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A revision of dragon millipedes III: the new genus *Gigaxytes* gen. nov., with the description of three new species (Diplopoda, Polydesmida, Paradoxosomatidae)

Ruttapon SRISONCHAI[1], Henrik ENGHOFF[2,*], Natdanai LIKHITRAKARN[3] & Somsak PANHA[4,*]

[1]Biological Sciences Program, Faculty of Science, Chulalongkorn University, Phaya Thai Road, Patumwan, Bangkok 10330, Thailand.
[2]Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, DK-2100 København Ø, Denmark.
[3]Division of Plant Protection, Faculty of Agricultural Production, Maejo University, San Sai, Chiang Mai 50290, Thailand.
[1,3,4]Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Phayathai Road, Patumwan, Bangkok 10330, Thailand.

[*]Corresponding authors: somsak.pan@chula.ac.th[4] and henghoff@snm.ku.dk[2]
[1]Email: ruttapon60104@yahoo.com
[3]Email: kongerrrr@hotmail.com

[1] urn:lsid:zoobank.org:author:4C9CB546-0A3E-4F0B-A9AB-618A6E9C2D6B
[2] urn:lsid:zoobank.org:author:9B9D901F-D6C8-4BCA-B11B-CF6EE85B16DC
[3] urn:lsid:zoobank.org:author:46C52EE1-A383-4C86-BF97-39E07C195075
[4] urn:lsid:zoobank.org:author:AC935098-D901-4F35-A414-4B0D4FE44E79

Abstract. The '*gigas*' group of dragon millipedes, formerly placed in the genus *Desmoxytes* Chamberlin, 1923, is revised and assigned to the new genus *Gigaxytes* gen. nov. *Desmoxytes gigas* Golovatch & Enghoff, 1994 is the type species of the new genus and is redescribed as *G. gigas* (Golovatch & Enghoff, 1994) gen. et comb nov. Three new species are described: *G. fusca* gen et sp. nov. from Thailand and Myanmar; *G. parvoterga* gen et sp. nov. and *G. suratensis* gen et sp. nov. from Thailand. All *Gigaxytes* species are endemic to small distribution areas in limestone habitats in South Thailand and South Myanmar. Illustrations of external morphological characters and an identification key to all known species are provided as well as a distribution map.

Keywords. Dragon millipede, endemic, new species, taxonomy, Thailand.

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Introduction

This is the third in a series of articles about revision of the dragon millipedes, the genus *Desmoxytes* Chamberlin, 1923, *sensu* Golovatch & Enghoff (1994). According to the approach for splitting the dragon millipedes into several genera outlined by Srisonchai *et al.* (2018a) which was based on morphological and genetic data, we here revise the '*gigas*' group. One formerly described species, '*Desmoxytes*' *gigas* Golovatch & Enghoff, 1994 and three further new species are assigned to the new genus *Gigaxytes*.

The new genus is narrowly distributed only in the Malay Peninsula (Thailand and Myanmar).

Material and methods

Specimen collecting and preservation

Specimens of *Gigaxytes* gen. nov. were hand-collected from many localities throughout southern Thailand and southern Myanmar during the rainy season. Most specimens were preserved in 70% ethanol for morphological study and some in 95% ethanol for molecular analysis. Coordinates and elevation were recorded by using Garmin GPSMAP 60 CSx and subsequently double-checked with Google Earth. Staff and students of the Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, referred to as ASRU members, are the main collectors.

Illustrations

Photographs of living specimen were taken with a Nikon 700D+AFS VR 105 mm lens at the collecting site. Scanning electron micrographs were generated with a JEOL, JSM–5410 LV. All objects analysed with SEM were dissected under microscope, mounted on aluminium stubs, then coated with gold. After imaging the objects were removed from the stubs and kept in dry condition. Morphological drawings were sketched under the stereo microscope and then made by using dot-line skills (stipple). All images were processed and organised in Adobe Photoshop CS6.

Morphological descriptions

We examined external morphology including non-gonopod, viz., size, colour, head, antennae, collum, tegument, prozona, metaterga, paraterga, telson, sterna, and legs, as well as gonopod characters. We use the morphological terminology according to previously published taxonomic papers (Jeekel 1964, 1980, 2003; Golovatch & Enghoff 1994; Golovatch *et al.* 2012; Enghoff *et al.* 2007; Srisonchai *et al.* 2016; Srisonchai *et al.* (2018a, b). Gonopod terms are shown in detail in the gonopod terminology section below.

Deposition of holotypes, paratypes and other new specimens

All holotypes of the new species, some paratypes and new specimens are deposited at CUMZ. Some paratypes are kept at ZMUC.

Institutional abbreviations

ASRU = Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn UniversitFy, Bangkok, Thailand
CUMZ = Chulalongkorn University Museum of Zoology, Bangkok, Thailand
ZMUC = Natural History Museum of Denmark (Zoological Museum), University of Copenhagen, Denmark

Other abbreviations used in the text

a.s.l. = above sea level
ca. = about, around (circa)
op = ozopore

Gonopod terminology for the genus *Gigaxytes* gen. nov., definitions and abbreviations

Acropodite = Apical part of gonopod including femorite, solenophore and solenomere
ca = cannula: a short tube, lever-like, curved, originating from coxa, tip inserted into concavity in prefemoral part
cx = coxa: basal part of gonopod, rather stout, connecting to seventh body ring, attached to apertural rim dorsally, with a distoanterior group of setae
fe = femorite: longest part of gonopod, curved, without lateral and mesal sulci, accommodates seminal groove
lm = lamina medialis: a small part distally on gonopod, lamella-like, obviously seen in mesal view
ll = lamina lateralis: a distinct lamella-like in distal part of gonopod, very long and broad
pfe = prefemoral part (= prefemur): basal portion of telopodite, densely setose
sg = seminal groove: a conspicuous groove, similar to a tunnel, seen as a transparent line, visible on femorite in mesal view
sl = solenomere: a usually long, flagellum-like appendage, originating on base of solenophore
sph = solenophore (= tibiotarsus) apical part of telopodite, consisting of lamina lateralis and lamina medialis
Telopodite = Main part of gonopod, pivoting on coxa, including prefemoral part, femorite, solenophore and solenomere

Positional/directional terms in gonopod description

Traditionally the gonopods are depicted as rotated 90º up from their *in situ* position (following the terminology of Srisonchai *et al.* 2018a).

Dorsal = position on the side nearest to the body ring
Ventral = position on the side farthest away from the body ring
Mesal = position on the side nearest to the midline
Lateral = position on the side furthest from the midline
Dorsad = direction towards the body ring
Ventrad = direction away from the body ring
Mesad = direction towards the midline
Laterad = direction away from the midline

We use ‘sub-’ as a prefix referring to positions and directions slightly different from the ones given above. For example, ‘subdorsal’ means a position close to, but not quite on the dorsal side.

Results

Taxonomy

Class Diplopoda Blainville-Gervais, 1844
Order Polydesmida Pocock, 1887
Family Paradoxosomatidae Daday, 1889
Subfamily Paradoxosomatinae Daday, 1889
Tribe Orthomorphini Brölemann, 1916

Genus ***Gigaxytes*** Srisonchai, Enghoff & Panha gen. nov.
urn:lsid:zoobank.org:act:71FC419F-3CB9-4F01-BB57-461E8DD2D771

Type species

Desmoxytes gigas Golovatch & Enghoff, 1994.

Diagnosis

The genus *Gigaxytes* is characterized by:
1. Paraterga subspiniform, long.
2. Metaterga with three regular rows of tubercles/cones/spines.
3. Metaterga 2–17 with a long caudolateral spine on each side.
4. Male femora 5, 6 or 5, 6, 7 with an apophysis (except. *G. gigas* comb. nov. without apophyses).
5. Postfemur of gonopod absent (mesal and lateral sulci poorly developed).
6. Lamina lateralis (ll) indistinctly demarcated from lamina medialis (lm).
7. Lamina lateralis (ll) larger and longer than lamina medialis (lm).

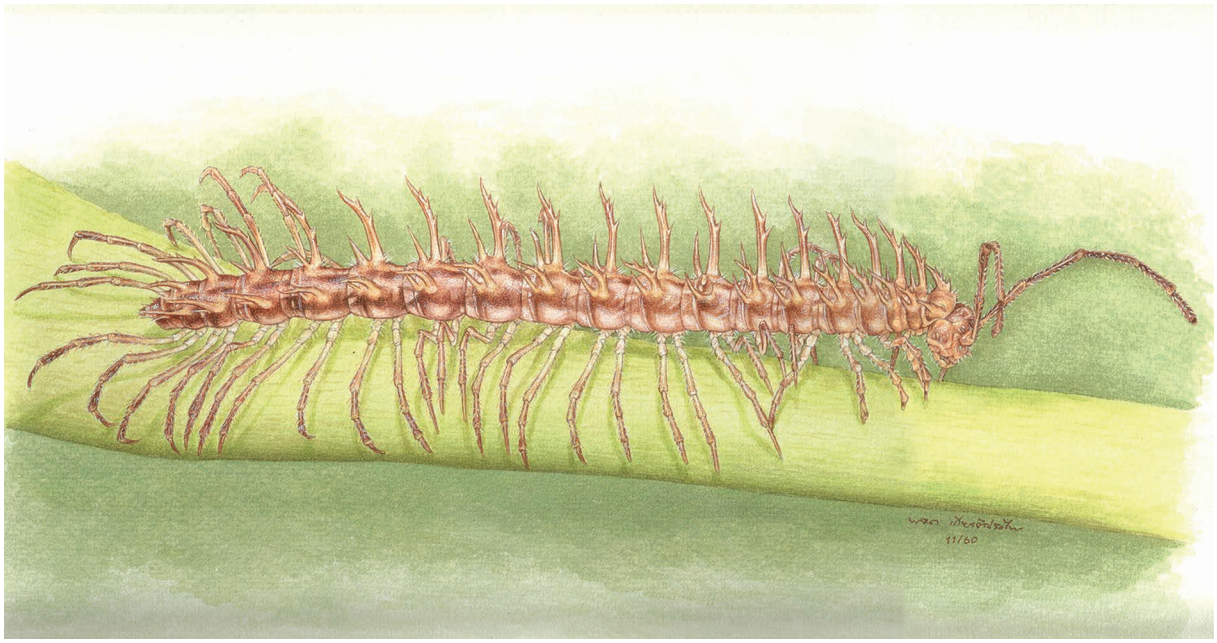

Fig. 1. *Gigaxytes fusca* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype. Watercolour by Photchana Kriatpraprai.

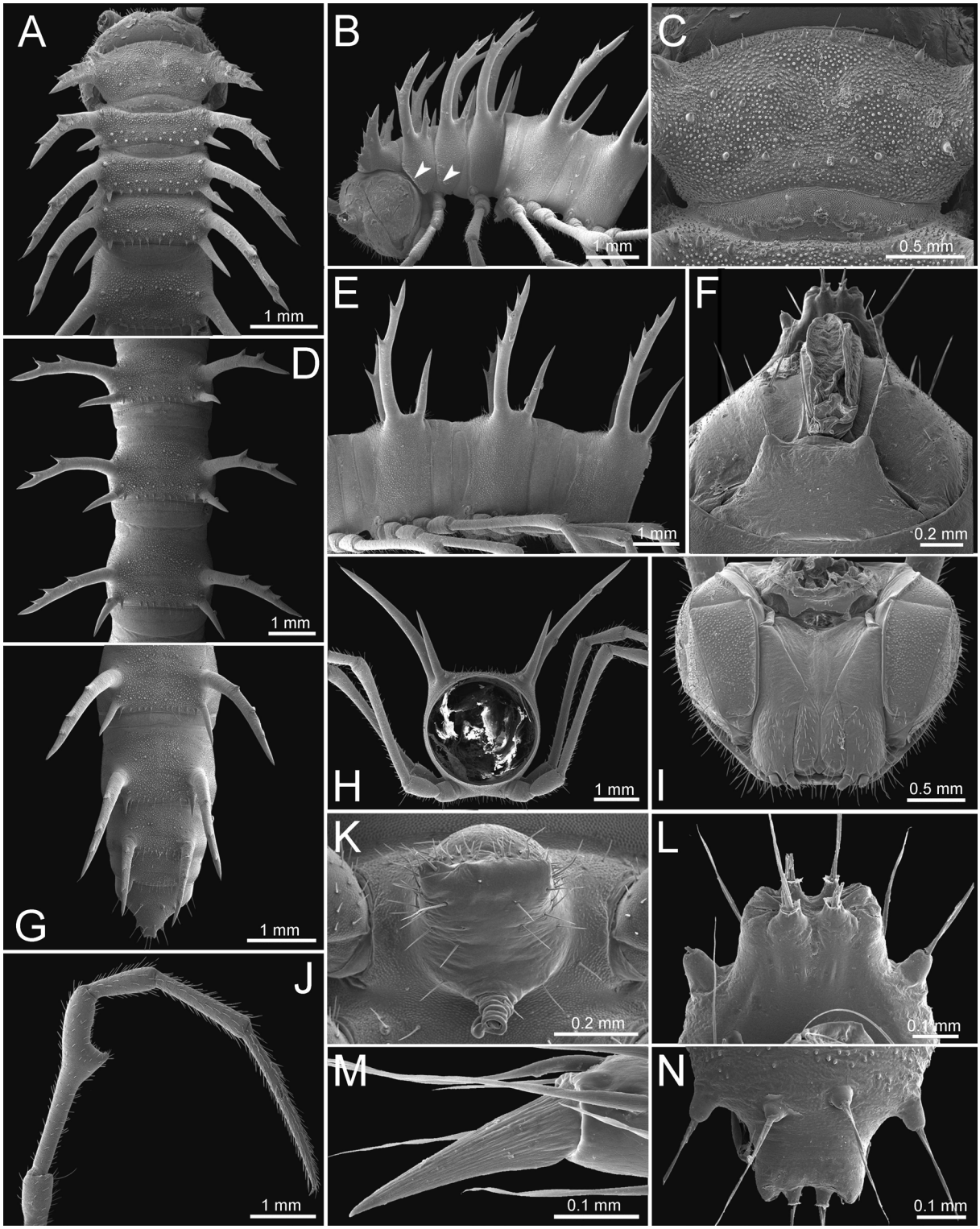

Fig. 2. General body characters of *Gigaxytes* gen. nov. (*G. fusca* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype) – SEM images. **A**–**B**. Anterior body part (arrowheads point to pleurosternal carinae). **C**. Collum. **D**. Body rings 9–10. **E**. Body rings 8–10. **F**. Telson. **G**. Posteriormost rings and telson. **H**. Body ring 10. **I**. Mouthparts, ventral view. **J**. ♂ leg 13. **K**. Sternal lobe between ♂ coxae 4. **L**, **N**. Tip of epiproct. **M**. Tip of tarsus and claw of leg 13.

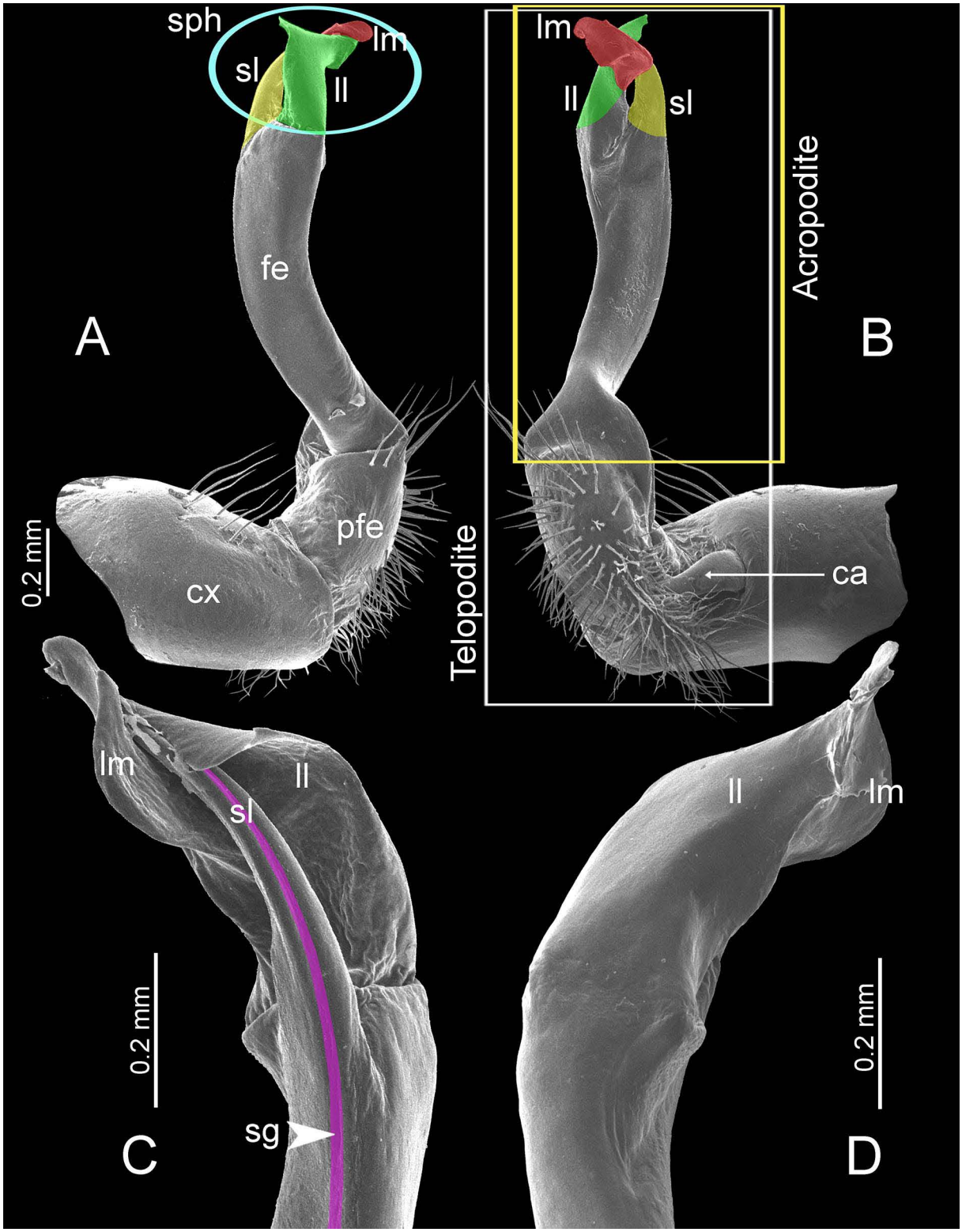

Fig. 3. SEM images of right gonopod of *Gigaxytes* Srisonchai, Enghoff & Panha gen. nov. – *Gigaxytes gigas* (Golovatch & Enghoff, 1994) gen. et comb. nov., ♂, specimen from Wat Tham Sue (Tiger Cave). **A**. Lateral view. **B**. Mesal view. **C**. Dorsal view. **D.** Ventral view. Colours: red = lamina medialis, yellow = solenomere, green = lamina lateralis, purple = seminal groove.

