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A New Species of the Pill Millipede Genus *Rhopalomeris* Verhoeff, 1906 (Diplopoda, Glomerida) from Southern Thailand

PICHSINEE SAPPAROJPATTANA[1], EKGACHAI JERATTHITIKUL[1] AND
NATDANAI LIKHITRAKARN[2]*

[1]*Animal Systematics and Molecular Ecology Laboratory, Department of Biology, Faculty of Science, Mahidol University, Bangkok 10400, THAILAND*
[2]*Program of Agriculture, Faculty of Agricultural Production, Maejo University, Chiang Mai 50290, THAILAND*
*Corresponding author. Natdanai Likhitrakarn (kongerrrr@hotmail.com)
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ABSTRACT.– A new species of pill millipede, *Rhopalomeris sirindhornae* sp. nov., is described from southern Thailand based on morphological characteristics and genetic barcoding. This species is distinguished from its congeners by light yellowish body with pale pink lateral margins on each tergum, a pair of black obtuse subtriangular patches on the dorsum, a pair of faded black dots on the lateral side of the thoracic shield, a light yellowish venter with faded light brown spots on pleurites 3–11, and a roundly triangular to spatulate syncoxital lobe of the telopod. Phylogenetic trees based on a fragment of the mitochondrial COI gene confirmed the entity of the new species and revealed a close relationship with *R. carnifex* and *R. nigroflava*. Interspecific genetic distances between *R. sirindhornae* sp. nov. and other *Rhopalomeris* species ranged from 9.97–14.36%, with the shortest distance to *R. carnifex*. Intraspecific genetic distances within each *Rhopalomeris* species ranged from 0–6.16%. A new distribution map of the presently known *Rhopalomeris* is also provided.

KEYWORDS: Myriapoda, biodiversity, taxonomy, phylogeny, Indochina

INTRODUCTION

The order Glomerida, commonly known as pill millipedes, is one of the most species-rich millipede groups, with more than 300 valid species inhabiting the northern hemisphere from Central and Southeast Asia to Europe, North Africa, and America (Minelli, 2015). Research on pill millipedes has intensified in recent years, with notable studies conducted in many regions such as Europe, China, and mainland Southeast Asia (Decker, 2010; Makarov et al., 2013; Golovatch and Semenyuk, 2016; Wesener and Conrad, 2016; Liu and Golovatch, 2020; Nguyen et al., 2019; Likhitrakarn et al., 2023a, 2024a;). In Thailand, recent studies have reported 14 species of pill millipedes belonging to two genera, *Hyleoglomeris* Verhoeff, 1910 and *Rhopalomeris* Verhoeff, 1906 (Likhitrakarn et al., 2023a, 2024a).

Rhopalomeris carnifex (Pocock, 1889) is the only taxon from the genus *Rhopalomeris* currently known from Thailand. The genus *Rhopalomeris* was described in 1906 by Verhoeff (Verhoeff, 1906) with *Glomeris bicolor* Wood, 1865 as the type species based on specimens from “Insel Salanga” or Salanga Island [= Phuket Island, Thailand]. Silvestri (1917) subsequently discovered that *Rhopalomeris bicolor* sensu Verhoeff (1906) had been misidentified, and therefore proposed *R. carnifex* (Pocock, 1889), from Tenasserim, Myanmar, as the valid type species of the genus. This re-designation was formally accepted and justified in later taxonomic works (Golovatch et al., 2011), and further clarified by Likhitrakarn et al. (2024b). Additional examination of specimens that were identified as *R. bicolor* by Verhoeff (1906) have confirmed them as *R. carnifex* (Silvestri, 1917; Golovatch et al., 2011). Later, the phylogenetic position of *R. carnifex* was verified by Likhitrakarn et al. (2024b) using molecular data and based on potential topotypes from Kala Island, Myanmar. The currently recognized distribution of *R. carnifex* was thus updated to cover limestone mountains located along the Tenasserim Mountain range in Myanmar and southern Thailand (Likhitrakarn et al., 2024b).

In the early efforts at *Rhopalomeris* taxonomy, the traditional morphological-based method was mainly used for species identification (e.g., Silvestri, 1917; Golovatch and Semenyuk, 2016). Later, molecular data became more popular for species delineation and evolutionary clarification (Nguyen et al., 2019, 2021; Likhitrakarn et al., 2024b). Despite the phylogenetic research that has been widely conducted in other regions, taxonomic study on this genus in Thailand is very scanty due to the lack of molecular information (Likhitrakarn et al., 2024a). However, Thailand is one of the most bio-diverse countries in mainland Southeast Asia (Myers et al., 2000), and therefore may have high diversity in the pill millipede genus *Rhopalomeris*.

In the present study, the hidden diversity of *Rhopalomeris* from Thailand is revealed using an integrative technique applying morphological characters and genetic barcoding from a DNA fragment of the mitochondrial COI gene. This study not only introduces a new species to the genus *Rhopalomeris* in Thailand but also initiates an in-depth exploration of its diversity and biogeography in Thailand to be pursued in the future.

