TAXONOMY AND SYSTEMATICS OF DRAGON MILLIPEDES GENUS *Desmoxytes* Chamberlin, 1923 IN THAILAND

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อนุกรมวิธานและซิสเทแมติกส์ของกิ้งกือมังกรสกุล *Desmoxytes* Chamberlin, 1923 ในประเทศไทย

นายรัฐพล ศรีสนไชย

วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรดุษฎีบัณฑิต
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Field of Study	Biological Sciences
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รัฐพล ศรีสนไชย : อนุกรมวิธานและซิสเทแมติกส์ของกิ้งกือมังกรสกุล *Desmoxytes* Chamberlin, 1923 ในประเทศไทย. (TAXONOMY AND SYSTEMATICS OF DRAGON MILLIPEDES GENUS *Desmoxytes* Chamberlin, 1923 IN THAILAND) อ.ที่ปรึกษาวิทยานิพนธ์หลัก : ศ. ดร.สมศักดิ์ ปัญหา, อ.ที่ปรึกษาวิทยานิพนธ์ร่วม : ศ. ดร.เฮนริก อิงฮอฟ

ศึกษาอนุกรมวิธานและซิสเทแมติกส์ของกิ้งกือมังกรสกุล *Desmoxytes* sensu Golovatch & Enghoff (1994) หรือ *Desmoxytes s.l.* ในวงศ์ Paradoxosomatidae โดยอาศัยวิธีบูรณาการจากข้อมูลลักษณะสัณฐานวิทยาและผลการวิเคราะห์ทางเทคนิคชีววิทยาเชิงโมเลกุลของยีน 3 ตำแหน่ง คือ COI, 16S rRNA และ 28S rRNA ตัวอย่างกิ้งกือมังกรได้ถูกเก็บจากประเทศไทยและบางพื้นที่บนแผ่นดินใหญ่เอเชียตะวันออกเฉียงใต้ จากนั้นทำการเปรียบเทียบกับตัวอย่างต้นแบบ จากการทบทวนอนุกรมวิธานนำไปสู่การจำแนกสกุลออกจากเดิมที่มี 1 สกุล เป็น 5 สกุล ดังนี้ *Desmoxytes s.s.*, *Hylomus* stat. rev., *Gigaxytes* gen. nov., *Nagaxytes* gen. nov. และ *Spinaxytes* gen. nov. โดย 3 สกุลหลังถูกตั้งเป็นสกุลใหม่ของโลก ซึ่งแต่ละสกุลมีลักษณะสัณฐานวิทยาที่แตกต่างกันอย่างชัดเจนและมีความแตกต่างกันทางพันธุกรรมสูง การศึกษาครั้งนี้ทำให้จำนวนสปีชีส์ของกิ้งกือมังกรเพิ่มขึ้นเป็น 68 สปีชีส์ แบ่งเป็น 18 สปีชีส์ในสกุล *Desmoxytes s.s.* 33 สปีชีส์ในสกุล *Hylomus* 4 สปีชีส์ในสกุล *Gigaxytes* 4 สปีชีส์ในสกุล *Nagaxytes* และ 9 สปีชีส์ในสกุล *Spinaxytes* ในจำนวนนี้พบว่าเป็นสปีชีส์ใหม่ทั้งสิ้น 27 สปีชีส์ ประกอบด้วย 23 สปีชีส์พบจากประเทศไทย 2 สปีชีส์จากประเทศพม่า และ 2 สปีชีส์จากประเทศมาเลเซีย กิ้งกือมังกรเกือบทุกสปีชีส์พบจากบริเวณเขาหินปูนเท่านั้น มีเพียงบางสปีชีส์พบอาศัยในป่าเขตร้อนทั่วไป และทุกสปีชีส์ถูกรายงานเป็นสปีชีส์เฉพาะถิ่นที่มีขอบเขตของการกระจายแคบ ยกเว้น 1 สปีชีส์ (*D. planata*) ที่มีการกระจายกว้าง

การศึกษาความสัมพันธ์ทางวิวัฒนาการเชิงโมเลกุล แสดงให้เห็นว่ากิ้งกือมังกรสกุล *Desmoxytes s.l.* มีความสัมพันธ์ทางวิวัฒนาการเป็นแบบเชิงวงศ์วานคู่ขนาน (paraphyly) โดยมีความสัมพันธ์ใกล้ชิดกับกิ้งกือตะเข็บสกุล *Orthomorpha* ซึ่งแผนภูมิต้นไม้ทางวิวัฒนาการแบ่งกิ้งกือมังกรออกเป็น 5 กลุ่ม สอดคล้องกับ 5 สกุลที่ถูกจำแนกโดยใช้ลักษณะสัณฐานวิทยา แต่ละสกุลที่ถูกแยกนั้นมีความสัมพันธ์เชิงวงศ์วานเดี่ยว (monophyly) ทั้งในวิธีวิเคราะห์แบบ Maximum Likelihood (ML) และ Bayesian Inference (BI) ผลการศึกษาสนับสนุนการใช้ลักษณะสัณฐานวิทยาของอวัยวะสืบพันธุ์เพศผู้ (gonopod) และโครงสร้างคล้ายแผ่นปีก (paraterga) เป็นลักษณะสำคัญในการจัดจำแนกสกุลของกิ้งกือมังกร นอกจากนี้ยังพบว่าข้อมูลทางพันธุกรรมสอดคล้องกับการกระจายตัวทางภูมิศาสตร์ด้วย การศึกษาในภาคสนามยังพบความสัมพันธ์ของกิ้งกือมังกรบางชนิดกับไรและรา ซึ่งเป็นการรายงานการค้นพบครั้งแรกในกิ้งกือกลุ่มนี้ ผลการวิเคราะห์และเก็บตัวอย่างที่ครอบคลุมที่สุดของการศึกษากิ้งกือมังกรในครั้งนี้ เป็นการขยายขอบเขตความรู้ด้านสัณฐานวิทยาและชีววิทยาเชิงโมเลกุล แสดงถึงหลักฐานบ่งชี้ว่ากิ้งกือมังกรมีความหลากหลายทางสปีชีส์สูงมาก นอกจากนี้ยังทำให้เข้าใจถึงความสัมพันธ์ทางวิวัฒนาการของสัตว์กลุ่มนี้อีกด้วย

ภาควิชา	ไม่สังกัดภาควิชา/เทียบเท่า	ลายมือชื่อนิสิต ....
สาขาวิชา	วิทยาศาสตร์ชีวภาพ	ลายมือชื่อ อ.ที่ปรึกษาวิทยานิพนธ์หลัก ....
ปีการศึกษา	2561	ลายมือชื่อ อ.ที่ปรึกษาวิทยานิพนธ์ร่วม ....

5672865323 : DOCTOR OF PHILOSOPHY
ENDEMIC / LIMESTONE AREA / NEW GENUS / PHYLOGENY

Ruttapon Srisonchai :
TAXONOMY AND SYSTEMATICS OF DRAGON MILLIPEDES GENUS *Desmoxytes* Chamberlin, 1923 IN TH AILAND. ADVISOR: Prof. Somsak Panha, D.Sc.,Prof. Henrik Enghoff, D.Sc.

Taxonomy and systematics of the dragon millipede genus *Desmoxytes* sensu Golovatch & Enghoff (1994) (= *Desmoxytes s.l.*) of the family Paradoxosomatidae has been analyzed and implemented based on an integrative approach by morphological revision and molecular phylogeny from three partial genes (COI, 16S rRNA and 28S rRNA). The specimens were collected mainly from Thailand and neighboring countries in mainland Southeast Asia, and were compared with available type material. Taxonomic revision resulted in the subdivision of *Desmoxytes s.l.* into five genera, viz., *Desmoxytes s.s.*, *Hylomus* stat. rev., *Nagaxytes* gen. nov., *Gigaxytes* gen. nov. and *Spinaxytes* gen. nov. All five genera showed distinctive morphological characteristics in agreement with high genetic divergences. The total number of dragon millipedes is currently brought up to 68: eighteen species in *Desmoxytes s.s.*; four species in *Nagaxytes*; four species in *Gigaxytes*; four species in *Spinaxytes* and 33 species in *Hylomus*. In this study, 27 species have been described as new species to science, of which 23 species are recorded from Thailand, two from Myanmar and two from Malaysia. Almost all species were found in limestone habitats; a few species inhabit tropical forest. All are regarded as locally endemic species according to their narrow distribution (except the tramp species *D. planata*).

The molecular phylogeny indicates paraphyly of *Desmoxytes s.l.* in terms of the outgroup genus *Orthomorpha.* The proposed tree delimits five clades of dragon millipedes corresponding to the five genera in accordance with the morphology-based classification and splitting approach. Each of the five genera was recovered as monophyletic in both Maximum Likelihood and Bayesian Inference analyses, and the results also support the significance of male genitalia (gonopod) and paraterga as diagnostic characters for genus identification. The results of the phylogenetic analysis interestingly show a high degree of compatibility between genetic structure and geographical distribution. Some biological traits such as mite and fungal associations were recorded for the first time in several species of these animals. By conducting the most comprehensive sampling of the dragon millipede to date, this study significantly expands the scope of morphological and molecular explorations, and reveals a much richer species diversity than previously known, finally leading to understanding of the relationships in this spectacular group of millipedes.

Department:	Common Course	Student's Signature ....
Field of Study:	Biological Sciences	Advisor's Signature ....
Academic Year:	2018	Co-advisor's Signature ....

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Ruttapon Srisonchai

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CHAPTER I

Introduction

Millipedes are common terrestrial invertebrates that play important roles in the decomposition and nutrient cycling in the forest ecosystem (Hopkin and Read, 1992; Lawrence, 1984). It is estimated that eighty thousand species of millipedes exist, but only 12,000 species have so far been described and allocated to 16 orders (Sierwald and Bond, 2007). The order Polydesmida is the largest order, and although many poldesmidans are quite large and colourful millipedes these animals are still quite poorly known. A peculiar somatic feature of (most) Polydesmida is wing-like dorsolateral extensions to the body rings called paranota. The paranota probably help the animal wedge itself into crevices in logs or leaf litter and protect its legs.

Among Polydesmida, the Paradoxosomatidae is the largest family, containing more than 1,100 described species distributed worldwide, except in North America and Antarctica (Nguyen and Sierwald, 2013; Zhang, 2011). Several species of paradoxosomatid millipedes exhibit swarming phenomena, in some cases causing a nuisance (Hopkin and Read, 1992). Moreover, polydesmidan millipedes secrete defensive chemicals such as hydrogen cyanide, which may be applied for medical researches and biological controls (Attygalle *et al.*, 1993; Eisner *et al.*, 1978; Enghoff *et al.*, 2014; Shear, 2015).

Paradoxosomatid species have been reported from all regions of Southeast Asia and contribute significantly to the status of Southeast Asia as an area containing a particularly high diversity of millipedes (Golovatch *et al.*, 2010). Located at the center of the Indo-Burma biodiversity hotspot, and not having had a colonial past, Thailand occupies a special position in terms of large numbers of species still awaiting discovery. For examples, more than 20 new species of the paradoxosomatoid genera *Orthomorpha* and *Tylopus* were recently described from Thailand (Likhitrakarn *et al.*, 2011).

Dragon millipedes – until very recently all classified in the genus *Desmoxytes* Chamberlin, 1923 (=*Desmoxytes sensu* Golovatch & Enghoff (1994), =*Desmoxytes* *sensu lato, =Desmoxytes s.l.*) are some of the most peculiar paradoxosomatids. The distinctive characters of dragon millipedes are conspicuously shaped paraterga, which may be antler-like, spiniform, or wing-shaped, often in combination with remarkably bright warning colourations (Fig. 1.1). Currently, 43 species of *Desmoxytes s.l.* are known from Southeast Asia and Central-Southern China. Specifically, the discovery of "the shocking pink dragon millipede", *Desmoxytes purpurosea,* in Thailand brought great attention to the endemic fauna of the region, and also stimulated research on myriapod taxonomy in Thailand (Enghoff *et al.*, 2007). However, the taxonomic study of dragon millipede in Thailand is still poorly known and seems to be scarce. Only some areas have been recorded to occur *Desmoxytes* (Fig. 1.2) whereas several remote locations or otherwise difficult-to-access places have never been explored yet.

The identification of dragon millipedes at the species level is based on characters derived from the striking paraterga and metaterga, and especially from the male copulatory organs called gonopods (Golovatch and Enghoff, 1994). However, many species are still taxonomically problematic due to similar morphologies of paraterga and gonopods, and even similar colour patterns (Golovatch *et al.*, 2012). Until now, dragon millipede classification has been based exclusively on morphological descriptions without any molecular analyses (Enghoff *et al.*, 2007; Golovatch *et al.*, 2012; Nguyen *et al.*, 2005).

In recent years, extensive surveys of millipedes, including dragon millipedes, have been made in several areas, mainly in Thailand, in some parts of Laos and Myanmar and to a lesser extent in peninsular Malaysia. After examination of newly collected specimens, and comparison with some original descriptions of all congeners, we found distinctive morphological characters, mainly in gonopods and paraterga, indicating heterogeneity of *Desmoxytes s.l.* Five groups of *Desmoxytes s.l.* can be clearly characterized based on differences of gonopods and paraterga. Therefore, *Desmoxytes s.l.* has been subdivided into five groups which are each monophyletic and are each regarded as a separate genus.

Objectives of the present thesis

1. To study the taxonomy of the dragon millipedes, genus *Desmoxytes* sensu Golovatch & Enghoff (1994) in Thailand

2. To reconstruct the molecular phylogeny for dragon millipedes, with emphasis on species from in Thailand

Figure 1.1 Photographs of live *Desmoxytes* s.l. (**A**: *Desmoxytes purpurosea* Enghoff, Sutcharit & Panha, 2007 **B**: *Desmoxytes* sp. 1 **C**: *Desmoxytes gigas* Golovatch & Enghoff, 1994 **D**: *Desmoxytes* sp. 2 **E**: *Desmoxytes* sp. 3 **F**: mating couple of *Desmoxytes* sp. 4)

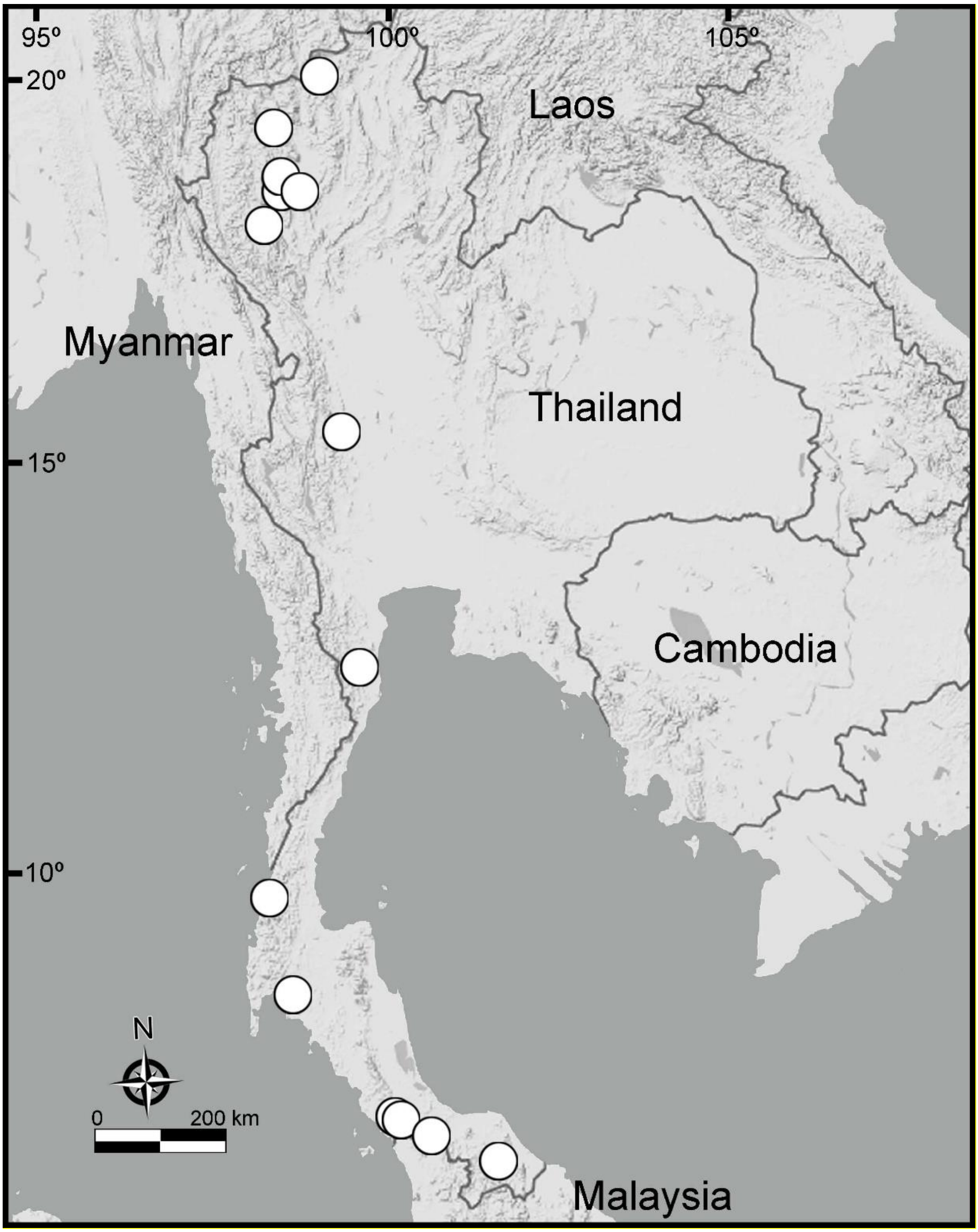

Figure 1.2 Collecting sites of the dragon millipede genus *Desmoxytes* s.l. in Thailand

CHAPTER II

Literature Review

Fundamental overview

Species of the genus *Desmoxytes s.l.,* belonging to the subfamily Paradoxosomatinae, are known as "dragon millipedes" (name introduced by Cook and Loomis 1924) because of the strikingly ornamented body, in particular the peculiar paraterga, often in combination with bright colours. Dragon millipedes are distributed from Central China down to northern peninsular Malaysia. Until recently the genus *Desmoxytes s.l.* contained 43 valid species; nineteen from China, ten from Vietnam, seven from Thailand, three from Myanmar, three from Laos and one from Malaysia. Most species seem to be endemic to specific habitats such as karst areas, limestone and caves. These habitats are actually quite unstable, changing through time because of limestone degradation by both physical and biological processes. In addition, human activities threaten the habitats and accelerate species extinction. There are many campaigns and rules for conservation from several world organizations such as CBD, UNDP, UNESCO but there is a great lack of serious complementary actions from member countries (CBD, 2010). These unique millipedes in their unique habitats may contribute to raising awareness of the necessity of biodiversity conservation. For instance, the finding of the shocking pink dragon millipede, *Desmoxytes purpurosea*, in only one karst cavern from Thailand, as well as three new cavernicolous species described from China, gained considerable publicity.

The study of dragon millipedes began in the late 19th century by Pocock (1895). Subsequently, several myriapodologists published and reported numerous dragon millipede species (Attems, 1937, 1953; Chamberlin, 1923; Cook and Loomis, 1924a; Enghoff *et al.*, 2007; Golovatch and Enghoff, 1994; Golovatch *et al.*, 2010; Golovatch *et al.*, 2012; Golovatch *et al.*, 2016; Jeekel, 1964; Likhitrakarn *et al.*, 2015; Liu *et al.*, 2014, 2016; Loksa, 1960; Nguyen *et al.*, 2005; Zhang, 1986; Zhang and Li, 1982). All described species were based on external morphological characters, e.g., gonopods, paraterga, sterna, metaterga, femora, tegument, telson. Although many morphological characteristics were used to describe those new species, the morphological similarities in body colour, gonopods and other body characteristics are still causing problems and have often lead to misidentification and erroneous classification. An example of the latter is *Desmoxytes philippina* Nguyen & Sierwald, 2010, which was shown not to belong to *Desmoxytes s.l.* by Golovatch *et al.* (2012) who proposed to move this species into an unspecified genus of subfamily Australiosomatinae due to the different shape of its gonopod.

The first, not very convincing attempt at a phylogenetic analysis of paradoxosomatid millipedes was made by Golovatch and Enghoff (1993) who performed a cladistic analysis of the species of the genus *Tylopus* Jeekel, 1968, based on 14 somatic and gonopodal characters. The same authors subsequently examined relationships of 19 species of *Desmoxytes s.l.* through a cladistic analysis based on 24 external and gonopodal characters. The result suggested that gonopods correlated poorly with paraterga (Golovatch and Enghoff, 1994). This conflict between characters derived from paraterga and gonopods has not yet been resolved.

Molecular techniques have been widely used in phylogenetic analyses and have helped to solve problems of evolutionary relationships, systematic classification, species delimitation and cryptic speciation in millipedes (Bond *et al.*, 2003). Bond and Sierwald (2002) studied cryptic speciation in the *Anadenobolus excisus* species complex of the order Spirobolida, using 1,000 base pairs of the mitochondrial 16S rRNA gene from 242 individual samples. The result revealed three highly divergent lineages, whereas the morphological phylogeny confirmed only one taxon. A combined analysis of the morphological and molecular data, however, strongly supported the recognition of three cryptic species were strongly recognized in the species complex.

The giant cylindrical millipedes of the genus *Thyropygus* (order Spirostreptida) provide an example of how evolutionary relationships of millipede species may be revealed by DNA sequences data. Pimvichai *et al.* (2014) analyzed parts of DNA sequences in the mitochondrial genes (COI and 16S rRNA) of numerous *Thyropygus* species. While this genus shows variant morphological characters, the molecular analysis recovered *Thyropygus* as monophyletic, and the indicated relationships were congruent with the morphological identification, thus supporting previous studies on species delimitation (Pimvichai *et al.*, 2014).

Up to now, molecular systematics of *Desmoxytes s.l.* has not been studied intensively. This group is vaguely supported by some diagnostic morphological characters. Moreover, the relationships among *Desmoxytes* species and related groups are also poorly understood. In the present thesis, combined studies of morphological and molecular characters are made, with a view to obtaining an acceptable classification and to reveal phylogenetic relationships between species of *Desmoxytes s.l.*

Clarification of species delimitation and relationships will contribute to understanding the evolution of the peculiar dragon millipedes, as well as be important for sustainable conservation of habitats, especially the limestone karsts of SE Asia.

The brief historical studies of the dragon millipede

Over the past 100 years, the concept of dragon millipedes (*Desmoxytes s.l.*) has involved six generic names which have been established/ reinstated/ synonymized through time, viz., *Prionopeltis* Pocock, 1895, *Pratinus* Attems, 1937, *Desmoxytes* Chamberlin, 1923, *Hylomus* Cook and Loomis, 1924, *Ceylonesmus* Chamberlin, 1941, *Pteroxytes* Jeekel, 1980.

The monotypic genus *Desmoxytes* was established by Chamberlin (1923) based on a single species, *D. coniger* Chamberlin, 1923 as the type species. Chamberlin created the new millipede genus based on the conspicuously elevated paraterga (= keels) in combination with distinct gonopod characters (a constriction between femur and postfemur). However, the name *Desmoxytes* was not widely used and accepted until (Jeekel, 1980a) recognized it as a senior synonym of *Prionopeltis* Pocock, 1895 (preoccupied), *Pratinus* Attems, 1931 and *Ceylonesmus* Chamberlin, 1941.

Just one year after the name *Desmoxytes* was published, (Cook and Loomis, 1924a) created the genus *Hylomus*, was established as new genus based on a single species, *H. draco* Cook & Loomis, 1924. Cook and Loomis were so impressed by the remarkable external features of the *H. draco*, viz., the strongly elevated (tree-like) paraterga, that they placed the new species not only in a new genus but even in a new family, Hylomidae. In the same year (Cook and Loomis, 1924b), they coined the common name “dragon millipede” which it relates to the external features of *H. draco*. *Hylomus* was synonymized under *Desmoxytes* by Golovatch and Enghoff (1994).

(Jeekel, 1980a) established the new genus *Pteroxytes* for a morphologically distinctly species of dragon millipede, *Pteroxytes terae* (Jeekel, 1964) which he had previously described in *Pratinus*. Subsequently, *Pteroxytes* was then synonymized under *Desmoxytes* by (Golovatch and Enghoff, 1994).

By the turn of the millennium, all dragon millipedes were thus classified in one genus, *Desmoxytes s.l*. New species of dragon millipedes described since then have also been assigned to this genus.

Apart from species described in the present thesis, *Desmoxytes s.l.* is comprises 43 nominal species:

1. *Desmoxytes acantherpestes* Golovatch & Enghoff, 1994
2. *Desmoxytes aspera* (Attems, 1937)
3. *Desmoxytes cattienensis* Nguyen, Golovatch & Anichkin, 2005
4. *Desmoxytes cervaria* (Attems, 1953)
5. *Desmoxytes cervina* (Pocock, 1895)
6. *Desmoxytes cornuta* (Zhang & Li, 1982)
7. *Desmoxytes delfae* (Jeekel, 1964)
8. *Desmoxytes draco* (Cook & Loomis, 1924)
9. *Desmoxytes enghoffi* Nguyen, Golovatch & Anichkin, 2005
10. *Desmoxytes eupterygota* Golovatch, Li, Liu & Geoffroy, 2012
11. *Desmoxytes getuhensis* Liu, Golovatch & Tian, 2014
12. *Desmoxytes gigas* Golovatch & Enghoff, 1994
13. *Desmoxytes grandis* Golovatch, VandenSpiegel & Semenyuk, 2016
14. *Desmoxytes hostilis* Golovatch & Enghoff, 1994
15. *Desmoxytes jeekeli* Golovatch & Enghoff, 1994
16. *Desmoxytes lingulata* Liu, Golovatch & Tian, 2014
17. *Desmoxytes laticollis* Liu, Golovatch & Tian, 2016
18. *Desmoxytes longispina* (Loksa, 1960)
19. *Desmoxytes lui* Golovatch, Li, Liu & Geoffroy, 2012

20. *Desmoxytes minutubercula* (Zhang, 1986)
21. *Desmoxytes nodulosa* Liu, Golovatch & Tian, 2014
22. *Desmoxytes parvula* Liu, Golovatch & Tian, 2014
23. *Desmoxytes phasmoides* Liu, Golovatch & Tian, 2016
24. *Desmoxytes pilosa* (Attems, 1937)
25. *Desmoxytes planata* (Pocock, 1895)
26. *Desmoxytes proxima* Nguyen, Golovatch a& Anichkin, 2005
27. *Desmoxytes pterygota* Golovatch & Enghoff, 1994
28. *Desmoxytes purpurosea* Enghoff, Sutcharit & Panha, 2007
29. *Desmoxytes rhinoceros* Likhitrakarn, Golovatch & Panha, 2015
30. *Desmoxytes rhinoparva* Likhitrakarn, Golovatch & Panha, 2015
31. *Desmoxytes rubra* (Jeekel, 1964)
32. *Desmoxytes scolopendroides* Golovatch, Geoffroy & Mauriès, 2010
33. *Desmoxytes scutigeroides* Golovatch, Geoffroy & Mauriès, 2010
34. *Desmoxytes similis* Liu, Golovatch & Tian, 2016
35. *Desmoxytes simplex* Golovatch, VandenSpiegel & Semenyuk, 2016
36. *Desmoxytes simplipoda* Liu, Golovatch & Tian, 2016
37. *Desmoxytes specialis* Nguyen, Golovatch & Anichkin, 2005
38. *Desmoxytes spectabilis* (Attems, 1937)
39. *Desmoxytes spinissima* Golovatch, Li, Liu & Geoffroy, 2012
40. *Desmoxytes spiniterga* Liu, Golovatch & Tian, 2016
41. *Desmoxytes taurina* (Pocock, 1895)
42. *Desmoxytes terae* (Jeekel, 1964)
43. *Desmoxytes variabilis* Liu, Golovatch & Tian, 2016

Previous phylogenetic studies of paradoxosomatid millipedes

Paradoxosomatidae is the largest family among all millipedes in terms of described genera and species. It is subdivided into several subfamilies and tribes, but phylogenetic relationships between these have never been analyzed. Only a few phylogenetic studies focusing on particular genera, based on morphology and molecular data, have been done.

The first integrative taxonomic study based on morphology and molecular phylogeny for a genus of paradoxosomatid millipede was recently published by Decker (2016a). Decker observed that the Australian genus *Oncocladosoma* Jeekel, 1985 (tribe Australosomatini) exhibited morphological similarities to genus *Somethus* Chamberlin, 1920. His analysis, based on morphological and molecular data (COI and 28S) for 25 specimens, showed that all species of *Oncocladosoma* fell within *Somethus*, and therefore, he synonymized *Oncocladosoma* under *Somethus*. At about the same time Decker (2016b) evaluated relationships within the likewise Australian genus *Pogonosternum* Jeekel, 1965 (tribe Australosomatini) using two mitochondrial (COI and 16S) and one nuclear (28S) gene. Decker found that the genus was recovered as monophyletic and consisted of five clades, morphologically congruent with five species groups. Each group displayed a pattern of high interspecific genetic variability, suggesting that they were geographically confined to multiple Pleistocene refugia on the southeastern Australian mainland. Decker's studies underlined the usefulness of combining morphological and genetic data for classification and species discrimination, as well as the importance of considering geographical distribution in order to understand the evolution of taxon.

Nguyen *et al.* (2017) revised the genus *Oxidus* Cook, 1911 (tribe Sulciferini) based on both morphological and molecular data. Two mitochondrial genes (COI and 16S) were used to reconstruct the phylogeny in order to compare with morphological characters. The monophyly of *Oxidus* was strongly supported, corresponding to the classification using gonopod characters. In the same year, Nguyen (2017) published phylogenetic relationship of the Vietnamese genus *Vietnamorpha* Golovatch, 1984 (tribe Sulciferini) based on sequence data form three partial genes (16S, 18S and 28S). The results showed that *Vietnamorpha* formed a monophyletic clade, and that morphological characteristics can be used for species delimitation also found earlier in the genus *Oxidus*.

The most recent phylogenetic studies focus on the genera *Antheromorpha* Jeekel, 1968 and *Nesorthomorpha* Jeekel, 1980 (tribe Orthomophini) (Nguyen *et al.*, 2018b). For *Antheromorpha*, a new species, *A. pumatensis,* was described based on morphological characters in combination with phylogenetic tree of 16S rRNA gene. For

Nesorthomorpha, the new species *N. montana* was based on two genes (COI and 16S rRNA). Nguyen *et al.* (2018a) included three species of *Desmoxytes s.l.* species (*D. cervaria*, *D. enghoffi* and *D. proxima*) as well as several other Vietnamese species to evaluate the position on the phylogenetic tree of the two new species. The results supported and were congruent with morphological characters. In addition, they also found that *Antheromorpha* and *Nesorthomorpha* were nested together with *Orthomorpha* Bollman, 1893, *Orthomorphoides* Likhitrakarn, Golovatch & Panha, 2011, and *Desmoxytes*.

For the dragon millipedes, the relationships within *Desmoxytes s.l.* were studied by Golovatch and Enghoff (1994) based on a cladistic analysis of 24 morphological characters derived from colour, body length, metatergal tubercles and surface texture, suture between pro- and metazona, paraterga, epiproct, hypoproct, the sternal lobe between male coxae 4, modifications of male femora, and gonopods. Golovatch and Enghoff's analysis was not designed to test monophyly of *Desmoxytes s.l.*, but their cladogram indicated that the correlation between gonopod and somatic characters (especially paraterga) is very poor.

Nguyen (2016) examined relationships within *Desmoxytes s.l.* using mitochondrial 16S gene of six Vietnamese species. The phylogenetic tree yielded two clades of *Desmoxytes s.l.*, with *Orthomorpha* and *Orthomorphoides* appearing as ingroups. *Desmoxytes s.l.* thus comes out as paraphyletic. However, only one group (6 species with anterlike paraterga) distributed in Vietnam was chosen to reconstruct the tree.

Summing up, only a few paradoxosomatid genera have been studied phylogenetically, and all studies have been mainly focused on intrageneric relationships. Within the tribe Orthomorphini, to which *Desmoxytes s.l.* belongs, relationships between some genera have been evaluated, but only a few species and genera have so far been sequenced. Considering the cladistic analysis by Golovatch and Enghoff (1994) and the recent phylogenetic tree of Vietnamese *Desmoxytes* species (Nguyen, 2016) which seems to contradict previous classification, relationships within *Desmoxytes s.l.* remain largely unresolved. Morphological and molecular characters need to be comprehensively integrated for a better resolution of the taxonomy and as well as for evaluating phylogenetic relationships.

CHAPTER III

Four colourful new species of dragon millipedes, genus *Desmoxytes* Chamberlin, 1923, from northern Thailand (Diplopoda: Polydesmida: Paradoxosomatidae)

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Abstract

Four new dragon millipede species of the genus *Desmoxytes* from northern Thailand are described and illustrated, *D. des* **sp. n.** from Chiang Mai Province, *D. breviverpa* **sp. n.** from Phrae Province, *D. takensis* **sp. n.** from Tak Province and *D. pinnasquali* **sp. n.** from Phitsanulok Province. The new species were compared with type specimens of closely related species and were all found to exhibit explicit morphological differences from these. They can be distinguished from other members of *Desmoxytes* by shape of gonopods, sternal process between male coxae 4, pattern of spines or tubercles on metaterga, and shape of paraterga. The colouration of all new species is clearly aposematic: ranging from purple pink to red. The new species are discussed in relation to congeners, and a distribution map is provided.

Key words: taxonomy, aposematic, endemism

Introduction

The dragon millipedes, genus *Desmoxytes* Chamberlin, 1923, are among the most outstanding paradoxosomatids. The genus is characterized by the unique shape of the paraterga, which may be antler-, spine-, or wing-shaped, and by remarkably bright body colours which attract the attention of myriapodologists as well as the general public. At present, *Desmoxytes* contains 41 described species which are chiefly distributed throughout mainland Southeast Asia including southern China. Almost all known species are narrowly distributed, many are known from a single or a few localities only and are thus to be regarded as local endemics. Several species from China seem to be troglobites: *D. longispina* (Loksa, 1960), *D. scutigeroides* Golovatch *et al*., 2010, *D. scolopendroides* Golovatch *et al*., 2010, *D. eupterygota* Golovatch *et al*., 2012, *D. spinissima* Golovatch *et al*., 2012, *D. lui* Golovatch *et al*., 2012, *D. nodulosa* Liu *et al*., 2014 , *D. getuhensis* Liu *et al*., 2014, *D. laticollis* Liu *et al*., 2016, *D. simplipoda* Liu *et al*., 2016, *D. similis* Liu *et al*., 2016, *D. phasmoides* Liu *et al*., 2016 and *D. variabilis* Liu *et al*., 2016 (Golovatch *et al.*, 2010; Golovatch *et al.*, 2012; Liu *et al.*, 2014, 2016; Loksa, 1960). Only a single species, *D. planata* (Pocock, 1895) had been found on widely separated localities and is clearly an anthropochore (Enghoff *et al.*, 2007; Golovatch *et al.*, 2012; Likhitrakarn *et al.*, 2015). The highest known species diversity has been found in China (20 species), followed by Vietnam (9 species), Thailand (8 species), Myanmar and Laos (each 2 species) and Malaysia (1 species).

Desmoxytes is best represented on limestone habitats or caves, mainly in humid tropical forest. Some species have a remarkable live colouration, no doubt aposematic, for example the spectacular, rather famous "shocking pink dragon millipede" *Desmoxytes purpurosea* Enghoff, Sutcharit & Panha, 2007. Another bright congener is the purplish pink *D. planata*, whilst *D. rubra* has red colour throughout.

In Thailand, nine species of *Desmoxytes* have been recorded so far, six of which were described from the South, one from the Central, and one from the North, one is widely distributed (Enghoff, 2005; Golovatch and Enghoff, 1994; Likhitrakarn *et al.*, 2015):

D. acantherpestes Golovatch and Enghoff, 1994: from Prachuap Khiri Khan Province

D. delfae (Jeekel, 1964): from Satun Province

D. jeekeli Golovatch and Enghoff, 1994: Chiang Mai Province, Chiang Rai Province

D. gigas Golovatch and Enghoff, 1994 from Krabi Province

D. planata (Pocock, 1895): wide distribution

D. pterygota Golovatch and Enghoff, 1994: from Ranong Province

D. purpurosea Enghoff, Sutcharit and Panha, 2007: from Uthai Thani Province

D. rubra Golovatch and Enghoff, 1994: from Satun Province

D. terae (Jeekel, 1964): from Satun Province, Yala Province

Although more than 20 new species of the family Paradoxosomatidae were recently described from Thailand (Likhitrakarn *et al.*, 2010, 2011, 2014a, 2014b), confirming the high diversity of this family in the country, no species of dragon millipede has been added to the Thai fauna for twenty years, except for *D. purpurosea*, added in 2007. Recent fieldwork in Thailand has, however, revealed a significant number of undescribed *Desmoxytes* species. The four species described here are from northern Thailand where they were collected on limestone habitats during the rainy season.

Material and methods

The dragon millipede specimens were carefully collected by hand from localities in northern Thailand during the rainy season, then preserved in 70% ethanol for morphological study and partly 95% ethanol for molecular study. Pictures of living colourful specimens were taken in the field and after collecting. Body parts with crucial morphological characters were photographed by using image stacking Cell-D automontage (Olympus DP72–SZX–16). In addition, photographs of gonopods were taken with a scanning electron microscope (JEOL, JSM–5410 LV), and drawings were made using a stereo microscope. The specimens were compared with the original descriptions and type specimens of the congeneric species. Abbreviations of gonopod structures used here are as follows: coxa (*cx*); cannula (*ca*); prefemorite (*pf*e); seminal grove (*sg*); femorite (*fe*); solenophore (*sph)*; lamina lateralis (*ll*); lamina medialis (*lm*) and solenomere (*sl*). All holotypes and several paratypes have been deposited at Museum of Zoology, Chulalongkorn University, Bangkok, Thailand (CUMZ). Additional paratypes have been donated for Natural History Museum of Denmark, University of Copenhagen, Denmark (ZMUC).

Results

Taxonomy

Family Paradoxosomatidae Daday, 1889

Tribe Orthomorphini Brölemann, 1916

Genus *Desmoxytes* Chamberlin, 1923

***Desmoxytes des* Srisonchai, Enghoff & Panha sp. n.**

(Figs. 3.1A, 3.1B, 3.2–3.4)

Holotype: male (CUMZ) THAILAND, Chiang Mai Province, Fang District, Doi Angkhang, near Royal Agricultural Station, 19°54'26"N, 99°2.0'26"E, ca. 1,425 m a.s.l., 12 August 2014, leg. N. Likhitrakarn.

Paratypes: 2 males, 2 females (CUMZ) same locality together with holotype; 1 male, 2 females (CUMZ), THAILAND, Chiang Mai Province, Chiang Dao District, Wat Tham Krab, 19°33'31.92"N, 99°3.0'46.91"E, ca. 620 m a.s.l., 25 October 2015, leg. C. Sutcharit, R. Srisonchai, T. Seesamut and A. Pholyotha.

Etymology: The species epithet is a noun in apposition and refers to the shape of the paraterga which reminds of an ancient Egyptian flint knife (des).

Diagnosis: Metaterga with 2 transverse rows of setae, 2+2 setae in anterior row, 2+2 in posterior one; shocking pink paraterga contrasting with a dark brown general body colour. *D. des* sp. n. shares these characters with *D. planata,* but differs from that species in having wing-shaped, knifelike paraterga, having the lateral sulcus between femorite and postfemorite poorly developed, having a prominent sulcus separating two ridges dorsally on lamina lateralis *(ll)*, having a dentiform lamella on lamina medialis (*lm*), having male femora 5 and 6 very strongly inflated and stout, and in having the hypoproct with a concave caudal margin.

Description: Length 26–34 mm (male), 30–34 mm (female), width of midbody prozona and metazona ca 1.8 and 2.5 mm (male), ca 2.2 and 3.0 mm (female).

Live colouration of body dark brownish; paraterga bright pink; surface below paraterga, head and metaterga dark brown; legs, antenna, epiproct and sterna brown; a few basal podomeres brownish pink (Figs. 3.1A, 3.1B, 3.2). Colouration in alcohol after twelve months faded to dark brown; metaterga and surface below paraterga dark brownish; paraterga, head, antenna, legs, sterna and epiproct brown.

Width of head < collum < segment 2 = 3 < 4 = 5 < 6–16, thereafter body gradually tapering towards telson. Head width 2.0–2.2 mm (male), 2.0–2.5 mm (female). Clypeolabral region sparsely setose, vertex bare; labrum and genae sparsely setose; epicranial suture distinct, shallow (Figs. 3.4A, 3.4D). Antennae quite long, surpassing segment 3 when stretched backward dorsally (both sexes) (Fig. 3.4D).

Collum ca 4.0 mm wide (both sexes), surface smooth and dull, with two transverse rows of inconspicuous setae; 3+3 anterior and 1+1 posterior setae; anterior margin subtruncate, posterior margin quite convex; paraterga strongly developed, wing-shaped, directed dorsolaterad at about 30°; with an inconspicuous notch on anterior margin (Fig. 3.4A).

Post-collar segments with surface of prozona and metazona finely shagreened, quite dull; paraterga smooth; surface below paraterga coarsely microgranulate with distinct wrinkles; sterna smooth (Figs. 3.2A–H, 3.4G). Suture between prozona and metazona wide, quite deep (Figs. 3.2A–F, 3.4B, 3.4E, 3.4G). Metaterga with two transverse rows of setiferous tubercles; metaterga 2–18 with 2+2 anterior and 2+2 posterior tubercles, all tubercles subequal in size; distance between the two mesal tubercles of anterior rows larger than distance between the mesal and the lateral tubercles on each side; distance between the two mesal tubercles of posterior rows smaller than distance between the mesal and the lateral tubercles on each side; metatergum 19 with 2+2 anterior and 2+2 posterior inconspicuous setae. Transverse sulcus on metaterga quite deep on segments 4–17, poorly expressed on segments 3 and 18, entirely missing on segments 2 and 19 (Figs. 3.2A, 3.2C, 3.2F, 3.4A–C). Axial line absent.

Paraterga strongly developed, very broad at base, wing-shaped, directed dorsolaterad at about ca 30° (Fig. 3.4F), tapering and curving backwards, ending in sharp point; shoulder present; anterior margin with two distinct denticles, on metaterga 9, 10, 12, 13, 15–18 with an additional tiny denticle close to the tip (Fig. 3.4H: *arrow*); calluses on anterior margin of pore-bearing segments distinct (Figs. 3.2C, 3.2E, 3.4H). Ozopore (op) visible from above, ovoid, located on anterior margin of paratergum (Fig. 3.4H). Pleurosternal carinae forming complete, tooth-like crests on segment 2, small incomplete ridges on segment 3, missing on remaining segments (Fig. 3.2B).

Epiproct conoid; tip truncate; apical papillae without tubercles; with 2 pairs of paramedian setae without supporting tubercles; lateral papillae with conspicuous tubercles lying close to the tip (Figs. 3.4J–L). Hypoproct subtrapeziform; caudal margin quite concave, with very small setiferous tubercles (Fig. 3.4I).

Sterna sparsely setose, cross-impression shallow; sternal process between male coxae 4 modified, sparsely setose, subquadrate, tip truncate, two sternal pores on sternal process visible from posterior view (Figs. 3.2G, 3.2H, 3.4M). Legs long and slender, 3–3.2 (male) or 3.1–3.2 times (female) as long as midbody height (Fig. 3.4P). Male femora 5 and 6 distinctly humped ventrally in middle part, femur 5 subequal in width and length to femur 6, delicately and sparsely setose, tarsal brush absent (Figs. 3.2I, 3.4N, 3.4O).

Gonopods (Figs. 3.3, 3.4Q–T) quite long, distal parts strongly condensed. Coxa (*cx*) about half as long as telopodite, dorsally densely setose, cannula quite long and slender. Prefemorite (*pfe*), almost half as long as telopodite, subequal in length to femorite, densely setose. Femorite (*fe*) elongated, with a prominent deep sulcus on mesal side demarcating the border between femorite and postfemoral part (Fig. 3.4Q, *arrow*), lateral sulcus poor-developed, seminal groove running entirely on mesal surface. Solenophore (*sph*) well-developed; lamina lateralis (*ll*) apically with a sulcus separating two ridges, inner ridge large, outer one smaller (Fig. 3.4T, *arrow*); lamina medialis (*lm*), broadly expanded, distally curving mesad, with dentiform lamella (Fig. 3.4S, *arrow*). Solenomere (*sl*) quite long, flagelliform, directed straight, twisted distally.

Distribution and habitat: This species is known only from its type locality and another locality in Chiang Mai Province, the two localities lie approximately 50 km apart. The holotype was taken from the limestone hill near the Royal Agricultural Station, Angkhang during the rainy season, additional specimens were also found on limestone habitats.

Remark: The colour of the living new species is clearly aposematic and remarkable by the contrast between dark brownish body combining pink paraterga.

Desmoxytes breviverpa **Srisonchai, Enghoff & Panha sp. n.**

(Figs. 3.1C, 3.1D, 3.5–3.7)

Holotype: male (CUMZ) THAILAND, Phrae Province, Long District, before Sareethai Cave, 18°16'43"N, 100°03'29"E, ca 264 m a.s.l., 21 October 2014, leg. C. Sutcharit, W. Siriwut, K. Inkhavilay and R. Srisonchai.

Paratypes: 27 males, 7 females (CUMZ), 3 males, 2 females (ZMUC) same locality together with holotype; 5 males, 3 females (CUMZ) same locality together with holotype, 21 July 2008, leg. N. Likhitrakarn; 1 male, 3 females (CUMZ) THAILAND, Lampang Province, Mae Tha District, Nakraua Subdistrict, Wat Tham Phra Sabai, 18°05'32"N, 99°32'03"E, ca 328 m a.s.l., 21 July 2008, leg. S. Panha, P. Tongkerd and N.

Likhitrakarn; 1 male, 5 females (CUMZ) THAILAND, Lampang Province, Mae Tha District, Tham Chakkrabhat monastery (Wat Tham Chakkrabhat), 18°06'02"N, 99°56'48"E, ca 237 m a.s.l., 8 October 2007, leg. U. Bantaowong, R. Chanabun, P. Pimvichai and T. Krutchuen.

Etymology: The name is Latin noun in apposition, meaning “short intromittent organ”, and referring to the short, flagelliform solenomere.

Diagnosis: Body colour shocking pink, paraterga wing-shaped, metaterga 2–8 with 2+2 spines in anterior row and 2+2 spines in posterior one, metaterga 9–19 with 2+2 spines in anterior row and 3+3 spines in posterior one. Similar in these respects to *D. taurina* (Pocock, 1895), *D. purpurosea* and *D. takensis* sp. n. Differs from *D. purpurosea* and *D. takensis* sp. n. by having 3+3 setiferous tubercles in anterior row of collum, by having the sternal process between male coxae 4 subquadrate with an emarginate tip, by having an emarginate process on lamina medialis (*lm*), and by having a very short solenomere. Differs from *D. taurina* by having strongly humped male femora 5 and 6, by having paraterga well developed, extremely elevated, and by having longer spines on metaterga.

Description: Length 28–30 mm (male), 33–35 mm (female), width of midbody prozona and metazona ca 1.7 and 2.0 mm (male), 2.5 and 3.0 mm (female).

Live colouration of body shocking pink to purple (Figs. 3.1C, 3.1D, 3.5); paraterga vivid pink; surface below paraterga and metaterga brown pink to brown purple; head brown; antenna dark brown; legs, sterna and epiproct pink. Colouration in alcohol after two years faded to pale brown; paraterga, surface below paraterga, metaterga, head, antenna, legs, sterna and epiproct brown to whitish.

Width of head < collum = segment 2 = 3 < 4 < 5 < 6–17 thereafter body gradually tapering towards telson. Head width ca 2.5 mm (male), 2.8 mm (female). Clypeolabral region sparsely setose, epicranial suture distinct (Figs. 3.7A, 3.7D). Antennae long and slender, reaching the end of segment 6 (male) or 5 (female) when stretched backward dorsally (Fig. 3.7D).

Collum width ca 3.0 mm (male) and 3.5–4.0 mm (female); surface coarsely microgranulate; with three transverse rows of setiferous tubercles, 3+3 anterior, 1+1 intermediate and 2+2 posterior tubercles; posterior margin concave; paraterga well-developed, wing-liked, elevated at ca 30° and directed dorsolaterad, tip pointed, anterior margin with two setiferous notches (Fig. 3.7A).

Post-collar segments with prozonae finely shagreened; surface below paraterga and metazonae coarsely microgranulate; paraterga and sterna quite smooth (Figs. 3.5A–H, 3.7G). Suture between prozona and metazona conspicuous, shallow, narrow on segments 5 and 6, thereafter much wider (Figs. 3.5A–F, 3.7B, 3.7E, 3.7G). Metaterga with two distinct transverse rows, rose-thornlike setiferous spines; metaterga 2–8 with 2+2 spines in anterior and 2+2 spines in posterior row, lateral spines of posterior rows larger than inner spines; metaterga 9–18 with 2+2 anterior and 3(4)+3(4) posterior spines, lateral spines of posterior row longest, intermediate ones shorter and mesal ones shortest, distance between the two mesal spines of posterior rows smaller than distance between the mesal and the lateral spines on each side; metatergum 19 with 2+2 anterior and 3+3 posterior spines, all spines equal in size. Transverse sulcus on metaterga conspicuous and quite deep on segments 5–17, poorly developed on segments 4 and 18 (Figs. 3.5A, 3.5C, 3.5F, 3.7A–C). Axial line missing.

Paraterga strongly developed, especially in male, winglike, directed dorsolaterad at about 45–50° (Fig. 3.7F); shoulder present, obviously rounded, fused to calluses; calluses on anterior margin of pore-bearing segments conspicuous; anterior margin with two conspicuous denticles; metaterga 9, 10, 12, 13, 15–17 with a very small additional denticle near tip (Fig. 3.7H); tip pointed, long (Figs. 3.5C, 3.5E, 3.7H). Ozopore (op) conspicuous, visible from above (Fig. 3.7H). Pleurosternal carinae forming a tooth-like crest on segment 2, a small tooth on segment 3, absent on remaining segment (both sexes) (Fig. 3.5B).

Epiproct conical, flattened ventrally; tip subtruncate; apical papillae without tubercles; paramedian setae with supporting by tiny tubercles; lateral papillae inconspicuous, small tubercles (Figs. 3.7J–L). Hypoproct subsemicircular; caudal margin quite convex, with a pair of small setigerous tubercles (Fig. 3.7I).

Sterna sparsely setose, cross-impression shallow; sternal process between male coxae 4 modified, subquadrate, tip emarginate, two sternal pores on sternal process visible from posterior view (Figs. 3.5G, 3.5H, 3.7M, 3.7N). Legs very long and slender, ca

3.2–3.5 (male) and 2.2–2.5 times (female) as long as mid body height (Fig. 3.7Q). Male femora 5 and 6 modified; distinctly humped at middle part, (Figs. 3.5I, 3.4O, 3.4P).

Gonopods (Figs. 3.6, 3.7R–U) quite long, distal parts strongly condensed. Coxa (*cx*) about half as long as telopodite; cannula (*ca*) quite long, broadened basally. Prefemorite (*pfe*) about 2/3 as long as telopodite. Femorite (*fe*) very long and slender, slightly separated from postfemoral part by distinct lateral and mesal sulcus (Figs. 3.7R, *black arrow*; 3.7S, *arrow*), with seminal groove running entirely on mesal surface. Solenophore (*sph*) condensed: lamina lateralis (*ll*) with a digitiform, vertical ventral lobe on ventral surface (Figs. 3.7R & 3.7T: *white arrow*); lamina medialis (*lm*) consisting of one process and two lobes; process prominent, directed mesad, spine-shaped, tip emarginate (Fig. 3.7U: *P arrow*); first lobe situated on top, terminating in two lamellae (Fig. 3.7U: L_1 *arrow*); second lobe long, blunt, twisted at base (Fig. 3.7U: L_2 *arrow*). Solenomere (*sl*) very short, flagelliform, straight, a bit curving distad.

Distribution and habitat: Known only from the type locality and nearby areas. The holotype and accompanying paratypes were sitting on logs and litter in limestone forest near the main road to Sareethai cave.

Remark: This species exhibits a remarkable shocking pink colour, no doubt aposematic. The specimens present some variation of the sternal process between male coxae 4, some specimens with a slightly emarginate tip, the others with deep emarginate tip (Figs. 3.7M, 3.7N). Very similar and probably closely related to *D. purpurosea*.

Desmoxytes takensis **Srisonchai, Enghoff & Panha sp. n.**

(Figs. 3.1E, 3.1F, 3.8–3.10)

Holotype: male (CUMZ) THAILAND, Tak Province, Phobphra District, Nangkruen waterfall, on litters and under decaying bark, 16°24'36"N, 98°41' 21"E, ca 398 m a.s.l., 15 January 2015, leg. R. Srisonchai, T. Seesamut, and P. Jirapatrasilp.

Paratypes: 12 males, 10 females, 1 juvenile (CUMZ), 2 males, 1 females (ZMUC) same locality, together with holotype; 2 males, 1 female (CUMZ) same locality, 18 January 2011, leg. C. Sutcharit, R. Chanabun, N. Likhitrakarn and T. Krutchuen.

Etymology: The name is Latin adjective referring to the province where the type locality belongs.

Diagnosis: Paraterga winglike, metaterga 2–8 with 2+2 anterior and 2+2 posterior spines, metaterga 9–19 with 2+2 anterior and 3+3 posterior spines. Sharing these characters with *D. taurina, D. purpurosea* and *D. breviverpa* sp. n., but differs by its red live colour; by smaller paraterga; by the sternal process between male coxae 4 being subtrapeziform; by lamina lateralis (*ll*) being subtriangular with a thumblike ventral lobe, and by having one conspicuous process and one lobe on lamina medialis (*lm*).

Description: Length 24–26 mm (male), 25–27 mm (female), width of midbody prozona and metazona ca 1.5 and 1.9 mm (male), 1.7 and 2.2 mm (female).

Live colouration of body bright red; paraterga, surface below paratega and metaterga red; head, antennae, legs and epiproct brown red (Figs. 3.1E, 3.1F). Colouration in alcohol after twelve months changed to pale brown; paraterga, surface below paraterga, legs and sterna brown to yellow; head, antenna and epiproct brown.

Width of head = collum = segment 2 = 3 = 4 < 5 < 6–16, thereafter body gradually tapering towards telson. Head width ca 2.0 mm (male), 2.5 mm (female). Clypeolabral region, labrum and genae sparsely setose; epicranial suture distinct as brownish stripe (Figs. 3.10A, 3.10D). Antennae very long and slender, surpassing segments 6 (male) and 5 (female), when stretch backward dorsally (Fig. 3.10D).

Collum width 2.5–3.0 mm (both sexes), with three transverse rows of setiferous tubercles; 4+4 anterior, 1+1 intermediate and 2+2 posterior tubercles, intermediate tubercles larger than other ones, lateral tubercles of posterior row displaced anteriad; paraterga wing-shaped, subhorizontal, elevated at 10–15°, ending in sharp point, with a setiferous notch at about halfway (Fig. 3.10A).

Post-collar segments with surface metazona and surface below paraterga microgranulate; prozona shagreened; sterna and paraterga smooth (Figs. 3.8A–H, 3.10G). Suture between prozonae and metazonae conspicuous, wide (Figs. 3.8C, 3.10B, 3.10E, 3.10G). Metaterga with two transverse rows of setiferous spines; metaterga 2–8 with 2+2 anterior and 2+2 posterior spines; metaterga 9–17 with 2+2 anterior and 3+3 posterior spines; lateral spines of posterior rows longer than mesal ones; metaterga 18 and 19 with 2+2 anterior spines and 3+3 posterior tubercles, subequal in size. Transverse sulcus on metaterga visible on segments 6–17, incomplete on segments 5 and 18, absent on segments 2, 3, 4 and 19. Axial line missing (Figs. 3.8A, 3.8C, 3.8F, 3.10A–C).

Paraterga strongly developed, especially well in male, winglike, directed dorsolaterad at about ca 45° (Fig. 3.10F); shoulder present, quite narrow; calluses present; anterior margin with two conspicuous denticles; on segments 9, 10, 12, 13, 15–18 with a very small additional denticle close to the tip (Fig. 3.10F); tip narrow and sharp; posterior margin almost straight (Figs. 3.8C, 3.8E, 3.10H). Ozopore (**op**) large, ovoid, visible from above (Figs. 3.8C, 3.8E, 3.10H). Pleurosternal carinae forming a complete, toothlike crest only on segment 2 (both sexes), a small crest on segment 3, absent on remaining segments (Fig. 3.8B).

Epiproct conical, flattened dorsoventrally; tip subtruncate; apical papillae inconspicuous, without tubercles; two pairs of paramedian setae without tubercles, lateral papillae conspicuous, lying close to the tip (Figs. 3.10J–K). Hypoproct subsemicircular, caudal margin slightly convex, very small inconspicuous tubercles on caudal edges (Fig. 3.10I).

Sterna sparsely setose, cross-impression shallow; sternal process between male coxae 4 modified, subtrapeziform, stout, tip rounded, with two pores in posterior view (Figs. 3.8G, 3.8H, 3.10M). Legs very long and slender, ca 3.0 (male), 2.6 times (female) as long as midbody height (Fig. 3.10P). Male femora 5 and 6 distinctly humped in ventral part (Fig. 3.8I, 3.10N, 3.10O).

Gonopods (Figs. 3.9, 3.10R–T) suberect and long, distal parts strongly condensed. Coxa (*cx*) about half as long as telopodite, with long sparse setation distoventrally. Prefemorite (*pfe*) densely setose, almost 1/3 as long as telopodite, a bit shorter than femorite. Femorite (*fe*) elongate and slender; seminal groove running on mesal surface; apically with conspicuous lateral and mesal sulcus demarcating femorite and postfemoral part (Fig. 3.10S: *arrow*). Solenophore (*sph*) well-developed: lamina lateralis (*ll*) subtriangular, inner surface subsided; with a huge thumblike ventral lobe, directed in vertical plane (Fig. 3.10R, *arrow*): lamina medialis (*lm*) with a prominent process, directed almost in vertical plane, tip sharp and a bit curving down

(Fig. 3.10T: *black arrow*); with a lamellar lobe curving in horizontal plane, tip terminated to solenomere (Fig. 3.10T: *white arrow*). Solenomere quite long, flagelliform, straight.

Distribution and habitat: Known only from the type locality. Almost all specimens of this species were found on humid litter surrounding the waterfall nearby a concreted natural board trail. Interestingly, we saw some specimens which were sitting on plastic garbages. The waterfall is a popular tourist attraction located just opposite the main road connecting to human habitation.

Remark: The noticeable red body colour is clearly aposematic.

Desmoxytes pinnasquali **Srisonchai, Enghoff & Panha sp. n.**

(Figs. 3.1G, 3.1H, 3.11–3.13)

Holotype: male (CUMZ) THAILAND, Phitsanulok Province, Noen Maprang District, near Pra Tham Mans Monastery (Tham Wangdaeng), 16°41'40"N, 100°40'42"E, ca 62 m a.s.l., 22 August 2014, leg. S. Panha, C. Sutcharit and U. Banthaowong.

Paratypes: 22 males, 5 females (CUMZ), 2 males, 1 female (ZMUC) same locality together with holotype; 10 males, 17 females (CUMZ) same locality together with holotype, leg. N. Likhitrakarn; 2 females (CUMZ) same locality together with holotype, 8 September 2009, leg. U. Bantaowong and R. Chanabun; 3 males, 6 females (CUMZ) THAILAND, Phitsanulok Province, Noen Maprang District, near Pa Ma Muang monastery, 16°34'00"N, 100°40'38"E, ca 92 m a.s.l., 23 July 2008, leg. C. Sutcharit and P. Tongkerd.

Ethymology: The name is Latin noun in apposition, meaning “shark fin” and referring to the shape of a process on lamina medialis.

Diagnosis: Metaterga with 2+2 anterior and 2+2 posterior spines, paraterga wing-like, shocking pink. Similar in these respect to *D. planata*, but differing by pink brown general body colour, epiproct with digitiform apical papillae, sternal process between male coxae 4 being subquadrate, lamina medialis (*lm*) being highly elevated with a shark finlike process.

Descriptions: Length 24–29 mm (male), 28–30 mm (female); width of midbody prozona and metazona ca 2.0 and 2.0 mm (male), 2.2 and 2.5 mm (female).

Live colouration vivid pink; paraterga shocking pink; surface below paraterga, metaterga, head and antenna brown pink; legs and epiproct pink; sterna brown (Figs. 3.1G, 3.1H). Colouration in alcohol after one year faded to pale brown; paraterga, legs and sterna yellow brown; surface below paraterga, metaterga, head, antenna and epiproct brown.

Width of head < collum < segment 2 < 3 = 4 < 5–16, thereafter body gradually tapering towards telson. Head broad ca 2.0 mm (male), 2.5 mm (female). Clypeolabral region sparsely setose; vertex bare so on; labrum and genae sparsely setose; epicranial suture visible as dark line, quite deep (Figs. 3.13A, 3.13D). Antennae very long and slender, reaching back to segments 5 (male) and 4 (female) when expanded dorsally (Fig. 3.13D).

Collum width ca 3.0 mm (both sexes), surface coarsely microgranulate, with three transverse rows of small setiferous tubercles, 3(4)+3(4) anterior, 1+1 intermediate and 2+2 posterior tubercles; paraterga wing-shaped, elevated at about 30° (male) and 20° (female), directed dorsolaterad, tip pointed, with two distinct setiferous notches on anterior margin (Fig. 3.13A).

Post-collar segments with surface of prozona finely shagreened; metazona coarsely microgranulate and shining; surface below paraterga finely microgranulate with inconspicuous wrinkles; paraterga and sterna quite smooth (Figs. 3.8A–H, 3.13G). Suture between prozonae and metazonae conspicuous, quite deep and wide, narrow only in segments 2–5, thereafter much wider (Figs. 3.11C, 3.11E, 3.13B, 3.13E, 3.13G). Metaterga with two transverse rows of setiferous spines; 2+2 anterior and 2+2 posterior spines; spines of anterior rows on metaterga 2–16 equal in size, lateral spines of posterior rows longer than mesal ones; metaterga 17–19 with all spines equal in size. Transverse sulcus on metaterga distinctly expressed on segments 5–17, quite deep, inconspicuous on segments 4 and 18, missing on segments 2, 3 and 19 (Figs. 3.11A, 3.11C, 3.11F, 3.13A–C). Axial line absent.

Paraterga strongly developed, especially in male, wing-shaped, directed dorsolaterad at ca 45° (Fig. 3.13F), thereafter curving backward; shoulder present; calluses conspicuous, broad anteriorly and continuing slightly narrowed near tip; lateral margin with two distinct denticles, segments 9, 10, 12 ,13, 15–18 with an additional very small denticle near the tip (Fig. 3.13H: *arrow*); tip of paraterga pointed and sharp, curving dorsolaterad; posterior margin of paraterga curving at base and almost straight near tip (Figs. 3.11C, 3.11E, 3.13H). Ozopore (op) visible from above, ovoid (Figs. 3.11C, 3.11E, 3.13H). Pleurosternal carinae forming complete crests on segment 2 (both sexes), small ridge on segment 3 and absent on following segments (Fig. 3.2B).

Epiproct conical; tip concave; apical papillae conspicuous, digitiform; with tiny tubercles supporting two pairs of paramedian setae; lateral papillae distinct (Figs. 3.13J–K). Hypoproct subsemicircular, with prominent setigerous tubercles on convex caudal margin (Fig. 3.13I).

Sterna sparsely setose, cross-impression shallow; sternal process between male coxae 4 modified, subquadrate, tip round, sternal pores visible from posterior view (Figs. 3.11G, 3.11H, 3.13M). Legs very long and slender, ca 2.5 (male), 2.0 times (female) as long as midbody height (Fig. 3.13P). Male femora 5 and 6 distinctly humped ventrally in middle part, femur 6 a bit bigger than 5 (Figs. 3.11I, 3.13N, 3.13O).

Gonopods (Figs. 3.12, 3.13Q–T) long and slender, suberect, distal parts strongly condensed. Coxa (*cx*) about 1/3 as long as telopodite. Prefemorite (*pfe*) about 1/3 as long as telopodite, quite stout. Femorite (*fe*) quite slender, very elongate, with seminal groove running entirely on mesal surface, postfemoral part demarcated by deep mesal and lateral sulcus (Fig. 3.13R: *black & white arrows*). Solenophore strongly developed: lamina lateralis (*ll*) swollen, without a lobe: lamina medialis (*lm*) broad and highly elevated, with one process and two lobes; process shark finlike, tip obtuse, directed mesad (Figs. 3.13Q, 3.13S, *P arrow*); first lobe lamellalike, terminating in two lamellae, outer one smaller than the inner one (Figs. 3.13Q, 3.13S, L_1 *arrow*); second lobe lamellalike, thick and broad (Figs. 3.13Q, 3.13S, L_2 *arrow*). Solenomere flagelliform, curving distad.

Distribution and habitat: This new species occurs in a small limestone area in the west of Thung Salaeng Luang National Park, northern Thailand, and was seen sitting on humid rocks, litter and vegetation under a shading tree.

Remark: This species shows a bizzare pink body colour which is clearly aposematic. It may be closely related to *D. planata* with which it shares the same patterns of colour and metatergal spines.

Discussion

The four new species described here all belong to the group of *Desmoxytes* species with winglike paraterga and a "condensed" gonopod, i.e., with the elements distal to the elongated femur folded closely together. Further, they all present stark bright live colours (Fig. 3.1), no doubt aposematic (Enghoff *et al.*, 2007). Such colours will probably make millipedes highly evident prey for diurnal predators, but because of their production of cyanide and their strong smell, the animals may be avoided by predators (Svádová *et al.*, 2009).

With SEM images, we could easily observe details of gonopodal processes. Gonopodal characters can be used reliably to identify *Desmoxytes* species, especially the postfemoral part of the gonopod is very important, together with other external morphological characters such as paraterga, sterna, femora, etc. *D. des* sp. n. and *D. pinnasquali* sp. n. share pink paraterga and 2+2 rows of setiferous spines on metaterga while *D. breviverpa* sp. n. and *D. takensis* sp. n. have 3+3 rows of setiferous spine and pink body colour throughout. All four are possibly related to *D. planata, D. delfae, D. rubra*, *D. terae, D. pterygota D. taurina* and *D. purpurosea* with which they share similar shapes of gonopods and sternal process between male coxae 4, as well as similar modifications of male femora 5 and 6. The remarkable colour of *D. planata, D. rubra*, *D. purpurosea* and all four new species combines them as a potentially monophyletic group. cf. Golovatch & Enghoff, 1994. However, we still need more information, including from molecular data, to suggest and support an appropriate evolutionary hypothesis for this genus.

With the addition of the four colourful new species described here to the Thai millipede fauna, *Desmoxytes* now contains thirteen known species distributed in the northern, central and southern parts of Thailand. However, the new species are described on specimens from just a few localities (Fig. 3.14). This suggests that several additional species probably remain to be discovered in Thailand.

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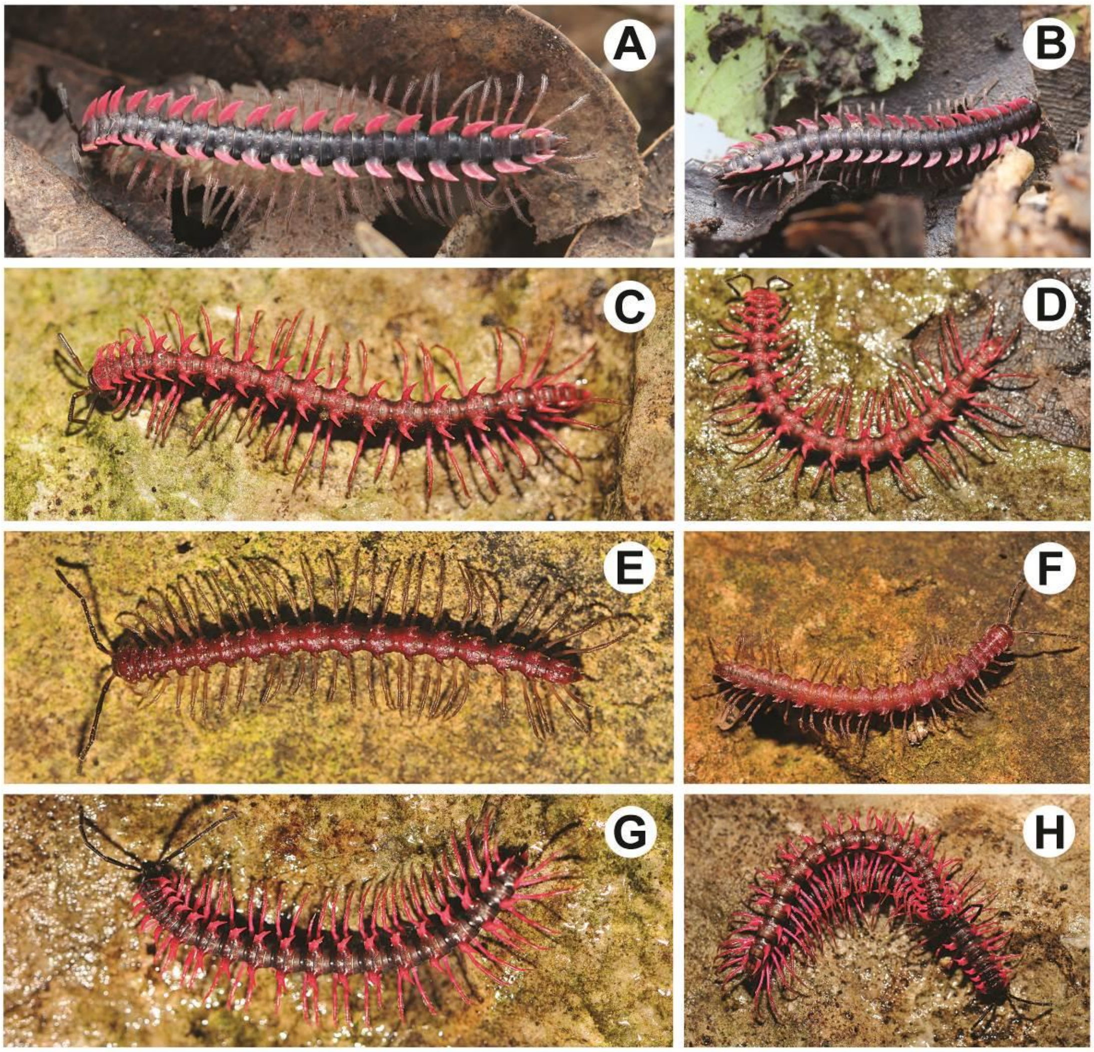

Figure 3.1 Live photographs of the new species. **A, B**: *Desmoxytes des* sp. n. – **A**: male holotype, **B**: female. **C, D**: *Desmoxytes breviverpa* sp. n. – male paratype. **E, F**: *Desmoxytes takensis* sp. n. – **E**: male paratype, **F**: female. **G, H**: *Desmoxytes pinnasquali* sp. n. – **G**: male holotype, **H**: mating couple.

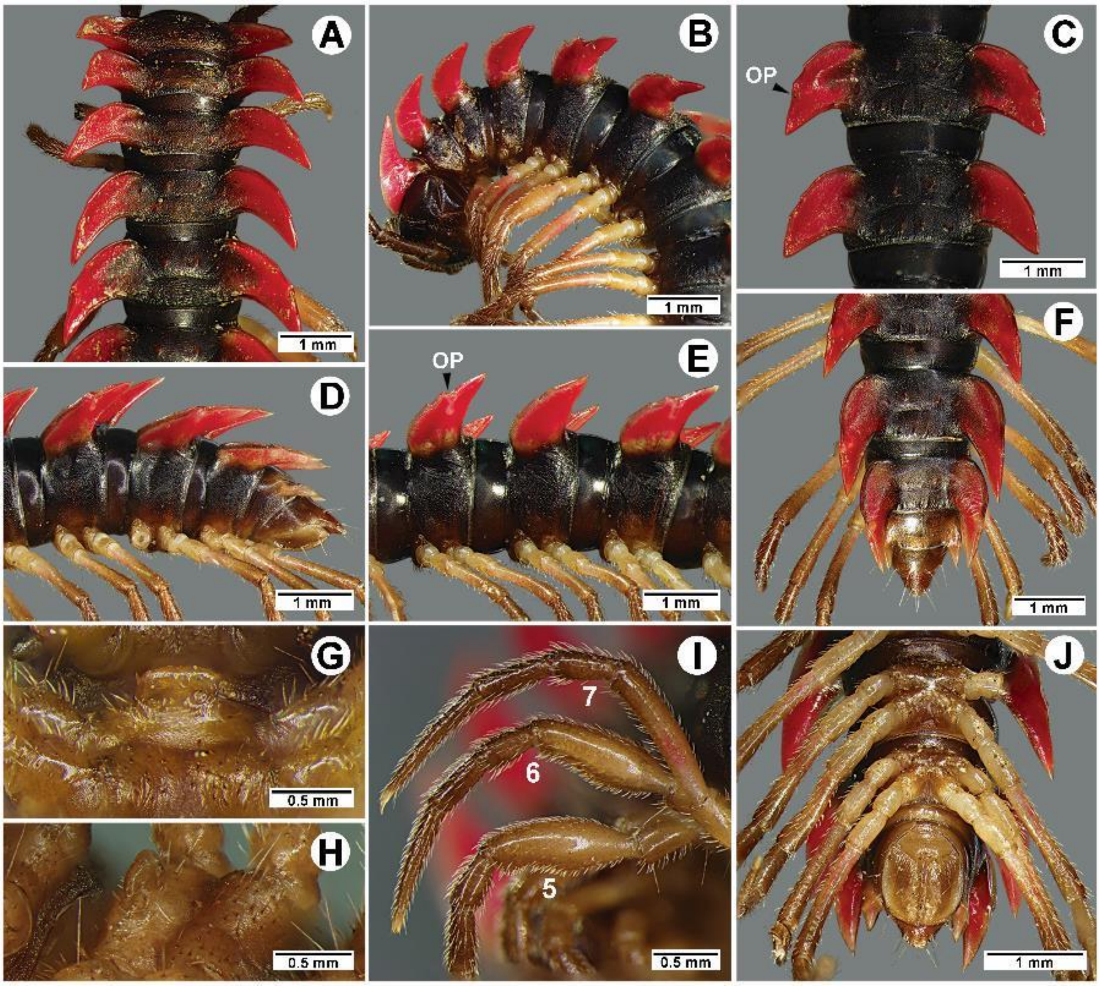

Figure 3.2 *Desmoxytes des* sp. n. (male holotype). **A, B**: anterior body parts – dorsal view (**A**) and lateral view (**B**). **C**: segments 10 and 11 (op = ozopore) – dorsal view. **D, F, J**: posterior body parts – lateral view (**D**), dorsal view (**F**) and ventral view (**J**). **E**: segments 10–12 (op = ozopore) – lateral view. **G, H**: sternal process between male coxae 4 – posterior view (**G**) and lateral view (**H**). I: legs 5–7 – posterior view.

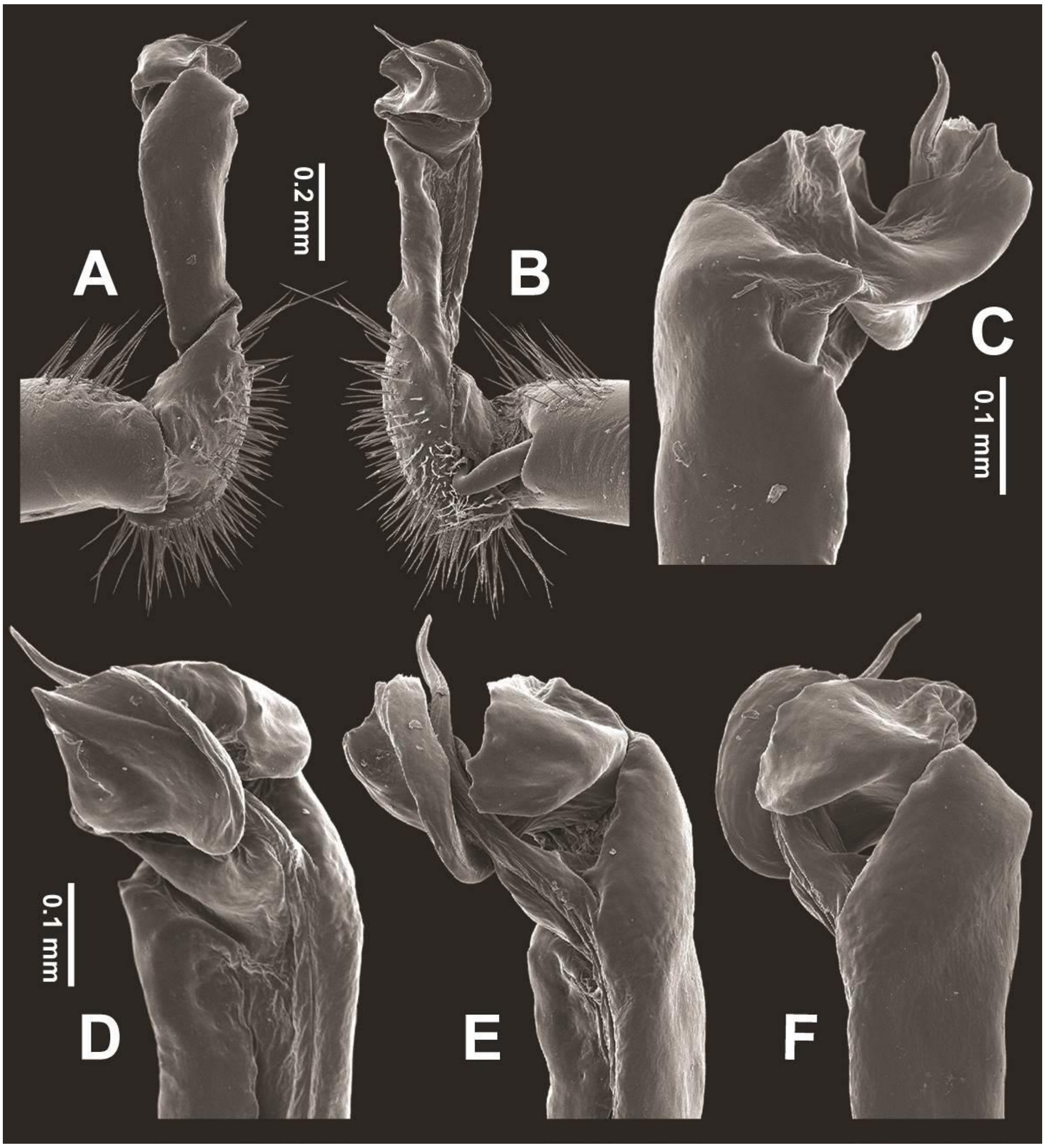

Figure 3.3 *Desmoxytes des* sp. n. (male paratype), right gonopod. **A**: lateral view. **B**: mesal view. **C**: ventral view. **D, F**: subdorsal view. **E**: dorsal view.

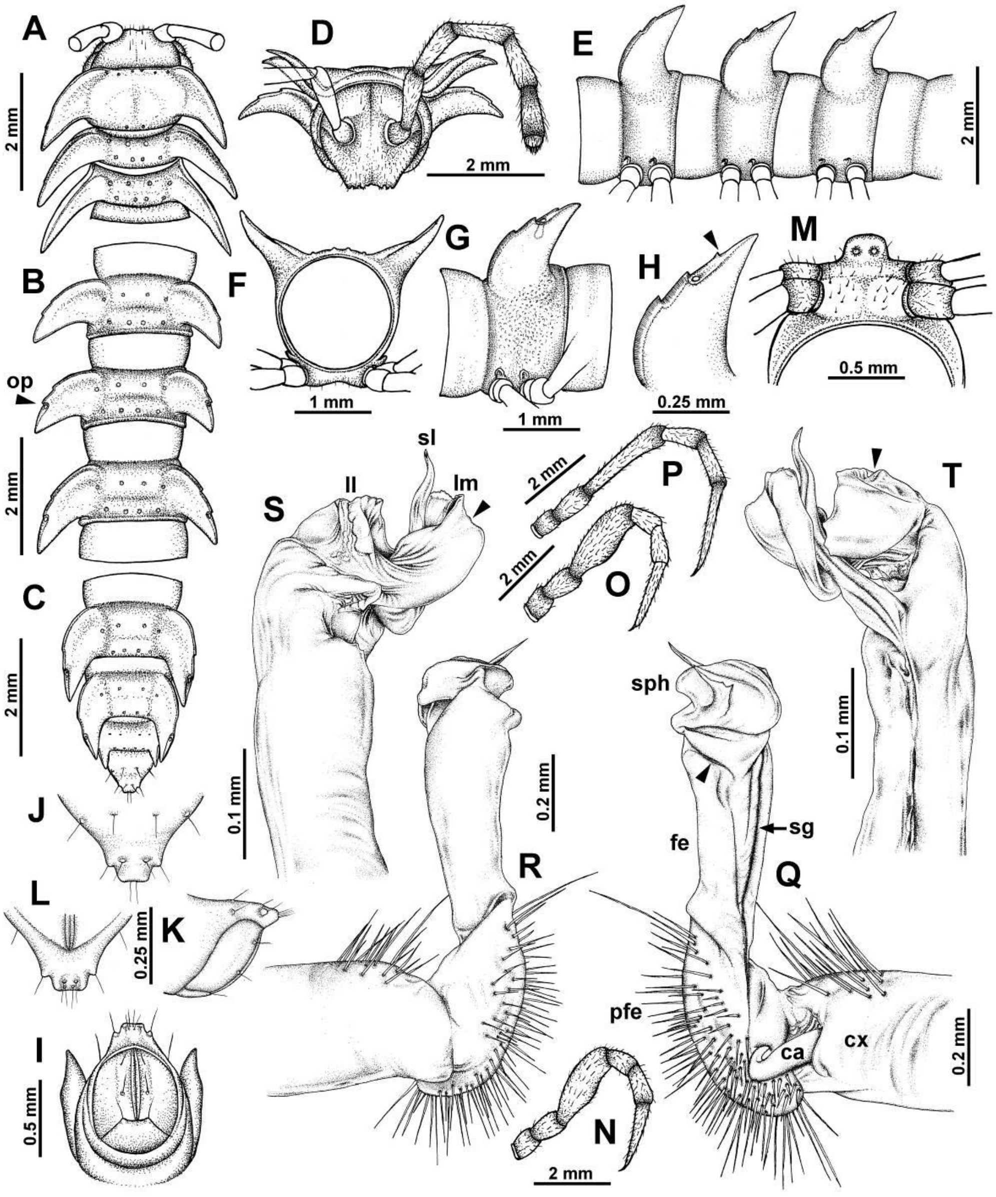

Figure 3.4 *Desmoxytes des* sp. n. (male holotype). **A**: head and segments 1–3 – dorsal view. **B**: segments 8–10 (op = ozopore) – dorsal view. **C**: posteriormost segments and telson segments – dorsal view **D**: head and antenna – anterior view. **E**: segments 8–10 – lateral view. **F**: segment 10 – posterior view. **G**: paraterga and sculpture of segment 10 – lateral view. **H**: paraterga of segment 10 (arrow = tiny denticle) – lateral view. **I**: last segment and telson; showing epiproct and hypoproct – ventral view. **J**–**L**: epiproct; **J**: dorsal view, **K**: lateral view, **L:** ventral view. **M**: sternal process between male coxae 4 – posterior view. **N**: male leg 5. **O**: male leg 6. **P**: male right anterior leg of segment 10. **Q**–**T**: right gonopod; **Q**: mesal view (*cx* = coxa, *ca* = cannula, *pfe* = prefemorite, *fe* = femorite, *sg* = seminal groove, *sph* = solenophore, arrow = sulcus on mesal side), **R**: lateral view, **S**: ventral view (*ll* = lamina lateralis, *lm* = lamina medialis, *sl* = solenomere, arrow = dentiform lamella), **T**: dorsal view (arrow = sulcus separating two ridges).

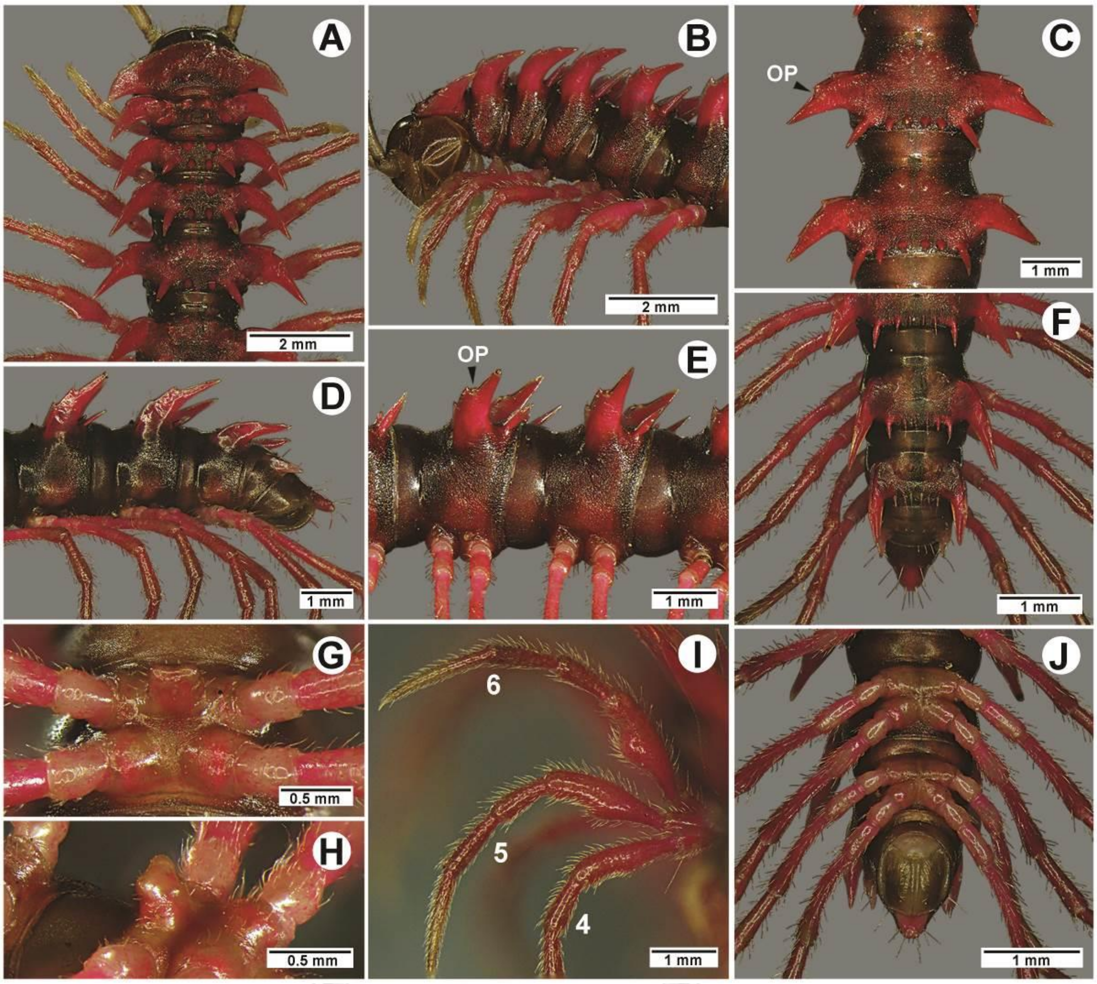

Figure 3.5 *Desmoxytes breviverpa* sp. n. (male holotype). **A, B**: anterior body parts – dorsal view (**A**) and lateral view (**B**). **C**: segments 10 and 11 (op = ozopore) – dorsal view. **D, F, J**: posterior body parts – lateral view (**D**), dorsal view (**F**) and ventral view (**J**). **E**: segments 10–11 (op = ozopore) – lateral view. **G, H**: sternal process between male coxae 4 – ventral view (**G**) and lateral view (**H**). **I**: legs 4–6 – anterior view.

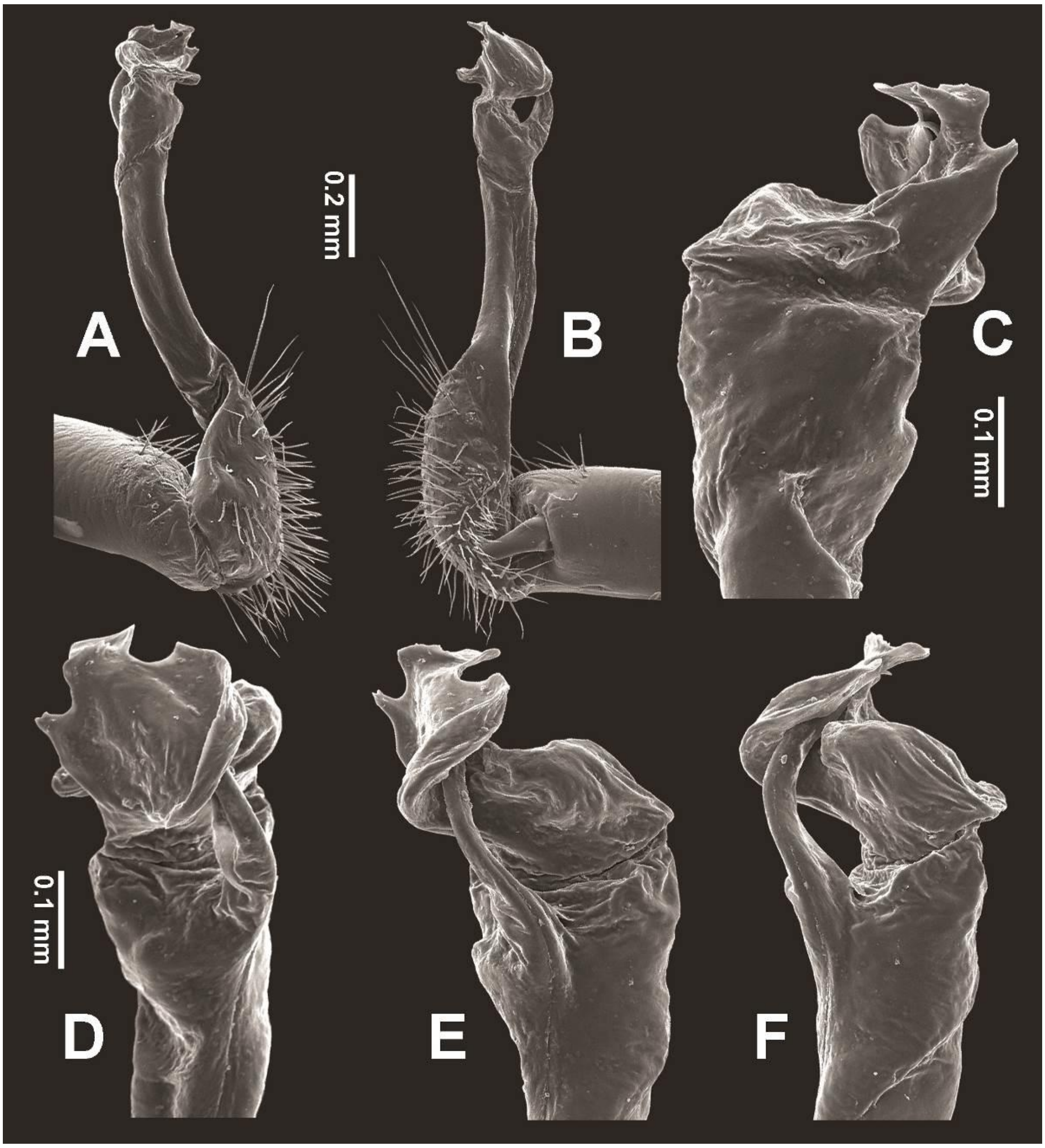

Figure 3.6 *Desmoxytes breviverpa* sp. n. (male paratype), right gonopod. **A**: lateral view. **B**: mesal view. **C**: ventral view. **D, F**: subdorsal view. **E**: dorsal view.

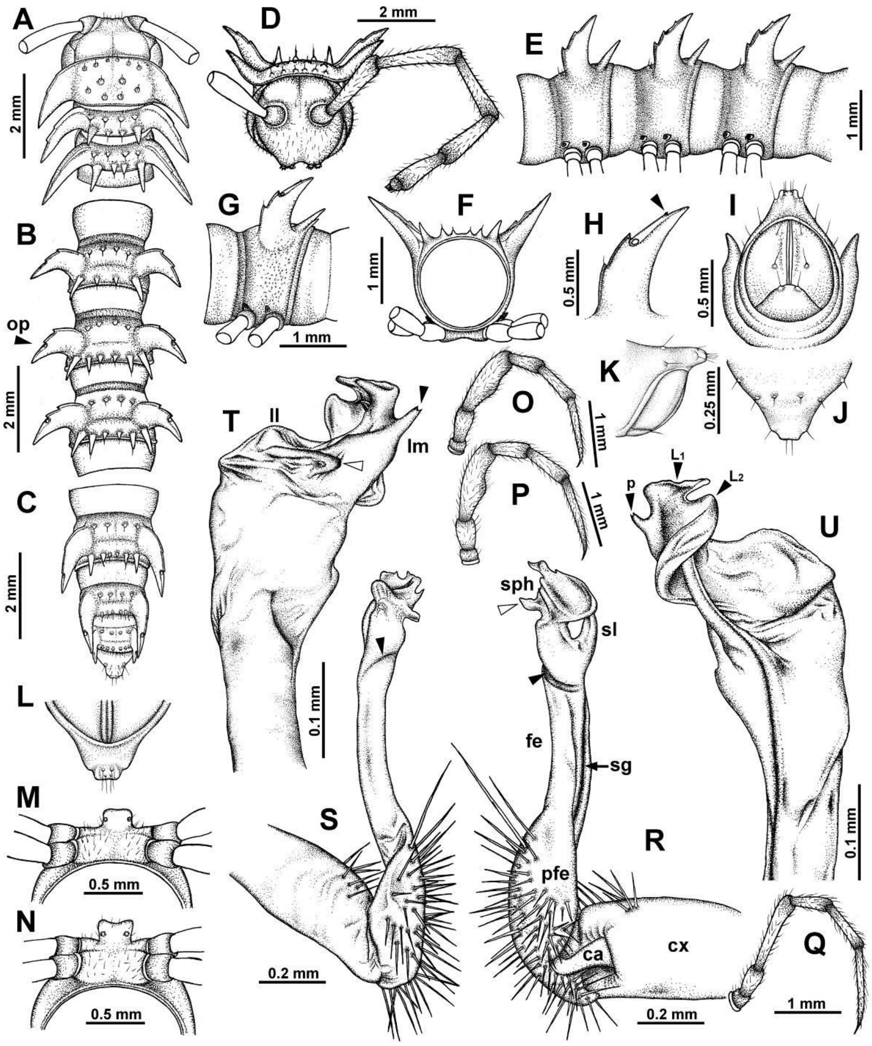

Figure 3.7 *Desmoxytes breviverpa* sp. n. (male holotype). **A**: head and segments 1–3 – dorsal view**.** **B**: segments 8–10 (op = ozopore) – dorsal view. **C**: posteriormost segments and telson segments – dorsal view **D**: head and antenna – anterior view. **E**: segments 8–10 – lateral view. **F**: segment 10 – posterior view. **G**: paraterga and sculpture of segment 10 **–** lateral view. **H**: paraterga of segment 10 (arrow = tiny denticle) – lateral view. **I**: last segment and telson; showing epiproct and hypoproct – ventral view. **J–L**: epiproct; **J**: dorsal view, **K**: lateral view, **L**: ventral view. **M**: sternal process between male coxae 4 (male holotype) – posterior view. **N**: sternal process between male coxae 4 – posterior view. **O**: male leg 5. **P**: male leg 6. **Q**: male right anterior leg of segment 10. **R–U**: right gonopod; **R**: mesal view (*cx* = coxa, *ca* = cannula, *pfe* = prefemorite, *fe* = femorite, *sg* = seminal groove, *sph* = solenophore, *sl* = solenomere, black arrow = sulcus on mesal side, white arrow = digitiform ventral lobe), **S**: lateral view (arrow = sulcus on lateral side), **T**: ventral view (*ll* = lamina lateralis, *lm* = lamina medialis, black arrow = process, white arrow = digitiform ventral lobe), **U**: dorsal view (*P arrow* = process, L_1 & L_2 *arrows* = lobes on lamina medialis).

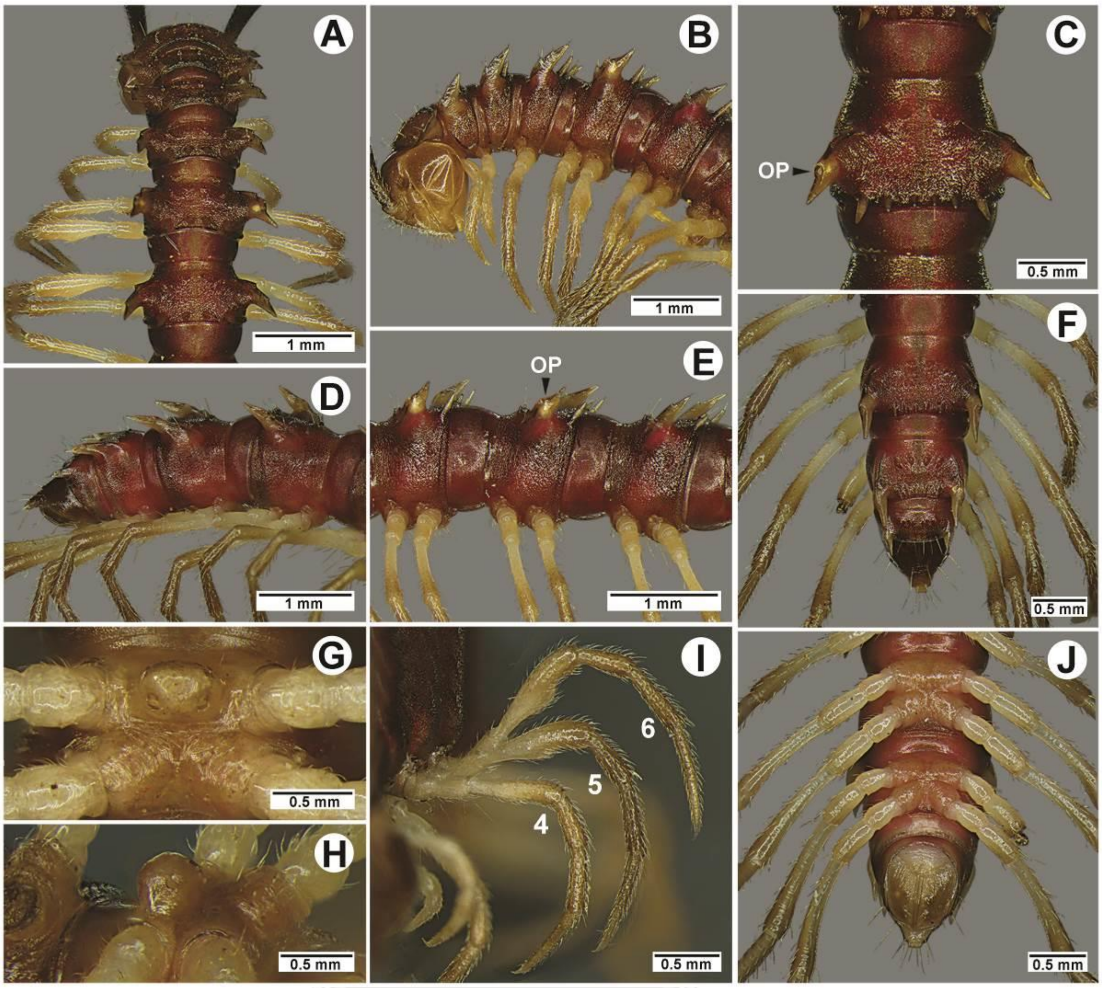

Figure 3.8 *Desmoxytes takensis* sp. n. (male holotype). **A, B**: anterior body parts – dorsal view (**A**) and lateral view (**B**). **C**: segment 10 (op = ozopore) – dorsal view. **D, F, J**: posterior body parts – lateral view (**D**), dorsal view (**F**) and ventral view (**J**). **E**: segments 10–12 (op = ozopore) – lateral view. **G, H**: sternal process between male coxae 4 – ventral view (**G**) and lateral view (**H**). **I**: legs 4–6 – anterior view.

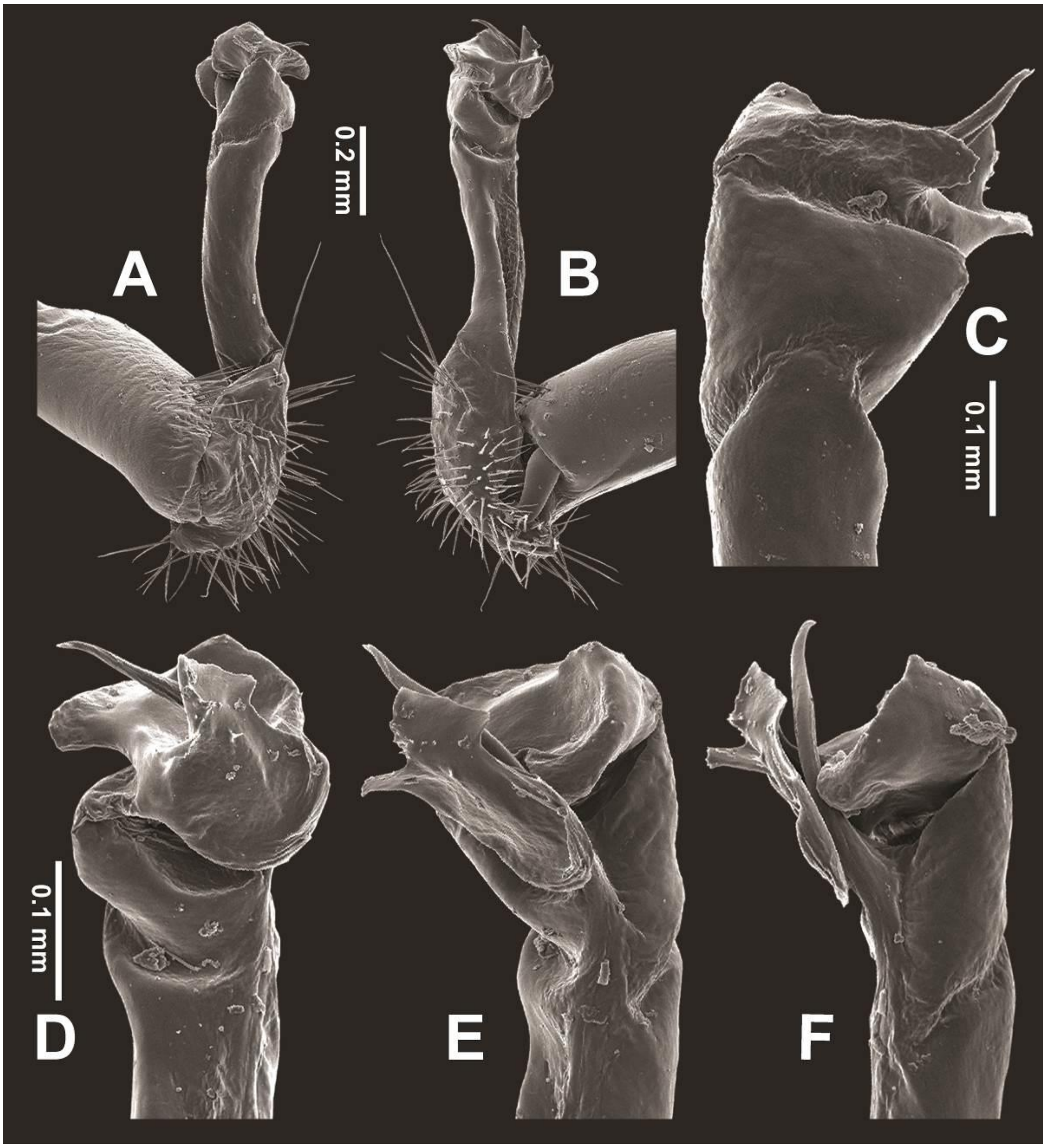

Figure 3.9 *Desmoxytes takensis* sp. n. (male paratype), right gonopod. **A**: lateral view. **B**: mesal view. **C**: ventral view. **D, F**: subdorsal view. **E**: dorsal view.

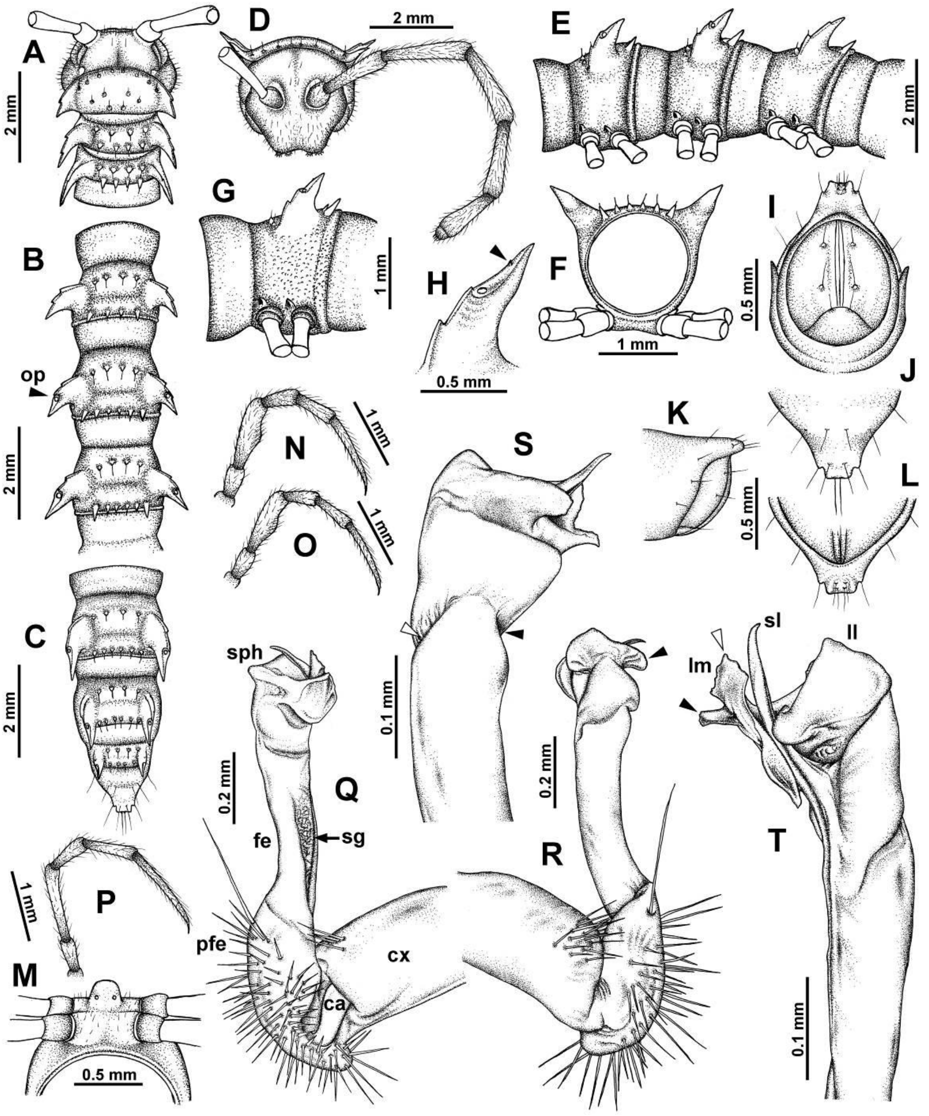

Figure 3.10 *Desmoxytes takensis* sp. n. (male holotype). **A**: head and segments 1–3 – dorsal view. **B**: segments 8–10 (op = ozopore) – dorsal view. **C**: posteriormost segments and telson segments – dorsal view **D**: head and antenna – anterior view. **E**: segments 8–10 – lateral view. **F**: segment 10 – posterior view. **G**: paraterga and sculpture of segment 10 – lateral view. **H**: paraterga of segment 10 (arrow = tiny denticle) – lateral view. **I**: last segment and telson; showing epiproct and hypoproct – ventral view. **J–L**: epiproct; **J**: dorsal view, **K**: lateral view, **L**: ventral view. **M**: sternal process between male coxae 4 – posterior view. **N**: male leg 5. **O**: male leg 6. **P**: male right anterior leg of segment 10. **Q–T**: right gonopod; **Q**: mesal view (*cx* = coxa, *ca* = cannula, *pfe* = prefemorite, *fe* = femorite, *sg* = seminal groove, *sph* = solenophore), **R**: lateral view (arrow = thumblike ventral lobe), **S**: ventral view (black arrow = mesal sulcus, white arrow = lateral sulcus), **T**: dorsal view (*sl* = solenomere, *ll* = lamina lateralis, *lm* = lamina medialis, black arrow = process, white arrow = lamellar lobe).

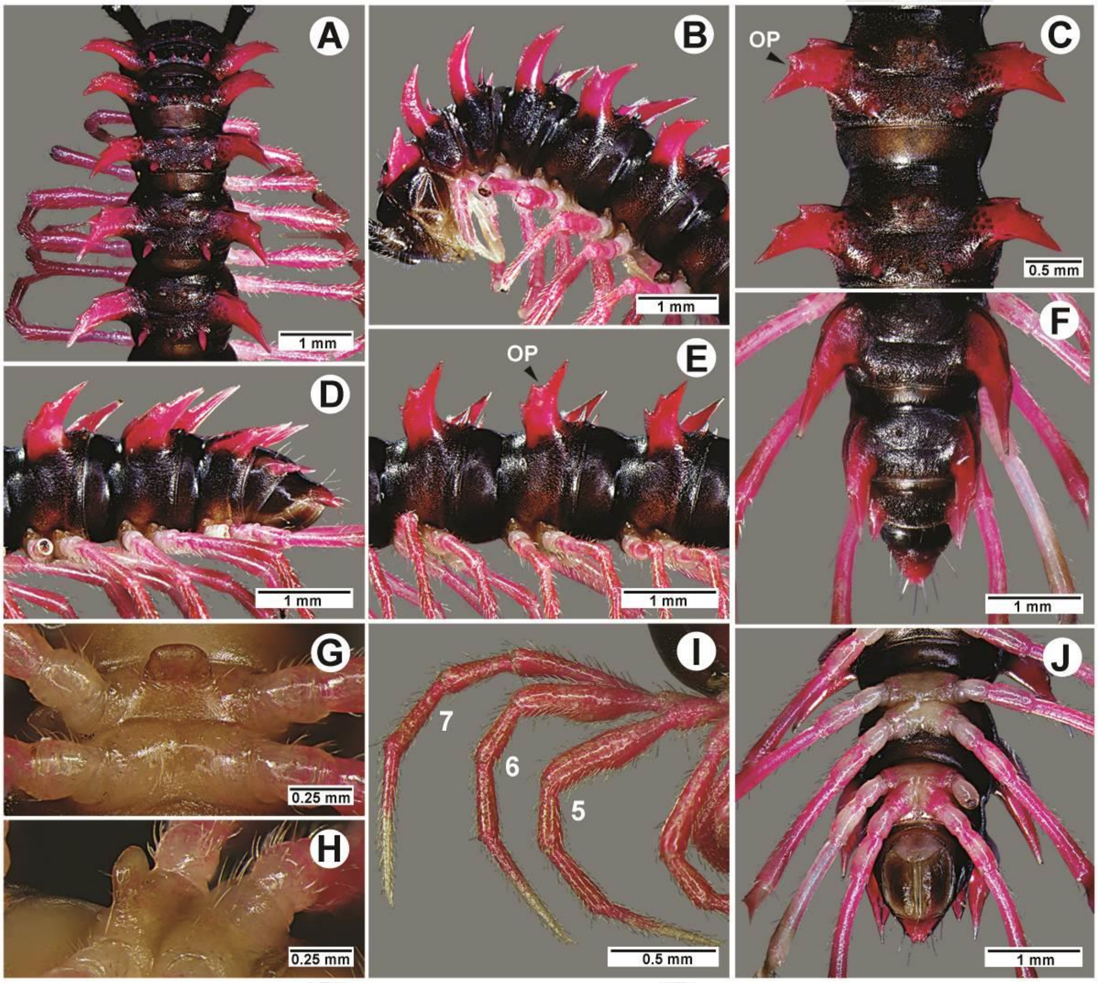

Figure 3.11 *Desmoxytes pinnasquali* sp. n. (male holotype). **A, B**: anterior body parts – dorsal view (**A**) and lateral view (**B**). **C**: segments 10 and 11 (op = ozopore) – dorsal view. **D, F, J**: posterior body parts **–** lateral view (**D**), dorsal view (**F**) and ventral view (**J**). **E**: segments 10–12 (op = ozopore) **–** lateral view. **G, H**: sternal process between male coxae 4 – ventral view (**G**) and lateral view (**H**). **I**: legs 5–7 – anterior view.

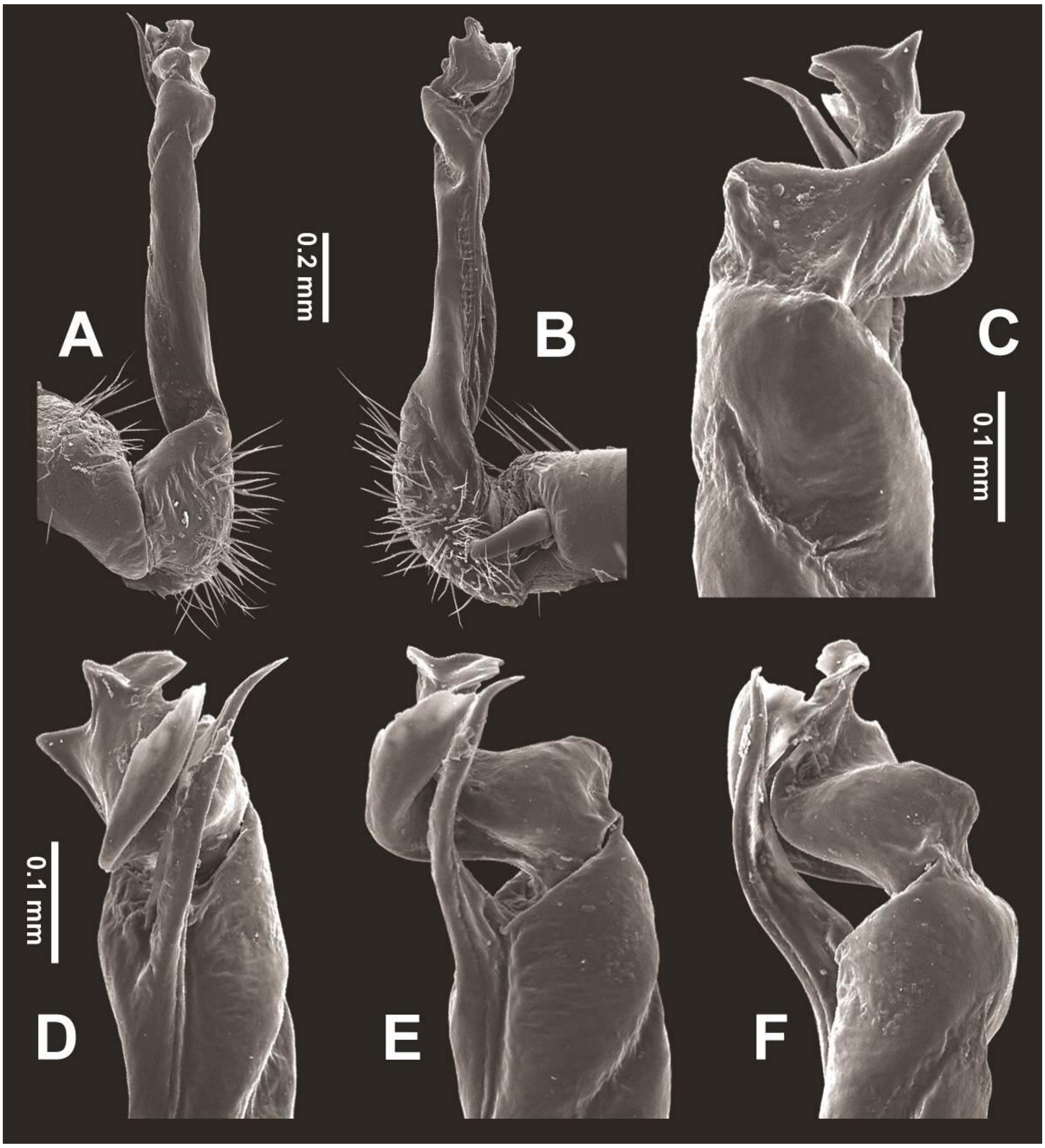

Figure 3.12 *Desmoxytes pinnasquali* sp. n. (male paratype), right gonopod. **A**: lateral view. **B**: mesal view. **C**: ventral view. **D, F**: subdorsal view. **E**: dorsal view.

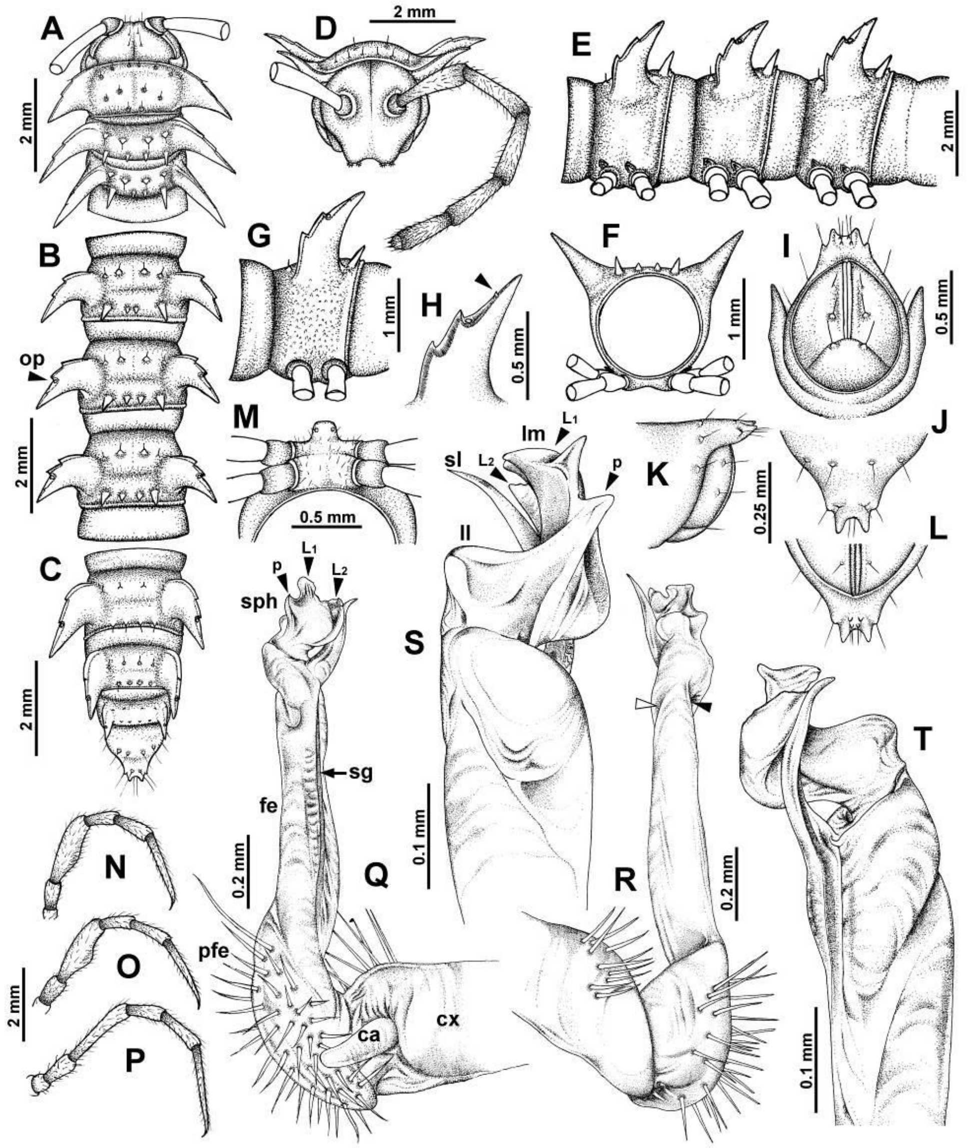

Figure 3.13 *Desmoxytes pinnasquali* sp. n. (male holotype). **A**: head and segments 1–3 – dorsal view. **B**: segments 8–10 (op = ozopore) – dorsal view. **C**: posteriormost segments and telson segments – dorsal view **D**: head and antenna – anterior view. **E**: segments 8–10 – lateral view. **F**: segment 10 – posterior view. **G**: paraterga and sculpture of segment 10 – lateral view. **H**: paraterga of segment 10 (arrow = tiny denticle) – lateral view. **I**: last segment and telson; showing epiproct and hypoproct – ventral view. **J**–**L**: epiproct; **J**: dorsal view, **K**: lateral view, **L**: ventral view. **M**: sternal process between male coxae 4 – posterior view. **N**: male leg 5. **O**: male leg 6. **P**: male right anterior leg of segment 10. **Q**–**T**: right gonopod; **Q**: mesal view (*cx* = coxa, *ca* = cannula, *pfe* = prefemorite, *fe* = femorite, *sg* = seminal groove, *sph* = solenophore, *P arrow* = finlike process, L_1 & L_2 arrows= lamellalike lobes), **R**: lateral view (black arrow = mesal sulcus, white arrow = lateral sulcus), **S**: ventral view (*sl* = solenomere, *ll* = lamina lateralis, *lm* = lamina medialis, *P arrow* = finlike process, L_1 & L_2 arrows= lamellalike lobes), **T**: dorsal view.

Figure 3.14 Known distribution of four new species of *Desmoxytes* in northern Thailand. Open triangle = *Desmoxytes des* sp. n.: Open star = *Desmoxytes breviverpa* sp. n.: Open square = *Desmoxytes takensis* sp. n.: Open circle = *Desmoxytes pinnasquali* sp. n.

CHAPTER IV

A revision of dragon millipedes I: genus *Desmoxytes* Chamberlin, 1923, with the description of eight new species (Diplopoda, Polydesmida, Paradoxosomatidae)

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Abstract

The dragon millipede genus *Desmoxytes* s.l. is split into five genera, based on morphological characters and preliminary molecular phylogenetic analyses. The present article includes a review of *Desmoxytes* s.s., while future articles will deal with *Hylomus* Cook and Loomis, 1924 and three new genera which preliminarily are referred to as the '*acantherpestes*', '*gigas*', and '*spiny*' groups. Diagnostic morphological characters of each group are discussed. *Hylomus* is resurrected as a valid genus and the following 33 species are assigned to it: *H. asper* (Attems, 1937) **comb. n.**, *H. cattienensis* (Nguyen, Golovatch and Anichkin, 2005) **comb. n.**, *H. cervarius* (Attems, 1953) **comb. n.**, *H. cornutus* (Zhang and Li, 1982) **comb. n.**, *H. draco* Cook and Loomis, 1924 **stat. rev.**, *H. enghoffi* (Nguyen, Golovatch and Anichkin, 2005) **comb. n.**, *H. eupterygotus* (Golovatch, Li, Liu and Geoffroy, 2012) **comb. n.**, *H. getuhensis* (Liu, Golovatch and Tian, 2014) **comb. n.**, *H. grandis* (Golovatch, VandenSpiegel and Semenyuk, 2016) **comb. n.**, *H. hostilis* (Golovatch and Enghoff, 1994) **comb. n.**, *H. jeekeli* (Golovatch and Enghoff, 1994) **comb. n.**, *H. lingulatus* (Liu, Golovatch and Tian, 2014) **comb. n.**, *H. laticollis* (Liu, Golovatch and Tian, 2016) **comb. n.**, *H. longispinus* (Loksa, 1960) **comb. n.**, *H. lui* (Golovatch, Li, Liu and Geoffroy, 2012) **comb. n.**, *H. minutuberculus* (Zhang, 1986) **comb. n.**, *H. nodulosus* (Liu, Golovatch and Tian, 2014) **comb. n.**, *H. parvulus* (Liu, Golovatch and Tian, 2014) **comb. n.**, *H. phasmoides* (Liu, Golovatch and Tian, 2016) **comb. n.**, *H. pilosus* (Attems, 1937) **comb. n.**, *H. proximus* (Nguyen, Golovatch and Anichkin, 2005) **comb. n.**, *H. rhinoceros* (Likhitrakarn, Golovatch and Panha, 2015) **comb. n.**, *H. rhinoparvus* (Likhitrakarn, Golovatch and Panha, 2015) **comb. n.**, *H. scolopendroides* (Golovatch, Geoffroy and Mauriès, 2010) **comb. n.**, *H. scutigeroides* (Golovatch, Geoffroy and Mauriès, 2010) **comb. n.**, *H. similis* (Liu, Golovatch and Tian, 2016) **comb. n.**, *H. simplex* (Golovatch, VandenSpiegel and Semenyuk, 2016) **comb. n.**, *H. simplipodus* (Liu, Golovatch and Tian, 2016) **comb. n.**, *H. specialis* (Nguyen, Golovatch and Anichkin, 2005) **comb. n.**, *H. spectabilis* (Attems, 1937) **comb. n.**, *H. spinitergus* (Liu, Golovatch and Tian, 2016) **comb. n.**, *H. spinissimus* (Golovatch, Li, Liu and Geoffroy, 2012) **comb. n.** and *H. variabilis* (Liu, Golovatch and Tian, 2016) **comb. n.** *Desmoxytes* s.s. includes the following species: *D. breviverpa* Srisonchai, Enghoff and Panha, 2016; *D. cervina* (Pocock,1895); *D. delfae* (Jeekel, 1964);

D. des Srisonchai, Enghoff and Panha, 2016; *D. pinnasquali* Srisonchai, Enghoff and Panha, 2016; *D. planata* (Pocock, 1895); *D. purpurosea* Enghoff, Sutcharit and Panha, 2007; *D. takensis* Srisonchai, Enghoff and Panha, 2016; *D. taurina* (Pocock, 1895); *D. terae* (Jeekel, 1964), all of which are re-described based mainly on type material. Two new synonyms are proposed: *Desmoxytes pterygota* Golovatch and Enghoff, 1994, **syn. n.** (= *Desmoxytes cervina* (Pocock, 1895)), *Desmoxytes rubra* Golovatch and Enghoff, 1994, **syn. n.** (= *Desmoxytes delfae* (Jeekel, 1964)). Six new species are described from Thailand: *D. aurata* Srisonchai, Enghoff and Panha **sp. n.**, *D. corythosaurus* Srisonchai, Enghoff and Panha **sp. n.**, *D. euros* Srisonchai, Enghoff and Panha **sp. n.**, *D. flabella* Srisonchai, Enghoff and Panha **sp. n.**, *D. golovatchi* Srisonchai, Enghoff and Panha **sp. n.**, *D. octoconigera* Srisonchai, Enghoff and Panha **sp. n.,** as well as one from Malaysia: *D. perakensis* Srisonchai, Enghoff and Panha **sp. n.**, and one from Myanmar: *D. waepyanensis* Srisonchai, Enghoff and Panha **sp. n.** The species can mostly be easily distinguished by gonopod structure in combination with other external characters; some cases of particularly similar congeners are discussed. All species of *Desmoxytes* s.s. seem to be endemic to continental Southeast Asia (except the 'tramp' species *D. planata*). Some biological observations (relationship with mites, moulting) are recorded for the first time. Complete illustrations of external morphological characters, an identification key, and distribution maps of all species are provided.

Key words: aposematic, dragon millipede, new species, Southeast Asia, taxonomy

Table of contents

Introduction

The dragon millipede genus *Desmoxytes* Chamberlin, 1923 is one of the most spectacular genera in the large family Paradoxosomatidae. The genus currently contains 45 described species which are broadly distributed in China, Laos, Malaysia, Myanmar, Thailand, and Vietnam. The "tramp" species *D. planata* (Pocock, 1895) has become widely dispersed to Fiji, French Polynesia, India, Indonesia, Seychelles, and Sri Lanka (Attems, 1936; Chamberlin, 1923, 1941; Golovatch and Korsós, 1992; Jeekel, 1980b; Mauriès, 1980b; Ramage, 2017; Shelley and Lehtinen, 1998; Tikader and Das, 1985). Most species are best represented in or even restricted to limestone habitats and caves (Enghoff *et al.*, 2007; Liu *et al.*, 2014, 2016; Srisonchai *et al.*, 2016), and some are probably troglobites (Golovatch *et al.*, 2010; Golovatch *et al.*, 2012; Liu *et al.*, 2014, 2016; Loksa, 1960).

Desmoxytes has been taxonomically discussed on several occasions (Golovatch and Enghoff, 1994; Golovatch *et al.*, 2012; Jeekel, 1964, 1980a). The genus was revised by Golovatch and Enghoff (1994), and further variable gonopod characters were added to the diagnosis by Golovatch *et al.* (2012). Several new species were described recently (Golovatch *et al.*, 2016; Likhitrakarn *et al.*, 2015; Liu *et al.*, 2014, 2016; Srisonchai *et al.*, 2016). However, for the time being, no updated diagnosis exists for *Desmoxytes*.

Intensive field surveys focusing on this genus were made by our team (ASRU), mainly in Southeast Asia (Malaysia, Myanmar, Laos, Thailand). After examination of newly collected specimens, and comparison with type material of all congeners, we found distinctive morphological characters, mainly in gonopods and paraterga, indicating heterogeneity of *Desmoxytes* s.s. A preliminary study on phylogeny of dragon millipedes based on mtDNA and nuclear DNA shows a perfect congruence with morphology (Srisonchai *et al.*, 2017) and further indicates that *Desmoxytes* as hitherto understood (i. e., *sensu* Golovatch and Enghoff 1994) is not a monophyletic taxon. Therefore, we find it necessary to subdivide the dragon millipedes into five genera. In the present study, the first in a series of articles about dragon millipedes, *Desmoxytes* is re-diagnosed, and the four other genera (*Hylomus* Cook and Loomis 1924, and three new genera yet to be named) are outlined. Ten species of *Desmoxytes* in the new, restricted sense are revised, eight new species are described, a new identification key to *Desmoxytes* species is provided, and 33 *Desmoxytes* species are assigned to the reinstated genus *Hylomus*.

Material and methods

Specimen collecting and preservation

The specimens were collected by hand from different localities in China, Laos, Malaysia, Myanmar, and Thailand during the rainy season. The GPS coordinates were recorded by using the Garmin GPSMAP 60CSx and the elevation was obtained by checking in Google Earth.

Intensive surveys in several parts of those countries, especially in Thailand, have been made since 2007 by staff and students from Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, referred to as “ASRU members” in the lists of material. Specimens were preserved in 70% ethanol for morphological study and partly in 95% ethanol for molecular study.

Illustrations

Photos of living specimens were taken in the field and after collecting using a Nikon 700D+AFS VR 105 mm lens. The gonopods were illustrated with a scanning electron microscope (JEOL, JSM–5410 LV); gonopods were coated with gold and mounted on aluminium stubs, and after imaging the gonopod was removed from the stub to be kept in dry condition. Drawings were made using dot-line techniques under a stereo microscope.

Morphological descriptions

General descriptions of the tribe and of the genus are provided. All specimens were carefully examined for non-gonopodal (male, female and juvenile) and gonopodal characters under a stereo microscope. Non-gonopodal characters were examined those of size, colour, head, antenna, collum, tegument, prozona, metaterga, paraterga, telson, sterna and legs. We use the terms of gonopod morphology from previous papers (Attems, 1937; Chamberlin, 1923, 1941; Enghoff *et al.*, 2007; Golovatch and Enghoff, 1994; Jeekel, 1964, 1980a, 2003; Pocock, 1895; Srisonchai *et al.*, 2016; Zhang, 1986), in part adapted, and we add further morphological characters (see Table 1).

Deposition of holotypes, paratypes and other new specimens

All holotypes, some paratypes of the new species, and most additional specimens will be deposited at CUMZ. Some paratypes and some new specimens will be donated to NHMUK, NHMW, ZMUC and ZMUM.

All species of *Desmoxytes* s.s. have been examined, notably Pocock's specimens in NHMUK, type material of *Hylomus draco* in USNM, and some material in ZMUC. Fig. 4.1 shows original labels of the type material for *Desmoxytes planata*, *D. cervina*, *D. taurina,* and *Hylomus draco*.

Abbreviation of institutions

ASRU = Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand

CUMZ = Chulalongkorn University Museum of Zoology, Bangkok, Thailand

MCZ = Museum of Comparative Zoology, Harvard University, USA

MHNG = Natural History Museum of Geneva, Switzerland

MSNG = Museo Civico di Storia Naturale, Genova, Italy

NBC = Naturalis Biodiversity Center (including the collections of the Zoological Museum Amsterdam), Leiden, the Netherlands

NHMUK = Natural History Museum of London, England

NHMW = Natural History Museum Vienna, Austria

USNM = National Museum of Natural History, Smithsonian Institution, Washington DC, USA

ZMH = Biozentrum Grindel und Zoologisches Museum, University of Hamburg, Germany

ZMUC = Natural History Museum of Denmark (Zoological Museum), University of Copenhagen, Denmark

ZMUM = Zoological Museum, University of Moscow, Russia

Other abbreviations used in the text

FFI = Fauna and Flora International, Myanmar

ca. = approximately, around (circa)

a.s.l. = above sea level

Positional/directional terms in gonopod description

Morphologically the gonopods are traditionally depicted as rotated 90° up from their position *in situ*.

Dorsal refers to a position on the side nearest to the body ring. *Ventral* refers to a position on the side farthest away from the body ring. *Mesal* refers to a position on the side nearest to the midline. *Lateral* refers to a position on the side away from the midline.

Dorsad refers to a direction towards the body ring. *Ventrad* refers to a direction away from the body ring. *Mesad* refers to a direction towards the midline. *Laterad* refers to a direction away from the midline.

We use “sub-” as a prefix to indicate positions and directions slightly different from the ones given above. For example, “submesal” means a position close to, but not quite on the mesal side.

Results

Taxonomy

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

Tribe Orthomorphini Brölemann, 1916

The tribe Orthomorphini was established by Brölemann (1916), as belonging to family Strongylosomidae. Later, the correct name for this family was found to be Paradoxosomatidae (Jeekel, 1963). The tribe Orthomorphini is characterized by the following gonopodal characters:

1. Femur separated from postfemur by distinct constriction (in most species).
2. Seminal groove running along mesal side of femur/femorite.
3. Apical part of telopodite consisting of a solenophore supporting the solenomere. The solenophore consists of a lamina lateralis and a lamina medialis.
4. Most species without a femoral process and a tibiotarsal process.

The tribe Orthomorphini currently contains 22 genera (Nguyen and Sierwald, 2013). Around 200 named species have been recorded so far. The tribe is broadly distributed mainly in Southeast Asia (Cambodia, Indonesia, Laos, Malaysia, Myanmar, Thailand, Vietnam, a few synanthropic species more or less globally widespread).

Subdivision of *Desmoxytes* s.l.

It is here proposed to split *Desmoxytes* s.l. into five groups. These groups are morphologically distinct, as detailed below, and are all supported by a molecular phylogeny (work ongoing). The molecular phylogenetic tree yields five groups of *Desmoxytes* s.l., and *Orthomorpha* Bollman, 1893 and *Antheromorpha* Jeekel, 1968 appear as ingroups. *Desmoxytes* s.l. thus comes out as non-monophyletic (Srisonchai *et al.*, 2017).

The present paper deals with one of the five groups, viz., *Desmoxytes* s.s. The remaining species (see Table 2) will be assigned to their proper genus in forthcoming papers. For one of the groups, a genus name is already available, viz, *Hylomus* Cook and Loomis, 1924, and this name is herewith re-instated as a valid genus name.

The five groups of *Desmoxytes* s.l. are characterized as follows (see Table 3 for all comparable characters, and Figs 4.2, 4.3):

***Desmoxytes* s.s.** (Figs 4.2A, 4.3A–D) can be easily distinguished from others by the following combination of characters: wing-shaped paraterga; male femora 5 and 6 swollen or humped (except *D. terae* without modification); lamina lateralis obviously separated from lamina medialis; lamina medialis and lamina lateralis equal in size, with process and lobes.

Two groups, the '*acantherpestes*' group and the '*gigas*' group are characterized by having subspiniform paraterga and tegument of metaterga microgranulate.

The '*acantherpestes*' group contains species with two rows of tubercles/cones/spines on metaterga; tegument of metaterga microgranulate; gonopodal telopodite straight; postfemur conspicuous, broad laterally, demarcated from femur by a deep mesal sulcus and a deep/shallow lateral sulcus; lamina lateralis obviously separated from lamina medialis; lamina lateralis shorter and smaller than lamina medialis; lamina medialis long and curved (Figs 4.2B, 4.3E).

The '*gigas*' group contain species with three rows of tubercles/cones/spines (uniform) on metaterga; tegument of metaterga microgranulate; long caudolateral spines on the metaterga; gonopodal telopodite curved, falcate; postfemur inconspicuous, mesal sulcus and lateral sulcus absent; lamina lateralis indistinctly separated from lamina medialis, larger than lamina medialis; lamina medialis short (Figs 4.2C, 4.3F).

The '*spiny*' group, still without described members, differs from the others by the following combination of characters: paraterga spiniform; tegument of metaterga smooth; gonopodal telopodite straight; postfemur conspicuous, narrow laterally, demarcated from femur by deep mesal and lateral sulci; lamina lateralis obviously separated from lamina medialis; lamina lateralis smaller than lamina medialis (lamina lateralis very small); lamina medialis long and curved, without process and lobe (Figs 4.2D, 4.3G).

The fifth group, corresponding to genus ***Hylomus*** and including numerous species, has wing-like, antler-like or spiniform paraterga, but is well-defined by gonopod characters: postfemur inconspicuous or absent (mesal and lateral sulci shallow or absent), lamina medialis short (except in a few species), lamina medialis mostly without lobe and process (except some species which have a process, a spine or a hook) (Figs 4.2E, F, 4.3H–P).

As Figs 4.2 and 4.3 clearly show, the differences in morphology (paraterga and gonopod) easily allow separation of the five groups of *Desmoxytes* s.l. species.

The distribution of each group based on data from both described and undescribed species is as follows (new records underlined):

- *Desmoxytes* s.s. – Malaysia, Myanmar, Thailand (includes the widely distributed 'tramp' species *D. planata*)
- The '*acantherpestes*' group – Thailand
- The '*gigas*' group – Thailand
- The '*spiny*' group – Malaysia, Myanmar, Thailand
- *Hylomus* – China, Laos, Myanmar, Vietnam, Thailand

Genus *Hylomus* Cook and Loomis, 1924, stat. rev.

Hylomus Cook and Loomis, 1924: 105

Hylomus was established as a monotypic genus by Cook and Loomis (1924a), who were so impressed by the remarkable external features of the type species, *H. draco*

Cook and Loomis, 1924, viz., the strongly elevated paraterga (like trees), that they placed the new species not only in a new genus but even in a new family, Hylomidae.

(Jeekel, 1964, 1968) maintained *Hylomus* as a valid genus, including only *H. draco,* and moved it into family Paradoxosomatidae, stating that the genus *Pratinus* Attems, 1937 (=*Desmoxytes*) was closely related to *Hylomus*.

Later, Jeekel (1980a) re-assessed the generic allocation of all members of *Hylomus*, *Desmoxytes* Chamberlin, 1923, *Pratinus* Attems, 1937, *Prionopeltis* Pocock, 1895 and *Ceylonesmus* Chamberlin, 1941, leading to the recognition of three genera: *Hylomus, Desmoxytes* (=*Prionopeltis*, *Pratinus*, *Ceylonesmus*) and *Pteroxytes* Jeekel, 1980. Jeekel (1980a) stated that the morphological characters of *Hylomus* showed clear differences from *Desmoxytes* and *Pteroxytes* (paranota antler-shaped and detail of gonopodal apex). The same author emphasized that his work was just a preliminary outline, and that “the discovery of new species … may considerably change the picture”.

Golovatch and Enghoff (1994) disagreed with Jeekel’s idea (1980a) to maintain *Hylomus* and *Pteroxytes* as separate genera. Based on new evidence from examination of old and new material, previous literature and the first cladistic analysis based on morphology, the authors synonymized *Hylomus* and *Pteroxytes* under *Desmoxytes* and assigned the genus to tribe Orthomorphini, of which they regarded Hylomini a synonym.

As mentioned above, our morphological analysis, as well as the initial molecular study, support recognition of *Hylomus* as a valid genus in agreement with Jeekel (1980a). We therefore consider *Hylomus* as a valid genus, separate from *Desmoxytes*. We further reallocate 33 species of *Desmoxytes* s.l. from China (19 species), Vietnam (10 species), Laos (3 species) and Thailand (1 species) to *Hylomus* (see Table 2).

Genus *Desmoxytes* Chamberlin, 1923

Prionopeltis Pocock, 1895: 828 (preoccupied name). Jeekel 1980a: 652 (synonymized with *Desmoxytes*).

Desmoxytes Chamberlin, 1923: 165.

Hylomus Cook and Loomis, 1924: 105. Golovatch and Enghoff 1994: 46 (synonymized with *Desmoxytes*).

Pratinus Attems, 1937: 113 (replacement name for *Prionopeltis*). Jeekel 1980a: 652 (synonymized with *Desmoxytes*).

Ceylonesmus Chamberlin, 1941: 33. Jeekel 1980a: 652 (synonymized with *Desmoxytes*).

Pteroxytes Jeekel, 1980a: 655. Golovatch and Enghoff 1994: 46 (synonymized with *Desmoxytes*).

Type species. *Desmoxytes coniger* Chamberlin, 1923 (MCZ, USA). This species was later synonymized with *Desmoxytes planata* by Jeekel (1980a).

Included species (18)

- *D. aurata* sp. n.
- *D. breviverpa* Srisonchai, Enghoff and Panha, 2016
- *D. cervina* (Pocock, 1895)
- *D. corythosaurus* sp. n.
- *D. delfae* (Jeekel, 1964)
- *D. des* Srisonchai, Enghoff and Panha, 2016
- *D. euros* sp. n.
- *D. flabella* sp. n.
- *D. golovatchi* sp. n.
- *D. octoconigera* sp. n.
- *D. perakensis* sp. n.
- *D. pinnasquali* Srisonchai, Enghoff and Panha, 2016
- *D. planata* (Pocock, 1895) (= *D. coniger* Chamberlin, 1923, type species)
- *D. purpurosea* Enghoff, Sutcharit and Panha, 2007
- *D. takensis* Srisonchai, Enghoff and Panha, 2016
- *D. taurina* (Pocock, 1895)
- *D. terae* (Jeekel, 1964)

- *D. waepyanensis* sp. n.

Desmoxytes s.l. was reviewed by Golovatch and Enghoff (1994), and the diagnosis of the genus was treated in detail again by Golovatch *et al.* (2012). Here we propose a restricted diagnosis for *Desmoxytes* s.s. based on morphological characters (gonopod, tegument, paraterga, metaterga, sterna, femora, epiproct, hypoproct) which have been extracted from previous taxonomic works (Chamberlin, 1923, 1941; Enghoff *et al.*, 2007; Golovatch and Enghoff, 1994; Jeekel, 1964, 1980a; Pocock, 1895; Srisonchai *et al.*, 2016).

The name "dragon millipede". For *Desmoxytes* sensu Golovatch and Enghoff (1994) we will retain the name "dragon millipede", originally coined by Cook and Loomis (1924a) for *Hylomus draco*. Golovatch *et al.* (2012) outlined the history of the name "dragon millipede" and further argued that *Desmoxytes philippina* Nguyen and Sierwald, 2010 (Philippine Isl.), and *Desmoxytoides hasenpuschorum* Mesibov, 2006 (Australia) have been wrongly assigned to *Desmoxytes* and "dragon millipedes", respectively.

Diagnosis. *Desmoxytes* s.s. differs from other genera of Orthomorphini by the combination of the following characters:

1. Gonopod suberect: solenophore strongly condensed; lamina lateralis developed, lobe-like, without process or spine; lamina medialis distinctly separated from lamina lateralis, bearing process and lobes.

2. Metaterga with 2 transverse rows of setiferous setae/ tubercles/ cones/ spines.

3. Paraterga wing-shaped, well-elevated.

4. Sternal cone between male coxae 4 present; subtrapeziform/ subquadrate/ subsemicircular/ incompletely bilobed.

5. Male femora 5 and 6 modified; swollen/humped (exception: *D. terae* without modification).

General description of the genus *Desmoxytes* s.s.

The description applies to adult males and females, except for the gonopods section and when “male” is specified (Figs 4.5, 4.6, 4.7, 4.8). The description hereunder is mainly based on illustrations of *D. planata*.

SIZE: Body length 16–35 mm (male) 20–38 mm (female), width ca. 1.7–2.5 mm (male) 2.0–3.6 mm (female); size varies between species, usually female wider and longer than male.

COLOUR: Most species in life with aposematic coloration: purplish pink, red, orange, brown, black, brownish black (piceous), brownish red (testaceous). Colour in alcohol: all specimens partly faded after one year’s preservation in alcohol; specimens kept in darkness faded more slowly.

HEAD (Figs 4.5C, 4.6A, B, I): Sparsely setose; vertex bare; labrum and genae sparsely setose; epicranial suture conspicuous as a brown or black stripe.

ANTENNAE (Fig. 4.5A–C): Often long and slender, rarely short, covered by delicate setation, usually reaching backwards to body ring 3–8 (male) and 3–6 (female) when stretched dorsally. Antennomere lengths 3 = 4 = 5 > 2 > 6 > 1 > 7 > 8.

COLLUM (Fig. 4.6A, C): With 1–3 transverse rows of setae/tubercles, the exact number in each row varying between species (sometimes lateral setae/tubercles of anterior row located nearly at the base of paraterga, on anterior margin). Paraterga wing-shaped, usually elevated at ca. 0°–30°.

TEGUMENT (Fig. 4.6A–E, G): Often shining, sometimes dull; collum and metaterga often microgranulate; surface below paraterga coarsely or finely microgranulate; prozona finely shagreened. Suture between prozona and metazona usually shallow, quite narrow.

METATERGA (Figs 4.5A, 4.6A, C, D, G): With 2 transverse rows of setae/tubercles/cones/spines, number in each row varying between species, lateral cones/spines of posterior row often longer and larger than inner and/or mesal ones. Suture (transverse sulcus) on metaterga present, usually conspicuous on body rings 5–17 in all species. Mid-dorsal (axial) line missing. Pleurosternal carinae forming complete, tooth-liked crests on ring 2, small ridges on ring 3, missing on remaining body rings.

PARATERGA (Figs 4.5A, B, D, 4.6A–E, G, H): Wing-shaped, well-elevated, directed caudolaterad. Callus and shoulder present, usually conspicuous, sometimes inconspicuous. Anterior margin with 2 distinct notches; on body rings 9, 10, 12, 13, 15–18 a tiny denticle present on lateral margin, near tip (but denticle virtually absent in some species). Elevation of paraterga in male usually higher than in female. Posterior edge concave. Tip pointed and sharp. Ozopore visible from above, round.

TELSON (Fig. 4.6F, G, N): Epiproct often flattened ventrally, tip often truncate or subtruncate, sometimes emarginate; lateral tubercles often conspicuous, sometimes inconspicuous; apical tubercles usually evident, sometimes indistinct, apically with two pairs of setae. Paraprocts convex. Hypoproct often subtrapeziform, sometimes subsemicircular, rarely subtriangular; caudal margin often round, sometimes emarginate, with two small setiferous tubercles.

STERNA (Figs 4.5E, 4.6K): Sparsely setose; cross-impressions faint, usually shallow, rarely quite deep. Sternal lobe between male coxae 4 usually subtrapeziform, subrectangular, subsemicircular or round, varying between species and sometimes varying between populations, usually with two pores on posterior side.

LEGS (Figs 4.5F, 4.6J, M): Very long and slender. Podomere lengths 3 = 6 > 5 > 2 = 4 > 1 > 7. Male femora 5 and 6 modified, often humped ventrally in middle part, sometimes swollen (exception: *D. terae*, without modification).

GONOPODS (Figs 4.6L, 4.7, 4.8): Coxa (cx) usually subequal in length to or longer than prefemur, with distoanterior group of seta. Prefemur (pfe) almost half or 2/3 as long as femur. Femur often long. Seminal groove (sg) running entirely on mesal surface of femur. Mesal sulcus (ms) conspicuous, deep; lateral sulcus (ls) conspicuous, usually deep, sometimes shallow. Postfemur shorter than femur, conspicuous. Solenophore (sph) variable between species: lamina lateralis (ll) swollen, sometimes with furrow(s) anterolaterally, sometimes with conspicuous ventral lobe (vll) or ventral ridge (vrl); lamina medialis (lm) variously species-specifically modified, consisting of one process (plm) and two lobes (distal lobe=dlm and broad lobe=blm, dlm and blm demarcated by indentation). Solenomere (sl) usually long, sometimes short.

Distribution and habitat. From south China to Malaysia. Most species seem to be local endemics (only *D. planata* is dispersed, certainly by anthropochory, through mainland Southeast Asia and in many islands). *Desmoxytes* specimens were usually found by ASRU personnel in limestone habitats or on granitic mountains, and some were seen crawling on rocks or vegetation or tree branches (Fig. 4.4).

Key to species of *Desmoxytes* s.s.

1. Male femora 5 and 6 without modification (Fig. 4.90H, I) ....***D. terae*** (Jeekel, 1964)

1. Male femora 5 and 6 modified (e.g., Fig. 4.11H, I) 2

2. Metaterga 2–8 with 2(1)+2(1) setae/tubercles/cones/spines in anterior row, 2+2 setae/ tubercles/ cones/ spines in posterior row (e.g., Figs 4.18A, B, 4.38A, B). Metaterga 9–19 with 2(1)+2(1) setae/ tubercles/ cones/ spines in anterior row, 2+2 setae/ tubercles/ cones/ spines in posterior row (e.g., Figs 4.18B, C, 4.38B, C) 3

2. Metaterga 2–8 with 2+2 or 3+3 tubercles/cones/spines in anterior row, 2+2 or 3+3 tubercles/ cones/ spines in posterior row (e.g., Figs 4.56A, B, 4.76A, B). Metaterga 9–19 with 2+2 or 3+3 or 4+4 tubercles/ cones/ spines in anterior row, 3+3 or 4(5)+4(5) tubercles/cones/spines in posterior row (e.g., Figs 4.56B, C, 4.76B, C) 12

3. Paraterga knife-like or blade-shaped (fig. 4B, E, H in Srisonchai *et al.* 2016) ....***D. des*** Srisonchai *et al.*, 2016

3. Paraterga wing-like (not knife-like or blade-shaped) (e.g., Fig. 4.3A–D) 4

4. Collum with one row of setae (anterior row) (e.g., Figs 4.18A, 4.24A, 4.44A). Metaterga with rows of tubercles (e.g., Fig. 4.18A–C). Gonopod; lamina lateralis (ll) with 1 or 2–3 conspicuous furrows (e.g., Figs 4.21B, D, 4.22F, 4.47B, 4.48E) 5

4. Collum with three rows of setae and/or tubercles (anterior, intermediate and posterior row) (e.g., Figs 4.38A, 4.50A, 4.56A). Metaterga with rows of cones/spines (e.g., Fig. 4.38A–C). Gonopod; lamina lateralis (ll) with an inconspicuous furrow or without furrow (e.g., Figs 4.41B, 4.53B) 10

5. Gonopod; lamina lateralis (ll) long, crest-like, without ventral ridge (vrl) (Fig. 4.27C); distal lobe (dlm) of lamina medialis long (Figs 4.27B–D, 4.28E); without or at most with inconspicuous indentation between distal lobe (dlm) and broad lobe (blm) of lamina medialis (Figs 4.27D, 4.28E) ....***D. corythosaurus*** **sp. n.**

5. Gonopod; lamina lateralis (ll) with ventral ridge (vrl) (e.g., Figs 4.21C, 4.22C); distal lobe (dlm) of lamina medialis short (e.g., Figs 4.21B, 4.22E, 4.47D, 4.48E); with conspicuous indentation between distal lobe (dlm) and broad lobe (blm) of lamina medialis (e.g., Figs 4.21D, 4.22D, 4.47D, 7.48E) 6

6. Gonopod; lamina lateralis (ll) anterolaterally with two or three furrows (e.g., Figs 4.47B, 4.48E) 7

6. Gonopod; lamina lateralis (ll) anterolaterally with one furrow (e.g., Figs 4.34E, 4.35F) 8

7. Paraterga wide (Fig. 4.61B). Gonopod; process (plm) of lamina medialis distinctly demarcated from distal lobe (dlm) of lamina medialis (Figs 4.64B, C, 4.65C, D); distal lobe (dlm) of lamina medialis with two lamellae (Figs 4.64B, 4.65D) ....***D. perakensis*** **sp. n.**

7. Paraterga narrow (Fig. 4.44B). Gonopod; process (plm) of lamina medialis indistinctly demarcated from distal lobe (dlm) of lamina medialis (Figs 4.47B, 4.48E); distal lobe (dlm) of lamina medialis with one lamella (Figs 4.47B, 4.48E) ....***D. flabella*** **sp. n.**

8. Body brownish red or brown. Paraterga strongly elevated (40°–45°) (Fig. 4.18E, F) .... ***D. cervina*** (Pocock, 1895)

8. Body orange. Paraterga at most moderately elevated (10°–35°) (e.g., Fig. 4.10E, F) 9

9. Paraterga of collum long (Fig. 4.10A). Gonopod; lateral sulcus (ls) shallow (Fig. 4.13E); lamina lateralis (ll) compact, stout (Figs 4.13B, C, 4.14C, E); ventral ridge (vrl) of lamina lateralis short (Figs 4.13C, 4.14C); distal lobe (dlm) of lamina medialis with one lamella (Figs 4.13B, 4.14E). Sternal lobe between male coxae 4 slender when seen in lateral view (Fig. 4.12A, B) ....***D. aurata* sp. n.**

9. Paraterga of collum short (Fig. 4.31A). Gonopod; lateral sulcus (ls) deep (Fig. 4.34E); lamina lateralis (ll) slender (Figs 4.34B, C, 4.35C, E); ventral ridge (vrl) of lamina lateralis well-developed, long, crest-like (Figs 4.34C, 4.35C); distal lobe (dlm) of lamina medialis with two lamellae (Figs 4.34B, 4.35E). Sternal lobe between male coxae 4 stout when seen in lateral view (Fig. 4.33A) ....***D. delfae*** (Jeekel, 1964)

10. Body brownish pink. Collum with 3(4)+3(4) tubercles in anterior row (fig. 13A in Srisonchai *et al.* 2016). Epiproct: tip extremely emarginate; apical setiferous tubercles conspicuous, very long, digitiform (fig. 13J, L in Srisonchai *et al.* 2016) ....***D. pinnasquali*** Srisonchai *et al.*, 2016

10. Body brown or black. Collum with 4+4 setae/tubercles in anterior row (e. g., Figs 4.38A, 4.69A). Epiproct: tip subtruncate or slightly emarginate; apical setiferous tubercles inconspicuous or conspicuous (if conspicuous – short, not digitiform) (Figs 4.39F, G, 4.70F, G) 11

11. Paraterga pink. Hypoproct subtrapeziform, with inconspicuous setiferous tubercles (Fig. 4.70C, D) ....***D. planata*** (Pocock, 1895)

11. Paraterga yellow to orange. Hypoproct subtriangular, with conspicuous setiferous tubercles (Fig. 4.39C, D) ....***D. euros* sp. n.**

12. Metaterga 9–19 with 2+2 tubercles/cones/spines in anterior row (e.g., Fig. 4.76B, C) 13

12. Metaterga 9–19 with 3+3 or 4+4 setae/tubercles/cones/spines in anterior row (e.g., Figs 4.50B, C, 4.56B, C) 16

13. Gonopod; lamina lateralis (ll) without ventral lobe (vll) (Fig. 4.87); process (plm) of lamina medialis short and thick (Fig. 4.87E) ....***D. taurina*** (Pocock, 1895)

13. Gonopod; lamina lateralis (ll) with ventral lobe (vll) (e.g., Figs 4.79F, 4.81C); process (plm) of lamina medialis quite long and slender (Figs 4.15B, 4.79E, 4.83B) 14

14. Gonopod; ventral lobe (vll) of lamina lateralis thumb-like, large, stout (Fig. 4.83C, D); distal lobe (dlm) of lamina medialis with one lamella (Fig. 4.83B) ....***D. takensis*** Srisonchai *et al.*, 2016

14. Gonopod; ventral lobe (vll) of lamina lateralis quite long and slender, digitiform (e.g., Figs 4.15C, 4.79F); distal lobe (dlm) of lamina medialis with two lamellae (e.g., Figs 4.15B, 4.79E) 15

15. Gonopod; lamina lateralis (ll) more swollen (Figs 4.79E, 4.81E), surface smooth (Figs 4.79D, 4.81F); tip of process (plm) of lamina medialis terminating in several spines (Fig. 4.80) ....***D. purpurosea*** Enghoff *et al.*, 2007

15. Gonopod; lamina lateralis (ll) less swollen (Fig. 4.15B), surface rough (Fig. 4.15E); tip of process (plm) of lamina medialis blunt or not terminating in spines (Fig. 4.15B) ....***D. breviverpa*** Srisonchai *et al.*, 2016

16. Metaterga 9–19 with 3(4)+3(4) tubercles/ cones/ spines in posterior row (Fig. 4.50B, C). Gonopod; broad lobe (blm) of lamina medialis expanded dorsally (Figs 4.53B, 4.54E) ....***D. golovatchi* sp. n.**

16. Metaterga 9–19 with 4(3)+4(3) or 4(5)+4(5) tubercles/cones/spines in post-erior row (Figs 4.56B, C, 4.94B, C). Gonopod; broad lobe (blm) of lamina medialis not expanded dorsally (e. g., Figs 4.59B, 4.97B) 17

17. Body dark brown or brown (Fig. 4.55A–C). Metaterga 9–19 with 4(3)+4(3) cones/spines in anterior row, 4(5)+4(5) cones /spines in posterior row (Fig. 4.56A–C). Male femora 5 and 6 swollen (Fig. 4.57H, I). Sternal lobe between male coxae 4 subtrapeziform (Fig. 4.58) ....***D. octoconigera* sp. n.**

17. Body pinkish brown (Fig. 4.93A, B, D). Metaterga 9–19 with 3+3 setae/tubercles/cones in anterior row, 4(3)+4(3) setae/tubercles/ cones/ spines in posterior row (Fig. 4.94A–C). Male femora 5 and 6 strongly humped in middle portion (Fig. 4.95H, I). Sternal lobe between male coxae 4 incompletely bilobed (Fig. 4.96) ....***D. waepyanensis* sp. n.**

Species descriptions

Desmoxytes aurata Srisonchai, Enghoff and Panha sp. n.

Figs 4.9–4.14

Holotype: Male (CUMZ), THAILAND, Surat Thani Province, Kanchanadit District, Khao Phanom Wang Cave, 9°05'27"N, 99°36'28"E, ca. 52 m a.s.l., 7 August 2015, leg. C. Sutcharit, R. Srisonchai, and ASRU members.

Paratypes: 10 males, 7 females (CUMZ), same data as holotype. 17 males, 3 females (CUMZ), 1 male, 1 female (ZMUC), 1 male (ZMUM), 1 male (NHMW), 1 male (NHMUK), THAILAND, Surat Thani Province, Kanchanadit District, Wat Praphutthabart Sri Surat, 9°11'11"N, 99°34'47"E, ca. 19 m a.s.l., 6 December 2016, leg. S. Panha and ASRU members.

Further specimens, not paratypes, all from THAILAND,

Surat Thani Province: 8 males, 18 females, 3 broken females, 1 broken male missing right gonopod (CUMZ), Donsak District, Nang Gam Beach, limestone mountain, 9°18'53"N, 99°45'40"E, ca. 20 m a.s.l., 10 October 2008, leg. S. Panha, P. Tongkerd, and ASRU members. 7 males, 1 male missing left gonopod, 6 females, 1 male missing gonopods, 1 broken male missing left gonopod (CUMZ), Ko Samui District, Mo Ko Ang

Thong National Marine Park, Ko Mae Koh, 9°39'06"N, 99°40'02"E, ca. 23 m a.s.l., 6 June 2009, leg. S. Panha and ASRU members. 1 broken male missing left gonopod, 4 males, 3 females, 1 male missing right gonopod, 1 male missing gonopods (CUMZ), Ko Samui District, Mo Ko Ang Thong National Marine Park, Ko Wua Talap, 9°38'08"N, 99°40'16"E, ca. 20 m a.s.l., 6 June 2009, leg. S. Panha and ASRU members. 1 male, 3 females (CUMZ), Donsak District, Nang Gam Beach, 9°18'53"N, 99°45'41"E, ca. 26 m a.s.l., 2 December 2015, leg. S. Panha, P. Tongkerd, and ASRU members.

Nakhon Si Thammarat Province: 1 male (CUMZ), Khanom District, Khao Krot Bureau of Monks, near Khao Krot Cave, 9°14'29"N, 99°48'07"E, ca. 19 m a.s.l., 23 October 2016, leg. W. Siriwut and ASRU members.

Diagnosis. Body bright orange, low degree of elevation of paraterga, femora 5 and 6 strongly humped ventrally in middle part, collum with row of 3+3 anterior setae and metaterga with rows of 2+2 anterior and 2+2 posterior small tubercles. Similar in these respects to *D. delfae* and *D. perakensis* sp. n., but differs from those by having paraterga of collum quite long; lateral sulcus (ls) quite shallow; lamina lateralis (ll) stout and compact, ventral ridge (vrl) short; process (plm) of lamina medialis crenate; sternal lobe between male coxae 4 thin when seen in lateral view.

Etymology. The name is Latin adjective and refers to the lamina lateralis (ll) of the gonopod which bears some resemblance to the “hooded” head of the oranda breed of goldfish (*Carassius auratus*).

Description.

SIZE: Length 21–24 mm (male), 25–27 mm (female); width of midbody metazona ca. 1.7 mm (male), 2.1 mm (female). Width of head < collum < body ring 2 < 3 = 4 < 5–16, thereafter body gradually tapering towards telson.

COLOUR (Fig. 4.9A–D): In life with body bright orange; antenna dark brown, except distal part of antennomere 7 and antennomere 8 whitish; head brown; paraterga, metaterga and surface below paraterga orange; legs, sterna and epiproct orange-ish yellow; a few basal podomeres whitish orange; prozona and metazona (metaterga) with wide black stripe, conspicuous on rings 4–19.

ANTENNAE (Fig. 4.10D): Moderately long and slender, reaching to body ring 6 (male) and 5 (female) when stretched dorsally.

COLLUM (Fig. 4.10A): With 1 transverse anterior row of 3+3 setae; paraterga of collum low, almost horizontal, directed caudolaterad, with two inconspicuous setiferous notches on lateral margin.

TEGUMENT: Strongly shining and smooth; prozona finely shagreened; collum, metaterga, sterna and epiproct smooth; surface below paraterga finely microgranulate.

METATERGA (Fig. 4.10A–C): With 2 transverse rows of setae and inconspicuous tubercles; metaterga 2–18 with 2+2 anterior and 2+2 posterior tubercles; metatergum 19 with 2+2 anterior and 2+2 posterior setae.

PARATERGA (Fig. 4.10E, F): Directed caudolaterad on body rings 2–17, elevated at ca. 30°–35° (male) 30° (female), directed increasingly caudad on body rings 18 and 19; anterior margin with 2 distinct notches, without tiny denticle near tip.

TELSON (Fig. 4.11C–G): Epiproct: tip emarginate; lateral setiferous tubercles small and inconspicuous; apical tubercles inconspicuous. Hypoproct subsemicircular; caudal margin round, with very small and inconspicuous setiferous tubercles.

STERNA (Fig. 4.12): Cross-impressions shallow. Sternal lobe between male coxae 4 subrectangular (in some specimens subtrapeziform), tip subtruncate (in some specimens subemarginate or round).