Etymology

The name is a combination of the species epithet of the type species, '*gigas*' from Latin, refers to the larger size of all species (30–40 mm in length); '*-xytes*' ensures harmony with *Desmoxytes* (and its synonym *Pteroxytes* Jeekel, 1980).

Included species (4)

- *Gigaxytes fusca* gen. et sp. nov.
- *Gigaxytes gigas* (Golovatch & Enghoff, 1994) gen. et comb. nov.
- *Gigaxytes parvoterga* gen. et sp. nov.
- *Gigaxytes suratensis* gen. et sp. nov.

Remarks

The new genus exhibits great morphological similarity with *Nagaxytes* Srisonchai, Enghoff & Panha, (2018a) (= the '*acantherpestes*' group) with which it shares subspiniform paraterga, but also resembles *Hylomus* Cook & Loomis, 1924 by having *Orthomorpha*-like gonopods.

General description of *Gigaxytes* gen. nov.

The description applies to adult males and females, except for the gonopods or when 'male' is specified (Figs 1, 2). The general description of gonopods is based mainly on *G. gigas* (Golovatch & Enghoff, 1994) gen. et comb. nov. (Fig. 3).

Size. Body length 30–40 mm (male) 34–40 mm (female), width ca. 2.8–3.0 mm (male) 3.5–3.7 mm (female), varies between species, usually female wider and longer than male.

Colour (Figs 4A–C, 9A–E, 14A, B, 19A–E). Most species pinkish brown/brownish pink in life, some species brown. Colour in alcohol: all specimens partly faded to pale brown after 4 year's preservation in alcohol; specimens kept in darkness faded more slowly.

Antennae. Long and slender, covered by delicate setation, usually reaching backwards to body ring 5–7 (male) and 4–6 (female) when stretched dorsally. Antennomere 2 = 3 = 4 > 5 > 6 > 1 > 7 > 8.

Head (Fig. 2I). Delicately setose; vertex, labrum and genae delicately setose; epicranial suture conspicuous as a long and deep, brown or black stripe.

Collum (Fig. 2A, C). With three regular rows of setiferous cones/spines; number of cones/spines in each row varies between species. Paraterga of collum subspiniform, usually elevated at ca. 20º–50º, directed caudolaterad, with two conspicuous notches at lateral margin.

Tegument (Fig. 2A–G, K–L, N). Dull; collum, metaterga, surface below paraterga and base of paraterga finely microgranulate; prozona finely shagreened; paraterga, epiproct and sterna smooth. Stricture between prozona and metazona wide; often deep, sometimes shallow.

Metaterga (Fig. 2A, D, G). With three transverse rows of setiferous cones and spines; number of cones/spines in each row varies between species. Caudolateral spine on ring 2–17 very long. Suture (transverse sulcus) on metaterga quite deep, conspicuous on body rings 5–17 in all species. Mid-dorsal (axial) line missing.

Pleurosternal Carinae (Fig. 2B). Forming a complete, tooth-like crest on ring 2, a long or short ridge on ring 3 and/or 4, missing on remaining body rings.

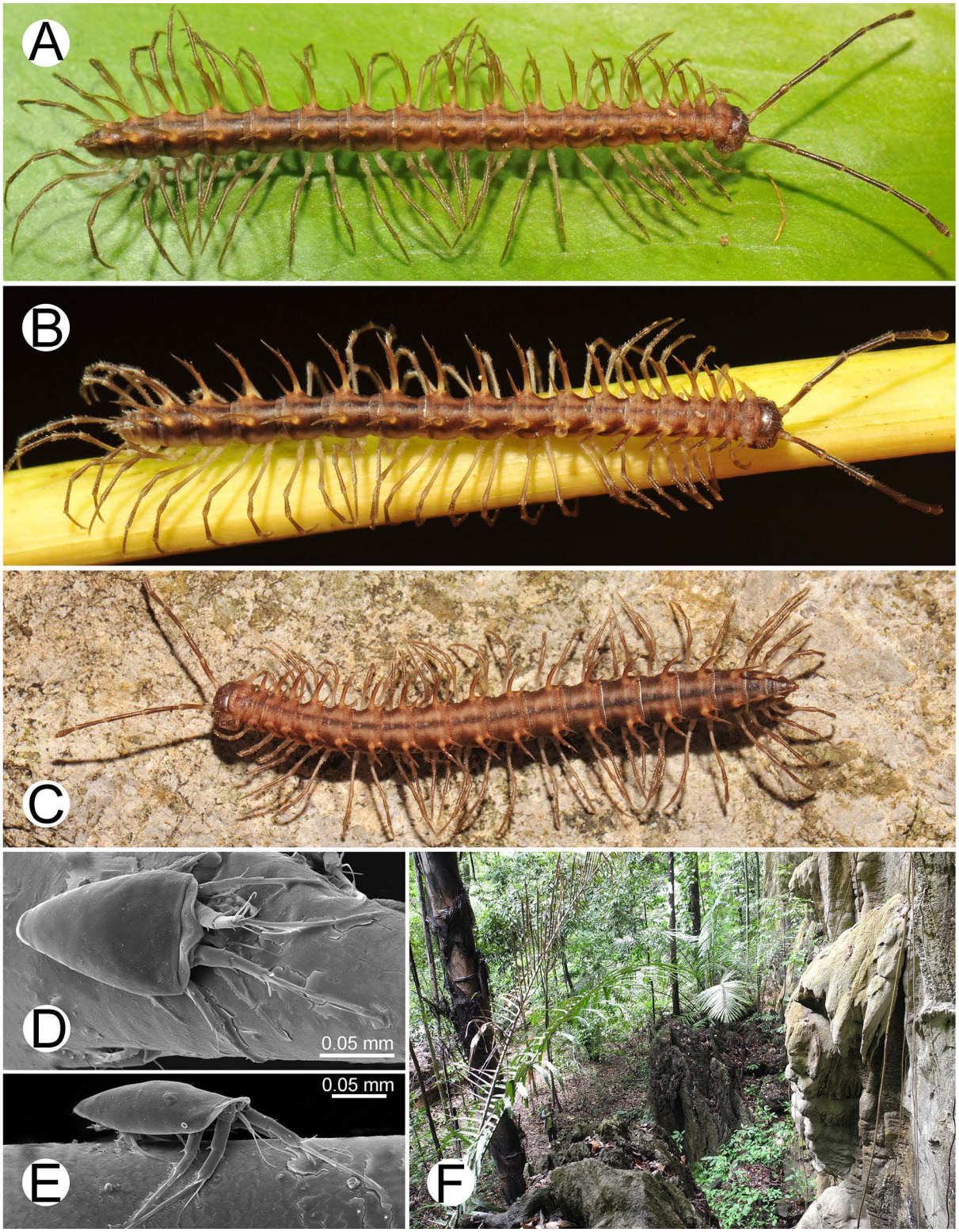

Fig. 4. A–C. Photographs of live *Gigaxytes fusca* Srisonchai, Enghoff & Panha gen. et sp. nov. **A**. ♂ paratype, specimen from Phitsadarn Cave. **B**. ♂ paratype, specimen from Phrayarhtan Cave (Buddha Cave). **C**. ♀ paratype, specimen from Phitsadarn Cave. **D–E**. Phoretic histiostomatid mites. **F**. Habitat.

Paraterga (Fig. 2A–B, D–E, G–H). Subspiniform, long, extremely elevated at ca. 40º–70º (male) 30º–60º (female), directed caudolaterad on rings 2–16 or 2–17, directed increasingly caudad on rings 17–19 or 18–19. Callus and shoulder poorly developed, inconspicuous. Anterior margin with two distinct notches; on body rings 9–10, 12–13, 15–19 with a denticle at lateral margin, near tip. Degree of elevation of paraterga in male usually higher than in female. Posterior angle concave; tip pointed and sharp. Ozopore visible from lateral view, round, small, slightly inconspicuous.

Telson (Fig. 2F–G, L, N). Epiproct quite short, flattened dorsoventrally, tip usually subtruncate, sometimes slightly emarginate; lateral setiferous tubercles conspicuous, long, digitiform; apical tubercles conspicuous, sometimes inconspicuous; epiproct apically with four spinnerets at the corners of a square, not in a depression, anterior pair close to apical tubercles. Paraprocts convex. Hypoproct usually subtrapeziform, sometimes subrectangular, sometimes subsemicircular; caudal margin often subtruncate, sometimes round, with two conspicuous or inconspicuous setiferous tubercles.

Sterna (Fig. 2K). Delicately setose, cross-impressions quite shallow. On body ring 5 with a swollen lobe, subtrapeziform; base swollen; tip subtruncate; with one pore seen in posterior view.

Legs (Fig. 2J). Very long and slender. Relative lengths of podomere: femur > tarsus > tibia > postfemur > prefemur > coxa > claw. Male femora 5, 6 or 5, 6, 7 with a ventral apophysis in most species, without modification in *G. gigas* gen. et comb. nov.

Gonopods (Fig. 3). *Orthomorpha*-like. Coxa longer than prefemoral part, subequal in length to femorite, with a distoanterior group of seta. Cannula mostly rather short, sometimes quite long. Telopodite curved (falcate). Prefemoral part ca. ⅔ as long as femorite. Femorite long and curved. Seminal groove running entirely on mesal surface of femorite. Mesal sulcus and lateral sulcus poorly developed. Solenophore sheath-like, curved: lamina lateralis lamella-like, thin, longer and wider than lamina medialis: lamina medialis indistinctly demarcated from lamina lateralis, tip *in situ* directed ventrad/mesoventrad. Solenomere long, slender, supported by solenophore.

Distribution and habitat

No sympatry between species of *Gigaxytes* gen. nov. has been found in this study; each species has a narrow distribution range. The four species (re)described here appear to be endemic to limestone habitats. The specimens were usually found living exclusively on the ground with leaf litter and hiding under dead leaves. Currently, *Gigaxytes* gen. nov. is distributed only in South Thailand and South Myanmar: Thailand – Krabi (Ao Luek, Muaeng Krabi, Plai Phraya), Nakhon Si Thammarat (Nopphitam, Thung Song), Phatthalung (Khuan Khanun, Kongra, Si Banphot, Srinagarinda), Songkhla (Rattaphum), Surat Thani (Ban Ta Khun, Khirirat Nikhom, Phanom) and Trang Provinces (Hui Yot, Na Yong, Palian, Ratsada); Myanmar – Thanintharyi Region.

Key to species of Gigaxytes *gen. nov. (based mainly on males)*

1. Male femora 5, 6, 7 without modification (Fig. 10E–F) ..... ***G. gigas*** (Golovatch & Enghoff, 1994) gen. et comb. nov.
– Male femora 5, 6 or 5, 6, 7 with an apophysis (e.g., Fig. 15E–G) 2

2. Body brown. Only male femora 5 and 6 with apophyses (Fig. 5E–F); solenophore narrow laterally (e.g., Figs 7C–D, 8C, E) ..... ***G. fusca*** Srisonchai, Enghoff & Panha gen. et sp. nov.
– Body pinkish brown or brownish pink. Male femora 5, 6 and 7 with apophyses (Figs 15E–G, 20E–G); solenophore (sph) broad laterally (e.g., Figs 17C, 18C, 22C, 23C) 3

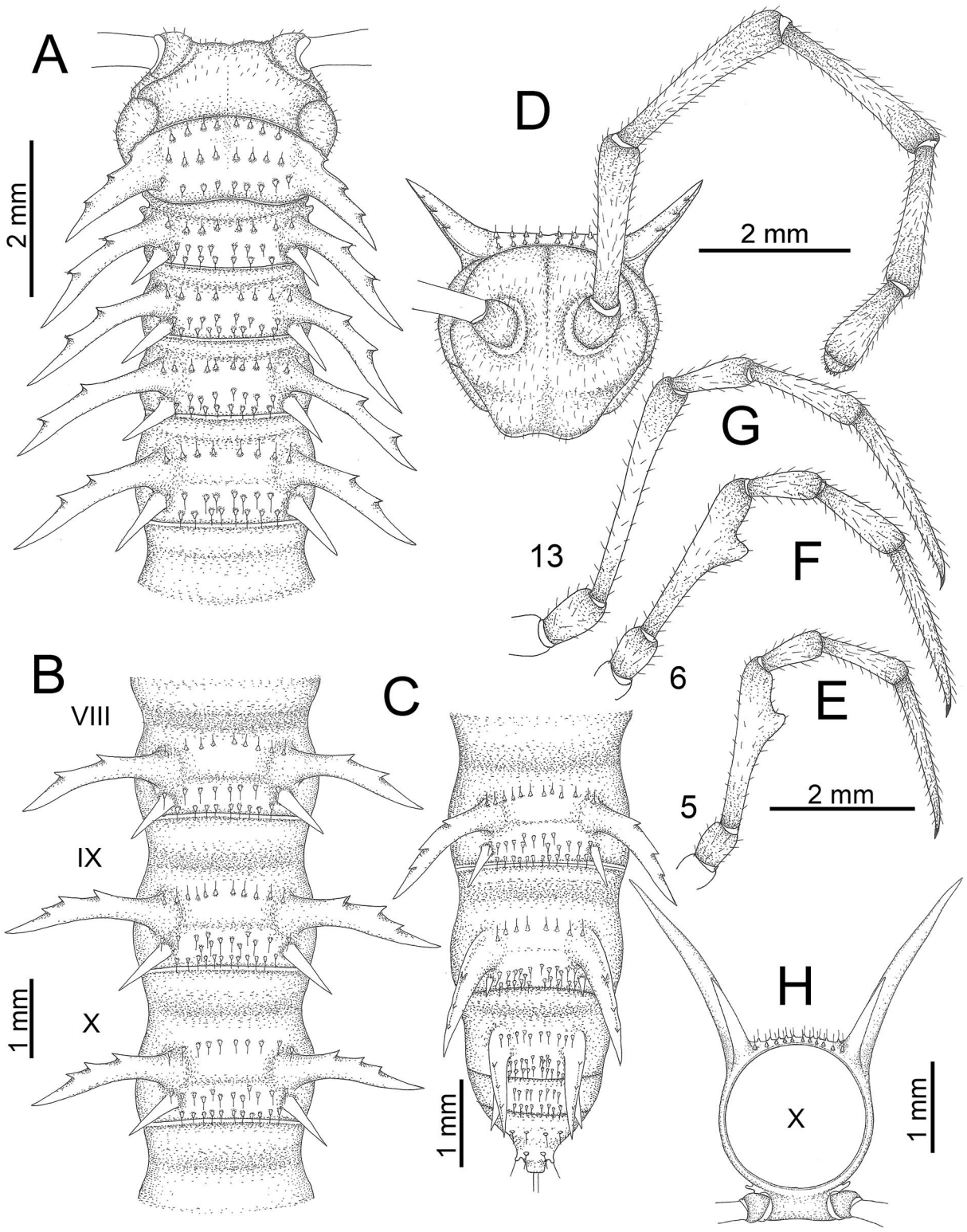

Fig. 5. *Gigaxytes fusca* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype. **A**. Anterior body part. **B**. Body rings 8–10. **C**. Posteriormost body rings and telson. **D**. Head and antenna. **E**. ♂ leg 5 (right). **F**. ♂ leg 6 (right). **G**. ♂ leg 13 (right). **H**. Midbody ring.

3. Paraterga short (Fig. 16A–B); collum usually with 3+3 cones/spines (intermediate row) (Fig. 15A); metaterga 2–8 usually with 4+4 cones/spines (anterior row), 3+3 cones/ spines (intermediate row) and 3+3 cones/spines (posterior row); metaterga 9–19 usually with 5+5 cones/spines (anterior row), 5+5 cones/spines (intermediate row) and 5+5 cones/spines (posterior row) (Fig. 15A–C) ..... ***G. parvoterga*** Srisonchai, Enghoff & Panha gen. et sp. nov.
– Paraterga long (Fig. 21A–B); collum usually with 4+4 cones/spines (intermediate row) (Fig. 20A); metaterga 2–8 usually with 4+4 cones/spines (anterior row), 4+4 cones/ spines (intermediate row) and 4+4 cones/spines (posterior row); metaterga 9–12 usually with 5+5 cones/spines (anterior row), 5+5 cones/spines (intermediate row) and 5+5 cones/spines (posterior row); metaterga 13–19 usually with 6+6 cones/spines (anterior row), 6+6 cones/ spines (intermediate row) and 6+6 cones/spines (posterior row) (Fig. 20A–C) ..... ***G. suratensis*** Srisonchai, Enghoff & Panha gen. et sp. nov.

Species descriptions

Gigaxytes fusca Srisonchai, Enghoff & Panha gen. et sp. nov.
urn:lsid:zoobank.org:act:9995F35F-6B9B-47E9-992A-1E2DEEE4BC36
(Figs 1, 2, 4–8, 24)

Diagnosis

Collum usually with 5+5 cones/spines in anterior row, 4+4 cones/spines in intermediate row and 4+4 cones/spines in posterior row. Metaterga 2–8 usually with 4+4 cones/spines in anterior row, 4+4 cones/ spines in intermediate row and 4+4 cones/spines in posterior row. Male femora 5 and 6 with an apophysis. Similar in these repects to *G. suratensis* gen. et sp. nov., but differs from this species by having brown body colouration; paraterga longer; male femora 7 unmodified; solenophore narrow laterally; lamina medialis apically sharp.

Etymology

The specific epithet is a Latin adjective meaning brown and refers to the brown body colour of living specimens.

Material examined

Holotype

THAILAND: ♂, Chumphon Province, Pathio District, Phitsadarn Cave (Tham Phitsadarn), 10º45′36″ N, 99°13′46″ E, ca. 103 m a.s.l., 29 Aug. 2015, ASRU members leg. (CUMZ-pxDGT00166).

Paratypes

THAILAND: 7 ♂♂, 1 ♀, same data as for holotype (CUMZ-pxDGT00167-174); 1 ♂, 1 ♀, same data as for holotype (ZMUC00040247).

Additional specimens

MYANMAR: 9 ♂♂, 5 ♀♀, 1 juveniles, Tanintharyi Region, Lenya National Park, approximately 10 km from Nam Yen Village, Phayarhtan Cave (Buddha Cave), 11º13′50″ N, 99°10′35″ E, ca. 85 m a.s.l., 6 Jun. 2015, Fauna & Flora International staffs, C. Sutcharit, R. Chanabun and R. Srisonchai leg. (CUMZ). – THAILAND: 1 broken ♂ – right gonopod lost, Chumphon Province, Pathio District, Phitsadarn Cave (Tham Phitsadarn), 10º45′36″ N, 99°13′46″ E, ca. 103 m a.s.l., 2 Oct. 2006, ASRU members leg. (CUMZ); 1 broken ♀, Prachuap Khiri Khan Province, Bang Saphan District, Wat Khao Tham Ma Rong, 11º12′05″ N, 99°29′52″ E, ca. 21 m a.s.l., 12 Oct. 2008, ASRU members leg. (CUMZ).

