อนุกรมวิธานและซิสเทแมติกส์ของตะขาบอันดับ Scolopendromorpha ในประเทศไทย

นายวรุฒ ศิริวุฒิ

วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรดุษฎีบัณฑิต
สาขาวิชาวิทยาศาสตร์ชีวภาพ
คณะวิทยาศาสตร์ จุฬาลงกรณ์มหาวิทยาลัย
ปีการศึกษา 2558

TAXONOMY AND SYSTEMATICS OF CENTIPEDES ORDER SCOLOPENDROMORPHA IN THAILAND

Mr. Warut Siriwut

A Dissertation Submitted in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy Program in Biological Sciences
Faculty of Science
Chulalongkorn University
Academic Year 2015

Thesis Title	TAXONOMY AND SYSTEMATICS OF CENTIPEDES ORDER SCOLOPENDROMORPHA IN THAILAND
By	Mr. Warut Siriwut
Field of Study	Biological Sciences
Thesis Advisor	Professor Somsak Panha, Ph.D.
Thesis Co-Advisor	Gregory D. Edgecombe, Ph.D.

Accepted by the Faculty of Science, Chulalongkorn University in Partial Fulfillment of the Requirements for the Doctoral Degree

....Dean of the Faculty of Science
(Associate Professor Polkit Sangvanich, Ph.D.)

THESIS COMMITTEE

....Chairman
(Noppadon Kitana, Ph.D.)
....Thesis Advisor
(Professor Somsak Panha, Ph.D.)
....Thesis Co-Advisor
(Gregory D. Edgecombe, Ph.D.)
....Examiner
(Assistant Professor Chirasak Sutcharit, Ph.D.)
....Examiner
(Assistant Professor Tosak Seelanan, Ph.D.)
....Examiner
(Assistant Professor Piyoros Tongkerd, Ph.D.)
....External Examiner
(Professor Visut Baimai, Ph.D.)

วรุฒ ศิริวุฒิ : อนุกรมวิธานและซิสเทแมติกส์ของตะขาบอันดับ Scolopendromorpha ในประเทศไทย (TAXONOMY AND SYSTEMATICS OF CENTIPEDES ORDER SCOLOPENDROMORPHA IN THAILAND) อ.ที่ปรึกษาวิทยานิพนธ์หลัก: ศ. ดร.สมศักดิ์ ปัญหา, อ.ที่ปรึกษาวิทยานิพนธ์ร่วม: ดร.เกร็กกอรี ดี เอ็ดจคอมบ์, 370 หน้า.

ได้ทำการเก็บตัวอย่างตะขาบในอันดับ Scolopendromorpha จากประเทศไทยและบางพื้นที่บนแผ่นดินใหญ่เอเชียตะวันออกเฉียงใต้ และทำการวิเคราะห์ทบทวนทางด้านอนุกรมวิธาน โดยใช้ลักษณะสัณฐานวิทยาทั่วไป ร่วมกับผลการวิเคราะห์ทางชีววิทยาโมเลกุล DNA เพื่ออธิบายสายสัมพันธ์ทางวิวัฒนาการโดยใช้ยีน 3 ตำแหน่ง คือ COI 16S และ 28S rRNA โดยพบว่า บริเวณที่ศึกษามีตะขาบทั้งสิ้น 24 สปีชีส์จาก 2 วงศ์ คือ Scolopendridae และ Cryptopidae โดยวงศ์ Scolopendridae มีสมาชิกมากที่สุดถึง 9 สกุล ได้แก่ *Scolopendra Otostigmus Rhysida Alluropus Cormocephalus Asanada Digitipes Sterropristes* และ *Ethmostigmus* โดยสกุล *Scolopendra* เป็นกลุ่มที่มีแสดงความดุร้ายมากที่สุดและจากผลการทบทวนทางอนุกรมวิธานในตะขาบ สกุลดังกล่าวนี้ พบว่า มีตะขาบในสกุล *Scolopendra* ทั้งสิ้น 9 สปีชีส์ โดย 8 สปีชีส์ ได้รับการบรรยายกำหนดชื่อไว้แล้ว และพบ 1 สปีชีส์ ที่ยืนยันว่าเป็นสปีชีส์ใหม่และได้รับการบรรยายลักษณะในการศึกษาครั้งนี้ นอกจากนี้พบว่า ตะขาบ 3 สปีชีส์ คือ *Scolopendra pinguis, S. cataracta* และ *S. dawydoffi* เป็นสปีชีส์เฉพาะถิ่นที่มีการกระจายพันธุ์ค่อนข้างแคบในพื้นที่ศึกษา และมีจำนวนประชากรค่อนข้างน้อยในพื้นที่ธรรมชาติ ในขณะเดียวกันตะขาบในสกุล *Otostigmus, Digitipes, Rhysida* และ *Alluropus* มีผันแปรในสัณฐานวิทยาและพันธุกรรมสูงมากเมื่อเทียบกับสกุลอื่นๆ และพบความสอดคล้องของความผันแปรดังกล่าวกับขอบเขตการกระจายพันธุ์ โดยเมื่อใช้เทคนิคทางด้านสัณฐานวิทยาเรขาคณิต เพื่อตรวจสอบความผันแปรของรูปร่างในลักษณะสัณฐานวิทยาภายนอก 3 ลักษณะของตะขาบในสกุล *Scolopendra* ในการจัดจำแนกและกำหนดชื่อวิทยาศาสตร์ของตะขาบอันดับนี้โดยวิธี CVA พบว่า รูปร่างของเปลือกหลังในปล้องที่ 21 เป็นลักษณะที่สามารถใช้จำแนกชนิดของตะขาบได้อย่างมีประสิทธิภาพที่สุด นอกจากนี้จากการเก็บตัวอย่างจากหลายพื้นที่ร่วมกับการถ่ายภาพในธรรมชาติ พบว่าตะขาบวงศ์นี้มีความผันแปรของสีสันลำตัวสูงมาก และพบว่า ความจำเพาะของสีสันลำตัวปรากฏเฉพาะกับประชากรในบางเขตภูมิศาสตร์ สำหรับตะขาบไม่มีตาในวงศ์ Cryptopidae พบเพียง 2 สปีชีส์ จาก 2 สกุล คือ *Cryptops* และ *Scolopocryptops* โดยตะขาบวงศ์ดังกล่าวมีประชากรหนาแน่นบริเวณพื้นที่ทางตอนเหนือของประเทศไทยและลาว

ผลการศึกษาสายสัมพันธ์ทางวิวัฒนาการเชิงโมเลกุลของตะขาบในอันดับ Scolopendromorpha พบว่า เป็นแบบสายสัมพันธ์เชิงเดี่ยว โดยวงศ์ Scolopendridae ซึ่งจำแนกเป็น 2 วงศ์ย่อย คือ Scolopendrinae และ Otostigminae มีลักษณะความสัมพันธ์เชิงวิวัฒนาการที่แตกต่างกัน โดยผลการวิเคราะห์ด้วยวิธี ML และ BI พบว่า Scolopendrinae มีความสัมพันธ์แบบสายสัมพันธ์เชิงเดี่ยว และพบว่า ในสกุล *Scolopendra* มีลักษณะทางพันธุกรรมสอดคล้องกับการแบ่งแยกทางภูมิศาสตร์ ซึ่งผลการวิเคราะห์ยังช่วยเป็นหลักฐานยืนยันความหลากสปีชีส์ และทำให้สามารถจำแนกออกได้เป็น 3 กลุ่มเขตภูมิศาสตร์ ซึ่งสอดคล้องกับการจำแนกโดยใช้ลักษณะทางสัณฐาน ในขณะที่ความสัมพันธ์ทางวิวัฒนาการของตะขาบวงศ์ย่อย Otostigminae ยังคงคลุมเครือ เนื่องจากความผันแปรของพันธุกรรมและสัณฐานวิทยาที่สูงมาก อย่างไรก็ตาม สมาชิกภายในวงศ์ย่อยดังกล่าว มีแนวโน้มความสัมพันธ์สอดคล้องกับพื้นที่และเขตการกระจายพันธุ์เช่นเดียวกัน นอกจากนี้ยังมีแนวโน้มที่จะพบ สปีชีส์ซ่อนเร้นอีก 4 สปีชีส์ ในขณะเดียวกันพบว่าลักษณะทางพันธุกรรมของตะขาบเขตอินเดีย-พม่าสกุล *Digitipes* มีความสัมพันธ์ทางวิวัฒนาการใกล้เคียงกับกลุ่มสปีชีส์ในพื้นที่ใกล้เคียง สำหรับสกุล *Rhysida* และ *Alluropus* พบว่า ลักษณะของเพศผู้ เป็นลักษณะสำคัญที่ใช้จำแนกตะขาบทั้ง 2 สกุล ซึ่งลักษณะสำคัญนี้พบในตะขาบกลุ่มอื่นๆเช่นเดียวกัน การศึกษาพฤติกรรมการเฝ้ารังและกินอาหารของตะขาบในประเทศไทยยังมีรายงานไม่มากนัก ซึ่งจากการศึกษาครั้งนี้ ได้บันทึกพฤติกรรมดังกล่าวในตะขาบหลายๆ สกุล เช่น *Otostigmus, Rhysida, Alluropus, Cormocephalus* และ *Scolopendra* ดังนั้นหากมีการประยุกต์รวมผลการศึกษาที่กล่าวมาแล้วจะทำให้ได้พัฒนาองค์ความรู้ทาง ด้านชีววิทยาของสัตว์ผู้ล่านี้ ที่จะสามารถนำไปสู่การประยุกต์ใช้ประโยชน์ต่อไปในอนาคต

สาขาวิชา	วิทยาศาสตร์ชีวภาพ	ลายมือชื่อนิสิต	....
ปีการศึกษา	2558	ลายมือชื่อ อ.ที่ปรึกษาหลัก	....
		ลายมือชื่อ อ.ที่ปรึกษาร่วม	....

5472851323 : MAJOR BIOLOGICAL SCIENCES
KEYWORDS: CENTIPEDE / TAXONOMY / SYSTEMATICS / PHYLOGENY / GEOMETRIC-MORPHOMETRIC / BEHAVIOUR / DISTRIBUTION

WARUT SIRIWUT: TAXONOMY AND SYSTEMATICS OF CENTIPEDES ORDER SCOLOPENDROMORPHA IN THAILAND. ADVISOR: PROF. SOMSAK PANHA, Ph.D., CO-ADVISOR: GREGORY D. EDGECOMBE, Ph.D., 370 pp.

Scolopendromorph centipede specimens were collected mainly in Thailand and from several other parts of mainland Southeast Asia. Taxonomic revision based on traditional morphology and molecular phylogeny from three partial gene datasets (COI, 16S rRNA and 28S rRNA) have been used to verify the taxonomic validity of this centipede group. Twenty-four described species were documented and classified into two families, Scolopendridae and Cryptopidae. Scolopendridae, the largest group, comprises nine genera: *Scolopendra*, *Otostigmus*, *Rhysida*, *Alluropus*, *Cormocephalus*, *Asanada*, *Digitipes*, *Sterropristes* and *Ethmostigmus*. The most aggressive and harmful group belong to the genus *Scolopendra*. Taxonomic revision of *Scolopendra* indicated 8 previously described and one new species from this region. *Scolopendra pinguis*, *S. cataracta* and *S. dawydoffi* were regarded as regionally endemic species according to their narrow distributions and lower population densities in natural habitats. *Otostigmus*, *Digitipes*, *Rhysida* and *Alluropus* reveal high morphological and genetic variability which is correlated with distribution patterns. Geometric-morphometric study has been implemented in *Scolopendra* to test the taxonomic potential of three traditional characters used for species identification in Scolopendromorpha. The result of shape variation tests by CVA indicated that the tergite of the ultimate leg-bearing segment is most powerful for species delimitation by this technique. Several scolopendrid species exhibit various kinds of colouration patterns, and light photographs of living specimens are used to document this morphological variability, which may be specific to geographical populations. The blind family Cryptopidae also occurs in this region, the two described species from the genera *Cryptops* and *Scolopocryptops* being found with their densest populations in the north of Thailand and Laos.

Molecular phylogeny depicted the monophyly of two families in this order. In Scolopendridae, which divides into two subfamilies, Scolopendrinae and Otostigminae, phylogenetic relationships within each subfamily show different traits. Scolopendrinae and its genera are monophyletic in both Maximum likelihood and Bayesian inference analyses. Species of the genus *Scolopendra* indicated compatibility between genetic composition and geographical distribution. Moreover, phylogenetic results also suggest evidence of transfer of regional biodiversity with neighboring faunas. Three *Scolopendra* species groups were found congruently with morphological and molecular identification. In the case of Otostigminae, relationships between genera are still ambiguous and the group depicts high morphological and genetic diversity. At least four putative morphological and molecularly distinct groupings within Otostigminae that likely represent new/cryptic species were found in this study. The genetic composition of some genera, such as the Indian-Burmese *Digitipes*, suggests that diversification within regional faunas may be shared with adjacent regions. Systematic revision of the genera *Rhysida* and *Alluropus* established the significance of male secondary characters as diagnostic characters for taxonomic identification. This morphological feature has also been recorded in other Scolopendromorpha during field surveys throughout Thailand and neighboring countries. Some information gaps in Southeast Asian centipedes such as feeding and brooding behaviours were recorded in several genera such as *Otostigmus*, *Rhysida*, *Alluropus*, *Cormocephalus* and *Scolopendra*. The integrative results from this study may improve the biological knowledge of these predatory animals in this region and may also suggest further utilization and applications in the future.

Field of Study: Biological Sciences
Academic Year: 2015

Student's Signature
Advisor's Signature
Co-Advisor's Signature

ACKNOWLEDGEMENTS

My respectful thanks are due to Prof. Dr. Somsak Panha who gave me an opportunity to enroll in a Ph.D. program at Chulalongkorn University under the Royal Golden Jubilee Ph.D. Program and also give appreciative thanks for his encouragement, challenges and all kinds of support during this study. My second appreciative thanks is to Dr. Gregory D. Edgecombe for his kind advice, suggestions and assistance during visits to the UK. Without these two mentors, I may not have successfully completed all my work, and the achievements done through my Ph.D. career should belong to them also. I sincerely thank the committee, Dr. Noppadon Kittana, Prof. Dr. Visut Baimai, Assist. Prof. Dr. Tosak Seelanan, Assist. Prof. Dr. Chirasak Sutcharit and Assist. Prof. Dr. Piyoros Tongkerd for their valuable comments and constructive suggestions that improved my study. I would like to give special thanks to Dr. Ratmanee Chanabun, Dr. Ueangfa Bantaowong, Dr. Natdanai Likhitrakarn, Dr. Piyatida Pimvichai, Dr. Ekgachai Jeratthitikul, Dr. Thanit Siriboon, Dr. Nattawadee Nantarat, Dr. Patchara Danaisawadi, Ms. Thita Krutchuen and Ms. Jaruwan Tubtimon for their true encouragement and assistance in several ways.

I would like to express my sincere thanks to all museum curators and technicians during my visits to the UK and EU, especially to Jan Beccaloni, Dr. Vladimir Blagoderov and Dr. Nesrine Akkari for their kind permission and facility support. A special thanks to Mr. Khamla Inkhavilay, Dr. Beewah Ng, Prof. Dr. Takahiro Asami,Prof. Dr. Jean-Jacques Jaeger, Dr. Yaowalak Chaimanee, Dr. John Lewis, Dr. Varpu Vahtera, Dr. Arkady Schileyko, Prof. Dr. Henrik Enghoff, and Prof. Dr. Sergei I Golovatch for their generous support, advice and constructive comments during writing.

I am also indebted to all members of Animal Systematic Research Unit and all staff members in the Department of Biology, Faculty of Science, Chulalongkorn University for their enormous assistance during field surveys and for much technical support during my study. I would like to sincerely thank the Plant Genetic Conservation Project under the Royal Initiative of Her Royal Highness Princess Maha Chakri Sirindhorn and the Royal Thai Navy for field collecting permissions and technical support during surveys in some remote areas. I would like to express my sincere thanks to the Royal Golden Jubilee Ph.D. Program, Newton Fund and British Council (Thailand) for their financial support. I also gratefully thank the Thailand Research Fund and Centre of Excellence on Biodiversity for the main financial budget during field surveys.

I express deep gratitude to my family for their support and true encouragement in all aspects of my life path and studies.

CONTENTS

Page

THAI ABSTRACT iv

ENGLISH ABSTRACT v

ACKNOWLEDGEMENTS vi

CONTENTS vii

LIST OF FIGURES 10

LIST OF TABLES 22

Chapter 1 Introduction 24

- Objectives 26
- Literature review 27

Chapter 2 A taxonomic review of the centipede genus *Scolopendra* Linnaeus, 1758 (Scolopendromorpha, Scolopendridae) in mainland Southeast Asia, with description of a new species from Laos 37

- Abstract 38
- Introduction 38
- Methodology 41
- Results 43
  - Phylogenetic relationships of mainland Southeast Asian *Scolopendra* and the position of *Scolopendra cataracta* sp. n. 43
  - Species diversity of *Scolopendra* in mainland Southeast Asia 45
  - Key to species of *Scolopendra* in mainland Southeast Asia 46
  - Systematics 47

Chapter 3 The centipede genus *Scolopendra* in mainland Southeast Asia: Molecular phylogenetics, geometric morphometrics and external morphology as tools for species delimitation 173

- Abstract 174
- Introduction 174
- Material and methods 176
- Results 183
  - Morphological identification 183

Page
Sequence annotation 183
Phylogenetic analysis 184
Geometric morphometrics 187
Discussion 191
The diversity of *Scolopendra* in mainland Southeast Asia 191
Morphological discrimination among nominal species 192
Molecular species delimitation 193
Taxonomic validity of some *Scolopendra* members in SE Asia 195
Phylogeography of *Scolopendra* in mainland SE Asia 196
Colouration patterns of *Scolopendra* 199
Taxonomic implications of shape variation 200
Conclusions 201
Chapter 4 Brooding behaviour of the centipede *Otostigmus spinosus* Porat, 1876 (Chilopoda: Scolopendromorpha: Scolopendridae) and its morphological variability in Thailand 220
Abstract 221
Introduction 221
Material and methods 223
Results 224
Description of broods and maternal care behaviour 224
Taxonomy 226
Variation and development of taxonomic characters 230
Discussion 231
Chapter 5 First record of the African-Indian centipede genus *Digitipes* Attems, 1930 (Scolopendromorpha: Otostigminae) from Myanmar, and the systematic position of a new species based on molecular phylogenetics 242
Abstract 243
Introduction 243
Material and methods 245
Results 247

Page
Systematics 247
Key to species of *Digitipes* 249
Molecular analysis 253
Discussion 254
Chapter 6 Systematic revision and phylogenetic reassessment of the centipede genera *Rhysida* Wood, 1862 and *Alluropus* Silvestri, 1912 (Chilopoda: Scolopendromorpha) in Southeast Asia, with further discussion of the subfamily Otostigminae 266
Abstract 267
Introduction 268
Material and methods 270
Results 273
Molecular phylogeny of the subfamily Otostigminae 273
Species diversity of mainland Southeast Asia Otostigminae 275
Taxonomic key to genera and species of *Rhysida* and *Alluropus* in SE-Asia . 276
Systematics 277
Discussion 297
Phylogenetic relationship of the subfamily Otostigminae 297
Phylogeny and taxonomic reassessment of *Alluropus* and *Rhysida* 301
Variation in some taxonomic characters 302
Species diversity and distribution trends of Southeast Asian Otostigminae ... 307
Chapter 7 Discussion and Conclusion 338
REFERENCES 347
VITA 370

LIST OF FIGURES

Figure 1.1 Four extant centipede orders: **A** Scutigeromorpha **B** Geophilomorpha **C** Lithobiomorpha **D** Scolopendromorpha 36

Figure 2.1 Maximum likelihood tree for *Scolopendra* in mainland Southeast Asia: colours for clades correspond to species and outgroups; black and white circles indicate statistical support values in both ML and BI analyses or only ML or BI analysis, respectively. Numbers at nodes are bootstrap support and posterior probability. Specimen codes in parentheses following localities correspond to Siriwut et al. (2015a, b: table 2) and Vahtera et al. (2013: table 1)..........................102

Figure 2.2 Colouration pattern during developmental stages of most *S. morsitans* populations in mainland Southeast Asia: **A** Juvenile stage **B** Adult stage (Colour morph 1)...103

Figure 2.3 *Scolopendra morsitans* (CUMZ 00344): **A–C** Spiracles 3, 5 and 8, respectively **D** Tooth-plates **E** Cephalic plate and trunk segments 1–2 **F** Forcipular segment **G** Tergites 9–11. 104

Figure 2.4 *Scolopendra morsitans* (CUMZ 00344, NHMUK 1889.7.15.14): **A** Sternites 9–11 **B** Coxopleura and ventral view of ultimate leg prefemora **C** Tergite of ultimate leg-bearing segment **D** Dorsal view of ultimate legs **E** Sternite of ultimate leg-bearing segment and coxopleura. 105

Figure 2.5 *Scolopendra morsitans* (CUMZ 00300, 00344): **A** Cephalic plate and basal antennal articles **B** Tergites 9–11 **C** Teeth on tooth-plates and trochanteroprefemoral process **D** Forcipular segment **E** Sternites 9–11. 106

Figure 2.6 *Scolopendra morsitans* (CUMZ 00300, 00344): **A** Tergite of ultimate leg-bearing segment **B** Lateral view of coxopleuron **C** Sternite of ultimate leg-bearing segment, coxopleura and ultimate legs **D** Spines on prefemoral process of ultimate leg **E–F** Spines on ultimate leg prefemora and margination on prefemora and femora (dorsal view). 107

Figure 2.7 Genital segments in some live Scolopendra specimens:**A** *Scolopendra dehaani* (male) **B** *Scolopendra dawydoffi* (male) **C** *Scolopendra morsitans* (male) **D** *Scolopendra japonica* (female) **E** *Scolopendra pinguis* (male) **F** *Scolopendra pinguis* (female). 108

Figure 2.8 Distribution map of *Scolopendra morsitans* in Southeast Asia: Filled triangles indicate data from material examined herein; blank triangles indicate localities in the literature (Shelley et al. 2005, Schileyko 2007). 109

Figure 2.9 Habitus photographs of *Scolopendra* species: **A** *Scolopendra subspinipes* (Singapore, CUMZ 00315) **B** *Scolopendra calcarata* (Thailand, CUMZ 00418) **C** *Scolopendra japonica* (Colour morph 2: Laos, CUMZ 00298). ... 110

Figure 2.10 *Scolopendra subspinipes* (NHMUK): **A** Cephalic plate and trunk segments 1–2 **B** Tergites 9–12 **C** Forcipular segment **D** Tooth-plates **E–G** Spiracles 3, 5 and 8, respectively. ... 111

Figure 2.11 *Scolopendra subspinipes* (NHMUK): **A** Sternites 8–11 **B** Sternite of ultimate leg-bearing segment and coxopleura **C** Lateral view of coxopleuron **D** Ventral view of ultimate leg-bearing segment and ultimate leg prefemora **E** Dorsal view of ultimate leg-bearing segment and prefemora. ... 112

Figure 2.12 *Scolopendra subspinipes* (Syntype NHMW 751 of *S. mutilans* Koch, 1878): **A** Tooth-plates **B** Cephalic plate and trunk segments 1–2 **C** Forcipular segment **D** Tergites 9–11 **E–G** Spiracles 3, 5 and 8, respectively. ... 113

Figure 2.13 *Scolopendra subspinipes* (Syntype NHMW 751 of *S. mutilans* Koch, 1878): **A** Sternite of ultimate leg-bearing segment and coxopleura **B** Sternites 10–12 **C** Sternite of ultimate leg-bearing segment, coxopleura and ventral view of ultimate leg prefemur **D** Tergite of ultimate leg-bearing segment **E** Ventral view of ultimate leg prefemur **F** Dorsal view of ultimate leg prefemur **G** Ventrolateral view of ultimate leg. ... 114

Figure 2.14 *Scolopendra subspinipes* (Syntypes NMB 391Va of "*piceoflava* Attems, 1934"): **A** Tooth-plates **B** Cephalic plate and trunk segments 1–3 **C** Forcipular segment **D** Tergites 9–12 **E** Sternites 8–10. ... 115

Figure 2.15 *Scolopendra subspinipes* (Syntypes NMB 391Va of "*piceoflava* Attems, 1934"): **A** Lateral view of coxopleuron **B** Tergite of ultimate leg-bearing segment and dorsal view of legs 20 and ultimate leg **C** Ventral view of Leg 20, coxopleura and ultimate leg **D** Sternite of ultimate leg-bearing segment, coxopleura and ultimate leg **E–F** Ventrolateral view of ultimate legs. ... 116

Figure 2.16 *Scolopendra subspinipes* (CUMZ 00315): **A** Cephalic plate and basal antennal articles **B** Tooth-plates and trochanteroprefemoral process **C** Tergites 9–11 **D** Forcipular segment. ... 117

Figure 2.17 *Scolopendra subspinipes* (CUMZ 00315): **A** Sternites 9–11 **B** Lateral view of coxopleuron **C** Tergite of ultimate leg-bearing segment **D** Sternite of ultimate leg-bearing segment, coxopleura, female genital segment and ultimate leg prefemora **E** Dorsal view of ultimate leg prefemora. ... 118

Figure 2.18 Distribution map of *Scolopendra dehaani* and *Scolopendra subspinipes* in Southeast Asia and China-Japan Sea (small map): Filled and blank colours refer to localities from the present study and in the literature, respectively. 119

Figure 2.19 Colouration changes and patterns during developmental stages of *Scolopendra dehaani*: **A** Juvenile stage **B** Subadult stage **C** Adult stage (specimen from northern Thailand)..120

Figure 2.20 Brooding and feeding behaviours: **A** *Scolopendra dehaani* exhibiting simple coiling with cluster of embryonic stadia (photograph by Natdanai Likhitrakarn) **B** *Scolopendra morsitans* exhibiting double coiling with postembryonic stadia **C–D** *Scolopendra dehaani* preying on snail eating snake *Pareas carinatus* **D** Flexibility of trunk segments during predation. 121

Figure 2.21 *Scolopendra dehaani* (CUMZ 00282): **A** Cephalic plate and trunk segments 1–2 **B** Tooth-plates **C** Forcipular segment **D–E** Spiracles 3, 5 and 8, respectively. 122

Figure 2.22 *Scolopendra dehaani* (CUMZ 00268 and 00282): **A** Tergites 10–11 **B** Sternites 10–11 **C** Lateral view of coxopleuron **D** Sternite of ultimate leg-bearing segment and coxopleura **E** Tergite of ultimate leg-bearing segment **F–G** ventral and dorsal view of ultimate leg prefemora. 123

Figure 2.23 *Scolopendra dehaani* (CUMZ 00365): **A** Forcipular segment **B** Tergites 9 and 10 **C–D** Variation in teeth on tooth-plates **E** Tergite of ultimate leg-bearing segment **F** Sternites 9 and 10. 124

Figure 2.24 *Scolopendra dehaani* (CUMZ 00365): **A** Sternites 9–11 **B–C** Spines on ultimate leg prefemora (dorsal and ventral views, respectively) **D** Tergite 9–11 **E** Lateral view of coxopleuron. 125

Figure 2.25 Genital segment(s) in some preserved *Scolopendra* specimens: **A** *Scolopendra dehaani* (male) **B** *Scolopendra calcarata* (female) **C** *Scolopendra pinguis* (male) **D** *Scolopendra morsitans* (male). 126

Figure 2.26 *Scolopendra multidens* (Holotype NHMUK): **A** Cephalic plate and trunk segments 1–3 **B** Sternites 9–11 **C** Forcipular segment **D–E** Spiracles 3 and 5, respectively. 127

Figure 2.27 *Scolopendra multidens* (Holotype NHMUK): **A** Tergites 9–10 **B** Sternite of ultimate leg-bearing segment, coxopleura, legs 20 and ventral view of ultimate legs **C** Tergite of ultimate leg-bearing segment and dorsal view of leg 20 and ultimate legs **D** Lateral view of ultimate leg and legs 20. 128

Figure 2.28 Genital segment(s) of **A–B** *Scolopendra multidens* (male; lateral and ventral views, respectively) **C–D** *Scolopendra cataracta* (female; lateral and ventral views, respectively). 129

Figure 2.29 Distribution map of six *Scolopendra* species in Southeast Asia and China-Japan Sea (small map): Filled and blank colours refer to localities from the present study and in the literature, respectively. 130

Figure 2.30 *Scolopendra calcarata* (CUMZ 00418): **A** Tooth-plates **B** Cephalic plate and trunk segments 1–3 **C** Forcipular segment **D–F** Spiracles 3, 5 and 8, respectively. 131

Figure 2.31 *Scolopendra calcarata* (CUMZ 00418): **A** Tergites 8–12 **B** Sternite of ultimate leg-bearing segment and coxopleura **C** Tergite of ultimate leg-bearing segment **D** Sternites 10–12 **E–F** Dorsal and ventral views of ultimate leg prefemora. 132

Figure 2.32 *Scolopendra calcarata* (Holotype NHRS–KASI 000000042): **A** Cephalic plate and trunk segments 1–5 **B** Tergites 8–11 **C** Tooth-plates **D** Forcipular segment **E–F** Spiracles 3 and 5, respectively. 133

Figure 2.33 *Scolopendra calcarata* (Holotype NHRS–KASI 000000042): **A** Sternites 10–12 **B** Sternite of ultimate leg-bearing segment, coxopleura and ventral view of ultimate legs **C** Tergite of ultimate leg-bearing segment and dorsal view of legs 20 and ultimate legs. 134

Figure 2.34 *Scolopendra calcarata* (CUMZ 00418): **A–B** Variation of teeth on tooth-plates **C** Cephalic plate and basal antennal articles **D** Tergites 9–11 **E** Forcipular segment. 135

Figure 2.35 *Scolopendra calcarata* (CUMZ 00418): **A** Sternites 9–11 **B–C** Dorsal and ventral views, respectively, of ultimate leg prefemora **D** Sternite of ultimate leg-bearing segment and coxopleura **E** Tergite of ultimate leg-bearing segment. 136

Figure 2.36 *Scolopendra japonica* (CUMZ 00297, 00298): **A** Cephalic plate and trunk segments 1–3 **B** Tooth-plates **C** Forcipular segment **D–F** Spiracles 3, 5 and 8, respectively. 137

Figure 2.37 *Scolopendra japonica* (CUMZ 00297, 00298): **A** Tergites 9–11 **B** Sternites 9–11 **C** Sternite of ultimate leg-bearing segment and coxopleura **D** Tergite of ultimate leg-bearing segment **E** and **F** Variation in ventral spines on ultimate leg prefemora **G** Dorsal view of ultimate legs. 138

Figure 2.38 *Scolopendra japonica* (Syntype NHMW 5368): **A** Cephalic plate and trunk segments 1–3 **B** Tooth-plates **C** Forcipular segment **D–F** Spiracles 3, 5 and 8, respectively **G** Sternites 9–11**H** Tergites 8–11. 139

Figure 2.39 *Scolopendra japonica* (Syntype NHMW 5368): **A** Sternite of ultimate leg-bearing segment and coxopleura **B** Tergite of ultimate leg-bearing segment **C–D** Ventral and dorsal views of ultimate leg prefemora **E–F** Variation in ventral spines of ultimate leg prefemora. 140

Figure 2.40 *Scolopendra japonica* (CUMZ 00297): **A** Cephalic plate and basal antennal articles **B** Tergites 9–11 **C** Forcipular segment **D–E** Variation in teeth on tooth-plates and trochanteroprefemural process. 141

Figure 2.41 *Scolopendra japonica* (CUMZ 00297, 00298): **A** Sternites 9–11 **B** Dorsal view of ultimate leg prefemora **C** Tergite of ultimate leg-bearing segment **D** Sternite of ultimate leg-bearing segment, coxopleura and ultimate legs. 142

Figure 2.42 Habitus photographs of *Scolopendra* species: **A** *Scolopendra pinguis* (Colour morph 1A: CUMZ 00309) **B** *Scolopendra pinguis* (Colour morph 2B) **C** *Scolopendra dawydoffi* (CUMZ 00272). 143

Figure 2.43 *Scolopendra pinguis* (CUMZ 00306, 00314): **A** Cephalic plate and trunk segments 1–3 (Colour morph 2) **B** Tergites 9–11 **C** Tooth-plates **D–F** Spiracles 3, 5 and 8, respectively. 144

Figure 2.44 *Scolopendra pinguis* (CUMZ 00306, 00314): **A** Cephalic plate and trunk segments 1–3 (Colour morph 1) **B** Forcipular coxosternite (Colour morph 1A and 1B) **C** Sternites 9–12 **D** Forcipular coxosternite (Colour morph 2) 145

Figure 2.45 *Scolopendra pinguis* (CUMZ 00306, 00314): **A** Sternites 9–11 (Colour morph 2) **B** Tergite of ultimate leg-bearing segment **C** Lateral view of coxopleuron **D–E** Sternite of ultimate leg-bearing segment and coxopleura in male and female, respectively **F–G** Dorsal and ventral views, respectively, of ultimate leg prefemora. 146

Figure 2.46 *Scolopendra pinguis* (CUMZ 00306, 00314): **A** Cephalic plate and basal antennal articles **B** Forcipular segment **C** Tergites 9–11 **D** Teeth on tooth-plates and trochanteroprefemoral process **E** Tergite of ultimate leg-bearing segment. 147

Figure 2.47 *Scolopendra pinguis* (CUMZ 00306, 00314): **A** Sternites 9–11 **B** Dorsal view of ultimate leg prefemora **C** Lateral view of coxopleuron **D** Sternite of ultimate leg-bearing segment, coxopleura and ultimate legs. 148

Figure 2.48 *Scolopendra dawydoffi* (CUMZ 00290, 00291): **A** Tooth-plates **B** Forcipular segment **C** Cephalic plate and trunk segments 1–3 **D** Sternites 9–11 **E–G** Spiracles 3, 5 and 8, respectively. 149

Figure 2.49 *Scolopendra dawydoffi* (CUMZ 00290, 00291, 00272): **A** Tergites 9–11 **B** Tergite of ultimate leg-bearing segment **C** Lateral view of coxopleuron, leg

20 and ultimate leg **D** Sternite of ultimate leg-bearing segment and coxopleura **E** and **F** Variation in ventral spines on ultimate leg prefemora **G** Dorsal view of ultimate leg prefemora. 150

Figure 2.50 *Scolopendra dawydoffi* (Syntypes NHMW 8234): **A** Cephalic plate and trunk segments 1–3 **B** Tergites 9–11 **C** Tooth-plates **D** Forcipular segment **E–G** Spiracles 3, 5 and 8, respectively. 151

Figure 2.51 *Scolopendra dawydoffi* (Syntypes NHMW 8234): **A** Sternites 9–11 **B** Sternite of ultimate leg-bearing segment and coxopleura **C** Tergite of ultimate leg-bearing segment **D** Lateral view of coxopleuron **E–F** Dorsal and ventral view of ultimate leg prefemora. 152

Figure 2.52 *Scolopendra dawydoffi* (CUMZ 00272): **A** Cephalic plate and basal antennal articles **B** Forcipular segment **C** Tergites 9–11 **D–F** Variation in teeth on tooth-plates and trochanteroprefemoral process. 153

Figure 2.53 *Scolopendra dawydoffi* (CUMZ 00272): **A** Sternites 9–11 **B–C** Variation in numbers of spines on prefemural process of ultimate leg **D** Sternite of ultimate leg-bearing segment, coxopleura and ultimate legs, showing lack of ventral and median spines on prefemora **E** Tergite of ultimate leg-bearing segment **F** Lateral view of coxopleuron. 154

Figure 2.54 *Scolopendra cataracta* sp. n.: **A** Habitus photograph of holotype CUMZ 00316 **B** Habitat at type locality **C** Genital region; GS – Genital segment...155

Figure 2.55 *Scolopendra cataracta* sp. n.: **A–B** Tooth-plates **C** Cephalic plate and trunk segments 1–3 **D** Forcipular segment **E** Sternites 9–11 and **F–H** Spiracles 3, 5 and 8, respectively. Holotype CUMZ 00316 (**A,C–H**) and paratype CUMZ 00317 (**B**). 156

Figure 2.56 *Scolopendra cataracta* sp. n.: **A** Tergites 9–11 **B** Tergite of ultimate leg-bearing segment **C–D** Sternite of ultimate leg-bearing segment and coxopleura **E–H** Variation in ventral spines on ultimate leg prefemora **F** Lateral view of coxopleuron **G** Dorsal view of ultimate legs. Holotype CUMZ 00316 (**A, B, D, G** and **H**) and paratype CUMZ 00317 (**C, E** and **F**). 157

Figure 2.57 *Scolopendra cataracta* sp. n. (Holotype: CUMZ 00316): **A** Cephalic plate and basal antennal articles **B** Tergites 9–11 **C** Tooth-plates and trochanteroprefemoral process **D** Forcipular segment **E** Sternites 9–11. 158

Figure 2.58 *Scolopendra cataracta* sp. n.: **A** Lateral view of coxopleuron **B** Tergite of ultimate leg-bearing segment **C** Sternite of ultimate leg-bearing segment, coxopleura and ultimate leg prefemora. **D** Asymmetry of spines on coxopleural process **E** Dorsal view of ultimate leg prefemora. Holotype CUMZ 00316 (**B–C, E**) and paratype CUMZ 00317 (**A, D**). 159

Figure 3.1 Phylogenetic tree of *Scolopendra* mainland Southeast Asia. Relationships among *Scolopendra* and two outgroups indicated similarly both in Maximum likelihood (ML) and Bayesian inference (BI) of the concatenated COI, 16S and COI partial gene analyses. Significant support values in ML and BI are indicated by three colouration circles; black circle = support both in ML and BI (above 70% bootstrap in ML and 0.95 posterior probability in BI), white circle = support only in ML, grey circle = support only in BI. The gradient colouration bars on the tree represent the genetic affinities of populations relative to morphological identification in each species. 204

Figure 3.2 Phylogenetic relationship of *S. dehaani* population (left) based on genetic structure among its populations relative to regional distribution in mainland Southeast Asia (middle); colours indicate the major populations. Five patterns of live colour morphs in *S. dehaani* were found (right); **A.** Dark colour morph; **B.** Light brownish colour morph; **C.** Reddish-brown body color morph, yellowish legs with reddish on distal part; **D.** Dichromatic pattern; cephalic plate, tergite 1, 20 and 21 reddish, tergites 2–19 brownish with yellowish legs; **E.** Reddish colour morph with dark band on anterior and posterior parts of tergites. ... 205

Figure 3.3 Phylogenetic tree of *S. morsitans*. Colour gradient indicates population structure; blue gradient indicates the northern population, yellow gradient the eastern population. *Scolopendra morsitans* exhibited two colour morphs: **colour morph 1**—antenna, cephalic plate, tergites 1, 20 and 21 and ultimate legs orange; **colour morph 2**—antenna, cephalic plate, tergites 1, 20 and 21 and ultimate legs blackish. 206

Figure 3.4 Phylogenetic tree of *S. pinguis* based on genetic structure of its populations. Colour gradient bar indicates colour morphs of sampled individuals that divide into two patterns; **colour morph 1**—blackish population (monochromatic); **colour morph 2**- yellowish—black population (dichromatic). Four live colour morph pictures depict the variability of colouration on legs of the two colour morphs in *S. pinguis*; colour morph **1A** and **2A**—animal with dark blue legs, colour morph **2A** and **2B**—animal with yellowish legs with blue stripes on distal part. 207

Figure 3.5 Phylogenetic tree of *S. dawydoffi* and *S. japonica*. **Clade A**, *S. dawydoffi*, **clade B**, *S. japonica*. In *S. japonica*, colour gradients indicate the colour morph of sampled individuals; colour morph 1—greenish body with reddish antenna, cephalic plate and legs; colour morph 2—greenish body with blue antenna, yellowish cephalic plate and legs. 208

Figure 3.6 Diagram of landmark locations on three constant characters and the CV plot of individual scores on each CV axis from canonical variates analysis (CVA). **A.** Cephalic plate; **B.** Forcipular coxosternite; **C.** Tergite 21. The CV plots represent the discrimination of classified individuals scored from CV axis comparison, showing comparisons of CV1 and CV2 axes (middle column) and CV2 and CV3 axes (right column). 209

Figure 3.7 Wireframe diagram from continuous linkage of all landmark positions in three features derived from CVA scores on three axes. CV1, CV2 and CV3 arranged vertically, respectively. In the wireframes, dotted lines represent shape changes relative to CV score moving from both negative and positive directions, solid lines represent the shape consensus in negative and positive groups. 210

Figure 3.8 Phylogenetic tree based on concatenation of three partial gene analysis. Support values of bootstrap and posterior probability were given at each node. 211

Figure 4.1 Distribution of *Otostigmus spinosus* Porat, 1876 in southern Thailand. .234

Figure 4.2 Six broods of *Otostigmus spinosus*: **A**, Brood sample from local resort near Khao Sok National Park, Surat Thani province; **B**, Brood sample from Wat Tham Wararam, Surat Thani province; **C–F**, Brood samples from Wat Tham Phung Chang, Phang-nga province. 235

Figure 4.3 Brooding behaviour of *Otostigmus spinosus*. **A–C**, Orientation of mother with cluster of hatchlings; **A**, Simple loop; **B**, Falcate coiling; **C**, S-shape posture; **D**, Forcipules being used by mother to catch 2nd adolescent stage hatchlings; **E**, Mother moving and carrying cluster of 2nd adolescent stage hatchlings under her body; **F**, Mother exhibiting filial cannibalism of 1st embryonic stage. 236

Figure 4.4 Schematic of brooding behaviour of *Otostigmus spinosus*. 237

Figure 4.5 *Otostigmus spinosus* Porat, 1876. Light photographs of specimens from southern Thailand (Fig. A–E; specimens from Surin Islands, Phang-nga province: CUMZ 00231; Fig. I–N; specimens from Wat Tham Wararam, Surat Thani province: CUMZ 00224). **A**, Cephalic plate and T1 with first pair of locomotory legs; **B**, Forcipular segment; **C**, Antenna with cephalic plate and TT1–5; **D**, Tergites 9–10; **E**, Sternites 9–10; **F–H**. Spiracles on segments 3, 5 and 8, respectively; **I**, Tergite and sternite of ultimate-leg bearing segment; **J**, Pore field on left and right coxopleura; **K**, Dorsal view of ultimate leg prefemur; **L**, Ventral view of ultimate leg prefemur; **M–N**, Leg 20 left and right with spine on distal part of prefemora..238

Figure 4.6 Variability in taxonomic characters in *Otostigmus spinosus* Porat, 1876 (examination materials: CUMZ 00224, Wat Tham Wararam, Phanom district, Surat Thani; CUMZ 00229, Tham Wang Thong, Phatthalung; CUMZ 00231, Surin Islands, Phang-nga). **A**, Ventral view of cephalic plate and antenna; **B**, Dorsal view of cephalic plate and antenna; **C**, Coxosternite; **D–F**, Variation in coxosternal teeth; **G**, Surface of TT5–7; **H**, Variability of depressions on surface of sternites 5–7; **I**, Leg 20 with projection on distal end of tarsus 1; **J**, Leg 21 with projection on tarsus 1; **K**, Ultimate leg-bearing segment, ventral view, with arrangement of ventral spines on prefemur of ultimate legs; **L**, Tergite of ultimate leg-bearing segment with arrangement of dorsal and corner spines on prefemur of ultimate legs; **M**, Pore field on coxopleuron (left). 239

Figure 5.1 Collecting area of *Digitipes kalewaensis* n. sp.; A. Location of collection area in Myanmar. B. Collecting locality (expanded magnification). C. Habitat type. 257

Figure 5.2 Morphological characters of *Digitipes kalewaensis* n. sp.; **A.** Forcipular coxosternite (Paratype; CUMZ 00234). **B-C.** Tergites and sternites 9–11 (Paratype; CUMZ 00241). **D**. Antenna, cephalic plate and T1 (Holotype). **E-G.** Spiracles 3, 5 and 8, respectively (Holotype). **H, J.** Ultimate legs (Paratypes; CUMZ 00234-00235). I. Projection on femur of ultimate leg in male (Holotype). **K.** Pore-field of coxopleuron (left and right; Paratype; CUMZ 00235). **L-M.** Ventral and dorsal view of ultimate leg-bearing segment (Paratype; CUMZ 00234). 258

Figure 5.3 Drawings depicting variation in some morphological characters; **A.** Cephalic plate and T1 (Holotype). **B.** Forcipular segment (Holotype). **C.** Tooth-plate with five teeth on right side (Paratype; CUMZ 00234). **D.** Articles 1–3 of telopodite of second maxilla (Paratype; CUMZ 00241). **E.** Tergites 9–11 (Holotype). **F.** Sternite 10 (Paratype; CUMZ 00240). **G.** Coxopleural pore area (Holotype). **H.** Sternite of ultimate leg-bearing segment with ultimate legs (Holotype; ventral view). **I.** Left ultimate leg (Paratype; CUMZ 00234). 259

Figure 5.4 Maximum likelihood consensus tree based on combined COI and 16S sequences. Numbers at nodes are bootstrap support in maximum likelihood (ML) and posterior probabilities in Bayesian inference (BI). Black circles refer to nodes supported from both ML and BI; grey circle refers to a node supported only by ML...260

Figure 6.1 Phylogenetic tree for the subfamily Otostigminae obtained from Bayesian inference; black circles indicate node support (>0.95 posterior probability)**.**..309

Figure 6.2 Maximum likelihood tree for the subfamily Otostigminae obtained from RAxML using GTR+CAT model; black circles indicate node support (>70% bootstrap value)..310

Figure 6.3 Holotype of *Rhysida lithobioides* (Newport, 1845): **A** Cephalic plate and tergites1-4 **B** Forcipular segment and sternites 1-4 **C** Tergites 8-13 **D** Forcipular segment **E** Sternite of ultimate leg-bearing segment, legs 20 and ultimate legs **F** Sternites 8-13 **G** Tergite of ultimate leg-bearing segment **H** Tergite of ultimate leg-bearing segment, legs 20 and ultimate legs **I** Spiracle 3 **J** Sternite of ultimate leg-bearing segment and coxopleura...311

Figure 6.4 Holotype of *Rhysida leviventer* Attems, 1953: **A** Cephalic plate and tergites1-4 **B** Forcipular segment and leg 1 **C** Ventral view of ultimate leg prefemora **D** Tergites 9-13 **E** Tooth-plates **F** Sternite of ultimate leg-bearing segment and coxopleura **G** Dorsal view of ultimate leg prefemora **H** Sternites 9-11 **I** Tergite of ultimate leg-bearing segment **J-L** Spiracles 3, 5 and 7-8.................312

Figure 6.5 Live habitus specimens of some *Rhysida* species in mainland Southeast Asia: **A** *Rhysida immarginata* (Porat, 1876) **B** *Rhysida longipes* (Newport, 1845) **C** *Rhysida singaporensis* Verhoeff, 1937. 313

Figure 6.6 Morphological characters of *Rhysida longipes* (Newport, 1845): **A** Cephalic plate and tergites 1-3 **B** Forcipular segment, sternites 1-2 and legs 1-2 **C** Sternite of ultimate leg-bearing segment, coxopleura, ultimate leg prefemora and legs 19-20 **D** Sternites 9-12 **E** Tergites 9-11 **F** Tergite of ultimate leg-bearing segment and ultimate leg prefemora **G** Coxopleuron **H-J** Spiracles 3, 5 and 7-8.....314

Figure 6.7 Morphological variation of *Rhysida longipes* (Newport, 1845): **A** Cephalic plate and glabrous antennal articles **B-C** Variation in teeth on tooth-plates **D** Tergites 9-11 **E** Sternite of ultimate leg-bearing segment, coxopleura and ultimate legs **F** Forcipular segment **G** Sternites 9-11 **H** Spines on distal part of coxopleural process **I** Tergite of ultimate leg-bearing segment **J** Coxopleuron........315

Figure 6.8 Syntype 1 of *Rhysida immarginata* (Porat, 1876): **A** Forcipular segment **B** Tergites 9-12 **C** Sternites 11-13 **D** Cephalic plate, antenna and tergites 1-3 **E-F** Tergite and sternite of ultimate leg-bearing segment **G-I** Spiracles 3, 5, 7 and 8...316

Figure 6.9 Syntype 2 and ultimate legs (loose in tube) of *Rhysida immarginata* (Porat, 1876): **A** Cephalic plate, antenna and tergites 1-3 **B** Forcipular segment, sternites 1-2 and legs 1-2 **C** Tergites 9-12 **D** Sternites 10-13 **E** Sternite 20, sternite of ultimate leg-bearing segment and coxopleura **F** Tergites 18-20 and tergite of ultimate leg-bearing segment and legs 19 **G** Coxopleuron and segments 19-20 **H-I** Ultimate legs **J-L** Spiracles 3, 5 and 7-8. 317

Figure 6.10 Morphological variation of *Rhysida immarginata* (Porat, 1876): **A** Forcipular segment **B** Cephalic plate and glabrous antennal articles **C-D** Variation in teeth on tooth-plates **E** Coxopleuron **F** Sternite of ultimate leg-bearing segment, coxopleura and ultimate legs **G** Tergites and sternites 9-11 **I** Tergite of ultimate leg-bearing segment **J** Sternite of ultimate leg-bearing segment and coxopleura. 318

Figure 6.11 Morphological characters of *Rhysida singaporensis* Verhoeff, 1937 (topotypes): **A** Tooth-plates **B** Cephalic plate, antenna and tergites 1-5 **C** Forcipular segment, sternites and legs 1 **D-E** Sternite and tergite of ultimate leg-bearing segment **F-G** Tergites and sternites 10-13 **H-I** Ventral and dorsal views of ultimate leg prefemora. 319

Figure 6.12 Morphological variation of *Rhysida singaporensis* Verhoeff, 1937 (topotypes): **A** Cephalic plate and glabrous antennal articles **B** Tooth-plates **C-D** Tergites and sternite 9-11 **E** Coxopleuron **F** Sternite of ultimate leg-bearing segment **G** Sternite of ultimate leg-bearing segment, coxopleura and ultimate legs **H** Lateral view of right ultimate leg. 320

Figure 6.13 Holotype of *Rhysida marginata* Attems, 1953: **A** Tooth-plates **B** Sternites 9-11 **C** Cephalic plate, antenna, tergites1-3 and legs 2 **D** Forcipular segment **E** Tergites 9-11 **F** Ventral view of ultimate leg prefemora **G** Sternite of ultimate leg-bearing segment and coxopleura **H** Coxopleuron **I-K** Spiracles 3, 5 and 7-8 **L** Tergite of ultimate leg-bearing segment and ultimate leg prefemora. 321

Figure 6.14 Live habitus specimens of *Alluropus calcarata* (Pocock, 1891); **A** Adult male (morphotype 1) **B** Adult female (morphotype 1) **C** lateral view of ultimate legs displaying male secondary sexual characters **D** Female coiling with brood. 322

Figure 6.15 Syntypes specimens of *A. calcarata* “*Alluropus demangei* Silvestri, 1912”: **A** Cephalic plate, antenna and tergites 1-3 **B** Forcipular segment and sternites 1-5 **C-D** Sternites and tergites 9-11 **E** Forcipular segment and sternites 1-2 **F** Sternite of ultimate leg-bearing segment and coxopleura **G** Tergite of ultimate leg-bearing segment **H** Ultimate leg **I** Lateral view of legs 20 and ultimate legs **J** Coxopleuron. 323

Figure 6.16 Morphological variation in morphotype 1 of *Alluropus calcarata* (Pocock, 1891); **A** Tooth-plates **B** Forcipular segment **C** Tergites 9-11 **D** Cephalic plate and glabrous antennal articles **E** Spines on coxopleural process **F** Sternite of ultimate leg-bearing segment, coxopleura and ultimate legs **G** Lateral view of ultimate leg (female) **H** Sternites 9-11 **I** Tergite of ultimate leg-bearing segment **J** Spines on prefemoral process on ultimate legs **K** Pretarsus with two accessory spurs **L** Coxopleuron. 324

Figure 6.17 Syntype specimen 1 of *Alluropus calcarata* (Pocock, 1891) [previously designated type of *R. calcarata*]: **A** Cephalic plate **B** Forcipular segment **C** Sternite 20 and sternite of ultimate leg-bearing segment **D-E** Tergites and sternites 8-10 **G** Coxopleuron. 325

Figure 6.18 Syntype specimen 2 of *Alluropus calcarata* (Pocock, 1891) [previously designated type of *R. calcarata*]; **A** Forcipular segment **B** Sternites 7-8 **C** Cephalic plate and left antenna **D** Sternites 7-9 **E** Sternite of ultimate leg-bearing segment, coxopleuron and female genital segments **F** Tergite 20 and tergite of ultimate leg-bearing segment. 326

Figure 6.19 Syntype specimen 3 of *Alluropus calcarata* (Pocock, 1891) [previously designated type of *R. calcarata*]: **A** Forcipular segment, sternite 1 and legs 1-2 **B** Cephalic plate, antenna and legs 1-3 **C** Sternites and tergites 8-10 **E** Tergite 20 and tergite of ultimate leg-bearing segment **F** Sternite 20 and sternite of ultimate leg-bearing segment. 327

Figure 6.20 Morphological characters of morphotype 2 in *Alluropus calcarata* (Pocock, 1891): **A** Cephalic plate, antenna and legs 1-2 **B** Coxopleuron **C** Cephalic plate and antenna **D** Tergites 9-12 **E** Tergite 20 and tergite of ultimate leg-bearing segment **F** Forcipular segment, sternites 1-2 and legs 1-3 **G** Tergite of ultimate leg-bearing segment **H** Sternites 7-10 **I** Tergite 20 and tergite of ultimate leg-bearing segment **J-L** Spiracles 3, 5 and 7-8. 328

Figure 6.21 Morphological variation in morphotype 2 of *Alluropus calcarata* (Pocock, 1891): **A** Tooth-plate **B** Cephalic plate and glabrous antennal articles **C-D** Tergites and sternites 9-12 **E** Forcipular segment **F** Coxopleuron **G** Sternite of ultimate leg-bearing segment, coxopleura and ultimate leg prefemora **H** Tergite of ultimate leg-bearing segment and ultimate leg prefemora..329

Figure 6.22 Distribution record of some *Rhyida* and *Alluropus calcarata* based on data from previous literatures and present study. 330

LIST OF TABLES

Table 2.1 *Scolopendra* sequences used in phylogenetic reconstruction of present study. The abbreviation name of voucher ID code refer to museum collection as follow; AMNH-American Museum of Natural History, CUMZ-Chulalongkorn University Museum of Zoology, MCZ-Museum of Comparative Zoology, Harvard University, NHMUK-Natural History Museum, London, UK. 160

Table 2.2 Sequence annotation of three partial genes used in this present study 163

Table 2.3 Genetic distance between *Scolopendra* species in mainland of Southeast Asia and outgroups; upper right and lower left distance collected from COI and 16S partial gene pair-wise comparisons 164

Table 2.4 Genetic distance under pairwise sequence comparison within populations of *Scolopedra* species in mainland of Southeast Asia...........................165

Table 2.5 Geographical variations from several populations of *Scolopendra morsitans* in Old world territory including Australia. 166

T**able 2.6** Morphological comparison of *Scolopendra subspinipes* populations from different geographical regions...167

Table 2.7 Morphological survey of geographical variation of *Scolopendra dehaani* populations from different regions..168

Table 2.8 Morphological comparison of *Scolopendra japonica* populations in the present study and the related species *S. cingulata* 169

Table 2.9 Morphological comparison of *Scolopendra pinguis, Scolopendra gracillima* and *S. calcarata*..170

Table 2.10 Morphological comparison of *S. dawydoffi* and *S. multidens;* data from present study and previous taxonomic studies, i.e., Attems (1938), Chao (2008), Kronmüller (2012). 171

Table 2.11 Morphological comparison of *Scolopendra cataracta* sp. n. and some related species in the adjacent sub-regions 172

Table 3.1 Diagnostic description of all examined species based on external morphology and common colouration schemes of voucher specimensin this analysis, with references to recent taxonomic descriptions with additional information...212

Table 3.2 List of voucher specimens of seven *Scolopendra* species and selected outgroups used in phylogenetic analyses. Each sample includes the collecting locality, GPS co-ordinates, CUMZ registration numbers, and GenBank accession number for three selected genes (COI, 16S and 28S). 213

Table 3.3 Characteristics of nucleotide sequence for three amplified genes and best fit models of heterogeneous nucleotide substitution for each gene calculated from jModel Test under AIC and BIC criteria. 216

Table 3.4 Corrected distance of interspecific variation in seven *Scolopendra* species from COI and 16S partial gene analyses under calculation model of K-2 parameter 217

Table 3.5 Corrected distance of intraspecific variation in six *Scolopendra* species from COI, 16S and 28S partial gene analysis under calculation model of K-2 parameter 218

Table 3.6 Results of CV discriminant function in three selected characters; the total number and percentage of correction of leave-one-out cross validation tests in CV discriminant function are in parentheses. 219

Table 4.1 Comparison of traditional taxonomic characters between adult female and 2nd adolescent stadium *O. spinosus* (samples from Brood A). * refers to character in damaged condition, ? refers to unclear character 240

Table 4.2 Taxonomic characters of *O. spinosus* from different geographic regions. ? refers to unclear character 241

Table 5.1 Accession number of all sampled taxa including outgroups. 1 = Murienne et al. (2010), 2= Joshi and Karanth (2011), 3 = Vahtera et al. (2013) and 4 = Joshi and Edgecombe (2013). “*” indicates the holotype. 261

Table 5.2 Corrected mean distance among Indian-Burmese *Digitipes* members. 262

Table 5.3 Comparative analysis of taxonomic characters in all *Digitipes* members; ? indicates unavailable data in the literature. (Continued).......................................263

Table 6.1 Collections used in molecular phylogenetic analysis...............................331

Table 6.2 Sequence annotation for three molecular markers (COI, 16S and 28S rRNA) 336

Table 6.3 Morphological comparison in some taxonomic characters of *R. lithobioides* subspecies. Abbreviation: PS, paramedian sutures; AP, apical spine; SAP, subapical spine; LP, lateral spine; L, left side; R, right side; ?, data insufficiency. References: [1] Attems, 1930, [2] Jangi and Dass, 1984, [3] Khanna, 1994, [4] This study...337

Chapter 1
Introduction

Centipedes or chilopods are terrestrial invertebrates that play very important roles in soil and leaf litter ecosystems as predators (Lewis, 1981) and are now becoming model animals for biological and medical research (Pemberton, 1999). The centipedes in the order Scolopendromorpha are most often encountered living closely to humans because they are well adapted to anthropogenic areas as well as in various natural habitats. However, these animals have still received relatively little attention from either the context of fundamental knowledge or conservation. Recent studies have documented some prospective uses of centipedes in general biology and as medical subjects, and they are relevant to both traditional medicine and commercial uses. There are some reports about local usage of roasted centipedes as traditional medicine for healing asthmatic disease in some regions, especially in Southeast Asia (Lawrence, 1984). This foundation seems to provide an interesting topic for further investigation and application to conservation management of these animals in the future.

The initial studies on centipedes focused mainly on taxonomy, dating back to the 18th -19th Centuries. The first scientific evidence of these animals was recorded in the 10th edition of “Systema Naturae” by Linnaeus (1758), in which nine species names for arthropods now recognized as myriapods were proposed and published. Leach (1816) divided the class Myriapoda into two orders, Syngnatha and Chilognatha, within which centipedes were assigned to Syngnatha. The names are based on characteristics of the mouth parts, Syngnatha possessing maxillary appendages. In addition, this investigation is also considered as the first classification hypothesis for Chilopoda. Many subsequent regional surveys and taxonomic studies have vastly increased the known species diversity of these animals. To date, more than 3,400 valid centipede species have been described.

Centipedes in the order Scolopendromorpha belong to a putative clade named Epimorpha based on their epimorphic post-embryonic development (the hatchling emerges from the egg with all segments already developed, rather than adding segments post-embryonically). A few taxa are distributed in all parts of the world, and a total of approximately 700 described species have been recorded in the order (Edgecombe and Bonato, 2011). Because of the toxicity of their venoms, scolopendromorphs are the most important centipede group in medical and toxicological research, a subject of considerable current attention to evolutionary biologists as well (Undheim et al., 2015). Some medical reports about the harmfulness of centipede envenomation to humans have been made in Asian countries such as Hong Kong (Fung et al., 2011). Most accidental cases of envenomation occurred in residential areas and at night. Only one case from the Philippines reported the effect of envenomation by a large centipede to cause death in childhood (Remington, 1950). However, the fatality evidently did not come directly from the centipede venom but by respiratory failure after inflammation.

In Thailand and neighboring countries, the taxonomy and systematics of centipedes are very scattered. Only one species of common large centipede, namely *Scolopendra subspinipes* Leach, 1816, is well-known in a broad sense. Few taxonomic works have been conducted on the biota of mainland Southeast Asia, including Thailand, e.g., Pocock (1891) and Flower (1901), the cited examples based on Burmese, Malaysian, Singaporean and Thai centipede collections made during British colonization of parts of Southeast Asia. Subsequently, a second phase of myriapod studies was done in the mid-20th Century, including work by Verhoeff (1937) and Attems (1953). Recently, several taxonomic revisions have focused on tropical regions because of biodiversity abundance and geographical richness. Lewis (2004) reassessed Indo-Chinese specimens of the genus *Otostigmus* and found that three described species were misidentified by previous authorities. This result suggests that knowledge of this diverse fauna needs further investigation. Schileyko (1992, 1995, 2007) documented species diversity of scolopendromorph centipedes in Vietnam and recorded three new species and updated twenty newly recorded species from seven genera into the national fauna list. However, he also suggested that the taxonomy of Vietnamese centipedes is still defective and incomplete because of a lack of opportunities to do comparative studies of specimens from nearby countries. Consequently, comprehensive work covering broad scale sampling in several part of

Southeast Asia may be needed to adequately explore the diversity of these fascinating myriapods.

Since 1930, only three species of Thai centipedes in the order Scolopendromorpha have been recognized. The latest survey on Thai scolopendromorphs fauna was conducted from Phang Nga Province (Muadsub et al., 2012). From this work, the genus *Sterropristes* Attems, 1934, was revised and a new species from Similan and Surin Islands described. Decker (2010) added a new record of *Otistigmus spinosus* into the Thai centipede fauna. To date, ten species in the order Scolopendromorpha were found in Thailand. However, further investigations on centipede taxonomy in other parts of Thailand have until now not been conducted. Thailand is located at the center of a biodiversity hotspot in the mainland Southeast Asian region, and as such the native fauna may share species diversity with neighbouring countries. Moreover, there are scolopendromorph records from several countries near to Thailand, i.e. three species are reported from Cambodia, six from Laos, 15 from Myanmar, and 14 from Malaysia (Bonato et al., 2016). However, the taxonomy of scolopendromorph species is still problematic because of variation in morphological characteristics. Consequently, there is still a great deal of information to be obtained from fundamental taxonomic work and other biological characteristics in this area. In this study, I focus on taxonomy and systematics of centipedes in the order Scolopendromorpha by collecting specimens throughout Thailand and also critically investigate specimens that are deposited in natural history museums both in Thailand and overseas. Taxonomic identification will be implemented by integrative morphological and molecular methods to minimize problems caused by geographical variation between populations. Comparative studies of geographical populations in light of molecular phylogenetic trees and available type specimens will form a basis for interpreting each species both evolutionarily and taxonomically.

Objectives

1. To revise the taxonomy of scolopendromorph centipedes in Thailand using morphology and molecular methods

2. To construct a molecular phylogeny of Scolopendromorpha in Thailand

Literature review

Fundamental overview of centipede classification

In the past, the classification of centipedes has been developed in concert with progress on taxonomic study of other myriapods. The first proposal of a classification hypothesis for these animals is from "Monograph of the class Myriapoda, order Chilopoda with observation on the general arrangement of the Articulata", published by Newport in 1845. Later, Chamberlin (1922) proposed that the order Chilopoda should be re-classified by raising its taxonomic rank up to the class level. Pocock (1895) classified centipedes into four orders: Scutigeromorpha, Lithobiomorpha, Scolopendromorpha and Geophilomorpha. Pocock (1902) later proposed the endemic centipede order Craterostigmomorpha from Tasmania, of which only two species have been recorded (Edgecombe and Giribet, 2008). Later, Shear and Bonamo (1988) reported fossils of an extinct centipede as a species which belonged to the new order Devonobiomorpha. Consequently, nowadays centipedes belong to the subphylum Myriapoda in the class Chilopoda. There are five extant and one extinct orders as follows (short diagnostic descriptions based on Shear and Bonamo (1988), Lewis (1981) and Edgecombe et al. (2011):

Order Scutigeromorpha (Figure 1.1A)

Body length up to 9 cm. Adults with 15 pair of legs. Antenna long. Head with compound eyes. Forcipular segment well-developed and more flexible than in other centipede orders. Trunk segments covered by eight elongated tergites dorsally. Spiracle located on dorso-median part of tergite. Locomotory legs very long and slender with small annulated articles on each tarsus. Last pair of leg is the longest compared with other leg pairs. Gonopods present in male and female. Post-embryonic development with several anamorphic stages. Approximately 95 described species from three families distributed worldwide.

Order Lithobiomorpha (Figure 1.1C)

Body length up to 6 cm. Adults with 15 pair of legs. Antenna long. Head with or without various numbers of ocelli on cephalic plate. Forcipular segment well-developed. Trunk segments covered with alternating long and short tergites dorsally. Spiracle located on lateral part of segments bearing long tergites, varied numbers of pairs. Locomotory legs short, with small coxal pores on basal part of posterior 2-5 legs. Gonopods well-developed in female, bearing two or more macrosetae (“spurs”) used to manipulate eggs. Post-embryonic development with several anamorphic stages. Approximately 1,100 described species from two families distributed worldwide, most abundant in temperate zones.

Order Craterostigmomorpha

Body length up to 5 cm. Adults with 15 pair of legs. Antenna quite long. Head with single ocellus on each side. Forcipular segment well-developed. Trunk segments covered by 21 tergites dorsally. Spiracle located on lateral part of segments. Sternites separated into two groups, presternite and metasternite. Anal region with bivalved capsule-like structure that covers four coxal/anal pore fields. Locomotory legs moderately long and slender, the last pair the longest. Small gonopods present in male. Post-embryonic development with a single anamorphic stage (12 leg pairs in hatchling). Only two endemic species, in New Zealand and Tasmania.

Order Devonobiomorpha (Extinct order; data from fossils)

Adults probably with more than 16 pair of legs. Antenna moderately long. Head without ocelli or Tömösváry organ. Forcipular segment well-developed. Trunk segments covered with small setae. Spiracle located on lateral part of segment, reported from segments 10 and 13. Locomotory legs moderately long. Coxal organ present. Genital system unknown. Only one fossilized species has been described based on fossils in Middle Devonian sediments from Gilboa, New York, USA.

Order Scolopendromorpha (Figure 1.1D)

Body length up to 30 cm. Adults usually with 21 or 23 pairs of legs (37 or 43 in a single species). They are the most aggressive centipedes. Body with varied colouration patterns. Antenna long or short, with 17 or more articles. Head with or without ocelli, usually with four or absent entirely. Forcipular segment enlarged, robust. Tergite of forcipular segment and first leg-bearing segment fused. Trunk segments with alternating long and short tergites. Spiracle located on lateral part of segment. Locomotory legs long and slender, often with tarsal or tibial spurs. Last pair of legs often modified in various shapes. Post-embryonic development epimorphic. Gonopods present or absent in male. Adult female displays brooding and maternal care behaviour by wrapping ventral side of body around brood. Approximately 700 described species in five families, distributed mainly in tropical and subtropical regions.

Order Geophilomorpha (Figure 1.1B)

Body length up to 22 cm. Adults with 27-191 pairs of legs. Antenna moderate long or short, invariantly with 14 articles. Head without ocelli. Forcipular segment well-developed and elongated anteriorly. Trunk segments covered by homonomous tergites. Spiracle located on lateral part of segments 2 to penultimate segment. Sternite surface mostly with fields of pore openings that secrete sticky mucous for defense. Locomotory legs short, with small setae. Last pair of legs small, often exhibiting sexual dimorphism. Gonopods present in male and female. Adult female displays brooding and maternal care behavior, in most families by wrapping dorsal side of body around brood. Approximately 1,250 described species in 13 families, distributed worldwide.

Biological remarks on centipedes

Centipedes are usually found in soil ecosystems as predatory animals. They can adapt their body flexibility for locomotion to search for prey in various kinds of habitats, such as the roofs of caves, streams, in leaf litter or even in households. Like other arthropods, the centipede body is bilaterally symmetrical, each segment covered by sclerotized integument on both the dorsal and ventral sides, called a tergite and sternite, respectively. Along the lateral part of each segment are small cutinized elements called pleurites. Centipedes are well-known as venomous terrestrial arthropods, as are scorpions, spiders and some insects. The first pair of trunk appendages is a functional part of the head, the appendage being modified into a pincer or claw-like structure that houses a venom producing gland. The mouthparts include three pairs of appendages; a mandible and first and second pairs of maxillae, from inside to outside, respectively.

The anterior part of the cephalic plate bears a group of sensory organs, including the antenna, Tömösváry organ, and (often) a group of ocelli which functionally associate with light and chemo- and/or mechanosensation. The surface of the antenna is covered by several kinds of small and medium-sized sensilla or setae that serve specific physiological functions, some being mechanosensory and others chemosensory (Ernst et al., 2009). The visual organs of centipedes are classified into two groups; first are the centipedes with compound eyes, which occur exclusively in the order Scutigeromorpha, and second are the centipedes with ocelli, as are usually present in the remaining orders. The evolutionary history of eyes in centipedes has been of recent interest (Müller and Meyer-Rochow, 2006a; Müller and Meyer-Rochow, 2006b) because several genera from different orders lack these visual organs and eyes are completely lacking in some families or even one entire order. Determining whether the three blind families of Scolopendromorpha likely had a blind common ancestor has been one of the questions driving phylogenetic studies.

The respiratory system is a tracheal system. In most centipede groups, the lateral part of a variable number of segments bears a small sclerite (called a stigmatopleurite) on which the opening of trachea (the spiracle) is situated. In Scutigeromorpha alone, this opening is located on the dorsal side of the body, at the rear margin of seven tergites. The characteristics of the spiracles and gross arrangement of the tracheal system plays a major role in classification among centipede orders and families (Edgecombe and Giribet, 2007), i.e., the split between Scutigeromorpha and the remaining centipedes being the basis for classifying centipedes as Notostigmophora and Pleurostigmophora, respectively. Recently, a survey of spiracle structure of Scolopendromorpha has been done (Vahtera et al., 2012b), revealing some informative data for centipede identification.

Each segment contains a pair of locomotory legs that is one of diagnostic characters separating centipedes from millipedes (two pair of legs per segment in the latter). The last pair of legs in some centipede orders has been modified for use in various purposes such as vibration for warning predators, a stinger-like structure for defense or display, and prey capture (Kronmüller and Lewis, 2015).

The genital segments of centipedes are located at the posterior end of the body, although in Scolopendromorpha in particular they are usually hidden above the sternite of the posterior body segment. In Scutigeromorpha and Lithobiomorpha, the genital segments present a conspicuous gonopod structure which differs from Geophilomorpha and especially from Scolopendromorpha. The internal reproductive system of Chilopoda has also been documented in previous literature (Demange and Richard, 1969). However, most of the documented characters were used for higher classification (Iorio, 2003) by sampling only a few representative groups or taxa and have never been investigated at a finer scale. For this reason, the significance of this system for classification and identification at the generic or species level in Scolopendromorpha is insufficient.

Taxonomy and systematics of scolopendromorph centipedes

The first formal taxonomic description of scolopendromorph centipedes appears in Systema Naturae by Linnaeus (1758), in which two species, namely *Scolopendra gigantea* and *S. morsitans* were named. Later, Kraepelin (1903) revised the centipedes in the family Scolopendridae in a monograph, gave some classification hypotheses by categorizing them into several tribes, and presented a phylogenetic tree depicting the interrelationships of genera. Up to now, the last comprehensive taxonomic monograph on the order was done by Attems in 1930. Keys to genera and species by Attems (1930) remain in widespread usage.

Currently, centipedes in the order Scolopendromorpha consist of five families; Cryptopidae, Mimopidae, Plutoniumidae, Scolopendridae and Scolopocryptopidae. Mimopidae consists of a single species from China, and Plutoniumidae includes seven species from North America, the Mediterranean region, and China. The other three families are more geographically widespread, including Southeast Asia. Morphological characters have been used to classify and identify centipedes since the 18th Century. Many taxonomists, e.g., Leach (1816), Pocock (1892), Newport (1845) and Schileyko (1992) remarked that some general characters such as the occurrence of visual organs and position and shape of the spiracles are diagnostic characters for species identification. However, those classification hypotheses have been revised in order to evaluate the significance of these characters (and instances of their convergent evolution) when compared between families or genera (Vahtera et al., 2012a; Vahtera et al., 2012b). Moreover, species identification in several centipede groups is still problematic because the taxonomic characters are sometime ambiguous (Edgecombe, 2007).

In late 20th Century, cladistics and phylogenetic studies on centipedes were initiated to clarify the relationships among centipede orders (Prunescu, 1965, Dohle 1985). The first numerical cladistic analysis of Scolopendromorpha was conducted by Schileyko and Pavlinov (1997). They published a paper on "A cladistic analysis of the order Scolopendromorpha (Chilopoda)", using 17 characters from morphological data. The result suggested that some families of the order Scolopendromorpha were paraphyletic groups, e.g. the family Cryptopidae, whereas the family Plutoniumidae was a monophyletic group.

Molecular techniques have also been applied to determine centipede relationships. Classification and identification hypotheses for groups at all taxonomic levels have been revised and verified. For example, Giribet et al. (1999) analyzed data from 18S and 28S rRNA gene fragments to construct the phylogenetic relationships between centipede orders and found congruence between phylogenetic relationships and morphology-based taxonomy of the Chilopoda. More recently, transcriptome-scale sampling has vastly increased the number of genes applied to inferring centipede ordinal relationships (Fernandez et al., 2014) as well as intraordinal relationships (Fernández et al., 2016). In the case of Scolopendromorpha, molecular work has focused on relationships between families, subfamilies and genera using nuclear ribosomal genes together with a few mitochondrial genes (Vahtera et al., 2012a, 2013). Molecular phylogenetics has also been applied to estimate species diversity and infer the ages of divergences in regional faunas, such as for Scolopendridae of India (Joshi and Karanth, 2011, 2012, 2013). Edgecombe and Koch (2008) reconstructed phylogeny of Scolopendromorpha based on a morphological dataset from several body systems. They proposed sixteen new informative characters from the epipharynx and hypopharynx (the preoral chamber) and used them in combination with 49 external body characters for phylogenetic tree reconstruction. The phylogenetic tree mostly confirmed relationships in the previous family-level classification. Updated versions of the Edgecombe and Koch (2008) morphological dataset have also been combined with sequence data from four molecular loci to infer scolopendromorph phylogeny (Vahtera et al., 2012, 2013). Recently, numerical morphometry and geometric morphometric analysis were used to study the morphological variation in populations of *Scolopendra cingulata* Latreille, 1829, in the Mediterranean region (Simaiakis et al., 2011). The results showed significant differences that result from geographic variation among its populations.

Systematists have also utilized additional taxonomic characters for classification and species identification, such as the internal structure of the spiracles (Vahtera et al., 2012), and structure of a region of the foregut known as a gizzard (Koch et al., 2009; Edgecombe and Koch, 2008). However, there are several problems in taxonomic works which still wait to be resolved such as the morphological variation among postembryonic developmental stages, colour variation, misidentifications caused by abnormality of specimens and sexual dimorphism in some groups, as well as a lack of revision of many primary type specimens (Lewis 1986, 2000, 2004). To resolve these problems, both morphological and molecular characters need to be comprehensively integrated for adequate interpretation of the classical taxonomy and phylogenetic relationship.

Historical study of centipedes in Southeast Asia

During the 19-20th Centuries, several taxonomic works reported on centipede collections from this area. In addition, some field expeditions were also done by European nations at that time such as the United Kingdom, Austria, Denmark and the Netherlands, which led to important collections for further investigation of this regional fauna (including most type specimens). Centipedes in the order Scolopendromorpha are especially well represented in collections because they are large, conspicuous animals that are readily hand-collected and because of their preferred habitats, often in or near anthropogenic areas. Recently, a compilation of a worldwide faunal checklist was carried out to develop an online database, named Chilobase, which summarizes past work in this area. The list of historical surveys and some important works related to Southeast Asia fauna are given below:

1. *Mainland Southeast Asia*

   Attems (1930, 1938, 1953). Decker (2010). Flower (1901). Haase (1887). Kronmüller (2012). Muadsub et al. (2012). Pocock (1889, 1891). Schileyko (1992, 1995, 1998, 2007). Sinclair (1901). Tran et al. (2013). Verhoeff (1937).

2. *Malay Archipelago*

   Attems (1907, 1909 1914, 1915, 1927, 1930, 1931, 1932, 1935, 1938, 1953). Brandt (1840). Decker (2013). Haase (1887). Lewis (1984, 1982, 2002, 2010, 2014, 2015). Pocock (1894). Silvestri (1895). Tömösváry (1885). Wang (1965, 1967). Wang and Tang (1965).

3. *Philippines Archipelago*

   Attems (1914, 1930, 1938, 1953). Kronmüller (2009). Chamberlin (1921). Muadsub et al. (2012). Wang (1951, 1962) .

According to those works, this region contains at least 65 described species, which belong to 12 genera from three families of the order Scolopendromorpha. Recently, Muadsub (2012) summarized the scolopendromorphs of Thailand as comprising nine species, five genera and two subfamilies, Scolopendrinae and Otostigminae. However, this study was done based on collections from only a small portion of Thai territory. It seems that there are several species that had been reported in neighboring countries near to Thailand or undescribed morphologically distinct species may await discovery in this area. Conspicuous gaps between species records of Thailand (9) and adjacent countries such as Vietnam (53) suggest that considerably more diversity is likely (Schileyko, 2007).

In order to address the paucity of data about Thai scolopendromorphs, field surveys since 2012 were conducted throughout Thailand, with further surveys in neighbouring countries such as Laos, Myanmar, Cambodia and Malaysia (Peninsular Malaysia). Centipede specimens were collected by hand. All specimens were paralyzed under a low concentration of ethanol for 10-15 minutes. During the state of paralysis, specimens were photographed by using a digital SLR camera under natural and artificial backgrounds in order to document their colouration. For preservation, centipedes were transferred into air-tight containers compatible with their body size, allowing the collector to manage their body orientation. Absolute ethanol was used as a fixative for preservation in both morphological and molecular aspects. This centipede collection has been registered and housed in Chulalongkorn University Museum of Natural History (Zoology), Bangkok, Thailand.

Figure 1.1 Four extant centipede orders: **A** Scutigeromorpha **B** Geophilomorpha **C** Lithobiomorpha **D** Scolopendromorpha

Chapter 2

A taxonomic review of the centipede genus *Scolopendra* Linnaeus, 1758 (Scolopendromorpha, Scolopendridae) in mainland Southeast Asia, with description of a new species from Laos

Warut Siriwut[1,2], Gregory D. Edgecombe[3], Chirasak Sutcharit[2], Piyoros Tongkerd[2], Somsak Panha[2]

1 *Biological Sciences Program, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand*
2 *AnimalSystematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand*
3 *Department of Earth Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, UK*
Corresponding author: *Somsak Panha* (somsak.pan@chula.ac.th)

ZooKeys 590: 1–124. doi: 10.3897/zookeys.590.7950

Abstract

The centipede genus *Scolopendra* in mainland Southeast Asia is reviewed taxonomically based on morphological characters, informed by a molecular phylogenetic analysis using sequences from three mitochondrial and nuclear genes (COI, 16S rRNA and 28S rRNA). Eight nominal species of *Scolopendra*, namely *S. morsitans* Linnaeus, 1758, *S. subspinipes* Leach, 1816, *S. dehaani* Brandt, 1840, *S. multidens* Newport, 1844, *S. calcarata* Porat, 1876, *S. japonica* Koch, 1878, *S. pinguis* Pocock, 1891, and *S. dawydoffi* Kronmüller, 2012, are redescribed together with some revision of type materials. Geographical variation in each species has been compiled with reference to samples that span their distribution ranges in Southeast Asia and some parts of neighbouring areas such as East Asia, the Indian Ocean, and Africa. Comparative study of traditional taxonomic characters from external morphology provides further information to distinguish some closely related species. *Scolopendra cataracta* Siriwut, Edgecombe and Panha, **sp. n.**, is described from the southern part of Laos, with additional records in Thailand and Vietnam. The phylogenetic framework for Southeast Asian *Scolopendra* recognizes *S. calcarata* + *S. pinguis*, *S. morsitans*, and a *S. subspinipes* group that unites the other six species as the main clades. Within the *S. subspinipes* group, two monophyletic groups can be distinguished by having either slender or short, thick ultimate leg prefemora and different numbers of apical spines on the coxopleuron. *Scolopendra arborea* Lewis, 1982, is placed in subjective synonymy with *S. dehaani*. A survey of external morphology of the genital segments confirms its potential for improving species identification in *Scolopendra*. Some observations on biology and behaviour are recorded based on field surveys in this area.

Keywords

Chilopoda, *Scolopendra*, systematics, distribution, phylogeny, species diversity

Introduction

The genus *Scolopendra* Linnaeus, 1758, is among the predominant centipede groups in tropical regions. These animals are generalist feeders that play an important role as one of the top carnivorous invertebrates in soil ecosystems. In several Asian countries, *Scolopendra* has symbolic status or figures in superstitions, and is used commercially in traditional medicine (Pemberton 1999). A few species have been proposed as model animals for medical and biological subjects (Minelli and Fusco 2004) but comprehensive work on the regional biota has not been consolidated since the last monograph on Scolopendromorpha (Attems 1930b).

The taxonomic study of *Scolopendra* dates back to the late 19th to mid 20th centuries (Kohlrausch, 1881; Pocock, 1891b; Kraepelin, 1903; Attems, 1930a, 1953). Several names have fallen into synonymy through the course of taxonomic revisions (Kohlrausch, 1881; Kraepelin, 1903; Attems, 1930a). Conversely, some populations that had been classified in geographically widespread species have recently been identified as distinct species e.g., *S. antananarivoensis* Kronmüller, 2010, versus *S. morsitans* Linnaeus, 1758, or *S. subcrustalis* Kronmüller, 2009 versus *S. subspinipes* Leach, 1816. The phylogenetic position of *Scolopendra* has been investigated in the context of broad scale phylogeny of Scolopendromorpha (Vahtera et al., 2012a, 2013). Combined molecular and morphological data supported a hypothesis that Old World species of *Scolopendra* can be distinguished from the New World species, and nested most Old World species in a clade with the genus *Asanada* Meinert, 1886. Morphological discrimination between two regional groups within *Scolopendra* is made mainly based on a transverse suture on tergite 1 in New World *Scolopendra* that is absent in nearly all Old World species. Some Old World species are polymorphic with respect to external phenotypic characters. For instance, *S. subspinipes* and *S. morsitans* are cosmopolitan species worldwide, and both of them include several colour variants (Kohlrausch, 1881; Attems, 1930a; Shelley et al., 2005). Previous scolopendrid studies proposed that morphological variation within species is influenced by geographic distribution and ontogeny (Lewis, 1968, 1972b). Ontogenetic variation in colouration patterns has been recorded in *S. dehaani* Brandt, 1840 from Southeast Asia, where the species has been investigated using both molecular and morphological data (Siriwut et al. 2015a).

To date, 99 described species of *Scolopendra* have been recorded (Bonato et al., 2016), of which fourteen species have been found in the Asian tropics (Schileyko, 2007; Lewis, 2010b; Kronmüller, 2012). Taxonomic studies have been undertaken in the following regions of Asia: the Indian Subcontinent (Jangi and Dass, 1984), Indochina including Burma (Pocock, 1889, 1891c; Attems, 1953), the Malay and

Philippine Archipelagos (Pocock, 1894; Wang Yu-Hsi, 1962; Wang Yu-Hsi and Tang, 1965; Wang Yu-Hsi, 1967b, a), and the East coast of the China Sea (Takakuwa, 1942a; Chamberlin and Wang, 1952; Wang Yu-Hsi, 1955b, a, 1956, 1957), including Taiwan (Schileyko, 2007; Chao, 2008). In Southeast Asia, the following *Scolopendra* species are endemics: *S. pinguis* Pocock, 1891, *S. gracillima* Attems, 1898, *S. spinosissima* Kraepelin, 1903 and *S. arborea* Lewis, 1982. There are also species which are widely distributed: *S. subspinipes*, *S morsitans*, *S. dehaani* and *S. japonica* Koch, 1878; each of them extends into neighbouring territories such as the Indian subcontinent and the Asian temperate region (Koch, 1878; Jangi and Dass, 1984).

In mainland Southeast Asia, *Scolopendra* comprises ten nominal species. Most of them are cosmopolitan species found synanthropically. For several species, geographical variation has not previously been documented, but we now have access to molecular evidence by which such variability can be mapped to genetic structure among and between populations. The validity of various scolopendrid species has been ambiguous because their distributions have not been comprehensively documented and/or because the diagnostic value of particular taxonomic characters has been unclear (Lewis, 1978; Lewis et al., 2006; Edgecombe, 2007). Infra specific variation within *Scolopendra* has long been noted as a fundamental problem for distinguishing between similar species (Newport, 1845; Attems, 1930a; Lewis, 2010b). Exclusive reliance on the traditional external morphological characters may not be sufficient to resolve some of these questions, not the least those involving problems of colour variation (Koch, 1982; Koch, 1983a; Shelley, 2005). The phylogenetic relationships of *Scolopendra* to other scolopendrid genera have also been contentious, as is the monophyly of the genus (Vahtera et al., 2013).

Recently, evidence has been presented that morphological identification, molecular phylogeny, and geometric morphometric analyses congruently support the traditional delimitation of *Scolopendra* species in mainland Southeast Asia (Pocock, 1891c; Flower, 1901; Schileyko, 1992, 1995; Kronmüller, 2012). Molecular sequence analyses of Southeast Asian species indicated previously unrecognized groups within nominal species (Siriwut et al. 2015a). These results may indicate that even within a morphologically conservative centipede group, cryptic species can potentially be identified. In this work, we review *Scolopendra* species in mainland Southeast Asia.

