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New Thai giant pill-millipede species, with new genetic barcoding data (Diplopoda, Sphaerotheriida, Zephroniidae)

SNEHA BHANSALI[1,2] & THOMAS WESENER[1,3]
[1]*Zoological Research Museum Alexander Koenig, Leibniz Institute for the Analysis of Biodiversity Change (LIB), Adenauerallee 160, D-53113 Bonn, Germany.*
[2]*Corresponding author, sneharbhansali@gmail.com; https://orcid.org/0000-0002-5440-9958*
[3] *T.Wesener@leibniz-zfmk.de; https://orcid.org/0000-0002-2028-3541*

Abstract

Three new species of giant pill-millipedes, *Sphaerobelum meridionalis* Bhansali & Wesener **sp. nov.**, *Zephronia chrysomallos* Bhansali & Wesener **sp. nov.** and *Zephronia erawani* Bhansali & Wesener **sp. nov.** are described based on museum samples from Thailand. All three species are described in an integrative manner, combining light microscopy, scanning electron microscopy, CT scans and genetic barcoding. Genetic barcoding was successfully conducted for all holotypes of the new species. In addition, genetic barcoding data of four recently described Thai *Zephronia* species, *Zephronia lannaensis* Likhitrakarn & Golovatch, 2021 in Likhitrakarn *et al.* 2021, *Z. phrain* Likhitrakarn & Golovatch, 2021, *Z. panhai* Srisonchai *et al.* 2021 and *Z. golovatchi* Srisonchai *et al.* 2021, together with new locality records, were added to the dataset. Our dataset includes all published sequences of the family Zephroniidae, including all but one (*Z. enghoffi* Srisonchai *et al.*, 2021) of the described species from Thailand, Laos and Cambodia. All new species are genetically distant from other Zephroniidae from Thailand and surrounding countries showing uncorrected p-distances of >10 %. *S. meridionalis* **sp. nov**. is genetically and morphologically close to a recently described aberrant *Sphaerobelum*, *S. aesculus* Rosenmejer & Wesener, 2021, as well as an unspecified specimen from Malaysia, and might represent a genus different from *Sphaerobelum* Verhoeff, 1924. Both new *Zephronia* species are geographically, morphologically and genetically close to *Z. panhai*, but differ from the latter by >10% p-distance in the COI gene and numerous morphological characters. Virtual cybertypes of the holotype of *Zephronia erawani* **sp. nov.** and of a paratype of *Z. chrysomallos* **sp. nov.** were created and made publicly accessible.

Key words: Cybertypes, CT Scan, DNA Barcoding, biodiversity, soil fauna

Introduction

The global diversity and distribution of one of the most species-rich groups of land arthropods in the world, the millipedes (class Diplopoda), remains understudied (Hoffman 1980; Shelley 2007; Brewer *et al.* 2012). These conspicuous soil arthropods are significant decomposers improving the quality of the soil in various vegetation types (Golovatch & Kime 2009; Alagesan 2016). In its evergreen to deciduous forest, Thailand harbors a species-rich millipede fauna (Enghoff 2005; Srisonchai *et al.* 2021), including giant pill-millipedes, Sphaerotheriida. Since the publication of the last catalog (Enghoff 2005) which mentions 105 species for Thailand, the millipede fauna of the country has received considerable attention in recent years, bringing the number of known species to ca. 240 from 48 genera (cf. Likhitrakarn *et al.* 2021). Of the five families representing Sphaerotheriida, Zephroniidae is the only family found in Southeast Asia (Wesener 2016). With only nine species of giant pill-millipedes known from Thailand, of which seven were described in 2021 (Rosenmejer *et al.* 2021; Likhitrakarn *et al.* 2021; Srisonchai *et al.* 2021), the number is still low compared to e.g. northeastern India, from which 22 species are known (Wesener 2015a). The Thai records contain species in the genus *Sphaerobelum* Verhoeff, 1924 and in the dominant and widely distributed genus *Zephronia* Gray, 1832. Hitherto, only two *Sphaerobelum* (*S. truncatum* Wongthamwanich *et al.*, 2012; *S. aesculus* Rosenmejer & Wesener, 2021) and seven *Zephronia* have been reported from Thailand (*Z. siamensis* Hirst, 1907; *Z. lannaensis* Likhitrakarn & Golovatch, 2021; *Z. phrain* Likhitrakarn & Golovatch, 2021;

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Z. viridisoma Rosenmejer & Wesener, 2021 in Rosenmejer *et al.* 2021; *Z. enghoffi*; *Z. golovatchi* and *Z. panhai* all Srisonchai *et al.*, 2021).

With eleven giant-pill millipede species documented from Laos since 2019 (Wesener 2019) and seven new species described from Thailand in 2021, it is clearly shown that many more species in SE Asia await discovery. With increased pressure on natural ecosystems due to rising anthropogenic changes, it has become ever more important to describe the unique fauna of biodiversity hotspots such as Thailand (Clements *et al.* 2006).

Recent studies have pointed out that genetic barcoding in combination with morphological characters is of great help in describing millipede species (e.g. Wesener 2015b). In this contribution we describe three new giant pill-millipede species from Thailand, adding molecular data to recent species descriptions, allowing genetic identification of almost all Thai, Laos, and Cambodian giant pill-millipede species. We describe all species integratively, combining morphology with genetic barcodes, and create a freely accessible cybertype for two of the new, not so easily identifiable *Zephronia* species.

Material and methods

Abbreviations:

CT—computer tomography

MHNG—Muséum d'histoire naturelle de la Ville de Genève, Geneva, Switzerland

SEM—scanning electron microscope

SMF—Senckenberg Museum Frankfurt, Germany

ZFMK—Zoological Research Museum A. Koenig, Leibniz Institute for Biodiversity Change (LIB), Bonn, Germany

NHMD—Zoological Museum, University of Copenhagen, Denmark

Map. The spatial information for the map was downloaded from GADM database v. 3.6 and the localities of the described species were mapped in QGis 3.16.14 Zanzibar (QGIS Development Team 2021).

Scanning electron microscopy. For scanning electron microscopy (SEM), the endotergum, left antennae, as well as for one species parts of the head were dissected. The samples were cleaned, and dehydrated via an ethanol series (2x 96%, 3x 100%) before being mounted on aluminum stubs. The samples were coated with gold for 240 seconds in a sputter coater. SEM images were taken using a Supra VR 300VP (Carl Zeiss AG) scanning electron microscope utilizing the Software SmartSEM V05.00, based at the ZFMK. After the study, dry coated SEM material was removed from stubs and returned to alcohol.

Dissecting, light microscopy, illustrations. Dissecting was done under a Zeiss Discovery V8 stereo microscope. Illustrations were produced by hand using pencil and paper, with a camera lucida mounted on the Zeiss Discovery V8 and later inked on tracing paper with Pigma Micron pens size 04 and 005. The scanned illustrations were edited in Adobe Photoshop before making plates on Adobe Illustrator. All terminology follows the recent literature (Wesener 2016).

Micro-computed tomography. Micro-computed tomography data were obtained for the male paratype of *Zephronia chrysomallos* **sp. nov.** and the male holotype of *Zephronia erawani* **sp. nov.** in 100% and 75% ethanol, respectively, at the ZFMK. Micro-CT data was obtained using a SkyScan 1272 (Bruker microCT, Kontich, Belgium) with the following scanning parameters: source voltage = 70 kV, source current = 142 µA, filter = AL 0.5 mm, exposure = 1700 ms, averaging = 5, random movement = 15, flat field correction = ON, geometrical correction = ON. The parameter for pixel size = 6.51583, 6.32032; rotation of 180°in rotation step = 0.200, 0.150 for *Zephronia chrysomallos* **sp. nov.** and *Zephronia erawani* **sp. nov.** respectively. Digital sections were reconstructed with NRecon ver. 1.7.0.4 (Bruker microCT, Kontich, Belgium) and the images were converted to 25bit grayscale images in Fiji Image J 1.52g (Schindelin *et al.* 2012). Volume rendering was performed in Drishti ver. 2.6.3 (Limaye 2012). The reconstructed µCT Data, i.e., the cybertypes were deposited in Zenodo freely accessible under their own digital identifier (https://doi.org/10.5281/zenodo.5820654). The voucher specimens are stored at the ZFMK (ZFMK MYR8826) and NHMD (K56-9) for *Zephronia chrysomallos* **sp. nov.** and *Zephronia erawani* **sp. nov.**, respectively.

DNA barcoding. In order to find relatives, match males to females, and investigate the intraspecific and interspecific COI distances of the species described here, a molecular genetic barcoding study (Hebert *et al.* 2003) was conducted. The DNA extraction, amplification, and sequencing of cytochrome c oxidase subunit I gene was done following the protocol similar to that employed in earlier studies (Sagorny & Wesener 2017; Wesener 2019), using the degenerate primer pair HCO-JJ/LCO-JJ (HCOJJ AWACTTCVGGRTGVCCAAARAATCA / LCOJJ CHACWAAYCATAAAGATATYGG) (Astrin & Stüben 2008). BLAST searches (Altschul *et al.* 1997) were performed to confirm sequence identities and to check for any contamination. Sequences were concatenated by hand or utilizing the software Seqman (DNASTAR Inc.). The whole dataset was translated into amino acids to rule-out the accidental amplification of pseudogenes. The 22 new sequences have been uploaded to GenBank under the accession codes OM509629– OM509650 (Table 1).

TABLE 1: Analyzed specimens, voucher and GenBank number. Specimens marked by an * have been newly sequenced. Abbreviations: **MHNG** = Muséum d'histoire naturelle de la ville de Genève, Geneva, Switzerland; **NHMD** = Natural History Museum of Denmark, University of Copenhagen; **QVMAG** = Queen Victoria Museum and Art Gallery, Tasmania, Australia; **SMF** = Senckenberg Museum Frankfurt, Germany; **ZFMK** = Zoological Research Museum Koenig, Bonn, Germany.

Species	Voucher #	GenBank #
Spirostreptida, *Doratogonus* sp. GG-2003	unknown	AY288738
Glomerida, *Glomeris marginata*	ZFMK Myr009	FJ409909
Sphaerotheriida, unknown family, *Epicyliosoma* sp. GB	unknown	AF370841
Sphaerotheriida, Procyliosomatidae, *Procyliosoma leae*	QVMAG 23:45801	FJ409910
Sphaerotheriida, Procyliosomatidae, *Procyliosoma* sp.	QVMAG 23:25721	FJ409911
Sphaerotheriida, Arthrosphaeridae, *Arthrosphaera brandti*	FMNH-INS 8650	FJ409915
Sphaerotheriida, Zephroniidae sp. Ia	ZFMK Myr014	FJ409912
Sphaerotheriida, Zephroniidae sp. Ib	ZFMK Myr015	FJ409913
Sphaerotheriida, Zephroniidae sp. II (unknown genus)	lost	FJ409914
Sphaerotheriida, Zephroniidae, *Sphaerobelum truncatum*	FMNH-INS 72673	JN885184
Sphaerotheriida, Zephroniidae, *Zephronia siamensis*	FMNH-INS-72669	JX486067
Sphaerotheriida, Zephroniidae, *Zephronia ovalis*	ZFMK Myr0832	JX486068
Sphaerotheriida, Zephroniidae, *Cryxus ovalis*	ZFMK Myr0824	JX486069
Sphaerotheriida, Zephroniidae, *Zephronia dawydoffi*	ZFMK Myr4504	MK330971
Sphaerotheriida, Zephroniidae, *Zephronia laotica*	ZFMK Myr3502	MK330977
Sphaerotheriida, *Sphaerobelum bolavensis*	MHNG LT-10/24	MK330982
Sphaerotheriida, Zephroniidae, *Sphaerobelum phouloei*	NHMD00040257	MK330974
Sphaerotheriida, Zephroniidae, *Sphaerobelum denticulatum*	MHNG LT-10/12	MK330983
Sphaerotheriida, Zephroniidae, *Sphaerobelum spinatum*	ZMUC00040258	MK330973
Sphaerotheriida, Zephroniidae, *Sphaerobelum lachneeis*	MHNG LT-10/12	MK330982
Sphaerotheriida, Zephroniidae, *Sphaerobelum peterjaegeri*	SMF SD553	MK330972
Sphaerotheriida, Zephroniidae, *Sphaerobelum nigrum*	SMF	MK330976
Sphaerotheriida, Zephroniidae, *Sphaerobelum laoticum*	SMF	MK330975
Sphaerotheriida Zephroniidae, *Sphaerobelum schwendingeri*	MHNG LT 10/03	MK330978
Sphaerotheriida Zephroniidae, *Sphaerobelum schwendingeri*	SMF	MK330981
Sphaerotheriida, Zephroniidae, *Sphaerobelum* sp. L07	NHMD00040261	MK330979
Sphaerotheriida, Zephroniidae, *Sphaerobelum* sp. L10	SMF	MK330980
Sphaerotheriida, Zephroniidae, *Sphaerobelum aesculus* M Holo	NHMD 621693	MW898737
Sphaerotheriida, Zephroniidae, *Sphaerobelum aesculus* F	NHMD 621694	MW898738
Sphaerotheriida, Zephroniidae, *Zephronia* sp., AowNoiTemple	NHMD K45	MW898741

......Continued on the next page

TABLE 1. (Continued)

