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Descriptions of two new species and a new record of the giant pill-millipede genus *Zephronia* Gray, 1832 from Thailand (Diplopoda, Sphaerotheriida, Zephroniidae)

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Abstract. Two new species of the millipede genus *Zephronia* Gray, 1832 are described from Thailand, viz., *Z. sukhothaiensis* Srimongkol & Srisonchai sp. nov. and *Z. tratensis* Srimongkol & Srisonchai sp. nov., based on an integrative taxonomic approach. The new species can be distinguished from all congeners by a combination of characters, especially the length of the bristles on the endotergum of the midbody tergite and the shape of the telopods. Mitochondrial COI gene divergences between the two new species and the closely related species are more than 11% for *Z. sukhothaiensis* sp. nov. and 12% for *Z. tratensis* sp. nov., which supports their recognition as separate species. The species *Zephronia ovalis* Gray, 1832 is recorded from Thailand for the first time and is redescribed based on newly collected specimens from Sisaket Province. This new record indicates a transboundary distribution for *Z. ovalis* and highlights the biogeographical connectivity between Thailand and Vietnam. Furthermore, morphological characters of a newly discovered population of *Zephronia macula* Srisonchai & Wesener, 2024 are also updated and discussed, and compared to the type material. The variation observed in this newly discovered population reveals an extreme colour plasticity within *Z. macula* and provides a cautionary example regarding the unreliability of colouration for species delimitation. Morphological illustrations of *Z. macula*, *Z. ovalis*, *Z. sukhothaiensis* sp. nov., *Z. tratensis* sp. nov., an identification key, and a distribution map of all species of *Zephronia* occurring in Thailand are also provided.

Keywords. Biodiversity, endemism, genetic barcoding, Southeast Asia, taxonomy.

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Introduction

The giant pill-millipede genus *Zephronia* Gray, 1832, represents one of the most diverse and distinctive groups within the family Zephroniidae Gray, 1843 of the order Sphaerotheriida Brandt, 1833. To date, more than 50 species have been described worldwide, with their distributions ranging from the Himalayas in western India to mainland Southeast Asia (Wesener 2016, 2019; Semenyuk *et al*. 2018, 2020; Srisonchai *et al*. 2024). Since 2019, the genus has received increasing attention, with numerous new species being described primarily from mainland Southeast Asia, especially Thailand and Laos. These regions are recognized as biodiversity hotspots (Clements *et al*. 2006).

In Thailand, the millipede diversity is notably high, comprising 287 recorded species, the majority of which are endemic and restricted to limited geographical ranges (Enghoff 2005; Likhitrakarn *et al.* 2023). Within this diversity, eleven species of the giant pill-millipede genus *Zephronia* have been documented, viz., *Z. chantaburiensis* Srisonchai & Wesener, 2024, *Z. chrysomallos* Bhansali & Wesener, 2022, *Z. enghoffi* Srisonchai, Sutcharit & Likhitrakarn, 2021, *Z. erawani* Bhansali & Wesener, 2022, *Z. golovatchi* Srisonchai, Sutcharit & Likhitrakarn, 2021, *Z. lannaensis* Likhitrakarn & Golovatch, 2021, *Z. macula* Srisonchai & Wesener, 2024, *Z. panhai* Srisonchai, Sutcharit & Likhitrakarn, 2021, *Z. phrain* Likhitrakarn & Golovatch, 2021, *Z. siamensis* Hirst, 1907, and *Z. viridisoma* Rosenmejer & Wesener, 2021. Seven of these have been described since 2019, and it is likely that additional, as yet undescribed species remain to be discovered.

A systematic study of the genus *Zephronia*, integrating both morphological characteristics and COI (cytochrome oxidase subunit I) data, has been initiated and is currently underway. In recent years, DNA barcoding has become widely used and have provided valuable insights into species delimitation within *Zephronia* and their closely related genera (Wesener 2019; Rosenmejer *et al*. 2021; Bhansali & Wesener 2022; Zhao *et al*. 2022).

Recent intensive field surveys across the country have revealed a significant number of newly described giant pill-millipedes (Likhitrakarn *et al*. 2021; Rosenmejer *et al*. 2021; Srisonchai *et al*. 2021, 2023, 2024; Bhansali & Wesener 2022; Srikampha *et al*. 2025). More recently, specimens were collected between 2022 and 2024 from central, eastern, and northeastern Thailand including individuals of several remarkable morphotypes. Two of these exhibit a striking yellowish, light brown and brownish-grey colouration, appearing morphologically distinct from most known congeners. This study presents the descriptions of two new species of *Zephronia* based on both morphological characteristics and COI gene data. Additionally, we provide a redescription of *Z. ovalis* Gray, 1832, recorded in Thailand for the first time along with further specimens of *Z. macula*.

Material and methods

Sample collections

Specimens were hand-collected during recent field surveys conducted in central, eastern, and northeastern Thailand. Live individuals were photographed in their natural habitats using a Canon 70D digital camera equipped with a Canon EF-S 60 mm f/2.8 Macro USM lens. Specimens were euthanized following the guidelines of the American Veterinary Medical Association (AVMA 2020), and then preserved in 70% ethanol for morphological examination or 95% ethanol for molecular analyses.

Coordinates of the collecting sites were recorded using a Garmin GPSMAP 60CSx device and subsequently verified with high precision via Google Earth. The background for the distribution map was sourced from Elastic Terrain Map (http://elasticterrain.xyz) (Willett *et al*. 2015) and edited using Adobe Photoshop CC2019.

This work was conducted in accordance with animal ethics regulations, and the research protocol was approved by the Animal Care and Use Committee of Khon Kaen University (Protocol Review No. IACUC-KKU-136/64).

Morphological study

A total of over 700 specimens were examined under a stereo microscope. For scanning electron microscopy (SEM), selected specimens were dried using a humidity-controlled cabinet (DRY-CABINET S32L desiccant), mounted on stubs, gold-coated, and examined using a JEOL JSM-5410 LV microscope. Illustrations of external morphological features were prepared and arranged using Adobe Photoshop CC2019.

Species identification and morphological descriptions were primarily based on previous taxonomic and systematic works, including those by Wesener (2016, 2019), Rosenmejer *et al*. (2021), Bhansali & Wesener (2022), and Srisonchai *et al*. (2024).

Holotypes, paratypes, and the majority of the newly collected specimens are deposited in the Museum of Zoology, Khon Kaen University, Thailand (MZKKU=KKUMZ). Additional paratypes are distributed between the Museum of Zoology, Chulalongkorn University, Thailand (CUMZ); Natural History Museum, United Kingdom (NHMUK); Natural History Museum of Denmark, Denmark (NHMD); Naturhistorisches Museum Wien, Austria (NHMW); Zoological Research Museum Koenig, Germany (ZFMK).

Other institutional abbreviations are: FMNH = Field Museum of Natural History, Chicago, USA; MHNG = Muséum d'histoire naturelle de la Ville de Genève, Geneva, Switzerland; SCAU = South China Agricultural University, China; SMF = Senckenberg Museum Frankfurt, Germany; ZMUC = Zoological Museum, University of Copenhagen, Denmark.

Morphological abbreviations used in the descriptions and captions

3it = 3-combed inner tooth
ac = apical cone
ad = antennal disc
ant = antenna
bu = bursa
cl = clypeus
Cl = claw
co = condyles
cp = cuticular impression
cpd = central pad
cr-t = crenulated teeth
cs = cuticular scales
ct = central tooth
cx = coxa
et = external tooth (teeth) of epipharynx
Et = external tooth of mandible
fe = femur
go = gonopore
hyp = hypopharynx
ia = inner area of endotergum
Ia = inner area of mandible
ih = inner horn
il = incisura lateralis
iL = inner lobes of telopod
ip = inner palpi
ll = lamellae linguales
ma = middle area of endotergum
me = mentum
ml = membranous lobe
mp = molar plate
Mp = membranous process

o = ommatidia
O = operculum
oa = outer area of endotergum
pl = pectinate lamellae
pm = posterior margin of endotergum
po = postfemur
pre = prefemur
rdg = femoral ridge
rsp = row of spines
sb = sensilla basiconica
sc = sensory cone
scl-s = sclerotized spots
sp = sclerotized spine
Sp = small triangular spines
st = stipites
st-pl = stigmatic plate
syn-cx = syncoxite
ta = tarsus
tib = tibia
to = organ of Tömösváry

DNA extraction, sequences and barcoding tree reconstruction

Mitochondrial cytochrome c oxidase subunit I (COI) gene sequences were analyzed in this study. Genomic DNA was extracted from leg tissues (12–13) of *Z. macula*, *Z. ovalis*, *Z. sukhothaiensis* Srimongkol & Srisonchai sp. nov., and *Z. tratensis* Srimongkol & Srisonchai sp. nov. using the standard protocol of the NucleoSpin® Tissue Kit (Macherey-Nagel). PCR amplification was performed following protocols outlined in Wesener (2015, 2018) and Srisonchai *et al*. (2024), using LCO-1490 as forward and HCO-2198 as reverse primers — LCO-1490 (5›-GGT CAA CAA ATC ATA AAG ATA TTG G-3›) and HCO-2198 (5›-TAA ACT TCA GGG TGA CCA AAA AAT CA-3›) (Folmer *et al*. 1994).

Newly generated sequence chromatograms were manually inspected for missing data using MEGA 7 (ver. 7.0, see https://www.megasoftware.net/) (Kumar *et al*. 2016) with ambiguous sites coded as "N" in the FASTA file. All COI sequences were translated into amino acid, aligned in the correct reading frame, and visually checked for misalignments and stop codons in MEGA 7. Final sequence alignment was performed using MAFFT ver. 7 (Katoh *et al*. 2019) via the online server (https://mafft.cbrc.jp/alignment/server/index.html).

A total of 19 sequences generated in this study were analyzed together with 97 additional sequences retrieved from GenBank, representing 20 ingroup and 27 outgroup species. All newly generated sequences have been deposited in GenBank (Table 1). The best-fit nucleotide substitution model for the COI fragment was determined using JModelTest2 via XSEDE 2.1.6 (Darriba *et al*. 2012) on the CIPRES Science Gateway (https://www.phylo.org/) (Miller *et al*. 2010). Model selection was based on the AICc criterion, identifying GTR+I+G as the best-fitting model. Sequences were partitioned by codon position (1st, 2nd, 3rd), and Kakusan 4 (Tanabe 2011) was used to assign models and generate the input files for subsequent genetic analyses. Barcoding trees were reconstructed using both maximum likelihood (ML) and Bayesian inference (BI) approaches on the CIPRES platform. An ML analysis was conducted with IQ-TREE on XSEDE ver. 1.6.6 (Minh *et al*. 2020) using 1000 ultrafast bootstrap replicates. BI analysis was performed in MrBayes on XSEDE ver. 3.2.7a (Ronquist *et al*. 2012), employing a Markov Chain Monte Carlo (MCMC) algorithm with two independent runs of four chains (nruns=2, nchains=4). The analysis was run for 20 million generations, sampling every 1000 generations.

Table 1 (continued on next six pages). List of species included in this study and their corresponding GenBank accession numbers for the COI gene fragment.

	Species	COI accession number	Voucher code	Locality	Reference
			Ingroups		
1	*Zephronia chantaburiensis* Srisonchai & Wesener, 2024	PP754582	CUMZ-Zeph0013 (M47)	THAILAND, Chanthaburi Province, Tha Mai District, Wat Khao Sukim.	Srisonchai *et al*. (2024)
2	*Zephronia chantaburiensis* Srisonchai & Wesener, 2024	PP754583	CUMZ-Zeph0013 (M48)	THAILAND, Chanthaburi Province, Tha Mai District, Wat Khao Sukim.	Srisonchai *et al*. (2024)
3	*Zephronia chrysomallos* Bhansali & Wesener, 2022	OM509649	ZFMK MYR8826	THAILAND, Kanchanaburi Province, Sai Yok District, Sai Yok Noi Waterfall.	Bhansali & Wesener (2022)
4	*Zephronia dawydoffi* Attems, 1953	MK330971	ZFMK Myr4504	N/A	Wesener (2019)
5	*Zephronia erawani* Bhansali & Wesener, 2022	OM509650	NHMD K56x9	THAILAND, Kanchanaburi Province, Si Sawat District, Erawan Waterfall, 50 km W of Kanchanaburi.	Bhansali & Wesener (2022)
6	*Zephronia golovatchi* Srisonchai, Sutcharit & Likhitrakarn, 2021	OM509646	ZFMK MYR6262	THAILAND, Nakhon Ratchasima Province, Pak Chong District.	Bhansali & Wesener (2022)
7	*Zephronia golovatchi* Srisonchai, Sutcharit & Likhitrakarn, 2021	OM509647	ZFMK K53	THAILAND, Nakhon Nayok Province, Khao Yai National Park.	Bhansali & Wesener (2022)
8	*Zephronia hui* Liu & Wesener, 2022	OP339790	SCAU YGM03	CHINA, Guizhou, Tongren City, Jiangkou County, Taiping Town, Yamugou Scenic Area.	Zhao *et al*. (2022)
9	*Zephronia hui* Liu & Wesener, 2022	OP339791	SCAU YGM02	CHINA, Guizhou, Tongren City, Jiangkou County, Taiping Town, Yamugou Scenic Area.	Zhao *et al*. (2022)
10	*Zephronia lannaensis* Likhitrakarn & Golovatch, 2021	OM509629	ZFMK MYR3498	THAILAND, Chiangmai Province, Mueang District, Doi Suthep.	Bhansali & Wesener (2022)
11	*Zephronia lannaensis* Likhitrakarn & Golovatch, 2021	OM509630	ZFMK MYR3501	THAILAND, Chiangmai Province, Mae Rim District, Traidhos School Campus.	Bhansali & Wesener (2022)
12	*Zephronia lannaensis* Likhitrakarn & Golovatch, 2021	OM509631	ZFMK MYR4911	THAILAND, Chiangmai Province, Mae Rim District, Mae Sa Valley.	Bhansali & Wesener (2022)
13	*Zephronia lannaensis* Likhitrakarn & Golovatch, 2021	OM509632	NHMD K57B	THAILAND, Chiangmai Province, Mueang District, Doi Suthep, Me Sa Waterfall.	Bhansali & Wesener (2022)
14	*Zephronia lannaensis* Likhitrakarn & Golovatch, 2021	OM509633	MHNG 3B	THAILAND, Chiangmai Province, Mueang District, Doi Suthep.	Bhansali & Wesener (2022)
15	*Zephronia laotica* Wesener, 2019	MK330977	ZFMK Myr3502	LAOS, Champasak Province, east of Mekong, Garden of Erawan Riverside Hotel.	Wesener (2019)
16	*Zephronia macula* Srisonchai & Wesener, 2024	PP754589	CUMZ (M54)	THAILAND, Sa Kaeo Province, Mueang Sa Kaeo District, Wat Tham Khao Maka.	Srisonchai *et al*. (2024)
17	*Zephronia macula* Srisonchai & Wesener, 2024	PP754590	CUMZ (M55)	THAILAND, Sa Kaeo Province, Mueang Sa Kaeo District, Wat Tham Khao Maka.	Srisonchai *et al*. (2024)

Table 1 (continued). List of species included in this study and their corresponding GenBank accession numbers for the COI gene fragment.

	Species	COI accession number	Voucher code	Locality	Reference
18	*Zephronia macula* Srisonchai & Wesener, 2024	PP754584	CUMZ- MYR 0015 (M417)	THAILAND, Chanthaburi Province, Khlung District, Thaeo Khlong Khlung Monastery.	Srisonchai *et al*. (2024)
19	*Zephronia macula* Srisonchai & Wesener, 2024	PP754585	CUMZ- MYR 0015 (M418)	THAILAND, Chanthaburi Province, Khlung District, Thaeo Khlong Khlung Monastery.	Srisonchai *et al*. (2024)
20	*Zephronia macula* Srisonchai & Wesener, 2024	PP754586	CUMZ- MYR 0015 (M421)	THAILAND, Chanthaburi Province, Tha Mai District, Wat Khao Sukim.	Srisonchai *et al*. (2024)
21	*Zephronia macula* Srisonchai & Wesener, 2024	PP754587	CUMZ- MYR 0015 (M422)	THAILAND, Chanthaburi Province, Tha Mai District, Wat Khao Sukim.	Srisonchai *et al*. (2024)
22	*Zephronia macula* Srisonchai & Wesener, 2024	PP754588	CUMZ- MYR 0015 (M424)	THAILAND, Chanthaburi Province, Tha Mai District, Wat Khao Sukim.	Srisonchai *et al*. (2024)
23	*Zephronia macula* Srisonchai & Wesener, 2024	PX526095	MZKKU (M400)	THAILAND, Sa Kaeo Province, Phra Phloeng District, Wat Tham Khao Chan.	This study
24	*Zephronia macula* Srisonchai & Wesener, 2024	PX526096	MZKKU (M401)	THAILAND, Sa Kaeo Province, Phra Phloeng District, Wat Tham Khao Chan.	This study
25	*Zephronia macula* Srisonchai & Wesener, 2024	PX526097	MZKKU (M437)	THAILAND, Rayong Province, Khao Chamao District, Wat Tham Suwan Phupha.	This study
26	*Zephronia macula* Srisonchai & Wesener, 2024	PX526098	MZKKU (M438)	THAILAND, Rayong Province, Khao Chamao District, Wat Tham Suwan Phupha.	This study
27	*Zephronia macula* Srisonchai & Wesener, 2024	PX526099	MZKKU (M456)	THAILAND, Chachoengsao Province, Phanom Sarakham District, Wat Khao Hin Sorn.	This study
28	*Zephronia macula* Srisonchai & Wesener, 2024	PX526100	MZKKU (M457)	THAILAND, Chachoengsao Province, Phanom Sarakham District, Wat Khao Hin Sorn.	This study
29	*Zephronia macula* Srisonchai & Wesener, 2024	PX526101	MZKKU (M458)	THAILAND, Chachoengsao Province, Phanom Sarakham District, Wat Khao Hin Sorn.	This study
30	*Zephronia macula* Srisonchai & Wesener, 2024	PX526102	MZKKU (M459)	THAILAND, Chachoengsao Province, Phanom Sarakham District, Wat Khao Hin Sorn.	This study
31	*Zephronia medongensis* Zhao & Liu, 2022	OP339793	SCAU XZ01	CHINA, Xizang Autonomous Region, Medog County.	Zhao *et al*. (2022)
32	*Zephronia ovalis* Gray, 1832	JX486068	ZFMK Myr 0832	VIETNAM, Dong Nai Province, Cat Tien National Park.	Golovatch *et al*. (2012)
33	*Zephronia ovalis* Gray, 1832	PX526103	MZKKU (M180)	THAILAND, Sisaket Province, Khun Han District, Hui Chan Waterfall.	This study
34	*Zephronia ovalis* Gray, 1832	PX526104	MZKKU (M181)	THAILAND, Sisaket Province, Khun Han District, Hui Chan Waterfall.	This study
35	*Zephronia ovalis* Gray, 1832	PX526105	MZKKU (M204)	THAILAND, Surin Province, Bua Chet District, Wat Tham Pha Sai.	This study

Table 1 (continued). List of species included in this study and their corresponding GenBank accession numbers for the COI gene fragment.

	Species	COI accession number	Voucher code	Locality	Reference
36	*Zephronia panhai* Srisonchai, Sutcharit & Likhitrakarn, 2021	OM509643	ZFMK MYR 8118	THAILAND Ratchaburi Province, Ratchabui-Photharam Districts.	Bhansali & Wesener (2022)
37	*Zephronia panhai* Srisonchai, Sutcharit & Likhitrakarn, 2021	OM509644	MHNG 3A	THAILAND, Ratchaburi Province, Chom Bueang District, Tham Kao Bin Forest Park.	Bhansali & Wesener (2022)
38	*Zephronia panhai* Srisonchai, Sutcharit & Likhitrakarn, 2021	OM509645	ZFMK MYR 8116	THAILAND, Ratchaburi Province, Ratchabui-Photharam Districts.	Bhansali & Wesener (2022)
39	*Zephronia phrain* Likhitrakarn & Golovatch, 2021	OM509634	ZFMK MYR 3499	THAILAND, Chiang Mai Province, Chiang Dao District, Padeng Lodge.	Bhansali & Wesener (2022)
40	*Zephronia phrain* Likhitrakarn & Golovatch, 2021	OM509635	ZFMK MYR3500	THAILAND, Chiangmai Province, Mueang District, Doi Suthep.	Bhansali & Wesener (2022)
41	*Zephronia phrain* Likhitrakarn & Golovatch, 2021	OM509636	SMF	THAILAND, Chiang Mai Province, Chiang Dao District, Tham Houay Luk.	Bhansali & Wesener (2022)
42	*Zephronia phrain* Likhitrakarn & Golovatch, 2021	OM509637	SMF	THAILAND, Chiang Mai Province, Chiang Dao District, Doi Chiang Dao, Ma Lee's Resort.	Bhansali & Wesener (2022)
43	*Zephronia phrain* Likhitrakarn & Golovatch, 2021	OM509638	SMF	THAILAND, Chiang Mai Province, Chai Prakan District, Tham Ngam.	Bhansali & Wesener (2022)
44	*Zephronia phrain* Likhitrakarn & Golovatch, 2021	OM509639	ZFMK MYR 4907	THAILAND, Chiang Mai Province, Chiang Dao.	Bhansali & Wesener (2022)
45	*Zephronia phrain* Likhitrakarn & Golovatch, 2021	OM509640	MHNG 5G	THAILAND, Lamphun Province, Mae Tha District, Doi Khuntan National Park.	Bhansali & Wesener (2022)
46	*Zephronia phrain* Likhitrakarn & Golovatch, 2021	OM509641	MHNG 5I	THAILAND, Chiang Mai Province, Chiang Dao District, Doi Chiang Dao.	Bhansali & Wesener (2022)
47	*Zephronia phrain* Likhitrakarn & Golovatch, 2021	OM509642	NHMD K35	THAILAND, Chiang Mai Province, Ban Musue.	Bhansali & Wesener (2022)
48	*Zephronia siamensis* Hirst, 1907	JX486067.2	FMNH-INS-72669	THAILAND, Chonburi Province, Sichang District, Koh Sichang.	Golovatch *et al*. (2012)
49	*Zephronia siamensis* Hirst, 1907	OR530089	CUMZ	THAILAND, Chonburi Province, Sichang District, Koh Sichang.	Srisonchai *et al*. (2023)
50	*Zephronia siamensis* Hirst, 1907	PP754591	CUMZ (D397)	THAILAND, Sa Kaeo Province, Khao Chakan District, Wat Tham Khao Chan.	Srisonchai *et al*. (2024)
51	*Zephronia siamensis* Hirst, 1907	PP754592	CUMZ (M455)	THAILAND, Chachoengsao Province, Phanom Sarakham District, Wat Khao Hin Sorn.	Srisonchai *et al*. (2024)
52	*Zephronia sukhothaiensis* Srimongkol & Srisonchai, sp. nov.	PX526106	MZKKU (L42)	THAILAND, Sukhothai Province, Ban Dan Lan Hoi District, Wat Khao Fang.	This study

Table 1 (continued). List of species included in this study and their corresponding GenBank accession numbers for the COI gene fragment.

	Species	COI accession number	Voucher code	Locality	Reference
53	*Zephronia sukhothaiensis* Srimongkol & Srisonchai, sp. nov.	PX526107	MZKKU (L43)	THAILAND, Sukhothai Province, Ban Dan Lan Hoi District, Wat Khao Fang.	This study
54	*Zephronia sukhothaiensis* Srimongkol & Srisonchai, sp. nov.	PX526108	MZKKU (M323)	THAILAND, Sukhothai Province, Ban Dan Lan Hoi District, Tham Yok Monastery.	This study
55	*Zephronia sukhothaiensis* Srimongkol & Srisonchai, sp. nov.	PX526109	MZKKU (M324)	THAILAND, Sukhothai Province, Ban Dan Lan Hoi District, Wat Khao Fang.	This study
56	*Zephronia sukhothaiensis* Srimongkol & Srisonchai, sp. nov.	PX526110	MZKKU (M325)	THAILAND, Sukhothai Province, Ban Dan Lan Hoi District, Tham Yok Monastery.	This study
57	*Zephronia* sp. (K45 Aow Noi Temple)	MW898741	NHMD K45	THAILAND, Prachuap Kiri Khan Province, Mueang District, Aow Noi Temple.	Rosenmejer *et al*. (2021)
58	*Zephronia* sp. (Aow Noi Temple)	MW898742	ZFMK MYR 8787	THAILAND, Prachuap Kiri Khan Province, Mueang District, Aow Noi Temple.	Rosenmejer *et al*. (2021)
59	*Zephronia tratensis* Srimongkol & Srisonchai, sp. nov.	PX526111	MZKKU (M414)	THAILAND, Trat Province, Mueang District, Khao Khun Tham Monastery.	This study
60	*Zephronia tratensis* Srimongkol & Srisonchai, sp. nov.	PX526112	MZKKU (M415)	THAILAND, Trat Province, Mueang District, Khao Khun Tham Monastery.	This study
61	*Zephronia tratensis* Srimongkol & Srisonchai, sp. nov.	PX526113	MZKKU (M416)	THAILAND, Trat Province, Mueang District, Khao Khun Tham Monastery.	This study
62	*Zephronia viridisoma* Rosenmejer & Wesener, 2021	MW898739	NHMD 621695	THAILAND, Nakhon Si Thammarat Province, Sichon District, Khao Lark Waterfall.	Rosenmejer *et al*. (2021)
63	*Zephronia viridisoma* Rosenmejer & Wesener, 2021	MW898740	ZFMK MYR 8822	THAILAND, Nakhon Si Thammarat Province, Sichon District, Khao Lark Waterfall.	Rosenmejer *et al*. (2021)
64	*Zephronia zhouae* Zhao & Liu, 2022	OP339794	SCAU YN02	CHINA, Yunnan Province, Diqing Tibetan Autonomous Prefecture, Laowo Village, Weixi County.	Zhao *et al*. (2022)
	Outgroups				
65	*Sphaerobelum aesculus* Rosenmejer & Wesener, 2021	MW898737	NHMD 621693	THAILAND, Phuket Province, Kathu District, Forest.	Rosenmejer *et al*. (2021)
66	*Sphaerobelum* cf. *aesculus* Rosenmejer & Wesener, 2021	MW898738	NHMD 621694	THAILAND, Nakhon Si Thammarat Province, Khao Luang NP.	Rosenmejer *et al*. (2021)
67	*Sphaerobelum benquii* Liu & Wesener, 2022	OP339792	SCAU MMY01	CHINA, Guizhou, Tongren City, Jiangkou County, Guanhe Town, Guanhe Village, Maomaoyan.	Zhao *et al*. (2022)
68	*Sphaerobelum bolavensis* Wesener, 2019	MK330982	MHNG LT-10/24	LAOS, Champasak Province, Bolaven Plateau, 3 km S of Ban Nong Luang, Tad Kameud.	Wesener (2019)

Table 1 (continued). List of species included in this study and their corresponding GenBank accession numbers for the COI gene fragment.

	Species	COI accession number	Voucher code	Locality	Reference
69	*Sphaerobelum denticulatum* Wesener, 2019	MK330984	MHNG LT-10/12	LAOS, Oudomxai Province, ca 3 km E of Tad Lak 11, SE of Oudomxai city.	Wesener (2019)
70	*Sphaerobelum huzhengkuni* Zhao, Yu & Liu, 2020	MT657327	SCAU SP02	CHINA, Guizhou Province, Tongren City, Fanjingshan National Nature Reserve.	Zhao *et al.* (2020)
71	*Sphaerobelum huzhengkuni* Zhao, Yu & Liu, 2020	MT657328	SCAU SP03	CHINA, Guizhou Province, Tongren City, Fanjingshan National Nature Reserve.	Zhao *et al.* (2020)
72	*Sphaerobelum lachneeis* Wesener, 2019	MK330983	MHNG LT-10/12	LAOS, Oudomxai Province, ca 3 km E of Tad Lak 11, SE of Oudomxai city.	Wesener (2019)
73	*Sphaerobelum laoticum* Wesener, 2019	MK330975	SMF	LAOS, Vientiane, Province, Vang Vieng.	Wesener (2019)
74	*Sphaerobelum meridionalis* Bhansali & Wesener, 2022	OM509648	MHNG 4B-2	THAILAND, Yala Province, Bannang Sata District, Bang Lang National Park, near Than To Waterfall.	Bhansali & Wesener (2022)
75	*Sphaerobelum nigrum* Wesener, 2019	MK330976	SMF	LAOS, Champasak Province, Muang Bachieng, Tad Etu, Ban Lak 35.	Wesener (2019)
76	*Sphaerobelum nonghinensis* Srikampha & Srisonchai, 2025	PQ838982	MZKKU (A35)	THAILAND, Loei Province, Nong Hin District, Suan Hin Pha Ngam (Hin Pha Ngam Park).	Srikampha *et al.* (2025)
77	*Sphaerobelum nonghinensis* Srikampha & Srisonchai, 2025	PQ838983	MZKKU (A36)	THAILAND, Loei Province, Nong Hin District, Suan Hin Pha Ngam (Hin Pha Ngam Park).	Srikampha *et al.* (2025)
78	*Sphaerobelum nonghinensis* Srikampha & Srisonchai, 2025	PQ838984	MZKKU (E28)	THAILAND, Loei Province, Nong Hin District, Suan Hin Pha Ngam (Hin Pha Ngam Park).	Srikampha *et al.* (2025)
79	*Sphaerobelum nonghinensis* Srikampha & Srisonchai, 2025	PQ838985	MZKKU (E29)	THAILAND, Loei Province, Nong Hin District, Suan Hin Pha Ngam (Hin Pha Ngam Park).	Srikampha *et al.* (2025)
80	*Sphaerobelum nonghinensis* Srikampha & Srisonchai, 2025	PQ838986	MZKKU (M237)	THAILAND, Loei Province, Nong Hin District, Suan Hin Pha Ngam (Hin Pha Ngam Park).	Srikampha *et al.* (2025)
81	*Sphaerobelum onyx* Srikampha & Srisonchai, 2025	PQ838987	MZKKU (M211)	THAILAND, Buang Kan Province, Seka District, Wat Tham Chum Chang (Nam Yaad Clift).	Srikampha *et al.* (2025)
82	*Sphaerobelum onyx* Srikampha & Srisonchai, 2025	PQ838988	MZKKU (M212)	THAILAND, Buang Kan Province, Seka District, Wat Tham Chum Chang (Nam Yaad Clift).	Srikampha *et al.* (2025)
83	*Sphaerobelum peterjaegeri* Wesener, 2019	MK330972	SMF SD553	LAOS, Luang Prabang Province, SE Luang Prabang, Nam Khan, Ban Pak Bak, Houay Kho.	Wesener (2019)
84	*Sphaerobelum petramurum* Srikampha & Srisonchai, 2025	PQ838989	MZKKU (E5)	THAILAND, Khon Kaen Province, Phu Pha Man District, Ban Khao Wong.	Srikampha *et al.* (2025)
85	*Sphaerobelum petramurum* Srikampha & Srisonchai, 2025	PQ838990	MZKKU (L127)	THAILAND, Khon Kaen Province, Phu Pha Man District, Ban Khao Wong.	Srikampha *et al.* (2025)

Table 1 (continued). List of species included in this study and their corresponding GenBank accession numbers for the COI gene fragment.