The type material of some species has been redescribed and, where available, type material is photographed and illustrated. All species are compared with the most closely allied congeners to provide distinguishing taxonomic characters. Variability in morphological characters is recorded in order to document geographical variation. The description of a new species is based on specimens from three SE Asian countries. Molecular phylogeny of three standard genes is analyzed, adding new samples to previous work on *Scolopendra*, to test the monophyly of each species and to determine the phylogenetic position of new species. An identification key to *Scolopendra* is presented and distribution ranges for species are updated.

Methodology

Material examined. Specimens were collected mainly throughout mainland Southeast Asia, principally from Thailand, Laos, Cambodia, Myanmar, Singapore and Malaysia and kept at Chulalongkorn University Museum of Zoology, Bangkok, Thailand. Examination of additional Southeast Asian and other Oriental regional collections including available type material was based on both identified and previously undetermined specimens in several museums. All specimens were observed by using either a LEICA MZ 16A, Nikon SMZ25 or Olympus stereo microscope. Morphological characters were photographed using montaged image stacks. Each morphological feature was serially captured with a Canon 700d linked to an automated calibration program, either Cell'D imaging or Helicon Focus on a desktop PC. In addition, illustration of some morphological variation was made by free hand drawings.

Institutional abbreviations: Chulalongkorn University Museum of Zoology, Bangkok (CUMZ), Museo Civico di Storia Naturale, Genova, Italy (MSNG), The Natural History Museum, London, UK (NHMUK), Naturhistorisches Museum Wien, Vienna (NHMW), Naturhistoriska Riksmuseet, Stockholm, Sweden (NHRS), Naturhistorisches Museum Basel, Switzerland (NMB) and Zoological Museum, University of Copenhagen, Copenhagen, Denmark (ZMUC).

Behaviour, biology and distribution. Feeding behaviour and brooding of eggs and hatchlings was observed and photographed both in the field and the laboratory. Characteristics of habitats and brood chambers are discussed in (Lewis, 1981; Mitić et al., 2012; Siriwut et al., 2014). The distributional ranges of all SE Asian *Scolopendra* species were reinvestigated based on field sampling, museum collections, and literature records from this region. Localities cited in the descriptions are arranged geographically and are separated in two sections:

I. A determined locality refers to the corrected name of a locality. In cases of inaccurate spelling and outdated names on old labels, we provide the corrected name in square parentheses based on resources from the internet and/or historical notes. Spellings of new collection localities in Thailand were transcribed by the Thai Romanization program (Wirote, 2001). Latitude and longitude coordinates are given for each new collecting locality, tracked by a GPS conductor via a Garmin GPS travelling device.

II. An undetermined locality refers to a name that is localized at only a regional scale such as by region or country. Distribution maps for each species include the records from recent field surveys and specimens from museum collections that provide sufficiently detailed locations. Each of those localities is marked by a filled symbol. Some localities from previous taxonomic work are included using a blank symbol. All undetermined localities and some specimens which were attributed only to a region, island or country have been excluded from the distribution maps.

Species identification and description. Morphological terminology follows the standardized terminology (Bonato et al. 2010). Taxonomic nomenclature and species identification followed Attems (1930b, 1938, 1953), Schileyko (1992, 1995, 2007), Shelley (2005), Shelley et al. (2005), Chao (2008), Lewis (2010b), Kronmüller (2012) and Siriwut et al. (2015a). The description of the genital segments is based on previous surveys of the genital system of Scolopendridae (Demange and Richard, 1969; Iorio, 2003). Abbreviations for terminology applied to morphology used in descriptions and some comparison tables are as follow: PS, paramedian suture; AP, apical spine; SAP, subapical spine; LS, lateral spine; DS, dorsal spine; V, ventral spine; VL, ventrolateral spine; VM, ventromedian spine; M, median spine; DM, dorsomedian spine; SP, spine on prefemoral process; ULBS, ultimate leg-bearing segment. Abbreviated terminology for the genital region used in figures is as follows: IM, intermediate membrane; AV, anal valve; GP, gonopod; LA, lamina adanalis; LS, lamina subanalis; PN, penis; SGS I, sternite of genital segment 1; SGS II, sternite of genital segment 2; TGS, tergite of genital segment. The list of synonyms for each *Scolopendra* species follows Chilobase (http://chilobase.biologia.unipd.it/). Diagnoses are revised from Siriwut et al. (2015a), and the range of geographical variation from the type, voucher specimens and previous surveys.

Phylogenetic reconstruction. Southeast Asian and some temperate Asian *Scolopendra* sequences were obtained from GenBank, based on previous phylogenetic analyses ((Joshi and Karanth, 2011; Vahtera et al., 2013; Siriwut et al., 2015b). We add more *Scolopendra* sequences from additional specimens collected during 2014 from various parts of the region (Table 2.1). DNA extraction methods follow Siriwut et al. (2015a). Three standard genes for centipede phylogeny (cytochrome *c* oxidase subunit I, 16S rRNA and 28S rRNA) were used to reconstruct phylogenetic trees. Maximum likelihood and Bayesian inference approaches were employed, using RAxML (Stamatakis, 2006) and MrBayes (Huelsenbeck and Ronquist 2001, Ronquist et al. 2012), respectively. Standard statistical tests were applied to evaluate branch support (bootstrap support and posterior probability). Algorithms and parameter settings for both analyses followed protocols detailed previously by (Siriwut et al., 2015a).

Results

Phylogenetic relationships of mainland Southeast Asian *Scolopendra* and the position of *Scolopendra cataracta* sp. n.

The phylogenetic tree from the updated concatenated DNA dataset aggregates studied specimens into eleven monophyletic groups within Scolopendrinae that are compatible with morphological identification (Fig. 2.1: Clade A). The phylogeny supports the monophyly of the genus *Scolopendra*, in contrast to a previous analysis in which a sampled species of *Cormocephalus* fell within *Scolopendra* (Siriwut et al., 2015a). The sequence annotation for each partial marker is given in Table 2.2. Genetic divergence was calculated by pairwise comparison of k2 parameter distance under one thousand bootstrap replicates (Table 2.3). The genetic distance among *Scolopendra* species ranges from 15.9–24.4% in COI and 8.3–25% in 16S (COI 13.5–16.8% and 16S 19.3–23.0% for European *Scolopendra* by Oeyen et al. (2014)). Comparing with different genera from the same/another subfamily, the distances are between 21.6–28.9% and 23.1–26.9% in COI, and 22.2–26.1% and 25.9–34.1% in 16S, respectively. Within populations, intraspecific variation is between 8.3–18.4% in COI and 5.2–11.3% in16S (Table 4).

Three main clades are identified in mainland Asian *Scolopendra* (Fig. 2.1: Clade B), corresponding to *pinguis-calcarata*, *subspinipes* and *morsitans* groups (Fig. 2.1: Clade C, D and E). The highest intraspecific variation is observed in *S. pinguis*, a species native to this region, and the lowest variation is in *S. dehaani*, which is widespread and the dominant species in the region. The high measure of genetic divergence among *S. pinguis* populations in our previous study prompted a re-examination of those specimens and additional ones that were added in this study. The updated phylogenetic tree revealed that the former *S. pinguis* clade (Siriwut et al., 2015a: fig. 1, clade C) can be divided into two species, *S. pinguis* and *S. calcarata* (Fig. 2.1: Clade C), and this separation can also be supported by diagnostic morphological characters. These two species are distributed along the montane areas of Burma and Thailand and occur eastward to the Indochina subregion in mountain ranges between Laos and Vietnam. Synapomorphic characters shared by these two species are the comparatively robust, vaulted shape of their body segments, the tergite of the ultimate leg-bearing segment being acute posteriorly, four glabrous antennal articles, and the dichromatic colouration on the cephalic plate in all *S. calcarata* specimens and most *S. pinguis* populations. In addition, the phylogeny indicates that even after recategorising a closely related species (*S. calcarata*) that had previously been classified as an aberrant clade within *S. pinguis*, the genetic distance within *S. pinguis* is still considerable. This distance might suggest cryptic speciation among different geographical populations.

The remaining *Scolopendra* species may be divided into two groups, one consisting of *S. morsitans* and another including former subspecies of *S. subspinipes* sensu Kronmüller (2012). In the case of *S. morsitans*, monophyly is corroborated with high bootstrap support and posterior probability in ML and BI analyses, respectively (Fig. 2.1: Clade D). Within the *S. subspinipes* group (Fig. 2.1: Clade E), a clade uniting *S. cingulata* Latreille, 1829 , *S. japonica*, *S. dawydoffi* and *S. multidens* (Fig. 2.1: Clade F) differs from a clade composed of *S. subspinipes*, *S. cataracta* and *S. dehaani* (Fig. 2.1: Clade I). A morphological feature shared by *S. cingulata*, *S. japonica*, *S. dawydoffi* and *S. multidens* is the *cingulata*-like ultimate legs, which have a dorsally flattened prefemur and femur and are much shorter and stouter than in the *subspinipes* clade (Fig. 2.1: Clade I). Attems (1938) referred to similar groupings based on form of the ultimate legs when describing *S. dawydoffi*. The number of apical spines on the coxopleural process might also be useful for discrimination of these two groups (one or two versus more than two spines in the *subspinipes* and *cingulata* groups, respectively). A monophyletic group composed of *S. subspinipes* and the two allied species (*S. cataracta* and *S. dehaani*) received statistical support both in ML and BI (Fig. 1: Clade I).

All samples of *S. cataracta* united as a clade with *S. dehaani* to the exclusion of *S. subspinipes* (Fig. 2.1: Clade J). This new *Scolopendra* species shares the following morphological similarities with various species of the *S. subspinipes* group: presence of two ventrolateral spines on the ultimate leg prefemur (as in *S. subspinipes*), long and slender ultimate legs (like *S. dehaani*), and incomplete paramedian sutures on the sternites (like *S. dawydoffi)*. However, *S. cataracta* is clearly distinguished from all of them by extremely short tergal paramedian sutures. Interspecific variation of DNA sequences ranges between 15.9–19.4% and 13.8–16.4% in COI and 16S, respectively, among these three related species.

Species diversity of *Scolopendra* in mainland Southeast Asia

In this region, nine species are identified from our survey. The taxomomic boundaries between species were based on information from both morphology and molecular analysis. Two other species of *Scolopendra* were not included in this paper, namely *S. mirabilis* (Porat, 1876), and *S. hardwickei* Newport, 1845. In the case of *S.*

mirabilis, an Africancentral Asian species, the single known specimen in SE Asia may be introduced, being found on an island in a coastal area of northern Vietnam (Schileyko, 1995). Likewise *S. hardwickei* was reported from Singapore, the largest port in Southeast Asia (Decker 2013). This species has been documented from India and the Nicobar and Andaman islands, and it probably occurs in Sumatra and Java (Khanna 2001, Lewis 2010b). Without further material from Singapore or neighbouring areas, the status of this recorded species in the mainland SE Asian fauna is questionable. *S. gracillima sternostriata* Schileyko, 1995, from Vietnam (Schileyko 1995, 1997), is similar to *S. pinguis* in most respects. We include it in the key below but have no new material of this subspecies, and accordingly have not revised it. The following key to native species of *Scolopendra* excludes only the two first aforementioned species.

Key to species of *Scolopendra* in mainland Southeast Asia

1 Tergite of ultimate leg-bearing segment with median suture………………………… ……………………………………………………………….***S. morsitans* Linnaeus, 1758**

– Tergite of ultimate leg-bearing segment without median suture................................**2**

2 Sternal paramedian sutures complete **3**

– Sternal paramedian sutures incomplete **4**

3 Coxopleural process with three or more apical spines, thick prefemur of ultimate leg with at least two ventrolateral and four spines on prefemoral process; average ratio of width:length of ultimate leg prefemur1:2 ………………..***S. japonica* Koch, 1878**

– Coxopleural process with 1–2 apical spines, slender prefemur of ultimate leg with two ventrolateral and two spines on prefemoral process; ratio of width:length of ultimate leg prefemur 1:3……………………….............. ***S. subspinipes* Leach, 1816**

4 Ultimate leg prefemur with at least one ventrolateral spine.......................................**5**

– Ultimate leg prefemur without ventrolateral spines……....***S. dehaani* Brandt, 1840**

5 Coxopleural process with one lateral and one dorsal spine; ultimate leg prefemur with numerous small scattered spines **6**

– Coxopleural process without lateral and dorsal spines; ultimate leg prefemur with a few enlarged spines in rows **8**

6 Legs 21 with a tarsal spur.. ***S. calcarata* Porat, 1876**

– Leg 21 without tarsal spurs **7**

7 Sternites of anterior body segments with complete paramedian sutures......................
……………………………….................***S. gracillima sternostriata* Schileyko, 1995**

–All sternites with incomplete paramedian sutures, reaching only 20–30% on anterior part of sternites..***S. pinguis* Pocock, 1891**

8 Complete paramedian sutures on tergites...**9**

– Short, incomplete paramedian sutures confined to anterior and posterior parts of tergites ……………………….***S. cataracta* Siriwut, Edgecombe and Panha, sp. n.**

9 Cephalic plate and tergite 1 densely punctate; tergites with short median sulcus on posterior part .... ***S. multidens* Newport, 1844**

– Cephalic plate and tergite 1 sparsely punctate; tergites without median sulcus on posterior part .... ***S. dawydoffi* Kronmüller, 2012**

Systematics

Family Scolopendridae Leach, 1816

Subfamily Scolopendrinae Kraepelin, 1903

Genus *Scolopendra* Linnaeus, 1758

Scolopendra morsitans Linnaeus, 1758

Figs 2.1–2.7

Scolopendra morsitans—Linnaeus, 1758: 638. Newport, 1844: 97, 1845: 378. Koch, 1847: 163. Wood, 1862: 23. Kohlrausch, 1881: 104. Meinert, 1886: 200. Haase, 1887: 52, pl. 3, figs. 52–54. Daday, 1889: 150, 1891: 150. Silvestri, 1895: 714. Kraepelin, 1903: 250. Attems, 1907: 80, 1909: 13, 1914a: 106, 1927: 61, 1930a: 23, figs. 38–39, 1930b: 175 1932: 5, 1938: 334. Brölemann, 1912: 54. Muralewicz, 1913: 200. Takakuwa, 1942a: 359, 1942b: 15, 1942c: 41, 1943: 171, 1947: 936. Bücherl, 1974: 107. Chamberlin and Wang, 1952: 180. Jangi, 1955: 597-607, 1959: 253–257. Wang, 1955a: 198, 1955b: 16, 1956: 158, 1957: 27, 1962: 101, 1965: 450, 1967b: 391. Würmli, 1975: 201–206. Koch, 1983a: 79–91. Jangi and Dass, 1984: 29, fig. 1. Lewis, 2002: 81, 2010b: 107, figs. 4, 33, 34. Shelley, 2005: 39, figs 57–64, 2006: 5. Shelley et al., 2005: 39–58.

Schileyko, 2007: 75. Akkari et al. , 2008: 83, map. 2. Decker, 2013: 19. Tran et al., 2013: 228. Chagas-Júnior et al., 2014: 138.

Scolopendra brandtiana Gervais, 1837: 16. Newport, 1845: 379.

Scolopendra bilineata Brandt, 1840: 155. Kohlrausch, 1881: 108.

Scolopendra crassipes Brandt, 1840: 153. Kohlrausch, 1881: 108.

Scolopendra erythrocephala Brandt, 1840: 155. Kohlrausch, 1881: 108.

Scolopendra limbata Brandt, 1840: 154. Kraepelin, 1903: 250.

Scolopendra platypus Brandt, 1840: 153. Newport, 1844: 97, 1845: 379.

Scolopendra elegans Brandt, 1841: 21. Kohlrausch, 1881: 107.

Scolopendra fulvipes Brandt, 1841: 22. Kohlrausch, 1881: 108.

Scolopendra morsitans scopoliana C.L. Koch, 1841: 222, pl. 11. Akkari et al., 2008: 83.

Scolopendra angulipes Newport, 1844: 97. Kohlrausch, 1881: 108.

Scolopendra leachii Newport, 1844: 97. Kraepelin, 1903: 251.

Scolopendra longicornis Newport, 1844: 97. Kohlrausch, 1881: 109.

Scolopendra platypoides Newport, 1844: 97. Kohlrausch, 1881: 111.

Scolopendra tuberculidens Newport, 1844: 97. Kohlrausch, 1881: 108.

Scolopendra algerina Newport, 1845: 387. Akkari et al., 2008: 83.

Scolopendra fabricii Newport, 1845: 384. Kohlrausch, 1881: 107.

Scolopendra formosa Newport, 1845: 383. Kohlrausch, 1881: 108.

Scolopendra richardsoni Newport, 1845: 385. Kohlrausch, 1881: 109.

Scolopendra tigrina Newport, 1845: 381. Kohlrausch, 1881: 108.

Scolopendra varia Newport, 1845: 380. Kohlrausch, 1881: 111.

Scolopendra tongana Gervais, 1847: 275. Kohlrausch, 1881: 110.

Scolopendra infesta Koch, 1847: 169. Kohlrausch, 1881: 112.

Scolopendra planipes Koch, 1847: 168. Kohlrausch, 1881: 106.

Scolopendra pella Wood, 1861: 13. Kohlrausch, 1881: 111.

Scolopendra porphyratainia Wood, 1861: 15. Kohlrausch, 1881: 108.

Scolopendra brachypoda Peters, 1862: 529, pl. 33, fig. 2. Kohlrausch, 1881: 107.

Scolopendra mossambica Peters, 1862: 527, pl. 33, fig. 4. Kohlrausch, 1881: 107.

Scolopendra compressipes Wood, 1862: 31. Haase, 1887: 52.

Scolopendra modesta Wood, 1862: 29. Kraepelin, 1903: 251.

Scolopendra carinipes Humbert and Saussure, 1870: 204. Kohlrausch, 1881: 111.

Scolopendra afzelii Porat, 1871: 1146. Meinert, 1886: 200.

Scolopendra attenuata Porat, 1871: 1148. Meinert, 1886: 200.

Scolopendra chlorocephala Porat, 1871: 1149. Meinert, 1886: 200.

Scolopendra cognata Porat, 1871: 1145 Meinert, 1886: 200.

Scolopendra intermedia Porat, 1871: 1145. Meinert, 1886: 200.

Scolopendra picturata Porat, 1871: 1144. Meinert, 1886: 200.

Scolopendra pilosella Porat, 1871: 1148. Meinert, 1886: 200.

Scolopendra saltatoria Porat, 1871: 1151. Meinert, 1886: 200.

Scolopendra vaga Porat, 1871: 1151. Kraepelin, 1903: 251.

Scolopendra wahlbergi Porat, 1871: 1150. Meinert, 1886: 200.

Eurylithobius slateri Butler, 1876: 446. Kraepelin, 1903: 250.

Scolopendra impressa Porat, 1876: 12. Meinert, 1886: 200.

Scolopendra morsitans procera Haase, 1887: 53, pl. 33, fig. 53. Kraepelin, 1903: 250.

Scolopendra morsitans sulcipes Haase, 1887: 54, pl. 33, fig. 54. Kraepelin, 1903: 250.

Scolopendra morsitans calcarata Daday, 1891: 150. Kraepelin, 1903: 250.

Scolopendra grandidieri Saussure and Zehntner, 1902: 302, pl. 3, fig. 13, pl. 12, fig. 6. Kraepelin, 1903: 251.

Scolopendra lineata Saussure and Zehntner, 1902: 308, pl. 15, fig. 19. Kraepelin, 1903: 251.

Scolopendra spinosella Saussure and Zehntner, 1902: 308, pl. 2, fig. 11. Kraepelin, 1903: 251.

Scolopendra morsitans fasciata Attems, 1930a: 372. Würmli, 1975: 205.

Scolopendra morsitans amazonica Bücherl, 1946: 135. Würmli, 1975: 205.

Trachycormocephalus jodhpurensis Khanna, 1977: 154, figs 5–8. Jangi and Dass, 1980: 67.

Type locality. India.

Material. Thailand — CUMZ 00343, one spm., Hui Hong Khrai, Chiang Mai (18°50'59.5"N, 99°13'16.4"E). CUMZ 00340, one spm., Lainan, Weing Sa, Nan (18°34'16.1"N, 100°46'59.7"E). CUMZ 00405, one spm., Wat Khao Isan, Pak Tho, Ratchaburi (13°23'2.458"N, 99°46'16.525"E). CUMZ 00302, two spms., Wat

Mahavanh, Buriram (14°41'09.8"N, 102°52'33.8"E). CUMZ 00342, one spm., Ban Khok Pho, Prasat, Surin (14°32'53.4"N, 103°22'19.1"E). CUMZ 00339, one spm., Ban Dan Chang, Ta Kantho, Kalasin (16°50'06.1"N, 103°16'32.0"E). CUMZ 00409, one spm., Nong Bo, Borabue, Maha Sarakham (16°1'35.695"N, 103°7'42.487"E). CUMZ 00410, two spms., Ban Tha Tum, Mueang, Maha Sarakham (16°10'45.231"N, 103°27'4.134"E). CUMZ 00411, one spm., Wat Pa Sai Mun, Sai Mun, Yasothon (15°56'45.092"N, 104°12'1.929"E). CUMZ 00412, two spms., Wat Tham Pha Koeng, Phu Wiang, Khon Kaen (16°42'10.303"N, 102°14'56.901"E). CUMZ 00414, two spms., Wan Tham Chia, Nong Ruea, Khon Kaen (16°32'27.014"N, 102°33'19.454"E). CUMZ 00413, two spms., Phu Wiang National Park, Nong Bua Rawe, Chaiyaphum (16°41'4.089"N, 102°14'38.477"E). CUMZ 00299, one spm., Wang Bua, Kabin Buri, Prachinburi (13°57'16.3"N, 101°36'37.3"E). CUMZ 00406, one spm., Wang Bo Waterfall, Mueang, Prachin Buri (14°10'33.933"N, 101°25'40.163"E). CUMZ 00407, 16 spms., Khram Yai Island, Sattahip, Chon Buri (12°42'18.095"N, 100°50'29.35"E). CUMZ 00341, one spm., Juang Island, Sattahip, Chonburi (12°31'46.4"N, 100°57'18.4"E). CUMZ 00408, three adult and numerous juvenile spms., Ta Phraya, Sa Kaeo (14°5'1.047"N, 102°45'36.389"E). CUMZ 00300, two spms., Mueang, Sa Kaeo (13°49'07.9"N, 102°03'10.5"E). CUMZ 00344, one spm., Tha Kra Bak Reservoir, Sa Kaeo (13°58'13.9"N, 102°15'57.6"E). CUMZ 00301, one spm., Kuiburi, Prachuab Khiri Khan (12°06'32.0"N, 99°45'53.0"E). CUMZ 00403, 12 spms., Hat Wanakon National Park, Tab Sakae, Prachuab Khiri Khan (11°38'6.012"N, 99°42'5.25’’). CUMZ 00404, five spms., Kui Buri National Park, Kui Buri, Prachuab Khiri Khan (12°8'57.096"N, 99°45'34.433"E). CUMZ 00402, two spms., Ban Laem Sai, Chaiya, Surat Thani (9°24’ 9.691"N, 99°17'19.719"E). CUMZ 00400, one spm., Ching Kho, Singhanakhon, Songkhla (7°16'44.261"N, 100°31'36.759"E). CUMZ 00401, eight spms., Nhai Plao Beach, Khanom, Nakhon Si Thammarat (9°7'52.64"N, 99° 52’ 39.415"E). NHMUK 1897.9.7.29, one spm., Betong, Yala, leg. S.S. Flower. NHMUK, one spm., Ko Kraew [Khao Kaeo, Chonburi]. NHMUK, one spm., Ko Kraam [Kram Islands, Chonburi], leg. S.S. Flower, 1897–1898.

Cambodia— CUMZ 00345, one spm., Wat Phanombak, Srisophon (13°36'05.5"N, 102°57'09.3"E). NHMW, two spms., Mount Cardamones [Cardamom Mountain], 500 m above sea level, Mission Dawydoff, April 1893. **Laos** — CUMZ 00419, two spms., Ban Na KaSom, Attapue (14°48'30.477"N, 106°50'49.948"E), CUMZ 00420, two spms., Wat Kao Kaeo, Pakse, Champasak (14°11'30.572"N, 105°54'30.821"E), CUMZ 00421, two spms., Savannhaket (16°38'25.053"N, 104°50'0.994"E).

Myanmar — CUMZ 00415, two spms., Old Bagan, Bagan (21°10'19.161"N, 94°51'34.61"E). CUMZ 00416, two spms., Kyaing, Pakokku (21°52'37.982"N, 94°37'47.384"E). NHMUK, one spm., Pyrimana [Pyinmana], Upper Burma. NHMUK 1889.7.15.1418, 21 spms., Teikiyi (Rangoon) [Yangon], leg. E.W. Oates. NHMUK 1889.7.1516, two spms., Moulmein. NHMUK 1889.7.15.17, five spms., Townwingyi (upper Burma) [Taunggyi, Shan State], leg. E.W. Oates. NHMUK 1889.7.15.15, six spms., Iharrawady [Ayeyarwady Region], leg. E.W. Oates. NHMUK 1889.7.1520, 20 spms., Mandalay, leg. E.W. Oates (Cap). NHMW Inv. No. 671, one spm., OslIndien, Aracan [Rakhine State], leg. Stoliczka, 1873.

Vietnam — NHMUK 1926.9.30.13, one spm., Thai Nien Basin, Heure Range, Tonkin, leg. SladenGodman, Trust Expedition. NHMUK, one spm., Annam, with label “?19”.

Brunei — NHMUK 1973.7.659, one spm., Jerudong, with label “CIE Coll. A6527”. NHMW Inv. No. 641, one spm., Brunei, don. Stimdarlmus.

Philippines — NHMUK, one spm., Mactan, Zebu Island. NHMUK 1913.6.18.851-853, one spm., Philippines. NHMW Inv. No. 646, two spms., Manila, Novara Expedition.

Indonesia — NHMW Inv. No. 659, one spm., Padang, Sumatra, leg. Comal Fehiel, 1901. NHMW Inv. No. 12?, one spm., Java, with label “adeusawer 8”. NHMW Inv. No. 636, five spms, Batavia, Java, Novara Expedition, 1857–1859. NHMUK 1913.6.18.849, one spm., Celebes, with label “Spec. No. 28”. NHMW Inv. No. 632, one spm., Celebes, leg. Beruh. Walt, 3 January 1894. NHMUK, one spm., Seram [Seram Island, Maluku Province], leg. Dr. R.F. Ellen, det. D. MacFarlane, 1975. NHMW Inv. No. 635, one spm., Amboina [Ambon], leg. Doleschal, 1859.

China — NHMUK 1928.3.16.4142, two spms., Amoy, leg. Prof. B. Ping 4/2/1926. NHMUK, two spms., China. NHMW Inv. No. 652, one spm., Hong Kong, April 1901. NHMW Inv. No. 638, two spms., Takao [Kaohsiung, Taiwan], leg. H. Sauler. NHMW Inv. No. 643, one spm., Fumasra [Formosa: Taiwan], leg. Breitenstein, 1884.

Japan — NHMUK 1913.6.18.853, one spm., Japan, leg. Koch. NHMUK1892.10.10, one spm., Loochoo [Ryukyu Islands], leg. Holst. NHMW Inv. No. 647, two spms., IshikagiJiwa, Liu Kiu Island [Ryukyu Islands], leg. H. Sauler.

Indian and Middle Asian Territory — NHMUK 1930.4.11.14, one spm., Ahmadabad, leg. Capt. J.B.E. Manning I.M.S. NHMUK, one spm., North Behar, Champharam, leg. Mrs. Campbell Martens with note “see letter 24/9/1930”. NHMUK, one spm., Mandras in 1925, leg. F.A. Turk. NHMUK, one spm., on porch at Bombay, leg. N.H. Soc, 1/8/1902. NHMUK 1894.10.24.7073, five spms., Madras, leg. J.R. Henderson. NHMUK 1910.4.10.31, one spm., Ceylon, Bainbridge Fletcher’s collection. NHMUK 1903.6.18.848, one spm., Bombay. NHMUK 1948.8.6.5, one spm., Kasual [Kansal], Punjab, leg. S.F. Woodward. NHMUK 1975.12, one spm., Ceylon. NHMUK, one spm., Andaman Island, leg. B.B. Osmaston and P.A. Buxton, London School of Hygiene and Tropical Medicine. NHMUK, one spm., Northern Baluchiotan [Balochistan, Pakistan], brought to Indian Museum, leg. Prof. P.A. Buxton, Indian School of Tropical Medicine. NHMUK, one spm., Calcutta, leg. Dr. S.P.R. Chaudhuri, relocated in 25.4.49. NHMUK, one spm., Indian Ocean, with label “Assumption of J.S. Gardiner in 1952.12.17”. NHMUK, 10 spms., Aldaima, Maldives, November, 1908, det. J.S. Gardiner. NHMUK, two spms., Aldaima,Maldives, 17/12/1952. NHMUK 1952.12.17.247, one spm., Astove Island, Indian Ocean, leg. J.S. Gardiner. NHMUK 1948.10.11.84, five spms., Delhi, leg. J.H. Graham. NHMUK 1896.10.2.34, two spms., Assam, leg. E.W.P. Cambridge. NHMW Inv. No. 665, one spm., Calcutta, leg. Stoliezka, 1865. NHMW Inv. No. 650, one spm., Kamoly?, Ceylon, leg. M. Hoelui, September, 1892. NHMW Inv. No. 673, two spms., Osindien [East India], with label “Parr.”. NHMW Inv. No. 642, one spm., Kagi Island, Maldives, leg. H. Sauler.

Africa — NHMUK, one spm., imported with bananas from West Africa, leg. J. Knight Co. Ltd Bermondsey, Indian S.E. on 17/5/1952. NHMUK, one spm., St. Helena Island, South Atlantic Ocean. NHMUK 1892.5.16.1, one spm., Delagoa Bay [Maputo], leg. J. de Coster. NHMUK 1954.7.5.17, one female, Tanga, Tanganyika territory, Tanzania, leg. R.H.C. Sweeney. NHMUK, two spms., St. Helena, leg. A. Loveridge. NHMUK, one spm., Shinyanga [Shinyanga, Tanzania?], Tanganyika, leg. P. Gettliffe.

Australia — NHMW Inv. No. 637, two spms., Gayndah [Queensland], NewHolland. NHMW Inv. No. 666, one spm., Neu Holland, leg. Dr. Millas, 1884.

South Pacific — NHMUK 1893.11.15.12, two spms., Tongatapu. NHMUK 1975.65, one spm., Samoan Island [Samoa]. NHMUK 1966.72, two spms., Samoan Island. NHMUK 1892.12.27.1113, two spms., Levuka, Fiji, leg. H. Hjorring, det. G.M. Thomson. NHMUK 1913.6.18.850, one spm., Vamma Levu [Vanua Levu, Fiji]. NHMUK 1976.31, two spms., Samoan Island. NHMW Inv. No. 634, one spm., Tahiti. NHMW Inv. No. 649, one spm., Tahiti, Museum Goddefroi, 3/3/1881.

Undetermined locality — NHMW Inv. No. 640, one spm., Yantempo, leg. H. Sauler. NHMUK 1985.29, three spms., with label “Lnas”.

Diagnosis. 17–23 antennal articles, 5–8 basal articles glabrous dorsally. Each tooth-plate with 5–6 teeth. Tergites 7(12)20 with paramedian sutures. Tergite of ultimate leg-bearing segment with median suture. Complete paramedian sutures on sternites 2–20. Coxopleural process with 3–4 apical and 0–1 lateral spines. Ultimate leg prefemora with three rows of ventral spines (2–6 VL, 3 V, 2–6 VM), 2–6 M, 2–6 DM and 0–8 spines on prefemoral process. One tarsal spur on legs 1–19 (in Southeast Asia).

Composite description. Body length up to 12.7 mm (In Australian populations according to Koch (1983a)). Reddishbrown or yellowish colour on body segments. Cephalic plate and tergites monochromatic or dichromatic in adult. Tergites usually reddishorange (Thai, Laos and Cambodian populations); dark band on posterior border of tergites. Cephalic plate with or without small punctae, median sulcus present on anterior part. Posterior part of cephalic plate without paramedian sutures.

Antenna usually with 18–20 articles (sometimes 17, 21 or 23 on one side), basal 5–7 glabrous dorsally, 5–8 articles glabrous ventrally. Antennae reach to segment 4. Forcipular trochanteroprefemoral process with denticles in two groups, 2–3 apical and one inner. Tooth-plates wider than long or nearly as long as wide, usually 5–6 teeth; rarely 3, 4 or 7. Tooth-plate with straight, transverse basal suture. Coxosternite without median suture. Article 2 of second maxillary telopodite with spur.

Anterior margin of T1 underlying cephalic plate. Complete paramedian sutures from TT4–5; margination typically starting on T14 (one spm., with margination restricted restricted to last two tergites). Tergite surface smooth. Tergite of ultimate leg-bearing segment curved posteriorly, with median suture; ratio of width: length of tergite of ultimate leg-bearing segment 1.34:1. Sternites with complete paramedian sutures. Sternites without depressions. Sternite of ultimate leg-bearing segment with sides converging posteriorly; surface without depression. Pore-field on coxopleuron terminating well beneath margin of tergite of ultimate leg--bearing segment, pore area slightly widened anteriorly. Coxopleural process moderately long or short, usually with 4–5 apical and 0–1 lateral spines ; porefree area extending 40–50% length from distal part of coxopleural process to margin of sternite of ultimate leg-bearing segment.

All legs without setae and tibial spurs. One tarsal spur on legs 1–19 (20 in some African and Indian populations). Ultimate legs: thick and moderately long, with ratios of lengths of prefemur and femur 1.2:1, femur and tibia 1.3:1, tibia and tarsus 2 1.7:1.; tarsus 1 and tarsus 2 2.8:1. In male, lateral margin of prefemora, femora and tibia marginated dorsally. Prefemoral spines: 2–4 VL, 3 V, 2–4 VM, 2–3 M, 2–3 DM and prefemoral process usually with 3–5 spines. Posterior margin of prefemur with shallow median groove.

Genital segments well developed, reaching longer than the distance between posterior margin of sternite of ultimate leg-bearing segment and distal part of coxopleural process. Sternite of genital segment 1 round and convex posteriorly, with median suture. In male, sternite of genital segment 2 attached to penis. Tergites of genital segments without small setae. Gonopods with small setae in male. Penis with fine posterior seta.

Colouration. *Scolopendra morsitans* demonstrates colour variation among its populations in SE Asia. Previously, colour variation has been recorded in African, Australian and Taiwanese populations (Lewis 1968, Koch 1983a, Chao 2008), those studies proposing that latitude and habitat composition might affect this variability. Recent molecular analyses of ThaiCambodian *S. morsitans* suggested that some colour morphs may be specific to local populations (Siriwut et al. 2015a), although similar patterns occur in each of three different continental faunas. We have recorded the colouration pattern in juvenile and adult specimens:

Colour morph 1. Dichromatic. Cephalic plate, T1 and tergite of ultimate leg-bearing segment orange, the remaining tergites brownish. Posterior borders and lateral margins of tergites dark. Antenna bright orange. Pleuron of leg-bearing segments with pale grey integument, pleurites orange. Legs 1–21 orangish or yellow. Ultimate legs orangish or light brown.

Colour morph 2. Dichromatic. Cephalic plate, T1 and tergite of ultimate leg-bearing segment dark brown or blackish, the remaining tergites brownish. Posterior borders and lateral margins of tergites dark. Antenna dark blue. Pleuron of leg-bearing segments with pale grey integument, pleurites orange or brown. Legs 1–20 yellowish or pale. Ultimate legs blackish or brown.

Discussion. *Scolopendra morsitans* is morphologically varied and subsumes many synonyms that are now attributed to geographical and/or ontogenetic variation. Intraspecific variation has been studied in Africa (Lewis 1969), India (Jangi 1955, 1959), and Australia (Koch 1983a), revealing that some diagnostic characters are inconsistent within its populations. These include: number of glabrous antennal articles, number of teeth on the forcipular tooth-plates, number of tergites that are marginated, and the number of legs with tarsal spurs. This species also demonstrates differences in colour patterns that might be correlated with its geographical distribution. Lewis (1969) noted that a population of *S. morsitans* from Bihe, Angola, demonstrated a dark body with red legs whereas specimens from Sudan were strawcoloured. Here we record two colouration patterns in Thai populations that do not occur sympatrically. In addition, some morphological characters might be restricted to certain geographical populations, such as a tarsal spur on leg 20, which has been reported from India and in some African populations.

For this reason, the utility of this character for defining boundaries between *S. morsitans* and other *Scolopendra* species that share some morphological characters with it, such as *S. laeta* Haase, 1887 and *S. antananarivoensis*, is not absolutely clear. Our survey of geographic variation in *S. morsitans* is presented in Table 5. Our phylogenetic analysis corroborates the monophyly of SE Asian populations of this species (Fig. 2.1). Previous molecular phylogenetic analyses of the *S. morsitans* complex in India suggested that *S. morsitans* was paraphyetic with respect to specimens that were determined as *S. amazonica*, the latter name being used for specimens with tarsal spurs on leg 20 (Joshi and Karanth 2011). From these results, it seems that molecular phylogenetics of this species complex throughout its geographic range may be necessary to clarify the taxonomic value of some variable morphological characters and to more confidently determine the taxonomic status of some phenotypically similar species. It is likely that some names currently treated as junior subjective synonyms of *S. morsitans* may be found to be applicable to cryptic species.

Distribution. This is one of the oldest described centipede species and it is distributed worldwide in the tropics.The native distribution is difficult to determine because of assumed introduction in several areas. Shelley et al. (2005) provided full distribution records. Here we provide a distribution map (Fig. 2.8) and summarise the occurrence of *S. morsitans* in Southeast Asia and some parts of East Asia as follows: **Southeast Asia:** Thailand (entirely), Laos (southern part; Khammouane, Champasak), Cambodia (probably entirely), Vietnam (fide Schileyko 2007: Bai Tu Long Archipelago, Nghe An (Vinh), Thua Thien Hue (Hai Van Pass), Dak Lak, Khanh Hoa, Ninh Thuan (Phan Rang), Lam Dong (Da Lat), Ba Ria, Tay Ninh and Ca Mau), Spratly Archipelago, Myanmar (probably entirely), Malaysia, Singapore, Indonesia, Philippines (Manilla and Zebu Island), and Brunei (Jerudong). **East Asia:** China (Amoy, Hong Kong, Taiwan) and Japan (Ryukyu Islands).

***Scolopendra subspinipes* Leach, 1816**

Figs 2.9A, 2.10–2.18

Scolopendra subspinipes Leach, 1816: 383. Newport, 1844: 96. Koch, 1847: 163. Kohlrausch, 1881: 96. Meinert, 1886: 202. Haase, 1887: 44, pl. 3, figs. 43–45. Daday, 1889: 150. Latzel, 1892: 185. Pocock, 1894: 312. Silvestri, 1894: 624, 1895: 714. Attems, 1897: 477, 1903: 81, 1914a: 106, 1914b: 568, 1914c: 380, 1915: 2, 1927: 1, 1930a: 29, fig. 43, 1930b: 175, 1932: 5, 1938: 334; 1953: 145. Flower, 1901: 21. Ribaut, 1912: 248. Chamberlin, 1918: 158, 1920a: 30, 1920b:

391. Muralewicz, 1913: 201. Chamberlin and Wang, 1952: 190. Takakuwa, 1942a: 1, 1942b: 15, 1942c: 41, 1943: 171. Wang, 1955b: 16, 1962: 101, 1965a: 449, 1967b: 391. Würmli, 1972: 91, Fig. 1. Shelley, 2000: 42. Lewis, 2002: 83, 2007: 10, 2010a: 129, 2010b: 111, 2010c: 380, figs. 1–3. Schileyko, 1995: 77, 2007: 75. Chao and Chang, 2003: 4, fig. 9, tables 1, 2. Chao, 2008: 35, figs. 37–39, table 2. Kronmüller, 2012: 20, table 1, figs. 3–5. Chagas-Júnior et al., 2014: 139.

Synonyms

Scolopendra audax Gevais, 1837: 50. Kohlrausch, 1881: 99.

Scolopendra septemspinosa Brandt, 1840: 152. Kraepelin, 1903; 256.

Scolopendra borbonica Blanchard, 1829: 7, pl. 1. Kohlrausch, 1881: 98.

Scolopendra sexspinosa Newport, 1844: 96, 1845: 391. Kohlrausch, 1881: 100. Daday, 1891: 149.

Rhombocephalus gambiae Newport, 1845: 392. Kraepelin, 1903: 256.

Scolopendra ceylonensis Newport, 1845: 391. Kohlrausch, 1881: 98.

Scolopendra flava Newport, 1845: 392. Kohlrausch, 1881: 98.

Scolopendra gervaisii Newport, 1845: 390. Kohlrausch, 1881: 100.

Scolopendra lutea Newport, 1845: 392. Kohlrausch, 1881: 99.

Scolopendra ornata Newport, 1845: 392. Koch 1863: 10, pl. 66, fig. 134. Kohlrausch, 1881: 100.

Scolopendra placeae Newport, 1845: 390. Kohlrausch, 1881: 100.

Scolopendra planiceps Newport, 1845: 391. Kohlrausch, 1881: 99.

Scolopendra rarispina Gervais, 1847: 270. Kohlrausch, 1881: 97.

Scolopendra sandwichiana Gervais, 1847: 276. Kohlrausch, 1881: 99.

Scolopendra mactans Koch, 1847: 16, 1863: pl. 41, fig. 79. Kohlrausch, 1881: 98.

Scolopendra sulphurea Koch, 1847: 156, 1863: 24, table. 11, fig. 21. Kohlrausch, 1881: 98.

Scolopendra byssina Wood, 1861: 10. Kohlrausch, 1881: 99.

Scolopendra cephalica Wood, 1861: 12. Kraepelin, 1903: 256.

Scolopendra cephalica gracilis Wood, 1861: 13. Kraepelin, 1903: 256.

Scolopendra dinodon Wood, 1861: 12. Kohlrausch, 1881: 98.

Scolopendra gracilipes Wood, 1861: 12. Kraepelin, 1903: 256.

Scolopendra parvidens Wood, 1861: 13. Kohlrausch, 1881: 98.

Scolopendra plumbeolata Wood, 1861: 14. Kohlrausch, 1881: 97.

Scolopendra bispinipes Wood, 1862: 28. Brölemann, 1909: 25.

Scolopendra nesuphila Wood, 1862: 31. Kraepelin, 1903: 256.

Scolopendra repens Wood, 1862: 31. Kraepelin, 1903: 256.

Scolopendra elongata Porat, 1871: 1143. Meinert, 1886: 202.

Rhombocephalus smaragdinus Butler, 1876: 446. Kraepelin, 1903: 256.

Scolopendra damnosa Koch, 1878: 789. Kraepelin, 1903: 256.

Scolopendra mutilans Koch, 1878: 791. Haase, 1881: 47, pl. 3, fig. 47. Takakuwa, 1947: 938.

Scolopendra aurantipes Tömösváry, 1885: 67. Haase, 1887: 44. Takakuwa 1936: 152.

Scolopendra variispinosa Tömösváry, 1885: 67. Haase, 1887: 44. Takakuwa 1936: 152.

Scolopendra rugosa Meinert, 1886: 202. Kraepelin, 1903: 257.

Scolopendra meyeri Haase, 1887: 49, pl. 3, fig. 50. Kraepelin, 1903: 257.

Scolopendra macracanthus Bollman, 1889: 213. Kraepelin, 1903: 257.

Scolopendra flavicornis Tömösváry, 1885: 67. Kraepelin, 1903: 256. Takakuwa 1936: 152.

Scolopendra subspinipes gracilipes Daday, 1891: 149. Kraepelin, 1903: 256.

Scolopendra subspinipes molleri Verhoeff, 1892: 199. Kraepelin, 1903: 256.

Scolopendra polyodonta Daday, 1893: 5; Kraepelin, 1903: 257.

Scolopendra machaeropus Attems, 1901: 136. Kraepelin, 1903: 257.

Scolopendra aringensis Sinclair, 1901: 529, pl. 31, fig. 46, pl. 32, figs. 67, 85, 86, 93. Kraepelin, 1903: 257.

Scolopendra subspinipes mutilans Kraepelin, 1903: 263. Attems, 1938: 334, 1953: 138. Takakuwa, 1943: 171. Takashima, 1952: 4. Shinohara, 1961: 75. Wang, 1993: 850, fig. 5. Schileyko, 1998: 268, 2007: 75. Chao and Chang, 2003: 8, table. 1–2, figs. 6–7. Chao, 2008: tab. 2. Lewis, 2010b: 111. Kronmüller, 2012: 20, table 1.

Scolopendra subspinipes gastroforeata Muralewicz, 1913: 201. Lewis, 2010b: 114. Kronmüller, 2012: table 1.

Scolopendra subspinipes piceoflava Attems, 1934: 51. Lewis, 2010b: 113. Kronmüller, 2012: 21, table 1.

Scolopendra subspinipes fulgurans Bücherl, 1946: 148, 1974: 107. Kronmüller, 2012: 21, table 1.

Type locality. Not designed. The whereabouts of the holotype are unknown.

Material. Specimens referred to *S. subspinipes* Leach, 1816: Malaysia— NHMUK 1897.1.25.12, one spm., Penang, Malaysia, leg. S.S. Flower, 26/11/1896, with label “PENANG 226”. NHMUK, two spms., Penang, Malay Peninsula, leg. H.N. Ridley. NHMUK (E): 2000110, one spm., C89, caught in base camp, Mulu, Sarawak, 5/8/1978, leg. J.G.E. Lewis. NHMUK (E): 2000110, one spm., Mulu, Sarawak, 21/8/1978, leg. Ian Baillie. NHMUK 1952.9.8.576, one spm., Sarawak, Borneo, with label “F.42.24.8.1932”, Oxford University Sarawak Expedition. NHMUK 1906.2.18.3, one spm., Malay Peninsula, leg. Annandale and Robinson, with label “No. 45”.

Singapore — CUMZ 00315, one spm., Kentridge Road, Singapore (1°17'08.9"N, 103°47'09.8"E). NHMUK 1886.115, one spm., Singapore, leg. Dr. Invine Russell, don. E.W. Holmes Zgar. NHMUK 1897.12.22.6364, two spms., Singapore, leg. S.S. Flower.

Indonesia — NHMUK 1893.5.13.30, two spms., east coast Sumatra, leg. Mrs. Findlay. NHMW, 12 spms., Singkarak, Klakah [Singkarak Lake, Sumatra, Indonesia]. NHMUK, one spm., Java, with label “No. 46/108”, 2/3/1885. NHMUK 1874.57, two spms., Java, leg. G. Lyon Esq. NHMW Inv. No. 726, six spms., Java, Indonesia, 1884, det. Attems C. NHMUK 1896.6.20.33, one spm., Surabaya, Java, leg. S.S. Flower, April 1896. NHMW Inv. No. 8596, two spms., Klakah, Lumajang Regency, East Java, Indonesia, leg. Thienemanm, October/November 1928, det. Attems C. NHMW Inv. No. 965, two spms., Java, 30/6/18571859, Novara expedition. NHMUK, one spm., found between base camp and corner camp near Utakawa River, Expedition to Dutch New Guinea [Irian Jaya]. NHMUK 1911.12.23.6364, two spms., Muisika River, South Dutch New Guinea, B.O.U. expedition, leg. Mr. Wollaston.

Philippines — NHMUK 1896.3.8.87, one spm., Philippines, leg. Pascal. NHMUK 1913.6.18.897, one spm., Philippines, with label “Typical form” and “Spec. 13”. NHMUK 1883.33, two spms., Manila, leg. S.W. Taylor.

China — NHMUK 1928.3.16.6468, one spm., Amoy, China, leg. Prof. C. Ping, 4/2/1926, with label “No.CAT.3”. NHMUK 1894.12.20.1, one spm., Central Formosa [Taiwan], leg. Holst. NHMUK, one spm., Changsha, Siang River (28o12'N, 112o59'E), leg. L.T. Loomer and R.H.S. Rodger R.N.

Japan — NHMUK, one spm., Japan, leg. Koch, with label “Number 2?”. NHMUK 1907.6.18.12, two spms., Goto Island, Japan, leg. R. Gordon Smith.

South Asia — NHMUK, one spm., India, with label “No. 45/29”. NHMUK, two spms., Ceylon, with label “No.46/104”.

Africa — NHMUK 1881.99, one spm., Kee Road, South Africa

Jamaica — NHMUK, two spms., in bananas from Jamaica, det. P.C. Jerrard. NHMUK, seven spms., Jamaica. NHMUK Entomology: 2000110, one spm., in case of bananas from Jamaica, 1987. NHMUK, one spm., in bananas from Jamaica, Longford, Kent, leg. Miss S. Truman, 1/11/1950.

Madagascar — NHMUK, one spm., West Africa, with label “n/a”. NHMUK 1989.3.12.37, five spms., Madagascant [Madagascar], det. Lewis and Ransome (cap.). NHMUK 1878.30, one spm., Madagascar.

Rodrigues — NHMUK Entomology: 2000110, six spms., under stones, heavily grazed grassland hill, west of port Mathunn, Rodrigues, 9/4/1995 (63o25'E, 9o41'S). NHMUK Entomology: 2000110, three spms., Solitude expedition to Rodrigues, 10.11.1995. NHMUK Entomology: 2000110, two spms., under forest cavern, Patate, Rodrigues (63o23.5'E, 19o45.5'S). NHMUK, six spms., Rodrigues, leg. Slater, October 1876, with label “refer to *Sc. mossambica* (Peter)”. NHMUK, one spm., probably from Rodriguez, with label “Rodriguez: Anse aux anglaise”. April 1983 CIE A14995”. NHMUK 1924.2.9.611, six adult spms. and brood, Rodrigues, leg. G.C. AddisonWilliamson.

Mauritius — NHMUK Entomology: 2000110, two spms., Raphael island, St. Brandon, Mauritius, January 1996.

Seychelles — NHMUK, one spm., with label “No. 13216?”, Praslin, January 1953, det. E.S. Brown. NHMUK 1952.12.17.248249, two spms., Silhouette Island, leg. J.S.

Gardiner. NHMUK, one spm., Mahe, leg. J.M and R.D. Pope, August 1976, det. MacFarlane. NHMUK 1867.76, two spms., Seychelles, leg. A. Newton Esq. NHMW Inv. No. 8597, two spms., Mahe, leg. Brauer, det. Attems C.

Comoros — NHMUK Entomology: 2000110, one spm., Comores, leg. Helen Read, May 1995.

Pacific Islands — NHMUK, one spm., South Pacific Islands, leg. J.M. Selfridge Mhl., 2/3/1885. NHMUK 1950.4.19.13, one spm., Nukualofa, Tonga, 22/2/1925, det. Brolemann. NHMUK 1950.4.19.6 and 11, two spms., Apia, Upolu, Samoa, leg. Buxton and Hopkins, 7/5/1924. NHMUK, one spm., Ahui, Tautira, Tahiti, 9/8/1925, leg. Cheesman. NHMUK, one spm., Pahenoo, Tahiti, South Pacific, 3/1925, leg. Col. S.Y. Sr. George P.H. Johnson S.Z.R.Q. NHMUK 1882.60, one spm., Ravatonga, leg. Sir J. Fulbock. NHMUK 1911.12.4.14, one spm., Savau, Friendly Island. NHMUK, one spm., Hawaiian Islands, leg. Henry Edward, 30/12/1875. NHMUK 1882.60, one spm., Rarotonga, Sir J. Lubbock’s collection. NHMUK 1926.1.24.465, one spm., on mango trunk, Fatu Hiva, Marquesas Island, leg. P.H. Johnson S.Z.R.A, 6/1/1925. NHMUK 1926.1.24.466470, five spms., Hiva Oa, Marquesas Island, January 1924, leg. P.H. Johnson.

United Kingdom — NHMUK, one spm., in flat over banana ripening store, Poplar, London, leg. E.Z.H.O.H., 9/10/1956. NHMUK 1894.12.23.1, one spm., Kew Gardens. NHMUK, one spm., imported with bananas, Windsor, 14/6/1965, det. P.C. Jerrard, 1965. NHMUK, one spm., West Indies dock, London. NHMUK, one spm., imported with bananas, Boston, Lincs [Lincolnshire, U.K.], det. P.C. Jerrard, 24/10/1960.

Caribbean Sea — NHMUK, two spms., Barbados, det. J. Locke Esq. NHMUK 1886.113116, one spm., Montserrat. NHMUK 1899.6.13, three adults, numerous juvenile spms., St. John (West Indies), leg. J.W. Gregory. NHMUK, one spm., leg. Morne Fortune, R.F.S., det. D.J. Clark. NHMUK, one spm., Bermuda, April, 1873. NHMUK 1896.3.17.21.22, two spms., Antigua, leg. W.R. Forrest. NHMUK, one spm., Bermuda, April, 1873.

Central and South America — NHMUK 1913.6.13.398399, two spms., Bogotia [Bogotá, Colombia]. NHMUK 1898.2.12.15, one spm., Rio Jurua, Amazons, leg. Dr. Bach. NHMUK 1913.6.18.900, one spm., Cayenne. NHMUK, one spm., Rio Sofiars, northwest Ecuador, 450 ft., leg. Rosenberg. NHMUK 1905.7.13.1, one spm., Isthmus of Panama, leg. Mr. H. Robert.

Undetermined locality — NHMUK, one spm., unknown locality, with label “No.47/21”. NHMUK 1813.6.18.201202, one spm., with label “*Scolopendra* Div.I seet. B.6 Cintillus”. NHMUK 1813.6.18.904, one spm., with label “*Sc. subspinipes* I (typical form)”. NHMUK 1916.10.4.48, one spm., unknown locality. NHMUK, one spm., Rei Islands, leg. Cahl. Lingen, with label “88100”. NHMW Inv. No. 703, one spm., Ostindien [East Indies].

Specimens referred to *S. mutilans* Koch, 1878: Japan—Syntype NHMW Inv. No. 751 of *S. mutilans* Koch, 1878, one spm., Japan, with label “Syntype”, leg. Roletz, don. Latzel, 1919 (Figs 2.12–2.13). NHMUK 1911.12.12.915916, two spms., Izu, Japan, leg. S. Akiyama. NHMUK, one spm., Yokohama, Japan, HMS Challenger Expedition, May 1875. NHMUK, two spms., Kole [Kobe], Japan, June 1875. NHMW Inv. No. 746, one spm., Nagasaki, Japan, leg. Rausonel, 1871. NHMW Inv. No. 738, seven spms., Japan, don. Roretz, 1/3/1881. NHMW Inv. No. 740, six spms., Japan.

China — NHMUK 1886.120, one spm., Snowy valley, Ningbo. NHMUK 1892.12.6.1, one spm., Chusan Island [Zhoushan], leg. J.J. Walkes.

Korea — NHMUK 1882.14, two spms., Southeast Korea. NHMUK, two spms., Kanghwa [Khangwhado], Korea, leg. Miss Scarlett.

Undetermined locality — NHMUK 1888.50, one spm., Seimer Island (Pabva), leg. H.O.F. NHMUK, two spms., Tsur Island, leg. Holst, JulyAugust 1891. NHMW, nine spms., unknown locality determined as “*Sc. mutilans”*.

Diagnosis. 17–19 antennal articles, 6 basal articles glabrous dorsally. Each tooth-plate with (4)57 teeth. Tergites 3(4)20 with paramedian sutures. Complete tergite margination on TT14 (17)21. Tergite of ultimate leg-bearing segment without depression or median suture. Complete paramedian sutures on sternites 2(3)20. Coxopleural process with 2 apical spines, without lateral and dorsal spine. Ultimate leg prefemora with 2 VL, 1–2 M, 0–3 DM and prefemoral process with 1–6 spines. One tarsal spur on legs 1–19 or 20.

Composite description. Body length up to 16 cm. Reddish brown colouration on entire body. Cephalic plate and segments monochromatic or dichromatic. Tergites reddish brown; dark band on posterior border of tergites. Cephalic plate with small punctae on anterior part; median sulcus present. Posterior part of cephalic plate without paramedian sulci. Antenna usually with 18–19 articles (16–17 articles on one side in some specimens), basal 6 subcylindrical and glabrous dorsally, 6 articles glabrous ventrally. Antennae reach segment 3–4. Forcipular trochanteroprefemoral process with denticles in two groups, 1–3 apical and 1–2 inner. Tooth-plates wider than long or nearly as long as wide, 5–7 teeth; atypically with 10 on one side (NHMUK specimen from western New Guinea). Tooth-plate with straight, transverse basal suture. Coxosternite without median suture. Article 2 of second maxillary telopodite with spur.

Anterior margin of T1 underlying cephalic plate. Complete paramedian sutures on TT3–4; margination typically starting on TT5–10 (atypically from TT12–13 in some specimens). Tergite surface smooth. Tergite of ultimate leg-bearing segment curved posteriorly, without median suture or depression; ratio of width: length of tergite of ultimate leg-bearing segment 0.8:1. Sternites with complete paramedian sutures. Surface of sternites smooth, without depression. Sternite of ultimate leg-bearing segment with sides converging posteriorly; surface without depression. Porefield on coxopleuron terminating far beneath margin of tergite of ultimate leg-bearing segment, dorsal margin of pore area gently sinuous. Coxopleural process moderately long, with two apical and 0–1 subapical spines; porefree area extending 30–70% length from distal part of coxopleural process to margin of sternite of ultimate leg-bearing segment.

All legs without setae and tibial spur. One tarsal spur on legs 1–19 or more commonly 1–20. Ultimate legs: moderately long and slender, with ratios of lengths of prefemur and femur 1.4:1, femur and tibia 1.2:1, tibia and tarsus 2 1.4:1.; tarsus 1 and tarsus 2 2:1. Prefemoral spines: 2 VL, 1–2 M, 0–3 DM and prefemoral process with 1–6 spines. Posterior margin of prefemur with short median groove.

Genital segments well developed, reaching longer than distance between posterior margin of sternite of ultimate leg-bearing segment and distal part of coxopleural process. Sternite of genital segment 1 round and convex posteriorly, with median suture. In male, sternite of genital segment 2 attached to penis. Tergite of genital segment without small setae. Gonopods with small setae in male. Penis with apical bristle.

Discussion. Recently, the taxonomic validity of *S. subspinipes* and its former subspecies has been evaluated both by morphology (Kronmüller 2012) and molecular methods (Chao et al. 2011, Siriwut et al. 2015a). Three former subspecies of *S. subspinipes*, namely *S. s. japonica*, *S. s. dehaani* and *S. s. cingulatoides* (= *S. dawydoffi*), have been raised to species rank (Kronmüller 2012), whereas the remaining four subspecies (in the classification of Attems (1930b)) have been synonymized with the nominotypical subspecies. However, some subspecies still remain of ambiguous status. Notably, *S. subspinipes mutilans* Koch, 1878, a nominal subspecies occurring in East Asia, corresponds to *S. subspinipes* in all respects apart from the cephalic plate and T1 showing reddish colouration. Recent morphological revisions have regarded this subspecies to be a synonym of *S. subspinipes* (Schileyko 2007, Kronmüller 2012), whereas molecular analyses based on four loci found it to either resolve as sister taxon to *S. subspinipes* s.str. or to group more closely with other species (Vahtera et al. 2013).

In this study, we document a syntype of *S. mutilans* Koch, 1878 in the NHMW collection (Figs 2.12–2.13) and reconfirmed its taxonomic status by using molecular analysis from the concatenated DNA dataset of *S. subspinipes* s.str. and *S. mutilans* Koch, 1878. The phylogenetic tree supports the proposition that this subspecies cannot be distinguished taxonomically from *S. subspinipes*. According to genetic divergence among examined populations, *S. mutilans* Koch, 1878 should be regarded as a geographical variant of *S. subspinipes*, as was suggested in other recent taxonomic studies (Schileyko 1995, 2007). Some morphological comparisons of several populations from Southeast and East Asia are provided in Table 2.6. *S. subspinipes piceoflava*, another former subspecies of *S. subspinipes* from Sulawesi, Indonesia, is currently treated as a synonym of *S. subspinipes* (see Kronmüller 2012), but may upon further study prove to be a valid species. Attems (1934) stated that it could be distinguished from other forms of *S. subspinipes* by yellowish colouration on the posterior part of its tergites. He also referred to the weakness or near absence of tergal paramedian sutures, which also occurs in some other SE Asian *Scolopendra* species (see Kronmüller 2012 and discussion of *S. cataracta* in this study). Re-examining the syntypes of *S. subspinipes piceoflava* leads us to dispute the taxonomic validity of this character because paramedian sutures are visible on the tergites in all syntypes. In order to provide a more complete evaluation of its taxonomic status, a redescription of its syntypes is as follows:

***Scolopendra subspinipes piceoflava* Attems, 1934**

Figs 2.14–2.15

Material. Syntypes NMB 391Va spec.1–3, one adult male and two adult females, Central Celebes, don. Z.U.F. Sarasin, 1895.

Type locality. Tomohon, Sulawesi, Indonesia [Tomohon, North Sulawesi Province, Indonesia].

Description. Body length 16.7 cm in male and 17.1 and 16.5 cm in female syntypes. Preserved male still exhibiting traces of its colouration pattern: cephalic plate and segments dark greenish or brown. Antenna yellowish. Tergites with yellowish or pale colour on posterior margin. All legs bluegreenish, distal part yellow. Cephalic plate without small punctae on anterior part, median sulcus present. Posterior part of cephalic plate without paramedian sulci. Antenna usually with 17–19 articles, basal 6 subcylindrical and glabrous both on dorsal and ventral sides. Antennae reach segment 4. Forcipular trochanteroprefemoral process bearing denticles in two groups, 2–3 apical and one inner. Tooth-plates wider than long or nearly equivalent, 6–7 teeth. Tooth-plate with straight, transverse basal suture. Coxosternite smooth without median suture, with shallow depression in male specimen. Article 2 of second maxillary telopodite with spur.

Anterior margin of T1 underlying cephalic plate. Complete paramedian sutures from T4; margination typically starting on TT5–7. Tergite surface smooth, without median sulci. Tergite of ultimate leg-bearing segment curved posteriorly, without median furrow or depression; ratio of width: length of tergite of ultimate leg-bearing segment 0.82:1. Sternites with incomplete paramedian sutures, extending 80% length of sternite on anterior segments. Surface of sternites smooth, without depression. Sternite of ultimate leg-bearing segment with sides converging posteriorly; surface typically without depression (with median depression in one female specimen; NMB391Va sp.1). Porefield on coxopleuron well developed, with gently curved dorsal margin, reaching nearly to margin of tergite of ultimate leg-bearing segment, anterior part of pore area widest. Coxopleural process long with 1–2 apical spine(s) and absence of lateral and dorsal spines; porefree area extending 30–50% length from distal part of coxopleural process to margin of sternite of ultimate leg-bearing segment.

All legs without setae and tibial spur. One tarsal spur on legs 1–20. Ultimate legs: slender and long, with ratios of lengths of prefemur and femur 1.2:1, femur and tibia 1.1:1, tibia and tarsus 2 1.3:1, tarsus 1 and tarsus 2 2.3:1. Prefemoral spines: 0–2 VL, 1–2 M, 1–2 DM and prefemoral process with 2–5 spines. Posterior margin of prefemur with acute median groove. Sternite of genital segment 1 round and convex posteriorly, with median suture. In male, sternite of genital segment 2 attached to penis. Tergite of genital segment without small setae. Gonopods present in male.

Discussion. Based on examination of the syntypes, we corroborate the assignment of this nominal subspecies to the *S. subspinipes* group. Some morphological characters that appear, however, not to be identical with *S. subspinipes* are the sharpness and length of the coxopleural process, which bears one or two strong apical spines, the ratio of ultimate leg podomeres, and the colouration pattern on the tergites that is clearly distinct from other geographical populations of *S. subspinipes* (the posterior part of the tergites exhibiting a yellowish colouration). On the other hand, the syntypes of *S. subspinipes piceoflava* also display morphological variation between each other with respect to the number of prefemoral spines on the ultimate legs: a male specimen has 4–6 spines on the prefemoral process whereas VL, M and DM spines are absent in one female specimen. The latter is similar to *S. dehaani* but it is possible that this absence may be due to regeneration in this individual. However, without additional material and lacking molecular data with which to test relationships among morphological similar species, we tentatively accept *S. subspinipes piceoflava* as a junior synonym of *S. subspinipes* as proposed by Kronmüller (2012).

Distribution. Previous studies regarded *S. subspinipes* s.l. as a cosmopolitan species in tropical regions (Schileyko 2007; Chao 2008; Lewis 2010b). In this study, most of the sampled specimens were collected on islands. Several old collections in the NHMUK identified as *S. subspinipes* sensu lato from mainland East and Southeast Asia instead refer to former subspecies of *S. subspinipes* that are now identified as distinct species, including *S. dawydoffi*, *S. dehaani, S. multidens* and *S. japonica*. For this reason, we removed occurrence records of *S. subspinipes* s.l. from Thailand and Laos due to our extensive surveys throughout these two countries, finding that no specimen of *S. subspinipes* s.str. was found in this area. The updated distribution of this species in Asia (Fig. 18) is as follows: **Southeast Asia:** Myanmar, Malaysia (Penang and Sarawak), Singapore, Vietnam (fide Schileyko 2007: Lao Cai, Vinh Phuc, HatTay, Hai Phong, Quang Binh, Thua Thien Hue, Da Nang, Dak Lak, Khanh Hoa and Dong Nai Provinces), Indonesia (Surabaya, Java, east coast of Sumatra, Lombok, Sumbawa and Mimika River, New Guinea) and Philippines (Manilla). **East Asia:** China (Zhouzhan Island, Ningbo and Changsha), Taiwan (Kanghwa), Japan (Izu and Goto Islands, Yokohama and Kobe) and South Korea.

Scolopendra dehaani Brandt, 1840

Figs 2.7A, 2.18–2.24 and 2.25A

Scolopendra dehaani Brandt, 1840: 152, 1841: 59. Newport, 1844: 96, 1845: 394. Kohlrausch, 1881: 47. Meinert, 1886: 203. Flower, 1901: 21. Siriwut et al., 2015: 7, table 1, figs. 1–2

Scolopendra subspinipes dehaani—Pocock, 1891: 409, 1894: 312. Silvestri, 1895: 714. Kraepelin, 1903: 260. Attems, 1907: 80, 1914a: 106, 1930a: 31, 1938: 334, 1953: 138. Takakuwa, 1942c: 41. Wang, 1955b: 16, 1956: 158, 1965b: 449.

Schileyko, 1998: 268, 2007: 75. Chao and Chang, 2003: 2. Lewis, 2010b: 113. Kronmüller, 2012: 24, figs. 3C, 4D, table 1. Tran et al., 2013: 230.

Scolopendra subspinipes—Jangi and Dass, 1984: 30, figs. 2–6.

Synonyms

Scolopendra childreni Newport, 1844: 96. Kraepelin, 1903: 260.

Scolopendra concolor Newport, 1845: 394. Daday, 1889: 150, 1891: 188. Kraepelin, 1903: 260.

Scolopendra inermis Newport, 1845: 393.Koch, 1863:64, pl. 29, fig. 55.

Scolopendra inermipes Koch, 1847: 153. Kraepelin, 1903: 260.

Scolopendra silhetensis Newport, 1845: 393. Kraepelin, 1903: 260.

Scolopendra lucasii Gervais, 1847: 270. Kraepelin, 1903: 260.

Scolopendra horrida Koch, 1847: 154. Kraepelin, 1903: 260.

Scolopendra limicolor Wood, 1861: 12. Kraepelin, 1903: 260.

Scolopendra bispinipes Wood, 1862: 28. Kraepelin, 1903: 260.

Scolopendra fissispina Koch, 1865: 891. Kraepelin, 1903: 260.

Scolopendra nudipes Tömösváry, 1885: 67. Kraepelin, 1903: 260.

Scolopendra foveolata Verhoeff, 1937: 220. Würmli, 1972: 91.

Scolopendra arborea Lewis, 1982: 389. Lewis, 2010: 97. **Syn. nov.**

Type locality. Java, Indonesia.

Material. Thailand — CUMZ 00325, one spm., Pha Mon Cave, Pang Ma Pha, Mae Hong Son (19°30'01.6"N, 98°16'43.5"E). CUMZ 00324, one spm., Wat Ban Mai, Mae Hong Son (19°17'55.3"N, 97°59'13.5"E). CUMZ 00323, one spm., Wat Tham Chiangdao, Chiang Mai (19°23'36.8"N, 98°55'42.6"E). CUMZ 00377, one spm., Wat Tham Pak Piang, Chiang Dao, Chiang Mai (19°24'10.498"N, 98°55'52.691"E). CUMZ 00378, one spm., Tham Chiang Dao, Chiang Dao, Chiang Mai (19°23'35.758"N, 98°55'44.412"E). CUMZ 00379, five spms., Huai Hong Khrai, Doi Saket, Chiang Mai (18°51'26.107"N, 99°13'21.827"E). CUMZ 00346, one spm., Hui Hong Khrai, Chiang Mai (18°50'58.6"N, 99°13'18.9"E). CUMZ 00380, one spm., Suan Hin Maharat Stone Park, Long, Phrae (18°9'15.072"N, 99°59'10.343"E). CUMZ 00381, one spm., Lai Nan, Wieng Sa, Nan (18°36'39.969"N, 100°53'17.242"E).

CUMZ 00382, two spms., Si Nan National Park, Na Noi, Nan (18°21'56.97"N, 100°49'56.393"E). CUMZ 00288, one spm., Phusang Waterfall, Phusang, Phayao (19°40'05.0"N, 100°23'25.1"E). CUMZ 00243, Hub PaTat, Larnsak, Uthai Thani. CUMZ 00276, one spm., Wat Tham Erawan, Ban Rai, Uthai Thani (15°02'01.5"N, 99°27'16.6"E). CUMZ 00329, one spm., Wat Phothikhun, Maesot, Tak (16°44'39.2"N, 98°36'17.2"E). CUMZ 00374, two spms., Wat Tham Namphu Khao Rong Kwang, Lansak, Uthai Thani (15°25'59.212"N, 99°35'7.924"E). CUMZ 00375, two spms., Wat Tham Khao Chakkachan, Chum Ta Bong, Nakhon Sawan (15°35'48.533"N, 99°32'38.758"E). CUMZ 00376, one spm., Wat Khao Huai Lung, Banphot Phisai, Nakhon Sawan (15°55'41.844"N, 99°52'20.407"E). CUMZ 00257, one spm., Wat Huai Lung, Banphot Phisai, Nakhon Sawan (15°55'29.6"N, 99°52'28.0"E). CUMZ 00256, one spm., Bang Ban, Ayutthaya (14°21'51.4"N, 100°29'22.3"E). CUMZ 00282, one spm., Wang Kanlueang Waterfall, Chai Badan, Lopburi (15°06'49.4"N, 101°06'38.8"E). CUMZ 00289, one spm., Wat Khao Somphot, Chai Badan, Lopburi (15°09'42.2"N, 101°16'49.5"E). CUMZ 00286, one spm., Chaloem Phra Kiat, Saraburi (14°40'11.9"N, 100°53'09.4"E). CUMZ 00371, one spm., Chet Sao Noi Waterfall, Muak Lek District, Saraburi (14°43'35.463"N, 101°11'22.63"E). CUMZ 00372, one spm., Phu Khae Botanical Garden, Chaloem Phra Kiat, Saraburi (14°40'10.455"N, 100°53'13.401"E). CUMZ 00373, one spm., Wat Tham Welu Wan, Suphanburi (14°57'6.824"N, 99°38'57.176"E). CUMZ 00364, one spm., Wat Mai Luak, Sai Yok, Kanchanaburi (14°26'16.384"N, 98°52'19.822"E). CUMZ 00365, two spms., Wat Tha Thung Na, Sai Yok, Kanchanaburi (14°29'40.864"N, 98°50'21.332"E). CUMZ 00268, one spm., Wat Namtok, Saiyok, Kanchanaburi (14°13'47.5"N, 99°03'59.8"E). CUMZ 00270, 00361, two spms., Wat Tham Lijia, Sangkhaburi, Kanchanaburi (15°04'12.6"N, 98°33'59.0"E). CUMZ 00362, two spms., Wat Khao Isan, Ratchaburi (13°22'57.897"N, 99°46'21.374"E). CUMZ 00363, one spm., Central Botanical Garden, Ratchaburi (13°36'24.229"N, 99°39'37.584"E). CUMZ 00253, one spm., Tham Khao Bin, Ratchaburi (13°35'35.6"N, 99°40'02.3"E). CUMZ 00241, one spm., Wat Huailat, Phu Ruea, Loei, Thailand (17°27'00.4"N, 101°24'45.4"E). CUMZ 00383, one spm., Wat Pa Huai Lat, Phu Ruea, Loei (17°26'20.14"N, 101°25'17.223"E). CUMZ 00277, two spms. and CUMZ 00384, five spms., Tham Pha Pu, Loei (17°34'41.5"N, 101°42'39.1"E). CUMZ

00292, one spm., Wat Tham Pak Khaew Chiang Khan, Loei (17°52'34.0"N, 101°40'20.8"E). CUMZ 00247, one spm., Ban Dong Savanh, Phang Khon, Sakon Nakhon (17°28'17.9"N, 103°30'12.6"E). CUMZ 00266, one spm. and CUMZ 00392, one spm., Kham Hom Waterfall, Sakon Nakhorn (17°07'19.9"N, 104°01'07.4"E). CUMZ 00393, one spm., Wat Nikhom Kaset, Mukdahan (16°48'26.312"N, 104°42'41.205"E). CUMZ 00394, one spm., Pak Maenam Songkhram, Nakhon Phanom (17°38'23.43"N, 104°27'13.517"E). CUMZ 00395, one spm., Cha Naen Waterfall, Bueng Kan (18°12'54.298"N, 103°53'18.422"E). CUMZ 00385, one spm., Tham Pu Lup, Chum Phae, Khon Kaen (16°47'48.98"N, 102°37'31.026"E). CUMZ 00386, two spms., Wat Tham Phra, Tha Khantho, Kalasin (16°51'46.069"N, 103°15'57.202"E) CUMZ 00249, two spms., Ban Dan Chang, Tha Kantho, Kalasin (14°49'29.3"N, 99°41'36.5"E). CUMZ 00271, one spm., Wat Tham Phupha, Thakantho, Kalasin (16°48'05.7"N, 103°12'37.5"E). CUMZ 00275, two spms., Tha Tum, Mueang, Maha Sarakham (16°10'32.2"N, 103°26'59.6"E). CUMZ 00387, one spm., Wat Pa Khok Hinlat, Mueang, Maha Sarakham (16°10'4.82"N, 103°28'57.255"E). CUMZ 00287, one spm., Ban Phon Thong, Kaset Wisai, RoiEt (15°39'59.6"N, 103°33'10.9"E). CUMZ 00369, one spm., Wat Pa Ka Thon, Wang Nam Khiao, Nakhon Ratchasima (14°24'38.479"N, 101°41'3.581"E). CUMZ 00370, two spms., Wat Tham Phrommachan Thamma Ram, Pak Chong, Nakhon Ratchasima (14°34'29.046"N, 101°16'39.524"E). CUMZ 00388, five spms., Khao Kradong Forest Park, Buriram (14°56'26.209"N, 103°5'21.1"E). CUMZ 00389, one spm., Phanom Sawai Forest Park, Surin (14°45'39.325"N, 103°22'2.067"E). CUMZ 00390, one spm., Mueang, Surin (14°52'9.914"N, 103°30'21.877"E). CUMZ 00284, one spm., and CUMZ 00391, six spms., Pa Son Nongkhu, Sangkhla, Surin (14°40'55.7"N, 103°45'51.9"E). CUMZ 00248, two spms., Kaeng Lamduan, Ubon Ratchathani (14°26'15.0"N, 105°06'06.7"E). CUMZ 00279, one spm., Nang Rong Waterfall, Nakhon Nayok (14°19'52.5"N, 101°19'09.1"E). CUMZ 00252, one spm., Si Chang Island, Chonburi (13°09'08.1"N, 100°48'29.3"E). CUMZ 00258, two spms., Wat Khao Maidaeng, Sriracha, Chonburi (12°56'56.0"N, 101°02'11.9"E). CUMZ 00320, one spm., Lan Island, Chonburi (12°55'05.8"N, 100°46'43.8"E). CUMZ 00285, one spm., Juang Island, Sattahip, Chonburi (12°31'46.4"N, 100°57'18.4"E). CUMZ 00269, two spms., Samet Island, Ban Phe, Rayong (12°34'04.3"N, 101°27'23.3"E).

CUMZ 00291, one spm., Wat Khao Sarp, Rayong (12°36'46.8"N, 101°23'18.8"E). CUMZ 00254, one spm., Wat Khao Chakan, Sa Kaeo (13°39'38.0"N, 102°05'02.7"E). CUMZ 00366, one spm., Wat Tham Khao Phrachan, Khao Chakan, Sa Kaeo (13°34'37.66"N, 102°5'39.42"E). CUMZ 00367, one spm., Tham Phet Pho Thong, Khlong Hat, Sa Kaeo (13°39'15.671"N, 102°29'28.066"E). CUMZ 00368, two spms., Wat Khao Phrom Suwan, Watthana Nakhon, Sa Kaeo (13°54'10.886"N, 102°30'49.344"E). CUMZ 00322, one spm., Tha Sen Waterfall, Trad (12°07'59.1"N, 102°42'22.6"E). CUMZ 00360, seven spms., Wat Khao Ma Rong, Bang Saphan, Prachuab Khiri Khan (11°12'23.041"N, 99°30'1.442"E). CUMZ 00326, one spm., Kreab Cave, Langsuan, Chumphon (9°49'01.8"N, 99°02'15.6"E). CUMZ 00359, one spm., Ban Tham Thong, Pathio, Chumphon (10°55'59.984"N, 99°29'27.521"E). CUMZ 00293, one spm., Tham Khao Kriab, Pathio, Chumphon (9°49'01.3"N, 99°02'17.9"E). CUMZ 00354, one spm., Tham Khao Phlu, Lamae, Chumphon (9°43'41.103"N, 99°6'10.996"E). CUMZ 00355, one spm., Wat Tham Khao Kriap, Chumphon (9°48'58.347"N, 99°2'10.364"E). CUMZ 00356, one spm., Ton Phet Waterfall, Kapong, Ranong (9°43'36.056"N, 98°37'7.853"E). CUMZ 00357, one spm., Wat Khao Sap, Ranong (9°57'50.532"N, 98°38'28.765"E) CUMZ 00358, one spm., Bok Krai Waterfall, Ranong (10°22'31.47"N, 98°51'15.943"E). CUMZ 00278, one spm., Bok Krai Waterfall, Kraburi, Ranong (10°22'34.6"N, 98°51'18.3"E). CUMZ 00262, one spm., King Rama V Stone park, Kraburi, Ranong (10°29'36.7"N, 98°54'35.7"E).CUMZ 00251, three spms., Sai Rung Waterfall, Takua Pa, Phang Nga (7°26'26.2"N, 99°48'47.5"E). CUMZ 00261, one spm., Surin Islands, Phang Nga (9°26'58.4"N, 97°52'37.8"E). CUMZ 00273, two spms., Khao Phlai Dam, Sichon, Nakhon Si Thammarat (9°05'33.4"N, 99°54'25.0"E). CUMZ 00281, two spms., Klong Phot Waterfall, Nop Phitam, Nakhon Si Thammarat (7°48'37.8"N, 99°12'20.0"E). CUMZ 00351, one spm., Wat Tha LiPhong, Chian Yai, Nakhon Si Thammarat (8°5'20.669"N, 100°7'59.627"E). CUMZ 00352, one spm., Tham Khamin, Ban Na San, Surat Thani (8°49'9.678"N, 99°22'19.029"E). CUMZ 00265, one spm., Kao Sok Resort, Phanom, Surat Thani (8°54'18.9"N, 98°31'21.1"E). CUMZ 00353, two spms., Ban Laem Thong, Chaiya, Surat Thani (9°24'33.236"N, 99°17'37.035"E). CUMZ 00267, one spm., Wat Huai To, Mueang, Krabi (8°13'37.6"N, 98°53'01.7"E). CUMZ 00263, two spms., Lanta Island, Krabi (7°29'55.7"N, 99°05'20.4"E). CUMZ 00283, 10 spms., Rog Nai Island, Koh Lanta, Krabi (7°13'12.7"N, 99°04'12.7"E). CUMZ CUMZ 00260, one spm., Wat Tham Suea, Krabi (8°07'26.1"N, 98°55'27.2"E). CUMZ 00250, two spms., Ron Waterfall, Khlong Thom, Krabi (7°56'07.4"N, 99°12'37.5"E). CUMZ 00255, one spm., Tham Rue Si, Kantang, Trang (7°28'35.9"N, 99°29'04.0"E). CUMZ 00259, one spm., Chao Mai Beach, Sikao, Trang (7°26'27.8"N, 99°20'45.0"E). CUMZ 00350, two spms., Thung Khai Botanical Garden, Trang (7°28'6.826"N, 99°38'8.117"E). CUMZ 00346, one spm., Wat Tham Khao Chin, Satun (6°38'33.161"N, 100°5'8.924"E). CUMZ 00347, one spm., Tham Ton Din, Kuan Don, Satun (6°43'16.848"N, 100°9'53.819"E). CUMZ 00348, one spm., Boriphat Waterfall, Rata Phum, Songkhla (6°59'41.991"N, 100°8'47.947'E). CUMZ 00349, one spm., Wat Hua Khao Chaison, Phatthalung (7°26'11.723"N, 100°7'44.344"E) 00264, one spm., Tham Malai, Phatthalung (7°38'58.3"N, 100°06'23.7"E). CUMZ 00244, two spms., Wat Tham Phuthakodom, Sinakharin, Phatthalung (7°33'37.2"N, 99°53'07.3"E). CUMZ 00274, five spms., Tham Wang Thong, Khuan Kanun, Phatthalung (7°40'55.1"N, 100°00'56.8"E). CUMZ 00280, one spm., Tham Su Mano, Srinakarin, Phatthalung (7°35'12.3"N, 99°52'04.3"E). NHMUK, one spm., Trang, leg. Dr. David A. Wamell. NHMUK, two spms., Lamphun. NHMUK 1898.4.528.32, two spms., Bangkok, two spms., Ko Si Chang Island and one spm., Dong Phaya Fai, leg. S.S. Flower. NHMUK 1898.6.28.1718, two spms., Kabin, Siam [Sa Kaeo, Thailand], leg. H. Way. NHMUK, one spm., Siam [Thailand], leg. W.H. Hillman. NHMW Inv. No. 774, one spm., XiengZang near Mekong, HinterIndien [Chiang Saen, Chiang Rai, Thailand], January 1886.

Laos — CUMZ 00335, one spm., Ban Bun Tai, Phongsaly (21°24'18.148"N, 101°57'27.294"E). CUMZ 00396, one spm., Mueang Phong Sali, Phongsaly (21°30'26.611"N, 102°10'27.28"E). CUMZ 00399, one spm., Luang Prabang (19°53'10.2"N, 102°08'16.2"E). CUMZ 00246, one spm., Ban Xai Na Pho, Xekong (15°25'28.3"N, 106°36'34.8"E). CUMZ 00245, one spm., Ban Ka Soam, Attapue (14°49'15.8"N, 106°49'05.0"E). CUMZ 00332, one spm., Thung Hin Tang 39 km from Vietnamese border, Attapue (14°45'57.353"N, 107°7'55.516"E). CUMZ 00397, one spm., TadFan, Pakse, Champasak (15°11'25.735"N, 106°7'39.408"E). CUMZ 00398, one spm., Khon Phapaeng Waterfall, Champasak (13°56'53.2"N, 105°56'27.1"E).

Cambodia — CUMZ 00330, one spm., Angkor Wat, Siem Reap (13°24'45.5"N, 103°52'14.7"E). CUMZ 00331, one spm., Wat Tham Ban Kele, Srisophon (13°36'05.5"N, 102°57'09.3"E).

Myanmar — NHMUK 1889.7.15.2, 16 juveniles and one adult spms., Thayelinyo, Burma, leg. E.W. Oates. NHMUK, eight spms., Mandalay, Burma, leg. Oates. NHMUK, one juvenile spm., Cqimana, Uflu, Burma [undetermined]. NHMUK 1889.7.15.10, one spm., Moulmein, Burma [Mawlamyaing District, Mon State], leg. E.W. Oates. NHMUK 1889.7.15.3, five spms., Tondwingyi, Burma. NHMUK 1889.5.15.5, one spm., Teikjyi near Rangoon [Yangon], Burma. NHMUK, two spms., Rangoon [Yangon], Burma, leg. Oates. NHMUK, one spm., Owen Island, Mergui Archipelago, Burma, leg. Dr. Anderson. NHMUK 1889.5.15.6, one spm., Ihawawaddy River [Irrawaddy River], Burma, leg. E.W. Oates (Cpt). NHMUK 1889.5.15.7, one spm., South Tenasserim Range, Burma, leg. E.W. Oates.

Malaysia — NHMUK 1885.8.15.3.6, two spms., Kualin, Kedah, Malaysia, leg. S.S. Flower. NHMW Inv. No. 773, one spm., Penang, Siam [now Malaysia], leg. Skind, 1/2/1882. CUMZ 00336, one spm., Gumpung Baru, Gunung Genting, Perak (4°41'39.9"N, 100°52'46.0"E). CUMZ 00338, one spm., Klinic Desa, Kampung Panit Luar, Perak (4°56'17.9"N, 100°59'00.1"E). NHMUK 1887.71, fiftytwo spms., Perak, Malaysia, leg. L. Way Esq. NHMUK 1889.5.26.1, one spm., Perak, Malaysia, leg. J.H. Leech. CUMZ 00337, Gua Musang, Kelantan (4°52'11.3"N, 102°00'40.6"E). NHMUK 1904.7.14.13, two spms., Kuala Kenting, Kelantan, Malaysia don. Imperial Institute. NHMUK(E) 200054 Chilo.1952.9.8.616, one spm., 2000 ft. in Koyan Forest, Sarawak, Oxford University Sarawak Expedition.

Singapore — NHMUK, one spm., Singapore, labelled "*Sc. subspinipes* var. *concolor*", by Senniry. NHMW Inv. No. 775, one spm., Singapore, 1/1/1887, Aurora Expedition, leg. Swoboda, det. Attems C.