MATERIALS AND METHODS

Specimen sampling and morphological examination

This study is based on new *Rhopalomeris* specimens collected from southern Thailand and voucher specimens deposited in Mahidol University Museum of Natural History, Department of Biology, Faculty of Science (MUMNH). 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). Living specimens were photographed using a Nikon camera (DSLR D850), then 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 and molecular studies. Holotype and paratypes are housed in Mahidol University Museum of Natural History, Department of Biology, Faculty of Science (MUMNH), Nakhon Pathom, Thailand.

The male telopod, leg-pair 17, and leg-pair 18 were dissected, and other morphological characters, includeing coloration pattern, ommatidia, Tomosvary's organ, antennae, sensory cones on antennal tip, striae tergites, and anal shield were examined under an Olympus SZX7 stereoscopic light microscope. The descriptions of morphological characters used in this research were based on previous studies (e.g. Wesener, 2012; Golovatch and Semenyuk, 2016; Likhitrakarn et al., 2024b). All characters were measured and imaged using a Dino-Eye Eyepiece Camera attached to a ZEISS Stemi 305 stereo microscope with DinoCapture 2.0 software.

Abbreviations for morphological terms

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
sn =syncoxite notch
sx =syncoxite
ta =tarsus
ti =tibia
tp =tibial process

Phylogenetic analyses

Fragments of the mitochondrial cytochrome c oxidase subunit I (COI) gene from two specimens of an undescribed *Rhopalomeris* species (MUMNH-GLO 189-1 and GLO235-1) were newly sequenced in this study. DNA extraction, polymerase chain reaction (PCR), sequencing, and sequence alignment were undertaken using the standard protocol described by Likhitrakarn et al. (2024b). The newly obtained DNA sequences were deposited in the GenBank nucleotide sequence database under accession numbers PV176402 to PV176403. Phylogenetic trees were conducted using maximum likelihood (ML) and Bayesian inference (BI), and both analyses were performed on-line through the Cyber Infrastructure for Phylogenetic Research (CIPRES) Science Gateway (Miller et al., 2010). The final data matrix included 660 base pairs (bp) of two added sequences of *Rhopalomeris* in this study, and 61 sequences previously used in by Likhitrakarn et al. (2024b), which contained 10 sequences of all available *Rhopalomeris* species, 49 sequences from other genera in family Glomeridae, as well as *Sphaerobelum truncatum* Wongthamwanich, 2012 and *Zephronia laotica* Wesener, 2019 as the distant outgroup.

The best-fit models of nucleotide substitution were identified using PartitionFinder2 v.2.3.4 (Lanfear et al., 2017) under the corrected Akaike information criterion (AICc). The program suggested the models SYM+I+G, HKY+I, GTR+I+G for the three COI codon positions. These nucleotide substitution models were applied in the subsequent phylogenetic analyses. The ML analysis was performed using IQ-Tree v.2.1.2 (Minh et al., 2020) with 1,000 ultrafast bootstrap replicates. The BI analysis was constructed using MrBayes v.3.2.7a (Ronquist et al., 2012) based on two simultaneous 10-million-generation runs and sampling every 1,000 generations, with the first 25% of samples discarded as burn-in. The average effective sample size (ESS) from the MCMC analysis was over 200 for all parameters. Nodes with ≥95% bootstrap support values (BS) from ML and/or ≥ 0.95 Bayesian posterior probabilities (BPP) from BI were considered as significant support (Hillis and Bull, 1993; Hoang et al., 2018; San Mauro and Agorreta, 2010). In addition, genetic distances among *Rhopalomeris* species and within each species were calculated using uncorrected *p*-distances as implemented in MEGA11 (Tamura et al., 2021).

