

Two New Species of the Giant Pill-Millipede Genus *Zephronia* Gray, 1832 from Thailand (Diplopoda: Sphaerotheriida: Zephroniidae)

NATDANAI LIKHITRAKARN^{1,2*}, SERGEI I. GOLOVATCH³,
RUTTAPON SRISONCHAI⁴ AND CHIRASAK SUTCHARIT⁵

¹Division of Plant Protection, Faculty of Agricultural Production, Maejo University, Chiang Mai 50290, THAILAND

²Biodiversity and Utilization Research Center of Maejo University, Maejo University, Chiang Mai 50290, THAILAND

³Institute for Problems of Ecology and Evolution, Russian Academy of Sciences,
Leninsky pr. 33, Moscow 119071, RUSSIA

⁴Department of Biology, Faculty of Science, Khon Kaen University, Khon Kaen, 40002 THAILAND

⁵Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University,
Bangkok 10330, THAILAND

*Corresponding author. Natdanai Likhitrakarn (kongerrrr@hotmail.com)

Received: 30 October 2020; Accepted: 8 December 2020

ABSTRACT.— Two new species of *Zephronia* sensu stricto, both coming from Chiang Mai Province, northern Thailand, are described: *Z. lannaensis*, new species and *Z. phrain*, new species. Both these species seem to be especially similar to *Z. laotica* Wesener, 2019, but clearly distinct by telopoditomere 2 of the anterior telopods showing a sclerotized process located inside a membranous area, coupled with leg-pair 3 featuring one or two dorso-apical spine(s).

KEY WORDS: giant pill-millipede, new species, arthropod, taxonomy, Thailand

INTRODUCTION

The giant pill-millipedes (order Sphaerotheriida) are among the most conspicuous, tropical or subtropical mega-invertebrates of the world. They are quite diverse and common in southern Africa (including Madagascar and the Seychelles), as well as Australasia: the Himalaya, most of India, Sri Lanka, the East Indies, entire Southeast Asia to southern China in the north, most of Indonesia (but excluding New Guinea), the Philippines, eastern Australia together with Tasmania, and entire New Zealand (Wesener and VandenSpiegel, 2009). Currently, the most recent and presently only slightly outdated catalogue of the Sphaerotheriida contains more than 350 species, of which over 150 were described before 1900 (Wesener, 2016a). Most of them are known

from type material alone and still require taxonomic revision. On the other hand, there are many places in the world remaining almost or totally unexplored in respect to pill-millipede diversity, while many species may have gone extinct before we knew of their existence. These animals are important decomposers in terrestrial ecosystems, improving the circulation of minerals and the humification of soil (Alagesan, 2016).

As regards the sphaerotheriidan fauna of Southeast Asia, it is exclusively represented by the family Zephroniidae which presently contains about 140 species in 15 genera, including the type genus *Zephronia* Gray, 1832 (Enghoff et al., 2015). Even though progress in diplopodological research in Thailand since the latest catalogue (Enghoff, 2005) has been very rapid and considerable (e.g., Likhitrakarn et al., 2017, 2019, 2020; Srisonchai et al., 2018a–d; Pimvichai et al.,

2018, 2020), bringing the millipede fauna of the country to a total of 238 species in 48 genera, 19 families and nine orders, the giant pill-millipede diversity still remains badly understudied. Thus, only three species in two genera of Sphaerotheriida have hitherto been recorded from Thailand (Wongthamwanich et al., 2012a, b).

Zephronia is one of the largest and most widespread genera both in the entire family Zephroniidae and the order Sphaerotheriida. The identity of *Zephronia* and its type species, *Z. ovalis* Gray, 1832, had remained obscure until Golovatch et al. (2012) selected and described a neotype of *Z. ovalis*, also providing refined diagnoses of both the genus and species. As a result, *Zephronia* has hitherto been known to contain 40 described species ranging from the Himalaya of India and Nepal in the west, through Myanmar, Cambodia and Laos, to Vietnam in the east (Jeekel, 2001; Semenyuk et al., 2018; Wesener, 2019). Only *Z. siamensis* Hirst, 1907 and *Z. cf. viridescens* Attems, 1936 have heretofore been reported from Thailand, confined to its southern and northern parts of the country, respectively (Hirst, 1907; Wongthamwanich et al., 2012b).

The present paper puts on record another two *Zephronia*, both new and coming from northern Thailand.

MATERIALS AND METHODS

Specimens were collected from Huai Hong Khrai Royal Development Study Centre, and Queen Sirikit Botanic Garden, both located in Chiang Mai Province, Thailand. The Animal Care and Use Protocol Review No. 1723018 was strictly followed. All specimens were hand-collected in forest habitats with visual spotting on open surfaces in daylight. The

collecting sites were located by GPS using a Garmin GPSMAP 60 CSx, and all coordinates and elevations were rechecked with Google Earth. Photographs of live animals were taken with a Canon 70D digital camera with a Canon EF-S 60mm f/2.8 Macro USM lens. The specimens were euthanized based on AVMA guidelines for the euthanasia of animals (AVMA, 2013) and then preserved in 75% ethanol for morphological study. Some ecological and behavioral data were recorded during collection.

The specimens were examined, measured, and photographed under a Nikon SMZ 745T trinocular stereo microscope, equipped with a Canon EOS 5DS R digital SLR camera. Scanning electron micrographs (SEM) were taken with a JEOL, JSM-5410 LV microscope using gold-coated samples, and the material was returned to alcohol upon examination. Digital images obtained were processed and edited with Adobe Photoshop CS5. Line drawings were based on photographs taken under the stereo microscope equipped with a digital SLR camera. The terminology of morphological structures used in the descriptions follows the most recent publications (Wesener and Sierwald, 2005; Wongthamwanich et al., 2012a; Wesener 2016a, b, 2019; Semenyuk et al., 2018, 2020).

The holotypes, as well as most of the paratypes are housed in the Museum of Zoology, Chulalongkorn University (CUMZ), Bangkok, Thailand; a few paratypes have also been donated to the collections of the Zoological Museum, State University of Moscow, Russia (ZMUM) and the Natural History Museum of Denmark, University of Copenhagen, Denmark (NHMD), as indicated in the text.

The following abbreviations listed below are used in the figures:

cr-T = crenulations/teeth

Cx = coxa

d = apical disc

ML = membranous lobe

O = operculum of vulva

Pre = prefemur

sb = sensilla basiconica

sc = sensory cones

SP = sclerotized process

St-Pl = stigmatic plate

Syn-Cx = syncoxite.

RESULTS

Family Zephroniidae Gray, 1843

Subfamily Zephroniinae Gray, 1843

Tribe Zephroniini Jeekel, 2001

Genus *Zephronia* Gray, 1832

Dignosis (after Enghoff et al., 2015, slightly amended to adopt the two new species described below).— Anterior telopods with three or four podomeres distal to syncoxite. Telopoditomere 2 with a large, curved process forming a clamp with simple telopoditomer 3 and 4. Posterior telopod with four telopoditomer 3 and 4. Immovable finger slender, curved apically, towards telopoditomer 3 and 4 with two membranous ledges. Telopoditomere 3 also with a membranous ledge and a row of large, crenulated, sclerotized teeth, much larger than telopoditomere 4. Antennae flattened laterally, axe-shaped. 18–50 mm long. Tarsi with several apical spines.