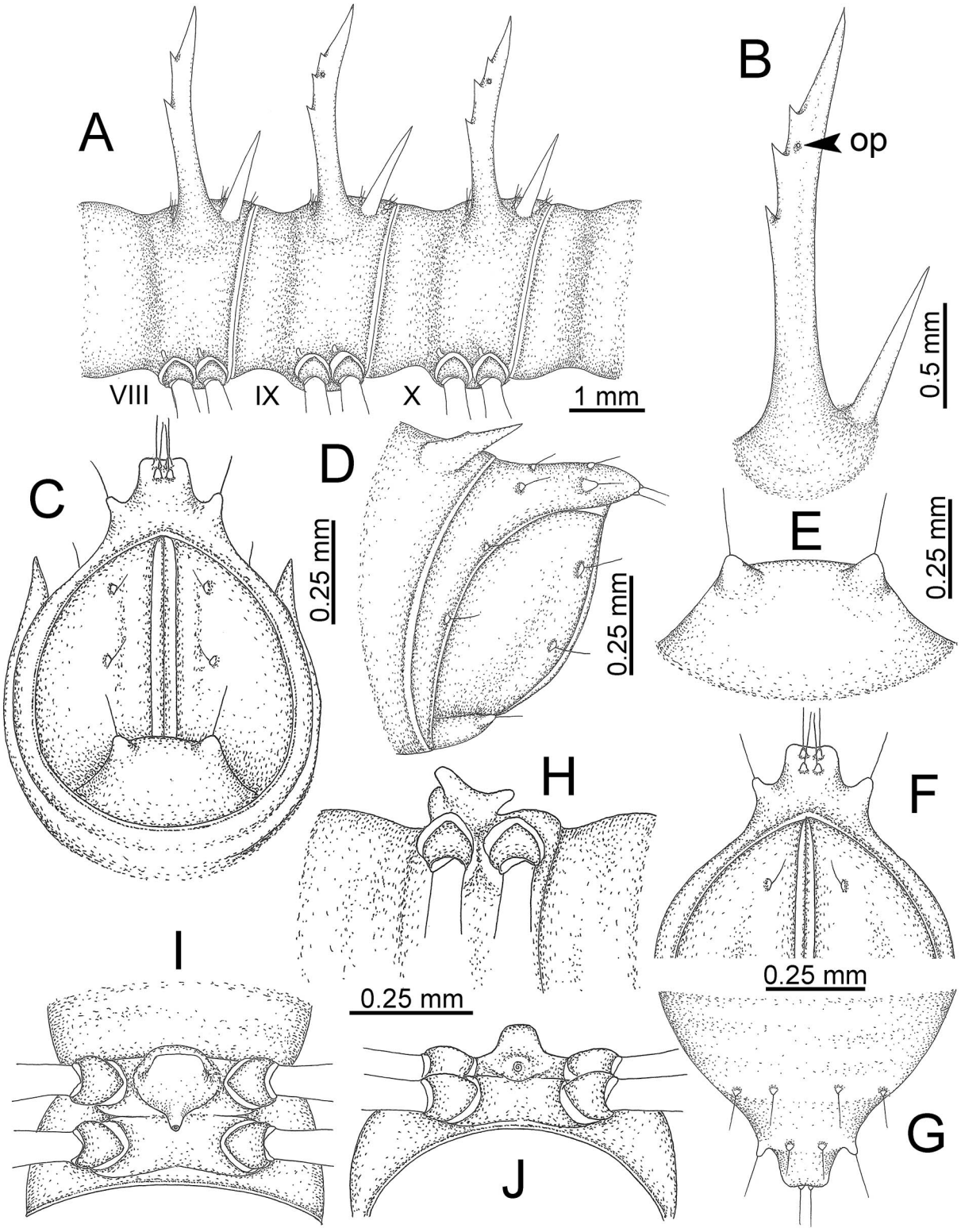

Fig. 6. *Gigaxytes fusca* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype. **A**. Body rings 8–10. **B**. Paraterga of ring 10 (arrowhead points to ozopore). **C**–**D**. Last ring and telson. **E**. Hypoproct. **F**–**G**. Epiproct. **H**–**J**. Sternal lobe between coxae 4.

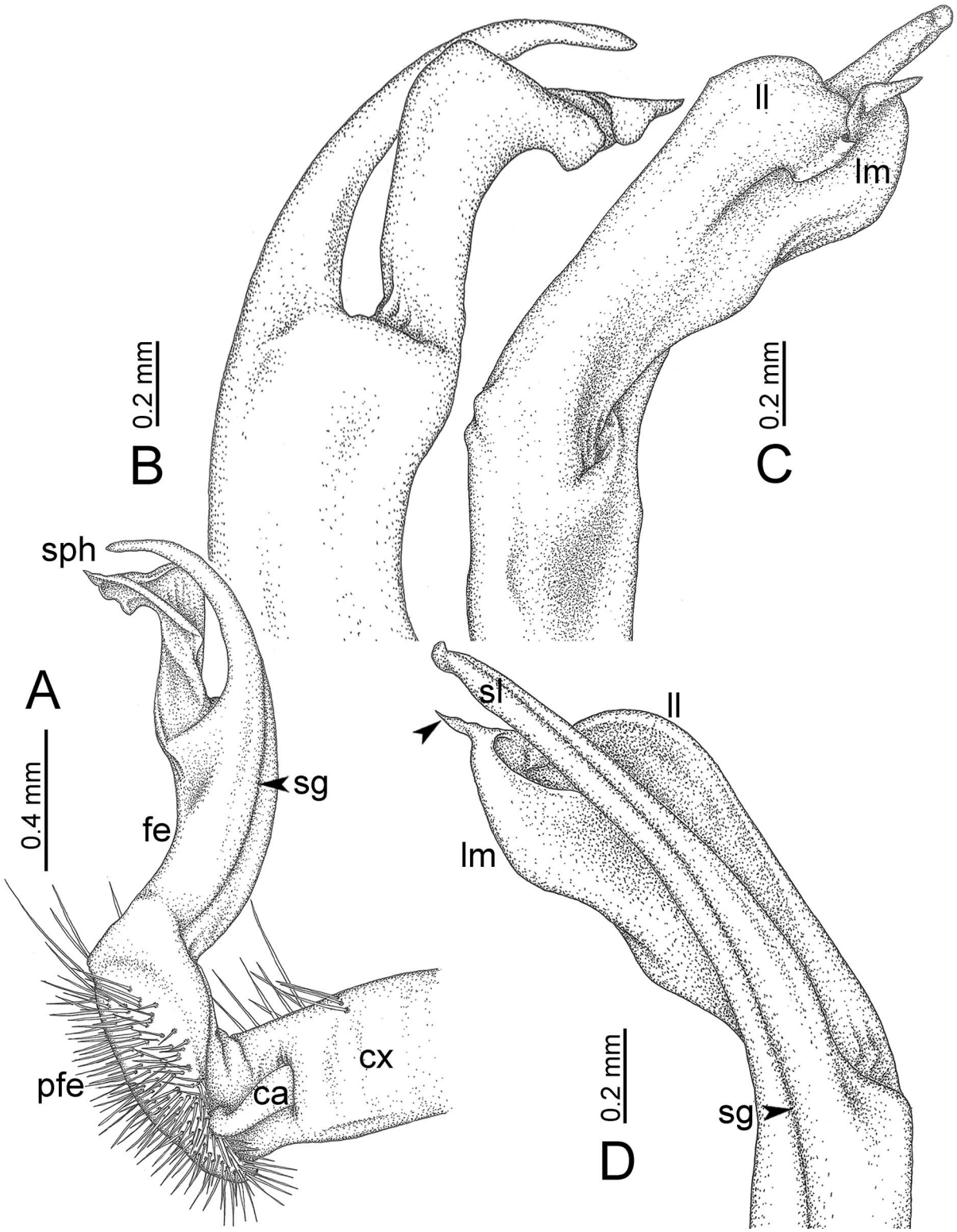

Fig. 7. *Gigaxytes fusca* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype – right gonopod. **A**. Mesal view. **B**. Lateral view. **C**. Ventral view. **D**. Dorsal view (arrowead points to sharp tip of lamina medialis).

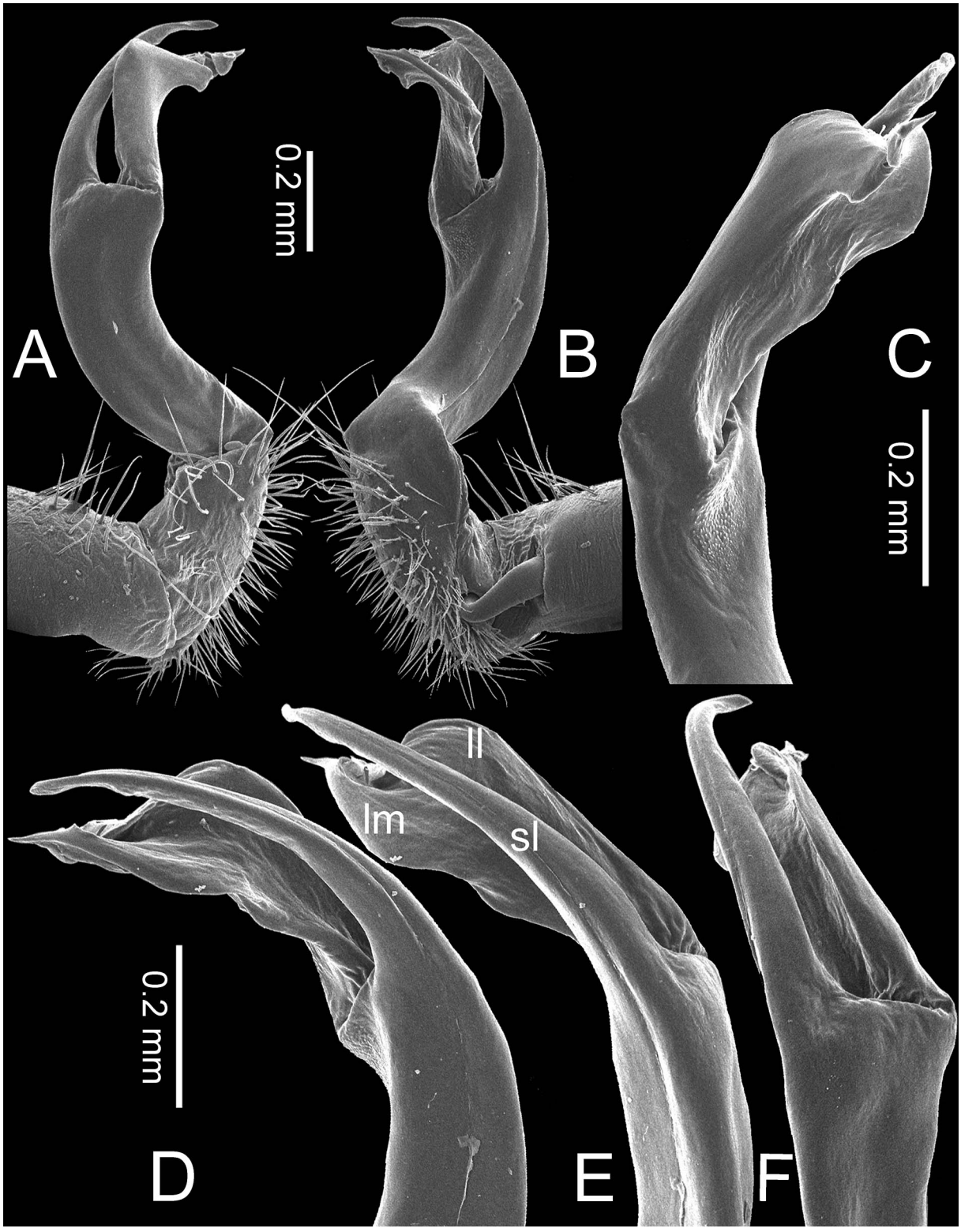

Fig. 8. *Gigaxytes fusca* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype – right gonopod. **A.** Lateral view. **B.** Mesal view. **C.** Ventral view. **D, F.** Subdorsal view. **E.** Dorsal view.

Description

Size. Length 35–38 mm (male), 35–40 mm (female); width of midbody metazona ca. 2.8 mm (male), 3.7 mm (female). Width of head < collum < 2 < 3 ≤ 4 < 5–17, thereafter body gradually tapering towards telson.

Colour (Fig. 4A–C). Specimens in life with body brown; head, collum, antennae, metaterga, prozona, surface below paraterga (upper part), paraterga, epiproct and legs brown; surface below paraterga (lower part), base of paraterga, sterna and a few basal podomeres pale brown. Colour in alcohol: after 10 years changed to pale brown; head, collum, metaterga, paraterga, surface below paraterga, sterna, epiproct pale brown or whitish brown.

Collum (Figs 2A, C, 5A). With three transverse rows of setiferous cones/spines, 5(6)+5 cones/spines in anterior row, 4(3/5)+4(3) cones/spines in intermediate row and 4(5)+4(3) cones/spines in posterior row (lateral cones/spines of anterior row located at base of collum paraterga; lateral cones/spines of posterior row displaced anteriad almost halfway to intermediate row); paraterga of collum elevated at ca. 40º–50º.

Antennae (Fig. 5D). Very long and slender, reaching to body ring 6 or 7 (male) and 5 or 6 (female) when stretched dorsally.

Tegument. Stricture between prozona and metazona wide, quite shallow.

Metaterga (Figs 2A, D, G, 5A–C). With three transverse rows of setiferous cones/spines; metaterga 2–8 with 4(3/5)+4(3/5) cones/spines in anterior row, 4(3/5)+4(3/5) cones/spines in intermediate row and 4(3/5)+4(3/5) cones/spines in posterior row; metaterga 9–19 with 6(5)+6(5) cones/spines in anterior row, 6(5/7/8)+6(5/7) cones/spines in intermediate row and 6(5/7)+6(5/7) cones/spines in posterior row; lateral cones/spines of posterior row larger and longer than others in some specimens.

Pleurosternal Carinae. On body ring 2 long, crest-like; on ring 3 a short ridge; thereafter missing.

Paraterga (Figs 2A–B, D–E, G–H, 5A–C, F, 6A–B). Extremely long; directed caudolaterad on body rings 2–16, elevated at ca. 50º–70º (male) 50º–60º (female), directed increasingly caudad on body rings 17–19.

Telson (Figs 2F, L–N, 6C–G). Tip of epiproct subtruncate; apical tubercles inconspicuous. Hypoproct subtrapeziform; caudal margin subtruncate, with conspicuous setiferous tubercles.

Sternum (Figs 2K, 6H–J). On body ring 5 with a swollen lobe; posterior surface of lobe with a pore borne on a long cylindrical stalk.

Legs (Figs 2J, 6E–G). Male femora 5 and 6 with an apophysis.

Gonopods (Figs 7–8). Coxa subequal in length to femorite. Cannula quite long and slender. Femorite quite long, a bit stout, curved. Solenophore narrow laterally: lamina lateralis narrow: lamina medialis quite long and narrow, distally sharp, tip *in situ* directed ventrad.

Distribution and habitat

Known only from Thailand (Chumphon and Prachuap Khiri Khan Provinces) and Myanmar (Lenya National Park). All specimens were encountered hiding under dead leaves in limestone habitats and some were found in syntopy with *Desmoxytes planata* (Pocock, 1895) at Phitsadarn Cave and Wat Khao Tham Ma Rong, or with *D. cervina* (Pocock, 1895) at Phayarhtan Cave. The new species appears to have a limited distribution near the Kra Isthmus (narrowest part of the Malay Peninsula), a few locations

have been recorded in Thailand and Myanmar. We regard this species to be endemic in this area. The type locality is a tourist attraction place, being a cave belonging to a bureau of monks. Some parts of a habitat where lot of specimens were collected in front of the cave are currently being destroyed, this has raised a concern about habitat loss for *G. fusca* gen. et sp. nov.

Remarks

Brown live specimens blended perfectly with the brown leaf litter on the ground, making them difficult to find. Specimens from Myanmar showed the same morphological characters as found in Thai material – no intrapopulational and interpopulational variations were found. On some specimens we found small white phoretic deutonymphs (the 'hypopus' stage) of mites of the family Histiostomatidae (Astigmata) (Fig. 4D, E). The mites can usually be found on specific sites especially on metaterga or paraterga, attaching to areas with a smooth surface.

Gigaxytes gigas (Golovatch & Enghoff, 1994) gen. et comb. nov.
(Figs 3, 9–13, 24)

Desmoxytes gigas Golovatch & Enghoff, 1994: 56, figs 49–52.
Desmoxytes gigas – Enghoff 2005: 96. — Nguyen & Sierwald 2013: 1241.

Diagnosis

Collum usually with 5+5 cones/spines in anterior row, 3+3 cones/spines in intermediate row and 4+4 cones/spines in posterior row. Similar in this respect to *G. parvoterga* sp. nov. Differs from this species by having paraterga longer; the degree of elevation of paraterga higher; male femora 5, 6 and 7 unmodified.

Material examined

Holotype

THAILAND: ♀, Krabi Province, road between Krabi and Phuket, 10 km South of Krabi, 8º09′ N, 98°50′ E, lowland rainforest, <200 m, 13 Oct. 1991, M. Anderson, O. Martin & N. Scharff leg. (ZMUC000101460) [the exact location is 10 km North of Krabi].