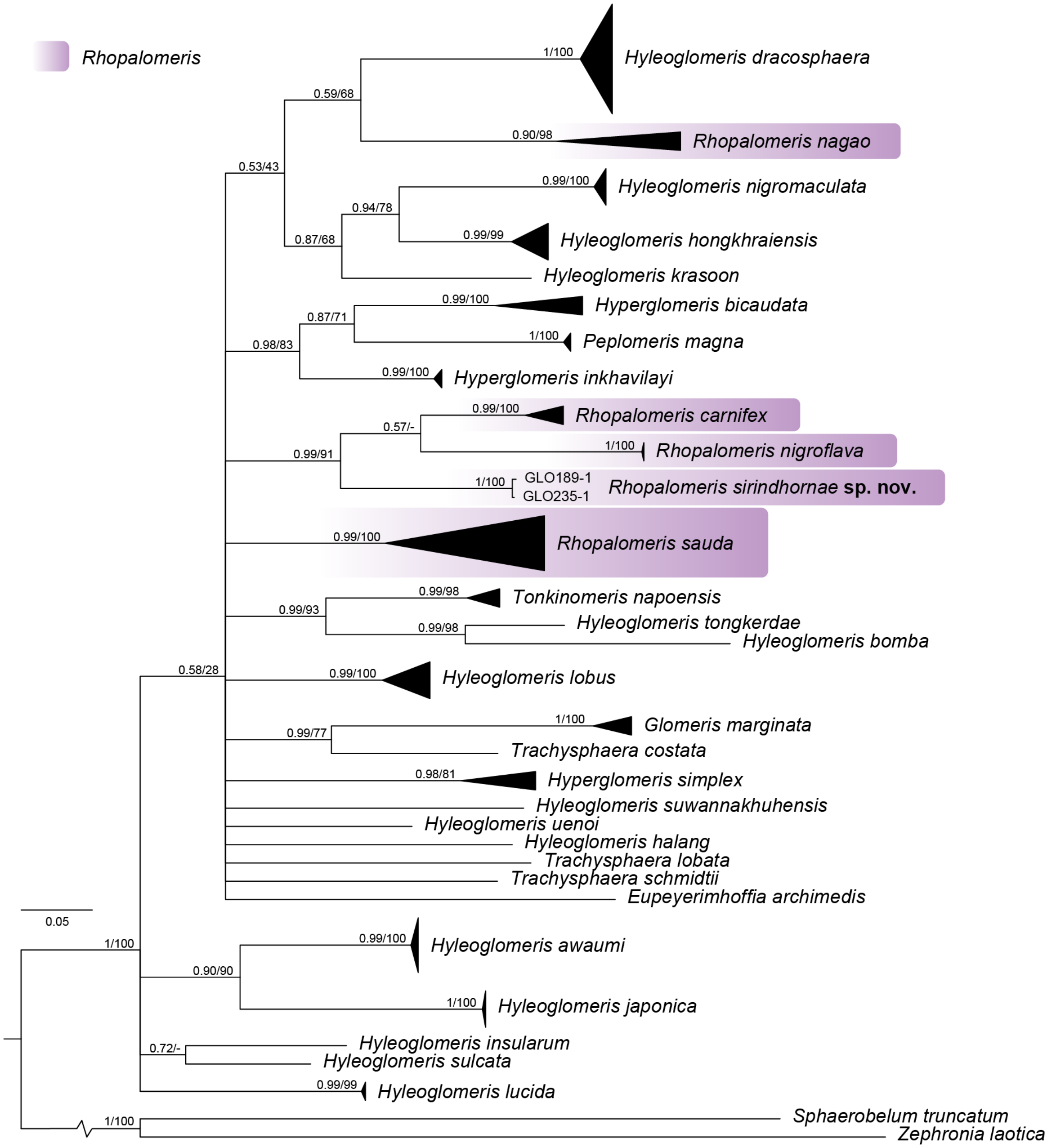

FIGURE 1. Bayesian inference tree of *Rhopalomeris* species and related taxa based on 660 bp of COI gene. Numbers at the nodes are the Bayesian posterior probabilities (BPP) from BI analysis and maximum likelihood ultrafast bootstrap values (BS) from ML analysis, and are shown as BPP/BS. Purple highlighted clades represent *Rhopalomeris* species.

RESULTS

Molecular phylogeny

The final alignment of the COI gene fragments used for phylogenetic analyses had a length of 660 bp, containing 272 (41.21%) parsimony informative sites and 333 (50.45%) variable sites. Topology of the COI gene trees from ML and BI were identical. Therefore, only the BI tree is presented in Figure 1. The obtained gene tree recovered all five taxa of *Rhopalomeris* as well-supported clades (BS = 98–100%, BPP = 0.90–1). Four of these are previously recognized species (i.e., *R. carnifex*, *R. sauda* Nguyen, Sierwald & Marek, 2019, *R. nagao* Nguyen, Nguyen & Eguchi, 2021, and *R.*

TABLE 1. Mean genetic divergence (uncorrected p-distance: %±SD) of *Rhopalomeris* species based on 660 bp COI gene. The interspecific genetic divergences are shown below the diagonal and the intraspecific genetic distances are shown in bold.

Taxa	1	2	3	4	5
1. *Rhopalomeris sirindhornae* sp. nov.	**0.17**				
2. *Rhopalomeris carnifex*	9.97 ± 0.01	**1.73**			
3. *Rhopalomeris nigroflava*	10.66 ± 0.001	10.05 ± 0.01	**0**		
4. *Rhopalomeris sauda*	12.05 ± 0.004	14.36 ± 0.01	12.48 ± 0.004	**6.16 ± 0.01**	
5. *Rhopalomeris nagao*	12.05 ± 0.01	12.69 ± 0.01	11.35 ± 0.003	11.76 ± 0.01	**5.02**

nigroflava Likhitrakarn, 2024 in Likhitrakarn et al., 2024b). The remaining unrecognized clade, from southern Thailand, is described herein as *R. sirindhornae* sp. nov. Interestingly, the COI gene tree failed to resolve relationships among members of the genus *Rhopalomeris* since the genus was not recovered as monophyletic, but instead *Rhopalomeris* species were mixed with members of other genera in the Glomeridae. Even though the overall phylogenetic relationships among genera were poorly resolved, the members of *Rhopalomeris* from Myanmar and southern Thailand (*R. carnifex*, *R. nigroflava*, and *R. sirindhornae* sp. nov.) were retrieved as a monophyletic clade, although with support only from BI (BS = 91%, BPP = 0.99).