Zephronia lan-naensis Likhitrakarn & Golovatch, new species

urn:lsid:zoobank.org:act:7BDF520A-4581-4E21-9CFD-FBB48F78DDDE

(Figs. 1A, B, 2A–C, G, 3, 4)

Material examined.— Holotype ♂ (CUMZ), Thailand, Chiang Mai Province, Doi Saket District, Huai Hong Khrai Royal Development Study Centre, 445 m a.s.l., 18°52'47"N 99°13'22"E, 29/07/2015, leg. N. Likhitrakarn. Paratypes 3 ♂, 3 ♀ (CUMZ), 1 ♂, 1 ♀ (ZMUM), same locality, together with holotype; 1 ♂, 1 ♀ (CUMZ), 1 ♂, 1 ♀ (NHMD), same locality, 02/09/2015, leg. N. Likhitrakarn.

Name.— To emphasize “Lan Na”, the old name of the region, referring to the Lan Na Kingdom (“kingdom of a million rice fields”) which ruled over northern Thailand from the 13th to 18th century; a noun in apposition.

Diagnosis.— This new species seems to be particularly similar to *Z. laotica* Wesener, 2019, but both differ from all known congeners in the anterior telopods sometimes showing a weak suture between telopoditomer 3 and 4, which is visible only in anterior view, but sometimes only three podomeres are discernible distal to the syncoxite. *Zephronia lan-naensis*, new species, differs in telopoditomere 2 being equipped with a large or small sclerotized process (SP) located inside a membranous area (Fig. 4C, F), coupled with leg-pair 3 featuring one or two dorso-apical spine(s), each of leg-pairs 4–21 is with 10–12 ventral spines (Fig. 3D) and each femur has a microdentate ventral margin (Fig. 3D) (vs. smooth), the tergites are beset with dense tiny setae (Fig. 1A, B) (vs. shiny, glabrous and weakly coriaceous) and a uniformly brown body (Fig. 1A) (vs. a bright green body with light brown posterior margins of the tergites). *Zephronia lan-naensis*, new species, fits in the general characteristics of the genus *Zephronia* because the anterior telopods show telopoditomere 2 forming a large and curved process as part of a clamp (Fig. 4C, F), the posterior telopods are with

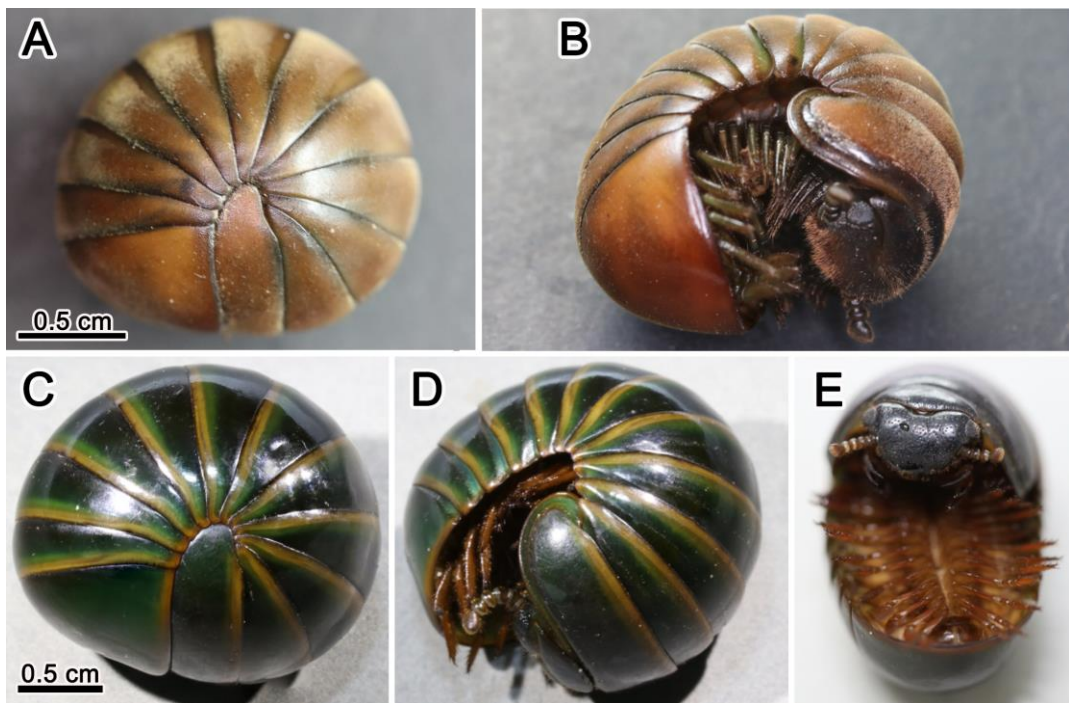


FIGURE 1. Habitus, live colouration. (A, B) *Zephronia lanmaensis*, new species, ♂ paratype; (C–E) *Zephronia phrain*, new species, ♀ paratype. (A) enrolled, lateral view; (B) unrolling, sublateral view; (C) enrolled, lateral view; (D, E) unrolling, sublateral and dorsal views, respectively. (B, D, E) Pictures taken not to scale.

four telopoditomer with two evident and membranous ledges (Fig. 4J), and the male antennae are flattened laterally and axe-shaped (Fig. 3A).

Description.— Measurements: Holotype ♂. Body length ca 29.5 mm. Width, of thoracic shield = 14.6 mm, of tergite 8 = 15.2 mm (= broadest). Height, of thoracic shield = 8.7 mm, of tergite 7 = 9.2 mm (= highest). ♂ body length = 28.8–36.2 mm. Width, of thoracic shield = 12.8–18.1 mm, of tergite 8 = 13.3–18.9 mm. Height, of thoracic shield = 8.2–10.8 mm, of tergite 7, 8.4–13.2 mm. ♀ body length = 31.8–38.2 mm. Width, of thoracic shield = 14.1–17.4 mm, of tergite 8 = 15.6–19.1 mm. Height, of thoracic shield = 9.0–11.8 mm, of tergite 7, 9.2–12.3 mm.

Colouration: live animals light brown to brown, setose parts with a golden sheen

(Fig. 1A, B), head, antennae and collum blackish to dark brown, groove of thoracic shield dark brown to brown, paratergite depressions and legs olive-green; venter light brown; colouration in alcohol, after six years of preservation, faded to brownish, head and collum dark brown, each following tergite with a dark posterior margin, legs pale yellowish, distal podomeres rusty brown, antennae dark green.

Head: trapezoid, anterior part of head clothed with numerous long setae, posterior part densely punctate; anterior margin of labrum with a single tooth. Each eye with >94 ommatidia. Aberrant ommatidium located inside antennal groove. Antennae short, with rounded joints, extending posteriorly to leg-pair 2. Lengths of antennomeres: $3 < 1 = 2 = 4 < 5 < 6$ (Fig. 3A).

