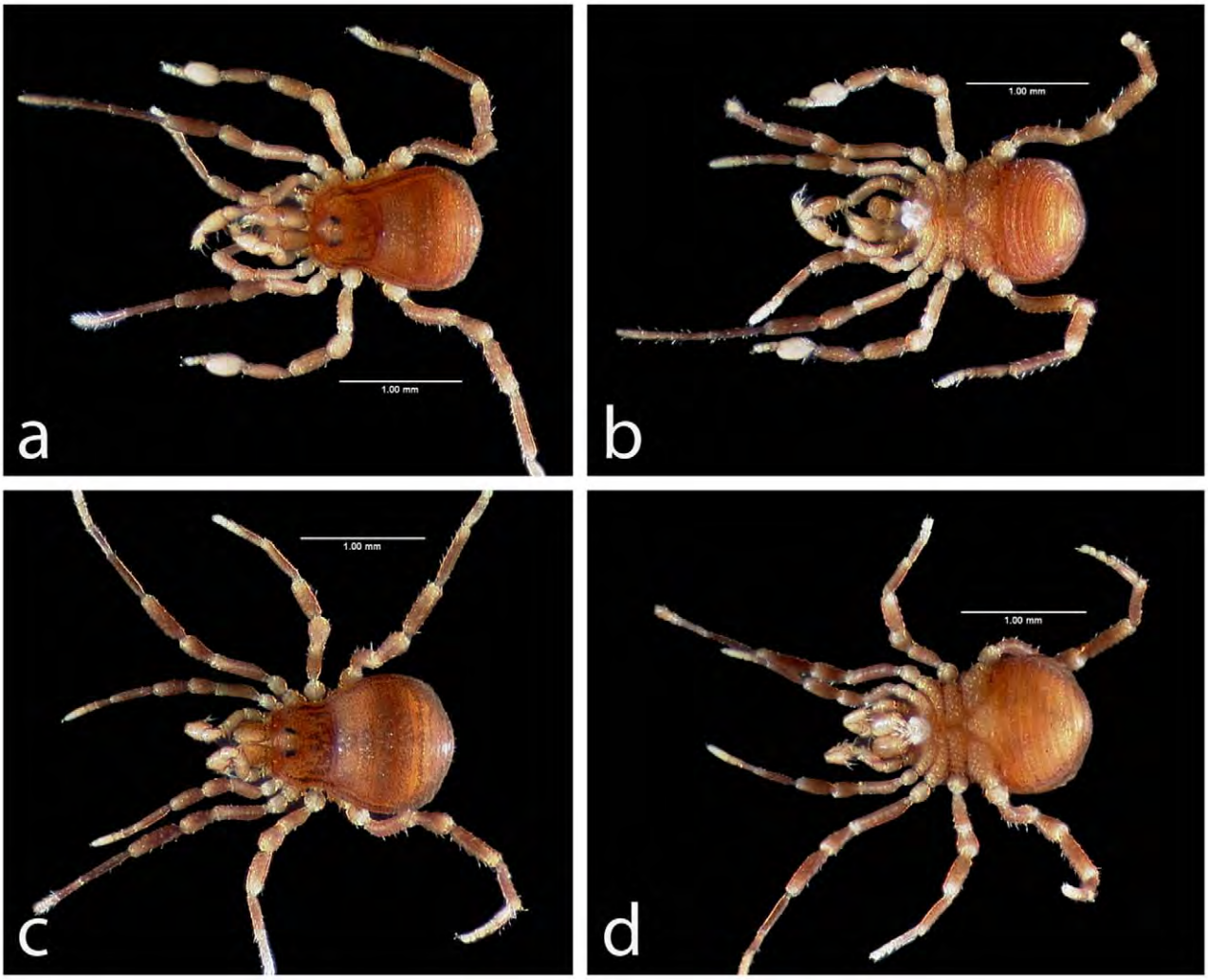

FIGURE 15. *Zalmoxis bendis* **sp. nov.** (a) Male holotype, dorsal view; (b) Male holotype, ventral view; (c) Female paratype, dorsal view; (d) Female paratype, ventral view.

Ventral prosomal complex of male with coxae II and III meeting in midline, coxae I and IV not so. Anterior and posterior margins of coxae III with tubercular bridges to adjacent coxae, and coxae I–III with setose tubercles. Coxae IV of male not greatly enlarged. Genital operculum sub-triangular. Spiracles not concealed, not braced posteriorly by row of tubercles. Opisthosomal sternites with regular belts of low setose tubercles tapering medially. Anal plate without prominent tubercles (Figs. 16a–b).

