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Five new species of the pill millipede genus *Rhopalomeris* Verhoeff, 1906 (Diplopoda, Glomerida) from Thailand

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Abstract

An integrative approach based on morphological characteristics and DNA data from the mitochondrial COI gene has revealed five new species of the pill millipede genus *Rhopalomeris* Verhoeff, 1906 from Thailand: *R. muka* Sapparojattana & Likhitrakarn, **sp. nov.**, *R. lentiginosa* Sapparojattana & Likhitrakarn, **sp. nov.**, *R. dulcia* Sapparojattana & Likhitrakarn, **sp. nov.**, *R. punctata* Sapparojattana & Likhitrakarn, **sp. nov.**, and *R. verhoeffi* Sapparojattana & Likhitrakarn, **sp. nov.** The five new species are distinguishable from their congeners by distinctive color patterns and telopod structure. The interspecific genetic divergences between the new species and other *Rhopalomeris* species ranged from 7.86 to 13.71%. Intraspecific genetic divergences within these five species ranged from 0 to 4.53%, with the highest divergences found in *R. carnifex* and *R. verhoeffi* **sp. nov.** This is consistent with both the wide distribution range and the significant intraspecific morphological variations observed in these latter two species. Furthermore, the taxonomic scope of *R. carnifex* in Thailand is reviewed, and intraspecific morphological variations within *R. carnifex* and *R. verhoeffi* **sp. nov.** are discussed. A distribution map, morphological illustrations from SEM, and an updated key to all known *Rhopalomeris* species are also provided.

Key words

DNA barcoding – Indochina – integrative taxonomy – phylogeny – systematics

Introduction

Thailand is part of the Indo-Burma Biodiversity Hotspot, a region famous for its diverse habitats and forest types, including a large collection of limestone mountains scattered throughout the country (Myers et al., 2000; Clements et al., 2006).

Limestone karst environments provide highly suitable conditions that promote the diversification of a wide range of flora and fauna taxa. This suitability stems from the unique geological, topographical, and microclimatic features characteristic of

these landscapes. The complex network of caves, fissures, and isolated rock outcrops creates a mosaic of highly specialized, stable, and often isolated habitats. These factors contribute to high levels of endemism, where species are restricted to a particular mountain or cave system. Furthermore, the geographical isolation of each karst system acts as a barrier to gene flow, driving allopatric speciation and resulting in numerous species with extremely restricted distributions (Rundle & Nosil, 2005; Clements et al., 2006).

In Thailand, numerous limestone-restricted species have been recorded, reflecting the notable diversity of fauna that these habitats support, including the land snails (e.g., Pholyotha et al., 2020), the bent-toed gecko (e.g., Ampai et al., 2024), as well as in several millipede genera (e.g., Srisonchai et al., 2018; Pimvichai et al., 2023; Likhitrakarn et al., 2024a; Srikampha et al., 2025; Benchapong et al., 2025). To date, more than 280 species of millipedes (Diplopoda) belonging to 58 genera, 18 families, and ten orders have been recorded from Thailand (Huynh et al., 2023; Likhitrakarn et al., 2023a, 2024a; Pimvichai et al., 2023; Srisonchai et al., 2023, 2024a, 2024b; Benchapong et al., 2025; Sapparoj Pattana et al., 2025; Srikampha et al., 2025).

The pill millipede order Glomerida is one speciose millipede group, comprising more than 300 species across 36 genera worldwide (Engelhof et al., 2015). The genus *Rhopalomeris* Verhoeff, 1906 is one of these and is known to be endemic to Indochina (Pocock, 1889; Verhoeff, 1906; Silvestri, 1917; Decker, 2010; Golovatch & Semenyuk, 2016; Nguyen et al., 2019; Nguyen et al., 2021; Likhitrakarn et al.,

2024b; Sapparoj Pattana et al., 2025). The genus was originally described as a monotypic genus with *Glomeris bicolor* Wood, 1865 from Phuket, Thailand, as the type species (Verhoeff, 1906). Later, Silvestri (1917) reexamined Verhoeff's materials and determined that the type species was misidentified, and therefore redesignated *Glomeris carnifex* Pocock, 1889, from Myanmar, as the type species. Golovatch et al. (2011) subsequently confirmed the identity and taxonomic status of *R. carnifex*, while the phylogenetic position has been clarified by Likhitrakarn et al. (2024). At present, this genus holds eight nominal species distributed from Peninsular Malaysia to southern Thailand and Myanmar, and was, surprisingly, recently recorded in Vietnam as well (Pocock, 1889; Silvestri, 1917; Golovatch & Semenyuk, 2016; Nguyen et al., 2019, 2021; Likhitrakarn et al., 2024b; Sapparoj Pattana et al., 2025).

The most prominent representative species of the genus is *R. carnifex* (Pocock, 1889), which is also known as the 'candy pill millipede' because of its vivid color pattern. Its current distribution covers a wide area in Myanmar and southern Thailand (Pocock, 1889; Verhoeff, 1906; Silvestri, 1917; Decker, 2010). This large and colorful species has also gained popularity in the exotic pet trade (e.g., <https://www.exotic-pets.co.uk/candy-red-pill-bug.html>, <https://thespidershops.co.uk/product/rhopalomeris-carnifex/>, <https://lotsoflegsth.com/product/rhopalomeris-carnifex-candy-pill-millipede/>), attracting attention from hobbyists worldwide.

In Thailand, *R. carnifex* is commonly found among limestone mountains in the southern region from Surat Thani to Krabi provinces (Verhoeff, 1906; Engelhof,

2005; Decker, 2010; Sapparojattana et al., 2025). However, due to the analogous color patterns of each population in *R. carnifex* as intraspecific variation, there has been minimal interest in conducting exhaustive investigations of this species (Engthoff, 2005; Decker, 2010). Recently, Sapparojattana et al. (2025) investigated *R. carnifex* s.l. populations in southern Thailand, and the results led to the discovery of a cryptic new species, *R. sirindhornae* Sapparojattana, Jeratthitikul & Likhitrakarn, 2025. Although similar to *R. carnifex*, this species differs in body size, coloration patterns on the dorsal and ventral sides, and the telopod structure. The discovery suggests that the diversity of *Rhopalomeris* remains underestimated, particularly in Thailand, which is a major distribution area for the genus, and in which many other *Rhopalomeris* populations have been poorly investigated. Furthermore, this study confirmed that despite similar coloration, an integrated approach combining molecular and morphological investigations can provide substantial differences across the species of *Rhopalomeris*. This is consistent with findings in other millipede groups, where even minute differences in the gonopod structure have been shown to correspond to significant molecular divergence (e.g., Srisonchai et al., 2018). In light of these findings, the discovery of cryptic species thus initiated a dedicated project to thoroughly re-evaluate the taxonomy of *R. carnifex* in Thailand using an integrative approach.

In the present study, the taxonomy and diversity of *Rhopalomeris* in Thailand are reviewed and updated through the description of five additional new species

using an integrated approach combining morphological examinations and molecular phylogeny from a fragment of the mitochondrial COI gene. The examined specimens provide a comprehensive dataset encompassing a broad geographic range from western to southern Thailand. Furthermore, we discuss the intraspecific morphological variation within some species of this genus, provide a distribution map, and present an updated identification key for all known species of *Rhopalomeris*.

Material and methods

Specimen sampling and morphological examination

All *Rhopalomeris* specimens examined in this study were based on voucher specimens deposited in the Mahidol University Museum of Natural History, Department of Biology, Faculty of Science (MUMNH), particularly those collected from western and southern Thailand between 2007 and 2022, together with specimens newly collected in 2023–2024. Geographic coordinates of the collecting sites were recorded using a GPS device (WGS84 datum) and were verified with Google Maps. Prior to preservation of the collected pill millipede specimens in the field, live specimens from each locality were photographed using a Nikon DSLR camera (D850). Then, they were euthanized using a two-step method following the AVMA Guidelines for the Euthanasia of Animals (AVMA, 2020), and preserved in 95% (v/v) ethanol for morphological examination and molecular analyses. The animal use in this study has been approved by the Faculty of Science,

Mahidol University Animal Care and Use Committee, SCMU-ACUC (No. MUSC66-033-663). All type specimens are housed in MUMNH, Nakhon Pathom Province, Thailand.

Standard protocols of species diagnosis and morphological description were based on previous glomerid literatures (Wesener, 2012; Golovatch & Semenyuk, 2016; Likhitrakarn et al., 2024b). The male telopod, leg-pair 17, and leg-pair 18 of each species were dissected. Some morphological diagnostic characters, including coloration pattern, ommatidia, Tömösváry organ, antennae (antennomeres 6 and 7, and sensory cones on the antennal tip), striae on the thoracic shield, striae on the tergites, and the anal shield were examined under an Olympus SZX7 stereoscopic light microscope. Key diagnostic characters were digitally imaged using a Dino-Eye Eyepiece Camera connected to the ZEISS Stemi 305 stereo microscope and operated by DinoCapture 2.0 software. The telopods were imaged by scanning electron microscopy (SEM; JEOL, JSM-6610 LV). Drawings depicting color pattern variation were made from the photographs of living specimens using the Procreate® application.

In the taxonomic catalogue sections, a letter system is applied to denote the status of taxonomic investigation:

- D** stands for the original description and subsequent descriptive notes;
- K** for the appearance in a key;
- L** for the appearance in a species list;
- M** for a mention;
- MI** for molecular investigation;
- R** for new subsequent records.

Morphological terms are used in accordance with those in recent studies (Golovatch & Semenyuk, 2016; Nguyen et al., 2019; Likhitrakarn et al., 2024b).

The following abbreviations of morphological characters are used in the figures:

- cx coxa
- cxl coxal lobe
- fe femur
- fp femoral process
- ft femoral trichostele of telopod
- pf prefemur
- pft prefemoral trichostele of telopod
- sh syncoxital horn of telopod
- sl syncoxital lobe of telopod
- slt syncoxital lobe tip
- sn syncoxite notch
- sx syncoxite
- ta tarsus
- ti tibia
- tp tibial process

DNA extraction and sequencing

A total of 73 individuals of the genus *Rhopalomeris* were used for DNA extraction. Genomic DNA was extracted from 2–3 legs of each specimen using the NucleoSpin® Tissue Kit (Macherey-Nagel, Germany), following the manufacturer's standard protocol. Fragments of the mitochondrial cytochrome c oxidase subunit I (COI) gene were amplified by Polymerase Chain Reaction (PCR) using the forward primer LCO1490 (Folmer et al., 1994) and the reverse primer HCOoutout (Schulmeister et al., 2002) or using the forward primer LOBOF1 and the reverse primer LOBOR1 (Lobo et al., 2013). The PCR reactions were performed with a final volume of 30 µL, including at least 10 ng of the DNA template, 1.5 µL each primer, 15 µL

of EmeraldAmp PCR Master Mix (TAKARA BIO INC.), and deionized H₂O until the final volume. The PCR thermal cycling was performed under the following conditions: initial denaturation at 94°C for 3 min followed by 35 cycles of 94°C for 45 s, 46 or 50°C for 45 s, and 72°C for 1 min, and then followed by a final extension at 72°C for 5 min. The amplified products were checked under UV transillumination after gel electrophoresis, then purified using MEGAquick-spin™ plus (Fragment DNA purification kit), and sent for commercial sequencing in both directions using an automated sequencer (ABI PRISM 3730XL).

Sequence alignment and phylogenetic analyses

DNA sequences from both directions were manually checked, aligned, and edited using the MUSCLE algorithm, as implemented in MEGA11 v.11.0.8 (Tamura et al., 2021). All newly obtained nucleotide sequences were deposited in the GenBank database under accession numbers PX220320–PX220392. Phylogenetic analyses were constructed using two model-based methods, maximum likelihood (ML) and Bayesian inference (BI), and performed online through the Cyber Infrastructure for Phylogenetic Research (CIPRES) Science Gateway (Miller et al., 2010). The final data matrix included 660 base pairs (bp) of 73 newly obtained sequences of *Rhopalomeris* in this study, and 63 sequences previously used by Sapparojpatana et al. (2025), which contained 12 sequences of all available *Rhopalomeris* species, 49 sequences from other genera in the family Glomeridae, and two distant outgroups, *Sphaerobelum*

truncatum Wongthamwanich, 2012 and *Zephronia laotica* Wesener, 2019 (Table 1).

The best-fit models of nucleotide substitution were identified under the Akaike information criterion (AICc) using PartitionFinder2 v.2.3.4 (Lanfear et al., 2017). The models GTR+I+G, HKY+I, GTR+G were suggested by the program for each of three COI codon positions, respectively. These nucleotide substitution models were subsequently applied in the ML and BI phylogenetic analyses. For ML analysis, IQ-Tree v.2.1.2 (Minh et al., 2020) was used to reconstruct the tree with 10,000 ultrafast bootstrap replicates. For BI analysis, the Bayesian inference phylogenetic tree was reconstructed using MrBayes v.3.2.7a (Ronquist et al., 2012) based on two independent 10-million-generation runs. Trees were sampled every 1,000 generations, and the first 25% of tree samples were discarded as burn-in. The average effective sample sizes (ESS) from the MCMC analysis were over 200 for all parameters. Nodes that exceeded 0.95 Bayesian posterior probabilities (BPP) for BI analysis and/or exceeded 95% bootstrap support values (BS) for ML analysis were considered as well supported (Hillis & Bull, 1993; Hoang et al., 2018; San Mauro & Agorreta, 2010). In addition, genetic divergence among *Rhopalomeris* species and within each species were calculated using uncorrected p-distances as implemented in MEGA11.

Species delimitation

Species delimitations were conducted using the COI dataset under two approaches: Automatic Barcode Gap Discovery (ABGD) (Puillandre et al., 2012) and a multi-rate Poisson Tree Processes

TABLE 1 List of the newly added sequences in this study. All specimens are from Thailand, unless specified otherwise (one specimen of *Rhopalomeris carnifex*).

Taxon	Locality	Latitude	Longitude	Voucher Number	GenBank accession numbers
<i>Rhopalomeris muka</i> sp. nov.	Kanchanaburi	14°07'38.9"N	99°09'30.3"E	GLO102-1	PX220349
				GLO102-2	PX220350
				GLO102-3	PX220351
				GLO223-1	PX220352
<i>Rhopalomeris lentiginosa</i> sp. nov.	Kanchanaburi	14°44'29.1"N	98°38'15.4"E	GLO042-1	PX220353
				GLO042-2	PX220354
				GLO086-1	PX220355
<i>Rhopalomeris dulcia</i> sp. nov.	Chumphon	10°26'46.2"N	99°02'06.5"E	GLO188-1	PX220356
				GLO188-2	PX220357
				GLO188-3	PX220358
<i>Rhopalomeris punctata</i> sp. nov.	Prachuap Khiri Khan	12°14'14.1"N	99°55'53.7"E	GLO056-1	PX220359
				GLO056-3	PX220360
				GLO056-4	PX220361
				GLO056-5	PX220362
<i>Rhopalomeris verhoeffi</i> sp. nov.	Phang-nga	8°26'33.7"N	98°30'56.5"E	GLO017-1	PX220367
				GLO017-2	PX220368
				GLO018-1	PX220369
				GLO018-2	PX220370
	Nakhon Si Thammarat	8°09'32.4"N	99°40'40.9"E	GLO025-1	PX220371
				GLO025-2	PX220372
				GLO025-3	PX220373
	Phang-nga	8°28'06.9"N	98°35'16.1"E	GLO061-1	PX220374
	Krabi	8°20'16.8"N	98°44'44.1"E	GLO062-1	PX220375
	Nakhon Si Thammarat	8°26'12.7"N	99°23'22.7"E	GLO080-1	PX220376
	Surat Thani	9°01'48.0"N	98°59'12.9"E	GLO081-1	PX220377
	Phuket	6°59'57.2"N	100°14'00.4"E	GLO099-1	PX220378
	Surat Thani	8°46'23.8"N	98°51'35.8"E	GLO125-1	PX220379
	Krabi	8°30'40.0"N	98°45'38.5"E	GLO132-1	PX220380
	Surat Thani	8°53'35.9"N	98°33'09.1"E	GLO142-1	PX220381
	Krabi	8°23'23.6"N	98°43'59.6"E	GLO154-1	PX220382
	Trang	7°47'36.4"N	99°38'39.7"E	GLO195-1	PX220383
	Krabi	8°07'25.4"N	98°55'30.5"E	GLO196-1	PX220384
		8°22'23.3"N	98°44'07.6"E	GLO197-1	PX220385
				GLO197-2	PX220386

TABLE 1 List of the newly added sequences in this study. All specimens are from Thailand (*cont.*)

Taxon	Locality	Latitude	Longitude	Voucher Number	GenBank accession numbers
<i>Rhopalomeris carnifex</i>	Phang-nga	8°31'51.4"N	98°34'40.8"E	GLO198-1	PX220387
		8°25'43.6"N	98°28'18.6"E	GLO199-1	PX220388
		8°26'33.7"N	98°30'56.5"E	GLO200-2	PX220389
				GLO200-3	PX220390
	Phuket	7°55'58.9"N	98°19'19.8"E	GLO201-1	PX220391
				GLO201-2	PX220392
	Krabi	8°22'20.4"N	98°44'08.4"E	TH49	PX220364
		8°01'55"N	98°50'12"E	TW135	PX220363
		8°12'35.0"N	98°56'22.1"E	CH138	PX220365
		8°12'31.7"N	98°56'05.2"E	CH139	PX220366
	Tanintharyi, Myanmar	11°40'18.1"N	99°13'30.1"E	GLO012-2	PX220323
	Prachuap Khiri Khan	12°04'02.7"N	99°39'53.8"E	GLO023-1	PX220324
				GLO023-2	PX220325
				GLO023-3	PX220326
				GLO024-1	PX220327
				GLO024-2	PX220328
	Prachuap Khiri Khan	11°51'43.0"N	99°49'21.5"E	GLO024-3	PX220329
				GLO066-1	PX220330
	Surat Thani	8°57'49.0"N	98°50'18.6"E	GLO074-1	PX220331
		8°35'32.4"N	99°23'06.5"E	GLO076-1	PX220332
	Phetchaburi	12°52'57.0"N	99°37'34.8"E	GLO101-1	PX220333
	Prachuap Khiri Khan	11°12'09.2"N	99°29'55.2"E	GLO104-1	PX220334
				GLO104-2	PX220335
	Chumphon	10°22'24.1"N	99°03'38.3"E	GLO105-1	PX220336
	Prachuap Khiri Khan	11°47'08.1"N	99°48'58.0"E	GLO112-1	PX220337
	Chumphon	10°30'24.2"N	99°07'50.5"E	GLO114-1	PX220338
				GLO114-2	PX220339
	Prachuap Khiri Khan	12°08'12.9"N	99°38'46.6"E	GLO119-1	PX220340
				GLO119-2	PX220341
	Surat Thani	9°00'50.1"N	98°52'40.1"E	GLO121-1	PX220342
	Prachuap Khiri Khan	11°38'09.4"N	99°42'09.4"E	GLO138-1	PX220343
		12°08'12.9"N	99°38'46.6"E	GLO157-1	PX220344
		11°44'56.6"N	99°47'15.5"E	GLO162-1	PX220345

TABLE 1 List of the newly added sequences in this study. All specimens are from Thailand (cont.)

Taxon	Locality	Latitude	Longitude	Voucher Number	GenBank accession numbers
	Chumphon	10°45'36.4"N	99°13'46.7"E	GLO187-1	PX220346
	Surat Thani	9°05'25.0"N	99°36'32.2"E	GLO190-1	PX220347
	Chumphon	10°32'09.6"N	99°08'59.2"E	GLO203-1	PX220348
	Surat Thani	9°46'00"N	99°58'00"E	TW134	PX220320
	Prachuap Khiri Khan	11°12'07"N	99°29'48"E	TW194	PX220321
	Chumphon	10°27'53"N	99°07'43"E	TW198	PX220322

(mPTP) (Kapli et al., 2017). The ABGD analysis was analyzed online using a web server (<https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html>) with relative gap width set to 1, and under the Kimura 2-parameter substitution model. For the mPTP, the analysis was performed via an online web server (<https://mptp.h-its.org/>) using the input tree generated from the previous IQ-Tree analysis, and parameters were set as default settings.

Results

Molecular phylogeny

Sequence fragments of the COI gene were successfully obtained from 73 *Rhopalomeris* individuals in this study. When aligned with sequences from previous studies and the outgroups, the final alignment used for phylogenetic analyses had a total length of 660 base pairs, containing 339 variable sites (51.36%) and 280 parsimony informative sites (42.42%).

The phylogenetic relationships inferred by the ML and BI analyses were similar. Therefore, only the tree topology from BI is presented in Figure 1.

Rhopalomeris specimens were recovered as ten clades. Nine of the clades received high support from both analyses (BPP = 0.99–1, BS = 99–100%); the clade of *R. nagao* Nguyen, Nguyen & Eguchi, 2021 from Vietnam was supported only from the ML analysis (BPP = 0.81, BS = 99%). Five of the ten clades are previously recognized species, namely *R. carnifex*, *R. nigroflava* Likhitrakarn, 2024 in Likhitrakarn et al., 2024b, *R. sirindhornae*, *R. nagao*, and *R. sauda* Nguyen, Sierwald & Marek, 2019. The other five clades could not be matched with any available species name. Therefore, we describe them in this study as *R. muka* sp. nov., *R. lentiginosa* sp. nov., *R. dulcia* sp. nov., *R. punctata* sp. nov., and *R. verhoeffi* sp. nov.