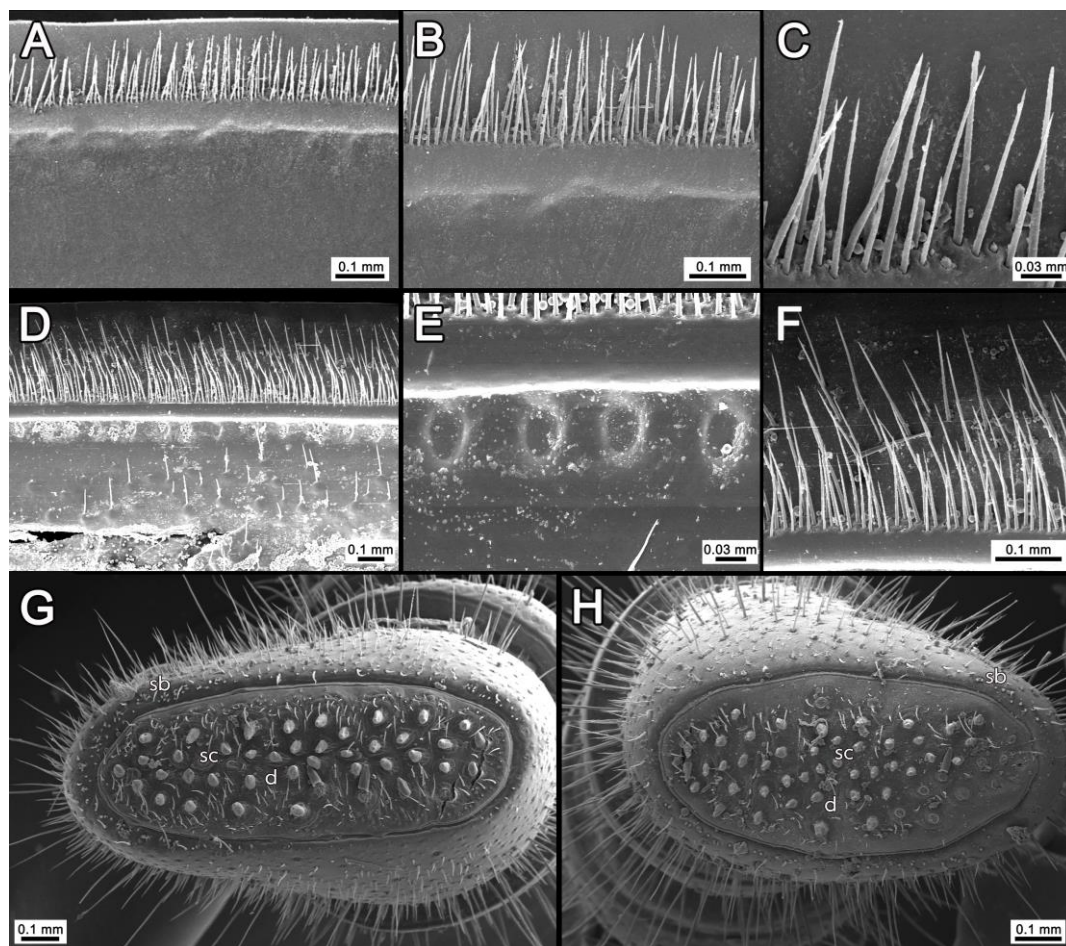


FIGURE 2. Endoterga of midbody segments, SEM micrographs. (A–C) *Zephronia lannaensis*, new species, ♂ paratype; (D–F) *Zephronia phrain*, new species, ♀ paratype; (G, H) apical disc with sensory cones; (G) *Zephronia lannaensis*, new species, ♂ paratype, right antenna; (H) *Zephronia phrain*, new species, ♀ paratype, left antenna.

Antennomere 6 densely pubescent, sensilla basiconica covering most of apical disc (Fig. 2G). Last antennomere thickened, widened apically and axe-shaped (Fig. 3A). Shape of antennae sexually dimorphic, cylindrical in ♀; thickened, widened apically and slightly flattened in ♂. Apical disc with 43–72 (♂) or 53–68 apical cones (♀). No sclerotized crest/ridge between antennal socket and ommatidia. Tömösváry's organ located separately at a projected brim between

ommatidia and antennal socket. Gnathochilarium: structure typical of the order. Palpi with sensory cones arranged in a single field. Mandibles not dissected.

Stigmatic plates: first stigmatic plate rounded, apex well-rounded, slightly curved towards coxa (Fig. 3B).

Laterotergites: each of laterotergites 1 and 2 with a broad and well-rounded projection. Collum: superficially glabrous, except for anterior and posterior margins

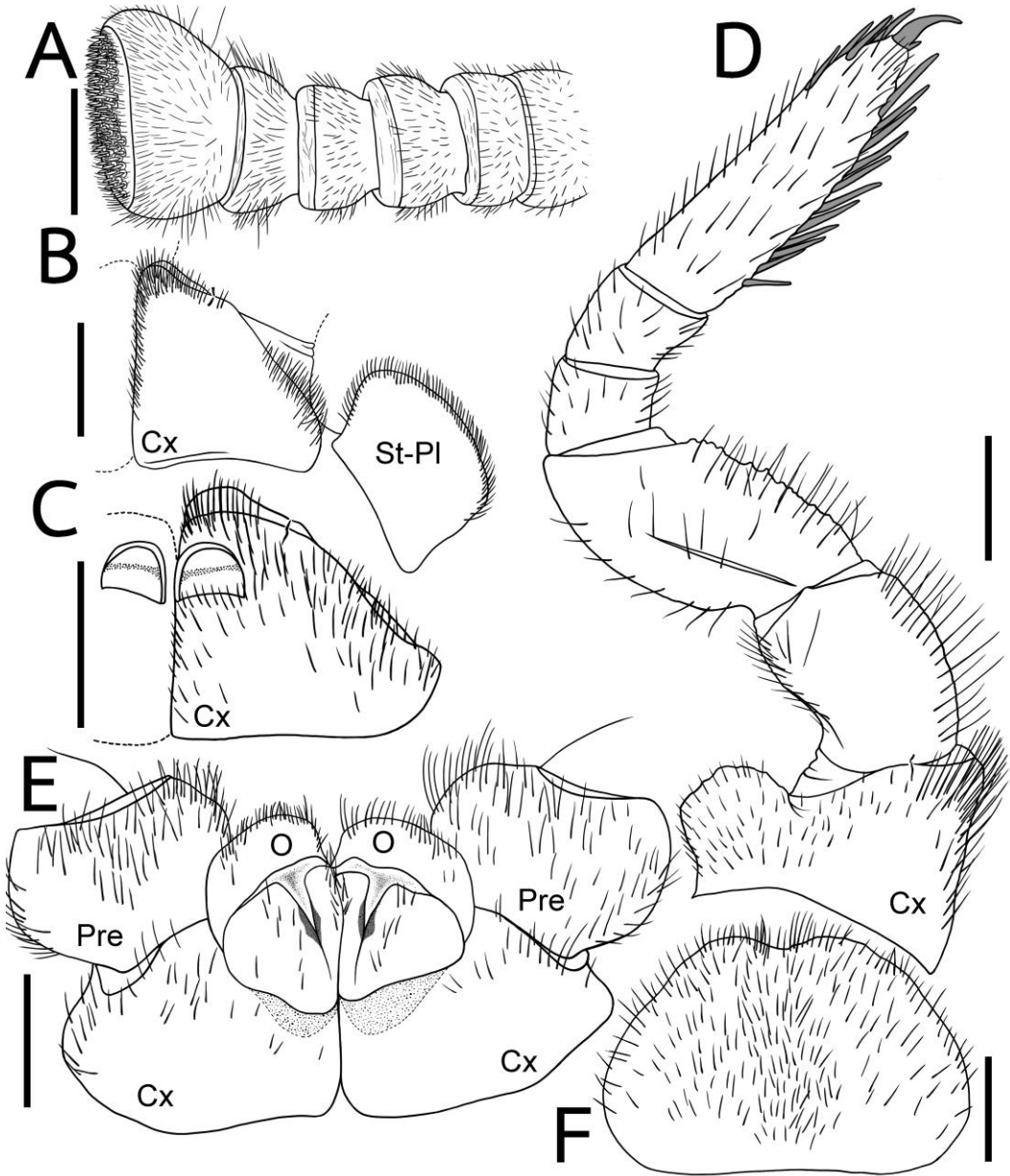


FIGURE 3. *Zephronia lannaensis*, new species. (A–C) holotype; (E, F) ♀ paratype. (A) right antenna, lateral view; (B) left first coxa with stigmatic plate; (C) coxa of second left leg with gonopore; (D) 9th right leg; (E) coxa and prefemur of second leg with vulva; (F) subanal plate. Scale bars: 1 mm.

supporting few isolated setae. Thoracic shield: surface superficially glabrous as in tergites. Shallow grooves filled with numerous long setae, no keels. Following

tergites: surface entirely clothed with dense tiny setae (Fig. 1A, B). Tips of paratergites of midbody tergites straight (Fig. 1B).

