



New species of *Paktongius* and convergent evolution of the gonyleptoid-like habitus in Southeast Asian Assamiidae (Opiliones: Laniatores)

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Abstract

The armored harvestman family Assamiidae (Arachnida: Opiliones: Laniatores) is widely distributed throughout the Old World tropics, specifically throughout tropical Asia and Central Africa. However, the systematics and intrafamilial relationships of the group remain poorly understood. This can be largely attributed to the complicated taxonomic history of the group, which is exemplified by poorly supported subfamily classifications and the prevalence of monotypic genera. Here, we describe four new species of the formerly monotypic genus *Paktongius* Suzuki, 1969, using specimens collected from Laos, Thailand, and West Malaysia, suggesting a degree of microendemism within the group, which underscores the need for greater sampling of the southeast Asian arachnofauna. Recent phylogenetic analysis has also suggested that *Mysorea thaiensis* Suzuki, 1985 nests within a clade composed of *Paktongius distinctus* Suzuki, 1969 and the species described herein (*P. sasukii* sp. nov., *P. spiculosus* sp. nov., *P. paritensis* sp. nov., *P. furculus* sp. nov.). We therefore transfer *Mysorea thaiensis* to *Paktongius* (*P. thaiensis* comb. nov.). We also comment on the unique morphology of this highly derived group of harvestmen, which appears to suggest convergent evolution of the gonyleptoid-like morphology, complete with the characteristic exaggerated leg four coxae and laterally expanded scutum.

Key words: Grassatores, Assamiodea, sexual dimorphism, southeast Asia, microendemism

Introduction

The armored harvestmen family Gonyleptidae Sundevall, 1833 (Arachnida: Opiliones: Laniatores) exhibits perhaps the most striking characteristics of the order, replete with an array of colorful pigmentation patterns and highly developed armature, that are typically sexually dimorphic (Kury & Pinto-da-Rocha *et al.* 2007). The most recognizable characteristic of the family is the highly exaggerated leg four coxae, often extending beyond the lateral margins of the scutum, which itself is expanded laterally. This creates the appearance of an incassate, dorsoventrally compressed opisthosoma (termed the “gonyleptoid” condition in the following text). Based on characterizations of postembryonic development in representative species of both Gonyleptidae and the closely related Cranidae Roewer, 1913, hypertrophy of the posterior portion of the scutum (typically of areas III and IV) occurs postembryonically, between the fourth and fifth instars (Townsend *et al.* 2009). Pigmentation also appears postembryonically, with progressive darkening of the prosoma and opisthosoma with each successive molt. The fifth instar also seems to correspond to the appearance of sharply pointed tubercles along the free tergites, and along the trochanter, femur, and tibia of the fourth leg (Townsend *et al.* 2009).

This same postembryonic expansion of the opisthosoma, however, also appears to characterize several members of the Assamiidae Sørensen, 1884. Within the now taxonomically defunct Polycoryphinae or Mysoreinae subfamilies (Palmieri *et al.* 2023), a curious case of convergent evolution of the gonyleptoid condition is observed in two southeast Asian species, *Mysorea thaiensis* Suzuki, 1985 and *Paktongius distinctus* Suzuki, 1969, although broader inference of this condition is limited by the relatively poor systematic understanding of these genera. Originally described by Roewer (1935), *Mysorea* seems to be characterized primarily by the absence of enlarged armature on the ocularium, areas I–V of the scutum, free tergites, and femora of the pedipalps. Roewer’s type species, *Mysorea brevipus*, is similarly limited in description, with no mention of any similarity with the expanded coxae of the fourth

leg, while the only available drawing is a lateral depiction of the pedipalpal profile (Roewer 1935). The first mention of the gonyleptoid condition in *Mysorea* thus appears in Suzuki's description of *Mysorea thaiensis*, characterized by "coxa IV remarkably larger than others." Exaggerated leg four coxae are also readily apparent in Suzuki's drawings of *Paktongius distinctus* Suzuki, 1969. However, given that the descriptions encompass only a singular female specimen, the full extent of this condition likely remains poorly understood, as Laniatores often exhibit marked sexual dimorphism, with males bearing the more exaggerated characteristics.

Here we describe four additional species of *Paktongius* collected from localities in Laos, Thailand, and West Malaysia, each demonstrating variations on the same gonyleptoid condition. The presence of distinct species across a small region within Southeast Asia suggests high microendemism within the genus, underscoring the necessity for more intensive surveys of the Southeast Asian opiliofauna. Based on recent phylogenetic analysis by Palmieri *et al.* (2023) utilizing five legacy molecular markers, the nested position of *Mysorea thaiensis* within *Paktongius* justifies the transfer of *M. thaiensis* to *Paktongius*. We note that *Paktongius thaiensis* **comb. nov.** is likely distantly related to the Indian species *Mysorea brevipes* Roewer, 1935 and their placement in the same genus is dubious. Roewer's description of *M. brevipes* is limited in detail and focused largely upon the absence of features common to other assamiids. Nevertheless, he noted that *M. brevipes* clearly lacked a "pseudonychium" (tarsal process), a character present in *P. thaiensis*, as well as all other *Paktongius* species described herein (Fig. 11). Similarly, the pedipalpal femur of *M. brevipes* bears only dorsal armature, whereas all *Paktongius* bear a characteristic row of ventral serrations that are proximally restricted. For this reason, we readily transfer the erstwhile *Mysorea thaiensis* to *Paktongius*.

Materials and Methods

Taxonomy

Examined specimens have been deposited in the following institutions: MHNG (Muséum d'histoire naturelle de la Ville de Genève) and UWZM (University of Wisconsin Zoological Museum). Specimens were additionally examined from MCZ (Museum of Comparative Zoology).

Type specimens were photographed using a Leica MC120 digital camera mounted on a Leica M60 stereomicroscope, driven by LAS X software (Leica). A series of images (from 5 to 15) was taken at different focal planes and assembled with the dedicated software Helicon Focus ver. 6.7.2. Specimens were examined with a Quanta FEI 200 scanning electron microscope (SEM). The genitalia of male types were also examined by SEM. Specimens previously used for DNA extraction are indicated as such among the type material. All measurements are given in millimeters unless otherwise indicated. Nomenclature on cuticular ornamentation follows Murphree (1988).

Material used for comparison consisted of non-type material of *Paktongius distinctus* Suzuki, 1969 (MHNG TH-09/04) and *P. thaiensis* (MCZ-92256/MCZ DNA104859).

Taxonomy

Order OPILIONES Sundevall, 1833

Suborder LANIATORES Thorell, 1876

Family ASSAMIIDAE Sørensen, 1884

Genus *Paktongius* Suzuki, 1969

Type species: *Paktongius distinctus* Suzuki, 1969, by original designation.

Material examined. ♀ (MHNG TH-09/04) THAILAND, Krabi Prov., Khlong Thom Distr., Khao Pra—Bang Khram Wildlife Sanctuary (7°54'38"N, 99°16'40"E), 80 m, semi-evergreen rainforest, 2.vi.2009, *leg.* P. Schwendinger.

***Paktongius suzukii* sp. nov.**

(Figs. 1–3, 11, 12; Tables 1–2)

Paktongius n. sp. 1, Palmieri *et al.* 2023

Type material. Holotype. ♂ (MHNG TH-11/05) THAILAND, Surat Thani Prov., Ko Samui, Nathon Distr., Hin Lad Waterfall (9°31'15" N, 99°57'47"E), 100 m, primary forest near stream, 5–6 VII 2011, *leg.* P.J. Schwendinger. Genitalia and appendages dissected and mounted for SEM. One leg III extracted for DNA by Palmieri *et al.* (2023).

Paratypes. 1 ♂ (UWZM Y.40170), 1 ♀ (UWZM Y.40169), same collecting data as holotype; appendages dissected and mounted on SEM stubs. 2 ♀ (MHNG TH-11/05), same collecting data as holotype.

Additional material studied. 1 subadult male (MHNG TH-11/05), same collecting data as holotype.

Etymology. The species epithet is a patronymic in honor of the late Seisho Suzuki, who described the genus *Paktongius*, its type species, *P. distinctus*, and *P. thaiensis* (as *Mysorea thaiensis*).

Diagnosis. Distinguished from congeners by the combination of the following characters: (1) dorsal surface of scutal areas I–IV with rings of dark pigmentation that do not cross the dorsal midline (*contra* solid patches in *P. distinctus*, *P. spiculosus*, *P. thaiensis*; rings crossing midline in *P. furculus*); (2) ventral pigmentation posterior to the genital operculum constituting winged shape with median anterior projection; (3) absence of two distinct lines of pigmentation extending posteriorly from the ocularium (*contra* *P. furculus*, *P. paritensis*); (4) absence of enlarged spines on the anal plate (*contra* *P. spiculosus*, *P. thaiensis*); (5) absence of enlarged tubercles along the anterolateral margins of the fourth coxae (*contra* *P. distinctus*, *P. thaiensis*); (6) tarsal formula 5: 9: 6: 7. Males additionally distinguished from congeners by genitalia with four pairs of lateral setae (*P. spiculosus*, *P. thaiensis* with five pairs; male *P. distinctus* unknown) and absence of paired cuticular projections dorso-apically (*contra* *P. spiculosus*).

TABLE 1. *Paktongius suzukii* sp. nov. Appendage measurements of male holotype (MHNG TH-11/05). All measurements in millimeters. Tr = trochanter; Fe = femur; Pa = patella; Ti = tibia; Me = metatarsus; Ta = tarsus.

	Tr	Fe	Pa	Ti	Me	Ta	Total
Leg I	0.272	1.482	0.566	0.981	1.835	0.821	5.957
Leg II	0.398	2.608	0.615	2.160	2.481	1.814	10.076
Leg III	0.399	2.008	0.574	1.427	2.191	0.728	7.327
Leg IV	0.544	3.096	0.922	3.068	3.342	0.965	11.937
Pedipalp	0.354	0.850	0.554	0.464	-	0.398	2.620
	Proximal	Second	Distal				
Chelicera	0.533	0.909	0.284				

TABLE 2. *Paktongius suzukii* sp. nov. Appendage measurements of female paratype (UWZM Y.40169). All measurements in mm.