Additional specimens

THAILAND – **Krabi Province**: 1 broken ♂ – gonopods lost, Ao Luek District, Than Bok Khorani, 8º23′28″ N, 98°44′07″ E, 15 Jan. 2014, ca. 46 m a.s.l., ASRU members leg. (CUMZ); 2 ♀♀, Ao Luek District, Than Bok Khorani, 8º23′28″ N, 98°44′07″ E, ca. 46 m a.s.l., 23 Aug. 2014, P. Pimvichai, P. Prasankok and N. Nantarat leg. (CUMZ); 1 juvenile, Ao Luek District, Than Bok Khorani, 8º23′28″ N, 98°44′07″ E, ca. 46 m a.s.l., 30 Aug. 2015, P. Pimvichai, P. Prasankok and N. Nantarat leg. (CUMZ); 1 ♀, Ao Luek District, Than Bok Khorani, 8º23′28″ N, 98°44′07″ E, ca. 46 m a.s.l., 12 Mar. 2017, ASRU members leg. (CUMZ); 1 ♂ – gonopods lost, Muaeng Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8º07′38″ N, 98°55′26″ E, ca. 87 m a.s.l., 25 Oct. 2007, ASRU members leg. (CUMZ); 1 broken ♀, Muaeng Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8º07′38″ N, 98°55′26″ E, ca 87 m a.s.l., 15 Jan. 2009, ASRU members leg. (CUMZ); 2 ♂♂, 1 ♂ – gonopods lost, 2 ♀♀, Muaeng Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8º07′38″ N, 98°55′26″ E, ca 87 m a.s.l., 18 May 2010, ASRU members leg. (CUMZ); 1 ♂, 2 ♀♀, Muaeng Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8º07′38″ N, 98°55′26″ E, ca. 87 m a.s.l., 15 Jan. 2013, ASRU members leg. (CUMZ); 9 ♂♂, 3 ♀♀, Muaeng Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8º07′38″ N, 98°55′26″ E, ca. 87 m a.s.l., 24 Aug. 2014, leg. ASRU members leg. (CUMZ); 1 ♂, 1 ♀, Muaeng Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8º07′38″ N, 98°55′26″ E, ca. 87 m a.s.l., 24 Aug. 2014, ASRU members leg. (ZMUC); 6 ♂♂, 5 ♀♀, Muaeng Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8º07′38″ N, 98°55′26″ E, ca. 87 m a.s.l., 30 Aug. 2015, ASRU members leg. (CUMZ); 3 ♂♂, 3 ♀♀, Muaeng Krabi

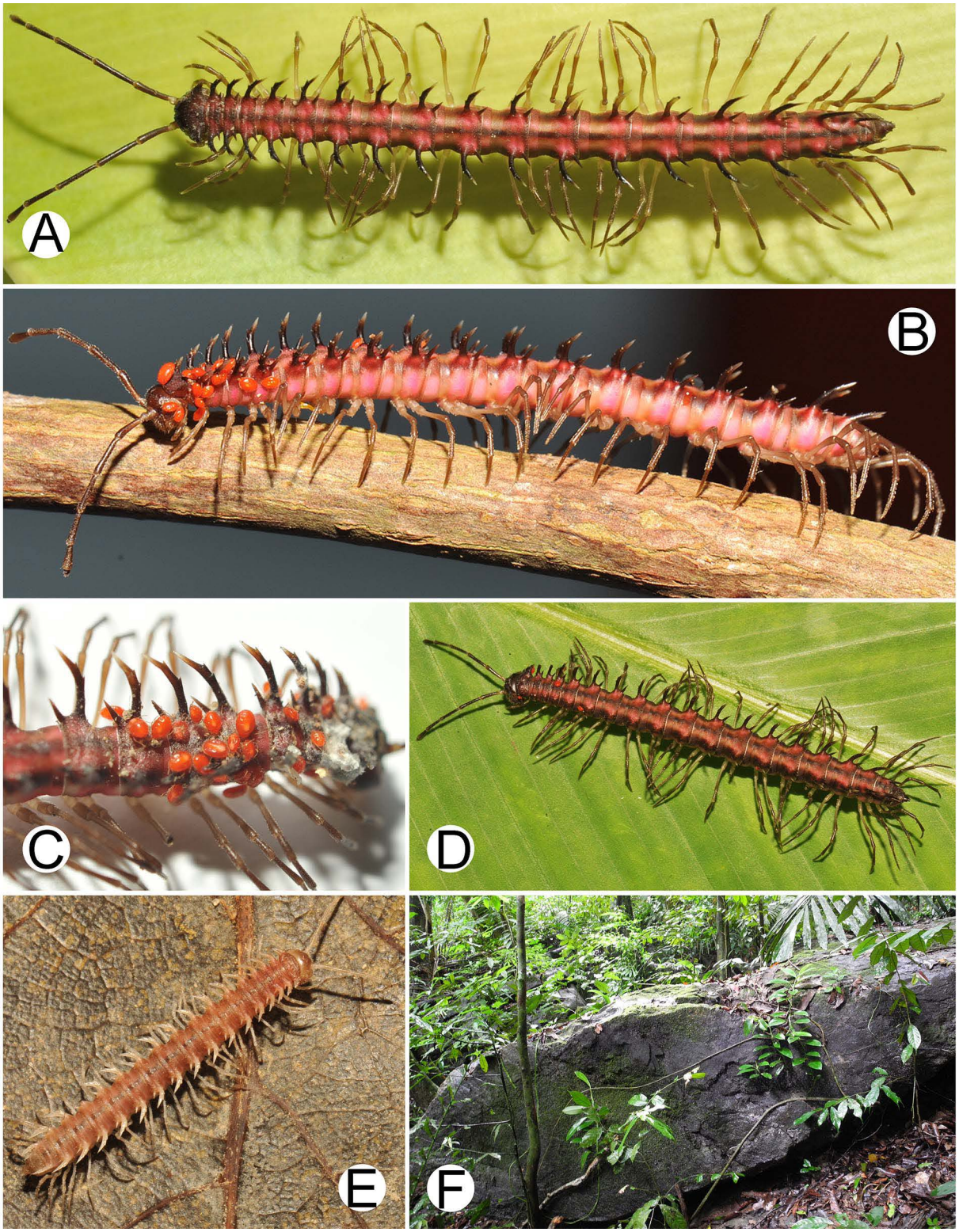

Fig. 9. A–E. Photographs of live *Gigaxytes gigas* (Golovatch & Enghoff, 1994) gen. et comb. nov. **A**. ♂, specimen from Wat Tham Sue (Tiger Cave). **B**. ♂, specimen from Wat Tham Phra Phut. **C**. Parasitic ?*Leptus* mites on ♂. **D**. ♀, specimen from Wat Tham Sue (Tiger Cave). **E**. Juvenile. **F**. Habitat.

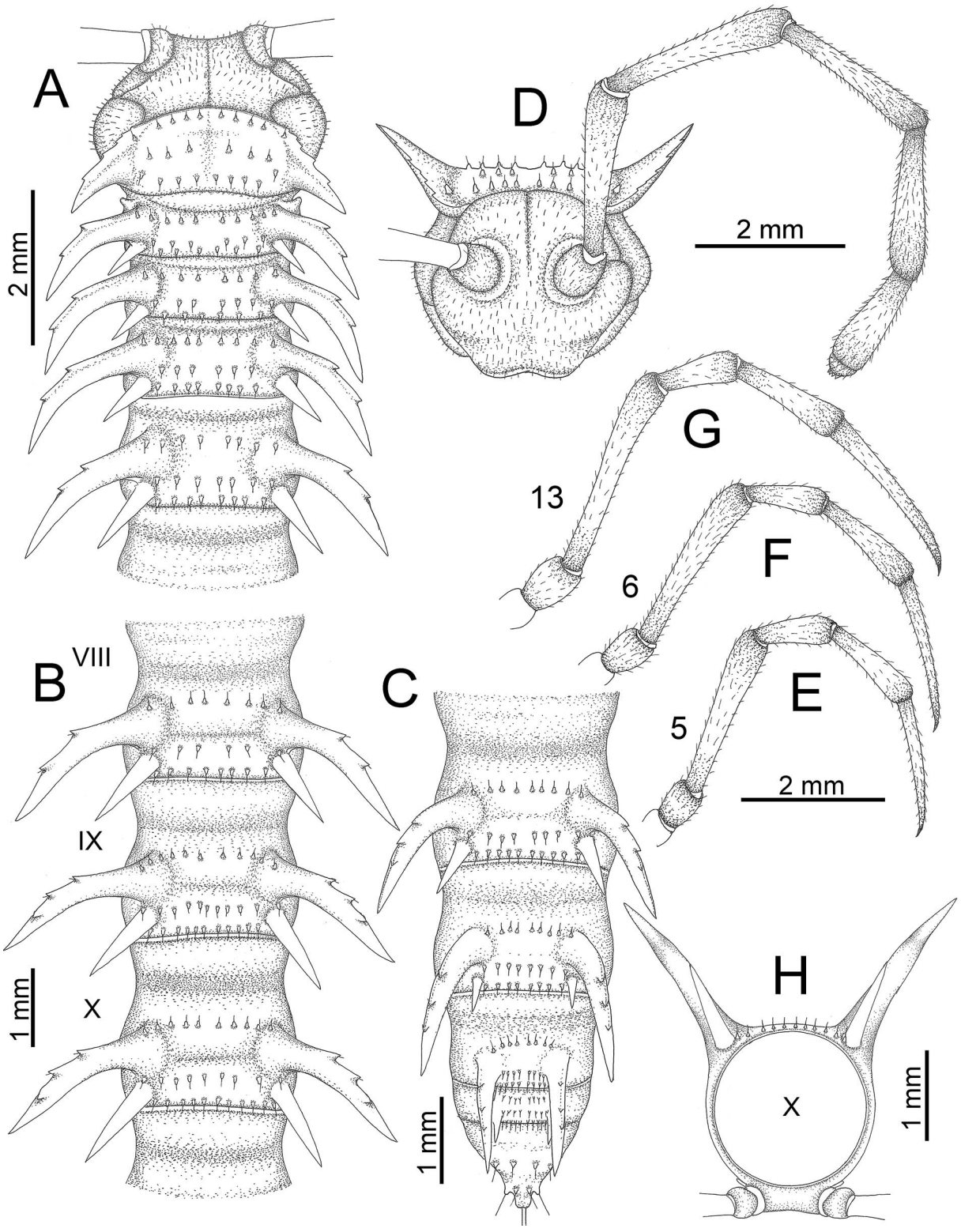

Fig. 10. *Gigaxytes gigas* (Golovatch & Enghoff, 1994) gen. et comb. nov., ♂, specimen from Wat Tham Sue (Tiger Cave). **A**. Anterior body part. **B**. Body rings 8–10. **C**. Posteriormost body rings and telson. **D**. Head and antenna. **E**. ♂ leg 5 (right). **F**. ♂ leg 6 (right). **G**. ♂ leg 13 (right). **H**. Midbody ring.

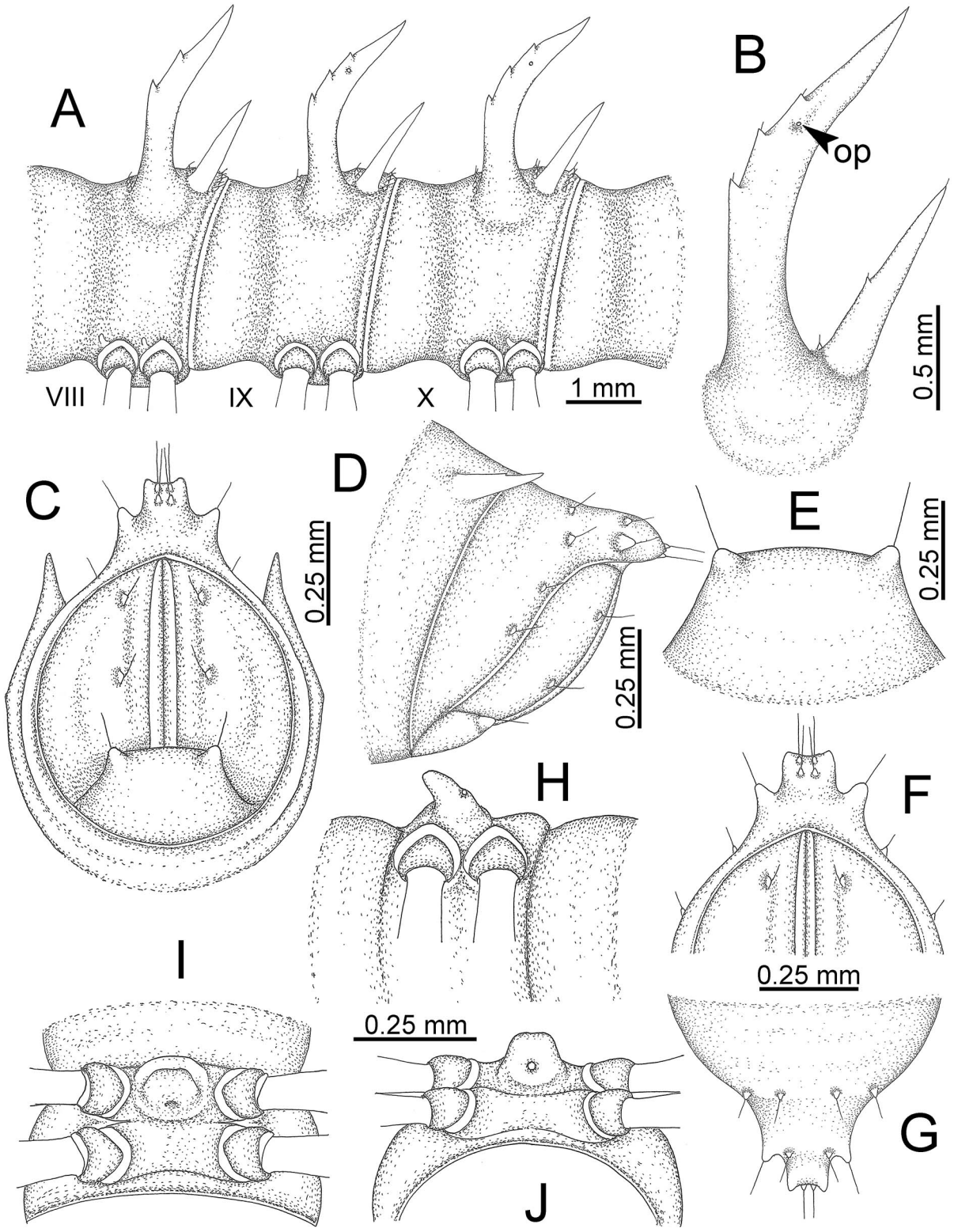

Fig. 11. *Gigaxytes gigas* (Golovatch & Enghoff, 1994) gen. et comb. nov., ♂, specimen from Wat Tham Sue (Tiger Cave). **A**. Body rings 8–10. **B**. Paraterga of ring 10 (arrowhead points to ozopore). **C**–**D**. Last ring and telson. **E**. Hypoproct. **F**–**G**. Epiproct. **H**–**J**. Sternal lobe between coxae 4.

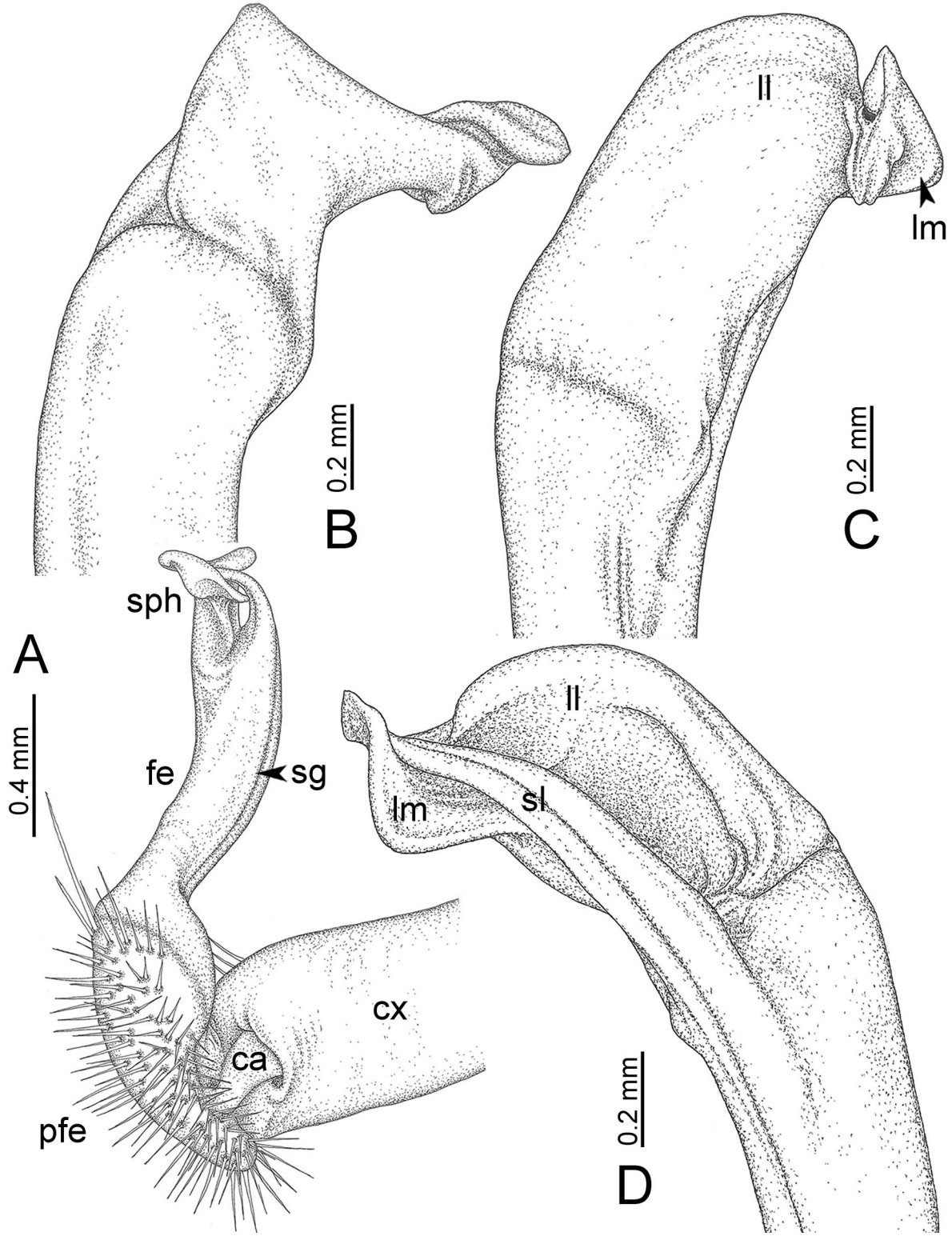

Fig. 12. *Gigaxytes gigas* (Golovatch & Enghoff, 1994) gen. et comb. nov., ♂, specimen from Wat Tham Sue (Tiger Cave) – right gonopod. **A**. Mesal view. **B**. Lateral view. **C**. Ventral view. **D**. Dorsal view.