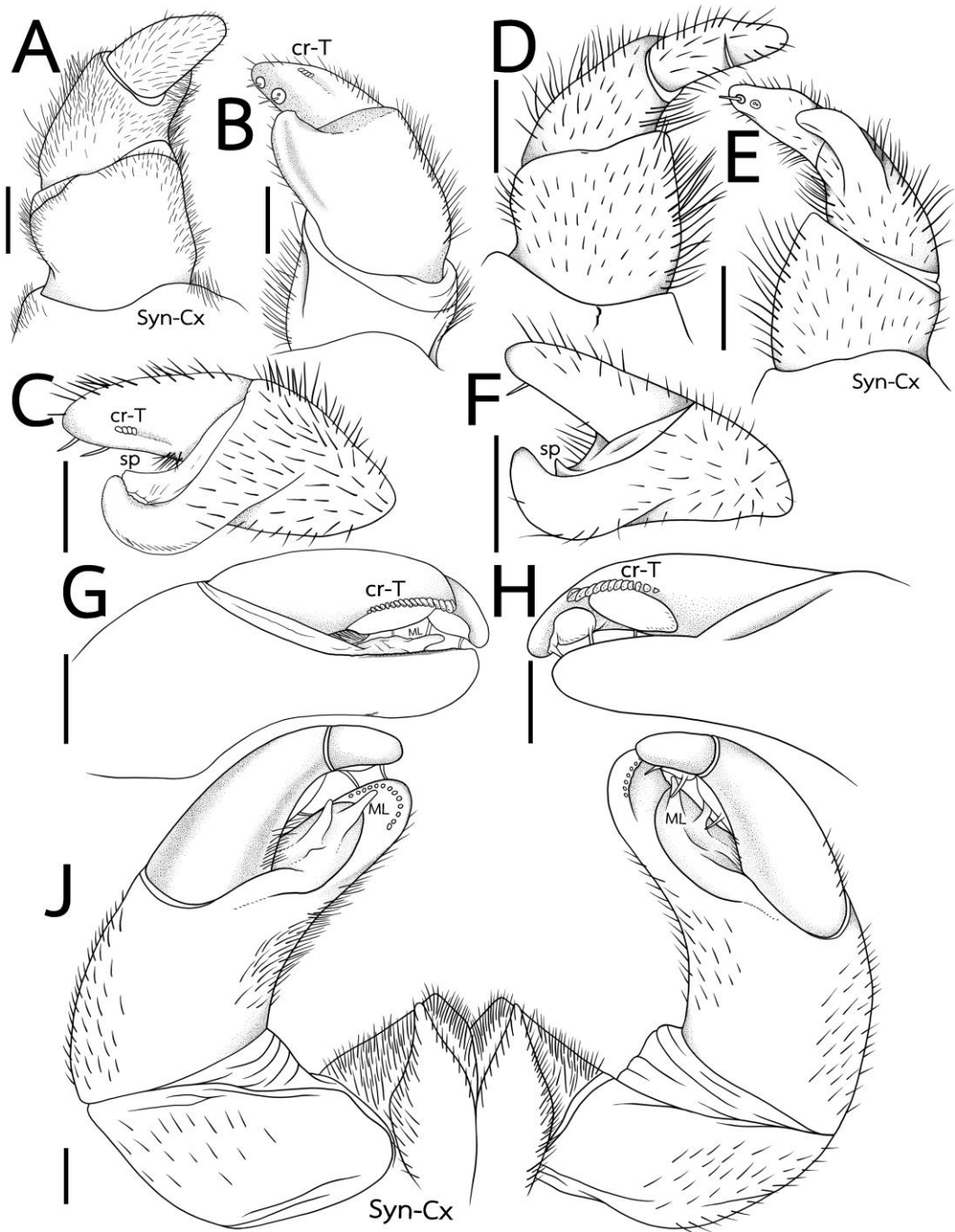


FIGURE 4. *Zephronia lannaensis*, new species. (A–C, G–J) holotype; (D–F) ♂ paratype. (A–F) left anterior telopods, anterior, subposterior, sublateral, subanterior, posterior and sublateral views, respectively; (G) left posterior telopod, subposterior view; (H) right posterior telopod, subposterior view; (J) posterior telopods, anterior view. Scale bars: 0.5 mm.

Endotergum: inner section lacking any spines or setae. Middle area lacking discernible cuticular impressions. Apically, 2–3 dense rows of short marginal bristles, tips of the longest setae not reaching tergal margin (Fig. 2A, B). Bristles smooth (Fig. 2C). Anal shield: slightly sexually dimorphic, in ♀ large and well-rounded (Fig. 1A), in ♂ slightly more rectangular, in both sexes glabrous. Surface similar to that of tergites, setose. Underside with a single black locking carina half as long as width of last laterotergite. Legs: leg-pair 1 with two ventral spines, leg-pair 2 with 4. First two leg-pairs devoid of an apical spine. Leg-pair 3 with 6–10 ventral spines and one or two dorso-apical spine(s). Leg-pairs 4–21 each with 10–12 ventral spines and 3(2)–5 dorso-apical ones. In leg 9, femur 1.7 times, tarsus 3.0 times longer than wide (Fig. 3D). All podomeres densely setose. Coxa with a large and well-rounded process. Coxal process absent from leg-pairs 1 (Fig. 3B) and 2 (Fig. 3C). Prefemur without any teeth. Femur with a microdenticulate ventral margin featuring 10–14 teeth (Fig. 3D).

Female sexual characters: vulva large, covering 1/2 coxa, located at mesal margin, extending distad to proximal third of prefemur (Fig. 3E). Operculum rounded.

Subanal plate: semi-circular, divided by a suture into two halves. Densely setose (Fig. 3F).

Male sexual characters: gonopore large, covered with a single, undivided, triangular, sclerotized plate (Fig. 3C).

Anterior telopods (Fig. 4A–F): First telopoditomere rectangular, slightly wider than long. Telopoditomere 2 large, more than as long as telopoditomere 3. Process of telopoditomere 2 located posteriorly, but partly visible laterally in anterior view, conspicuously unciform, projecting as high as basal part of telopoditomere 4, apically

with a well-rounded tip (Fig. 4B, C, E, F). Process of telopoditomere 2 with a membranous area carrying a massive and sclerotized process (SP) showing a rounded tip (Fig. 4C), while telopoditomere 3 of younger males with a small and sclerotized process (SP) (Fig. 4F). Telopoditomeres 3 and 4 divided by a short and weak suture, this suture being visible only in anterior view (Fig. 4D) and disappearing in older males (Fig. 4A–C). Telopoditomere 3 large, cylindrical, slender, 1.5X longer than wide, 3X longer than telopoditomere 4 (Fig. 4D). Telopoditomere 4 short, well-rounded, posterior face with three or four small and sclerotized spines located inside two small, thin, sclerotized fields (Fig. 4B, E). Lateral side of podomere 4 carrying three or four small crenulations/teeth (cr-T) (Fig. 4B, C), but invisible in younger males (Fig. 4E, F). All podomeres covered with long setae.