	Tr	Fe	Pa	Ti	Me	Ta	Total
Leg I	0.283	1.370	0.516	0.880	1.714	0.817	5.580
Leg II	0.321	2.406	0.664	2.021	2.532	1.758	9.702
Leg III	0.442	1.856	0.599	1.222	1.995	0.776	6.890
Leg IV	0.527	2.573	0.729	2.065	2.883	0.905	9.682
Pedipalp	0.409	0.827	0.572	0.445	-	0.277	2.530
	Proximal	Second	Distal				
Chelicera	0.539	0.847	0.335				

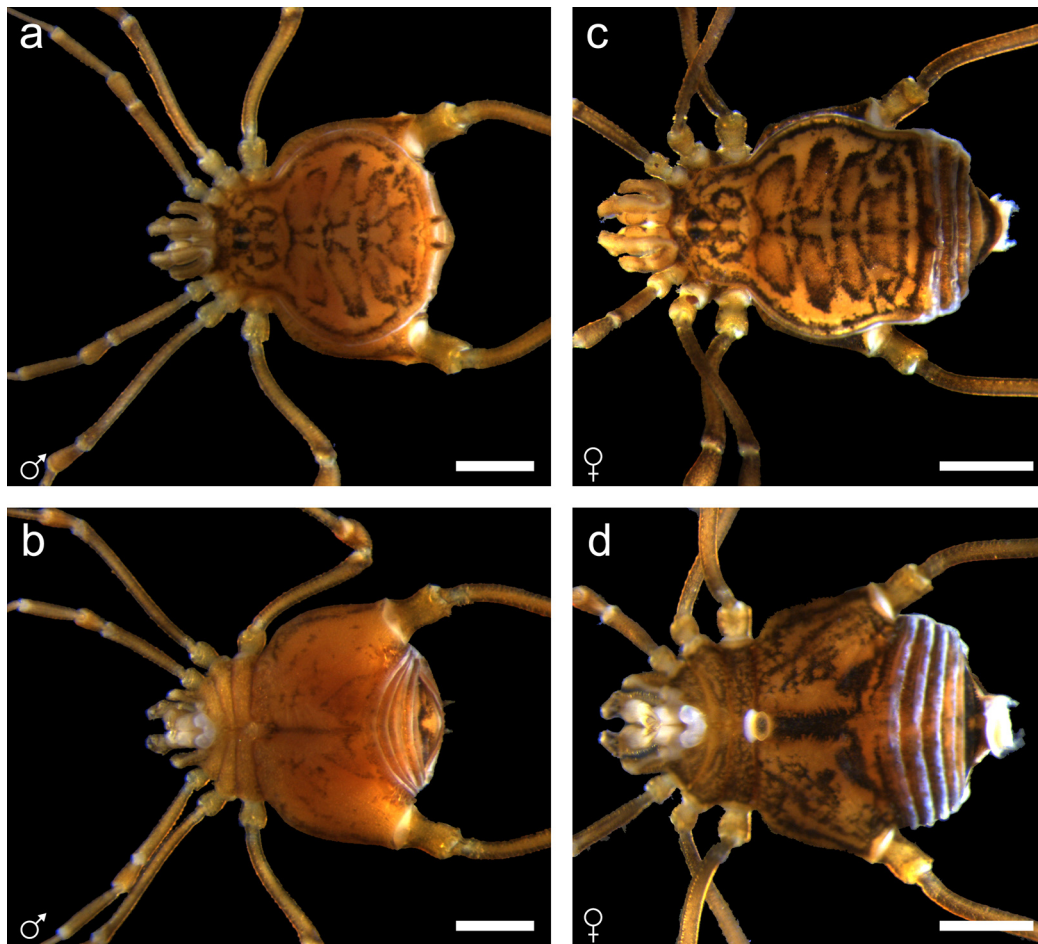


FIGURE 1. *Paktongius suzukii* sp. nov. Male holotype, dorsal view (a). Male holotype, ventral view (b). Female paratype, dorsal view (c). Female paratype, ventral view (d). Scale bars: 1.0 mm.

Description

Total length of male holotype (female paratype in parentheses) 2.95 mm (2.92 mm), greatest width of prosoma 1.46 mm (1.44 mm), greatest width of opisthosoma 2.77 mm (2.64 mm); length-to-width ratio 1.06 (1.11). Body either campaniform with rounded posterior margin (holotype) or campaniform with sub-rectangular posterior margin (female) (Fig. 1a, 1c). Body reddish brown in color with darker mottling (in alcohol, depending on incidence of light), almost entirely with a dense microgranulate surface microstructure. Eyes present on small, unornamented ocularium that is set back from anterior margin of the carapace. Ocularium 0.29 mm (0.37 mm) long, 0.30 mm (0.35 mm) wide. Anterior margin of carapace with five pegs (two pairs on lateral margins, one at the dorsal midline), typical of Assamiidae. Scutal grooves of mesotergum indistinct. Posterior margin of carapace with two prominent spines flanking midline and projecting posteriorly. Free tergites granulated, unarmed.

Ventral prosoma complex (Fig. 1b, 1d) of male and female, with coxae II and III meeting in midline, coxae I not so. Genital operculum subtriangular in male, elliptical in female. Spiracles not apparent. Coxae IV of both male and female massively enlarged (for Grassatores). Anal plate unarmed.

Dorsal pigmentation of male with continuous band of pigment along lateral margins of the carapace; rings of dark pigmentation immediately posterior to ocularium; variable wing-shaped patches of pigmentation on scutal areas I–IV; and dark patches of pigmentation abutting pedipalpal coxae. Ventral pigmentation of male indistinct except along ventral midline of opisthosomal segment II (between coxae IV), lateral margins of coxae IV, and flanking the midline at the posterior of coxae IV. Darker pigmentation flanking midline of anal plate. Female with comparable pigmentation dorsally, but richer patterns of mottling on ventral surface; pigmentation most prominent along midline of opisthosomal segment II and posterior margins of coxae IV.

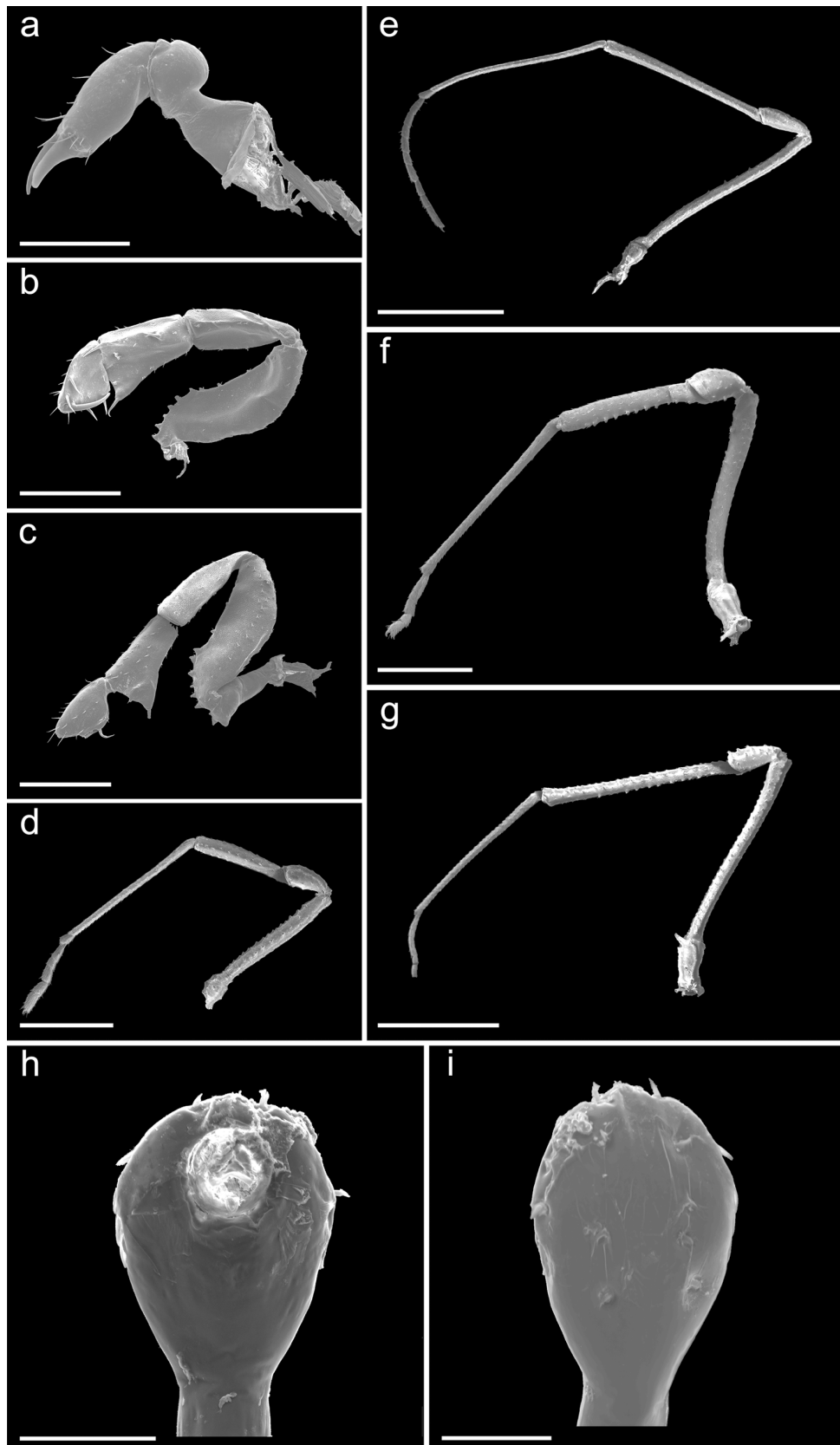


FIGURE 2. *Paktongius suzukii* sp. nov. Appendages are presented in ectal view unless otherwise indicated. Left chelicera of male holotype (a). Right pedipalp of male holotype, mesal view (b). Left pedipalp of male holotype (c). Left leg I of male holotype (d). Left leg II of male holotype (e). Left leg III of male holotype (f). Left leg IV of male holotype (g). Genitalia of male holotype, dorsal view (h). Genitalia of male holotype, ventral view (i). Scale bars: 500 μ m (a–c), 1 mm (d, f), 2 mm (e, g), 100 μ m (h–i).