District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8º07′38″ N, 98°55′26″ E, ca. 87 m a.s.l., 9 Jul. 2017, ASRU members leg. (CUMZ); 1 ♂, Muaeng Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8º07′38″ N, 98°55′26″ E, ca. 87 m a.s.l., 25 Jul. 2017, ASRU members leg. (CUMZ); 1 ♂, Muaeng Krabi District, near Ban Na Mee, Tham Na Mee (Na Mee Cave), 8º08′12″ N, 98°48′23″ E, ca. 70 m a.s.l., 30 Aug. 2015, ASRU members leg. (CUMZ); 2 ♂♂, Plai Phraya District, Wat Khao Hua Sing, 8º30′47″ N, 98°45′34″ E, ca. 155 m a.s.l., 12 Mar. 2017, ASRU members leg. (CUMZ). – **Nakhon Si Thammarat Province**: 1 ♀, Thung Song District, Weruwan Bureau of Monks (Tham Rad), 8º02′48″ N, 99°43′43″ E, ca. 83 m a.s.l., 11 Jan. 2009, ASRU members leg. (CUMZ); 1 ♂, 2 ♀♀, Thung Song District, Talod Cave Park (Talod Cave), 8º09′32″ N, 99°40′42″ E, ca. 74 m a.s.l., 5 Jan. 2017, ASRU members leg. (CUMZ); 1 ♀, Nopphitam District, Krung Ching Waterfall, 8º43′27″ N, 99°40′04″ E, ca. 173 m a.s.l., 17 Jan. 2013, ASRU members leg. (CUMZ). – **Phatthalung Province**: 1 ♂ – gonopods lost, Khuan Khanun District, Tham Wang Thong, 7º40′57″ N, 100°00′58″ E, ca. 44 m a.s.l., 11 Jan. 2009, ASRU members leg. (CUMZ); 2 broken ♀♀, Khuan Khanun District, Tham Wang Thong, 7º40′57″ N, 100°00′58″ E, ca. 44 m a.s.l., 6 Jul. 2017, ASRU members leg. (CUMZ); 1 ♂ – gonopods lost, Si Banphot District, Khao Pu-Khao Ya National Park, 11 Jan. 2009, ASRU members leg. (CUMZ); 1 ♂, Srinagarindra District, Wat Tham Sumano (Sumano Cave Temple), 7º35′08″ N, 99°52′08″ E, ca. 75 m a.s.l., 23 Oct. 2010, ASRU members leg. (CUMZ); 6 ♂♂, Srinagarindra District, Wat Tham Sumano (Sumano Cave Temple), 7º35′08″ N, 99°52′08″ E, ca. 75 m a.s.l., 16 Jan. 2013, ASRU members leg. (CUMZ); 1 ♂, Srinagarindra District, Wat Tham Sumano (Sumano Cave Temple), 7º35′08″ N, 99°52′08″ E, ca. 75 m a.s.l., 16 Jan. 2013, ASRU members leg. (CUMZ); 2 ♂♂, 1 ♀, Kong Ra District, Khao Phaya Hong, 7º27′46″ N, 99°57′50″ E, ca. 55 m a.s.l., 6 Jul. 2017, ASRU members leg. (CUMZ). – **Trang Province**: 1 ♀, Hui Yot District, Khao Phra Yot, Bua Nguen-Bua Thong Pagoda, 7º48′10″ N, 99°37′05″ E, ca. 66 m a.s.l., 14 Jan. 2009, ASRU members leg. (CUMZ); 4 ♂♂, Hui Yot District, Wat Khao Huai Hang, 7º47′37″ N, 99°38′40″ E, ca. 83 m a.s.l., 24 Aug. 2014, ASRU members leg. (CUMZ); 1 broken ♂ – gonopods lost, 1 ♀, Na Yong District, Khao Chang Hai Cave, 7º35′23″ N, 99°40′08″ E, ca. 35 m a.s.l., 15 Jan. 2009, ASRU members leg. (CUMZ); 1 ♂, 2 ♀♀, Na Yong District, Khao Chang Hai Cave, 7º35′23″ N, 99°40′08″ E, ca. 35 m a.s.l., 25 Aug. 2014, ASRU members leg. (CUMZ); 1 ♂, 2 juveniles, Na Yong District, Khao Chang Hai Cave, 7º35′23″ N, 99°40′08″ E, ca. 35 m a.s.l., 9 Jul. 2017, ASRU members leg. (CUMZ); 5 ♂♂, 3 ♀♀, Ratsada District, Wat Tham Phra Phut, 7º57′42″ N, 99°44′42″ E, ca. 103 m a.s.l., 5 Jul. 2017, ASRU members leg. (CUMZ).

Redescription (first description of male)

Size. Length 30–40 mm (male), 34–40 mm (female); width of midbody metazona ca. 3.0 mm (male), 3.5 mm (female). Width of head < collum < 2 ≤ 3 ≤ 4 < 5–16, thereafter body gradually tapering towards telson.

Colour (Fig. 9A–E). Specimens in life with body brownish pink/pinkish brown; head and antennae brown/dark brown (except distal part of antennomere 7 and antennomere 8 whitish); prozona, metaterga and surface below paraterga brownish pink/pinkish brown; paraterga dark brown/black; collum, epiproct and leg brown; tip of paraterga, sterna and a few basal podomeres pale brown. Colour in alcohol: after 5–16 years changed to pale brown; head, antennae, collum, metaterga, paraterga, surface below paraterga, sterna, epiproct and legs pale brown.

Collum (Fig. 10A). With three transverse rows of setiferous cones/spines, 5(6)+5(6) cones/spines in anterior row, 3(4/5)+3(4/5) cones/spines intermediate row and 4(3)+4(3) cones/spines in posterior row (lateral cones/spines of anterior row located at base of collum paraterga); paraterga of collum elevated at ca. 30º–40º.

Antennae (Fig. 10D). Very long and slender, reaching to body ring 7 or 6 (male) and 5 or 4 (female) when stretched dorsally.

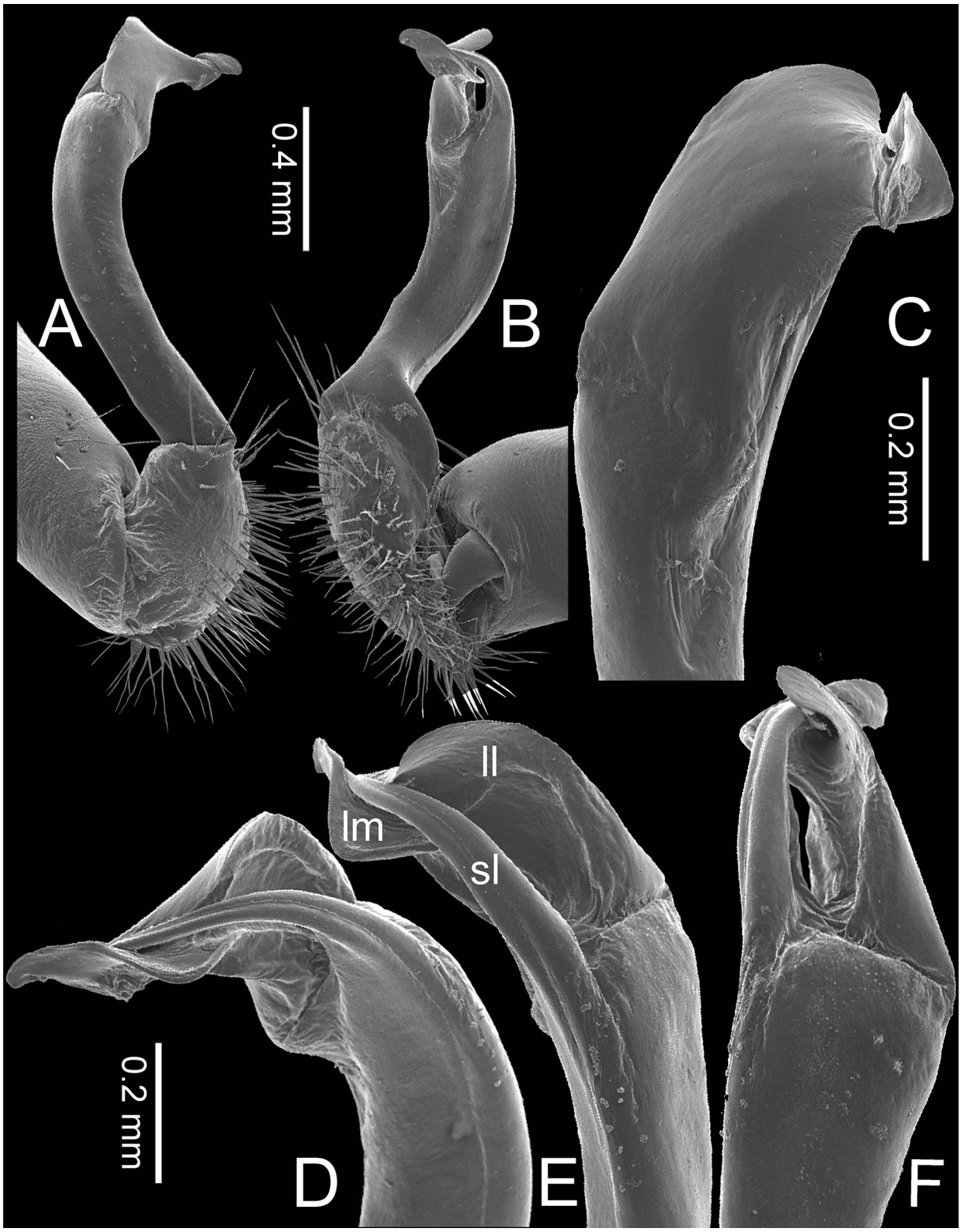

Fig. 13. *Gigaxytes gigas* (Golovatch & Enghoff, 1994) gen. et comb. nov., ♂, specimen from Wat Tham Sue (Tiger Cave) – right gonopod. **A**. Lateral view. **B**. Mesal view. **C**. Ventral view. **D**, **F**. Subdorsal view. **E**. Dorsal view.

Tegument. Stricture between prozona and metazona wide, quite deep.

Metaterga (Fig. 10A–C). With three transverse rows of setiferous cones/spines; metaterga 2–8 with 4(5)+4(5) cones/spines in anterior row, 4(3/5)+4(3/5) cones/spines in intermediate row and 4(3)+4(3) cones/spines in posterior row; metaterga 9–19 with 5(4/6)+5(4/6) cones/spines in anterior row, 5(4)+5(4) cones/spines in intermediate row and 5(4/6)+5(4/6) cones/spines in posterior row.

Pleurosternal Carinae. On body ring 2 long, crest-like; on ring 3 a long ridge; on ring 4 a short ridge; thereafter missing.

Paraterga (Figs 10A–C, H, 11A–B). Moderately long, directed caudolaterad on body rings 2–17, elevated at ca. 50º–70º (male) 40º–60º (female), directed increasingly caudad on body rings 18 and 19.

Telson (Fig. 11C–G). Tip of epiproct usually subtruncate (in some specimens slightly emarginate); apical tubercles inconspicuous. Hypoproct usually subtrapeziform (in some specimens subrectangular); caudal margin subtruncate, with conspicuous setiferous tubercles (in specimens from Khao Phaya Hong inconspicuous).

Sternum (Fig. 11H–J). On body ring 5 with a swollen lobe; posterior surface of lobe with a pore, pore not borne on a stalk.

Legs (Fig. 11E–G). Male femora without modification (Male femora 5, 6 and 7 unmodified).

Gonopods (Figs 3, 12–13). Coxa subequal in length to femorite or longer than femorite. Cannula quite short and stout. Femorite long and slender, curved. Solenophore wide laterally: lamina lateralis broad: lamina medialis wide, distally blunt, *in situ* directed mesoventrad.

Distribution and habitat

Gigaxytes gigas gen. et comb. nov. is presently known only from Krabi, Nakhon Si Thammarat, Phatthalung and Trang Provinces. Specimens were collected from limestone habitats and were mostly seen hiding under dead leaves, sometimes crawling on leaf litter. It has been found in syntopy with two species of other dragon millipedes at several locations across its distribution: *Desmoxytes cervina* and *Desmoxytes delfae* (Jeekel, 1964). Notably, *G. gigas* gen. et comb. nov. was usually seen living and crawling on the ground whereas *D. cervina* and *D. delfae* were collected from rocks and tree branches.

Based on extensive fieldwork focused on this genus in southern Thailand, *G. gigas* gen. et comb. nov. is one of the most common and widely distributed dragon millipedes in many provinces. It is sometimes encountered close to the areas that have been developed as tourist attractions such as caves, as well as a temple or bureau of monks. However, it is still found in natural habitats and has a rather limited distribution in southern Thailand; we here regard this species as endemic for the Thai fauna.

Note on material

'*Desmoxytes*' *gigas* Golovatch & Enghoff, 1994 was described on the basis of a single adult female (in ZMUC) collected from Krabi Province. We have collected additional specimens in many areas, males as well as females. After examination of all material, it is clear that morphological characters of adult females collected from Krabi, Nakhon Si Thammarat, Phatthalung and Trang Provinces match perfectly with the female holotype.

Remarks

The living colouration of adults is generally pinkish brown that blends perfectly with brown/pinkish brown leaves or litter on the ground; juveniles are brown.

Two main populations, eastern and western, can be distinguished on the basis of morphological differences in combination with distribution. The two populations differ in characters of paranota and gonopod femorite: specimens of the western population have obviously longer paraterga and the femorite more slender than those of the eastern one. Intrapopulational variation also exists: epiproct with conspicuous apical setiferous tubercles in some specimens, inconspicuous in others; hypoproct subtrapeziform in some specimens, subrectangular in others.

Some specimens of *G. gigas* gen. et comb. nov. were infested with parasitic mite larvae, probably belonging to the genus *Leptus* Latreille, 1896. Several mites appeared on metaterga in anteriormost rings and could easily be discerned (Fig. 9B, C) by their remarkable orange colour. Mite larve assigned to the genus *Leptus* were reported from a few dragon millipede species (genera *Desmoxytes* and *Nagaxytes*) by Srisonchai *et al.* (2018a, b). We suspect that all ?*Leptus* larvae from dragon millipedes might belong to the same species. However, an exact identification of the mite species has not been undertaken, and in any case, the relationship between the millipede and *Leptus* still requires further studies.

As mentioned in the diagnosis, the new species is noticeably different from other *Gigaxytes* species due to its unmodified male femora 5–7.

Gigaxytes parvoterga Srisonchai, Enghoff & Panha gen. et sp. nov.
urn:lsid:zoobank.org:act:6D14B1A7-3F10-4502-93FE-52CAD606C93D
(Figs 14–18, 24)

Diagnosis

Male femora 5, 6 and 7 with an apophysis. Similar in this respect to *G. suratensis* gen. et sp. nov., but differs from this by having paraterga shorter; collum usually with 3+3 cones/spines (intermediate row); metaterga 2–8 usually with 4+4 cones/spines (anterior row), 3+3 cones/spines (intermediate row) and 3+3 cones/spines (posterior row); metaterga 9–19 usually with 5+5 cones/spines (anterior row), 5+5 cones/spines (intermediate row) and 5+5 cones/spines (posterior row).

Etymology

The specific epithet is a Latin noun in apposition, combining '*parvus*' meaning small, and '*terga*' referring to paraterga, and alludes to the shorter subspiniform paraterga compared to other species.

Material examined

Holotype

THAILAND: ♂, Trang Province, Palian District, Tham Khao Ting, 7º09′30″ N, 99°48′10″ E, ca. 42 m a.s.l., 31 Aug. 2015, ASRU members leg. (CUMZ-pxDGT00175).

Paratypes

THAILAND: 5 ♂♂, 1 ♀, same data as for holotype (CUMZ-pxDGT00176-181).

Additional specimens

THAILAND: 1 juvenile, Trang Province, Palian District, Tham Khao Ting, 7º09′30″ N, 99°48′10″ E, ca. 42 m a.s.l., 31 Aug. 2015, ASRU members leg. (CUMZ); 2 ♀♀, Songkhla Province, Rattaphum District, Tham Sri Khaesorn (Sri Khaesorn Cave), 7º00′47″ N, 100°09′43″ E, ca. 348 m a.s.l., 12 Jan. 2009, ASRU members leg. (CUMZ).

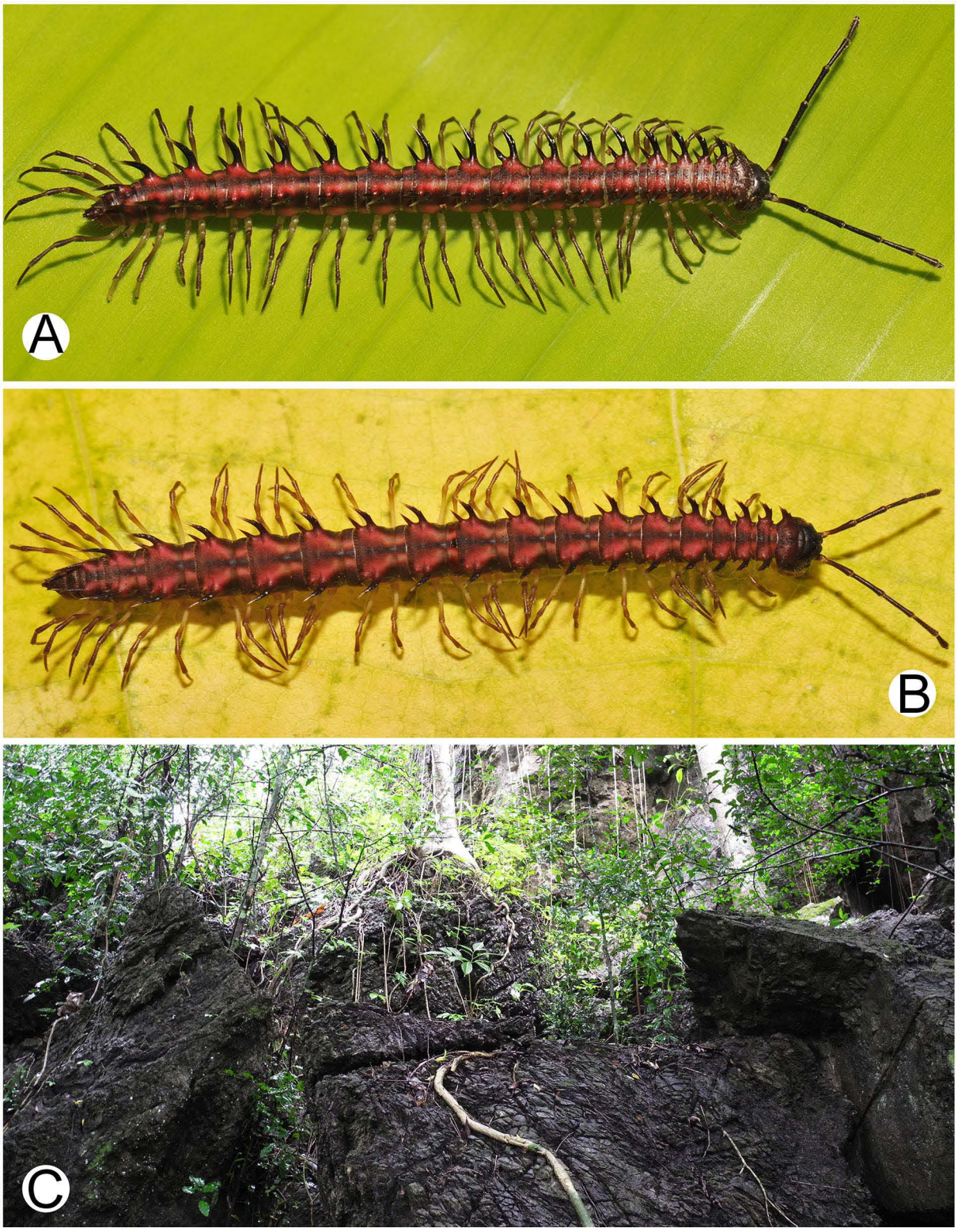

Fig. 14. A–B. Photographs of live *Gigaxytes parvoterga* Srisonchai, Enghoff & Panha gen. et sp. nov., specimens from Tham Khao Ting **A**. ♂ paratype. **B**. ♀ paratype. **C**. Habitat.