Posterior telopods (Fig. 4G–J): inner horns with sharply edged tips, slightly curved caudad (Fig. 4J). Telopodite consisting of four podomeres. First podomere stout and short, twice as wide as long. Immobile finger (process of telopoditomere 2) as long as movable finger; the latter consisting of telopoditomeres 3 and 4, wide, twice as long as wide, not curved, distally glabrous, at tip, opposite to tip of telopoditomere 4, with a semi-circular row of 10–14 sclerotized spots (Fig. 4J). Margin towards movable finger with two massive, triangular, membranous lobes. Telopoditomere 3 elongated, slightly curved, twice as long as telopoditomere 4, with a large, swollen, membranous ledge, and a short and sclerotized spine (Fig. 4J), postero-apically slightly enlarged, with a row of 12–17 crenulate and sclerotized teeth (cr-T) (Fig. 4G, H), Telopoditomere 4 slender, twice as long as wide, slightly tapering apically, with a large, swollen, membranous ledge, and two long and sclerotized spines

(Fig. 4G–J). Telopoditomer 1 and 2 on both sides covered with few setae (Fig. 4J). Telopoditomer 3 at base of inner margin with a few setae, remaining parts of telopoditomer 3 and 4 almost glabrous (Fig. 4J).

Remarks.— This new species was found creeping on the leaf litter during the rainy season (June to August). The air was very humid, but the temperatures generally remained high (daily average temperatures around 28–34°C), this being characteristic of the rainy season in northern Thailand. Then, when the rainy season ends, the millipedes would disappear from the forest floor and hide into humid shelters such as under rocks, near tree roots or damp hollows waiting for the next rainy season. The specimens were found in a dry dipterocarp forest.

***Zephronia phrain* Likhitrakarn & Golovatch, new species**

urn:lsid:zoobank.org:act:C080E8E6-168E-4E89-9324-393C3CED7DE3

(Figs. 1C–E, 2D–F, H, 5, 6)

Material examined.— Holotype ♂ (CUMZ), Thailand, Chiang Mai Province, Mae Rim District, Queen Sirikit Botanic Garden, ca 650 m a.s.l., 18°53'52"N 98°51'40"E, 21 August 2020, leg. W. Srisuka and N. Likhitrakarn. Paratypes 1 ♂, 1 ♀ (CUMZ), 1 ♂, 1 ♀ (ZMUM), 1 ♂, 1 ♀ (NHMD), same locality, together with holotype; 9 ♂, 2 ♀ (CUMZ), same locality, 25 August 2014, leg. P. Nunthamontree.

Name.— To emphasize “Phra In”, referring to a deity in Thai mythology in order to emphasize a greenish body and also the Thai common name for the giant pill-millipedes (Sphaerotheriida); a noun in apposition.

Diagnosis.— This new species is similar to both *Z. lannaensis*, new species, and *Z. laotica* Wesener, 2019, all three of which

feature the anterior telopod with a weak suture between telopoditomer 3 and 4 visible only in anterior view. However, *Z. phrain*, new species, differs from *Z. lannaensis*, new species, in a smooth ventral margin of the femora (Fig. 5D) (vs. a microdenticulate margin (Fig. 3D)), tergites shiny and glabrous (Fig. 1C, D) (vs. tergites beset with dense tiny setae (Fig. 1A, B)), as well as a green body with contrasting yellow posterior margins of the tergites (Fig. 1C) (vs. a uniformly brown body (Fig. 1A)). In addition, *Z. phrain*, new species, differs from *Z. laotica* Wesener, 2019 also in the presence of a small membranous ledge on each anterior telopod (Fig. 6C), coupled with leg-pair 3 showing one or two dorso-apical spine(s), and each of leg-pairs 4–21 with 7–11 ventral spines and 2–4 dorso-apical ones (Fig. 5D), as well as the head, antennae, collum and legs blackish to brown (Fig. 1D, E) (vs. all green).

Description.— Measurements: Holotype ♂. Body length 33.5 mm. Width, of thoracic shield = 17.7 mm, of tergite 8 = 18.2 mm (= broadest). Height, of thoracic shield = 10.2 mm, of tergite 7 = 11.2 mm (= highest). ♂ body length = 29.5–41.2 mm. Width, of thoracic shield = 14.2–18.6 mm, of tergite 8 = 14.6–19.3 mm. Height, of thoracic shield = 7.5–12.0 mm, of tergite 7 = 8.4–12.5 mm. ♀ body length = 33.2–40.6 mm. Width, of thoracic shield = 16.8–18.7 mm, of tergite 8 = 17.7–19.7 mm. Height, of thoracic shield = 9.2–11.6 mm, of tergite 7 = 11.8–13.8 mm.

Colouration: live animals dark olive-green to bright green, posterior margins of tergites contrasting yellow (Fig. 1C, D), head and collum blackish to dark brown (Fig. 1E), groove of thoracic shield light green, legs and antennae light brown to brown, venter brown to yellow brownish (Fig. 1D, E); colouration in alcohol, after six