Indonesia — NHMUK 1893.5.13.2.30, two spms., east coast of Sumatra, Indonesia, leg. Mrs. Findlay. NHMW Inv. No. 8603, one spm., Java, Indonesia, with old label "Soumarak near Java", leg. Plason A., det. Attems C., 1874. NHMW Inv. No. 772, one spm., Java, 1882. NHMW Inv. No. 8602, one spm., West Java, leg. Ausbeute Kainy, det. Attems C. NHMW Inv. No. 37U, one spm., Java, Novara Expedition. NHMW, one spm., Java, 1/2/1882, leg. Breitensl. NHMW Inv. No. 1648, one spm., Java, 1/5/1879, don. Moscovics. NHMW Inv. No. 8604, one spm., Java, Indonesia, don. Moscovics, det. Attems C. in 1/5/1879. NHMW Inv. No. 8600, one spm., Buitenzorg [Bogor], Java, Indonesia, leg. Müller, det. Attems C. NHMW Inv. No. 8605, six spms., Java, Indonesia. NHMW Inv. No. 8598, one spm., Java, Indonesia, leg. Adensamer, det. Attems C. NHMW Inv. No. 778, one spm., Java, Indonesia, don. Moscovics, det. Attems C. NHMW Inv. No. 779, one spm., Java, Indonesia, Novara Expedition.

China — NHMUK, one spm., Hong Kong by G. Browning.

Indian Territory — NHMW Inv. No. 768, one spm., India or Aracan, leg. Stoliczka in 1873. NHMUK, one spm., Chamba, Himalaya in Schlogin.

Mexico — NHMUK, one spm., Mexico, leg. California Academy of Science [probably introduced, if not mislabeled].

Undetermined locality — NHMUK, 1894.8.23.7, one spm., unknown locality, leg. C. Hose Esq. NHMUK 1913.6.18.903, two spms., Côte Malaga, Koch’s collection; NHMUK, one spm., near mouth of Patam R. [possibly Karandag (Patam) River, Bangladesh].

Diagnosis. 17–21 antennal articles, 6 basal articles glabrous dorsally. Each tooth-plate with 5–6 teeth. Tergites 3(4)–20 with paramedian sutures. Complete tergite margination from T7. Tergite of ultimate leg-bearing segment without depression or suture. Complete or incomplete paramedian sutures on sternites. Coxopleural process with two apical spines, absent lateral and dorsal spines. Ultimate leg prefemora with 0–1 M, 0–1 DM and prefemoral process with 1–4 spines. One tarsal spur on legs 1–19(20).

Composite description. Body length up to more than 25 cm (collections from Java, NHMW). Varied colouration; cephalic plate and segments monochromatic. Tergites usually brownishorange with or without dark band on posterior border of tergites. Cephalic plate with small punctate on anterior part; median sulcus present. Posterior part of cephalic plate without paramedian sulci. Antenna usually with 18 articles (17, 19 and 21 articles in some specimens), basal 6 subcylindrical and glabrous dorsally, 5–5.5 glabrous ventrally. Antennae reach segment 3–4. Forcipular trochanteroprefemoral process bearing denticles in two groups, one apical and 2–3 inner. Tooth-plates wider than long or nearly equivalent, 4–5 teeth on each side; rarely 3, 7, 8 or 10. Tooth-plate with straight, transverse basal suture. Coxosternite smooth, without median suture. Article 2 of second maxillary telopodite with spur.

Anterior margin of T1 underlying cephalic plate. Complete paramedian sutures from T4; margination typically starting on TT9–12 (14 in one spm. from Burma; NHMUK 1889.5.1.7). Tergite surface smooth, without median sulci. Tergite of ultimate leg-bearing segment curved posteriorly, without median furrow or depression; ratio of width: length of tergite of ultimate leg-bearing segment 0.84:1. Paramedian sutures usually complete on sternites, atypically confined to anterior 30–50%. Surface of sternite smooth (atypically with small pit on posterior part). Sternite of ultimate leg-bearing segment with sides converging posteriorly; surface of sternite without depression. Porefield on coxopleuron terminating well beneath margin of tergite of ultimate leg-bearing segment, anterior part of pore area widest. Coxopleural process moderately long or short with two apical spines (atypically 0–1 spines); pore-free area extending 90–100% length from distal part of coxopleural process to margin of sternite of ultimate leg-bearing segment.

All legs without setae and tibial spur. One tarsal spur on legs 1–19 or 20 in equal frequency. Ultimate legs: moderately long and slender, with ratios of lengths of prefemur and femur 1.1:1, femur and tibia 1.2:1, tibia and tarsus 2 1.6:1.; tarsus 1 and tarsus 2 2.3:1. Prefemora long and slender, flattened dorsally. Prefemoral spines: 0 VL, 0–1 M, 0–1 DM and prefemoral process with 1–4 spines. Posterior margin of prefemur with shallow median groove. Genital segments well developed, reaching longer than distance between posterior margin of sternite of ultimate leg-bearing segment and distal part of coxopleural process. Sternite of genital segment 1 round and convex posteriorly, with median suture. In male, sternite of genital segment 2 attached to penis. Tergites of genital segments without small setae. Gonopods with or without small setae. Penis with apical bristle.

Colouration. This species is among those that exhibited the most varied colouration patterns. Chao (2008) suggested two major types of *Scolopendra* colouration, referred to as monochromatic and dichromatic. The variability in colouration of *S. dehaani* has been reported in Southeast Asia over the past century (Flower 1901). In the present study, the colour patterns of growth stages have been photographed (Fig. 2.19). Recently, ontogenetic variation including specific changes in colouration has been discussed with reference to geographical distribution (Siriwut et al. 2015a). These findings indicated that the colouration change might involve a heritable component among populations. A descriptive classification of colouration in *S. dehaani* is as follows:

Colour morph 1: Dichromatic. All segments including cephalic plate dark brownish. Posterior border of tergites with a dark band. Antenna reddish brown. Pleuron with pale grey integument, all pleurites brownish. Legs chestnut brown, tibiae and tarsi dark purplish.

Colour morph 2: Dichromatic. All segments brown or yellowish orange. Posterior border of tergites with a dark band. Antenna yellowish orange. Pleuron with pale grey integument, pleurites pale grey. Legs dark brownish, tibiae and tarsi dark purplish.

Colour morph 3: Monochromatic. All segments including cephalic plate reddish brown. Antenna reddish brown. Pleuron with pale grey integument, pleurites brownish. Legs 1–18 yellowish, tibiae and tarsi reddish brown. Leg 20 and ultimate legs entirely reddish brown.

Colour morph 4: Dichromatic. Cephalic plate, TT1–2 and 19–21 bright reddish, rest of tergites brown. Posterior border of tergites with a dark band. Antenna yellowish or bright orange. Pleuron with pale grey integument, pleurites orange. Legs 1–19 yellowish, without secondary colouration on distal part. Leg 20 and ultimate legs entirely reddish.

Colour morph 5: Dichromatic. All segments including cephalic plate cherry reddish. Posterior border of tergites with a dark band. Antenna reddish or orange. Pleuron with grey integument, pleurites orange. All legs reddish.

Discussion. This is the largest centipede in Asia. A consistent character that is treated as diagnostic for this species is the absence of ventral spines on the ultimate leg prefemur. *Scolopendra dehaani* possesses characters of the *S. subspinipes* s.l. sensu Lewis (2010) but after morphological survey (Kronmüller 2012) and molecular delimitation (Siriwut et al. 2015b) a species rank has been conferred to this name. The morphological variability in the extent of paramedian sutures recorded in some specimens might demand further examination. Three morphotypes of *S. dehaani* within the examined collections can de delimited as follow:

Morphotype 1: Complete paramedian sutures on tergites and sternites. This is the typical form of *S. dehaani*, according to Attems (1930b) and Jangi and Dass (1984), observed throughout the geographic range of the species.

Morphotype 2: Paramedian sutures complete on tergites, confined to 20–30% length of sternites. This morphotype is observed in a specimen apparently from Bangladesh.

Morphotype 3: Paramedian sutures lacking on tergites on all segments (Fig. 2.24D) and confined to 10–20% length of sternites (Fig. 2.23F). This morphotype has been observed in spec. from Hong Kong and northern India and is common in Java.

Based on these morphotypes, we surmise that this variability might have a geographic basis and could suggest evidence of cryptic speciation. Molecular data are presently lacking for morphotype 3 in particular and, presently, we apply the specific name *S. dehaani* Brandt, 1840, throughout the entire geographic range. A morphological comparison through the species' geographical range is given in Table 2.7. In addition, we recorded some brooding and feeding behaviour of individuals in their natural habitat. *Scolopendra dehaani* exhibited double coiling when guarding offspring in the brood chamber (Fig. 2.20A), similar to *S. morsitans* (Fig. 2.20B). Two stages of feeding behaviour have been observed, which may be described as late foraging (Fig. 2.20D) and consumption stages (Fig. 2.20C). The centipede attached itself to the posterior part of the body of the snaileating snake *Pareas carinatus* Boie, 1828 and then advanced to the anterior part of the prey's body, stabbing the snake several times. The posterior part of the centipede hung twisted with a palm trunk by using the locomotory and ultimate legs. The period of consumption of the prey lasted approximately one to two hours after the initial recording; all somatic tissue was completely eaten by the centipede.

One new subjective synonym is proposed for *S. dehaani*. The holotype and sole known specimen of *S. arborea* Lewis, 1982 (NHMUK 1952.9.8.616) is approximately 40 mm in length, from an elevation of 2,000 ft. at Koyan Forest, Sarawak. It is here regarded as an immature specimen of *S. dehaani*. Lewis (1982, 2010) noted that morphological characteristics of *S. arborea* are similar to some other Asian and one Pacific island species, namely *S. dehaani*, *S. puensis* Jangi and Dass, 1984, *S. gracillima*, *S. hardwickei* Newport, 1844, and *S. metuenda* Pocock, 1895. In its original description, *S. arborea* was noted to have a colouration pattern similar to juveniles of *S. dehaani*, i.e., the cephalic plate and last two segments black, the other tergites bright orange, the legs bright blue with blackish lateral lines. Its taxonomic characters appear very close to *S. dehaani*, the apparent differences being the number of spines on the coxopleural process (one in *S. arborea* versus two in *S. dehaani*) and tergite margination starting from T20 or only T21 margination (reaching more forward to anterior segments in *S. dehaani*). According to our study, the number of apical spines on the coxopleural process of adults of *S. dehaani* is quite strictly two, but on some occasions a single minute apical spine is present in small subadult and juvenile specimens. Morover, our reexamination of the holotype of *S. arborea* indicated that tergite margination starts from T15, which decreases the distinction from *S. dehaani*. An unusual morphological feature of *S. arborea* is the expansion of the peritrema on the spiracle of segment 3 to cover part of the tricrescentic flaps. This atypical feature may be ontogenetic variation or the effect of muscle contraction or extension around the spiracle margin which might be affected by fixation. Without other significant diagnostic characters to distinguish this species from *S. dehaani*, which is abundant on the mainland and on some islands in Southeast Asia, we synonymise *S. arborea* with *S. dehaani*.

Distribution. Widespread species in the Southeast Asian mainland and some islands (Fig. 2.18). The first occurrence was reported from Java, Indonesia. In this study, we provide all recorded localities of this species in Asian territory, together with some localities in which the species might be introduced, as follows: **Southeast Asia:** probably this is the native distribution area of this species according to population abundance and genetic structure. Population density is high throughout mainland territory especially in synanthropic areas but populations are more scattered in montane areas. The currently known distribution is as follows: Thailand (entirely), Laos (Vientiane, Khammouane, Phongsaly and Savannakhet), Cambodia (Siem Reap), Vietnam (fide Tran et al. 2013: Poulo Condore, Quang Binh, Nghe An, Dak

Lak, Kon Tum, Ba Ria), Myanmar (Mergui Archipelago, Rangoon (Yagon) and Mandalay), Malaysia (Kelantan, Perak, Penang, Kedah, Selangor, Johore and Sarawak), Singapore, Indonesia (Kota Bogor (Java), Solok, SiRambe?, Singgalang Mountain (Sumatra), Anambas and Ambon islands) and Philippines. **East Asia:** China (Hong Kong and Hainan), Japan (Okinawa) and Taiwan (Hualien). **South Asia:** India (Himachal Pradesh (Chamba Himalaya), West Bengal (Calcutta), Karnakata, Andaman and Nicobar Islands), Bangladesh and Sri Lanka. **Central America:** Mexico probably introduced).

Scolopendra multidens Newport, 1844

Figs 2.26, 2.27, 2.28A–B, 2.29

Scolopendra multidens Newport, 1844: 97, 1845: 391. Gervais, 1847: 288. Kohlrausch, 1881: 101. Haase, 1887: 46, pl. 3, fig. 46. Chao, 2003: 7, 2008: 30, table 2, figs. 31–36. Lewis, 2010b: 108. Kronmüller, 2012: 26. Siriwut et al., 2015a: 22.

Scolopendra rugosa—Meinert, 1886: 202.

Scolopendra subspinipes multidens—Kraepelin, 1903: 264. Attems, 1907: 81, 1914a: 107, 1914b: 568, 1930a: 31. Muralewicz, 1913: 201. Takakuwa, 1942: 359, 1943: 171. Takashima, 1949: 11. Takashima and Shinohara, 1952: 4. Wang, 1955: 16, 1956: 158, 1962: 101. Zhang, 1992: 8, fig. 1.

Type locality. Not designated.

Material. Holotype NHMUK, one adult, dry condition, Newport’s collection (Figs 2.26, 2.27).

Additional material. NHMUK, one spm., Qiang Binh, Vietnam (17.47001°N 106.38168°E), leg. F. Naggs and J. Ablett, 4/3/2012. NHMUK, one spm., Annam [Vietnam], leg. A. Graham (C.). NHMUK, one spm., in bottle “*Scolopendra multidens*”, Hong Kong, July 1954, leg. I.D. Romer. NHMUK, spm. numbers 2, 6, 8, 11, 13 and 14 in bottle “*Scolopendra multidens*”, Hong Kong.

Diagnosis. 17–18 antennal articles, 6 basal articles glabrous dorsally. Each tooth-plate with 5–10 teeth. Tergites 2(3)–20 with paramedian sutures. Complete tergite margination from TT12 (14)–21. Tergite of ultimate leg bearing segment without depression or suture. Paramedian sutures 20–60% on anterior part of sternites. Coxo pleural process with 2–3 apical spines. Ultimate leg prefemora with 2 VL, 1 M, 1–2 DM and 1–3 spines on prefemoral process. One tarsal spur on legs 1–19.

Composite description. Body length 11.4 cm in syntype. Dried holotype brownish on entire body. Cephalic plate with small punctae; median sulcus present. Posterior part of cephalic plate without paramedian sulci. Antennae with 17–18 articles, basal 6 subcylindrical and glabrous dorsally on left side, 6 articles glabrous ventrally. Antennae reach segment 4. Forcipular trochanteroprefemoral process with denticles in two groups, one apical and three inner. Tooth-plates quadrate, with 5 teeth (total of 12–14 teeth in original description). Tooth-plate with straight, transverse basal suture. Coxosternite smooth, without median suture. Article 2 of second maxillary telopodite with spur.

Anterior margin of T1 underlying cephalic plate. Complete paramedian sutures on TT2; margination typically starting on T9 (T13 in specimen from Hong Kong; NHMUK). Tergite surface smooth, with median sulci on posterior part. Tergite of ultimate leg-bearing segment relatively broad, curved posteriorly, without median furrow or depression; ratio of width: length of tergite of ultimate leg-bearing segment 0.72:1. Sternites with short paramedian sutures on approximately 40–60% of anterior part. Surface of sternites smooth. Sternite of ultimate leg-bearing segment with sides converging posteriorly, surface without depression. Porefield on coxopleuron terminating beneath margin of tergite of ultimate leg-bearing segment, dorsal margin of pore area sinous. Coxopleural process moderately long or short with 1–2 apical and 1–2 subapical spines; porefree area extending 80% length from distal part of coxopleural process to margin of sternite of ultimate leg-bearing segment.

All legs without setae and tibial spur. One tarsal spur on legs 1–19; holotype lacking leg 20. Ultimate legs thick and moderately long, with ratios of lengths of prefemur and femur 1.2:1, femur and tibia 1.7:1, tibia and tarsus 1 1.8:1; tarsus 1 and tarsus 2 1.5:1. Prefemora flattened dorsally, atypically rounded, with enlarged blackish spines. Prefemoral spines as follow: 3 VL, 2 M, 2 DM, prefemoral process with 3 spines (3 V, 2 D, prefemoral process with 3 spines in original description). Posterior margin of prefemur with shallow median groove.

Genital segments well developed, reaching longer than distance between posterior margin of sternite of ultimate leg-bearing segment and distal part of coxopleural process. Sternite of genital segment 1 round and convex posteriorly, with median suture. In male, sternite of genital segment 2 welldeveloped. Tergite of genital segment without small setae. Gonopods and penis absent.

Colouration. According to Chao (2008), juvenile specimens have a reddish orange cephalic plate and T1. Basal part of antenna reddish orange, distal part greenish. The remaining tergites dark green. All legs reddish orange. In adult, all tergites reddish orange.

Discussion. Morphological characters are similar to *S. subspinipes* sensu Chao, 2008. The validity of *S. multidens* as a separate species was reestablished by the absence of gonopods on the first genital segment in males (Chao 2008). Two species of *Scolopendra* in the region, *S. hainanum* Kronmüller, 2012 from Hainan Island, China, and *S. multidens*, distributed in eastern coastal Asia, have been reported to lack gonopods. Study of the type specimens of both *S. multidens* and *S. dawydoffi* indicates a close relationship between these two species. The lack of gonopods in males of *S. dawydoffi* from Thailand was found in the present study, which might provide a synapomorphic character for a clade composed of these species. However, the species boundaries between these taxa are complicated by disjunct distributional data, with previous records indicating that *S. multidens* mostly occurs in the East China Sea and possibly ranges as far as Japan. Vahtera et al. (2013) reported the occurrence of *S. multidens* from northern Vietnam and provided DNA sequences for a specimen. In this present study, we analyzed molecular data for numerous specimens of *S. dawydoffi* as well as the Vietnamese specimen of *S. multidens* to explore their relationships. The phylogenetic tree based on mitochondrial and nuclear genes indicated that *S. multidens* is sister taxon to *S. dawydoffi* and both are genetically distinct from other members of the *S. subspinipes* group (Fig. 2.1). Based on to these results, an absence of gonopods is corroborated as a synapomorphy for this clade. Only geographical distribution and molecular data (i.e., branch length) can be used to distinguish these two species. COI is the only molecular marker available for *S. multidens* from East Asia (unpublished results from sequences in GenBank from Taiwan), and analyses of our COI data with these included groups the Vietnamese specimen together with other *S. multidens*. Because of their genetic distinctness and reciprocal monophyly, we regard *S. multidens* and *S. dawydoffi* as valid species until further morphological examination throughout their distribution ranges has been done to clarify species boundaries.

Distribution. Widespread species in Asia (Fig. 2.29). The original description did not designate a type locality. Kohlrausch (1881) reported the collecting locality of this species as China based on a specimen in the Godeffroy collection, Hamburg, Germany. Subsequent publications reported further localities of this species as follows: **Southeast Asia:** Vietnam, Philippines (Mindanao) and Indonesia (Java and north New Guinea?). **East Asia:** China (Yunnan, Guanxi, Hainan, Hong Kong and Taiwan (Keelung, Nuannuan and Taipei)).

Scolopendra calcarata Porat, 1876

Figs 2.9B, 2.25B, 2.29–2.35

Scolopendra calcarata Porat, 1876: 10. Haase, 1887: 51. Attems, 1930a: 33. Zhang, 1992: 6, map 1. Schileyko, 1995: 77, fig. 3, 1998: 268, 2001: 434, 2007: 74. Lewis, 2010b: 98. Tran et al., 2013: 227.

Type locality. China.

Material. Holotype: NHRSKASI 000000042, one female with label "*Scolopendra calcarata* v. Por" from Kina [China] in Kinberg collection (Figs 2.32, 2.33).

Additional material. Thailand — CUMZ 00417, one spm., Wat Mae Long, Mae Chaem, Chiang Mai (18°13'42.315"N, 98°26'23.003"E). CUMZ 00418, one spm., Lan Sang Waterfall, Mueang, Tak (16°46'36.861"N, 99°0'39.441"E). CUMZ 00312, one spm., Chong Kao Khat (Hellfire Pass), Kanchanaburi (14°22'47.6"N, 98°55'47.7"E).

Diagnosis. 17 antennal articles, 4–6 basal articles glabrous dorsally. Each tooth-plate with 5–8 teeth. Tergites 3–20 with paramedian sutures. Complete margination only on tergite of ultimate leg-bearing segment. Tergite of ultimate leg-bearing segment without depression or median suture. Incomplete paramedian sutures on sternites. Coxopleural process with 3–4 apical, 0–3 subapical and 0–1 lateral spines, without dorsal spine. Ultimate leg prefemora with 4–12 VL, 0–12 VM, 1–5 M, 2 DM, prefemoral process with 3–5 spines. One tarsal spur on legs 1–21.

Composite description. Body length up to 5.3 cm. Blackish colouration on most of dorsal part of body. Cephalic plate dichromatic; anterior part of cephalic plate dark blue or black, posterior margin green yellowish. Antenna dark blue. Tergites dark blue or nearly blackish. All legs light blue, their basal part yellowish. Cephalic plate with median sulcus on anterior part. Posterior part of cephalic plate without paramedian sulci. Antenna usually with 17 articles, basal 4–6 subcylindrical, glabrous dorsally, 3.3 glabrous articles ventrally. Antenna reaching segments 3–4. Forcipular trochanteroprefemoral process with denticles in two groups, one apical and 2–3 inner. Tooth-plates with 5–8 teeth. Tooth-plate with straight, transverse basal suture. Coxosternite smooth, without median suture. Article 2 of second maxillary telopodite with spur.

Anterior margin of T1 underlying cephalic plate. Complete paramedian sutures from TT3–4; tergite margination only on T21 (starting on T15 in holotype). Tergite surfaces smooth, without median sulci. Tergite of ultimate leg-bearing segment with curved, acute posterior margin, lacking median furrow or depression; ratio of width: length of tergite of ultimate leg-bearing segment 0.87:1. Sternites with incomplete paramedian sutures occupying anterior 10–30%. Surface of sternites smooth, without depression. Sternite of ultimate leg-bearing segment with sides converging posteriorly. Porefield on coxopleuron terminating well beneath margin of tergite of ultimate leg-bearing segment, dorsal margin of pore area elevated equally along its length. Coxopleural process moderately long, with 3–4 apical, 0–3 subapical and 0–1 lateral spines, without dorsal spine. Porefree area extending 50–75% length from distal part of coxopleural process to margin of sternite of ultimate leg-bearing segment.

All legs with small setae, without tibial spur. One tarsal spur on legs 1–21. Ultimate legs moderately long and slender, with ratios of lengths of prefemur and femur 1.2:1, femur and tibia 1.2:1, tibia and tarsus 2 1.4:1.; tarsus 1 and tarsus 2 2.6:1. Prefemoral spines: 4–7 VL, 0–3 VM, 1–5 M, 1–7 DM, prefemoral process with 2–5 spines.

Genital segments well developed, reaching longer than distance between posterior margin of sternite of ultimate leg-bearing segment and distal part of coxopleural process. Sternite of genital segment 1 round and convex posteriorly, with median suture. In male, sternite of genital segment 2 well developed. Tergites of genital segments with small setae.

Discussion. This montane species was sometimes collected together with other scolopendrids such as species of *Otostigmus* and *Rhysida*. External phenotypic characters are similar to *S. pinguis* but the unique, diagnostic character that permits species identification is the presence of a tarsal spur on the ultimate legs, which is atypical for *Scolopendra*. However, this character has been reported in some individuals of a few other *Scolopendra* species in Southeast Asia, notably *S. subcrustalis* (see Kronmüller 2009, Lewis 2010b). We also recorded the occurrence of a tarsal spur on the ultimate leg in two juveniles of *S. subspinipes* from Yokohama, Japan (NHMW 758). For this reason, variation in tarsal spurs on legs needs to be used cautiously for justification of species boundaries when sample size is limited. However, *S. calcarata* is readily distinguished morphologically from *S. subspinipes* s.l. and *S. subcrustalis* by the number of glabrous antennal articles (four glabrous dorsally), only the tergite of the ultimate leg-bearing segment showing margination, sternites with incomplete paramedian sutures, and 4–5 apical and subapical spines on the coxopleural process. All specimens from Thailand and the description of Vietnamese populations by Schileyko (1995) consistently exhibited a tarsal spur on the ultimate legs. However, some characteristics seem to be variable between these two populations, such as a count of six glabrous antennal articles in Vietnam versus four in Thailand (four in the original description), the last 4–6 tergites marginated versus only the tergite of the ultimate leg-bearing segment (but in original description, margination starting from TT12 (13)), the sternite of the ultimate leg-bearing segment with a median depression versus its absence, and the arrangement of spines on the ultimate leg prefemur. With respect to the latter, Vietnamese populations exhibited 9–12 VL, 11–12 VM, 2–3 both M and DM, and 2 spines on the prefemoral process versus 4–7 VL, 0–3 VM, 1–2 M, 1–2 DM, and 2–4 spines on the prefemoral process in Thai populations.

Morphological similarity between *S. calcarata* and *S. pinguis* is indicated by several characteristics, including the number of antennal articles, the shape of teeth on theforcipular tooth-plates (these being in the form of minute denticles), and the number of spines on the coxopleural process. In addition, the habitat preferences of these two species resemble each other, both of them being found only in montane territory, and they also show similar dichromatic colouration patterns. There is no evidence from our survey that these two species are distributed sympatrically. These characters are consistent with the molecular phylogeny, which resolves these two species as sister taxa.

Distribution. This species is quite rare in tropical mainland Southeast Asia, usually distributed along mountain ranges in the western territory of Thailand (Fig. 2.29). A few specimens were found in the eastern plateau. Schileyko (1995, 2007) also reported material from northern Vietnam, and Zhang (1992) recorded *S. calcarata* in southern China. We combine all records of this species from previous literature and our new collections to provide and updated distribution as follows: **Southeast Asia:** Thailand (Kanchanaburi, Tak and Chiang Mai) and Vietnam (fide Schileyko (2007): Mai Chau, Tam Dao National Park, Cat Ba National Park and Ba Vi National Park). **East Asia:** South China.

Scolopendra japonica Koch, 1878

Figs 2.7D, 2.9C, 2.29, 2.36–2.41

Scolopendra japonica Koch, 1878: 790. Daday, 1889: 149. Haase, 1887: 48, pl. 3, fig. 48. Takakuwa, 1942: 41, 1943: 171, 1947: 938. Kronmüller, 2012: 24, figs. 3D, 4B.

Scolopendra subspinipes japonica – Kraepelin, 1903: 263. Attems, 1909: 10, 13, 1914: 107, 1930a: 30. Shinohara, 1949: 81, 1961: 75. Takashima, 1949: 11, 1952: 4. Chamberlin and Wang, 1952: 180. Miyosi, 1955: 151. Wang, 1955: 16. Takano, 2001: 211. Lewis, 2010b: 114.

Otostigmus politoides Attems, 1953: 147. Lewis, 2004: 32, figs. 14–17. Kronmüller, 2012: 25.

Otostigmus puncticep Attems, 1953: 146, figs. 16–17. Lewis, 2004: 30, figs 8–13. Kronmüller, 2012: 25.

Type locality. Japan.

Material. Syntype: NHMW Inv. No. 5368, one female from Japan, leg. Roletz, don. Latzel, 1919, det. Attems C (Figs 2.38, 2.39). **Probable syntypes:** NHMW Inv. No. 762, seven spms., Japan, leg. Roletz, red (type) label in bottle.

Additional material. Laos — CUMZ 00297.13, two spms., Phu Fah Mountain, Phongsaly, Laos (21°41'19.6"N, 102°06'30.4"E). CUMZ 00298.15, five spms., Plain of Jar, Xiang Khouang, Laos (19°25'51.5"N, 103°09'10.4"E).

Japan — CUMZ 00319, one spm., Shinshu University, Matsumoto, Japan (36°13'22.4"N, 137°54'35.0"E). NHMUK 1893.1.15.3, one spm., Tokyo. NHMUK 1912.12.12.914, two spms., Izu Peninsula. NHMUK 1937.9.9.59, one spm., Japan, det. K.W. Verhoeff. NHMW Inv. No. 758, six spms., Yokohama. NHMW Inv. No. 755, seven spms., Japan. NHMW Inv. No. 757, one spm., Okayama, leg. H. Sauler. NHMW Inv. No. 759, one spm., Kioto [Kyoto] with anther label "344". NHMW Inv. No. 760, two spms., Kioto [Kyoto], leg. H. Sauler. NHMW Inv. No. 756, two spms., Kanagava [Kanagawa], leg. H. Sauler, 17/11/1905, bottle with labels, "Hans Lauter 4122, Kanagawa 17/11/1905 Jan Haus" and "Hans Lauter 3236, Kanagawa 25/6/1905 Sichen".

Indonesia — NHMUK 1882.62, one spm., Sumatra.

China — NHMUK, one spm., Loc. 273, Peak of Flat No. 2, Hong Kong. NHMUK 1904.7.23.5–8, two spms., YunnanFu [Kunming], South China.

Undetermined — NHMW Inv. No. 761, 17 spms., Kuile? [Possibly referring to Korea?].

Diagnosis. 17–19 antennal articles, 6 basal articles glabrous dorsally. Each tooth-plate with 4–6 teeth. Tergites (3)4–20 with paramedian sutures. Complete margination from TT(10)12–21. Tergite of ultimate leg-bearing segment without depression or suture.

Complete paramedian sutures on sternites 2–20. Coxopleural process with 3 apical spines. Ultimate leg prefemora with 2–3 VL, 1–2 M, 1–3 DM and prefemoral process with 0–5 spines. One tarsal spur on legs 1–19(20).

Composite description. Body length up to 12.9 cm. Two colour morphs; morph 1 with antenna and legs 1–20 yellowish, morph 2 with antenna and legs 1–20 reddish. All tergites greenish brown. Cephalic plate with median sulcus. Paramedian sulci or sutures absent on posterior part. Antenna usually with 18 articles (atypically with 17 or 19), basal 6 subcylindrical and glabrous dorsally), the rest spherical. Antennae reach to tergite 2. Forcipular trochanteroprefemoral process bearing denticles in two groups, one apical and 2–3 inner. Tooth-plates wider than long, with 4–6 teeth. Tooth-plate with straight, transverse basal suture. Coxosternite smooth without median suture. Article 2 of second maxillary telopodite with spur.

Anterior margin of T1 underlying cephalic plate. Complete paramedian sutures from TT3–4; margination typically starting on T10. Tergite surface with median posterior sulci in TT10–20. Tergite of ultimate leg-bearing segment curved posteriorly, without median furrow or depression; ratio of width: length of tergite of ultimate leg-bearing segment 0.82:1. Sternites with complete paramedian sutures, without depression or pit on surface. Sternite of ultimate leg-bearing segment with sides converging posteriorly, surface with obscure depression on median part. Lateral part of coxopleuron with porefield terminating beneath margin of tergite of ultimate leg-bearing segment. Coxopleural process moderately long, usually with three apical spines; porefree area extending 70–90% length from distal part of coxopleural process to margin of sternite of ultimate leg-bearing segment.

All legs without setae and tibial spur. One tarsal spur on legs 1–19 (on leg 20 in one spm.). Ultimate legs: moderately thick and long, with ratios of lengths of prefemur and femur 1.1:1, femur and tibia 1.3:1, tibia and tarsus 2 1.4:1; tarsus 1 and tarsus 2 1.8:1. Prefemoral spines: 2–3(4) VL, 1–2 VM, 1–3 DM, prefemoral process with 0–5 spines.

Genital segments well developed, reaching longer than distance between posterior margin of sternite of ultimate leg-bearing segment and distal part of coxopleural process. Sternite of genital segment 1 round and convex posteriorly, with median suture. Tergites of genital segment without small setae. Gonopod present in male.

Discussion. The validity of *Scolopendra japonica* at the species level was defended by Kronmüller (2012) from morphological surveys of former subspecies of *S. subspinipes*. Diagnostic characters of this species by comparison to the other former subspecies are the number of apical spines on the coxopleural process (*S. subspinipes* s.str. having two apical spines versus *S. japonica* having three spines, including a subapical spine), and the number of ventral spines on the prefemur of the ultimate legs. With respect to the latter, *S. japonica* has three spines whereas *S. subspinipes* s.str. has only two, although in this study an asymmetrical number of spines in *S. japonica* was also found in syntypes (Fig. 2.39C–F). Four specimens among the *japonica* syntypes have been recorded as presenting only two or three ventral spines on the prefemur of the ultimate leg either on only one side or on both (six spines is the observed maximum). This variability might represent ontogenetic variation more so than geographical variation. Chao (2008) cited the lack of a tarsal spur on leg 20 as an additional diagnostic character for this species but from our study one specimen of *S. japonica* from the Izu Peninsula, Japan (NHMUK 1912.12.12.914), also exhibits a tarsal spur on leg 20. As such, the occurrence of a spur on leg 20 and number of ventral spines on the ultimate leg prefemur are not completely reliable for diagnosing *S. japonica*.

The sympatric distribution of this species and former subspecies of *S. subspinipes* as well as other Asian temperate *Scolopendra* complicates morphological delimitation of species boundaries except using the three phenotypic characters discussed above. In this paper, we compared taxonomic characters based on collections in the NHMUK and NHMW (Table 2.8). Additional characters of these two species that might be useful for species identification are the proportions of the ultimate leg podomeres and the number of spines on the prefemoral process on the ultimate leg. In *S. subspinipes* s.str., two spines are usually present on the prefemoral process whereas in *S. japonica* there are typically three. The length of the antenna also permits a distinction berween these two species; the antenna extends backwards only as far as TT2–3 in *S. japonica* whereas it can reach to TT4–5 in *S. subspinipes* (Figs

2.10A, 2.14B and 2.36A). Moreover, molecular analysis of three combined genes (COI, 16S and 28S) indicated a genetic distinction between *S. japonica* and *S. subspinipes* (Fig. 2.1), and the validity of these species has been corroborated herein. Ratios of ultimate leg podomeres have been used as diagnostic characters of some putative species of *Scolopendra* in Asia, such as *S. negrocapitis* Zhang and Wang, 1999 from Jingshan (northeast coastal area of China). The authors mentioned the close similarity between that species and *S. japonica* but the Chinese species can be distinguished from the latter only by the width:length ratio of the ultimate leg prefemur, which is twice as long as broad. The lack of further information from fresh material from the type locality and molecular data from *S. negrocapitis* renders the status of these two closely related species questionable.

In the current phylogenetic framework of *Scolopendra*, *S. japonica* is resolved in the same clade as *S. cingulata* Latreille, 1829. The two species are morphologically similar despite their markedly disjunct distributions, i.e., *S. cingulata* in the Mediterranean versus *S. japonica* in East Asia (Table 2.8). However, exploration of microrefugia of populations of *S. cingulata* during glacial maxima in Europe (Simaiakis et al. 2012, Oeyen et al. 2014) and a record of *S. japonica* in the northern part of Laos could indicate that these two species may be more widespread than previously recognised. However, distributional data for *S. japonica* are patchy due to incomplete faunistic surveys in several parts in Asia. For these reasons, the relationship between these two species warrants further scrutiny in both morphological and molecular studies.

Distribution. Probably distributed throughout the temperate zone of East Asia including mainland and insular territory (Fig. 2.29). The distribution range is likely to be sympatric with several Asian species (*S. subspinipes*, *S. multidens*, *S. dawydoffi* and *S. dehaani*). Previous study on the subspecies complex of *S. subspinipes* indicated that *S. japonica* might occur in northern Vietnam (Tonkin) and Cambodia, based on the type localities of "*Otostigmus politoides* Attems, 1953" and "*Otostigmus puncticeps* Attems, 1938" (= *S. subspinipes* fide Lewis 2004), the types of both of which are adolescent stages (Kronmüller 2012) that are compatible with *S. japonica*. The current distribution of this species gathered from previous literature and this study is as follows: **Southeast Asia:** Vietnam (Chapa, Tonkin [probably referring to Sa Pa, Lao Cai Province, northern Vietnam]), Laos (Phongsaly and Xieng Khuang), Cambodia (Ream, Koh Kong Island and Sre Umbell [Sre Ambel]), Indonesia (Sumatra). **East Asia:** Japan (Yokohama, Enoshima, Murayama, Tokyo, Matsumoto, Kanakawa, Sendai, Kii, Hachijo island and Izu Peninsula), Taiwan and China (Hong Kong, YunnanFu [Kunming] and Ningbo).

Scolopendra pinguis **Pocock, 1891**

Figs 2.7E–F, 2.25C, 2.29, 2.42A–B, 2.43–2.47

Scolopendra pinguis Pocock, 1891b: 411, 1894: 312, pl. 19, fig. 4. Kraepelin, 1903: 249. Attems, 1907: 80, 1914a: 106, 1930b: 27. Lewis, 2010b: 109.

Type locality. 1,000–2,000 ft., Carin Mountain, Cheba District, Burma [KayahKaren Mountains, Myanmar].

Material. Type material. This species was described based on one specimen and the holotype was probably destroyed. It was collected during a field expedition to Burma (Myanmar) by Leonardo Fea, the assistant zoologist at the Museo Civico di Storia Naturale di Genova, Genova, Italy. In 1891, Pocock published on the myriapods of Burma based on Fea and Oates's collections. Subsequently most of Oates's collection was deposited in the NHMUK while Fea's collection was sent back to Genova. The holotype of *S. pinguis* was explicitly identified as part of Fea's collection (Pocock 1891: 411). In 1970, the basement of the museum in Genova was flooded and parts of the collection were irreparably damaged. The holotype of *S. pinguis* cannot presently be found (M. Tavano, written comm., November 2015) and is presumed to have been lost during that flood.

Additional material. Thailand — CUMZ 00314, one spm., Phamone Cave, Pangmapha, Maehongson (19°30'01.6"N, 98°16'43.5"E). ZMUC 00101107, one spm., Siribhum Waterfall, Chomthong, Chiang Mai (18º32'49"N, 98º30'57"E), 1315 m, leg. C. Sutcharit, 13/10/2009. ZMUC, four specimens, 0–1.400 m, Doi Suthep National Park, leg. Bergit Degerbol, specimen Nos. 1841, 1828, 694 Loc. 3 and 2026. CUMZ 00313, one spm., Ban Pang Pan, Maetaeng, Chiang Mai (19°12'17.4"N, 98°40'00.7"E).CUMZ 00305, one spm., Phusang Waterfall, Phayao (19°37'10.2"N, 100°21'54.7"E). CUMZ 00307, one spm., Hui NamUn, Wiangkhum, Nan (18°30'22.8"N, 100°31'49.1"E). CUMZ 00311, one spm., Tat Ton Waterfall, Chaiyaphum (16°01'05.2"N, 102°01'24.4"E). CUMZ 00303, one spm., Wat Tham Lijia, Sangkhlaburi, Kanchanaburi (15°04'12.8"N, 98°33'56.4"E).

Laos — CUMZ 00304, one spm., Wiang Thong Hot Spring, Mueang Ieam, Houaphanh (20°04'45.2"N, 103°44'33.3"E). CUMZ 00310, two spms., Kra Cham Waterfall, Luang Prabang (19°32'27.3"N, 101°59'02.3"E). CUMZ 00306, one spm., Ban NaTon, Muang Khun, Xieng Khouang (17°52'31.4"N, 104°51'44.7"E). CUMZ 00309, one spm., Kao Rao Cave, Bo Kaeow (20°41'56.6"N, 101°05'46.8"E).

Diagnosis. 17 antennal articles, 3–4 basal articles glabrous dorsally. Each tooth-plate with 6 teeth. Tergites 3–20 with paramedian sutures. Complete tergite margination from TT16 (18)–21. Tergite of ultimate leg-bearing segment without depression or suture. Paramedian sutures on anterior 10–30% of sternites. Coxopleural process with 3–7 apical + subapical, 1–2 lateral and 0–1 dorsal spines. Ultimate leg prefemora with 6–12 VL, 1–12 VM, 2–3 M, 3–4 DM and prefemoral process with 3–4 spines. One tarsal spur on legs 1–19(20).

Composite description. Body length up to 85 mm. Darkish blue colouration on entire body. Cephalic plate dichromatic in some populations. Tergites dark blue or nearly black. Cephalic plate with small punctae on anterior part, median sulcus present. Posterior part of cephalic plate without paramedian sulci. Antenna usually with 17 articles, basal 3–4 subcylindrical and glabrous dorsally, 5–5.5 articles glabrous ventrally. Antennae reach segment 4. Forcipular trochanteroprefemoral process bearing denticles in two groups, one apical and 2–3 inner. Tooth-plates wider than long or nearly equivalent, with 6 teeth. Tooth-plate with straight, transverse basal suture. Coxosternite smooth, without median suture. Article 2 of second maxillary telopodite with spur.

Anterior margin of T1 underlying cephalic plate. Complete paramedian sutures from T3; margination typically from TT16–18 (atypically, only on ter gite of ultimate leg-bearing segment in one specimen: CUMZ 00311). Tergite surface smooth, without median sulci. Tergite of ultimate leg-bearing segment curved and acute posteriorly, without median furrow or depression; ratio of width: length of tergite of ultimate leg-bearing segment 0.82:1. Anterior part of sternites with short paramedian sutures reaching approximately 20–30% length of sternite (atypically to 60%). Surface of sternites smooth. Sternite of ultimate leg-bearing segment with sides converging posteriorly; without depression. Porefield on coxopleuron reaching to margin of tergite of ultimate leg-bearing segment, dorsal margin of pore field sinuous. Coxopleural process moderately long or short with 3 apical, 0–3 subapical, 0–1 dorsal and 1 lateral spine(s). Porefree area extending 30–45% length from distal part of coxopleural process to margin of sternite of ultimate leg-bearing segment.

All legs with small setae on tarsus 2. Tibial spur absent on all legs. One tarsal spur on legs 1–19(20). Ultimate legs: thick and moderately long, with ratios of lengths of prefemur and femur 1.3:1, femur and tibia 1:1; tibia and tarsus 2 1.2:1; tarsus 1 and tarsus 2 2.2:1. Prefemora and femora flattened posteriorly, with robust or acute blackish prefemoral spines. Prefemoral spines: 6–12 VL, 1–12 VM, 2–3 M, 3–4 DM, prefemoral process with 3–4(7) spines. Posterior margin of prefemur with short median groove.

Genital segments well developed, reaching longer than distance between posterior margin of sternite of ultimate leg-bearing segment and distal part of coxopleural process. Sternite of genital segment 1 round and convex posteriorly, with median suture. Gonopod present in male. Lamina subanalis situated between genitalia and anal valve; lamina analis between anal valve and tergite of genital segment. In male, tergite and sternite of genital segment and gonopods with small setae.

Colouration. According to Siriwut et al. (2015a), *S. pinguis* exhibits four colour morphs which can classified as either monochromatic or dichromatic. All of these patterns are specific to populations, with no mixing or sympatry found in our surveys. The full description of each colour morph is given below:

Colour morph 1A: Monochromatic, all segments including cephalic plate dark blue. Antenna dark blue on basal part, light blue on distal part. Pleuron with pale blue integument, all pleurites black. All legs blue, legs 19–21 dark blue. This morph has been found only in Thailand.

Colour morph 1B: Monochromatic, all segments including cephalic plate dark blue. Antenna dark blue on basal part, light blue on distal part. Pleuron with pale blue integument, all pleurites black. Most legs yellowish on prefemur, other podomeres dark blue with yellowish band bordering articulations; last three legs dark blue or black. This morph has been found only in Thailand.

Colour morph 2A: Dichromatic, cephalic plate dark blue on anterior part, yellowish on posterior part and T1. Antenna dark blue on basal part, light blue on distal part. Pleuron with pale blue integument, all pleurites black. All legs dark blue or black. This morph has been found both in Thailand and NorthCentral Laos.

Colour morph 2B: Dichromatic, cephalic plate dark blue on anterior part, yellowish on posterior part and T1. Antenna dark blue on basal part, light blue on distal part. Pleuron with pale blue integument, all pleurites black. All legs yellowish on prefemur, other podomeres light blue with yellowish band bordering articulations. This morph has been found both in Thailand and NorthCentral Laos.

Discussion. *Scolopendra pinguis* has not been revised since Pocock (1891) described the holotype from Burma. Two additional records from BataviaBuitenzorg (Bogor, Java) expanded its geographical distribution across Southeast Asia (Pocock 1894). Kraepelin (1903) confirmed additional material from Buitenzorg; Bogor, Java. Attems' (1930b) monograph followed Kraepelin's description and argued that this species is similar to another Javan species, *S. gracillima*. This argument has been followed in several subsequent taxonomic reviews (Schileyko 1995, 2007, Lewis 2010b). Comparative taxonomic characters of these two species (Table 2.9) can, in the present state of knowledge, be used to defend species validity until further data (e.g., molecular data for both species from Java) can be considered. Another related species from northwestern India, *Scolopendra ellorensis* Jangi and Dass, 1984, was also noted to be morphologically similar to *S. pinguis.* However, this Indian species was decribed from one juvenile specimen (31 mm) that might not permit confident comparison (Lewis 2010b). Molecular phylogenetic analysis of *S. pinguis* revealed a high level of genetic divergence among populations that might suggest regional endemism and the possibility of cryptic species. The latter would be consistent with the marked degree of colour polymorphism noted above.

Distribution. A native species in Southeast Asia, distributed along the montane ranges between the ThailandBurma borders (Fig. 2.29). The updated distribution of *S. pinguis* is as follows: **Southeast Asia:** Myanmar (type locality), Thailand (Kanchanaburi, Mae Hong Son, Chiang Mai, Phayao, Chiyaphume and Loei), Laos (Bo Kaew, Luang Prabang, Vientien and Houaphanh) and Indonesia (Batavia, Buitenzorg [Bogor], Java).

Scolopendra dawydoffi **Kronmüller, 2012**

Figs 2.7B, 2.29, 2.42C, 2.48–2.53

Scolopendra subspinipes cingulatoides Attems, 1938: 335, fig. 307, 1953: 138. Schileyko, 1998: 268, 2001: 434, 2007: 76. Lewis, 2010b: 112, fig. 24. Tran et al., 2013: 229.

Scolopendra dawydoffi Kronmüller, 2012: 22, table 1, fig. 4E [new replacement name]. Tran et al., 2013: 229. Siriwut et al., 2015a: 1.

Type locality. Two localities were reported in the original description, Hagiang, Haut Tonkin [Hà Giang Province, northern Vietnam], and Thakek, Laos [Thakhek, Khammouane Province, Laos].

Material. Syntypes NHMW Inv. No. 8234, two females labeled "*Scolopendra subspinipes cingulatoides* Attems, 1934 typus by Attems", Thakek, Laos (Figs 50, 51).

Additional material. Thailand — ZMUC 1/7.59, one adult female and 13 juvenile spms., labeled as "*Scolopendra subspinipes*", Phu Kradueng, Loei, 1300 m, evergreen forest, 24/11/1958, leg. B. Degerbol. CUMZ 00294 two adult spms., Wat Thang Biang, Pak Chong, Nakhon Ratchsrima (14°32'22.0"N, 101°21'54.6"E). CUMZ 00290, one spm., Sakaerat Biosphere Reserve Center, Nakon Ratchasima (14°30'36.5"N, 101°55'51.5"E). CUMZ 00272.1–2, two spms., Saphan Hin Waterfall, Khlong Yai, Trad (12°06'06.0"N, 102°42'39.2"E) **Malaysia** — NHMUK.1950.4.19.12, one spm., Kelantan, Malay Peninsula (labeled as "*Scolopendra subspinipes*").

Diagnosis. 17–18 antennal articles, 6 basal articles glabrous dorsally. Each tooth-plate with 5–10 teeth. Tergites 2(3)20 with paramedian sutures. Complete tergite margination from TT11–21. Tergite of ultimate leg-bearing segment without depression or suture. Paramedian sutures on anterior 15–60% of sternites. Coxopleural process with 2–3 apical+subapical spines. Ultimate leg prefemora with 1–2 VL, 0–2 M, 0–2 DM, prefemoral process with 1–5 spines. One tarsal spur on legs 1–19.

Composite description. Body length up to 16.2 cm (14.7 and 15.1 cm in syntypes). Reddish colouration on entire body. Cephalic plate and tergites dichromatic. Cephalic plate and tergites reddish orange; posterior border of tergites with dark band. Cephalic plate with small punctae; median sulcus present. Posterior part of cephalic plate without paramedian sulci. Antenna usually with 18 articles (sometimes 17 on one side in some specimens), basal 6 subcylindrical and glabrous dorsally, 5–5.5 articles glabrous ventrally. Antennae reach segment 4. Forcipular trochanteroprefemoral process with denticles in two groups, one apical and 2–3 inner. Anterior part of coxosternite with tooth-plates, wider than long or nearly equivalent, 5–7 robust teeth; atypically with 10 teeth (CUMZ 00272). Tooth-plate with straight, transverse suture. Coxosternal surface smooth, without median suture. Article 2 of second maxillary telopodite with spur.

Anterior margin of T1 underlying cephalic plate. Complete paramedian sutures on TT2–3; margination typically from TT11–14. Tergite surfaces smooth, without median sulci. Tergite of ultimate leg-bearing segment curved posteriorly, without median furrow or depression; ratio of width: length of tergite of ultimate leg-bearing segment 0.7:1. Anterior part of sternites with short paramedian sutures reaching approximately 15–30% (atypically, to 60% in one specimen: CUMZ 00272). Surface of sternites smooth, mostly with depression (small circular pit present on posterior median part of sternite in one specimen: CUMZ 00294). Sternite of ultimate leg-bearing segment with sides converging posteriorly. Porefield on coxopleuron terminating beneath margin of tergite of ultimate leg-bearing segment, dorsal margin of pore area sinuous, most elevated anteriorly. Coxopleural process moderately long or short with two apical spines and one subapical spine (atypically only two apical spines); porefree area extending 65–90% length from distal part of coxopleural process to margin of sternite of ultimate leg-bearing segment.

All legs without setae and tibial spur. One tarsal spur on legs 1–19. Ultimate legs: thick and moderately long, with ratios of lengths of prefemur and femur 1.3:1, femur and tibia 1.3:1, tibia and tarsus 2 1.8:1, tarsus 1 and tarsus 2 1.7:1. Prefemora flattened dorsally (atypically rounded), with robust blackish spines. Prefemoral spines: 1–2 VL, 0–2 M, 0–2 DM, prefemoral process with 1–3 spines, atypically with 5 spines. Posterior margin of prefemur with shallow median groove

Genital segments well developed, reaching longer than distance between posterior margin of sternite of ultimate leg-bearing segment and distal part of coxopleural process. Sternite of genital segment 1 round and convex posteriorly, with median suture. Sternite of genital segment 2 developed. Gonopod absent in male. Lamina subanalis between genitalia and anal valve; lamina analis between anal valve and tergite of genital segment. Tergite and sternite of genital segments with small setae. Penis with apical bristle.

Discussion. This species is distinguished from *S. subspinipes* by its short, robust ultimate legs and three apical/subapical spines on the coxopleural process. The characteristic of incomplete paramedian sutures on the sternites further distinguishes it from *S. subspinipes* and *S. japonica* (which have complete paramedian sutures on the sternites). However, *S. dawydoffi* is similar to *S. multidens* in the absence of gonopods in the male. The distribution of *S. dawydoffi* is restricted to mainland Southeast Asia whereas *S. multiden*s occurs in temperate regions of Asia, including both inland and insular parts. A specimen identified as *S. multidens* from Vietnam is genetically differentiated from Thai populations (see discussion of *S. multidens* above for molecular arguments in favour of the two taxa being separate species). Moreover, to test the hypothesis that characteristics of *S. dawydoffi* might indicate affinities to the *cingulata* group (with reference to the Mediterranean species *S. cingulata*; Attems 1930a), as implied by the original "*cingulatoides*" name for *S. dawydoffi,* our phylogenetic analysis included *S. cingulata* sequences from Spain. The result (Fig. 2.1) demonstrated that *S. dawydoffi* was not grouped together with *S. cingulata* but should be recognized as a distinct species based on its genetic distance and geographical distribution. A morphological comparison between these two species is presented in Table 2.10.

Distribution. This species was formerly reported from only two occurrences in Southeast Asia, one in each of Laos and Vietnam (Attems 1938). We add more material from Thailand and some adjacent areas based on museum collections. The updated distribution range (Fig. 2.29) is as follows: **Southeast Asia:** Thailand (Nakhon Ratchasima, Loei and Trad), Laos (Thakhek), Malaysia (Kelantan state) and Vietnam (fide Tran et al. 2013: Ha Giang, Hanoi, Thai Nguyen and Ha Tinh).

Scolopendra cataracta **Siriwut, Edgecombe and Panha, sp. n.**
http://zoobank.org/
Figs 2.28C–D, 2.29, 2.54–2.58

Type locality. Tad Etu Waterfall, Bolaven Plateau, Pakse, Champasak, Laos (15°13'10.6"N, 105°55'31.3"E) (Fig. 2.54B).

Materials. Holotype CUMZ 00316, adult specimen from type locality (Fig. 54A). **Paratypes** CUMZ 00317, one adult, TadYueang Waterfall, Mueang Singh, Luang Namtha, Laos (15°09'55.1"N, 106°06'10.6"E). NHMUK 010305528, one adult, Kao Sok National Park, Surat Thani, Thailand, labeled as "a distinct population of *Scolopendra subspinipes* but without paramedian sutures on the tergites", det. J.G.E. Lewis, leg. G. Beccaloni, 2001. NHMUK 1928.5.30.7, one adult, BacKan, Vietnam, labelled as "*Scolopendra subspinipes*". NHMUK 1928.5.30.6, one female, DacTo, Annam [Vietnam], DelacourLowe expedition.

Etymology. From "*cataract*", meaning waterfall, for the type locality at Tad Etu Waterfall.

Diagnosis. 18–19 antennal articles, 6 basal articles glabrous dorsally. Cephalic plate punctate. 5–6 teeth on tooth-plate. Tergites 7(14)20 with paramedian sutures, all incomplete, present only on anterior and posterior parts. Tergite of ultimate leg-bearing segment without depression or suture. Paramedian sutures confined to anterior 15–20% of sternites. Coxopleural process with 1–3 apical+subapical spines, 0–1 dorsal spine, without lateral spine. Ultimate leg prefemora with 1–2 VL, 1–2 M, 0–2 DM and prefemoral process with 1–3 spines. Tarsal spur on legs 1–19(20).

Holotype description (variation of paratypes is given in parentheses). Body length 12.8 cm (up to ca. 20 cm long in paratype NHMUK 1928.v.30.6). Blackish colouration on entire body. Cephalic plate and segments monochromatic. Tergites dark greenish or black. Cephalic plate without small punctae on anterior part; median sulcus present. Posterior part of cephalic plate without paramedian sulci. Antenna usually with 19 articles (atypically with 18 articles on one side), basal 6 glabrous dorsally, 5–5.5 glabrous ventrally. Antennae reach segment 4(5). Forcipular trochanteroprefemoral process with denticles in two groups, one apical tooth and (2)3–4 inner. Tooth-plates wider than long or nearly as long as wide, with 6 teeth (5 in NHMUK 1928.5.30.6). Tooth-plate with straight, transverse basal suture. Coxosternal surface smooth, without median suture. Article 2 of second maxillary telopodite with spur.

Anterior margin of T1 underlying cephalic plate. Incomplete paramedian sutures on all tergites; margination typically starting on T7 (TT10–14). Tergite surface smooth, with median sulci starting from TT5–20. Tergite of ultimate leg-bearing segment curved posteriorly, without median furrow or depression; ratio of width: length of tergite of ultimate leg-bearing segment 1.1:1. Anterior part of sternites with short paramedian sutures confined to approximately 20–45% length of sternite. Surface of sternites smooth. Sternite of ultimate leg-bearing segment with sides converging posteriorly; surface without depression. Porefield on coxopleuron extending to and overlapped by margin of tergite of ultimate leg-bearing segment, dorsal margin of pore area sinuous, most elevated anteriorly. Coxopleural process moderately long or short with 2–3 apical+subapical spines (spines atypically absent on one side; CUMZ 00317), without lateral spine (one paratype with one dorsal spine on one side: CUMZ 00317). Pore free area extending 30–90% length from distal part of coxopleural process to margin of sternite of ultimate leg-bearing segment.

All legs without setae and tibial spur. One tarsal spur on legs 1–20 (1–19 in one paratype, CUMZ 00317). Ultimate leg: long and slender, with ratios of lengths of prefemur and femur 1.1:1, femur and tibia 1.1:1, tibia and tarsus 2 1.3:1; tarsus 1 and tarsus 2 1.9:1. Prefemora flattened dorsally with acute blackish spines. Prefemoral spines: 2 VL, 1 M, 0–1 DM, prefemoral process with 2 spines (Paratypes: 1–2 VL, 1–2 M, 0–2 DM and prefemural process with 1–3 spines).

Genital segments well developed, reaching longer than distance between posterior margin of sternite of ultimate leg-bearing segment and distal part of coxopleural process. Sternite of genital segment 1 round and convex posteriorly, with median suture. Tergites of genital segment lacking small setae. Presence of gonopods and penis uncertain because genitalia are mostly retracted in holotype and paratypes; only two female specimens show genital segments (NHMUK 010305528 and 1928.5.30.6).

Remarks. The paratype collected in Thailand in 2001 (NHMUK 010305528) was observed to display apparent amphibious habits. The following account is based on observations by G. Beccaloni (pers. comm., Jan. 2016). The centipede was initially observed under a rock slab beside a stream ca. 1.5 m wide and 20 cm deep. It escaped into the stream and concealed itself under a rock. After extraction from the stream it was placed in a glass container of water, in which it swam powerfully on the bottom of the container with vigorous horizontal undulating motions.

Discussion. This species exhibits an atypical characteristic for scolopendromorphs, namely incomplete paramedian sutures on the tergites. Very few members in only three genera share this character, these being within *Scolopocryptops* Newport, 1844, *Scolopendra* and *Rhysida* Wood, 1862. Within *Scolopendra*, only two described species, *S. hainanum* from Hainan Island, China, and “*S. subspinipes piceoflava*” (treated above as a synonym of *S. subspinipes* following Kronmüller (2012)), from Sulawesi, Indonesia, have been reported to lack or have nearly absent paramedian sutures on the tergites. *Scolopendra cataracta* and “*S. subspinipes piceoflava*” can be distinguished from each other by: paramedian sutures confined to the posterior part of tergites in *S. cataracta* vs complete sutures in “*S. subspinipes piceoflava*”, very short paramedian sutures on the sternites vs sutures extending along 80–100% the length of the sternites, and three apical/subapical spines on the coxopleural process vs one or two.

Scolopendra cataracta differs from *S. hainanum* by the short paramedian sutures on the sternites versus being nearly complete in *S. hainanum*, the number of spines on the coxopleural process (three vs one or two), and the number of VL spines on the ultimate leg prefemora. The two species can also be distinguished by their colouration patterns and their distributions, though the latter are closely associated. For these reasons, we regard *S. cataracta* as distinct from *S. hainanum*, and its sampled populations group as monophyletic for each partial gene analysis (see Table 2.11 for morphological comparison). It is likewise morphologically distinct from *S. subspinipes*, *S. multidens* and *S. dawydoffi*. DNA sequences are not available for *S. hainanum* but would be useful to study the relationship between these two apparently related species.

Distribution. All localities are in mainland territory. The currently known distribution (Fig. 2.29) is as follows: **Southeast Asia:** Laos (Champasak and Luang Namtha), Thailand (Surat Thani) and Vietnam (Bac Kan and DacTo).

Acknowledgment

The authors sincerely thank all members of the Animal Systematics Research Unit and Department of Biology, Faculty of Science, Chulalongkorn University, for field collecting and technical support. We give special thanks to T. Krutchuen for her excellent drawings and to T. Asami, K. Inkhavilay and B. Ng for collecting in Japan, Laos and Malaysia. We also extend thanks to N. Akkari, H. Sattmann, V. Stagl and E. Schiller at NHMW, and to J. and G. Beccaloni, V. Blagoderov and R. Summerfield at NHMUK for their valuable assistance, field collection data and hospitality during visits by WS, GDE and SP. H. Enghoff (ZMUC), K.S. Kronestedt (NHRS) and E. Stöckli (NMB) kindly arranged loans of specimens, including types, and R. Poggi and M. Tavano (MSNG) provided type information. We gratefully acknowledge the Thailand Research Fund for financial support through the Royal Golden Jubilee Ph.D. Program (Grant No. PHD/0066/2553) and a cofunded Scholarship for oneyear Ph.D. placement in the UK by Newton Fund to SP and WS. The main funding for this project is from the Thailand Research Fund (TRF) under TRF Senior Research Scholar RTA 5880002 (2015–2017) to SP. The authors thank the Plant Genetic

Conservation Project under the Initiative of Her Royal Highness Princess Maha Chakri Sirindhorn, Centre of Excellence on Biodiversity and Sakaerat Environmental Research Station for permission and support in several remote and restricted areas. Sincere thanks are extended to the journal's referees, J.G.E. Lewis, A.A. Schileyko and V. Vahtera, for valuable comments that substantially improved the manuscript.

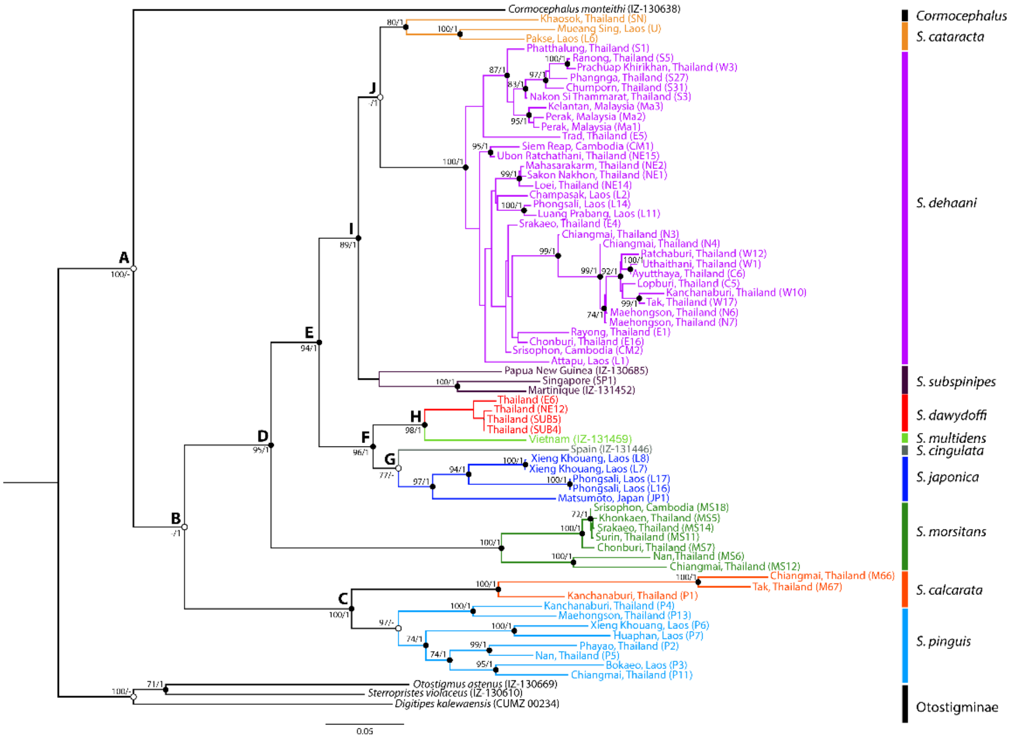


Figure 2.1 Maximum likelihood tree for *Scolopendra* in mainland Southeast Asia: colours for clades correspond to species and outgroups; black and white circles indicate statistical support values in both ML and BI analyses or only ML or BI analysis, respectively. Numbers at nodes are bootstrap support and posterior probability. Specimen codes in parentheses following localities correspond to Siriwut et al. (2015a, b: table 2) and Vahtera et al. (2013: table 1)

Figure 2.2 Colouration pattern during developmental stages of most *S. morsitans* populations in mainland Southeast Asia: **A** Juvenile stage **B** Adult stage (Colour morph 1).

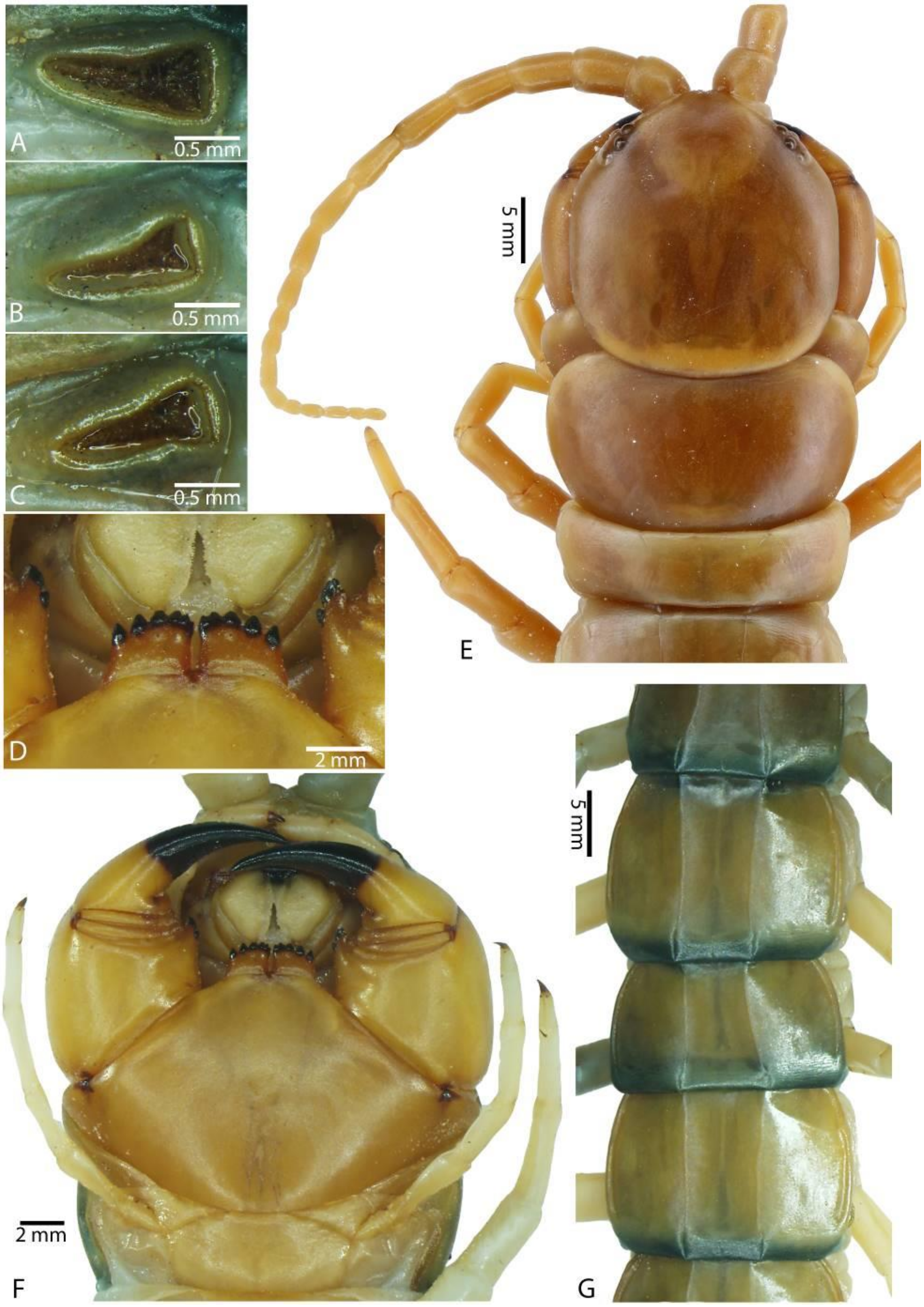


Figure 2.3 *Scolopendra morsitans* (CUMZ 00344): **A–C** Spiracles 3, 5 and 8, respectively **D** Tooth-plates **E** Cephalic plate and trunk segments 1–2 **F** Forcipular segment **G** Tergites 9–11.

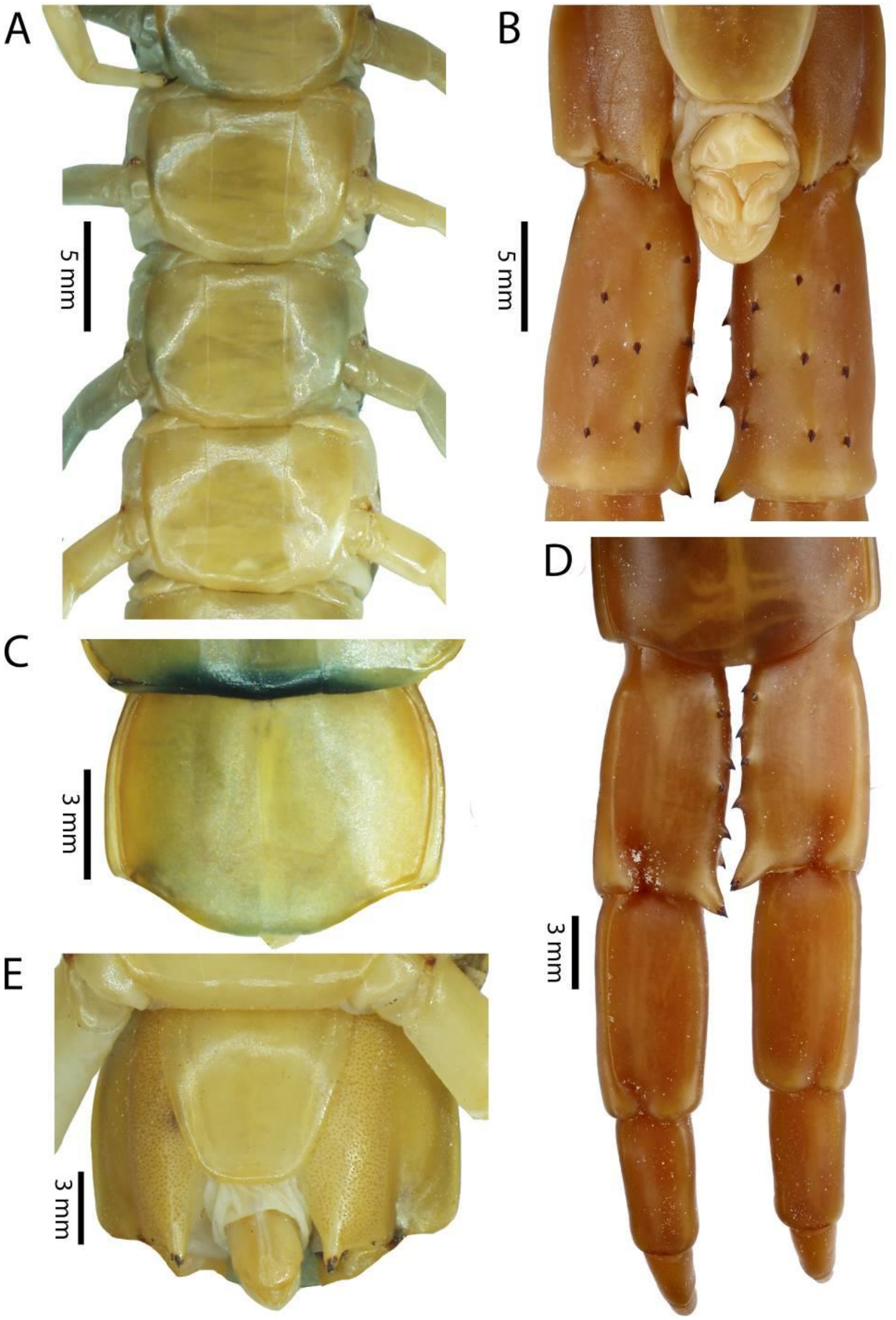


Figure 2.4 *Scolopendra morsitans* (CUMZ 00344, NHMUK 1889.7.15.14): **A** Sternites 9–11 **B** Coxopleura and ventral view of ultimate leg prefemora **C** Tergite of ultimate leg-bearing segment **D** Dorsal view of ultimate legs **E** Sternite of ultimate leg-bearing segment and coxopleura.

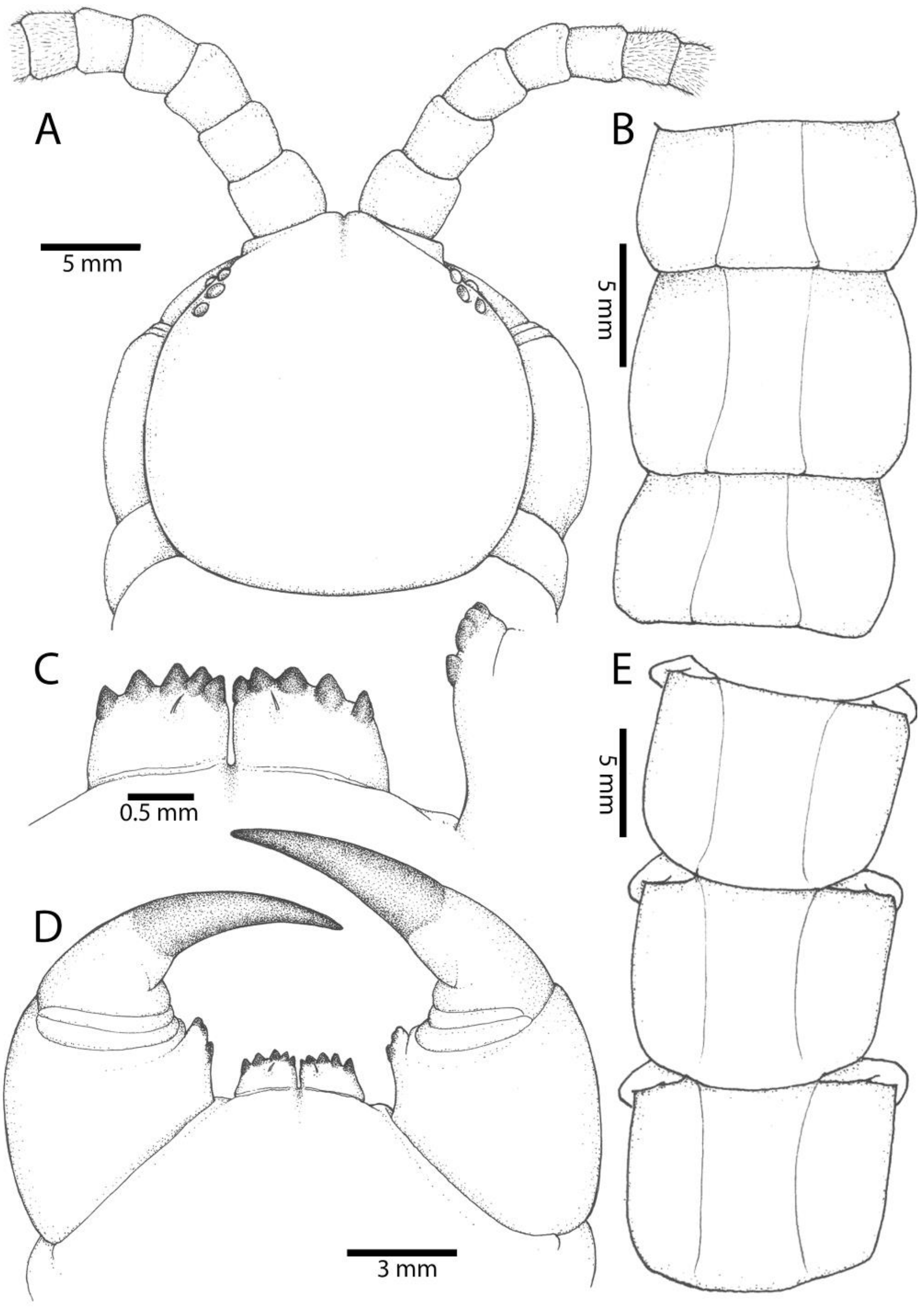


Figure 2.5 *Scolopendra morsitans* (CUMZ 00300, 00344): **A** Cephalic plate and basal antennal articles **B** Tergites 9–11 **C** Teeth on tooth-plates and trochanteroprefemoral process **D** Forcipular segment **E** Sternites 9–11.

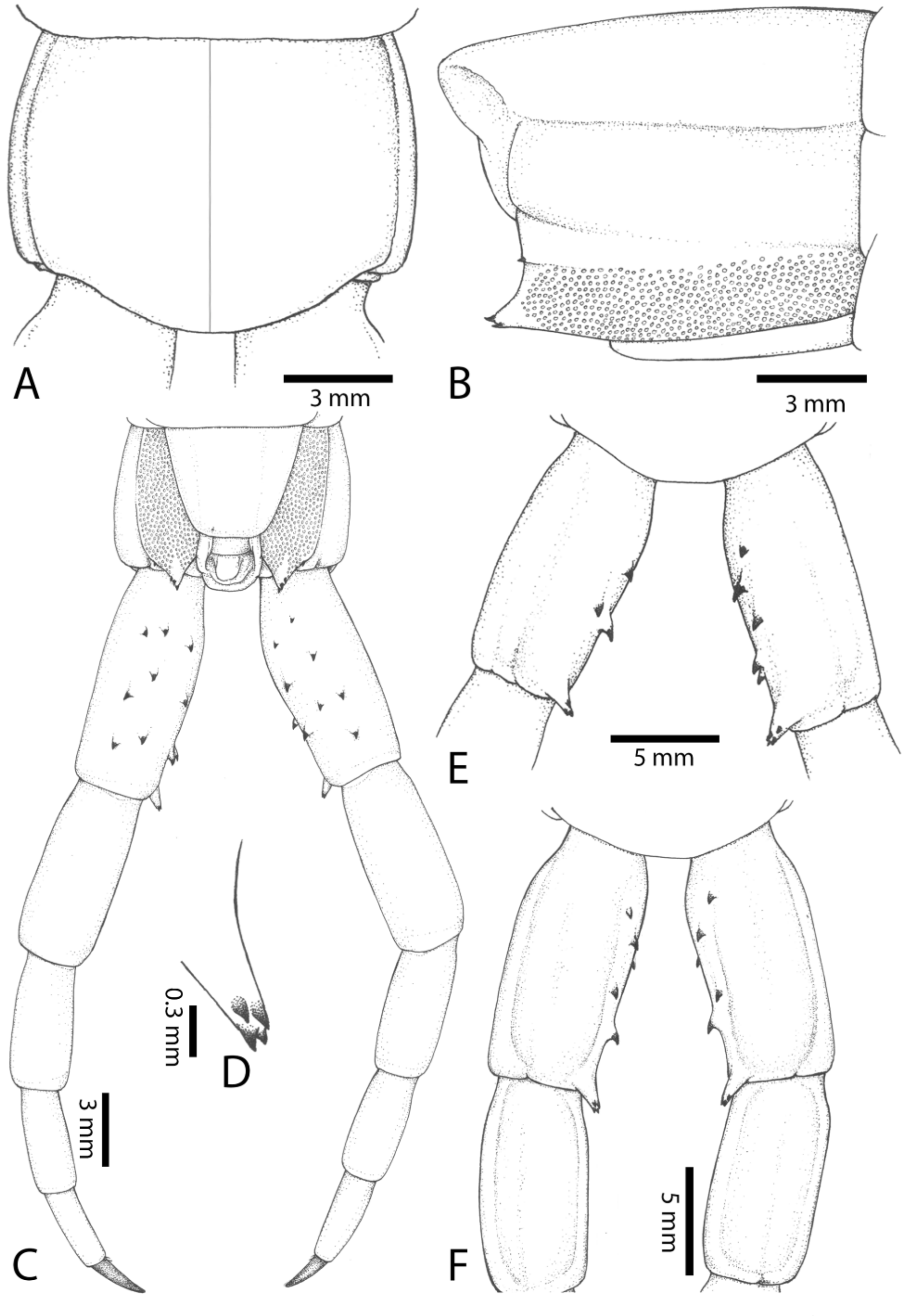


Figure 2.6 *Scolopendra morsitans* (CUMZ 00300, 00344): **A** Tergite of ultimate leg-bearing segment **B** Lateral view of coxopleuron **C** Sternite of ultimate leg-bearing segment, coxopleura and ultimate legs **D** Spines on prefemoral process of ultimate leg **E**–**F** Spines on ultimate leg prefemora and margination on prefemora and femora (dorsal view).

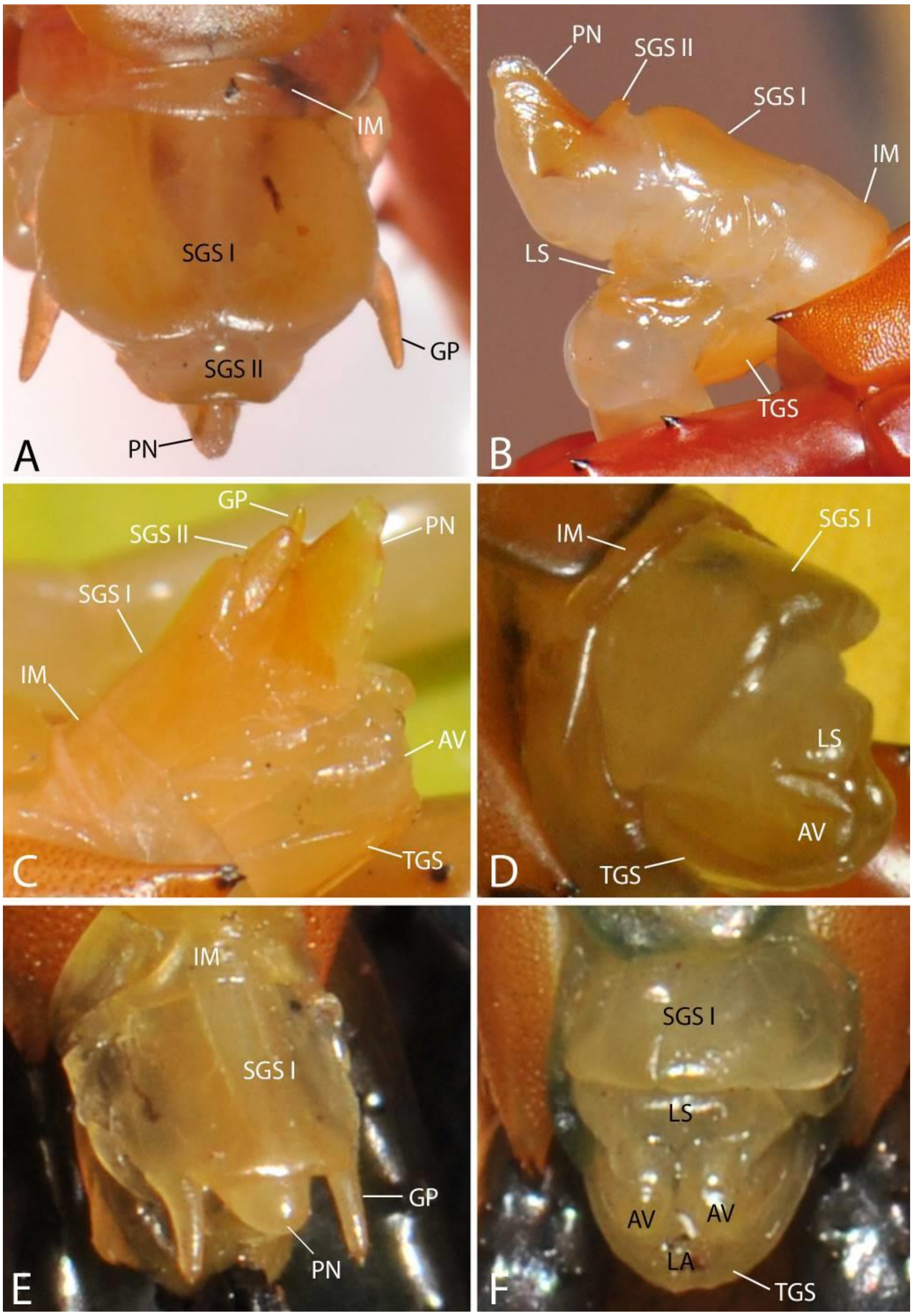


Figure 2.7 Genital segments in some live *Scolopendra* specimens:**A** *Scolopendra dehaani* (male) **B** *Scolopendra dawydoffi* (male) **C** *Scolopendra morsitans* (male) **D** Scolopendra japonica (female) **E** *Scolopendra pinguis* (male) **F** *Scolopendra pinguis* (female).

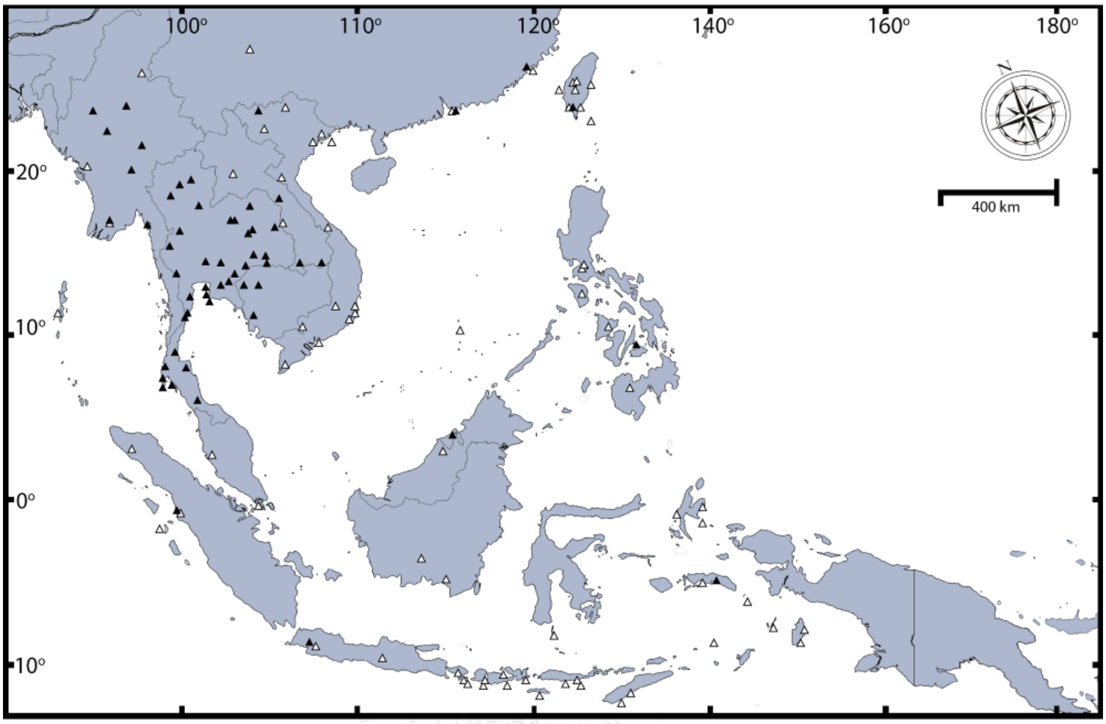


Figure 2.8 Distribution map of *Scolopendra morsitans* in Southeast Asia: Filled triangles indicate data from material examined herein; blank triangles indicate localities in the literature (Shelley et al. 2005, Schileyko 2007).