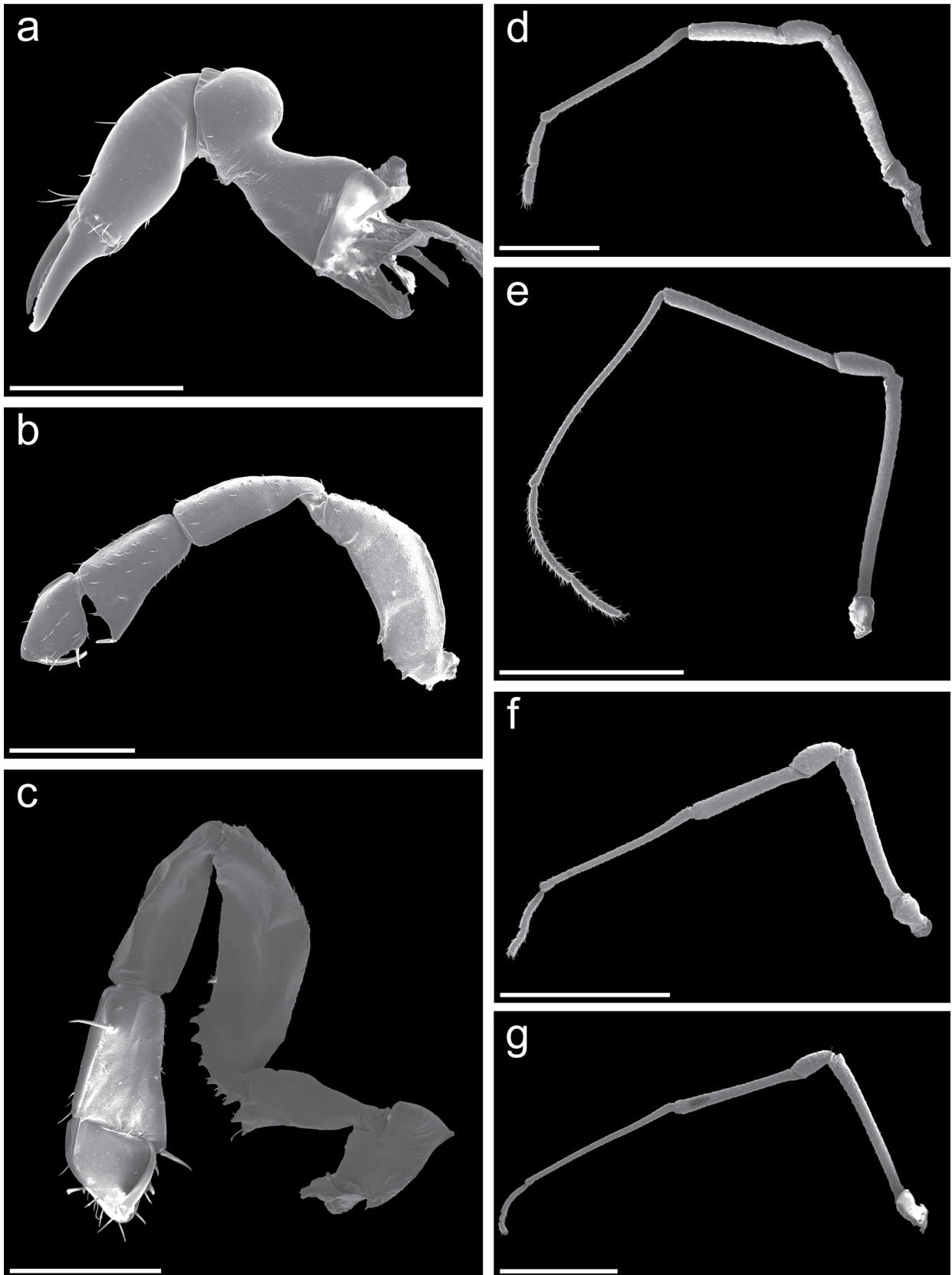


FIGURE 3. *Paktongius suzukii* sp. nov. Appendages are presented in ectal view unless otherwise indicated. Left chelicera of female paratype (a). Left pedipalp of female paratype (b). Right pedipalp of female paratype, mesal view (c). Left leg I of female paratype (d). Left leg II of female paratype (e). Left leg III of female paratype (f). Left leg IV of female paratype (g). Scale bars: 500 μ m (a–c), 1 mm (d), 2 mm (e–g).

Chelicerae (Fig. 2a, 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 and latero-distal margin bearing several setae. Distal article with delicate dentition, free of ornamentation. Pedipalps (Fig. 2b–c, 3b–c) spoon-shaped and folded over chelicerae. Pedipalpal trochanter slender with two setose tubercles at ventro-distal margin. Pedipalpal femur ventrally with eight small tubercles, lacking megaspines and located in proximal half of femur; dorsally with small setose tubercles distally. Pedipalpal tibia with a single, ventrally oriented spine. Spine length 0.20 mm (0.25 mm). Pedipalpal tarsus with two small ventral spines, four megaspines, and unornamented tarsal claw. Legs I–IV (Fig. 2d–g) slender, elongate, finely granulated, with small and irregularly distributed setiferous tubercles on femora, patellae, tibiae, and metatarsi. Male leg IV with more prominent setiferous tubercles in the patellae and tibiae, and two prominent spines in distal margin of trochanter. Tarsal claws I–IV smooth, unmodified, double claws on legs III and IV (typical of Grassatores). Legs III and IV with tarsal process (Fig. 11a). Tarsal formula 5: 9: 6: 7.

Male genitalia (Fig. 2h–i) typical of Assamiidae, with two dorsal setae distally; four pairs of setae on lateral margins of ventral plate; and three pairs of setae on ventral plate.

Distribution. Known only from the type locality (Fig. 12).

***Paktongius spiculosus* sp. nov.**

(Figs. 4–6, 11, 12; Tables 3–4)

Type material. Holotype. ♀ (MHNG LT-10/18) LAOS, Khammouan Province, Nam Kading NPA, Tad Mouang, ca. 1km northeast of Nahin, 18°13'13"N, 104°32'08"E, 270 m, disturbed primary forest, 26.ix.2010, *leg.* P. Schwendinger. L2-4 extracted for DNA; one of each appendage (L1-4; chelicera), both pedipalps dissected and mounted for SEM imaging.

Paratypes. ♂ (UWZM Y.40171) Same collecting data as holotype. LAOS, Bolikhamxai Province, Phou Khao Khouay NPA, north of Ban Hadkhai, trail to Tad Xay, 18°27'05"N, 103°08'59"E, 300 m (secondary forest), 22.ix.2010, *leg.* P. Schwendinger. LT-10/15. Genitalia and one of each appendage dissected and mounted for SEM imaging.

Etymology. The species epithet is derived from the Latin for “spike” (*spiculo*) and highlights the prominent cluster of tubercles adorning the anal plate of the male, reminiscent of thorns or spikes.

Diagnosis. Distinguished from congeners by the combination of the following characters: (1) dorsal pigmentation composed of solid dark patches that do not cross dorsal midline (*contra* rings in *P. suzukii*, *P. paritensis*, *P. furculus*; anterior-most patches crossing midline in *P. thaiensis*); (2) ventral pigmentation posterior to the genital operculum constituting subtriangular shape, without prominent “wings”; (3) absence of two distinct lines of pigment stretching posteriorly from the ocularium (*contra* *P. furculus*, *P. paritensis*); (4) presence of eight enlarged tubercles on the anal plate (males only); (5) absence of enlarged tubercles along the posterior margin of the scutum; (6) tarsal formula: 5: 9: 6: 6. Males additionally distinguished from congeners by the combination of three enlarged tubercles on the lateral margin of the leg IV femur (*contra* *P. suzukii*), and genitalia with five pairs of lateral setae (*contra* *P. suzukii*) and two dorso-apical cuticular projections (*contra* *P. thaiensis*).

TABLE 3. *Paktongius spiculosus* sp. nov. Appendage measurements of female holotype (MHNG LT-10/18). All measurements in mm.

	Tr	Fe	Pa	Ti	Me	Ta	Total
Leg I	0.292	1.216	0.453	0.790	1.471	0.747	4.969
Leg II	0.350	1.967	0.624	1.622	2.088	1.661	8.312
Leg III	0.303	1.352	0.442	0.926	1.672	0.691	5.386
Leg IV	0.507	2.067	0.599	1.585	2.682	0.899	8.339
Pedipalp	0.344	0.738	0.528	0.390	-	0.330	2.330
	Proximal	Second	Distal				
Chelicera	0.442	0.750	0.260				

TABLE 4. *Paktongius spiculosus* sp. nov. Appendage measurements of male paratype (UWZM Y.40171). All measurements in mm.

	Tr	Fe	Pa	Ti	Me	Ta	Total
Leg I	0.315	1.263	0.491	0.801	1.651	0.830	5.351
Leg II	0.343	2.118	0.592	1.656	2.368	1.718	8.795
Leg III	0.388	1.640	0.570	1.103	1.926	0.731	6.358
Leg IV	0.521	2.355	0.674	1.989	2.784	0.968	9.291
Pedipalp	0.360	0.733	0.537	0.345	-	0.246	2.221

	Proximal	Second	Distal
Chelicera	0.461	0.722	0.224

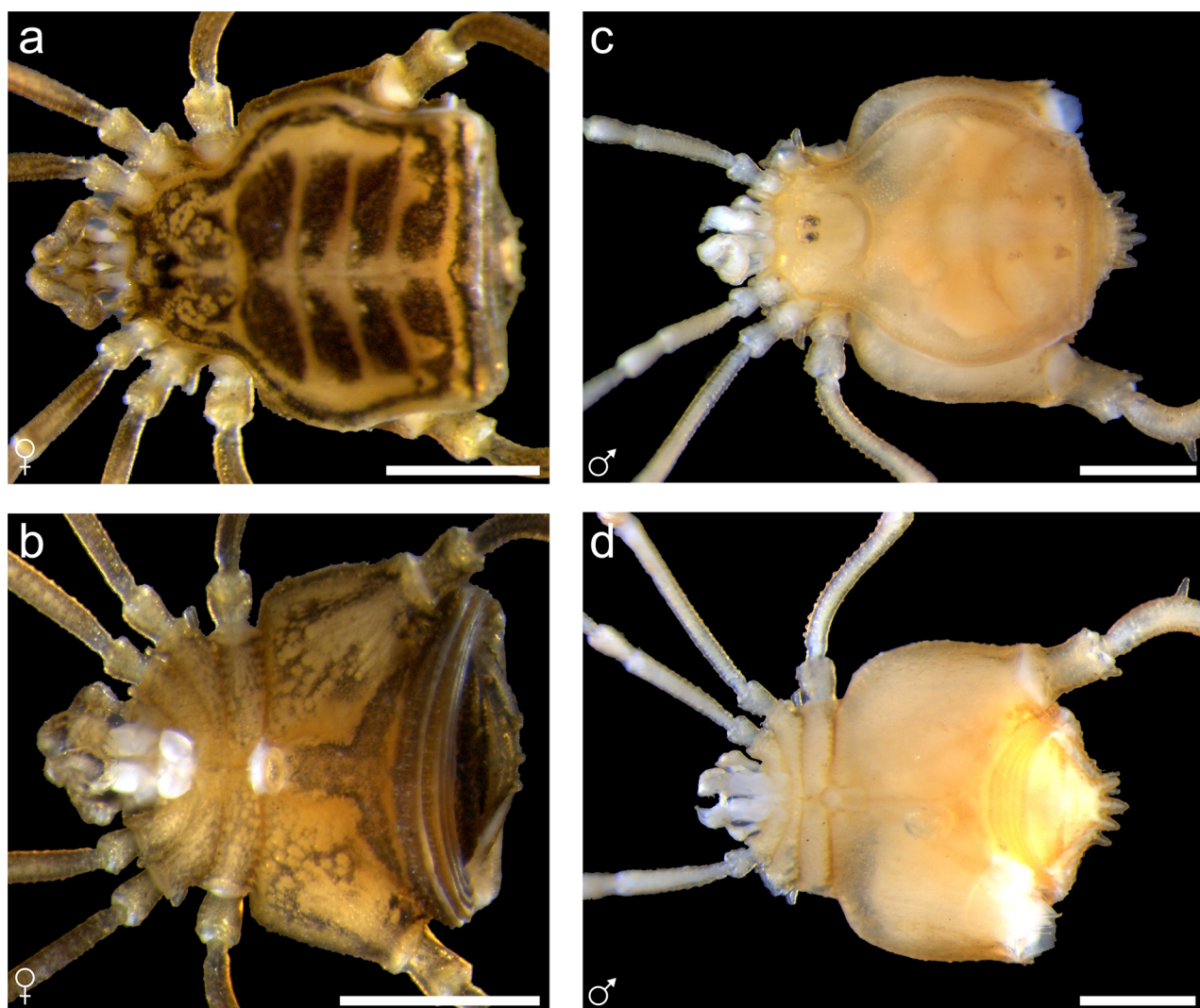


FIGURE 4. *Paktongius spiculosus* sp. nov. Female holotype, dorsal view (a). Female holotype, ventral view (b). Male paratype, dorsal view (c). Male paratype, ventral view (d). Scale bars: 1.0 mm.

