

A taxonomic revision of the family Oncopodidae III. Further new species of *Gnomulus* Thorell (Opiliones, Laniatores)

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A taxonomic revision of the family Oncopodidae III. Further new species of *Gnomulus* Thorell (Opiliones, Laniatores). - Twenty-one new *Gnomulus* species are described and placed in nine species groups. The new taxa are: *G. carinatus* (Kalimantan), *G. claviger* (Philippines), *G. crassipes* (Philippines), *G. exsudans* (Sarawak, Sabah), *G. hamatus* (Philippines), *G. hutan* (Sarawak), *G. javanicus* (Java), *G. latoperculum* (Sulawesi), *G. leofeae* (Myanmar), *G. lomani* (Borneo), *G. marginatus* (Thailand), *G. matabesar* (Halmahera), *G. monticola* (peninsular Malaysia), *G. obscurus* (Sarawak), *G. pilosus* (peninsular Malaysia), *G. rostratoideus* (peninsular Malaysia), *G. ryssie* (Thailand), *G. sinensis* (southern China), *G. spiniceps* (Vietnam), *G. tuberculatus* (Sumatra) and *G. tumidifrons* (Halmahera). Additional specimens of *G. armillatus* (Thorell) and *G. laruticus* Martens & Schwendinger are reported and illustrated, respectively. Relationships and zoogeography are discussed.

Key-words: Opiliones - Oncopodidae - *Gnomulus* - new species - taxonomy - zoogeography - Asia.

INTRODUCTION

In our preceding paper on the Oncopodidae (Schwendinger & Martens, 1999b) we have re-examined the 27 known species of *Gnomulus* without taking new taxa into account. Here we add 21 new species to this genus. Most of them were collected fairly recently by means of leaf litter sifting and soil extraction; a few others were found in old collections, where they had been misidentified by previous taxonomists who did not examine the genitalia of these specimens. The present number of 48 nominal *Gnomulus* species is remarkable when considering that oncopodids were long regarded as being extremely rare. Prior to a partial revision by Schwendinger in 1992, merely 21 species (including *G. thorelli* Sørensen, which was then overlooked) were known for the whole family.

In an attempt to keep some degree of order within this species-rich and presumably further expanding genus, 11 preliminary species groups are distinguished.

This grouping has no nomenclatural relevance; it is done for purely practical reasons and does not represent the results of a thorough phylogenetic analysis. Some (hopefully the majority) of our species groups may actually correspond with monophyletic lineages, others may not. A few species, which stand isolated and do not fit in well with any group of related species, are placed in monotypical species groups. It is hoped that additional new species will be found, which will either link these outsiders to other groups or will prove that they belong to distinct lineages (as in the case of the *sumatranus*-group in here).

Four of the six groups distinguished by Schwendinger & Martens (1999b: 979) are re-evaluated and five additional groups are added. The *aborensis*-group (with three species from central Nepal, northeastern India and northern Thailand) is excluded, because no new material has become available. The *rostratus*-group (with two described species from peninsular Malaysia) is not treated here either. Several new species have meanwhile been discovered in peninsular Malaysia and Thailand, which also belong to this very distinct species group. They will be treated separately.

MATERIALS AND METHODS

External structures were studied and drawn with a ZEISS SV11 stereomicroscope, the penes with a NIKON Optiphot compound microscope (each with a drawing tube). The penes were expanded by placing them in hot lactic acid and then in distilled water. Expansion is reversed when the penes are transferred to 70% alcohol.

Body measurements refer to the dorsal scutum. Leg articles were measured on their dorsal side, from joint to joint. All measurements are given in mm. Terminology of penis morphology follows that of Martens & Schwendinger (1998: fig. 1).

Abbreviations used in the text: AMNH American Museum of Natural History, New York; BMH Bishop Museum, Honolulu; MAR collection of J. Martens, Mainz; MSNG Museo Civico di Storia Naturale, Genova; NHML Natural History Museum, London [formerly British Museum (Natural History)]; MHNG Muséum d'histoire naturelle, Genève; NSMT National Science Museum, Tokyo; SMF Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt; ZMB Museum für Naturkunde der Humboldt-Universität, Berlin; ZMC Zoologisk Museum, København; ZMH Zoologisches Institut und Museum, Universität Hamburg.

TAXONOMY

Gnomulus Thorell, 1890

Synonymy and diagnosis: See Martens & Schwendinger (1998: 526) and Schwendinger & Martens (1999b: 946).

Type species: *Gnomulus sumatranus* Thorell, 1891. Designated by ruling of the International Commission on Zoological Nomenclature (2001), following an application by Schwendinger & Martens (1999a). See also Schwendinger & Martens (1999b: 946).

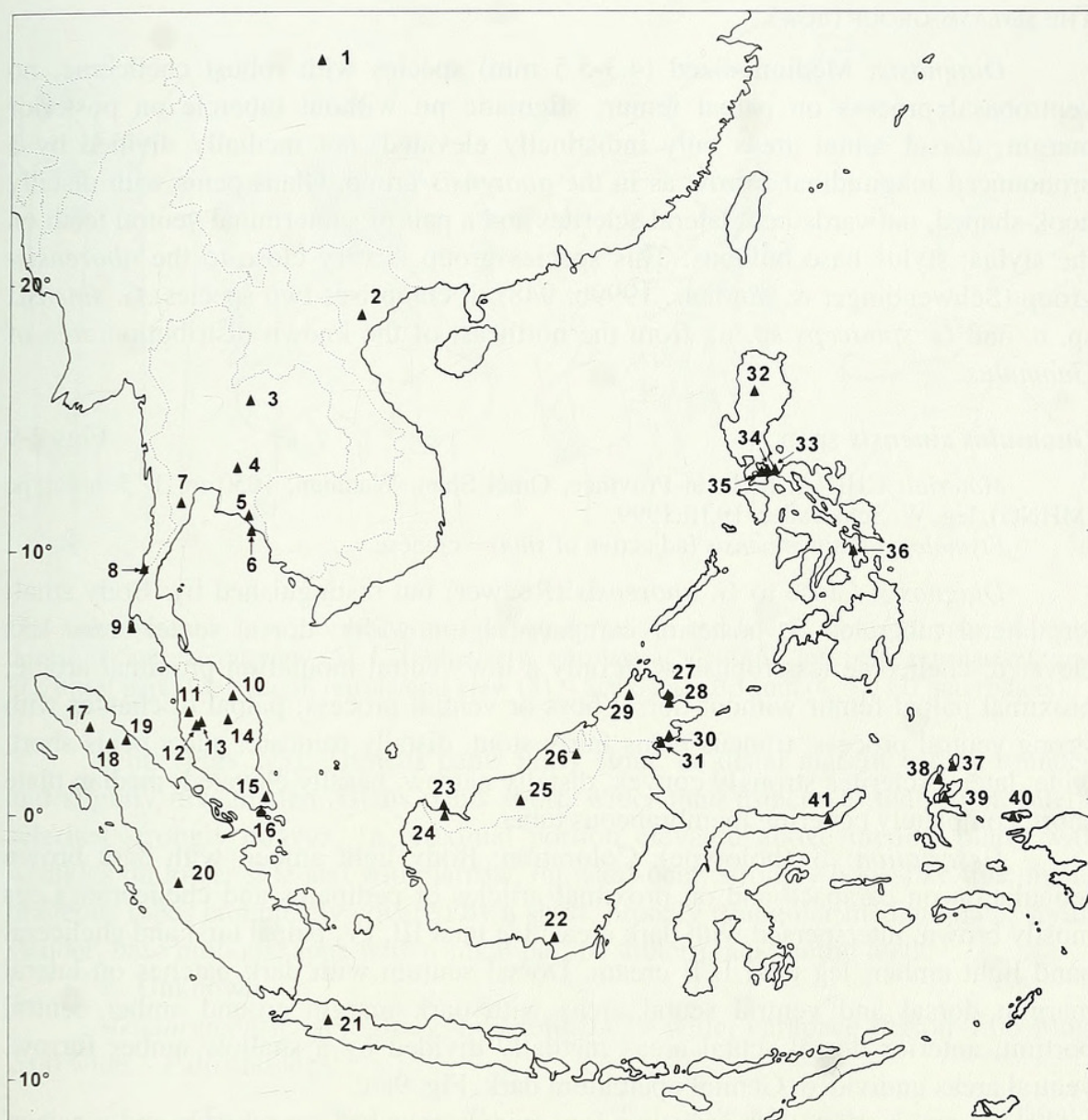


FIG. 1

Records of *Gnomulus* species treated in this paper. - 1 Omei Shan (*G. sinensis* sp. n.), 2 Cuc Phuong (*G. spiniceps* sp. n.), 3 Tham Pu Lub (*Gnomulus* sp.), 4 Khao Yai N. P. (*Gnomulus* sp.), 5 Nam Tok Phliu N. P. (*G. marginatus* sp. n.), 6 Ko Chang N. P. (*G. marginatus* sp. n.), 7 Kaeng Krachan N. P. (*G. ryssie* sp. n.), 8 Malewoon (*G. leofeae* sp. n.), 9 Ko Siray (*Gnomulus* sp.), 10 Jeram Pasu (*Gnomulus* sp.), 11 Maxwell Hill (*G. laruticus* Martens & Schwendinger; *Gnomulus* sp.), 12 Chenderiang (*Gnomulus* sp.), 13 Cameron Highlands (*G. monticola* sp. n.), 14 Taman Negara (*G. pilosus* sp. n.), 15 Kota Tinggi (*G. rostratoideus* sp. n.), 16 Bukit Timah (*G. rostratoideus* sp. n.), 17 Ketambe (*G. tuberculatus* sp. n.), 18 Bukit Lawang (*Gnomulus* sp.), 19 Deli (*Gnomulus* sp.), 20 Gunung Kerinci (*G. armillatus* (Thorell)), 21 Mt. Gede (*G. javanicus* sp. n.), 22 Bandjermasin (*G. carinatus* sp. n.), 23 Santubong (*Gnomulus* sp.), 24 Kuching (*G. obscurus* sp. n.), 25 Kapit (*G. hutan* sp. n.), 26 Gunung Mulu N. P. (*G. exsudans* sp. n.), 27 Sepilok (*G. exsudans* sp. n.), 28 Sapagaya (*G. exsudans* sp. n.), 29 Mt. Kinabalu (*Gnomulus* sp.), 30 Tiger Hill (*Gnomulus* sp.), 31 Nunukan Island (*Gnomulus* sp.), 32 Sagada (*Gnomulus* sp.), 33 Quezon N. P. (*Gnomulus* sp.), 34 Mt. Banahaw (*G. hamatus* sp. n., *G. claviger* sp. n., *G. crassipes* sp. n.), 35 Mt. Makiling (*G. hamatus* sp. n., *G. claviger* sp. n.), 36 Baybay (*Gnomulus* sp.), 37 Morotai (*Gnomulus* sp.), 38 Tobelo (*G. matabesar* sp. n.), 39 Buli (*G. tumidifrons* sp. n.), 40 Waigeo (*Gnomulus* sp.), 41 Dumoga - Bone N. P. and Gunung Tongara (*G. latoperculum* sp. n.).

THE *SINENSIS*-GROUP (new)

Diagnosis: Medium-sized (4.3-5.5 mm) species with robust chelicerae; no ventrobasal process on palpal femur; stigmatic pit without tubercle on posterior margin; dorsal scutal areas only indistinctly elevated, not medially divided by a pronounced longitudinal furrow as in the *aborensis*-group. Glans penis with distally hook-shaped, outwards-bent lateral sclerites and a pair of subterminal ventral teeth on the stylus; stylus base bulbous. This species group is very close to the *aborensis*-group (Schwendinger & Martens, 1999b: 948); it comprises two species, *G. sinensis* sp. n. and *G. spiniceps* sp. n., from the northeast of the known distribution area of *Gnomulus*.

***Gnomulus sinensis* sp. n.**

Figs 2-9

Material: CHINA, Sichuan Province, Omei Shan, Wannian, 1050 m, 1 ♂ holotype (MHNG), leg. W. Schawaller, 19.III.1999.

Etymology: Latin: *sinensis* (adjective of *sina*) = chinese.

Diagnosis: Close to *G. aborensis* (Roewer) but distinguished by: Body smaller; lateral tubercles on posterior carapace region wider; dorsal scutal areas less elevated; chelicerae less robust, with only a low ventral mound on proximal article; proximal palpal femur without dorsal boss or ventral process; palpal trochanter with strong ventral process; truncus penis fairly stout, distally truncate; glans penis short, wide; lateral sclerites strongly convex, distally narrow, basally elevated; median plate short, completely covering membraneous tubes.

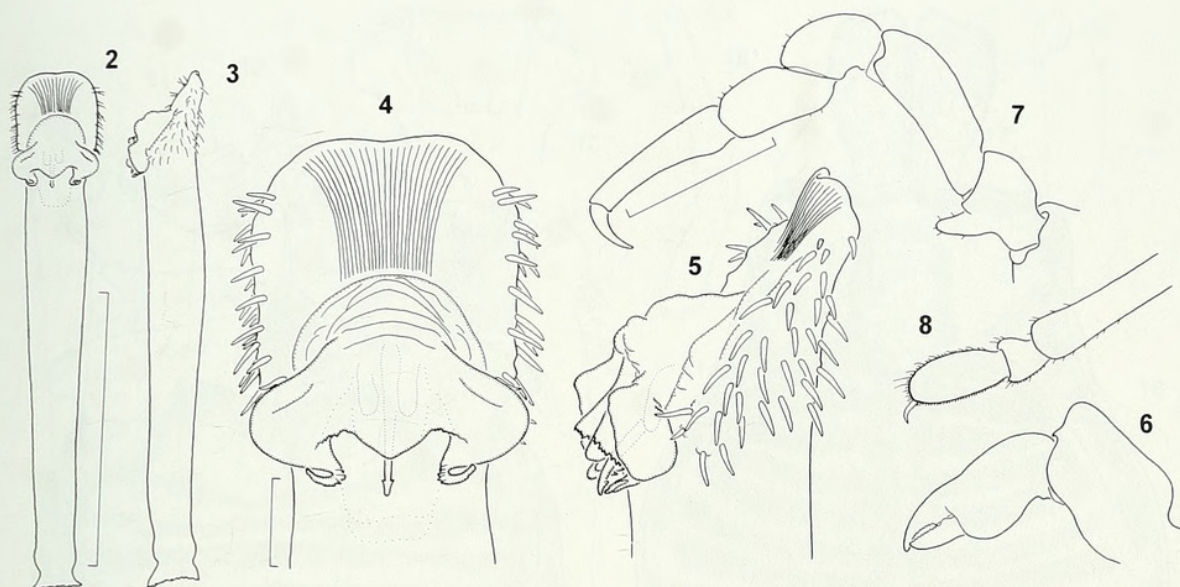
Description: ♂ (holotype). Coloration: Body light amber, with dark brown reticulation on carapace and on proximal articles of pedipalps and chelicerae. Legs mostly brown, interspersed with dark areas; leg tarsi III, IV, palpal tarsi and chelicerall hand light amber, leg tarsi I, II cream. Dorsal scutum with dark patches on lateral margin; dorsal and ventral scutal areas with dark margin around amber central portion; anterior dorsal scutal areas medially divided by a shallow amber furrow, ventral areas undivided. Genital operculum dark. Fig. 9a-c.

Carapace short, with indistinct low, widely rounded eye tubercle and a pair of broadly rounded lateral tubercles below wide, undivided carapace-abdomen bridge (Fig. 9a, c). Dorsal scutum with anterior areas only slightly elevated, posterior ones more distinctly so; ventral scutal areas only moderately swollen (Fig. 9c), bearing "encrusted" hairs (see Schwendinger & Martens, 1999b: fig. 69a, b). Palpal coxa with large ventral process; ventral side of leg coxa I without anterolateral process; ventral side of leg coxa II with small anteroproximal process (no posteroproximal one), coxa III without process. Genital operculum quite large, somewhat triangular in shape, slightly wider than long; posterior margin of stigmatic pit without tubercle (Fig. 9b).

Chelicerae (Fig. 6) fairly robust; proximal article with distinct dorsodistal to dorsomedian boss; ventral side with low, wide mound.

Palps (Fig. 7): Ventral side of femur without proximal process; trochanter with strong, slightly distad-inclined ventral process.

Legs 1324, tarsal formula 2-2-3-3. Distitarsus of leg II 2.2 times longer than wide (Fig. 8).



FIGS 2-8

Gnomulus sinensis sp. n., ♂ holotype. - Penis, dorsal (2) and lateral view (3); apex of penis, dorsal (4) and lateral view (5). Left chelicera, retrolateral view (6); left palp, retrolateral view (7); distal part of left leg II, retrolateral view (8). - Scale lines 0.1 mm (4, 5), 1.0 mm (others).

Penis (Figs 2-5): Truncus penis fairly stout, its distal margin widely rounded and slightly invaginated. Glans penis short, wider than truncus at that point; lateral sclerites strongly convex, in proximal portion elevated above median plate, with wrinkles on lower side and with narrow, outward-bent, strongly hook-like tips; membranous tubes completely covered by a short, broadly triangular median plate; stylus slender, base bulbous, apex with a small pair of subterminal ventral teeth.

♀. Unknown.

Measurements: (♂): Body 4.32 long, 3.29 wide; carapace region 1.06 long, 2.00 wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.67	0.96	0.62	0.44	-	0.91	3.60
Leg I	0.52	1.58	0.77	0.82	1.43	0.74	5.86
Leg II	0.59	2.03	1.01	1.26	2.03	1.11	8.03
Leg III	0.52	1.48	0.79	0.86	1.63	0.59	5.87
Leg IV	0.64	1.93	1.03	1.31	2.42	0.74	8.07

Relationships: *Gnomulus sinensis* sp. n. is closest to *G. spiniceps* sp. n.

Distribution and bionomics: Known only from Mount Omei (3079 m) in southern China. The specimen was sifted from the forest floor of a subtropical broad-leaf-forest. This is so far the northernmost record for the family Oncopodidae [Fig. 1 (1)].

Gnomulus spiniceps sp. n.

Figs 10-19

Material: VIETNAM, Ninh Binh Province, Cuc Phuong National Park, 450 m, about 40 km NW of Ninh Binh, ♂ holotype (NSMT-Ad 174), leg. S. Nomura, 15.X.1995.

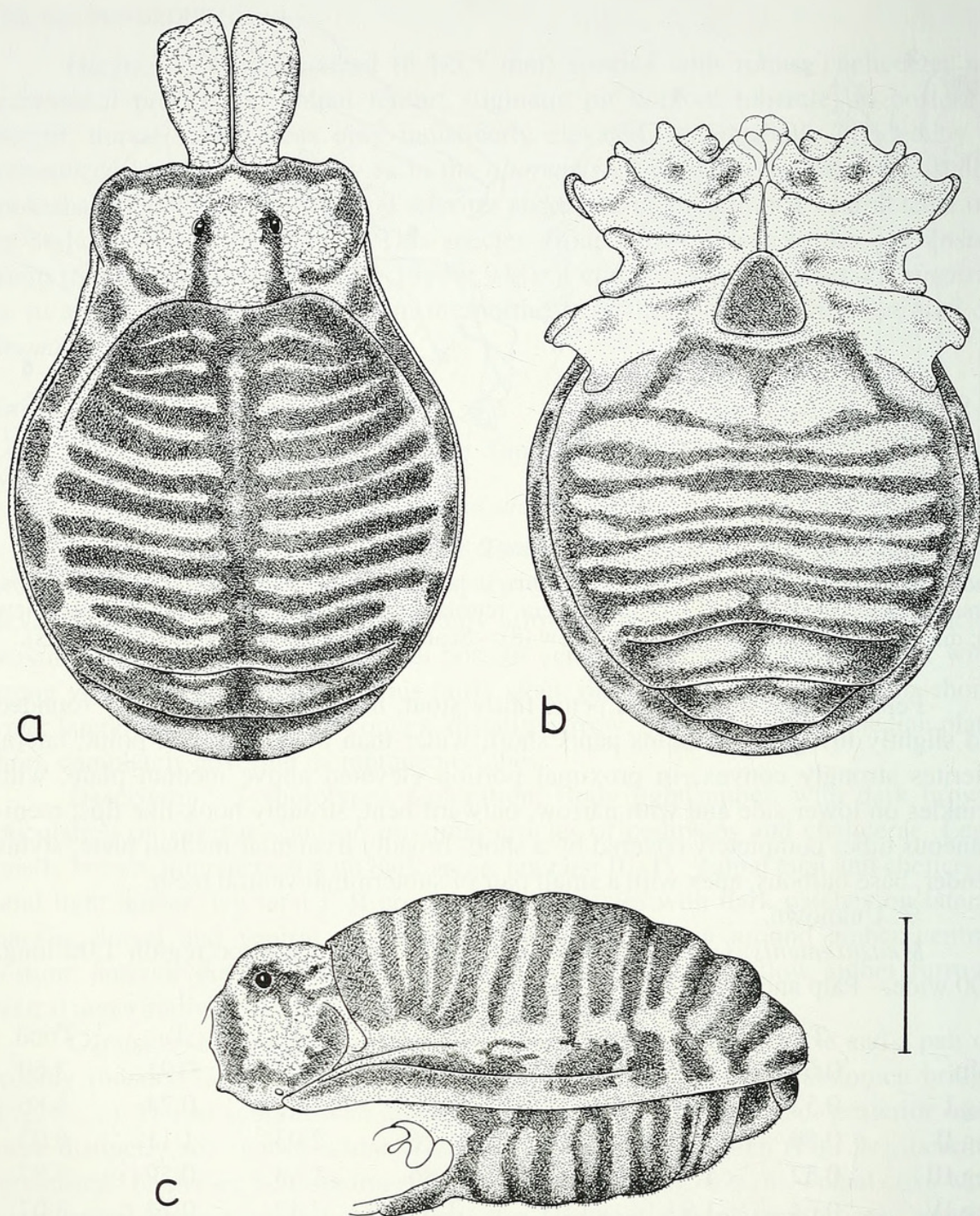
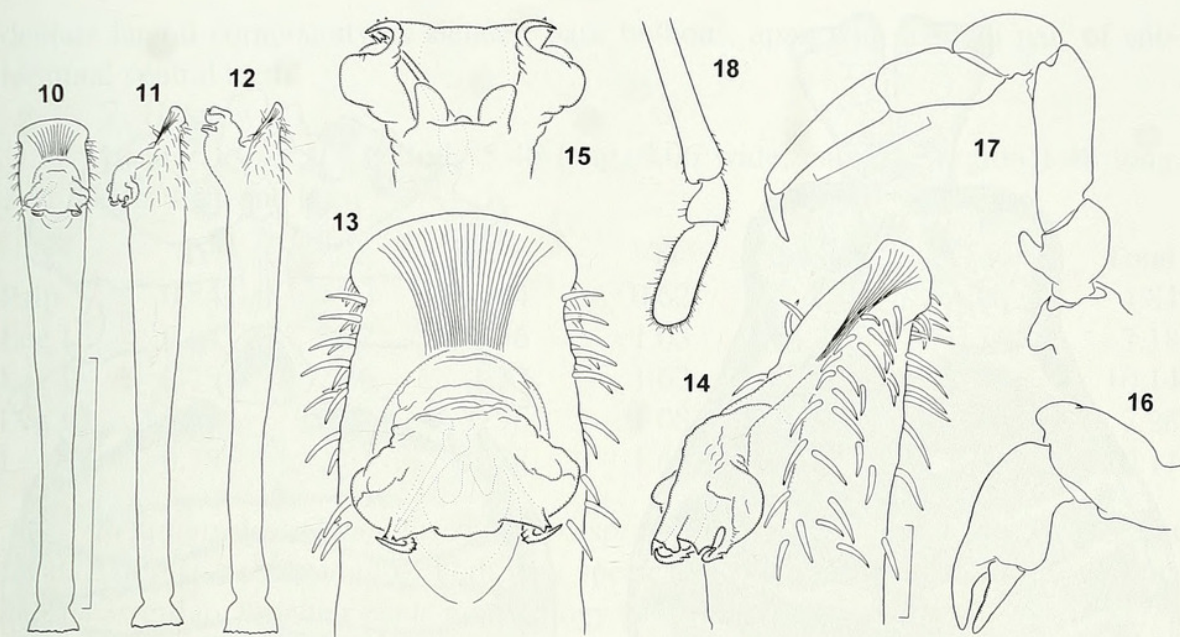


FIG. 9

Gnomulus sinensis sp. n., ♂ holotype. - Body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1.0 mm.

Etymology: Latin: *spina* = thorn, spine, *ceps* (from *caput*) = head; noun in apposition. The specific epithet refers to the long and pointed eye tubercle of the holotype.

Diagnosis: Closest to *G. sinensis* sp. n., distinguished by: Eye tubercle pronounced, pointed; posterior scutal areas less elevated; distitarsus II longer; penis more slender, with a narrower glans and a widely truncate median plate.



FIGS 10-18

Gnomulus spiniceps sp. n., ♂ holotype. - Penis, dorsal (10) and lateral view (11); penis with expanded glands, lateral view (12); apex of penis, dorsal (13) and lateral view (14); expanded glans, dorsal view (15). Left chelicera, retrolateral view (16); left palp, retrolateral view (17); distal part of left leg II, retrolateral view (18). - Scale lines 0.1 mm (13-15), 1.0 mm (others).

Description: ♂ (holotype). Coloration: Body light amber, with dark brown reticulation on carapace and on proximal articles of pedipalps and chelicerae. Dorsal scutum with dark pattern on scutal elevations and with dark patches on light lateral and posterior margin (Fig. 19a, c). Ventral side of body light amber, ventral scutal elevations pale, with dark fringes; genital operculum darkened in its centre (Fig. 19b). Trochanters and femora of palps and trochanters to metatarsi of legs darkened (on posterior legs most distinctly so in proximal portion), palpal tarsi and cheliceral hand light amber, leg tarsalia II cream.

Carapace with distinct, acutely pointed eye tubercle; carapace-abdomen bridge wide, undivided, with very wide, low tubercles below. Dorsal scutal areas slightly elevated, medially indistinctly broken by a shallow longitudinal furrow; ventral scutal areas moderately swollen, without modified hairs (Fig. 19a, c). Palpal coxa with large ventral process; leg coxa I with small anterolateral process; leg coxa II with distinct anteroproximal and indistinct posteroproximal processes; coxa III without process. Genital operculum anteriorly rounded, slightly wider than long; posterior margin of stigmatic pits without tubercle (Fig. 19b).

Chelicerae (Fig. 16) fairly robust; proximal article with distinct, forward-inclined dorsodistal to dorsomedian boss and knob-shaped proventral subdistal process.

Palps (Fig. 17): Ventral side of femur without proximal process; trochanter with long, slightly distad-inclined ventral process.

Legs 1342, tarsal formula 2-2-3-3. Distitarsus II about 2.9 times longer than wide (Fig. 18).

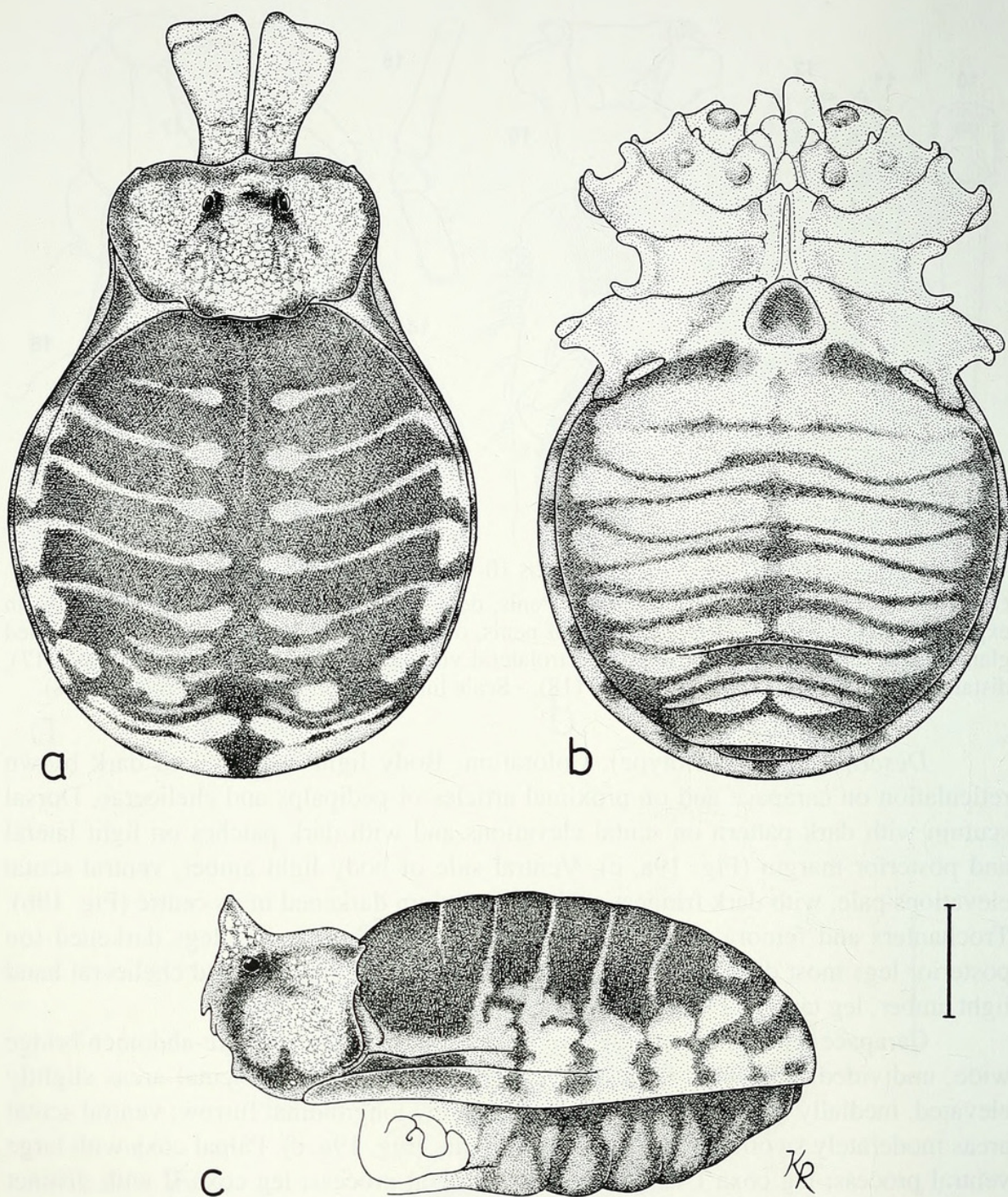


FIG. 19

Gnomulus spiniceps sp. n., ♂ holotype. - Body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1.0 mm.

Penis (Figs 10-15): Truncus penis relatively slender, its anterior margin widely arched. Glans short, narrower than truncus at that point; lateral sclerites strongly convex, elevated at proximolateral margins, with strongly outward-bent hook-like tips carrying transversal wrinkles on lower side; membranous tubes completely covered by short, very wide median plate with almost straight distal margin and distinctly

dentate lateral corners; stylus slender, base bulbous, apex with a small pair of sub-terminal ventral teeth.

♀. Unknown.

Measurements: (♂): Body 5.46 long, 4.06 wide; carapace region 1.48 long, 2.31 wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.84	1.23	0.84	0.62	-	1.28	4.81
Leg I	0.64	2.02	0.96	1.03	1.77	0.76	7.18
Leg II	0.79	2.66	1.33	1.67	2.53	1.16	10.14
Leg III	0.59	2.02	0.96	1.08	1.94	0.69	7.28
Leg IV	0.79	2.61	1.28	1.67	2.95	0.81	10.11

Relationships: *Gnomulus spiniceps* sp. n. is most closely related to *G. sinensis* sp. n. External morphology of both new species shows a clear relationship with the *aborensis*-group, but their penis morphology is distinct.