	Species	COI accession number	Voucher code	Locality	Reference
86	*Sphaerobelum petramurum* Srikampha & Srisonchai, 2025	PQ838991	MZKKU (L128)	THAILAND, Khon Kaen Province, Phu Pha Man District, Ban Khao Wong.	Srikampha *et al*. (2025)
87	*Sphaerobelum petramurum* Srikampha & Srisonchai, 2025	PQ838992	MZKKU (L6)	THAILAND, Khon Kaen Province, Phu Pha Man District, Ban Khao Wong.	Srikampha *et al*. (2025)
88	*Sphaerobelum petramurum* Srikampha & Srisonchai, 2025	PQ838993	MZKKU (M217)	THAILAND, Khon Kaen Province, Phu Pha Man District, Ban Khao Wong.	Srikampha *et al*. (2025)
89	*Sphaerobelum petramurum* Srikampha & Srisonchai, 2025	PQ838994	MZKKU (M218)	THAILAND, Khon Kaen Province, Phu Pha Man District, Ban Khao Wong.	Srikampha *et al*. (2025)
90	*Sphaerobelum phouloei* Wesener, 2019	MK330974	ZMUC00040257	LAOS, Houaphan Province, Phou Loei.	Wesener (2019)
91	*Sphaerobelum schwendingeri* Wesener, 2019	MK330978	MHNG LT-10/03	LAOS, Vientiane Province, W. of Vang Vieng, trail to Tham Pou Kham.	Wesener (2019)
92	*Sphaerobelum schwendingeri* Wesener, 2019	MK330981	SMF	LAOS, Vientiane Province, Vang Vieng, Tham Pou Kham.	Wesener (2019)
93	*Sphaerobelum* sp. L07	MK330979	ZMUC00040261	LAOS, Khammouane Province, Ban Khounkham [Khun Kham] (Nahin).	Wesener (2019)
94	*Sphaerobelum* sp. L10	MK330980	SMF	LAOS, Vientiane Province, Vang Vieng, W. of Nam Song, Tham Nam Or Khem.	Wesener (2019)
95	*Sphaerobelum spinatum* Wesener, 2019	MK330973	ZMUC00040258	LAOS, Vientiane Province, Phou Khao Khouay.	Wesener (2019)
96	*Sphaerobelum truncatum* Wongthamwanich, 2012	JN885184	FMNH-INS 0000 072 674	THAILAND, Nan Province, Song Khwae District, Na Rai Luang Subdistrict, Pang Hi Village.	Wongthamwanich *et al*. (2012)
97	*Sphaerobelum turcosa* Srisonchai & Pimvichai, 2023	OR530087	CUMZ-Zeph0012	THAILAND, Loei Province, Mueang Loei District, Phu Pha Lom Forest Park.	Srisonchai *et al*. (2023)
98	*Sphaerobelum turcosa* Srisonchai & Pimvichai, 2023	OR530087	CUMZ-Zeph0012	THAILAND, Loei Province, Mueang Loei District, Phu Pha Lom Forest Park.	Srisonchai *et al*. (2023)
99	*Sphaerobelum tujiaphilum* Zhao & Liu, 2022	OP339783	SCAU SD01	CHINA, Guizhou, Tongren City, Jiangkou County, Guanhe Town, Sidu Village.	Zhao *et al*. (2022)
100	*Sphaerobelum tujiaphilum* Zhao & Liu, 2022	OP339784	SCAU SD02	CHINA, Guizhou, Tongren City, Jiangkou County, Guanhe Town, Sidu Village.	Zhao *et al*. (2022)
101	*Sphaerobelum tujiaphilum* Zhao & Liu, 2022	OP339785	SCAU BHS01	CHINA, Guizhou, Tongren City, Jiangkou County, Taiping Town, Baiheshan Village.	Zhao *et al*. (2022)
102	*Sphaerobelum tujiaphilum* Zhao & Liu, 2022	OP339786	SCAU JXT01	CHINA, Guizhou, Tongren City, Jiangkou County, Taiping Town, Jiang-xitun Village.	Zhao *et al*. (2022)

Table 1 (continued). List of species included in this study and their corresponding GenBank accession numbers for the COI gene fragment.

	Species	COI accession number	Voucher code	Locality	Reference
103	*Sphaerobelum tujiaphilum* Zhao & Liu, 2022	OP339787	SCAU JXT02	CHINA, Guizhou, Tongren City, Jiangkou County, Taiping Town, Jiang-xitun Village.	Zhao *et al*. (2022)
104	*Sphaerobelum tujiaphilum* Zhao & Liu, 2022	OP339788	SCAU SD03	CHINA, Guizhou, Tongren City, Jiangkou County, Guanhe Town, Sidu Village.	Zhao *et al*. (2022)
105	*Sphaerobelum tujiaphilum* Zhao & Liu, 2022	OP339789	SCAU DW01	CHINA, Guizhou, Tongren City, Jiangkou County, Dewang Town, Xiaobang Village.	Zhao *et al*. (2022)
106	*Arthrosphaera brandtii* (Humbert, 1865)	FJ409915	FMNH-INS 8650	TANZANIA, Usambara hills.	Wesener *et al*. (2010)
107	*Cryxus ovalis* (Linnaeus, 1758)	JX486069.2	ZFMK MYR0824	VIETNAM, Dong Nai Province, Cat Tien National Park.	Golovatch *et al*. (2012)
108	*Glomeris marginata* (Villers, 1789)	FJ409909	ZFMK Myr009	GERMANY, Bonn, Venusberg.	Wesener *et al*. (2010)
109	*Epicyliosoma* sp.	AF218270	NA	NA	Edgecombe & Giribet (2004)
110	*Prionobelum inthanonense* Donworth & Wesener, 2024	PP297645	MHNG 4E-2	THAILAND, Chiang Mai Province, Chom Thong District, Doi Inthanon National Park.	Donworth & Wesener (2024)
111	*Prionobelum inthanonense* Donworth & Wesener, 2024	PP297646	MHNG 7A	THAILAND, Chiang Mai Province, Chom Thong District, Doi Inthanon National Park.	Donworth & Wesener (2024)
112	*Prionobelum naevium* Donworth & Wesener, 2024	PP297647	MHNG 4B-1	THAILAND, Yala Province, Than To District, Bang Lang National Park, Than To Waterfall.	Donworth & Wesener (2024)
113	*Prionobelum naevium* Donworth & Wesener, 2024	PP297648	NHMD 1184671	THAILAND, Yala Province, Than To District, Bang Lang National Park.	Donworth & Wesener (2024)
114	*Prionobelum naevium* Donworth & Wesener, 2024	PP297649	NHMD 1184672	THAILAND, Yala Province, Than To District, Bang Lang National Park.	Donworth & Wesener (2024)
115	*Prionobelum naevium* Donworth & Wesener, 2024	PP297650	NHMD 1184673	THAILAND, Yala Province, Than To District, Bang Lang National Park.	Donworth & Wesener (2024)
116	*Sphaeromimus splendidus* Wesener & Sierwald, 2005	FJ409917	FMMC-INS 6702	MADAGASCAR, Sainte Luce S9	Wesener *et al*. (2010)

Resulting barcoding trees were visualized and annotated in FigTree (ver. 1.4.4, see https://github.com/rambaut/figtree/releases) (Rambaut 2018). Trees were rooted using *Arthrosphaera brandti* (Humbert, 1865), *Cryxus ovalis* (Linnaeus, 1758), *Epicyliosoma* sp., *Glomeris marginata* (Villers, 1789), *Prionobelum* spp., *Sphaerobelum* spp. and *Sphaeromimus splendidus* Wesener & Sierwald, 2005, selected based on previously published phylogenetic studies. Node support was considered strong when ML bootstrap (BS) exceeded 70% and Bayesian posterior probability (PP) exceeded 0.95. Interspecific and intraspecific genetic distances were calculated in MEGA 7 using uncorrected *p*-distances with pairwise deletion of missing data.

Results

COI genetic distances

The aligned COI sequences consisted of 658 base pairs, of which 373 sites were variable, 285 conserved, and 311 parsimony-informative. Genetic distances as a percentage between the most distantly related outgroups (*Arthrosphaera brandtii*, *Epicyliosoma* sp., and *Sphaeromimus splendidus*) and the large clade comprising *Zephronia*, *Sphaerobelum* Verhoeff, 1924, *Prionobelum* Verhoeff, 1924, and *Cryxus* Leach, 1814 ranged from 20.55 to 32.52%.

Intergeneric distances were as follows: between *Zephronia* and *Sphaerobelum* 6.85–25.27%, between *Zephronia* and *Prionobelum* 16.44–22.98%, and between *Zephronia* and *Cryxus* 18.02–23.38%.

Interspecific distances within genera ranged from 9.28–24.20% for *Zephronia*, 10.15–24.58% for *Sphaerobelum*, and 17.38–18.42% for *Prionobelum*.

For the two newly described species and additional newly collected material, the intraspecific genetic distances were as follows: *Z. sukhothaiensis* sp. nov. 0–1.07%, *Z. tratensis* sp. nov. 0–0.30%, *Z. macula* (between "green" and "spotted" morphs) 3.20–5.02%, and *Z. ovalis* (between Thai and Vietnamese populations) 0.61–5.63%.

The two new species are clearly distinguishable from other congeners, with interspecific genetic distances ranging from 11.26–21.19% for *Z. sukhothaiensis* Srimongkol & Srisonchai sp. nov. and 12.63–22.68% for *Z. tratensis* Srimongkol & Srisonchai sp. nov. (Supp. file 1).

COI-based barcoding tree

In both maximum likelihood (ML) and Bayesian inference (BI) analyses, the terminal clades were consistent and strongly supported, although the deeper nodes remained unresolved (Figs 1–2 and Supp. file 2). The low support values observed at these deeper nodes in both trees, based solely on the COI gene, are insufficient to reliably resolve the deeper relationships among species of *Zephronia*, *Sphaerobelum*, *Prionobelum*, and *Cryxus*. Because the primary focus of this study is the placement of the two newly described species, the ML tree was chosen as the main figure, as it provides a clearer overall topology and facilitates visualization of their positions. The BI tree is presented in Supp. file 2 for reference.

Despite topological differences, both ML and BI hypotheses consistently support the distinctiveness and positions of the two new species (Figs 1–2). In the ML tree, *Z. sukhothaiensis* Srimongkol & Srisonchai sp. nov. represents the earliest diverging lineage within the main *Zephronia* clade, while *Z. tratensis* Srimongkol & Srisonchai sp. nov. is recovered as the sister species to *Z. golovatchi* with strong bootstrap support (BS = 98) (Figs 1–2). In the BI tree *Z. sukhothaiensis* is placed as a sister taxon to *Z. erawani* (PP = 0.99), while *Z. tratensis* remains closely allied with *Z. golovatchi* (PP = 1.0) (Supp. file 2).

The northeastern Thai population of *Z. ovalis* formed a well-supported clade with the Vietnamese population, supporting their morphological similarity. Similarly, the "green" and "spotted" morphs of *Z. macula* from eastern Thailand are recovered as a strongly supported monophyletic group (BS = 100, PP = 1.0), corroborating the morphological observations (Figs 1–2) (see more details of both morphs in the section on *Z. macula* below).

Both newly described species grouped together with members of the *Zephronia* s. str. clade (*Z. chantaburiensis*, *Z. chrysomallos*, *Z. dawydoffi*, *Z. erawani*, *Z. golovatchi*, *Z. lannaensis*, *Z. laotica*, *Z. macula*, *Z. medogensis*, *Z. ovalis*, *Z. panhai*, *Z. siamensis*, and *Z. zhouae*). In the ML tree, this clade is well resolved, whereas in the BI analysis it collapses into a polytomy, reflecting the limitations of single-gene phylogenetic inference (Figs 1–2 and Supp. file 2).

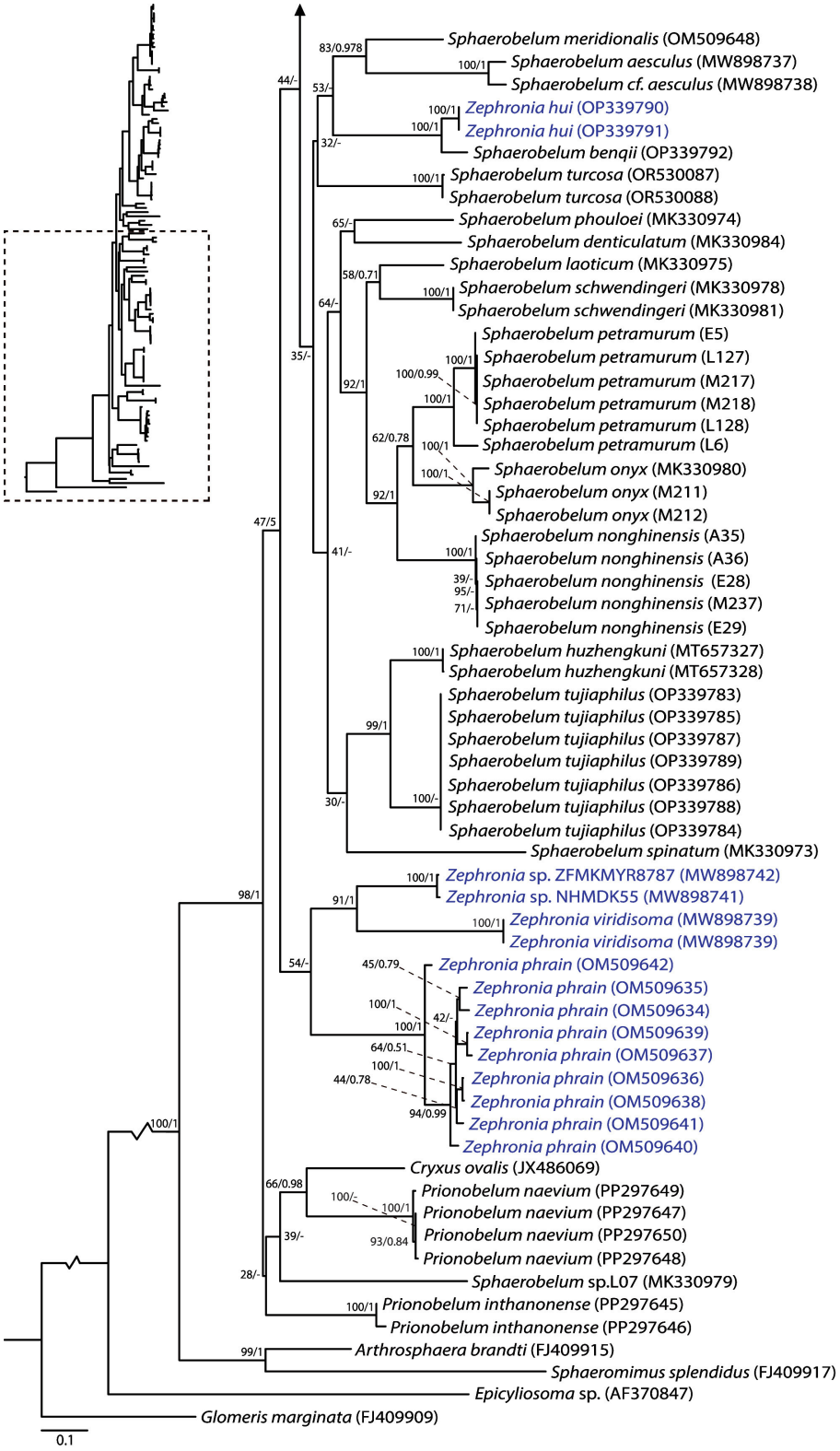

Fig. 1. COI-based barcoding tree of the genus *Zephronia* Gray, 1832 (part 1), inferred using maximum likelihood (ML) analysis. Numbers at the nodes indicate bootstrap support (BS) from ML and posterior probabilities (PP) from Bayesian inference (BI), shown as ML/BI. A hyphen "-" at nodes indicates a different topology between the ML and BI analyses. The scale bar represents branch length. The blue letters represent species of the genus *Zephronia*, while the black letters indicate other genera.

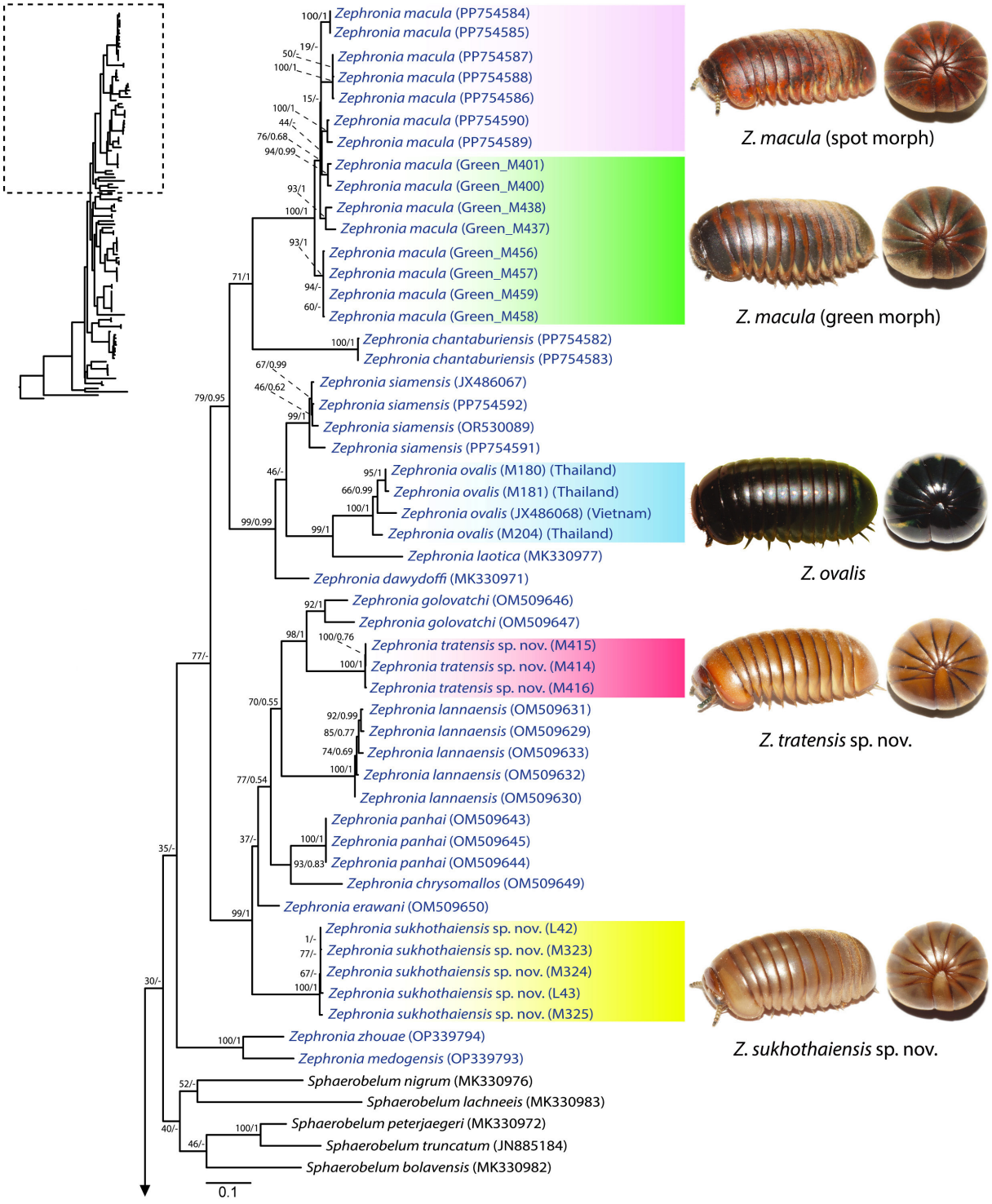

Fig. 2. COI-based barcoding tree of the genus *Zephronia* Gray, 1832 (part 2), inferred from a maximum likelihood (ML) analysis. Numbers at the nodes indicate bootstrap support (BS) from ML and posterior probabilities (PP) from Bayesian inference (BI), shown as ML/BI. A hyphen "-" at nodes indicates a different topology between the ML and BI analyses. The scale bar represents branch length. Background colours indicate species: purple = *Z. macula* Srisonchai & Wesener, 2024 "spotted" morph; green = *Z. macula* "green" morph; sky blue = *Z. ovalis* Gray, 1832; pink = *Z. tratensis* Srimongkol & Srisonchai sp. nov.; yellow = *Z. sukhothaiensis* Srimongkol & Srisonchai sp. nov. Scale bar represents branch length.

Taxonomy

Class Diplopoda de Blainville in Gervais, 1844
Order Sphaerotheriida Brandt, 1833
Family Zephroniidae Gray, 1843
Subfamily Zephroniinae Gray, 1843
Tribe Zephroniini Jeekel, 2001

Genus ***Zephronia*** Gray, 1832

Type species

Zephronia ovalis Gray, 1832.

Species members

57 species, including the two species described herein.

Distribution

Cambodia, China, Himalaya, Hongkong, India (NE), Indonesia (Borneo), Laos, Malaysia, Myanmar, Nepal, Singapore, Sumatra, Thailand and Vietnam.

Differential diagnosis

See differential diagnosis for *Zephronia* and *Zephronia* s. str. in Srisonchai *et al*. (2024: 38).

Zephronia can be distinguished from all other genera of Zephroniinae by the following combination of characters: antennae flattened laterally, usually axe-shaped, with numerous (>4) apical cones; tarsi of legs 5–21 often bearing more than one apical spine and several ventral spines; anterior telopods with four podomeres distal to syncoxite; telopoditomere 2 with a large, curved process forming a clamp-like; telopoditomeres 3 and 4 simple; posterior telopod with four telopoditomeres; immovable finger slender, apically curved towards telopoditomeres 3 and 4, always with two membranous lobes; telopoditomere 3 with a membranous lobe and a row of conspicuous, crenulated, sclerotized teeth; telopoditomere 4 also with a membranous lobe, and with 1 or 2 sclerotized spines.

For a more detailed differential diagnosis of *Zephronia* and *Zephronia* s. str., see Srisonchai *et al*. (2024: 38).

***Zephronia* s. str.**

Zephronia s. str. currently includes 20 species: *Z. chantaburiensis* Srisonchai & Wesener, 2024, *Z. chrysomallos* Bhansali & Wesener, 2022, *Z. dawydoffi* Attems, 1953, *Z. enghoffi* Srisonchai, Sutcharit & Likhitrakarn, 2021, *Z. erawani* Bhansali & Wesener, 2022, *Z. golovatchi* Srisonchai, Sutcharit & Likhitrakarn, 2021, *Z. hui* Liu & Wesener, 2022, *Z. konkakinhensis* Semenyuk *et al*., 2018, *Z. lannaensis* Likhitrakarn & Golovatch, 2021, *Z. laotica* Wesener, 2019, *Z. macula* Srisonchai & Wesener, 2024, *Z. medongensis* Zhao & Liu, 2022, *Z. montis* Semenyuk *et al*., 2018, *Z. ovalis* Gray, 1832, *Z. panhai* Srisonchai, Sutcharit & Likhitrakarn, 2021, *Z. phrain* Likhitrakarn & Golovatch, 2021, *Z. siamensis* Hirst, 1907, *Z. sukhothaiensis* Srimongkol & Srisonchai sp. nov., *Z. tratensis* Srimongkol & Srisonchai sp. nov., and *Z. zhouae* Zhao & Liu, 2022.

List of 14 species of *Zephronia* occurring in Thailand

All 14 species of *Zephronia* in Thailand are as follows: *Z. chantaburiensis*, *Z. chrysomallos*, *Z. enghoffi*, *Z. erawani*, *Z. golovatchi*, *Z. lannaensis*, *Z. macula*, *Z. ovalis*, *Z. panhai*, *Z. phrain*, *Z. siamensis*, *Z. sukhothaiensis* Srimongkol & Srisonchai sp. nov., *Z. tratensis* Srimongkol & Srisonchai sp. nov. and *Z. viridisoma*.

Zephronia chantaburiensis Srisonchai & Wesener, 2024
Figs 2–3

Zephronia chantaburiensis Srisonchai & Wesener in Srisonchai *et al*., 2024: 39.

Distribution

Chanthaburi Province (Fig. 3).

Remarks

Endemic. Known to occur in granitic habitats. See Srisonchai *et al*. (2024: figs 2–7).

Zephronia chrysomallos Bhansali & Wesener, 2022
Figs 2–3, 4A–F

Zephronia chrysomallos Bhansali & Wesener, 2022: 367.

Zephronia chrysomallos – Likhitrakarn *et al*. 2023: 56.

Distribution

Kanchanaburi Province (Fig. 3).

Remarks

Endemic. Known to occur in limestone habitats. See Bhansali & Wesener (2022: figs 7–11).

Zephronia enghoffi Srisonchai, Sutcharit & Likhitrakarn, 2021
Figs 3, 5A–F

Zephronia enghoffi Srisonchai, Sutcharit & Likhitrakarn, 2021: 32.

Zephronia enghoffi – Likhitrakarn *et al*. 2023: 56.

Distribution

Khon Kaen and Loei Provinces (Fig. 3).

Remarks

Endemic. Known to occur in limestone habitats. See Srisonchai *et al*. (2021: figs 7–8).

Zephronia erawani Bhansali & Wesener, 2022
Figs 2–3, 4G–L

Zephronia erawani Bhansali & Wesener, 2022: 370.

Zephronia erawani – Likhitrakarn *et al*. 2023: 56.

Distribution

Kanchanaburi Province (Fig. 3).

Remarks

Endemic to limestone habitats. See Bhansali & Wesener (2022: figs 12–14).

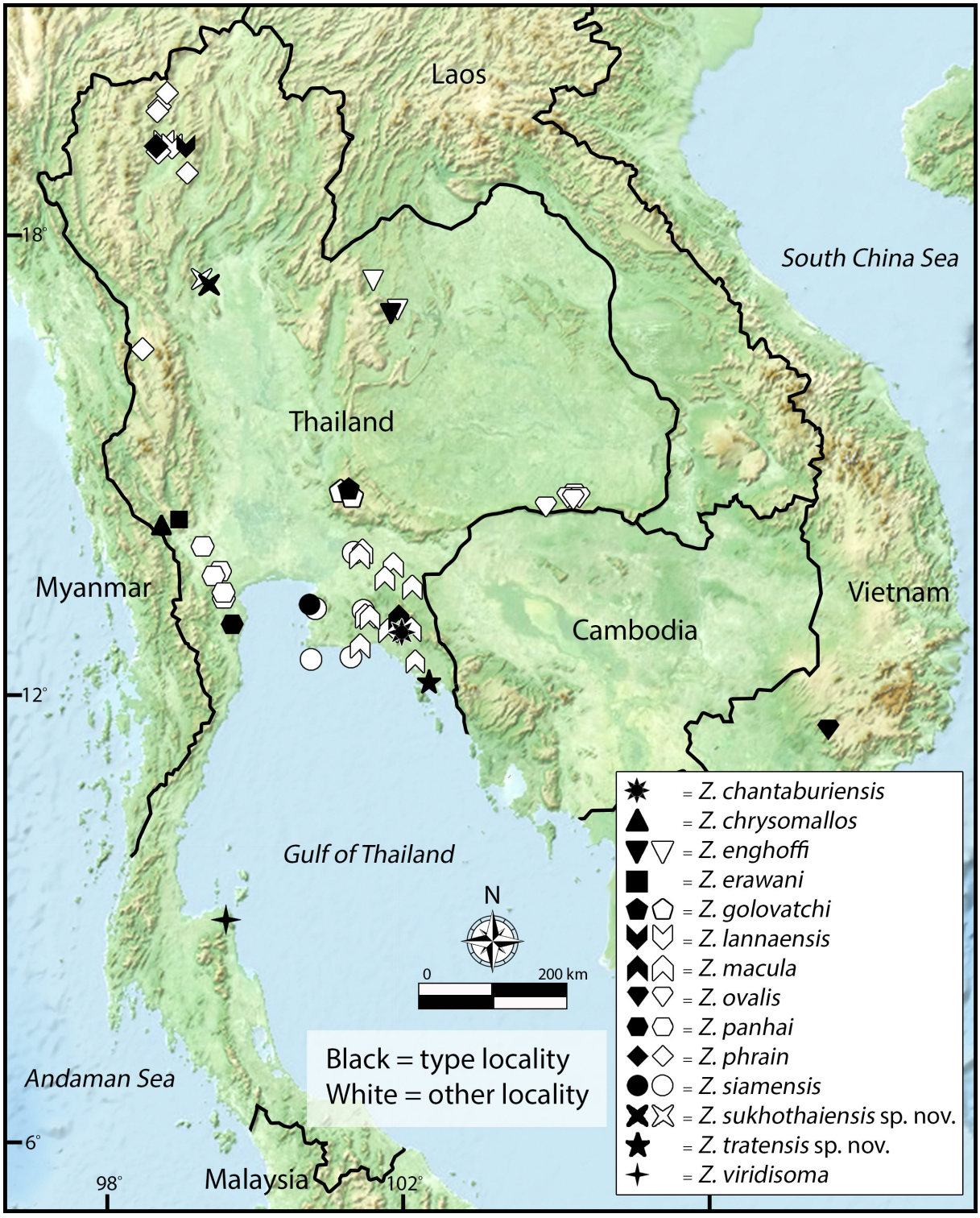

Fig. 3. Distribution map of *Zephronia* Gray, 1832 in Thailand and nearby areas. Identical shapes of both black and white symbols represent same species.