Interestingly, the COI gene trees did not recover monophyletic relationships among all *Rhopalomeris* species, as *R. sauda*

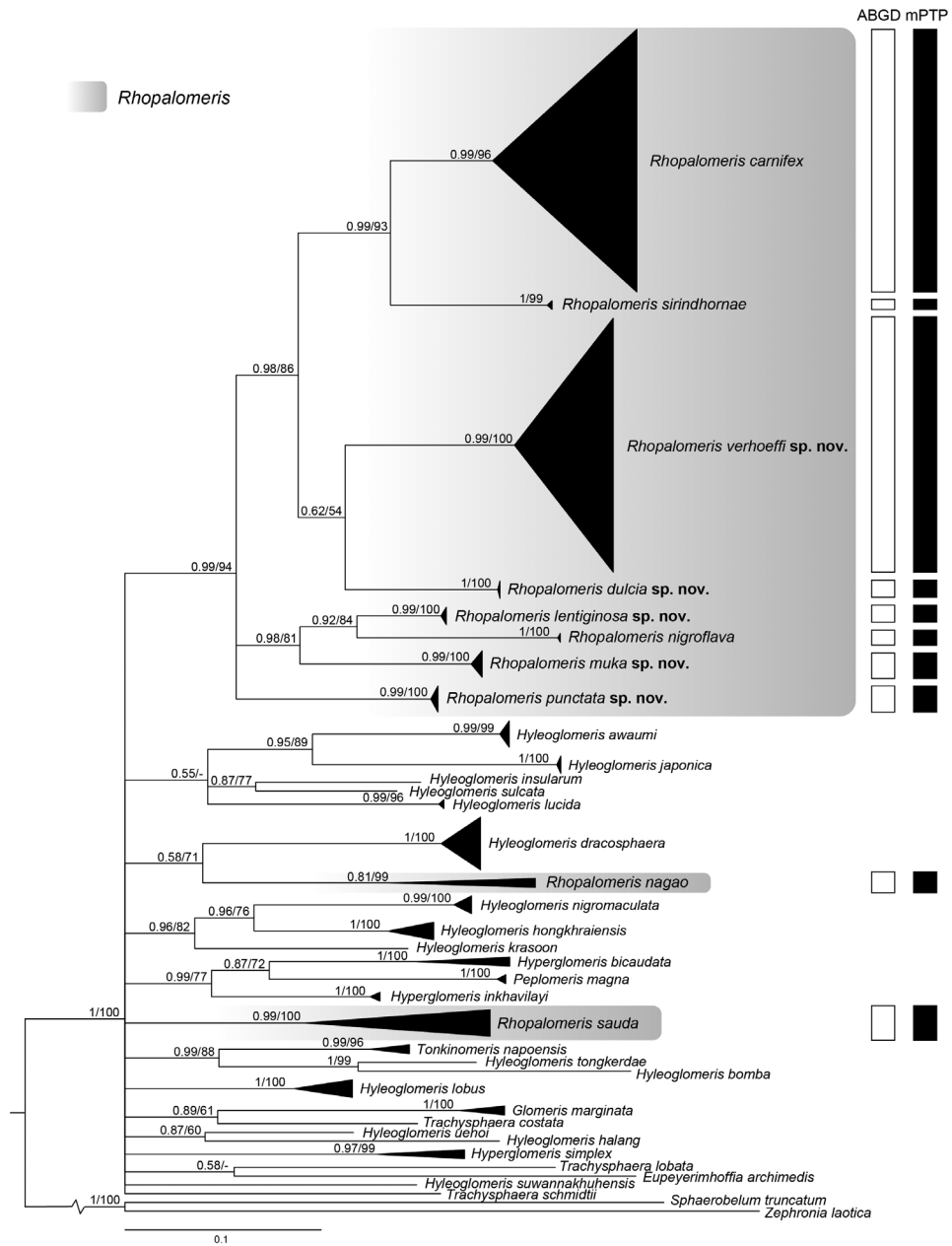


FIGURE 1 Bayesian inference tree of *Rhopalomeris* species and related taxa reconstructed from 660-bp COI dataset, and species delimitation clustering results. Numbers on nodes indicate Bayesian posterior probabilities (BPP) from Bayesian inference analysis (BI) and bootstrap values (BS) from maximum likelihood analysis (ML) and are shown as BPP/BS. Grey highlighted clades refer to *Rhopalomeris* species.

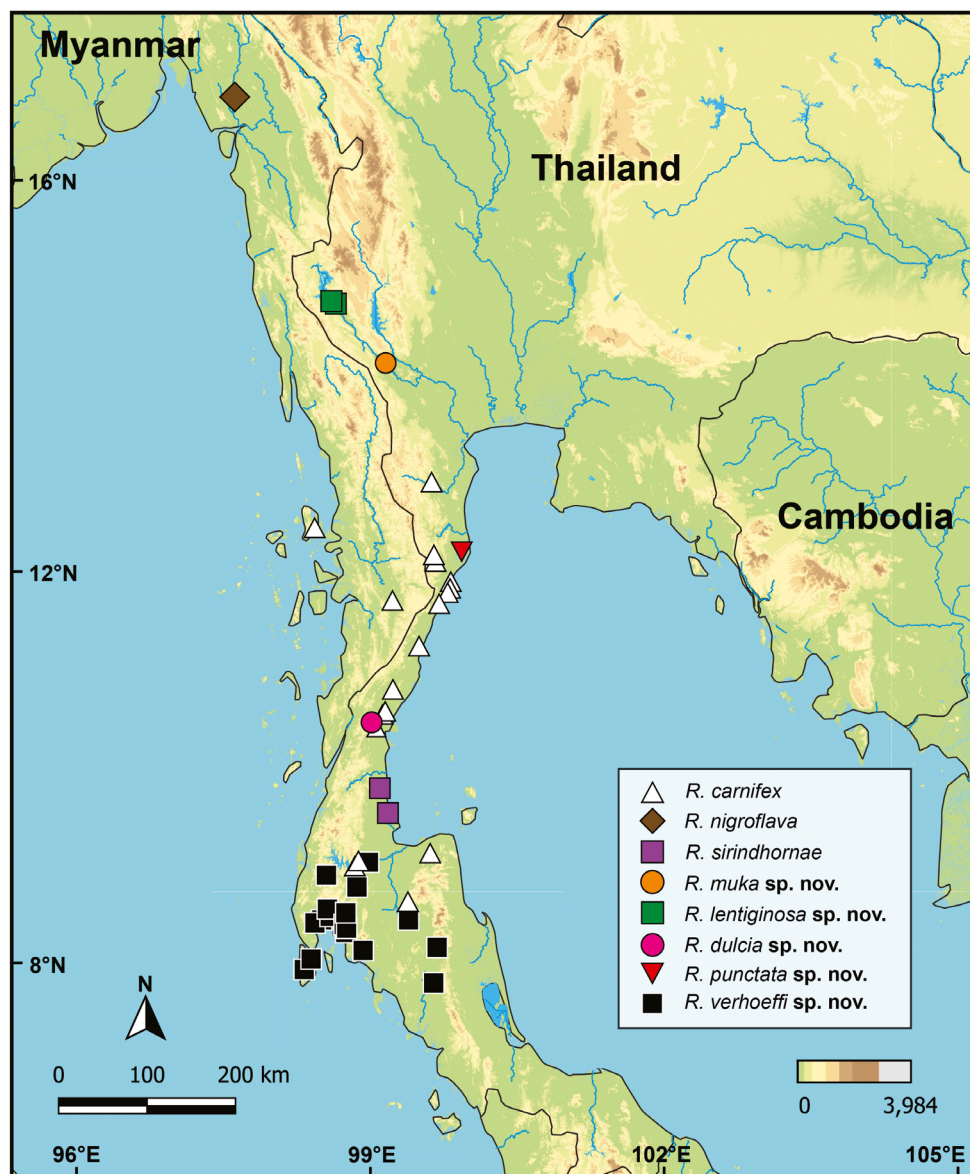


FIGURE 2 Distributions of currently known *Rhopalomeris* species in Thailand and Myanmar

and *R. nagao*, both from Vietnam, were not clustered with other *Rhopalomeris* lineages and were instead nested with other genera in the Glomeridae family. Although the relationships between glomerid genera remain unclear, the species of *Rhopalomeris* from Myanmar and

Thailand, including three previously recognized species (*R. carnifex*, *R. nigroflava*, and *R. sirindhornae*) and five new species from this study, were nested together and recovered as a strongly supported clade (BPP = 0.99, BS = 94%). Within this clade, *R. nigroflava* from Myanmar was sister

to *R. lentiginosa* **sp. nov.**, although with moderate support values (BPP = 0.92, BS = 81%). The clade of these two species was then grouped with *R. muka* **sp. nov.** (BPP = 0.98, BS = 81%). Both *R. lentiginosa* **sp. nov.** and *R. muka* **sp. nov.** were collected from Kanchanaburi Province in western Thailand (Fig. 2). The other two new species from southern Thailand, *R. verhoeffi* **sp. nov.** and *R. dulcia* **sp. nov.**, were clustered as sister taxa, but with low support (BPP = 0.62, BS = 54%). They were then sister to a clade of *R. carnifex* and *R. sirindhornae* (BPP = 0.99, BS = 93%),

TABLE 2 Average interspecific genetic divergence (uncorrected p-distance) matrix for the 660-bp COI gene sequences between *Rhopalomeris* species (lower diagonal) and average intraspecific genetic distances within each taxon (in bold).

Taxon	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
<i>Rhopalomeris muka</i> sp. nov.	0.29 ± 0.00									
<i>Rhopalomeris lentiginosa</i> sp. nov.	7.86 ± 0.00	0.13 ± 0.00								
<i>Rhopalomeris dulcia</i> sp. nov.	8.38 ± 0.00	10.07 ± 0.00	0.00 ± 0.00							
<i>Rhopalomeris punctata</i> sp. nov.	10.64 ± 0.00	10.26 ± 0.00	10.00 ± 0.00	0.20 ± 0.00						
<i>Rhopalomeris verhoeffi</i> sp. nov.	12.17 ± 0.01	10.76 ± 0.01	9.07 ± 0.01	12.88 ± 0.01	4.53 ± 0.02					
<i>Rhopalomeris carnifex</i>	10.62 ± 0.01	9.42 ± 0.01	10.69 ± 0.01	13.27 ± 0.00	10.95 ± 0.01	3.69 ± 0.02				
<i>Rhopalomeris nigroflava</i>	9.56 ± 0.00	7.91 ± 0.00	10.59 ± 0.00	10.88 ± 0.00	12.28 ± 0.01	10.66 ± 0.00	0.00 ± 0.00			
<i>Rhopalomeris sirindhornae</i>	10.83 ± 0.00	10.23 ± 0.00	9.41 ± 0.00	12.06 ± 0.00	9.56 ± 0.01	9.04 ± 0.01	11.67 ± 0.00	0.20 ± 0.00		
<i>Rhopalomeris sauda</i>	12.33 ± 0.01	12.37 ± 0.00	12.35 ± 0.01	13.33 ± 0.01	13.71 ± 0.01	13.32 ± 0.01	12.7 ± 0.00	12.4 ± 0.00	6.96 ± 0.01	
<i>Rhopalomeris nagao</i>	12.23 ± 0.01	10.92 ± 0.00	11.57 ± 0.00	11.86 ± 0.00	12.71 ± 0.01	12.06 ± 0.01	11.37 ± 0.00	12.35 ± 0.01	11.47 ± 0.01	5.29 ± 0.00

although this relationship was supported only by the BI analysis (BPP = 0.98, BS = 86%). Meanwhile, *R. punctata* **sp. nov.** from the upper part of southern Thailand was placed as polytomy to the clade of *Rhopalomeris* from Thailand and Myanmar.

The average uncorrected p-distance of the COI gene of examined *Rhopalomeris* species was 11.13% (Table 2). The minimum divergence was 7.86% between *R. muka* **sp. nov.** and *R. lentiginosa* **sp. nov.**, both from Kanchanaburi Province, Thailand; the maximum divergence was 13.71% between *R. verhoeffi* **sp. nov.** from southern Thailand and *R. sauda* from Vietnam. The intraspecific genetic distances within each *Rhopalomeris* lineage ranged from 0–6.96% (Table 2). The highest intraspecific mean sequence divergence of COI within *Rhopalomeris* in Thailand was observed in *R. verhoeffi* **sp. nov.** (4.53%), followed by *R. carnifex* (3.69%); the lowest intraspecific genetic distance was observed in *R. dulcia* **sp. nov.** (0%).

Species delimitation from both methods, ABGD and mPTP, were consistent with the phylogenetic analyses and morphological examination, and congruently supported the validity of all examined *Rhopalomeris* species (Fig. 1).

Taxonomy

Class Diplopoda Blainville in Gervais, 1844
Order Glomerida Leach, 1814

Family Glomeridae Leach, 1815

Genus *Rhopalomeris* Verhoeff, 1906

Type species. *Glomeris carnifex* Pocock, 1889 (see Silvestri, 1917 for the subsequent designation of the type species)

Species included. Currently, the genus comprises 13 valid species, including five newly described species in this study:

Rhopalomeris carnifex (Pocock, 1889)

Rhopalomeris dulcia **sp. nov.**

Rhopalomeris lentiginosa **sp. nov.**

Rhopalomeris monacha Silvestri, 1917

Rhopalomeris muka **sp. nov.**

Rhopalomeris nagao Nguyen, Nguyen & Eguchi, 2021

Rhopalomeris nigroflava Likhitrakarn, 2024

Rhopalomeris punctata **sp. nov.**

Rhopalomeris sauda Nguyen, Sierwald & Marek, 2019

Rhopalomeris sirindhornae Sapparojpatana, Jeratthitikul & Likhitrakarn, 2025

Rhopalomeris tonkinensis Silvestri, 1917

Rhopalomeris variegata Golovatch & Semenyuk, 2016

Rhopalomeris verhoeffi **sp. nov.**

Diagnosis. The genus *Rhopalomeris* is characterized by a relatively large body size, approximately 11–20 mm in length. Antenna particularly enlarged, with a strongly curved antennomere 6, and numerous apical sensory cones on the antennal tip. The telopods are strongly enlarged and stout, bearing both pre-femoral and femoral trichosteles, with the femur exhibiting a distinctive distocaudal process.

Distribution. Myanmar, Thailand, Malaysia, and Vietnam (Pocock, 1889; Verhoeff, 1906; Silvestri, 1917; Enghoff, 2005; Decker, 2010; Golovatch & Semenyuk, 2016; Nguyen et al., 2019, 2021; Likhitrakarn et al., 2024b; Sapparojpatana et al., 2025; this study)

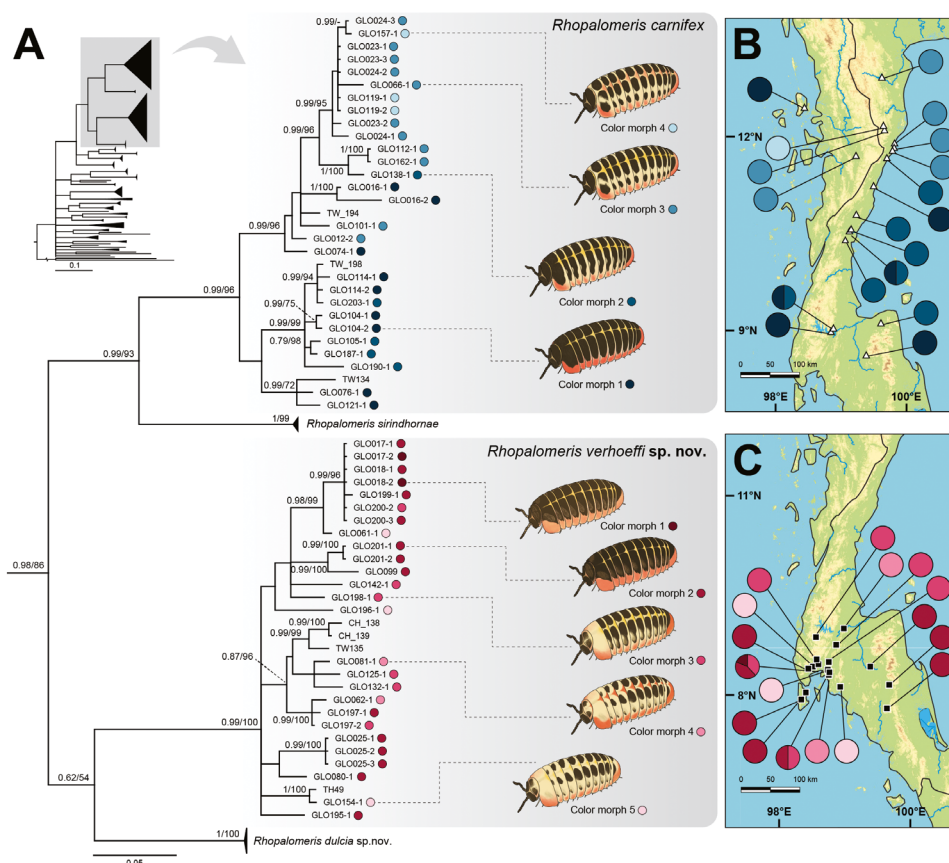


FIGURE 3 (A) Bayesian inference tree focusing on the detailed topology of *Rhopalomeris carnifex* (Pocock, 1889) and *R. verhoeffi* sp. nov., with colored drawings illustrating the color variations within each species. All millipede drawings are not to scale. (B, C) Maps of southern Thailand showing the distributions of color morphs for (B) *R. carnifex* and (C) *R. verhoeffi* sp. nov. The different shaded colors in each pie chart represent the proportion of the corresponding color morphs in that locality.

Rhopalomeris carnifex (Pocock, 1889)

Glomeris carnifex Pocock, 1889: 290 (D).

Type locality. Tenasserim.

Glomeris carnifex var. *pallida* Pocock, 1889: 290 (D). *Type locality.* Elphinstone Island [= Thayawthadangyi Island, Mergui Archipelago, Myanmar]

Glomeris carnifex – Pocock 1890: 385 (R); Attems 1914: 138 (L); Hoffman 1980: 66 (M).

Glomeris carnifex var. *pallida* – Attems 1914: 138 (L).

Rhopalomeris carnifex – Silvestri 1917: 142 (D); Attems 1936: 194 (R); Enghoff 2005: 88 (in part) (R); Decker 2010: 24 (in part) (R); Golovatch et al. 2011: 6 (in part) (D); Golovatch & Semenyuk 2016: 411 (in part) (M, K); Likhitrakarn et al. 2017: 6 (in part) (L); Nguyen et al. 2019: 292 (M); Nguyen et al. 2021: 259 (in part) (M); Likhitrakarn et al. 2023: 55 (in part) (L); Likhitrakarn et al. 2024: 241 (in part) (D, R, K, M1); Sapparojpattana et al. 2025: 58 (in part) (M).

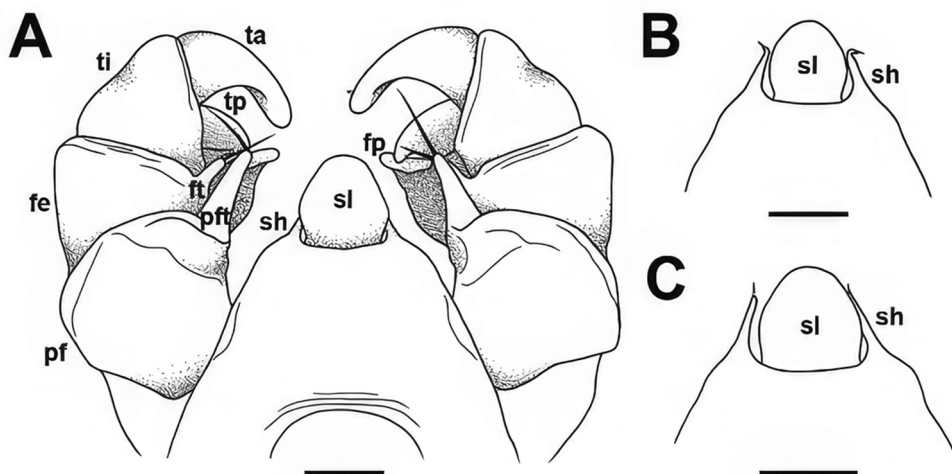


FIGURE 4 *Rhopalomeris carnifex* (Pocock, 1889), (A) telopods (MUMNH-GLO101), anterior view, (B, C) syncoxital lobe and horns, anterior view, (B) MUMNH-GLO109, (C) MUMNH-GLO023. Scale bar = 0.5 mm. Abbreviations: cx = coxa, cxl = coxal lobe, fe = femur, fp = femoral process, ft = femoral trichostele, pf = prefemur, pft = prefemoral trichostele of telopod, sh = syncoxital horn of telopod, sl = syncoxital lobe of telopod, sn = syncoxite notch, sx = syncoxite, ta = tarsus, ti = tibia, tp = tibial process

Rhopalomeris carnifex var. *pallida* – Silvestri 1917: 143 (in part) (D); Attems 1936: 194 (in part) (L).