Species	Voucher #	GenBank #
Sphaerotheriida, Zephroniidae, *Zephronia* sp., AowNoiTemple	ZFMK MYR8822	MW898742
Sphaerotheriida, Zephroniidae, *Zephronia viridisoma* Holotype	NHMD 621695	MW898739
Sphaerotheriida, Zephroniidae *Zephronia viridisoma* F Paratype	ZFMK MYR8787	MW898740
Sphaerotheriida, Zephroniidae, *Zephronia lannaensis* Chiang Mai*	ZFMK MYR3498	OM509629
Sphaerotheriida, Zephroniidae, *Zephronia lannaensis* Chiang Mai*	ZFMK MYR3501	OM509630
Sphaerotheriida, Zephroniidae, *Zephronia lannaensis* Chiang Mai*	ZFMK MYR4911	OM509631
Sphaerotheriida, Zephroniidae, *Zephronia lannaensis* Doi Suthep - Mae Sa*	NHMD K57B	OM509632
Sphaerotheriida, Zephroniidae, *Zephronia lannaensis* Doi Suthep*	MHNG 3B	OM509633
Sphaerotheriida, Zephroniidae, *Zephronia phrain* Chiang Mai*	ZFMK MYR3499	OM509634
Sphaerotheriida, Zephroniidae, *Zephronia phrain* Chiang Mai*	MYR3500	OM509635
Sphaerotheriida, Zephroniidae, *Zephronia phrain* Tham Houay Luk*	SMF	OM509636
Sphaerotheriida, Zephroniidae, *Zephronia phrain* Ma Lee*	SMF	OM509637
Sphaerotheriida, Zephroniidae, *Zephronia phrain* Tham Ngam*	SMF	OM509638
Sphaerotheriida, Zephroniidae, *Zephronia phrain* Chiang Dao*	ZFMK MYR4907	OM509639
Sphaerotheriida, Zephroniidae, *Zephronia phrain* Doi Khuntan*	MHNG 5G	OM509640
Sphaerotheriida, Zephroniidae, *Zephronia phrain* Doi Chiang Dao*	MHNG 5I	OM509641
Sphaerotheriida, Zephroniidae, *Zephronia phrain* Ban Musoe*	NHMD K35	OM509642
Sphaerotheriida, Zephroniidae, *Zephronia panhai* Ratchabourri R1*	ZFMK MYR8118	OM509643
Sphaerotheriida, Zephroniidae, *Zephronia panhai* Tham Khao Bin*	MHNG 3A	OM509644
Sphaerotheriida, Zephroniidae, *Zephronia panhai* Ratchabourri R2*	ZFMK MYR8116	OM509645
Sphaerotheriida, Zephroniidae, *Zephronia golovatchi* Route3052*	ZFMK MYR6262	OM509646
Sphaerotheriida, Zephroniidae, *Zephronia golovatchi* Khao Yai*	NHMD K53	OM509647
Sphaerotheriida, Zephroniidae, *Sphaerobelum meridionalis* **sp. nov.** holotype, Bang Lang*	MHNG 4B-2	OM509648
Sphaerotheriida, Zephroniidae, *Zephronia* chrysomallos **sp. nov.** holotype*	ZFMK MYR8826	OM509649
Sphaerotheriida, Zephroniidae, *Zephronia erawani* **sp. nov.** holotype*	NHMD K56x9	OM509650

Phylogenetic and distance analyses. The 22 new COI sequences were added to a dataset from a previous study, containing all published sequences of the Zephroniidae (at 06.2020) in addition to far- and near-outgroups (Rosenmejer *et al.* 2021). All sequences were aligned in Bioedit (Hall 1999). The final dataset contained 55 terminal and 674 base pairs (Table 1).

The number of base differences per site between sequences was calculated (p-distance analysis, see Supplemental material 1). The analysis involved 55 nucleotide sequences. Codon positions included were 1st+2nd+3rd. All ambiguous positions were removed for each sequence pair. There were a total of 674 positions in the final dataset. Evolutionary analyses were conducted in MEGA6 (Tamura *et al.* 2013).

The best fitting substitution model for a maximum likelihood analysis was calculated with Modeltest (Tamura & Nei 1993) as implemented in MEGA6. The best fitting model was the general time reversible (GTR)-Model (Tavaré 1986) with gamma distribution and invariant sites (GTR+G+I) (lnL = -11225.478, Invariant = 0.389508456, Gamma = 0.654092826, R = 2.741554897; Freq A: 0.273683638, T: 0.333813575, C: 0.231304537, G: 0.160790497).

Phylogenetic analysis were performed in MEGA6 based on General Time Reversible model (GTR+G+I). A species tree was constructed using maximum likelihood method with a gamma distribution of 5 categories. The tree with the highest log likelihood (-1125.9025) is shown in Fig. 1. An initial tree for the heuristic search was obtained automatically by applying Neighbor-joining and BioNj algorithms to a matrix of pairwise distance estimated using the Maximum Composite Likelihood (MLC) approach. Codon positions included were 1st+2nd+3rd. All positions with less than 5% site coverage were eliminated. The final dataset contained a total of 674 positions. The bootstrap consensus tree was calculated from 1000 replicates (Felsenstein 1985) in MEGA6 (Tamura *et al.* 2013). The obtained tree was edited in Adobe Illustrator CS2 with all bootstrap values >70% as well as any nodes discussed in the text illustrated.

Results

Tree description and genetic distances between species. Interspecific distances in our dataset of Zephroniidae varied between 10.8–24% (Sup. file 1). *S. meridionalis* **sp. nov**. shows the lowest genetic distance to *Sphaerobelum aesculus*, found 330 km apart (Fig. 2), with 17 % divergence. *Z. chrysomallos* **sp. nov**. and *Z. erawani* **sp. nov**. show the lowest genetic distance to the three *Zephronia panhai* specimens, with a p-distance of 10.8% and 11.6% respectively. Both new species differ from one another by 11.9%. Our genetic distance analysis discovered surprisingly high intraspecific distances in *Z. phrain*. While most populations differ by 3–5%, one geographical satellite population from Ban Musoe differs by 6.4–7.6%. In addition, our two populations tentatively identified as *Z. golovatchi* (one containing only female specimens) differ by 8.2% from one another (Fig. 1).

The gene tree might not be suitable to reconstruct deeper phylogenies, nevertheless are the order Sphaerotheriida (88% bootstrap support) and the family Zephroniidae (51%) recovered as monophyletic (Fig. 1). In the maximum likelihood tree, several high bootstrap support value of 100% were received for shallow nodes and a few deeper nodes received high support (>/= 70%.).

Inside the family Zephroniidae, *Cryxus* was recovered in a basal position (albeit without statistical support) juxtaposed to all other Zephroniidae (Fig. 1). The next basal branch (statistically unsupported) unites a likely wrongly identified female *Sphaerobelum* from Laos, an unidentified Zephroniidae from Malaysia together with recently described Thai *Zephronia* which are morphologically aberrant (they have only one apical spine on the tarsi). The next split (statistically unsupported) divides the analyzed species into most *Sphaerobelum* and all other *Zephronia* specimens combined with *Sphaerobelum nigrum*. Inside *Sphaerobelum*, little resolution is achieved, but *Sphaerobelum meridionalis* **sp. nov.** is in a clade with an undetermined Zephroniidae from Malaysia and *Sphaerobelum aesculus* from Phuket with low branch support (41%). Inside *Zephronia*, *Z. phrain* is sister taxon to *Sphaerobelum nigrum* from Laos, while the remaining species are in the *Zephronia* "sensu stricto" group with good statistical support (81%). Here *Zephronia lannaensis, Zephronia panhai*, *and Zephronia* cf. *golovatchi* along with *Z. chrysomallos* **sp. nov**. and *Z. erawani* **sp. nov**. form a clade with high statistical support (99%). *Z. erawani* **sp. nov**. was recovered as a sister-group to a well-supported clade (70%) formed by *Zephronia panhai* and *Z. chrysomallos* **sp. nov**. (Fig. 1).

Taxonomy

Class Diplopoda de Blainville in Gervais, 1844

Order Sphaerotheriida Brandt, 1833

Family Zephroniidae Gray, 1842

Remarks. See Wesener (2016) for a catalogue of the family.

Genus *Sphaerobelum* Verhoeff, 1924

Remarks. For a recent revision and a key see Semenyuk *et al.* (2018), Wesener (2019), Semenyuk *et al.* (2020), Zhao *et al.* (2020), Rosenmejer *et al.* (2021).

Type species. *Sphaerobelum clavigerum* Verhoeff, 1924 (subsequently designated by Jeekel 1971: 28), from Vietnam.

Species included. 20 (including the one described below).

Distribution. Vietnam, Thailand, Laos, China.

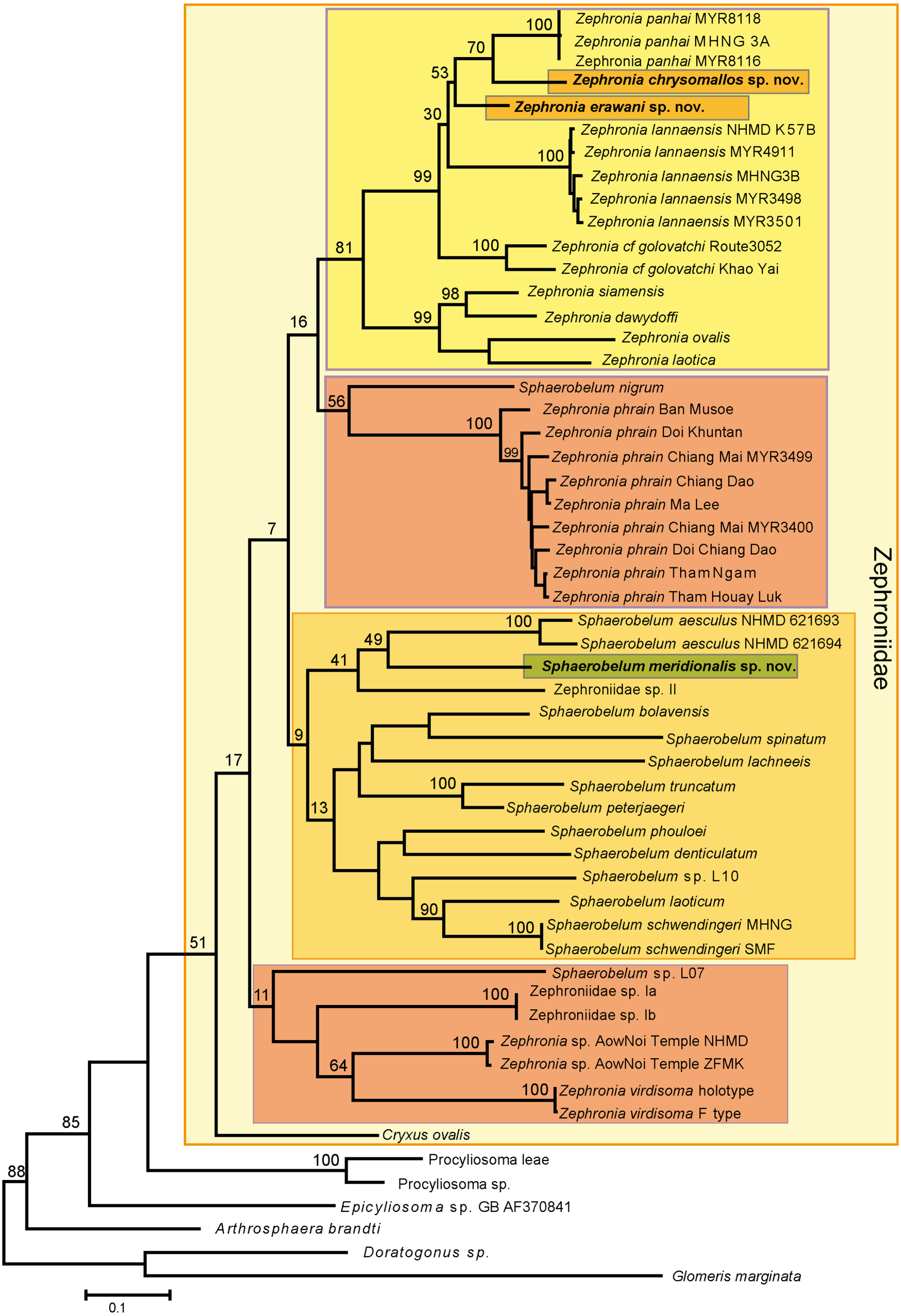

FIGURE 1. Maximum likelihood tree based on the COI sequence after 1000 bootstrap replicates analyzed with the General Time Reversible Model. Numbers on branches indicate bootstrap support. Codon positions included were 1st+2nd+3rd. All positions with less than 5% site coverage were eliminated. The tree is drawn to scale, with branch length indicating genetic distance. Orange and green box represent new species of *Zephronia* and *Sphaerobelum,* respectively.