Description. Total length of female holotype (male paratype in parentheses) 2.56 mm (2.98 mm), greatest width of the prosoma 1.23 mm (1.28 mm), greatest width of the opisthosoma 2.20 mm (2.34 mm); length-to-width ratio 1.16 (1.27). Body campaniform with sub-rectangular posterior margin (Fig. 4). Body reddish brown in color with darker mottling (in alcohol, depending on incidence of light) in holotype, almost entirely with a dense microgranulate surface microstructure. Eyes present on small, unornamented ocularium that is set back from anterior margin of the

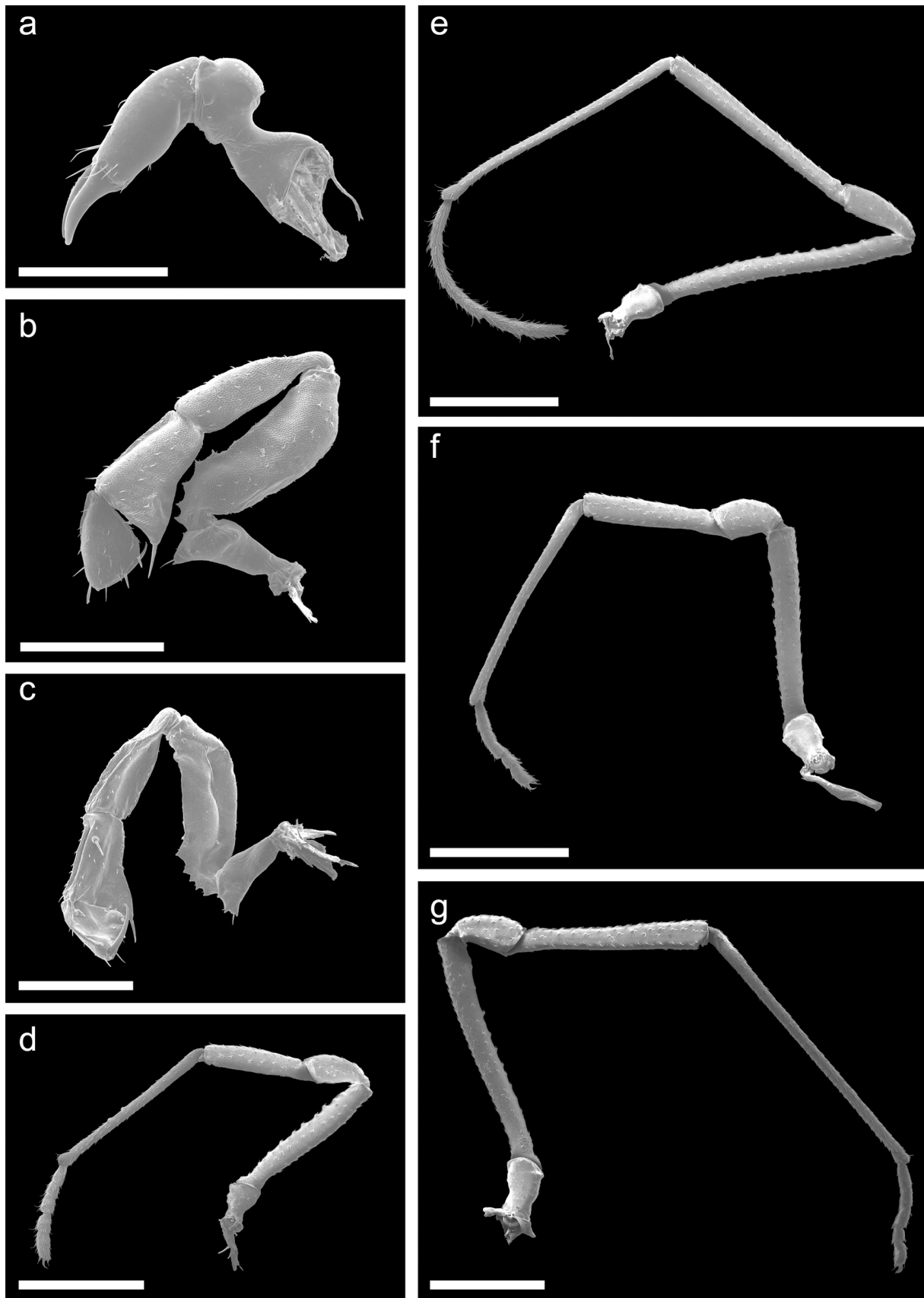


FIGURE 5. *Paktongius spiculosus* sp. nov. Appendages are presented in ectal view unless otherwise indicated. Left chelicera of female holotype (a). Left pedipalp of female holotype (b). Right pedipalp of female holotype, mesal view (c). Left leg I of female holotype (d). Left leg II of female holotype (e). Left leg III of female holotype (f). Left leg IV of female holotype (g). Scale bars: 500 μ m (a–c), 1 mm (d–g).

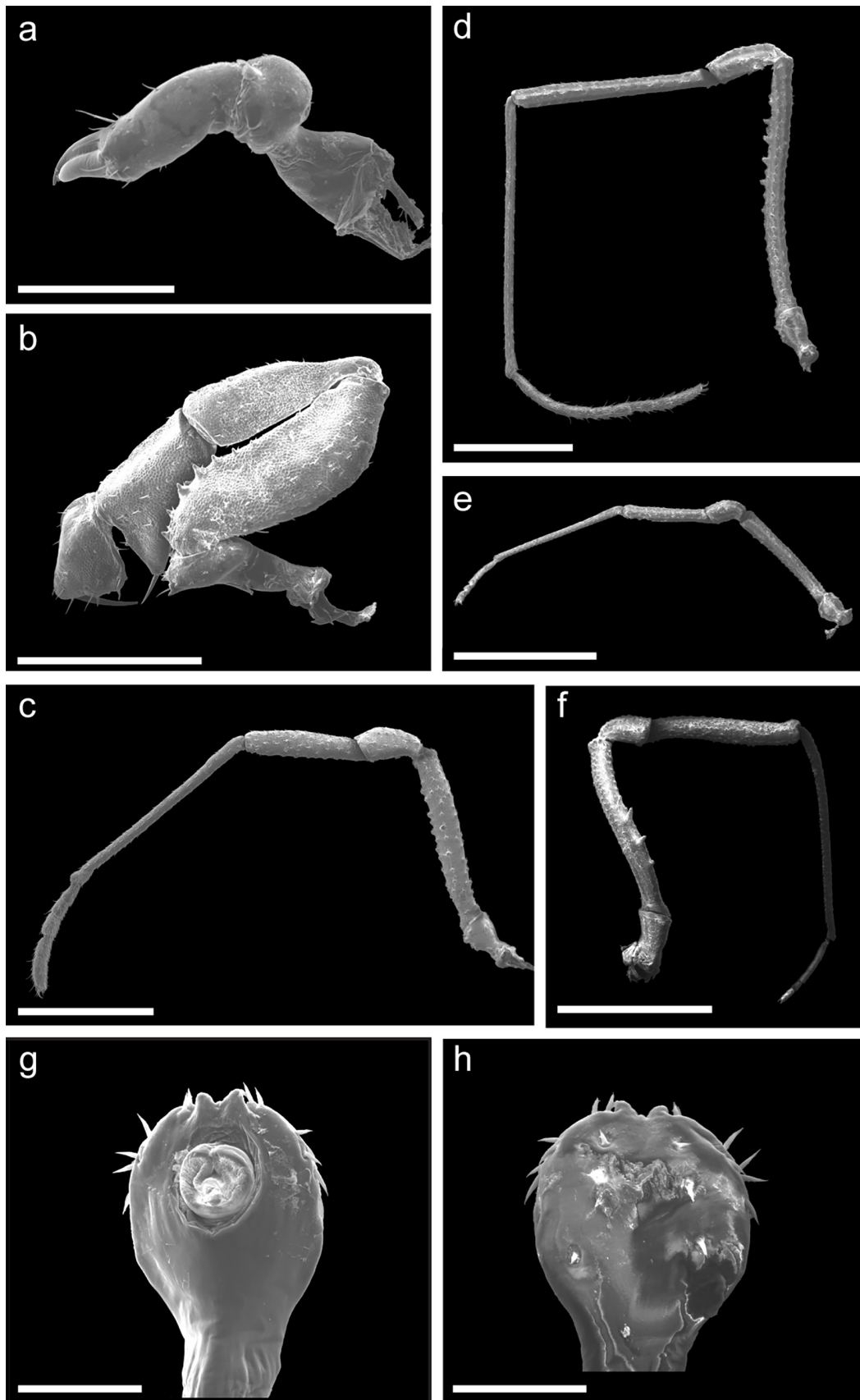


FIGURE 6. *Paktongius spiculosus* sp. nov. Appendages are presented in ectal view unless otherwise indicated. Left chelicera of male paratype (a). Left pedipalp of male paratype (b). Left leg I of male paratype (c). Left leg II of male paratype (d). Left leg III of male paratype (e). Left leg IV of male paratype (f). Genitalia of male paratype, dorsal view (g). Genitalia of male paratype, ventral view (h). Scale bars: 500 μ m (a–b), 1 mm (c–d), 2 mm (e–f), 100 μ m (g–h).

carapace. Ocularium 0.24 mm (0.23 mm) long, 0.30 mm (0.32 mm) wide. Anterior margin of carapace with five pegs (two pairs on lateral margins, one at the dorsal midline), typical of Assamiidae. Scutal grooves of mesotergum indistinct. Scutal areas III–IV with pairs of small spines flanking the midline. Free tergites unarmed.

Ventral prosoma complex (Fig. 4b, d) of male and female, with coxae II and III meeting in midline, coxae I not so. Genital operculum subtriangular in male, elliptical in female. Spiracles not apparent. Coxae IV of both male and female massively enlarged (for Grassatores). Anal plate armed with eight prominent tubercles in male, same number of small and blunt tubercles in female.

Dorsal pigmentation of male absent (likely due to recent ecdysis event) (Fig. 4c, d). Dorsal pigmentation of female with continuous band of pigment along lateral margins of the carapace (Fig. 4a, b); mottled rings of dark pigmentation immediately posterior to ocularium; solid wing-shaped patches of pigmentation on scutal areas I–IV flanking the midline; and dark patches of pigmentation on both lateral pairs of pegs at anterior margin of the carapace. Ventral pigmentation of female indistinct except along ventral midline of opisthosomal segment II (between coxae IV), lateral margins of coxae IV, and flanking the midline at the posterior of coxae IV. Sternites posterior to opisthosomal segment II uniformly with darker pigmentation.

Chelicerae (Figs. 5a, 6a) 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 and latero-distal margin bearing several setae. Distal article with delicate dentition, free of ornamentation. Pedipalps (Fig. 5b–c, 6b) spoon-shaped and folded over chelicerae. Pedipalpal trochanter slender with two prominent setose tubercles at ventro-distal margin. Pedipalpal femur ventrally with eight small tubercles, lacking megaspines and located in proximal half of femur; dorsally with small setose tubercles distally. Pedipalpal tibia with two ventrally oriented spines at the distal margin and one smaller spine at a ventro-lateral and proximal position. Spine length 0.23 mm (0.21 mm). Pedipalpal tarsus with four megaspines and unornamented tarsal claw. Legs I–IV (Fig. 5d–g, 6c–f) slender, elongate, finely granulated, with small and irregularly distributed setiferous tubercles on femora, patellae, tibiae, and metatarsi. Femur I of both male and female ventrally with prominent row of setose tubercles. Coxa II of both male and female with prominently projecting pegs, particularly at the posterior of trochanter II. Male femur IV ectally with four prominent setiferous tubercles (not present in female). Tarsal claws I–IV smooth, unmodified, double claws on legs III and IV (typical of Grassatores). Legs III and IV with tarsal process (Fig. 11b). Tarsal formula 5: 9: 6: 6.