LEGS (Fig. 4.11H–J): Long and slender. Male femora 5 and 6 strongly humped ventrally in middle portion.

GONOPODS (Figs 4.13, 4.14): Coxa (cx) longer than prefemur. Cannula (ca) slightly stout. Telopodite quite stout. Prefemur (pfe) ca. 2/3 as long as femur. Femur (fe) somewhat stout. Mesal sulcus (ms) conspicuous and very deep; lateral sulcus (ls) shallow. Postfemur (pof) conspicuous, ventrally narrow and short. Solenophore (sph) well-developed: lamina lateralis (ll) swollen, stout and compact, anterolaterally with a distinct furrow; ventral ridge (vrl) short: lamina medialis (lm) well-developed; process (plm) short, wide and thin, tip crenate; distal lobe (dlm) distally with one lamella, tip directed anteriad; broad lobe (blm) indistinctly separated from distal lobe (dlm) by a shallow indentation. Solenomere (sl) long.

Distribution and habitat. Known only from Surat Thani and Nakhon Si Thammarat Provinces. All specimens were collected in limestone mountains (on the mainland and on two islands) (Fig. 4.9E). We also surveyed other islands in Mo Ko Ang Thong National Marine Park, but found no specimens of *D. aurata* sp. n. The new species is probably distributed along the islands in the Gulf of Thailand and also on the mainland near the type locality. We regard it as endemic for Thailand.

Desmoxytes aurata sp. n. is morphologically similar to *D. delfae* and *D. perakensis* sp. n. in the remarkable orange colouration, as well as some morphological characters (except characters in diagnosis). These three species show allopatric distribution ranges, and the big mountain ranges known as the Nakhon Si Thammarat and Sunkala Khiri mountains possibly act as dispersal barriers.

Remarks. The bright orange colouration is without doubt aposematic. There is some distinct variation within populations in the sternal lobe between male coxae 4, especially its shape: in most specimens the lobe is subrectangular, in others subtrapeziform, and its tip also varies – subtruncate/ subemarginate/ round. The shape of the sternal lobe of the new species is similar to that seen in *D. delfae* and *D. perakensis* sp. n., however, it looks thinner than those when seen in lateral view.

Coexisting species. *Desmoxytes cervina* was found together with the new species in some localities.

***Desmoxytes breviverpa* Srisonchai, Enghoff and Panha, 2016**

Fig. 4.15

Desmoxytes breviverpa Srisonchai, Enghoff and Panha, 2016: 99.

Material examined.

Holotype: Male (CUMZ), THAILAND, Phrae Province, Long District, in front of Sareethai Cave, 18°16'43"N, 100°03'29"E, ca. 292 m a.s.l., 21 October 2014, leg. C. Sutcharit, W. Siriwut, K. Inkhavilay and R. Srisonchai.

Paratypes: 27 males, 7 females (CUMZ), 3 males, 2 females (ZMUC), same data as holotype. 5 males, 3 females (CUMZ), THAILAND, Phrae Province, Long District, in front of Sareethai Cave, 18°16'43"N, 100°03'29"E, ca. 292 m a.s.l., 21 July 2008, leg. N. Likhitrakarn. 1 male, 3 females (CUMZ), THAILAND, Lampang Province, Mae Tha District, Nakraua Subdistrict, Wat Tham Phra Sabai, 18°05'32"N, 99°32'03"E, ca. 328 m a.s.l., 21 July 2008, leg. S. Panha, P. Tongkerd and N. Likhitrakarn. 1 male, 5 females (CUMZ), THAILAND, Lampang Province, Mae Tha District, Tham Chakkrabhat Monastery (Wat Tham Chakkrabhat), 18°06'02"N, 99°56'48"E, ca. 210 m a.s.l., 8 October 2007, leg. U. Bantaowong, R. Chanabun, P. Pimvichai and T. Krutchuen.

Further specimens, all from THAILAND: 2 males, 5 broken males, 1 male with rings 1–8, 6 broken females (CUMZ), Uttaradit Province, Thong Saen Khan District, Tham Chan (Chan Cave), 17°35'00"N, 100°25'21"E, ca. 164 m a.s.l., 22 July 2008, leg. S. Panha and ASRU members. 1 male, 1 female (CUMZ), Lampang Province, Mae Tha District, Nakraua Subdistrict, Wat Tham Phra Sabai, 18°05'32"N, 99°32'03"E, ca. 328 m a.s.l., 21 July 2008, leg. S. Panha and ASRU members.

Diagnosis. Differs from all other *Desmoxytes* species by the combination of the following characters; body purple pink; collum with rows of 3+3 anterior, 1+1 intermediate and 2+2 posterior setiferous tubercles; sternal lobe between male coxae 4 subrectangular, quite long and thick when seen in lateral view; ventral lobe (vll) of lamina lateralis quite long, digitiform, directed ventrad; distal lobe (dlm) distally with two lamellae (mesal lamella smaller than lateral one; lateral lamella thin, tip directed almost in vertical plane); broad lobe (blm) thick, obviously demarcated from distal lobe by a deep and wide indentation; solenomere (sl) short.

Type locality. THAILAND, Phrae Province, Long District, in front of Sareethai Cave.

Redescription (updated from Srisonchai *et al.* 2016).

SIZE: Length 28–33 mm (male), 33–38 mm (female); width of midbody metazona ca. 2.2 mm (male), 3.5 mm (female). Width of head < collum = body ring 2 = 3 ≤ 4 < 5 < 6–17, thereafter body gradually tapering toward telson.

COLOUR: In life with body shocking pink to purple (some female specimens brownish pink); paraterga vivid pink; metaterga and surface below paraterga brownish pink to brownish purple; head brown; antenna blackish brown (except distal part of antennomere 7 and antennomere 8 whitish); legs, sterna and epiproct pink; a few basal podomeres whitish pink. Colour in alcohol: after two years changed to pale brown.

ANTENNAE: Long and slender, reaching to body ring 6 (male), and 5 (female) when stretched dorsally.

COLLUM: With 3 transverse rows of setiferous tubercles, 3+3 anterior, 1+1 intermediate and 2+2 posterior tubercles (excluding small setiferous notches at base of paraterga), lateral tubercles of posterior row located at almost halfway to intermediate row; paraterga of collum low, elevated at ca. 30°, directed caudolaterad, with two setiferous notches on lateral margin (first inconspicuous notch located at the base of paratergum, second one conspicuous).

TEGUMENT: Moderately shining; collum, metaterga and surface below paraterga coarsely microgranulate; prozona finely shagreened; paraterga, sterna and epiproct smooth.

METATERGA: With 2 transverse rows of setiferous tubercles and rose thorn-like spines; metaterga 2–18 with 2+2 anterior and 2+2 posterior spines; metatergum 19 with 2+2 anterior and 2+2 posterior spines (tubercles in some specimens).

PARATERGA: Directed caudolaterad on body rings 2–17, elevated at ca. 45° (male) 40° (female); directed increasingly caudad on body rings 18 and 19; anterior margin with 2 distinct notches, on lateral margin of body rings 9, 10, 12, 13, 15–18 with tiny denticle near the tip.

TELSON: Epiproct: tip subtruncate; lateral setiferous tubercles inconspicuous; apical tubercles inconspicuous. Hypoproct subsemicircular (in some specimens subtrapeziform); caudal margin round, with inconspicuous setiferous tubercles.

STERNA: Cross-impressions shallow. Sternal lobe between male coxae 4 swollen, usually subrectangular (in some specimens subtrapeziform), quite long and slightly thick when seen in lateral view, tip usually emarginate (some specimens subtruncate).

LEGS: Very long and slender. Male femora 5 and 6 strongly humped ventrally in middle part.

GONOPODS (Fig. 4.15): Coxa (cx) longer than prefemur. Cannula (ca) long and slender. Prefemur (pfe) ca. 2/3 as long as femur. Femur (fe) long and slender. Mesal sulcus (ms) and lateral sulcus (ls) very deep and wide. Postfemur (pof) conspicuous, ventrally very wide. Solenophore (sph) well-developed: lamina lateralis (ll) swollen, surface rough; ventral lobe (vll) quite long, digitiform, directed ventrad: lamina medialis (lm) well-developed; process (plm) long, spine-like, tip emarginate – not terminating in spines (in some specimens almost blunt), directed mesoanteriad; distal lobe (dlm) distally with two distinct lamellae (mesal lamella slightly smaller than lateral one; lateral lamella thin and broad, tip directed almost in vertical plane); broad lobe (blm) thick, obviously demarcated from distal lobe (dlm) by a deep and wide indentation. Solenomere (sl) quite short.

Distribution and habitat. Known only from the type locality and nearby areas. *Desmoxytes breviverpa* was collected from limestone forest, crawling on logs and litter (Srisonchai *et al.* 2016). We believe it may be distributed though the central and southern parts of north Thailand. This species has been reported from Phrae, Lampang and Uttaradit Provinces. Therefore, *D. breviverpa* should be regarded as endemic for Thailand.

Remarks. Specimens collected from Uttaradit Province south of the type locality showed the same morphological characters as the type specimens. No variation was found between populations although most limestone areas in north Thailand are geographically isolated by several big mountain ranges and quite far from each other.

Srisonchai *et al.* (2016) discussed variation of the tip of sternal lobe between male coxae 4; we found additional variation within populations as follows:

- Tip of sternal lobe in some specimens almost truncate (=subtruncate), albeit other specimens show an emarginate tip (slightly or deeply emarginate).

- Tip of hypoproct in some individuals subsemicircular, in others subtrapeziform.

- Tip of process (plm) of lamina medialis emarginate in most specimens, but almost blunt in some.

Coexisting species. None known.

Corrections to Srisonchai *et al.* (2016). Srisonchai *et al.* (2016, pp. 99–103) wrote in the description of this species that the paraterga (including paraterga of collum) are directed dorsolaterad. In fact they are directed caudolaterad as described above.

***Desmoxytes cervina* (Pocock, 1895)**

Figs 4.16–4.22

Prionopeltis cervinus Pocock, 1895: 831. Attems 1914: 203; 1936: 215.

Pratinus cervinus – Attems 1937: 120. Jeekel 1964: 63. Jeekel 1968: 61.

Desmoxytes cervina – Jeekel 1980a: 654. Golovatch and Enghoff 1994: 61. Nguyen and Sierwald 2013: 1241. Likhitrakarn *et al.* 2017: 19.

Desmoxytes pterygota Golovatch and Enghoff, 1994: 55, syn. n. Enghoff 2005: 96. Decker 2010: 30. Nguyen and Sierwald 2013: 1242.

Desmoxytes sp. – Golovatch and Enghoff 1994: 60.

Material examined.

Lectotype: Male (NHMUK, Bm 1892.5.4.76), MYANMAR, south Tenasserim, leg. E. W. Oates, most legs missing. Lectotype here designated.

Holotype (*D. pterygota*): Male (ZMUC), THAILAND, Ranong Province, Kapoe District, in forest at big waterfalls south of Kapoe (Khao Phra Narai Waterfall?), 15 November 1990, leg. M. Andersen and A. R. Rasmussen.

Paratypes (*D. pterygota*): 2 males (ZMUC), 1 male (ZMUM), THAILAND, Ranong Province, Kapoe District, in forest at big waterfalls south of Kapoe, 15 November 1990, leg. M. Andersen and A. R. Rasmussen.

Other material examined.

MYANMAR: 10 males, 7 females (CUMZ), Tanintharyi Division, Lenya National Park, Phayarhtan Cave (Buddha Cave), approximately 10 km from Ban Nam Yen Village, inside the deep rainforest near limestone mountain, on decaying wood and under bark, 11°13'50''N, 99°10'35''E, ca. 85 m a.s.l., 6 June 2015, leg. C. Sutcharit, R. Chanabun and R. Srisonchai.

THAILAND:

Chumphon Province: 1 male, 2 females (CUMZ), Mueang Chumphon District, Tham Chang Phuek Bureau of Monks, 10°26'47"N, 99°02'06"E, ca. 93 m a.s.l., 13 March 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members. 1 male (CUMZ), Sawi District, Wat Nam Cha, 10°17'54"N, 99°01'57"E, ca. 105 m a.s.l., 3 July 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Krabi Province: 1 male (CUMZ), Ao-Luek District, P.N. Moutain Resort, 8°24'09''N, 98°44'18''E, ca. 60 m a.s.l., 30 August 2015, leg. C. Sutcharit and ASRU members. 1 male remaining rings 7–20 (CUMZ), Khlong Thom District, Emerald Blue Pool, 7°55'30''N, 99°16'05''E, ca. 67 m a.s.l., 15 January 2009, leg. S. Panha and ASRU members. 1 female (CUMZ), Muang Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'38''N, 98°55'27''E, ca. 86 m a.s.l., 18 May 2010, leg. S. Panha and ASRU members. 2 males, 3 females, 1 broken male and missing gonopods (CUMZ), Muang Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'38''N, 98°55'27''E, ca. 86 m a.s.l., 7 October 2006, leg. S. Panha and ASRU members. 1 male, 4 females (CUMZ), Muang Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'38''N, 98°55'27''E, ca. 86 m a.s.l., 24 August 2014, leg. S. Panha and ASRU members. 2 males, 1 female, 1 juvenile (CUMZ), Muang Krabi District, Wat Tham Sue

(Tiger Cave), valley behind Tiger Cave, 8º07'38''N, 98°55'27''E, ca. 86 m a.s.l., 30 August 2015, leg. C. Sutcharit, R. Srisonchai and ASRU members. 15 males, 3 females, 1 juvenile (CUMZ), Muang Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8º07'38''N, 98°55'27''E, ca. 86 m a.s.l., 9 July 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members. 11 males, 6 females, 1 juvenile (CUMZ), Muang Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8º07'38''N, 98°55'27''E, ca. 86 m a.s.l., 25 July 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Nakhon Si Thammarat Province: 2 males, 2 females, 4 juveniles (ZMUC), Sichon District, Khao Lark Waterfall, 25 August 2007, leg. ASRU members. 1 female (CUMZ), Thung Song District, Yong Waterfall, 8°10'21''N, 99°44'34''E, ca. 138 m a.s.l., 20 July 2008, leg. S. Panha and ASRU members. 1 male missing gonopods (CUMZ), Nopphitam District, Krung Ching Waterfall, 8°43'27''N, 99°40'04''E, ca. 173 m a.s.l., 17 January 2013, leg. C. Sutcharit, R. Srisonchai and ASRU members. 1 female (CUMZ), Khanom District, Nai Plao Beach, 9º07'26''N, 99°52'60''E, ca. 20 m a.s.l., 4 December 2015, leg. S. Panha and ASRU members. Many specimens (CUMZ), Tham Phannara District, Wat Tham Kanlaya Namit, 8°30'48''N, 99°22'52''E, ca. 51 m a.s.l., 4 July 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members. Many specimens (CUMZ), Tham Phannara District, Wat Tham Thong Phannara, 8°25'21''N, 99°22'47''E, ca. 32 m a.s.l., 4 July 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Phang Nga Province: 1 male missing gonopods, 3 males, 1 female (CUMZ), Thai Mueang District, Khaolak-Lumru National Park, 8°37'35''N, 98°14'25''E, ca. 72 m a.s.l., 7 October 2006, leg. S. Panha and ASRU members. 1 male, 1 female (ZMUC), Thap Put District, Highway No. 4 Phet Kasem Road ca. 0.5 km north of the Headquarters of the Khao Lak–Lamru National Park, on the street next to secondary rainforest. 8°37'N, 98°14'E, ca. 30–40 m a.s.l., 29 August–12 September 2008, leg. N. Laufer. 1 male missing gonopods, 1 male (CUMZ), Khura Buri District, Mu Koh Surin National Park, Koh Surin Nuea, 9°26'27''N, 97°52'11''E, ca. 39 m a.s.l., 8 April 2012, leg. S. Panha and ASRU members. 1 broken male and missing gonopods (CUMZ), Mueang Phang Nga District, Tham Nam Pud, 8°27'50''N, 98°32'36''E, ca. 58 m a.s.l., 7 October 2006, leg. S. Panha and ASRU members. Many specimens (CUMZ), Mueang Phang Nga District, Tham Nam Pud, 8°27'50''N, 98°32'36''E, ca. 58 m a.s.l., 5 August 2015, leg. C. Sutcharit, R. Srisonchai and ASRU members. 1 male (CUMZ), Mueang Phang Nga District, Tham Pha Sue Bureau of Monks, 8°28'24''N, 98°32'15''E, ca. 78 m a.s.l., 10 July 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members. 2 females (CUMZ), Mueang Phang Nga District, Tham Nam Pud Bureau of Monks, 8 October 2006, leg. S. Panha and ASRU members. 1 male, 1 female (CUMZ), Mueang Phang Nga District, Tao Thong Waterfall, 8°29'08''N, 98°35'09''E, ca. 25 m a.s.l., 7 October 2006, leg. S. Panha and ASRU members. 1 female (CUMZ), Mueang Phang Nga District, Phung Chang Cave, 8°26'34"N, 98°30'59"E, ca. 24 m a.s.l., 26 September 2009, leg. S. Panha and ASRU members. 3 males, 2 females, 14 juveniles (CUMZ), Mueang Phang Nga District, Phung Chang Cave, 8°26'34"N, 98°30'59"E, ca. 24 m a.s.l., 6 August 2014, leg. C. Sutcharit, R. Srisonchai and ASRU members. Many specimens (CUMZ), Mueang Phang Nga District, Phung Chang Cave, 8°26'34"N, 98°30'59"E, ca. 24 m a.s.l., 5 August 2015, leg. C. Sutcharit, R. Srisonchai and ASRU members. 5 males, 4 females (CUMZ), Mueang Phang Nga District, Phung Chang Cave, 8°26'34"N, 98°30'59"E, ca. 24 m a.s.l., 8 August 2016, leg. C. Sutcharit, R. Srisonchai, and ASRU members. 3 males, 2 juveniles (CUMZ), Takua Thung District, Wat Suwan Khuha (Monkey Cave), 8°25'42"N, 98°28'22"E, ca. 25 m a.s.l., 8 August 2016, leg. C. Sutcharit, R. Srisonchai, and ASRU members. Many specimens (CUMZ), Thap Put District, Wat Khiri Wong (Tham Kob), 8°31'57"N, 98°34'40"E, ca. 97 m a.s.l., 9 July 2017, leg. C. Sutcharit, R. Srisonchai, and ASRU members.

Phuket Province: 1 male of *Desmoxytes* sp. (ZMUC), Thalang District, Thepkrasattree Subdistrict, Tonsai Waterfall, 8°01'44''N, 98°21'45''E, ca. 67 m a.s.l., 12 October 1991, leg. M. Anderson, O. Martin, and N. Scharff. 1 female (CUMZ), Mueang Phuket District, Panwa Cave, 7°48'04''N, 98°24'34''E, ca. 25 m a.s.l., June 2007, leg. S. Panha and ASRU members. 1 female (CUMZ), Mueang Phuket District, Panwa Cave, 7°48'04''N, 98°24'34''E, ca. 25 m a.s.l., 5 November 2007, leg. S. Panha and ASRU members.

Ranong Province: 1 male (CUMZ), Kra Buri District, Tham Phra Khayang, 10°19'35''N, 98°45'54''E, ca. 51 m a.s.l., 21 November 2015, leg. S. Panha, P. Tongkerd, and A. Pholyotha. 1 female (CUMZ), Kra Buri District, Bok Krai Waterfall, 10°22'35''N, 98°51'22''E, ca. 106 m a.s.l., 3 January 2013, leg. S. Panha, P. Tongkerd, and A. Pholyotha.

Surat Thani Province: 2 broken and mixed females, 2 females remaining rings 13–20, 1 broken female (CUMZ), Phanom District, Khlong Phanom National Park, 8°52'44''N, 98°40'26''E, ca. 68 m a.s.l., 28 August 2007, leg. S. Panha and ASRU members. 1 male, 6 juveniles (CUMZ), Phanom District, Khlong Phanom National Park, Pha Daeng, 8°53'41''N, 98°33'12''E, ca. 67 m a.s.l., 7 August 2016, leg. C. Sutcharit, R. Srisonchai, and ASRU members. 8 males, 3 females (CUMZ), Phanom District, Khlong Phanom National Park, Pha Daeng, 8°53'41''N, 98°33'12''E, ca. 67 m a.s.l., 1 August 2017, leg. C. Sutcharit, R. Srisonchai, and ASRU members. 4 males (CUMZ), Phanom District, Ban Song Phi Nong, 8°50'51''N, 98°44'16''E, ca. 74 m a.s.l., 7 August 2016, leg. C. Sutcharit, R. Srisonchai, and ASRU members. 10 males, 3 females, 1 broken male missing gonopods (CUMZ), Ban Ta Khun District, Ratchaprapa Dam, 8°57'22''N, 98°48'22''E, ca. 53 m a.s.l., 8 October 2008, leg. S. Panha and ASRU members. Many specimens (CUMZ), Ban Ta Khun District, Ratchaprapa Dam, 8°57'22''N, 98°48'22''E, ca. 53 m a.s.l., 4 August 2014, leg. C. Sutcharit, R. Srisonchai, and ASRU members. Many specimens (CUMZ), Ban Ta Khun District, Ratchaprapa Dam, 8°57'22''N, 98°48'22''E, ca. 53 m a.s.l., 3 August 2015, leg. C. Sutcharit, R. Srisonchai, and ASRU members. 1 male (CUMZ), Ban Ta Khun District, Ratchaprapa Dam, 8°57'22''N, 98°48'22''E, ca. 53 m a.s.l., 5 August 2016, leg. C. Sutcharit, R. Srisonchai, and ASRU members. 1 male (CUMZ), Ban Ta Khun District, Khlong Hoi, 8 October 2008, leg. S. Panha and ASRU members. 2 males, 1 male missing gonopods, 1 juvenile, 1 broken juvenile (CUMZ), Ban Ta Khun District, Khao Wong Water Supply Station, 8°55'47''N, 98°56'25''E, ca. 97 m a.s.l., 9 October 2008, leg. S. Panha and ASRU members. 2 males (CUMZ), Ban Ta Khun District, Wat Khao Pang (Suspension Bridge), 8°56'54''N, 98°49'21''E, ca. 24 m a.s.l., 5 May 2017, leg. S. Panha and ASRU members. 1 male, 1 male missing gonopods, 2 females, 2 broken females, 1 juvenile (CUMZ), Khirirat Nikhom District, Wat Satit Khirirom, 9°01'48''N, 98°59'12''E, ca. 47 m a.s.l., 8 October 2008, leg. S. Panha and ASRU members. 1 male (CUMZ), Khirirat Nikhom District, Wat Satit Khirirom, 9°01'48''N, 98°59'12''E, ca. 47 m a.s.l., 5 September 2009, leg. S. Panha and ASRU members. 27 males, 10 females (CUMZ), 2 males, 1 female (ZMUC), 1 male, 1 female (ZMUM), 1 male, 1 female (NHMW), 1 male, 1 female (NHMUK), Khirirat Nikhom District, Wat Satit Khirirom, 9°01'48''N, 98°59'12''E, ca. 47 m a.s.l., 10 July 2017, leg. C. Sutcharit, R. Srisonchai, and ASRU members. 1 male missing right gonopod

(CUMZ), Khirirat Nikhom District, km3 near Khirirat Nikhom City, 9 October 2008, leg. S. Panha and ASRU members. 1 male, 1 female (CUMZ), Khirirat Nikhom District, Tham Wang Badan Bureau of Monks, 8°56'09''N, 98°57'28''E, ca. 69 m a.s.l., 3 August 2017, leg. C. Sutcharit, R. Srisonchai, and ASRU members. 3 broken males (CUMZ), Ko Samui District, Na Muang Waterfall, 9°27'58''N, 99°59'02''E, ca. 53 m a.s.l., 27 January 2006, leg. S. Panha and ASRU members. 1 female (CUMZ), Ko Samui District, Na Muang Waterfall, 9°27'58''N, 99°59'02''E, ca. 53 m a.s.l., 4 December 2015, leg. S. Panha, P. Tongkerd and A. Pholyotha. 1 male remaining rings 1–11, 1 female (ZMUM), Ko Samui, Thailand, June 2013, leg. Korabushkin Daniil. 10 males, 5 females, 4 juveniles (CUMZ), Wiang Sa District, Khiri Rat Pattana Bureau of Monks (Wat Khao Poon), 8°31'37''N, 99°22'59''E, ca. 68 m a.s.l., 4 July 2017, leg. C. Sutcharit, R. Srisonchai, and ASRU members. 1 male, 1 female (CUMZ), Ban Na San District, Khao Kok Maharat Bureau of Monks, 8°41'33''N, 99°22'45''E, ca. 71 m a.s.l., 4 July 2017, leg. C. Sutcharit, R. Srisonchai, and ASRU members.

Diagnosis. Differs from other *Desmoxytes* species by the combination of the following characters: body colour brownish red/brown/pale brown; paraterga brownish red/red/yellowish brown; metaterga 2–4 with 2+2 (anterior row) and 2+2 (posterior row) tubercles, metaterga 5–19 with 2(1)+2(1) (anterior row) and 2+2 (posterior row) tubercles; lamina lateralis (ll) stout; anterolaterally with a long, distinct, deep and wide furrow; ventral ridge (vrl) of lamina lateralis very long, wide, conspicuous; process (plm) of lamina medialis long, distinctly demarcated from distal lobe, irregularly shaped, directed mesodorsad; distal lobe (dlm) of lamina medialis distally with one distinct lamella; broad lobe (blm) slightly thick at the edge, distinctly demarcated from distal lobe (dlm) by a wide and shallow indentation.

Type locality. MYANMAR, southern Myanmar, Tenasserim [Tanintharyi Division].

Redescription.

SIZE: Length 25–31 mm (male), 33–39 mm (female); width of midbody metazona ca. 2.1 mm (male), 3.6 mm (female). Width of head < collum < body ring 2 ≥ 3 = 4 < 5–16, thereafter body gradually tapering towards telson.

COLOUR (Figs 4.16, 4.17A–E): In life with two colour morphs. Brownish red morph – body brownish red (testaceous); head and antenna brownish black (except distal part of antennomere 7 and antennomere 8 whitish); collum, epiproct and legs brown; rings 2–3 brownish red or brown; metaterga, surface below paraterga and sterna brownish red; paraterga brownish red or red; a few basal podomeres reddish brown. Brown morph – body brown (female pale brown); head and antenna (except distal part of antennomere 7 and antennomere 8 whitish) brownish black or black; collum and rings 2–3 brownish black; metaterga, surface below paraterga, epiproct and legs brown; paraterga yellowish brown; sterna pale brown; a few basal podomeres brownish white. Colour in alcohol: after 100 years changed to greenish dark or greenish brown, after 5–10 years changed to pale brown.

ANTENNAE (Fig. 4.18D): Very long and slender, reaching to body ring 6 or 7 (male) and 5 or 6 (female) when stretched dorsally.

COLLUM (Fig. 4.18A): With 1 transverse row of setae, 3+3 anterior setae; paraterga of collum low, elevated at ca. 15°–20°, directed caudolaterad, with two inconspicuous notches on lateral margin.

TEGUMENT: Moderately shining; collum coarsely microgranulate; prozona finely shagreened; metaterga and surface below paraterga finely microgranulate; paraterga, sterna and epiproct smooth.

METATERGA (Fig. 4.18A–C): With 2 transverse rows of tubercles; metaterga 2–4 with 2+2 anterior tubercles and 2+2 posterior tubercles; metaterga 5–19 with 2(1)+2(1) anterior tubercles and 2+2 posterior tubercles (lateral setae of anterior row in some specimens very distinct, in some specimens poorly developed).

PARATERGA (Fig. 4.18E, F): Long, strongly developed; directed caudolaterad on body rings 2–17, elevated at ca. 45° (male) 40° (female); directed increasingly caudad on body rings 18 and 19; anterior margin with 2 distinct notches, on lateral margin of body rings 9, 10, 12, 13, 15–18 with tiny denticle near the tip.

TELSON (Fig. 4.19C–G): Epiproct: tip usually truncate (in some specimens slightly emarginate); lateral setiferous tubercles and apical setiferous tubercles conspicuous, coniform. Hypoproct subtrapeziform; caudal margin slightly round (in some specimens subtruncate), with inconspicuous setiferous tubercles.

STERNA (Fig. 4.20): Cross-impressions shallow (in some specimens slightly deep). Sternal lobe between male coxae 4 swollen, usually subtrapeziform (in some specimens subsemicircular), usually thick when seen in lateral view (in some specimens thin), slightly attenuated near tip, tip round/subtruncate/slightly emarginate.

LEGS (Fig. 4.19H–J): Very long and slender. Male femora 5 and 6 strongly humped ventrally in middle portion.

GONOPODS (Figs 4.21, 4.22): Coxa (cx) longer than prefemur. Cannula (ca) long and slender. Prefemur (pfe) ca. 2/3 as long as femur. Femur (fe) long and slender. Mesal sulcus (ms) and lateral sulcus (ls) conspicuous, very deep and narrow. Postfemur (pof) conspicuous, ventrally narrow. Solenophore (sph) well-developed: lamina lateralis (ll) stout; anterolaterally with a long, distinct, deep and wide furrow; with a long, wide and conspicuous ventral ridge (vrl): lamina medialis (lm) well-developed; process (plm) long, of irregular shape (varies within population), distinctly demarcated from distal lobe, tip blunt (in some specimens terminating in spines), directed mesodorsad; distal lobe (dlm) distally with one distinct lamella; broad lobe (blm) slightly thick at the edge, distinctly demarcated from distal lobe (dlm) by a wide and shallow indentation. Solenomere (sl) long.

Distribution and habitat. *Desmoxytes cervina* is known from Myanmar (Lenya National Park) and Thailand (Chumphon, Krabi, Nakhon Si Thammarat, Phang Nga, Phuket, Ranong, and Surat Thani Provinces). The type locality is in south of Tenasserim, but we do not know the exact location, probably somewhere near Taninthayi township. The locality of the paralectotype (see below) "Malewoon, Tenasserim", is currently known as Maliwan Village.

Almost all specimens were collected from limestone habitats, a few specimens were collected from granitic areas. Interestingly, *D. cervina* was also found in some islands in both the Andaman Sea and the Gulf of Thailand (Mu Koh Surin National Park, Phuket, and Ko Samui).

Decker (2010) classified "*D. pterygota*" as endemic for Thailand due to its narrow range near the type locality. After intensive collecting and synonymising of *D.*

cervina and "*D. pterygota*", the known distribution range has expanded to southern Myanmar and southern Thailand.

This species was found living together with *D. delfae* and *D. corythosaurus* sp. n. According to our observations, it is probable that they may even share microhabitat: humid rocks, branches of trees and rock walls.

Note on material. This species was described based on two males, one of which was collected by L. Fea (Malewoon, Tenasserim – MSNG) and the other collected by E. W. Oates (south Tenasserim – NHMUK).

Jeekel (1964) revised this species by examining the male in MSNG; he stated that "in anticipation of the designation as holotype of the specimen collected by Oates in the British Museum, I have labelled this specimen as paratype". However, the holotype has never been designated in the original description. R.L. Hoffman visited NHMUK and labelled the specimen collected by Oates as paratype, but he did not publish this designation, which is in conflict with Jeekel's (1964) paratype designation. Therefore, we here designate the male collected by Oates and belonging to NHMUK as lectotype to stabilize the name. The male in MSNG (which we have not examined) is considered to be a paralectotype.

Some specimens kept in MHNG and identified as "*D. pterygota*" by Decker (2010), are probably *D. cervina* because the localities fall within the distribution range of this species.

Remarks. This is the first report of the colour of living specimens for this species; the brownish red colour is apparently aposematic. Pocock (1895) and Golovatch and Enghoff (1994) did not mention the colour of living specimens. We found two colour morphs of *D. cervina*: brownish red and brown. The majority of specimens are brownish red, and the minority are brown; the latter colour can be found in a few specimens within a population.

Interestingly, brownish red and brown morphs occur in the same habitat in the valley behind Tiger Cave and Ban Song Phi Nong. The brown morph was found at Wat Tham Kanlaya Namit, Wat Tham Thong Phannara, Tham Nam Pud, Phung Chang Cave and Wat Suwan Khuha (Monkey Cave). Specimens from the remaining localities are of the brownish red morph. We examined the morphological characters of all specimens of both colour morphs; all specimens exhibit the same morphology, especially in the gonopods which are identical. Perhaps the difference in colour is caused by environmental factors and/or genetic variation.

We assume that the type material of both *D. cervina*, collected by Oates and Fea a hundred years ago, and “*D. pterygota*” collected by M. Andersen and A.R. Rasmussen 17 years ago, did probably exhibit brownish red colour because all specimens near the type localities are brownish red. We found additionally that the colour of some females is pale brownish red or pale brown, and the colour of juveniles is pale brown.

Jeekel (1964) wrote in his redescription that *D. cervina* shows collum without setae, metaterga 2–19 with 1+1 anterior tubercles and 2+2 posterior tubercles. Golovatch and Enghoff (1994) distinguished “*D. pterygota*” from *D. cervina* by having smooth metaterga. They also described “*D. pterygota*” as having no pleurosternal carinae, antenna reaching to ring 4 in male, collum with 2 rows of 3+3 anterior setae and 1+1 intermediate setae, metaterga 2–19 with 2+2 anterior cones and 2+2 posterior cones. After examination of all type material and newly collected specimens of *D. cervina* and “*D. pterygota*”, we found that:

- all specimens of *D. cervina* and “*D. pterygota*” display fine microgranulation on the metaterga.

- all specimens have pleurosternal carinae, in body ring 2 very distinct and crest-like, in ring 3 very small, thereafter absent.

- antenna reaches to ring 6–7 in male and to ring 5–6 in female of both *D. cervina* and “*D. pterygota*”.

- collum has 3+3 anterior setae in all specimens – because Jeekel studied old preserved specimens, the setae may have been lost over time.

- metaterga 5–19 varies within populations; metaterga 2–4 with 2+2 anterior tubercles and 2+2 posterior tubercles, metaterga 5–19 with 2+2/1+1 anterior and 2+2 posterior tubercles.

Several other characters show variability, as follows:

I. variation within populations

- size of tubercles on metaterga: tubercles conspicuous in some specimens, inconspicuous in the others (bigger and more obvious in the holotype of "*D. pterygota*" than in the lectotype of *D. cervina*).

- tip of process (plm) of lamina medialis: in some specimens terminating in one blunt process, in others terminating in a sharp spine.

- shape of sternal lobe between male coxae 4: in some individuals subtrapeziform, in others subsemicircular.

- tip of sternal lobe between male coxae 4: in some specimens round, in some subtruncate, in others emarginate.

- cross-impressions on sternum: in some individuals shallow and faint, in others slightly deep.

- tip of epiproct: in some individuals truncate, in others slightly emarginate.

- caudal margin of hypoproct: in some specimens slightly round, in others subtruncate.

- size of sternal lobe between male coxae 4 when seen in lateral view in specimens from Wat Satit Khirirom: in some specimens thick, in others thin.

II. variation between populations

- colour: all individuals in the same population usually have the same colour: brown or brownish red. However, in some populations (valley behind Tiger Cave and Ban Song Phi Nong) brownish red and brown individuals coexist.

Although the male paralectotype of *D. cervina* (in MSNG) has not been examined by us, the morphological characters for this specimen as redescribed by Jeekel (1964) perfectly match the morphology of the numerous other specimens we have seen. Based on our analysis of morphology and variation of these specimens we have synonymized "*D. pterygota*" under *D. cervina*.

Distribution data support the synonymization: the type localities of "*D. pterygota*" (Ranong Province) and *D. cervina* (Tenasserim = Taninthayi) are very close to each other. Our intensive surveys prove that this species is distributed quite widely, but nevertheless is found in south Myanmar and south Thailand only.

During the field survey, we noticed several adult males of *D. cervina* which were infested with red mites. The mites are probably larvae of the genus *Leptus* Latreille, 1796 (Prostigmata, family Erythraeidae). Associations between mites and millipedes may be of a phoretic or a parasitic nature (Gerdeman *et al.* 2000, Swafford and Bond 2010, Farfan and Klompen 2012, Mwabvu 2014). In Figs 4.17C and 4.17D, several engorged mites are seen along with a few small, non-engorged ones, and we therefore assume that the mite species found in *D. cervina* is parasitic, like other *Leptus* larvae. Southcott (1992) described *Leptus millipedius* from julid millipedes, but this is the first record of a parasitic prostigmatan mite from a paradoxosomatid millipede. The only record of a mite from Paradoxosomatidae concerns the widespread *Oxidus gracilis* (C. L. Koch, 1847) which was reported as associated with *Cosmolaelaps hortensis* Ishikawa, 1986 (Mesostigmata, family Laelapidae) (Ishikawa 1986).

Golovatch and Enghoff (1994) reported one broken male of "*Desmoxytes* sp." from Phuket Province, Thailand. According to the remarks of Golovatch and Enghoff (1994), the gonopod characters of this specimen were similar to *D. delfae*, but the paraterga showed a higher degree of elevation. We examined this specimen again and found it to share gonopod and other characters with *D. cervina*. We therefore treat "*Desmoxytes* sp." as *D. cervina*.

Coexisting species. *D. delfae* at Wat Tham Sue (Tiger Cave), Krung Ching Waterfall, Khiri Rat Pattana Bureau of Monks (Wat Khao Poon); *D. corythosaurus* sp. n. at Ban Song Phi Nong.

***Desmoxytes corythosaurus* Srisonchai, Enghoff and Panha sp. n.**

Figs 4.23–4.28

Holotype: Male (CUMZ), THAILAND, Surat Thani Province, Phanom District, Ban Song Phi Nong, huge limestone mountain, 8°50'51"N, 98°44'16"E, ca. 74 m a.s.l., 7 August 2014, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Paratypes: 5 males, 1 female (CUMZ), 1 male (ZMUC), same data as holotype.

Further specimens, not paratypes, all from THAILAND,

Surat Thani Province, Phanom District: 1 male, 2 females (CUMZ), Wat Tham Wararam, 8°53'07"N, 98°40'01"E, ca. 51 m a.s.l., 5 August 2014, leg. C. Sutcharit, R. Srisonchai and ASRU members. 1 male, 1 female (CUMZ), Wat Tham Wararam, 8°53'07"N, 98°40'01"E, ca. 51 m a.s.l., 6 August 2016, leg. C. Sutcharit, R. Srisonchai and ASRU members. 1 male, 1 broken female (CUMZ), Wat Tham Wararam, 8°53'07"N, 98°40'01"E, ca. 51 m a.s.l., 1 August 2017, leg. C. Sutcharit and A. Pholyotha and ASRU members. 2 males, 1 female (CUMZ), Tham Nam Lod, near Anurak Community Lodge Resort, big limestone mountain, 8°52'43"N, 98°40'50"E, ca. 51 m a.s.l., 7 August 2014, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Etymology. The name is a Latin noun in apposition, referring to the similarity of the lamina lateralis (ll) to the crest-liked structure on the head of the dinosaur genus *Corythosaurus*.

Diagnosis. Body dark brown to black; paraterga with brown or black patches contrasting against whitish at base and along the edges; metaterga 2–18 with rows of 2+2 anterior and 2+2 posterior tubercles. Similar in these respects to *D. terae*, but differing by having paraterga much longer and higher; sternal lobe between male coxae 4 subtrapeziform; male femora 5 and 6 modified; lamina lateralis (ll) apically crest-like; distal lobe with one very long lamella; indentation between distal lobe (dlm) and broad lobe (blm) inconspicuous.

Description.

SIZE: Length 32–33 mm (male), 33–34 mm (female); width of midbody metazona ca. 2.3 mm (male), 3.0 mm (female). Width of head < collum < body ring 2 < 3 = 4 < 5–16, thereafter body gradually tapering towards telson.

COLOUR (Fig. 4.23A–D): In life with body brownish black; antenna and head dark brown (except distal part of antennomere 7 and antennomere 8 whitish); metaterga and surface below paraterga brownish black; paraterga whitish, dorsally with brown patches in the middle; legs, sterna and epiproct brown; a few basal podomeres sometimes whitish.

ANTENNAE (Fig. 4.24D): Moderately long and slender, reaching to the posterior end of body ring 6 (male) and 5 (female) when stretched dorsally.

COLLUM (Fig. 4.24A): With 1 transverse anterior row of 3+3 setae; paraterga of collum low, elevated at ca. 10°–15°, directed caudolaterad, with two distinct notches on lateral margin.

TEGUMENT: Moderately shining and smooth; prozona finely shagreened; collum, metaterga, surface below paraterga, sterna and epiproct smooth; lateral surface at base of paraterga with wrinkles.

METATERGA (Fig. 4.24A–C): With 2 transverse rows of setae and tubercles, mostly inconspicuous; metaterga 2–18 with 2+2 anterior and 2+2 posterior tubercles; metatergum 19 with 2+2 anterior and 2+2 posterior setae.

PARATERGA (Fig. 4.24E, F): Directed caudolaterad on body rings 2–17, elevated at ca. 30° (male) 25° (female); directed increasingly caudad on body rings 18 and 19; tip of paraterga in female slightlty curved caudad; anterior margin with 2 distinct notches, without a tiny denticle near the tip.

TELSON (Fig. 4.25C–G): Epiproct: tip subtruncate; lateral setiferous tubercles and apical tubercles inconspicuous. Hypoproct subtrapeziform; caudal margin round, with very small and inconspicuous setiferous tubercles.

STERNA (Fig. 4.26): Cross-impressions shallow. Sternal lobe between male coxae 4 subtrapeziform; tip usually slightly round (in some specimens subemarginate), base broad and stout.

LEGS (Fig. 4.25H–J): Long and slender. Male femora 5 and 6 strongly humped ventrally in middle portion (hump of male femora 6 more developed than 5).

GONOPODS (Figs 4.27, 4.28): Coxa (cx) longer than prefemur. Cannula (ca) somewhat stout. Telopodite erect. Prefemur (pfe) ca. 2/3 as long as femur. Femur (fe) quite long and slender. Mesal sulcus (ms) and lateral sulcus (ls) conspicuous, very deep. Postfemur (pof) conspicuous, ventrally narrow and short. Solenophore (sph) well-developed: lamina lateralis (ll) conspicuous, apically crest-like, quite thin; anterolaterally with a wide and conspicuous furrow: lamina medialis (lm) well-developed; process (plm) very short; distal lobe (dlm) very long and broad, indentation between distal lobe (dlm) and broad lobe (blm) inconspicuous; broad lobe (blm) moderately thick. Solenomere (sl) long.

Distribution and habitat. This species is known only from a narrow distribution range in Phanom district. We consider *D. corythosaurus* sp. n. to be endemic for Surat Thani Province, Thailand.

Remarks. The shape of the sternal lobe between male coxae 4 is variable: the tip is emarginate in the populations from Wat Tham Wararam and Tham Nam Lod, whereas specimens from the type locality have a truncate tip. The new species shares a similar shape of gonopodal solenophore with *D. terae*.

This species is almost impossible to find at first glance. We collected all specimens that were found on the humid rock walls by using flashlight. It blended in perfectly with the brown or black rock, this way probably avoiding being detected by predators.

Coexisting species. *Desmoxytes cervina* (brown morph) at Ban Song Phi Nong, was collected from rock walls, same habitat as the new species.

Desmoxytes delfae (Jeekel, 1964)

Figs 4.29–4.35

Pratinus delfae Jeekel, 1964: 66; 1968: 51.

Desmoxytes delfae Jeekel 1980a: 654. Golovatch and Enghoff 1994: 61. Enghoff 2005: 96. Decker 2010: 28. Nguyen and Sierwald 2013: 1241.

Desmoxytes rubra Golovatch and Enghoff, 1994: 54, syn. n. Enghoff 2005: 96. Decker 2010: 30. Nguyen and Sierwald 2013: 1242.

Material examined.

Holotype: Male (NHMUK), THAILAND, Bukit Besar, on leaves in clearing, late evening, 3 September 1901.

Paratypes: 1 male, 1 female (NHMUK), 1 male (NBC), THAILAND, Bukit Besar, Nawnchila, crawling on low foliage in clearing, 2500 feet a.s.l., 29 September 1901.

Holotype (*D. rubra*): Male (ZMUC), THAILAND, Satun Province, Thale Ban National Park, lowland rainforest, on vegetation and under bark, 6°42'N, 100°10'E, ca. 400 m a.s.l., 20 October 1991, leg. M. Andersen, O. Martin, N. Scharff.

Paratypes (*D. rubra*): 6 males, 5 females (ZMUC), same data as holotype.

Further specimens, all from THAILAND,

Krabi Province: 1 female (CUMZ), Mueang Krabi District, Huai To Waterfall, 8°14'27''N, 98°54'51''E, ca. 110 m a.s.l., 16 January 2006, leg. S. Panha and ASRU members. 1 male missing right gonopod (CUMZ), Mueang Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'39''N, 98°55'27''E, ca. 85 m a.s.l., 7 October 2009, leg. S. Panha and ASRU members. 1 male (CUMZ), Mueang Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'39''N, 98°55'27''E, ca. 85 m a.s.l., 28 April 2014, leg. C. Sutcharit, R. Srisonchai and ASRU members. 5 males, 2 females (CUMZ), Mueang Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'39''N, 98°55'27''E, ca. 85 m a.s.l., 9 July 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members. 1 male, 1 female (CUMZ), Mueang Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'39''N, 98°55'27''E, ca. 85 m a.s.l., 25 July 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Nakhon Si Thammarat Province: 2 broken males (CUMZ), Nopphitam District, Krung Ching Waterfall, 8°43'27''N, 99°40'07''E, ca. 171 m a.s.l., 28 October 2006, leg. S. Panha and ASRU members. 1 female (CUMZ), Thung Song District, Talod Cave Park (Talod Cave), 8º09'32"N, 99°40'42"E, ca. 73 m a.s.l., 5 July 2017, leg. C. Sutcarit, R. Srisonchai and ASRU members. 2 males, 1 female (CUMZ), Thung Song District, Weruwan Bureau of Monks (Tham Rad), 8°02'48''N, 99°43'43''E, ca. 82 m a.s.l., 5 July 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Phatthalung Province: 2 males,1 female (CUMZ), Khao Chaison District, Khao Chaison Hot Spring, 7°26'59''N, 100°07'48''E, ca. 37 m a.s.l., 12 January 2009, leg. S.

Panha and ASRU members. 1 broken male missing gonopods, 2 females (CUMZ), Khao Chaison District, Khao Chaison Hot Spring, 7°26'59''N, 100°07'48''E, ca. 37 m a.s.l., 13 January 2009, leg. C. Sutcharit and ASRU members. 1 female (CUMZ), Khuan Khanun District, Tham Wang Thong, 7°40'57''N, 100°00'58''E, ca. 45 m a.s.l., 12 January 2009, leg. C. Sutcharit and ASRU members. 3 males, 1 female (CUMZ), Khuan Khanun District, Tham Wang Thong, 7°40'57''N, 100°00'58''E, ca. 45 m a.s.l., 6 July 2017, leg. C. Sutcharit and ASRU members. 3 males, 3 females (CUMZ), Kong Ra District, Khao Phaya Hong, 7°27'46"N, 99°57'50"E, ca. 55 m a.s.l., 6 July 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Satun Province: 1 male (ZMUC), Thale Ban National Park, lowland rainforest, 6°42''37'N, 100°10''09'E, ca. 93 m a.s.l., 15–18 October 2003, leg. ATOL expedition (ZMUC staff). 7 males, 2 females (CUMZ), Thung Wa District, Tham Khan Ti Phol, 7°05'11"N, 99°47'53"E, ca. 82 m a.s.l., 8 July 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members. 26 males, 4 females (CUMZ), 2 males, 1 female (ZMUC), 1 male (ZMUM), 1 male (NHMW) ,1 male (NHMUK), Thung Wa District, Tham Khan Ti Phol, 7°05'11"N, 99°47'53"E, ca. 82 m a.s.l., 7 July 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members. 2 males, 2 females (CUMZ), Khuan Don District, Thale Ban National Park, Tham Tone Din (Tone Din Cave), 6°43'35''N, 100°09'45''E, ca. 154 m a.s.l., 7 July 2017, leg. S. Sutcharit, R. Srisonchai and ASRU members. 1 female (CUMZ), La-ngu District, limestone mountain near Ao Noon (Mu Ko Petra National Park), 6°50'17"N, 99°45'41"E, ca. 37 m a.s.l., 31 August 2015, leg. C. Sutcharit, R. Srisonchai and ASRU members. 2 males (CUMZ), La-ngu District, limestone mountain near La-ngu Subdistrict, 6°53'41"N, 99°46'49"E, ca. 18 m a.s.l., 17 July 2017, leg. P. Danaisawadi.

Songkhla Province: 1 male missing gonopods (CUMZ), Hat Yai District, Ton Nga Chang Waterfall, 6°56'53''N, 100°14'03''E, ca. 157 m a.s.l., 12 January 2009, leg. S. Panha and ASRU members. Many broken and mixed specimens (CUMZ), Hat Yai District, Ton Nga Chang Waterfall, 6°56'53''N, 100°14'03''E, ca. 157 m a.s.l., 13 December 2011, leg. S. Panha and ASRU members. 4 males, 4 females (CUMZ), Sa Dao District, Khao Wong Pra Chan Bureau of Monks, 6°42'38''N, 100°16'34''E, ca. 100 m a.s.l., 7–8 July 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members. 2 females (CUMZ), Sa Dao District, Tham

Nang Phaya Lued Kao Bureau of Monks, 6°44'26''N, 100°15'27''E, ca. 124 m a.s.l., 7 July 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Surat Thani Province: 2 males, 1 female (CUMZ), Wiang Sa District, Khiri Rat Pattana Bureau of Monks (Wat Khao Poon), 8°31'38''N, 99°22'59''E, ca. 49 m a.s.l., 4 July 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members. 2 males, 1 female (CUMZ), Tham Phannara District, Wat Tham Kanlaya Namit, 8°30'49''N, 99°22'53''E, ca. 62 m a.s.l., 4 July 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Trang Province: 3 males, 3 females, 2 juveniles (CUMZ), Palian District, Tham Khao Ting, 7°09'31"N, 99°48'10"E, ca. 42 m a.s.l., 31 August 2015, leg. C. Sutcarit, R. Srisonchai and ASRU members. 9 males, 2 females (CUMZ), Palian District, Tham Khao Ting, 7°09'31"N, 99°48'10"E, ca. 42 m a.s.l., 8 July 2017, leg. C. Sutcarit, R. Srisonchai and ASRU members.

Yala Province: 1 male (ZMUC), Bang Lang National Park, lowland rainforest, 6°4'N, 101°11'E, ca. 400 m a.s.l., 20 October 1991, leg. M. Andersen, O. Martin, N. Scharff.

Diagnosis. Differs from congeners in the combination of the following characters; sternal lobe between male coxae 4 thick and stout, round/ subtrapeziform/ subrectangular; lamina lateralis (ll) swollen, round crest-like, laterally with a distinct and wide furrow, mesally with deep subsided surface; process (plm) of lamina medialis short, distally curving dorsad, tip blunt.

Type locality. Thailand, Bukit Besar [Thale Ban National Park, Khuan Don District, Satun Province].

The redescription hereunder is modified from Jeekel (1964), and Golovatch and Enghoff (1994). We ‘harmonized’ descriptions of all morphological characters and added some morphological characteristics from additional collected specimens.

Redescription.

SIZE: Length 21–24 mm (male), 23–27 mm (female); width of midbody metazona ca. 1.8 mm (male), 2.3 mm (female). Width of head ≥ collum < body ring 2 < 3 < 4 < 5–16, thereafter body gradually tapering towards telson.

COLOUR (Figs 4.29, 4.30A–C): In life body bright orange or brownish orange (newly moulted adults pale pink); head, paraterga, surface below paraterga and epiproct yellowish orange; metaterga bright orange; antenna brownish orange or blackish orange (except antennomere 7 blackish, distal part of antennomere 7 and antennomere 8 whitish); legs brownish orange or brownish black; a few basal podomeres whitish yellow; sterna whitish yellow or orange; prozona and metazona (metaterga) with wide black stripe, conspicuous on rings 4–19. Colour in alcohol: after 116 years changed to white, after 26 years changed to brownish white.

ANTENNAE (Fig. 4.31D): Moderately long and slender, reaching to body ring 6 (male) and 4–5 (female) when stretched dorsally.

COLLUM (Fig. 4.31A): With 1 transverse anterior row of 3+3 setae; paraterga of collum low, almost horizontal, directed almost caudad, with two setiferous notches on lateral margin.

TEGUMENT: Strongly shining and smooth; prozona finely shagreened; collum, metaterga, paraterga, sterna and epiproct smooth; surface below paraterga coarsely microgranulate.

METATERGA (Fig. 4.31A–C): With 2 transverse rows of small tubercles; metaterga 2–19 with 2+2 anterior and 2+2 posterior tubercles.

PARATERGA (Fig. 4.31E, F): Directed caudolaterad on body rings 2–17, elevated ca. 10°–20° above the horizontal plane (ca. 20° in male, ca. 10° in female), directed increasingly caudad on body rings 18 and 19; anterior margin with 2 distinct notches, on lateral margin of body rings 9, 10, 12, 13, 15–18 with tiny denticle near the tip.

TELSON (Fig. 4.32C–G): Epiproct: tip truncate; lateral setiferous tubercles usually conspicuous (in some specimens inconspicuous); apical tubercles inconspicuous. Hypoproct subtriangular; caudal margin round and narrow, with inconspicuous setiferous tubercles.

STERNA (Fig. 4.33): Cross-impressions shallow. Sternal lobe between male coxae 4 round/ subtrapeziform/ subrectangular (varies within population); erect, stout, thick, and broad when seen in ventral view; tip subtruncate/ round/ emarginate (varies within population).

LEGS (Fig. 4.32H–J): Long and slender. Male femora 5 and 6 strongly humped ventrally in middle portion.

GONOPODS (Figs 4.34, 4.35): Coxa (cx) longer than prefemur. Cannula (ca) long and slender. Prefemur (pfe) ca. 2/3 as long as femur. Femur (fe) quite long. Mesal sulcus (ms) and lateral sulcus (ls) conspicuous, deep and wide. Postfemur (pof) conspicuous, ventrally narrow, and short. Solenophore (sph) well-developed: lamina lateralis (ll) swollen, round crest-like, laterally with a distinct furrow, mesally with deep subsided surface; ventral ridge (vrl) conspicuous: lamina medialis (lm) well-developed; process (plm) short, distally curving dorsad, tip blunt; distal lobe (dlm) distally with two lamellae, mesal lamella thin and smaller than lateral one; broad lobe (blm) somewhat thick, distinctly separated from distal lobe (dlm) by a deep and wide indentation. Solenomere (sl) long.

Distribution and habitat. *Desmoxytes delfae* is known from several provinces in southern Thailand. All new specimens were collected by us from limestone habitats (the recorded locations in previous papers are also limestone); most specimens were seen crawling on leaf litter and climbing on branches of trees (Fig. 4.30D).

The type locality, Bukit Besar, may be part of what is now Thale Ban National Park in Khuan Don District, Satun Province, and refers to the big mountain which is probably Khao Chin (ca. 2500 ft. or 756 m). Specimens collected by us from Thale Ban National Park may thus be topotypes. The other paratype locality (Bukit Besar, Nawnchila) has not been exactly located, but it is probably near Thale Ban National Park (Thailand–Malaysia border), possibly close to the type locality.

We assume that *D. delfae* is distributed mainly in Thailand and possibly south to Malaysia near the Thailand–Malaysia border.

This species was reported as endemic for Thailand (Decker 2010), and we would agree that it should be regarded as endemic for the southern part of Thailand due to its narrow distribution. However, two males of *D. delfae* were reported from Khaosok National Park in west of Surat Thani Province by Decker (2010); it is probable that the specimens from this location belong to another species because all the specimens of *D. delfae* which we have seen are from an area in south Thailand (Krabi, east of Surat Thaini, Nakhon Si Thammarat, Phatthalung, Satun, Songkhla, and Yala Provinces). Furthermore, Decker (2010) also identified one male, which was collected from Nakhon Si Thammarat Province (Lan Saka District, Khao Luang National Park, near Karom Waterfall) as *D. rubra*. Re-examination of those specimens in MHNG is necessary to evaluate the distribution of this species.

Remarks. The remarkable and vivid bright orange colouration is clearly aposematic.

Golovatch and Enghoff (1994) distinguished *D. rubra* from *D. delfae* based on *D. rubra* having 1+1 anterior and 2+2 posterior metatergal tubercles, the mid-dorsal (axial) line traceable, the sternal lobe between male coxae 4 roundly subtriangular and lamina medialis (lm) more strongly produced mesally than dorsally. After examination of all type material and new specimens of both *D. delfae* and "*D. rubra"* collected by us, we found that:

- There is a variation in the size of tubercles on metaterga (metaterga with two rows of 2+2 anterior and 2+2 posterior tubercles, lateral tubercles of anterior row in some specimens (tiny and very inconspicuous).

- All specimens are without mid-dorsal line.

- The sternal lobe between male coxae 4 is highly variable in shape, even within populations, as round/ subtrapeziform/ subrectangular; we found this variation in both *D. delfae* and "*D. rubra"* specimens. Its tip also varies as subtruncate/ round/ emarginate.

- SEM images clearly show that specimens of these two nominal species have identical gonopods, especially in details of lamina lateralis and lamina medialis.

Due to this variation, we have synonymized *D. rubra* under *D. delfae*.

Jeekel (1964) described this species as lacking a tiny denticle near the tip of paraterga on the lateral margin of rings 9, 10, 12, 13, 15–18, and collum as having 2 rows of 3+3 conspicuous setae (anterior row) and 1?+1? inconspicuous tubercles (posterior row). All specimens studied by us have a tiny denticle near the tip (conspicuous in some specimens, inconspicuous in others), and we regard this character as variable within populations.

For *D. rubra*, Golovatch and Enghoff (1994) described the colour of alcohol-preserved specimens as bright pinkish, that of living specimens as bright red, collum with 3 rows of setae (anterior conspicuous, intermediate and posterior inconspicuous), mid-dorsal line traceable. Based on the re-examination of type material of *D. rubra* and examination of newly collected specimens we have found that *D. rubra* (= *D. delfae*) exhibits:

- Specimens in life with bright orange colouration, newly moulted adult stage pinkish or pinkish orange, late adult stage reddish orange or dark orange. As Golovatch and Enghoff (1994) reported that living specimens have a bright red colour, it is possible that the type specimens of *D. rubra* were collected at late adult stage (red = reddish orange?).

- Collum with one row of setae (3+3 anterior setae), intermediate and posterior rows absent. Therefore, we here report collum with only one row of setae (3+3 anterior setae).

- All specimens without mid-dorsal line.

- Sternal lobe between male coxae 4 varies within population, round/ subtrapeziform/ subrectangular.

As we mentioned above, this species shows high variability in morphology, e.g., colour, rows of setae on collum, size of metatergal tubercles, occurrence of a tiny denticle near tip of paraterga, shape of sternal lobe between male coxae 4. All variations are typically present within a population. Although there are deviations in several morphological characters, interestingly, gonopod characters of all specimens are quite stable, looking exactly the same in details.

Coexisting species. *Desmoxytes cervina* in several places, *D. terae* at Tham Tone Din, *D. flabella* sp. n. at Tham Khao Ting and Tham Khan Ti Phol.

***Desmoxytes des* Srisonchai, Enghoff and Panha, 2016**

Fig. 4.36

Desmoxytes des Srisonchai, Enghoff and Panha, 2016: 94.

Material examined.

Holotype: Male (CUMZ), THAILAND, Chiang Mai Province, Fang District, Doi Angkhang, near Royal Agricultural Station, 19°54'26"N, 99°02'26"E, ca. 1426 m a.s.l., 12 August 2014, leg. N. Likhitrakarn.

Paratypes: 2 males, 2 females (CUMZ), same data as holotype. 1 male, 2 females (CUMZ), THAILAND, Chiang Mai Province, Chiang Dao District, Wat Tham Krab, 19°33'32"N, 99°03'47"E, ca. 622 m a.s.l., 25 October 2015, leg. C. Sutcharit, R. Srisonchai, T. Seesamut and A. Pholyotha.

Type locality. THAILAND, Chiang Mai Province, Fang District, Doi Angkhang, near Royal Agricultural Station.

Diagnosis. Differs from all other *Desmoxytes* species by the combination of the following characters: paraterga knife-like; lateral sulcus (ls) of gonopod shallow; lamina lateralis (ll) separated into two ridges by a deep and wide furrow; process (plm) of lamina medialis long and thin, lamellar, tip dentate or crenate; distal lobe (dlm) of lamina medialis quite long, tip directed ventroanteriad; caudal margin of hypoproct concave or truncate.

Redescription (updated from Srisonchai *et al.* 2016).

SIZE: Length 26–34 mm (male), 30–34 mm (female); width of midbody metazona ca. 2.5 mm (male), 3.0 mm (female). Width of head < collum < body ring 2 = 3 < 4 ≤ 5 < 6–16, thereafter body gradually tapering toward telson.

COLOUR: In life with body dark brown; paraterga bright pink; head, metaterga and surface below paraterga dark brown; antenna (except distal part of antennomere 7 and antennomere 8 whitish), leg, sterna and epiproct brown; a few basal podomeres pinkish brown or brown. Colour in alcohol: after two years changed to dark brown or pale brown.

ANTENNAE: Quite short, reaching to body ring 3 or 4 (male), and 3 (female) when stretched dorsally.

COLLUM: With 3 transverse rows of setiferous tubercles, 3+3 anterior, 1+1 posterior setae (posterior setae inconspicuous); paraterga of collum low, elevated at ca. 20°–30°, directed almost caudolaterad, with two inconspicuous setiferous notches on lateral margin.

TEGUMENT: Quite dull, but slightly shining; prozona finely shagreened; metaterga and surface below paraterga coarsely microgranulate; collum, paraterga, sterna and epiproct smooth.

METATERGA: With 2 transverse rows of setiferous tubercles; metaterga 2–18 with 2+2 anterior and 2+2 posterior tubercles; metatergum 19 with 2+2 anterior and 2+2 posterior setae.

PARATERGA: Directed caudolaterad on body rings 2–16, elevated at ca. 45° (male) 40° (female); directed increasingly caudad on body rings 17, 18 and 19; anterior margin with 2 distinct notches, on lateral margin of body rings 9, 10, 12, 13, 15–18 with tiny denticle near the tip.

TELSON: Epiproct: tip truncate; lateral setiferous tubercles conspicuous, small; apical tubercles inconspicuous. Hypoproct subtrapeziform; caudal margin quite concave or truncate, with inconspicuous setiferous tubercles.

STERNA: Cross-impressions shallow. Sternal lobe between male coxae 4 swollen, subrectangular, flat when seen in lateral view, tip truncate.

LEGS: Long and slender. Male femora 5 and 6 slightly stout, moderately humped ventrally in middle part.

GONOPODS (Fig. 4.36): Coxa (cx) longer than prefemur. Cannula (ca) slender. Telopodite quite stout. Prefemur (pfe) half to 2/3 as long as femur. Femur (fe) slightly stout. Mesal sulcus (ms) very deep and narrow, lateral sulcus (ls) shallow (= “poorly developed” in Srisonchai *et al.* 2016). Postfemur (pof) conspicuous, ventrally narrow. Solenophore (sph) well-developed: lamina lateralis (ll) swollen, laterally with a conspicuous, deep and wide furrow (= sulcus) separating ll into two ridges (inner ridge larger than outer one): lamina medialis (lm) well-developed; process (plm) lamellar, slightly short and thin, base long, tip dentate or crenate, indistinctly separated from distal lobe; distal lobe (dlm) quite long, tip directed ventroanteriad; broad lobe (blm) thick, indentation between broad lobe (blm) and distal lobe (dlm) inconspicuous. Solenomere (sl) quite long, distally twisted.

Distribution and habitat. Known only from the type locality and nearby areas. This species seems to be rare because we made intensive surveys again in 2015 and 2016, no further specimens were found. As mentioned by Srisonchai *et al.* (2016), *D. des* is known only from two localities (Doi Angkhang and Wat Tham Krab), and we consider it to be endemic to Thailand.

Remarks. This species exhibits some variation in the gonopods: the tip of process (plm) of lamina lateralis is dentate in some specimens, crenate in others.

D. des is easy to discriminate from other dragon millipedes by the distinct shape of paraterga and unique gonopod characters.

Coexisting species. None known.

Corrections to Srisonchai *et al.* (2016). Srisonchai *et al.* (2016, pp. 99–103) wrote in the description of this species that paraterga (including paraterga of collum) are directed dorsolaterad at ca. 30°. They are in fact directed caudolaterad and are elevated at ca. 45° as stated in the updated redescription above. Moreover, Srisonchai *et al.* also described the surface of metaterga as finely shagreened, but we now regard it as being coarsely microgranulate.

***Desmoxytes euros* Srisonchai, Enghoff and Panha sp. n.**

Figs 4.37–4.42

Holotype: Male (CUMZ), THAILAND, Chanthaburi Province, Kaeng Hang Maeo District, Khao Wong Kot Cave, 12°53'53"N, 101°49'00"E, ca. 53 m a.s.l., 4 August 2016, leg. S. Panha, P. Tongkerd ans ASRU members.

Paratypes: 13 males, 5 females (CUMZ), same data as holotype. 3 males, 4 females (CUMZ), 2 males, 1 female (ZMUC), 1 male (NHMW), THALAND, Rayong Province, Khao Chamao District, Wat Tham Suwan Phupha, 12°59'16"N, 101°39'32"E, ca. 64 m a.s.l., 8 August 2017, leg. P. Tongkerd and ASRU members.

Further specimens, not paratypes, all from THAILAND,

Chantaburi Province: 1 male, 1 female (CUMZ), Kaeng Hang Maeo District, Khao Wong Kot Cave, 12°53'53"N, 101°49'00"E, ca. 53 m a.s.l., 15 September 2009, leg. S. Panha and ASRU members. 1 male, 1 female (CUMZ), Kaeng Hang Maeo District, Khao Wong Kot Cave, 12°53'53"N, 101°49'00"E, ca. 53 m a.s.l., 1 October 2009, leg. S. Panha and ASRU members. 2 males, 1 female (CUMZ), Kaeng Hang Maeo District, near Khao Wong Kot Cave, 12°53'53"N, 101°49'00"E, ca. 53 m a.s.l., 15 October 2010, leg. S. Panha and ASRU members. 1 male, 2 females (CUMZ), Kaeng Hang Maeo District, near Khao Wong Kot Cave, 12°53'53"N, 101°49'00"E, ca. 53 m a.s.l., 24 October 2010, leg. S. Panha and ASRU members. 4 males, 4 females, 2 juveniles (CUMZ), Kaeng Hang Maeo District, Khao Wong Kot Cave, 12°53'53"N, 101°49'00"E, ca. 53 m a.s.l., 17 October 2015, leg. C. Sutcharit and R. Srisonchai. 1 female (CUMZ), Kaeng Hang Maeo District, Khao Wong Kot Cave, 12°53'53"N, 101°49'00"E, ca. 53 m a.s.l., 8 August 2017, leg. S. Panha, P. Tongkerd ans ASRU members. 5 males, 3 females (CUMZ), Kaeng Hang Maeo District, Khao Sip Ha Chan National Park, 13°10'33"N, 102°00'09"E, ca. 118 m a.s.l., 7 October 2010, leg. S. Panha and ASRU members. 2 males, 1 female (CUMZ), Khlung District, Makok Waterfall, 12°35'14"N, 102°15'21"E, ca. 58 m a.s.l., 3 September 2007, leg. ASRU members. 1 male, 1 female (CUMZ), Khlung District, Makok Waterfall, 12°35'14"N, 102°15'21"E, ca. 59 m a.s.l., 3 September 2007, leg. ASRU members. 3 males, 3 females, 4 females (CUMZ), Khlung District, Makok Waterfall, 12°35'14"N, 102°15'21"E, ca. 58 m a.s.l., 10 August 2014, leg. ASRU members. 5 males, 3 females (CUMZ), Mueang Chantaburi District, Phlio Waterfall, 12°31'44"N 102°10'57"E, ca. 104 m a.s.l., 19 October 2015, leg. S. Panha and ASRU members. 2 males, 2 females (CUMZ), Tha Mai District, Wat Khao Su Kim (Khao Su Kim Temple), 12°45'47"N, 102°01'56"E, ca. 148 m a.s.l., 29 September 2009, leg. S. Panha and ASRU members. 3 males, 5 females (CUMZ), Tha Mai District, Wat Khao Su Kim (Khao Su Kim Temple), 12°45'47"N, 102°01'56"E, ca. 148

m a.s.l., 14 October 2010, leg. S. Panha and ASRU members. 2 males, 2 females (CUMZ), Tha Mai District, Wat Khao Su Kim (Khao Su Kim Temple), 12°45'47"N, 102°01'56"E, ca. 148 m a.s.l., 6 August 2011, leg. S. Panha and ASRU members. 2 males, 1 female, 1 juvenile (CUMZ), Tha Mai District, Wat Khao Su Kim (Khao Su Kim Temple), 12°45'47"N, 102°01'56"E, ca. 148 m a.s.l., 8 August 2017, leg. S. Panha, P. Tongkerd and ASRU members.

Chonburi Province: 2 males, 3 females (CUMZ), Bo Thong District, Wat Tham Khao Cha-ang Oune, 13°12'35"N, 101°39'09"E, ca. 151 m a.s.l., 15 September 2009, leg. ASRU members. 2 males, 3 females (CUMZ), Bo Thong District, Wat Tham Khao Cha-ang Oune, 13°12'35"N, 101°39'09"E, ca. 151 m a.s.l., 15 October 2010, leg. ASRU members. 2 males (CUMZ), Bo Thong District, Wat Tham Khao Cha-ang Oune, 13°12'35"N, 101°39'09"E, ca. 151 m a.s.l., 24 September 2012, leg. S. Panha and ASRU members. 2 males, 2 females (CUMZ), Bo Thong District, Wat Tham Khao Cha-ang Oune, 13°12'35"N, 101°39'09"E, ca. 151 m a.s.l., 6 July 2016, leg. A. Pholyotha and ASRU members. 1 male, 1 female (CUMZ), Bo Thong District, Wat Tham Khao Cha-ang Oune, 13°12'35"N, 101°39'09"E, ca. 151 m a.s.l., 25 October, leg. ASRU members.

Rayong Province: 1 male, 1 female (CUMZ), Khao Chamao District, Wat Tham Watana Monkhol, 13°05'45"N, 101°36'28"E, ca. 76 m a.s.l., Unknown date, leg. S. Panha and ASRU members. 3 males (CUMZ), Khao Chamao District, Wat Tham Khao Loy (Wat Ma Duae), 13°03'26"N, 101°36'28"E, ca. 71 m a.s.l., 5 September 2008, leg. S. Panha and ASRU members. 1 male, 1 female (CUMZ), Khao Chamao District, Wat Tham Khao Loy (Wat Ma Duae), 13°03'26"N, 101°36'28"E, ca. 71 m a.s.l., 23 October 2010, leg. S. Panha and ASRU members. 1 male, 3 females (CUMZ), Khao Chamao District, Wat Tham Khao Loy (Wat Ma Duae), 13°03'26"N, 101°36'28"E, ca. 71 m a.s.l., 9 November 2013, leg. S. Panha and ASRU members. 1 male, 1 female (CUMZ), Khao Chamao District, Tham Khao Pratun Monastery, 13°07'26"N, 101°35'52"E, ca. 107 m a.s.l., 24 October 2010, leg. S. Panha and ASRU members. 1 male, 1 female (CUMZ), Khao Chamao District, Khlong Pra Kang Waterfall, 12°55'59"N, 101°42'58"E, ca. 69 m a.s.l., 15 September 2009, leg. S. Panha and ASRU members. 1 male, 1 female (CUMZ), Khao Chamao District, Tham Khao Boath Bureau of Monks, 13°02'13"N, 101°38'08"E, ca. 102 m a.s.l., 23 October 2010, leg. S. Panha and ASRU members. 2 males, 2 females (CUMZ), Khao Chamao

District, Wat Nong Tha Khian, 12°57'49"N, 101°40'24"E, ca. 64 m a.s.l., 5 September 2008, leg. C. Sutcharit and ASRU members. 1 male, 1 female (CUMZ), Khao Chamao District, Wat Tham Khao Chamao, 23 October 2008, leg. C. Sutcharit and ASRU members.

Sa Kaeo Province: 1 male, 1 female (CUMZ), Khlong Hat District, Phet Pho Thong Cave, 13°24'50"N, 102°19'33"E, ca. 240 m a.s.l., 28 October 2010, leg. C. Sutcharit and ASRU members. 1 male, 1 female (CUMZ), Khao Chakan District, near Wat Tham Khao Chakan, 13°39'40"N, 102°05'11"E, ca. 75 m a.s.l., 28 August 2014, leg. S. Panha and ASRU members. 2 males, 1 female (CUMZ), Khlong Hat District, Phet Pho Thong Cave, 13°24'50"N, 102°19'33"E, ca. 240 m a.s.l., 28 August 2014, leg. S. Panha and ASRU members. 1 male, 3 females (CUMZ), Khao Chakan District, near Wat Tham Khao Chakan, 13°39'40"N, 102°05'11"E, ca. 75 m a.s.l., 3 September 2015, leg. S. Panha and ASRU members.

Diagnosis. Body black or brownish black; collum with 3 transverse rows of setae and setiferous tubercles (4+4 anterior setae, 1+1 intermediate setae and 2+2 posterior tubercles); metaterga 2–16 with two rows of 2+2 (anterior) setiferous cones and 2+2 (posterior) setiferous spines; ventral ridge (vrl) of lamina lateralis conspicuous; process (plm) of lamina medialis long, directed almost mesad; distal lobe (dlm) distally with two distinct lamellae. Similar in these respects to *D. planata*, but differs from that species by having paraterga yellow to orange and hypoproct subtriangular with conspicuous setiferous tubercles.

Etymology. "*Euros*" (noun in apposition) is the name of the ancient Greek god of the east wind; the name refers to the occurrence of this species in the eastern part of Thailand.

Description.

SIZE: Length 25–27 mm (male), 28–29 mm (female); width of midbody metazona ca. 1.6 mm (male), 2 mm (female). Width of head < collum = body ring 2 < 3 = 4 < 5–16, thereafter body gradually tapering towards telson.

COLOUR (Fig. 4.37A–D): In life with body dark or brownish black; paraterga yellow to orange; head, antenna, metaterga and surface below paraterga dark brown (except distal part of antennomere 7 and antennomere 8 whitish); epiproct, sterna and a few basal podomeres brown to whitish; legs otherwise brown.

ANTENNAE (Fig. 4.38D): Moderately long and slender, reaching to body ring 6 (male) and 5 (female) when stretched dorsally.

COLLUM (Fig. 4.38A): With 3 transverse rows of setae and setiferous tubercles, 4+4 anterior setae, 1+1 intermediate setae and 2+2 posterior tubercles (lateral seta in anterior row located almost at base of paraterga in some specimens); paraterga of collum low, elevated at ca. 15°–20°, directed caudolaterad, with one inconspicuous notch on lateral margin.

TEGUMENT: Quite dull, slightly shining; collum and metaterga microgranulate; prozona finely shagreened; surface below paraterga finely microgranulate; sterna and epiproct smooth.

METATERGA (Fig. 4.38A–C): With 2 transverse rows of setiferous tubercles, cones and spines; metaterga 2–8 with 2+2 anterior cones and 2+2 posterior spines; metaterga 9–16 with 2+2 anterior cones and 2+2 posterior spines; metaterga 17–18 with 2+2 anterior and 2+2 posterior cones; metatergum 19 with 2+2 anterior and 2+2 posterior tubercles.

PARATERGA (Fig. 4.38E, F): Directed caudolaterad on body rings 2–17, elevated at ca. 45° (male) 40° (female); directed increasingly caudad on body rings 18 and 19; anterior margin with 2 distinct notches, on lateral margin of body rings 9, 10, 12, 13, 15–18 with tiny denticle near the tip.

TELSON (Fig. 4.39C–G): Epiproct: tip emarginate; lateral setiferous tubercles and apical tubercles conspicuous. Hypoproct subtriangular; caudal margin subtriangular, with conspicuous setiferous tubercles.

STERNA (Fig. 4.40): Cross-impressions shallow. Sternal lobe between male coxae 4 swollen, base stout, slightly attenuated near tip, knob-like when seen in lateral view, tip subtruncate.

LEGS (Fig. 4.39H–J): Long and slender. Male femora 5 and 6 moderately humped ventrally in middle portion.

GONOPODS (Figs 4.41, 4.42): Coxa (cx) longer than prefemur. Cannula (ca) long and slender. Prefemur (pfe) ca. 2/3 as long as femur. Femur (fe) long and slender. Mesal sulcus (ms) and lateral sulcus (ls) conspicuous, very deep. Postfemur (pof) conspicuous, ventrally narrow and short. Solenophore (sph) well-developed: lamina lateralis (ll) well-developed, inner surface subsided, anterolaterally with an inconspicuous furrow; with conspicuous ventral ridge (vrl): lamina medialis (lm) well-developed; process (plm) long, tip blunt, directed mesad; distal lobe (dlm) distally with two distinct lamellae (equal in size); broad lobe (blm) dorsally thick at the edge, with a wide and conspicuous indentation between broad lobe (blm) and distal lobe (dlm). Solenomere (sl) very long.

Distribution and habitat. Known only from east Thailand (Chantaburi, Chonburi, Sa Kaeo and Rayong Provinces). Interestingly, this species exists in both limestone areas and granitic mountains. It was seen crawling on rocks during the rainy season and occurs only in natural habitat inside primary forest. On the basis of current data, the distribution area is quite narrow, and the species seems to be restricted to the eastern part of Thailand. We thus regard *D. euros* sp. n. to be an endemic for the Thai fauna.

Remarks. The observation of all living specimens reveals variation on colour of paraterga within a population; yellow in some specimens, yellowish orange to orange in others.

Desmoxytes euros sp. n. strongly resembles *D. planata* in several morphological characters (except for the characters mentioned in the diagnosis); notably the gonopod characters are identical. However, our initial study on DNA barcoding gene (COI) revealed that *D. planata* and the new species are separated enough to support the suggestion that *D. planata* and the new species are indeed different species (paper in preparation).

Because of the similarity in gonopod morphology, it is difficult to discriminate old material of *D. planata* and *D. euros* sp. n. However, they can be distinguished by colour of paraterga (yellow or yellow orange in *D. euros* sp. n., pink in *D. planata*), and by characters of hypoproct (subtriangular in *D. euros* sp. n., subtrapeziform in *D. planata*).

We kept several adults in an acrylic box with litter at room temperature. Two weeks later, we found a nest with eggs and a cluster of stadium 1 juveniles at ca. 2 cm depth in the soil and leaf litter (Fig. 4.37E, F).

Coexisting species. None known.

***Desmoxytes flabella* Srisonchai, Enghoff and Panha sp. n.**

Figs 4.43–4.48

Holotype: Male (CUMZ), THAILAND, Trang Province, Palian District, Tham Khao Ting, 7°09'31"N, 99°48'10"E, ca. 42 m a.s.l., 8 July 2017, leg. C. Sutcarit, R. Srisonchai and ASRU members.

Paratypes: 13 males, 4 females (CUMZ), 1 male, 1 female (ZMUC), 1 male (ZMUM), 1 male (NHMW), 1 male (NHMUK), same data as holotype. 3 males, 3 females, 2 juveniles (CUMZ), THAILAND, Trang Province, Palian District, Tham Khao Ting, 7°09'31"N, 99°48'10"E, ca. 42 m a.s.l., 31 August 2015, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Further specimens, not paratypes: 7 males, 3 females (CUMZ), THAILAND, Satun Province, Thung Wa District, Tham Khan Ti Phol, 7°05'08"N, 99°47'54"E, ca. 80 m a.s.l., 8 July 2017, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Diagnosis. Collum with one row of 3+3 setae (anterior row); paraterga wing-like (not knife-shaped); metaterga 2–19 with 2+2 tubercles in anterior row and 2+2 tubercles in posterior row; male femora 5 and 6 modified; lamina lateralis (ll) distally rough, anterolaterally with 2–3 distinct furrows; process (plm) of lamina medialis very short. Similar in these respects to *D. perakensis* sp. n. Differs from that species by having body black or brownish black contrasting with yellowish brown paraterga; paraterga narrower; process (plm) of lamina medialis indistinctly demarcated from distal lobe (dlm); distal lobe (dlm) of lamina medialis with one lamella.

Etymology. The name is a Latin noun, referring to the shape of process (plm) and the distal lobe (dlm) on lamina medialis which somewhat resemble a handheld fan or flyswatter.

Description.

SIZE: Length 32–35 mm (male), 34–36 mm (female); width of midbody metazona ca. 2.2 mm (male), 2.5 mm (female). Width of head < collum = body ring 2 = 3 = 4 < 5–16, thereafter body gradually tapering toward telson.

COLOUR (Fig. 4.43A–C): In life with body brownish black or black; metaterga and antenna black (except distal part of antennomere 7 and antennomere 8 whitish); surface below paraterga, head and epiproct brownish black; paraterga yellowish brown; sterna and legs brown; a few basal podomeres brownish white.

ANTENNAE (Fig. 4.44D): Moderately long and slender, reaching to body ring 6 (male) and 4–5 (female).

COLLUM (Fig. 4.44A): With 1 transverse anterior row of 3+3 setae; paraterga of collum low, elevated at ca. 10°–15°, directed caudolaterad, with 2 distinct notches on lateral margin.

TEGUMENT: Moderately shining; collum and metaterga coarsely microgranulate; prozona finely shagreened; surface below paraterga coarsely microgranulate; sterna and epiproct smooth.

METATERGA (Fig. 4.44A–C): With 2 transverse rows of conspicuous tubercles; metaterga 2–19 with 2+2 anterior and 2+2 posterior tubercles.

PARATERGA (Fig. 4.44E, F): Directed caudolaterad on body rings 2–17, elevated at ca. 45° (male) 45° (female); directed increasingly caudad on body rings 18 and 19; anterior margin with 2 distinct notches, on lateral margin of body rings 9, 10, 12, 13, 15–18 with tiny denticle near the tip.

TELSON (Fig. 4.45C–G): Epiproct: tip emarginate; lateral setiferous tubercles inconspicuous; apical tubercles conspicuous, small, knob-like. Hypoproct subtrapeziform, broad; caudal margin round, with two conspicuous setiferous tubercles.

STERNA (Fig. 4.46): Cross-impressions shallow. Sternal lobe between male coxae 4 swollen, suberect, subtrapeziform when seen in posterior view, tip usually truncate (in some specimens slightly round).

LEGS (Fig. 4.45H–J): Long and slender. Male femora 5 and 6 strongly humped ventrally in middle portion.

GONOPODS (Figs 4.47, 4.48): Coxa (cx) subequal in length to prefemur. Cannula (ca) quite long and slender. Telopodite quite stout. Prefemur (pfe) ca. 2/3 as long as femur. Femur (fe) somewhat stout, slightly enlarged distally. Mesal sulcus (ms) and lateral sulcus (ls) conspicuous, very deep. Postfemur (pof) conspicuous, ventrally narrow and short. Solenophore (sph) well-developed: lamina lateralis (ll) rough, anterolaterally with 2–3 distinct furrows, deep; ventral ridges (vrl) conspicuous: lamina medialis (lm) well-developed; process (plm) very short, indistinctly demarcated from distal lobe; distal lobe (dlm) distally with one lamella; broad lobe (blm) thick, clearly demarcated from distal lobe (dlm) by a narrow and deep indentation. Solenomere (sl) long, apically twisted.

Distribution and habitat. Known only from the type locality and a few nearby localities. The new species is restricted to limestone habitats (Fig. 4.43D), and it is sympatric with *D. delfae* at Tham Khao Ting and Tham Khan Ti Phol. Unlike the bright orange *D. delfae*, which was easily spotted crawling on branches of shrubs and on rocks, the new species, blackish brown, was found on rocks where it was quite hard to see. This suggests that these two species, although sharing the same habitat, may show microhabitat differences, but this has not yet been studied in detail. We assume that the new species is distributed along limestone mountain ranges in a narrow area at the border between Trang and Satun Provinces. This species should be regarded as endemic to the Thai fauna.

Coexisting species. *Desmoxytes delfae* co-occurs at the same localities.

***Desmoxytes golovatchi* Srisonchai, Enghoff and Panha sp. n.**

Figs 4.49–4.54

Holotype: Male (CUMZ), THAILAND, Kanchanaburi Province, Thong Pha Phum District, Prang Ka Sri Temple, 14°39'05"N, 98°40'08"E, ca. 107 m a.s.l., 15 August 2016, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Paratypes: 19 males (CUMZ), 2 males (ZMUC), 1 male (ZMUM), 1 male (NHMW), 1 male (NHMUK), same data as holotype.

Further specimens, not paratypes, all from THAILAND, Kanchanaburi Province,

Thong Pha Phum District: 4 males (CUMZ), Tham Khao Noi Bureau of Monks (Wat Tham Khao Noi), 14°41'55"N, 98°31'33"E, ca. 225 m a.s.l., 21 August 2015, leg. E. Jeratthitikul and R. Srisonchai. 3 males, 1 female (CUMZ), Tham Khao Noi Bureau of Monks (Wat Tham Khao Noi), 14°41'55"N, 98°31'33"E, ca. 225 m a.s.l., 15 August 2016, leg. C. Sutcharit, R. Srisonchai and ASRU members. 6 males, 1 female (CUMZ), Wat Huay Charoen Srattha Tham, 14°39'27"N, 98°31'38"E, ca. 202 m a.s.l., 11 October 2015, leg. C. Sutcharit and R. Srisonchai. 1 female (CUMZ), Huay Kayeng Subdistrict, Tham Pong Chang Monastery, 14°44'38"N, 98°30'26"E, ca. 209 m a.s.l., 11 October 2015, leg. C. Sutcharit and R. Srisonchai. 3 males, 5 females (CUMZ), Wat Pak Lam Philok, 14°37'39"N, 98°34'27"E, ca. 280 m a.s.l., 11 October 2015, leg. C. Sutcharit and R. Srisonchai. 4 males, 1 female (CUMZ), Prang Ka Sri temple, 14°39'05"N, 98°40'08"E, ca. 107 m a.s.l., 24 July 2016, leg. P. Pimvichai and P. Prasankok.

Sai Yok District: 2 males, 2 females (CUMZ), Daowadueng Cave, 14°28'23"N, 98°50'04"E, ca. 132 m a.s.l., 15 August 2016, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Diagnosis. Metaterga 2–8 with 2+2 tubercles/cones/spines in anterior row and 2+2 tubercles/cones/spines in posterior row; metaterga 9–19 with 3+3 tubercles/cones/spines in posterior row. Similar in these respects to *D. breviverpa*, *D. purpurosea*, *D. takensis* and *D. taurina*. Differs from those by having: metaterga 9–19 with two rows of 3(2)+3(2) tubercles/cones/spines in anterior row; lamina lateralis (ll) round and compact; tip of process (plm) of lamina medialis terminating in a sharp spine; distal lobe (dlm) of lamina medialis long; broad lobe (blm) dorsally expanded.

Etymology. The name honours Sergei I. Golovatch, a myriapodologist at the Institute for Problems of Ecology and Evolution, Russian Academy of Sciences, who has enthusiastically encouraged millipede research in Thailand, in recognition of his extensive work on the taxonomy of millipedes – especially in family Paradoxosomatidae.

Description.

SIZE: Length 27–31 mm (male), 32 mm (female); width of midbody metazona ca. 1.9 mm (male), 2.3 mm (female). Width of head < collum < body ring 2 = 3 = 4 < 5–16, thereafter body gradually tapering towards telson.

COLOUR (Fig. 4.49A–C): In life with body vivid pink; paraterga, metaterga, surface below paraterga and epiproct pink; head brown; antenna black, except distal part of antennomere 7 and antennomere 8 whitish; sterna and legs pinkish brown; a few basal podomeres brown to whitish.

ANTENNAE (Fig. 4.50D): Very long and slender, reaching to body ring 7 (male) and 5 (female) when stretched dorsally.

COLLUM (Fig. 4.50A): With 3 transverse rows of setae and setiferous tubercles, 4+4 anterior setae, 1+1 intermediate setae and 2+2 posterior tubercles (lateral seta in anterior row located almost at base of paraterga in some specimens; lateral tubercles in posterior row located almost halfway to intermediate row); paraterga of collum low, elevated at ca. 15°–20°, directed caudolaterad, with one conspicuous notch on lateral margin.

TEGUMENT: Slightly shining; collum and metaterga microgranulate; prozona finely shagreened; surface below paraterga finely microgranulate; sterna and epiproct relatively smooth.

METATERGA (Fig. 4.50A–C): With 2 transverse rows of setiferous tubercles, cones and spines; metaterga 2–8 with 2+2 anterior cones and 2(3)+2(3) posterior spines; metaterga 9–17 with 3(2)+3(2) anterior cones and 3(4)+3(4) posterior spines; metatergum 18 with with 3+3 anterior cones and 3+3 posterior cones; metatergum 19 with with 3+3 anterior tubercles and 3+3 posterior tubercles.

PARATERGA (Fig. 4.50E, F): Directed caudolaterad on body rings 2–17, elevated at ca. 45° (male) 40° (female); directed increasingly caudad on body rings 18 and 19; anterior margin with 2 distinct notches, on lateral margin of body rings 9, 10, 12, 13, 15–18 with tiny denticle near the tip.

TELSON (Fig. 4.51C–G): Tip subtruncate; lateral setiferous tubercles inconspicuous, apical tubercles small and inconspicuous. Hypoproct subtrapeziform; caudal margin round, with small inconspicuous setiferous tubercles.

STERNA (Fig. 4.52): Cross-impressions shallow. Sternal lobe between male coxae 4 subtrapeziform; base slightly enlarged; tip emarginate; swollen near pores.

LEGS (Fig. 4.51H–J): Long and slender. Male femora 5 and 6 strongly humped ventrally in middle portion.

GONOPODS (Figs 4.53, 4.54): Coxa (cx) longer than prefemur. Cannula (ca) slender. Prefemur (pfe) ca. 2/3 as long as femur. Femur (fe) long, slightly curved. Mesal sulcus (ms) and lateral sulcus (ls) conspicuous, deep. Postfemur (pof) conspicuous, ventrally wide. Solenophore (sph) well-developed: lamina lateralis (ll) round and compact (obvious when seen in ventral view): lamina medialis (lm) well-developed; process (plm) somewhat short, tip terminating in a sharp spine (in some specimens with a tiny spine-like process situated between process (plm) and distal lobe (dlm)); distal lobe (dlm) quite long, distally with two indistinctly separated lamellae; broad lobe (blm) dorsally expanded, indentation between broad lobe (blm) and distal love (dlm) very wide and shallow. Solenomere (sl) relatively long.

Distribution and habitat. Known from the type locality and nearby areas in Kanchanaburi Province only. The type locality is situated on a small, isolated limestone mountain near Khwae Noi river. All specimens were found in limestone habitats (Fig. 4.49D).

This species is distributed along the limestone mountain ranges in Sai Yok and Thong Pha Phum districts. Based on many intensive surveys, the current distribution of the new species is evidently quite narrow, ca. 100 km^2. Thus, *D. golovatchi* sp. n. should be regarded as a Thai endemic.

Remarks. *Desmoxytes golovatchi* sp. n. is aposematic in its vivid pink body. During the field trips, this animal was noticeable by the contrast of its bright colour to green leaves or brown rocks, it thus was easy to see and collect after rain.

This species is morphologically similar to *D. breviverpa*, *D. purpurosea*, *D. takensis,* and *D. waepyanensis* sp. n. with which it shares colourful pink or red body colour, as well as further characters, viz., the same patterns of row of cones on metaterga (metaterga 2–8 with 2+2 cones in anterior row).

Coexisting species. The new species was found in one place together with *D. octoconigera* sp. n. (see detail in *D. octoconigera* sp. n.), with *D. planata* at Wat Huay Charoen Srattha Tham and Tham Khao Noi Bureau of Monks, and with *D. purpurosea* at Daowadueng Cave. This species and *D. purpurosea* were hand-collected after rain when lots of them were climbing on vegetation and limestone rocks. Microhabitat differences have not yet been observed. Moreover, *D. planata* also occurs near the new species, but the habitats of these two species are clearly different: *D. planata* was found on humid cement and on construction materials whereas *D. golovatchi* sp. n. was seen crawling on limestone rock.

Desmoxytes octoconigera Srisonchai, Enghoff and Panha sp. n.

Figs 4.55–4.60

Holotype: Male (CUMZ), THAILAND, Kanchanaburi Province, Sangkhla Buri District, Wat Tham Kaeo Sawan Bandal, 15°18'18"N, 98°24'57"E, ca. 334 m a.s.l., 16 August 2016, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Paratypes: 22 males, 11 females (CUMZ), 1 male, 1 female (ZMUC), same data as holotype; 1 female; 1 broken female (CUMZ), same locality as holotype, 10 July 2009, leg. S. Panha and ASRU members.

Further specimens, not paratypes, all from THAILAND, Kanchanaburi Province,

Sangkhla Buri District: 3 broken males, 1 female, 2 broken and mixed specimens, 2 broken and mixed females? (CUMZ), Kra Teng Cheng Waterfall, 15°01'30"N, 98°36'05"E, ca. 208 m a.s.l., 10 July 2009, leg. C. Sutcharit, R. Srisonchai and ASRU members. 1 broken male missing gonopods, 5 males, 2 females (CUMZ), Kroeng Krawia Waterfall, 14°58'53"N, 98°37'54"E, ca. 255 m a.s.l., 10 July 2009, leg. S. Panha and ASRU members. 2 males, 3 juveniles (CUMZ), Takhian Thong Waterfall, 15°17'58"N, 98°26'56"E, ca. 241 m a.s.l., 10 July 2009, leg. S. Panha and ASRU members. 1 broken male (CUMZ), mountain near the Three Pagodas Pass, 15°18'20"N, 98°24'01"E, ca. 368 m a.s.l., 19 December 2010, leg. S. Panha and ASRU members. 3 males (CUMZ), Kra Teng Cheng Waterfall, 15°01'30"N, 98°36'05"E, ca. 208 m a.s.l., 16 August 2016, leg. C. Sutcharit, R. Srisonchai and ASRU members. 2 males, 2 females (CUMZ), near Ban Songkaria (Songkaria Village), limestone mountain, 15°13'01"N, 98°27'06"E, ca. 206 m a.s.l., 16 August 2016, leg. C. Sutcharit, R. Srisonchai and ASRU members. 7 males (CUMZ), Wat Tham Sukhlo, 15°02'14"N, 98°34'59"E, ca. 196 m a.s.l., 16 August 2016, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Thong Pha Phum District: 4 males (CUMZ), Kroeng Krawia Checkpoint, 14°56'32"N, 98°40'11"E, ca. 347 m a.s.l., 16 August 2016, leg. C. Sutcharit, R. Srisonchai and ASRU members. 2 males, 1 female (CUMZ), Tham Khao Noi Bureau of Monks (Wat Tham Khao Noi), 14°41'55"N, 98°31'33"E, ca. 225 m a.s.l., 21 August 2015, leg. E. Jeratthitikul and R. Srisonchai. 2 males (CUMZ), Tham Khao Noi Bureau of Monks (Wat Tham Khao Noi), 14°41'55"N, 98°31'33"E, ca. 225 m a.s.l., 15 August 2016, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Diagnosis. Differs from all other *Desmoxytes* species by the combination of the following characters; collum with three rows of 5+5 anterior, 1(2)+1(2) intermediate, and 3+3 posterior setiferous tubercles; metaterga 2–8 with two rows of 3+3 (anterior row) and 3+3 (posterior row) setiferous cones; metaterga 9–17 with two rows of 4(3)+4(3) (anterior row) and 4(5)+4(5) (posterior row) setiferous cones; sternal cone between male coxae 4 incompletely bilobed, cordiform; lateral lamella of distal lobe (dlm) on lamina medialis broad and thin, demarcated from broad lobe (blm) by a deep indentation.

Etymology. The name is a Latin adjective, referring to the two rows each with eight setiferous cones on metaterga 9–17.

Description.

SIZE: Length 24–30 mm (male), 30–32 mm (female); width of midbody metazona ca. 1.75 mm (male), 2.0 mm (female). Width of head > collum = body ring 2 = 3 = 4 < 5–16, thereafter body gradually tapering toward telson.

COLOUR (Fig. 4.55A–C): In life with body dark brown (male), brown (female); paraterga and sterna brown to whitish; metaterga, surface below paraterga and antenna dark brown (except antennomeres 6–8 whitish); head and epiproct brown; a few basal podomeres brown to whitish.

ANTENNAE (Fig. 4.56D): Very long and slender, reaching to body ring 7–8 (male) and 6 (female) when stretched dorsally.

COLLUM (Fig. 4.56A): With 3 transverse rows of setiferous tubercles, 5+5 anterior, 1(2)+1(2) intermediate and 3+3 posterior tubercles (lateral tubercles of anterior row located almost at base of paraterga in some specimens); paraterga of collum low, elevated at ca. 20°, directed caudad, with one distinct notch on lateral margin.

TEGUMENT: Quite dull, slightly shining; collum and metaterga coarsely microgranulate; prozona finely shagreened; surface below paraterga finely microgranulate; sterna and epiproct smooth.

METATERGA (Fig. 4.56A–C): With 2 transverse rows of setae, setiferous tubercles and setiferous cones; metaterga 2–8 with 3+3 anterior and 3+3 posterior cones; metaterga 9–17 with 4(3)+4(3) anterior and 4(5)+4(5) posterior cones; metatergum 18 with 4+4 anterior and 4+4 posterior tubercles; metatergum 19 with 4+4 anterior and 4+4 posterior setae.

PARATERGA (Fig. 4.56E, F): Directed caudolaterad on body rings 2–17, elevated at ca. 50° (male) 45° (female); directed increasingly caudad on body rings 18 and 19; anterior margin with 2 distinct notches, on lateral margin of body rings 9, 10, 12, 13, 15–18 with tiny denticle near the tip.

TELSON (Fig. 4.57C–G): Epiproct: tip subemarginate; lateral setiferous tubercles small but conspicuous; apical tubercles conspicuous. Hypoproct subtrapeziform; caudal margin round, with inconspicuous setiferous tubercles.

STERNA (Fig. 4.58): Cross-impressions shallow. Sternal lobe between male coxae 4 swollen, tip emarginate to incompletely bilobed, cordiform when seen in ventral view.

LEGS (Fig. 4.57H–J): Very long and slender. Male femora 5 and 6 swollen in middle part.

GONOPODS (Figs 4.59, 4.60): Coxa (cx) longer than prefemur. Cannula (cx) slender. Prefemur (pfe) ca. 2/3 as long as femur. Femur (fe) long and slender. Mesal sulcus (ms) and lateral sulcus (ls) very deep and wide. Postfemur (pof) conspicuous, ventrally wide. Solenophore (sph) well-developed: lamina lateralis (ll) swollen, lobe-like when seen in ventral view, conspicuous: lamina medialis (lm) well-developed; process (plm) long, directed mesoanteriad, tip almost blunt (in some specimens tip bifurcating into two sharp small spines); distal lobe (dlm) well-developed, distally with two lamellae (lateral lamella broad and thin, projecting laterad, *in situ* terminating close to tip of solenomere (sl); mesal lamella shorter than lateral one, apical margin serrate); broad lobe (blm) thick, distinctly demarcated from distal lobe (dlm) by a very deep and narrow indentation. Solenomere (sl) quite long.

Distribution and habitat. *D. octoconigera* sp. n. is known only from Kanchanaburi Province. At the type locality where the holotype and the majority of the paratypes were collected, the animals were crawling on litter inside rock holes; some specimens were seen crawling on rock walls near the cave.

Interestingly, some specimens of *D. planata* were also found near the cave, however, according to our surveys this species is usually found in places with human activity. We assume that it was probably accidentally introduced to the cave by human actions. Therefore, *D. planata* and the new species might not share microhabitat, although they live syntopically.

The new species and *D. golovatchi* sp. n. are sympatric in one location at Tham Khao Noi Bureau of Monks (Wat Tham Khao Noi), and they both have narrow distribution ranges (<100 km^2). Currently, the type locality of *D. octoconigera* sp. n. is situated in an area with considerable human activity (Bureau of Monks and tourist cave), where the forest habitat is cut every year.

We have tried in vain to find this species in another area nearby. Given the narrow distribution range, the new species is probably endemic to Thailand.

Remarks. There is considerable variation in tip of process (plm) of lamina medialis within populations. The process tip in some specimens is bifurcate as two small spines whereas in other specimens it may be relatively blunt.

Coexisting species. *Desmoxytes golovatchi* sp. n. and *D. planata*.

Desmoxytes perakensis Srisonchai, Enghoff and Panha sp. n.

Figs 4.61–4.65

Holotype: Male (CUMZ), MALAYSIA, Perak, Ipoh, Ulu Kinta, near The Lost World Tambun Theme Park, limestone mountain, 4°37'45"N, 101°09'21"E, ca. 73 m a.s.l., 27 September 2007, leg. B. W. Ng, S. Panha and ASRU members.

Paratypes: 4 males (CUMZ), same data as holotype.

Diagnosis. Differing from all other species, except *D. delfae* and *D. aurata* sp. n., by having a low degree of elevation of paraterga, femora 5 and 6 strongly humped ventrally in middle part, collum with a row of 3+3 anterior setae and metaterga 2–18 with rows of 2+2 anterior and 2+2 posterior small tubercles. Differs from *D. delfae* and *D. aurata* sp. n. by having paraterga wider than those species; lamina lateralis (ll) with two distinct furrows ventrolaterally; process (plm) of lamina medialis lamellar, tip blunt.

Etymology. The name is a Latin adjective referring to the type locality.

Description.

SIZE: Length 24–26 mm (male), 27–29 mm (female); width of midbody metazona ca. 1.9 mm (male), 2.2 mm (female). Width of head < collum < body ring 2 = 3 < 4 < 5–16, thereafter body gradually tapering towards telson.

COLOUR: In life with bright orange. Colour in alcohol: after 10 years in alcohol pale yellow to whitish.

ANTENNAE (Fig. 4.61D): Moderately long and slender, reaching to body ring 6 (male) and 5 (female) when stretched dorsally.

COLLUM (Fig. 4.61A): With 1 transverse anterior row of 3+3 setae; paraterga of collum low, almost horizontal, directed caudolaterad, with two inconspicuous setiferous notches on lateral margin.

TEGUMENT: Slightly shining and smooth; collum, metaterga, sterna and epiproct smooth; prozona finely shagreened; surface below paraterga finely microgranulate.

METATERGA (Fig. 4.61A–C): With 2 transverse rows of small, inconspicuous setae and tubercles; metaterga 2–18 with 2+2 anterior and 2+2 posterior tubercles; metatergum 19 with 2+2 anterior and 2+2 posterior setae.

PARATERGA (Fig 4.61E, F): Directed caudolaterad on body rings 2–17, elevated at ca. 25°–30° (male) 25° (female); directed increasingly caudad on body rings 18 and 19; anterior margin with 2 distinct notches, on lateral margin of body rings 9, 10, 12, 13, 15–18 with tiny denticle near the tip.

TELSON (Fig. 4.62C–G): Epiproct: tip truncate; lateral setiferous tubercles and apical tubercles inconspicuous. Hypoproct subtriangular; caudal margin round, with very small and inconspicuous setiferous tubercles.

STERNA (Fig. 4.63): Cross-impressions shallow. Sternal lobe between male coxae 4 subtrapeziform, tip subtruncate, base slightly enlarged.

LEGS (Fig. 4.62H–J): Long and slender. Male femora 5 and 6 strongly humped ventrally in middle portion.

GONOPODS (Figs 4.64, 4.65): Coxa (cx) longer than prefemur. Cannula (ca) somewhat stout. Prefemur (pfe) ca. 2/3 as long as femur. Femur (fe) quite long and slender. Mesal sulcus (ms) and lateral sulcus (ls) conspicuous, very deep. Postfemur (pof) conspicuous, ventrally narrow and short. Solenophore (sph) well-developed:

lamina lateralis (ll) swollen, quite thin, anterolaterally with two distinct furrows, dorsolaterally subsided, ventral ridge (vrl) conspicuous: lamina medialis (lm) well-developed; process (plm) short, lamellar, tip blunt; distal lobe (dlm) distally with two lamellae (mesal lamella smaller than lateral one); broad lobe (blm) dorsally somewhat thick, demarcated from distal lobe (dlm) by conspicuous indentation. Solenomere (sl) long.

Distribution and habitat. Known only from the type locality. Currently, the habitats at this site are being destroyed and disturbed by human activities, e.g. deforestation for tourist attractions. Our extensive surveys in 2007 allow us to consider this species to be endemic to Malaysia.

Remarks. *D. perakensis* sp. n. is morphologically similar to *D. delfae* and *D. aurata* sp. n.

Unfortunately, we did not photograph a living specimen during the field trip; however, one collector noticed orange colouration similar to *D. aurata* sp. n. and *D. delfae*.

Coexisting species. None known.

Desmoxytes pinnasquali **Srisonchai, Enghoff and Panha, 2016**

Fig. 4.66

Desmoxytes pinnasquali Srisonchai, Enghoff and Panha, 2016: 107.

Material examined.

Holotype: Male (CUMZ), THAILAND, Phitsanulok Province, Noen Maprang District, near Pra Tham Mans Monastery (Tham Wangdaeng), 16°41'40"N, 100°40'42"E, ca. 76 m a.s.l., 22 August 2014, leg. S. Panha, C. Sutcharit and U. Banthaowong.

Paratypes: 22 males, 5 females (CUMZ), 2 males, 1 female (ZMUC), same data as holotype. 10 males, 17 females (CUMZ), THAILAND, Phitsanulok Province, Noen

Maprang District, near Pra Tham Mans Monastery (Tham Wangdaeng), 16°41'40"N, 100°40'42"E, ca. 76 m a.s.l., 23 July 2008, leg. N. Likhitrakarn. 2 females (CUMZ), THAILAND, Phitsanulok Province, Noen Maprang District, near Pra Tham Mans Monastery (Tham Wangdaeng), 16°41'40"N, 100°40'42"E, ca. 76 m a.s.l., 8 September 2009, leg. U. Bantaowong and R. Chanabun. 3 males, 6 females (CUMZ), THAILAND, Phitsanulok Province, Noen Maprang District, near Pa Ma Muang monastery, 16°34'00"N, 100°41'41"E, ca. 113 m a.s.l., 23 July 2008, leg. C. Sutcharit and P. Tongkerd.

Further specimens, all from THAILAND,

Phitsanulok Province, Noen Maprang District: 1 male, 2 females (CUMZ), Pra Tham Mans Monastery (Tham Wangdaeng), 16°41'40"N, 100°40'42"E, ca. 76 m a.s.l., 29 July 2016, leg. P. Pimvichai, T. Backeljau, P. Prasankok and N. Nantarat. 3 males, 4 females (CUMZ), Pa Ma Muang Bureau of Monks (= Pa Ma Muang Monastery), 16°34'00"N, 100°41'41"E, ca. 113 m a.s.l., 29 July 2016, leg. P. Pimvichai, T. Backeljau, P. Prasankok and N. Nantarat.

Type locality. THAILAND, Phitsanulok Province, Noen Maprang District, Pra Tham Mans Monastery (Tham Wangdaeng).

Diagnosis. Differs from all other *Desmoxytes* species by the combination of the following characters; sternal lobe between male coxae 4 subrectangular or subtrapeziform, flattened when seen in lateral view; apical tubercles of epiproct conspicuous, long, digitiform; process (plm) of lamina medialis sharkfin-like, long.

Redescription (updated from Srisonchai *et al.* 2016).

SIZE: Length 24–30 mm (male), 28–33 mm (female); width of midbody metazona ca. 2.0–2.2 mm (male), 2.4 mm (female). Width of head < collum < body ring 2 < 3 ≤ 4 < 5–16, thereafter body gradually tapering toward telson.

COLOUR: In life with body vivid pink or brownish pink; paraterga vivid pink; metaterga and surface below paraterga brownish pink; head and antenna blackish brown (except distal part of antennomere 7 and antennomere 8 whitish); legs pink or brownish pink; a few basal podomeres whitish pink; sterna brown or pinkish brown; epiproct pink. Colour in alcohol: after two years changed to pale brown.

ANTENNAE: Long and slender, reaching to body ring 5 or end of 5 (male), and 4 (female) when stretched dorsally.

COLLUM: With 3 transverse rows of setiferous tubercles, 3(4)+3(4) anterior, 1+1 intermediate and 2+2 posterior tubercles (excluding small setiferous notches at base of collum paraterga); paraterga of collum low, elevated at ca. 10°–15°, directed almost laterad, with two setiferous notches on lateral margin (first notch located at the base of paratergum, second one conspicuous).

TEGUMENT: Moderately shining; collum and metaterga coarsely microgranulate; prozona finely shagreened; surface below paraterga finely microgranulate; paraterga, sterna and epiproct smooth.

METATERGA: With 2 transverse rows of setiferous tubercles, setiferous cones and setiferous spines; metaterga 2–17 with 2+2 anterior cones and 2+2 posterior spines; metaterga 18 and 19 with 2+2 anterior tubercles and 2+2 posterior tubercles.

PARATERGA: Directed caudolaterad on body rings 2–17, elevated at ca. 45° (male) 40° (female); directed increasingly caudad on body rings 18 and 19; anterior margin with 2 distinct notches, on lateral margin of body rings 9, 10, 12, 13, 15–18 with tiny denticle near the tip.

TELSON: Epiproct: tip extremely concave; lateral setiferous tubercles inconspicuous, very short; apical tubercles conspicuous, very long, digitiform. Hypoproct subsemicircular; caudal margin round, with big and conspicuous setiferous tubercles.

STERNA: Cross-impressions shallow. Sternal lobe between male coxae 4 swollen, usually subrectangular (in some specimens subtrapeziform), flat when seen in lateral view, tip subtruncate.

LEGS: Very long and slender. Male femora 5 and 6 moderately humped ventrally in middle part (hump of femora 6 bigger than 5).

GONOPODS (Fig. 4.66): Coxa (cx) longer than prefemur. Cannula (ca) slender. Prefemur (pfe) ca. 2/3 as long as femur. Femur (fe) long and slender. Mesal sulcus (ms) and lateral sulcus (ls) very deep and wide. Postfemur (pof) conspicuous, ventrally quite wide. Solenophore (sph) well-developed: lamina lateralis (ll) swollen: lamina medialis (lm) well-developed; process (plm) long, sharkfin-like, tip slightly blunt (in some specimens slightly sharp), directed mesad; distal lobe (dlm) distally with two lamellae (mesal lamella slightly smaller than second one); broad lobe (blm) thick, obviously demarcated from distal lobe (dlm) by a wide and shallow indentation. Solenomere (sl) quite long.

Distribution and habitat. Known only from the type locality and nearby area. It was found in limestone habitats. Given the narrow distribution in the small limestone area in the west of Thung Salaeng Luang National Park (Srisonchai *et al.* 2016), we regard this species as endemic for Thailand.

Remarks. We collected additional topotypes during the rainy season. Some morphological variation was found. Thus, in some individuals, the sternal lobe between male coxae 4 is subrectangular, in others subtrapeziform. Gonopod variation is also found in this species; the tip of process (plm) of lamina medialis seems to be slightly blunt in some specimens, slightly sharp in others.

Coexisting species. None known.

Corrections to Srisonchai *et al.* (2016). Srisonchai *et al.* (2016, pp. 99–103) wrote in the description of this species that the paraterga (including paraterga of collum) are directed dorsolaterad at ca. 30°. They are in fact directed caudolaterad and elevated at ca. as 45°. Moreover, Srisonchai *et al.* also described the type of tubercles on metaterga as spines in body rings 2–19. We prefer to change terms, from spine to tubercle and cone – thus, metaterga 2–17 with rows of 2+2 anterior cones and 2+2 posterior spines, metaterga 18–19 with rows of 2+2 anterior tubercles and 2+2 posterior tubercles.

***Desmoxytes planata* (Pocock, 1895)**

Figs 4.5–4.8, 4.67–4.74

Prionopeltis planatus Pocock, 1895: 829. Attems 1914: 204; 1936: 215; 1937: 114.

Pratinus planatus – Jeekel 1964: 63 (in key); 1968: 61. Mauriès 1980: 161.

Desmoxytes planata – Jeekel 1980a: 652; 1980b: 124. Golovatch and Korsós 1992: 25. Golovatch and Enghoff 1994: 60. Shelley and Lehtinen 1998: 88. Enghoff 2005: 96. Decker 2010: 29. Nguyen and Sierwald 2013: 1240. Zoysa *et al.* 2016: 474. Golovatch and Wesener 2016: 45. Likhitrakarn *et al.* 2017: 20.

Desmoxytes coniger Chamberlin, 1923: 165. Jeekel 1980a: 652 (synonymized).

Euphyodesmus greeni (Silv.) Attems, 1936: 213. Jeekel 1980a: 652 (synonymized).

Euphyodesmus greeni – Attems 1937: 128.

Pratinus greeni – Jeekel 1964: 63 (in key).

Euphyodesmus (*Ceylonesmus*) *vector* Chamberlin, 1941: 33. Jeekel 1980a: 652 (synonymized).

Pratinus vector – Jeekel 1964: 63 (in key).

Pratinus rastrituberus Zhang, 1986: 255. Golovatch and Enghoff 1994: 60 (synonymized).

Material examined.

Lectotype: Male (NHMUK, 1892.5.4.64–74), MYANMAR, Andaman Sea, Great Cocos Island, leg. E. W. Oates; designated by Mauriès (1980).

Paralectotypes: 1 male, 2 females pinned through body (>10 males and >15 females broken and mixed) (NHMUK), MYANMAR, Andaman Sea, Great Cocos Island, leg. E. W. Oates.

Other material examined.

CHINA: 8 males, 2 females (CUMZ), Yunnan, Xishuangbanna, Mengla, 213 national road near Menglunzhen, Munlun Village, 21°56'40"N, 101°13'45"E, ca. 576 m a.s.l., 26 November 2016, leg. S. Panha, C. Sutcharit and E. Jeratthitikul.

FIJI: 1 female, 1 juvenile (ZMUC), Viti Levu Suva, in garden, 2–3 September 1995, leg. A. Van Harten. 1 male (ZMUC), Upper Sigataka Valley, 6 March 1995, leg. A. Van Harten. 1 female (ZMUC), Colo-i-Suva Forest Park, 10 January 1995, leg. A. Van

Harten. 3 females (ZMUC), Viti Levu, Colo-i-Suva Forest Park, 23–27 August 1995, leg. A. Van Harten. 1 male (ZMUC), Viti Levu, Colo-i-Suva Forest Park, 3 March 1995, leg. A. Van Harten. 4 males (ZMUC), Viti Levu, Colo-i-Suva Forest Park, 22 October 1995, leg. A. Van Harten. 1 male (ZMUC), Viti Levu, Colo-i-Suva Forest Park, 1995, leg. A. Van Harten. 1 male (ZMUC), Colo-i-Suva Forest Park, 29 March–6 April 1995, leg. A. Van Harten.

MYANMAR: 4 males (CUMZ), Tanintharyi State, Myeik, 20 km northeast of Monoron, near Lenya National Park, Lampane Village, Ngawun Chuang River, 11°40'18"N, 99°13'29"E, ca. 44 m a.s.l., 9 June 2015, leg. ASRU members and FFI staff.

SEYCHELLES: 2 females (ZMUC), Mahé, ca. 50 m above Hotel Reef (near airport), under dead banana leaves, 8 October 1997, leg. H. Sturm.

THAILAND:

Chiang Mai Province: 1 female (ZMUC), Mae Rim District, Queen Sirikit Botanical Garden, June 1998. leg. R. Meier. 2 males, 6 females (ZMUC), Chiang Mai Province, Chiang Mai, in garden, ca. 300 m a.s.l., 26 September 1981, leg. ZMUC staff. 1 male, 1 female (ZMUC), Chiang Mai, in garden, ca. 300 m a.s.l., 2 October 1981, leg. ZMUC staff. 1 female (ZMUC), Doi Inthanon National Park, Siripum Waterfall, ca. 1200–1300 m a.s.l., 2 October 1981, leg. ZMUC staff. 1 female (ZMUC), Fang Horticultural Station, ca. 1200–1300 m a.s.l., 21 October 1981, leg. ZMUC staff. 2 females, 2 juveniles (CUMZ), Chiang Dao District, Wat Tham Chiang Dao, 19°23'46"N, 98°55'45"E, ca. 442 m a.s.l., 20 July 2008, leg. ASRU members. 1 female (CUMZ), Mueang Chiang Mai District, 700 years house of Chiang Mai, 2 October 2009, leg. S. Panha and ASRU members. 1 female (CUMZ), Mueang Chiang Mai District, 700 years house of Chiang Mai, 2 October 2009, leg. S. Panha and ASRU members. 1 female (CUMZ), Mae On District, Mae Kampong Waterfall, 18°51'56"N, 99°21'18"E, ca. 1069 m a.s.l., 27 September 2009, leg. S. Panha and ASRU members.

Chiang Rai Province: 7 males, 4 females (CUMZ), Mae Lao District, Dong Mada Subdistrict, Huai Kon Kom, beside road no.118, 19°44'55"N, 99°39'33"E, ca. 472 m a.s.l., 27 November 2009, leg. ASRU members.

Chumphon Province: 1 male, 1 female (CUMZ), Pathio District, Phitsadarn Cave (Tham Phitsadarn), 10°45'36"N, 99°13'46"E, ca. 106 m a.s.l., 29 August 2015, leg. ASRU members. 2 females (CUMZ), Pathio District, Phitsadarn Cave (Tham Phitsadarn), 10°45'36''N, 99°13'46''E, ca. 106 m a.s.l., 5 January 2017, leg. ASRU members.

Kanchanaburi Province: 14 males, 11 females, 2 juveniles (CUMZ), Thong Pha Phum District, Thong Pha Phum Forest Garden, 14°40'06"N, 98°35'42"E, ca. 171 m a.s.l., 8 May 2014, leg. ASRU members. 1 male, 5 females (CUMZ), Thong Pha Phum District, Thong Pha Phum Forest Garden, 14°40'06"N, 98°35'42"E, ca. 171 m a.s.l., 24 July 2016, leg. P. Pimvichai, T. Backeljau, P. Prasankok and N. Nantarat. 2 males, 2 females, (CUMZ), Thong Pha Phum District, Huai Ka Yeng Hot Spring, 14°38'57"N, 98°31'28"E, ca. 202 m a.s.l., 9 May 2014, leg. ASRU members. 1 male (CUMZ), Thong Pha Phum District, Wat Huay Charoen Srattha Tham, 14°39'27"N, 98°31'38"E, ca. 202 m a.s.l., 9 May 2014, leg. ASRU members. 2 males, 2 females (CUMZ), Sangkhla Buri District, Kroeng Krawia Waterfall, 14°58'55''N, 98°37'54''E, ca. 258 m a.s.l., 10 July 2009, leg. ASRU members. 2 females, 1 juvenile (CUMZ), Sri Sawat District, Erawan Waterfall National Park, 14°22'09''N, 99°08'41''E, ca. 102 m a.s.l., 28 August 2011, leg. ASRU members. 1 male, 1 broken fragment (CUMZ), Thong Pha Phum District, Tham Khao Noi Bureau of Monks, 14°41'55''N, 98°31'34''E, ca. 233 m a.s.l., 21 August 2015, leg. R. Srisonchai and C. Sutcharit. 3 females, 6 juvenile (CUMZ), Thong Pha Phum District, Kroeng Krawia Check Point, 14°56'32''N, 98°40'10''E, ca. 343 m a.s.l., 12 October 2015, leg. C. Sutcharit and ASRU members. 8 males, 9 females (CUMZ), Sangkhla Buri District, Wat Tham Su Kho, 15°02'14''N, 98°34'58''E, ca. 194 m a.s.l., 16 August 2016, leg. C. Sutcharit and ASRU members. 1 female (CUMZ), Sangkhla Buri District, Kra Teng Jeng Waterfall, 15°01'30''N, 98°36'03''E, ca. 202 m a.s.l., 16 August 2016, leg. C. Sutcharit and ASRU members. 7 males, 1 female (CUMZ), Sangkhla Buri District, Ban Song Karia, beside road no. 323, 15°13'01''N, 98°27'06''E, ca. 204 m a.s.l., 16 August 2016, leg. C. Sutcharit and ASRU members. 19 males, 26 females (CUMZ), Sangkhla Buri District, Tham Thep Prachao Praya Nak Kharach, 16 August 2016, leg. C. Sutcharit and ASRU members. 1 female (CUMZ), Sangkhla Buri District, Tham Kaeo Sawan Bandhan, 15°18'18''N, 98°24'57''E, ca. 339 m a.s.l., 16 August 2016, leg. C. Sutcharit and ASRU members. 2 females (CUMZ), Thong Pha Phum District, Wat Tha Kha-nun, 14°44'36''N, 98°38'19''E, ca. 113 m a.s.l., 16 August 2016, leg. C. Sutcharit and ASRU members. 4 males, 9 females (CUMZ), Thong Pha Phum District, Phuphrai Thannam Resort, 14°44'07''N, 98°38'39''E, ca. 110 m a.s.l., 16 August 2016, leg. C. Sutcharit and ASRU members. 3 males (CUMZ), Mueang Kanchanaburi District, Lat Ya Subdistrict, Klong Ta Ploen, 19 December 2016, leg. E. Jeratthitikul.

Lampang Province: 1 male, 5 male fragments, 5 females (CUMZ), Mae Mo District, Chao Por Pra Thu Pha Shrine, 18°30'48"N, 99°49'13"E, ca. 587 m a.s.l., 23 October 2008, leg. ASRU members. 1 female (CUMZ), Mae Mo District, Chao Por Pra Thu Pha Shrine, 18°30'48"N, 99°49'13"E, ca. 587 m a.s.l., 22 October 2015, leg. ASRU members.

Mae Hong Son Province: 12 males, 12 females (CUMZ), Mueang Mae Hong Son District, Tham Pla-Namtok Pha Suea National Park, 19°30'07"N, 98°00'23"E, ca. 398 m a.s.l., 19 July 2008, leg. ASRU members. 1 male, 5 females, 6 juveniles (CUMZ), Mae Sariang District, Mae Sariang Highway Division, 18°12'37"N, 97°56'15"E, ca. 296 m a.s.l., 16 January 2015, leg. ASRU members. 9 males, 14 females (CUMZ), Mueang Mae Hong Son District, Tham Phadaeng, 19°25'23"N, 97°59'04"E, ca. 288 m a.s.l., 19 September 2008, leg. ASRU members.

Phayao Province: 5 males, 6 females (CUMZ), Phusang District, Phu Sang Waterfall, 19°39'49"N, 100°22'36"E, ca. 472 m a.s.l., 24 October 2008, leg. ASRU members. 1 male (CUMZ), Phusang District, Phu Sang Waterfall, 19°39'49"N, 100°22'36"E, ca. 472 m a.s.l., 11 October 2014, leg. ASRU members. 1 broken male, 3 females (CUMZ), Phusang District, Phu Sang Waterfall, 19°39'49"N, 100°22'36"E, ca. 472 m a.s.l., 19 November 2012, leg. ASRU members. 1 male, 3 females (CUMZ), Chiang Kham District, Tham Phadaeng, 19°30'00"N, 100°27'10"E, ca. 495 m a.s.l., 24 October 2008, leg. ASRU members.

Phetchaburi Province: Mixed rings – probably 2 males (CUMZ), Kaeng Krachan District, Huai Mae Priang Subdistrict, Ban Dan Ngo, 12°48'41"N, 99°33'46"E, ca. 252 m a.s.l., 1 September 2007, leg. ASRU members. 1 male, 4 females, 1 juvenile (CUMZ), Khao Yoi District, Wat Paung Malai (Wat Tham Khao Iko), 13°18'42"N, 99°47'03"E, ca. 42 m a.s.l., 24 August 2016, leg. ASRU members. 17 males, 16 females (CUMZ), Khao Yoi District, Wat Paung Malai (Wat Tham Khao Iko), 13°18'42"N, 99°47'03"E, ca. 42 m a.s.l., 24 October 2016, leg. ASRU members.

Phrae Province: 3 males, 3 females (CUMZ), Rong Kwang District, Huai Rong Waterfall, 18°26'28"N, 100°26'60"E, ca. 441 m a.s.l., 31 August 2014, leg. ASRU members. 2 females (CUMZ), Den Chai District, Suan Sai Thong Restaurant, 17°58'17"N, 100°04'22"E, ca. 170 m a.s.l., 9 October 2008, leg. ASRU members. 1 male, 2 females (CUMZ), Den Chai District, Suan Sai Thong Restaurant, 17°58'17"N, 100°04'22"E, ca. 170 m a.s.l., 24 August 2014, leg. ASRU members. 31 males, 30 females (CUMZ), Den Chai District, Suan Sai Thong Restaurant, 17°58'17"N, 100°04'22"E, ca. 170 m a.s.l., 31 August 2014, leg. ASRU members.

Prachuap Khiri Khan Province: 1 male, 1 female, broken and mixed rings (CUMZ), Bang Saphan District, Wat Khao Tham Ma Rong, 11°12'05"N, 99°29'52"E, ca. 22 m a.s.l., 12 October 2008, leg. ASRU members. 8 males, 4 females (CUMZ), Kui Buri District, Hat Kham Subdistrict, near Kui Buri National Park, 12°03'13"N, 99°37'53"E, ca. 141 m a.s.l., 7 August 2014, leg. ASRU members. 7 males, 4 females (CUMZ), Kui Buri District, Hat Kham Subdistrict, near Kui Buri National Park, 12°03'13"N, 99°37'53"E, ca. 141 m a.s.l., 9 August 2016, leg. ASRU members. 4 males, 1 female (CUMZ), Kui Buri District, Hat Kham Subdistrict, near Kui Buri National Park, 12°03'13"N, 99°37'53"E, ca. 141 m a.s.l., 11 October 2010, leg. ASRU members. 9 males, 12 females (CUMZ), Mueang Prachuap Khiri Khan District, Khao Ta Mong Lai Forest Park, 11°50'49"N, 99°49'35"E, ca. 14 m a.s.l., 24 October 2016, leg. ASRU members.

Ratchaburi Province: 1 female (CUMZ), Mueang District, Khao Bin Cave, 13°35'37"N, 99°40'00"E, ca. 73 m a.s.l., 8 September 1973, leg. CUMZ staff.

Sa Kaeo Province: 2 males, 2 females (CUMZ), Mueang Sa Kaeo District, Tayak Subdistrict, near Pang Sida National Park, 13°58'26"N, 102°12'15"E, ca. 68 m a.s.l., 17 July 2016, leg. A. Pholyotha.

Saraburi Province: 1 male (CUMZ), Muak Lek District, Chet Sao Noi Waterfall, 14°44'07"N, 101°11'30"E, ca. 158 m a.s.l., 11 October 2014, leg. S. Panha, P. Tongkerd and A. Pholyotha.

Tak Province: 2 males, 3 females, 1 fragment of male (CUMZ), Phop Phra District, Pha Charoen Waterfall, 16°30'04"N, 98°45'06"E, ca. 649 m a.s.l., 5 July 2009, leg. ASRU members. 3 males, 2 females, 1 juvenile, broken and mixed fragments (CUMZ), Umphang District, Khun Danai Restaurant, 16°02'32"N, 98°50'55"E, ca. 466 m a.s.l., 6 July

2009, leg. ASRU members. 1 broken male (CUMZ), Mae Sot District, PK House Hotel, 16°43'39''N, 98°34'13''E, ca. 217 m a.s.l., 5 July 2009, leg. ASRU members. 2 males, 4 females, 6 juveniles (CUMZ), Phop Phra District, Um Piam Village, 16°24'33''N, 99°00'22''E, ca. 1088 m a.s.l., 1 July 2015, leg. ASRU members. 7 males, 1 female, 1 juvenile (CUMZ), Umphang District, Thi Lo Su Riverside Resort, 16°02'47''N, 98°51'09''E, ca. 470 m a.s.l., 1 July 2015, leg. ASRU members. 20 specimens (CUMZ), Phop Phra District, Chao Por Phawo Phop Phra Shrine, near Ban Ja Dee Kho, 16°34'10''N, 98°40'03''E, ca. 554 m a.s.l., 2 July 2015, leg. ASRU members. 1 male (CUMZ), Umphang District, Mae Klong Kee Bureau of Monks, 16°13'46''N, 98°55'12''E, ca. 586 m a.s.l., 30 June 2015, leg. ASRU members.

Diagnosis. Body black or brownish black; collum with 3 transverse rows of setae and setiferous tubercles (4+4 anterior setae, 1+1 intermediate and 2+2 posterior tubercles); metaterga 2–16 with two rows of 2+2 (anterior) setiferous cones and 2+2 (posterior) setiferous spines; ventral ridge (vrl) of lamina lateralis conspicuous; process (plm) of lamina medialis long, directed almost mesad; distal lobe (dlm) distally with two distinct lamellae. Similar in these respects to *D. euros* sp. n., but differs from that species by having paraterga vivid pink and hypoproct subtrapeziform with inconspicuous setiferous tubercles.

Type Locality. Great Cocos Island, Andaman Sea [Myanmar, Yangon Region].

Redescription.

SIZE: Length 16–26 mm (male), 20–28 mm (female); width of midbody metazona ca. 1.8 mm (male), 2.1 mm (female). Width of head ≤ collum ≥ body ring 2 ≥ 3 = 4 < 5–16, thereafter body gradually tapering towards telson.

COLOUR (Figs 4.67, 4.68A, B): In life with body black or brownish black; head, antenna (except distal part of antennomere 7 and antennomere 8 whitish), metaterga and surface below paraterga brownish black; paraterga vivid pink; sterna pinkish brown; epiproct brown; legs brownish pink; a few basal podomeres pinkish white. Colour in alcohol: after 120 years changed to pale brown, after 2–10 years changed to brown or pale brown.

ANTENNAE (Fig. 4.69D): Moderately long and slender, reaching to body ring 5 or 6 (male) and 4 or 5 (female) when stretched dorsally.

COLLUM (Fig. 4.69A): With 3 transverse rows of setae and setiferous tubercles, 4+4 anterior setae, 1+1 intermediate and 2+2 posterior tubercles (lateral seta in anterior row located almost at base of paraterga in some specimens, posterior tubercles in posterior row bigger than others); paraterga of collum low, elevated at ca. 10°–15°, directed caudolaterad, with one inconspicuous notch on lateral margin.

TEGUMENT: Slightly shining; prozona finely shagreened; metaterga and surface below paraterga finely microgranulate; collum, sterna and epiproct smooth.

METATERGA (Fig. 4.69A–C): With 2 transverse rows of setiferous tubercles/cones/spines; metaterga 2–17 with 2+2 anterior tubercles/cones and 2+2 posterior cones/spines (lectotype and paralectotypes all with 2+2 anterior tubercles and 2+2 posterior tubercles/cones on metaterga 2–17); metaterga 18 and 19 with 2+2 anterior and 2+2 posterior tubercles.

PARATERGA (Fig. 4.69E, F): Directed caudolaterad on body rings 2–17, elevated at ca. 45° (male) 40° (female), in lectotype and paralectotypes less elevated than in others: at ca. 40° in male and 35° in female; directed increasingly caudad on body rings 18 and 19; anterior margin with 2 distinct notches, on lateral margin of body rings 9, 10, 12, 13, 15–18 with tiny denticle near the tip (tiny denticle of lectotype and paralectotypes poorly developed).

TELSON (Fig. 4.70C–G): Epiproct: tip usually subtruncate (in some specimens slightly emarginate); lateral setiferous tubercles and apical tubercles usually conspicuous (in some specimens inconspicuous). Hypoproct subtrapeziform; caudal margin round, with inconspicuous setiferous tubercles.

STERNA (Fig. 4.71): Cross-impressions shallow. Sternal lobe between male coxae 4 swollen subtrapeziform/subsemicircular when seen in caudal view (round in lectotype and paralectotypes); base stout; slightly attenuated near tip; tip usually subtruncate (in some specimens round).

LEGS (Fig. 4.70H–J): Long and slender. Male femora 5 and 6 slightly humped ventrally in middle portion.

GONOPODS (Figs 4.7, 4.8, 4.72, 4.73, 4.74): Coxa (cx) longer than prefemur. Cannula (ca) long and slender. Prefemur (pfe) ca. 2/3 as long as femur. Femur (fe) long and slender. Mesal sulcus (ms) and lateral sulcus (ls) conspicuous, very deep. Postfemur (pof) conspicuous, ventrally narrow, and short. Solenophore (sph) well-developed: lamina lateralis (ll) swollen, anterolaterally with an inconspicuous furrow; with conspicuous ventral ridge (vrl): lamina medialis (lm) well-developed; process (plm) long, spear-like, tip sharp (blunt in some specimens), directed mesad; distal lobe (dlm) distally with two distinct lamellae (mesal lamella smaller than second one); broad lobe (blm) dorsally thick at the edge, distinctly demarcated from distal lobe (dlm) by a conspicuous indentation. Solenomere (sl) very long.

Distribution and habitat. This species was collected at several places together with *D. octoconigera* sp. n., *D. golovatchi* sp. n. and *D. purpurosea*, but these species apparently occupy different microhabitats. *D. planata* can be found all year round in humid places in environments strongly influenced by humans. It was very easy to find, mostly in plant farms or shaded gardens. Although *D. planata* was sometimes seen in areas close to another *Desmoxytes* species, the habitats where it was collected are clearly different: *D. planata* is often found in human-influenced habitats while the other ones live in natural habitats.

However, some specimens from Tham Khoa Ma Rong, Khoa Ta Mong Lai, Ban Yang Chum (all in Prachuap Khiri Khan Province) seem to be indigenous as they were found in limestone habitats, although not too far from human-influenced habitats. Certain introduced paradoxosomatid species seem to have penetrated natural habitats and have become more dominant and abundant than the native ones (Jeekel 1980b), and *D. planata* at the above-mentioned locations may similarly have dispersed into the forest.

This species has been reported from Hawaii (Chamberlin 1923, 1941). Because the only reliable records concern specimens taken from quarantine in Honolulu, it seems reasonable to delete *D. planata* from the Hawaii fauna. We believe that this species is transported easily by global commerce, most probably in soil-containing or plant-associated materials.

The origin of *D. planata* was assumed to be Burma or Malaya by Jeekel (1980a). Later, Shelley and Lehtinen (1998) regarded it more probable that this species occurs naturally in Thailand and China. Based on all recent data analysed by us, *D. planata* may originally be native to Thailand or Myanmar. Surprisingly, however, no specimen of *D. planata* has yet been found in Cambodia, Laos or Malaysia, possibly owing to insufficient surveys in these areas.

Decker (2010) reported *D. planata* from eastern Thailand, viz., Namtok Phliu (Chantaburi Province), Khao Chamoa National Park (Rayong Province) and Ko Chang National Park (Trat Province). However, these localities all lie in the distribution range of the very similar *D. euros* sp. n., and Decker's specimens may well belong to the latter species.

Note on type material. The lectotype was designated by Mauriès (1980). In the jar which contains lectotype and paralectotypes in NHMUK, there are three small vials:

- one vial contains the male lectotype with a label "*Pratinus planatus* (Poc.) male lectotype vid. Mauriès (Paris)", pinned through the body; collum and telson were broken off.
- a second vial with one male and two female paralectotypes (one female with only rings 10–20), all specimens pinned through the body.
- a third vial with broken specimens (>5 specimens).

There is also one more vial containing many broken and mixed specimens (>15 specimens).

Remarks. The vivid pink paraterga are obviously aposematic.

According to many previous works, as well as our own results, this species seems to be almost pantropical. In order to assess morphological variability, we compared the gonopods of several specimens (including illustrations) reported from different localities: *D. planata* from Myanmar (lectotype and paralectotypes); *D.*

coniger – (Jeekel 1980b) from Hawaii taken from Java (Bogor); *D. planata* – (Mauries 1980) from Seychelles; *D. planata* – (Shelley and Lehtinen 1998) and (Golovatch and Enghoff 1994) from Fiji; *Pratinus rastrituberus* – (Zhang, 1986) from China. Combining the examination of previous works and the newly collected specimens from China, Myanmar and Thailand, variation in morphological characters was as follows.

I. Variation within populations (Fig. 4.71)

- anterior row of tubercles on collum (usually with 4+4 anterior setae): in some specimens lateral setae located in anterior margin (conspicuous tubercles), in others lateral setae located almost at base of paraterga (inconspicuous tubercles).
- type of metatergal projections (anterior row and posterior row) on body rings 2–17: anterior tubercles/cones in some specimens, posterior cones/spines in others.
- tip of sternal lobe between male coxae 4: truncate in some specimens, quite round in others.
- process (plm) of lamina medialis: short in some individuals, long in others.
- tip of process (plm) of lamina medialis of specimens from Great Cocos Island: slightly emarginate in some, sharp in others.
- epiproct tip: in some specimens subtruncate, in others slightly emarginate.

II. Variation between populations

- Fiji population: posterior tubercles on collum seem to be bigger than in other populations.
- Fiji population: sternal lobe between male coxae 4 more round than in others.
- Great Cocos Island population: size seems to be smaller than in others (16–20 mm in male, 20-23 mm in female).
- Great Cocos Island population: metatergal tubercles shorter than in others.

On this basis, we strongly agree with Jeekel (1980a) and Golovatch and Enghoff (1994) with the synonymy of *D. coniger, E. greeni, E. vector* and *P. rastrituberus* under

Desmoxytes planata. Although the type material of *D. coniger* in MCZ has not been examined by us, its identity with *D. planata* is clear from the photo and remarks given by Jeekel (1980a). The morphological characters of this specimen match perfectly with the others.

Desmoxytes planata is morphologically similar to *D. euros* sp. n. with which it shares the metaterga with 2+2 anterior tubercles/cones and 2+2 posterior cones/spines. Moreover, gonopod characters of these species are very similar in shape and processes. Based on morphological characters only, they could be supposed to be the same species. However, the color of living specimens (paraterga) and shape of hypoproct are totally different, as well as ongoing COI analysis supports to separate them as different species.

Coexisting species. *D. golovatchi* sp. n., and *D. octoconigera* sp. n. (see details under these species).

***Desmoxytes purpurosea* Enghoff, Sutcharit and Panha, 2007**

Figs 4.75–4.81

Desmoxytes purpurosea Enghoff, Sutcharit and Panha, 2007: 32. Nguyen and Sierwald 2013: 1242.

Material examined.

Hototype: Male (CUMZ), THAILAND, Uthai Thani Province, Department of National Parks, Tam Pratun Non-Hunting Area, Hup Pa Tard. 15°22'38"N, 99°37'50"E, ca. 113 m a.s.l., 28 August 2006, leg. S. Panha, H. Enghoff, P. Pimwichai and C. Sutcharit.

Paratypes: 16 males, 30 females (CUMZ), 4 males, 3 females (ZMUC), same data as holotype.

Further specimens, all from THAILAND,

Kanchanaburi Province: 8 males, 5 females, 1 broken male, 1 male missing gonopods, 1 male missing left gonopod, 1 fragment, 1 juvenile (CUMZ), Sai Yok District, Daowadueng Cave, 14°28'23"N, 98°50'04"E, ca. 132 m a.s.l., 11 July 2009, leg. S. Panha and ASRU members. 1 male (CUMZ), Sai Yok District, Daowadueng Cave, 14°28'23"N, 98°50'04"E, ca. 132 m a.s.l., 12 October 2015, leg. C. Sutcharit and R. Srisonchai. 14 males, 7 females (CUMZ), Sai Yok District, Daowadueng Cave, 14°28'23"N, 98°50'04"E, ca. 132 m a.s.l., 15 August 2016, leg. C. Sutcharit, R. Srisonchai and ASRU members. 3 males, 1 female (CUMZ), Sai Yok District, Ban Thung Kang Yang, 14°24'17"N, 98°55'04"E, ca. 264 m a.s.l., 15 August 2016, leg. C. Sutcharit, R. Srisonchai and ASRU members. 38 males, 13 females (CUMZ), Sai Yok District, Wat Sunantha Wanaram, 14°32'11"N, 98°49'51"E, ca. 161 m a.s.l., 17 August 2016, leg. C. Sutcharit, R. Srisonchai and ASRU members. 1 male (CUMZ), Si Sawat District, Chalermrattanakosin National Park, Tham Than Lod Cave, 14°40'06"N, 99°19'02"E, ca. 255 m a.s.l., 9 September 1973, leg. CUMZ staff. Many specimens (CUMZ), Si Sawat District, Chalermrattanakosin National Park, Tham Than Lod Cave, 14°40'06"N, 99°19'02"E, ca. 255 m a.s.l., 10 July 2006, leg. CUMZ staff. 6 males, 4 females (CUMZ), Si Sawat District, Chalermrattanakosin National Park, Tham Than Lod Cave, 14°40'06"N, 99°19'02"E, ca. 255 m a.s.l., 13 October 2015, leg. C. Sutcharit and R. Srisonchai. 1 male missing gonopods, 2 females (CUMZ), Sangkhla Buri District, Kroeng Krawia Waterfall, 14°58'56"N, 98°37'55"E, ca. 264 m a.s.l., 10 July 2009, leg. S. Panha and ASRU members. 7 males, 12 females (CUMZ), Thong Pha Phum District, Kroeng Krawia Checkpoint, 14°56'32"N, 98°40'11"E, ca. 347 m a.s.l., 16 August 2016, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Lamphun Province: 1 male (CUMZ), Pasang District, Tham Erawan (Erawan Cave), 18°19'35"N, 98°52'24"E, ca. 551 m a.s.l., 26 October 2015, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Suphan Buri Province: 3 juveniles (CUMZ), Dan Chang District, Tham Weruwan, 14°57'17"N, 99°38'49"E, ca. 121 m a.s.l., 5 June 2017, leg. C. Sutcharit, A. Pholyotha and ASRU members.

Uthai Thani Province: 1 male missing gonopods (CUMZ), Lansak District, Hup Pa Tard, 15°22'26"N, 99°37'58"E, ca. 113 m a.s.l., 8 June 2008, leg. S. Panha and ASRU members. 7 males, 9 females, 1 broken female, 1 male missing gonopods (CUMZ), Lansak District, Hup Pa Tard, 15°22'26"N, 99°37'58"E, ca. 113 m a.s.l., 15 May 2009, leg. S. Panha and ASRU members. 5 females (CUMZ), Lansak District, Hup Pa Tard, 15°22'26"N, 99°37'58"E, ca. 113 m a.s.l., April 2009, leg. S. Panha and ASRU members. 1 male, 3 broken and mixed males (CUMZ), Lansak District, Hup Pa Tard, 15°22'26"N, 99°37'58"E, ca. 113 m a.s.l., 27 October 2013, leg. S. Panha and ASRU members. Many specimens (CUMZ), Lansak District, Hup Pa Tard, 15°22'26"N, 99°37'58"E, ca. 113 m a.s.l., 31 May 2009, leg. S. Panha and ASRU members. Many specimens (CUMZ), Lansak District, Hup Pa Tard, 15°22'26"N, 99°37'58"E, ca. 113 m a.s.l., 7 June 2008, leg. S. Panha and ASRU members. Many specimens (CUMZ), Lansak District, Hup Pa Tard, 15°22'26"N, 99°37'58"E, ca. 113 m a.s.l., 10 September 2006, leg. S. Panha and ASRU members. Many specimens (CUMZ), Lansak District, Hup Pa Tard, 15°22'26"N, 99°37'58"E, ca. 113 m a.s.l., unknown date, unknown collector. 1 female (CUMZ), Lansak District, Hup Pa Tard, 15°22'26"N, 99°37'58"E, ca. 113 m a.s.l., 27 October 2013, leg. S. Panha and ASRU members. 2 males, 1 female (CUMZ), Lansak District, Hup Pa Tard, 15°22'26"N, 99°37'58"E, ca. 113 m a.s.l., 1 August 2014, leg. S. Panha and ASRU members. 34 specimens (CUMZ), Lansak District, Hup Pa Tard, 15°22'26"N, 99°37'58"E, ca. 113 m a.s.l., 20 October 2015, leg. C. Sutcharit and R. Srisonchai. 4 males, 1 female (CUMZ), Lansak District, Hup Pa Tard, 15°22'26"N, 99°37'58"E, ca. 113 m a.s.l., 27 July 2006, leg. C. Sutcharit, R. Srisonchai and ASRU members. 1 male, 1 female (ZMUC), 1 male, 1 female (ZMUM), 1 male, 1 female (NHMW), 1 male, 1 female (NHMUK), Lansak District, Hup Pa Tard, 15°22'26"N, 99°37'58"E, ca. 113 m a.s.l., 27 July 2016, leg. C. Sutcharit, R. Srisonchai and ASRU members. 9 males, 1 female, 6 broken males and 4 broken females mixed together (CUMZ), Lansak District, Hup Pa Tard, 15°22'26"N, 99°37'58"E, ca. 113 m a.s.l., 19 August 2017, leg. R. Srisonchai and ASRU members. Many specimens (CUMZ), Lansak District, Tham Pha Nam Thip Bureau of Monks, 15°26'03"N, 99°35'24"E, ca. 245 m a.s.l., 27 July 2016, leg. C. Sutcharit, R. Srisonchai and ASRU members. 17 males, 6 females (CUMZ), Lansak District, Tham Pha Nam Thip Bureau of Monks, 15°26'03"N, 99°35'24"E, ca. 245 m a.s.l., 19 August 2017, leg. R. Srisonchai and ASRU members. 4 males, 6 females, 1 broken male, 2 broken females (CUMZ), Lansak District, Wat Wang Pong (Wat Tham Khoa Chong Lom), 15°16'50"N, 99°43'11"E, ca. 90 m a.s.l., 28 July 2016, leg. C. Sutcharit, R. Srisonchai and ASRU members. Many specimens (CUMZ), Ban Rai District, Wat Khao Chuak Charoen Tham, 15°16'19"N, 99°41'43"E, ca. 86 m a.s.l., 8 July 2009, leg. S. Panha and ASRU members. 3 males (CUMZ), Ban Rai District, Wat Tham Khao Wong, 15°01'57"N, 99°27'21"E, ca. 259 m a.s.l., 27 October 2013, leg. S. Sutcharit, R. Chanabun and S. Siriwut.

Diagnosis. Differs from all other *Desmoxytes* species by the combination of the following characters; body purple pink; collum with rows of 4+4 anterior, 1+1 intermediate and 2+2 posterior setiferous tubercles; tip of epiproct slightly or moderately concave; lateral sulcus (ls) deep, long and narrow; lamina lateralis (ll) swollen, surface smooth; ventral lobe (vll) of lamina lateralis long and slender, digitiform, tip round; process (plm) of lamina medialis very long, spine-like, tip usually bifurcating into two distinct spines (in some populations tip terminating in 3–5 spines); distal lobe (dlm) of lamina medialis quite long, distally with two distinct lamellae (mesal lamella smaller and thinner than lateral lamella, tip crenate; lateral lamella broad).

Type locality. THAILAND, Uthai Thani Province, Lansak District, Department of National Parks, Tam Pratun Non–Hunting Area, Hup Pa Tard.

The updated redescription hereunder is modified from Enghoff *et al.* 2007; we have added some morphological characteristics which were extracted from the type material and all recently collected specimens.

Redescription.

SIZE: Length 22–34 mm (male), 26–38 mm (female); width of midbody metazona ca. 2 mm (male), 3.4 mm (female). Width of head < collum = body ring 2 < 3 = 4 < 5–17, thereafter body gradually tapering toward telson.

COLOUR (Fig. 4.75A–D): In life with body purple to vivid pink; paraterga and metaterga vivid pink to purple; surface below paraterga brownish pink or pink; head brown or blackish brown; antenna black or blackish brown (except distal part of antennomere 7 and antennomere 8 whitish); leg, sterna and epiproct pink; a few basal podomeres pale pink. Colour in alcohol: after 10–11 years changed brownish white, after 2–5 years changed to pale brown.

ANTENNAE (Fig. 4.76D): Very long and slender, reaching to body ring 7 or 8 (male), and 6 (female) when stretched dorsally.

COLLUM (Fig. 4.76A): With 3 transverse rows of setiferous tubercles, 4+4 anterior, 1+1 intermediate and 2+2 posterior tubercles, lateral tubercles of posterior row located almost halfway anteriad to intermediate row; paraterga with one conspicuous setiferous notch on lateral margin, elevated at 15°–20°.

TEGUMENT: Slightly shining; collum and metaterga coarsely microgranulate; surface below paraterga finely microgranulate; prozona finely shagreened; paraterga, sterna and epiproct smooth.

METATERGA (Fig. 4.76A–C): With 2 transverse rows of setiferous rose thorn-like spines; metaterga 2–18 with 2+2 anterior and 2+2 posterior spines; metatergum 19 with 2+2 anterior and 2+2 posterior spines/tubercles.

PARATERGA (Fig. 4.76E, F): Directed caudolaterad on body rings 2–17, elevated at ca. 45° (male) 40° (female); directed increasingly caudad on body rings 18 and 19; anterior margin with 2 distinct notches, on lateral margin of body rings 9, 10, 12, 13, 15–18 with tiny denticle near the tip.

TELSON (Fig. 4.77C–G): Epiproct: tip slightly or moderately concave; lateral setiferous tubercles inconspicuous, short; apical tubercles conspicuous, usually short (very long and distinct in Kanchanaburi B population). Hypoproct trapeziform; caudal margin round, with inconspicuous setiferous tubercles.

STERNA (Fig. 4.78): Cross-impressions shallow. Sternal lobe between male coxae 4 swollen and stout, usually trapeziform (in specimen from Lamphun Province subsemicircular), tip usually round or truncate (in some specimens slightly emarginate).

LEGS (Fig. 4.77H–J): Very long and slender. Male femora 5 and 6 strongly humped ventrally in middle part.

GONOPODS (Figs 4.79, 4.80, 4.81): Coxa (cx) longer than prefemur. Cannula (ca) long and slender. Prefemur (pfe) ca. 2/3 as long as femur. Femur (fe) long and slender. Mesal sulcus (ms) very deep and wide, lateral sulcus (ls) very deep, long and narrow. Postfemur (pof) conspicuous, ventrally very wide and stout. Solenophore (sph) well-developed: lamina lateralis (ll) swollen, surface smooth; ventral lobe (vll) long and slender, digitiform, tip round, directed ventrad: lamina medialis (lm) well-developed;

process (plm) very long, spine-like, tip usually bifurcating into two distinct spines (in some populations tip terminating in 3–5 spines), directed mesoanteriad; distal lobe (dlm) quite long, distally with two distinct lamellae (mesal lamella slightly smaller than lateral one, tip crenate; lateral lamella broad); broad lobe (blm) thick, obviously demarcated from distal lobe (dlm) by conspicuous indentation. Solenomere (sl) long, twisted distally.

Distribution and habitat. Known from several places in many provinces (Kampaeng Phet, Kanchanaburi, Lamphun, Suphan Buri, and Uthai Thani). All specimens were collected from limestone habitats (Fig. 4.75E); they were very easy to collect because of their aposematic coloration. We noticed that August–September is an annual peak period for adult swarming.

Although this species has been found in several places, it is distributed only in central, west, and north Thailand. So, we regard *D. purpurosea* as endemic for the Thai fauna.

A specimen from Nakhon Sawan Province (Mae Wong National Park, near the type locality of *D. purpurosea*) which really looks very much like *D. purpurosea* is shown on YouTube ("shocking pink dragon millipede - living treasure of the forest at Mae Wong National Park" (https://youtu.be/jQsn6rOrlA8 - in Thai)). Although we cannot confirm this record because we did not examine specimens from this location, according to the known distribution of *D. purpurosea*, the specimen from Nakhon Sawan Province may possibly be this species.

Remarks. Interestingly, all adult specimens in all populations show exactly the same colour as reported in the original description: vivid pink to purple. However, we found morphological variation between four main populations delimited as follows:

1. Lamphun – Tham Erawan.
2. Uthai Thani – Tham Pha Nam Thip, Wat Wang Pong, Wat Khao Chuak Charoen Tham, Wat Tham Khao Wong and Tham Weruwan.
3. Kanchanaburi A – Tham Than Lod Cave.

4. Kanchanaburi B – Daowadueng Cave, Ban Thung Kang Yang, Wat Sunantha Wanaram, Kroeng Krawia Waterfall and Kroeng Krawia Checkpoint.

- Size: Specimens from the Lamphun and Uthai Thani populations are larger than others (length 28–34 mm in male, 32–38 mm in female), whereas specimens from the Kanchanaburi B population seems to be smaller than others (length 22–26 mm in male, 26–28 mm).

- Sternal lobe between male coxae 4: The only studied specimen from the Lamphun population has a subsemicircular and quite short lobe, while in others the lobe is trapeziform.

- Apical tubercles of epiproct: Distinctly longer in the Kanchanaburi B population than in others.

- Process (plm) of lamina lateralis: A bifurcate tip, as two conspicuous spines, in the Lamphun and Uthai Thani populations, but terminating in several spines in the Kanchanaburi A and B populations.

The shape of the hypoproct varies within populations: in some specimens it is trapeziform, in others it is subsemicircular.

D. purpurosea shares some morphological characters with *D. breviverpa* and *D. takensis,* viz., metaterga 9–19 with rows of 2+2 (anterior) and 3+3 (posterior) setiferous tubercles/cones/spines. However, the differences in gonopod characters are sufficient for separating these as different species.

Coexisting species. *D. octoconigera* sp. n. and *D. golovatchi* sp. n. (see details under these species).

Desmoxytes takensis Srisonchai, Enghoff and Panha, 2016

Figs 4.82, 4.83

Desmoxytes takensis Srisonchai, Enghoff and Panha, 2016: 103.

Material examined.

Holotype: Male (CUMZ), THAILAND, Tak Province, Phobphra District, Nangkruen Waterfall, on litters and under decaying bark, 16°24'36.0"N, 98°41'21.0"E, ca. 383 m a.s.l., 15 January 2015, leg. R. Srisonchai, T. Seesamut, and P. Jirapatrasilp.

Paratypes: 12 males, 10 females, 1 juvenile (CUMZ), 2 males, 1 female (ZMUC), same data as holotype. 2 males, 1 female (CUMZ), same locality as holotype, 18 January 2011, leg. C. Sutcharit, R. Chanabun, N. Likhitrakarn and T. Krutchuen.

Further specimens, all from THAILAND,

Kamphaeng Phet Province: 2 males missing gonopods, 1 female, 2 males (CUMZ), Khlong Lan District, Khlong Lan Waterfall, 16°07'40"N, 99°17'11"E, ca. 189 m a.s.l., 31 May 2009, leg. S. Panha and ASRU members.

Tak Province, Tha Song Yang District: 1 male, 8 females, 2 broken males, 1 male missing gonopods, 1 male missing right gonopod (CUMZ), Km 89 on road no. 105 from Mae Sot to Mae Hong Son, limestone mountain, 18 July 2008, leg. S. Panha and ASRU members. 13 juveniles (CUMZ), Km 131 on road no. 105 from Mae Sot to Mae Hong Son, limestone moutain, 30 June 2015, leg. C. Sutcharit, R. Srisonchai and ASRU members.

Tak Province, Mae Sot District: 3 males (CUMZ), Chao Por Phawo Shrine, 16°46'19"N, 98°41'11"E, ca. 668 m a.s.l., 17 July 2010, leg. S. Panha and ASRU members. 4 males, 14 females, 1 broken male and missing gonopods, 6 broken males, (12 males, all remaining rings 1–8), many broken and mixed specimens (CUMZ), Chao Por Phawo Shrine, 16°46'19"N, 98°41'11"E, ca. 668 m a.s.l., 17 July 2010, leg. S. Panha and ASRU members. 1 male missing gonopods, 1 male, 1 broken male (CUMZ), Chao Por Phawo Shrine, 16°46'19"N, 98°41'11"E, ca. 668 m a.s.l., 26 September 2010, leg. S. Panha and ASRU members. 10 males, 8 females (CUMZ), Chao Por Phawo Shrine, 16°46'19"N, 98°41'11"E, ca. 668 m a.s.l., 29 June 2015, leg. C. Sutcharit and ASRU members. 15 mixed specimens (CUMZ), Chao Por Phawo Shrine, 16°46'19"N, 98°41'11"E, ca. 668 m a.s.l., 19 October 2015, leg. C. Sutcharit and R. Srisonchai. 3 females (CUMZ), Chao Por Phawo Shrine, 16°46'19"N, 98°41'11"E, ca. 668 m a.s.l., 27 July 2016, leg. P. Pimvichai, P. Prasankok and N. Nantarat. 54 males, 16 females (CUMZ), Chao Por Phawo Shrine, 16°46'19"N, 98°41'11"E, ca. 668 m a.s.l., 29 August 2016, leg. S. Panha and ASRU members. 15 specimens (CUMZ), Wat Tham Inthanin, 16°45'59"N, 98°40'21"E, ca. 671 m a.s.l., 19 October 2015, leg. C. Sutcharit and R. Srisonchai. 13 males, 11 females (CUMZ), Wat Pho Thi Khun (Wat Huai Toey), 16°45'42"N, 98°38'49"E, ca. 432 m a.s.l., 29 August 2016, leg. C. Sutcharit and R. Srisonchai.

Tak Province, Umphang District: 15 males, 13 females, 1 male missing right gonopod, 1 male missing left gonopod, 4 males missing gonopods (CUMZ), Tham Takhobi (Takhobi Cave), 16°03'15"N, 98°49'14"E, ca. 511 m a.s.l., 5 July 2009, leg. S. Panha and ASRU members. 7 males, 11 females (CUMZ), Tham Takhobi (Takhobi Cave), 16°03'15"N, 98°49'14"E, ca. 511 m a.s.l., 5 July 2009, leg. S. Panha and ASRU members. 2 males, 5 females, 1 male missing right gonopod, 8 males missing gonopods, 2 broken males, many broken and mixed specimens (CUMZ), Doi Hua Mod, 15°57'30"N, 98°51'13"E, ca. 893 m a.s.l., 5 July 2009, leg. S. Panha and ASRU members. 6 males, 7 females (CUMZ) Doi Hua Mod, 15°57'30"N, 98°51'13"E, ca. 893 m a.s.l., 1 July 2015, leg. S. Panha and ASRU members. 1 male, 1 female (CUMZ), Mae Klong Kee Bureau of Monks, 16°13'46''N 98°55'12''E, ca. 586 m a.s.l., 5 July 2009, leg. C. Sutcharit, R. Srisonchai and ASRU members. 1 male, 1 female (CUMZ), Ban Ta Per Pru – Wa Krue Kro, 16°10'49"N, 98°52'48"E, ca. 523 m a.s.l., 30 June 2015, leg. C. Sutcharit, R. Srisonchai and ASRU members. 29 males, 47 females, 5 broken males, 4 broken females; 1 male missing gonopods, 1 broken male and missing gonopods, 1 male remaining rings 7–20, 1 female remaining rings 1–10 (CUMZ), Km 162 on road no.1090 from Mae Sot to Umphang (near Chao Por Phawo Shrine Umphang), 16°02'23"N, 98°50'60"E, ca. 483 m a.s.l., 6 July 2009, leg. S. Panha and ASRU members. 3 males, 7 females, 1 juvenile (CUMZ), Ban Ta Per Pru – Wa Krue Kro Village, 16°10'49"N, 98°52'48"E, ca. 523 m a.s.l., 30 June 2015, leg. C. Sutcharit and ASRU members. 3 males, 1 female, 4 juveniles (CUMZ), Ban Kra Per Pru, 16°12'15"N, 98°52'04"E, ca. 628 m a.s.l., 2 July 2015, leg. C. Sutcharit and ASRU members.

Type locality. THAILAND, Tak Province, Phobphra District, Nangkruen Waterfall.

Diagnosis. Differs from all other *Desmoxytes* species by the combination of the following characters; lamina lateralis (ll) subtriangular; ventral lobe (vll) of lamina lateralis thumb-like, large and long; broad lobe (blm) of lamina medialis indistinctly demarcated from distal lobe (dlm) of lamina medialis by very shallow or slightly deep indentation.

Redescription (updated from Srisonchai *et al.* 2016).

SIZE: Population A (see Remarks): Length 24–26 mm (male), 25–27 mm (female); width of midbody metazona ca. 1.9 mm (male), 2.2 mm (female). Width of head = collum = body ring 2 = 3 = 4 < 5 < 6–16, thereafter body gradually tapering toward telson. Population B (see Remarks): Length 29–31 mm (male), 32–35 mm (female); width of midbody metazona ca. 1.9 mm (male), 2.3 mm (female). Width of head < collum > body ring 2 > 3 > 4 < 5–16, thereafter body gradually tapering toward telson.

COLOUR (Fig. 4.82A–D): Population A (see below): In life with body bright red; paraterga, metaterga and surface below paraterga red; head, antennae (distal part of antennomere 7 and antennomere 8 whitish), a few basal podomeres, sterna and epiproct brownish red. Population B (see below): In life with body bright pink; paraterga, metaterga and surface below paraterga bright pink; head brown; antenna blackish brown (except distal part of antennomere 7 and antennomere 8 whitish); legs brownish pink to brown; a few basal podomeres pale brown to whitish; sterna and epiproct brownish pink. Colour in alcohol: after one year changed to pale brown or almost whitish in some specimens.

ANTENNAE: Very long and slender, reaching to body ring 6 or beginning of 7 (male) and 5 (female) when stretched dorsally.

COLLUM: With 3 transverse rows of setiferous tubercles, 4+4 anterior, 1+1 intermediate and 2+2 posterior tubercles (lateral tubercles of posterior row located almost halfway to intermediate row); paraterga of collum low, elevated at ca. 10°–15°, directed caudolaterad, with one distinct notch on lateral margin.

TEGUMENT: Slightly shining; collum and metaterga coarsely microgranulate; prozona finely shagreened; surface below paraterga finely microgranulate; paraterga, sterna and epiproct smooth.

METATERGA: With 2 transverse rows of setae, setiferous tubercles and setiferous spines; metaterga 2–8 with 2+2 anterior and 2+2 posterior spines; metaterga 9–17 with 2+2 anterior and 3+3 posterior spines; metatergum 18 with 2+2 anterior spines and 3+3 posterior tubercles; metatergum 19 with 2+2 anterior and 3+3 posterior setae or tubercles.

PARATERGA: Directed caudolaterad on body rings 2–17, elevated at ca. 45° (male) 40° (female); directed increasingly caudad on body rings 18 and 19; anterior margin with 2 distinct notches, on lateral margin of body rings 9, 10, 12, 13, 15–18 with tiny denticle near the tip.

TELSON: Epiproct: tip subtruncate; lateral setiferous tubercles conspicuous, short; apical tubercles inconspicuous. Hypoproct subsemicircular (population B subtrapeziform); caudal margin round, with inconspicuous setiferous tubercles.

STERNA: Cross-impressions shallow. Sternal lobe between male coxae 4 swollen, subtrapeziform when seen in caudal view; base enlarged, slightly attenuated near tip; tip round (in population B subtruncate).

LEGS: Very long and slender. Male femora 5 and 6 strongly humped ventrally in middle part.

GONOPODS (Fig. 4.83): Coxa (cx) longer than prefemur. Cannula (ca) slender. Prefemur (pfe) ca. 2/3 as long as femur. Femur (fe) long and slender. Mesal sulcus (ms) and lateral sulcus (ls) very deep and wide. Postfemur (pof) conspicuous, ventrally wide. Solenophore (sph) well-developed: lamina lateralis (ll) swollen, like a triangular lobe when seen in lateral view; ventral lobe (vll) thumb-like, large (in population B thumb-like, longer and more slender than in population A), directed ventrad: lamina medialis (lm) well-developed; process (plm) long, directed mesad, tip usually sharp (in some specimens almost blunt); distal lobe (dlm) well-developed, distally with one broad and thin lamella (in population B distally with two lamellae; mesal lamella very small, crest-like; lateral lamella broad and thin, *in situ* terminating close to tip of solenomere); broad lobe (blm) thick, indistinctly demarcated from distal lobe (dlm) by a usually wide and shallow indentation (in some specimens demarcated from distal lobe (dlm) by a deep indentation). Solenomere (sl) quite long.