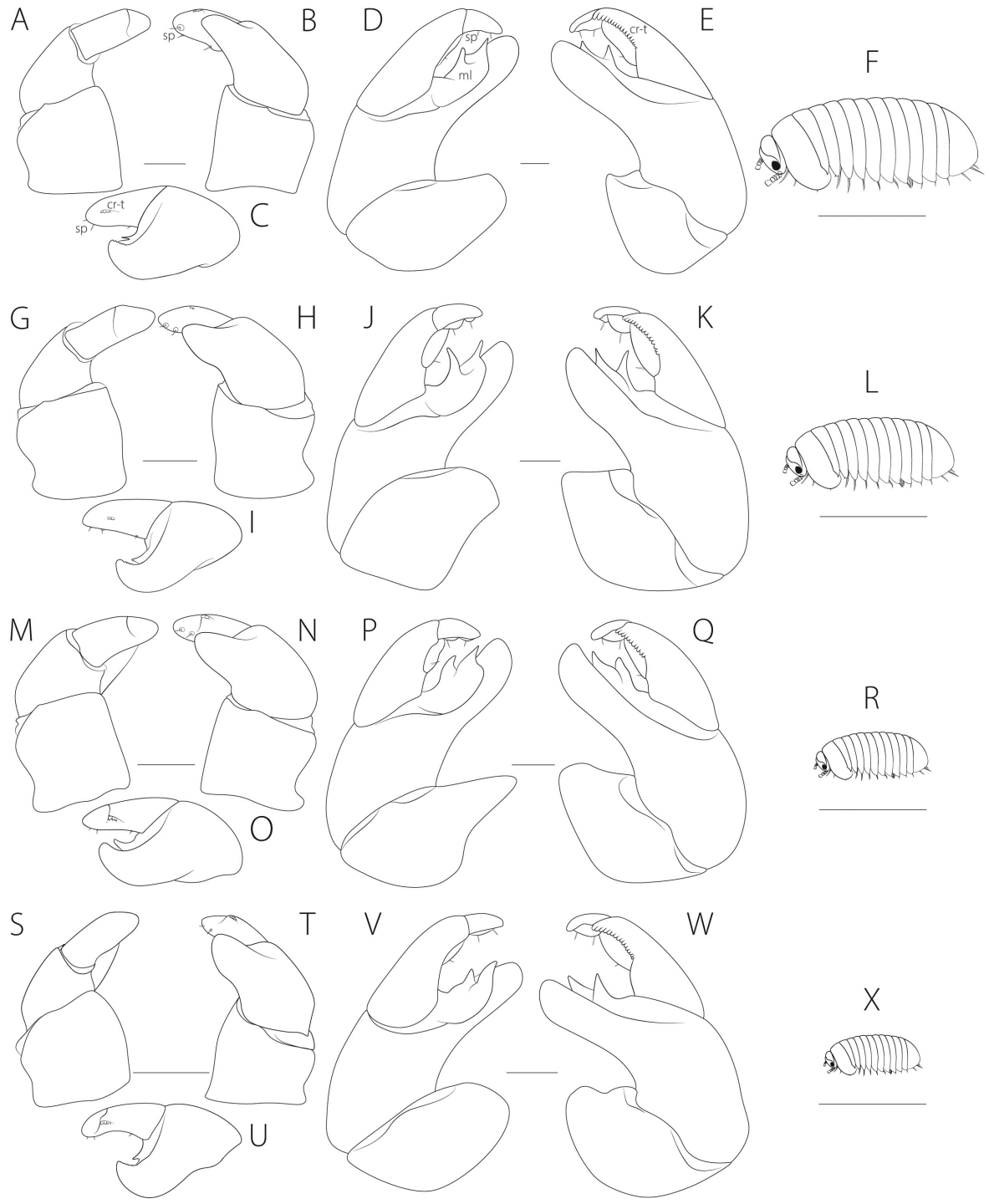

Fig. 4. Line drawings of male telopods and average body length of *Zephronia sukhothaiensis* Srimongkol & Srisonchai sp. nov. (paratype), compared with the three closely related species. **A**–**F**. *Zephronia chrysomallos* Bhansali & Wesener, 2022. **G**–**L**. *Zephronia erawani* Bhansali & Wesener, 2022. **M**–**R**. *Zephronia panhai* Srisonchai, Sutcharit & Likhitrakarn, 2021. **S**–**X**. *Zephronia sukhothaiensis* Srimongkol & Srisonchai sp. nov. **A**–**C**, **G**–**I**, **M**–**O**, **S**–**U**. Left anterior telopods. **D**–**E**, **J**–**K**, **P**–**Q**, **V**–**W**. Left posterior telopods. **F**, **L**, **R**, **X**. Comparison of average body length of each species. **A**, **D**, **G**, **J**, **M**, **P**, **S**, **V**. Anterior views. **B**, **E**, **H**, **K**, **N**, **Q**, **T**, **W**. Posterior views. **C**, **I**, **O**, **U**. Lateral views. Abbreviations: cr-t = crenulated teeth; ml = membranous lobe; sp = sclerotized spine. Scale bars: A–E, G–K, M–Q, S–W = 0.5 mm; F, L, R, X = 20 mm.

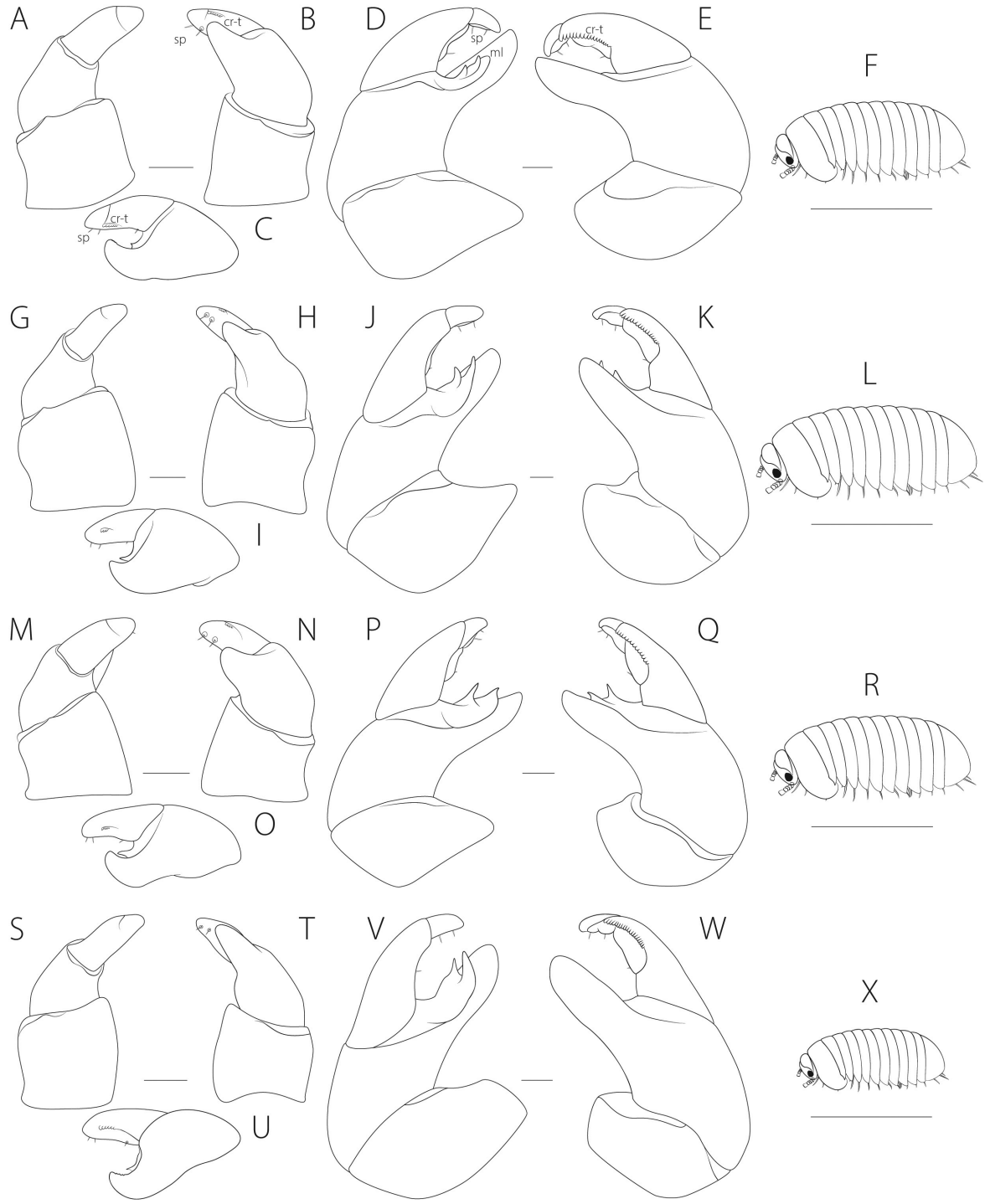

Fig. 5. Line drawings of male telopods and average body length of *Zephronia tratensis* Srimongkol & Srisonchai sp. nov. (paratype) compared with the three closely related species. **A**–**F**. *Zephronia enghoffi* Srisonchai, Sutcharit & Likhitrakarn, 2021. **G**–**L**. *Zephronia golovatchi* Srisonchai, Sutcharit & Likhitrakarn, 2021. **M**–**R**. *Zephronia lannaensis* Likhitrakarn & Golovatch, 2021. **S**–**X**. *Zephronia tratensis* Srimongkol & Srisonchai sp. nov. **A**–**C**, **G**–**I**, **M**–**O**, **S**–**U**. Left anterior telopods. **D**–**E**, **J**–**K**, **P**–**Q**, **V**–**W**. Left posterior telopods. **F**, **L**, **R**, **X**. Comparison of average body length of each species. **A**, **D**, **G**, **J**, **M**, **P**, **S**, **V**. Anterior view. **B**, **E**, **H**, **K**, **N**, **Q**, **T**, **W**. Posterior view. **C**, **I**, **O**, **U**. Lateral view. Abbreviations: cr-t = crenulated teeth; ml = membranous lobe; sp = sclerotized spine. Scale bars: A–E, G–K, M–Q, S–W = 0.5 mm; F, L, R, X = 20 mm.

Zephronia golovatchi Srisonchai, Sutcharit & Likhitrakarn, 2021
Figs 2–3, 5G–L

Zephronia golovatchi Srisonchai, Sutcharit & Likhitrakarn, 2021: 37.

Zephronia golovatchi – Bhansali & Wesener 2022: 376. — Likhitrakarn *et al*. 2023: 56.

Distribution

Nakhon Ratchasima and Nakhon Nayok Provinces (Fig. 3).

Remarks

Endemic. Known to occur in both limestone and sandstone habitats. See Srisonchai *et al*. (2021: figs 9–10).

Zephronia lannaensis Likhitrakarn & Golovatch, 2021
Figs 2–3, 5M–R

Zephronia lannaensis Likhitrakarn & Golovatch in Likhitrakarn *et al*., 2021: 13.

Zephronia lannaensis – Bhansali & Wesener 2022: 376. — Likhitrakarn *et al*. 2023: 56.

Distribution

Chiang Mai Province (Fig. 3).

Remarks

Endemic. This species was found in a dipterocarp forest (granitic habitat). See Likhitrakarn *et al*. (2021: figs 3–4)

Zephronia macula Srisonchai & Wesener, 2024
Figs 2–3, 6–9, 22A–B, 23A–B

Zephronia macula Srisonchai & Wesenerin Srisonchai *et al*., 2024: 48.

Diagnosis (updated from Srisonchai *et al*. 2024)

Zephronia macula belongs to the *Zephronia* s. str. species group based on the position of Tömösváry's organ, located next to the aberrant ocelli, not inside the antennal socket. Adult body length 8.6–18.5 mm; posterior margin of midbody endotergum flat, not modified in green morph but relatively undulate in spotted morph; posterior telopods usually with 9 or 10 crenulated teeth, and tarsi of legs 3–21 with only one apical spine. Similar in these aspects to *Z. chantaburiensis*, but differs from it by having a combination of the following characters: apical disc of antenna with 38–57 cones (vs 25–35 cones); femur of walking legs less widened, slightly longer than wide (vs wider than long in *Z. chantaburiensis*), mesal margin of operculum of vulva round and not protruding (vs more slender and slightly protruding). See also Table 2.

Material examined

THAILAND • 6 ♂♂, 11 ♀♀; Chachoengsao Province, Phanom Sarakham District, Wat Khao Hin Sorn; 13°45′36.0″ N, 101°30′44.0″ E; 69 m a.s.l.; 1 Jun. 2023; N. Srimongkol and MZKKU students leg.; MZKKU • 5 ♂♂, 18 ♀♀; same locality as for preceding; 13°45′35.8″ N, 101°30′43.7″ E; 71 m a.s.l.; 15 Jun. 2023; N. Srimongkol, R. Srisonchai and MZKKU students leg.; MZKKU • 42 ♂♂, 54 ♀♀;

Table 2 (continued on next two pages). Morphological comparison between the two new species and related species of *Zephronia* Gray, 1832.

Species	Morphological characters								
	Body size (mm)	**Colouration**	**Apical cone on antenna**	**Endotergum of midbody tergite (posterior margin = pm, row of bristles, tip of bristles)**	**Legs 5–21 (apical spine = a, ventral spine = v)**	**Subanal plate (shape, apical margin)**	**Anterior telopods (length of immovable finger = imf vs movable finger = mf, crenulated teeth = cr-t)**	**Posterior telopods (length of immovable finger = imf vs movable finger = mf, (crenulated teeth = cr-t)**	**Female vulva (shape, width dorsoventrally, apical margin of operculum)**
Z. chantaburiensis Srisonchai & Wesener, 2024	♂ = 19–23, ♀ = 19–22	brown	♂ = 30–41, ♀ = 25–35	• flat/regular • 1 row • slightly protruding above pm	a = 1, v = 7–9	• semicircular • strongly concave	• imf = mf • 2 cr-t	• imf > mf • 9–12 cr-t	• slender • narrow • protruding into an oval-like lobe
Z. chrysomallos Bhansali & Wesener, 2022	ca 40	greyish brown	78/88	• flat/regular • 2 rows • not reaching to pm (reaching ⅘ of outer area)	a = 3 or 4, v = 10–12	NA	• imf < mf • 4 cr-t	• imf < mf • 17 or 18 cr-t	NA
Z. dawydoffi Attems, 1953	11–13	dark green	♂ = 39–43	• modified to small lobes, 'rectangle-wavy' margin • 2 rows • not reaching to pm	a = 2–4, v = 7–9	• trapeziform • slightly concave	• imf < mf • 4 cr-t	• imf < mf (as long as telopoditomere 3) • 8–10 cr-t	• round • wide • not protruding
Z. enghoffi Srisonchai & Likhitrakarn, 2021	♂ = 29–33, ♀ = 30–36	light brown to brown	ca 75	• flat/regular • 2 rows • extended over pm	a = 1–3, v = 7–10	• subsemicircular • shallowly concave	• imf = mf • 6 cr-t	• imf = mf • 17–19 cr-t	• slender • slightly narrow • not protruding
Z. erawani Bhansali & Wesener, 2022	31.4	greyish brown	91/96	• flat/regular • 3 rows • not extended beyond pm (reaching ⅘ of outer area)	a = 2 or 3, v = 8–10	NA	• imf < mf • 2 cr-t	• imf < mf • 15 cr-t	NA
Z. golovatchi Srisonchai & Likhitrakarn, 2021	♂ = 35–36.5, ♀ = 35–37	brown	90–100	• flat/regular • 2 rows • extended over pm	a = 1–3, v = 8–12	• trapeziform • strongly concave	• imf < mf • 2 or 3 cr-t	• imf < mf • 17 or 18 cr-t	• round • wide • not protruding
Z. lannaensis Likhitrakarn & Golovatch, 2021	♂ = 28.8–36.2, ♀ = 31.8–38.2	light brown to brown	♂ = 43–72, ♀ = 53–68	• flat/regular • 2–3 rows • not reaching to pm	a = 3(2)–5, v = 10–12	• semicircular • slightly concave	• imf < mf • 3 or 4 cr-t	• imf = mf • 12–17 cr-t	• round • wide • not protruding
Z. laotica Wesener, 2019	♂ = 15.6, ♀ ca 14.1	bright green (posterior half of tergite light brown)	♂ = 61/65, ♀ = 32/34	• modified to lobes, 'rectangle-wavy' margin • 1–2 rows • extended over pm	a = 3–5, v = 7–9	• triangular • well-rounded, sometimes slightly concave	• imf < mf • without any teeth	• imf = mf • 11 cr-t	• round • wide • not protruding

Table 2 (continued). Morphological comparison between the two new species and related species of *Zephronia* Gray, 1832.

Species	Morphological characters								
	Body size (mm)	**Colouration**	**Apical cone on antenna**	**Endotergum of midbody tergite (posterior margin = pm, row of bristles, tip of bristles)**	**Legs 5–21 (apical spine = a, ventral spine = v)**	**Subanal plate (shape, apical margin)**	**Anterior telopods (length of immovable finger = imf vs movable finger = mf, crenulated teeth = cr-t)**	**Posterior telopods (length of immovable finger = imf vs movable finger = mf, (crenulated teeth = cr-t)**	**Female vulva (shape, width dorsoventrally, apical margin of operculum)**
Z. macula Srisonchai & Wesener, 2024 (spotted morph)	♂ = 18–20, ♀ = 18–20	brown/ greenish brown/ reddish brown	♂ = 48–57, ♀ = 36–43	• flat/regular • 1 row • reaching to pm	a = 1, v = 7–9	• semicircular • slightly concave, rarely truncate or obtuse	• imf = mf • 2 or 3 cr-t	• imf = mf • 9 or 10 cr-t	• round • wide • not protruding
Z. macula Srisonchai & Wesener, 2024 (green morph)	♂ = 8.6–17, ♀ = 12.5–18.5	dark green	♂ = 36–38, ♀ = 22–24	• modified, undulate • 1 row • extended beyond pm	a = 1, v = 5–9	• semicircular • truncate, sometimes slightly concave	• imf = mf • 2 or 3 cr-t	• imf = mf • 9 or 10 cr-t	• round • wide • not protruding
Z. ovalis Gray, 1832 (Vietnam)	♂ = 14.7, ♀ = 17.5–18.9	dark olive blackish (tergites dorsally with two golden-yellow stripes)	♂ = 62–65, ♀ = 71–73	• modified (margin well-rounded) • 3 rows • extended over pm	a = 2 or 3, v = 6–8	• trapeziform • truncate, sometimes slightly concave	• imf < mf • 3 or 4 cr-t	• imf = mf • 16 cr-t	• slightly round • wide • not protruding
Z. ovalis Gray, 1832 (Thailand)	♂ = 7–10.8, ♀ = 7.2–12.5	greenish dark or dark olive green, (tergites dorsally with two yellowish patches	♂ = 35–47, ♀ = 35–43	• modified to trapezoidal lobes, trapezoidal-wavy • 2 rows • not reaching to pm	a = 1–3, v = 3–6	• trapeziform • slightly concave	• imf = mf • 1 or 2 cr-t (small)	• imf > mf • 8 or 9 cr-t	• slightly round • wide • slightly protruding
Z. panhai Srisonchai & Likhitrakarn, 2021	♂ = 19–22, ♀ = 20–23	light grey	ca 50	• flat/regular • 2 rows • not extended over pm or not reaching pm	a = 1–3, v = 7–11	• trapeziform • slightly round/ truncate	• imf < mf • 3 cr-t	• imf < mf • 11–12 cr-t	• slightly concave • slightly narrow (sometimes wide) • not protruding

Table 2 (continued). Morphological comparison between the two new species and related species of *Zephronia* Gray, 1832.

Species	Morphological characters								
	Body size (mm)	**Colouration**	**Apical cone on antenna**	**Endotergum of midbody tergite (posterior margin = pm, row of bristles, tip of bristles)**	**Legs 5–21 (apical spine = a, ventral spine = v)**	**Subanal plate (shape, apical margin)**	**Anterior telopods (length of immovable finger = imf vs movable finger = mf, crenulated teeth = cr-t)**	**Posterior telopods (length of immovable finger = imf vs movable finger = mf, (crenulated teeth = cr-t)**	**Female vulva (shape, width dorsoventrally, apical margin of operculum)**
Z. phrain Likhitrakarn & Golovatch, 2021	♂ = 29.5–41.2, ♀ = 33.2–40.6	dark olive• green to bright green	♂ = 72–89, ♀ = 52–71	• flat/regular • 4–6 rows • not reaching to pm	a = 2–4, v = 7–11	• semicircular • undivided	• imf = mf • inconpicuous	• imf < mf • 5–6 cr-t	• round • narrow • not protruding
Z. siamensis Hirst, 1907	♂ = 15–26.5, ♀ = 15–23	dark green (tergites dorsally with two brown/ yellowish brown patches)	♂ = 51–61, ♀ = 49–54	• modified to lobes, 'rectangle-wavy' margin • 1 row • not extended over pm or not reaching to pm	a = 2 or 3, v = 5–9	• semicircular • concave	• imf < mf • 7 cr-t	• imf < mf • 11 or 12 cr-t	• regularly round • wide • not protruding
Z. sukhothaiensi sp. nov.	♂ = 15.8–18.3, ♀ = 16.5–22.9	brownish grey	♂ = 38–45, ♀ = 24–36	• flat/regular • 1 row • not reaching to pm	a = 3, v = 7–10	• trapeziform • slightly concave/ truncate	• imf < mf • 3–4 cr-t	• imf < mf • 10–12 cr-t	• slightly round • narrow • projecting into a well-rounded lobe
Z. tratensis sp. nov.	♂ = 19.1–28.5, ♀ = 22.8–32	light brown (golden brown)	♂ = 80–85, ♀ = 60–65	• flat/regular • 2 rows • reaching to pm or extended beyond pm	a = 3, v = 7–12	• semicircular • slightly round or convex	• imf > mf • 3–4 cr-t	• imf > mf • 21 or 22 cr-t	• slightly concave • wide • not protruding
Z. viridisoma Rosenmejer & Wesener, 2021	♂ = 25.6 (based on holotype) ♀ = 25.6 (based on female paratype)	green	♂ = 32/44, ♀ = 25/25	• flat/regular • 3 row • extended beyond pm	a = 1, v = 5 or 6	• well-rounded • N/A	• imf < mf • 3 cr-t	• imf < mf • 8 or 9 cr-t	• slender • narrow • slightly protruding

Rayong Province, Khao Chamao District, Wat Tham Suwan Phupha; 12°59′21.3″ N, 101°39′33.1″ E; 64 m a.s.l.; 14 Jun. 2023; N. Srimongkol, R. Srisonchai and MZKKU students leg.; MZKKU • 5 ♂♂, 1 ♀; Sa Kaeo Province, Khao Chakan District, Wat Tham Khao Chan; 13°34′44.8″ N, 102°05′33.6″ E; 100 m a.s.l.; 13 Jun. 2023; N. Srimongkol, R. Srisonchai and MZKKU students leg.; MZKKU.

All specimens described by Srisonchai *et al*. (2024) consistently exhibit distinctive spots on their tergites. In contrast, the newly collected specimens lack any such markings on their bodies. We therefore refer to the spotted specimens as the "spotted" morph and those without spots as the "green" morph.

Type locality

Thailand, Chanthaburi Province, Tha Mai District, Wat Khao Sukim.

Description of "green" morph specimens

Measurements. Males: body length 8.6–17.0 mm; width (=broadest) of head=3.3–5.3 mm, of collum=3.0–5.1 mm, of thoracic shield=4.6–8.6 mm, of tergite 7=4.7–8.5 mm, of anal shield=4.5–7.2 mm; height (=highest) of head=2.0–2.6 mm, of collum ca 2.8–3.7 mm, of thoracic shield ca 3.2–4.8 mm, of tergite 7 ca 3.4–5.2 mm, of anal shield ca 3.2–4.6 mm. Females: body length 12.5–18.5 mm; width (=broadest) of head=4.0–5.4 mm, of collum=3.6–5.2 mm, of thoracic shield=6.1–8.9 mm, of tergite 7=6.2–9.3 mm, of anal shield=5.2–8.3 mm; height (=highest) of head=2.1–3.0 mm, of collum ca 3.2–4.0 mm, of thoracic shield=3.5–5.3 mm, of tergite 7=3.7–6.2 mm, of anal shield=3.6–5.4 mm.

Colouration (Fig. 6C–F). Live specimens brownish green. Antennae, head, collum and thoracic shield dark green. Paratergites brown. Legs bluish green. Tergites without spots (here referred to "green" morph); anterior part of tergites brown; lateral and posterior parts of tergites dark green. Posterior half of anal shield brown contrast with dark green anterior one. Colour in alcohol after one year of preservation changed to greenish brown.

Head (Fig. 7A). Trapeziform. Anterior part of clypeus (cl) clothed with numerous long setae; central part covered with numerous short setae; posterior part sparsely punctate. Anterior margin of labrum with a single tooth. Each eye with 50–52 ommatidia (o). Aberrant ocellus located at brim of antennal groove.

Antenna (Figs 7A, 8A–D). Short; with rounded joints; covered by long and dense setae. Last antennomere (antennomere 6) extending posteriorly to tarsus of leg-pair 2; with sensilla basiconica (sb) surrounding apical disc (ad). Lengths of antennomeres: 6>5>4>3>2=1. Antennomere 6 thickened and stout, widened apically, axe-shaped. Shape of antennae sexually dimorphic, in female more cylindrical, strongly flattened in male. Apical disc with 36–38 apical cones (ac) in males and 22–24 cones in females. No sclerotized crest/ridge between antennal socket and ommatidia.

Tömösváry's organ (Fig. 7A–C). Tömösváry's organ (to) distinctly separated from ommatidium, located close to anterior margin of ommatidia, not inside antennal socket. Smaller in size than an individual ommatidium, with dentate inner structure.

Epipharynx (Fig. 7D). Apically with single central tooth (ct), centrally (inner region) with one conspicuous and swollen sclerotized plate (inner tooth), laterally surrounded by single row of conical spines (row of spines=rsp), outer area (next to row of spines) with group of long spines (external teeth=et), with ca 20 small cuticular scales (cs) at base of each side.

Gnathochilarium (Fig. 7E–I). Lamellae linguales (ll) oval, conspicuous. Central pads (cpd) modified, with two types of sensory cones (sc), large one with a pillow and small one without pillow. Stipites (st) stout. Mentum (me) large, broad, fused; laterally protruding. Inner palpi (ip) with numerous sensory

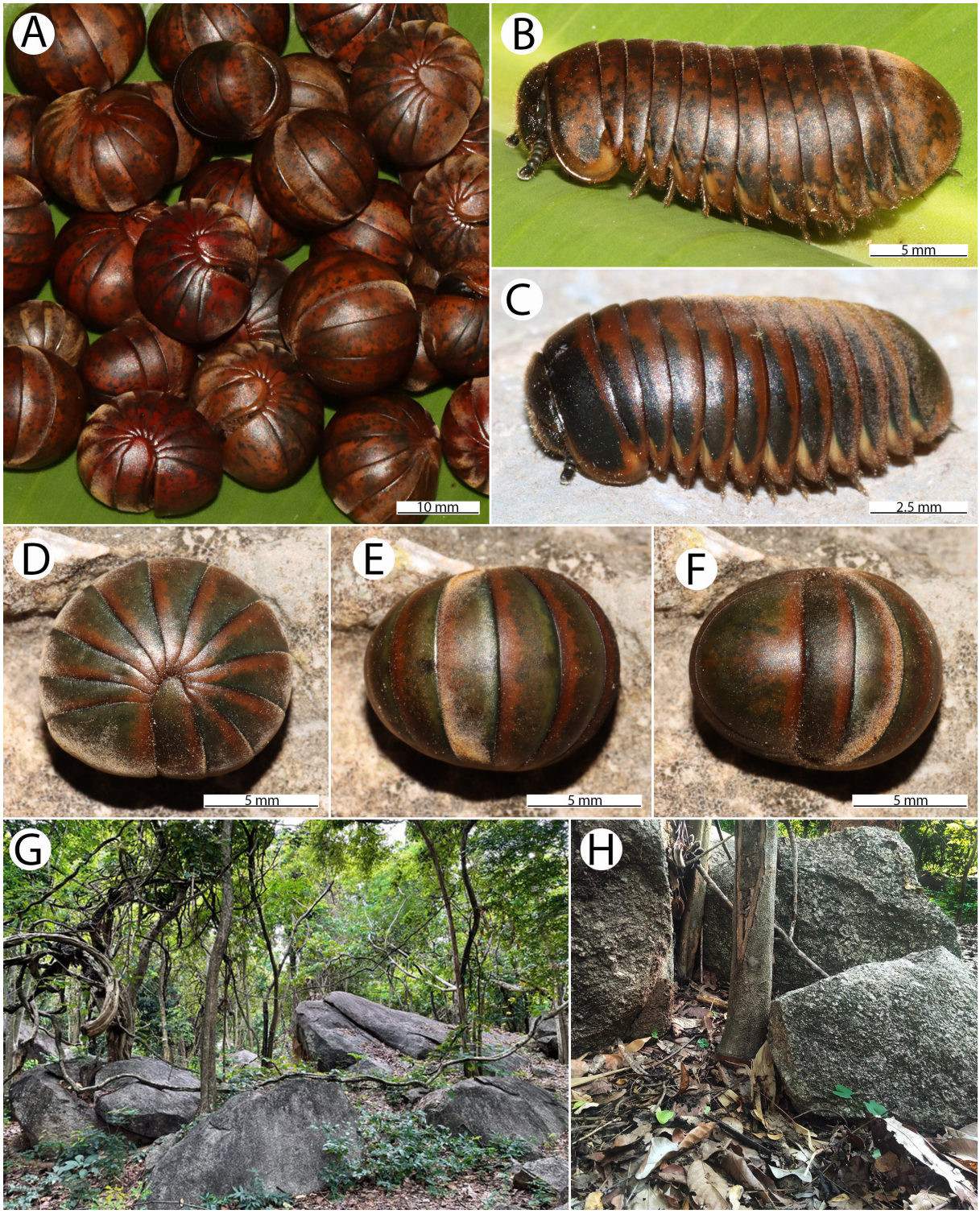

Fig. 6. Photographs of live *Zephronia macula* Srisonchai & Wesener, 2024 and habitat. **A–B**. Specimens from Chanthaburi Province described by Srisonchai *et al*. (2024), "spotted" morph (paratypes CUMZ-zeph0016). **C–F**. Newly collected "green" morph specimens from Wat Khao Hin Sorn, Chachoengsao Province and Wat Tham Khao Chan, Sa Kaeo Province, respectively. **G–H**. Habitat at Wat Khao Hin Sorn.