Distribution: Known only from the type locality in northern Vietnam [Fig. 1 (2)].

THE *ASLI*-GROUP (see Schwendinger & Martens, 1999b: 956)

Diagnosis: These small (2.3-4.2 mm) species can be further characterized by: Palpal trochanter with a distinctly distad-directed ventral process; tubercle on posterior margin of stigmatic pit distinct (*G. laruticus*, *G. monticola* sp. n., *G. pilosus* sp. n.), indistinct or absent (other species); stylus penis with a ventral pair of sub-terminal teeth and a bulbous base.

Species account and distribution: Five species are known from the western and central parts of peninsular Malaysia, i.e. *G. asli* Martens & Schwendinger, *G. hirsutus* Martens & Schwendinger, *G. laruticus* Martens & Schwendinger, *G. monticola* sp. n. and *G. pilosus* sp. n.

Gnomulus laruticus Martens & Schwendinger, 1998

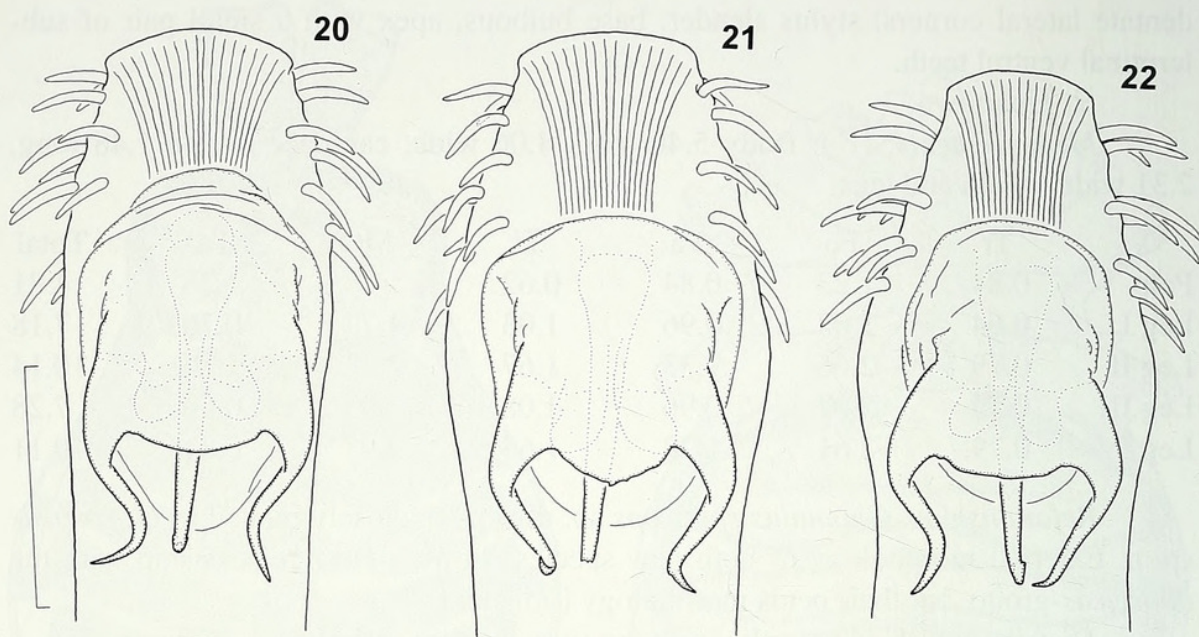
Figs 20-22

Gnomulus laruticus Martens & Schwendinger (1998: 539-542, figs 105-113).

New material: MALAYSIA (peninsula), Perak, Maxwell Hill near Taiping (type locality) [Fig. 1 (11)], at 1150 m, 2 ♂, 7 ♀, 24.-25.XI.1999, at 1250 m, 1 ♂, 23.XI.1999; all specimens leg. G. Cuccodoro & I. Löbl (1 ♂, 1 ♀ in MAR, others in MHNG).

Remarks: All newly collected specimens possess the unusual tarsal formula (2-2-2-2), which confirms that this is a diagnostic character for *G. laruticus*. The amber coloration and dark markings of the new specimens are more pronounced than in the holotype and they all possess a genital operculum with a dark central zone. Their penes largely correspond with that of the holotype, but one ♂ has a distinctly narrower apex and a lateral glans sclerite with an inwards pointing apex (only on one side, probably deformed; Fig. 22).

The ♀ from the same locality (at 1200 m) mentioned in Martens & Schwendinger (1998: 549) clearly belongs to a different, presumably undescribed species.



FIGS 20-22

Gnomulus laruticus Martens & Schwendinger. - Apex of penis of three males, dorsal view. - Scale line 1.0 mm.

***Gnomulus monticola* sp. n.**

Figs 23-35

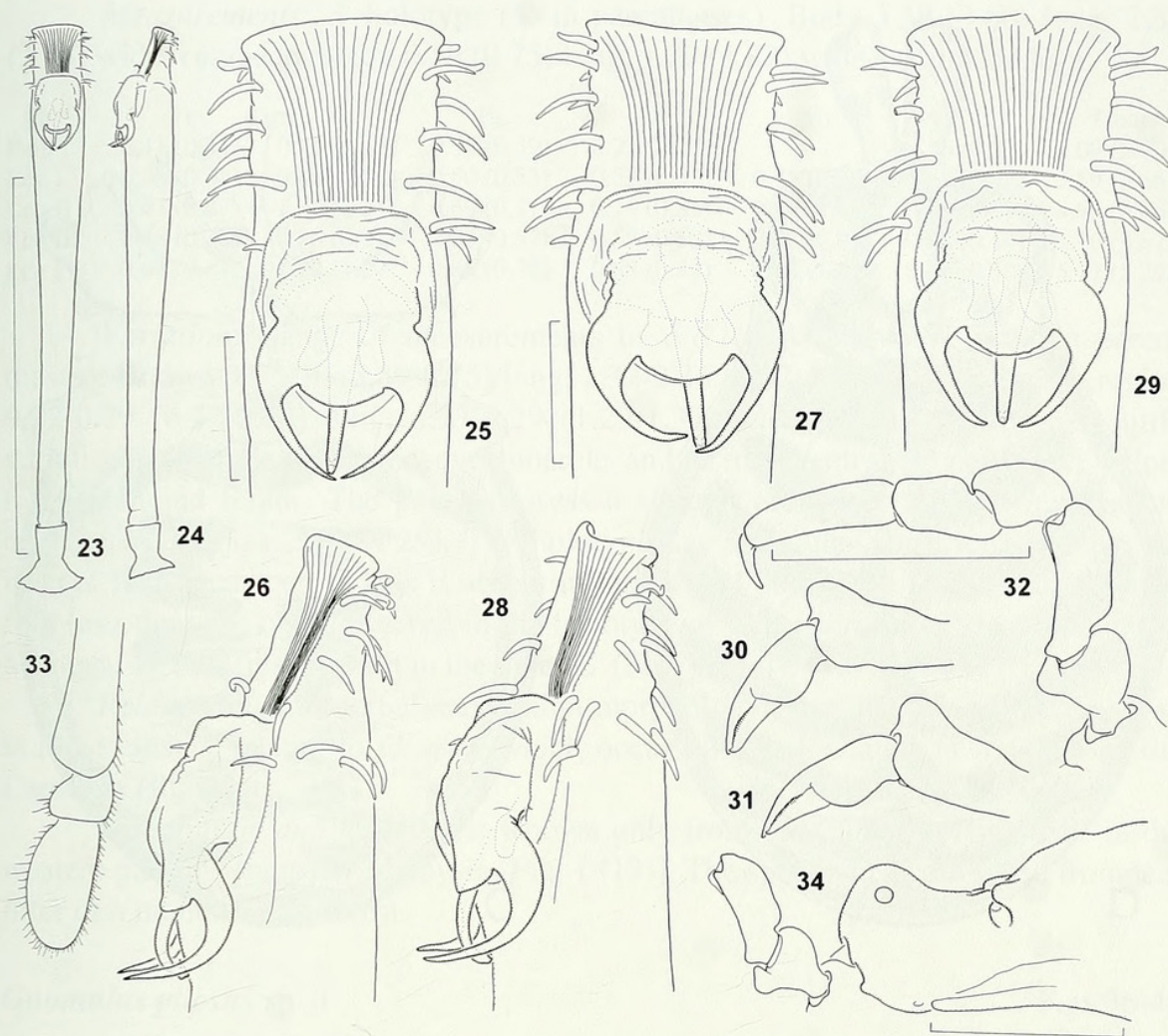
Material: MALAYSIA (peninsula), Pahang, Cameron Highlands, near Tanah Rata: Gunung Jasar, 1550 m, trail 11, ♂ holotype (MHNG), 1 ♂, 1 ♀ paratypes, 3 juv., 24.III.1993; G. Jasar, 1720 m, 1 ♂, 2 ♀ paratypes, 25.III.1993; trails 4 and 13 (E of Tanah Rata), 1500 m, 1 ♂ paratype, 23.III.1993; trail 9 (between Tanah Rata and Robinson Fall), 1400 m, 2 ♀ paratypes, 27.III.1993, all leg. I. Löbl & F. Calame. - Ringlet, 960 m, 1 juv., leg. T. Jaccoud. 1 ♂, 1 ♀ paratypes in MAR, others in MHNG.

Etymology: Latin: *monticola* = mountain dweller; noun (male gender) in apposition.

Diagnosis: Close to *G. asli*, distinguished by: Body larger; colour pattern different; anterior dorsal scutal margin less rounded; teeth of carapace-abdomen bridge longer, more widely separated; glans penis with more rounded median plate; tips of lateral glans sclerites very close to each other.

Description: ♂ (holotype). Coloration: Body light amber, ventral scutum more reddish; characteristic dark pattern on dorsal and ventral scuta. Genital operculum reddish amber with dark central zone (Fig. 35a-c). Leg segments (except tarsi) darkened, with light circular distal band on all tibiae and light median bands on metatarsi III and IV and (less distinct) on all femora. Palps and chelicerae light amber, with a dark reticulation (faint on tarsus and chelicerar hand, respectively).

Carapace with low rounded eye tubercle; no lateral tubercles present. Carapace-abdomen bridge distinctly divided, composed of two widely separated opposing pairs of fairly long conical processes. Dorsal and ventral scutal areas only slightly elevated (Fig. 35a, c). Ventral scutum covered with fine short hairs (much denser than on dorsal scutum). Palpal coxa with distinct ventral process; leg coxa I with low, wide anterolateral one; ventral side of leg coxae II and III with small anteroproximal



FIGS 23-34

Gnomulus monticola sp. n., ♂ holotype (27, 28, 30, 32, 33), ♂ paratypes (23-26, 29), ♀ paratype (31, 34). - Penis, dorsal (23) and lateral view (24); apex of penis, dorsal (25, 27, 29) and lateral view (26, 28). Left chelicera, retrolateral view (30, 31); left palp, retrolateral view (32); distal part of left leg II, retrolateral view (33); anterior body and proximal palp (34). - Scale lines 0.1 mm (25-29), 1.0 mm (others).

processes, coxa II also with small posteroproximal one. Genital operculum slightly wider than long; a small but distinct tubercle on posterior margin of stigmatic pit (Fig. 35b).

Chelicerae (Fig. 30): Hand weak, proximal article with distinct dorsodistal and indistinct dorsomedian boss, no ventral tubercle.

Palps (Fig. 32): Ventral side of femur with small proximal process; trochanter with basally wide, distad-inclined ventral process.

Legs 1324, tarsal formula 2-2-3-3. Distitarsus II about 2 times longer than wide (Fig. 33).

Penis (Figs 23-28; holotype: 27, 28): Truncus fairly slender, continually widening towards apex, with almost straight distal margin. Glans distinctly remote from tip of truncus, with quadrangular membranous socket; short, widely rounded

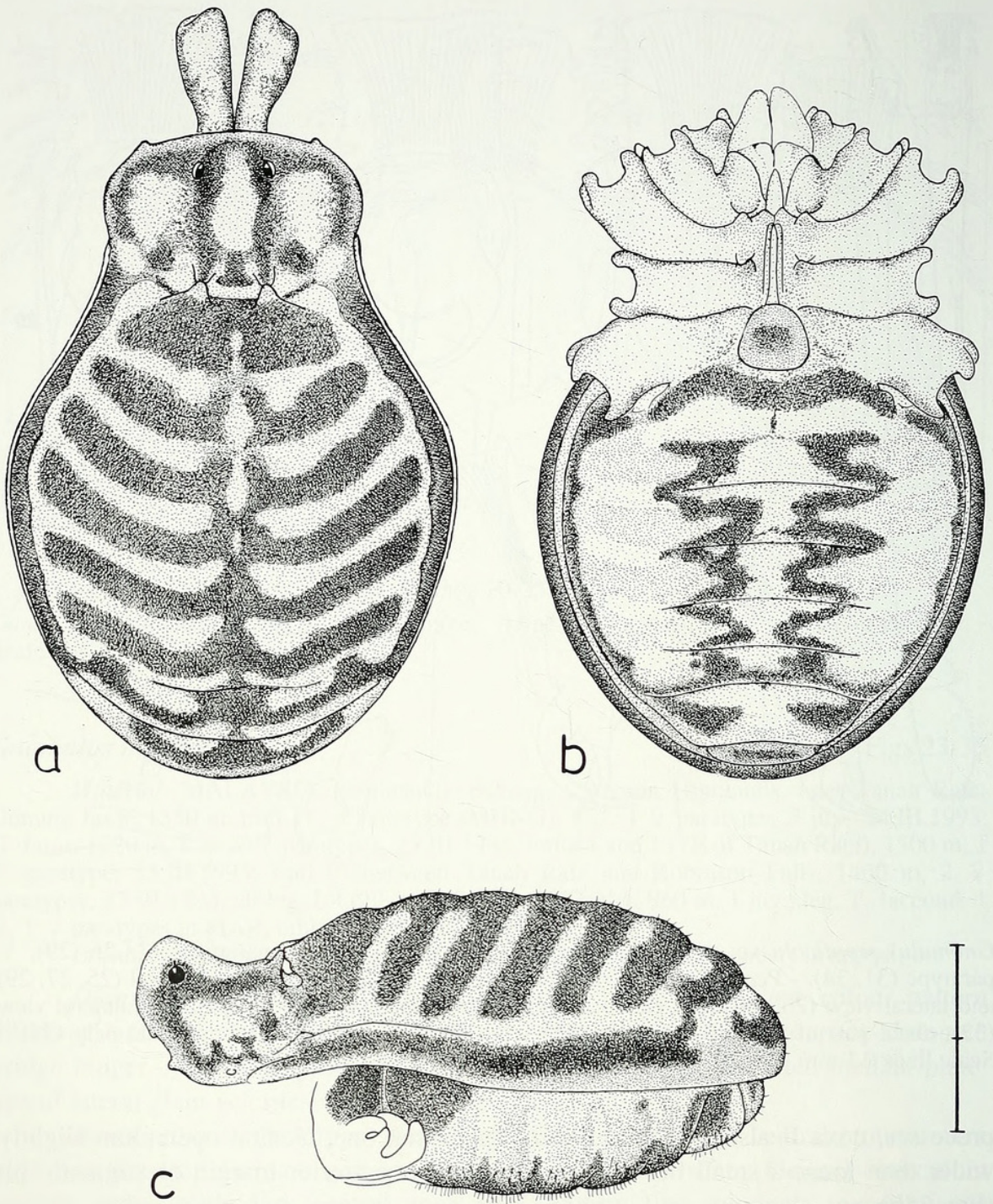


FIG. 35

Gnomulus monticola sp. n., ♂ holotype. - Body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1.0 mm.

median plate covering membranous tubes; lateral sclerites sickle-shaped, bent away from the truncus, their tips almost touching each other; stylus slender, base bulbous, apex with a small pair of subterminal ventral teeth.

♀. As the male, no external sexual dimorphism discernible.

Measurements: ♂ holotype (♀ in parentheses): Body 3.38 (3.60) long, 2.32 (2.54) wide; carapace region 0.79 (0.75) long, 1.29 (1.32) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.41 (0.41)	0.47 (0.47)	0.38 (0.39)	0.27 (0.27)	- -	0.56 (0.56)	2.09 (2.10)
Leg I	0.38 (0.38)	0.86 (0.89)	0.50 (0.53)	0.52 (0.53)	0.75 (0.75)	0.58 (0.58)	3.59 (3.66)
Leg II	0.47 (0.47)	1.16 (1.21)	0.69 (0.71)	0.79 (0.82)	1.16 (1.16)	0.69 (0.69)	4.96 (5.06)
Leg III	0.38 (0.38)	0.86 (0.91)	0.53 (0.57)	0.58 (0.60)	0.97 (0.97)	0.44 (0.44)	3.76 (3.87)
Leg IV	0.44 (0.47)	1.22 (1.27)	0.69 (0.72)	0.88 (0.89)	1.44 (1.44)	0.50 (0.50)	5.17 (5.29)

Variation: Range of measurements in ♂♂ (n=4) and ♀♀ (n=5; in parentheses): Body 3.31-3.38 (3.39-3.75) long, 2.32-2.36 (2.32-2.59) wide, carapace region 0.72-0.79 (0.72-0.79) long, 1.27-1.29 (1.29-1.37) wide. There is only very little variation in the shape of the eye tubercle and of the ventral processes on palpal trochanter and femur. The penes possess a slightly arched or slightly invaginated distal margin (Figs 25, 27, 29). The holotype has a circular constriction above the base of its truncus penis. This is absent in one ♂ and developed into a small circular fold [as otherwise only observed in the lectotype of *G. sumatranus* (Schwendinger & Martens, 1999b: figs 70, 71)] in the other ♂ (Figs 23, 24).

Relationships: External and genital morphology show that *G. monticola* sp. n. is most closely related to *G. asli*, which occurs in the lowlands at the foot of the Cameron Highlands.

Distribution and bionomics: Known only from the Cameron Highlands in the western part of peninsular Malaysia [Fig. 1 (13)]. The specimens were sifted from leaf litter of a montane rain forest.

Gnomulus pilosus sp. n.

Figs 36-45

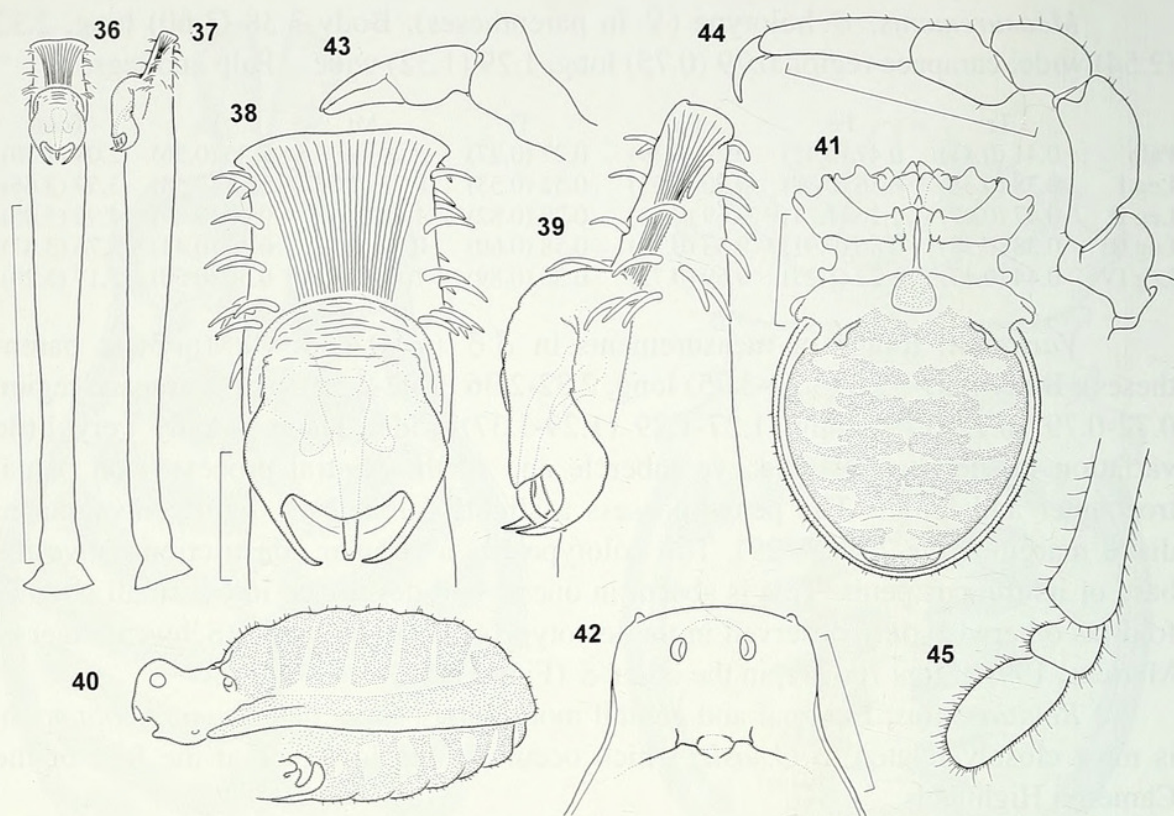
Material: MALAYSIA (peninsula), Pahang, Taman Negara (= National Park), Tembeling Trail, 90-120 m, ♂ holotype, 10./13.III.1993, leg. I. Löbl & F. Calame (MHNG).

Etymology: Latin: *pilosus* = hairy.

Diagnosis: Similar to *G. hirsutus*, distinguished by: Hair cover less dense; colour pattern on ventral scutum different; anterior dorsal scutal margin less rounded; teeth of carapace-abdomen bridge more widely separated; ventral process on palpal femur smaller; glans penis with a shorter, more V-shaped median plate and more strongly converging lateral sclerites with a wider base.

Description: ♂ (holotype). Coloration: Body amber, with dark reticulation in carapax region and with dark pattern on dorsal (shaped as in *G. hirsutus*) and ventral scuta. Genital operculum dark. Palps and chelicerae light amber, with a dark reticulation (except on palpal tarsus). Legs mostly dark brown, with a light circular median band on metatarsi III and IV and (less distinct) on femur IV; tarsi light amber, with distitarsus I dorsally darkened.

Carapace with rounded eye tubercle, no lateral tubercles. Left and right processes of carapace-abdomen bridge distinctly separated from each other (Fig. 42). Dorsal and ventral scutal areas moderately elevated (Fig. 40). Palpal coxa with distinct ventral process; leg coxa I with widely triangular anterolateral process; ventral side of leg coxae II and III with conical anteroproximal processes, the latter



FIGS 36-45

Gnomulus pilosus sp. n., ♂ holotype. - Penis, dorsal (36) and lateral view (37); apex of penis, dorsal (38) and lateral view (39). Body, lateral (40) and ventral view (41); anterior body, dorsal view (42); left chelicera, retrolateral view (43); left palp, retrolateral view (44); distal part of left leg II, retrolateral view (45). - Scale lines 0.1 mm (38, 39), 1.0 mm (others).

overlapped by rounded posteroproximal process on coxa II. Genital operculum slightly wider than long; a distinct tubercle present on posterior margin of stigmatic pit (Fig. 41). Whole body, except for carapace region, covered by fine hairs (Fig. 40).

Chelicerae (Fig. 43): Hand weak, proximal article with distinct dorsodistal and indistinct dorsomedian boss and with indistinct retroventral tubercle.

Palps (Fig. 44): Ventral side of femur with small rounded proximal process; trochanter with distad-inclined ventral process.

Legs 1324, tarsal formula 2-2-3-3. Distitarsus II 2.1 times longer than wide (Fig. 45).

Penis (Figs 36-39): Truncus continually widening towards apex, with widely arched, indistinctly invaginated distal margin. Glans quite remote from tip of truncus, with rounded membraneous socket and short, widely V-shaped median plate covering membraneous tubes; lateral sclerites sickle-shaped, their bases wide (as seen in lateral view; Fig. 39), distal parts bent away from the truncus and towards each other; stylus slender, base bulbous, apex with a small pair of subterminal ventral teeth.

♀. Unknown.

Measurements: ♂: Body 3.45 long, 2.32 wide; carapace region 0.74 long, 1.28 wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.38	0.50	0.39	0.27	-	0.57	2.11
Leg I	0.38	0.98	0.55	0.57	0.82	0.66	3.96
Leg II	0.49	1.32	0.71	0.88	1.34	0.71	5.45
Leg III	0.39	0.98	0.58	0.61	1.07	0.46	4.09
Leg IV	0.49	1.39	0.77	0.96	1.61	0.53	5.75

Relationships: Externally the new species is very similar to *G. hirsutus* (especially in hair cover and dorsal colour pattern), but penis morphology indicates a closer relationship with *G. monticola* sp. n.

Distribution and bionomics: Known only from the type locality in the southern part of Taman Negara, in the centre of peninsular Malaysia [Fig. 1 (14)]. The type specimen was sifted from leaf litter of a lowland rain forest.

THE *ROSTRATOIDEUS*-GROUP (new)

Diagnosis: Medium-sized (about 5.5 mm) species with strongly forward-inclined, beak-like eye tubercle and distinct carapace-abdomen bridge; ventral process on palpal trochanter distad-directed; dark margin around dorsal scutum unbroken; posterior margin of stigmatic pit without tubercle; stylus penis with invaginated base and without subterminal ventral teeth.

Species account and distribution: This species group is represented only by *G. rostratoideus* sp. n. from the southern end of the Malay Peninsula.

Gnomulus rostratoideus sp. n.

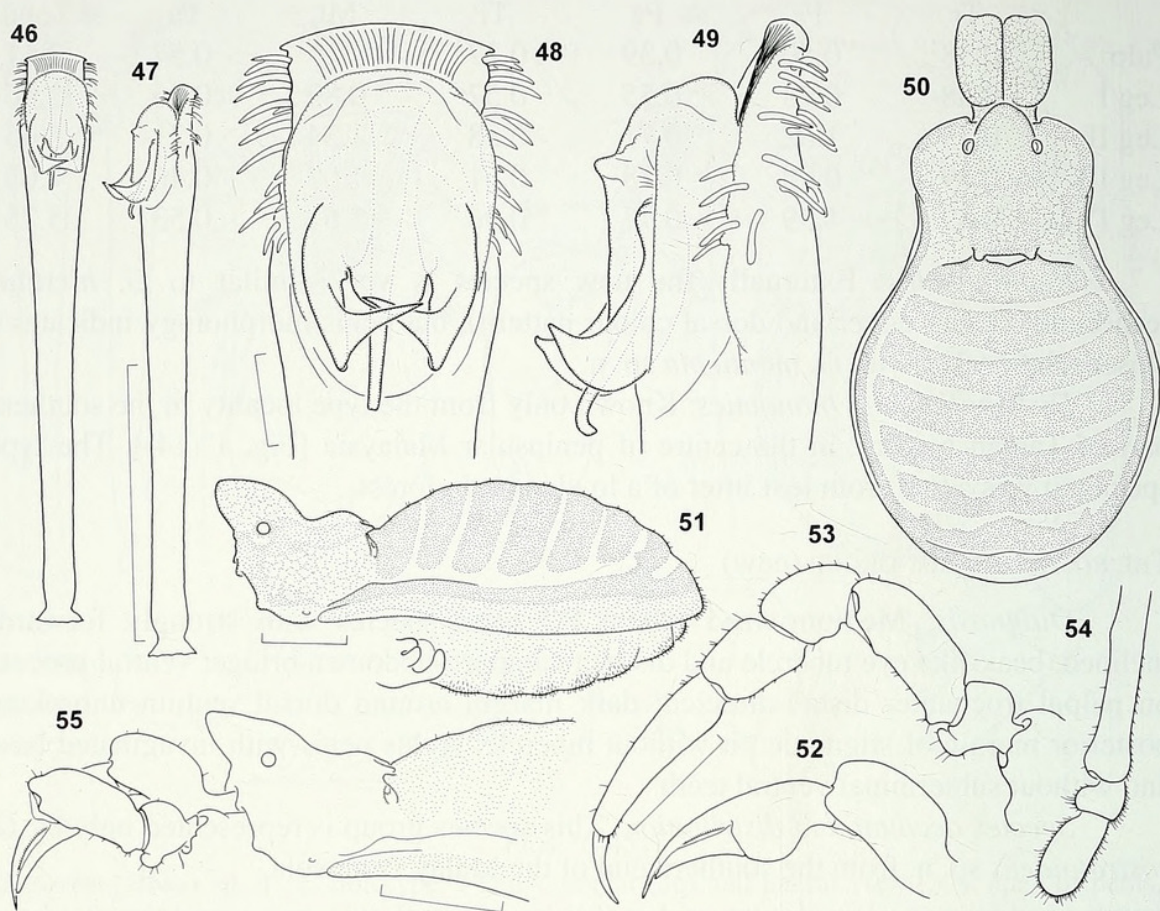
Figs 46-55

Material: MALAYSIA (peninsula), Kota Tinggi Waterfalls, 170 m, at the foot of Gunung Muntahak, ca. 15 km NW of Kota Tinggi, Johor, ♂ holotype, 5.II.2000, leg. P. J. Schwendinger. - SINGAPORE, Bukit Timah Nature Reserve, 1 ♀ (not a type), 4.VII.1969, leg. D. H. Murphy; same locality, Jungle Fall Valley, 100 m, 1 ♀ (not a type), 9.VI.2001, leg. P. Schwendinger. All specimens in MHNG.

Etymology: The latinized Greek suffix *-oideus* refers to similarities with *G. rostratus* Thorell.

Diagnosis: Externally similar to *G. rostratus* Thorell, distinguished by a narrower eye tubercle (in dorsal view), by a more arched dorsal and ventral scutum and by an unbroken dark margin around the dorsal scutum. Penis very different in shape: Truncus more slender, distal margin widely rounded; glans with convex pincer-like lateral sclerites ending in undivided apices, with a rounded median plate covering short membraneous tubes, and with a thin, tubular stylus without subterminal ventral teeth.

Description: ♂ (holotype). Coloration: Body amber, with dark brown reticulation on carapace, chelicerae, pedipalps and ventral side of prosoma. Abdominal part of dorsal scutum framed by an unbroken dark margin; dark transversal bands on scutal elevations, medially interconnected in areas III-V (Figs 50, 51). Legs mostly dark brown; tarsi light brown, with reddish grey on proximal part of dorsal distitarsi I and II. Ventral scutal areas with faint dark transversal bands; genital operculum dark reddish brown.



FIGS 46-55

Gnomulus rostratoideus sp. n., ♂ holotype (46-54), ♀ (55). - Penis, dorsal (46) and lateral view (47); apex of penis, dorsal (48) and lateral view (49). Body, dorsal (50) and lateral view (51); left chelicera, retrolateral view (52); left palp, retrolateral view (53); distal part of left leg II, retrolateral view (54). Anterior body, chelicera and proximal palp, lateral view (55). - Scale lines 0.1 mm (48, 49), 1.0 mm (others).

Carapace with large pointed, anteriad-inclined eye tubercle and with a rounded hump behind it; no lateral tubercles present; carapace-abdomen bridge composed of two opposing pairs of widely separated teeth (Figs 50, 51). Abdominal part of dorsal scutum moderately arched; ventral and dorsal scutal areas only slightly elevated, the ventral ones bearing "encrusted" hairs (Fig. 51). Palpal coxa with large ventral process; ventral side of leg coxa I with distinct anterolateral process; ventral side of leg coxa II with pronounced anteroproximal and posteroproximal processes, coxa III with distinct anteroproximal one. Genital operculum as long as wide, anteriorly rounded; posterior margin of stigmatic pit without tubercle but with distinct ledge.

Chelicerae (Fig. 52) weak; proximal article with dorsodistal to dorsomedian boss (distally low) and without ventral tubercle. Cheliceral fingers very long and slender.

Palps (Fig. 53): Ventral side of femur with small proximal process and bulging distal margin; trochanter with distad-directed ventral process.

Legs 1324, tarsal formula 2-2-3-3. Distitarsus of leg II 2.2 times longer than wide (Fig. 54).