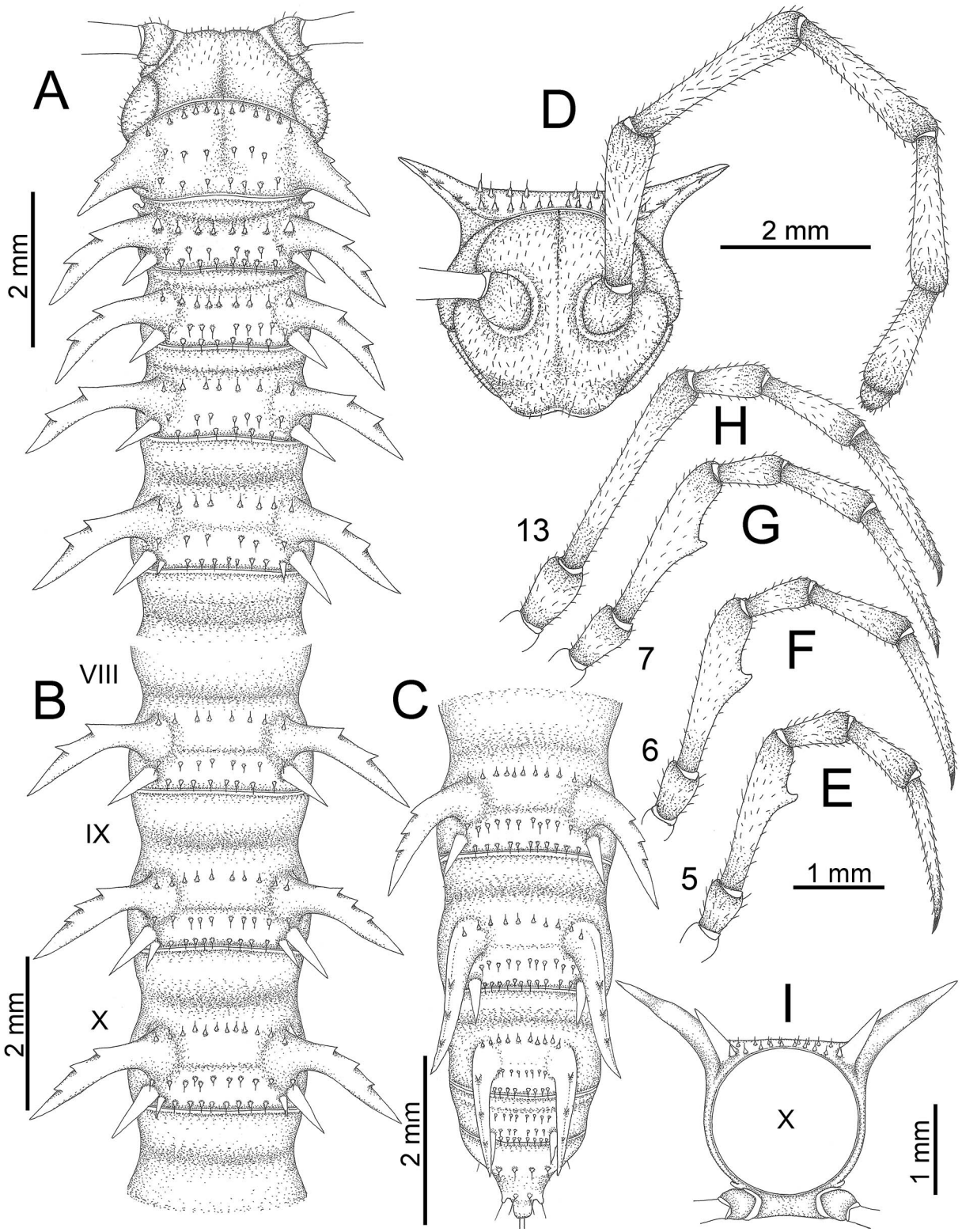

Fig. 15. *Gigaxytes parvoterga* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype. **A**. Anterior body part. **B**. Body rings 8–10. **C**. Posteriormost body rings and telson. **D**. Head and antenna. **E**. ♂ leg 5 (right). **F**. ♂ leg 6 (right). **G**. ♂ leg 7 (right). **H**. ♂ leg 13 (right). **I**. Midbody ring.

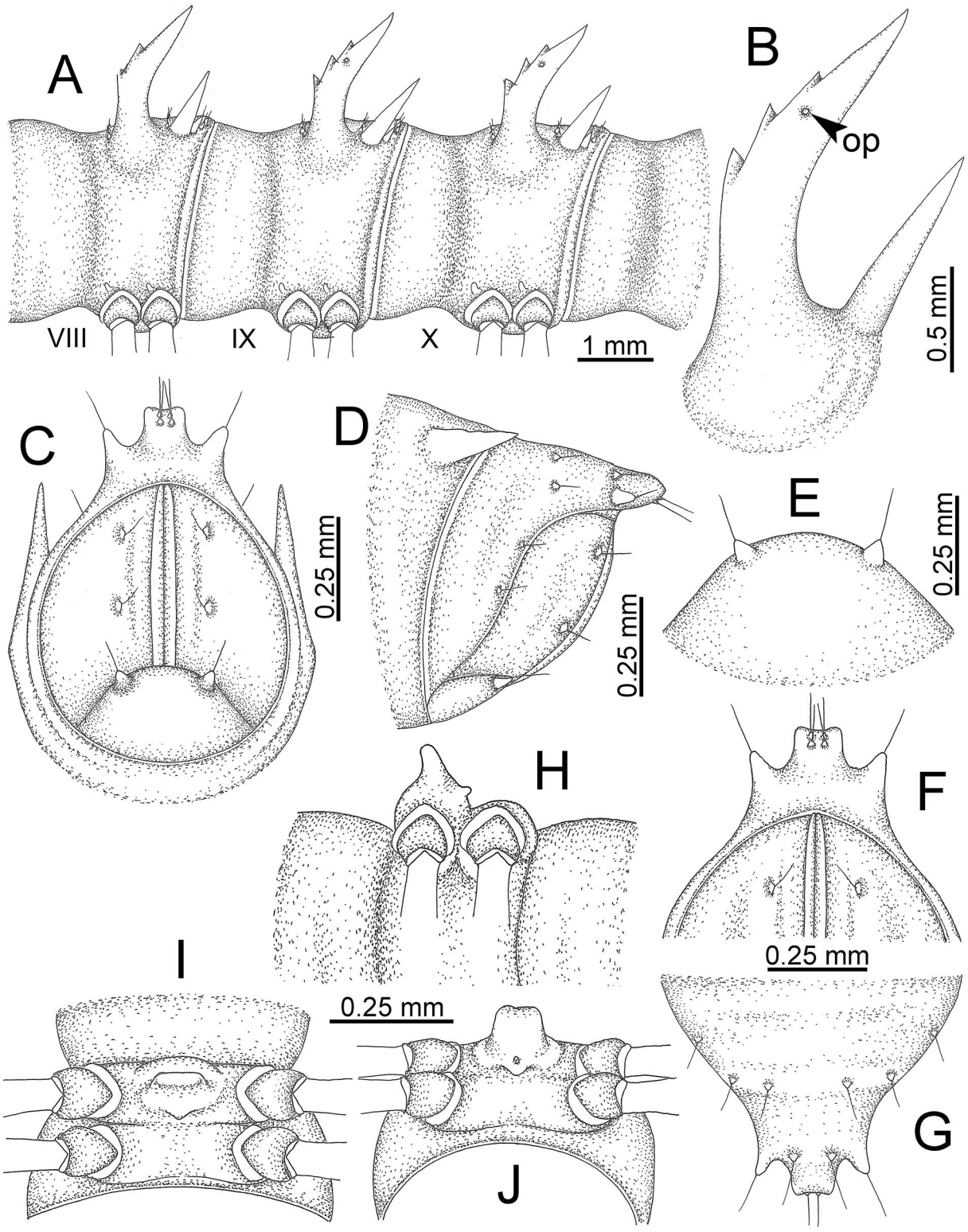

Fig. 16. *Gigaxytes parvoterga* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype. **A**. Body rings 8–10. **B**. Paraterga of ring 10 (arrowhead points to ozopore). **C**–**D**. Last ring and telson. **E**. Hypoproct. **F**–**G**. Epiproct. **H**–**J**. Sternal lobe between coxae 4.

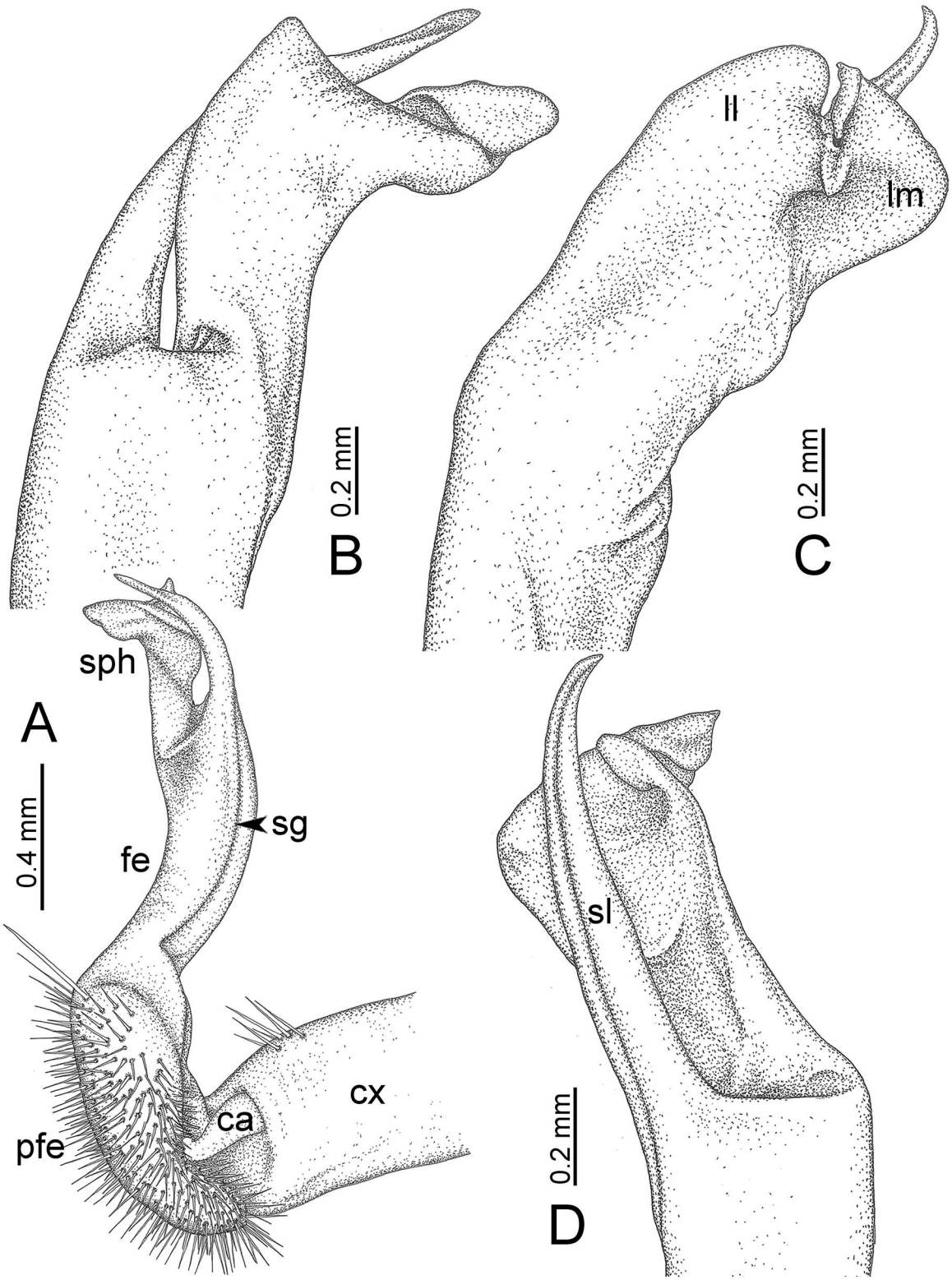

Fig. 17. *Gigaxytes parvoterga* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype – right gonopod. **A**. Mesal view. **B**. Lateral view. **C**. Ventral view. **D**. Dorsal view.

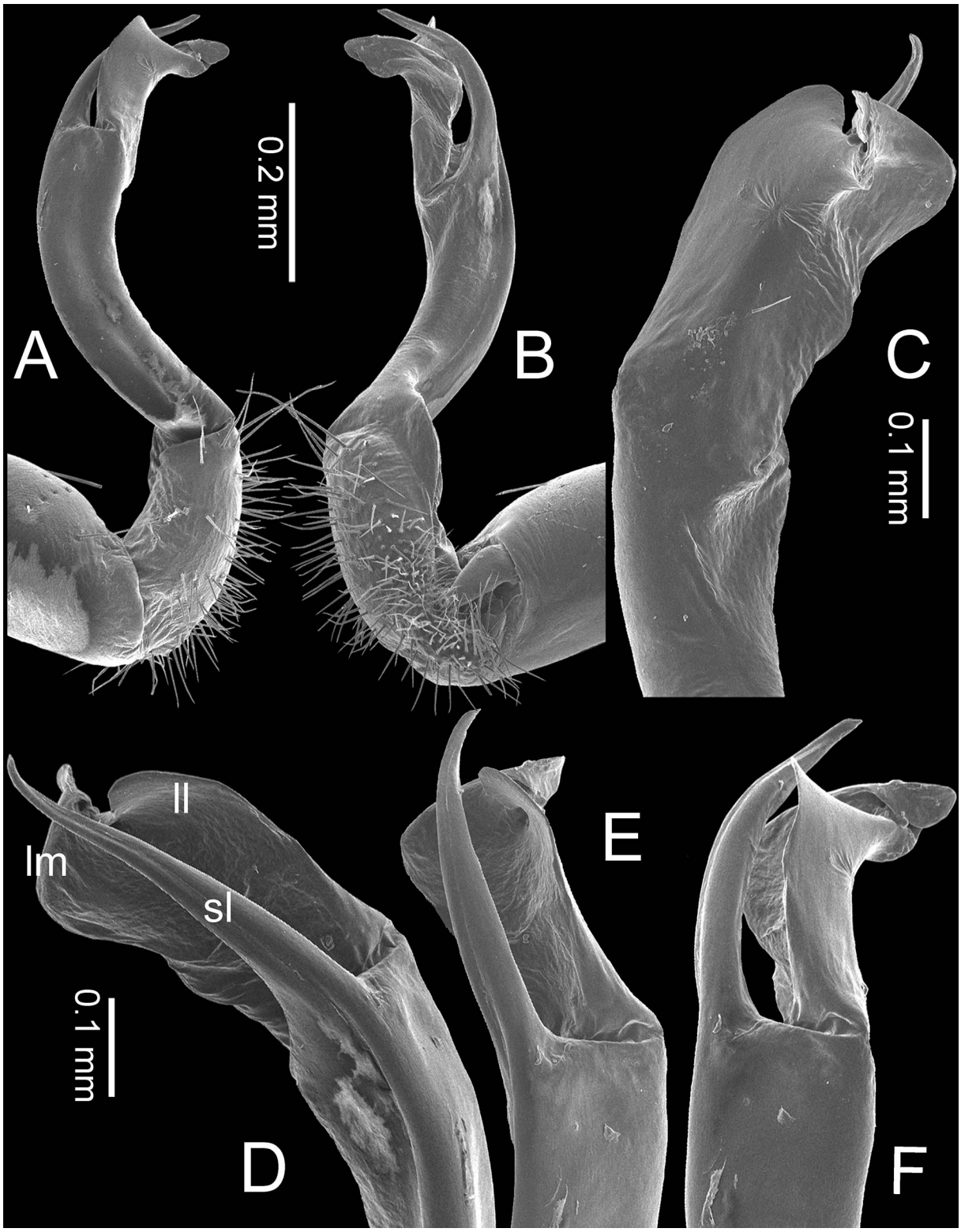

Fig. 18. *Gigaxytes parvoterga* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype – right gonopod. **A**. Lateral view. **B**. Mesal view. **C**. Ventral view. **D**, **F**. Subdorsal view. **E**. Dorsal view.

Description

Size. Length 35–37 mm (male), 36–40 mm (female); width of midbody metazona ca. 3.0 mm (male), 3.4 mm (female). Width of head < collum < 2 = 3 < 4 < 5–16, thereafter body gradually tapering towards telson.

Colour (Fig. 14A–B). Specimens in life with body pinkish brown (recently moulted adult brownish pink); head and antennae (except distal part of antennomere 7 and antennomere 8 whitish); metaterga, prozona and surface below paraterga pinkish brown; a dark brown triangular zone on metaterga of each ring; collum, epiproct and legs brown; paraterga dark brown; sterna and a few basal podomeres pale brown; tip of paraterga white. Colour in alcohol: after 9 years changed to brown; head, antennae, collum, metaterga, paraterga, surface below paraterga, sterna, epiproct and legs brown or pale brown.

Collum (Fig. 15A). With three transverse rows of setiferous cones/spines, 5(6)+5(6) cones/spines in anterior row, 3(4/5)+3(4) cones/spines in intermediate row and 4(3)+4 cones/spines in posterior row (lateral cones/spines of anterior row located at base of collum paraterga; paraterga of collum elevated at ca. 20º–40º.

Antennae (Fig. 15D). Moderately long and slender, reaching to body ring 5 or 6 (male) and 4 or 5 (female) when stretched dorsally.

Tegument. Stricture between prozona and metazona wide, quite deep.

Metaterga (Fig. 15A–C). With three transverse rows of setiferous cones/spines; metaterga 2–8 with 4(5)+4(5) cones/spines in anterior row, 3(4/5)+3(4/5) cones/spines in intermediate row and 3(4)+3(4/5) cones/spines in posterior row; 9–19 with 5(6)+5(6) cones/spines in anterior row, 5(4/6)+5(4/6) cones/spines in intermediate row and 5(4/6/7)+5(4/6/7) cones/spines in posterior row; lateral cones/spines of posterior row larger and longer than others in some specimens.

Pleurosternal Carinae. On body ring 2 long, crest-like; on ring 3 a long ridge; on ring 4 a short ridge; thereafter missing.

Paraterga (Figs 15A–C, F, 16A–B). Moderately long, directed caudolaterad on body rings 2–16, elevated at ca. 40º–50º (male) 30º–40º (female), directed increasingly caudad on body rings 17–19.

Telson (Fig. 16C–G). Tip of epiproct subtruncate; apical tubercles inconspicuous. Hypoproct usually subsemicircular (some specimens subtrapeziform); caudal margin slightly round, with conspicuous setiferous tubercles.

Sternum (Fig. 16H–J). On body ring 5 with a swollen lobe; posterior surface of lobe with a pore borne on a short cylindrical stalk.

Legs (Fig. 15E–H). Male femora 5, 6 and 7 with an apophysis.

Gonopods (Figs 17–18). Coxa longer than prefemoral part, subequal in length to femorite. Cannula quite short and stout. Femorite long and slender, curved. Solenophore wide laterally: lamina lateralis broad: lamina medialis very wide, distally blunt, *in situ* directed ventrad.