The interspecific genetic distances of the COI gene observed among *Rhopalomeris* species ranged from 9.97% to 14.36% (Table 1). The nearest taxon to the new species was *R. carnifex* with the distance of 9.97%. The intraspecific genetic distances within each species of *Rhopalomeris* ranged between 0 and 6.16% (Table 1). The genetic distance within *R. sirindhornae* sp. nov. was observed at 0.17%.

Taxonomy

Order Glomerida Leach, 1814
Family Glomeridae Leach, 1815
Genus *Rhopalomeris* Verhoeff, 1906

Type species.– *Rhopalomeris carnifex* (Pocock, 1889).

Diagnosis.– The genus *Rhopalomeris* could be distinguished by an enlarged, strongly curved antennomere 6, and antennal tip with numerous apical sensory cones. The telopods are enlarged and stout, bearing both prefemoral and femoral trichosteles. The femur of the telopod has a distinctive distocaudal process. Adults are comparatively large, typically 11–20 mm in length. Coloration is variable and often useful for species identification.

Species included.– *Rhopalomeris carnifex*, *R. monacha* Silvestri, 1917, *R. tonkinensis* Silvestri, 1917, *R. variegata* Golovatch & Semenyuk, 2016, *R. sauda*, *R. nagao*, *R. nigroflava*, and *R sirindhornae* sp. nov.

Rhopalomeris sirindhornae sp. nov.

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(Figs 2, 3)

Type Material.– Holotype: ♂ (MUMNH-GLO189), Thailand, Chumphon Province, Lang Suan District, Wat Tham Khao Kriap, ca. 60–80 m a.s.l., 9°49'02.8"N 99°02'17.3"E, 16 May 2023, leg. R. Srisonchai, E. Jeratthitikul, and P. Sapparojpattana. Paratype: 29 ♂♂, 35 ♀♀ (MUMNH–GLO189), same locality, together with holotype; 59 ♂♂, 95 ♀♀ (MUMNH-GLO235), Thailand, Surat Thani Province, Tha Chana District, Wat Tham Sila Tiap, ca. 20–40 m a.s.l., 9°31'01.0"N 99°11'28.8"E, 11 June 2024, leg. R. Srisonchai.

Etymology.– The specific epithet *sirindhornae* pays honor to Her Royal Highness Princess Maha Chakri Sirindhorn in recognition of her dedication and great interest in science and the natural history of the flora and fauna in Thailand.

Diagnosis.– Differs from its congeners by light yellowish body with pale pink lateral margin on each tergum (*vs* body mostly blackish with vibrant red lateral margin in *R. carnifex* and body without pink margin in *R. sauda* and *R. nagao*). Dorsum with a pair of black, obtuse, subtriangular patches. Thoracic shield with a pair of faded black dots on the lateral side. Venter with faded light brown spots on pleurites 3–11 (*vs* no spots observed on ventral side in any described *Rhopalomeris* species). The body size is smaller than *R. carnifex* (8.3–12.7 mm in length and 4.2–5.8 mm in width *vs* 17.5–17.9 mm in length and 8.9–9.1 mm in width). The syncoxital lobe of telopod is roundly triangular to spatulate (*vs* roundly pentagonal in *R. carnifex*, narrowly round in *R. nigroflava*, and concave medially in *R. nagao*).

Description.–

Measurements: Body length of unrolled holotype, 10.6 mm; width 5.7 mm. Body length of unrolled paratypes, 8.3–10.7 mm (♂), 9.9–12.7 mm (♀); width 4.2–5.7 mm (♂), 5.1–5.8 mm (♀).