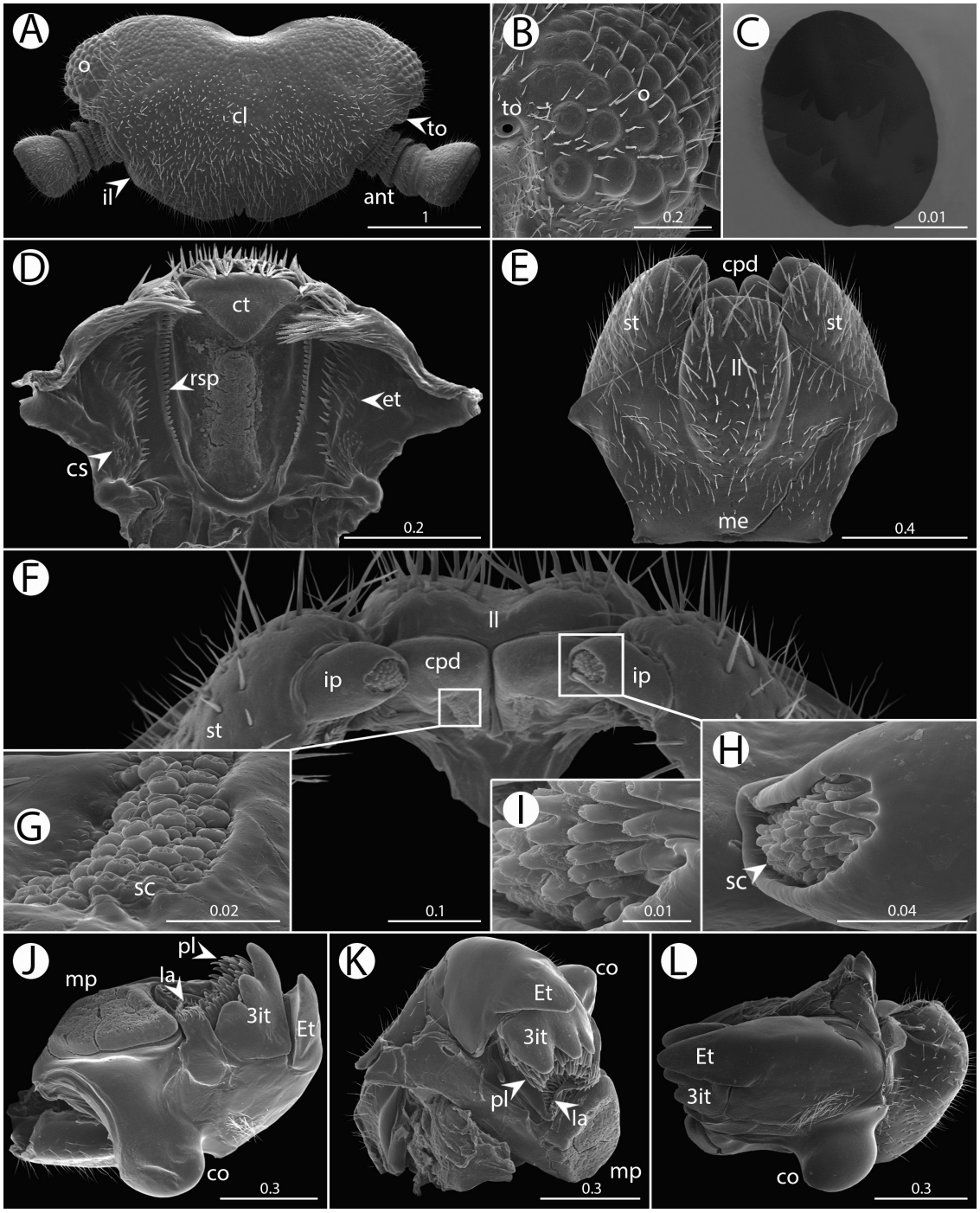

Fig. 7. *Zephronia macula* Srisonchai & Wesener, 2024, a male specimen from Wat Khao Hin Sorn, Chachoengsao Province, Thailand — SEM. **A**. Head, anterior view. **B**. Left ommatidia, lateral view. **C**. Left Tömösváry's organ, lateral view. **D**. Epipharynx, ventral view. **E–F**. Gnathochilarium, ventral and frontal views, respectively. **G**. Left central pad, frontal view. **H–I**. Right lateral palpi, frontal view. **J–L**. Right mandible, dorsal, mesal and anterior views, respectively. Abbreviations: 3it = 3-combed inner tooth; ant = antenna; cl = clypeus; co = condylus; cpd = central pad; cs = cuticular scales; ct = central tooth; et = external tooth of epipharynx; Et = external tooth of mandible; Ia = inner area of mandible; il = incisura lateralis; ip = inner palpi; ll = lamellae lingulales; me = mentum; mp = molar plate; o = ommatidia; pl = pectinate lamellae; rsp = row of spines; sc = sensory cone; st = stipites; to = organ of Tömösváry. Scale bars in micrometres (μm).

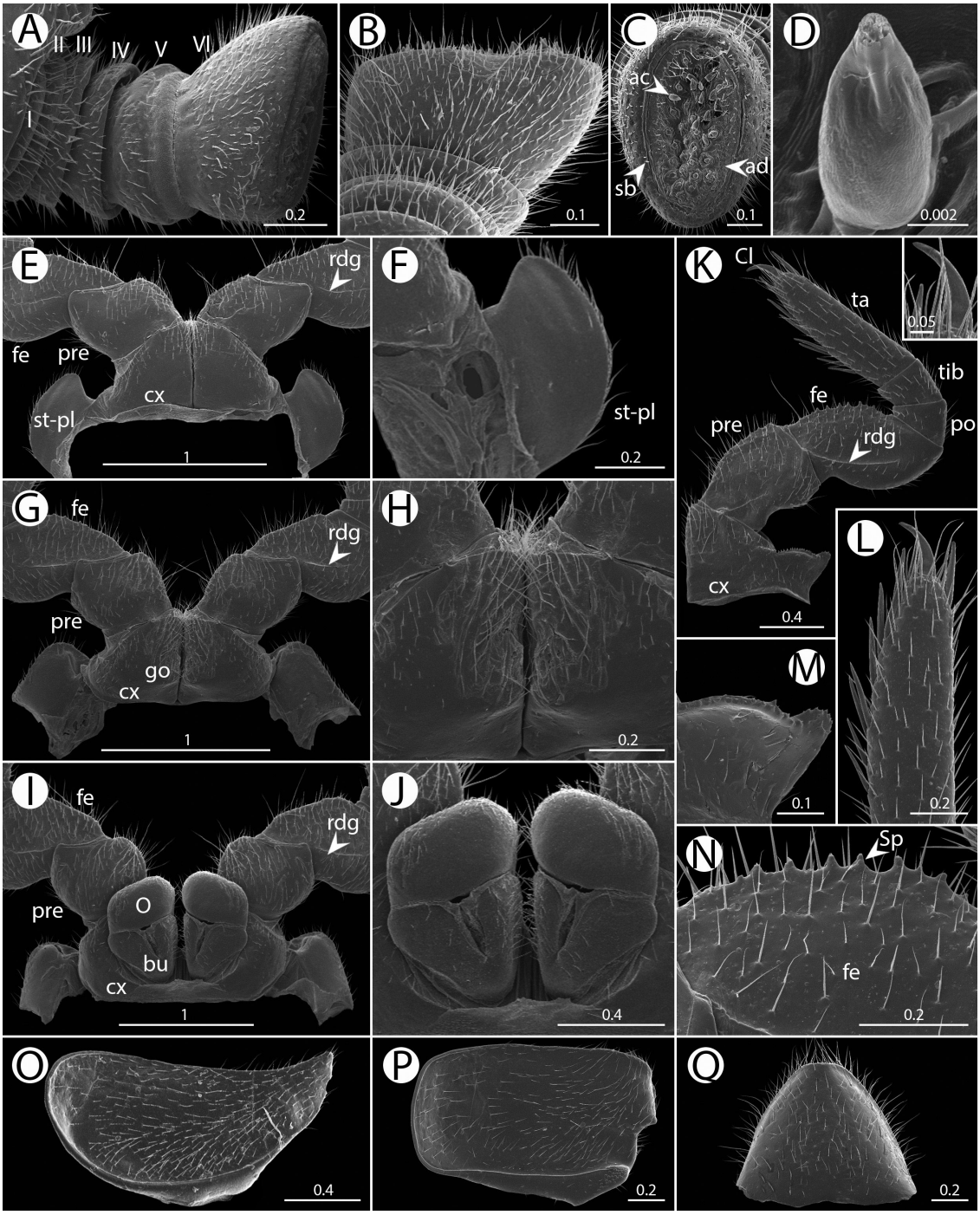

Fig. 8. *Zephronia macula* Srisonchai & Wesener, 2024, specimens from Wat Khao Hin Sorn, Chachoengsao Province, Thailand — SEM. **A–H**, **K–P**. Male. **I–J**, **Q**. Female. **A–B**. Antenna, anterior and mesal views. **C–D**. Antennal disc and apical cone. **E–F**. First coxae with stigmatic plates, posterior views. **G–H**. Coxae of legs 2 with gonopores, posterior views. **I–J**. Coxae of legs 2 with vulvae, posterior view. **K–L**. Left leg 10, posterior views. **M**. Left coxal process on leg 10, posterior view. **N**. Femur of left leg 10, posterior view. **O**. Right first pleurite, ventral view. **P**. Right midbody pleurite, ventral view. **Q**. Subanal plate, ventral view. Abbreviations: ac = apical cone; ad = antennal disc; bu = bursa; Cl = claw; cx = coxa; fe = femur; go = gonopore; O = operculum; po = postfemur; pre = prefemur; rdg = femoral ridge; sb = sensilla basiconica; Sp = small triangular spines; st-pl = stigmatic plate; ta = tarsus; tib = tibia. Scale bars in micrometres (μm).

cones (sc) arranged in a single field; each sensory cone long and slender. Lateral palpi inconspicuous. Stipes and mentum covered by numerous long setae.

Mandibles (gnathal lobe) (Fig. 7J–L). With undivided external tooth (Et); with conspicuous 3-combed inner tooth (3it). Pectinate lamellae (pl) with ca 5 rows. Inner area (Ia) consists of several rows of tiny spines. Condylus (co) at anterior margin with distinct and shallow ridges. Molar plate (mp) flat, regular.

Tegument (Fig. 6C–F). Dull. Collum, thoracic shield, tergite and anal shield covered by tiny setae; each seta located in small pit. Posterior margin of tergite with dense setae, anterior one sparsely setose.

Collum. Dull, subsemicircular, densely setose cover. Tip of lateral margin obtuse.

Thoracic shield. Anteriorly with shallow, large groove. Laterally without ridge.

Midbody tergite. Anterior margin with small crests, with single row of oval impressions; inner area with crenate barrier separating broad and shallow groove. Tips of midbody paratergites weakly curved and projecting posteroventrad.

Paratergites (Fig. 6C). First paratergite slender, with sharp tip; tips of paratergites 2–10 gradually obtuse. All paratergites curved; tip directed posteroventrad.

Anal shield. Sexually dimorphic; large and well-rounded in female, weakly bell-shaped and more slender in male. Surface similar to tergites. Inner surface (underside) with a single black locking carina; long; half as long as width of last laterotergite.

Endotergum of thoracic shield and midbody tergite (Figs 22A–B, 23A–B). Thoracic shield similar to midbody tergite, except for posterior margin (pm) of thoracic shield flat and regular, bristles very short, each seta situated on tubercles. Posterior margin of midbody tergite modified, undulate. Outer area (oa) smooth, without setae. Bristles arranged in one row, tip of longest bristles reaching to posterior margin. Middle area (ma) with single row of conspicuous, oval cuticular impressions (cp), distance between impressions twice as long as individual diameter. Inner area (ia) smooth, without setae and tubercles.

Pleurites (laterotergites) (Fig. 8O–P). First pleurite boomeranglike, slender, apex sharp, weakly projecting posteriorly. Pleurite 2 short, with obtuse apex, projecting less than first one. Pleurites 3–11 flat, wide, lamella-like, with well-rounded apex and not projecting. Sparsely setose.

Subanal plate of female (Fig. 8Q). Sparsely setose; semicircular; undivided; narrow; central margin (apical margin) truncate/obtuse (some specimens slightly concave).

Stigmatic plates (Fig. 8E–F). First stigmatic plate (st-pl) subtriangular; large; flattened; apex well-rounded. Second stigmatic plates in both male and female triangular.

Legs (Fig. 8E–N). All podomeres sparsely setose. Coxa (cx) large; as long as prefemur (pre). Coxal process absent in leg-pairs 1 and 2; legs 3–21 marginally with conspicuous coxal process; dentate; projecting laterally. Prefemur stout; apico-mesally without projection; mesal margin usually with 5–7 small triangular spines. Femur (fe) ca 1.4 times as long as wide; short and stout; as long as prefemur; apico-mesally with strong projection and with 7–9 small triangular spines; with long femoral ridge (rdg). Postfemur (po) and tibia (ti) short. Tarsus (ta) quite short; 2.8 times as long as wide. Leg-pairs 1 and 2 without apical spine. Leg-pair 1 with 2–4 ventral spines. Leg-pair 2 with 3–4 ventral spines. Leg-pair 3 with 4–6 ventral spines and 1 apical spine. Leg-pair 4 with 6–7 ventral spines and 1 apical spine. Leg pairs 5–19 with 6–9 ventral spines and 1 apical spine. Last two leg-pairs with 5–7 ventral spines and 1 apical spine. Claw (cl) normal; at base with conspicuous notch.

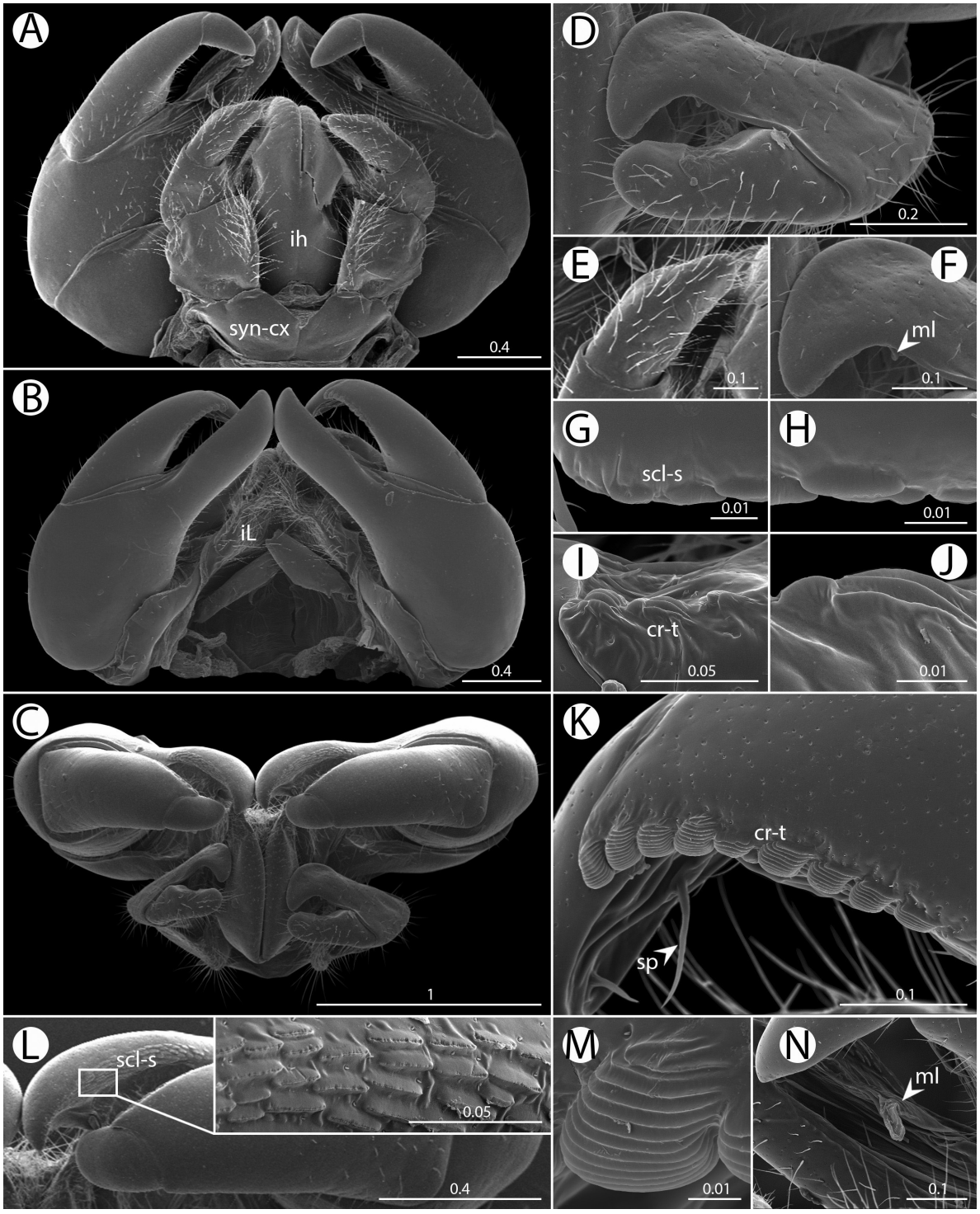

Fig. 9. *Zephronia macula* Srisonchai & Wesener, 2024, a male specimen from Wat Khao Hin Sorn, Chachoengsao Province, Thailand — SEM. **A–C**. Telopods, anterior, posterior and ventral views, respectively. **D**, **F**. Right anterior telopod, ventral views. **E**. Left anterior telopod, anterior view. **G–H**. Sclerotized spots on right anterior telopod, ventral views. **I–J**. Crenulated teeth on right anterior telopod, ventral views. **K**, **M**. Crenulated teeth on left posterior telopod, posterior views. **L**. Sclerotized spots on right posterior telopod, ventral view. **N**. Membranous lobe on right posterior telopod, anterior view. Abbreviations: cr-t = crenulated teeth; ih = inner horns; iL = inner lobes of telopod; ml = membranous lobe; scl-s = sclerotized spots; sp = sclerotized spine; syn-cx = syncoxite. Scale bars in micrometres (μm).

Male sexual characters (Fig. 8G–H). Male gonopore (go) small; located at mesal margin; covered by single, triangular, divided sclerotized plate. Apical part of coxae 2 without membranous processes (Mp).

Anterior telopods (Fig. 9A, C–J). With four conspicuous telopoditomeres; all telopoditomeres sparsely setose, except apical part of telopoditomere 2. First telopoditomere trapeziform; stout; longer than wide. Telopoditomere 2 large and stout. Process of telopoditomere 2 (= immovable finger) long; as long as combination of telopoditomeres 3+4 (= movable finger); ca 1.4 times as long as wide; tip obtuse, strongly curved, directed anteriad; apical margin with sclerotized spots (scl-s); margin towards telopoditomere 3 with membranous lobe (ml). Telopoditomere 3 clearly demarcated from telopoditomere 4, longer than telopoditomere 4, with one small, short, sclerotized spine (sp) located on conspicuous membranous lobe at inner margin, apically with 2 or 3 small crenulated teeth (cr-t). Telopoditomere 4 conspicuous, ca 1.5 times shorter than telopoditomere 3; tip round and directed mesad, with two small membranous lobes, each with one sclerotized spine on posterior side.

Posterior telopods (Fig. 9A–C, K–N). With four telopoditomeres. Telopoditomeres 1–3 sparsely setose; dorsal side of process of telopoditomere 2, apical part of telopoditomere 3 and complete telopoditomere 4 without setae. Syncoxite conspicuous. Inner lobes (iL) densely setose, sharply edged. Inner horns (ih) glabrous at base, tip attenuate and curved. First telopoditomere stout. Telopoditomere 2 large. Process of telopoditomere 2 (= immovable finger) long and slender; equal in length to combination of telopoditomeres 3+4 (= movable finger). Immovable finger 2.5 times as long as wide; apically curved; with conspicuous sclerotized spots (scl-s), clearly visible in ventral view; margin towards movable finger with two massive, triangular, membranous lobes (ml). Telopoditomere 3 long, tip attenuate, 4 times as long as telopoditomere 4, postero-apically with a row of 9 or 10 crenulated teeth (cr-t), inner side with membranous ledge and one sclerotized spine (sp). Telopoditomere 4 slender, abruptly curved, with round tip and two long sclerotized spines located on swollen and large membranous lobe.

Female sexual characters (Fig. 8I–J). Vulva large and stout; covering ca ⅓ of coxa; located at mesal margin, mesally extended to base of prefemur. Bursa (bu) large; distal margin separated from operculum by a triangular groove. Operculum (O) large; wide dorsoventrally; broad; well-rounded; swollen; mesal margin not protruding.

Distribution and habitat

Zephronia macula is currently found in eastern Thailand, specifically in the provinces of Chanthaburi, Chonburi, Rayong, and Sa Kaeo (Fig. 3). The species is endemic to limestone and granitic habitats.

Remarks

Specimens collected from Chachoengsao (Wat Khao Hin Sorn), Rayong (Wat Suwan Phupha), and Sa Kaeo (Wat Tham Khao Chan) show notable differences from the type specimens described by Srisonchai *et al*. (2024). These include a dark green body colouration without prominent tergal spots; an antennal disc bearing only 22–38 apical cones (compared to 36–57); a large and conspicuous process at the tip of the mentum (vs absent); and a longer process on telopoditomere 2 of the anterior telopod, as long as the combined length of telopoditomeres 3 and 4 (vs as long as telopoditomere 3 only). Interestingly, although the variation in the endotergum between the two populations is minimal, one noticeable difference is the flat posterior margin in the "spotted" morph whilst undulating in the green morph.

Considerable intraspecific variation in the structure of the endotergum is of particular taxonomic interest, as this character has previously been regarded as fixed and species-specific within *Zephronia*. Despite this variation, both morphs are consistent in all other diagnostic characters, and molecular evidence (COI) strongly supports their conspecificity. The finding indicates that variation in endotergum should be interpreted with caution to prevent potential taxonomic confusion.

Zephronia ovalis Gray, 1832
Figs 2–3, 10–13, 22C–D, 23C–D

Zephronia ovalis Gray, 1832: 796.

Zephronia ovalis – Gervais 1837: 42. — Newport 1844: 264. — Butler 1873: 180. — Olliff 1882: 30. — Attems 1914: 146. — Jeekel 2001: 20. — Golovatch *et al*. 2012: 286. — Wesener 2014: 204; 2016: 34.
Sphaerotherium ovale – C.L. Koch 1847: 99.

Diagnosis

Zephronia ovalis belongs to the *Zephronia* s. str. species group based on the position of Tömösváry's organ, located next to the aberrant ocelli, not inside the antennal socket. Colour pattern unique for the order; body with dark olive-green (greenish dark) and two large patches (stripes), the latter either golden brown or yellowish gold dorsally, running from the thoracic shield to the anal shield; adults with body length 7–18.9 mm; process of telopoditomere 2 of anterior telopods relatively short, shorter than combination of telopoditomeres 3+4. Similar in these aspects to *Z. dawydoffi*, *Z. laotica* and *Z. siamensis*. Differs from these three species by a combination of these characters: surface of tergites, thoracic shield, and anal shield more glabrous and shining; bristles of midbody endotergum arranged in 2 or 3 rows; posterior margin of endotergum modified: 'trapezoidal-wavy' or undulate; process of telopoditomere 2 of posterior telopods equal to or longer than the combination of telopoditomeres 3+4. See also Table 2.

Material examined

THAILAND • 24 ♂♂, 46 ♀♀; Sisaket Province, Khunhan District, Huai Chan Waterfall; 14°31′44.9″ N, 104°21′25.9″ E; 222 m a.s.l.; 25 Jun. 2022; N. Srimongkol leg.; MZKKU • 39 ♂♂, 60 ♀♀, 5 broken specimens; Sisaket Province, Khunhan District, Rubber Plantation 1, near Huai Chan Waterfall; 14°31′45.4″ N, 104°21′14.3″ E; 232 m a.s.l.; 10 Jun. 2023; N. Srimongkol leg.; MZKKU • 4 ♂♂, 2 ♀♀; Sisaket Province, Khunhan District, Rubber Plantation 2, near Huai Chan Waterfall; 14°31′32.1″ N, 104°21′10.6″ E; 250 m a.s.l.; 10 Jun. 2023; N. Srimongkol leg.; CUMZ • 9 ♂♂, 7 ♀♀; Sisaket Province, Khunhan District, Rubber Plantation 3, near Huai Chan Waterfall; 14°29′58.6″ N, 104°20′09.4″ E; 256 m a.s.l.; 10 Jun. 2023; N. Srimongkol leg.; CUMZ • 8 ♂♂, 5 ♀♀; Surin Province, Bua Chet District, Wat Tham Pha Sai; 14°28′27″ N, 104°00′19″ E; 200 m a.s.l.; 30 Jul. 2022; N. Srimongkol, N. Tungpairojwong and MZKKU students leg.; MZKKU • 2 ♂♂, 2 ♀♀; same locality as for preceding; 14°28′27″ N, 104°00′19″ E; 200 m a.s.l.; 30 Jul. 2022; N. Srimongkol, N. Tungpairojwong and MZKKU students leg.; CUMZ.

Type locality

Vietnam, Dong Nai Province, Cat Tien National Park.

Description of specimens from Thailand

For the full description of type specimens, see Gray (1832) and Golovatch *et al*. (2012).

Measurements. Males: body length 7.0–10.8 mm (neotype and Vietnamese specimens = 14.7–18.9 mm); width (= broadest) of head = 2.9–3.8 mm, of collum = 2.5–3.6 mm, of thoracic shield = 4.5–5.5 mm, of tergite 7 = 4.4–5.6 mm, of anal shield = 4.2–5.3 mm; height (= highest) of head = 2.3–2.7 mm, of collum = 2.9–3.4 mm, of thoracic shield = 3.2–3.5 mm, of tergite 7 = 3.4–3.7 mm, of anal shield = 2.9–3.1 mm. Females: body length 7.2–12.5 mm; width (= broadest) of head = 3.0–4.0 mm, of collum = 2.8–3.8 mm, of thoracic shield = 4.7–5.9 mm, of tergite 7 = 4.6–6.3 mm, of anal shield = 4.4–5.7 mm; height (= highest) of head = 2.4–2.9 mm, of collum = 2.8–3.7 mm, of thoracic shield = 3.3–4.1 mm, of tergite 7 = 3.5–4.2 mm, of anal shield = 3.0–4.0 mm.

Colouration (Fig. 10A–F). Live specimens greenish dark (dark olive green). Antennae, head and collum dark or greenish dark. Thoracic shield, pleurites and legs greenish dark. Tergites with two big, separated patches, yellowish brown or yellowish gold, arranged in almost central part of anterior half; lateral part of tergites greenish dark, posterior edge dark brown. Anal shield with two colours, contrasting each other;

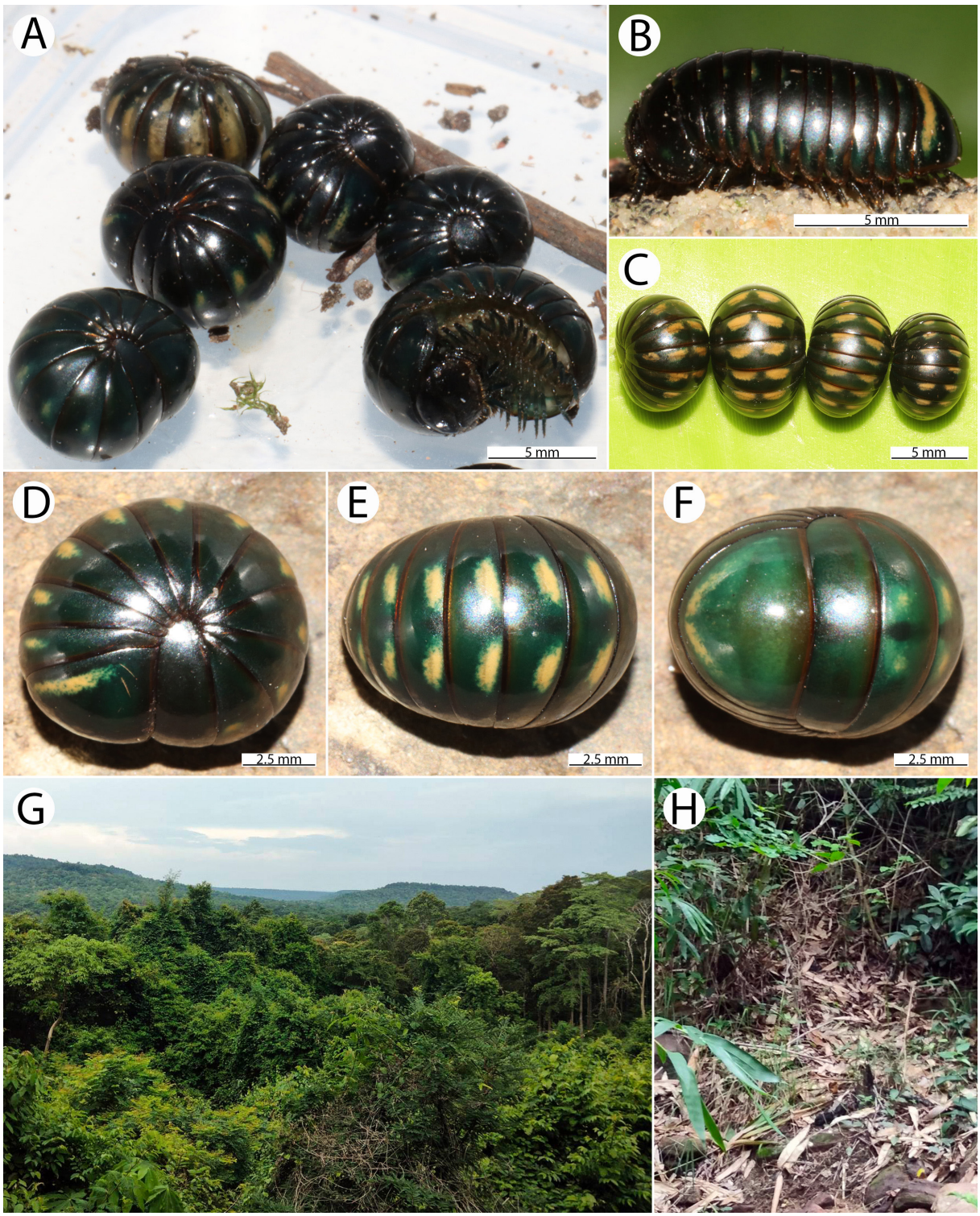

Fig. 10. Photographs of live *Zephronia ovalis* Gray, 1832 and habitat. **A–F**. Specimens of a population from Sisaket Province, Thailand. **G–H**. Sandstone forest habitat.

posterior half greenish dark; anterior half yellowish brown or yellowish gold. Colour in alcohol after 1 year of preservation not changed.