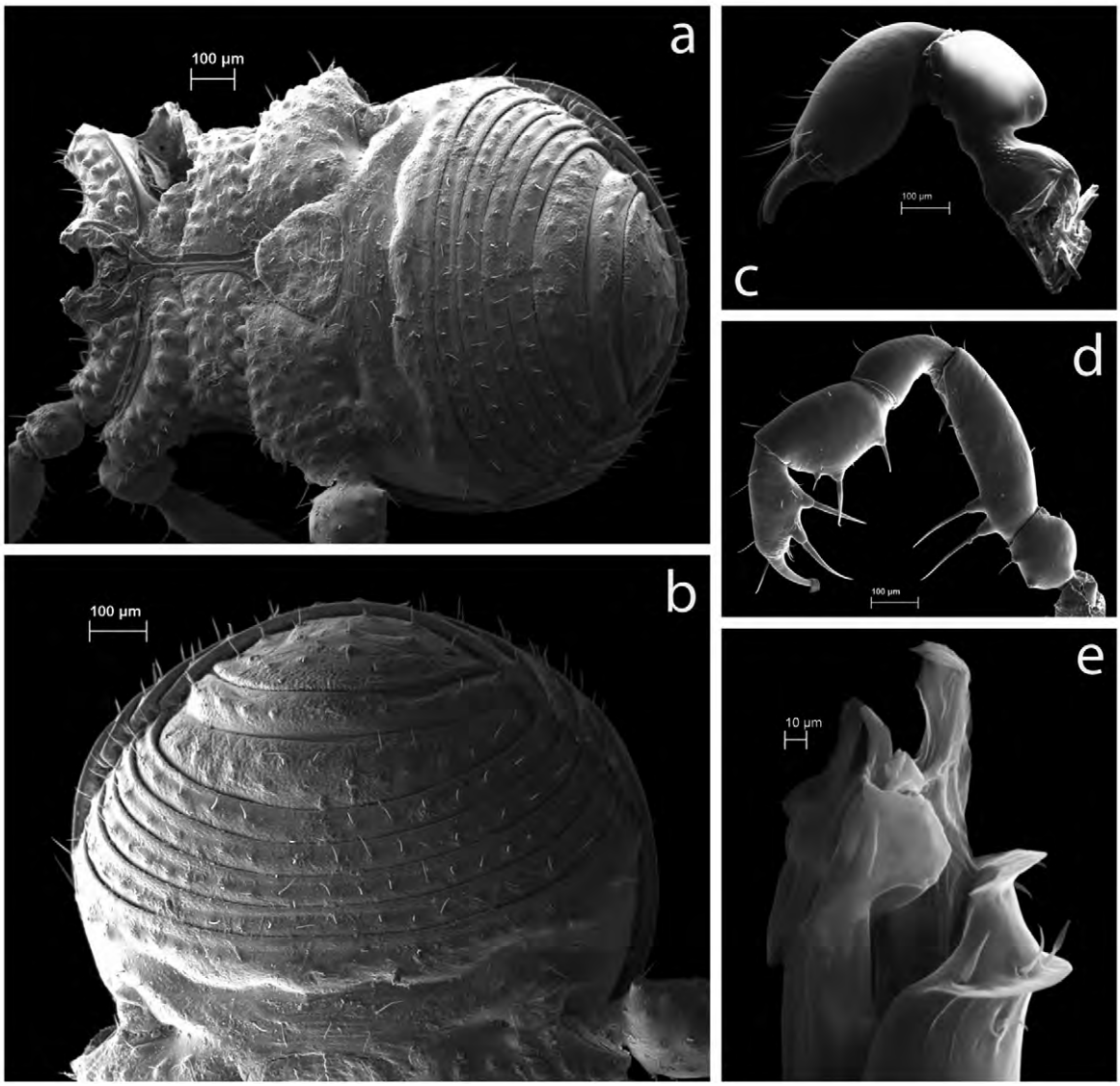

FIGURE 16. *Zalmoxis bendis* **sp. nov.** (a) Ventral view of male paratype; (b) Opisthosomal region of male paratype; (c) Left chelicer of male paratype; (d) Left palp of male paratype; (e) Pars distalis of male genitalia, lateral view.

Chelicerae (Fig. 16c) 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. 16d) robust and spined ventrally and/or ventrolaterally, typical of zalmoxids. Palpal tarsus with two pairs of megaspines.

Legs (Figs. 17a–f) finely granulated. Trochanters, patellae, and tibiae of all legs bearing irregular rows of setose tubercles. Leg I (Fig. 17a) trochanter with one small tubercle ventrally. Femur IV of both sexes (Figs. 17e–f) with ventral row of tubercles. Femur of male leg III (Fig. 17c) with prominent two ventromesal tubercles. Tarsus of male leg III bearing four tarsomeres and sexually dimorphic, with most proximal tarsomere greatly incrassate. Tarsus of female leg III (Fig. 17d) with five tarsomeres. Male leg IV (Fig. 17e) not sexually dimorphic, neither elongated nor armed. Metatarsi I–IV divided distally, with calcaneus less ornamented but generally more setose. Calcaneus of metatarsus IV in both sexes with prominent dorsal tubercle. Tarsal claws I–IV smooth, unmodified. Tarsal segmentation 3: 5: 4: 5 (male) or 3: 5: 5: 5 (female).