Distribution and habitat. Known only from Tak and Kamphaeng Phet Provinces. This species is restricted to limestone habitats and was seen crawling on litter and decaying bark (Fig. 4.82F). Srisonchai *et al.* (2016) reported that *D. takensis* was found on humid plastic garbage, a sign that the type locality is clearly under human influence. There is a long, broad concrete natural trail into the waterfall, and lots of garbage littered the type locality. However, the species has also been found in other natural habitats.

During our intensive surveys in western Thailand, we found this species in many places. However, it has a narrow range and occurs in only two provinces. Thus, *D. takensis* should be regarded to be endemic to the Thai fauna.

Remarks. Based on morphology, we divided our material specimens into two main populations: Population A includes specimens from Nangkruen Waterfall (type locality), Tham Takhobi, Doi Hua Mod, Mae Klong Kee Bureau of Monks, Ban Ta Per Pru – Wa Krue Kro, Km 162 on road no.1090 near Chao Por Phawo Shrine Umphang and Ban Kra Per Pru. Population B includes specimens from Khlong Lan Waterfall, Km 89 on road no. 105 from Mae Sot to Mae Hong Son, Km 131 on road no. 105 from Mae Sot to Mae Hong Son, Chao Por Phawo Shrine (Mae Sot), Wat Tham Inthanin and Wat Pho Thi Khun.

The two populations differ in some characters as follows:

- Colour: The remarkable body colour of the two populations apparently differs: bright red in population A, vivid pink in population B (some old females strongly pinkish to reddish).

- Size: Population B individuals seem to be bigger than population A ones in both width and length (see size description).

- Hypoproct: The shape of the hypoproct in population A is subsemicircular whereas it is subtrapeziform in population B.

- Gonopods: The ventral lobe (vll) of lamina lateralis of population B specimens is large, thumb-like, longer and more slender than that of population A ones. The distal lobe (dlm) of lamina medialis in population A specimens consists of one lamella while population B specimens have two lamellae distally.

Although the two populations vary in some morphological characters, they show an overall gonopodal resemblance. According to the differences in morphology of the two populations, this might an example of ongoing speciation in allopatry, supported by the confinement of the two populations to two large isolated limestone regions located in the northern (Population B) and southern (Population A) parts of the distribution area.

We collected some juveniles during the field trip and kept them with litter until they moulted. Interestingly, the juveniles made a moulting chamber which was apparently produced by fecal material and silk; it is probable that the building process is the same as in the families Polydesmidae, Pyrgodesmidae and in order Callipodida (Adis *et al.* 2000, Youngsteadt 2009, Reboleira and Enghoff 2016). This is the first observation of moulting in dragon millipedes; however, we did not keep an eye on them in detail. After moulting and emerging from the chamber, the specimens were in an early adult stage showing a pale whitish colouration. Nearly 2 weeks later, they became vivid pink (Fig. 4.82D, E).

Coexisting species. None known.

Corrections to Srisonchai *et al.* (2016). Srisonchai *et al.* (2016, pp. 99–103) wrote in the description of this species that the paraterga (including paraterga of collum) are directed dorsolaterad at ca. 30°. They are in fact directed caudolaterad and are elevated at ca. as 45°.

Desmoxytes taurina (Pocock, 1895)

Figs 4.84–4.87

Prionopeltis taurinus Pocock, 1895: 830. Attems 1914: 204. Weidner 1960: 89. Jeekel 1965: 124.

Pratinus taurinus – Attems 1937: 121. Jeekel 1964: 63; 1968: 61.

Desmoxytes taurina – Jeekel 1980a: 655. Golovatch and Enghoff 1994: 57. Nguyen and Sierwald 2013: 1243. Likhitrakarn *et al.* 2017: 20.

Material examined.

Lectotype: Male (rings 1–11 only, with gonopod – pinned through body) (ZMUC), MYANMAR, Pegu (Taikkyii and Palon), leg. Fea. Lectotype here designated.

Paralectotypes: 1 male (2–3 broken rings in very poor condition, without gonopods) (ZMUC), MYANMAR, Pegu (Taikkyii and Palon), leg. Fea. 2 females (1 female, complete – pinned through body; 1 female, remaining rings 11–20 – pinned through body) (NHMUK), MYANMAR, Rangoon, leg. E. W. Oates [Yangon].

Diagnosis. Metaterga 9–19 usually with 2+2 cones/spines (anterior row) and 3+3 cones/spines (posterior row). Similar in this respect to *D. breviverpa, D. purpurosea* and *D. takensis*. Differs from these species by the following combination of characters; process (plm) of lamina medialis short, thick and broad, directed mesad, tip blunt; distal lobe (dlm) apically with two distinct lamellae, mesal and lateral lamellae equal in size, very broad and thick; epiproct short; male femora 5 and 6 slightly humped ventrally.

Type locality. Myanmar, Pegu (Taikkyii and Palon).

Redescription.

SIZE: Length ca. 23 mm (male), ca. 27 mm (female) width of midbody metazona ca. 1.7 mm (male), 2.3 mm (female). Width of head < collum < body ring 2 < 3 = 4 < 5–16, thereafter body gradually tapering toward telson.

COLOUR: In life with body probably brownish black (Pocock, 1895) or castaneous brown? (Golovatch and Enghoff, 1994). Colour in alcohol: after ca. 100 years changed to pale brown (lectotype) or rusty brown (paralectotypes).

ANTENNAE (Fig. 4.84D): Long and slender, probably reaching to body ring 5 (male) and 4–5 (female) when stretched dorsally.

COLLUM (Fig. 4.84A): With 3 transverse rows of setiferous tubercles, 4+4 anterior, 1+1 intermediate and 2+2 posterior tubercles (lateral tubercles of anterior row located near base of paraterga); paraterga of collum low, elevated almost in horizontal plane, directed caudolaterad, with one inconspicuous notch on lateral margin.

TEGUMENT: Quite dull; collum and metaterga coarsely microgranulate; prozona finely shagreened; surface below paraterga and sterna finely microgranulate; paraterga and epiproct smooth.

METATERGA (Fig. 4.84A–C): With 2 transverse rows of setiferous tubercles and setiferous cones; metaterga 2–8 with 2+2 anterior and 2(3)+2(3) posterior cones; metaterga 9–18 with 2+2 anterior and 3(2)+3(2) posterior cones (anterior cones shorter than posterior ones); metatergum 19 with 2+2 anterior and 3+3 posterior tubercles.

PARATERGA (Fig. 4.84E, F): Directed caudolaterad on body rings 2–17, elevated at ca. 50° (male) 45° (female); directed increasingly caudad on body rings 18 and 19; anterior margin with 2 distinct notches, on lateral margin of body rings 9, 10, 12, 13, 15–18 with tiny denticle near the tip.

TELSON (Fig. 4.85C–G): Epiproct short; tip truncate; lateral setiferous tubercles and apical tubercles inconspicuous. Hypoproct subtrapeziform; caudal margin round, with inconspicuous setiferous tubercles.

STERNA (Fig. 4.86): Cross-impressions shallow. Sternal lobe between male coxae 4 swollen, stout, subquadrate when seen in caudal view; base enlarged, slightly attenuated near tip; tip slightly emarginate.

LEGS (Fig. 4.85H–J): Very long and slender. Male femora 5 and 6 slightly humped ventrally in middle part.

GONOPODS (Fig. 4.87): Coxa (cx) longer than prefemur. Cannula (ca) slender. Prefemur (pfe) ca. 2/3 as long as femur. Femur (fe) long and slender. Mesal sulcus (ms) and lateral sulcus (ls) very deep. Postfemur (pof) conspicuous, ventrally wide. Solenophore (sph) well-developed: lamina lateralis (ll) swollen, stout: lamina medialis (lm) well-developed; process (plm) slightly short, thick and broad, directed mesad, tip blunt; distal lobe (dlm) well-developed, distally with two distinct lamellae (mesal lamella and lateral lamella equal in size, very broad and thick); broad lobe (blm) very thick, distinctly demarcated from distal lobe (dlm) by a conspicuous, shallow indentation. Solenomere (sl) quite long.

Distribution and habitat. This species is known from Myanmar – Rangoon and Pegu (Taikkyii and Palon). [Rangoon is currently Yangon. Pegu is presently Bago township (Hanthawaddy), Bago region. Taikkyii is Taikkyi township, Yangon region. Palon is probably a small village located in the area north to Taikkyii in the west of Pegu, Yangon region]. Taikkyii and Palon were formerly parts of Pegu region, now they belong to Yangon region. Therefore, the label of specimens collected by Fea gives the locality as Pegu (Taikkyii and Palon).

Habitat details for this species have never been reported; however, all locations are supposed to be granitic and limestone mountain ranges based on geological data, and the two locations were approximately 20 km apart.

We assume that *D. taurina* is distributed in a narrow range. A field survey near Yangon in 2015 revealed no further specimens of *D. taurina*. Therefore, we regard this species as endemic to Myanmar.

Note on material. In the original description Pocock (1895), wrote that all specimens were collected from Rangoon by Oates and from Pegu (Taikkyii and Palon) by Fea. Two females collected by Oates are now in NHMUK, one specimen collected by Fea in ZMH and two males collected by Oates in ZMUC.

The two males in ZMUC collected by Fea are labelled “cotypes”, and only “Palon” is given as locality whereas in the original description Pocock gave “Pegu (Taikkyii and Palon)”. We assume that these two males were probably collected from different locations, one from Taikkyii and one from Palon.

Weidner (1960) classified a specimen (unknown sex, not studied by us) of *Prionopeltis taurinus* (= *Desmoxytes taurina*) in ZMH as a “paratypoid”. However, Pocock (1895) and the following authors did not designate a holotype or lectotype for this species, thus, all specimens are syntypes.

The lectotype chosen is the ZMUC male with one remaining gonopod. The other ZMUC, ZMH and NHMUK specimens are designated here as paralectotypes.

Colour of type specimens: the lectotype is brown without metallic oxidation of the pin while the paralectotypes in NHMUK have become greenish black with metallic oxidation of the pin.

Remarks. This species has not been revised since Golovatch and Enghoff gave a good description in 1994. Golovatch and Enghoff (1994) described the collum with rows of 3(4?)+3(4?) anterior tubercles, suture between prozona and metazona distinctly beaded, pleurosternal carinae absent. After examining all known specimens except the one in ZMH, we found:

- collum with rows of 4+4 anterior tubercles (lateral tubercles near base of paraterga).

- suture between prozona and metazona not beaded, but with very small ridges of irregular shape.

- pleurosternal carinae of all specimens conspicuously present on body ring 2, very small ridges on body ring 3, thereafter missing.

We noticed that the number of cones (posterior row) on metaterga varies between individuals. Most specimens have metaterga 8 with 2+2 tubercles in the posterior row, but some have 3+2 tubercles. Metaterga 9–19 usually have 3+3 tubercles in the posterior row, whereas some individuals have with 3+4 or 4+3 tubercles.

The length of antenna in male could not be examined (antennae missing in both males), but the antennae are supposed to reach to ring 5 (Pocock 1895).

Coexisting species. None known.

Desmoxytes terae **(Jeekel, 1964)**

Figs 4.88–4.92

Pratinus terae Jeekel, 1964: 69; 1968: 51.

Pteroxytes terae – Jeekel 1980a: 655.

Desmoxytes terae – Golovatch and Enghoff 1994: 59. Enghoff 2005: 97. Nguyen and Sierwald 2013: 1243.

Material examined.

Holotype: Male (NBC), MALAYSIA, Perlis, Kaki Bukit, near Kampong Wang Tangga, 19 December 1958, leg. W.S.S van der Feen-van Benthem Jutting.

Paratypes: 1 female, 1 female fragment (NBC), same data as holotype.

Further specimens, all from THAILAND,

Satun Province: 1 male (ZMUC), Thale Ban National Park, in logs, litter, under stones, 6°42'N, 100°10'E, 8 November 1990, leg. M. Andersen and A. R. Rasmussen. 1 female (CUMZ), Khuan Don District, Thale Ban National Park, Tham Tone Din (Tone Din Cave), 6°43'35"N, 100°09'45"E, ca. 154 m a.s.l., 31 August 2015, leg. S. Sutcharit, A. Pholyotha, T. Seesamut and R. Srisonchai. 2 males, 6 females (CUMZ), 1 female (ZMUC), Khuan Don District, Thale Ban National Park, Tham Tone Din (Tone Din Cave), 6°43'35"N, 100°09'45"E, ca. 154 m a.s.l., 7 July 2017, leg. S. Sutcharit, R. Srisonchai and ASRU members.

Diagnosis. Differs from all other *Desmoxytes* species by the combination of the following characters; body black or brownish black contrasting with yellowish white paraterga with a triangular dorsal, dark spot; sternal lobe between male coxae 4 short and stout, broad at base, trapeziform or semicircular; male femora 5 and 6 without modification; lamina lateralis (ll) with big and long lobe-like structure projecting ventroanteriad.

Type locality. MALAYSIA, Perlis, Kaki Bukit, near Kampong Wang Tangga.

The redescription hereunder is modified from Jeekel (1964); we 'harmonized' descriptions of all morphological characters and added some morphological characteristics from additional specimens.

Redescription.

SIZE: Length 28–32 mm (male), 28–34 mm (female); width of midbody metazona ca. 2.4 mm (male), 3.1 mm (female). Width of head < collum ≤ body ring 2 ≤ 3 = 4 < 5–17, thereafter body gradually tapering toward telson.

COLOUR (Fig. 4.88A, B): In life with body black or brownish black; paraterga yellowish white (dorsal side with triangular dark brown spot); metaterga, surface below paraterga and prozona black or brownish black; head black; antenna brownish black (except distal part of antennomere 7 and antennomere 8 whitish); legs brown; sterna brown to yellowish brown; a few basal podomeres and epiproct pale brown. Colour in alcohol: after 49 years changed to whitish brown, 2–5 years changed to pale blackish brown.

ANTENNAE (Fig. 4.89D): Long and slender, reaching to body ring 6 (male), and 5 (female) when stretched dorsally.

COLLUM (Fig. 4.89A): With 3 transverse rows of setae and tubercles, 3+3 anterior setae, 1+1 intermediate tubercles and 2+2 posterior tubercles (tubercles small, without setae), lateral tubercles of posterior row located more anteriorly, almost halfway to intermediate row; paraterga of collum with two distinct setiferous notches on lateral margin, directed caudolaterad, almost horizontal.

TEGUMENT: Quite dull, sometimes shining; collum coarsely microgranulate; prozona, metaterga and surface below paraterga finely microgranulate; paraterga smooth (dorsal side finely microgranulate); sterna and epiproct smooth.

METATERGA (Fig. 4.89A–C): With 2 transverse rows of tubercles; metaterga 2–19 with 2+2 anterior and 2+2 posterior tubercles.

PARATERGA (Fig. 4.89E, F): Directed caudolaterad on body rings 2–17, elevated ca. 5°–10° above the horizontal plane in both sexes; directed increasingly caudad on body rings 18 and 19; anterior margin with 2 distinct notches, on lateral margin of body rings 9, 10, 12, 13, 15–18 with very small and tiny denticle near the tip.

TELSON (Fig. 4.90C–G): Epiproct: tip usually subtruncate (in some specimens slightly emarginate); lateral setiferous tubercles usually conspicuous (in some specimens inconspicuous), quite short; apical tubercles inconspicuous. Hypoproct trapeziform; caudal margin usually subtruncate (in some specimens slightly round), with big and conspicuous setiferous tubercles.

STERNA (Fig. 4.91): Cross-impressions quite deep. Sternal lobe between male coxae 4 swollen, short and stout, broad at base, usually trapeziform (in some specimens semicircular), tip usually truncate (in some specimens round).

LEGS (Fig. 4.90H–J): Long and slender. Male femora 5 and 6 without modification.

GONOPODS (Fig. 4.92): Coxa (cx) longer than prefemur. Cannula (ca) slender. Prefemur (pfe) ca. 2/3 as long as femur, quite short and stout. Femur (fe) long and slender. Mesal sulcus (ms) and lateral sulcus (ls) deep. Postfemur (pof) conspicuous, ventrally wide. Solenophore (sph) well-developed: lamina lateralis (ll) swollen, with a big and long lobe-like structure projecting ventroanteriad: lamina medialis (lm) well-developed, longer than lamina lateralis; process (plm) short; distal lobe (dlm) quite broad, distally with two lamellae (mesal lamella shorter than lateral one); broad lobe (blm) long and thick, obviously demarcated from distal lobe (dlm) by a slightly deep and wide indentation. Solenomere (sl) very long.

Distribution and habitat. This species is known only from the Malaysia–Thailand borderland (Kaki Bukit and Thale Ban National Park). We noticed that it prefers to live on humid mosses, logs or litter in limestone habitats (Fig. 4.88C). The localities are all on limestone mountains. The species is probably distributed in a narrow range in limestone areas near the Thai–Malay border. *D. terae* has so far been recorded from three localities (near Kaki Bukit, Thale Ban National Park and Tham Tone Din) which are located only 10–15 km apart. Despite several attempts by us, *D. terae* was not found in other areas. Hence, this species should be regarded as endemic to the Malaysia and Thailand faunas.

Remarks. In the recent field surveys we noticed that the colour of living specimens is black or brownish black with contrasting white paraterga as reported earlier by Jeekel (1964) and Golovatch and Enghoff (1994). This species blends so perfectly with its environment that it is difficult to collect specimens without a flashlight.

In the original description, Jeekel (1964) stated about the collum: “near the anterior margin a transverse row of six hairs, which may be present partly rubbed off, the lateral pair placed on the low tubercles”. This means collum with 1 row of 3+3 anterior setae/tubercles. Moreover, Jeekel also described paraterga without a tiny denticle near the tip. After we examined all specimens, it is clear that:

- Collum with 3 rows of 3+3 anterior setae, 1+1 intermediate tubercles and 2+2 posterior tubercles (tubercles without setae, quite small but conspicuous).

- Paraterga of body rings 9, 10, 12, 13, 15–18 with tiny denticle near ther tip, albeit all quite small.

The sternal lobe between male coxae 4 shows some variation within populations; the lobe of some specimens is trapeziform whereas in others it is semicircular. We also found some variability on the telson: tip of epiproct subtruncate in some individuals, in others slightly emarginate; lateral setiferous tubercles conspicuous in some specimens, inconspicuous in others; caudal margin of hypoproct truncate in some individuals, slightly round in others.

Coexisting species. This species and *D. delfae* are sympatric at Tam Ton Din.

Desmoxytes waepyanensis **Srisonchai, Enghoff and Panha sp. n.**

Figs 4.93–4.98

Holotype: Male (CUMZ), MYANMAR, Kayin State, 12 km south of Kamarmuang City, Wae Pyan Cave, 17°13'38"N, 97°37'24"E, ca. 24 m a.s.l., 20 June 2015, leg. S. Panha and FFI staffs.

Paratypes: 5 males, 12 females, 1 juvenile (CUMZ), 1 male, 1 female (ZMUC), same data as holotype.

Diagnosis. Differs from all congeners by having: metaterga 2–8 with two rows of 2+2 (anterior) setiferous cones and 3(2)+3(2) (posterior) setiferous spines; metaterga 9–18 with two rows of 3+3 (anterior) setiferous cones and 4(3)+4(3) (posterior) setiferous spines; ventral lobe (vll) of lamina lateralis short and stout, digitiform; process (plm) of lamina lateralis tube-like, quite long.

Etymology. The name is a Latin adjective, referring to the type locality.

Description.

SIZE: Length 29–33 mm (male), 33–35 mm (female); width of midbody metazona ca. 2.2 mm (male), 2.8 mm (female). Width of head < collum = body ring 2 < 3 = 4 < 5–16, thereafter body gradually tapering towards telson.

COLOUR (Fig. 4.93A–D): In life with body pinkish brown; paraterga pink; antenna brownish black, except distal part of antennomere 7 and antennomere 8 whitish; collum and metaterga pinkish brown; head, surface below paraterga, sterna and epiproct brown; legs brownish black; a few basal podomeres pink.

ANTENNAE (Fig. 4.94D): Moderately long and slender, reaching to body ring 6 (male) and 4–5 (female) when stretched dorsally.

COLLUM (Fig. 4.94A): With 3 transverse rows of setiferous tubercles, 4(5)+4(5) anterior, 1+1 intermediate and 3(2)+3(2) posterior tubercles (lateral tubercles of anterior row located almost at base of paraterga in some specimens); paraterga of collum low, elevated at ca. 15°–20°, directed caudolaterad, with one conspicuous setiferous notch on lateral margin.

TEGUMENT: Quite dull, but slightly shining; collum and metaterga microgranulate; prozona finely shagreened; surface below paraterga finely microgranulate; sterna and epiproct somewhat smooth.

METATERGA (Fig. 4.94A–C): With 2 transverse rows of setiferous cones and spines; metaterga 2–8 with 2+2 anterior cones and 3(2)+3(2) posterior spines; metaterga 9–18 with 3+3 anterior cones and 4(3)+4(3) posterior spines; metatergum 19 with 3+3 anterior cones and 4+4 posterior cones.

PARATERGA (Fig. 4.94E, F): Directed caudolaterad on body rings 2–17, elevated at ca. 50° (male) 45° (female); directed increasingly caudad on body rings 18 and 19; anterior margin with 2 distinct notches, on lateral margin of body rings 9, 10, 12, 13, 15–18 with tiny denticle near the tip.

TELSON (Fig. 4.95C–G): Epiproct: tip subtruncate, lateral setiferous tubercles and apical tubercles inconspicuous. Hypoproct subtrapeziform; caudal margin round, with small but conspicuous setiferous tubercles.

STERNA (Fig. 4.96): Cross-impressions shallow. Sternal lobe between male coxae 4 trapeziform, tip truncate, thin in lateral view.

LEGS (Fig. 4.95H–J): Long and slender. Male femora 5 and 6 moderately humped ventrally in middle portion.

GONOPODS (Figs 4.97, 4.98): Coxa (cx) longer than prefemur. Cannula (ca) slender. Prefemur (pfe) ca. 2/3 as long as femur. Femur (fe) long and slender. Mesal sulcus (ms) and lateral sulcus (ls) conspicuous, deep. Postfemur (pof) conspicuous, ventrally wide. Solenophore (sph) well-developed: lamina lateralis (ll) swollen, broad; ventral lobe (vll) conspicuous, short and stout, digitiform: lamina medialis (lm) well-developed; process (plm) somewhat long, tube-like, tip usually terminating in three or two sharp small spines (in some specimens just one spine or tip blunt); distal lobe (dlm) distally with two lamellae, mesal lamella smaller and shorter than lateral one; broad lobe (blm) thick dorsally with ridges on edge. Solenomere (sl) relatively long.

Distribution and habitat. Known only from the type locality in a limestone area (Fig. 4.93E). We assume that it is distributed in Kayin State. We made an intensive search for this species in September 2016 in Mawlamyine State (very close to Kayin State), however, no further specimens were found. Since it is so far known only from the type locality, *D. waepyanensis* sp. n. should be regarded as endemic to Myanmar.

Remarks. The tip of process (plm) on lamina medialis is quite variable, having one, two, or three small spine(s), or being almost blunt in some specimens.

This species seems to be aposematic, to judge by the remarkable pink paraterga and pinkish brown body.

Coexisting species. None known.

Discussion

Our analyses of morphology, as well as our preliminary molecular phylogeny, supports the subdivision of *Desmoxytes s.l.* into five groups (*Desmoxytes* s.s., the '*acantherpestes*' group, the '*gigas*' group, the '*spiny*' group and *Hylomus*). All groups are clearly defined on morphological characters, especially of the gonopods and paraterga (Figs 4.2, 4.3). The distribution areas of the groups seem to be clear in their boundaries. The *Hylomus* group is more diverse in shape of paraterga, however, its members show a notable similarity in gonopod shape (Fig. 4.2E, F).

Desmoxytes s.s., the focus of the present paper, is well-defined based on gonopod characters especially the solenophore (lamina lateralis (ll) and lamina medialis (lm)). Species of *Desmoxytes* s.s. share several morphological similarities including wing-like paraterga; lamina lateralis (ll) swollen; lamina medialis (lm) comprised of process (plm), distal lobe (dlm) and broad lobe (blm); and the modification of male femora 5 and 6 only (exception: *D. terae*). Certain morphological characters show intra- and inter-population variations within the same species. The most variable characters within populations are:

- colour: variation seen in *D. cervina*, *D. delfae*, *D. takensis* and *D. euros* sp. n.

- tubercles/cones/spines on metaterga 9–19: number of tubercles/cones/spines sometimes decrease or increase in some rings – seen in *D. taurina*, *D. purpurosea*, *D. breviverpa*, *D. takensis*, *D. golovatchi* sp. n., *D. octoconigera* sp. n. and *D. waepyanensis* sp. n. This variable character is not significant for species identification.

- sternal lobe between male coxae 4: many species seem to be variable in the shape of the tip – seen in *D. planata*, *D. cervina*, *D. delfae*, *D. purpurosea*, *D. aurata* sp. n., *D. corythosaurus* sp. n. and *D. golovatchi* sp. n.

- process (plm) of lamina medialis: tip terminating in one or more spines – seen in *D. cervina*, *D. purpurosea* and *D. octoconigera* sp. n.: tip sharp or blunt – seen in *D. breviverpa*, *D. pinnasquali* and *D. takensis*.

Inter-population variation was also found in some species as follows:

- size: In *D. purpurosea*, specimens in the two main northern populations are clearly bigger than those from the two main southern populations. Specimens in a population of *D. planata* from Great Cocos Island seem to be smaller than others.

- colour: colour variation of living specimens of dragon millipedes is reported here for the first time. *D. cervina* includes brownish red as well as brown individuals. Specimens from the northern populations of *D. takensis* are red and those from southern populations are pink; however, the other morphological characters are identical.

Variation of colour and size within and between populations may at least in part be due to quality and quantity of food, differences in the physical environment (temperature, soil, humidity), like in other arthropods. Hagen (1881) and Buckton (1879) found that the colour of some arthropods was affected by nutrients and temperature. Many studies, e.g. Baker (1989) and Juliano (1986), have shown that food is one of the main factors controlling growth rate, body size, etc. in arthropods. For millipedes, there is the study by Berns and Keeton (1968) on *Narceus annularis* (order Spirobolida) showing that semi-starved individuals attained smaller body sizes than well-fed ones. David and Célérier (1997) showed that individuals of *Polydesmus angustus* kept on a diet of leaf litter plus yeast attained larger body sizes than individuals fed on leaf litter alone. On this background we assume that food and the physical environment may affect colour and size in *Desmoxytes*. Another possible factor controlling differences in colour and size might be the genetic variation within and between populations.

There are some species showing great resemblance in gonopod characters. In particular, *D. planata* and *D. euros* sp. n. are remarkable in having identical gonopods. Nevertheless, the yellow paraterga, shape of hypoproct and the initial study on mitochondrial COI gene supports to separate them as different species. The *D. planata*-*D. euros* sp. n. case reminds of what Pimvichai *et al.* (2011b) found for *Thyropygus induratus* Attems, 1936 vs *T. quietus* Attems, 1938: a pair of species with virtually identical gonopods but significant genetic and non-gonopodal morphological differences.

Desmoxytes (and other dragon millipedes) are particularly attractive animals because of the peculiar paraterga, in combination with the unusual vivid colour in some species. The bright colour probably is a warning signal (Marek and Moore, 2015; Shear, 2015; Svádová *et al.*, 2009). Many mating couples were found during our field surveys, and we collected some representative couples and reared a few specimens of *D. euros* sp. n. and *D. takensis* in acrylic boxes, feeding them with natural litter. We observed that the millipedes made moulting chambers using fecal material and silk as found in other polydesmidan families such as Polydesmidae and Pyrgodesmidae, as well as in the order Callipodida (Adis *et al.*, 2000; Reboleira and Enghoff, 2016; Youngsteadt, 2009). We also observed a host-parasitic association between millipedes and mites in *D. cervina* (probably the mites belong in genus *Leptus* Latreille, 1976). We assume that the mite species is a parasite, like in other *Leptus* spp. (Southcott, 1992) which use the millipede host for nourishment and dispersal purposes.

Figs 4.99 and 4.100 clearly show that all *Desmoxytes* species (except *D. planata*) are narrowly distributed, and all are restricted to limestone habitats or granitic mountains. The narrow distributional ranges of *Desmoxytes* species are perhaps the result of their poor dispersal capacities.

Desmoxytes planata, a pantropical species, has been recorded from widely scattered places. According to our survey we suspect that *D. planata* is probably originally native to Thailand or Myanmar. Especially in Thailand, we noticed that it ranges from Chiang Rai (northern end) to Chumphon Province (middle) (Fig. 4.100).

The species diversity of dragon millipedes is impressive. At the moment, Thailand, Malaysia, and Myanmar contain 18 species of *Desmoxytes*. We believe that many more new species remain to be discovered, especially in Thailand, Myanmar, Malaysia, Cambodia, and Laos.

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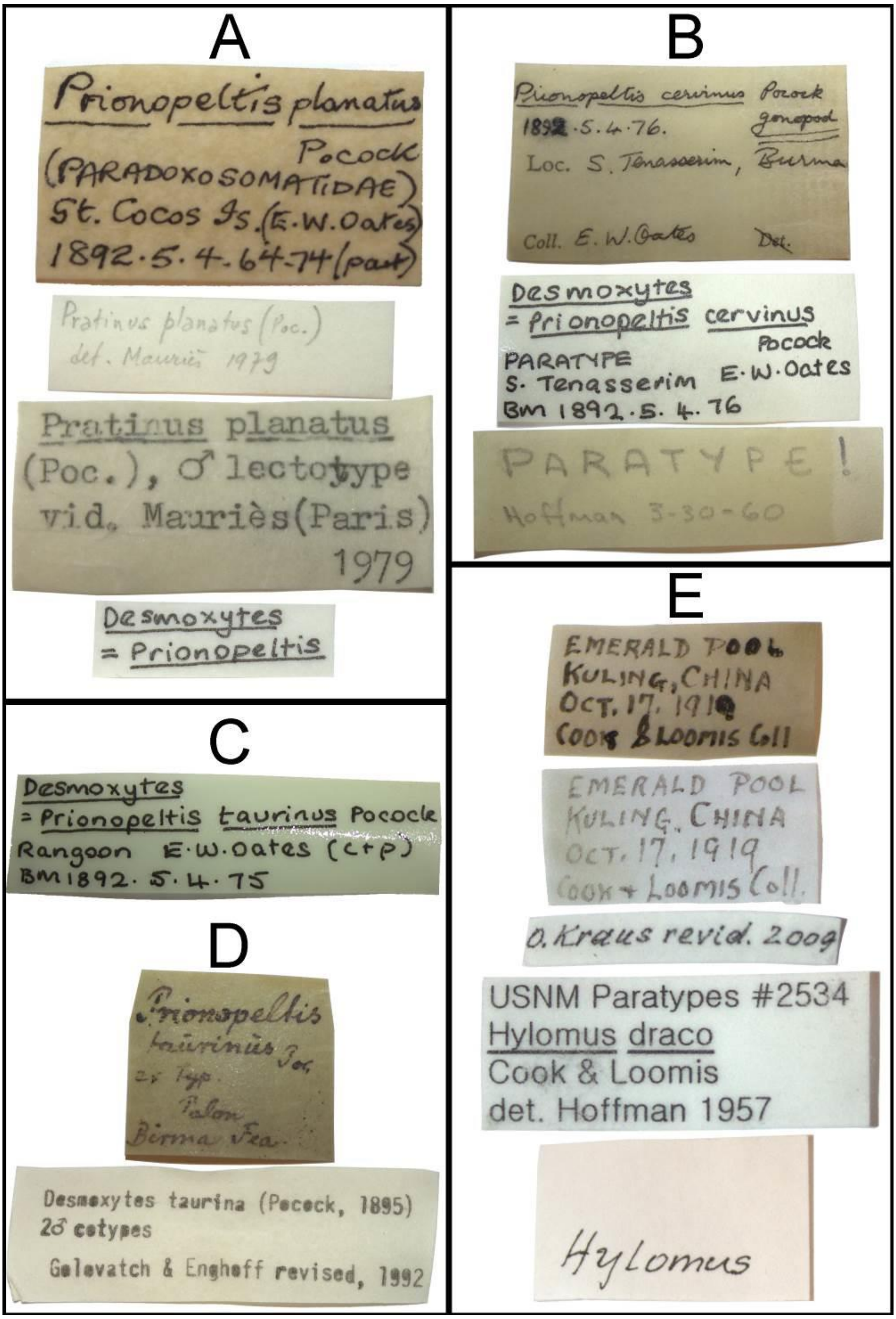

Figure 4.1 Some original and additional labels of some lectotypes and paratypes. **A** *Desmoxytes planata* (Pocock, 1895) (NHMUK) **B** *D. cervina* (Pocock, 1895) (NHMUK) **C** *D. taurina* (Pocock, 1895) (NHMUK) **D** *D. taurina* (Pocock, 1895) (ZMUC) **E** *Hylomus draco* Cook and Loomis, 1924 (USNM).

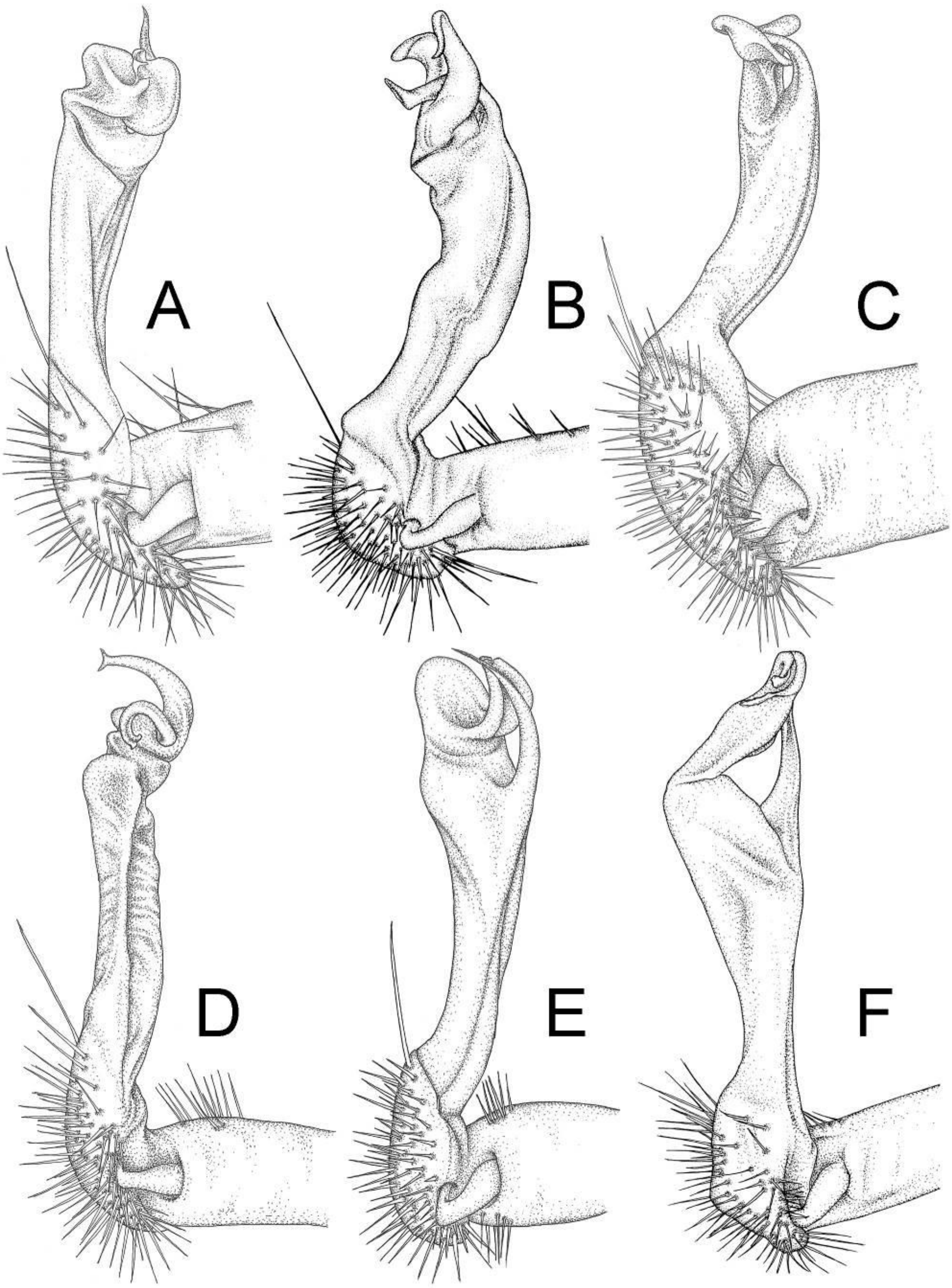

Figure 4.2 Shape of gonopod of *Desmoxytes s.l.* **A** *Desmoxytes* s.s. (*D. planata* (Pocock, 1895)) – specimen from Wat Puang Malai **B** the '*acantherpestes*' group (specimen from Kanchanaburi, Thailand) **C** the '*gigas*' group (specimen from Krabi, Thailand) **D** the 'spiny' group (specimen from Krabi, Thailand) **E, F** *Hylomus* Cook and Loomis, 1924 (**E** = *H. draco* Cook and Loomis, 1924 stat. rev. (paratype) **F** = *Hylomus* sp. (specimen from Laos)).

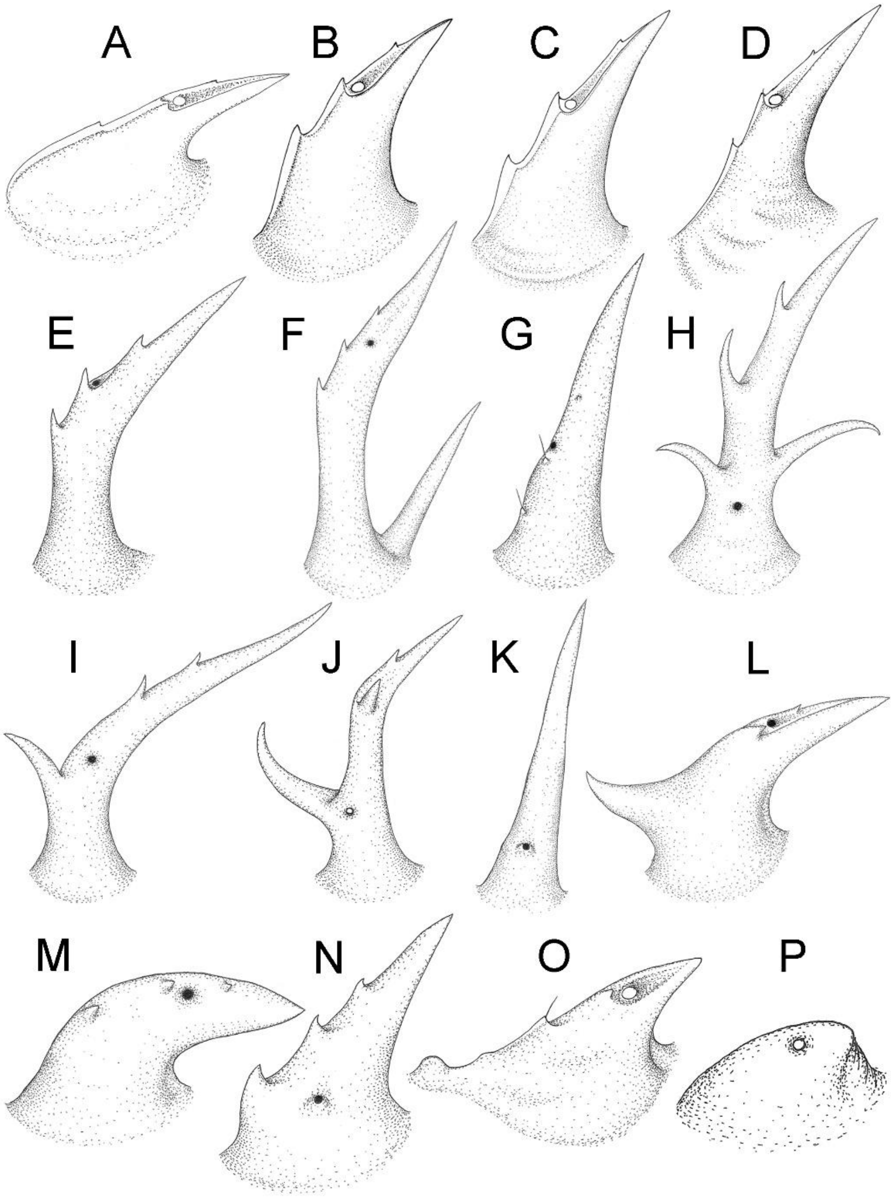

Figure 4.3 Type of paranota (paraterga) of *Desmoxytes s.l.* **A–D** *Desmoxytes s.s.* **A** *D. delfae* (Jeekel, 1964), specimen from Tham Khan Ti Phol **B** *D. planata* (Pocock, 1895), specimen from Suan Sai Thong Restaurant **C** = *D. purpurosea* Enghoff *et al.*, 2007, specimen from Hup Pa Tard **D** *D. cervina* (Pocock, 1895), specimen from Wat Satit Khirirom **E** the '*acantherpestes*' group **F** the '*gigas*' group **G** the 'spiny' group **H–P** *Hylomus* Cook and Loomis, 1924 **H** *H. draco* Cook and Loomis, 1924 stat. rev., paratype **I** *H. cervarius* (Attems, 1953) comb. n., ZMUM specimen **J** *H. rhinoceros* (Likhitrakarn *et al.*, 2015) comb. n., paratype **K** *H. scolopendroides* (Golovatch *et al.*, 2010) comb. n., paratype **L** *H. nodulosus* (Liu *et al.*, 2014) comb. n., paratype **M** *H. eupterygotus* (Golovatch *et al.*, 2012) comb. n., paratype **N** *H. scutigeroides* (Golovatch *et al.*, 2010) comb. n., paratype **O** *H. simplex* (Golovatch *et al.*, 2016) comb. n., paratype **P** *H. laticollis* (Liu *et al.*, 2016) comb. n., paratype.

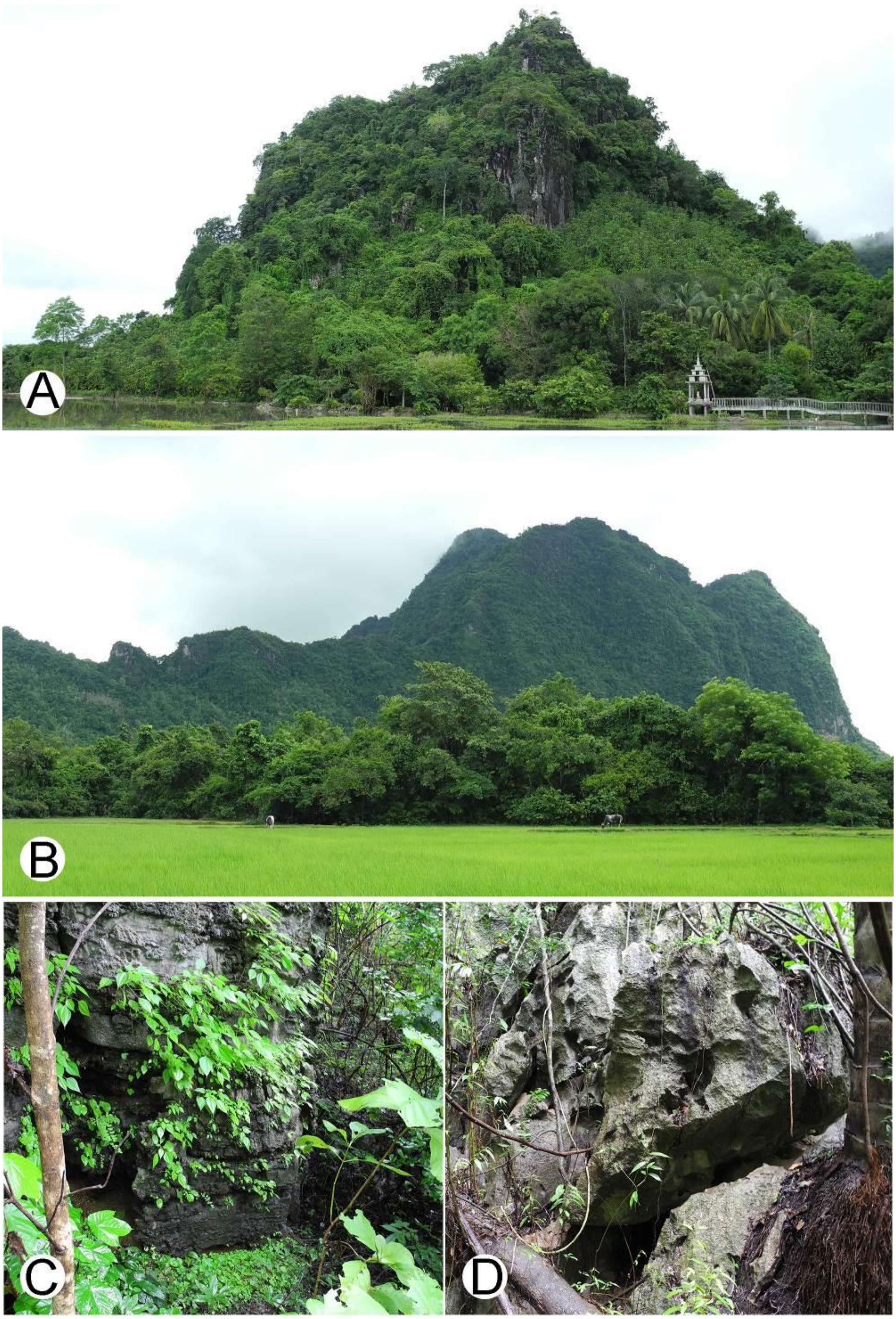

Figure 4.4 Common habitats for *Desmoxytes* Chamberlin, 1923. **A, B** limestone mountain **C** rock wall and plants **D** rock wall and small cave.

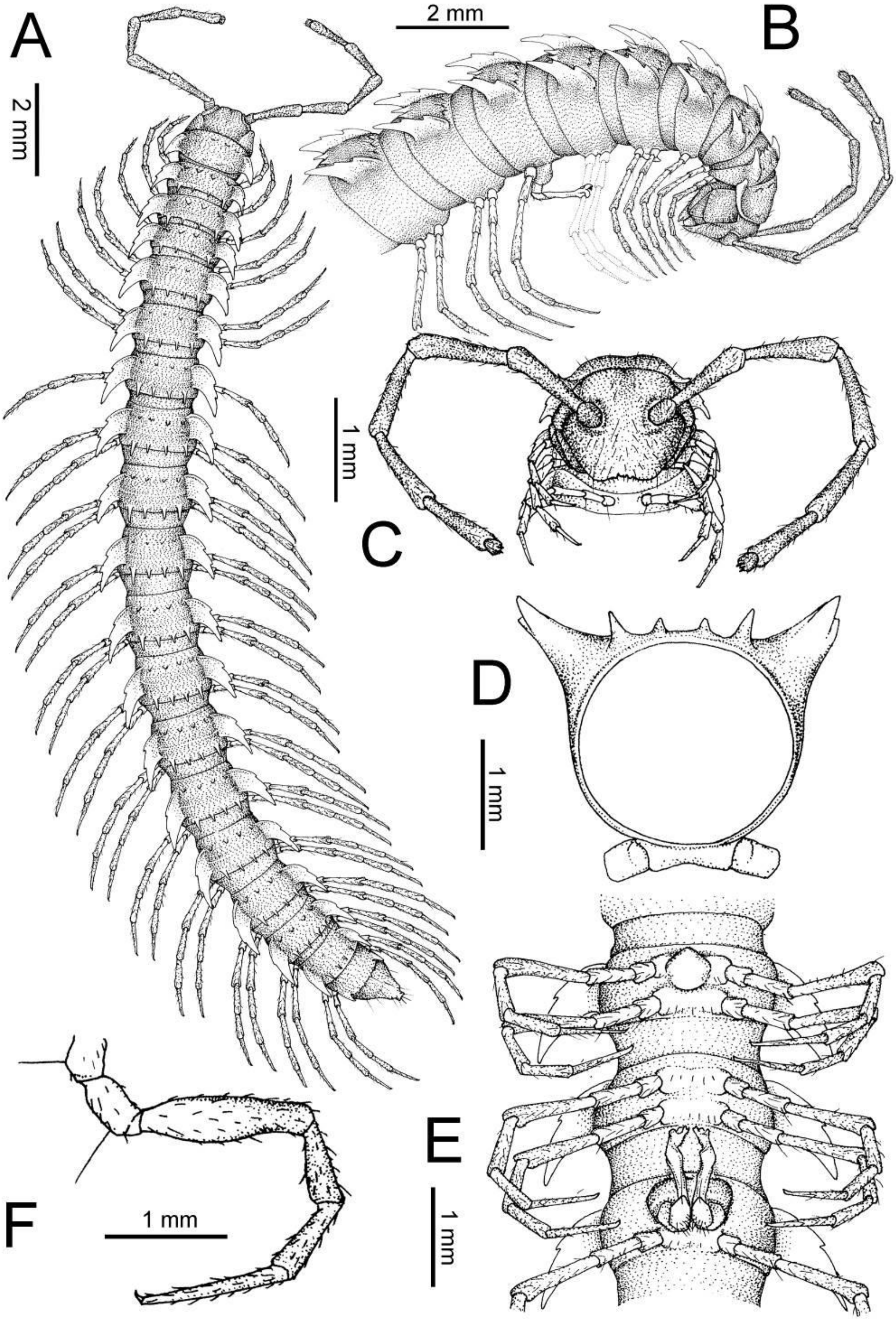

Figure 4.5 General body characters of *Desmoxytes* – *D. planata* (Pocock, 1895), male specimen from Wat Puang Malai**.** **A** whole body **B** anterior body part **C** head region **D** body ring **E** body rings 5–7, showing sternal lobe between coxae 4 and gonopods on ring 7 **F** male femora 5 or 6.

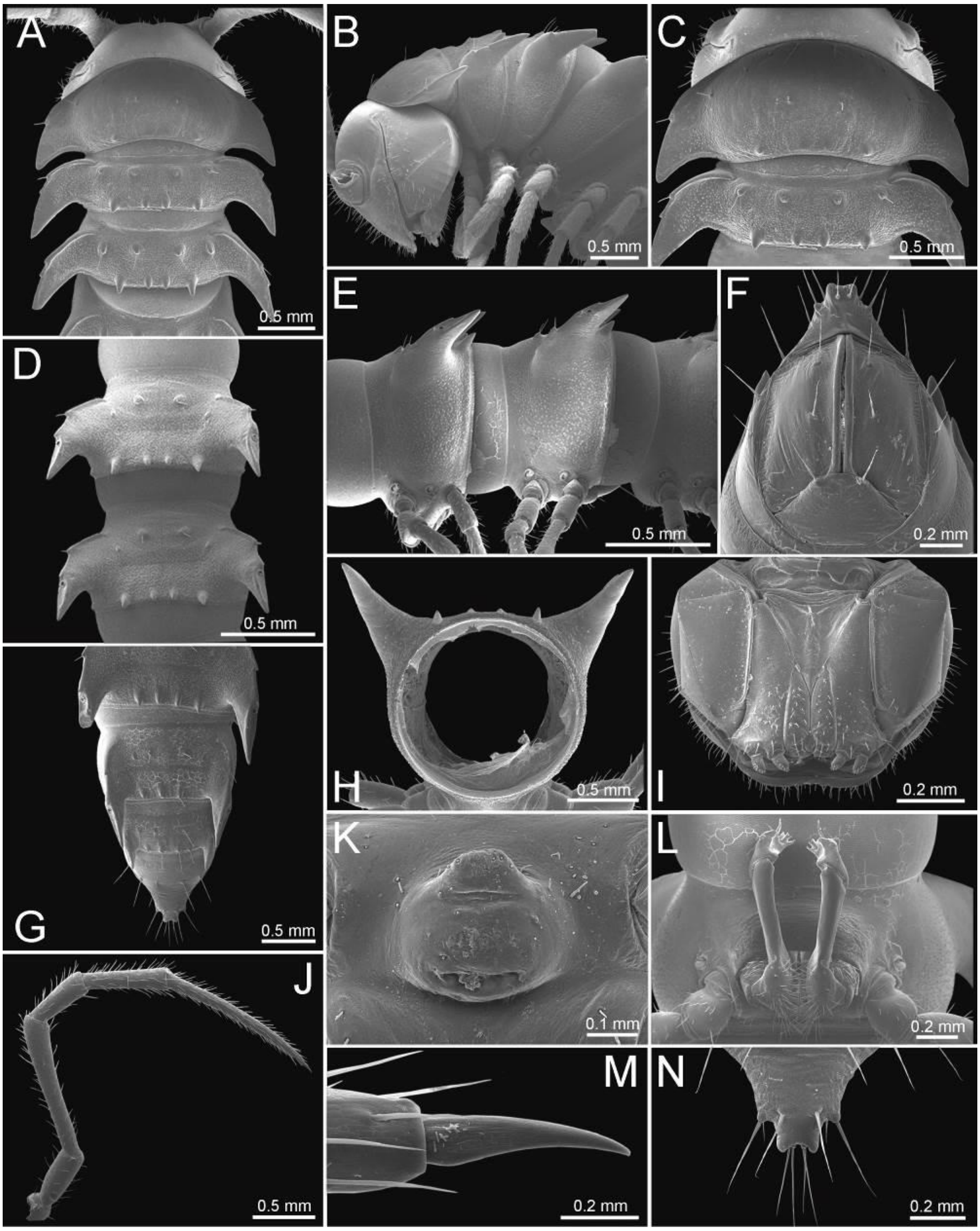

Figure 4.6 General body characters of *Desmoxytes* (*D. planata* (Pocock, 1895), male specimen from Wat Puang Malai) – SEM images**. A, B** anterior body part **C** collum **D, E** body rings 9–10 **F** last ring and telson **G** posteriormost rings **H** body ring 10 **I** mouth parts **J** leg 13 (right) **K** sternal lobe between male coxae 4 **L** gonopods on ring 7 **M** tip of tarsus and claw of leg 13 **N** tip of epiproct.

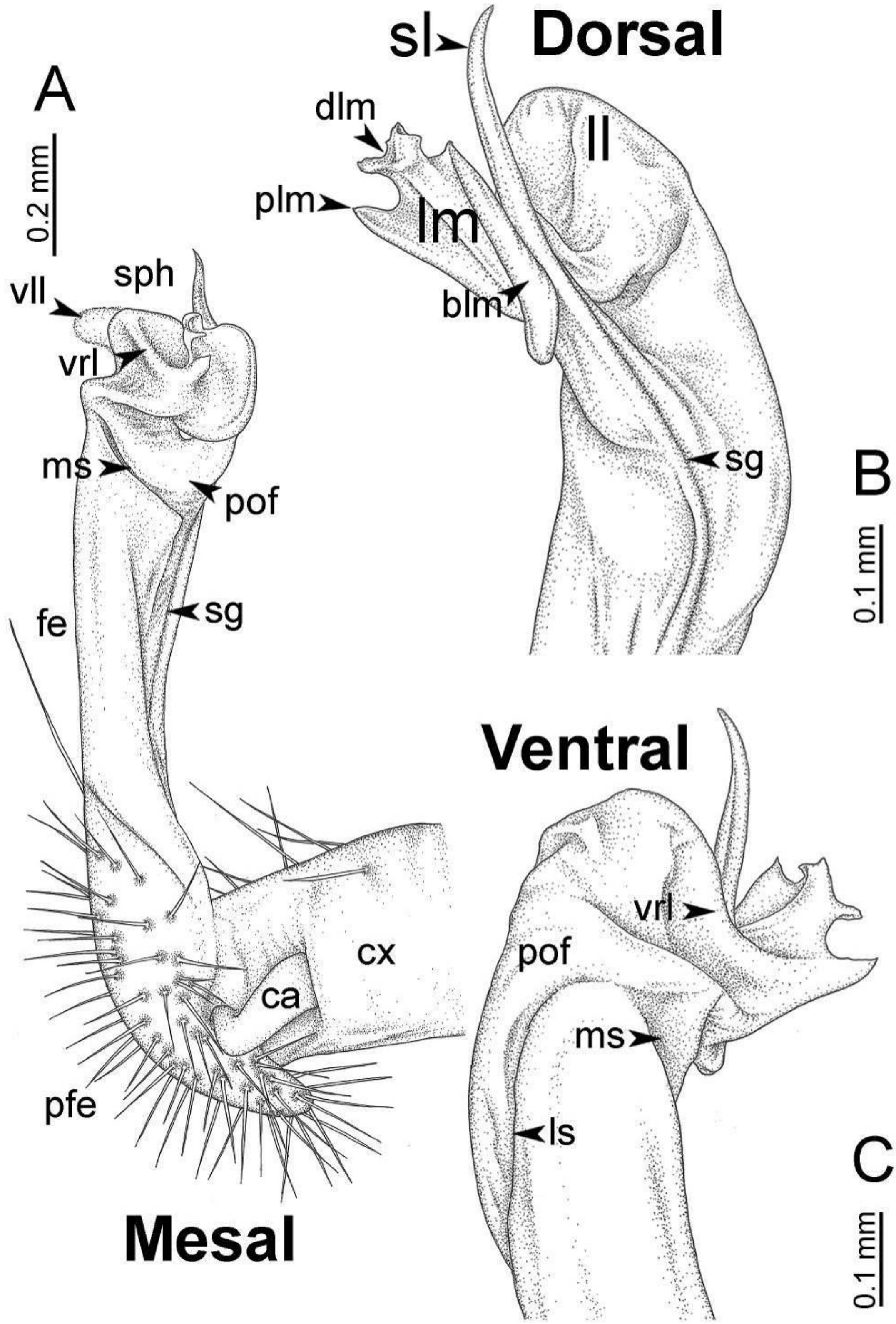

Figure 4.7 Diagrammatic drawings of right gonopod of *Desmoxytes D. planata* (Pocock, 1895), specimen from Wat Puang Malai. **A** mesal view **B** dorsal view **C** ventral view.

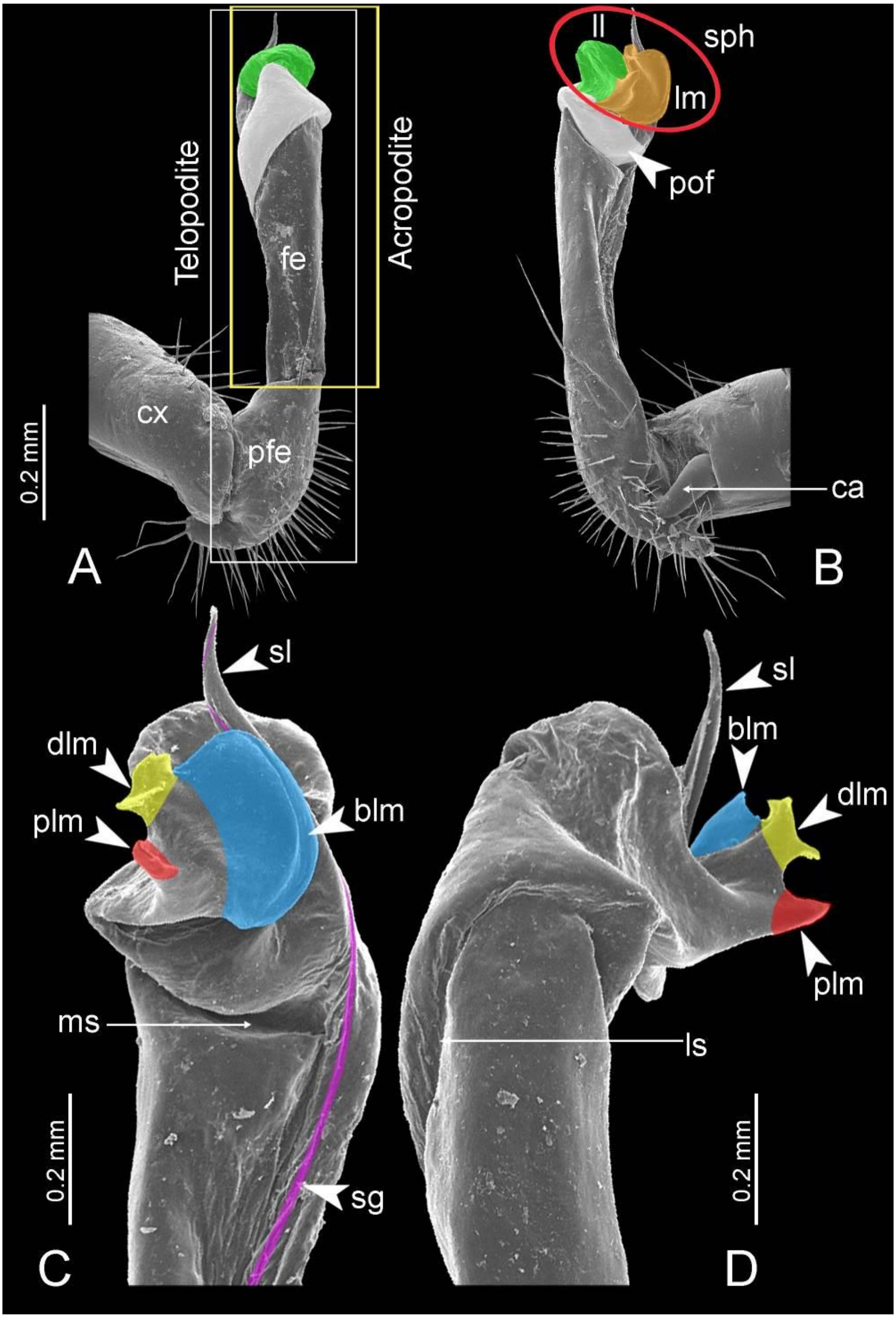

Figure 4.8 SEM images of right gonopod of *Desmoxytes planata* (Pocock, 1895), specimen from Wat Puang Malai. **A** lateral view **B** mesal view **C** submesal view **D** ventral view.

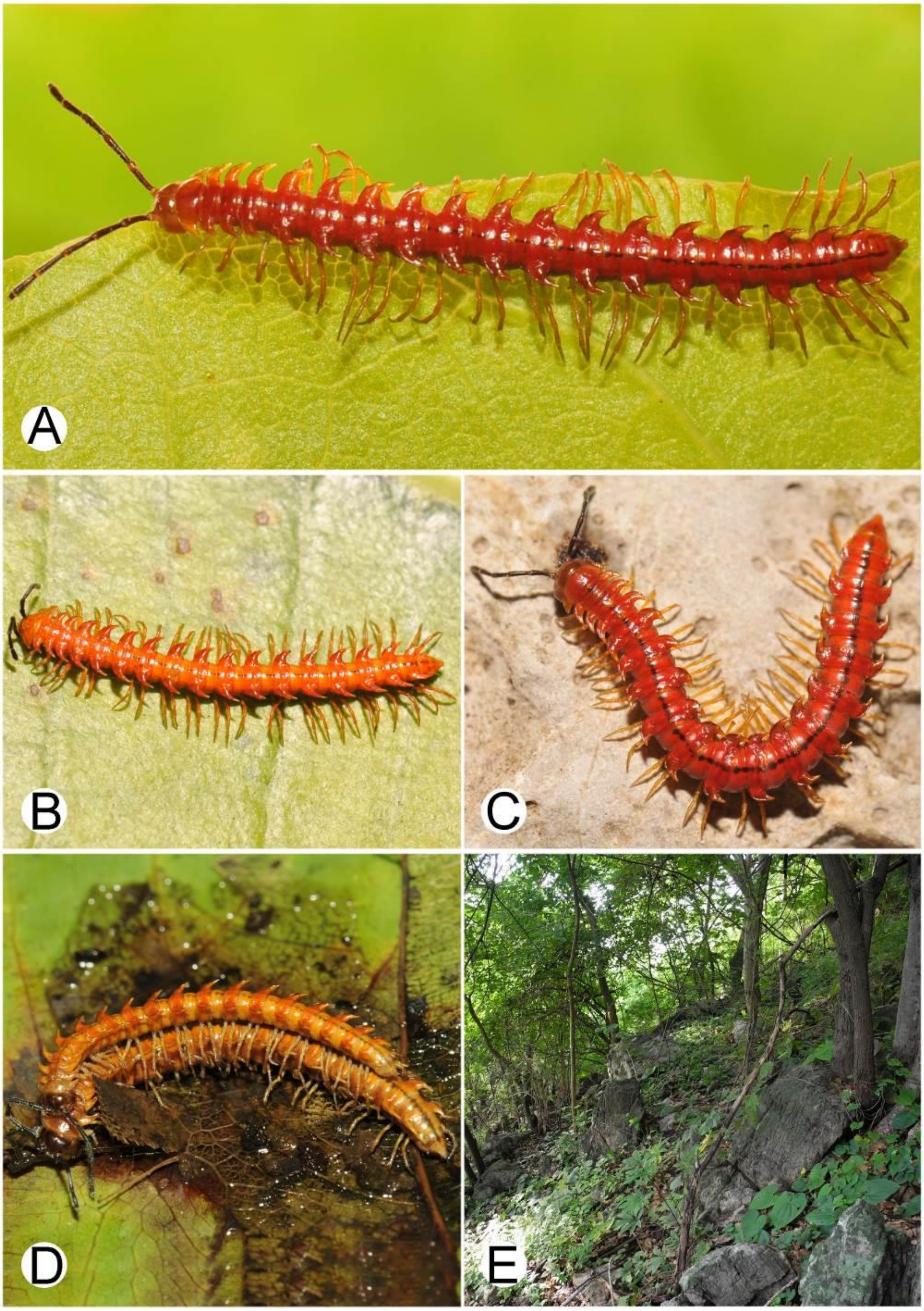

Figure 4.9 Photographs of live *Desmoxytes aurata* sp. n. and habitat. **A, B** male paratype **C** female paratype **D** mating couple **E** habitat.

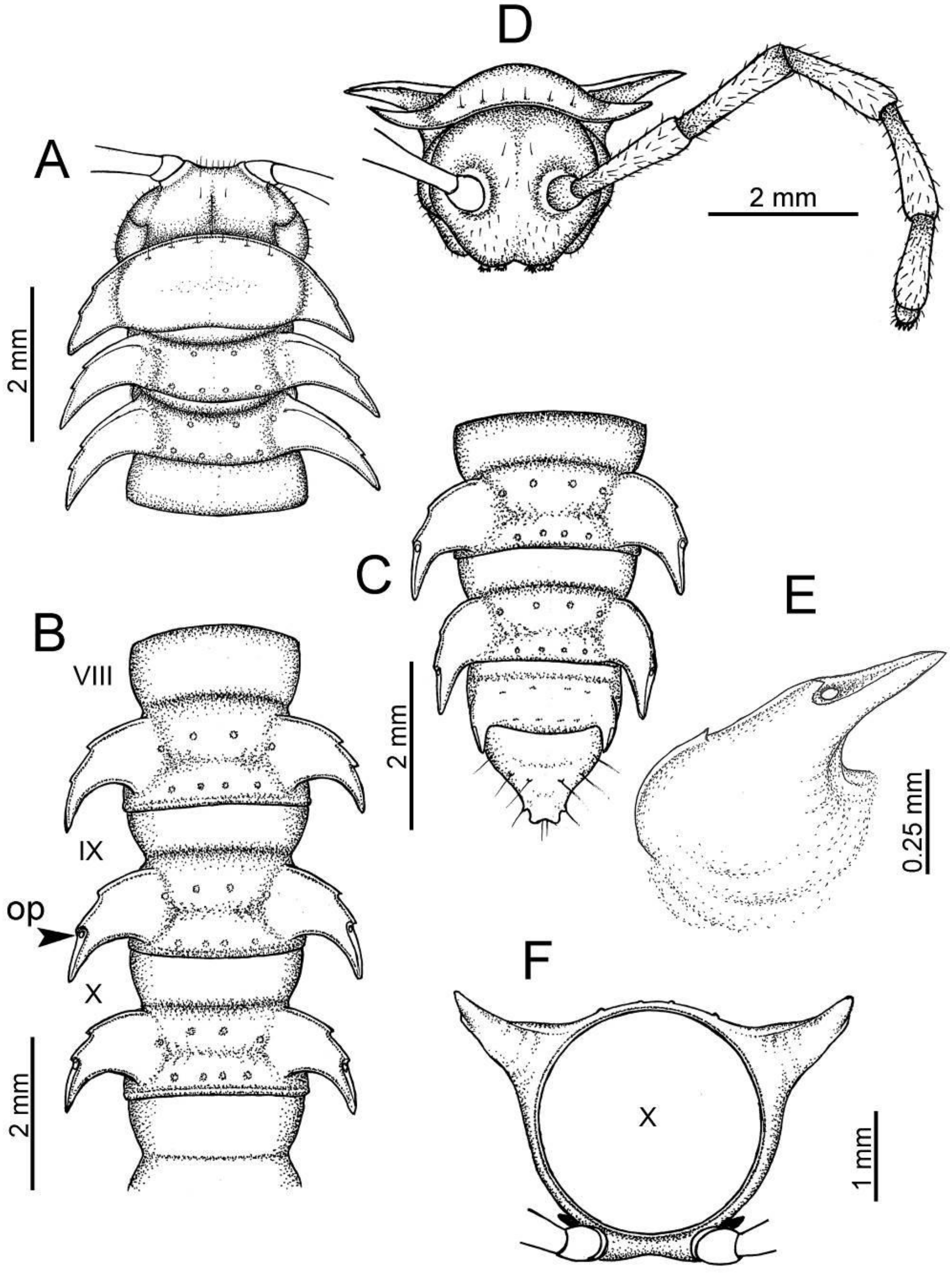

Figure 4.10 *Desmoxytes aurata* sp. n. (male paratype). A anterior body part B body rings 8–10 (op = ozopore) C posteriormost body rings and telson D head and antenna E paraterga of ring 10 F body ring 10.

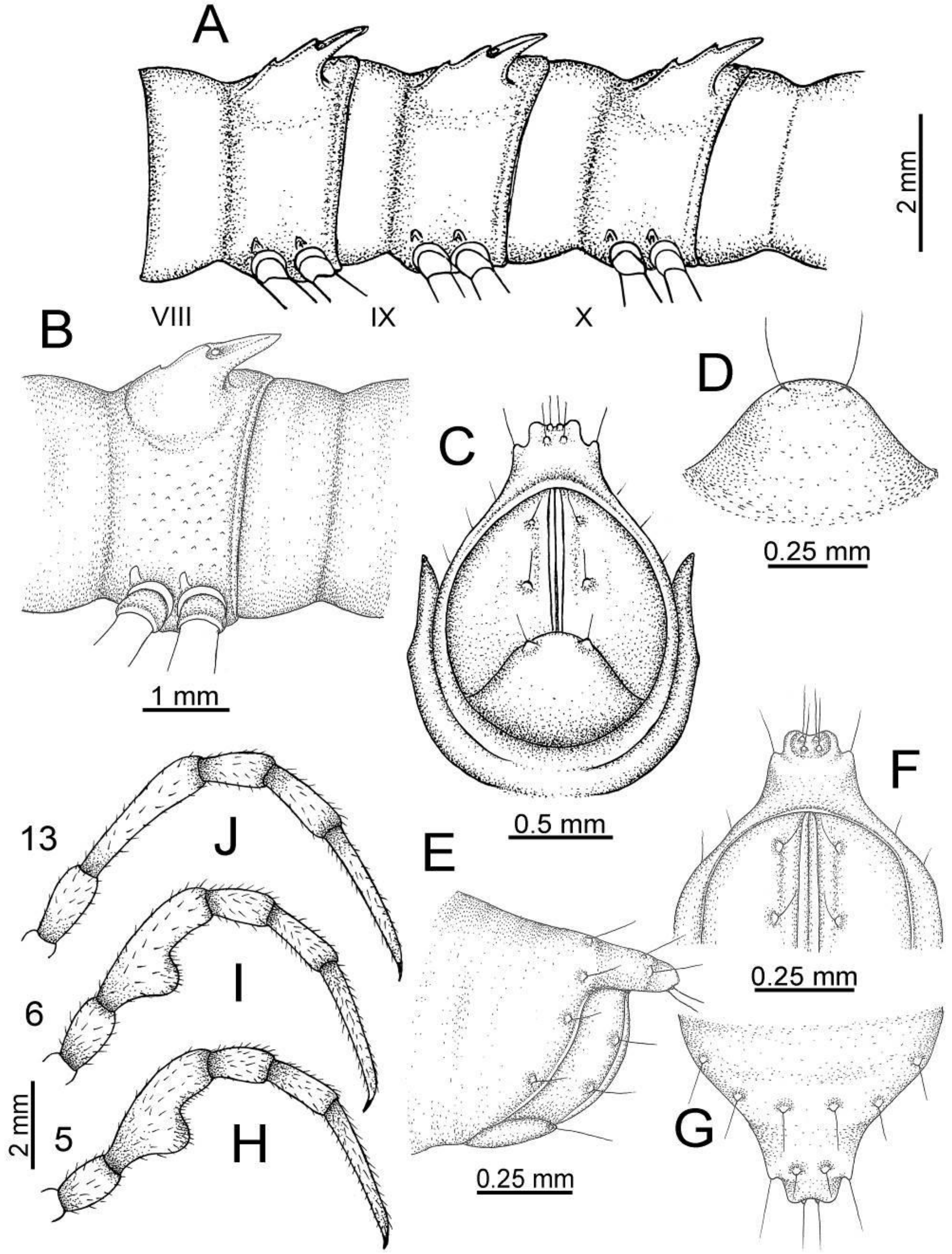

Figure 4.11 *Desmoxytes aurata* sp. n. (paratypes). **A** body rings 8–10 **B** sculpture of ring 10 **C, E** last ring and telson **D** hypoproct **F, G** epiproct **H** male leg 5 (right) **I** male leg 6 (right) **J** male leg 13 (right).

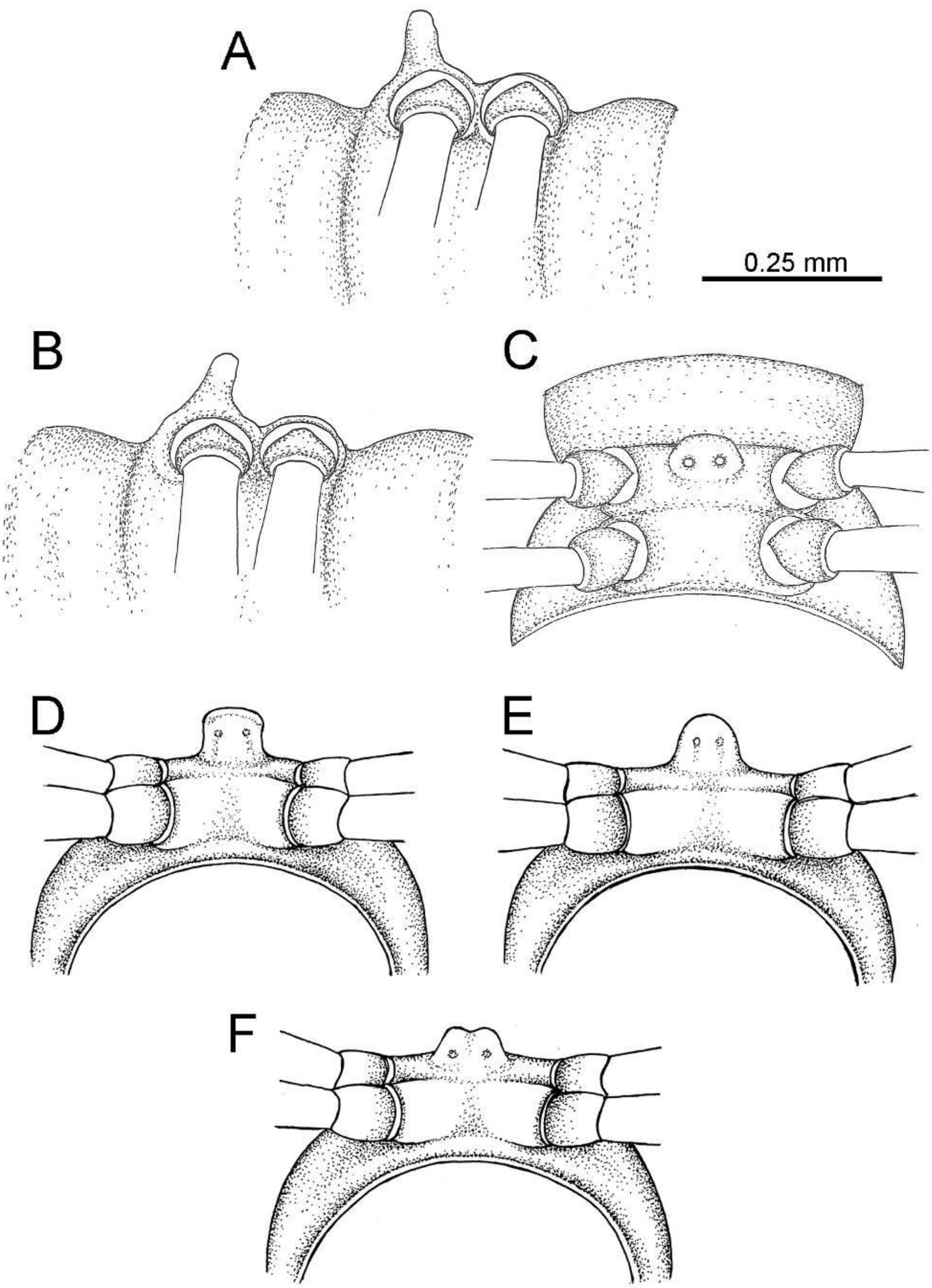

Figure 4.12 *Desmoxytes aurata* sp. n. (male holotype, male paratypes) – sternal lobe between male coxae 4. **A, B** ventral view **C** ventral view **D–F** caudal view.

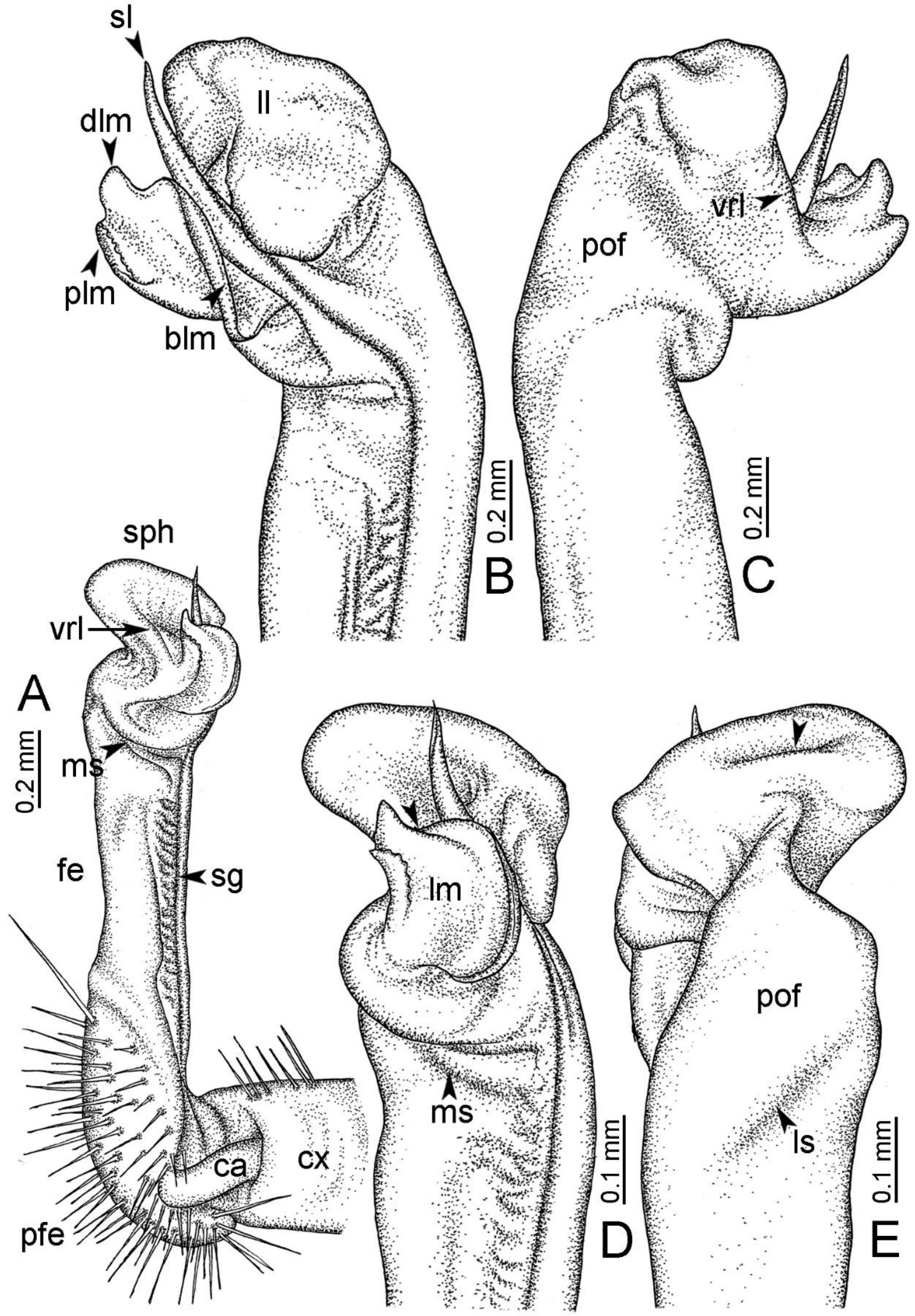

Figure 4.13 *Desmoxytes aurata* sp. n. (paratype) – right gonopod. **A** mesal view **B** dorsal view **C** ventral view **D** submesal view (arrow = indentation) **E** subdorsal view (arrow = furrow).

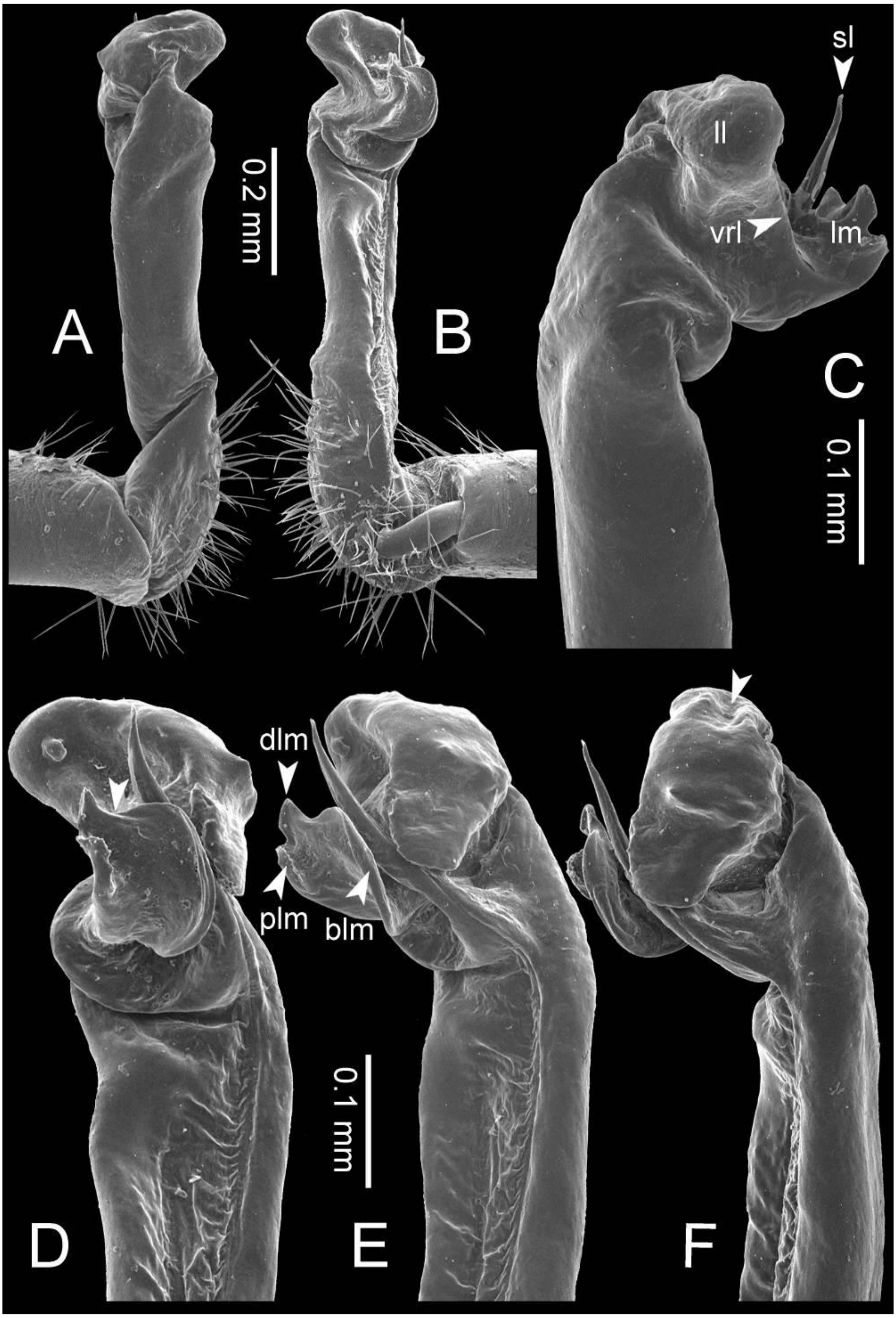

Figure 4.14 *Desmoxytes aurata* sp. n. (paratype) – right gonopod. **A** lateral view **B** mesal view **C** ventral view **D** subdorsal view (arrow = indentation) **E** dorsal view **F** subdorsal view (arrow = furrow).

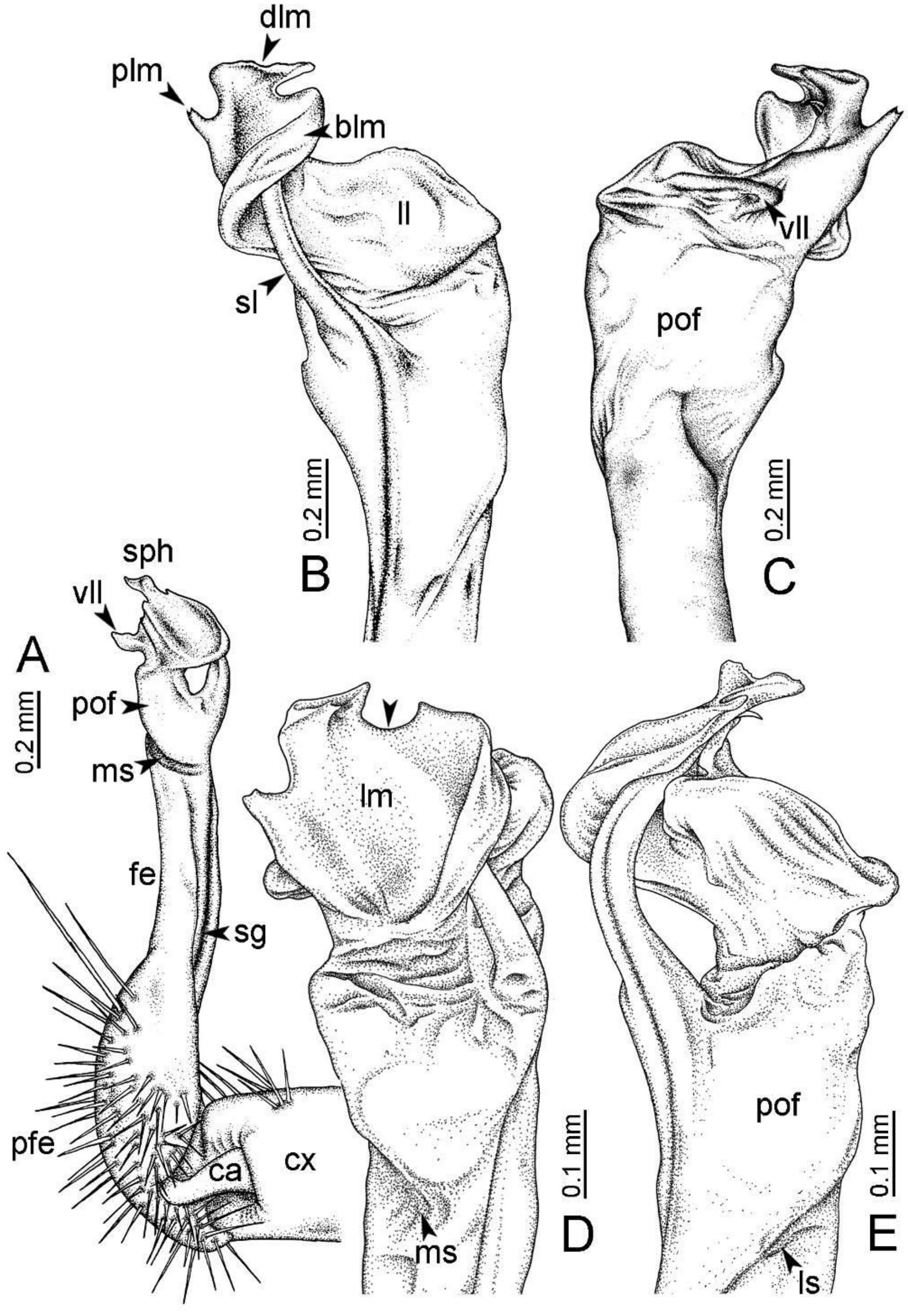

Figure 4.15 *Desmoxytes breviverpa* Srisonchai *et al.*, 2016 (paratype) – right gonopod (modified from Srisonchai *et al.* 2016). **A** mesal view **B** dorsal view **C** ventral view **D** submesal view subdorsal view (arrow = indentation) **E** lateral view.

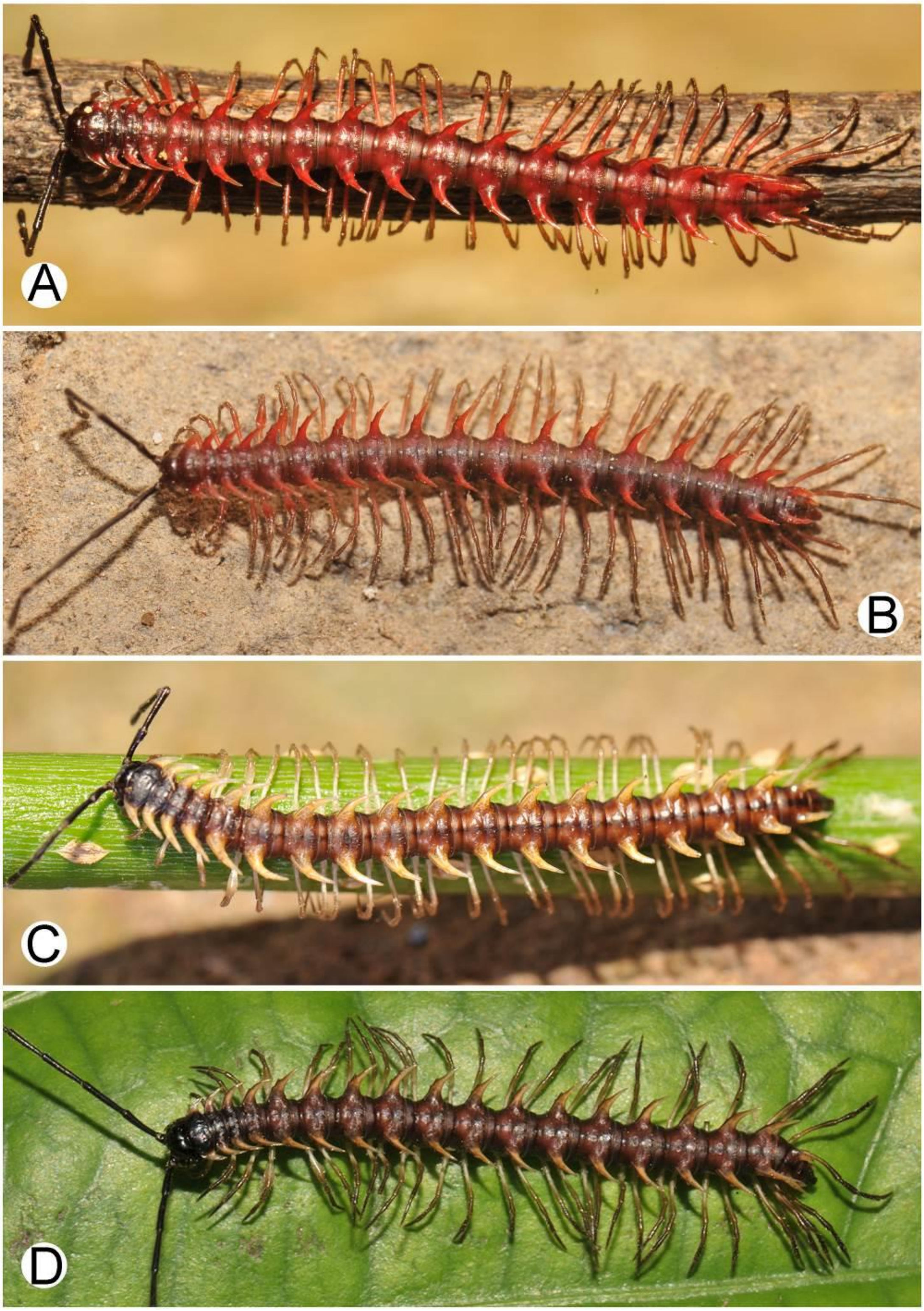

Figure 4.16 Photographs of live *Desmoxytes cervina* (Pocock, 1895) – males. **A** specimen from Wat Satit Khiri Rom **B** specimen from Phrayathtan Cave (Myanmar) **C** specimen from Ban Song Phi Nong **D** specimen from Wat Suwan Khuha.

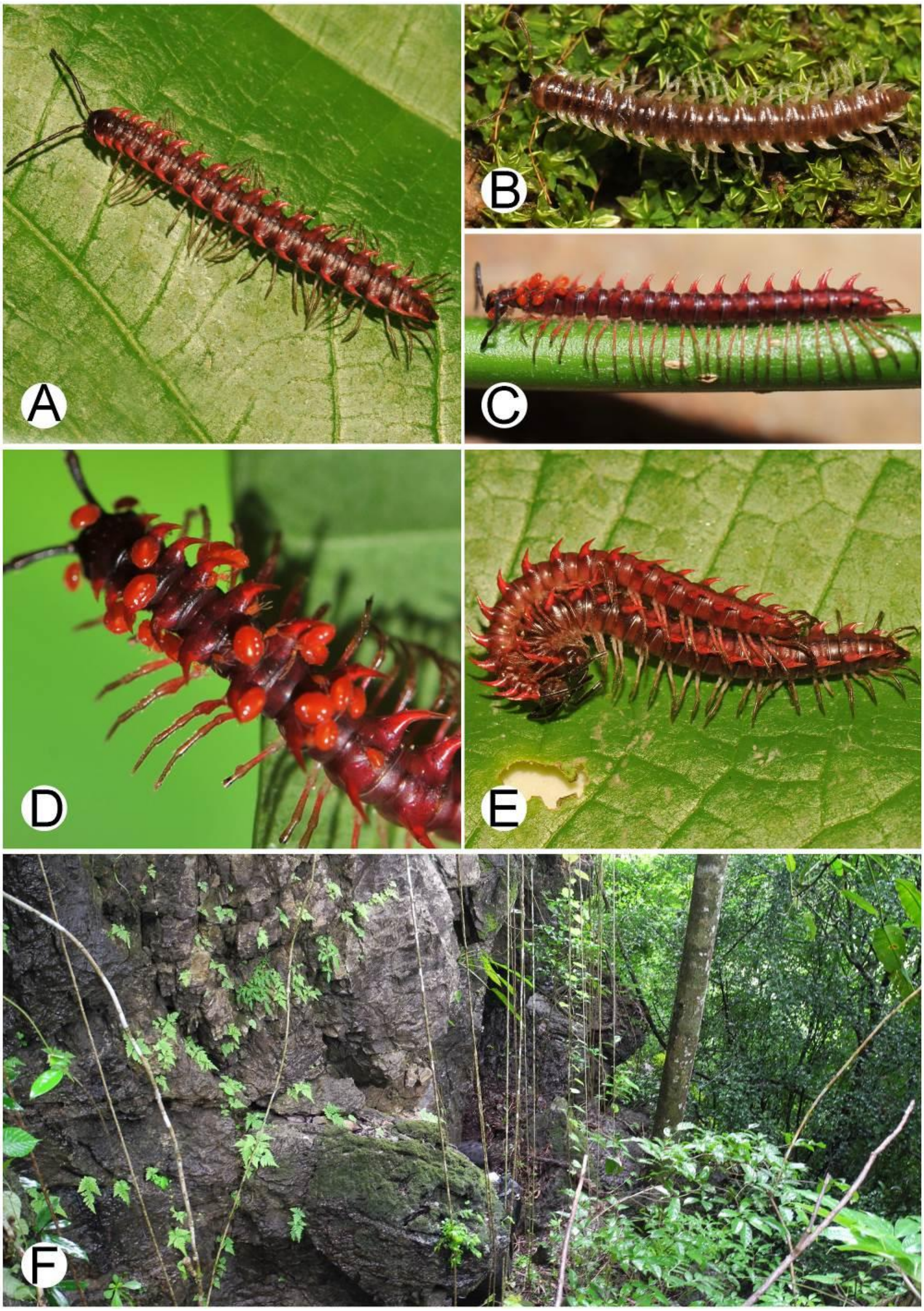

Figure 4.17 Photographs of live *Desmoxytes cervina* (Pocock, 1895) and habitat. **A–E** specimens from Ratchaprapa Dam **A** female **B** juvenile **C**, **D** male with parasitic mites **E** mating couple **F** habitat.

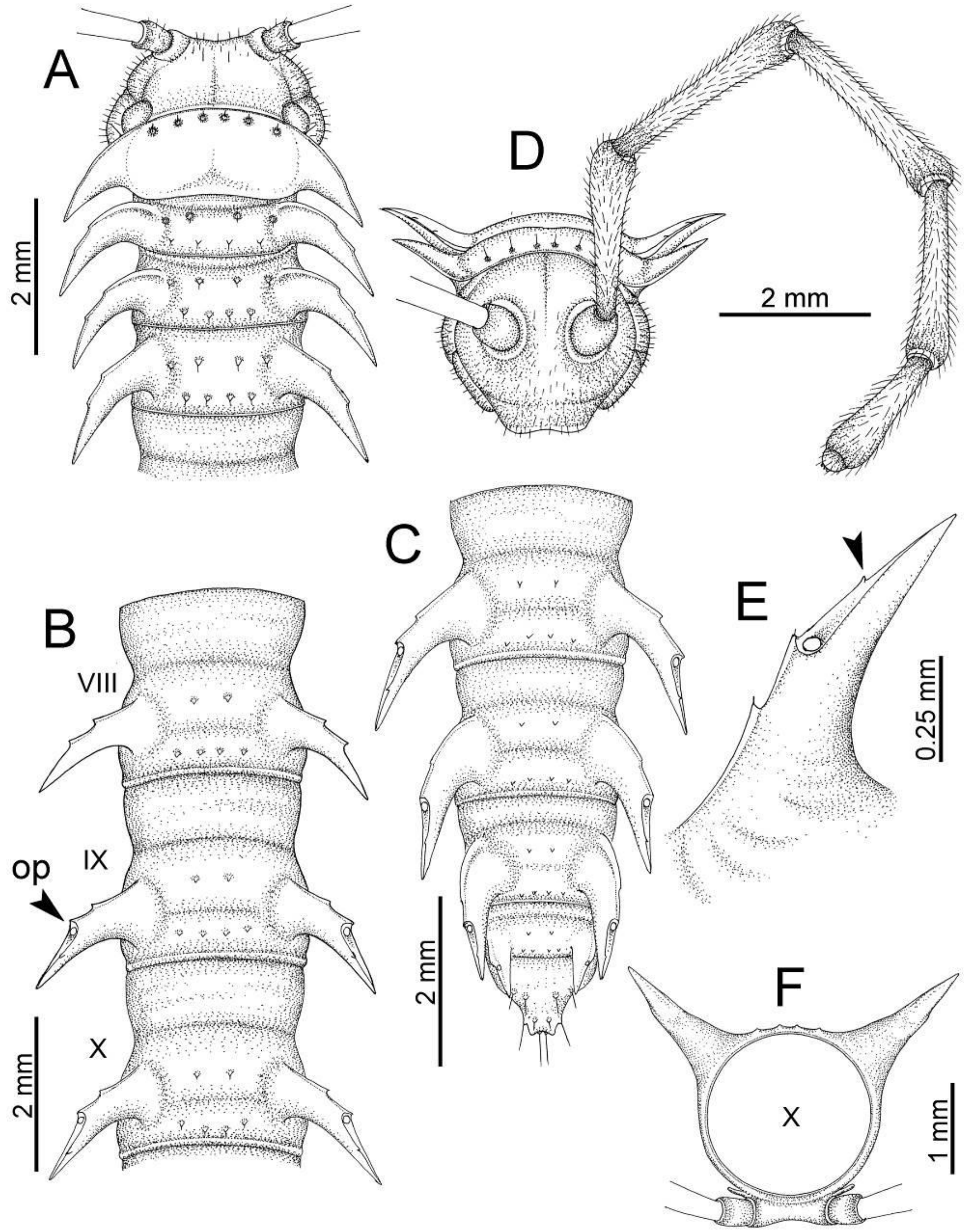

Figure 4.18 *Desmoxytes cervina* (Pocock, 1895) – specimen from Wat Satit Khirirom. **A** anterior body part **B** body rings 8–10 (op = ozopore) **C** posteriormost body rings and telson **D** head and antenna **E** paraterga of ring 10 (arrow = tiny denticle) **F** body ring 10.

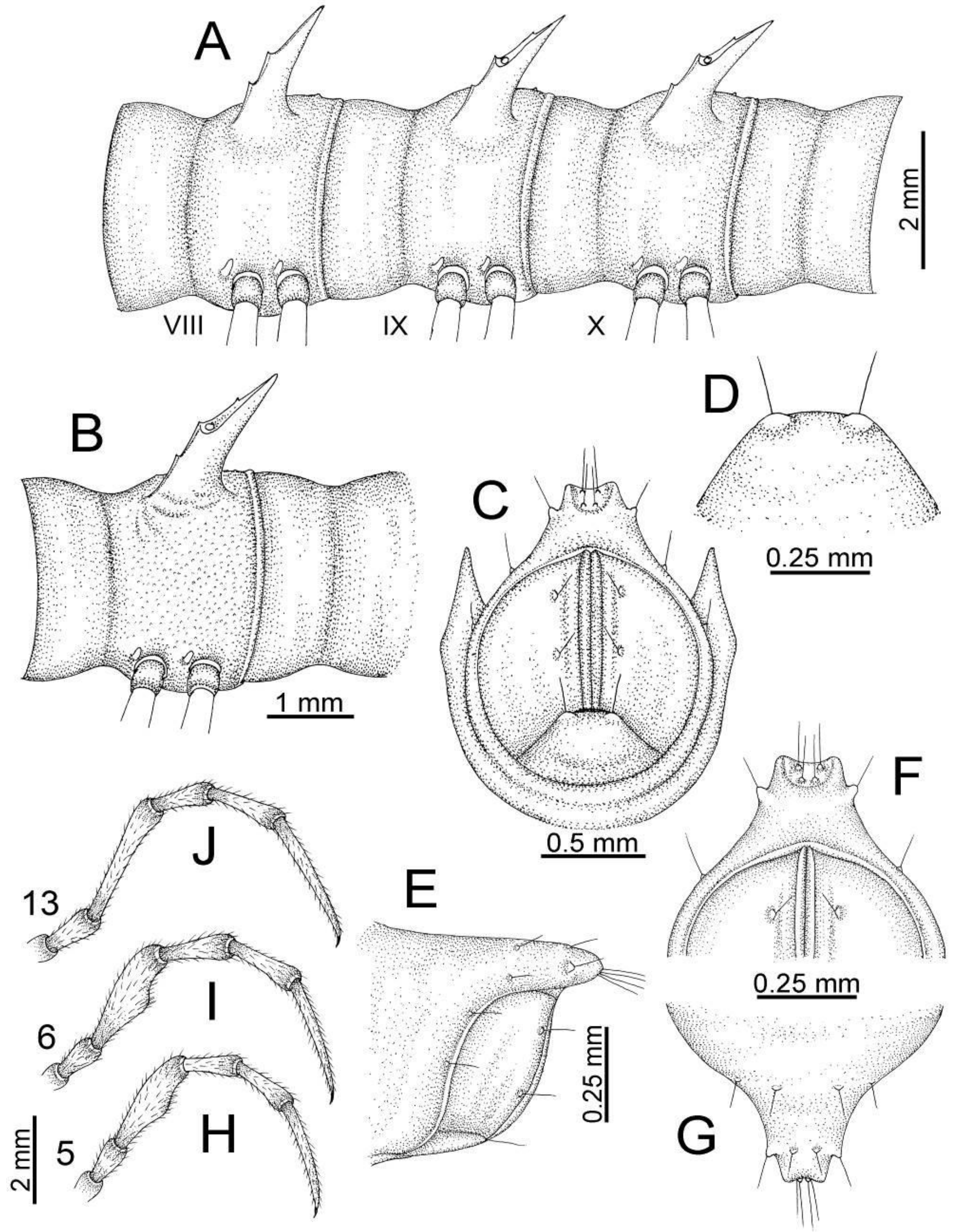

Figure 4.19 *Desmoxytes cervina* (Pocock, 1895) – specimen from Wat Satit Khirirom. **A** body rings 8–10 **B** sculpture of ring 10 **C, E** last ring and telson **D** hypoproct **F, G** epiproct **H** male leg 5 (right) **I** male leg 6 (right) **J** male leg 13 (right).

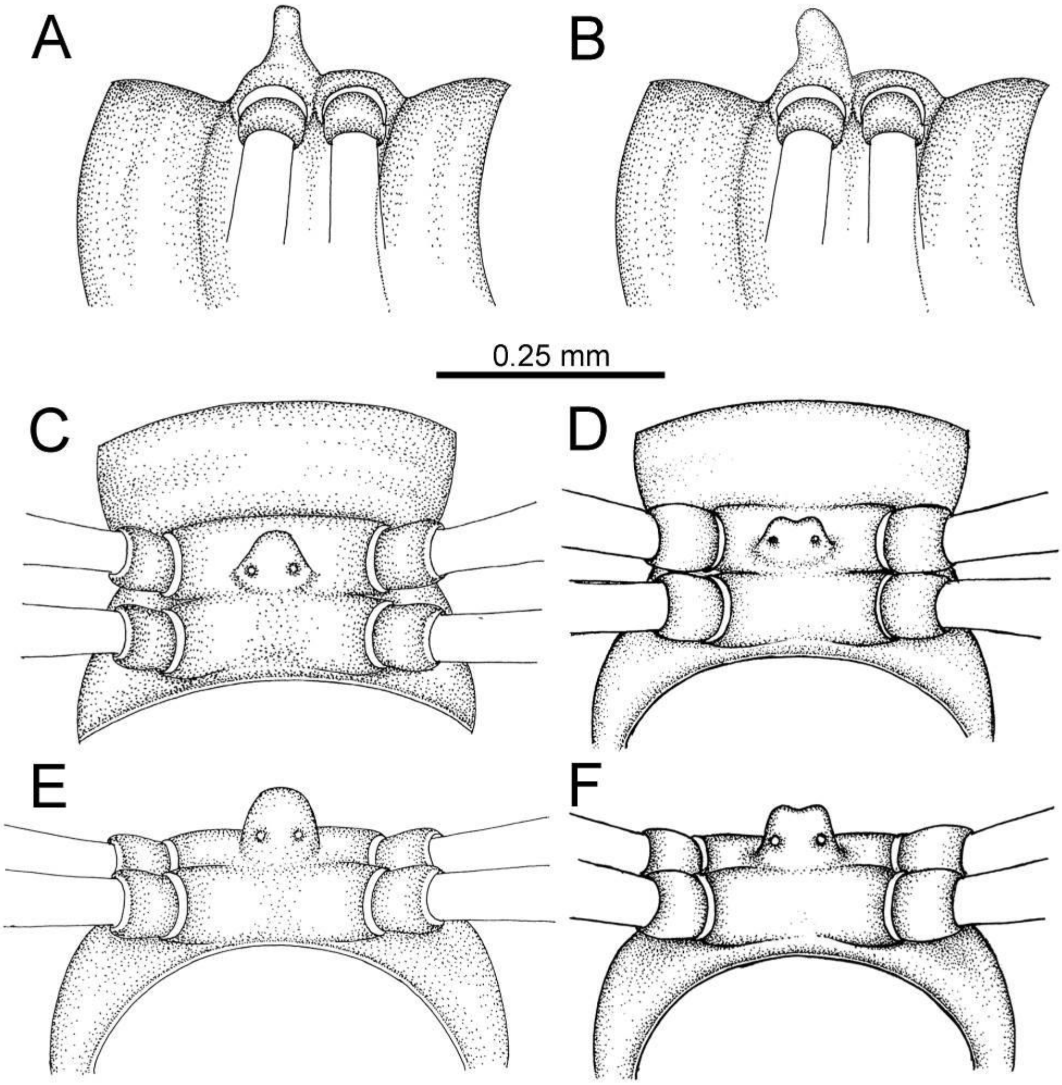

Figure 4.20 *Desmoxytes cervina* (Pocock, 1895), specimens from Wat Satit Khirirom – sternal lobe between male coxae 4. **A, B** lateral view **C, D** ventral view **E, F** caudal view.

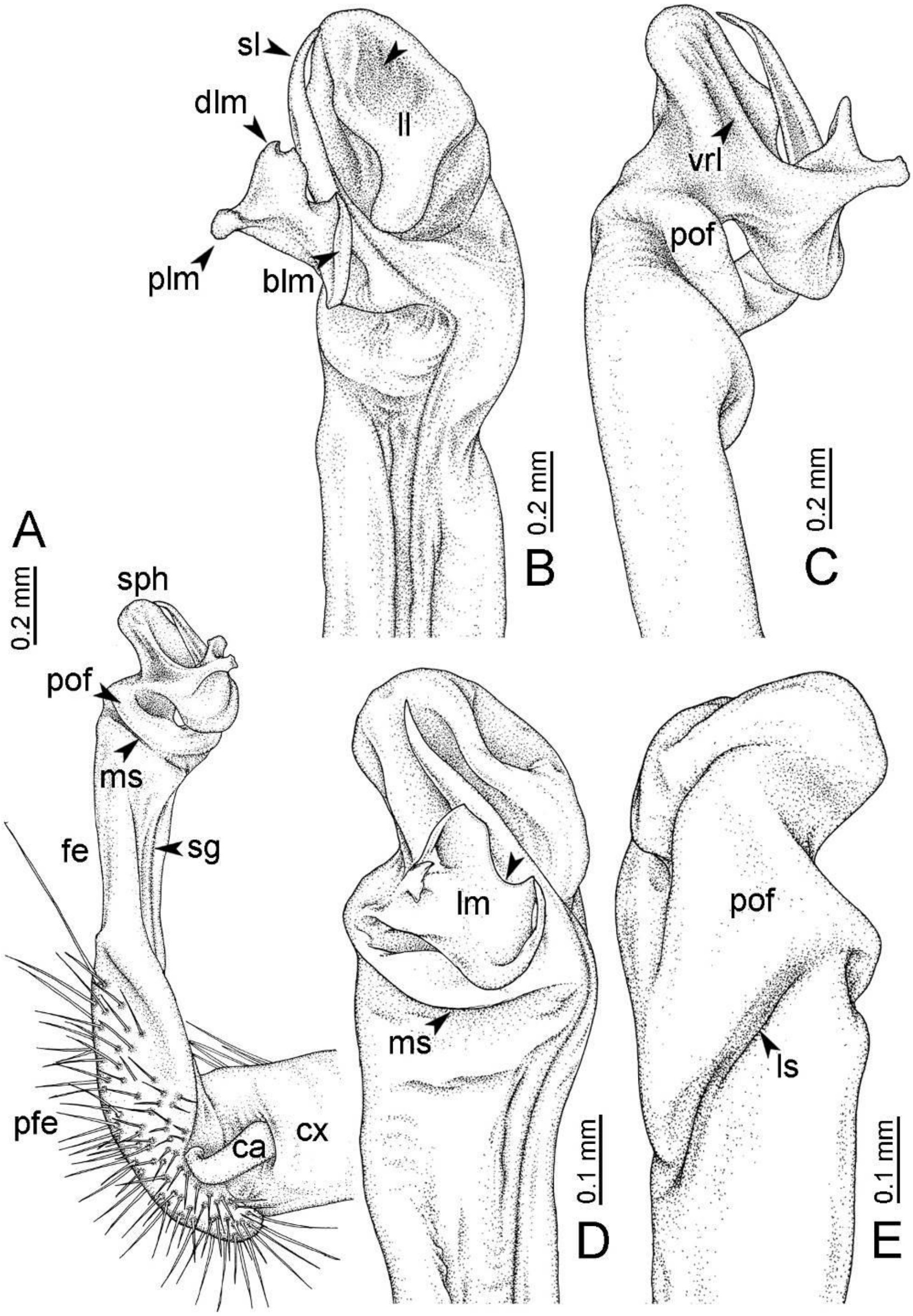

Figure 4.21 *Desmoxytes cervina* (Pocock, 1895), specimen from Wat Satit Khirirom – right gonopod. **A** mesal view **B** dorsal view (arrow = furrow) **C** ventral view **D** submesal view (arrow = indentation) **E** lateral view.

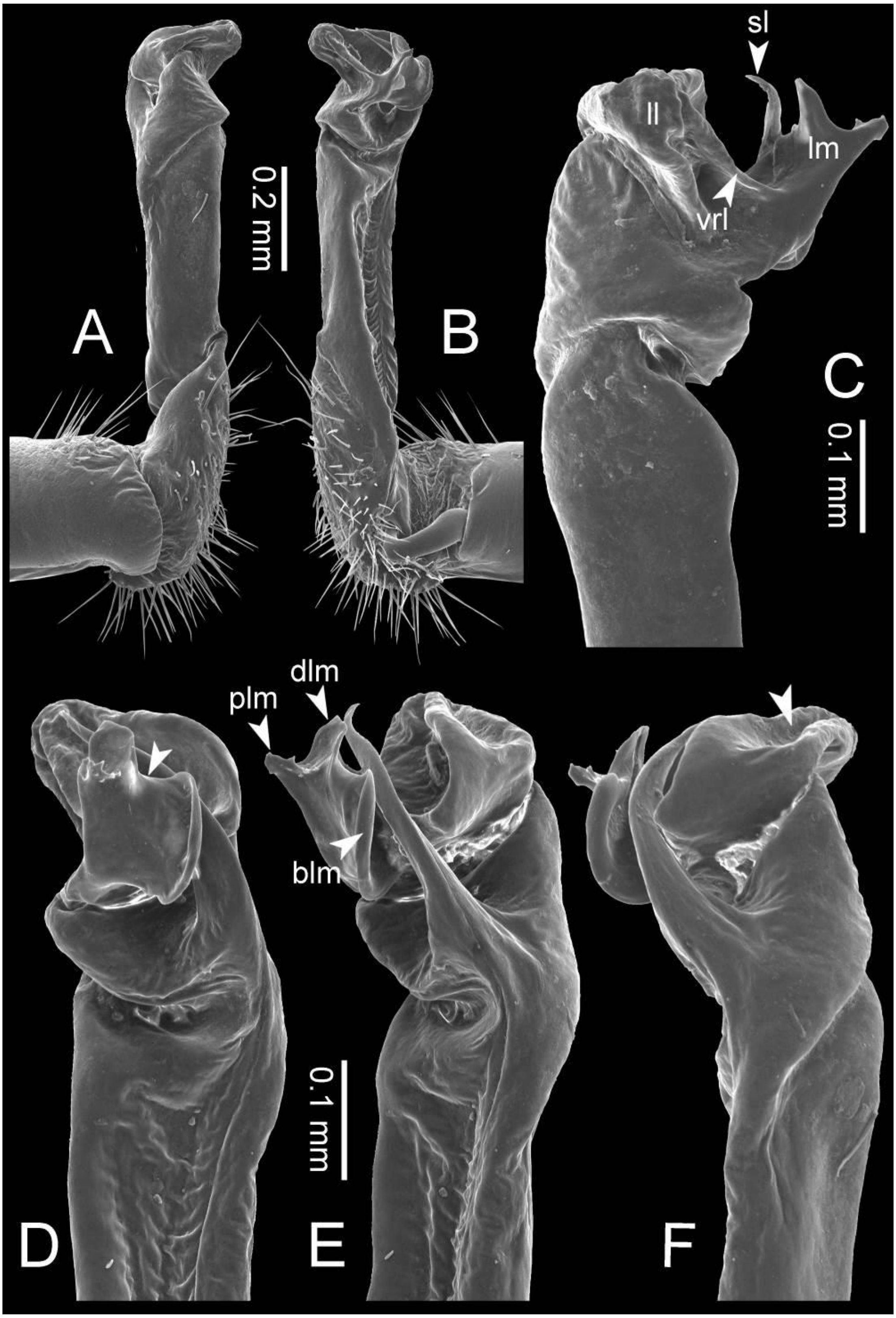

Figure 4.22 *Desmoxytes cervina* (Pocock, 1895), specimen from Wat Satit Khirirom – right gonopod. **A** lateral view **B** mesal view **C** ventral view **D** subdorsal view (arrow = indentation) **E** dorsal view, **F** subdorsal view (arrow = furrow).

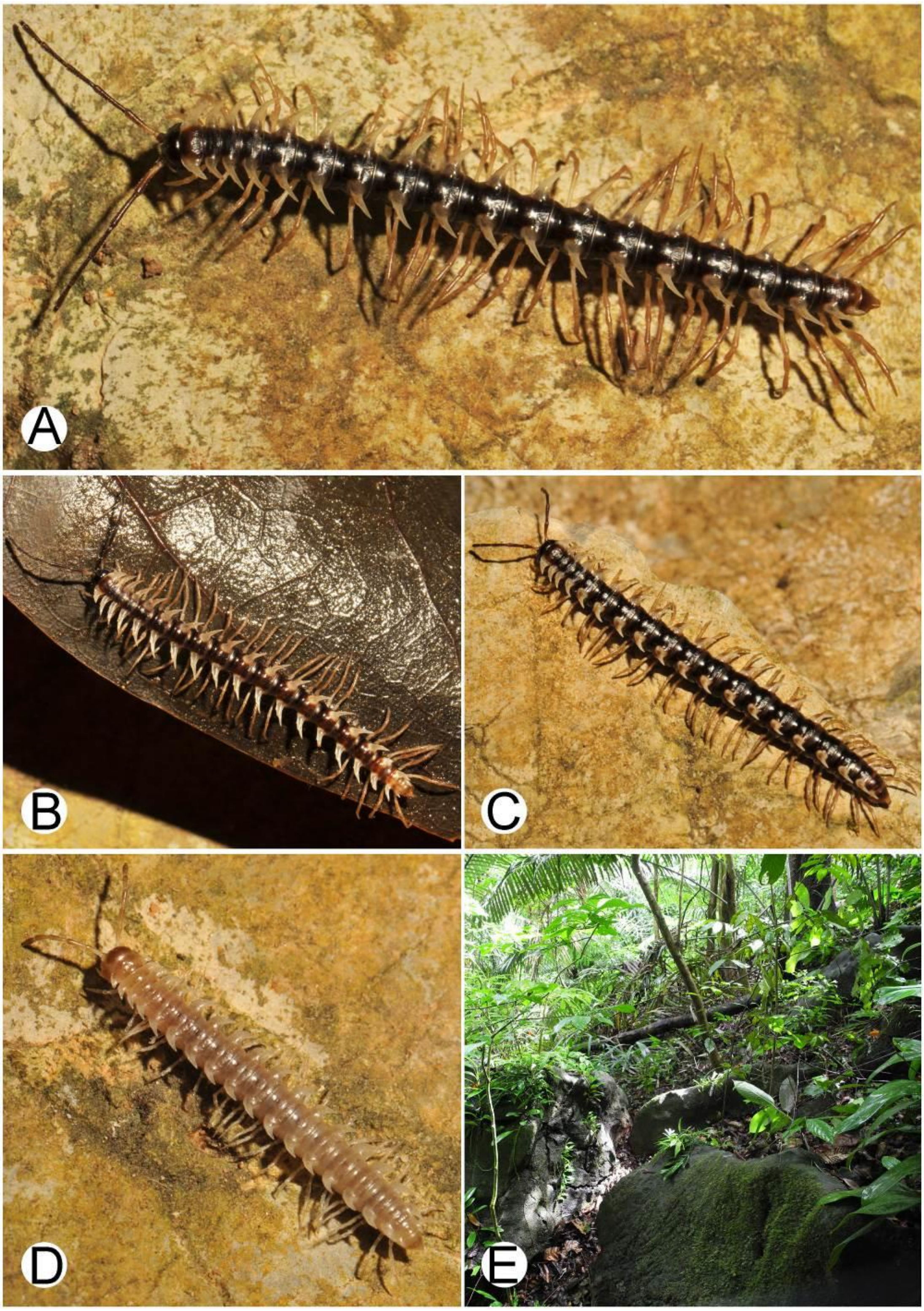

Figure 4.23 Photographs of live *Desmoxytes corythosaurus* sp. n. and habitat **A, B** male paratypes **C** female paratype **D** juvenile **E** habitat.

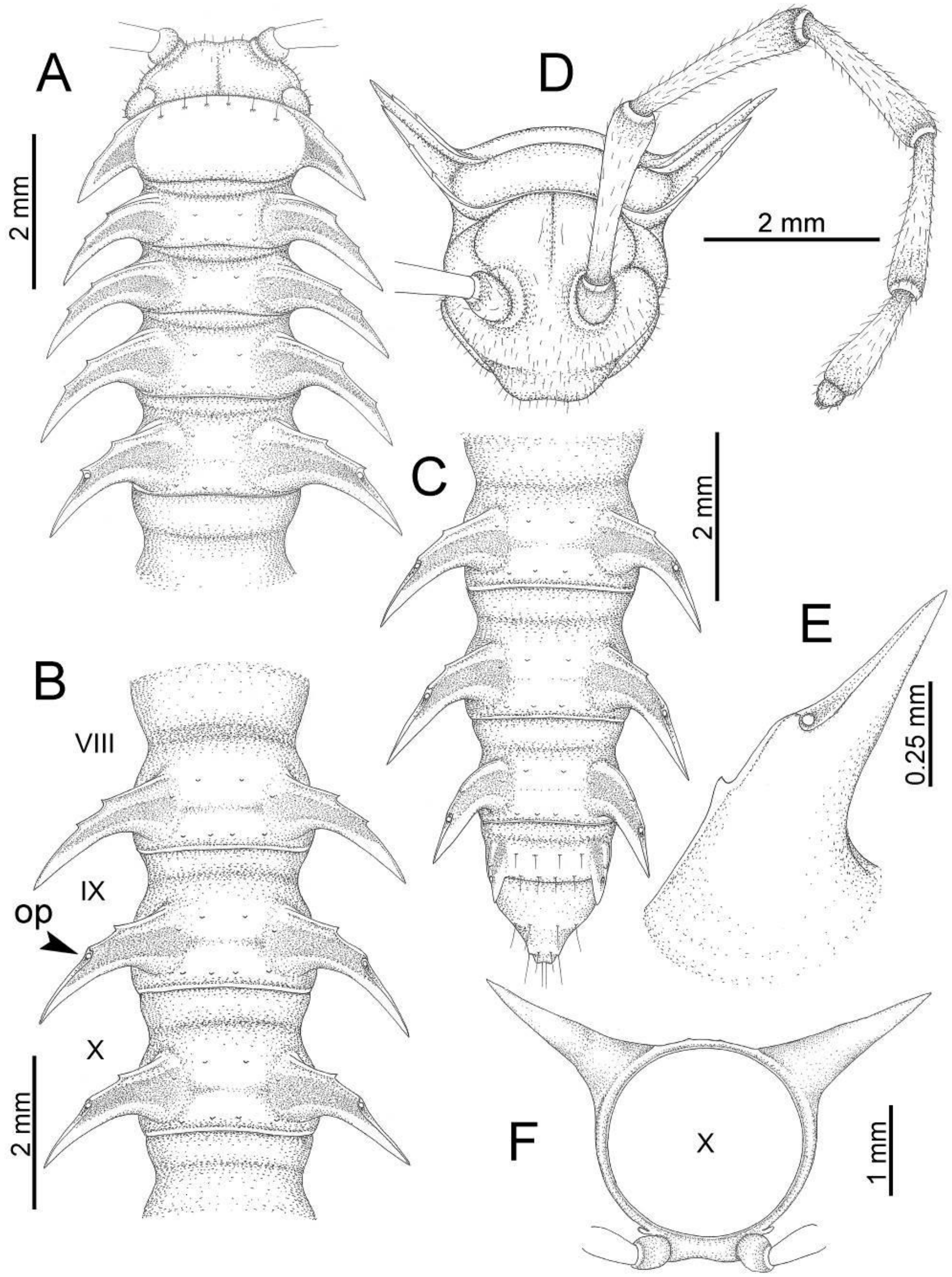

Figure 4.24 *Desmoxytes corythosaurus* sp. n. (male paratype). **A** anterior body part **B** body rings 8–10 (op = ozopore) **C** posteriormost body rings and telson **D** head and antenna **E** paraterga of ring 10 **F** body ring 10.

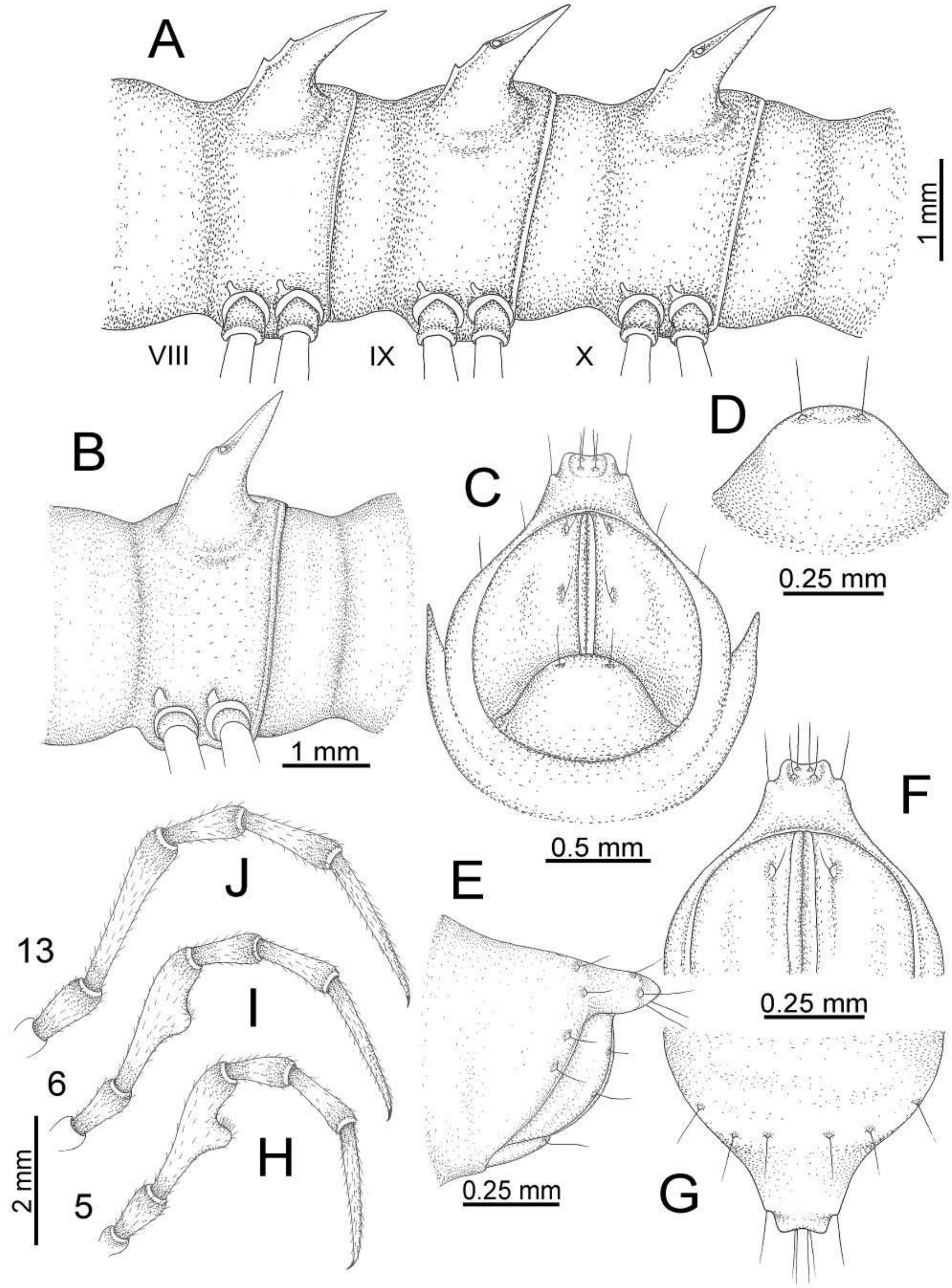

Figure 4.25 *Desmoxytes corythosaurus* sp. n. (male paratypes). **A** body rings 8–10 **B** sculpture of ring 10 **C, E** last ring and telson **D** hypoproct **F, G** epiproct **H** male leg 5 (right) **I** male leg 6 (right) **J** male leg 13 (right).

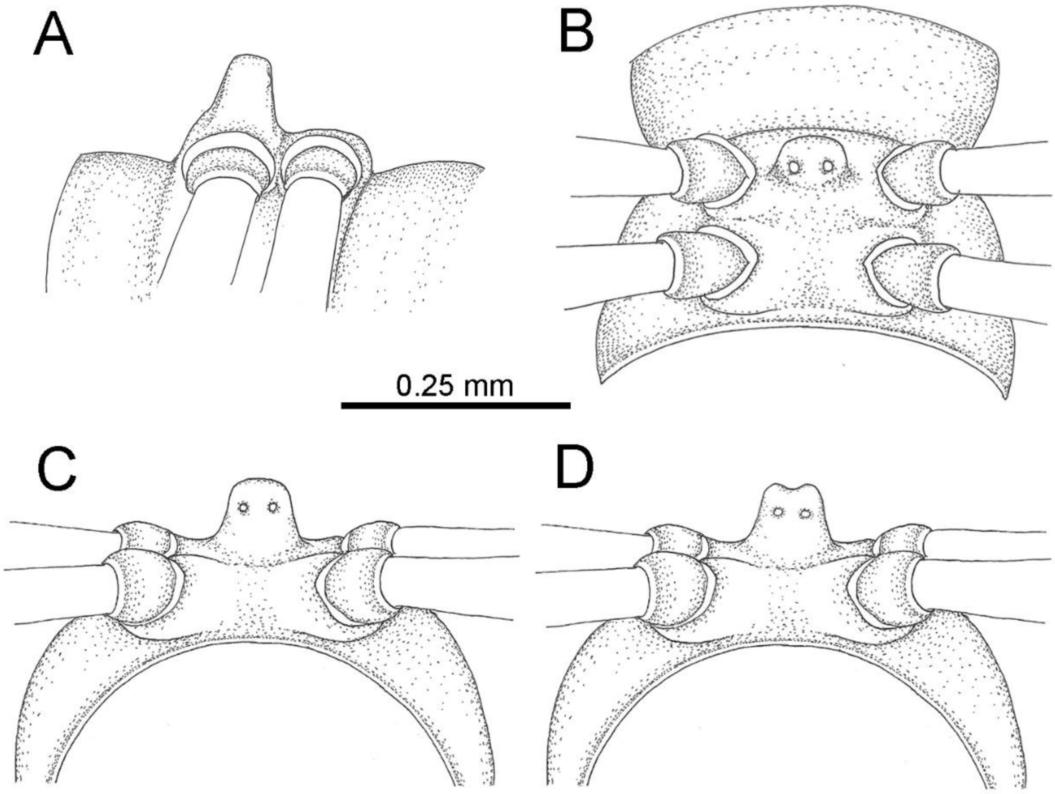

Figure 4.26 *Desmoxytes corythosaurus* sp. n. – sternal lobe between male coxae 4. **A** lateral view (male holotype) **B** ventral view (male holotype) **C** caudal view (male holotype) **D** caudal view (male paratype).

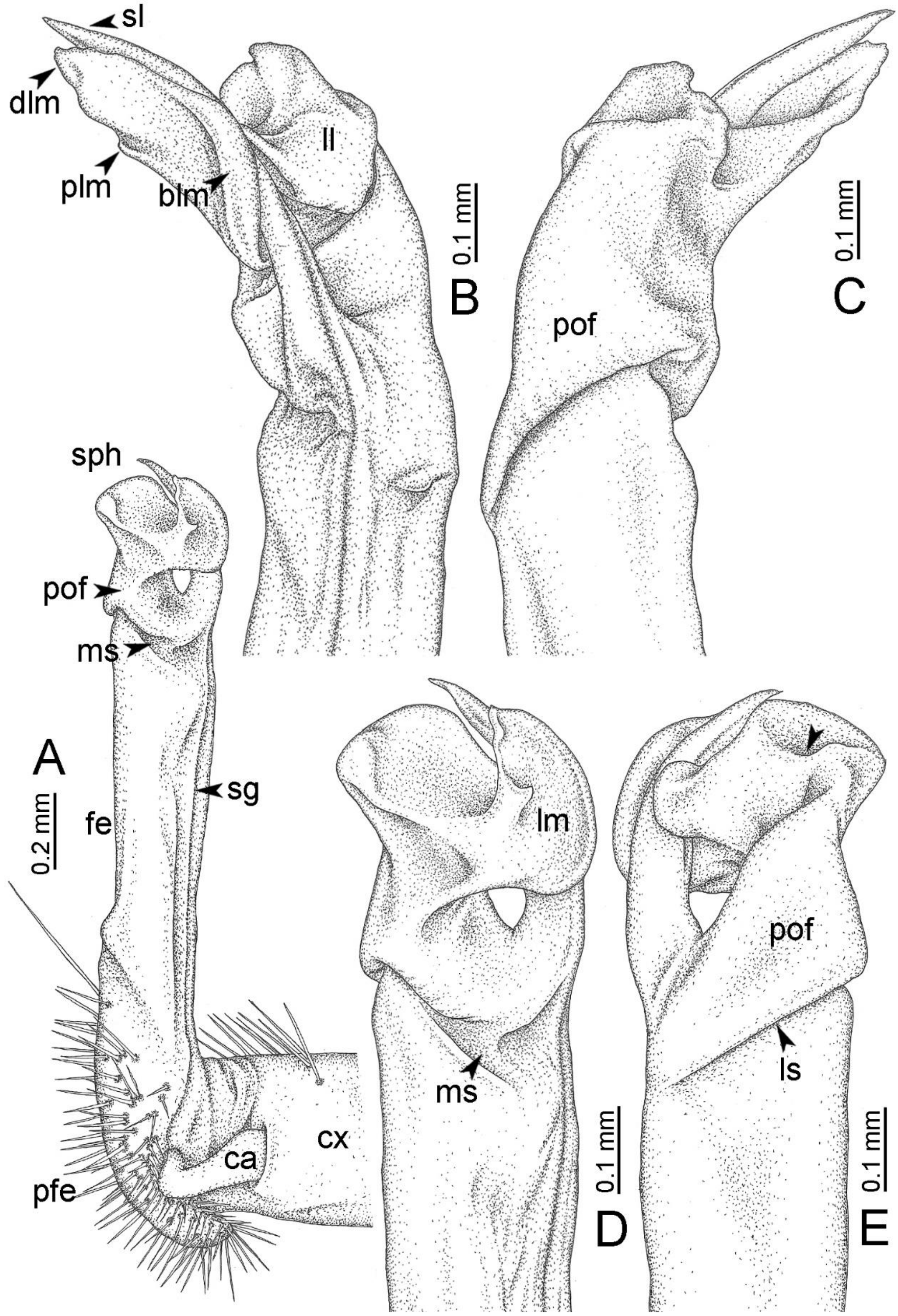

Figure 4.27 *Desmoxytes corythosaurus* sp. n. (paratype) – right gonopod. **A** mesal view **B** dorsal view **C** ventral view **D** submesal view **E** lateral view (arrow = furrow).

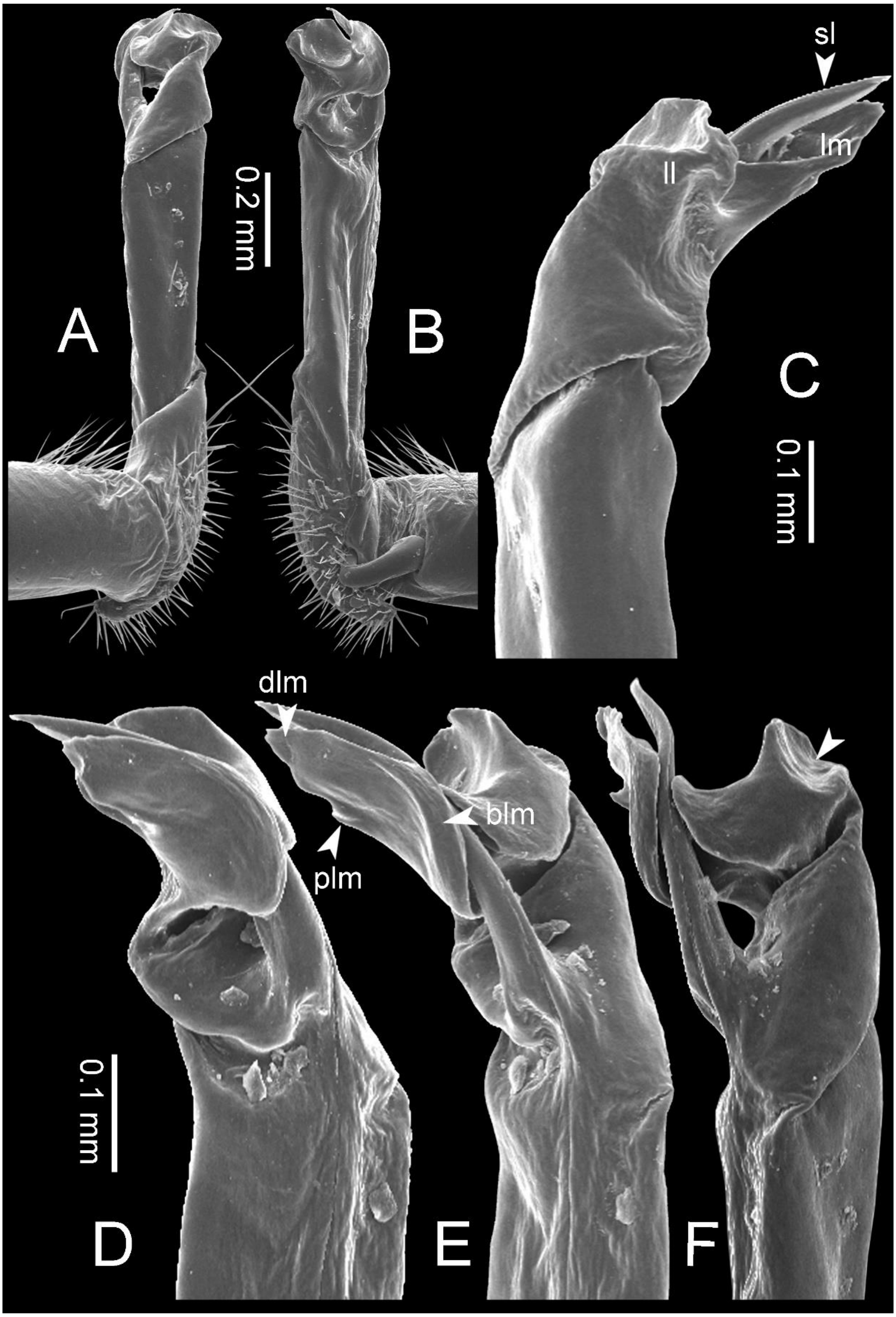

Figure 4.28 *Desmoxytes corythosaurus* sp. n. (paratype) – right gonopod. **A** lateral view **B** mesal view **C** ventral view **D, F** subdorsal view **E** dorsal view (arrow = furrow).

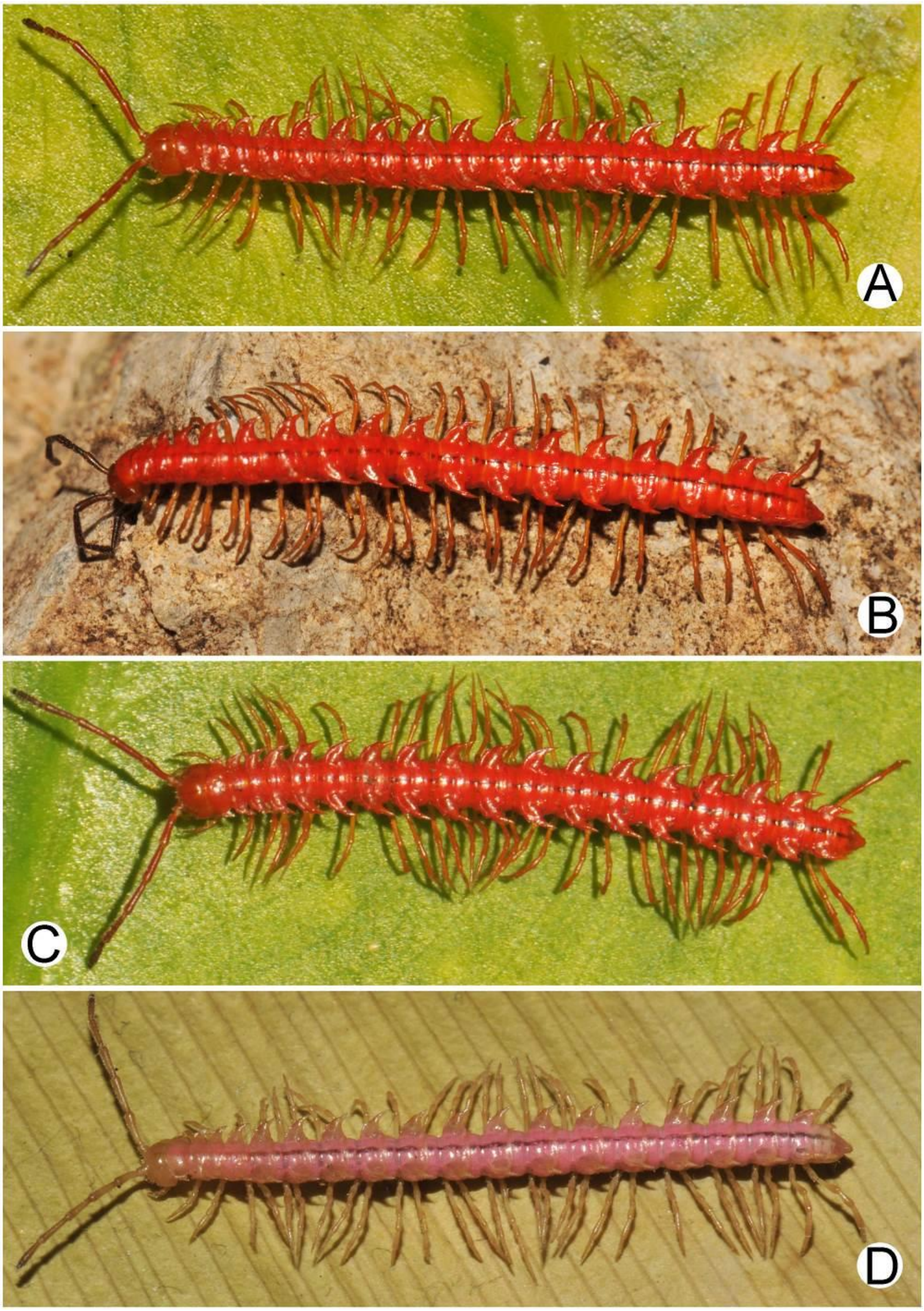

Figure 4.29 Photographs of live *Desmoxytes delfae* (Jeekel, 1964) – males. **A** specimen from Khao Chi Chan Bureau of Monks **B** specimen from Tham Tone Din **C** specimen from Wat Tham Sue (Tiger Cave) **D** early adult from La-ngu Subdistrict.

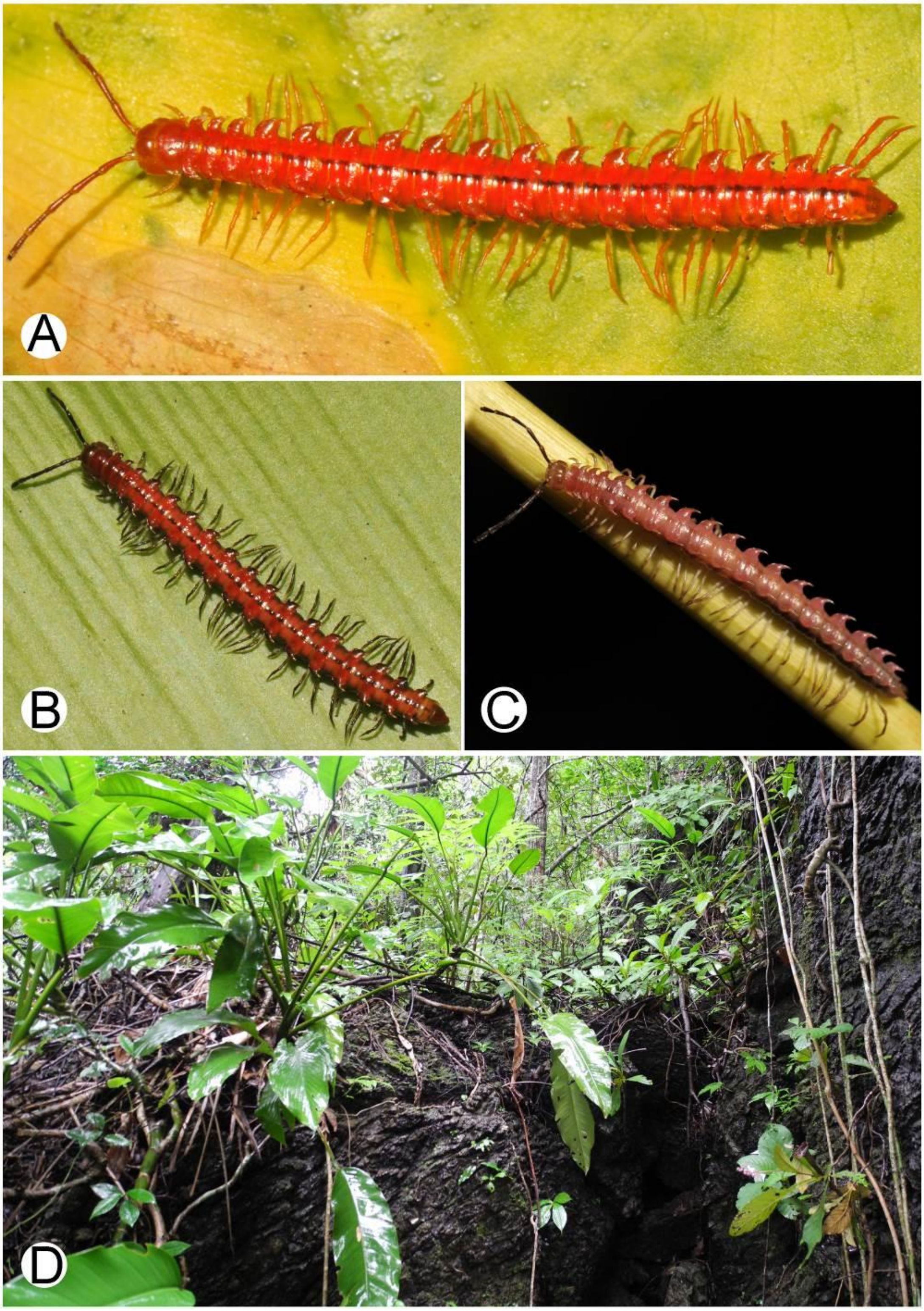

Figure 4.30 Photographs of live *Desmoxytes delfae* (Jeekel, 1964) and habitat. **A–C** specimens from Tham Khan Ti Phol **A** female **B** old female **C** newly moulted adult female **D** habitat.

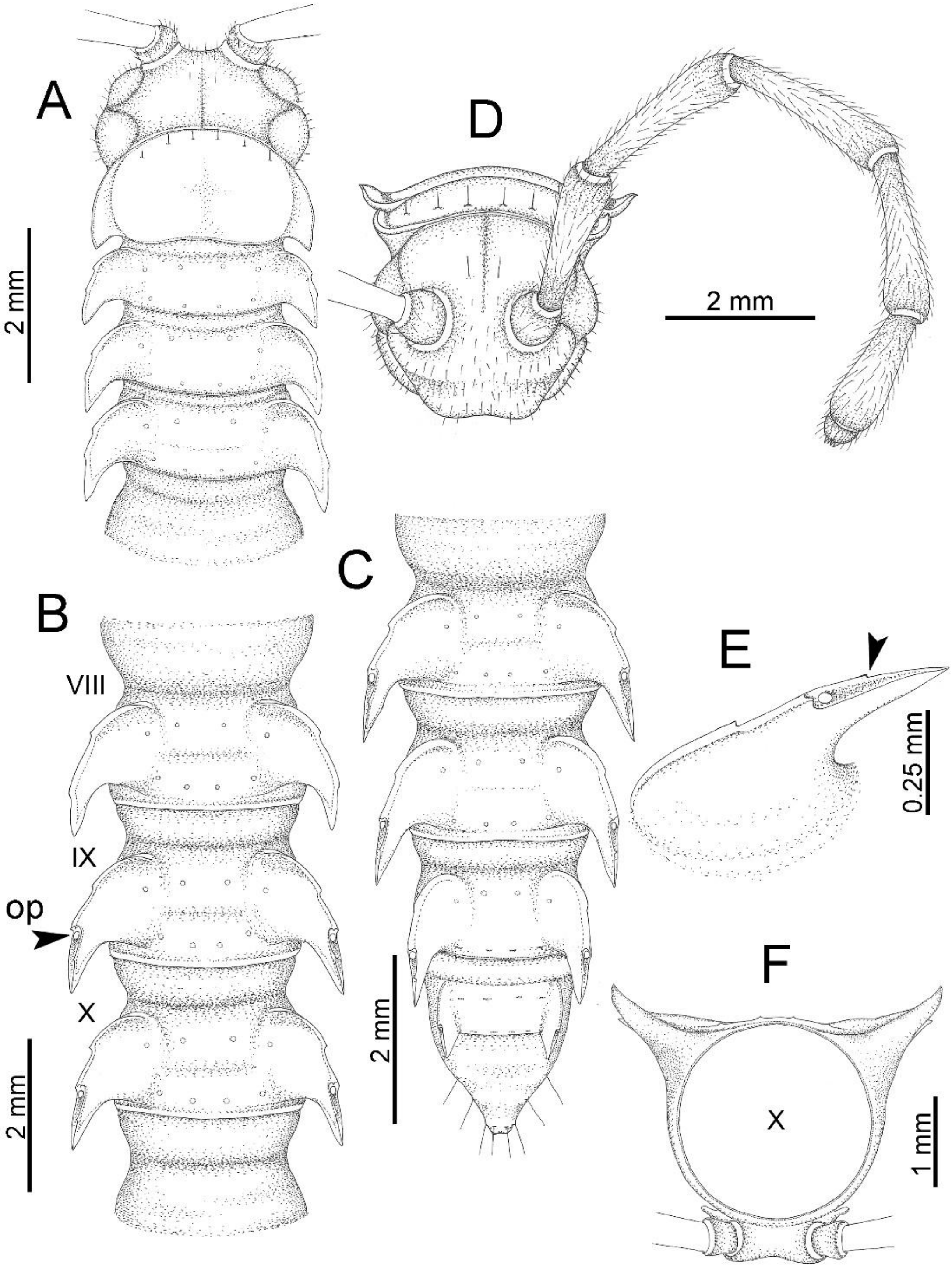

Figure 4.31 *Desmoxytes delfae* (Jeekel, 1964), specimen from Tham Khan Ti Phol. **A** anterior body part **B** body rings 8–10 (op = ozopore) **C** posteriormost body rings and telson **D** head and antenna **E** paraterga of ring 10 (arrow = tiny denticle) **F** body ring 10.

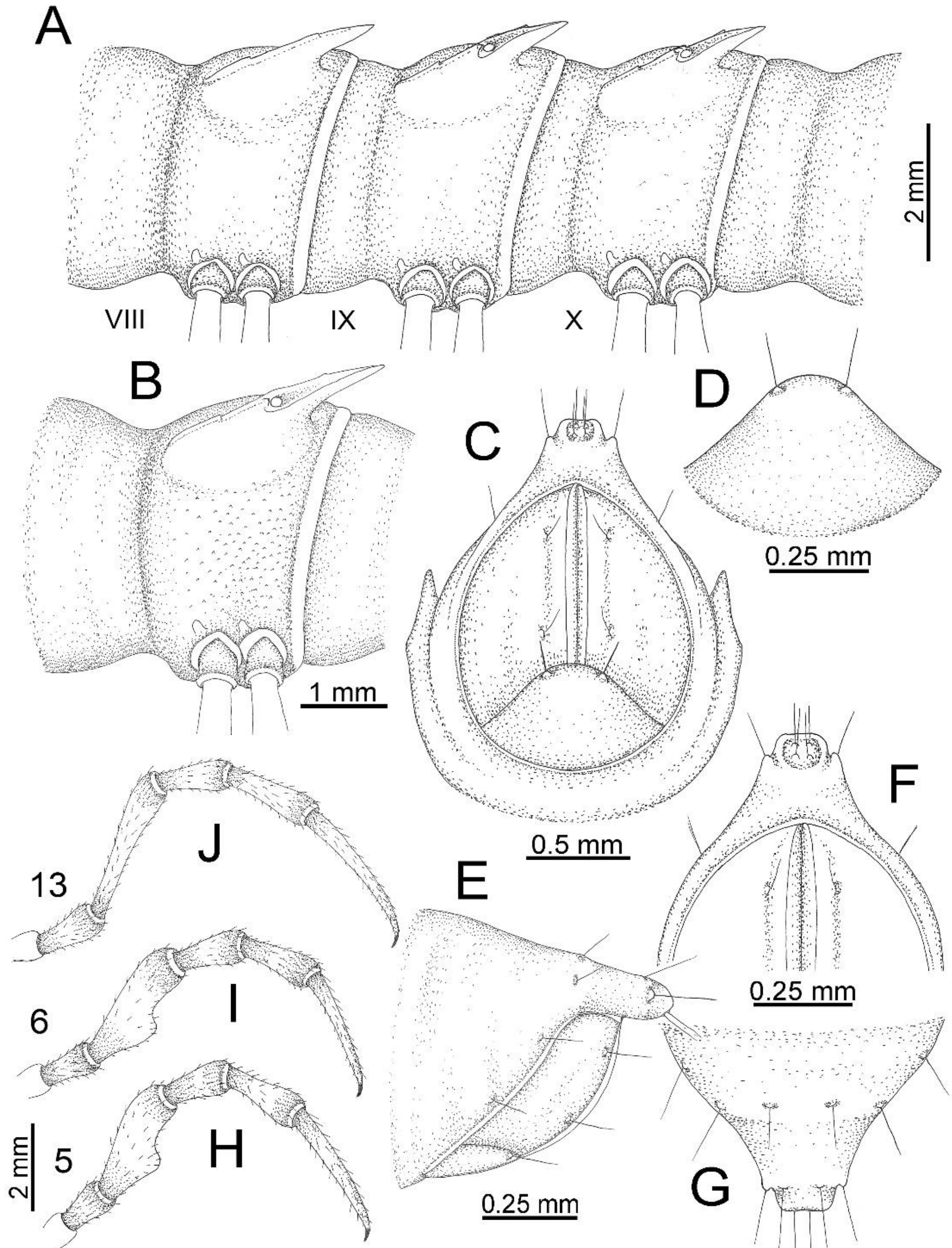

Figure 4.32 *Desmoxytes delfae* (Jeekel, 1964), specimens from Tham Khan Ti Phol. **A** body rings 8–10 **B** sculpture of ring 10 **C, E** last ring and telson **D** hypoproct **F, G** epiproct **H** male leg 5 (right) **I** male leg 6 (right) **J** male leg 13 (right).

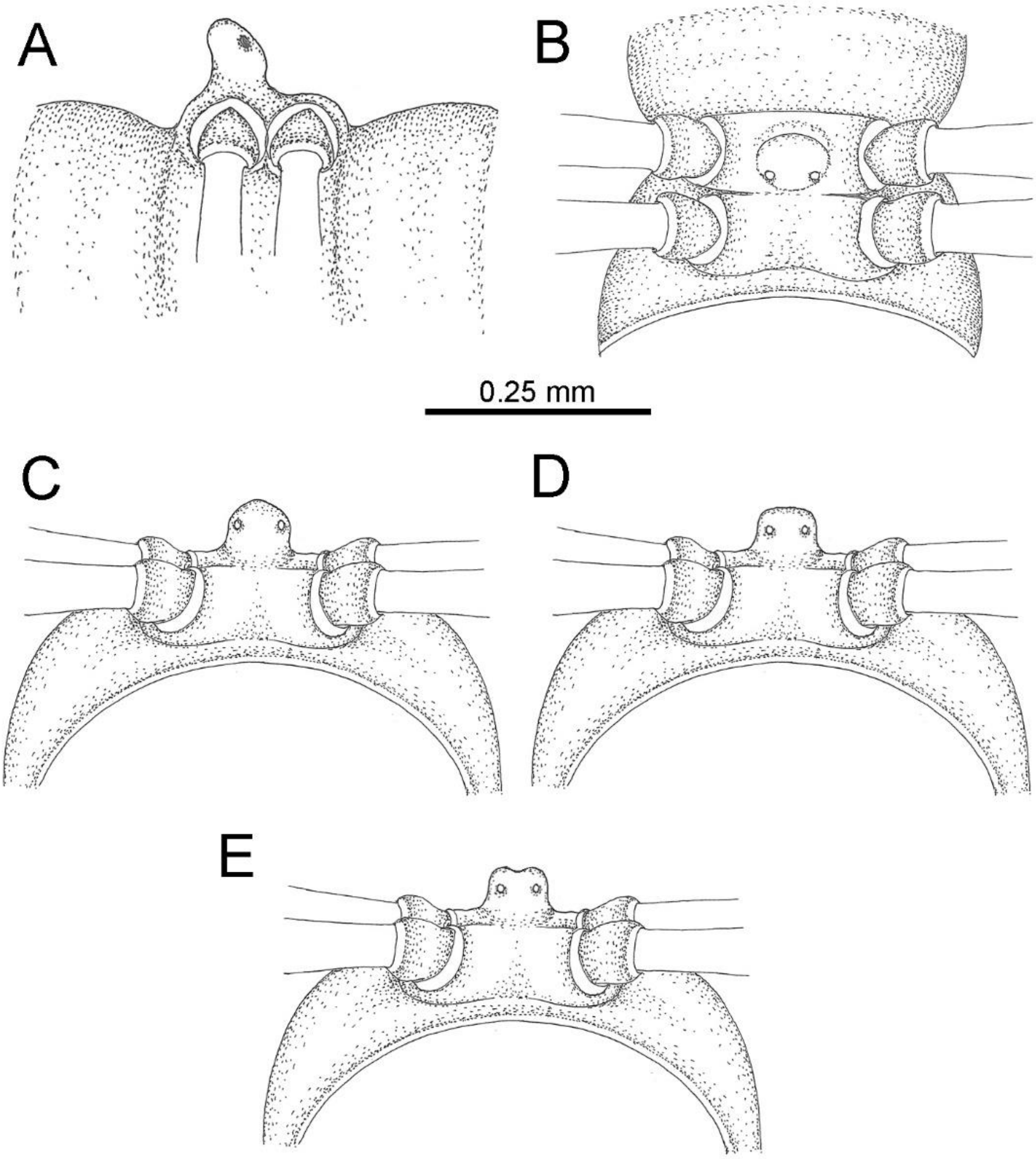

Figure 4.33 *Desmoxytes delfae* (Jeekel, 1964), specimens from Tham Khan Ti Phol – sternal lobe between male coxae 4. **A** lateral view **B** ventral view **C**, **D** caudal view **E** some specimens from Tham Khao Ting – caudal view.

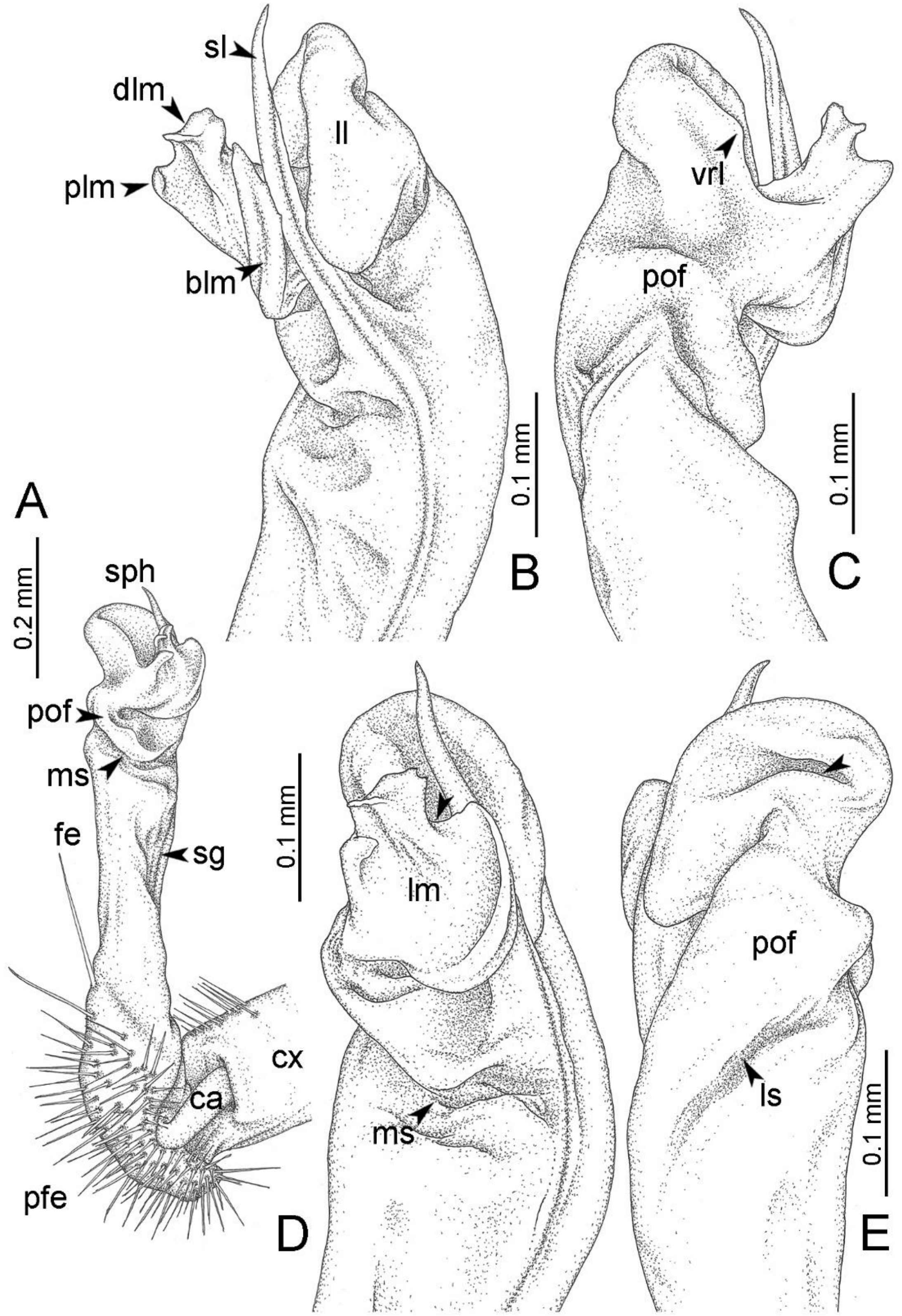

Figure 4. 34 *Desmoxytes delfae* (Jeekel, 1964), specimen from Khao Chi Chan Bureau of Monks – right gonopod. **A** mesal view **B** dorsal view **C** ventral view **D** submesal view (arrow = indentation) **E** lateral view (arrow = furrow).