Distribution and habitat

Known only from a small area in Trang and Songkhla Provinces. All specimens were collected in limestone habitats during the rainy season. Adults males and females were seen hiding under dead leaves while juveniles were found crawling on leaf litter. It is noteworthy that despite several intensive

surveys during 2016–2017 in Trang and Songkhla as well as nearby areas, no further specimens of this species have yet been found. We consider *G. parvoterga* gen. et sp. nov. as an endemic species for Thailand. The new species has been found in syntopy with *Desmoxytes delfae* and *Desmoxytes flabella* Srisonchai, Enghoff & Panha, 2018.

Remarks

Specimens blended perfectly with the environment by hiding under brown/red leaves, it therefore was really difficult to find them. We could not find males at Tham Sri Khaesorn, only two females were collected, but the morphological characters of these perfectly agree with a female specimen from the type locality. *Gigaxytes parvoterga* gen. et sp. nov. exhibits some variation in shape of hypoproct: subtrapeziform in some specimens, subsemicircular in the others.

Gigaxytes suratensis Srisonchai, Enghoff & Panha gen. et sp. nov.
urn:lsid:zoobank.org:act:8F348BCF-8785-40C0-AF0C-B5DA034FF7E1
(Figs 19–24)

Diagnosis

Male femora 5, 6 and 7 with an apophysis. Similar in this respect to *G. parvoterga* gen. et sp. nov., but differs from this species by having paraterga longer; collum usually with 4+4 cones/spines (intermediate row); metaterga 2–8 usually with 4+4 cones/spines (anterior row), 4+4 cones/spines (intermediate row) and 4+4 cones/spines (posterior row); metaterga 9–12 usually with 5+5 cones/spines (anterior row), 5+5 cones/spines (intermediate row) and 5+5 cones/spines (posterior row); metaterga 13–19 usually with 6+6 cones/spines (anterior row), 6+6 cones/spines (intermediate row) and 6+6 cones/spines (posterior row).

Etymology

The specific epiteth is a Latin adjective, referring to the province where the type locality occurs.

Material examined

Holotype

THAILAND: ♂, Surat Thani Province, Phanom District, Ban Song Phi Nong, 8º50′54″ N, 98°44′16″ E, ca. 117 m a.s.l., 7 Aug. 2016, ASRU members leg. (CUMZ-pxDGT00182).

Paratypes

THAILAND: 3 ♂♂, 6 ♀♀, 13 juveniles, same data as for holotype (CUMZ-pxDGT00183-204); 1 ♂, 1 ♀, same data as for holotype (ZMUC00040248).

Additional specimens

THAILAND – **Surat Thani Province**: 1 ♂, 1 broken ♂ – right gonopod lost, 1 ♀, 1 broken ♀, 4 juveniles, Ban Ta Khun District, Ratchaprapa Dam, 8º57′22″ N, 98°48′22″ E, ca. 53 m a.s.l., 8 Oct. 2008, ASRU members leg. (CUMZ); 1 ♂ – gonopods lost, Ban Ta Khun District, Khao Wong Water Supply Station, 8º55′47″ N, 98°56′25″ E, ca. 91 m a.s.l., 9 Oct. 2008, ASRU members leg. (CUMZ); 1 ♂, Khirirat Nikhom District, Wat Satit Khirirom, 9º01′48″ N, 98°59′12″ E, ca. 50 m a.s.l., 10 Jul. 2017, ASRU members leg. (CUMZ); 4 broken ♂♂, 3 broken ♂♂ – gonopods lost, 1 ♀, Phanom District, Khlong Phanom National Park, 8º52′44″ N, 98°40′26″ E, ca. 68 m a.s.l., 28 Aug. 2007, ASRU members leg. (CUMZ); 1 juvenile, Phanom District, Wat Tham Wararam, 8º53′07″ N, 98°40′01″ E, ca. 51 m a.s.l., 5 Aug. 2014, ASRU members leg. (CUMZ); 1 ♂ remaining rings 14–20, 1 ♂ – gonopods lost, 1 broken ♀, Unknown location (probably in Ban Ta Khun District), ASRU leg. (CUMZ).

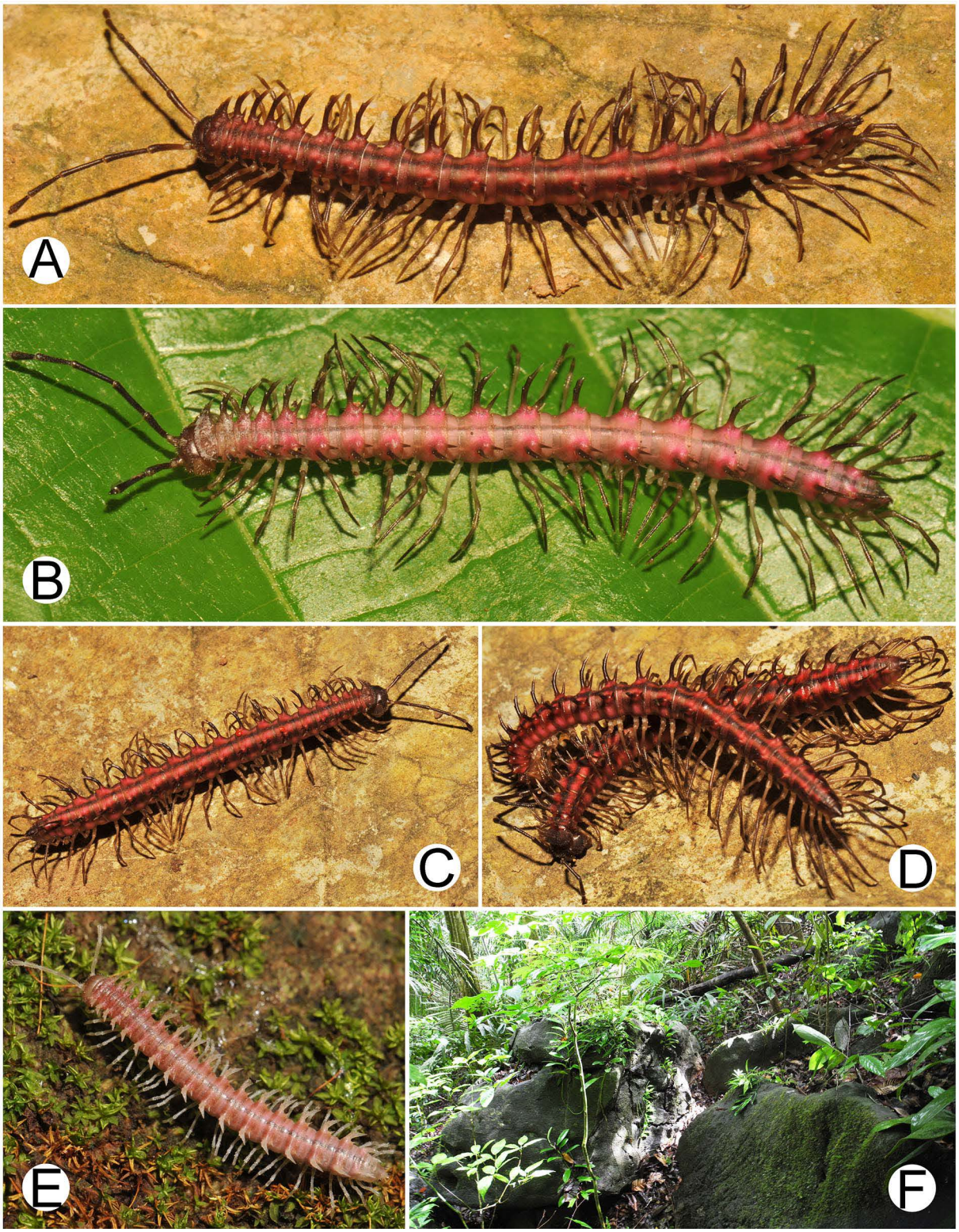

Fig. 19. A–E. Photographs of live *Gigaxytes suratensis* Srisonchai, Enghoff & Panha gen. et sp. nov. **A**. ♂ paratype, specimen from Ban Song Phi Nong. **B**. ♂, specimen from Wat Satit Khirirom. **C**. ♀ paratype, specimen from Ban Song Phi Nong. **D**. Mating couple (paratypes). **E**. Juvenile. **F**. Habitat.

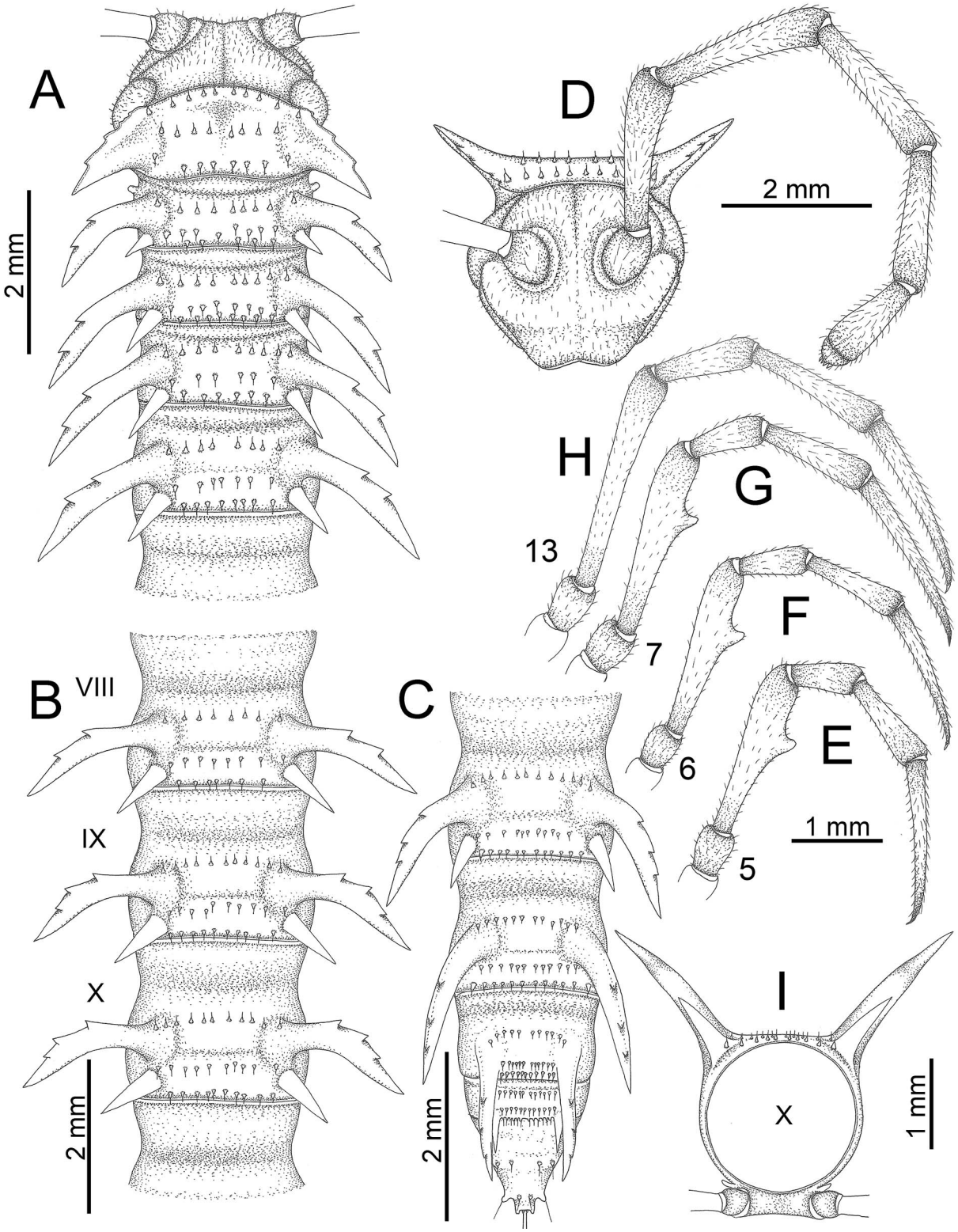

Fig. 20. *Gigaxytes suratensis* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype. **A**. Anterior body part. **B**. Body rings 8–10. **C**. Posteriormost body rings and telson. **D**. Head and antenna. **E**. ♂ leg 5 (right). **F**. ♂ leg 6 (right). **G**. ♂ leg 7 (right). **H**. ♂ leg 13 (right). **I**. Midbody ring.

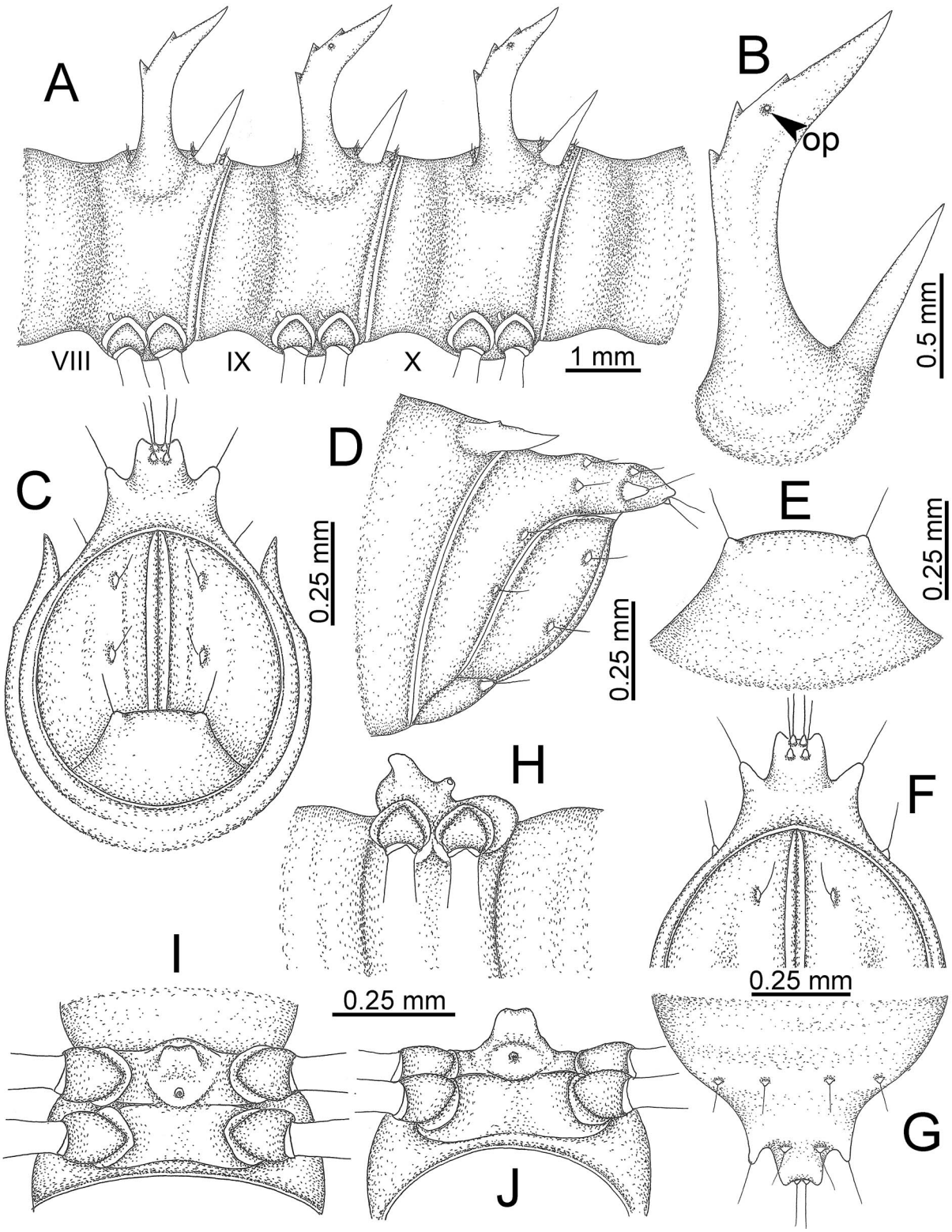

Fig. 21. *Gigaxytes suratensis* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype. **A**. Body rings 8–10. **B**. Paraterga of ring 10 (arrowhead points to ozopore). **C**–**D**. Last ring and telson. **E**. Hypoproct. **F**–**G**. Epiproct. **H**–**J**. Sternal lobe between coxae 4.

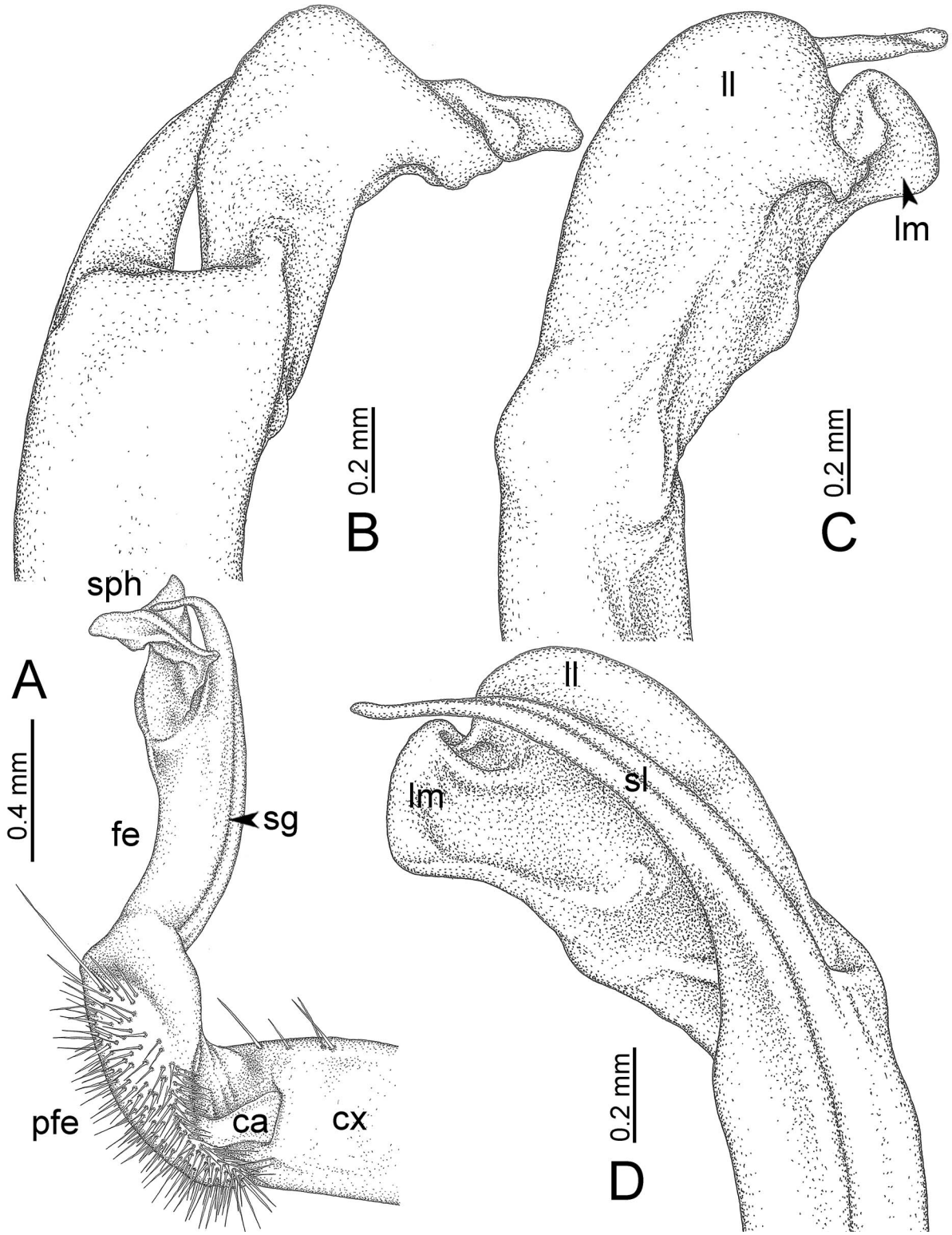

Fig. 22. *Gigaxytes suratensis* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype – right gonopod. **A**. Mesal view. **B**. Lateral view. **C**. Ventral view. **D**. Dorsal view.