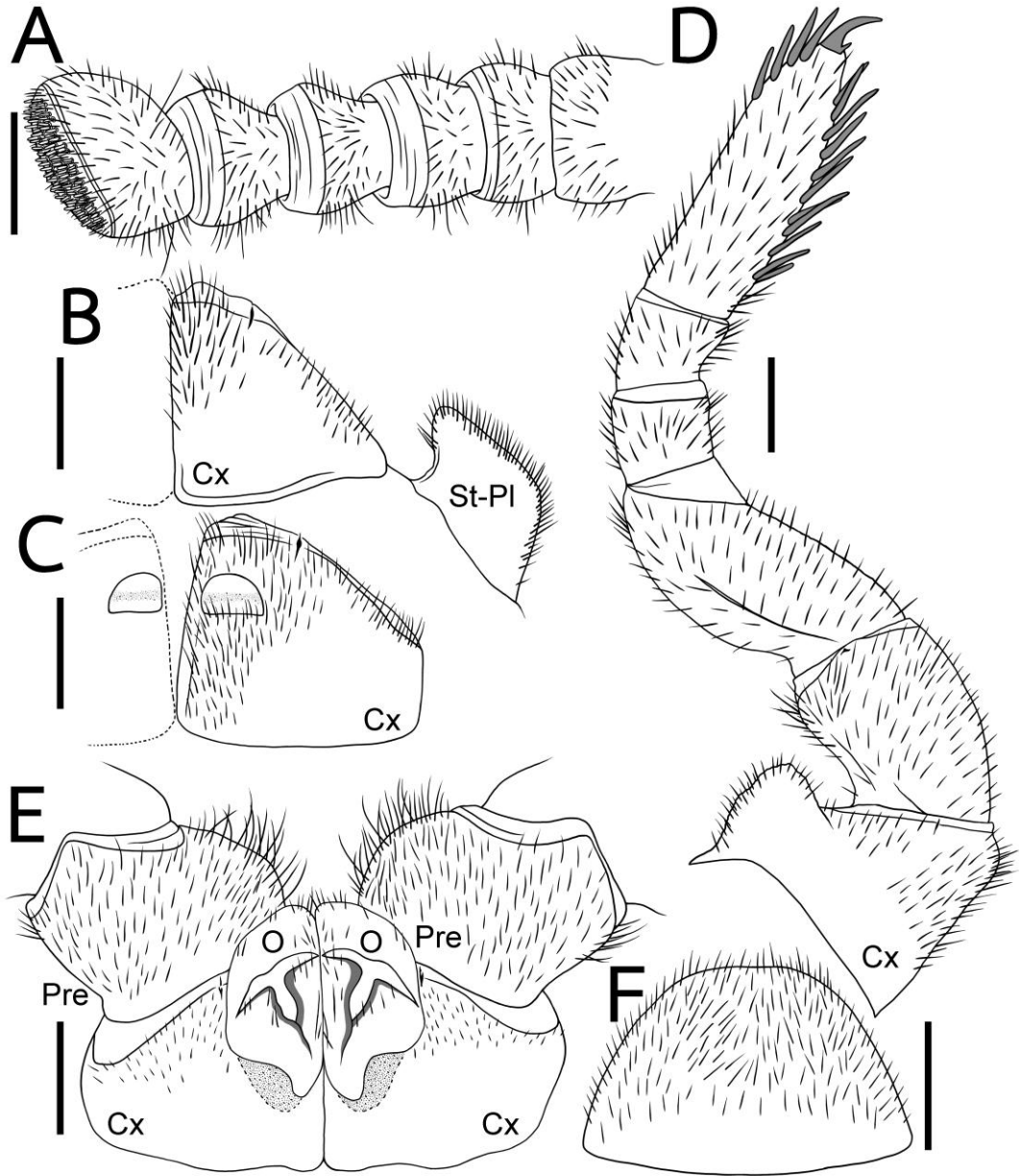


Figure 5. *Zephronia lannaensis*, new species. (A–C, G–J) holotype; (D–F) ♂ paratype. (A–F) left anterior telopods, anterior, subposterior, sublateral, subanterior, posterior and sublateral views, respectively; (G) left posterior telopod, subposterior view; (H) right posterior telopod, subposterior view; (J) posterior telopods, anterior view. Scale bars: 0.5 mm.

years of preservation, faded to olive-green to yellow greenish, head and collum brown to brownish green, ommatidia dark green,

paratergite depressions and groove of thoracic shield yellowish, legs, antennae and venter brown to brownish yellow.

Head: trapezoid, anterior part of head clothed with numerous long setae, posterior part densely punctate; anterior margin of labrum with a single tooth. Each eye with 60–90 ommatidia. Aberrant ocellus located inside antennal groove. Antennae short, with rounded joints, extending posteriorly to leg-pair 2. Lengths of antennomeres: $3 < 1 = 2 = 4 < 5 < 6$. Antennomere 6 densely pubescent, sensilla basiconica covering most of apical disc (Fig. 2H). Last antennomere thickened, widened apically and axe-shaped (Fig. 5A). Shape of antennae sexually dimorphic, cylindrical in ♀; thickened, widened apically and slightly flattened in ♂. Apical disc with 72–89 (♂) or 52–71 apical cones (♀). No sclerotized crest/ridge between antennal socket and ommatidia. Tömösváry's organ located separately at a projecting brim between ommatidia and antennal socket. Gnathochilarium: structure typical of the order. Palpi with sensory cones arranged in clusters. Mandibles not dissected.

Stigmatic plates: first stigmatic plate subtriangular, apex broadly rounded, slightly curved towards coxa (Fig. 5B). Laterotergites: laterotergite 1 strongly projecting into a sharp tip. Laterotergite 2 with a broad rounded process. Laterotergite 3 with a broad, stout, much shorter projection. Collum: glabrous, except for anterior and posterior margins supporting few isolated setae. Thoracic shield: surface glabrous as in other tergites. Shallow grooves filled with numerous long setae, no keels. Following tergites: surface glabrous, shining, but paratergite grooves filled with numerous long setae, no keels. Tips of paratergites of midbody tergites slightly projecting posteriorly (Fig. 1D). Endotergum: inner section with few shorter setae (Fig. 2D). Middle area with a single row of large, dense, elliptical, cuticular impressions.

Distance between impressions as wide as their diameter (Fig. 2E). Apically, 4–6 dense rows of marginal bristles, tips of the longest setae not reaching tergal margin (Fig. 2D, F). Bristles smooth (Fig. 2F). Anal shield: slightly sexually dimorphic, in ♀ large and only slightly concave (Fig. 1D), in ♂ more angular, in both sexes glabrous. Surface similar to that of tergites. Underside with a single black locking carina nearly as long as width of last laterotergite. Legs: leg-pair 1 with 3 or 4 ventral spines, leg-pair 2 with 3–7 ones. First two leg-pairs without an apical spine. Leg-pair 3 with 6–9 ventral spines and 1 or 2 dorso-apical spine(s). Leg-pairs 4–21 with 7–11 ventral spines and 2–4 dorso-apical ones. In leg 9, femur 1.9 times, tarsus 3.0 times longer than wide (Fig. 5D). All podomeres densely setose. Coxa with a large, high, narrowly rounded process. Coxal process absent from leg-pairs 1 (Fig. 5B) and 2 (Fig. 5C). Prefemur and femur without any teeth (Fig. 5D).

Female sexual characters: vulva large, covering 2/3 coxa, located at mesal margin, extending mesally to anterior third of prefemur (Fig. 5E). Operculum rounded.

Subanal plate: semi-circular, large and wide, undivided. Densely setose (Fig. 5F).

Male sexual characters: gonopore large, covered with a single, undivided, triangular, sclerotized plate (Fig. 5C).

Anterior telopods (Fig. 6A–D): First telopoditomere rectangular, as long as wide. Telopoditomere 2 large, more than half as long as telopoditomere 3 and 4 combined. Process of telopoditomere 2 located posteriorly, mostly visible laterally in anterior view (Fig. 6A, B). Process of telopoditomere 2 large, evidently curved towards apical part of telopoditomere 4, apically with a well-rounded tip (Fig. 6C). Process of telopoditomere 2 with a membranous area carrying a small and