Fig. 3, 4

New material examined. Thailand – 1 ♂ (MUMNH-GLO101) Phetchaburi Province, Kaeng Krachan District, near Kaeng Krachan National Park, elev. ca. 100 m a.s.l., 12°52'57.0"N 99°37'34.8"E, 4 Aug 2022, leg. C. Sutcharit; 1 ♂ (MUMNH-GLO066) Prachuap Khiri Khan Province, Mueang District, Tham Phra Non, 40 m a.s.l., 11°51'43.0"N 99°49'21.5"E, 26 Sep 2022, leg. E. Jeratthitikul; 3 ♀♀ (MUMNH-GLO112) Prachuap Khiri Khan Province, Mueang District, Khao Lom Muak, Ao Manao, elev. ca. 120 m a.s.l., 11°47'08.1"N 99°48'58.0"E, 9 Mar 2007, leg. C. Sutcharit; 1 ♀ (MUMNH-GLO138) Prachuap Khiri Khan Province, Mueang District, Hat Wanakon, elev. ca. 0–10 m a.s.l., 11°38'09.4"N 99°42'09.4"E,

14 Jan 2014, leg. C. Sutcharit; 5 ♂♂, 7 ♀♀ (MUMNH-GLO162) Prachuap Khiri Khan Province, Mueang District, Wat Klong Wan, elev. ca. 0–10 m a.s.l., 11°44'56.6"N 99°47'15.5"E, 14 Jan 2014, leg. C. Sutcharit; 16 ♂♂, 20 ♀♀ (MUMNH-GLO023) Prachuap Khiri Khan Province, Kui Buri District, Ban Yang Chum, near Kui Buri National Park, elev. ca. 60–100 m a.s.l., 12°04'02.7"N 99°39'53.8"E, 7 Aug 2014, leg. N. Likhitrakarn and C. Sutcharit; 1 ♀ (MUMNH-GLO024) Prachuap Khiri Khan Province, Kui Buri District, Ban Yang Chum, near Kui Buri National Park, elev. ca. 60–100 m a.s.l., 12°04'02.7"N 99°39'53.8"E, 7 Aug 2015, leg. N. Likhitrakarn and C. Sutcharit; 7 ♂♂, 7 ♀♀ (MUMNH-GLO119) Prachuap Khiri Khan Province, Kui Buri District, near Kui Buri National Park, elev. ca. 160–180 m a.s.l., 12°08'12.9"N 99°38'46.6"E, 11 Oct 2010, leg. C. Sutcharit; 2 ♂♂, 5 ♀♀ (MUMNH-GLO157) Prachuap Khiri Khan

Province, Kui Buri District, near Kui Buri National Park, elev. ca. 160–180 m a.s.l., 12°08'12.9"N 99°38'46.6"E, 9 Aug 2016, leg. N. Likhitrakarn and R. Srisonchai; 28 ♂♂, 37 ♀♀ (MUMNH-GLO104) Prachuap Khiri Khan Province, Bang Saphan District, Wat Khao Tham Ma Rong, elev. ca. 20 m a.s.l., 11°12'09.2"N 99°29'55.2"E, 12 Oct 2008, leg. C. Sutcharit; 1 ♂, 13 ♀♀ (MUMNH-GLO114) Chumphon Province, Mueang District, Wat Uthaitam, elev. ca. 10–20 m a.s.l., 10°30'24.2"N 99°07'50.5"E, 12 Oct 2008, leg. C. Sutcharit; 4 ♂♂, 3 ♀♀ (MUMNH-GLO203) Chumphon Province, Mueang District, Wat Tham Khao Ma Yang, elev. ca. 20 m a.s.l., 10°32'09.6"N 99°08'59.2"E, 25 May 2023, leg. R. Srisonchai, N. Likhitrakarn, and P. Sapparojattana; 3 ♀♀ (MUMNH-GLO105) Chumphon Province, Sawi District, Chola Khiri Monastery, elev. ca. 60 m a.s.l., 10°22'24.1"N 99°03'38.3"E, 11 Jul 2017, leg. R. Srisonchai and N. Likhitrakarn; 5 ♂♂, 3 ♀♀ (MUMNH-GLO187) Chumphon Province, Pathio District, Tham Pisadan, elev. ca. 100 m a.s.l., 10°45'36.4"N 99°13'46.7"E, 15 May 2023, leg. R. Srisonchai; 7 ♂♂, 8 ♀♀ (MUMNH-GLO074) Surat Thani Province, Ban Ta Khun District, Wat Khao Phang, elev. ca. 40 m a.s.l., 8°57'49.0"N 98°50'18.6"E, 5 May 2017, leg. E. Jeratthitikul and R. Srisonchai; 15 ♂♂, 5 ♀♀ (MUMNH-GLO076) Surat Thani Province, Wiang Sa District, Wat Tham Khao Khok, elev. ca. 120 m a.s.l., 8°35'32.4"N 99°23'06.5"E, 4 Jul 2017, leg. N. Likhitrakarn; 2 ♂♂, 1 ♀ (MUMNH-GLO121) Surat Thani Province, Khiri Rat Nikhom District, Tham Phueng, elev. ca. 60–80 m a.s.l., 9°00'50.1"N 98°52'40.1"E, 20 Jun 2018, leg. N. Likhitrakarn; 2 ♂♂ (MUMNH-GLO190) Surat Thani Province, Kanchanadit District, Wat Khao

Phanom Wang, elev. ca. 40 m a.s.l., 9°05'25.0"N 99°36'32.2"E, 16 May 2023, leg. R. Srisonchai and P. Sapparojattana; 1 ♀ (ZFMK MYR4912) [TW134] Surat Thani Province, Mo Ko Samui, Ko Phangan, Haad Gruad, elev. ca. 5 m a.s.l., 9°46'00"N 99°58'00"E, 20 Aug 2015, leg. P. Autt; 1 ♀ (ZFMK MYR8109) [TW194] Prachuap Khiri Khan, 2 km SSW Bang Saphan, elev. ca. 50 m a.s.l., 11°12'07"N 99°29'48"E, Aug 2018, leg. P. Autt; 3 ♂♂, 1 ♀ (ZFMK MYR8126) [TW198] Chumphon, 6 km SW Chumphon, elev. ca. 90 m a.s.l., 10°27'53"N 99°07'43"E, Aug 2018, leg. P. Autt. **Myanmar** – 1 ♂, 2 ♀♀ (MUMNH-GLO012) Tanintharyi Region, Limestone Forest near Lampane Village, elev. ca. 40–100 m a.s.l., 11°40'18.1"N 99°13'30.1"E, 7 Jun 2015, leg. C. Sutcharit and R. Srisonchai.

Variation. The newly collected specimens from Thailand displayed four distinct color morphs, as described below and illustrated in Fig. 3A.

Color morph 1: Blackish body with red lateral margin and a narrow yellow axial line of tergites 2–11. Posterior margin of each tergite narrow, light yellowish. Head and antenna blackish. Pygidium blackish with carmine or reddish margin. Venter light yellowish. Legs light yellowish to brownish. This color morph is the same as described in specimens from Myanmar (Likhitrakarn et al., 2024b).

Color morph 2: Blackish body with pale red lateral margin and yellow axial line of tergites 2–11. The blackish patch on tergite narrower than in color morph 1. Posterior margin of each tergite broad, light yellowish. Head and antenna blackish. Pygidium blackish with red margin. Venter light yellowish. Legs light yellowish to brownish.

Color morph 3: Blackish body with pale red lateral margin and yellow axial line of tergites 2–11. The blackish patch separated into a pair of large oval or wide subtriangular spots on the paramedian of each tergite and a pair of small oval spots on each lateral side, the paramedian and lateral spots somewhat connected by a narrow black band in some specimens. Thoracic shield black, occasionally with light yellowish marbled spot at the middle of black part. Posterior margin of each tergite broad, light yellowish. Head and antenna blackish. Pygidium blackish with red margin. Venter light yellowish. Legs light yellowish to brownish.

Color morph 4: Color similar to color morph 3, but with a pale red or pink mid-posterior tergal margin.

Several characters of the newly collected specimens from Thailand were also studied and are provided here:

Collum with 2–4 transverse striae. Telopod enlarged and stout. Telopodite (Fig. 4A) similar to the original description, syncoxital lobe height varied from reaching at the same level of its horns to reaching double of syncoxital horn height (Fig. 4B, C). Other characters are consistent with the redescription provided in Likhitrakarn et al. (2024).

Distribution. This species exhibits a broad distribution range, extending across Myanmar and Thailand (from Phetchaburi to Surat Thani province; figs 2, 3B), and has partial sympatry with *R. verhoeffi* sp. nov. in Surat Thani Province, with no evidence of co-occurrence in the same locality. In Thailand, color morphs 1 and 2 are distributed in Prachuap Khiri Khan, Chumphon, and Surat Thani provinces (Fig. 3B), while color morphs 3 and 4 are only distributed

in Phetchaburi and northern Prachuap Khiri Khan (Fig. 3B).

Remarks. The distribution of *R. carnifex* has been previously reported along the Tenasserim range, from Myanmar to Malay Peninsula, including several localities in southern Thailand (Phuket, Krabi, Phangnga, and Surat Thani provinces) (Pocock, 1889; Verhoeff, 1906; Silvestri, 1917; Enghoff, 2005; Decker, 2010). However, the genetic results showed that the southernmost distribution of this species is demarcated in Wiang Sa District, Surat Thani Province, Thailand (approximately above 8°35' N; Fig. 2). Populations further southward that have been previously recognized as either '*R. carnifex*' or '*R. carnifex* var. *pallida*' (e.g., Silvestri, 1917; Attems, 1936; Enghoff, 2005; Decker, 2010; Golovatch et al., 2011; Golovatch & Semenyuk, 2016; Nguyen et al., 2021; Likhitrakarn et al., 2023a, 2024b; Sapparoj Pattana et al., 2025) are here recognized as *R. verhoeffi* sp. nov.

***Rhopalomeris muka* Sapparoj Pattana & Likhitrakarn, sp. nov.**

Fig. 5–7

Holotype. ♂ (MUMNH-GLO102) Thailand, Kanchanaburi Province, Sai Yok District, Mahidol University Kanchanaburi Campus (MUKA), elev. ca. 260 m a.s.l., 14°07'38.9"N 99°09'30.3"E, 8 October 2022, leg. E. Jeratthitikul and P. Paejaroen.

Paratypes. 2 ♂♂, 5 ♀♀ (MUMNH-GLO102) same collection data as for the holotype; 9 ♂♂, 11 ♀♀ (MUMNH-GLO223) same locality as the holotype, 7 October 2023, leg. E. Jeratthitikul and P. Paejaroen.

Etymology. The specific epithet '*muka*' is a noun in apposition, derived from the acronym of the type locality, Mahidol

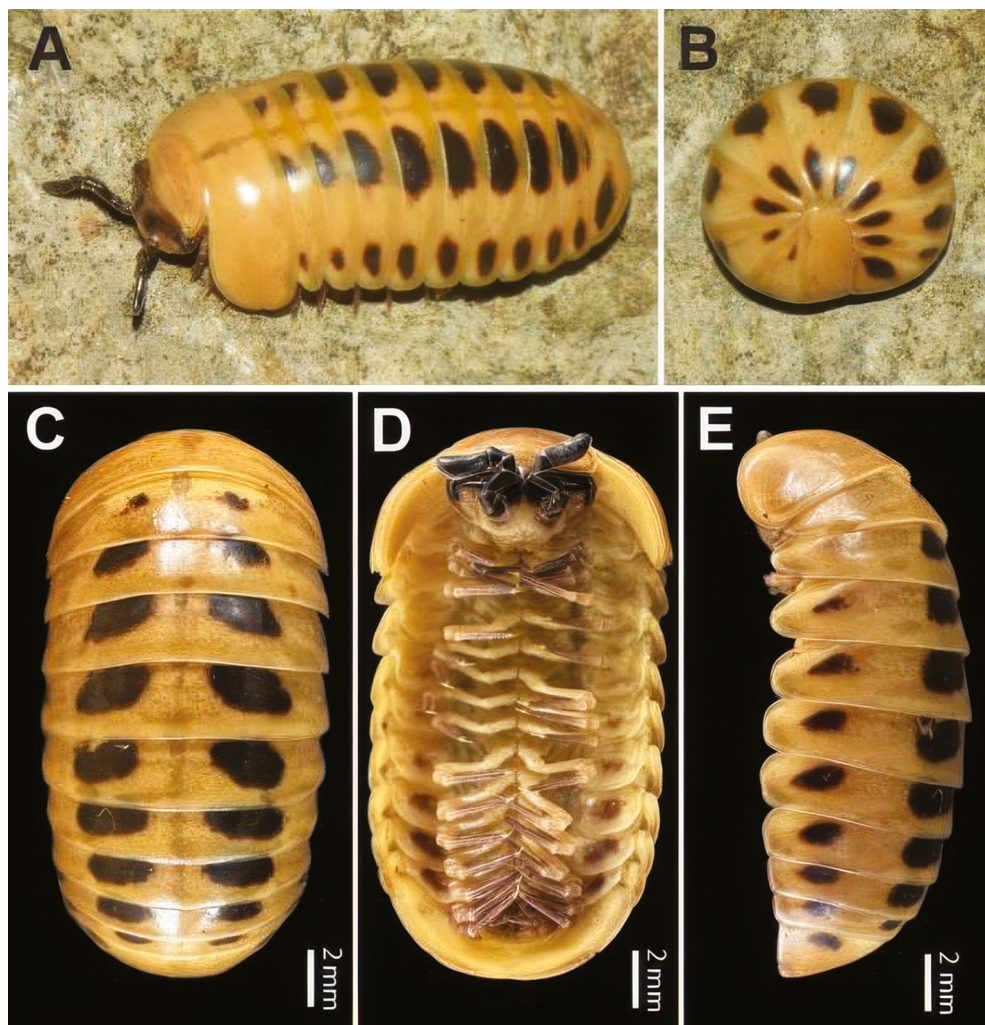


FIGURE 5 *Rhopalomeris muka* sp. nov., (A, B) paratype (MUMNH-GLO223), habitus, live coloration (C–E) ♂ paratype (MUMNH-GLO223), alcohol preserved, in dorsal, ventral, and lateral views (A) unrolled in sublateral view (B) rolled in sublateral view. (A, B) image not to scale (C–E) scale bars: 2 mm

University Kanchanaburi Campus (MUKA).

Diagnosis. Yellowish body with a pair of dark brown paramedian spots and lateral sides with dark brown oval spots on tergites 3 to 11 (Fig. 5). Venter light yellowish with a large brown spot on pleurites 6–11. The syncoxital lobe of telopod with a

narrow-pointed tip, longer than its horns (Fig. 6D, E).

Diagnostical notes. Differs from other *Rhopalomeris* species by the yellowish body with a pair of dark brown paramedian spots and lateral sides with dark brown oval spots on tergites 3 to 11, a relatively larger body size (about 15.6–22.3

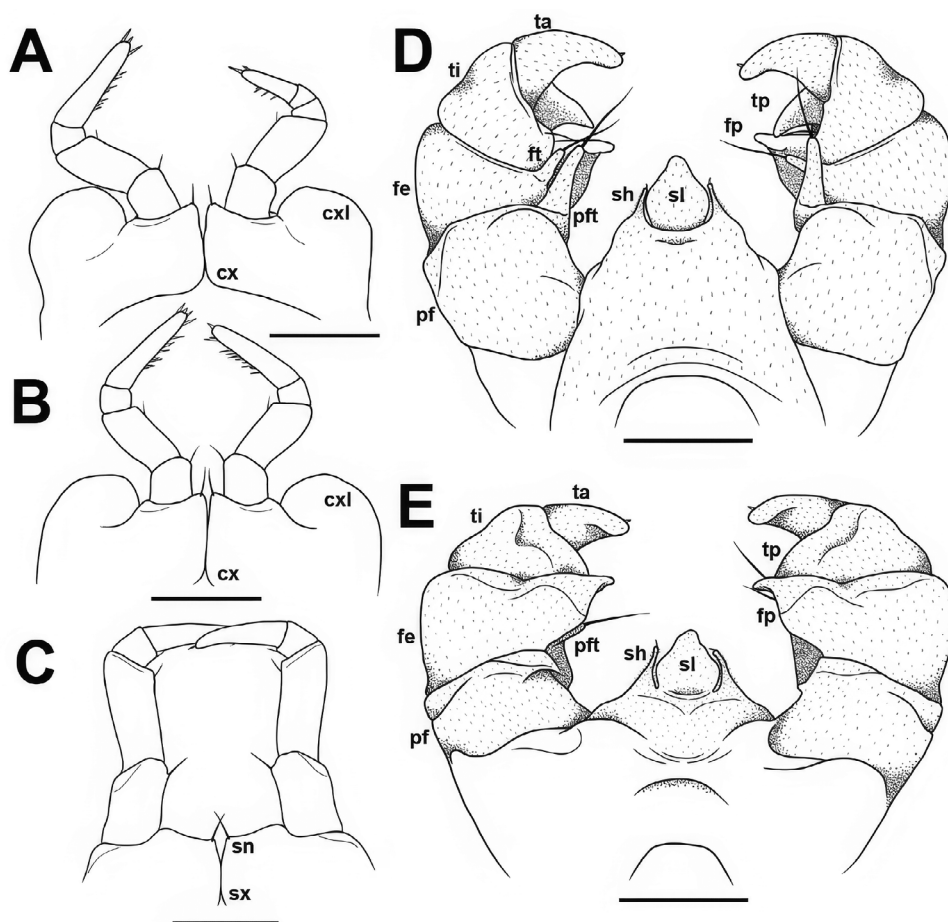


FIGURE 6 *Rhopalomeris muka* sp. nov., (A, C-E) ♂ Holotype (B) ♂ Paratype, (A, B) legs 17, anterior view, (C) legs 18, anterior view, (D, E) telopods, anterior and posterior views. Scale bar = 1 mm. Abbreviations: cx = coxa, cxl = coxal lobe, fe = femur, fp = femoral process, ft = femoral trichostele, pf = prefemur, pft = prefemoral trichostele of telopod, sh = syncoxital horn of telopod, sl = syncoxital lobe of telopod, sn = syncoxite notch, sx = syncoxite, ta = tarsus, ti = tibia, tp = tibial process

mm), and the characteristic of a narrow-pointed tip on central lobe of the telopod syncoxite. The new species differs from *R. nigroflava* from Myanmar in the marking pattern on the tergites (dark brown paramedian spots and dark brown lateral spots vs brown to blackish markings). The new species is clearly distinguishable from *R. sauda* and *R. nagao* from Vietnam in the color pattern on the thoracic shield (black

color absent vs black color present in both *R. sauda* and *R. nagao*).

Description. Body length of unrolled holotype, 17.4 mm; width 8.9 mm. Body length of unrolled paratypes, 15.6–19.8 mm (♂; n = 4), 14.9–22.3 mm (♀; n = 6); width of second tergite 8.6–10.0 mm (♂; n = 4), 8.3–10.3 mm (♀; n = 6).

Color. Generally yellowish with a pair of dark brown paramedian spots,

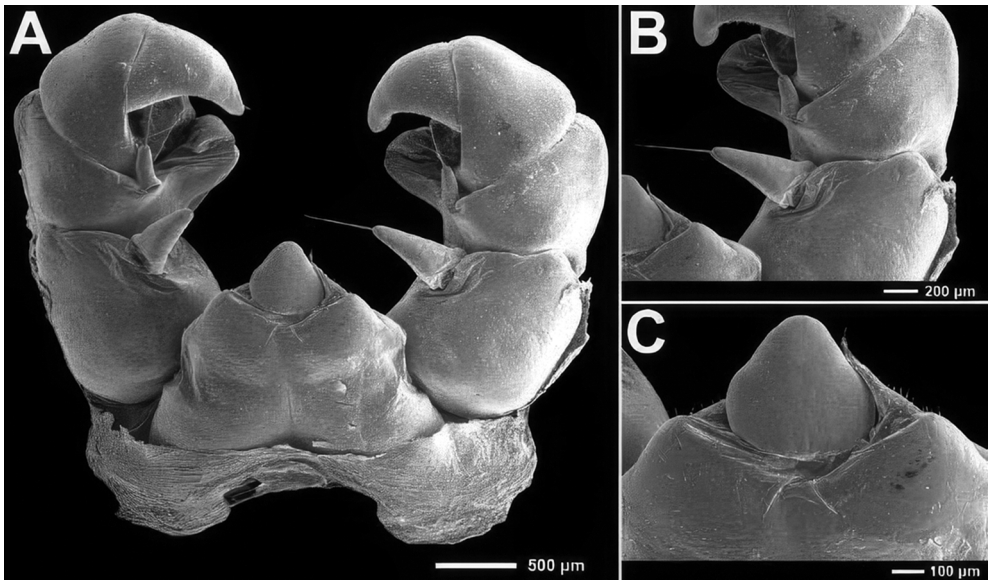


FIGURE 7 (A–C) *Rhopalomeris muka* sp. nov., ♂ paratype (MUMNH-GLO223), from Mahidol University Kanchanaburi Campus, Kanchanaburi. (A) telopods, anterior view (B) prefemoral and femoral trichostyles (C) syncoxital lobe and horns

parallelly arranged, and a pair of small, lateral, dark brown oval spots on each of tergites 3 to 11; this latter pair smaller on tergites 3–4 and 10–11 (Fig. 5A, C). Anal shield (= pygidium) yellowish with a pair of lateral blackish-brown oval spots (Fig. 5A, E). Body with translucent bands at both lateral and caudal edges of all tergites. Head yellowish with a pair of curved dark brown patches above the antennal sockets; antennae blackish. Ventral tergites light yellowish with a large brown spot on pleurites 6–11; legs yellowish to brown (Fig. 5D).

Head. Ommatidia 8(9)+1, lenses blackish and convex cornea. Organ of Tömösváry transverse-oval, approximately 1.6–1.7 times as long as wide, strongly horseshoe-shaped. Labrum scantily setose. Gnathochilarium with 2+2 palps subequal in length. Antennomere 6 long, slightly curved, approximately 1.6–1.8 times as

long as high (Fig. 5D). Antennal tip with 44–95 small sensory cones.

Body. Collum semicircular as usual, with 3–5 transverse striae. Thoracic shield with barely broad hyposchism field, almost reaching the caudal tergal margin, 7–8 striae; 3–4 lying above schism, 2 equal to schism, remaining 2 beneath schism, 6–8 completely crossing the dorsum. Pygidium rounded, slightly concave medio-caudally.