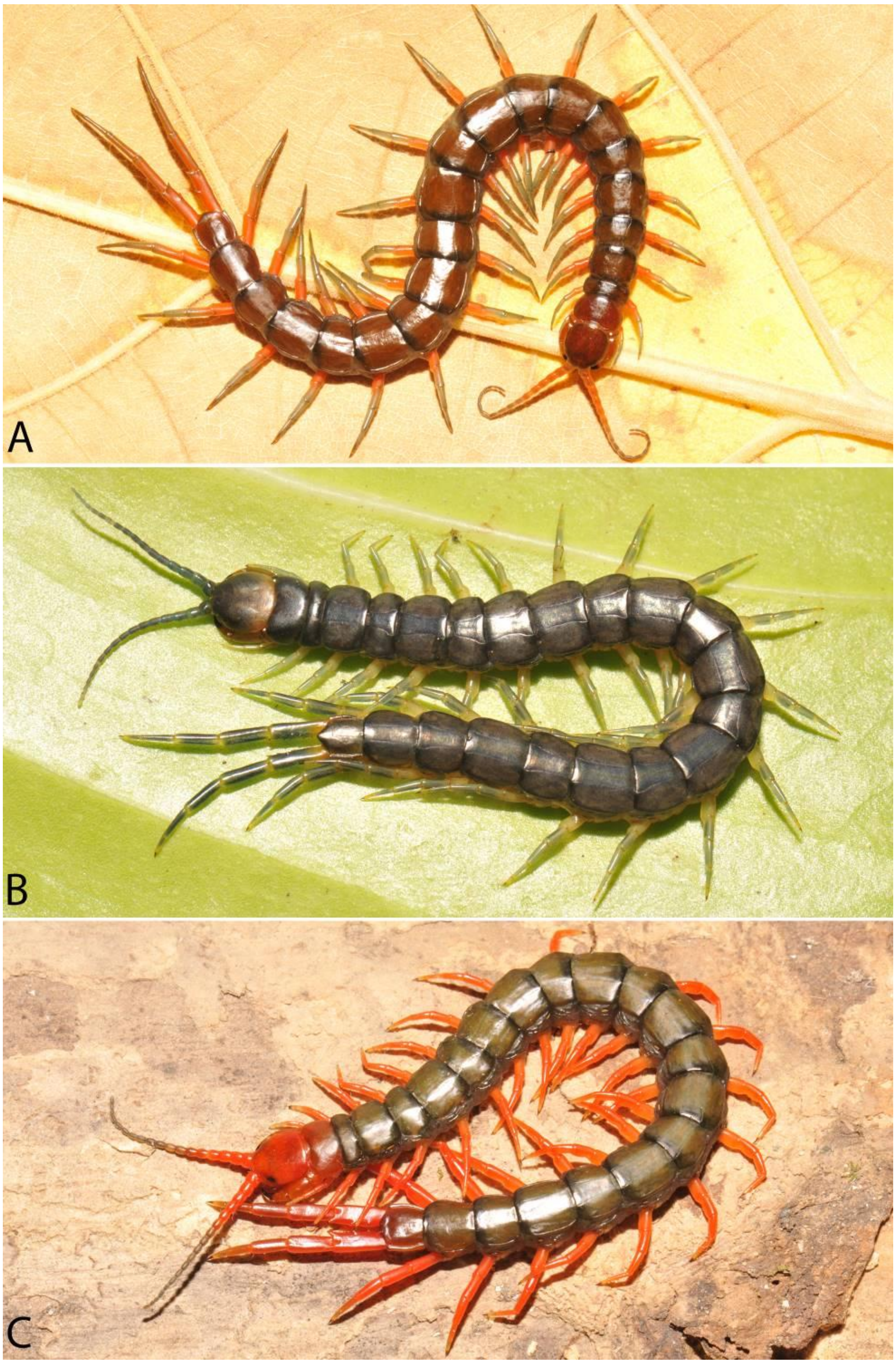


Figure 2.9 Habitus photographs of *Scolopendra* species: **A** *Scolopendra subspinipes* (Singapore, CUMZ 00315) **B** *Scolopendra calcarata* (Thailand, CUMZ 00418) **C** *Scolopendra japonica* (Colour morph 2: Laos, CUMZ 00298).

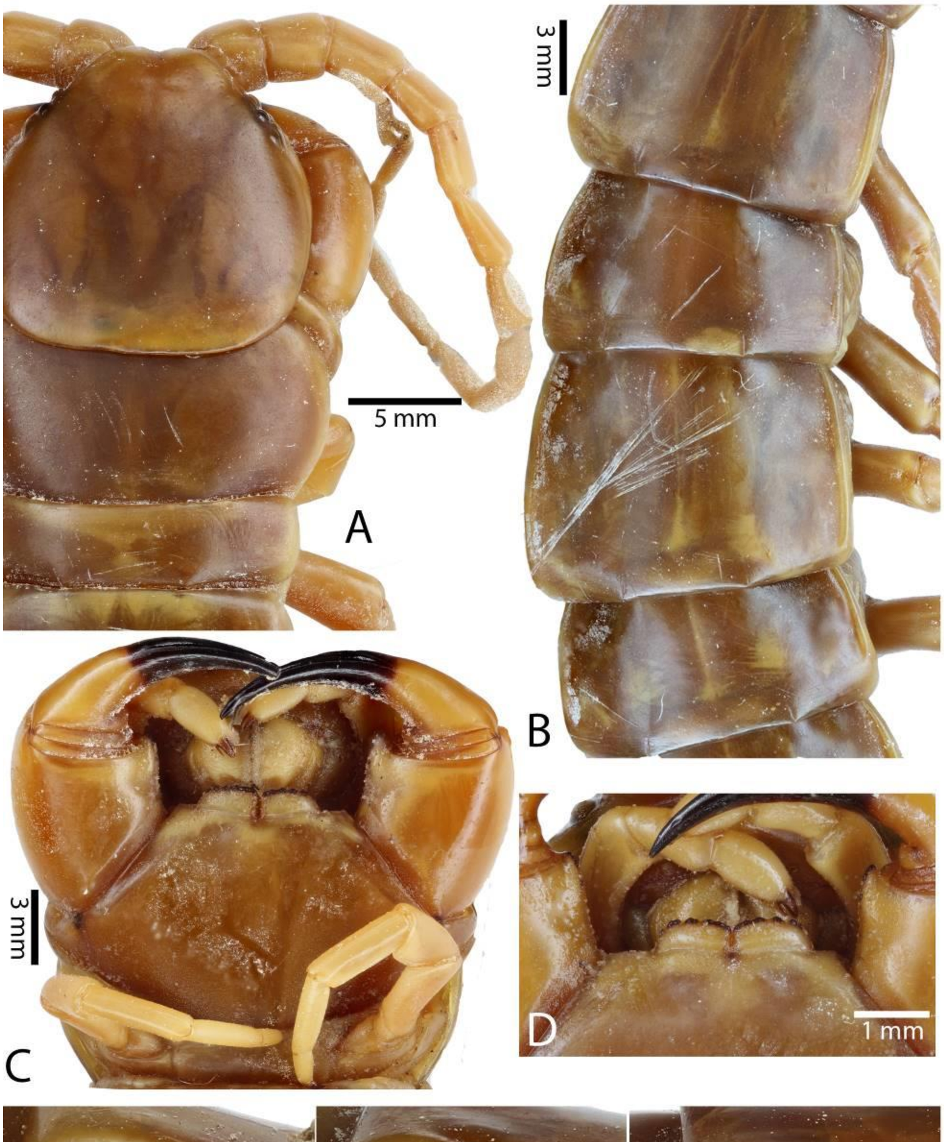


Figure 2.10 *Scolopendra subspinipes* (NHMUK): **A** Cephalic plate and trunk segments 1–2 **B** Tergites 9–12 **C** Forcipular segment **D** Tooth-plates **E**–**G** Spiracles 3, 5 and 8, respectively.

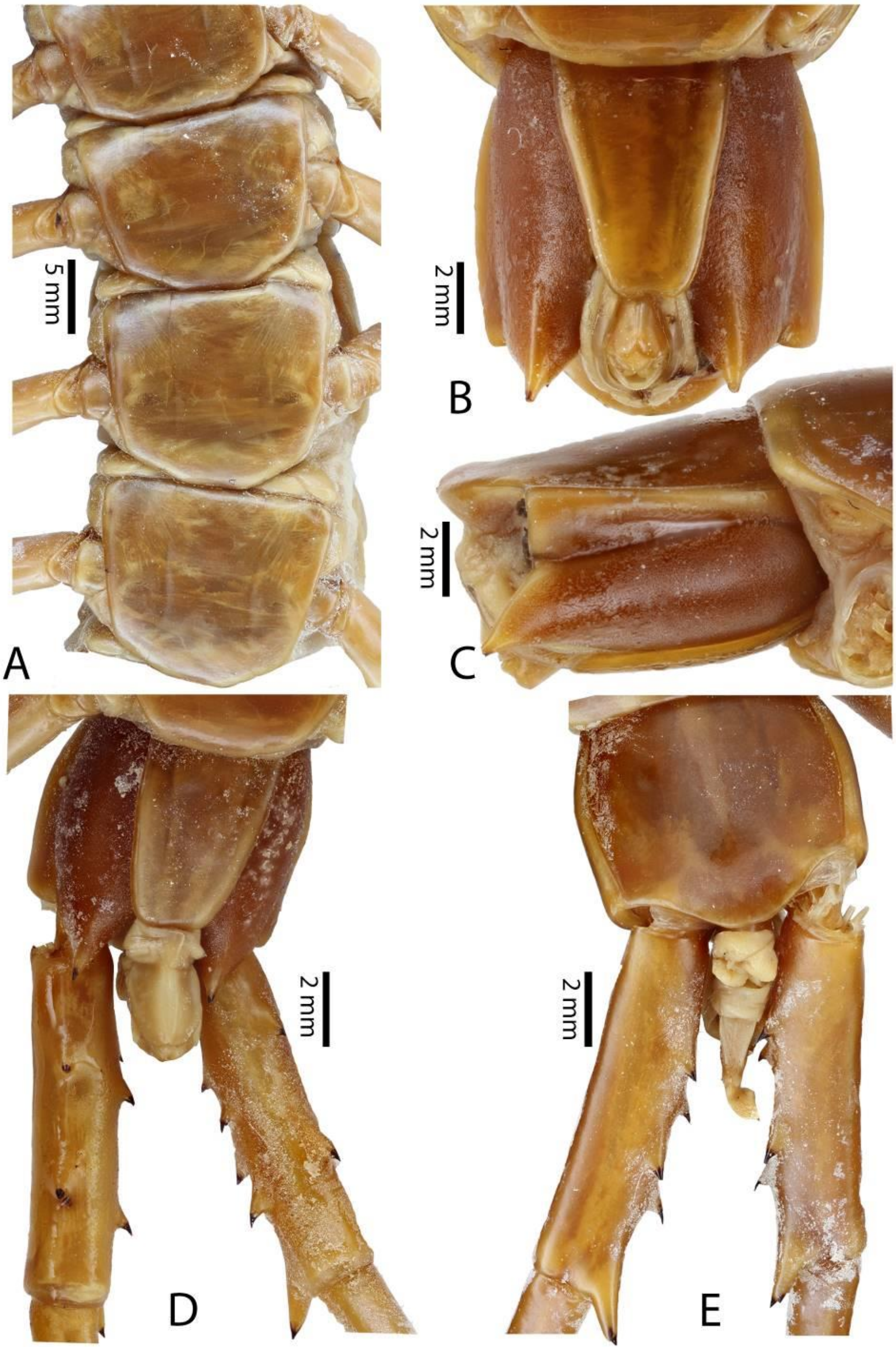


Figure 2.11 *Scolopendra subspinipes* (NHMUK): **A** Sternites 8–11 **B** Sternite of ultimate leg-bearing segment and coxopleura **C** Lateral view of coxopleuron **D** Ventral view of ultimate leg-bearing segment and ultimate leg prefemora **E** Dorsal view of ultimate leg-bearing segment and prefemora.

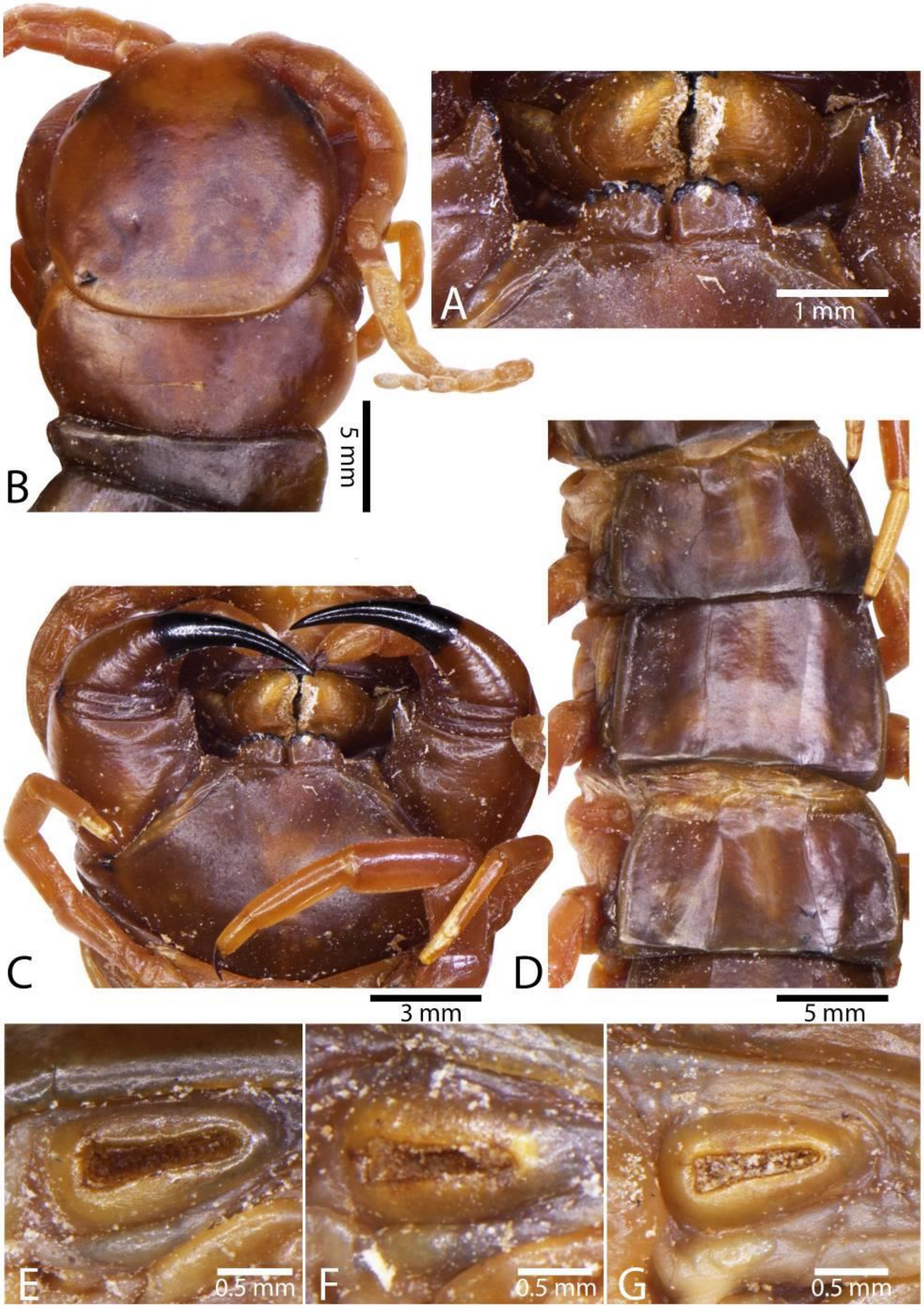


Figure 2.12 *Scolopendra subspinipes* (Syntype NHMW 751 of S. mutilans Koch, 1878): **A** Tooth-plates **B** Cephalic plate and trunk segments 1–2 **C** Forcipular segment **D** Tergites 9–11 **E–G** Spiracles 3, 5 and 8, respectively.

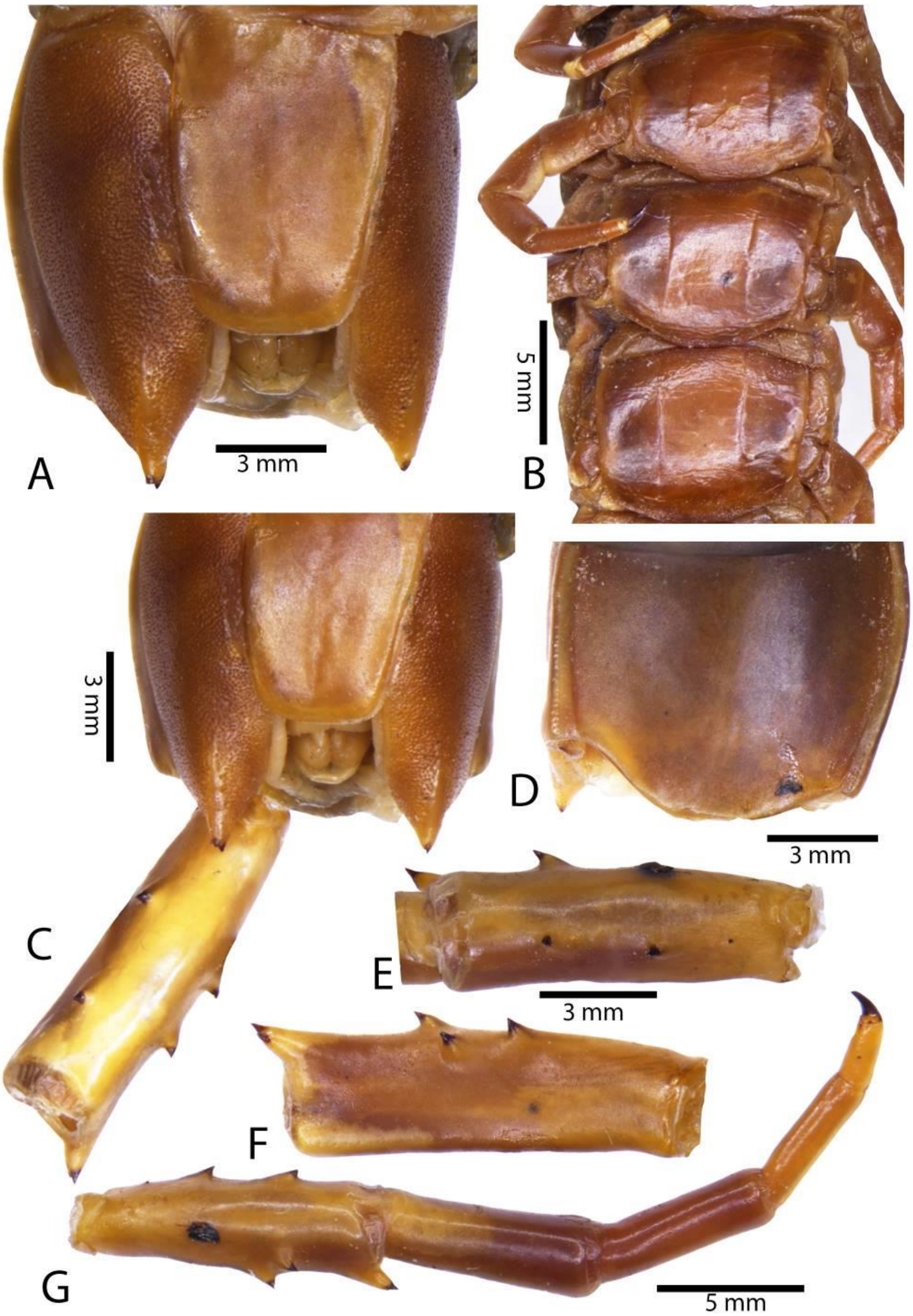


Figure 2.13 *Scolopendra subspinipes* (Syntype NHMW 751 of S. mutilans Koch, 1878): **A** Sternite of ultimate leg-bearing segment and coxopleura **B** Sternites 10–12 **C** Sternite of ultimate leg-bearing segment, coxopleura and ventral view of ultimate leg prefemur **D** Tergite of ultimate leg-bearing segment **E** Ventral view of ultimate leg prefemur **F** Dorsal view of ultimate leg prefemur **G** Ventrolateral view of ultimate leg.

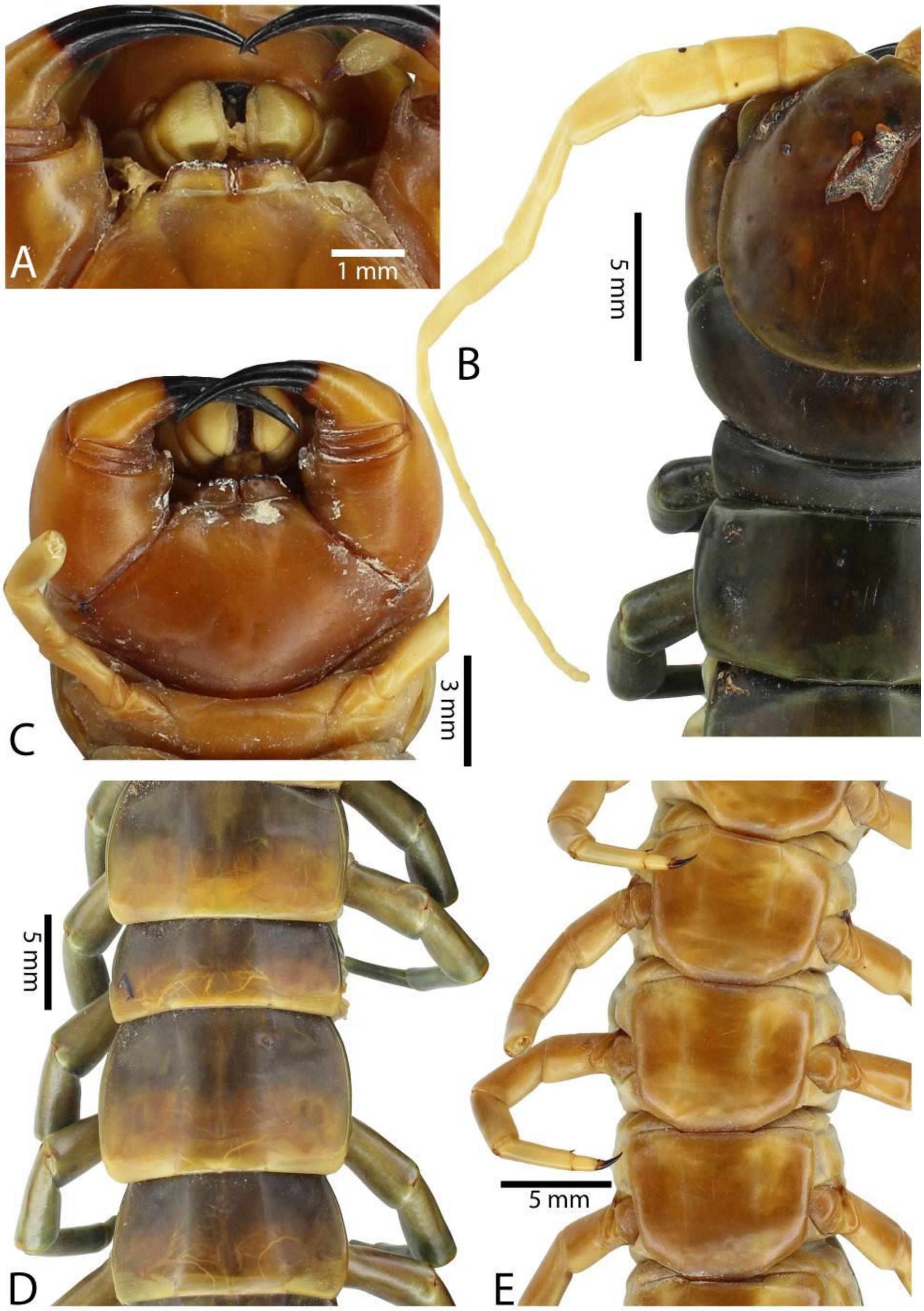


Figure 2.14 *Scolopendra subspinipes* (Syntypes NMB 391Va of "*piceoflava* Attems, 1934"): **A** Tooth-plates **B** Cephalic plate and trunk segments 1–3 **C** Forcipular segment **D** Tergites 9–12 **E** Sternites 8–10.

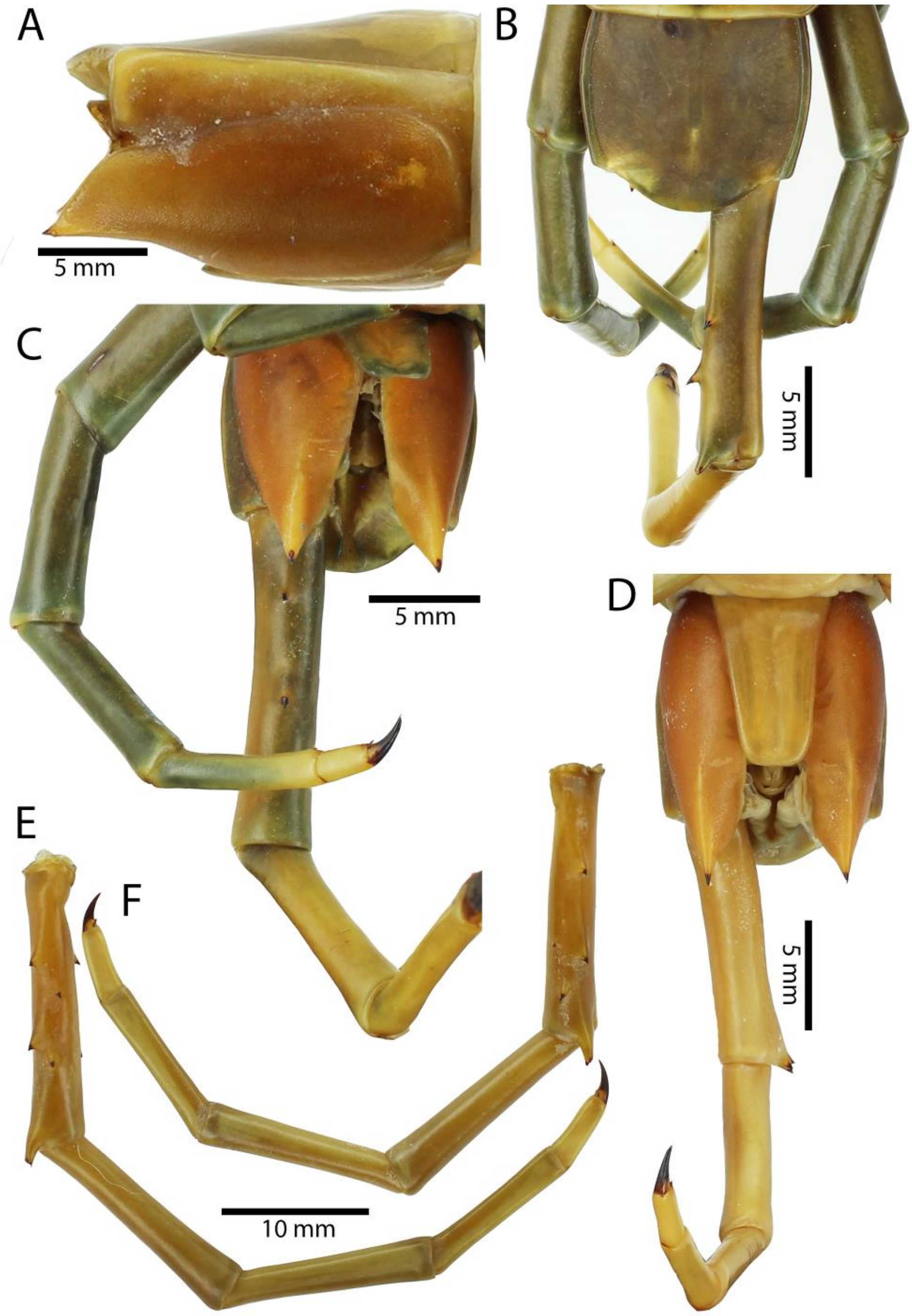


Figure 2.15 *Scolopendra subspinipes* (Syntypes NMB 391Va of "*piceoflava* Attems, 1934"): **A** Lateral view of coxopleuron **B** Tergite of ultimate leg-bearing segment and dorsal view of legs 20 and ultimate leg **C** Ventral view of Leg 20, coxopleura and ultimate leg **D** Sternite of ultimate leg-bearing segment, coxopleura and ultimate leg **E**–**F** Ventrolateral view of ultimate legs.

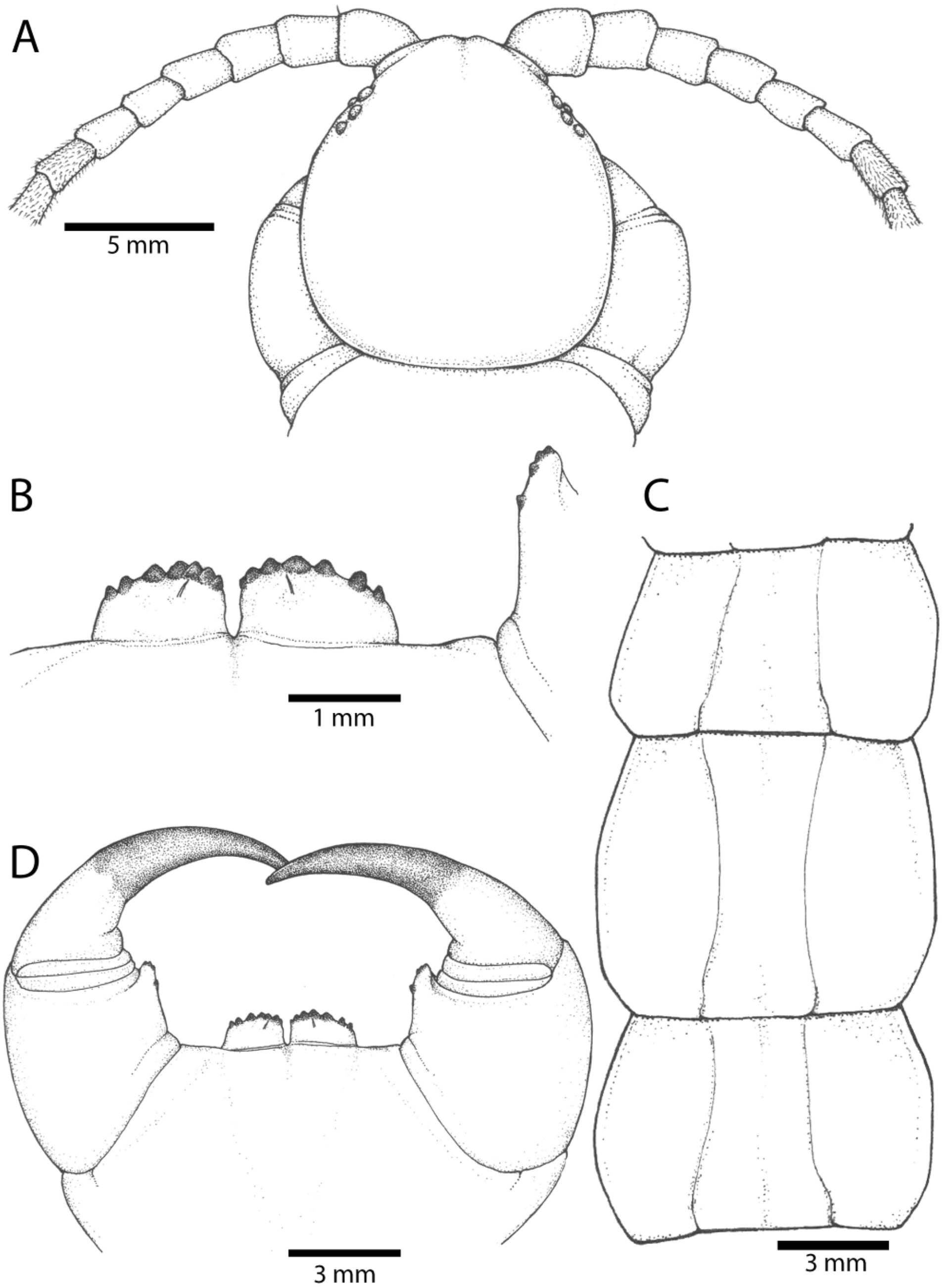


Figure 2.16 *Scolopendra subspinipes* (CUMZ 00315): **A** Cephalic plate and basal antennal articles **B** Tooth-plates and trochanteroprefemoral process **C** Tergites 9–11 **D** Forcipular segment.

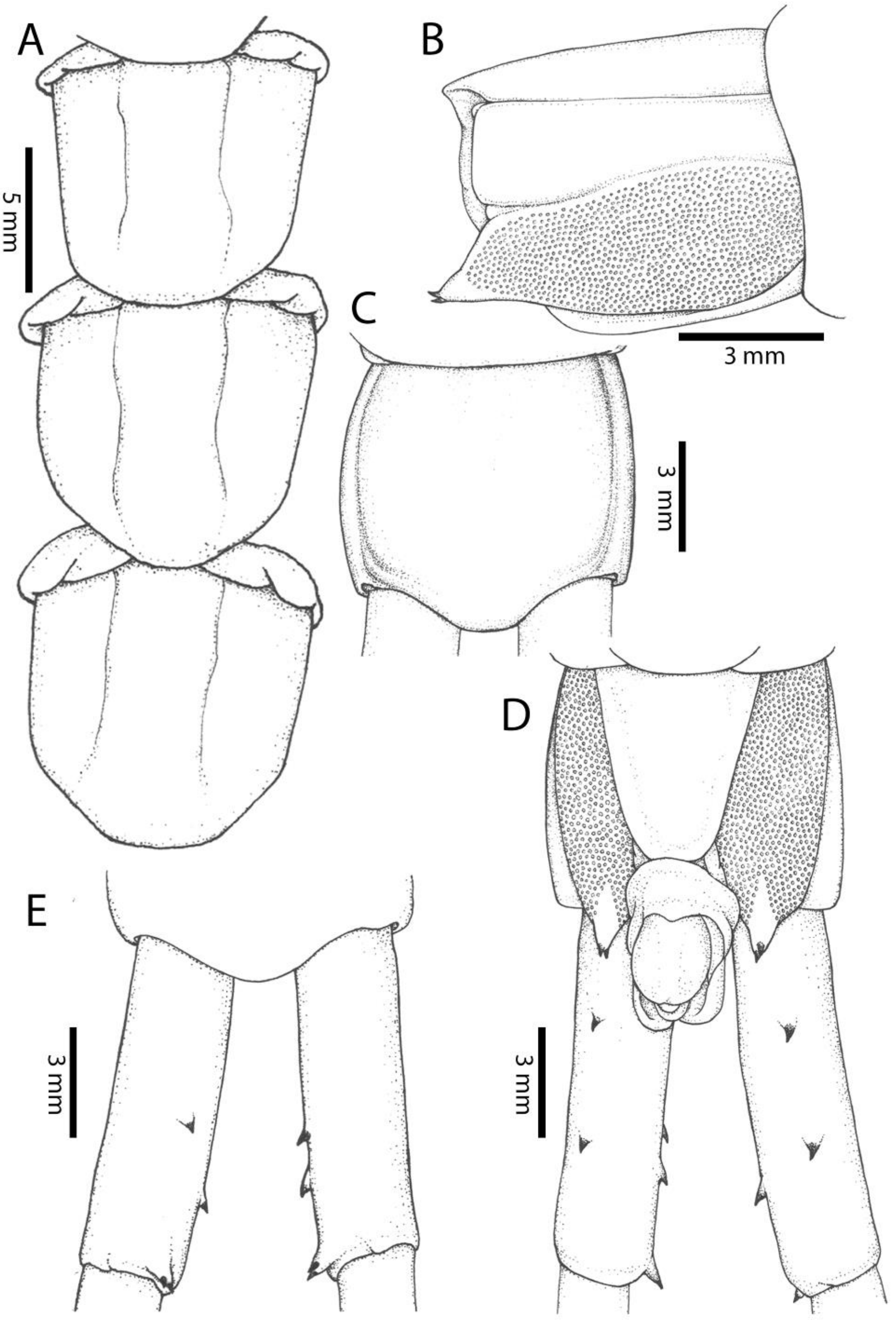


Figure 2.17 *Scolopendra subspinipes* (CUMZ 00315): **A** Sternites 9–11 **B** Lateral view of coxopleuron **C** Tergite of ultimate leg-bearing segment **D** Sternite of ultimate leg-bearing segment, coxopleura, female genital segment and ultimate leg prefemora **E** Dorsal view of ultimate leg prefemora.

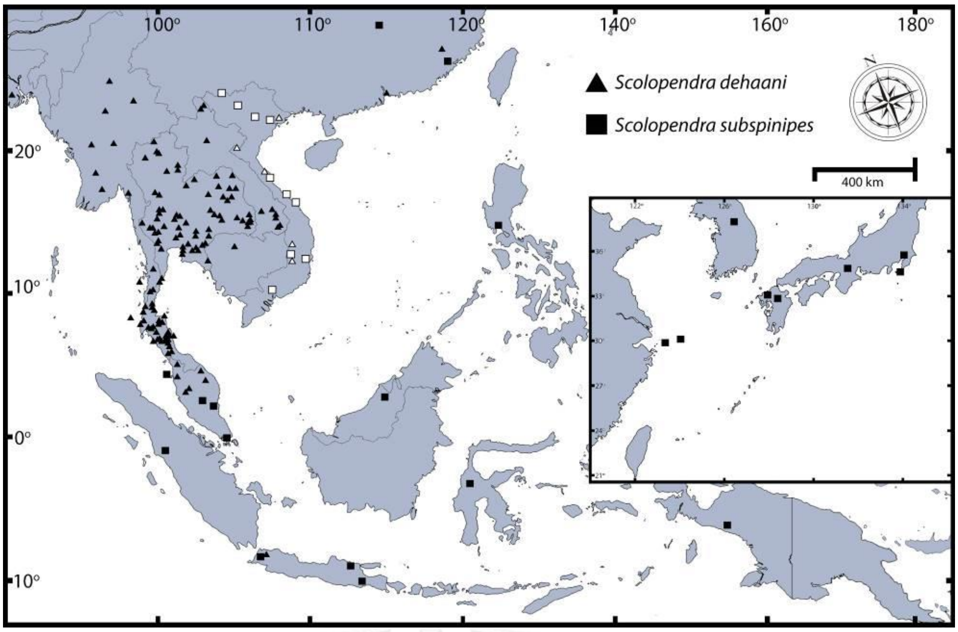


Figure 2.18 Distribution map of *Scolopendra dehaani* and *Scolopendra subspinipes* in Southeast Asia and ChinaJapan Sea (small map): Filled and blank colours refer to localities from the present study and in the literature, respectively.

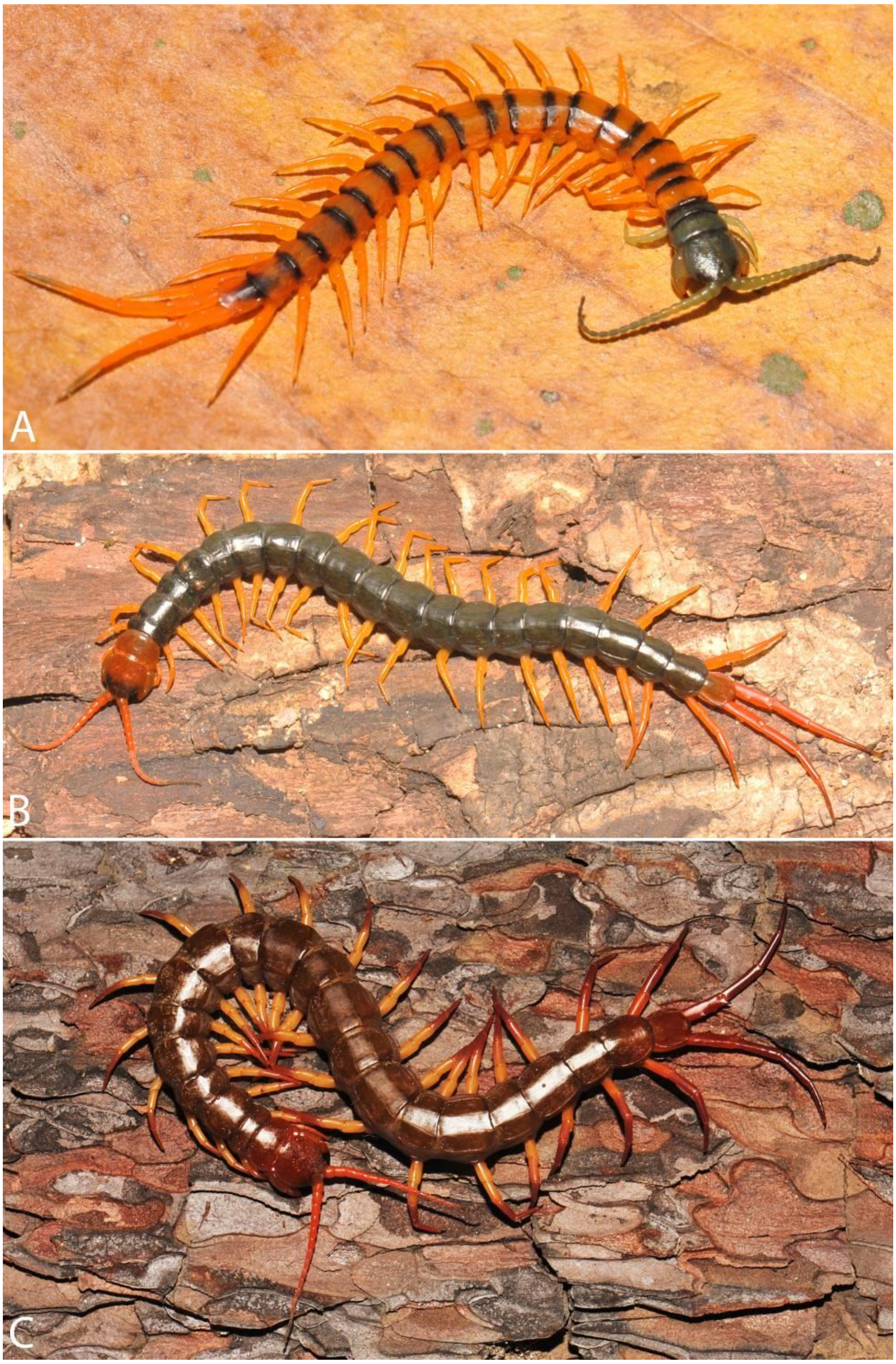


Figure 2.19 Colouration changes and patterns during developmental stages of *Scolopendra dehaani*: **A** Juvenile stage **B** Subadult stage **C** Adult stage (specimen from northern Thailand).

Figure 2.20 Brooding and feeding behaviours: **A** *Scolopendra dehaani* exhibiting simple coiling with cluster of embryonic stadia (photograph by Natdanai Likhitrakarn) **B** *Scolopendra morsitans* exhibiting double coiling with postembryonic stadia **C–D** *Scolopendra dehaani* preying on snaileating snake Pareas carinatus **D** Flexibility of trunk segments during predation.

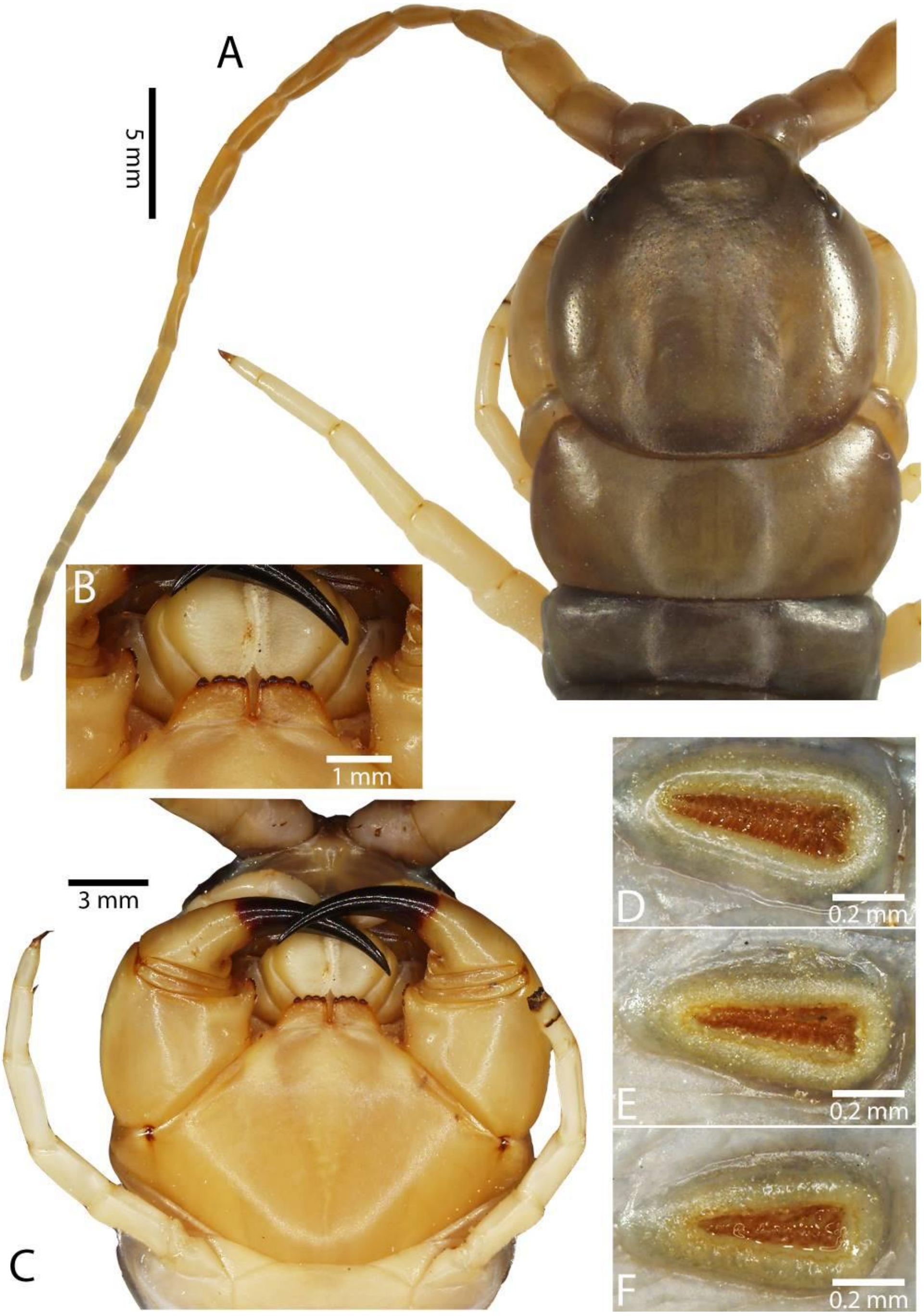


Figure 2.21 *Scolopendra dehaani* (CUMZ 00282): **A** Cephalic plate and trunk segments 1–2 **B** Tooth-plates **C** Forcipular segment **D–E** Spiracles 3, 5 and 8, respectively.

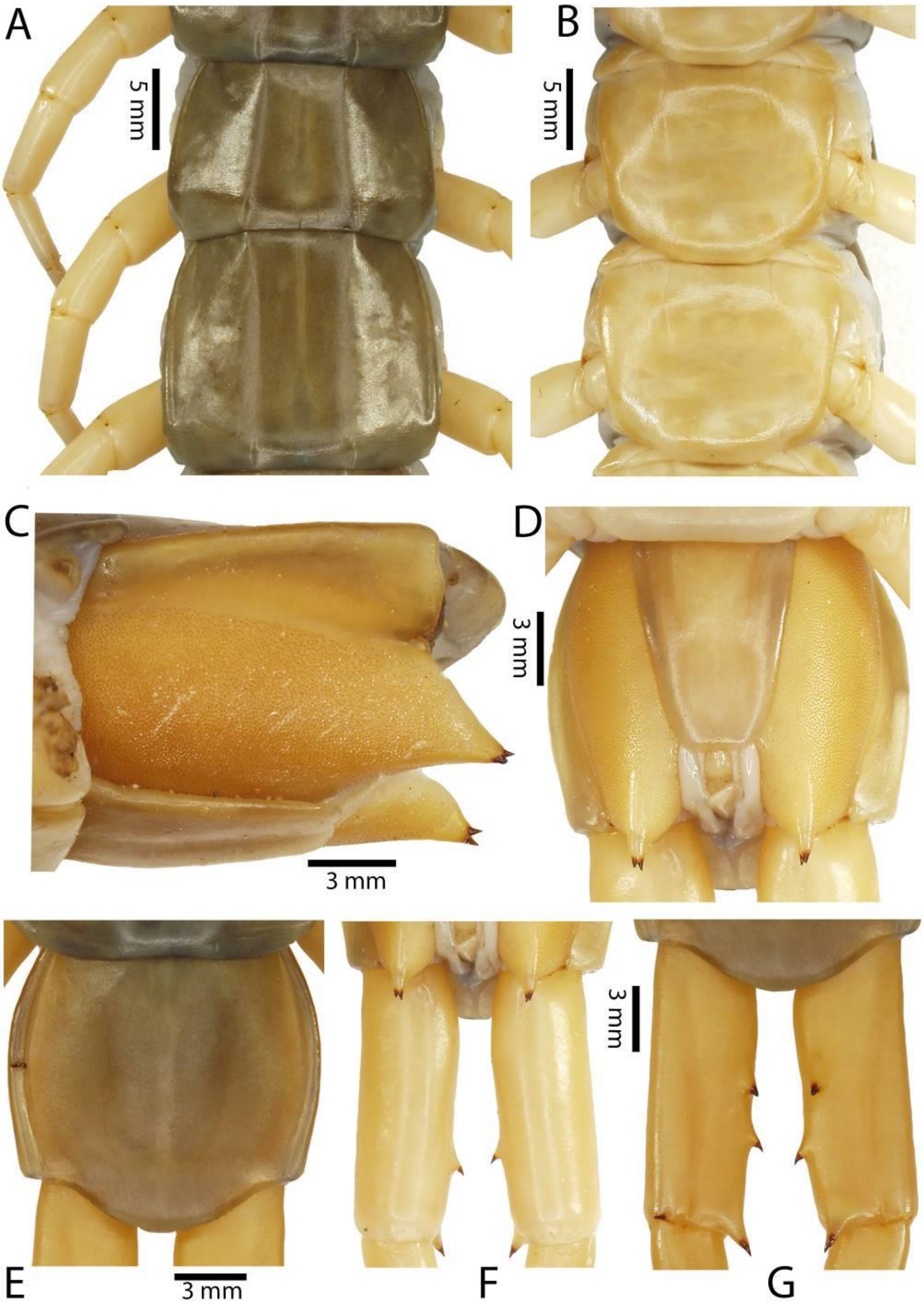


Figure 2.22 *Scolopendra dehaani* (CUMZ 00268 and 00282): **A** Tergites 10–11 **B** Sternites 10–11 **C** Lateral view of coxopleuron **D** Sternite of ultimate leg-bearing segment and coxopleura **E** Tergite of ultimate leg-bearing segment **F–G** ventral and dorsal view of ultimate leg prefemora.

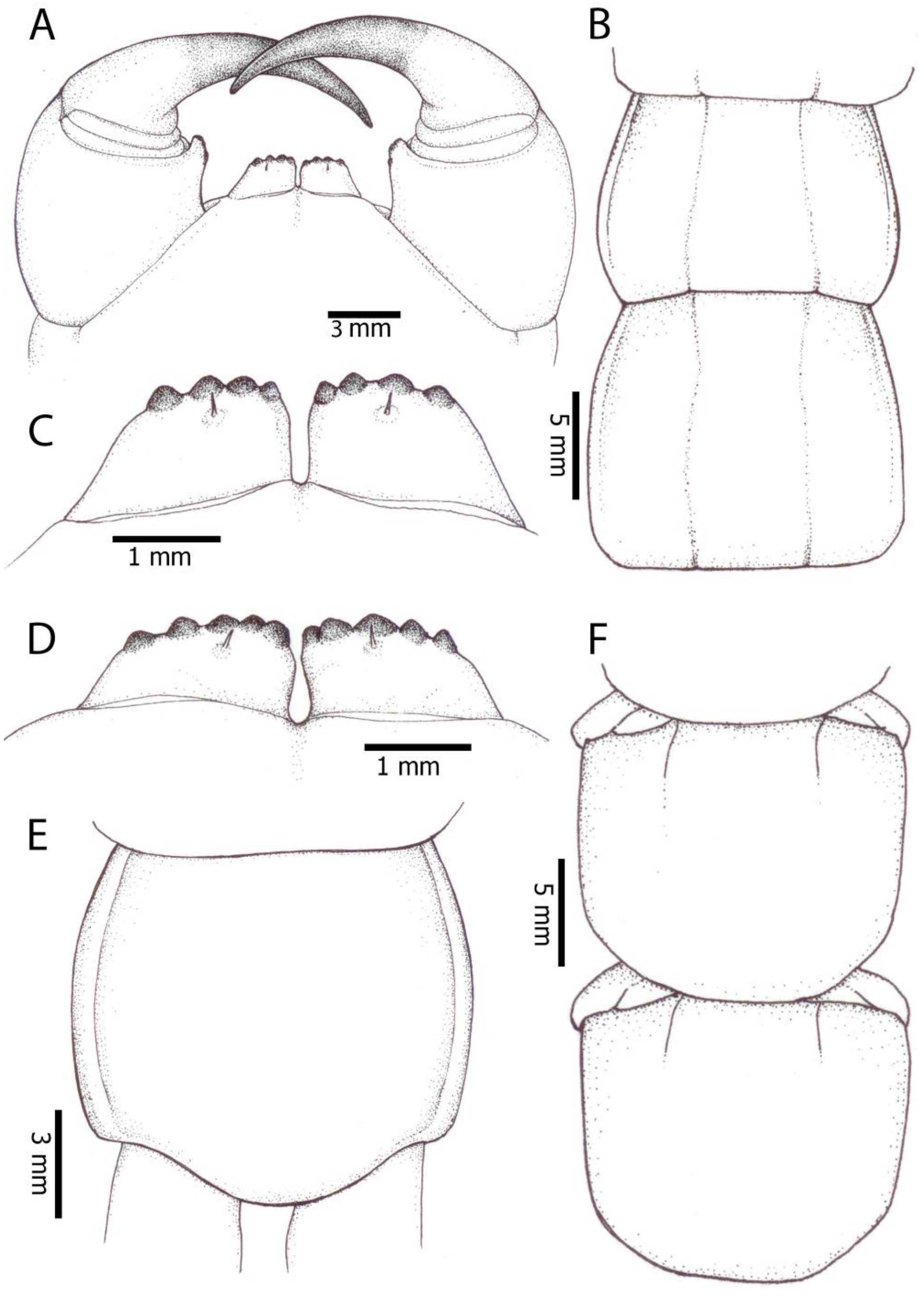


Figure 2.23 *Scolopendra dehaani* (CUMZ 00365): **A** Forcipular segment **B** Tergites 9 and 10 **C–D** Variation in teeth on tooth-plates **E** Tergite of ultimate leg-bearing segment **F** Sternites 9 and 10.

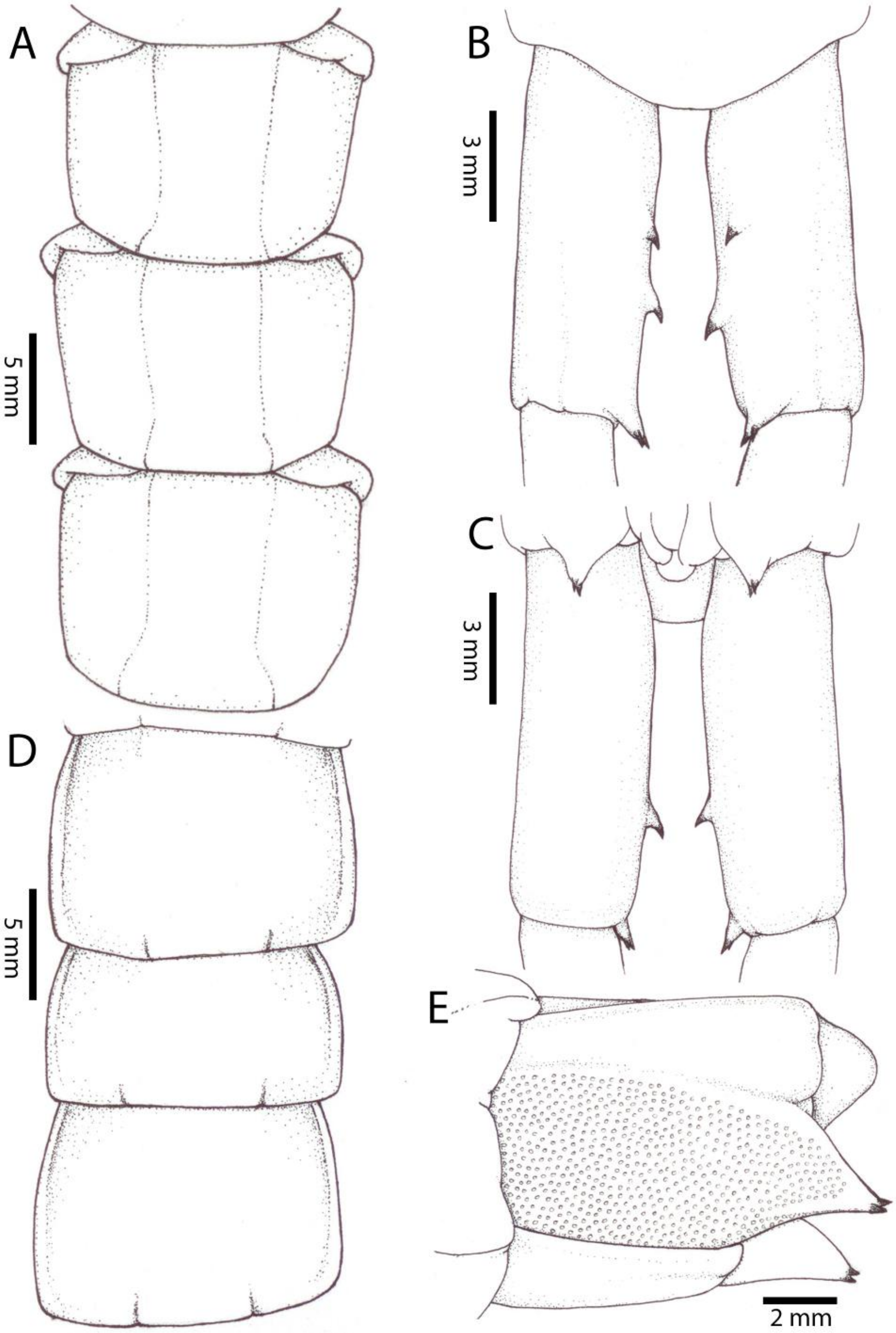


Figure 2.24 *Scolopendra dehaani* (CUMZ 00365): **A** Sternites 9–11 **B–C** Spines on ultimate leg prefemora (dorsal and ventral views, respectively) **D** Tergite 9–11 **E** Lateral view of coxopleuron.

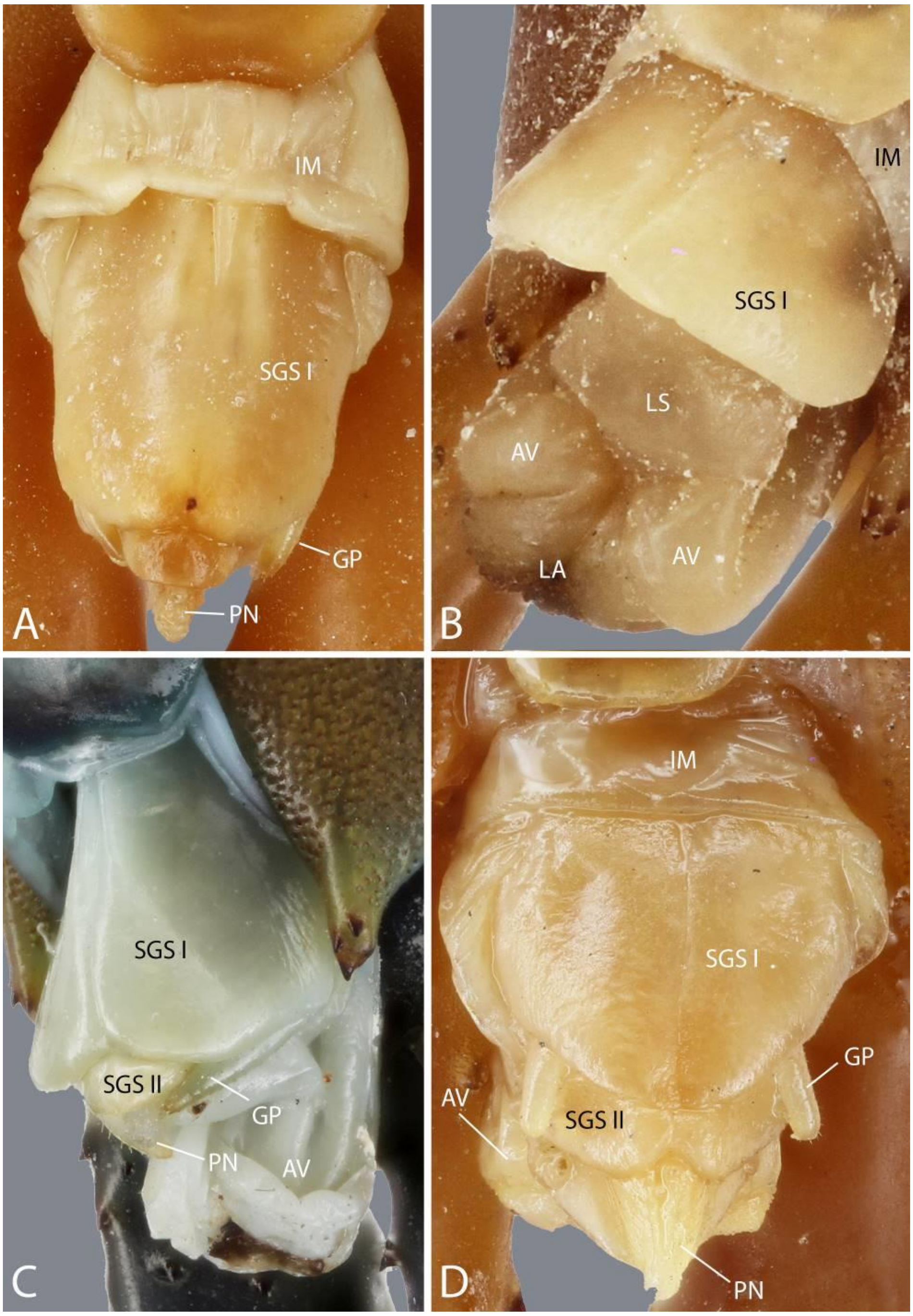


Figure 2.25 Genital segment(s) in some preserved *Scolopendra* specimens: **A** *Scolopendra dehaani* (male) **B** *Scolopendra calcarata* (female) **C** *Scolopendra pinguis* (male) **D** *Scolopendra morsitans* (male).

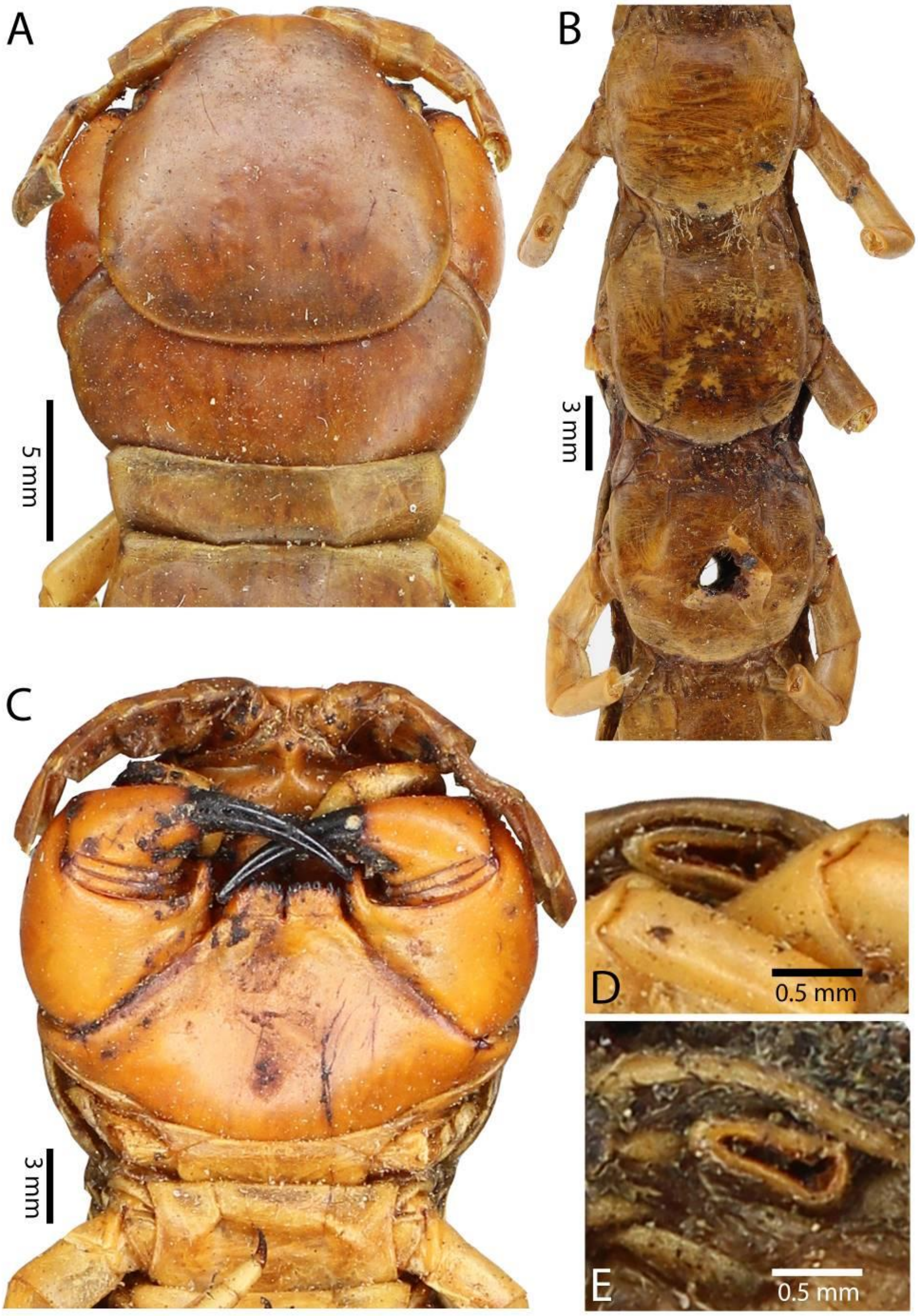


Figure 2.26 *Scolopendra multidens* (Holotype NHMUK): **A** Cephalic plate and trunk segments 1–3 **B** Sternites 9–11 **C** Forcipular segment **D–E** Spiracles 3 and 5, respectively.

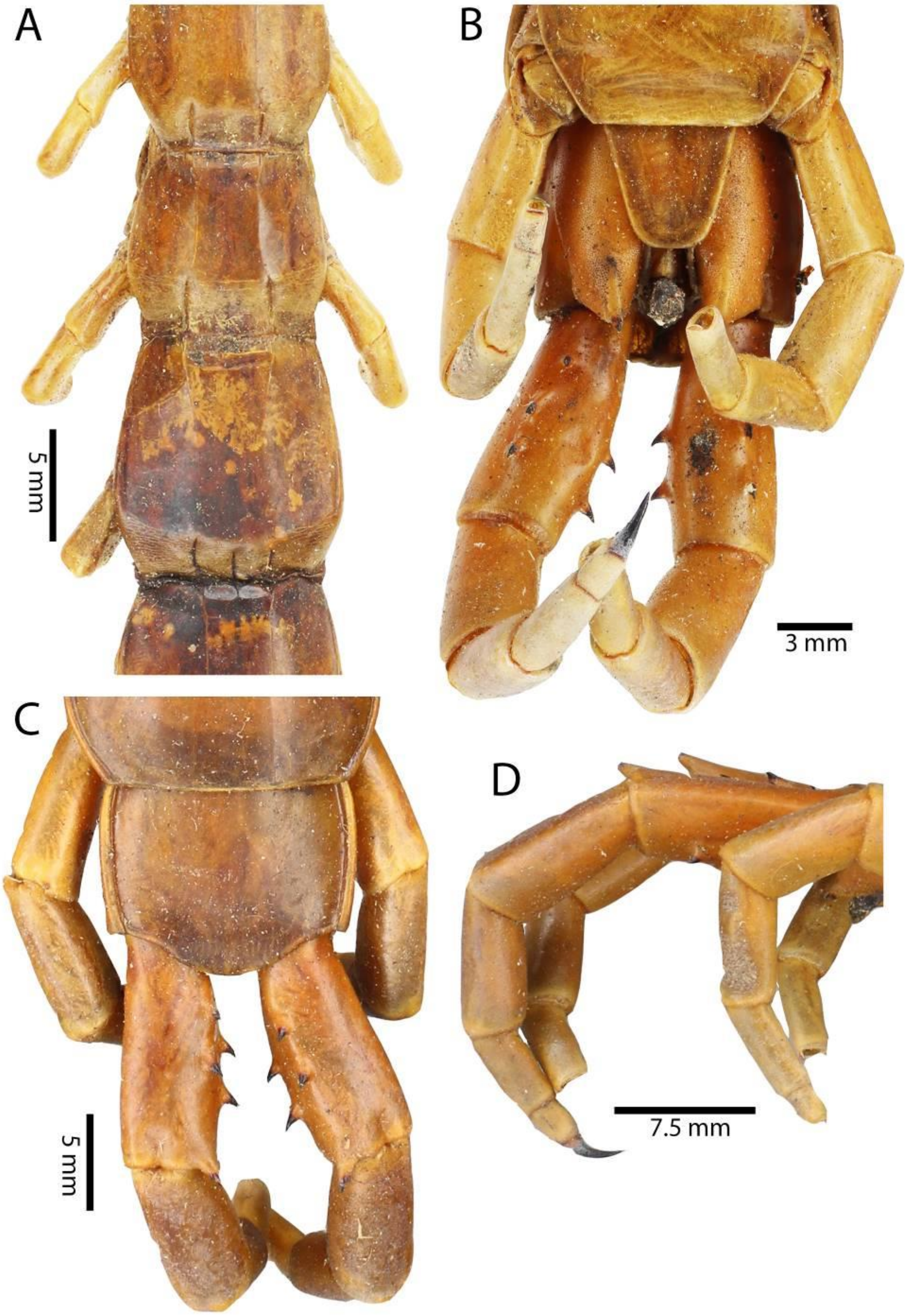


Figure 2.27 *Scolopendra multidens* (Holotype NHMUK): **A** Tergites 9–10 **B** Sternite of ultimate leg-bearing segment, coxopleura, legs 20 and ventral view of ultimate legs **C** Tergite of ultimate leg-bearing segment and dorsal view of leg 20 and ultimate legs **D** Lateral view of ultimate leg and legs 20.

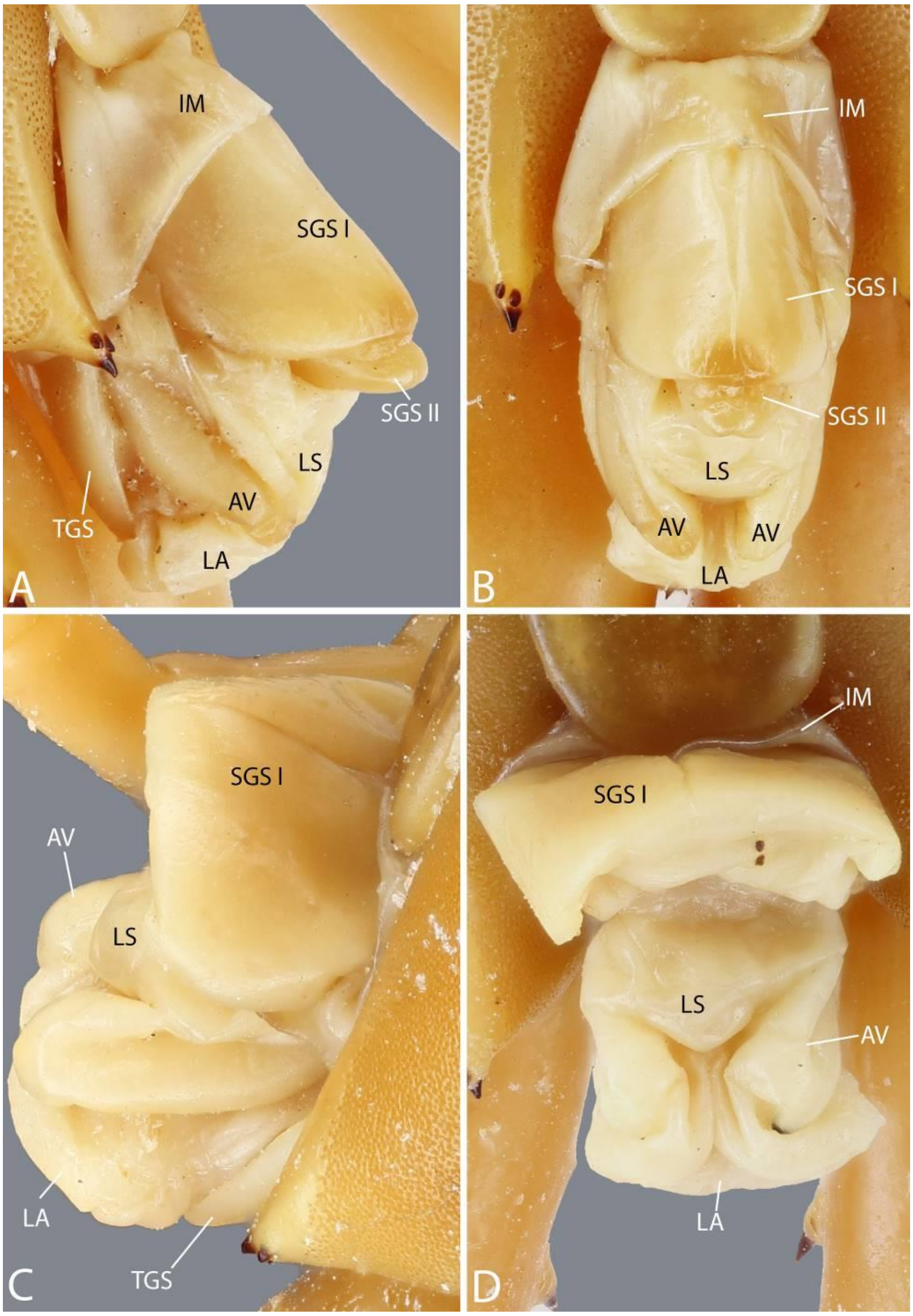


Figure 2.28 Genital segment(s) of **A–B** *Scolopendra multidens* (male; lateral and ventral views, respectively) **C–D** *Scolopendra cataracta* (female; lateral and ventral views, respectively).

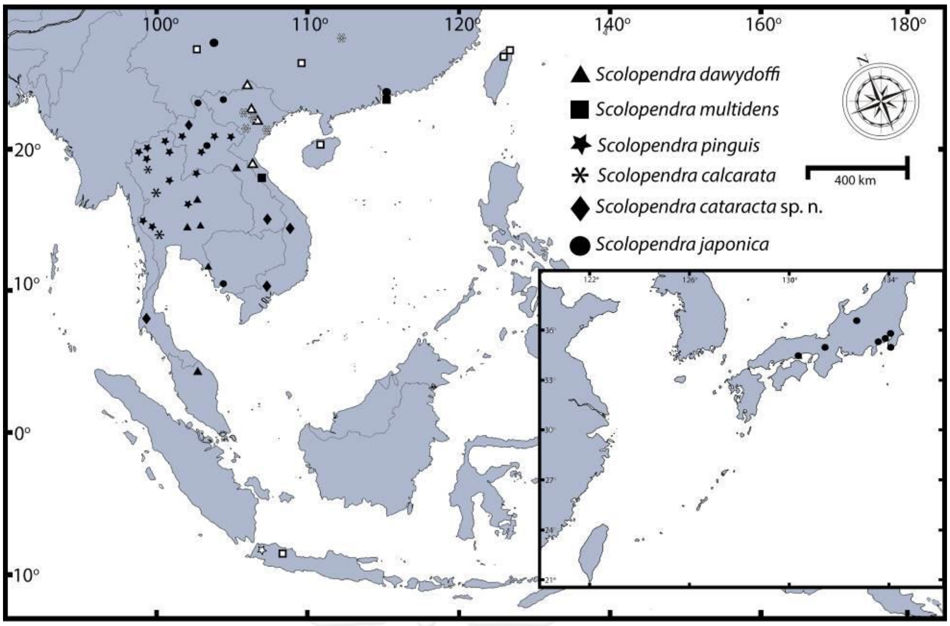


Figure 2.29 Distribution map of six *Scolopendra* species in Southeast Asia and China-Japan Sea (small map): Filled and blank colours refer to localities from the present study and in the literature, respectively.

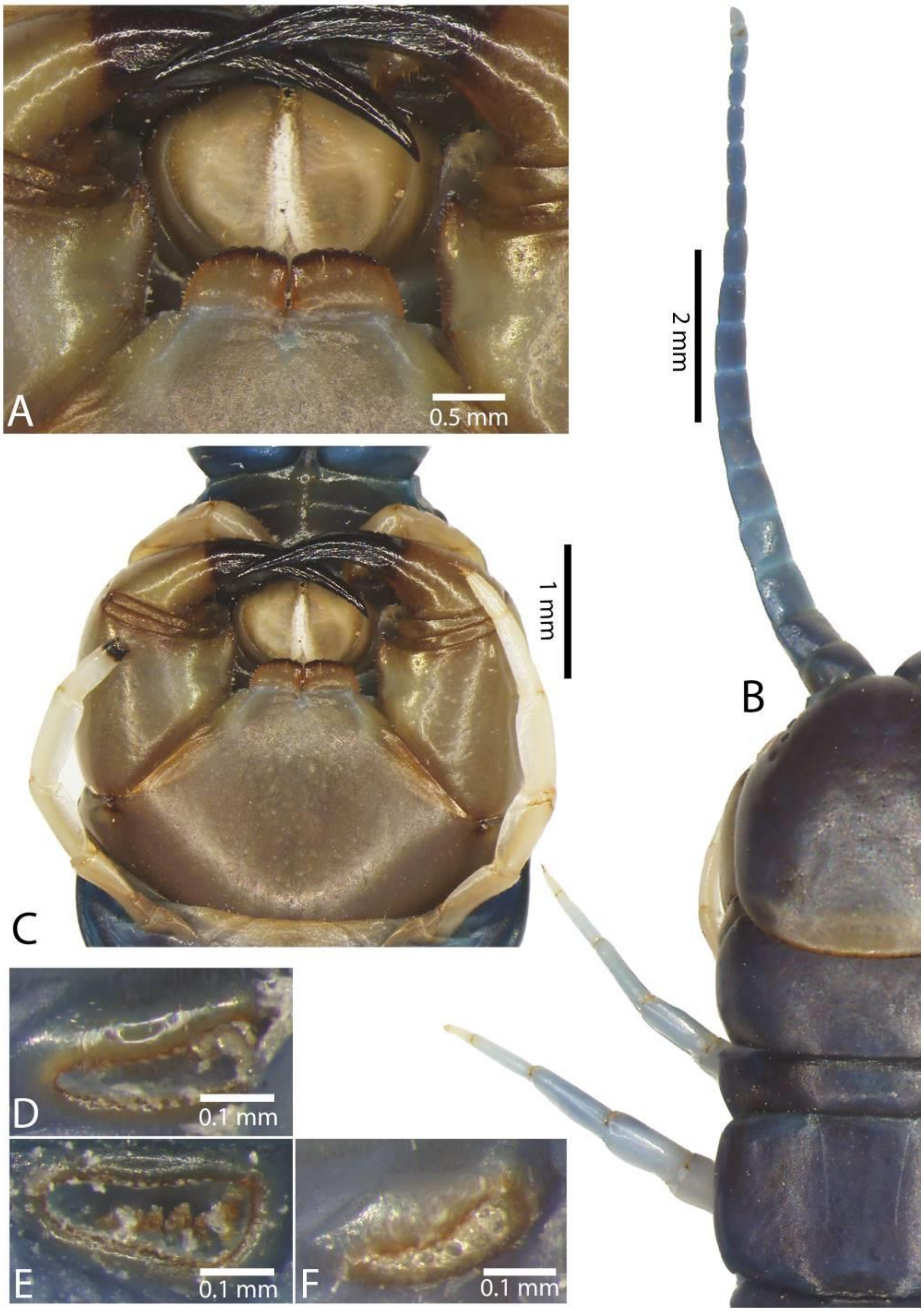


Figure 2.30 *Scolopendra calcarata* (CUMZ 00418): **A** Tooth-plates **B** Cephalic plate and trunk segments 1–3 **C** Forcipular segment **D–F** Spiracles 3, 5 and 8, respectively.

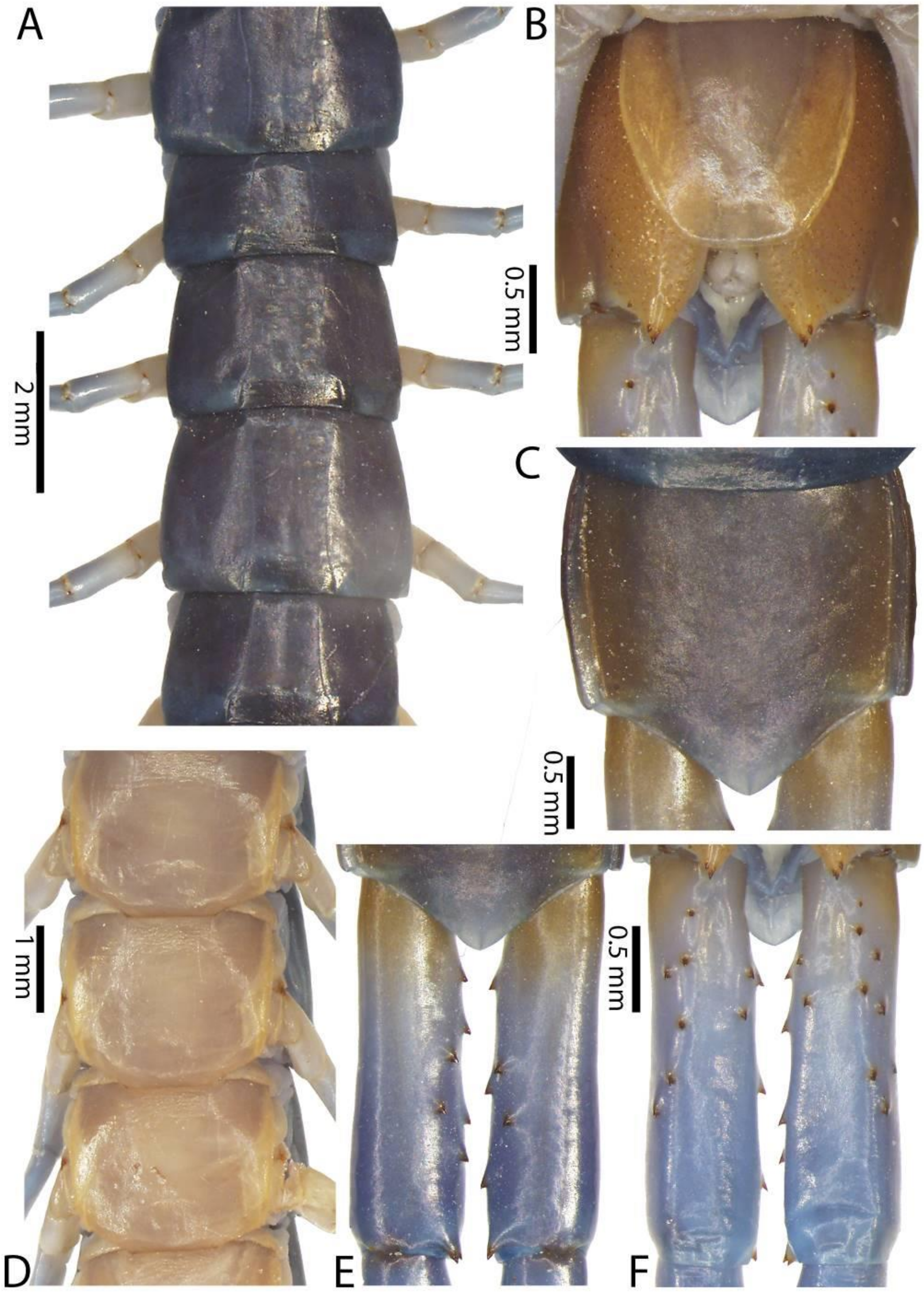


Figure 2.31 *Scolopendra calcarata* (CUMZ 00418): **A** Tergites 8–12 **B** Sternite of ultimate leg-bearing segment and coxopleura **C** Tergite of ultimate leg-bearing segment **D** Sternites 10–12 **E–F** Dorsal and ventral views of ultimate leg prefemora.