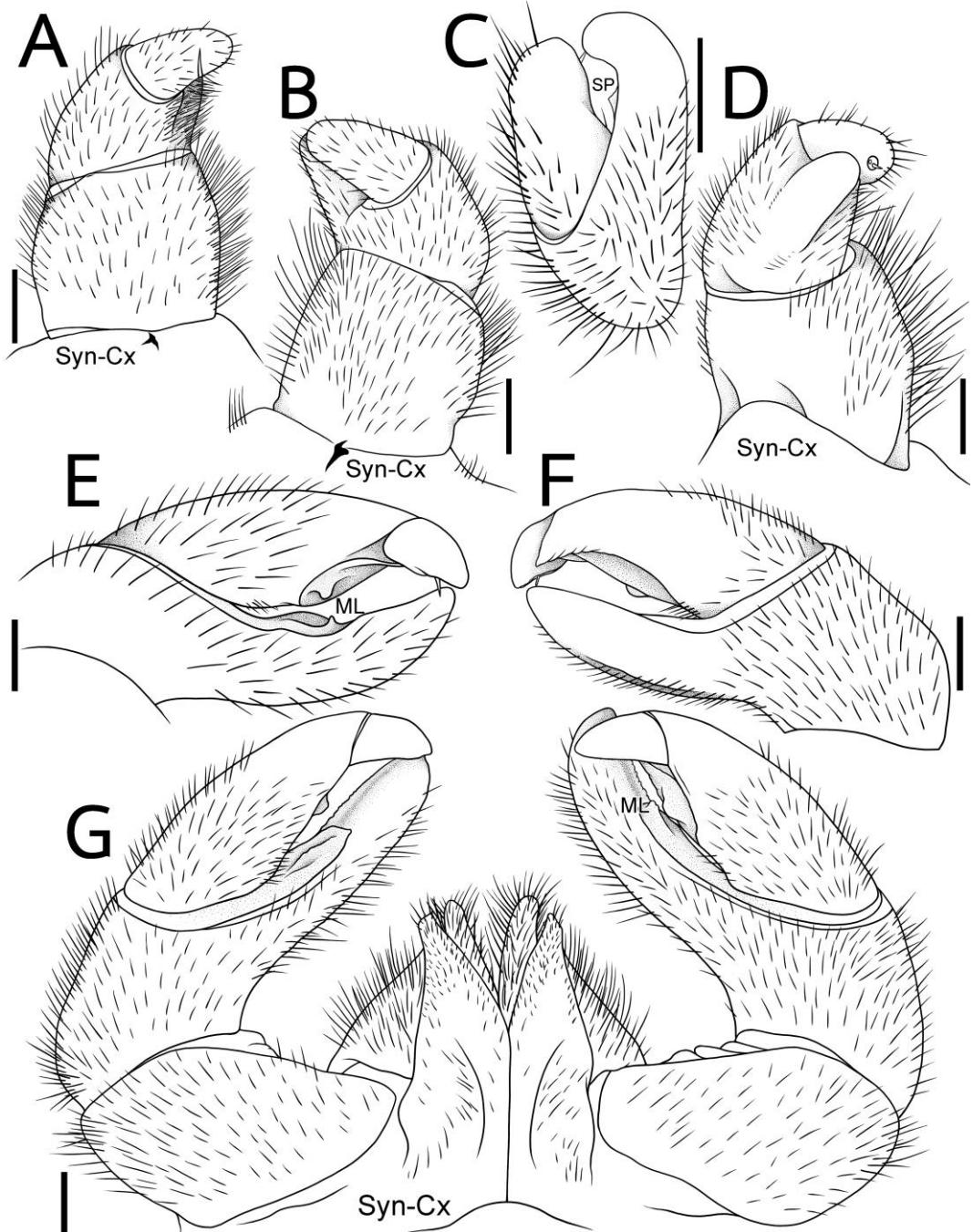


FIGURE 6. *Zephronia phrain*, new species. (A) ♂ paratype; (A–G) holotype. (A) left anterior telopods, anterior view; (B–D) right anterior telopod, subanterior, posterior and sublateral views, respectively; (E) right posterior telopod, subanterior view; (F) right posterior telopod, subposterior view; (G) posterior telopods, anterior view. Scale bars: 0.5 mm.

sclerotized process (Fig. 6C). Telopoditomer 3 and 4 divided by a short and weak suture, this visible only in anterior view (Fig. 6A) and disappearing in older males (Fig. 6B–D). Telopoditomer 3 large, rectangular, straight, twice as long as telopoditomer 4 (Fig. 6A). Telopoditomer 4 very short, well-rounded, posterior face with one or two small and sclerotized spine(s) located inside two small, thin, sclerotized fields (Fig. 6A). All podomeres covered with long setae.

Posterior telopods (Fig. 6E–G): inner horns with sharply edged tips, slightly curved caudad (Fig. 6G). Telopodite consisting of four podomeres. First podomere short, 1.5X longer than wide. Immobile finger (process of telopoditomer 2) shorter than movable finger, consisting of telopoditomer 3 and 4. Immobile finger stout and narrow, 2.5X longer than wide, slightly curved, glabrous distally. Margin towards movable finger with a rather wide, low, membranous ledge (Fig. 6G). Telopoditomer 3 elongated, slightly curved, 3X longer than telopoditomer 4, with a large, membranous area carrying a sclerotized process (Fig. 6E, G), postero-apically enlarged and with a row of 5–6 sclerotized teeth (Fig. 6F). Telopoditomer 4 slender, 1.5X longer than wide, slightly tapering apically, 1–2 sclerotized spine(s) located on a small, thin, separated, sclerotized plate. All podomeres densely setose on both sides, except for distally almost glabrous telopoditomer 4 and telopoditomer 2 and 3 (Fig. 6E–G).

Remarks.— This new species was found during the rainy season near the Pill Millipede Trail in Queen Sirikit Botanic Garden. The trail was named after this new species of giant pill-millipede which could easily be spotted and collected during the rainy season in the garden

(<https://www.chiangmaicitylife.com/citynews/general/new-nature-trail-opened-queen-sirikit-botanic-garden/>). This trail was the first one officially named so in order to inspire gaining fundamental knowledge of Thai pill-millipedes.

DISCUSSION

Considering both new congeners described above, *Zephronia* presently comprises 42 species. Two groups have been recognized within *Zephronia*, one of which, *Zephronia* sensu stricto, shows the organ of Tömösváry located at a projecting brim close to the ommatidia. The other group shows the organ of Tömösváry situated inside the antennal groove (Semenyuk et al., 2018; Wesener, 2019). Provisionally, *Z. lannaensis*, new species, and *Z. phrain*, new species, are to be classified in *Zephronia* sensu stricto, a group that encompasses *Z. ovalis* Gray, 1832, *Z. konkakinhensis* Semenyuk et al., 2018, and *Z. montis* Semenyuk et al., 2018, all from Vietnam; *Z. laotica* Wesener, 2019 from Laos, *Z. dawydoffi* Attems, 1953 from Cambodia, and *Z. siamensis* Hirst, 1907 from Thailand.

As regards the presence of a (weak) suture between telopoditomer 3 and 4 of the anterior telopods in both new species and in *Z. laotica* Wesener, 2019, all members of *Zephronia* s. str., as well as in several other, taxonomically more remote congeners from Myanmar, it often tends to be treated amongst the most important taxonomic characters to separate the different genera or generic groups in Zephroniidae. However, because this suture is variable both intra- and interspecifically, and it tends to disappear even in some older conspecific males, we prefer to slightly



FIGURE 7. Distributions of four *Zephronia* species recorded in Thailand. **Square** *Zephronia phrain*, new species; **Triangle** *Zephronia lannaensis*, new species; **Circle** *Zephronia cf. viridescens* Attems, 1936; **Cross** *Zephronia siamensis* Hirst, 1907.

amend the diagnosis of *Zephronia* (see above) and to refrain from further evaluating this distinction before more information becomes amassed to attempt a representative phylogenetic analysis. Further numerous new species of *Zephronia* and Zephroniidae from Thailand and elsewhere undoubtedly await discovery and description. Additional molecular evidence

is definitely ahead, too. In addition, variations in the number of podomeres in the anterior gonopods (three or four) in some congeners is sometimes difficult to ascertain, likewise being observed, e.g., in *Sphaerobelum* Verhoeff, 1924, a genus closely related to and largely sympatric with *Zephronia* (Enghoff et al., 2015). No less significantly, the development of all

Sphaerotheriida is with hemianamorphosis, when the growth is gradual and often causes modifications in some taxonomically important structures from one moult to the next (Enghoff et al., 1993).

Because both new species described in this paper were discovered in the Chiang Mai area alone, and their type localities are not too distant from each other (ca 40 air-km, Fig. 7), there can hardly be any doubt that a lot of important novelties are still ahead. Even the material already available in various museum collections contains further *Zephronia* species. Only such an approach is deemed appropriate to significantly improve the first, highly fragmentary and preliminary insights in the evolution of Zephroniidae, both morphology- and molecular-based, as presented recently by Wesener (2019).

ACKNOWLEDGEMENTS

This project was partly funded through grants received from the Office of the Royal Development Projects Board (RDPB), while most of the financial support was obtained from TRF Strategic Basic Research BDG 6080011 (2017–2019) to CS and NL, and Centre of Excellence on Biodiversity (BDC-PG2-161002). We thank the members of the Animal Systematics Research Unit for their invaluable assistance in the field. One of us (SIG) was partly supported by the Presidium of the Russian Academy of Sciences, Program No. 41 “Biodiversity of natural systems and biological resources of Russia”.

Special thanks go to both reviewers, whose valuable corrections and suggestions have allowed us to considerably improve our paper.