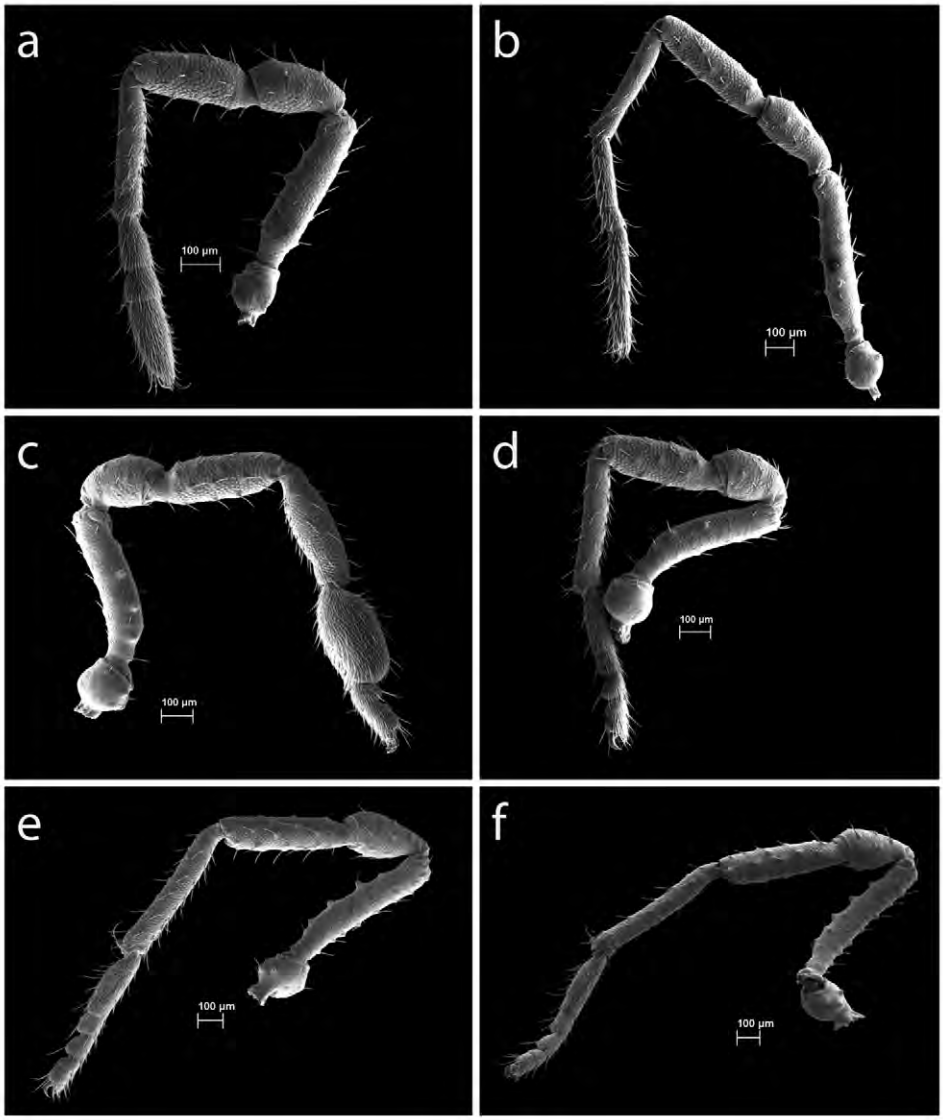

FIGURE 17. *Zalmoxis bendis* **sp. nov.** (a) Male left leg I; (b) Male left leg II; (c) Male right leg III; (d) Female left leg III; (e) Male left leg IV; (f) Female left leg IV.

Appendage measurements of holotype (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.13/0.11	0.44/0.10	0.24/0.13	0.30/0.12	0.39/0.07	0.44/0.09	1.94
Leg II	0.14/0.14	0.60/0.10	0.32/0.14	0.44/0.12	0.47/0.07	0.74/0.08	2.71
Leg III	0.15/0.18	0.51/0.12	0.28/0.17	0.37/0.15	0.44/0.14	0.52/0.19	2.27
Leg IV	0.18/0.20	0.63/0.12	0.33/0.18	0.49/0.13	0.62/0.09	0.59/0.10	2.84
Palp	0.15/0.14	0.40/0.14	0.20/0.13	0.24/0.18	—	0.25/0.11	1.24
	Proximal	Second	Distal				
Chelicera	0.40/0.20	0.57/0.21	0.15/0.04				

Appendage measurements of female paratype (NMP) (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.14/0.11	0.41/0.11	0.24/0.14	0.28/0.13	0.39/0.06	0.42/0.08	1.88
Leg II	0.15/0.14	0.59/0.13	0.31/0.14	0.44/0.13	0.48/0.06	0.78/0.06	2.75
Leg III	0.15/0.15	0.44/0.13	0.24/0.16	0.33/0.14	0.46/0.07	0.46/0.06	2.08
Leg IV	0.17/0.17	0.57/0.12	0.31/0.18	0.45/0.14	0.62/0.09	0.58/0.08	2.70
Palp	0.15/0.13	0.35/0.12	0.18/0.12	0.23/0.15	—	0.24/0.10	1.15
	Proximal	Second	Distal				
Chelicera	0.34/0.17	0.49/0.16	0.14/0.04				

Penis (Fig. 16e) with two pairs of setae on rutrum and three pairs of setae on pergula (one ventral and median, one ventrolateral, one lateral). One small ventrolateral pair of setae posterior to pergula. Rutrum without lateral extensions, smaller than stragulum, with distal margin directed ventrally. Pergula protruding ventrally.

Distribution. Known from two sites in East Kalimantan Province, Borneo, Indonesia.

***Zalmoxis kotys* sp. nov.**
Figs. 18–21, 22c

Types. Male holotype (MHNG) from East Kalimantan Province, Berau District, Hutan Wisata Sei Tangap, ca. 8 km west of Tanjungredeb, Borneo (2º 8’ 4” N, 117º 24’ 39” E), Indonesia, 30 m elevation, collected 2 October 2008 by P.J. Schwendinger. 1 male (used for DNA extraction [ex MCZ DNA104064-1]) paratype, same collecting data as holotype (MHNG). 2 male (1 dissected for genitalia and mounted on SEM stub 124600; 1 mounted on SEM stubs MCZ 124598–124599) paratypes, same collecting data as holotype (MCZ 124597). 1 male (used for DNA extraction [ex MCZ DNA104065-2]) paratype (NMP) from East Kalimantan Province, Berau District, Hutan Mayang Mangurai, ca. 15 km southwest of Tanjungredeb, Borneo (2º 6’ 13” N, 117º 24’ 5” E), Indonesia, 20 m elevation, collected 30 September 2008 by P.J. Schwendinger. 1 male (used for DNA extraction [ex MCZ DNA104068]; dissected for anal plate, mounted on SEM stub MCZ 124602) paratype (MCZ 124601) from East Kalimantan Province, Berau District, 1 km of road between Tanjungredeb and Tanjungselor, ca. 45 km north of Tanjungredeb, Borneo (2º 29’ 13” N, 117º 28’ 46” E), Indonesia, 190 m elevation, collected 29 September 2008 by P.J. Schwendinger.

Additional material studied. 1 subadult male, same collecting data as holotype.

Etymology. The specific epithet, a noun in apposition, refers to a goddess of the Getae (or Thracians). Kotys was the goddess of sexuality and promiscuity.

Diagnosis. Distinguished from congeners in the armature of the anal plate, which bears four prominent tubercles, the middle pair greater in size; and the armature of male leg IV, which bears two ventral rows of spiny tubercles on tibia IV enlarging distally.

Description. Total length of male holotype 2.36, greatest width of prosoma 0.92, greatest width of opisthosoma 1.70; length-to-width ratio 1.39. Body campaniform, orange to dark brown (in ethanol, 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 forming obtuse “V” shape anteriorly. Mesotergum and free tergites with six regular belts of setose tubercles (Fig. 18).