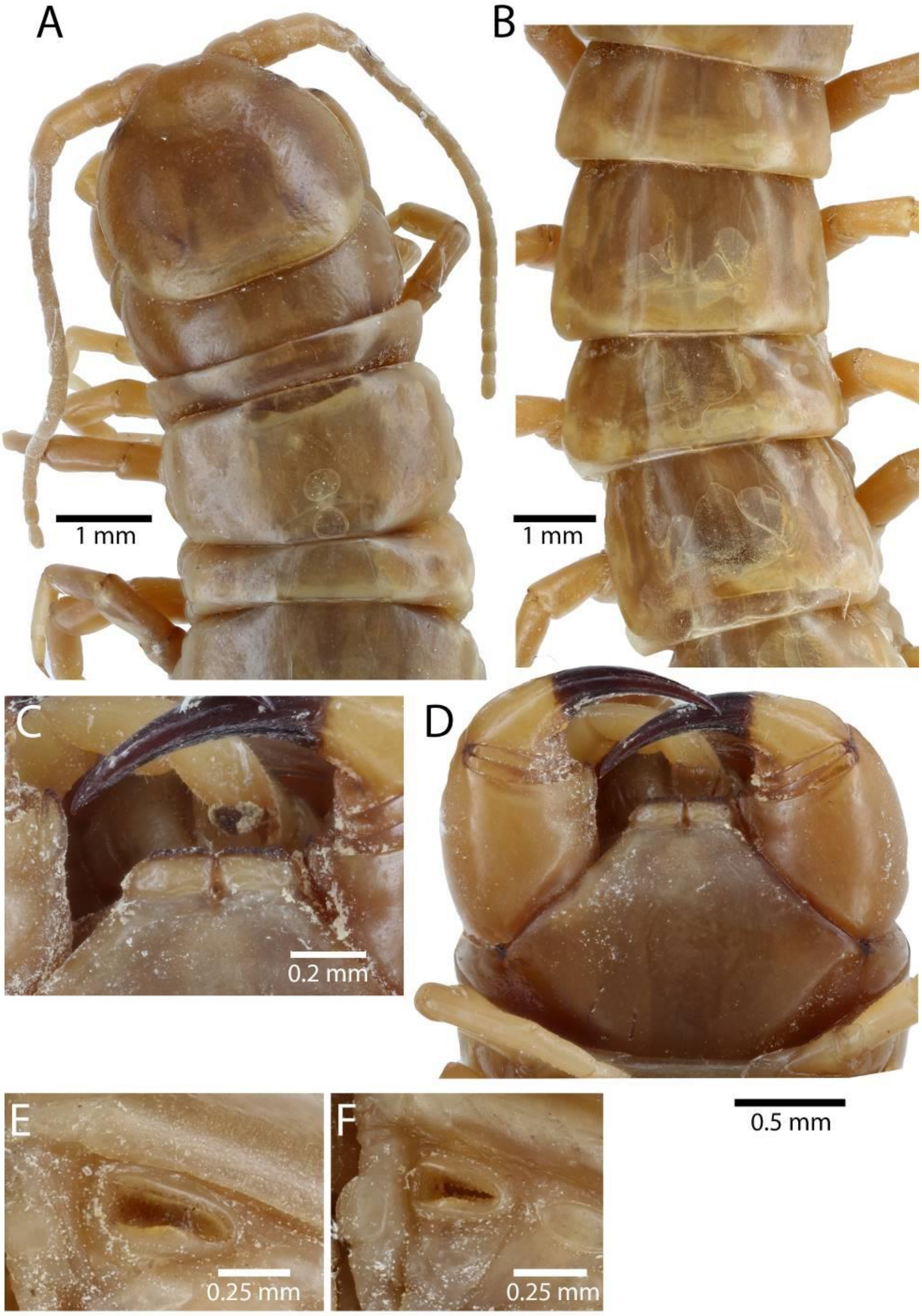


Figure 2.32 *Scolopendra calcarata* (Holotype NHRS–KASI 000000042): **A** Cephalic plate and trunk segments 1–5 **B** Tergites 8–11 **C** Tooth-plates **D** Forcipular segment **E–F** Spiracles 3 and 5, respectively.

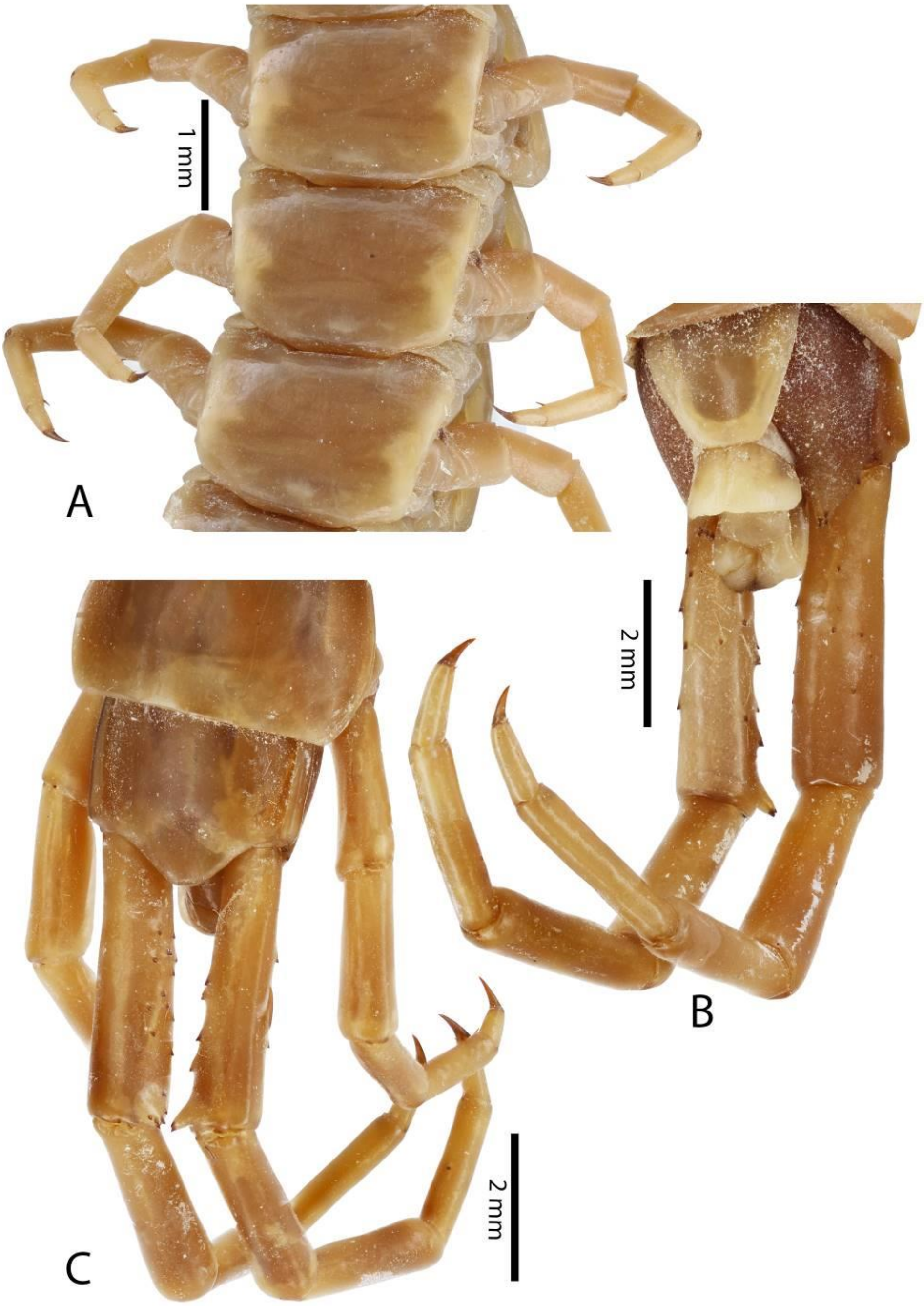


Figure 2.33 *Scolopendra calcarata* (Holotype NHRS–KASI 000000042): **A** Sternites 10–12 **B** Sternite of ultimate leg-bearing segment, coxopleura and ventral view of ultimate legs **C** Tergite of ultimate leg bearing segment and dorsal view of legs 20 and ultimate legs.

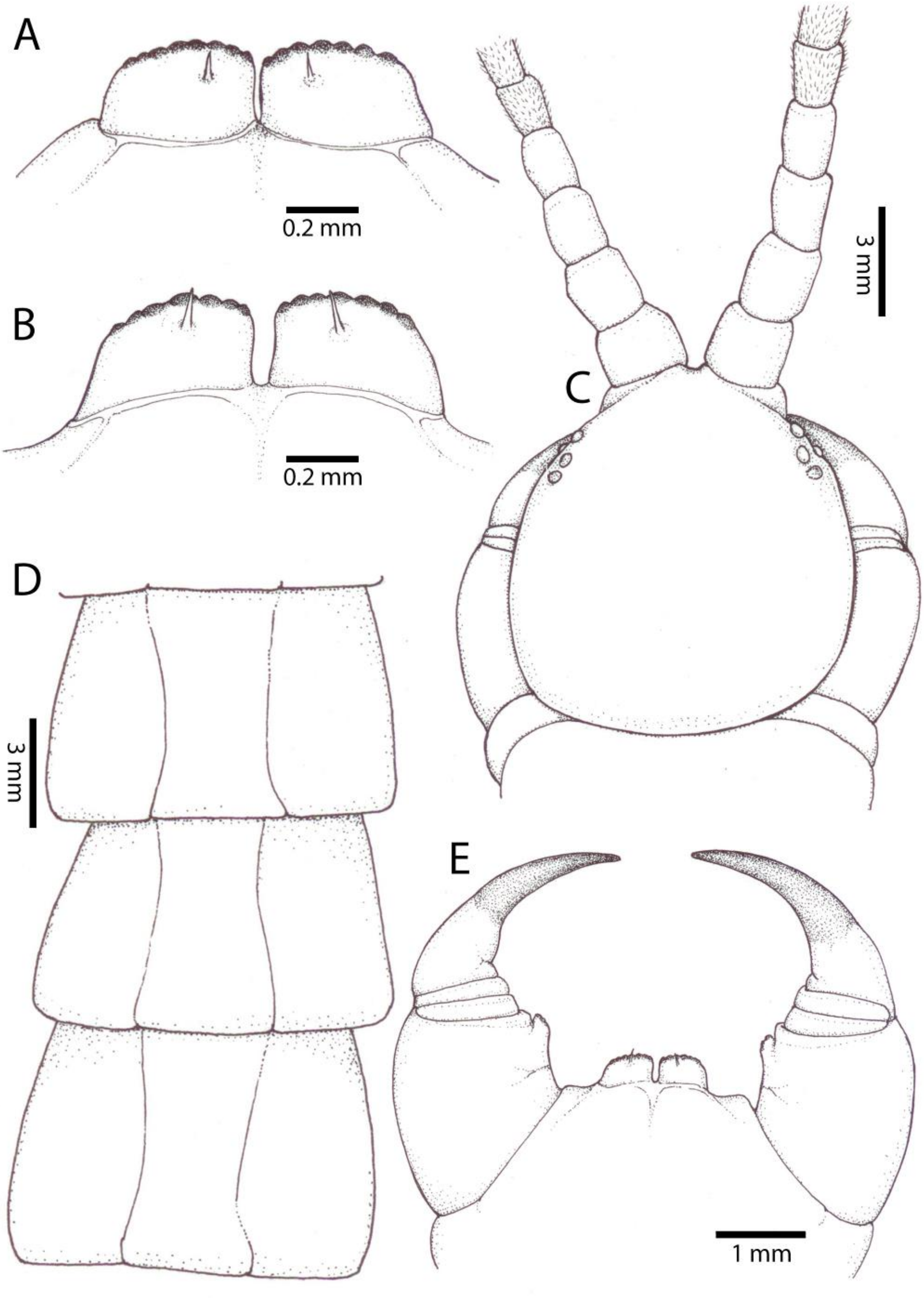


Figure 2.34 *Scolopendra calcarata* (CUMZ 00418): **A–B** Variation of teeth on tooth-plates **C** Cephalic plate and basal antennal articles **D** Tergites 9–11 **E** Forcipular segment.

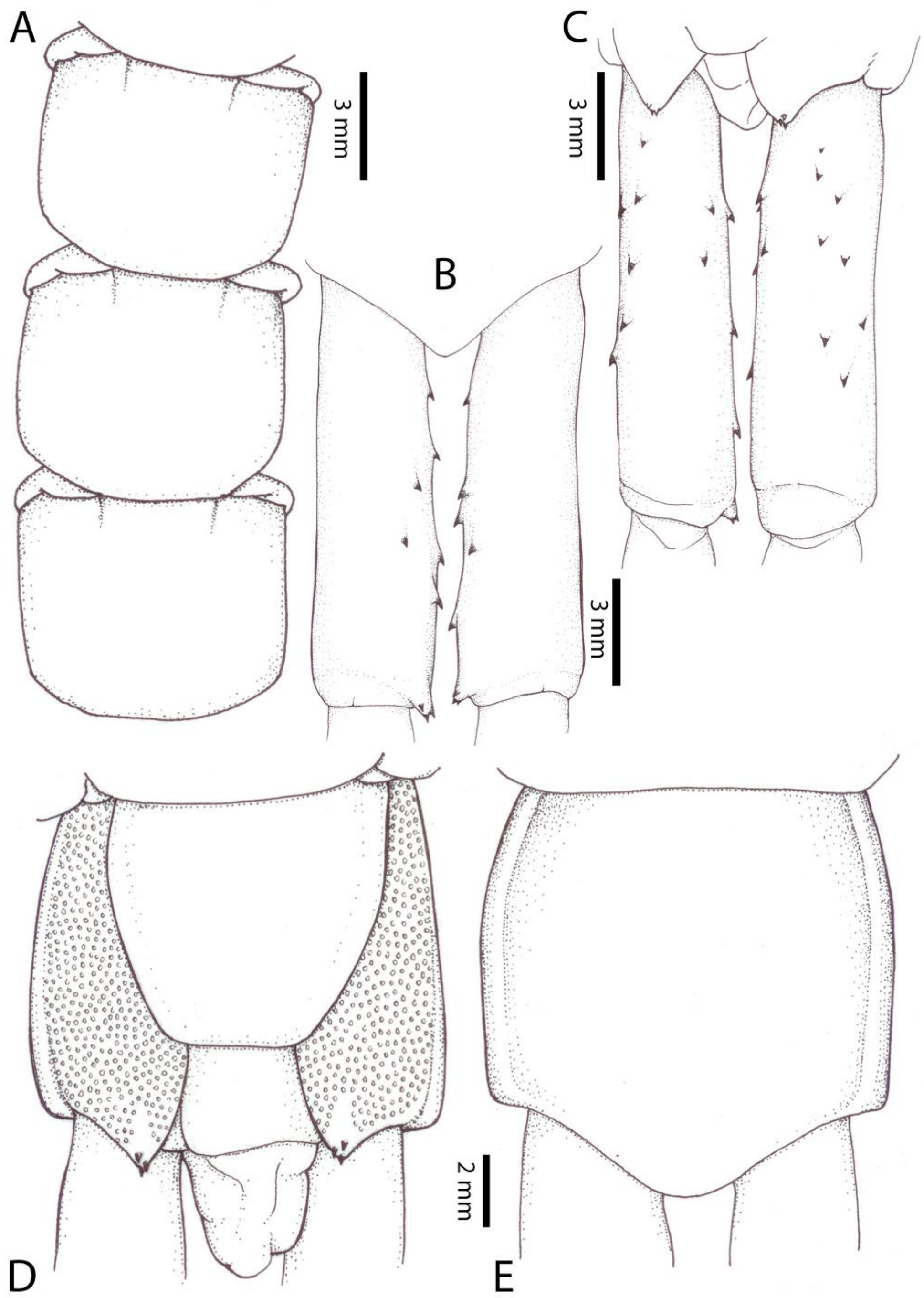


Figure 2.35 *Scolopendra calcarata* (CUMZ 00418): **A** Sternites 9–11 **B–C** Dorsal and ventral views, respectively, of ultimate leg prefemora **D** Sternite of ultimate leg-bearing segment and coxopleura **E** Tergite of ultimate leg-bearing segment.

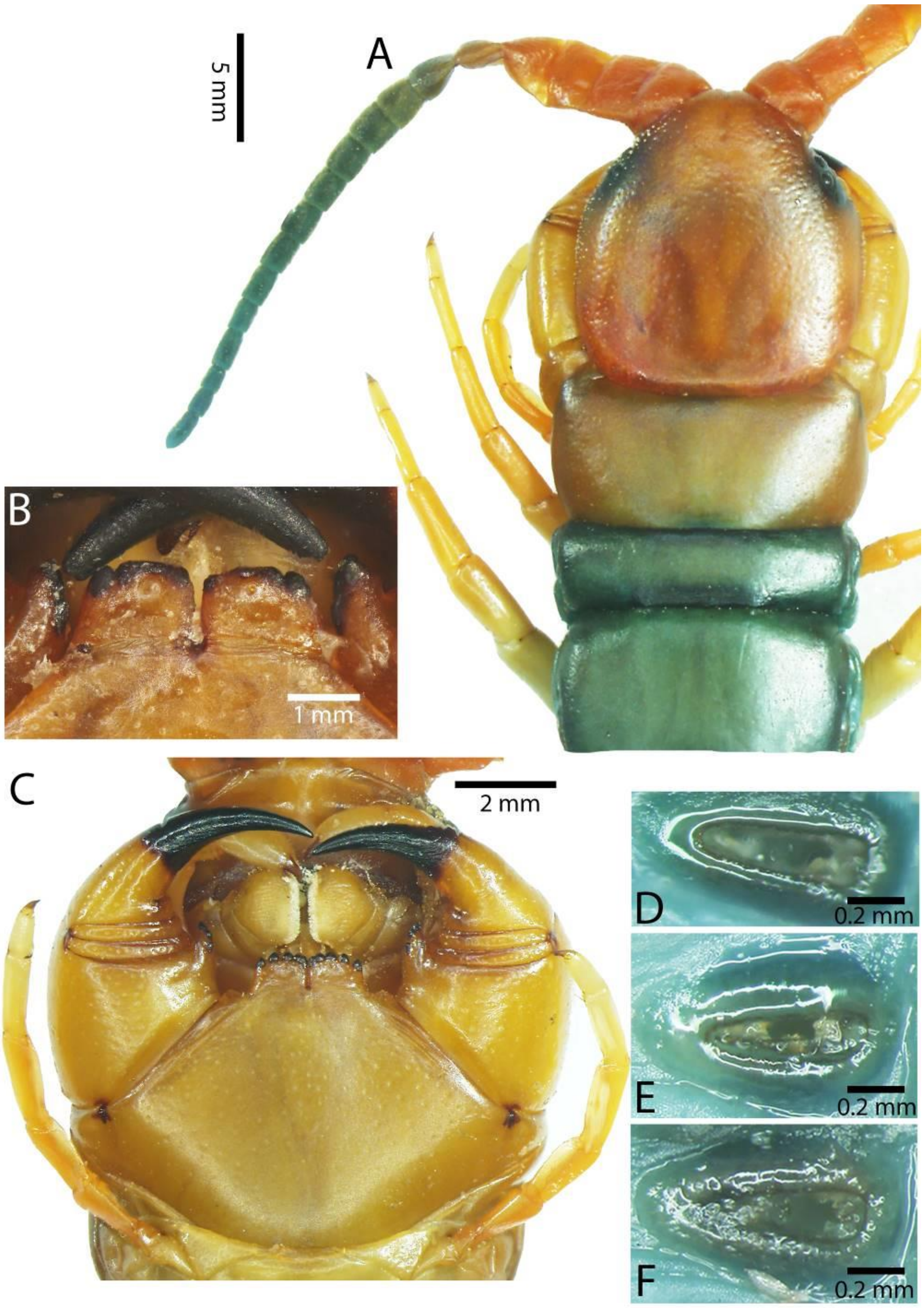


Figure 2.36 *Scolopendra japonica* (CUMZ 00297, 00298): **A** Cephalic plate and trunk segments 1–3 **B** Tooth-plates **C** Forcipular segment **D–F** Spiracles 3, 5 and 8, respectively.

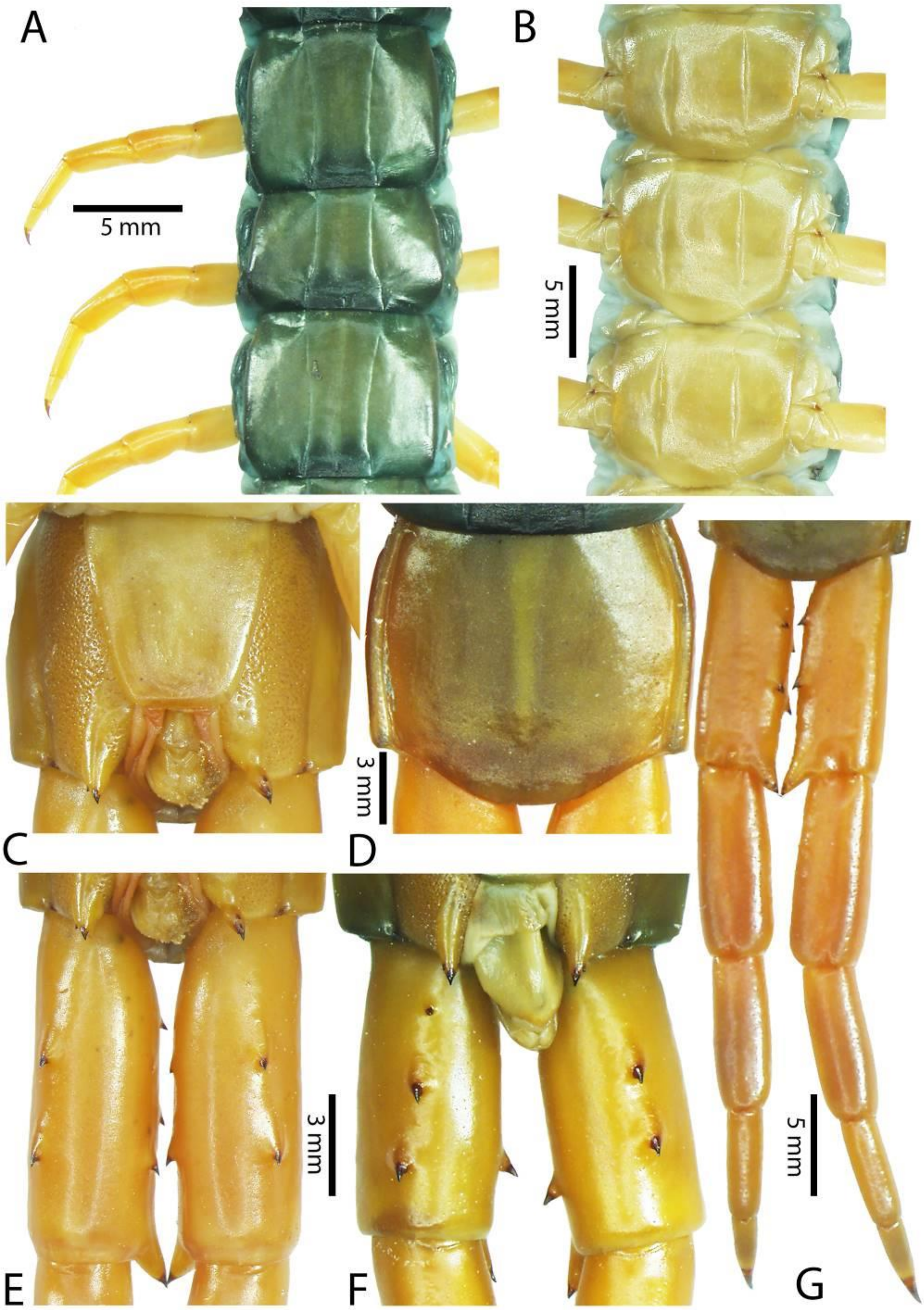


Figure 2.37 *Scolopendra japonica* (CUMZ 00297, 00298): **A** Tergites 9–11 **B** Sternites 9–11 **C** Sternite of ultimate leg-bearingsegment and coxopleura **D** Tergite of ultimate leg-bearing segment **E** and **F** Variation in ventral spines on ultimate leg prefemora **G** Dorsal view of ultimate legs.

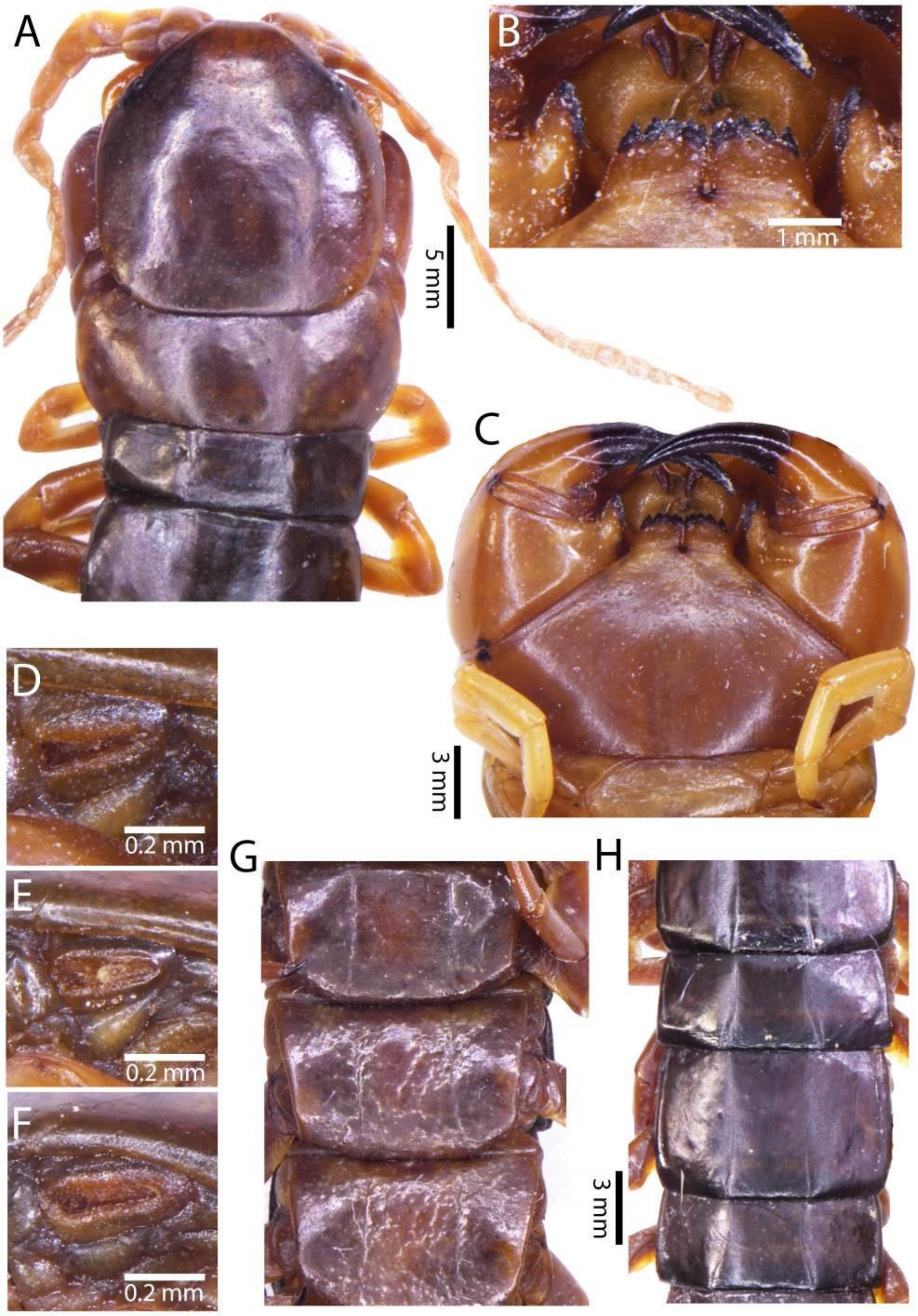


Figure 2.38 *Scolopendra japonica* (Syntype NHMW 5368): **A** Cephalic plate and trunk segments 1–3 **B** Tooth-plates **C** Forcipular segment **D–F** Spiracles 3, 5 and 8, respectively **G** Sternites 9–11**H** Tergites 8–11.

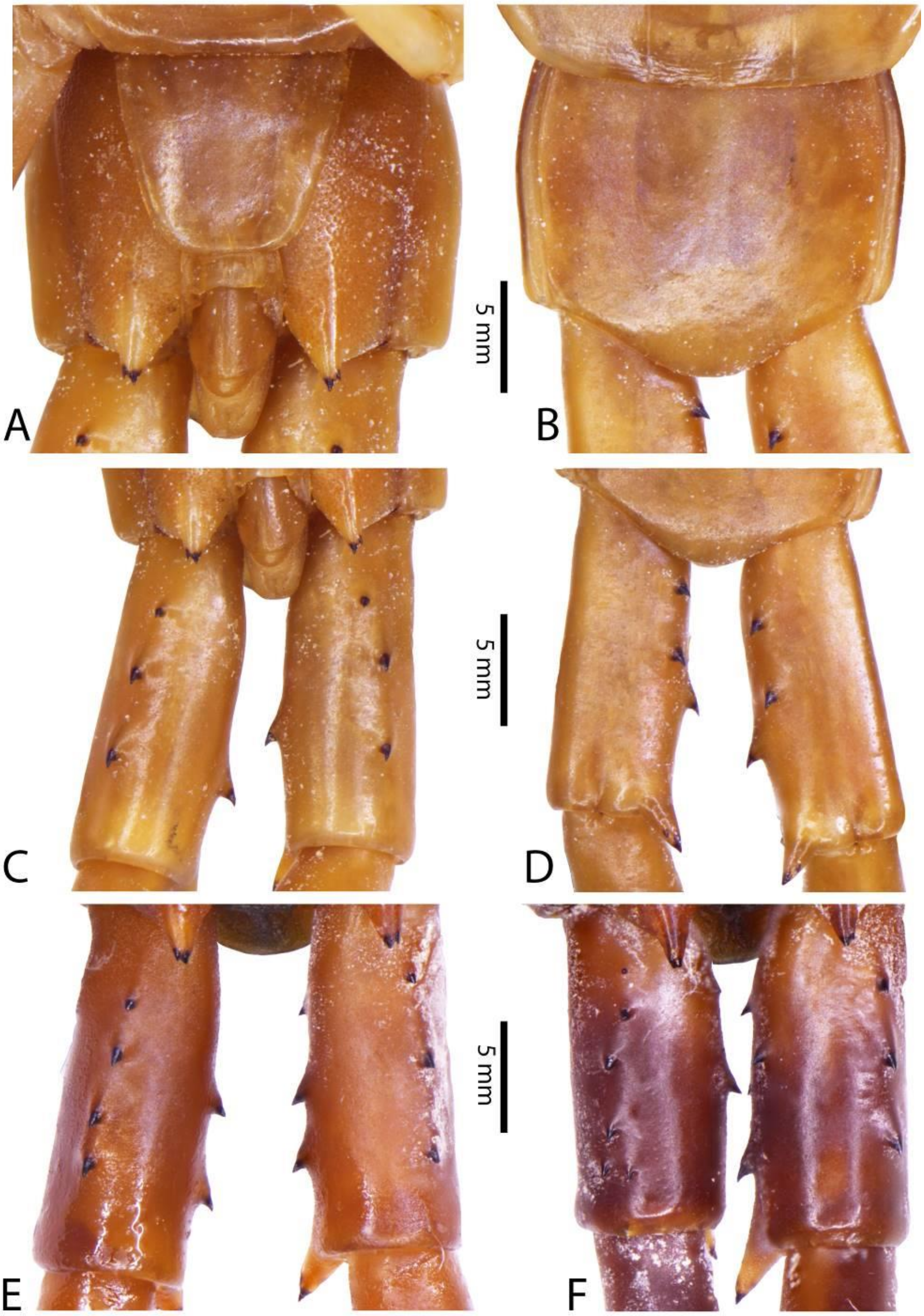


Figure 2.39 *Scolopendra japonica* (Syntype NHMW 5368): **A** Sternite of ultimate leg-bearing segment and coxopleura **B** Tergite of ultimate leg-bearing segment **C–D** Ventral and dorsal views of ultimate leg prefemora **E–F** Variation in ventral spines of ultimate leg prefemora.

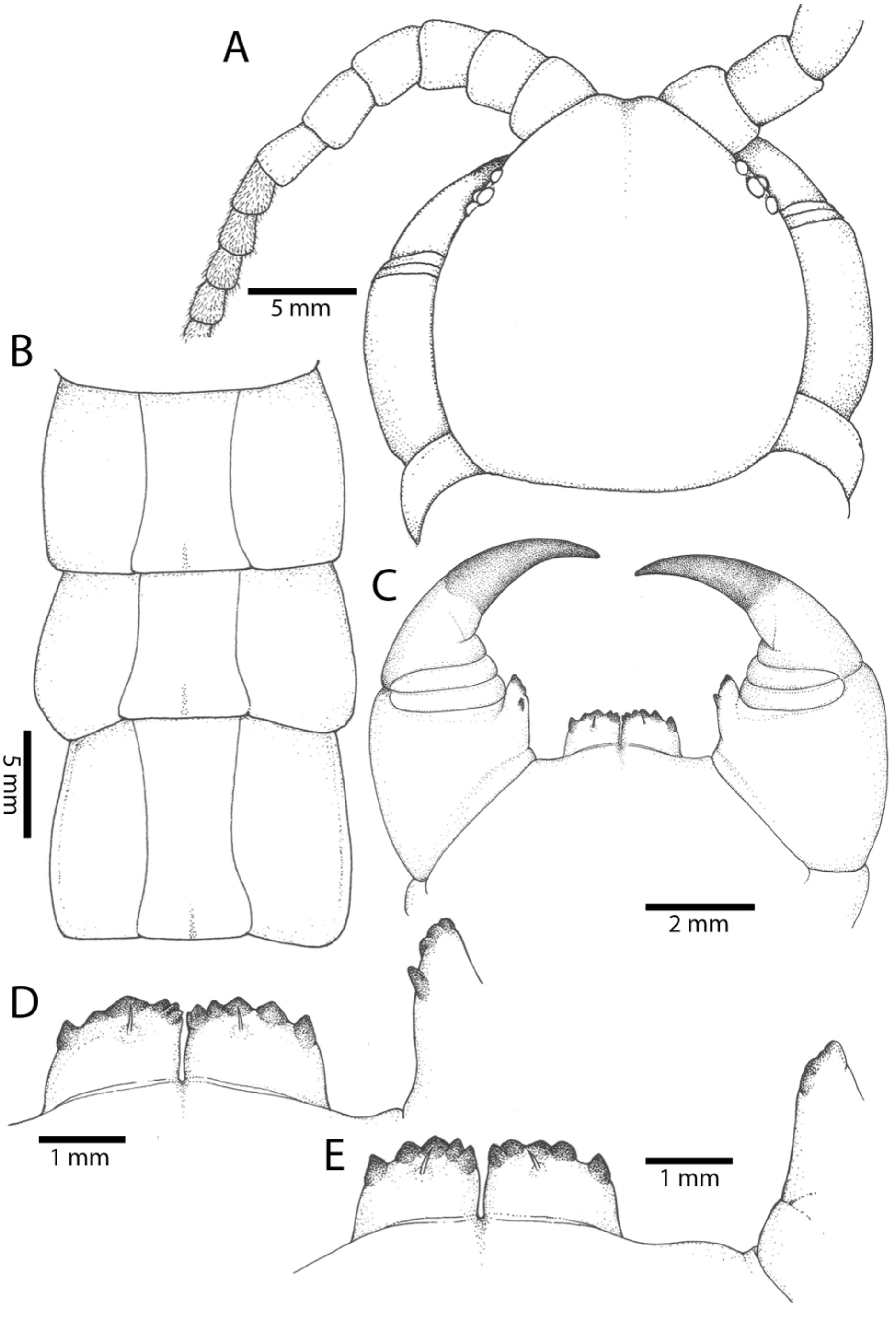


Figure 2.40 *Scolopendra japonica* (CUMZ 00297): **A** Cephalic plate and basal antennal articles **B** Tergites 9–11 **C** Forcipular segment **D–E** Variation in teeth on tooth-plates and trochanteroprefemural process.

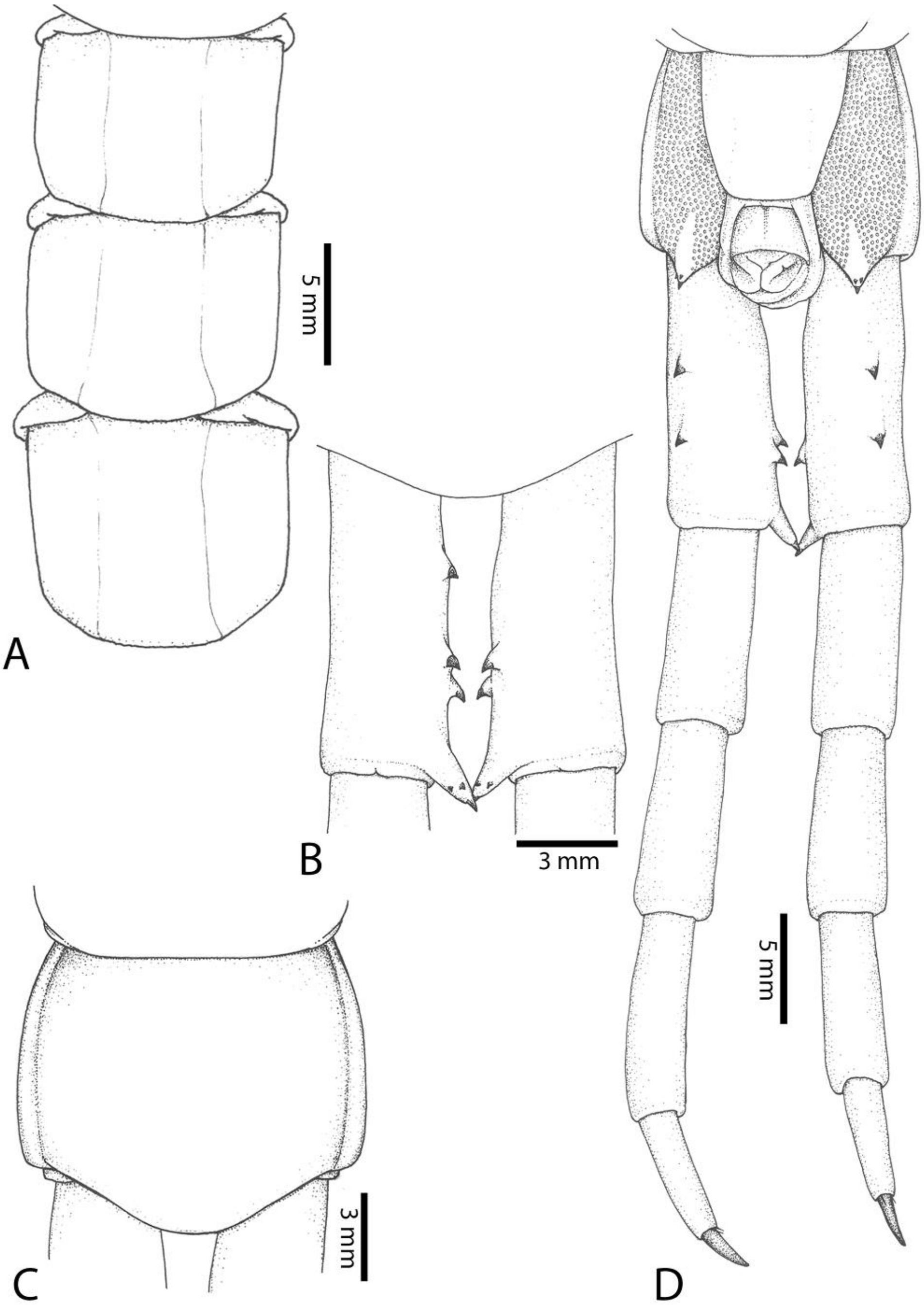


Figure 2.41 *Scolopendra japonica* (CUMZ 00297, 00298): **A** Sternites 9–11 **B** Dorsal view of ultimate leg prefemora **C** Tergite of ultimate leg-bearing segment **D** Sternite of ultimate leg-bearing segment, coxopleura and ultimate legs.

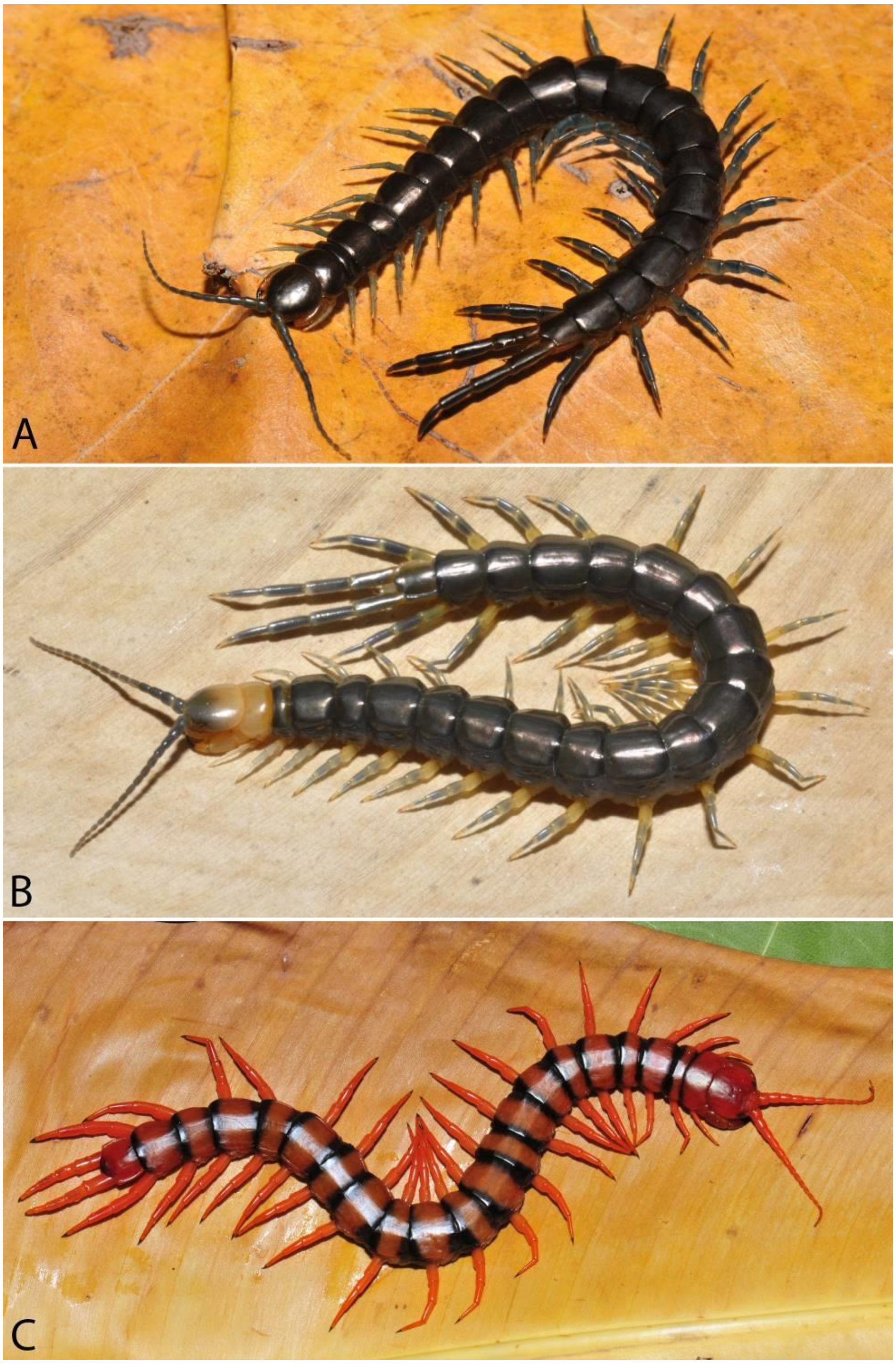


Figure 2.42 Habitus photographs of *Scolopendra* species: **A** *Scolopendra pinguis* (Colour morph 1A: CUMZ 00309) **B** *Scolopendra pinguis* (Colour morph 2B) **C** *Scolopendra dawydoffi* (CUMZ 00272).

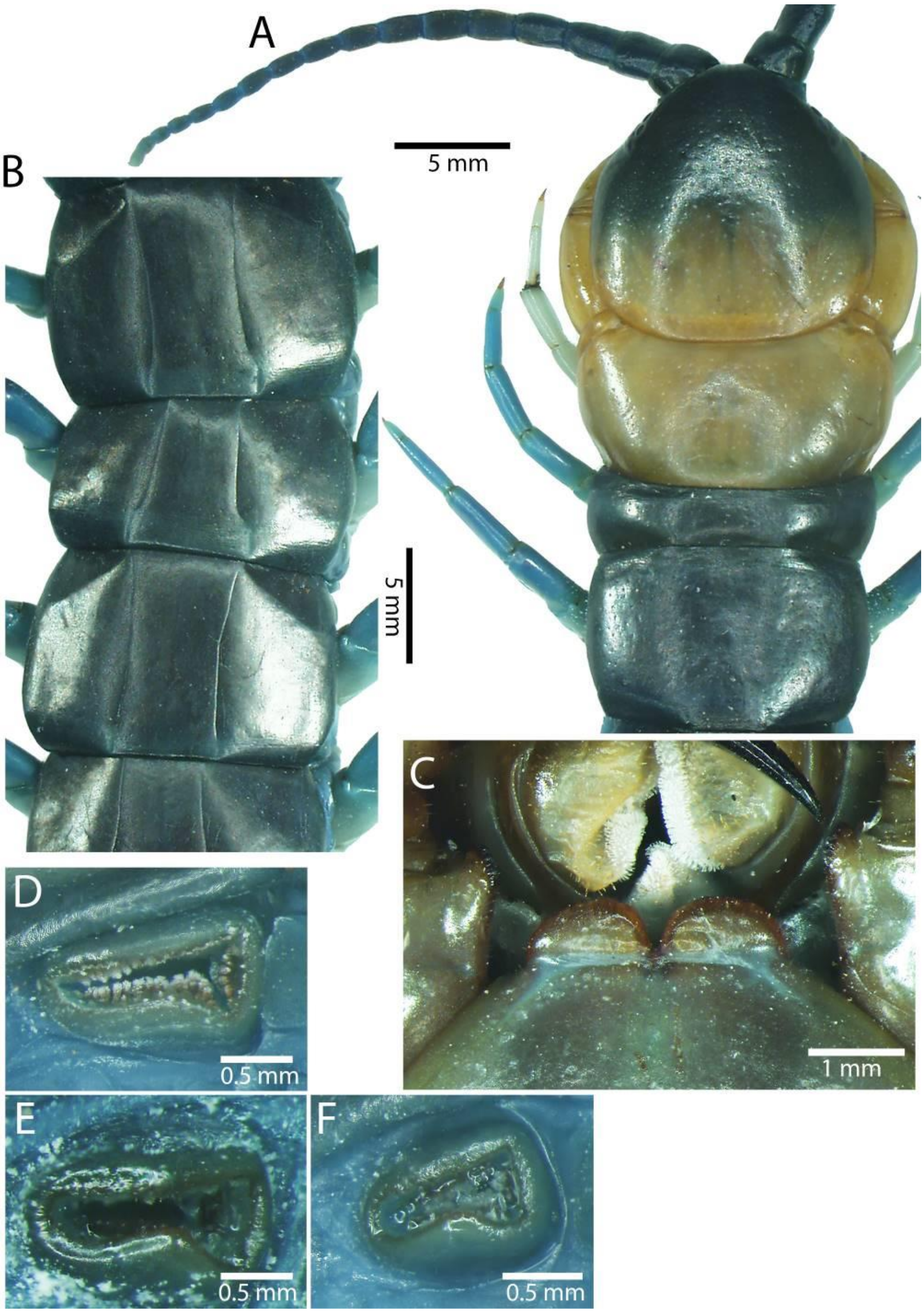


Figure 2.43 *Scolopendra pinguis* (CUMZ 00306, 00314): **A** Cephalic plate and trunk segments 1–3 (Colour morph 2) **B** Tergites 9–11 **C** Tooth-plates **D–F** Spiracles 3, 5 and 8, respectively.

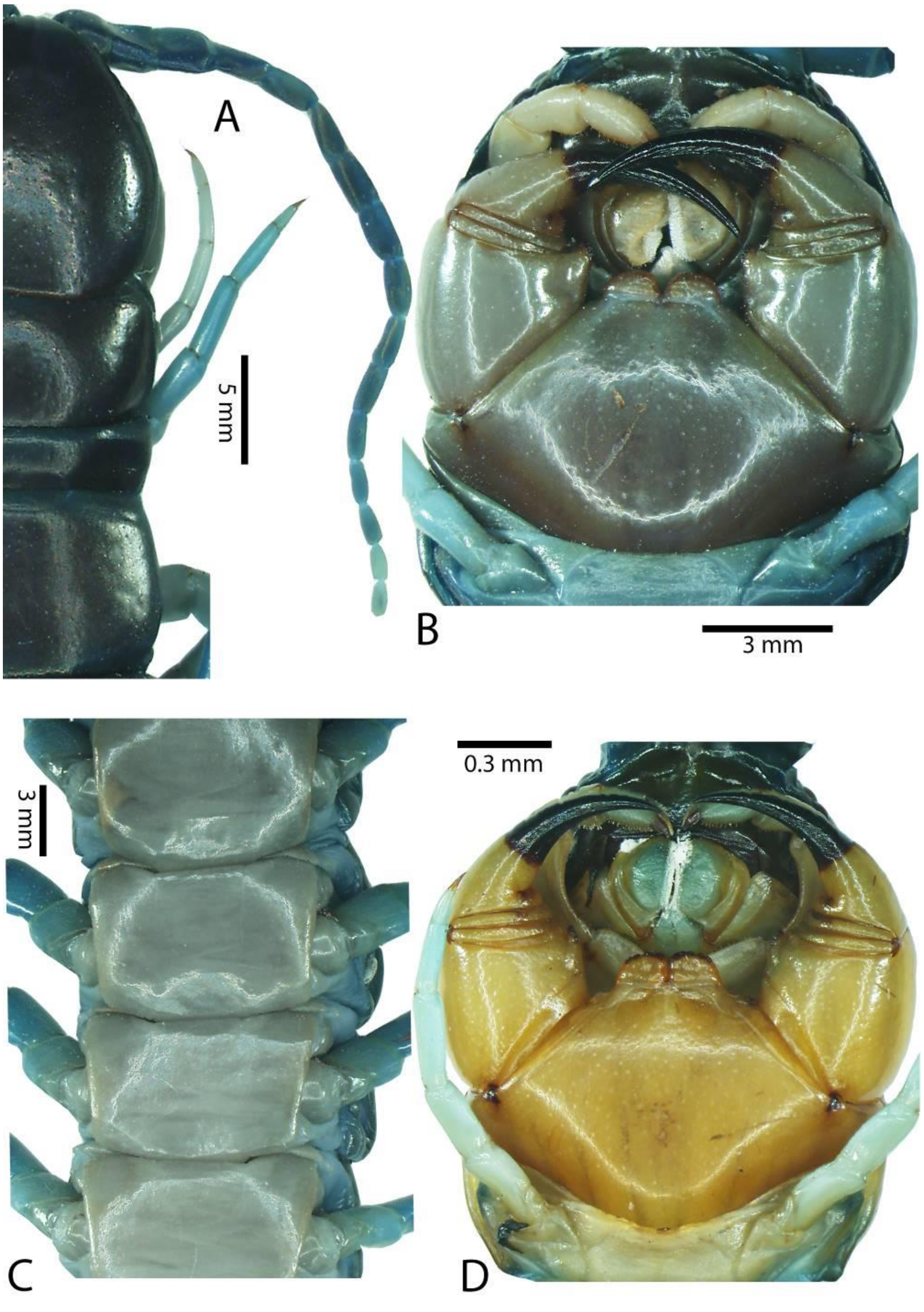


Figure 2.44 *Scolopendra pinguis* (CUMZ 00306, 00314): **A** Cephalic plate and trunk segments 1–3 (Colour morph 1) **B** Forcipular coxosternite (Colour morph 1A and 1B) **C** Sternites 9–12 **D** Forcipular coxosternite (Colour morph 2)

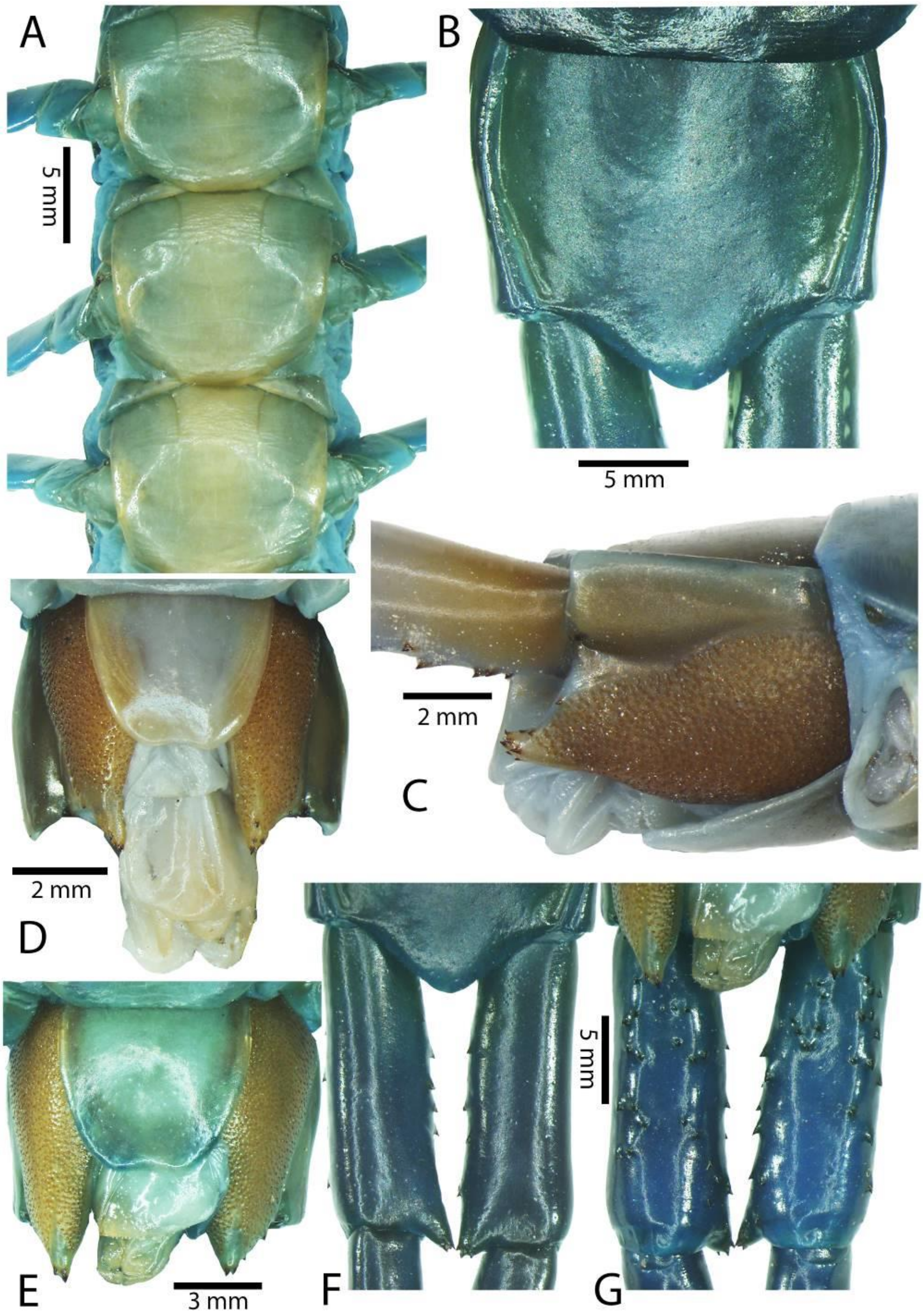


Figure 2.45 *Scolopendra pinguis* (CUMZ 00306, 00314): **A** Sternites 9–11 (Colour morph 2) **B** Tergite of ultimate leg-bearing segment **C** Lateral view of coxopleuron **D**–**E** Sternite of ultimate leg-bearing segment and coxopleura in male and female, respectively **F**–**G** Dorsal and ventral views, respectively, of ultimate leg prefemora.

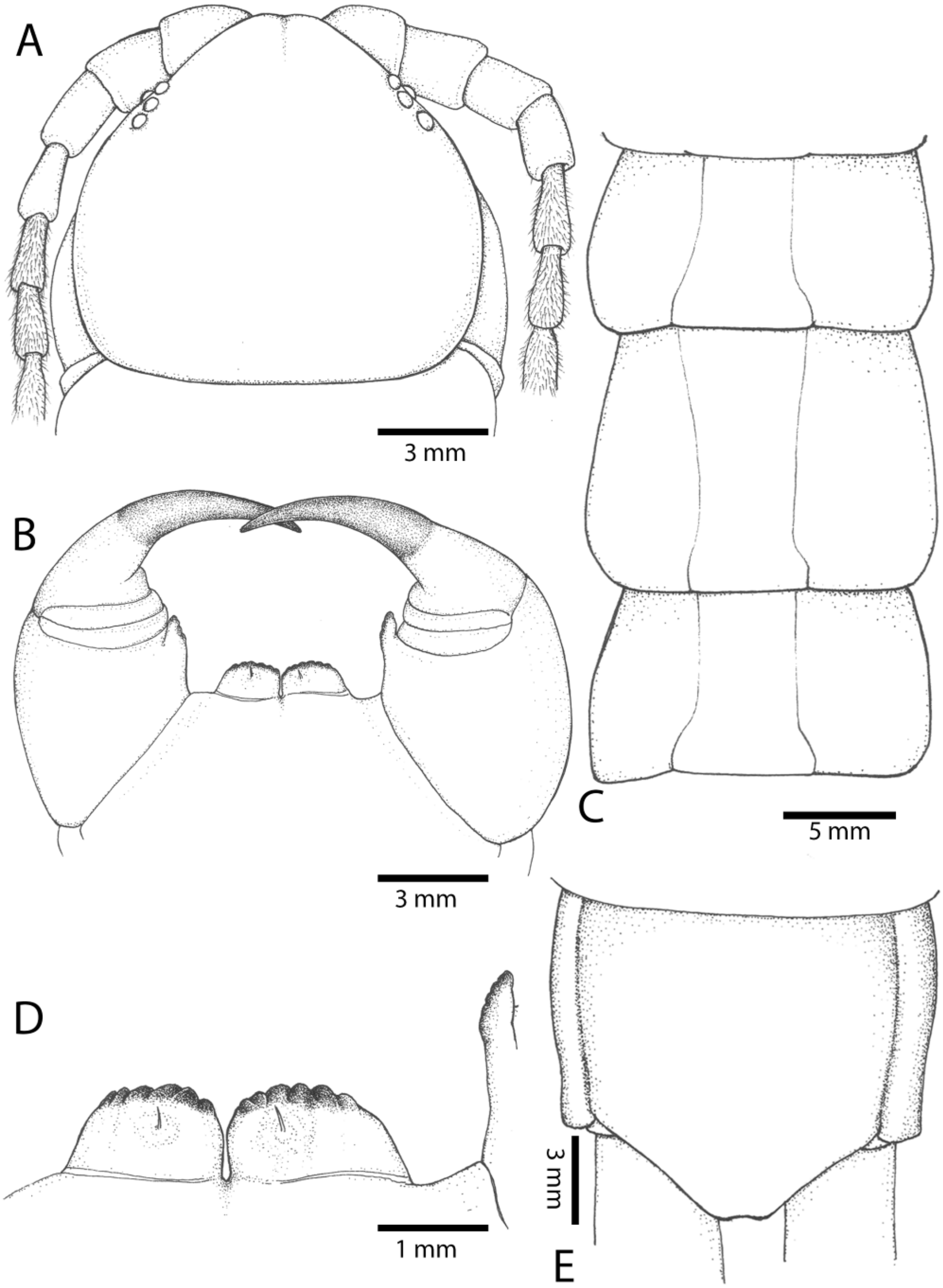


Figure 2.46 *Scolopendra pinguis* (CUMZ 00306, 00314): **A** Cephalic plate and basal antennal articles **B** Forcipular segment **C** Tergites 9–11 **D** Teeth on tooth-plates and trochanteroprefemoral process **E** Tergite of ultimate leg-bearing segment.

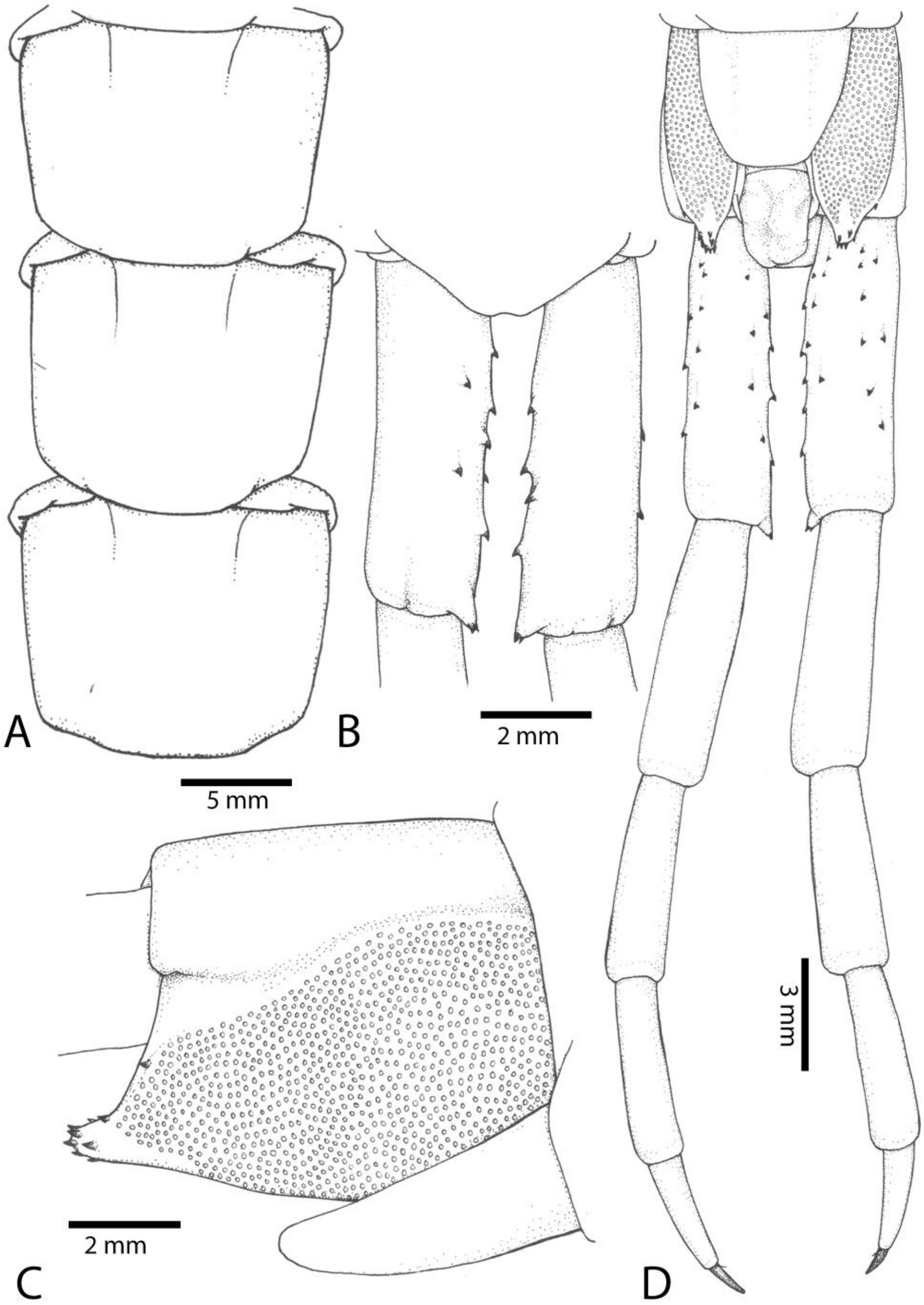


Figure 2.47 *Scolopendra pinguis* (CUMZ 00306, 00314): **A** Sternites 9–11 **B** Dorsal view of ultimate leg prefemora **C** Lateral view of coxopleuron **D** Sternite of ultimate leg-bearing segment, coxopleura and ultimate legs.

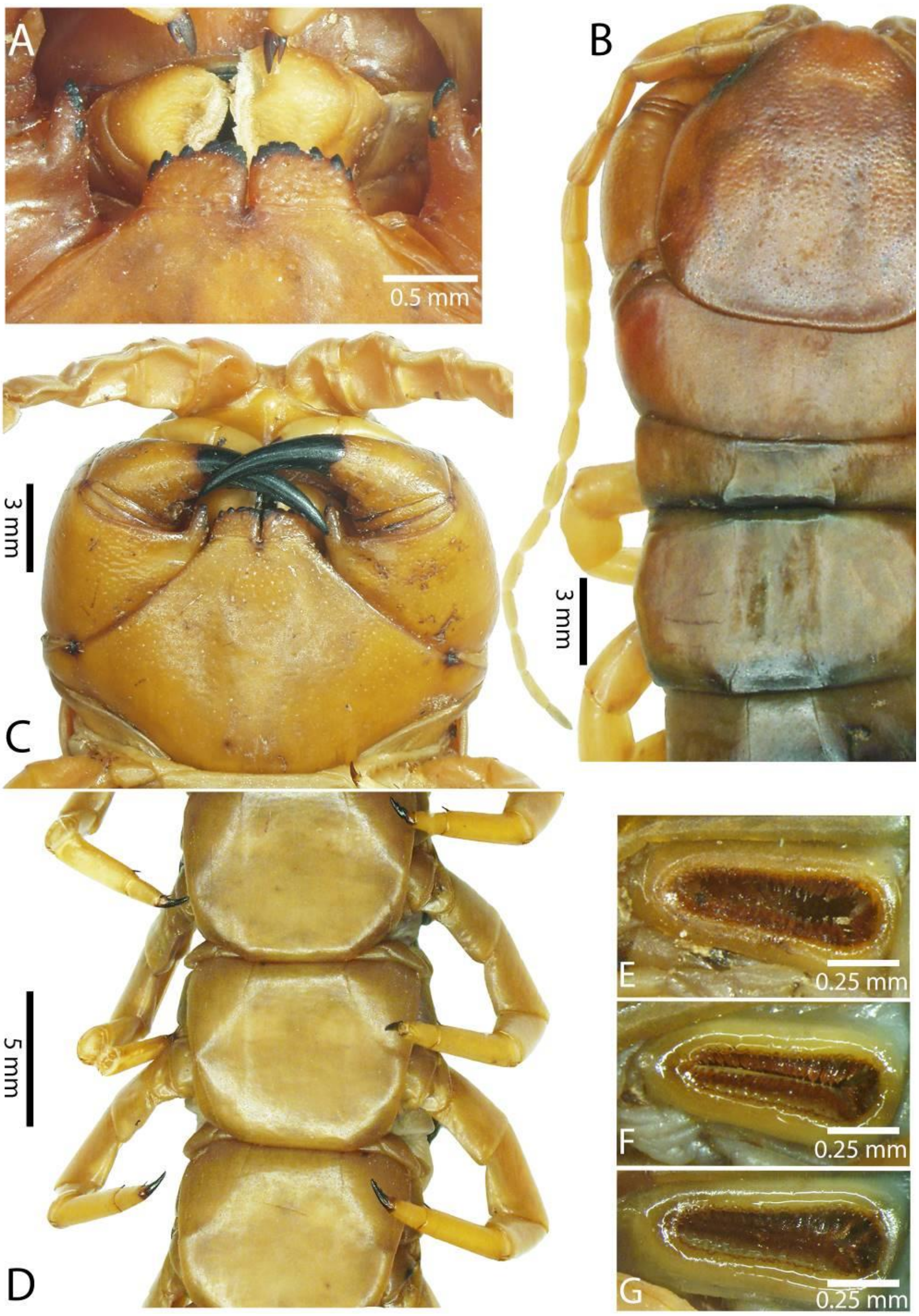


Figure 2.48 *Scolopendra dawydoffi* (CUMZ 00290, 00291): **A** Tooth-plates **B** Forcipular segment **C** Cephalic plate and trunk segments 1–3 **D** Sternites 9–11 **E–G** Spiracles 3, 5 and 8, respectively.

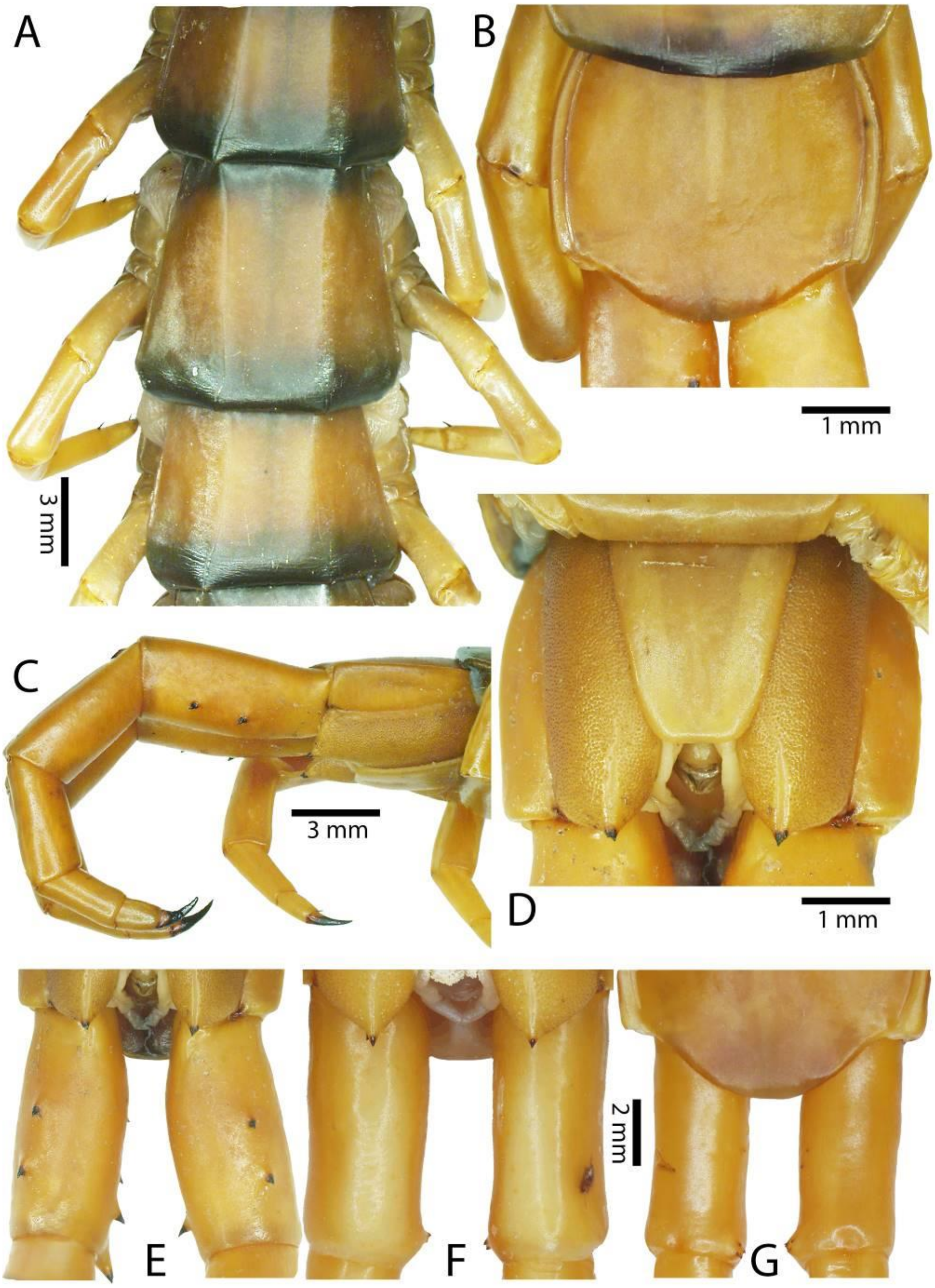


Figure 2.49 *Scolopendra dawydoffi* (CUMZ 00290, 00291, 00272): **A** Tergites 9–11 **B** Tergite of ultimate leg-bearing segment **C** Lateral view of coxopleuron, leg 20 and ultimate leg **D** Sternite of ultimate leg-bearing segment and coxopleura **E** and **F** Variation in ventral spines on ultimate leg prefemora **G** Dorsal view of ultimate leg prefemora.

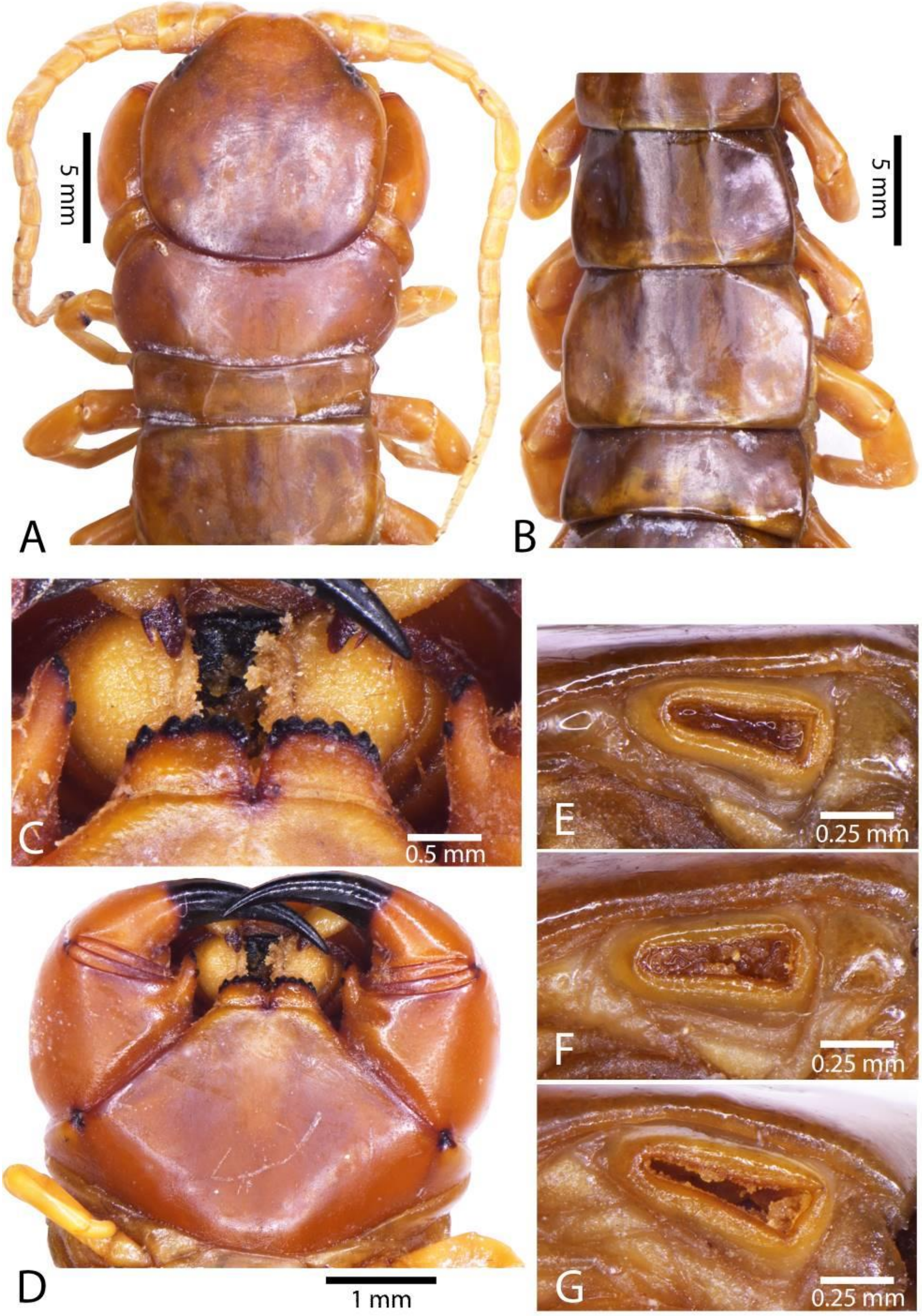


Figure 2.50 *Scolopendra dawydoffi* (Syntypes NHMW 8234): **A** Cephalic plate and trunk segments 1–3 **B** Tergites 9–11 **C** Tooth-plates **D** Forcipular segment **E–G** Spiracles 3, 5 and 8, respectively.

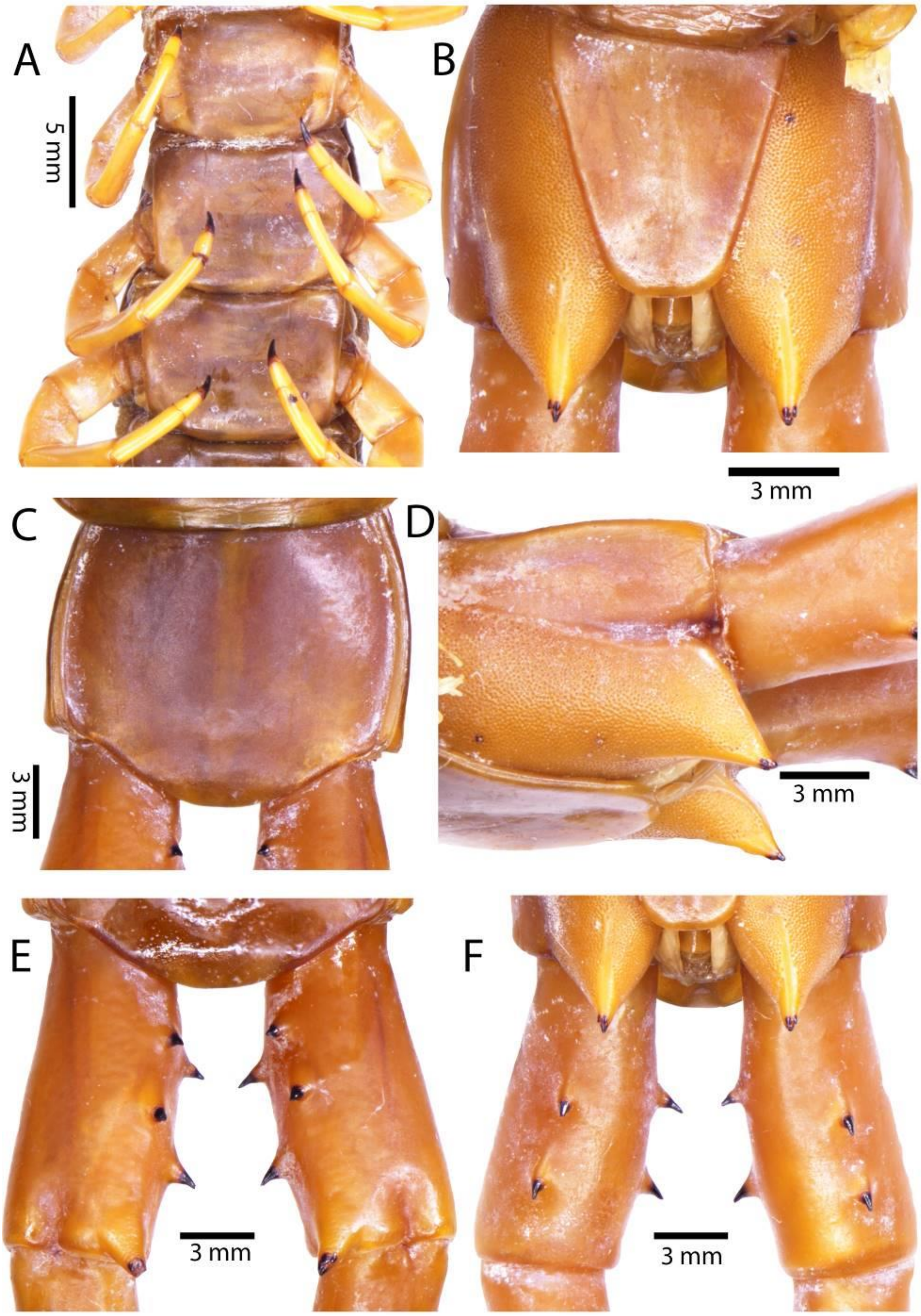


Figure 2.51 *Scolopendra dawydoffi* (Syntypes NHMW 8234): **A** Sternites 9–11 **B** Sternite of ultimate leg-bearing segment and coxopleura **C** Tergite of ultimate leg-bearing segment **D** Lateral view of coxopleuron **E–F** Dorsal and ventral view of ultimate leg prefemora.

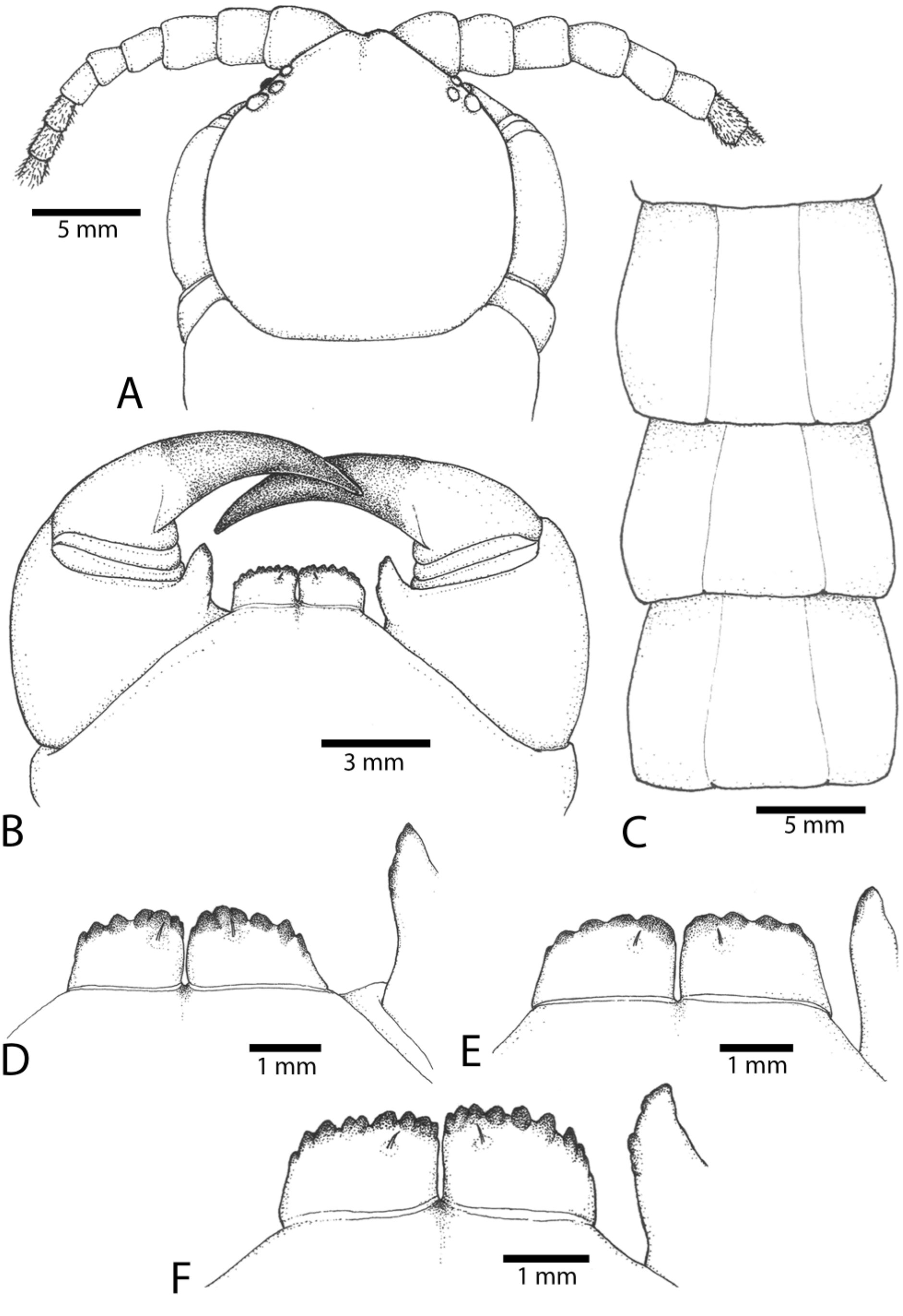


Figure 2.52 *Scolopendra dawydoffi* (CUMZ 00272): **A** Cephalic plate and basal antennal articles **B** Forcipular segment **C** Tergites 9–11 **D–F** Variation in teeth on tooth-plates and trochanteroprefemoral process.

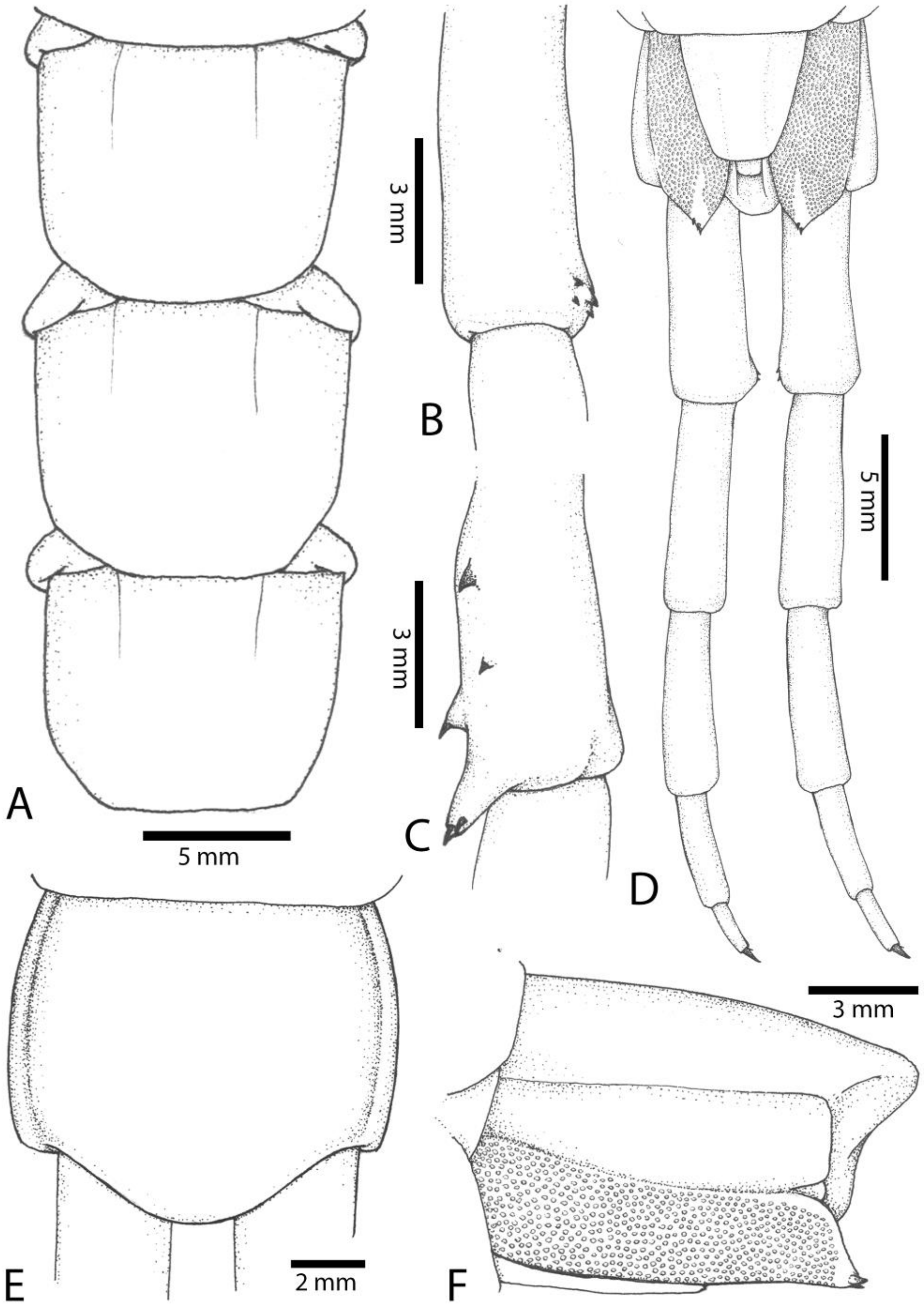


Figure 2.53 *Scolopendra dawydoffi* (CUMZ 00272): **A** Sternites 9–11 **B–C** Variation in numbers of spines on prefemural process of ultimate leg **D** Sternite of ultimate leg-bearing segment, coxopleura and ultimate legs, showing lack of ventral and median spines on prefemora **E** Tergite of ultimate leg-bearing segment **F** Lateral view of coxopleuron.