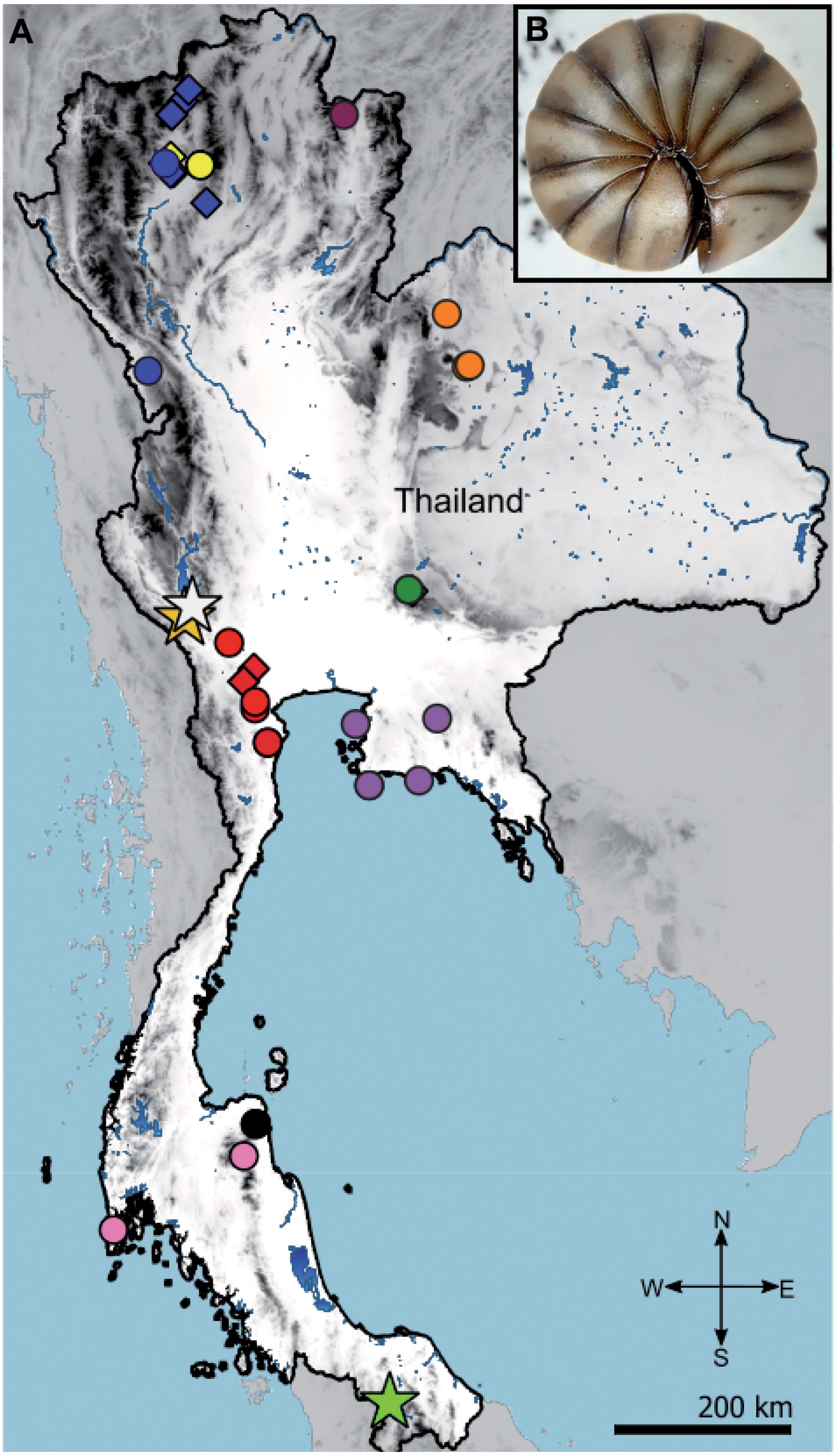

FIGURE 2. Map of Thailand with known distribution of *Sphaerobelum* spp. and *Zephronia* spp. Star represents new species. Diamonds represent new localities. Fluorescent Green = *S. meridionalis* Bhansali & Wesener **sp. nov**.; Pink = *S. aesculus*; Brown = *S. truncatum*; Chrome yellow = *Z. chrysomallos* Bhansali & Wesener **sp. nov**.; White = *Z. erawani* Bhansali & Wesener **sp. nov**.; Black = *Z. viridisoma*; Red = *Z. panhai*; Dark green = *Z. golovatchi*; Purple = *Z. siamensis*; Orange = *Z. enghoffi*; Yellow = *Z. lannaensis*; Blue = *Z. phrain*. **B.** Habitus photograph of *Z. chrysomallos* Bhansali & Wesener **sp. nov**., holotype ♀ (**ZFMK MYR8826**).

Sphaerobelum meridionalis **Bhansali & Wesener, new species**
Figures 2A, 3, 4, 5, 6A.

Diagnosis. Differs from all other species of the genus *Sphaerobelum* aside from *S. aesculus* in the shape of the posterior telopod, where there is a swelling at the tip of the immovable finger, but the swelling does not extend above the margin (Fig. 5B). Both species also share numerous other characteristics, such as general size and color, the glabrous, leather-like surface of the tergites and the shape of the anal shield, the low number of ventral spines on the legs, as well as the absence of apical spines on leg 3. *S. meridionalis* **sp. nov.** differs from *S. aesculus* in several characters, such as the presence of a distinct mesal process on the prefemur of midbody legs (Fig. 4B, arrow) (absent in *S. aesculus*), a mesal coxal process on the first coxae (Fig. 4A) (absent in *S. aesculus*), the telopoditomeres 3 and 4 of the anterior telopods being clearly separated (Fig. 4F) (being almost fused in *S. aesculus*) as well as some minor characters such as the lower number of ventral spines on the first tarsi (1 versus 4 in *S. aesculus*) and the slightly higher number of apical cones on the antenna (68–73 versus 52–56 in *S. aesculus*) (Fig. 3B). *S. meridionalis* **sp. nov.** differs from *S. aesculus* by an uncorrected p-distance on the COI gene of 17% (Sup. file 1).

Derivatio nominis. meridionalis, Latin for southern, adjective used as noun. Noun in apposition.

Material examined (total: 1 ♂)

Holotype

THAILAND: 1 ♂ (fragmented), **MHNG 4B-2**, Yala Province Yala, Bannang Sata District, Bang Lang National Park, near Than To Waterfall, [probably 6°11'47.50"N, 101° 9'50.90"E], 150 m, 1.II.1991, leg. P. Schwendinger.

Description (based on holotype)

Size. Length 26.8 mm. Width of thoracic shield 13.3 mm, of widest segment 14.4 mm. Height of thoracic shield 7.9 mm, Height of highest segment (8) 8.8mm.

Color. Faded after 30 years in 75% ethanol. Head medium brown. Antenna pale light brown with traces of green and a brown border. Last antennomere distinctly light green. Legs pale brown, tarsi greenish. Tergites and anal shield medium brown with green color, ventral side light green. Posterior margin of tergites medium brown. Thoracic shield-like tergites but groove greenish.

Head. Number of ommatidia low, 61–65. Tömösváry organ located in antennal groove. Antennae short, reaching to center of head, antennomere lengths: 6>1>3=4>2=5. Last antennomere apically slightly swollen (Fig. 3A), number of apical cones 73/68 (Fig. 3B).

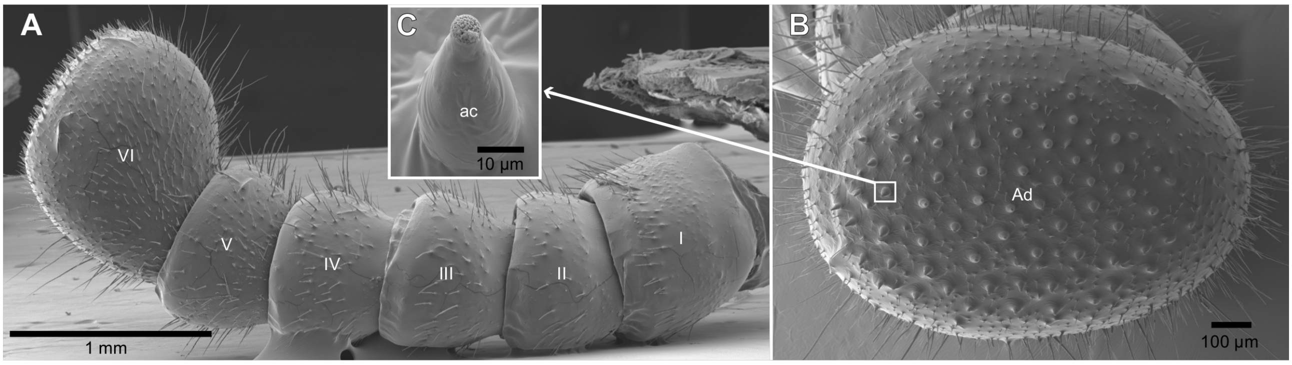

FIGURE 3. *Sphaerobelum meridionalis* Bhansali & Wesener **sp. nov.**, holotype ♂ (**MHNG 4B-2**), scanning electron micrographs. **A.** Left antenna, lateral view. **B.** Right antenna, disc. **C.** Detail of apical cone. **Abbreviations**: ac = apical cone; Ad = antennal disc.

Mandible. Not dissected.

Gnathochilarium. Lingual lamella with numerous long setae. Palpi with sensory cones arranged in single field.

Collum. Setae distributed towards borders, more concentrated at lateral ends. Glabrous on posterior and median region.

Thoracic shield. Grooves wide and deep, with 5 or 6 sclerotized ledges along inner ridge. Surface like tergites.

Tergites. Paratergite tips on posterior half projecting backwards. Tergites glabrous with dull leather-like surface.

Endotergum (Fig. 6A). With a regular flat margin. Outer zone with three rows of irregular marginal setae, not extending beyond posterior margin, but reaching 4/5 of outer area. Middle section with a single row of distant, oval cuticular impressions. Distance between impressions twice the diameter. Inner area with numerous rows of setae, widely distributed, shorter than marginal setae.

First stigmatic plate (Fig. 4A). Large, larger than coxa, with a well-rounded apex.

Pleurites. Pleurite 1 weakly projecting posteriorly with a sharp apex. Pleurite 2 short with well-rounded apex, not projecting.

Legs. Ventral spines on leg 1 1/1, on 2 2/2, on 3 4/4. Apical spine absent on leg 3. Three apical and 6 or 7 ventral spines on midbody legs (Fig. 4B). Inner margin of femur with up to 20 small teeth, but not excavated. Femur 1.7, tarsus 3.8 times longer than wide. Prefemur with conspicuous mesal process (Fig. 4B arrow). First coxae with conspicuous mesal process (Fig. 4A).

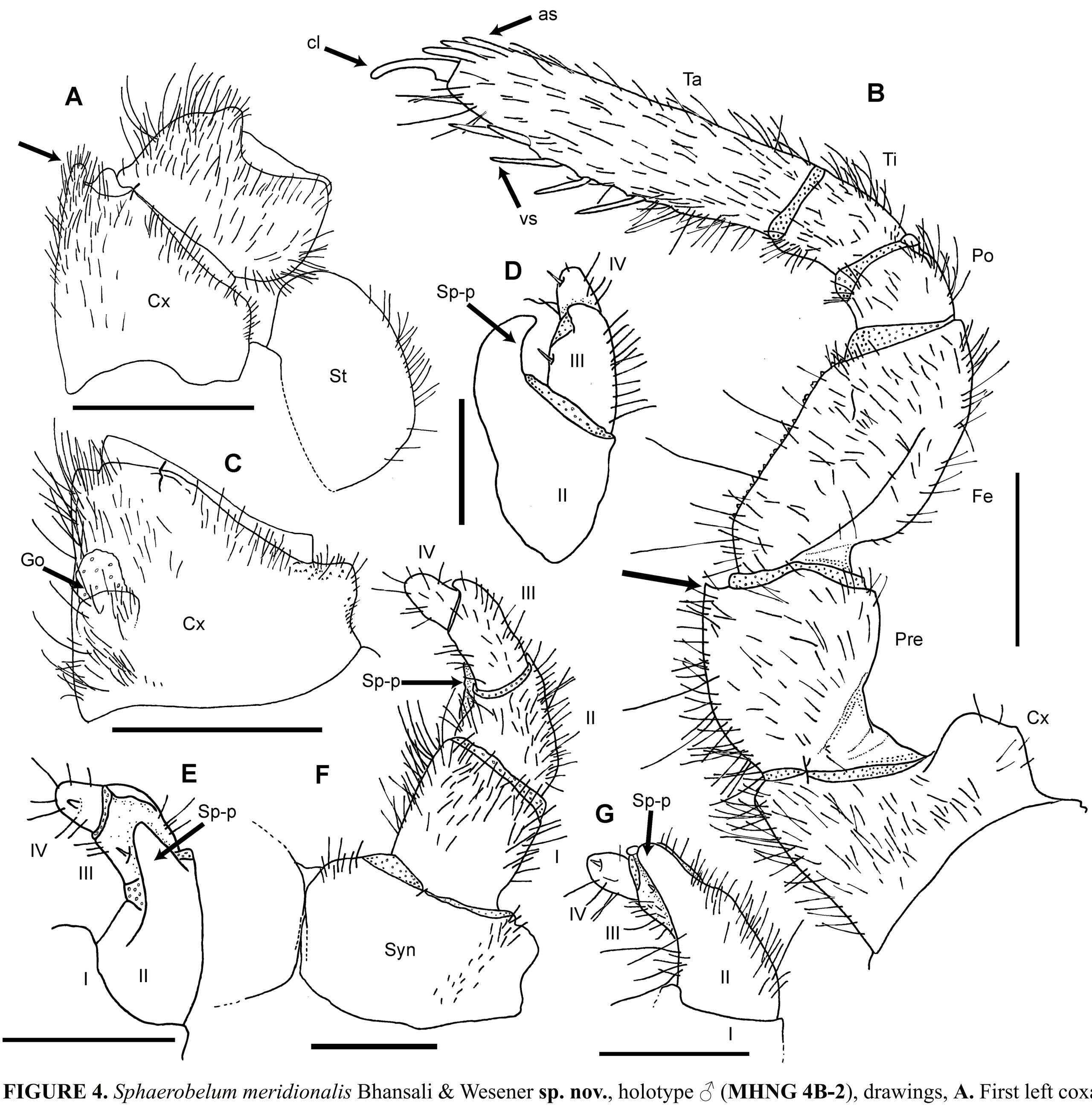

FIGURE 4. *Sphaerobelum meridionalis* Bhansali & Wesener **sp. nov.**, holotype ♂ (**MHNG 4B-2**), drawings, **A.** First left coxa with stigmatic plate, posterior view, arrow points to mesal coxal process. **B.** Left leg 9, posterior view, arrow points to mesal process on prefemur. **C.** Second left coxa with gonopore, posterior view. **D.** Left anterior telopod, lateral view. **E**. Right anterior telopod, meso-posterior view. **F.** Right anterior telopod, anterior view. **G.** Right anterior telopod, posterior view. **Abbreviations**: as = apical spine; cl = claw; Cx = coxa; Fe = femur; Go = gonopore; Po = postfemur; Pre = prefemur; Sp-p = second podomere process; St = stigmatic plate; Syn = syncoxite = tarsus; Ti = tibia; vs = ventral spines. **Scale bars** = 1 mm.