Head (Fig. 11A). Trapeziform; sparsely setose. Clypeus (cl) covered by numerous long setae; posterior portion with a few setae. Anterior edge of labrum with single conspicuous tooth. Each eye with 60–80 ommatidia (o). Aberrant ocellus located almost inside antennal groove.

Antennae (Figs 11A, 12A–D). Short and stout; all antennomeres covered by long and dense setae; last antennomere extending posteriorly to tarsus of leg pair 2. Lengths of antennomeres: 6>5>4>3>2=1. Antennomere 6 thickened and stout, widened apically, axe-shaped, with sensilla basiconica (sb) surrounding antennal disc. Shape of antennae sexually dimorphic, slightly flattened in males, and more cylindrical in females. Antennal disc (ad) flat, slightly concave; with 35–47 apical cones (ac) in males and 35–43 cones in females. Between antennal socket and ommatidia without ridges or crests.

Tömösváry's organ (Fig. 11A–C). Tömösváry's organ (to) isolated from ommatidium, located at a projecting brim between ommatidia and antennal socket, close to anterior margin of ommatidia. Smaller in size than individual ommatidium.

Epipharynx (Fig. 11D). Apically with single and conspicuous central tooth (ct); centrally with one inner tooth (sclerotized plate), conspicuous and swollen; laterally (inner area) surrounded by single row of conical spines (rsp); outer area with several rows of long external teeth (et), each side with 26–28 small cuticular scales (=cs).

Gnathochilarium (Fig. 11E–I) Sparsely setose. Lamellae linguales (ll) oval and slightly concave apically. Central pads (cpd) modified, with two types of papillae or sensory cones (sc), large and small ones; large papilla circular, located on pillow; second one smaller, without pillow. Stipites (st) large and quite stout. Mentum (me) fused; large and broad; apico-laterally portion not protruding (without mentum process). Inner palpi (ip) with numerous sensory cones (sc) arranged in single field; each sensory cone short and swollen. Hypopharynx (hyp) with single tooth; laterally with single row of sclerotized spines. Lateral palpi inconspicuous.

Mandibles (gnathal lobes) (Fig. 11J–L). External tooth (Et) undivided. Inner tooth with 3-cusped (3-combed inner tooth=3it); each equal in size. Pectinate lamellae (pl) with 5 rows of teeth. Inner area (Ia) with two types of teeth; innermost one large and outermost one small. Condylus (co) at anterior margin with two distinct ridges. Molar plate (mp) almost flat in general.

Tegument (Fig. 10A–F). Shining. Collum, thoracic shield, tergite, and anal shield densely microscopic setose; each seta located in a tiny pit.

Collum. Dull; subsemicircular; densely setose cover. Tip of lateral margin obtuse.

Thoracic shield. Anteriorly with a large groove, separated by a long ridge. Laterally with conspicuous ridges.

Midbody tergite. Dorsally with conspicuous crest (circular impressions) and small crests at anterior margin. Inner area with single row of sclerotized grains (crenate barrier) separating wide and shallow groove. Tips of paratergites slightly projecting posteroventrad.

Paratergites (Fig. 10B). Paratergites weakly curved and directed posteroventrad; tip of first paratergite slender and sharp; tip of paratergites 2–10 obtuse and wide.

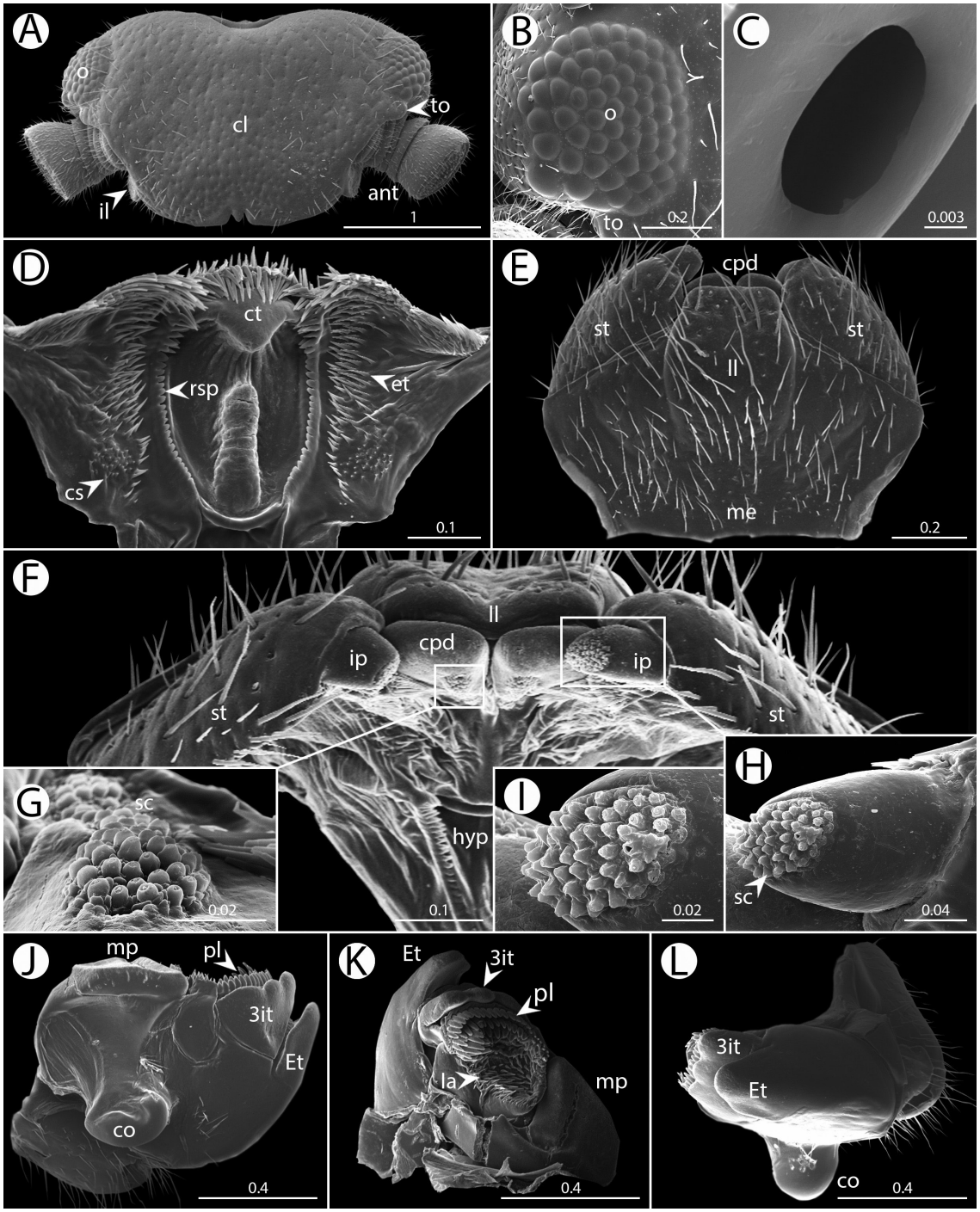

Fig. 11. *Zephronia ovalis* Gray, 1832, a male specimen from Huai Chan Waterfall, Sisaket Province, Thailand — SEM. **A**. Head, anterior view. **B**. Right ommatidia, lateral view. **C**. Left Tömösváry's organ, lateral view. **D**. Epipharynx, ventral view. **E–F**. Gnathochilarium, ventral and frontal views, respectively. **G**. Left central pad, frontal views. **H–I**. Right lateral palpi, frontal views. **J–L**. Right mandible, dorsal, mesal and anterior views, respectively. Abbreviations: 3it = 3-combed inner tooth; ant = antenna; cl = clypeus; co = condylus; cpd = central pad; cs = cuticular scales; ct = central tooth; et = external tooth of epipharynx; Et = external tooth of mandible; hyp = hypopharynx; Ia = inner area of mandible; il = incisura lateralis; ip = inner palpi; ll = lamellae lingulales; me = mentum; mp = molar plate; o = ommatidia; pl = pectinate lamellae; rsp = row of spines; sc = sensory cone; st = stipites; to = organ of Tömösváry. Scale bars in micrometres (μm).

Anal shield. Sexually dimorphic, more rectangular in males, large and more rounded in females. Surface covered by dense and tiny setae. Inner surface (underside) with single, long, black locking carina, located almost half breadth of last laterotergite.

Endotergum of thoracic shield and midbody tergite (Figs 22C–D, 23C–D). Thoracic shield somewhat similar to midbody tergite. Midbody tergite with modified posterior margin (pm), 'trapezoidal-wavy', marginal edge of each trapezoidal lobe overlapped to one another. Outer area (oa) with crests or ridges, without setae. Inner area (ia) with small setiferous tubercles. Middle area (ma) with single row of large, elliptic, cuticular impressions (cp); distance between impressions slightly longer than individual diameter. Bristles arranged in two rows, longest bristles not reaching to posterior margin.

Pleurites (laterotergites) (Fig. 12O–P). First pleurite slender, boomerang-like; apical margin attenuated, projecting towards paratergite 1. Pleurite 2 short with obtuse apex; well-rounded; tip obtuse; projecting less than first one. All remaining pleurites with oblong lamella-like; flat; well-rounded apex; not projecting. Sparsely setose.

Subanal plate of female (Fig. 12Q). Sparsely setose. Trapeziform; undivided; slender; tip narrow; apical margin (central margin) slightly concave.

Stigmatic plates (Fig. 12E–F). First stigmatic plate (st-pl) subtriangular; wide; apex round, slightly curved towards coxa. Second stigmatic plate in both sexes triangular; swollen; slightly curved towards coxa.

Legs (Fig. 12E–N). All podomeres sparsely long setose. Coxa (cx) large; as long as prefemur (pre). Coxal process absent in leg pairs 1 and 2; legs 3–21 laterally with large and well-rounded dentate process. Prefemur (pre) of leg 10 quite stout; apico-mesally without projection, mesal margin without teeth. Femur (fe) of leg 10 ca 1.8 times as long as wide; slightly long and slender; apico-mesally with small spines (Sp), forming dentate margin; with long ridge (rdg) in all leg-pairs (clearly seen in posterior view), except for leg-pair 1 without long ridge. Postfemur (po) and tibia (ti) of leg 10 quite short; tarsus (ta) of leg 10 quite long, ca 3.2 times as long as wide. Leg-pairs 1–3 without apical spine. Leg-pair 1 with 1 ventral spine. Leg-pair 2 with 2–3 ventral spines. Leg-pair 3 with 4–5 ventral spines. Leg-pairs 4–18 with 5 or 6 ventral spines and 2 or 3 apical spines. Leg-pairs 19–21 with 3–4 ventral spines and 1 or 2 apical spines. Claw (cl) normal, with a conspicuous notch at base.

Male sexual characters (Fig. 12G–H). Gonopore (go) small but conspicuous; covered by single, triangular, sclerotized membranous plate. Coxae 2 without membranous process (Mp) at mesal margin.

Anterior telopods (Fig. 13A, C–J). Consisting of 4 telopoditomeres. All telopoditomeres sparsely setose, except for process of telopoditomere 2 without setae. First telopoditomere rectangular. Telopoditomere 2 slender. Process of telopoditomere 2 (= immovable finger) unciform, relatively short, as long as telopoditomere 3; tip curved, reaching to halfway of telopoditomere 4, apically with conspicuous sclerotized spots (scl-s); margin towards telopoditomere 3 with small membranous lobe (ml). Telopoditomere 3 longer than telopoditomere 4, ca 1.5 times as long as wide; with one tiny, short, sclerotized spine (sp) located on conspicuous membranous lobe at inner margin; apically with 1–2 tiny crenulated teeth (cr-t). Telopoditomere 4 short, stout, clearly demarcated from telopoditomere 3, apically round; tip directed mesad, with two small membranous lobes, each with one sclerotized spine on posterior side.

Posterior telopods (Fig. 13A–C, K–N). Inner lobes (iL) densely setose. Inner horns (ih) glabrous; tip slightly curved caudad. Telopod with four telopoditomeres; sparsely setose; dorsal side of process of telopoditomere 2, apical part of telopoditomere 3 and all of telopoditomere 4 without setae. First

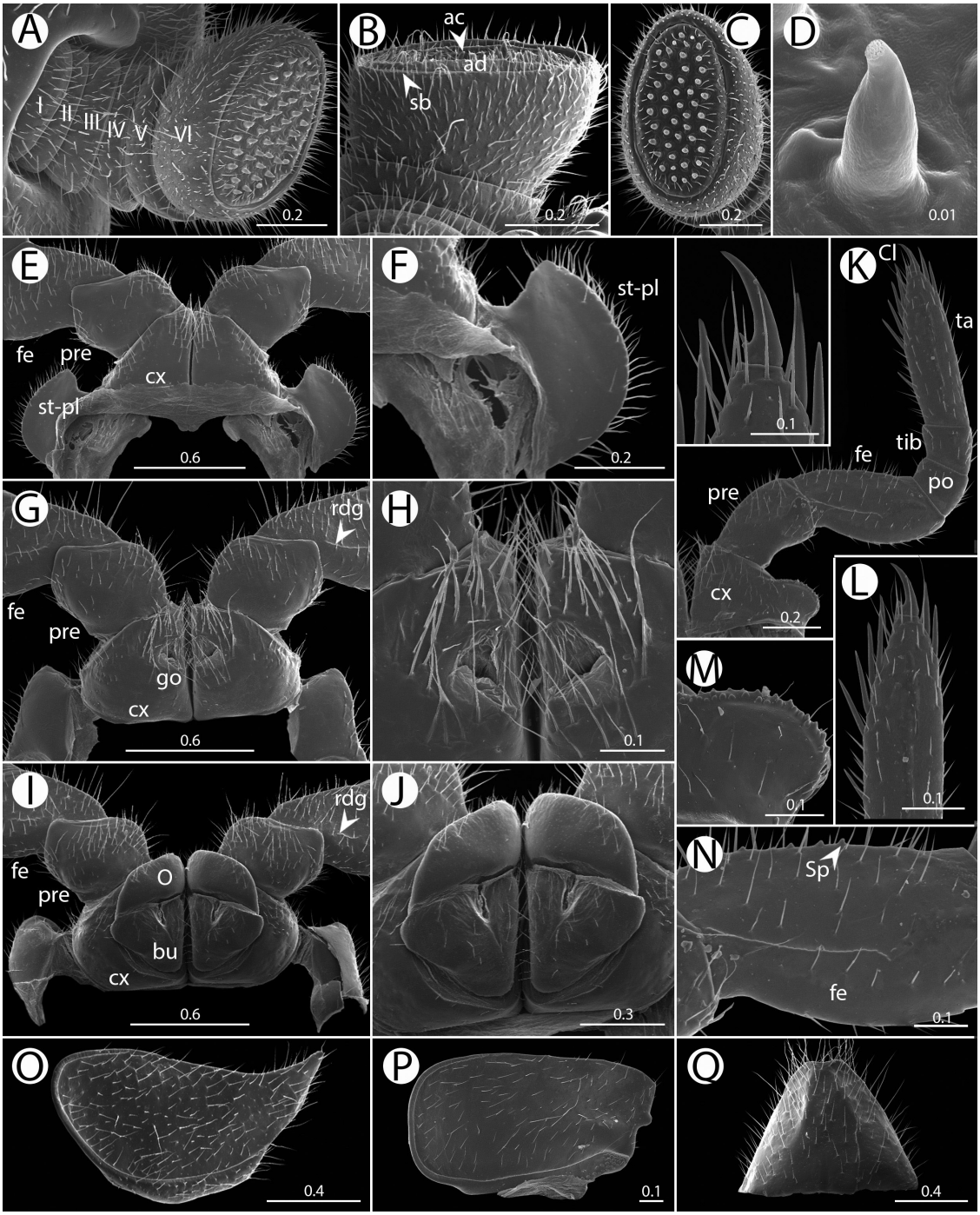

Fig. 12. *Zephronia ovalis* Gray, 1832, specimens from Huai Chan Waterfall, Sisaket Province, Thailand — SEM. **A–H**, **K–P**. Male. **I–J**, **Q**. Female. **A–B**. Antenna, anterior and mesal views. **C–D**. Antennal disc and apical cone. **E–F**. First coxae with stigmatic plates, posterior views. **G–H**. Coxae of legs 2 with gonopores, posterior views. **I–J**. Coxae of legs 2 with vulvae, posterior views. **K–L**. Left leg 10, posterior views. **M**. Left coxal process on leg 10, posterior view. **N**. Femur of left leg 10, posterior view. **O**. Right first pleurite, ventral view. **P**. Right midbody pleurite, ventral view. **Q**. Subanal plate, ventral view. Abbreviations: ac = apical cone; ad = antennal disc; bu = bursa; Cl = claw; cx = coxa; fe = femur; go = gonopore; O = operculum; po = postfemur; pre = prefemur; rdg = femoral ridge; sb = sensilla basiconica; Sp = small triangular spines; st-pl = stigmatic plate; ta = tarsus; tib = tibia. Scale bars in micrometres (μm).

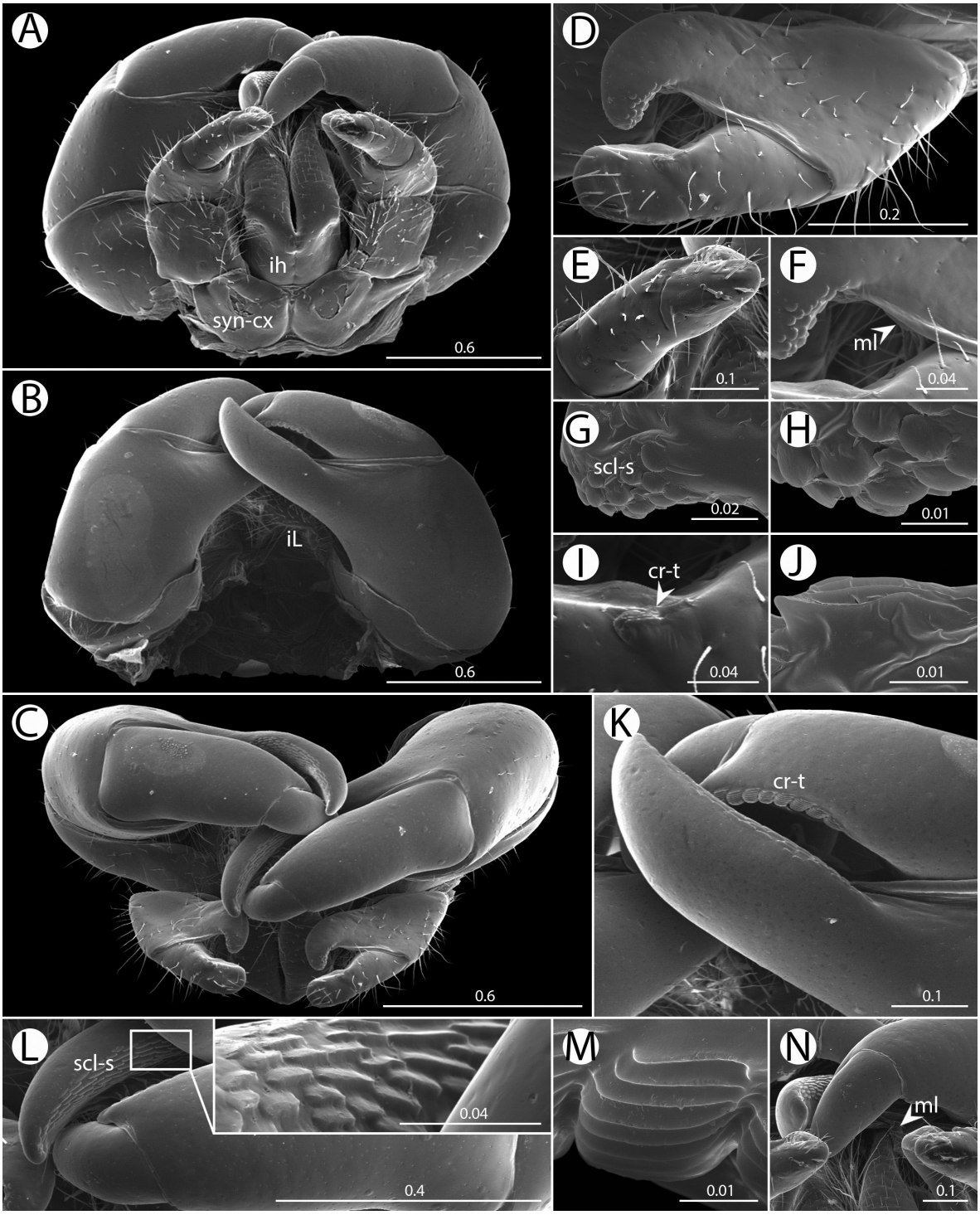

Fig. 13. *Zephronia ovalis* Gray, 1832, male specimens from Huai Chan Waterfall, Sisaket Province, Thailand — SEM. **A–C**. Telopods, anterior, posterior and ventral views, respectively. **D**, **F**. Right anterior telopod, ventral views. **E**. Left anterior telopod, anterior view. **G–H**. Sclerotized spots on right anterior telopod, ventral views. **I–J**. Crenulated teeth on right anterior telopod, ventral views. **K**, **M**. Crenulated teeth on left posterior telopod, posterior views. **L**. Sclerotized spots on right posterior telopod, ventral view. **N**. Membranous lobe on right posterior telopod, anterior view. Abbreviations: cr-t = crenulated teeth; ih = inner horns; iL = inner lobes of telopod; ml = membranous lobe; scl-s = sclerotized spots; syn-cx = syncoxite. Scale bars in micrometres (μm).

telopoditomere wide and stout, almost twice as wide as long. Telopoditomere 2 large. Process of telopoditomere 2 (= immovable finger) as long as combination of telopoditomeres 3+4 (= movable finger); slender; 3 times as long as wide; apically curved; posterior side with sclerotized spots (scl-s); margin towards movable finger with two massive, digitiform, membranous lobes (ml). Telopoditomere 3 long; 2.5 times as long as wide; mesal margin with large, swollen, membranous lobe and one sclerotized spine (sp); postero-apically enlarged, with row of 8 or 9 sclerotized, crenulated teeth (cr-t). Telopoditomere 4 slender; apex round, curving dorsad, with two long sclerotized spines located on swollen membranous lobe.

Female sexual characters (Fig. 12I–J). Vulva large, covering ca ½ of coxa, located at mesal side, extending mesally to basal of prefemur. Bursa (bu) separated from operculum by triangular groove. Operculum (O) conspicuous, wide dorsoventrally, mesal margin slightly round; distally not protruding.

Distribution and habitat

Zephronia ovalis has a wide distribution, extending from its type locality in southern Vietnam to northeastern Thailand, covering a range of at least 500 kilometers (Fig. 3). All newly collected specimens were found in mixed deciduous forests within sandstone mountain regions (Fig. 10G–H), whereas the type specimens were originally discovered in lowland tropical forests.

Remarks

The newly collected specimens from Thailand exhibit notable morphological differences from the neotype designated by Golovatch *et al*. (2012) from Vietnam. Specifically, the Thai material possesses 35–47 apical cones on the antennal disc, compared to 62–73 in the Vietnamese neotype. The midbody endotergum features two rows of bristles, whereas the neotype displays three. Additionally, the tip of the longest bristle in the Thai specimens does not extend beyond the posterior margin, in contrast to the Vietnamese specimen where it does. The posterior margin of the endotergum in the Thai specimens is wavy-rectangular, while it is slightly undulate in the neotype. Furthermore, the movable finger of the posterior telopod bears 8–9 crenulated teeth in the Thai material, as opposed to 16 in the neotype. The COI sequence divergence between the Thai and Vietnamese specimens ranges from 4.87% to 5.63%, indicating a modest genetic distance. See also Table 2.

Zephronia panhai Srisonchai, Sutcharit & Likhitrakarn, 2021
Figs 2–3, 4M–R

Zephronia panhai Srisonchai, Sutcharit & Likhitrakarn, 2021: 41.

Zephronia panhai – Bhansali & Wesener 2022: 376. — Likhitrakarn *et al*. 2023: 56.

Distribution

Kanchanaburi, Phetchaburi, and Ratchaburi Provinces (Fig. 3).

Remarks

Endemic. Known to occur in limestone habitats. See Srisonchai *et al.* (2021: figs 11–12).

Zephronia phrain Likhitrakarn & Golovatch, 2021
Figs 1, 3

Zephronia phrain Likhitrakarn & Golovatch in Likhitrakarn *et al*., 2021: 19.

Zephronia phrain – Srisonchai *et al*. 2021: 29. — Bhansali & Wesener 2022: 375. — Likhitrakarn *et al*. 2023: 56.

Distribution

Chiang Mai, Lamphun and Tak Provinces (Fig. 3).

Remarks

Endemic. Known to occur in limestone and granitic habitats. See Likhitrakarn *et al*. (2021: figs 5–6).

Zephronia siamensis Hirst, 1907
Figs 2–3

Zephronia siamensis Hirst, 1907: 218.

Zephronia siamensis – Attems 1914: 147; 1936: 182. — Jeekel 2001: 21. — Enghoff 2005: 89. — Golovatch *et al*. 2012: 276. — Wongthamwanich *et al*. 2012: 30. — Wesener 2016: 35. — Srisonchai *et al*. 2021: 22. — Likhitrakarn *et al*. 2023: 56.
Zephronia cf. *siamensis* – Decker 2010: 25.

Distribution

Chachoengsao, Chonburi, Rayong, and Sa Kaeo provinces (Fig. 3).

Remarks

Endemic. Known to occur in limestone and granitic habitats. See Srisonchai *et al*. (2021: figs 3–4).

Zephronia sukhothaiensis Srimongkol & Srisonchai sp. nov.
urn:lsid:zoobank.org:act:0EA66571-EEF8-4E5F-98CE-0291B2266B3D
Figs 2–3, 4S–X, 14–17, 22E–F, 23E–F

Diagnosis

Zephronia sukhothaiensis sp. nov. belongs to the *Zephronia* s. str. species group based on the position of Tömösváry's organ, located next to the aberrant ocelli, not inside the antennal socket. Body grey / brownish, grey / greyish brown; leg-pairs 3 usually with 5–7 ventral spines; longest bristles of midbody endotergum not reaching to posterior margin; immovable finger (process) of telopoditomere 2 of anterior telopods relatively short, shorter than the combination of telopoditomeres 3+4. Similar in these aspects to *Z. chrysomallos*, *Z. erawani* and *Z. panhai*, but differs from them by a combination of the following characters: endotergum of midbody tergite with one row of bristles (vs 2 or 3 rows); leg-pair 3 usually with 1–3 apical spines (vs 1 spine); coxa of leg-pair 2 in male with conspicuous, long, membranous process, being unique among grey-bodied congeners (vs without membranous process).

Etymology

The name is a Latin adjective and refers to the province where the type locality is located.

Type material

Holotype

THAILAND • ♂; Sukhothai Province, Ban Dan Lan Hoi District, Wat Khao Fang; 17°09′13.7″ N, 99°33′13.0″ E; 100 m a.s.l.; 29 Jul. 2023; N. Srimongkol, R. Srisonchai and MZKKU students leg.; MZKKU-MYR0017.

Paratypes

THAILAND • 26 ♂♂, 24 ♀♀; same data as for holotype; MZKKU-MYR0018 • 1 ♂, 1 ♀; same data as for holotype; NHMUK • 1 ♂, 1 ♀; same data as for holotype; NHMD • 1 ♂, 1 ♀; same data as for holotype; NHMW • 2 ♂♂, 2 ♀♀; same data as for holotype; ZFMK • 1 ♂, 1 ♀; same data as for holotype; CUMZ-zeph0039.

Additional material examined

THAILAND • 3 ♂♂, 11 ♀♀, 6 juveniles; Sukhothai Province, Ban Dan Lan Hoi District, Tham Yok Monastery; 17°08′16.1″ N, 99°33′00.4″ E; ca 100 m a.s.l.; 16 Sep. 2022; N. Likhitrakarn leg.; MZKKU • 111 ♂♂, 163 ♀♀, 12 juveniles; same data as for holotype; MZKKU.

Description

Measurements of male holotype. Body length 18.2 mm; width (=broadest) of head=5.5 mm, of collum=5.6 mm, of thoracic shield=9.6 mm, of tergite 7=10.2 mm, of anal shield=9.2 mm; height (=highest) of head=3.2 mm, of collum=2.0 mm, of thoracic shield=5.2 mm, of tergite 7=6.3 mm, of anal shield=5.8 mm.

Measurements of paratypes. Males: body length 15.8–18.3 mm; width (=broadest) of head=4.2–5.6 mm, of collum=4.3–5.7 mm, of thoracic shield=7.4–9.8 mm, of tergite 7=7.9–10.3 mm, of anal shield=7.2–9.3 mm; height (=highest) of head=2.6–3.3 mm, of collum=1.6–2.1 mm, of thoracic shield=4.4–5.4 mm, of tergite 7=5.1–6.4 mm, of anal shield=4.9–5.8 mm. Females: body length 16.5–22.9 mm; width (=broadest) of head=4.7–6.2 mm, of collum=5.0–7.0 mm, of thoracic shield=7.5–11.5 mm, of tergite 7=8.3–12.1 mm, of anal shield=7.5–10.9 mm; height (=highest) of head=3.1–4.0 mm, of collum=1.7–2.6 mm, of thoracic shield=4.6–6.1 mm, of tergite 7=5.6–7.9 mm, of anal shield=5.1–7.6 mm.

Colouration (Fig. 14A–F). Specimens in life brownish grey. Head and collum brown to dark brown. Thoracic shield light brown. Antenna greenish grey. Tergites and anal shield brownish grey, except posterior margins dark brown and paratergites light brown. Middle part of tergites (dorsal view) with dark brown stripe when curled up. Legs greenish grey. A few basal podomeres of legs light brown. Colour in alcohol after 1 year of preservation changed to light grey.