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. Genital operculum sub-triangular. Spiracles not concealed, anterior to row of tubercles. Opisthosomal sternites with regular belts of low setose tubercles tapering medially. Anal plate armed with three rows of tubercles: anterior and posterior rows both with two low tubercles flanking the midline; and median row with six tubercles, enlarging medially, with innermost pair larger than all others (Figs. 19, 22c).

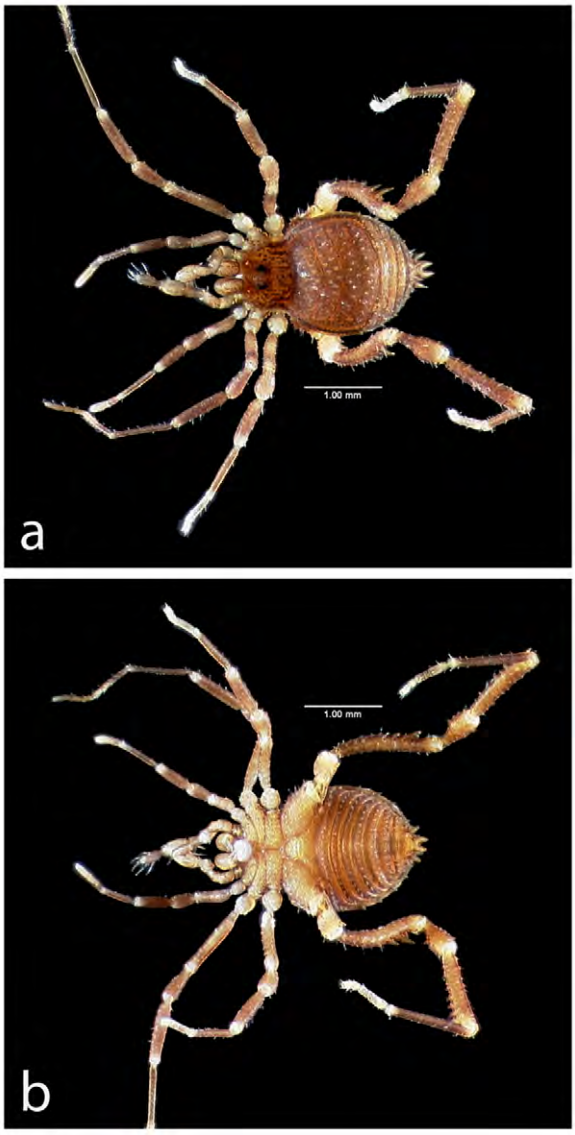

FIGURE 18. *Zalmoxis kotys* **sp. nov.** (a) Male holotype, dorsal view; (b) Male holotype, ventral view.

Chelicerae (Fig. 20a) 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. 20b) robust and spined ventrally and/or ventrolaterally, typical of zalmoxids. Palpal tarsus with two pairs of megaspines.

Legs (20c–f) finely granulated. Trochanters, patellas, and tibias of all legs bearing irregular rows of setose tubercles. Leg I (Fig. 20c) trochanter with one small tubercle dorsally and two small tubercles ventrally. Femora of legs I and II with ventral row of small tubercles. Male leg IV (Fig. 20f) elongate and armed. Femur IV arcuate, bearing ventral and ventrolateral row of tubercles; ventral row enlarging distally with largest ventral tubercle flanked by two abruptly smaller tubercles distally, with one additional hook-like tubercle at distal-most part of segment. Patella IV with two ventral tubercles. Tibia IV with two ventral rows of tubercles enlarging distally. Metatarsi I–IV divided distally, with calcaneus less ornamented but generally more setose. Calcaneus of metatarsus IV with small setose dorsal tubercle. Tarsal claws I–IV smooth, unmodified. Tarsal segmentation 3: 6: 5: 6.

Appendage measurements of holotype (length/width):

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.16/0.18	0.67/0.15	0.37/0.17	0.49/0.15	0.73/0.08	0.61/0.10	3.03
Leg II	0.33/0.26	1.08/0.16	0.56/0.21	0.86/0.17	1.05/0.08	1.10/0.09	4.98
Leg III	0.25/0.23	0.83/0.17	0.41/0.23	0.75/0.17	0.92/0.10	0.66/0.10	3.82
Leg IV	0.53/0.28	1.56/0.22	0.79/0.30	1.30/0.24	1.33/0.13	0.79/0.13	6.30
Palp	0.18/0.19	0.51/0.18	0.20/0.16	0.33/0.20	—	0.34/0.14	1.56
	Proximal	Second	Distal				
Chelicera	0.49/0.24	0.72/0.23	0.20/0.05				