Male genitalia (Fig. 6g–h) typical of Assamiidae, with two cuticular dorsal projections distally; two pairs of apical setae; five pairs of setae on lateral margins of ventral plate; three pairs of setae on ventral plate.

Distribution. Known from Khammouan and Bolikhamxai Provinces, Laos (Fig. 12).

***Paktongius paritensis* sp. nov.**

(Figs. 7–8, 11, 12; Table 5)

Type material. Holotype. ♀ (MHNG), MALAYSIA, Pahang, Cameron Highlands, Tanah Rata, near Parit Falls, 4°28.52'N, 101°23.02'E, ca. 1500 meters, sitting on leaf litter, 26.iv.2009, *leg.* P. Banar; four legs extracted for DNA, remaining appendages removed and mounted for SEM imaging.

Etymology. The species epithet is referred to the collection locality near Parit Falls in the Cameron Highlands of West Malaysia.

Diagnosis. Distinguished from congeners by the combination of the following characters: (1) dorsal surface of scutal areas I–IV with rings of dark pigmentation that do not cross the dorsal midline (*contra* solid patches in *P. distinctus*, *P. spiculosus*, *P. thaiensis*; rings crossing midline in *P. furculus*); (2) ventral pigmentation posterior to the genital operculum constituting three discontinuous patches, as a central arrowhead shape and lateral wings; (3) presence of two distinct lines of pigment stretching posteriorly from the ocularium (see Fig. 7a; *contra* *P. distinctus*, *P. spiculosus*, *P. suzukii*, *P. thaiensis*); (4) presence of two to three enlarged tubercles along the anterolateral margins of the fourth coxae (*contra* *P. spiculosus*, *P. suzukii*, *P. thaiensis*); (5) absence of enlarged tubercles on the anal plate (*contra* *P. thaiensis*, male *P. spiculosus*); (6) tarsal formula: 5: 10: 6: 6.

Description. Female holotype, total length 2.57 mm, greatest width of prosoma 1.27 mm, greatest width of opisthosoma 1.76 mm; length-to-width ratio 1.46. Body pandurate (fiddle-shaped; Fig. 7a). Body light-brown in color with mottling, densely microgranulate surface microstructure. Eyes present on small ocularium with a single

enlarged tubercle abutting the anterior margin of the carapace. Ocularium 0.34 mm long, 0.23 mm wide. Anterior margin of carapace with five pegs (two pairs on lateral margins with outermost longest, one at dorsal midline), typical of Assamiidae. Posterior margin of scutum with two prominent spines flanking midline and projecting posteriorly.



FIGURE 7. *Paktongius paritensis* sp. nov. Female holotype, dorsal view (a). Female holotype, ventral view (b). Scale bars: 1.0 mm.

TABLE 5. *Paktongius paritensis* sp. nov. Appendage measurements of female holotype (MHNG). All measurements in mm.

	Tr	Fe	Pa	Ti	Me	Ta	Total
Leg I	0.280	1.275	0.507	0.901	1.625	1.125	5.713
Leg II	0.357	2.097	0.682	1.805	2.294	2.434	9.669
Leg III	0.331	1.523	0.602	1.073	1.968	1.008	6.505
Leg IV	0.414	2.213	0.659	1.498	2.889	1.130	8.803
Pedipalp	0.415	0.949	0.729	0.466	-	0.397	2.956
	Proximal	Second	Distal				
Chelicera	0.518	0.911	0.260				

Ventral prosomal complex (Fig. 7b) with coxae II and III meeting in midline, coxae I not so. Genital operculum subtriangular. Spiracles not apparent. Coxae IV highly enlarged (typical of Grassatores) with one enlarged tubercle along anterolateral margin and an enlarged tubercle laterally abutting trochanter IV projecting posteriorly. Cuticular projections span the gap between coxa IV and the anterior margin of sternite I, creating a bridge near the distal end of coxa IV. Free tergites smooth. Anal plate unarmed.

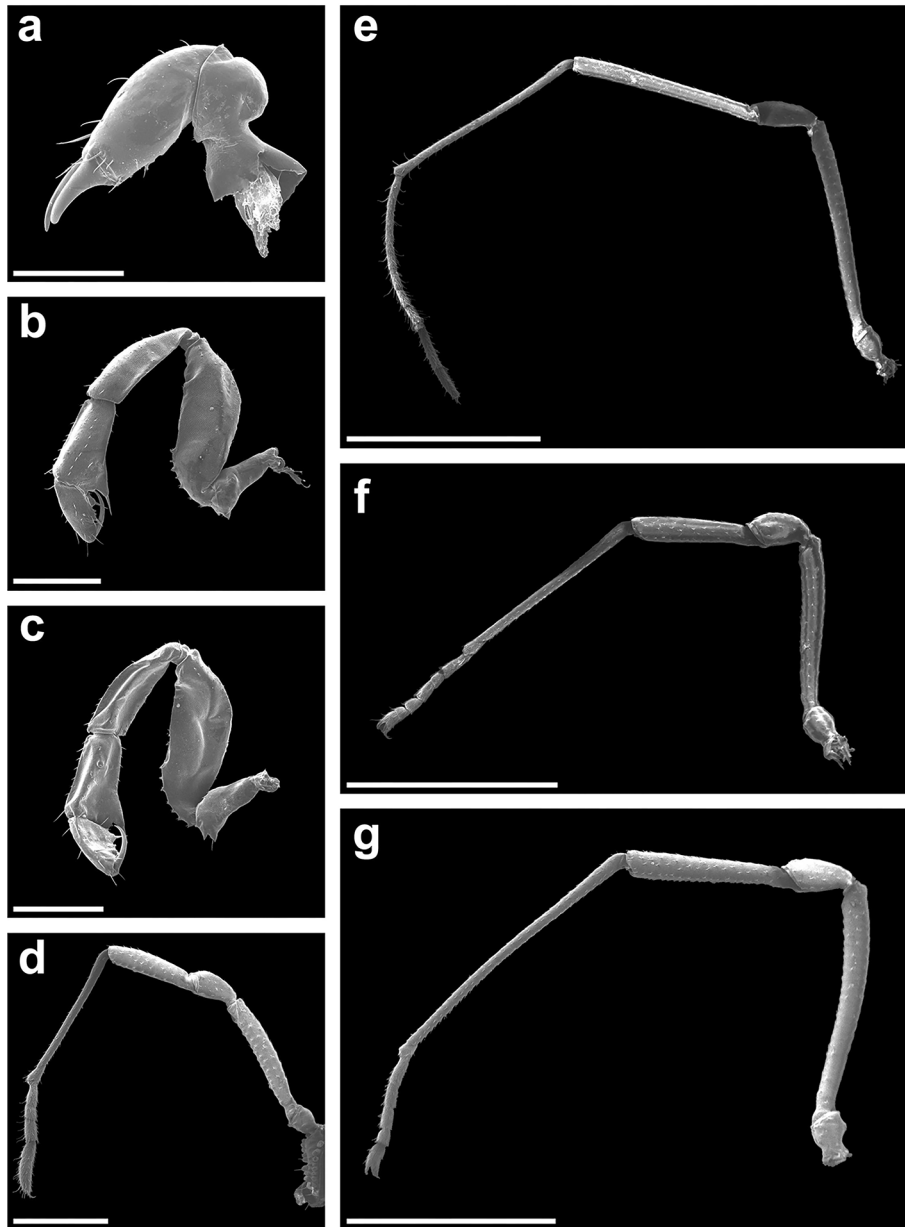


FIGURE 8. *Paktongius paritensis* **sp. nov.** Appendages are presented in ectal view unless otherwise indicated. Left chelicera of female holotype (a). Left pedipalp of female holotype (b). Right pedipalp of female holotype, mesal view (c). Left leg I of female holotype (d). Left leg II of female holotype (e). Left leg III of female holotype (f). Left leg IV of female holotype (g). Scale bars: 400 μ m (a), 500 μ m (b–c), 1 mm (d), 2 mm (e–g).

Dorsal pigmentation with continuous band of dark pigment along lateral margin of the carapace; two solid patches of pigment flanking anterior-posterior axis immediately posterior to the ocularium and meeting in the midline; two arcuate patches of pigment toward posterior-lateral margin of the prosoma; prominent and complex arcs of pigmentation on scutal areas I–IV overlapping the midline; pegs at anterior margin of carapace indistinctly mottled; and spines on scutal area V pigmented. Ventral pigmentation prominently flanking ventral midline of opisthosomal segment II and the posterior margins of the leg IV coxae, creating slender and non-contiguous winged shapes with prominent anterior projection. Leg IV coxae also with lighter bands of pigment extending posteriorly to the junction of the leg IV trochanter and at the distal margin of coxae III. Pigmentation of opisthosoma present along ventral midline of sternites and complex wing-shaped pigmentation pattern on segment anterior to anal plate.

Chelicerae (Fig. 8a) with prominent bulla on proximal article. Proximal article with denticulate granulation throughout basal territory. Article sparsely setose. Second article not incrassate, smooth, free of ornamentation.

Several prominent setae along the length of the dorsal territory and along margin of distal article. Distal article with delicate dentition, free of ornamentation. Pedipalps (Fig. 8b, 8c) spoon-shaped and folded over chelicerae. Pedipalpal trochanter slender with two prominent setose tubercles at ventro-distal margin. Femur ventrally with a series of seven small, adjacent tubercles, lacking megaspines, restricted to proximal-most territory, and two additional disjunct tubercles midway along ventral surface. Femur dorsally with small setose tubercles toward distal end. Pedipalpal tibia with two large spines, one ventrally oriented at apex of prominent triangular projection, other dorso-laterally oriented. Pedipalpal tarsus with unornamented tarsal claw and four megaspines. Tarsal claw 0.27 mm long. Tarsus sparsely setose, with four megaspines ventro-distally, two flanking each side of the claw. Legs I–IV (Fig. 8d–g) slender, elongate, finely granulated, and with setiferous tubercles roughly arranged into rows along femora, patellae, tibiae, and metatarsi. Tarsal claws I–IV smooth, unmodified, double claws on legs III and IV (typical of Grassatores). Legs III and IV with tarsal process (Fig. 11c). Tarsal formula 5: 10: 6: 6.

Male: Unknown.

Distribution. Known only from the type locality (Fig. 12).

***Paktongius furculus* sp. nov.**

(Figs. 9–12; Table 6)

Bandonia sp., Palmieri *et al.* 2023

Type material. Holotype. ♀ (MCZ 92229), Thailand, Kanchanaburi: Khuean Srinagarindra NP, tourist center, 16–17.viii.2008, 14°38.136'N, 98°59.837'E. Chatchawan, Boonkam, collectors. Field Number: T3433. Collection method: pan trap. L2-3 extracted for DNA; one of each appendage dissected and mounted for SEM imaging.