Legs. Mid-body legs: tarsus with one apical spine, 6–7 lateral spines, and 19–22 ventral spines. Claw narrow and elongate. Male leg pair 1: similar to mid-body legs, but coxae protruding and elongate, with two long spines. Tarsus with only 14–16 ventral spines. Male leg pair 2: similar to mid-body legs, but coxae with two long spines. Gonopore covering 1/3 of coxa. Male leg pair 17 (Fig. 6A, B): strongly reduced, 4 podomeres, coxa with a setiferous tubercle, often rounded coxal lobe, tarsus with

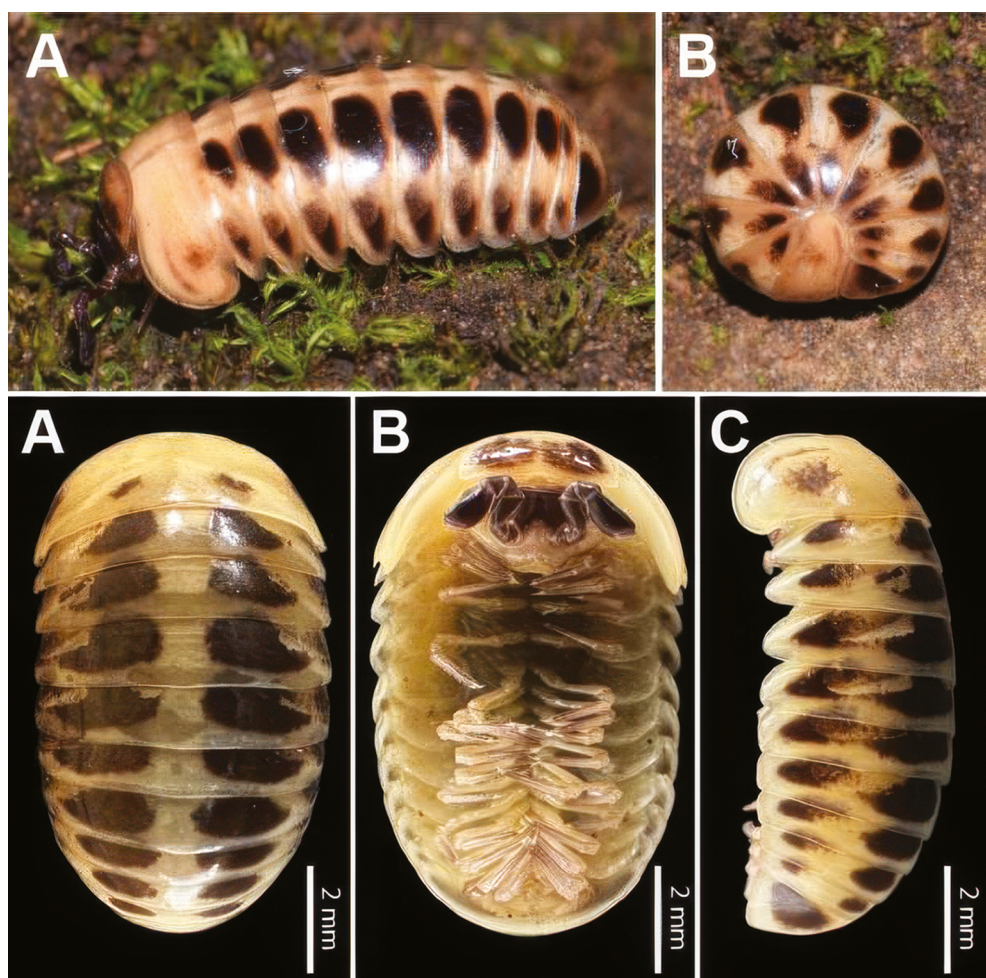


FIGURE 8 *Rhopalomeris lentiginosa* sp. nov., (A, B) paratype (MUMNH-GLO086), habitus, live coloration (C–E) ♂ paratype (MUMNH-GLO042), alcohol preserved, in dorsal, ventral, and lateral views (A) unrolled in sublateral view (B) rolled in sublateral view. (A, B) image not to scale (C–E) scale bars: 2 mm

2–4 strong apical and 7–8 strong median spines. Male leg pair 18 (Fig. 6C): less strongly reduced, 4 podomeres, with a small, narrow arch-shape syncoxite notch, tarsus with one apical spine.

Telopods. Enlarged and stout, with a relatively high, central, syncoxital lobe subtriangular with a narrow, drop-shaped (guttiform) tip, flanked by two setose horns, each shorter than the syncoxital

lobe, with small bulbous structures apically, being crowned by a subapical setoid filament (Fig. 6D, E). Prefemur distroventrally with a long trichostele anteriorly. Femur with a small anterior trichostele and a large posterior outgrowth, holding a pointed membranous apical sac slightly folded anteriad. Tibia with an anterior seta, a large distolateral tibial process, and a round parabasal tubercle posteriorly.

Tarsus elongated, slightly sigmoid, with a strong apical spine.

Distribution. Currently known only from the type locality, Mahidol University Kanchanaburi Campus (MUKA), which is located among limestone mountains of the Tenasserim range in western Thailand.

Habitats. The type locality is surrounded by mixed deciduous forest, where the millipedes were primarily found under litter on the campus grounds or on the sides of large limestone rocks.

Rhopalomeris lentiginosa

Sapparojpattana & Likhitrakarn, sp. nov.

Fig. 8–10

Holotype. ♂ (MUMNH-GLO086) Thailand, Kanchanaburi Province, Thong Pha Phum District, Wat Tha Khanun, elev. ca. 100 m a.s.l., 14°44'29.1"N 98°38'15.4"E, 16 August 2016, leg. R. Srisonchai.

Paratypes. 2 ♀♀ (MUMNH-GLO086) same collection data as for the holotype; 13 ♂♂, 14 ♀♀ (MUMNH-GLO042) same locality as the holotype, 6 October 2022, leg. E. Jeratthitikul.

Etymology. The specific epithet '*lentiginosa*' is derived from the Latin '*lentigo*', meaning 'small spots or freckled', referring to the characteristic dark brown markings on the lateral side of the thoracic shield.

Diagnosis. Body light yellowish with a pair of large blackish brown subtriangular oval paramedian spots on tergites 2–11 and a small dark brown oval spot on the lateral side of tergites 3–11. Thoracic shield with a dark brown marbled spot and curved line on lateral side. Venter light yellowish with a light brown spot on pleurites 6–11, this

spot darker on pleurites 9–11. The syncoxital horns large, distantly separated from syncoxital lobe.

Diagnostical notes. Its color pattern resembles that of *R. muka* sp. nov. but differs in the smaller body size (length 7.6–11.8 mm, width 4.3–6.2 mm vs length 14.9–22.3 mm, width 8.3–10.3 mm), the color marking on the first tergite and thoracic shield (dark brown vs absent), the head color (mostly blackish brown vs mostly yellowish), the syncoxital lobe of the telopod (small and slightly shorter than horns vs large and higher than horns), and the different structure of the syncoxital horns (large, distantly separated from central lobe vs short, close to central lobe). *R. lentiginosa* sp. nov. is clearly distinguishable from *R. nigroflava* from Myanmar in the color pattern on the tergites (large blackish brown subtriangular oval paramedian spots and dark brown lateral spots vs brown to blackish markings), and the thoracic shield color pattern (dark brown marbled spot and curved line on lateral side vs black color absent).

Description. Body length of unrolled holotype, 9.2 mm; width 4.8 mm. Body length of unrolled paratypes, 7.6–10.8 mm (♂; n = 5), 9.4–11.8 mm (♀; n = 6); width of second tergite 4.3–5.8 mm (♂; n = 5), 5.3–6.2 mm (♀; n = 6).

Color. Collum light yellowish with a pair of large blackish brown subtriangular oval spots, parallelly arranged along the mid-dorsal of tergites 2–11 and a small dark brown oval spot on the lateral side of tergites 3–11; the latter spot growing broader and longer on tergites 5–8 (Fig. 8A). The first tergite yellowish to yellowish brown with a pair of large dark brown patches; the thoracic shield with a dark brown marbled

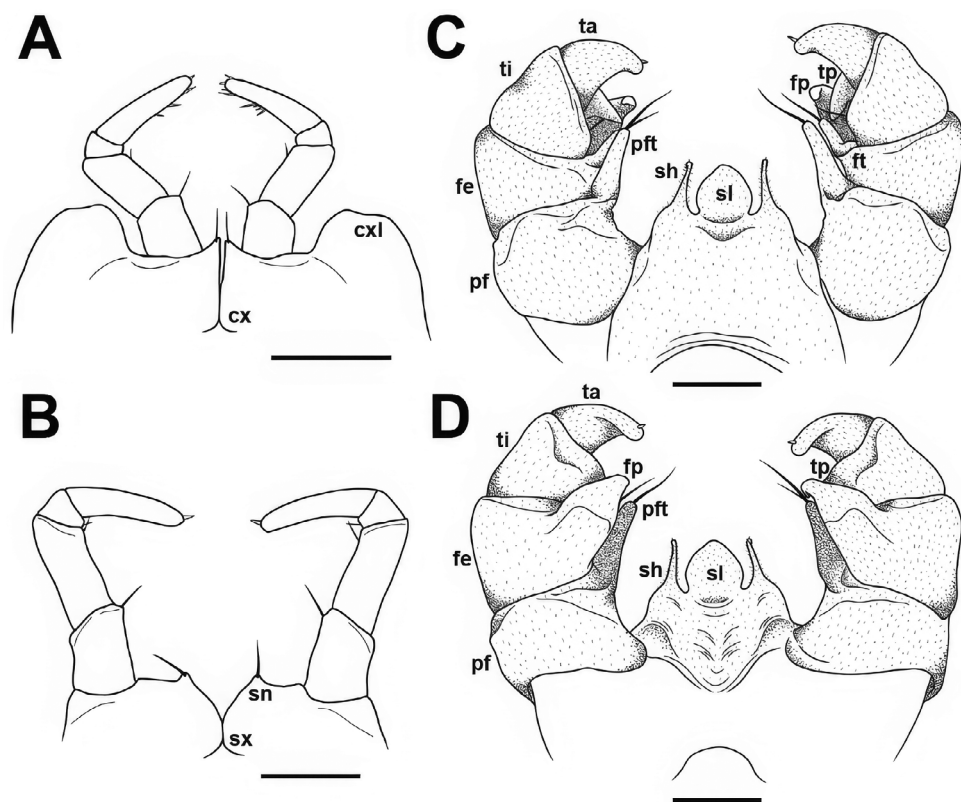


FIGURE 9 *Rhopalomeris lentiginosa* sp. nov., ♂ Holotype, (A) legs 17, anterior view, (B) legs 18, anterior view, (C, D) telopods, anterior and posterior views. Scale bar = 1 mm. Abbreviations: cx = coxa, cxl = coxal lobe, fe = femur, fp = femoral process, ft = femoral trichostele, pf = prefemur, pft = prefemoral trichostele of telopod, sh = syncoxital horn of telopod, sl = syncoxital lobe of telopod, sn = syncoxite notch, sx = syncoxite, ta = tarsus, ti = tibia, tp = tibial process

spot and curved line on lateral, anteriorly placed. Head blackish brown, except the labrum and Tömösváry's organ light yellow; antennae blackish (Fig. 8B). Pygidium light yellowish with a pair of rather large, lateral, subtriangular spots, almost reaching the anterior margin (Fig. 8C). Venter light yellowish with a light brown spot on pleurites 6–11, this spot darker on pleurites 9–11; legs pale yellowish to brown (Fig. 8B).

Head. Ommatidia 8(9)+1, with blackish and convex cornea. Tömösváry organ transverse-oval, approximately 1.3–1.5 times as long as broad, strongly

horseshoe-shaped. Labrum scantily setose. Gnathochilarium with 2+2 palps subequal in length. Antennomere 6 slightly curved, approximately 1.4–1.7 times as long as high (Fig. 8B). Antennal tip with 38–57 small sensory cones.

Body. Collum as usual, with 2–3 transverse striae. Thoracic shield with a narrow hyposchism field, not projecting behind the caudal tergal margin, 6–7 striae; 3 lying above schism, 1 or 2 equal to schism, remaining 2 beneath schism, 5 completely crossing the dorsum. Pygidium rounded, not concave medio-caudally.

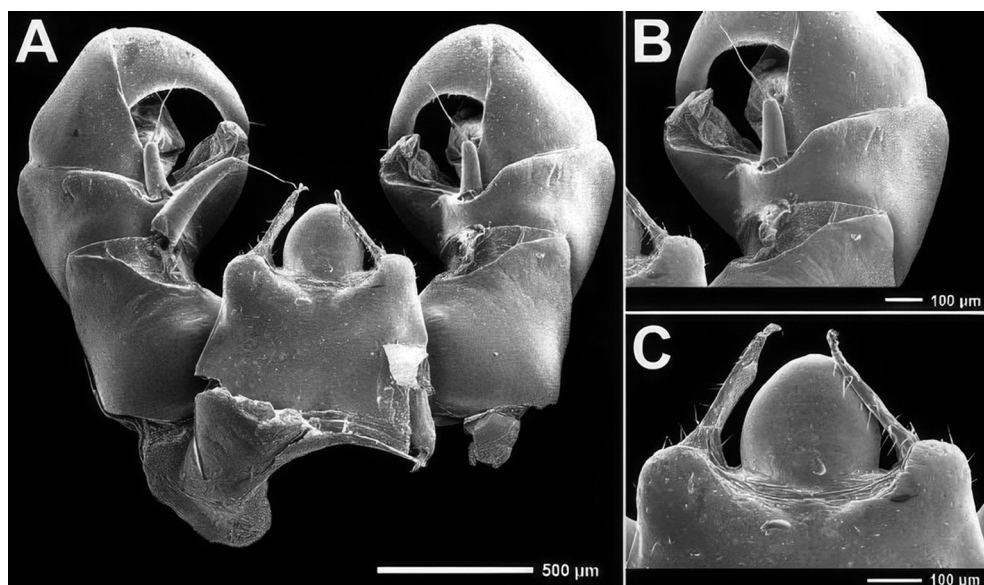


FIGURE 10 (A–C) *Rhopalomeris lentiginosa* sp. nov., ♂ paratype (MUMNH-GLO042), from Tha Khanun, Thong Pha Phum, Kanchanaburi. (A) telopods, anterior view (B) prefemoral and femoral trichostyles (C) syncoxital lobe and horns

Legs. Mid-body legs: tarsus with one apical spine, 10–13 lateral spines, and 16–19 ventral spines. Claw narrow and elongate. Male leg pair 1: similar to mid-body legs, but coxae protruding and elongate, with two long spines. Tarsus with 16–19 ventral spines. Male leg pair 2: similar to mid-body legs, but coxae with two long spines. Gonopore covering 1/3 of coxa. Male leg pair 17 (Fig. 9A): simple, particularly strongly reduced, 4 podomeres, with a setiferous tubercle on coxa, tarsus with 2–3 strong apical and 2–4 strong median spines. Male leg pair 18 (fig. 9B): simple, less strongly reduced, 4 podomeres, with a moderate, wide, V-shaped syncoxital notch, tarsus with one apical spine.

Telopods. Enlarged and stout, with a small, round, subtriangular, central, syncoxital lobe outcurve on both sides, flanked by two large, spiniform, setose horns (fig.

9C, D). The horns slightly bent at the tip, distantly separated, somewhat longer than the syncoxital lobe, being crowned by a small subapical setoid filament. Prefemur subrectangular, with an elongated, distroventral trichostele anteriorly. Femur with a relatively short anterior trichostele and posterior with a large, elongated, femoral process, holding a membranous apical sac folded antieriad. Tibia with an anterior seta, bearing a moderate, strongly curved, distolateral tibial process, and a round parabasal tubercle posteriorly. Tarsus elongated, faintly sigmoid, with a strong terminal spine.

Variation. In a few individuals, the lateral marbled dark brown spot and the paramedian spots on the thoracic shield may be absent, or the light brown spots on the venter may be present only on pleurites 9–11.

Distribution. Currently known only from the type locality.

Habitats. The type locality is an isolated limestone mountain surrounded by agricultural land and human settlements, where the millipedes were found climbing on the large limestone rocks and forest ground. The type locality is situated approximately 87 kilometers north from the type locality of *R. muka* sp. nov. and located in an area with a higher degree of human disturbance than the type locality of *R. muka* sp. nov.

***Rhopalomeris dulcia* Sapparojpattana & Likhitrakarn, sp. nov.**

Fig. 11–13

Holotype. ♂ (MUMNH-GLO188) Thailand, Chumphon Province, Mueang District, Tham Chang Puek Monastery, elev. ca. 100 m a.s.l., 10°26'46.2"N 99°02'06.5"E, 16 May 2023, leg. R. Srisonchai, E. Jerattitikul, and P. Sapparojpattana.

Paratypes. 2 ♂♂, 2 ♀♀ (MUMNH-GLO188) same collection data as for the holotype.

Etymology. The specific epithet '*dulcia*' is a plural noun from the Latin word '*dulce*' or '*dulcis*' meaning 'sweets' or 'candy', referring to the striking coloration reminiscent of candy.

Diagnosis. Body light yellowish with bright red lateral margin and a yellow posterior margin on each tergite. The dark patches on the first tergite are oblique and subtriangular on the lateral side. Thoracic shield with a large black dot on each lateral side. Venter light yellowish with a brown spot on pleurites 8–11. The syncoxital lobe of telopod large, like a conical mushroom cap. The syncoxital horns are shorter and

more posteriorly placed than the syncoxital lobe.

Diagnostical notes. The color of *R. dulcia* sp. nov. resembles that of *R. sirindhornae*, but both species differ in their significantly larger body size (length 15.3–23.5 mm, width 8.4–11.9 mm vs length 8.3–12.7 mm, width 4.22–5.8 mm), the color pattern on the thoracic shield (a pair of large black dots laterally with a bright red lateral margin vs a pair of faded black dots on the lateral side with a pale pink lateral margin), and the structure of the syncoxital horns (shorter and more posteriorly placed to syncoxital lobe vs slightly shorter or at the level of the syncoxital lobe). It can also be distinguished from *R. carnifex* in the color pattern on the thoracic shield (a pair of large black dots laterally with a bright red lateral margin vs black patch or black color with a red or pale red lateral margin) and in the shape of the syncoxital lobe (large, round, subtriangular, like a conical mushroom cap vs subtriangular, with a low ridge at the base of the lobe on the posterior side).

Description. Body length of unrolled holotype, 22.8 mm; width 12.0 mm. Body length of unrolled paratypes, 15.3–19.8 mm (♂; n = 2), 20.3–23.5 mm (♀; n = 2); width of second tergite 8.4–10.5 mm (♂; n = 2), 10.8–11.9 mm (♀; n = 2).

Color. Tergites light yellowish with bright red lateral margin and yellow posterior margin. The first tergite with a pair of oblique, subtriangular black patches on lateral side. Thoracic shield holds a pair of black dots on lateral side (fig. 11A, E). A pair of large black subtriangular patches on mid-dorsal and a pair of large black oval spots on lateral side of the 3rd–11th tergites, usually rather parallel-sided, the

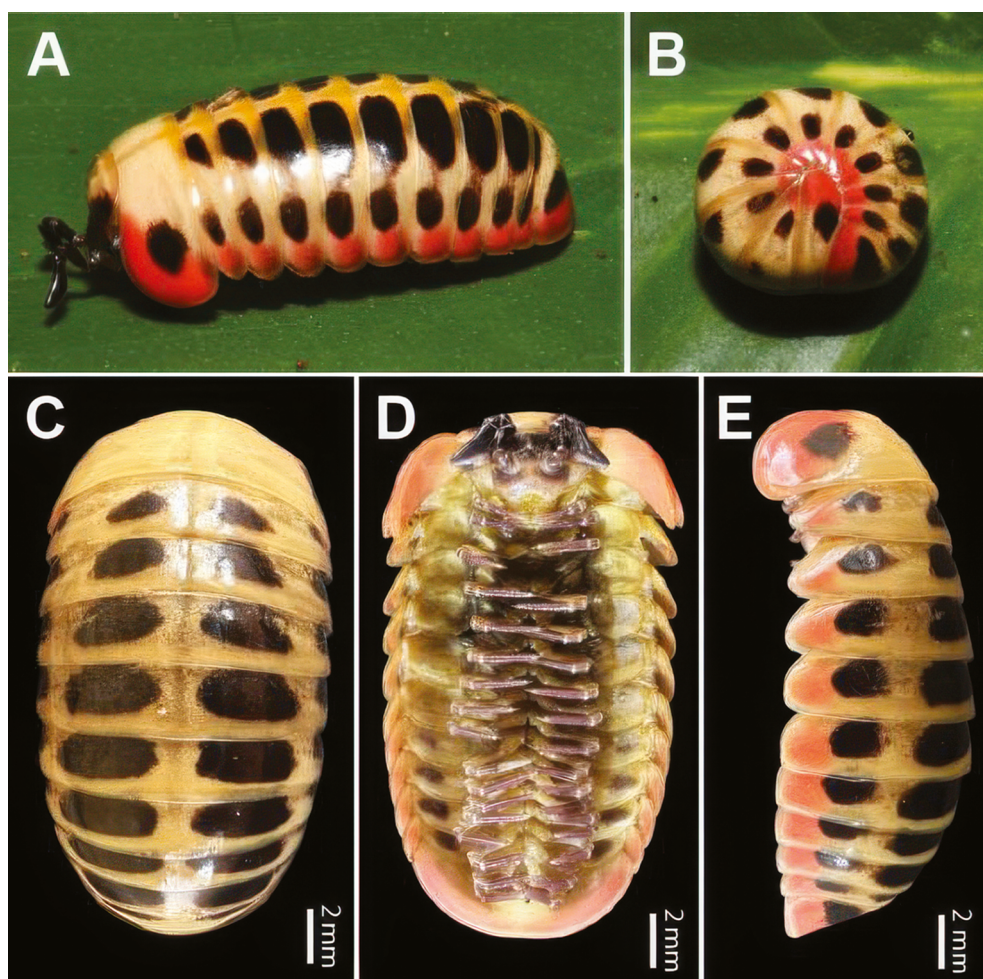


FIGURE 11 *Rhopalomeris dulcia* sp. nov., (A, B) paratype (MUMNH-GLO188), habitus, live coloration (C–E) ♀ paratype (MUMNH-GLO188), alcohol preserved, in dorsal, ventral, and lateral views (A) unrolled in sublateral view (B) rolled in sublateral view. (A, B) image not to scale (C–E) scale bars: 2 mm

latter growing broader on tergites 6–11 (Fig. 11A–C). Head and antennae blackish. Pygidium light yellowish with a thick red caudal margin and a pair of black spots (Fig. 11A, E). Venter light yellowish with a brown spot on pleurites 8–11, legs brownish purple (Fig. 11D).

Head. Ommatidia 8(9)+1, with blackish brown and convex cornea. Tömösváry organ oblong-oval, about 1.0–1.2 times as

long as wide, strongly horseshoe-shaped. Labrum scantily setose. Gnathochilarium with 2+2 palps subequal in length. Antennae clavate with 71–74 small apical cones. Antennomere 6 large, strongly curved, about 1.6–1.8 times as long as high (Fig. 11D). Antennomere 7 elongated, slightly curved.