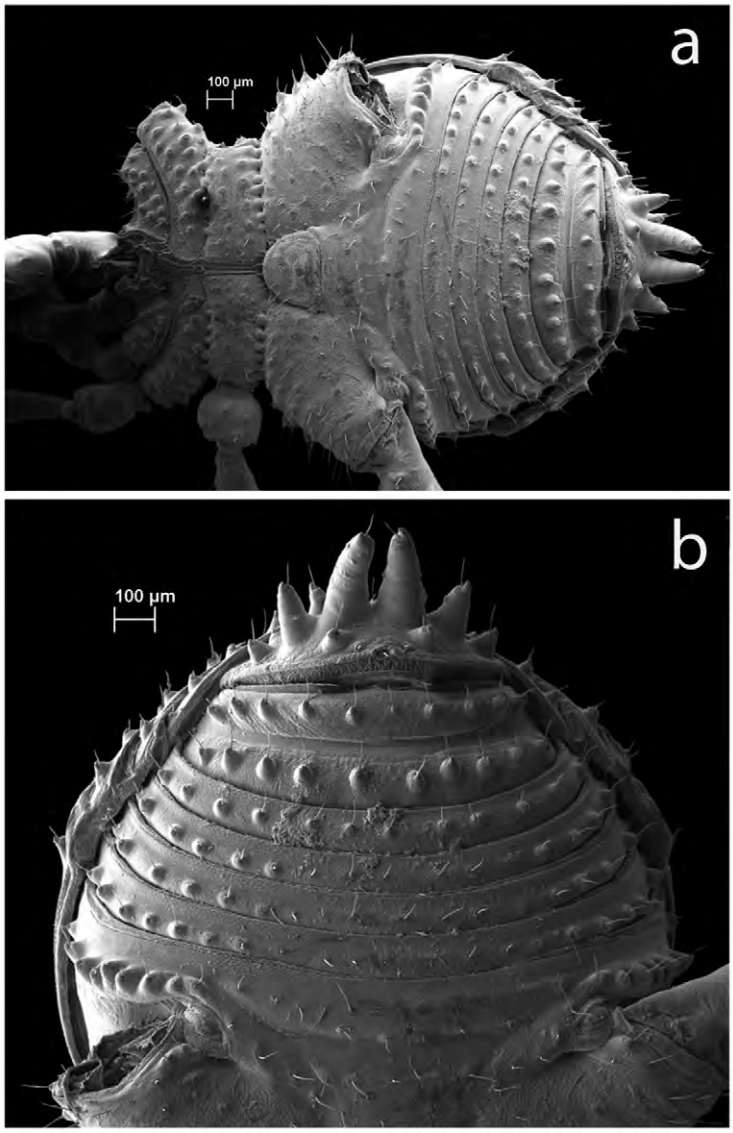

FIGURE 19. *Zalmoxis kotys* **sp. nov.** (a) Ventral view of male paratype; (b) Opisthosomal region of male paratype.

Penis (Fig. 21) with two pairs of setae on distal part of rutrum and three pairs of setae on pergula (one median, two ventrolateral). One small dorsolateral pair of setae posterior to pergula. Rutrum of arrowhead shape with lateral extensions. Pergula protruding ventrally.

Distribution. Known from three sites in East Kalimantan Province, Borneo, Indonesia.

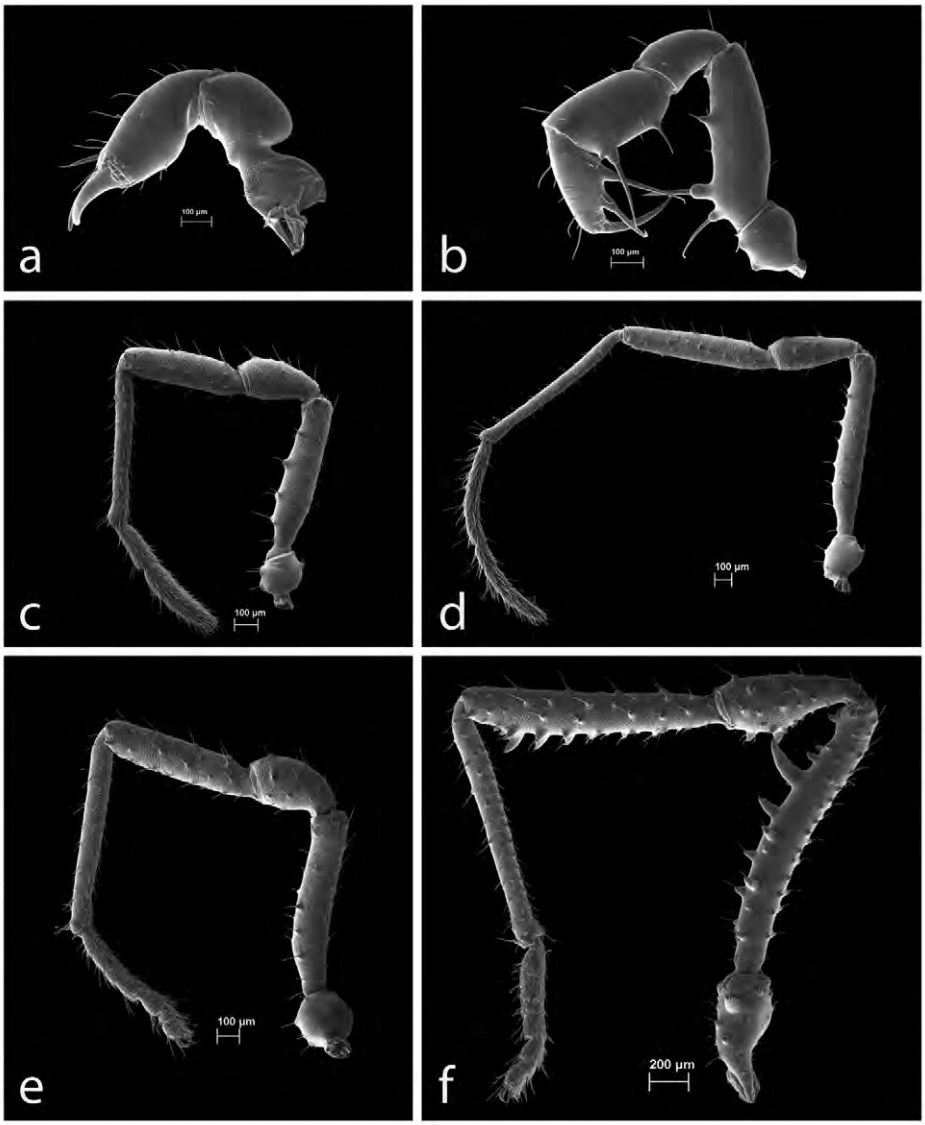

FIGURE 20. *Zalmoxis kotys* **sp. nov.** (a) Left chelicer of male paratype; (b) Left palp of male paratype; (c) Male left leg I; (d) Male left leg II; (e) Male left leg III; (f) Male left leg IV.