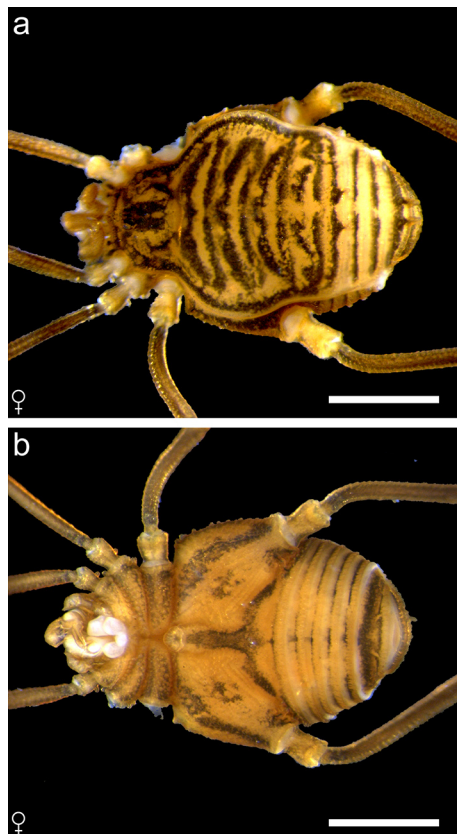


FIGURE 9. *Paktongius furculus* sp. nov. Female holotype, dorsal view (a). Female holotype, ventral view (b). Scale bars: 1.0 mm.

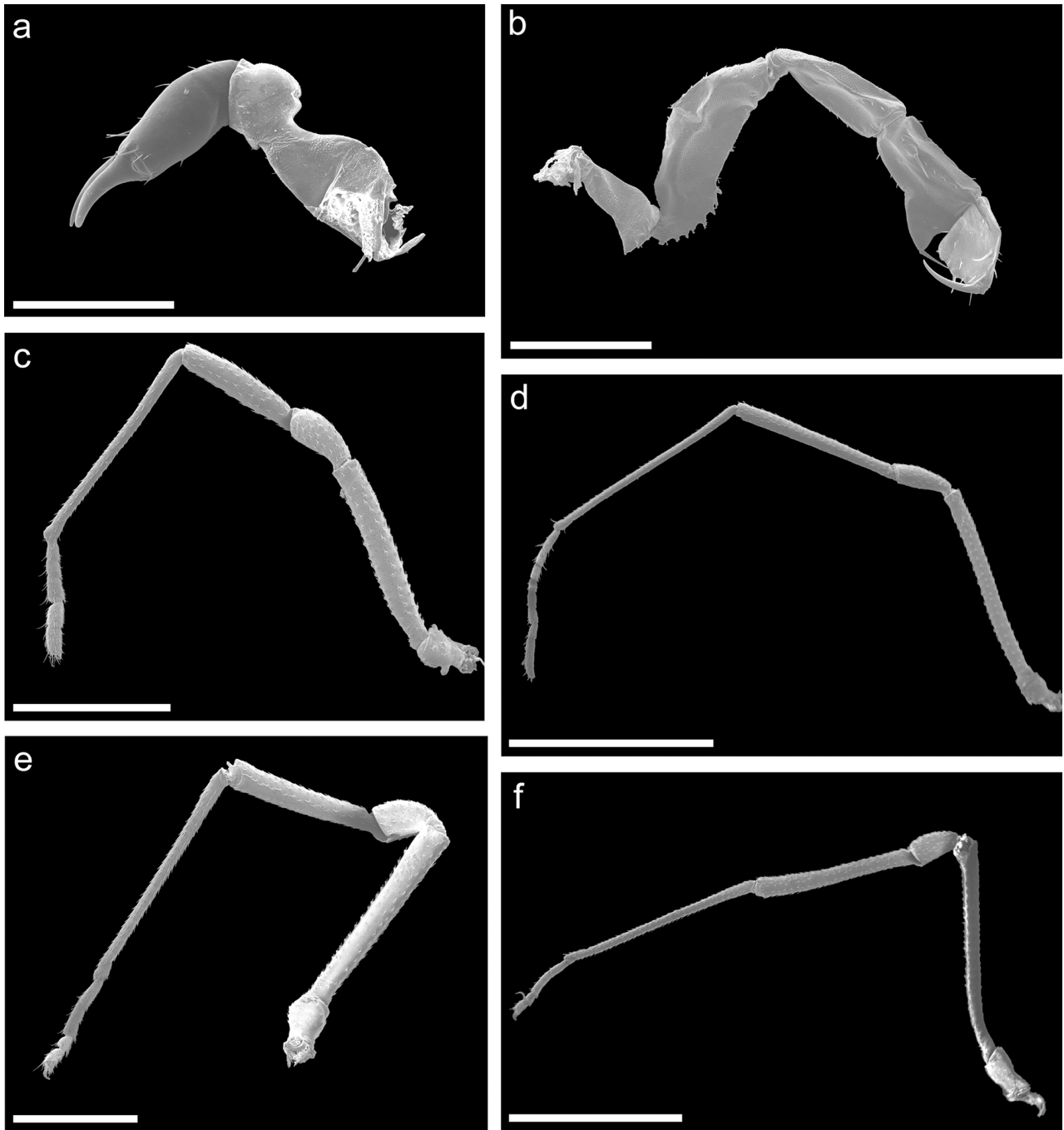


FIGURE 10. *Paktongius furculus* sp. nov. Appendages are presented in ectal view unless otherwise indicated. Left chelicera of female holotype (a). Left pedipalp of female holotype (b). Left leg I of female holotype (c). Left leg II of female holotype (d). Left leg III of female holotype (e). Left leg IV of female holotype (f). Scale bars: 500 μ m (a–b), 1 mm (c, e), 2 mm (d, f).

Etymology. The species epithet is derived from the Latin for “wishbone” (*furculum*) and highlights the prominent pigmentation along the ventral midline and posteriolateral margins of the leg IV coxae, superficially resembling a bird wishbone or furcula.

Diagnosis. Distinguished from congeners by the combination of the following characters: (1) dorsal surface of scutum areas I–IV with rings of dark pigmentation that overlap the midline (*contra* solid patches in *P. distinctus*, *P. spiculosus*, *P. thaiensis*; rings not overlapping midline in *P. furculus*, *P. suzukii*); (2) ventral pigmentation posterior to genital operculum constituting a central column with attached, thin wings, and a small posterior projection at the midline; (3) presence of distinct lines of pigment stretching posteriorly from the ocularium (*contra* *P. distinctus*, *P.*

spiculosus, *P. suzukii*, *P. thaiensis*); (4) presence of two to three enlarged tubercles along the anterolateral margins of the fourth coxae (*contra P. suzukii*, *P. spiculosus*, *P. thaiensis*); (5) absence of enlarged tubercles on the anal plate (*contra P. thaiensis*, male *P. spiculosus*); (6) tarsal formula: 5: 9: 6: 6.

Description. Female holotype, total length 2.88 mm, greatest width of prosoma 1.09 mm, greatest width of opisthosoma 1.89 mm; length-to-width ratio 1.52. Body shape pandurate (fiddle-shaped; Fig. 9). Body reddish-brown in color with darker mottling, densely microgranulate surface microstructure. Eyes present on small ocularium with a single enlarged tubercle, set back from anterior margin of the carapace. Ocularium 0.15 mm long, 0.23 mm wide. Anterior margin of carapace with five pegs (two pairs on lateral margins with outermost longest, one at dorsal midline), typical of Assamiidae. Anterior margin of carapace also adorned with a single row of slightly enlarged tubercles, most prominent at the dorsal midline. Final three segments of scutum each with rows of slightly enlarged tubercles, largest of which flanking midline and projecting posteriorly. Free tergite III also with two prominent spines flanking midline. Free tergite I and II with eight enlarged tubercles, four on either side of dorsal midline.

Ventral prosomal complex (Fig. 9b) with coxae II and III meeting in midline, coxae I not so. Genital operculum sub-triangular to reniform. Spiracles not apparent. Coxae IV highly enlarged (typical of Grassatores) and with enlarged tubercles along anterolateral margin. Coxae IV also with single enlarged tubercle laterally at junction with trochanter IV and projecting posteriorly. Posterior-most tergite with two tubercles projecting ventrally. Anal plate unarmed.

TABLE 6. *Paktongius furculus* **sp. nov.** Appendage measurements of female holotype (MCZ 92229). All measurements in mm.

	Tr	Fe	Pa	Ti	Me	Ta	Total
Leg I	0.271	1.237	0.448	0.800	1.480	0.756	4.992
Leg II	0.295	2.005	0.595	1.650	2.122	1.468	8.135
Leg III	0.334	1.517	0.444	1.052	1.783	0.739	5.869
Leg IV	0.504	2.176	0.541	1.745	2.317	0.771	8.054
Pedipalp	0.305	0.725	0.469	0.393	-	0.227	2.119

	Proximal	Second	Distal
Chelicera	0.498	0.752	0.295

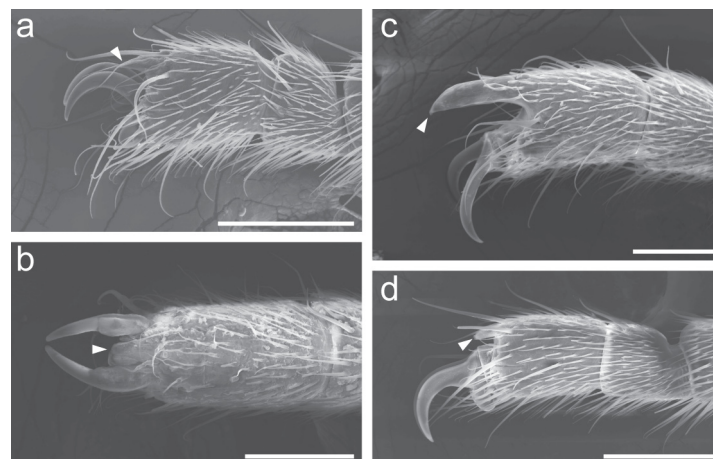


FIGURE 11. Condition of the leg IV tarsal process in all newly described *Paktongius* species. *Paktongius suzukii* **sp. nov.**, left leg IV of female paratype (a). *Paktongius spiculosus* **sp. nov.**, left leg IV of male paratype (b). *Paktongius paritensis* **sp. nov.**, left leg IV of female holotype (c). *Paktongius furculus* **sp. nov.**, left leg IV tarsus of female holotype (d). Location of tarsal process indicated by white arrowheads. Scale bars: 100 μ m.

Dorsal pigmentation with continuous band of dark pigment along lateral margin of the carapace; two solid patches of pigment flanking anterior-posterior axis immediately posterior to the ocularium; two arcuate patches of pigment toward posterior-lateral margin of the prosoma; prominent arcuate rings of pigmentation on scutal areas

I–IV overlapping the midline; pegs above pedipalpal coxae pigmented; and anterior margins of free tergites with stripes of pigment. Ventral pigmentation prominently flanking ventral midline of opisthosomal segment II and the posterior margins of the leg IV coxae, creating a winged-shape with prominent anterior projection. Leg IV coxae also with arched bands of pigment extending posteriorly to the junction of the leg IV trochanter; patches of pigment medially; and patches of pigment at posterior margin near trochanter. Pigmentation of coxae I–III consisting of indistinct mottling. Sternites with stripes of pigmentation at anterior margins.