Penis (Figs 46-49): Truncus penis fairly slender, continually widening from base to the height of glans, narrower between middle of glans and widely rounded distal margin. Glans penis with large membraneous socket, about as wide as truncus at that point; lateral sclerites convex, sickle-shaped, with acutely pointed tips crossing each other; membraneous tubes short, completely covered by a rounded, U-shaped median plate; stylus long and slender, its base slightly invaginated, its apex without subterminal ventral teeth.

♀ (Identification uncertain). As the male, but eye tubercle less elevated and more pointed in dorsal view, region behind eye tubercle less elevated, abdominal part of dorsal scutum less arched, ventral process on palpal trochanter shorter, more knob-shaped (Fig. 55).

Measurements: ♂ holotype (♀ in parentheses): Body 5.48 (5.43) long, 3.48 (3.33) wide; carapace region 1.70 (1.50) long, 2.06 (1.90) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.63 (0.51)	1.15 (0.91)	0.79 (0.65)	0.61 (0.53)	- -	1.47 (1.31)	4.65 (3.91)
Leg I	0.63 (0.53)	1.74 (1.43)	0.83 (0.75)	1.03 (0.87)	1.50 (1.27)	0.83 (0.69)	6.56 (5.54)
Leg II	0.75 (0.71)	2.30 (1.96)	1.19 (1.17)	1.66 (1.39)	2.30 (1.90)	1.03 (0.87)	9.23 (8.00)
Leg III	0.55 (0.55)	1.72 (1.39)	0.91 (0.75)	1.07 (0.87)	1.72 (1.50)	0.61 (0.55)	6.58 (5.61)
Leg IV	0.77 (0.67)	2.38 (1.98)	1.21 (1.07)	1.62 (1.39)	2.65 (2.28)	0.75 (0.63)	9.38 (8.02)

Variation: The second ♀ measures: Body length 5.26, width 3.22, carapace length 1.49, width 1.78. Both ♀ from Singapore are smaller than the ♂ from Malaysia and differ in some details of external morphology. These specimens may therefore not be conspecific, but the common presence of an unbroken dark dorsal scutal margin, a fairly distinct hair cover and geographical proximity clearly show that they are more closely related with each other than with any of the species of the *rostratus*-group. Until this uncertainty is solved by the discovery of a ♂ from Singapore, we tentatively place the ♀♀ examined in *G. rostratoideus* sp. n., but we do not designate them as paratypes.

Relationships: *Gnomulus rostratoideus* sp. n. appears to be the sister taxon of the *rostratus*-group. Congruence in penis morphology with the species of the *good-nighti*-group is considered to be due to convergence (see discussion).

Distribution and bionomics: Known from rainforests in the south of peninsular Malaysia [Fig. 1 (15)] and on nearby Singapore Island [Fig. 1 (16)].

THE *SUMATRANUS*-GROUP (see Schwendinger & Martens, 1999b: 957)

Diagnosis: The new species possesses a distinctly elevated eye tubercle and posteroproximal processes on coxae II, but no transversal keels on its dorsal scutum. Therefore the diagnosis of this group has to be modified. The *sumatranus*-group is essentially characterized by: Body large (6.8-9.0 mm); chelicerae robust (at least in the ♂), with a distad-inclined proventral tooth (pointed process) on proximal article; a subdistal process present on ventral side of palpal femur (indistinct in some females); proximal process on ventral side of palpal femur slightly to distinctly distad-directed; distodorsal tubercle present on palpal trochanter; posterior margin of stigmatic pit with tubercle; lateral sclerites on glans penis cylindrical, acutely pointed, only slightly bent; stylus penis with ventral pair of subterminal teeth and bulbous base.

Species account and distribution: This group comprises two species from Sumatra, i.e. *G. sumatranus* Thorell and *G. tuberculatus* sp. n.

***Gnomulus tuberculatus* sp. n.**

Figs 56-73

Material: INDONESIA, Sumatra, Aceh Province, Gunung Leuser National Park, Ketambe Research Station, 300-500 m, ♂ holotype (MHNG), 1 ♂, 3 ♀ paratypes, 3 juv., 23.-30.XI.1989, leg. I. Löbl, D. Agosti & D. Burckhardt (1 ♀ paratype in MAR, others in MHNG).

Etymology: Latin: *tuberculatus* = tuberculate. The specific epithet refers to the presence of two tubercles on the dorsal side of leg coxa IV and of one tubercle on the anterolateral side of trochanter III.

Diagnosis: Close to *G. sumatranus*, distinguished by: Body smaller; carapace shorter in the ♂, with a distinct eye tubercle in both sexes; ventral side of leg coxa II with an anteroproximal process, process on coxa III larger; trochanter III with a small prolateral tubercle; proximal process on ventral side of palpal femur smaller, not distad-inclined, subdistal process indistinct; distitarsus II shorter; penis without circular fold around subbasal truncus; distal margin of truncus less arched; two setae present on each side of glans penis; tips of lateral sclerites slightly inclined towards each other.

Description: ♂ (holotype). Coloration: Body amber, with dark reticulation on carapace, chelicerae and pedipalps; dorsal scutal elevations dark brown, separated by a light median, longitudinal, partly broken stripe in areas I-IV and by pairs of light transversal stripes ending in light paramedian patches (Fig. 73a, c). Legs dark brown; tarsi I, II cream (slightly darkened on dorsal side of distitarsus I), tarsi III, IV light brown.

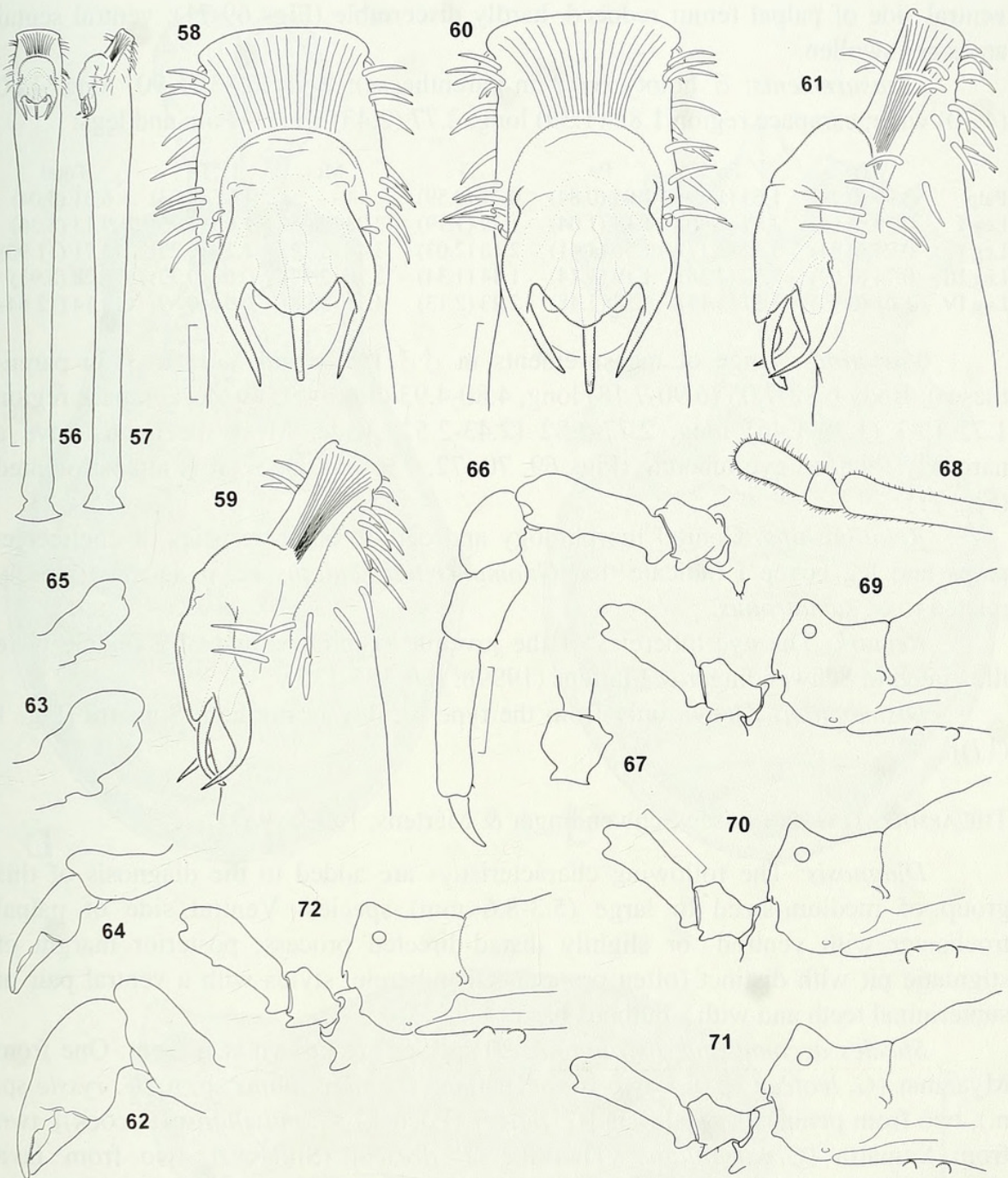
Carapace with conical, distally rounded eye tubercle and an indistinct pair of lateral tubercles below wide undivided carapace-abdomen bridge. Dorsal scutal areas only slightly elevated; ventral scutal areas distinctly swollen, without hairs (Figs 73a, c). Palpal coxa with distinct ventral process; leg coxa I with long, outwards-inclined anterolateral one; ventral leg coxae II and III with distinct anteroproximal processes, coxa II additionally with low posteroproximal one (Fig. 73b); dorsal side of leg coxa IV with two knob-shaped tubercles (Figs 69-72, 73c). Genital operculum about as long as wide; rounded tubercle on posterior margin of stigmatic pit (Fig. 73b).

Chelicerae (Figs 62, 63): Hand strong, cutting edges of fingers each with a strong subbasal tooth; proximal article with forward-inclined dorsodistal to dorso-median boss and with two distad-inclined proventral teeth (the subbasal one smaller than the subterminal one; Fig. 63).

Palps (Fig. 66): Ventral side of femur with indistinct subdistal and distinct proximal process; trochanter with low dorsal tubercle and with small, slightly distad-inclined ventral process.

Legs 1324, tarsal formula 2-2-3-3. Trochanter of leg III with prolateral tubercle (Fig. 67); distitarsus II about 2.2 times longer than wide (Fig. 68).

Penis (Figs 56-61; holotype: 60, 61): Truncus fairly slender, with very widely arched distal margin; membranous socket of glans penis laterally bordered by two pairs of setae. Glans with subtriangular median plate partly covering membranous tubes; distal portion of lateral sclerites cylindrical, acutely pointed, not sigmoid and only moderately bent away from the truncus, tips slightly inclined towards each other; stylus slender, base bulbous, apex with a small pair of subterminal ventral teeth.



FIGS 56-72

Gnomulus tuberculatus sp. n., ♂ holotype (60, 61, 62, 63, 66-68), ♂ paratype (56-59, 72), ♀ paratypes (64, 65, 69-71). - Penis, dorsal (56) and lateral view (57); apex of penis, dorsal (58, 60) and lateral view (59, 61). Left chelicera, retrolateral view (62, 64); proximal article of left chelicera, prolateral view (63, 65); left palp, retrolateral view (66); trochanter of left leg III, dorsal view (67); distal part of left leg II, retrolateral view (68); anterior body and proximal palp, lateral view (69-72). - Scale lines 0.1 mm (58-61), 1.0 mm (others).

♀. As the male but coloration generally more reddish; carapace region slightly smaller; chelicerae weaker, subbasal tooth on cutting edge of both cheliceral fingers indistinct, no dorsomedian boss on proximal article (Figs 64, 65); subdistal process on

ventral side of palpal femur reduced, hardly discernible (Figs 69-71); ventral scutal areas not swollen.

Measurements: ♂ holotype (♀ in parentheses): Body 6.83 (6.90) long, 4.80 (4.70) wide; carapace region 1.83 (1.39) long, 2.77 (2.43) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.99 (0.79)	1.63 (1.29)	1.04 (0.84)	0.77 (0.59)	--	1.88 (1.53)	6.31 (5.04)
Leg I	0.79 (0.69)	2.57 (2.40)	1.14 (1.04)	1.29 (1.19)	2.28 (2.05)	1.06 (0.99)	9.13 (8.36)
Leg II	0.94 (0.84)	3.32 (3.17)	1.56 (1.41)	2.18 (2.03)	3.42 (3.22)	1.29 (1.29)	12.71 (11.96)
Leg III	0.74 (0.69)	2.52 (2.38)	1.19 (1.14)	1.44 (1.34)	2.70 (2.57)	0.69 (0.79)	9.28 (8.91)
Leg IV	1.01 (0.99)	3.27 (3.17)	1.58 (1.48)	2.23 (2.13)	4.11 (3.98)	0.94 (0.89)	13.14 (12.64)

Variation: Range of measurements in ♂♂ (n=2) and ♀♀ (n=3; in parentheses): Body 6.83-7.05 (6.90-7.18) long, 4.80-4.93 (4.60-4.95) wide, carapace region 1.73-1.83 (1.39-1.46) long, 2.77-2.82 (2.43-2.52) wide. Most specimens have a narrowly rounded eye tubercle (Figs 69, 70, 72, 73c), in one ♀ it is almost pointed (Fig. 71).

Relationships: Genital morphology and certain characteristics of chelicerae, palps and leg coxae I indicate that *Gnomulus tuberculatus* sp. n. is most closely related to *G. sumatranus*.

Remark: The eye tubercles of the juvenile specimens and of a female were illustrated in Schwendinger & Martens (1999b: figs 135-137).

Distribution: Known only from the type locality in northern Sumatra [Fig. 1 (17)].

THE ARMILLATUS-GROUP (see Schwendinger & Martens, 1999b: 958)

Diagnosis: The following characteristics are added to the diagnosis of this group of medium-sized to large (5.3-8.6 mm) species: Ventral side of palpal trochanter with ventrad- or slightly distad-directed process; posterior margin of stigmatic pit with distinct (often pronounced) tubercle; stylus with a ventral pair of subterminal teeth and with a bulbous base.

Species account and distribution: 20 species are known at present: One from Myanmar (*G. leofeae* sp. n.), two from Thailand (*G. marginatus* sp. n., *G. ryssie* sp. n.), two from peninsular Malaysia [*G. piliger* (Pocock), *G. pulvillatus* (Pocock)], two from Sumatra [*G. armillatus* (Thorell), *G. drescoi* (Šilhavý)], two from Java [*G. javanicus* sp. n., *G. thorelli* (Sørensen) (male unknown, uncertain assignment)] and 10 from Borneo [*G. annulipes* (Pocock), *G. baharu* Schwendinger, *G. carinatus* sp. n., *G. conigerus* (Schwendinger), *G. exsudans* sp. n., *G. hutan* sp. n., *G. laevis* (Roewer), *G. lomani* sp. n., *G. obscurus* sp. n., *G. sundaicus* (Schwendinger)] and one from Palawan, the Philippines [*G. palawanensis* (Suzuki), male unknown, uncertain assignment].

Gnomulus marginatus sp. n.

Figs 74-91

Material: THAILAND, Chanthaburi Province and District, Nam Tok Phliu - Khao Sabap National Park, near Phliu Waterfall, 50 m, ♂ holotype, 2 ♂, 1 ♀ paratypes, 12.XI.1998. - Trat Province, Laem Ngop District, Ko Chang (= Elephant Island) National Park, forest above White Sand Beach, 20-50 m, 3 ♂ paratypes, 6.-8.IX.1993, 1 juv., 24.VIII.1992 (all specimens

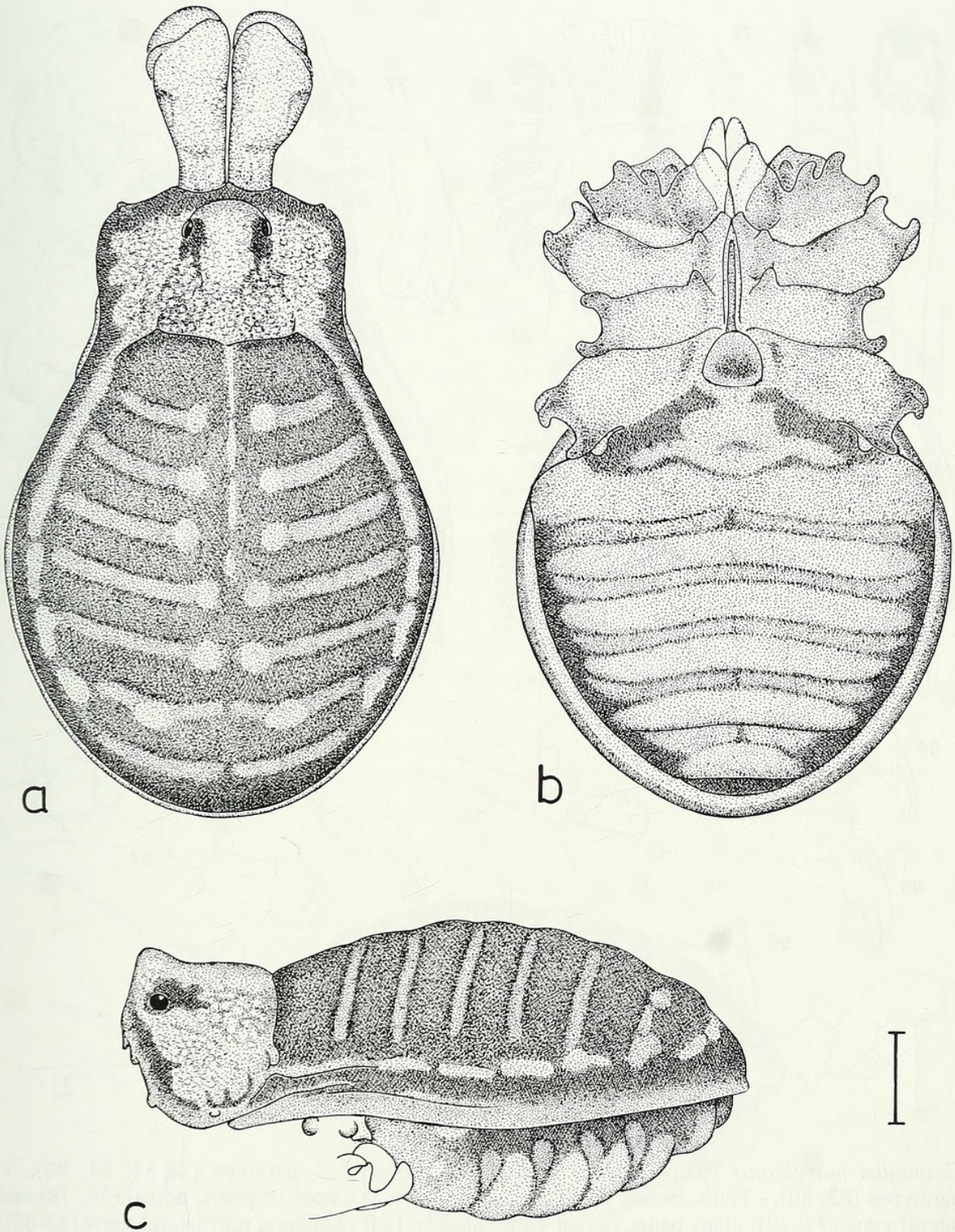
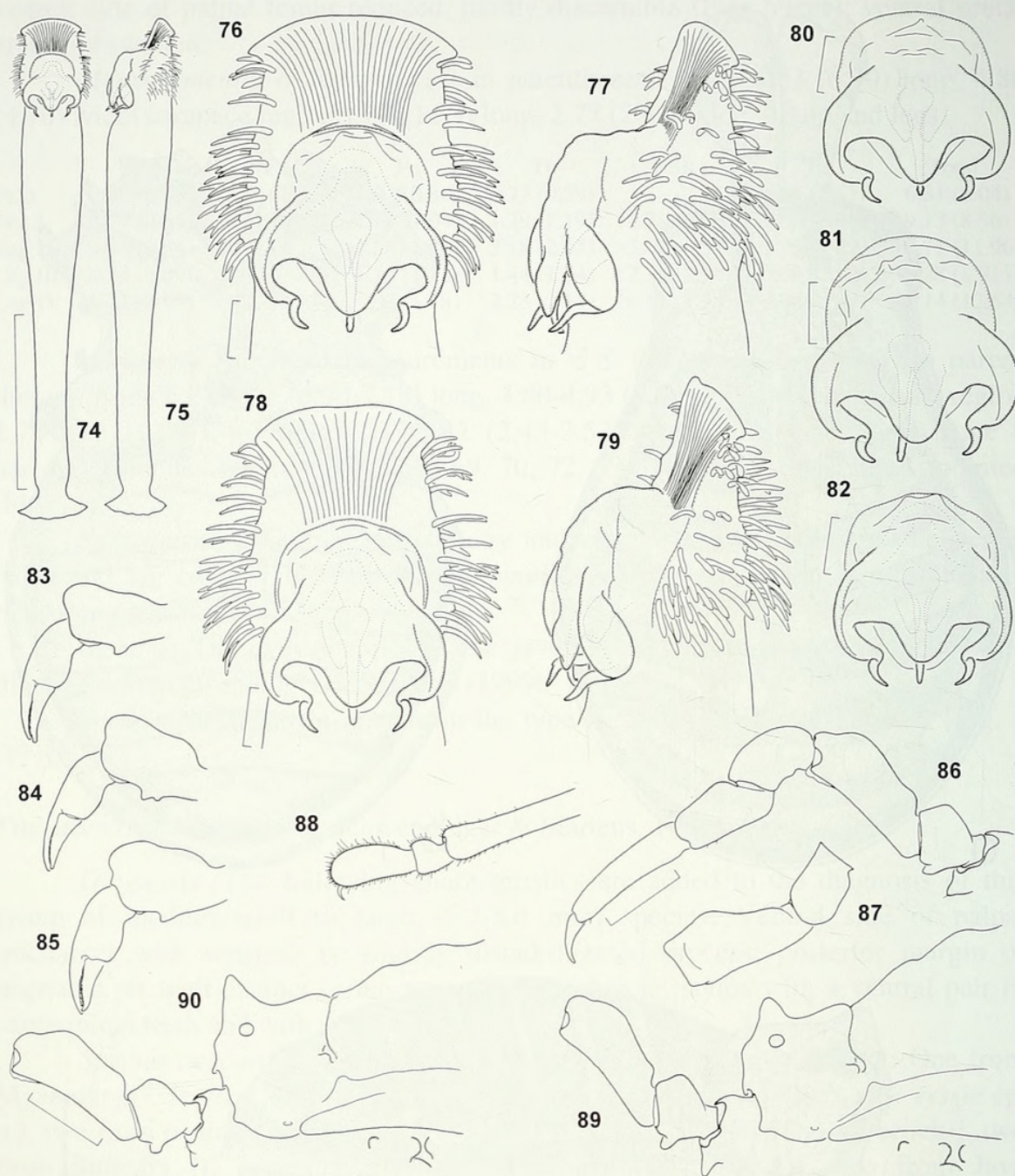


FIG. 73

Gnomulus tuberculatus sp. n., ♂ holotype. - Body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1.0 mm.

leg. P.J. Schwendinger); same island, west side, 12°03'N, 102°18'E, 50-200 m, 1 ♂ paratype, 3.-23.XII.1999 (leg. A. Schulz). 1 ♂ paratype in MAR, others in MHNG.

Etymology: Latin: *marginatus* (adjective of *margo*) = framed. The specific epithet refers to the conspicuous dark marginal and light submarginal band around the abdominal part of the dorsal scutum.



FIGS 74-90

Gnomulus marginatus sp. n., ♂ holotype (74-77, 85-88), ♂ paratype (78-82, 84, 90), ♀ paratypes (83, 89). - Penis, dorsal (74) and lateral view (75); apex of penis, dorsal (76, 78) and lateral view (77, 79); glans penis, dorsal view (80-82). Left chelicera, retrolateral view (83-85); left palp, retrolateral view (86); trochanter and femur of left palp, dorsal view (87); distal part of left leg II, retrolateral view (88); anterior body and proximal palp, lateral view (89, 90). - Scale lines 0.1 mm (76-82), 1.0 mm (others).

Diagnosis: Similar to *G. armillatus*, distinguished by: Light submarginal band on abdominal part of dorsal scutum; retroventral tooth on proximal cheliceral article more distinct and pointed; ventral processes on palpal femur and trochanter smaller; two tubercles on dorsal side of leg coxa IV and one on lateral side of abdominal

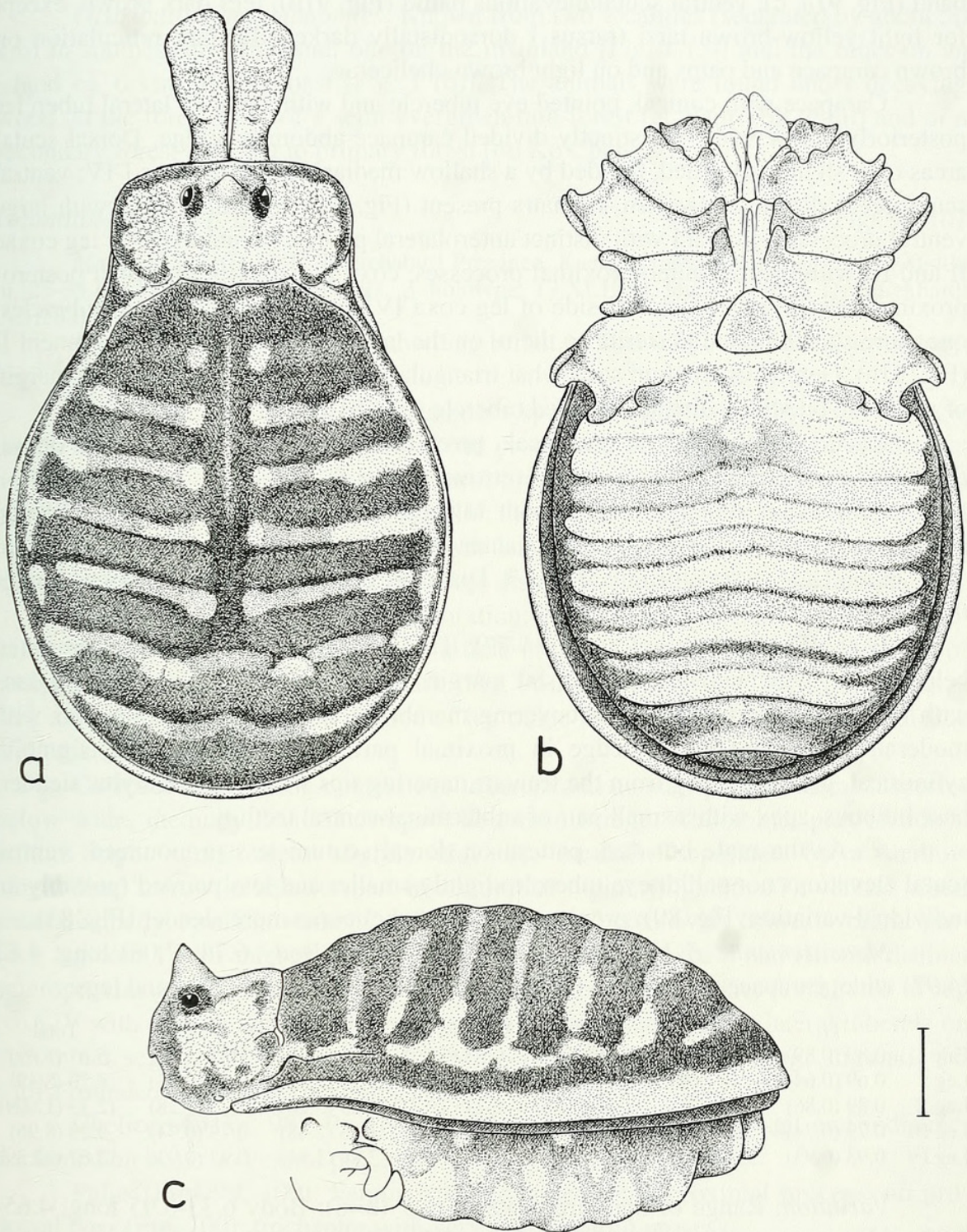


FIG. 91

Gnomulus marginatus sp. n., ♂ holotype. - Body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1.0 mm.

segment II; penis more stout, glans wider, its lateral sclerites more convex and basally more elevated, its median plate longer, tongue-shaped.

Description: ♂ (holotype). Coloration: Body brown, dorsal scutum with dark brown pattern and clearly outlined red-brown margin below light brown submarginal

band (Fig. 91a, c); ventral scutal elevations pallid (Fig. 91b); legs dark brown, except for light yellow-brown tarsi (tarsus I dorsodistally darkened); dark reticulation on brown carapace and palps and on light brown chelicerae.

Carapace with conical, pointed eye tubercle and with a pair of lateral tubercles posteriorly below wide, indistinctly divided carapace-abdomen bridge. Dorsal scutal areas only slightly elevated, divided by a shallow median furrow in areas I-IV; ventral scutal areas distinctly swollen, no hairs present (Fig. 91a, c). Palpal coxa with large ventral process; leg coxa I with distinct anterolateral process; ventral side of leg coxae II and III with distinct anteroproximal processes, coxa II also with indistinct postero-proximal one (Fig. 91b); dorsal side of leg coxa IV with two knob-shaped tubercles; one more such tubercle posterior to them, on the lateral side of abdominal segment II (Fig. 91c). Genital operculum somewhat triangular, wider than long; posterior margin of stigmatic pit with a distinct rounded tubercle (Fig. 91b).

Chelicerae (Fig. 85): Hand weak, proximal article fairly strong, with dorso-distal to dorsomedian boss and distinct retroventral tooth.

Palps (Figs 86, 87): Femur with low prodorsal median boss (Fig. 87) and indistinct ventroproximal process; trochanter with low ventral process.

Legs 1324, tarsal formula 2-2-3-3. Distitarsus of leg II about 2.3 times longer than wide (Fig. 88).

Penis (Figs 74-82; holotype: 74-77): Truncus fairly stout, slightly constricted below glans, with widely arched distal margin and plenty of subapical setae. Glans with tongue-shaped median plate covering membranous tubes; lateral sclerites with moderately elevated dorsal ledge in proximal part, distal part slender, sigmoid, cylindrical, pointing away from the truncus, tapering tips widely apart; stylus slender, base bulbous, apex with a small pair of subterminal ventral teeth.

♀. As the male but dark pattern on dorsal scutum less pronounced, ventral scutal elevations not pallid; eye tubercle slightly smaller and less pointed (possibly an individual variation; Fig. 89); proximal article of chelicerae more slender (Fig. 83).

Measurements: ♂ holotype (♀ in parentheses): Body 6.74 (7.08) long, 4.82 (4.97) wide; carapace region 1.48 (1.38) long, 2.61 (2.58) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.89 (0.89)	1.48 (1.40)	1.08 (1.08)	0.81 (0.79)	- -	1.55 (1.53)	5.81 (5.69)
Leg I	0.69 (0.64)	2.46 (2.41)	1.16 (1.11)	1.25 (1.28)	2.16 (2.12)	0.98 (0.93)	8.70 (8.49)
Leg II	0.89 (0.86)	3.17 (3.15)	1.48 (1.48)	2.21 (2.12)	3.25 (3.20)	1.33 (1.28)	12.33 (12.09)
Leg III	0.79 (0.74)	2.51 (2.41)	1.21 (1.21)	1.43 (1.38)	2.56 (2.48)	0.79 (0.74)	9.29 (8.96)
Leg IV	0.93 (0.93)	3.20 (3.15)	1.53 (1.48)	2.19 (2.09)	3.89 (3.81)	0.93 (0.93)	12.67 (12.39)

Variation: Range of measurements in ♂♂ (n=6): Body 6.33-6.95 long, 4.65-4.82 wide, carapace region 1.45-1.56 long, 2.54-2.61 wide. One ♂ paratype with a bifid ventral tooth on proximal cheliceral article (Fig. 84) and with a truncate ventral process on palpal trochanter (Fig. 90).