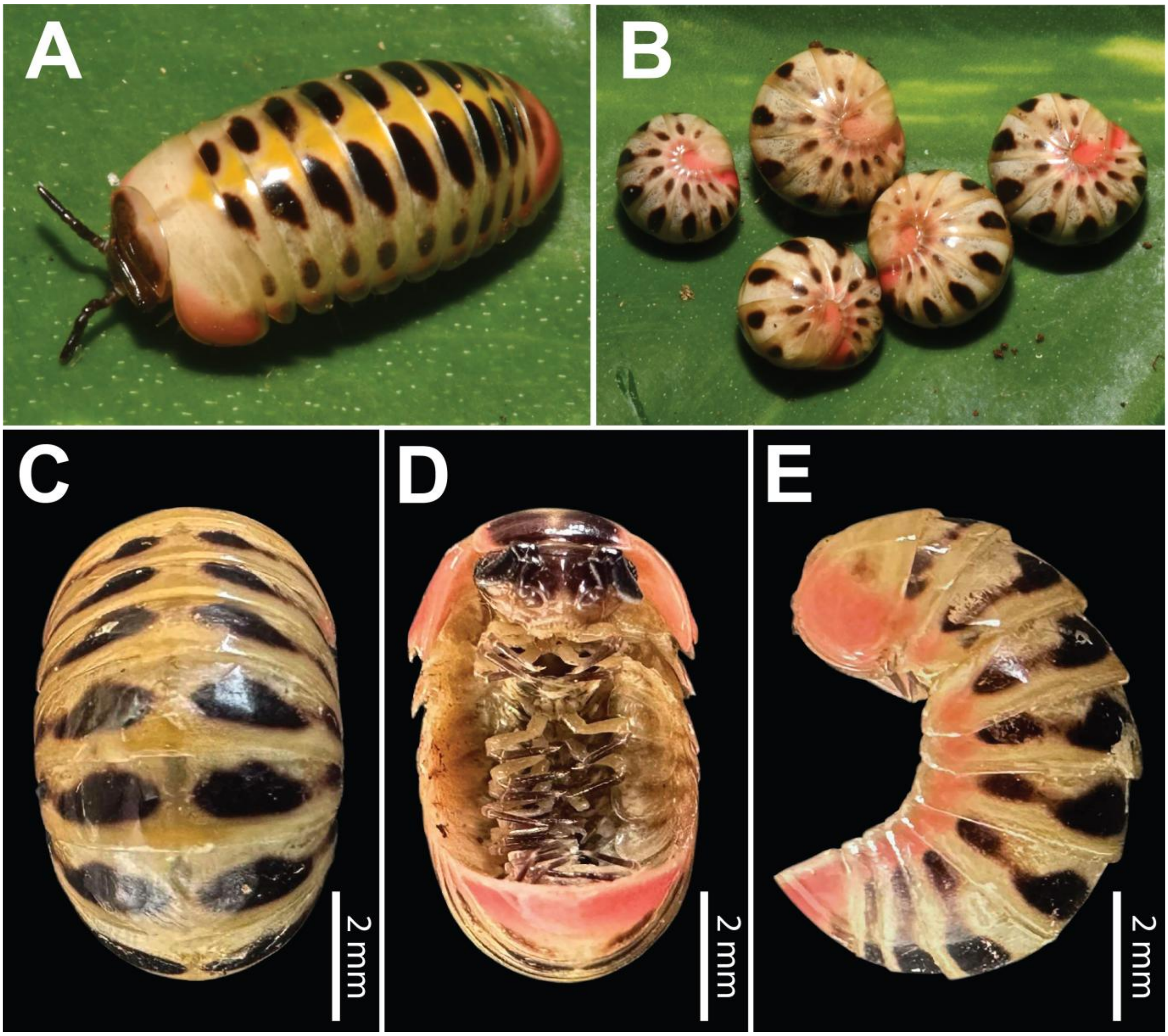

FIGURE 2. *Rhopalomeris sirindhornae* sp. nov. **A, B.** paratypes (MUMNH–GLO189), habitus, live coloration; **A.** unrolled in sublateral view; **B.** rolled in sublateral view; **C–E.** ♀ paratype (MUMNH–GLO189), alcohol preserved, in dorsal, ventral, and lateral views, respectively. **A, B.** pictures taken without scale; **C–E.** scale bars: 2 mm.

Coloration: Terga light yellowish with pale pink lateral margin and yellow at middle of posterior margin (Fig. 2A, C). The first tergum with a pair of black patches, thoracic shield with a pair of faded black dots on lateral side (Fig. 2A, D). A pair of black obtuse, subtriangular patches on mid-dorsal connected with a black oval spot on each lateral side of the 3rd–11th tergites (Fig. 2A–C, E). Pygidium light yellowish with pinkish caudal margin and a pair of black spots on anterior (Fig. 2A, B, D, E). Venter light yellowish with a faded light brown spot on pleurites 3–11, legs brownish (Fig. 2D).

Head: Dark brown, 7–9+1, blackish ommatidia, lenses convex (Fig. 2D). Tömösváry's organ oblong-oval, ca. 2.25–2.45 times as long as wide, strongly horseshoe-shaped. Labrum scantly setose. Gnathochilarium with 2+2 palps subequal in length. Antennae clavate with 25–57 small apical cones (♂), 29–50 small apical cones (♀). Antennomere 6 large, strongly curved, ca. 1.26–1.28 times as long as high (Fig. 2D). Antennomere 7 elongated, slightly curved.

Body: Collum semicircular, with 2 or 3 transverse striae. Thoracic shield with a narrow hyposchism field, not reaching behind the caudal tergal margin, 7 striae: 3–4 lying above schism, one at level to schism, remaining 3 beneath schism, 5–6 completely crossing the dorsum. Pygidium rounded, slightly concave mediocaudally.