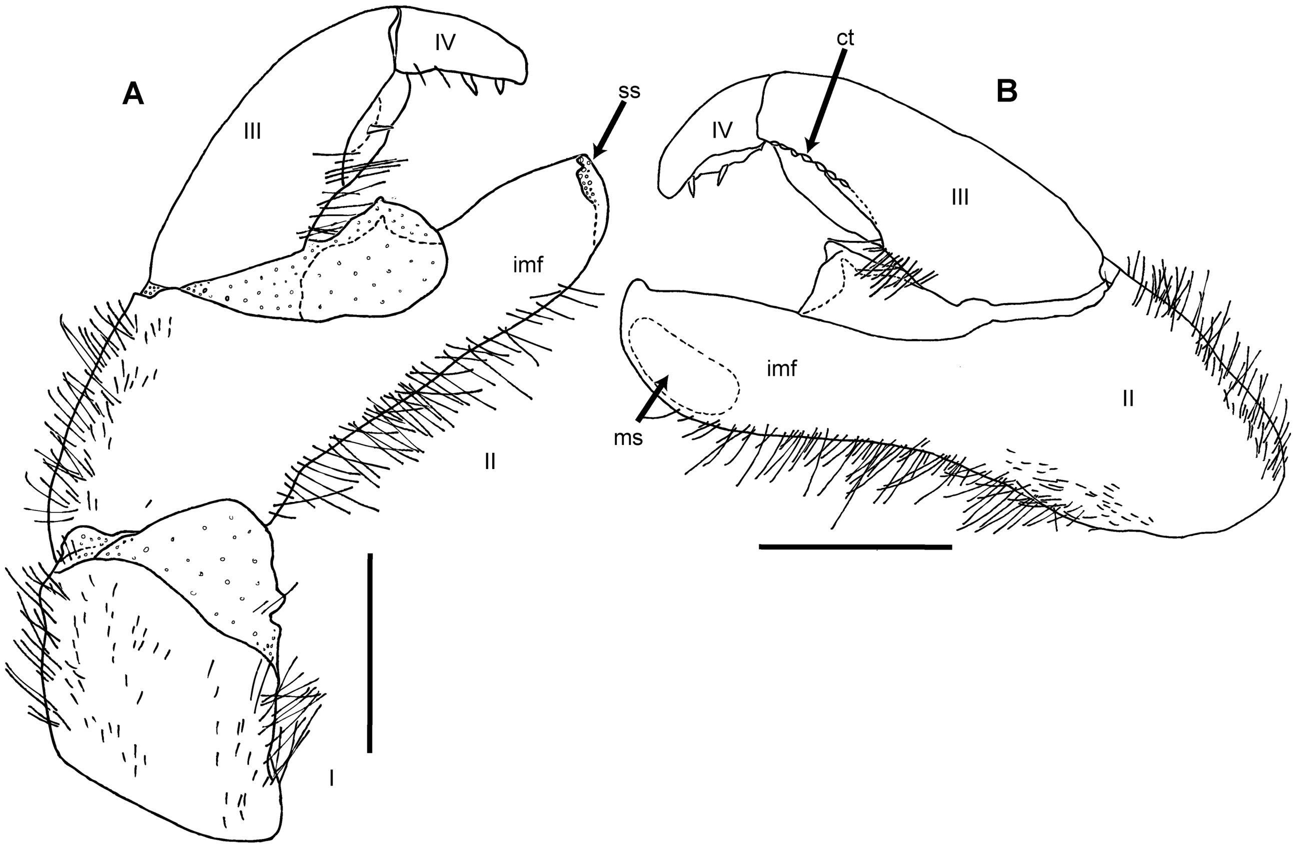

FIGURE 5. *Sphaerobelum meridionalis* Bhansali & Wesener **sp. nov.**, holotype ♂ (**MHNG 4B-2**), drawings, **A.** Left posterior telopod, anterior view. **B.** Left posterior telopod, posterior view. **Abbreviations**: ct = crenulated teeth; imf = immovable finger; ms = membranous spot; ss = sclerotized spot. **Scale bars** = 1 mm.

Anal shield. Well-rounded and glabrous. Ventral side with single medium length locking carina, placed close to margin.

Male sexual characters. Gonopore (Fig. 4C) large, consisting of large membranous opening located directly at mesal margin of second coxa, covered posteriorly by a single semicircular sclerotized plate.

Anterior telopods (Figs 4D–G). Syncoxite with few setae. Podomere 1 rectangular 1.2 times longer than wide, more densely covered with setae in apical half than at basal margin, with longer setae medially, basal margin glabrous. Podomere 2 with wide process visible in anterior view, protruding to half-length of podomere 3. Process curved, well-rounded, apically slightly tapering (Fig. 4D). Podomere 3 cylindrical, almost twice as long as wide, latero-apical process juxtaposed to process of podomere 2. One spine visible in lateral view. Podomere 4 clearly separated from podomere 3, cylindrical, of half-length of podomere 3, with one spine below apex visible in posterior and lateral view.

Posterior telopods (Fig. 5). Syncoxite inner horns (not drawn): well-rounded, apically tapering. Podomere 1 rectangular, as long as wide, with moderately long setae. Podomere 2 with a single, large triangular membranous lobe at base of immovable finger. Immovable finger wide, straight, slightly wider anteriorly and apex tapering towards movable finger in a small process. Process with sclerotized round spots in anterior view. Single large oval membranous spot visible in posterior view. Surface of finger glabrous except for margins. Podomere 3 circa 3 times longer than wide. Membranous ledge with a single spine, Posterior side with a row of 7 small crenulated teeth. Glabrous except for several long setae clustered at lower inner margin. Podomere 4 short, apically tapering, slightly curved towards immovable finger, ca. 2.5 times longer than wide. Membranous ledge and 2 spines present mesal margin. Glabrous.

Distribution

Only known from the area near the Than To Waterfall in the very south of Thailand (Fig. 2A).

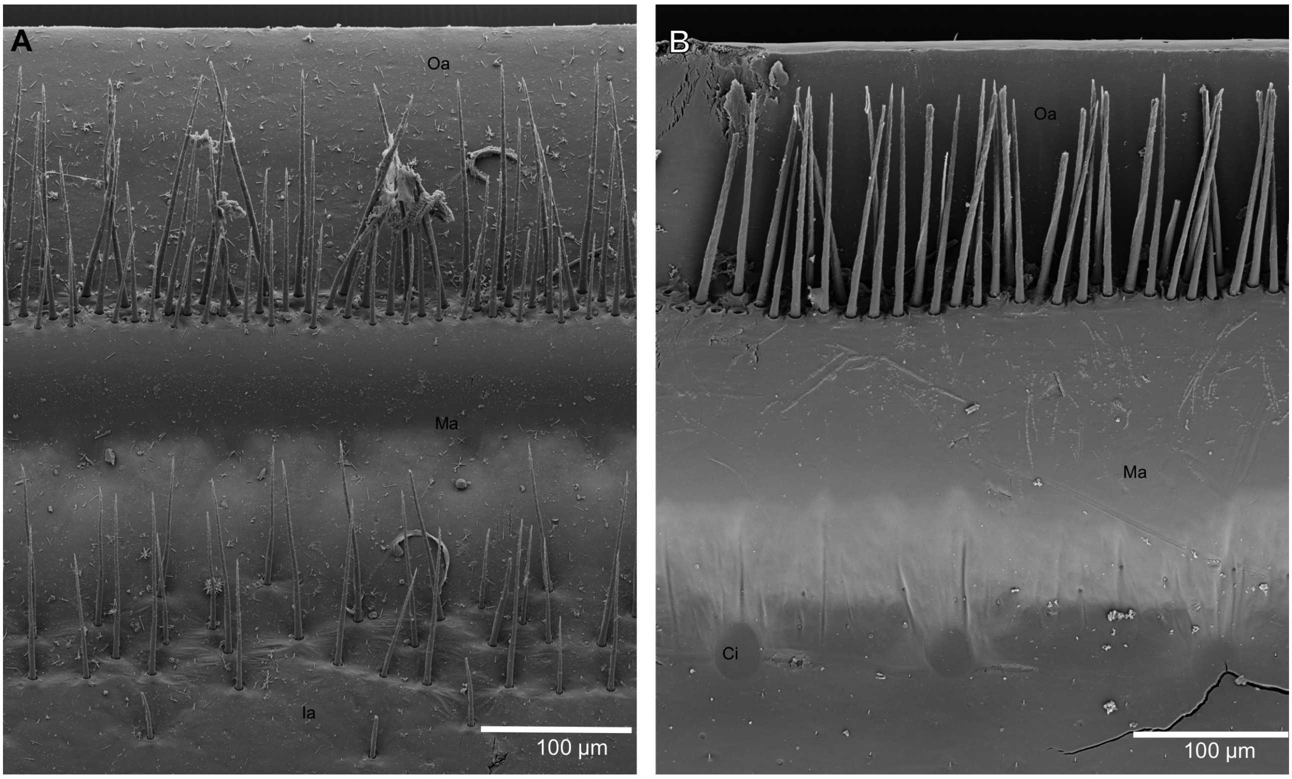

FIGURE 6. Endoterga of midbody tergites, scanning electron micrographs. **A.** *Sphaerobelum meridionalis* Bhansali & Wesener **sp. nov.**, holotype ♂ (**MHNG 4B-2**). **B.** *Zephronia chrysomallos* Bhansali & Wesener **sp. nov.**, holotype ♂ (**ZFMK MYR8826**). **Abbreviations**: Ci = cuticular impression; Ia = inner area; Ma = middle area; Oa = outer area.

Genus *Zephronia* Gray, 1832

Type species. *Zephronia ovalis* Gray, 1832 (by monotypy).

Species included. 48, including the two described below (Wesener 2016a, 2019; Semenyuk *et al.* 2018, 2020; Likhitrakarn *et al.* 2021; Rosenmejer *et al.* 2021; Srisonchai *et al.* 2021).

Distribution. NE India, Nepal, Myanmar, with a few species also in other SE Asian countries.

Zephronia chrysomallos Bhansali & Wesener, new species

Figures 2A–B, 6B, 7, 8, 9, 10, 11.

Diagnosis. The position of the organ of Tömösváry at the brim and not in the antennal groove identifies this species as a member of the *Zephronia* sensu stricto group, with which it also aligns weakly genetically (Fig. 1). The sensory cones on the palpi of the gnathochilarium are arranged in a single field, not in separate clusters (Fig. 8D) and the body is covered in a dense coat of golden setae like in several other Thai *Zephronia*. The greyish brown tergites color resembles those of *Z. erawani* **sp. nov.** and *Z. panhai* (Fig. 2B). The male second leg mesal coxal margin is not extended into a membranous process, a character shared only with *Z. lannaensis* and *Z. panhai*. *Zephronia chrysomallos* **sp. nov.** differs from *Z. lannaensis* in the color (grey versus brown), telopod characters as well as the endotergum. *Z. chrysomallos* **sp. nov.** differs from *Z. panhai* in being much larger in size (40 mm versus 20 mm), the higher number of ventral spines on the walking legs (10–12 versus 7–9), the higher number of apical cones on the antenna (78–88 versus around 50), the higher number of rows of marginal bristles on the endotergum (3 versus 2) and the shape of the first pleurite, which is weakly extended and well-rounded in *Z. chrysomallos* **sp. nov.** but with a long sharp process in *Z. panhai*. *Z. chrysomallos* **sp. nov.** differs genetically in the COI barcoding fragment from *Z. panhai* by a p-distance of 10.8%, from *Z. erawani* **sp. nov.** by a p-distance of 11.9% and from *Z. lannaensis* by 14.8–15.2% (Sup. file 1).

Derivatio nominis. chrysomallos, Greek, meaning Golden Wool, and also the flying sheep ram Chrysomallos from Greek mythology, which was sacrificed to Zeus in order to obtain the famous Golden Fleece. Noun in apposition.

Material examined (total:7 ♂♂)

Holotype

THAILAND: 1 ♂, **ZFMK MYR8826**, Kanchanaburi Province, Sai Yok District, Sai Yok Noi Waterfall, 14°14'12" N, 99°03'46" E, 150 m.

Paratypes

THAILAND: 1 ♂, **ZFMK MYR11366**, CT scan voucher, same data as for holotype; 1 ♂, **ZFMK MYR11365**, same data as for holotype.

Other material

THAILAND: 4 ♂♂, **CUMZ**, Kanchanaburi Province, Sai Yok District, Sai Yok Noi Waterfall (Khao Phang WF), 14°14'21" N, 99°03'28" E, ca. 160 m a.s.l., 11.VII.2009, leg. ASRU members.

Description (based on holotype)

Size. Length: ca. 40 mm. Width of thoracic shield 16.3 mm, of widest segment (8th) 16.9 mm. Height of thoracic shield 9.4 mm, of highest segment (8th) 11.5 mm.

Color (from living specimens). Head, collum and anterior margin of thoracic shield dark brown to black. Antenna dark brown, legs pale brown. Tergites and anal shield greyish-brown (fading to light brown in ethanol), darker towards posterior margin. Thoracic shield-like tergite with darker anterior and posterior margins. (Fig. 2B).

Head (Fig. 7D). Number of ommatidia more than 90. Tömösváry organ placed on rim of antennal groove. Antennae (Fig. 7A–D) short, axe-shaped (Fig. 8A–C), not reaching to center of head (Fig. 7C), antennomere lengths: 6>1>5=4=3=2. Antennomere 1 basally with scales (Fig. 8A). Antennomere 6 apically wide, and flattened, axe-shaped, with 78/88 apical cones (Fig. 8C).