Body. Collum semicircular, with 4–5 transverse striae. Thoracic shield with

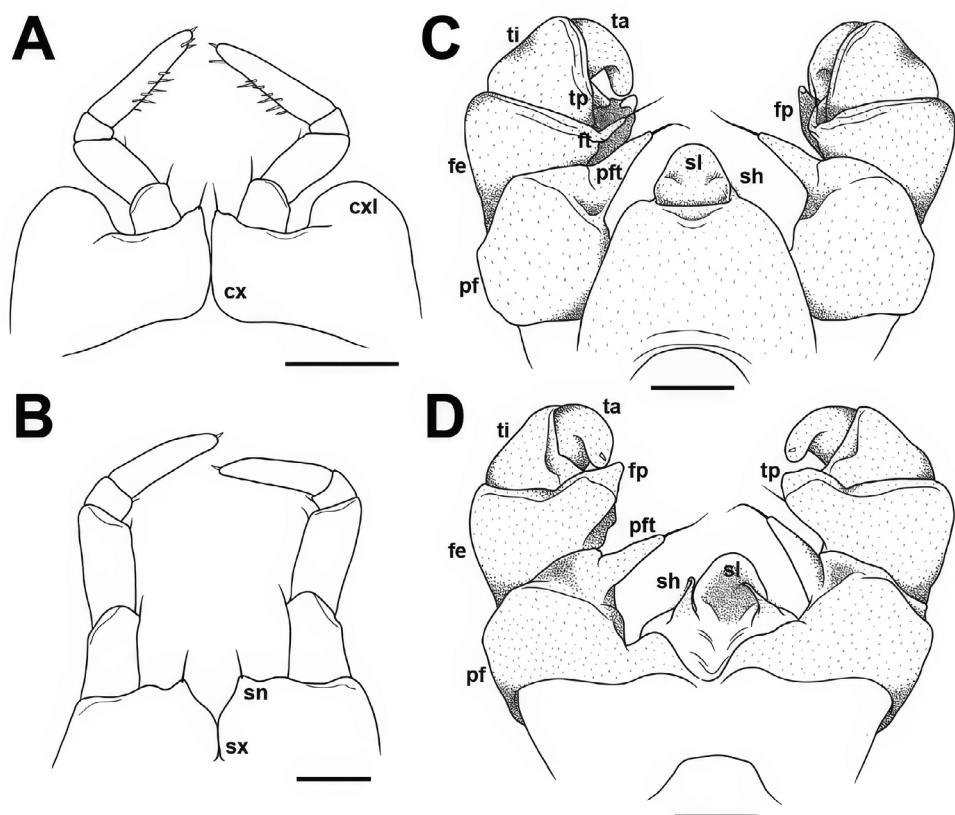


FIGURE 12 *Rhopalomeris dulcia* sp. nov., ♂ Holotype, (A) legs 17, anterior view, (B) legs 18, anterior view, (C, D) telopods, anterior and posterior views. Scale bar = 1 mm. Abbreviations: cx = coxa, cxl = coxal lobe, fe = femur, fp = femoral process, ft = femoral trichostele, pf = prefemur, pft = prefemoral trichostele of telopod, sh = syncoxital horn of telopod, sl = syncoxital lobe of telopod, sn = syncoxite notch, sx = syncoxite, ta = tarsus, ti = tibia, tp = tibial process

a narrow hyposchism field, not reaching behind the caudal tergal margin, 7 striae; 3 lying above schism, 1 equal to schism, remaining 3 beneath schism, 5–7 completely crossing the dorsum. Pygidium rounded, strongly concave medio-caudally.

Legs. Mid-body legs: tarsus with one apical spine, 8–15 lateral spines, and 20–24 ventral spines. Claw narrow and elongate. Male leg pair 1: similar to mid-body legs, but coxae protruding and elongate, with two long spines. Tarsus with only

16–19 ventral spines. Male leg pair 2: similar to mid-body legs, but coxae with two long spines. Gonopore covering 1/3 of coxa. Male leg pair 17 (Fig. 12A): strongly reduced, 4 segmented, coxa with a regular outer lobe and a setiferous tubercle, tarsus with 2–3 strong apical and 7–8 strong median spines. Male leg pair 18 (Fig. 12B): less reduced, 4 segmented, with a simple syncoxital notch, tarsus with one apical spine.

Telopods. Enlarged, stout, and trapeziform, with a large, round, subtriangular,

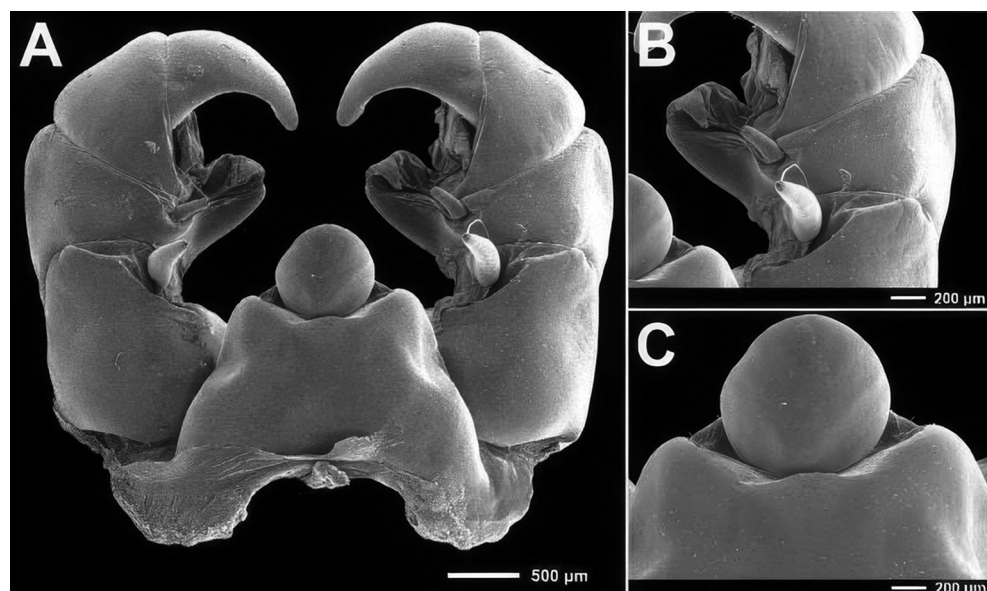


FIGURE 13 (A–C) *Rhopalomeris dulcia* sp. nov., ♂ paratype (MUMNH-GLO188), from Tham Chang Puek Monastery, Chumphon. (A) telopods, anterior view (B) prefemoral and femoral trichosteles (C) syncoxital lobe and horns

central, syncoxital lobe like a conical mushroom cap, flanked by two setose horns (Fig. 12C, D). Syncoxital horns shorter, placed slightly behind the syncoxital lobe, with subapical setoid filament on each horn. Prefemur distroventrally with a large, long trichostele anteriorly. Femur with a tiny anterior trichostele and a large posterior tuberculiform process, distal part bowed anteriad. Tibia with a posterior outgrowth bearing a small sigmoid membranous apical sac folded anteriad and a small parabasal tubercle. Tarsus strongly curved, with a terminal spine.

Distribution. Currently known only from the type locality.

Habitats. The type locality, Tham Chang Puek Monastery, is situated on the south-west side of a limestone hill and is surrounded by palm plantations. The millipedes were observed outside the Chang

Puek cave, on the forest floor in high-humidity soil beneath large rocks.

Remarks. The vivid red and yellow colors remain bright even after two years of preservation in ethanol.

***Rhopalomeris punctata* Sapparojpattana & Likhitrakarn, sp. nov.**

Fig. 14–16

Holotype. ♂ (MUMNH-GLO056) Thailand, Prachuap Khiri Khan Province, Sam Roi Yot District, Bueng Bua Buddhist Park, elev. ca. 20 m a.s.l., 12°14'14.1"N 99°55'53.7"E, 26 September 2022, leg. R. Srisonchai.

Paratypes. 1 ♂, 3 ♀♀ (MUMNH-GLO056) same collection data as for the holotype.

Etymology. The specific epithet '*punctata*' is derived from the Latin '*punctatus*', meaning 'dot' or 'spotted', referring to the dark spot on the tergites.

Diagnosis. Body light yellowish with a pair of large, blackish spots on paramedian side and a small, dark oval spot on lateral side of tergites 3–11, the latter growing broader on tergites 6–9. Venter light yellowish with no color marking. The telopod with a roundly pentagonal syncoxital lobe, slightly shorter than the horns.

Diagnostical notes. The color pattern of *R. punctata* sp. nov. resembles that of *R. muka* sp. nov. but both species differ in their smaller body size (length 8.3–10.3 mm, width 4.3–4.9 mm vs length 14.9–22.3 mm, width 8.3–10.3 mm), marking on venter (absent vs present on pleurites 6–11), telopod shape (strongly stout vs slightly stout), and the syncoxital lobe of telopod (small and slightly shorter than horns vs large and higher than horns). This species can also be distinguished from *R. nigroflava* from Myanmar in the color pattern on the tergites (blackish paramedian spots

and small dark oval lateral spots vs brown to blackish markings) and the syncoxital lobe of the telopod (roundly pentagonal vs small subtrapeziform, narrowly and roundly emarginated. The new species differs from *R. sauda* and *R. nagao* from Vietnam in the color pattern on the thoracic shield (black color absent vs black color present in both *R. sauda* and *R. nagao*).

Description. Body length of unrolled holotype, 9.9 mm; width 4.9 mm. Body length of unrolled paratypes, 9.5 mm (σ ; $n = 1$), 8.3–10.3 mm ($\varnothing$; $n = 3$); width of second tergite 4.9 mm (σ ; $n = 1$), 4.3–4.8 mm ($\varnothing$; $n = 3$).

Color. Color faded from preservation in ethanol. Collum light yellowish with a pair of large, blackish spots on paramedian and a pair of small, dark oval spots on lateral side of tergites 3–11, the latter growing broader on tergites 6–9 (Fig. 14A, C).

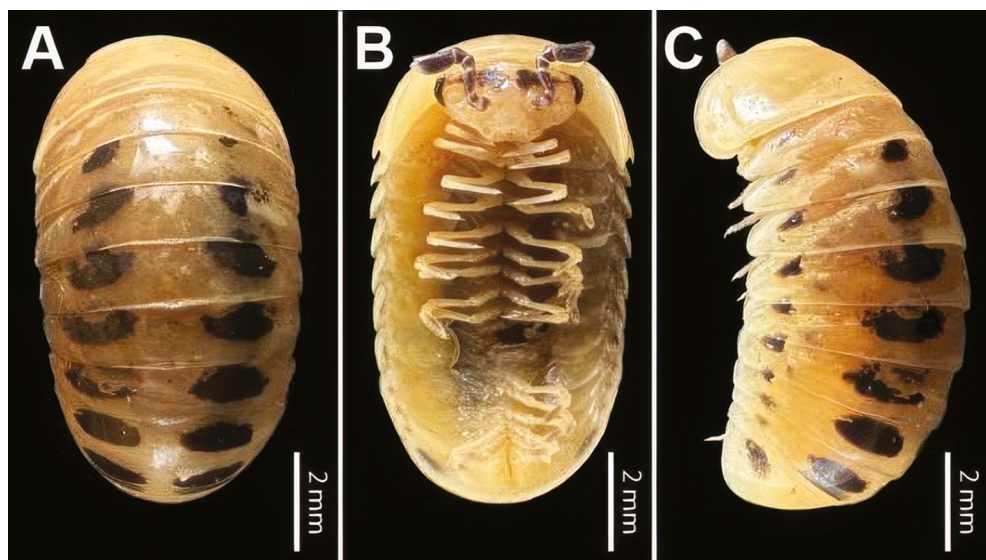


FIGURE 14 *Rhopalomeris punctata* sp. nov., (A–C) ♀ paratype (MUMNH-GLO056), alcohol preserved, in dorsal, ventral, and lateral views. Scale bars: 2 mm

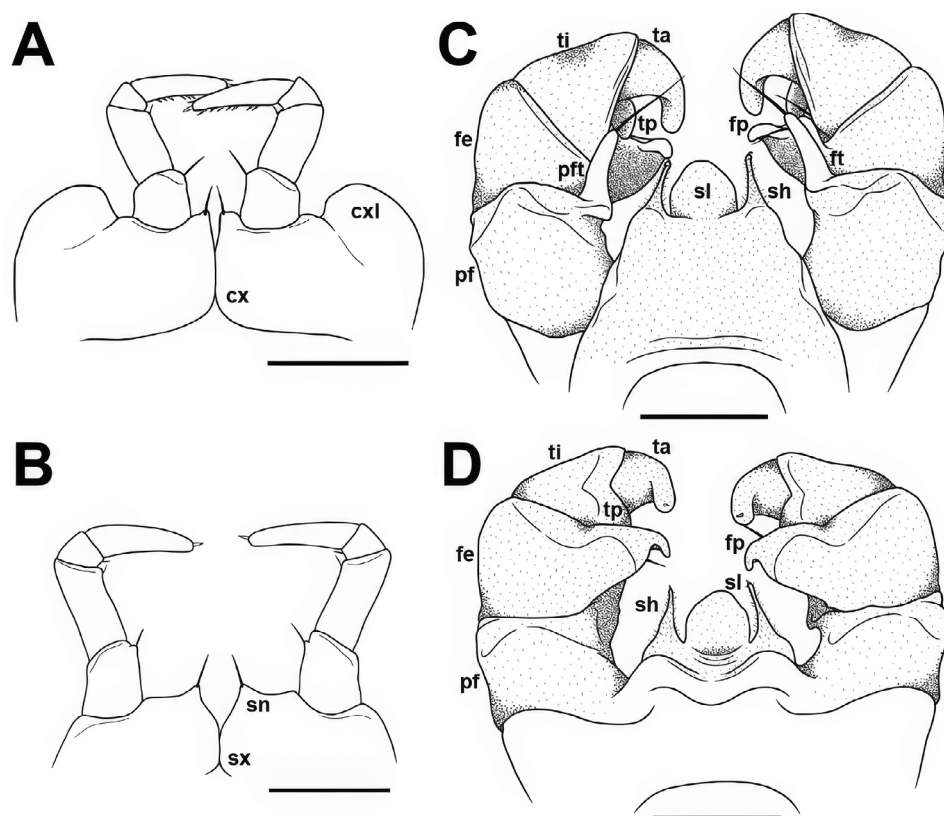


FIGURE 15 *Rhopalomeris punctata* sp. nov., ♂ Holotype, (A) legs 17, anterior view, (B) legs 18, anterior view, (C, D) telopods, anterior and posterior views. Scale bar = 0.5 mm. Abbreviations: cx = coxa, cxl = coxal lobe, fe = femur, fp = femoral process, ft = femoral trichostele, pf = prefemur, pft = prefemoral trichostele of telopod, sh = syncoxital horn of telopod, sl = syncoxital lobe of telopod, sn = syncoxite notch, sx = syncoxite, ta = tarsus, ti = tibia, tp = tibial process

The first tergite and thoracic shield light yellowish with no dark marking. Head yellowish with dark brown patches above the antennal socket; antennae blackish. Pygidium light yellowish with a pair of small, oval spots placed on lateral side of the tergite (Fig. 14C). Venter light yellowish with no coloration pattern, legs yellowish to light brown (Fig. 14B).

Head. Ommatidia 6(7–8)+1, with blackish and convex cornea. Tömösváry organ

strongly horseshoe-shaped, oblong-oval, about 1.7–1.9 times as long as wide. Labrum scantily setose. Gnathochilarium with 2+2 palps subequal in length. Antennae clavate with 26–32 small apical cones. Antennomere 6 large, almost straight with slight curve, about 1.5–1.8 times as long as high (Fig. 14B). Antennomere 7 short and thick.

Body. Collum semicircular, with 2–3 transverse striae. Thoracic shield with a

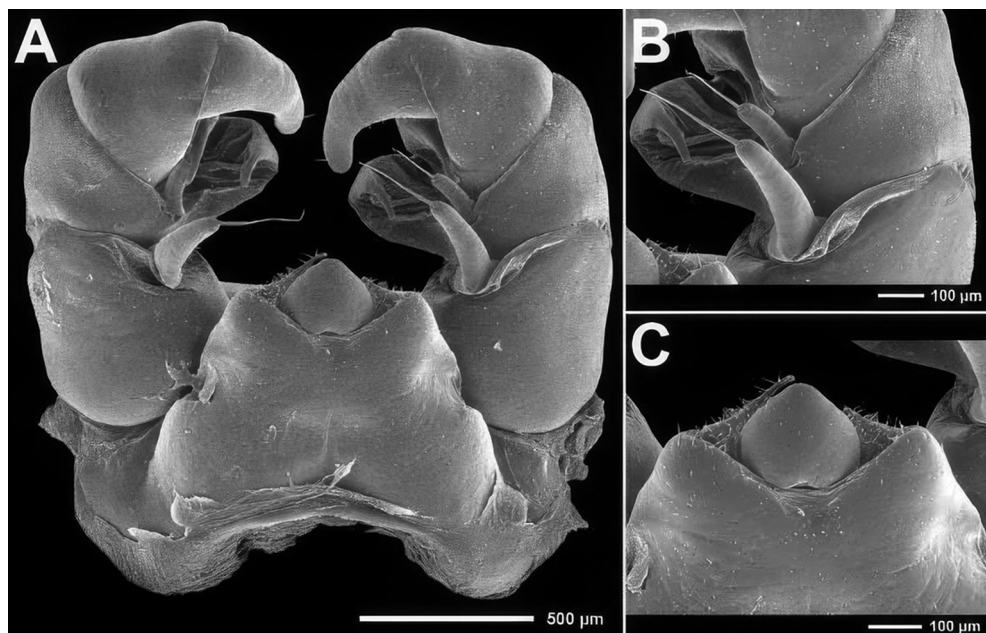


FIGURE 16 (A–C) *Rhopalomeris punctata* sp. nov., ♂ paratype (MUMNH-GLO056), from Bueng Bua Buddhist Park, Prachuap Khiri Khan. A telopods, anterior view B prefemoral and femoral trichostyles C syncoxital lobe and horns

narrow hyposchism field, not reaching behind the caudal tergal margin, 5–7 striae; 2 lying above schism, 1 equal to schism, remaining 2–4 beneath schism, 4–5 completely crossing the dorsum. Pygidium rounded, strongly concave medio-caudally.

Legs. Mid-body legs: tarsus with one apical spine, 12–16 lateral spines, and 13–16 ventral spines. Claw narrow and elongate. Male leg pair 1: similar to mid-body legs, but coxae protruding and elongate, with two long spines. Tarsus with 15 ventral spines. Male leg pair 2: similar to mid-body legs, but coxae with two long spines. Gonopore covering 1/3 of coxa. Male leg pair 17 (Fig. 15A): strongly reduced, 4 segmented, coxa with a slightly slanted outer lobe and a setiferous tubercle, tarsus with 2–3 strong apical and

5–8 strong median spines. Male leg pair 18 (Fig. 15B): less reduced, 4 segmented, with a simple syncoxital notch, tarsus with one apical spine.

Telopods. Enlarged, strongly stout, trapeziform, no color marking (Fig. 15C, D). Syncoxital lobe roundly pentagonal, with two setose horns paramedially, each horn slightly longer than the central lobe and being crowned by a long setoid filament. Prefemur distroventrally with a large, long trichostele anteriorly. Femur with a tiny anterior trichostele and a large posterior tuberculiform process, distal part thick, elongate, bowed anteriorly. Tibia with a posterior outgrowth bearing a small sigmoid membranous apical sac folded anteriorly and a small parabasal tubercle.

Tarsus slender, strongly curved, bearing an apical seta.

Distribution. Currently known only from the type locality.

Habitats. Bueng Bua Buddhist Park is situated on the north-west side of a large, isolated limestone mountain, approximately 4.2 km wide and 13.8 km long. The type locality is surrounded by a large lotus pond, agricultural lands, and urban areas. The millipedes were found on the forest ground under leaf litter.

Rhopalomeris verhoeffi Sapparojattana & Likhitrakarn, sp. nov.

Rhopalomeris bicolor [non Wood, 1865] – Verhoeff 1906: 189 (M); Verhoeff 1910: 241 (M); Verhoeff 1914: 143 (M); Attems 1914: 138 (in part) (L).

Glomeris bicolor [non Wood, 1865] – Hoffman 1980: 66 (in part) (M).