Head (Fig. 15A). Subtrapeziform. Anterior portion of clypeus (cl) covered by numerous long setae; posterior portion with sparse setae, each seta situated inside tiny pit. Labrum with single tooth on anterior margin. Each eye with 70–75 ommatidia (o). Aberrant ocellus located near brim of antennal groove (at upper part of groove).

Antennae (Figs 15A, 16A–D). Short and stout; all antennomeres covered by long and dense setae; last antennomere extending posteriorly to tarsus of leg pair 2 or 3. Lengths of antennomeres: 6>5>4=3>2=1. Antennomere 6 thickened, slightly flattened apically, axe-shaped, with sensilla basiconica (sb) surrounding antennal disc. Shape of antennae sexually dimorphic, slightly flattened in males, and more cylindrical in females. Antennal disc (ad) flat, slightly concave, with 38–45 apical cones (ac) in males and 24–36 cones in females. Between antennal socket and ommatidia without ridges or crests.

Tömösváry's organ (Fig. 15A–C). Tömösváry's organ (to) separated from ommatidium, located at projecting brim between ommatidia and antennal groove; equal in size to individual ommatidium. Pore with dentate inner structure.

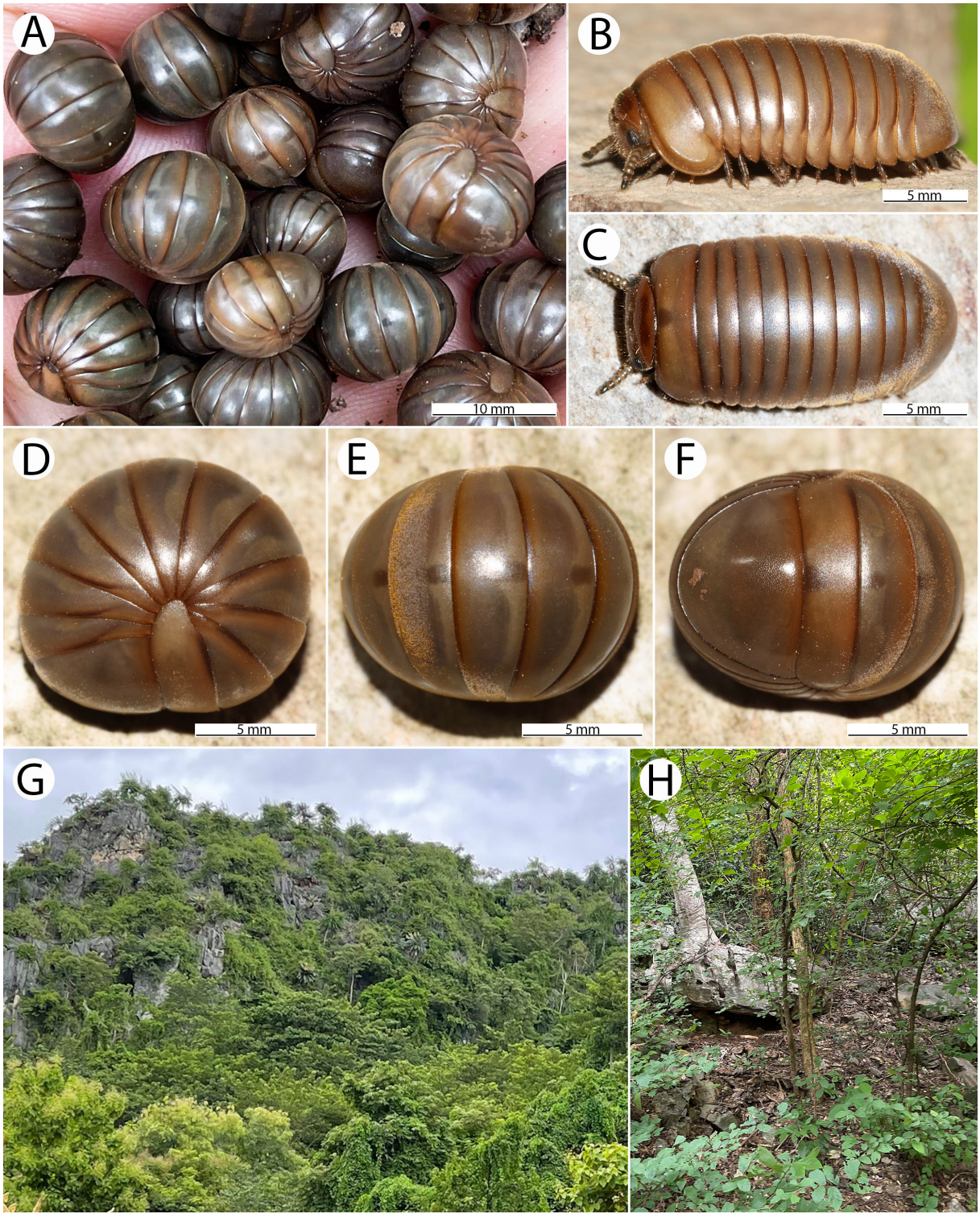

Fig. 14. Photographs of live *Zephronia sukhothaiensis* Srimongkol & Srisonchai sp. nov. and habitat. **A–F**. Male paratypes MZKKU-MYR0018. **G–H**. Habitat at the type locality.

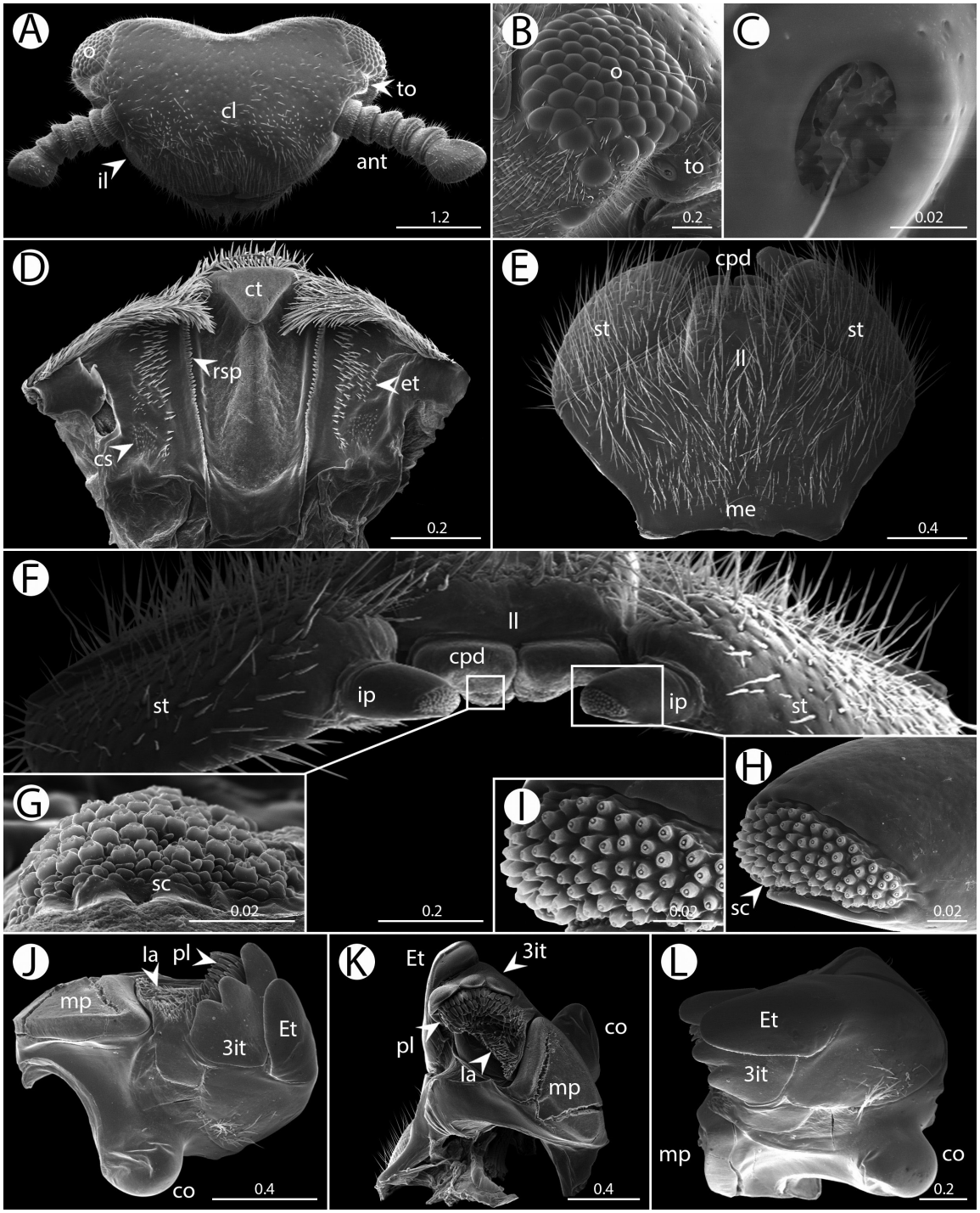

Fig. 15. *Zephronia sukhothaiensis* Srimongkol & Srisonchai sp. nov., male paratype MZKKU-MYR0018 — SEM. **A**. Head, anterior view. **B**. Right ommatidia, lateral view. **C**. Left Tömösváry's organ, lateral view. **D**. Epipharynx, ventral view. **E–F**. Gnathochilarium, ventral and frontal views, respectively. **G**. Left central pad, frontal view. **H–I**. Right lateral palpi, frontal views. **J–L**. Right mandible, dorsal, mesal and anterior views, respectively. Abbreviations: 3it = 3-combed inner tooth; ant = antenna; cl = clypeus; co = condylus; cpd = central pad; cs = cuticular scales; ct = central tooth; et = external tooth of epipharynx; Et = external tooth of mandible; Ia = inner area of mandible; il = incisura lateralis; ip = inner palpi; ll = lamellae lingulales; me = mentum; mp = molar plate; o = ommatidia; pl = pectinate lamellae; rsp = row of spines; sc = sensory cone; st = stipites; to = organ of Tömösváry. Scale bars in micrometres (µm).

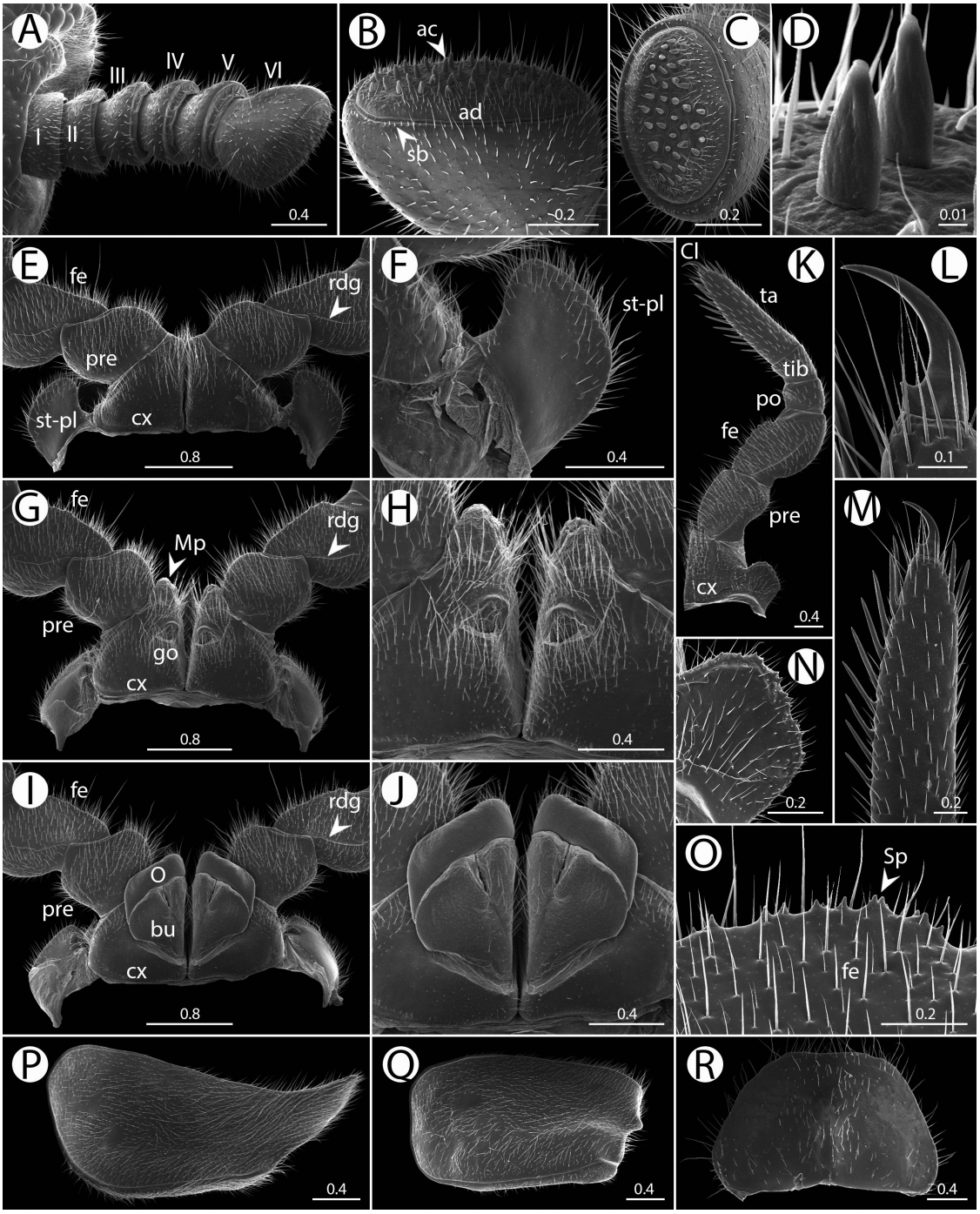

Fig. 16. *Zephronia sukhothaiensis* Srimongkol & Srisonchai sp. nov., paratypes MZKKU-MYR0018 — SEM. **A–H**, **K–Q**. Male. **I–J**, **R**. Female. **A–B**. Antenna, anterior and mesal views. **C–D**. Antennal disc and apical cone. **E–F**. First coxae with stigmatic plates, posterior views. **G–H**. Coxae of legs 2 with gonopores, posterior views. **I–J**. Coxae of legs 2 with vulvae, posterior views. **K–M**. Left leg 10, posterior views. **N**. Left coxal process on leg 10, posterior view. **O**. Femur of left leg 10, posterior view. **P**. Right first pleurite, ventral view. **Q**. Right midbody pleurite, ventral view. **R**. Subanal plate, ventral view. Abbreviations: ac = apical cone; ad = antennal disc; bu = bursa; Cl = claw; cx = coxa; fe = femur; go = gonopore; Mp = membranous process; O = operculum; po = postfemur; pre = prefemur; rdg = femoral ridge; sb = sensilla basiconica; Sp = small triangular spines; st-pl = stigmatic plate; ta = tarsus; tib = tibia. Scale bars in micrometres (μm).

Epipharynx (Fig. 15D). Apically with large central tooth (ct); inner region with large, conspicuous tooth; laterally (inner area) surrounded by single row of short conical spines (rsp); outer area with group of several external teeth (et); at base close to et with 45–50 small triangular, cuticular scales (cs) on each side.

Gnathochilarium (Fig. 15E–I). Densely setose. Lamellae linguales (ll) oval, quite narrow, apically truncate. Central pads (cpd) modified, with large and small sensory cones (sc), large one with pillow and small one without pillow. Stipites (st) large and stout. Mentum (me) broad, fused, apico-laterally without mentum process. Inner palpi (ip) with numerous sensory cones (sc) arranged in single field, each cone conical, with apical depression containing inner plug-liked structure. Lateral palpi (lp) inconspicuous.

Mandibles (gnathal lobes) (Fig. 15J–L). With conspicuous undivided external tooth (Et) and 3-cusped inner tooth (3it). Pectinate lamellae (pl) with 5–6 rows of teeth. Inner area (Ia) with numerous rows of spine-liked teeth. Condylus (co) conspicuous, apically with 2–3 ridges. Molar plate (mp) flat, regular.

Tegument (Fig. 14A–F). Quite shiny. Collum, thoracic shield, tergite and anal shield densely setose; each seta located in tiny pit. Anterior margin of tergite with lower number of setae than posterior margin.

Collum. Subsemicircular; covered by a few short setae. Tip of lateral margin obtuse.

Thoracic shield. Anteriorly with large, conspicuous groove, separated by long ridge. Laterally with conspicuous ridges.

Midbody tergite. Anterior margin with small tubercles and single row of circular impressions. Inner area with single row of crenate barrier (sclerotized grains / ridges), separating wide and shallow groove. Tips of midbody paratergite slightly curved, directed posteroventrad.

Paratergites (Fig. 14B). Paratergites weakly curved and directed posteroventrad; tip of first paratergite slender and sharp; tip of paratergites 2–10 obtuse and wide.

Anal shield. Sexually dimorphic, large and well-rounded in female, more slender in male. Ventral side with long locking carina; ca ⅔ as long as last laterotergite.

Endotergum of thoracic shield and midbody tergite (Figs 22E–F, 23E–F). Thoracic shield resembling midbody tergite. Midbody tergite with flat and regular posterior margin (pm). Outer area (oa) without setae or tubercles. Inner area (ia) filled with numerous conspicuous long setae. Middle area (ma) with single row of conspicuous, elliptical cuticular impressions (cp); distance between impressions 2–4 times as long as individual diameter. Bristles short, arranged in one row, tip of longest bristles reaching to middle part of outer area.

Pleurites (laterotergites) (Fig. 16P–Q). First pleurite slender, boomerang-like, apical margin (apex) sharp, strongly projecting posterioriad towards paratergite 1. Pleurite 2 short, wider than first one, apical margin obtuse, weakly curved posteriorly. All remaining pleurites flat and wide, lamella-like, with well-rounded apex, not projecting. Densely setose.

Subanal plate of female (Fig. 16R). Trapeziform, undivided, large and broad, apical margin (tip) truncate/slightly concave. Sparsely setose.

Stigmatic plates (Fig. 16E–F). First stigmatic plate (st-pl) large, subsemicircular, tip obtuse. Second stigmatic plates in both sexes subtriangular, not curving.

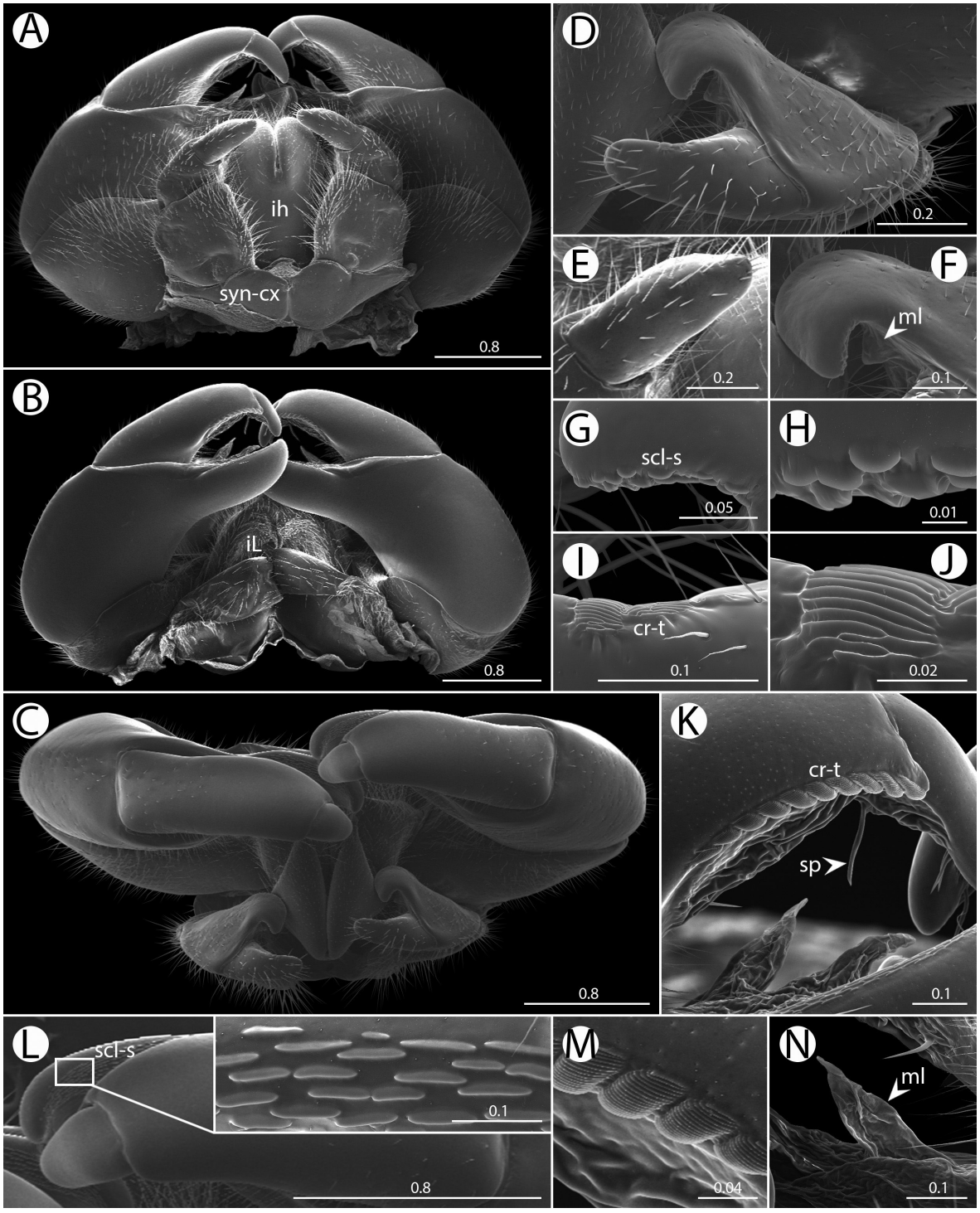

Fig. 17. *Zephronia sukhothaiensis* Srimongkol & Srisonchai sp. nov., male paratype MZKKU-MYR0018 — SEM. **A–C**. Telopods, anterior, posterior and ventral views, respectively. **D**, **F**. Right anterior telopod, ventral views. **E**. Left anterior telopod, anterior view. **G–H**. Sclerotized spots on right anterior telopod, ventral views. **I–J**. Crenulated teeth on right anterior telopod, ventral views. **K**, **M**. Crenulated teeth on left and right posterior telopod, posterior views, respectively. **L**. Sclerotized spots on right posterior telopod, ventral view. **N**. Membranous lobe on right posterior telopod, anterior view. Abbreviations: cr-t = crenulated teeth; ih = inner horns; iL = inner lobes of telopod; ml = membranous lobe; scl-s = sclerotized spots; sp = sclerotized spine; syn-cx = syncoxite. Scale bars in micrometres (μm).

Legs (Fig. 16E–O). All podomeres densely setose. Coxa (cx) large, as long as femur (fe). Coxal process absent in leg-pairs 1 and 2, but present in legs 3–21 with dentate process marginally. Coxa of leg pair 2 in males mesally with conspicuous membranous process (Mp), but absent in females. Prefemur (pre) of leg 10 stout, apico-mesally without projection, mesal margin with inconspicuous spines. Femur of leg 10 slightly short and stout, ca 1.6 times as long as wide, apico-mesally extended, carrying 10–13 small triangular spines (Sp). Femoral ridge (rdg) present and conspicuous in all femurs. Postfemur (po) and tibia (ti) of leg 10 short, tarsus (ta) long, ca 4 times as long as wide. Leg-pairs 1 and 2 without apical spine. Leg-pair 1 with 2–3 ventral spines. Leg-pair 2 with 6–7 ventral spines. Leg-pair 3 with 7–8 ventral spines and 1–3 apical spines. Leg-pair 4 with 7–9 ventral spines and 3 apical spines. Leg-pairs 5–18 with 9–10 ventral spines and 3 apical spines. Leg-pairs 19–21 decreased to 7–8 ventral spines and 3 apical spines. Claw (cl) normal, at base with a notch, conspicuous.

Male sexual characters (Fig. 16G–H). Gonopore (go) large, located at mesal margin, covered by single, triangular, sclerotized, membranous plate, surrounded by long setae. Apical margin of coxae with conspicuous membranous process (Mp), large and long, projecting ventrad.

Anterior telopods (Figs 4S–U, 17A, C–J). With 4 telopoditomeres. Densely setose, except for basal part of telopoditomere 1 and process of telopoditomere 2 (= immovable finger) without setae. First telopoditomere rectangular, large, slightly longer than wide. Telopoditomere 2 stout. Process of telopoditomere 2 quite short, shorter than combination of telopoditomeres 3+4 (= movable finger); tip obtuse, strongly curved and directed anteriad; inner margin with conspicuous membranous lobe (ml), apically with sclerotized spots (scl-s). Telopoditomere 3 twice as long as telopoditomere 4, partly demarcated from telopoditomere 4 by conspicuous suture (clearly visible only in ventral view), with small, short, sclerotized spine (sp), located on conspicuous membranous lobe at inner margin, apically with 3–4 small crenulated teeth (cr-t). Telopoditomere 4 short, tip round, with two small membranous lobes, each with one sclerotized spine on posterior side.

Posterior telopods (Figs 4V–W, 17A–C, K–N). Inner lobes (iL) densely setose. Inner horns (ih) glabrous at base, sharp-edged tip, slightly curving caudad. Telopod with 4 telopoditomeres, covered by numerous long setae, clearly visible in anterior view; base of telopoditomere 1, apical margin of telopoditomeres 2–3 and telopoditomere 4 without setae. First telopoditomere large and stout, slightly longer than wide. Telopoditomere 2 large and stout. Process of telopoditomere 2 (= immovable finger) slightly shorter than combination of telopoditomeres 3+4 (= movable finger); tip obtuse, strongly curved, directed anteroventrad, reaching towards tip of telopoditomere 4; inner margin with conspicuous rows of sclerotized spots (scl-s); margin towards movable finger with two large, swollen, membranous lobes (ml). Telopoditomere 3 long, ca 2.7 times as long as wide, apically curved, inner margin with one sclerotized spine (sp), located on large membranous lobe, posteriorly with row of 10–12 small crenulated teeth (cr-t). Telopoditomere 4 short, 3 times as short as telopoditomere 3, ca 1.5 times as long as wide; inner margin with large, conspicuous, swollen membranous lobe carrying two long evident sclerotized spines; tip slightly round, directed dorsomesad.

Female sexual characters (Fig. 16I–J). Vulva large, covering almost ⅓ of coxa, extending mesally to basal part of prefemur. Bursa (bu) large, apically divided from operculum by triangular groove. Operculum (O) slightly round, narrow dorsoventrally, mesal margin slightly projecting into a well-rounded lobe.

Distribution and habitat

Currently, the new species is known only from its type locality in Sukhothai Province (Fig. 3), specifically near Wat Khao Fang and Tham Yok Monastery. It appears to have a limited distribution and is likely endemic to this region. All specimens were collected from limestone areas (Fig. 14G–H).

Remarks

The new species is characterized by a long and prominent membranous process (Mp) on the second pair of male coxa, a feature also observed in *Z. enghoffi*. In contrast, other closely related species in this group, typically exhibiting a grey body colouration such as *Z. chrysomallos*, *Z. erawani*, and *Z. panhai*, lack this large membranous process. The genetic divergence between the new species and its closest relative, *Z. erawani*, exceeds 11.3%.

Zephronia tratensis Srimongkol & Srisonchai sp. nov.
urn:lsid:zoobank.org:act:3C5B26FF-F3D5-43A0-B20C-533CCF4D7853
Figs 2–3, 5S–X, 18–21, 22G–H, 23G–H

Diagnosis

Zephronia tratensis sp. nov. belongs to the *Zephronia* s. str. species group based on the position of Tömösváry's organ, located next to the aberrant ocelli, not inside the antennal socket. Adult body length medium to large > 19.0 mm (19–38 mm); antenna usually with > 60 apical cones; bristles of midbody endotergum arranged in 2 or 3 rows; legs 4–21 usually with 3 apical spines; posterior telopods with 12–22 crenulated teeth. Similar in these aspects to *Z. enghoffi*, *Z. golovatchi,* and *Z. lannaensis*, but *Z. tratensis* differs from them by having the combination of these characters: light brown or golden brown body colour (vs brown or dark brown); apical margin of operculum of vulva slightly concave (vs round); telopoditomeres 3 and 4 of anterior telopod incompletely demarcated from each other (vs clearly demarcated); process of telopoditomere 2 of anterior telopod very long and curved (vs short).

Etymology

The name is a Latin adjective referring to the province where the type locality occurs.

Type material

Holotype

THAILAND • ♂; Trat Province, Mueang District, Khao Khun Tham Monastery; 12°15′50.6″ N, 102°25′43.7″ E; 53 m a.s.l.; 14 Jun. 2023; N. Srimongkol, R. Srisonchai and MZKKU students leg.; MZKKU- MYR0019.

Paratypes

THAILAND • 13 ♂♂, 18 ♀♀; same data as for holotype; MZKKU- MYR0020 • 1 ♂, 1 ♀; same data as for holotype; NHMUK • 1 ♂, 1 ♀; same data as for holotype; NHMD • 1 ♂, 1 ♀; same data as for holotype; NHMW • 2 ♂♂, 2 ♀♀; same data as for holotype; ZFMK • 1 ♂, 1 ♀; same data as for holotype; CUMZ-zeph0040.

Additional material examined

THAILAND • 19 ♂♂, 23 ♀♀, 1 juvenile; same data as for holotype; MZKKU • 2 ♀♀, broken specimens; same data as for holotype; MZKKU.

Description

Measurements of male holotype. Body length 26.4 mm; width (=broadest) of head=8.4 mm, of collum=8.3 mm, of thoracic shield=15.1 mm, of tergite 7=15.6 mm, of anal shield=14.0 mm; height (=highest) of head=4.2 mm, of collum=7.0 mm, of thoracic shield=7.6 mm, of tergite 7=9.2 mm, of anal shield=7.7 mm.