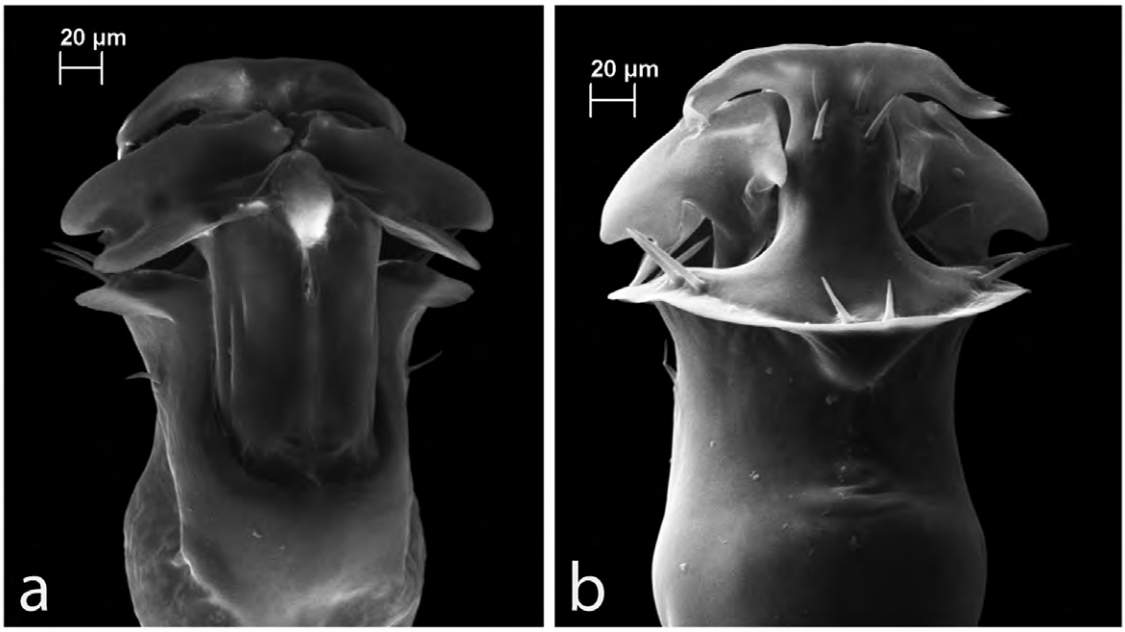

FIGURE 21. *Zalmoxis kotys* **sp. nov.** (a) Pars distalis of male genitalia, dorsal view; (b) Pars distalis of male genitalia, ventral view.

Discussion

The six new species reported here add to the known morphological diversity of the genus in two ways. Firstly, males of *Zalmoxis bendis* **sp. nov.** have a sexually dimorphic third leg, which is contrary to the usual pattern in the superfamily Zalmoxoidea, *i.e.*, a sexually dimorphic fourth leg (Kury & Pérez-González 2007; Sharma & Giribet 2011). Moreover, the sexually dimorphic part of the third leg is a tarsomere, not a podomere as in other Zalmoxidae; and the tarsal formula is additionally sexually dimorphic (likely a result of fusion of the two basal tarsal articles to form the incrassate tarsal article in males). A similar condition occurs in the third leg of male *Ethobunus tarsalis* (Banks, 1909), which is endemic to Costa Rica (tarsal formulae 3: 7: 4: 6 and 3: 7: 5: 6 in males and females, respectively), although this species also bears sexually dimorphic and armored fourth legs, like most zalmoxids (Goodnight & Goodnight, 1983). Some other Central American *Ethobunus* also have enlarged sexually dimorphic tarsomeres, although the tarsal formula does not vary among males and females (reviewed in Goodnight & Goodnight, 1983).

Secondly, we describe here some of the smallest known *Zalmoxis*—two of the Bornean species (*Zalmoxis zibelthiurdos* **sp. nov.** and *Zalmoxis bendis* **sp. nov.**) are less than 2 mm in length. The small size of Bornean *Zalmoxis* may have contributed to their being overlooked despite large amounts of suitable habitat, as was the case for the unrelated and minute Philippine Petrobunidae (Sharma & Giribet, 2011).