LITERATURE CITED

- Alagesan, P. 2016. Millipedes: diversity, distribution and ecology. In: CHAKRAVARTHY A.K. and SRIDHARA, S. (Eds.) *Arthropod Diversity and Conservation in the Tropics and Subtropics*. Springer, Singapore, Pp. 119–137.
- AVMA, 2013. AVMA guidelines for the euthanasia of animals. Available from: <https://www.avma.org/KB/Policies/Documents/euthanasia.pdf> (19 October 2020)
- Enghoff, H. 2005. The millipedes of Thailand (Diplopoda). *Steenstrupia*, 29(1): 87–103.
- Enghoff, H., Dohle, W. and Blower J.G. 1993. Anamorphosis in millipedes (Diplopoda)—the present state of knowledge with some developmental and phylogenetic considerations. *Biological Journal of the Linnean Society*, 109: 103–234.
- Enghoff, H., Golovatch, S.I., Short, M., Stoev, P. and Wesener, T. 2015. Diplopoda – taxonomic overview. In: Minelli A. (Ed.). *Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda*, 2(16): 363–453. https://www.researchgate.net/publication/304660831_Treatise_on_Zoology_Anatomy_Taxonomy_Biology_The_Myriapoda_Vol_2
- Golovatch, S.I., Wesener, T., Mauriès, J.-P. and Semenyuk, I.I. 2012. On the identities of *Cryxus* Leach, 1814 and *Zephronia* Gray, 1832, the oldest generic names in the millipede order Sphaerotheriida (Diplopoda). *Arthropoda Selecta*, 21(4): 273–294. https://kmkjournals.com/upload/PDF/ArthropodaSelecta/21/21_4%20273_294%20Golovatch_Cryxus%20for%20Inet.pdf
- Hirst, A.S. 1907. On four new pill-millipedes from the Malay Peninsula and Siam. *Annals and Magazine of Natural History*, series 7, 20: 215–219. <https://www.biodiversitylibrary.org/item/61719#page/3/mode/1up>
- Jeekel, C.A.W. 2001. A bibliographic catalogue of the Asiatic Sphaerotheriida (Diplopoda). *Myriapod Memoranda*, 3: 5–38.
- Likhitrakarn, N., Golovatch, S.I. and Panha, S. 2017. The first record of the pantropical millipede, *Chondromorpha xanthotricha* (Attems, 1898) (Diplopoda: Polydesmida: Paradoxosomatidae), from Thailand. *Arthropoda Selecta*, 26(4): 281–287. https://kmkjournals.com/upload/PDF/ArthropodaSelecta/26/26_4_281_287_Likhitr_et_al_for_Inet.pdf
- Likhitrakarn, N., Golovatch, S.I., Srisonchai, R., Sutcharit, C. and Panha, S. 2019. A new species of the millipede genus *Cryptocorypha* Attems, 1907,

- from northern Thailand (Polydesmida, Pyrgodesmidae). *ZooKeys*, 833: 121–132.
<https://doi.org/10.3897/zookeys.833.32413>
- Likhitrakarn, N., Golovatch, S.I., Jeratthitikul, E., Srisonchai, R., Sutcharit, C. and Panha, S. 2020. A remarkable new species of the millipede genus *Trachyjulus* Peters, 1864 (Diplopoda, Spirostreptida, Cambalopsidae) from Thailand, based both on morphological and molecular evidence. *ZooKeys*, 925: 55–72.
<https://doi.org/10.3897/zookeys.925.49953>
- Pimvichai, P., Enghoff, H., Panha, S. and Backeljau, T. 2018. Morphological and mitochondrial DNA data reshuffle the taxonomy of the genera *Atopochetus* Attems, *Litostrophus* Chamberlin and *Tonkinbolus* Verhoeff (Diplopoda: Spirobolida: Pachybolidae), with descriptions of nine new species. *Invertebrate Systematics*, 32: 159–195.
<https://doi.org/10.1071/IS17052>
- Pimvichai, P., Enghoff, H., Panha, S. and Backeljau, T. 2020. Integrative taxonomy of the new millipede genus *Coxobolellus*, gen. nov. (Diplopoda: Spirobolida: Pseudospirobolellidae), with descriptions of ten new species. *Invertebrate Systematics*, 34: 591–617.
<https://doi.org/10.1071/IS20031>
- Semenyuk, I., Golovatch, S.I. and Wesener, T. 2018. Some new or poorly-known Zephroniidae (Diplopoda, Sphaerotheriida) from Vietnam. *ZooKeys*, 930: 37–60.
<https://doi.org/10.3897/zookeys.930.47742>
- Semenyuk, I., Golovatch, S.I. and Wesener, T. 2020. Four new species of giant pill-millipedes from Vietnam (Sphaerotheriida, Zephroniidae). *Zootaxa*, 4459(3): 535–550.
<https://doi.org/10.11646/zootaxa.4459.3.7>
- Srisonchai, R., Enghoff, H., Likhitrakarn, N. and Panha, S. 2018a. A revision of dragon millipedes I: Genus *Desmoxys* 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., Enghoff, H., Likhitrakarn, N. and Panha, S. 2018b. A revision of dragon millipedes II: The new genus *Nagaxytes*, with the description of three new species (Diplopoda, Polydesmida, Paradoxosomatidae). *European Journal of Taxonomy*, 462: 1–44.
<https://doi.org/10.5852/ejt.2018.462>
- Srisonchai, R., Enghoff, H., Likhitrakarn, N. and Panha, S. 2018c. A revision of dragon millipedes III: The new genus *Gigaxytes*, with the description of three new species (Diplopoda, Polydesmida, Paradoxosomatidae). *European Journal of Taxonomy*, 463: 1–43.
<https://doi.org/10.5852/ejt.2018.463>
- Srisonchai, R., Enghoff, H., Likhitrakarn, N. and Panha, S. 2018d. A revision of dragon millipedes IV: The new genus *Spinaxytes*, with the description of nine new species (Diplopoda, Polydesmida, Paradoxosomatidae). *ZooKeys*, 797: 19–69.
<https://doi.org/10.3897/zookeys.797.29510>
- Wesener, T. 2016a. The giant pill-millipedes, order Sphaerotheriida – An annotated species catalogue with morphological atlas and list of apomorphies (Arthropoda: Diplopoda). *Bonn Zoological Bulletin Supplementum*, 63: 1–104.
- Wesener, T. 2016b. Redescription and phylogenetic analysis of the type species of the giant pill-millipede genus *Sphaeropoeus* Brandt, 1833 (Diplopoda, Sphaerotheriida, Zephroniidae). *Zootaxa*, 4184(1): 141–157.
<http://doi.org/10.11646/zootaxa.4184.1.9>
- Wesener, T. 2019. First records of giant pill-millipedes from Laos (Diplopoda, Sphaerotheriida, Zephroniidae). *Zootaxa*, 4563(2): 201–248.
<https://doi.org/10.11646/zootaxa.4563.2.1>
- Wesener, T. and Sierwald, P. 2005. The giant pill-millipedes of Madagascar: Revision of the genus *Sphaeromimus*, with a review of the morphological terminology (Diplopoda, Sphaerotheriida, Sphaerotheriidae). *Proceedings of the California Academy of Sciences*, 56(29): 557–599.
- Wesener, T. and VandenSpiegel, D. 2009. A first phylogenetic analysis of giant pill-millipedes (Diplopoda: Sphaerotheriida), a new model Gondwanan taxon, with special emphasis on island gigantism. *Cladistics*, 25(6): 545–573.
<https://doi.org/10.1111/j.1096-0031.2009.00267.x>
- Wongthamwanich, N., Panha, S., Sierwald, P., Wesener, T. and Thirakhupt, K. 2012a. 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: 29–43.
- Wongthamwanich, N., Panha, S., Sitthicharoenchai, D., Pradatsundarasar, A., Seelanan, P., Enghoff, H. and Thirakhupt, K. 2012b. Daily activities of the giant pill-millipede *Zephronia* cf. *viridescens* Attems, 1936 (Diplopoda: Sphaerotheriida: Zephroniidae) in a deciduous forest in northern Thailand. *Zoological Studies*, 51(7): 913–926.