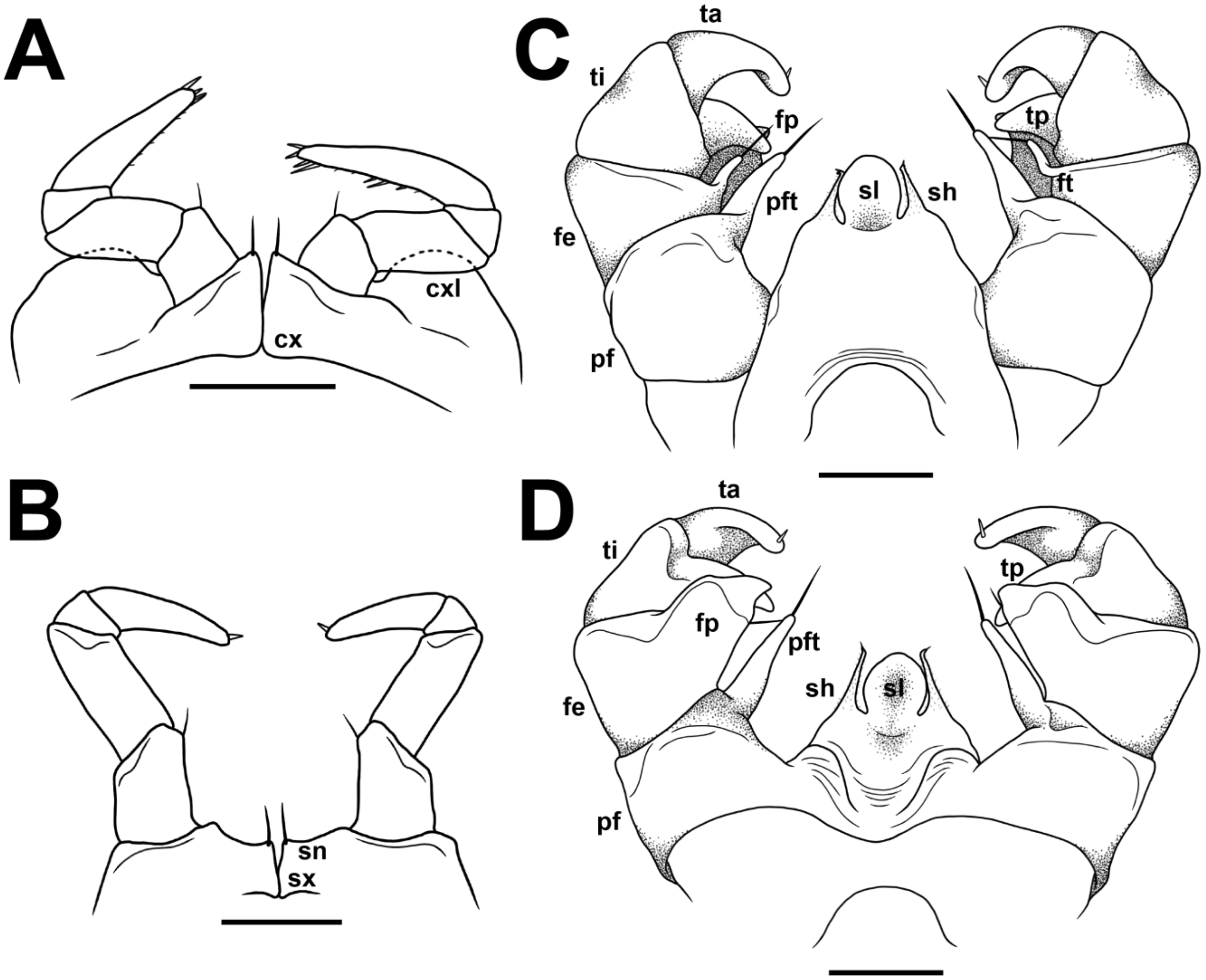

FIGURE 3. *Rhopalomeris sirindhornae* sp. nov., ♂ holotype. **A.** legs 17, anterior view; **B.** legs 18, anterior view; **C, D.** telopod, anterior and posterior views. Abbreviations: cx, coxa; cxl, coxal lobe; fe, femur; fp, femoral process; ft, femoral trichostele; pf, prefemur; pft, prefemoral trichostele; sh, syncoxital horn; sl, syncoxital lobe; sn, syncoxite notch; sx, syncoxite; ta, tarsus; ti, tibia; tp, tibial process. Scale bar = 1 mm.

Legs: Mid-body legs; tarsus with one apical spine, 7–11 lateral spines, and 16–20 ventral spines. Claw narrow and elongate. Male leg pair 1; similar to mid-body legs, but coxae protrude and elongate, with two long spines. Tarsus with only 14–17 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. 3A); strongly reduced, 4 segmented, coxa with a round, obtuse outer lobe and a setiferous tubercle, tarsus with 3–4 strong apical and 0–3 strong median spines (Fig 3A). Male leg pair 18 (Fig. 3B); less reduced, 4 segmented, with a simple syncoxital notch, tarsus with one apical spine.

Telopods (Fig. 3C, D): enlarged, stout, and trapeziform, with a roundly triangular to spatulate, central, syncoxital lobe, flanked by two spiniform, setose horns. Syncoxital horns at the level of syncoxital lobe or slightly shorter than syncoxital lobe (Fig. 3C), projecting posteriorly to the lobe (sometimes appearing equal or slightly longer than the lobe in posterior view in Fig. 3D). Each latter with a subapical setoid filament. Prefemur distroventrally with a large, long trichostele anteriorly (Fig. 3C, D). Femur with a tiny anterior trichostele and a large posterior tuberculiform process, distal part bent anteriad (Fig. 3C). Tibia with a posterior outgrowth bearing a small sigmoid membranous apical sac folded anteriad and a small parabasal tubercle (Fig. 3C). Tarsus strongly curved, with apical spine.

Distribution.– The new species is known to occur in Lang Suan District, Chumphon Province and Tha Chana District, Surat Thani Province, southern Thailand (Fig. 4).