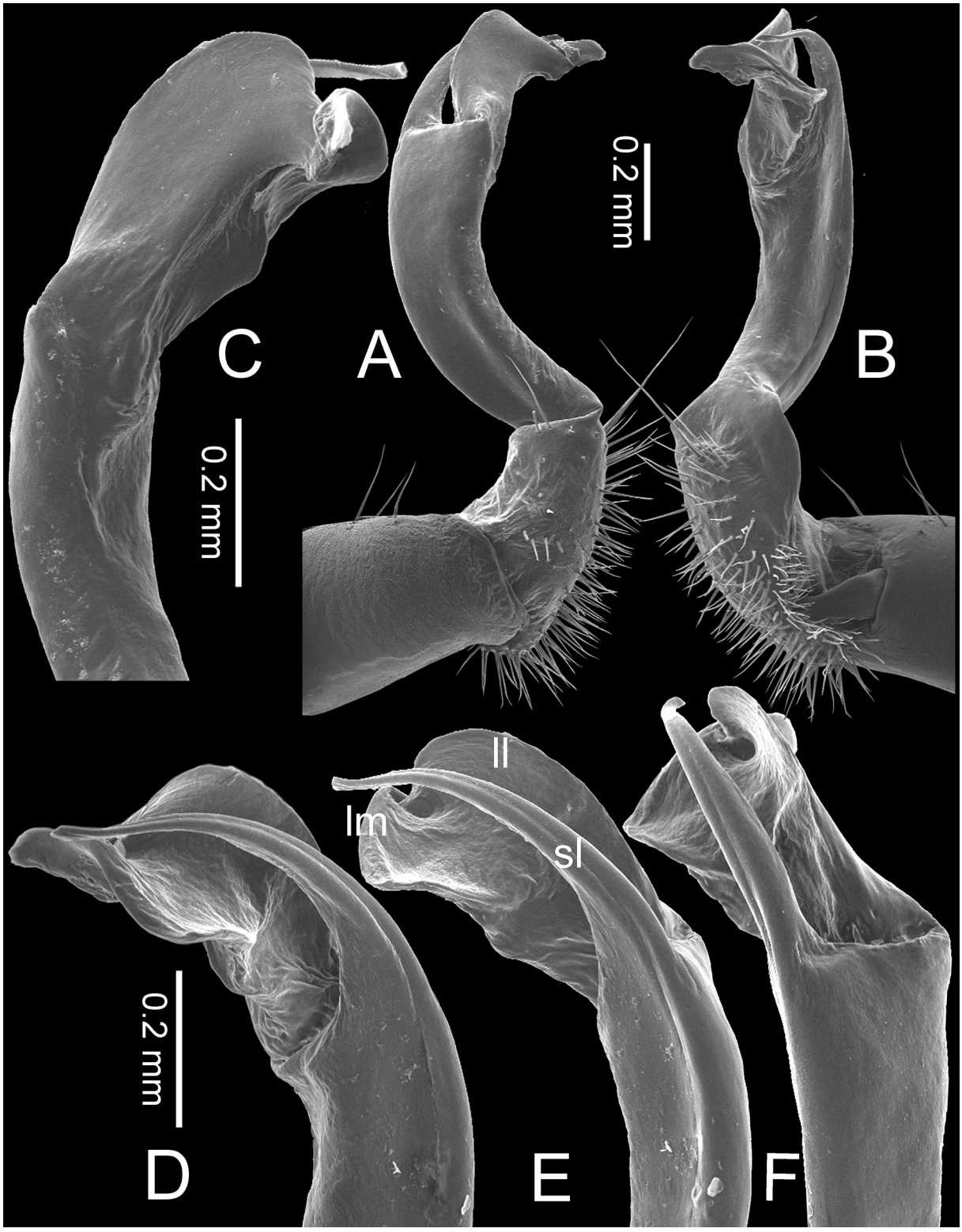

Fig. 23. *Gigaxytes suratensis* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂, paratype – right gonopod. **A**. Lateral view. **B**. Mesal view. **C**. Ventral view. **D**, **F**. Subdorsal view. **E**. Dorsal view.

Description

Size. Length 36–40 mm (male), 38–40 mm (female); width of midbody metazona ca. 2.9 mm (male), 3.7 mm (female). Width of head < collum < 2 ≤ 3 < 4 < 5–16, thereafter body gradually tapering towards telson.

Colour (Fig. 19A–E). Specimens in life with body pinkish brown; some specimens with a dark mid-dorsal band; paraterga and antennae dark brown (except distal part of antennomere 7 and antennomere 8 whitish); head, epiproct and legs brown; metaterga, prozona and surface below paraterga (upper part) pinkish brown; collum pinkish brown/brown; surface below paraterga (lower part) brownish pink; tip of paraterga and sterna pale brown to whitish; a few basal podomeres pale brown. Colour in alcohol: after 10 years changed to pale brown; head, antennae, collum, metaterga, paraterga, surface below paraterga, sterna, epiproct and legs pale brown.

Collum (Fig. 20A). With three transverse rows of setiferous cones/spines, 5(6)+5 cones/spines in anterior row, 4(3)+4(3) cones/spines in intermediate row and 4(3/5)+4(5) cones/spines in posterior row (lateral cones/spines of anterior row located at base of collum paraterga; lateral cones/spines of posterior row displaced anteriad almost halfway to intermediate); paraterga of collum elevated at ca. 30º–45º.

Antennae (Fig. 20D). Moderately long and slender, reaching to body ring 5 or 6 (male) and 4 or 5 (female) when stretched dorsally.

Tegument. Stricture between prozona and metazona wide, quite deep.

Metaterga (Fig. 20A–C). With three transverse rows of setiferous cones/spines; metaterga 2–8 with 4(5)+4(5) cones/spines in anterior row, 4(3)+4(3/5) cones/spines in intermediate row and 4(3/5)+4(3/5) cones/spines in posterior row; metaterga 9–12 with 5(6/7)+5(6) cones/spines in anterior row, 5(6)+5(6) cones/spines in intermediate row and 5(6/7)+5(6/7) cones/spines in posterior row; metaterga 13–19 with 6(5/7/8)+6(5/7/8) cones/spines in anterior row, 6(5/7/8)+6(5/7/8) cones/spines in intermediate row and 6(5/7/8)+6(5/7/8) cones/spines in posterior row.

Pleurosternal Carinae. On body ring 2 long, crest-like; on ring 3 a long ridge; on ring 4 a short ridge; thereafter missing.

Paraterga (Figs 20A–C, I, 21A–B). Moderately long, directed caudolaterad on body rings 2–17, elevated at ca. 45º–60º (male) 40º–50º (female), directed increasingly caudad on body rings 18–19.

Telson (Fig. 21C–G). Tip of epiproct usually subtruncate (in some specimen slightly emarginate); apical tubercles inconspicuous. Hypoproct subtrapeziform; caudal margin usually subtruncate (in some specimens slightly round), with inconspicuous setiferous tubercles.

Sternum (Fig. 21H–J). On body ring 5 with a swollen lobe; posterior surface of lobe with a pore borne on a short cylindrical stalk.

Legs (Fig. 20E–H). Male femora 5, 6 and 7 with an apophysis.

Gonopods (Figs 22–23). Coxa subequal in length to femorite. Cannula quite short and stout. Femorite long, slender, curved. Solenophore wide laterally: lamina lateralis broad: lamina medialis very wide, distally blunt, *in situ* directed mesoventrad.

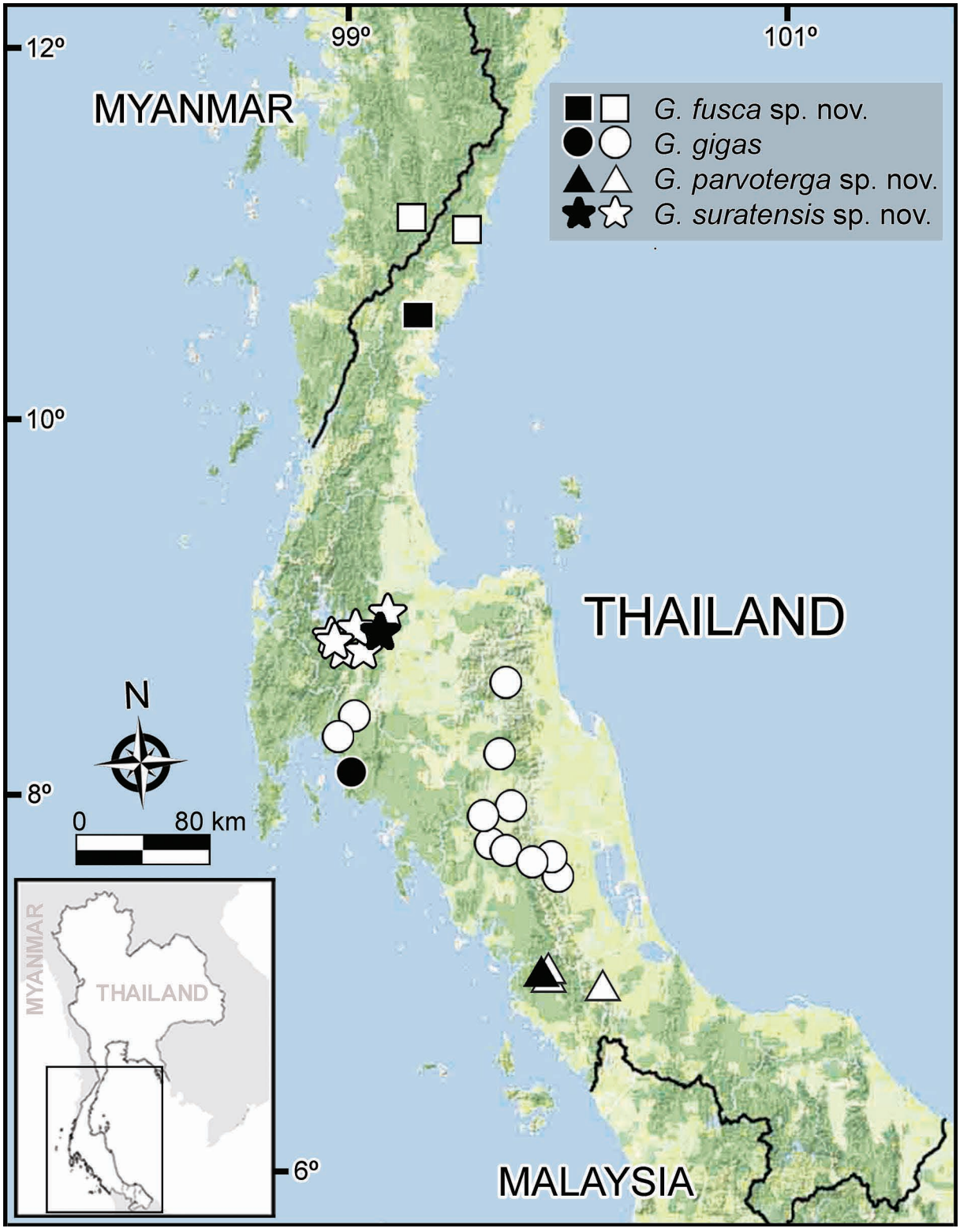

Fig. 24. Known distribution of all *Gigaxytes* gen. nov. species (black symbol = type locality, white symbol = other localities).

Distribution and habitat

Gigaxytes suratensis gen. et sp. nov. is known only from Surat Thani Province. It has been collected from limestone habitats hiding under dead leaves. We cound not access many isolated limestone moutains nearby the type locality, we assume, however, that this species might have a distribution running along the huge limestone mountain ranges in Khaosok and Khlong Phanom National Parks. According to the current data, the new species is dispersed narrowly, we therefore regard *G. suratensis* gen. et sp. nov. as endemic for Thailand. The new species was found together with *Desmoxytes corythosaurus* Srisonchai, Enghoff & Panha, 2018 at Ban Song Phi Nong and Wat Satit Khirirom; *Desmoxytes cervina* at Wat Satit Khirirom.

Remarks

Across the range of this species there are some variations in tip of epiproct (subtruncate in some specimens, slightly emarginate in others) and in shape of caudal margin of hypoproct (subtruncate in some specimens, in others slightly round).

Discussion

Four species of the new dragon millipede genus *Gigaxytes* are here reported for Thailand and Myanmar, of which three are new species to science. All species belonging to the new genus exhibit notable characters: long subspiniform paraterga; three regular rows of cones/spines on metaterga combined with very long caudolateral spines; an *Orthomorpha*-like shape of the gonopod; postfemoral part poorly developed and a small lamina medialis indistinctly demarcated from a large lamina lateralis. These characters can be used to distinguish the new genus from other dragon millipede genera.

Previous to this study, species of dragon millipede have mainly been distinguished on the base of morphological characteristics, especially male gonopods (Pocock 1895; Chamberlin 1923, 1941; Cook & Loomis 1924; Attems 1936, 1937, 1938, 1953; Loksa 1960; Jeekel 1964, 1980; Zhang & Li 1982; Zhang 1986; Golovatch & Enghoff 1994; Nguyen *et al.* 2005; Enghoff *et al.* 2007; Golovatch *et al.* 2010, 2012, 2016; Liu *et al.* 2014, 2016; Likhitrakarn *et al.* 2015; Srisonchai *et al.* 2016, 2018a). Our study has been based upon both gonopod and other characters (e.g. male femora 5–7 and numbers of cones/spines on metaterga, paraterga, etc.) in combination with our on-going analysis of the mitochondrial COI gene, which all can potentially be used for species discrimination. Among the four species of *Gigaxytes*, *G. gigas* gen. et comb. nov., *G. parvoterga* gen. et sp. nov. and *G. suratensis* gen. et sp. nov. show great similarity in gonopod morphology, sharing a broad and wide solenophore (lamina lateralis broad; lamina medialis short and wide). Based on gonopod characters alone, these species can not be reliably distinguished. However, male femora 5–7 and numbers of cones/spines on metaterga have shown to be useful for separation of species. In the case of *G. parvoterga* gen. et sp. nov. and *G. suratensis* gen. et sp. nov., although they are morphologically most similar (gonopod shape and modification of male femora 5–7), *G. parvoterga* gen. et sp. nov. can be differentiated from *G. suratensis* gen. et sp. nov. due to the shorter paraterga, the caudal margin of hypoproct with inconspicuous setiferous tubercles and differences in numbers of cones/spines on metaterga. Their (small) distributions areas are also widely separated.

All four species are notable by their very long, subspiniform paraterga. As for other dragon millipede species, these structures are thought to be used for the protection against predators and might support the spread of the defensive substances. However, for the time being this is still hypothetical; experiments have not yet been carried out (Liu *et al.* 2017). Another remarkable trait is the live colouration of three species: *G. gigas* gen. et comb. nov., *G. parvoterga* gen. et sp. nov. and *G. suratensis* gen. et sp. nov. are pinkish brown and seem able to be blend in well with the environment. We therefore suspect that their colouration is not aposematic.

We found two types of mites associated with two *Gigaxytes* species. Parasitic larvae of ?*Leptus* sp. were found on *G. gigas* gen. et comb. nov. Similar mites have also been encountered on *Desmoxytes cervina*, *Nagaxytes acantherpestes* (Golovatch & Enghoff, 1994) and *N. erecta* Srisonchai, Enghoff & Panha as reported by Srisonchai *et al.* (2018a, b). A very different type of mite was found on *G. fusca* gen. et sp. nov. as shown in Fig. 4D, E; according to examination under light microscope these tiny mites exhibit a very flat venter and convex dorsum, lack mouthparts, have suckers on the ventral side and have backward-directed 'knees' of leg-pairs 3 and 4. These characters make it possible to identify them as deutonymphs (the hypopus stage) of the family Histiostomatidae (cohort Astigmatina) (Farfan & Klompen 2012; OConnor 2009). This type of astigmatidan deutonymph is considered to be a great example of phoretic relationship (OConnor 2009). Histiosomatid mites had not yet been documented before in any previously known species of the order Polydesmida. Only one species of histiostomatid mite, *Histiostoma feroniarum* (Dufour, 1839) has been reported with a millipede, the julid *Ommatoiulus moreleti* (Lucas, 1860) by Baker (1985).

The new genus has a rather limited distribution in southern Myanmar and southern Thailand (Fig. 24). Its distribution is bounded to the South by the Tenasserim mountain range. These millipedes are all restricted to limestone areas. Our observations in the field suggest that the preferred microhabitat of all species in this genus is on the ground, underneath leaf litter with which the colour of the millipede blends in perfectly. Of the five species of *Gigaxytes*, only one is currently known to have a relatively wide distribution range, viz., *G. gigas* gen. et comb. nov., dispersed across middle part of southern Thailand, whereas the other three species have been found to occur exclusively within such a very restricted area. No sympatry between *Gigaxytes* species was observed, but all can be found in syntopy with *Desmoxytes* species in some localities, sharing the same habitat.

The number of known dragon millipede species (*Desmoxytes*, *Hylomus*, *Nagaxytes*, *Gigaxytes* gen. nov.) has increased substantially during the recent few years (Liu *et al*. 2014, 2016; Likhitrakarn *et al*. 2015; Golovatch *et al*. 2016; Srisonchai *et al*. 2016, 2018a) including the new genus *Gigaxytes* described herein. Further collecting in so far unexplored isolated limestone areas of difficult access in several countries in mainland Southeast Asia, especially Laos, Malaysia, Myanmar, and South Thailand, will probably reveal many new, peculiar species.

Correction to Srisonchai *et al.* (2018a)

Srisonchai *et al.* (2018a) in page 107 failed to mention two female paratypes of *Desmoxytes perakensis*. The paratypes should be indicated as follows: Paratypes. 4 ♂♂, 2 ♀♀ (CUMZ), same data as holotype.

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