Relationships: *Gnomulus marginatus* sp. n. clearly belongs to the *armillatus*-group; it appears most closely related to *G. piliger*, *G. pulvillatus* from the Malayan Peninsula and to *G. armillatus* from Sumatra. Striking similarities in external and penis morphology are also evident between *G. marginatus* sp. n. and *G. annulipes* from Sarawak. These are regarded as convergences.

Distribution and bionomics: Known from two localities (separated by about 50 km) in southeastern Thailand, one on the mainland [Fig. 1 (5)] and the other on an island ca. 6 km off the coast [Fig. 1 (6)]. The animals were found under decaying wood on the forest floor of a semi-evergreen rain forest (at Nam Tok Phliu) and of a secondary forest adjacent to primary forest (on Ko Chang).

Gnomulus ryssie sp. n.

Figs 92-101

Material: THAILAND, Phetchaburi Province, Kaeng Krachan National Park, 300-400 m, 25-30 km W of park headquarters, ♂ holotype, 17.XI.1985, leg. I. Löbl & D. Burckhardt (MHNG).

Etymology: Ryssie is a forest-dwelling hermit in Thai (originally Hindu) mythology. Noun in apposition.

Diagnosis: Closest to *G. marginatus* sp. n., distinguished by: Eye tubercle larger; abdominal region higher; no ventral process on proximal article of chelicerae; no prodorsal boss on palpal femur; ventral process on palpal trochanter smaller; no posterior tubercle on dorsal side of coxa IV; lateral tubercles on abdominal segment II indistinct; penis more slender, with fewer subapical setae; glans with longer, subtriangular median plate; lateral sclerites less distinctly elevated above median plate.

Description: ♂ (holotype). Coloration: Body light amber, with dark reticulation in carapace region, on proximal article of chelicerae and on femur to tarsus of pedipalps; dorsal scutal elevations dark (Fig. 96), ventral ones pallid; legs and palps dark amber, all tarsi and distal portion of leg tibiae III and IV light brown; dorsal side of distitarsus I darkened.

Carapace with strong conical eye tubercle and a small pair of lateral tubercles below wide, medially divided carapace-abdomen bridge. Abdominal part of dorsal scutum high; scutal areas slightly elevated, medially separated by a shallow longitudinal furrow in anterior part of abdominal region (Figs 96, 97); ventral scutal areas distinctly swollen, without pubescence. Palpal coxa with conical ventral process; leg coxa I with anterolateral one; ventral side of leg coxae II and III with distinct anteroproximal processes, coxa II with small posteroproximal one; dorsal side of leg coxa IV with distinct anterior tubercle, posterior one absent; pair of lateral tubercle on abdominal segment II indistinct. Genital operculum wider than long; stigmatic pit with a rounded tubercle on posterior margin.

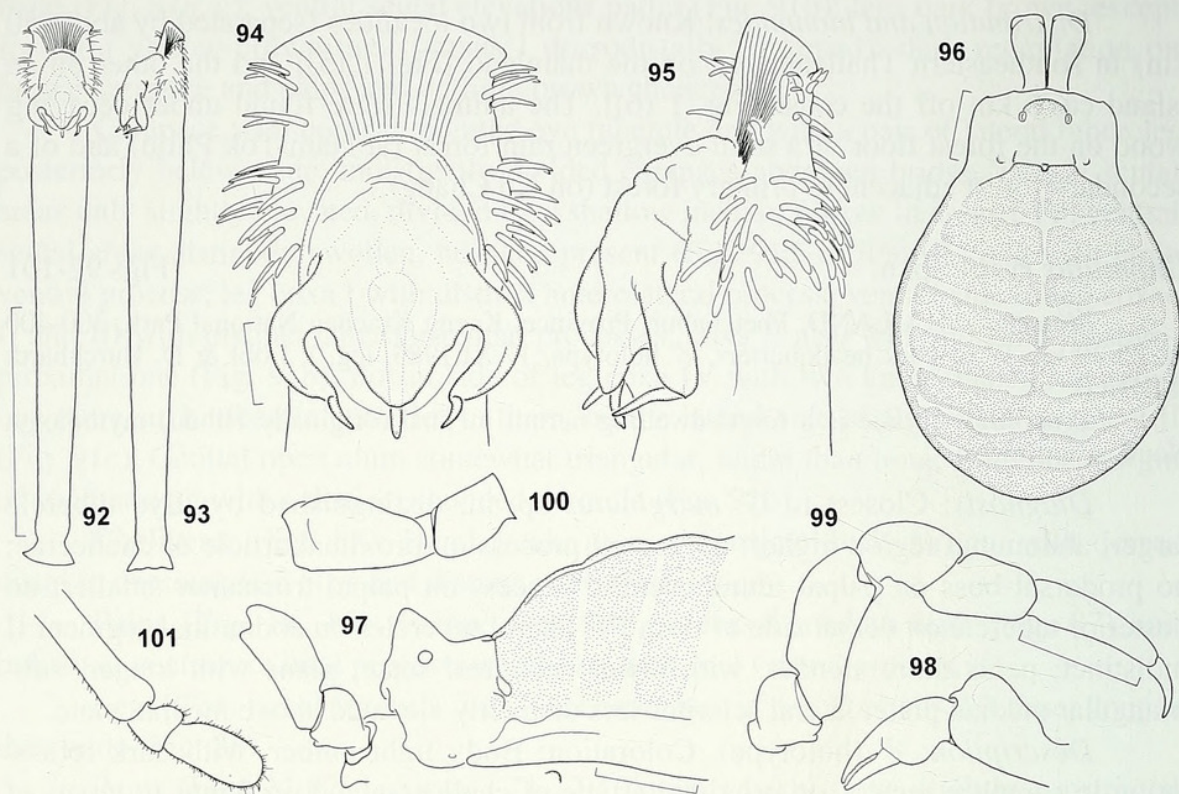
Chelicerae (Fig. 98): Proximal article with distinct dorsodistal and indistinct dorsomedian boss; no ventral process.

Palps (Figs 99, 100): Femur with indistinct ventroproximal process, no prodorsal boss (Fig. 100); trochanter with very small ventral process.

Legs 1324, tarsal formula 2-2-3-3. Distitarsus II about 2.2 times longer than wide (Fig. 101).

Penis (Figs 92-95): Truncus slightly constricted below glans, with widely arched distal margin; glans with large subtriangular median plate covering membranous tubes; lateral sclerites convex, with slightly elevated ledge in proximal part; distal part slender, sigmoid, tapering, pointing away from the truncus, tips widely apart; stylus slender, base bulbous, apex with a small pair of subterminal ventral teeth.

♀. Unknown.



FIGS 92-101

Gnomulus ryssie sp. n., ♂ holotype. - Penis, dorsal (92) and lateral view (93); apex of penis, dorsal (94) and lateral view (95). Body, dorsal view (96); anterior body and proximal palp, lateral view (97). Left chelicera, retrolateral view (98); right palp, retrolateral view (99); trochanter and femur of left palp, dorsal view (100); distal part of left leg II, retrolateral view (101). - Scale lines 0.1 mm (94, 95), 1.0 mm (others).

Measurements: (♂): Body 6.22 long, 4.38 wide; carapace region 1.13 long, 2.21 wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.69	1.03	0.83	0.59	-	1.15	4.29
Leg I	0.54	1.92	0.89	0.98	1.62	0.79	6.74
Leg II	0.64	2.51	1.13	1.77	2.51	0.98	9.54
Leg III	0.57	1.92	0.98	1.18	2.02	0.59	7.26
Leg IV	0.74	2.56	1.21	1.80	3.10	0.69	10.1

Relationships: *Gnomulus ryssie* sp. n. is closest to *G. marginatus* sp. n.

Distribution: Known only from the type locality in the southwestern part of central Thailand [Fig. 1 (7)].

Gnomulus leofeae sp. n.

Figs 102-111

Pelitus segnipis Loman: Roewer (1935: 13).

Material: MYANMAR, Tenasserim, Malewoon (= Maliwun), ♂ holotype (MSNG, Nr. 10203), leg. L. Fea, VIII-IX 1887.

Etymology: This species is dedicated to the Italian naturalist Leonardo Fea, who travelled and collected in Myanmar in the years 1885-1888. The genitive ending “-ae” is linguistically correct (and accepted by the International Code of Zoological Nomenclature) for names with a terminal “-a”, also when referring to a man.

Diagnosis: Closest to *G. pulvillatus*, distinguished by: Eye tubercle lower; lateral tubercles in posterior carapace region present; median dorsal scutal elevations keeled; palpal femur more slender, its ventroproximal process more distad-inclined; leg coxa II without posteroproximal process; penis not constricted at position of glans; glans narrower and less convex in dorsal view, its lateral sclerites longer and more slender; isolated pair of lateral setae on each side of membranous socket situated more proximally.

Description: ♂ (holotype). Coloration: Body and limbs light amber throughout (bleached), except for slightly darker leg tarsi.

Carapace with widely conical, pointed eye tubercle and a pair of small lateral tubercles (Fig. 106) below wide, medially divided carapace-abdomen bridge (Fig. 108). Dorsal scutal areas slightly elevated, the median ones keeled (Fig. 106). Ventral scutum heart-shaped (probably deformed due to preservation), areas swollen, without pubescence (Fig. 107). Palpal coxa with digitiform ventral process; leg coxa I with pronounced anterolateral one; ventral side of leg coxae II and III with distinct anteroproximal processes, no posteroproximal one coxa II; no tubercles on dorsal side of leg coxa IV. Genital operculum somewhat triangular, slightly wider than long; posterior margin of stigmatic pit with pronounced tubercle (Fig. 107).

Chelicerae (Fig. 109): Proximal article with distinct dorsodistal and indistinct dorsomedian boss, ventral side with low, wide hump.

Palps (Fig. 110): Strong, slightly distad-inclined ventral processes on proximal femur and on trochanter.

Legs 1324, tarsal formula 2-2-3-3. Distitarsus II about 2.8 times longer than wide (Fig. 111).

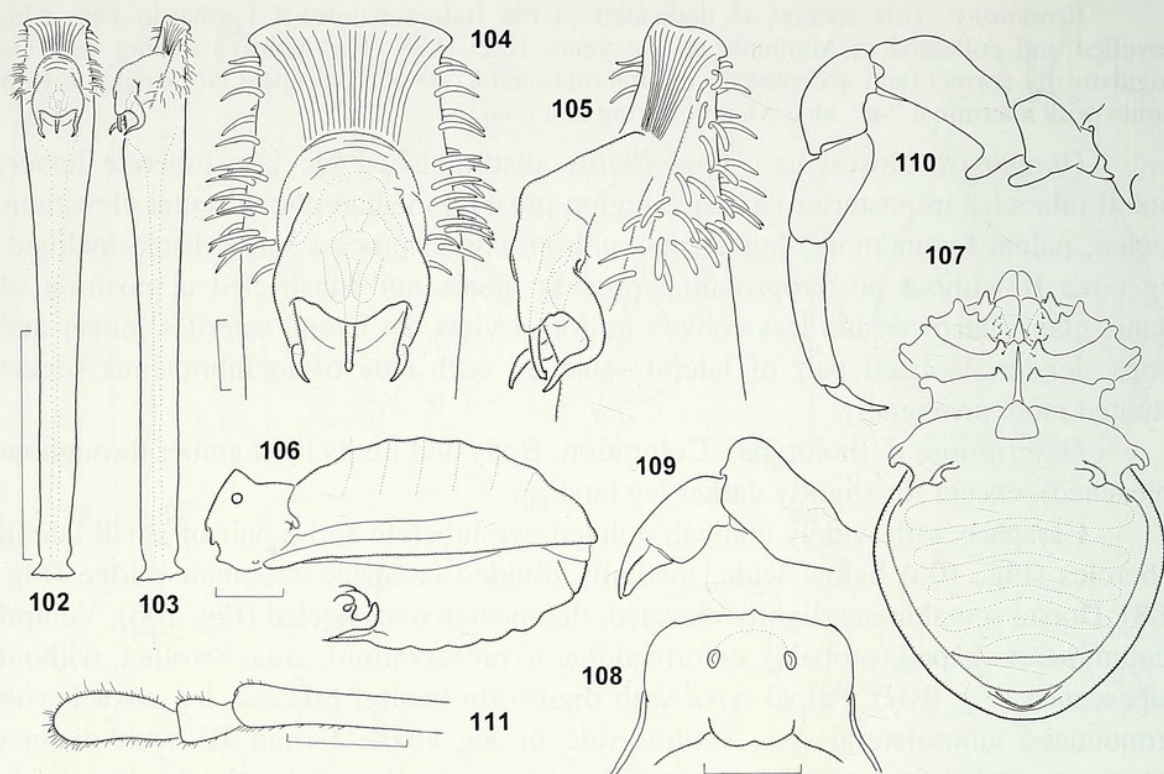
Penis (Figs 102-105): Truncus widest at position of glans, distal margin indistinctly invaginated. Glans with short, widely rounded median plate covering membranous tubes; lateral sclerites cylindrical, fairly long and slender, their distal parts sigmoid, tapering, pointing away from the truncus; stylus slender, base bulbous, apex with a small pair of subterminal ventral teeth.

♀. Unknown.

Measurements: (♂): Body 5.74 long, 4.21 wide; carapace region 1.44 long, 2.13 wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.87	1.24	0.99	0.64	-	1.29	5.03
Leg I	0.69	2.45	1.16	1.34	2.08	1.06	8.78
Leg II	0.82	3.37	1.58	2.33	3.22	1.34	12.66
Leg III	0.72	2.50	1.29	1.56	2.57	1.14	9.78
Leg IV	0.89	3.32	1.56	2.28	3.86	1.29	13.20

Relationships: *Gnomulus leofeae* sp. n. is closely related to *G. pulvillatus* from central peninsular Malaysia and to *G. piliger* from southern Thailand.



FIGS 102-111

Gnomulus leofeae sp. n., ♂ holotype. - Penis, dorsal (102) and lateral view (103); apex of penis, dorsal (104) and lateral view (105). Body, lateral view (106); body, ventral view (107); anterior body, dorsal view (108). Left chelicera, retrolateral view (109); left palp, retrolateral view (110); distal part of left leg II, retrolateral view (111). - Scale lines 0.1 mm (104, 105), 1.0 mm (others).

Remarks: *Gnomulus leofeae* sp. n., *G. piliger* and *G. pulvillatus* are quite similar to each other in external and genital characters, and each species is known only from a single specimen. Additional conspecific material from the Malay Peninsula may show whether these are really three distinct species or just individual or population-dependent variations of a widely distributed and unusually variable species.

Distribution: Known only from the type locality at the southernmost tip of Myanmar [Fig. 1 (8)].

***Gnomulus armillatus* (Thorell, 1891)**

Synonyms: See Schwendinger & Martens (1999: 963).

Remark: A new ♂ specimen was collected on Gunung (= Mount) Kerinci (2160 m, 17.-18.II.2000, leg. P. J. Schwendinger, MHNG), Jambi Province, Sumatra [Fig. 1 (20)], which largely accords with the ♂ from the same locality mentioned by Schwendinger & Martens (1999b: 963, 965, figs 114, 122). The new ♂ also possesses a fairly low, rounded eye tubercle, but its ventral processes on palpal femur and trochanter are larger (more typical for males of this species) and the ventral tubercle on the proximal cheliceral article is indiscernible. The median plate of the glans penis

is more distinctly V-shaped, with clearly discernible lateral teeth, well-according with conspecific males from close to the type locality (see Schwendinger & Martens, 1999b: figs 110, 112).

***Gnomulus javanicus* sp. n.**

Figs 112-124

Pelitnus segnipes Loman. - Loman (1902: 182, partim). - Roewer (1923: 63, partim).

Material: INDONESIA, Java, Mt. Gede, SE of Bogor, ♂ holotype (ZMH, with labels: “*Pelitnus segnipes*, Loman det. 1901/02, H. Fruhstorfer vend. 18.II.1897” and “*Pelitnus segnipes*, Roewer det. 1914, No. 1258”). - Java, without exact locality, 2 ♀ paratypes (SMF 1602, with label: “*Pelitnus javanus* n. sp. Roewer, typus, 1 ♂, 1 ♀, Roewer det. 1929”).

Diagnosis: Similar to *G. laevis*, distinguished by: Body smaller; palp without prolateral boss and with distinct ventrobasal process on femur; ventral process on palpal trochanter longer; distitarsus II shorter; penis with narrower apex and less strongly arched distal margin; glans narrower, its lateral sclerites less convex, with more distinctly pointed apices; median plate shorter.

Description: ♂ (holotype). Coloration mostly dark reddish brown; transversal bands on dorsal scutal elevations slightly darker, medially disconnected in areas I-III; chelicerae and proximal article of pedipalps slightly lighter.

Carapace with low, rounded eye tubercle, without lateral tubercles posteriorly below wide, indistinctly divided carapace-abdomen bridge (Figs 116, 124). Dorsal scutal areas distinctly elevated, anterior ones rounded, posteriors keeled; ventral scutal areas swollen, without modified hairs. Palpal coxa with distinct ventral process; leg coxa I with small anterolateral one; ventral side of leg coxae II and III with distinct anteroproximal processes, coxa II with indistinct posteroproximal one; dorsal side of coxa IV without tubercle. Genital operculum narrow, slightly longer than wide (Fig. 117); posterior margin of stigmatic pit with tubercle.

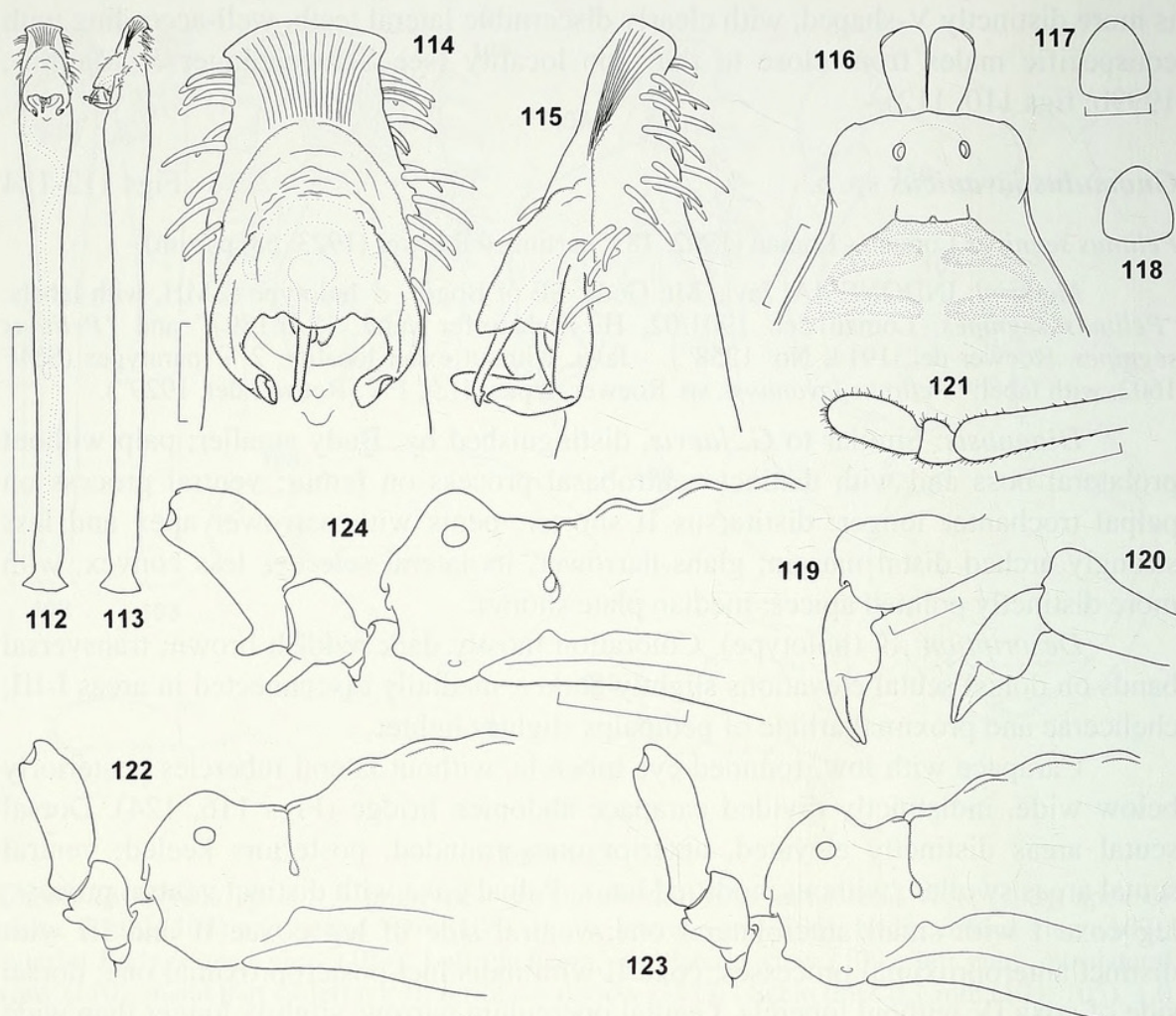
Chelicerae (Fig. 119) weak, proximal article with distinct dorsodistal and less distinct dorsomedian boss; no ventral tubercle.

Palps (Fig. 124): Femur stout, with strong ventroproximal process and long dorsodistal to dorsoproximal boss; trochanter with long, digitiform, slightly distad-inclined ventral process.

Legs 13(24?), tarsal formula 2-2-3-3. Distitarsi of legs II missing.

Penis (Figs 112-115): Truncus slender, widest below glans, with narrow, slightly arched apex. Glans slightly narrower than truncus at that point; lateral sclerites convex and with a moderately elevated dorsal ledge in proximal half, distal half narrowly paddle-shaped, pointing away from the truncus, both sides parallel to each other; knee between proximal and distal part of lateral sclerites bent at right angles, not bulged towards truncus (Fig. 115); median plate very short, widely rounded, with a pair of rounded lateral teeth; membranous tubes distally not covered by median plate; stylus slender, base bulbous, apex with a small pair of subterminal ventral teeth.

♀. As the male but with much shorter ventral processes on palpal femur and trochanter; palpal femur without dorsal boss (Figs 122, 123); proximal article of chelicera without dorsomedian boss (Fig. 120); dorsal scutal areas less elevated and



FIGS 112-124

Gnomulus javanicus sp. n., ♂ holotype (112-117, 119, 124), ♀ paratypes (118, 120-123). - Penis, dorsal (112) and lateral view (113); apex of penis, dorsal (114) and lateral view (115). Anterior body and chelicerae, dorsal view (116); genital operculum (117, 118); left chelicera, retrolateral view (119, 120); distal part of left leg II, retrolateral view (121); anterior body and proximal palp, lateral view (122-124). - Scale lines 0.1 mm (114, 115), 1.0 mm (others).

ventral scutal areas not swollen. Legs 1324; distitarsus II about 2.1 times longer than wide (Fig. 121).

Measurements: ♂ holotype (♀ in parentheses): Body 5.86 (5.92) long, 4.05 (4.02) wide; carapace region 1.25 (1.08) long, 2.23 (2.10) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.81 (0.69)	1.12 (1.04)	0.94 (0.74)	0.69 (0.54)	--	1.18 (1.08)	4.74 (4.09)
Leg I	0.56 (0.54)	2.24 (1.68)	1.06 (0.89)	1.31 (1.04)	1.93 (1.63)	0.94 (0.84)	8.04 (6.62)
Leg II	0.69 (0.64)	3.24 (2.32)	1.53 (1.16)	2.37 (1.63)	3.24 (2.32)	? (1.13)	? (9.20)
Leg III	0.69 (0.59)	2.43 (1.75)	1.18 (0.99)	1.62 (1.16)	2.37 (1.92)	1.00 (0.84)	9.29 (7.25)
Leg IV	1.03 (0.89)	3.18 (2.42)	1.50 (1.21)	2.24 (1.77)	3.58 (2.91)	1.18 (0.94)	12.71 (10.14)

Variation: Range of measurements in ♀♀ (n=2): Body 5.67-5.92 long, 3.86-4.02 wide, carapace region 1.08-1.18 long, 1.99-2.10 wide. One ♀ has a very low eye tubercle (Fig. 122).

Relationships: *Gnomulus javanicus* sp. n. is closest to *G. lomani* sp. n.

Remarks: The specimens examined are clearly distinct from *G. thorelli*, which also occurs on Java. However, males and females of *G. javanicus* sp. n. (both from the same island) differ from each other in a number of characters (see above), which either reflect a pronounced sexual dimorphism or indicate that they belong to different species. Until further evidence for the contrary becomes available, these specimens are regarded as conspecific.

As far as we know "*Pelitnus javanus* Roewer" has never been described and was never mentioned in the literature. It thus is an unpublished name without nomenclatural relevance.

Distribution: Known only from one or two localities on Java [Fig. 1 (21)]. The exact locality of the presumably conspecific female paratypes is unknown. *Gnomulus thorelli* was found at Cibodas (Schwendinger & Martens, 1999b: 969) and possibly occurs syntopically with *G. javanicus* sp. n.

Gnomulus lomani sp. n.

Figs 125-140

Pelitnus segnipipes Loman. - Loman (1902: 182, partim). - Roewer (1923: 63, partim).

Material: BORNEO, Telang (locality not identified), ♂ holotype, ♂ paratype (ZMB 4247), with one label saying "*Pelitnus segnipipes* Loman, 1892, Fundort (= find locality): Telang, Broneo (Burma)" and another in Gothic handwriting (probably by Roewer) "*Pelitnus segnipipes* Loman, von Loman falsch bestimmt (= misidentified by Loman)"; both specimens leg. F. Grabonsky. - SUMATRA, BORNEO, without exact locality, 2 ♂, 1 ♀, "leg. ?, leg. Schwaner?" (ZMA; no types).

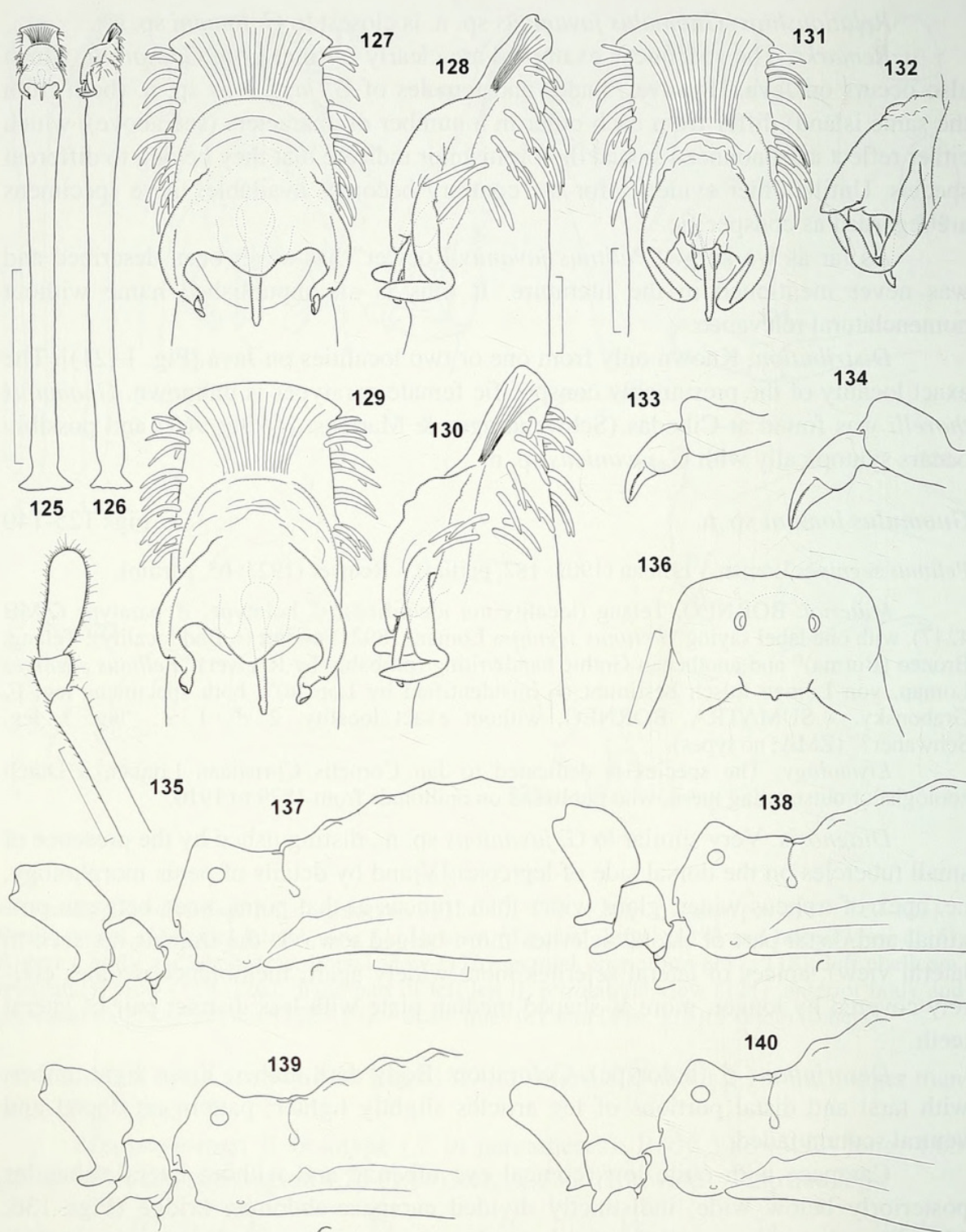
Etymology: The species is dedicated to Jan Cornelis Christiaan Loman, a Dutch zoologist of outstanding merit, who published on opilionids from 1879 to 1910.

Diagnosis: Very similar to *G. javanicus* sp. n., distinguished by the presence of small tubercles on the dorsal side of leg coxa IV and by details of penis morphology, i.e. apex of truncus wider; glans wider than truncus at that point; knee between proximal and distal part of lateral sclerites more bulged towards the truncus (as seen in lateral view); apices of lateral sclerites more widely apart; membraneous tubes entirely covered by longer, more V-shaped median plate with less distinct pair of lateral teeth.

Description: ♂ (holotype). Coloration: Body dark amber, limbs light amber, with tarsi and distal portions of leg articles slightly lighter; pattern on dorsal and ventral scutum faded.

Carapace with quite low, conical eye tubercle and without lateral tubercles posteriorly below wide, indistinctly divided carapace-abdomen bridge (Figs 136, 137). Dorsal scutal areas distinctly elevated, anterior ones rounded, posteriors keeled; ventral scutal areas swollen, without modified hairs. Palpal coxa with strong ventral process; leg coxa I with small anterolateral one; ventral side of leg coxae II and III with distinct anteroproximal processes, no posteroproximal one on coxa II; dorsal side of coxa IV with a small anterior tubercle. Genital operculum about as long as wide; posterior margin of stigmatic pit with low tubercle.

Chelicerae (Fig. 134) weak, proximal article with distinct dorsodistal to dorsomedian boss; no ventral process.



FIGS 125-140

Gnomulus lomani sp. n., ♂ holotype (125-128, 134, 136, 137), ♀ paratypes (129-130, 139), presumably conspecific ♂ (138) and ♀ (133, 140). - Penis, dorsal (125) and lateral view (126); apex of penis, dorsal (127, 129, 131) and lateral view (128, 130); glans penis, lateral view (132). Left chelicera, retrolateral view (133, 134); distal part of left leg II, retrolateral view (135); anterior body, dorsal view (136); anterior body and proximal palp, lateral view (137-140). - Scale lines 0.1 mm (127-132), 1.0 mm (others).