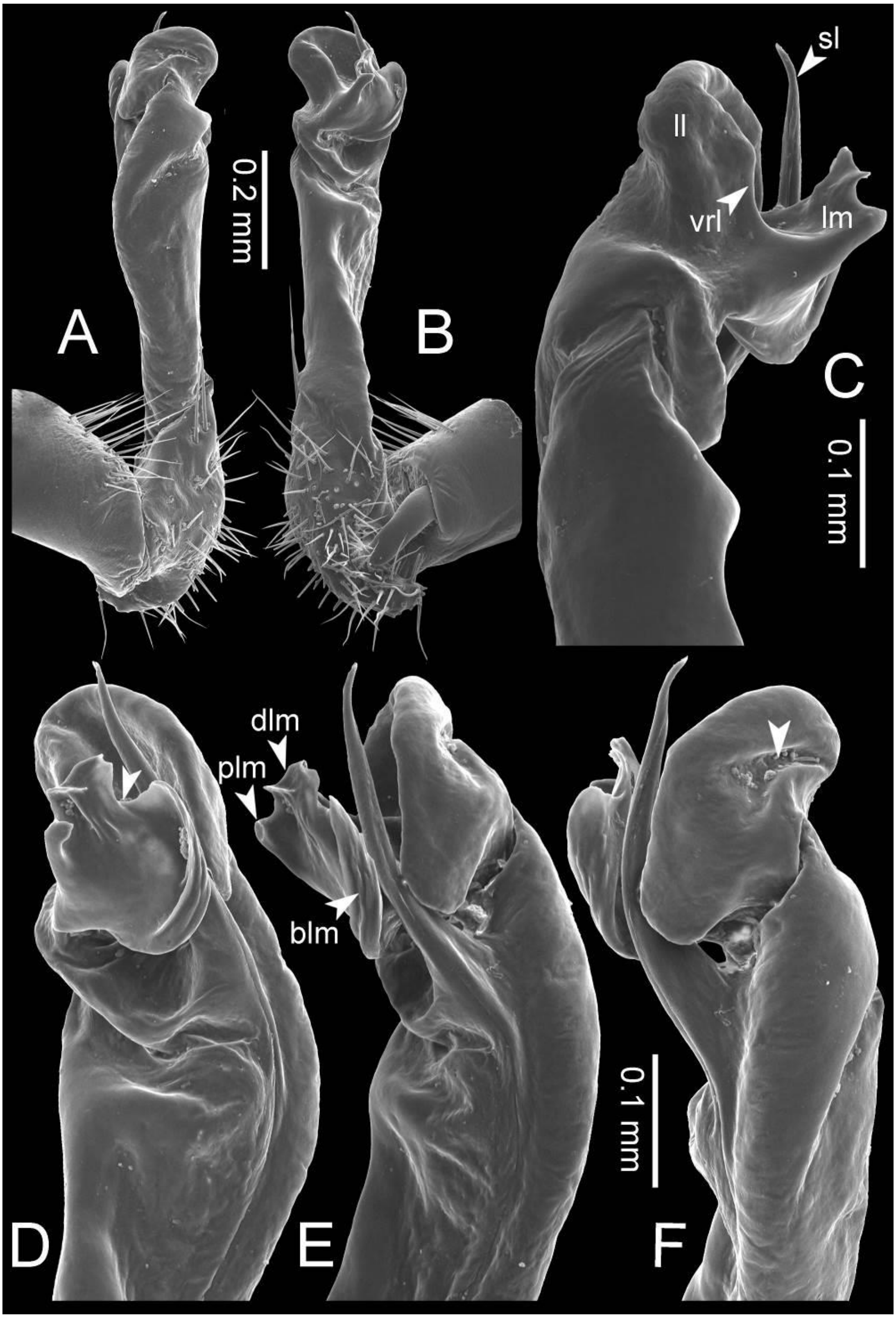

Figure 4.35 *Desmoxytes delfae* (Jeekel, 1964), specimen from Khao Chi Chan Bureau of Monks – right gonopod. **A** lateral view **B** mesal view **C** ventral view **D** subdorsal view (arrow = indentation) **E** dorsal view **F** subdorsal view (arrow = furrow).

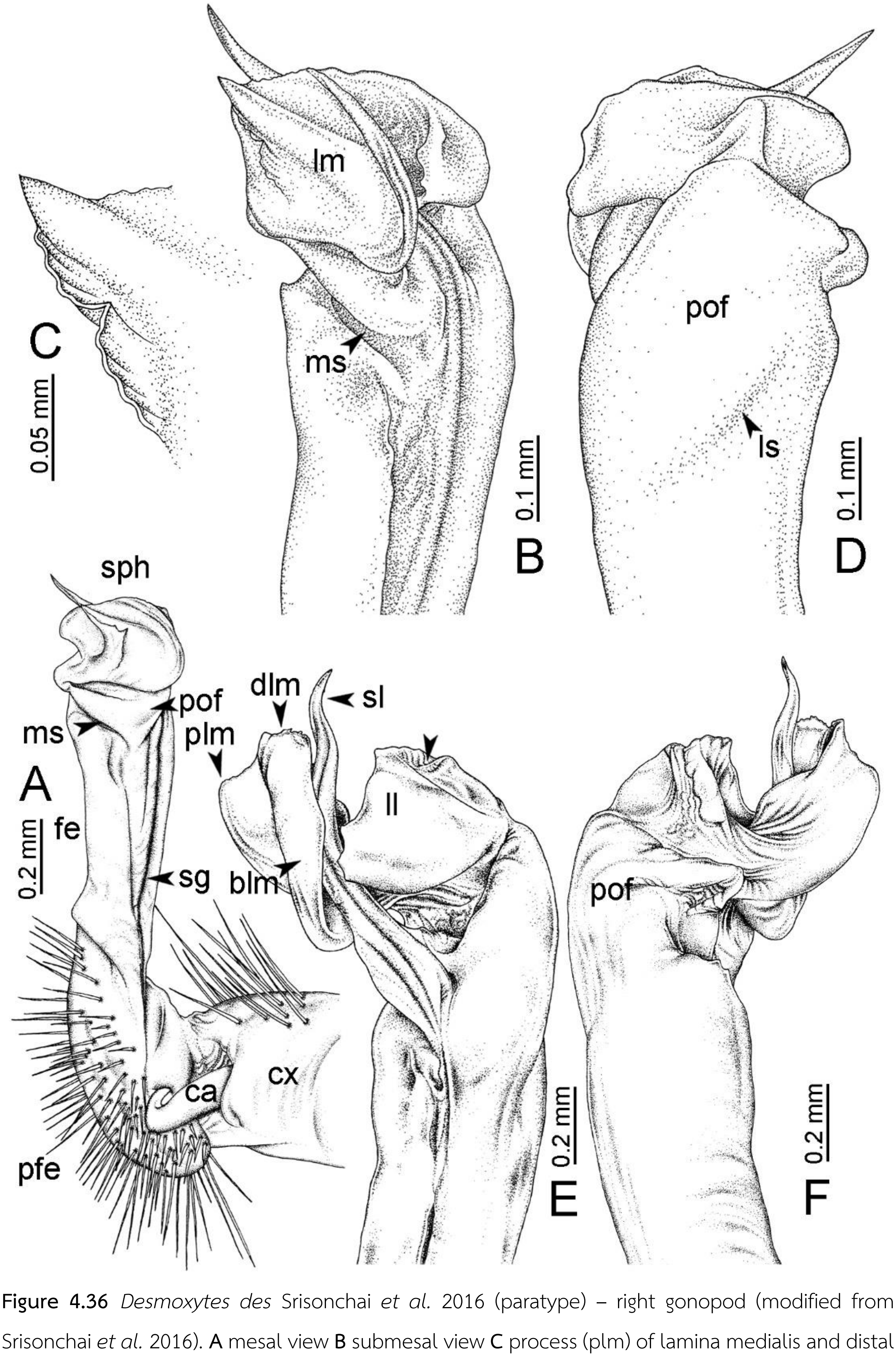

Figure 4.36 *Desmoxytes des* Srisonchai *et al.* 2016 (paratype) – right gonopod (modified from Srisonchai *et al.* 2016). **A** mesal view **B** submesal view **C** process (plm) of lamina medialis and distal lobe (dlm) of lamina medialis **D** lateral view **E** dorsal view (arrow = indentation) **F** ventral view.

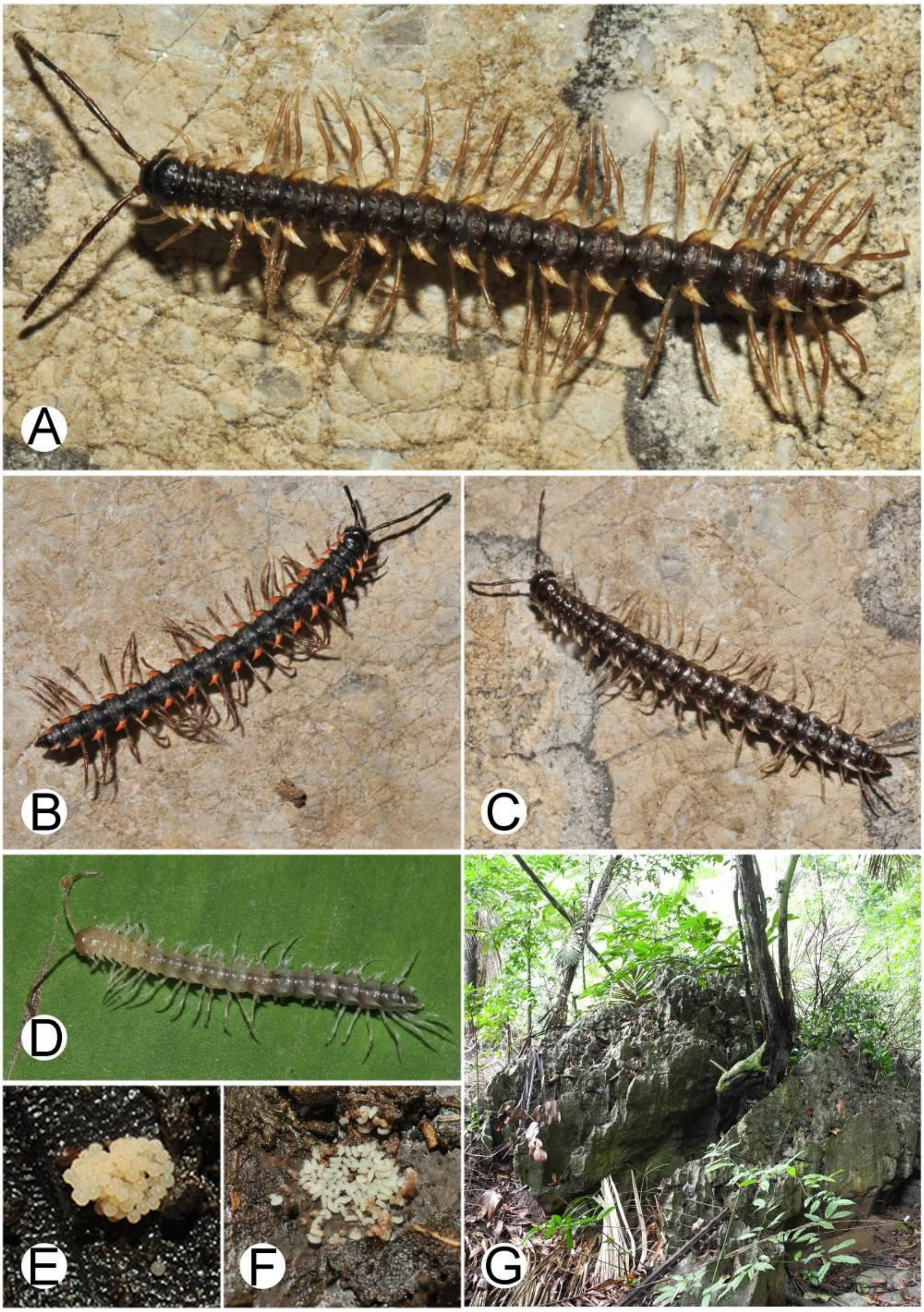

Figure 4.37 Photographs of live *Desmoxytes euros* sp. n. and habitat. **A, B** male paratypes **C** female paratype **D** juvenile **E** egg cluster **F** cluster of stadium 1 juveniles **G** habitat.

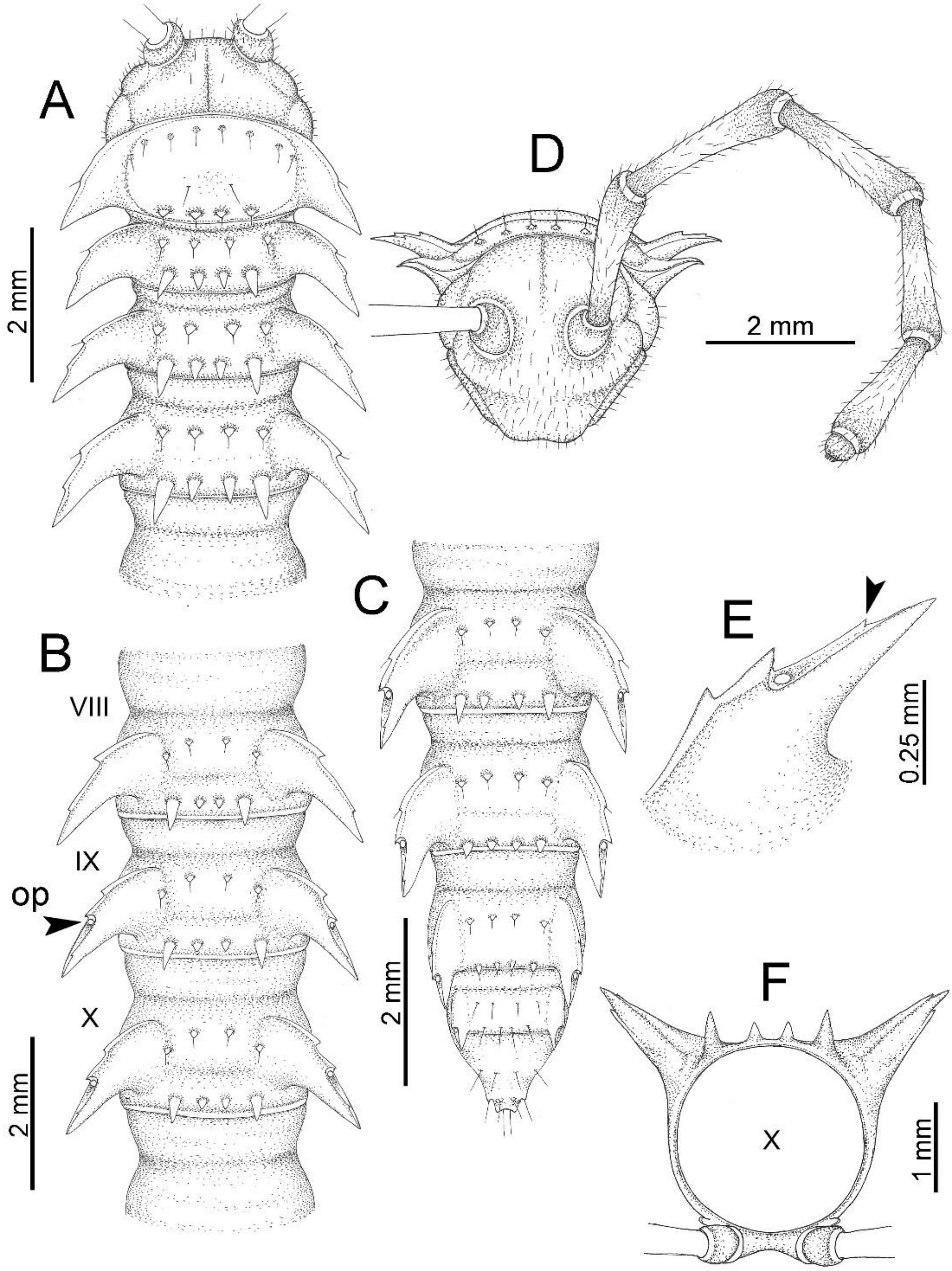

Figure 4.38 *Desmoxytes euros* sp. n. (male paratype). **A** anterior body part **B** body rings 8–10 (op = ozopore) **C** posteriormost body rings and telson **D** head and antenna **E** paraterga of ring 10 (arrow = tiny denticle) **F** body ring 10.

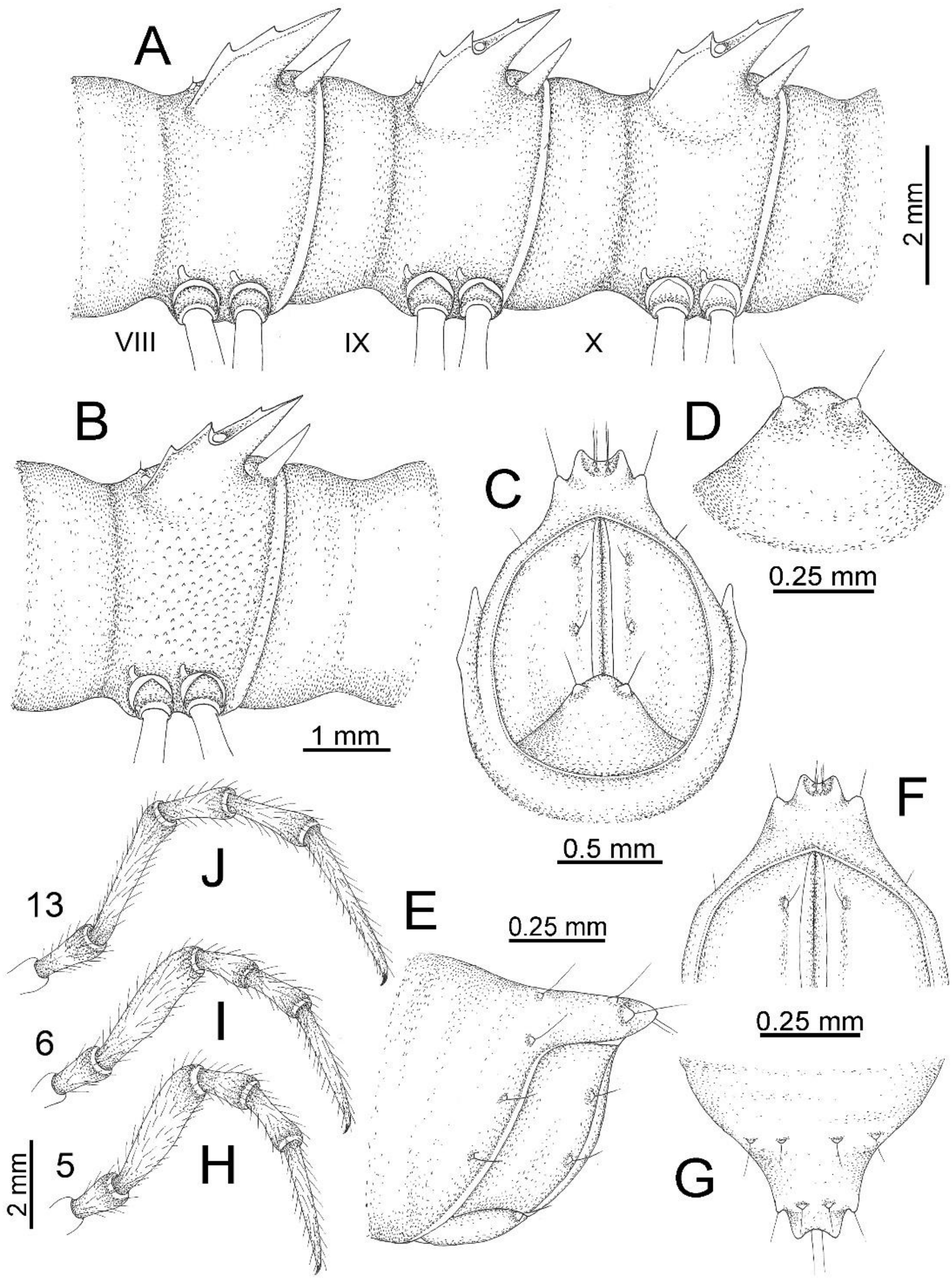

Figure 4.39 *Desmoxytes euros* sp. n. (male paratype). **A** body rings 8–10 **B** sculpture of ring 10 **C, E** last ring and telson **D** hypoproct **F, G** epiproct **H** male leg 5 (right) **I** male leg 6 (right) **J** male leg 13 (right).

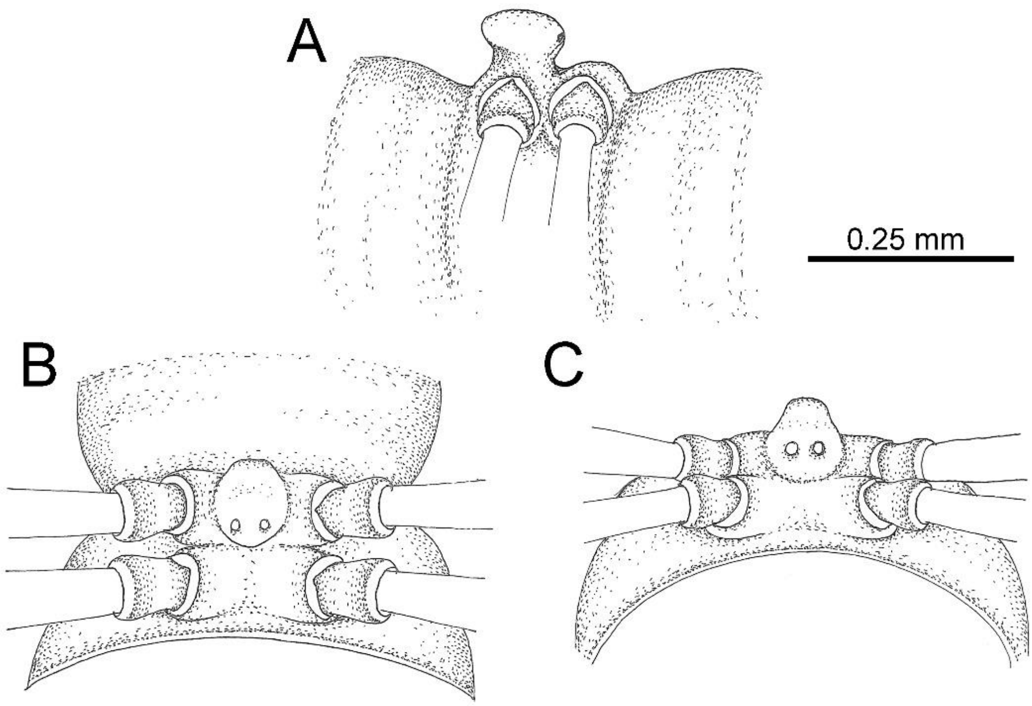

Figure 4.40 *Desmoxytes euros* sp. n. (male paratype) – sternal lobe between male coxae 4. **A** lateral view **B** ventral view **C** caudal view.

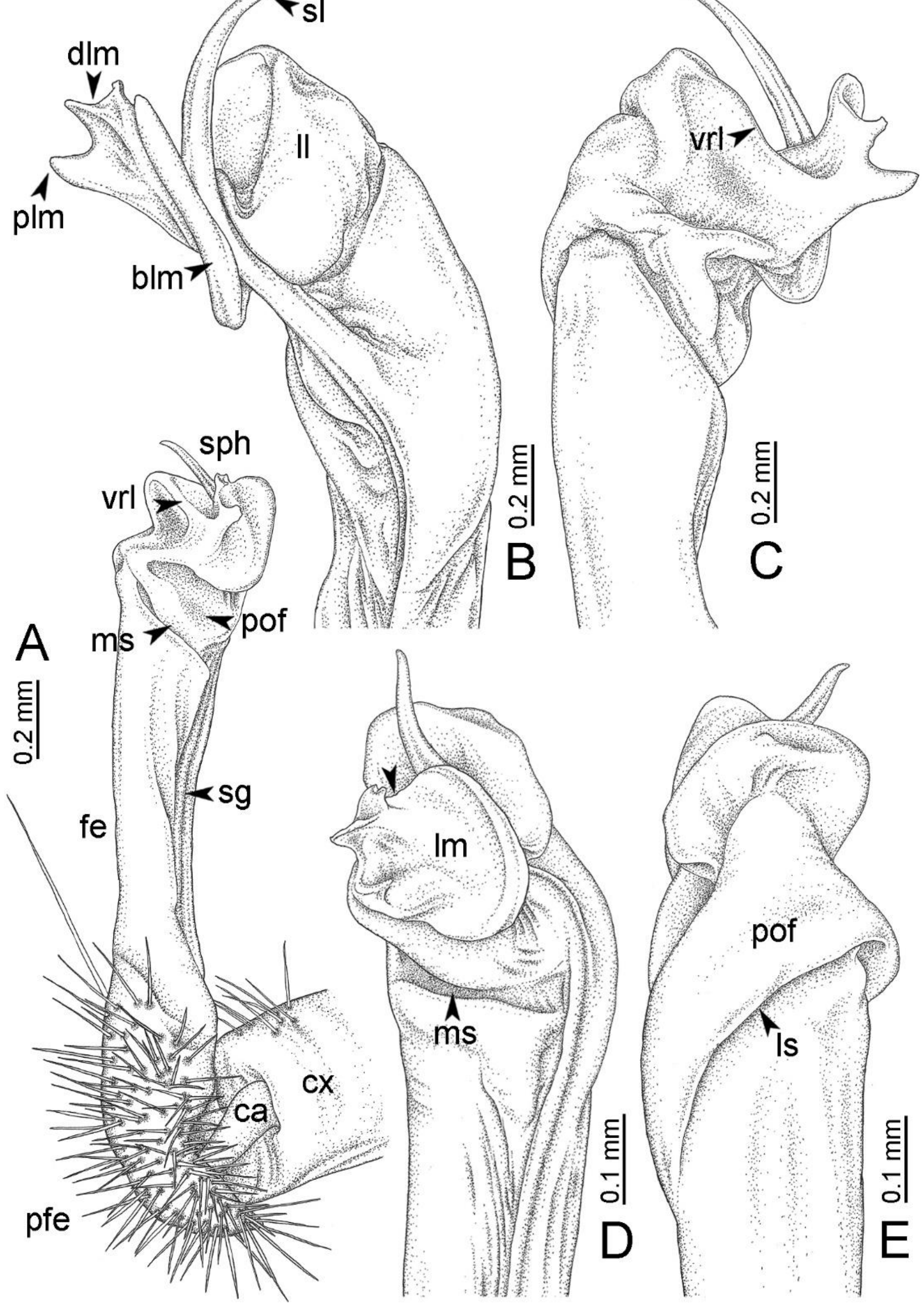

Figure 4.41 *Desmoxytes euros* sp. n. (paratype) – right gonopod. **A** mesal view **B** dorsal view **C** ventral view **D** submesal view (arrow = indentation) **E** lateral view.

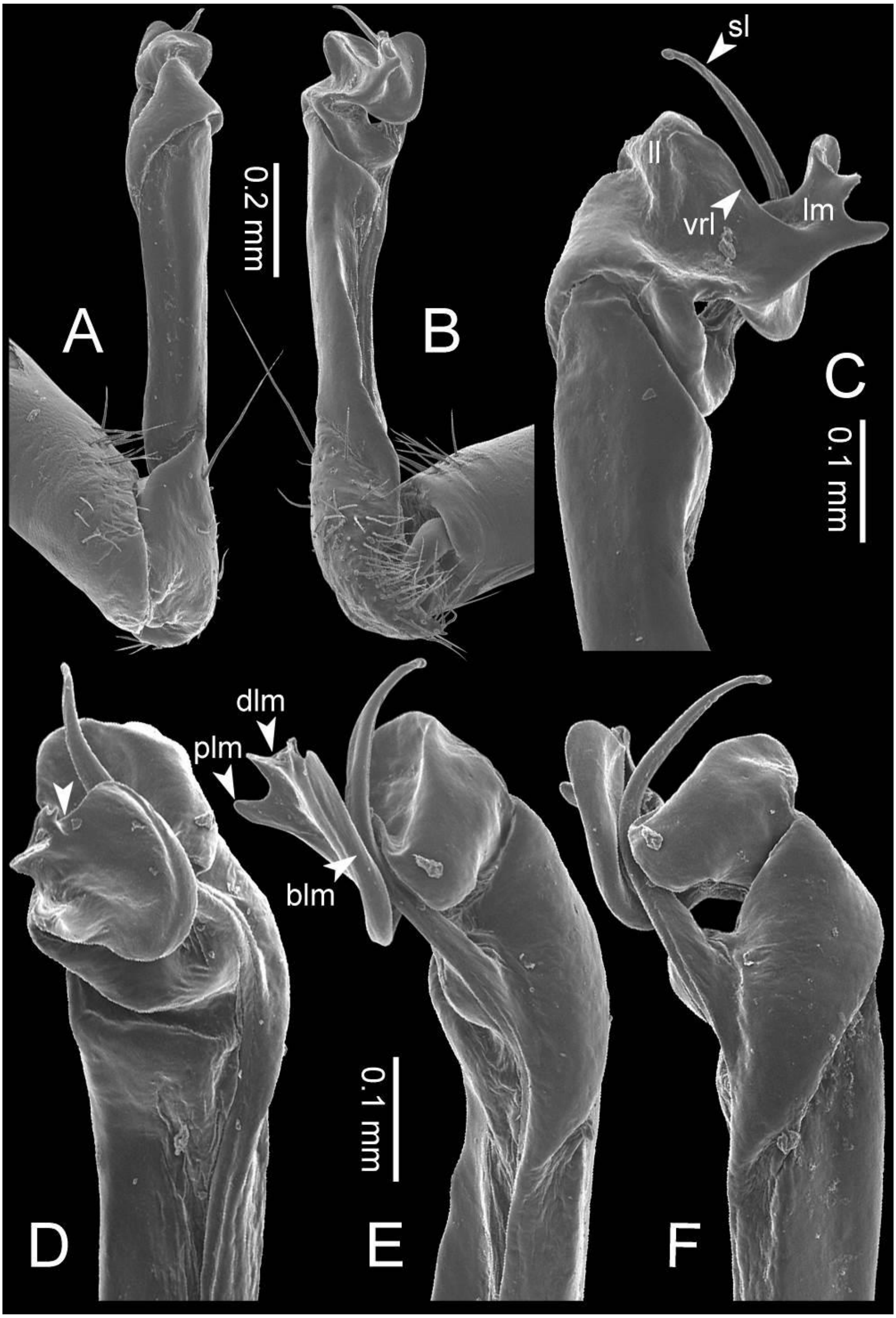

Figure 4.42 *Desmoxytes euros* sp. n. (paratype) – right gonopod. **A** lateral view **B** mesal view **C** ventral view **D, F** subdorsal view **E** dorsal view.

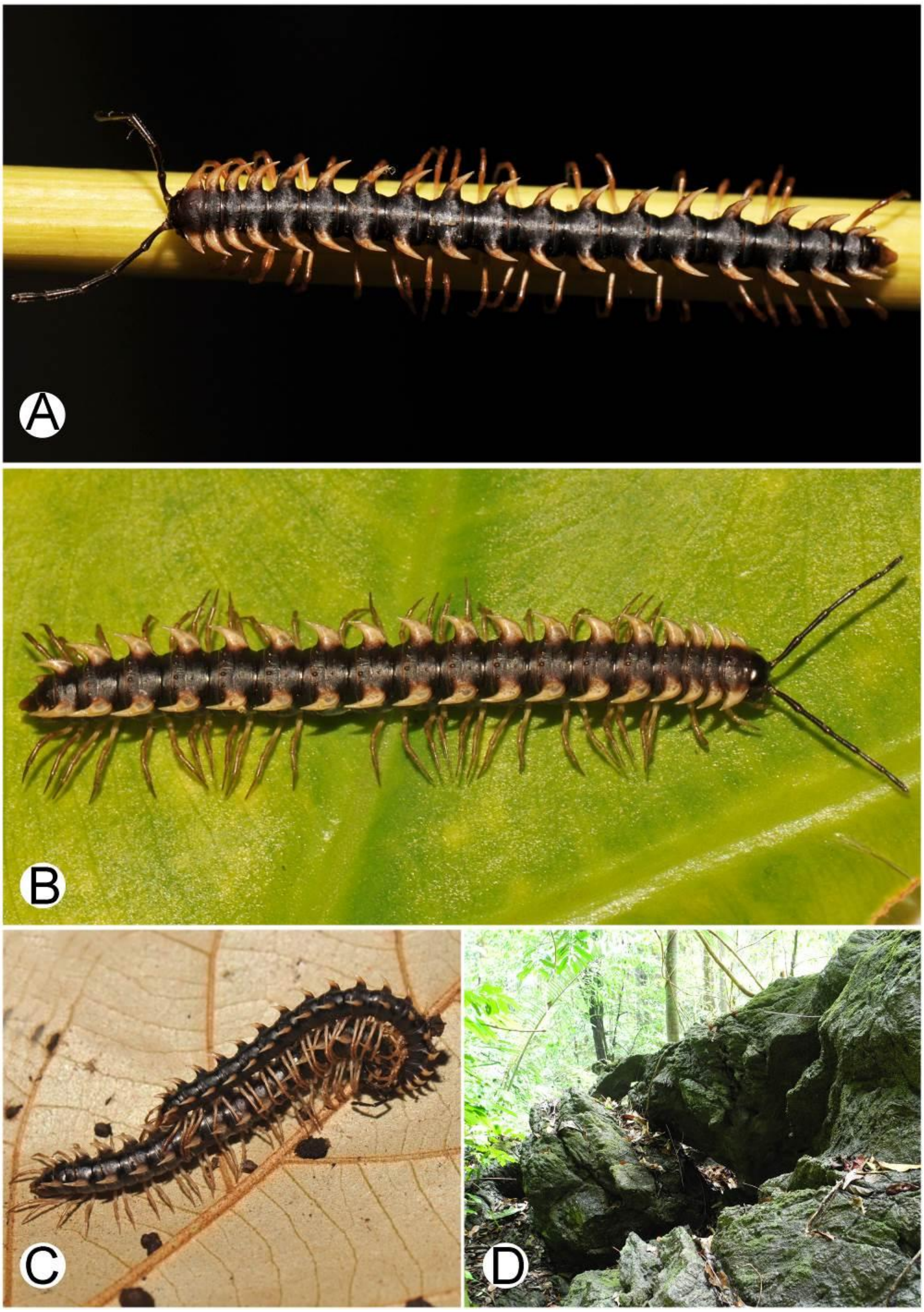

Figure 4.43 Photographs of live *Desmoxytes flabella* sp. n. and habitat. **A** male paratype **B** female paratype **C** mating couple **D** habitat.

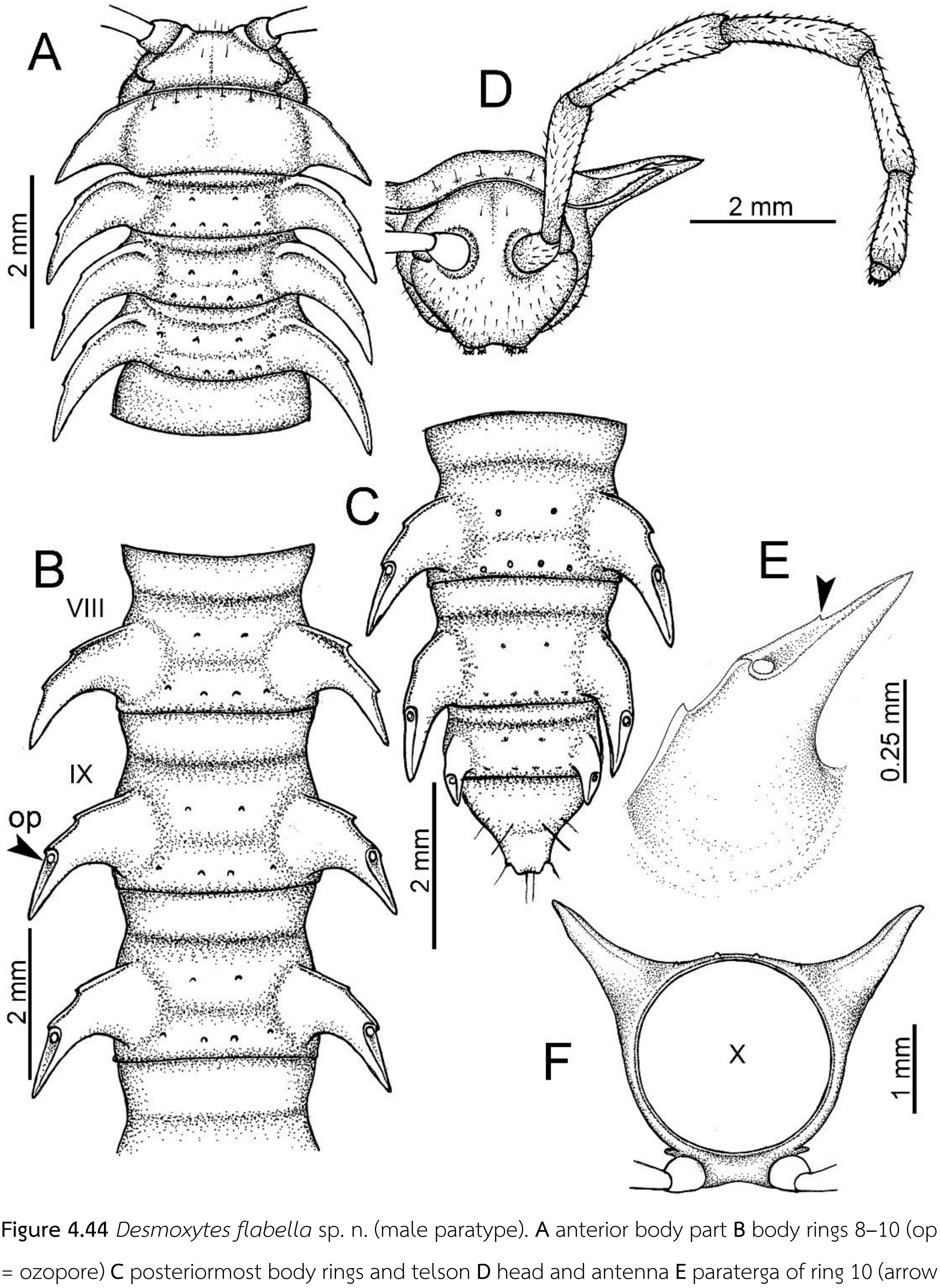

Figure 4.44 *Desmoxytes flabella* sp. n. (male paratype). **A** anterior body part **B** body rings 8–10 (op = ozopore) **C** posteriormost body rings and telson **D** head and antenna **E** paraterga of ring 10 (arrow = tiny denticle) **F** body ring 10.

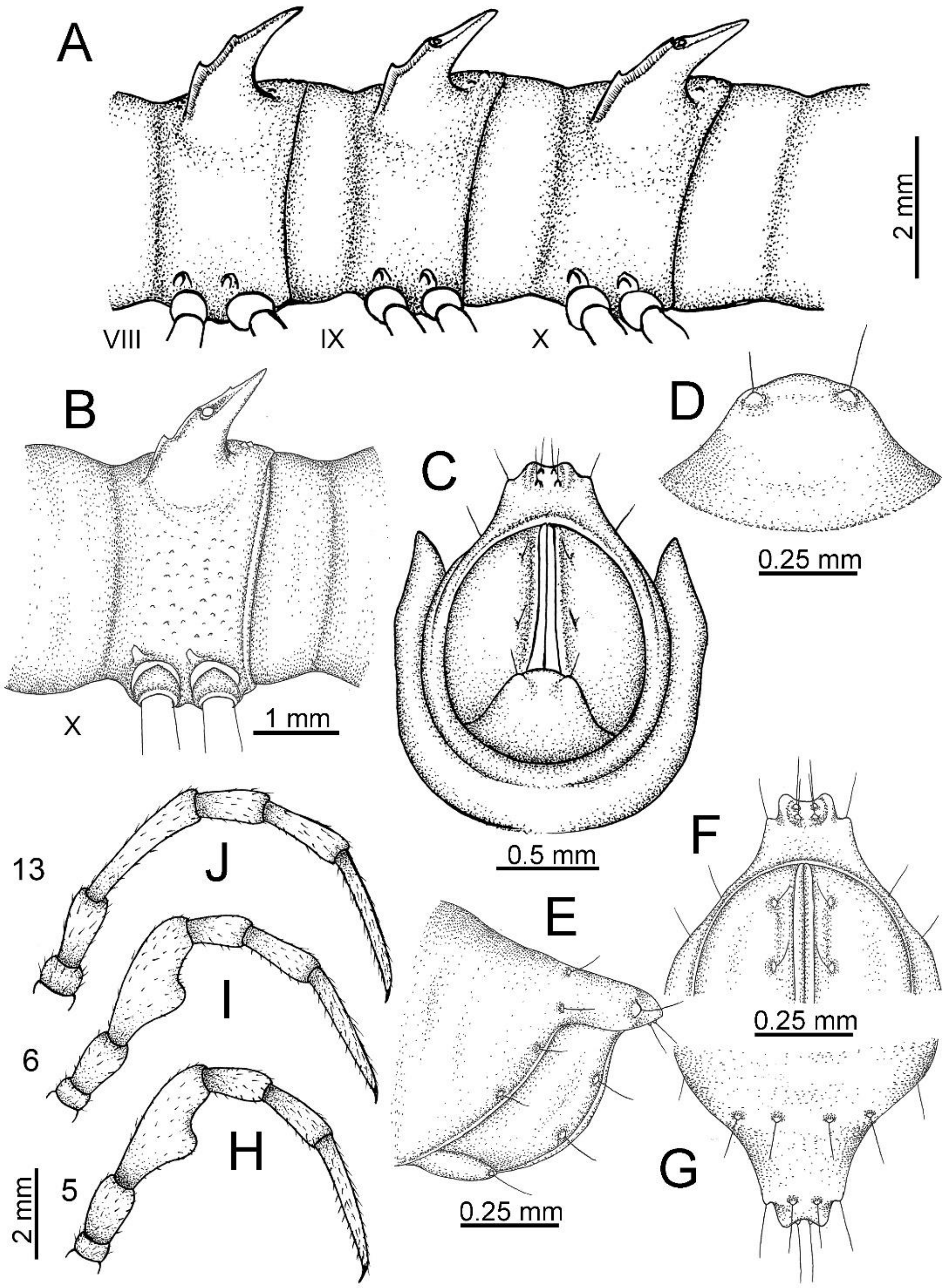

Figure 4.45 *Desmoxytes flabella* sp. n. (male paratype) **A** body rings 8–10 **B** sculpture of ring 10 **C, E** last ring and telson **D** hypoproct **F, G** epiproct **H** male leg 5 (right) **I** male leg 6 (right) **J** male leg 13 (right).

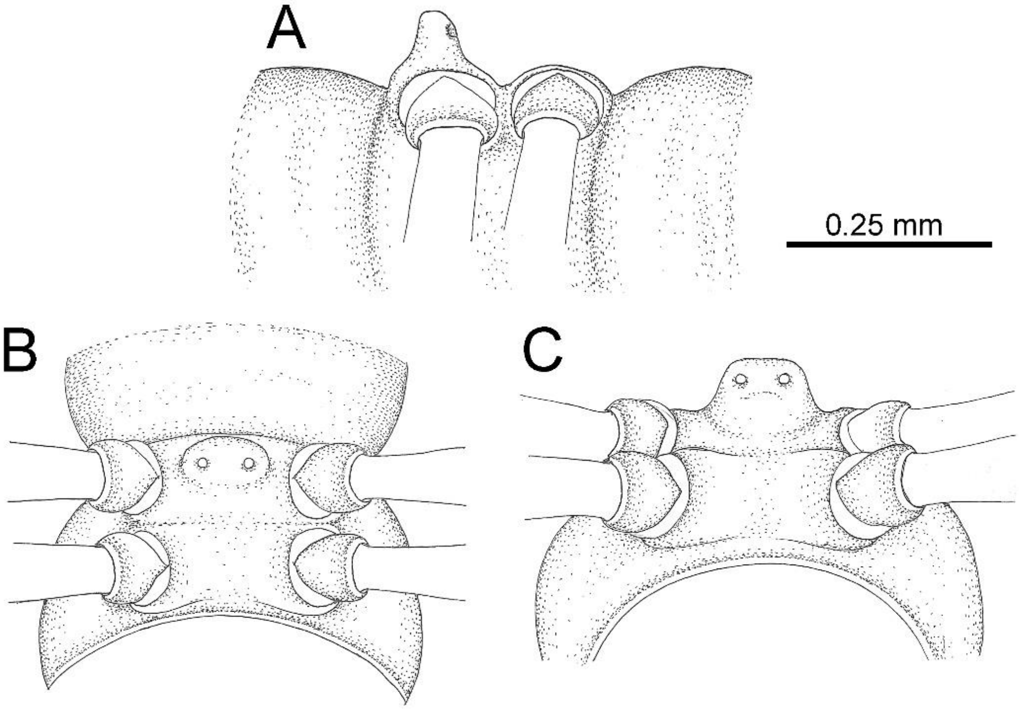

Figure 4.46 *Desmoxytes flabella* sp. n. (male paratype) – sternal lobe between male coxae 4. **A** lateral view **B** ventral view **C** caudal view.

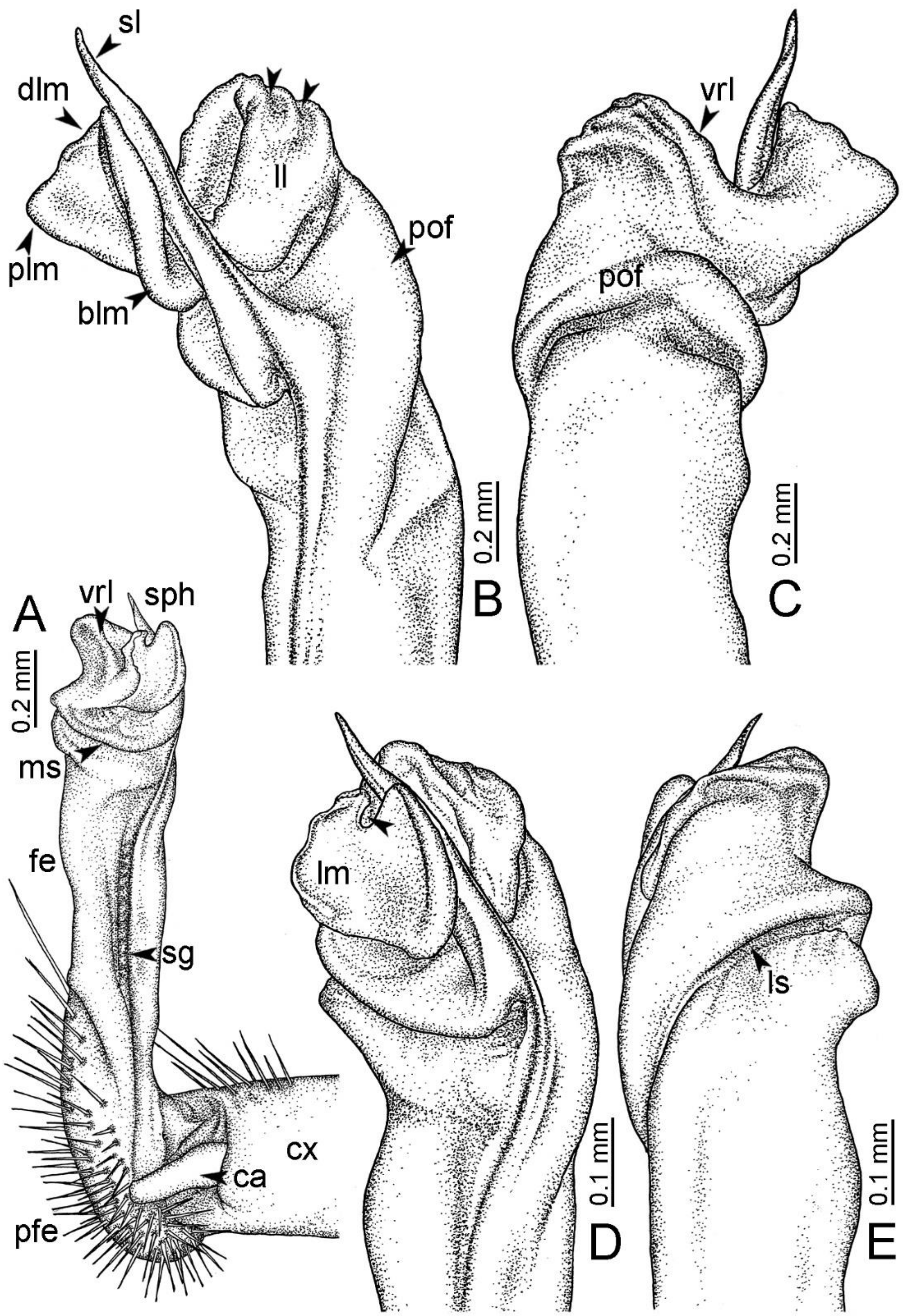

Figure 4.47 *Desmoxytes flabella* sp. n. (paratype) – right gonopod. **A** mesal view **B** dorsal view (arrows = furrows) **C** ventral view **D** submesal view (arrow = indentation) **E** lateral view.

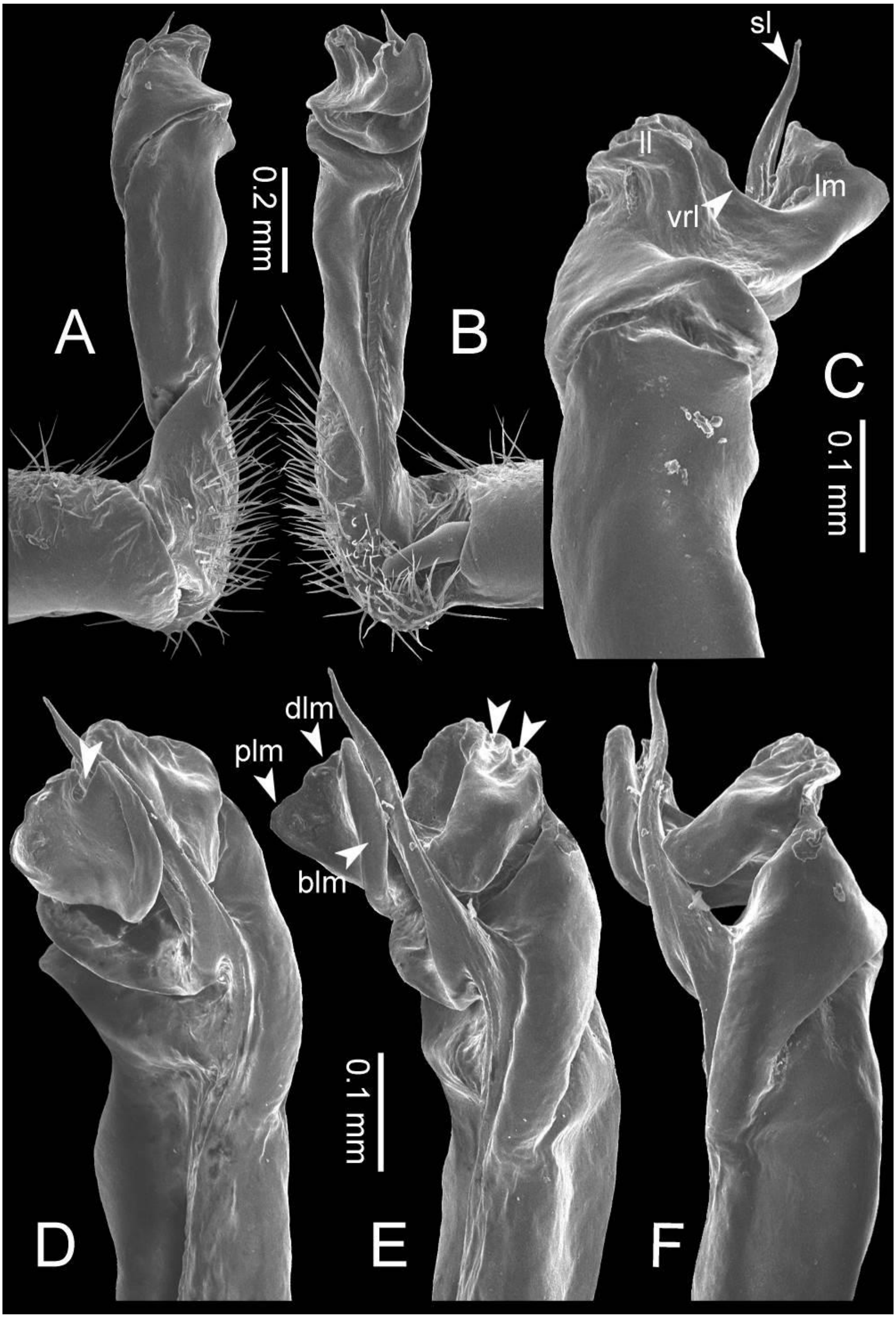

Figure 4.48 *Desmoxytes flabella* sp. n. (paratype) – right gonopod. **A** lateral view **B** mesal view **C** ventral view **D** subdorsal view (arrows = indentations) **E** dorsal view (arrows = furrows) **F** subdorsal view.

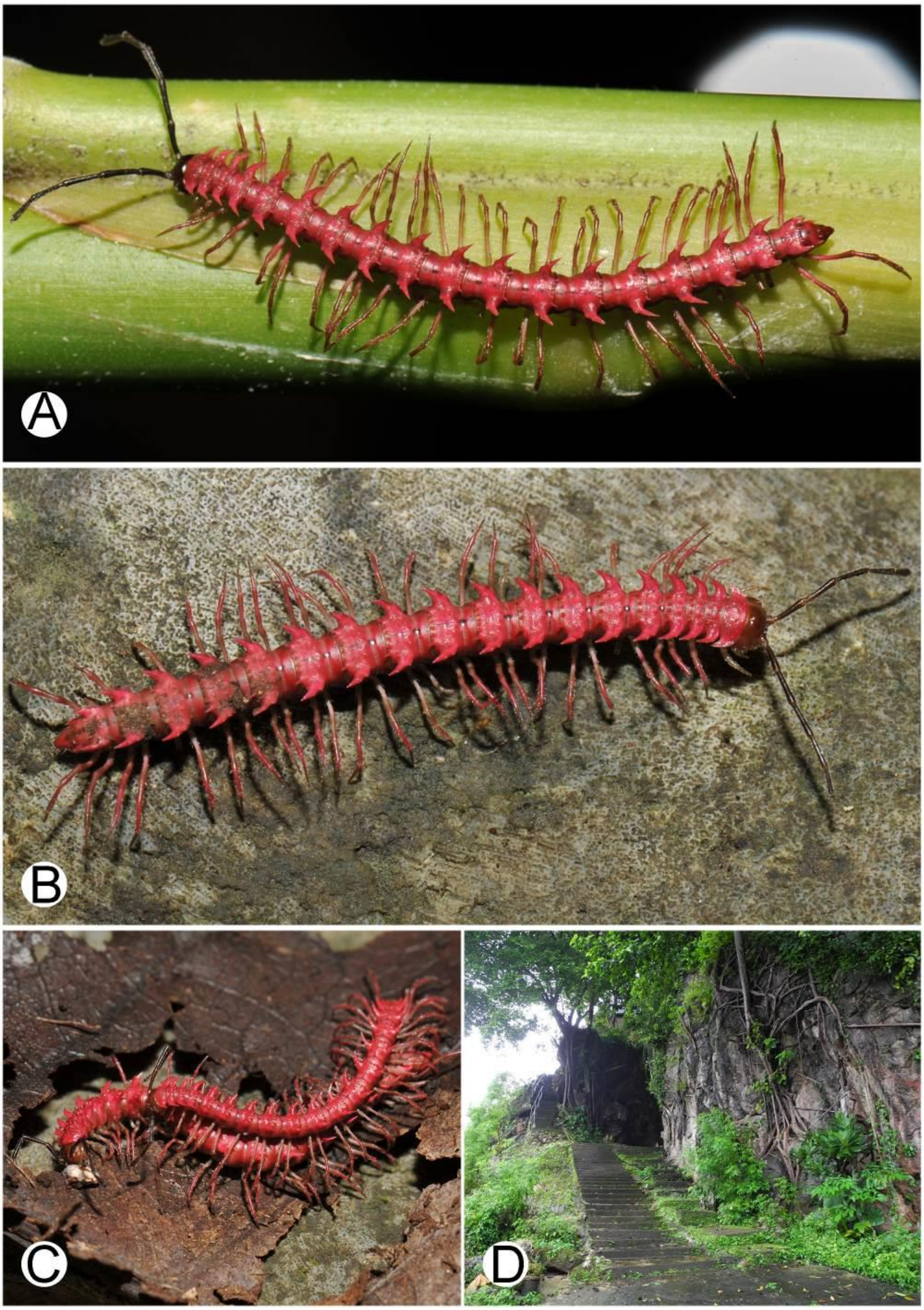

Figure 4.49 Photographs of live *Desmoxytes golovatchi* sp. n. and habitat. **A** male paratype **B** female paratype **C** mating couple **D** habitat.

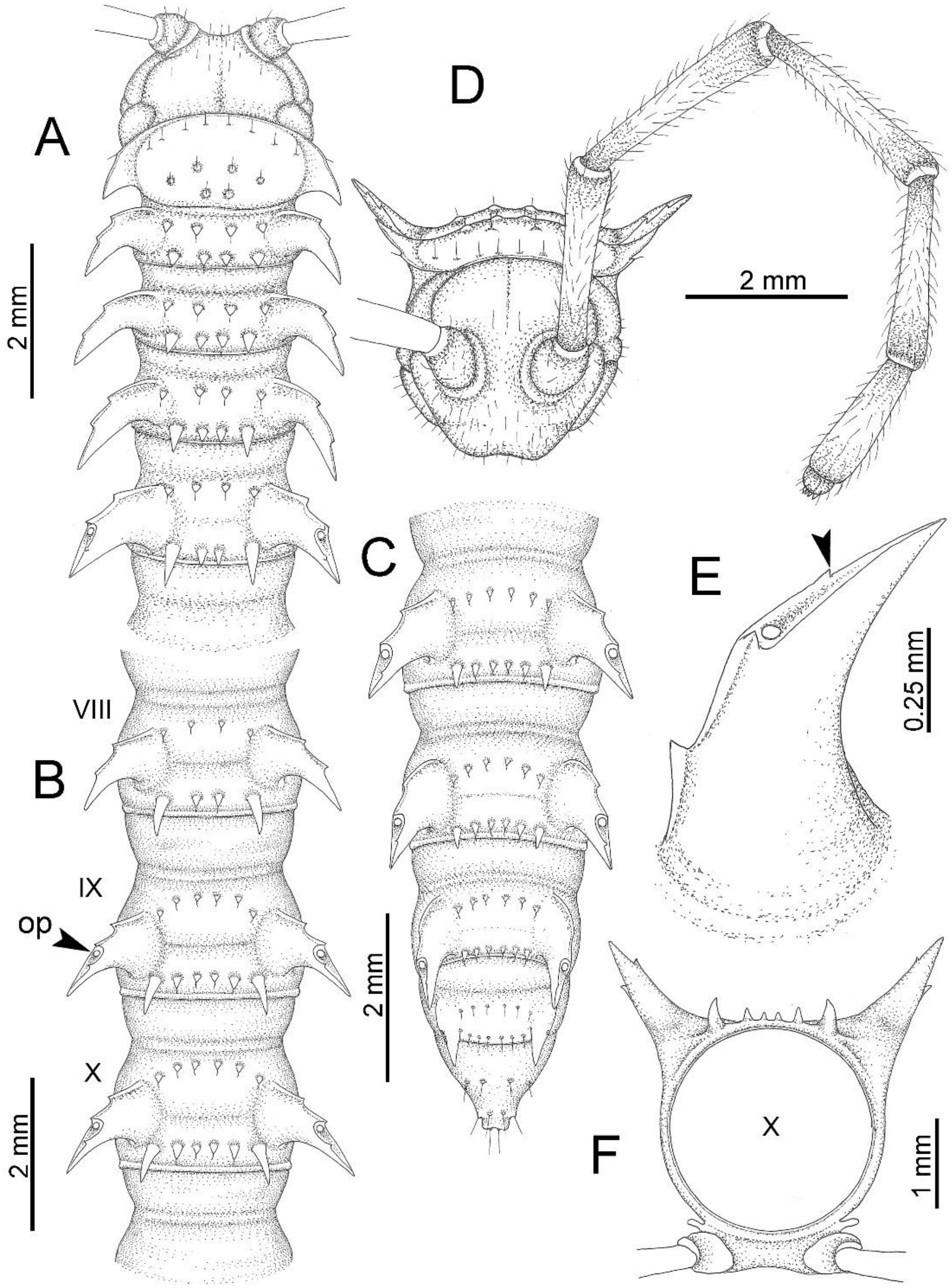

Figure 4.50 *Desmoxytes golovatchi* sp. n. (male paratype). **A** anterior body part **B** body rings 8–10 (op = ozopore) **C** posteriormost body rings and telson **D** head and antenna **E** paraterga of ring 10 (arrow = tiny denticle) **F** body ring 10.0

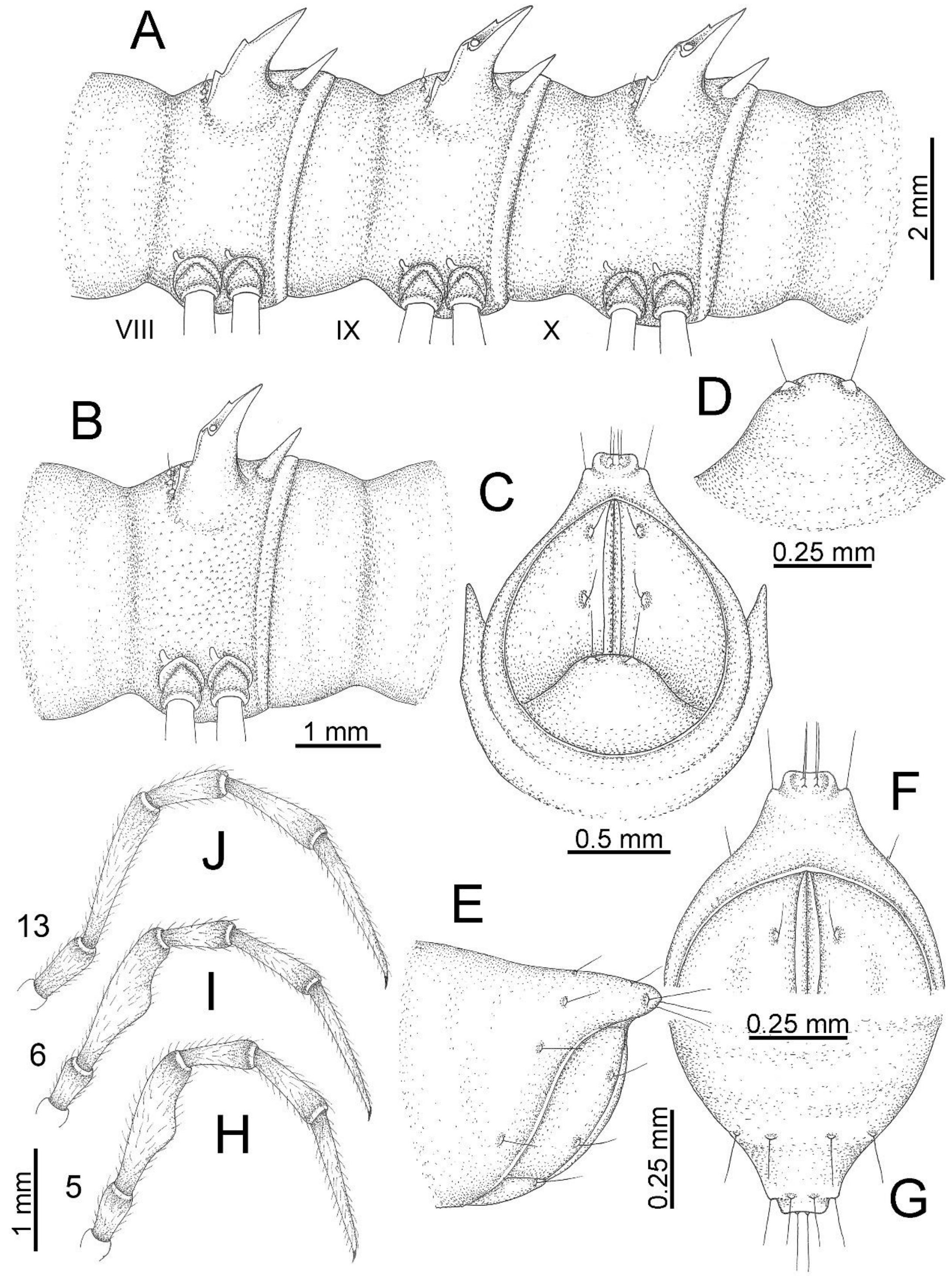

Figure 4.51 *Desmoxytes golovatchi* sp. n. (male paratype). **A** body rings 8–10 **B** sculpture of ring 10 **C, E** last ring and telson **D** hypoproct **F, G** epiproct **H** male leg 5 (right) **I** male leg 6 (right) **J** male leg 13 (right).

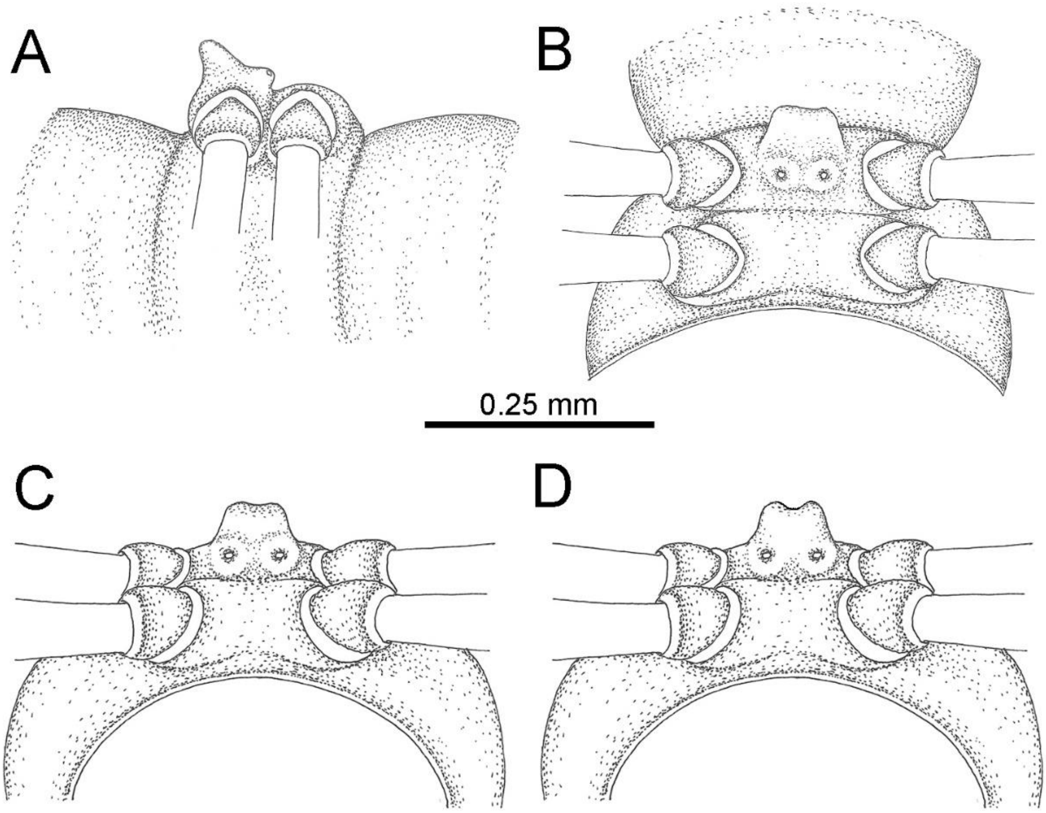

Figure 4.52 *Desmoxytes golovatchi* sp. n. (male paratype) – sternal lobe between male coxae 4. **A** lateral view **B** ventral view **C, D** caudal view.

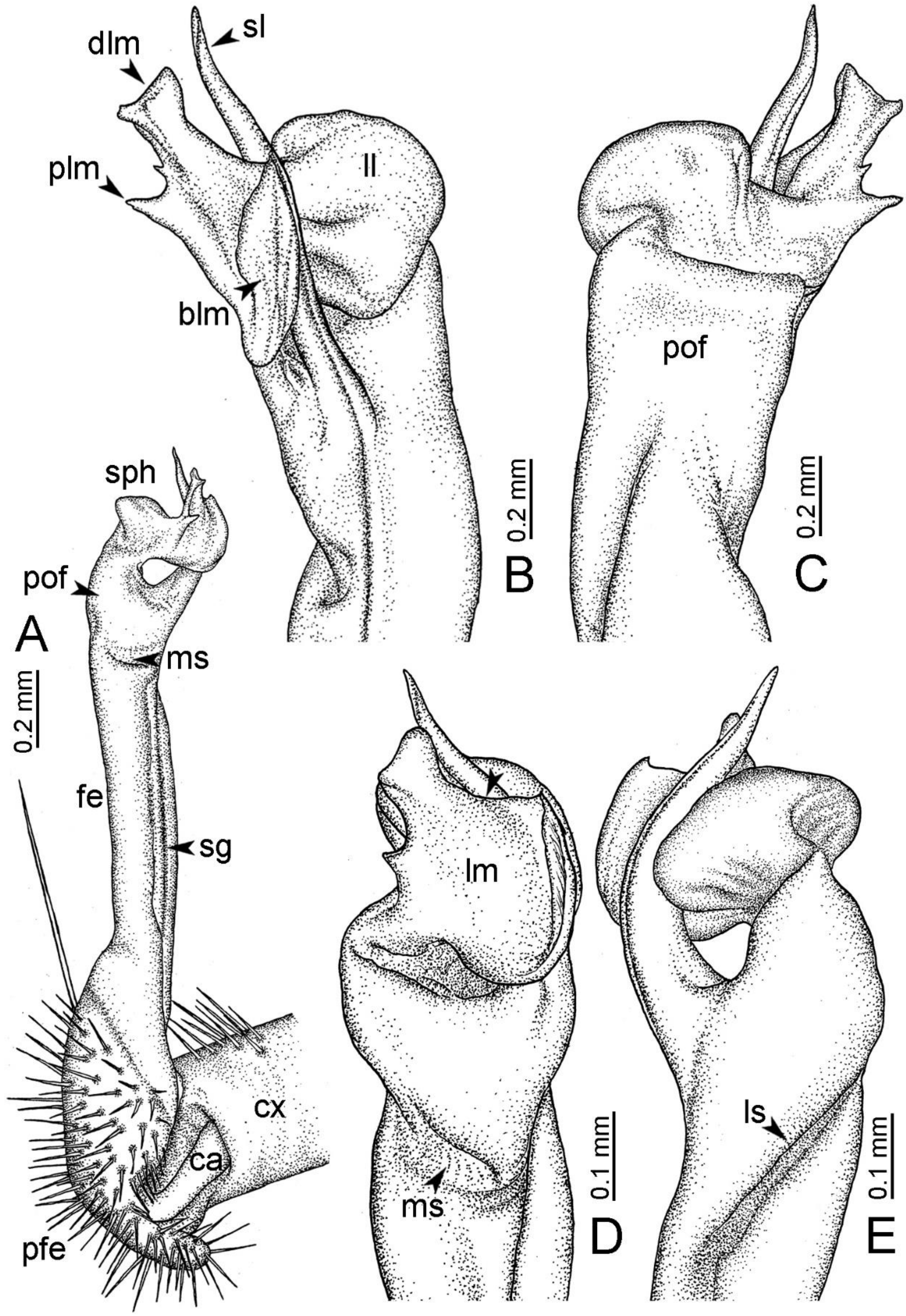

Figure 4.53 *Desmoxytes golovatchi* sp. n. (paratype) – right gonopod. **A** mesal view **B** dorsal view **C** ventral view **D** submesal view (arrow = indentation) **E** lateral view.

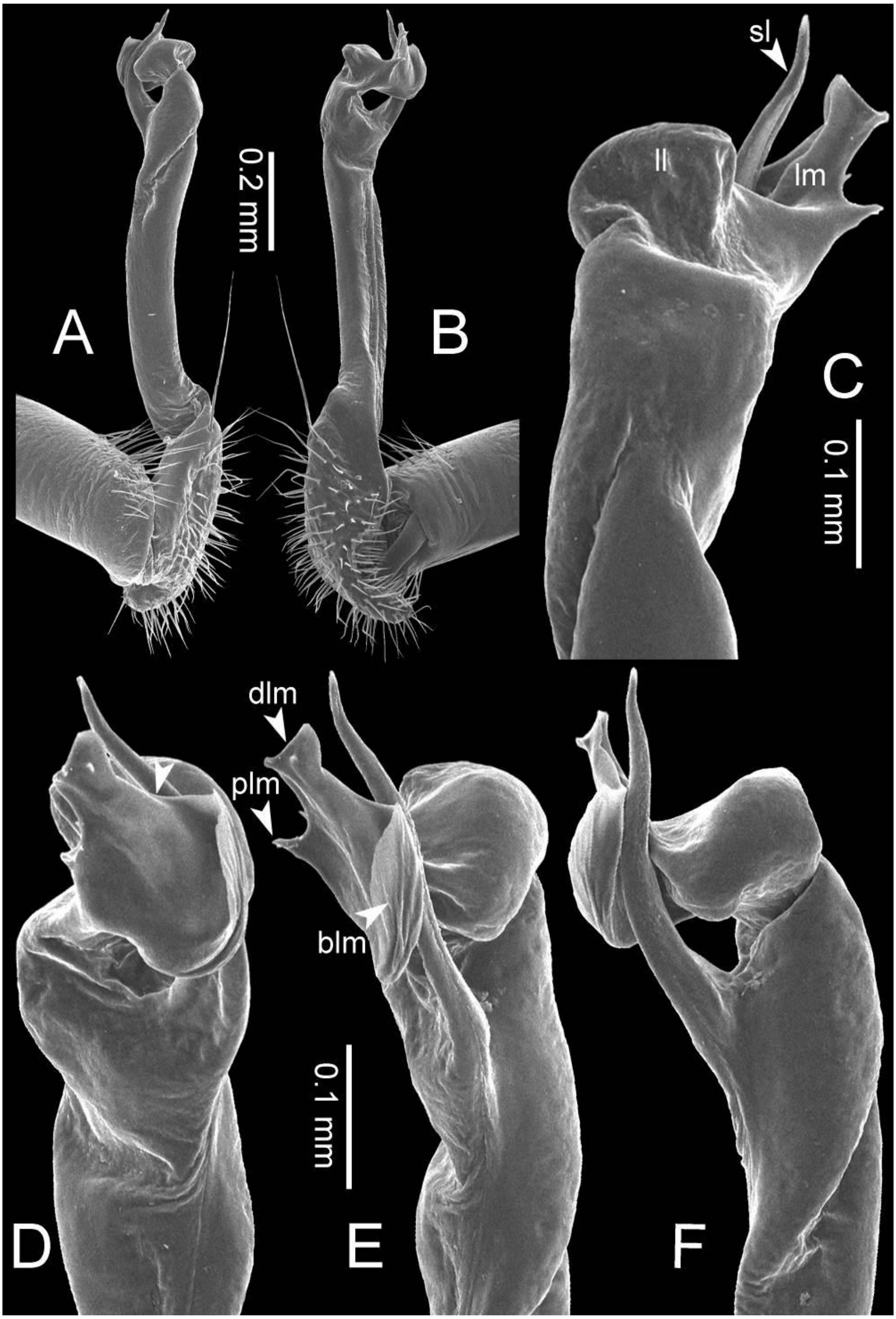

Figure 4.54 *Desmoxytes golovatchi* sp. n. (paratype) – right gonopod. **A** lateral view **B** mesal view **C** ventral view **D** subdorsal view (arrow = indentation) **E** dorsal view **F** subdorsal view.

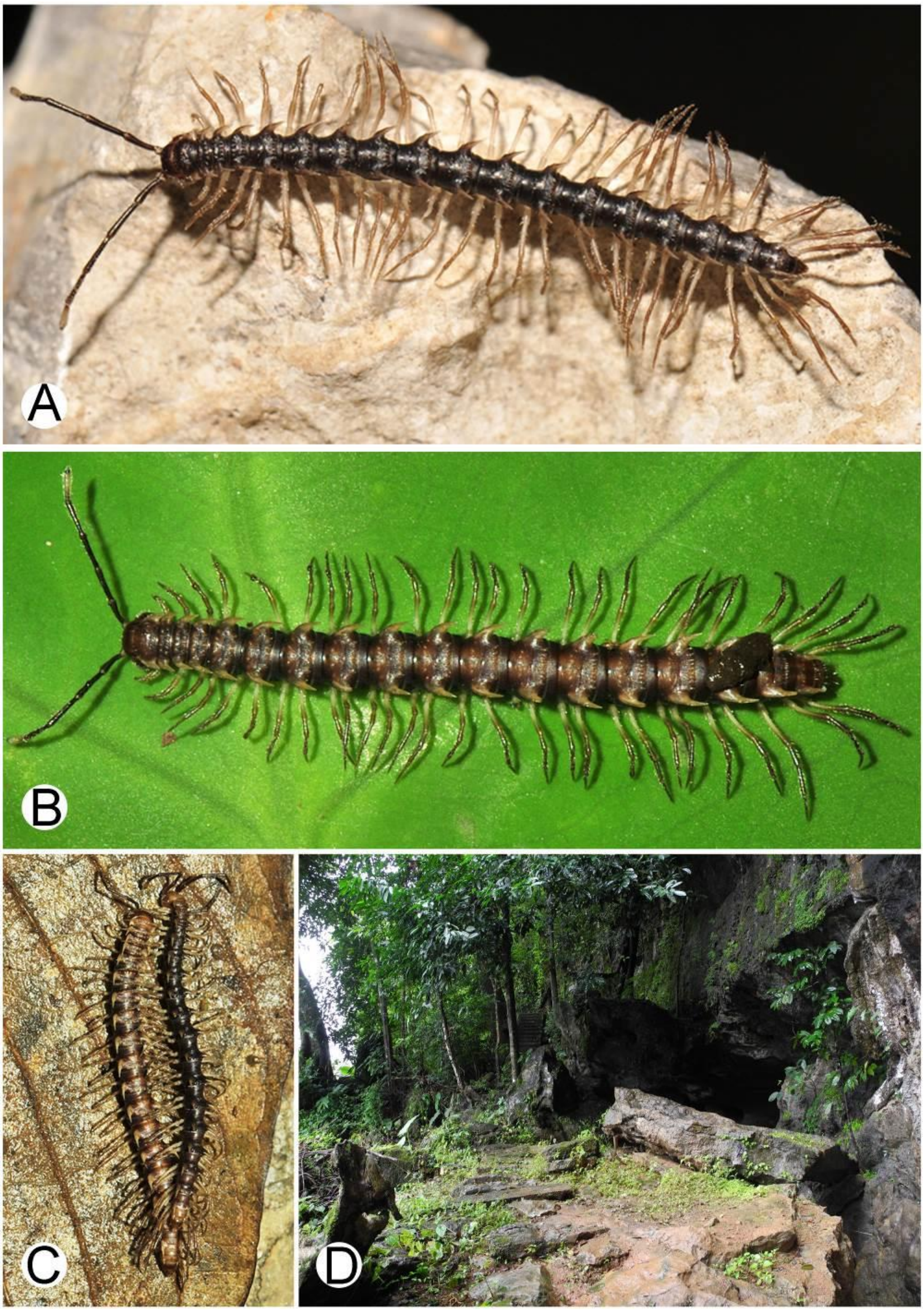

Figure 4.55 Photographs of live *Desmoxytes octoconigera* sp. n. and habitat. **A** male paratype **B** female paratype **C** mating couple **D** habitat.

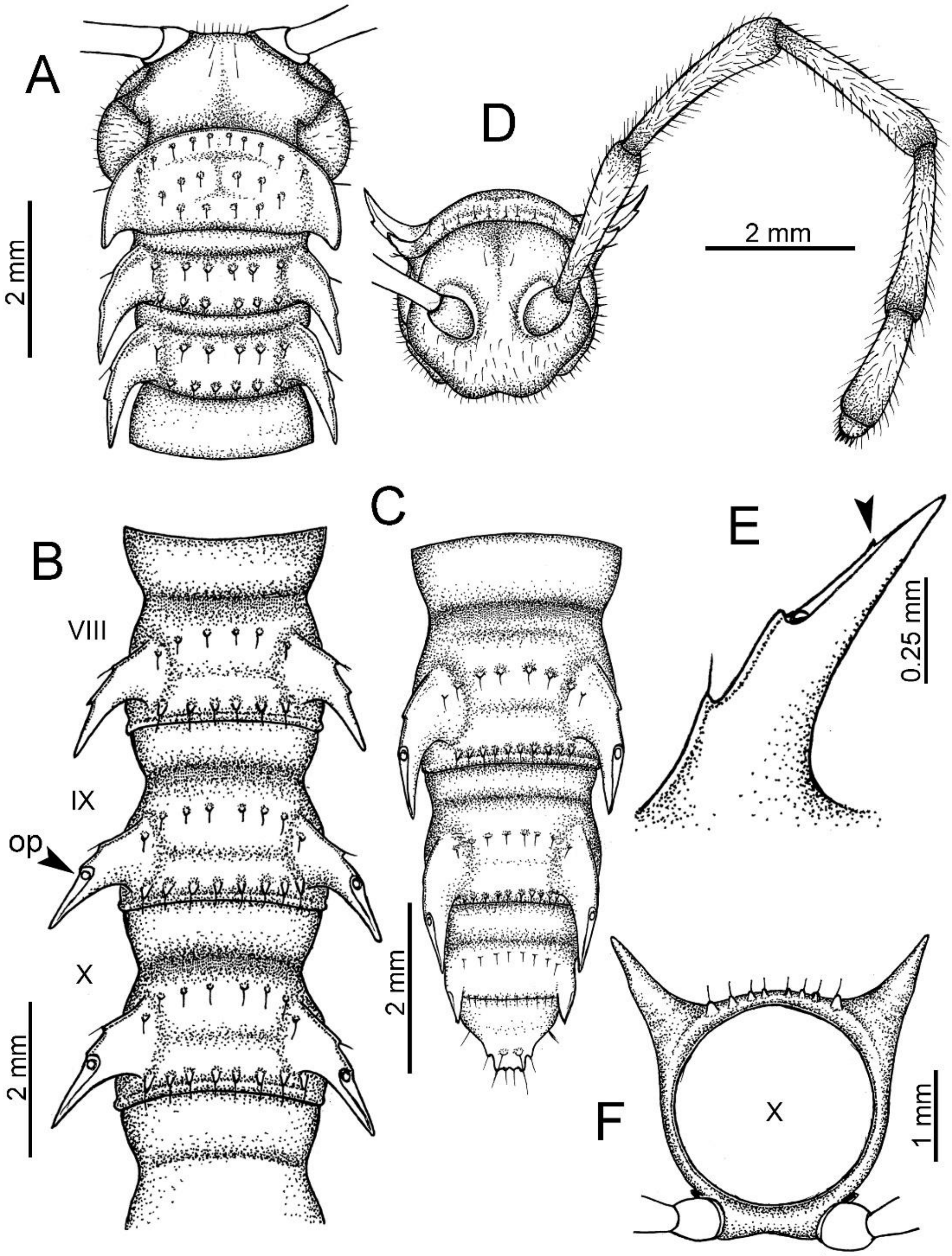

Figure 4.56 *Desmoxytes octoconigera* sp. n. (male paratype). **A** anterior body part **B** body rings 8–10 (op = ozopore) **C** posteriormost body rings and telson **D** head and antenna **E** paraterga of ring 10 (arrow = tiny denticle) **F** body ring 10.

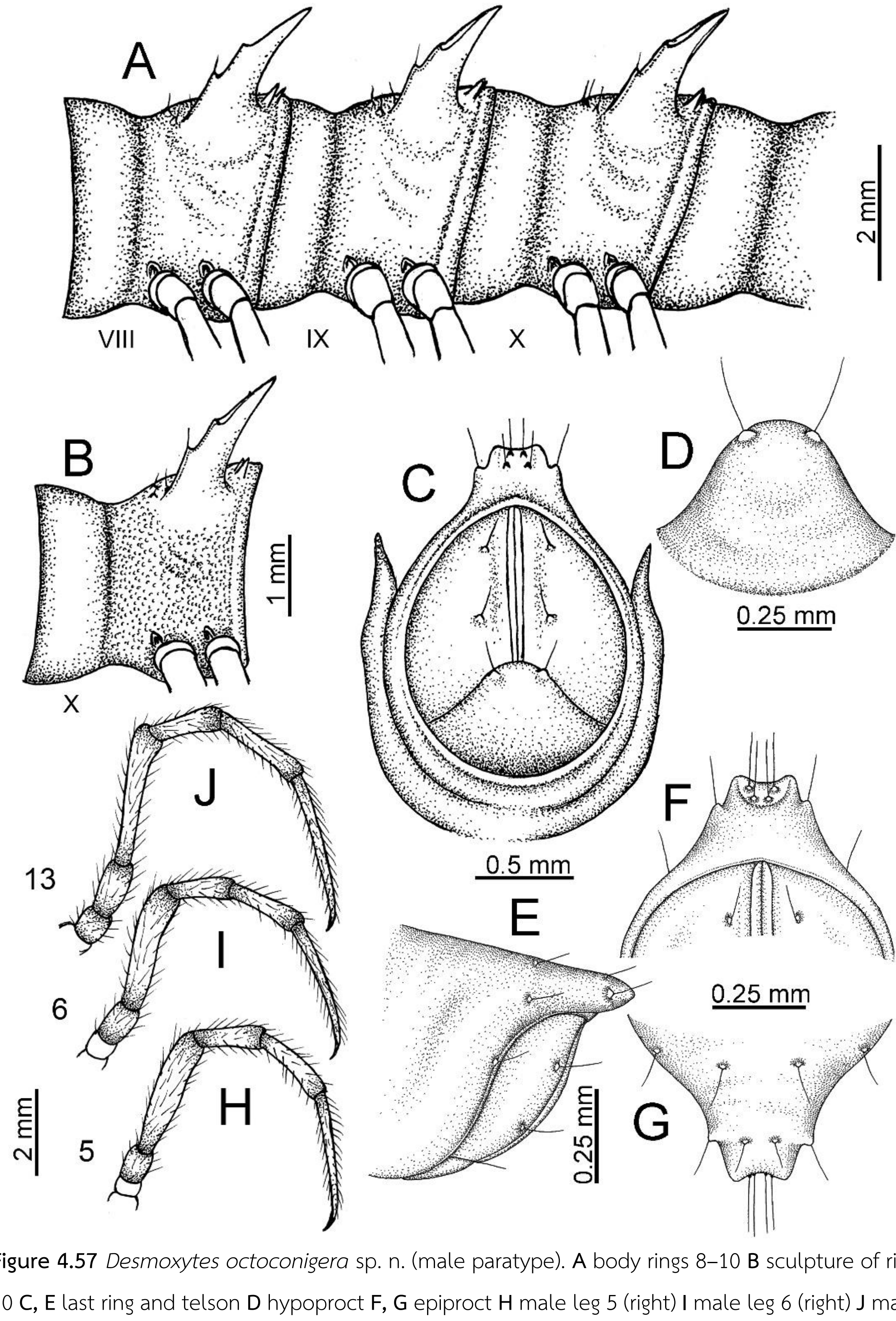

Figure 4.57 *Desmoxytes octoconigera* sp. n. (male paratype). **A** body rings 8–10 **B** sculpture of ring 10 **C, E** last ring and telson **D** hypoproct **F, G** epiproct **H** male leg 5 (right) **I** male leg 6 (right) **J** male leg 13 (right).

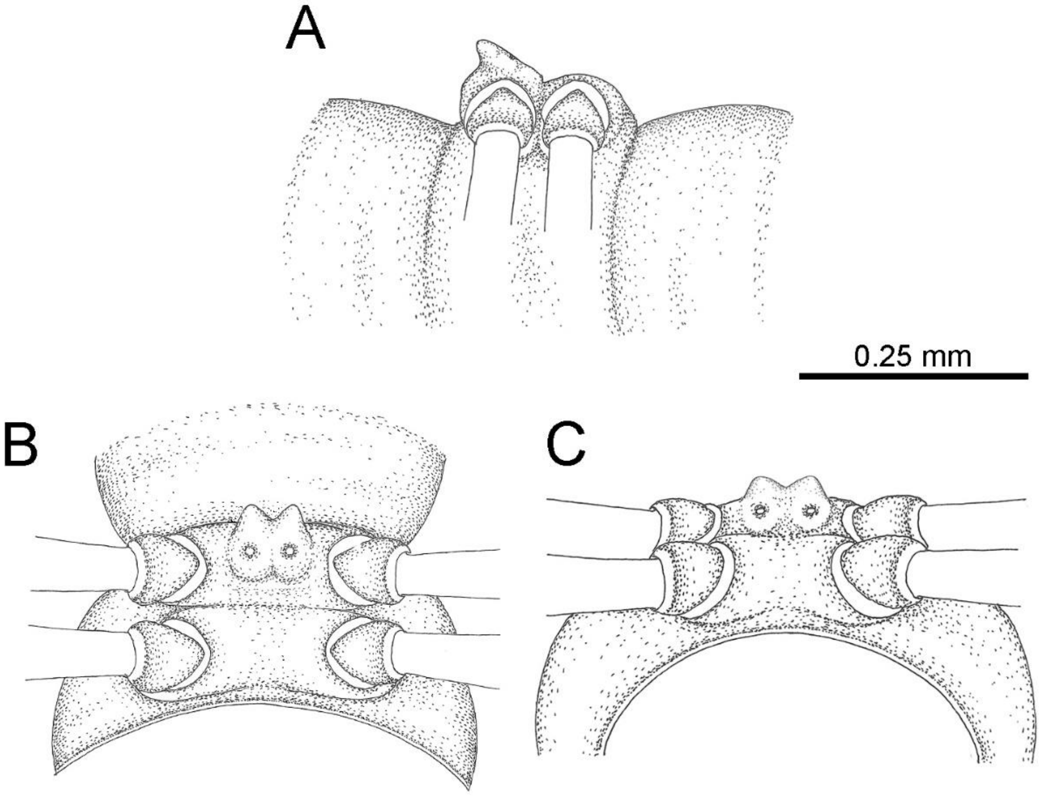

Figure 4.58 *Desmoxytes octoconigera* sp. n. (male paratype) – sternal lobe between male coxae 4. **A** lateral view **B** ventral view **C** caudal view.

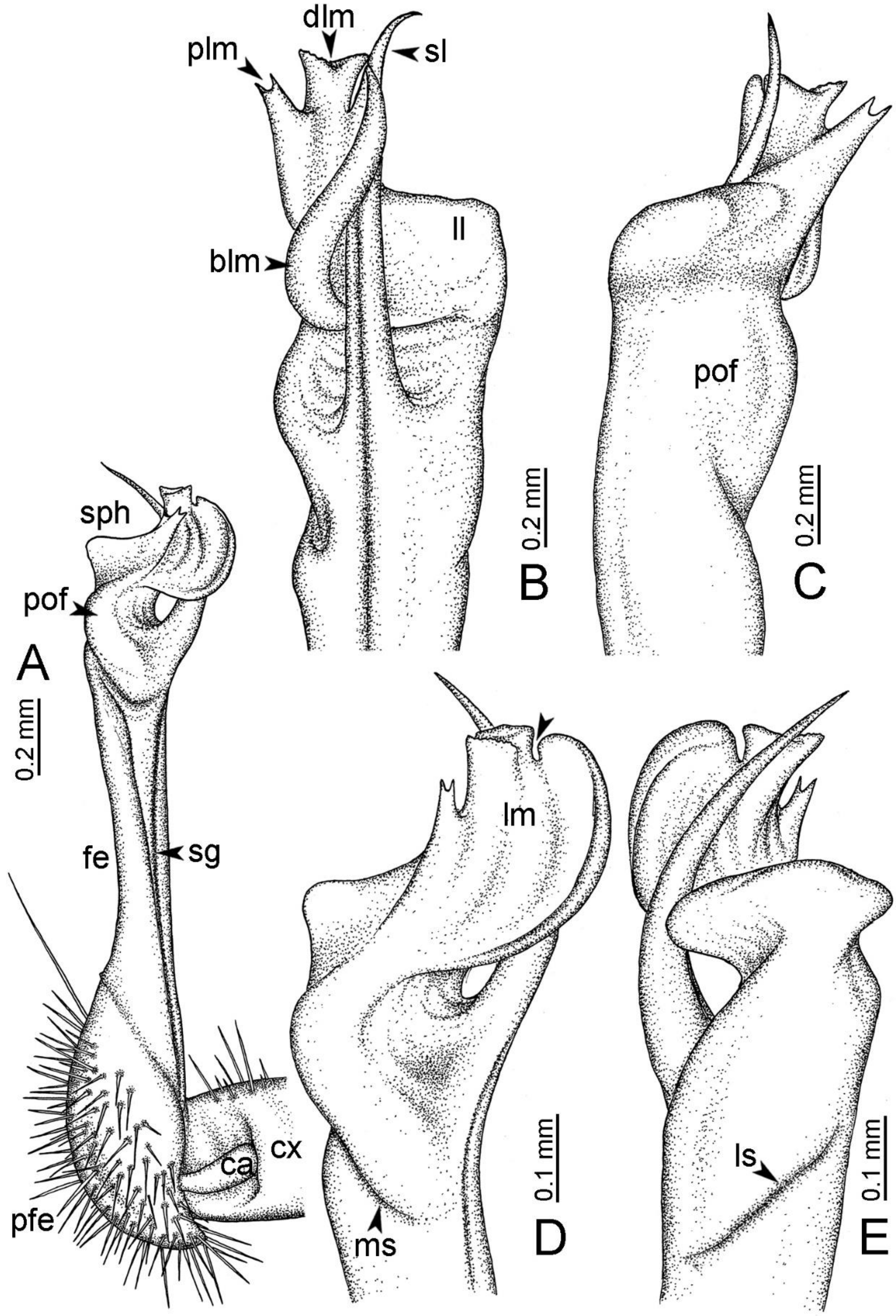

Figure 4.59 *Desmoxytes octoconigera* sp. n. (paratype) – right gonopod. **A** mesal view **B** dorsal view **C** ventral view **D** submesal view (arrow = indentation) **E** lateral view.

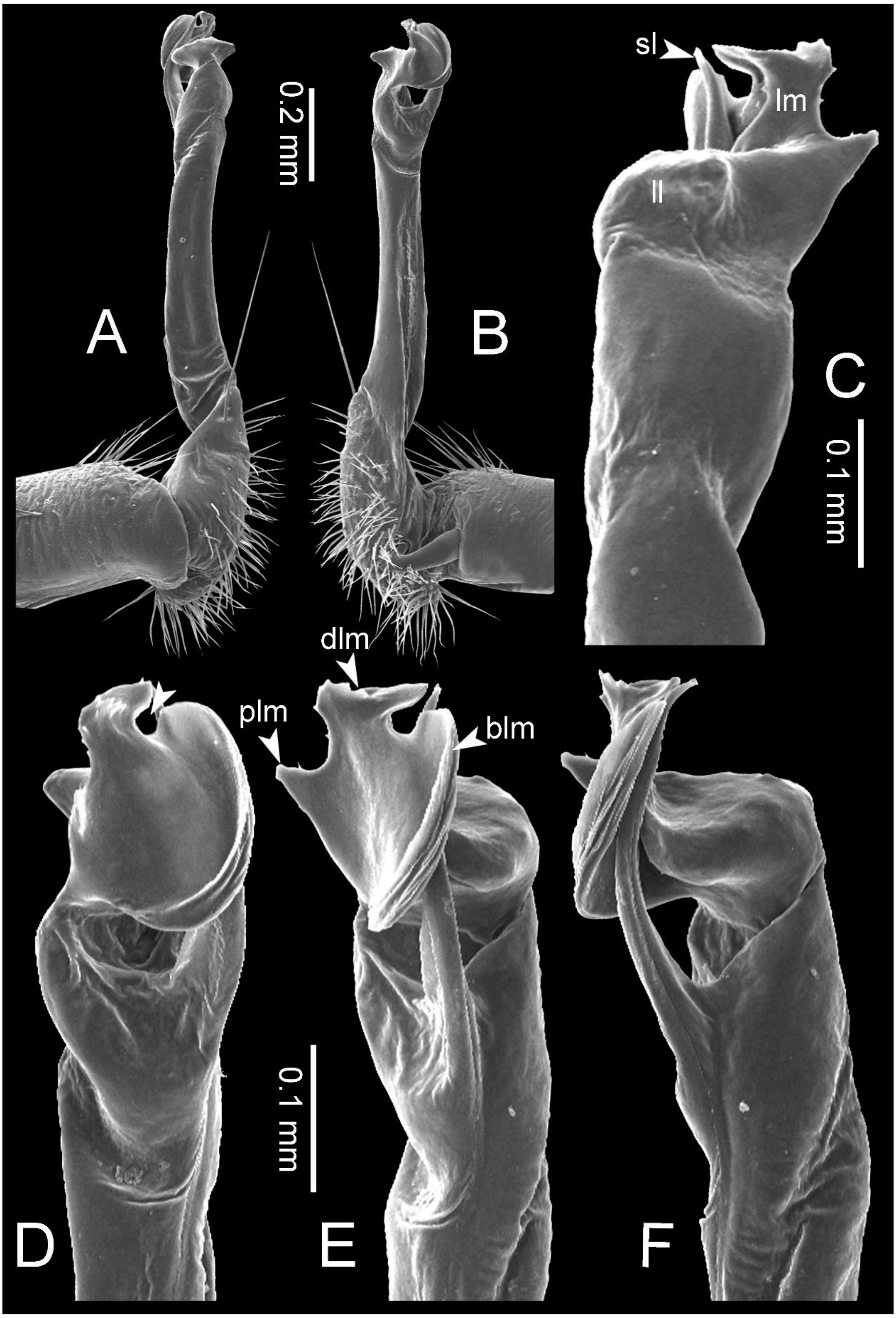

Figure 4.60 *Desmoxytes octoconigera* sp. n. (paratype) – right gonopod. **A** lateral view **B** mesal view **C** ventral view **D** subdorsal view (arrow = indentation) **E** dorsal view **F** subdorsal view.

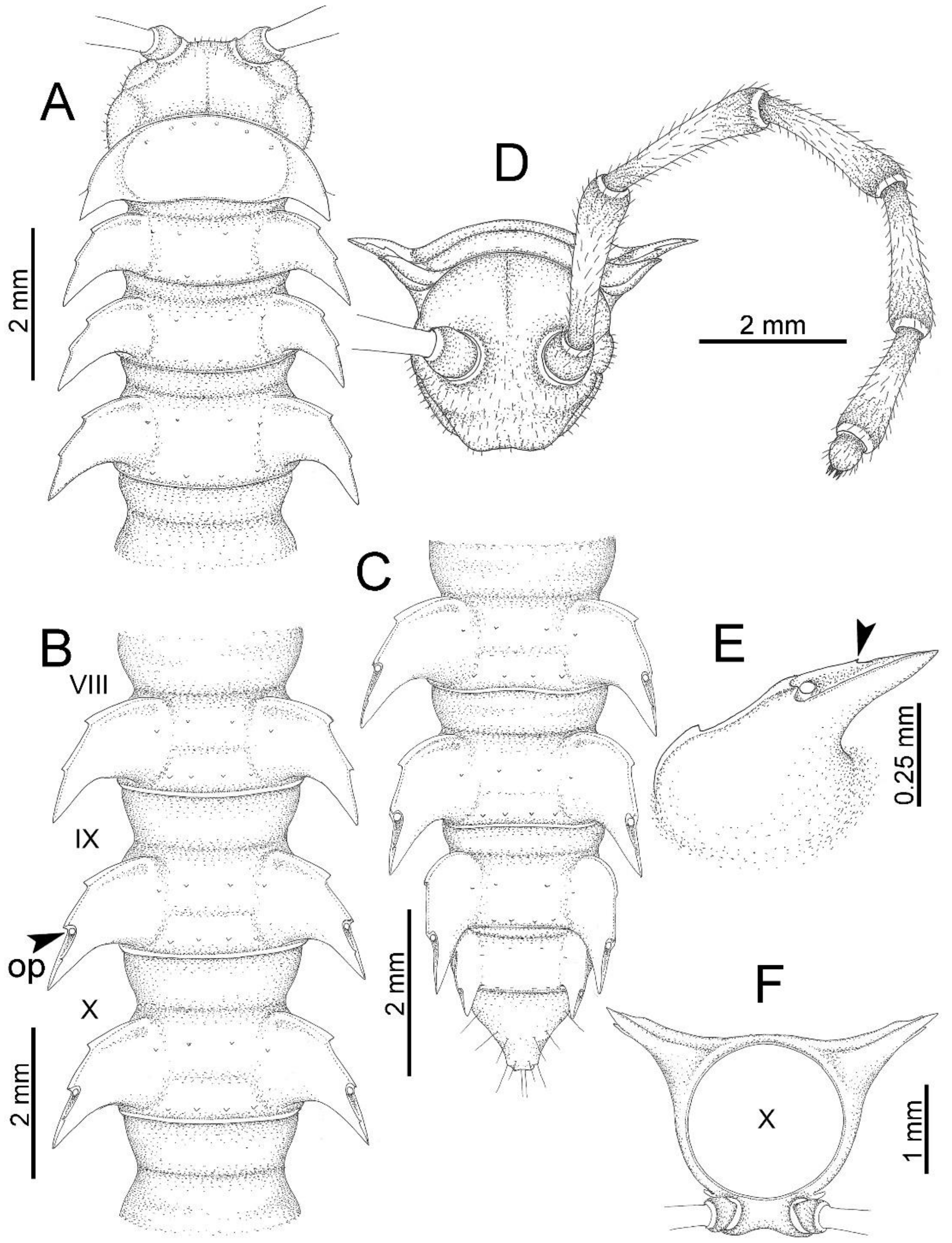

Figure 4.61 *Desmoxytes perakensis* sp. n. (male paratype). **A** anterior body part **B** body rings 8–10 (op = ozopore) **C** posteriormost body rings and telson **D** head and antenna **E** paraterga of ring 10 (arrow = tiny denticle) **F** body ring 10.

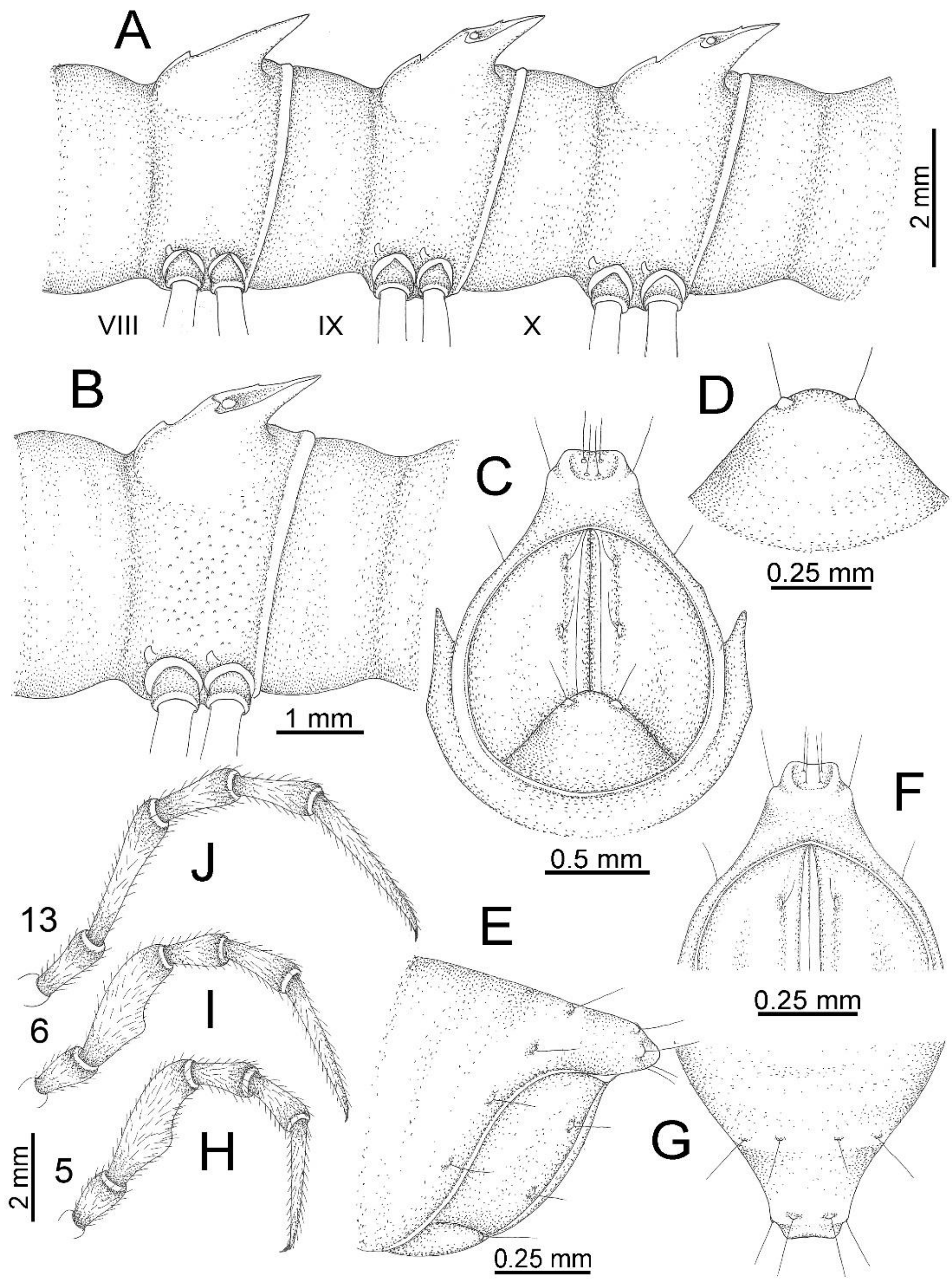

Figure 4.62 *Desmoxytes perakensis* sp. n. (male paratype). **A** body rings 8–10 **B** sculpture of ring 10 **C, E** last ring and telson **D** hypoproct **F, G** epiproct **H** male leg 5 (right) **I** male leg 6 (right) **J** male leg 13 (right).

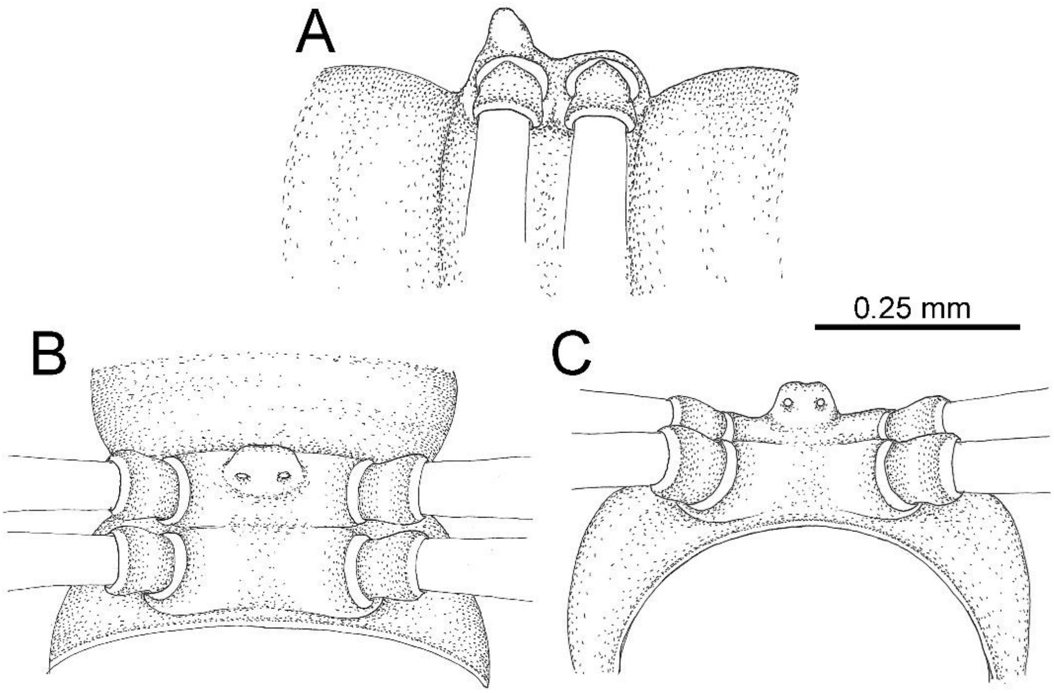

Figure 4.63 *Desmoxytes perakensis* sp. n. (male paratype) – sternal lobe between male coxae 4. **A** lateral view **B** ventral view **C** caudal view.

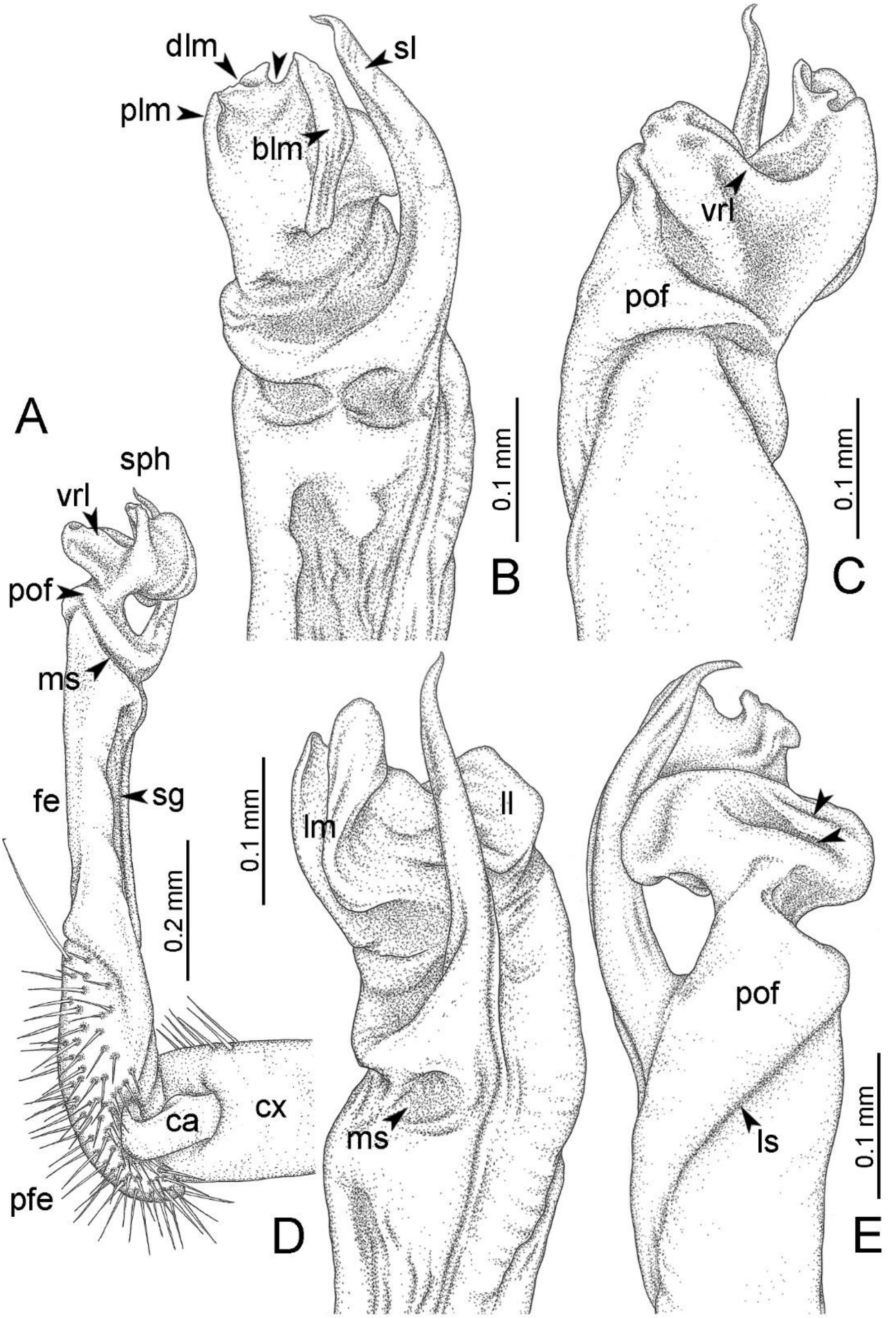

Figure 4.64 *Desmoxytes perakensis* sp. n. (paratype) – right gonopod. **A** mesal view **B** submesal view (arrow = indentation) **C** ventral view **D** dorsal view **E** lateral view (arrows = furrows).

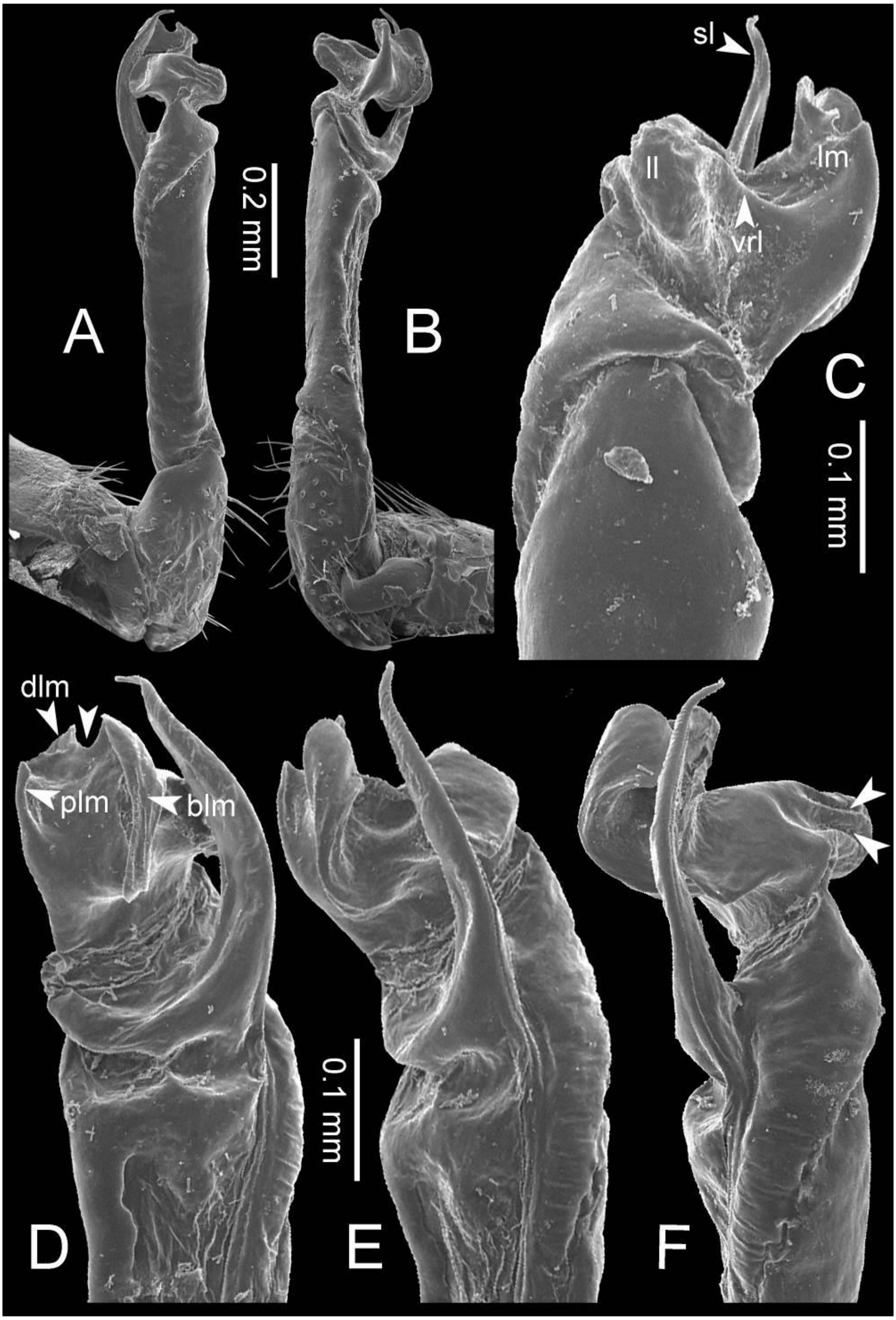

Figure 4.65 *Desmoxytes perakensis* sp. n. (paratype) – right gonopod. **A** lateral view **B** mesal view **C** ventral view **D** subdorsal view (arrow = indentation) **E** dorsal view **F** subdorsal view (arrows = furrows).

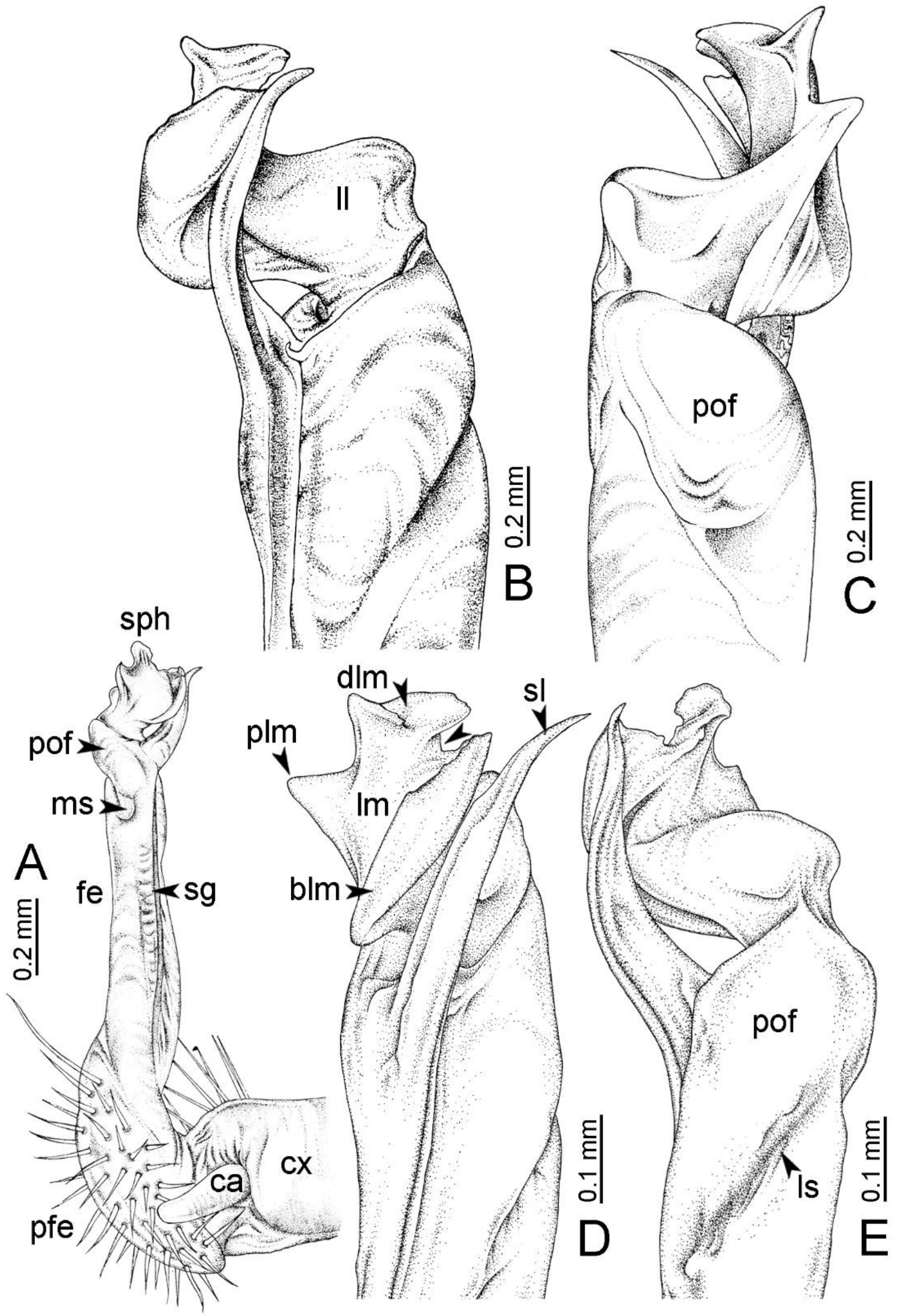

Figure 4.66 *Desmoxytes pinnasquali* Srisonchai *et al.*, 2016 (paratype) – right gonopod (modified from Srisonchai *et al.* 2016). **A** mesal view **B** dorsal view **C** ventral view **D** subdorsal view (arrow = indentation) **E** lateral view.

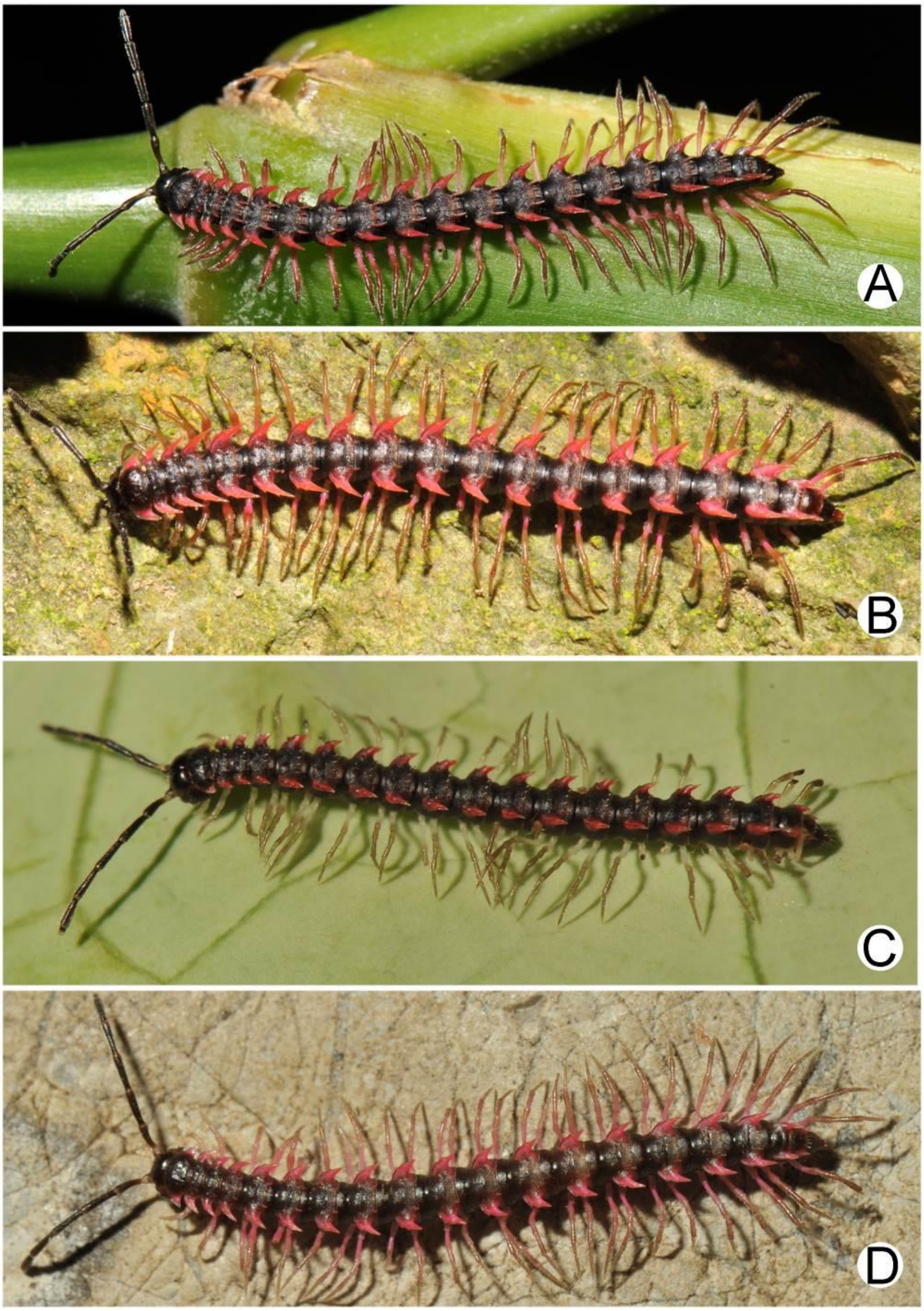

Figure 4.67 Photographs of live *Desmoxytes planata* (Pocock, 1895) – males. **A** specimen from Xishuangbanna, Mengla (China) **B** specimen from Suan Sai Thong restaurant, Phrae (Thailand) **C** specimen from Lampane Village, Nguwun Chuang River (Myanmar) **D** specimen from Wat Khao Tham Ma Rong, Prachuap Khiri Khan (Thailand).

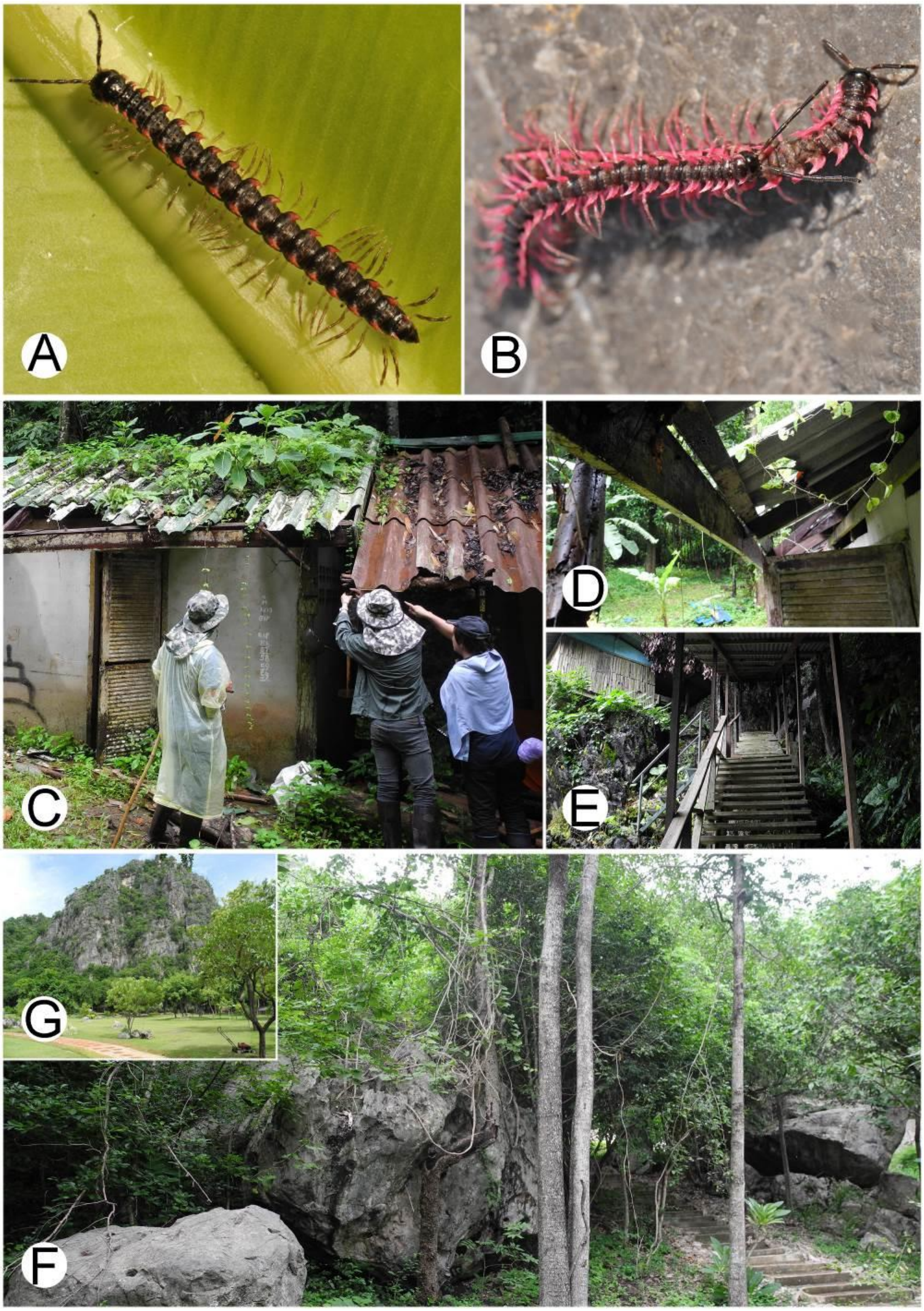

Figure 4.68 Photographs of live *Desmoxytes planata* (Pocock, 1895) and habitats. **A** female **B** mating couple **C–E** synanthropic areas **F, G** limestone area near synanthropic area.

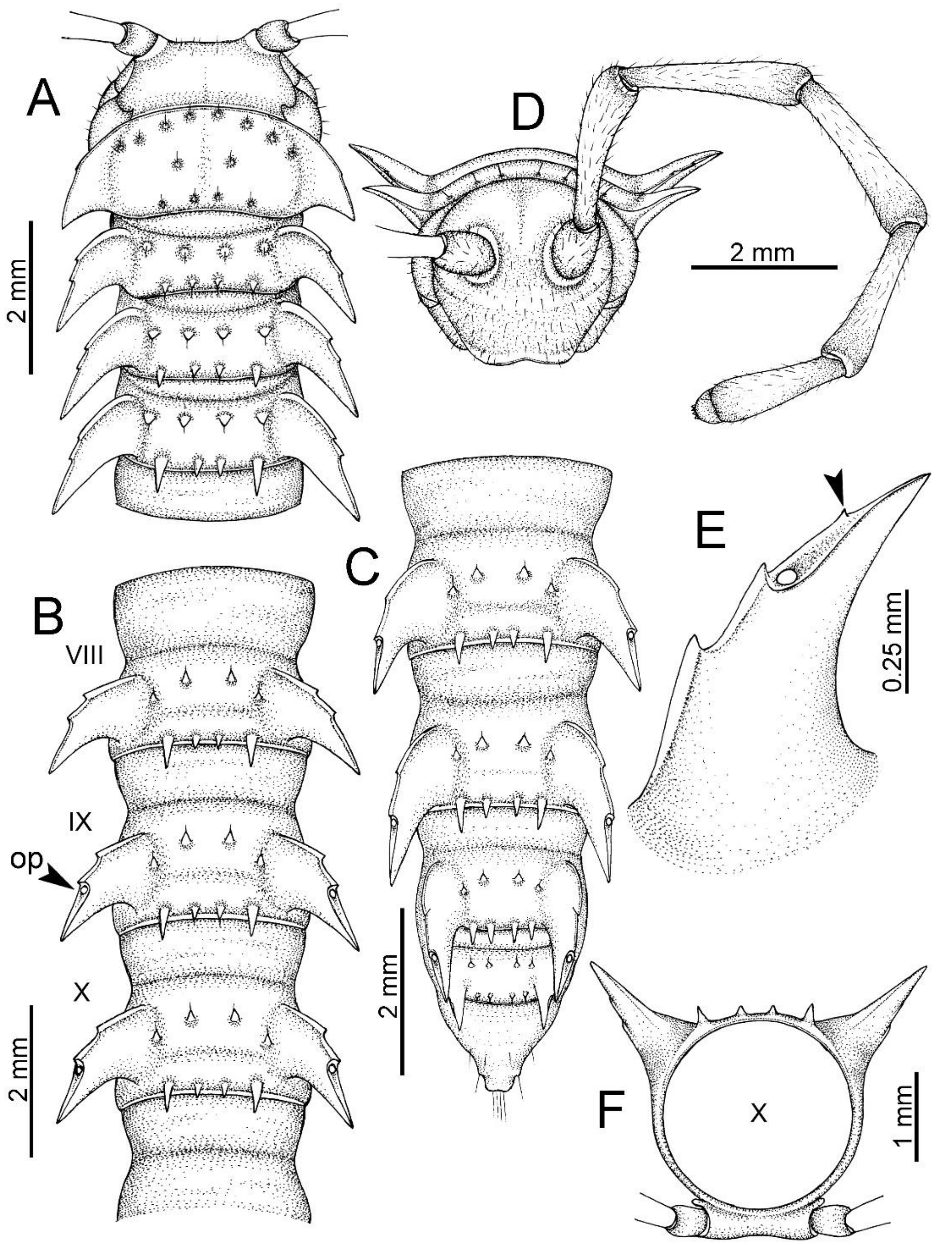

Figure 4.69 *Desmoxytes planata* (Pocock, 1895), specimen from Suan Sai Thong Restaurant. **A** anterior body part **B** body rings 8–10 (op = ozopore) **C** posteriormost body rings and telson **D** head and antenna **E** paraterga of ring 10 (arrow = tiny denticle) **F** body ring 10.

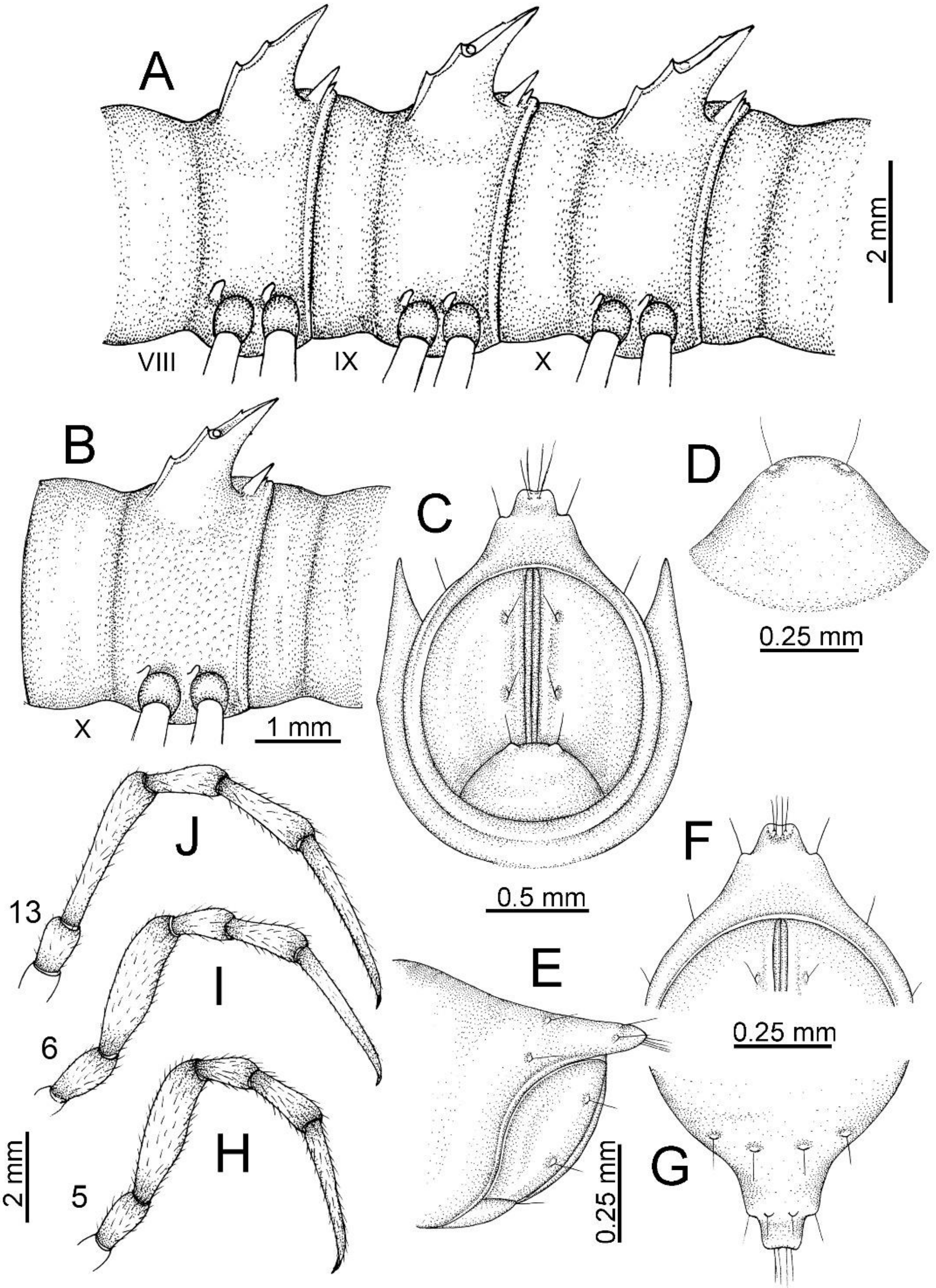

Figure 4.70 *Desmoxytes planata* (Pocock, 1895), specimen from Suan Sai Thong Restaurant. **A** body rings 8–10 **B** sculpture of ring 10 **C, E** last ring and telson **D** hypoproct **F, G** epiproct **H** male leg 5 (right) **I** male leg 6 (right) **J** male leg 13 (right).

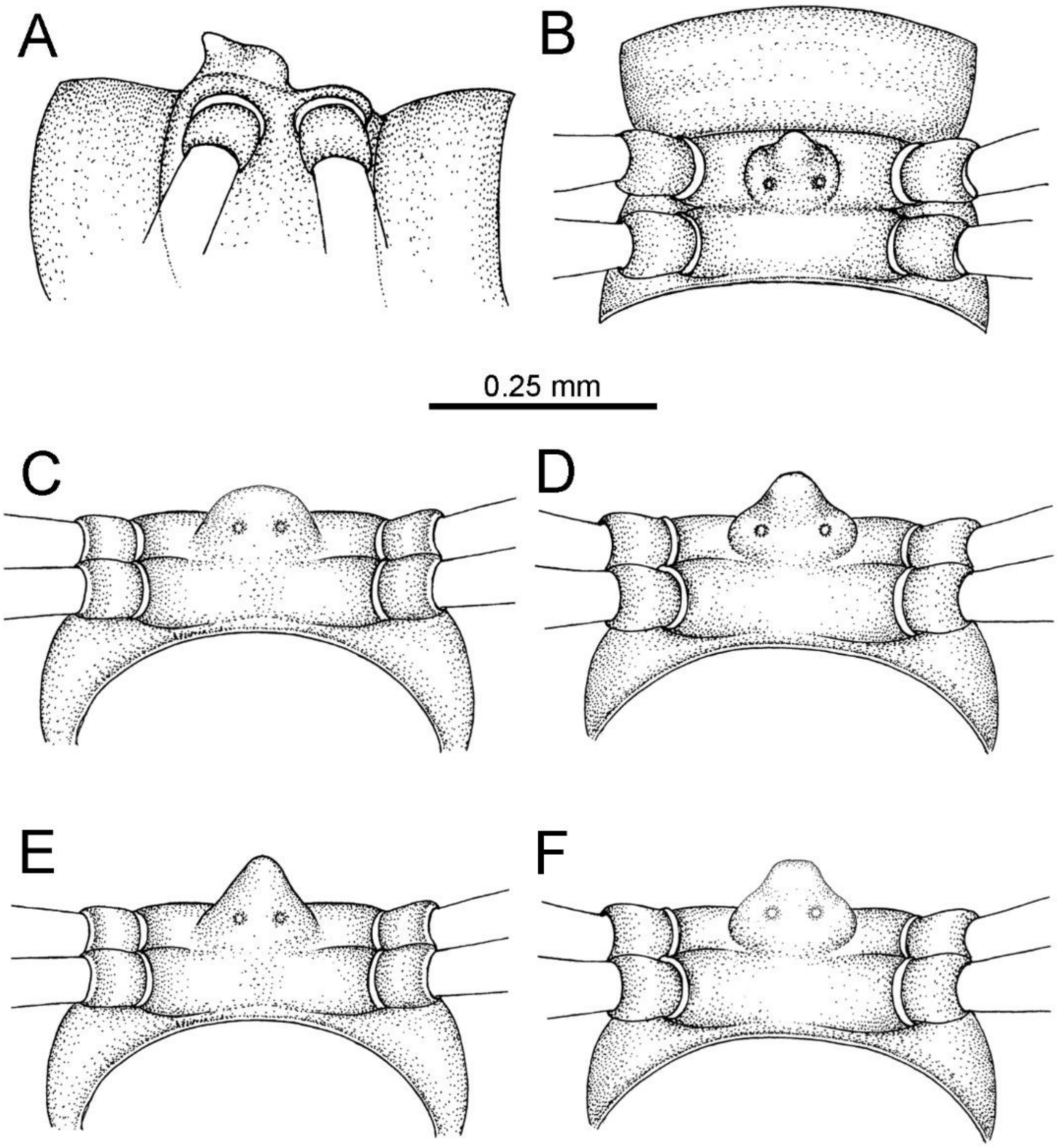

Figure 4.71 *Desmoxytes planata* (Pocock, 1895), population from Suan Sai Thong Restaurant – sternal lobe between male coxae 4. **A** lateral view **B** ventral view **C** caudal view (specimen from Fiji only) **D–F** caudal view.

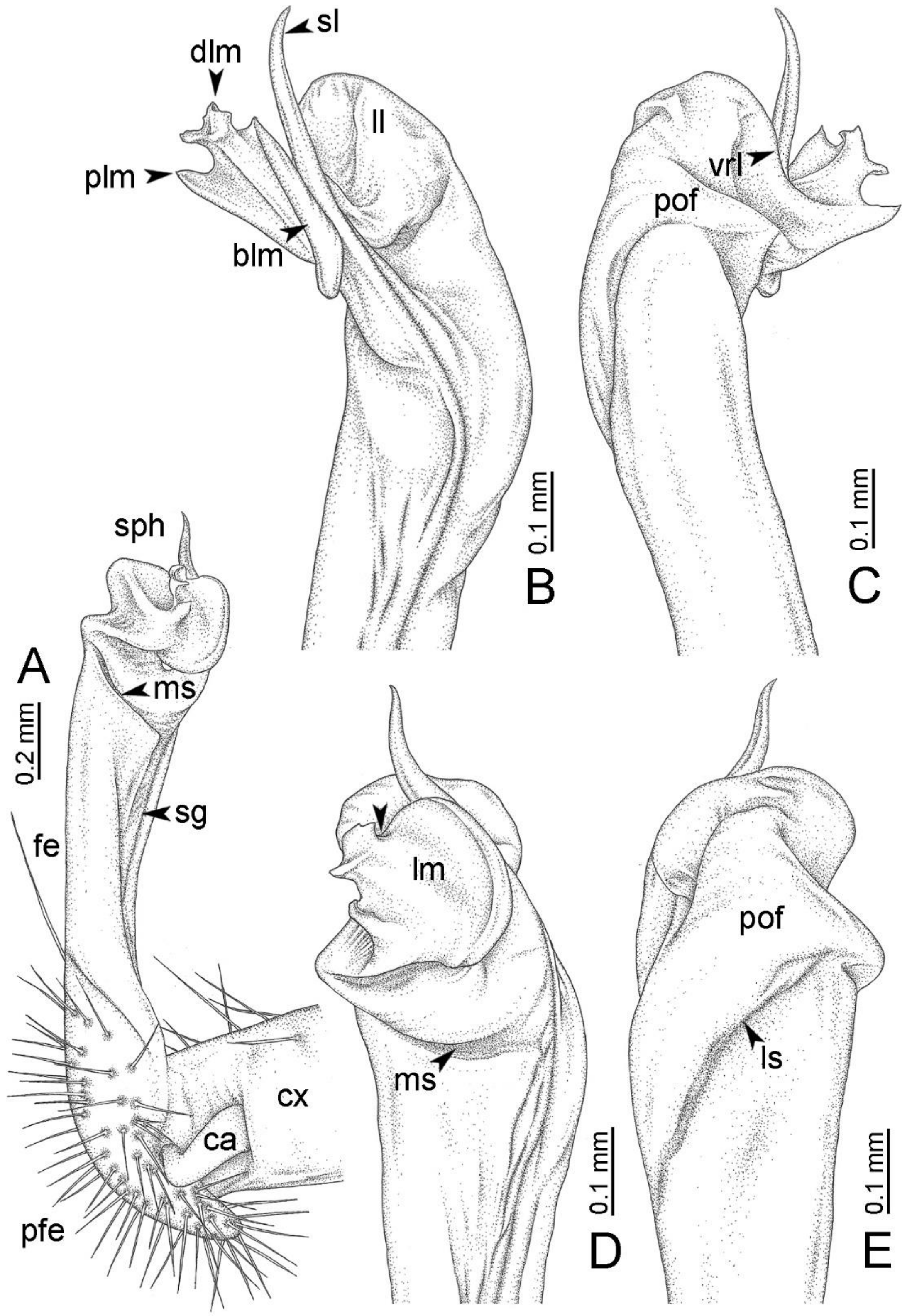

Figure 4.72 *Desmoxytes planata* (Pocock, 1895), specimen from Wat Puang Malai – right gonopod. **A** mesal view **B** dorsal view **C** ventral view **D** submesal view (arrow = indentation) **E** lateral view.

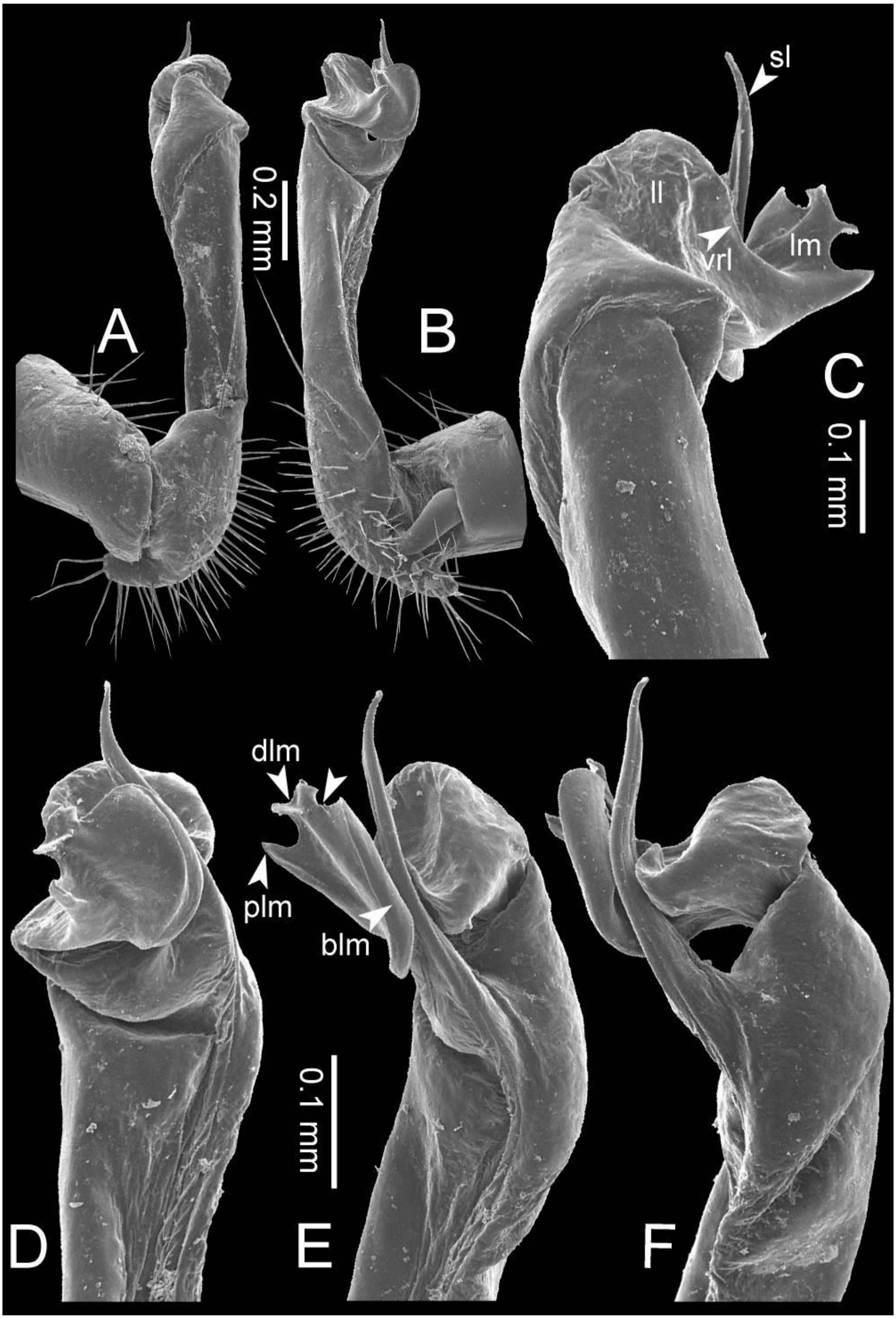

Figure 4.73 *Desmoxytes planata* (Pocock, 1895), specimen from Wat Puang Malai – right gonopod. **A** lateral view **B** mesal view **C** ventral view **D** subdorsal view (arrow = indentation) **E** dorsal view **F** subdorsal view.

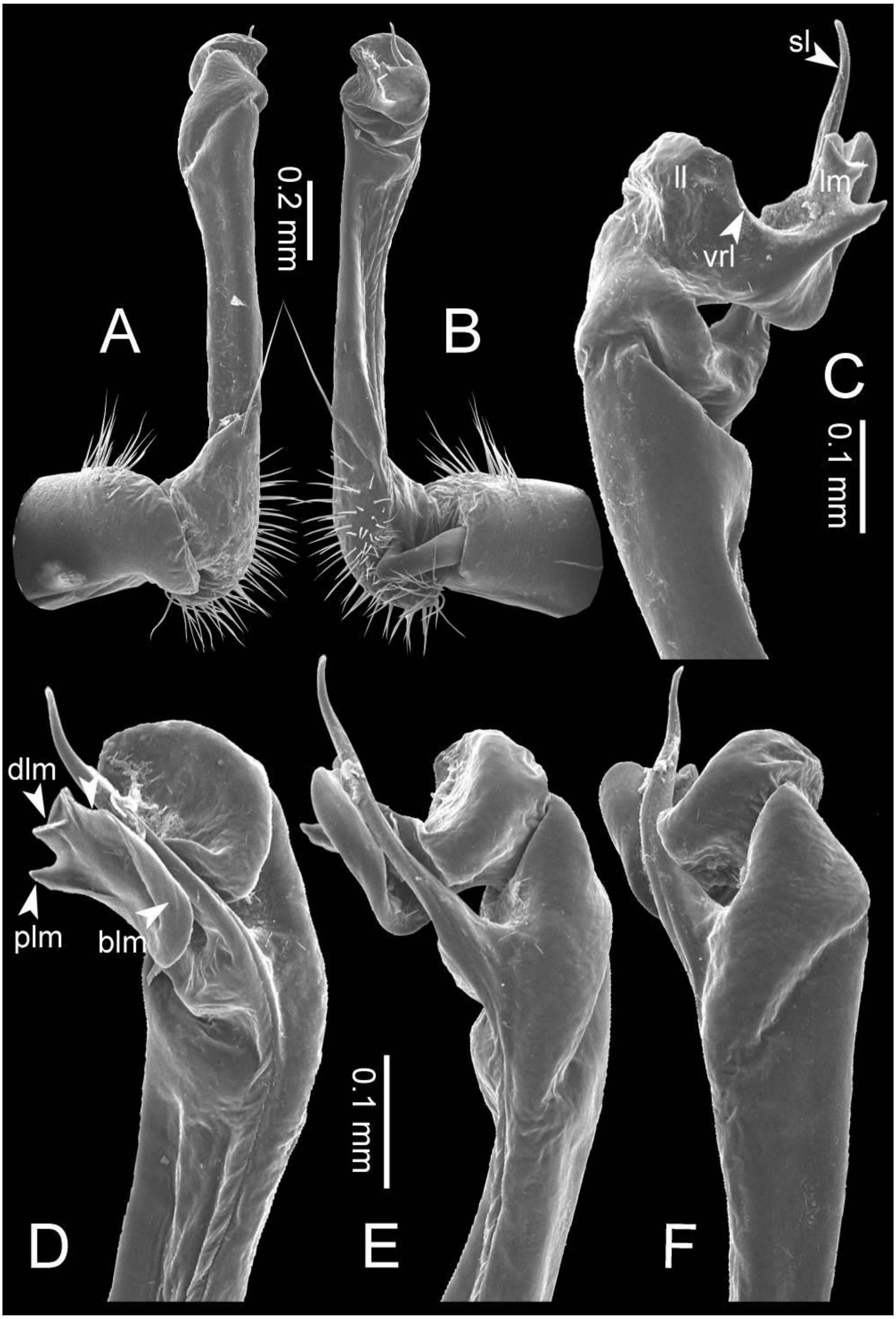

Figure 4.74 *Desmoxytes planata* (Pocock, 1895), specimen from Fiji, Viti Levu – right gonopod. **A** lateral view **B** mesal view **C** ventral view **D** subdorsal view (arrow = indentation) **E** dorsal view **F** subdorsal view.

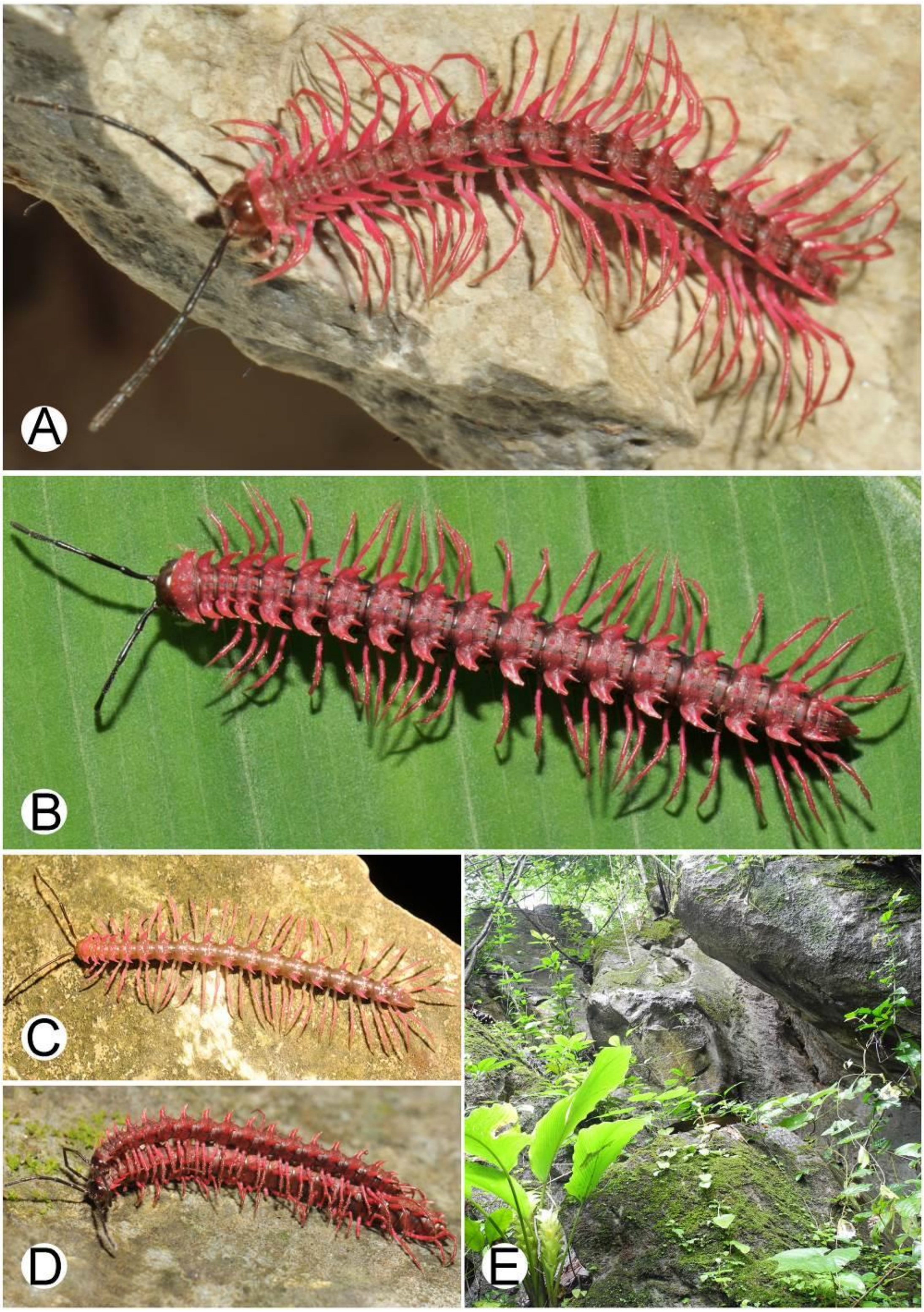

Figure 4.75 Photographs of live *Desmoxytes purpurosea* Enghoff *et al.*, 2007 (specimens from Hup Pa Tard) and habitat. **A** male **B** female **C** early adult male **D** mating couple **E** habitat.

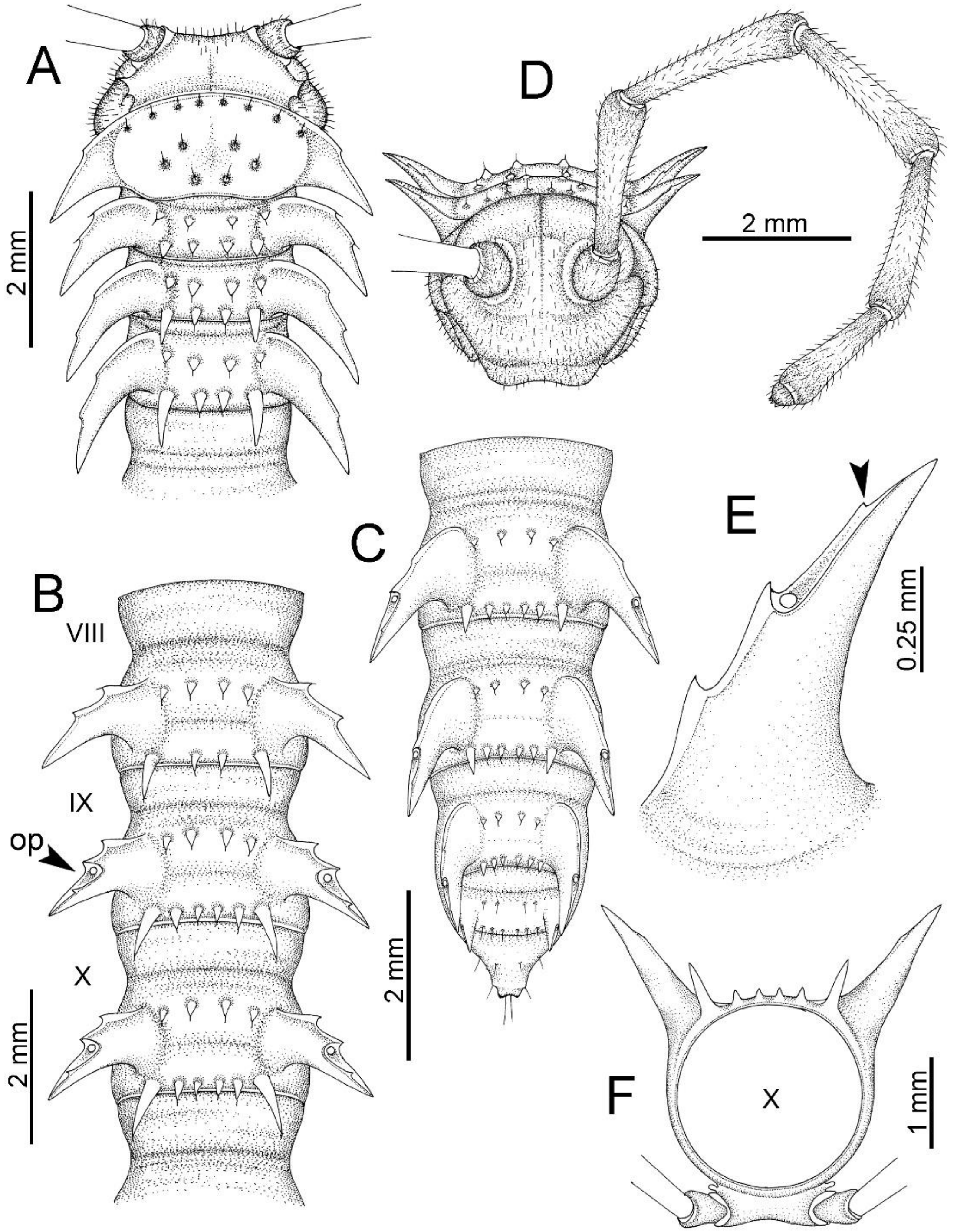

Figure 4.76 *Desmoxytes purpurosea* Enghoff *et al.*, 2007 (male paratype). **A** anterior body part **B** body rings 8–10 (op = ozopore) **C** posteriormost body rings and telson **D** head and antenna **E** paraterga of ring 10 (arrow = tiny denticle) **F** body ring 10.

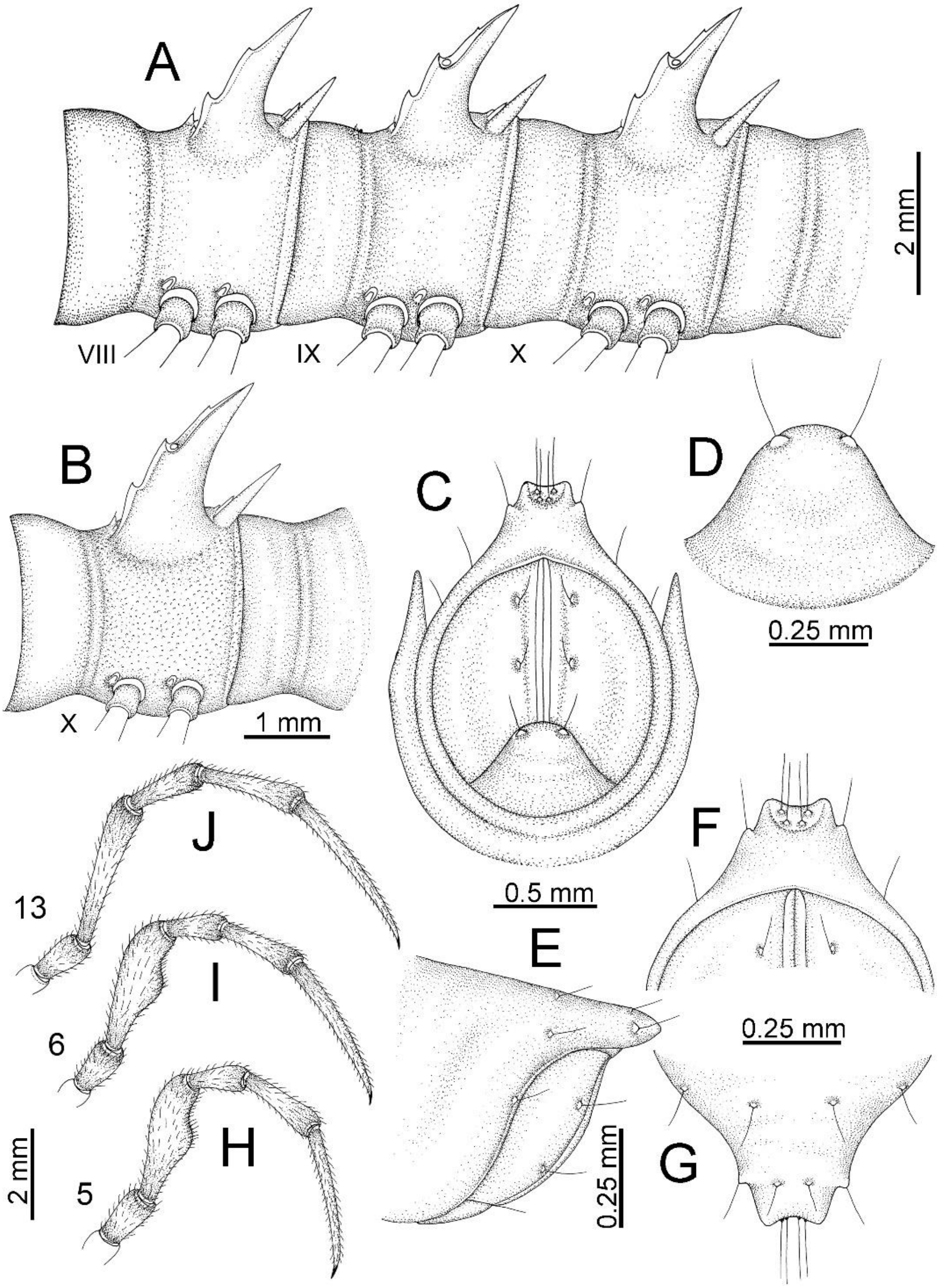

Figure 4.77 *Desmoxytes purpurosea* Enghoff *et al.*, 2007 (male paratype). **A** body rings 8–10 **B** sculpture of ring 10 **C, E** last ring and telson **D** hypoproct **F, G** epiproct **H** male leg 5 (right) **I** male leg 6 (right) **J** male leg 13 (right).