Figure 2.54 *Scolopendra cataracta* sp. n.: **A** Habitus photograph of holotype CUMZ 00316 **B** Habitat at type locality **C** Genital region; GS – Genital segment.

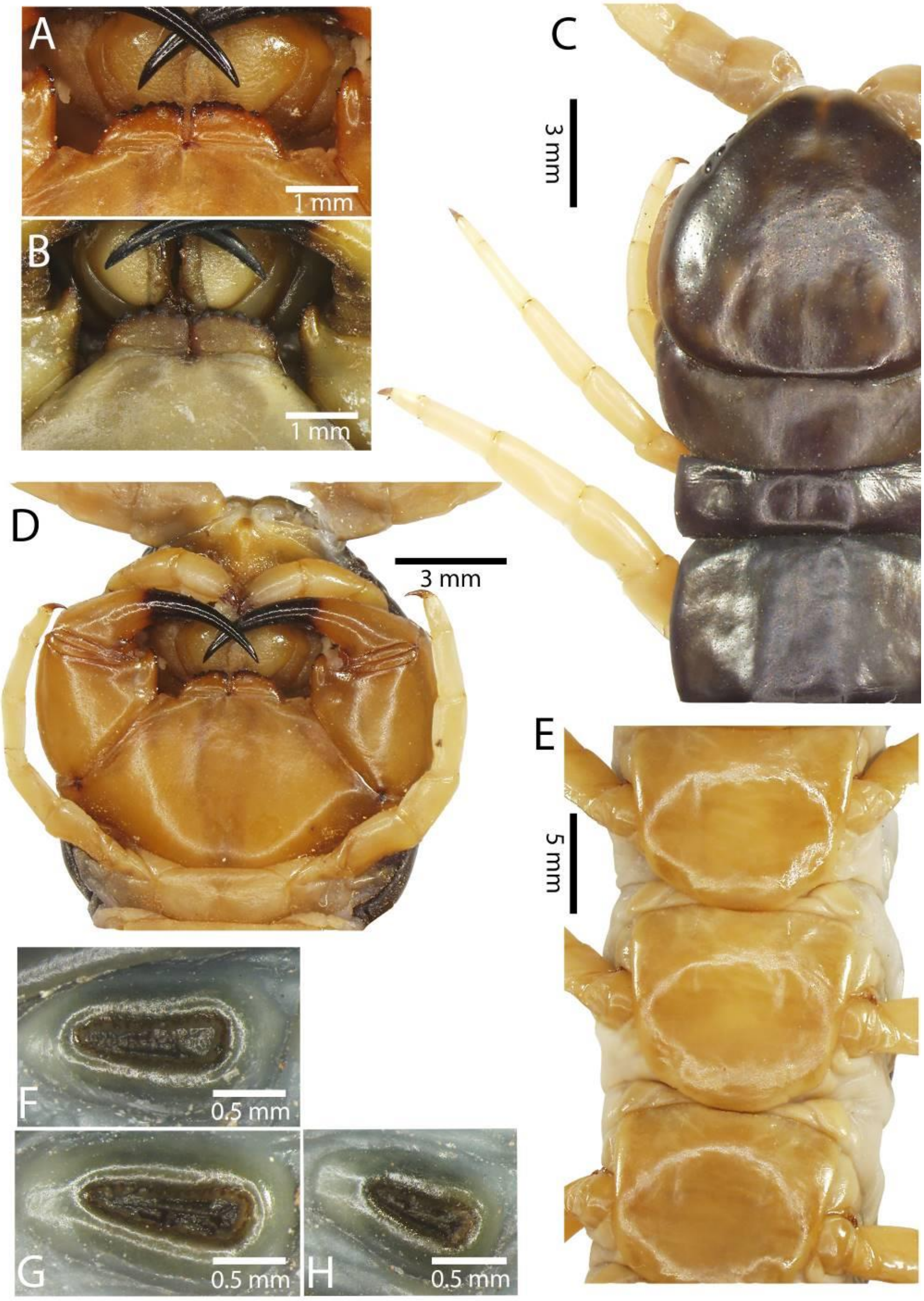


Figure 2.55 *Scolopendra cataracta* sp. n.: **A–B** Tooth-plates **C** Cephalic plate and trunk segments 1–3 **D** Forcipular segment **E** Sternites 9–11 and **F–H** Spiracles 3, 5 and 8, respectively. Holotype CUMZ 00316 (**A,C–H**) and paratype CUMZ 00317 (**B**).

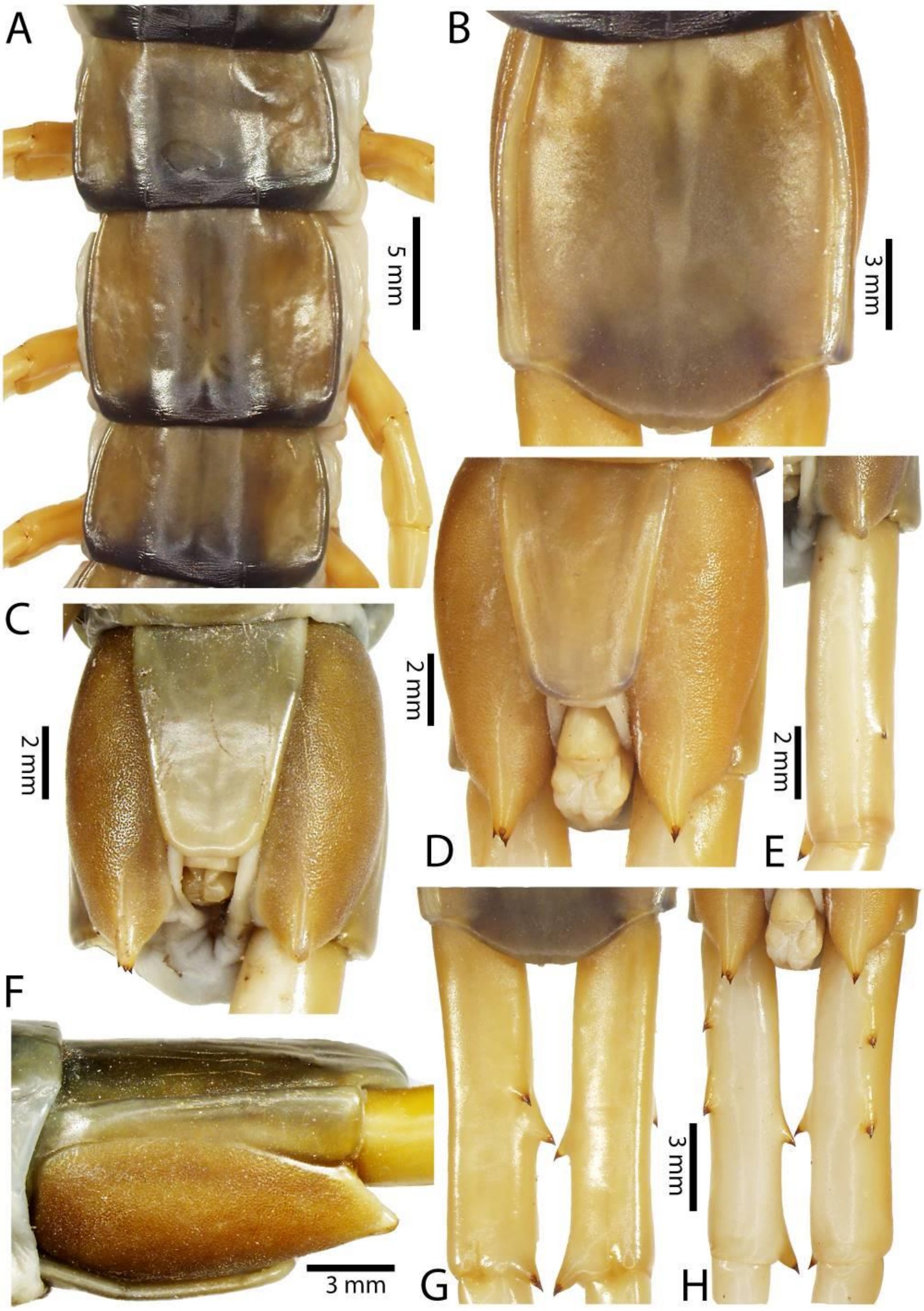


Figure 2.56 *Scolopendra cataracta* sp. n.: **A** Tergites 9–11 **B** Tergite of ultimate leg-bearing segment **C–D** Sternite of ultimate leg-bearing segment and coxopleura **E–H** Variation in ventral spines on ultimate leg prefemora **F** Lateral view of coxopleuron **G** Dorsal view of ultimate legs. Holotype CUMZ 00316 (**A, B, D, G** and **H**) and paratype CUMZ 00317 (**C, E** and **F**).

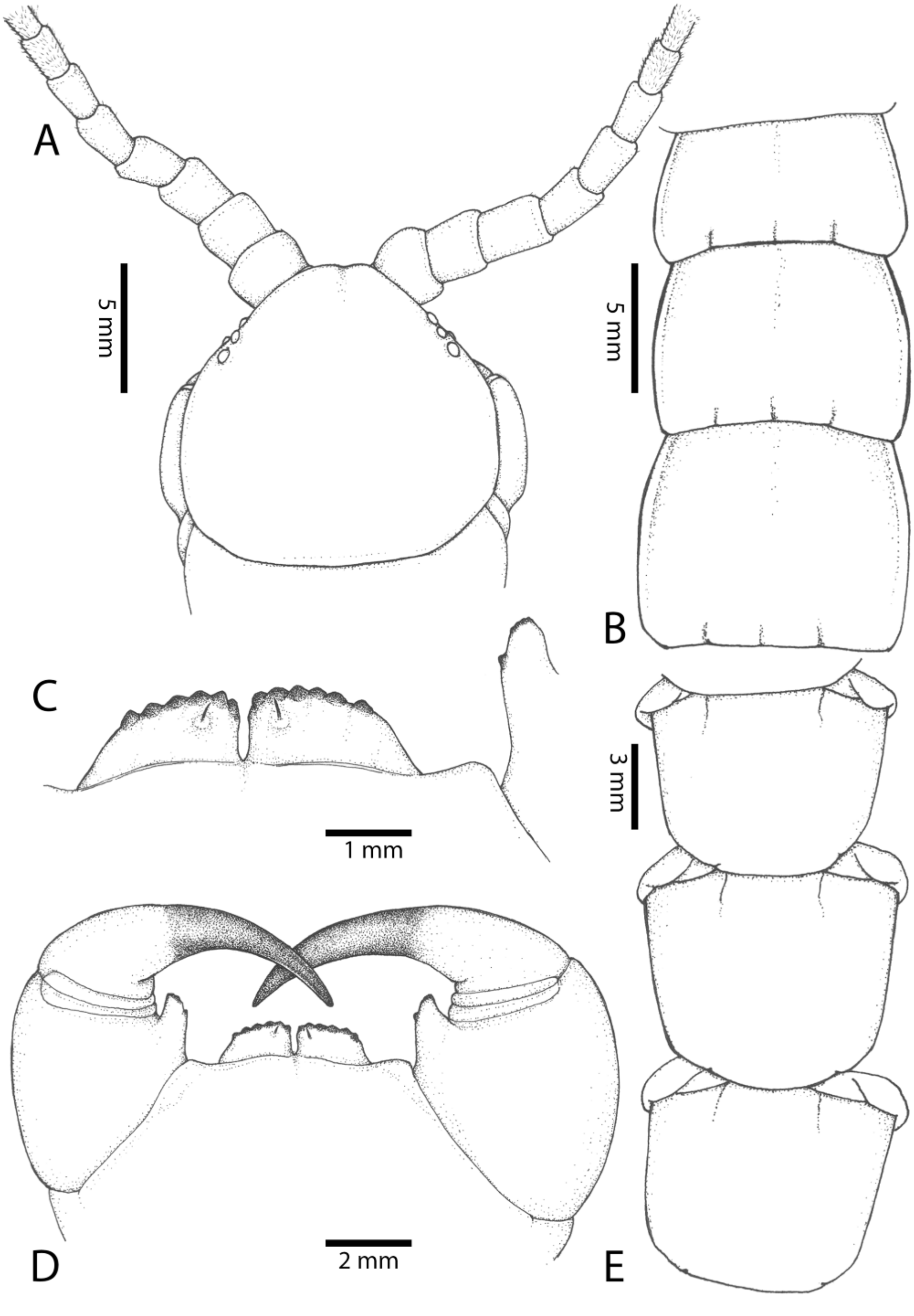


Figure 2.57 *Scolopendra cataracta* sp. n. (Holotype: CUMZ 00316): **A** Cephalic plate and basal antennal articles **B** Tergites 9–11 **C** Tooth-plates and trochanteroprefemoral process **D** Forcipular segment **E** Sternites 9–11.

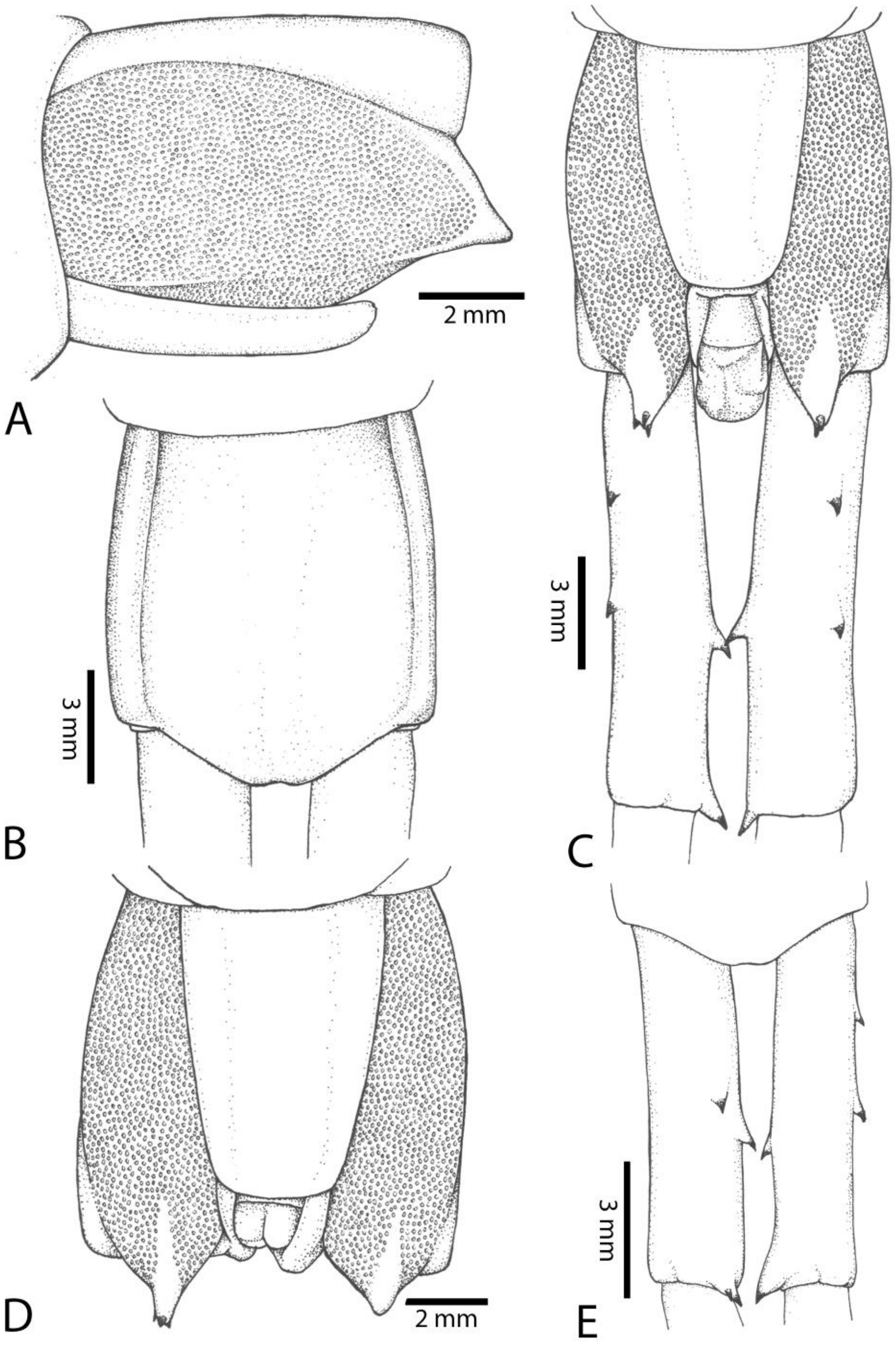


Figure 2.58 *Scolopendra cataracta* sp. n.: **A** Lateral view of coxopleuron **B** Tergite of ultimate leg-bearing segment **C** Sternite of ultimate leg-bearing segment, coxopleura and ultimate leg prefemora. **D** Asymmetry of spines on coxopleural process **E** Dorsal view of ultimate leg prefemora. Holotype CUMZ 00316 (**B–C, E**) and paratype CUMZ 00317 (**A, D**).

Table 2.1 *Scolopendra* sequences used in phylogenetic reconstruction of present study. The abbreviation name of voucher ID code refer to museum collection as follow; AMNH-American Museum of Natural History, CUMZ-Chulalongkorn University Museum of Zoology, MCZ-Museum of Comparative Zoology, Harvard University, NHMUK-Natural History Museum, London, UK.

Species	Taxon locality	Voucher ID number	COI	16S	28S	Reference
Scolopendra morsitans Linnaeus, 1758	Khon Kaen, Thailand	CUMZ 00339	KR705662	KR705600	KR705724	1
	Nan, Thailand	CUMZ 00340	KR705661	KR705599	KR705723	1
	Chonburi, Thailand	CUMZ 00341	KR705660	KR705598	KR705722	1
	Surin, Thailand	CUMZ 00342	KR705666	KR705604	KR705728	1
	Chiang Mai, Thailand	CUMZ 00343	KR705665	KR705603	KR705727	1
	Sa Kaeo, Thailand	CUMZ 00344	KR705664	KR705602	KR705726	1
	Sisophon, Cambodia	CUMZ 00345	KR705663	KR705601	KR705725	1
	Singapore	CUMZ 00315	KR705636	KR705574	KR705698	1
Scolopendra subspinipes Leach, 1816	Papua New Guinea	MCZ IZ-130685	KF676528	KF676488	-	3
	Martinique	AMNH LP3879, MCZ IZ-131452	HQ402554	HQ402502	-	3
Scolopendra cingulata Latreille, 1829	Spain	MCZ IZ-131446	HM453310	HM453220	-	3
Scolopendra dehaani Brandt, 1840	Lopburi, Thailand	CUMZ 00282	KR705689	KR705627	KR705751	1
	Ayutthaya, Thailand	CUMZ 00256	KR705688	KR705626	KR705750	1
	Lan Island, Rayong, Thailand	CUMZ 00320	KR705684	KR705622	KR705746	1
	Sa Kaeo, Thailand	CUMZ 00321	KR705682	KR705620	KR705744	1
	Trad, Thailand	CUMZ 00322	KR705681	KR705619	KR705743	1
	Sichang Island, Chonburi, Thailand	CUMZ 00252	KR705683	KR705621	KR705745	1
	Chiang Mai, Thailand	CUMZ 00323	KR705659	KR705597	KR705721	1
	Chiang Mai, Thailand	CUMZ 00346	KR705658	KR705596	KR705720	1
	Maehongson, Thailand	CUMZ 00324	KR705657	KR705595	KR705719	1
	Maehongson, Thailand	CUMZ 00325	KR705656	KR705594	KR705718	1
	Sakon Nakhon, Thailand	CUMZ 00247	KR705655	KR705593	KR705717	1
	Mahasarakarm, Thailand	CUMZ 00275	KR705651	KR705589	KR705713	1
	Loei, Thailand	CUMZ 00277	KR705653	KR705591	KR705715	1
	Ubon Ratchathani, Thailand	CUMZ 00248	KR705652	KR705590	KR705714	1

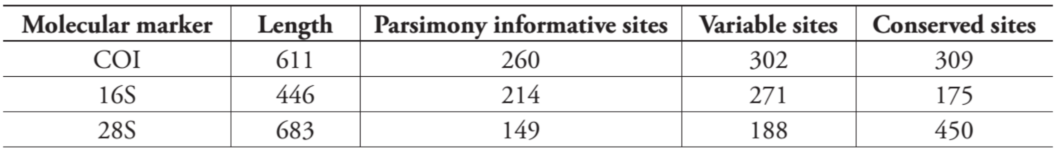
Table 2.1 *Scolopendra* sequences used in phylogenetic reconstruction of present study. The abbreviation name of voucher ID code refer to museum collection as follow; AMNH-American Museum of Natural History, CUMZ-Chulalongkorn University Museum of Zoology, MCZ-Museum of Comparative Zoology, Harvard University, NHMUK-Natural History Museum, London, UK. (Continues)

Species	**Taxon locality**	**Voucher ID number**	**COI**	**16S**	**28S**	**Reference**
	Phatthalung, Thailand	CUMZ 00274	KR705641	KR705579	KR705703	1
	Nakhon Si Thammarat, Thailand	CUMZ 00281	KR705639	KR705577	KR705701	1
	Ranong, Thailand	CUMZ 00262	KR705637	KR705575	KR705699	1
	Phang Nga, Thailand	CUMZ 00251	KR705640	KR705578	KR705702	1
	Chumphon, Thailand	CUMZ 00326	KR705638	KR705576	KR705700	1
	Uthai Thani, Thailand	CUMZ 00243	KR705632	KR705570	KR705694	1
	Prachuap Khiri Khan, Thailand	CUMZ 00327	KR705628	KR705566	KR705690	1
	Kanchanaburi, Thailand	CUMZ 00328	KR705631	KR705569	KR705693	1
	Ratchaburi, Thailand	CUMZ 00253	KR705630	KR705568	KR705692	1
	Tak, Thailand	CUMZ 00329	KR705629	KR705567	KR705691	1
	Siem Reap, Cambodia	CUMZ 00330	KR705687	KR705625	KR705749	1
	Srisophon, Cambodia	CUMZ 00331	KR705686	KR705624	KR705748	1
	Attapue, Laos	CUMZ 00332	KR705678	KR705616	KR705740	1
	Champasak, Laos	CUMZ 00333	KR705673	KR705611	KR705735	1
	Luang Prabang, Laos	CUMZ 00334	KR705677	KR705615	KR705739	1
	Phongsaly, Laos	CUMZ 00335	KR705676	KR705614	KR705738	1
	Perak, Malaysia	CUMZ 00336	KR705669	KR705607	KR705731	1
	Kelantan, Malaysia	CUMZ 00337	KR705668	KR705606	KR705730	1
	Perak, Malaysia	CUMZ 00338	KR705667	KR705605	KR705729	1
Scolopendra multidens Newport, 1844	Qiang Binh, Vietnam	NHMUK, MCZ IZ-131459	KF676540	KF676485	-	3
Scolopendra calcarata Porat, 1876	Kanchanaburi, Thailand	CUMZ 00312	KR705650	KR705588	KR705712	1
	Wat Mae Long, Mae Chaem, Chiang Mai, Thailand	CUMZ 00417	KU512629	KU512632	KU512635	This study
	Lan Sang Waterfall, Mueang, Tak, Thailand	CUMZ 00418	KU512630	KU512633	KU512636	This study
Scolopendra japonica Koch, 1878	Matsumoto, Japan	CUMZ 00319	KR705679	KR705617	KR705741	1
	Xieangkhuang, Laos	CUMZ 00298.1-2	KR705671, KR705670	KR705609, KR705608	KR705733, KR705732	1
	Phongsaly, Laos	CUMZ 00297.1-2	KR705675, KR705674	KR705613, KR705612	KR705737, KR705736	1

Table 2.1 *Scolopendra* sequences used in phylogenetic reconstruction of present study. The abbreviation name of voucher ID code refer to museum collection as follow; AMNH-American Museum of Natural History, CUMZ-Chulalongkorn University Museum of Zoology, MCZ-Museum of Comparative Zoology, Harvard University, NHMUK-Natural History Museum, London, UK. (Continues)

Species	**Taxon locality**	**Voucher ID number**	**COI**	**16S**	**28S**	**Reference**
Scolopendra pinguis Pocock, 1891	Bo Kaeo, Laos	CUMZ 00309	KR705646	KR705584	KR705708	1
	Kanchanaburi, Thailand	CUMZ 00303	KR705646	KR705584	KR705708	1
	Nan, Thailand	CUMZ 00307	KR705644	KR705582	KR705706	1
	Xieangkhuang, Laos	CUMZ 00306	KR705643	KR705581	KR705705	1
	Huaphun, Laos	CUMZ 00304	KR705642	KR705580	KR705704	1
	Chiang Mai, Thailand	CUMZ 00313	KR705649	KR705587	KR705711	1
	Mae Hong Son, Thailand	CUMZ 00314	KR705648	KR705586	KR705710	1
Scolopendra dawydoffi Kronmüller, 2012	Trad, Thailand	CUMZ 00272	KR705680	KR705618	KR705742	1
	Nakhon Ratchasima, Thailand	CUMZ 00290	KR705654	KR705592	KR705716	1
	Nakhon Ratchasima, Thailand	CUMZ 00294.1-2	KR705635, KR705634	KR705573, KR705572	KR705697, KR705696	1
Scolopendra cataracta sp. n.	Tad E-tu Waterfall, Bolaven Plateau, Pakse, Champasak, Laos	Holotype CUMZ 00316	KR705672	KR705610	KR705734	1
	Tad-Yueang Waterfall, Mueang Singh, Luang Namtha, Laos	Paratype CUMZ 00317	KR705633	KR705571	KR705695	1
	Kao Sok National Park, Surat Thani, Thailand	Paratype NHMUK 010305528	KU512631	KU512634	KU512637	This study
Cormocephalus monteithi Koch, 1983	Queensland, Australia	MCZ IZ-130638	HM453309.1	AF370861.1	HM453274	3
Digitipes kalewaensis Siriwut, Edgecombe & Panha, 2015	Kalewa, Sagaing, Burma	CUMZ 00234	KP204116	KP204112	-	2
Otostigmus astenus Kohlrausch, 1878	Fiji / Vanuatu	MCZ IZ-130669/130670	HM453312	HM453221	-	3
Sterropristes violaceus Muadsub & Panha, 2012	Similan,Thailand	MCZ IZ-130610	KF676519	KF676477	-	3

Table 2.2 Sequence annotation of three partial genes used in this present study

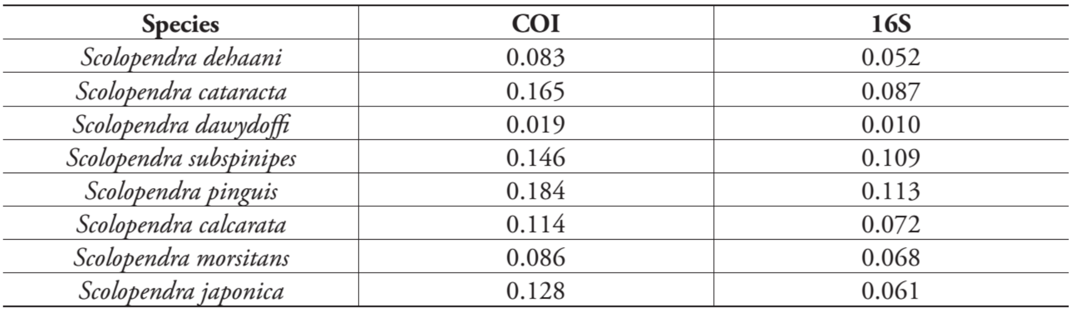


Molecular marker	Length	Parsimony informative sites	Variable sites	Conserved sites
COI	611	260	302	309
16S	446	214	271	175
28S	683	149	188	450

Table 2.3 Genetic distance between *Scolopendra* species in mainland of Southeast Asia and outgroups; upper right and lower left distance collected from COI and 16S partial gene pair-wise comparisons

Species		**16S**													
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
COI	*S. dehaani*^{1}		0.143	0.159	0.148	0.216	0.216	0.210	0.159	0.142	0.185	0.253	0.259	0.265	0.294
	S. cataracta^{2}	0.159		0.164	0.138	0.238	0.213	0.199	0.156	0.158	0.175	0.259	0.262	0.288	0.300
	S. dawydoffi^{3}	0.171	0.190		0.164	0.209	0.220	0.217	0.123	0.127	0.083	0.222	0.292	0.285	0.293
	S. subspinipes^{4}	0.167	0.194	0.177		0.229	0.238	0.212	0.162	0.166	0.174	0.257	0.271	0.303	0.291
	S. pinguis^{5}	0.219	0.247	0.215	0.224		0.171	0.240	0.246	0.230	0.233	0.234	0.280	0.298	0.322
	S. calcarata^{6}	0.228	0.240	0.212	0.230	0.219		0.241	0.237	0.223	0.250	0.255	0.270	0.278	0.315
	S. morsitans^{7}	0.204	0.230	0.204	0.233	0.244	0.242		0.214	0.215	0.231	0.274	0.323	0.341	0.290
	S. japonica^{8}	0.202	0.227	0.163	0.208	0.218	0.219	0.232		0.123	0.135	0.258	0.287	0.297	0.307
	S. cingulata^{9}	0.188	0.197	0.177	0.214	0.224	0.228	0.221	0.181		0.131	0.261	0.274	0.291	0.322
	S. multidens^{10}	0.196	0.203	0.107	0.178	0.216	0.214	0.229	0.163	0.188		0.230	0.304	0.326	0.323
	Cormocephalus^{11}	0.236	0.263	0.234	0.238	0.269	0.239	0.267	0.243	0.231	0.233		0.266	0.296	0.322
	Digitipes^{12}	0.234	0.216	0.227	0.255	0.249	0.252	0.289	0.260	0.237	0.229	0.279		0.213	0.246
	Sterropristes^{13}	0.234	0.246	0.228	0.249	0.233	0.240	0.245	0.217	0.232	0.242	0.244	0.205		0.199
	Otostigmus^{14}	0.217	0.237	0.222	0.237	0.250	0.232	0.251	0.248	0.267	0.236	0.261	0.219	0.208	

Table 2.4 Genetic distance under pairwise sequence comparison within populations of *Scolopedra* species in mainland of Southeast Asia



Species	**COI**	**16S**
Scolopendra dehaani	0.083	0.052
Scolopendra cataracta	0.165	0.087
Scolopendra dawydoffi	0.019	0.010
Scolopendra subspinipes	0.146	0.109
Scolopendra pinguis	0.184	0.113
Scolopendra calcarata	0.114	0.072
Scolopendra morsitans	0.086	0.068
Scolopendra japonica	0.128	0.061

Table 2.5 Geographical variations from several populations of *Scolopendra morsitans* in Old world territory including Australia.

Character	**India[3]**	**Burma[1]**	**Indochina[1,2]**	**Malay Archipelago[1,2]**	**Philippines[1]**	**East Asia[1,6]**	**Australia[5]**	**Africa[2,4]**
Number of antennal articles	19–20	18–22	20–21	18–20	17–19	18–20	17–23	17–21
Number of glabrous articles	6–9	6–7	5	6–7	6–7	5–7?	3–8	5–7
Teeth on tooth-plate	5	4–5	3–7	4–5	4–5	5	3–6	5
First tergite with complete paramedian sutures	2	3	4–5	2–3	2–3	3	2–4	2–4
First tergite with margination	7–17	6–17	5–14	6–13	12–13	10–14	5	2–7 (15)
Tergite surface	smooth	smooth	smooth	smooth	smooth	smooth	smooth	smooth
Median furrow on tergite of ULBS	present	present	present	present	present	present	present	present
Paramedian sutures on sternites	incomplete	incomplete	incomplete	incomplete	incomplete	incomplete	incomplete	incomplete
Sternite of ULBS	?	without depression	without depression	without depression	without depression	without depression	without depression	?
Spines on coxopleural process	AP: 3–5 LS: 0–1	AP: 3–5 LS: 1	AP: 1–5 SAP: 0–1 LS: 0–1	AP: 3–5 LS: 0–1	AP: 4–5 LS: 0–1	AP: 4 LS: 0–1	AP: 2–6	AP: 2–6 LS: 0–1
Spine formula on prefemora of ultimate legs	VS: 3 rows DS: 4–5 2 rows (4–5) SP: 4–10	V: 5–10 (3 rows) M: 2–4 DM: 2–4 SP: 3–7	V: 5–10 (3 rows) M: 0–6 DM: 0–5 SP: 2–6	V: 5–10 (3 rows) M: 2–4 DM: 2 SP: 3–7	V: 9–10 (3 rows) M: 2–4 DM: 2 SP: 3–7	V: 7–9 (3 rows) M: 0–3 DM: 2–6 SP: 0–4	VL: 2–6 VM: 2–8 M: 2–6 DM: 2–6 SP: 4–8	VL: 6–12 M: 2–6 DM: 3–6 SP: 3–8
Legs with one tarsal spur	1–19(20)	1–19	1–19	1–19	1–19	1–19	1–19	1–19(20)

Note: each superscript number refers to description in previous and present studies as follow; [1]= this study, [2]= Attems (1930b, 1953), [3]= Jangi and Dass (1955), [4]= Lewis (1967, 1969), [5]= Koch (1983), [6]= Chao (2003, 2008).

Table 2.6 Morphological comparison of *Scolopendra subspinipes* populations from different geographical regions

Character	Bay of Bengal and Indian Ocean[1]	Malay Peninsula[1]	Vietnam [2]	Indonesia[1]	Philippines[1]	Taiwan [3]	China[1]	Japan[1]
Number of antennal articles	18	18–19	18–19	17–19	17–18	18–19	16–18	15–19
Number of glabrous articles	6	6	6	6	6	6	6	6
Teeth on tooth-plate	5+5	4+6, 5+5, 6+5, 6+6, 7+7	4–9 (each side?)	5+5, 6+7, 7+7, 6+10	5+5, 10+5, 7+7	5+5	5+5	4+5, 5+5, 6+5, 6+6
First tergite with complete paramedian sutures	3	3	2(9) (poorly defined in some specimens)	3–4	3–4	4–6	3–6	3–6
First tergite with margination	5	4–10	14–15	4–11	3–5	5–9	5–8	5–16
Tergite surface	smooth	smooth	smooth	smooth	smooth	smooth	smooth	smooth
Median furrow on tergite of ULBS	absent	absent	absent	absent	absent	absent	absent	absent
Paramedian sutures on sternites	complete	complete	complete	complete	complete	incomplete	complete	complete
Sternite of ultimate leg-bearing segment	without pit	pit-like median furrow	?	pit-like median furrow	without pit	?	pit-like median furrow	pit-like median furrow
Spines on coxopleural process	AP: 2	AP: 2 SAP: 0–1	AP: 2	AP: 2 SAP: 0–1	AP: 2 SAP: 0–1	AP: 2–3	AP: 1–2 SAP: 0–1	AP: 0–2 SAP: 0–1
Spine formula on prefemora of ultimate legs	VL: 2 M: 1 DM: 1 SP: 2	VL: 2–3 M: 1–2 DM: 1–2 SP: 2–3	VL: 0–3 M: 0–2 DM: 0–3 SP: 1≥	VL: 2 M: 1–2 DM: 1–2 SP: 2–5	VL: 2 M: 1–2 DM: 1–2 SP: 2	VL: 2 VM: 1 DM: 2 SP: 2–4	VL: 2–3 M: 1 DM: 1 SP: 1–2	VL: 0–3 M: 0–2 DM: 0–2 SP: 1–6
Legs with one tarsal spur	1–20(R)	1–19(20)	1–19	1–19 (20)	1–19 (20)	1–20	1–20	1–19(20)

Note: each superscript number refers to description in previous and present studies as follow: [1] = this study, [2] = Schileyko (1995), [3] = Chao (2008).

Table 2.7 Morphological survey of geographical variation of *Scolopendra dehaani* populations from different regions

Characters	Geographical distribution area						
	Java[1,2]	**Thailand, Laos and Cambodia[1]**	**Burma[1]**	**Malay Peninsula[1]**	**India[3]**	**China- Japan[1]**	**Mexico[1]**
Number of antennal articles	14–18	18–21	17–19	17–19	18–19	18	18
Number of glabrous articles	6	6	6	6	6	6	6
Teeth on tooth-plate	5+4,5+5	5+5	5+5,5+6,6+6	5+5,6+6,7+8,8+10	6+6	6+7	6+6
First tergite with complete paramedian sutures	incomplete	4	2–6	3–4	4	3–5 or incomplete	incomplete
First tergite with margination	7–10	13	10–14	7–13	5	8	7
Tergite surface	smooth	smooth	smooth	smooth	smooth	smooth	smooth
Median furrow on tergite of ULBS	absent	absent	absent	absent	absent	absent	absent
Extent (percentage) of paramedian sutures on sternites	10–15% (rarely with complete PS)	90–100%	100%	30–100%	80–100%	80–100%	20%
Sternite of ultimate leg-bearing segment	with or without pit-like median depression	with pit- like median depression	with or without pit- like median depression	with or without pit-like median depression	without pit-like median depression	without pit-like median depression	without pit-like median depression
Spines on coxopleural process	AP: 2 SAP: 0–1	AP: 2	AP: 2	AP: 0–2	AP: 2	AP: 2	AP: 1 SAP: 0–1
Spinulation formula on prefemora of ult. legs	M: 0–2 DM: 0–2 SP: 2–4	M: 1 DM: 1 SP: 2–3	M: 0–2 DM: 0–2 SP: 2	M: 1 DM: 1 SP: 1–3	DM: 1 SP: 2	M: 0–1 DM: 1–2 SP: 1–2	M: 0–1 DM: 1 SP: 2
Legs with one tarsal spur	1–20	1–19	1–19 (20)	1–19 (20)	1–20	1–20	1–20

Note: each superscript number refers to data from recent and earlier studies as follow: [1] = This study, [2] = Brandt (1840), [3] = Jangi and Dass (1984).

Table 2.8 Morphological comparison of *Scolopendra japonica* populations in the present study and the related species *S. cingulata*

Characters	*S. japonica*			*S. cingulata*
	Japan (Syntypes)	**Japan-China**	**Laos**	
Number of antennal articles	17–19	17–19	12–18	17–22
Number of glabrous articles	6	6	6	6
Teeth on tooth-plate	5+5	4+5, 5+5	6+6, 5+5	4+4,5+5
First tergite with complete paramedian sutures	3–4	3–4	4	2–3
First tergite with margination	10–13	11–15	12	7–12
Tergite surface	smooth	smooth	short median furrow on posterior part of TT7–19	smooth
Median furrow on tergite of ULBS	absent	absent	absent	absent
Paramedian sutures on sternites	complete	complete	complete	complete
Sternite of ultimate leg-bearing segment	sides converging posteriorly	sides converging posteriorly	sides converging posteriorly	sides converging posteriorly
Spines on coxopleural process	AP: 0–3 SAP: 0–1	AP: 0–3 SAP: 0–1	AP: 3	AP+SAP: 1–5
Spine formula on prefemora of ultimate legs	VL: 2–3 M: 1–2 DM: 1–3 SP: 0–3	VL: 2–3 M: 1–2 DM: 1–2 SP: 1–5	VL: 2–3 M: 1 DM: 2 SP: 3–4	VL: 1–2 M+DM: 4–8 SP: 1–11
Legs with one tarsal spur	1–19 (20)	1–19 (1–20)	1–19	19

Table 2.9 Morphological comparison of *Scolopendra pinguis*, *Scolopendra gracillima* and *S. calcarata*

Characters	*S. pinguis*			*S. gracillima*		*S. calcarata*		
	Pocock (1891, 1893)	**Kraepelin (1903) and Attems (1930)**	**This study**	**Attems (1930)**	**Schileyko (1995)**	**Porat (1876)**	**Schileyko (1995)**	**This study**
Number of antennal articles	17	17	17	17	17	17	17	17
Number of glabrous articles	3	3	4	5	6	4	5–6	4
Teeth on tooth-plate	?	?	6+6	5+5	4+4, 5+5	10–12 (in total)	5+5, 6+6	5+5
First tergite with complete paramedian sutures	T3	T3	T3	?	T3	?	T3	T3
First tergite with margination	20–21	20–21	T16–18	20–21	only 21	T12–14	TT15–21	only T21
Tergite surface	?	?	smooth	punctate on TT3(4)–19(20)	?	smooth	?	smooth
Median furrow on tergite of ULBS	absent	absent	absent	absent	absent	present	absent	absent
Extent (percentage) of paramedian sutures on sternites	nearly complete on anterior part of body	nearly complete on anterior part of body	incomplete (20–30%)	incomplete	complete only on anterior part of body	?	incomplete	incomplete (20–50%)
Sternite of ultimate leg-bearing segment	wide, sides converging	wide, sides converging	sides converging posteriorly	narrow, posterior margin rounded	narrow, posterior margin rounded	?	trapeziform with shallow depression	sides converging
Spines on coxopleural process	AP+SAP: 5 L: 1	AP: 3 SAP: 0–3 LS: 1 DS: 1	AP: 3 SAP: 0–3 LS: 1–2 DS: 0–1	AP+SAP: 3–5 LS: 1	AP+SAP: 5–6 LS: 1	AP+SAP: 5	AP+SAP: 5 LS: 1 DS: 1	AP: 3–4 SAP: 0–3 LS: 1 DS: 1
Spine formula on prefemora of ult. legs	V: 14–22 D: 2–8	V: 14–22 D: 2–8 (5–8)	VL: 6–12 VM: 1–12 M: 2–6 DM: 3–4	VL: 6–8 VM: 3–4 M: 3–4 D: 1–3 SP:4–5	VL: 7 VM: 5–6 D: 3–4 SP: 4	V: 9 M: 5 D: 7 SP: 5	VL: 9–12 VM: 11–12 M: 2–3 D: 2–3	VL: 4–7 VM: 0–3 M: 1–2 DM+SP: 3–4
Legs with one tarsal spur	1–20 (?)	1–19	1–19 (20)	1–20	1–20	1–21	1–21	1–21

Table 2.10 Morphological comparison of *S. dawydoffi* and *S. multidens;* data from present study and previous taxonomic studies, i.e., Attems (1938), Chao (2008), Kronmüller (2012).

Characters	***S. dawydoffi***		***S. multidens***	
	Laos (Syntypes)	**Thailand**	**China (Holotype)**	**Hong Kong and Taiwan**
Number of antennal articles	18	17–18	7/4, damaged	17–19
Number of glabrous articles	6	6	6	6
Teeth on tooth-plate	6+6	5+5, 7+6, 10+9	5+7	7+7
First tergite with complete paramedian sutures	3	2–3	2	2–4
First tergite with margination	11	12–14	9	13
Tergite surface	smooth	smooth	short median furrow on posterior part	short transverse groove on anterior-lateral part (TT2–20)
Median furrow on tergite of ULBS	absent	absent	absent	absent
Extent (percentage) of paramedian sutures on sternites	incomplete (15–35%)	incomplete (20–60%)	incomplete (40–60%)	incomplete (20–100%)
Sternite of ultimate leg-bearing segment	sides converging posteriorly	sides converging posteriorly	sides converging posteriorly	sides converging posteriorly
Spines on coxopleural process	AP: 1 SAP: 2	AP: 1–2 SAP: 1–2	AP: 1 SAP: 2	AP: 1–2 SAP: 1–2
Spine formula on prefemora of ultimate legs	VL: 2 M: 2 DM: 2 SP: 2–3	VL: 0–2 M: 0–1 DM: 0–2 SP: 1–5	VL: 3 M: 2 DM: 2 SP: 2–3	VL: 2 M: 2 DM: 2 SP: 1–3
Legs with one tarsal spur	1–19	1–19	1–19 (20?)	1–19 (20L)
Podomeres of ultimate legs with shallow groove on posterior part	prefemur and femur	prefemur and femur	prefemur and femur	prefemur and femur
Gonopods on genital segment	? (female)	absent	?	absent

Table 2.11 Morphological comparison of *Scolopendra cataracta* sp. n. and some related species in the adjacent sub-regions

Characters	***S. cataracta* sp. n.**				***S. subspinipes piceoflava* (Syntypes)**	***S. hainanum****
	Laos (Holotype)	**Thailand (Paratype)**	**Vietnam (Paratypes)**	**Laos (Paratype)**		
Number of antennal articles	19	19	19	18(19)	17–18	17–19
Number of glabrous articles	6	6	6	6	6	6
Teeth on tooth-plate	6+6	6+6	5+5, 6+6	6+6	5+5, 6+6	6+6,7+7
First tergite with complete paramedian sutures	incomplete (short PS on anterior and posterior part)	incomplete (short PS on posterior parts from TT5–20)	incomplete (short PS on anterior and posterior parts from TT3–20)	incomplete (short PS on anterior and posterior part)	complete, starting from T3	incomplete, starting from T3–4
First tergite with margination	7	14	7 and 10	12	5–7	5
Tergite surface	smooth	smooth	smooth	smooth	punctate	smooth
Extent (percentage) of paramedian sutures on sternites	15–20%	20–45%	10–25%	15%	complete	nearly complete
Sternite of ultimate leg-bearing segment	sides converging posteriorly	sides converging posteriorly	sides converging posteriorly, with pit like-furrow	sides converging posteriorly	sides converging posteriorly, with pit like-furrow	sides converging posteriorly, with pit like-furrow
Spines on coxopleural process	AP: 3(2) DP: 0–1	AP: 1–2	AP: 1 SAP: 2	AP: 3 DP: 1	AP: 1	AP: 1–2
Spine formula on prefemora of ultimate legs	VL: 2 M: 1 DM: 0–1 SP: 2	VL: 1 M: 0–1 DM: 1–2 SP: 1	VL: 2 M: 1–2 DM: 1–2 SP: 2–3	VL: 1 M: 0 DM: 0 SP: 2	V: 0–2 SP: 2–5	VL: 1 VM: 1 DM: 2 SP: 2
Legs with one tarsal spur	1–20	1–20	1–19, 20(R)	1–19	1–20	1–19
Gonopods on genital segment	female specimen	?	female specimens	?	present	absent

Chapter 3

The centipede genus *Scolopendra* in mainland Southeast Asia: Molecular phylogenetics, geometric morphometrics and external morphology as tools for species delimitation

Warut Siriwut[1,2], Gregory D. Edgecombe[3], Chirasak Sutcharit[2], and Somsak Panha[2]*

[1] Biological Sciences Program, Faculty of Science, Chulalongkorn University, Bangkok, Thailand
[2] Animal Systematics Research Unit, Department of Biology, Chulalongkorn University, Bangkok , Thailand
[3] Department of Earth Sciences, The Natural History Museum , London, UK.
*Corresponding author
E-mail: somsak.pan@chula.ac.th

PLoS ONE 10(8): e0135355. doi:10.1371/journal.pone.0135355

Abstract

Seven *Scolopendra* species from the Southeast Asian mainland delimited based on standard external morphological characters represent monophyletic groups in phylogenetic trees inferred from concatenated sequences of three gene fragments (cytochrome *c* oxidase subunit 1, 16S rRNA and 28S rRNA) using Maximum likelihood and Bayesian inference. Geometric morphometric description of shape variation in the cephalic plate, forcipular coxosternite, and tergite of the ultimate leg-bearing segment provides additional criteria for distinguishing species. Colouration patterns in some *Scolopendra* species show a high degree of fit to phylogenetic trees at the population level. The most densely sampled species, *Scolopendra dehaani* Brandt, 1840, has three subclades with allopatric distributions in mainland SE Asia. The molecular phylogeny of *S. pinguis* Pocock, 1891, indicated ontogenetic colour variation among its populations. The taxonomic validation of *S. dawydoffi* Kronmüller, 2012, *S. japonica* Koch, 1878, and *S. dehaani* Brandt, 1840, each a former subspecies of *S. subspinipes* Leach, 1814 sensu Lewis, 2010, as full species was supported by molecular information and additional morphological data. Species delimitation in these taxonomically challenging animals is facilitated by an integrative approach that draws on both morphology and molecular phylogeny.

Introduction

Several lines of evidence suggest that Southeast Asia, one of world’s biodiversity hotspots, might be a migration corridor for animals (de Bruyn et al., 2014). Currently, Southeast Asian biodiversity is classified as two zoogeographical sub-regions, Indochina and Malesia (Lohman et al., 2011). Associated with the geographical richness of this area, cryptic speciation has been reported in several endemic groups, including molluscs (Nantarat et al., 2014b), decapods (Chia and Ng, 2006), insects (Menezes et al., 2015), fish (Lourie and Vincent, 2004) and amphibians (Emerson et al., 2000), and has been attributed to allopatric and sympatric speciation, both on land and on islands (Brown and Stuart, 2012).

Molecular phylogeny has emerged as a powerful tool for evolutionary studies across the Tree of Life (Dunn et al., 2008; Giribet and Edgecombe, 2012). Drawing on molecular techniques, the classification and evolutionary history of organisms has been revised and refined (Field et al., 1988; Emerson et al., 2000; Edgecombe and Giribet, 2008; Nishikawa et al., 2012; Laakmann et al., 2013; Nantarat et al., 2014a; Pimvichai et al., 2014; Menezes et al., 2015). Recent studies on a global scale of phylogenetic biogeography of evolutionarily ancient animal taxa such as onychophorans (Monge-Najera, 1995; Murienne et al., 2013) and centipedes in the order Scutigeromorpha (Edgecombe and Giribet, 2009; Giribet and Edgecombe, 2013) revealed insights on genetic affinity and evolutionary history through past geological events. Moreover, smaller scale phylogeographic studies have proven valuable for exploring spatial and phylogenetic patterns in the diversification in some groups of centipedes, such as the geographically restricted Australasian order Craterostigmomorpha (Edgecombe and Giribet, 2008). However, this approach to historical biogeography has not yet been applied to any centipedes in Southeast Asia.

The genus *Scolopendra* Linnaeus, 1758 comprises common large scolopendromorph centipedes that are distributed worldwide, especially in tropical territories, and nowhere more than in Southeast Asia (Bonato et al., 2016). In the Old World, *Scolopendra* consists of 42 nominal species (Lewis, 2010b). However, because of its scattered distributional records, the fine details of the distributional range of several species are still unknown and need to be revised. Some *Scolopendra* species, such as *S. morsitans* Linnaeus, 1758, and *S. subspinipes* Leach, 1814 (Leach, 1816), have been interpreted as widespread species and recognized as introduced by human transportation because of their habitat preferences, and in some cases their commercial usage (Shelley et al., 2005). Recent studies on molecular phylogeny of Mediterranean *S. cingulata* (Latreille, 1829) (Latreille, 1829)explored the genetic affinity between adjacent populations and also interpreted the evolutionary history of its geographical distribution in the past in relation to geological events (Simaiakis et al., 2012; Oeyen et al., 2014).

However, there remains considerable morphological ambiguity among members of *Scolopendra*, a problem that has been discussed in relation to a shortage of informative taxonomic characters that can be used for species delimitation (Edgecombe and Giribet, 2007). Moreover, the validity of some members needs to be reassessed because their purportedly diagnostic characters show a high degree of geographic variability (Lewis, 2010b). The status of various nominal taxa within *Scolopendra* as either full species, as subspecies, or as variants within species that do not warrant taxonomic recognition is especially acute in *S. subspinipes*. This nominal species had long been assigned as many as seven subspecies (Attems, 1930a), the status of which has been repeatedly debated (Kronmüller, 2012). Recently, geometric and meristic morphometrics has been proposed as a method for helping to clarify shape problems in some centipede groups such as Scutigeromorpha (Bolton et al., 2009; Lopez Gutierrez et al., 2011) and Scolopendromorpha, including species of *Scolopendra* (Simaiakis et al., 2011). These studies invite the application of such techniques for attempting to resolve taxonomic problems in other groups.

According to many previous taxonomic studies, colouration patterns in the body of *Scolopendra* vary among populations from different geographical regions (Koch, 1982; Shelley, 2005). However, there are still limited data for evaluating this character for its taxonomic value, and its relationship to phylogenetic and phylogeographic patterns are all but unexplored.

In this study, seven *Scolopendra* species from the Southeast Asian mainland have been collected and examined. The concatenated sequences of three gene fragments, specifically the barcode region of cytochrome *c* oxidase subunit 1, 16S mitochondrial DNA, and partial 28S nuclear ribosomal DNA, have been used to construct phylogenetic trees and perform a biogeographic study. Geometric morphometrics has been implemented to record shape variation in three selected features using landmark methods. These features are the forcipular coxosternite, the cephalic plate, and the tergite of the ultimate leg-bearing segment. Moreover, colouration patterns in some *Scolopendra* species have been recorded at both the species and population levels, allowing this variation to be mapped on phylogenetic trees. We apply these different data sources and analytical approaches together with traditional external morphological characters to the question of species delimitation in *Scolopendra*.

Material and methods

Specimen collection and identification

Centipede specimens were collected from both natural and urban habitats through the course of biodiversity surveys in Thailand and adjacent countries under grants to SP since 2010. Permission to enter remote and natural reserve areas was granted by The Plant Genetic Conservation Project under the Initiative of Her Royal Highness Princess Maha Chakri Sirindhorn (grant proposals 2010-2015). During field surveys, some individuals were photographed with either a Nikon D700 or D90 camera equipped with a Nikon AF-S DX Micro-Nikkor 40 mm f/2.8G lens and two Nikon SB 600 Speed light flash sources to record their living colouration pattern. Collected samples were relaxed with 50% ethanol concentration mixture for 5-20 minutes and then transferred to a higher ethanol concentration for setting their posture for photography. Species identification was made based on previous literature on scolopendrid taxonomy, i.e. studies by Attems (Attems, 1930a, 1953), Chao (Chao, 2008), Lewis (Lewis, 1982b; Lewis, 2001; Lewis, 2010b) Shelley et al. (Shelley, 2005; Shelley et al., 2005) Schileyko (Schileyko, 1992, 1995, 2007), Koch (Koch, 1982), Kronmüller (Kronmüller, 2009; Kronmüller, 2012) and Verhoeff (Verhoeff, 1937). Terminology applied to taxonomic characters used the standardized nomenclature for centipede morphology by Bonato et al. (2010) (Bonato et al., 2010). All taxonomic characters were observed under an Olympus stereo microscope connected with a montage imaging system operated under the Cell'D program. All examined materials are housed at Chulalongkorn University, Museum of Zoology, Bangkok, Thailand. Molecular samples are kept in absolute ethanol at -40 degrees Celsius to prevent DNA degradation.

DNA extraction, amplification and sequencing

Sixty-one *Scolopendra* samples were dissected to separate tissue from locomotory legs for DNA extraction. The commercial Geneaid DNA extraction and Nucleospin purification kits were used for harvesting genomic DNA. Genomic DNA yields were determined using DNA quantification loading dye blue, loaded in 1X TBE-Agarose gel and run under a 135 V electrical gradient impulse for 15 minutes. Standardized conditions of PCR amplification were edited based on previous molecular works on centipede phylogeny as follow; Edgecombe and Giribet, 2008 , Joshi and Karanth, 2011; 2012 (Joshi and Karanth, 2012), Murienne et al. 2010; 2011

(Murienne et al., 2010), Vahtera et al. 2012, 2013 (Vahtera et al., 2013) and Siriwut et al. 2015 (Siriwut et al., 2015b). Three partial gene fragments were used in this study; the barcode region of cytochrome *c* oxidase subunit I (COI), 16S ribosomal DNA (16S rRNA), and 28S nuclear ribosomal DNA (28S rRNA)

The PCR mixture consisted of the following: 0.6-1 µl of DNA template, 2.5 µl of forward and reverse primers, 25 µl of Ultra-Pure *Taq* PCR Master Mix combined with ruby and emerald loading dye and 18 µl of ddH_2O. All gene fragments were amplified using the selected primers for each region as follow: COI was assembled using forward universal primers for COI for animal phylogeny LCO1490 (Folmer et al., 1994) and the modified reverse primer for centipede phylogeny HCOoutout (Schwendinger and Giribet, 2005; Murienne et al., 2010), 16S rRNA used primers 16Sa and 16Sb (Xiong and Kocher, 1991; Vahtera et al., 2013), and 28S rRNA was amplified by 28SF4 and 28SR5 (Morgan et al., 2002)

All PCR mixtures were activated by an Eppendorf Mastercycler Pro S machine with manual and gradient functions. The COI, 16S and 28S gene amplifications were performed under standard conditions of PCR reactions cycled at 94 °C for 5 min of an initial step, followed by 35 cycles of 94 °C for 30 s in a denaturation step. The selected temperatures of the annealing step were 42.5-44.1°C for COI, 45-48 °C for 16S, and 55-58.1°C for 28S, for 30 s, 72 °C for 15 s in an extension step, and then a final extension step at 72 °C for 10 min. PCR cycler was installed at a holding temperature at 4°C as the final step.

The PCR products were inspected under 1% (w/v) agarose gel electrophoresis in 0.5x TBE buffer. The fluorescence of PCR bands was enhanced with SYBR Safe illuminant and observed under a UV light source. The gene target products were purified using a QIAquick purification kit (QIAGEN Inc.). The purified PCR products were directly cycle-sequenced using the original amplification primers with an Applied Biosystems automatic sequencer (ABI 3730XL) at Macrogen and Bioneer Inc. (Korea). Sequences were aligned with libraries in GenBank using the BLASTn algorithm to verify the correct group of organisms from product sequences.

Phylogenetic reconstruction

DNA sequences were assembled in Sequence Navigator (Parker, 1997). Double strand sequence comparisons were made by a shadow pair-wise alignment function analysis to detect missing sites and gaps in nucleotide sequences, and correlated with chromatograms for each sequence sample. Seven *Scolopendra* species were used in this analysis: *S. dawydoffi* Kronmüller, 2012 (Kronmüller, 2012), *S. dehaani* Brandt, 1840 (Brandt, 1840), *S. japonica* Koch, 1878 (Koch, 1878), *S. morsitans* Linnaeus, 1758 (Linnaeus, 1758), *S. pinguis* Pocock, 1891 (Pocock, 1891c), *S. subspinipes* Leach, 1816 (Leach, 1816) and *Scolopendra* sp. Moreover, sequences of two scolopendromorph taxa from GenBank, *Cormocephalus monteithi* Koch, 1983 (Koch, 1983b) and *Cryptops doriae* Pocock, 1891 (Pocock, 1891c), were chosen as outgroups to root the trees. DNA alignment was carried in MEGA 6 (Tamura et al., 2013b) using MUSCLE (Edgar, 2004) with the default parameter set. File format preparation, i.e. FASTA, PHYLIP and NEXUS, for further phylogenetic analysis was implemented in MEGA 6 and Mesquite 3.03v (Maddison and Maddison, 2011). The heterogeneity of nucleotide substitution model fit was calculated by JModelTest v.1.7 (Posada, 2008) based on the PhyML likelihood algorithm of heuristic search (Guindon et al., 2010) and MEGA 6. Eleven nucleotide substitution schemes (Lanfear et al., 2012) and 88 candidate models were set at the beginning of an analysis for each gene fragment in JModelTest. Gaps and missing data were discarded. For the best fit DNA substitution model, the three fragments were analyzed independently. Kakusan 4 (Tanabe, 2007), implemented in MOLPHY, was used to assemble the final concatenated file.

In this study, Maximum likelihood (ML) and Bayesian inference (BI) were applied to construct phylogenetic trees from the combination of the partitioned DNA dataset. For ML analysis, the concatenated files were analyzed with Treefinder (Jobb et al., 2004) and RAxML 8.0.0v (Stamatakis, 2006). A single search was conducted to find the starting tree in Treefinder. Fast likelihood-based analyses were performed with 1,000 bootstrap pseudo-replicates. Bayesian inference was conducted in MrBayes, ver. 3.2.5. (Huelsenbeck and Ronquist, 2001a; Ronquist et al., 2012) using four metropolis-coupled, Markov chain Monte Carlo runs (Larget and Simon, 1999). The program was ordered for random sampling of starting trees before more exhaustive analyses. The number of pseudo-replicates was set at 10,000,000 generations, with simultaneous tree sampling at every 500 random replicates. Sixteen nucleotide substitution schemes and the invisible gamma parameter were applied. Seventy percent of harvested trees were removed as burn-in. The analyses were terminated after the standard deviation of proportional frequency reached below 0.01. The consensus tree implemented from 50% majority rules was obtained at the final stage, and draft tree topology files were reconstructed by FigTree. Node support values have been depicted on the trees in those instances where bootstrap values exceed 70% (ML) and posterior probabilities exceed 0.95 (BI) (Huelsenbeck and Hillis, 1993; Larget and Simon, 1999). A Kimura 2-Parameter model (Kimura, 1980) was used to calculate corrected distance of all gene fragments in MEGA 6. Genetic distance was compared for both interspecific and intraspecific variation within and between populations. Finally, species justification and validation of the selected *Scolopendra* species based on genetic affinities are discussed in relation to morphological identification in previous literature.

Geometric-morphometric analysis

One-hundred seventeen *Scolopendra* specimens were used in this analysis (see S1 Table). Because of morphological changes through the course of ontogeny, a minimum size for sampled individuals was set at 40 mm, following a suggested standard for scolopendrid taxonomy (Lewis, 1978). Three morphological features were examined in this analysis: the cephalic plate, the forcipular coxosternite, and the tergite of the ultimate leg-bearing segment (tergite 21). All samples were photographed in the same orientations and magnifications under a light stereo-microscope. Each feature was analyzed independently by using landmark geometric methods (Bookstein, 1996, 1997). The landmark points were digitized from a set of stable, conserved parts of each feature, the position detail of each landmark point being as follows:

(1) Cephalic plate

Landmark 1: anterior end of median sulcus of cephalic plate
Landmark 2: interior basal part of first antennal article (right side)
Landmark 3: anterior end of anterior ocellus (right side)
Landmark 4: posterior end of posterior ocellus (right side)

Landmark 5: intersection point between pleurite of forcipular segment and trochanteroprefemur (right side)

Landmark 6: intersection point between pleurite of forcipular segment and Tergite 1 (right side)

Landmark 7: intersection point between pleurite of forcipular segment and Tergite 1 (left side)

Landmark 8: intersection point between pleurite of forcipular segment and trochanteroprefemur (left side)

Landmark 9: posterior end of posterior ocellus (left side)

Landmark 10: anterior end of anterior ocellus (left side)

Landmark 11: interior basal part of first antennal article (left side)

(2) Forcipular coxosternite

Landmark 1: median diastema

Landmark 2: inner end of oblique suture (left tooth-plate)

Landmark 3: outer end of oblique suture (left tooth-plate)

Landmark 4: left upper corner of forcipular coxosternite

Landmark 5: coxosternal condyle (left side)

Landmark 6: inner end of coxosternite collar (left side)

Landmark 7: left junction between presternite and sternite of first leg-bearing segment

Landmark 8: right junction between presternite and sternite of first leg-bearing segment

Landmark 9: inner end of coxosternite collar (right side)

Landmark 10: coxosternal condyle (right side)

Landmark 11: right upper corner of coxosternite

Landmark 12: outer end of oblique suture (right tooth-plate)

Landmark 13: inner end of oblique suture (right tooth-plate)

(3) Tergite of ultimate leg-bearing segment

Landmark 1: anterior interior margin (right side)

Landmark 2: anterior exterior margin (right side)

Landmark 3: posterior exterior margin (right side)

Landmark 4: posterior exterior margin (right side)

Landmark 5: distal point of postero-median margin
Landmark 6: posterior exterior margin (left side)
Landmark 7: posterior exterior margin (left side)
Landmark 8: lower exterior margin (left side)
Landmark 9: upper interior margin (left side)

All landmark points were marked manually by WS with tpSDig2 (Rohlf, 2001). The standard image of each constant character of all samples was randomly chosen with tpsUtil (Rohlf, 2002) in order to avoid personal bias. MorphoJ 1.06b (Klingenberg, 2011) was used for testing shape variation. Procrustes superimposition was calculated to minimize effects such as sample size, orientation and depth (Goodall, 1991; Rohlf, 1999). The covariance metric was generated as two-dimensional axes for each feature. Multivariate regression was performed using the Procrustes superimposed data to define allometry and statistically test for correlation between centroid origin and shape variation (Mosimann, 1979). A category of sampled specimens was classified based on morphological identification. Canonical variates analysis (CVA) implemented the relative determination of two or more classified groups under Mahalanobis and Procrustes distance values (Mahalanobis, 1936; Dryden and Mardia, 1998). A permutation test for pairwise distance was set at 10,000 permutation rounds for calculation of Mahalanobis distance in both between- and among-classified groups. From the CVA results, the shape variation detected from landmark positions was linked serially as Wire-frame outlines to visualize shape reformation between negative and positive canonical variates groups on a three-dimensional axis. Confidence ellipses were calculated to indicate the centroid origin of each defined sample group in a three-dimensional CVA graph. Comparative CVA plots were generated separately in each dimension for CV1-CV2 and CV2-CV3. All graphs were exported in Encapsulated Postscript Vector Graphics format (EPS) for processing in Adobe Illustrator.

Results

Morphological identification

This study is based on 176 centipede specimens collected from 134 localities in mainland Southeast Asia and one voucher specimen from the Japanese archipelago. All specimens were observed by light microscopy, with taxonomy based on traditional external morphological characters of scolopendrids. These are as follow: the number of antennal articles, as well as the number of those that are sparsely hirsute ("glabrous"); number of teeth on the forcipular coxosternal tooth-plates; the first tergite to possess complete paramedian sutures; the first tergite with complete margination; the extent of paramedian sutures on the sternites (complete or confined anteriorly to a variable extent); the number of spines on the coxopleuron (specifically, the number of apical spines and the presence/numbers of subapical and dorsal spines); the prefemoral spine arrangement on the ultimate legs; the presence or absence of tarsal spurs on legs 19 and 20; and, presence or absence of a gonopod ("genital appendage") on the first genital segment of the male. The taxonomic results show six nominal species that can be identified as named species and one putative new species in the sampling area as follow: *Scolopendra dawydoffi*, *S. dehaani*, *S. japonica*, *S. morsitans*, *S. subspinipes* and *Scolopendra* sp. Diagnostic character combinations of all assigned species are summarized in Table 3.1.

Sequence annotation

Sixty nucleotide sequences from partial gene targets for cytochrome *c* oxidase subunit 1, 16S rDNA and 28S rDNA were obtained (Table 3.2). All raw nucleotide sequences were blasted with other available scolopendromorph sequences in GenBank as a check for contamination. The compatibility values of all sequence reached up to 80% of available scolopendromorph sequences, suggesting that outgroup contamination is not affecting the genomic DNA. The final aligned sequences obtained from sequence editing and the alignment program, consisted of 814 bp for COI, 446 bp for 16S, and 638 bp for 28S. Sequence annotation (Table 3.3) of each gene is as follows: COI sequences consist of 334 parsimony-informative sites, and 403 and 411 variable and conservative sites, respectively; 16S sequences comprise 197 parsimony-informative sites, and 271 and 175 variable and conservative sites, respectively; 28S sequences include 110 parsimony-informative sites, and 206 and 432 variable and conservative sites, respectively. Corrected genetic distances were calculated under the Kimura-2-parameter model for DNA sequence alignment. Interspecific variation in each partial sampling of genes is 15-24.2% for COI, 10.6-22.4% for 16S, and 0.8-10.8% for 28S. A summary of inter-intra specific variation and best fit scores for the nucleotide substitution model is given in Tables 3.4 and 3.5.

Phylogenetic analysis

The best fit models of heterogeneous nucleotide substitution under the two optimality criteria (Maximum likelihood and Bayesian inference) for each partial gene analysis are JC, GTR+G+I and GTR+G (Table 3). The output trees for the concatenated analyses have congruent topologies in both analyses (Fig. 3.1; see Fig. 3.8 for node support). They depict the expected monophyly of the subfamily Scolopendrinae Kraepelin, 1903 (Kraepelin, 1903), with all species of *Scolopendra* and the outgroup OTU of *Cormocephalus monteithi* nesting together with strong posterior probability support in BI (Fig. 3.1A). Inside the Scolopendrinae, however, the monophyly of the genus *Scolopendra* is contradicted by the interpolation of *C. monteithi* within it (Fig. 3.1D). In the case of examined *Scolopendr*a taxa, seven genetically delimited taxa can be discriminated that are congruent with their morphological identification as species, and phylogeographic structure is resolved within each of these species. The tree separates members of *Scolopendra* into three main clades. One clade includes *S. dehaani*, a putatively new species that we refer to as *Scolopendra* sp., and *S. subspinipes* (labeled as clade B in Fig. 3.1), and another unites *S. morsitans* and *S. pinguis* (clade C in Fig. 3.1). The third clade (clade E in Fig. 3.1) groups *S. japonica* and *S. dawydoffi*. From the tree topology, short internal branch lengths are characteristic of populations within *S. dehaani* (Fig. 3.1, clade F therein) while the remaining species showed greater amounts of genetic diversity between their populations.

In *S. dehaani* (Fig. 3.2), the phylogenetic tree indicates three major groups that have clear relationships to geographical zones as follow: the Chao Phraya Basin population (CPB; Clade A), the Mekong River Basin population (MRB; Clade C), and the Lower Tenasserim Range population (LTR; Clade B). The CPB clade unites populations from the northern, western (upper part of the Tenasserim Range) and central parts of Thailand. The northern population is separated from the others with strong node support in ML and BI analysis (73/1) while the relationship between MRB and LTR remains unresolved, with weak support values in ML and BI (64/0.86). The MRB clade consists of all populations from northeastern and eastern parts of Thailand, Laos and some western Cambodian populations. Inside the MRB clade, node support values indicate that the western Cambodian population and the lower northeastern Thailand population are closely related (98/1; ML and BI) while relationships in the other populations are undefined. The LTR clade includes southern populations starting from the Isthmus of Kra through the coastal part of Thailand to the northern part of the Malay Peninsula. In this clade, the tree topology indicates two main populations, one northern and other southern. The split between these two clades received strong support both in ML and BI (98/1). In addition, genetic relationships are congruent with colouration among regional populations of *S. dehaani* in the Southeast Asian mainland. During field surveys, five colouration patterns have been recorded (Fig. 3.2A-E). Colour morphs 2-4 are found throughout most regions whereas morphs 1 and 5 (Fig. 3.2A and 3.2E) are specific to only some populations. Colour morph 1 (Fig. 3.2A) has been reported only from some specimens of the CPB population. This colour morph has a dark brown body and dark violet legs, with most specimens coming from the north western part of Thailand, close to the Thailand-Myanmar border. Also geographically restricted is colour morph 5 (Fig. 3.2E), which has been found only in the LTR population. In this, the body is bright reddish with a dark band on the posterior part of the tergites while all legs are usually reddish or yellowish.

Scolopendra sp. and *S. subspinipes* are the closest relatives of *S. dehaani* (Fig. 3.1; clade B), although the precise sister group relationships are equivocal because the putative clade that unites *Scolopendra* sp. and *S. dehaani* to the exclusion of *S. subspinipes* has low support values in both ML and BI (39/0.63). The union of the two sampled populations of *Scolopendra* sp. from northern and southern Laos supports the validity of this species, as is indicated by diagnostic morphological characters, notably the incomplete paramedian sutures on the tergites. In case of *S.*

subspinipes, the tree topology indicated the separation of *S. subspinipes* from *S. dehaani* as well as *Scolopendra* sp. according to both support values (56/0.97) and corrected distances (12.9-13.7% and 17-19.9% in COI and 16S, respectively).

S. morsitans was nested in the same clade with *S. pinguis* and an outgroup (*C. monteithi*) (Fig. 3.1; clade C). All *S. morsitans* populations were nested together as monophyletic. However, the genetic affinity divided *S. morsitans* into two minor populations (Fig. 3.3), one of which is found in the northern part of Thailand (clade A in Fig. 3.3) whereas the other is located in northeastern Thailand and some populations from Cambodia. This separation was supported with strong nodal support in both ML and BI (100/1) whether between or within the two populations. Furthermore, observation of colour patterns indicated two colour morphs for *S. morsitans* in this region (Fig. 3.3). The most common pattern, called colour morph 1, covers most populations in this region. The cephalic plate, tergite 21 and ultimate legs of this morph are red-yellowish, while colour morph 2 has the cephalic plate, tergite 21 and ultimate leg blackish. This latter morph is only found in the north-western population.

The tree shows marked genetic diversity between populations of *S. pinguis*, as indicated both by branch lengths and the corrected within-species distances (18% and 11% in COI and 16S, respectively). Monophyly of the species is supported (Fig. 3.4), as is consistent with its diagnostic morphological characters, and groupings within the species received strong support in both ML and BI analysis. The genetic structure of *S. pinguis* showed that Thai populations exhibited a genetic connection with all examined populations from Laos. Moreover, the tree topology depicts a relationship between western and northwestern Thailand, which showed closer affinities with each other than with other populations. However, one population (Fig. 3.4; P1) from the western part of Thailand did not group with the adjacent population (Fig. 3.4; P4) and the former is resolved basally relative to all other *S. pinguis* populations. This species also exhibited colour variation among its populations, as for the previously discussed species. Four colouration patterns (Fig. 3.4) have been recorded both in the Thai and Laotian faunas. The major colouration pattern is seen on the cephalic plate, which differs between yellowish and blackish colour morphs. Minor variability has also been detected on the legs, these exhibiting two colour forms, either being monochrome or dichromatic. The tree topology indicated that all populations with the yellowish cephalic plate were grouped together but one of the two blackish populations is nested within the yellowish population. The blackish populations are divided into two lineages, one of which is sister lineage to a clade that unites all other sampled individuals. With regards to their geographical distribution, the blackish cephalic plates are specific to the north western area of Thailand whereas the other forms are distributed both in Thailand and Laos.

Scolopendra dawydoffi and *S. japonica* unite as a clade in which both species are reciprocally monophyletic (Fig. 3.5). The taxonomic validity of these two species has been corroborated by strong node support (96/0.99). The corrected distances indicated low genetic diversity among *S. dawydoffi* populations as depicted by short branch lengths in the phylogenetic tree (Fig. 3.5; clade A). In case of *S. japonica* (Fig. 3.5; clade B), individuals from the sampled populations unite as well-supported clades, the corrected distance within the species being 12.4% and 5.3% in COI and 16S, respectively. A Japanese specimen was resolved as sister taxon to a group composed of the *S. japonica* populations from Laos. With regards to colouration, there is no evidence in our collections for *S. dawydoffi* exhibiting colour variation. In contrast, *S. japonica* has two morphs that can be distinguished by colour of the legs: in colour morph 1, the legs are reddish, whereas colour morph 2 has green-yellowish legs. The Laos fauna includes both colour morphs whereas the specimen from Japan shows similarity to the Laotian population classified as colour morph 1. However, the phylogenetic tree indicated that the colouration does not precisely correlate with genetic affinities in this species.

Geometric morphometrics

Six species of *Scolopendra* in the Southeast Asian mainland (excluding *S. subspinipes*) have been identified based on morphological taxonomy. Specimen numbers used in this analysis are as follow: five specimens of *S. dawydoffi*, 84 specimens of *S. dehaani*, eight specimens of *S. japonica*, 10 specimens of *S. morsitans*, 12 specimens of *S. pinguis*, and two specimens of *Scolopendra* sp. The Procrustes ANOVA statistical test found no measurement error in all analyses (*p*<0.0001; S2 Table). CVA plots were performed based on group classified datasets with 10,000 replicates of permutation testing for pairwise distance. Eigenvalue and variable percentages of selected characters are summarized in S3 Table. The three dimensions of CVA plots have been used for species discrimination from shape variation (Fig. 3.6). The discriminant results of *Scolopendra* species from CVA analysis with statistical testing in three selected features are described as follows.

Cephalic plate (Fig. 3.6A): The CV1 axis captured 46.468 % of shape variation while the CV2 and 3 axes exhibited 26.269% and 15.575%, respectively. The CVA plot clearly indicated the differentiation of centroid origin in the CV1-CV2 axis. From this CVA plot, all individuals of the same species were grouped together. The clusters of individuals of both *S. morsitans* and *S. japonica* separated from other species, whereas *S. dawydoffi*, *S. dehaani* and *Scolopendra* sp. were grouped closely together. In contrast, a poorer discriminant resolution was found in the CV2-CV3 axes, with all species apart from *Scolopendra* sp. overlapping with the range of variation in *S. dehaani*. From the statistical result, the *p*-values from permutation tests of Mahalanobis distances among groups supported the discrimination of four *Scolopendra* species, these being *S. dehaani*, *S. japonica*, *S. morsitans* and *S. pinguis* (p<0.0001). However, no significant difference among groups was indicated by *p*-values of Procrustes distances.

Forcipular coxosternite (Fig. 3.6B): Forcipular coxosternal shape showed appreciable variability in most *Scolopendra* species except in *Scolopendra* sp., although it need be noted that the sample size of the latter species is small. The percentages of variability contributed by the CV1, CV2 and CV3 axes are 54.298%, 30.728% and 7.995%, respectively. The CV1-CV2 pairwise comparison plot showed that individuals of each species show a marked clustering. Variation in the shape range of the forcipular coxosternite in *S. japonica* and *S. dawydoffi* overlapped and extended into the range of *S. dehaani*, whereas *S. morsitans* and *S. pinguis* are well delineated. In the CV2-CV3 plot, all individuals of *S. pinguis* were pooled separately with each other while the remaining species were grouped closely. All individuals of *S. morsitans* and *S. dawydoffi* were interpolated inside the range of variation of *S. dehaani*. From permutation tests of Mahalanobis distances among groups, *p*-values indicated the distinctness of four *Scolopendra* species, i.e., *S. dehaani*, *S. japonica*, *S. morsitans* and *S. pinguis*, with significant support (p<0.0001). The Procrustes distances significantly differed only in three examined species, *S. dehaani*, *S. morsitans* and *S. pinguis*.

Tergite 21 (Fig. 3.6C): The shape variation percentages of the three CV axes are as follow: CV1 explained 64.358%, CV2 28.756%, and CV3 5.558%. The CVA analysis exhibited the discriminant centroid origin of CV1-CV2 comparison plot in all examined species. *Scolopendra dehaani*, *S. pinguis* and *Scolopendra* sp. depicted wholly or mostly unique ranges of variation. The three remaining species exhibited shape variability against each other. However, the CV2-CV3 comparison plot allowed *S. pinguis* and *Scolopendra* sp. to be distinguished from other species. In this comparison, most individuals of *S. dawydoffi*, *S. japonica* and *S. morsitans* were gathered inside the variation of *S. dehaani*. The Mahalanobis and Procrustes distances among groups indicated four distinct species, i.e., *S. dawydoffi*, *S. dehaani*, *S. japonica*, *S. morsitans* and *S. pinguis*, with statistical support (p<0.0001).

Based on the CVA analyses for each assigned feature, the Eigenvalue and percentage of variance were generated in S3 Table. The variation of the landmarks in the three selected morphological features has been recorded and described as follows:

Cephalic plate: In the CV1 axis, variable reformation was found on Landmarks 1, 2, 3, 4, 5, 6, 7 and 8 (see column A in Fig. 7). The position of Landmark 1 shifts posteriorly as CV scores trend positively. This position describes a deeper median sulcus on the anterior part of the cephalic plate. Landmarks 2, 3 and 4 (as well as Landmarks 9, 10 and 11) are displaced medially as CV scores trend from negative to positive. This variation relates to the shape of the cephalic plate, the size of basal antennal article, and relative length of the basal article and the ocelli. The movement of Landmarks 5 and 6 (also 7 and 8) record an increase in width of the posterolateral part of the cephalic plate from positive to negative. In the CV2 axis (column B in Fig. 3.7), variable sites were found to relate to Landmarks 1, 4, 5, 6, 7, 8, 9 and 10. The most extreme change was recognized both in CV negative and positive groups, this being located between Landmarks 5 and 6 (and 7 and 8), affecting length of the cephalic plate. In the CV3 axis (column C in Fig. 3.7), only six landmarks showed slight variability, these being Landmarks 1, 2, 3, 6, 7 and 8 in both CV positive and negative score datasets. This variation again impacted on the length of the cephalic plate.

Forcipular coxosternite: In the CV1 axis, shape variation was detected in all landmark points (column A). Movement in Landmarks 3-12 describes the shape of the coxosternite in both CV negative and positive groups. The forcipular coxosternite in the CV positive group is relatively shorter than in the negative. Landmarks 3 and 4 (also 11 and 12) shift laterally from negative to positive, describing a broadening of the anterolateral corner of the coxosternite. Landmarks 6, 7, 8 and 9 moves anteriorly from negative to positive. In the case of the CV2 axis (column B in Fig. 3.7), the outline between Landmarks 12-13 and 2-3 showed variation. Specifically, landmarks describing the course of the anterior parts of the forcipular coxosternite shift from more curved to straighter towards the positive group. Moreover, the posterior part of the forcipular coxosternite also showed high variability at Landmarks 7 and 8, which shift anteriorly from negative to positive groups. Simultaneously, the coxosternal condyles are situated more posteriorly from negative to positive groups. From this variability, the outline of the forcipular coxosternite in the CV positive group is more trapezoidal and straighter / more transverse across both its anterior and posterior parts whereas the CV negative group exhibited a more curved diamond shape on its anterior and posterior parts. From the CV3 axis (column C in Fig. 3.7), the shape variation of the forcipular coxosternite in both the CV negative and positive groups showed only slight change, this being captured by Landmarks 2, 3, 4, 5, 6, 7, 8 and 10.

Tergite 21: In the CV1 axis, shape variation exhibited substantial changes in both CV negative and positive groups (Column A in Fig. 3.7). Tergite 21 depicts relatively elongate versus broad rectangular shapes in the CV negative and positive groups, respectively. According to Landmark 5 in particular, the posterior margin of tergite 21 shifts posteriorly from positive to negative, and combined with movements of other landmarks corresponds to the change in length: width ratio of the tergite. Landmarks 1, 2, 8 and 9 shift laterally from negative to positive groups, whereas Landmarks 2, 3, 7 and 8 shift so that the tergite transforms from longer than wide to the reverse. In CV 2 axis (column B in Fig. 3.7), a stable landmark was identified in Landmark 5, which showed consistency in both CV extremes. However, the visualized shape outline of tergite 21 also reflected the distinctness between CV populations, similar to the case for the CV1 axis. The CV positive group shows a displacement of Landmarks 3 and 4 (also 6 and 7) so that the posterior margin of the tergite changes from a broad V-shape to having the short extent delimiting the margination being transverse, and then flexing to its V-shaped extent. In the CV3 axis (column C in Fig. 3.7), the shape of tergite 21 showed less variation than did the CV1 and CV2 axes. Landmarks 1, 3, 5, 7, 8 and 9 all exhibited variability on this axis. In the CV negative group, tergite 21 has the lateral margin (between Landmarks 2 and 3 / 7 and 8) more strongly diverging posteriorly than in the CV positive group

From the results of discriminant function analysis among classification categories (Table 3.6), five assigned categories of morphometric samples were confirmed by the percentage of correct classification in two features, the forcipular coxosternite and tergite 21 (>80% in all categories). However, the percentage of correct classification based on variation in the cephalic plate was lower (<50%) in *S. dawydoffi* and *Scolopendra* sp. The cross-validation of discriminant function analysis showed a low percentage of correct classification in all sampled characters and taxa except for *S. dehaani*, which received 89% correct classification when defined by the forcipular coxosternite and tergite 21.

Discussion

The diversity of *Scolopendra* in mainland Southeast Asia

The field survey in this study identified the occurrence of *S. japonica* in mainland SE Asia, its character data conforming to a recent taxonomic review (Kronmüller, 2012). The distribution range of all species has been refined and it is now possible to make inferences on several species usually reported as regional widespread species (Lewis, 2010b). In this study, seven *Scolopendra* species have been found in both natural and anthropogenic areas. Previous records of *Scolopendra* in SE Asia (Haase, 1887a; Kraepelin, 1903; Schileyko, 2007) indicated that there are three additional species that can potentially be found in this area: *S. gracillima* Attems, 1898 (Attems, 1898), *S. calcarata* Porat, 1876 (Porat, 1876), and *S. hardwickei* Newport, 1844 (Newport, 1844b). However, very few specimens were reported in the relevant studies and the species listed above were treated as likely introductions (Schileyko, 2007). In mainland SE Asia, *S. dehaani* has been found to be the dominant, widespread species throughout the sampling territory, whereas *S. subspinipes* (*S. subspinipes subspinipes* of most previous studies) is rarely found, as conforms to previous work (Haase, 1887a; Flower, 1901; Decker, 2013). In contrast to those species, some species seem to be endemic and have scattered distributions and sparse populations in nature, i.e., *S. dawydoffi*, *S. japonica*, *Scolopendra* sp. and *S. pinguis*. From phylogenetic analysis, the regional populations of some examined species such as *S. dehaani*, *S. morsitans* and *S. pinguis* suggested the genetic affinities among geographically neighboring members, infraspecific structure that might be affected by the geographical richness of the region. Several areas have been promoted as corridors for dispersal or land bridges (Outlaw and Voelker, 2008; Metcalfe, 2013; de Bruyn et al., 2014), and the mechanisms that sculpt the gene pool among regional populations may derive from these boundaries, as has been proposed for other invertebrates and vertebrates (Bird et al., 2005; Clouse and Giribet, 2010; Yodthong et al., 2015).