Palps (Fig. 137): Femur with strong ventroproximal process and extended dorsodistal to dorsoproximal boss; trochanter with long, digitiform ventral process.

Legs 1324, tarsal formula 2-2-3-3. Distitarsus II 2.9 times longer than wide (Fig. 135).

Penis (Figs 125-132; holotype: 125-128): Truncus slender, continuously widening towards apex; distal margin broadly arched. Glans wider than truncus at that point; lateral sclerites convex and with a slightly elevated dorsal ledge in proximal half, distal part narrowly paddle-shaped, pointing away from the truncus (Fig. 128), both sides parallel to each other; knee between proximal and distal half distinctly bulged towards the truncus; apices of lateral sclerites widely apart; median plate quite short, more or less distinctly V-shaped, distally rounded, with lateral teeth reduced to low bulges; membranous tubes completely covered by median plate; stylus slender, base bulbous, apex with a small pair of subterminal ventral teeth.

♀ (uncertain identification). As the male but with a more slender palpal femur, distinctly smaller ventral processes on palpal trochanter and femur and with a smaller dorsomedian boss on the proximal cheliceral article.

Measurements: ♂ holotype (♂ paratype in parentheses; no measurements of available ♀ given because of uncertain identification): Body 5.70 (5.67) long, 4.05 (3.99) wide; carapace region 1.19 (1.19) long, 2.22 (2.20) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.78	1.06	0.90	0.65	-	1.12	4.51
Leg I	0.56	2.06	1.06	1.25	1.87	0.94	7.74
Leg II	0.72	2.99	1.56	2.28	2.99	1.31	11.85
Leg III	0.69	2.24	1.22	1.50	2.31	1.00	8.96
Leg IV	0.97	2.81	1.50	2.12	3.40	1.18	11.98

Variation: The ♂ paratype has indistinct posteroproximal processes on coxa II, more strongly elevated dorsal scutal areas (Fig. 139) and a longer median plate on glans penis (Fig. 129).

Relationships: *Gnomulus lomani* sp. n. is closest to *G. javanicus* sp. n.; both are in the same phyletic lineage with *G. exsudans* sp. n., *G. hutan* sp. n., *G. laevis*, *G. obscurus* sp. n. and *G. sundaicus*.

Remarks: The indication of the type locality ["Telang, Broneo (Burma)"], as given on the label with the types, is misleading. According to information from Jason Dunlop, the ZMB houses extensive material collected by Fritz Grabonsky in Borneo, but none from Burma. Broneo was obviously misspelled for Borneo, but it is unclear why Burma was added in parentheses.

2 ♂ and 1 ♀ (dried and pinned specimens transferred to alcohol) with label reading "Sumatra, leg. ?, Borneo, leg. Schwaner (?)", lodged in the ZMA and recorded by Loman (1902: 182), are very similar to the types of *G. lomani* sp. n. but cannot be assigned to this species with certainty. In one ♂ the distal part of the penis is missing, in the other the penis is bent and its glans partly collapsed (caused by the pin which passed beside the tip of the penis; Figs 131, 132).

The weaker palpal femur, smaller ventral processes on palpal trochanter and femur (Fig. 140) and smaller dorsomedian boss on the proximal cheliceral article (Fig. 133) of the female (conspecific?) are probably due to sexual dimorphism. The same is seen in *G. armillatus* (see Schwendinger & Martens 1999b, figs 116-123) and - less distinctly so - also in *G. exsudans* sp. n. (Figs 181-184); it presumably also holds true for *G. javanicus* sp. n. (Figs 122-124).

Distribution: The type locality cannot be identified, but there are three localities which may correspond: 1) Pulau Talang (1°55'N, 109°46'E), an island off the coast at the western end of Sarawak, 2) Telang (2°07'S, 115°00'E) in southern Kalimantan and 3) Pulau Telang (0°43'N, 104°37'E), an island in the Riau Archipelago, south of Singapore.

Gnomulus obscurus sp. n.

Figs 141-149

Material: MALAYSIA (east), Sarawak, Kuching, ♂ holotype (SMF 7373/12, with label: "*Pelitnus segnipes*, Roewer det. 1939").

Etymology: Latin: *obscurus* = hidden, unknown. The specific epithet refers to the previous misidentification of the type specimen.

Diagnosis: Similar to *G. annulipes*, distinguished by: Body smaller; eye tubercle lower, more rounded; penis more slender, with basally narrower, distally wider lateral sclerites and with a W-shaped median plate.

Description: ♂ (holotype). Coloration (bleached): Body and cheliceral fingers light amber, no colour pattern on scuta discernible; limbs mostly light orange.

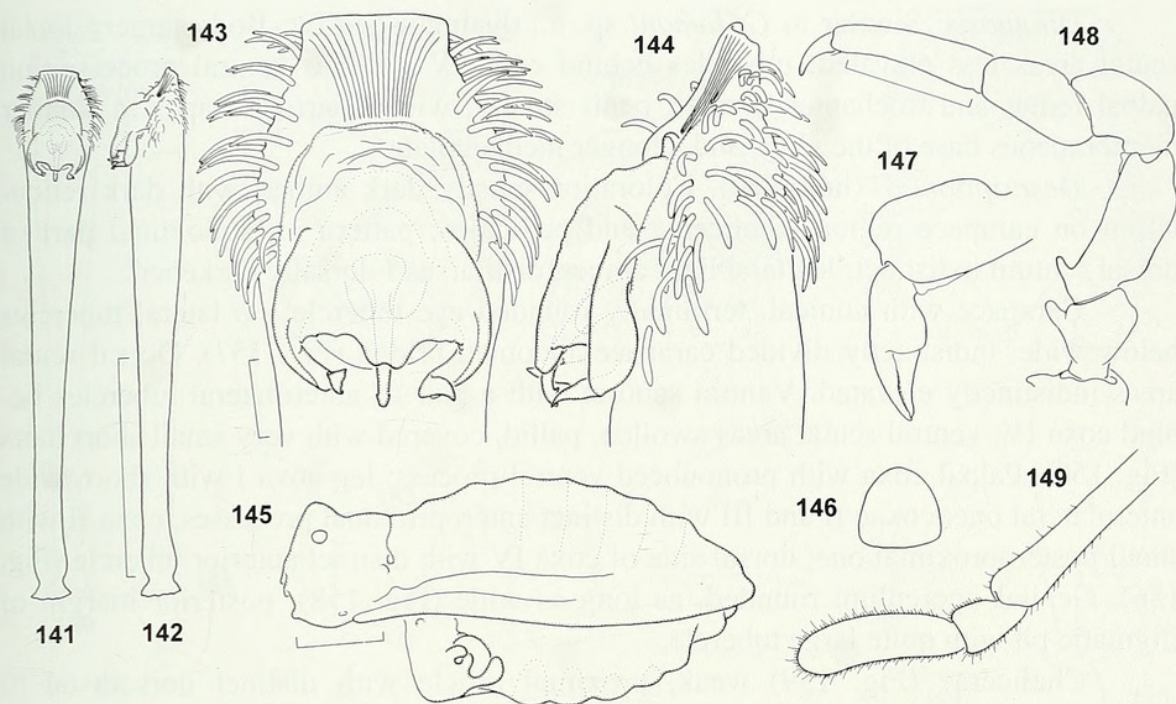
Carapace with widely conical, distally rounded eye tubercle and with a pair of small lateral tubercles below wide, indistinctly divided carapace-abdomen bridge. Anterior dorsal scutal areas little elevated, indistinctly keeled, posterior ones rounded (Fig. 145); a low longitudinal furrow separating anterior areas medially. Ventral scutal areas swollen, without modified hairs. Palpal coxa with large ventral process; leg coxa I with distinct anterolateral one; coxa II with strong, coxa III with small anteroproximal process, coxa II with posteroproximal one. Genital operculum almost semicircular (Fig. 146); posterior margin of stigmatic pit with small tubercle.

Chelicerae (Fig. 147) weak, proximal article with distinct dorsodistal to dorsomedian boss; no ventral process.

Palps (Fig. 148): Ventral side of femur with narrow, slightly anteriad-inclined proximal process and moderately developed dorsodistal to dorsoproximal boss; trochanter with slightly distad-inclined ventral process.

Legs 1324, tarsal formula 2-2-3-3. Distitarsus II about 3.5 times longer than wide (Fig. 149).

Penis (Figs 141-144) slender, widest at height of membranous socket of glans; apex narrow, carrying plenty of setae; distal margin of truncus almost straight. Glans narrower than truncus at that point; lateral sclerites convex and with a moderately elevated dorsal ledge in basal half, in distal half laterally compressed, tapering and pointing away from the truncus; median plate short, with a narrow, protruding, somewhat W-shaped median portion; membranous tubes completely covered by



FIGS 141-149

Gnomulus obscurus sp. n., ♂ holotype. - Penis, dorsal (141) and lateral view (142); apex of penis, dorsal (143) and lateral view (144). Body, lateral view (145); genital operculum, ventral view (146); left chelicera, retrolateral view (147); left palp, retrolateral view (148); distal part of left leg II, retrolateral view (149). - Scale lines 0.1 mm (143, 144), 1.0 mm (others).

median plate; stylus slender, base bulbous, apex with a small pair of subterminal ventral teeth.

♀. Unknown.

Measurements: (♂): Body 5.64 long, 3.99 wide; carapace region 1.33 long, 2.12 wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.84	1.11	0.89	0.62	-	1.23	4.69
Leg I	0.64	2.42	1.11	1.36	2.12	1.13	8.78
Leg II	0.74	3.30	1.53	2.51	3.30	1.58	12.96
Leg III	0.67	2.47	1.23	1.63	2.56	1.18	9.74
Leg IV	0.94	3.30	1.48	2.34	3.77	1.33	13.16

Relationships: Penis morphology shows that *G. obscurus* sp. n. is close to *G. exsudans* sp. n., *G. javanicus* sp. n., *G. hutan* sp. n., *G. laevis*, *G. lomani* sp. n. and *G. sundaicus*.

Distribution: Known only from Kuching in Sarawak, northern Borneo, where *G. obscurus* sp. n. apparently occurs sympatrically with *G. sundaicus* [Fig. 1 (24)].

Gnomulus hutan sp. n.

Figs 150-163

Material: MALAYSIA (east), Sarawak, confluent of Sun Oyan and Mujong rivers, E of Kapit, 50 m, ♂ holotype, ♂ paratype, 18.V.1994, leg. I. Löbl & D. Burckhardt (MHNG).

Etymology: Malay and Indonesian: *hutan* = forest; noun in apposition.

Diagnosis: Similar to *G. lomani* sp. n., distinguished by: Body larger; dorsal scutal areas less elevated; tubercles behind coxa IV present; ventral processes on palpal femur and trochanter smaller; penis stouter, with a narrower apex, a smaller membraneous base of the glans and a longer median plate.

Description ♂ (holotype). Coloration mostly dark amber, with dark reticulation on carapace region, chelicerae and pedipalps; pattern on abdominal part of dorsal scutum indistinct; leg tarsi light amber, distitarsus I dorsally darkened.

Carapace with conical, terminally rounded eye tubercle; no lateral tubercles below wide, indistinctly divided carapace-abdomen bridge (Fig. 157). Dorsal scutal areas indistinctly elevated. Ventral scutum with a pair of anterolateral tubercles behind coxa IV; ventral scutal areas swollen, pallid, covered with very small short hairs (Fig. 156). Palpal coxa with pronounced ventral process; leg coxa I with short, wide anterolateral one; coxae II and III with distinct anteroproximal processes, coxa II with small posteroproximal one; dorsal side of coxa IV with distinct anterior tubercle (Fig. 156). Genital operculum rounded, as long as wide (Fig. 158); posterior margin of stigmatic pit with quite large tubercle.

Chelicerae (Fig. 159) weak, proximal article with distinct dorsodistal to dorsomedian boss; no ventral process.

Palps (Figs 160, 161): Femur with small ventroproximal process, with distinct dorsodistal to dorsoproximal boss and with wide, low prodorsal boss (Fig. 161); trochanter with digitiform, slightly distad-inclined ventral process.

Legs 1324, tarsal formula 2-2-3-3. Distitarsus II about 2.8 times longer than wide (Fig. 162).

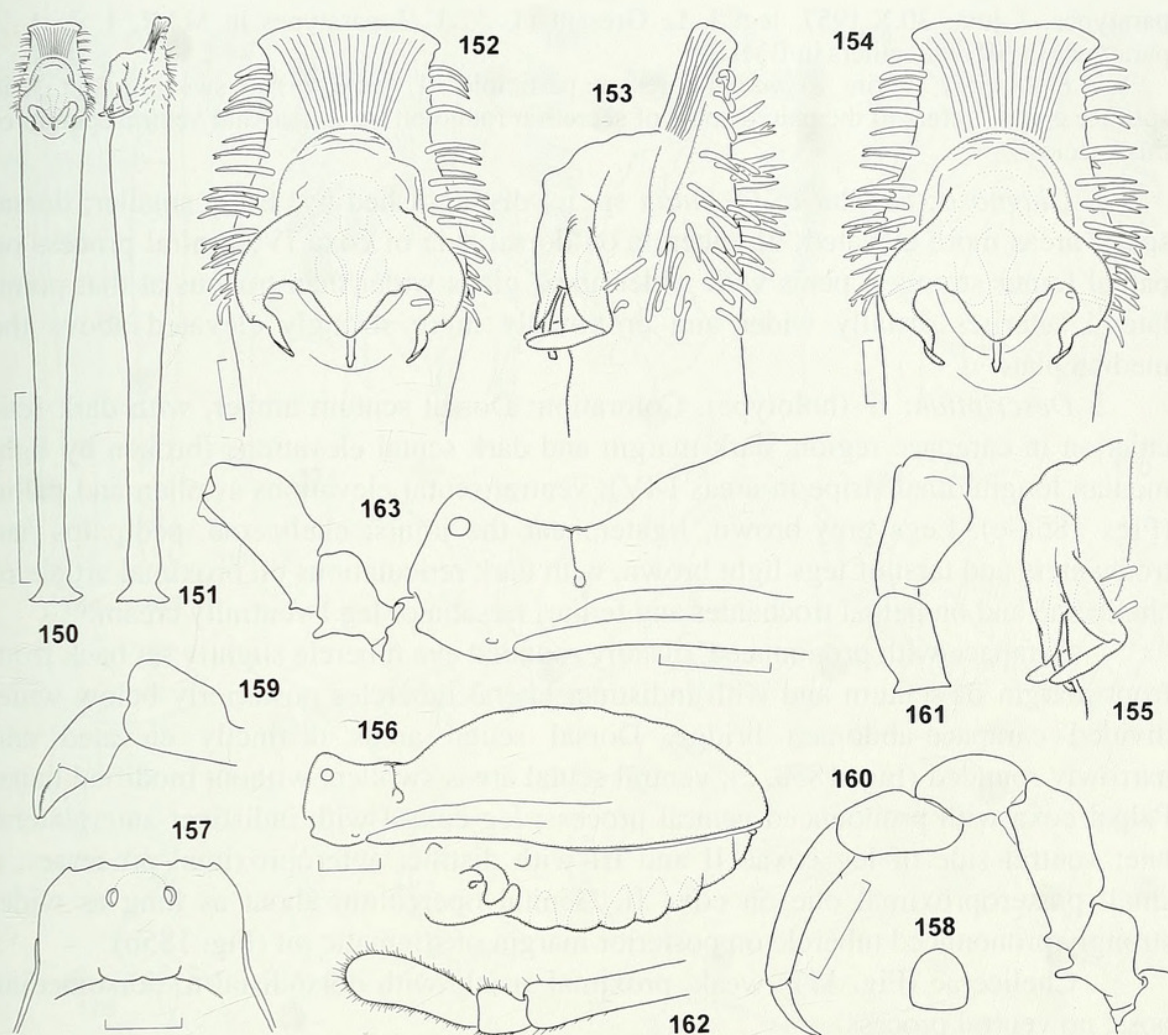
Penis (Figs 150-155; holotype: 152, 153) fairly stout, widening in distal half, distal margin slightly invaginated; apex narrow, carrying plenty of setae. Glans slightly narrower than truncus at that point; lateral sclerites strongly convex, basal half with moderately elevated dorsal ledge, distal half narrowly paddle-shaped, pointing away from the truncus; median plate long, V-shaped, with a small pair of lateral teeth; membraneous tubes completely covered by median plate; stylus slender, base bulbous, apex with a small pair of ventral subterminal teeth.

♀. Unknown.

Measurements: ♂ holotype (♂ paratype in parentheses): Body 7.44 (7.47) long, 4.96 (5.08) wide; carapace region 1.49 (1.46) long, 2.70 (2.67) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.96	1.30	0.99	0.81	-	1.55	5.61
Leg I	0.81	2.42	1.21	1.43	2.23	1.24	9.34
Leg II	0.99	3.32	1.55	2.39	3.47	1.64	13.36
Leg III	0.87	2.45	1.30	1.61	2.79	1.12	10.14
Leg IV	1.24	3.41	1.67	2.42	4.43	1.30	14.47

Variation: The paratype has smaller ventral processes on its palpal femur and trochanter (Fig. 163) than the holotype (Fig. 160).



FIGS 150-163

Gnomulus hutan sp. n., ♂ holotype (152, 153, 156-162), ♂ paratype (150, 151, 154, 155, 163). - Penis, dorsal (150) and lateral view (151); apex of penis, dorsal (152, 154) and lateral view (153); glans penis, lateral view (155). Body, lateral view (156); anterior body, dorsal view (157); genital operculum, ventral view (158); left chelicera, retrolateral view (159); left palp, retrolateral view (160); trochanter and femur of left palp, dorsal view (161); distal part of left leg II, retrolateral view (162); anterior body and proximal palp, lateral view (163). - Scale lines 0.1 mm (152-155), 1.0 mm (others).

Relationships: This species appears most closely related to *G. lomani* sp. n., followed by *G. javanicus* sp. n. and *G. exsudans* sp. n.

Distribution: Known only from the environs of Kapit, in the central part of Sarawak [Fig. 1 (25)].

Gnomulus exsudans sp. n.

Figs 164-185

Material: MALAYSIA (east), Sarawak, Gunung Mulu National Park, Base Camp (= Paku Camp, 150 m?), ♂ holotype, 1 ♂, 1 ♀ paratypes, 1 juv., VI.1978, leg. F. Wanless (NHML). - Sabah, Sandakan Bay (southwest), Sapagaya Lumber Camp, 2-20 m, 1 ♂ paratype (BMH; penis dissected and retained by W. A. Shear), 7 ♀ paratypes, 2 juv., 4.-7.XI.1957, leg. J. L. Gressitt (BMH); Sandakan Bay (northwest), Sepilok Forest Reserve, 1-10 m, 7 ♂, 5 ♀

paratypes, 1 juv., 30.X.1957, leg. J. L. Gressitt (1 ♂, 1 ♀ paratypes in MAR, 1 ♂, 1 ♀ paratypes in MHNG, others in BMH).

Etymology: Latin: *exsudans* (present participle of *exsudare*) = sweating out. The specific epithet refers to the paired spots of secretion found on the dorsal and ventral scutum of this species.

Diagnosis: Similar to *G. hutan* sp. n., distinguished by: Body smaller; dorsal scutal areas more elevated; no tubercle on dorsal side of coxa IV; ventral process on palpal femur stronger; penis with wider apex; glans wider than truncus at that point, lateral sclerites distally wider and proximally more strongly elevated above the median plate.

Description: ♂ (holotype). Coloration: Dorsal scutum amber, with dark reticulation in carapace region, dark margin and dark scutal elevations (broken by light median longitudinal stripe in areas I-IV); ventral scutal elevations swollen and pallid (Figs 185a-c). Legs grey-brown, lighter near the joints; chelicerae, pedipalps and trochanters and tarsi of legs light brown, with dark reticulations on proximal article of chelicerae and on palpal trochanter and femur; tarsalia of leg I ventrally cream.

Carapace with pronounced, distally rounded eye tubercle slightly set back from front margin of scutum and with indistinct lateral tubercles posteriorly below wide, divided carapace-abdomen bridge. Dorsal scutal areas distinctly elevated and narrowly rounded (Fig. 185a, c); ventral scutal areas swollen, without modified hairs. Palpal coxa with pronounced ventral process; leg coxa I with indistinct anterolateral one; ventral side of leg coxae II and III with distinct anteroproximal processes, a small posteroproximal one on coxa II. Genital operculum about as long as wide; strongly pronounced tubercle on posterior margin of stigmatic pit (Fig. 185b).

Chelicerae (Fig. 177) weak, proximal article with dorsodistal to dorsomedian boss; no ventral process.

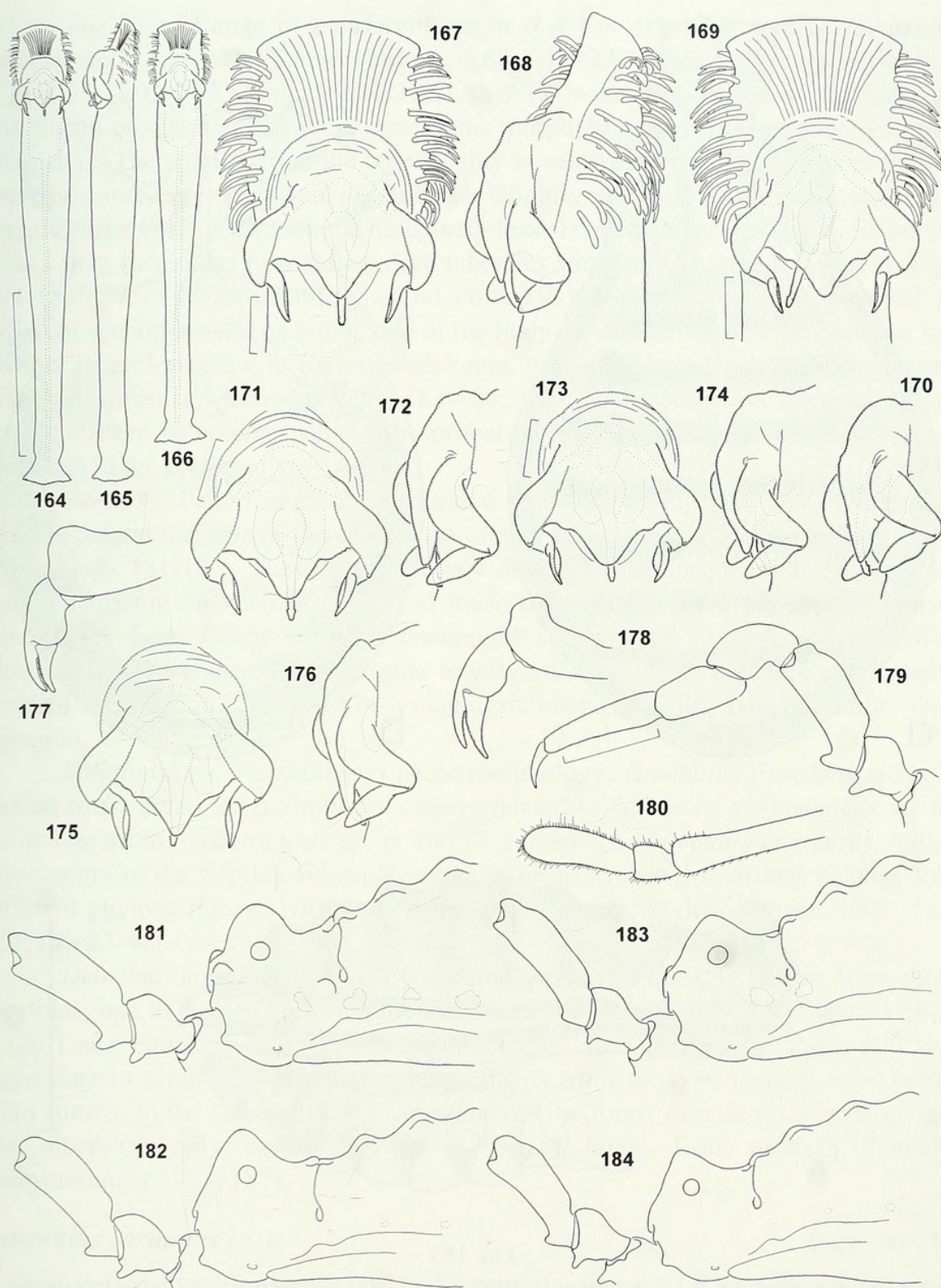
Palps (Fig. 179): Ventral side of femur with slightly distad-inclined proximal process, about as long as ventrad-directed process on ventral side of trochanter.

Legs 1324, tarsal formula 2-2-3-3. Distitarsus of leg II 3.2 times longer than wide (Fig. 180).

Penis (Figs 164-176; holotype: 164, 165, 167, 168): Truncus slightly constricted at height of glans, distal margin broadly arched. Glans wider than truncus at that point; lateral sclerites convex, proximal half with dorsal ledge strongly elevated above median plate, distal half widely paddle-shaped, pointing away from the truncus; knee between proximal and distal half of lateral sclerites rounded, somewhat bulged towards the truncus; median plate V-shaped, with an indistinct pair of lateral teeth; membraneous tubes completely covered by median plate; stylus slender, base bulbous, apex with a small pair of subterminal ventral teeth.

♀. As the male but: Carapace region relatively smaller; ventral processes on palpal femur and trochanter slightly weaker (Figs 183, 184); proximal article of chelicera without dorsomedian boss (Fig. 178); ventral scutal areas not swollen; distitarsus II only 3.0 times longer than wide.

Measurements: ♂ holotype (♀ from type locality in parentheses): Body 5.95 (6.12) long, 4.18 (4.38) wide; carapace region 1.33 (1.16) long, 2.21 (2.12) wide. - Palp and legs:



FIGS 164-184

Gnomulus exsudans sp. n., ♂ holotype (164, 165, 167, 168, 177, 179, 180), paratypes: ♂ from the type locality (181), ♂♂ from Sabah (166, 169-176, 182), ♀ from the type locality (178, 183), ♀ from Sabah (184). - Penis, dorsal (164, 166) and lateral view (165); apex of penis, dorsal (167, 169) and lateral view (168); glans penis, dorsal (171, 173, 175) and lateral view (170, 172, 174, 176). Left chelicera, retrolateral view (177, 178); left palp, retrolateral view (179); distal part of left leg II, retrolateral view (180); anterior body and proximal palp, lateral view (181-184). - Scale lines 0.1 mm (167-176), 1.0 mm (others).

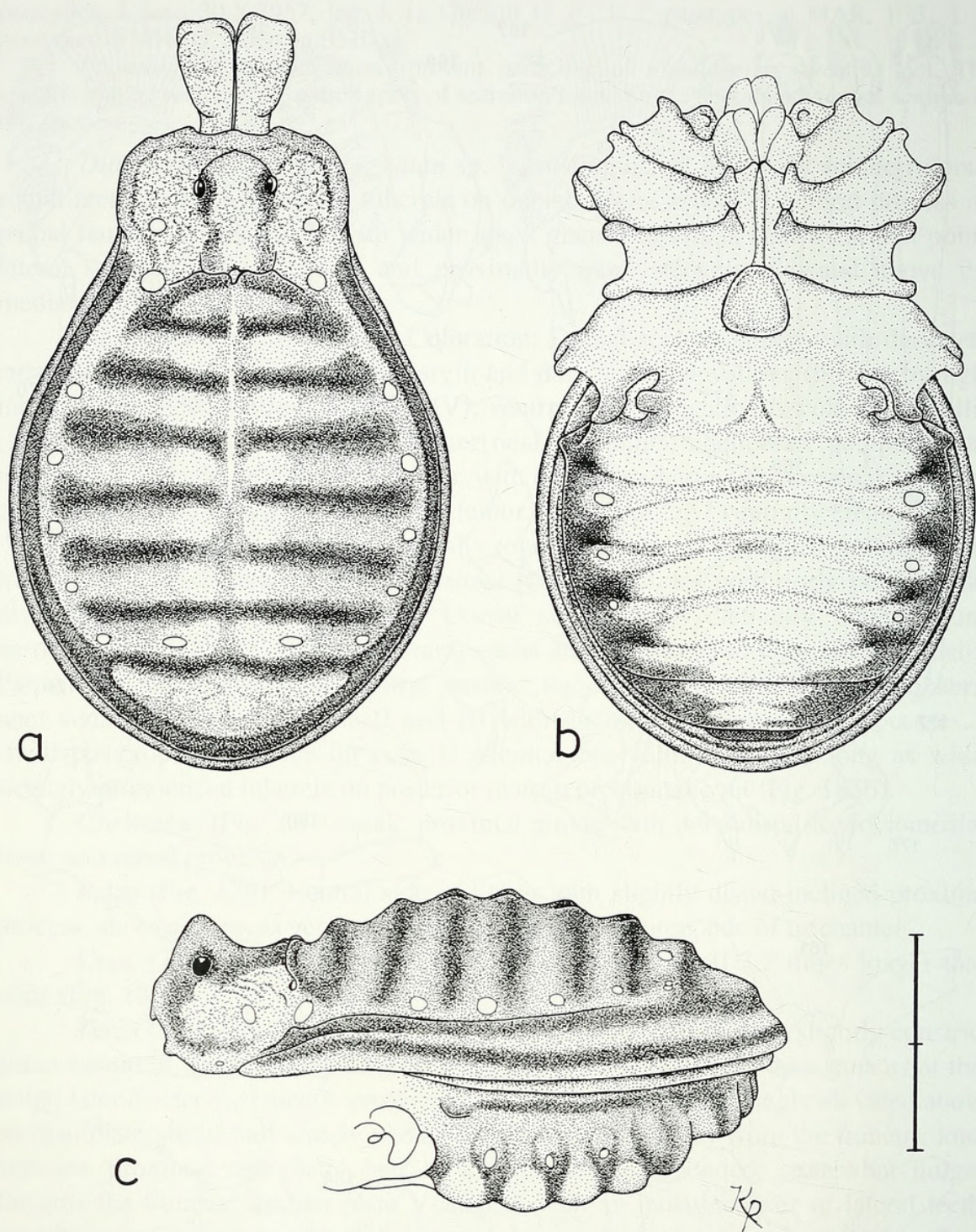


FIG. 185

Gnomulus exsudans sp. n., ♂ holotype. - Body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1.0 mm.

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.79 (0.79)	1.18 (1.18)	0.93 (0.89)	0.64 (0.59)	--	1.18 (1.23)	4.72 (4.68)
Leg I	0.79 (0.64)	2.51 (2.31)	1.08 (1.03)	1.40 (1.28)	2.16 (2.07)	1.16 (1.13)	9.10 (8.46)
Leg II	0.84 (0.84)	3.64 (3.35)	1.57 (1.50)	2.68 (2.56)	3.39 (3.25)	1.50 (1.40)	13.62 (12.90)
Leg III	0.69 (0.69)	2.66 (2.46)	1.28 (1.21)	1.67 (1.67)	2.68 (2.56)	1.38 (1.35)	10.36 (9.94)
Leg IV	1.03 (0.93)	3.44 (3.35)	1.53 (1.48)	2.41 (2.39)	3.91 (3.76)	1.43 (1.40)	13.75 (13.31)

Variation: Range of measurements in ♂♂ (n= 10) [♀♀ (n= 13) in parentheses]: Body 5.26-5.95 (5.53-6.18) long, 3.68-4.45 (3.89-4.45) wide, carapace region 1.11-1.33 (1.02-1.17) long, 1.95-2.21 (1.88-2.12) wide. Specimens of the Sarawak and Sabah populations show the same penis morphology but differ in a few external characters. The animals from the type locality in eastern Sarawak have a more bulged anterior carapace margin, an eye tubercle slightly set back from the scutal front margin (Figs 181, 183, 185c) and a distinctly less elevated anterolateral process on leg coxa I than specimens from Sabah. Eye tubercles vary from pointed to rounded (Figs 181-184, 185c). The tubercles behind coxa IV are more or less pronounced in different specimens and on either side of the body. The ♂ paratype from Sarawak has distinct tubercles below its carapace-abdomen bridge (Fig. 181); these are indistinct or absent in other specimens (Figs 182-184, 185c). All specimens from Sabah are clearly darker in colour, which was probably caused by humid acids (from soil particles) in the preservative.