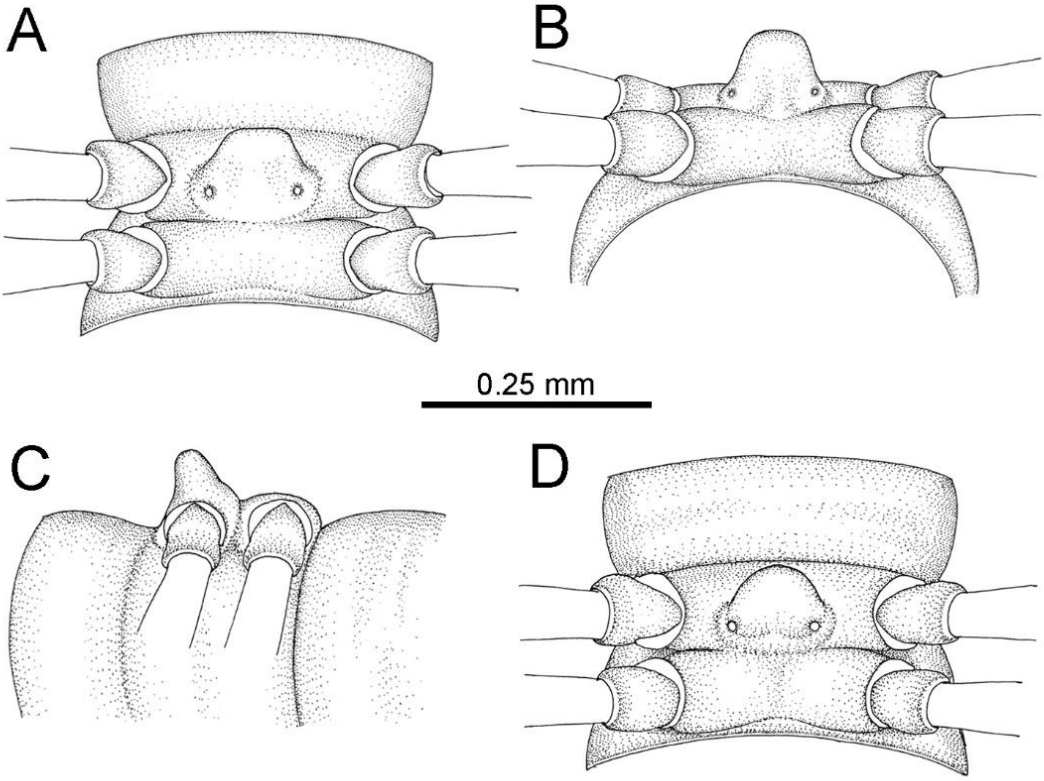

Figure 4.78 *Desmoxytes purpurosea* Enghoff *et al.*, 2007 (male paratypes) – sternal lobe between male coxae 4. **A, D** ventral view **B** caudal view **C** lateral view.

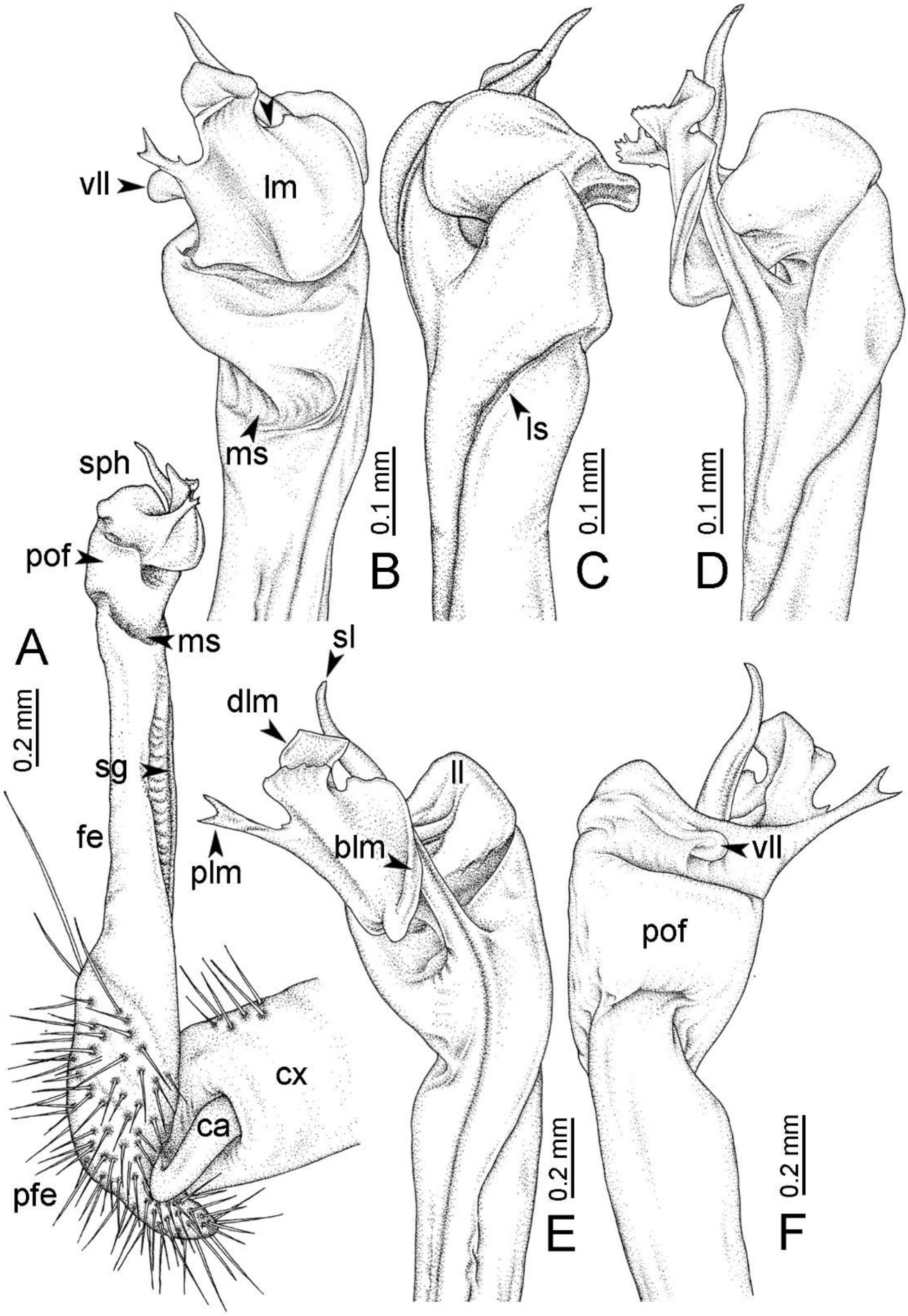

Figure 4.79 *Desmoxytes purpurosea* Enghoff *et al.*, 2007 (specimen from Hup Pa Tard) – right gonopod. **A** mesal view **B** submesal view (arrow = indentation) **C** lateral view **D** dorsal view (Kanchababuri A and B populations) **E** subdorsal view **F** ventral view.

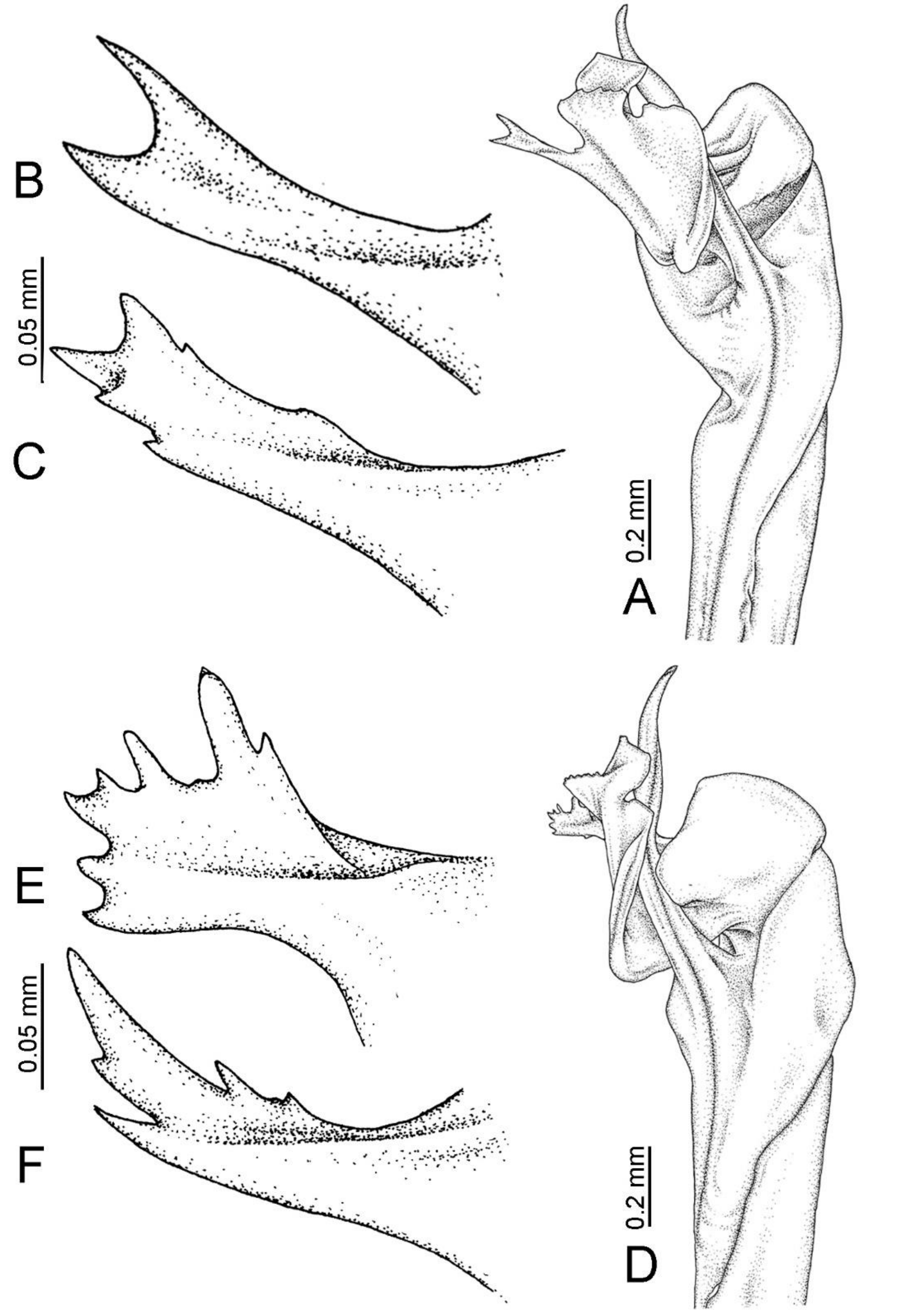

Figure 4.80 *Desmoxytes purpurosea* Enghoff *et al.*, 2007 – right gonopod. **A** mesal view (specimen from Hup Pa Tard) **B, C** process (plm) of lamina medialis (Lamphun and Uthai Thani populations) **D** dorsal view (specimen from Tham Than Lod cave) **E, F** process (plm) of lamina medialis (Kanchababuri A and B populations).

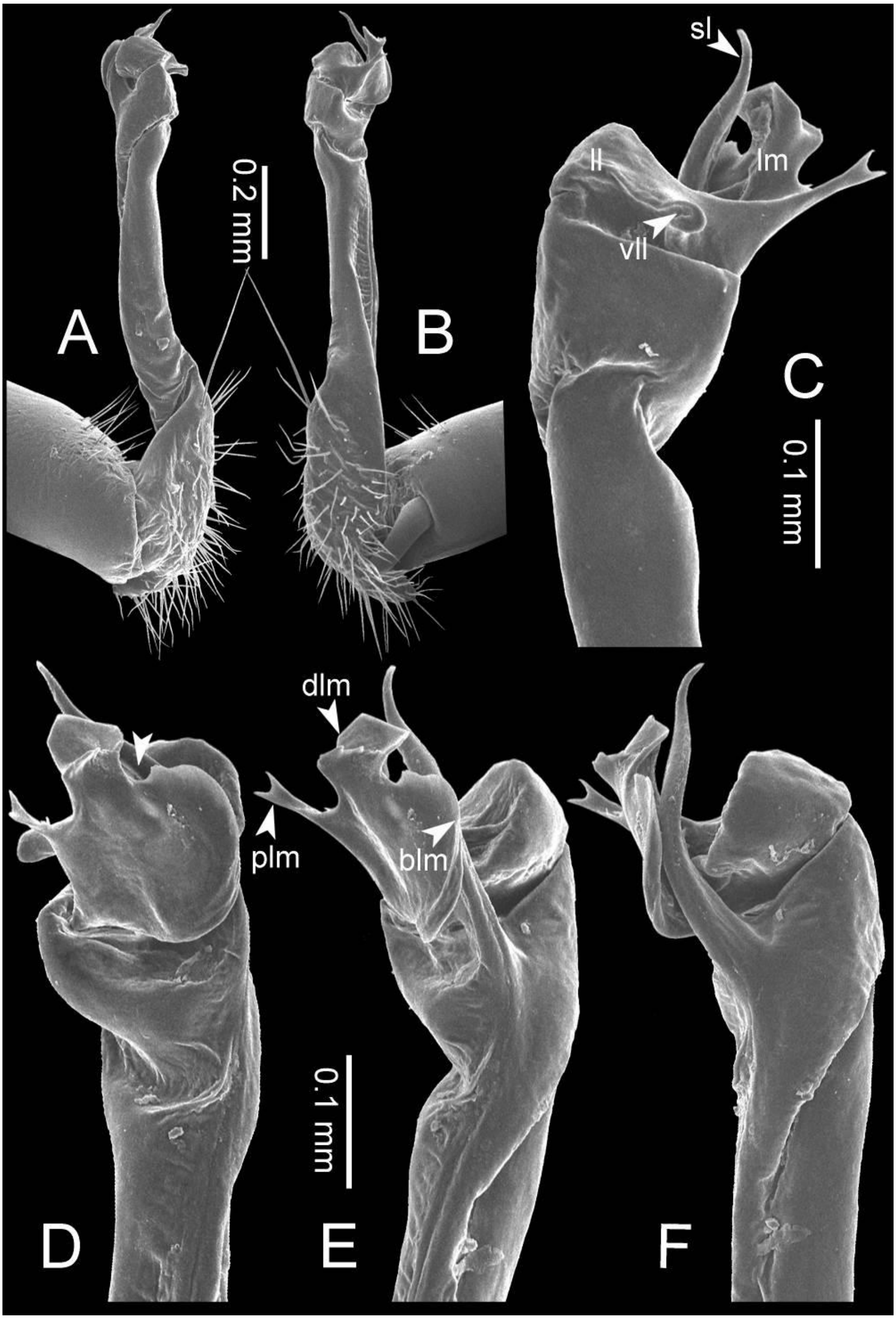

Figure 4.81 *Desmoxytes purpurosea* Enghoff *et al.*, 2007 (specimen from Hup Pa Tard) – right gonopod. **A** lateral view **B** mesal view **C** ventral view **D** subdorsal view (arrow = indentation) **E** dorsal view **F** subdorsal view.

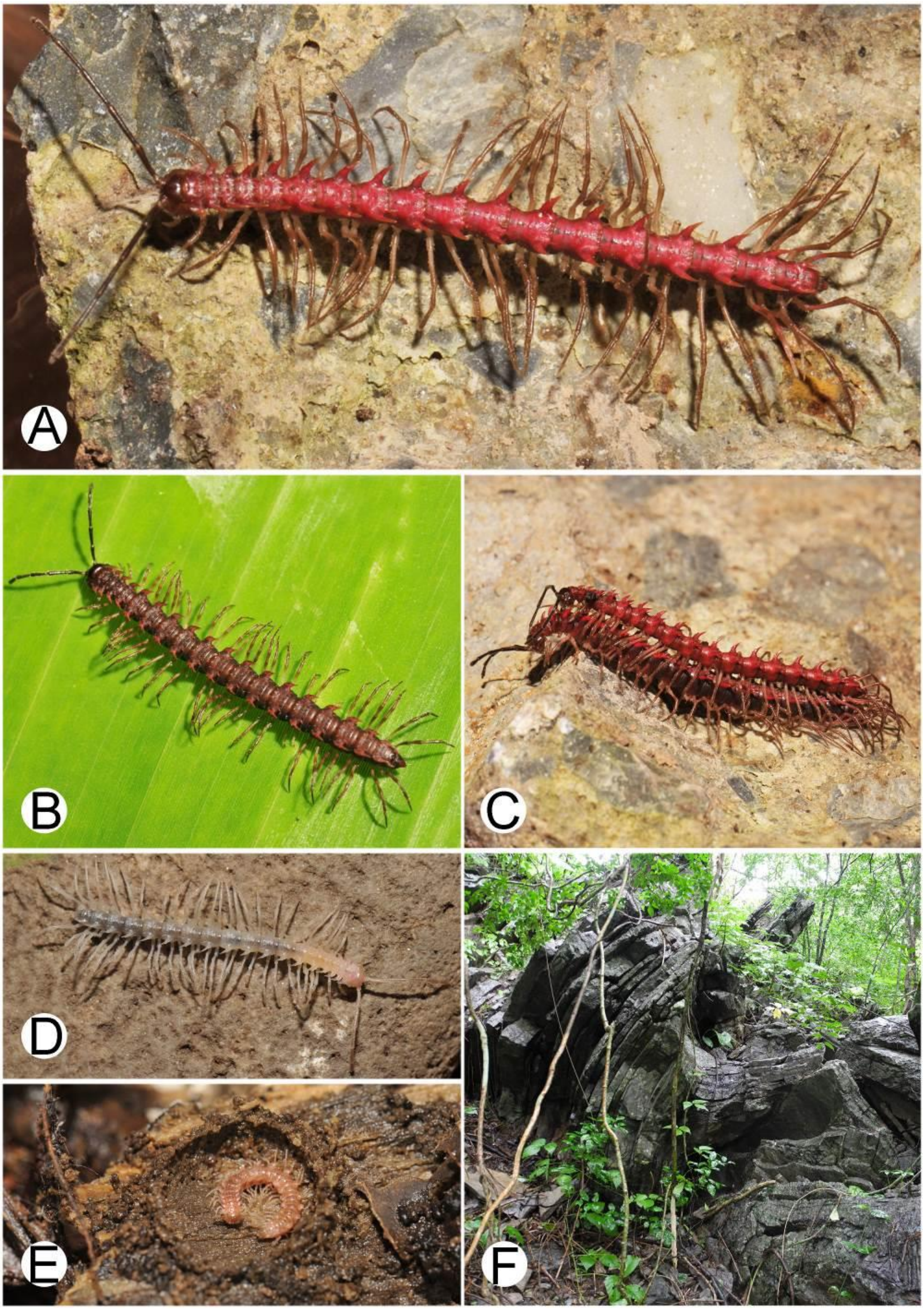

Figure 4.82 *Desmoxytes takensis* Srisonchai *et al.*, 2016 (specimen from Chao Por Phawo Shrine) and habitat. **A** male **B** female **C** mating couple **D** early adult **E** moulting chamber **F** habitat.

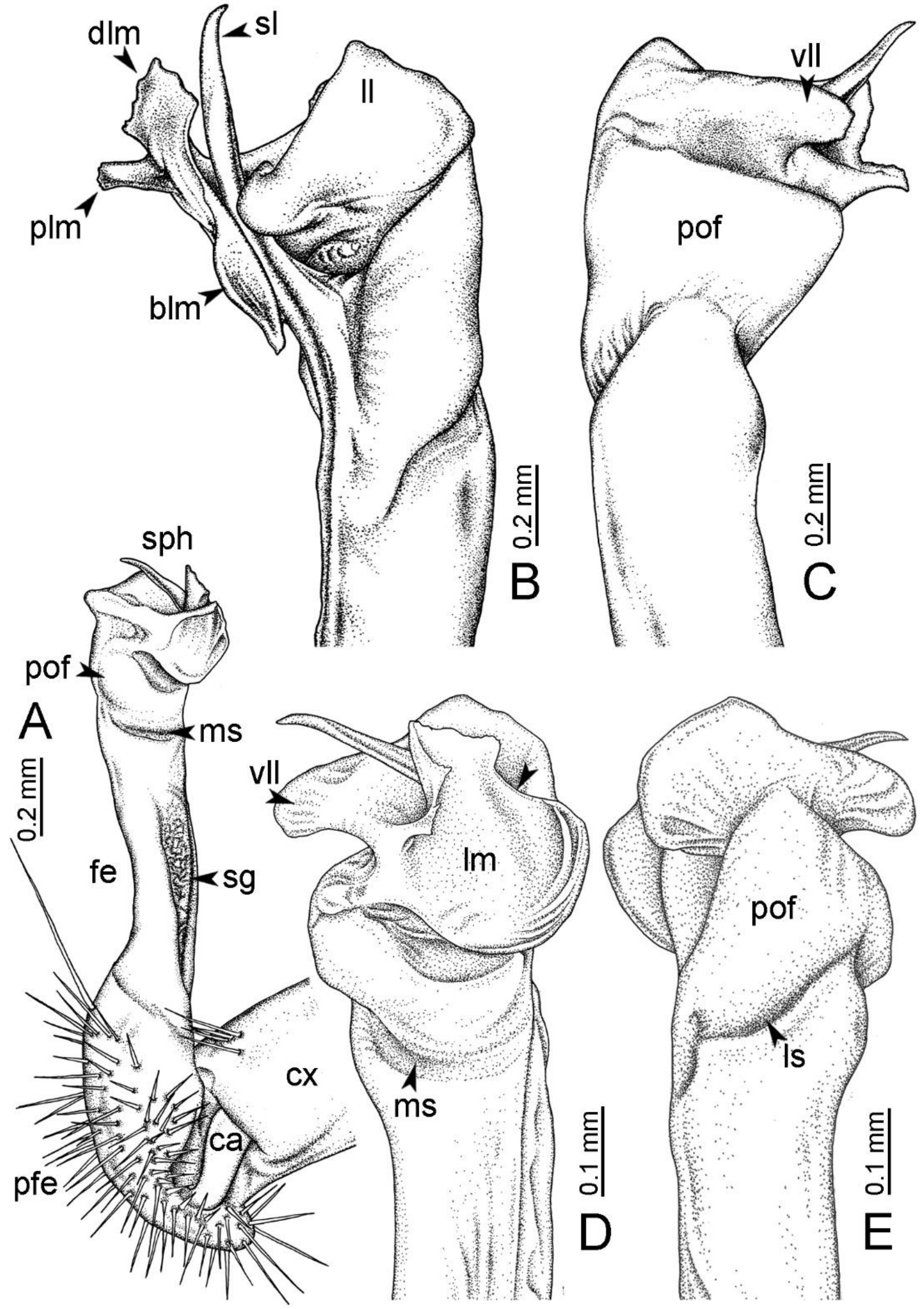

Figure 4.83 *Desmoxytes takensis* Srisonchai *et al.*, 2016 (paratype) – right gonopod (modified from Srisonchai *et al.* 2016). **A** mesal view **B** dorsal view **C** ventral view **D** submesal view (arrow = indentation) **E** lateral view.

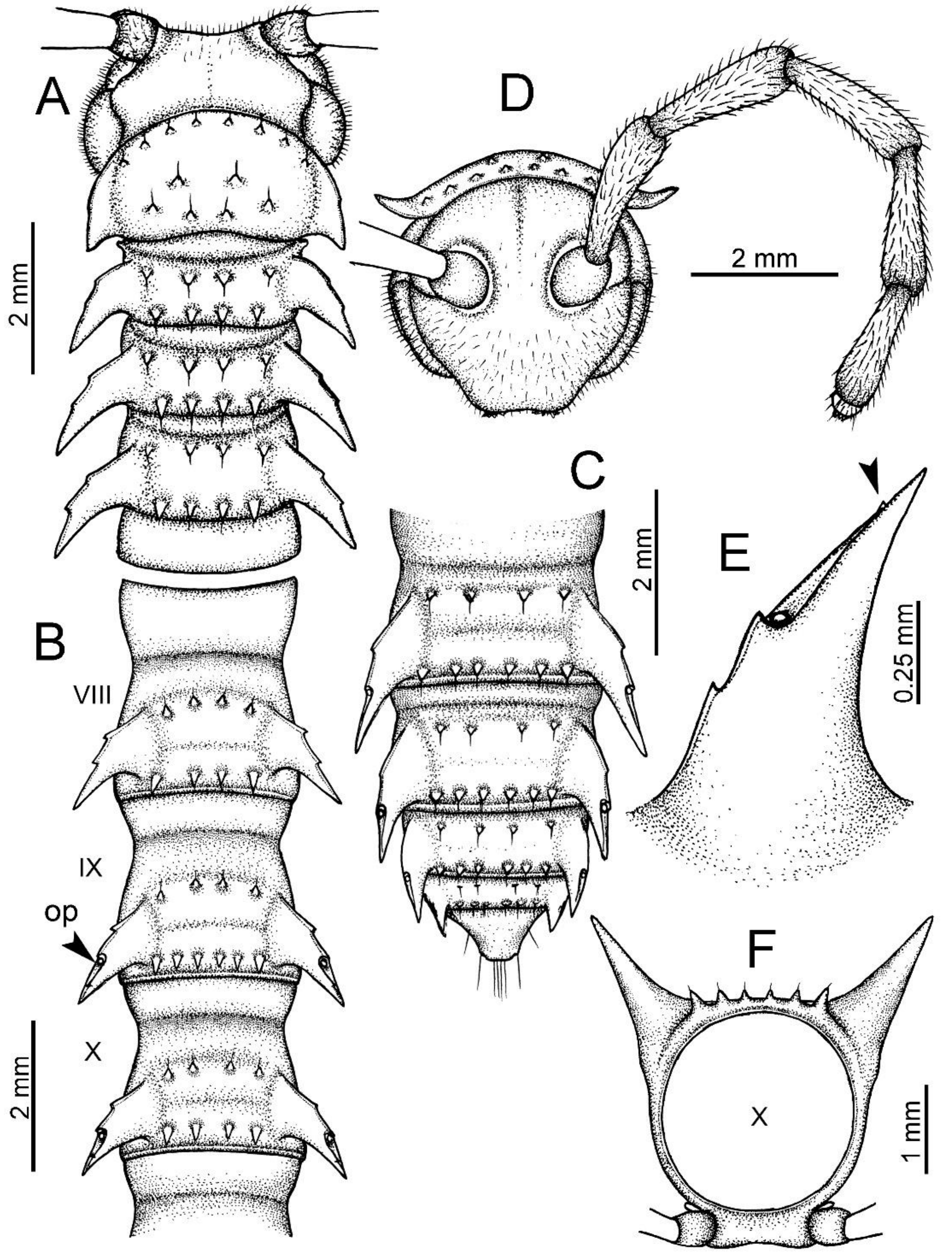

Figure 4.84 *Desmoxytes taurina* (Pocock, 1895), lectotype. **A** anterior body part **B** body rings 8–10 (op = ozopore) **C** posteriormost body rings and telson **D** head and antenna **E** paraterga of ring 10 (arrow = tiny denticle) **F** body ring 10.

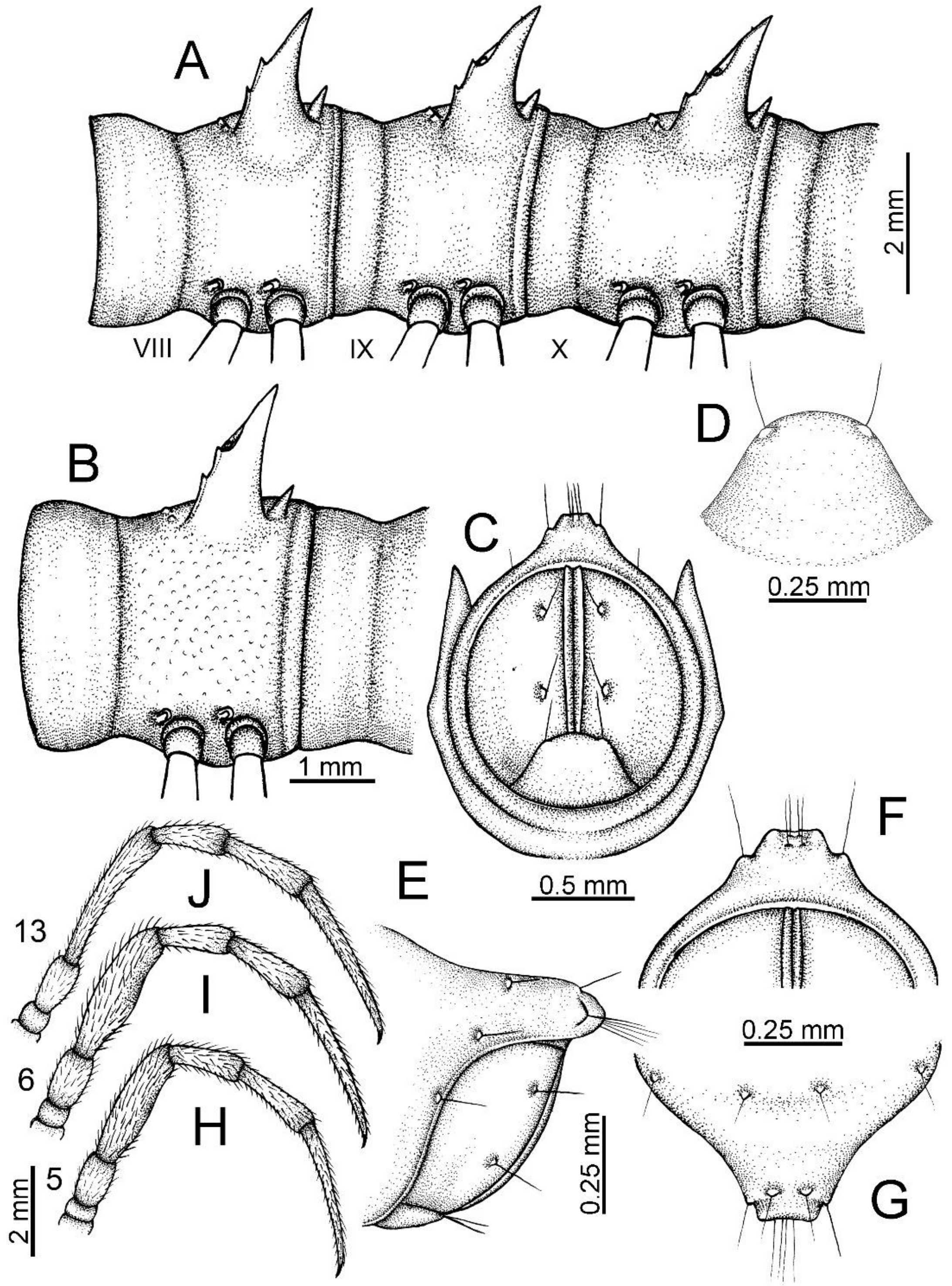

Figure 4.85 *Desmoxytes taurina* (Pocock, 1895), lectotype. **A** body rings 8–10 **B** sculpture of ring 10 **C, E** last ring and telson **D** hypoproct **F, G** epiproct **H** male leg 5 (right) **I** male leg 6 (right) **J** male leg 13 (right).

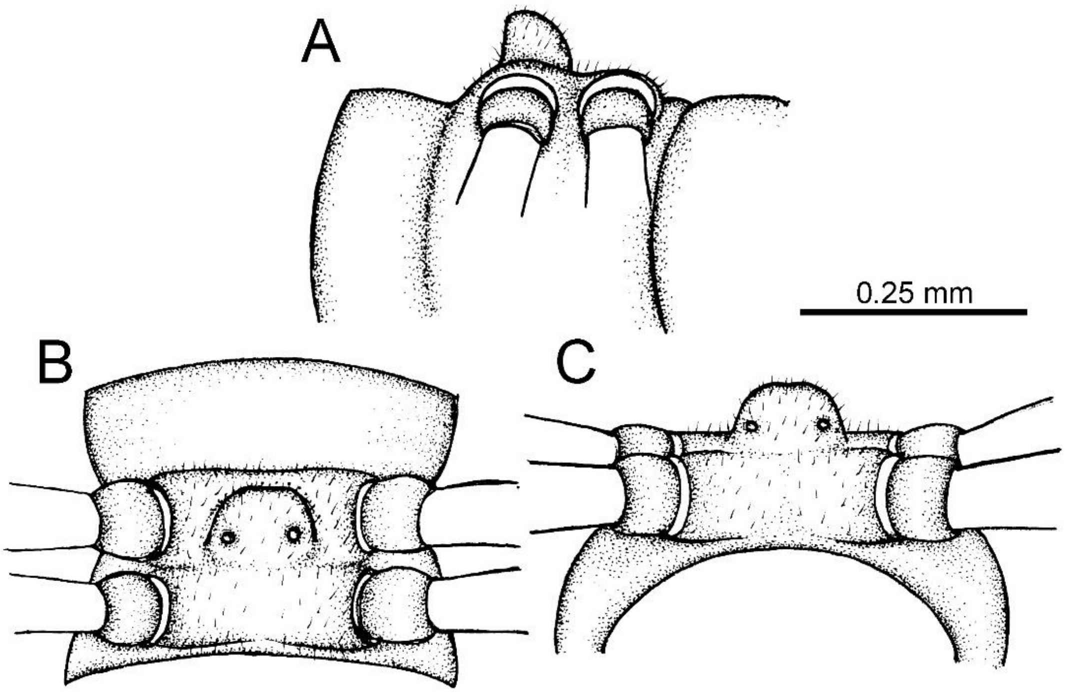

Figure 4.86 *Desmoxytes taurina* (Pocock, 1895), lectotype – sternal lobe between male coxae 4. **A** lateral view **B** ventral view **C** caudal view.

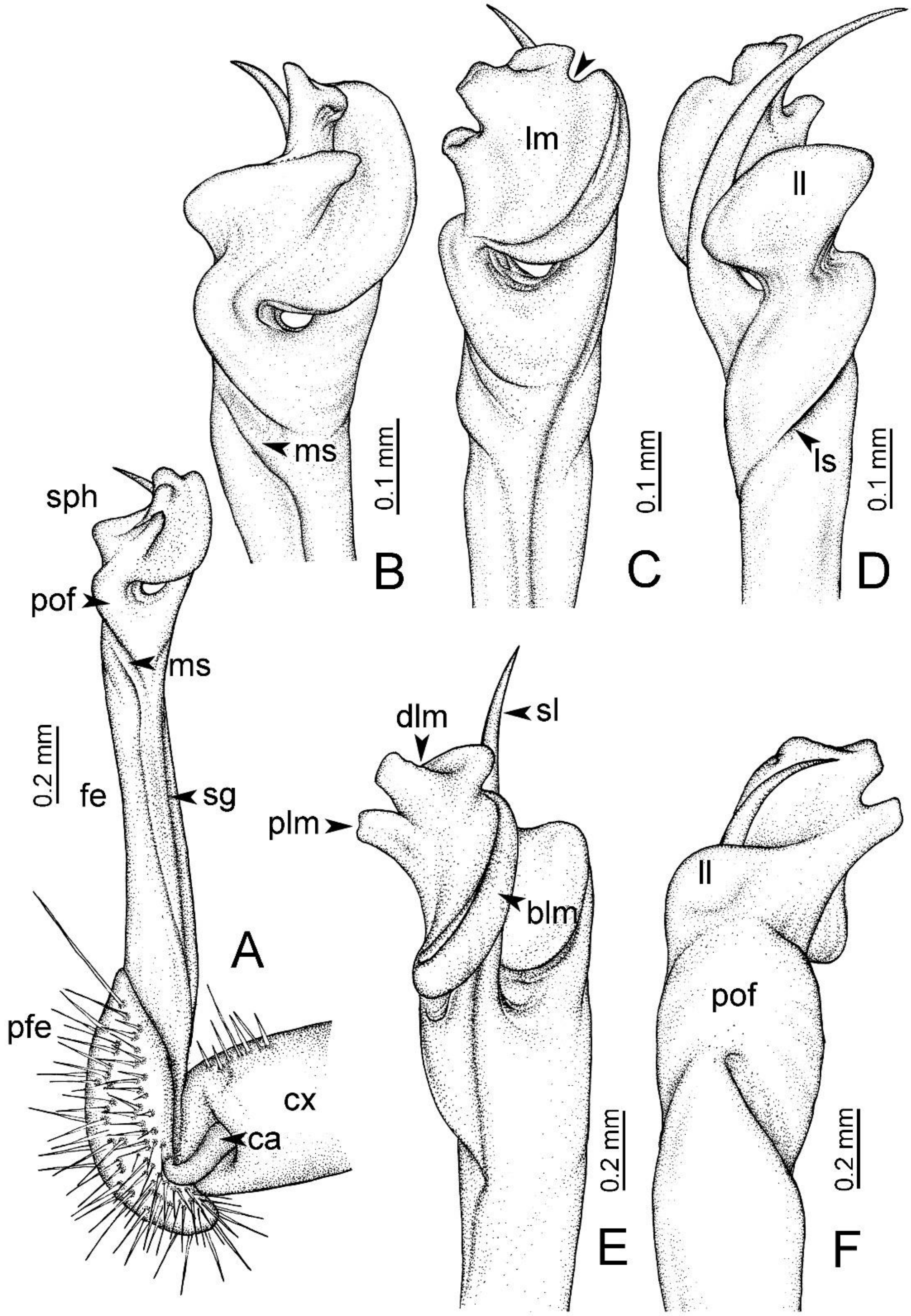

Figure 4.87 *Desmoxytes taurina* (Pocock, 1895), lectotype – right gonopod. **A** mesal view **B** mesal view **C** submesal view (arrow = indentation) **D** lateral view **E** dorsal view **F** ventral view.

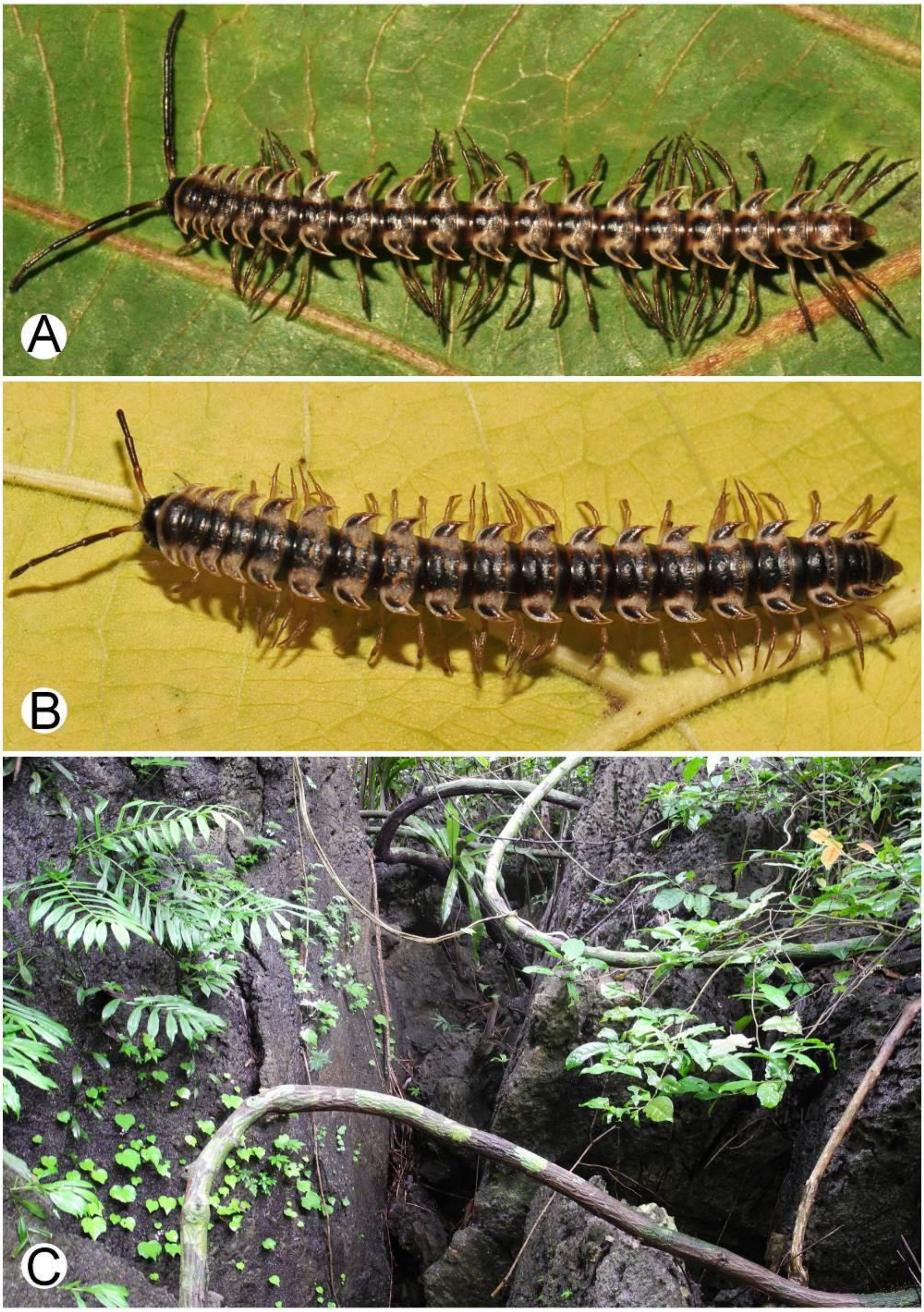

Figure 4.88 Photographs of live *Desmoxytes terae* (Jeekel, 1964) (specimens from Tham Tone Din) and habitat. **A** male **B** female **C** habitat.

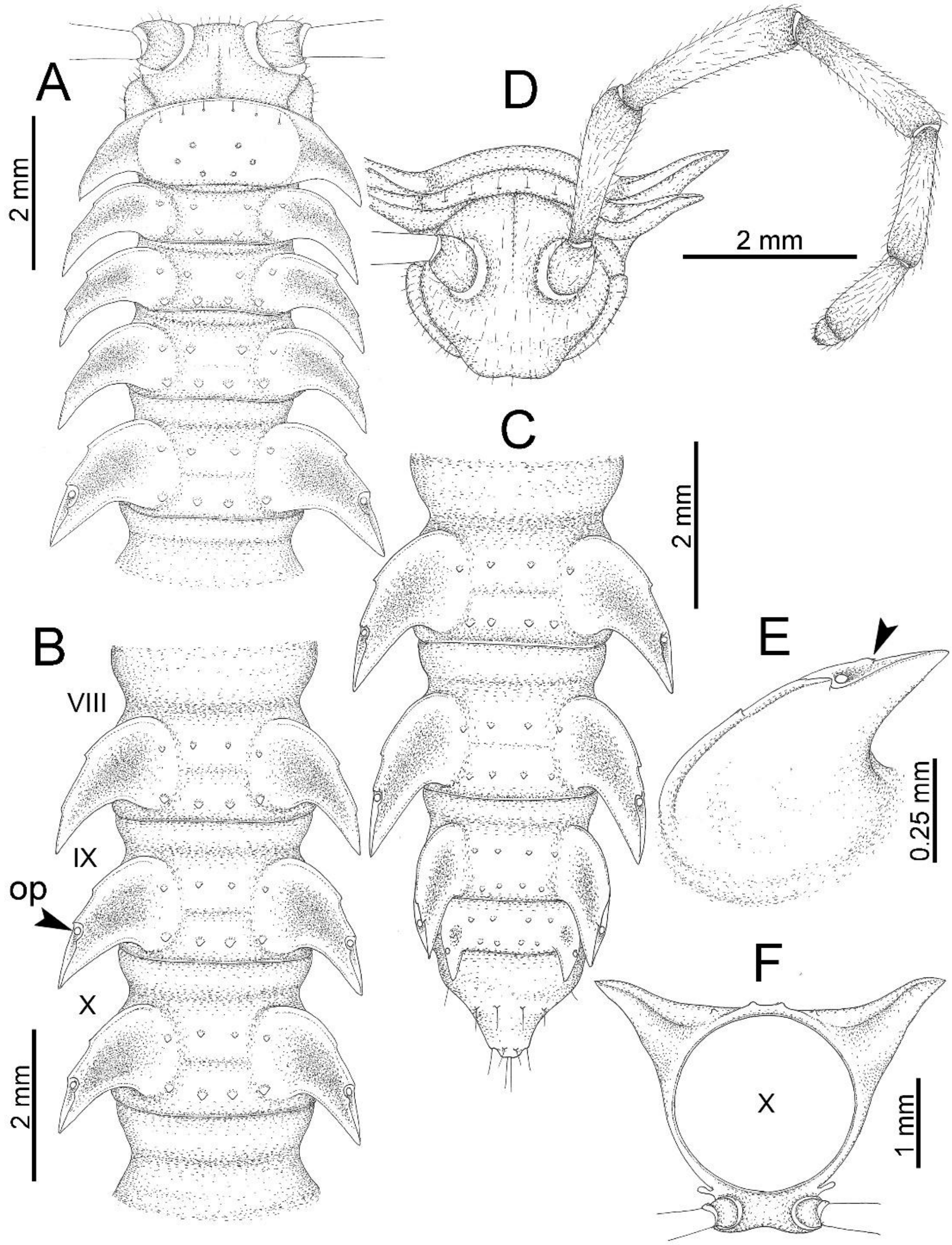

Figure 4.89 *Desmoxytes terae* (Jeekel, 1964), specimen from Tham Tone Din. **A** anterior body part **B** body rings 8–10 **C** posteriormost body rings and telson **D** head and antenna **E** paraterga of ring 10 **F** body ring 10.

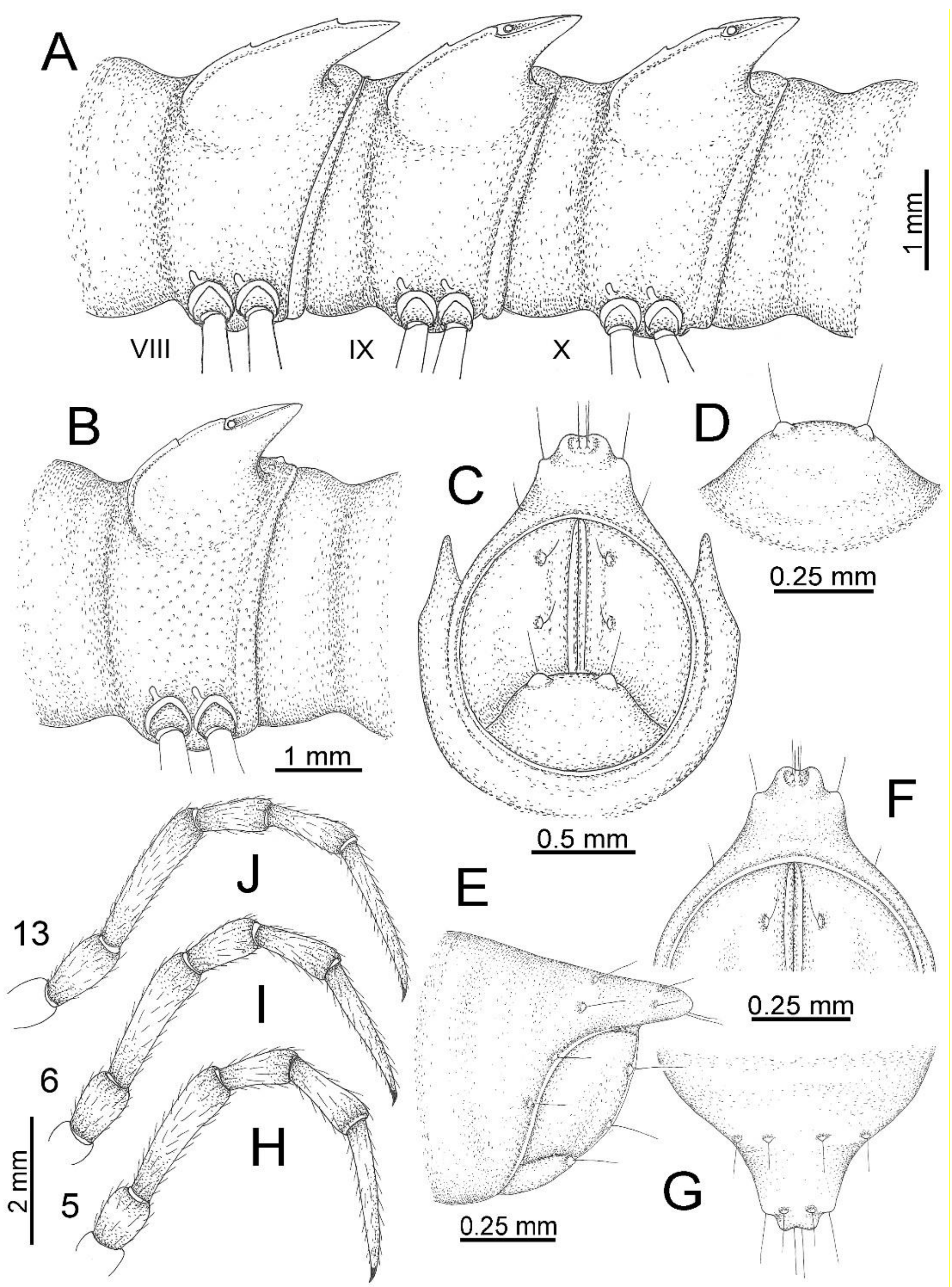

Figure 4.90 *Desmoxytes terae* (Jeekel, 1964), specimen from Tham Tone Din. **A** body rings 8–10 **B** sculpture of ring 10 **C, E** last ring and telson **D** hypoproct **F, G** epiproct **H** male leg 5 (right) **I** male leg 6 (right) **J** male leg 13 (right).

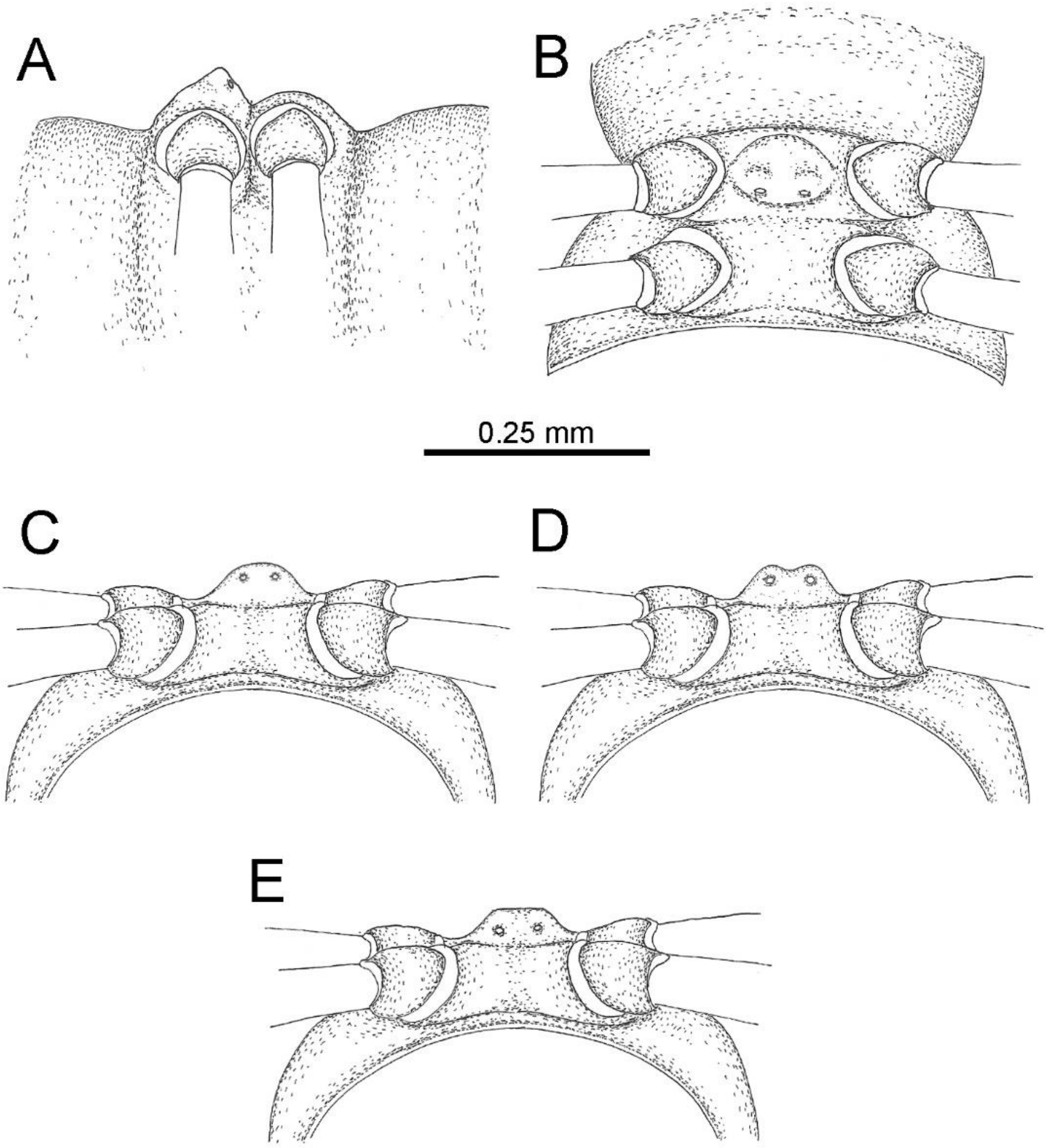

Figure 4.91 *Desmoxytes terae* (Jeekel, 1964), specimen from Tham Tone Din – sternal lobe between male coxae 4. **A** lateral view **B** mesal view **C–E** caudal view.

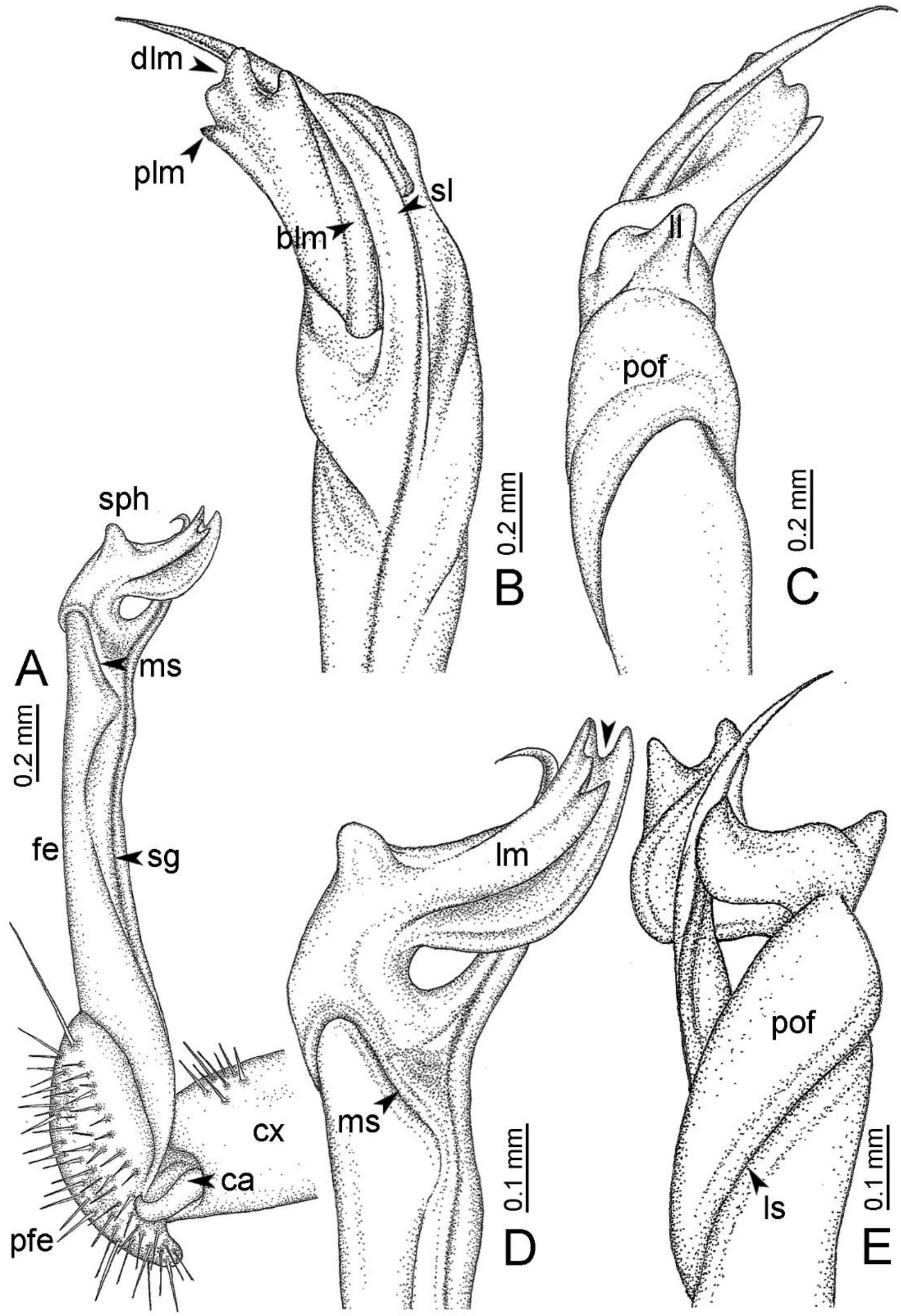

Figure 4.92 *Desmoxytes terae* (Jeekel, 1964), holotype – right gonopod. **A** mesal view **B** dorsal view **C** ventral view **D** submesal view (arrow = indentation) **E** lateral view.

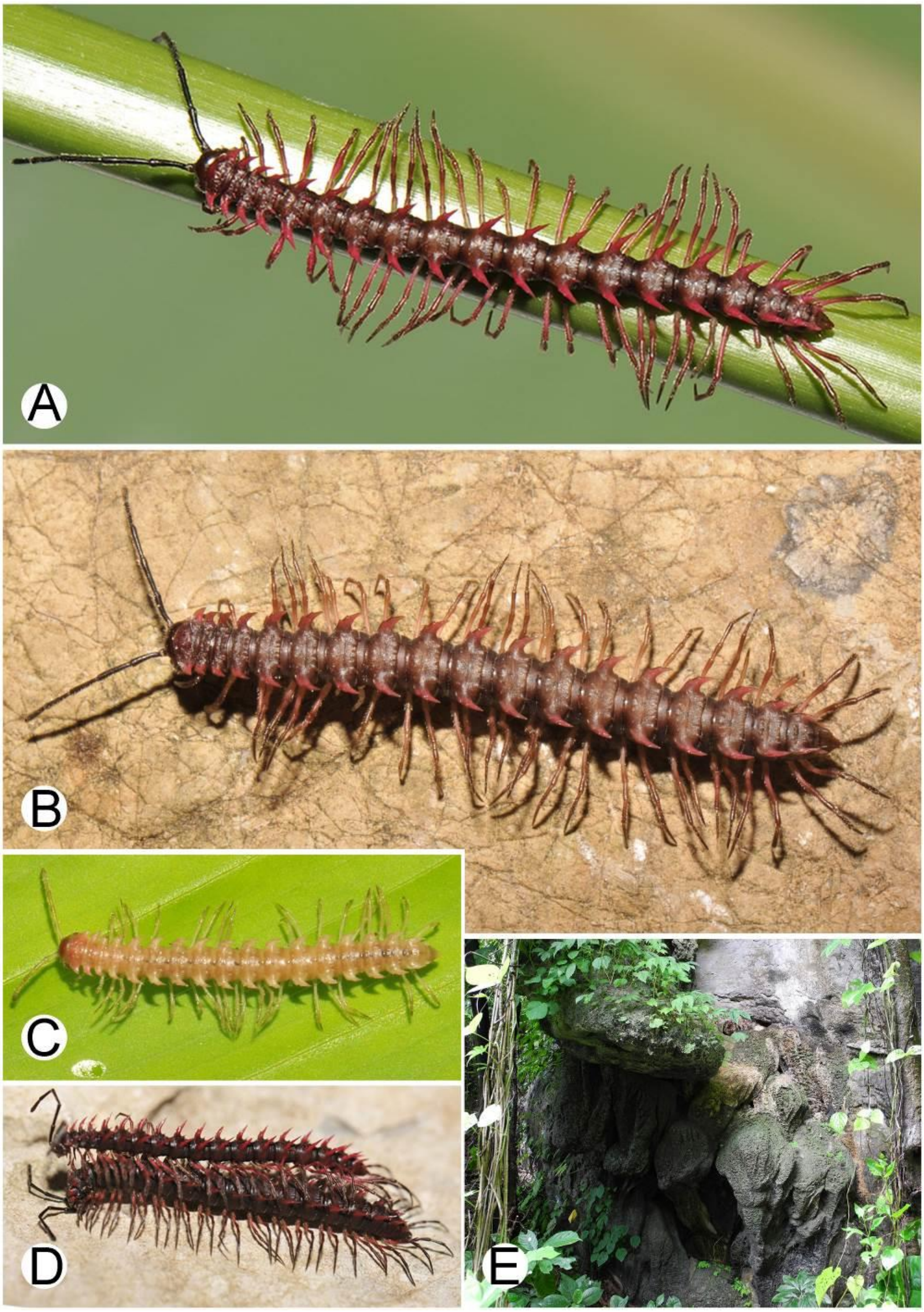

Figure 4.93 Photographs of live *Desmoxytes waepyanensis* sp. n. and habitat. **A** male paratype **B** female paratype **C** juvenile **D** mating couple **E** habitat.

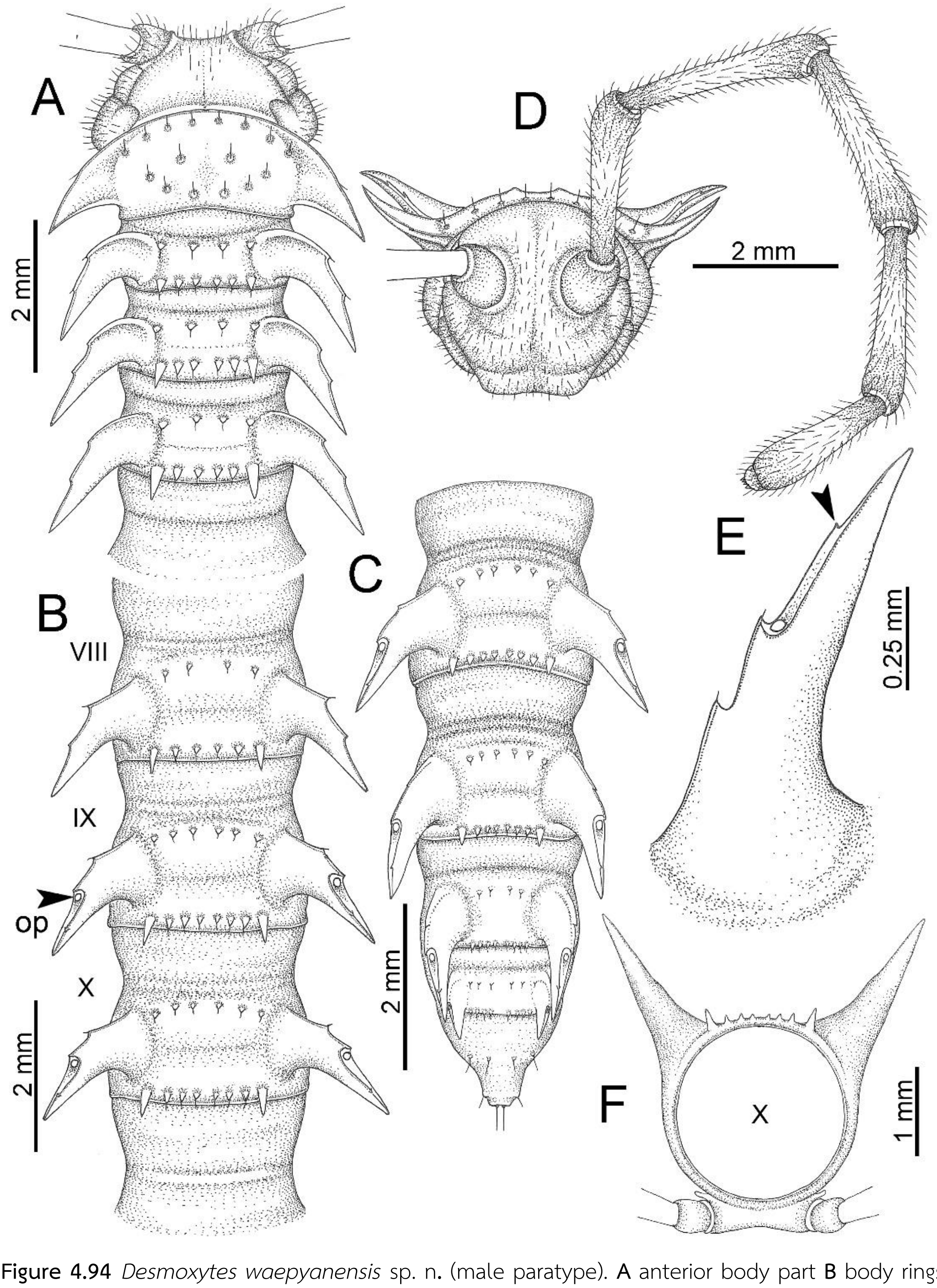

Figure 4.94 *Desmoxytes waepyanensis* sp. n. (male paratype). **A** anterior body part **B** body rings 8–10 (op = ozopore) **C** posteriormost body rings and telson **D** head and antenna **E** paraterga of ring 10 (arrow = tiny denticle) **F** body ring 10.

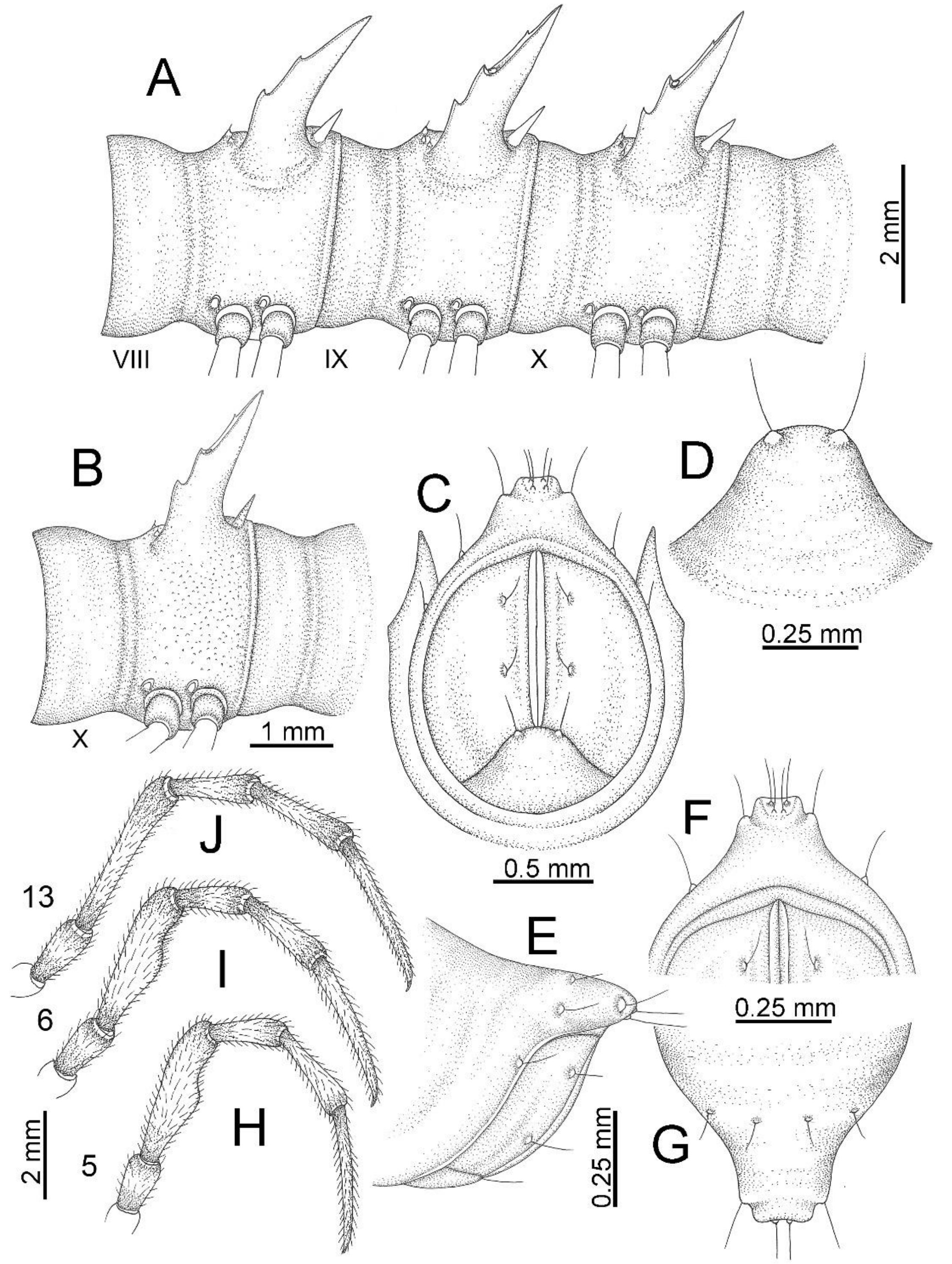

Figure 4.95 *Desmoxytes waepyanensis* sp. n. (male paratype). **A** body rings 8–10 **B** sculpture of ring 10 **C, E** last ring and telson **D** hypoproct **F, G** epiproct **H** male leg 5 (right) **I** male leg 6 (right) **J** male leg 13 (right).

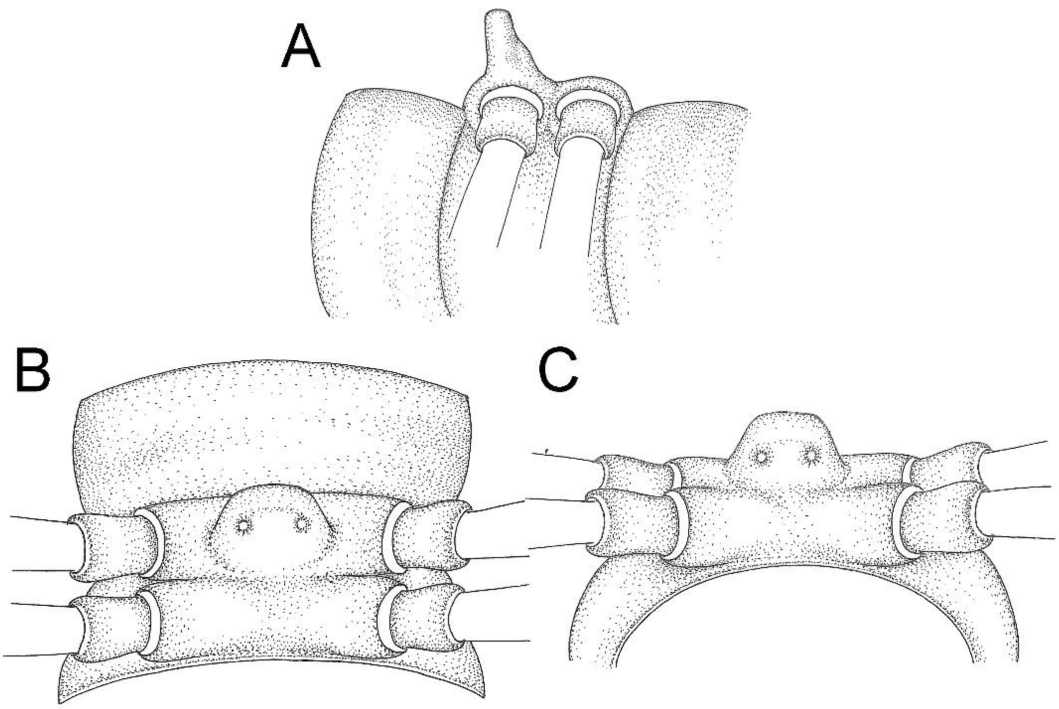

Figure 4.96 *Desmoxytes waepyanensis* sp. n. (male paratype) – sternal lobe between male coxae 4. **A** lateral view **B** ventral view **C** caudal view.

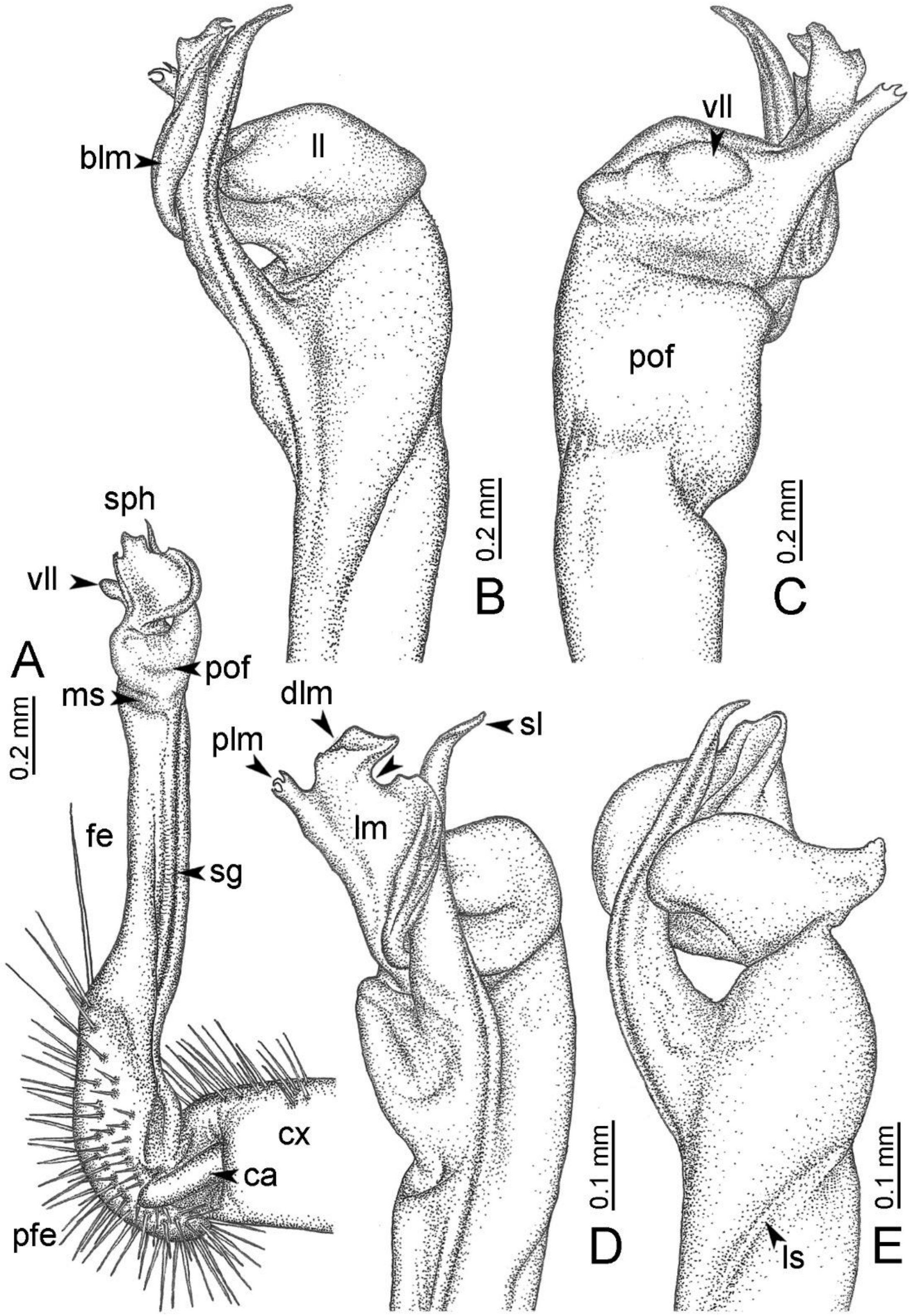

Figure 4.97 *Desmoxytes waepyanensis* sp. n. (paratype) – right gonopod. **A** mesal view **B** dorsal view **C** ventral view **D** subdorsal view (arrow = indentation) **E** lateral view.

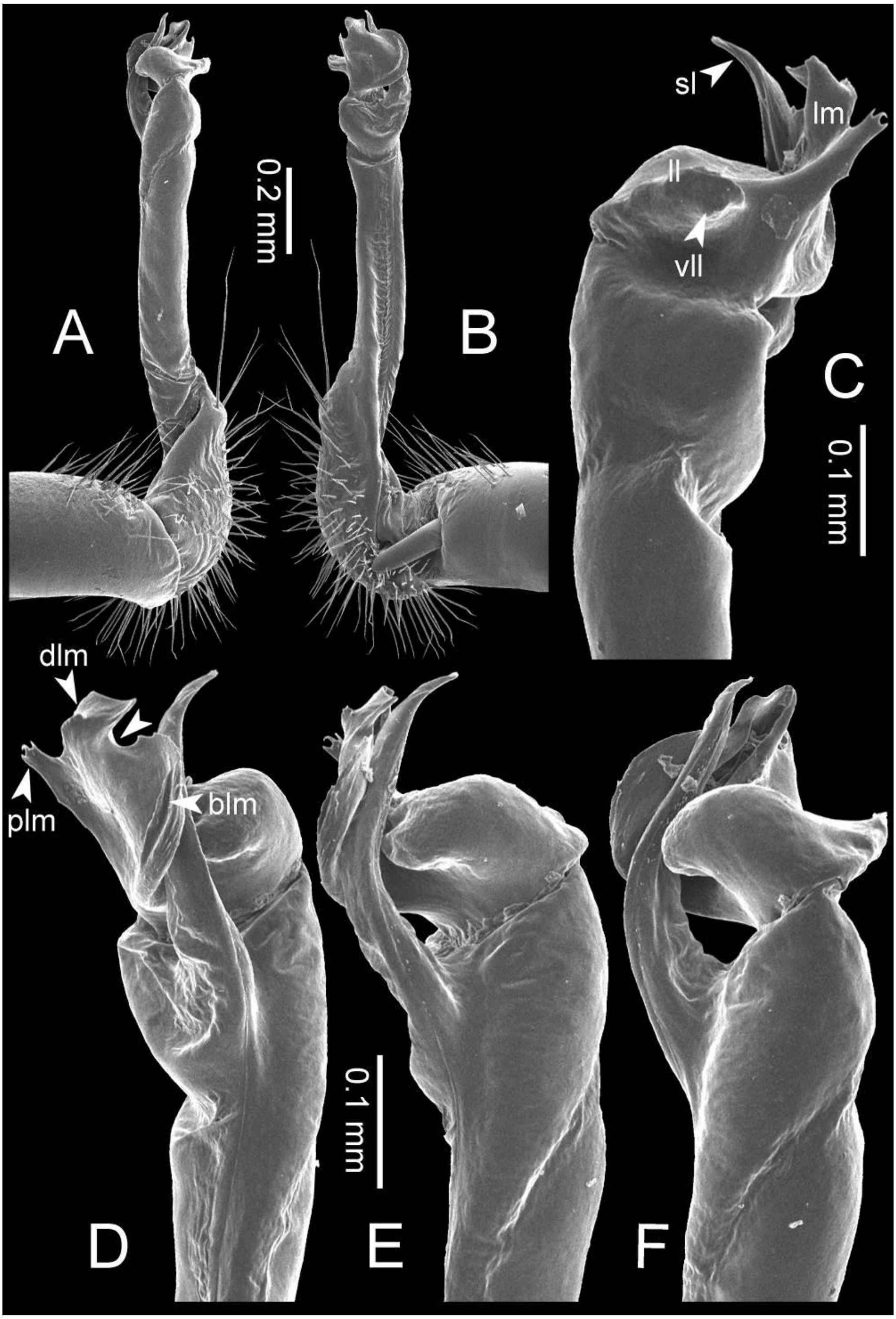

Figure 4.98 *Desmoxytes waepyanensis* sp. n. (paratype) – right gonopod. **A** lateral view **B** mesal view **C** ventral view **D** subdorsal view (arrow = indentation) **E** dorsal view **F** subdorsal view.

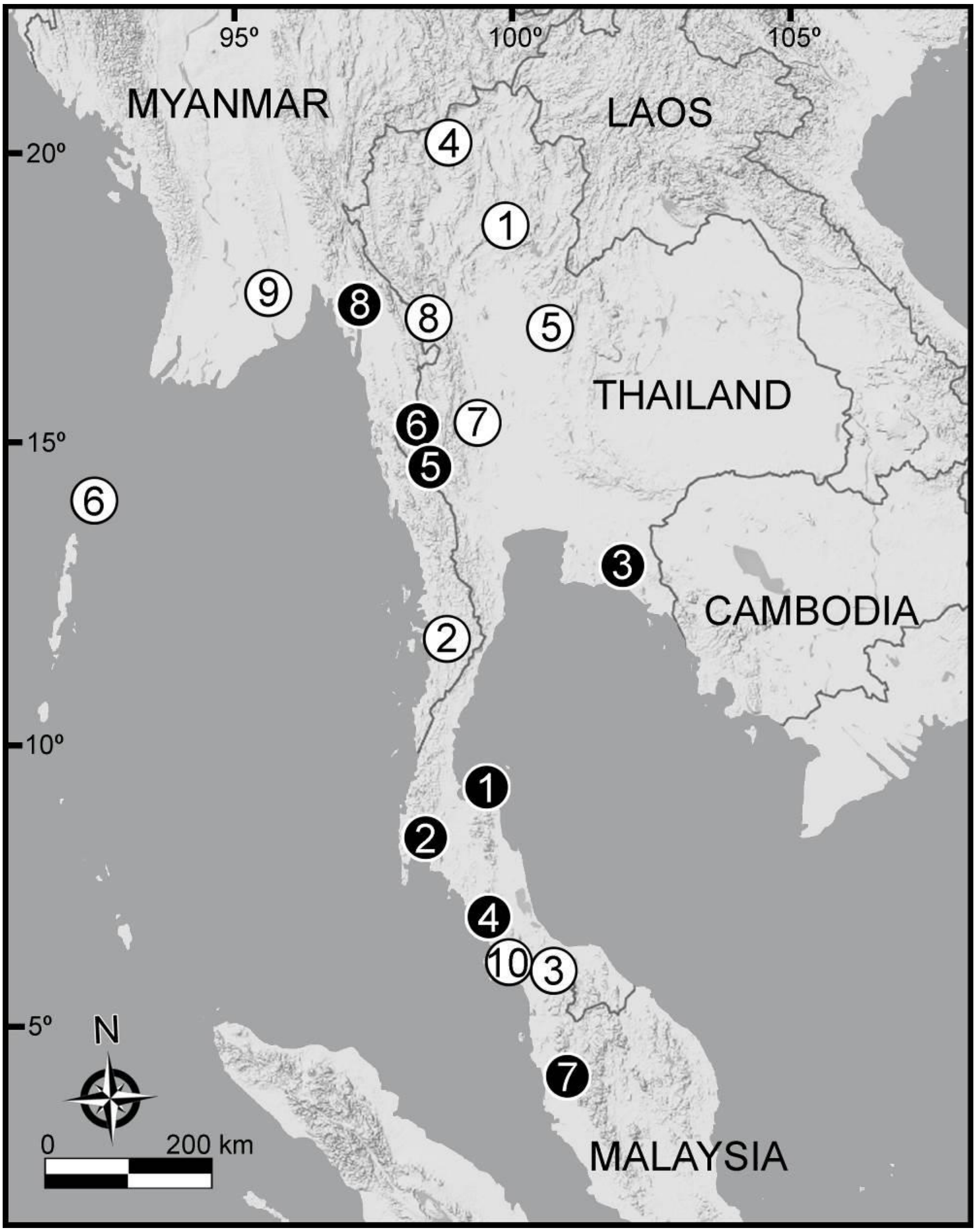

Figure 4.99 Type localities of all *Desmoxytes* species. white circle = described species (1 = *D. breviverpa*, 2 = *D. cervina*, 3 = *D. delfae*, 4 = *D. des*, 5 = *D. pinnasquali*, 6 = *D. planata*, 7 = *D. purpurosea*, 8 = *D. takensis*, 9 = *D. taurina*, 10 = *D. terae*). black circle = new species described in this study (1 = *D. aurata*, sp. n. 2 = *D. corythosaurus* sp. n., 3 = *D. euros* sp. n., 4 = *D. flabella* sp. n., 5 = *D. golovatchi* sp. n., 6 = *D. octoconigera* sp. n., 7 = *D. perakensis* sp. n., 8 = *D. waepyanensis* sp. n.).

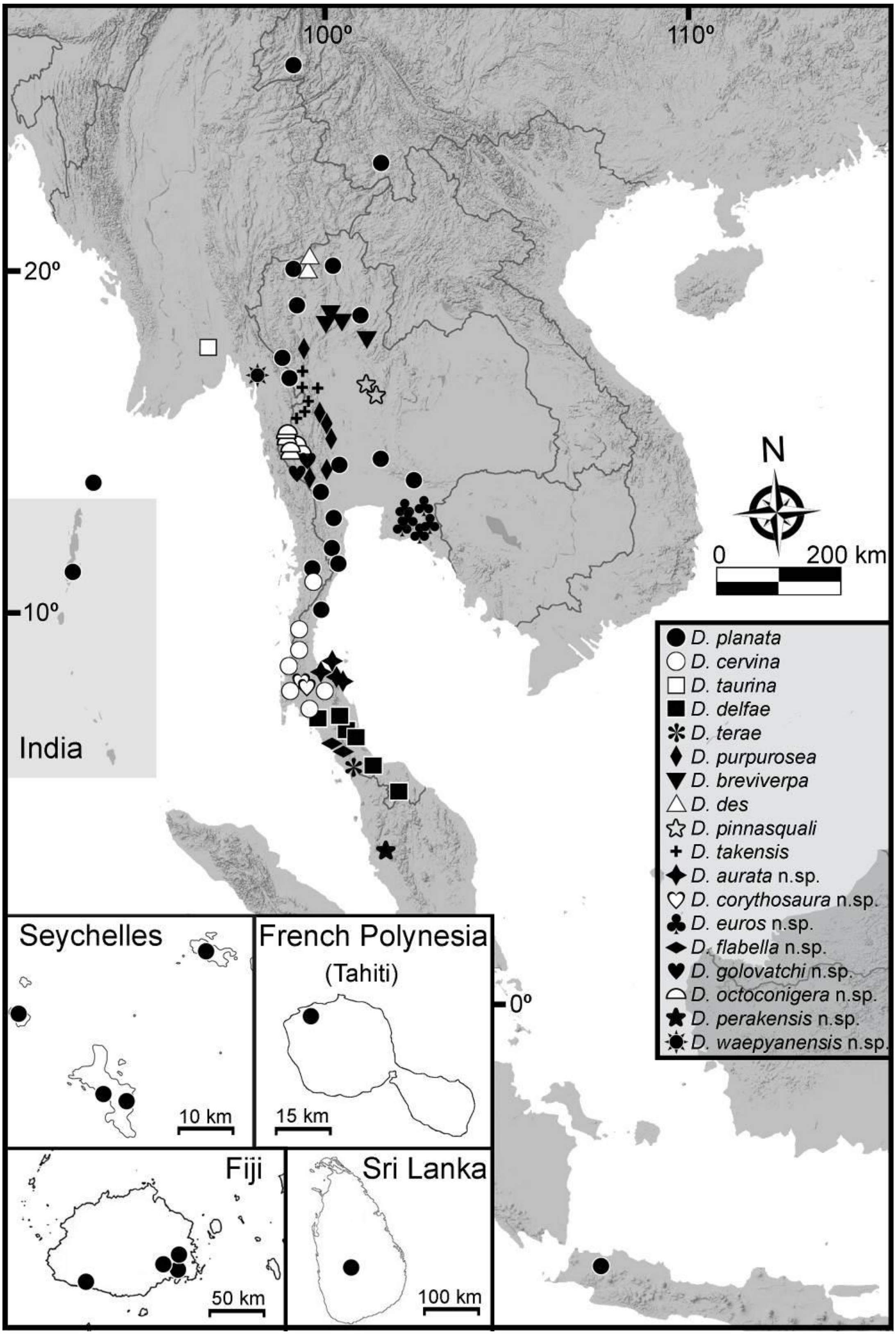

Figure 4.100 Known distribution of all *Desmoxytes* species based on all recorded data (*D. planata*, *D. cervina* and *D. delfae* are shown in the representative localities).

Table 4.1 Gonopod structures in *Desmoxytes s.s.*, and their abbreviations (in **Bold**: structure only occurring in certain species).

Gonopodal part	Abb.	Description
Acropodite		The apical part of the gonopod; including femorite, solenophore and solenomere.
Coxa	cx	The basal part of the gonopod, connecting to body ring, attached to the apertural rim dorsally; rather stout; ca. half as long as femur, sometimes quite short (equal in length with prefemur); with distoanterior group of setae.
Broad lobe of lamina medialis	blm	A broad lobe originating from lamina medialis, lamella-like; normally broad with thick edge.
Cannula	ca	A short tube, lever-like, curved, long and slender; originating from coxa, tip inserted into concavity in prefemur.
Distal lobe of lamina medialis	dlm	A lamella-like process, situated on the top of lamina medialis, consisting one or two small lobe(s)/ lamella(e).
Femur	fe	The longest part of the gonopod, straight; accommodates the seminal groove.
Lamina medialis	lm	A large part distally on the gonopod, normally with one process and one/two lobe(s)
Lamina lateralis	ll	A distinct lobe in the distal part of gonopod; sometimes comprising a ridge and/or lobe
Lateral sulcus	ls	A distinct sulcus distally on femur, visible in lateral view
Mesal sulcus	ms	A distinct sulcus distally on femur, usually seen in mesal view.
Postfemur	pof	A short part of telopodite, supporting solenophore and solenomere, demarcated from femur by lateral sulcus and mesal sulcus.

Prefemur	pfe	The basal portion of the telopodite, with densely setose.
Process of lamina medialis	plm	A protruding process originating from lamina medialis
Seminal groove	sg	A conspicuous groove, similar to a tunnel, seen as a transparent line, visible on femur in mesal view.
Solenomere	sl	A usually long, flagella-like appendage, originating on base of solenophore.
Solenophore (= tibiotarsus)	sph	Apical part of telopodite, consisting of lamina lateralis and lamina medialis.
Telopodite		The main part of the gonopod pivoting on coxa; including prefemur, femorite, solenophore and solenomere.
Ventral lobe of lamina lateralis	vll	An additional lobe on lamina lateralis, normally digitiform, visible in ventral view, seen in *D. purpurosea, D. breviverpa, D. takensis, D. waepyanensis* sp. n.
Ventral ridge of lamina lateralis	vrl	An additional ridge on lamina lateralis, seen in ventral view, present in *D. aurata* sp. n., *D. cervina*, *D. delfae*, *D. euros* sp. n., *D. flabella* sp. n., *D. perakensis* sp. n., *D. planata*.

Table 4.2 Species assigned to *Desmoxytes s.l.* and their placement according to our analysis.

	Placement
1	*Desmoxytes acantherpestes* Golovatch and Enghoff, 1994 (to be placed in new genus)
2	*Desmoxytes aspera* (Attems, 1937) = *Hylomus asper* (Attems, 1937) comb. n.
3	*Desmoxytes breviverpa* Srisonchai, Enghoff and Panha, 2016 (in *Desmoxytes* s.s.)
4	*Desmoxytes cattienensis* Nguyen, Golovatch and Anichkin, 2005 = *Hylomus cattienensis* (Nguyen, Golovatch and Anichkin, 2005) comb. n.
5	*Desmoxytes cervaria* (Attems, 1953) = *Hylomus cervarius* (Attems, 1953) comb. n.
6	*Desmoxytes cervina* (Pocock, 1895) (in *Desmoxytes* s.s.)
7	*Desmoxytes cornuta* (Zhang and Li, 1982) = *Hylomus cornutus* (Zhang and Li, 1982) comb. n.
8	*Desmoxytes delfae* (Jeekel, 1964) (in *Desmoxytes* s.s.)
9	*Desmoxytes des* Srisonchai, Enghoff and Panha, 2016 (in *Desmoxytes* s.s.)
10	*Desmoxytes draco* (Cook and Loomis, 1924) = *Hylomus draco* Cook and Loomis, 1924 stat. rev.
11	*Desmoxytes enghoffi* Nguyen, Golovatch and Anichkin, 2005 = *Hylomus enghoffi* (Nguyen, Golovatch and Anichkin, 2005) comb. n.
12	*Desmoxytes eupterygota* Golovatch, Li, Liu and Geoffroy, 2012 = *Hylomus eupterygotus* (Golovatch, Li, Liu and Geoffroy, 2012) comb. n.
13	*Desmoxytes getuhensis* Liu, Golovatch and Tian, 2014 = *Hylomus getuhensis* (Liu, Golovatch and Tian, 2014) comb. n.
14	*Desmoxytes gigas* Golovatch and Enghoff, 1994 (to be placed in new genus)
15	*Desmoxytes grandis* Golovatch, VandenSpiegel and Semenyuk, 2016

	Placement
	= *Hylomus grandis* (Golovatch, VandenSpiegel and Semenyuk, 2016) comb. n.
16	*Desmoxytes hostilis* Golovatch and Enghoff, 1994 = *Hylomus hostilis* (Golovatch and Enghoff, 1994) comb. n.
17	*Desmoxytes jeekeli* Golovatch and Enghoff, 1994 = *Hylomus jeekeli* (Golovatch and Enghoff, 1994) comb. n.
18	*Desmoxytes lingulata* Liu, Golovatch and Tian, 2014 = *Hylomus lingulatus* (Liu, Golovatch and Tian, 2014) comb. n.
19	*Desmoxytes laticollis* Liu, Golovatch and Tian, 2016 = *Hylomus laticollis* (Liu, Golovatch and Tian, 2016) comb. n.
20	*Desmoxytes longispina* (Loksa, 1960) = *Hylomus longispinus* (Loksa, 1960) comb. n.
21	*Desmoxytes lui* Golovatch, Li, Liu and Geoffroy, 2012 = *Hylomus lui* (Golovatch, Li, Liu and Geoffroy, 2012) comb. n.
22	*Desmoxytes minutubercula* (Zhang, 1986) = *Hylomus minutuberculus* (Zhang, 1986) comb. n.
23	*Desmoxytes nodulosa* Liu, Golovatch and Tian, 2014 = *Hylomus nodulosus* (Liu, Golovatch and Tian, 2014) comb. n.
24	*Desmoxytes parvula* Liu, Golovatch and Tian, 2014 = *Hylomus parvulus* (Liu, Golovatch and Tian, 2014) comb. n.
25	*Desmoxytes phasmoides* Liu, Golovatch and Tian, 2016 = *Hylomus phasmoides* (Liu, Golovatch and Tian, 2016) comb. n.
26	*Desmoxytes pilosa* (Attems, 1937) = *Hylomus pilosus* (Attems, 1937) comb. n.
27	*Desmoxytes pinnasquali* Srisonchai, Enghoff and Panha, 2016 (in *Desmoxytes* s.s.)
28	*Desmoxytes planata* (Pocock, 1895) (in *Desmoxytes* s.s.)
29	*Desmoxytes proxima* Nguyen, Golovatch and Anichkin, 2005 = *Hylomus proximus* (Nguyen, Golovatch and Anichkin, 2005) comb. n.
30	*Desmoxytes purpurosea* Enghoff, Sutcharit and Panha, 2007 (in *Desmoxytes* s.s.)

	Placement
31	*Desmoxytes rhinoceros* Likhitrakarn, Golovatch and Panha, 2015 = *Hylomus rhinoceros* (Likhitrakarn, Golovatch and Panha, 2015) comb. n.
32	*Desmoxytes rhinoparva* Likhitrakarn, Golovatch and Panha, 2015 = *Hylomus rhinoparvus* (Likhitrakarn, Golovatch and Panha, 2015) comb. n.
33	*Desmoxytes scolopendroides* Golovatch, Geoffroy and Mauriès, 2010 = *Hylomus scolopendroides* (Golovatch, Geoffroy and Mauriès, 2010) comb. n.
34	*Desmoxytes scutigeroides* Golovatch, Geoffroy and Mauriès, 2010 = *Hylomus scutigeroides* (Golovatch, Geoffroy and Mauriès, 2010) comb. n.
35	*Desmoxytes similis* Liu, Golovatch and Tian, 2016 = *Hylomus similis* (Liu, Golovatch and Tian, 2016) comb. n.
36	*Desmoxytes simplex* Golovatch, VandenSpiegel and Semenyuk, 2016 = *Hylomus simplex* (Golovatch, VandenSpiegel and Semenyuk, 2016) comb. n.
37	*Desmoxytes simplipoda* Liu, Golovatch and Tian, 2016 = *Hylomus simplipodus* (Liu, Golovatch and Tian, 2016) comb. n.
38	*Desmoxytes specialis* Nguyen, Golovatch and Anichkin, 2005 = *Hylomus specialis* (Nguyen, Golovatch and Anichkin, 2005) comb. n.
39	*Desmoxytes spectabilis* (Attems, 1937) = *Hylomus spectabilis* (Attems, 1937) comb. n.
40	*Desmoxytes spiniterga* Liu, Golovatch and Tian, 2016 = *Hylomus spinitergus* (Liu, Golovatch and Tian, 2016) comb. n.
41	*Desmoxytes spinissima* Golovatch, Li, Liu and Geoffroy, 2012 = *Hylomus spinissimus* (Golovatch, Li, Liu and Geoffroy, 2012) comb. n.
42	*Desmoxytes takensis* Srisonchai, Enghoff and Panha, 2016 (in *Desmoxytes* s.s.)
43	*Desmoxytes taurina* (Pocock, 1895) (in *Desmoxytes* s.s.)
44	*Desmoxytes terae* (Jeekel, 1964) (in *Desmoxytes* s.s.)
45	*Desmoxytes variabilis* Liu, Golovatch and Tian, 2016 = *Hylomus variabilis* (Liu, Golovatch and Tian, 2016) comb. n.

Table 4.3 Comparison of the five groups (genera) of *Desmoxytes* s.l. ....

	Desmoxytes s.s.	'*acantherpestes*'	'*gigas*'	'*spiny*'	*Hylomus*
Paraterga	Wing-like	Subspiniform	Subspiniform	Spiniform	Wing-like, antler-like, spiniform
Tegument (metaterga)	Microgranulate	Microgranulate	Microgranulate	Smooth	Microgranulate (some spp. smooth)
Row of setae/tubercles/cones/spines on metaterga 2–19	2 rows	2 rows	3 rows (uniform)	2 rows	1, 2, 3 (uniform/random), or 4 rows
Caudolateral spine	Absent	Absent	Present - long	Absent	Absent
Femora 5 6 7 8 9 Modified/Unmodified	Modified (ex. *D. terae*)	Unmodified	Modified and unmodified	Modified and unmodified	Modified and unmodified
- If modified	5 6		5 6 or 5 6 7	6 7 or 7 or 8 9	5 6 or 5 6 7 or 6 or 6 7 or 6 7 8
- Shape	Swollen/humped		Apophysis	Apophysis	Mostly apophysis (some spp. humped, some spp. mixed - apophysis+humped)
Pores on lobe of sternum 5	2 pores	2 pores	1 pore	1 or 2 pores	2 pores
Gonopod telopodite overall shape (especially femorite)	Straight	Straight	Curved (falcate)	Straight	Curved (some spp. straight)
Postfemoral part	Conspicuous, broad laterally	Conspicuous, broad laterally	Inconspicuous	Conspicuous, narrow laterally	Inconspicuous
Mesal sulcus (ms)/lateral sulcus (ls)	ms deep, ls deep/ shallow	ms deep, ls deep/shallow	ms absent, ls absent	ms deep, ls deep	ms shallow/absent, ls shallow/absent
Lamina lateralis (ll)	Obviously separated from lm	Obviously separated from lm	Indistinctly separated from lm	Obviously separated from lm	Mostly - indistinctly separated from lm (some spp. obvious)
ll larger/smaller than lm	Equal size	Smaller than lm	Larger than lm	Smaller than lm (ll very small)	Mostly larger than lm (some spp. smaller than lm)
Lamina medialis (lm)	Short	Long, curved	Short	Long, curved	Short
Process on Lamina medialis (lm)	With process	Absent	Absent	Absent	Absent
Lobe(s) on Lamina medialis (lm)	With 1 or 2 lobe(s)	Absent	Absent	Absent	Absent (ex. some spp. with process/spine/hook)

CHAPTER V

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

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Abstract

The '*acantherpestes*' group of dragon millipedes, formerly placed in genus *Desmoxytes* Chamberlin, 1923, is revised and assigned to the new genus *Nagaxytes* gen. nov. *Desmoxytes acantherpestes* Golovatch & Enghoff, 1994 is the type species of the new genus and is redescribed as *N. acantherpestes* (Golovatch & Enghoff, 1994) gen. et comb. nov. Three new species are described from Thailand: *N. erecta* gen. et sp. nov. and *N. gracilis* gen. et sp. nov. from Kanchanaburi province, and *N. spatula* gen. et sp. nov. from Tak province. All new species are endemic to western Thailand and all are restricted to limestone habitats. Complete illustrations of external morphological characters, an identification key, and a distribution map are provided.

Key words. endemic, dragon millipede, new species, taxonomy, Thailand.

Introduction

Srisonchai *et al.* (2018a) subdivided the dragon millipede genus *Desmoxytes* Chamberlin, 1923, *sensu* Golovatch & Enghoff (1994) into five groups based on morphological characters and DNA sequence data; they regarded each of the groups as a separate genus. In the present article, the second in a series of articles about revision of the dragon millipedes, we revise the '*acantherpestes*' group *sensu* Srisonchai *et al.* For this group we erect the new genus *Nagaxytes* gen. nov. to include *Desmoxytes acantherpestes* Golovatch & Enghoff, 1994 from western Thailand as well as three new species.

The new genus *Nagaxytes* is narrowly distributed and restricted to limestone areas. All species are known only from western Thailand: Kanchanaburi, Prachuap Khiri Khan and Tak provinces.

Material and methods

Specimen collecting and preservation

Nagaxytes specimens were collected by hand from many localities in the western part of Thailand. The main collectors are staff and students from Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, referred to as "ASRU members". Coordinates and elevation were recorded by using Garmin GPSMAP 60 CSx, and were subsequently double-checked with Google Earth.

After collecting and photographing, most specimens were preserved in 70% ethanol for morphological study and some in 95% ethanol for molecular analysis (specimens kept in 95% ethanol at room temperature were later stored at -20°C in a freezer).

Illustrations

Living specimens were photographed using a Nikon 700D+AFS VR with a 105 mm lens. Scanning electron microscope images (SEMs) of gonopods were generated with a JEOL JSM–5410 LV. All objects were mounted on aluminium stubs and coated with gold; after imaging the objects were removed from the stubs and kept dry in eppendorf tubes. Drawings were sketched under a stereo microscope and finished using dot-line techniques.

Morphological descriptions

Specimens were studied for non-gonopod and gonopod characters under a stereo microscope and under SEM. Non-gonopod characters include size, colour, head, antennae, collum, tegument, prozona, metaterga, paraterga, telson, sterna, and legs. We use the terms of morphology according to previous taxonomic publications (Enghoff *et al.*, 2007; Golovatch and Enghoff, 1994; Jeekel, 1964, 1980a, 2003; Srisonchai *et al.*, 2016, 2018a). Details of gonopod characters are provided in the gonopod terminology section below.

Deposition of holotypes, paratypes and other new specimens

All holotypes, some paratypes of the new species and new specimens will be housed in CUMZ. Some paratypes and some new specimens will be deposited at NHMUK, NHMW, ZMUC and ZMUM.

Abbreviation of institutions

CUMZ	=	Chulalongkorn University Museum of Zoology, Bangkok, Thailand

MHNG	=	Natural History Museum, Geneva, Switzerland
NHMUK	=	Natural History Museum, London, England
NHMW	=	Natural History Museum, Vienna, Austria
ZMUC	=	Natural History Museum of Denmark (Zoological Museum), University of Copenhagen, Denmark
ZMUM	=	Zoological Museum, University of Moscow, Russia

Other abbreviations used in the text

ASRU	=	Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand
ca.	=	about, around (circa)
a.s.l.	=	above sea level

Gonopod terms for the genus Nagaxytes*, and their abbreviations*

Acropodite	=	Apical part of gonopod; including femorite, solenophore and solenomere.
Coxa (cx)	=	Basal part of gonopod, rather stout, connecting to seventh body ring, attached to apertural rim dorsally; with a distoanterior group of setae.
Cannula (ca)	=	A short tube, lever-like, curved, slender; originating from coxa, tip inserted into concavity in the prefemoral part.
Femur (fe)	=	Longest part of gonopod, straight; accommodates seminal groove.
Lamina medialis (lm)	=	A large part distally on gonopod, very long, snake-like.
Lamina lateralis (ll)	=	A distinct lobe on distal part of gonopod; sometimes short, stout, compact; sometimes long; rarely with a spatulate lobe.
Lateral sulcus (ls)	=	A distinct sulcus distally on femur, conspicuously deep or shallow, visible in lateral view.

Mesal sulcus (ms)	=	A distinct sulcus distally on femur, conspicuous and deep, usually seen in mesal view.
Prefemoral part (= prefemur) (pfe)	=	Basal portion of telopodite, densely setose.
Postfemoral part (postfemur) (pof)	=	A short part of telopodite, supporting solenophore and solenomere, demarcated from femur by lateral sulcus and mesal sulcus.
Seminal groove (sg)	=	A conspicuous groove, similar to a tunnel, seen as a transparent line, visible on femur in mesal view.
Solenomere (sl)	=	A usually long, flagellum-like appendage, originating on base of solenophore.
Solenophore (=tibiotarsus) (sph)	=	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 90° up from their *in situ* position (following the terminology of Srisonchai *et al.* (2018a)).

Dorsal refers to a position on the side nearest to the body ring.

Ventral refers to a position on the side farthest away from the body ring.

Mesal refers to a position on the side nearest to the midline.

Lateral refers to a position on the side furthest from the midline.

Dorsad refers to a direction towards the body ring.

Ventrad refers to a direction away from the body ring.

Mesad refers to a direction towards the midline.

Laterad refers to a 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

Suborder Strongylosomatidea Brölemann, 1916

Family Paradoxosomatidae Daday, 1889

Subfamily Paradoxosomatinae Daday, 1889

Tribe Orthomorphini Brölemann, 1916

Nagaxytes Srisonchai, Enghoff & Panha gen. nov.

Type species

Desmoxytes acantherpestes Golovatch & Enghoff, 1994

Diagnosis

The genus *Nagaxytes* is characterized by:

1. Paraterga subspiniform.
2. Metaterga with 2 rows of tubercles/cones/spines (lateral spines of posterior row very long).
3. Male femora 5 and 6 without modification.
4. Postfemoral part of gonopod conspicuous, demarcated from femur by a deep mesal sulcus (ms) and a shallow/deep lateral sulcus (ls).
5. Lamina lateralis (ll) obviously separated from lamina medialis (lm).
6. Lamina medialis (lm) long and curved, apically fringed/hooked.

Etymology

'*Naga'* is a Sanskrit and Pali word, relating to a category of snake-like spirits in Buddhist and Hindu mythology, and refers to the snake-like shape of the lamina medialis (lm) of the gonopod; '–*xytes*' ensures harmony with *Desmoxytes* (and its synonym *Pteroxytes* Jeekel, 1980).

Included species (4)

- *N. acantherpestes* (Golovatch & Enghoff, 1994) comb. nov.
- *N. erecta* sp. nov.
- *N. gracilis* sp. nov.
- *N. spatula* sp. nov.

Remarks

Srisonchai *et al.* (2018a) proposed to subdivide *Desmoxytes* sensu Golovatch & Enghoff (1994) into five genera. The '*acantherpestes*' group (= *Nagaxytes* gen. nov.) is well-defined by several distinct morphological characters (see diagnosis), especially the distinctive subspiniform paraterga and the very long lamina medialis (lm) of the gonopods. Even though the subspiniform paraterga are relatively similar to those of the '*gigas*' group, the gonopod details are very different.

General description of the genus *Nagaxytes*

The description applies to adult males and females, except for the part on the gonopods and when "male" is specified (Figs 5.1, 5.2, 5.3). The general description of gonopods is based mainly on *Nagaxytes gracilis* sp. nov. (Figs 5.4, 5.5).

SIZE. Body length 22–34 mm (male) 24–38 mm (female), width ca. 2.0–2.4 mm (male) 2.8–3.4 mm (female), varies between species, usually female wider and longer than male.

COLOUR (Figs 5.1, 5.11, 5.12, 5.17, 5.22). Specimens in life with brown or reddish brown colour or pinkish brown (possibly aposematic coloration). Colour in alcohol: all specimens partly faded to pale whitish brown after one year's preservation in alcohol; specimens kept in darkness faded more slowly.

ANTENNAE (Fig. 5.2A, B, D). Long and slender, covered by delicate setation, usually reaching backwards to body ring 5–7 (male) and 4–6 (female) when stretched dorsally. Antennomere 3 = 4 > 5 ≥ 2 > 6 > 1 > 7 > 8.

HEAD. Delicately setose; vertex, labrum and genae delicately setose; epicranial suture conspicuous as brown stripe.

COLLUM (Fig. 5.3A, C). With three transverse rows of setae/tubercles and spines; 3+3 setae/tubercles (anterior row), 1+1 setae/tubercles (intermediate row) and 2+2 spines (posterior row); lateral spines of posterior row very long. Paraterga of collum wing-like, usually elevated at ca. 25°–40°, with two conspicuous notches at lateral margin.

TEGUMENT (Fig. 5.3A–G). Often dull, sometimes quite shining; collum, metaterga (except anterior part of metaterga smooth) and surface below paraterga finely microgranulate; prozona finely shagreened; paraterga, sterna and epiproct smooth. Stricture between prozona and metazona wide, usually quite shallow, sometimes quite deep.

METATERGA (Figs 5.2A, 5.3A, D, G). With one or two transverse rows of setae/tubercles and spines; usually with 2+2 setae/tubercles/cones/spines in anterior row and 2+2 spines in posterior row (sometimes setae/tubercles/cones/spines in anterior row poorly developed or absent); lateral spines of posterior row longer and larger than mesal ones. Suture (transverse sulcus) on metaterga quite deep, conspicuous on body ring 5–17 in all species. Mid-dorsal (axial) line missing.

PLEUROSTERNAL CARINAE (Fig. 5.3B). Forming a complete crest on ring 2, a small ridge on ring 3 and/or 4, missing on remaining body rings.

PARATERGA (Fig. 5.3A, B, D, E, G, H). Subspiniform, long, elevated at ca. 50°–70° (male) or 45°–70° (female), directed caudolaterad on rings 2–17 or 2–18, directed increasingly caudad on ring 19 or 18–19. Callus and shoulder poorly developed. Anterior margin with two distinct notches; on body rings 9, 10, 12, 13, 15–18 a denticle usually present at lateral margin near tip (denticle absent in some rings). Degree of elevation of paraterga in male usually higher than in female. Posterior edge concave; posterior angle pointed and sharp. Ozopore visible in lateral and dorsal views, round, small, somewhat inconspicuous.

TELSON (Fig. 5.3F, G, L, N). Epiproct quite short, often flattened dorsoventrally, tip usually subtruncate, sometimes emarginate; lateral setiferous tubercles conspicuous, digitiform; apical tubercles mostly conspicuous, sometimes inconspicuous; setiferous tubercles beyond lateral setiferous tubercles long, digitiform; epiproct apically with two pairs of conspicuous setae (= spinnerets). Four spinnerets (Fig. 5.3L) at the corners of a square, not in a depression, anterior pair close to apical tubercles. Paraprocts convex. Hypoproct subtriangular or subtrapeziform; caudal margin often subtriangular, sometimes round, with two conspicuous or inconspicuous setiferous tubercles.

STERNA (Figs 5.2C, 5.3K). Sparsely setose; cross-impressions somewhat deep, sometimes quite shallow. Sternal lobe between male coxae 4 modified; usually subtrapeziform, sometimes incompletely bilobed, varying between species; tip slightly emarginate, sometimes deeply emarginate or even incompletely bilobed; with two pores seen in posterior view.

LEGS (Fig. 5.2A–C). Very long and slender. Relative lengths of podomeres: femur > tarsus > tibia > prefemur = postfemur > coxa > claw. Male femora 5 and 6 without modification in all species.

GONOPODS (Figs 5.4, 5.5). Coxa (cx) longer than prefemoral part, with a distoanterior group of setae. Cannula (ca) long or short. Telopodite straight. Prefemoral part (pfe) usually shorter than femur, sometimes subequal in length to femur. Femur usually long, sometimes quite short. Seminal groove (sg) running entirely on mesal surface of femur. Mesal sulcus (ms) and lateral sulcus (ls) conspicuous. Postfemoral part conspicuous, shorter than femur. Solenophore (sph) well-developed: lamina lateralis (ll) variously modified; swollen, sometimes long digitiform/lamella-like and projecting, sometimes with spatula-like lobe: lamina medialis (lm) longer than lamina lateralis, snake-like, tip curving down. Solenomere (sl) relatively long.

Distribution and habitat

This genus is known only from the western part of Thailand: Prachuap Khiri Khan Province (Hua Hin and Kui Buri Districts), Kanchanaburi Province (Sai Yok and Thong Pha Phum Districts) and Tak Province (Mae Sot and Umphang Districts) (Fig. 5.27). All four species seem to be local endemics which are highly restricted to limestone habitats, and all have narrow distribution ranges. The specimens were usually found on humid rocks, rock walls, leaf litter or surface roots of trees. Some species can be found syntopically in the same habitat with other dragon millipede species.

Key to species of *Nagaxytes* (based mainly on males)

1. Gonopod with lamina lateralis (ll) long (e.g., Figs 5.15B, 5.16C, 5.20B, 5.21C), or with lobe (e.g. Figs 5.25B, 5.26C) 2
– Lamina lateralis (ll) short, swollen, stout, compact, without lobe (e.g., Figs 5.9B, 5.10C, F) ....***N. acantherpestes*** (Golovatch & Enghoff, 1994) comb. nov.

2. Body length 22–26 mm in male, 24–28 mm in female. Lamina lateralis (ll) with a curved, long, spatulate lobe (Figs 5.25, 5.26); solenomere (sl) terminating in two curved processes (Figs 5.25B, 5.26E) ....***N. spatula*** sp. nov.
– Body length 30–36 mm in male, 35–38 mm in female. Lamina lateralis (ll) without spatulate lobe; solenomere (sl) terminating in one process (e.g., Figs 5.15D, 5.16D, 5.20D, 5.21D) 3

3. Metaterga 4–19 with conspicuous anterior row of tubercles/cones/spines (Fig. 5.13A–C). Sternal lobe between male coxae 4 subtrapeziform (Fig. 5.14J). Lamina lateralis (ll) erect, digitiform, thick, tip directed anteriad (Figs 5.15B–D, 5.16C, E, F) ....***N. erecta*** sp. nov.
– Metaterga 4–19 without anterior row of tubercles/cones/spines (Fig. 5.18A–C). Sternal lobe between male coxae 4 not subtrapeziform, incompletely bilobed, tip deeply emarginate (Fig. 5.19J). Lamina lateralis (ll) lamella-like, curved, broad, thin, tip directed mesoventrad (Figs 5.20B–D, 5.21C–F) ....***N. gracilis*** sp. nov.

Species descriptions

Nagaxytes acantherpestes (Golovatch & Enghoff, 1994) comb. nov.

(Figs 5.2, 5.6–5.10)

Desmoxytes acantherpestes Golovatch & Enghoff, 1994: 51–53, figs 21–28.

Desmoxytes acantherpestes – Enghoff 2005: 96. — Decker 2010: 28. — Nguyen & Sierwald 2013: 1240.

Material examined

Holotype

THAILAND: ♂, Western Coast of Siam Gulf (Gulf of Thailand), Hua Hin [Prachuap Khiri Khan Province, Hua Hin District], 8 Aug. 1979, B. Petersen leg. (ZMUC).

Other material

THAILAND: 2 ♂♂, 1 ♂ – gonopods lost, 1 ♀, Prachuap Khiri Khan Province, Kui Buri District, Hat Kham Subdistrict, Ban Yan Sue, 12°03'12"N, 99°37'52"E, ca. 147 m a.s.l., 31 Aug. 2007, ASRU members leg. (CUMZ).

Diagnosis

Metaterga 4–19 with one row of 2+2 posterior spines (anterior row absent). Similar in this respect to *N. gracilis* sp. nov. but differs from this species by having paraterga shorter; degree of elevation of paraterga lower; sternal lobe between male coxae 4 subtrapeziform; lamina lateralis (ll) swollen, stout, short.

Redescription

SIZE. Length 32–34 mm (male), 36 mm (female); width of midbody metazona ca. 2.2 mm (male), 3.0 mm (female). Width of head < body rings 2 = 3 < collum < 4 < 5–16, thereafter body gradually tapering towards telson.

COLOUR. Specimens in life brown. Colour in alcohol: after 29 years changed to pale brown; head, antennae, collum, metaterga, surface below paraterga, sterna, epiproct pale brown; paraterga brownish white.

COLLUM (Fig. 5.7A). With setae in anterior row and intermediate row, spines in posterior row; paraterga of collum elevated at ca. 35–40°, directed caudolaterad, with two conspicuous notches at lateral margin.

ANTENNAE (Fig. 5.7D). Moderately long and slender, reaching to body ring 5 or 6 (male) and 5 (female) when stretched dorsally.

TEGUMENT. Quite dull. Stricture between prozona and metazona shallow, wide.

METATERGA (Fig. 5.7A–C). With one or two transverse rows of setae and spines; metatergum 2 with ?1+?1 anterior setae (inconspicuous) and 2+2 posterior spines; metaterga 3–19 with 2+2 posterior spines (lateral spines very long).

PLEUROSTERNAL CARINAE. On body ring 2 long, crest-like; on body ring 3 a small ridge; thereafter missing.

PARATERGA (Figs 5.7F–G, 5.8B). Directed caudolaterad on body rings 2–18, elevated at ca. 60° (male) 50°–60° (female), directed increasingly caudad on body ring 19.

TELSON (Fig. 5.8C–G). Epiproct quite short; tip usually subtruncate (in some specimens slightly emarginate); lateral setiferous tubercles conspicuous, long, digitiform; apical tubercles conspicuous. Hypoproct subtriangular; caudal margin subtriangular, with inconspicuous setiferous tubercles.

STERNA (Fig. 5.8H–J). Cross-impressions quite deep. Sternal lobe between male coxae 4 swollen, subtrapeziform when seen in caudal view; base broad; tip slightly or deeply emarginate.

GONOPODS (Figs 5.9, 5.10). Coxa (cx) subequal in length to femur. Cannula (ca) long and slender. Telopodite quite long and slender. Prefemoral part (pfe) ca. 2/3 as long as femur. Femur (fe) quite long and slender. Mesal sulcus (ms) conspicuous, deep, wide; lateral sulcus (ls) conspicuous, very deep. Postfemoral part (pof) conspicuous, quite short. Solenophore (sph) well-developed: lamina lateralis (ll) swollen, stout, short, compact: lamina medialis (lm) very long; with a swollen base, gradually becoming thinner towards tip; apically fringed with several small spines; tip directed mesoventrad. Solenomere (sl) quite long, curved, tip directed ventrad.

Distribution and habitat

This species is known from two locations (Hua Hin and Ban Yan Sue) in Prachuap Khirikhan Province. We believe that the holotype was probably collected from limestone habitats because the type locality (near Hua Hin) lies in a limestone area. Specimens collected by us were from limestone habitats. It has been found crawling on rocks or on leaf litter.

This species is likely to be syntopic with *Desmoxytes planata* (Pocock, 1895) at Ban Yan Sue; however, we noticed that the habitats of these two species are clearly different. *N. acantherpestes* lives on the ground or on limestone rocks while *D. planata* was found on tree trunks near garbage.

Decker (2010) identified one male in NHMG, collected from Thanboke Khorani National Park, Krabi Province (8°23'12"N, 98°44'16"E) as *D. acantherpestes*. This specimen might perhaps be '*D.' gigas* Golovatch & Enghoff, 1994 (in the '*gigas*' group) because the location falls in the distribution range for this group in South Thailand whereas *Nagaxytes* (the '*acantherpestes*' group) is limited to western Thailand. Moreover, Thanboke Khorani National Park and Hua Hin are far apart, about 500 km.

The new species is distributed in a narrow area; we regard *N. acantherpestes* as endemic to Prachuap Khiri Khan Province, Thailand.

Remarks

In the original description, Golovatch and Enghoff (1994) did not comment on the live colouration of this species. We did not photograph living specimens, but our collector noticed brown colouration. Golovatch and Enghoff (1994) also described *D. acantherpestes* as lacking pleurosternal carinae, but after we re-examined the holotype and examined all newly collected specimens, we found the pleurosternal carinae as crest-like on ring 2, as small ridges on ring 3, thereafter absent. There is variation in the tip of the epiproct which in some specimens is subtruncate, in others slightly emarginate.

On some specimens we found parasitic mites, probably of the genus *Leptus* Latreille, 1795 (Fig. 5.6B). The mites infested the millipede on the metaterga. This association reminds us of what Srisonchai *et al.* (2018a) found in *Desmoxytes cervina* (Pocock, 1895): several engorged *Leptus* mites attached to the millipede body.

Nagaxytes erecta Srisonchai, Enghoff & Panha sp. nov.

(Figs 5.3, 5.11–5.16)

Material examined

Holotype

THAILAND: ♂, Kanchanaburi Province, Thong Pha Phum District, Phuphrai Thannam Resort, 14°44'0.6"N, 98°38'36"E, ca. 112 m a.s.l., 17 Aug. 2016, ASRU members leg. (CUMZ).

Paratypes

THAILAND: 52 ♂♂, 36 ♀♀, same data as holotype (CUMZ); 1 ♂, 1 ♀, same data as holotype (ZMUC); 1 ♂, 1 ♀, same data as holotype (ZMUM); 1 ♂, 1 ♀, same data as holotype (NHMW); 1 ♂, 1 ♀, same data as holotype (NHMUK).

Further specimens, not paratypes, all from THAILAND, Kanchanaburi Province

Thong Pha Phum District: 1 ♂ – gonopods lost, 4 ♀♀, Vajiralongkorn Dam, 28 Aug. 2011, ASRU members leg. (CUMZ); 2 ♂♂, 2 ♀♀, Ban Nong Bang (near Wat Pha Sukit Suwannaket), 14°34'31"N, 98°49'04"E, ca. 151 m a.s.l., 12 Oct. 2015, ASRU members leg. (CUMZ); 4 ♂♂, 3 ♀♀, Wat Pak Lam Pilock, 14°37'41"N, 98°34'26"E, ca. 257 m a.s.l., 11 Oct. 2015, ASRU members leg. (CUMZ); 1 ♂, 3 ♀♀, Wat Tha Kha-nun, 14°44'36"N, 98°38'18"E, ca. 114 m a.s.l., 24 Jul. 2016, P. Pimvichai, P. Prasankok and N. Nantarat leg. (CUMZ); 12 ♂♂, 21 ♀♀, Wat Tha Kha-nun, 14°44'36"N, 98°38'18"E, ca. 114 m a.s.l., 16 Aug. 2016, ASRU members leg. (CUMZ); 20 ♂♂, 46 ♀♀, Prang Ka Sri Temple (Wat Prang Ka Sri), 14°39'05"N, 98°40'08"E, ca. 106 m a.s.l., 15 Aug. 2016, leg. ASRU members (CUMZ).

Sai Yok District: 1 broken ♂ – gonopods lost, Daowadueng Cave, 14°28'23"N, 98°50'04"E, ca. 133 m a.s.l., 8 Sept. 2008, ASRU members leg. (CUMZ); 4 ♂♂, 5 broken ♂♂, 1 broken ♂ – right gonopod lost, 2 ♂♂ – left gonopod lost, 1 ♂ remaining rings 1–8, 10 ♀♀, 1 juvenile, Daowadueng Cave, 14°28'23"N, 98°50'04"E, ca. 133 m a.s.l., 11 Jul. 2009, ASRU members leg. (CUMZ); 5 ♂♂, 4 ♀♀, Daowadueng Cave, 14°28'23"N, 98°50'04"E, ca. 133 m a.s.l., 12 Oct. 2015, ASRU members leg. (CUMZ); 6 ♂♂, 2 ♀♀, Daowadueng Cave, 14°28'23"N, 98°50'04"E, ca. 133 m a.s.l., 15 Aug. 2016, ASRU members leg. (CUMZ); 6 ♂♂, 2 ♀♀, Wat Sunantha Wanaram, 14°32'11"N, 98°49'51"E, ca. 161 m a.s.l., 17 Aug. 2016, ASRU members leg. (CUMZ).

Etymology

The name is a Latin adjective and refers to the erect lamina lateralis (ll) of the gonopod telopodite.

Diagnosis

Metaterga 2–8 with two rows of spines (1+1 or 2+2 spines in anterior row, 2+2 spines in posterior row). Similar in this respect to *N. spatula* sp. nov. but differs by having: degree of elevation of paraterga lower; apical tubercles of epiproct conspicuous; surface near lateral sulcus (ls) without ridge (not swollen); lamina lateralis (ll) erect, long, thick, digitiform, tip round and directed anteriad; lamina medialis (lm) very long, apically fringed.

Description

SIZE. Length 32–36 mm (male), 36–38 mm (female); width of midbody metazona ca. 2.4 mm (male), 3.4 mm (female). Width of head < collum < body rings 2 = 3 < 4 < 5–17, thereafter body gradually tapering towards telson.

COLOUR (Figs 5.11, 5.12A–C). Specimens in life falling into two colour morphs: Reddish brown morph – body reddish brown; paraterga pinkish red; collum, metaterga and epiproct reddish brown; head, antennae (except whitish distal part of antennomere 7 and antennomere 8), prozona, surface below paraterga, sterna and legs brown; a few basal podomeres whitish brown. Brown morph – body brown; paraterga pinkish red; head, antennae (except whitish distal part of antennomere 7 and antennomere 8), collum, prozona, metaterga, epiproct and legs brown; paraterga and sterna pale brown; surface below paraterga brown or dark brown; a few basal podomeres whitish brown. Colour in alcohol: after 3–10 years changed to pale brown; head, antennae, collum, metaterga, surface below paraterga, sterna, epiproct, legs pale brown or whitish brown; paraterga brownish white.

COLLUM (Fig. 5.13A). With three transverse rows of setiferous tubercles and spines, 3+3 tubercles in anterior row, 1+1 tubercles in intermediate row and 2+2 spines in posterior row; paraterga of collum long and broad, elevated at ca. 40°–45° (male) 35°–40° (female), directed caudolaterad, with two conspicuous notches at lateral margin.

ANTENNAE (Fig. 5.13D). Moderately long and slender, reaching to body ring 5 or 6 (male) and 4 or 5 (female) when stretched dorsally.

TEGUMENT. Quite dull. Stricture between prozona and metazona shallow, wide.

METATERGA (Fig. 5.13A–C). With two transverse rows of cones and spines; metaterga 2–15 with 2+2 anterior spines and 2+2 posterior spines (posterior spines longer and thicker than anterior ones; lateral spines of posterior row very long); metaterga 16–18 with 2+2 anterior cones/spines and 2+2 posterior cones/spines (brown morph – anterior cones/spines inconspicuous; lateral spines of posterior row very long); metatergum 19 with 1+1 anterior small tubercles/cones and 2+2 posterior spines (brown morph – anterior tubercles/cones poorly developed).

PLEUROSTERNAL CARINAE. On body ring 2 long, crest-like; on ring 3 long ridges; on ring 4 small ridges; thereafter missing.

PARATERGA (Figs 5.13F–G, 5.14B). Directed caudolaterad on body rings 2–17, elevated at ca. 60°–70° (male) 50°–60° (female), directed increasingly caudad on body ring 18–19.

TELSON (Fig. 5.14C–G). Epiproct quite short; tip usually subtruncate (in some specimens slightly emarginate); lateral setiferous tubercles conspicuous, long, digitiform; apical tubercles conspicuous. Hypoproct usually subtriangular (in some specimens subtrapeziform); caudal margin subtriangular or round, with conspicuous setiferous tubercles.

STERNA (Fig. 5.14H–J). Cross-impressions quite deep. Sternal lobe between male coxae 4 subtrapeziform, stout; base broad; tip emarginate.

GONOPODS (Figs 5.15, 5.16). Coxa (cx) subequal in length to femur. Cannula (ca) long and slender. Telopodite quite long and slender. Prefemoral part (pfe) ca. half as long as femur. Femur (fe) quite long and slender, slightly enlarged distad. Mesal sulcus (ms) conspicuous, deep, wide; lateral sulcus (ls) quite deep and wide. Postfemoral part (pof) conspicuous, short. Solenophore (sph) well-developed: lamina lateralis (ll) erect, long, thick, digitiform; tip round, directed anteriad: lamina medialis (lm) very long; apically fringed with several small spines; tip directed mesad. Solenomere (sl) long and slender, tip directed anterolateriad.

Distribution and habitat

N. erecta sp. nov. is known only from Kanchanaburi province, Thailand. All specimens were collected from limestone habitats during the rainy season (July–October). Lots of specimens were usually found near human areas, where some habitats are being destroyed for construction of a temple or bureau of monks.

At Daowadueng Cave, the new species lives syntopically with *N. gracilis* sp. nov. and *Desmoxytes purpurosea* Enghoff *et al.*, 2007, in the same habitat. *D. planata* was also found near the habitat of the new species at Phuphrai Thannam Resort and Wat Tha Kha-nun. We assume that *D. planata* occurs in a different microhabitat because the areas where we collected *D. planata* are very strongly influenced by humans, and all specimens were seen crawling on statues and concrete.

We have only found *N. erecta* sp. nov. in a narrow area (100 km^2) along the huge limestone mountain range in Sai Yok and Thong Pha Phum districts. Therefore, we regard this species as endemic for the Thai fauna.

Remarks

There is considerable variation in live colouration; two colour morphs can be distinguished – brownish red and brown. All specimens from Ban Nong Bang (near Wat Pha Sukit Suwannaket) show brownish red colour whereas specimens from the remaining localities exhibit brown colour (except at Daowadueng Cave: both reddish brown and brown colour morphs occur in the same place, even the same habitat). A further morphological difference between these two colour morphs concerns the size of cones/spines (anterior row) on metaterga 16–19: conspicuous in the reddish brown colour morph, inconspicuous in the brown morph. However, the gonopod characters are virtually identical. A similar phenomenon is also found in *Desmoxytes cervina* in which two colour morphs share identical gonopod characters (Srisonchai *et al.*, 2018a). Therefore, we regard the differences in colour as interpopulational variation. Intrapopulational variation was also found:

- tip of epiproct: in some specimens subtruncate, in others slightly emarginate.
- shape of hypoproct: in some individuals subtriangular, in others subtrapeziform.

Some specimens of this species are infested by engorged mites (possibly of the genus *Leptus*) (Fig. 5.12C), as also found in *D. cervina* by Srisonchai *et al.* (2018a) and *N. acantherpestes* as mentioned above.

Nagaxytes gracilis Srisonchai, Enghoff & Panha sp. nov.

(Figs 5.4, 5.5, 5.17–5.21)

Material examined

Holotype

THAILAND: ♂, Kanchanaburi Province, Sai Yok District, Daowadueng Cave, 14°28'23"N, 98°50'04"E, ca. 133 m a.s.l., 15 Aug. 2016, ASRU members leg. (CUMZ).

Paratypes

THAILAND: 7 ♂♂, 21 ♀♀, same data as holotype (CUMZ); 1 ♂, 1 ♀, same data as holotype (ZMUC).

Further specimens, not paratypes, all from THAILAND, Kanchanaburi Province, Sai Yok District

1 ♂, 1 broken ♂, 1 broken ♂ – right gonopod lost, 5 ♀♀, Daowadueng Cave, 14°28'23"N, 98°50'04"E, ca. 133 m a.s.l., 8 Sept. 2008, ASRU members leg. (CUMZ); 2 ♂♂, 6 ♀♀, Daowadueng Cave, 14°28'23"N, 98°50'04"E, ca. 133 m a.s.l., 11 Jul. 2009, ASRU members leg. (CUMZ); 2 ♂♂, Daowadueng Cave, 14°28'23"N, 98°50'4"E, ca. 133 m a.s.l., 12 Oct. 2015, ASRU members leg. (CUMZ); 8 ♂♂, 21 ♀♀, 1 broken ♂, 1 ♂ – right gonopod lost, 1 ♂ fragment – gonopods lost, Wat Tham Phrom Lok Khao Yai, 14°12'15"N, 99°07'57"E, ca. 122 m a.s.l., 9 Jul. 2009, ASRU members leg. (CUMZ); 1 ♂, Wat Tham Phrom Lok Khao Yai, 14°12'15"N, 99°07'57"E, ca. 122 m a.s.l., 15 Aug. 2016, ASRU members leg. (CUMZ); 1 ♂, Kra Sae Cave, 14°06'05"N, 99°10'09"E, ca. 79 m a.s.l., 10 Dec. 2006, ASRU members leg. (CUMZ); 3 ♂♂, 3 broken ♂♂, 1 ♂ – right gonopod lost, 5 ♀♀, Hellfire Pass, 14°21'20"N, 98°57'09"E, ca. 216 m a.s.l., 29 Aug. 2011, ASRU members leg. (CUMZ); 2 ♂♂, 2 ♀♀, Hellfire Pass, 14°21'20"N, 98°57'09"E, ca. 216 m a.s.l., Aug. 2014, ASRU members leg. (CUMZ); 1 ♂, 1 ♀, Ban Thung Kang Yang, 14°24'17"N, 98°55'04"E, ca. 263 m a.s.l., 15 Aug. 2016, ASRU members leg. (CUMZ); 4 ♂♂, 5 ♀♀, Wat Sunantha Wanaram, 14°32'11"N, 98°49'51"E, ca. 161 m a.s.l., 17 Aug. 2016, ASRU members leg. (CUMZ); 7 ♂♂, 6 ♀♀, Wat Phuttha Vimooddhi Wanaram (Wat Tham Phu Mood), 14°18'07"N, 98°59'27"E, ca. 213 m a.s.l., 17 Aug. 2016, ASRU members leg. (CUMZ).

Etymology

The name is a Latin adjective, referring to the slender lamina lateralis (ll) of the gonopod telopodite.

Diagnosis

Metaterga 4–19 with one row of 2+2 posterior spines (anterior row absent). Similar in this respect to *N. acantherpestes* but differs from this species by having paraterga longer; degree of elevation of paraterga higher; sternal lobe between male coxae 4 incompletely bilobed; lamina lateralis (ll) long, lamella-like, thin, slender, tip round and directed ventrad.

Description

SIZE. Length 30–33 mm (male), 35–38 mm (female); width of midbody metazona ca. 2.2 mm (male), 3.1 mm (female). Width of head < collum < body rings 2 = 3 = 4 < 5–17, thereafter body gradually tapering towards telson.

COLOUR (Fig. 5.17A–B). Specimens in life with body pinkish brown; paraterga vivid pink or reddish pink; collum, prozona, metaterga, surface below paraterga pinkish brown; head, antennae (except whitish distal part of antennomere 7 and antennomere 8) sterna and legs brown; a few basal podomeres whitish brown; epiproct pink. Colour in alcohol: after 3–9 years changed to pale brown; head, collum, metaterga, surface below paraterga, sterna, epiproct pale brown or whitish brown; paraterga brownish white.

COLLUM (Fig. 5.18A). With three transverse rows of setae/tubercles and spines, 3+3 setae/tubercles in anterior row, 1+1 setae/tubercles in intermediate row (tubercles small) and 2+2 spines in posterior row; paraterga of collum long and broad, elevated at ca. 40°–45° (male) 35°–40° (female), directed caudolaterad, with 2 conspicuous notches at lateral margin.

ANTENNAE (Fig. 5.18D). Moderately long and slender, reaching to body ring 5 or 6 (male) and 4 or 5 (female) when stretched dorsally.

TEGUMENT. Quite shining. Stricture between prozona and metazona shallow, wide.

METATERGA (Fig. 5.18A–C). Metatergum 2 with 1(2)+1(2) anterior tubercles/cones and 2+2 posterior spines; metatergum 3 with 1+1 anterior tubercles (inconspicuous) and 2+2 posterior spines; metaterga 4–19 with 2+2 posterior spines (anterior row absent; lateral spines of posterior row in all rings very long, longer than mesal ones).

PLEUROSTERNAL CARINAE. On body ring 2 long, crest-like; on body rings 3 and 4 small ridges; thereafter missing.

PARATERGA (Figs 5.18F–G, 5.19B). Directed caudolaterad on body rings 2–18, elevated at ca. 70° (male) 60°–70° (female), directed increasingly caudad on body ring

19; notch near the tip at lateral margin of body rings 5–7, 9, 10, 12, 13, 15–18 absent on some rings in some specimens.

TELSON (Fig. 5.19C–G). Epiproct quite short; tip usually subtruncate (in some specimens slightly emarginate); lateral setiferous tubercles conspicuous, long, digitiform; apical tubercles conspicuous. Hypoproct subtriangular; caudal margin subtriangular, with inconspicuous setiferous tubercles.

STERNA (Fig. 5.19H–J). Cross-impressions quite deep. Sternal lobe between male coxae 4 incompletely bilobed; base broad; tip deeply emarginate; surface near pores swollen.

GONOPODS (Figs 5.4, 5.5, 5.20, 5.21). Coxa (cx) subequal in length to femur. Cannula (ca) long and slender. Telopodite quite long and slender. Prefemoral part (pfe) ca. half as long as femur. Femur (fe) long and slender, slightly enlarged distally. Mesal sulcus (ms) conspicuous, deep, wide; lateral sulcus (ls) quite deep and very wide. Postfemoral part (pof) conspicuous, short. Solenophore (sph) well-developed: lamina lateralis (ll) long, lamella-like, thin, slender; tip round, directed ventrad: lamina medialis (lm) very long; slightly enlarged distally; apically fringed with several small spines; tip directed mesoventrad. Solenomere (sl) long and slender, tip directed ventrad.

Distribution and habitat

N. gracilis sp. nov. is known only from Sai Yok district, Kanchanaburi province. All specimens were collected on humid rocks, superficial tree roots and litter in limestone habitats. It lives in the same habitat with *D. purpurosea*, *D. golovatchi* Srisonchai, Enghoff & Panha, 2018 and *N. erecta* sp. nov. (q.v.). The new species occurs in a narrow distribution area along the huge limestone range which is entirely contained within Sai Yok district. We thus consider this species to be endemic to Kanchanaburi province, Thailand.

Remarks

The vivid pink paraterga are probably aposematic. *N. gracilis* sp. nov. was noticeable in the field by the contrast of its bright pink colour to brown rocks.

There is variability in the tip of epiproct: in some specimens subtruncate, in others slightly emarginate.

Nagaxytes spatula Srisonchai, Enghoff & Panha gen. et sp. nov.
(Figs 5.22–5.26)

Material examined

Holotype

THAILAND: ♂, Tak Province, Mae Sot District, Chao Por Phawo Shrine, 16°46'19"N, 98°41'11"E, ca. 688 m a.s.l., 29 Aug. 2016, ASRU members leg. (CUMZ).

Paratypes

THAILAND: 27 ♂♂, 19 ♀♀, same data as holotype (CUMZ); 1 ♂, 1 ♀, same data as holotype (ZMUC); 1 ♂, 1 ♀, same data as holotype (ZMUM); 1 ♂, 1 ♀, same data as holotype (NHMW); 1 ♂, 1 ♀, same data as holotype (NHMUK).

Further specimens, not paratypes, all from THAILAND, Tak Province

Mae Sot District: 1 ♀, Chao Por Phawo Shrine, 16°46'19"N, 98°41'11"E, ca. 688 m a.s.l., 29 Jun. 2015, ASRU members leg. (CUMZ); 1 ♂, 1 ♀, Wat Tham Inthanin, 16°45'59"N, 98°40'21"E, 671 m a.s.l., 18 Oct. 2015, ASRU members leg. (CUMZ); 10 broken specimens, Wat Pho Thi Khun (Wat Huai Toey), 16°45'42"N, 98°38'49"E, ca. 431 m a.s.l., 27 Jul. 2016, leg. P. Pimvichai, P. Prasankok and N. Nantarat leg. (CUMZ); 3 ♂♂, 6 ♀♀, Wat Pho Thi Khun (Wat Huai Toey), 16°45'42"N, 98°38'49"E, ca. 431 m a.s.l., 29 Aug. 2016, ASRU members leg. (CUMZ).

Umphang District: 1 ♂, 1 ♂ – left gonopod lost, 4 ♀♀, Tham Takhobi (Takhobi Cave), 16°03'15"N, 98°49'14"E, ca. 510 m a.s.l., 5 Jul. 2009, ASRU members leg. (CUMZ); 1 ♂, 1 ♀, Tham Takhobi (Takhobi Cave), 16°03'15"N, 98°49'14"E, ca. 510 m a.s.l., 1 Jul. 2015, ASRU members leg. (CUMZ); 4 ♂♂, 6 ♀♀, many broken specimens, Doi Hua Mod, 15°57'30"N, 98°51'13"E, ca. 894 m a.s.l., 5 Jul. 2009, ASRU members leg. (CUMZ); 1 ♂, 1 ♀, 1 juvenile, Doi Hua Mod, 15°57'30"N, 98°51'13"E, ca. 894 m a.s.l., 1 Jul. 2015, ASRU members leg. (CUMZ).

Etymology

The name is a Latin noun in apposition, referring to the spatulate lobe on lamina lateralis (ll).

Diagnosis

Metaterga 2–8 with two rows of spines (1+1 or 2+2 spines in anterior row, 2+2 spines in posterior row). Similar in this respect to *N. erecta* sp. nov. but differs by having: degree of elevation of paraterga higher; apical tubercles of epiproct inconspicuous; surface near lateral sulcus (ls) swollen as long ridge; lamina lateralis (ll) broad, with a long and conspicuous spatula-like lobe; lamina medialis (lm) very long, curved, apically hook-like; tip of solenomere (sl) terminating in two curved processes.

Description

SIZE. Length 22–26 mm (male), 24–28 mm (female); width of midbody metazona ca. 2.0 mm (male), 2.8 mm (female). Width of head < collum = body rings 2 = 3 = 4 < 5–17, thereafter body gradually tapering towards telson.

COLOUR (Fig. 5.22A–C). Specimens in life with body usually reddish brown (some specimens brown); prozona, metaterga, surface below paraterga and sterna reddish brown; antennae brown to dark brown (except whitish distal part of antennomere 7 and antennomere 8); head, paraterga, epiproct and leg brown; a few basal podomeres pale brown. Colour in alcohol: after 3–10 years changed to pale brown; head, antennae, collum, metaterga, surface below paraterga, sterna, epiproct, legs pale brown or whitish brown; paraterga brownish white.

COLLUM (Fig. 5.23A). With three transverse rows of setiferous tubercles and spines, 3+3 tubercles in anterior row, 1+1 tubercles in intermediate row and 2+2 spines in posterior row; paraterga of collum long and broad, elevated at ca. 25°–35° (male)

20°–30° (female), directed caudolaterad, with two conspicuous notches at lateral margin.

ANTENNAE (Fig. 5.23D). Very long and slender, reaching to body ring 6 or 7 (male) and 5 or 6 (female) when stretched dorsally.

TEGUMENT. Quite dull. Stricture between prozona and metazona quite deep, wide.

METATERGA (Fig. 5.23A–C). Male – metaterga 2–8 with 2(1)+2(1) anterior spines and 2+2 posterior spines (anterior spines small and sometimes inconspicuous; posterior spines longer and larger than anterior ones; lateral spines of posterior row very long); metaterga 9–19 with ?1+?1 anterior small tubercles and 2+2 posterior spines (lateral spines of posterior row very long). Female – metaterga 2–10 with 2+2 anterior spines and 2+2 posterior spines (posterior spines longer and larger than anterior ones; lateral spines of posterior row very long); metaterga 11–18 with 1+1 anterior spines and 2+2 posterior spines (lateral spines of posterior row very long); metatergum 19 with ?1+?1 anterior small tubercles and 2+2 posterior spines.

PLEUROSTERNAL CARINAE. On body ring 2 long, crest-like; on ring 3 long ridge; on ring 4 small ridge; thereafter missing.

PARATERGA (Figs 5.23F–G, 5.24B). Directed caudolaterad on body rings 2–18, elevated at ca. 50°–60° (male) 45°–50° (female), directed increasingly caudad on body ring 19.

TELSON (Fig. 5.24C–G). Epiproct quite short; tip subtruncate; lateral setiferous tubercles conspicuous, long, digitiform; apical tubercles inconspicuous. Hypoproct subtriangular, short and broad; caudal margin round, with conspicuous setiferous tubercles.

STERNA (Fig. 5.24H–J). Cross-impressions shallow. Sternal lobe between male coxae 4 stout; base broad; tip deeply emarginate to incompletely bilobed.

GONOPODS (Figs 5.25, 5.26). Coxa (cx) shorter than femur. Cannula (ca) quite short and stout. Telopodite quite short and stout. Prefemoral part (pfe) subequal in length to femur. Femur (fe) quite stout, slightly enlarged distad. Mesal sulcus (ms) conspicuous, deep, wide; lateral sulcus (ls) quite shallow and wide, surface near lateral sulcus swollen as long ridge. Postfemoral part (pof) conspicuous, wide, laterally demarcated from femur by a long ridge. Solenophore (sph) well-developed: lamina lateralis (ll) broad; with a long, flattened, conspicuous spatulate lobe, apically round, directed anteriad (Figs 5.25D, 5.26C); lamina medialis (lm) very long; curved; apically hook-like. Solenomere (sl) long, tip terminating in two curved processes.

Distribution and habitat

Known only from Tak province. Almost all specimens were seen crawling on rocks, some on leaf litter in limestone habitats. Some juveniles were collected from the leaf litter (probably in moulting chambers). In the field, the specimens blended perfectly with brown rocks and leaf litter.

The type locality for this species is situated beside road no. 12 (Tak – Mae Sot) near Khun Phawo National Park. We noticed that the forest beside the road is being destroyed for road construction, some parts of the limestone forest are being cut down.

For the time being, only five recorded locations are reported in the quite narrow distribution range of this species. Several intensive surveys allow us to consider *N. spatula* gen. et sp. nov. to be endemic to Tak Province, Thailand.

Remarks

We divide this species into two main populations, each restricted to a separate limestone areas:

- North populations: Chao Por Phawo Shrine, Wat Tham Inthanin and Wat Pho Thi Khun (Wat Huai Toey).

- South populations: Tham Takhobi (Takhobi Cave) and Doi Hua Mod.

Specimens of the North populations (24–26 mm in male, 26–28 mm in female) seem to be longer than those of the South populations (22–24 mm in male, 24–25 mm in female). However, other morphological characteristics, especially gonopod characters, are identical.

Discussion

On the basis of our morphological study and a preliminary DNA sequence analysis (work in progress), the '*acantherpestes*' group as defined by Srisonchai *et al.* (2018a) is here described as a new genus which includes '*Desmoxytes*' *acantherpestes* and three new species. The new genus *Nagaxytes* is well-characterized by having subspiniform paraterga, unmodified male femora, as well as a curved and long lamina medialis (lm). Each of the four species can be easily distinguished from its congeners by distinctive gonopod characters, especially the shape of the lamina lateralis (ll) in combination with other morphological characters.

Nagaxytes erecta gen. et sp. nov. includes two colour morphs: brownish red and brown. Moreover, the size of tubercles/cones/spines (anterior row) on metaterga 16–19 also differs between the two colour morphs: anterior row of tubercles/cones/spines conspicuous in the brownish red morph, inconspicuous in the brown morph. However, other morphological characters are clearly identical, especially gonopod characters: lamina lateralis (ll) long, thick, digitiform (Figs 5.14, 5.17). Interestingly, the two morphs mainly occur allopatrically, although at Daowadueng Cave and Wat Sunantha Wanaram, they were found syntopically in the same habitat. This case is similar to that of *Desmoxytes cervina*: similarity in several morphological characters, but differences in colour between two allopatric and/or sympatric populations (Srisonchai *et al.*, 2018a). We hope that our molecular phylogeny work combined with morphological studies will shed more light on relationships within populations, within species, within the genus *Nagaxytes*, as well as among its closely related genera.

Nagaxytes erecta sp. nov. has been found in partial sympatry with *N. gracilis* sp. nov. at Daowadueng Cave and Wat Sunantha Wanaram in Kanchanaburi province. Both species show a similar pattern of gonopod shape and share a long lamina lateralis (ll) (e.g., Figs 5.15D, 5.21D), yet they are not identical. The differences in shape of the sternal lobe between male coxae 4 and the pattern of row of spines on metaterga support regarding them as different taxa. Although *N. erecta* gen. et sp. nov. and *N. gracilis* gen. et sp. nov. have been found to be syntopic, even collected from the same habitat, the detail of their microhabitats have not yet been observed and they may not co-occur in a strict sense.

During the field surveys, we found associations of mites with two *Nagaxytes* species, *N. acantherpestes* and *N. erecta* gen. et sp. nov. The mites probably belong to the genus *Leptus* Latreille, 1796 (Southcott, 1992). As in the association between parasitic mites and millipedes of the genus *Desmoxytes* reported by Srisonchai *et al.* (2018a), it seems likely that the mites use their hosts for nourishment and dispersal purposes, as in other mite-millipede associations (Kethley, 1978; Swafford and Bond, 2010).

The new species described here are further examples of the peculiar dragon millipedes. Their long subspiniform paraterga may provide protection against predators and possibly enhance the spreading of their defense fluid (Liu *et al.*, 2017; Shear, 2015). In addition, one of the new species, *N. gracilis* gen. et sp. nov., is spectacularly aposematic, like several dragon millipedes in the genus *Desmoxytes* (Enghoff *et al.*, 2007; Srisonchai *et al.*, 2018a).

Based on our surveys and observations, all species of *Nagaxytes* have narrow distribution ranges within limestone habitats (Fig. 5.27). Therefore, we regard all *Nagaxytes* species as endemic to the Thai fauna. We would not be surprised if so far unsurveyed limestone areas will yield more new species of this peculiar genus.

Correction to Srisonchai *et al.* (2018)

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 males, 2 females (CUMZ), same data as holotype.

Acknowledgements

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Figure 5.1 *Nagaxytes gracilis* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂, paratype (CUMZ-pxDGT00095). Watercolour by R. Srisonchai and P. Kriatpraprai.

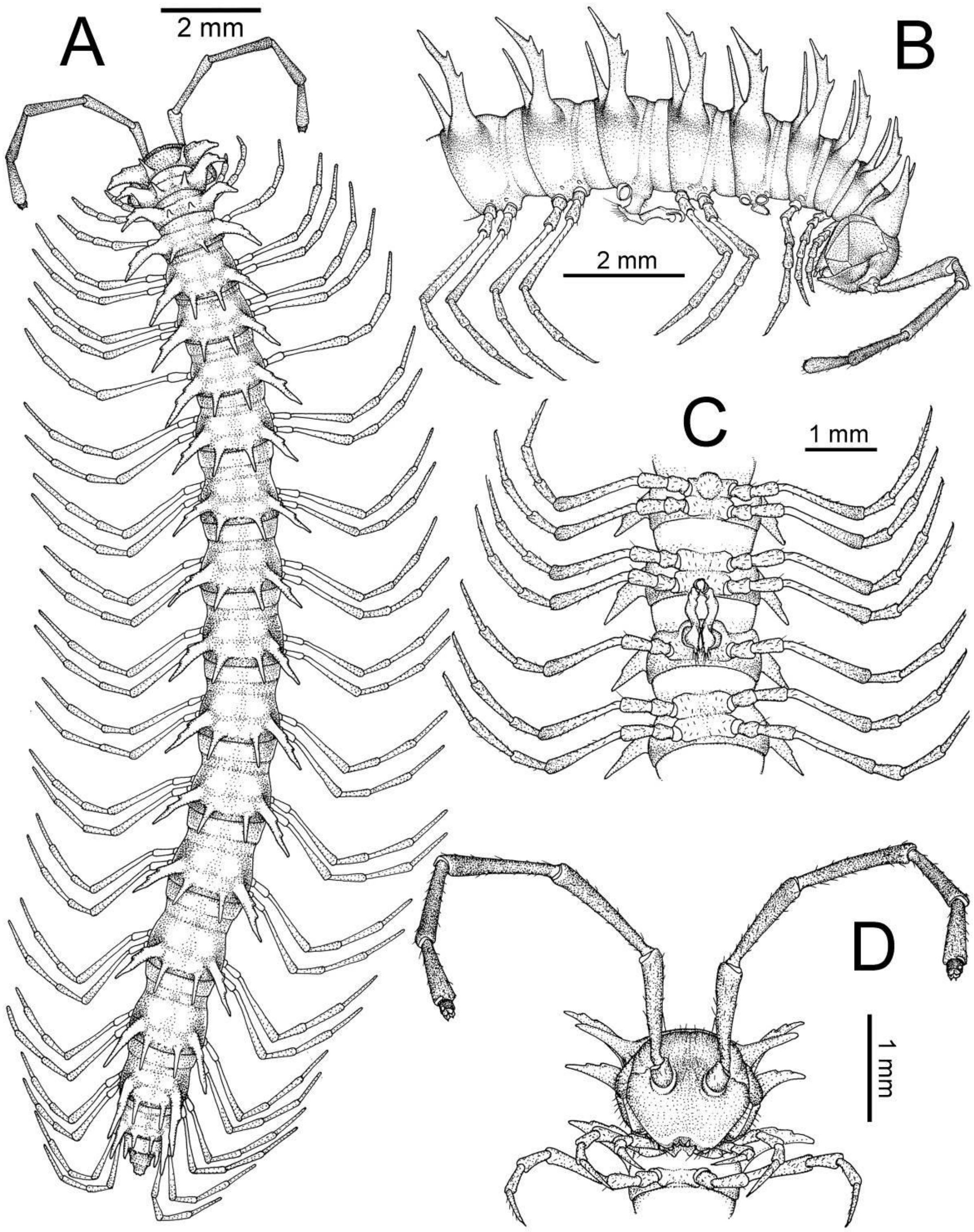

Figure 5.2 General body characters of *Nagaxytes* gen. nov. – *N. acantherpestes* (Golovatch & Enghoff, 1994) gen. et comb. nov., ♂, holotype, Prachuap Khiri Khan Province, Hua Hin District (ZMUC000101457). **A**. Entire body. **B**. Anterior body part. **C**. Body rings 5–8, showing sternal lobe between coxae 4 and gonopods on ring 7. **D**. Head and antennae.

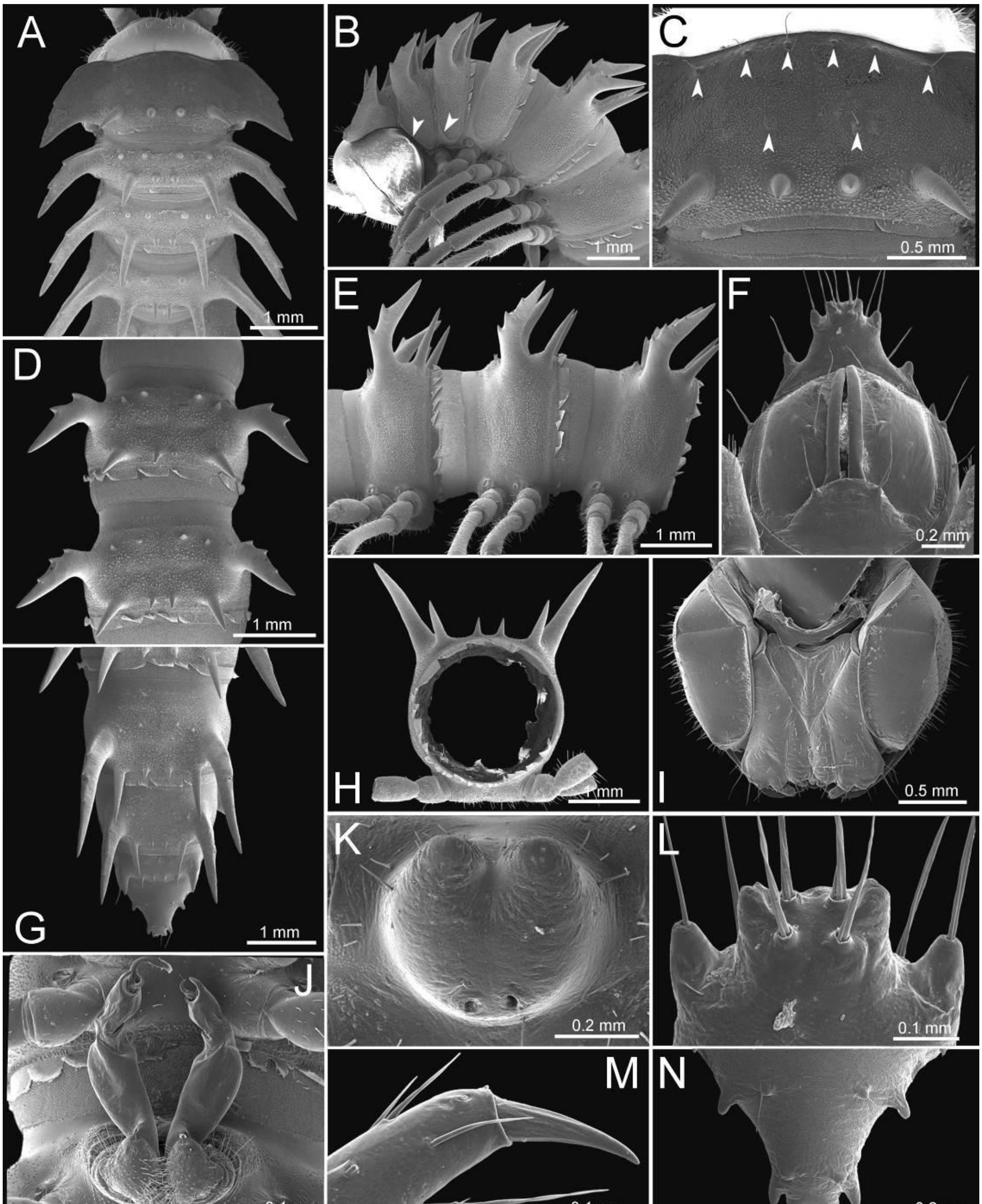

Figure 5.3 General body characters of *Nagaxytes* gen. nov. (*N. erecta* Srisonchai, Enghoff & Panha gen. et sp. nov., specimen from Prang Ka Sri Temple, Thailand), SEM images. **A–B**. Anterior body part (arrowheads point to pleurosternal carinae). **C**. Collum (arrowheads point to the setae/tubercles of the anterior and intermediate rows). **D**. Body rings 9–10. **E**. Body rings 8–10. **F**. Telson. **G**. Posteriormost rings and telson. **H**. Body ring 10. **I**. Mouth parts, ventral view. **J**. Gonopods in situ. **K**. Sternal lobe between male coxae 4. **L, N**. Tip of epiproct. **M**. Tarsus and claw of leg 13.

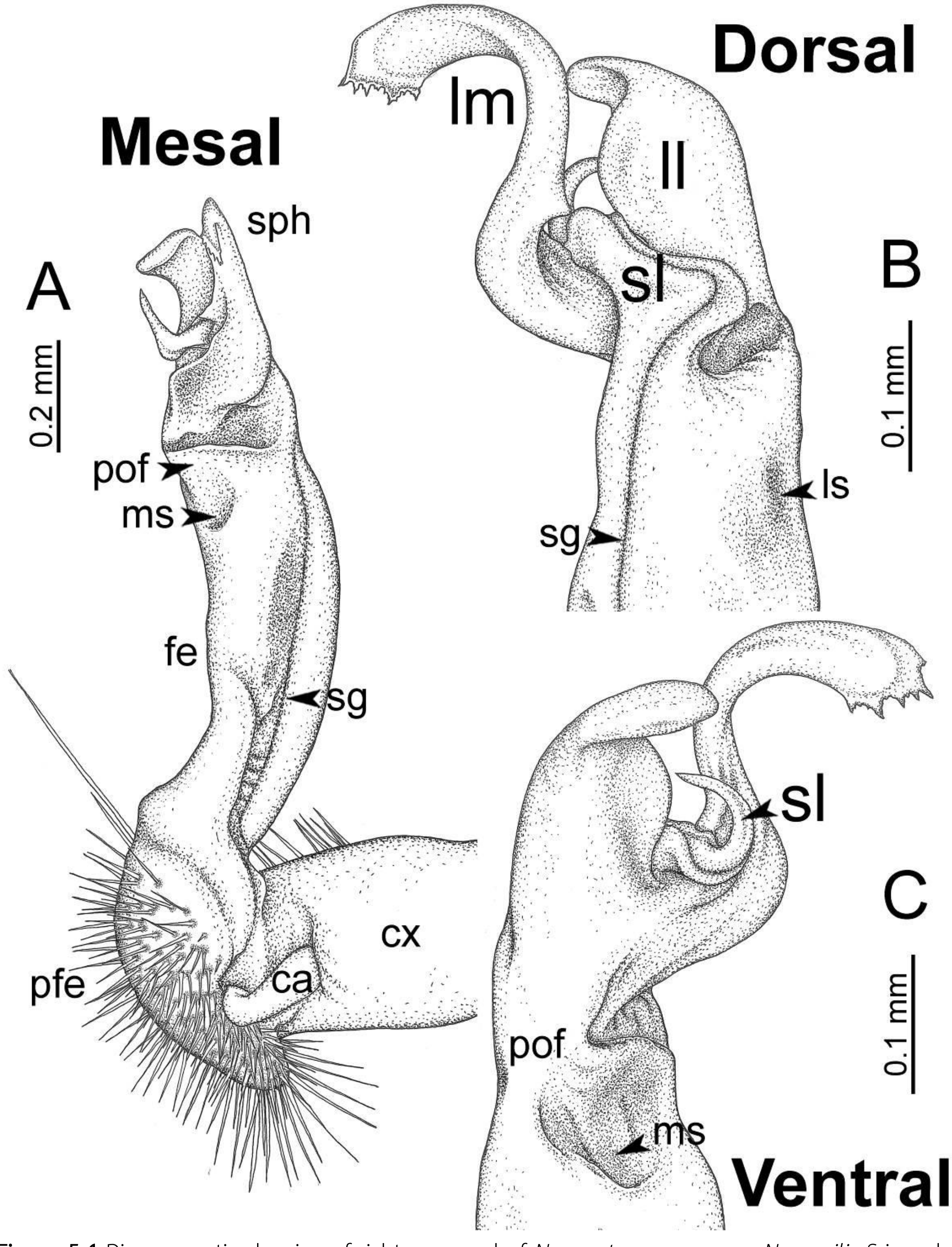

Figure 5.4 Diagrammatic drawing of right gonopod of *Nagaxytes* gen. nov. – *N. gracilis* Srisonchai, Enghoff & Panha gen. et sp. nov., specimen from Wat Vimooddhi Wanaram, Thailand. **A**. Mesal view. **B**. Dorsalview. **C**. Ventral view.