Morphological discrimination among nominal species

In the past, the status of several scolopendrid genera such as *Cormocephalus* Newport, 1844 (Newport, 1844a), *Trachycormocephalus* Kraepelin, 1903, and *Arthrorhabdus* Pocock, 1891 (Pocock, 1891b) has been debated relative to their distinction from *Scolopendra*. Because of its morphological variability and distribution, several species have now been revised (Kronmüller, 2012) while some of them were relegated to synonymy with particular members of *Scolopendra* (Lewis et al., 2006). From the available collections, sourced from different geographical localities throughout mainland SE Asia, some examined species such as *S. japonica* and *S. dawydoffi* exhibited morphological variation among their populations. Diagnostic characters such as the number of teeth on the coxosternal tooth-plates, tergite margination, and the number of spines on the ultimate leg prefemur showed high variability, as has previously been recognized in various species of *Scolopendra* (Kronmüller, 2012). Overlapping proportions and a shortage of diagnostic characters are more pervasive challenges in Scolopendromorpha, affecting other genera as well, such as *Otostigmus* Porat, 1876 (Porat, 1876), *Digitipes* Attems, 1930 (Attems, 1930c), *Rhysida* Wood, 1862 (Wood, 1862) and *Cryptops* Leach, 1816 (Leach, 1816).

In our examined species, *S. dehaani* exhibited morphological consistency of its diagnostic characters in all populations. The morphology of *S. dawydoffi* and *S. japonica* is most similar, as demonstrated by the flattened ultimate leg in both species, but they can be distinguished by the extent of the sternal paramedian sutures.

A taxonomic issue for *S. dawydoffi* is its morphological similarity with another tropical-temperate species, *S. multidens* Newport, 1844. Only one character, the male genital segment without appendages (gonopods), has been proposed to be diagnostic for *S. multidens* (Chao, 2008), but we have found that this character also occurs in *S. dawydoffi* from Thailand, and it is furthermore shared by another insular species, *S. hainanum* Kronmüller, 2012, from Hainan Island, China. We presently decline to synonymise *S. dawydoffi* with *S. multidens* because preliminary phylogenetic results suggest they are genetically distinct (Chao et al., 2011). Species nomenclature uses geographical information, *S. dawydoffi* being distributed in the Indochina subregion whereas *S. multidens* is distributed in Taiwan and other part of the East Asian temperate zone. The problem of uncertain diagnostic characters was also recognized between *S. pinguis* and *S. gracillima*, as discussed in recent taxonomic reviews (Lewis, 2010b). Solving such taxonomic problems in *Scolopendra* will likely require comprehensive description and DNA sequence data for samples from across the distributional ranges of the relevant nominal species.

Molecular species delimitation

The phylogenetic tree from partial gene analysis showed informative resolution for the purpose of species delimitation. The clade corresponding to the subfamily Scolopendrinae showed reasonable support in BI analysis for its monophyly, but *Scolopendra* itself cannot be defended as monophyletic. Even for the present sampling of SE Asian species, the exemplar species of *Cormocephalus* nested within *Scolopendra* rather than resolving as sister group to a monophyletic *Scolopendra*. This is not an especially surprising finding because recent broad-scale molecular and morphology-based phylogenetic analyses of Scolopendromorpha found *Scolopendra* to be paraphyletic or polyphyletic with respect to other genera of Scolopendrini (Vahtera et al., 2013). The genus in its traditional (and current) guise is diagnosed by a combination of characters (e.g., the cephalic plate overlapping T1, tooth-plates shorter than those of *Arthrorhabdus*, presence of tarsal spurs, accessory spurs on the pretarsus), all of which are likely symplesiomorphies for Scolopendrini, without an obvious autapomorphy that would signal monophyly.

In contrast to the unsettled status of the genus, part of a more pervasive problem with the diagnoses and delimitation of genera in Scolopendridae, our analyses provide clearer insights into the phylogenetic status of species. In this study, the former subspecies of *S. subspinipes* sensu Lewis 2010 (here determined as *S. dehaani*, *S. subspinipes*, *S. japonica* and *S. dawydoffi*) have been taxonomically validated, as was suggested by the most recent morphological classification (Kronmüller, 2012). However, comprehensive description of their morphology is needed to improve species discrimination.

Previously, evaluation of barcode gaps in members of *Scolopendra* has been undertaken only in three species: *S. cingulata*, *S. cretica* Lucas, 1853 (Lucas, 1853) and *S. canidens* Newport, 1844 (Newport, 1844b) . These showed an average interspecific variation between 13.4-14.8% in the universal COI barcode region (Oeyen et al., 2014). Species of *Scolopendra* in the present analysis exhibited greater genetic distance than in previous studies, the relative morphospecies comparison depicting genetic distances from 15% to 19.9% in COI. The high genetic distance both between and within species might be useful for species delimitation of *Scolopendra*, being similar to previous evidence from phylogenetic studies of scolopendromomorphs, including *Digitipes* (Indian populations; 14.2-19.4% for COI (Joshi and Karanth, 2012), Burmese-Indian populations; 14.5-21.3% (Siriwut et al., 2015b)) and *Cryptops* (Pacific island populations; 19.8-23.7% (Murienne et al., 2011)). In the case of intraspecific variation, genetic distances in this analysis were 8.6% for COI in two cosmopolitan species (*S. dehaani* and *S. morsitans*) whereas the more narrow-ranged species, *S. pinguis*, *S. japonica* and *Scolopendra* sp., show greater genetic diversity (18.3%, 12.2% and 12.4% in COI, respectively).

Genetic distance in *S. pinguis* in particular is indicated by branch lengths in the phylogenetic tree and high intraspecific variation in COI, 16S and 28S genes (Table 5). This pattern is often ascribed in invertebrates to the process of cryptic speciation (Puillandre et al., 2010; Chen and Hare, 2011; Joshi and Karanth, 2012; Nantarat et al., 2014a; Nantarat et al., 2014b). For this reason, the sample of *S. pinguis* might contain more than one species or may at least be in the early stage of cryptic speciation. *Scolopendra morsitans*, a cosmopolitan pantropical species, showed two lineages from their genetic structure. An eastern population that shows low genetic diversity among its populations seems to indicate high genetic transfer in this species in this area because this situation also occurred in another widespread species, *S. dehaani*, in which all populations exhibited low genetic diversity. Dispersal mechanisms among these widespread species are of interest and may be clarified by population genetic and demographical historical studies as have been undertaken for some other *Scolopendra* species (Simaiakis et al., 2012; Oeyen et al., 2014)

Taxonomic validity of some *Scolopendra* members in SE Asia

Currently, the species diversity of *Scolopendra* in Southeast Asia comprises 13 species that are distributed in the mainland and insular faunas (Bonato et al., 2016). Among them, morphological examination is adequate for species delimitation in some species, such as *S. morsitans* and *S. dehaani*. However, there are other species that show high morphological variability, indeed more than previously estimated, such as *S. dawydoffi*, *S. japonica* and *S. pinguis*. As noted above, their variability might overlap with other related species in this region such as *S. multidens* (in the case of *S. dawydoffi*) and *S. gracillima* (in the case of *S. pinguis*) (Attems, 1930a). *Scolopendra dehaani* was originally established as a full species [56] but because of its morphological similarity with *S. subspinipes*, subsequent taxonomists treated it as a subspecies of *S. subspinipes*, until it was only recently revalidated as a separate species (Kronmüller, 2012). Another two former subspecies of *S. subspinipes*, *S. dawydoffi* and *S. japonica* (previously known as *S. subspinipes cingulatoides* Attems, 1938, and *S. subspinipes japonica* Koch, 1878, respectively), have likewise most recently been elevated to the ranks of separate species (Kronmüller, 2012). Our molecular examination confirmed the validation of these two species, not the least because they are resolved as more closely related to each other than either is to *S. subspinipes* (Fig. 1 and 3), and was supported by new additional characters for species discrimination. For these reasons, we consider that three former subspecies of *S. subspinipes* sensu Lewis, 2010 are valid species, as likewise determined based on external morphology alone (Kronmüller, 2012).

Phylogeography of *Scolopendra* in mainland SE Asia

Phylogeography has been introduced for centipede systematic studies in the past decade (Edgecombe and Giribet, 2009; Puillandre et al., 2010; Simaiakis et al., 2012; Giribet and Edgecombe, 2013). Geological events in the past that potentially bear on the distribution range of these animals include the drift and collision of former fragments of Gondwana during the Jurassic (Joshi and Karanth, 2011), micro-refugia in the last glacial period during the Pleistocene (Simaiakis et al., 2012; Oeyen et al., 2014), and the debated hypothesis of biotic shuttle for some insular centipedes (Murienne et al., 2011). Phylogenetic results in this study depict genetic relationships of some *Scolopendra* populations that are congruent with geographical barriers in mainland Southeast Asia. These findings may relate to the two sub-regional faunas of the Indo-Burmese biodiversity hotspot, Indochina and Malesia (Woodruff and Turner, 2009a; Woodruff, 2010; Koh et al., 2013; de Bruyn et al., 2014). The genetic structure of *S. dehaani* populations suggested a separation into three lineages. The CPB population occupies the northern, central and some western elements of Thailand while the MRB population contained the entire eastern element of the Indochina sub-region, including the northeast and east of Thailand, Laos and Cambodia. The separation between these two major populations is located on the western margin of Korat Plateau along the Phetchabun, Dong Paya Yen and Sankambeng mountain ranges. Uplift of the Korat Plateau has been estimated to date to the middle-late Triassic (Lovatt Smith et al., 1996; Racey, 2009). This plateau is delimited by the mountain block between northeastern Thailand and Cambodia, which is likely to have initiated speciation and divergences between these two faunas, as exemplified by amphibians (Nishikawa et al., 2012) and reptiles (Lukoschek et al., 2011). However, our analysis groups together the entire population of *S. dehaani* from northern Laos to the eastern coast of Thailand, demonstrating less sensitivity to vicariance than in some other animal groups.

In the case of the CPB population, the northwest and central Thai samples were united as a core group. The one sample from the upper northern region exhibited genetic difference from the rest, being resolved as the basal clade of the CPB population. The genetic distance may reflect the genetic transfer among neighbouring populations along a geographical gradient. The parallel mountain range along the western and northern parts of Thailand may not limit the dispersal of this population only to the northwestern part of Thailand. Collision of the Indian subcontinent with the Laurasian plate during the Eocene (55 Mya) (Ali and Aitchison, 2008; Metcalfe, 2013; Monod and Prendini, 2015) is likely to have contributed to dispersal of *S. dehaani*, which is known from India (Jangi and Dass, 1984). Other elements of the SE Asian and Indian biotas, both extinct (Rust et al., 2010) and extant (Joshi and Karanth, 2012), show similar patterns of diversification. Moreover, a hypothesis that refers to some Indian centipede taxa dispersing into SE Asia is consistent with molecular dating and genetic composition among populations (Siriwut et al., 2015b).

Similar to the previous population, the LTR population is divided into two main groups. The first covered the population along the Isthmus of Kra, which is assumed to be a transitional zone for animals in this region (Woodruff, 2003; de Bruyn et al., 2004; Woodruff and Turner, 2009a). The second lineage is the lower Tenasserim Range population, which extends from the central part of southern Thailand to the Malay Peninsula. These two minor populations were separated by the mountain valley between the Phuket Range in the west coast and the Titiwangsa Range in the lower east coast of the Thai-Malay Peninsula. Sea level fluctuation in the South China Sea and its role in habitat change/loss has been discussed as a factor impacting on population-level patterns in this region (Voris, 2000; Lambeck and Chappell, 2001; Horton et al., 2005; Woodruff, 2010; Lambeck et al., 2014; Niedermeyer et al., 2014), and also contributed to exposure of the Sunda Shelf along the coastal areas of Indochina and the Malay Archipelago (Hanebuth et al., 2000; Bird et al., 2005; Hanebuth et al., 2009; Woodruff, 2010; Metcalfe, 2011; Morley, 2012). These geological events seem to be driving mechanisms for the migration of both flora (Cannon et al., 2009) and fauna (Gorog et al., 2004; Quek et al., 2007; Woodruff and Turner, 2009a; Lukoschek et al., 2011; Nishikawa et al., 2012) in this area. Our result showed that one sample from the eastern coast of Thailand exhibited genetic affinity with the entire southern population. This result is congruent with data from taxonomic studies on other animal groups that report relationships between populations from the same two regions, including butterflies (Muadsub and Pinkaew, 2014) as well as centipedes (Schileyko, 2007; Siriwut et al., 2014). These repeated patterns are suggestive of a cause that is linked to the geographical history of Sundaland. However, passive dispersal from anthropogenic activity is also a possibility because of the habitat preference of this species, *S. dehaani* often being collected in disturbed sites with human modification.

Contrary to the widespread *S. dehaani,* the rare species *S. pinguis* exhibited high genetic diversity among its populations. The updated distribution from this study showed a limit to dispersal along the northwestern and northeastern mountain ranges of mainland SE-Asia. Genetic distances indicated that population structure relates to geography in that western, central and eastern populations are differentiated along the northern region. Genetic variability likewise reported in other morphologically conservative groups of vertebrates and invertebrates has often been found to signal cryptic species, as exemplified by amphibians (Stuart et al., 2006), molluscs (Nantarat et al., 2014a), diplopods (Pimvichai et al., 2014), and even in some scolopendrid centipedes (Joshi and Karanth, 2012). Accordingly, some of the distinct populations of *S. pinguis* in the west should be monitored to test the hypothesis that cryptic species may be involved.

In case of *S. japonica*, the phylogenetic result showed two regional populations. This genetic relationship provides evidence for shared animal diversity between the eastern coast of the Palearctic (here sampled by Japan) and Indo-Malay ecozones, as reported in other invertebrates, e.g. dragon flies (Heiser and Schmitt, 2013), scorpions (Lourenço and Pham, 2015), and spiders (Moyle et al., 2011; Thoma et al., 2014). Populations within *S. dawydoffi* depict close relationships to each other (i.e., short branch lengths). However, the population from the east coast of Thailand was resolved as sister group to the remaining conspecific populations. The continuous geography of this area may facilitate genetic transfer among these populations, as is likewise the case for populations of *S. morsitans* from Northeastern and Eastern Thailand and Cambodia. The ecological richness of this area likely contributes to it being a migration route for some organisms throughout the Indochina sub-region (Luo et al., 2014). However, the precise distribution range of *S. dawydoffi* is unknown (records are scattered in Laos and Vietnam) and additional material will be needed to reveal the fine detail of its genetic structure.

Colouration patterns of *Scolopendra*

The colour variation on animal bodies has been promoted as an interesting topic for evolutionary studies of various kinds of organisms, such as nudibranchs (Rudman, 1991), land snails (Schilthuizen, 2013), and butterflies (Zhan et al., 2014), as well as in centipedes (Oeyen et al., 2014). Recently, molecular phylogeny has been used to explain the relationship between two different colour morphs distributed sympatrically with each other (Oeyen et al., 2014). In our survey, colour variation in populations was recorded for all examined species, *Scolopendra* being the only centipede genus in the biota that shows highly diverse patterns of colour morphs (Koch, 1982; Shelley, 2005). Several species exhibited extreme difference as bright or contrasted colour morphs between populations. The number of patterns differs in various species (Flower, 1901), for example *S. laeta* Haase, 1887 from Australia exhibited five colour morphs (Koch, 1982), two colour morphs of *S. cingulata* were found in the Mediterranean (Oeyen et al., 2014), and four colour morphs have been documented in *S. morsitans amazonica* Bücherl, 1946 (Bücherl, 1946) (=*S. morsitans*) from Africa (Lewis, 1972b). Moreover, the significance of colour variation in several species has been debated in the literature with regards to its taxonomic value. In previous studies, authors usually assigned the different colour morphs of centipedes to new species (Humbert and Saussure, 1870; Chamberlin, 1912) or treated them as subspecies or varieties of species (Koch, 1878). Recently, several taxonomic revisions argued against this approach. The number of fresh specimens for examination in several species is limited, and when colours have faded in preserved museum specimens the taxonomic utility of colour is compromised. For these reasons, several nominal species in the past, which had been identified by colouration pattern, have fallen into synonymy with other widespread species (Shelley, 2005; Kronmüller, 2012). However, our study revealed the relationship of these morphological changes to the genetic structure of some species, in several cases showing that colour morphs correspond to monophyletic groups.

In this study, the species with most diverse colour morphs is *S. dehaani*. This centipede exhibited five colouration patterns. Colour morphs 2, 3 and 4 are standard colour morphs which are usually found in all populations of *S. dehaani* whereas colour morphs 1 and 5 are specific to only two regional populations, CPB and TLH.

Environmental factors such as humidity and other habitat characteristics were assumed to affect this variability. Comparable variability in colouration has been reported and discussed in systematic studies on tropical organisms, e.g., snakes (Wilson et al., 2007), amphibians (Ohler and Grosjean, 2005), and sea cucumbers (Purcell and Tekanene, 2006). These results suggest a correlation between colouration and such factors such as habitat type (Langkilde and Boronow, 2012) and predation (Stuart-Fox et al., 2006).

The distinct colouration patterns in *S. pinguis* populations differ from other species in our analysis. In general, juvenile *Scolopendra* show different colour patterns compared to adult stages, e.g., in *S. morsitans* and *S. dehaani*. In the case of *S. pinguis*, however, colouration patterns are consistent through an observed series of post-embryonic developmental stages, such that paedomorphosis may account for this variation. Ontogenetic data such as these have been suggested as necessary to clarify some taxonomic problems in scolopendromorphs (Edgecombe, 2007; Edgecombe et al., 2015).

The remaining examined species, *S. morsitans* and *S. japonica*, exhibited specific colour morphs in different populations. Interestingly, the black and reddish patterns found in *S. morsitans* were also reported in African and Australian populations (Lewis, 1968; Koch, 1982). The pattern of colouration change is specific to particular morphological characters such as the cephalic plate and tergite of the ultimate leg-bearing segment (Flower, 1901; Koch, 1982), as often noted in taxonomic descriptions of *Scolopendra*. According to the colour variation of these samples, we can separate the colouration pattern among SE Asia *Scolopendra* into either monochrome or dichrome (Table 3.1), following similar descriptions in some previous *Scolopendra* studies (Chao, 2008). The colour polymorphism of *Scolopendra* populations might be useful as a model for molecular ecology and evolutionary studies in SE Asian centipedes.

Taxonomic implications of shape variation

Shape variation tests in morphology have been widely used in fossilized material because of a frequent shortage of morphological characters for species identification (Lohmann, 1983; Sheets et al., 2004; Perez et al., 2006). These techniques have also been applied to systematic study of varied organisms for species discrimination (Davis and Baker, 1974; Vanhooydonck et al., 2009; Nantarat et al., 2014b). In this study, the three surveyed features show results that appear to be useful as taxonomic signal for species-level taxonomy, as exemplified by plots from canonical variates analysis (Fig. 3.6) and CV discriminant functions (Table 3.6). Each of the examined characters had been documented in some scolopendrid literature over the past century (Pocock, 1891c; Attems, 1930a) , but this study showed the first indications of taxonomic value of these features based on their discrete shape variation among *Scolopendra* species. Shape variation in tergite 21 seems to be the most variable of the features explored in our analysis and, indeed, this character has been used as diagnostic for some scolopendrid species, e.g., *Cormocephalus cupipes* Pocock, 1891 (Newport, 1844a) and *Otostigmus caudatus* Brölemann, 1902 (Brölemann, 1902b). To reduce confounding effects and improve accuracy, further shape analysis techniques such as combined outline and semi-landmark methods that have been used in scutigeromorph centipedes (Bolton et al., 2009; Lopez Gutierrez et al., 2011), as well as meristic measurements (Simaiakis et al., 2011), are likely to be promising topics for further study.

Conclusions

Taxonomy of scolopendrid centipedes at the species level has classically used external morphology, and *Scolopendra* is no exception. The phenotypic characters used herein for species delimitation in SE Asia (Table 3.1) are ones that have been employed by experts in scolopendrid taxonomy over many decades. Despite their widespread usage, the taxonomic reliability of these characters has at some time been called into question because they depict variability within particular scolopendrid species (Lewis, 1978, 2000; Shelley, 2005; Kronmüller, 2012). External morphology offers an accessible toolkit for identifying scolopendrid species but whether or not these entities (morphospecies) correspond to monophyletic groups has usually not been clear because taxonomy has usually been conducted separately from phylogenetic analysis. At the same time, *Scolopendra* has been subjected to perennial discussion about whether various taxa are species, subspecies or infraspecific variants undeserving of formal taxonomic recognition, a situation best exemplified by the unstable taxonomy of *S. subspinipes* and the dozens of nominal species now considered as junior synonyms of *S. morsitans*.

We have aimed to test the status of morphospecies in *Scolopendra* in SE Asia by applying additional data sources, specifically DNA sequences and geometric morphometric approaches to shape analysis. The results of these tests demonstrate that morphospecies are monophyletic groups supported by strong node support in probabilistic molecular analyses. Furthermore, these same formulations of species can be identified by statistical morphometric methods using such features as the shape of the forcipular coxosternite and the tergite of the ultimate leg-bearing segment. These shapes had generally not been used in prior taxonomy, possibly because the subtle differences between species are less amenable to qualitative description than to quantitative analysis. We are hesitant to generalize on whether the concordance between species delimited by external characters and molecular tree topologies seen in this set of *Scolopendra* species is representative of centipede taxonomy more broadly. At least some previous analyses, such as for the Neotropical scolopendromorph genus *Newportia* Gervais, 1847 (Gervais, 1847), have found that at least some morphospecies correspond to para- or polyphyletic groups based on molecular phylogeny (Edgecombe et al., 2015). Other analyses, as for Indian species of the scolopendrid *Digitipes*, have found a better match between morphological and molecular estimates of species, though some instances of cryptic species are likely (Joshi and Karanth, 2012; Joshi and Edgecombe, 2013). Finally, our study suggests that colour variation and genetic diversity of SE Asian *Scolopendra* populations can likely be attributed both to natural and anthropogenic pressures that affected genetic composition and ontogeny of these centipedes.

Acknowledgments

The authors are grateful to members of the Animal Systematics Research Unit for kind help during field collecting and data analysis, especially Dr. Ekgachai Jiratthitikul for his kind advice on morphometric analysis. Cordial thanks for accommodation and technical support during this study are given to all staff in the Department of Biology, Faculty of Science, Chulalongkorn University. Surveys in many restricted areas, especially some islands in both the Gulf of Thailand and the

Andaman Sea, were possible because of the great support and permission granted from The Plant Genetic Conservation Project under the Initiative of Her Royal Highness Princess Maha Chakri Sirindhorn, The Royal Thai Navy, The Department of National Parks, Wildlife and Conservation, and Sakaerat Environmental Research Station, Sakaerat Biosphere Reserve. Studies of some museum collections were generously facilitated by Dr. Nesrine Akkari (Naturhistorisches Museum Wien), Prof. Henrik Enghoff (National Museum of Denmark), and Ms. Janet Beccaloni (The Natural History Museum, London). The authors would like to express our thanks for constructive comments from Prof. Alessandro Minelli and Dr. Varpu Vahtera that improved the manuscript.

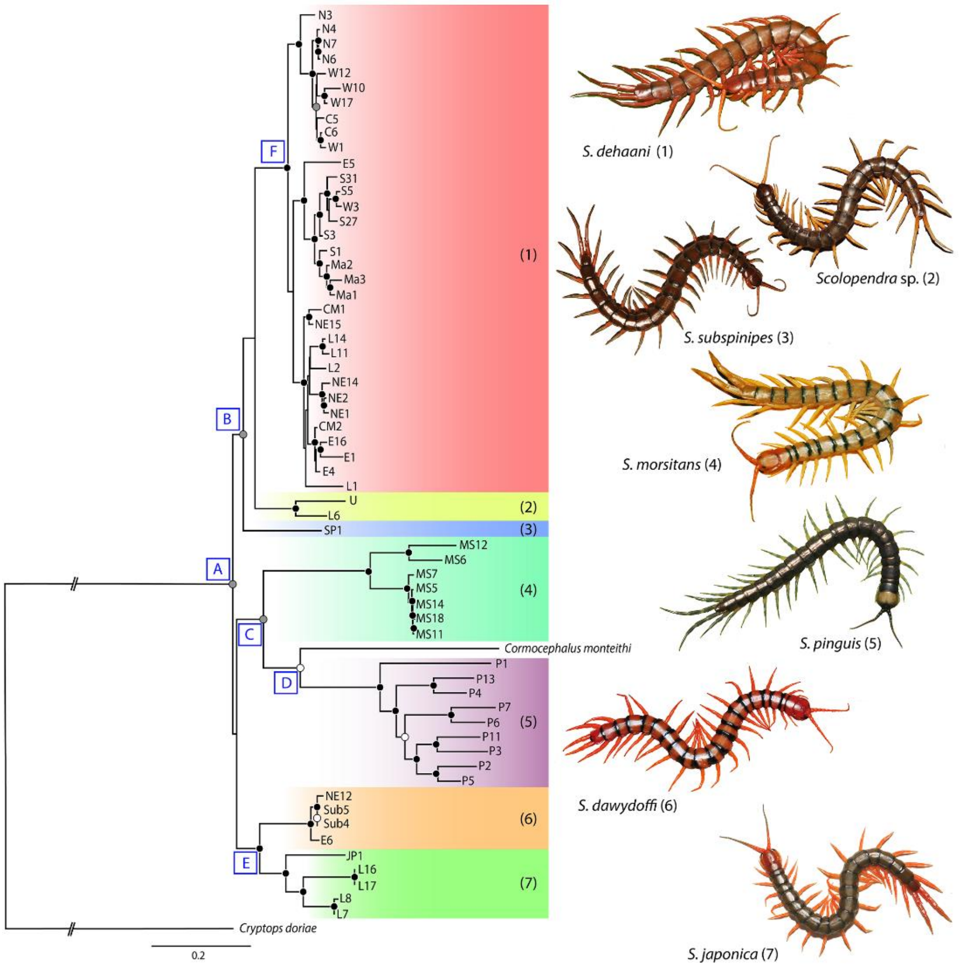


Figure 3.1 Phylogenetic tree of *Scolopendra* mainland Southeast Asia. Relationships among Scolopendra and two outgroups indicated similarly both in Maximum likelihood (ML) and Bayesian inference (BI) of the concatenated COI, 16S and COI partial gene analyses. Significant support values in ML and BI are indicated by three colouration circles; black circle = support both in ML and BI (above 70% bootstrap in ML and 0.95 posterior probability in BI), white circle = support only in ML, grey circle = support only in BI. The gradient colouration bars on the tree represent the genetic affinities of populations relative to morphological identification in each species.

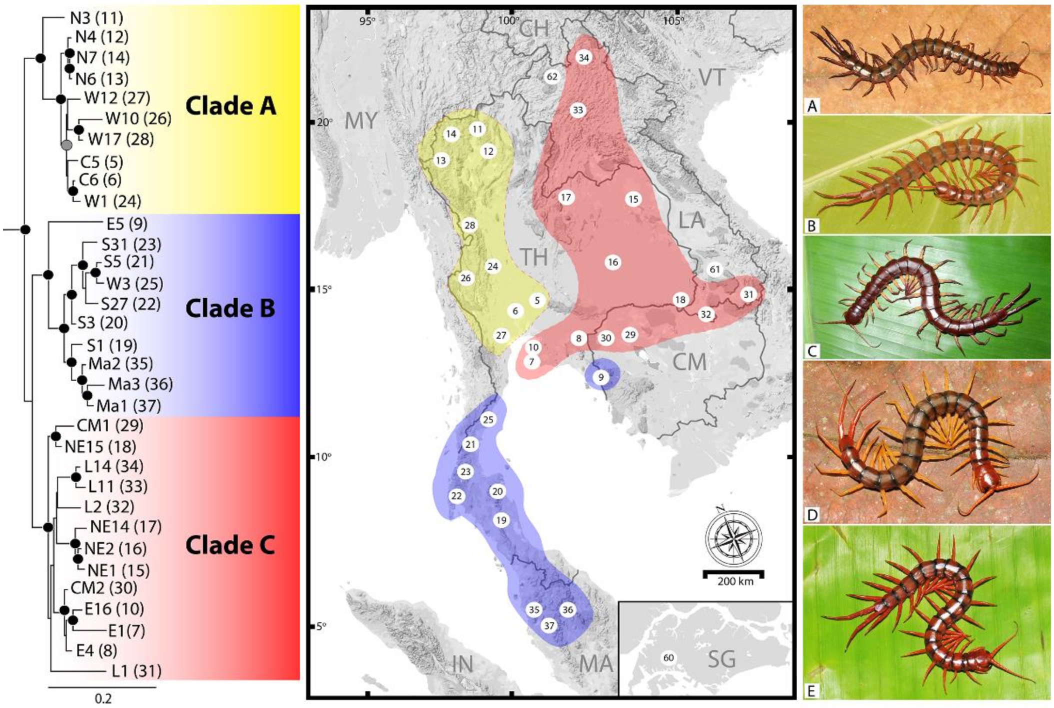


Figure 3.2 Phylogenetic relationship of *S. dehaani* population (left) based on genetic structure among its populations relative to regional distribution in mainland Southeast Asia (middle); colours indicate the major populations. Five patterns of live colour morphs in *S. dehaani* were found (right); **A.** Dark colour morph; **B.** Light brownish colour morph; **C.** Reddish-brown body color morph, yellowish legs with reddish on distal part; **D.** Dichromatic pattern; cephalic plate, tergite 1, 20 and 21 reddish, tergites 2–19 brownish with yellowish legs; **E.** Reddish colour morph with dark band on anterior and posterior parts of tergites.

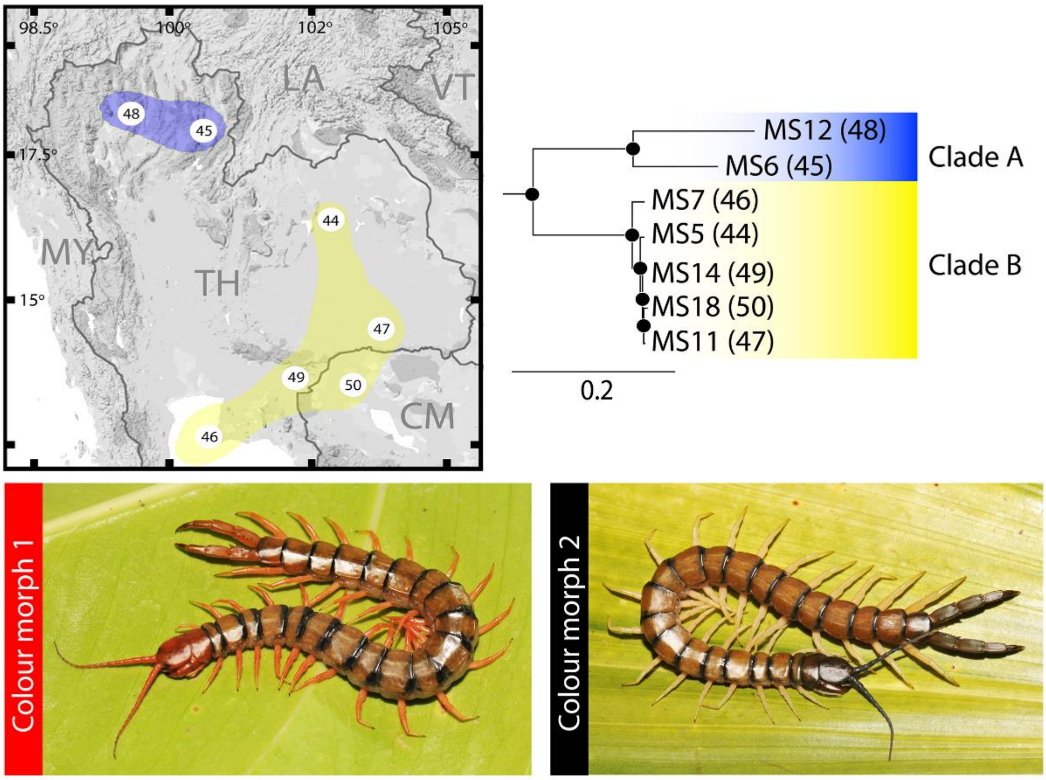


Figure 3.3 Phylogenetic tree of *S. morsitans*. Colour gradient indicates population structure; blue gradient indicates the northern population, yellow gradient the eastern population. *Scolopendra morsitans* exhibited two colour morphs: **colour morph 1**—antenna, cephalic plate, tergites 1, 20 and 21 and ultimate legs orange; **colour morph 2**—antenna, cephalic plate, tergites 1, 20 and 21 and ultimate legs blackish.

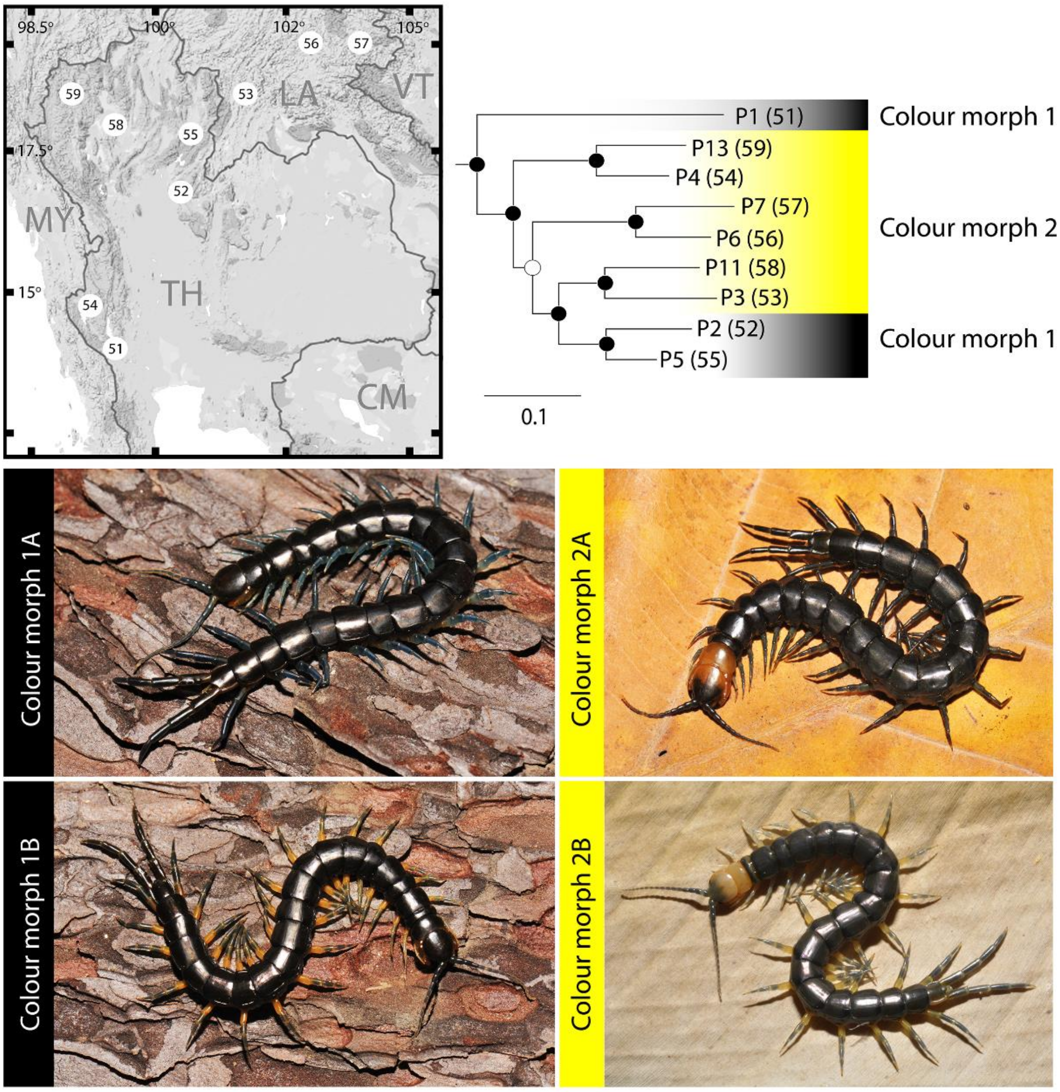


Figure 3.4 Phylogenetic tree of *S. pinguis* based on genetic structure of its populations. Colour gradient bar indicates colour morphs of sampled individuals that divide into two patterns; **colour morph 1**—blackish population (monochromatic); **colour morph 2**- yellowish—black population (dichromatic). Four live colour morph pictures depict the variability of colouration on legs of the two colour morphs in *S. pinguis*; colour morph **1A** and **2A**—animal with dark blue legs, colour morph **2A** and **2B**—animal with yellowish legs with blue stripes on distal part.

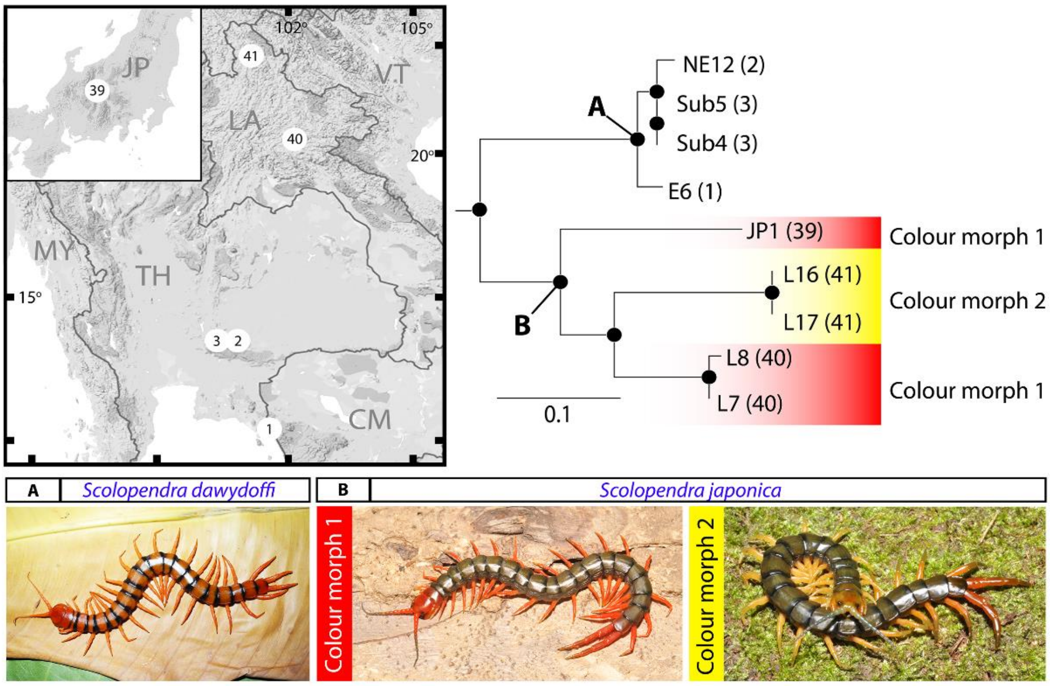


Figure 3.5 Phylogenetic tree of *S. dawydoffi* and *S. japonica*. **Clade A**, *S. dawydoffi*, **clade B**, *S. japonica*. In *S. japonica*, colour gradients indicate the colour morph of sampled individuals; colour morph 1—greenish body with reddish antenna, cephalic plate and legs; colour morph 2—greenish body with blue antenna, yellowish cephalic plate and legs.

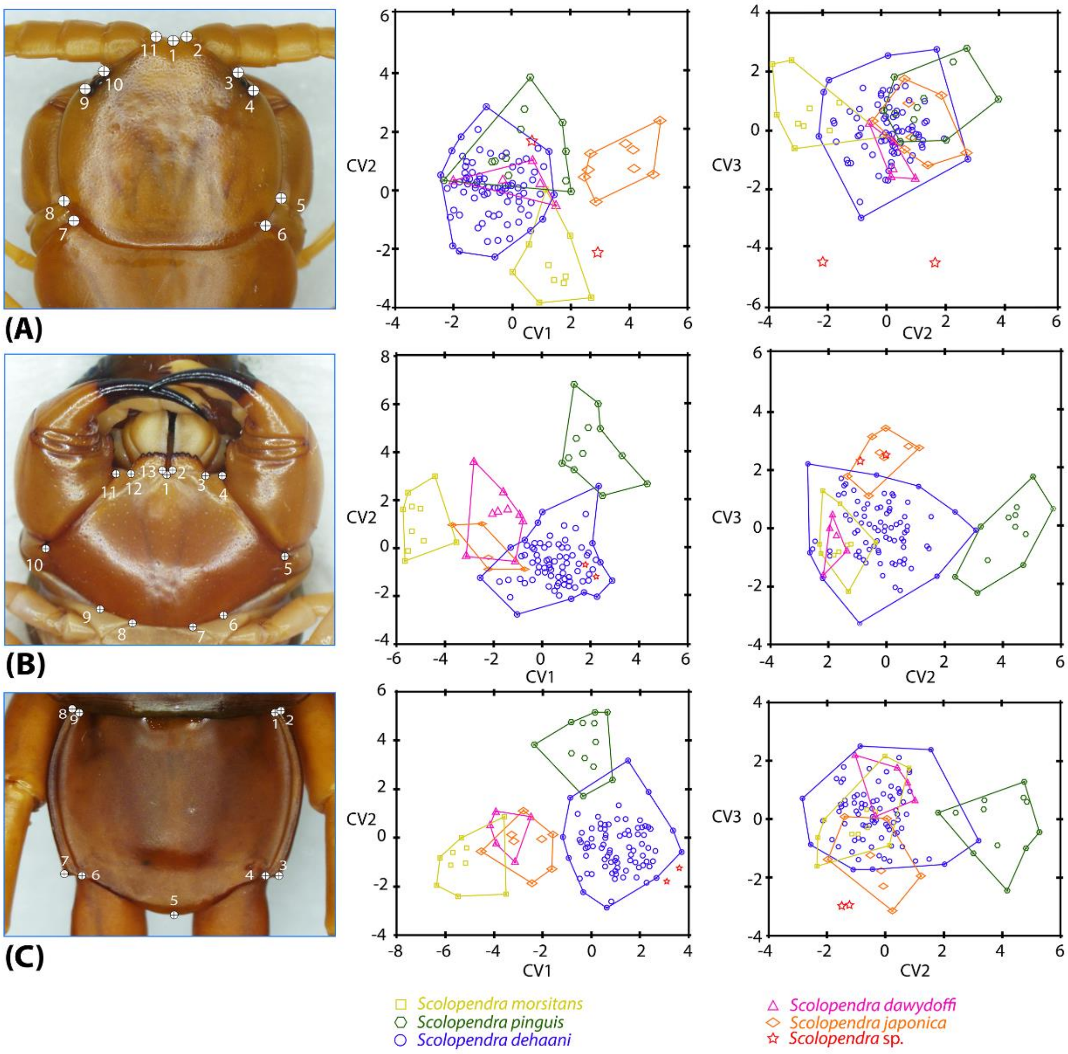


Figure 3.6 Diagram of landmark locations on three constant characters and the CV plot of individual scores on each CV axis from canonical variates analysis (CVA). **A.** Cephalic plate; **B.** Forcipular coxosternite; **C.** Tergite 21. The CV plots represent the discrimination of classified individuals scored from CV axis comparison, showing comparisons of CV1 and CV2 axes (middle column) and CV2 and CV3 axes (right column).

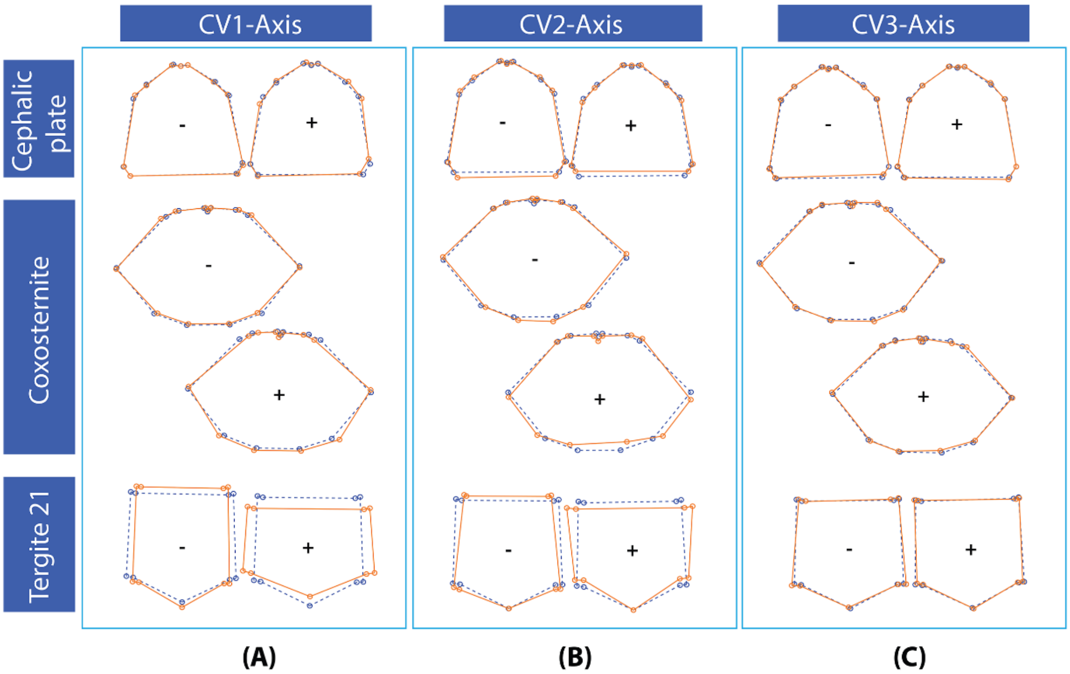


Figure 3.7 Wireframe diagram from continuous linkage of all landmark positions in three features derived from CVA scores on three axes. CV1, CV2 and CV3 arranged vertically, respectively. In the wireframes, dotted lines represent shape changes relative to CV score moving from both negative and positive directions, solid lines represent the shape consensus in negative and positive groups.

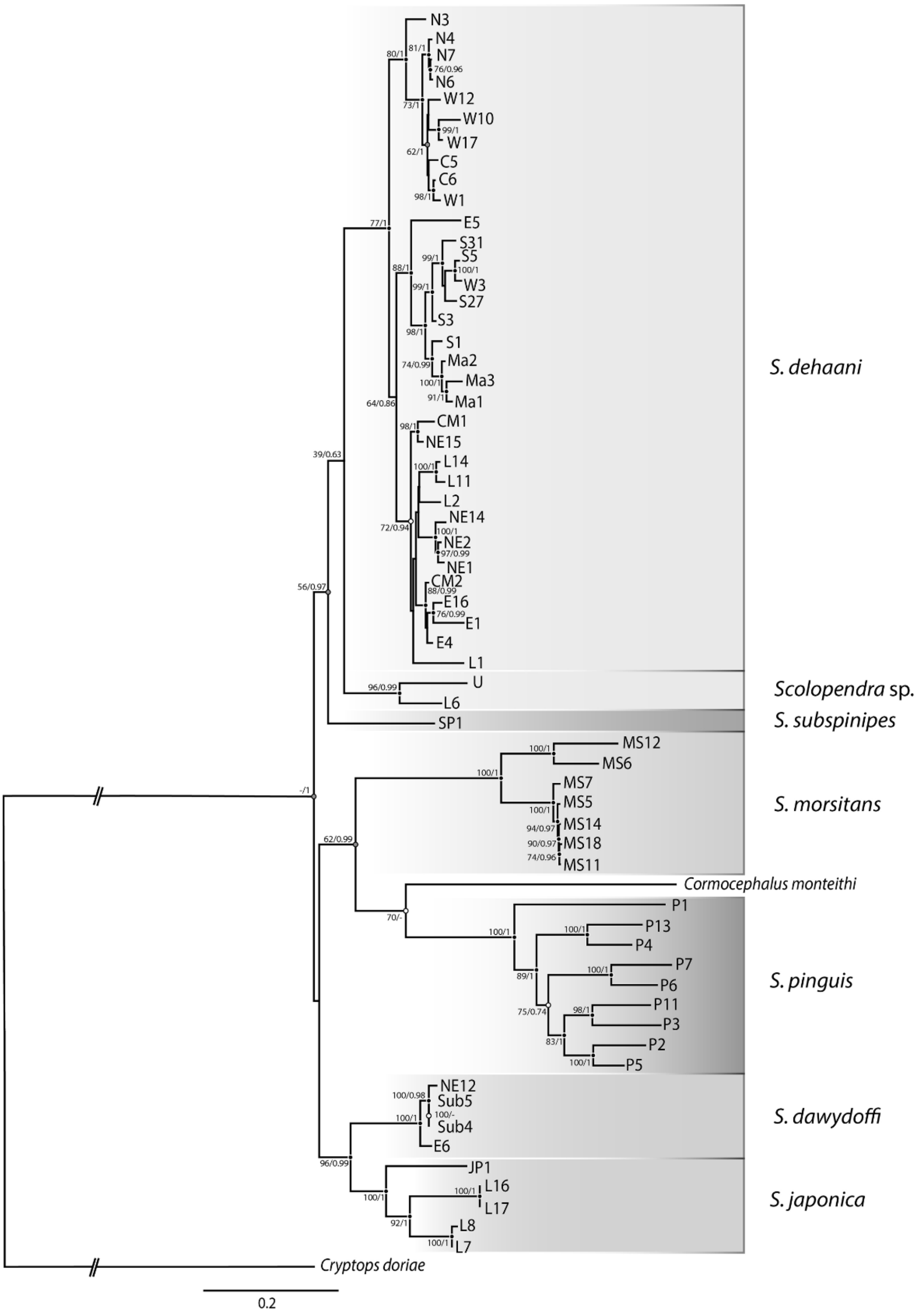
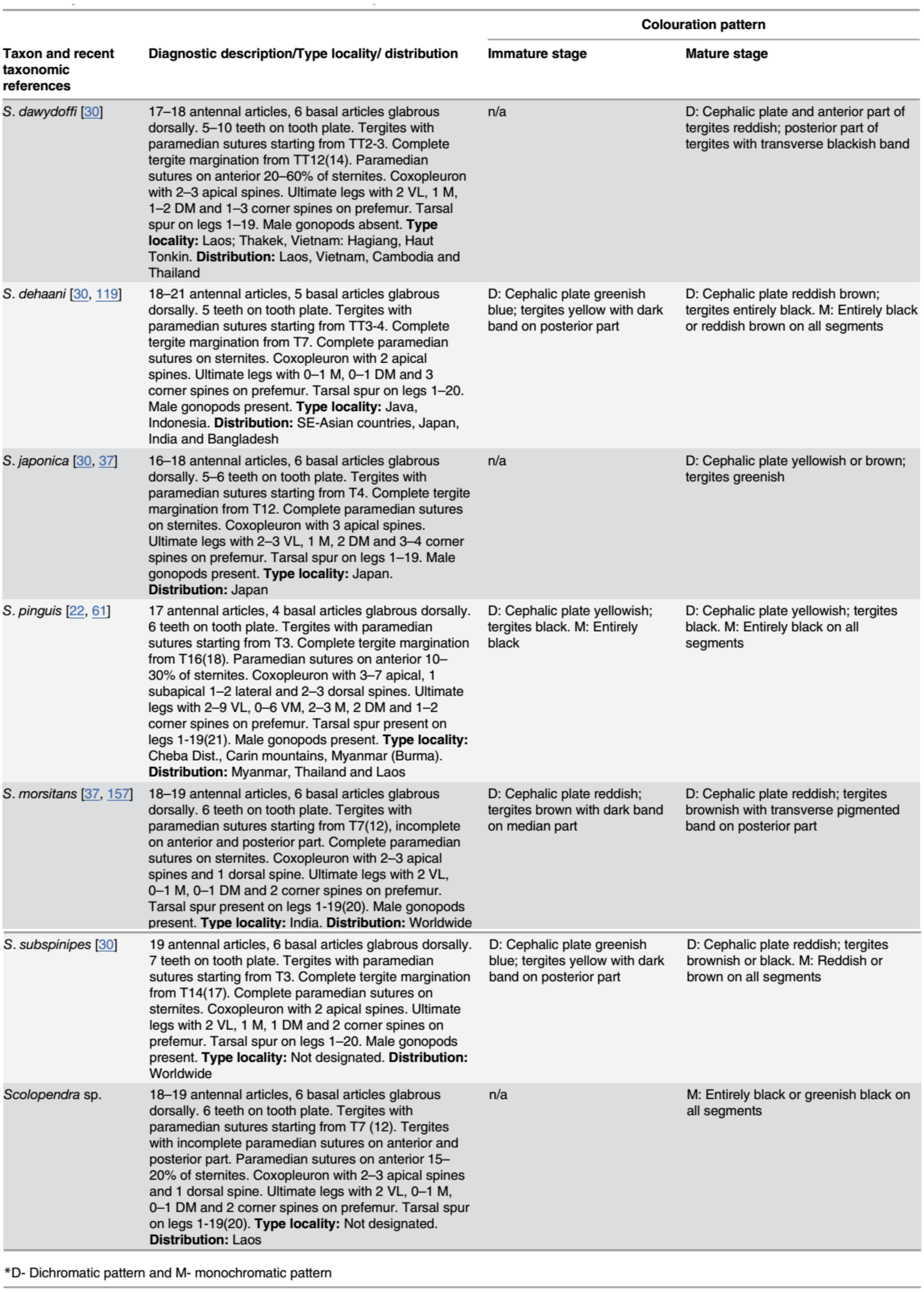


Figure 3.8 Phylogenetic tree based on concatenation of three partial gene analysis. Support values of bootstrap and posterior probability were given at each node.

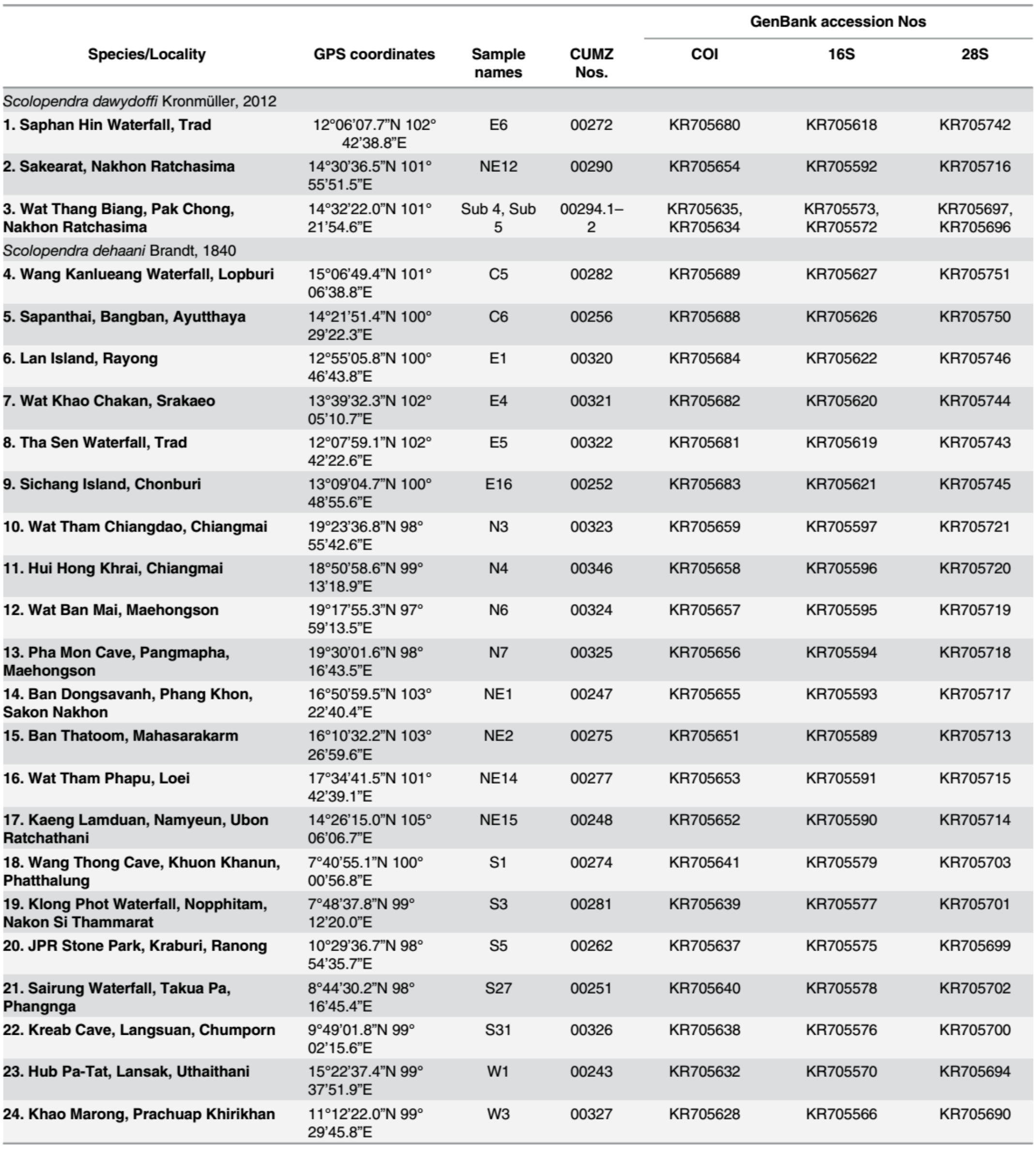
Table 3.1 Diagnostic description of all examined species based on external morphology and common colouration schemes of voucher specimensin this analysis, with references to recent taxonomic descriptions with additional information.



		Colouration pattern	
Taxon and recent taxonomic references	**Diagnostic description/Type locality/ distribution**	**Immature stage**	**Mature stage**
S. dawydoffi [30]	17–18 antennal articles, 6 basal articles glabrous dorsally. 5–10 teeth on tooth plate. Tergites with paramedian sutures starting from TT2-3. Complete tergite margination from TT12(14). Paramedian sutures on anterior 20–60% of sternites. Coxopleuron with 2–3 apical spines. Ultimate legs with 2 VL, 1 M, 1–2 DM and 1–3 corner spines on prefemur. Tarsal spur on legs 1–19. Male gonopods absent. **Type locality:** Laos; Thakek, Vietnam: Hagiang, Haut Tonkin. **Distribution:** Laos, Vietnam, Cambodia and Thailand	n/a	D: Cephalic plate and anterior part of tergites reddish; posterior part of tergites with transverse blackish band
S. dehaani [30, 119]	18–21 antennal articles, 5 basal articles glabrous dorsally. 5 teeth on tooth plate. Tergites with paramedian sutures starting from TT3-4. Complete tergite margination from T7. Complete paramedian sutures on sternites. Coxopleuron with 2 apical spines. Ultimate legs with 0–1 M, 0–1 DM and 3 corner spines on prefemur. Tarsal spur on legs 1–20. Male gonopods present. **Type locality:** Java, Indonesia. **Distribution:** SE-Asian countries, Japan, India and Bangladesh	D: Cephalic plate greenish blue; tergites yellow with dark band on posterior part	D: Cephalic plate reddish brown; tergites entirely black. M: Entirely black or reddish brown on all segments
S. japonica [30, 37]	16–18 antennal articles, 6 basal articles glabrous dorsally. 5–6 teeth on tooth plate. Tergites with paramedian sutures starting from T4. Complete tergite margination from T12. Complete paramedian sutures on sternites. Coxopleuron with 3 apical spines. Ultimate legs with 2–3 VL, 1 M, 2 DM and 3–4 corner spines on prefemur. Tarsal spur on legs 1–19. Male gonopods present. **Type locality:** Japan. **Distribution:** Japan	n/a	D: Cephalic plate yellowish or brown; tergites greenish
S. pinguis [22, 61]	17 antennal articles, 4 basal articles glabrous dorsally. 6 teeth on tooth plate. Tergites with paramedian sutures starting from T3. Complete tergite margination from T16(18). Paramedian sutures on anterior 10–30% of sternites. Coxopleuron with 3–7 apical, 1 subapical 1–2 lateral and 2–3 dorsal spines. Ultimate legs with 2–9 VL, 0–6 VM, 2–3 M, 2 DM and 1–2 corner spines on prefemur. Tarsal spur present on legs 1-19(21). Male gonopods present. **Type locality:** Cheba Dist., Carin mountains, Myanmar (Burma). **Distribution:** Myanmar, Thailand and Laos	D: Cephalic plate yellowish; tergites black. M: Entirely black	D: Cephalic plate yellowish; tergites black. M: Entirely black on all segments
S. morsitans [37, 157]	18–19 antennal articles, 6 basal articles glabrous dorsally. 6 teeth on tooth plate. Tergites with paramedian sutures starting from T7(12), incomplete on anterior and posterior part. Complete paramedian sutures on sternites. Coxopleuron with 2–3 apical spines and 1 dorsal spine. Ultimate legs with 2 VL, 0–1 M, 0–1 DM and 2 corner spines on prefemur. Tarsal spur present on legs 1-19(20). Male gonopods present. **Type locality:** India. **Distribution:** Worldwide	D: Cephalic plate reddish; tergites brown with dark band on median part	D: Cephalic plate reddish; tergites brownish with transverse pigmented band on posterior part
S. subspinipes [30]	19 antennal articles, 6 basal articles glabrous dorsally. 7 teeth on tooth plate. Tergites with paramedian sutures starting from T3. Complete tergite margination from T14(17). Complete paramedian sutures on sternites. Coxopleuron with 2 apical spines. Ultimate legs with 2 VL, 1 M, 1 DM and 2 corner spines on prefemur. Tarsal spur on legs 1–20. Male gonopods present. **Type locality:** Not designated. **Distribution:** Worldwide	D: Cephalic plate greenish blue; tergites yellow with dark band on posterior part	D: Cephalic plate reddish; tergites brownish or black. M: Reddish or brown on all segments
Scolopendra sp.	18–19 antennal articles, 6 basal articles glabrous dorsally. 6 teeth on tooth plate. Tergites with paramedian sutures starting from T7 (12). Tergites with incomplete paramedian sutures on anterior and posterior part. Paramedian sutures on anterior 15–20% of sternites. Coxopleuron with 2–3 apical spines and 1 dorsal spine. Ultimate legs with 2 VL, 0–1 M, 0–1 DM and 2 corner spines on prefemur. Tarsal spur on legs 1-19(20). **Type locality:** Not designated. **Distribution:** Laos	n/a	M: Entirely black or greenish black on all segments

*D- Dichromatic pattern and M- monochromatic pattern

Table 3.2 List of voucher specimens of seven *Scolopendra* species and selected outgroups used in phylogenetic analyses. Each sample includes the collecting locality, GPS co-ordinates, CUMZ registration numbers, and GenBank accession number for three selected genes (COI, 16S and 28S).



Species/Locality	GPS coordinates	Sample names	CUMZ Nos.	GenBank accession Nos		
				COI	16S	28S
Scolopendra dawydoffi Kronmüller, 2012						
1. Saphan Hin Waterfall, Trad	12°06’07.7”N 102° 42’38.8”E	E6	00272	KR705680	KR705618	KR705742
2. Sakearat, Nakhon Ratchasima	14°30’36.5”N 101° 55’51.5”E	NE12	00290	KR705654	KR705592	KR705716
3. Wat Thang Biang, Pak Chong, Nakhon Ratchasima	14°32’22.0”N 101° 21’54.6”E	Sub 4, Sub 5	00294.1–2	KR705635, KR705634	KR705573, KR705572	KR705697, KR705696
Scolopendra dehaani Brandt, 1840						
4. Wang Kanlueang Waterfall, Lopburi	15°06’49.4”N 101° 06’38.8”E	C5	00282	KR705689	KR705627	KR705751
5. Sapanthai, Bangban, Ayutthaya	14°21’51.4”N 100° 29’22.3”E	C6	00256	KR705688	KR705626	KR705750
6. Lan Island, Rayong	12°55’05.8”N 100° 46’43.8”E	E1	00320	KR705684	KR705622	KR705746
7. Wat Khao Chakan, Srakaeo	13°39’32.3”N 102° 05’10.7”E	E4	00321	KR705682	KR705620	KR705744
8. Tha Sen Waterfall, Trad	12°07’59.1”N 102° 42’22.6”E	E5	00322	KR705681	KR705619	KR705743
9. Sichang Island, Chonburi	13°09’04.7”N 100° 48’55.6”E	E16	00252	KR705683	KR705621	KR705745
10. Wat Tham Chiangdao, Chiangmai	19°23’36.8”N 98° 55’42.6”E	N3	00323	KR705659	KR705597	KR705721
11. Hui Hong Khrai, Chiangmai	18°50’58.6”N 99° 13’18.9”E	N4	00346	KR705658	KR705596	KR705720
12. Wat Ban Mai, Maehongson	19°17’55.3”N 97° 59’13.5”E	N6	00324	KR705657	KR705595	KR705719
13. Pha Mon Cave, Pangmapha, Maehongson	19°30’01.6”N 98° 16’43.5”E	N7	00325	KR705656	KR705594	KR705718
14. Ban Dongsavanh, Phang Khon, Sakon Nakhon	16°50’59.5”N 103° 22’40.4”E	NE1	00247	KR705655	KR705593	KR705717
15. Ban Thatoom, Mahasarakarm	16°10’32.2”N 103° 26’59.6”E	NE2	00275	KR705651	KR705589	KR705713
16. Wat Tham Phapu, Loei	17°34’41.5”N 101° 42’39.1”E	NE14	00277	KR705653	KR705591	KR705715
17. Kaeng Lamduan, Namyeun, Ubon Ratchathani	14°26’15.0”N 105° 06’06.7”E	NE15	00248	KR705652	KR705590	KR705714
18. Wang Thong Cave, Khuon Khanun, Phatthalung	7°40’55.1”N 100° 00’56.8”E	S1	00274	KR705641	KR705579	KR705703
19. Klong Phot Waterfall, Nopphitam, Nakon Si Thammarat	7°48’37.8”N 99° 12’20.0”E	S3	00281	KR705639	KR705577	KR705701
20. JPR Stone Park, Kraburi, Ranong	10°29’36.7”N 98° 54’35.7”E	S5	00262	KR705637	KR705575	KR705699
21. Sairung Waterfall, Takua Pa, Phangnga	8°44’30.2”N 98° 16’45.4”E	S27	00251	KR705640	KR705578	KR705702
22. Kreab Cave, Langsuan, Chumporn	9°49’01.8”N 99° 02’15.6”E	S31	00326	KR705638	KR705576	KR705700
23. Hub Pa-Tat, Lansak, Uthaithani	15°22’37.4”N 99° 37’51.9”E	W1	00243	KR705632	KR705570	KR705694
24. Khao Marong, Prachuap Khirikhan	11°12’22.0”N 99° 29’45.8”E	W3	00327	KR705628	KR705566	KR705690

Table 3.2 List of voucher specimens of seven *Scolopendra* species and selected outgroups used in phylogenetic analyses. Each sample includes the collecting locality, GPS co-ordinates, CUMZ registration numbers, and GenBank accession number for three selected genes (COI, 16S and 28S). (Continued)

Species/Locality	GPS coordinates	Sample names	CUMZ Nos.	GenBank accession Nos		
				COI	16S	28S
25. Wat Tham Lijia, Sangkhlaburi, Kanchanaburi	15°04'12.8"N 98° 33'56.4"E	W10	00328	KR705631	KR705569	KR705693
26. Tham Khao Bin, Ratchaburi	13°35'35.6"N 99° 40'02.3"E	W12	00253	KR705630	KR705568	KR705692
27. Wat Phothikhun, Maesot, Tak	16°44'39.2"N 98° 36'17.2"E	W17	00329	KR705629	KR705567	KR705691
28. Angkor Wat, Siem Reap, Cambodia	13°24'45.5"N 103° 52'14.7"E	CM1	00330	KR705687	KR705625	KR705749
29. Wat Tham Ban Kele, Srisophon, Cambodia	13°36'05.5"N 102° 57'09.3"E	CM2	00331	KR705686	KR705624	KR705748
30. Hin Tang Stone field, 39 Km. before Vietnam border, Attapu, Laos	14°43'18.6"N 107° 17'39.6"E	L1	00332	KR705678	KR705616	KR705740
31. Khon Phapaeng Waterfall, Champasak, Laos	13°56'53.2"N 105° 56'27.1"E	L2	00333	KR705673	KR705611	KR705735
32. Luang Prabang, Laos	19°53'10.2"N 102° 08'16.2"E	L11	00334	KR705677	KR705615	KR705739
33. Ban Bun-Tai, Bun-Tai, Phongsali, Laos	21°26'50.8"N 101° 58'30.5"E	L14	00335	KR705676	KR705614	KR705738
34. Gumpung Baru, Gunung Getting, Perak, Malaysia	4°41'39.9"N 100° 52'46.0"E	Ma1	00336	KR705669	KR705607	KR705731
35. Gua Musang, Kelantan, Malaysia	4°52'11.3"N 102° 00'40.6"E	Ma2	00337	KR705668	KR705606	KR705730
36. Klinic Desa, Kampung Panit Luar, Perak, Malaysia	4°56'17.9"N 100° 59'00.1"E	Ma3	00338	KR705667	KR705605	KR705729
Scolopendra japonica Koch, 1860						
37. Shinshu University, Matsumoto, Japan	36°13'22.4"N 137° 54'35.0"E	JP1	00319	KR705679	KR705617	KR705741
38. Plain of Jar, Xieang Khouang, Laos	19°25'51.5"N 103° 09'10.4"E	L7, L8	00298.1–2	KR705671, KR705670	KR705609, KR705608	KR705733, KR705732
39. Phu Fah Mountain, Phongsali, Laos	21°41'19.6"N 102° 06'30.4"E	L16, L17	00297.1–2	KR705675, KR705674	KR705613, KR705612	KR705737, KR705736
Scolopendra morsitans Linnaeus, 1758						
40. Ban Dan Chang, Ta Kantho, Khonkaen	16°50'06.1"N 103° 16'32.0"E	MS5	00339	KR705662	KR705600	KR705724
41. Lainan, Weing Sa, Nan	18°34'16.1"N 100° 46'59.7"E	MS6	00340	KR705661	KR705599	KR705723
42. Juang Island, Sattahip, Chonburi	12°31'46.4"N 100° 57'18.4"E	MS7	00341	KR705660	KR705598	KR705722
43. Ban Khok Pho, Prasat, Surin	14°32'53.4"N 103° 22'19.1"	MS11	00342	KR705666	KR705604	KR705728
44. Hui Hong Khrai, Chiangmai	18°50'59.5"N 99° 13'16.4"E	MS12	00343	KR705665	KR705603	KR705727
45. Tha Kra Bak Reservoir, Srakaeo	13°58'13.9"N 102° 15'57.6"E	MS14	00344	KR705664	KR705602	KR705726
46. Wat Phanombak, Srisophon, Cambodia	13°36'05.5"N 102° 57'09.3"E	MS18	00345	KR705663	KR705601	KR705725
Scolopendra pinguis Pocock, 1891						
47. Chong Kao Khat, Kanchanaburi	14°22'47.6"N 98° 55'47.7"E	P1	00312	KR705650	KR705588	KR705712

(*Continued*)

Table 3.2 List of voucher specimens of seven *Scolopendra* species and selected outgroups used in phylogenetic analyses. Each sample includes the collecting locality, GPS co-ordinates, CUMZ registration numbers, and GenBank accession number for three selected genes (COI, 16S and 28S). (Continued)

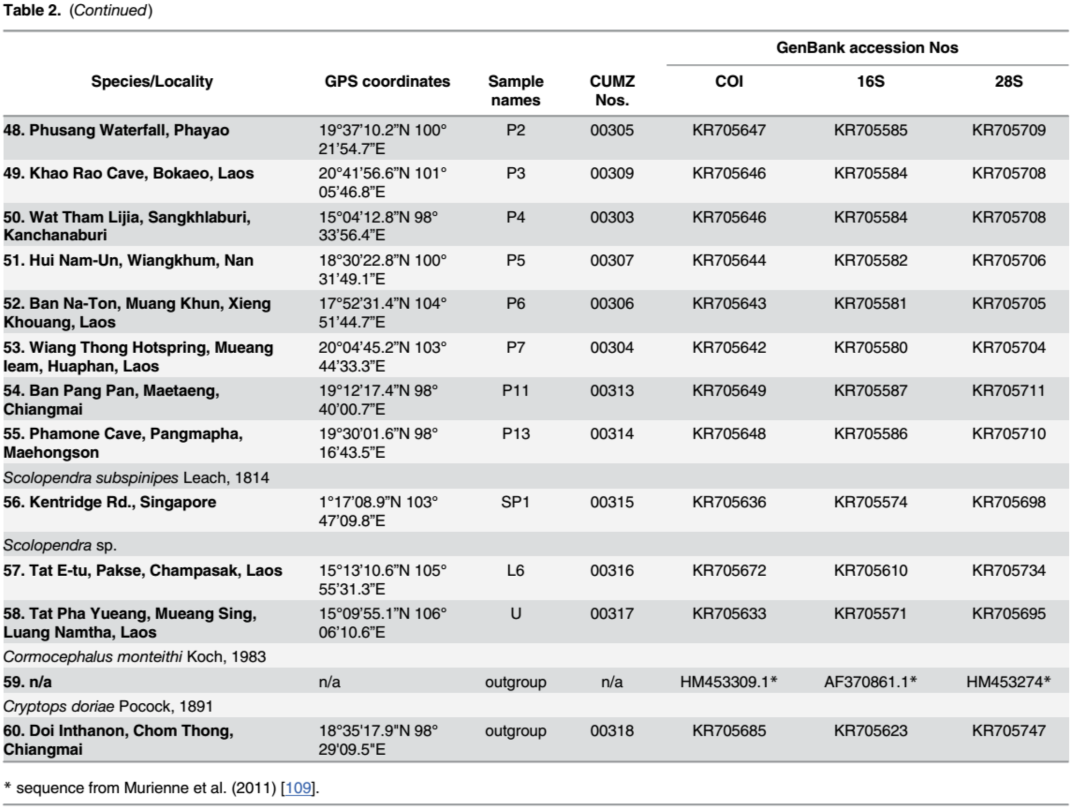
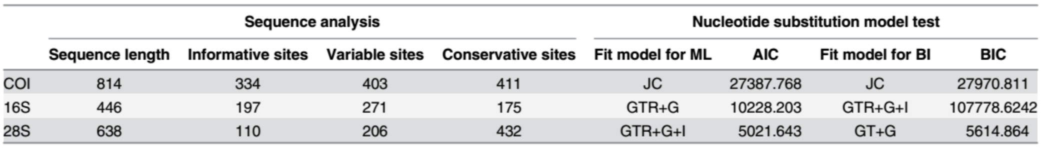


Table 2. (*Continued*)

Species/Locality	GPS coordinates	Sample names	CUMZ Nos.	GenBank accession Nos COI	16S	28S
48. Phusang Waterfall, Phayao	19°37'10.2"N 100° 21'54.7"E	P2	00305	KR705647	KR705585	KR705709
49. Khao Rao Cave, Bokaeo, Laos	20°41'56.6"N 101° 05'46.8"E	P3	00309	KR705646	KR705584	KR705708
50. Wat Tham Lijia, Sangkhlaburi, Kanchanaburi	15°04'12.8"N 98° 33'56.4"E	P4	00303	KR705646	KR705584	KR705708
51. Hui Nam-Un, Wiangkhum, Nan	18°30'22.8"N 100° 31'49.1"E	P5	00307	KR705644	KR705582	KR705706
52. Ban Na-Ton, Muang Khun, Xieng Khouang, Laos	17°52'31.4"N 104° 51'44.7"E	P6	00306	KR705643	KR705581	KR705705
53. Wiang Thong Hotspring, Mueang Ieam, Huaphan, Laos	20°04'45.2"N 103° 44'33.3"E	P7	00304	KR705642	KR705580	KR705704
54. Ban Pang Pan, Maetaeng, Chiangmai	19°12'17.4"N 98° 40'00.7"E	P11	00313	KR705649	KR705587	KR705711
55. Phamone Cave, Pangmapha, Maehongson	19°30'01.6"N 98° 16'43.5"E	P13	00314	KR705648	KR705586	KR705710
Scolopendra subspinipes Leach, 1814						
56. Kentridge Rd., Singapore	1°17'08.9"N 103° 47'09.8"E	SP1	00315	KR705636	KR705574	KR705698
Scolopendra sp.						
57. Tat E-tu, Pakse, Champasak, Laos	15°13'10.6"N 105° 55'31.3"E	L6	00316	KR705672	KR705610	KR705734
58. Tat Pha Yueang, Mueang Sing, Luang Namtha, Laos	15°09'55.1"N 106° 06'10.6"E	U	00317	KR705633	KR705571	KR705695
Cormocephalus monteithi Koch, 1983						
59. n/a	n/a	outgroup	n/a	HM453309.1*	AF370861.1*	HM453274*
Cryptops doriae Pocock, 1891						
60. Doi Inthanon, Chom Thong, Chiangmai	18°35'17.9"N 98° 29'09.5"E	outgroup	00318	KR705685	KR705623	KR705747

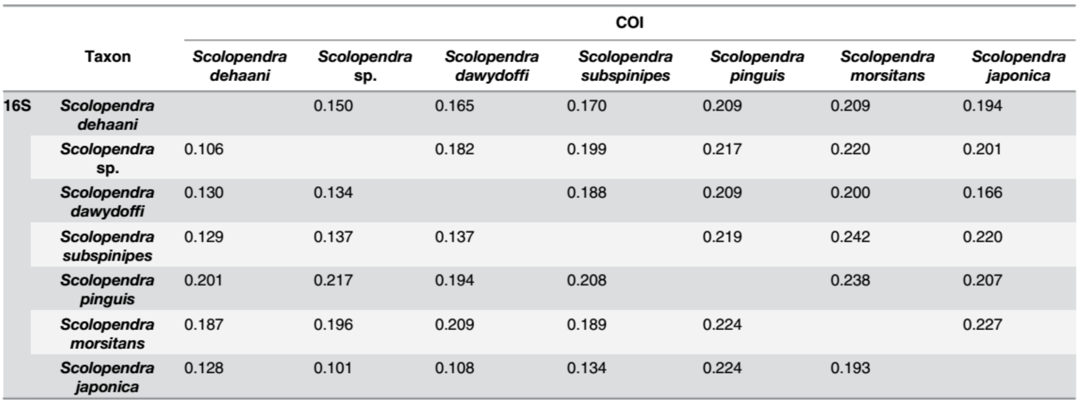
* sequence from Murienne et al. (2011) [109].

Table 3.3 Characteristics of nucleotide sequence for three amplified genes and best fit models of heterogeneous nucleotide substitution for eachgene calculated from jModel Test under AIC and BIC criteria.



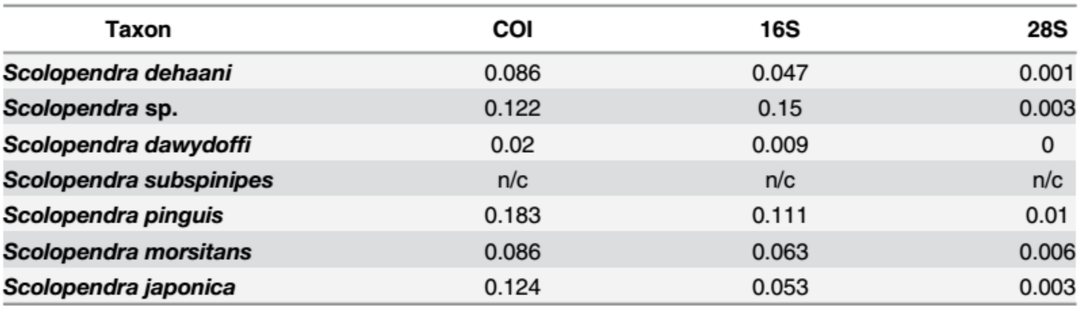
	Sequence analysis				Nucleotide substitution model test			
	Sequence length	Informative sites	Variable sites	Conservative sites	Fit model for ML	AIC	Fit model for BI	BIC
COI	814	334	403	411	JC	27387.768	JC	27970.811
16S	446	197	271	175	GTR+G	10228.203	GTR+G+I	107778.6242
28S	638	110	206	432	GTR+G+I	5021.643	GT+G	5614.864

Table 3.4 Corrected distance of interspecific variation in seven Scolopendra species from COI and 16S partial gene analyses under calculation model of K-2 parameter.



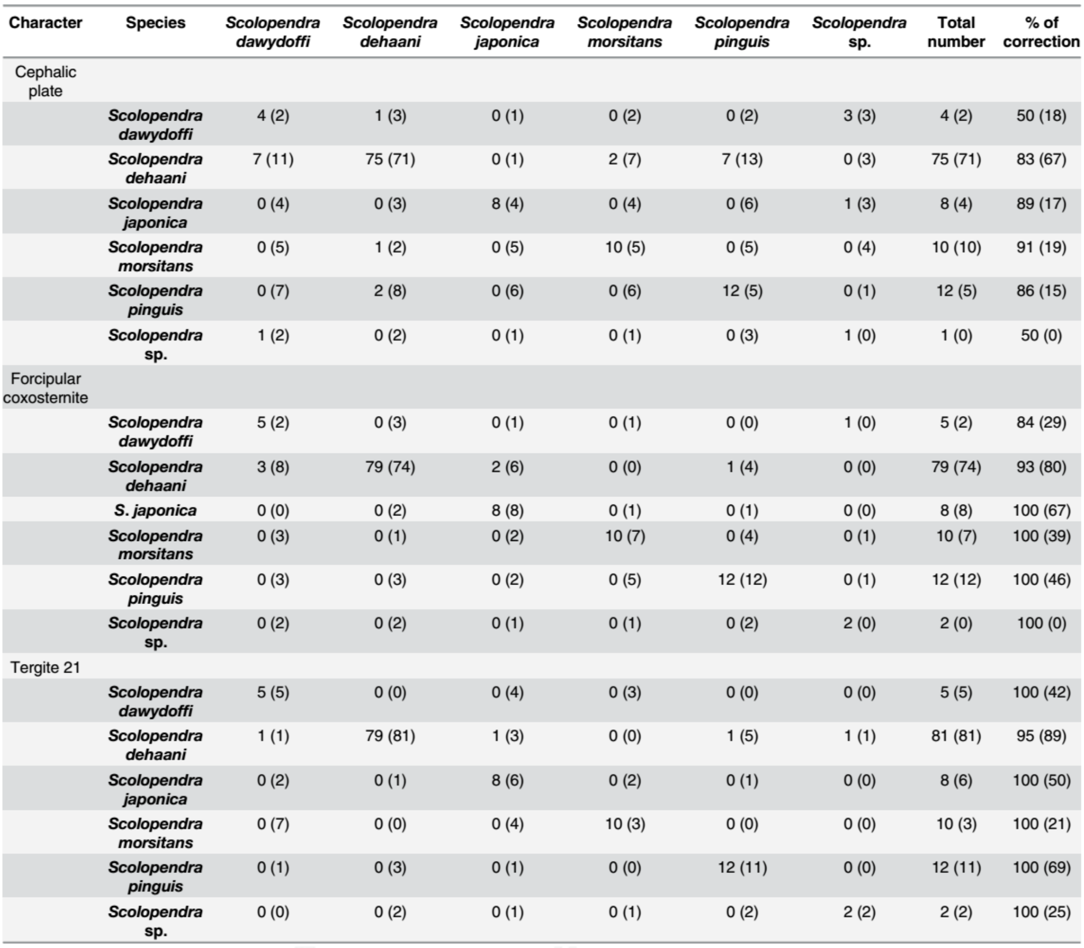
		COI						
	Taxon	***Scolopendra dehaani***	***Scolopendra* sp.**	***Scolopendra dawydoffi***	***Scolopendra subspinipes***	***Scolopendra pinguis***	***Scolopendra morsitans***	***Scolopendra japonica***
16S	***Scolopendra dehaani***		0.150	0.165	0.170	0.209	0.209	0.194
	***Scolopendra* sp.**	0.106		0.182	0.199	0.217	0.220	0.201
	Scolopendra dawydoffi	0.130	0.134		0.188	0.209	0.200	0.166
	Scolopendra subspinipes	0.129	0.137	0.137		0.219	0.242	0.220
	Scolopendra pinguis	0.201	0.217	0.194	0.208		0.238	0.207
	Scolopendra morsitans	0.187	0.196	0.209	0.189	0.224		0.227
	Scolopendra japonica	0.128	0.101	0.108	0.134	0.224	0.193	

Table 3.5 Corrected distance of intraspecific variation in six *Scolopendra* species from COI, 16S and 28S partial gene analysis under calculation model of K-2 parameter.



Taxon	COI	16S	28S
Scolopendra dehaani	0.086	0.047	0.001
***Scolopendra* sp.**	0.122	0.15	0.003
Scolopendra dawydoffi	0.02	0.009	0
Scolopendra subspinipes	n/c	n/c	n/c
Scolopendra pinguis	0.183	0.111	0.01
Scolopendra morsitans	0.086	0.063	0.006
Scolopendra japonica	0.124	0.053	0.003

Table 3.6 Results of CV discriminant function in three selected characters; the total number and percentage of correction of leave-one-out cross validation tests in CV discriminant function are in parentheses.