Remarks.– There were variations on the black paramedian spots on the dorsum. These spots can be connected to the lateral spots, and the black spots on the thoracic shield may fade to almost disappearing in some individuals. In addition, after nearly two years of preservation in ethanol, their pink, yellow, and black colors remain vibrant. All specimens were found buried under the soil in May and June, which are dry season months in Thailand (temperature around 28–33°C).

DISCUSSION

There are currently eight known species of the pill millipede genus *Rhopalomeris*. All species are distributed in Southeast Asia, including *R. carnifex* in southern Thailand and Myanmar, *R. monacha* in Malaysia, *R. tonkinensis* in northern Vietnam, *R. variegata* in southern Vietnam, *R. sauda* in northern Vietnam, *R. nagao* in northern Vietnam, *R. nigroflava* in Myanmar, and *R. sirindhornae* sp. nov. in southern Thailand (Fig. 4). Only two species have been reported in Thailand, *R. carnifex* and *R. sirindhornae* sp. nov., the new species described in this study. The new species was found in isolated limestone mountains, surrounded by agricultural and urban areas, it is presently known only from the type locality and another locality about 38 kilometers away (Fig. 4). This species might be endemic to Thailand, and thus suggests that several localities in Thailand potentially serve as suitable microhabitats for pill millipede speciation and endemism. However, further field surveys are required to confirm the distribution range of this species. Moreover, the pill millipede genus *Rhopalomeris* in Thailand likely arbors greater diversity than currently known. This is supported by the recent description of several new species within the related genus *Hyleoglomeris* from Thailand (Likhitrakarn et al., 2024a). Furthermore, several specimens collected during our preliminary survey suggest the presence of undescribed *Rhopalomeris* taxa, thus warranting further taxonomic investigation.

In this study, specimens were morphologically examined based on characters of the male telopod and color patterns on both dorsal and ventral sides (Fig. 2, 3). Most of the telopod characters of *R. sirindhornae* sp. nov. were similar to the closely related taxa, *R. carnifex* and *R. nigroflava*, indicating the close evolutionary relationship among them. In contrast, the syncoxital lobe shapes were obviously different and could be used as a strong distinguishable character between species. Similarly, this character has been used as a solid identifiable character in other genera of pill millipedes such as *Nearctomeris*, *Hyperglomeris*, and *Hyleoglomeris* (Wesener, 2012; Kuroda et al., 2022a; Likhitrakarn et al., 2023b).

The color patterns could also be among the important distinguishing characteristics used for species identification, which is consistent with the previous works on pill millipedes (Wesener, 2019a; Likhitrakarn et al., 2024a). Although the black and red/pink color on terga were similarly presented in both *R. sirindhornae* sp. nov. and *R. carnifex*, the detail of color patterns in each species was unique. However, color may sometimes fade after preservation in ethanol for a long period of time and could be difficult to ascertain. Consequently, DNA characteristics, which have recently shown their utility in classification, were essential in delimiting the scope of species within the glomerid family (Wesener and Conrad, 2016; Likhitrakarn et al., 2023b, 2024a).

This study also investigated the inter- and intraspecific genetic distances among the *Rhopalomeris* species based on partial mitochondrial COI gene fragments (Table 1). The genetic distances between *Rhopalomeris* species in this study (9.97–14.36%) were congruent with previous studies on glomerid pill millipedes: 8.81–16.45% in *Hyperglomeris* species (Likhitrakarn et al., 2023b), 9.12–17.95% in *Hyleoglomeris* species (Likhitrakarn et al., 2024a), 13.0–15.8% in Vietnamese glomeridan genera (*Rhopalomeris*, *Hyleoglomeris*, *Hyperglomeris*, *Peplomeris*, and *Tonkinomeris*; Nguyen et al., 2021), and 6.7–15.9% in *Glomeris* species (Wesener and Conrad, 2016). The pattern of low intraspecific genetic distance observed in *R. sirindhornae* sp. nov. (0.17%) was also exhibited by its congener *R. nigroflava* (0%), which may be related to the endemism and narrow distribution range of these species.

Furthermore, this work highlights that genetic data is important for the designation of species boundaries in morphologically similar or cryptic species, as our results show strong genetic differences between species with similar coloration (*R. sirindhornae* sp. nov. and *R. carnifex*). The species *R. carnifex*, which was recently reported to have high variation in color patterns during a preliminary survey in Thailand (Likhitrakarn et al., 2024b), may be mingled with other hidden species. However, species examination using only morphological characteristics as in previous studies in *R. carnifex* (Verhoeff, 1906; Enghoff, 2005; Decker, 2010) is insufficient to distinguish between the cryptic species. Therefore, future works should collect and study samples comprehensively together with molecular analysis to prove the species boundary of *R. carnifex* in Thailand.