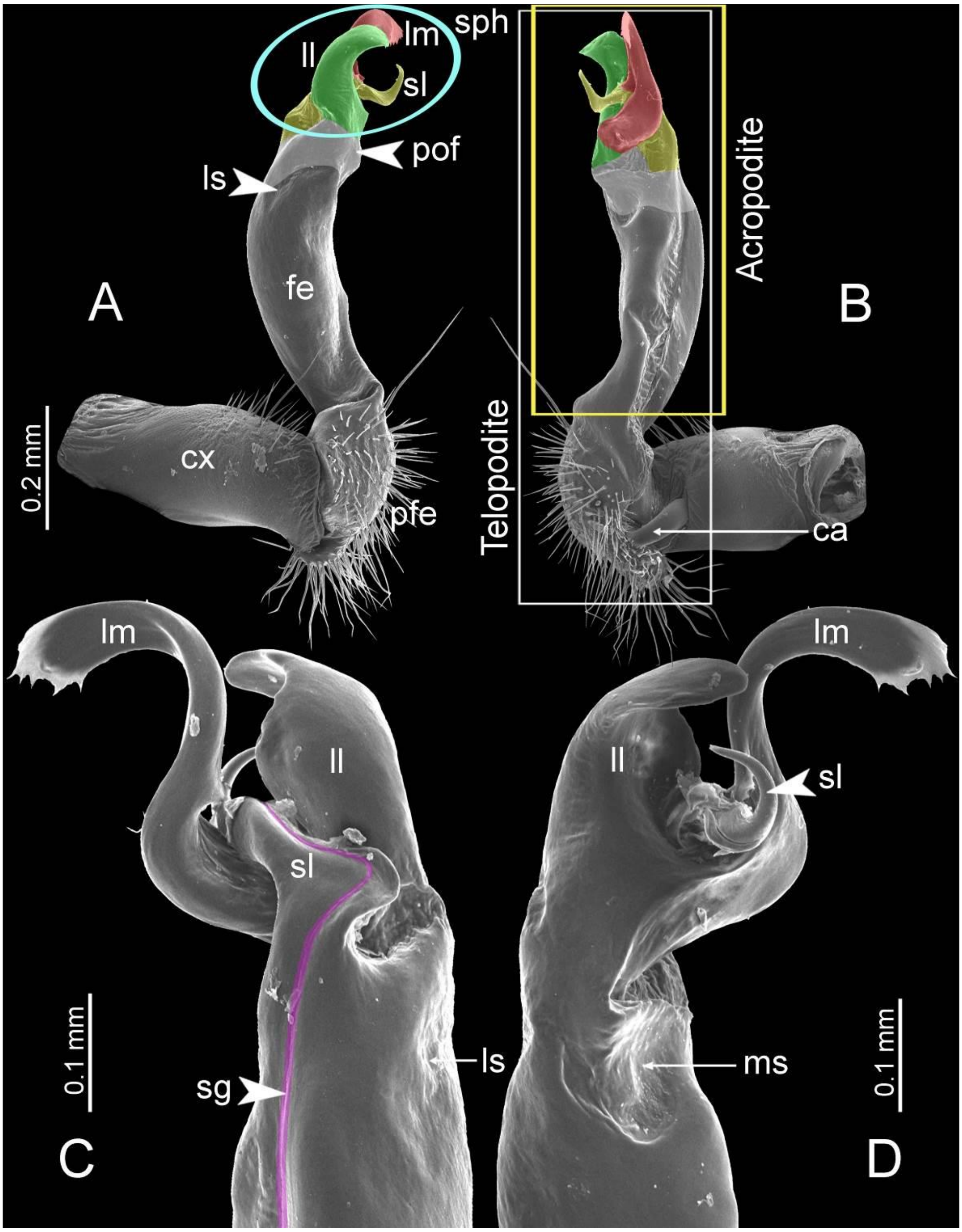

Figure 5.5 SEM images of right gonopod of *Nagaxytes* gen. nov. – *N. gracilis* gen. et sp. nov., specimen from Wat Vimooddhi Wanaram, Thailand. **A**. Lateral view. **B**. Mesal view. **C**. Dorsal view. **D**. Ventral view. Colours: red = lamina medialis (lm), green = lamina lateralis (ll), yellow = solenomere (sl), purple = seminal groove (sg).

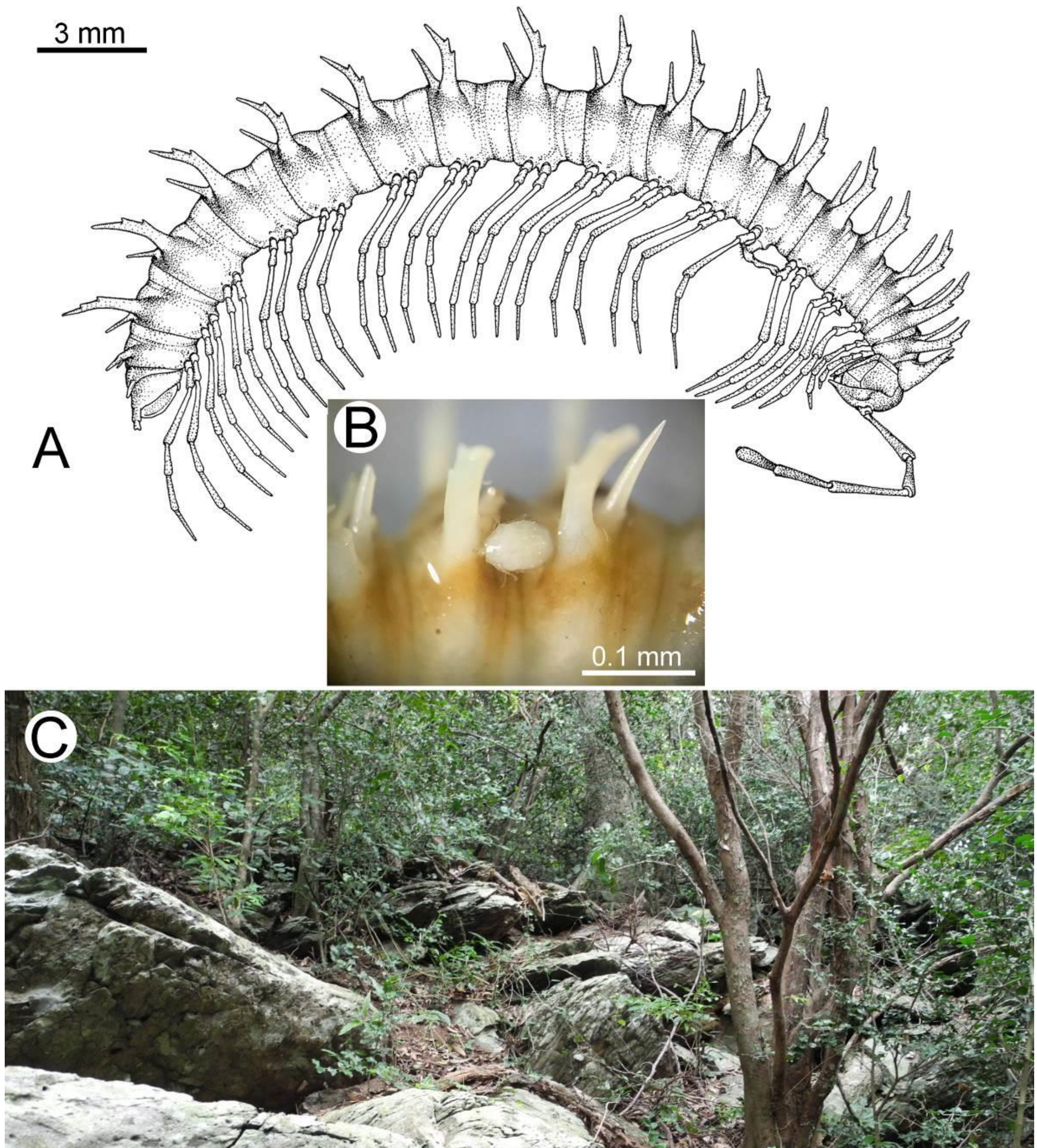

Figure 5.6 *Nagaxytes acantherpestes* (Golovatch & Enghoff, 1994) gen. et comb. nov. **A**. Drawing of ♂, holotype (ZMUC000101457). **B**. Parasitic mite. **C**. Habitat.

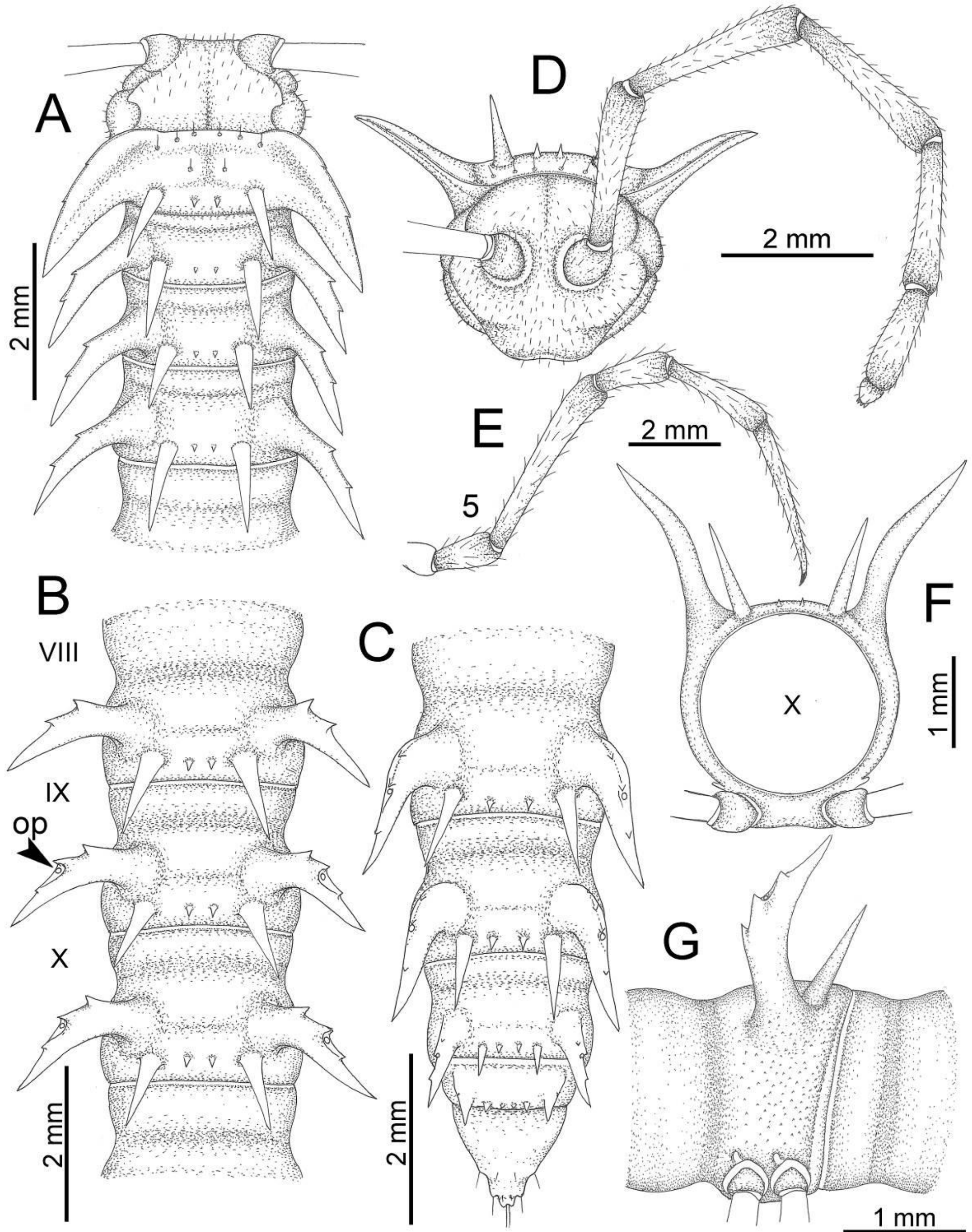

Figure 5.7 *Nagaxytes acantherpestes* (Golovatch & Enghoff, 1994) gen. et comb. nov., ♂, holotype (ZMUC000101457). **A**. Anterior body part. **B**. Body rings 8–10 (op = ozopore). **C**. Posteriormost body rings and telson. **D**. Head and antenna. **E**. ♂ leg 5 (right). **F–G**. Midbody ring.

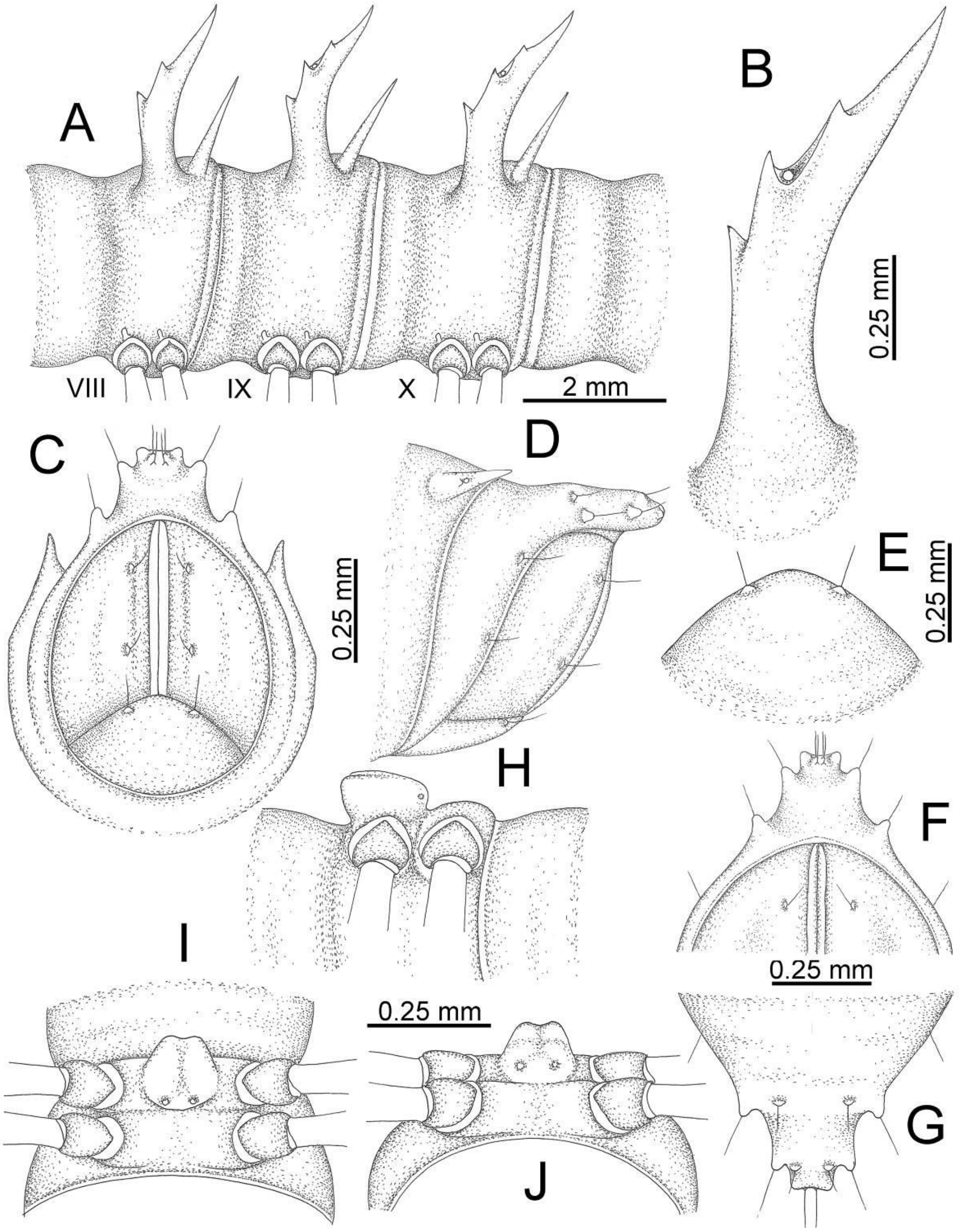

Figure 5.8 *Nagaxytes acantherpestes* (Golovatch & Enghoff, 1994) gen. et comb. nov., ♂, holotype (ZMUC000101457). **A**. Body rings 8–10. **B**. Paraterga of ring 10. **C–D**. Last ring and telson. **E**. Hypoproct. **F–G**. Epiproct. **H–J**. Sternal lobe between coxae 4.

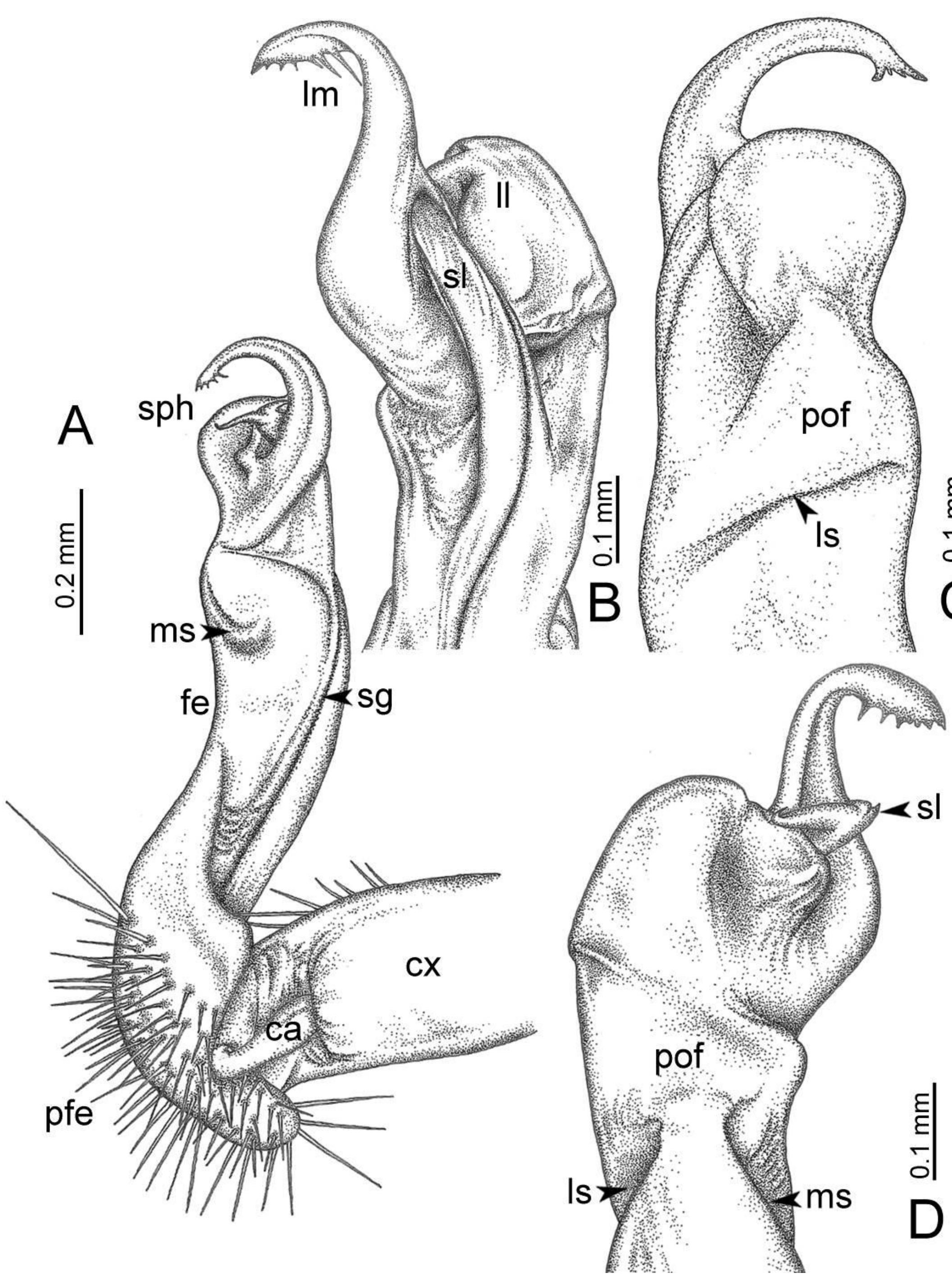

Figure 5.9 *Nagaxytes acantherpestes* (Golovatch & Enghoff, 1994) gen. et comb. nov., specimen from Ban Yan Sue, Thailand – right gonopod. **A**. Mesal view. **B**. Dorsal view. **C**. Lateral view. **D**. Ventral view.

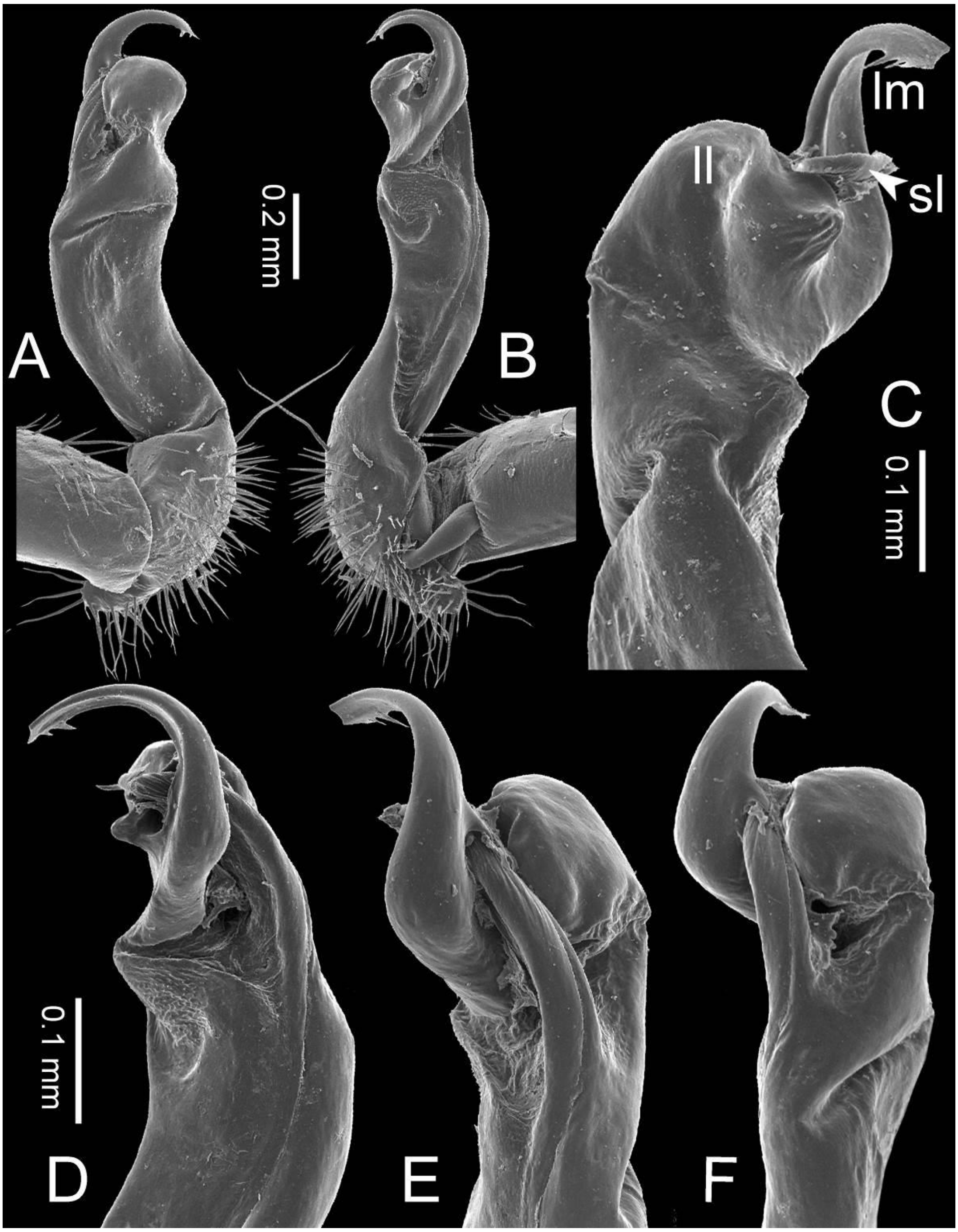

Figure 5.10 *Nagaxytes acantherpestes* (Golovatch & Enghoff, 1994) gen. et comb. nov., specimen from Ban Yan Sue, Thailand – right gonopod. **A**. Lateral view. **B**. Mesal view. **C**. Ventral view. **D**, **F**. Subdorsal view. **E**. Dorsal view.

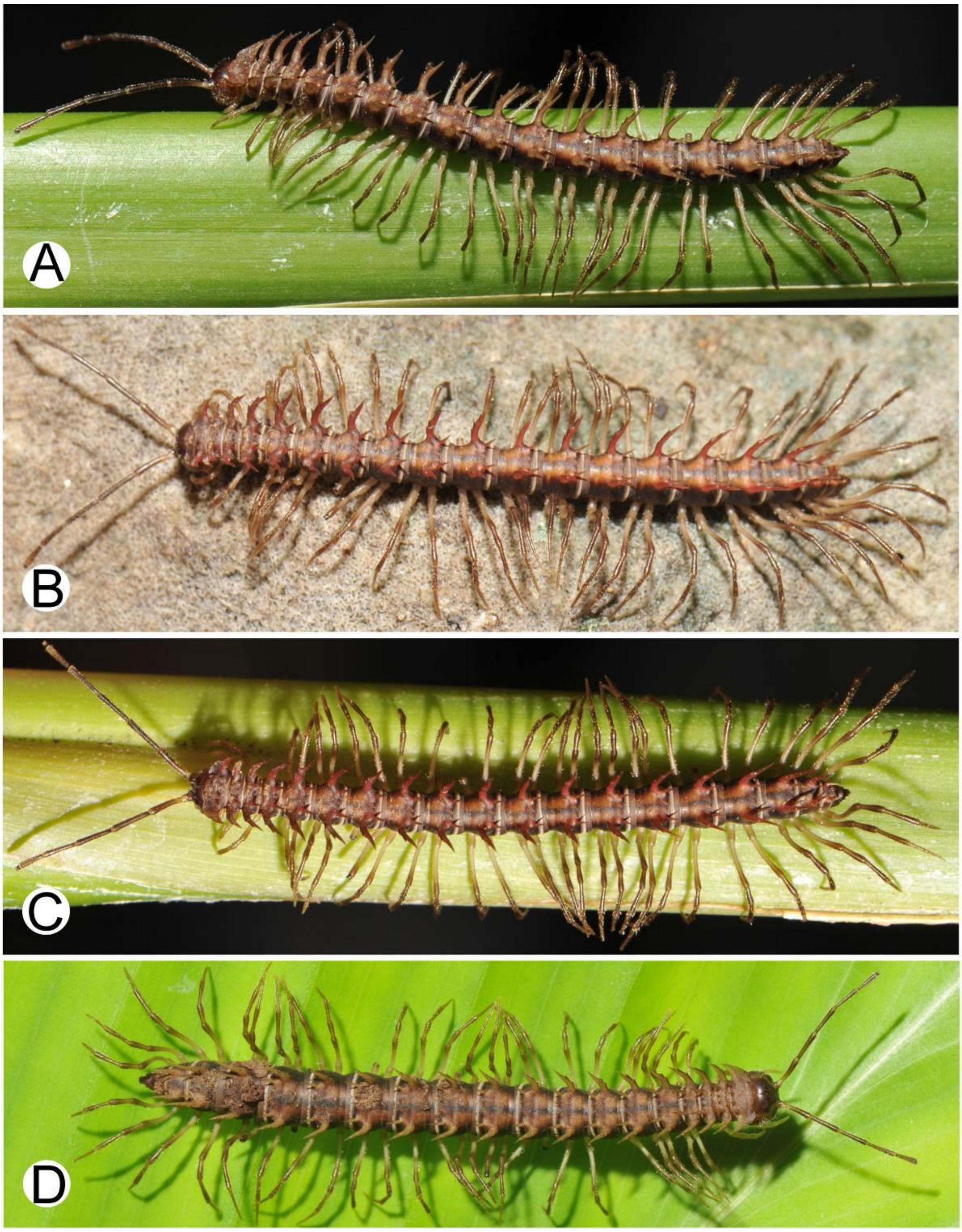

Figure 5.11 Live photographs of *Nagaxytes erecta* Srisonchai, Enghoff & Panha gen. et sp. nov. **A–B**. Specimens from Phuphrai Thannam Resort (♂♂, paratypes, CUMZ-pxDGT00002-3). **C**. Specimen from Ban Nong Bang, Thailand (♂). **D**. Specimen from Phuphrai Thannam Resort, Thailand (♀, CUMZ-pxDGT00054).

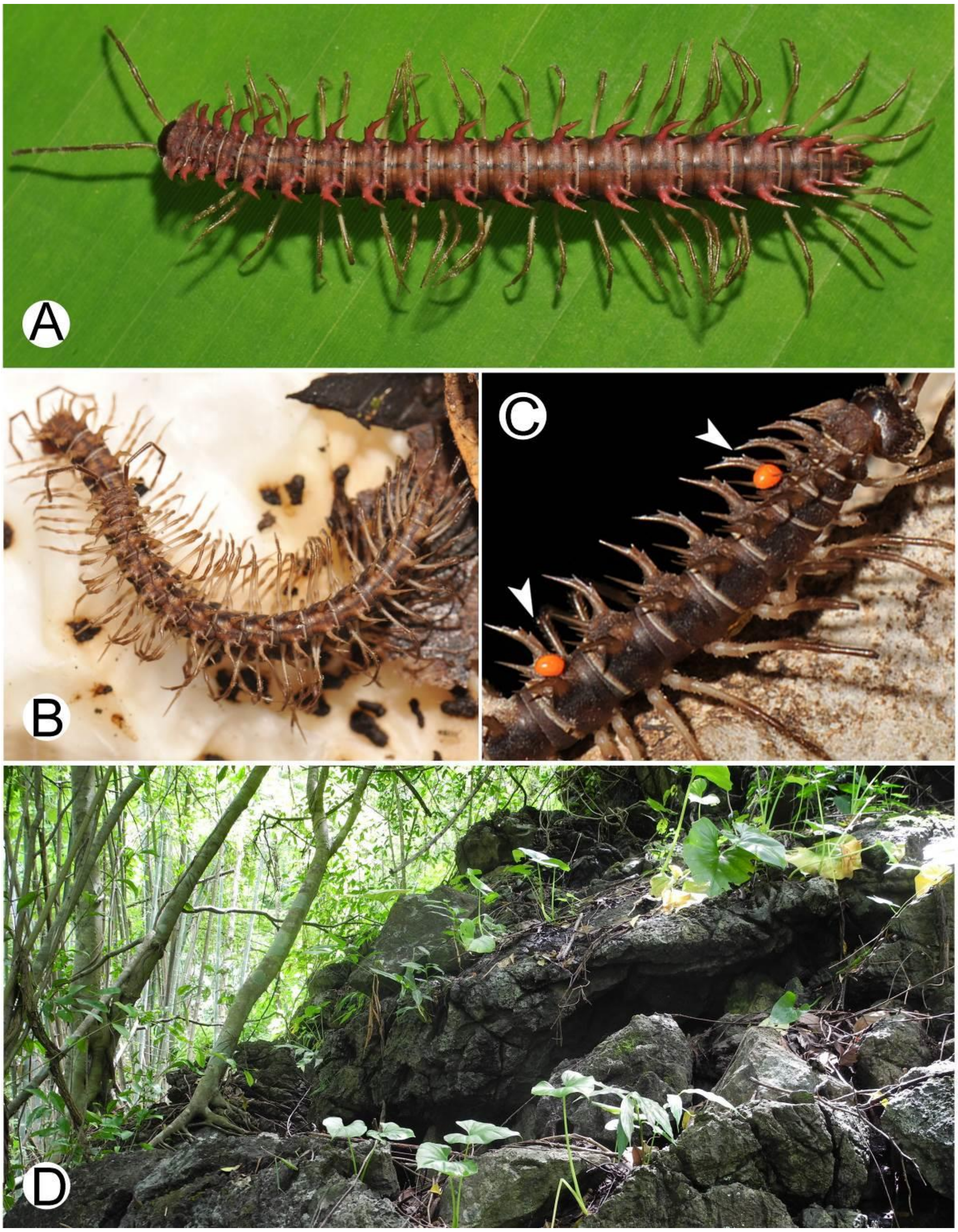

Figure 5.12 Live photographs and habitat of *Nagaxytes erecta* Srisonchai, Enghoff & Panha gen. et sp. nov. **A**. Specimen from Ban Nong Bang, Thailand (♀). **B**. Mating couple. **C**. ♂ with parasitic mites. **D**. Habitat.

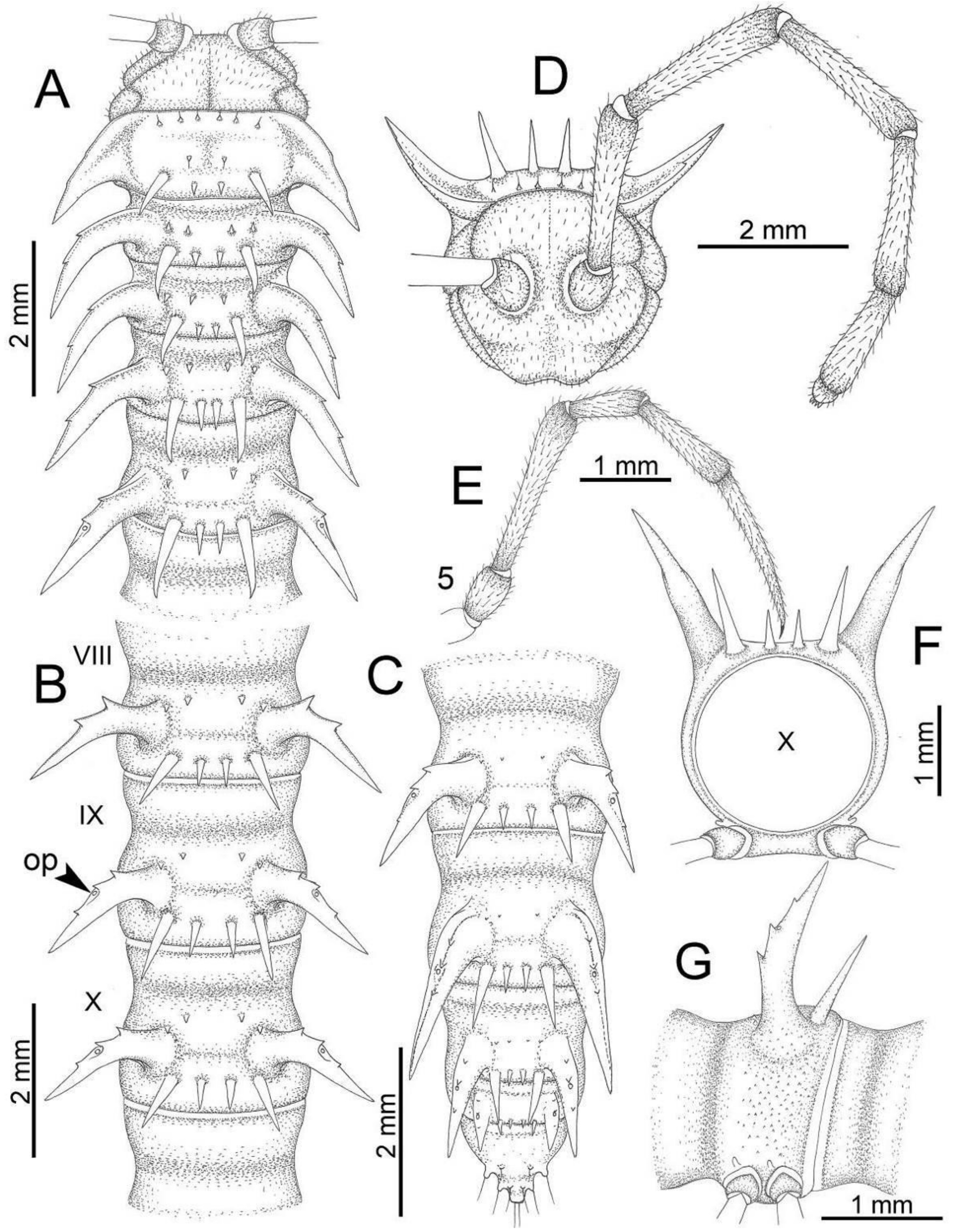

Figure 5.13 *Nagaxytes erecta* sp**.** nov., ♂, paratype, CUMZ-pxDGT00002. **A**. Anterior body part. **B**. Body rings 8–10 (op=ozopore). **C**. Posteriormost body rings and telson. **D**. Head and antenna. **E.** ♂ leg 5 (right). **F**, **G**. Midbody ring.

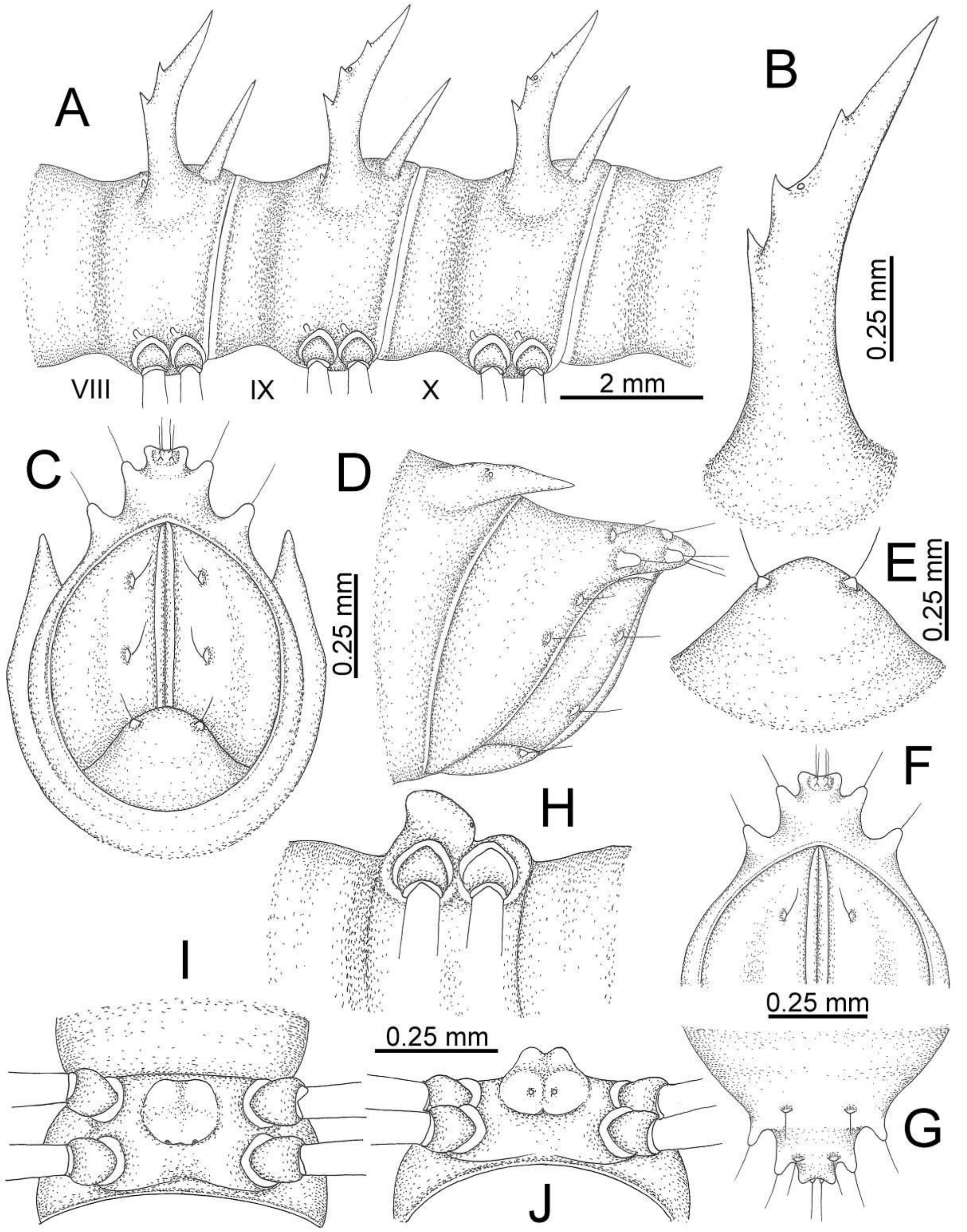

Figure 5.14 *Nagaxytes erecta* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂, paratype (CUMZ-pxDGT00002). **A**. Body rings 8–10. **B**. Paraterga of ring 10. **C–D**. Last ring and telson. **E**. Hypoproct. **F–G**. Epiproct. **H–J**. Sternal lobe between coxae 4.

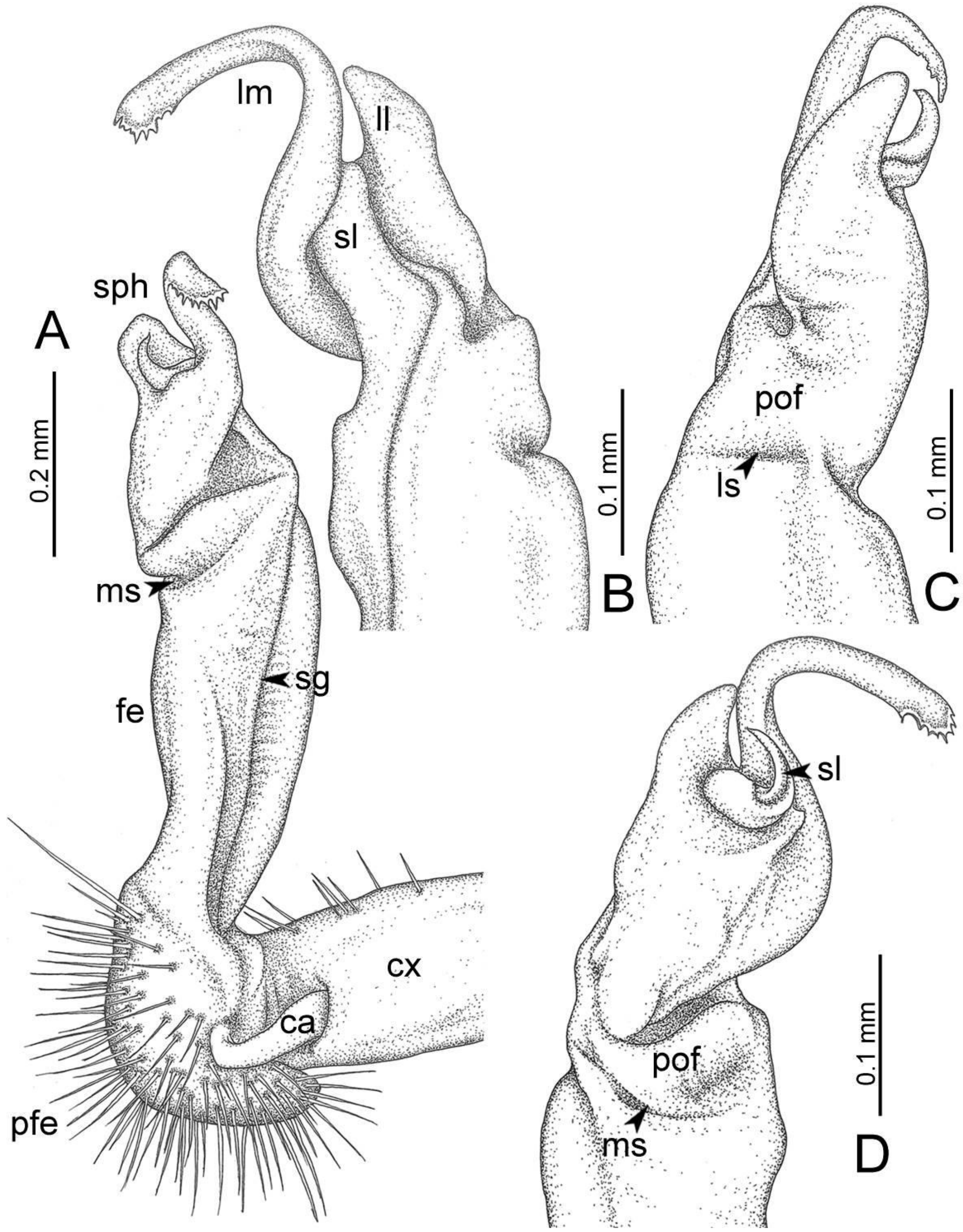

Figure 5.15 *Nagaxytes erecta* Srisonchai, Enghoff & Panha gen. et sp. nov. (paratype, CUMZ-pxDGT00002), right gonopod. **A**. Mesal view. **B**. Dorsal view. **C**. Lateral view. **D**. Ventral view.

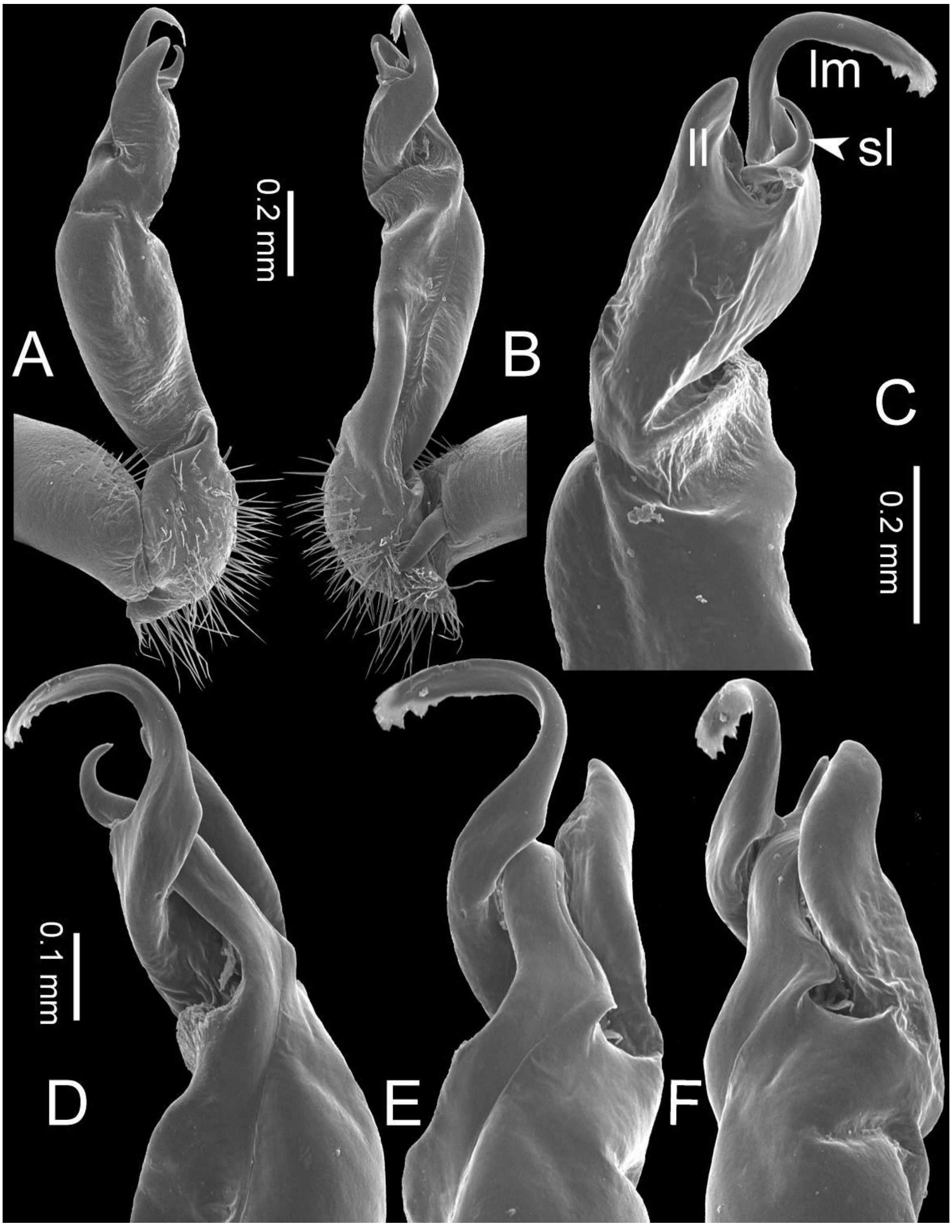

Figure 5.16 *Nagaxytes erecta* Srisonchai, Enghoff & Panha gen. et sp. nov. (paratype, CUMZ-pxDGT00002), right gonopod. **A**. Lateral view. **B**. Mesal view. **C**. Ventral view. **D, F**. Subdorsal view. **E**. Dorsal view.

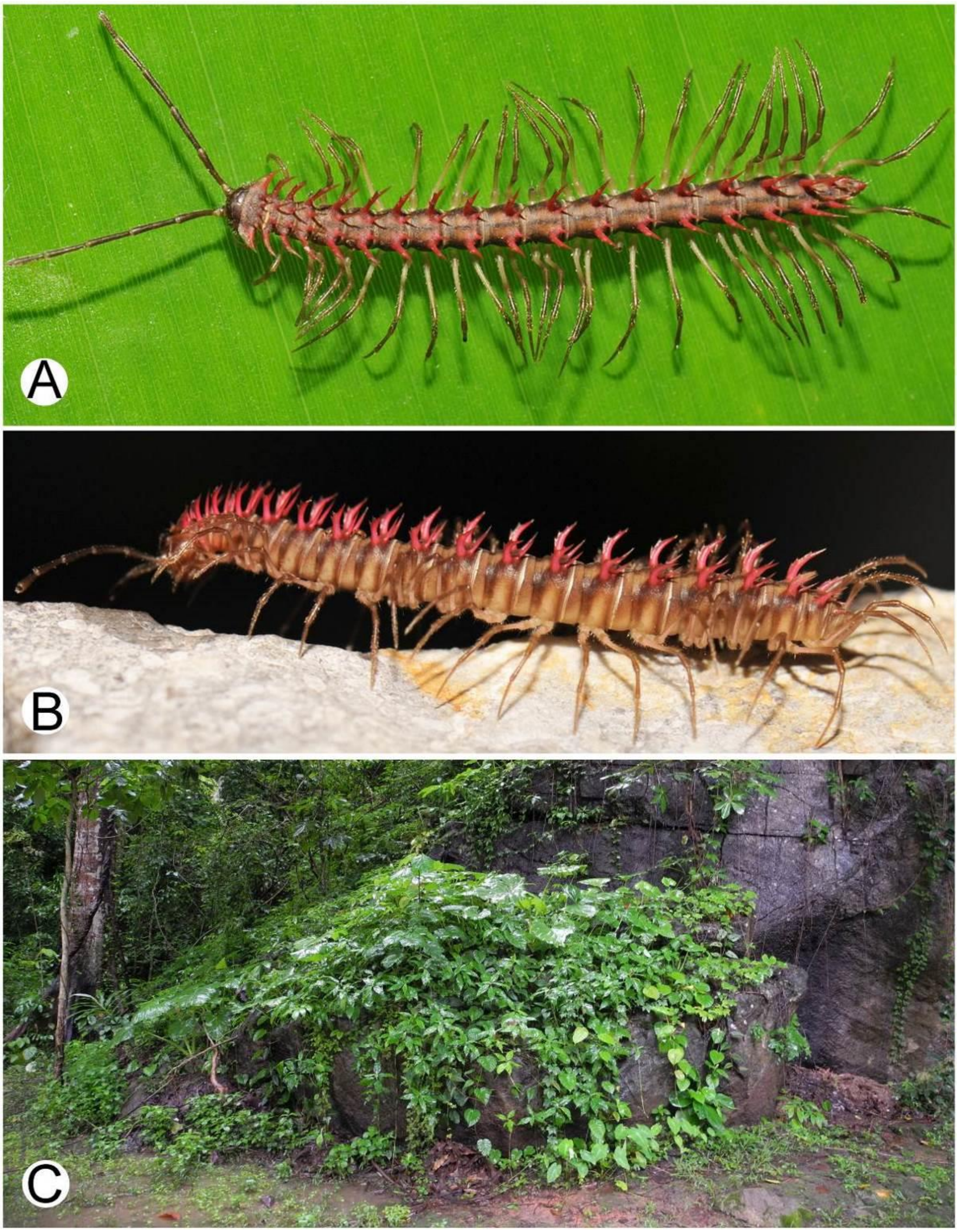

Figure 5.17 Live photographs and habitat of *Nagaxytes gracilis* Srisonchai, Enghoff & Panha gen. et sp. nov. (specimens from Daowadueng Cave, Thailand). **A**. ♂, paratype (CUMZ-pxDGT00091). **B**. ♀, paratype (CUMZ-pxDGT00098). **C**. Habitat.

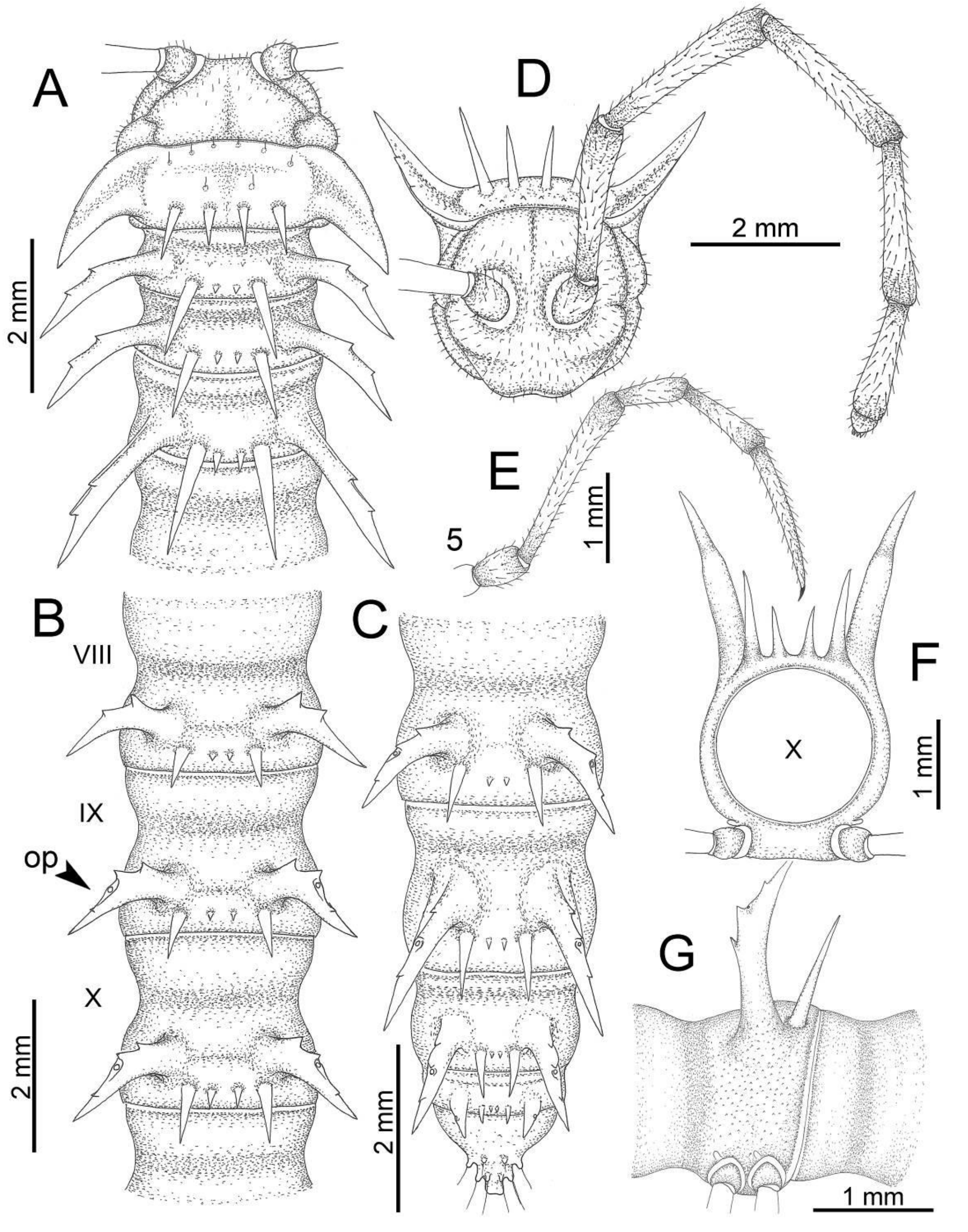

Figure 5.18 *Nagaxytes gracilis* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂, paratype (CUMZ-pxDGT00091). **A**. Anterior body part. **B**. Body rings 8–10 (op = ozopore). **C**. Posteriormost body rings and telson. **D**. Head and antenna. **E**. ♂, leg 5 (right). **F–G**. Midbody ring.

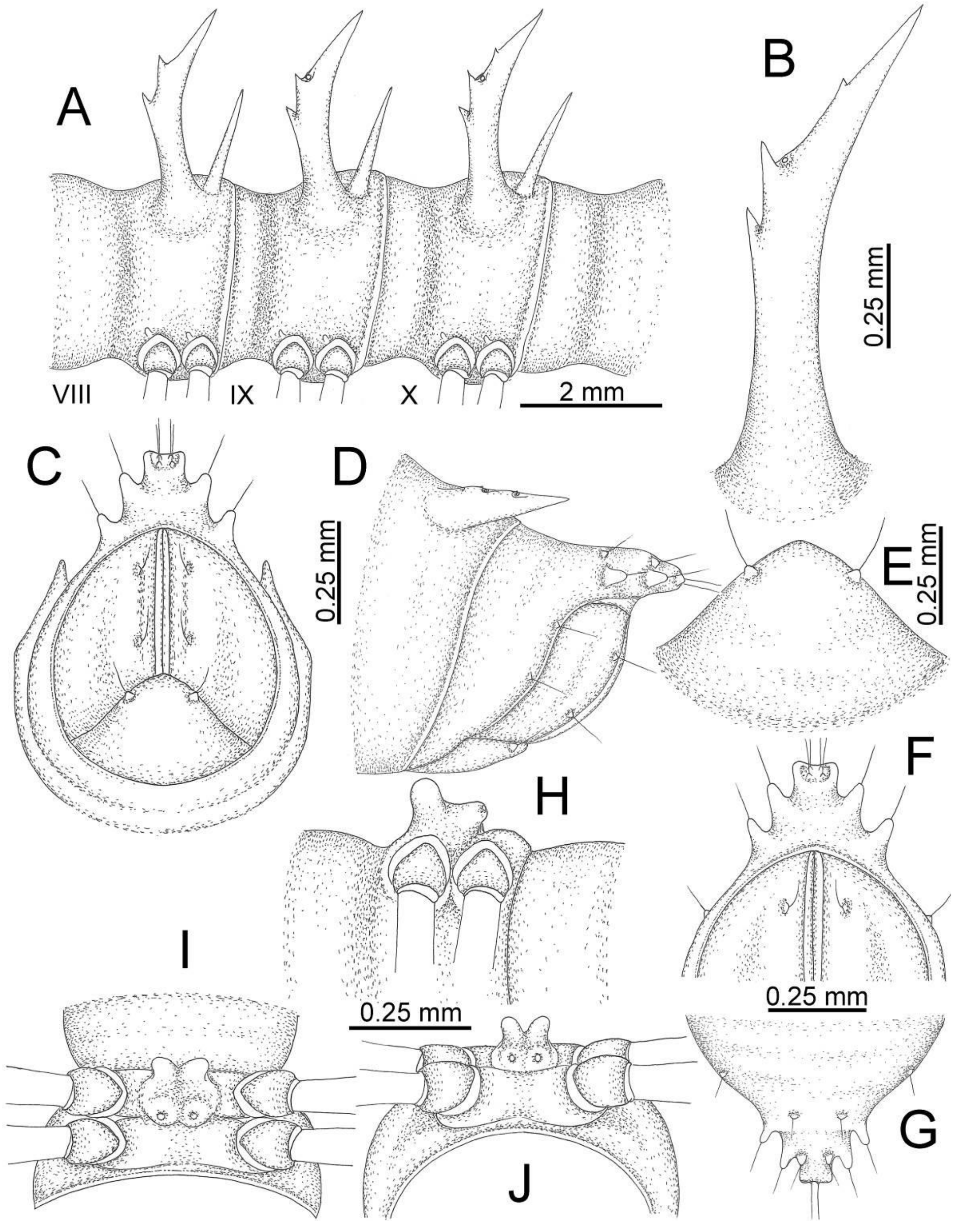

Figure 5.19 *Nagaxytes gracilis* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂, paratype (CUMZ-pxDGT00091). **A**. Body rings 8–10. **B**. Paraterga of ring 10. **C–D**. Last ring and telson. **E**. Hypoproct. **F–G**. Epiproct. **H–J**. Sternal lobe between coxae 4.

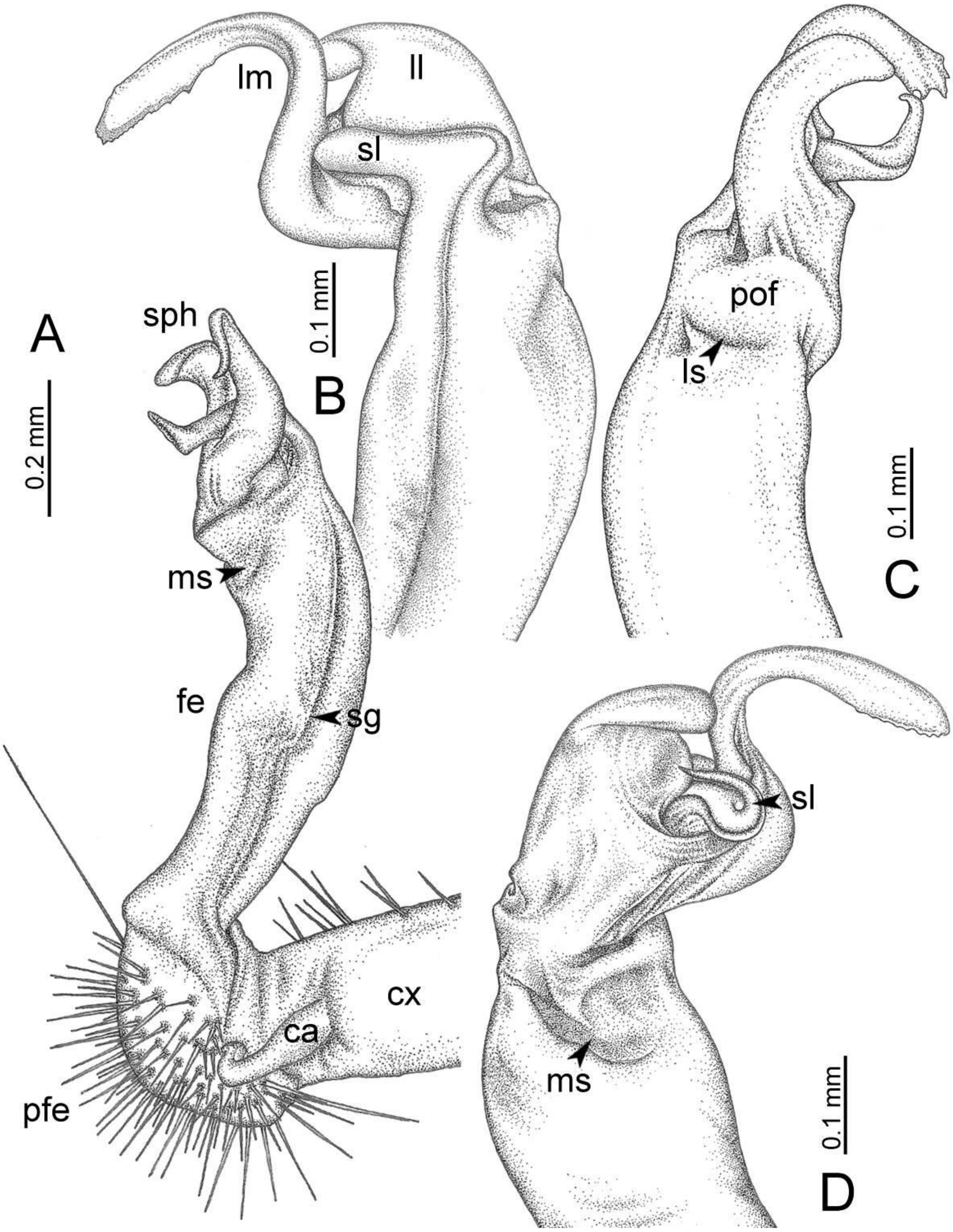

Figure 5.20 *Nagaxytes gracilis* Srisonchai, Enghoff & Panha gen. et sp. nov., paratype (CUMZ-pxDGT00092), right gonopod. **A**. Mesal view. **B**. Dorsal view. **C**. Lateral view. **D**. Ventral view.

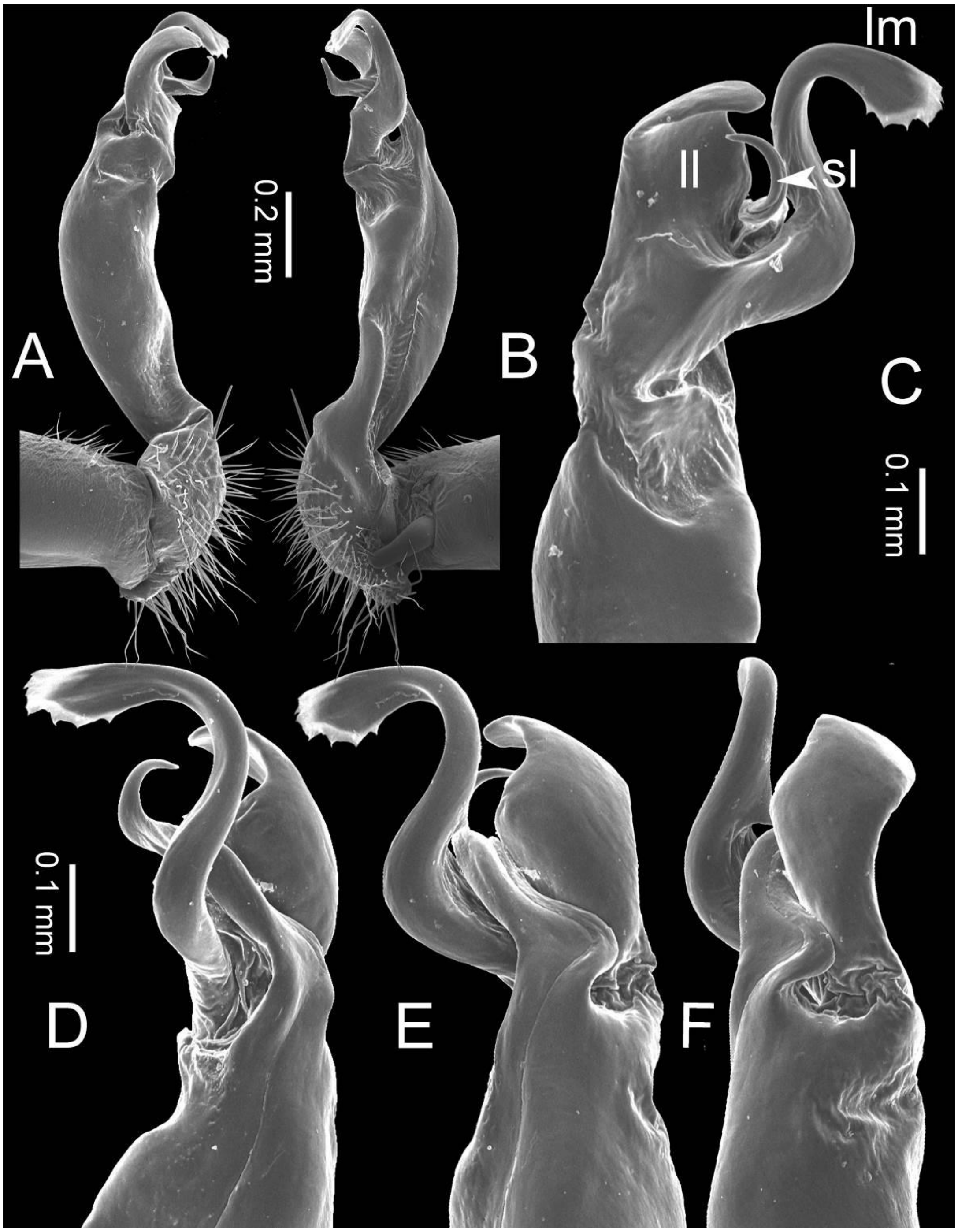

Figure 5.21 *Nagaxytes gracilis* Srisonchai, Enghoff & Panha gen. et sp. nov., paratype (CUMZ-pxDGT00092), right gonopod. **A**. Lateral view. **B**. Mesal view. **C**. Ventral view. **D, F**. Subdorsal view. **E**. Dorsal view.

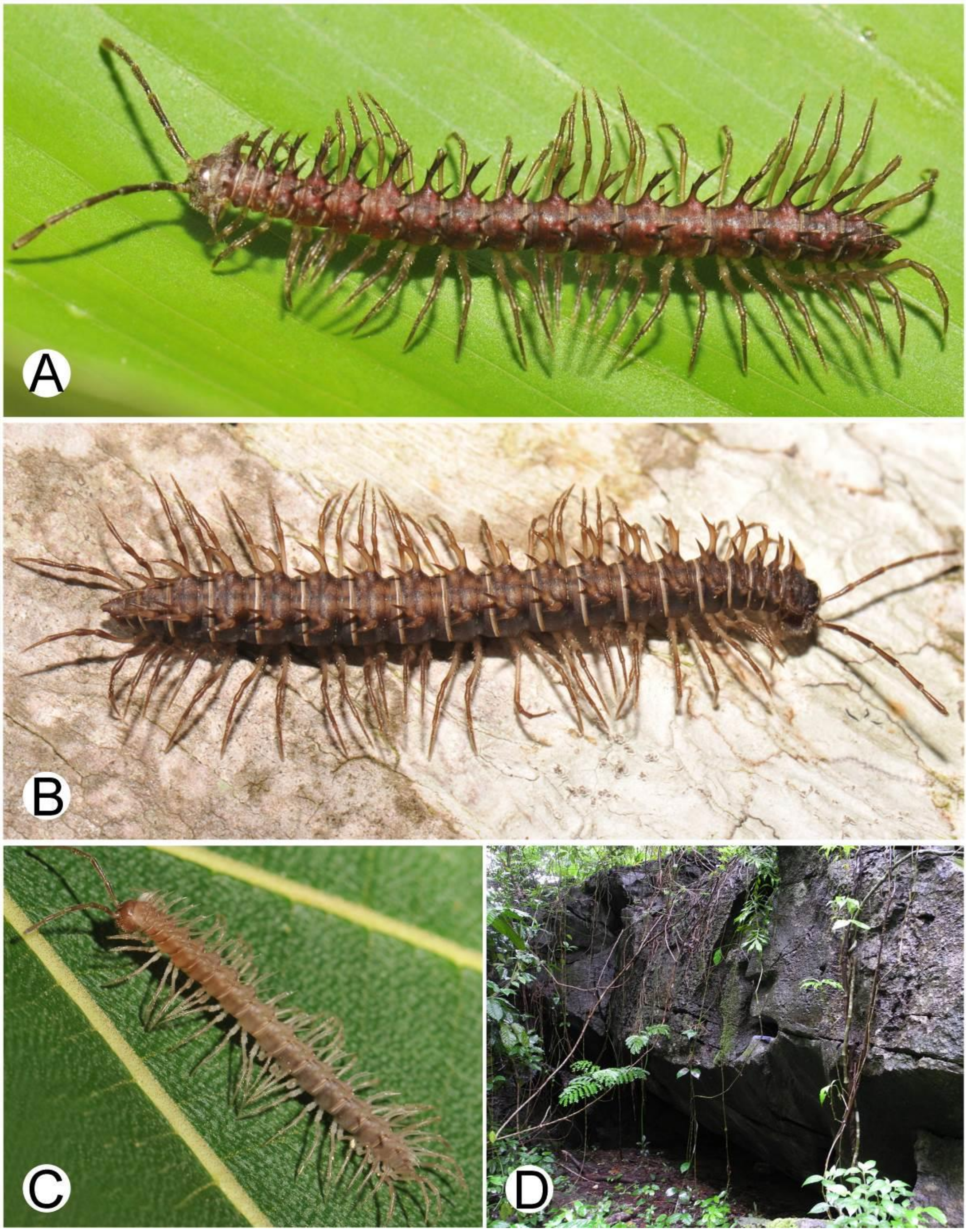

Figure 5.22 Live photographs and habitat of *Nagaxytes spatula* Srisonchai, Enghoff & Panha gen. et sp. nov. (specimens from Chao Por Phawo Shrine, Thailand). **A.** ♂, paratype (CUMZ-pxDGT00120). **B.** ♀, paratype (CUMZ-pxDGT00147). **C.** ♂, paratype (CUMZ-pxDGT00146), newly moulted adult. **D.** Habitat.

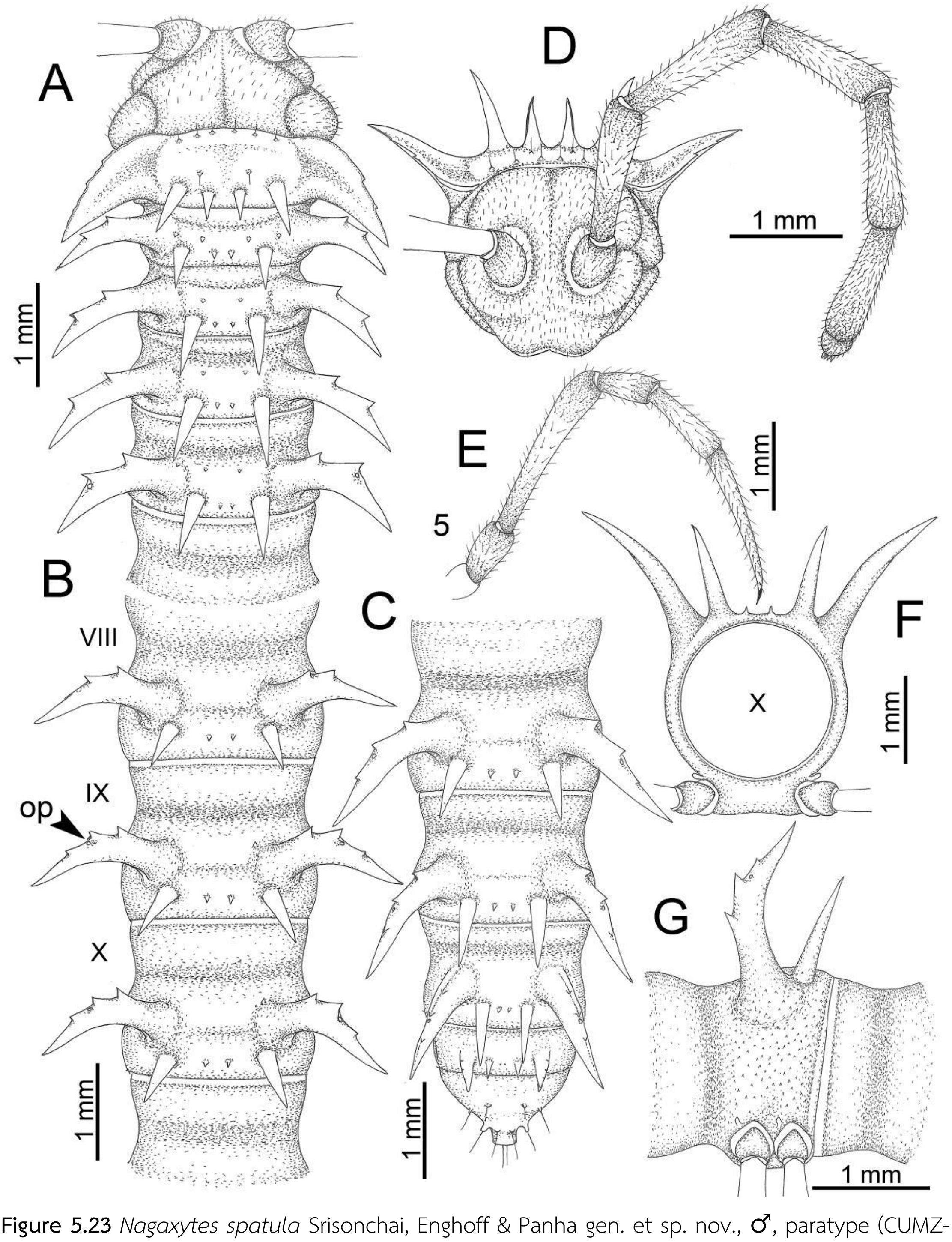

Figure 5.23 *Nagaxytes spatula* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂, paratype (CUMZ-pxDGT00120). **A**. Anterior body part. **B**. Body rings 8–10 (op = ozopore). **C**. Posteriormost body rings and telson. **D**. Head and antenna. **E**. ♂, leg 5 (right). **F–G**. Midbody ring.

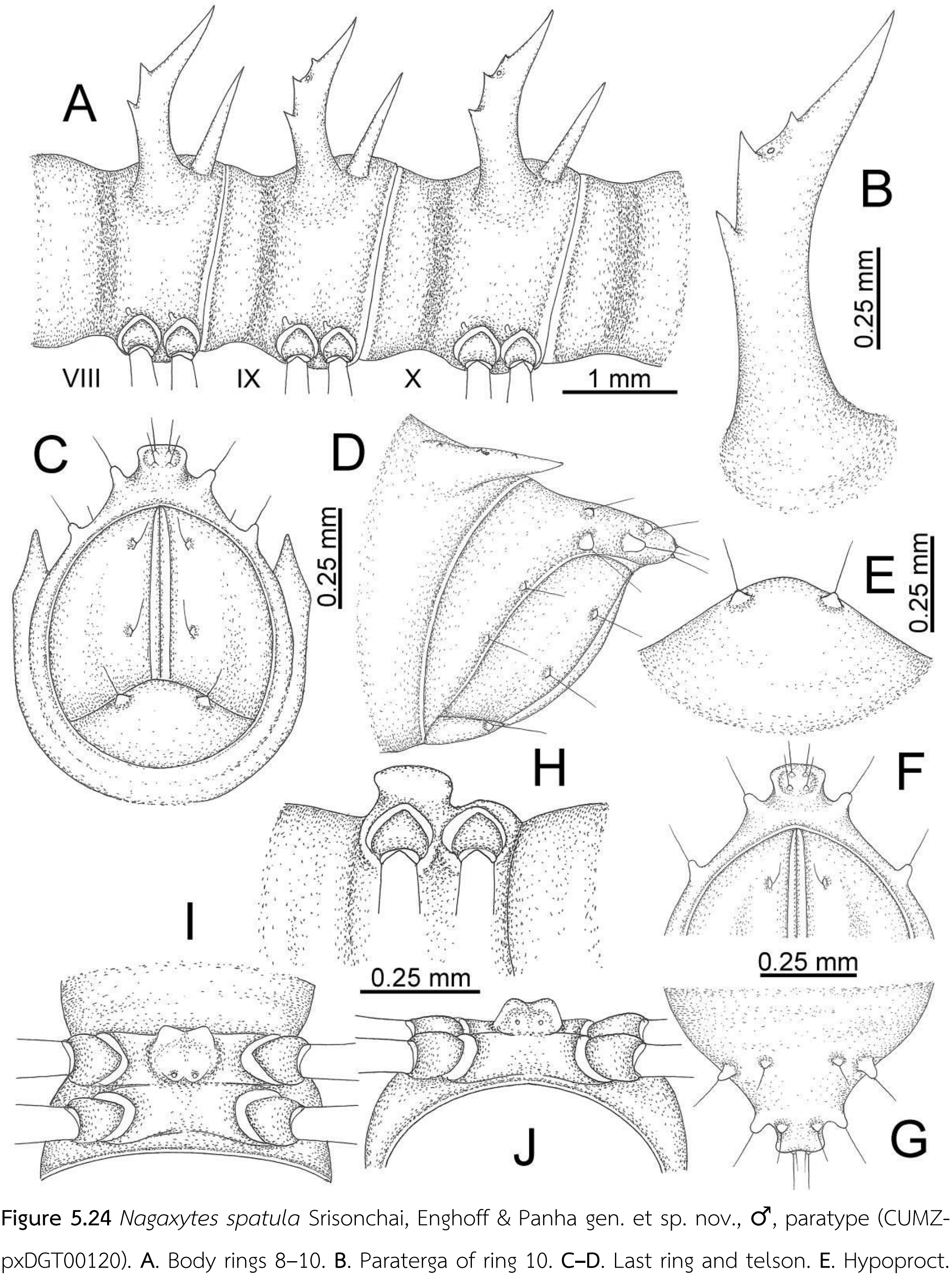

Figure 5.24 *Nagaxytes spatula* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂, paratype (CUMZ-pxDGT00120). **A**. Body rings 8–10. **B**. Paraterga of ring 10. **C–D**. Last ring and telson. **E**. Hypoproct. **F–G**. Epiproct. **H–J**. Sternal lobe between coxae 4.

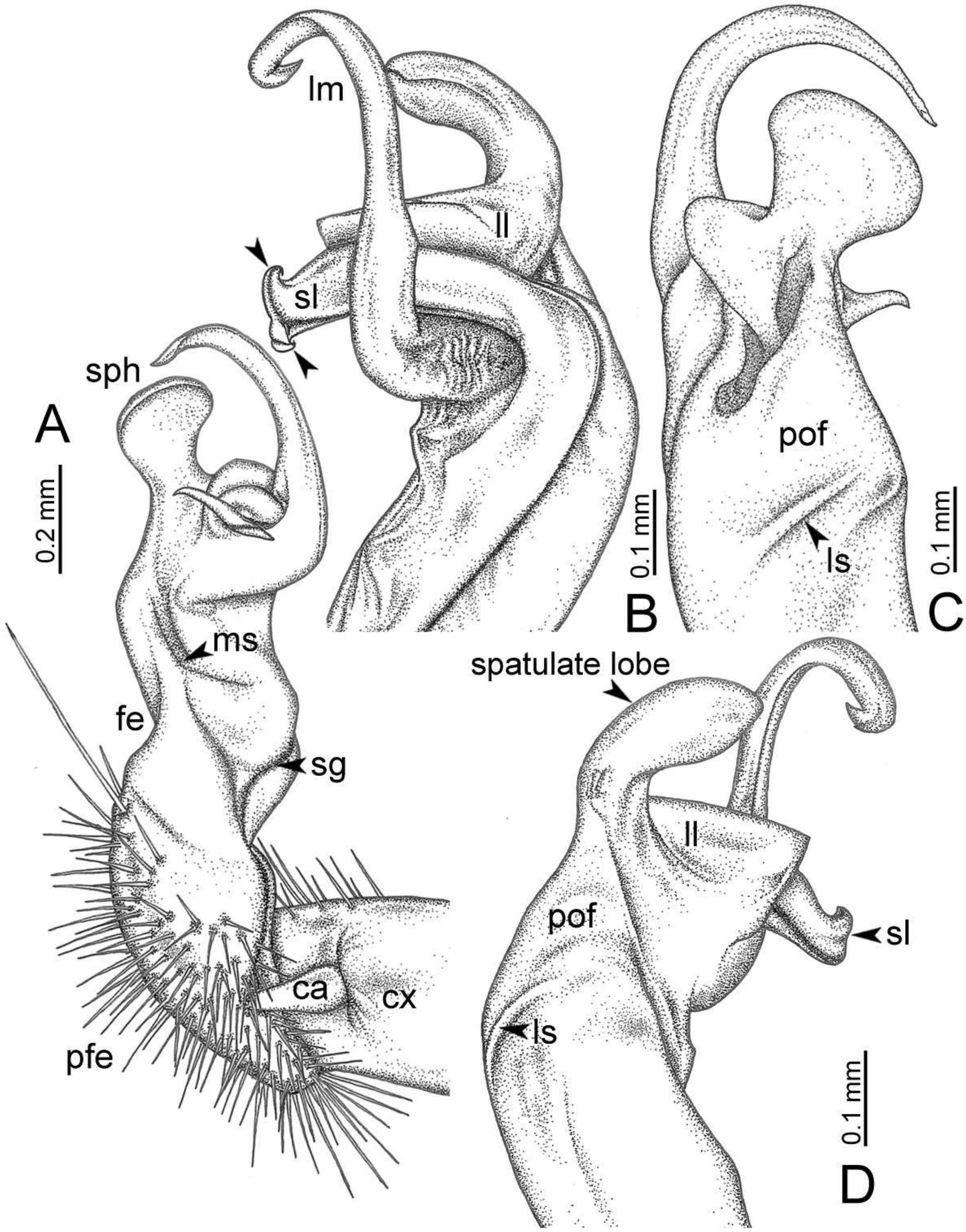

Figure 5.25 *Nagaxytes spatula* Srisonchai, Enghoff & Panha gen. et sp. nov., paratype (CUMZ-pxDGT00121), right gonopod. **A**. Mesal view. **B**. Dorsal view (arrowheads = tip of solenomere terminating in two curved processes). **C**. Lateral view. **D**. Ventral view.

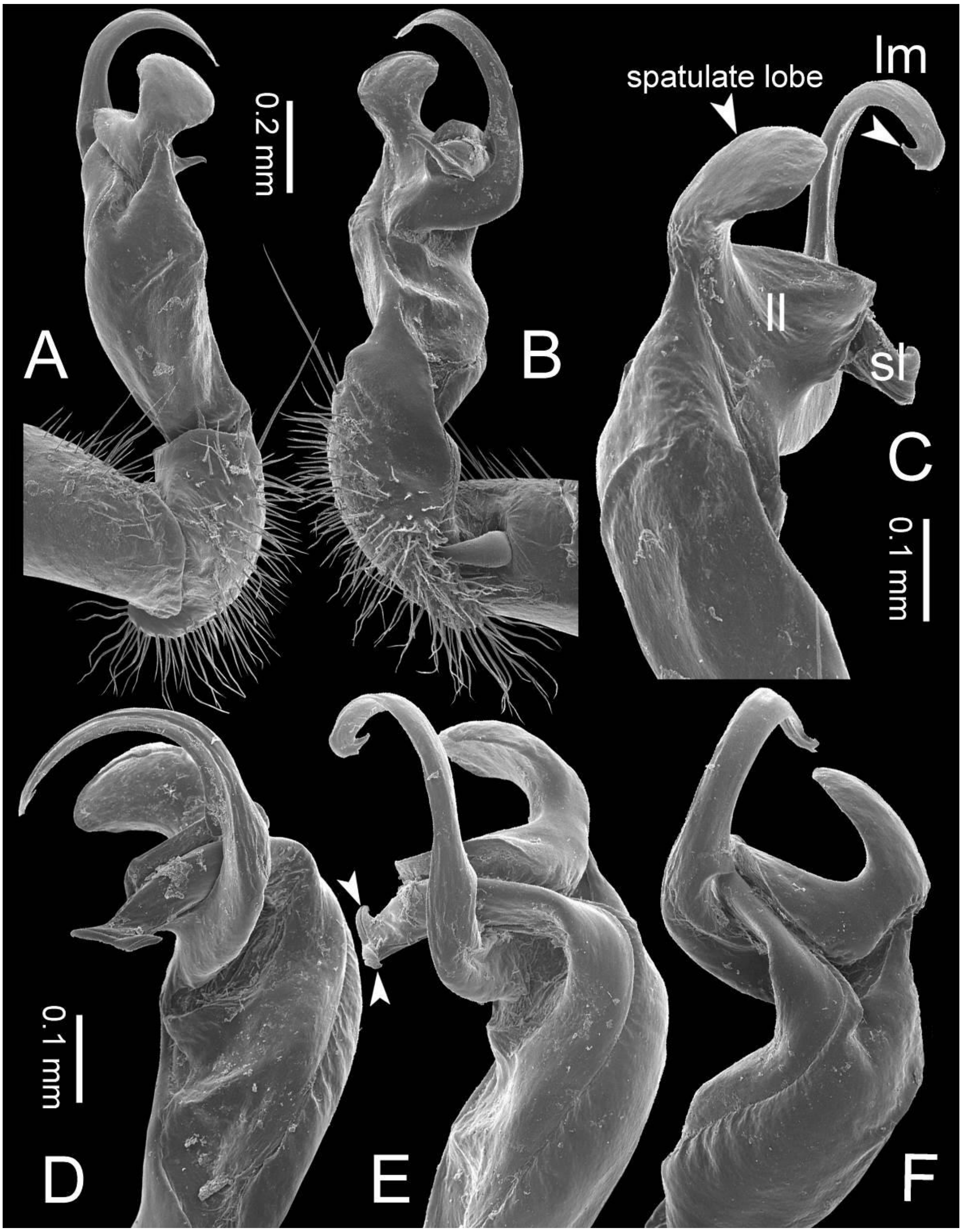

Figure 5.26 *Nagaxytes spatula* Srisonchai, Enghoff & Panha gen. et sp. nov., paratype (CUMZ-pxDGT00121), right gonopod. **A**. Lateral view. **B**. Mesal view. **C**. Ventral view (arrowhead = hook-like tip). **D, F**. Subdorsal view. **E**. Dorsal view (arrowheads = tip of solenomere terminating in two curved processes).

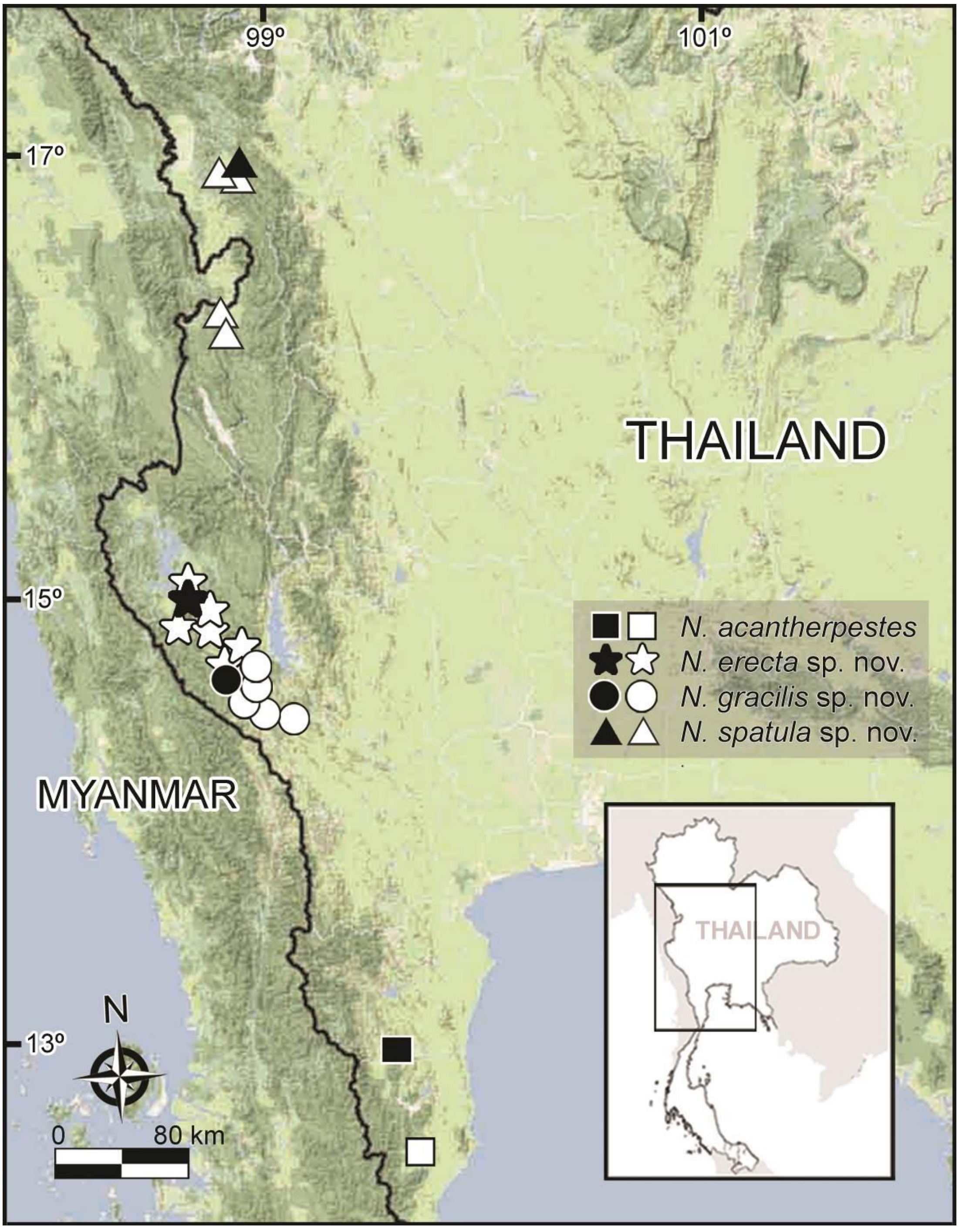

Figure 5.27 Known distribution of all *Nagaxytes* species (black symbol= type locality, white symbol=other localities).

CHAPTER VI

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

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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) comb. nov. Three new species are described: *G. fusca* sp. nov. from Thailand and Myanmar; *G. parvoterga* sp. nov. and *G. suratensis* 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.

Key words. dragon millipede, endemic, new species, taxonomy, Thailand.

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

Gigaxytes specimens 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

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. The morphological terminology is mainly based on previous taxonomic papers (Enghoff *et al.*, 2007; Golovatch and Enghoff, 1994; Golovatch *et al.*, 2012; Jeekel, 1964, 1980a, 2003; Srisonchai *et al.*, 2016, 2018a). 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 will be kept at ZMUC.

Abbreviation of institutions and other abbreviations used in the text

ASRU	=	Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand
CUMZ	=	Chulalongkorn University Museum of Zoology, Bangkok, Thailand

ZMUC	=	Natural History Museum of Denmark (Zoological Museum), University of Copenhagen, Denmark
ca.	=	approximately, around (circa)
a.s.l.	=	above sea level

Gonopod terminology for the genus Gigaxytes*, and their abbreviations*

Acropodite	=	Apical part of gonopod; including femorite, solenophore and solenomere.
Coxa (cx)	=	Basal part of gonopod, rather stout, connecting to seventh body ring, attached to apertural rim dorsally; with a distoanterior group of setae.
Cannula (ca)	=	A short tube, lever-like, curved; originating from coxa, tip inserted into concavity in prefemoral part.
Femorite (fe)	=	Longest part of gonopod, curved; without lateral and mesal sulci; accommodates seminal groove.
Lamina medialis (lm)	=	A small part distally on gonopod, lamella-like; obviously seen in mesal view.
Lamina lateralis (ll)	=	A distinct lamella-like in distal part of gonopod; very long and broad
Prefemoral part (Prefemur) (pfe)	=	Basal portion of telopodite, densely setose.
Seminal groove (sg)	=	A conspicuous groove, similar to a tunnel, seen as a transparent line, visible on femur in mesal view.
Solenomere (sl)	=	A usually long, flagellum-like appendage, originating on base of solenophore.

Solenophore (= tibiotarsus) (sph)	=	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 90° up from their *in situ* position (following the terminology of Srisonchai *et al.* (2018a)).

Dorsal refers to a position on the side nearest to the body ring.

Ventral refers to a position on the side farthest away from the body ring.

Mesal refers to a position on the side nearest to the midline.

Lateral refers to a position on the side furthest from the midline.

Dorsad refers to a direction towards the body ring.

Ventrad refers to a direction away from the body ring.

Mesad refers to a direction towards the midline.

Laterad refers to a 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

Type species

Desmoxytes gigas Golovatch & Enghoff, 1994 (ZMUC).

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)

Etymology

The name is a combination of the species epithet of the type species, ‘*gigas*’, 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* sp. nov.
- *Gigaxytes gigas* (Golovatch & Enghoff, 1994) comb. nov.
- *Gigaxytes parvoterga* sp. nov.
- *Gigaxytes suratensis* sp. nov.

Remarks

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

General description of the genus *Gigaxytes*

The description applies to adult males and females, except for the part on the gonopods and when “male” is specified (Figs 6.1, 6.2). The general description of gonopods is based mainly on *G. gigas* (Golovatch & Enghoff, 1994) comb. nov. (Fig. 6.3).

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 6.4A–C, 6.9A–E, 6.14A, B, 6.19A–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. 6.2I). Delicately setose; vertex, labrum and genae delicately setose; epicranial suture conspicuous as a long and deep, brown or black stripe.

COLLUM (Fig. 6.2A, 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. 20°–50°, directed caudolaterad, with two conspicuous notches at lateral margin.

TEGUMENT (Fig. 6.2A–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. 6.2A, 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. 6.2B). 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.

PARATERGA (Fig. 6.2A, B, D, E, G, H). Subspiniform, long, extremely elevated at ca. 40°–70° (male) 30°–60° (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. 6.2F, 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 two pairs of conspicuous setae. 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. 6.2K). 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. 6.2J). 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* comb. nov.

GONOPODS (Fig. 6.3). *Orthomorpha*-like. Coxa (cx) longer than prefemoral part, subequal in length to femorite, with a distoanterior group of seta. Cannula (ca) mostly rather short, sometimes quite long. Telopodite curved (falcate). Prefemoral part (pfe) ca. 2/3 as long as femorite. Femorite long and curved. Seminal groove (sg) running entirely on mesal surface of femorite. Mesal sulcus (ms) and lateral sulcus (ls) poorly developed. Solenophore (sph) sheath-like, curved: lamina lateralis (ll) lamella-like, thin, longer and wider than lamina medialis: lamina medialis (lm) indistinctly demarcated from lamina lateralis, tip *in situ* directed ventrad/mesoventrad. Solenomere (sl) long, slender, supported by solenophore.

Distribution and habitat

No sympatry between species of *Gigaxytes* 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* (based mainly on males)

1. Male femora 5, 6, 7 without modification (Fig. 6.10E, F) ....***G. gigas*** (Golovatch & Enghoff, 1994) comb. nov.
– Male femora 5, 6 or 5, 6, 7 with an apophysis (e.g., Fig. 6.15E–G) 2

2. Body brown. Only male femora 5 and 6 with apophyses (Fig. 6.5E, F); solenophore (sph) narrow laterally (e.g., Figs 6.7C–D, 6.8C, E) ....***G. fusca*** sp. nov.
– Body pinkish brown or brownish pink. Male femora 5, 6 and 7 with apophyses (Figs 6.15E–G, 6.20E–G); solenophore (sph) broad laterally (e.g., Figs 6.17C, 6.18C, 6.22C, 23C) 3

3. Paraterga short (Fig. 6.16A, B); collum usually with 3+3 cones/spines (intermediate row) (Fig. 6.15A); 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. 6.15A–C) ....***G. parvoterga*** sp. nov.

– Paraterga long (Fig. 6.21A, B); collum usually with 4+4 cones/spines (intermediate row) (Fig. 6.20A); 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. 6.20A–C) ....***G. suratensis*** sp. nov.

Species descriptions

Gigaxytes fusca Srisonchai, Enghoff & Panha sp. nov.

(Figs 6.1, 6.2, 6.4–6.8)

Material examined

Holotype

THAILAND: ♂, Chumphon Province, Pathio District, Phitsadarn Cave (Tham Phitsadarn), 10°45'36"N, 99°13'46"E, ca. 103 m a.s.l., 29 Aug. 2015, ASRU members leg. (CUMZ).

Paratypes

THAILAND: 7 ♂♂, 1 ♀, same data as holotype (CUMZ); 1 ♂, 1 ♀, same data as holotype (ZMUC).

Further specimens, not paratypes

MYANMAR: 9 ♂♂, 5 ♀, 1 juveniles, Tanintharyi Region, Lenya National Park, approximately 10 km from Nam Yen Village, Phayarhtan Cave (Buddha Cave), 11°13'50"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), 10°45'36"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, 11°12'05"N, 99°29'52"E, ca. 21 m a.s.l., 12 Oct. 2008, ASRU members leg. (CUMZ).

Etymology

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

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* sp. nov., but differs from this species by having brown body colouration; paraterga longer; male femora 7 unmodified; solenophore (sph) narrow laterally; lamina medialis (lm) apically sharp.

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. 6.4A–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 6.2A, C, 6.5A). 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. 40°–50°.

ANTENNAE (Fig. 6.5D). 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 6.2A, D, G, 6.5A–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 6.2A, B, D, E, G, H, 6.5A–C, F, 6.6A, B). Extremely long; directed caudolaterad on body rings 2–16, elevated at ca. 50°–70° (male) 50°–60° (female), directed increasingly caudad on body rings 17–19.

TELSON (Figs 6.2F, L–N, 6.6C–G). Tip of epiproct subtruncate; apical tubercles inconspicuous. Hypoproct subtrapeziform; caudal margin subtruncate, with conspicuous setiferous tubercles.

STERNUM (Figs 6.2K, 6.6H–J). On body ring 5 with a swollen lobe; posterior surface of lobe with a pore borne on a long cylindrical stalk.

LEGS (Figs 6.2J, 6.6E–G). Male femora 5 and 6 with an apophysis.

GONOPODS (Figs 6.7, 6.8). Coxa (cx) subequal in length to femorite. Cannula (ca) quite long and slender. Femorite (fe) quite long, a bit stout, curved. Solenophore (sph) narrow laterally: lamina lateralis (ll) narrow: lamina medialis (lm) 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* 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. 6.4D, 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) comb. nov.

(Figs 6.3, 6.9–6.13)

Desmoxytes gigas Golovatch & Enghoff, 1994: 56, figs 49–52.

Desmoxytes gigas – Enghoff 2005: 96. — Nguyen & Sierwald 2013: 1241.

Material examined

Holotype

THAILAND: ♀, Krabi Province, road between Krabi and Phuket, 10 km South of Krabi, 8°09'N, 98°50'E, lowland rainforest, <200 m, 13 Oct. 1991, M. Anderson, O. Martin & N. Scharff leg. (ZMUC) [the exact location is 10 km North of Krabi].

Other material examined, all from THAILAND

Krabi Province: 1 broken ♂ – gonopods lost, Ao Luek District, Than Bok Khorani, 8°23'28"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, 8°23'28"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, 8°23'28"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, 8°23'28"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, 8°07'38"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, 8°07'38"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, 8°07'38"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, 8°07'38"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, 8°07'38"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, 8°07'38"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, 8°07'38"N, 98°55'26"E, ca. 87 m a.s.l., 30 Aug. 2015, ASRU members leg. (CUMZ); 3 ♂♂, 3 ♀♀, Muaeng Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'38"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, 8°07'38"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), 8°08'12"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, 8°30'47"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), 8°02'48"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), 8°09'32"N, 99°40'42"E, ca. 74 m a.s.l., 5 Jan. 2017, ASRU members leg. (CUMZ); 1 ♀, Nopphitam District, Krung Ching Waterfall, 8°43'27"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, 7°40'57"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, 7°40'57"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), 7°35'08"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), 7°35'08"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), 7°35'08"N, 99°52'08"E, ca. 75 m a.s.l., 16 Jan. 2013, ASRU members leg. (ZMUC); 2 ♂♂, 1 ♀, Kong Ra District, Khao Phaya Hong, 7°27'46"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, 7°48'10"N, 99°37'05"E, ca. 66 m a.s.l., 14 Jan. 2009, ASRU members leg. (ZMUC); 4 ♂♂, Hui Yot District, Wat Khao Huai Hang, 7°47'37"N, 99°38'40"E, ca. 83 m a.s.l., 24 Aug. 2014, ASRU members leg. (ZMUC); 1 broken ♂ – gonopods lost, 1 ♀, Na Yong District, Khao Chang Hai Cave, 7°35'23"N, 99°40'08"E, ca. 35 m a.s.l., 15 Jan. 2009, ASRU members leg. (ZMUC); 1 ♂, 2 ♀♀, Na Yong District, Khao Chang Hai Cave, 7°35'23"N, 99°40'08"E, ca. 35 m a.s.l., 25 Aug. 2014, ASRU members leg. (ZMUC); 1 ♂, 2 juveniles, Na Yong District, Khao Chang Hai Cave, 7°35'23"N, 99°40'08"E, ca. 35 m a.s.l., 9 Jul. 2017, ASRU members leg. (ZMUC); 5 ♂♂, 3 ♀♀, Ratsada District, Wat Tham Phra Phut, 7°57'42"N, 99°44'42"E, ca. 103 m a.s.l., 5 Jul. 2017, ASRU members leg. (ZMUC).

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.

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. 6.9A–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. 6.10A). 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. 30°–40°.

ANTENNAE (Fig. 6.10D). Very long and slender, reaching to body ring 7 or 6 (male) and 5 or 4 (female) when stretched dorsally.

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

METATERGA (Fig. 6.10A–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 6.10A–C, H, 6.11A, B). Moderately long, directed caudolaterad on body rings 2–17, elevated at ca. 50°–70° (male) 40°–60° (female), directed increasingly caudad on body rings 18 and 19.

TELSON (Fig. 6.11C–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. 6.11H–J). On body ring 5 with a swollen lobe; posterior surface of lobe with a pore, pore not borne on a stalk.

LEGS (Fig. 6.11E–G). Male femora without modification (Male femora 5, 6 and 7 unmodified).

GONOPODS (Figs 6.3, 6.12, 6.13). Coxa (cx) subequal in length to femorite or longer than femorite. Cannula (ca) quite short and stout. Femorite (fe) long and slender, curved. Solenophore (sph) wide laterally: lamina lateralis (ll) broad: lamina medialis (lm) wide, distally blunt, *in situ* directed mesoventrad.

Distribution and habitat

G. gigas 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* 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* 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 and 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* 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. 6.9B, 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, 2018b). 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 sp. nov.

(Figs 6.14–6.18)

Material examined

Holotype

THAILAND: ♂ male, Trang Province, Palian District, Tham Khao Ting, 7°09'30"N, 99°48'10"E, ca. 42 m a.s.l., 31 Aug. 2015, ASRU members leg. (CUMZ).

Paratypes

THAILAND: 5 ♂♂, 1 ♀, same data as holotype (CUMZ).

Further specimens, not paratypes

THAILAND:1 juvenile, Trang Province, Palian District, Tham Khao Ting, 7°09'30"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), 7°00'47"N, 100°09'43"E, ca. 348 m a.s.l., 12 Jan. 2009, ASRU members leg. (CUMZ).

Etymology

The name 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.

Diagnosis

Male femora 5, 6 and 7 with an apophysis. Similar in this respect to *G. suratensis* 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).

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. 6.14A, 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. 6.15A). 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. 20°–40°.

ANTENNAE (Fig. 6.15D). 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. 6.15A–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 6.15A–C, F, 6.16A, B). Moderately long, directed caudolaterad on body rings 2–16, elevated at ca. 40°–50° (male) 30°–40° (female), directed increasingly caudad on body rings 17–19.

TELSON (Fig. 6.16C–G). Tip of epiproct subtruncate; apical tubercles inconspicuous. Hypoproct usually subsemicircular (some specimens subtrapeziform); caudal margin slightly round, with conspicuous setiferous tubercles.

STERNUM (Fig. 6.16H–J). On body ring 5 with a swollen lobe; posterior surface of lobe with a pore borne on a short cylindrical stalk.

LEGS (Fig. 6.15E–H). Male femora 5, 6 and 7 with an apophysis.

GONOPODS (Figs 6.17, 6.18). Coxa (cx) longer than prefemoral part, subequal in length to femorite. Cannula (ca) quite short and stout. Femorite (fe) long and slender, curved. Solenophore (sph) wide laterally: lamina lateralis (ll) broad: lamina medialis (lm) 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* 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. *G. parvoterga* sp. nov. exhibits some variation in shape of hypoproct: subtrapeziform in some specimens, subsemicircular in the others.

Gigaxytes suratensis Srisonchai, Enghoff & Panha sp. nov.

(Figs 6.19–6.23)

Material examined

Holotype

THAILAND: ♂, Surat Thani Province, Phanom District, Ban Song Phi Nong, 8°50'54"N, 98°44'16"E, ca. 117 m a.s.l., 7 Aug. 2016, ASRU members leg. (CUMZ).

Paratypes

THAILAND: 3 ♂♂, 6 ♀♀, 13 juveniles, same data as holotype (CUMZ); 1 ♂, 1 ♀, same data as holotype (ZMUC).

Further specimens, not paratypes

THAILAND, Surat Thani Province: 1 ♂, 1 broken ♂ – right gonopod lost, 1 ♀, 1 broken ♀, 4 juveniles, Ban Ta Khun District, Ratchaprapa Dam, 8°57'22"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, 8°55'47"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, 9°01'48"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, 8°52'44"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, 8°53'07"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).

Etymology

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

Diagnosis

Male femora 5, 6 and 7 with an apophysis. Similar in this respect to *G. parvoterga* 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).

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. 6.19A–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. 6.20A). 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. 30°–45°.

ANTENNAE (Fig. 6.20D). 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. 6.20A–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 (Fig. 6.2B). On body ring 2 long, crest-like; on ring 3 a long ridge; on ring 4 a short ridge; thereafter missing.

PARATERGA (Figs 6.20A–C, I, 6.21A, B). Moderately long, directed caudolaterad on body rings 2–17, elevated at ca. 45°–60° (male) 40°–50° (female), directed increasingly caudad on body rings 18–19.

TELSON (Fig. 6.21C–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. 6.21H–J). On body ring 5 with a swollen lobe; posterior surface of lobe with a pore borne on a short cylindrical stalk.

LEGS (Fig. 6.20E–H). Male femora 5, 6 and 7 with an apophysis.

GONOPODS (Figs 6.22, 6.23). Coxa (cx) subequal in length to femorite. Cannula (ca) quite short and stout. Femorite (fe) long, slender, curved. Solenophore (sph) wide laterally: lamina lateralis (ll) broad: lamina medialis (lm) very wide, distally blunt, *in situ* directed mesoventrad.

Distribution and habitat

G. suratensis 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* 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

(Attems, 1936, 1937, 1938, 1953; Chamberlin, 1923, 1941; Cook and Loomis, 1924a; Enghoff *et al.*, 2007; Golovatch and Enghoff, 1994; Golovatch *et al.*, 2010; Golovatch *et al.*, 2012; Golovatch *et al.*, 2016; Jeekel, 1964, 1980a; Likhitrakarn *et al.*, 2015; Liu *et al.*, 2014, 2016; Nguyen *et al.*, 2005; Pocock, 1895; Srisonchai *et al.*, 2016, 2018a, 2018b; Zhang, 1986; Zhang and Li, 1982). 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* comb. nov., *G. parvoterga* sp. nov. and *G. suratensis* 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* sp. nov. and *G. suratensis* sp. nov., although they are morphologically most similar (gonopod shape and modification of male femora 5–7), *G. parvoterga* sp. nov. can be differentiated from *G. suratensis* 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* comb. nov., *G. parvoterga* sp. nov. and *G. suratensis* 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* 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, 2018b). A very different type of mite was found on *G. fusca* sp. nov. as shown in Fig. 6.4D, 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 and 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. 6.24). 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 *Gigixytes*, only one is currently known to have a relatively wide distribution range, viz., *G. gigas* 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 (Golovatch *et al.*, 2016; Likhitrakarn *et al.*, 2015; Liu *et al.*, 2014, 2016; Srisonchai *et al.*, 2016, 2018a, 2018b) 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.

Acknowledgements

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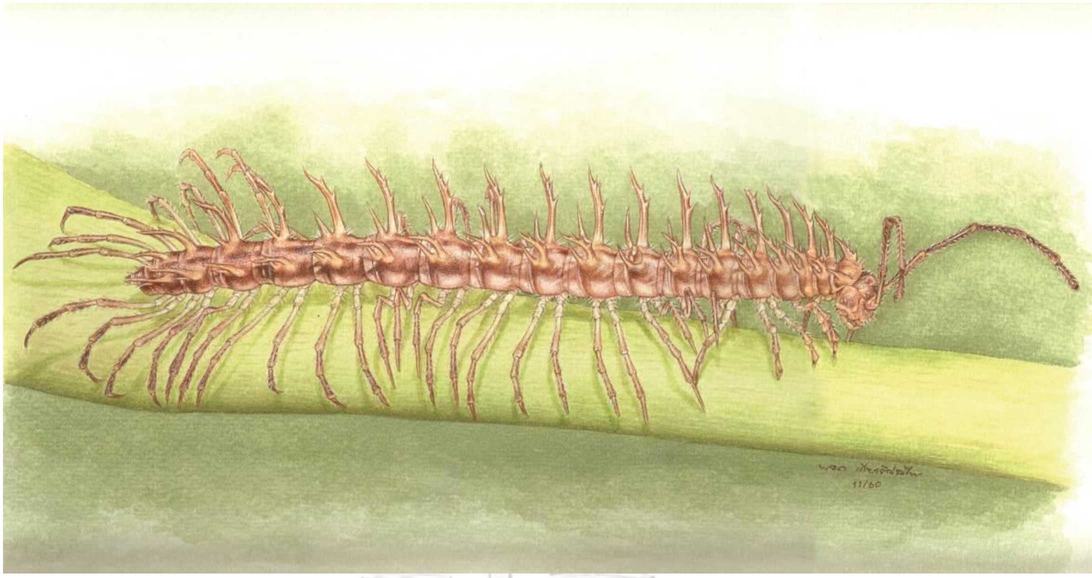

Figure 6.1 *Gigaxytes fusca* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype. Watercolour by Photchana Kriatpraprai.

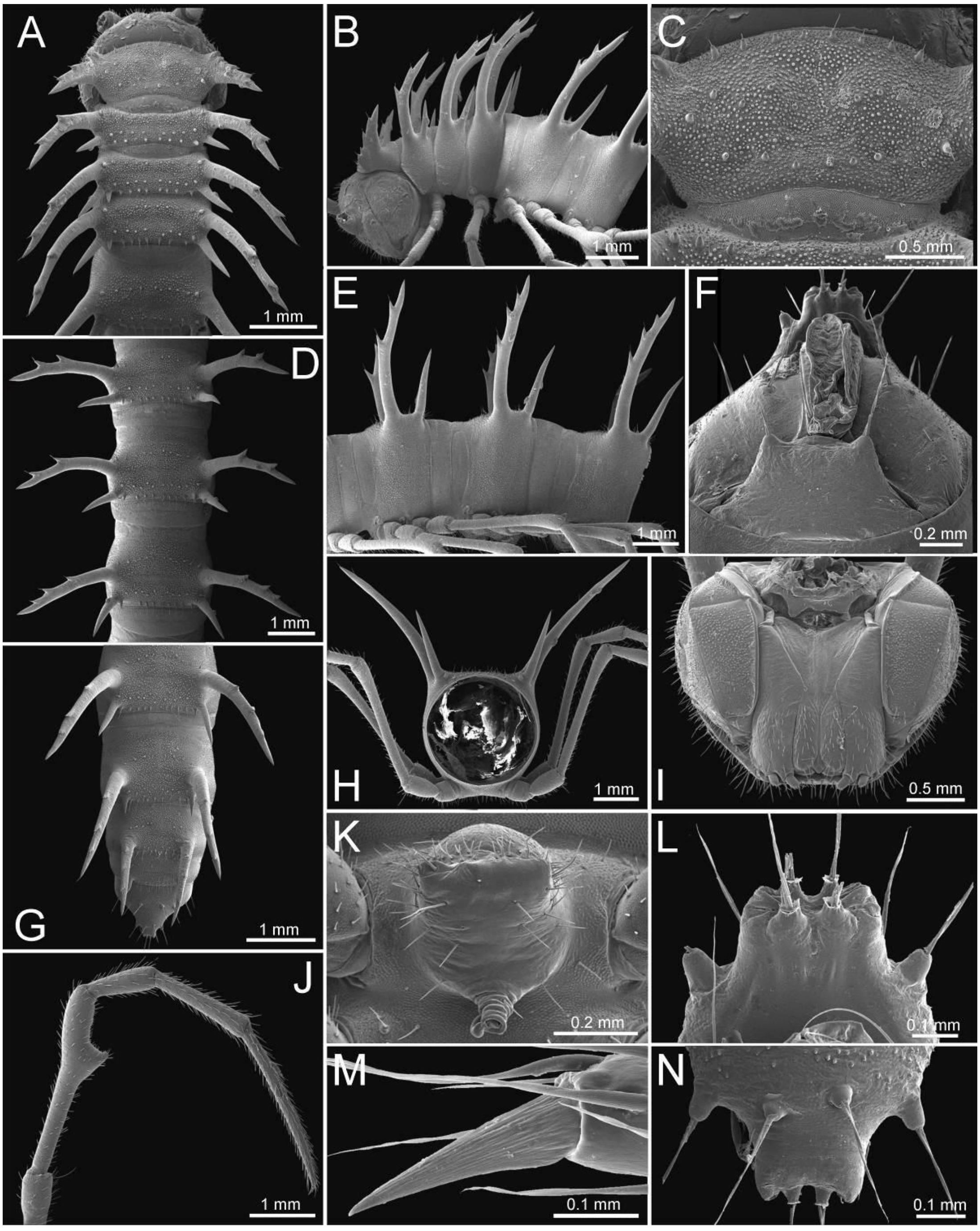

Figure 6.2 General body characters of *Gigaxytes* gen. nov. (*G. fusca* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype) – SEM images. **A**, **B**. Anterior body part (arrows point to pleurosternal carinae). **C**. Collum. **D**. Body rings 9–10. **E**. Body rings 8–10. **F**. Telson. **G**. 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.

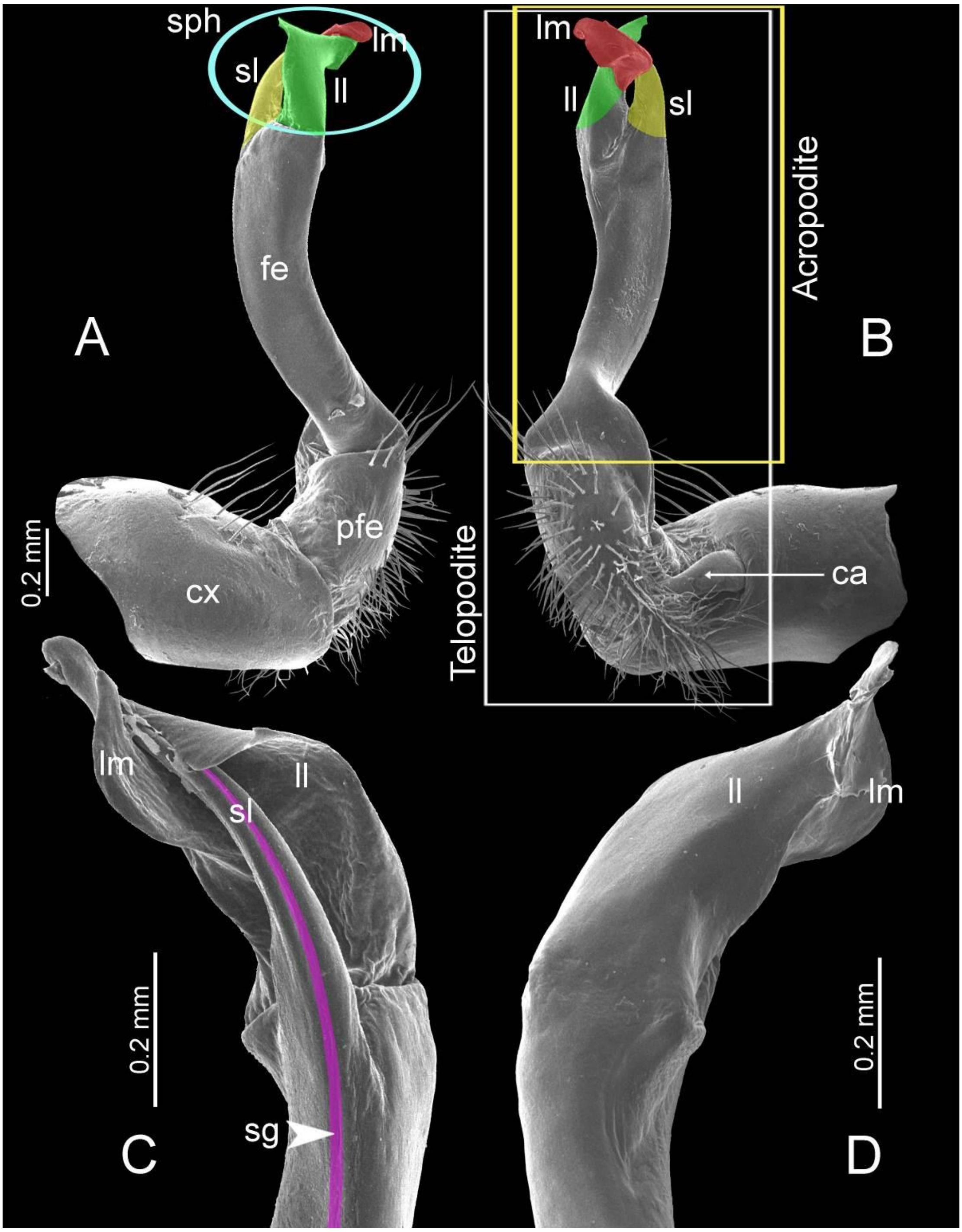

Figure 6.3 SEM images of right gonopod of *Gigaxytes* Srisonchai, Enghoff & Panha gen. nov. – *Gigaxytes gigas* (Golovatch & Enghoff, 1994) gen. et comb. nov., specimen from Wat Tham Sue (Tiger Cave). **A**. Lateral view. **B**. Mesal view. **C**. Dorsal view. **D**. Ventral view. Colours: red = lamina medialis (lm), yellow = solemomere (sl), green = lamina lateralis (ll), purple = seminal groove (sg).

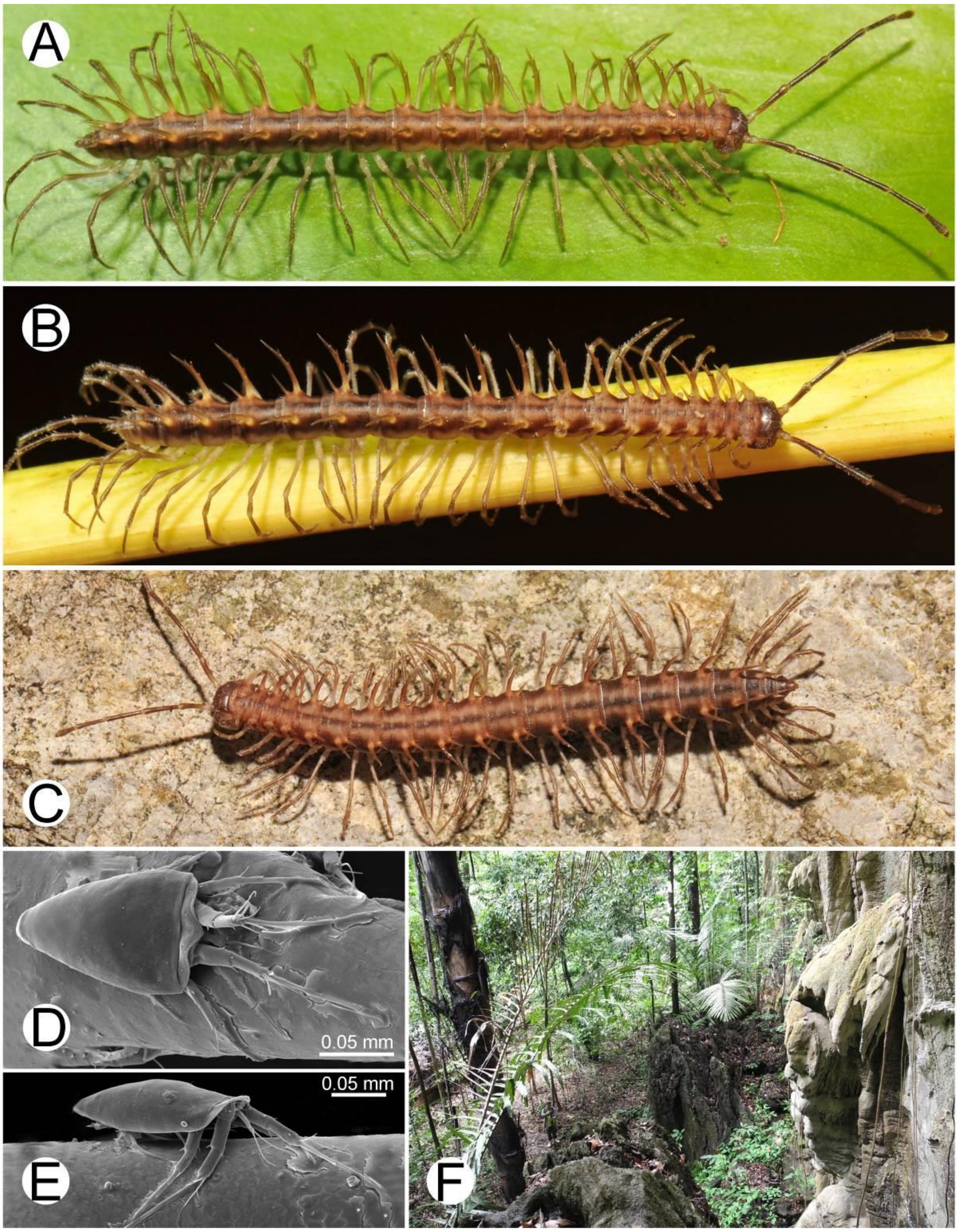

Figure 6.4 Photographs of live *Gigaxytes fusca* Srisonchai, Enghoff & Panha gen. et sp. nov. **A.** ♂ paratype, specimen from Phitsadarn Cave. **B.** ♂ paratype, specimen from Phrayarhtan Cave (Buddha Cave). **C.** ♀ paratype, specimen from Phitsadarn Cave. **D**, **E**. Phoretic histiostomatid mites. **F**. Habitat.

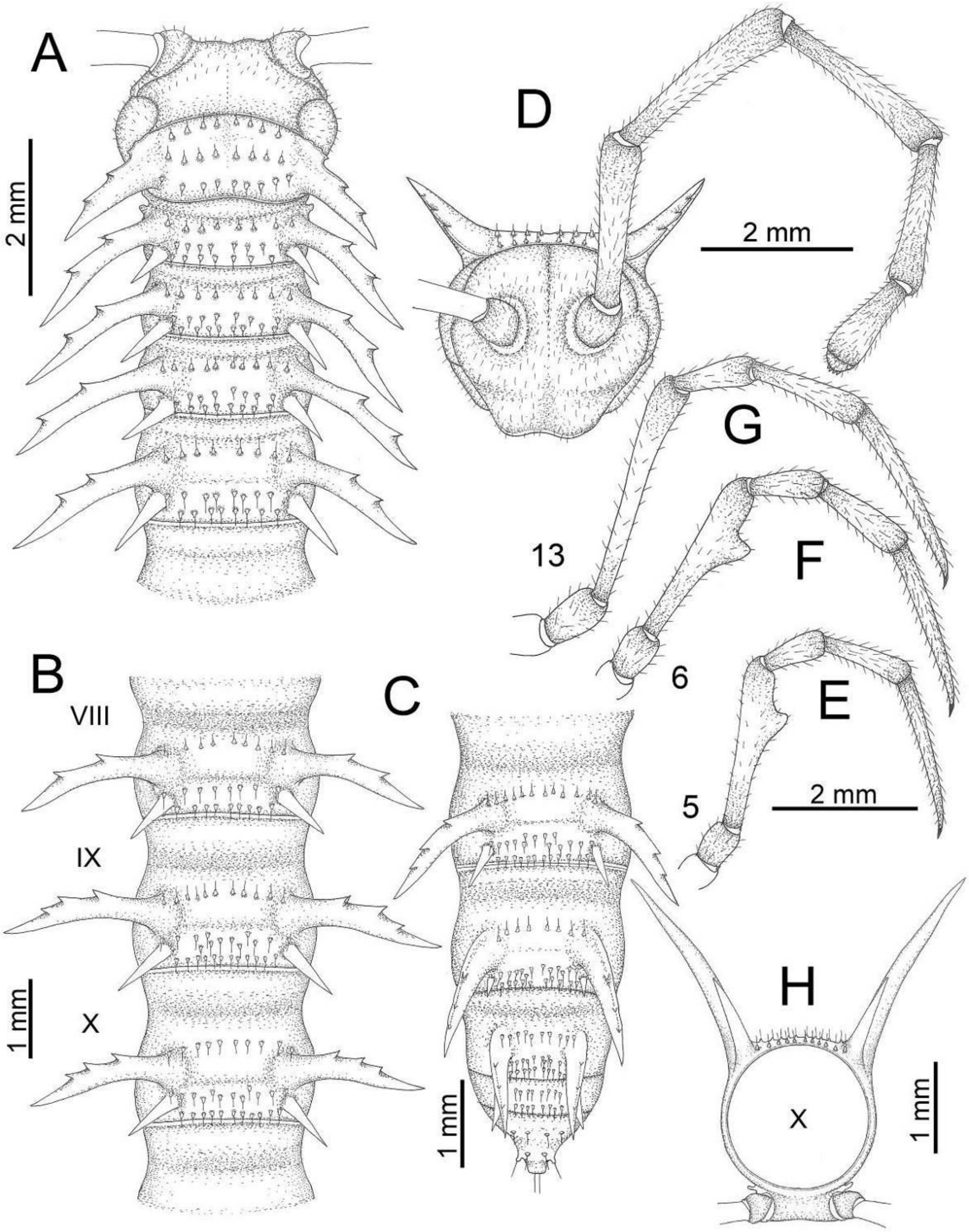

Figure 6.5 *Gigaxytes fusca* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype. **A**. Anterior body part. **B**. Body rings 8–10. **C**. Posteriormost body rings and telson. **D**. Head and antenna. **E.** ♂ leg 5 (right). **F.** ♂ leg 6 (right). **G.** ♂ leg 13 (right). **H.** Midbody ring.

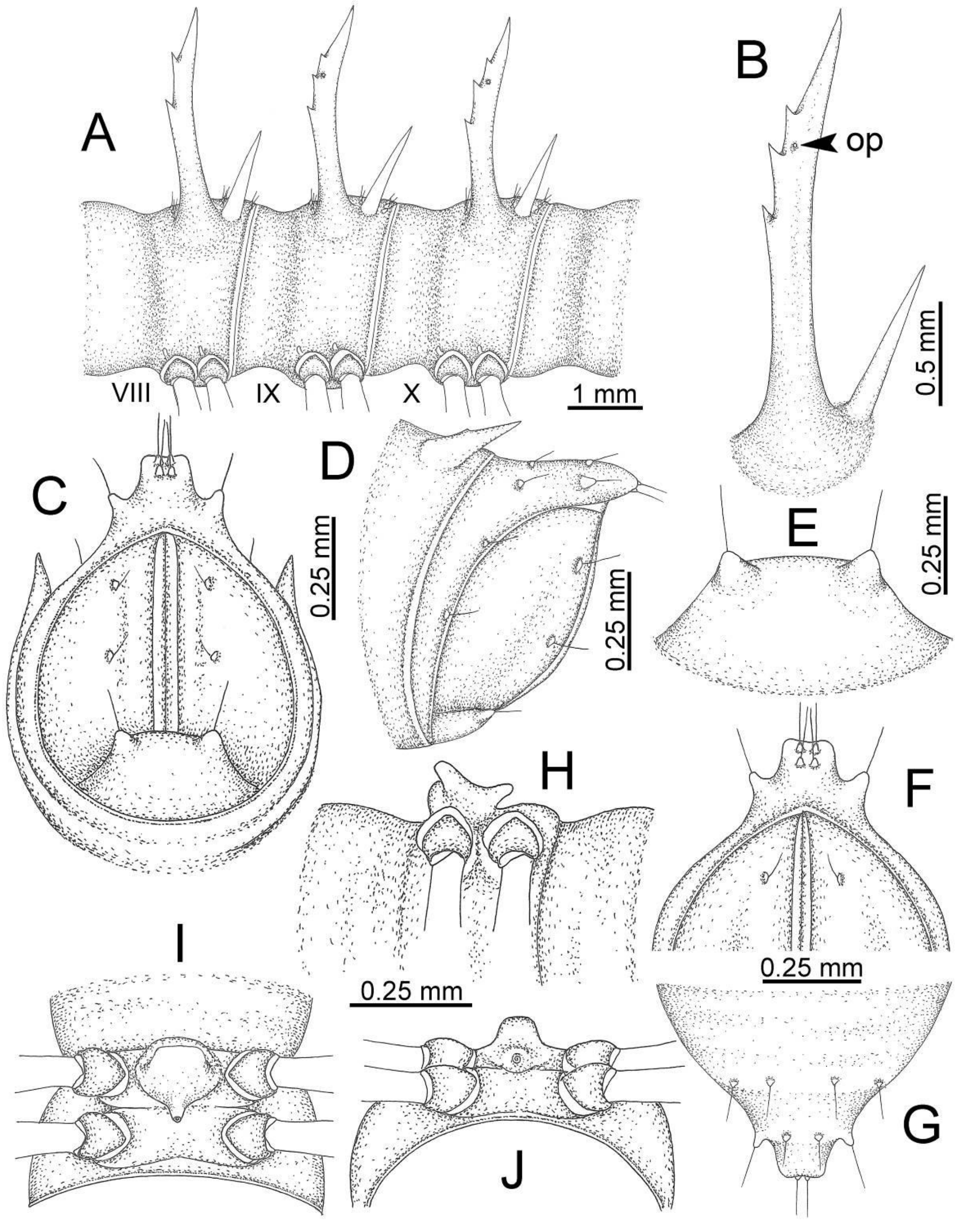

Figure 6.6 *Gigaxytes fusca* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype. **A**. Body rings 8–10. **B**. Paraterga of ring 10 (op = ozopore). **C**, **D**. Last ring and telson. **E**. Hypoproct. **F**, **G**. Epiproct. **H–J**. Sternal lobe between male coxae 4.

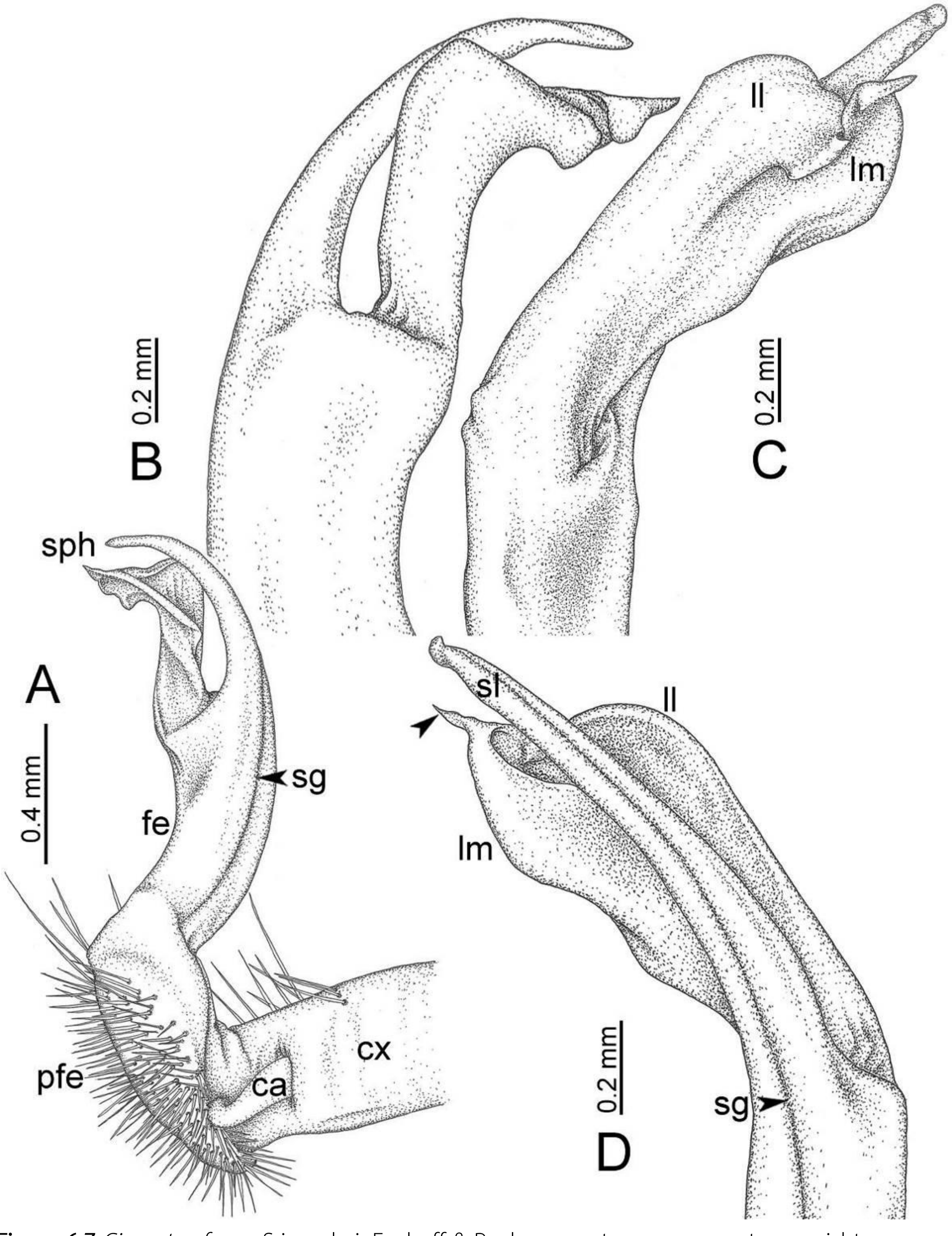

Figure 6.7 *Gigaxytes fusca* Srisonchai, Enghoff & Panha gen. et sp. nov., paratype – right gonopod. **A**. Mesal view. **B**. Lateral view. **C**. Ventral view. **D**. Dorsal view (arrow = sharp tip of lm).

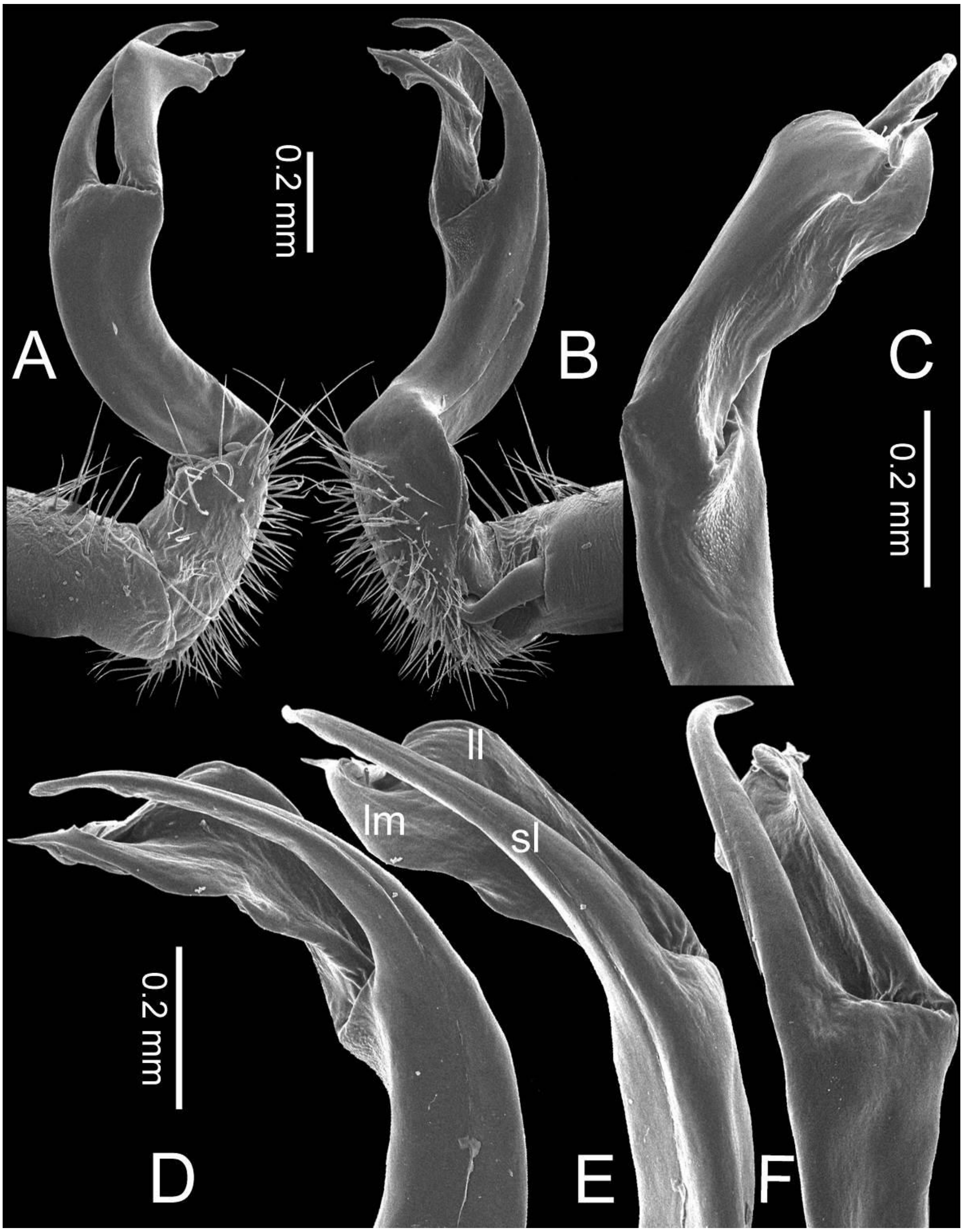

Figure 6.8 *Gigaxytes fusca* Srisonchai, Enghoff & Panha gen. et sp. nov., paratype – right gonopod. **A**. Lateral view. **B**. Mesal view. **C**. Ventral view. **D**, **F**. Subdorsal view. **E**. Dorsal view.

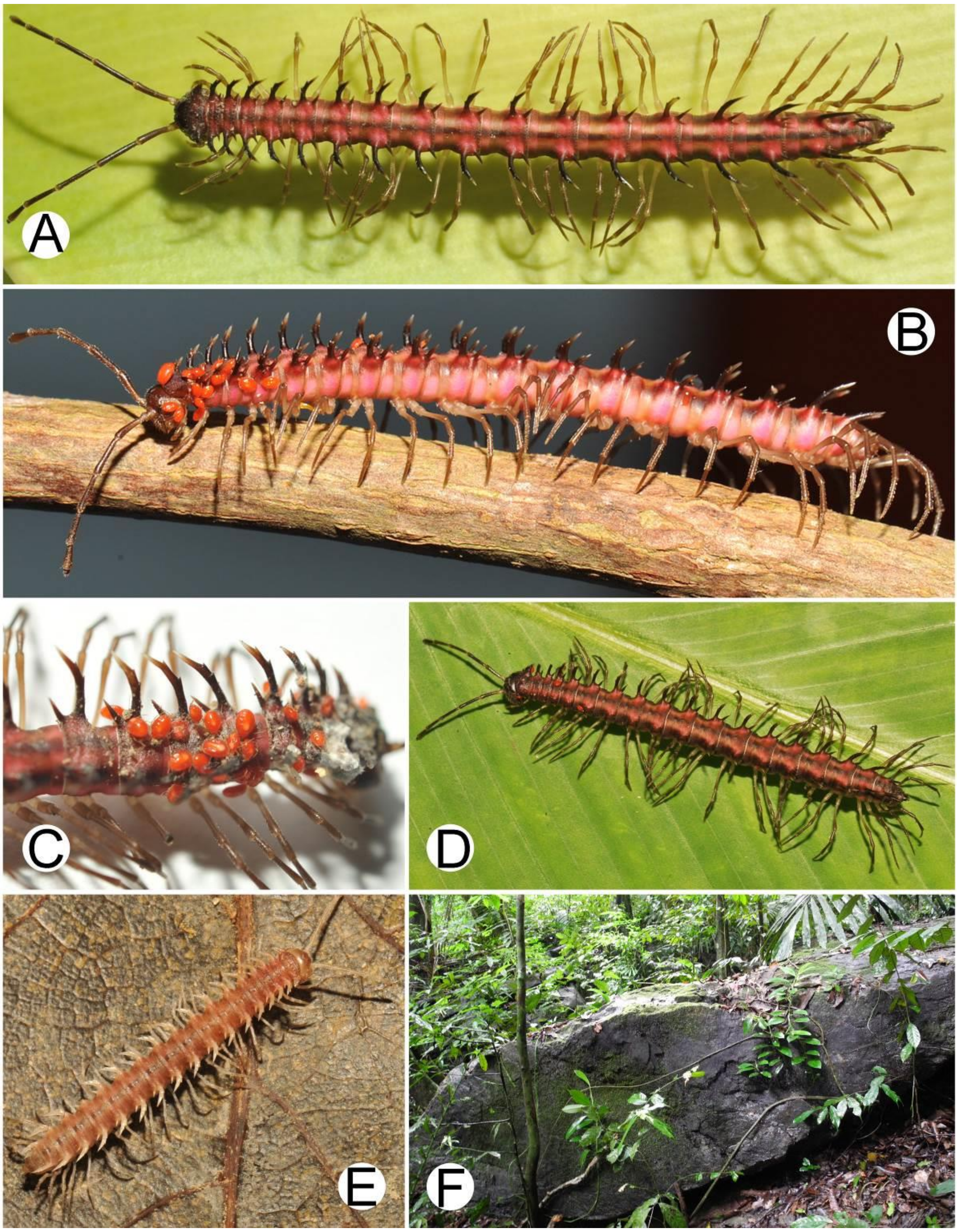

Figure 6.9 A–E. Photographs of live *Gigaxytes gigas* (Golovatch & Enghoff, 1994) gen. et comb. nov. **A**. ♂, specimen from Wat Tham Sue (Tiger Cave). **B**. ♂, specimen from Wat Tham Phra Phut. **C**. Parasitic ?*Leptus* mites on ♂. **D**. ♀, specimen from Wat Tham Sue (Tiger Cave). **D**, **E**. Juvenile. **F**. Habitat.

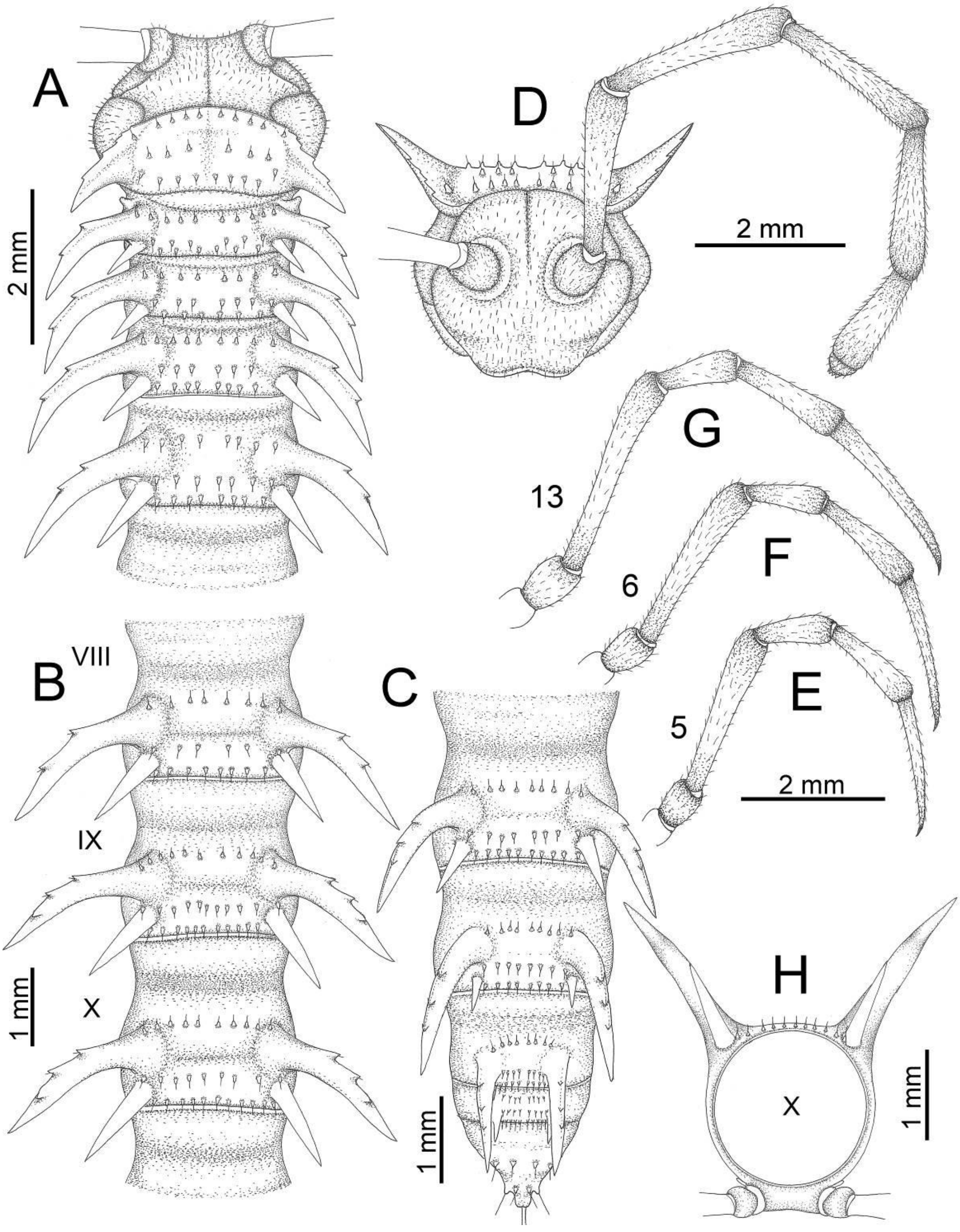

Figure 6.10 *Gigaxytes gigas* (Golovatch & Enghoff, 1994) gen. et comb. nov., ♂ specimen from Wat Tham Sue (Tiger Cave). **A**. Anterior body part. **B**. Body rings 8–10. **C**. Posteriormost body rings and telson. **D**. Head and antenna. **E**. ♂ leg 5 (right). **F**. ♂ leg 6 (right). **G**. ♂ leg 13 (right). **H**. Midbody ring.

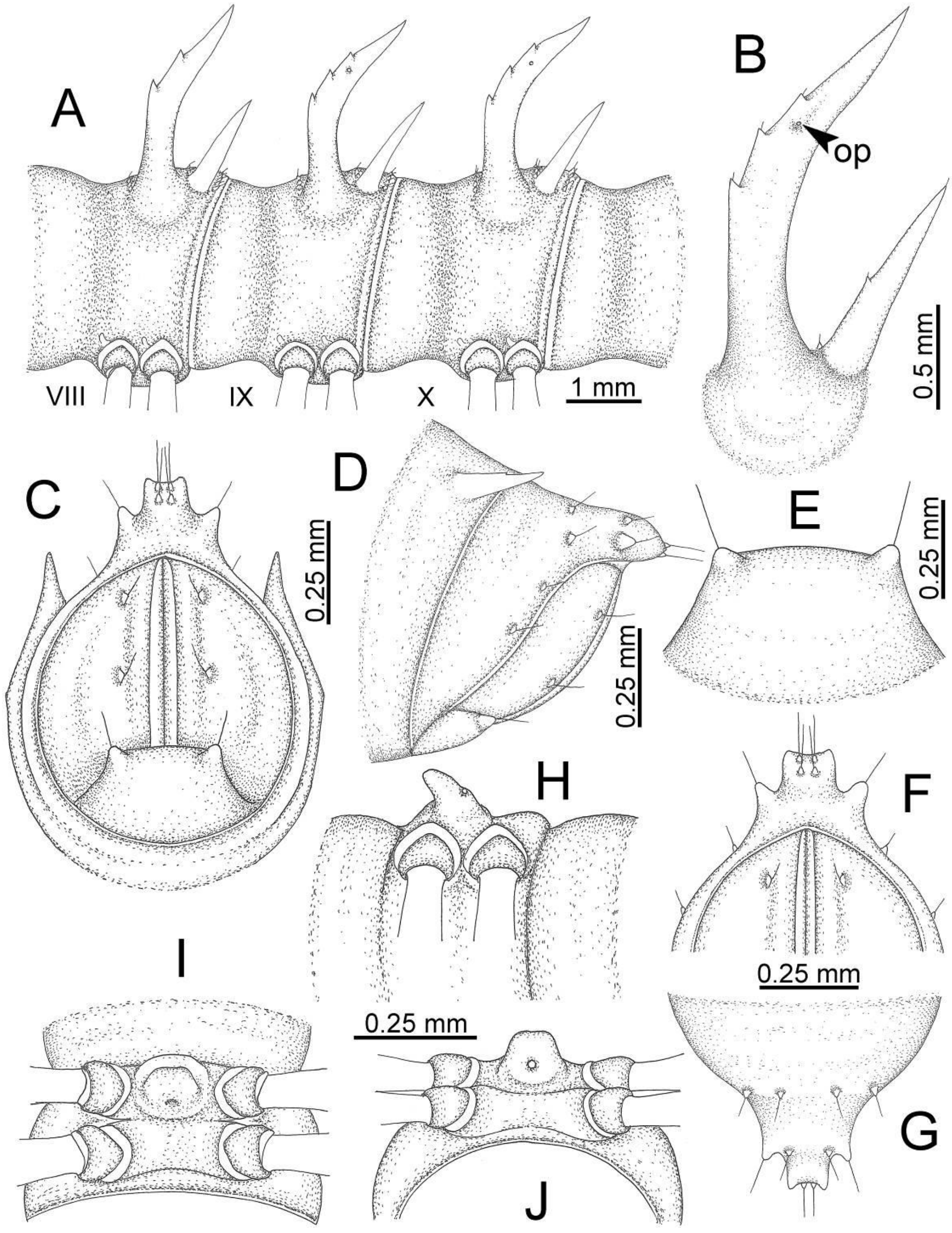

Figure 6.11 *Gigaxytes gigas* (Golovatch & Enghoff, 1994) gen. et comb. nov., ♂ specimen from Wat Tham Sue (Tiger Cave). **A**. Body rings 8–10. **B**. Paraterga of ring 10 (op). **C**, **D**. Last ring and telson. **E**. Hypoproct. **F**, **G**. Epiproct. **H–J**. Sternal lobe between male coxae 4.

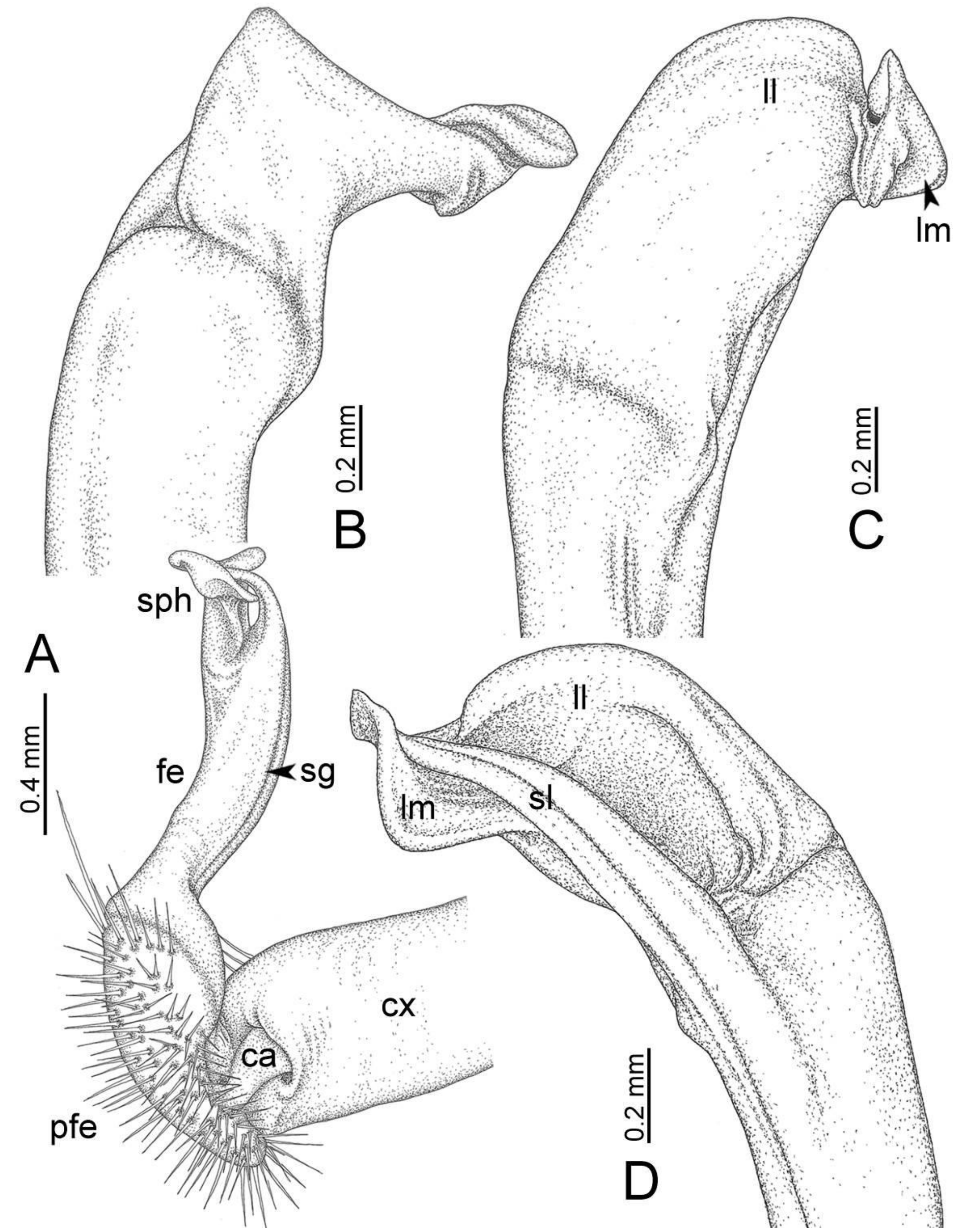

Figure 6.12 *Gigaxytes gigas* (Golovatch & Enghoff, 1994) gen. et comb. nov., specimen from Wat Tham Sue (Tiger Cave) – right gonopod. **A**. Mesal view. **B**. Lateral view. **C**. Ventral view. **D**. Dorsal view.

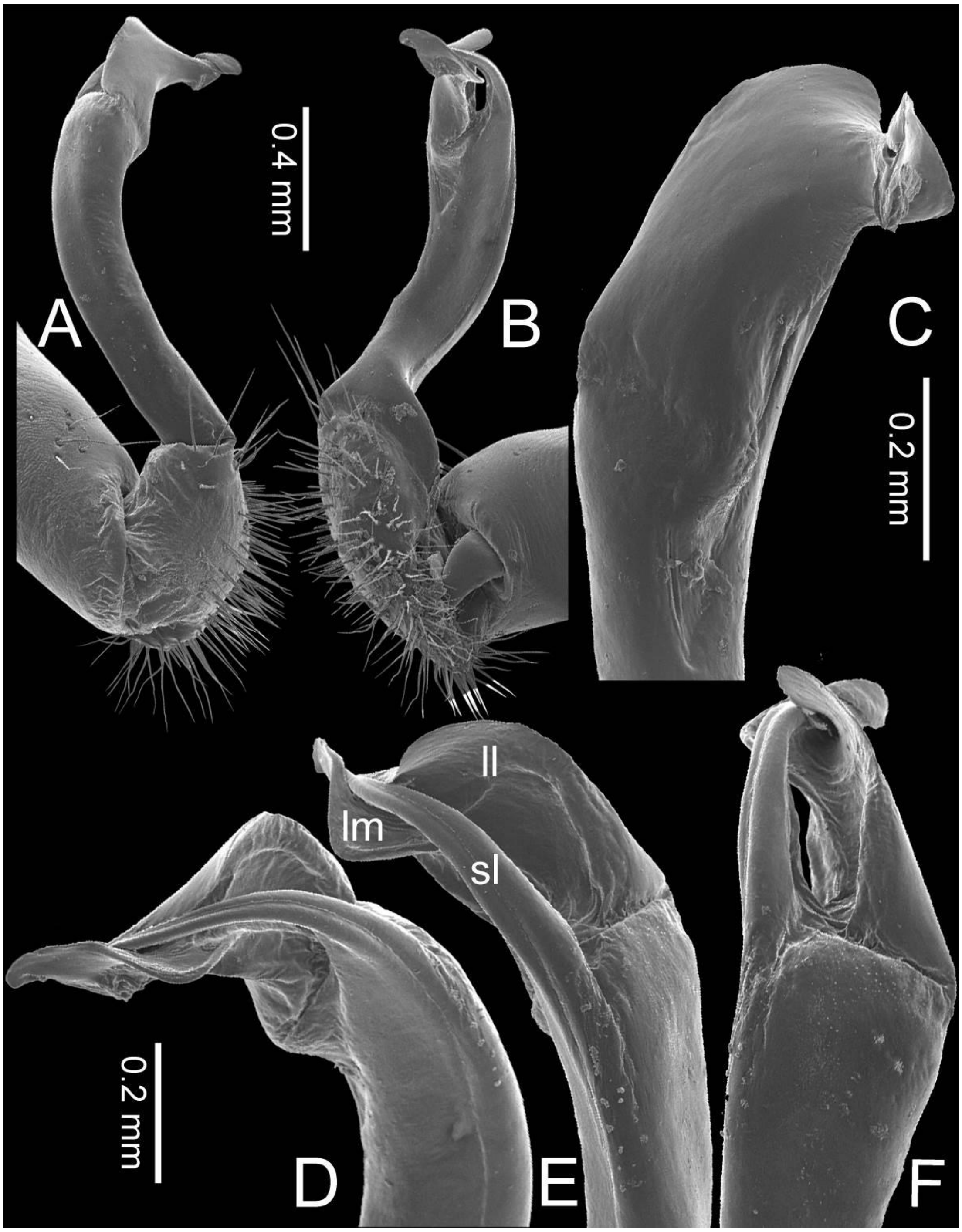

Figure 6.13 *Gigaxytes gigas* (Golovatch & Enghoff, 1994) gen. et comb. nov., specimen from Wat Tham Sue (Tiger Cave) – right gonopod. **A**. Lateral view. **B**. Mesal view. **C**. Ventral view. **D**, **F**. Subdorsal view. **E**. Dorsal view.

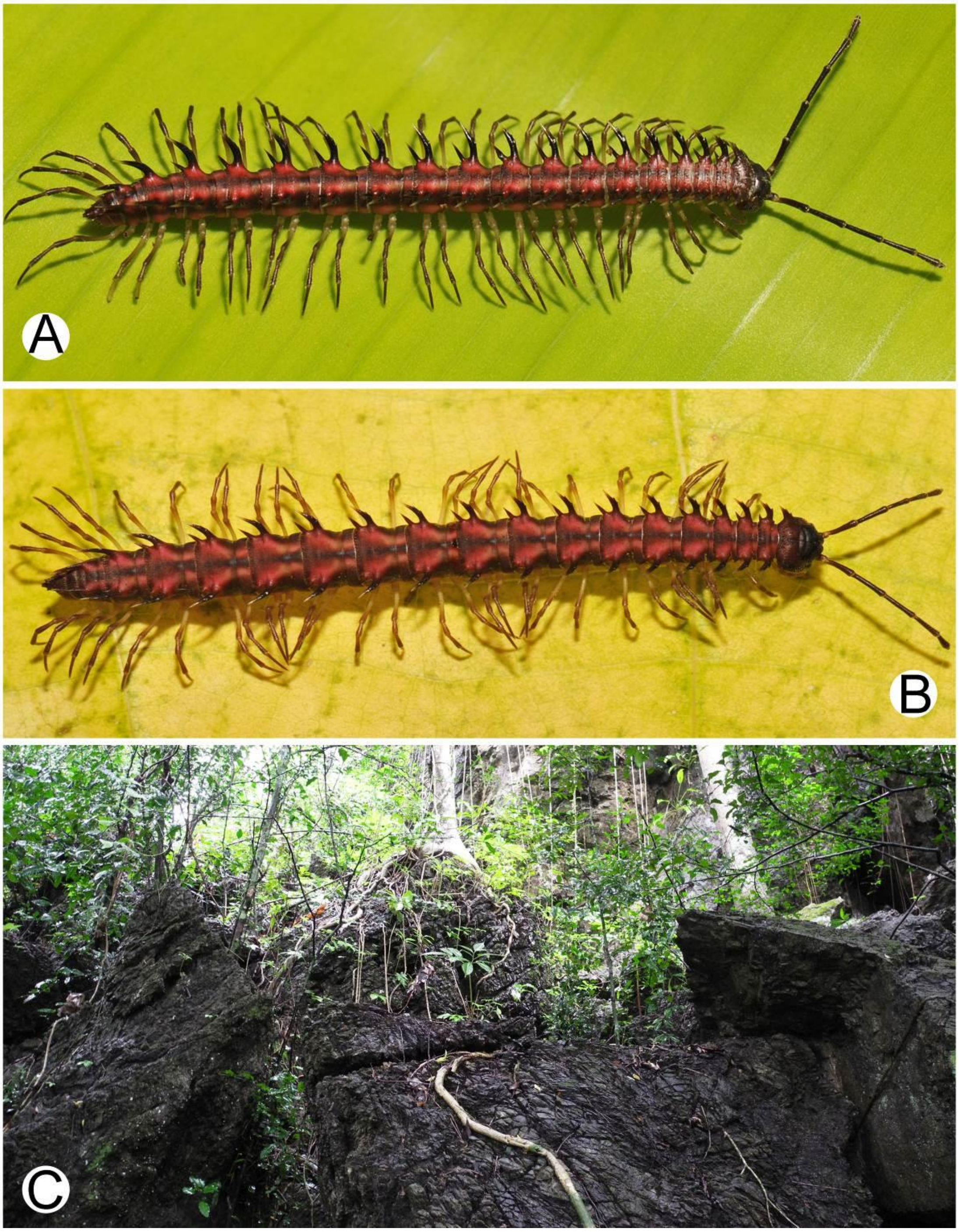

Figure 6.14 **A**, **B**. Photographs of live *Gigaxytes parvoterga* Srisonchai, Enghoff & Panha gen. et sp. nov., specimen from Tham Khao Ting **A.** ♂ paratype. **B.** ♀ paratype. **C.** Habitat.