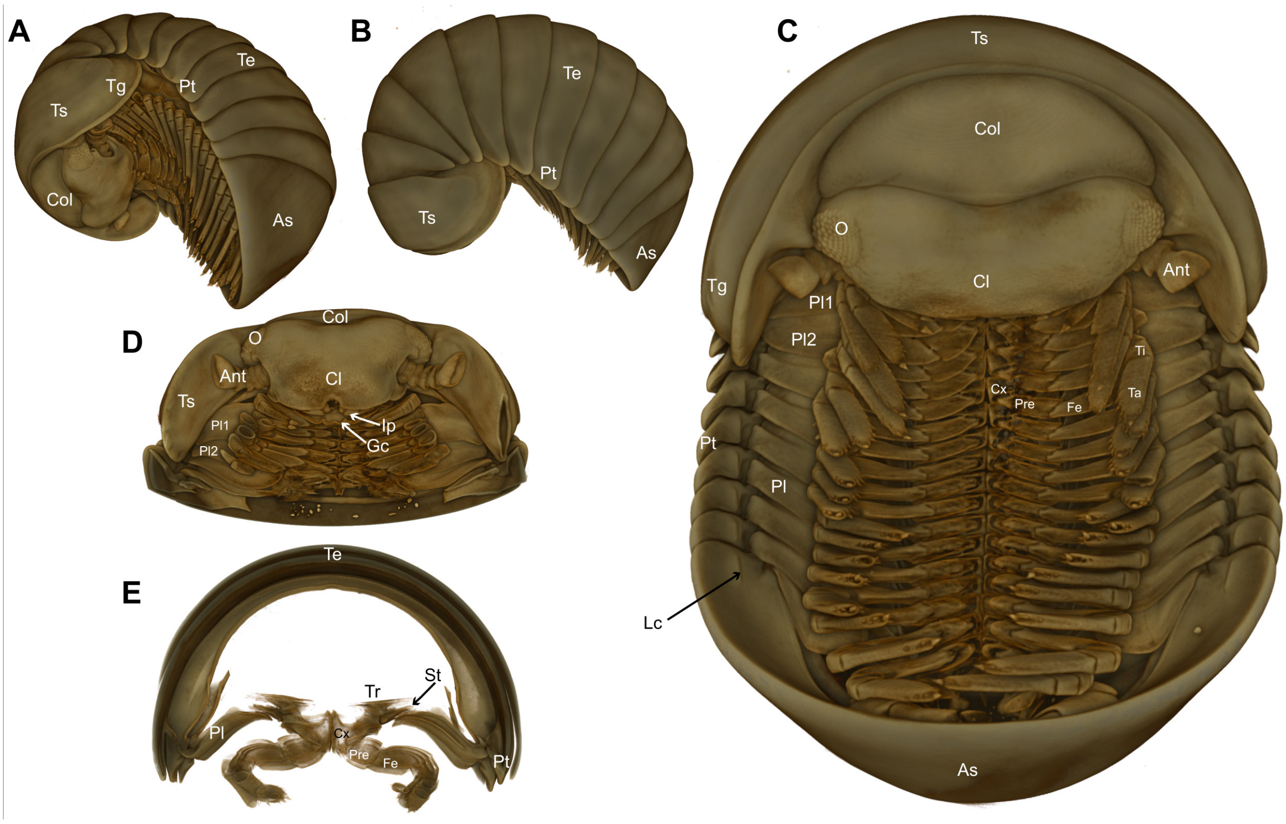

FIGURE 7. *Zephronia chrysomallos* Bhansali & Wesener **sp. nov.**, paratype ♂ (ZFMK **MYR11366**), volume rendering based on micro-computed tomography. **A.** Habitus, lateral view. **B.** Habitus, ventro-lateral view. **C.** Habitus, ventral view. **D.** Habitus, anterior view. **E.** Body-ring architecture, cross section trough midbody-ring. **Abbreviations**: Ant = Antennae; As = anal shield; Cl = clypeus; Col = collum; Cx = coxa; Fe = femur; Gc = gnathochilarium; Go = gonopore; Ip = inner palpi; Lc = locking carina; O = ommatidia; Pl = pleurite; Pl1= pleurite 1; Pl2= pleurite 2; Pre = prefemur; Pt = paratergite; St = stigmatic plate; Ta = tarsus; Te = tergite; Tg = thoracic shield groove; Ti = tibia; Tr = tracheal apodeme; Ts = thoracic shield. Not to scale.

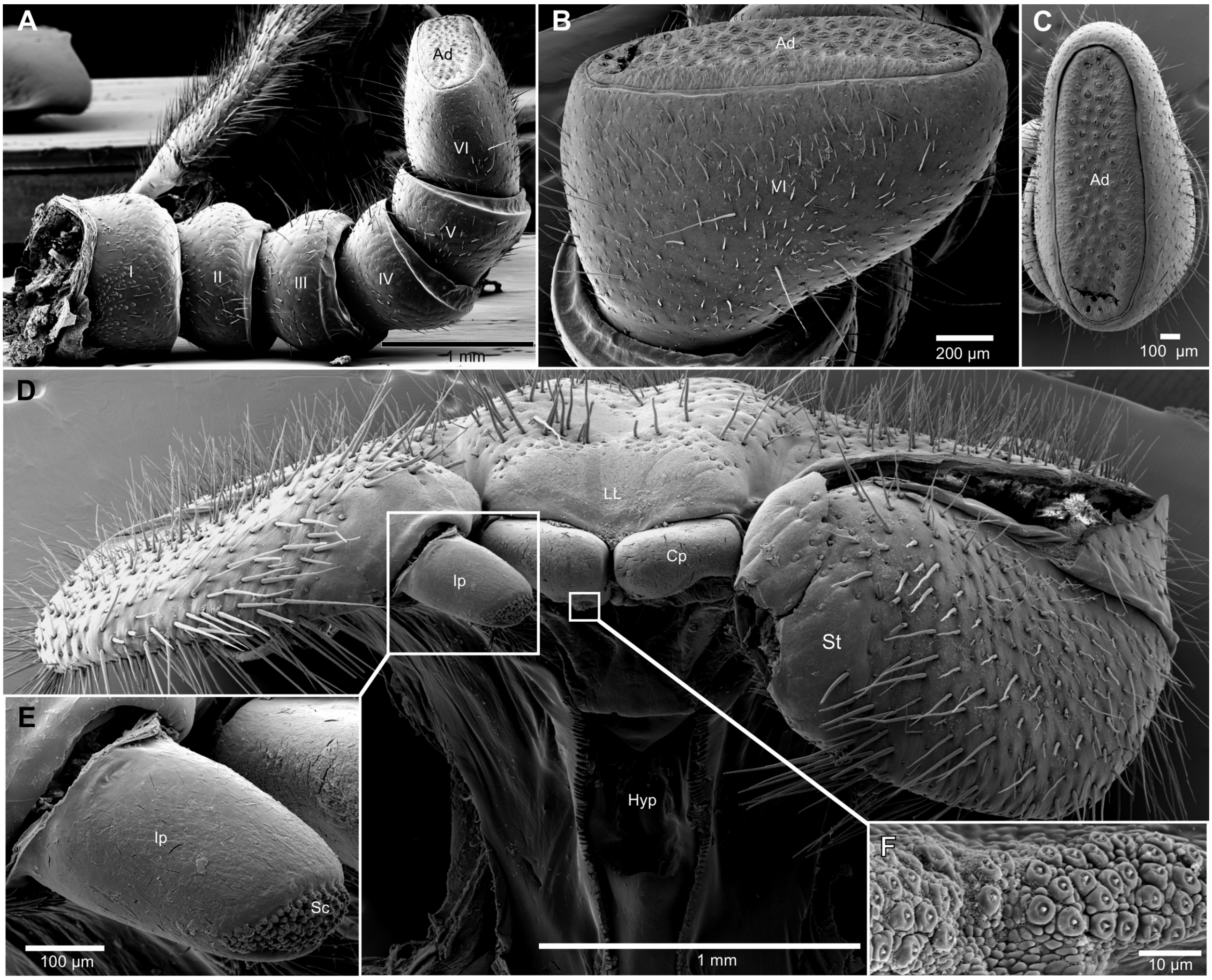

FIGURE 8. *Zephronia chrysomallos* Bhansali & Wesener **sp. nov.**, holotype ♂ (**ZFMK MYR8826**), scanning electron micrographs. **A.** Left antennae, lateral view. **B.** Left sixth antennomere with antennal disc. **C.** Left antenna, disc. **D.** Gnathochilarium, apical view. **E.** Left lateral palpi. **F.** Left central pad, two types of sensory cones on central pad, detail. **Abbreviations**: ac = apical cone; ad = antennal disc; Cp = central pad; Hyp = hypopharynx; Ip = inner palpi; LL = lamellae lingulales; Sc = sensory cone; St = stipites.

Epipharynx. With a large inner tooth.

Gnathochilarium (Figs 7D, 8D–F, 9A). Lamellae linguales with numerous long setae, more towards the margins. Stipes and mentum with numerous long setae in a regular pattern (Fig. 9A). Gnathochilarium palpi with sensory cones arranged in single field (Fig. 8E). 'Pillows' of central pads with two types of sensory cones (Fig. 8F).

Mandible (Fig. 9B). External tooth undivided, inner tooth with 3 lobes. Pectinate lamellae with 6 or 7 rows. Condylus at anterior margin with two distinct ridges.

Collum (Figs 7A, C). With few setae distributed towards the margins, more concentrated towards lateral ends.

Thoracic shield. Thoracic shield grooves wide and shallow (Figs 7A–C), without sclerotized ledges.

First stigmatic plate (Fig. 10A). Smaller than coxa, with rounded sub-triangular apex.

Tergites. Tergites densely covered in short, dense setae visible at higher magnification, with dull orange skin-like surface (Fig. 2B). Paratergite tips only weakly projecting backwards (Fig. 7B).

Pleurites. Pleurite 1 well-rounded, weakly projecting. Pleurite 2 well-rounded, not projecting (Fig. 7C).

Endotergum (Fig. 6B). With a regular flat margin. Outer area with two dense rows of marginal setae, reaching 4/5 of outer area. Middle section with a single row of rounded cuticular impression, distance between impression 2–3 times their diameter. Inner area without setae or spines.

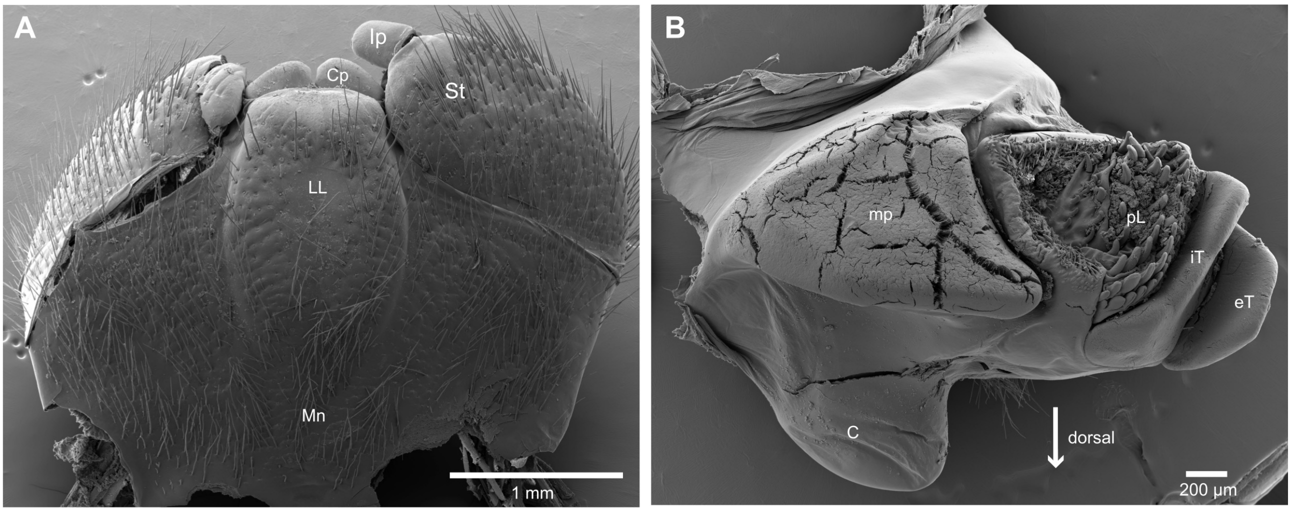

FIGURE 9. *Zephronia chrysomallos* Bhansali & Wesener **sp. nov.**, holotype ♂ (**ZFMK MYR8826**), scanning electron micrographs. **A.** Gnathochilarium, ventral view. **B. Right** mandible, mesal view. **Abbreviations**: C = condyles; Cp = cental pad; eT = external tooth; Ip = inner palpi; iT = internal combined tooth; LL = lamellae linguales; Mn = mentum; pL = pectinate lamellae; St = stipites.

Legs. Ventral spines on leg 1 2/2, at 2 4 /4, at 3 5/5. Leg 3 with single apical spine. Mid-body legs with 3 or 4 apical and 10–12 ventral spines (Fig. 10B). Inner margin of femur with 12–15 small triangular teeth, concentrated at apical half, but not excavated. Femur 1.5, tarsus 3.3 times longer than wide.

Anal shield. Well-rounded and like tergites covered with short dense setae visible at higher magnification (Fig. 2B). Ventral side with dark-colored medium-sized locking carina placed slightly closer to pleurite than margin (Fig. 7C).

Male sexual characters. Male gonopore consisting of large membranous opening located directly at mesal margin of coxa 2 (Fig. 10C). Coxae 2 without membranous processes.