Remarks: Paired spots of denaturated secretion, arranged in a regular pattern near the lateral margins of the dorsal and ventral scutum, occur in all specimens examined (Figs 181-185). These spots are very distinct in the specimens from Sarawak, less so (missing on ventral scutum) in those from Sabah. Such peculiar secretions have never been found in other oncopodid species and are probably specific. However, as these secretions are quite loosely attached to the cuticle and are easily brushed off, we don't use them as a diagnostic character. They deserve further examination.

Relationships: According to penis morphology, *Gnomulus exsudans* sp. n. is closest to *G. hutan* sp. n.; both are closely related to *G. laevis*, *G. javanicus* sp. n., *G. lomani* sp. n., *G. obscurus* sp. n. and *G. sundaicus*. *Gnomulus conigerus*, which also occurs in the Sepilok Forest Reserve, is clearly more distant and belongs to a different phyletic lineage within the *armillatus*-group (cf. Schwendinger, 1992: 183, 184, figs 27-41).

Distribution and bionomics: *Gnomulus exsudans* sp. n. is known from three localities, one in eastern Sarawak, the other two in eastern Sabah. The Sarawak [Fig. 1 (26)] and Sabah [Fig. 1 (27, 28)] populations are separated by about 400 km. According to a note on the label, the specimens from the type locality were swept from shrubs. In the Oncopodidae occurrence off the forest floor is most unusual and has otherwise only been observed in *G. sundaicus* from western Sarawak (Schwendinger 1992: 187).

Gnomulus carinatus sp. n.

Figs 186-190

Pelitnus segnipes Loman. - Loman (1902: 182, partim). - Roewer (1923: 63, partim, fig. 66). - Schwendinger (1992: 187, figs 57-61).

Material: INDONESIA, South Kalimantan, Bandjermasin (= Banjarmasin), ♂ holotype, leg. Suck (SMF 1259).

Etymology: Latin: *carinatus* = keeled. The specific epithet refers to the keeled dorsal scutal elevations of this species.

Diagnosis: Externally similar to *G. thorelli* (male unknown), distinguished by keeled elevations on posterior part of dorsal scutum and by a longer subbasal process

on ventral side of palpal femur. Penis similar to that of *G. armillatus* but: Truncus with wider apex; glans shorter, wider; lateral sclerites more convex; median plate more rounded and carrying distinct lateral teeth.

Description: ♂ (holotype). Coloration: Body reddish brown, colour pattern faded; legs yellow-brown, tarsi I, II cream.

Carapace with conical, pointed eye tubercle and with a pair of small lateral tubercles posteriorly below wide, indistinctly divided carapace-abdomen bridge. Dorsal scutal elevations rounded in areas I-II, distinctly keeled in posterior areas; ventral scutal areas swollen, covered by few very small hairs without incrustations (Fig. 187). Palpal coxa with large ventral process; leg coxa I with distinct antero-lateral one; ventral side of leg coxae II and III with small anteroproximal processes, coxa II without posteroproximal one. Genital operculum somewhat triangular, slightly wider than long; posterior margin of stigmatic pit with tubercle.

Chelicerae (Fig. 188) weak, proximal article with distinct dorsodistal and indistinct dorsomedian boss; no ventral process.

Palps (Fig. 189): Ventral side of femur with strong subbasal, slightly distad-directed process; trochanter with short, ventrad-directed process.

Legs 1324, tarsal formula 2-2-3-3. Distitarsus of leg II about 2.5 times longer than wide (Fig. 190).

Penis (Fig. 186; Schwendinger, 1992: figs 58-61): Truncus in its distal half wider than in proximal half; distal margin broadly arched, median part almost straight. Glans slightly wider than truncus at that point; lateral sclerites strongly convex in proximal portion, with dorsal ledge moderately elevated above median plate, distal half cylindrical, weakly sigmoid, tapering and pointing away from the truncus; median plate short, widely rounded, with a distinct pair of lateral teeth; stylus slender, base bulbous, apex with a small pair of subterminal ventral teeth.

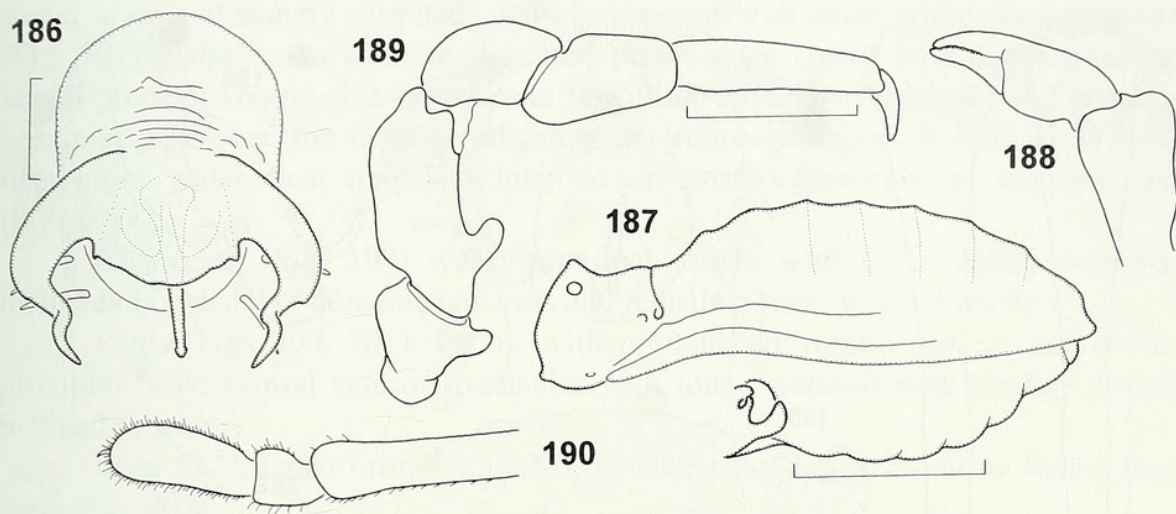
♀. Unknown.

Measurements: (♂): Body 6.00 long, 3.98 wide; carapace region 1.23 long, 2.16 wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.79	1.13	0.89	0.59	-	1.13	4.53
Leg I	0.64	2.02	1.08	1.18	1.82	0.84	7.58
Leg II	0.74	2.66	1.38	1.82	2.61	1.28	10.49
Leg III	0.69	2.02	1.08	1.28	2.21	0.84	8.12
Leg IV	0.79	2.56	1.38	1.87	3.35	0.93	10.88

Relationships: *Gnomulus carinatus* sp. n. appears most closely related to *G. thorelli* (♂ unknown). These are the only two *Gnomulus* species known at present, which possess a ventral process distinctly remote from the base of the palpal femur. Regarding penis morphology, most congruence is seen between *G. carinatus* sp. n. and *G. armillatus*.

Remark: *Gnomulus carinatus* sp. n. could be the conspecific male to the female syntypes of *G. thorelli*, since most differences between them correspond with sexual dimorphism found in other *Gnomulus* species. However, a wide geographic



FIGS 186-190

Gnomulus carinatus sp. n., ♂ holotype. - Glans penis, dorsal view (186). Body, lateral view (187); left chelicera, retrolateral view (188); right palp, retrolateral view (189); distal part of left leg II, retrolateral view (190). - Scale lines 0.1 mm (186), 1.0 mm (others).

separation and the presence of keeled dorsal scutal elevations in *G. carinatus* sp. n. (rarely seen in *Gnomulus*) indicate distinctiveness.

Distribution: Known only from the type locality in southern Borneo [Fig. 1 (22)].

THE *HAMATUS*-GROUP (new)

Diagnosis: Medium-sized (5.1-5.3 mm) species with rounded eye tubercle and without carapace-abdomen bridge; posterior margin of stigmatic pit without tubercle; ventral side of palpal trochanter with slightly distad-directed, spatulate process. Penis subdistally widened; glans with an extensive membraneous socket; lateral sclerites distally truncate; median plate long, very narrow, turned upwards; stylus with a bulbous base and with a pair of subterminal teeth.

Species account and distribution: Only a single species, *G. hamatus* sp. n., from Luzon, the Philippines.

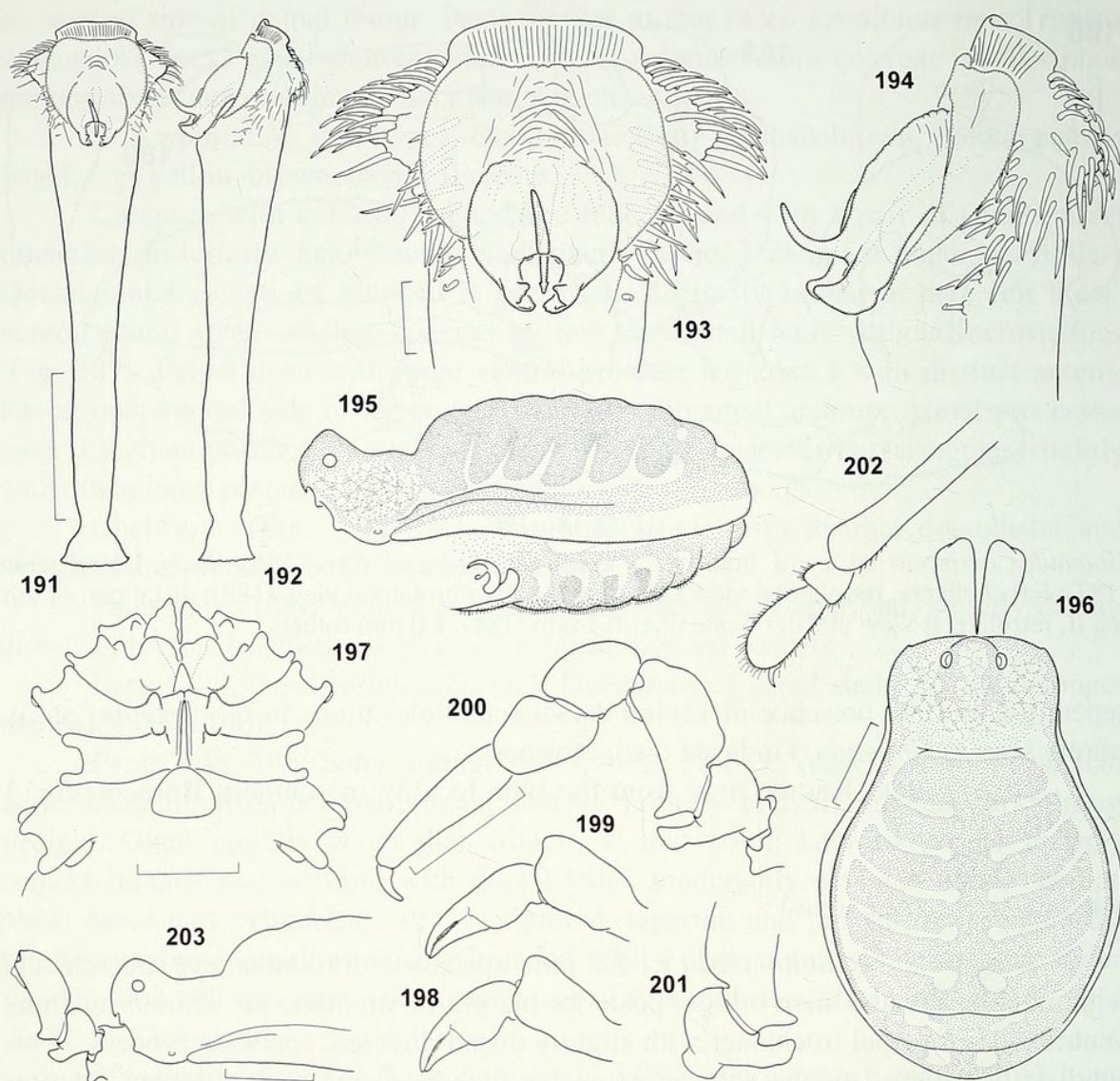
Gnomulus hamatus sp. n.

Figs 191-203

Material: PHILIPPINES, Luzon, Lagunas, Mt. Banahaw, above Kinabuhayan, trail to Crystalino, 600-700 m, ♂ holotype, 24.XI.1995. - Mt. Makiling, south of Los Baños, near Mad Springs, 400-450 m, ♀ paratype, 19.XI.1995; leg. I. Löbl (both in MHNG).

Etymology: Latin: *hamatus* = furnished with a hook. The specific epithet refers to the upturned, hook-like median plate of the glans penis.

Diagnosis: Externally similar to *G. minor* (♂ unknown), distinguished by: Body larger; interocular area elevated; dorsal and ventral scutal areas higher; ventral processes on palpal femur and trochanter longer. Distinguished from all other *Gnomulus* species by a stout, subdistally very wide penis; its glans with a large membraneous base and an upturned, hook-like median plate.



FIGS 191-203

Gnomulus hamatus sp. n., ♂ holotype (191-197, 199-202), ♀ paratype (198, 203). - Penis, dorsal (191) and lateral view (192); apex of penis, dorsal (193) and lateral view (194). Body, lateral (195) and dorsal view (196); anterior body, ventral view (197); left chelicera, retrolateral view (198, 199); left palp, retrolateral view (200); proximal part of right palp, retrolateral view (201); distal part of left leg II, retrolateral view (202); anterior body and proximal palp, lateral view (203). - Scale lines 0.1 mm (193, 194), 0.5 mm (191, 192), 1.0 mm (others).

Description: ♂ (holotype). Coloration: Dorsal scutum amber, with dark reticulation in carapace region, dark margin and dark, medially interconnected, transverse bands (Figs 195, 196); central portion of each ventral scutal elevation somewhat pallid. Legs dark amber, except for light amber tarsalia (with darkened dorsal sides on tarsi I, III and IV).

Carapace with widely conical, distally rounded eye tubercle; no lateral tubercles in posterior portion; carapace-abdomen bridge absent. Dorsal scutal areas moderately elevated, the first one rising steeply behind the carapace region; ventral

scutal areas indistinctly elevated, densely covered with short white truncate hairs (Fig. 195). Palpal coxa with small ventral process; leg coxa I with distinct antero-lateral process; ventral side of leg coxa II with distinct anteroproximal and postero-proximal processes, the latter overlapping anteroproximal one on coxa II. Genital operculum wider than long; no tubercle on posterior margin of stigmatic pit (Fig. 197).

Chelicerae (Fig. 199) weak, proximal article with low, slightly forward-inclined dorsodistal to dorsomedian boss and indistinct retroventral tubercle.

Palps (Figs 200, 201): Femur with pronounced ventral process and dorso-proximal boss; ventral side of trochanter with long, spade-shaped, slightly distad-inclined process.

Legs 1324, tarsal formula 2-2-3-3. Distitarsus of leg II 2.1 times longer than wide (Fig. 202).

Penis (Figs 191-194): Truncus stout; apex with wide subterminal lateral lobes carrying plenty of setae; distal margin broadly arched. Glans narrower than truncus at that point; membraneous socket very large, shaped like a plate; lateral sclerites short, with broadly truncate tips close to each other; median plate narrow, hook-like, pointing away from the truncus and slightly distad; membraneous tubes mostly covered by basal part of median plate; stylus slender, base bulbous, apex with a small pair of subterminal ventral teeth.

♀. As the male but palp with shorter ventral processes on femur and trochanter, proximodorsal boss on palpal femur less distinct (Fig. 203); ventral scutal areas darker and less elevated, covered with fewer hairs.

Measurements: ♂ (♀ in parentheses): Body 5.09 (5.29) long, 3.46 (3.66) wide; carapace region 1.28 (1.24) long, 1.95 (1.90) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.67 (0.59)	0.94 (0.89)	0.74 (0.69)	0.54 (0.49)	- -	1.24 (1.24)	4.13 (3.90)
Leg I	0.52 (0.49)	1.48 (1.53)	0.79 (0.74)	0.86 (0.84)	1.38 (1.33)	0.84 (0.77)	5.87 (5.70)
Leg II	0.67 (0.69)	1.95 (1.98)	1.03 (1.01)	1.33 (1.33)	2.07 (2.07)	0.99 (0.94)	8.04 (8.02)
Leg III	0.59 (0.54)	1.46 (1.46)	0.84 (0.79)	0.91 (0.89)	1.70 (1.68)	0.62 (0.62)	6.12 (5.98)
Leg IV	0.74 (0.74)	2.15 (2.10)	1.09 (1.09)	1.48 (1.46)	2.67 (2.52)	0.74 (0.74)	8.87 (8.65)

Relationships: In the shape of the stylus, in the slightly distad-inclined ventral process on palpal trochanter and in medium body size, *G. hamatus* sp. n. corresponds with species of the *armillatus*-group. The lack of a carapace-abdomen bridge and the presence of aberrant modifications of the penis, however, indicate that this species is closer to the *goodnighti*-group.

Distribution: Known from two mountains near San Pablo City in central Luzon [Fig. 1 (34, 35)].

THE *TUMIDIFRONS*-GROUP (new)

Diagnosis: Small (3.4-4.0 mm) species with relatively large eyes, without a carapace-abdomen bridge and with a distad-directed proximal process on ventral side of palpal trochanter; dorsal scutal elevations lighter in colour than areas in between them; posterior margin of stigmatic pit without tubercle. Truncus penis with circular

wrinkles in basal portion; glans with long, golfclub-shaped membraneous tubes protruding from under a narrow, pointed median plate; stylus strong, with a seemingly bulbous base and without subterminal ventral teeth.

Species account and distribution: This group is close to the *goodnighti*-group and it comprises two species, *G. tumidifrons* sp. n. and *G. matabesar* sp. n., from the Moluccas.

***Gnomulus tumidifrons* sp. n.**

Figs 204-216

Material: INDONESIA, Moluccas, Halmahera, Buli, Maba, 20 m, ♂ holotype, 3 ♀ paratypes, 6.-7.XI.1999; leg. A. Riedel (1 ♀ paratype in MAR, others in MHNG).

Etymology: Latin: *tumidus* = swollen, *frons* = forehead; noun in apposition. The specific epithet refers to the characteristic frontal hump on the eye tubercle of this species.

Diagnosis: Similar to *G. coniceps*, distinguished by: Eyes larger; interocular tubercle smaller, with a distinct hump on frontal side; carapace-abdomen bridge absent; dorsal scutal areas light, less elevated; penis with narrower apex; lateral sclerites of glans wider in distal portion, not covering long, golfclub-shaped membraneous tubes.

Description: ♂ (holotype). Coloration: Body light amber, with dark reticulation in carapace region and dark pattern on dorsal and ventral scuta; dorsal scutal elevations light, separated by dark transversal bands and by a dark longitudinal median stripe; ventral scutal elevations I-V pallid (Fig. 216a-c). Chelicerae, pedipalps and leg coxae and trochanters light yellow-brown; other leg segments mostly darkened, except for light amber tarsi and distal portions of tibiae and metatarsi; distitarsus I ventrally cream.

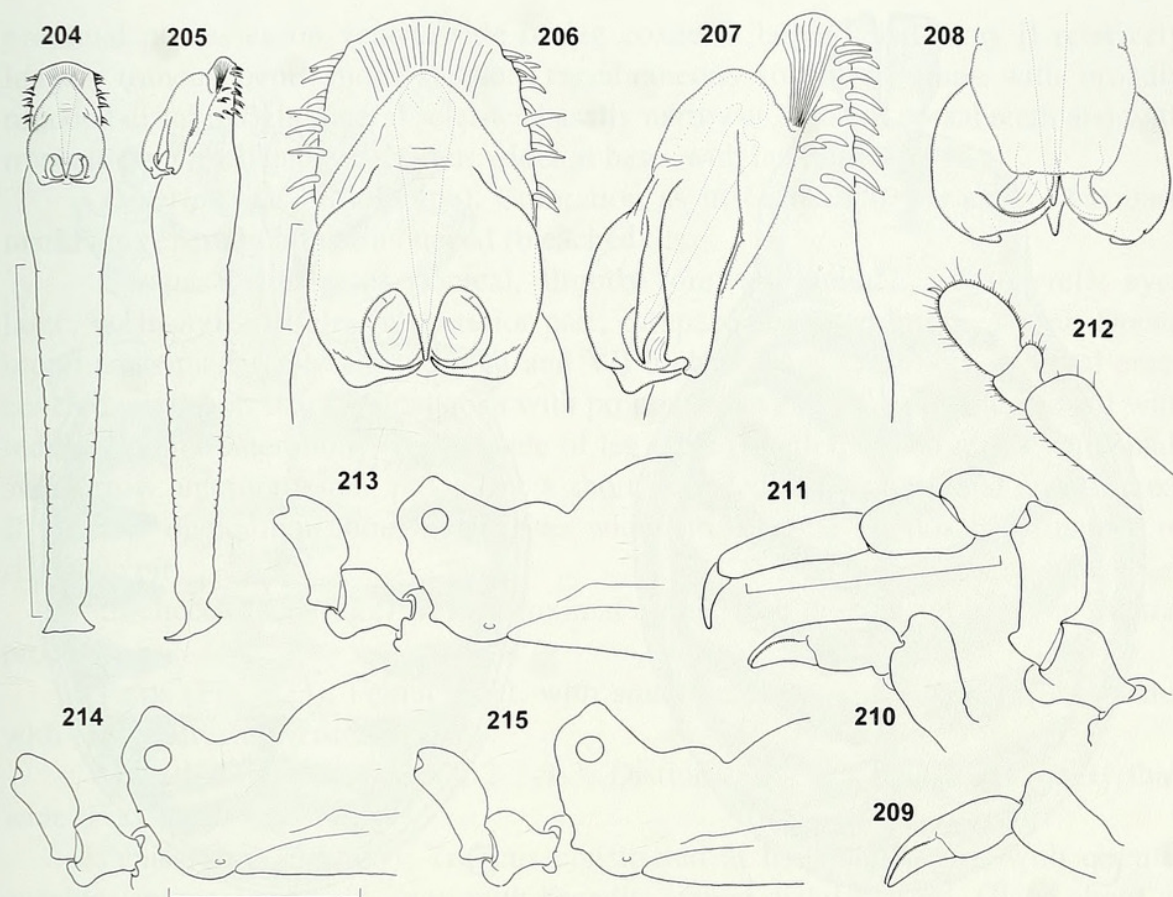
Carapace with small conical eye tubercle bearing a hump on its front side; eyes large; no lateral tubercles on posterior carapace; carapace-abdomen bridge absent. Dorsal scutal areas moderately elevated, VI and VII most strongly so; ventral scutal areas indistinctly swollen (Fig. 216a, c) and covered with short hairs. Palpal coxa with strong ventral process; leg coxa I with indistinct anterolateral one; ventral side of leg coxae II and III with small anteroproximal processes, indistinct posteroproximal one on coxa II. Genital operculum about as long as wide; no tubercle on posterior margin of stigmatic pit (Fig. 216b).

Chelicerae (Fig. 210) weak, proximal article with distinct dorsodistal and indistinct dorsomedian boss; no ventral process.

Palps (Fig. 211): Femur stout, ventral side with small proximal process; trochanter with distad-directed ventral process.

Legs 1324, tarsal formula 2-2-3-3. Distitarsus of leg II 1.6 times longer than wide (Fig. 212).

Penis (Figs 204-208): Truncus fairly stout, widest below glans, slightly constricted at height of glans, with circular wrinkles in proximal part; distal margin broadly arched. Glans slightly wider than truncus at that point; membraneous socket distally pointed; lateral sclerites massiv and convex, proximal portion wide, with a strong dorsal tooth on each side; tips of lateral sclerites fang-like, pointing towards each other; median plate long, narrowly triangular; membraneous tubes long, golf-



FIGS 204-215

Gnomulus tumidifrons sp. n., ♂ holotype (204-208, 210-212), ♀ paratypes (209, 213-215). - Penis, dorsal (204) and lateral view (205); apex of penis, dorsal (206) and lateral view (207); glans penis, ventral view (208). Left chelicera, retrolateral view (209, 210); left palp, retrolateral view (211); distal part of left leg II, retrolateral view (212); anterior body and proximal palp, lateral view (213-215). - Scale lines 0.1 mm (206, 207), 1.0 mm (others).

club-shaped, clearly visible in between median plate and lateral sclerites; stylus strong, fairly wide at bulbous base, tip pointed, without subterminal ventral teeth, completely covered by the median plate.

♀. As the male, apart from very slightly less pallid ventral scutal elevations.

Measurements: ♂ (♀ in parentheses): Body 3.42 (3.34) long, 2.28 (2.25) wide; carapace region 0.90 (0.83) long, 1.20 (1.18) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.45 (0.40)	0.49 (0.47)	0.41 (0.38)	0.28 (0.27)	--	0.57 (0.57)	2.20 (2.09)
Leg I	0.35 (0.32)	0.82 (0.81)	0.47 (0.45)	0.47 (0.45)	0.69 (0.68)	0.46 (0.47)	3.26 (3.18)
Leg II	0.41 (0.40)	1.04 (1.04)	0.63 (0.60)	0.72 (0.69)	1.07 (1.07)	0.54 (0.56)	4.41 (4.36)
Leg III	0.35 (0.33)	0.72 (0.72)	0.50 (0.50)	0.49 (0.48)	0.87 (0.84)	0.39 (0.40)	3.32 (3.27)
Leg IV	0.47 (0.45)	1.01 (0.99)	0.66 (0.66)	0.79 (0.77)	1.28 (1.26)	0.44 (0.42)	4.65 (4.55)

Variation: Range of measurements in ♀ ♀ (n= 3): Body 3.34-3.70 long, 2.25-2.33 wide, carapace region 0.83-0.90 long, 1.18-1.23 wide.

Relationships: This species is most closely related to *G. matabesar* sp. n.

Distribution and bionomics: Known only from the type locality in the eastern region of Halmahera Island [Fig. 1 (39)]. The animals were collected by sifting leaf litter in a disturbed primary rain forest.

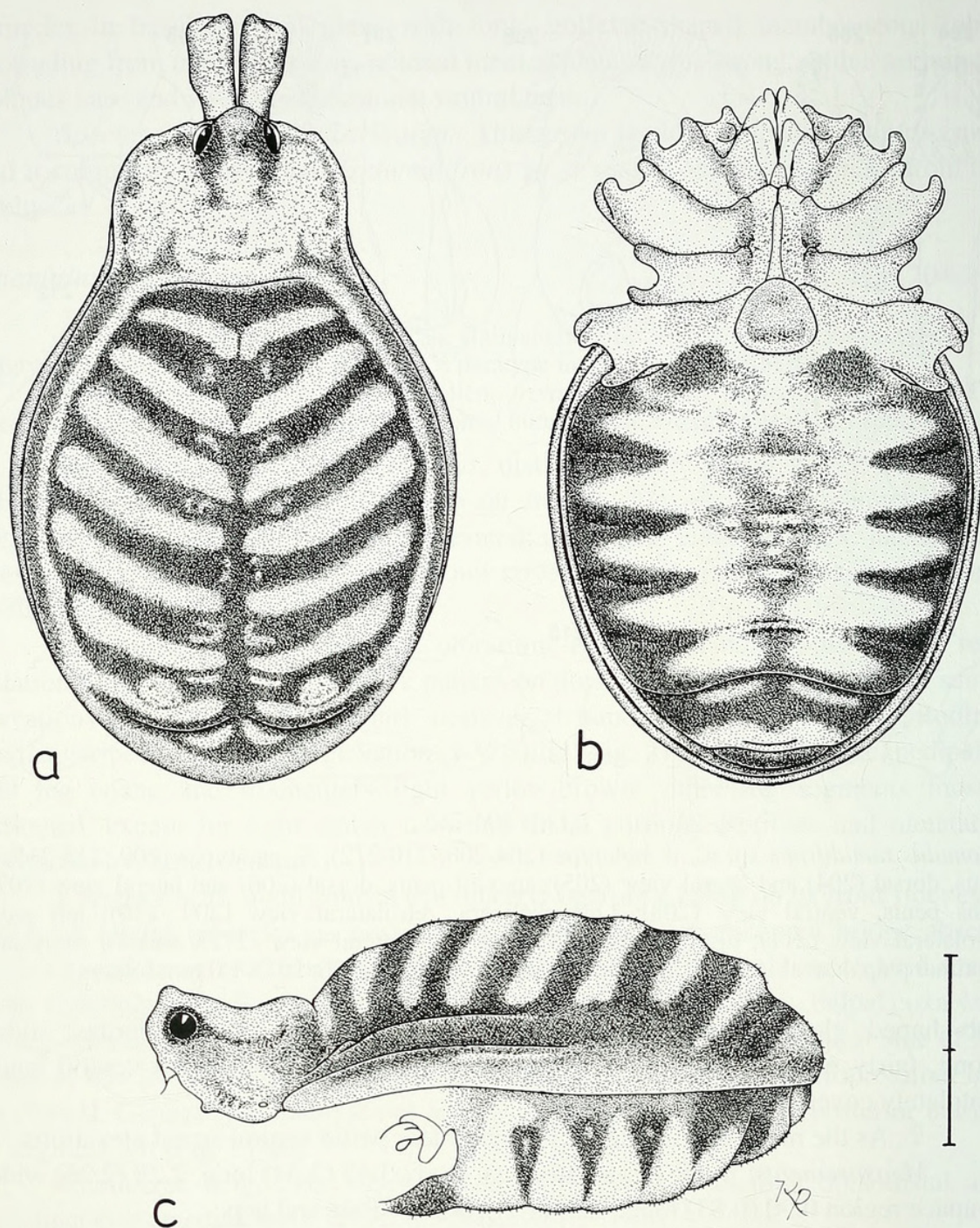


FIG. 216

Gnomulus tumidifrons sp. n., ♂ holotype. - Body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1.0 mm.

***Gnomulus matabesar* sp. n.**

Figs 217-224

Material: INDONESIA, Moluccas, Halmahera, mountains SW of Tobelo, 850 m, ♂ holotype, 2 juv., 1.XI.1999; leg. A. Riedel (MHNG).

Etymology: Malay and Indonesian: *mata* = eye, *besar* = big; noun in apposition. The specific epithet refers to the unusually large eyes of this species.

Diagnosis: Closely related to *G. tumidifrons* sp. n., distinguished by: Eye tubercle without frontal hump; colour pattern on dorsal scutum less marked; antero-

proximal processes on ventral side of leg coxae II larger; distitarsus II relatively longer; truncus penis more slender; membranous socket of glans with broadly rounded distal margin; lateral sclerites basally narrower, without dorsal teeth and with truncate tips; median plate shorter, wider at base, with lateral teeth.

Description: ♂ (holotype). Coloration as in *G. tumidifrons* sp. n., but dark markings generally less pronounced (bleached?).

Carapace with stout, conical, slightly forward-inclined eye tubercle; eyes large; no lateral tubercles in posterior part; carapace-abdomen bridge absent. Dorsal scutal areas moderately elevated, VI and VII highest (Fig. 221); ventral scutal areas covered with short hairs. Palpal coxa with pronounced ventral process; leg coxa I with indistinct anterolateral one; ventral side of leg coxa II with quite large, III with small and narrow anteroproximal processes, a short, rounded posteroproximal one on coxa II. Genital operculum about as long as wide; no tubercle on posterior margin of stigmatic pit.

Chelicerae (Fig. 222) weak, proximal article with dorsodistal boss; no ventral process.

Palps (Fig. 223): Femur stout, with small ventroproximal process; trochanter with distad-directed ventral process.

Legs 1324, tarsal formula 2-2-3-3. Distitarsus of leg II 2 times longer than wide (Fig. 224).