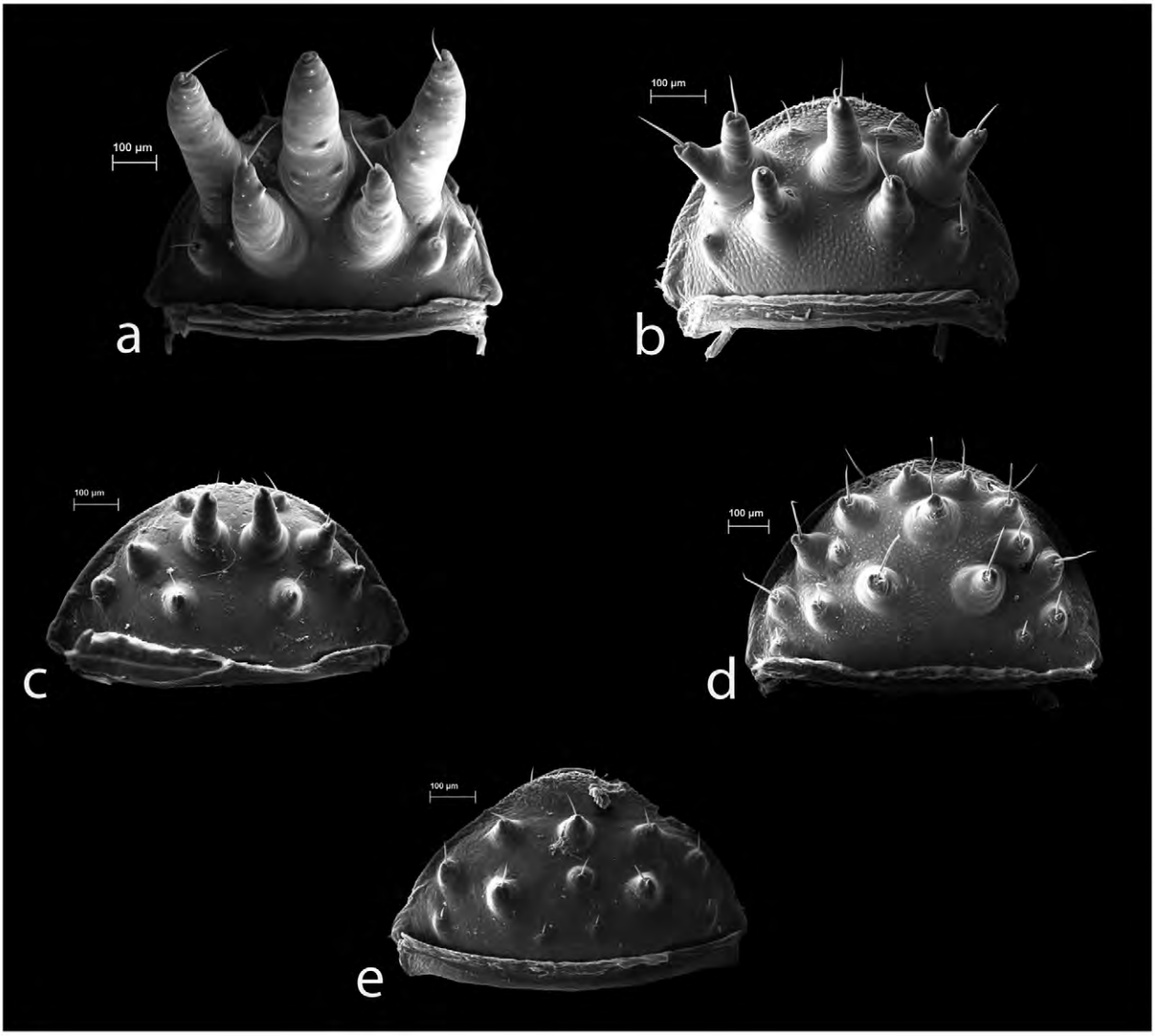

FIGURE 22. Variation in anal plate armature; anterior end oriented up. (a) *Zalmoxis cuspanalis* Roewer, 1927; (b) *Zalmoxis gebeleizis* **sp. nov.**; (c) *Zalmoxis kotys* **sp. nov.**; (d) *Zalmoxis mitobatipes* (Roewer, 1926); (e) *Zalmoxis derzelas* **sp. nov.**

Re-examination of previously described species from Luzon (*Zalmoxis mitobatipes* and *Zalmoxis cuspanalis*) underscores the diversity of anal plate armature (Fig. 22) and suggests a relationship between the Bornean *Zalmoxis kotys* **sp. nov.** and the two Philippine species, *Zalmoxis gebeleizis* **sp. nov.** and *Zalmoxis cuspanalis*, all of which bear anal opercula armed with prominent tubercles. However, examination of male genitalic morphology (Figs. 4, 8, 10, 14, 16e, 21, 23) suggests that armor and spination in Zalmoxidae may constitute a conflicting set of characters with respect to genitalic ones. Specifically, a disjunct pergula occurs in *Zalmoxis mitobatipes*, *Zalmoxis cuspanalis*, and *Zalmoxis gebeleizis* **sp. nov.**, favoring a closer relationship of these taxa; by contrast, the continuous pergula and the rutral setation of *Zalmoxis kotys* **sp. nov.** (Borneo) is similar to those of *Zalmoxis derzelas* **sp. nov.** (Mindoro) and *Zalmoxis sabazios* **sp. nov.** (Palawan), suggesting disparate affinities within Philippine species. We anticipate that a molecular phylogeny may shed more light on interspecific relationships and vindicate certain character systems when the phylogenetic signal of morphology is conflicted.