Even though the overall phylogenetic relationships among genera were poorly resolved, the members of

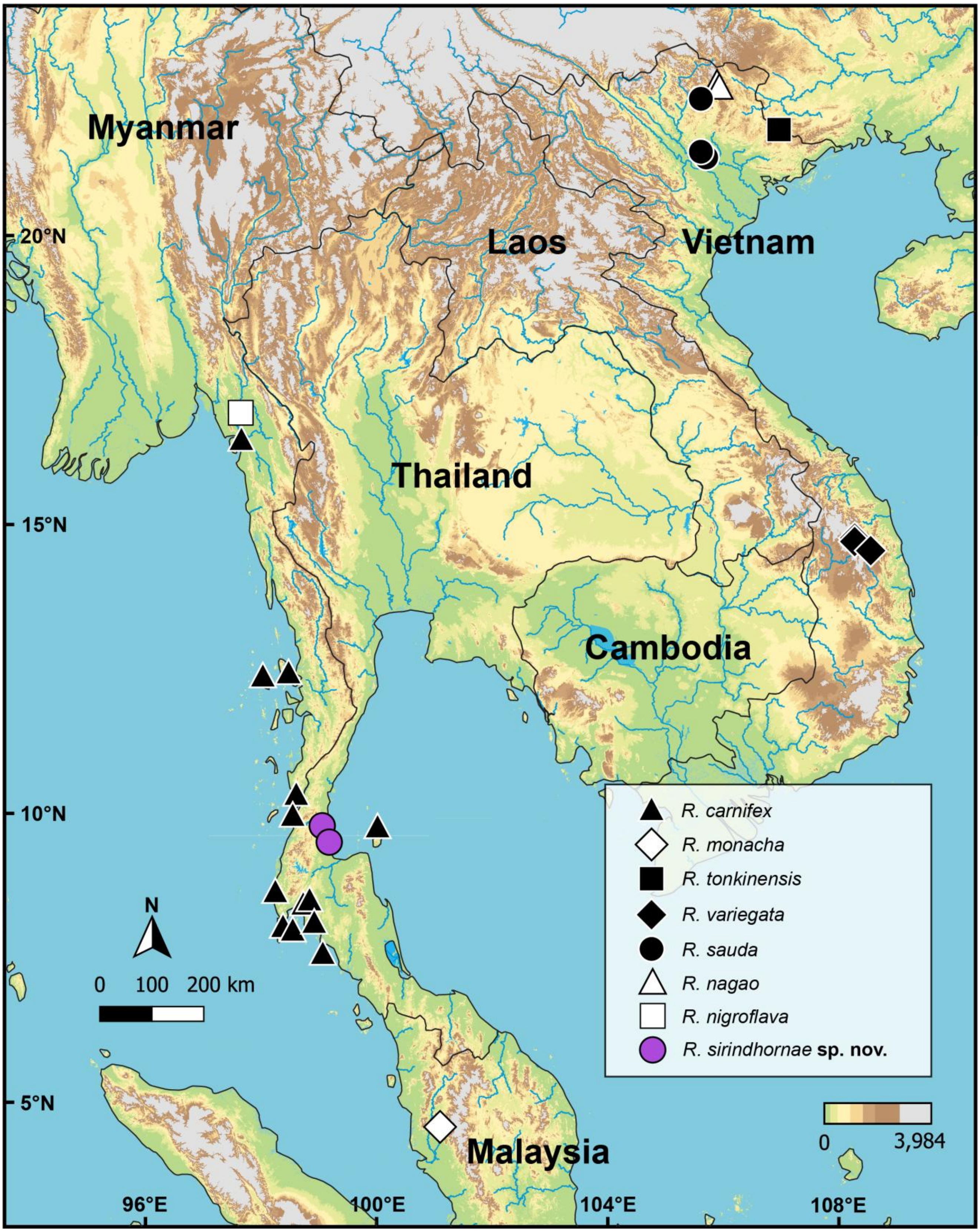

FIGURE 4. Distributions of all currently known *Rhopalomeris* species.

Rhopalomeris from Myanmar and southern Thailand (*R. carnifex*, *R. nigroflava*, and *R. sirindhornae* sp. nov.) were grouped together and exhibited a monophyletic relationship. These three species share some morphological characteristics such as the color patterns of red or pink lateral margins in *R. carnifex* and *R.*

sirindhornae sp. nov., and the black stripe on terga in *R. carnifex* and *R. nigroflava* (Likhitrakarn et al., 2024b). The black color on terga in *R. carnifex* and *R. nigroflava* was also found in *R. monacha* from Malaysia (Silvestri, 1917). However, the Vietnamese taxa (*R. sauda* and *R. nagao*) were not grouped with *Rhopalomeris* from Myanmar and southern Thailand in phylogenetic analyses in this study nor in a previous study (Likhitrakarn et al., 2024b). In fact, the telopodite shape in Vietnamese *Rhopalomeris* species is more finger-like when compared to the stout telopod in *R. carnifex*, *R. nigroflava*, and *R. sirindhornae* sp. nov. (Nguyen et al., 2021). Moreover, *Rhopalomeris* from Myanmar and southern Thailand are distantly distributed from Vietnamese *Rhopalomeris* (approximately 1,000–1,400 km), and these species may be separated by some biogeographic barriers or geological events in the interstitial areas. Nevertheless, determining the relationship between glomerid pill millipedes by using only the mitochondrial COI gene is inadequate. We thus suggest that further research combined with other genetic markers for phylogenetic analyses will be necessary to clarify the relationship of this group, and that these efforts may reveal other interesting issues in Southeast Asian pill millipede evolution.

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