Penis (Figs 217-220): Truncus constricted at height of glans, with circular wrinkles in proximal half; apex with broadly arched distal margin. Glans about as wide as truncus at that point, its membranous socket widely rounded distally; lateral sclerites short, their broadly rounded tips covering lateral parts of long, golfclub-shaped membranous tubes; median plate short, its distal part narrowly triangular, its base wide, with distinct lateral teeth; stylus fairly strong, base seemingly bulbous, tip pointed, without subterminal teeth, completely covered by the median plate.

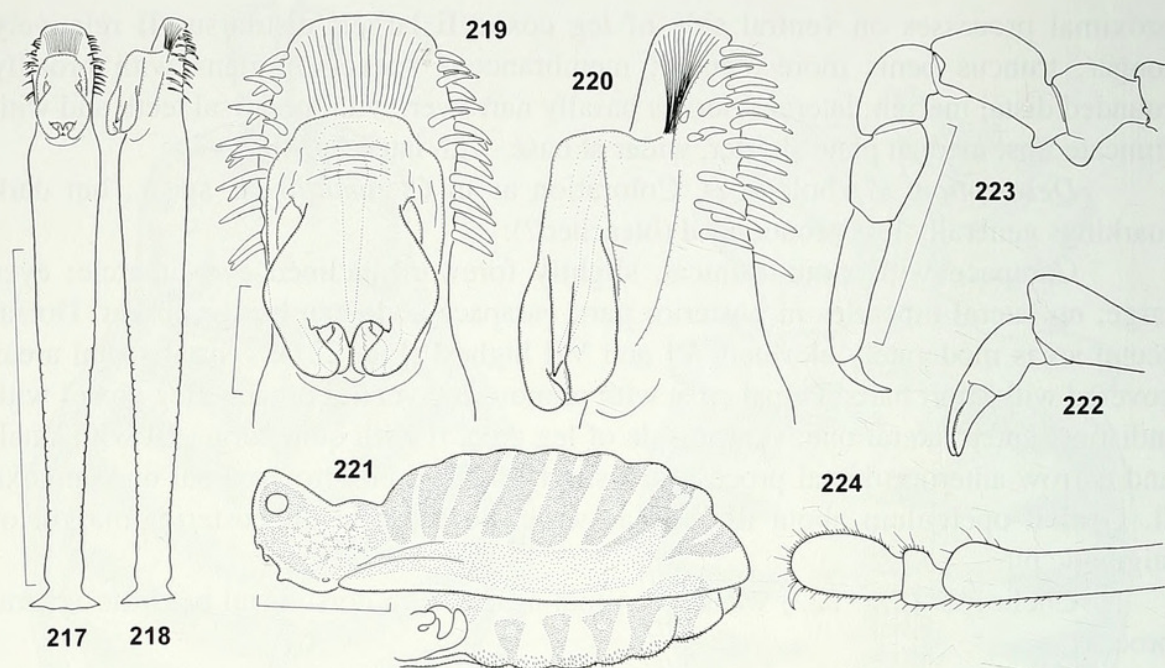
♀. Unknown.

Measurements: ♂: Body 3.59 long, 2.35 wide; carapace region 0.93 long, 1.29 wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.55	0.58	0.46	0.32	-	0.64	2.55
Leg I	0.37	0.97	0.55	0.55	0.86	0.55	3.85
Leg II	0.47	1.24	0.72	0.89	1.39	0.67	5.38
Leg III	0.42	0.84	0.56	0.58	1.08	0.47	3.95
Leg IV	0.52	1.19	0.72	0.95	1.55	0.52	5.45

Remarks: The juveniles examined possess a high, conical, but not forward-inclined eye tubercle.

Relationships: *Gnomulus matabesar* sp. n. and *G. tumidifrons* sp. n. are closest relatives. Small body size, a distad-directed ventral process on palpal trochanter and modifications of membranous tubes and stylus indicate phylogenetic proximity to the *goodnighti*-group from the Philippines. The shape of the membranous tubes also points to a fairly close relationship with *G. latoperculum* sp. n. from Sulawesi.



FIGS 217-224

Gnomulus matabesar sp. n., ♂ holotype. - Penis, dorsal (217) and lateral view (218); apex of penis, dorsal (219) and lateral view (220). Body, lateral view (221); left chelicera, retrolateral view (222); left palp, retrolateral view (223); distal part of left leg II, retrolateral view (224). - Scale lines 0.1 mm (219, 220), 1.0 mm (others).

Distribution: Known only from the type locality in the northern part of Halmahera Island [Fig. 1 (38)].

THE LATOPERCULUM-GROUP (new)

Diagnosis: Large (5.7-6.7 mm) species with a wide, undivided carapace-abdomen bridge and with a slightly distad-inclined process on ventral side of palpal trochanter; posterior margin of stigmatic pit with tubercle; genital operculum very wide; penis scoop-shaped, carrying an enlarged pointed stylus with an invaginated base and without subterminal ventral teeth.

Species account and distribution: At present, this group is represented only by *G. latoperculum* sp. n. from northern Sulawesi.

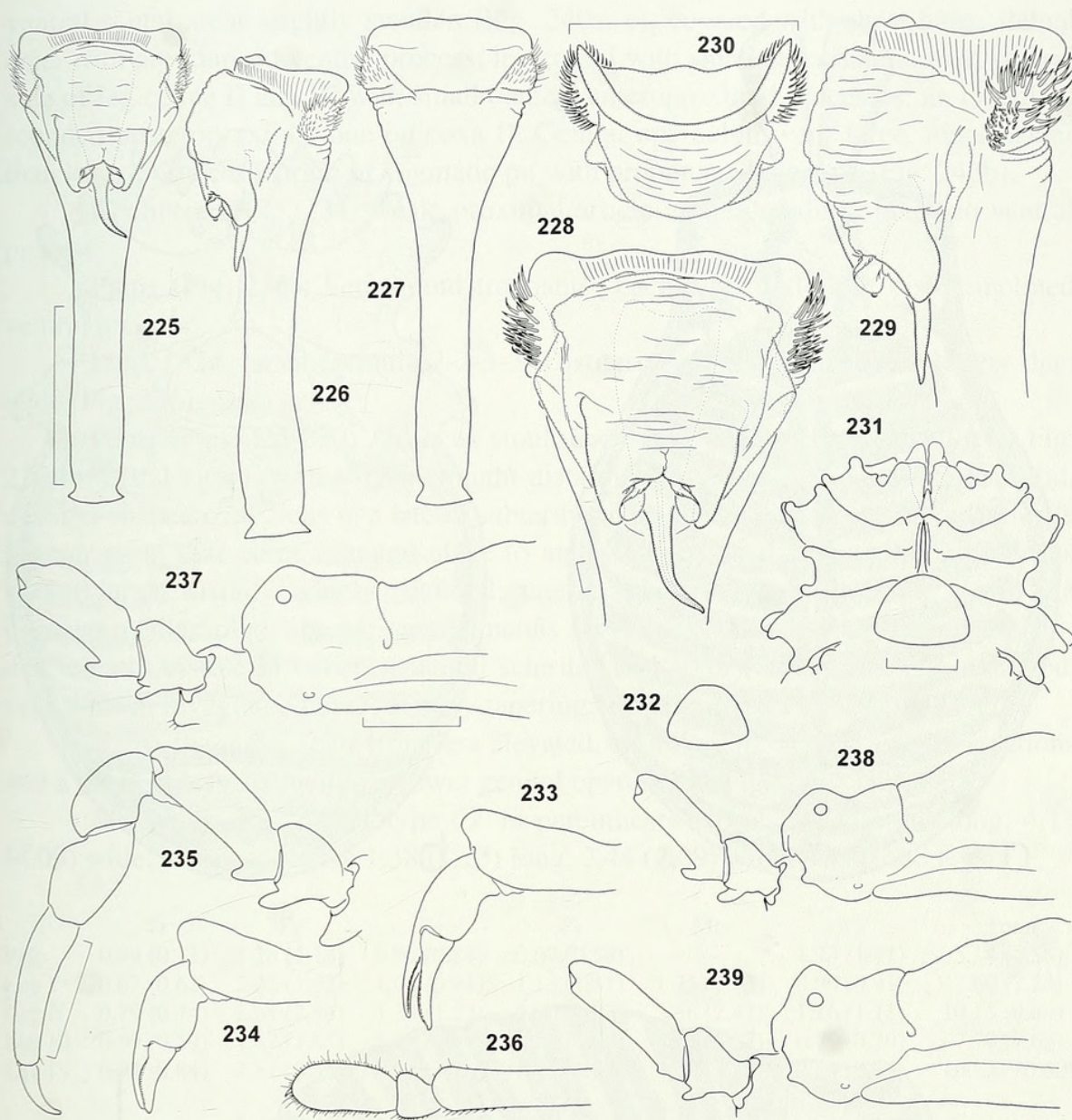
Gnomulus latoperculum sp. n.

Figs 225-240

Material: INDONESIA, Sulawesi, Northern Sulawesi Province, Dumoga - Bone National Park, ♂ holotype, ♂ paratype (penis not examined), 2 juv., XI.1985, leg. P. D. Hillyard (Project Wallace Expedition; NHML). - Same province, Kotamobagu, Matalibaru, Gunung Tongara, 800-900 m, 2 ♀ paratypes, 5.-9.XII.1999, leg. A. Riedel (MHNG).

Etymology: Latin: *latus* = wide, extensive, *operculum* = cover, lid; noun in apposition. The specific epithet refers to the unusually wide genital operculum (especially in males) of this species.

Diagnosis: Similar to *G. claviger* sp. n., distinguished by: Body much larger; eye tubercle lower; carapace-abdomen bridge wider, undivided; genital operculum



FIGS 225-239

Gnomulus latoperculum sp. n., ♂ holotype (225-230, 237), ♂ paratype (234-236), ♀ paratypes (231-233, 238, 239). - Penis, dorsal (225), lateral (226) and ventral view (227); apex of penis, dorsal (228), lateral (229) and distal view (230). Anterior body, ventral view (231); genital operculum, ventral view (232). Left chelicera, retrolateral view (233, 234); left palp, retrolateral view (235); distal part of left leg II, retrolateral view (236); anterior body and proximal palp, lateral view (237-239). - Scale lines 0.1 mm (228, 229), 1.0 mm (others).

wider; truncus penis scoop-shaped; glans carrying lobate lateral sclerites and a basally thick, distally tapering stylus; median plate absent.

Description: ♂ (paratype). Coloration quite pale, light yellow-brown (newly moulted specimen). Dark reticulation in carapace region and dark pattern on dorsal and ventral scuta; dark transversal bands on dorsal scutal elevations broken by light, narrow, longitudinal stripe in areas I-VI; dorsal and ventral scutal elevations each with a pallid transversal band in its centre (Fig. 240a-c). Chelicerae and pedipalps

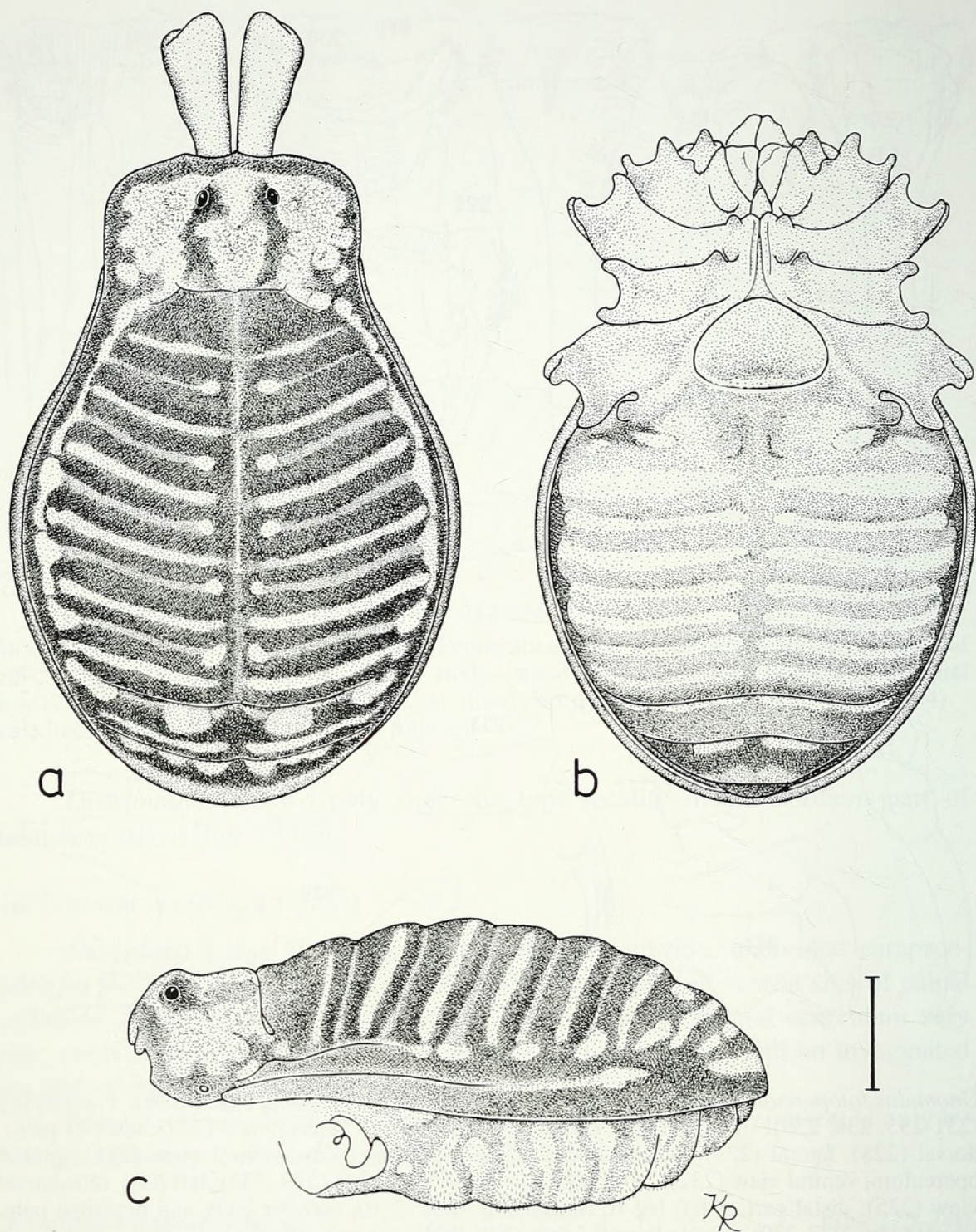


FIG. 240

Gnomulus latoperculum sp. n., ♂ paratype. - Body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1.0 mm.

with dark reticulation. Legs mostly dark, except for light distal portion on tibiae and light median zone on metatarsi of posterior legs and light tarsi on all legs.

Carapace with small, low, rounded eye tubercle; no lateral tubercles below wide, undivided carapace-abdomen bridge. Dorsal scutal areas moderately elevated;

ventral scutal areas slightly swollen (Fig. 240a, c), covered with short hairs. Palpal coxa with pronounced ventral process; leg coxa I with small anterolateral one; ventral side of leg coxae II and III with small conical anteroproximal processes, an indistinct rounded posteroproximal one on coxa II. Genital operculum very large, much wider than long; posterior margin of stigmatic pit with pronounced tubercle (Fig. 240b).

Chelicerae (Fig. 234) weak, proximal article with dorsodistal boss; no ventral process.

Palps (Fig. 235): Femur and trochanter each with a slightly distad-inclined ventral process.

Legs 1324, tarsal formula 2-2-3-3. Distitarsus of leg II 2.3 times longer than wide (Fig. 236).

Penis (Figs 225-230): Truncus stout, apex very wide, scoop-shaped (see Fig. 230 for distal view), with almost straight distal margin; setae restricted to two pallid, cushion-shaped oval areas in a lateral subterminal position. Glans large, about as wide as truncus at that point, situated close to anterior margin of truncus; membraneous socket large, distally widely rounded; lateral sclerites lobate, pointing down the truncus; median plate absent; membraneous tubes long, distally flat, wide and rounded, clearly visible in between lateral sclerites and stylus; stylus strongly enlarged, very wide at invaginated base, distally tapering, without ventral subterminal teeth.

♀. As the male, apart from less elevated, entirely dark ventral scutal elevations and a more or less distinctly narrower genital operculum (Figs 231, 232).

Measurements: ♂ holotype (♀ in parentheses): Body 6.21 (6.36) long, 4.12 (4.09) wide; carapace region 1.38 (1.23) long, 2.44 (2.29) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.89 (0.71)	1.26 (1.13)	0.99 (0.84)	0.67 (0.59)	- -	1.33 (1.31)	5.14 (4.58)
Leg I	0.67 (0.62)	2.02 (1.92)	1.04 (0.94)	1.13 (1.11)	1.75 (1.73)	0.99 (0.91)	7.60 (7.23)
Leg II	0.79 (0.74)	2.61 (2.54)	1.33 (1.23)	1.70 (1.75)	2.56 (2.47)	1.16 (1.11)	10.15 (9.84)
Leg III	0.69 (0.59)	1.87 (1.85)	1.06 (0.99)	1.26 (1.23)	2.12 (2.17)	0.79 (0.79)	7.79 (7.62)
Leg IV	0.94 (0.84)	2.51 (2.54)	1.33 (1.26)	1.85 (1.87)	3.20 (3.20)	0.89 (0.89)	10.72 (10.60)

Variation: Range of measurements in ♂♂ (n= 2) and ♀♀ (n=2; in parentheses): Body 5.74-6.21 (6.36-6.68) long; 3.99-4.12 (4.09-4.51) wide, carapace region 1.26-1.38 (1.23-1.48) long, 2.29-2.44 (2.29-2.56) wide. The ♂ paratype has distinct pale transversal bands in the central zones of its dark dorsal scutal elevations (Fig. 240a). This is not observable in the holotype, where the underlying pigmentation is partly detached from the cuticle (due to preservation?). One ♀ has a distinctly higher eye tubercle and smaller ventral processes on palpal femur and trochanter (Fig. 239). Variation in the size of the genital operculum, see Figs 231, 232, 240b.

Relationships: The relationships of *G. latoperculum* sp. n. are unclear. Judging from penis morphology it appears most closely related to the *goodnighti*-species group.

Distribution: Known only from two localities (close to each other) in northern Sulawesi [Fig. 1 (41)]. The ♀ paratypes were collected by sifting leaf litter in a selectively logged primary rain forest.

THE *GOODNIGHTI*-GROUP (see Schwendinger & Martens, 1999b: 974)

Diagnosis: Small (1.9-3.8 mm) species, additionally characterized by: Ventral process on palpal trochanter distinctly distad-directed; posterior margin of stigmatic pit without tubercle; carapace-abdomen bridge absent (*G. crucifer*, *G. minor*, *G. crassipes* sp. n.) or present (all others); glans penis usually with quite long membranous tubes; stylus enlarged (often strongly modified), if slender, then without ventral pair of subterminal teeth (*G. coniceps*, *G. imadatei*?); base of stylus bulbous (*G. coniceps*, *G. goodnighti* and *G. crassipes* sp. n.) or invaginated (all others).

Species account and distribution: Nine species: One from Brunei [*G. imadatei* (Suzuki)] and eight from the Philippines [*G. claviger* sp. n., *G. coniceps* Martens & Schwendinger, *G. crassipes* sp. n., *G. crucifer* Martens & Schwendinger, *G. goodnighti* (Suzuki), *G. leyteensis* Martens & Schwendinger, *G. maculatus* Martens & Schwendinger, *G. minor* Tsurusaki (male unknown - assignment uncertain)].

***Gnomulus claviger* sp. n.**

Figs 241-255

Material: PHILIPPINES, Luzon, Mt. Banahaw, above Kinabuhayan, trail to Cristalino, 600-700 m, ♂ holotype, 24.XI.1995, leg. I. Löbl (MHNG). - Los Baños, Mt. Makiling (= Mt. Maquiling), 2 ♂ paratypes, XI.1968 and 5.V.1968, leg. R. A. Morse (AMNH).

Etymology: Latin: *clava* = club, cudgel; *ger* (suffix derived from *gerere*) = furnished with. The specific epithet refers to the club-shaped penis of this species.

Diagnosis: Close to *G. maculatus*, distinguished by: Colour pattern different; ventroproximal process on palpal femur larger; penis stouter, distally wider, with membranous socket extending beyond apex of truncus; sclerites of glans, especially stylus, different in shape.

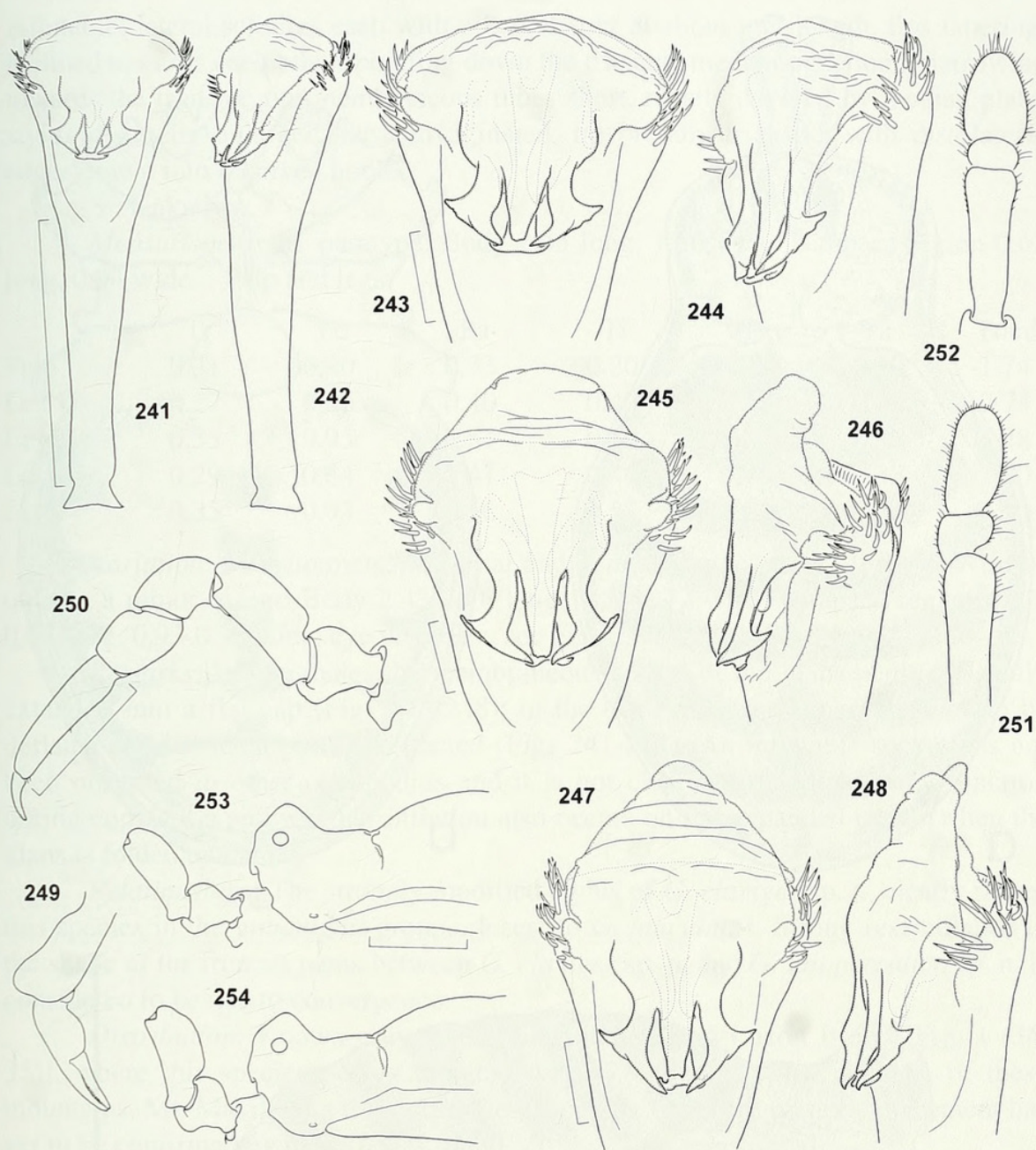
Description: ♂ (paratype). Coloration: Body amber, with dark reticulation in carapace region and dark margin and transversal bands on dorsal scutum (cf. Fig. 255a, c); dark transversal bands on ventral scutum less distinct (median portion most clearly pronounced). Genital operculum light throughout (cf. Fig. 255b). Chelicerae and pedipalps with dark reticulation, except for light yellow-brown hand and tarsus, respectively. Legs mostly darkened, except for light tarsi and light distal portion on tibiae and metatarsi.

Carapace with low, widely conical, terminally rounded eye tubercle bearing a small hump on its front side; no lateral tubercles in posterior part; carapace-abdomen bridge formed by two opposing pairs of tubercles. Dorsal scutal areas only indistinctly elevated; ventral scutal areas with few fine hairs, not recognizably modified (cf. Fig. 255a, c). Palpal coxa with strong ventral process; leg coxa I with indistinct anterolateral one; ventral side of leg coxae II and III with small conical anteroproximal processes, a knob-shaped posteroproximal one on coxa II. Genital operculum clearly wider than long; posterior margin of stigmatic pit without tubercle (Fig. 255b).

Chelicerae (Fig. 249) weak, proximal article with distinct dorsodistal and indistinct dorsomedian boss; no ventral process.

Palps (Fig. 250): Femur short, ventral side with small, ventrad-directed proximal process; trochanter with distad-directed ventral process.

Legs 1324, tarsal formula 2-2-3-3. Distitarsus II 2.1 times longer than wide



FIGS 241-254

Gnomulus claviger sp. n., ♂ holotype (245, 246, 254), ♂ paratypes (241-244, 247-253). - Penis, dorsal (241) and lateral view (242); apex of penis, dorsal (243, 245, 247) and lateral view (244, 246, 248). Left chelicera, retrolateral view (249); left palp, retrolateral view (250); distal part of left leg II, retrolateral view (251); distal part of left leg I, dorsal view (252). Anterior body and proximal palp, lateral view (253, 254). - Scale lines 0.1 mm (243-248), 0.5 mm (others).

(Fig. 251); distitarsus I somewhat egg-shaped, clearly wider than preceding leg segments (Fig. 252).

Penis (Figs 241-248; holotype: 245, 246): Truncus stout, strongly widening in distal half; apex very wide, with broadly arched distal margin. Glans very close to tip of truncus, slightly narrower than truncus at that point; membraneous socket distally

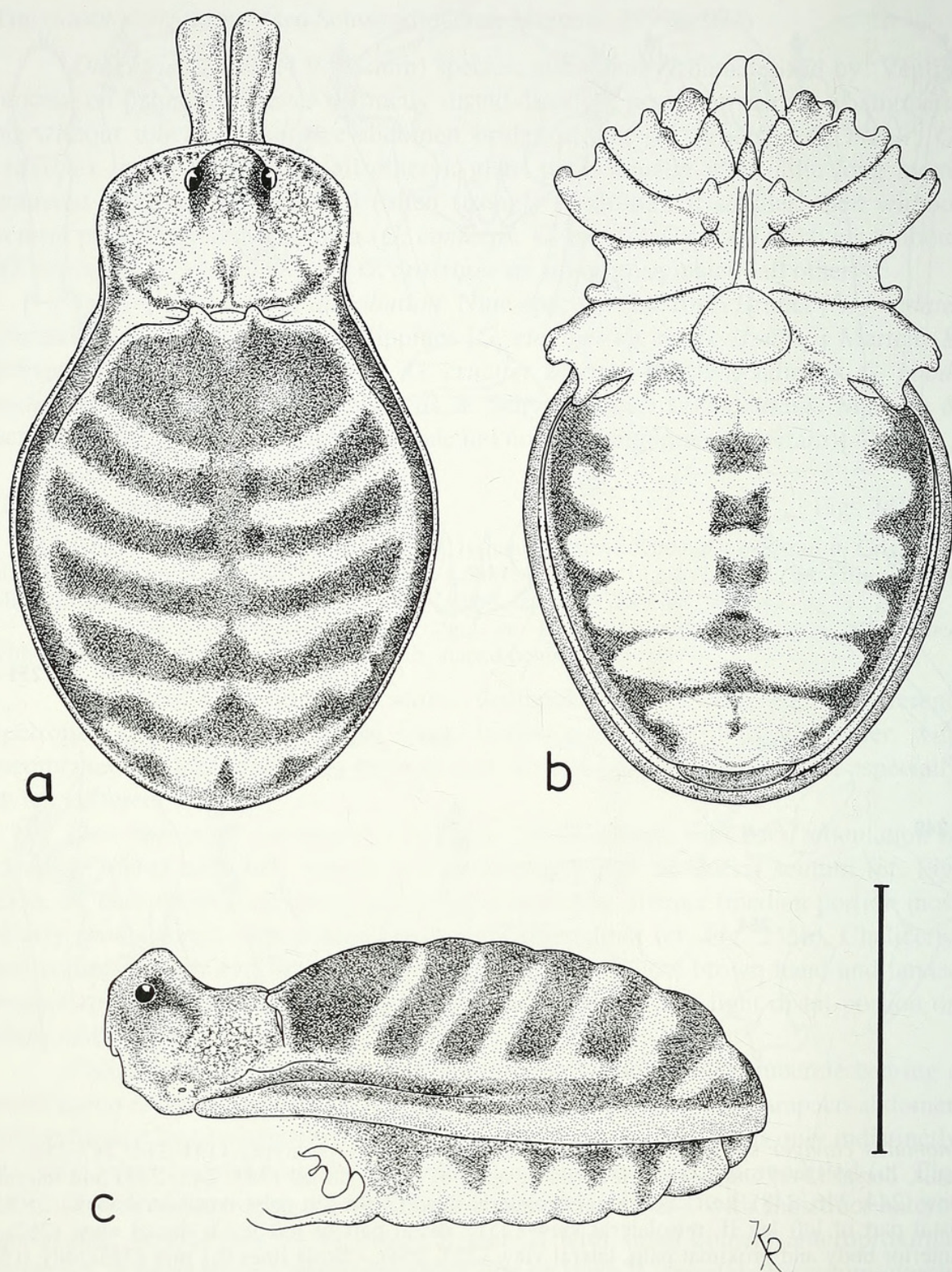


FIG. 255

Gnomulus claviger sp. n., ♂ paratype. - Body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1.0 mm.

inflatable; lateral sclerites each with a lateral spur at about mid-length, tips tapering, inclined towards each other, pointing down the truncus; median plate long, narrowing towards the truncate tip; membraneous tubes short, mostly covered by median plate; stylus distinctly enlarged, base invaginated, tip broadly truncate, with distolateral edges drawn into recurved hooks.

♀. Unknown.

Measurements: ♂ paratype: Body 2.45 long, 1.56 wide; carapace region 0.62 long, 0.94 wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.31	0.40	0.33	0.20	-	0.50	1.74
Leg I	0.27	0.68	0.40	0.40	0.57	0.42	2.74
Leg II	0.35	0.93	0.51	0.60	0.88	0.51	3.78
Leg III	0.29	0.64	0.41	0.40	0.73	0.33	2.80
Leg IV	0.35	0.93	0.56	0.68	1.01	0.37	3.90

Variation: Measurements, external and genital characters of all three ♂ differ only to a minor extent: Body 2.43-2.56 long, 1.56-1.72 wide, carapace region 0.62-0.64 long, 0.93-0.98 wide; eye tubercles, see Figs 253, 254, 255c.

Remarks: In two males the membraneous socket of the glans penis is distally extended into a flat cap (Figs 245-248); in the third male the socket appears to be deflated and its distal portion retracted (Figs 241-244). An inflatable socket has not been observed in other oncopodids and it is not clear whether it has any function during copulation and whether inflation also occurs on the expanded penis (when the glans is folded upwards).

Relationships: The strongly modified stylus of *G. claviger* sp. n. clearly places this species in the *goodnighti*-group, closest to *G. maculatus*. Strong resemblance in the shape of the truncus penis between *G. claviger* sp. n. and *G. latoperculum* sp. n. is considered to be due to convergence.