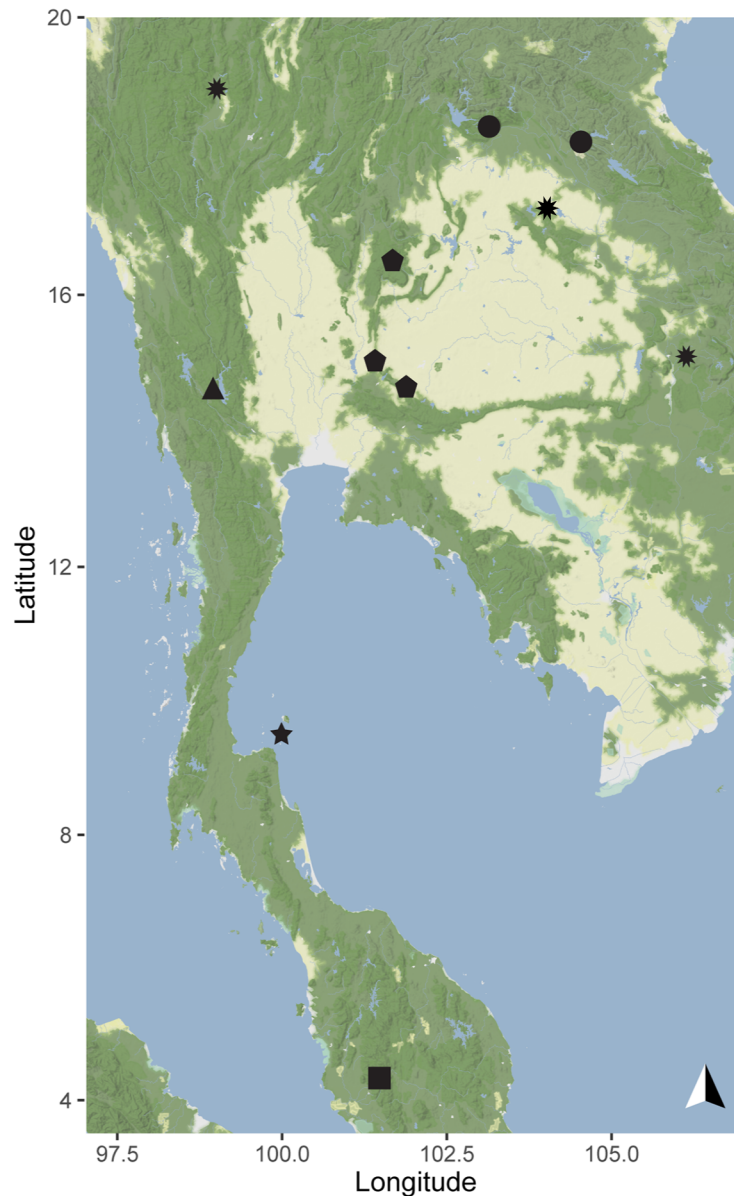


FIGURE 12. Distribution of *Paktongius* species in the Thai-Malay Peninsula. Icons correspond to the following species: star: *Paktongius suzukii* **sp. nov.**; circle: *Paktongius spiculosus* **sp. nov.**; square: *Paktongius paritensis* **sp. nov.**; triangle: *Paktongius furculus* **sp. nov.**; pentagon: *Paktongius distinctus* Suzuki, 1969; ten-pointed star: *Paktongius thaiensis* (Suzuki, 1985) **comb. nov.**

Chelicerae (Fig. 10a) with prominent bulla on proximal article. Proximal article with denticulate granulation throughout basal territory with notable smoothening of the cuticle towards the dorsal side of the bulla. Proximal article sparsely setose. Second article not incrassate, smooth, free of ornamentation. Several prominent setae along the length of the dorsal territory and along margin of distal article. Distal article with delicate dentition, free of ornamentation. Pedipalps (Fig. 10b) spoon-shaped and folded over chelicerae. Pedipalpal trochanter slender with two prominent setose tubercles at ventro-distal margin. Femur ventrally with a series of eight small, adjacent tubercles,

lacking megaspines, restricted to proximal-most territory, and an additional disjunct tubercle midway along ventral surface. Femur dorsally with small setose tubercles toward distal end. Pedipalpal tibia with two megaspines, one ventrally oriented at apex of prominent triangular projection, other dorso-laterally oriented. Laterally, tibia also with exaggerated proximal megaspine. Sparsely setose ventrally and laterally. Pedipalpal tarsus with unornamented tarsal claw and four megaspines ventro-distally, two flanking each side of the claw. Tarsal claw 0.25 mm long. Legs I–IV (Fig. 10c–f) slender, elongate, finely granulated, and with setiferous tubercles roughly arranged into rows along femora, patellae, tibiae, and metatarsi. Leg I trochanter with several notable cuticular projections. Tarsal claws I–IV smooth, unmodified, double claws on legs III and IV (typical of Grassatores). Legs III and IV with tarsal process (Fig. 11d). Tarsal formula 5: 9: 6: 6.

Male. Unknown.

Distribution. Known only from the type locality (Fig. 12).

***Paktongius thaiensis* (Suzuki, 1985) comb. nov.**

Mysorea thaiensis Suzuki, 1985, p. 102–104, fig. 19, Table 15; Zhang & Zhang, 2015, p. 336–341, figs. 1–25, table 1.

Material examined. ♂ (MCZ-92256/MCZ DNA104859) THAILAND, Sakon Nakhon, Phu Phan National Park (16°48.63'N, 103°53.59'E), 1-4.vi.2007, 522 m, dry evergreen forest near house, *leg.* W. Kongnara.

Diagnosis. Distinguished from congeners by the combination of the following characters: (1) anal plate with three large spines; (2) free tergite III with a transverse row of six tubercles; (3) scutal areas II–V with two median tubercles at posterior margin; (4) tarsal formula 5:9:6:6.

Distribution. Known from: Chiang Mai (Suzuki 1985) and Sakon Nakhon Provinces, Thailand; Champasak Province, Laos (Zhang & Zhang 2015) (Fig. 12).

Discussion

Using a ten-locus dataset, Palmieri *et al.* (2023) inferred the internal relationships within Assamiidae and recovered a nested position of *Mysorea thaiensis* within *Paktongius* in tree topologies inferred under both maximum likelihood and Bayesian inference frameworks. *Mysorea thaiensis* closely resembles species of *Paktongius* in most aspects, with emphasis on the hypertrophy of coxa IV and the *scutum magnum*. A recent redescription of *M. thaiensis* also showed considerable similarity of male genitalia with respect to *Paktongius* species described here (Zhang & Zhang 2015). By contrast, the description of *Mysorea brevipes* Roewer, 1935, the type species of *Mysorea*, is markedly different from *M. thaiensis* or *Paktongius* species, especially given the absence of the exaggerated body shape characteristic of the Thai Peninsula species in *M. brevipes*. Thus, *M. thaiensis* is transferred to *Paktongius* establishing the **new combination** *P. thaiensis*. Additionally, a specimen previously thought to be a female of the genus *Bandonia* (see Palmieri *et al.* 2023, fig. 3, “As006 *Bandonia* sp.”) in previous phylogenetic studies (Palmieri *et al.* 2023; Sharma & Giribet 2011) has here been formally described and designated *Paktongius furculus* **sp. nov.** given broad morphological similarity and its stable placement in *Paktongius* based on molecular sequence data. The three additional novel species of *Paktongius* described above now increases the diversity of the formerly monotypic genus to six species.

The occurrence of the “gonyleptoid habitus”—characterized here contextually by the lateral expansion of scutal areas III and IV and the hypertrophy of coxae IV—within *Paktongius* presents an interesting case of convergent evolution. The gonyleptoid habitus is also observed within derived families of Gonyleptoidea, such as Cranaiidae, Cosmetidae, Ampycidae, and Metasarcidae (Monteiro & Pinto-da-Rocha 2015; Benavides *et al.* 2021). In addition, various species of Pyramidopidae (the putative sister group of Assamiidae) likewise exhibit the lateral expansion of the scutum (Sharma *et al.* 2011; Aharon *et al.* 2019). While the placement of Assamiidae within the Laniatores is not fully resolved (whether sister to the clade of superfamilies Samooidea and Zalmoxoidea, or as a derived member of a clade also containing the families Pyramidopidae and Beloniscidae (Aharon *et al.* 2019; Derkarabetian *et al.* 2023; Palmieri *et al.* 2023), Assamiidae is always recovered as distantly related to Gonyleptoidea. We interpret these phylogenetic placements to imply multiple, independent origins of the gonyleptoid habitus, rather than a less parsimonious series of losses across a subset of Grassatores. This apparent morphological convergence is suggestive

of similar selective forces. Assamiidae and Gonyleptoidea are primarily tropical in distribution, although restricted to the Old World and New World, respectively. It has long been observed that tropical species tend to show a higher degree of ornamentation and more elaborate coloration than their temperate counterparts (Wright 1878). This pattern holds for highly divergent taxa, from butterflies to freshwater fishes (Adams *et al.* 2014; Sumarto *et al.* 2020). The exaggeration of morphological traits and ornaments is believed to reflect the latitudinal temperature gradient and its impact on the length of the reproductive season (Tarr *et al.* 2019). In the lower latitudes, higher average temperatures equate to a lower magnitude of seasonal differences, yielding longer reproductive seasons. It has been proposed that latitudinal variation in temperature will also cause latitudinal variation in operational sex ratio (OSR), or the ratio of males to females seeking mating partners (Fujimoto *et al.* 2015). At higher latitudes, with the reproductive season limited to a short window of favorable conditions, mature males and females are expected to appear in synchrony, producing OSRs that are more equal, limiting the strength of sexual selection as competition becomes primarily exploitative. On the other hand, the constant aseasonality in tropical environments is more likely to cause asynchronous appearances of mature females and yield more biased OSRs, increasing the strength of sexual selection and direct competition between mature males.

An increased strength of sexual selection is readily apparent in the armature of the largely tropical and subtropical Laniatores, by comparison to harvestman groups dominant in temperate regions (e.g., temperate Eupnoi and Dyspnoi; Buzatto & Machado 2014). Although detailed life history observations are often limited for tropical Opiliones, male-male combat has been documented within various species of Gonyleptoidea (e.g., García-Hernández & Machado 2018; Osses *et al.* 2008; Zatz *et al.* 2011). Male-male combat in many harvestmen species involves the use of large, elaborate spines and elongated appendages. Members of Cranidae and Gonyleptidae, for example, extend their elongated second pair of walking legs laterally when facing off against another male and use them to strike the similarly positioned second legs of their opponent (García-Hernández & Machado 2018; Zatz *et al.* 2011). Additionally, other gonyleptoid harvestmen, when such fights escalate, will turn and interlock their armored fourth pair of legs and attempt to pinch the opponent's leg between the spines of their femur and coxa (Osses *et al.* 2008; Willemart *et al.* 2009). This combat behavior is possibly shared in various lineages of Laniatores that exhibit sexually dimorphic leg IV hypertrophy, but for which behavioral data are lacking (e.g., Zalmoxidae; Sharma 2012). If similar sexual selection is generated in conjunction with the aseasonality of tropical environments, it could explain the convergent hypertrophy of the *Paktongius* leg IV and scutum, which yields the gonyleptoid opisthosomal condition when these structures expand laterally. The mechanisms that underlie the patterning and operation of the gonyleptoid habitus are not understood with respect to either developmental genetics or biomechanics.