Rhopalomeris carnifex [non Pocock, 1889] – Enghoff 2005: 88 (in part) (R); Decker 2010: 24 (in part) (R); Golovatch et al. 2011: 6 (in part) (D); Golovatch

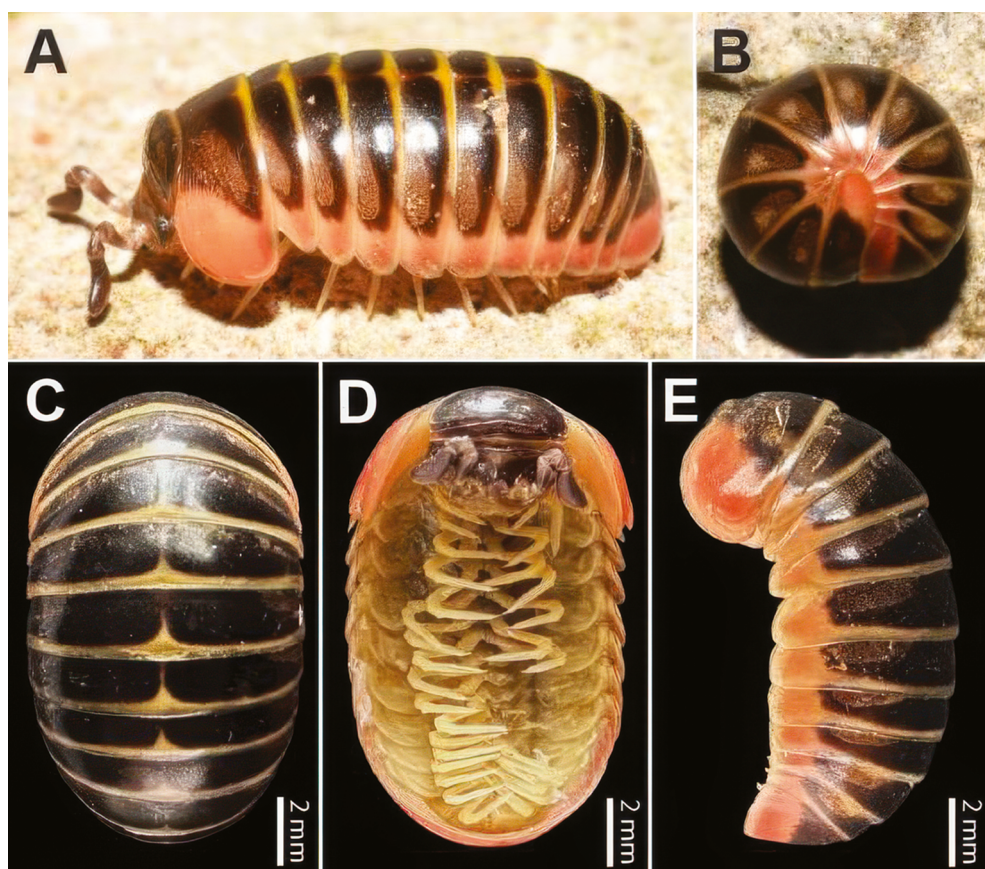


FIGURE 17 *Rhopalomeris verhoeffi* sp. nov., (A, B) paratype (MUMNH-GLO201), habitus, live coloration of color morph 2 (C–E) ♀ paratype (MUMNH-GLO201), alcohol preserved specimen of color morph 2 in dorsal, ventral, and lateral views (A) unrolled in sublateral view (B) rolled in sublateral view. (A, B) image not to scale (C–E) scale bars: 2 mm

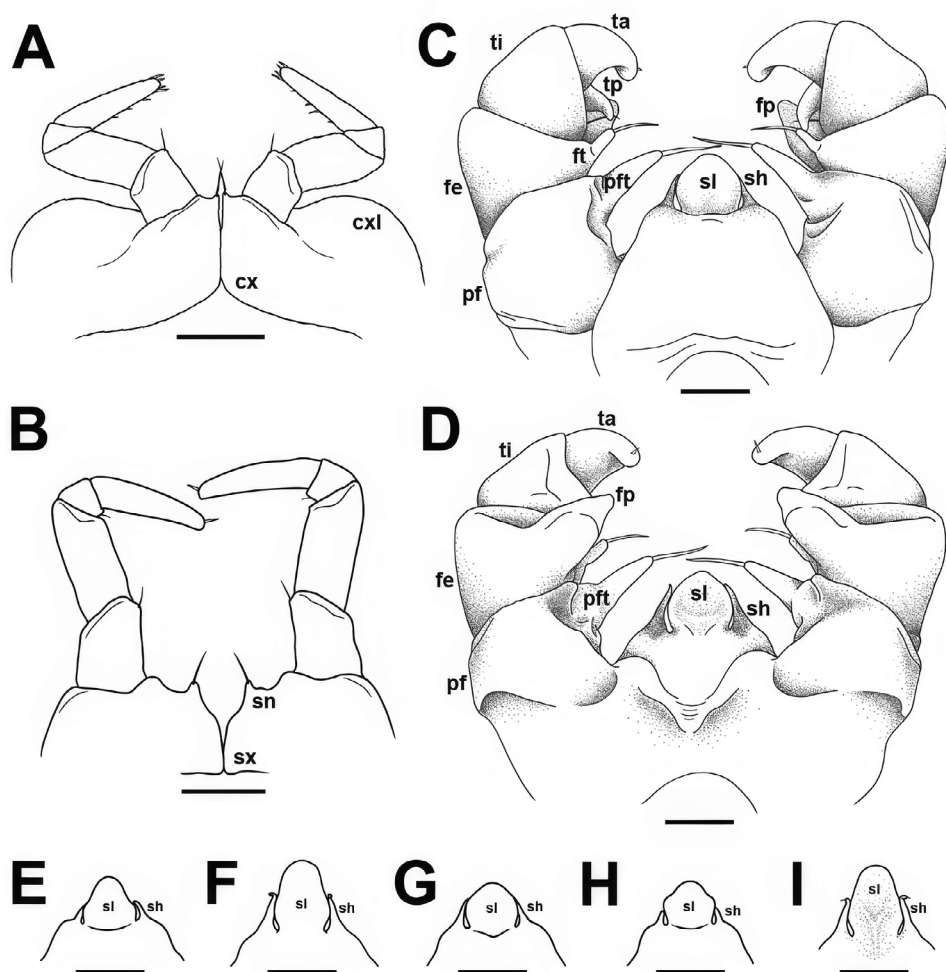


FIGURE 18 *Rhopalomeris verhoeffi* sp. nov., (A-D) ♂ Holotype, (E-I) ♂ Paratypes, (A) legs 17, anterior view, (B) legs 18, anterior view, (C, D) telopods, anterior and posterior views, (E-H) syncoxital lobe and horns, anterior view, (I) syncoxital lobe and horns, posterior view. Scale bar = 0.5 mm. Abbreviations: cx = coxa, cxl = coxal lobe, fe = femur, fp = femoral process, ft = femoral trichostele, pf = prefemur, pft = prefemoral trichostele of telopod, sh = syncoxital horn of telopod, sl = syncoxital lobe of telopod, sn = syncoxite notch, sx = syncoxite, ta = tarsus, ti = tibia, tp = tibial process

& Semenyuk 2016: 411 (in part) (M, K); Likhitrakarn et al. 2017: 6 (in part) (L); Nguyen et al. 2019: 292 (in part) (M); Nguyen et al. 2021: 259 (in part) (M); Likhitrakarn et al. 2023: 55 (in part) (L); Likhitrakarn et al. 2024: 241 (in part) (D, R, K, M1); Sapparojpattana et al. 2025 (in part) (M).

Rhopalomeris carnifex var. *pallida* – Silvestri 1917: 143 (in part) (D); Attems 1936: 194 (in part) (L).
Fig. 3, 17, 18

Holotype. ♂ (MUMNH-GLO201)
Thailand, Phuket Province, Kathu District, Kathu Waterfall, elev. ca. 80–100 m a.s.l.,

7°55'58.9"N 98°19'19.8"E, 24 May 2023, leg. N. Likhitrakarn, R. Srisonchai, and P. Sapparojpatana.

Paratypes. 2 ♂♂, 1 ♀ (MUMNH-GLO201), same collection data as for the holotype.

Other material examined. Thailand—2 ♀♀ (MUMNH-GLO099) Phuket Province, Thalang District, Bang Pae Waterfall, elev. ca. 80–100 m a.s.l., 6°59'57.2"N 100°14'00.4"E, 4 Dec 2022, leg. E. Jeratthitikul; 4 ♂♂, 5 ♀♀ (MUMNH-GLO017) Phang-nga Province, Mueang District, Tham Phung Chang, elev. ca. 40 m a.s.l., 8°26'33.7"N 98°30'56.5"E, 23 May 2023, leg. C. Sutcharit; 2 ♂♂, 8 ♀♀ (MUMNH-GLO018) Phang-nga Province, Mueang District, Tham Phung Chang, elev. ca. 40 m a.s.l., 8°26'33.7"N 98°30'56.5"E, 8 Aug 2016, leg. C. Sutcharit; 6 ♂♂, 6 ♀♀ (MUMNH-GLO200) Phang-nga Province, Mueang District, Tham Phung Chang, elev. ca. 40 m a.s.l., 8°26'33.7"N 98°30'56.5"E, 23 May 2023, leg. C. Sutcharit; 10 ♂♂, 19 ♀♀ (MUMNH-GLO061) Phang-nga Province, Thap Put District, Tham Chang, elev. ca. 20 m a.s.l., 8°28'06.9"N 98°35'16.1"E, 1 Oct 2022, leg. R. Srisonchai and E. Jeratthitikul; 4 ♂♂, 7 ♀♀ (MUMNH-GLO198) Phang-nga Province, Thap Put District, Wat Khiriwong, elev. ca. 80 m a.s.l., 8°31'51.4"N 98°34'40.8"E, 23 May 2023, leg. N. Likhitrakarn, R. Srisonchai, and P. Sapparojpatana; 3 ♂♂, 3 ♀♀ (MUMNH-GLO199) Phang-nga Province, Takua Thung District, Wat Suwan Khuha, elev. ca. 60 m a.s.l., 8°25'43.6"N 98°28'18.6"E, 23 May 2023, leg. N. Likhitrakarn, R. Srisonchai, and P. Sapparojpatana; 10 ♂♂, 17 ♀♀ (MUMNH-GLO081) Surat Thani Province, Khiri Rat Nikhom District, Tham Sathit Khirirom, elev. ca. 60 m a.s.l., 9°01'48.0"N 98°59'12.9"E, 10 Jul 2017, leg. R. Srisonchai; 2 ♂♂ (MUMNH-GLO125) Surat Thani

Province, Phanom District, Tham Kang Kao, elev. ca. 80 m a.s.l., 8°46'23.8"N 98°51'35.8"E, 19 Jun 2018, leg. R. Srisonchai and N. Likhitrakarn; 1 ♂ (MUMNH-GLO142) Surat Thani Province, Phanom District, near Khao Sok National Park, elev. ca. 60–80 m a.s.l., 8°53'35.9"N 98°33'09.1"E, 5 Aug 2014, leg. C. Sutcharit; 6 ♂♂, 8 ♀♀ (MUMNH-GLO025) Nakhon Si Thammarat Province, Thung Song District, Talod Cave, elev. ca. 60–80 m a.s.l., 8°09'32.4"N 99°40'40.9"E, 5 Jul 2017, leg. R. Srisonchai; 4 ♂♂, 2 ♀♀ (MUMNH-GLO080) Nakhon Si Thammarat Province, Tham Phannara District, Tham Phannara, elev. ca. 40–60 m a.s.l., 8°26'12.7"N 99°23'22.7"E, 15 Jan 2014, leg. C. Sutcharit; 5 ♂♂, 2 ♀♀ (MUMNH-GLO062) Krabi Province, Ao Luek District, Tham Klang, elev. ca. 40 m a.s.l., 8°20'16.8"N 98°44'44.1"E, 1 Oct 2022, leg. E. Jeratthitikul and R. Srisonchai; 2 ♂♂, 3 ♀♀ (MUMNH-GLO154) Krabi Province, Ao Luek District, near Than Bok Khorani National Park, elev. ca. 20–40 m a.s.l., 8°23'23.6"N 98°43'59.6"E, 30 Aug 2015, leg. N. Likhitrakarn and R. Srisonchai; 16 ♂♂, 26 ♀♀ (MUMNH-GLO197) Krabi Province, Ao Luek District, Toh Chong Toh Yuan Shrine, elev. ca. 20–40 m a.s.l., 8°22'23.3"N 98°44'07.6"E, 23 May 2023, leg. N. Likhitrakarn, R. Srisonchai, and P. Sapparojpatana; 2 ♀♀ (MUMNH-GLO196) Krabi Province, Mueang District, Wat Tham Suea, elev. ca. 20–40 m a.s.l., 8°07'25.4"N 98°55'30.5"E, 23 May 2023, leg. N. Likhitrakarn, R. Srisonchai, and P. Sapparojpatana; 1 ♂ (MUMNH-GLO132) Krabi Province, Plai Phraya District, Wat Khao Hua Sing, elev. ca. 100 m a.s.l., 8°30'40.0"N 98°45'38.5"E, 12 Mar 2017, leg. R. Srisonchai and C. Sutcharit; 8 ♂♂, 5 ♀♀ (MUMNH-GLO195) Trang Province, Huai Yot District, Wat Khao Huai Haeng, elev. ca.

80–100 m a.s.l., 7°47'36.4"N 99°38'39.7"E, 22 May 2023, leg. N. Likhitrakarn, R. Srisonchai, and P. Sapparojpattana; 1 ♂ (ZFMK MYR4913) [TW135] Krabi Province, Ao Nang, elev. ca. 40 m a.s.l., 8°01'55"N 98°50'12"E, 25 Aug 2015, leg. P. Autt; 1 ♂ (ZFMK MYR5550) [CH138] Krabi Province, ca. 20 km N Krabi, Phanom Bencha, elev. ca. 80 m a.s.l., 8°12'35.0"N 98°56'22.1"E, 1 Aug 2016, leg. P. Autt; 1 ♂ (ZFMK MYR5553) [CH139] Krabi Province, ca. 20 km N Krabi, Phanom Bencha, elev. ca. 114 m a.s.l., 8°12'31.7"N 98°56'05.2"E, 31 Jul 2016, leg. P. Autt; 1 ♀ (ZFMK MYR14527) [TH49] Krabi Province, Ao Luk Thai, N of road, elev. ca. 42 m a.s.l., 8°22'20.4"N 98°44'08.4"E, 27 Jul 2017, leg. T. Wesener & L. Moritz.

Etymology. The specific name is given in honour of Karl Wilhelm Verhoeff, the renowned German myriapodologist who established the genus *Rhopalomeris* based on specimens from Salanga Island (the historical name for Phuket, Thailand).

Diagnosis. Body blackish or brownish with a red or pale red lateral margin and a narrow yellow axial line or body light yellowish with a pair of paramedian and lateral black spots, and a red or pale red lateral margin, and a yellow or red mid-posterior margin. The first tergite blackish with a marble pattern or light yellowish with a pair of black patches. Thoracic shield blackish or brownish or light yellowish with a broad red or pale red lateral margin and an oval marble spot on lateral side. Other tergites with a red or pale red lateral margin and an oval marble spot on lateral side. The syncoxital lobe of telopod with a low ridge at base of lobe on posterior side.

Diagnostical notes. The color pattern of *R. verhoeffi* sp. nov. resembles that of

R. carnifex; but differs in the oval marble spots on the lateral side of tergites (present vs absent), the black color on the first tergite (blackish with marble or brownish with marble or a pair of black patches vs fully plain blackish), the color on the thoracic shield (blackish with marble or brownish with marble or no black color vs blackish or faded blackish color), and the syncoxital lobe of telopod (with a low ridge at the base of the lobe on posterior side vs ridge absent). It can also be distinguished from *R. sirindhornae* in the color pattern on the thoracic shield (blackish with marble or brownish with marble or no black color vs a pair of faded black dots on lateral side with a pale pink lateral margin) and the syncoxital lobe of the telopod (with a low ridge at the base of the lobe on posterior side vs ridge absent).

Description. Body length of unrolled holotype, 15.4 mm; width 7.7 mm. Body length of unrolled paratypes and other materials, 8.6–18.3 mm (♂; n = 10), 13.5–20.2 mm (♀; n = 14); width of second tergite 4.7–9.6 mm (♂; n = 10), 6.3–9.9 mm (♀; n = 14).

Color. Collum blackish with red lateral margin and narrow yellow axial line (Fig. 17A, C). The first tergite blackish with marble pattern. Thoracic shield and other tergites with broad red lateral margin and oval marble spot on lateral of each side (Fig. 17A, B, E). Caudal margin of each tergite light yellowish and blending to red near lateral side (Fig. 17A, C). Head and antennae blackish brown. Pygidium blackish with red margin (Fig. 17A, E). Venter light yellowish with no coloration pattern, legs yellowish (Fig. 17D).

Head. Ommatidia 7–10+1, with dark brown to blackish and convex cornea.

Tömösváry organ oblong-oval, approximately 1.5–2.0 times as long as wide, strongly horseshoe-shaped. Labrum scanty setose. Gnathochilarium with 2+2 palps subequal in length. Antennomere 6 large, clavate, strongly curved, approximately 1.2–1.4 times as long as high (Fig. 17D). Antennomere 7 slightly elongated and curved, with 66–97 small apical cones.

Body. Collum semicircular as usual, with 2–4 transverse striae. Thoracic shield with a narrow hyposchism field, not reaching behind the caudal tergal margin, 7–12 striae; 3–5 lying above schism, 1 or 2 equal to schism, remaining 2–5 beneath schism, 5–6 completely crossing the dorsum. Pygidium rounded, strongly concave medio-caudally.

Legs. Mid-body legs: tarsus with one apical spine, 10–13 lateral spines, and 16–21 ventral spines. Claw narrow and elongate. Male leg pair 1: similar to mid-body legs, but coxae protruding and elongate, with two long spines. Tarsus with only 14 ventral spines. Male leg pair 2: similar to mid-body legs, but coxae with two long spines. Gonopore covering $\frac{1}{3}$ of coxa. Male leg pair 17 (Fig. 18A): strongly reduced, 4 segmented, coxa with a low, widely round outer lobe and a setiferous tubercle, tarsus with 4 strong apical and 3 or 4 strong median spines. Male leg pair 18 (Fig. 18B): less reduced, 4 segmented, with a simple syncoxital notch, tarsus with one apical spine.

Telopods. Enlarged, stout and trapeziform with a subtriangular syncoxital lobe (Fig. 18C, D). The central lobe with a low ridge at the base of the lobe on posterior side. The syncoxital lobe flanked by two setose horns, each horn shorter than the

lobe, folded apically, being crowned by a subapical setoid filament. Prefemur distroventrally with a long trichostele anteriorly. Femur with a tiny anterior trichostele and a large posterior outgrowth, holding a pointed membranous apical sac slightly folded anteriad. Tibia with an anterior seta, a large distolateral tibial process, and a round parabasal tubercle posteriorly. Tarsus elongated, slightly sigmoid, with a strong apical spine.

Variation. This species is highly variable in both color pattern and telopod morphology. Five distinct color morphs were observed among populations (Fig. 3A, C), as follows:

Color morph 1: Brownish body with pale red lateral margin and narrow yellow axial line. Tergites with oval marble spot on lateral of each side. Caudal margin of each tergite light yellowish and blending to pale red near lateral side. Head and antennae brownish. Pygidium brownish with pale red margin. Venter and legs light yellowish.

Color morph 2: Blackish body with red lateral margin and narrow yellow axial line. Tergites with oval marble spot on lateral of each side. Caudal margin of each tergite light yellowish and blending to red near lateral side. Head and antennae blackish. Pygidium blackish with red margin. Venter and legs light yellowish.

Color morph 3: Blackish body with pale red lateral margin and wide yellow axial line. The lateral side of tergites with oval marble spot and faded black color on each side. The first tergite with a pair of black patches and the thoracic shield with no black color. Caudal margin, head, antennae, pygidium, and venter similar to color morph 2.

Color morph 4: Light yellowish body with a pair of paramedian and lateral black spots. Tergites with red lateral margin and a red subtriangular mid-posterior margin. The first tergite with a pair of black patches and the thoracic shield with no black color. Pygidium blackish with red margin and yellow axial line. Head, antennae, and venter similar to color morph 2.

Color morph 5: Color similar to color morph 4, but with a yellow mid-posterior margin.

Moreover, the shape of syncoxital lobe of the telopod in this species varies from subtriangular to elongated obtuse subtriangular (Fig. 18E–H). The posterior side of the lobe can be convex or with a linear ridge or Y-shaped ridge (Fig. 18I).

Distribution. The distribution range of this new species covers an area from Surat Thani to Trang province (figs 2, 3C), and has partial sympatry with *R. carnifex* in Surat Thani province, with no evidence of co-occurrence in the same locality.

Remarks. The genus *Rhopalomeris* was described by Verhoeff (1906) with *Glomeris bicolor* Wood, 1865 as the type species, based on specimens from Phuket, Thailand. Afterward, Silvestri (1917) reexamined Verhoeff's specimens and concluded that *R. bicolor* sensu Verhoeff (1906) was misidentified. As a result, he redesignated *Glomeris carnifex* Pocock, 1889 from Tenasserim, Myanmar, as the type species of *Rhopalomeris*. Golovatch et al. (2011) then reexamined Verhoeff's materials housed in the Museum für Naturkunde Berlin (ZMB), Germany, and confirmed the identity of these specimens as *R. carnifex*. Subsequently, *R. carnifex* has remained in taxonomic usage for populations from Phuket Island to the present.

However, the phylogenetic analyses in this study have revealed that specimens from Phuket Island and several nearby localities in the mainland form a clade separate from the clade *R. carnifex* s.s. (figs 1, 3A) To maintain the monophyletic concept of the species, we thus recognize this clade as a distinct species and describe it as *R. verhoeffi* **sp. nov.**

As the known distribution of *R. verhoeffi* **sp. nov.** extends from Surat Thani to Trang, populations from these areas formerly identified as '*R. carnifex*' and '*R. carnifex* var. *pallida*' (e.g., Silvestri, 1917; Attems, 1936; Enghoff, 2005; Decker, 2010; Golovatch et al., 2011; Golovatch & Semenyuk, 2016; Nguyen et al., 2021; Likhitrakarn et al., 2023a, 2024b; Sapparojpattana et al., 2025) belong to this species.

The vivid red and yellow pigments in the color pattern tend to fade and had almost disappeared after long-term preservation (more than 10 years in ethanol in our cases).