Anterior telopods (Figs 10D–F). Syncoxite setaceous. Podomere 1 rectangular, as long as wide. Few setae, mainly at margins and in apical half. Podomere 2 in anterior view as wide as but slightly narrower as podomere 1. Process massive, visible in anterior view (Fig. 10E), relatively short and wide. Process protruding above basal half of podomere 3, triangular (Figs 10E, F). Podomere 3 cylindrical, 1.4 longer than wide, with one spine in the mesal membranous region, apically with 4 crenulated teeth (Fig. 10D). Podomere 4 clearly separated from podomere 3, conical bearing a black spot at apex. Meso-posterior margin with two spines.

Posterior telopods (Fig. 11). Syncoxite inner horns (not drawn): apex well rounded, apically diverging. Podomere 1 rectangular, as wide as long, with short setae. Podomere 2 with long and narrow immovable finger, 5 times longer than wide. Immovable finger slightly wider posteriorly and apically very slightly curved towards movable finger. Immovable finger glabrous, remaining part of podomere 2 setose. Membranous lobe bearing 2 elongated processes, fused at base. Podomere 3 in posterior view glabrous, in anterior view basal half setose. With a row of 17 or 18 large crenulated square teeth on posterior side (Fig. 11B). Membranous ledge on podomere 3 with single spine. Podomere 4 on both sides glabrous, slightly curved towards immovable finger, membranous lobe with 2 spines. Immovable finger shorter than movable finger.

Distribution

Z. chrysomallos **sp. nov.** is currently only known from the type locality near the Sai Yok Noi Waterfall (Fig. 2A) and might be microendemic, as are other, closely related species in nearby forests.

***Zephronia erawani* Bhansali &Wesener, new species**

Figures 2A, 12, 13, 14.

Diagnosis. The position of the organ of Tömösváry at the brim and not in the antennal groove identifies this species as a member of the *Zephronia* senso-stricto group with which it also aligns weakly genetically. The sensory cones on the palpi of the gnathochilarium are arranged in a single field, not in separate clusters and the body is covered in a dense coat of golden setae like in several other Thai *Zephronia*. The greyish-brown color resembles those of *Z. chrysomallos* **sp. nov.** and *Z. panhai*. The male second leg mesal coxal margin is extended into a membranous process (Fig. 13B arrow), a character shared only with *Z. golovatchi* and *Z. enghoffi*. *Z. erawani* **sp. nov.** differs from both *Z. golovatchi* and *Z. enghoffi* in the shorter marginal bristles of the endotergum which end well before the margin, while the bristles are projecting above the two in both other species.

Z. erawani **sp. nov.** differs genetically in the COI barcoding fragment from *Z. panhai* by a p-distance of 11.6%, from *Z. chrysomallos* **sp. nov.** by a p-distance of 11.9% and from *Z. lannaensis* by 12.6–13.3% (Sup. file 1).

Derivatio nominis. Named after the type locality, the Erawan waterfalls. Erawan is a mythological elephant, similar to the Hindi Airavata. Noun in apposition.

Material examined (total: 1 ♂)

Holotype:

THAILAND: 1 ♂, **NHMD K56-9**, Kanchanaburi Province, Si Sawat District, 50 km W of Kanchanaburi, Erawan Waterfall, [probably: 14°21'31.32"N, 99° 8'26.23"E, 377 m], 6.VI.1990, leg. A. R. Rasmussen & B. Helwigh.

Description (based on holotype)

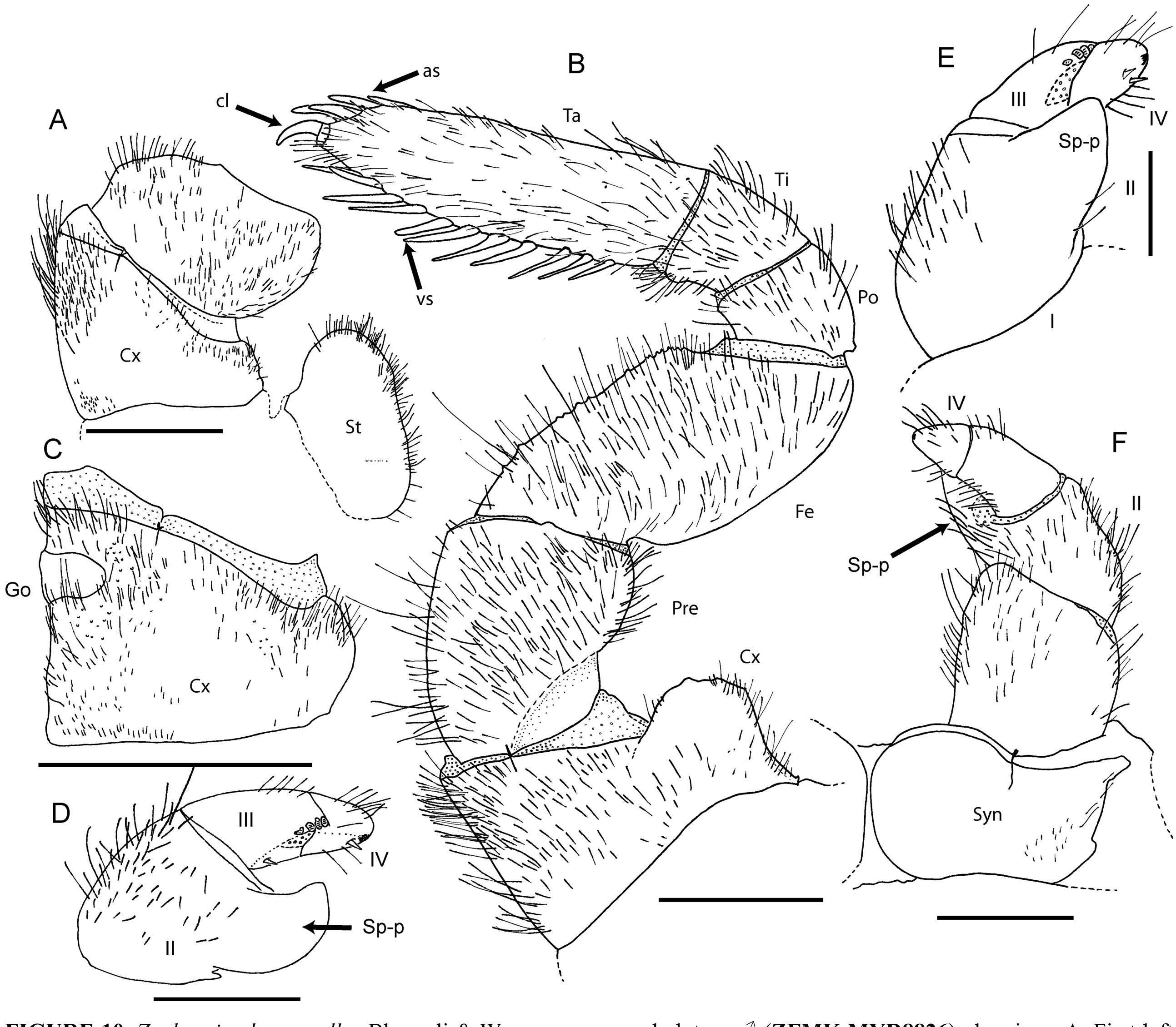

FIGURE 10. *Zephronia chrysomallos* Bhansali & Wesener **sp. nov.**, holotype ♂ (**ZFMK MYR8826**), drawings, **A.** First left coxa with stigmatic plate, posterior view. **B.** Left leg 9, posterior view. **C.** Second left coxa with gonopore, posterior view. **D.** Right anterior telopod, lateral view. **E.** Right anterior telopod, posterior view. **F.** Right anterior telopod, anterior view. **Abbreviations**: as = apical spine; cl = claw; Cx = coxa; Fe = femur; Go = gonopore; Po = postfemur; Pre = prefemur; Sp-p = second podomere process; St = stigmatic plate; Syn = syncoxite; Ta = tarsus; Ti = tibia; vs = ventral spines. **Scale bars** = 1 mm.

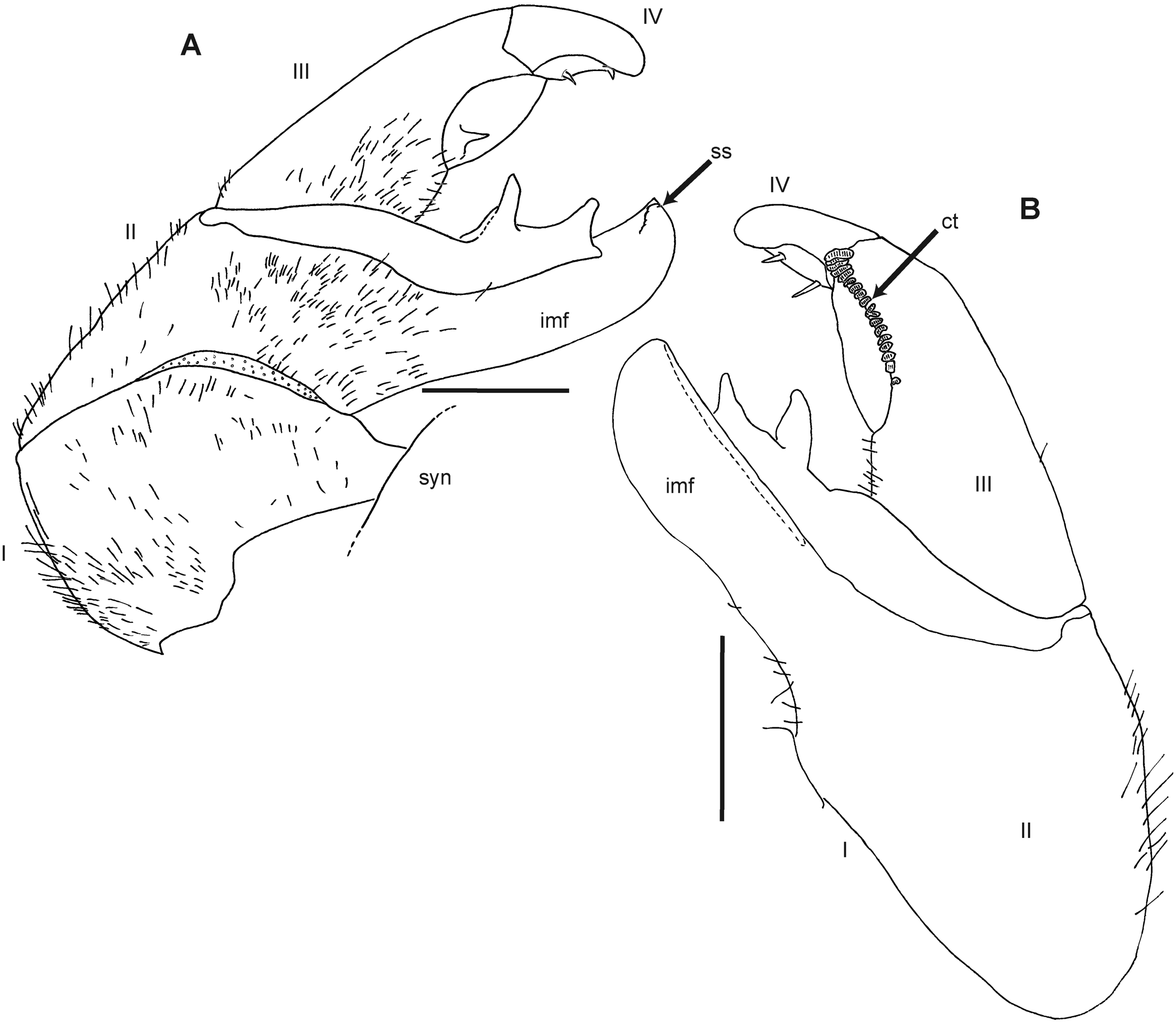

FIGURE 11. *Zephronia chrysomallos* Bhansali & Wesener **sp. nov.**, holotype ♂ (**NHMD MYR8826**), drawings, **A.** Left posterior telopod, anterior view. **B.** Left posterior telopod, posterior view. **Abbreviations**: ct = crenulated teeth; imf = immovable finger; ss = sclerotized spot. **Scale bars** = 1 mm.

Size. Length: 31.4 mm. Width of thoracic shield 14.8 mm, of widest segment (6) 16.5 mm. Height of thoracic shield 9.3 mm, of highest segment (6) 9.8 mm.

Colour. Faded after 30 years in 75% ethanol. Collum medium brown, head and legs with traces of green. Antenna green. Tergites and anal shield pale greyish-brown, darker brown towards posterior margin. Thoracic shield-like tergite with darker groove and margins. Anal shield colour like tergite.

Head. Number of ommatidia 95. Tömösváry organ placed on the rim of antennal groove. Antennae short, not reaching to center of head (Fig. 12A–D). Antennomere lengths: 1>2=3=4=5<<6. Antennomer 6 laterally flattened, apically widened, axe-shaped, carrying 91/96 apical cones.

Epipharynx. Not dissected.

Gnathochilarium (Fig. 12D). Gnathochilarium palpi with the sensory cones arranged in single field.

Mandible. Not dissected.

Collum. Numerous setae, distributed towards margins, few setae in central region.

Thoracic shield. Thoracic shield grooves shallow and wide with 2 or 3 weak ledges (Fig. 12A, B).

First stigmatic plate. Smaller than coxa, rounded apex.

Tergites. Tergites covered in short, dense setae visible at higher magnification, with dull orange skin-like surface. Paratergite tips weakly projecting backwards (Fig. 12A, B).

Pleurites (Fig. 12C). Pleurite 1 projecting, tip well-rounded. Pleurite 2 well-rounded, weakly projecting.

Endotergum. With a regular flat margin. Outer zone with three dense rows of irregular marginal setae, not extending beyond posterior margin, but reaching 4/5 of the outer area. Middle section with cuticular impressions. Inner area without setae.