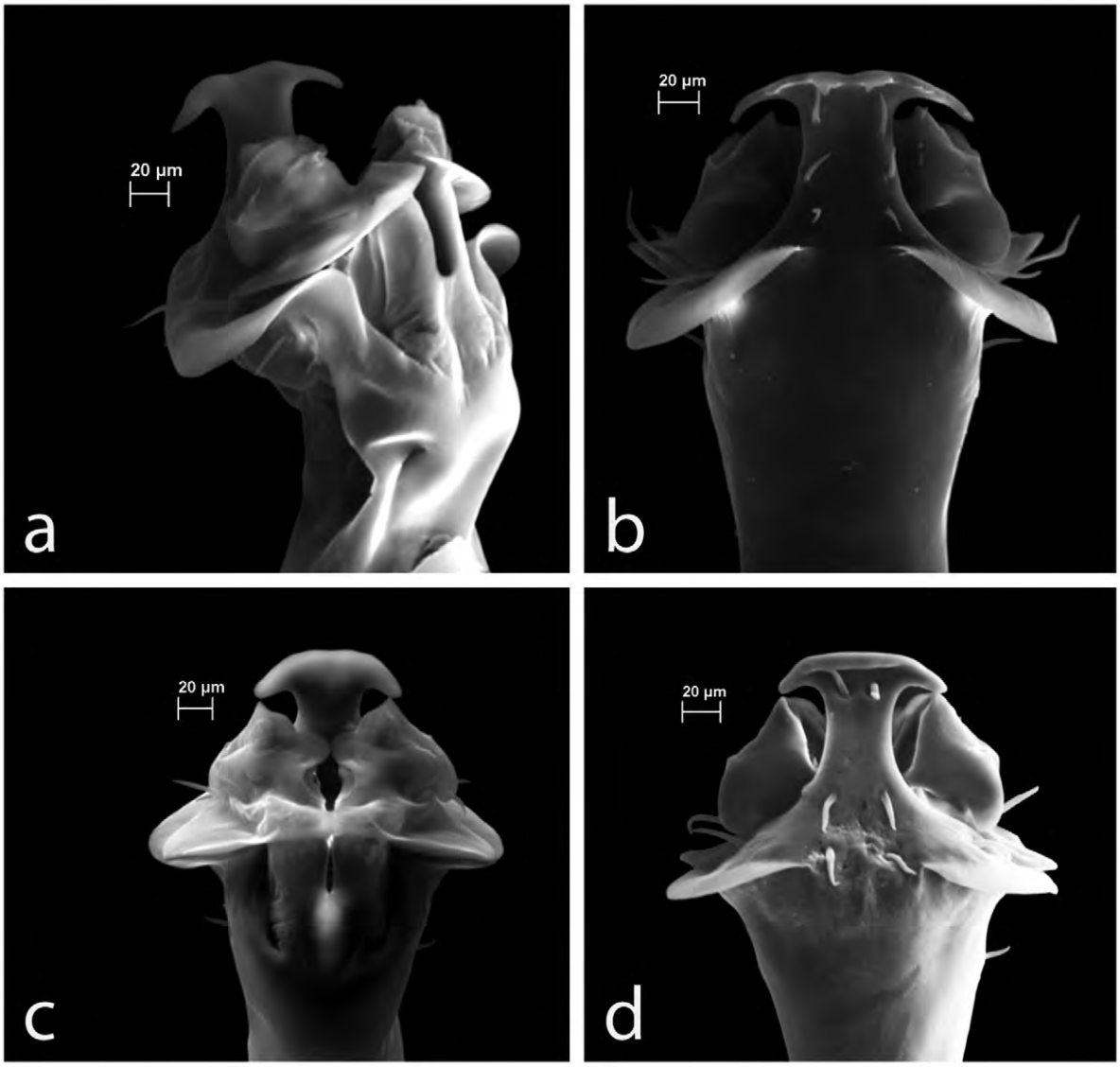

FIGURE 23. Pars distalis of male genitalia. (a) *Zalmoxis cuspanalis* Roewer, 1927, dorsolateral view; (b) *Zalmoxis cuspanalis* Roewer, 1927, ventral view; (c) *Zalmoxis mitobatipes* (Roewer, 1926), dorsal view; (d) *Zalmoxis mitobatipes* (Roewer, 1926), ventral view.

The description of these new species of Zalmoxidae also expands the known range of zalmoxids, insofar as *Zalmoxis* were previously unreported from Borneo and known only from Luzon and Mindanao in the Philippine Islands (Fig. 24). The discovery of *Zalmoxis* from Borneo, Palawan, Panay, and Mindoro, in addition to their narrow distributions, suggests that potentially dozens of species may inhabit these landmasses, including other islands whence zalmoxids have not yet been reported (*e.g.*, Negros, Leyte, Samar).

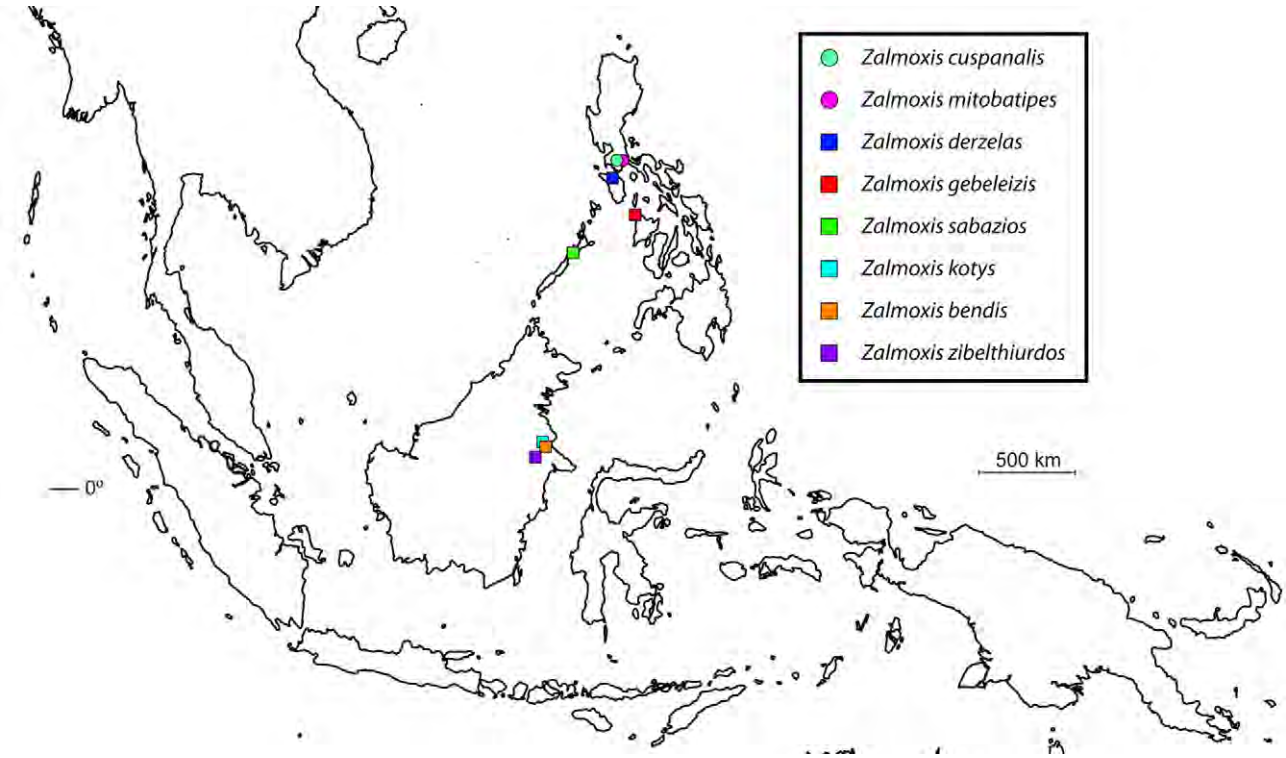

FIGURE 24. Map of Southeast Asia showing type localities for *Zalmoxis* species examined in this study. Circles indicate type localities of previously described species; squares indicate type localities of newly described species.

Acknowledgements

We are indebted to Peter J. Schwendinger for contributing numerous collections for study. Special thanks go to Rafe Brown and Dave General for facilitating the availability of Philippine collections. Laura Leibensperger sorted and accessioned Zalmoxidae collections from Southeast Asia, 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 the Philippines and other Pacific islands was supported by an MCZ Putnam Expedition Grant awarded to R.M.C and P.P.S (2009). Abel Pérez-González, Ricardo Pinto-da-Rocha, and Nobuo Tsurusaki revised and greatly improved an early draft of the manuscript.

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