Distribution: Known only from two mountains on Luzon Island [Fig. 1 (34, 35)], where this species occurs together with *G. hamatus* sp. n. On one of these mountains, Mt. Makiling, a third congeneric species, *G. minor* (generic placement has yet to be confirmed by males), was found.

Gnomulus crassipes sp. n.

Figs 256-273

Material: PHILIPPINES, Luzon, Mt. Banahaw, near school, 500 m, about 1 km from Kinabuhayan, ♂ holotype, 2 ♂, 1 ♀ paratypes, 1 juv., 26.XI.1995; summit trail, 800 m, 1 ♂ paratype, 25.XI.1995; above Kinabuhayan, trail to Cristalino, 600-700 m, 3 ♀ paratypes, 24.XI.1995. All specimens leg. I. Löbl (1 ♂, 1 ♀ paratypes in MAR, others in MHNG).

Etymology: Latin: *crassus* = thick, stout, *pes* = leg; noun in apposition. The specific epithet refers to the incrassate metatarsus III of males in this species.

Diagnosis: Close to *G. crucifer* (also possessing the unusual tarsal formula 2-2-2-2), distinguished by: Body smaller; colour pattern different; ventroproximal process on palpal femur larger; truncus penis subdistally constricted; glans with longer lateral sclerites; stylus different in shape.

Description: ♂ (holotype). Coloration: Body light brown, with dark reticulation on carapace region, chelicerae and pedipalps; abdominal region of dorsal scutum amber, with dark margin and dark transversal bands (laterally more or less distinctly touching each other) on all areas (Fig. 273a, c); transversal bands on ventral scutum weakly pronounced (Fig. 273). Femora to metatarsi of legs darkened, tarsi light brown.

Carapace with very low, widely rounded eye tubercle; posterior portion of carapace elevated, slightly higher than eye tubercle; no lateral tubercles in posterior part; carapace-abdomen bridge absent. Dorsal scutal areas only indistinctly elevated, ventral scutal areas slightly more so, without hairs (Fig. 273a, c). Palpal coxa with pronounced ventral process; leg coxa I with indistinct anterolateral one; ventral side of leg coxae II and III with conical anteroproximal processes, a knob-shaped postero-proximal one on coxa II. Genital operculum wider than long; no tubercle on posterior margin of stigmatic pit (Fig. 273b).

Chelicerae (Fig. 266) weak, proximal article with slightly forward-inclined dorsodistal and indistinct dorsomedian boss; no ventral process.

Palps (Fig. 267): Femur short, with widely rounded ventroproximal process; trochanter with distad-directed ventral process.

Legs 3142, tarsal formula 2-2-2-2. Distitarsus II 1.2 times longer than wide (Fig. 268); metatarsus III recognizably inflated (Figs 269, 270).

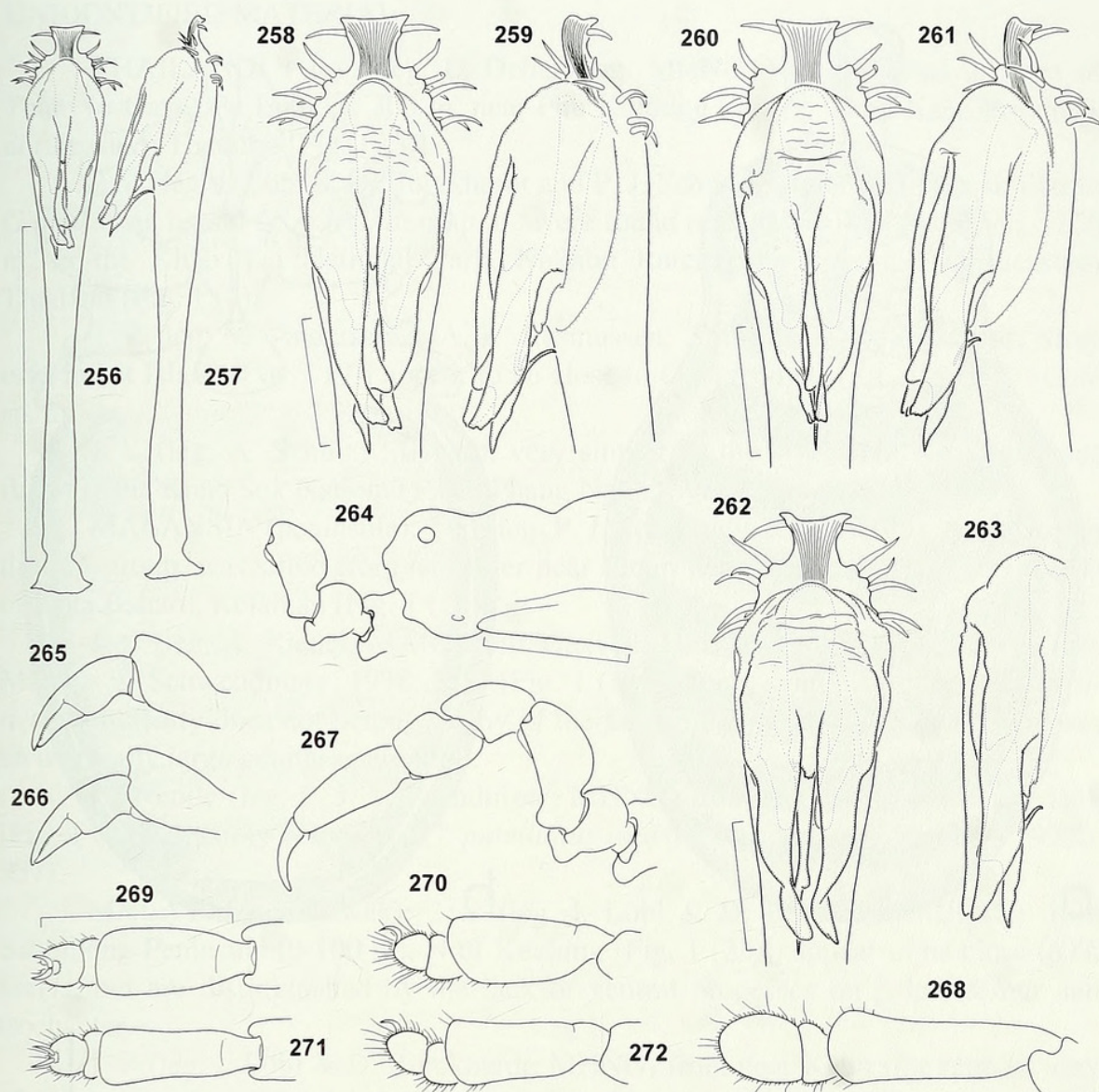
Penis (Figs 256-263; holotype: 260, 261): Truncus slender, strongly constricted below axe-shaped (in dorsal view) apex; distal margin almost straight; a pair of lateral setae situated above constriction, few other setae below it. Glans slightly wider than truncus at that point; membranous socket distally wide, rounded; lateral sclerites long, pointing down the truncus, their tips unevenly rounded; median plate short, pointed, mostly covered by lateral sclerites; membranous tubes long, covered by lateral sclerites; stylus enlarged, base bulbous, distal portion compressed at the sides, with a dorsal boss at some distance from the blade-shaped tip, sperm duct opening on the tip of a narrow medioventral spine pointing towards the truncus.

♀. As the male but metatarsus III not incrassate (Figs 271, 272).

Measurements: ♂ holotype (♀ in parentheses): Body 1.94 (2.09) long, 1.17 (1.26) wide; carapace region 0.56 (0.60) long, 0.70 (0.72) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.20 (0.21)	0.25 (0.25)	0.24 (0.24)	0.16 (0.16)	- -	0.32 (0.33)	1.17 (1.19)
Leg I	0.21 (0.21)	0.42 (0.44)	0.29 (0.30)	0.21 (0.22)	0.25 (0.36)	0.22 (0.23)	1.70 (1.76)
Leg II	0.24 (0.27)	0.54 (0.57)	0.36 (0.38)	0.31 (0.32)	0.54 (0.55)	0.27 (0.28)	2.26 (2.37)
Leg III	0.21 (0.21)	0.33 (0.35)	0.28 (0.29)	0.23 (0.23)	0.41 (0.41)	0.15 (0.15)	1.61 (1.64)
Leg IV	0.25 (0.27)	0.50 (0.52)	0.37 (0.39)	0.37 (0.39)	0.56 (0.58)	0.17 (0.17)	2.22 (2.31)

Variation: Range of measurements in ♂♂ (n = 4) and ♀♀ (n= 4; in parentheses): Body 1.90-1.98 (1.99-2.09) long, 1.13-1.20 (1.22-1.26) wide, carapace region 0.55-0.56 (0.56-0.60) long, 0.68-0.70 (0.72) wide. In some specimens the dark transversal bands on the dorsal scutum are broken by light, narrow longitudinal stripes in areas II and III; the ventral scutal bands are partly broken in some specimens. In one male the median plate of the glans penis is narrowly truncate instead of pointed (Fig. 262).



FIGS 256-272

Gnomulus crassipes sp. n., ♂ holotype (260, 261, 266, 267-270), ♂ paratypes (256-259, 262, 263), ♀ paratype (264, 271, 272). - Penis, dorsal (256) and lateral view (257); apex of penis, dorsal (258, 260, 262) and lateral view (259, 261); glans penis, lateral view (263). Left chelicera, retrolateral view (265, 266); left palp, retrolateral view (267); distal part of left leg II, retrolateral view (268); distal part of left leg III, dorsal (269, 271) and lateral view (270, 272). - Scale lines 0.1 mm (258-263), 0.5 mm (others).

Relationships: Modifications of the glans (especially of its stylus) and a distad-directed ventral process on the palpal trochanter place *G. crassipes* sp. n. in the *goodnighti*-group. Congruence in external morphology (tarsal formula 2-2-2-2, no carapace-abdomen bridge) and penis morphology (especially the reduction of the median plate) suggest closest relationship with *G. crucifer*.

Distribution: Known only from a mountain on Luzon Island [Fig. 1 (34)], where the new species occurs together with *G. claviger* sp. n. and *G. hamatus* sp. n.

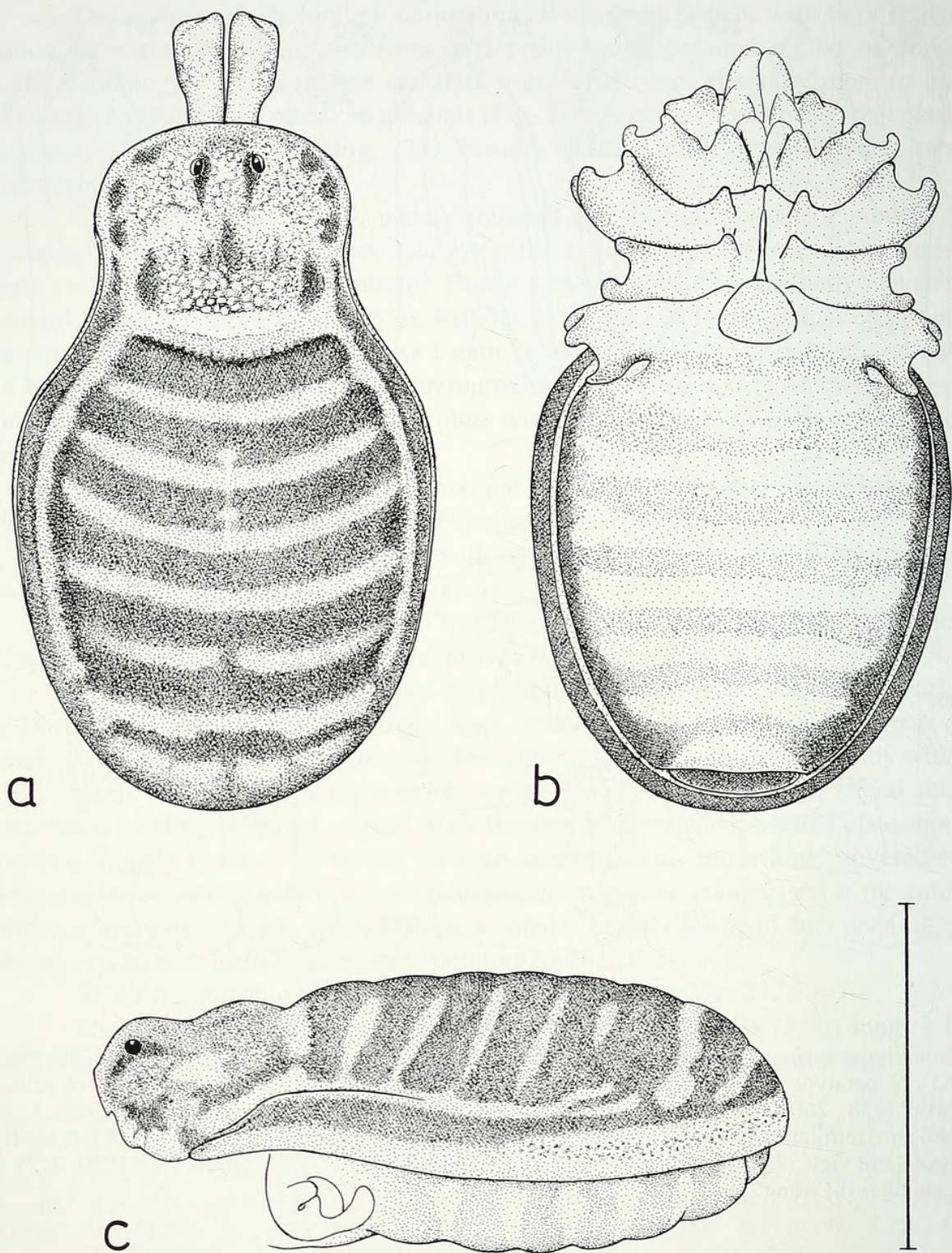


FIG. 273
Gnomulus crassipes sp. n., ♂ paratype. - Body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1.0 mm.

UNIDENTIFIED MATERIAL

THAILAND: 1 juv. (leg. L. Deharveng; MHNG) was collected in front of Tham (= Cave) Pu Lub, ca. 300 m, near Phu Kradung village, Khon Kaen Province, northeastern Thailand [Fig. 1 (3)].

2 ♀ (leg. I. Löbl & D. Burckhardt and P. J. Schwendinger; MHNG), similar to *G. ryssie* sp. n. and *G. marginatus* sp. n., were found on Khao (= Mount) Khieo, 1150 m, in the Khao Yai National Park, Nakhon Ratchasima Province, northeastern Thailand [Fig. 1 (4)].

4 ♀ (leg. M. Andersen & A. R. Rasmussen; ZMC) from Ko (= Island) Siray off Phuket Island [Fig. 1 (9)] appear to be close to *G. marginatus* sp. n. and *G. ryssie* sp. n.

1 ♀ (leg. A. Schulz; MHNG), very similar to the 4 ♀ from Ko Siray, was found in the Khao Sok National Park (Phang Nga Province; not indicated on Fig. 1).

MALAYSIA (peninsula): 1 ♀ (leg. P. J. Schwendinger; MHNG), belonging to the *asli*-group, was sifted from leaf litter near Jeram Pasu Waterfall, ca. 30 km south of Kota Baharu, Kelantan [Fig. 1 (10)].

1 ♀ (leg. A. Riedel; MAR) from Maxwell Hill, 1200 m, Taiping, Perak (see Martens & Schwendinger, 1998: 549) [Fig. 1 (11)] occurs syntopically with *G. larticus* but clearly does not belong to any of the known *asli*-group species. It possesses an unusually large genital operculum.

1 juvenile (leg. P. J. Schwendinger; MHNG) from a forest near Chenderiang [Fig. 1 (12)] possibly belongs to *G. pulvillatus* (see Schwendinger & Martens, 1999b: 957).

MALAYSIA (Sarawak): 2 ♀ (leg. I. Löbl & D. Burckhardt; MHNG) from Santubong Peninsula (0-100 m), N of Kuching [Fig. 1 (23)], appear to be close to *G. laevis*, but are distinguished by the lack of ventral processes on palpal femur and trochanter.

1 ♀ (leg. I. Löbl & D. Burckhardt; MHNG) from near Kapit (the type locality of *G. hutan* sp. n.) [Fig. 1 (25)] is distinct by the lack of a ventral process on palpal trochanter and by the rare tarsal formula 2-2-2-2.

MALAYSIA (Sabah): 1 ♀ (leg. R. Leakey?; NHML) from Mount Kinabalu National Park, 1540 m [Fig. 1 (29)] and a large juvenile (leg. W. Schawaller; MAR) from the same mountain at 1500-1600 m externally largely correspond with *G. exsudans* sp. n., but presumably belong to a different species.

The same also applies to 4 juveniles (leg. P. Lehtinen; Zoological Museum Turku) from Tiger Hill near Tawau, southeastern Sabah [Fig. 1 (30)].

INDONESIA (Sumatra): 1 ♀ (collector unknown; MHNG) from Deli near Medan, Northern Sumatra Province [Fig. 1 (19)] seemingly belongs to the *sumatranus*-group. A juvenile (leg. A. Riedel; MHNG) from Bukit Lawang (west of Medan) [Fig. 1 (18)] may also be conspecific.

INDONESIA (Kalimantan): 1 ♀ (leg. P. Beron & T. Ivanova; National Museum of Natural History, Sofia) from Nunukan Island (near the border to Sabah) [Fig. 1 (31)] is externally similar to *G. exsudans* sp. n. but possesses a distinctly larger body and a lower eye tubercle.

INDONESIA (Moluccas): 1 juv. (leg. A. Riedel; MHNG) from Morotai Island (north of Halmahera) [Fig. 1 (37)] is similar to the species of the *tumidifrons*-group but has a different colour pattern than the juveniles from Halmahera.

INDONESIA (Irian Jaya): 1 ♀, 1 juv. (leg. A. Riedel; MHNG) from Gunung Susu on Waigeo Island is externally similar to *G. tumidifrons*.

PHILIPPINES (Luzon): 1 ♀ (leg. L. Deharveng; MAR) from near Sagada [Fig. 1 (32)] resembles *G. crucifer* but differs by larger size and the common tarsal formula 2-2-3-3.

1 juv. (leg. L. Deharveng; MAR) from the Quezon National Park [Fig. 1 (33)] clearly differs from the species found at the nearby mountains, Mt. Makiling and Mt. Banahaw.

PHILIPPINES (Leyte): 1 ♀ (fairly large; mentioned in Martens & Schwendinger 1998: 549) and 1 juv. (leg. J. Martens & W. Schawaller; MAR) from north of Baybay [Fig. 1 (36)] differ from *G. leyteensis*, which occurs at the same locality.

DISCUSSION

THE SPECIES GROUPS

At present 48 *Gnomulus* species are known, which we arrange in 11 preliminary species groups. Two of them (*aborensis*-group, *rostratus*-group) were treated earlier (Schwendinger & Martens, 1999b) and are not further considered here.

1. *Gnomulus sinensis* sp. n. and *G. spiniceps* sp. n., here placed in the *sinensis*-group, are both close to the *aborensis*-group. Discoveries of further new species in the northern part of the distribution area of *Gnomulus* will most likely close the narrow gap between these two groups.

2. In the most species-rich assembly, the *armillatus*-group with 20 spp., details of penis morphology indicate four different phyletic lineages:

A) *Gnomulus piliger* from southern Thailand, *G. leofeae* sp. n. from southern Myanmar, *G. pulvillatus* from peninsular Malaysia, *G. armillatus* from Sumatra and *G. carinatus* sp. n. from southern Kalimantan all possess narrow, cylindrical, pointed, slightly sigmoid lateral glans sclerites pointing away from the truncus, in addition to a short, broadly rounded median plate.

B) *Gnomulus ryssie* sp. n. and *G. marginatus* sp. n. from central and south-eastern Thailand are similar but have a long, more or less pointed median plate.

C) *Gnomulus baharu* from Brunei and *G. conigerus* from Sabah also have cylindrical, pointed lateral sclerites, but they are U-shaped instead of sigmoid and their median plate is quite long and pointed. Genitalic characters of all these species appear to be plesiomorphic, as cylindrical, pointed lateral sclerites are also present in the primitive *Palaeoncopus*. Therefore these three subgroups are possibly not monophyletic.

D) *Gnomulus javanicus* sp. n. (from Java), *G. exsudans* sp. n., *G. hutan* sp. n., *G. laevis*, *G. lomani* sp. n., *G. obscurus* sp. n. and *G. sundaicus* (from northern Borneo), on the other hand, all possess paddle-shaped or blade-shaped lateral sclerites with laterally compressed apices, which are probably apomorphic. These 7 *Gnomulus*

species, presumably together with *G. annulipes* (the apices of its small and hook-like lateral sclerites are not clearly compressed), seem to form a distinctly monophyletic group.

In *G. thorelli* from Java and *G. drescoi* from Sumatra the males are still unknown and therefore their relationships remain unclear. We assume that the former species is close to *G. carinatus* sp. n. and the latter close to (or even identical with) *G. armillatus*.

3. The *asli*-group is a distinct, seemingly quite primitive lineage, restricted in its distribution to peninsular Malaysia. The fortunate find of further *G. laruticus* specimens confirms that the unusual tarsal formula 2-2-2-2 is in fact a specific character and not just a deformity of the holotype. The same is presumably also the case in the unrelated *G. crucifer* (with the same tarsal formula) from the Philippines.

4. *Gnomulus tuberculatus* sp. n., the second species of the *sumatranus*-group, makes an external distinction from the *armillatus*-group and from the *aborensis*-group less clear-cut than before. With regard to penis morphology, however, the two species of the *sumatranus*-group show more congruence with the externally much different *asli*-group species. The synapomorphic presence of a subdistal process on the ventral side of their palpal femur, in addition to their large size, show that *G. sumatranus* and *G. tuberculatus* sp. n. belong to a distinct lineage and do not just present links between the *armillatus*- (or *aborensis*-) group and the *asli*-group.

5. *Gnomulus rostratoideus* sp. n. is externally almost indistinguishable (except for an unbroken dark margin around the dorsal scutum) from the species of the *rostratus*-group, which are characterised by a strong, beak-like, forward-inclined eye tubercle. The penis of the new species, however, does not show the same derived morphology (i.e. stylus shaped like a flattened bell). Instead it resembles the penes of the *goodnighti*-group species in that its cylindrical stylus lacks ventral subterminal teeth. This congruence is considered to be due to convergent reduction. Therefore *G. rostratoideus* sp. n. is probably a primitive relative of the species in the *rostratus*-group. We place it here in a species group of its own, the *rostratoideus*-group, and regard it as sister to the distinct and clearly monophyletic *rostratus*-group.

6. *Gnomulus hamatus* sp. n., the only representative of the *hamatus*-group, possesses several characters which appear to be primitive for the genus *Gnomulus* (i.e. medium body size, an only slightly distad-inclined ventral process on palpal trochanter and stylus penis slender, with bulbous base and with a pair of subterminal ventral teeth). The absence of a carapace-abdomen bridge and the presence of pronounced modifications on the truncus penis and certain parts of the glans (i.e. sub-distally wide truncus, enlarged membraneous socket, truncate lateral sclerites, hook-shaped median plate), however, show that this species is much closer to the *goodnighti*-group than to the *armillatus*-group. Therefore we place *G. hamatus* sp. n. in a species group of its own and regard it as the sister of the *goodnighti*-group.

7. With 11 species known at present, the *goodnighti*-group is second to the *armillatus*-group in species-richness but it is more diverse with regard to penis morphology. Moreover, the group has a fairly restricted distribution in the Philippines and northern Borneo, which indicates that this is a relatively young phylogenetic lineage undergoing rapid speciation. This group is probably paraphyletic.

Gnomulus goodnighti and *G. leyteensis* show the primitive situation of retaining a ventral pair of subdistal teeth on their stylus penis. Otherwise both species perfectly correspond with others from this group, mostly because their styli are distinctly enlarged. *Gnomulus coniceps* and seemingly also *G. imadatei* (not examined; see Suzuki, 1969: fig. 4d, e), on the other hand, lack subdistal teeth on their styli (and are otherwise quite typical for this group), but these styli appear to be slender, not enlarged. Hence, the presence of an enlarged stylus or the absence of subterminal teeth on the stylus alone are not exclusive characteristics of the *goodnighti*-group (see also the *rostratoideus*-, *tumidifrons*- and *latoperculum*-group).

Gnomulus crassipes sp. n. and *G. crucifer* are related by the unusual tarsal formula 2-2-2-2, by the reduction of their carapace-abdomen bridge and by similar modifications of the glans penis. The lack of a carapace-abdomen bridge appears to link them with *G. minor* (male unknown) and with the *tumidifrons*-group, but this is not reflected in a similar penis morphology. The carapace-abdomen bridge probably has been reduced parallel in different lineages, i.e. in the *goodnighti*-group, in the *tumidifrons*-group and in the *hamatus*-group.

8. *Gnomulus tumidifrons* sp. n. and *G. matabesar* sp. n. from the Moluccas, here placed in the *tumidifrons*-group, clearly represent a distinct phyletic lineage close to the *goodnighti*-group. Small body size, a distad-directed ventral process on palpal trochanter, fairly long membraneous tubes in the glans and an enlarged stylus are shared by both groups. The two species of the *tumidifrons*-group are characterized by large eyes, a glans penis with fairly large, golfclub-shaped membraneous tubes, which are not covered by the narrow, spike-like median plate. Similar membraneous tubes are also found in *G. latoperculum* sp. n. The *tumidifrons*-group is possibly an offshoot of the *goodnighti*-group, which in this case would be paraphyletic.

9. *Gnomulus latoperculum* sp. n. (*latoperculum*-group) appears intermediate between three species groups. In external morphology it resembles species of the *armillatus*-group (by its fairly large size, its wide, undivided carapace-abdomen bridge and by a slightly distad-inclined ventral process on palpal trochanter), but its penis shows modifications otherwise mostly found in the *goodnighti*-group (i.e. enlarged cylindrical stylus with invaginated base and without subdistal pair of teeth, long membraneous tubes, reduced median plate, lobate lateral sclerites). As in the case of the *tumidifrons*-group, *G. latoperculum* sp. n. is presumably also a highly derived descendant of the (then paraphyletic) *goodnighti*-group. Most similarities in penis morphology are found between *G. latoperculum* sp. n. and *G. claviger* sp. n., but we consider these as convergent. A close relationship possibly also exists between *Gnomulus latoperculum* sp. n. and both species of the *tumidifrons*-group from the Moluccas, as indicated by geographical proximity and by the long, distally flattened and widened (golfclub-shaped) membraneous tubes of the glans penis. The latter may, however, be yet another case of convergence.

ZOOGEOGRAPHY

Gnomulus has clearly the largest distribution of all oncopodid genera, covering the entire range of the family (Fig. 1 and Schwendinger & Martens, 1999b: fig. 1). The newly discovered species considerably expand the previously known distribution

of the Oncopodidae towards the northeast and the southeast. *Gnomulus sinensis* sp. n. marks the northeasternmost occurrence in this family and *G. spiniceps* sp. n. stands at the eastern periphery of the known distribution on mainland Asia. Looking at the sparse and widely separated oncopodid records in this region (with the exception of a relatively well-investigated peninsular Malaysia), one can see how little we still know about the diversity of these enigmatic opilionids, let alone about their biology. These patchy records are not least due to restricted accessibility of certain areas, either because of the political situation in Myanmar and northeastern India, or because of dangers from land mines and unexploded bombshells in Indochina. Unfortunately this restricts zoological investigations in situ, but not large-scale habitat destruction in these areas.

The most surprising discovery from the new material is the occurrence of oncopodids beyond Wallace's line, i.e. *Gnomulus latoperculum* sp. n. in northern Sulawesi, *G. matabesar* sp. n. and *G. tumidifrons* sp. n. in the northern Moluccas and an unidentified species (only ♀ and juvenile available) on an island off the north-western tip of New Guinea. Considering that oncopodids require constantly high humidity and looking at the relationships between these three nominal species and at their taxonomic distinctiveness from congeners west of Wallace's line, we can exclude that they have been introduced by man. The closest relatives of these three species are found in the Philippines and not on the Greater Sunda Islands. Therefore it appears that the ancestors of these autochthonous taxa have arrived from the north, probably in fairly recent geological times. It will be exciting to learn from further collections on the Lesser Sunda Islands and on New Guinea, how far the Oncopodidae have advanced into the Australian region.

The different species groups occupy quite distinctly outlined geographical ranges with only few disjunctions. The *aborensis*-group species occur in and around the Himalayas and its foothills extending into northern Thailand, whereas the *sinensis*-group occupies the northeastern part of the generic range on mainland Asia, i. e. southern China and northern Vietnam. The *asli*-group and the *rostratus*-group are known only from peninsular Malaysia (new finds for the latter also in Thailand), the *sumatranus*-group only from Sumatra and the *tumidifrons*-group so far only from the Moluccas (probably also from Waigeo Island off New Guinea). The monotypic *rostratoideus*-group, *latoperculum*-group and *hamatus*-group occur in southern peninsular Malaysia, on Sulawesi and on Luzon Island (Philippines), respectively. The *goodnighti*-group is found on the Philippine islands and one of its species also on Borneo. Only the *armillatus*-group has a wide distribution, ranging from northeastern Thailand to Sumatra, Java and probably the whole of Borneo. Most species appear to have small distribution areas, only two members of the *armillatus*-group are noteworthy exceptions: The known range of *G. armillatus* stretches over 170 km, that of *G. exsudans* sp. n. over about 400 km.

Remarkable is the seemingly syntopical occurrence of three congeneric species (*G. hamatus* sp. n., *G. claviger* sp. n. and *G. crassipes* sp. n.) on Mt. Banahaw, Luzon Island. The latter two species even belong to the same derived species-group. From the nearby Mt. Makiling also three species are known, i.e. *G. hamatus* sp. n., *G. claviger* sp. n. and *G. minor*. In this case, however, it is not clear whether the latter

species (male unknown) is really congeneric with the other two. At the same mountain there is additionally an undescribed *Biantoncopus* and an oncopodid species, which at present we cannot attribute to any genus. The presence of presumably yet another *Gnomulus* species (1 juvenile available) in the nearby Quezon National Park shows that the Oncopodidae have experienced an exceptionally vivid process of speciation in the Philippines and on Luzon Island in particular.

ACKNOWLEDGEMENTS

We gratefully acknowledge loans and donations of specimens from the following colleagues: Petar Beron (National Museum of Natural History, Sofia), Giulio Cuccodoro and Ivan Löbl (MHNG), Hieronymus Dastych (ZMH), Louis Deharveng (Laboratoire d'Ecologie Terrestre, Toulouse), Giuliano Doria (MSNG), Jason Dunlop (ZMB), Manfred Grasshoff (SMF), Janet Beccaloni and Paul Hillyard (NHML), Pekka Lehtinen (Zoological Museum Turku), Hirotugu Ono (NSMT), Norman Platnick (AMNH), Nikolaj Scharff (ZMC), Wolfgang Schawaller and Alexander Riedel (Staatliches Museum für Naturkunde, Stuttgart), Andreas Schulz (Leichlingen). J. Dunlop also provided information on the collection of Fritz Grabonsky. William Shear (Hampden-Sydney College) kindly sent us material from different collections, which he intended to study himself. Käthe Rehbinder (Universität Mainz) most skillfully and patiently produced the whole-animal figures. Jürgen Gruber (Naturhistorisches Museum Wien) commented on the manuscript. The German Academic Exchange Service (Deutscher Akademischer Austauschdienst, Bonn) supported P.J.S. with a 1-months research grant at the beginning of this project. The Feldbausch and Wagner Foundations of the University of Mainz provided travel funds to J.M.

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Added in proof: We have only recently received further *Gnomulus* specimens from the Philippines, Malaysia and Singapore (all in MHNG; leg. L. Deharveng, S. Huber, L. Monod, A. Schulz, P. J. Schwendinger), which will be treated in a later paper.



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<https://doi.org/10.5962/bhl.part.79580>.

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