Additional characteristics of Assamiidae suggest similar selective pressures to Gonyleptoidea in shaping both morphology and possibly behavior. Various assamiids possess the flattened, spoon-shaped pedipalps characteristic of Cosmetidae, another gonyleptoid family. However, the function of the spoon-shaped pedipalps remain unknown (Pagoti *et al.* 2019), and similar morphology between males and females would not suggest sexual selection as the driver of this particular convergence in morphology. But, paralleling many Gonyleptoidea, the Nepalese assamiid *Lepchana spinipalpis* exhibits evidence of paternal care of flattened egg clutches underneath stones and wood debris (Martens 1993). In Gonyleptoidea, exclusive paternal care has evolved multiple times, as exemplified by Manaosbiidae and several species of Gonyleptidae (Buzatto & Machado 2014). The phylogenetic distance between Assamiidae and Gonyleptidae suggests independent origins of this behavior as well and the intriguing possibility of behavioral convergence driven by comparable sexual selection pressures in tropical environments. However, we add the caveat that parental care behavior is based on only a handful of observations outside Gonyleptoidea and virtually no data are available for the behavioral ecology of numerous Old World families.

The apparent convergence in morphology of the Assamiidae and Gonyleptoidea may provide a promising system for studying the parallel evolution of appendage hypertrophy in Laniatores. The microendemism of much of the Old World opiliofauna, exemplified by the distribution of five of the now six species of *Paktongius* in the Thai-Malay peninsula (Fig. 12), leaves the true extent of behavioral and ecological convergences largely unknown. Yet, this convergence and support for the longstanding connection between the intensity of sexual selection and latitudinal temperature variation underscores the necessity for more thorough surveying of the tropical Laniatores in conjunction with detailed life history observations.

Conclusion

Here, we expanded upon the known diversity of the formerly monotypic genus *Paktongius* with guidance from a recent molecular phylogeny of Assamiidae. Broad uncertainty of internal relationships within Assamiidae remains a challenge, given a plethora of mono- or ditypic genera whose descriptions were accompanied by limited illustration and abbreviated morphological depictions in Roewer's monographs. The morphological convergence exhibited by *Paktongius* and various Gonyleptoidea may offer an opportune system for understanding the drivers of morphological convergence within Laniatores.

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References

- Adams, J.M., Kang, C. & June-Wells, M. (2014) Are tropical butterflies more colorful? *Ecological Research*, 29, 685–691.
<https://doi.org/10.1007/s11284-014-1154-1>
- Aharon, S., Ballesteros, J.A., Crawford, A.R., Friske, K., Gainett, G., Langford, B., Santibáñez-López, C.E., Ya'aran, S., Gavish-Regev, E. & Sharma, P.P. (2019) The anatomy of an unstable node: a Levantine relict precipitates phylogenomic dissolution of higher-level relationships of the armoured harvestmen (Arachnida: Opiliones: Laniatores). *Invertebrate Systematics*, 31, 2553–21.
<https://doi.org/10.1071/is19002>
- Benavides, L.R., Pinto-da-Rocha, R. & Giribet, G. (2021) The phylogeny and evolution of the flashiest of the armored harvestmen (Arachnida: Opiliones). *In*: Barrow, L. (Ed.), *Systematic Biology*, 70, pp. 648–659.
<https://doi.org/10.1093/sysbio/syaa080>
- Buzatto, B.A. & Machado, G. (2014) Male dimorphism and alternative reproductive tactics in harvestmen (Arachnida: Opiliones). *Behavioral Processes*, 109, 2–13.
<https://doi.org/10.1016/j.beproc.2014.06.008>
- Derkarabetian, S., Lord, A., Angier, K., Frigvik, E. & Giribet, G. (2023) An Opiliones-specific ultraconserved element probe set with a near-complete family-level phylogeny. *Molecular Phylogenetics and Evolution*, 187, 107887.
<https://doi.org/10.1016/j.ympev.2023.107887>
- Fujimoto, S., Miyake, T. & Yamahira, K. (2015) Latitudinal variation in male competitiveness and female choosiness in a fish: Are sexual selection pressures stronger at lower latitudes? *Evolutionary Biology*, 42, 75–87.
<https://doi.org/10.1007/s11692-014-9300-9>
- García-Hernández, S. & Machado, G. (2018) Convergent fighting behavior in two species of Neotropical harvestmen (Opiliones): insights on the evolution of maternal care and resource defense polygyny. *The Journal of Arachnology*, 46, 165–169.
<https://doi.org/10.1636/JoA-S-17-070.1>
- Kury, A.B. & Pinto-da-Rocha, R. (2007) Gonyleptidae Sundevall, 1833. *In*: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (Eds.), *Harvestmen, the biology of Opiliones*. Harvard University Press, Cambridge, Massachusetts, pp. 196–203.
- Martens, J. (1993) Further cases of paternal care in Opiliones (Arachnida). *Tropical Zoology*, 6 (1), 97–107.
<https://doi.org/10.1080/03946975.1993.10539212>
- Monteiro, Y.G. & Pinto-da-Rocha, R. (2015) Revision of the genus *Ferkeria* Roewer, 1947, with the description of a new species (Opiliones: Laniatores: Cosmetidae). *Zootaxa*, 4006 (2), 361–373.
<https://doi.org/10.11646/zootaxa.4006.2.7>
- Murphree, C.S. (1988) Morphology of the dorsal integument of ten opilionid species (Arachnida, Opiliones). *The Journal of Arachnology*, 16 (2), 237–252.
- Osses, F., Nazareth, T.M. & Machado, G. (2008) Activity pattern of the Neotropical harvestman *Neosadocus maximus* (Opiliones, Gonyleptidae): sexual and temporal variations. *The Journal of Arachnology*, 36, 518–526.
<https://doi.org/10.1636/St06-48.1>
- Palmieri, L., Giribet, G. & Sharma, P.P. (2023) Too early for the ferry: The biogeographic history of the Assamiidae of southeast Asia (Chelicerata: Opiliones, Laniatores). *Molecular Phylogenetics and Evolution*, 178, 107647.
<https://doi.org/10.1016/j.ympev.2022.107647>
- Pagoti, G.F., Portela, E., Campanha, J.S., Dias, J.M. & Willemart, R.H. (2019) On the function of the spoon-shaped pedipalps of harvestmen in the family Cosmetidae (Opiliones, Laniatores). *Journal of Natural History*, 53 (33–34), 2087–2098.
<https://doi.org/10.1080/00222933.2019.1692086>

- Roewer, C.F. (1913) Die Familie der Gonyleptiden der Opiliones—Laniatores. [Part 2]. *Archiv für Naturgeschichte*, Abteilung A, 79 (5), 257–472.
- Roewer, C.F. (1935) Alte und neue Assamiidae. Weitere Weberknechte VIII. *Veröffentlichungen aus dem Deutschen Kolonial- und Übersee-Museum in Bremen*, 1 (1), 1–168.
- Sharma, P.P., Prieto, C.E. & Giribet, G. (2011) A new family of Laniatores (Arachnida: Opiliones) from the Afrotropics. *Invertebrate Systematics*, 25, 143–154.
<https://doi.org/10.1071/IS11003>
- Sharma, P.P. & Giribet, G. (2011) The evolutionary and biogeographic history of the armoured harvestmen—Laniatores phylogeny based on ten molecular markers, with the description of two new families of Opiliones (Arachnida). *Invertebrate Systematics*, 25, 106–142.
<https://doi.org/10.1071/IS11002>
- Sharma, P.P. (2012) New Australasian Zalmoxidae (Opiliones: Laniatores) and a new case of male polymorphism in Opiliones. *Zootaxa*, 3236 (1), 1–35.
<https://doi.org/10.11646/zootaxa.3236.1.1>
- Sørensen, W.E. (1884) Opiliones Laniatores (Gonyleptides W.S. Olim) Musei Hauniensis. *Naturhistorisk Tidsskrift*, 14, 555–646.
- Sumarto, B.K.A., Kobayashi, H., Kakioka, R., Tanaka, R., Maeda, K., Tran, H.D., Koizumi, N., Morioka, S., Bounsong, V., Watanabe, K., Musikasinthorn, P., Tun, S., Yun, L.K.C., Anoop, V.K., Raghavan, R., Masengi, K.W.A., Fujimoto, S. & Yamahira, K. (2020) Latitudinal variation in sexual dimorphism in a freshwater fish group. *Biological Journal of the Linnean Society*, 131, 898–908.
<https://doi.org/10.1093/biolinnean/blaa166>
- Sundevall, C.J. (1833) *Conspectus Arachnidum*. C.F. Berling, Londini Gothorum, 39 pp.
- Suzuki, S. (1969) Some phalangids from Thailand. *Journal of Science of the Hiroshima University*, Series B, Division 1 (Zoology), 22 (3), 79–101, pl. I.
- Suzuki, S. (1985) A synopsis of the Opiliones of Thailand (Arachnida) I. Cyphophthalmi and Laniatores. *Streenstrupia*, 11 (3), 69–110.
- Tarr, S., Meiri, S., Hicks, J.J. & Algar, A.C. (2019) A biogeographic reversal in sexual size dimorphism along a continental temperature gradient. *Ecography*, 42, 706–716.
<https://doi.org/10.1111/ecog.03593>
- Thorell, T.T.T. (1876) Sopra alcuni Opilioni (Phalangidea) d'Europa e dell' Asia occidentale, con un quadro dei generi europei di quest' Ordine. *Annali del Museo Civico di Storia Naturale di Genova*, 8, 452–508.
- Townsend, V.R., Rana, N.J., Proud, D.N., Moore, M.K., Rock, P. & Felgenhauer, B.E. (2009) Morphological changes during postembryonic development in two species of neotropical harvestmen (Opiliones, Laniatores, Cranidae). *Journal of Morphology*, 270 (9), 1055–1068.
<https://doi.org/10.1002/jmor.10742>
- Willemart, R.H., Osses, F., Chelini, M.C., Macías-Ordóñez, R. & Machado, G. (2009) Sexually dimorphic legs in a neotropical harvestman (Arachnida, Opiliones): Ornament or weapon? *Behavioural Processes*, 80, 51–59.
<https://doi.org/10.1016/j.beproc.2008.09.006>
- Wright, E.P. (1878) Tropical Nature and other Essays. *Nature*, 18, 140–141.
<https://doi.org/10.1038/018140a0>
- Zatz, C., Werneck, R.M., Macías-Ordóñez, R. & Machado, G. (2011) Alternative mating tactics in dimorphic males of the harvestman *Longiperna concolor* (Arachnida: Opiliones). *Behavioral Ecology and Sociobiology*, 65, 995–1005.
<https://doi.org/10.1007/s00265-010-1103-0>
- Zhang, C. & Zhang, F. (2015) The assamiids harvestmen (Opiliones: Laniatores: Assamiidae) from Champasak Province, Laos. *Zootaxa*, 3964 (3), 335–351.
<https://doi.org/10.11646/zootaxa.3964.3.3>