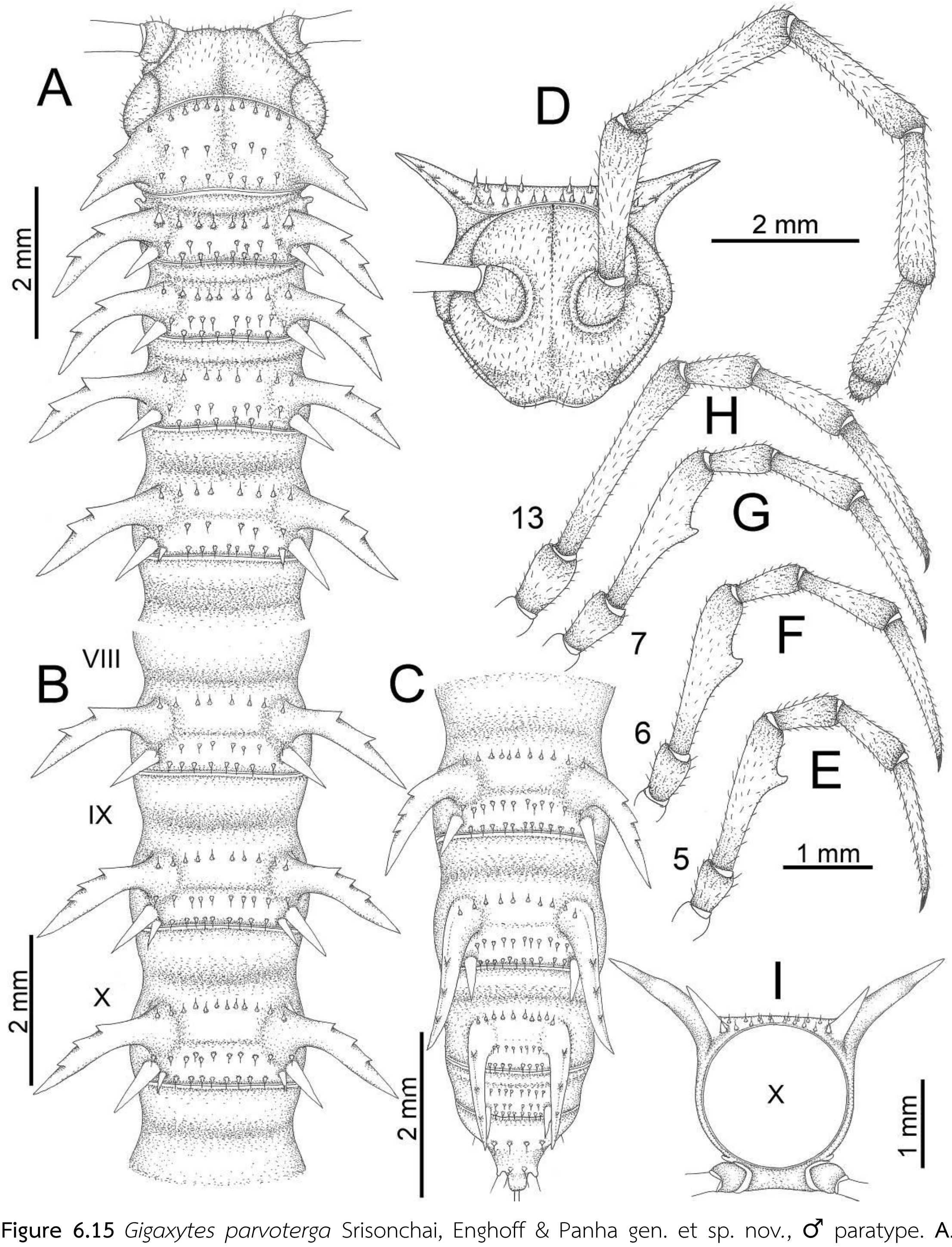

Figure 6.15 *Gigaxytes parvoterga* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype. **A**. Anterior body part. **B**. Body rings 8–10. **C**. Posteriormost body rings and telson. **D**. Head and antenna. **E**. ♂ leg 5 (right). **F**. ♂ leg 6 (right). **G**. ♂ leg 7 (right). **H**. ♂ leg 13 (right). **I**. Midbody ring.

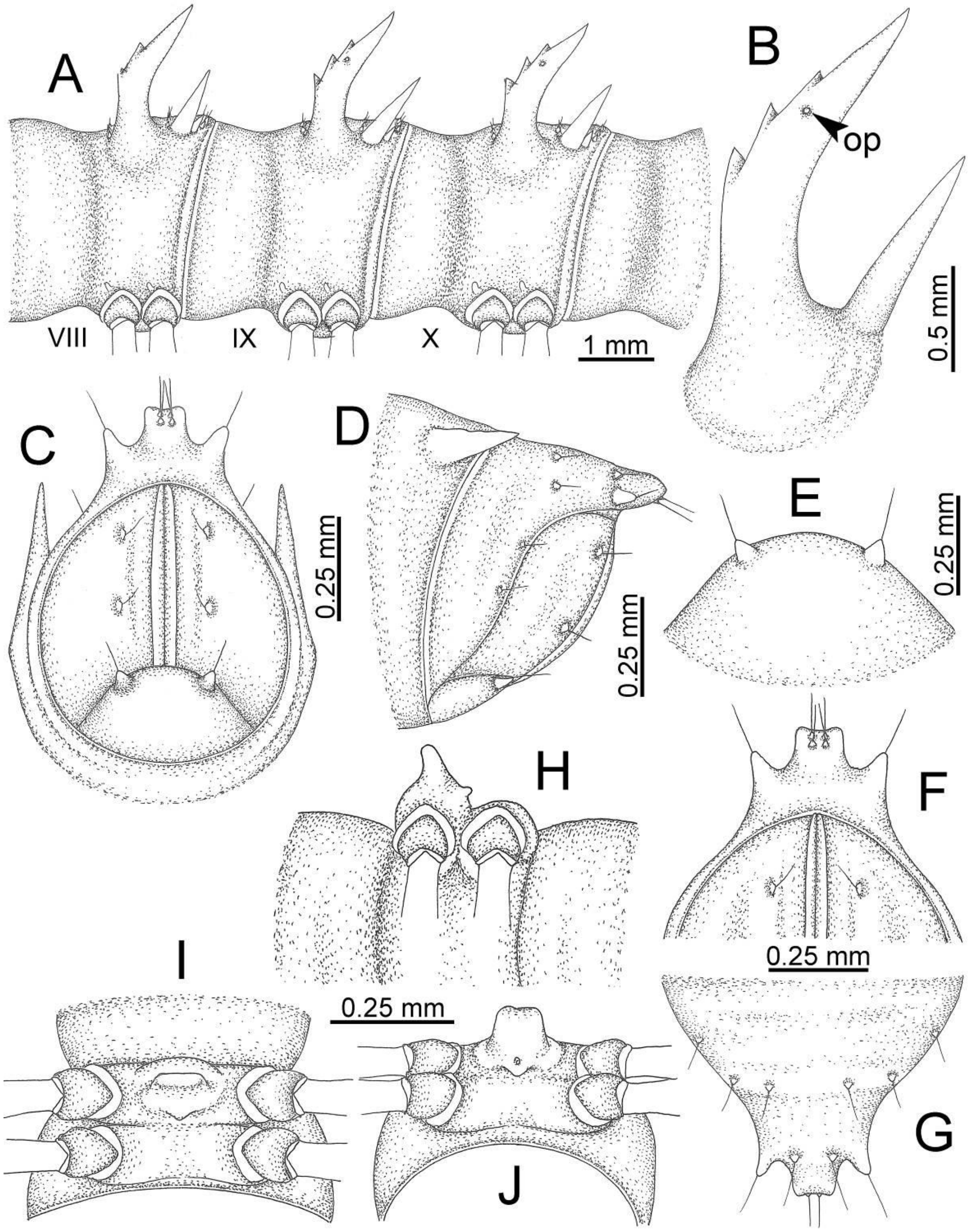

Figure 6.16 *Gigaxytes parvoterga* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype. **A**. Body rings 8–10. **B**. Paraterga of ring 10 (op = ozopore). **C**, **D**. Last ring and telson. **E**. Hypoproct. **F**, **G**. Epiproct. **H–J**. Sternal lobe between male coxae 4.

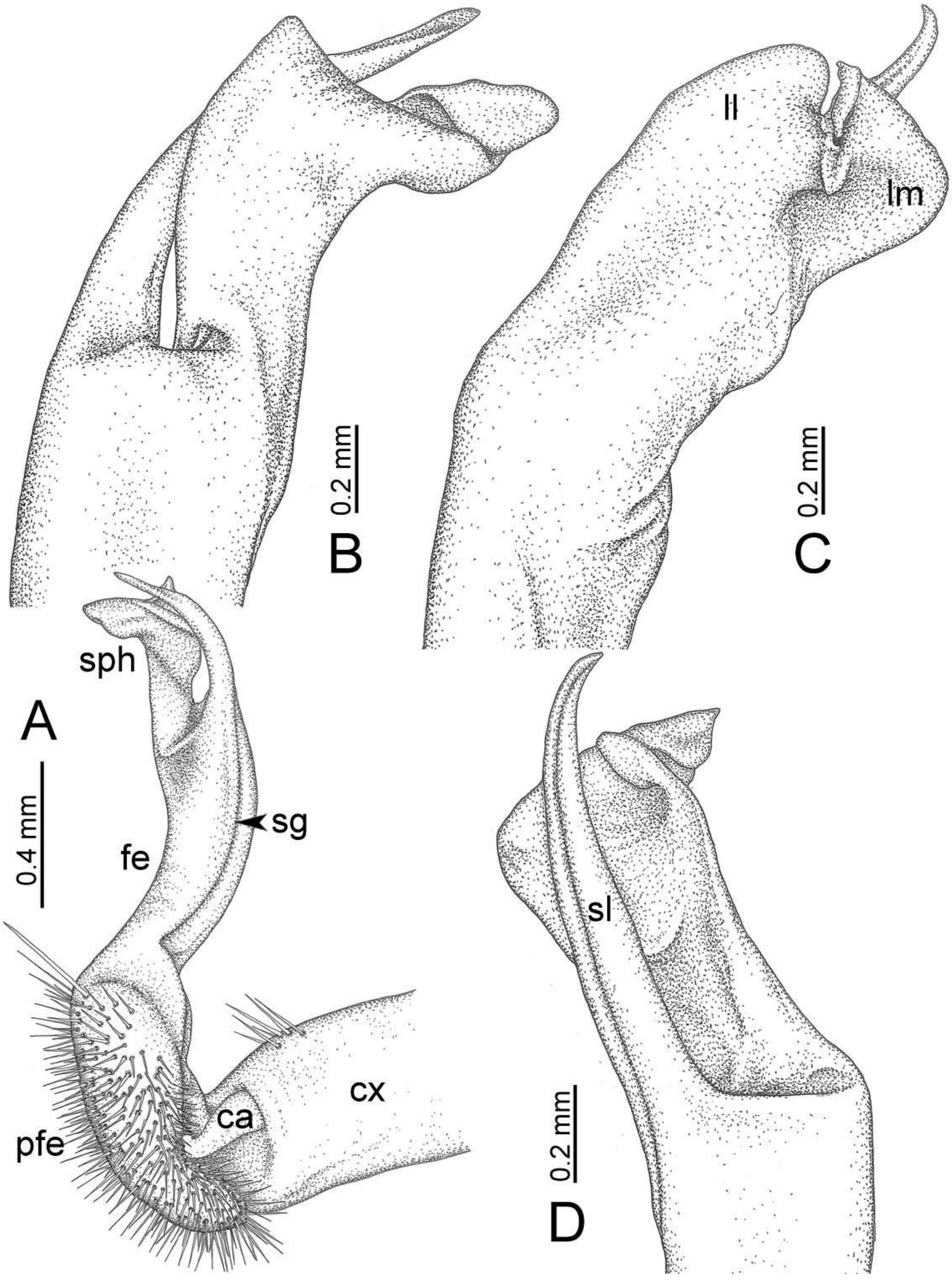

Figure 6.17 *Gigaxytes parvoterga* Srisonchai, Enghoff & Panha gen. et sp. nov., paratype – right gonopod. **A**. Mesal view. **B**. Lateral view. **C**. Ventral view. **D**. Dorsal view.

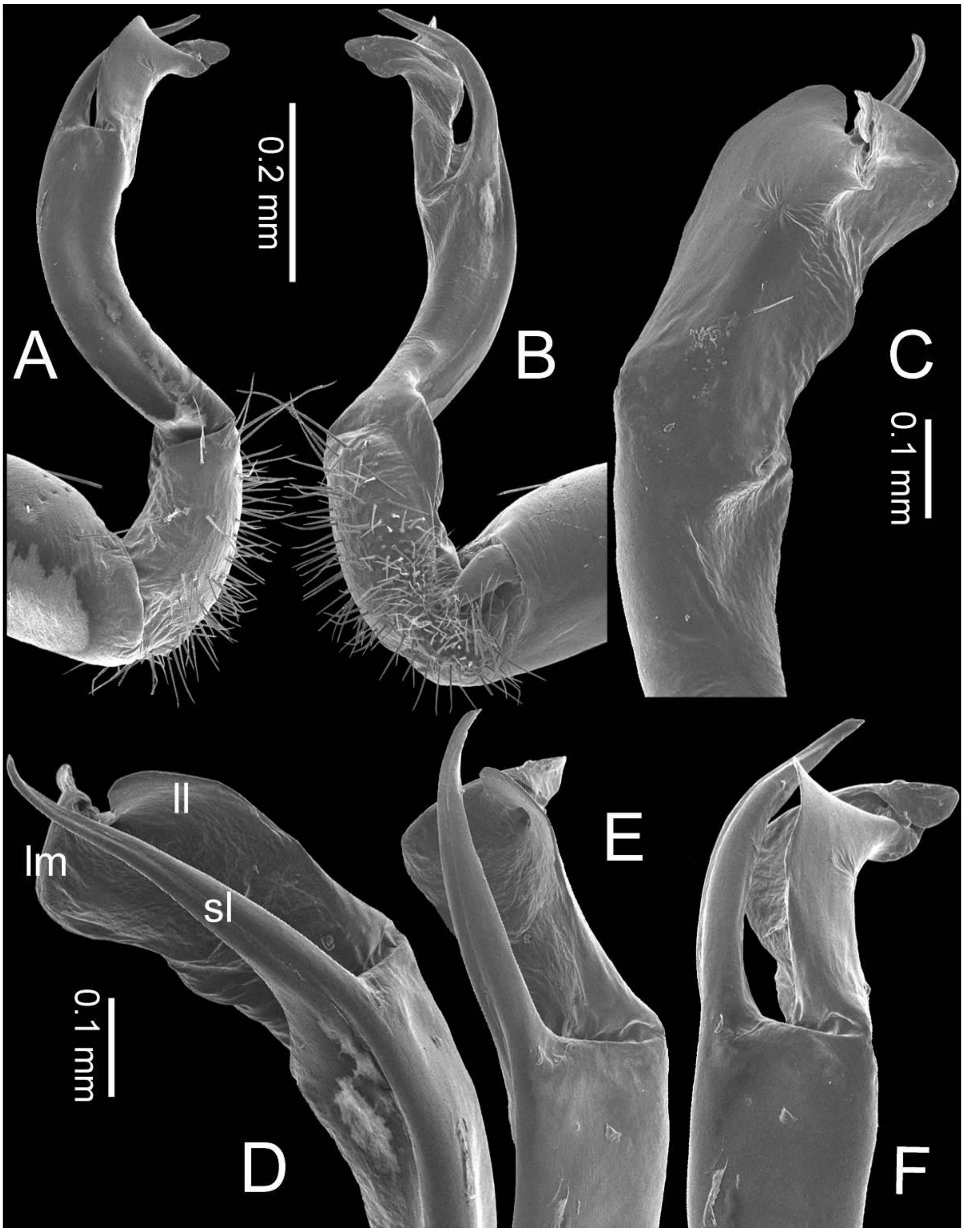

Figure 6.18 *Gigaxytes parvoterga* Srisonchai, Enghoff & Panha gen. et sp. nov., paratype – right gonopod. **A**. Lateral view. **B**. Mesal view. **C**. Ventral view. **D**, **F**. Subdorsal view. **E**. Dorsal view.

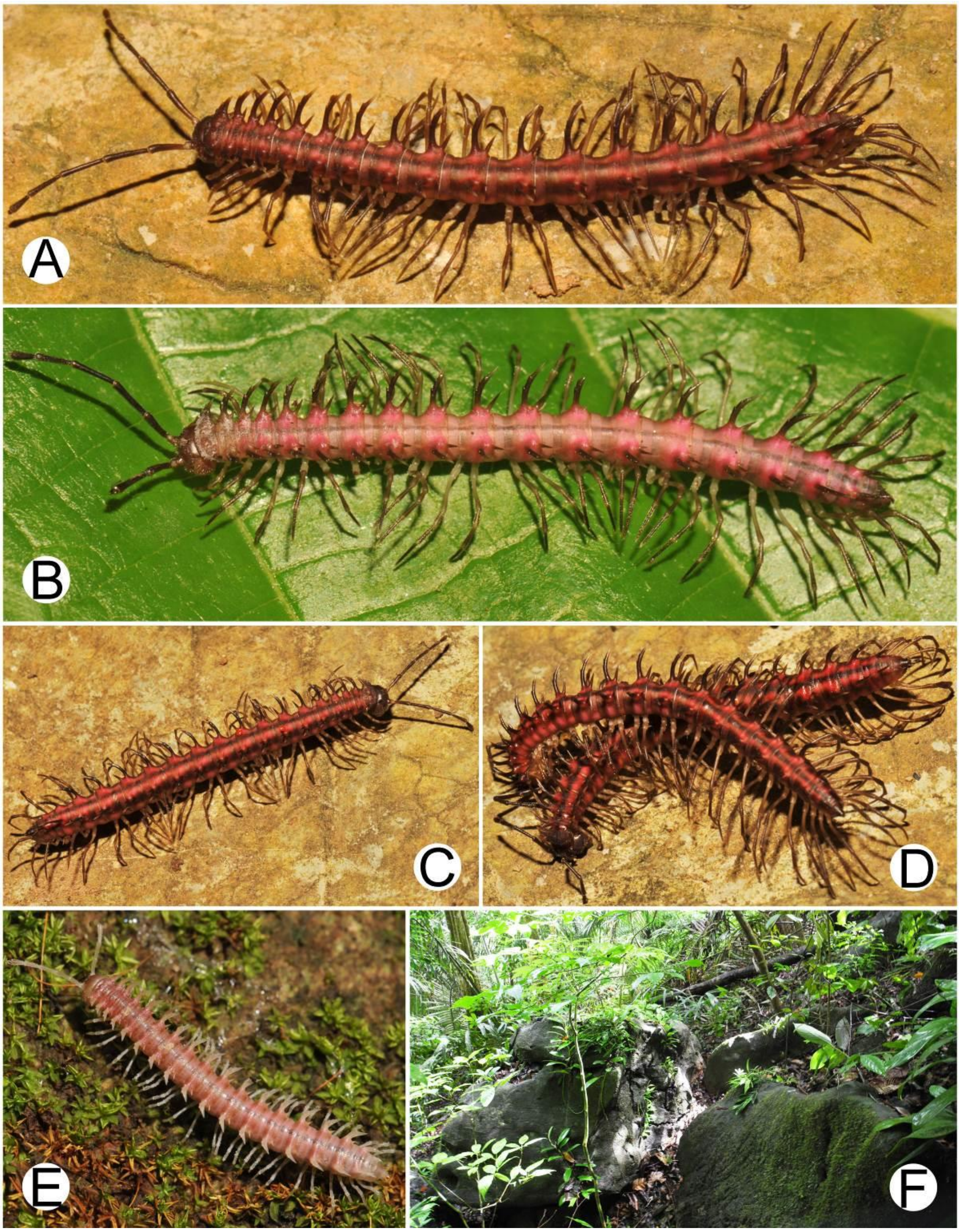

Figure 6.19 A–E. Photographs of live *Gigaxytes suratensis* Srisonchai, Enghoff & Panha gen. et sp. nov. **A**. ♂ paratype, specimen from Ban Song Phi Nong. **B**. ♂, specimen from Wat Satit Khirirom. **C**. ♀ paratype, specimen from Ban Song Phi Nong. **D**. Mating couple (paratypes). **E**. Juvenile. **F**. Habitat.

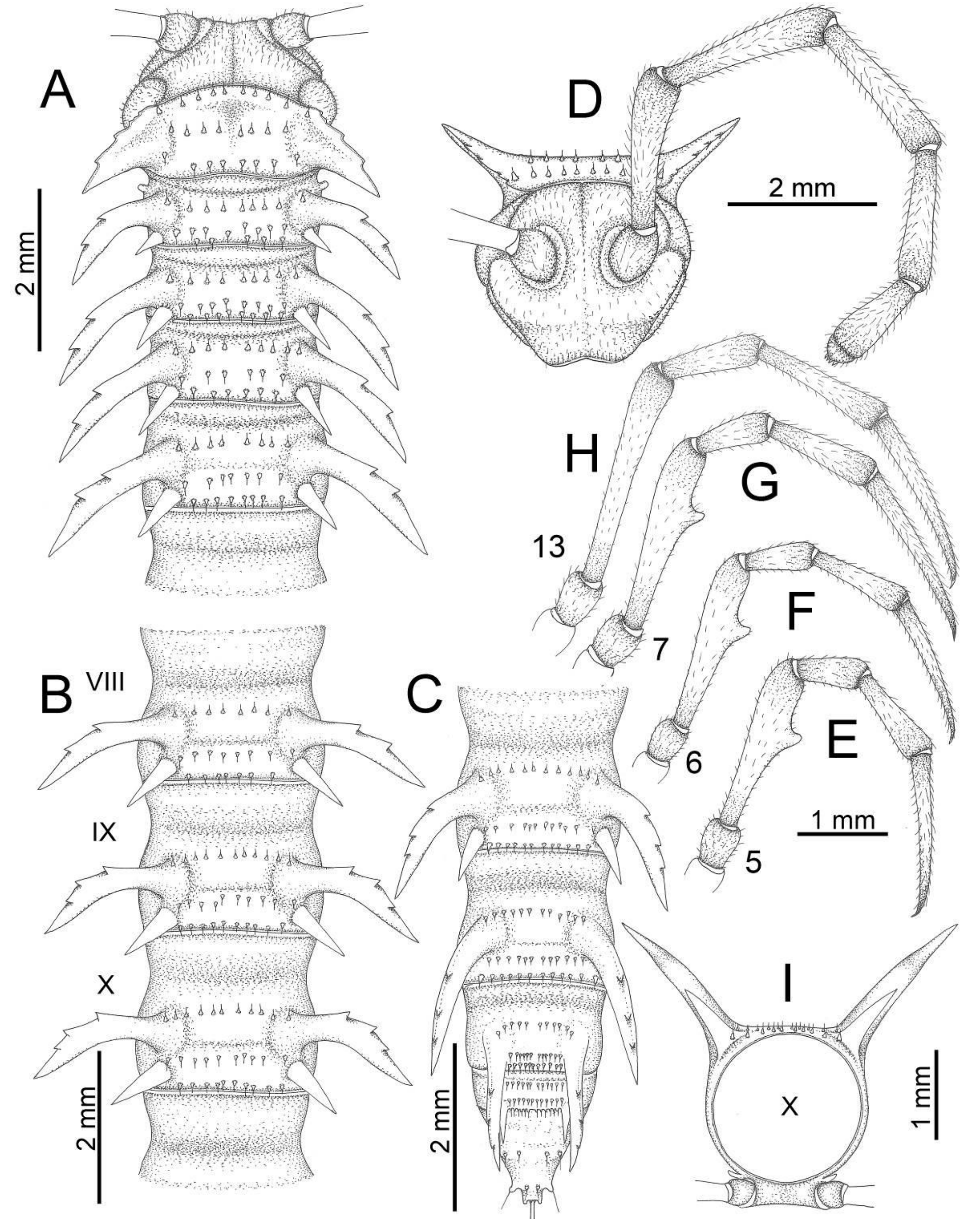

Figure 6.20 *Gigaxytes suratensis* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype. **A**. Anterior body part. **B**. Body rings 8–10. **C**. Posteriormost body rings and telson. **D**. Head and antenna. **E**. ♂ leg 5 (right). **F**. ♂ leg 6 (right). **G**. ♂ leg 7 (right). **H**. ♂ leg 13 (right). **I**. Midbody ring.

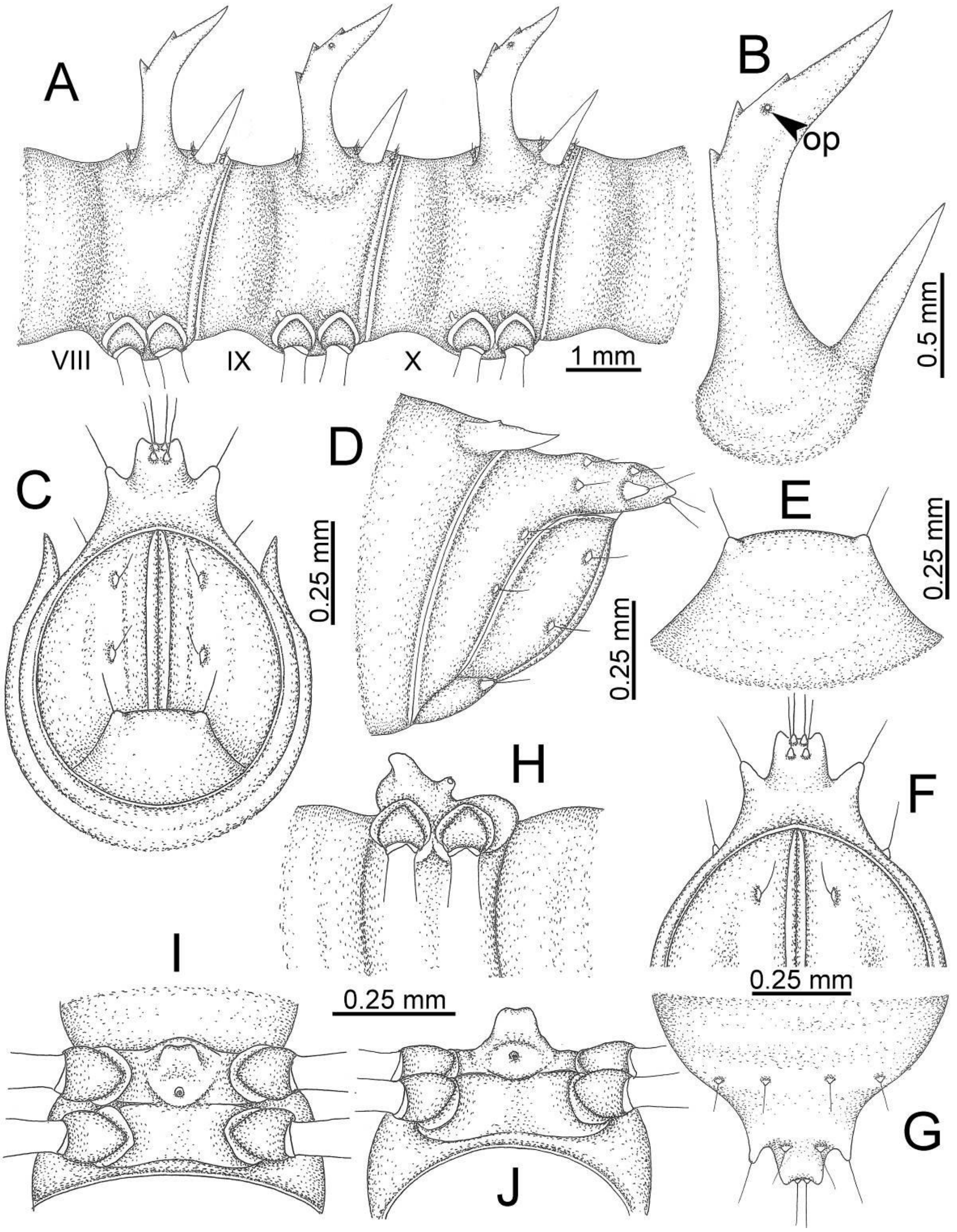

Figure 6.21 *Gigaxytes suratensis* Srisonchai, Enghoff & Panha gen. et sp. nov., ♂ paratype. **A**. Body rings 8–10. **B**. Paraterga of ring 10 (op = ozopore). **C**, **D**. Last ring and telson. **E**. Hypoproct. **F**, **G**. Epiproct. **H–J**. Sternal lobe between male coxae 4.

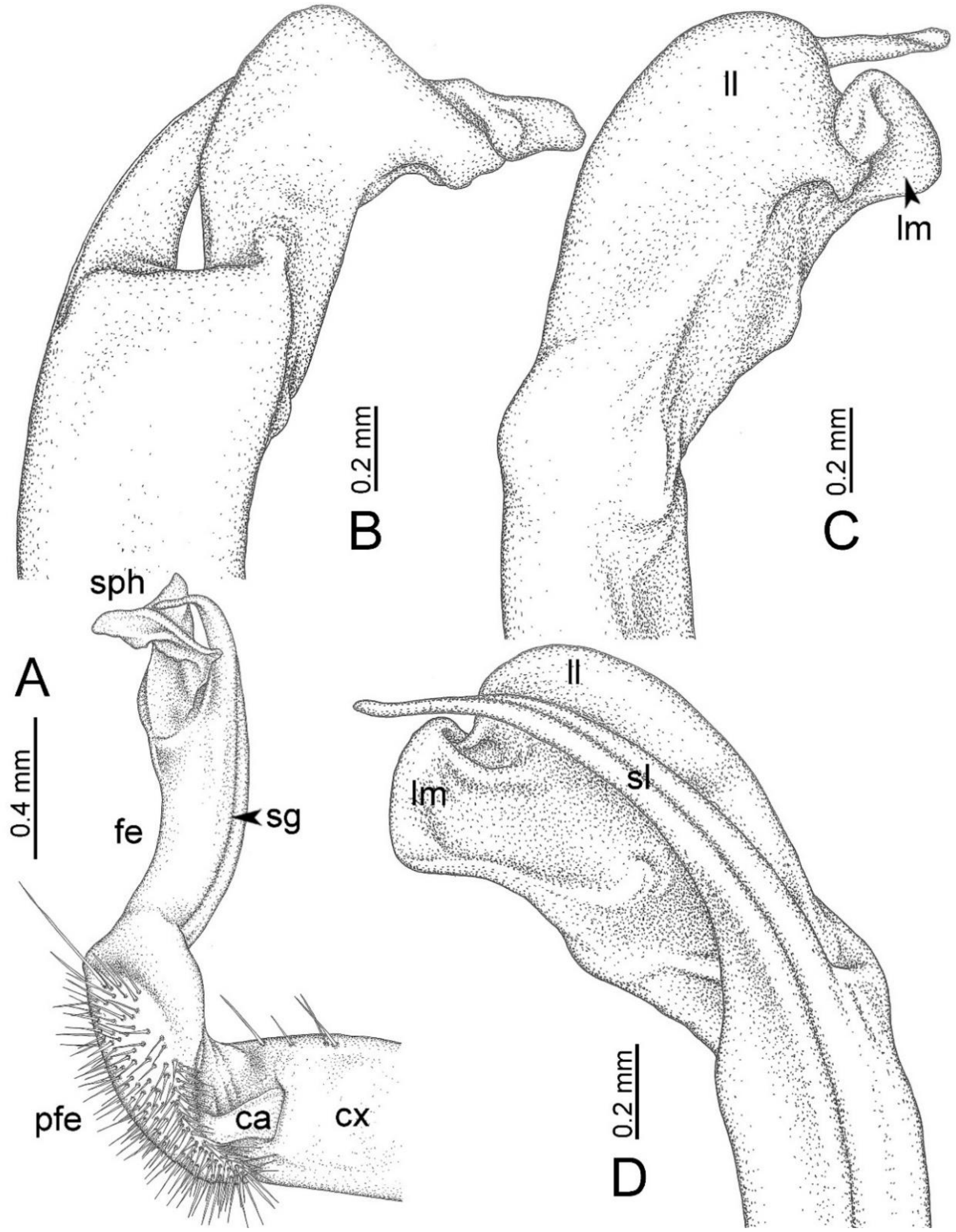

Figure 6.22 *Gigaxytes suratensis* Srisonchai, Enghoff & Panha gen. et sp. nov., paratype – right gonopod. **A**. Mesal view. **B**. Lateral view. **C**. Ventral view. **D**. Dorsal view.

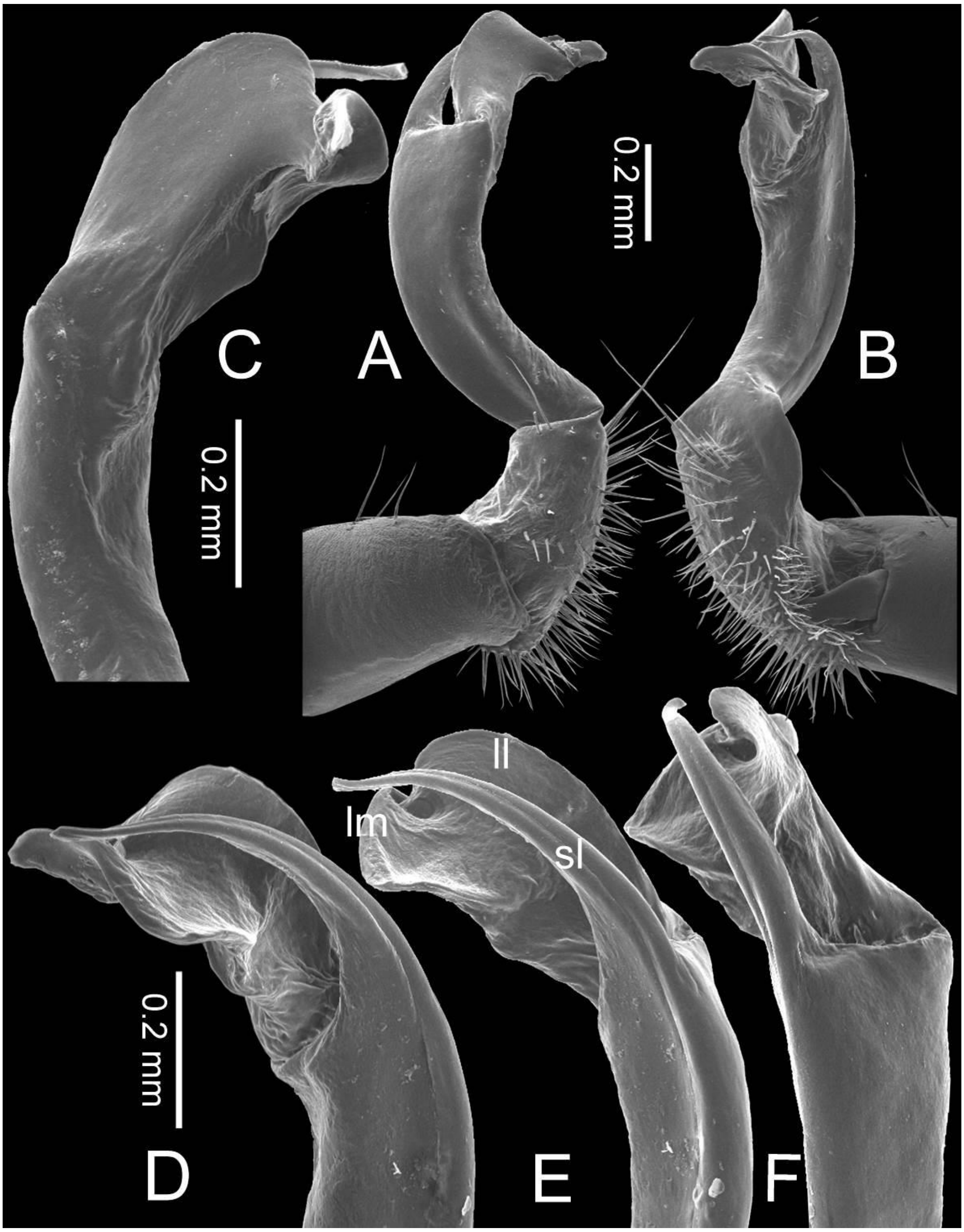

Figure 6.23 *Gigaxytes suratensis* Srisonchai, Enghoff & Panha gen. et sp. nov., paratype – right gonopod. **A**. Lateral view. **B**. Mesal view. **C**. Ventral view. **D**, **F**. Subdorsal view. **E**. Dorsal view.

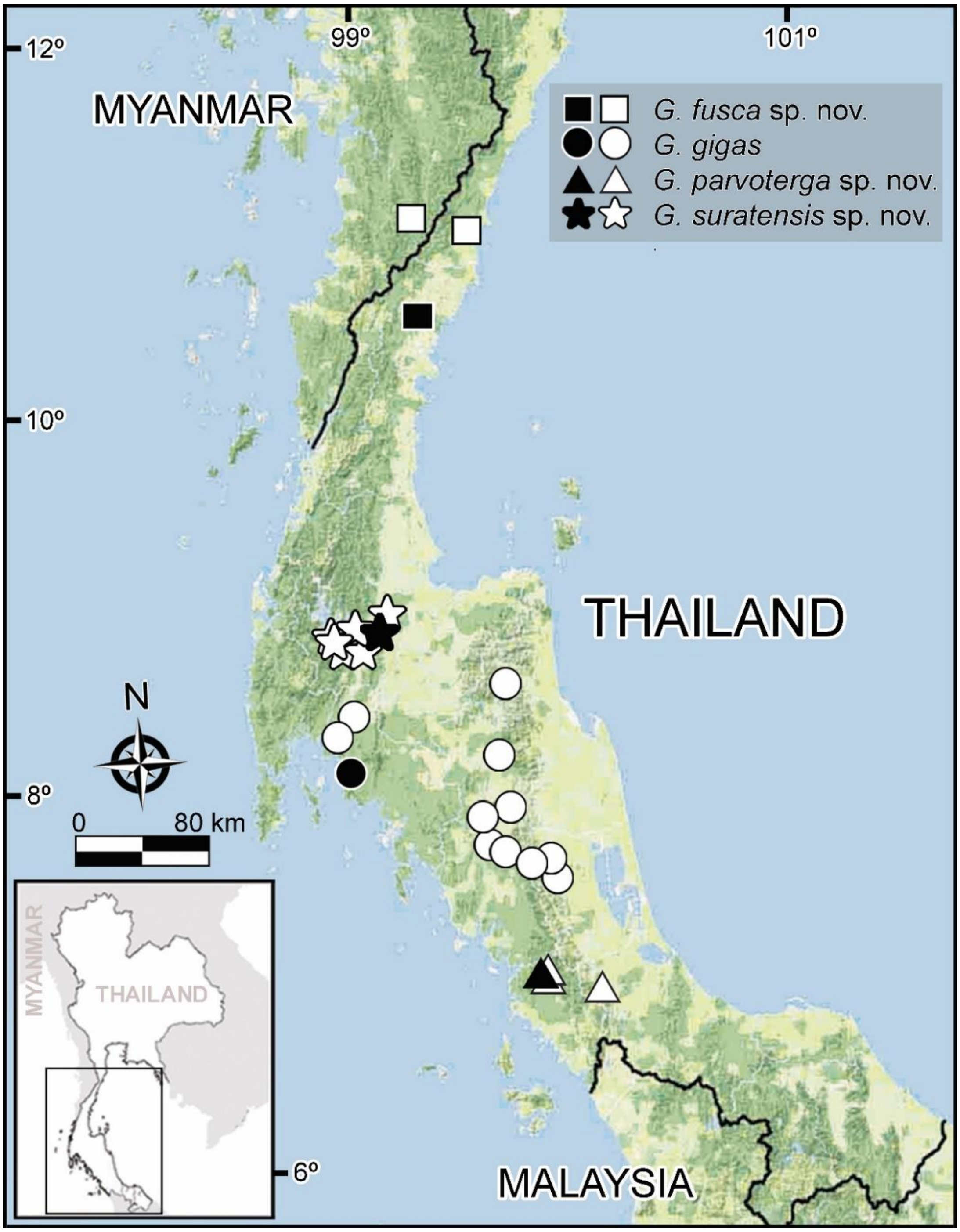

Figure 6.24 Known distribution of all *Gigaxytes* gen. nov. (black symbol = type locality, white symbol = other localities).

CHAPTER VII

A revision of dragon millipedes IV: the new genus *Spinaxytes*, with the description of nine new species (Diplopoda, Polydesmida, Paradoxosomatidae)

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Abstract

Nine new species constituting the '*spiny*' group of dragon millipedes are assigned to the new genus *Spinaxytes* Srisonchai, Enghoff & Panha, **gen. n.** Seven new species are described from Thailand: *S. biloba* Srisonchai, Enghoff & Panha, **sp. n.** and *S. palmata* Srisonchai, Enghoff & Panha, **sp. n.** from Surat Thani Province, *S. hasta* Srisonchai, Enghoff & Panha, **sp. n.** from Chumphon Province, *S. krabiensis* Srisonchai, Enghoff & Panha, **sp. n.** (type species) and *S. sutchariti* Srisonchai, Enghoff & Panha, **sp. n.** from Krabi Province, *S. uncus* Srisonchai, Enghoff & Panha, **sp. n.,** and *S. macaca* Srisonchai, Enghoff & Panha, **sp. n.** from Phang Nga Province; as well as one from Malaysia, *S. tortioverpa* Srisonchai, Enghoff & Panha, **sp. n.**, and one from Myanmar, *S. efefi* Srisonchai, Enghoff & Panha, **sp. n.** The new genus is endemic to South Myanmar, South Thailand, and Malaysia, and all new species are restricted to limestone habitats. All were exclusively found living on humid rock walls and/or inside small caves. Complete illustrations of external morphological characters, an identification key, and a distribution map are provided.

Key words

dragon millipede, endemic, new species, taxonomy, Thailand

Introduction

This is the fourth paper in a series of articles about revision of the dragon millipedes. Srisonchai *et al.* (2018a) provided general information on dragon millipedes, split *Desmoxytes* Chamberlin, 1923, *sensu* Golovatch & Enghoff (1994) into five genera based on morphological and genetic data, and revised the genus *Desmoxytes* in its new, restricted sense. Subsequently, Srisonchai *et al.* (2018a, 2018b) described two new genera of dragon millipedes containing several new species and several species transferred from *Desmoxytes*. In the present study, we describe nine new species constituting the group that we (Srisonchai *et al.*, 2018a) provisionally named the '*spiny*' group, of which no species has hitherto been named, and assign them to *Spinaxytes* gen. n.

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

Materials and methods

Specimen collection and preservation

Specimens were hand-collected from many localities throughout South Thailand, in some parts of Malaysia and in southern Myanmar. We also observed the habitats of all specimens. Specimens were mostly stored in 70% ethanol for morphological study and partly in 95% ethanol for molecular analysis. Latitude, longitude, and elevation were recorded by using a Garmin GPSMAP 60 CSx, and all coordinates and elevations were checked with Google Earth.

The main collectors in this work were staff and students of the Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University which we here refer to as 'ASRU members'.

Illustrations

All living specimen photos were taken with a Nikon D700 equipped with a AF-S VR Micro-Nikkor 105 mm lens during fieldwork. Newly collected specimens preserved in ethanol were imaged with an Olympus DP72 camera on an Olympus SZX16 stereomicroscope, using image stacking Cell-D auto-montage software. Scanning electron micrographs were generated with a JEOL - JSM–5410 LV. All samples studied with SEM were carefully dissected under a microscope, mounted on aluminium stubs, and coated with gold. After imaging with SEM, all objects were removed and kept in dry condition. Drawings were outlined under a stereo microscope (Leica Wild M10) with a drawing tube and finished using dot-line technique (stipple). Plates were composed in Adobe Photoshop CS6.

Morphological descriptions

We use morphological terminology according to previous taxonomic publications (Enghoff *et al.*, 2007; Golovatch and Enghoff, 1994; Golovatch *et al.*, 2012; Jeekel, 1964, 1980a, 2003; Srisonchai *et al.*, 2016, 2018a, 2018b, 2018c). Details of gonopodal terms are shown in the gonopod terminology section below.

Gonopod terms for the genus Spinaxytes *gen. n., and their abbreviations*

acropodite	=	Apical part of the gonopod; including femur, postfemoral part, solenophore and solenomere
ca	=	Cannula: a tube, lever-like, curved and slender; originating from coxa, tip inserted into concavity in prefemoral part
cx	=	Coxa: basal part of the gonopod, rather long, connecting to seventh body ring, attached to apertural rim dorsally; with a distoanterior group of setae
fe	=	Femur: longest part of the gonopod, straight; with lateral and mesal sulci distally; accommodates seminal groove (terminology for femorite vs femur, see Jeekel (2003 p. 48)
ll	=	Lamina lateralis: a small lobe on distal part of gonopod; seen in lateral view
lm	=	Lamina medialis: the longest part distally on the gonopod, very long, curved
ls	=	Lateral sulcus: a distinct sulcus distally on femur, seen obviously in lateral view
ms	=	Mesal sulcus: a distinct sulcus distally on femur, seen obviously in mesal view
pfe	=	Prefemoral part (=prefemur): basal portion of the telopodite, densely setose

pof	=	Postfemoral part (=postfemur): short part of telopodite, supporting solenophore and solenomere, demarcated from femur by lateral and mesal sulci
sg	=	Seminal groove: a conspicuous groove, similar to a tunnel, seen as a transparent line, visible on femur in mesal view
sl	=	Solenomere: a long and curved, flagellum-like appendage, originating from base of solenophore
sph	=	Solenophore (=tibiotarsus): apical part of telopodite, consisting of lamina lateralis and lamina medialis
telopodite	=	Main part of the gonopod, pivoting on coxa; including prefemoral part, femur, postfemoral part, solenophore and solenomere

Deposition of holotypes, paratypes, and other new specimens

All holotypes and most paratypes are kept at CUMZ. Some paratypes are deposited at NHMUK, NHMW, ZMUC, and ZMUM.

Abbreviations

ASRU	=	Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand
CUM	=	Chulalongkorn University Museum of Zoology, Bangkok, Thailand
FFI	=	Fauna and Flora International, Myanmar
NHMUK	=	Natural History Museum of London, England
NHMW	=	Natural History Museum, Vienna, Austria

ZMUC = Natural History Museum of Denmark (Zoological Museum), University of Copenhagen, Denmark

ZMUM = Zoological Museum, University of Moscow, Russia

a.s.l. = above sea level

Positional and directional terms in gonopod descriptions

Traditionally the gonopods are depicted as rotated 90° up from their in situ position. Following Srisonchai *et al.* (2018a), we use the following terms:

Dorsal = nearest to the body ring.

Ventral = farthest away from the body ring.

Mesal = nearest to the midline.

Lateral = furthest from the midline.

Dorsad = towards the body ring.

Ventrad = away from the body ring.

Mesad = towards the midline.

Laterad = 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 in Gervais, 1844

Order Polydesmida Pocock, 1887

Family Paradoxosomatidae Daday, 1889

Subfamily Paradoxosomatinae Daday, 1889

Tribe Orthomorphini Brölemann, 1916

Spinaxytes Srisonchai, Enghoff & Panha, gen. n.

Type species. *Spinaxytes krabiensis* Srisonchai, Enghoff & Panha, gen. et sp. n.

Diagnosis. The genus *Spinaxytes* gen. n. is characterized by:

1. Paraterga spiniform.
2. Metaterga with two rows of tubercles/cones/spines.
3. Postfemoral part of gonopod conspicuous, demarcated from femur by deep mesal and lateral sulci.
5. Lamina lateralis distinctly demarcated from lamina medialis.
6. Lamina medialis very long, curved, larger and longer than lamina lateralis.

Etymology. The name is a noun in apposition; from the Latin '*spina*', referring to the spine-like paraterga of all constituent species; '–*xytes*' ensures harmony with *Desmoxytes* (and its synonym '*Pteroxytes*').

Included species

1. *Spinaxytes biloba* Srisonchai, Enghoff & Panha, sp. n.
2. *Spinaxytes efefi* Srisonchai, Enghoff & Panha, sp. n.
3. *Spinaxytes hasta* Srisonchai, Enghoff & Panha, sp. n.
4. *Spinaxytes krabiensis* Srisonchai, Enghoff & Panha, sp. n.
5. *Spinaxytes macaca* Srisonchai, Enghoff & Panha, sp. n.
6. *Spinaxytes palmata* Srisonchai, Enghoff & Panha, sp. n.
7. *Spinaxytes sutchariti* Srisonchai, Enghoff & Panha, sp. n.
8. *Spinaxytes tortioverpa* Srisonchai, Enghoff & Panha, sp. n.
9. *Spinaxytes uncus* Srisonchai, Enghoff & Panha, sp. n.

Remarks. The new genus is easily distinguished from other genera of dragon millipedes by having spiniform paraterga, lamina lateralis smaller and shorter than lamina medialis, lamina medialis long and curved. Some species of the genus *Hylomus* Cook & Loomis, 1924, share spine-like paraterga; however, the gonopod details are totally different.

General description of the genus *Spinaxytes*. The description applies to adult males and females, except for the gonopods and when "male" is specified (Figs 7.1, 7.2, 7.4). The general description of the gonopods is based mainly on *Spinaxytes krabiensis* gen. et sp. n. (Figs 7.3, 7.5).

SIZE. Body length ca. 18–33 mm (male) ca. 16–33 mm (female), width 1.0–2.2 mm (male) 1.3–2.9 mm (female), size varies between species, usually female a bit longer than male.

COLOUR. Most species in life with dark brown colour. Colour in alcohol: all specimens partly faded to pale brown after 5 years' preservation in alcohol; specimens kept in darkness faded more slowly.

ANTENNAE (Figure 7.1A–C). Extremely long and slender, covered by delicate setation, usually reaching backwards to body rings 7–10 (male) and 6–8 (female) when stretched dorsally. Antennomere 3 = 4 > 5 ≥ 2 > 6 > 1 > 7 > 8.

HEAD. Delicately setose; vertex, labrum and genae sparsely setose; epicranial suture conspicuous as a deep, brown or black stripe.

COLLUM (Figure 7.2A, C). With three regular transverse rows of setiferous tubercles/cones; number of tubercles/cones in each row varies between species. Paraterga wing-like/spiniform, usually elevated at ca. 10°–30°, directed laterally/caudolaterally/caudally, with one or two conspicuous/inconspicuous notches at lateral margin.

TEGUMENT. Quite dull, sometimes shining; collum, metaterga and surface below paraterga smooth/microgranulate; prozona finely shagreened; paraterga, epiproct and sterna smooth. Stricture between prozona and metazona shallow, wide.

METATERGA (Figure 7.2A, D, G). With two regular transverse rows of setiferous cones/tubercles (in anterior row) and cones/spines (in posterior row); number of tubercles/cones/spines in each row varies between species. Transverse sulcus on metaterga shallow and wide in body rings 5–18. Mid-dorsal (axial) line missing.

PLEUROSTERNAL CARINAE (Figure 7.2B). Forming a complete, tooth-like crest on ring 2, a short ridge on ring 3, missing on remaining body rings.

PARATERGA (Figs 7.1A, B, D; 7.2A, B, D, E, G, H). Spiniform, long (except *S. biloba* sp. n.: quite short), extremely elevated at ca. 45°–80° (male) 40°–70° (female). Callus and shoulder poorly developed, inconspicuous. Anterior margin with two distinct denticles; on body rings 9, 10, 12, 13, 15–19 without a third denticle at lateral margin near tip. Degree of elevation of paraterga in male usually higher than in female. Posterior angle straight. Tip pointed and sharp. Ozopore visible from dorsal/dorsolateral/lateral view, round, small.

TELSON (Figure 7.2F, G, L, N). Epiproct usually long, apically with two pairs of conspicuous setae (spinnerets) arranged at the corners of a square, not in a depression, anterior pair close to apical tubercles. Paraprocts convex. Hypoproct usually subtrapeziform, sometimes subsemicircular/subtriangular; caudal margin often round, sometimes subtruncate/angular, with two conspicuous/ inconspicuous setiferous tubercles.

STERNA (Figs 7.1E, 7.2K). Sparsely setose, cross-impressions shallow in all species. Sternal lobe between male coxae 4 varies in shape; subtrapeziform/long subrectangular/bifurcate/spear-like; one or two pores seen in posterior view.

LEGS (Figs 7.1F, 7.2M). Extremely long and slender. Relative length of podomeres: femur ≥ tibia > tarsus ≥ postfemur > prefemur > coxa > claw. Male femora mostly without modification, sometimes male femora 6, 7 or 7 or 8, 9 with hump/apophysis ventrally in distal part.

GONOPODS (Figure 7.3). Coxa shorter than femur, sometimes subequal in length to femur. Cannula long and slender. Telopodite erect. Prefemoral part usually almost half as long, sometimes ca. 2/3 as long as femur. Acropodite erect. Femur long and straight. Seminal groove running entirely on mesal surface of femur. Mesal sulcus and lateral sulcus conspicuous, deep. Postfemoral part conspicuous, usually small and narrow, sometimes broad and wide, rarely very large. Solenophore variously modified in shape between species: lamina lateralis obviously demarcated from lamina medialis, smaller and shorter than lamina medialis; lamina medialis long, base stout, slightly attenuated near the curved tip. Solenomere long, slender, curved, supported by solenophore.

Distribution and habitat. All species of the new genus are allopatric. However, some of the new species can be found in syntopy with some species of *Desmoxytes*. The nine species described here are confined to limestone habitats and have narrow distributions; we therefore regard them as endemic. All species blend perfectly with habitat environment, mostly living on humid rock walls and/or inside small caves.

According to the current knowledge, *Spinaxytes* gen. n. is distributed only in the Malay Peninsula (south Myanmar, south Thailand, and north Malaysia): Myanmar: Thanintharyi Region; Thailand: Chumphon Province (Thung Tako, Mueng Chumphon, Lang Suan and Sawi Districts), Surat Thani Province (Phanom District), Phang Nga Province (Mueng Phang Nga and Takua Thung Districts), Krabi Province (Ao Luek and Muaeng Krabi Districts); Malaysia: Perak State (Figure 7.30).

Key to species of *Spinaxytes* gen. n. (based mainly on males)

1. Male femora 6–9 without modification (e.g., Figs. 7.4E, G; 7.10J; 7.13J) **2**

– Male femora 6 and 7, or 7, or 8 and 9 humped/with apophyses (e.g., Figs. 7.4B, C, L, M; 7.7J; 7.15J) **6**

2. Collum with 5+5 tubercles in anterior row, 2+2 tubercles in intermediate row, 3+3 tubercles in posterior row (Figure 7.10A). Metaterga 2–8 with 3+3 cones in anterior row and 3+3 cones in posterior row; metaterga 9–19 with 3+3 cones in anterior row and 4+4 cones in posterior row (Fig. 7.2A, C, E) .... ***S. efefi* sp. n.**

– Collum with 4+4 tubercles/cones in anterior row, 1+1 in intermediate row, 2+2 in posterior row (e.g., Figs 7.16A, 7.28A). Metaterga 2–19 with 2+2 tubercles/cones in anterior row and 2+2/3+3 tubercles/cones/spines in posterior row (e.g., Figs 7.16A, C, E; 7.28A, C, E) **3**

3. Sternal lobe between male coxae 4 bilobed/bifurcate/subtrapeziform (e.g., Figs 7.4A, K, P, R; 7.7F, G; 7.19F, G) **4**

– Sternal lobe between male coxae 4 spear-like (not bilobed, not bifurcate, not subtrapeziform) (Figs 7.4F; 7.13F, G) .... ***S. hasta* sp. n.**

4. Postfemoral part very large, angled 90 degrees with femoral part (Figs 7.5H, 7.26C–F). Lamina lateralis divided into two lobes; first lobe spine-like, long; second lobe smaller, ridge-like (Figs 7.5H; 7.26A, C, D). Lamina medialis curving up (Figs 7.5H; 7.26C, E). Solenomere longer than lamina medialis (Figs 7.5H; 7.26A–D) .... ***S. tortioverpa* sp. n.**

– Postfemoral part small, not angled 90 degrees with femoral part (e.g., Figs 7.5F, G; 7.23C; 7.25C). Lamina lateralis not divided into two lobes (e.g., Figs 7.5F, G; 7.23C; 7.25C, F). Lamina medialis curving down (e.g., Figs 7.5F, G; 7.23C; 7.25C, D). Solenomere approximately equal in length to lamina medialis (e.g., Figs 7.5F, G; 7.23C; 7.25C) **5**

5. Lamina lateralis small (Figs 7.5F, 7.23C). Solenomere circular in transverse section, curving down (Fig. 7.23C, E) .... ***S. palmata* sp. n.**

– Lamina lateralis large (Figs 7.5G; 7.25C, F). Solenomere flat in transverse section, curving up (Fig. 7.25C–E) .... ***S. sutchariti* sp. n.**

6. Only male femora 7 modified (Figs 7.4V, 7.28J) .... ***S. uncus* sp. n.**

– Male femora 6 and 7, or 8 and 9 modified (e.g. Figs 7.4B, C, L, M; 7.7J; 7.19J) . **7**

7. Lamina medialis with process-like lobe at base (Fig. 7.8D). Sternal lobe between male coxae 4 subtrapeziform (Figs 7.4A; 7.7F, G). Male femora 8 and 9 with apophyses .... ***S. biloba* sp. n.**

– Lamina medialis without process-like lobe at base (Figs 7.17D, E; 7.20D, E). Sternal lobe between male coxae 4 incompletely bilobed, fork-like (Figs 7.4H, K; 7.16F, G; 7.19F, G). Male femora 6 and 7 modified as humped ventrally in distal portion **8**

8. Paraterga extremely long (Fig. 7.16D). Lamina lateralis distally round (Fig. 7.17C). Tip of lamina lateralis terminating in two lobes (Figs 7.3C, D; 7.17C, D, E) .... ***S. krabiensis*** **sp. n.**

– Paraterga moderately long (Fig. 7.19D). Lamina lateralis distally protruding, lobe-like (Fig. 7.20C). Tip of lamina lateralis bent, terminating in one lobe (Fig. 7.20C, D, E) .... ***S. macaca*** **sp. n.**

Species descriptions

Spinaxytes biloba Srisonchai, Enghoff & Panha, sp. n.

Figs 7.4A–C, 7.5A, 7.6–7.8

Material examined. Holotype. ♂, THAILAND, Surat Thani Province, Phanom District, Khlong Phanom National Park, Pha Daeng, 8°53'41"N, 98°33'12"E, ca. 67 m a.s.l., 7 Aug. 2016, ASRU members leg. (CUMZ-pxDGT00205). **Paratypes.** 17 ♂♂, 24 ♀♀, same data as for holotype (CUMZ- pxDGT00206); 1 ♂, 1 ♀, same data as for holotype (ZMUC0040249); 1 ♂, 1 ♀, same data as for holotype (NHMW9423). **Further specimens, not paratypes.** 5 ♂♂, 3 ♀♀, THAILAND, Surat Thani Province, Phanom District, Khlong Phanom National Park, Pha Daeng, 8°53'41"N, 98°33'12"E, ca. 67 m a.s.l., 6 Aug. 2015, ASRU members leg. (CUMZ).

Etymology. The species name is an adjective, refers to the two additional process-like lobes on the solenophore (one on lamina lateralis and one on lamina medialis).

Diagnosis. Differs from other species by having: metaterga 5–19 with 2+2 cones in anterior row and 3+3 cones in posterior row; sternal lobe between male coxae 4 subtrapeziform; male femora 8 and 9 with apophyses distally; lamina lateralis with an additional process-like protruding lobe; lamina medialis basally with an additional protruding process-like lobe.

Description. SIZE. Length 15–17 mm (male), 16–18 mm (female); width of midbody metazona 1.0–1.2 mm (male), 1.3–1.5 mm (female). Width of rings 2 = 3 $<$ 4 $<$ collum $<$ 5 $<$ head = 6–17, thereafter body gradually tapering towards telson.

COLOUR (Figure 7.6A, B). Specimens in life brown/pale brown; paraterga brownish white; head, antennae (except whitish distal part of antennomeres 7 and 8) and collum brown; prozona, metaterga (except white spines in posterior row) and surface below paraterga brown/pale brown; sterna pale brown/whitish brown; epiproct and legs whitish brown; a few basal podomeres whitish brown/white.

ANTENNAE. Reaching to body ring 7 or 8 (male) and 6 (female) when stretched dorsally.

COLLUM (Figure 7.7A). With three transverse rows of setiferous cones, 4+4 in anterior row, 1+1 in intermediate row and 2+2 in posterior row; with one inconspicuous setiferous notch at lateral margin; paraterga wing-like, quite short, tip blunt, elevated at ca. 15°–20° (male) 10°–20° (female), directed almost caudad.

TEGUMENT. Quite shining; collum coarsely microgranulate; metaterga and surface below paraterga finely microgranulate.

METATERGA (Figure 7.7A, C, E). With two transverse rows of setiferous cones; metaterga 2–4 with 2+2 cones in anterior row and 2(3)+2(3) cones in posterior row; metaterga 5–19 with 2+2 cones in anterior row and 3+3 cones in posterior row; all cones subequal in length and size. An additional cone-like denticle at base of paraterga near anterior row of cones.

PARATERGA (Figure 7.7A–D, H). Quite short; directed dorsocaudad on body rings 3–17, elevated at ca. 60°–70° (male) 55°–70° (female), directed more caudad on body ring II and increasingly so on rings 18 and 19. Denticle of paraterga located at base of paraterga and very close to anterior row of cones on metaterga. Ozopore visible in lateral view.

TELSON (Figure 7.7E, I, H). Epiproct quite long; tip subemarginate; lateral setiferous tubercles conspicuous; apical tubercles conspicuous. Hypoproct subtrapeziform, wide; caudal margin round (in some specimens subtruncate), with inconspicuous setiferous tubercles.

STERNA (Figs 7.4A; 7.7F, G). Sternal lobe between male coxae 4 subtrapeziform, broad, and thin, tips subtruncate, in situ directed ventroanteriad; posterior surface of sternal lobe with two pores borne on swollen and short lobe.

LEGS (Figs 7.4B, C; 7.7J). Male femora 8 and 9 with apophyses distally.

GONOPODS (Figs 7.5A, 7.8). Coxa shorter than femur. Prefemoral part ca. half as long as femur. Femur not enlarged distally. Postfemoral part broad. Mesal sulcus wide; lateral sulcus narrow. Solenophore subequal in size to postfemoral part: lamina lateralis small and short; with a protruding lobe, process-like, directed mesad; apically round: lamina medialis long; base enlarged and stout, slightly attenuated near the tip, basally with a protruding lobe, process-like, directed mesad; tip curving down, bifurcating into two small spines. Solenomere curving down, compressed in transverse section, tip directed posteriad.

Distribution and habitat (Figure 7.6C). Known only from the type locality which is a small isolated limestone mountain between Khao Sok and Khlong Phanom National Parks. The new species blended perfectly with the humid rock walls, and most specimens were found inside rock holes/crevices. *S. biloba* sp. n. co-occurs with *Desmoxytes cervina* (Pocock, 1895) (Srisonchai *et al.*, 2018a) in the same habitat. Several attempts (2017–2018) have been made to find further specimens near the type locality, but none were found. As the new species has only been found at the type locality only, we regard *S. biloba* sp. n. as endemic to Thailand.

Remarks. Among all *Spinaxytes* species, *S. biloba* sp. n. is obviously the smallest (length 15–18 mm, width of midbody metazona 1.0–1.5 mm), and the live pale brown colouration is lighter than that of other species.

Spinaxytes efefi Srisonchai, Enghoff & Panha, sp. n.

Figs 7.4D, E; 7.5B; 7.9–7.11

Material examined, Holotype. ♂, MYANMAR, Tanintharyi Region, Myeik, 20 km northeast of Monoron, Lenya National Park, limestone mountain near Ngawun Chaung River, 11°40'20"N, 99°13'30"E, ca. 64 m a.s.l., 9 Jun. 2015, FFI staff and ASRU members leg. (CUMZ-pxDGT00207). **Paratypes.** 20 ♂♂, 25 ♀♀, same data as for holotype (CUMZ-pxDGT00208); 1 ♂, 1 ♀, same data as for holotype (ZMUC00040250); 1 ♂, 1 ♀, same data as for holotype (ZMUM); 1 ♂, 1 ♀, same data as for holotype (NHMW9422); 1 ♂, 1 ♀, same data as for holotype (NHMUK).

Etymology. The name is an artificially constructed homophone (*efefi* = FFI) honouring FFI (Fauna and Flora International, Myanmar), an organization for biodiversity conservation; in recognition of their hard work to protect wildlife including invertebrates.

Diagnosis. Sternal lobe between male coxae 4 not bilobed and male femora without modification. Similar in this respect to *S. hasta* sp. n., but differs by having: collum with 5(4)+5(4) tubercles in anterior row, 2+2 tubercles in intermediate row and 3+3 tubercles in posterior row; metaterga 2–8 with 3+3 cones in anterior row and 3+3 cones in posterior row; metaterga 9–18 with 3+3 cones in anterior row and 4+4 cones in posterior row; metatergum 19 with 3+3 tubercles/cones in anterior row and 4+4 tubercles/cones in posterior row; postfemoral part of gonopod with a triangular process and a triangular ridge.

Description. SIZE. Length 26–30 mm (male), 30–32 mm (female); width of midbody metazona 2.1–2.2 mm (male), 2.7–2.9 mm (female). Width of collum = ring 2 = 3 = 4 < head = 5–17, thereafter body gradually tapering towards telson.

COLOUR (Figure 7.9A, B). Specimens in life with body brown/yellowish brown; paraterga yellow; antennae (except whitish distal part of antennomeres 7 and 8), head and prozona brown/blackish brown; collum, metaterga and surface below paraterga brown/yellowish brown; sterna, epiproct and legs brown; a few basal podomeres pale brown/whitish brown.

ANTENNAE. Reaching to body ring 9 or 10 (male) and 7 or 8 (female) when stretched dorsally.

COLLUM (Figure 7.10A). With three transverse rows of setiferous tubercles, 5(4)+5(4) tubercles in anterior row, 2+2(1) tubercles in intermediate row and 3+3 tubercles in posterior row; with two inconspicuous setiferous notches at lateral margin;

paraterga wing-like, quite short and small, tip obtuse, elevated at ca. 15°–25° (male) 10°–15° (female), directed caudolaterad.

TEGUMENT. Quite dull; collum, metaterga (posterior part) and surface below paraterga coarsely microgranulate; metaterga (anterior part) smooth.

METATERGA (Figure 7.10A, C, E). With two transverse rows of setiferous cones; metaterga 2–8 with 3+3 cones in anterior row and 3+3 cones in posterior row; metaterga 9–19 with 3(4)+3(4) cones in anterior row and 4(5)+4(5) cones in posterior row; all cones subequal in length and size.

PARATERGA (Figure 7.10A–D, H). Very long; directed almost dorsad on body rings 2–16, elevated at ca. 65°–80° (male) 60°–70° (female); directed dorsocaudad on ring 17; directed increasingly caudad on body rings 18 and 19. Ozopore visible in lateral view.

TELSON (Figure 7.10E, H, I). Epiproct quite long; tip subtruncate; lateral setiferous tubercles conspicuous; apical tubercles inconspicuous. Hypoproct subsemicircular; caudal margin round (in some specimens angular), with conspicuous setiferous tubercles.

STERNA (Figs 7.4D; 7.10F, G). Sternal lobe between male coxae 4 erect, long subrectangular, very long; tips emarginate, in situ directed ventrad; posterior surface bearing one pore near tip.

LEGS (Figs 7.4E, 7.10J). Male femora without modification.

GONOPODS (Figs 7.5B, 7.11). Coxa subequal in length to femur. Prefemoral part ca. 2/3 as long as femur. Femur not enlarged distally, ventrally swollen in middle part. Postfemoral part broad; mesally with a long triangular process (directed mesoanteriad) and a long triangular ridge, between process and ridge with a wide furrow. Mesal sulcus and lateral sulcus wide. Solenophore bigger and longer than postfemoral part; basally very broad: lamina lateralis long and slender, curved, tip round: lamina medialis long and slender; with two ridges in middle portion; slightly attenuated near tip; tip in situ resting very close to solenomere, terminating in small spines. Solenomere flat, curving down; tip terminating in three sharp spines, directed mesoventrad.

Distribution and habitat (Figure 7.9C). Known only from the type locality. The specimens were found exclusively on rock walls or in caves. We have tried to vain to find this species in other places near the type locality, but no further specimens have been collected. Given the finding only at the type locality, the new species is considered to be endemic to southern Myanmar.

Remarks. No variation was found. Body ring 19 of *S. efefi* sp. n. seems to be shorter than in other species, and the tip of paraterga on collum is obtuse whereas in other species (except *S. biloba* sp. n.) it is sharp.

Spinaxytes hasta **Srisonchai, Enghoff & Panha, sp. n.**

Figs 7.4F, G; 7.5C; 7.12–7.14

Material examined. Holotype. ♂, THAILAND, Chumphon Province, Thung Tako District, Khao Ma Ngaen, 10°05'27"N, 99°04'25"E, ca. 28 m a.s.l., 23 Oct. 2016, ASRU members leg. (CUMZ-pxDGT00209). **Paratypes.** 5 ♂♂, 6 ♀♀, same data as for holotype (CUMZ-pxDGT00210); 1 ♂, 1 ♀, same data as for holotype (ZMUC00040251). **Further specimens, not paratypes, all from THAILAND, Chumphon Province. Mueang Chumphon District:** 8♂♂, 1 ♀, Wat Tham Sanook, 10°28'52"N, 99°04'29"E, ca. 54 m a.s.l., 3 Jul. 2017, ASRU members leg. (CUMZ). **Lang Suan District:** 2 ♀♀, Wat Ratcha Burana School, 9°56'21"N, 99°02'26"E, ca. 34 m a.s.l., 10 Sep. 2016, ASRU members leg. (CUMZ); 1 ♂, 5 ♀♀, Wat Tham Khao Kriap (Khao Kriap Cave), 9°49'08"N, 99°02'22"E, ca. 102 m a.s.l., 5 Jun. 2009, ASRU members leg. (CUMZ). **Sawi District:** 8 ♂♂, 3 ♀♀, Wat Nam Cha, 10°17'54"N, 99°01'57"E, ca. 95 m a.s.l., 5 Jun. 2009, ASRU members leg. (CUMZ).

Etymology. The name is a Latin noun in apposition meaning spear, referring to the shape of the sternal lobe between male coxae 4 which is somewhat similar to a spear.

Diagnosis. Sternal lobe between male coxae 4 not bilobed, not bifurcate; male femora without modification. Similar in this respect to *S. efefi* sp. n., but differs by having: collum with 4+4 tubercles in anterior row, 1+1 tubercles in intermediate row and 2+2 tubercles in posterior row; metaterga 2–8 with 2+2 cones in anterior row and 2+2 cones in posterior row; metaterga 9–18 with 2+2 cones in anterior row and 2+2 cones in posterior row; metatergum 19 with 2+2 tubercles/cones in anterior row and 2+2 tubercles/cones in posterior row; lamina medialis (lm) with a large lobe in middle part.

Description. SIZE. Length 23–33 mm (male), 26–33 mm (female); width of midbody metazona 1.7–2.2 mm (male), 2.1–2.8 mm (female). Width of collum = ring 2 = 3 = 4 < head = 5–16, thereafter body gradually tapering towards telson.

COLOUR (Figure 7.12A–C). Specimens in life with body black/brownish black; paraterga white/yellowish white/whitish yellow; antennae (except whitish distal part of antennomeres 7 and 8) and metaterga (posterior part) brown/brownish black; head and collum brown/blackish brown; prozona and metaterga (anterior part) black; surface below paraterga black/brownish black; sterna and epiproct brown; legs brown/pale brown; a few basal podomeres pale whitish brown.

ANTENNAE (Figure 7.13M). Reaching to body ring 9 or 10 (male) and 7 (female) when stretched dorsally.

COLLUM (Figure 7.13A). With three transverse rows of setiferous tubercles, 4+4 tubercles in anterior row, 1(0)+1 tubercles in intermediate row and 2+2 tubercles in posterior row; with two inconspicuous setiferous notches at lateral margin; paraterga wing-like, quite short and broad, tip sharp, elevated at ca. 10°–15° (male) 10°–15° (female), directed caudolaterad.

TEGUMENT. Quite dull; collum, metaterga and surface below paraterga finely microgranulate.

METATERGA (Figure 7.13A, C, E). With two transverse rows of setiferous tubercles/cones and spines; metaterga 2–8 with 2+2 tubercles/cones in anterior row and 2+2 spines in posterior row; metaterga 2–18 with 2+2 tubercles/cones in anterior row and 2+2 spines in posterior row; metatergum 19 with 2+2 tubercles in anterior row and 2+2 tubercles in posterior row; lateral spines of posterior row bigger and longer than mesal ones, gradually reduced in length and size on the following rings.

PARATERGA (Figure 7.13A–E, H). Very long; directed dorsolaterad on body rings 4–16, elevated at ca. 60°–70° (male) 50°–60° (female); directed caudolaterad on rings 2, 3 and 17; directed increasingly caudad on body rings 18 and 19. Ozopore visible in lateral view.

TELSON (Figure 7.13E, H, I). Epiproct long; tip subtruncate; lateral setiferous tubercles conspicuous (in some specimens inconspicuous); apical tubercles inconspicuous. Hypoproct subtrapeziform (in some specimens subsemicircular); caudal margin round (in some specimens angular), with inconspicuous setiferous tubercles.

STERNA (Figs 7.4F; 7.13F, G). Sternal lobe between male coxae 4 coniform, long, spear-like; base stout; tips sharp, in situ directed almost ventrad; posterior surface bearing one pore.

LEGS (Figs 7.4G, 7.13J). Male femora without modification.

GONOPODS (Figs 7.5C, 7.14). Coxa shorter than femur. Prefemoral part ca. 2/3 as long as femur. Femur not enlarged distally, basally indented. Postfemoral part narrow. Mesal sulcus and lateral sulcus wide. Solenophore bigger and longer than postfemoral part: lamina lateralis broad and long, flattened laterally: lamina medialis long; base enlarged, slightly attenuated near the tip; middle part with a large lobe; tip a bit curving up, terminating in several small spines. Solenomere circular in transverse section, curving up, tip directed anteriad.

Distribution and habitat (Figure 7.12D). The specimens were found on rocks or walls with plants, and some were found in a small cave. *S. hasta* sp. n. is distributed only in Chumphon Province, and we regard the new species as endemic for the Thai fauna. At Wat Nam Cha the new species coexists with *Desmoxytes cervina.*

Remarks. There are some variations: the lateral setiferous tubercles of the epiproct are conspicuous in some specimens, inconspicuous in others; the hypoproct is subtrapeziform in some individuals, subsemicircular in others; the caudal margin of the hypoproct is rounded in some specimens, angular in others.

Spinaxytes krabiensis Srisonchai, Enghoff & Panha, sp. n.

Figs 7.3; 7.4H–J; 7.5D; 7.15–7.17

Material examined. Holotype. ♂, THAILAND, Krabi Province, Mueang Krabi District, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'38"N, 98°55'26"E, ca. 87 m a.s.l., 9 Jul. 2017, ASRU members leg. (CUMZ-pxDGT00211). **Paratypes.** 5 ♂♂, 9 ♀♀, 1 juvenile, same data as for holotype (CUMZ-pxDGT00212); 1 ♂, 1 ♀, same data as for holotype (ZMUC00040252). **Further specimens, not paratypes, all from THAILAND, Krabi Province. Ao Luek District:** 2 ♂♂, 1 ♀, Than Bok Khorani, 8°23'28"N, 98°44'07"E, ca. 46 m a.s.l., 14 Jan. 2013, ASRU members leg. (CUMZ); 5 ♂♂, 1 ♀, Than Bok Khorani, 8°23'28"N, 98°44'07"E, ca. 46 m a.s.l., 23 Aug. 2014, ASRU members leg. (CUMZ); 12 ♂♂, 7 ♀♀, 1 juvenile, Than Bok Khorani, 8°23'28"N, 98°44'07"E, ca. 46 m a.s.l., 30 Aug. 2015, ASRU members leg. (CUMZ); 3 ♂♂, Than Bok Khorani, 8°23'28"N, 98°44'07"E, ca. 46 m a.s.l., Jan. 2016, ASRU members leg. (CUMZ); 1 ♂, 5 ♀♀, P.N. Mountain Resort, 8°24'09"N, 98°44'18"E, ca. 46 m a.s.l., 30 Aug. 2015, ASRU members leg. (CUMZ); 1 ♂, 1 broken ♂, Tham Sa Yuan Thong (Sa Yuan Thong Cave), 8°23'29"N, 98°46'17"E, ca. 7 m a.s.l., 9 Oct. 2006, ASRU members leg. (CUMZ). **Muaeng Krabi District:** 1 broken ♂, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'38"N, 98°55'26"E, ca. 87 m a.s.l., 25 Oct. 2007, ASRU members leg. (CUMZ); 1 broken ♂, 1 ♀, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'38"N, 98°55'26"E, ca. 87 m a.s.l., 7 Oct. 2009, ASRU members leg. (CUMZ); 1 ♂, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'38"N, 98°55'26"E, ca. 87 m a.s.l., 24 Aug. 2014, ASRU members leg. (CUMZ); 1 ♀, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'38"N, 98°55'26"E, ca. 87 m a.s.l., 30 Aug. 2015, P. Pimvichai, P. Prasankok and N. Natarat leg. (CUMZ); 2 ♂♂, 1 ♀, 1 broken ♀, Wat Tham Sue (Tiger Cave), valley behind Tiger Cave, 8°07'38"N, 98°55'26"E, ca. 87 m a.s.l., 25 Jul. 2017, ASRU members leg. (CUMZ).

Etymology. The new species is named after the province where the type locality lies.

Diagnosis. Male femora 6 and 7 humped distally. Similar in this respect to *S. macaca* sp. n., but differs by having: paraterga orange, longer; male femora 6 smaller; tip of lamina lateralis round, not protuding as digitiform; tip of lamina medialis terminating in two lobes.

Description. SIZE. Length 28–31 mm (male), 30–33 mm (female); width of midbody metazona 1.8–2.0 mm (male), 2.2–2.5 mm (female). Width of rings 2 = 3 = 4 < collum < head = 5–16, thereafter body gradually tapering towards telson.

COLOUR (Figure 7.15A–D). Specimens in life with body black/brownish black; paraterga orange; head, antennae (except whitish distal part of antennomeres 7 and 8), collum, prozona and epiproct black; metaterga and surface below paraterga black/brownish black; sterna brown; legs brown/blackish brown; a few basal podomeres whitish brown.

ANTENNAE (Figure 7.16M). Reaching to body ring 8 (male) and 6 (female) when stretched dorsally.

COLLUM (Figure 7.16A). With three transverse rows of setiferous tubercles/cones, 4+4 in anterior row, 1+1 in intermediate row and 2+2 in posterior row; with one conspicuous setiferous notch at lateral margin; paraterga spiniform, long, tip sharp, elevated at ca. 20°–30° in both male and female, directed caudolaterad.

TEGUMENT. Quite shining; collum coarsely microgranulate; metaterga and surface below paraterga smooth.

METATERGA (Figure 7.16A, C, E). With two transverse rows of setiferous tubercles and setiferous cones/spines; metaterga 2–7 with 2+2 tubercles in anterior row and 2+2 spines in posterior row; 8–19 with 2+2 tubercles in anterior row and 2+2 cones in posterior row; lateral cones/spines of posterior row bigger and longer than mesal ones, gradually reduced in size and length on the following rings.

PARATERGA (Figure 7.16A–E, H). Extremely long; directed dorsolaterad on body rings 2–16, elevated at ca. 45°–60° (male) 40°–50° (female), directed dorsocaudad on ring 17, directed increasingly caudad on body rings 18 and 19. Ozopore visible in subdorsal view.

TELSON (Figure 7.16E, H, I). Epiproct long; tip subtruncate; lateral setiferous tubercles mostly inconspicuous (in some specimens conspicuous); apical tubercles inconspicuous. Hypoproct subtrapeziform; caudal margin round, with inconspicuous setiferous tubercles.

STERNA (Figs 7.4H; 7.16F, G). Sternal lobe between male coxae 4 bifurcate, long; tips sharp, in situ directed ventroanteriad; posterior surface bearing one pore.

LEGS (Figs 7.4I, J; 7.16J). Male femora 6 a bit humped; male femora 7 strongly humped.

GONOPODS (Figs 7.3, 7.5D, 7.17). Coxa subequal in length to femur. Prefemoral part ca. half as long as femur. Femur obviously enlarged distally. Postfemoral part narrow. Mesal sulcus and lateral sulcus wide. Solenophore bigger than postfemoral part: lamina lateralis small, compact, tip round: lamina medialis long; basally enlarged and slightly attenuated near the tip; tip a bit curved, terminating in two lobes. Solenomere curved and twisted, compressed in transverse section, tip directed lateroposteriad.

Distribution and habitat (Figure 7.15E). *S. krabiensis* sp. n. inhabits Krabi Province. Considering its narrow distribution, we regard this species as endemic for the Thai fauna. It is syntopic with *Desmoxytes delfae* (Jeekel, 1964), *Desmoxytes cervina* and *Gigaxytes gigas* (Golovatch & Enghoff, 1994), which were collected from the same location (Than Bok Khorani and Wat Tham Sue (Tiger Cave)), but the new species was encountered living on rock walls or in small caves while the others were usually found on leaf litter or on tree branches.

Remarks. We found variations in the lateral setiferous tubercles of the epiproct: conspicuous in some specimens, inconspicuous in others.

Spinaxytes macaca Srisonchai, Enghoff & Panha, sp. n.

Figs 7.4K–M; 7.5E; 7.18–7.20

Material examined. Holotype. ♂, THAILAND, Phang Nga Province, Takua Thung District, Wat Suwan Khuha (Monkey Cave), 8°25'42"N, 98°28'22"E, ca. 27 m a.s.l., 8 Aug. 2016, ASRU members leg. (CUMZ-pxDGT00213). **Paratypes.** 7 ♂♂, 2 ♀♀, same data as for holotype (CUMZ-pxDGT00214); 1 ♂, 1 ♀, same data as for holotype (ZMUC00040253); 1 ♂ same data as for holotype (ZMUM).

Etymology. The species is named after the monkey, long-tailed macaque (*Macaca fascicularis*) living at the type locality (Monkey Cave).

Diagnosis. Male femora 6 and 7 humped distally. Similar in this respect to *S. krabiensis* sp. n., but differs from it by having: paraterga brownish white, shorter; male femora 6 larger; tip of lamina lateralis (ll) protruding as a small lobe, digitiform; tip of lamina medialis (lm) bent, terminating in one lobe.

Description. SIZE. Length 27–29 mm (male), 29–32 mm (female); width of midbody metazon 1.8–1.9 mm (male), 2.0–2.3 mm (female). Width of collum = 2 = 3 < 4 < head = 5–16, thereafter body gradually tapering towards telson.

COLOUR (Figure 7.18A, B). Specimens in life with body black; paraterga brownish white; head, antennae (except whitish distal part of antennomeres 7 and 8), collum, metaterga, prozona and surface below paraterga black; sterna brown; epiproct black/brownish black; legs blackish brown; a few basal podomeres pale brown/whitish brown.

ANTENNAE (Figure 7.19M). Reaching to body ring 8 or 9 (male) and 7 (female) when stretched dorsally.

COLLUM (Figure 7.19A). With three transverse rows of setiferous tubercles/cones, 4+4 tubercles/cones in anterior row, 1+1 tubercles/cones in intermediate row and 2+2 tubercles/cones in posterior row; with one conspicuous setiferous notch at lateral margin; paraterga spiniform, long, tip sharp, elevated at ca. 15°–20° in both male and female, directed caudolaterad.

TEGUMENT. Quite shining; collum, metaterga and surface below paraterga smooth.

METATERGA (Figure 7.19A, C, E). With two transverse rows of setiferous tubercles and cones/spines; metaterga 2–19 with 2+2 tubercles in anterior row and 2+2 cones/spines in posterior row; lateral cones/spines of posterior row bigger and longer than mesal ones, gradually reduced in length and size on the following rings.

PARATERGA (Figure 7.19A–E, H). Long; directed dorsolaterad on body rings 2–16, elevated at ca. 60°–70° (male) 50°–60° (female), directed dorsocaudad on ring 17, directed increasingly caudad on body rings 18 and 19. Ozopore visible in dorsolateral view.

TELSON (Figure 7.19E, H, I). Epiproct quite short; tip subtruncate; lateral setiferous tubercles conspicuous; apical tubercles inconspicuous. Hypoproct subtrapeziform; caudal margin round, with conspicuous setiferous tubercles.

STERNA (Figs 7.4K; 7.19F, G). Sternal lobe between male coxae 4 bifurcate, long; base stout; tips very sharp, in situ directed ventroanteriad; posterior surface bearing 1 pore.

LEGS (Figs 7.4L, M; 7.19J). Male femora 6 and 7 humped ventrally in distal part.

GONOPODS (Figs 7.5E, 7.20). Coxa shorter than femur. Prefemoral part ca. half as long as femur. Femur quite enlarged distally. Postfemoral part short and narrow. Mesal sulcus and lateral sulcus wide. Solenophore longer than postfemoral part: lamina lateralis small, compact; apically protruding as a small lobe, directed mesoventrad: lamina medialis long; basally enlarged and slightly attenuated near the tip; tip bent, sharp and curving up. Solenomere curved and twisted, compressed in transverse section, tip directed posteriad.

Distribution and habitat (Figure 7.18C). All specimens were collected in small caves near the big Monkey Cave, crawling on rock walls. It is difficult to see the new species without using a flashlight/torch as the black body colour blends in with dark rocks. This species can be found in syntopy with *Desmoxytes cervina*. For the time being, *S. macaca* sp. n. is known only from the type locality and we regard it as endemic to Thailand.

Remarks. *S. macaca* sp. n. is morphologically similar to *S. krabiensis* sp. n. and *S. uncus* sp. n. with which it shares a fork-like sternal lobe between male coxae 4 and a small lamina lateralis.

Spinaxytes palmata Srisonchai, Enghoff & Panha, sp. n.

Figs 7.2; 7.4N, O; 7.5F; 7.21–7.23

Material examined. Holotype. ♂, THAILAND, Surat Thani Province, Phanom District, Wat Tham Wararam, 8°53'07"N, 98°40'01"E, ca. 51 m a.s.l., 6 Aug. 2016, ASRU members leg. (CUMZ-pxDGT00215). **Paratypes.** 23 ♂♂, 22 ♀♀, same data as for holotype (CUMZ-pxDGT00216); 1 ♂, 1 ♀, same data as for holotype (ZMUC00040254); 1 ♂, 1 ♀, same data as for holotype (ZMUM); 1 ♂, 1 ♀, same data as for holotype (NHMW9425); 1 ♂, 1 ♀, same data as for holotype (NHMUK). **Further specimens, not paratypes.** THAILAND: 1 ♂, 2 ♀♀, Surat Thani Province, Phanom District, Wat Tham Wararam, 8°53'07"N, 98°40'01"E, ca. 51 m a.s.l., 5 Aug. 2014, ASRU members leg. (CUMZ).

Etymology. The species name is a Latin adjective, referring to the tip of lamina medialis which is somewhat hand-shaped.

Diagnosis. Male femora without modification. Similar in this respect to *S. efefi* sp. n., *S. hasta* sp. n., *S. sutchariti* sp. n. and *S. tortioverpa* sp. n., but differs from them by having: anterior part of sternal lobe between male coxae 4 bifurcate, fork-like; tip of lamina medialis expanded, hand-shaped.

Description. SIZE. Length 26–30 mm (male), 27–32 mm (female); width of midbody metazona 1.9–2.2 mm (male), 2.0–2.4 mm (female). Width of collum = 2 = 3 = 4 < head < 5–16, thereafter body gradually tapering towards telson.

COLOUR (Figure 7.21A–C). Specimens in life with body black; paraterga orange; head, antennae (except whitish distal part of antennomeres 7 and 8), collum, prozona, metaterga (except white spines in posterior row) and surface below paraterga black; sterna and legs brown; epiproct pale brown; a few basal podomeres whitish brown.

ANTENNAE (Figure 7.22M). Reaching to body ring 8 (male) and 6 or 7 (female) when stretched dorsally.

COLLUM (Figure 7.22A). With three transverse rows of setiferous tubercles/cones, 4+4 in anterior row, 1(0)+1(0) in intermediate row and 2(1)+2(1) in posterior row; with one conspicuous setiferous notch at lateral margin; paraterga spiniform, long, tip sharp, elevated at ca. 15°–20° (male) 10°–15° (female), directed almost laterad.

TEGUMENT. Very shining; collum coarsely microgranulate; metaterga and surface below paraterga smooth.

METATERGA (Figure 7.22A, C, E). With two transverse rows of setiferous cones and setiferous spines; metaterga 2–19 with 2+2 cones in anterior row and 2+2 spines in posterior row; lateral cones/spines of posterior row bigger and longer than mesal ones, gradually reduced in size and length on the following rings.

PARATERGA (Figure 7.22A–E, H). Very long; directed dorsolaterad on body rings 2–17, elevated at ca. 50°–60° (male) 45°–60° (female), directed increasingly caudad on body rings 18 and 19. Ozopore visible in dorsolateral view.

TELSON (Figure 7.22E, H, I). Epiproct quite short; tip subtruncate; lateral setiferous tubercles conspicuous; apical tubercles inconspicuous. Hypoproct subtrapeziform (in some specimens subtriangular); caudal margin round (in some specimens angular), with inconspicuous setiferous tubercles.

STERNA (Figs 7.4N; 7.22F, G). Sternal lobe between male coxae 4 with two parts; anterior part bifurcate, tuning-fork-like, long, tips sharp, in situ directed ventroanteriad; posterior margin of anterior part bearing 1 pore; posterior part swollen, short.

LEGS (Figs 7.4O, 7.22J). Male femora without modification.

GONOPODS (Figs 7.5F, 7.23). Coxa shorter than femur. Prefemoral part ca. half as long as femur. Femur not enlarged distally. Postfemoral part broad. Mesal sulcus and lateral sulcus wide. Solenophore a bit bigger than postfemoral part: lamina lateralis small, oval, tip round: lamina medialis long; basally enlarged and slightly attenuated near the tip; tip fringed, hand-shaped; tip curving down, in situ resting close to solenomere. Solenomere curved and twisted, compressed in transverse section, tip directed posteriad.

Distribution and habitat (Figure 7.21D). *S. palmata* sp. n. is known only from the type locality. We regard this species as endemic for the Thai fauna. The new species can be found in syntopy with *Desmoxytes corythosaurus* Srisonchai, Enghoff & Panha, 2018, crawling on humid rock walls.

Remarks. There are variations in the hypoproct: subtrapeziform in some specimens, subtriangular in the others; caudal margin in some individuals round, angular in the others.

Spinaxytes sutchariti Srisonchai, Enghoff & Panha, sp. n.

Figs 7.4P, Q; 7.5G; 7.24; 7.25

Material examined. Holotype. ♂, THAILAND, Krabi Province, Muang Krabi District, Tham Na Mee (Na Mee Cave), 8°08'12"N, 98°48'23"E, ca. 70 m a.s.l., 31 Aug. 2015, C. Sutcharit leg. (CUMZ-pxDGT00217). **Paratypes.** 7 ♂♂, 4 ♀♀, same data as for holotype (CUMZ-pxDGT00218).

Etymology. The name honours associate professor Dr. Chirasak Sutcharit, malacologist of ASRU (CUMZ), collector of this new species and numerous other dragon millipedes.

Diagnosis. Male femora without modification, sternal lobe between male coxae 4 incompletely bilobed. Similar in these respects to *S. palmata* sp. n., but differs by having: a large and round lamina lateralis; tip of lamina medialis terminating in two spines; distal part of solenomere circular in tranverse section.

Description. SIZE. Length 20–25 mm (male), 23–27 mm (female); width of midbody metazona 1.5–1.8 mm (male), 1.9–2.2 mm (female). Width of collum = 2 = 3 = 4 < head = 5–16, thereafter body gradually tapering towards telson.

COLOUR (Figure 7.24A–C). Specimens in life with body black; paraterga brownish white; head, antennae (except whitish distal part of antennomeres 7 and 8), collum, prozona, metaterga and epiproct black; surface below paraterga black/brownish black; sterna brown; legs brown/blackish brown; a few basal podomeres whitish brown.

ANTENNAE. Reaching to body ring 8 or 9 (male) and 6 (female) when stretched dorsally.

COLLUM. With three transverse rows of setiferous tubercles, 4+4 tubercles in anterior row, 1+1 tubercles in intermediate row and 2+2 tubercles in posterior row; with one inconspicuous setiferous notch at lateral margin; paraterga spiniform, quite short, tip sharp, elevated at ca. 15°–20° in both male and female, directed caudolaterad.

TEGUMENT. Quite dull; collum and metaterga (posterior part) coarsely microgranulate; metaterga (anterior part) and surface below paraterga smooth.

METATERGA. With two transverse rows of setiferous tubercles and setiferous spines; metaterga 2–19 with 2+2 tubercles in anterior row and 2+2 spines in posterior row; lateral spines of posterior row bigger and longer than mesal ones, subequal in size and length on all body rings.

PARATERGA. Long; directed dorsolaterad on body rings 2–16, elevated at ca. 45°–50° (male) 40°–50° (female), directed dorsocaudad on ring 17, directed increasingly caudad on body rings 18 and 19. Ozopore visible in lateral view.

TELSON. Epiproct quite long; tip subtruncate; lateral setiferous tubercles conspicuous; apical tubercles inconspicuous. Hypoproct subtrapeziform (in some specimens subtriangular); caudal margin round (in some specimens angular), with inconspicuous setiferous tubercles.

STERNA (Figure 7.4P). Sternal lobe between male coxae 4 incompletely bilobed; tips sharp, in situ directed laterad; posterior surface bearing 2 pores.

LEGS (Figure 7.4Q). Male femora without modification.

GONOPODS (Figs 7.5G, 7.25). Coxa subequal in length to femur. Prefemoral part ca. 2/3 as long as femur. Femur not enlarged distally. Postfemoral part narrow. Mesal sulcus and lateral sulcus wide. Solenophore bigger and longer than postfemoral part: lamina lateralis oval, large, long, tip round: lamina medialis long and slender; base enlarged, slightly attenuated near the tip; tip curving down, with two sharp spines (one smaller, one bigger). Solenomere curving up, circular in transverse section, tip directed anteriad.

Distribution and habitat (Figure 7.24D). *S. sutchariti* sp. n. is known only from the type locality, and we regard it as endemic to Thailand. The new species can be found in the same area as *Gigaxytes gigas*, but we assume that they live in different microhabitats: *G. gigas* was collected from the ground in leaf litter, whereas the new species was found on humid rock walls.

Remarks. We found variation in the hypoproct: in some specimens subtrapeziform, in others subtriangular; caudal margin in some individuals round, in others angular. Parasitic mite larvae, probably of the genus *Leptus* Latreille, 1796, were found attached to the anterior body part of some female specimens. Larvae of ?*Leptus* have previously been found on species of *Desmoxytes* (*D. cervina*) and *Nagaxytes* (*N. acantherpestes* (Golovatch & Enghoff, 1994)) Srisonchai *et al.* (2018a, 2018b), see also Southcott (1992).

Spinaxytes tortioverpa Srisonchai, Enghoff & Panha, sp. n.

Figs 7.1; 7.4R, S; 7.5H; 7.26

Material examined. Holotype. ♂, MALAYSIA, Perak State, Ipoh City, Gua Tempurung, limestone mountain, 4°24'58"N, 101°11'16"E, ca. 92 m a.s.l., 27 Sep. 2007, B. W. Ng and ASRU members leg. (CUMZ-pxDGT00219). **Paratypes.** 1 ♂, 1 ♂ gonopods missing, 1 ♀, same data as for holotype (CUMZ-pxDGT00220).

Etymology. The name is a noun in apposition, from the Latin *tortio* meaning torsion and *verpa* for penis, refers to the distal part of gonopod (postfemoral part, solenophore and solenomere) which makes a 90 degrees torsion relative to the femoral part.

Diagnosis. Male femora without modification; collum with 4+4 tubercles in anterior row, 1+1 tubercles in intermediate row and 2+2 tubercles in posterior row. Similar in these respects to *S. hasta* sp. n. and *S. palmata* sp. n., but differs from them by having: a completely bilobed sternal lobe between male coxae 4; postfemoral part, solenophore and solenomere angled 90 degrees with femoral part; lamina lateralis with two lobes – the lateral one spine-like, the mesal one shorter and ridge-like; solenomere very long, longer than lamina medialis.

Description. SIZE. Length 28–30 mm (male), 30–33 mm (female); width of midbody metazona 2.0 mm (male), 2.8 mm (female). Width of rings 2 = 3 = 4 < head = 5–16, thereafter body gradually tapering towards telson.

COLOUR. Specimens in life with body black/brownish black. Colour in alcohol: after 10 years changed to brown; paraterga brownish white; antennae brown (except whitish distal part of antennomeres 7 and 8); head, collum, metaterga and prozona blackish brown; surface below paraterga brown/blackish brown; sterna, epiproct and legs pale brown; a few basal podomeres whitish brown.

ANTENNAE. Reaching to body ring 8 or 9 (male) and 6 or 7 (female) when stretched dorsally.

COLLUM. With three transverse rows of setiferous tubercles, 4+4 tubercles in anterior row, 1+1 tubercle in intermediate row and 2+2 tubercles in posterior row; anterior margin truncate; with one inconspicuous setiferous notch at lateral margin; paraterga wing-like, long and broad, tip sharp, elevated at ca. 15°–20° in both male and female, directed caudolaterad.

TEGUMENT. Quite dull; collum, metaterga and surface below paraterga finely microgranulate.

METATERGA. With two transverse rows of setiferous tubercles/cones and spines; metaterga 2–8 with 2+2 cones in anterior row and 2+2 spines in posterior row; metaterga 9–19 with 2+2 tubercles/cones in anterior row and 2+2 spines in posterior row; mesal spines of posterior row bigger and longer than lateral ones, gradually reduced in length and size on posterior rings.

PARATERGA. Very long; directed dorsolaterad on body rings 2–17, elevated at ca. 65°–70° (male) 60°–70° (female), directed increasingly caudad on body rings 18 and 19. Ozopore visible in dorsolateral view.

TELSON. Epiproct quite short; tip subtruncate; lateral setiferous tubercles inconspicuous; apical tubercles inconspicuous. Hypoproct subsemicircular; caudal margin round, with inconspicuous setiferous tubercles.

STERNA (Figure 7.4R). Sternal lobe between male coxae 4 completely divided into two lobes, long, spine-like; tips in situ directed ventrad; posterior surface a bit swollen, bearing 2 pores.

LEGS (Figure 7.4S). Male femora without modification.

GONOPODS (Figs 7.5H, 7.26). Coxa subequal in length to femur. Prefemoral part about 2/3 as long as femur. Femur quite enlarged distally. Postfemoral part large, broad and wide; angled 90 degrees with femur. Mesal sulcus and lateral sulcus wide. Solenophore smaller than postfemoral part: lamina lateralis apparently with two lobes demarcated from each other; lateral lobe very long, process-like, its tip in situ directed ventrad; mesal lobe short and wide, supporting solenomere: lamina medialis long, base not enlarged, tip directed mesad. Solenomere obviously longer than lamina medialis, circular in transverse section, curving down, tip directed laterad.

Distribution and habitat. Known only in the type locality which is currently a tourist attraction (cave). We regard this species as endemic to Malaysia.

Remarks. A photograph of a live specimen was not taken during the field survey, but our collector noticed its black or brownish black colour. All specimens were seen crawling on rock walls where they seem to blend perfectly with the substrate. No variation in morphological characters was found.

Spinaxytes uncus **Srisonchai, Enghoff & Panha, sp. n.**

Figs 7.4T–V; 7.5I; 7.27–7.29

Material examined. Holotype. ♂, THAILAND, Phang Nga Province, Mueang Phang Nga District, Phung Chang Cave, 8°26'34"N, 98°30'59"E, ca. 24 m a.s.l., 8 Aug. 2016, ASRU members leg. (CUMZ-pxDGT00221). **Paratypes.** 15 ♂♂, 16 ♀♀, same data as for holotype (CUMZ-pxDGT00222); 1 ♂, 1 ♀, same data as for holotype (ZMUC00040255); 1 ♂, 1 ♀, same data as for holotype (ZMUM); 1 ♂, 1 ♀, same data as for holotype (NHMW9424). **Further specimens, not paratypes, all from THAILAND, Phang Nga Province. Muaeng Phang Nga District:** 4 ♂♂, 2 ♀♀, Phung Chang Cave, 8°26'34"N, 98°30'59"E, ca. 24 m a.s.l., 6 Aug. 2014, ASRU members leg. (CUMZ); 4 ♂♂, Phung Chang Cave, 8°26'34"N, 98°30'59"E, ca. 24 m a.s.l., 5 Aug. 2015, ASRU members leg. (CUMZ); 2 ♂♂, 4 broken ♀♀, Tham Nam Pud, 8°27'50"N, 98°32'36"E, ca. 58 m a.s.l., 8 Oct. 2006, ASRU members leg. (CUMZ); 3 ♂♂, 2 ♀♀, Tham Nam Pud, 8°27'50"N, 98°32'36"E, ca. 58 m a.s.l., 5 Aug. 2015, ASRU members leg. (CUMZ); 2 ♂♂, 1 ♀, Wat Tham Bang Toei, 8°27'52"N, 98°34'10"E, ca. 24 m a.s.l., 10 Jul. 2017, ASRU members leg. (CUMZ); 8 ♂♂, 2 ♀♀, Tham Pha Phueng Bureau of Monks, 8°28'24"N, 98°32'15"E, ca. 78 m a.s.l., 10 Jul. 2017, ASRU members leg. (CUMZ). **Thap Put District:** 11 ♂♂, 3 ♀♀, Wat Kerewong (Tham Koab), 8°31'52"N, 98°34'39"E, ca. 76 m a.s.l., 9 Jul. 2017, ASRU members leg. (CUMZ).

Etymology. The name is a Latin noun in apposition (*uncus*), meaning hook, and refers to the hook-like lamina medialis of gonopod.

Diagnosis. Differs from other species by having only male femora 7 strongly humped distally, in combination with the distal part of lamina medialis hook-like, tip long and sharp.

Description. SIZE. Length 20–27 mm (male), 25–29 mm (female); width of midbody metazon 1.4–1.6 mm (male), 2.1–2.3 mm (female). Width of collum < 2 = 3 < 4 < head = 5–16, thereafter body gradually tapering towards telson.

COLOUR (Figure 7.27A–E). Specimens in life with body black; paraterga yellow/whitish yellow; head, antennae (except whitish distal part of antennomeres 7 and 8) and prozona black; collum, metaterga and surface below paraterga black/brownish black; sterna and epiproct brown; legs yellow; a few basal podomeres white.

ANTENNAE (Figure 7.28M). Reaching to body ring 8 or 9 (male) and 6 or 7 (female) when stretched dorsally.

COLLUM (Figure 7.28A). With three transverse rows of setiferous cones, 4+4 in anterior row, 1+1 in intermediate row and 2+2 in posterior row; with two conspicuous setiferous notches at lateral margin (first notch located at base of paraterga very close to cones of anterior row; paraterga spiniform, long, tip sharp, elevated at ca. 20°–30° in both male and female, directed almost laterad.

TEGUMENT. Quite shining; collum, metaterga (posterior part) and surface below paraterga finely microgranulate; metaterga (anterior part) coarsely microgranulate.

METATERGA (Figure 7.28A, C, E). With two transverse rows of setiferous cones and setiferous spines; metaterga 2–19 with 2+2 cones in anterior row and 2+2 spines in posterior row; lateral spines of posterior row very long, bigger and longer than mesal ones.

PARATERGA (Figure 7.28A–E, H). Very long; directed dorsolaterad on body rings 2–16, elevated at ca. 40°–50° (male) 40°–45° (female), directed dorsocaudad on ring 17, directed increasingly caudad on body rings 18 and 19. Ozopore visible in dorsolateral view.

TELSON (Figure 7.28E, I, H). Epiproct short; tip subtruncate; lateral setiferous tubercles inconspicuous; apical tubercles inconspicuous. Hypoproct subtrapeziform (in some specimens subsemicircular); caudal margin round, with conspicuous setiferous tubercles (in some specimens inconspicuous).

STERNA (Figs 7.4T; 7.28F, G). Sternal lobe between male coxae 4 bifurcate, long; tips sharp, in situ directed ventroanteriad; posterior surface bearing one pore.

LEGS (Figs 7.5U, V; 7.28J). Male femora 7 strongly humped ventrally in distal part.

GONOPODS (Figs 7.5I, 7.29). Coxa subequal in length to femur. Prefemoral part almost half as long as femur. Femur obviously enlarged distally. Postfemoral part small, narrow. Mesal sulcus wide; lateral sulcus narrow. Solenophore bigger and longer than postfemoral part: lamina lateralis very small, compact, tip round: lamina medialis long; basally enlarged and slightly attenuated near the tip; apically sharp, long, hook-like; tip curving down, in situ resting close to solenomere, compressed in transverse section, tip directed posteriad.

Distribution and habitat (Figure 7.27F). Known only from Phang Nga Province; we regard *S. uncus* sp. n. as endemic for the Thai fauna. Most specimens were found on rock walls near the cave, some were seen crawling on leaf litter on the rock. The new species has been encountered in syntopy with *Desmoxytes cervina* at Phung Chang Cave, Tham Nam Pud and Wat Kerewong (Tham Koab).

Remarks. Some variation in the hypoproct was observed in this species: in some specimens subtrapeziform, in others subsemicircular; caudal margin in some individuals conspicuous, in others inconspicuous. In addition, specimens from Wat Kerewong (Tham Koab) have smaller and shorter paraterga than other specimens.

Discussion

The new genus *Spinaxytes,* defined by Srisonchai *et al.* (2018a) as the "spiny" group of dragon millipedes, at that time without described members, adds to the challenge of understanding the patterns of paratergal and gonopod evolution in the dragon millipedes. The nine species, all new, described here are recorded from Malaysia, Myanmar, and Thailand. They are united in the new genus by sharing the diagnostic characters of subspiniform paraterga; lamina lateralis distinctly demarcated from lamina medialis; and the lamina medialis long and curved, larger and longer than lamina lateralis.

Based on a comparatively large number of specimens and species of the new genus, our study confirmed that gonopod characters can be used confidently to discriminate the species, just as we found in *Desmoxytes* and *Nagaxytes* (Srisonchai *et al.*, 2018a, 2018b). Using the gonopods in combination with other morphological characters, such as modification of male femora, sternal lobe between male coxae 4, and number of tubercles/cones/spines on collum and on metaterga, further facilitates reliable taxonomic identification. It is particularly interesting that a process on the postfemoral part of the gonopod is found in *S. efefi* sp. n. Only two species of dragon millipede, *Hylomus specialis* (Nguyen et al. 2005) and *H. spectabilis* (Attems, 1937), have hitherto been known to have this process (z-spine) at the base of the solenophore. However, the overall gonopod characters of *S. efefi* sp. n. are markedly different from the gonopod of the two mentioned *Hylomus* species, warranting its inclusion in the new genus. *Spinaxytes* gen. n., is quite possibly a monophyletic group, considering both gonopodal and non-gonopodal characters. A phylogenetic study using molecular as well as morphological characters seems warranted in order to better understand the taxonomic position and the true relationship of the genus with other dragon millipede genera.

Almost all specimens collected by us were found on humid rock walls in small caves. Therefore, we strongly suspect that all species in this genus prefer to live on rock walls. The black or dark brown body colour makes them difficult to see against dark-coloured rocks. Quite often some specimens of *Desmoxytes* and *Gigaxytes* species are encountered in the same habitat as species of the new genus, but it seems likely that those species live on leaf litter, on the ground or on tree branches instead of rock walls. Considering currently known distributions of species of *Spinaxytes* gen. n., and their restriction to small limestone areas (Figure 7.30), we regard all described species here as locally endemic. Of the nine species of *Spinaxytes* gen. n., only one (*S. hasta* sp. n.) has been shown to have a somewhat wider range, but it still inhabits less than approximately 50 km^2 along the coast of Thailand.

The discovery rate of new dragon millipede species has been increasing in recent years (Golovatch *et al.*, 2016; Likhitrakarn *et al.*, 2015; Liu *et al.*, 2014, 2016; Srisonchai *et al.*, 2016, 2018b, 2018c). Including the nine new species described here, the diversity of dragon millipedes (*Desmoxytes* + *Hylomus* + *Nagaxytes* + *Gigaxytes* + *Spinaxytes* gen. n.) has now reached 59 species. Dragon millipedes are thus a significant element in the biodiversity of Southeast Asia, especially Thailand and the Malay Peninsula. We believe that the number of endemic dragon millipede species will certainly increase further when collecting efforts in very remote or otherwise difficult-to-access places are made.

Acknowledgements

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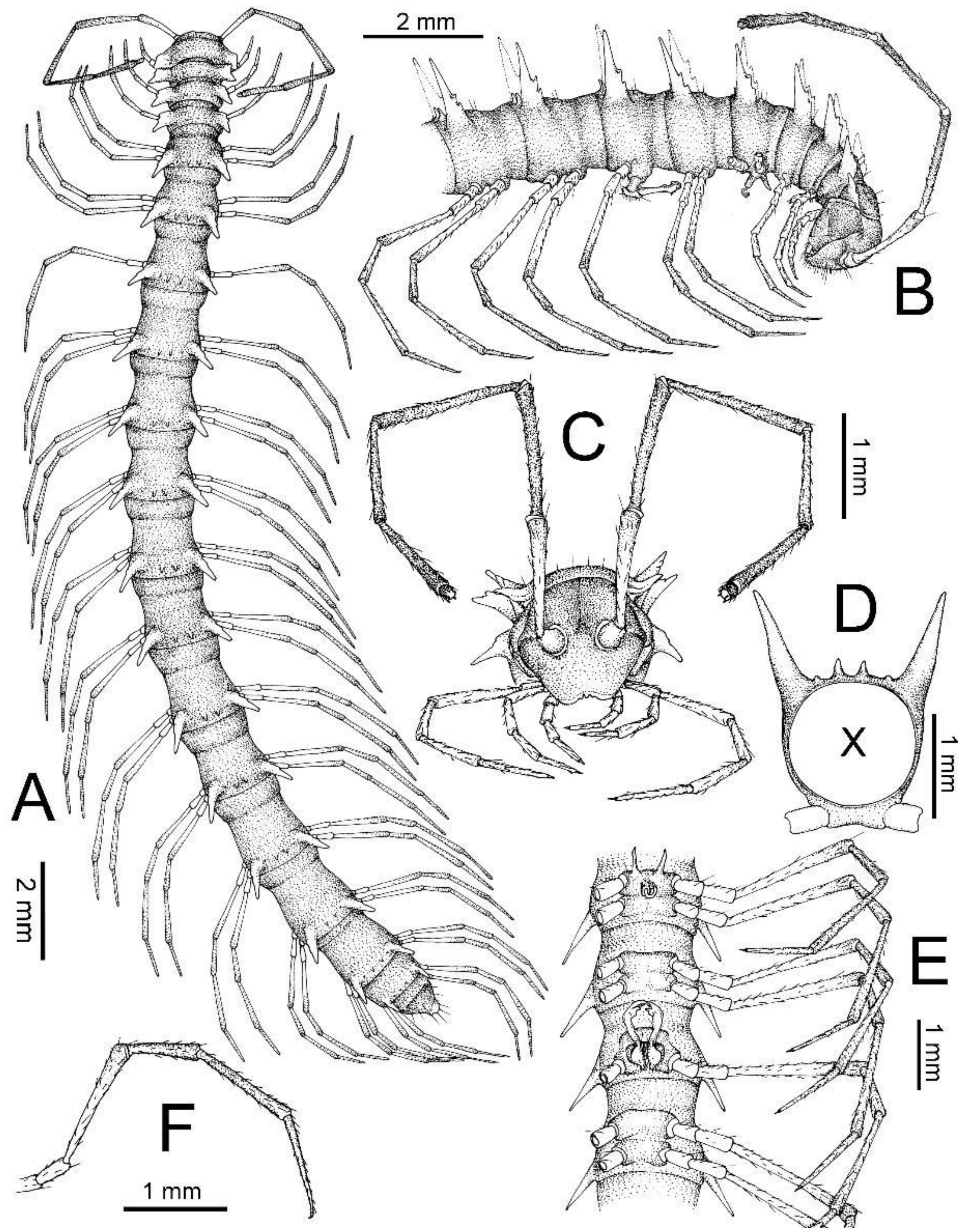

Figure 7.1 General body characters of *Spinaxytes* gen. n. (*S. tortioverpa* sp. n., ♂ paratype, CUMZ-pxDGT00220) **A** Whole body **B** Anterior body part **C** Head and antennae **D** Midbody ring **E** Body rings 5–8, showing gonopods and sternal lobe between coxae 4 **F** Leg 13.

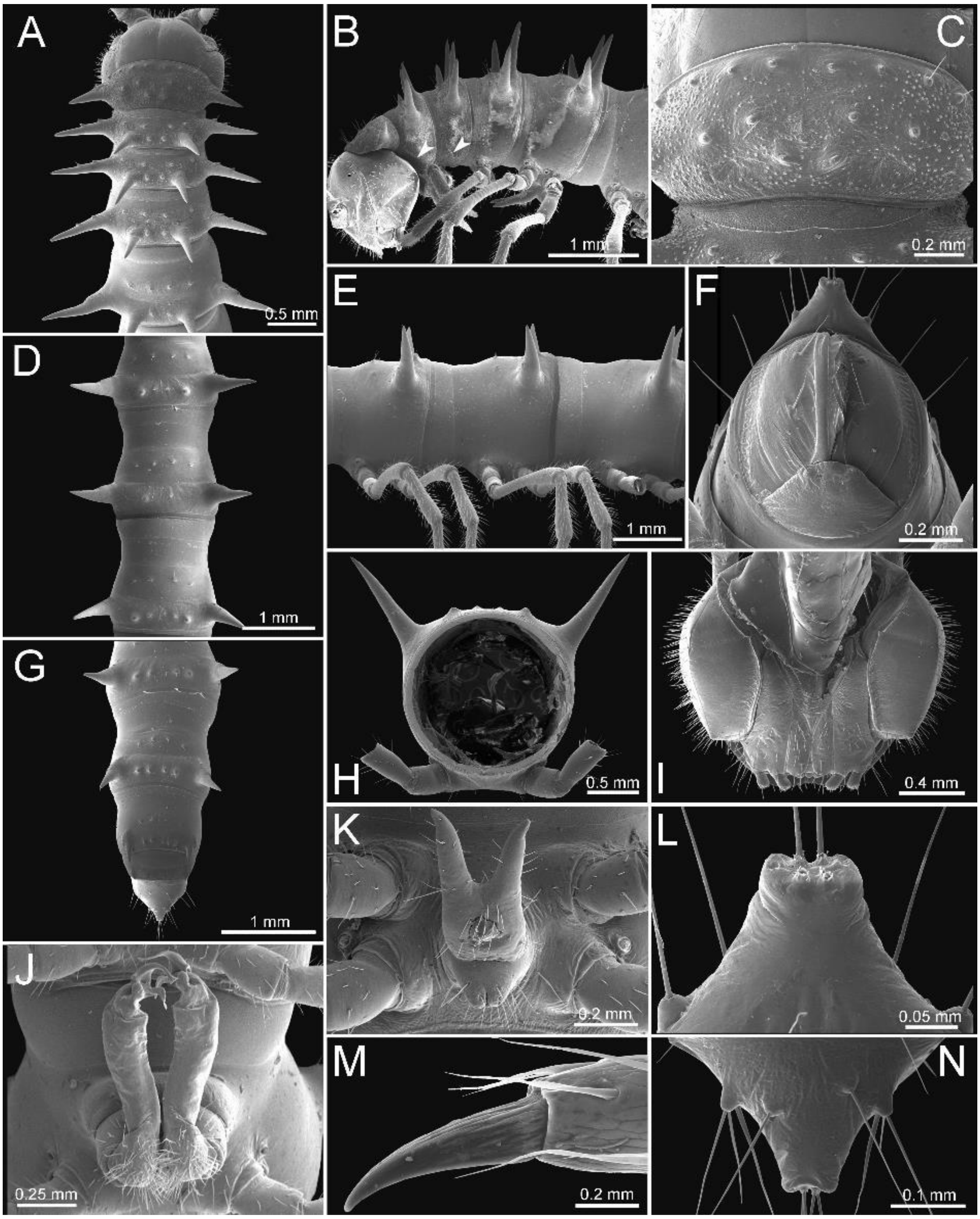

Figure 7.2 General body characters of *Spinaxytes* gen. n. (*S. palmata* sp. n., ♂ paratype, CUMZ-pxDGT00216) – SEM images **A, B** Anterior body part (arrowheads point to pleurosternal carinae) **C** Collum **D, E** Body rings 9–11 **F** Telson **G** Posteriormost rings and telson **H** Body ring 10 **I** Mouth parts, ventral view **J** Gonopods **K** Sternal lobe between coxae 4 **L, N** Tip of epiproct **M** Tip of tarsus and claw of leg 13.

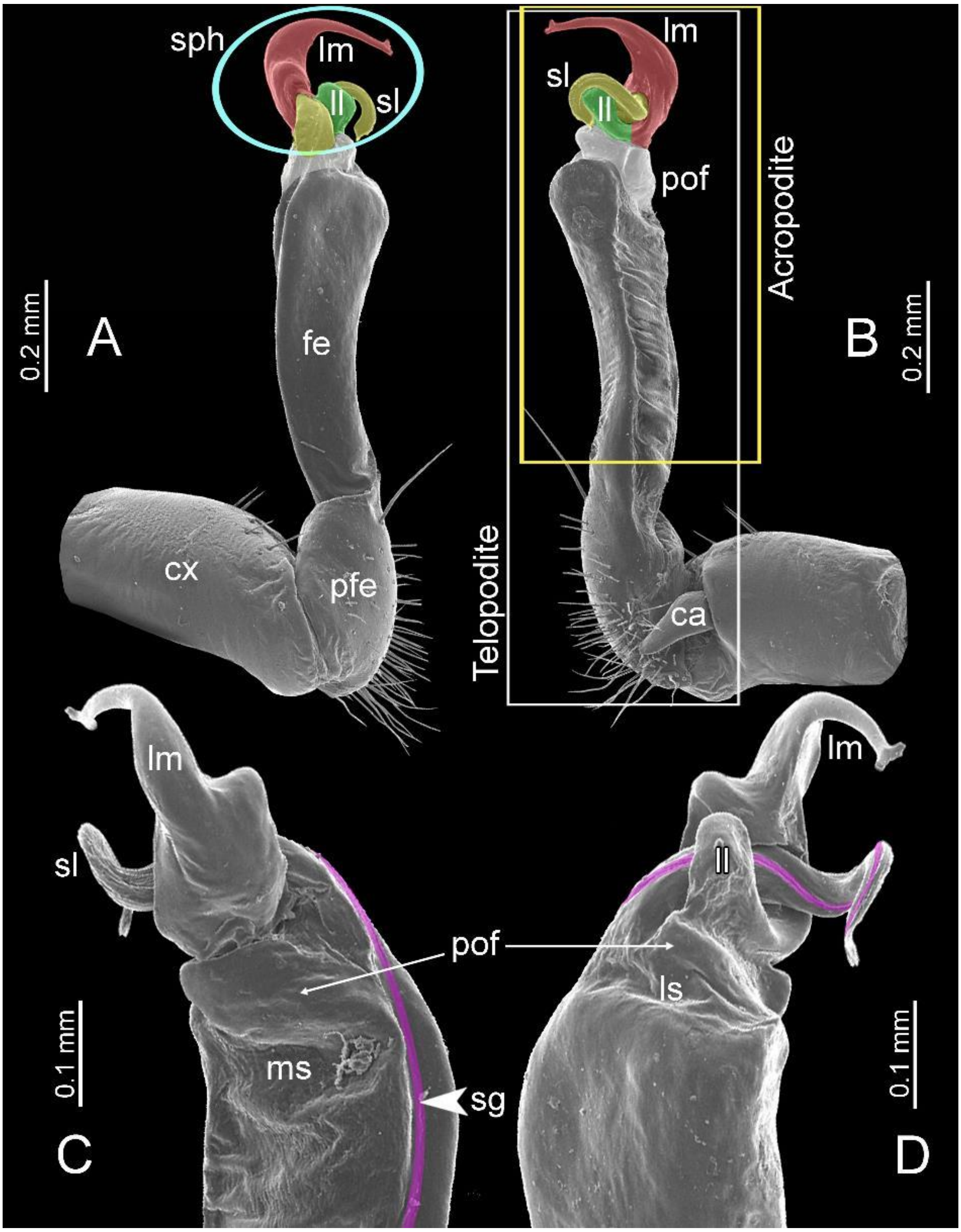

Figure 7.3 SEM images of right gonopod of *Spinaxytes* gen. n. (*Spinaxytes krabiensis* sp. n., ♂ paratype, CUMZ-pxDGT00212) **A** Lateral view **B** Mesal view **C** Dorsal view **D** Ventral view. Colour: red = lamina medialis (lm), yellow = solenomere (sl), green = lamina lateralis (ll), purple = seminal groove (sg).

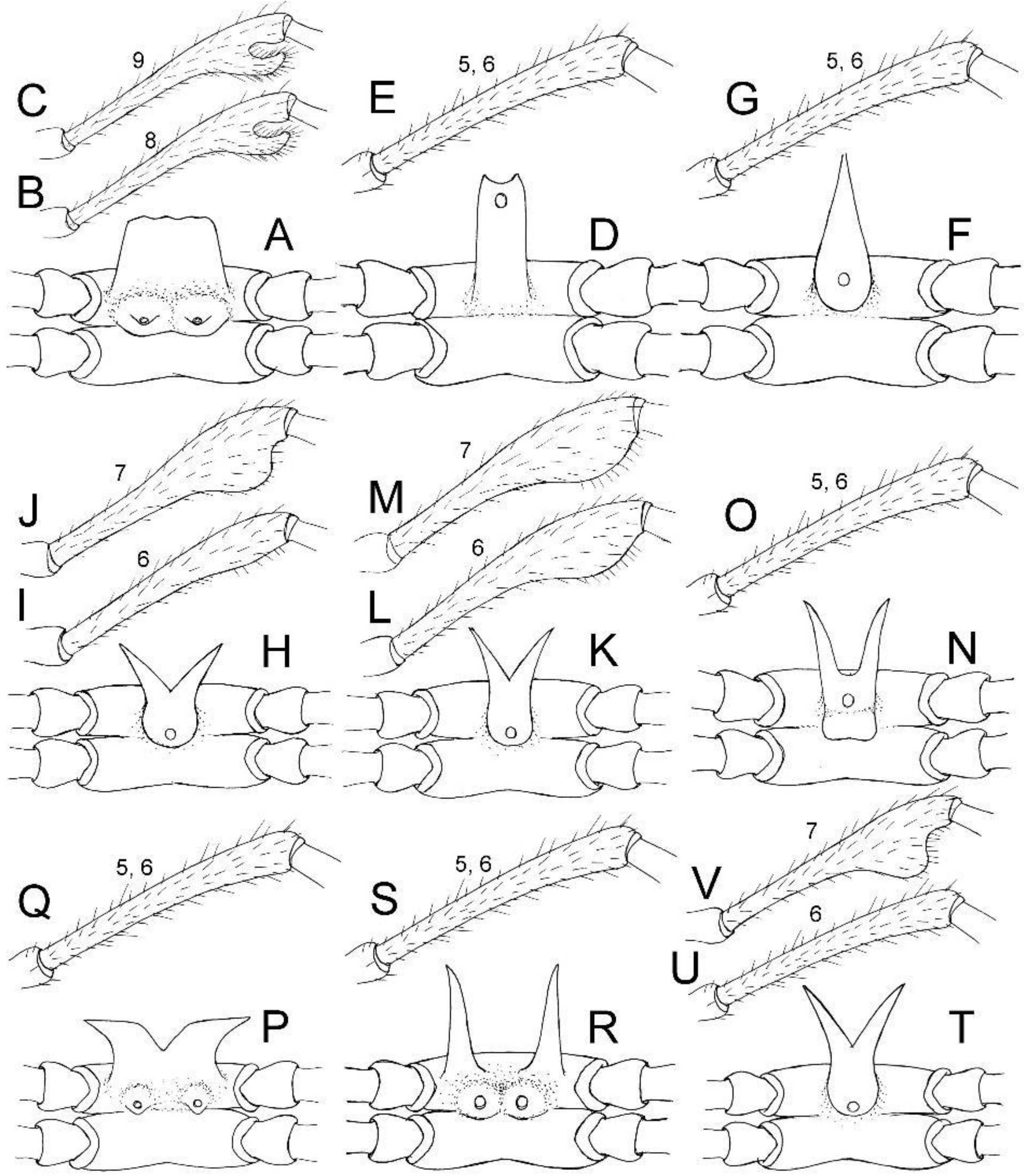

Figure 7.4 Male femora and sternal lobe between male coxae 4 of *Spinaxytes* gen. n. **A–C** *S. biloba* sp. n. (**A** Sternal lobe **B** Femur 8 **C** Femur 9). **D, E** *S. efefi* sp. n. (**D** Sternal lobe **E** Femur 5 or 6) **F, G** *S. hasta* sp. n. (**F** Sternal lobe **G** Femur 5 or 6) **H–J** *S. krabiensis* sp. n. (**H** Sternal lobe **I** Femur 6 **J** Femur 7) **K–M** *S. macaca* sp. n. (**K** Sternal lobe **L** Femur 6 **M** Femur 7) **N, O** *S. palmata* sp. n. (**N** Sternal lobe **O** Femur 5 or 6) **P, Q** *S. sutchariti* sp. n. (**P** Sternal lobe **Q** Femur 5 or 6) **R, S** *S. tortioverpa* sp. n. (**R** Sternal lobe **S** Femur 5 or 6) **T–V** *S. uncus* sp. n. (**T** Sternal lobe **U** Femur 6 **V** Femur 7).

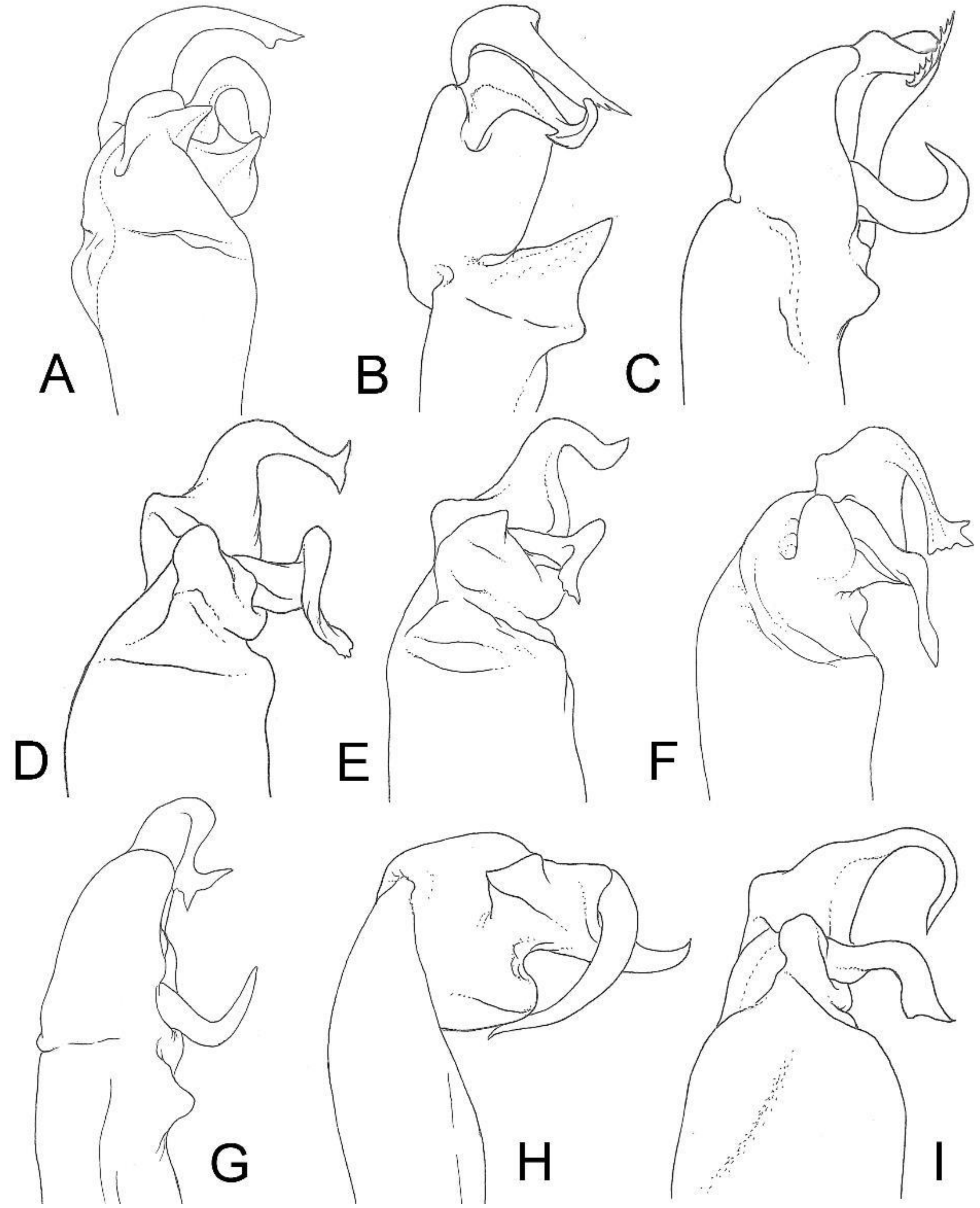

Figure 7.5 Right gonopods of *Spinaxytes* gen. n. (ventral view) **A** *S. biloba* sp. n. **B** *S. efefi* sp. n. **C** *S. hasta* sp. n. **D** *S. krabiensis* p. n. **E** *S. macaca* sp. n. **F** *S. palmata* sp. n. **G** *S. sutchariti* sp. n. **H** *S. tortioverpa* sp. n. **I** *S. uncus* sp. n.

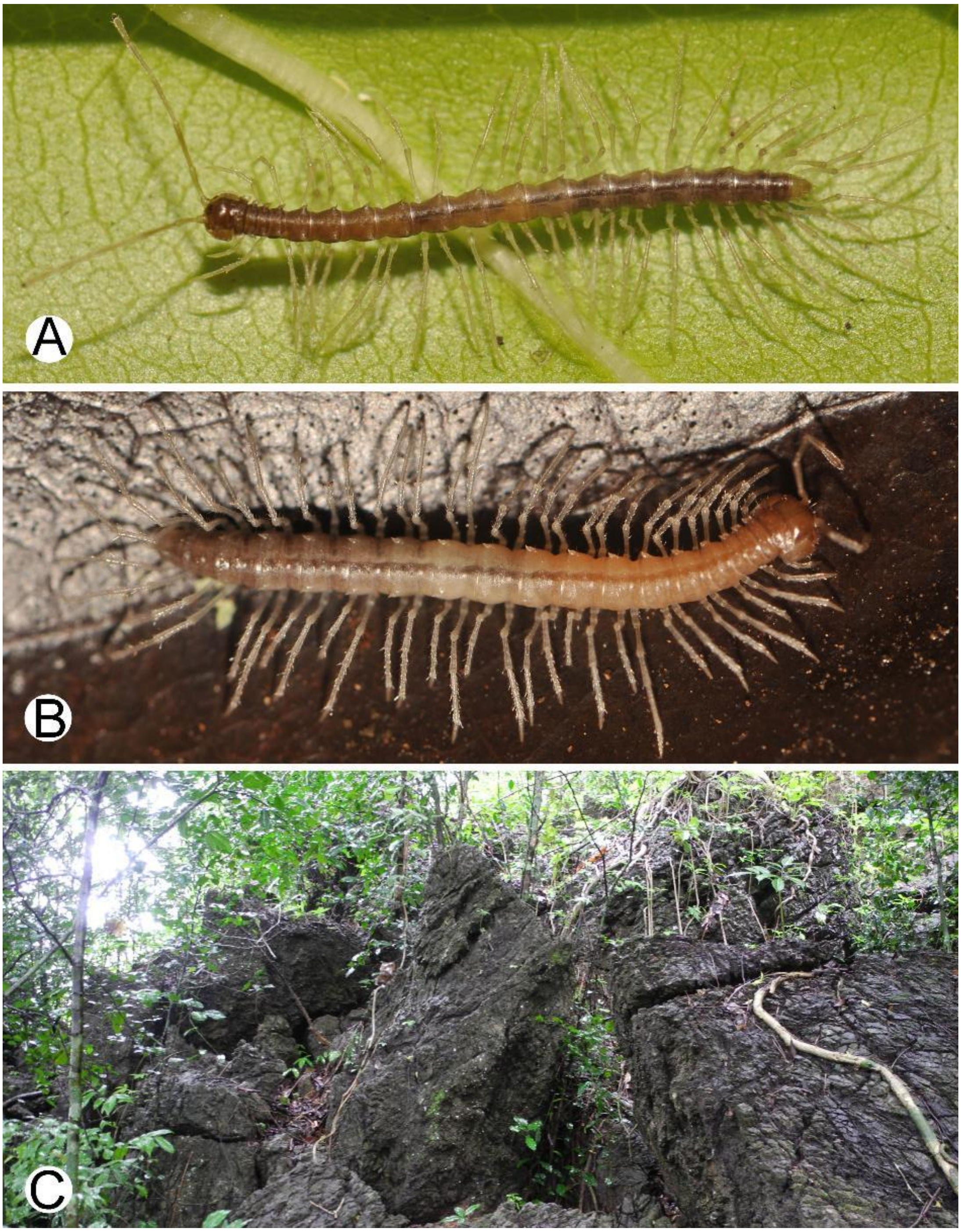

Figure 7.6 Photographs of live *Spinaxytes biloba* sp. n. and habitat **A** ♂ paratype, CUMZ-pxDGT00206 **B** ♀ paratype, CUMZ-pxDGT00206 **C** Habitat.

Figure 7.7 *Spinaxytes biloba* sp. n., ♂ paratype, CUMZ-pxDGT00206 **A**, **B**. Anterior body part **C, D** Body rings 8–10 **E, H, I** Posteriormost body rings and telson **F, G** Sternal lobe between coxae 4 **J**

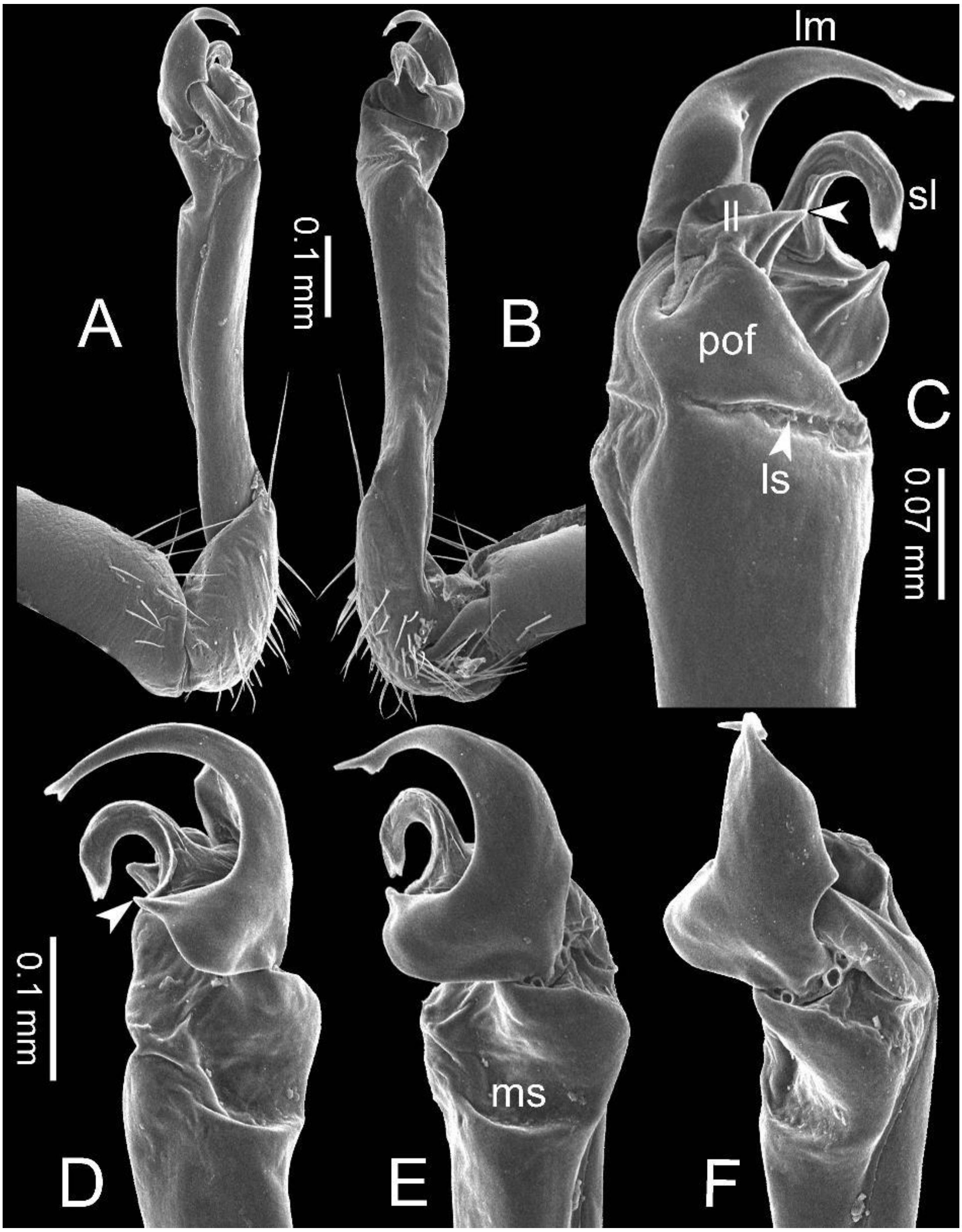

Figure 7.8 *Spinaxytes biloba* sp. n., paratype, CUMZ-pxDGT00206 – right gonopod **A** Lateral view **B** Mesal view **C** Ventral view (arrowhead points to lobe on lamina lateralis) **D** Mesodorsal view (arrow points to lobe at base of lamina medialis) **E** Dorsal view **F** Laterodorsal view.

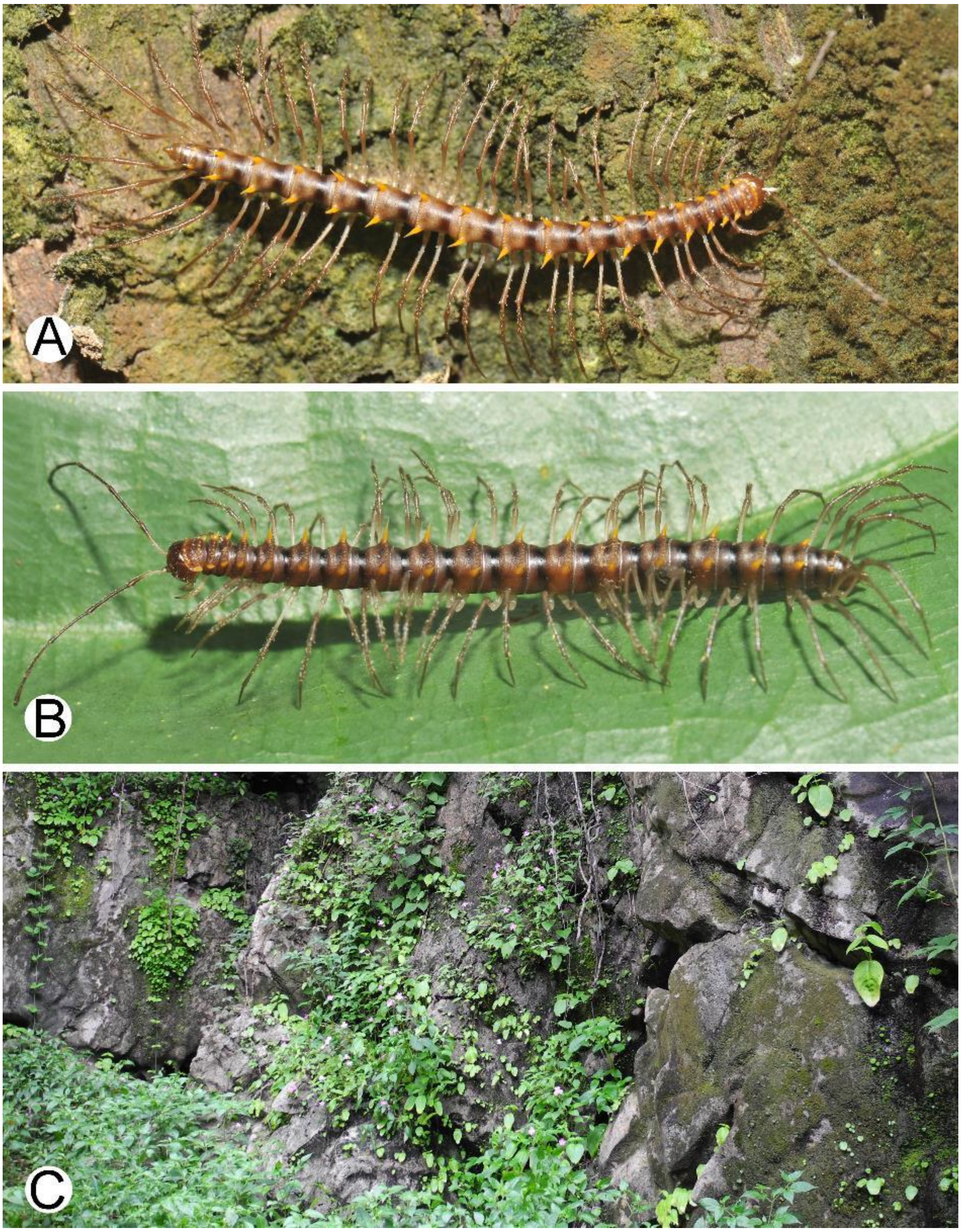

Figure 7.9 Photographs of live *Spinaxytes efefi* sp. n. and habitat **A** ♂ paratype, CUMZ-pxDGT00208 **B** ♀ paratype, CUMZ-pxDGT00208 **C** Habitat.

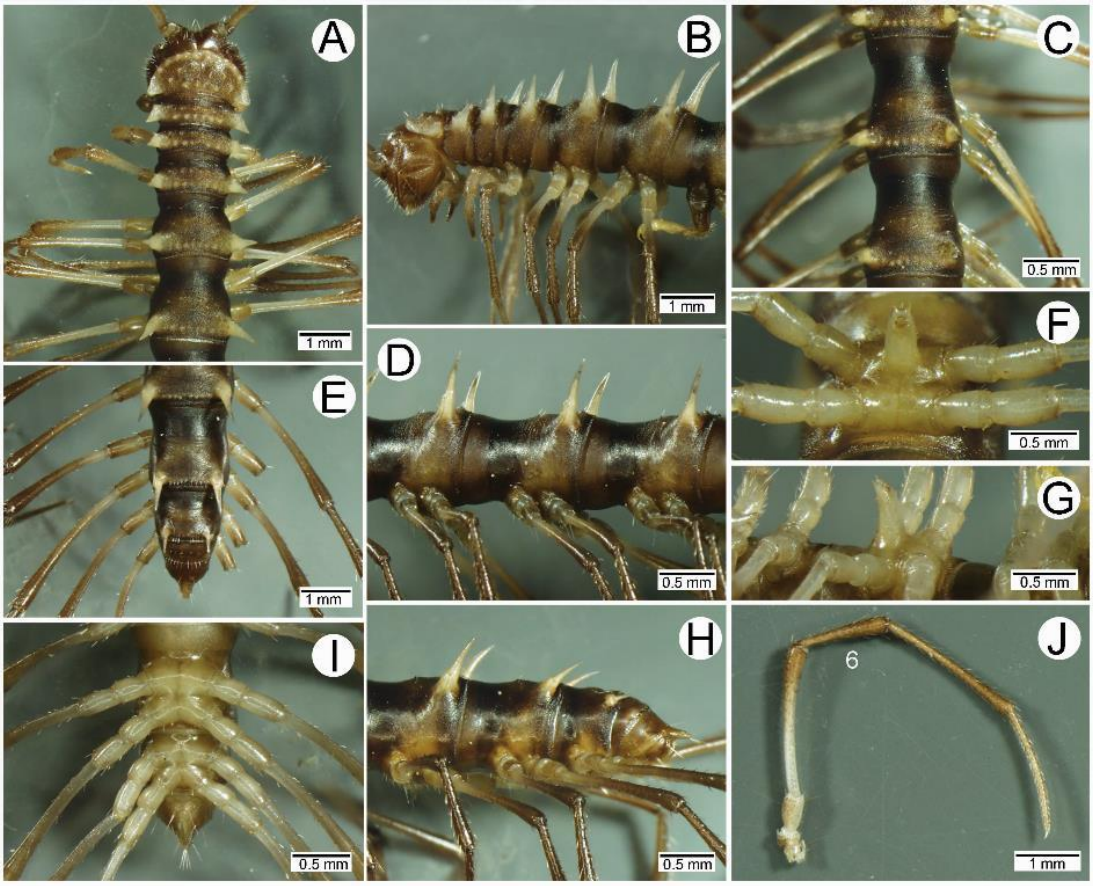

Figure 7.10 *Spinaxytes efefi* sp. n., ♂ paratype, CUMZ-pxDGT00208 **A**, **B** Anterior body part **C, D** Body rings 9–11 **E, H, I** Posteriormost body rings and telson **F, G** Sternal lobe between coxae 4 **J** Leg 6.

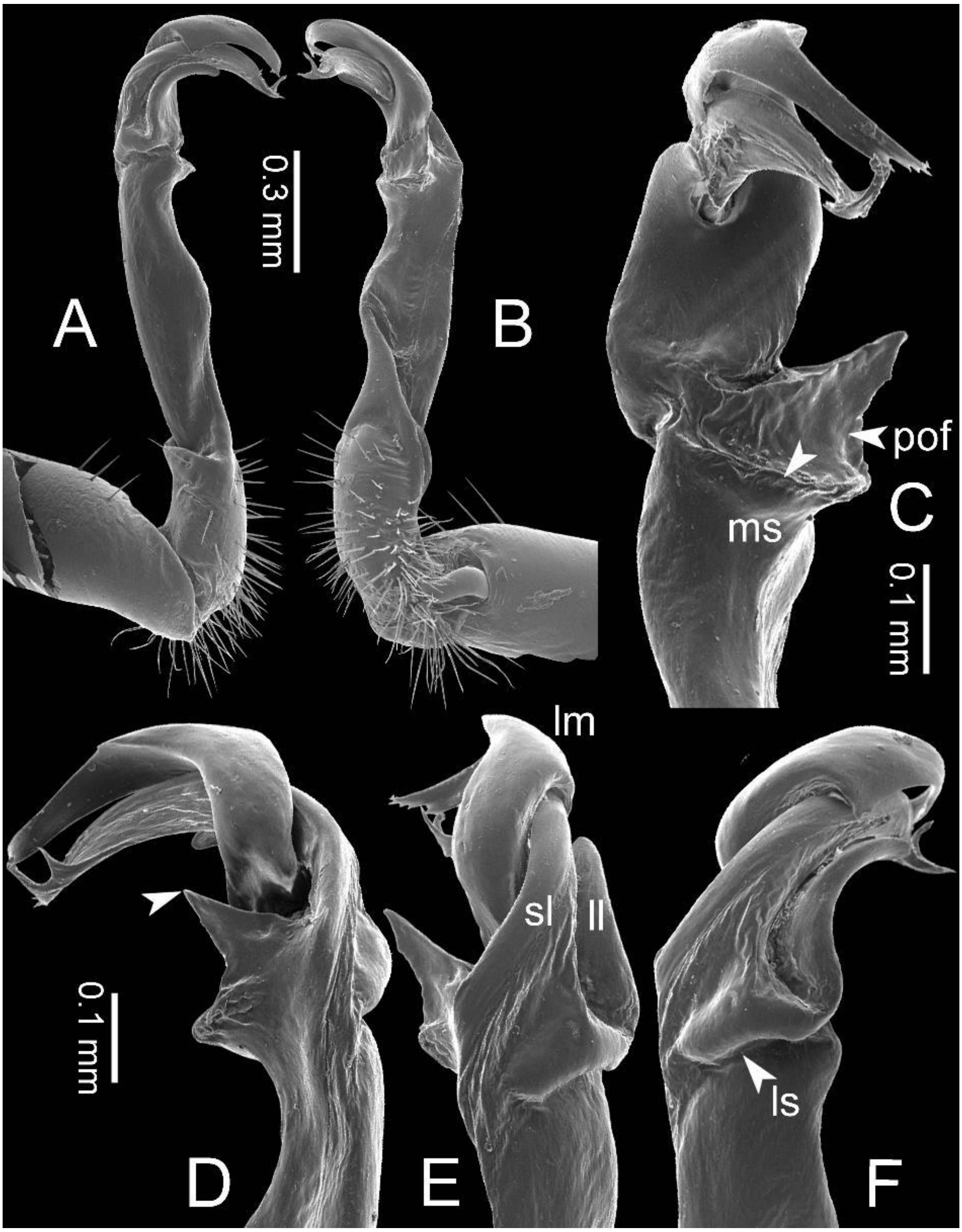

Figure 7.11 *Spinaxytes efefi* sp. n., paratype, CUMZ-pxDGT00208 – right gonopod **A** Lateral view **B** Mesal view **C** Ventral view (arrow points to a ridge on postfemoral part) **D** Mesodorsal view (arrowhead points to a triangular process on postfemoral part) **E** Dorsal view **F** Laterodorsal view.

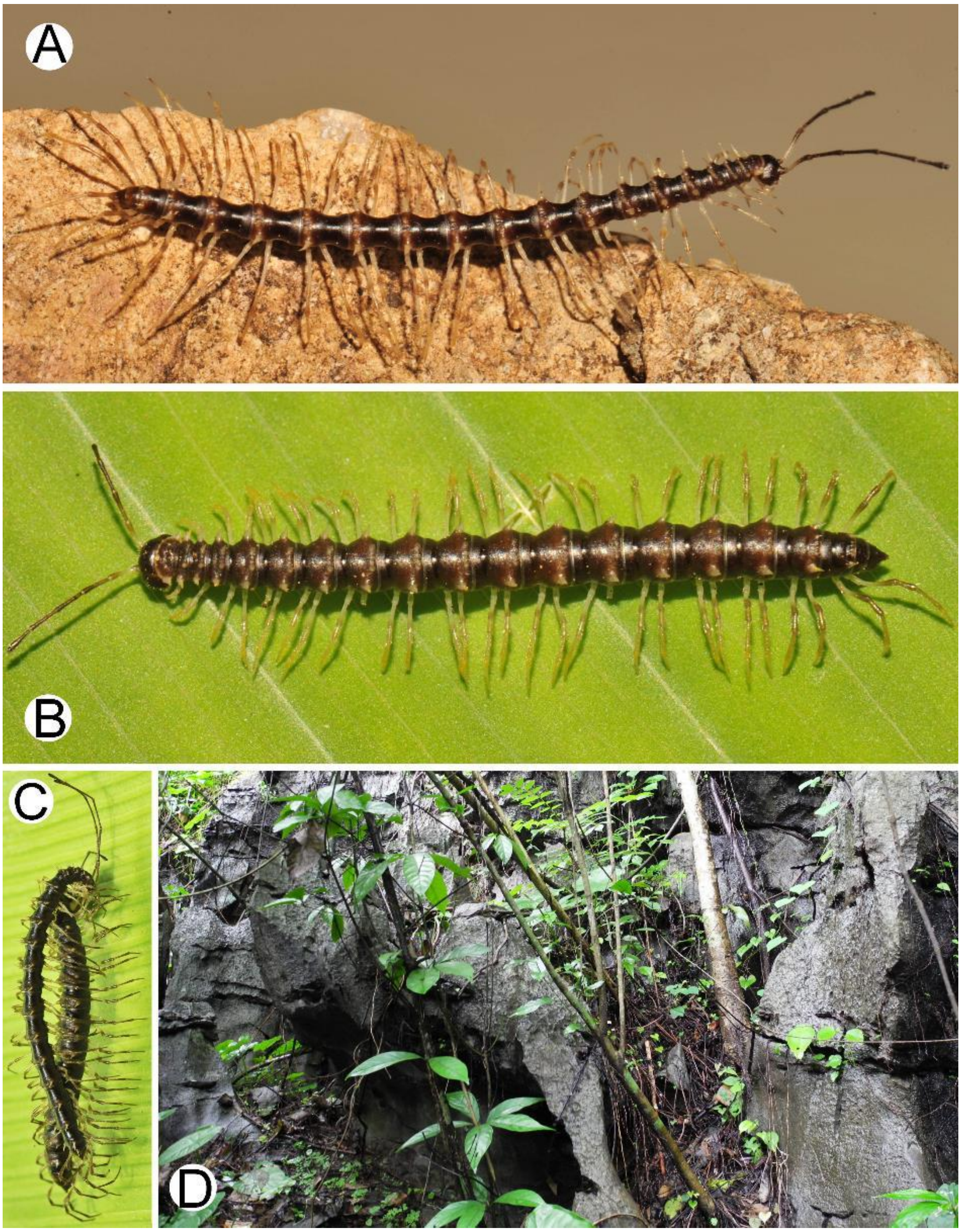

Figure 7.12 Photographs of live *Spinaxytes hasta* sp. n. and habitat **A** ♂ paratype, CUMZ-pxDGT00210 **B** ♀ paratype, CUMZ-pxDGT00210 **C** Mating couple **D** Habitat.

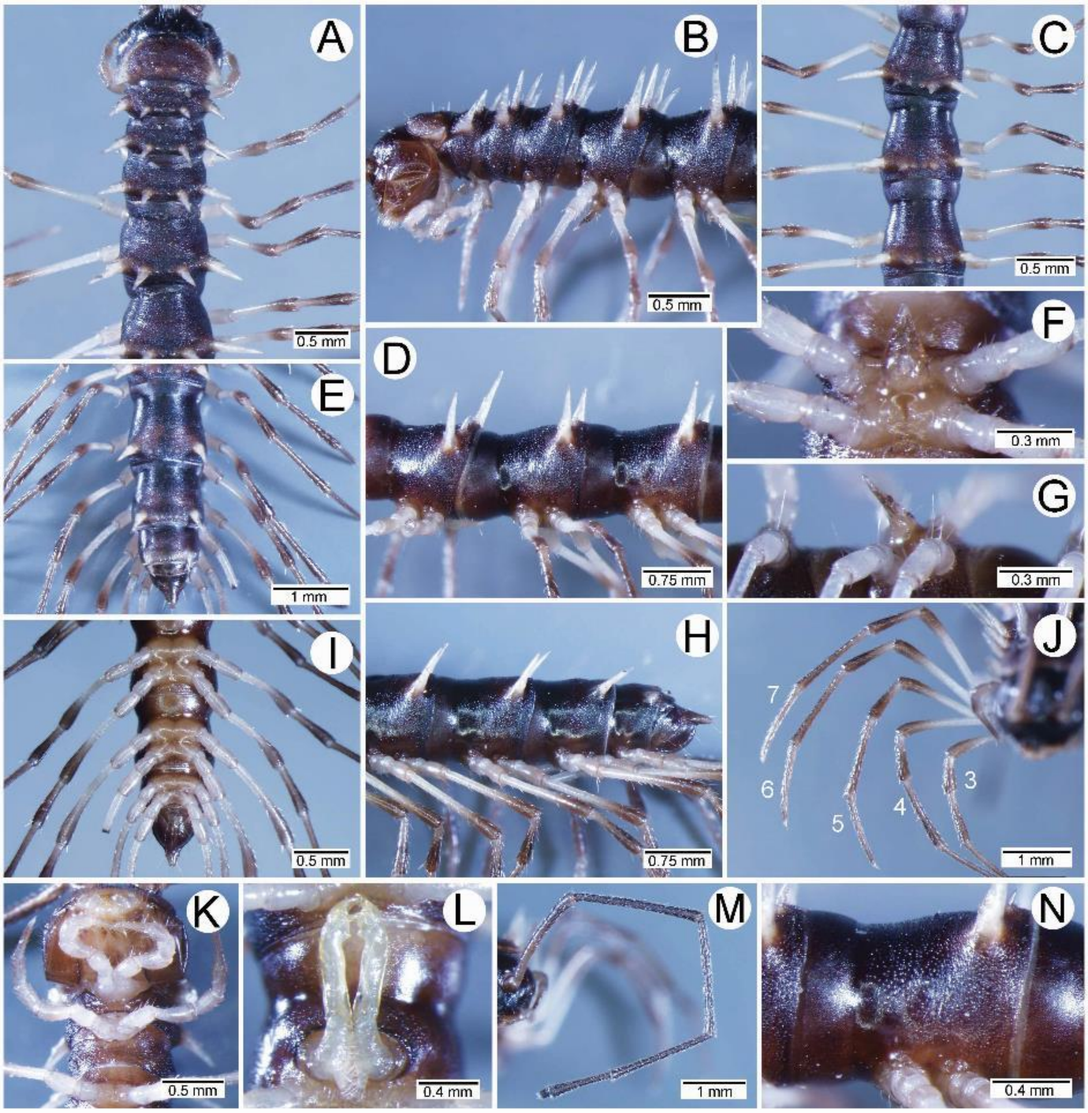

Figure 7.13 *Spinaxytes hasta* sp. n., ♂ paratype, CUMZ-pxDGT00210 **A, B** Anterior body part **C, D** Body rings 8–10 **E, H, I** Posteriormost body rings and telson **F, G** Sternal lobe between coxae 4 **J** Legs 3–7 **K** Legs 1–3 **L** Gonopods **M** Left antenna **N** Sculpture of body ring 10.

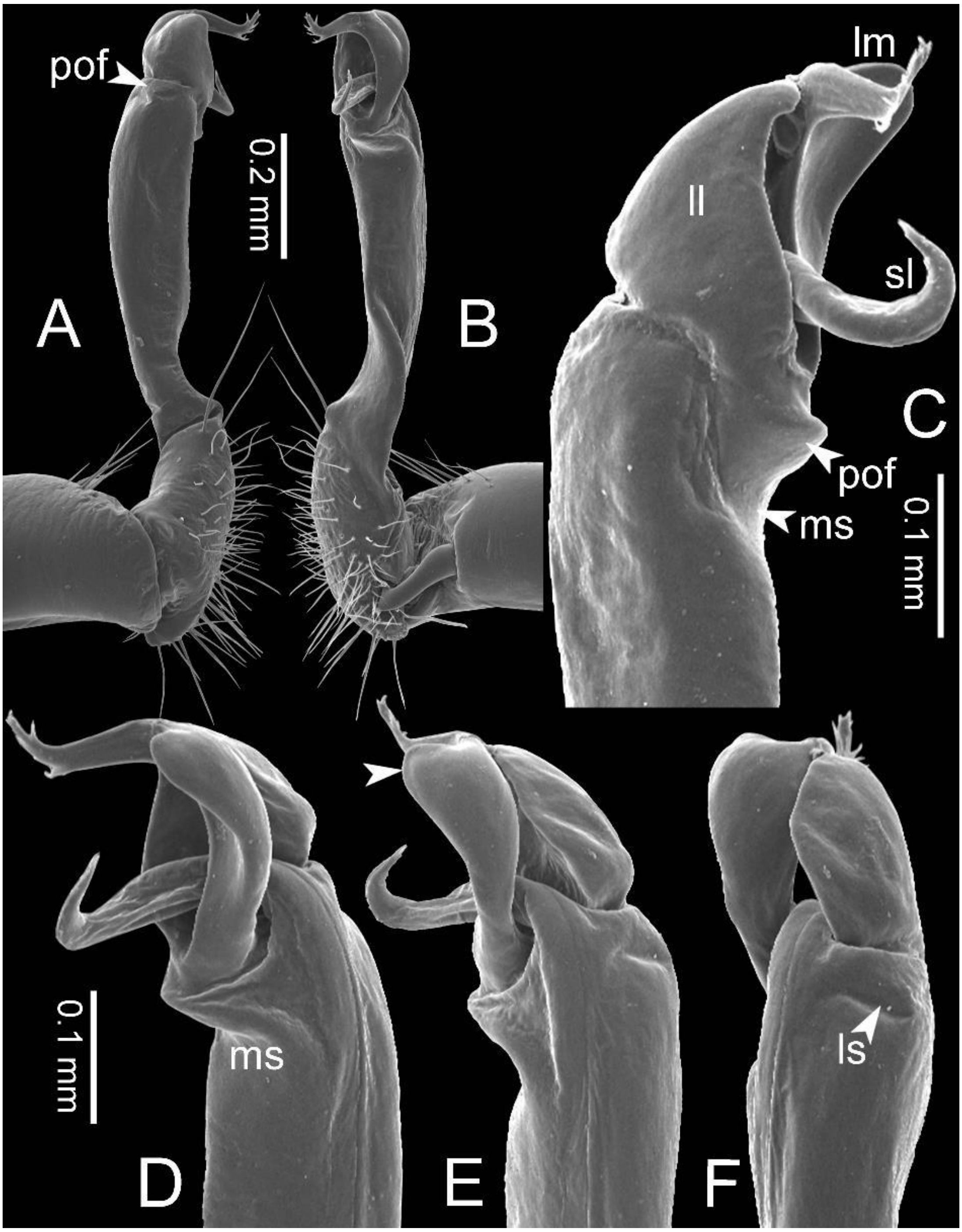

Figure 7.14 *Spinaxytes hasta* sp. n., paratype, CUMZ-pxDGT00210 – right gonopod **A** Lateral view **B** Mesal view **C** Ventral view **D** Mesodorsal view **E** Dorsal view (arrowhead points to lobe on lamina medialis) **F** Laterodorsal view.