Legs. Ventral spines on leg 1 2/2, at 2 4 /4, at 3 7/7. Leg 3 with single apical spine. Mid-body legs with 2 or 3 apical and 8–10 ventral spines (Fig. 13A). Inner margin of femur with 14 small triangular teeth, concentrated at apical half, but not excavated. Femur 1.7, tarsus 3.6 times longer than wide.

Anal shield. Bell-shaped and like tergites covered with short dense setae visible at higher magnification. Underside with single black locking carina of medium length, located close to pleurite (Fig. 12C).

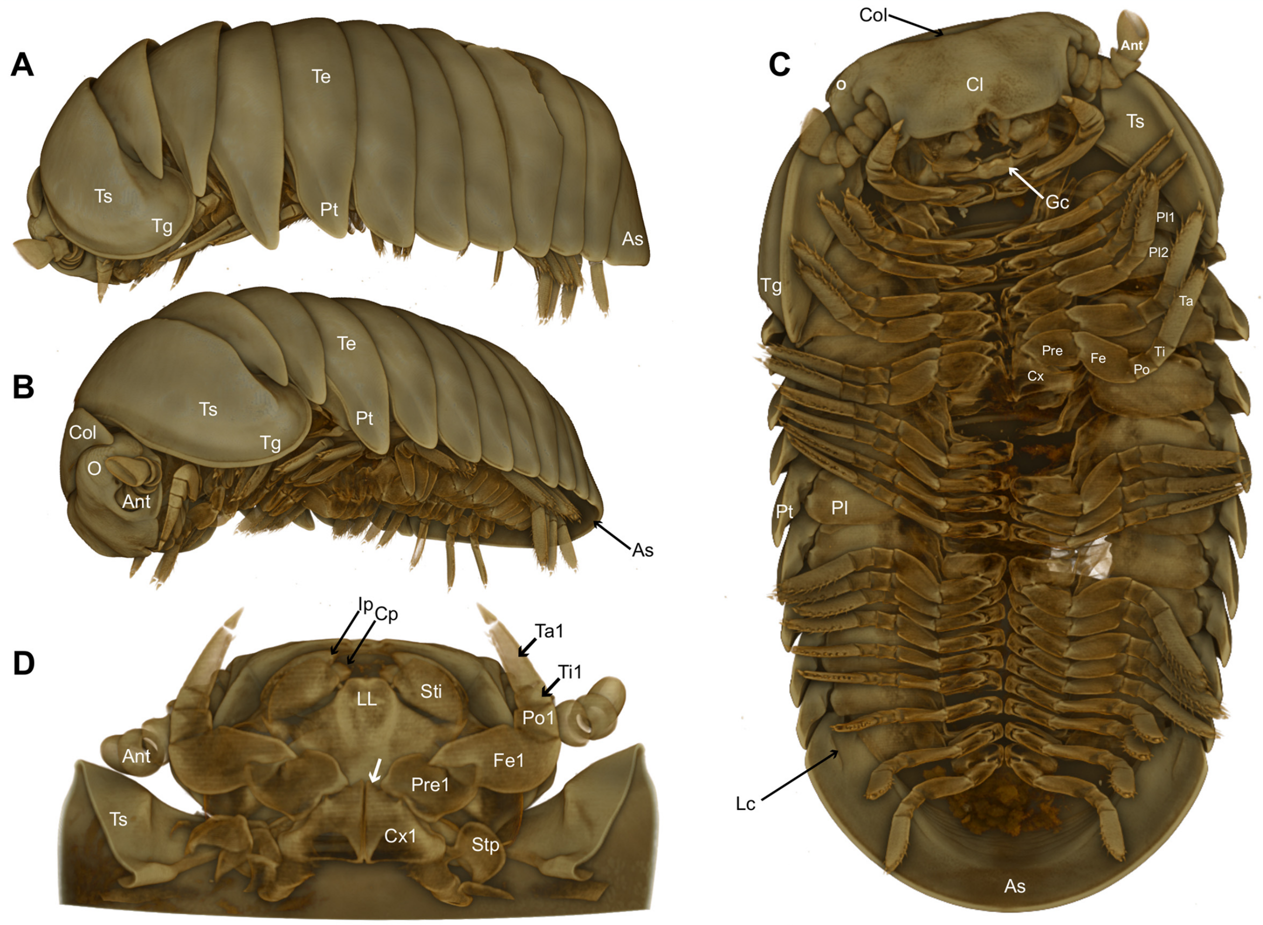

FIGURE 12. *Zephronia erawani* Bhansali & Wesener **sp. nov.**, holotype ♂ (**NHMD K56-9**), volume rendering based on micro-computed tomography. **A.** Habitus, lateral view. **B.** Habitus, ventro-lateral view. **C.** Habitus, ventral view. **D.** Habitus, anterior view. **E.** Body-ring architecture, cross section trough midbody-ring. **Abbreviations**: Ant = Antennae; As = anal shield; Cl = clypeus; Col = collum; Cp = central pad; Cx = coxa; Fe = femur; Gc = gnathochilarium; Go = gonopore; Ip = inner palpi; Lc = locking carina; o = ommatidia; Pl = pleurite; Pl1= pleurite 1; Pl2= pleurite 2; Po = postfemur; Pre = prefemur; Pt = paratergite; Stp = stigmatic plate; St = stipites; Ta = tarsus; Te = tergite; Tg = thoracic shield groove; Ti = tibia; Ts = thoracic shield. Not to scale.

Male gonopore. Located directly on mesal margin of coxa 2, covered posteriorly by a single semicircular sclerotized plate. Membrane rising mesally into a projection (Fig. 13B).

Anterior telopods (Fig. 13C–E). Syncoxite with few setae. Podomere 1 rectangular, as long as wide. Numerous setae, mainly at median margins. Podomere 2 slightly narrower than podomere 1. Process massive, well-rounded, apically slightly tapering, relatively short and wide (Fig. 13D, E). Process visible protruding and exceeding podomere 3 in anterior view (Fig. 13D). Podomere 3 cylindrical, with a black spot at the anterior margin visible in posterior view. Podomere 4 partially fused to podomere 3, suture can be seen in anterior view (Fig. 13C), while it is completely fused in posterior, lateral and mesal views. Podomere 4 small, narrowing at the apex. Meso-anterior margin with one spine and a black spot at apex visible in posterior and lateral view.

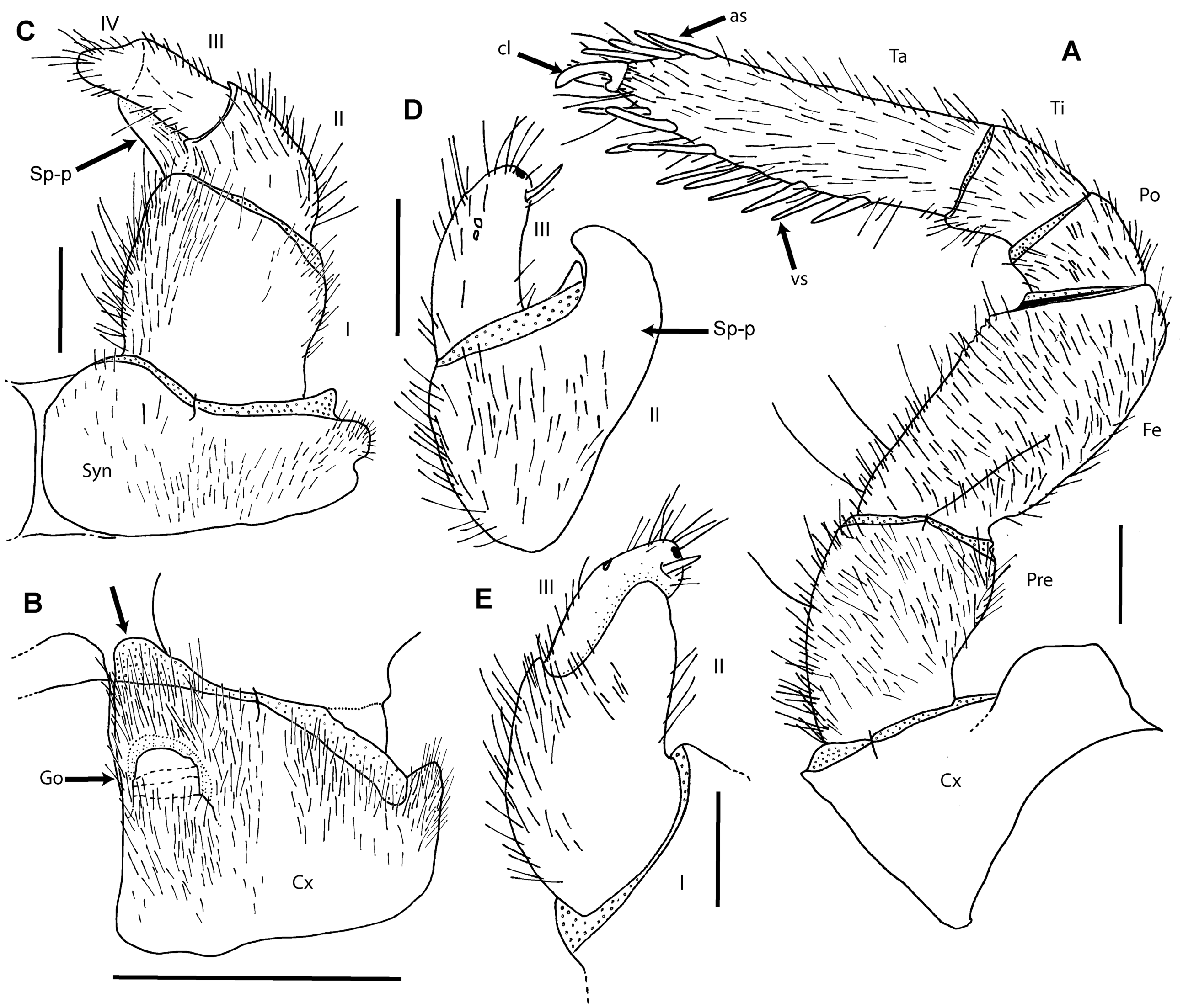

FIGURE 13. *Zephronia erawani* Bhansali & Wesener **sp. nov.**, holotype ♂ (**ZMUC K56-9**), drawings, **A.** Left leg 9, posterior view **B.** Second left coxa with gonopore, posterior view. **C.** Right anterior telopod, anterior view. **D.** Right anterior telopod, lateral view. **E.** Right anterior telopod, posterior view. **Abbreviations**: as = apical spine; cl = claw; Cx = coxa; Fe = femur; Go = gonopore; Po = postfemur; Pre = prefemur; Sp-p = second podomere process; St = stigmatic plate; Syn = syncoxite; Ta = tarsus; Ti = tibia; vs = ventral spines. **Scale bars** = 1 mm.

Posterior telopods (Fig. 14). Syncoxite inner horns (not drawn): apex well rounded, apically diverging. Podomere 1 with short setae distributed in median and lateral margin, median margin glabrous. Podomere 2 with long and wide immovable finger, 2.5 times longer than wide. Podomere 2 with numerous setae visible in anterior view, almost entirely glabrous in posterior view. Immovable finger slightly narrow anteriorly and straight. Apical process with sclerotized round spots in anterior view (Fig. 14A, arrow). Membrane toward podomere 3 with a two-tipped membranous lobe. Podomere 3 setose in anterior view, with more setae concentrated medially. With row of 15 large, crenulated teeth on posterior side (Fig. 14B, arrow). Large membranous ledge on podomere 3 with single spine present basal region. Podomere 4 glabrous on both sides, slightly curved towards immovable finger. Membranous lobe with 2 long spines. Immovable finger shorter than movable finger.

Distribution

Z. erawani **sp. nov.** is currently only known from the type locality (Fig. 2A) and might be microendemic, as are other, closely related species in nearby forests.