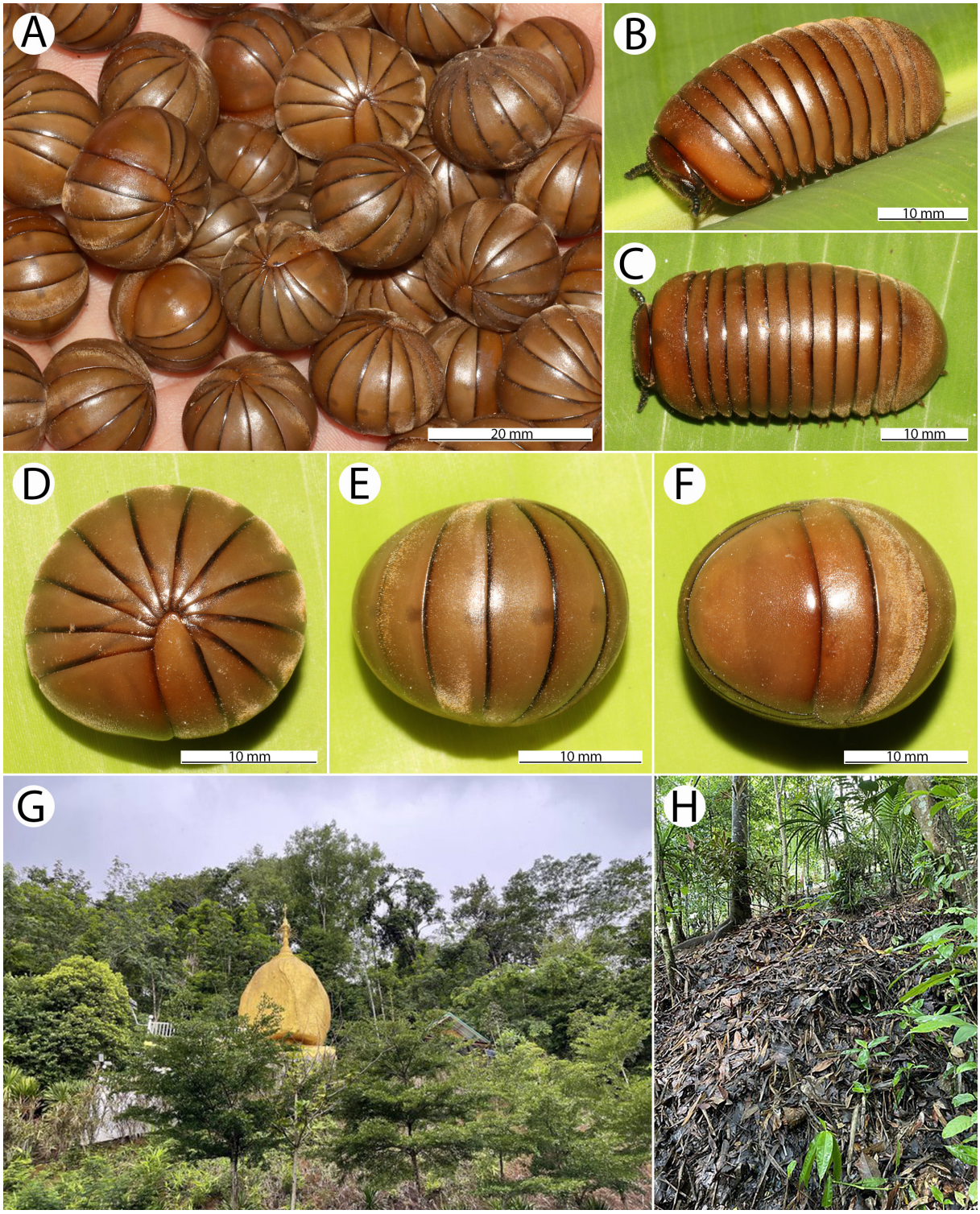

Fig. 18. Photographs of live *Zephronia tratensis* Srimongkol & Srisonchai sp. nov. and habitat. **A–F**. Male paratypes MZKKU-MYR0020. **G–H**. Habitat at the type locality.

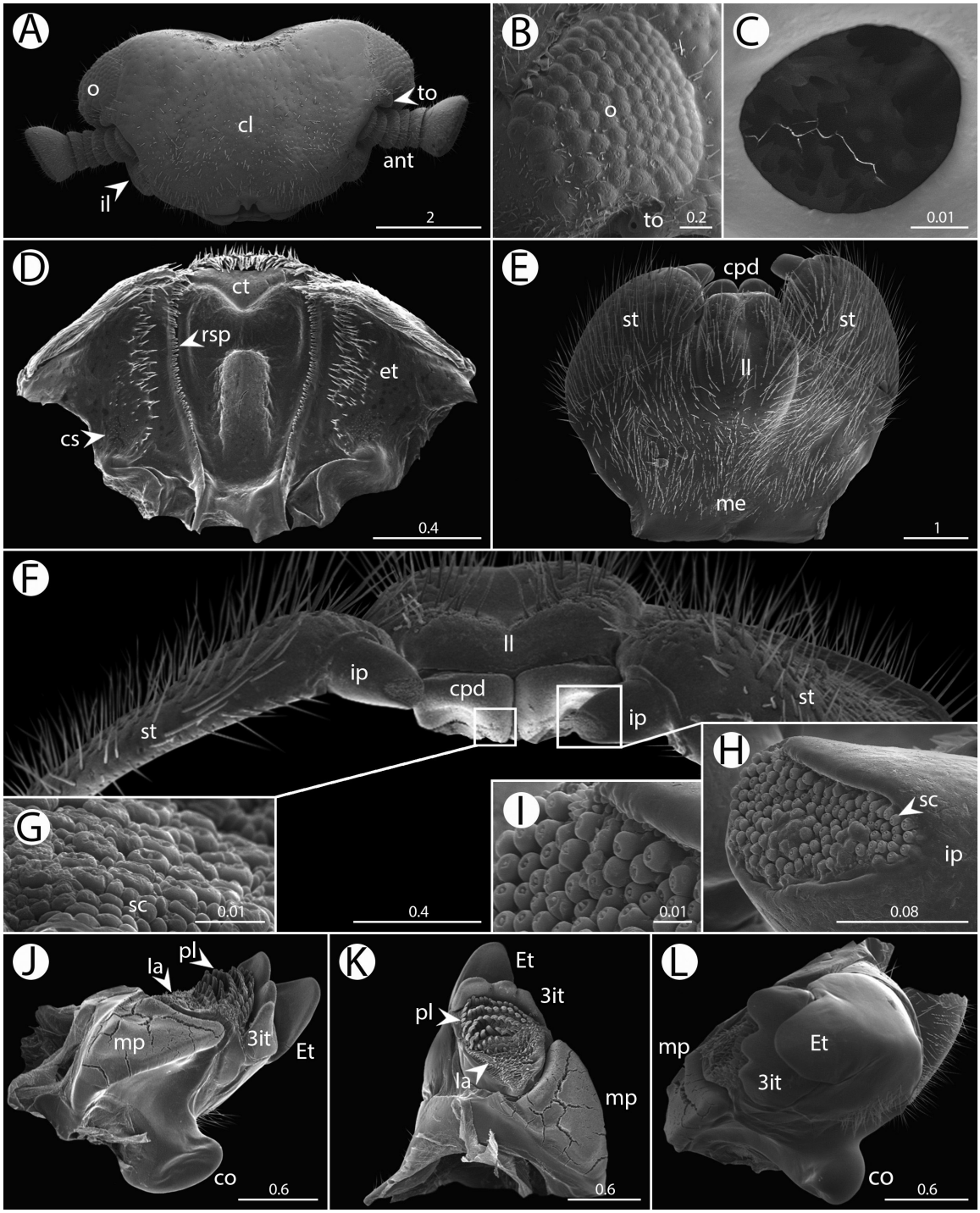

Fig. 19. *Zephronia tratensis* Srimongkol & Srisonchai sp. nov., male paratype MZKKU-MYR0020 — SEM. **A**. Head, anterior view. **B**. Right ommatidia, lateral view. **C**. Left Tömösváry's organ, lateral view. **D**. Epipharynx, ventral view. **E–F**. Gnathochilarium, ventral and frontal views, respectively. **G**. Left central pad, frontal view. **H–I**. Right lateral palpi, frontal views. **J–L**. Right mandible, dorsal, mesal and anterior views, respectively. Abbreviations: 3it = 3-combed inner tooth; ant = antenna; cl = clypeus; co = condylus; cpd = central pad; cs = cuticular scales; ct = central tooth; et = external tooth of epipharynx; Et = external tooth of mandible; Ia = inner area of mandible; il = incisura lateralis; ip = inner palpi; ll = lamellae lingulales; me = mentum; mp = molar plate; o = ommatidia; pl = pectinate lamellae; rsp = row of spines; sc = sensory cone; st = stipites; to = organ of Tömösváry. Scale bars in micrometres (μm).

Measurements of paratypes. Males: body length 19.1–28.5 mm; width (=broadest) of head=6.3–8.9 mm, of collum=5.7–8.6 mm, of thoracic shield=10.6–15.7 mm, of tergite 7=11.0–16.4 mm, of anal shield=9.7–15.0 mm; height (=highest) of head=3.1–4.4 mm, of collum=4.9–7.3 mm, of thoracic shield=5.5–7.5 mm, of tergite 7=7.0–10.4 mm, of anal shield=5.9–9.7 mm. Females: body length 22.8–32.0 mm; width (=broadest) of head=6.9–9.7 mm, of collum=6.5–9.1 mm, of thoracic shield=12.4–17.8 mm, of tergite 7=12.6–18.6 mm, of anal shield=11.8–16.5 mm; height (=highest) of head=4.0–5.7 mm, of collum=5.4–7.8 mm, of thoracic shield=6.2–8.9 mm, of tergite 7=8.1–11.8 mm, of anal shield=6.4–10.0 mm.

Colouration (Fig. 18A–F). Specimens in life light brown or golden brown. Antennae greenish dark. Head, collum, posterior margin of tergites dark brown. Thoracic shield golden brown. Tergites, paratergites, anal shield and a few basal podomeres of legs light brown. Legs greenish brown to greenish dark. Colour in alcohol after 1 year not changed.

Head (Fig. 19A). Subtrapeziform, wide, stout, apically glabrous. Clypeus (cl) with sparse and short setae. Labrum with single tooth on anterior margin. Each eye with 90–100 ommatidia (o). Aberrant ocellus situated near antennal groove (at upper part of groove).

Antennae (Figs 19A, 20A–D). Short; covered with long and dense setae. Lengths ca 4–5 mm; reaching backward to tarsus of leg 2 or 3. Lengths of antennomeres: 6>5>4=3=2=1. Antennomere 6 thickened, extremely widened, flattened apically, axe-shaped; with sensilla basiconica (sb) surrounding antennal disc. Shape of antennae sexually dimorphic, flattened in males. Antennal disc (ad) flat; with 80–85 apical cones (ac) in males and 60–65 cones in females. No sclerotized ridge between antennal socket and ommatidia.

Tömösváry's organ (Fig. 19A–C). Organ of Tömösváry' separated from ommatidium, located midway along protruding brim between antennal groove and ommatidia, smaller in diameter than individual ommatidium. Pore with conspicuous typical coral-liked structure.

Epipharynx (Fig. 19D). Apically with single large central tooth (ct); inner region with one conspicuous sclerotized plate (longitudinal tooth), large and swollen; inner area covered by single row of short conical spines (rsp); outer area of both sides with group of numerous external teeth (et). On each side close to et with field of several cuticular scales (cs).

Gnathochilarium (Fig. 19E–I). Lamellae linguales (ll) oval, slightly truncate apically. Central pads (cpd) with two large and small sensory cones (sc), large one with pillow and small one without a pillow. Stipites (st) stout. Mentum (me) fused, without mentum process. Inner palpi (ip) with big and small sensory cones (sc), big ones oval, arranged together, surrounded by small ones at edge. Lateral palpi inconspicuous.

Mandibles (gnathal lobes) (Fig. 19J–L). Gnathal lobe with undivided external tooth (Et). Inner tooth with 3-cusped (3it). Pectinate lamellae (pl) with 6 rows of conical teeth. Inner area (Ia) consisting of several rows of tiny teeth, spinelike. Condylus (co) with 2–3 distinct ridges at anterior margin. Molar plate (mp) flat, regular.

Tegument (Fig. 18A–F). Quite dull. Thoracic shield, tergite and anal shield covered by short golden setae; each seta located in a tiny pit. Anterior margin of tergite with a lower number of setae than posterior one.

Collum. Quite glabrous; subsemicircular; covered by a few short setae. Tip of lateral margin obtuse.

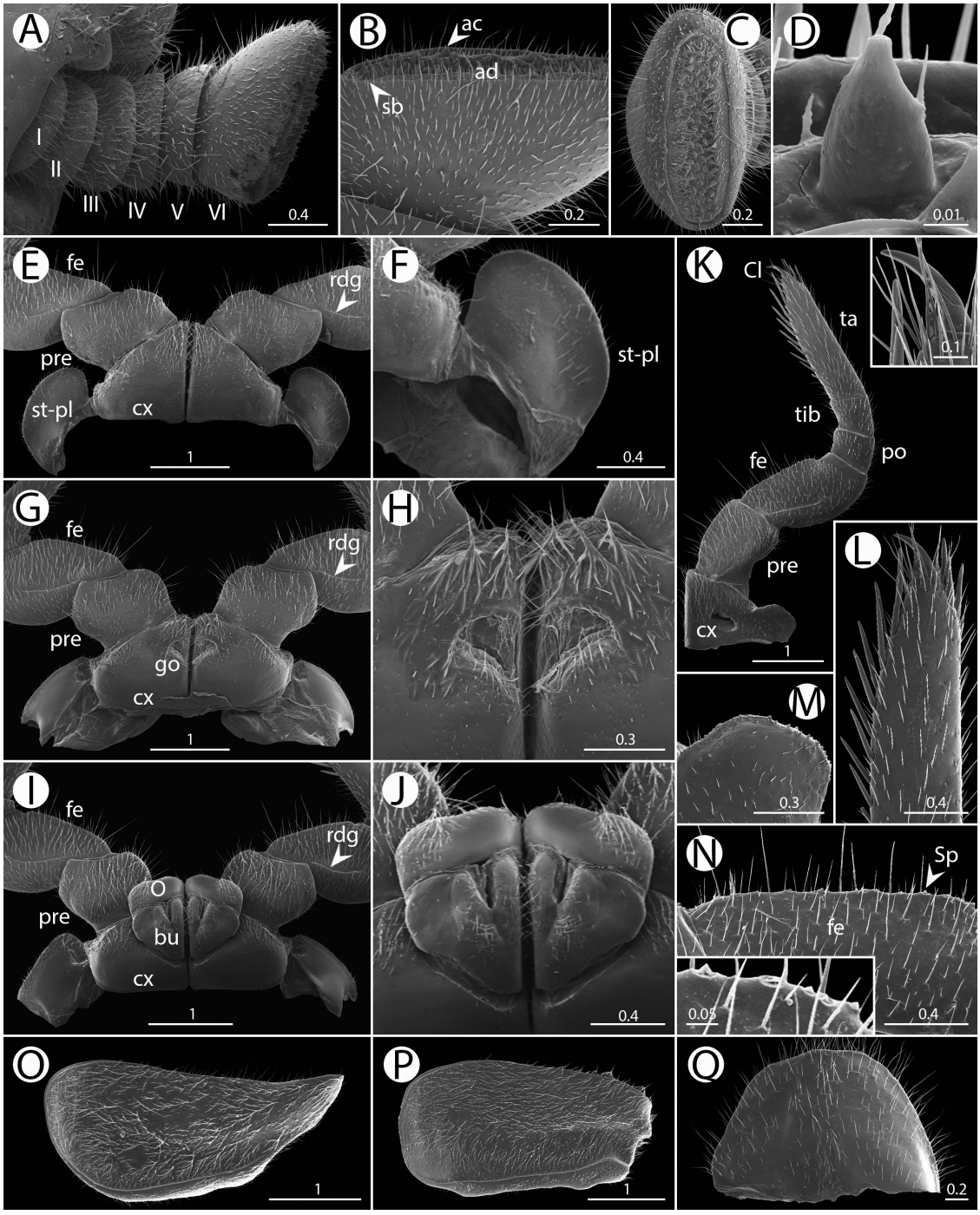

Fig. 20. *Zephronia tratensis* Srimongkol & Srisonchai sp. nov., paratypes MZKKU-MYR0020 — SEM. **A–H**, **K–P**. Male. **I–J**, **Q**. Female. **A–B**. Antenna, anterior and mesal views. **C–D**. Antennal disc and apical cone. **E–F**. First coxae with stigmatic plates, posterior views. **G–H**. Coxae of legs 2 with gonopores, posterior views. **I–J**. Coxae of legs 2 with vulvae, posterior views. **K–L**. Left leg 10, posterior views. **M**. Left coxal process on leg 10, posterior view. **N**. Femur of left leg 10, posterior view. **O**. Right first pleurite, ventral view. **P**. Right midbody pleurite, ventral view. **Q**. Subanal plate, ventral view. Abbreviations: ac = apical cone; ad = antennal disc; bu = bursa; Cl = claw; cx = coxa; fe = femur; go = gonopore; O = operculum; po = postfemur; pre = prefemur; rdg = femoral ridge; sb = sensilla basiconica; Sp = small triangular spines; st-pl = stigmatic plate; ta = tarsus; tib = tibia. Scale bars in micrometres (μm).

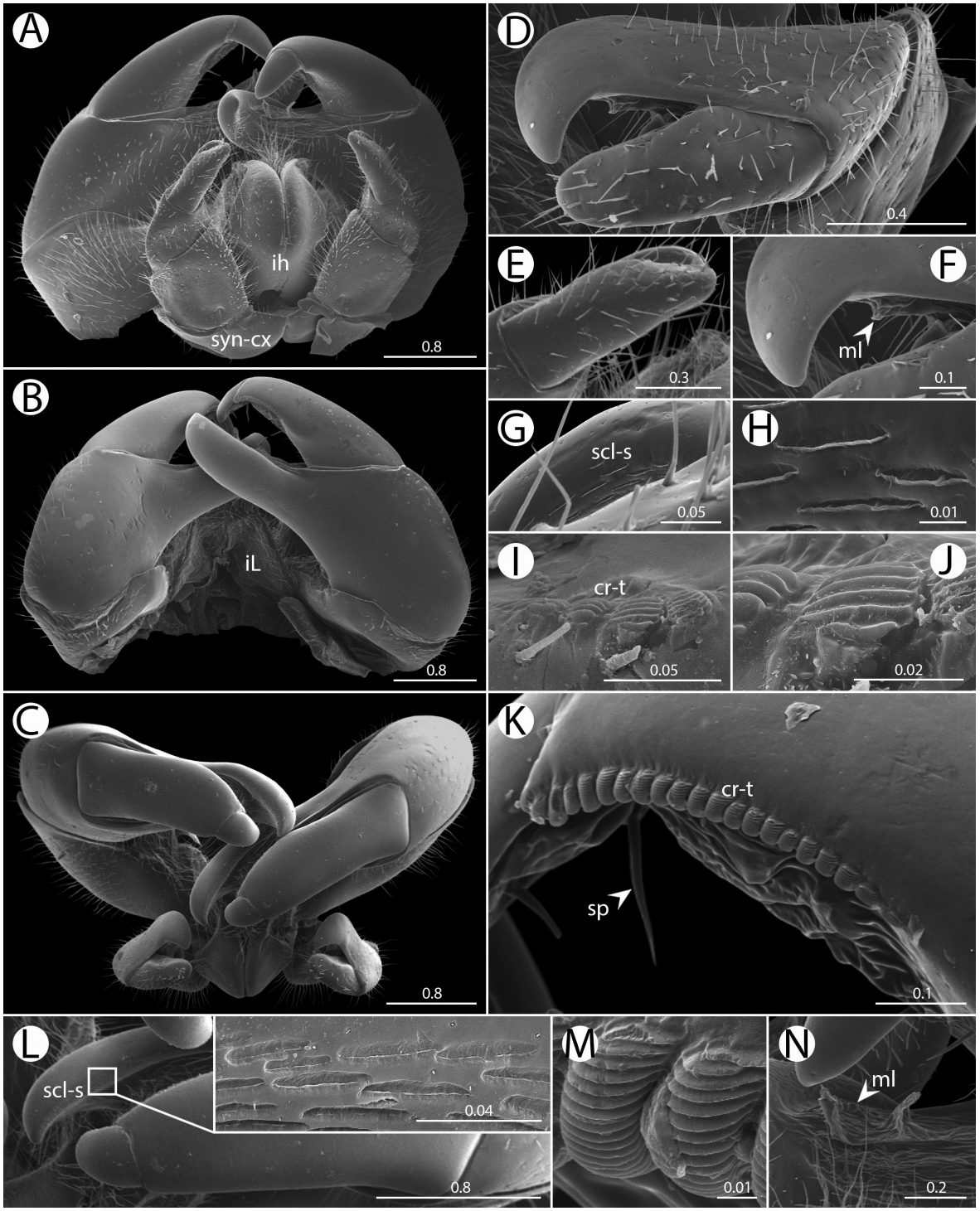

Fig. 21. *Zephronia tratensis* Srimongkol & Srisonchai sp. nov., male paratype MZKKU-MYR0020 — SEM. **A–C**. Telopods, anterior, posterior and ventral views, respectively. **D**, **F**. Right anterior telopod, ventral views. **E**. Left anterior telopod, anterior view. **G–H**. Sclerotized spots on right anterior telopod, ventral views. **I–J**. Crenulated teeth on right anterior telopod, ventral views. **K**, **M**. Crenulated teeth on left posterior telopod, posterior views. **L**. Sclerotized spots on right posterior telopod, ventral view. **N**. Membranous lobe on right posterior telopod, anterior view. Abbreviations: cr-t = crenulated teeth; ih = inner horns; iL = inner lobes of telopod; ml = membranous lobe; scl-s = sclerotized spots; sp = sclerotized spine; syn-cx = syncoxite. Scale bars in micrometres (μm).

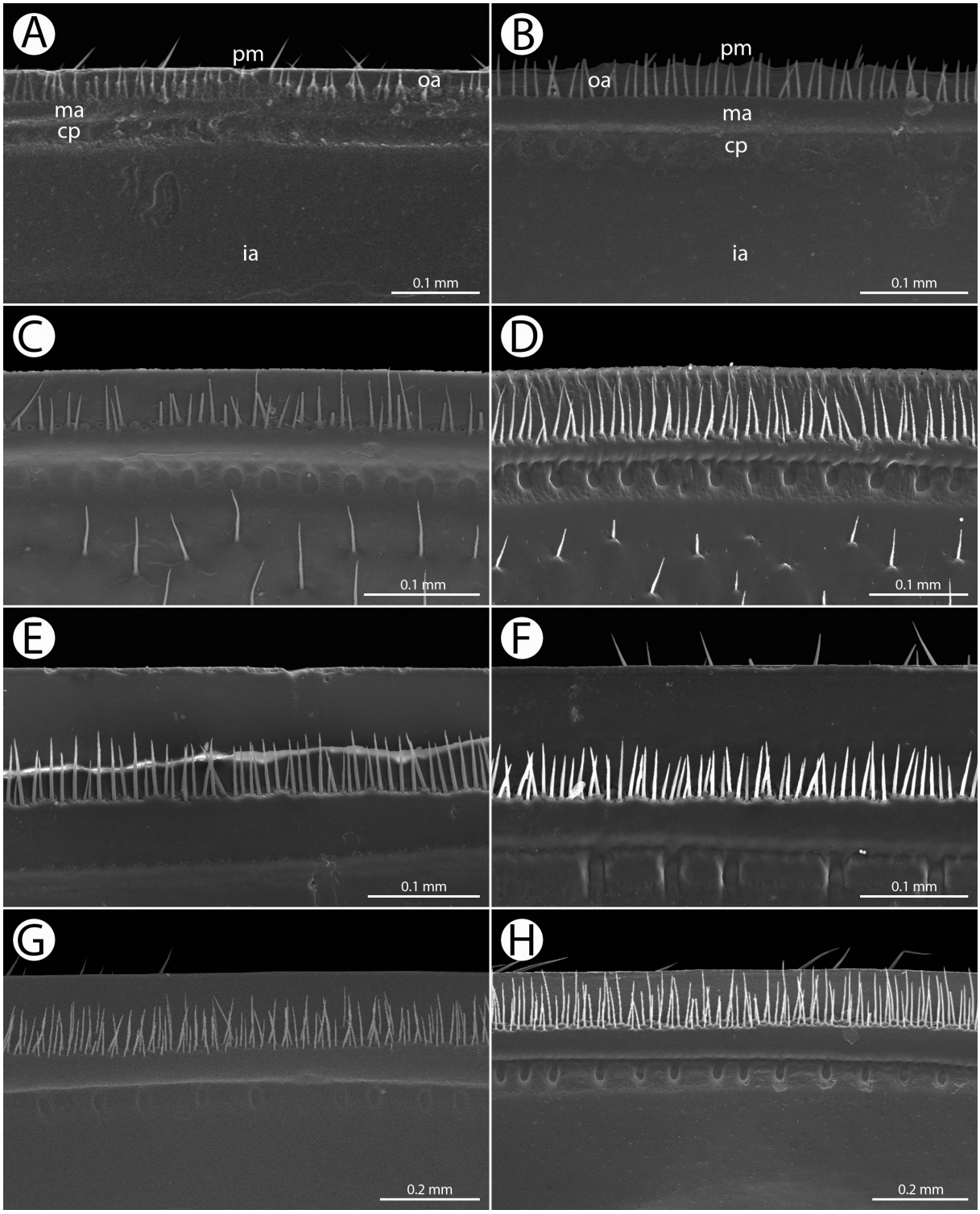

Fig. 22. Endoterga of thoracic shield and tergite 7, all in ventral view — SEM. **A–B**. *Zephronia macula* Srisonchai & Wesener, 2024 (Wat Khao Hin Sorn). **C–D**. *Zephronia ovalis* Gray, 1832 (Huai Chan Waterfall). **E–F**. *Zephronia sukhothaiensis* Srimongkol & Srisonchai sp. nov., male paratype MZKKU-MYR0018. **G–H**. *Zephronia tratensis* Srimongkol & Srisonchai sp. nov., male paratype MZKKU-MYR0020. Abbreviations: cp = cuticular impression; ia = inner area; ma = middle area; oa = outer area; pm = posterior margin.

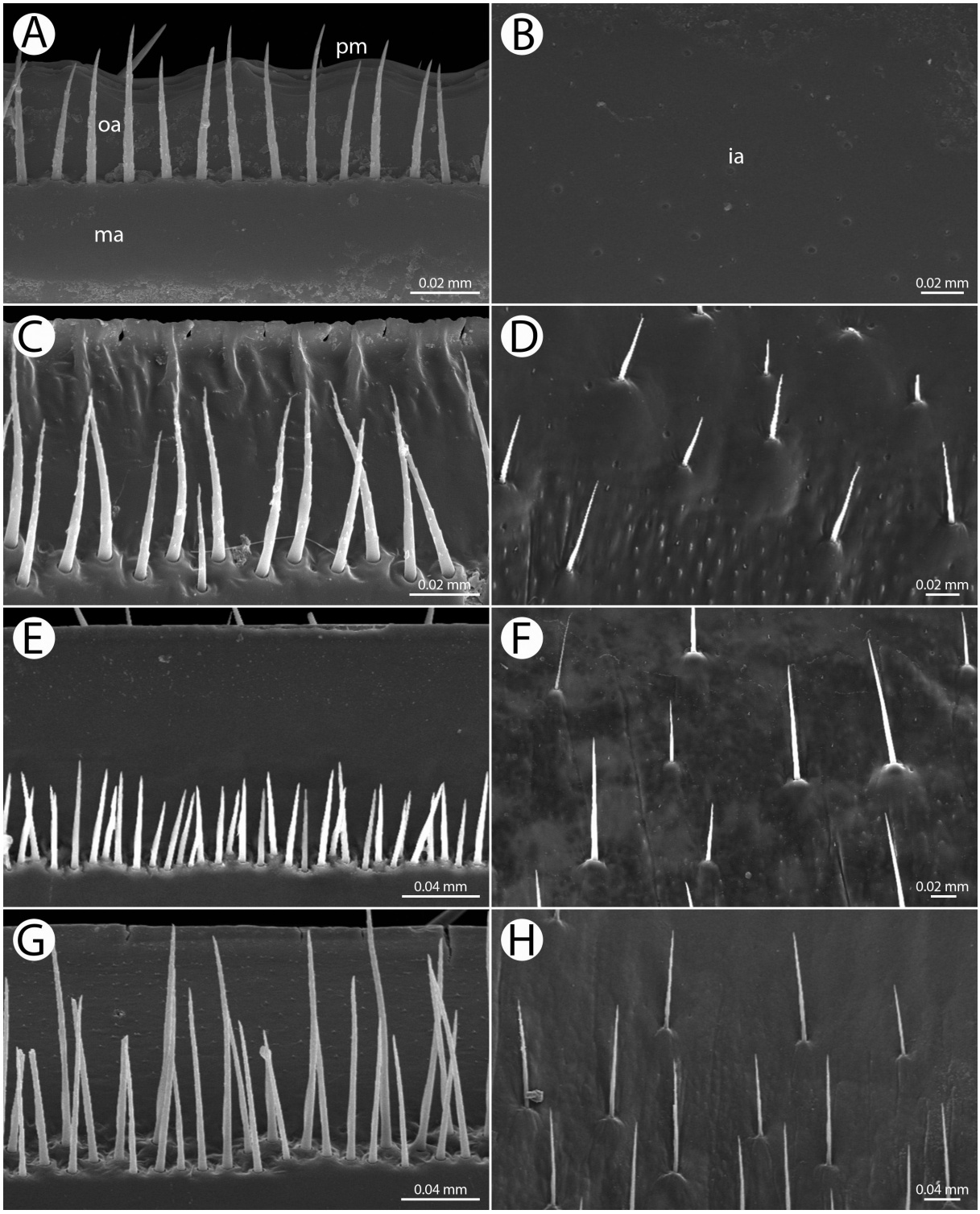

Fig. 23. Endoterga of tergite 7, all in ventral view — SEM. **A–B**. *Zephronia macula* Srisonchai & Wesener, 2024 (Wat Khao Hin Sorn). **C–D**. *Zephronia ovalis* Gray, 1832 (Huai Chan Waterfall, Thailand). **E–F**. *Zephronia sukhothaiensis* Srimongkol & Srisonchai sp. nov., male paratype CUMZ-zeph0018. **G–H**. *Zephronia tratensis* Srimongkol & Srisonchai sp. nov., male paratype CUMZ-zeph0020. Abbreviations: cp = cuticular impression; ia = inner area; ma = middle area; oa = outer area; pm = posterior margin.