Key to known species of *Rhopalomeris* based on adults (modified from Likhitrakarn et al., 2024):

1. Body with red or pale pink coloration, at least on lateral margins of tergites 2
- Body without red or pale pink coloration; coloration brown, black, or yellowish 5
2. Thoracic shield with a distinct, black, round spot on each lateral side..... 3
- Thoracic shield without distinct, black, round spots on lateral side..... 4

3. Body larger, 15.3–23.5 mm in length and 8.4–12.0 mm in width. Dorsum light yellowish with red lateral margin, a pair of paramedian, and lateral black spots on tergites 3–11 (Fig. 11A, C). Chumphon, Thailand
R. dulcia sp. nov.
- Body smaller, 8.3–12.7 mm in length and 4.2–5.8 mm in width. Dorsum light yellowish body with pale pink lateral margin, a pair of paramedian, and lateral black spots on tergites 3–11. Thoracic shield with a pair of faded black dots on the lateral side. Chumphon and Surat Thani, Thailand
R. sirindhornae Sapparojattana, Jeratthitikul & Likhitrakarn, 2025
4. Body size 8.6–20.2 mm long and 4.7–9.9 mm wide. Dorsum blackish to brownish with an obvious oval marbled spot on lateral side in specimens with blackish or brownish thoracic shield (Fig. 3A, 17). Dorsum mostly light yellowish with black stripe or two pairs of subtriangular spots and a pair of dark patches on the first tergite, mid-posterior edge with yellow or red color (Fig. 3A). Southern Thailand
R. verhoeffi sp. nov.
- Dorsum mostly dark on all tergites. Dark color sometimes narrow or faded and discontinuous. Mid-posterior margin with yellow or pale red color. Axial stripe from thoracic shield to pygidium. Southern Thailand and Myanmar
R. carnifex (Pocock, 1889)
5. Body mostly dark (blackish to dark brown), sometimes with contrasting yellow markings6
- Body mostly yellowish or light brown, with a distinct pattern of dark brown or black spots/patches9
6. Body large, ca. 20 mm long and 11 mm wide (♀). Dorsum uniformly blackish, not variegated. Mount Mau Son, Lang Son Province, northern Vietnam
R. tonkinensis Silvestri, 1917
- Body smaller, 20 mm in length and 11 mm in width. Dorsum with variegated coloration or with contrasting patterns7
7. Body almost entirely dark with four yellow lateral spots on each of tergites 3–11. Telopods with a medially slightly concave syncoxital lobe. Prefemoral trichostele short, not extending to about half the distal boundary of femur. Femoral process long, narrow, acute at tip. Tibial process short and lobuliform. Northern Vietnam
R. nagao Nguyen, Nguyen & Eguchi, 2021
- Body color variegated. Telopods with a medially slightly convex syncoxital lobe. Prefemoral trichostele long, extending to about half or distal boundary of femur. Femoral process large, subtrapeziform, rounded at tip. Tibial process long and sigmoid mesally8
8. Body larger, 15–18 mm long and 7–8 mm wide. Dorsum mostly

brown to blackish, with variegated pattern. Antennomere 6 slightly shorter, ca. 2.0 times as long as height. Thoracic shield with 8–10 striae. Central Vietnam

R. variegata Golovatch & Semenyuk, 2016

- Body smaller, 11 mm long and 6 mm wide. Dorsum blackish, with contrasting yellowish, lateral, oval bands on each of tergite 2–11. Antennomere 6 longer, 2.5–3 times as long as height. Thoracic shield with 2–3 striae. Northern Vietnam

R. sauda Nguyen, Sierwald & Marek, 2019

- 9. Marked with black spots.....10
- Mostly black.....12
- 10. Body small, 7.6–11.8 mm in length and 4.3–6.2 mm in width. Body light yellowish, with a pair of large blackish brown subtriangular oval spots on tergites 2–11 and a small dark brown oval spot on lateral side of tergites 3–11 (Fig. 8A, C). The first tergite and thoracic shield with faded dark brown markings (Fig. 8A–C). Thong Pha Phum, Kanchanaburi, Thailand

R. lentiginosa sp. nov.

- Body light yellowish, with a pair of dark brown paramedian spots and lateral sides with brown or dark brown oval spots on tergites 3–11. The first tergite and thoracic shield without faded dark brown spots11
- 11. Body larger, 14.9–22.3 mm in length and 8.3–10.3 mm in width. Yellowish body with a pair of

dark brown paramedian spots and lateral sides with dark brown oval spots on tergites 3–11 (Fig. 5A, C). Head yellowish with a pair of dark brown patches above the antennal sockets.

Ventral with a large brown spot on tergites 6–11 (Fig. 5D). Narrow-pointed tip central lobe of the telopod syncoxite like a water drop (Fig. 6D, E). Mahidol University Kanchanaburi Campus, Kanchanaburi, Thailand

R. muka sp. nov.

- Body smaller, 8.3–10.3 mm in length and 4.3–4.9 mm in width. Yellowish body with a pair of dark brown paramedian spots and lateral sides with small brown oval spots on tergites 3–11 (Fig. 14A, C). Head mostly yellowish. No marking on venter (Fig. 14B). Sam Roi Yot, Prachuap Khiri Khan, Thailand

R. punctata sp. nov.

- 12. Body larger, ca. 12 mm long and 6 mm wide. Head, collum and thoracic shield light yellowish, body mostly blackish thereafter with a light, rather broad, axial stripe. Perak State, western Malaysia

R. monacha Silvestri, 1917

- Body smaller, 5.1–9.7 mm long and 2.6–4.7 mm wide. Dorsum yellowish to yellowish-brown, and blackish on tergites 4–9. Head and collum brown to dark brownish. Kayin State, Myanmar

R. nigroflava
Likhitrakarn, 2024

Discussion

Diversity and diagnostic morphology of Rhopalomeris

The genus *Rhopalomeris* currently comprises 13 species, and all of them are endemic to Indochina (Pocock, 1889; Silvestri, 1917; Golovatch & Semenyuk, 2016; Nguyen et al., 2019, 2021; Likhitrakarn et al., 2024b; Sapparojpattana et al., 2025; this study). The discovery of five new species significantly expands the known diversity and indicates that western and southern Thailand are a possible primary center of diversification of the genus, as evidenced by the high diversity of seven recorded species. In the past, *Rhopalomeris* in Thailand has been reported as being represented by only one species, *R. carnifex*, and since 2025 by a second species (*R. sirindhornae*) and their distribution was assumed to be restricted to the southern region (Verhoeff, 1906; Silvestri, 1917; Enghoff, 2005; Decker, 2010; Likhitrakarn et al., 2024b; Sapparojpattana et al., 2025). In this study, the distribution range of *Rhopalomeris* is extended into the western and southern regions of the country from Kanchanaburi to Trang province (Fig. 2). This finding fills a previous geographical gap between *Rhopalomeris* in Thailand and the newly described species in Myanmar reported earlier by Likhitrakarn et al. (2024).

Interestingly, the current known distribution of *Rhopalomeris* appears restricted to the Tenasserim Range, extending from southern Thailand northward to adjacent parts in Myanmar. This restricted range is intriguing as it creates a non-overlapping distribution with species of the related genus *Hyleoglomeris*, which

occupy the central and northern regions of Thailand (Likhitrakarn et al., 2024a). This clear separation strongly suggests a potential biogeographic boundary between these taxa. Similar distribution patterns along the Tenasserim Range from southern Thailand to Myanmar have also been observed in other taxa, such as the Southeast Asian macrophagous leech genus *Gastrostomobdella* Moore, 1929 (Nakano et al., 2018) and the carnivorous land snail family Streptaxidae Gray, 1860 (Man et al., 2022).

The five new species of *Rhopalomeris* in this study were well characterized and supported by morphological characters, particularly regarding the shape and size of the syncoxital lobe and horns, telopodite process, femoral process, tibial process, and coloration on each part of the tergites. These characteristics not only differ among the five newly described species but are also essential to distinguish them from other congeners. Accordingly, the morphological characters, including the telopod structure and coloration patterns, were reliable and effective for distinguishing between species. These characteristics are also commonly used as strong recognizable characters in other pill millipedes, such as in *Hyleoglomeris*, *Hyperglomeris*, *Glomeris*, and *Nearctomeris* (Wesener, 2012; Wesener, 2019a; Kuroda et al., 2022a; Likhitrakarn et al., 2023b, 2024a).

In addition, SEM photographs of the telopod offer a more detailed view of surface features. For instance, the morphology of small setae structures on the surface, a level of detail unattainable with a standard stereo microscope, can be clearly observed and quantified using SEM (Fig. 10C). However, no additional distinguishing

microcharacters as shown in SEM examination were observed in this study. Species identification of *Rhopalomeris* relying on the characteristics used in previous studies may be sufficient. Nevertheless, incorporating SEM imaging could enhance the confirmation of these characters and may reveal additional diagnostic structures in future studies.

Furthermore, the integration of DNA information in the present study not only supports the use of morphological characteristics but also validates the distribution range of *Rhopalomeris* species. The distribution of *R. carnifex* in Thailand, which was previously reported in the literature from Phang-nga, Surat Thani, Krabi, and Phuket provinces (Silvestri, 1917; Enghoff, 2005; Decker, 2010; Likhitrakarn et al., 2023a, 2024b; Sapparojpattana et al., 2025) was in fact limited to Phetchaburi to Surat Thani provinces in this study. In contrast, the populations from Phang-nga, Krabi, and Phuket provinces belonged to *R. verhoeffi* sp. nov. The integration of genetic data in taxonomy could enhance the accuracy of species boundary designation and emphasize the importance of using integrative methods combining morphological characters, molecular data, and distributional information.

***Rhopalomeris carnifex* species complex**

This study demonstrates the high efficiency of species delimitation using molecular data to detect the presence of cryptic species. Previously, all the pill millipedes of the genus *Rhopalomeris* from southern Thailand were recognized as only one species, *R. carnifex* s.l. (Verhoeff 1906; Silvestri, 1917; Enghoff, 2005; Decker, 2010). However, with the integration of DNA data,

these populations were shown here to consist of at least four distinct species: *R. carnifex* s.s., *R. verhoeffi* sp. nov., *R. dulcia* sp. nov., and *R. sirindhornae*. Additional undescribed species are also likely hidden, particularly those from highly isolated limestone mountains. These species share similar color patterns, such as black stripes or black spots on the dorsum, and with red or pale pink lateral margins. Further morphological examination indicates that these patterns are not completely similar between the species. There are subtle differences in detail but these may obscure species boundaries and introduce confusion during species-level identification. Consequently, the integration of molecular data is crucial for precisely defining species boundaries and for confirming the monophyly of each lineage.

In addition, the distributions of *R. carnifex*, *R. verhoeffi* sp. nov., *R. dulcia* sp. nov., and *R. sirindhornae* show that these species are largely allopatric. *R. dulcia* sp. nov. and *R. sirindhornae* are only known from their type localities, while *R. carnifex* and *R. verhoeffi* sp. nov. have wider ranges but occupy different areas (*R. carnifex* in the upper part of southern Thailand, ca. 8°35' N to 12°52' N, and *R. verhoeffi* sp. nov. in the lower part of southern Thailand, ca. 7°47' N to 9°01' N). Although their ranges partially overlap in Chumphon and Surat Thani provinces, no evidence of sympatry at the same locality has been found. The resemblance in coloration between these species may reflect an adaptation to similar environmental conditions. Alternatively, these color patterns may represent an ancestral characteristic shared among *R. carnifex*, *R. verhoeffi* sp. nov., *R. dulcia* sp. nov., and *R.*

sirindhornae, with subsequent radiation resulting from geographic isolation. The findings of this study indicate that using only morphological characters may be inadequate for accurate species delimitation; incorporating molecular data and other information is essential.

Genetic divergences within *Rhopalomeris* species

The genetic divergences between and within *Rhopalomeris* species were also analyzed in this study. The interspecific genetic distances among the *Rhopalomeris* species based on a fragment of COI gene ranged from 7.86–13.71%, which is consistent ranges for the other genera of glomerid pill millipedes as reported in the literature, such as 6.7–16.1% in the European genus *Glomeris* (Wesener & Conrad, 2016), 13–15.8% in several Vietnamese genera (Nguyen et al., 2021), and 9.12–16.92% in the genus *Hyleoglomeris*, another Indochinese endemic genus (Likhitrakarn et al., 2024a).

Furthermore, *Rhopalomeris* species showed both low and high genetic divergence within species, ranging from 0–6.96%. From five newly described species in this study, four species were observed with a low genetic distance, which are *R. muka* sp. nov., *R. lentiginosa* sp. nov., *R. dulcia* sp. nov., and *R. punctata* sp. nov., reflecting their narrow distributions. In contrast, *R. verhoeffi* sp. nov., the species with a wide geographic range, had a higher genetic distance at 4.53%. The high genetic divergence has also been found in other species, such as *R. carnifex*, *R. sauda*, and *R. nagao*. The pattern of high genetic divergence is likely associated with their broad distribution, which allows

genetic variation accumulated among distant geographical populations.

Intraspecific morphological variations within the populations of widespread *Rhopalomeris* species

Two widespread *Rhopalomeris* species in Thailand, *R. carnifex* and *R. verhoeffi* sp. nov., display considerable intraspecific variation in morphology (Fig. 3A). The color patterns distinctly varied from light to dark color morphs and were observed on the first tergite, thoracic shield, and other tergites on the dorsal side. The expression of melanin-based colors in arthropods, where lighter color morphs have less melanin deposition and darker color morphs have more, may correlate with environmental factors such as temperature, humidity, precipitation, and seasonal variation (Hinton & Jarman, 1973; Haque et al., 2024). For instance, male *Dynastes hercules* (Linnaeus, 1758) beetles exhibit a color change in their elytra, transitioning from black during the night to yellow in the morning, in response to a drop in humidity (Hinton & Jarman, 1973). Moreover, seasonal morphs have been observed in the butterfly *Eurema hecabe* (Linnaeus, 1758) from Japan, characterized by variation in wing coloration intensity between summer and autumn populations. The fringe color on the forewing's upper side exhibits a broader black border in the typical summer morph but is comparatively narrower in the typical autumn morph (Kato, 2000).

The color variation within *R. carnifex* appears to follow a geographical trend, with lighter color morphs (color morphs 3 and 4) occurring in northern populations, and progressively darker morphs (color

morphs 1 and 2) observed further south (Fig. 3B). This color variation may be associated with the precipitation and humidity in the southern region of Thailand. This area is known for notable climatic variation, as the rainfall and humidity patterns differ significantly between the upper and lower parts of the region. The area around the Isthmus of Kra serves as a transitional zone between the more seasonal upper zone and the high-rainfall, low-seasonality lower zone (Hughes et al., 2011; Parnell, 2013). This gradual increase in precipitation and humidity toward the lower part of southern Thailand appears to be related to a shift in color morphs in *R. carnifex*, which tends to darken progressively along the latitudinal gradient (Fig. 3B). Therefore, the observed color variation in *R. carnifex* may be influenced by humidity levels and climatic transitions.

However, some *R. carnifex* populations do not conform to this pattern. For example, the population from Kala Island, which is the northernmost population in Myanmar, exhibits a dark color morph (color morph 1; Fig. 3B). The presence of dark coloration in this population may be attributed to its geographic location. Kala Island, located within the Myeik Archipelago, is exposed to high humidity driven by the Southwest Monsoon from the Andaman Sea. In contrast to inland regions, this island is not affected by the rain shadow caused by the surrounding mountain ranges, i.e., the Tenasserim Range, in this case (Hughes et al., 2011; Parnell, 2013; Sein et al., 2018). Therefore, the consistently high humidity in Kala Island may also be correlated with the darker coloration observed in this population.

While there were some patterns among the color variation within *R. carnifex*, the color variation observed in *R. verhoeffi* sp. nov. showed a weak correlation with geographic distribution along the latitudinal gradient (Fig. 3C). Although the populations on the eastern side appeared to follow the latitudinal gradient pattern, the overall trend was not particularly clear. This could be due to the lower part of southern Thailand experiencing consistently high rainfall throughout the area. Moreover, the climate in this region is complex and influenced by monsoons from both the Andaman Sea and the Gulf of Thailand (Ridd et al., 2011; Parnell, 2013). Nevertheless, the weak correlation between color variation and geographic distribution observed in *R. verhoeffi* sp. nov. may also be affected by other factors, such as the complexity of the microclimate in the habitats (Law et al., 2020).

Our field surveys also revealed that more than one color morph of the same species can be found in the same place, but such co-occurrences are infrequent. The presence of multiple color morphs in a single locality may be associated with microhabitat heterogeneity in the area, such as large limestone rocks and dry leaf litter habitats. The complexity of microhabitat results in diverse background environments, which can reduce predation pressure and may facilitate the coexistence of multiple color morphs (Fark et al., 2022).

For the telopod, the syncoxital lobe in *R. verhoeffi* sp. nov. varied distinctly in size and shape (Fig. 18E–I). These morphological variations may have arisen as adaptations to their specific habitats or may be evidence of ongoing evolutionary

processes. Therefore, the use of multiple morphological characters is essential for accurate species identification and for distinguishing closely related taxa.

Species distribution and local endemism

Among all *Rhopalomeris* species, *R. carnifex*, is the most widely distributed species, ranging in the upper part of southern Thailand, covering areas from Phetchaburi to Surat Thani province (figs 2, 3B). The second widest distributed species is *R. verhoeffi* **sp. nov.**, which occupies an area in the lower part of southern Thailand from Surat Thani to Trang province (figs 2, 3C). The broad distribution of these species may be related to a high degree of adaptability to diverse environmental conditions or a greater dispersal ability relative to the other species. Although limestone-associated millipedes are typically restricted to small areas, some species can exhibit a wide distribution. Similar broad distribution patterns have also been reported in other millipedes, such as the dragon millipede *Desmoxytes cervina* (Pocock, 1895) and *D. delfae* (Jeekel, 1964), which are widely distributed across southern Thailand (>250 km and >350 km, respectively) (Srisonchai et al., 2018).

However, most of the *Rhopalomeris* species exhibit relatively narrow distribution ranges or are restricted to their type locality, suggesting a high degree of local endemism. The limited distribution pattern may be influenced by the habitat specialization, geographic isolation, and adaptation ability of each species. For example, *R. punctata* **sp. nov.** is found only in Sam Roi Yot District, Prachuap Khiri Khan Province. The type locality is in an

isolated limestone karst surrounded by agricultural land and urban areas. Several terrestrial invertebrates in Thailand have also been reported as endemic, with highly restricted distribution ranges — for example, the land snail *Siamochlamys panhai* Pholyotha, 2023 (Pholyotha et al., 2023) and the giant pill millipede *Sphaerobelum nonghinensis* Srikampha & Srisonchai, 2025 (Srikampha et al., 2025). Interestingly, these highly endemic faunas are restricted to limestone mountains, which are ecologically fragile and experiencing significant degradation across numerous regions (Latinne et al., 2013; Chen et al., 2020). Given the high level of endemism observed in various *Rhopalomeris* species, these taxa are likely to be highly susceptible to habitat disturbance and environmental change. Therefore, it is crucial to conserve their natural habitats and mitigate further anthropogenic impacts. Moreover, comprehensive and spatially representative sampling is essential for ensuring the accuracy of biodiversity assessments. In this study, we conducted extensive sampling of *Rhopalomeris* species across a broad geographic range, encompassing areas from the western to the southern regions of Thailand. In the long term, this distribution data will be essential for conservation strategies and future biodiversity management plans.

Concluding Remarks

In total, seven *Rhopalomeris* species have been reported from Thailand, including five new species described in this study (Likhitrakarn et al., 2024b;

Sapparojpattana et al., 2025; this study). These findings suggest that the diversity of the millipede fauna in Thailand still remains underestimated. There is a high probability that more diversity of the genus *Rhopalomeris* in Thailand is waiting to be discovered, as there are still many isolated limestone and forest areas in Thailand that have not been surveyed yet. Moreover, the distribution and diversification of each species appear to have an interesting correlation with the biogeographic transitions in Thailand. Analyzing more data using biogeographic approaches by including more genetic markers and more examined localities could provide crucial information for the pill millipede's evolutionary history. Beyond the scope of this study, *Rhopalomeris* appears to have a broader distribution, with additional species discovered in Vietnam and China that will be reported in forthcoming publications (Golovatch, personal communication). Therefore, future studies should also focus on the underexplored regions, such as limestone areas in Malaysia, due to their connection to southern Thailand. Moreover, there may be some patterns of coloration gradients associated with geographic distribution along the whole Thai-Malay Peninsula.

Furthermore, this study used only the mitochondrial COI gene as a genetic marker and could not resolve the deeper phylogenetic relationships among glomerid genera, as has also evidenced in other studies (Nguyen et al., 2019; Liu & Golovatch, 2020; Nguyen et al., 2021; Likhitrakarn et al., 2024b; Sapparojpattana et al., 2025). Adding more genetic markers, such as the mitochondrial 16S rRNA

gene, nuclear 18S rRNA, and 28S rRNA genes or phylogenomic data, should give more phylogenetic information and could help clarify higher-level relationships (e.g., Fernández et al., 2018; Pholyotha et al., 2020; Gao et al., 2025). Nevertheless, to gain a comprehensive understanding of the pill millipede genus *Rhopalomeris*, it is essential to collect data from several perspectives. Thus, integrative approaches using molecular data, morphological characters, and ecological data are also important in the understanding of the pill millipede genus *Rhopalomeris* evolution, and should receive focus on the future.