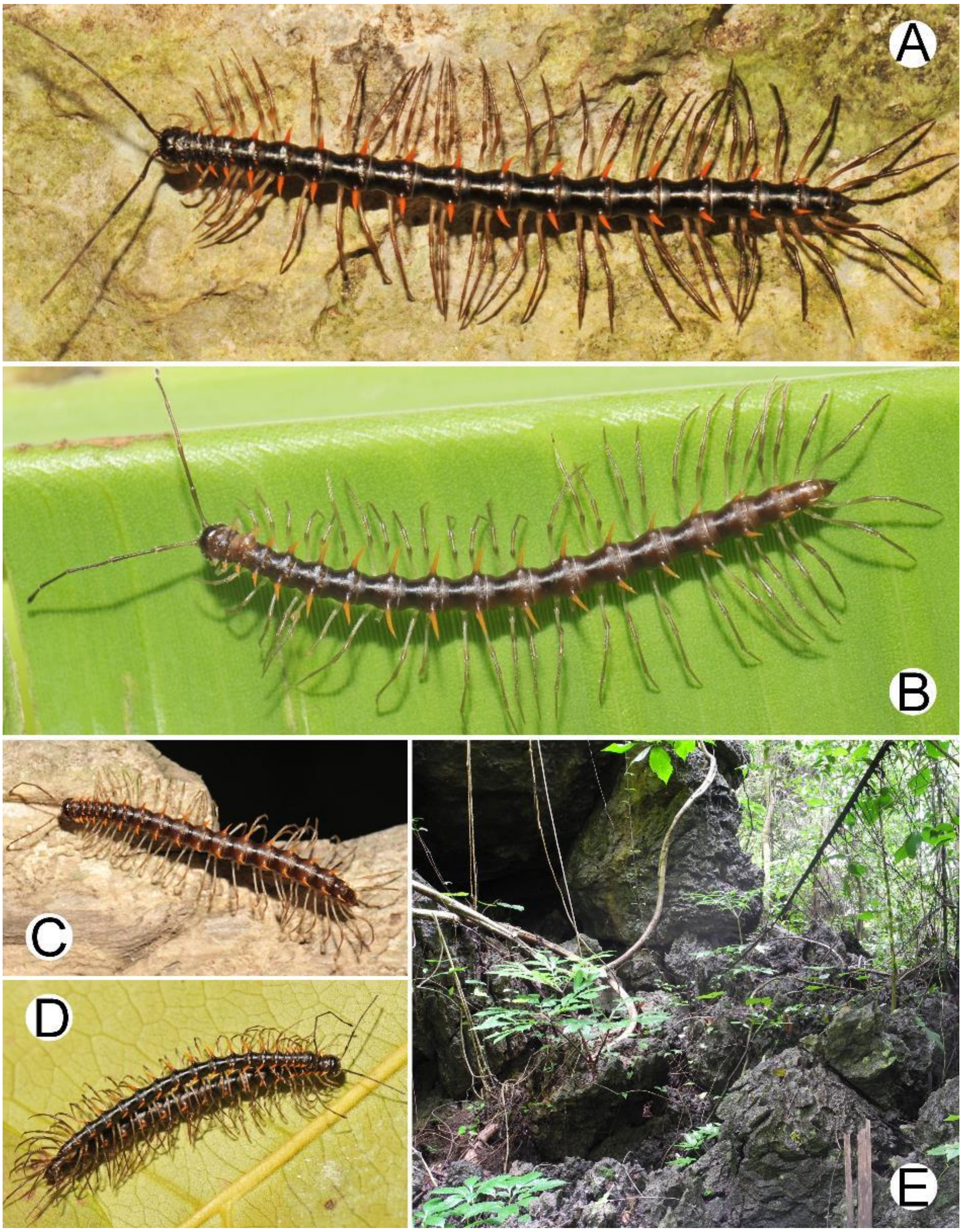

Figure 7.15 Photographs of live *Spinaxytes krabiensis* sp. n. and habitat **A** ♂ paratype, CUMZ-pxDGT00212 **B** ♂, specimen from Tham Sa Yuan Thong (Sa Yuan Thong Cave) **C** ♀ paratype **D** Mating couple **E**. Habitat.

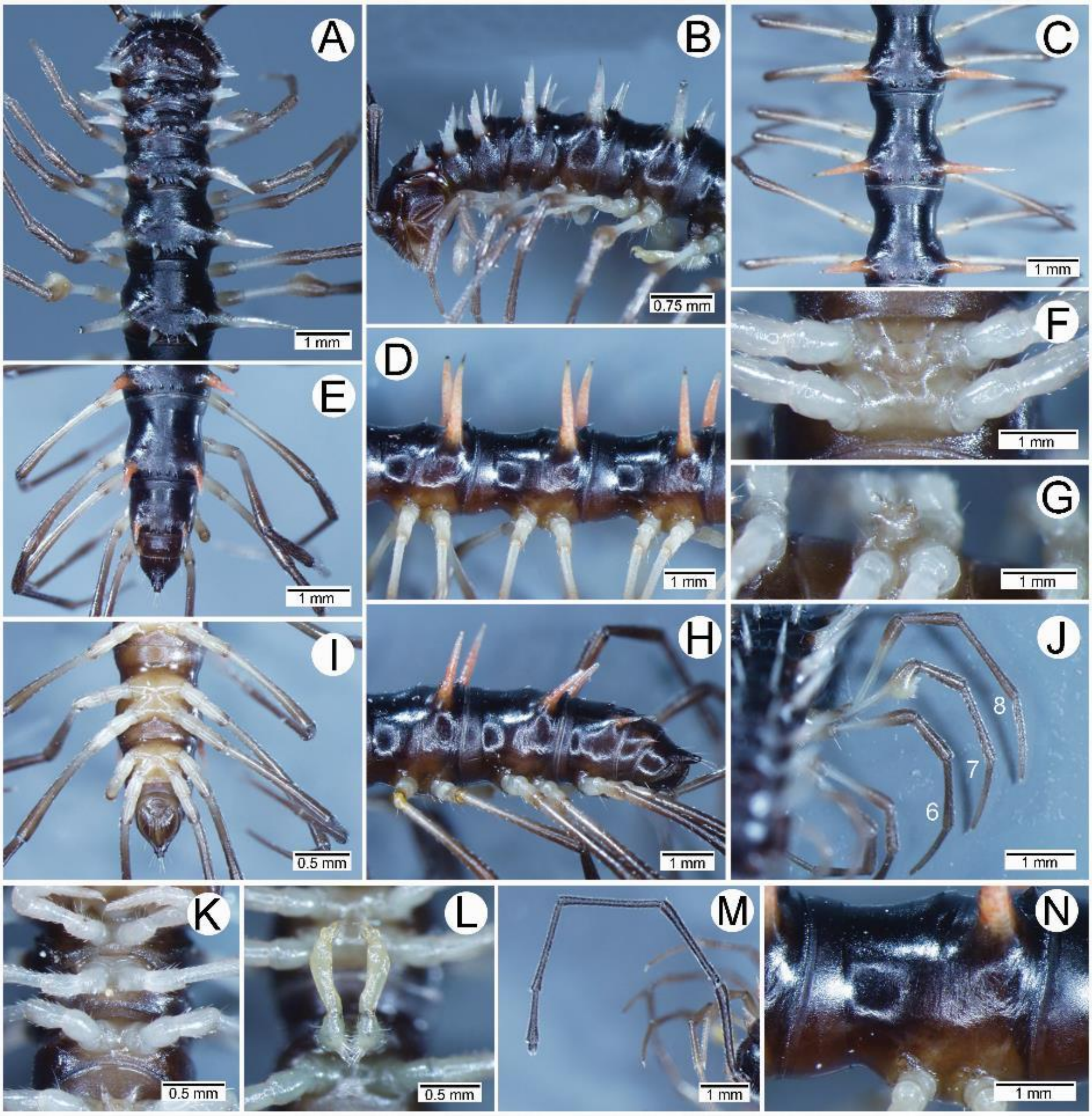

Figure 7.16 *Spinaxytes krabiensis* sp. n., ♂ paratype, CUMZ-pxDGT00212 **A, B** Anterior body part **C, D** Body rings 9–11 **E, H, I** Posteriormost body rings and telson **F, G** Sternal lobe between coxae 4 **J** Legs 4–8 **K** Legs 1–3 **L** Gonopods **M** Right antenna **N** Sculpture of body ring 10.

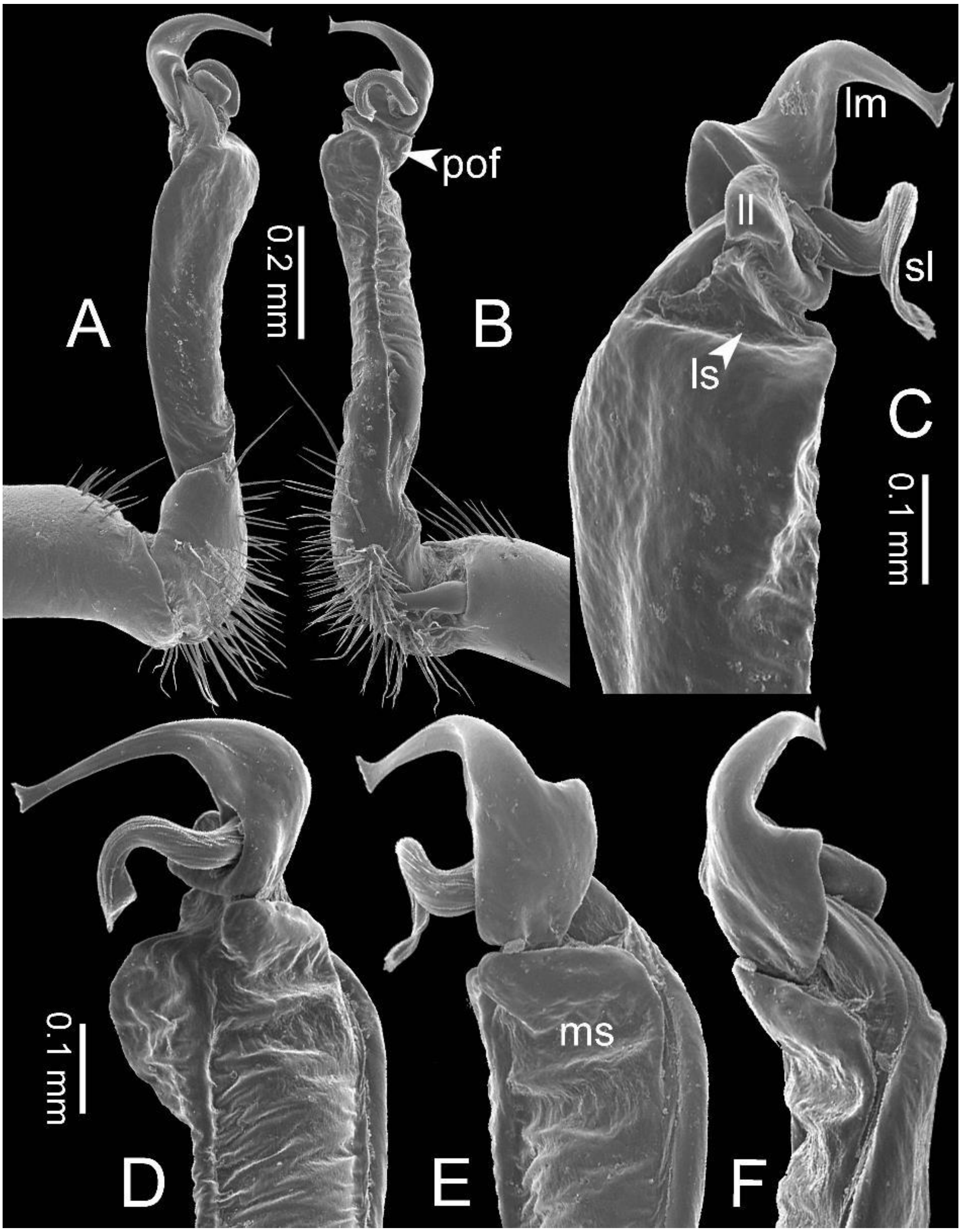

Figure 7.17 *Spinaxytes krabiensis* sp. n., paratype, CUMZ-pxDGT00212 – right gonopod **A** Lateral view **B** Mesal view **C** Ventral view **D** Mesodorsal view **E** Dorsal view **F** Laterodorsal view.

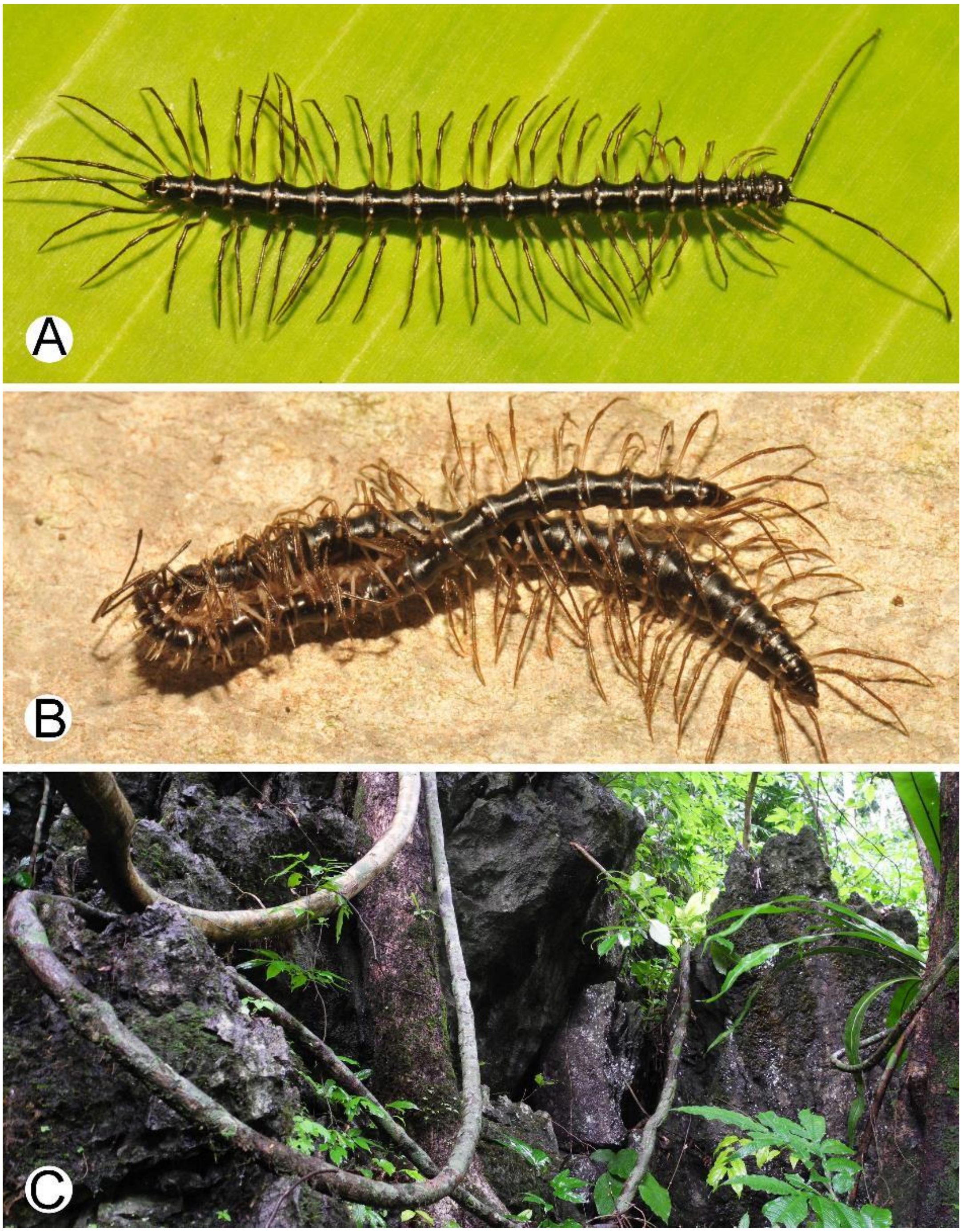

Figure 7.18 Photographs of live *Spinaxytes macaca* sp. n. and habitat **A** ♂ paratype, CUMZ-pxDGT00214 **B** Mating couple **C** Habitat.

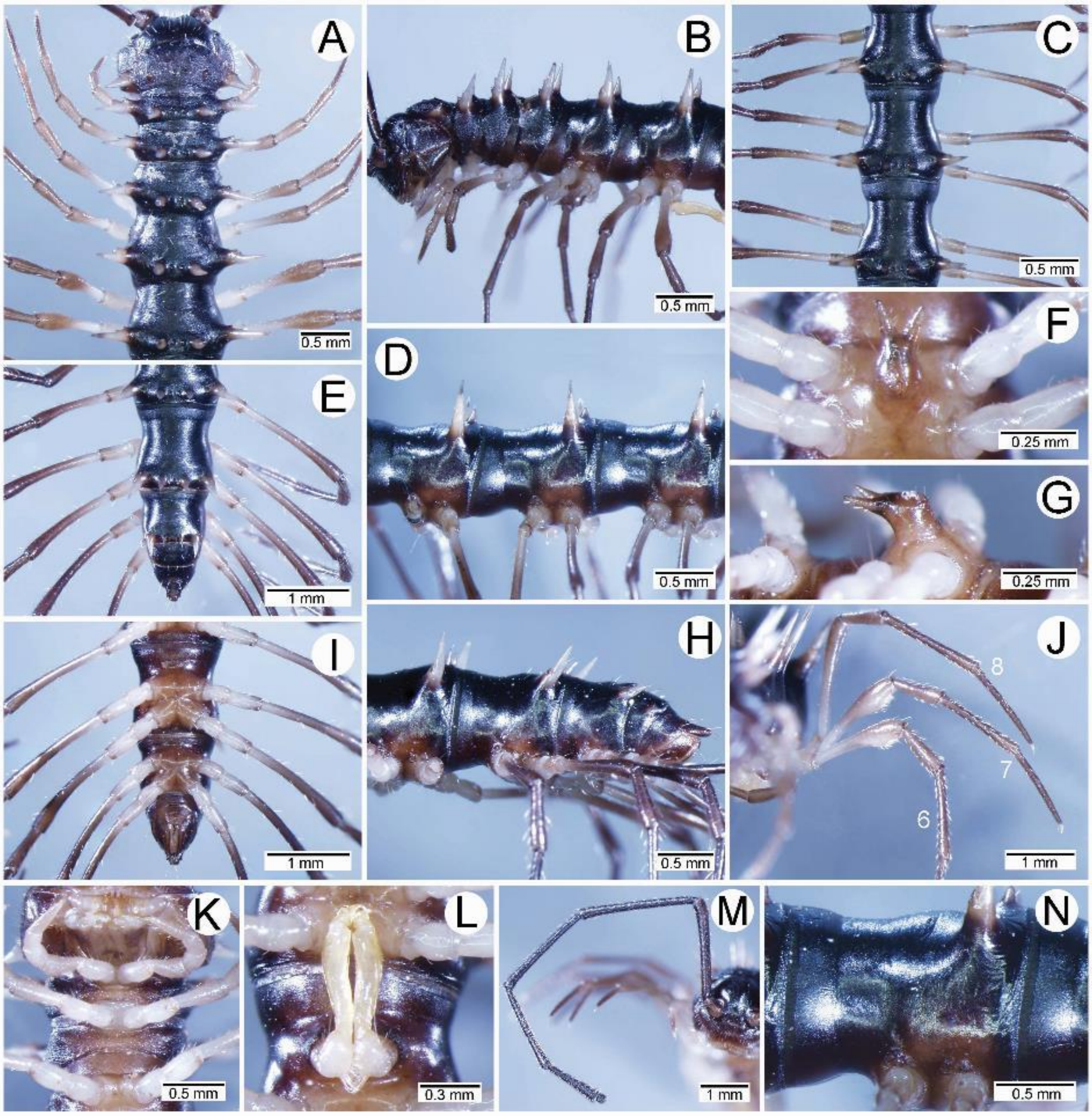

Figure 7.19 *Spinaxytes macaca* sp. n., ♂ paratype, CUMZ-pxDGT00214 **A, B** Anterior body part. **C, D** Body rings 8–10 **E, H, I** Posteriormost body rings and telson **F, G** Sternal lobe between coxae 4. **J** Legs 6–8 **K** Legs 1–3 **L** Gonopods **M** Right antenna **N** Sculpture of body ring 10.

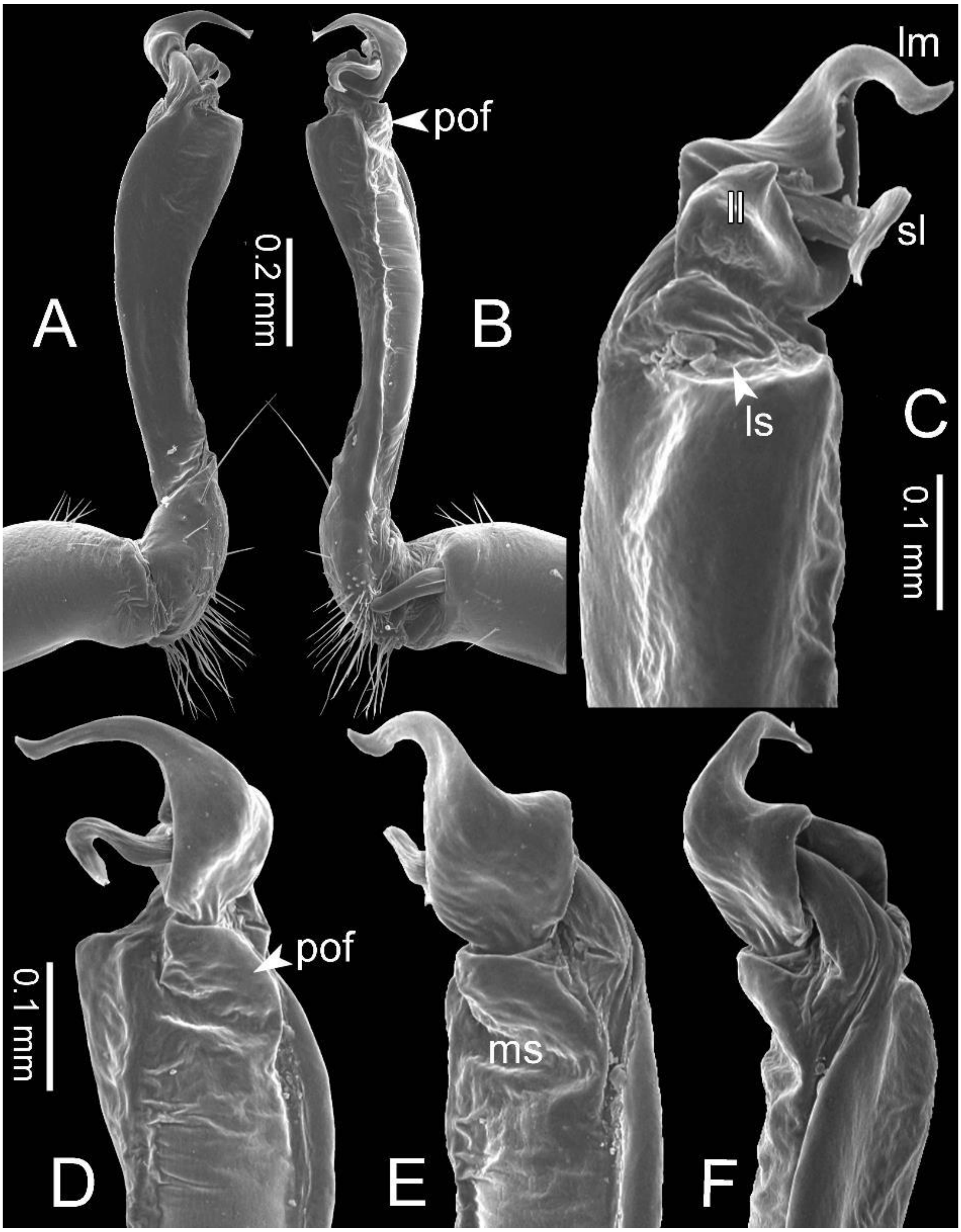

Figure 7.20 *Spinaxytes macaca* sp. n., paratype, CUMZ-pxDGT00214 – right gonopod **A** Lateral view **B** Mesal view **C** Ventral view **D** Mesodorsal view **E** Dorsal view **F** Laterodorsal view.

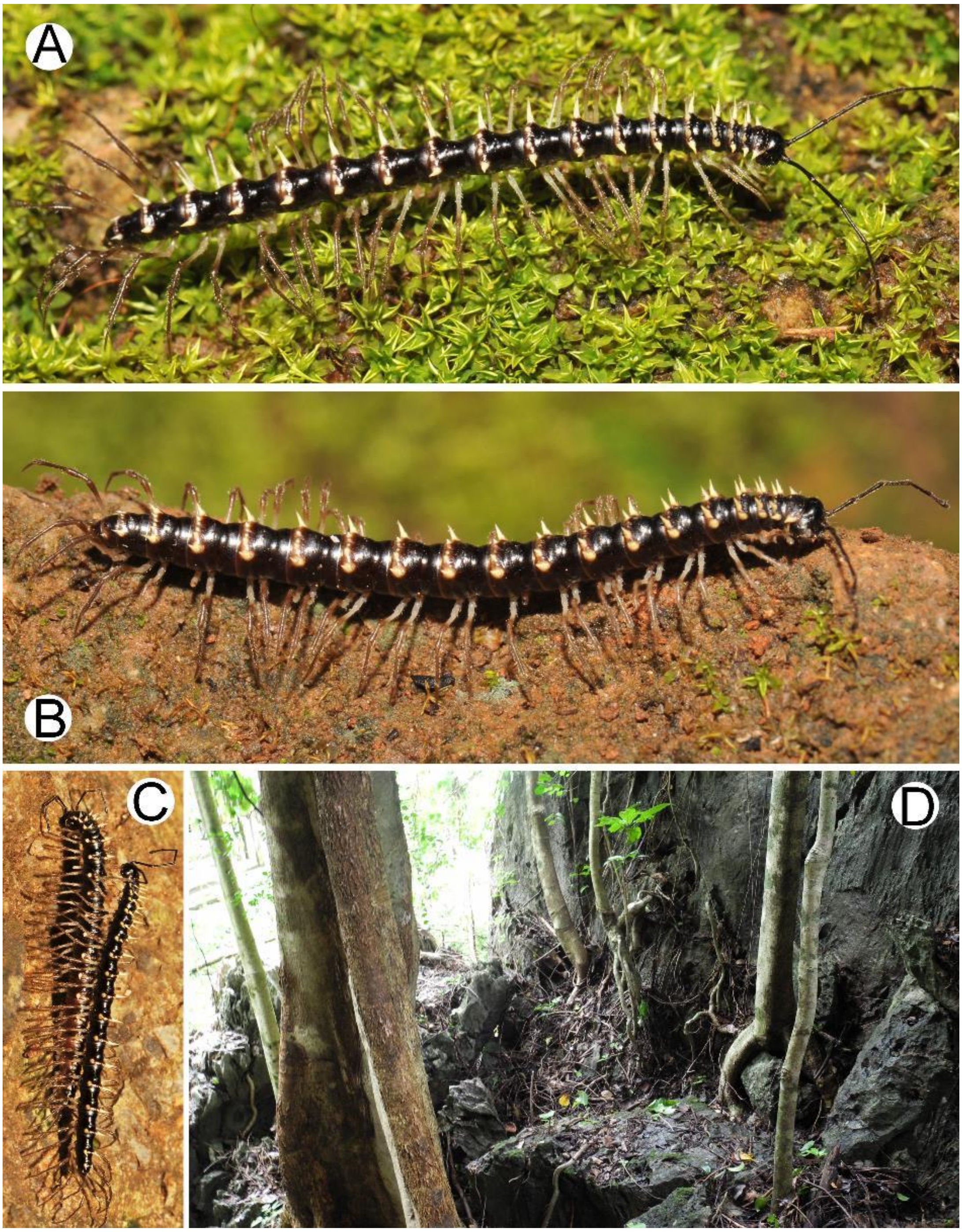

Figure 7.21 Photographs of live *Spinaxytes palmata* sp. n. and habitat **A** ♂ paratype, CUMZ-pxDGT00216 **B** ♀ paratype, CUMZ-pxDGT00216 **C** Mating couple **D** Habitat.

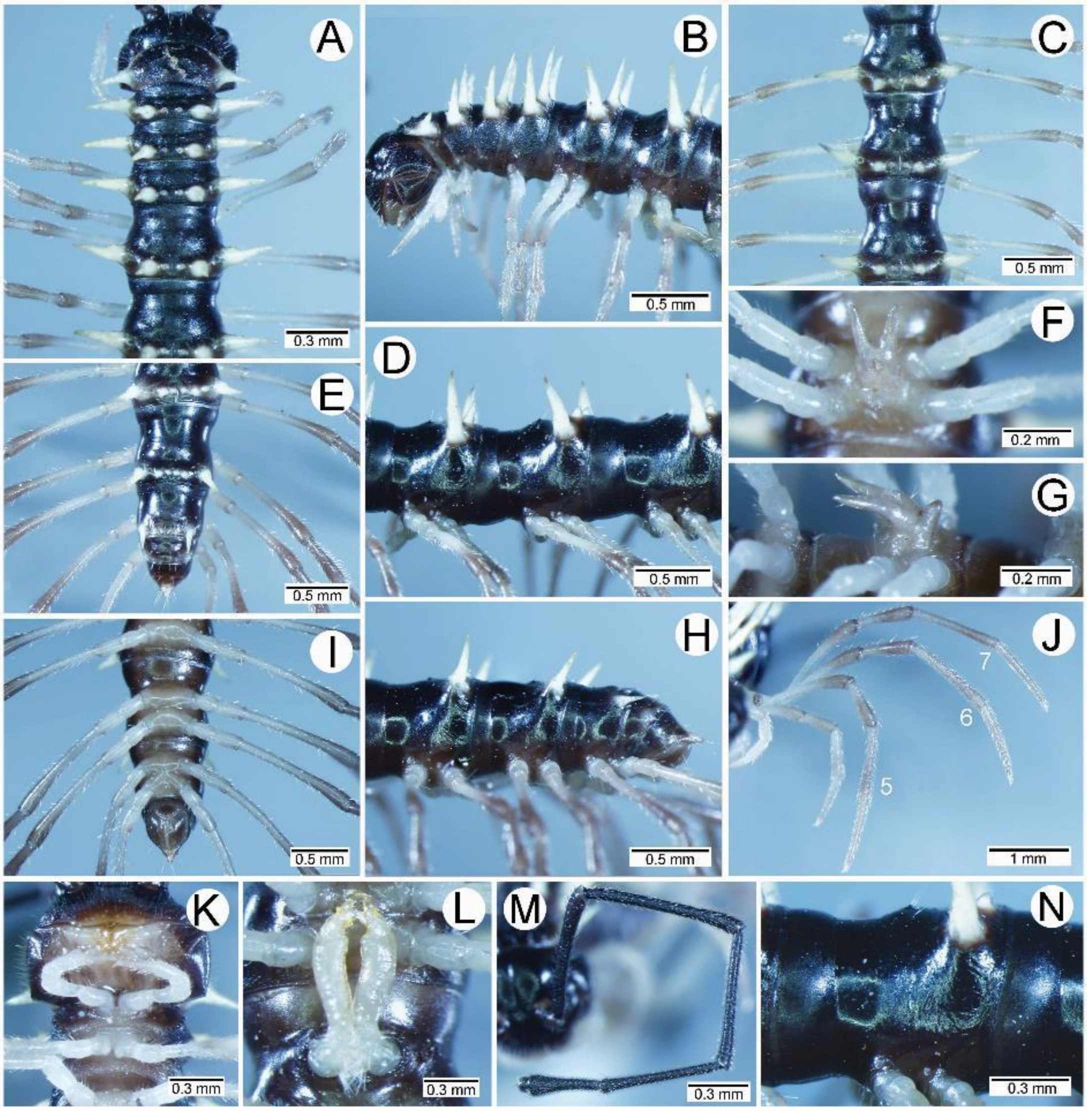

Figure 7.22 *Spinaxytes palmata* sp. n., ♂ paratype, CUMZ-pxDGT00216 **A, B** Anterior body part **C, D** Body rings 8–10 **E, H, I** Posteriormost body rings and telson. **F, G** Sternal lobe between coxae 4 **J** Legs 5–7 **K** Legs 1–3 **L** Gonopods **M** Left antenna **N** Sculpture of body ring 10.

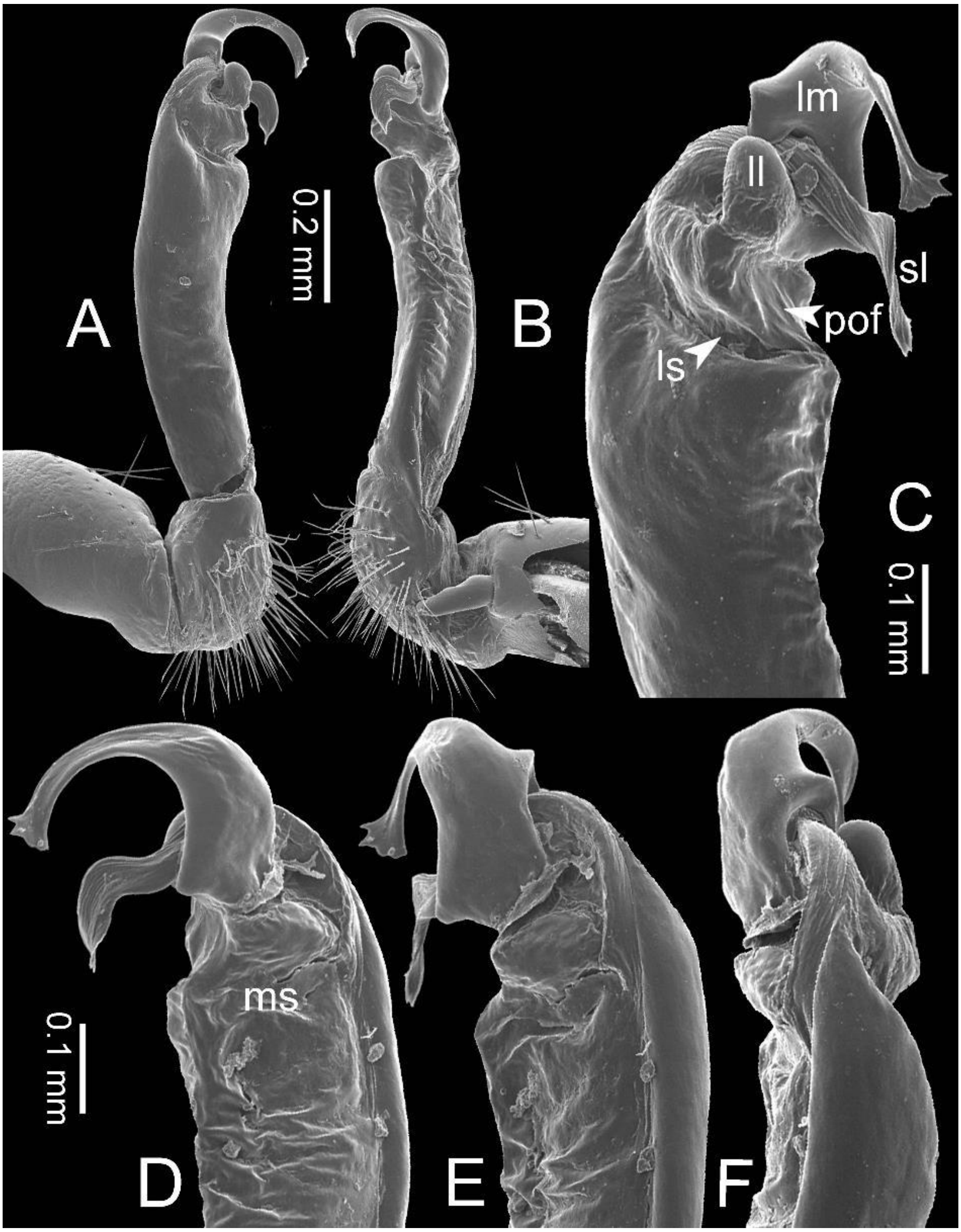

Figure 7.23 *Spinaxytes palmata* sp. n., paratype, CUMZ-pxDGT00216 – right gonopod **A** Lateral view **B** Mesal view **C** Ventral view **D** Mesodorsal view **E** Dorsal view **F** Laterodorsal view.

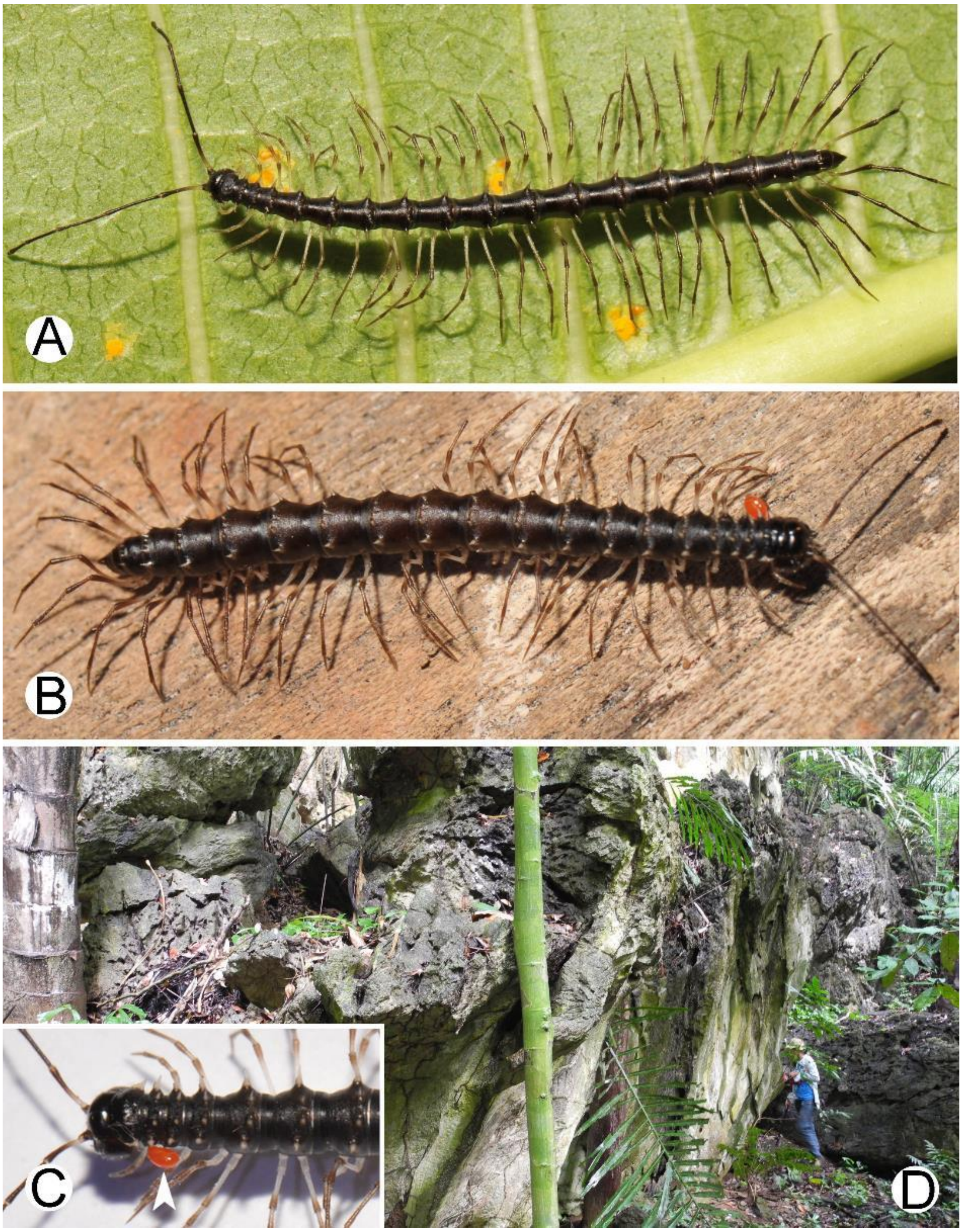

Figure 7.24 Photographs of live *Spinaxytes sutchariti* sp. n. and habitat **A** ♂ paratype, CUMZ-pxDGT00218 **B** ♀ paratype, CUMZ-pxDGT00218 **C** Parasitic mite (arrowhead) **D** Habitat.

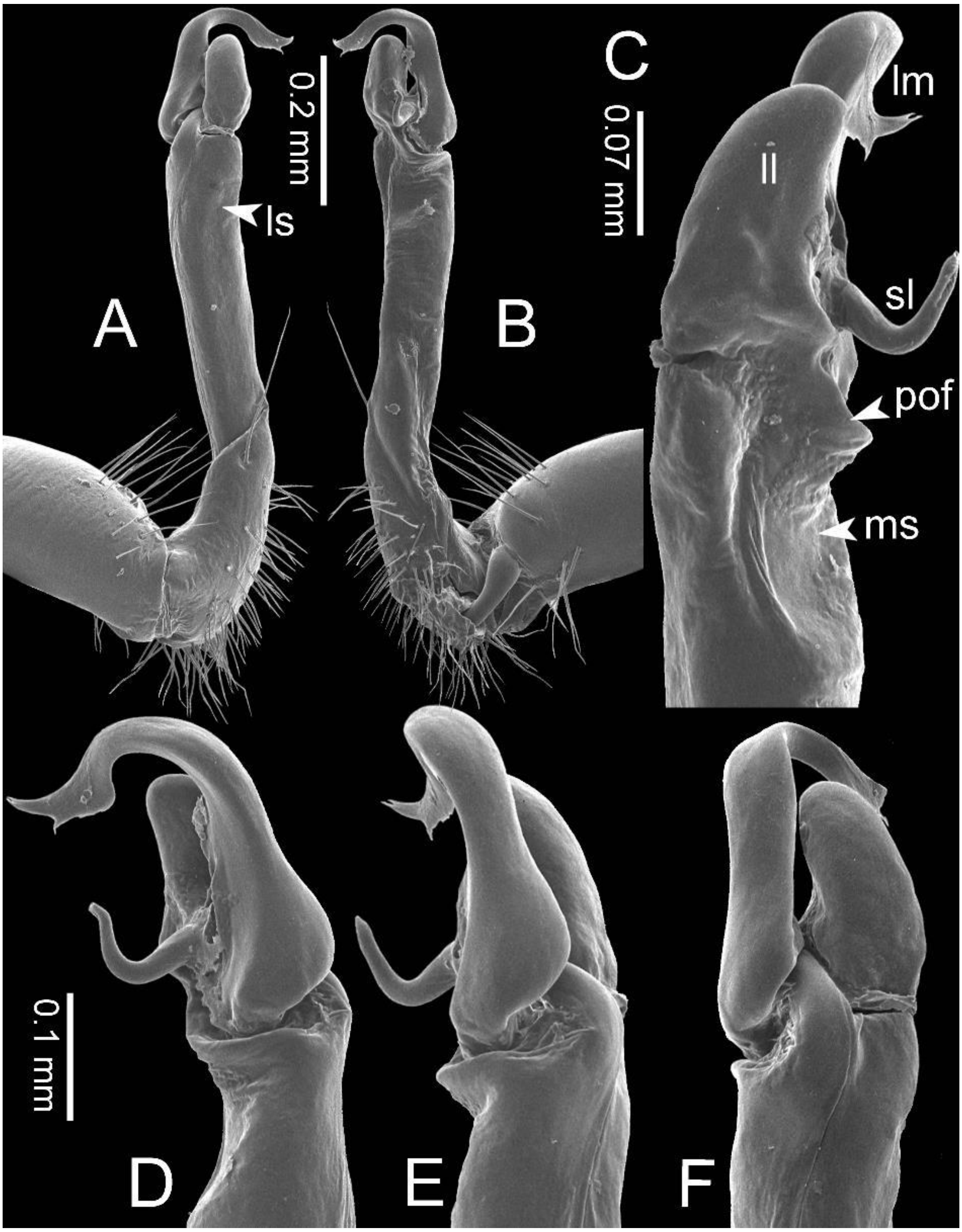

Figure 7.25 *Spinaxytes sutchariti* sp. n., paratype, CUMZ-pxDGT00218 – right gonopod **A** Lateral view **B** Mesal view **C** Ventral view **D** Mesodorsal view **E** Dorsal view **F** Laterodorsal view.

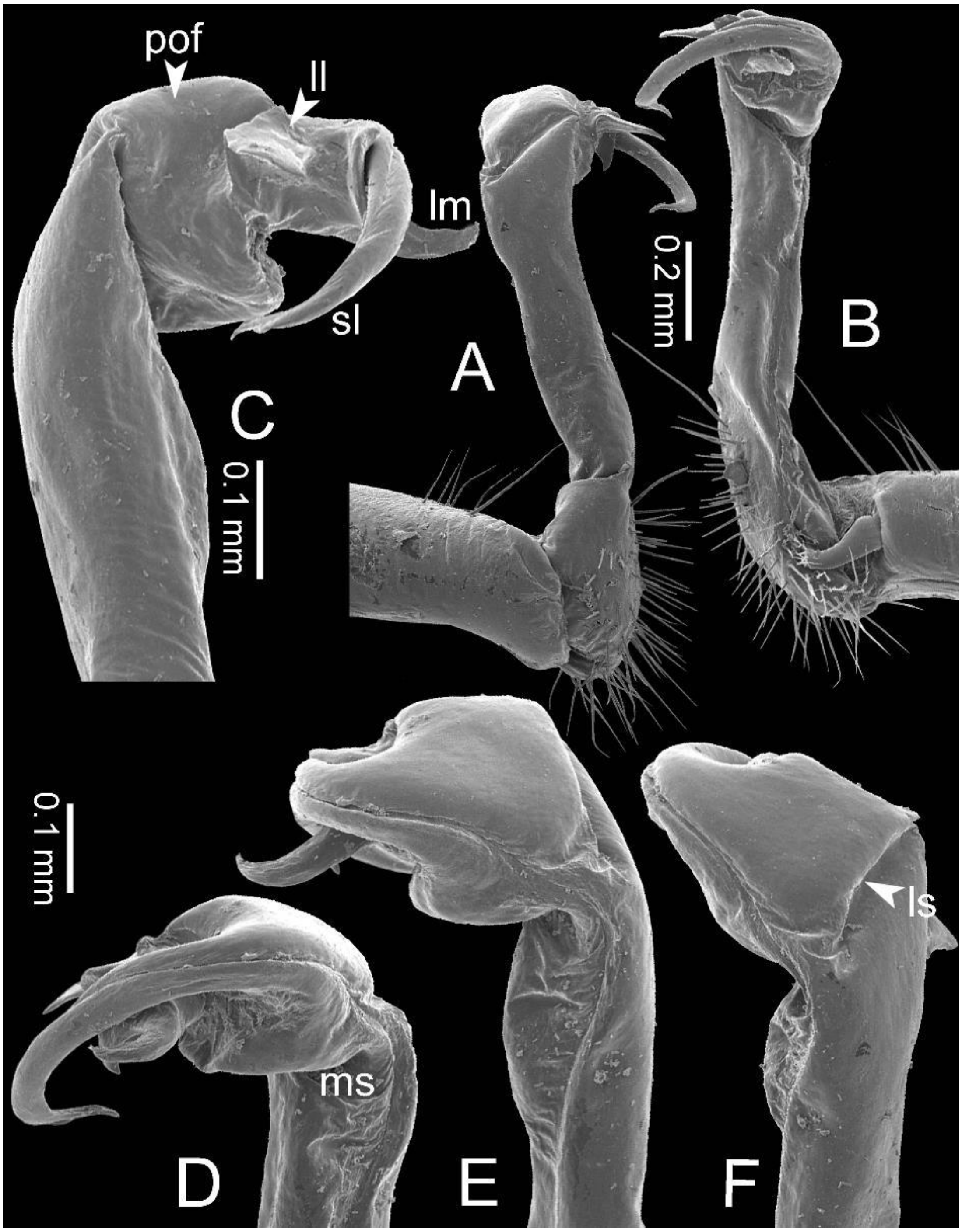

Figure 7.26 *Spinaxytes tortioverpa* sp. n., paratype, CUMZ-pxDGT00220 – right gonopod **A** Lateral view **B** Mesal view **C** Ventral view **D** Mesodorsal view **E** Dorsal view **F** Laterodorsal view.

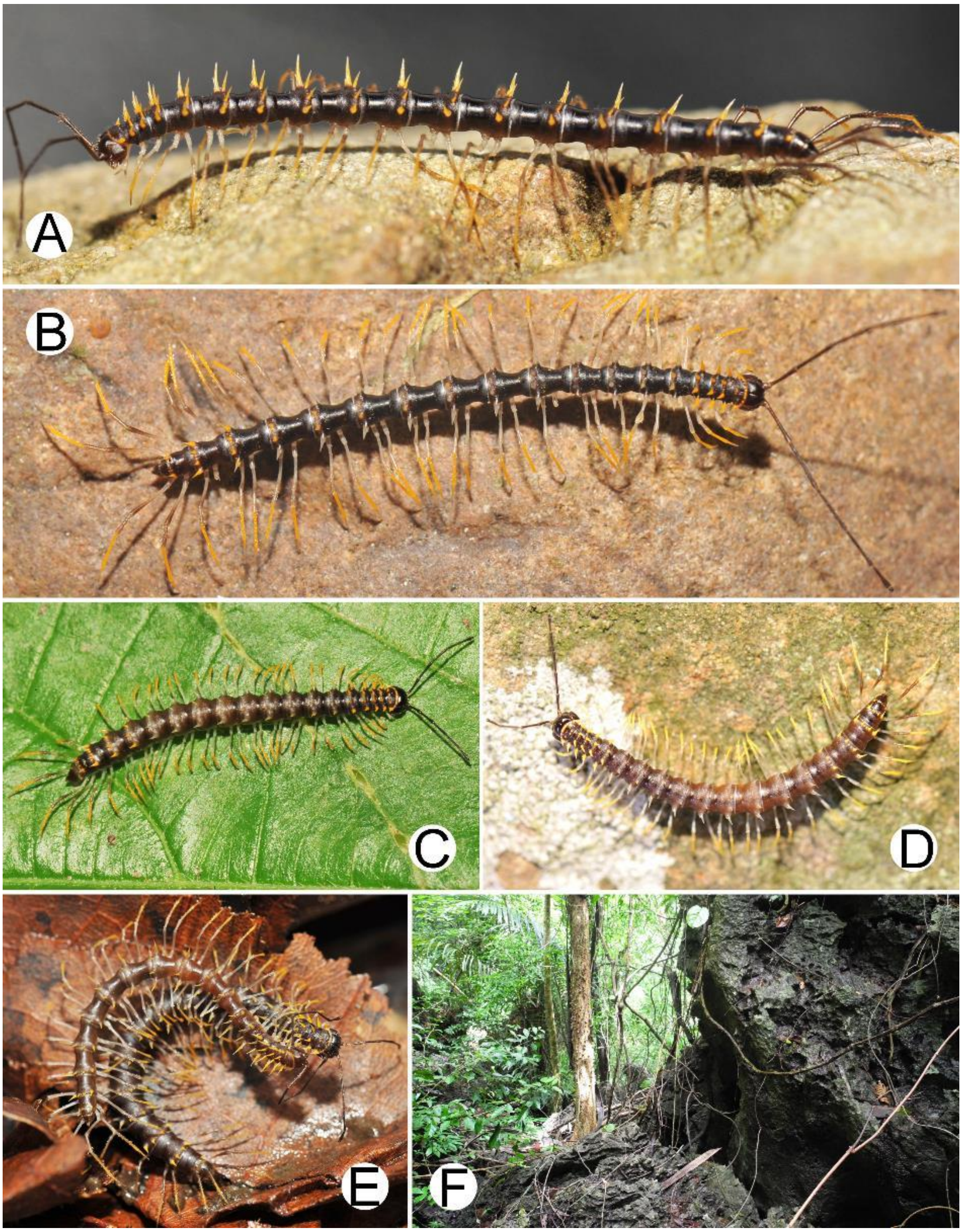

Figure 7.27 Photographs of live *Spinaxytes uncus* sp. n. and habitat **A** ♂ paratype, CUMZ-pxDGT00222 **B** ♂, specimen from Wat Kerewong (Tham Koab) **C** ♀ paratype, CUMZ-pxDGT00222 **D** ♀, specimen from Wat Kerewong (Tham Koab) **E** Mating couple **F** Habitat.

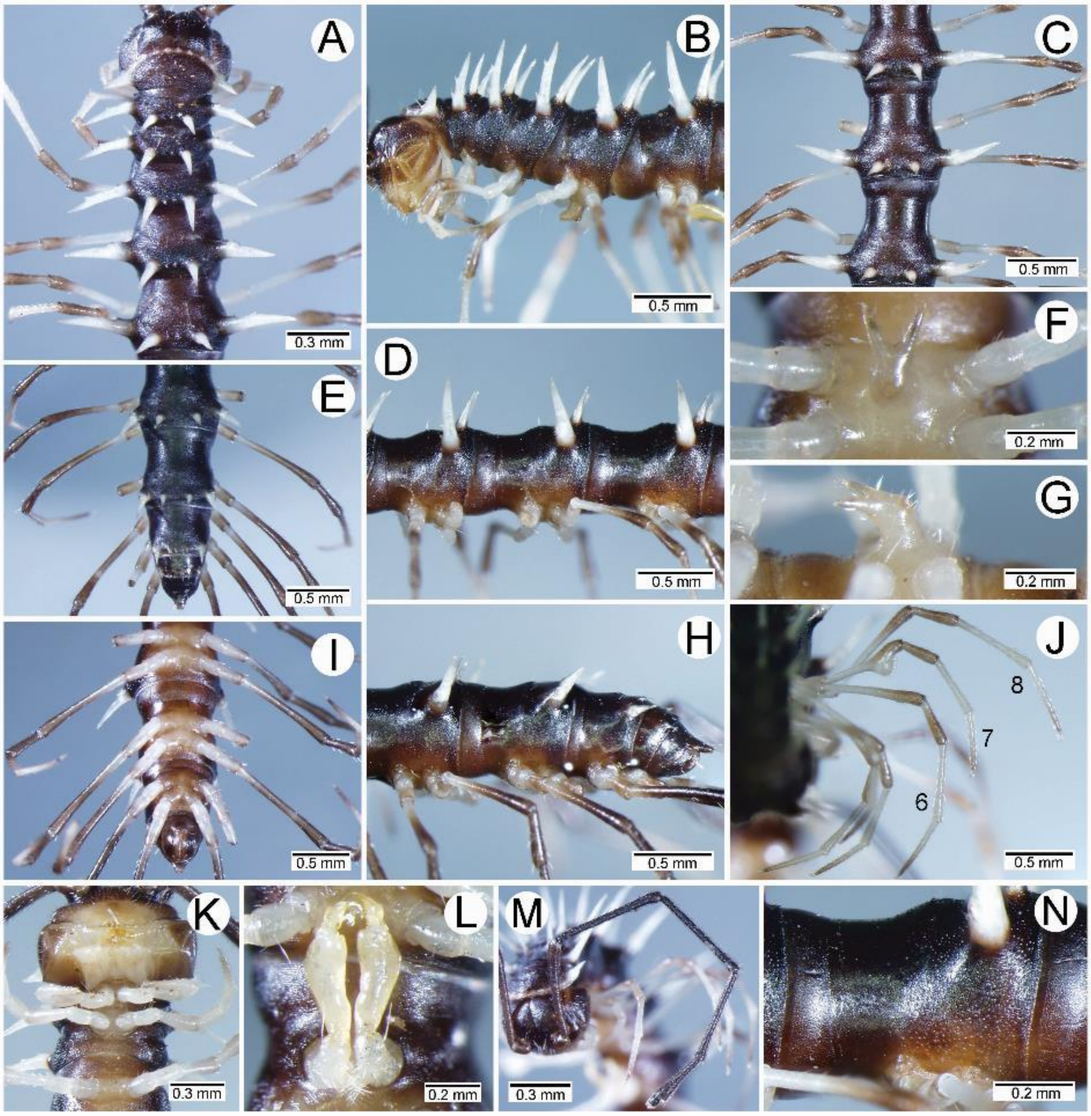

Figure 7.28 *Spinaxytes uncus* sp. n., ♂ paratype, CUMZ-pxDGT00222 **A, B** Anterior body part **C, D** Body rings 8–10 **E, H, I** Posteriormost body rings and telson **F, G** Sternal lobe between coxae 4 **J** Legs 6–8 **K** Legs 1–3 **L** Gonopods **M** Left antenna **N** Sculpture of body ring 10.

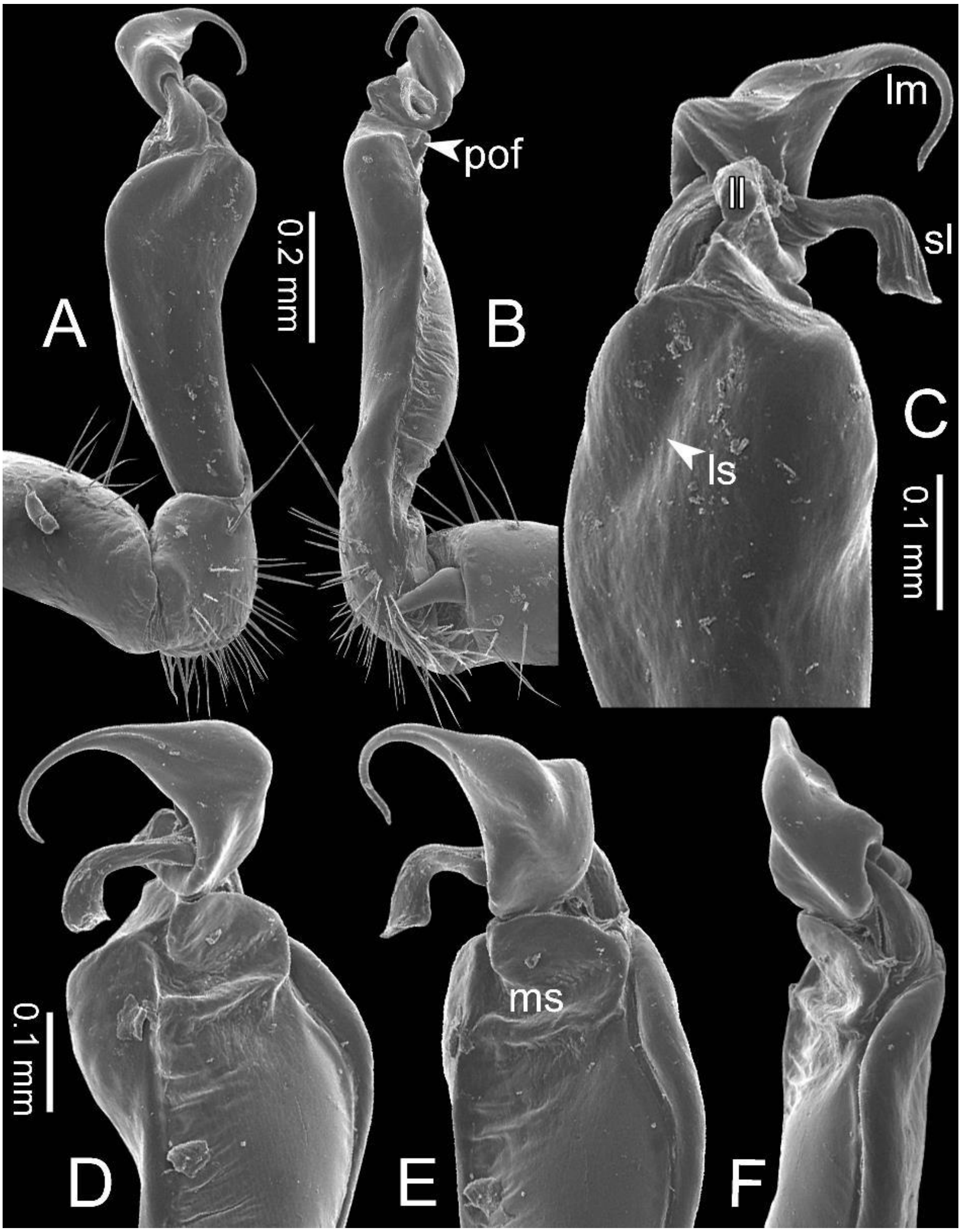

Figure 7.29 *Spinaxytes uncus* sp. n., paratype, CUMZ-pxDGT00222 – right gonopod **A** Lateral view **B** Mesal view **C** Ventral view **D** Mesodorsal view **E** Dorsal view **F** Laterodorsal view.

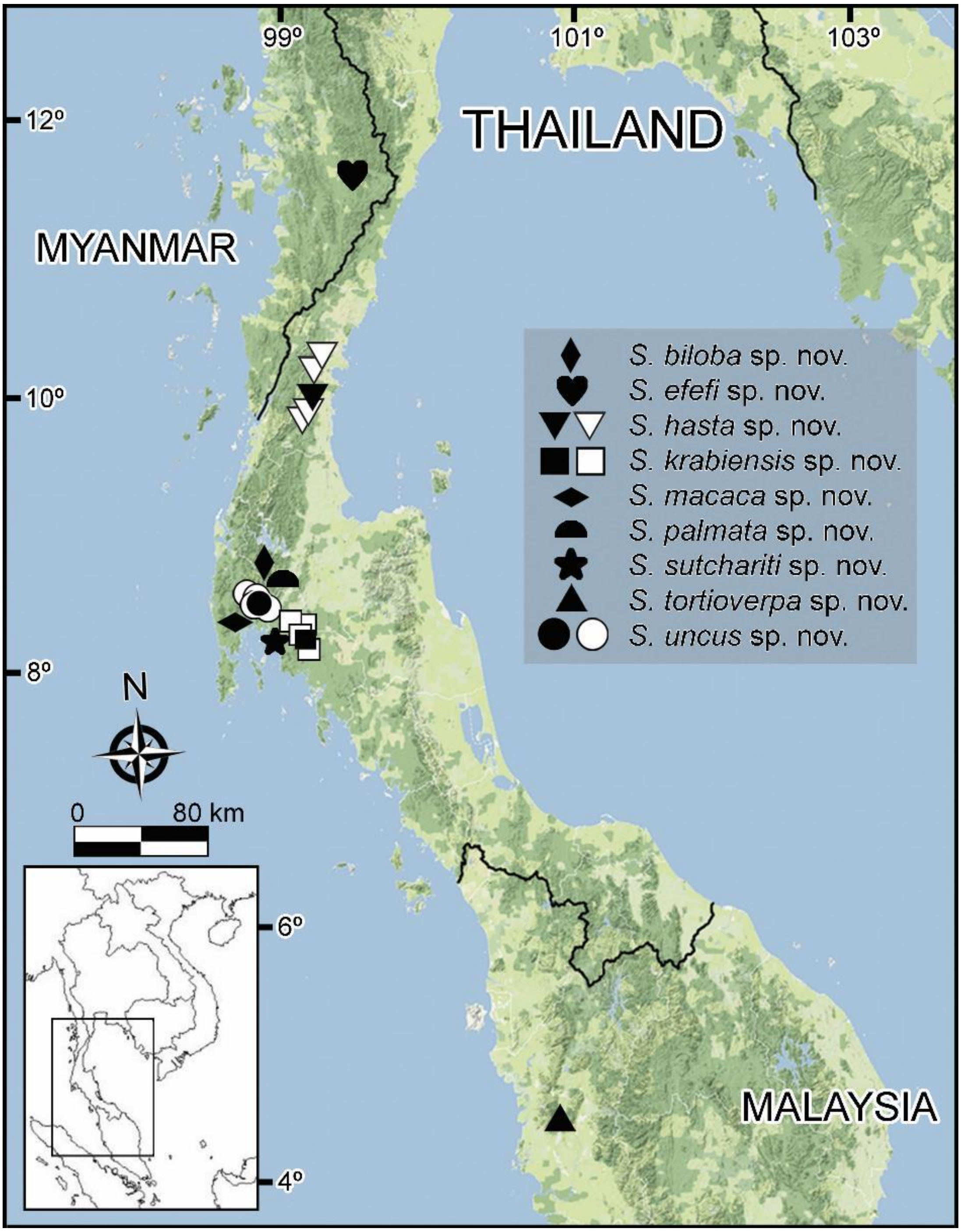

Figure 7.30 Known distribution of all *Spinaxytes* gen. n. species (black symbols = type locality, white symbols = other locality).

CHAPTER VIII

Molecular phylogenetic analysis inferred from mitochondrial and nuclear markers supports splitting of the dragon millipede genus *Desmoxytes* sensu Golovatch and Enghoff, 1994 (Diplopoda, Polydesmida, Paradoxosomatidae)

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(MS in preparation)

Abstract

The spectacular Southeast Asian dragon millipedes, genus *Desmoxytes s.l.* (*sensu* Golovatch and Enghoff, 1994), are analyzed based on an integration of morphological and molecular data. Traditionally, dragon millipedes have been considered to belong to a single genus, *Desmoxytes* Chamberlin, 1923. Although the genus is seemingly well defined by several characters, dragon millipedes show a great deal of diversity in morphology including paraterga, color patterns and gonopod characters. After an extensive taxonomic revision, including study of type specimens, the study found that a generic division is warranted, based mainly on gonopod and paraterga characters, and *Desmoxytes* is accordingly split into five genera. In the present paper, a well resolved molecular phylogeny of the dragon millipedes based on genes from mitochondria and nucleus are presented, in support of the previous studies. Phylogenetic relationships were estimated from three partial gene fragments (COI, 16S rRNA mtDNA and nuclear 28S rRNA) using Bayesian Inference and Maximum likelihood incorporating morphological characters. The phylogenetic analyses all found the dragon millipede, genus *Desmoxytes s.l.*, to be paraphyletic in terms of a group of *Orthomorpha* species. However, each of the morphologically defined genera that it was split is recovered as monophyletic with very strong bootstrap, which supports previous splitting approach. The molecular analyses thus strongly support the usefulness of morphological characters and also are in accordance with geographical distribution. The results can be hypothesized two possible ways in evolution of paraterga in the dragon millipede that (1) the high degree of elevation of paraterga may have evolved in parallel in the five different lineages of dragon millipedes which is also supported by the presence of this character in some species belonging to another paradoxosomatid tribe, or (2) the ancestor of *Desmoxytes* + *Orthomorpha* had highly elevated paraterga and that *Orthomorpha* has reverted to a low degree of elevation. This is the first comprehensive study on the dragon millipedes and as such it expands the scope of morphological and molecular explorations, and reveals a much richer species diversity than previously known, finally leading to understanding of the relationships in this spectacular group of millipedes.

Introduction

The Paradoxosomatidae is the most species-rich family of the millipede order Polydesmida, containing about 220 genera and more than 1,050 species distributed worldwide except in the Arctic, Antarctica and North America. The family has received considerable attention from myriapodologists due to peculiar features such as the variously developed paranota, and huge diversity in gonopod characters (Nguyen and Sierwald, 2013). However, the molecular phylogenetic studies on paradoxosomatids are still scarce. Within the Paradoxosomatidae, the dragon millipedes, genus *Desmoxytes s.l.* (*sensu* Golovatch and Enghoff (1994)) are among the most peculiar genera because of the remarkably developed, often highly elevated paraterga in combination with a colourful body. A total of 68 species of dragon millipedes have been recognized, inhabiting SE Asia from South China down to the Malay Peninsula. Dragon millipedes show a relatively high diversity in morphology, especially in paranota which may be spiniform, subspiniform, antlerlike or winglike (Srisonchai *et al.*, 2016, 2018a, 2018b, 2018c, 2018d).

Traditional classification of the dragon millipedes has been based on morphological characters, especially paraterga and gonopods (Attems, 1937, 1953; Chamberlin, 1923; Cook and Loomis, 1924a; Enghoff *et al.*, 2007; Golovatch and Enghoff, 1994; Golovatch *et al.*, 2010; Golovatch *et al.*, 2012; Golovatch *et al.*, 2016; Jeekel, 1964; Likhitrakarn *et al.*, 2015; Liu *et al.*, 2014, 2016; Loksa, 1960; Nguyen *et al.*, 2005; Pocock, 1895; Zhang, 1986; Zhang and Li, 1982). However, these characters have sometimes been misleading, e.g., in the case of *“D.” philippina* Nguyen and Sierwald, 2010. Based on its paraterga alone, this species should be placed in genus *Desmoxytes*, but gonopod characters support placing it in another genus (*Euphyodesmus*) in another tribe (Golovatch *et al.*, 2012). In an even trickier case, *D. planata* and *D. euros* exhibit the same shape of gonopods which may lead to identifying them as the same species, although in molecular characters they are clearly different. All in all, some morphological characters need to be used with caution. The lack of phylogenetic work may also lead to instability of genus or species limits. An early effort to evaluate relationships between dragon millipedes using a phylogenetic approach was made by Golovatch and Enghoff (1994), but with little success. Thus, molecular phylogenetic analysis is needed as a powerful tool to reveal relationships between both genera and species.

Recent molecular phylogenetic studies have potentially improved the status of knowledge about species limits and relationships in some groups of millipedes (Means and Marek, 2017; Pimvichai *et al.*, 2014; Pimvichai *et al.*, 2016). For the family Paradoxosomatidae, phylogenetic studies have recently been conducted in some genera: Decker (2016a, 2016b) revised genera *Pogonosternum* Jeekel, 1965 and *Oncocladosoma* Jeekel, 1985 (tribe Australosomatini); Nguyen *et al.* (2017) and Nguyen (2017) analyzed and revised the genera *Oxidus* Cook, 1911 and *Vietnamorpha* Golovatch, 1984 (tribe Sulciferini). A year later, phylogenetic relationships in genera *Antheromorpha* Jeekel, 1968 and *Nesorthomorpha* Jeekel, 1980 (tribe Orthomophini) were made to evaluate the position on the phylogenetic tree of new species (Nguyen *et al.*, 2018a; Nguyen *et al.*, 2018b). So far, no intensive studies on molecular phylogeny of *Desmoxytes s.l.*, have been published. However, a preliminary molecular analysis using a single gene from mitochondria of six species of dragon millipedes from Vietnam has been reported (Nguyen, 2016).

Recently, the intensive field surveys in several areas in Mainland Southeast Asia have made and have found numerous species of dragon millipedes. Intensive morphological work has lead us to separate the dragon millipedes into five genera, i.e. *Desmoxytes* Chamberlin, 1923, *Nagaxytes* Srisonchai, Enghoff and Panha, 2018, *Gigaxytes* Srisonchai, Enghoff and Panha, 2018, *Spinaxytes* Srisonchai, Enghoff and Panha, submitted, and *Hylomus* Cook and Loomis, 1924 (Srisonchai *et al.*, 2018a, 2018b, 2018c, 2018d).

The main aim is to clarify the status of the genus *Desmoxytes s.l.* using an integrative method, as well as to examine relationships between dragon millipede species. A phylogenetic approach for the dragon millipedes based on three molecular markers from representative species is presented.

Material and methods

1. Taxon sampling and identification

In the present study, 84 samples (207 sequences of 26 species as ingroup, 40 sequences of 12 species as outgroup) were analyzed, see Table 1 for details. The specimens were hand-collected during the rainy season, mainly in Thailand, but also in some parts of Laos, Myanmar and Malaysia. Latitude, longitude and elevation were recorded, and photographs of live specimens were also taken. The samples were preserved in 70% ethanol for morphological study and in 95% ethanol for molecular analysis. Specimens in 95% were later stored at -20°C. Most specimens are deposited at CUMZ. Some specimens belonging to ZMUC and ZMUM were partly dissected for the molecular analysis (CUMZ = Chulalongkorn University Museum of Zoology, Bangkok, Thailand; ZMUC = Natural History Museum of Denmark (Zoological Museum), University of Copenhagen, Denmark; ZMUM = Zoological Museum, University of Moscow, Russia).

Morphological characters were examined under a stereo microscope. Species identification and nomenclature were based on Chamberlin (1923); Enghoff *et al.* (2007); Golovatch and Enghoff (1994); Golovatch *et al.* (2012); Jeekel (1964, 1980a, 2003); Srisonchai *et al.* (2016, 2018a, 2018b, 2018c, 2018d).

Abbreviations for gonopodal structures used in the text and figures are as follows: ll = lamina lateralis; lm = lamina medialis; plm = process of lamina medialis; dlm = distal lobe of lamina medialis; blm = broad lobe of lamina medialis.

2. Molecular markers

Three partial gene fragments including Cytochrome *C* Oxidase Subunit 1 (COI) and 16S ribosomal DNA (16S rRNA) from the mitochondria, and one from nucleus which is 28S ribosomal DNA (28S rRNA) were analyzed. The numbers of base pairs of each gene fragment are as follows: COI = 658 bp; 16S rRNA = 640 bp; 28S rRNA = 383 bp.

Initially, both Maximum Likelihood (ML) and Bayesian Inference (BI) trees were reconstructed based on a single gene. However, tree topology differed significantly between single-gene trees. Therefore, we prefer to present only a combined gene tree. For the combined data of COI + 16S rRNA + 28S rRNA, we analyzed 84 specimens of 10 genera, 38 named species.

3. DNA extraction and amplification

DNA was harvested from tissue of legs and body rings 13-15. The total genomic DNA was isolated using the standard protocol by DNA extraction Kits (NucleoSpin @Tissue Kits). The target DNA gene was amplified using the Polymerase Chain Reaction (PCR) (Saiki *et al.*, 1988). Polymerase chain reaction were carried out using the following primers

– COI: 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),

– 16S rRNA: 16Sar (5'-CGC CTG TTT AAC AAA AAC AT-3') and 16Sbr (5'-CCG GTC TGA ACT CAG ATC ACG T-3') (Simon *et al.*, 1994),

– 28S rRNA: 28Sar (5'-AGC GCC AGT TCT GCT TAC CAA AA-30') and 28Sbr (5'-TGG GTG AAC AAT CCA ACG CTT GG-3') (Colgan *et al.*, 2000).

The PCR amplification was conducted in a total 50.0 µL composed of 2.0 µL of DNA template, 2.0 µL of the primers (Forward + Reverse), 30.0 µL of *Taq* PCR Master Mix, and 16.0 µL of ddH_2O. All PCR procedures were processed with the Eppendorf Master Cycler Pro S machine using standard and gradient functions. The thermal cycling for amplification of COI was performed as: 94 °C for 5 mins as an initial step, followed by 36 cycles at 94 °C for 2 mins in a denaturation step, 43 °C for 2 mins as an annealing step, then 72 °C for 2 mins as an extension step. The final step took place at 4 °C. All products were stored at 4 °C in refrigerator before sending for sequencing. For 16S rRNA and 28S rRNA, the same conditions were used, except in annealing step which was 48 °C for 2 mins and 50 °C for 1 min, respectively. The amplified genes were checked in 1% agarose gel electrophoresis with 0.5x TBE buffer, substantially stained with SYBR Safe and observed under UV trans-illumination. The target DNA was purified using PEG precipitation and a QIAquick purification kits. We sent all PCR products to be sequenced commercially at Macrogen and Bioneers Co. (Korea) using the same primers as mentioned above. To confirm and verify the samples, all sequences were carefully double-checked via GenBank under the BLAST function.

3. DNA alignment and model selection

DNA sequencing chromatograms were carefully checked for gaps and missing sites by using MEGA 6.0 (Tamura *et al.*, 2013). Both mitochondrial and nuclear sequences were aligned in MAFFT version 7.0 (Katoh and Standley, 2013). For COI, all codon positions were inspected for saturation, however, no saturation was found which means that we used all positions in the analysis. In case of the appearance of divergence regions in sequences of 16S rRNA and 28S rRNA genes, some gaps were excluded using GBlocks Server (Talavera and Castresana, 2007) with settings under the following parameters: allow smaller final blocks, allow gap positions within the final block and allow restrict flanking positions. All sequences were carefully checked again after deleting some divergent regions. The length of each gene fragments is shown in table 2. DNA alignment was prepared properly in many types of files i.e. FASTA, NEXUS and/or PHYLIP.

The best-fit substitution model of nucleotide evolution for each gene was implemented using JModelTest2 on XSDXE 2.1.6 through Cipres Gateway (Darriba *et al.*, 2012) based on Akaike Information Criterion (AIC) under PhyML likelihood heuristic search algorithm. The program Kakusan 4.0 (Tanabe, 2011) were used for concatenating data of the three gene fragments. This program automatically selects the best fit model. If the selected best-fit model was not incorporated with JModelTest2, and did not appear in MrBayes and IQ tree programs, the closest one with a higher complexity would be used.

5. Phylogenetic reconstruction

Two approaches were used to reconstruct the phylogenies: Maximum Likelihood (ML) and Bayesian Inference (BI). Analyses were initially conducted on a single gene of mitochondrial DNA data (COI, 16S rRNA) separately, and then on concatenated data from all three genes. However, all trees based on single gene were not resolved, we therefore show a tree based on combined datasets only in the results. Maximum Likelihood analysis was conducted using IQ tree 1.6.6 (Hoang *et al.*, 2018; Nguyen *et al.*, 2015). The support values for branches on the best ML tree were assessed with 1000 bootstrap replicates. For the Bayesian approach, we used MrBayes version 3.2.2 on XSEDE via Cipres Science Gateway Portal (Huelsenbeck and Ronquist, 2001;

Ronquist *et al.*, 2012). BI analyses were performed with Markov Chains Monte Carlo algorithms (MCMC) with a random starting tree, run for 50 million generations, sampling every 1,000 generations and disregarding 25% of the samples as burn in, and then the initial 2000 trees were discarded.

The final ML and BI trees were visualized using FigTree version 1.4.0 (Rambaut, 2012) and the ML and BI trees (also bootstrap support and posterior probability) were combined to a single figure using Adobe Illustrator CS6. Node support of ML was based on bootstrap values (BV) – more than 70% was considered to be a strong support. Node robustness of BI was based on Bayesian posterior probabilities (PP) – more than 95% was regarded as strong support for a given clade (Huelsenbeck and Hillis, 1993; Larget and Simon, 1999). In the combined dataset tree, we use "-" to depict nodes that were not present on the ML tree.

4. Genetic distance

For comparing the intraspecific and interspecific genetic distance, all sequences were compared and estimated for uncorrected P-distance using MEGA 6.0 (Tamura *et al.*, 2013) under calculation model of K-2 parameter. See table 4 for genetic divergences of dragon millipede genera.

Results

1. Sequence annotations and distance analysis

207 nucleotide sequences of dragon millipedes from partial genes (cytochrome *C* oxidase subunit 1, 16S rRNA and 28S rRNA) were obtained (Table 1). All sequences were blasted in GenBank to check the similarity with other closely related millipedes, confirming that there was no contamination. The final aligned sequences, after editing in GBlock were composed of 658 bp for COI, 465 bp for 16S rRNA, and 339 bp for 28S rRNA. Sequence annotation (Table 2) of each gene is as follows: COI sequences yield 344 variable sites, 314 conservative sites and 324 parsimony-informative sites; 16S rRNA sequences contain 313 variable sites, 152 conservative sites and 295 parsimony-informative sites; 28S rRNA sequences consist of 42 variable sites, 297 conservative sites and 40 parsimony-informative sites.

A summary of intra- and interspecific variation (uncorrected *P*-distances) in each partial gene fragment after calculating under the Kimura-2-parameter model for DNA sequence alignment is given in tables 3 and 4.

2. Phylogenetic analysis

For separate analyses of single genes, multiple runs for BI and ML resulted in trees topology, and all were poorly supported with low values of PP and BV. The topologies of BI and ML trees for the same gene were clearly different in the arrangements of several basal and terminal nodes (not shown). Therefore, only the phylogenetic tree of the concatenated datasets is presented (Figs 8.1, 8.2). For these trees, the topologies based on BI and ML methods are identical and differ only in bootstrap support values. The results from BI and ML are shown together based on BI topology with PP (> 95%) and BV (> 70%) (Figs 8.1, 8.2).

2.1 Paraphyly of the dragon millipedes

The combined dataset of three genes revealed that *Desmoxytes s.l.* + *Orthomorpha* form a well-supported clade in both BI and ML (PP = 1, BV = 98) and thus that dragon millipedes (*Desmoxytes s.l.*) are paraphyletic in terms of *Orthomorpha.* The genus *Orthomorpha* is joined as a sister group to the dragon millipede genus *Hylomus* (clade C), though the support for this clade was very strong by BI only (BV = 1), but not for ML.

The analysis separates the dragon millipede into five main clades, all strongly supported in both BI and ML: *Desmoxytes s.s.* (Clade A) (PP = 1, BV = 100), *Gigaxytes* (Clade B) (PP = 1, BV = 100), *Hylomus* (Clade C) (PP = 1, BV = 93), *Spinaxytes* (Clade D) (PP = 1, BV = 99) and *Nagaxytes* (Clade E) (PP = 1, BV = 100). The chosen outgroup taxa, however, are not nested together, but separated in several clades: *Orthomorpha* clade (PP = 1, BV = 92), sister group to the dragon millipede clade C (= *Hylomus*); the others are *Pogosternum-Kronopolites-Tylopus-Oxidus* at base of phylogeny.

Clade A (= *Desmoxytes s.s.*) is recovered as sister group to **Clade B** (= *Gigaxytes*) with full support of BI and of ML (PP = 1, BV = 92). Clades A and B were both fully supported by both BI and ML (PP = 1, BV = 100 in both cases).

Clades A+B together constitute the sister group to Clade C (= *Hylomus*) + Clade *Orthomorpha*.

Clade C (= *Hylomus*) is well-supported (PP = 1, BV = 93) for BI and ML. Obviously, this clade is sister to *Orthomorpha* with full bootstrap value of BI (PP = 1).

Clade D (= *Spinaxytes*) is recovered as the sister group to clades A+B+C+*Orthomorpha*. The relationship is, however, neither supported in BI nor ML. *Spinaxytes* itself is strongly supported strong support (PP = 1, BV = 99).

Clade E (= *Nagaxytes*) is fully supported (PP = 1, BV = 100). This clade is the basal group among dragon millipedes (+*Orthomorpha*) with strong statistical support (PP = 1, BV = 98) for the clade consisting of all non-*Nagaxytes*, dragon millipedes + *Orthomorpha.*

Short branch lengths are particularity prominent in the genus *Gigaxytes* (Clade B) whilst the remaining genera had greater genetic distances between their constituent species.

2.2 Relationships within genus *Desmoxytes s.s.* (Fig. 8.3)

Clade A (= *Desmoxytes s.s.*), the second largest genus of dragon millipedes in terms of described species, contains three subclades that each contain a group of species with a coherent geographical distribution. Fourteen genetically delimited taxa can be discriminated of which which all are congruent with morphologically characterized species.

The first subclade (**A1**) joins six species from northern Thailand with full bootstrap support (PP = 1). Here, the remarkable pink/red/purple colour species, *D. breviverpa*, *D. takensis*, *D. waepyanensis*, *D. purpurosea* and *D. golovatchi* ("infraclade" A1A), are grouped together with the black *D. octoconigera* as the basal sister group.

The second subclade **(A2),** distributed in southern Thailand, groups *D. aurata* as the sister taxon to *D. perakensis*, *D. delfae* and *D. terae*, with full support (PP = 1, BV = 87). These four species together are recovered with high bootstrap value (PP = 1, BV = 100) as the sister group to *D. flabella*.

The third subclade **(A3),** distributed in southern and eastern Thailand, joins four species supported by strong bootstrap of BI (PP = 0.97), viz., *D. euros*, *D. planata*, *D. corythosaurus* and *D. cervina*. *D. euros* + *D. planata* form the sister group to *D. corythosaurus* + *D. cervina*. Subclade A3 it can be further grouped in two “infraclades”. The split between these two “infraclades” received a strong bootstrap support in only BI (PP = 0.97).

- “Infraclade” A3A, composed of *D. planata* and *D. euros*, is distributed on the western and eastern sides of the Gulf of Siam and is very well-supported by BI and ML (PP = 1, BV = 100). Interestingly, these two species exhibit identical gonopod characters.

- “Infraclade” A3B join *D. corythosaurus* and *D. cervina* with strong support (PP = 1, BV = 730), both are distributed only in southern Thailand.

2.3 Relationship within genus *Gigaxytes* (Fig. 8.4)

Gigaxytes (**clade B**) forms a monophyletic group with very strong support (PP = 1, BV = 100), containing three species. *G. parvoterga* and *G. gigas* were recovered together by full support (PP = 1, BV = 100) with *G. fusca* as the sister group. Clade B is comprised of three subclades:

- subclade **B1** contains one species, *D. gigas*. Inside this subclade, the tree topology indicated monophyly of each of three populations as follows: B1A (Krabi), B1B (Phattalung) and B1C (Trang), all receiving full support in both BI and ML (PP = 1, BV = 100). The split between the three populations is congruent with their geographical distribution. B1A is dispersed in the western part of the distribution area, B1B in the northeastern, and B1C in the southeastern area.

- subclade **B2** comprised of *G. parvoterga* only

- subclade **B3** is fully supported (PP = 1, BV = 100) and consists of *G. fusca.*

2.4 Relationship within genus *Hylomus*

Hylomus (**clade** C) is the largest genus of dragon millipedes in number of described species; however, only three *Hylomus* sequences have been analyzed in this study, representing *Hylomus* n. sp. Laos and *H. rhinoceros*. Clade C is strongly supported (PP = 1, BV = 93), and surprisingly, *Hylomus* is recovered as the sister group to the outgroup *Orthomorpha* although the two genera are strongly dissimilar morphologically.

2.5 Relationship within genus *Spinaxytes* (Fig. 8.5)

Spinaxytes (**clade D)** is strongly supported as monophyletic (PP = 1, BV = 99). Of the trhee included species *S. biloba* and *S. unca* are grouped together, with *S. hasta* as the basal sister taxon. **Clade D** can be separated in three subclades (**D1**, **D2** and **D3**), **D1** and **D3** are well-supported by high bootstrap values. Subclade D3 (*S. hasta*), is divided into two "infraclades", one of which (D3A) is found in the northern area of distribution while the other (D3B) is limited to southern area of distribution (D3B).

2.6 Relationship within genus *Nagaxytes* (Fig. 8.6)

Nagaxytes (**clade E**) consists of *N. spatula*, *N. gracilis* and *N. erecta*, all grouped together with high support (PP = 1, BV = 100). *N. spatula* is recovered as a sister group to *N. gracilis* + *N. erecta*.

Clade E comprises:

- subclade **E1**, fully supported, contains *N. spatula*.

- subclade **E2** (not supported) contains *N. gracilis* and can be further subdivided into two "infraclades": (1) D3A with three specimens from Thong Pha Phum in the northern part of the distribution area, and (2) D3B with two specimens from Sai Yok the southern part.

- subclade **E3** contains *N. erecta*, supported by full bootstrap value.

3. Geographical distribution of the dragon millipedes

The genetic relationships of dragon millipedes as found by the present study seem to be related to geographical boundaries in mainland Southeast Asia (Fig. 8.2). Each genus tends to occupy its own area; however, some overlap exists. Among the five genera, *Desmoxytes s.s.* and *Hylomus* have the largest distribution areas.

Desmoxytes s.s. (clade A) inhabits a large area from southern China, through Laos and Vietnam, and northern Thailand (one synanthropic tramp species, *D. planata,* has become widespread far beyond this area, however).

Gigaxytes (clade B) is limited to southern Myanmar and southern Thailand.

Hylomus (Clade C) is widely distributed across southern China, through Laos and Vietnam, to northern Thailand.

Spinaxytes (clade D) is confined to southern Myanmar, southern Thailand, and northern Malaysia.

Nagaxytes (Clade E) is found only in western Thailand.

All species of dragon millipedes analyzed in this study are confined to small distribution areas (except the tramp species *D. planata*). Only a few species (*D. cervina*, *D. delfae*, *N. spatula* and *G. gigas*) seem to be somewhat more widely distributed, nevertheless, their distribution areas area are all < 200 km^2.

Desmoxytes s.s., *Gigaxytes*, *Spinaxytes* and *Nagaxytes* species have often been found to inhabit limestone habitats exclusively, whereas *Hylomus* species have been encountered in both limestone areas and primary forest.

Discussion and conclusion

Previous taxonomic studies suggested that all species of dragon millipede should be placed together in the single genus *Desmoxytes* Chamberlin, 1923 *sensu* Golovatch and Enghoff (1994) (= *Desmoxytes s.l.*) based on morphological characters of paraterga (high degree of elevation) and gonopods (Golovatch and Enghoff, 1994; Golovatch *et al.*, 2012). However, dragon millipede classification was recently revised by Srisonchai *et al.* (2018a) who, after an extensive morphological study including re-examination of all relevant type material, suggested a subdivision of *Desmoxytes s.l.* into five genera. In order to confirm the splitting approach, we here investigate the relationships between dragon millipedes based mainly on DNA from three genes, in combination with morphological characters. The analyses clearly resolve relationships among the dragon millipedes and support the subdivision into five genera, with strong statistical support for most branches. *Desmoxytes s.l.* is recovered as paraphyletic in terms of the non-dragon millipede genus *Orthomorpha*, further supporting the subdivision of *Desmoxytes s.l.*

Each genus of dragon millipedes (*Desmoxytes s.s.*, *Gigaxytes*, *Hylomus*, *Spinaxytes* and *Nagaxytes*) is recovered as monophyletic under BI and ML analyses with very strong support, confirming the results of the recent classification proposed by Srisonchai *et al.* (2018a) in which the species were group into genera based on similarities in the shape of gonopods and paraterga. These characters match perfectly with the molecular phylogeny, and thus seem to be useful for discrimination at genus level. The apical part of the gonopod, called solenophore, clearly demarcated and divided into two main parts (lamina lateralis (ll) and lamina medialis (lm)) as well as paratergal shape (antlerlike, winglike, spiniform and subspiniform) can reliably be used for classification.

The preliminary phylogenetic study on the genus *Hylomus* (Nguyen, 2016) suggested that *Hylomus* is not monophyletic and that the genera *Orthomorpha*, *Antheromorpha* Jeekel, 1968 and *Orthomorphoides* Likhitrakarn, Golovatch & Panha, 2011 appear to be closely related to *Hylomus*. This is in agreement with our study where we also found that *Orthomorpha* is closely related to *Hylomus*. However, we analyzed only two *Hylomus* species. Therefore, the relationship of *Hylomus* species could not be assessed properly. It is possible that a more comprehensive analysis of *Hylomus* will render the genus non-monophyletic, in accordance with the rather diverse morphology in this genus, as suggested by Nguyen (2016).

Although our study has provided strong evidence for non-monophyly of dragon millipedes, the inclusion of only one outgroup of Orthomorphini (*Orthomorpha*) is a limitation. The inclusion of more paradoxosomatid genera is needed in order to provide a deeper insight into the relationships of dragon millipedes.

1. Species diversity of dragon millipede in Mainland Southeast Asia

According to the previous taxonomic and phylogenetic studies, Southeast Asia is an important biodiversity hotspot (Clements *et al.*, 2006), and the high species richness of millipedes including the dragon millipedes is indeed remarkable. During the recent few years, many new dragon millipede species have been discovered in this region (Golovatch *et al.*, 2016; Likhitrakarn *et al.*, 2015; Liu *et al.*, 2014, 2016; Srisonchai *et al.*, 2016, 2018a, 2018b, 2018c, 2018d). According to available data, 67 out of 68 species are endemic to local areas and can often be found inhabiting limestone habitat/tropical forest.

Our molecular phylogeny shows great genetic variation within genera, within species and even within populations. In particular, the regional populations of some species such as *D. cervina* and *N. gracilis* suggested that genetic affinities might be significantly affected by the geographical features, perhaps leading to speciation.

The limestone areas in China, Myanmar, Thailand, Laos, Vietnam and Malaysia, where the vast majority of dragon millipedes are found, may be major foci for speciation and important biodiversity arks. We strongly believe that many new dragon millipedes are waiting for discovery by further collecting in so far unexplored areas in the mentioned countries. Actually, very recently collected but still not described material from those areas contains at least ten more new candidate species of the dragon millipede.

2. Distribution

All species of *Desmoxytes s.s.*, *Gigaxytes*, *Spinaxytes*, *Nagaxytes* and most species of *Hylomus* inhabit limestone areas only. *Desmoxytes* species can be found living on rocks or on branches of trees; *Gigaxytes* species prefer to live on the ground with leaf litter; *Spinaxytes* species were found crawling on rock walls and inside small caves; *Nagaxytes* species can be found on rocks. For *Hylomus*, according to recorded data, most species were found in limestone habitats, and some species can be encountered in tropical forest.

A few species of *Desmoxytes s.s.* and *Nagaxytes* have been found coexisting with others species, e.g., *D. terae* and *D. delfae* were collected from the same spot, but one lived on rocks whilst the other existed on tree branches. *Desmoxytes corythosaurus* and *D. cervina* have been reported occurring in the same microhabitat (on rocks). Also, *Nagaxytes gracilis* and *N. erecta* hae been found living in the same habitat and even possibly in the same microhabitat. However, the microhabitat details have not been studied in detail. In contrast, no case of sympatry has been recorded within *Spinaxytes*, *Gigaxytes* and *Hylomus,* perhaps due to low dispersal capacity. Most species belonging to these genera are highly endemic, being restricted to one or a few localities.

D. planata is the only species of dragon millipede which is distributed in a wide range as a pantropical species. It has been encountered in many countries, viz., China, Fiji, French Polynesia, USA (Hawaii), India, Indonesia, Myanmar, Seychelles, Sri Lanka, Thailand and Vietnam. Jeekel (1980b) assumed that the origin of this species could possibly be in Thailand, Myanmar or Malaysia. Srisonchai *et al.* (2018a) also found that numerous specimens of this species collected from the western and southern parts of Thailand and inhabiting natural limestone habitats, all seem to be indigenous. According to the phylogenetic tree, *D. planata* is grouped together with other species from western and southern Thailand/Myanmar. It is possible that the origin of this species might be in western/southern Thailand. Further evidence to support this area as its original place is the habitat where it was collected. Specimens collected from western/southern Thailand were from natural limestone habitats, whereas other recorded distribution data suggest that the occurrence of *D. planata* in Myanmar (type locality), northern Thailand, China, India, Fiji, Seychelles, French Polynesia, Sri Lanka and Hawaii is due to anthropochory although in some cases the species may subsequently have spread to natural habitats.

3. The usefulness of gonopod characters

It is generally believed that the gonopods of millipedes are useful for species identification, like the aedeagus of insects and other intromittent organs which evolve rapidly and divergently during speciation via reproductive isolation (Eberhard, 1985; Eberhard and Noor, 2004). Consistent with this hypothesis, our phylogenetic results are perfectly congruent with the previous morphological studies and support the value of morphological characters, particularly gonopods. Each genus of dragon millipedes can be characterized based on gonopods as follows: *Desmoxytes s.s.* – solenophore with processes plm, blm and dlm, lm and ll obviously demarcated: *Gigaxytes* – solenophore without process and lobes, lm and ll indistinctly demarcated; *Nagaxytes* – solenophore without process, lm and ll obviously demarcated; *Spinaxytes* – solenophore without process, lm and ll obviously demarcated; *Hylomus* – solenophore without process, lm and ll indistinctly demarcated.

Species in the genera *Nagaxytes*, *Spinaxytes* and *Hylomus* all have distinctive gonopods, while there are cases of identical/very similar gonopods in the genera *Desmoxytes s.s.* and *Gigaxytes*. A case of identical gonopods is provided by the sister pair *D. planata* and *D. euros*: the molecular phylogeny strongly supports separating them as different species, as indicated by the genetic divergence, 13.5-16.5% from three genes. In addition, their geographical distributions are also clearly separated: although *D. planata* is a widespread species (see above), no sympatry exists between these two species. Another case of species with similar gonopods is *G. gigas* and *G. parvoterga*. They appear as sister species on our tree, and the low genetic distance between them (4.3%) suggests that they may be the same species. However, male femora 5 6 and 7 are different: modified in *G. parvoterga* and unmodified in *G. gigas*. Moreover, these two species are allopatric, *G. gigas* occurring in a northern area and *G. parvoterga* in a southern one. Both these cases could probably be examples of allopatric speciation in dragon millipedes, reminding of the findings in some other millipede genera (Evsyukov *et al.*, 2016; Pimvichai *et al.*, 2014).

For *Nagaxytes gracilis*, two main populations are recognized based on the phylogenetic tree, showing high genetic divergence (11.4%). However, their gonopod details are totally identical, as well as overall morphological characters, and furthermore, the two populations are not completely isolated from each other. We thus regarded these two populations as belonging to the same species, although this still requires confirmation in the form of more sampling, more molecular analysis and perhaps study of hitherto unexploited morphological characters.

In earlier studies, the identification of dragon millipedes was mainly based on gonopods. Attems (1953); Golovatch and Enghoff (1994); Jeekel (1964, 1980a) discussed the relationship between *Orthomorpha* and those dragon millipedes which we here refer to genus *Hylomus* because they appeared to have partly/entirely similar in gonopod structure. Our phylogenetic results confirmed the close relationship between these genera, although BI analysis was the only one to provide a strong support. Morphologically, a sister-group relationships between *Hylomus* and *Orthomorpha* is supported by some shared characters: solenophore without a process (in most species), and lm and ll indistinctly demarcated. Their distribution ranges of the two genera roughly cover the same area, mainly in China, Laos and Vietnam.

Golovatch and Enghoff (1994) proposed evolutionary pathways of gonopod structure in dragon millipedes. They suggested two alternative hypotheses: that the shape of gonopod has proceeded from the strongly condensed type towards a less condensed type, and vice versa. In order to understand how dragon millipede gonopods have evolved, we investigated morphological data in combination with a molecular analysis. Our previous study based on morphology revealed that the dragon millipedes exhibit two types in shape of gonopod: (1) strongly condensed (*Desmoxytes s.s.*, *Spinaxytes*, *Nagaxytes*), and (2) uncondensed i.e., similar to *Orthomorpha* (*Hylomus*, *Gigaxytes*).

Considering the distribution of strongly condensed and uncondensed gonopods on the tree (Fig. 8.3), it seems likely that the common ancestor of the dragon millipede and *Orthomorpha* had the strongly condensed type which is thus to be regarded as plesiomorphic at this level, and that 'uncondensation' subsequently happened twice (once in *Hylomus* + *Orthomorpha*, once in *Gigaxytes*). However, this is just a hypothesis. Including more outgroup genera in the analysis, as well as adding more molecular markers, could potentially shed more light on this hypothesis.

4. Paraterga characters

Almost all paradoxosomatid millipedes have paranota (lateral extensions of the dorsal surface) that extend laterad and upward at an angle and may be armed with sharp teeth or spikes, often supplemented by rows or groups of long spines on the dorsum. It is believed that having wide paranota may be a way to extend the reach of secretions from the ozopores and/or deter predation , and probably help the animal wedge itself into crevices in logs or leaf litter (Liu *et al.*, 2017; Shear, 2015). For the time being, the function of the paraterga in Paradoxosomatidae is still debatable and has never been studied.

In all dragon millipedes, the degree of elevation of paranota (= paraterga) is high. Four main types of paraterga may been recognized, viz., winglike, spinelike, subspiniform, antlerlike. Several previous taxonomic studies suggested that the shape of paraterga is very useful for genus and species discrimination, i.a., in dragon millipedes (Attems, 1937, 1953; Chamberlin, 1923; Cook and Loomis, 1924a; Golovatch and Enghoff, 1994; Golovatch *et al.*, 2010; Golovatch *et al.*, 2012; Jeekel, 1964; Pocock, 1895). Our morphological observation revealed that this character can indeed be of help for classifying dragon millipede at the genus level (Srisonchai *et al.*, 2018a).

Pathways of paratergal evolution in Paradoxosomatidae have not been analyzed yet. According to the phylogenetic tree, it is probable that either the ancestor of dragon millipedes + *Orthomorpha* had highly elevated paraterga and that *Orthomorpha* has reverted to a low degree of elevation, or that dragon millipedes developed a high degree of elevation multiple times in the different lineages. The latter notion is supported by the presence of highly elevated paraterga in other paradoxosomatid genera such as *Borneochiropus* and *Euphyodesmus* (spiniform paraterga) and *Desmoxytoides* (antlerlike) (Mesibov, 2006). An even more interesting piece of evidence is provided by the fossil order Archipolypoda (Late Carboniferous/ Early Permian). Kraus (2012) discussed that the extinct archipolypod *Euphoberia* sp. might be related to dragon millipedes with which it shares antlerlike paraterga. However, the similarity between the paraterga of *Euphoberia* and dragon millipedes, as well as those of the other paradoxosomatid genera mentioned above, is clearly due to parallel evolution, and the same applies to *Tridontomus procerus* Loomis and Hoffman, 1962 and *Aenigmopus alatus* Loomis and Hoffman, 1962 (Tridontomidae), also considered by Kraus (2012).

5. Comments on selected morphological characters

In addition to gonopods and paraterga, some other morphological characters exhibit variation and instability in certain genera and species of dragon millipedes which has implication for their usefulness for classification and identification.

Collum: Charaters of the collum have long been used just for species identification in dragon millipedes. All dragon millipede genera have three rows of setae/ tubercles/ cones/ spines on the collum, like other genera in tribe Orthomorphini and Sulciferini, e.g., *Orthomorpha* , *Antheromorpha*, *Enghoffosoma* and *Tylopus.*

Each species, however, shows differences in the numbers of setae/ tubercles/ cones/ spines which can be reliably used for discrimination. Nevertheless, characters of collum do not seem to be useful at the genus level.

Sternal lobe between male coxae 4: This structure may be a copulating facility that is used for deceiving female by providing edible secretions through two pores. The sternal lobe is quite highly variable among the genera: mostly angular/round in *Desmoxytes s.s.*, *Nagaxytes* and *Gigaxytes*; mostly long forklike or tubulifirm in *Spinaxytes*; very diverse in shape, rectangular, tapeziform, or even only represented by the two pores, in *Hylomus*.

A sternal lobe between male coxae 4 is often found in several genera of Paradoxosomatidae especially in the tribe Orthomorphini. In dragon millipedes, the shape of the sternal lobe can be used for species delimitation in some cases, e.g., *D. octoconigera*, *G. fusca*, *S. biloba*, *S. efefi*, *S. hasta*, *S. tortioverpa*, *S. sutchariti*, *N. erecta*, as well as several species in *Hylomus* such as *H. nodulosa*, *H. draco*, *H. parvula, H. lingulata*, *H. rhinoceros*.

Femora of male legs 5-9: There are three major types of modifications of male femora 5-9: swollen, humped and apophysis. Such modifications are present in most species of *Desmoxytes s.s.*, *Gigaxytes*, *Spinaxytes* and *Hylomus*, whereas *Nagaxytes* species have unmodified femora. Also, some species of *Desmoxytes s.s.*, *Gigaxytes*, *Spinaxytes* and *Hylomus* have unmodified femora. Therefore, modifications of femora seem not to be useful for generic diagnoses. In contrast, they are very useful for distinguishing species within genera.

Setae/ tubercles/ cones/ spines on metaterga: Most genera in the family Paradoxosomatidae presented two rows of setae/ tubercles/ cones/ spines on the metaterga. This also applies to: *Desmoxytes s.s.*, *Nagaxytes* and *Spinaxytes*, whereas *Gigaxytes* species have three rows, and *Hylomus* species may have either two or three rows. For species distinguishing, the number of rows and the type of setae/ tubercles/ cones/ spines is very useful.

Telson: The telson of millipedes is composed of three parts: (1) epiproct (preanal ring), (2) paraproct (anal valves) and (3) hypoproct (subanal scale). Telson structure varies little among dragon millipedes, only epiproct and hypoproct seem to differ. A few previous taxonomic studies (Golovatch and Enghoff, 1994; Liu *et al.*, 2016; Nguyen *et al.*, 2005; Srisonchai *et al.*, 2016) suggested using these for distinguishing some dragon millipede species within the same genus, viz., *Desmoxyte*s *s.s.* and *Hylomus*. After intensive examination, we found that these characters differ in such small degrees within a genus that they do not seem to be useful for species discrimination in general. As an exceptional case, one species of the genus *Desmoxytes s.s.* can be distinguished from other closely related species based on the epiproct, viz., *D. pinnasquali* with an extremely emarginated tip of the epiproct (Srisonchai *et al.* 2016: fig. 13K-L).

6. The remarkable colour in some dragon millipede species

The dragon millipedes belong to a group of millipedes which defend themselves by secreting highly poisonous hydrogen cyanide, giving out the typical almond-like smell. The strong pink colour of several species certainly serves as a warning to would-be predators (aposematism) (Enghoff *et al.*, 2007). Some of the pink species have been observed proudly siting and crawling with an ‘easy-going attitude’ on open ground and vegetation during daytime, no doubt relying on the aposematic colouration.

Some species are easily recognized by their colour, the most well-known and spectacular one being the shocking pink dragon millipede, *D. purpurosea* (Enghoff *et al.*, 2007). However, other dragon millipede species also have remarkable pink body colours (*D. golovatchi*, *D. breviverpa*, *D. pinnasquali*, *D. takensis*, *D. waepyanensis*, *H. enghoffi*), and some are bright orange red (*D. aurata*, *D. delfae*, *D. perakensis*).

Many other species of paradoxosomatid millipedes exhibit similarly vivid colours, e.g., *Antheromorpha uncinata* (Attems, 1931) and *Helicorthomorpha holstii* (Pocock, 1895) (Likhitrakarn *et al.*, 2016; Nguyen and Sierwald, 2013). In one case, our analysis found a monophyletic group of species with similar colours: The genus *Desmoxytes s.s.* contains species with vivid pink, red, purple and orange colours, and all species with pink/purple/red colour body were grouped together in the subclade (A1A) with full support by BI analysis. Moreover, all members in this subclade also exhibit the similar shape of gonopod characters, shape of paraterga and same number of tubercles/ cones/ spines on metaterga 2-19, etc.

These results thus in part partly support the use of colour as a supplementary tool for identifying and grouping dragon millipedes. However, colour may not always be reliable because colour variation occurs in some species such as *D. cervina*, *D. delfae*, *D. takensis* and *N. erecta*. Moreover, old preserved museum specimens are usually more or less faded. Whenever possible, photos of living specimens should be made during fieldwork.

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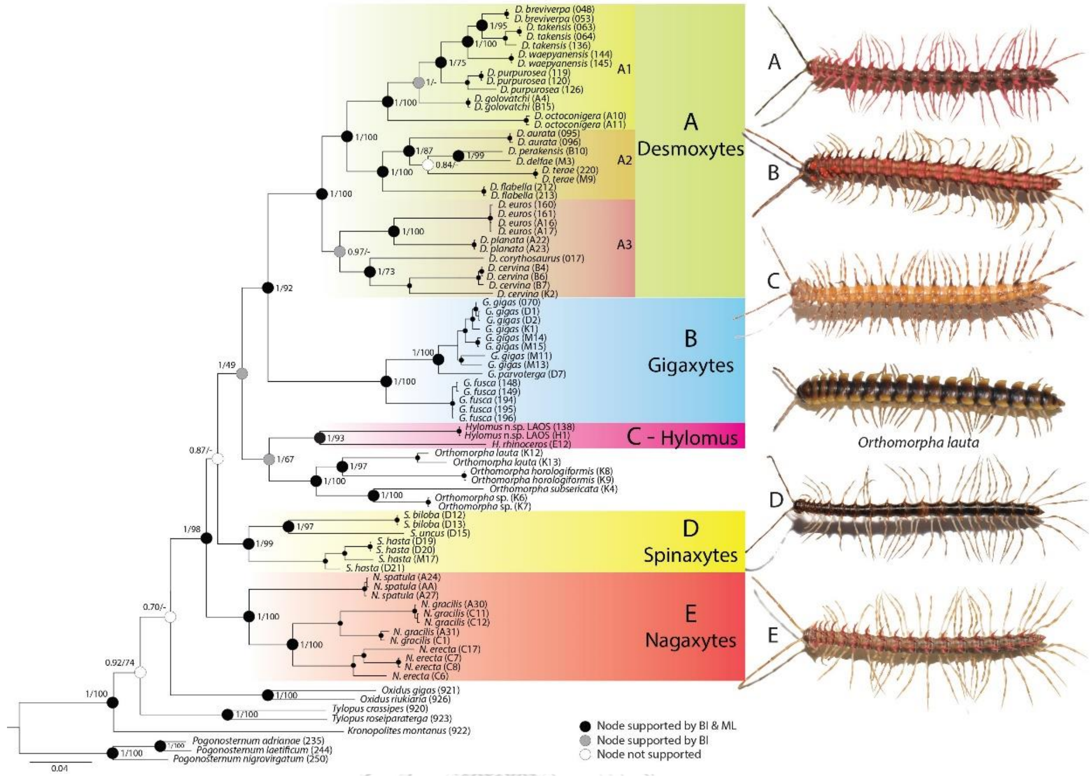

Figure 8.1 Phylogenetic tree of dragon millipedes based on Bayesian Inference Analysis of the combined dataset of COI, 16S rRNA and 28S rRNA. Number at nodes correspond to Bayesian Posterior Probability (PP) and Maximum Likelihood Bootstrap Support Values (BV). Black circle = node supported by both BI and ML. Grey circle = node supported by BI only. White circle = node not supported. The number at each terminal taxon refers to the specimens number in Table 1. Live photos of representative specimens representing each clade: A = *Desmoxytes purpurosea*, B = *Gigaxytes gigas*, C = *Hylomus* n.sp. LAOS, D = *Spinaxytes krabiensis*, E = *Nagaxytes gracilis*, *Orthomorpha lauta* as outgroup).

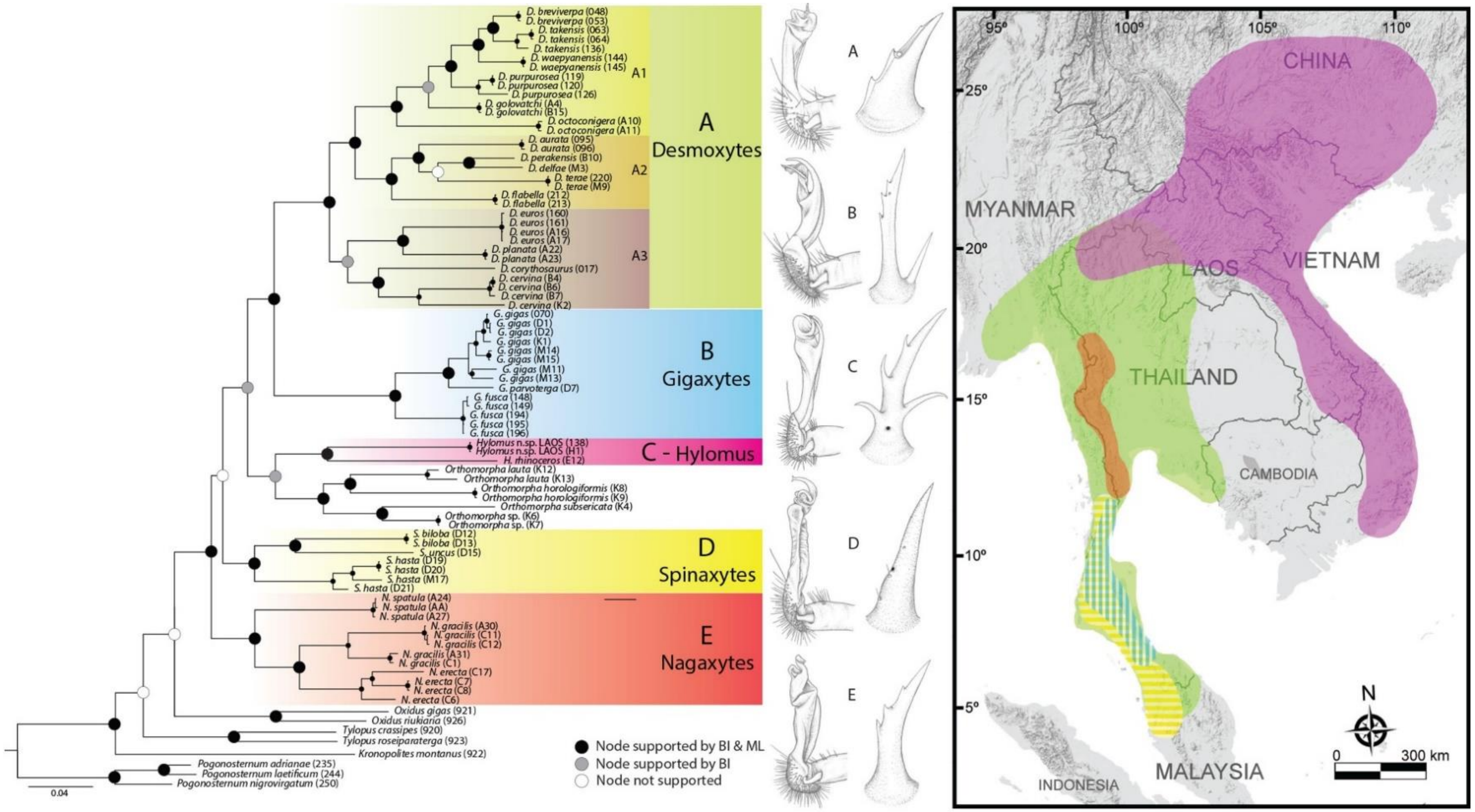

Figure 8.2 Phylogenetic relationship of dragon millipedes combining with gonopod and paraterga characters relative to distribution. Gonopodal and paratergal illustrations represent each clades (A = *Desmoxytes planata*, B = *Gigaxytes fusca*, C = *Hylomus draco*, D = *Spinaxytes krabienesis*, E = *Nagaxytes erecta*). The number at each terminal taxon refers to the specimens number in Table 1. Distribution map based on all recorded data of all species.

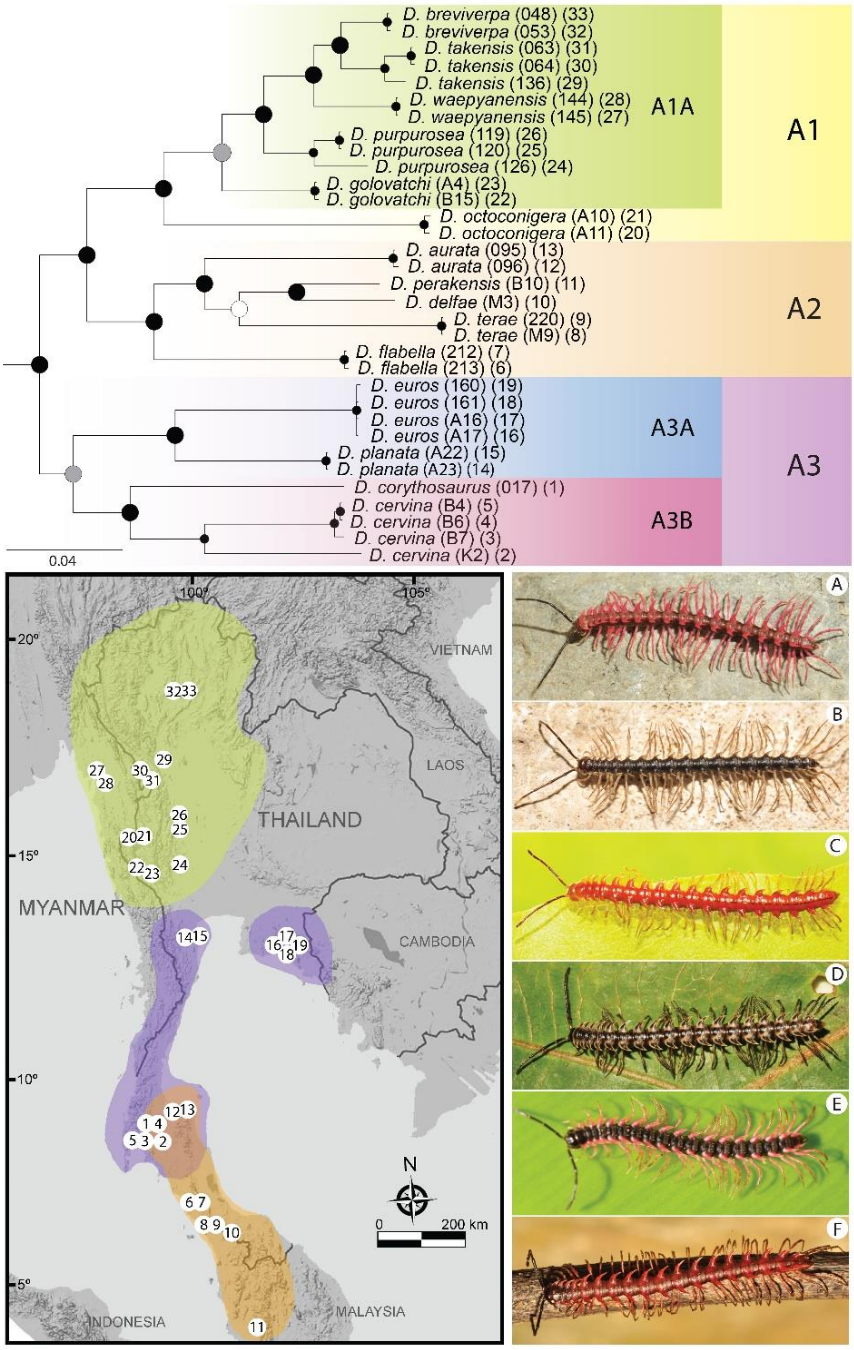

Figure 8.3 Phylogenetic tree of the genus *Desmoxytes* based on Bayesian Inference Analysis of the combined dataset of three gene fragments relative to regional distribution in mainland Southeast Asia. Black circle = node supported by both BI and ML. Grey circle = node supported by BI only. White circle = node not supported. The number at each terminal taxon refers to the specimens number in Table 1, the second number corresponds to the locality numbers on the map. Live photos of representative specimens *s*, showing colouration: A = *D. purpurosea*, B = *D. octoconigera*, C = *D. delfae*, D = *D. terae*, E = *D. planata*, F = *D. cervina*.

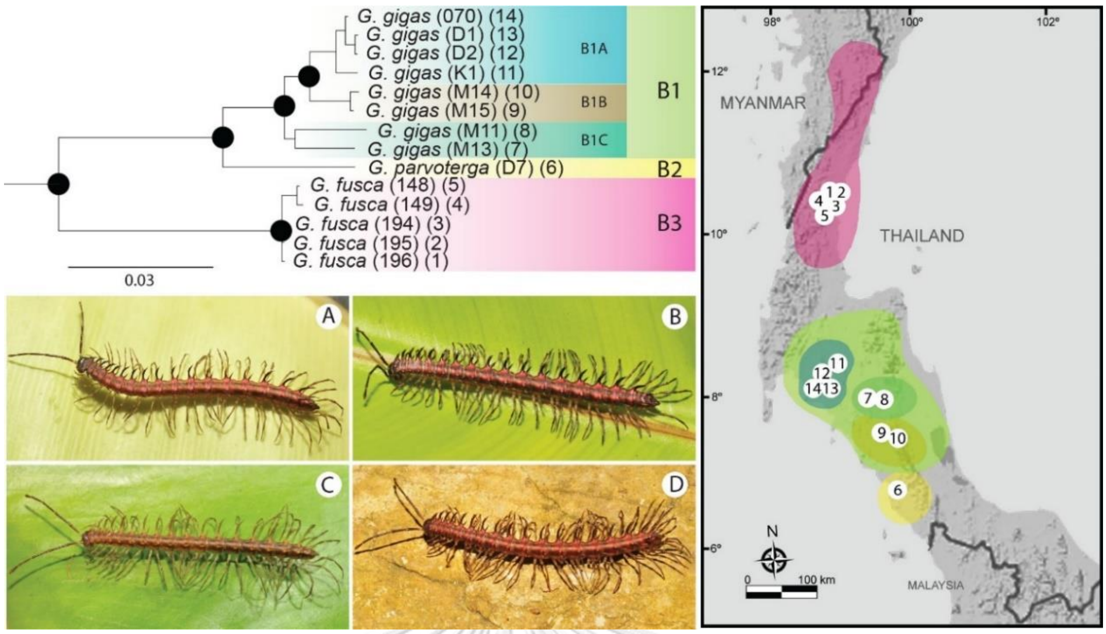

Figure 8.4 Phylogenetic tree of the genus *Gigaxytes* based on Bayesian Inference Analysis of the combined dataset of three gene fragments relative to regional distribution in mainland Southeast Asia. Black circle = node supported by both BI and ML. The number at each terminal taxon refers to the specimens number in Table 1, the second number corresponds to the locality numbers on the map. Live photos of representative specimens: A = *G. gigas* specimen from Tiger Cave, B = *G. gigas* specimen from Khao Chang Hai Cave, C = *G. fusca*, D = *G. parvoterga*.

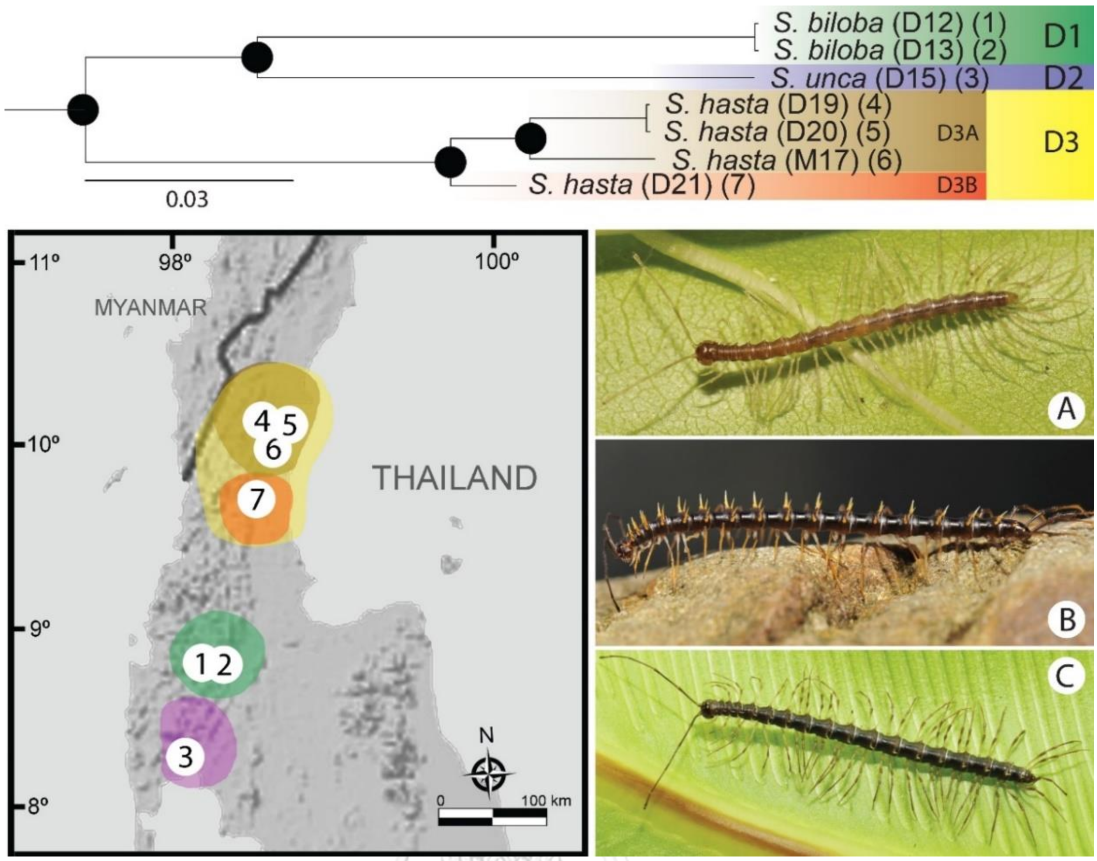

Figure 8.5 Phylogenetic tree of the genus *Spinaxytes* based on Bayesian Inference Analysis of the combined dataset of three gene fragments relative to regional distribution in mainland Southeast Asia. Black circle = node supported by both BI and ML. The number at each terminal taxon refers to the specimens number in Table 1, the second number corresponds to the locality numbers on the map. Live photos of representative specimens: A = *S. biloba*, B = *S. uncus*, C = *S. hasta*.

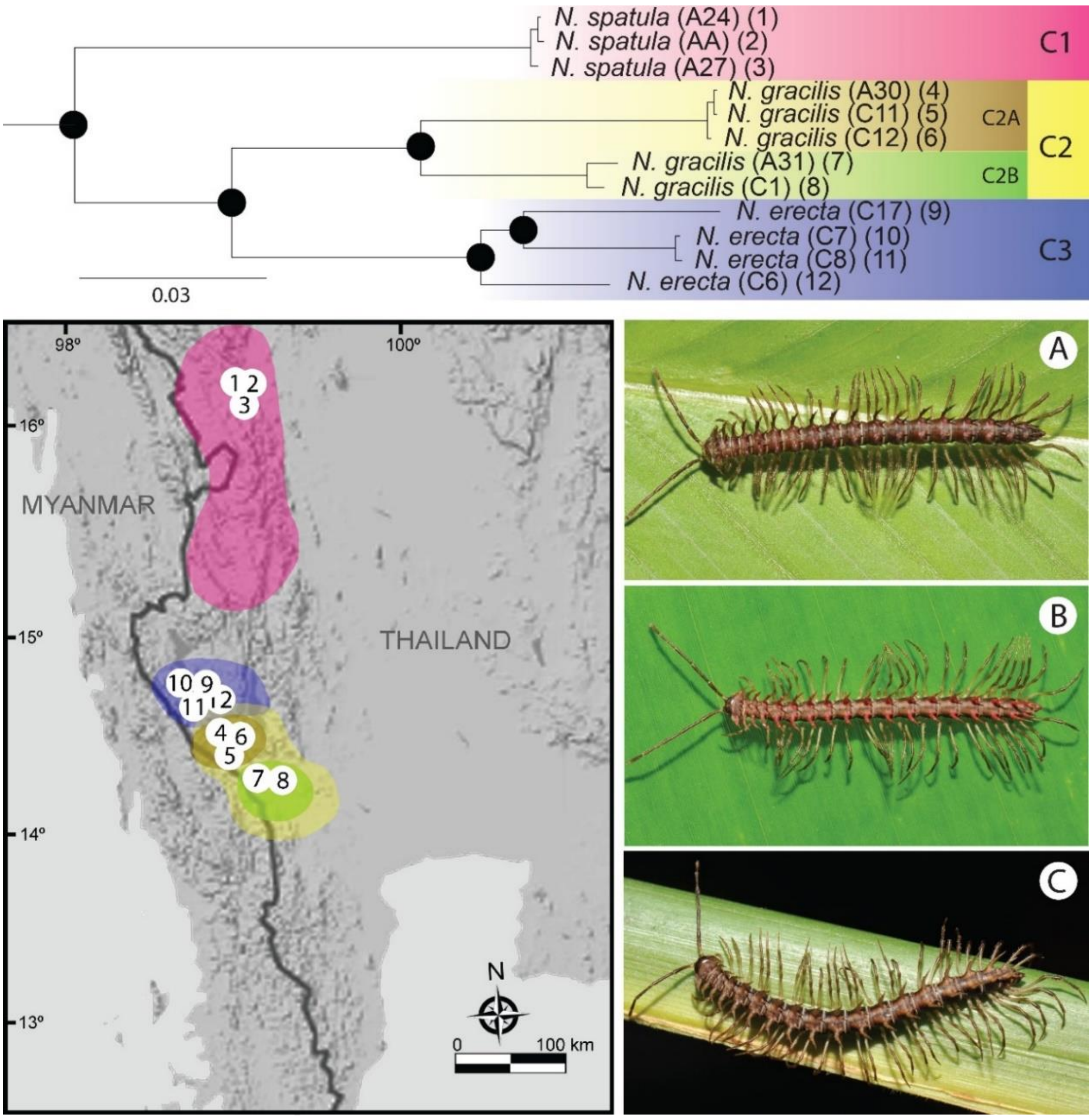

Figure 8.6 Phylogenetic tree of the genus *Nagaxytes* based on Bayesian Inference Analysis of the combined dataset of three gene fragments relative to regional distribution in mainland Southeast Asia. Black circle = node supported by both BI and ML. The number at each terminal taxon refers to the specimens number in Table 1, the second number corresponds to the locality numbers on the map. Live photos of representative specimens: A = *N. spatula*, B = *N. gracilis*, C = *N. erecta*.

Table 8.1 Lists of specimens used in this study: species, localities, voucher number, number and name used in phylogenetic tree, and GenBank accession number.

	Species/Locality	Voucher code	No.	GenBank accession number		
				COI	16S	28S
	Ingroup					
	Tribe Orthomorphini, genus *Desmoxytes* Chamberlin, 1923					
1.	*Desmoxytes aurata* Srisonchai, Enghoff and Panha, 2018					
	Khao Phanom Wang Cave, Kanchanadit, Suratthani	CUMZ-DP-D0001 CUMZ-DP-D0002	095 096	-	-	-
	Desmoxytes breviverpa Srisonchai, Enghoff and Panha, 2016					
2	Sareethai Cave, Long, Phrae	CUMZ-DP-DE0003 CUMZ-DP-DE0004	048 053			
3.	*Desmoxytes cervina* (Pocock, 1985)					
	Wat Suwan Khuha (Monkey Cave), Takua Thung, Phang Nga	CUMZ-DP-DE0005	B4	-	-	-
	Ban Song Phi Nong, Phanom, Surat Thani	CUMZ-DP-DE0006	B6	-	-	-
	Phoung Chang Cave, Mueang, Phang Nga	CUMZ-DP-DE0007	B7	-	-	-
	Wat Khao Hua Sing, Plai Phraya, Krabi	CUMZ-DP-DE0008	K2	-	-	-
4.	*Desmoxytes corythosaurus* Srisonchai, Enghoff and Panha, 2018					
	Wat Tham Wararam, Phanom, Surat Thani	CUMZ-DP-DE0009	017	-	-	-
5.	*Desmoxytes delfae* (Jeekel, 1964)					
	Khao Wong Pra Chan Bureau of Monks, Sa Dao, Songkhla	CUMZ-DP-DE0010	M3	-	-	-
6.	*Desmoxytes euros* Srisonchai, Enghoff and Panha, 2018					
	Khao Wong Kot Cave, Kaeng Hang Maeo, Chantaburi	CUMZ-DP-DE0011	160	-	-	-

	Species/Locality	Voucher code	No.	GenBank accession number		
				COI	16S	28S
		CUMZ-DP-DE0012	161			
		CUMZ-DP-DE0013	A16			
		CUMZ-DP-DE0014	A17			
7.	*Desmoxytes flabella* Srisonchai, Enghoff and Panha, 2018					
	Tham Khao Ting, Palian, Trang	CUMZ-DP-DE0015	212	-	-	-
		CUMZ-DP-DE0016	213			
8.	*Desmoxytes golovatchi* Srisonchai, Enghoff and Panha, 2018					
	Prang Ka Sri Temple, Thong Pha Phum, Kanchanaburi	CUMZ-DP-DE0017	A4	-	-	-
		CUMZ-DP-DE0018	B15			
9.	*Desmoxytes octoconigera* Srisonchai, Enghoff and Panha, 2018					
	Wat Tham Kaeo Sawan Bandal, Sangkhla Buri, Kanchanaburi	CUMZ-DP-DE0019	A10	-	-	-
		CUMZ-DP-DE0020	A11			
10.	*Desmoxytes perakensis* Srisonchai, Enghoff and Panha, 2018					
	The Lost World Tambun Theme Park, Perak, Malaysia	CUMZ-DP-DE0021	B10	-	-	-
11.	*Desmoxytes planata* (Pocock, 1985)					
	Wat Puang Malai (Wat Tham Khao Iko), Khao Yoi, Phrtchaburi	CUMZ-DP-DE0022	A22	-	-	-
		CUMZ-DP-DE0023	A23			

	Species/Locality	Voucher code	No.	GenBank accession number		
				COI	16S	28S
12.	*Desmoxytes purpurosea* Enghoff, Sutcharit and Panha, 2007					
	Hup Pa Tard, Lansak, Uthai Thani	CUMZ-DP-DE0024 CUMZ-DP-DE0025	119 120	-	-	-
	Than Lod Cave, Srisawat, Kanchanaburi	CUMZ-DP-DE0026	126			
13.	*Desmoxytes takensis* Srisonchai, Enghoff and Panha, 2016					
	Nangkruen Waterfall, Phobphra, Tak	CUMZ-DP-DE0027 CUMZ-DP-DE0028	063 064	-	-	-
	Chao Por Phawo, Mae Sot, Tak	CUMZ-DP-DE0029	136	-	-	-
14.	*Desmoxytes terae* (Jeekel, 1964)					
	Tham Tone Din (Tone Din Cave), Khuan Don, Satun	CUMZ-DP-DE0030 CUMZ-DP-DE0031	220 M9	-	-	-
15.	*Desmoxytes waepyanensis* Srisonchai, Enghoff and Panha, 2018					
	Wae Pyan Cave, Kayin, Myanmar	CUMZ-DP-DE0032 CUMZ-DP-DE0033	144 145	-	-	-
	Tribe Orthomorphini, genus *Gigaxytes* Srisonchai, Enghoff and Panha, 2018					
16.	*Gigaxytes fusca* Srisonchai, Enghoff and Panha, 2018					

	Species/Locality	Voucher code	No.	GenBank accession number		
				COI	16S	28S
	Phitsadarn Cave (Tham Phitsadarn), Pathio, Chumphon	CUMZ-DP-GX0001 CUMZ-DP-GX0002 CUMZ-DP-GX0003 CUMZ-DP-GX0004 CUMZ-DP-GX0005	148 149 194 195 196	-	-	-
17.	*Gigaxytes gigas* (Golovatvh and Enghoff, 1994)					
	Wat Tham Sue (Tiger Cave), Mueang, Krabi	CUMZ-DP-GX0006 CUMZ-DP-GX0007 CUMZ-DP-GX0008	070 D1 D2	-	-	-
	Wat Khao Hua Sing, Plai Phraya, Krabi	CUMZ-DP-GX0009	K1	-	-	-
	Wat Tham Phra Put, Ratsada, Trang	CUMZ-DP-GX0010 CUMZ-DP-GX0011	M14 M15	-	-	-
	Wat Tham Wang Thong, Na Yong, Trang	CUMZ-DP-GX0012	M11	-	-	-
	Khao Chang Hai Cave, Na Yong, Trang	CUMZ-DP-GX0013	M13	-	-	-
18.	*Gigaxytes parvoterga* Srisonchai, Enghoff and Panha, 2018					
	Tham Khao Ting, Palian, Trang	CUMZ-DP-GX0014	D7	-	-	-

	Species/Locality	Voucher code	No.	GenBank accession number		
				COI	16S	28S
	Tribe Orthomorphini, genus *Hylomus* Cook and Loomis, 1924					
19.	*Hylomus rhinoceros* (Likhitrakarn, Golovatch and Panha, 2015)					
	Ban Teu, Kafey, Sekong, Laos	CUMZ-DP-HY0001	E12	-	-	-
20.	*Hylomus* n. sp.					
	Phuthalang Forest Protected Area, Phongsali, Laos	CUMZ-DP-HY0002 CUMZ-DP-HY0003	138 H1	-	-	-
	Tribe Orthomorphini, genus *Nagaxytes* Srisonchai, Enghoff and Panha, 2018					
21.	*Nagaxytes erecta* Srisonchai, Enghoff and Panha, 2018					
	Ban Nong Bang (near Wat Pha Sukit Suwannaket, Thong Pha Phum, Kanchanaburi	CUMZ-DP-NX0001	C6	-	-	-
	Wat Pak Lam Pilock, Thong Pha Phum, Kanchanaburi	CUMZ-DP-NX0002 CUMZ-DP-NX0003	C7 C8	-	-	-
	Wat Tha Kha-nun, Thong Pha Phum, Kanchanaburi	CUMZ-DP-NX0004	C17	-	-	-
22.	*Nagaxytes gracilis* Srisonchai, Enghoff and Panha, 2018					
	Tham Doawadueng, Sai Yok, Kanchanaburi	CUMZ-DP-NX0005 CUMZ-DP-NX0006 CUMZ-DP-NX0007	A30 C11 C12	-	-	-

	Species/Locality	Voucher code	No.	GenBank accession number		
				COI	16S	28S
	Wat Phu Mood, Sai Yok, Kanchanaburi	CUMZ-DP-NX0008 CUMZ-DP-NX0009	A31 C1	-	-	-
23.	*Nagaxytes spatula* Srisonchai, Enghoff and Panha, 2018					
	Chao Por Phawo, Mae Sot, Tak	CUMZ-DP-NX0010 CUMZ-DP-NX0011	AA A24	-	-	-
	Wat Pho Thi Khun (Wat Huai Toey), Mae Sot, Tak	CUMZ-DP-NX0012	A27	-	-	-
	Tribe Orthomorphini, genus *Spinaxytes* Srisonchai, Enghoff and Panha, 2018					
24.	*Spinaxytes biloba* Srisonchai, Enghoff and Panha, 2018					
	Pha Daeng, Phanom, Surat Thani	CUMZ-DP-SX0001 CUMZ-DP-SX0002	D12 D13	-	-	-
25.	*Spinaxytes hasta* Srisonchai, Enghoff and Panha, 2018					
	Khao Ma Ngaen, Thung Tako, Chumphon	CUMZ-DP-SX0003 CUMZ-DP-SX0004	D19 D20	-	-	-
	Wat Nam Cha, Sawi, Chumphon	CUMZ-DP-SX0005	M17	-	-	-
	Wat Ratcha Burana School, Lang Suan, Chumphon	CUMZ-DP-SX0006	D21	-	-	-
26.	*Spinaxytes unca* Srisonchai, Enghoff and Panha, 2018					
	Phoung Chang Cave, Mueang, Phang Nga	CUMZ-DP-SX0007	D15	-	-	-
	Outgroup					
	Tribe Orthomorphini, genus *Orthomorpha* Bollman, 1893					

	Species/Locality	Voucher code	No.	GenBank accession number		
				COI	16S	28S
27.	*Orthomorpha horologiformis* Golovatch, 1998					
	Tham Boon Raksa Phu Pha Ram, Lam Thap, Krabi	CUMZ-DP-OR0004 CUMZ-DP-OR0005	K8 K9	-	-	-
28.	*Orthomorpha lauta* Golovatch, 1998					
	Tham Lod, Noppkitam, Nakhon Si Thammarat	CUMZ-DP-OR0006 CUMZ-DP-OR0007	K12 K13	-	-	-
29.	*Orthomorpha* sp.					
	Wat Khao Hua Sing, Plai Phraya, Krabi	CUMZ-DP-OR0001 CUMZ-DP-OR0002	K6 K7	-	-	-
30.	*Orthomorpha subsericata* Golovatch, 1998					
	Tham Chang Phuek Bureau of Monks, Mueang, Chumphon	CUMZ-DP-OR0003	K4	-	-	-
	Tribe Sulciferini, genus *Oxidus* Cook, 1911					
31.	*Oxidus gigas* (Attems, 1953)					
	Sapa, Lao Cai, Vietnam	IEBR-Myr 113	921	KX096921	KX096912	*
32	*Oxidus riukiaria* (Verhoeff, 1940)					
	Okinawa, Japan	IEBR-H500	926	KX096926	KX096915	*
	Tribe Sulciferini, genus *Kronopolites* Attems, 1914					

	Species/Locality	Voucher code	No.	GenBank accession number		
				COI	16S	28S
33.	*Kronopolites montanus* (Golovatch, 2009)					
	Pu Mat, Nghe An, Vietnam	IEBR-Myr 175	922	KX096922	KX096908	*
	Tribe Sulciferini, genus *Tylopus* Jeekel, 1968					
34.	*Tylopus crassipes* Golovatch, 1984					
	Sapa, Lao Cai, Vietnam	IEBR-Myr 92	920	KX096920	KX096907	*
35.	*Tylopus roseiparaterga* Nguyen, 2012					
	Tam Dao, Vinh Phuc, Vietnam	IEBR-Myr 185A	923	KX096923	KX096909	*
	Tribe Antichiropodini, genus *Pogonosternum* Jeekel, 1965					
36.	*Pogonosternum adrianae* Jeekel, 1982					
	S Dargo, Victoria, Australia	NMV K-12203	235	KU745235	KU745194	KU745185
37.	*Pogonosternum laetificum* Jeekel, 1982					
	SE Narbethong, Victoria, Australia	SMNG VNR016987	244	KU745244	KU745203	KU745187
38.	*Pogonosternum nigrovirgatum* (Carl, 1902)					
	SE Traralgon South, Victoria, Australia	NMV K-12205	250	KU745250	KU745209	KU745188

(*) sequence not available in GenBank, (-) sequences not yet submitted to GenBank.

Table 8.2 Nucleotide sequences of the three genes and the best-fit models of the nucleotide substitution

	Nucleotide sequences					Best-fit model	
	No. of bp (origin)	No. of bp after checking In-Del	Parsimony informative sites	Variable sites	Conservative sites	ML	BI
COI	658	658	324	344	314	GTR+I+G	GTR+I+G
16S rRNA	640	465	295	313	152	GTR+I+G	GTR+I+G
28S rRNA	383	339	40	42	297	K80+I+G	K80+I+G

Table 8.3 Ranges of intergeneric distances for COI and 16S rRNA genes of all genera analyzed in this study (genus in Bold = dragon millipedes)

		COI (%)									
		Dragon millipede (Orthomorphini)					Orthomorphini	Sulciferini			Antichiropodini
		Desmoxytes	***Hylomus***	***Gigaxytes***	***Nagaxytes***	***Spinaxytes***	*Orthomorpha*	*Kronopolites*	*Tylopus*	*Oxidus*	*Pogonosternum*
16S rRNA (%)	***Desmoxytes***		20.3-28.1	19.6-29.3	17.7-30.4	18.2-28.8	17.8-29.6	17.7-26.9	18.7-32.1	18.2-31.9	20.1-31.5
	Hylomus	29.2-40.2		21.2-24.3	23.1-28.5	20.8-24.3	16.0-26.6	19.4-22.6	18.1-25.1	24.1-25.7	26.1-29.8
	Gigaxytes	28.3-38.2	33.8-38.8		20.2-28.1	20.0-24.9	22.4-30.0	22.1-25.4	23.7-27.6	23.6-28.3	25.1-31.1
	Nagaxytes	22.9-32.4	28.7-38.3	25.7-35.1		16.5-23.9	18.4-25.4	16.7-20.1	17.8-23.0	16.3-24.2	18.5-23.0
	Spinaxytes	25.3-35.4	26.4-35.1	28.1-38.8	24.2-38.8		16.9-24.1	15.8-20.6	17.6-22.2	17.4-24.7	17.0-21.5
	Orthomorpha	23.1-34.5	25.9-39.5	25.5-32.7	20.0-31.0	23.7-29.2		19.4-22.6	18.5-25.1	18.9-23.7	20.3-23.8
	Kronopolites	31.9-42.2	39.4-43.9	36.2-38.3	32.1-40.9	35.0-37.2	30.8-37.7		16.9-21.2	17.4-22.3	17.6-19.0
	Tylopus	28.8-36.5	27.9-38.0	30.1-37.6	26.3-30.1	25.9-30.1	24.9-32.5	34.0-34.8		18.6-22.7	17.4-20.9
	Oxidus	26.9-38.3	31.1-39.9	29.7-33.2	23.3-29.0	25.5-29.5	25.3-30.7	30.7-34.1	21.2-23.5		17.3-21.5
	Pogonosternum	29.4-36.6	30.8-39.2	33.5-34.8	26.8-32.5	26.0-30.1	22.9-29.2	34.0-36.1	22.8-26.2	24.5-31.0	

Table 8.4 Ranges of intergeneric distances for 28 rRNA gene of all genera analysed in this study (genus in **Bold** = dragon millipedes)

		COI (%)									
		Dragon millipede (Orthomorphini)					Orthomorphini	Sulciferini			Antichiropodini
		Desmoxytes	***Hylomus***	***Gigaxytes***	***Nagaxytes***	***Spinaxytes***	*Orthomorpha*	*Kronopolites*	*Tylopus*	*Oxidus*	*Pogonosternum*
	Desmoxytes		2.1-2.7	2.1-3.6	3.3-4.2	2.1-3.0	4.3-7.2	-	-	-	4.5-4.9
	Hylomus			1.5-2.4	1.2-2.4	0.9-2.4	2.7-5.9	-	-	-	4.1-4.5
	Gigaxytes				3.3-5.8	1.2-2.4	3.0-4.6	-	-	-	3.7-4.5
	Nagaxytes					3.3-5.2	2.7-7.8	-	-	-	3.7-4.1
	Spinaxytes						2.7-5.9	-	-	-	4.1-4.9
	Orthomorpha							-	-	-	4.9-6.0
	Kronopolites								-	-	-
	Tylopus									-	-
	Oxidus										-
	Pogonosternum										

CHAPTER IX
Discussion and Conclusion

The taxonomy of the dragon millipedes (genus *Desmoxytes* Chamberlin, 1923, *s.l.*) in mainland Southeast Asia is now quite well known. Whereas most classical taxonomic work on dragon millipedes, was conducted in South China and Vietnam whereas, corresponding studies in Thailand, Laos, Myanmar and Malaysia were scarce, although, the spectucular "shocking pink dragon millipede" *Desmoxytes purpurosea* was described from Thailand and gained worldwide fame. In the present study, comprehensive surveys and intensive studies have been made throughout Thailand and in neighboring countries i.e. Laos, Myanmar and Malaysia. The authors came across numerous species of dragon millipedes in many parts of those countries. In addition to describing new species, all 43 previously described species have been revised, including re-study of available type specimens. Furthermore a molecular phylogenetic study, based on three gene fragments, has been conducted in order to better understand the relationships of dragon millipedes and to obtain a robust classification. No less than twenty-three new species have been discovered from limestone habitats, all are regarded to be endemic to the narrow areas that they inhabit.

Morphological re-examination of the dragon millipedes resulted in the recognition of five morphological groups which they were initially named as the *Desmoxytes*, *acantherpestes*, *gigas*, 'spiny' and *Hylomus* groups (Srisonchai *et al.*, 2018a). This classification conforms to the previous taxonomic idea proposed by Jeekel (1980a). Taxonomic survey from both morphological and molecular studies reveals either validated or synonymized several former genus/species of the dragon millipedes. In this study, the taxonomic reallocation was confirmed the possible resurrection of a synonym, genus *Hylomus*, based on potential morphological diagnosibility after type specimen re-examination and genetic investigation. Subsequently, each of these groups, except the *Hylomus* group, has been treated in detail and assigned to formal genus rank. *Desmoxytes s.l.* (i.e., *sensu* Golovatch & Enghoff 1994) has thus been split into five genera, i.e., *Desmoxytes s.s.*, *Hylomus* stat.

rev., *Gigaxytes* gen. nov., *Nagaxytes* gen. nov. and *Spinaxytes* gen. nov. All previously described species members were assigned and placed into the proper genus: 35 species previously placed in *Desmoxytes* were moved to *Nagaxytes*, *Gigaxytes* or *Hylomus*. At the species level, two synonyms were proposed: *D. pterygota* Golovatch & Enghoff, 1994 = *D. cervina*, *D. rubra* Golovatch & Enghoff, 1994 = *D. delfae*.

As a result, the total number of the dragon millipede species currently stands at 68, of which 27 species were described as new by us. Of the 27 new species, 23 were from Thailand, two from Myanmar, and two from Malaysia.

The genus *Desmoxytes s.s.* (= the *Desmoxytes* group) contains 18 species, of which 12 are new species to science:

D. aurata Srisonchai, Enghoff & Panha, 2018

D. breviverpa Srisonchai, Enghoff & Panha, 2016

D. cervina (Pocock, 1895)

D. corythosaurus Srisonchai, Enghoff & Panha, 2018

D. delfae (Jeekel, 1964)

D. des Srisonchai, Enghoff & Panha, 2016

D. euros Srisonchai, Enghoff & Panha, 2018

D. flabella Srisonchai, Enghoff & Panha, 2018

D. golovatchi Srisonchai, Enghoff & Panha, 2018

D. octoconogera Srisonchai, Enghoff & Panha, 2018

D. perakensis Srisonchai, Enghoff & Panha, 2018

D. pinnasqulai Srisonchai, Enghoff & Panha, 2016

D. planata (Pocock, 1895)

D. purpurosea Enghoff, Sutcharit & Panha, 2007

D. takensis Srisonchai, Enghoff & Panha, 2016

D. terae (Jeekel, 1964)

D. taurina (Pocock, 1895)

D. waepyanensis Srisonchai, Enghoff & Panha, 2018

The new genus *Nagaxytes* (= the '*acantherpestes*' group) contains 4 species, 3 of which are new to science:

N. acantherpestes (Golovatch & Enghoff, 1994)

N. erecta Srisonchai, Enghoff & Panha, 2018

N. gracilis Srisonchai, Enghoff & Panha, 2018

N. spatula Srisonchai, Enghoff & Panha, 2018

The new genus *Gigaxytes* (= the '*gigas*' group) contains 4 species, 3 of which are new to science:

G. fusca Srisonchai, Enghoff & Panha, 2018

G. gigas (Golovatch & Enghoff, 1994)

G. parvoterga Srisonchai, Enghoff & Panha, 2018

G. suratensis Srisonchai, Enghoff & Panha, 2018

The new genus *Spinaxytes* (= the 'spiny' group), consists of 9 species, all new to two science:

S. biloba Srisonchai, Enghoff & Panha, 2018

S. efefi Srisonchai, Enghoff & Panha, 2018

S. hasta Srisonchai, Enghoff & Panha, 2018

S. krabiensis Srisonchai, Enghoff & Panha, 2018

S. macaca Srisonchai, Enghoff & Panha, 2018

S. palmata Srisonchai, Enghoff & Panha, 2018

S. sutchariti Srisonchai, Enghoff & Panha, 2018

S. tortioverpa Srisonchai, Enghoff & Panha, 2018

S. uncus Srisonchai, Enghoff & Panha, 2018

Finally, the resurrected genus *Hylomus* stat. rev. (= the *Hylomus* group), contains 33 described species:

Hylomus asper (Attems, 1937)

Hylomus cattienensis (Nguyen, Golovatch & Anichkin, 2005)

Hylomus cervarius (Attems, 1953)

Hylomus cornutus (Zhang & Li, 1982)

Hylomus draco Cook & Loomis, 1924

Hylomus enghoffi (Nguyen, Golovatch & Anichkin, 2005)

Hylomus eupterygotus (Golovatch, Li, Liu & Geoffroy, 2012)

Hylomus getuhensis (Liu, Golovatch & Tian, 2014)

Hylomus grandis (Golovatch, VandenSpiegel & Semenyuk, 2016)

Hylomus hostilis (Golovatch & Enghoff, 1994)

Hylomus jeekeli (Golovatch & Enghoff, 1994)

Hylomus lingulata (Liu, Golovatch & Tian, 2014)

Hylomus laticollis (Liu, Golovatch & Tian, 2016)

Hylomus longispinus (Loksa, 1960)

Hylomus lui (Golovatch, Li, Liu & Geoffroy, 2012)

Hylomus minutuberculus (Zhang, 1986)

Hylomus nodulosus (Liu, Golovatch & Tian, 2014)

Hylomus parvulus (Liu, Golovatch & Tian, 2014)

Hylomus phasmoides (Liu, Golovatch & Tian, 2016)

Hylomus pilosus (Attems, 1937)

Hylomus proximus (Nguyen, Golovatch & Anichkin, 2005)

Hylomus rhinoceros (Likhitrakarn, Golovatch & Panha, 2015)

Hylomus rhinoparvus (Likhitrakarn, Golovatch & Panha, 2015)

Hylomus scolopendroides (Golovatch, Geoffroy & Mauriès, 2010)

Hylomus scutigeroides (Golovatch, Geoffroy & Mauriès, 2010)

Hylomus similis (Liu, Golovatch & Tian, 2016)

Hylomus simplex (Golovatch, VandenSpiegel & Semenyuk, 2016)

Hylomus simplipodus (Liu, Golovatch & Tian, 2016)

Hylomus specialis (Nguyen, Golovatch & Anichkin, 2005)

Hylomus spectabilis (Attems, 1937)

Hylomus spinitergus (Liu, Golovatch & Tian, 2016)

Hylomus spinissimus (Golovatch, Li, Liu & Geoffroy, 2012)

Hylomus variabilis (Liu, Golovatch & Tian, 2016)

It should be borne in mind that by far most of the species found during this study were collected in Thailand. It is believed that the number endemic dragon millipede species will increase significantly when collecting efforts in very remote or otherwise difficult-to-access places throughout SE Asia will be made.

The most diverse genus is *Hylomus*, which includes several morphological conspicuous species such as *Hylomus draco* with antlerlike paraterga, *Hylomus spinissimus* with spinelike paraterga, and *Hylomus simplex* with winglike paraterga. Several morphotypes of *Hylomus*, probably corresponding to habitat types, have been recognized (Liu *et al.*, 2014, 2016; Liu *et al.*, 2017). *Hylomus* species can be found in both limestone areas, in caves and outside caves, and even in tropical forests, and dispersed through South China, all parts of Vietnam and Laos, and some parts of Thailand. In this study all these diverse species were grouped in a single genus *Hylomus* because of gonopod similarity, although other characters, notably the paraterga, are quite diverse. This study has, however, not focused an attention on *Hylomus*, and further studies may well result in its splitting into more than one genus. Also for molecular analysis, DNA sequences from several further *Hylomus* species are required.

In contrast, paratergal morphology is similar in species within the second most diverse genus (*Desmoxytes s.s.*) and within each of the three smaller genera (*Spinaxytes*, *Nagaxytes* and *Gigaxytes*). These genera, can be clearly diagnosed by gonopods, each genus has its own, quite distinct shape. Moreover, the phylogenetic analysis strongly supports the monophyly of each of these genera.

At the species level within each genus, several morphological characters are useful for identification. As normal in millipede, the goponods provide good characters for identifying species (except in the case of two species of *Desmoxytes s.s.*: *D. euros* and *D. planata*). Other characteristics can help although they are sometimes ambiguous due either to the variation or to similarity with other species; such characters include male femur 5, sternal lobe between male coxae 4, number of setaes/tubercles/cones/spines on collum and on metaterga. Previous authors have suggested that non-gonopodal characters have potential in species identification (Golovatch *et al.*, 2012; Jeekel, 1964, 1968), however, this is not always true. For reliable taxonomic identification the combination of several characters should be considered.

The problem of species identification and generic classification relying on traditional morphological characters has become evident in several cases: *Desmoxytes philippina* Nguyen & Sierwald, 2010 was placed in genus *Desmoxytes* because of paratergal morphology, but the gonopods suggested to place it in a different genus in a different tribe (Golovatch *et al.*, 2012). The unique high degree of elevation in paraterga could thus not guarantee an accurate classification. Sometimes only a low number of specimens have been examined, leading to under-estimation of the range of the variation. For example, *D. pterygota* was described based on one male and one female. It was distinguished from *D. cervina* mainly by the sculpture on metaterga. By examining type material and newly collected the study found considerable variation among populations in this character and therefore have synonymized *D. pterygota* under *D. cervina*. Another case of a variable species concerns *D. delfae* of which it is now considered *D. rubra* to be a synonym. According to the original description of *D. rubra*, they can be discriminated from each other by the different colour. After the intensive field experience including the collecting of living specimens, this study can now state that all individuals of *delfae/rubra* displayed the same orange colour. Problems like those discussed above may be solved by means of molecular analysis. Molecular phylogenetic study is currently considered to be one of the most powerful tools for taxonomic classification and identification in several paradoxosomatid millipede genera (Decker, 2016a, 2016b; Nguyen, 2017; Nguyen *et al.*, 2017; Nguyen *et al.*, 2018a; Nguyen *et al.*, 2018b).

Previous molecular analyses of paradoxosomatids, cited above, have suggested the usefulness of DNA sequences such as DNA barcoding gene (COI) and 16S rRNA, as well as nuclear markers (28S rRNA) for obtaining reliable estimates of relationships and evolutionary history of millipedes. These three genes (COI, 16S rRNA and 28S rRNA) of many dragon millipede and several outgroup species were sequenced. Analysis (Maximum Likelihood and Bayesian Inference) of the sequences strongly support five monophyletic groups of *Desmoxytes s.l.*, corresponding to the five genera *Desmoxytes* *s.s.*, *Nagaxytes*, *Gigaxytes*, *Spinaxytes* and *Hylomus* which it is recognized on a morphological basis.

This phylogenetic study only included two species of *Hylomus*, and they are nested together. Interestingly, *Hylomus* is grouped together with an outgroup genus *Orthomorpha*. This has lead us to realize that, except for the paraterga which are not elevated and modified in *Orthomorpha*, the two genera share many characters; in particular the gonopods looks very similar in shape and structure and are quite different from those of *Desmoxytes s.s.*, *Nagaxytes*, *Gigaxytes* and *Spinaxytes*.

Within *Desmoxytes s.s.*, three clades were supported which correspond to distinctly separate distribution areas. The three subgroups can be diagnosed by different shapes of gonopod and numbers of setae/tubercles/cones/spines on metaterga. Moreover, the colour is likely to be different: the first subgroup with vivid colour as pink/red/purple; the second subgroup with orange body colour; and the third subgroup with black/brownish red/brown. *Desmoxytes s.s.* inhabits a large area from southern China, through Laos and Vietnam, and northern Thailand (one synanthropic tramp species, *D. planata,* has become widespread far beyond this area).

The phylogenetic tree suggests that dragon millipedes are paraphyletic in terms of the non-dragon genus *Orthomorpha.* This means that either the dragon millipede "habitus" has evolved independently in several lineages, or that *Orthomorpha* has secondarily lost the "dragon-ness". Multiple origins of dragon millipede-like paraterga is supported by the occurrence of similar modification in other paradoxosomatid genera, genera *Desmoxytoides*, *Euphyodesmus* and *Borneochiropus* (Attems, 1931; Golovatch, 1996; Golovatch *et al.*, 2012; Mesibov, 2006). Moreover, this character can also be found in some non-paradoxosomatid millipedes (*Tridontomus*, *Aenigmopus*) and even in fossil millipedes of the genus *Euphoberia* (Kraus, 2012). The function of the elevated paraterga is probably defensive.

Trend of distribution are conformed to the boundaries of each genus which seem to have their own ranges relative to the molecular results. All five genera are confined to mainland Southeast Asia, of which some have shown in overlapping with others especially *Desmoxytes s.s* (except the tramp species *D. planata*). This genus is dispersed from North down to South Thailand, and some part of Myanmar and

Malaysia: northern area of distribution shared with *Hylomus*, western and southern shared with *Nagaxytes*, *Gigaxyte*s and *Spinaxytes*, respectively (Fig. 8.2). *Gigaxytes* is limited to southern Myanmar and southern Thailand. *Hylomus* widely distributed across southern China, through Laos and Vietnam, to northern Thailand. *Spinaxytes* is confined to southern Myanmar, southern Thailand, and northern Malaysia. *Nagaxytes* is found only in western Thailand. All species of dragon millipedes analyzed in this study are confined to small distribution areas (except the tramp species *D. planata*). Only a few species (*D. cervina*, *D. delfae*, *N. spatula* and *G. gigas* seems to be somewhat more widely distributed, nevertheless, their distribution areas area all < 200 km^2.

All species of dragon millipedes collected during this study were found in limestone areas, especially in sites with high humidity. Of the five genera, only *Hylomus* seems to occur in both limestone area and tropical forests, while other genera are limited to limestone habitats. This is assumed that such habitats provide a favourable environment in terms of temperature, humidity, availability of organic material. However, the restriction to limestone areas has not yet been analyzed in detail. Because the vast majority of studied material was collected by ourselves, information on microhabitat is also available, and some differences between the genera were observed. Species of *Desmoxytes s.s.* and *Hylomus* seem to live in various type of microhabitats because many species have been collected from different microhabitats such as on rocks, on branch of tree, on cave wall, or even on the ground. In contrast, the other genera (*Nagaxytes*, *Gigaxytes* and *Spinaxytes*) exclusively inhabit specific microhabitats. Thus, species of *Gigaxytes* can be found on the ground, underneath leaf litter and dead leaf with which their colour blends in perfectly. *Nagaxytes* species were exclusively encountered on humid rocks. An even more specific microhabitat preference is shown by *Spinaxytes*, specimens of this genus were always found living on rock walls and/or inside small caves. In spite of their partial association with caves *Spinaxytes* species don't exhibit troglomorphic characters such as lighter pigmentation and must be regarded as trogloxenes. Several species are often found in syntopy, in some cases even at the microhabitat level. Most often syntopic species from the same habitat don't share the same microhabitat. For instance, *D. terae* and *D. delfae*, were found to coexist in the same spot, but one lived on rocks whilst the other was found on tree branches. There are a few cases of sympatric species probably sharing the same microhabitat: *D. corythosaurus* and *D. cervina* has been reported occurring together on rocks. Also *N. erecta* and *N. gracilis* were found to share the same microhabitat in syntopy (on humid rocks).

Of the 68 dragon millipede species, 67 are endemic to small areas, only one (*D. planata*) has a wide distribution. *D. planata* has been recorded in several areas in many countries (Attems, 1936; Chamberlin, 1923, 1941; Jeekel, 1980b; Mauriès, 1980a; Pocock, 1895; Ramage, 2017; Shelley and Lehtinen, 1998; Tikader and Das, 1985). It has been suggested to have been introduced to many of these places by human action (Chamberlin, 1941; Jeekel, 1980b). *D. planata* seems to be highly adaptable, because it has been collected from many different habitat types such as natural limestone areas, agricultural areas, even in modern cities. In this respect *D. planata* resembles certain other widespread, synanthropic paradoxosomatids, such as *Oxidus gracilis* (C.L. Koch, 1847) and *Asiomorpha coarctata* (DeSaussure, 1860) (Nguyen & Sierwald 2013).

In life several species exhibit vivid colours such as shocking pink, red, purple and orange (also white in an undescribed species). Most species with remarkable colours are in the genus *Desmoxytes s.s.*, some in *Hylomus*. As discussed by the authors of the most vivid pink species, the shocking pink dragon millipede, *Desmoxytes purpurosea* (Enghoff *et al.* 2007), such colours are clearly aposematic. However, species of *Gigaxytes*, *Nagaxytes* and *Spinaxytes* have more drab colours and are not aposematic. Their colours blend perfectly with background, and living specimens can hardly be seen in the field, where collectors had to use torches to find them.

During the field surveys, two types of mites were found in parasitic and phoretic associations with five dragon millipede species. Mite larvae of the genus ?*Leptus* were encountered living on *Desmoxytes cervina*, *Nagaxytes acantherpestes*, *Gigaxytes gigas* and *Spinaxytes sutchariti*. These mites infested parts of the anterior body by attaching to the metaterga. Like other *Leptus* spp. found in other arthropods, they are clearly parasite (Southcott 1992). ?*Leptus* mites was here recorded for the first time in the millipede family Paradoxosomatidae. A very different type of tiny mite was also found on *Gigaxytes fusca*, showing a very flat venter and convex dorsum, lacking mouthparts, having suckers on the ventral side and having backward-directed “knees” of leg-pairs 3 and 4. These characters perfectly match the deutonymphs (the hypopus stage) of the family Histiostomatidae (cohort Astigmatina) (Farfan and Klompen, 2012; OConnor, 2009). Histiostomatid deutonymphs are known to enter phoretic relationships with millipedes (OConnor 2009), but no case involving Polydesmida has hitherto been documented. Only one species of histiostomatid mite, *Histiostoma feroniarum* (Dufour, 1839) has been reported from a millipede of the order Julida, *Ommatoiulus moreleti* (Lucas, 1860) by Baker (1985).

A specimen of *Hylomus laticollis* from China was found to carry a phoretic fungus, probably the ‘amphoromorph’ stage of the genus *Basidiobolus* Eidam (Zygomycota, Mucoromycotina, family Basidiobolaceae). The fungus has the shape of a minute amphora with an attachment disk. Similar fungi have been reported in association with different millipedes including species of Paradoxosomatidae, genera *Eviulisoma* Silvestri, 1910 and *Boreviulisoma* Brolemann, 1928 (Enghoff 2018; Enghoff and Reboleira 2017).

Summing-up, a comprehensive integrative approach for taxonomy and systematics has revealed and extended the knowledge on species diversity of the dragon millipedes in Thailand and some neighboring countries. These discoveries of several morphologically and genetically distinct species may encourage further comprehensive study and surveys of these millipedes. Molecular phylogeny helps to reveal and understand the richness of species in relation to geological characteristics of this region.

The main aim of this study is to understand species diversity and evolutionary history, as well as to resolve systematic problems such as genus- and species-level classification. As previous suggested, the multidisciplinary approach seems to be helpful for conventional taxonomic studies as well as for ascertaining evolutionary history and the effect of geological barriers to diversification processes. Moreover, the integrative results of this study suggest that some endemic species are in an evolutionary process as indicated by their genetic affinities. An intensive survey on phylogenetic relationships involving several additional genetic markers or even at the whole genome level, as well as the integration of classical taxonomy, distributional patterns, fossil data (if available) and some fundamental biological knowledge to evaluate species delimitation, will beyond doubt shed further light on these remarkable millipedes. Given the high degree of endemism, and thus vulnerability, in almost all species of dragon millipedes, the protection of them should be a high priority. At a more general level, dragon millipedes provide a strong argument for conservation of limestone habitats in Mainland Southeast Asia.

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AWARD RECEIVED Best oral presentation in 7th conference on taxonomy and systematics in Thailand