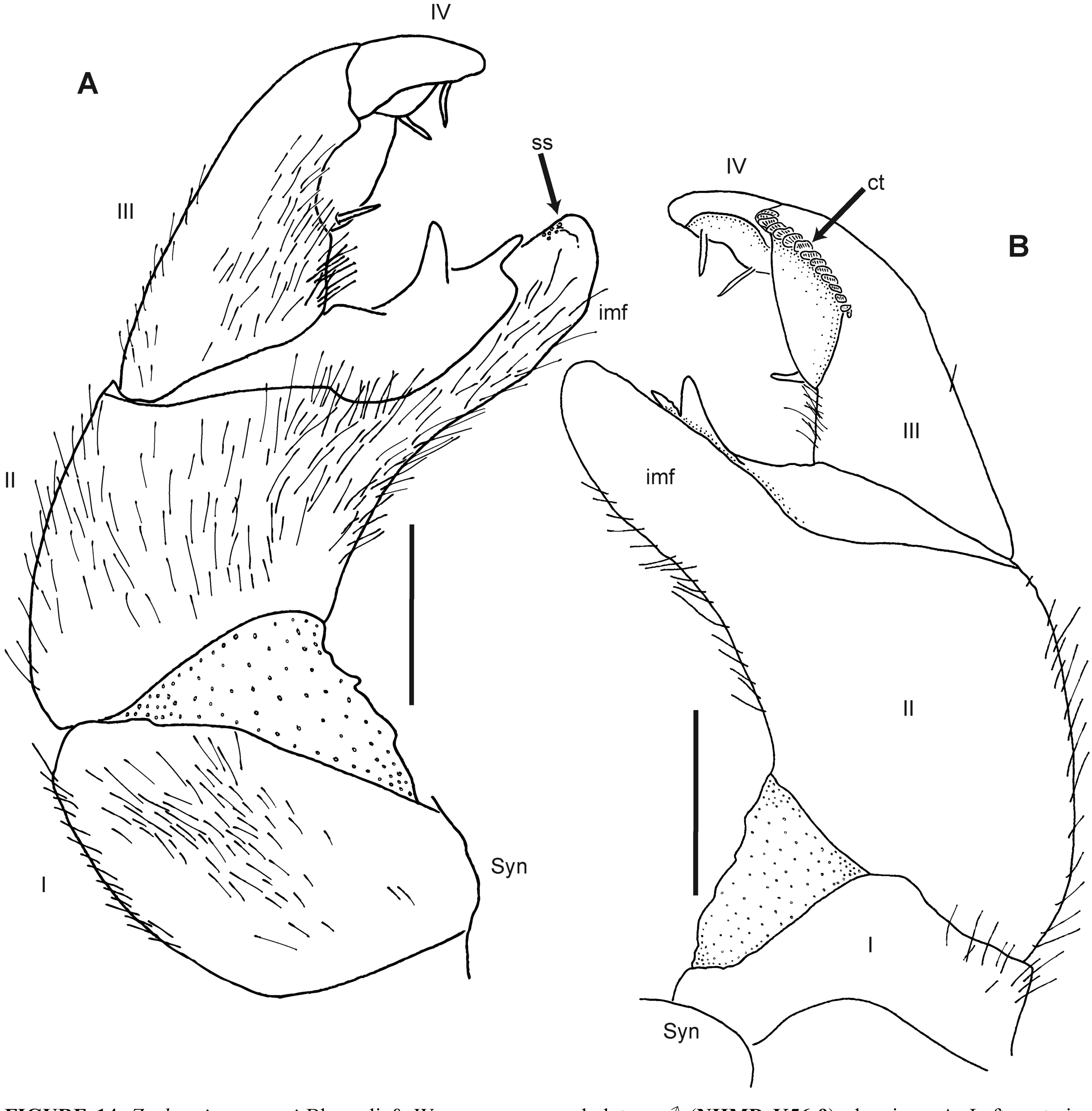

FIGURE 14. *Zephronia erawani* Bhansali & Wesener **sp. nov**., holotype ♂ (**NHMD K56-9**), drawings, **A.** Left posterior telopod, anterior view. **B.** Left posterior telopod, posterior view. **Abbreviations**: ct = crenulated teeth; imf = immovable finger; ss = sclerotized spot. **Scale bars** = 1 mm.

New locality data for Thai Zephroniidae

Zephronia phrain Likhitrakarn & Golovatch in Likhitrakarn *et al.* 2021

New locality data: 1 ♂, **SMF**, Chiang Mai Province, Chiang Dao District 20 km NNE of Chiang Dao, Tham Houay Luk, 19°32'18"N, 99°2'44"E, 623 m, outside cave, by hand, leg. 26.VI.2014, P. Jäger & E. Grall; 1 ♂, **SMF**, Chiang Mai Province, Chiang Dao District, Doi Chiang Dao, Ma Lee's Resort, 19°24'12"N, 98°55'34"E, 470 m, garden, by hand, by day and night, leg. 24–30.VI.2014, P. Jäger & E. Grall; 1 ♂, 1 ♀, **SMF**, Chiang Mai Province, Chai Prakan District, near Si Dong Yen, ThamNgam [=pretty cave], 19°39'19.46"N, 99°6'11.10"E, 660 m, inside cave and in front of cave, by day, by hand, leg. 29.VI.2014, P. Jäger & E. Grall; 1 ♂, **ZFMK MYR4907**, Chiang Mai, Chiang Dao, 19°23'54" N, 98°55'47" E, 448 m; 2 ♂♂, **MHNG 5G**, Lamphun Province, Mae Tha District, Doi Khuntan National

Park, 1100 m, evergreen hill forest, 18°29'35.83"N, 99°17'6.43"E, 8.X.1992, leg. A. Schwendinger; 1 ♂, **MHNG 5I**, Province Chiang Mai, Chiang Dao District, Doi Chiang Dao, 400 m, 7.VII.1987, leg. P. Schwendinger; 1 ♂, **ZFMK MYR3499**, Chiang Mai Province, District Chiang Dao, Padeng Lodge, 03.VII.2014, leg. S. Huber; 1 ♂, **ZFMK MYR3500**, Chiang Mai Province and District, Doi Suthep, behind tourist market, 18°48'03" N, 98°55'05" E, 2040 m, leg. 29.VI.2014, S. Huber; 1 ♂, **ZFMK MYR4907**, Chiang Mai Province, Chiang Dao, 19°23'54"N, 98°55'47" E, 448 m, 14–16.VIII.2015.

Remarks. This species, as already mentioned previously (Srisonchai *et al.* 2021), is more widespread than previously thought (Fig. 2A). We observed a lot of intraspecific variation in the genetic barcode (Sup. file 1) as well as in the telopods of *Z. phrain*, so there might be cryptic species under this name.

Zephronia lannaensis Likhitrakarn & Golovatch, 2021 in Likhitrakarn *et al.* 2021

New locality data: 3 ♂♂, **ZFMK MYR4911**, Chiang Mai Province, Mae Rim District, Mae Sa Valley, 18°53'54"N, 98°51'16"E, 650 m, 31.VIII–03.IX.2015; 2 ♂♂, **NHMD K57B**, Chiang Mai Province and District, Doi Suthep, Mae Sa Waterfall, 29.V.1991, leg. C.C. Kinze; 1 ♂, **MHNG 3B**; Chiang Mai Province & District, Doi Suthep, 800 m, evergreen gallery forest, 12.V.1986, leg. P. Schwendinger; 1 ♀, **ZFMK MYR3498**, Chiang Mai Province and District, foot of western side of Doi Suthep, 18°48'30" N, 98°56'49" E, 360 m. 05.VII.2014, leg S. Huber; 1 ♂, **ZFMK MYR3501**, Chiang Mai Province, Mae Rim District, Traidhos School Campus, 18°57'57" N, 98°55'05" E, 330 m, 30.VI.2014, leg. S. Huber; 3 ♂♂, **ZFMK MYR4912**, Chiang Mai Province, Mae Rim District, Mae Sa Valley, 18°53'54" N, 98°51'16" E, 650 m, 31.VIII–03.IX.2015.

Remarks. The localities mentioned above lie close to the type locality (Fig. 2A).

Zephronia panhai Srisonchai, Sutcharit & Likhitrakarn, 2021

New locality data: 1 ♀, **ZFMK MYR8116**, Ratchaburi Province, Ratchaburi and Photharam District, 18–20 km WNW of Ratchaburi, N: 13°35'17"–13°43'07", E: 99°40'07"–99°46'21", 30–80 m; 1 ♀, **ZFMK MYR8118**, same data as previous; 1 ♂, 1 ♀, 3 imm., **ZFMK MYR8128**, same data as previous; 5 ♂♂, 4 ♀♀, **ZFMK MYR8134**, same data as previous; 4 ♂♂, 1 ♀, **MHNG 3A**, Ratchaburi Province, Chombueng District, Tham Khao Bin Forest Park, 70 m, secondary forest on limestone, 13°35'12"N, 99°40'01"E, 27/28.VI.2011, leg. P. Schwendinger, sample TH-11/01.

Remarks. The localities mentioned above are close to the type locality (Fig. 2A).

Zephronia golovatchi Srisonchai, Sutcharit & Likhitrakarn, 2021

New locality data: 1 ♂, **ZFMK MYR6262**, Nakhon Ratchasima Province, Pak Ching District, near Highway 3052, 14°30'59.2"N, 101°23'52.9"E, 10.VI.2017; 1 ♂, 2 ♀♀, **ZFMK MYR6779**, same data as previous; 1 ♂, **ZFMK MYR7236**, same data as previous; 2 ♀♀, **NHMD K53**, Nakhon Nayok Province, Khao Yai National Park, 700 m, leg. 29.IX–6.X.1984, leg. Karsholt, Lomholdt & Nielsen.

Remarks. Both localities lie close to the type locality (Fig. 2A). However, specimens from both localities differ significantly genetically and might represent two different species.

Updated key to confirmed species of *Zephronia* in Thailand

1: Tarsi of leg pair 4–21 with single apical spine, third leg pair without apical spine. Male antennae, antennomere 6 swollen, not axe-shaped. . . . . *Z. viridisoma* Rosenmejer & Wesener in Rosenmejer *et al.* 2021

\- Tarsi of leg pair 4–21 with 3 apical spines, third leg pair with apical spine. Male antennae, antennomere 6 axe-shaped. **2**

2: Conspicuous colour pattern with a vivid green, glabrous or dull, not golden setae. Palpi of gnathochilarium, sensilla in clusters. **3**

\- Brown, grey, or brown-greenish color pattern with dense coat of 'golden' setae. Palpi of gnathochilarium, sensilla in single field. **4**

3: Small bodied, around 20 mm. Unique color pattern, green-whitish with red on the anal shield. Tergites setose, dull. Anterior telopod, podomere 3 with up to 7 crenulated teeth. Antennae, antennomere 6 with 50–60 cones. . . . *Z. siamensis* Hirst, 1907

- Large, around 40 mm. Unique color pattern, with a vivid green-lightbrownish stripes. Tergite glabrous, shiny. Anterior telopod variable, without or only very few sclerotized teeth. Antennae, antennomere 6 with 70–90 cones. . . . . *Z. phrain* Likhitrakarn & Golovatch in Likhitrakarn *et al.* 2021

4: Male second leg, mesal margin extended in short membranous process. **5**

- Male second leg, mesal margin not extended. **7**

5: Endotergum, two rows of marginal bristles which project beyond tergite margin. **6**

- Endotergum, two rows of marginal bristles which end clearly before the tergite margin. . . . .*Z. erawani* **sp. nov.**

6: Female vulval operculum margin straight and wide. Antennae, antennomere 6 with 90–100 cones. Male anal shield bell-shaped. . . . . *Z. golovatchi* Srisonchai *et al.*, 2021

- Female vulval operculum narrow in posterior view. Antennae, antennomere 6 with around 75 cones. Male anal shield rectangular. . . . . *Z. enghoffi* Srisonchai *et al.* 2021

7: Brown. Inner area of endotergum without setae. . . . . *Z. lannaensis* Likhitrakarn & Golovatch in Likhitrakarn *et al.* 2021

- Greyish. Inner area of endotergum with setae. **8**

8: Small, 20–22 mm long. Legs with 7–9 ventral spines. Male antennae, antennomere 6 with ca. 50 cones. Pleurite 1 extended into long, sharp tip. Endotergum with two rows of marginal bristles. . . . . *Z. panhai* Srisonchai *et al.* 2021

- Medium, 40 mm long. Legs with 10–12 ventral spines. Male antennae, antennomere 6 with 78–88 apical cones. Pleurite 1 weakly extended, well-rounded. Endotergum with three rows of marginal bristles. . . . . *Z. chrysomallos* **sp. nov.**

Discussion

Biogeography and genetic distance of newly described *Sphaerobelum*. *Sphaerobelum meridionalis* **sp. nov.** and *S. aesculus* differ from all previously described *Sphaerobelum* morphologically, geographically, and genetically. The immovable finger with a swollen apex is an important character for the characterization of the genus *Sphaerobelum* (Enghoff *et al.* 2015; Wesener 2019; Zhao *et al.* 2020). Unlike other *Sphaerobelum* species which possess a swollen apex of the immovable finger (Wongthamwanich *et al.* 2012; Wesener 2019), *S. meridionalis* **sp. nov.** and *S. aesculus* have a weak swelling in the center of the posterior side of the immovable finger, which is in other characters usual for Zephroniidae millipedes (Wesener 2016). Being quite distant geographically and genetically (p-distance of >17%) from other *Sphaerobelum* species, there is a possibility that both *S. meridionalis* **sp. nov.** and *S. aesculus* need to be placed in a genus different from *Sphaerobelum*. Malaysian giant pill-millipedes need to be reviewed in order to see if the two recently described *Sphaerobelum* might belong to a Malaysian genus (Jeekel 2000; Mauriès 2001). Especially a revision of Malaysian species, not done since the 1950s, is urgently needed.

Intra- and interspecific genetic distances. DNA barcoding is becoming an increasingly important tool for efficiently delimiting organisms at species-level using the mitochondrial COI gene (Hebert *et al.* 2003). Genetic barcoding helps to correctly determine samples only represented by females or juveniles at the genus- and species-level, as well as identify cryptic species (Wesener & Conrad 2016), or color variants of widespread species (Reip & Wesener 2018). In our new dataset, the observed interspecific distances of the three new Thai Zephroniidae species in comparison with related species are similar (minimum 10.8%) to those observed in giant pill-millipedes from Madagascar, where the species of *Sphaeromimus* de Saussure & Zehntner, 1902 show interspecific distances of 8.3–20.8% (Wesener *et al.* 2014; Moritz & Wesener 2017), while the interspecific distances in the less well-sampled genus *Zoosphaerium* Pocock, 1895 are 9.1–20% (Sagorny & Wesener 2017; Wesener & Anilkumar 2020; Wesener & Sagorny 2021). One reason behind the large interspecific distances between our three new species from southern Thailand might be that their closest relatives have not been discovered or sampled yet. *Z. panhai* and *Z. lannaensis* show intraspecific distances as seen between most populations of millipedes. On the other hand, our results show surprisingly high intraspecific distances in between populations of *Z. phrain* and *Z. golovatchi*. Future morphological studies should test whether the high intraspecific distances observed in these two species are in fact due to intraspecific variation, or whether these populations represent additional undescribed Thai *Zephronia* species.

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SUPPLEMENTAL MATERIAL

Sup. file 1. Estimates of Evolutionary Divergence between sequences. The number of base differences per site from between sequences are shown. The analysis involved 34 nucleotide sequences. Codon positions included were 1st+2nd+3rd. All ambiguous positions were removed for each sequence pair. There were a total of 674 positions in the final dataset. Evolutionary analyses were conducted in MEGA6 (Tamura *et al.* 2013).