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References

- Ampai, N., Rujirawan, A., Yodthong, S., Termprayoon, K., Stuart, B.L. & Aowphol, A. (2024) A new species of karst-dwelling bent-toed gecko of the *Cyrtodactylus intermedius* group (Squamata, Gekkonidae) from eastern Thailand and the phylogenetic placement of *C. intermedius*. *ZooKeys*, 1211, 101–130. <https://doi.org/10.3897/zookeys.1211.122563>.
- Attems, C. (1914) Die indo-australischen Myriopoden. *Archiv für Naturgeschichte*, 80A, 1–398.
- Attems, C. (1936) Diplopoda of India. *Memoirs of the Indian Museum*, 11(4), 133–323.
- American Veterinary Medical Association (AVMA) (2020) AVMA guidelines for the euthanasia of animals. Available at <https://www.avma.org/sites/default/files/2020-02/Guidelines-on-Euthanasia-2020.pdf> [Accessed on: 2025-8-6].
- Benchapong, T., Enghoff, H., Likhitrakarn, N., Chanabun, R., Aoonkum, A. & Srisonchai, R. (2025) Three new species of the millipede genus *Enghoffosoma* Golovatch, 1993 from Thailand (Diplopoda, Polydesmida, Paradoxosomatidae). *Zoosyst. Evol.*, 101(2), 509–532.
- Bohlen, J., Dvořák, T., Šlechta, V. & Šlechtová, V. (2020) Sea water shaping the freshwater biota: Hidden diversity and biogeographic history in the *Paracanthocobitis zonalternans* species complex (Teleostei: Nemacheilidae) in western Southeast Asia. *Mol. Phyl. Evol.*, 148, 106806. <https://doi.org/10.1016/j.ympev.2020.106806>.
- Chen, J., Yu, J., Bai, X., Zeng, Y. & Wang, J. (2020) Fragility of karst ecosystem and environment: Long-term evidence from lake sediments. *Agr. Ecosyst. Environ.*, 294, 106862. <https://doi.org/10.1016/j.agee.2020.106862>.
- Clements, R., Sodhi, N.S., Schilthuizen, M. & Ng, P.K.L. (2006) Limestone karsts of Southeast Asia: Imperiled arks of biodiversity. *BioScience*, 56(9), 733–742. [https://doi.org/10.1641/0006-3568\(2006\)56\[733:LKOSA1\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[733:LKOSA1]2.0.CO;2).
- Decker, P. (2010) Contributions to the myriapod fauna of Thailand – New records of millipedes and centipedes from Thailand (Myriapoda: Diplopoda, Chilopoda). *Schubartiana*, 4, 23–34.
- Enghoff, H. (2005) The millipedes of Thailand (Diplopoda). *Steenstrupia*, 29(1), 87–103.
- Enghoff, H., Golovatch, S., Short, M., Stoev, P. & Wesener, T. (2015) Diplopoda – taxonomic overview. In: Minelli A. (Ed) *Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda, Volume: 2*, pp. 363–453. Brill, Leiden. https://doi.org/10.1163/9789004188273_017.
- Fark, S.N., Gerber, S., Alonzo, S.H., Kindsvater, H.K., Meier, J.I. & Seehausen, O. (2022) Multispecies colour polymorphisms associated with contrasting microhabitats in two Mediterranean wrasse radiations. *J. Evol. Biol.*, 35(4), 633–647. <https://doi.org/10.1111/jeb.13999>.
- Fernández, R., Edgecombe, G.D. & Giribet, G. (2018) Phylogenomics illuminates the backbone of the Myriapoda tree of life and reconciles morphological and molecular phylogenies. *Sci. Rep.*, 8(1), 83. <https://doi.org/10.1038/s41598-017-18562-w>.
- Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotechnol.*, 3(5), 294–299.
- Gao, K., He, X., Wang, H., Chen, C., Gu, X., Lai, Q., Perez, M., Kojima, S., Amano, K. & Sun, J. (2025) Phylogenomic analyses

- of Pliocardiinae (Bivalvia: Vesicomidae) update genus-level taxonomy and shed light on trait evolution. *Cladistics*, 41(4), 372–387. <https://doi.org/10.1111/cla.70001>.
- Golovatch, S.I., Hoffman, R.L. & Chang, H.-W. (2011) Identity of *Glomeris bicolor* Wood, 1865, and the status of the generic names *Hyleoglomeris* Verhoeff, 1910 and *Rhopalomeris* Verhoeff, 1906 (Diplopoda, Glomeridae). *Trop. Nat. His.*, 11(1), 1–8. <https://doi.org/10.58837/tnh.11.1.103004>.
- Golovatch, S.I. & Semenyuk, I. (2016) Two new species of the millipede family Glomeridae from Vietnam (Diplopoda: Glomerida). *Russ. Entomol. J.*, 25(4), 411–416.
- Haque, M.T., Khan, M.K. & Herberstein, M.E. (2024) Current evidence of climate-driven colour change in insects and its impact on sexual signals. *Ecol. Evol.*, 14(7), e11623. <https://doi.org/10.1002/ece3.11623>.
- Hillis, D.M. & Bull, J.J. (1993) An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Syst. Biol.*, 42(2), 182–192. <https://doi.org/10.1093/sysbio/42.2.182>.
- Hinton, H.E. & Jarman, G.M. (1973) Physiological colour change in the elytra of the hercules beetle, *Dynastes hercules*. *J. Insect. Physiol.*, 19(3), 533–549. [https://doi.org/10.1016/0022-1910\(73\)90064-4](https://doi.org/10.1016/0022-1910(73)90064-4).
- Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B.Q. & Vinh, L.S. (2018) UFBoot2: Improving the ultrafast bootstrap approximation. *Mol. Biol. Evol.*, 35, 518–522. <https://doi.org/10.1093/molbev/msx281>.
- Hoffman, R.L. (1980) *Classification of the Diplopoda*. *Muséum d'Histoire Naturelle*, Genève, Switzerland, 237 pp.
- Hughes, A.C., Satasook, C., Bates, P.J.J., Bumrungsri, S. & Jones, G. (2011) Explaining the causes of the zoogeographic transition around the Isthmus of Kra: using bats as a case study. *J. Biogeogr.*, 38(12), 2362–2372. <https://doi.org/10.1111/j.1365-2699.2011.02568.x>.
- Huynh, C., Veenstra, A.A. & Likhitrakarn, N. (2023) First records of penicillate millipedes (Diplopoda, Polyxenidae) from Thailand, with descriptions of two new species. *Zootaxa*, 5383(4), 514–536. <https://doi.org/10.11646/zootaxa.5383.4.5>.
- Kapli, P., Lutteropp, S., Zhang, J., Kobert, K., Pavlidis, P., Stamatakis, A. & Flouri, T. (2017). Multi-rate Poisson tree processes for single-locus species delimitation under maximum likelihood and Markov chain Monte Carlo. *Bioinformatics*, 33(11), 1630–1638. <https://doi.org/10.1093/bioinformatics/btx025>.
- Kato, Y. (2000). Overlapping distribution of two groups of the butterfly *Eurema hecabe* differing in the expression of seasonal morphs on Okinawa-jima Island. *Zool. Sci.*, 17(4), 539–547. [https://doi.org/10.2108/0289-0003\(2000\)17\[539:ODOTGO\]2.0.CO;2](https://doi.org/10.2108/0289-0003(2000)17[539:ODOTGO]2.0.CO;2).
- Kuroda, M., Eguchi, K., Oguri, E. & Nguyen, A.D. (2022a) Two new cave *Hyleoglomeris* species (Glomerida, Glomeridae) from northern Vietnam. *ZooKeys*, 1108, 161–174. <https://doi.org/10.3897/zookeys.1108.85423>.
- Kuroda, M., Susukida, M., Sakamoto, K., Tsukamoto, S., Nguyen, A.D., Oguri, E. & Eguchi, K. (2022b) A new species of the genus *Hyleoglomeris* Verhoeff 1910 from Central Japan (Diplopoda: Glomerida: Glomeridae). *Acta Arachnol.*, 71(2), 115–124. <https://doi.org/10.2476/asjaa.71.115>.
- Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. & Calcott, B. (2017) PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Mol. Bio. Evol.*, 34(3), 772–773. <https://doi.org/10.1093/molbev/msw260>.
- Latinne, A., Waengsothorn, S., Rojanadilok, P., Eiamampai, K., Sribuarod, K. & Michaux,

- J.R. (2013) Diversity and endemism of Murinae rodents in Thai limestone karsts. *Syst. Biodiver.*, 11(3), 323–344. <https://doi.org/10.1080/14772000.2013.818587>
- Law, S.J., Bishop, T.R., Eggleton, P., Griffiths, H., Ashton, L. & Parr, C. (2020) Darker ants dominate the canopy: Testing macroecological hypotheses for patterns in colour along a microclimatic gradient. *J. Anim. Ecol.*, 89, 347–359. <https://doi.org/10.1111/1365-2656.13110>.
- Leach, W.E. (1814) Crustaceology. In: Brewster, D. (Ed) *The Edinburgh Encyclopaedia. Balfour, Edinburgh*, vol. 7(2), 385–437, 765–766.
- Leach, W.E. (1815) A tabular view of the external characters of four classes of animals, which Linné arranged under Insecta; with the distribution of the genera comprising three of these classes into orders, &c. and descriptions of several new genera and species. *Trans. Linn. Soc. London*, 11(2), 306–400.
- Likhitrakarn, N., Golovatch, S.I., Jirapatrasilp, P., Panha, S. (2017) A checklist of the millipedes (Diplopoda) of Myanmar, with an updated list of Leonardo Fea's collecting localities. *Zootaxa*, 4350(1), 1–46. <https://doi.org/10.11646/zootaxa.4350.1.1>.
- Likhitrakarn, N., Srisonchai, R. & Golovatch, S.I. (2023a) An updated catalogue of the millipedes (Diplopoda) of Thailand. *Trop. Nat. His.*, 23(7), 51–92. <https://doi.org/10.58837/tnh.23.7.258815>.
- Likhitrakarn, N., Srisonchai, R., Siriwtut, W., Jirapatrasilp, P., Jeratthitikul, E., Panha, S. & Sutcharit, C. (2023b) Review of the pill millipede genus *Hyperglomeris* Silvestri, 1917 (Diplopoda, Glomerida, Glomeridae) with description of two new species from Laos. *ZooKeys*, 1163, 177–198. <https://doi.org/10.3897/zookeys.1163.103950>.
- Likhitrakarn, N., Jeratthitikul, E., Sapparoj-pattana, P., Siriwtut, W., Srisonchai, R., Jirapatrasilp, P., Seesamut, T., Poolprasert, P., Panha, S. & Sutcharit, C. (2024a) Six new species of the pill millipede genus *Hyleoglomeris* Verhoeff, 1910 (Diplopoda, Glomerida, Glomeridae) in Thailand revealed by dna-barcoding. *Contrib. Zool.*, 93(4), 289–323. <https://doi.org/10.1163/18759866-bja10062>.
- Likhitrakarn, N., Golovatch, S.I., Srisonchai, R., Jirapatrasilp, P., Sapparoj-pattana, P., Jeratthitikul, E., Panha, S. & Sutcharit, C. (2024b) A new species of the pill millipede genus *Rhopalomeris* Verhoeff, 1906 (Diplopoda, Glomerida, Glomeridae) from Myanmar, and notes on *Rhopalomeris car-nifex* (Pocock, 1889). *ZooKeys*, 1215, 235–257. <https://doi.org/10.3897/zookeys.1215.130919>.
- Liu, W. & Golovatch, S.I. (2020) The first representatives of the millipede family Glomeridellidae (Diplopoda, Glomerida) recorded from China and Indochina. *ZooKeys*, 954, 1–15. <https://doi.org/10.3897/zookeys.954.54694>.
- Lobo, A.J., Costa, P., Teixeira, M., Ferreira, M., Costa, M.H. & Costa, F. (2013) Enhanced primers for amplification of DNA barcodes from a broad range of marine metazoans. *BMC Ecol.*, 13, 34. <https://doi.org/10.1186/1472-6785-13-34>.
- Man, N.S., Siriboon, T., Lin, A., Sutcharit, C. & Panha, S. (2022) Revision of the carnivorous land snail family Streptaxidae (Stylommatophora, Achatinina) in Myanmar, with description of four new species. *ZooKeys*, 1110, 39–102. <https://doi.org/10.3897/zookeys.1110.85399>.
- Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing

- Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA, USA.
- Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D., Woodhams, M.D., von Haeseler, A. & Lanfear, R. (2020) IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. *Mol. Bio. Evol.*, 37(5), 1530–1534. <https://doi.org/10.1093/molbev/msaa015>.
- Mock, A., Tajovský, K., Žurovcová, M., Jarošová, A., Kocourek, P., Gruber, J., Angyal, D. & Spelda, J. (2016) *Hungarosoma bokori* Verhoeff, 1928 (Diplopoda: Chordeumatida): new insights into its taxonomy, systematics, molecular genetics, biogeography and ecology. *Zootaxa*, 4178(2), 234–256. <https://doi.org/10.11646/zootaxa.4178.2.4>.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853–858. <https://doi.org/10.1038/35002501>.
- Nakano, T., Eto, K., Nishikawa, K., Hossman, M.Y. & Jeratthitikul, E. (2018) Systematic revision of the Southeast Asian macrophagous leeches, with the description of two new gastrostomobdellid species (Hirudinida: Arhynchobdellida: Erpobdelliformes). *Zool. J. Linn. Soc.*, 184(1), 1–30. <https://doi.org/10.1093/zoolinnean/zlx097>.
- Nguyen, A.D., Sierwald, P. & Marek, P.E. (2019) The pill millipedes of Vietnam: a key to genera and descriptions of five new species (Diplopoda: Glomerida: Glomeridae). *Raffles B. Zool.*, 67, 260–297. <https://doi.org/10.26107/RBZ-2019-0020>.
- Nguyen, A.D., Nguyen, S.G. & Eguchi, K. (2021) A new *Rhopalomeris* species (Diplopoda: Glomerida: Glomeridae), and notes on the phylogenetic relationships between glomeridans in Vietnam. *Zootaxa*, 4927(2), 257–264. <https://doi.org/10.11646/zootaxa.4927.2.5>.
- Oeyen, J.P. & Wesener, T. (2015) Steps towards a phylogeny of the pill millipedes: non-monophyly of the family Protoglomeridae, with an integrative redescription of *Eupeyerimhoffia archimedis* (Diplopoda, Glomerida). *Zookeys*, 510, 49–64. <https://doi.org/10.3897/zookeys.510.8675>.
- Parnell, J. (2013) The biogeography of the Isthmus of Kra region: a review. *Nord. J. Bot.*, 31(1), 001–015. <https://doi.org/10.1111/j.1756-1051.2012.00121.x>.
- Pholyotha, A., Sutcharit, C., Tongkerd, P., Jeratthitikul, E. & Panha, S. (2020) Integrative systematics reveals the new land-snail genus *Taphrenalla* (Eupulmonata: Ariophantidae) with a description of nine new species from Thailand. *Contrib. Zool.*, 90(1), 21–69. <https://doi.org/10.1163/18759866-BJA10013>.
- Pholyotha, A., Tongkerd, P. & Sutcharit, C. (2023) *Siamochlamys panhai*, a new limestone karst-restricted terrestrial snail from Thailand (Eupulmonata: Helicarionidae). *Trop. Nat. His.*, 23(7), 41–50. <https://doi.org/10.58837/tnh.23.7.258814>.
- Pimvichai, P., Enghoff, H. & Backeljau, T. (2023) Morphological and DNA sequence data of two new millipede species of the *Thyropygus induratus* Subgroup (Diplopoda: Spirostreptida: Harpagophoridae). *Trop. Nat. His.*, 23(7), 107–122. <https://doi.org/10.58837/tnh.23.7.258818>.
- Pocock, R.I. (1889) Contributions to the fauna of Mergui and its archipelago, Volume 1: Myriopoda. *Zool. J. Linn. Soc.*, 21(132), 287–303. <https://doi.org/10.1111/j.1096-3642.1889.tb00980.x>.
- Pocock, R.I. (1890) On the myriapods of Burma. Pt. 1. Report on the Oniscomorpha collected by Sig. L. Fea, by Mr. L. W. Oates and by the late Sig. G.B. Comotto. *Annalidel Museo*

- Civico di Storia Naturale di Genova, Series 2*, 10, 399–432.
- Puillandre, N., Lambert, A., Brouillet, S. & Achaz, G. (2012) ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Mol. Ecol.*, 21(8), 1864–1877. <https://doi.org/10.1111/j.1365-294X.2011.05239.x>.
- Reip, H.S. & Wesener, T. (2018) Intraspecific variation and phylogeography of the millipede model organism, the black pill millipede *Glomeris marginata* (Villers, 1789) (Diplopoda, Glomerida, Glomeridae). *ZooKeys*, 741, 93–131. <https://doi.org/10.3897/zookeys.741.21917>.
- Ridd, M.F., Barber, A.J. & Crow, M.J. (2011) Introduction to the geology of Thailand. In: Ridd, M.F., Barber, A.J. & Crow, M.J. (Eds) *The Geology of Thailand*, pp. 1–18. Geological Society, London. <https://doi.org/10.1144/GOTH.1>.
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.*, 61(3), 539–542. <https://doi.org/10.1093/sysbio/sys029>.
- Rundle, H.D. & Nosil, P. (2005) Ecological speciation. *Ecol. Lett.*, 8, 336–352. <https://doi.org/10.1111/j.1461-0248.2004.00715.x>.
- San Mauro, D. & Agorreta, A. (2010) Molecular systematics: A synthesis of the common methods and the state of knowledge. *Cell. Mol. Biol. Lett.*, 15(2), 311–341. <https://doi.org/10.2478/s11658-010-0010-8>.
- Sapparojpatana, P., Jeratthitikul, E. & Likhitrakarn, N. (2025) A new species of the pill millipede genus *Rhopalomeris* Verhoeff, 1906 (Diplopoda, Glomerida) from southern Thailand. *Trop. Nat. His.*, 25(8), 52–61.
- Schulmeister, S., Wheeler, W.C. & Carpenter, J.M. (2002) Simultaneous analysis of the basal lineages of Hymenoptera (Insecta) using sensitivity analysis. *Cladistics*, 18(5), 455–484. [https://doi.org/10.1016/S0748-3007\(02\)00100-7](https://doi.org/10.1016/S0748-3007(02)00100-7).
- Sein, K.K., Chidthaisong, A. & Oo, K.L. (2018) Observed trends and changes in temperature and precipitation extreme indices over Myanmar. *Atmosphere*, 9(12), 477. <https://doi.org/10.3390/atmos9120477>.
- Shear, W.A. (2011) Class Diplopoda de Blainville in Gervais, 1844. In: Zhang, Z.Q. (Ed) *Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness*. *Zootaxa*, 3148(1), 159–164.
- Silvestri, F. (1917) Contributions to a knowledge of the oriental Diplopoda Oniscomorpha. I. The family Glomeridae. *Rec. Indian Mus.*, 13(3, 9), 103–151.
- Srikampha, K., Wesener, T., Likhitrakarn, N., Sutcharit, C. & Srisonchai, R. (2025) The millipede genus *Sphaerobelum* Verhoeff, 1924, in Thailand, with descriptions of three new species (Diplopoda, Sphaerotheriida, Zephroniidae). *Zoosyst. Evol.*, 101(1), 273–300. <https://doi.org/10.3897/zse.101.143073>.
- Srisonchai, R., Enghoff, H., Likhitrakarn, N. & Panha, S. (2018) A revision of dragon millipedes I: genus *Desmoxytes* Chamberlin, 1923, with the description of eight new species (Diplopoda, Polydesmida, Paradoxosomatidae). *ZooKeys*, 761, 1–177. <https://doi.org/10.3897/zookeys.761.24214>.
- Srisonchai, R., Likhitrakarn, N., Sutcharit, C., Backeljau, T. & Pimvichai, P. (2023) A new jewel-like species of the pill-millipede genus *Sphaerobelum* Verhoeff, 1924 (Diplopoda, Sphaerotheriida, Zephroniidae) from Thailand. *ZooKeys*, 1181, 41–57. <https://doi.org/10.3897/zookeys.1181.109076>.

- Srisonchai, R., Enghoff, H., Likhitrakarn, N., Jeratthitikul, E., Jirapatrasilp, P., Panha, S. & Sutcharit, C. (2024a) Molecular phylogeny of dragon millipedes (Diplopoda: Polydesmida: Paradoxosomatidae) from mainland South-East Asia, with description of a new genus and species. *Zool. J. Linn. Soc.*, 202(1), zlad164. <https://doi.org/10.1093/zoolinnea/zlad164>.
- Srisonchai, R., Likhitrakarn, N., Sutcharit, C. & Wesener, T. (2024b) Integrative taxonomy reveals two new giant pill-millipedes of the genus *Zephronia* Gray, 1832 from eastern Thailand (Diplopoda, Sphaerotheriida, Zephroniidae). *ZooKeys*, 1212, 29–64. <https://doi.org/10.3897/zookeys.1212.126536>.
- Tamura, K., Stecher, G. & Kumar, S. (2021) MEGA11: Molecular Evolutionary Genetics Analysis Version 11. *Mol. Bio. Evol.*, 38(7), 3022–3027. <https://doi.org/10.1093/molbev/msab120>.
- Verhoeff, K.W. (1906) Über Diplopoden. 4. (24). Aufsatz: Zur kenntnis der Glomeriden (zugleich Vorläufer einer Glomeris-Monographie). *Archiv für Naturgeschichte*, 72, 107–226.
- Verhoeff, K.W. (1910) Über Diplopoden. 41. Aufsatz: Indomalayische Glomeriden. *Sber. Ges. Naturf. Freunde Berl.*, 1910(5), 240–249.
- Verhoeff, K.W. (1914) *Die Diplopoden Deutschlands zusammenfassend bearbeitet, zugleich eine allgemeine Einführung in die Kenntnis der Diplopoden – Systematik, der Organisation, Entwicklung, Biologie, Geographie*. C.F. Winter'sche Verlagsbuchhandlung.
- Wesener, T. (2012) *Nearctomeris*, a new genus of pill millipedes from North America, with a comparison of genetic distances of American pill millipede genera (Glomerida, Glomeridae). *Zootaxa*, 3258(1), 58–68. <https://doi.org/10.11646/zootaxa.3258.1.5>.
- Wesener, T. (2019a) The oldest pill millipede fossil: A species of the Asiatic pill millipede genus *Hyleoglomeris* in Baltic amber (Diplopoda: Glomerida: Glomeridae). *Zool. Anz.*, 283, 40–45. <https://doi.org/10.1016/j.jcz.2019.08.009>.
- Wesener, T. (2019b) First records of giant pill-millipedes from Laos (Diplopoda, Sphaerotheriida, Zephroniidae). *Zootaxa*, 4563(2), 205–209. <https://doi.org/10.11646/zootaxa.4563.2.1>.
- Wesener, T. & Conrad, C. (2016) Local hotspots of endemism or artifacts of incorrect taxonomy? The status of microendemic pill millipede species of the genus *Glomeris* in Northern Italy (Diplopoda, Glomerida). *PLoS One*, 11(9), e0162284. <https://doi.org/10.1371/journal.pone.0162284>.
- Wilbrandt, J., Lee, P., Read, H. & Wesener, T. (2015) A first integrative study of the identity and origins of the British dwarf pill millipede populations, *Trachysphaera* cf. *lobata* (Diplopoda, Glomerida, Glomeridae). *Bio-divers. Data J.*, 3, e5176. <https://doi.org/10.3897/BDJ.3.e5176>.
- Wood, H.C. (1865) New Polyzoniidae, Gervais. In: *Proceedings of the Academy of Natural Sciences of Philadelphia 1865*, 172–173.
- Wongthamwanich, N., Panha, S., Sierwald, P., Wesener, T. & Thirakhupt, K. (2012) A new species of the giant pill-millipede genus *Sphaerobelum* Verhoeff, 1924 from northern Thailand, with an extensive description and molecular characters (Diplopoda: Sphaerotheriida: Zephroniidae). *Zootaxa*, 3220(1), 29–43. <https://doi.org/10.11646/zootaxa.3220.1.2>.