Thoracic shield. Anteriorly with shallow, large groove, separated by long ridge. Laterally with conspicuous ridges.

Midbody tergite. Anterior margin with tubercles and single row of conspicuous circular impressions. Inner area with single row of ridges (crenate barrier), separated by shallow groove. Tip of midbody paratergite weakly projecting.

Paratergites (Fig. 18B). Tips of paratergites curved, projecting posteroventrad. Paratergite 1 slender, tip sharp. Paratergites 2–10 wide (wider from front to back), tip obtuse.

Anal shield. Sexually dimorphic, bell-shaped in males and well-rounded in females. Outer surface covered by dense and tiny setae. Inner surface (underside) with single locking carina, ca ⅓ as long as last laterotergite.

Endotergum of thoracic shield and midbody tergite (Figs 22G–H, 23G–H). Thoracic shield as typical as midbody tergites. Midbody tergite with flat margin (pm). Outer area (oa) with tiny scale-liked tubercles. Inner area (ia) covered with setae. Middle area (ma) with single row of elliptical cuticular impressions (cp), distance between impressions 2 times as long as individual diameter. Bristles arranged in two rows, longest one reaching to posterior margin (pm).

Pleurites (laterotergites) (Fig. 20O–P). Densely setose. First pleurite slender, boomerang-like, tip attenuate. Pleurite 2 slightly shorter than first one, tip obtuse. All remaining pleurites flat, wide, lamella-like; apical margins not extended.

Subanal plate of female (Fig. 20Q). Large and wide; semicircular; undivided; central margin (tip) round or convex. Sparsely setose.

Stigmatic plates (Fig. 20E–F). First stigmatic plate (st-pl) oval, wide and broad, apex round. Second stigmatic plate of both sexes subtriangular, without any curve.

Legs (Fig. 20E–N). All podomeres sparsely setose. Coxa (cx) large, as long as prefemur (pre), without membranous process. Coxal process absent in leg-pairs 1 and 2, but present in legs 3–21 with a large and broad dentate ridge. Prefemur (pre) of leg 10 large, apico-mesally without projection or spine. Femur (fe) of leg 10 rather short, ca 1.5 times as long as wide, as long as prefemur, apico-mesally slightly extended mesally, with 9–11 small triangular spines (Sp). Femoral ridge (rdg) conspicuous in all legs. Postfemur (po) and tibia (ti) of leg 10 short. Tarsus (ta) of leg 10 long, ca 3.7 times as long as wide. Leg-pairs 1 and 2 without apical spine. Leg-pair 1 with 2 ventral spines. Leg-pair 2 with 4 ventral spines. Leg-pair 3 with 5–7 ventral spines and 1 apical spine. Leg-pair 4 with 8–10 ventral spines and 2 or 3 apical spines. Leg pairs 5–19 with 8–12 ventral spines and 3 apical spines. Last two leg-pairs with 7–8 ventral spines and 3 apical spines. Claw (cl) normal, at base with notch, conspicuous.

Male sexual characters (Fig. 20G–H). Gonopore (go) large; sparsely setose; covered by single, undivided, triangular membranous plate. Apical margin without membranous process (Mp).

Anterior telopods (Figs 5S–U, 21A, C–J). With 4 telopoditomeres, telopoditomere 3 indistinctly demarcated from telopoditomere 4. Densely setose, except for process of telopoditomere 2 and lower margin of telopoditomere 1 without setae. First telopoditomere large, relatively long, as long as combination of telopoditomeres 3+4 (= movable finger). Telopoditomere 2 large and stout, as long as telopoditomere 3. Process of telopoditomere 2 (= immovable finger) very long and slender, longer than movable finger, tip strongly curved, directed anteriad, close to apex telopoditomere 4; inner margin with sclerotized spots (scl-s) and membranous lobe (ml). Telopoditomere 3 slender, 2 times as long as

telopoditomere 4, incompletely demarcated from telopoditomere 4 when seen in anterior view, with one small, short, sclerotized spine (sp) located on a conspicuous membranous lobe at inner margin, ventrally with 3–4 small crenulated teeth (cr-t). Telopoditomere 4 short, narrows towards tip; tip round, directed mesad, with two small membranous lobes, each with one sclerotized spine on posterior side.

Posterior telopods (Figs 5V–W, 21A–C, K–N). Inner lobes (iL) densely setose. Inner horns (ih) glabrous at base, with sharp-edged tip, strongly curving caudad. With four telopoditomeres. Telopoditomeres 1 and 2 sparsely setose, except for glabrous process of telopoditomere 2. First telopoditomere large and stout, as long as wide. Telopoditomere 2 large. Process of telopoditomere 2 (= immovable finger) slender, slightly longer than combination of telopoditomeres 3+4 (= movable finger), apically curved, directed anteroventrad, reaching towards tip of telopoditomere 4, with conspicuous rows of sclerotized spots (scl-s), margin towards movable finger with two conical membranous lobes (ml). Telopoditomere 3 very long and slender, strongly curved apically, 4 times as long as telopoditomere 4, with one sclerotized spine (sp) located on a large, swollen, membranous lobe, posteriorly with single row of 21 or 22 crenulated teeth (cr-t). Telopoditomere 4 slender, inner margin with large, conspicuous, swollen, membranous lobe carrying two evident sclerotized spines, tip directed dorsomesad.

Female sexual characters (Fig. 20I–J). Vulva large and broad, covering ca ⅓ of coxa, located at mesal side, extending mesally to basal half of prefemur. Bursa (bu) large, with triangular groove. Operculum (O) slightly wide dorsoventrally, tip truncate/slightly concave, not protruding.

Distribution and habitat

Currently, the new species is known only from the type locality in Trat Province (Fig. 3). We assume that this species occurs in a small distribution area regarded here as endemic to the Thai fauna. All specimens were seen crawling on the thick leaf litter beside the trail (Fig. 18G–H).

Remarks

The interspecific distance between the new species to the closely related species (*Z. golovatchi*) is more than 13%.

Zephronia viridisoma Rosenmejer & Wesener, 2021
Figs 1, 3

Zephronia viridisoma Rosenmejer & Wesener in Rosenmejer *et al*., 2021: 121.

Zephronia viridisoma – Likhitrakarn *et al*. 2023: 57.

Distribution

Nakhon Si Thammarat Province (Fig. 3).

Remarks

Endemic. Known to occur in limestone habitats. See Rosenmejer *et al*. (2021: figs 7–12).

Key to species of Zephronia Gray, 1832 in Thailand

1. Adult body coloration in life grey/greyish brown/brownish grey/light grey. Western Thailand 2
– Adult body coloration in life brown/golden brown/dark brown/greenish brown/reddish brown/green. All regions of Thailand 5

2. Body small to medium (length ca 20 mm) (Figs 4X, 14A–F). Bristles of midbody endotergum arranged in one row (Figs 22E–F, 23E). Antennomere 6 of antenna with ca 20–45 apical cones. Second coxa in male with a large and conspicuous membranous process (Fig. 16G–H). Anterior telopods: process of telopoditomere 2 strongly curved (Figs 4U, 17C–D, F) ..... ***Z. sukhothaiensis*** Srimongkol & Srisonchai sp. nov.
– Body medium to large (length 20–40 mm) (Fig. 4F, L, R). Bristles of midbody endotergum arranged in 2 or 3 rows. Antennomere 6 of antenna with ca 50–90 apical cones. Second coxa in male without membranous process. Anterior telopods: process of telopoditomere 2 slightly curved (Fig. 4C, I, O) 3

3. Endotergum: posterior margin with 3 rows of bristles ..... ***Z. erawani*** Bhansali & Wesener, 2022
– Endotergum: posterior margin with 2 rows of bristles 4

4. Body length 19–23 mm (Fig. 4R). Antennomere 6 of antenna with ca 50 apical cones. Tarsus of leg-pairs 5–21 usually with 7–11 ventral spines and 1–3 apical spines ..... ***Z. panhai*** Srisonchai, Sutcharit & Likhitrakarn, 2021
– Body length ca 40 mm (Fig. 4F). Antennomere 6 of antenna with 78/88 apical cones. Tarsus of leg-pairs 5–21 usually with 10–12 ventral spines and 3 or 4 apical spines ..... ***Z. chrysomallos*** Bhansali & Wesener, 2022

5. Tarsus of leg-pairs 5–21 with only one apical spine 6
– Tarsus of leg-pairs 5–21 with 2 apical spines or more 8

6. Body green. Antennomere 6 of antenna apically swollen, not axe-shaped. Bristles of midbody endotergum arranged in 3 rows ..... ***Z. viridisoma*** Rosenmejer & Wesener, 2021
– Body brown/greenish, brown/reddish, brown/dark green. Antennomere 6 of antenna apically axe-shaped, apically expanded. Bristles of midbody endotergum arranged in one row 7

7. Tergite without spots. Subanal plate: apical margin usually concave. Vulva: operculum of vulva narrow dorsoventrally; mesal margin protruding into an oval lobe ..... ***Z. chantaburiensis*** Srisonchai & Wesener, 2024
– Tergite with dark or greenish dark spots (Fig. 6A–B) and without spots (Fig. 6C–F). Subanal plate: apical margin usually truncate (Fig. 8Q). Vulva: operculum broad and wide dorsoventrally; mesal margin not protruding (Fig. 8I–J) ..... ***Z. macula*** Srisonchai & Wesener, 2024

8. Body length 15–20 mm (< 26.5 mm). Tergites with two yellowish brown or yellowish gold patches 9
– Body length 30–40 mm (<41.2 mm). Tergites without patches 10

9. Posterior telopods: process of telopoditomere 2 (immovable finger) shorter than combination of telopoditomeres 3+4 ..... ***Z. siamensis*** Hirst, 1907
– Posterior telopods: process of telopoditomere 2 equal in length to / longer than telopoditomeres 3+4 (Fig. 13B–C) ..... ***Z. ovalis*** Gray, 1832

10. Body dark green. Bristles of midbody endotergum arranged in 4–6 rows ..... ***Z. phrain*** Likhitrakarn & Golovatch, 2021
– Body brown. Bristles of midbody endotergum arranged in 2 or 3 rows 11

11. Anterior telopods: process of telopoditomere 2 very long, longer than combination of telopoditomeres 3+4 (Figs 5U, 21C–D) .....***Z. tratensis*** Srimongkol & Srisonchai sp. nov.
– Anterior telopods: process of telopoditomere 2 shorter than/equal in length to combination of telopoditomeres 3+4 (Fig. 5C, I, O) 12

12 Bristles of midbody endotergum arranged in 2 or 3 rows; tip of longest bristles not reaching to posterior margin ..... ***Z. lannaensis*** Likhitrakarn & Golovatch, 2021
– Bristles of midbody endotergum arranged in 2 rows of marginal bristles; tip of longest bristles reaching above posterior margin 13

13. Second coxa in male with conspicuous membranous process. Vulva: operculum slender and narrow. Subanal plate subsemicircular; apical margin (tip) shallowly concave, narrow ....***Z. enghoffi*** Srisonchai, Sutcharit & Likhitrakarn, 2021
– Second coxa in male without membranous process. Vulva: operculum round and wide. Subanal plate trapeziform; apical margin (tip) strongly concave, wide .... ***Z. golovatchi*** Srisonchai, Sutcharit & Likhitrakarn, 2021

Discussion

Previous comprehensive work (Wesener 2019; Srisonchai *et al*. 2024) has provided valuable insights into key taxonomic characters essential for distinguishing species within the genus *Zephronia*. The two new species described in this study clearly belong to the *Zephronia* sensu stricto species group, as evidenced by the Tömösváry organ being located on the edge (brim) rather than within the antennal groove (see diagnostic details in Srisonchai *et al*. 2024). In addition, both species exhibit a unique colouration: *Z. sukhothaiensis* Srimongkol & Srisonchai sp. nov. is characterized by a distinct brownish-grey body, while *Z. tratensis* Srimongkol & Srisonchai sp. nov. displays a yellowish-brown appearance.

The two new species are morphologically, genetically, and geographically distinct from all known congeners. Genetic barcoding analysis based on a 658 bp fragment of mitochondrial COI barcode gene reveals substantial genetic divergence from other species in the genus, ranging from 11.26% to 21.19% for *Z. sukhothaiensis* sp. nov. and from 12.63% to 22.68% for *Z. tratensis* sp. nov. These values fall well within the range considered sufficient for species-level differentiation and are consistent with ranges reported in previous studies (Rosenmejer *et al*. 2021; Bhansali & Wesener 2022; Srisonchai *et al*. 2024). Although the COI-based barcoding results provide tentative insights into position of two new species, it does not offer strong resolution regarding the evolutionary relationships within *Zephronia* and its closely related genus *Sphaerobelum*. Clarifying these relationships will likely require a more comprehensive approach, including multi-gene phylogenetic analyses in combination with detailed morphological comparisons.

As *Zephronia* is a large and morphologically diverse genus with a wide distribution, a full systematic revision remains challenging, especially given the scarcity of molecular data for many previously described species. For the time being, the most effective approach is to progressively describe new species and document local records using integrative evidence from smaller groups or regional faunas. This stepwise accumulation of morphological and molecular data from different countries will ultimately provide the foundation for a comprehensive revision of the entire genus.

This study also records *Z. ovalis* for the first time from northeastern Thailand. Although originally described from Cat Tien National Park in Vietnam, its distribution almost certainly extends into southern Vietnam, southern Laos, and northeastern Cambodia. It is expected in provinces such as Mondulkiri, Kratie, Stung Treng, Ratanakiri, and Preah Vihear, which are geographically connected to Vietnam and Thailand. These regions are linked by continuous lowland forests along the Mekong River basin

which likely served as ecological corridors facilitating dispersal of *Z. ovalis* across mainland Southeast Asia. Such broad transboundary distributions are rarely present among giant pill-millipedes, examples include *Z. phrain*, *S. aesculus* Rosenmejer & Wesener, 2021, and *S. onyx* Srikampha & Srisonchai, 2025, which have been documented up to 200–300 km from their original type localities (Rosenmejer *et al*. 2021; Srisonchai *et al*. 2021; Srikampha *et al*. 2025). Populations of *Z. ovalis* from Thailand and Vietnam are morphologically almost identical, sharing a characteristic dark-greenish body. Minor differences in antennal cones, posterior telopod dentition, and endotergal bristle arrangement are negligible. Genetic data support this conclusion, with a COI divergence of about 5.6% between Thai and Vietnamese populations, which is at a level that is consistent with intraspecific variation among giant pill-millipedes. This finding represents a clear example of isolation by distance, where geographically separated populations of the same species begin to diverge genetically, indicating that evolutionary processes are ongoing (Srikampha *et al*. 2025).

Based on a comparatively large number of newly collected specimens, *Zephronia macula* is here newly recorded from the Chachoengsao and Rayong provinces. Notably, all individuals from these populations exhibited a uniform green body colour without any spots on the tergites ("green" morph) which clearly contrasts with the originally described "spotted" morph reported by Srisonchai *et al*. (2024). Nevertheless, the detailed morphological examination confirms a close correspondence with the spotted morph, supporting their inclusion within *Z. macula*. Genetic data further corroborate this, grouping the two morphs as a single species with strong support (BS = 100, PP = 1), despite showing intraspecific divergence of 3.2–5.0%. This extreme morphological plasticity serves as an example for the taxonomist by demonstrating that reliance on external traits such as colouration or colour patterns is sometimes inadequate for accurate species identification within the genus. Similar cases of morphological variation within a single species have been observed in other giant pill-millipedes, such as *Z. phrain* which includes two colour forms: dark green in the type locality and dark brown in another population (Srisonchai *et al*. 2021). Comparable extensive intraspecific variation has also been reported in the pill millipede *Glomeris klugii* Brandt, 1833, which exhibits more than 40 distinct colour morphs while still being treated as a single species (Wesener & Conrad 2016). Moreover, in the Australian millipede *Antichiropus variabilis* Attems, 1911, substantial morphological differences in genital traits occur within genetically cohesive populations, underscoring that striking phenotypic divergence does not necessarily equate to species-level separation (Wojcieszek & Simmons 2012). Additional undescribed species from southern Thailand also show distinct colour variation despite being genetically similar (T. Wesener unpublished data). The evidence presented here underscores the need for an integrative approach incorporating molecular data to ensure taxonomic accuracy. Whether the observed colour variation in *Z. macula* reflects natural phenotypic plasticity, as seen in other arthropods (Schielzeth & Dieker 2020), or results from differences in diet, habitat, or a combination of these factors, remains an open question that merits further study.

With the addition of these records, the number of species of *Zephronia* known from Thailand now totals 14. This strongly suggests that further undescribed taxa remain to be discovered. The surge in millipede discoveries in the country since 2019 (Pimvichai *et al*. 2020; Srisonchai *et al*. 2018, 2021) underscores Thailand's rich but underexplored biodiversity, particularly within natural habitats that remain poorly surveyed (Clements *et al*. 2006; Grismer *et al*. 2020). Giant pill-millipedes thus represent a significant component of Southeast Asia's faunal diversity, especially in Thailand and neighboring regions.

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References

American Veterinary Medical Association. 2020. *AVMA Guidelines for the Euthanasia of Animals: 2020 Edition*. Available from https://www.avma.org/sites/default/files/2020-02/Guidelines-on-Euthanasia-2020.pdf [accessed 14 Mar. 2025].

Attems C. 1914. Die indo-australischen Myriopoden. *Archiv für Naturgeschichte* 80A: 1–398. Berlin. Available from https://www.biodiversitylibrary.org/page/13260451#page/557/mode/1up [accessed 18 Apr. 2026].

Attems C. 1936. Diplopoda of India. *Memoirs of the Indian Museum* 11: 133–323.

Bhansali S. & Wesener T. 2022. New Thai giant pill-millipede species, with new genetic barcoding data (Diplopoda, Sphaerotheriida, Zephroniidae). *Zootaxa* 5105 (3): 357–380. https://doi.org/10.11646/zootaxa.5105.3.2

Butler A.G. 1873. A monographic revision of the genera *Zephronia* and *Sphaerotherium*, with descriptions of new species. *Proceedings of the Zoological Society of London* 1873: 172–182. Available from https://www.biodiversitylibrary.org/part/325937 [accessed 18 Apr. 2026].

Clements R., Sodhi N.S., Schilthuizen M. & Ng P.K. 2006. Limestone karsts of Southeast Asia: Imperiled arks of biodiversity. *BioScience* 56 (9): 733–742. https://doi.org/10.1641/0006-3568(2006)56[733:LKOSAI]2.0.CO;2

Darriba D., Taboada G.L., Doallo R. & Posada D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772–772. https://doi.org/10.1038/nmeth.2109

Decker P. 2010. Contributions to the myriapod fauna of Thailand – new records of millipedes and centipedes from Thailand (Myriapoda: Diplopoda, Chilopoda). *Schubartiana* 4: 23–34. Available from http://www.schubartiana.de/issues/pdf/vol4/Decker-2010-Myriapod_fauna_of_Thailand.pdf [accessed 18 Apr. 2026].

Donworth P. & Wesener T. 2024. The first record of the giant pill-millipede genus *Prionobelum* Verhoeff, 1924 from Thailand, with the integrative description of two species (Diplopoda, Sphaerotheriida, Zephroniidae). *Zootaxa* 5419 (4): 545–562. https://doi.org/10.11646/zootaxa.5419.4.4

Edgecombe G.D. & Giribet G. 2004. Adding mitochondrial sequence data (16S rRNA and cytochrome c oxidase subunit I) to the phylogeny of centipedes (Myriapoda: Chilopoda): an analysis of morphology and four molecular loci. *Journal of Zoological Systematics and Evolutionary Research* 42 (2): 89–134. https://doi.org/10.1111/j.1439-0469.2004.00245.x

Enghoff H. 2005. The millipedes of Thailand (Diplopoda). *Steenstrupia* 29 (1): 87–103.

Folmer O., Black M., Hoeh W., Lutz R. & Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3 (5): 294–299.

Gervais P. 1837. Études pour servir à l'histoire naturelle des Myriapodes. *Annales des Sciences naturelles, Zoologie* Série 2 7: 35–60. Available from https://www.biodiversitylibrary.org/part/28836 [accessed 18 Apr. 2026].

Golovatch S.I., Wesener T., Mauriès J.P. & 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://doi.org/10.15298/arthsel.21.4.01

Gray G. 1832. The Myriapods (Myriapoda – Mitosata). *In*: Griffith E. & Pidgeon E. (eds) *The Class Insecta arranged by the Baron Cuvier. Vol. 2*: 1–769. London.

Grismer L.L., Wood P.L. Jr, Le M.D., Quah E.S.H. & Grismer J.L. 2020. Evolution of habitat preference in 243 species of bent-toed geckos (Genus *Cyrtodactylus* Gray, 1827) with a discussion of karst habitat conservation. *Ecology and Evolution* 10 (24): 13717–13730. https://doi.org/10.1002/ece3.6961

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://doi.org/10.1080/00222930709487327

Jeekel C.A.W. 2001. A bibliographic catalogue of the Asiatic Sphaerotheriida (Diplopoda). *Myriapod Memoranda* 3: 5–38.

Katoh K., Rozewicki J. & Yamada K.D. 2019. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics 20 (4): 1160–1166. https://doi.org/10.1093/bib/bbx108

Koch C.L. 1847. *System der Myriapoden, mit den Verzeichnissen und Berichtigungen zu Deutschlands Crustaceen, Myriapoden und Arachniden*. Pustet, Regensburg. https://doi.org/10.5962/bhl.title.49866

Kumar S., Stecher G. & Tamura K. 2016. MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33 (7): 1870–1874. https://doi.org/10.1093/molbev/msw054

Likhitrakarn N., Golovatch S.I., Srisonchai R. & Sutcharit C. 2021. Two new species of the giant pill-millipede genus *Zephronia* Gray, 1832 from Thailand (Diplopoda: Sphaerotheriida: Zephroniidae). *Tropical Natural History* 21: 12–26. https://doi.org/10.58837/tnh.21.1.247730

Likhitrakarn N., Srisonchai R. & Golovatch S.I. 2023. An updated catalogue of the Millipedes (Diplopoda) of Thailand. *Tropical Natural History Supplement* 7: 51–92. https://doi.org/10.58837/tnh.23.7.258815

Miller M.A., Pfeiffer W. & Schwartz T. 2010. Creating the CIPRES science gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*: 1–8. IEEE, New Orleans, Louisiana, USA. https://doi.org/10.1109/GCE.2010.5676129

Minh B.Q., Schmidt H.A., Chernomor O., Schrempf D., Woodhams M.D., von Haeseler A. & Lanfear R. 2020. IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* 37: 1530–1534. https://doi.org/10.1093/molbev/msaa015

Newport G. 1844. A list of the species of Myriapoda, Order Chilognatha, contained in the cabinets of the British Museum, with descriptions of a new genus and thirty-two new species. *Annals and Magazine of Natural History; Zoology, Botany, and Geology* 13 (84): 263–270. https://doi.org/10.1080/03745484409442605

Olliff A.S. 1882. Description of a new species of the genus *Zephronia*, from Borneo. *Cistula Entomologica* 3 (26): 29–30. Available from https://www.biodiversitylibrary.org/part/403019 [accessed 18 Apr. 2026].

Pimvichai P., Enghoff H., Panha S. & 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 (6): 591–617. https://doi.org/10.1071/IS20031

Rambaut A. 2018. Figtree ver. 1.4.4. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh. Available from https://github.com/rambaut/figtree/releases [accessed 11 Sep. 2024].

Ronquist F., Teslenko M., van der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M.A. & Huelsenbeck J.P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61 (3): 539–542. https://doi.org/10.1093/sysbio/sys029

Rosenmejer T., Enghoff H., Moritz L. & Wesener T. 2021. Integrative description of new giant pill-millipedes from southern Thailand (Diplopoda, Sphaerotheriida, Zephroniidae). *European Journal of Taxonomy* 762: 108–132. https://doi.org/10.5852/ejt.2021.762.1457

Schielzeth H. & Dieker P. 2020. The green-brown polymorphism of the club-legged grasshopper *Gomphocerus sibiricus* is heritable and appears genetically simple. *BMC Ecology and Evolution* 20: 63. https://doi.org/10.1186/s12862-020-01630-7

Semenyuk I., Golovatch S.I. & Wesener T. 2018. 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

Semenyuk I., Golovatch S.I. & Wesener T. 2020. Some new or poorly-known Zephroniidae (Diplopoda, Sphaerotheriida) from Vietnam. *ZooKeys* 930: 37–60. https://doi.org/10.3897/zookeys.930.47742

Srikampha K., Wesener T., Likhitrakarn N., Sutcharit C. & Srisonchai R. 2025. The millipede genus *Sphaerobelum* Verhoeff, 1924, in Thailand, with descriptions of three new species (Diplopoda, Sphaerotheriida, Zephroniidae). *Zoosystematics and Evolution* 101 (1): 273–300. https://doi.org/10.3897/zse.101.143073

Srisonchai R., Enghoff H., Likhitrakarn N. & Panha S. 2018. A revision of dragon millipedes I: Genus *Desmoxytes* Chamberlin, 1923, with the description of eight new species (Diplopoda, Polydesmida, Paradoxosomatidae). *ZooKeys* 761: 1–177. https://doi.org/10.3897/zookeys.761.24214

Srisonchai R., Sutcharit C. & Likhitrakarn N. 2021. The giant pill-millipede genus *Zephronia* Gray, 1832 from Thailand, with a redescription of *Z. siamensis* Hirst, 1907 and descriptions of three new species (Diplopoda, Sphaerotheriida, Zephroniidae). *ZooKeys* 1067: 19–56. https://doi.org/10.3897/zookeys.1067.72369

Srisonchai R., Likhitrakarn N., Sutcharit C., Backeljau T. & Pimvichai P. 2023. A new jewel-like species of the pill-millipede genus *Sphaerobelum* Verhoeff, 1924 (Diplopoda, Sphaerotheriida, Zephroniidae) from Thailand. *ZooKeys* 1181: 41–57. https://doi.org/10.3897/zookeys.1181.109076

Srisonchai R., Likhitrakarn N., Sutcharit C. & Wesener T. 2024. Integrative taxonomy reveals two new giant pill-millipedes of the genus *Zephronia* Gray, 1832 from eastern Thailand (Diplopoda, Sphaerotheriida, Zephroniidae). *ZooKeys* 1212: 29–64. https://doi.org/10.3897/zookeys.1212.126536

Tanabe A.S. 2011. Kakusan4 and Aminosan: two programs for comparing nonpartitioned, proportional and separate models for combined molecular phylogenetic analyses of multilocus sequence data. *Molecular Ecology Resources* 11: 914–921. https://doi.org/10.1111/j.1755-0998.2011.03021.x

Wesener T. 2014. A new phylogenetic analysis of the Sphaerotheriida (Diplopoda) with a revision of the Australian giant pill-millipedes. *Invertebrate Systematics* 28 (2): 196–213. https://doi.org/10.1071/IS13048

Wesener T. 2015. Integrative redescription of a forgotten Italian pill millipede endemic to the Apuan Alps – *Glomeris apuana* Verhoeff, 1911 (Diplopoda, Glomerida, Glomeridae). *Zootaxa* 4039 (2): 391–400. https://doi.org/10.11646/zootaxa.4039.2.11

Wesener T. 2016. 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. 2018. An integrative and citizen science based approach to the rediscovery and redescription of the only known high-altitude endemic pill millipede, *Glomeris aurita* Koch (Diplopoda, Glomerida). *PeerJ* 6: e5569. https://doi.org/10.7717/peerj.5569

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. & Conrad C. 2016. Local hotspots of endemism or artifacts of incorrect taxonomy? The status of microendemic pill millipede species of the genus *Glomeris* in northern Italy (Diplopoda, Glomerida). *PLoS ONE* 11 (9): e0162284. https://doi.org/10.1371/journal.pone.0162284

Wesener T., Raupach M.J. & Sierwald P. 2010. The origins of the giant pill-millipedes from Madagascar (Diplopoda: Sphaerotheriida: Arthrosphaeridae). *Molecular Phylogenetics and Evolution* 57: 1184–1193. https://doi.org/10.1016/j.ympev.2010.08.023

Willett W., Jenny B., Isenberg T. & Dragicevic P. 2015. Lightweight relief shearing for enhanced terrain perception on interactive maps. *Proceedings of the 33rd ACM Conference on Human Factors in Computing Systems (CHI 2015)*: 3563–3572. AMC, Seoul, South Korea. https://doi.org/10.1145/2702123.2702172

Wongthamwanich N., Panha S., Sierwald P., Wesener T. & Thirakhupt K. 2012. A new species of the giant pill-millipede genus *Sphaerobelum* Verhoeff, 1924 from northern Thailand, with an extensive description and molecular characters (Diplopoda: Sphaerotheriida: Zephroniidae). *Zootaxa* 3220: 29–43. https://doi.org/10.11646/zootaxa.3220.1.2

Wojcieszek J.M. & Simmons L.W. 2012. Evidence for stabilizing selection and slow divergent evolution of male genitalia in a millipede (*Antichiropus variabilis*). *Evolution* 66 (4): 1138–1153. https://doi.org/10.1111/j.1558-5646.2011.01509.x

Zhao Y., Yu J. & Liu W. 2020. A molecular-based phylogeny of the millipede genus *Sphaerobelum* Verhoeff, 1924, with the first record of the genus from mainland China (Diplopoda: Sphaerotheriida: Zephroniidae). *Annales de la Société entomologique de France (N.S.)* 56 (4): 341–348. https://doi.org/10.1080/00379271.2020.1811153

Zhao Y., Hu L., Wesener T. & Liu W. 2022. Five new species of the giant pill-millipedes of the genera *Zephronia* and *Sphaerobelum*, from China (Diplopoda: Sphaerotheriida: Zephroniidae). *Annales de la Société entomologique de France (N.S.)* 58 (6): 499–524. https://doi.org/10.1080/00379271.2022.2137059

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Supplementary files

Supp. file 1. Estimates of cytochrome C oxidase I (COI) sequence divergences (uncorrected *p*-distances) within and among species of *Zephronia* Gray, 1832 and related genera.
https://doi.org/10.5852/ejt.2026.1053.3275.14455

Supp. file 2. COI-based barcoding tree of the genus *Zephronia* Gray, 1832 and related genera inferred using Bayesian inference (BI) analysis. https://doi.org/10.5852/ejt.2026.1053.3275.14456