Character	**Species**	***Scolopendra dawydoffi***	***Scolopendra dehaani***	***Scolopendra japonica***	***Scolopendra morsitans***	***Scolopendra pinguis***	***Scolopendra* sp.**	**Total number**	**% of correction**
Cephalic plate									
	Scolopendra dawydoffi	4 (2)	1 (3)	0 (1)	0 (2)	0 (2)	3 (3)	4 (2)	50 (18)
	Scolopendra dehaani	7 (11)	75 (71)	0 (1)	2 (7)	7 (13)	0 (3)	75 (71)	83 (67)
	Scolopendra japonica	0 (4)	0 (3)	8 (4)	0 (4)	0 (6)	1 (3)	8 (4)	89 (17)
	Scolopendra morsitans	0 (5)	1 (2)	0 (5)	10 (5)	0 (5)	0 (4)	10 (10)	91 (19)
	Scolopendra pinguis	0 (7)	2 (8)	0 (6)	0 (6)	12 (5)	0 (1)	12 (5)	86 (15)
	***Scolopendra* sp.**	1 (2)	0 (2)	0 (1)	0 (1)	0 (3)	1 (0)	1 (0)	50 (0)
Forcipular coxosternite									
	Scolopendra dawydoffi	5 (2)	0 (3)	0 (1)	0 (1)	0 (0)	1 (0)	5 (2)	84 (29)
	Scolopendra dehaani	3 (8)	79 (74)	2 (6)	0 (0)	1 (4)	0 (0)	79 (74)	93 (80)
	S. japonica	0 (0)	0 (2)	8 (8)	0 (1)	0 (1)	0 (0)	8 (8)	100 (67)
	Scolopendra morsitans	0 (3)	0 (1)	0 (2)	10 (7)	0 (4)	0 (1)	10 (7)	100 (39)
	Scolopendra pinguis	0 (3)	0 (3)	0 (2)	0 (5)	12 (12)	0 (1)	12 (12)	100 (46)
	***Scolopendra* sp.**	0 (2)	0 (2)	0 (1)	0 (1)	0 (2)	2 (0)	2 (0)	100 (0)
Tergite 21									
	Scolopendra dawydoffi	5 (5)	0 (0)	0 (4)	0 (3)	0 (0)	0 (0)	5 (5)	100 (42)
	Scolopendra dehaani	1 (1)	79 (81)	1 (3)	0 (0)	1 (5)	1 (1)	81 (81)	95 (89)
	Scolopendra japonica	0 (2)	0 (1)	8 (6)	0 (2)	0 (1)	0 (0)	8 (6)	100 (50)
	Scolopendra morsitans	0 (7)	0 (0)	0 (4)	10 (3)	0 (0)	0 (0)	10 (3)	100 (21)
	Scolopendra pinguis	0 (1)	0 (3)	0 (1)	0 (0)	12 (11)	0 (0)	12 (11)	100 (69)
	***Scolopendra* sp.**	0 (0)	0 (2)	0 (1)	0 (1)	0 (2)	2 (2)	2 (2)	100 (25)

Chapter 4

Brooding behaviour of the centipede *Otostigmus spinosus* Porat, 1876 (Chilopoda: Scolopendromorpha: Scolopendridae) and its morphological variability in Thailand

Warut Siriwut[1, 2], Gregory D Edgecombe[3], Chirasak Sutcharit[2] & Somsak Panha[2*]

[1]Biological Sciences Program, Faculty of Science, Chulalongkorn University, Phayathai Road, Bangkok 10330, Thailand
[2]Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand; Email: somsak.pan@chula ac.th (*corresponding author)
[3]Department of Earth Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

Raffles Bulletin of Zoology: published 62: 339-351 (2014)

Abstract

Maternal care is shared by three of the five living orders of centipedes and is generally thought to have a single evolutionary origin in this group. Literature on brooding behaviour in the order Scolopendromorpha is scattered, with observations available for six genera. Brooding in the diverse genus *Otostigmus* Porat, 1876, with ca 120 species mostly distributed in the tropics, has been documented in only two species from Brazil. Six broods of *O. spinosus* representing different embryonic and adolescent (post-embryonic) stages are documented from southern Thailand. Size of the brood is similar to other species of *Otostigmus*, and this species exhibits filial cannibalism also documented in the Neotropical *O. scabricauda*. *Otostigmus spinosus* is redescribed with emphasis on a large sample of Thai material and is reported from Laos for the first time. Sexual dimorphism is apparently exhibited by a distal projection on tarsus 1 of legs 20 and 21 in males. Considerable variability in taxonomic characters within and between populations renders a consistent distinction from *O. punctiventer* (Tömösváry, 1885) less clear-cut than previously suspected.

Introduction

Parental investment appears both in invertebrates and vertebrates. In terrestrial arthropods, this behaviour is classified into three forms: female uni-parental (maternal) care, male uni-parental (paternal) care, and bi-parental care. There are many reports of terrestrial arthropod groups exhibiting these behavioural characteristics, among them arachnids, insects, millipedes, and centipedes (Zeh and Smith, 1985). Centipedes are a terrestrial arthropod group that plays an important role in ecosystems as top consumers in the trophic level of soil macro-invertebrates. In the case of extant orders, parental care behaviour and brooding are limited to three orders: Craterostigmomorpha, Scolopendromorpha and Geophilomorpha (Bonato and Minelli, 2002; Edgecombe and Giribet, 2007), and this behaviour has led to heightened interest in these animals. In the order Scolopendromorpha, brooding and maternal care have been reported in six genera; *Scolopendra* Linnaeus, 1758, *Cryptops* Leach, 1815, *Cormocephalus* Newport, 1844, *Scolopocryptops* Newport, 1844, *Rhysida* Wood, 1862, and *Otostigmus* Porat, 1876 (Bonato and Minelli, 2002;

Chao, 2008; Mitić et al., 2012). The scolopendrid genus *Otostigmus*, the subject of the present study, is widely distributed in tropical areas. It is a diverse group, with approximately 120 described species in three subgenera (Bonato et al., 2016). Most of them live in leaf litter, coastal forest, and rotting wood; occasionally, however, they are also found in human habitations.

Presently, there are very few reports about development and brooding behaviour of *Otostigmus*, only two species having been studied, both in the New World/African tropical subgenus *O.* (*Parotostigmus*): *O.* (*P.*) *tibialis* Brölemann, 1902 and *O.* (*P.*) *scabricauda* (Humbert and Saussure, 1870), both from Brazil. Bücherl (1971) provided succinct accounts of maternal care in these species. The mother constructs a brood chamber to lay eggs in a dark, protected area. The cluster of eggs consists of 15–30 individuals, of yellowish colour, and 1–2 mm in diameter. During brooding, the mother remains coiled around the hatchlings until the young leave. Machado (2000) gave a more detailed account of brooding by *O. scabricauda* based on a sample of three egg clusters and six first instar hatchling clusters.

In this paper, we present observations on maternal care behaviour and the brooding period in natural habitats for *Otostigmus* in Thailand. The documented species is *Otostigmus spinosus*, originally described from Java and until now known from eastern India, Burma, Vietnam, Peninsular Malaysia, Singapore, and Indonesia (Sumatra and Krakatau as well as Java) (Schileyko, 2007; Lewis, 2010d). It is reported here for the first time from Thailand and Laos. The aims of this study are to describe maternal care during the brooding period and to provide comparative data for some external morphological characters between hatchlings and their mothers to clarify changes in taxonomic characters during post-embryonic development. Also, the distribution and description of Thai *O. spinosus* are given based on the range of variation in traditionally employed taxonomic characters for *Otostigmus*. Variability in these characters creates problems for taxonomists to identify the limits of species within this species-rich genus. Some taxonomic characters may be affected by such factors as geographic and individual variation, regeneration, and changes through growth (Lewis, 1978).

Material and methods

Specimen collection

Centipedes were collected and observed in natural habitats throughout Thailand during 2012–2013. In the field, hand sorting was used to collect and characteristics of the animals' habitats were recorded. GPS coordinates for each locality are provided. Collected specimens were fixed in 95% ethanol and are housed in the Chulalongkorn University Museum of Zoology, Bangkok (prefix CUMZ).

Behavioural study

Behaviour was recorded and photographed only in natural habitats. Behavioural postures were recorded during the first 15 minutes after discovering animals in a brood chamber. Video recording was performed by using DSLR and pro-compact digital cameras (Nikon D700 and Canon G12). After observation, most of the brooding centipedes were collected and preserved in 95% ethanol. Descriptions of parental care are given. A brooding behaviour scheme of *O. spinosus* was made by integrating data from our observations and comparing with previous behavioural literature on Scolopendridae.

Systematics and comparative morphological studies

Taxonomic study has been conducted with reference to standard monographs (Attems, 1930a) and the most recent revisions (Lewis, 2010). Nomenclature for taxonomic characters is based on standard terminology for centipede external morphology (Bonato et al., 2010). Specimens from Thailand were compared with specimens deposited in the Natural History Museum, London, and also compared with holotype descriptions in recent revisions of *Otostigmus* species. Drawings were made to depict variability in taxonomic characters of all atypical specimens. For comparative study, traditional taxonomic characters of this species have been recognised and compared between the mother and hatchlings. Developmental stages of hatchlings have been recorded and identified by using previous literature on post-embryonic development of Scolopendridae. Variable characteristics have been recorded and photographed by using the Cell'D© program connected with an Olympus stereomicroscope.

Results

Description of broods and maternal care behaviour

The patterns of development of scolopendrids have been described using different schemes. Drawing upon *Scolopendra cingulata* and *S. dalmatica*, Heymons (1901) recognised a first embryonic stadium, a foetus or intermediate stadium, and an adolescent stadium, based on observations on molting. Subsequently, Lawrence (1947) divided the phase of maternal care in *Cormocephalus multispinus* into two parts that consist of six stages, these comprising three embryonic stages and three adolescent stages based on morphological characteristics (summarized by Lewis, 1981). The same six stages were described for *Cormocephalus anceps* by Brunhuber (1970).

Six broods of *O. spinosus* were found in this survey (Fig. 4.2A–F). Dates of collection are as follow: brood A (9 October 2012); brood B (10 October 2012); broods C–F (9 August 2013). Their habitats are diverse, including under broken roof tiles near a residential resort (brood A), under a clump of moss (brood B), and under coconut shells on the soil surface near human habitats (broods C–F). All collecting localities are located in the southern part of Thailand which had very high humidity and storms on some occasions. The distribution and schematic of brooding behaviour of *O. spinosus* in Thailand are given in Figs. 4.1 and 4.4, respectively.

Brood A (Fig. 4.2B): After clearing the surface of the brood chamber, we found hatchlings, with morphology corresponding to the second adolescent stage sensu Lawrence (1947) (see Table 4.1 for morphological comparison of the mother and adolescents). The mother (body length 26 mm) was coiled around a brood of 19 hatchlings. When disturbed she moved to find a new place to hide in an adjacent area, leaving the hatchlings two or three times. The mother subsequently returned and carried the hatchling cluster to the new place using her forcipules (Fig. 4.3D) and anterior legs to hold part of the hatchling cluster under her head and the ventral side of her body (Fig. 4.3E). All individuals were collected but the cluster of hatchlings had already dispersed and some had disappeared, with only six hatchlings and the mother surviving. The disappearance of hatchlings suggests filial cannibalism, as has been directly observed in brood F (see below).

Brood B (Fig. 4.2A): The hatchlings in this brood were at the third embryonic stadium (sensu Lawrence, 1947), covered by egg shell (see brood E for description). There were 27 hatchlings in the brood chamber with their mother (Fig. 4.2A). The mother exhibited body posture as an S-shape over the upper part of the hatchling cluster (Fig. 4.3C). She occasionally exhibited falcate coiling (Fig. 4.3B) or simple loop coiling (Fig. 4.3A) around the hatchlings, and adjusted their position on her ventral surface using the forcipules. After observation, five hatchlings were collected, the remainder being returned to the brood chamber.

Brood C (Fig. 4.2C): This brood consisted of 19 cleavage stage eggs. All of them were coated with thin, sticky mucous that combined all together as a massive cluster. The mother (body length 32 mm) nestled her eggs and carried the egg cluster under her body using locomotory legs. The mother’s posture switched between a simple loop and an S-shape.

Brood D (Fig. 4.2D): The hatchlings were at the first adolescent stage. They are white in colour, and the antennae have scattered, short setae. Coxosternal teeth, paramedian sutures on the tergites and sternites, spurs on the locomotory legs and ultimate legs, and the coxopleural process spines are undeveloped. The posture of the mother (body length 33 mm) was a simple loop for the first five minutes after exposure of the nest; subsequently, S-shape posture and falcate coiling were exhibited. Subsequently, the mother moved to find a new location. The cluster of hatchlings (20 individuals) was moved to the ventral posterior part of her body. Locomotory and ultimate legs were used to reposition and protect the hatchling cluster during the search for a new nest position.

Brood E (Fig. 4.2E): This brood contained 21 hatchlings at the third embryonic stage, as was brood B. The number of antennal articles is consistently 17, the tergites and sternites are fully segmented but weakly sclerotised and colourless, the ocelli are distinct but unpigmented and the legs are articulated but lack pretarsal claws. The mother (body length 36 mm) surrounded the hatchling cluster in an S-shape posture. Most of the hatchlings were covered by the ventral side of the mother’s body but two of them had been separated from the brood.

Brood F (Fig. 4.2F): The mother (body length 35 mm) exhibited S-shape posture, partially covering the eggs. The eggs were at the first embryonic stage (sensu

Lawrence, 1947), 16 eggs being present. The eggs lay on the soil surface for a while and afterwards the mother used the forcipules to collect them under her body and coil round them. The mother displayed filial cannibalism, eating some embryos after recollecting the cluster (Fig. 4.3F).

Taxonomy

Family Scolopendridae Leach, 1816
Subfamily Otostigminae Kraepelin, 1903
Genus *Otostigmus* Porat, 1876

Type species. *Otostigmus carinatus* Porat, 1876; by subsequent designation of Pocock (1891).

***Otostigmus spinosus* Porat, 1876**
(Figs. 4.5, 4.6)
Otostigmus spinosus Porat, 1876: 22
Branchiotrema nitidulum Tömösváry, 1885: 26, table 3, figs. 19, 20
Otostigmus spinosum: Haase, 1887: 71, Taf. 4, fig. 70a–d
Otostigmus spinosum ab. *hirtipes* Haase, 1887: 71, Taf. 4, fig. 71a–c
Otostigma spinosum: Pocock, 1891b: 414; Pocock, 1894: 312
Otostigmus spinosus: Kraepelin, 1903: 116, fig. 53; Kraepelin, 1904: 247; Attems, 1930a: 152, fig. 182; Attems, 1930b: 118; Verhoeff, 1937: 212; Chamberlin, 1939: 3; Chamberlin, 1944: 1; Lewis, 1991: 340, figs. 11–14; Khanna, 1994: 467; Lewis, 2001: 37, figs. 75–78; Khanna, 2001: 206; Schileyko, 2007: 81, fig. 5; Lewis, 2010: 6, figs. 8–13
nec *Otostigmus* (*O.*) *spinosus*: Lewis, 1982: 365, figs. 25–31; Lewis,1984: 37, fig. 3.15

Type locality. Indonesia: Java.

Distribution. Java, Sumatra, New Guinea, Burma, Laos, Thailand, Vietnam, Malaysia, India?

Material examined. Malaysia: BMNH 1898.9.15.75–76 general collection, 2 of 3 specimens in tube labeled “Otostigmus sp.” from Penang. Laos: CMUZ 00232, one specimen from Ban KraSom, Attopue, Laos (15°0'27.2" N 106°51'14.6" E). Thailand: CUMZ 00224, one specimen from Wat Tham Wararam, Phanom district, Surat Thani (8°53'2.7" N 98°40'1.4" E). CUMZ 00228, two specimens from Khao Sok, Phanom district, Surat Thani (8°53'37.3" N 98°33'107" E). CUMZ 00225, five specimens from Wat Kerewong, Thap Put district, Phang-nga (8°31'54.8" N 98°34'37.8" E). CUMZ 00226, one specimen from Sairung waterfall, Takua Pa district, Phang-nga (8°44'28.3" N 98°16' 43.1" E). CUMZ 00231, 53 specimens from Surin islands, Phang-nga (9°26'41" N 97°53'30.3" E). CUMZ 00230, one specimen from Sichon district, Nakhon Si Thammarat (9°5'31.4" N 99°54'23.2" E). CUMZ 00229, three specimens from Tham Wang Thong, Khuan Khanun district, Phatthalung (7°40'53.5" N. 100°0'56.6" E.). CUMZ 00223, one specimen from Tham Sumano, Srinagarindha district, Phatthalung (7°35'11.9" N 99° 52'3.2" E), CUMZ 00227, one specimen from Huaito waterfall, Khao Phanom district, Krabi (8°13'35.5" N 98°53'2.5" E).

Diagnosis. 17–22(24) antennal articles, basal 2.3–2.8 articles glabrous dorsally. Forcipular coxosternum with 4–6 main teeth. Forcipular trochanteroprefemoral process with one apical and two inner teeth. Tergite surface smooth, without keels, but with scattered small spines or setae; paramedian sutures starting from TT4–7 and complete margination from TT7–15. Tergite of ultimate leg-bearing segment with or without depression. Sternites with incomplete paramedian sutures occupying 10–30% of anterior part of sternite, posterior part with shallow depression. Posterior margin of sternite of ultimate leg-bearing segment concave, lateral margins converging. Coxopleural process with one to three apical spines, one sub-apical or none, one lateral or none, and one dorsal spine. Ultimate legs long and slender, spine formula on prefemur VL-4 or 5, VM-2–4, M-2–5 and DM- 1–4 (including corner spine). Locomotory legs with two accessory spurs; legs 1–3 to 1–5 in equal frequency (rarely 2, 6 or 7) with two tarsal spurs, legs 5–21 (rarely 3, 7 and 8) with one tarsal spur. One tibial spur on legs 1–3 (rarely leg 4). Femoral spur only on leg 1. Dorsal side of leg 20 with one spine at end of prefemur.

Description. Maximum body length approximately 38 mm. Body colour of living animal greenish black except tergite of ultimate leg-bearing segment, which is reddish black. Trochanteroprefemur yellowish white or light brown. Legs light blue or purple except prefemur, which is light yellow. Cephalic plate without sulci or sutures. Preserved specimens dark purple. Antennae with 17–22 articles, 24 articles in one specimen. Basal 2.5–2.8 articles glabrous dorsally; atypically 2.3. Basal 2.5–2.8 articles glabrous ventrally. Antennae reach segments 4–6 (5 or 6 in large specimens). Forcipular trochanteroprefemoral process bearing one apical and two inner teeth (rarely 3). Coxosternal tooth-plate wider than long with 4, 5 or 6 main teeth in equal frequency (rarely 3 or 7), separated into two groups; inner three or four teeth usually fused and outer 1 or 2 acute, basal part with one transparent, fine seta on each side, atypically with 1 transparent spine and 2 small spines in a depression. One specimen shows an abnormal condition with both tooth-plates fused together. Coxosternum lacking median suture in some specimens, median diastema reaching to base of tooth-plate, connecting with basal oblique sutures. Angle of basal oblique sutures ca 105–110°. Telopodite 2 of second maxilla with one strong transparent spine on each side.

First tergite overlapping cephalic plate, without transverse sulcus. Tergites with paramedian sutures complete from TT5 to 6 (rarely TT7); margination typically starting on TT11 to 15 (atypically TT9–10). Tergite surface with oblique suture anteriorly on TT3 to 5 and with paramedian sulci on TT3 or 4 to 18 (to TT19 to 20 in large specimens). Tergite of ultimate leg-bearing segment usually with median furrow on posterior part (rarely absent). Sternites with short paramedian sutures on anterior part, occupying 10–30% length of sternite. Surface of some sternites with small scattered setae and depressions grouped in triangular arrangement (one atypical specimen with depression continued behind end of paramedian suture), all mostly found on posterior part of sternite. Sternite of ultimate leg-bearing segment with sides converging posteriorly, posterior margin concave (one specimen with depression on surface). Oval spiracles present on segments 3, 5, 8, 10, 12, 14, 16, 18 and 20. Coxopleural process moderately long with two apical spines (rarely 1 or 3), one subapical spine or none, one to two lateral spines or none, and one dorsal spine or none. Coxopleura with dense pore field covering whole area except on ventro-distal part of coxopleural process, pore-free area on coxopleural process extending 50–70%

length from distal part to the margin of sternite of ultimate leg-bearing segment (Fig. 5I). Ultimate legs long and slender with ratios of lengths of prefemur and femur 6:4, tibia and tarsus 2 1.5:1; tarsus 1 and tarsus 2 03:2. Prefemoral spines in four rows, formula VL-4–5 (rarely 2, 6 and 7), VM-3–4 (rarely 1 or 2), M-2–5 (usually 4), DM-1–4 including corner spine (rarely 5 or 6).

Locomotory legs with or without short setae, usually legs 1–5 with two tarsal spurs (rarely 1–2 or up to 6 and 7), the subsequent legs to 21 with one tarsal spur. One tibial spur on legs 1–2 or 3 in equal frequency (rarely 1–4). Leg 1 with femoral spur (rarely absent). Two accessory spurs and pretarsal claw present on all legs. Dorsal part of prefemur of leg 20 with one spine at the margin of prefemur (atypically found only on one side). Anterior face of leg 20 in some males with a short, rounded, variably depigmented projection on distal end of tarsus 1 (Fig. 6I); similarly proportioned projection on tarsus 1 of leg 21 in two of four specimens with a projection on leg 20; projections most strongly developed in the largest specimen.

Remarks. The taxonomic status of *O. spinosus* and *O. punctiventer* Tömösváry, 1885 is still unclear, the two species possessing the synapomorphic character of a distal prefemoral spine on leg 20. In this study, we found that the range of variation of some taxonomic characters in O. spinosus to overlap with the description of *O. punctiventer* sensu Lewis, 2010 (see Table 4.2). Moreover, the geographic distributions of *O. punctiventer* and *O. spinosus* overlap at least on peninsular Malaysia. For these reasons, the identification based on morphology of *O. spinosus* and *O.punctiventer* is complicated and needs to be reassessed. The nominate subspecies of *O. spinosus* is recognised in this work; *O. spinosus spinosus* Porat, 1876 and *O. spinosus nannus* Chamberlin, 1939 are currently valid subspecies, though the latter has been questioned as possibly being based upon a juvenile specimen of *Ethmostigmus rubripes spinosus* (Newport, 1845) (Schileyko and Stagl, 2004). The type locality of *O. spinosus nannus* is Doormanpad, Irian Jaya/West Papua (New Guinea). We found one specimen of *Otostigmus* in the NHM from Mimika River, Irian Jaya, that we identified as *O. spinosus* but its associated label indicated affinities to *O. punctiventer*.

In Thailand, *O. spinosus* is widespread throughout the southern part of the country (Fig. 4.1). In all localities this species was found together with other

Otostigmus species such as *O. multidens*, *O. rugulosus*, *O. astenus*, and *O. scaber*. As some taxonomic characters, such as the range of appearances of tibial and tarsal spurs on the locomotory legs, number of antennal articles, and numbers of apical and lateral spines on the coxopleural process are variable (Table 4.1), there can be problems in determining species. On some occasions we found animals in which the spine on the prefemur of leg 20, a diagnostic character, was absent on one side. The characteristic of leg 20 (and variably 21) bearing a distal projection on the anterior face of tarsus 1 is apparently unique to this species and, with the data at hand, appears to be a secondary sexual characteristic. The three specimens possessing this feature that exhibit the genital segments are all males and its elaboration with growth is consistent with it being sex-specific. Other Otostigminae have distal processes on different articles of the ultimate leg-pair in males, e.g., on the inner side of the femur in *Digitipes* Attems, 1930, and on the inner side of the tibia in *Otostostigmus* (*Parotostigmus*) *tibialis* Brölemann, 1902. The inconsistency of taxonomic characters may be problematic when it involves the purported diagnostic characters of species and may lead to misidentifications. Molecular data could assist with revaluating species delimitation in the *Otostigmus rugulosus* group (sensu Lewis, 2010).

Variation and development of taxonomic characters

In this study, we found two broods that belong to adolescent stages that permitted investigating the development of some taxonomic characters. In hatchlings in brood D, an early first adolescent stage, most taxonomic characters are incompletely developed. Contrastingly, in the four surviving hatchlings of brood A, some taxonomic characters (including some species-diagnostic characters) are fully developed. Our observations reveal that some traditional taxonomic characters such as number of antennal articles, number of glabrous articles, and number of apical spines on the ultimate leg coxopleuron vary during the life span. A distinguishing character of this species (the prefemoral spine on leg 20) is strongly fixed, being conserved between the mother and second adolescent stage hatchlings except in one specimen (see Table 4.2) presumably due to abnormal development. Colouration differs between young and the mother; hatchlings show a very light yellowish or brown and magenta colour whereas others are dark greenish brown.

Discussion

Otostigmus spinosus exhibits similar hatching and maternal care to other scolopendromorphs. The season in which eggs are laid and brooded varies between different geographic regions, presumably affected by factors such as humidity and temperature. The Neotropical *O. scabricauda* seems to start brooding in early October (Machado, 2000) while *O. spinosus* in Thailand exhibited this behaviour during June–July. In contrast to a debate over whether the mother broods with dorsal or ventral side towards the brood in Geophilomorpha (Bonato and Minelli, 2002; Edgecombe et al., 2010), the position of the mother's body coiling around the cluster of hatchlings is conserved across all families of Scolopendromorpha. The benefit of this brooding posture has been demonstrated in experimental study of *Scolopendra cingulata* Latreille, 1829 (Radl, 1992). That study showed that eggs or hatchlings cannot develop without their mother coiling around them, and survival efficiency of hatchlings decreases when they are separated from the mother. Development of embryonic stages in scolopendrids has been described in a few previous works (Heymons, 1901; Lawrence, 1947; Lewis, 1981). In this study, we found stages corresponding to first (brood D) and the second adolescent stages (brood A) and the first (brood F) and third embryonic stages (broods B and E) as described by Lawrence (1947, 1984). The number of segments is fixed at 21 in all studied specimens, conforming to epimorphic development. Bücherl (1971) described the cluster of eggs in *O. tibialis* and *O. scabricauda* numbering 15–30 in each brood, and for *O. scabricauda* Machado (2000) observed a range of 16–58 (mean 29.1) for nine broods. In this study we found 19, 27, 19, 21, 20, and 16 eggs or adolescents in broods A–F, respectively. Body size of adults differs substantially between these three species, with *O. spinosus* having a body length of 38 mm (holotype description 45 mm.), *O. tibialis* 80 mm, and *O. scabricauda* 70 mm (Attems, 1930a; Lewis, 2010). This demonstrates that size of the mother does not appear to influence reproductive efficiency.

Embryonic development has been a focus of developmental biologists studying gene expression during differentiation and growth of centipedes (Brena and Akam, 2012). However, development in taxonomic characters during the life span of these animals still lacks data for many species, although some variation during post-embryonic development has been documented for species of *Otostigmus* and *Scolopendra* by Lewis (1968, 2000). In our study, the results support previous records that some taxonomic characters change during post-embryonic development, among them length of the coxopleural process, number of spines and the arrangement of spines on the coxopleural process, the presence of paramedian sutures on the sternites and tergites, tergite margination, and number of antennal articles. Filial cannibalism has now been confirmed in *O. spinosus* (direct observation of the mother consuming the eggs in brood F, and suggested by the disappearance of hatchlings in brood A in the laboratory), as has been observed in other scolopendromorphs (Brunhuber, 1970; Lawrence, 1984), including *O. scabricauda* (Machado, 2000). This phenomenon has been reported throughout the animal kingdom when parents and their young live together in high selective pressure environments such as high predation, limited feeding and poor environment, which influence survival efficiency of the hatchlings and parent (Klug and Lindstrom, 2008; Chin-Baarstad et al., 2009). Understanding on behaviour and development of scolopendrids contributes to knowledge of their biology and ecology. Moreover it clarifies problems involving variability of morphological characters and thus contributes to an improved classification of the group.

Acknowledgements

We would like to thank all members of the Animal Systematics Research Unit and Department of Biology, Faculty of Science, Chulalongkorn University for help during field collecting and for technical support. We thank T. Backeljau for his kindness in finding literature. We would like to express our grateful thanks to the Thai Navy and Army and The Plant Genetic Conservation Project under the Initiative of Her Royal Highness Princess Maha Chakri Sirindhorn for support and permission to collect in some restricted natural reserve areas. We are grateful for financial support from the Thailand Research Fund through the Royal Golden Jubilee PhD Program (Grant No. PHD/0066/2553). The main funding support for this project is from The Thailand Research Fund (TRF) under TRF Senior Research Scholar (RTA 5880001) to SP. We sincerely thank faculty of Science and Graduate school for Oversea

Academic Presentation Scholarship. We give special thanks to John Lewis and Varpu Vahtera for their valuable input as referees.

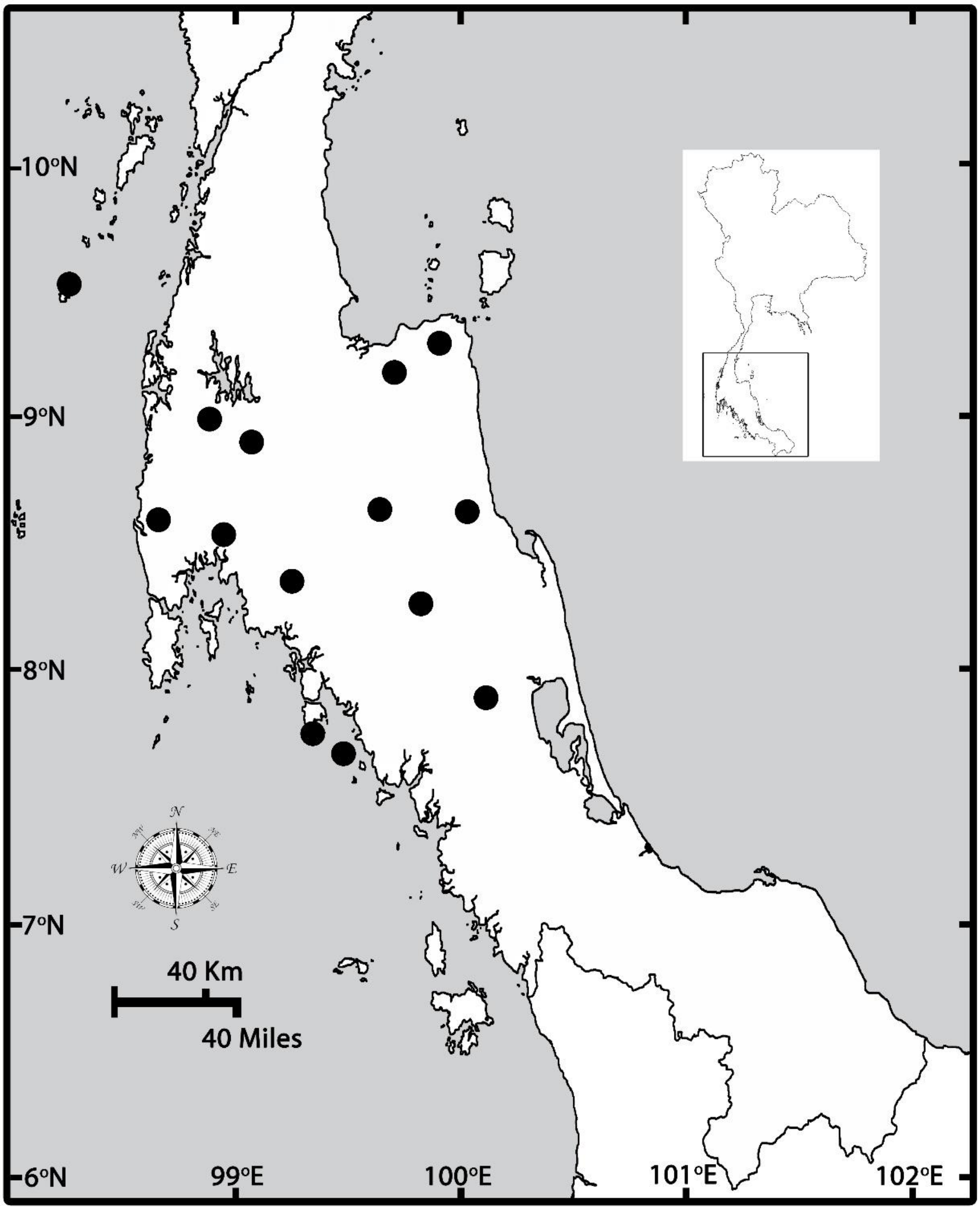


Figure 4.1 Distribution of *Otostigmus spinosus* Porat, 1876 in southern Thailand.

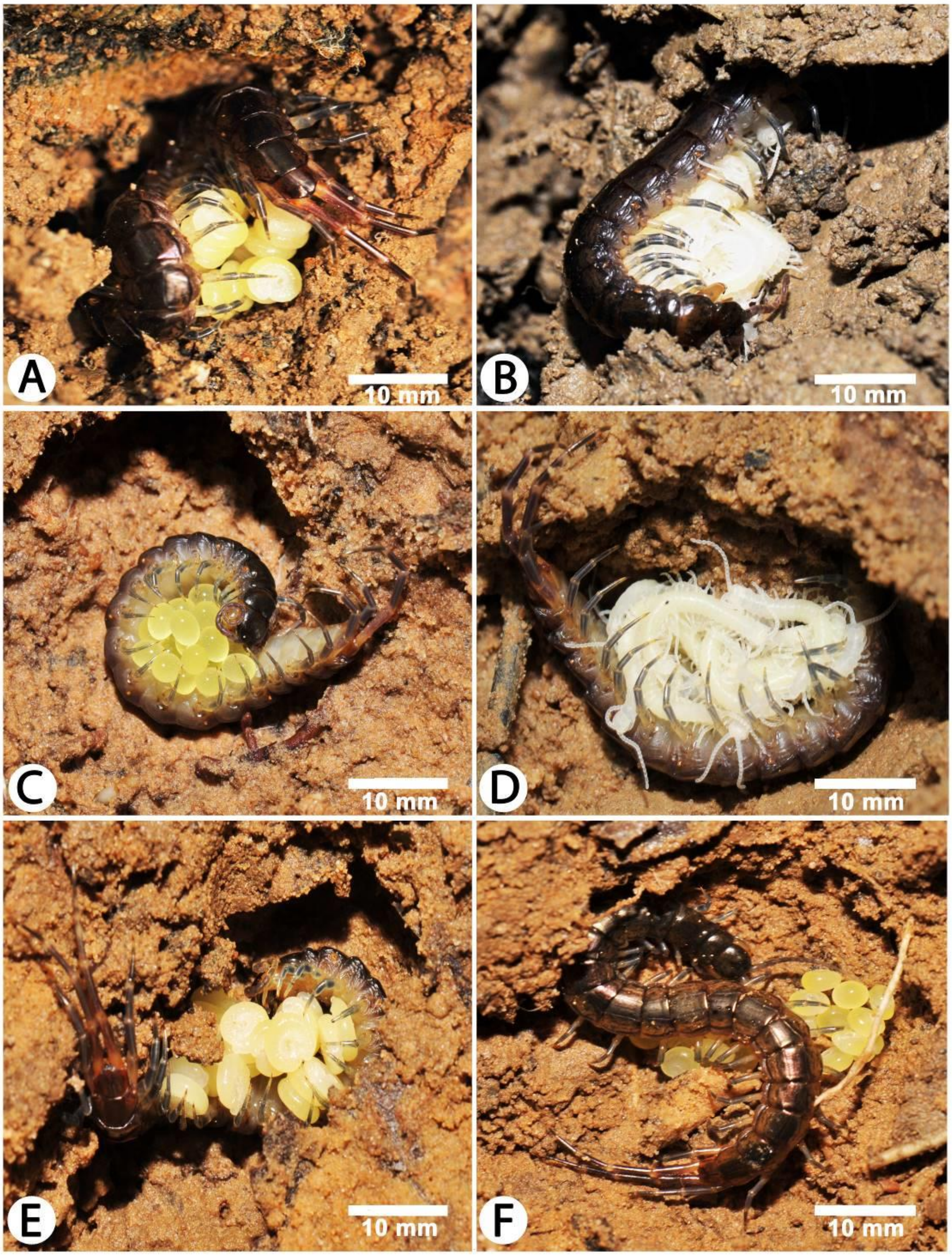


Figure 4.2 Six broods of *Otostigmus spinosus*: **A**, Brood sample from local resort near Khao Sok National Park, Surat Thani province; **B**, Brood sample from Wat Tham Wararam, Surat Thani province; **C–F**, Brood samples from Wat Tham Phung Chang, Phang-nga province.

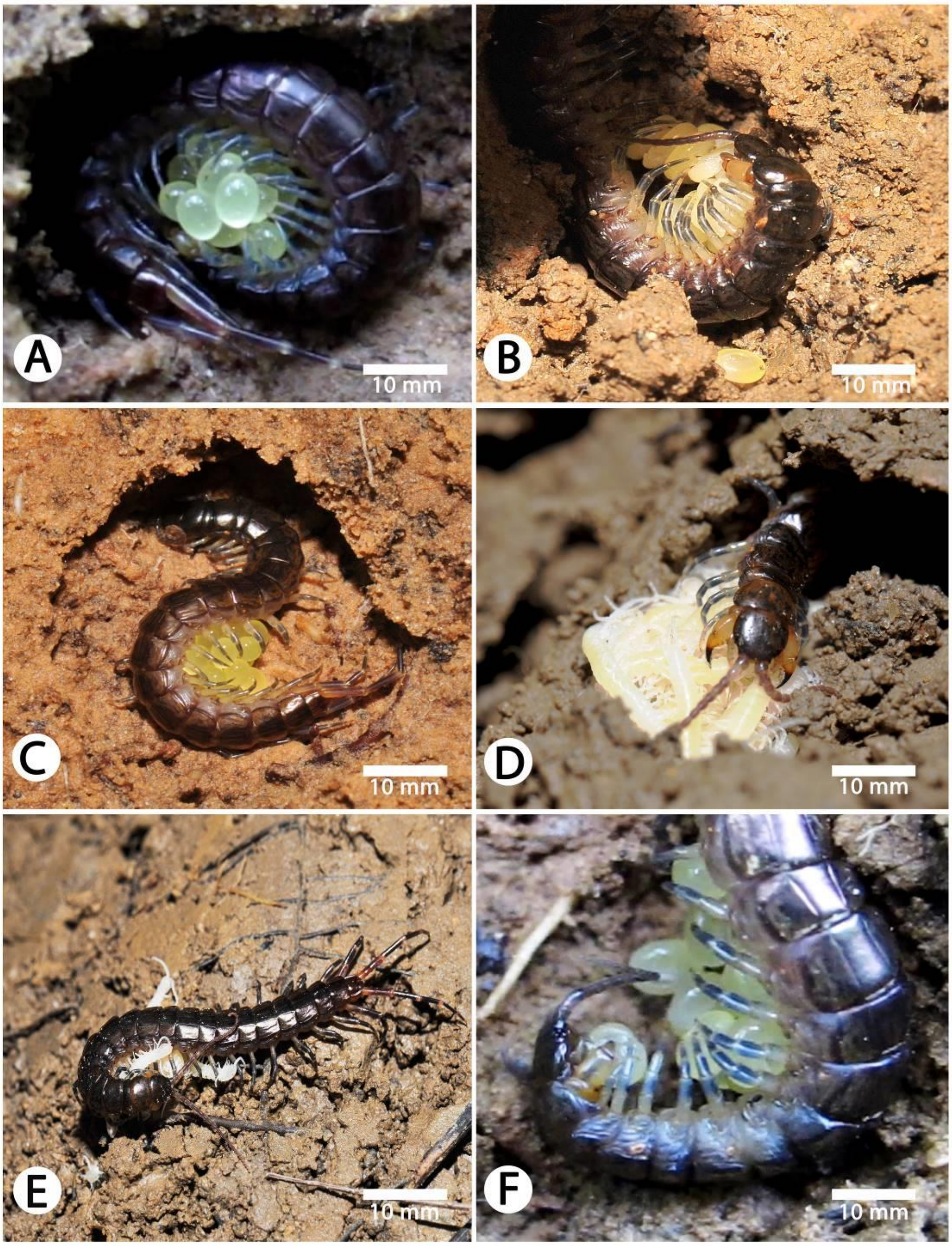


Figure 4.3 Brooding behaviour of *Otostigmus spinosus*. **A**–**C**, Orientation of mother with cluster of hatchlings; **A**, Simple loop; **B**, Falcate coiling; **C**, S-shape posture; **D**, Forcipules being used by mother to catch 2nd adolescent stage hatchlings; **E**, Mother moving and carrying cluster of 2nd adolescent stage hatchlings under her body; **F**, Mother exhibiting filial cannibalism of 1st embryonic stage.

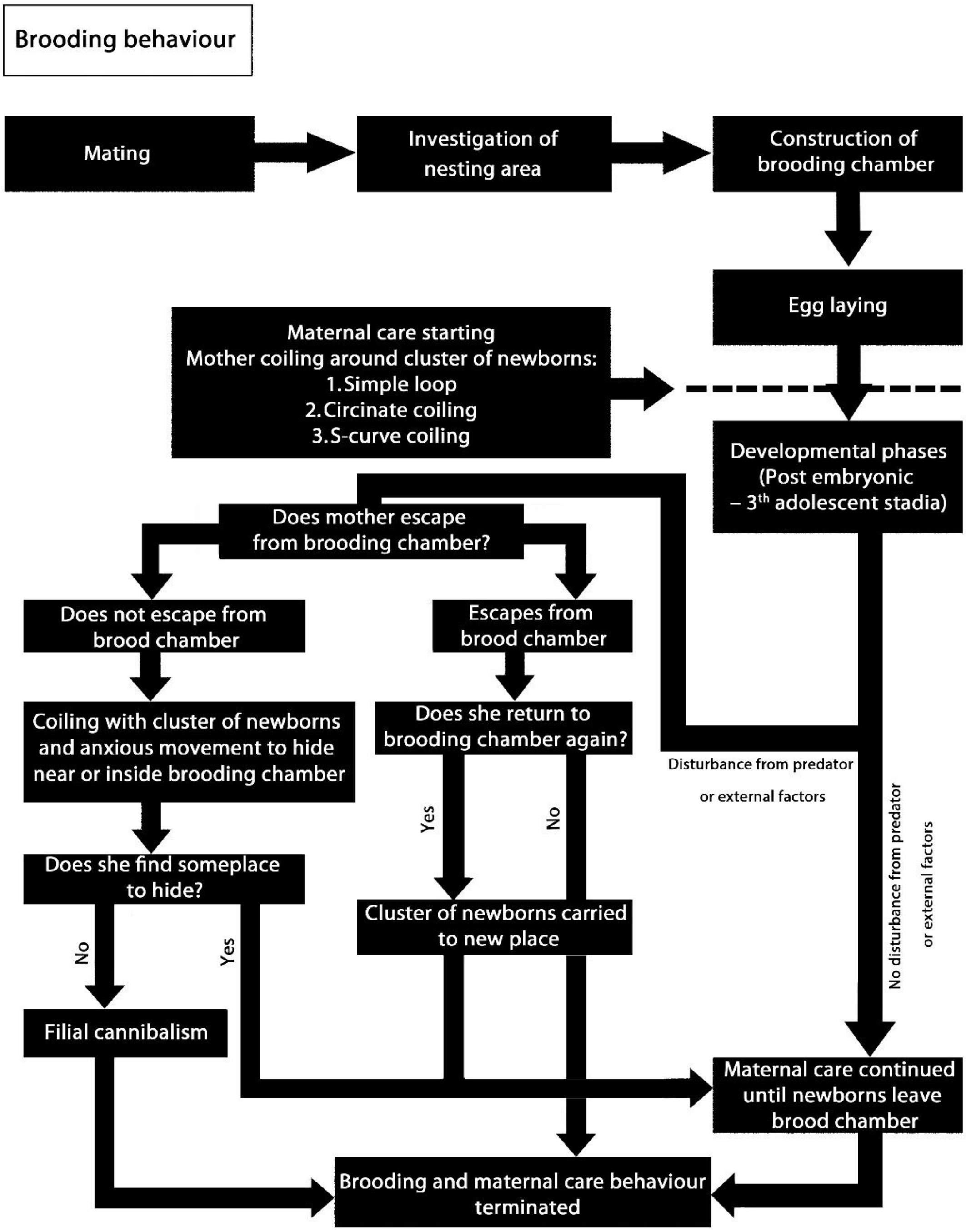


Figure 4.4 Schematic of brooding behaviour of *Otostigmus spinosus.*

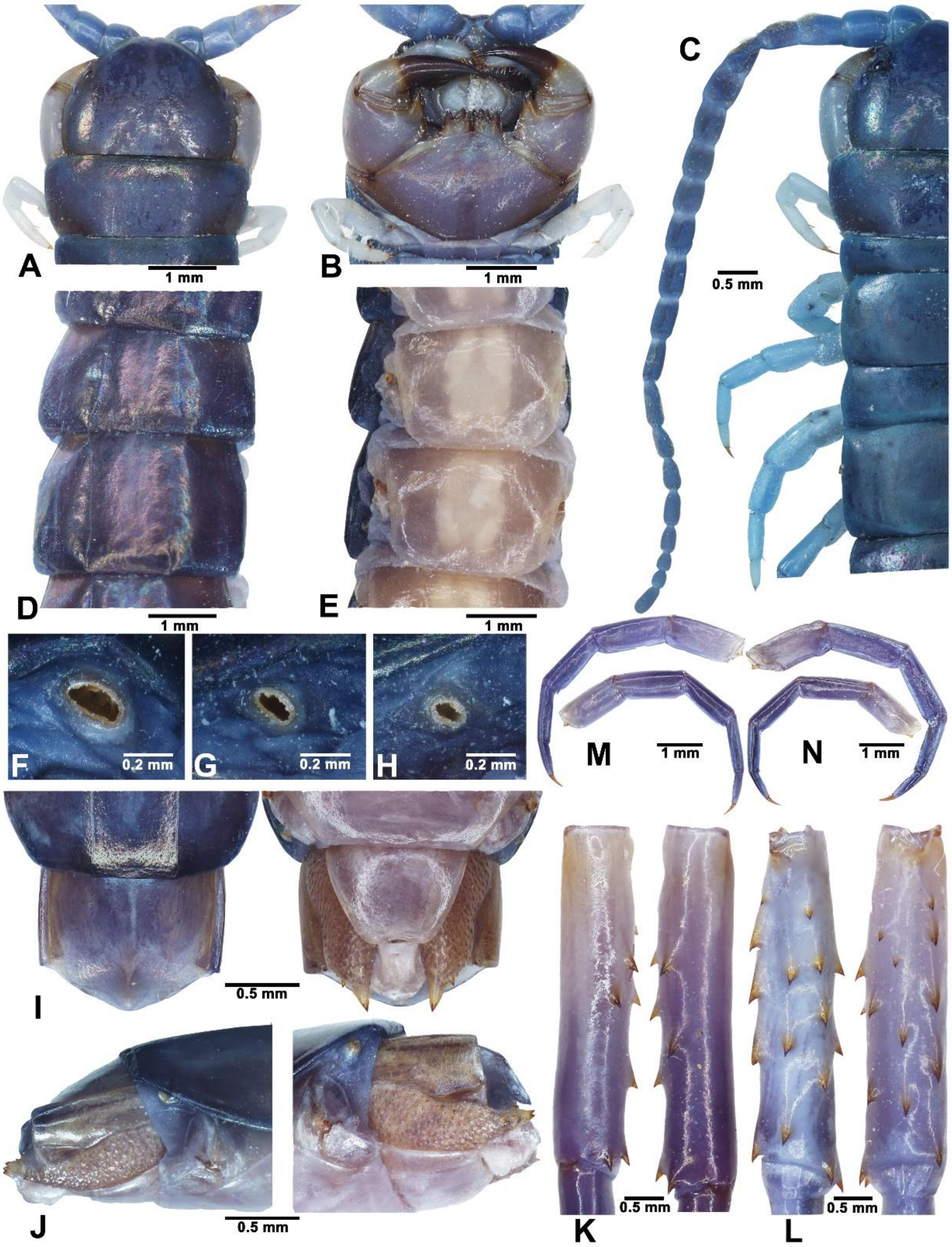


Figure 4.5 *Otostigmus spinosus* Porat, 1876. Light photographs of specimens from southern Thailand (Fig. A–E; specimens from Surin Islands, Phang-nga province: CUMZ 00231; Fig. I–N; specimens from Wat Tham Wararam, Surat Thani province: CUMZ 00224). **A**, Cephalic plate and T1 with first pair of locomotory legs; **B**, Forcipular segment; **C**, Antenna with cephalic plate and TT1–5; **D**, Tergites 9–10; **E**, Sternites 9–10; **F–H**. Spiracles on segments 3, 5 and 8, respectively; **I**, Tergite and sternite of ultimate-leg bearing segment; **J**, Pore field on left and right coxopleura; **K**, Dorsal view of ultimate leg prefemur; **L**, Ventral view of ultimate leg prefemur; **M–N**, Leg 20 left and right with spine on distal part of prefemora.

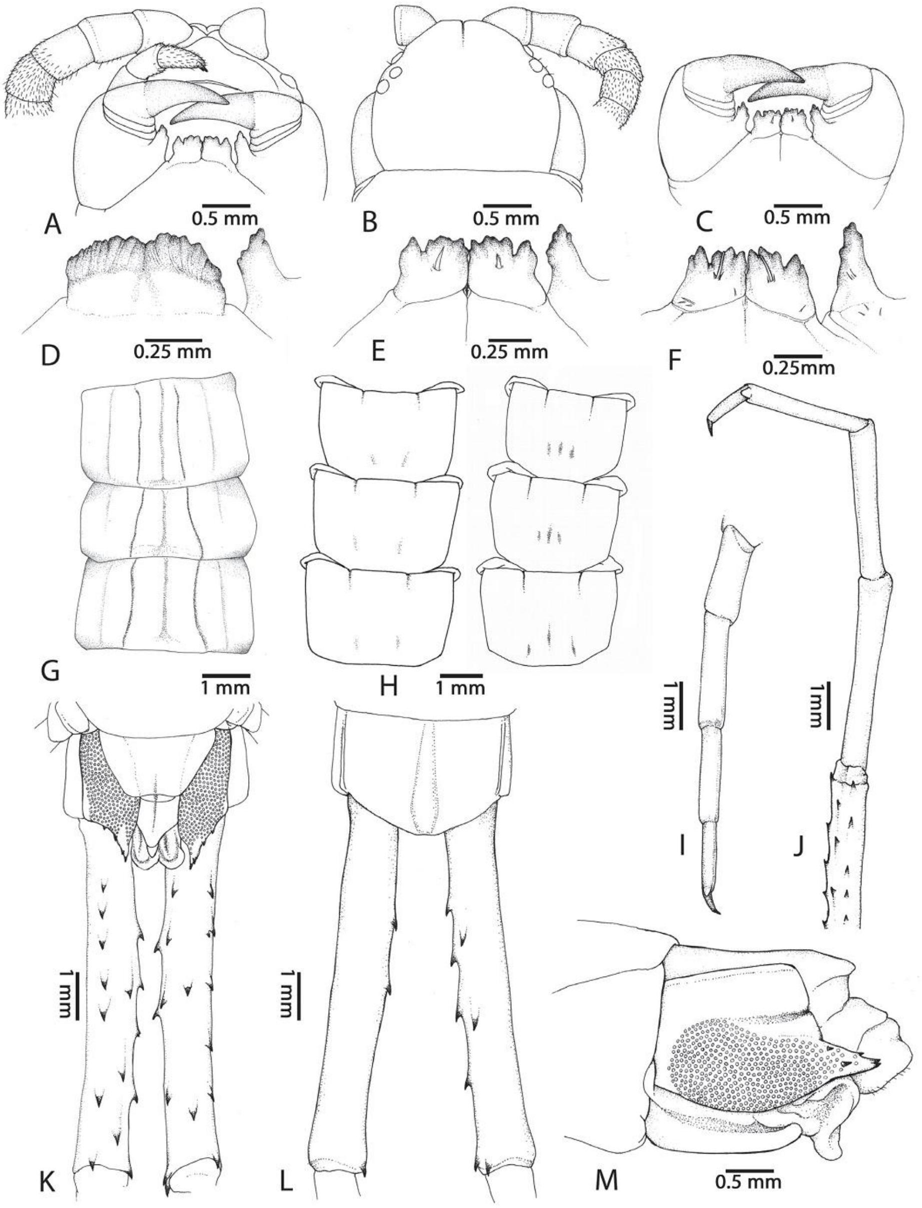


Figure 4.6 Variability in taxonomic characters in *Otostigmus spinosus* Porat, 1876 (examination materials: CUMZ 00224, Wat Tham Wararam, Phanom district, Surat Thani; CUMZ 00229, Tham Wang Thong, Phatthalung; CUMZ 00231, Surin Islands, Phang-nga). **A**, Ventral view of cephalic plate and antenna; **B**, Dorsal view of cephalic plate and antenna; **C**, Coxosternite; **D–F**, Variation in coxosternal teeth; **G**, Surface of TT5–7; **H**, Variability of depressions on surface of sternites 5–7; **I**, Leg 20 with projection on distal end of tarsus 1; **J**, Leg 21 with projection on tarsus 1; **K**, Ultimate leg-bearing segment, ventral view, with arrangement of ventral spines on prefemur of ultimate legs; **L**, Tergite of ultimate leg-bearing segment with arrangement of dorsal and corner spines on prefemur of ultimate legs; **M**, Pore field on coxopleuron (left).

Table 4.1 Comparison of traditional taxonomic characters between adult female and 2nd adolescent stadium *O. spinosus* (samples from Brood A). * refers to character in damaged condition, ? refers to unclear character

Taxonomic Characters	**Specimens**				
	Mother	**Hatchling 1**	**Hatchling 2**	**Hatchling 3**	**Hatchling 4**
No. of antennal articles	23/21	18/19	19/17	18/18	15*/18
No. of glabrous articles	2.5/2.3	2/2	2/2	2/2	2.5/2.5
No. of forcipular teeth	4+4	4+4	4+4	4+4	4+4
Paramedian suture complete from tergite No.	5	6	6	6	4
Margination starting from tergite No.	11	11	11	11	11
Sternal paramedian sutures	Incomplete	?	?	?	?
Number of apical spines on coxopleuron	2	1	1	1	2
Number of lateral spines on coxopleuron	2	2	1	1	1
Number of dorsal spine on coxopleuron	1	1	?	?	?
Length of coxopleural process	Moderate length VL-5	Moderate length V-4	Moderate length VL-4	Moderate length VL-4	Moderate length VL-
Prefemoral spine formula of ultimate leg	VL-4 VM-3 DM-2	V-2 VM-2 DM-2	V-3 VM-3 DM-2	V-3 VM-3 DM-2	V-3 VM-3 DM-2
No. of corner spines on prefemoral process of ultimate legs	2+2	1+1	1+1	1+1	1+1
Legs No. with 2 tarsal spurs	1–3	1–4	1–3	1–4	1–4
Legs No. with tibial spur	1	?	?	?	?
Leg 20 with prefemoral process	1+1	1+?	absent	1+1	1+1

Table 4.2 Taxonomic characters of *O. spinosus* from different geographic regions. ? refers to unclear character

Taxonomic Characters	Regional Area of Examined Specimens					
	Burma[1]	Peninsula Malaysia and Singapore[2]	Thailand and Laos[3]	Java and Sumatra[4]	New Guinea[5]	*O. punctiventer*[6]
No. of antennal articles	?	20–21	18–24	17–20	20–21	19–22
No. of glabrous articles	?	2.2–2.3	2.2–2.7	2.5	2.2	2–2.3
No. of forcipular teeth	?	3/3 or 4/4	3/3, 4/4, 5/5 or 6/6	4/4	4/3	3/3
Paramedian suture complete from tergite no.	?	5 or 6	5,6 or 7	5	6	5–7
Margination starting from tergite no.	?	7, 9 or 11	9, 10, 11, 13 or 15	9	9	7–9
Sternal paramedian sutures	?	Present (10–20% on anterior)	Present (10–30% on anterior)	Present	Present (20% on anterior)	20–27%
Number of apical spines on coxopleuron	?	1 or 2	1 or 2 (rarely 3)	2–3	2	1–2
Number of lateral spines on coxopleuron	?	1 or absent	1 or 2	1	1	2
Number of dorsal spines on coxopleuron	?	1–2	1	1	1	1
Length of coxopleural process	?	Long	Moderately long	?	Moderately long	Moderately long
Prefemoral spine formula of ultimate leg	?	VL-4 to 5 VM-2 to 3 M-3 to 4 DM-3	VL-2 to 7 VM-2, 3 to 4 M-2 to 5 DM-1 to 6	VL-5 VM-3 DM-5	VL-4 to 5 VM-2 to 3 M-2 to 3 DM-0 to 2	VL- 4 to 5 VM-2 to 3 M-2 to 3 DM-0 to 2
No. of corner spines on prefemoral process of ultimate legs	?	2	1–2	1	1–5	1
Leg No. with 2 tarsal spurs	?	1–2 or 1–4	1, 1–2, 1–3, 1–4, 1–5 or 1–6	?	1–3,4?,5?	1–2
Leg No. with 1 tarsal spur	Reach to 21	3, 5–21	2, 3, 4, 5, 6 or 7–21	?	6–21	?
Femoral and tibial spur on leg no.	?	1 or absent	1–2, 1–3 or only 1	?	1	?
Leg 20 with prefemoral spine	present	present	present	present	?	present

Note: Superscripts refer to cited literature and examined specimen; 1= Pocock, 1891; 2= Verhoeff, 1937; 3= Thai & Laos specimens; 4= Haase, 1887; 5= BMNH collection (1 specimen); 6= Lewis, 2010

Chapter 5

First record of the African-Indian centipede genus *Digitipes* Attems, 1930 (Scolopendromorpha: Otostigminae) from Myanmar, and the systematic position of a new species based on molecular phylogenetics

Warut Siriwut[1,2], Gregory D. Edgecombe[3], Chirasak Sutcharit[2], Piyoros Tongkerd[2] & Somsak Panha[2,4]

[1]Biological Sciences Program, Faculty of Science, Chulalongkorn University, Bangkok, Thailand
E-mail: boligozx_mix@yahoo.com
[2]Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand
E-mails: boligozx_mix@yahoo.com, jirasak4@yahoo.com, piyorose@hotmail.com and somsak.pan@chula.ac.th
[3]Department of Earth Sciences, The Natural History Museum, London, UK
E-mail: g.edgecombe@nhm.ac.uk
[4]Corresponding author

Zootaxa: published 3931(1): 071-081 (2015)

Abstract

The first Southeast Asian record of the scolopendrid centipede *Digitipes* Attems, 1930, has been collected and analyzed based on a new species from Myanmar, males possessing a distomedial process on the ultimate leg femur that is diagnostic of the genus. *Digitipes kalewaensis* n. sp., described herein, is distinguished from other members of *Digitipes* by its 2.5 to 2.7 dorsally glabrous antennal articles, an unusually long basal suture on the tooth-plates, absence of a lateral spine on the coxopleural process, and a lack of median and dorso-median spines on the ultimate leg prefemur. Maximum likelihood and Bayesian analyses of two molecular markers (mitochondrial COI and 16S rRNA) supported the proposal of a new species from Myanmar. The phylogenetic tree identifies *Digitipes barnabasi* from the Western Ghats, India, in a polytomy with members of other genera of Otostigminae (*Otostigmus*, *Ethmostigmus* and *Rhysida*) and a robust Indian-Burmese *Digitipes* clade in which *D. kalewaensis* n. sp. is resolved as sister group to a clade composed of most Indian species. Available molecular dates for the diversification of Indian *Digitipes* are consistent with introduction of the genus into SE Asia when the Indian subcontinent made contact with Myanmar in the early Palaeogene.

Key words: Scolopendridae, *Digitipes*, phylogenetics, biogeography

Introduction

The centipede genus *Digitipes* Attems, 1930, is considered as a relatively narrow-range endemic in the subfamily Otostigminae Kraepelin, 1903, being distributed only in the African and Indian regions (Jangi and Dass, 1984; Joshi and Edgecombe, 2013). The validity of this genus had been debated because it is supported by only a few unique morphological characters, the most distinctive of which are confined to one sex only (the male), and its geographic distribution overlaps with that of the widespread *Otostigmus* Porat, 1876 (Attems, 1930a, c; Lewis, 2004a). Evidence of variability in morphological characters within species of tropical scolopendromorph centipedes has been documented for several decades (Lewis, 1978, 2000) and, as discussed below, some of the purportedly diagnostic characters of *Digitipes* are among those known to be subject to variability within species. However, recent molecular phylogenetic analyses of the Indian members of Digitipes have added novel support to its recognition as a distinct genus because its species united as a monophyletic group and were separated from other genera by considerable genetic divergence (Joshi and Karanth, 2012).

The distribution of *Digitipes* is limited to former regions of Gondwana. The timing of diversification of *Digitipes* and other Indian Scolopendromorpha has been estimated using molecular dating (Joshi and Karanth, 2011; Joshi and Edgecombe, 2013). The deepest divergences within Indian *Digitipes* correspond to drift of peninsular India during the Late Cretaceous, though some speciation may post-date accretion of India to the Eurasian Plate. Furthermore, coalescent analysis predicted the distributions of populations of Indian *Digitipes*, suggesting that they may be related to habitat types based on ecological modeling (Joshi and Karanth, 2012). Molecular analyses have been used to infer the phylogenetic position of new species in some endemic centipede groups such as *Craterostigmus* (Edgecombe and Giribet, 2008; Giribet et al., 2009). Allopatric speciation driven by geographic barriers is likely to affect species' distributions in Chilopoda, although the impact of such barriers through geological time has been studied only in certain parts of the world, such as the Mediterranean (Simaiakis et al., 2012) and the Australian region (Giribet and Edgecombe, 2006). Conversely, the phenomenon of some scolopendromorphs becoming adventitious introductions or widespread species can be found in several species (e.g., Shelley et al. (2005)). The centipede diversity of Myanmar has received little attention over the past century, with only 27 species having been reported thus far (Pocock, 1891c; Attems, 1930a; Bonato et al., 2016). The Burmese centipede fauna may be allied to those known from India and Indo-China, but the reassessment of indigenous groups awaits further exploration. In this study, a new species of *Digitipes* from northwestern Myanmar is described based on traditional morphological characters. Molecular data obtained from two mitochondrial genes widely used in centipede phylogenetics are analyzed to determine the systematic position of this new species relative to Indian congeners, in the context of other genera of Otostigminae. In addition, the geographic distribution of the genus is discussed, with particular reference to molecular dating and biotic exchange between India and SE Asia.

Material and methods

Specimen collecting and identification. Centipedes were collected in 2013 and 2014 during a Myanmar-French expedition to the northwestern part of Myanmar, the Kale District, Sagaing Division (Fig. 5.1). The GPS coordinates of the type locality were recorded and the habitat type photographed. All collected specimens were fixed in 95%ethanol for morphological and molecular studies. Specimens were identified based on the classic monograph by Attems (1930a), together with previous systematic work on *Digitipes* (Jangi and Dass, 1984; Joshi and Edgecombe, 2013). Nomenclature for taxonomic characters in species description was based on standard terminology for centipede morphology (Bonato et al., 2010). Traditional morphological characters were photographed using the Cell'D© program connected and automated with an Olympus stereo-microscope. The holotype and paratypes are housed at Chulalongkorn University Museum of Zoology, Bangkok (CUMZ).

DNA extraction, amplification and sequencing. Genomic DNA was extracted from locomotory legs (legs 9and 10) using QiagenTM and GeneaidTM DNA extraction kits for tissue samples. Quality of genomic DNA was quantified using TBE-Agarose gel electrophoresis under an electromagnetic field of 135 V gradients for 20 minutes. Cytochrome c oxidase subunit I (COI) and 16S ribosomal DNA (16S rRNA) were amplified. The PCR mixture consisted of the following: 0.6-1 µl of DNA template, 2.5 µl of forward and reverse primers, 25 µl of Ultra-Pure Taq PCR Master Mix with ruby and emerald Dye (16S and COI, respectively), and 18 µl of ddH2O. The COI fragment was amplified using universal forward primers for metazoans LCO1490, and the modified reverse primer HCOoutout (Prendini et al., 2005; Schwendinger and Giribet, 2005; Murienne et al., 2010; Vahtera et al., 2012a).The partial 16S rRNA gene was amplified using primers 16Sa and 16Sb (Xiong and Kocher, 1991; Edgecombe et al., 2002). The PCR reactivation conditions for COI were performed with the reactions cycled at 94 °C for 5 min of an initial step, followed by 36 cycles of 94 °C for 30 s in a denaturation step, 41–45 °C for 40 sec in an annealing step, 72 °C for 15 s in an extension step, and then a final extension step at 72 °C for 10 min. Reactivation conditions for 16S rRNA were the same except that the annealing temperature was 45–48 °C for 30 s. The amplified PCR products were checked using 1% (w/v) agarose gel electrophoresis in 0.5x TBE buffer and visualized with SYBR Safe under a UV Tran-simulator device. DNA products were purified using a QIAquick purification kit (QIAGEN Inc.). Double-stranded amplified PCR products were directly cycle-sequenced using the original amplification primers, and sequencing reaction products were performed with an Applied Biosystems Automatic Sequencer (ABI 3730XL) at Macrogen, Inc. (Korea). The DNA sequences were aligned with sequences from GenBank by using the BLASTn algorithm to confirm the amplification products.

Phylogenetic reconstruction. DNA sequences of the COI and 16S genes were corrected in Sequence Navigator (Parker, 1997) and MEGA 6 (Tamura et al., 2013a). Chromatograms were used to detect erroneous sequences by pair-wise comparisons between each DNA sample. Phylogenetic analyses were conducted in MOLPHY ver. 32, which includes utility programs such as Kakusan 4 (Tanabe, 2007). The data preparation of FASTA, PHYLIB and NEXUS files for both molecular markers was provided in MEGA and Mesquite (Maddison and Maddison, 2011). The Kakusan 4 program was applied for the preparation of ordinary command line and molecular parameter settings before a DNA substitution model test. All sequences were aligned and edited in MEGA 6. Available Indian *Digitipes* sequences from previous molecular works (Joshi and Karanth, 2011, 2012) were downloaded from GenBank together with other selected scolopendrids for appropriate outgroup rooting (Table 5.1). Sequences of species of the genera *Otostigmus*, *Rhysida* Wood, 1862 and *Ethmostigmus* Pocock, 1898 were used to test relationships within the subfamily Otostigminae. A specimen of *Scolopendra morsitans* (Linnaeus, 1758) from Thailand was sequenced and used for outgroup rooting for both ML and BI analyses. Nucleotide substitution was modelled with Jmodel test (Guindon and Gascuel, 2003; Darriba et al., 2012) based on Neighbour-Joining tree analysis using four nucleotide sequences and nucleotide bases combined as 1st+2nd+3rd+non-coding codons. All positions containing gaps and missing data were eliminated. Each gene fragment was analyzed independently with a fitted substitution model to improve tree accuracy. The combined sequences for all gene fragments were used in the final analysis to estimate the phylogenetic position of all available *Digitipes* species. For the Maximum likelihood criterion, the aligned sequences in an interleaved PHYLIP file format were analyzed in PHYML 3.0 (Guindon (Guindon et al., 2010) et al. 2010) and POY (Varón et al., 2010). A GTR plus Gamma distribution and irreversible substitution model were observed to be the best fit maximum likelihood model, supported by the lowest Bayesian Information Criterion score and Maximum Likelihood value. 16 nucleotide substitution rate categories were used with estimated gamma shape parameters. BIONJ was implemented for tree search under SPR and NNI tree improvement methods, with tree topology and branch length optimized. The fast likelihood-based analysis was performed under 1,000 bootstrap pseudo-replicates. As an alternative phylogenetic analysis,

Bayesian inference was also undertaken. The Nexus file was extracted from Mesquite and analyzed with MrBayes ver. 3.3.2 (Huelsenbeck and Ronquist, 2001b). The analytical parameters were settled and analyzed under 10,000,000 pseudoreplicates. The execution files of each DNA fragment consisted of four Metropolis-Coupled Markov chains with a random starting tree topology. Sixteen nucleotide substitution rate categories and an invisible gamma criterion were used. To avoid tree topology convergence effects, 50% of tree yields were removed as burn-in. Simultaneous trees were sampled every 1,000 random replicates, and runs were terminated after the standard deviation of portioning frequency value reached 0.01. A 50% majority rules consensus was used to interpret the tree topology in the final stage, and the posterior probability values of clades taken as a measure of support for the tree. Tree topologies in each analysis were viewed with the programs FigTree and TreeView. In each topology, branches were regarded as reasonably supported when bootstrap values and posterior probabilities exceeded 70% in ML or 0.95 in BI, respectively (Huelsenbeck and Hillis, 1993; Larget and Simon, 1999).

Results

Systematics

Family Scolopendridae Leach, 1816

Subfamily Otostigminae Kraepelin, 1903

Genus *Digitipes* Attems, 1930

Digitipes Attems, 1930a: 167; 1930b: 291.

Type species. *Digitipes verdascens* Attems, 1930, by monotypy.

Composite description. 16–18 antennal articles, 2.5–3.5 articles glabrous dorsally. Cephalic plate with anterior median sulcus that may be posteriorly bifurcated. Forcipular coxosternite without median suture. Tooth-plate wider than long, with four teeth on each side separated into two groups of two lateral and two median teeth. Trochanteroprefemoral process bearing one apical tooth and two or three inner teeth.

Tergite 1 overlapping cephalic plate, without transverse sulcus or suture. Tergites with or without keels; oblique suture starting from T4 or 5 to T19. Paramedian sutures complete from at least TT 7 to 20. Tergite margination usually starting at least from T5; exceptionally only tergite of ultimate leg-bearing segment marginated. Tergite of ultimate leg-bearing segment with convex lateral margins. Sternites with small punctae, occasionally with median sulcus; depressionlike pits on posterior part of sternite. Paramedian sutures at least 10% length of sternite, nearly complete in a few species. Sternite of ultimate leg-bearing segment trapezoidal, with sides converging posteriorly.

Coxopleural process short to moderately long, with two apical spines, one lateral spine or absent, dorsal spine absent. Pore-field on lateral part of coxopleuron extending to dorsal margin or terminating beneath that margin. Spine formula on ultimate leg prefemur: VL 1–4 or absent, VM 1–5 or absent, M 0–1 and DM 1–2 or absent. Locomotory legs usually with two tarsal spurs on at least legs 1–3, usually one tarsal spur on legs 4–20. Tibial and femoral spur on leg 1 or absent. Male with blunt conical distal process on ultimate leg femur; shallow longitudinal furrow along medial surface of femur terminating at the process. Spiracles rounded or oval, on segments 3, 5, 8, 10, 12, 14, 16, 18 and 20.

Remarks. *Digitipes* is similar to the widespread, mostly tropical genus *Otostigmus* in most respects, but three distinguishing characters were proposed (Attems 1930b). Most noteworthy is the distal process on the ultimate leg femur that is present in males of *Digitipes* but is absent in *Otostigmus*. Attems also considered the absence of a large spine on article 2 of the telopodite of the second maxilla and an absence of accessary spines on the second maxillary pretarsus as diagnostic of

Digitipes. The lack of a spine on article 2 has proven to be unreliable because it is on the one hand present in all Indian species of *Digitipes* (Joshi and Edgecombe 2013) and on the other hand is likewise absent in various species of the related genus *Otostigmus* (Lewis 2004 (Lewis, 2004b; Chagas Júnior et al., 2007). In some species of *Otostigmus* it is even subject to geographic variability between conspecific populations (Schileyko, 1995; Lewis, 2004a). In the case of pretarsal accessory spines on the second maxilla, an absence in at least two African species (*D. verdascens* and *D. reichardti* (Kraepelin, 1903)) is not matched by *Digitipes* species from India, where they are demonstrably present (Joshi and Edgecombe 2013). The most reliable morphological autapomorphy of *Digitipes* remains the presence of the femoral process in the male, coupled with a longitudinal furrow that extends along the medial surface of the femur and terminates at the process in male. These characters remain unknown in *D. periyarensis* Joshi and Edgecombe, 2013 and *D. krausi* Dobroruka, 1968, for which males have not been documented. Immature and limited material of unsexed specimens may be subject to misidentification at both the genus and species levels.

Currently the genus comprises three species from central Africa and six species from western India (Attems, 1930a, c; Jangi and Dass, 1984; Joshi and Edgecombe, 2013). Molecular distances (Table 5.2) and the composite data of morphological characters for all members (Table 5.3) suggest that the number of glabrous antennal articles, the posterior bifurcation of a median sulcus on the cephalic plate, the extent of paramedian sutures on the sternites, as well as the presence or absence of a lateral spine on the coxopleural process are taxonomically informative anduseful for species discrimination. Our key has been constructed based on a combination of the taxonomic keys to species by Jangi and Dass (1984) and Joshi and Edgecombe (2013), together with additional taxonomic characters.

Key to species of *Digitipes*

1a. Tergite surface with rugose ridges, keels a…………….…………..…… ***D. barnabasi***
1b. Tergite surface lacking rugose ridges, keels and tubercles…………..……………2
2a. 2.5–2.7 basal articles of antenna glabrous dorsally……..…………………………3
2b. At least 3 basal articles of antenna glabrous ………………..……………………4

3a. Dorsal spine absent on coxopleural …..………………...………… ***D. chhotanii***

3b. Dorsal spine present on coxopleural process………………..***D. kalewaensis* n. sp.**

4a. Longitudinal median sulcus on cephalic plate with posterior bifurcation…………..
…………………………………………………………………………….***D. pruthii***

4b. Longitudinal median sulcus on cephalic plate without posterior bifurcation….… 5

5a. Paramedian sutures nearly complete or complete on most sternites...................... 6

5b. Paramedian sutures only on anterior part of sternites ………….…………………8

6a. Tergite margination starting at least from T5………………….………………..7

6b. Only tergite of ultimate leg-bearing segment with margination…..….***D. reichardti***

7a. All legs without femoral, tibial and tarsal spurs…..………………….***D. periyarensis***

7b. At least leg 1 with femoral, tibial and tarsal…………………...……***D. verdascens***

8a. Posterior part of cephalic plate with pair of short sulci…...……..………..***D. jangii***

8b. Posterior part of cephalic plate without pair of short sulci …………...…...………9

9a. All legs without tibial and tarsal spurs ……....………………...………..***D. krausi***

9a. At least 3 pairs of legs with tibial and tarsal spurs…………………...……… 10

10a. Pore-field reaching to dorsal margin of coxopleuron………...….***D. coonoorensis***

10b. Pore-field terminating beneath dorsal margin of coxopleuron……..…..***D. jonesii***

Digitipes kalewaensis **Siriwut, Edgecombe and Panha n. sp.**

Figs. 5.1–5.3

Type specimens. Holotype CUMZ 00233 and GenBank ID for COI and 16S as KP204116 and KP204112, respectively; adult male from the type locality (length 43 mm, width 3.8 mm; Figs. 2D, 2E–G, 2I, 3A, 3B, 3E, 3G and 3H). Paratypes CUMZ 00234 (adult male), CUMZ 00235 (adult male), CUMZ 00236 (two females), CUMZ 00237 (juvenile), CUMZ 00238.1–2 (two juveniles), CUMZ 00240 (adult female), CUMZ 00241 (adult male). All paratypes are from the type locality.

Etymology. The name "kalewaensis" refers to the northwestern Burmese town which is the type locality.

Type locality. Semi-arid dry-dipterocarp forest on the bank of the Chindwin River, Kalewa Township, Sagaing Division, northwestern Myanmar (23º12’52.2” N, 94º18’7.2” E). It is located at the tip of drainage between two river systems, the Mayittha and Chindwin Rivers.

Diagnosis. 17 antennal articles, basal 2.7 glabrous dorsally. Tooth-plate with four main teeth; suture at base of tooth-plate extending laterally subparallel to margin of coxosternite. Tergite surfaces smooth. Tergite of ultimate leg-bearing segment with weak depression on posterior part. Sternites with incomplete paramedian sutures occupying 15 to 25% of anterior part of sternite, posterior part with circular pit. Lateral and dorsal spines on coxopleural process absent. Ultimate legs lacking M and DM spines. Locomotory legs with accessory spurs; legs 1–5 with two tarsal spurs, legs 6–20 with one tarsal spur; ultimate legs without tarsal spurs.

Description. Body length ranges from 23–47 mm. Body colour of preserved material greenish-brown; only cephalic plate and anterior three trunk segments dark blue. Locomotory legs light blue. Sternites 4–21 light yellowish. Cephalic plate with small, fine setae. Anterior median part of cephalic plate with short, straight sulcuswithout bifurcation posteriorly.

Antenna with 17 articles, basal 2.5–2.7 articles glabrous dorsally; 2.5 articles glabrous ventrally. Antenna reaches only to T2. Process of forcipular trochanteroprefemur bearing one apical and one or two inner teeth. Coxosternal tooth-plate wider than long, with four main teeth, separated into two groups, two inner and two outer; basal part with a clear, fine seta on each side or without. Interior part of article 2 of telopodite of second maxilla with a fine pigmented spine. Coxosternite without median suture, coxosternal median diastema reaching to base of tooth-plate, basal part of tooth-plate with curved sutures extending laterally subparallel to margin of coxosternite. Angulation of basal sutures ca 130º–135º.

T1 overlapping cephalic plate, without transverse suture. Tergites with paramedian sutures complete from TT7–8; margination starting on TT8–9. Tergite of ultimate leg-bearing segment usually without median furrow on posterior part (furrow present in one specimen). Sternites with short paramedian sutures on anterior part, occupying 15–25% length of sternite. Surface of sternites with two discontinuous longitudinal median sulci. Sternite of ultimate leg-bearing segment with sides converging posteriorly, posterior margin slightly concave.

Coxopleural process moderately long, with two apical spines; lateral and dorsal spines absent. Dense pore field covering whole area of coxopleuron except on ventro-distal part of coxopleural process, pore-free area reaching to 10% the distance to margin of sternite of ultimate leg-bearing segment. On lateral side of coxopleura, dense pore area not covered by lateral margin of tergite of ultimate leg-bearing Ultimate legs long and slender with ratio of ultimate leg articles as follow; 1:1.9 between tarsus 1 and tarsus 2, 1.9:2.1 between tarsus 2 and tibia, 2.1:2.4 between tibia and femur and 2.4:2.7 between femur and prefemur. Prefemoral spines in two rows, arranged as VL-1 or 2, VM-1 to 2, without M and DM spines.

Locomotory legs with short setae on anterior segments; legs 1 to 5 usually with two tarsal spurs (occasionally, two tarsal spurs on only one side), subsequent legs to leg 20 with one tarsal spur. One tibial and femoral spur on leg 1. Two accessory spurs and pretarsal claw present on all legs. Ultimate leg femur with conical projection in male. Pretarsus and tarsus 2 of ultimate legs with or without small setae. Spiracles oval or rounded, present on segments 3, 5, 8, 10, 12, 14, 16, 18 and 20. Spiracle of segment 3 oval shape and largest; spiracles on segments 5 and 8 rounded.

Remarks. *Digitipes kalewaensis* n. sp. is the first record of *Digitipes* from outside central Africa and western India (Fig. 5.1). By comparing the species with the closely related Indian *Digitipes* species, *D. kalewaensis* n. sp. differs from *D. chhotanii* Jangi and Dass, 1984 and *D. pruthii* Jangi and Dass, 1984 by having 2.5–2.7 glabrous antennal articles, without a posterior bifurcated sulcus on the anterior-medial part of the cephalic plate, having femoral, tibial and tarsal spurs on leg 1, and a prefemoral spine arrangement on the ultimate legs as VL 1–2, VM 2(1), with M and DM absent. The variability of some morphological characters such as the number of glabrous antennal articles, number of teeth on the coxosternal tooth-plates, margination of tergites, spinulation of the coxopleural process, and numbers of legs with tarsal spurs may cause problems for species delimitation. An inconsistency in several characters indicates the need to further clarify the extent of intraspecific variability within this group. For this reason, a summary of comparative diagnostic characters for each previously named species with *D. kalewaensis* n. sp. is given in Table 3.

Molecular analysis

The sequences of the new Burmese *Digitipes* species are represented by 445 base pairs for COI (152 informative sites) and 332 base pairs for 16S (143 informative sites). 182 sites are variable for COI and 189 for 16S, whereas 263 and 143 sites are conservative for the two genes, respectively. Corrected mean distance analysis of Indian and Burmese *Digitipes* species (Table 5.2) shows a corrected mean distance for COI between 13.8–21.3% among interspecific populations, whereas intraspecific populations showed proportion ranges between 2 and 11% of corrected mean distance. In the case of 16S, the corrected mean distance for interspecific population ranged between 13.1–27% while intraspecific populations were between 0.4 and 13% of corrected mean distance. The proportional ranges of corrected mean distance values between *Digitipes* and other selected genera in the subfamilies Otostigminae and Scolopendrinae Leach, 1814 are 17.0–26.3% in COI and 17.3–34.7% in 16S. The maximum likelihood and Bayesian trees yield the same topology (Fig. 5.4). This depicts monophyly of the subfamily Otostigminae, in this analysis represented by species of *Otostigmus*, *Rhysida*, *Ethmostigmus* and *Digitipes*. Within the Otostigminae, members of *Digitipes* were separated into two clades, but these are part of a polytomy that also includes the other members of Otostigminae. The four specimens of Burmese *Digitipes* were grouped together and resolved as sister clade within the Indian-Burmese group, with moderate nodal support and considerable branch length both in maximum likelihood and Bayesian inference (81/0.9). Among Indian *Digitipes* species, *D. barnabasi* Jangi and Dass, 1984 was separated from the other species. Relationships of the main Indian *Digitipes* clade are as follow; *D. coonoorensis* Jangi and Dass, 1984 and *D. jonesii* (Verhoeff, 1938) were grouped together, supported by 76/1 (ML/BI), whereas *D. jangii* Joshi & Edgecombe, 2013 and *D. periyarensis* were unresolved. In case of three selected species of genus *Otostigmus*, *O. ruficeps* Pocock, 1890 and *O. scaber* Porat, 1876 were grouped together but with weak nodal support, while the position of *O. multidens* Haase, 1887 is ambiguous and unresolved.

Discussion

Phylogenetic position of *D. kalewaensis* n. sp. The phylogenetic position of a new Burmese species suggested the relationship among two geographically distinct populations by grouping it with the main clade of most Indian *Digitipes* members (Fig. 5.4). The four OTUs of *D. kalewaensis* n. sp. form the sister group of an Indian clade that includes *D. coonoorensis*, *D. jangii*, *D. jonesii* and *D. periyarensis*. This Indian-Burmese group is supported both in ML and BI analyses. Diagnostic characters of the Burmese species are its number of glabrous antennal articles, the arrangement of prefemoral spines on the ultimate legs, and leg 20 bearing a tarsal spur. However, it also shared some characters with Indian species such as two apical spines on the coxopleural process, a consistent number of antennal articles, and a nearly fixed number of teeth on the forcipular tooth-plates. Within the main clade of Indian-Burmese *Digitipes*, *D. coonoorensis* is sister species to *D. jonesii*, as is supported by several shared characters such as the arrangement of prefemoral spines on ultimate legs, and the variable presence or absence of a lateral spine on the coxopleural process. The occurrences of depressions on the sternites may serve as additional characters, as in related genera such as *Otostigmus* (see Lewis 2010). The congruent position and details of depressions on the sternites from different species here is noteworthy (see Table 5.3). The proportion of legs bearing two tarsal spurs is confined to anterior pairs of legs in most Indian-Burmese *Digitipes* except for one Indian (*D. periyarensis*) and one African species (*D. krausi*) that lack tarsal spurs entirely. The coincidence in number of teeth on the coxosternal tooth-plates and their separation into two groups should be recognized as plesiomorphic characters shared by all members of the genus.

A character not found in Indian-Burmese members is tergite margination confined to the ultimate leg-bearing segment; this character occurs only in two African species (Dobroruka, 1968; Lewis, 2004b). The complete or nearly complete paramedian sutures on sternites in two species (*D. periyarensis* and *D. reichardti*) should be emphasized because they resemble a condition found in other genera of Otostigminae (e.g., some species of *Otostigmus*). Morphologically, *D. periyarensis* is the most anomalous member of *Digitipes*, and comparisons can be made with species of *Otostigmus* in its robust, dorsally-grooved ultimate legs. Indeed, the membership of this species within *Digitipes* is heavily reliant on its molecular placement (Fig. 5.4). The contradictory result of *D. barnabasi* failing to cluster with the remaining Indian species of *Digitipes* was also detected by Vahtera et al. (2013) and Vahtera and Edgecombe (2014). Monophyly of *D. barnabasi* finds support from the presence of keels, rugosity and tubercles on tergite surfaces, as well as the relatively posterior extent of legs with two tarsal spurs, character states not observed elsewhere in the genus. The polytomy at the base of Otostigminae may be affected by the limited taxon sampling. However, even expanded sampling has shown that the status and interrelationships of genera in Otostigminae are ambiguous because of weakly supported, unstable nodes (Vahtera et al., 2013; Vahtera and Edgecombe, 2014). For further study, the topic of the relationship between the two scattered groups within *Digitipes* (i.e., *D. barnabasi* and the remaining Indian-Burmese clade) should be explored because the current tree leaves the monophyly of Indian members open, as well as the entire genus. Sequence data for African members of *Digitipes* are also needed to further evaluate the monophyly and biogeography of the genus, as well as for nomenclatural reasons (the type species being African).

Geographic distribution of *Digitipes*. The first three named species in the genus *Digitipes* were described from central and eastern Africa (Attems 1930a, b; Kraus, 1957; Dobroruka, 1968; Lewis, 2004). Subsequent discoveries have all come from the western parts of peninsular India (Jangi and Dass, 1984; Joshi and Edgecombe, 2013), a pattern consistent with geological evidence for connections between the biotas of the Indian and African plates before the former was attached to the Eurasian plate (Ali and Aitchison, 2008). This endemicity of *Digitipes* has been confirmed by phylogenetic analysis under the estimated climate surface modeling of global land areas (Hijmans et al., 2005; Joshi and Karanth, 2012). The diversification of Indian scolopendromorphs, including *Digitipes*, has been dated, estimating lineage diversity relative to tectonic history. The split between *D. barnabasi* and other Indian species of *Digitipes* (and, we infer, the Burmese *D. kalewaensis* n. sp. based on the tree in Fig. 5.4) is dated to some 86–78 Ma (Joshi and Karanth, 2011; Joshi and Edgecombe, 2013), approximately corresponding to the Late Cretaceous split of India from Madagascar. The molecular phylogenetic analysis supports closest affinities between the Burmese *Digitipes* and a clade composed of most known Indian *Digitipes* species. The latter are estimated to have begun diversifying in the early Palaeogene (Joshi and Karanth, 2011, 2012), suggesting that most recent common ancestry with *D. kalewaensis* n. sp. dates to the Late Cretaceous or earliest Palaeogene. This substantially post-dates the connection between the West Burma terrane and East Gondwana, from which it is inferred to have drifted from the Australian margin by the Late Triassic and was already incorporated into SE Asia in the Cretaceous (Metcalfe, 1998). Rather than inferring that current molecular dates grossly underestimate an earlier Mesozoic history for *Digitipes*, an alternative timing for introduction of *Digitipes* into Myanmar relates to the contact of the northeastern corner of peninsular India with SE Asia in the late Palaeocene-early Eocene. In any case, the conspicuous gaps between occurrences in both Africa and India-SE Asia suggest that current distributional data are likely incomplete.

Acknowledgements

The authors kindly thank all members of the Animal Systematics Research Unit and Department of Biology, Faculty of Science, Chulalongkorn University, for technical support. We would like to make a special thanks to U. Bantaowong who collected the first samples from Myanmar to include Digitipes. Special thanks also go to Prof. Dr. J.J. Jaeger, Dr. Y. Chaimanee and French-Myanmar colleagues for their kindness in inviting U. Bantaowong and WS to join the field expeditions in Myanmar in 2013 and 2014. We are grateful to Dr. E. Jeratthitikul for comments and suggestions on molecular analysis and to T. Krutchuen for her excellent scientific drawings. We gratefully thank the Thailand Research Fund for financial support through the Royal Golden Jubilee Ph.D. Program (Grant No. PHD/0066/2553). The main funding for this project is from The Thailand Research Fund (TRF) under TRF Senior Research Scholar (RTA 5880001) to SP. We also give special thanks for valuable comments and suggestions from Dr. A. Schileyko that improved this manuscript.

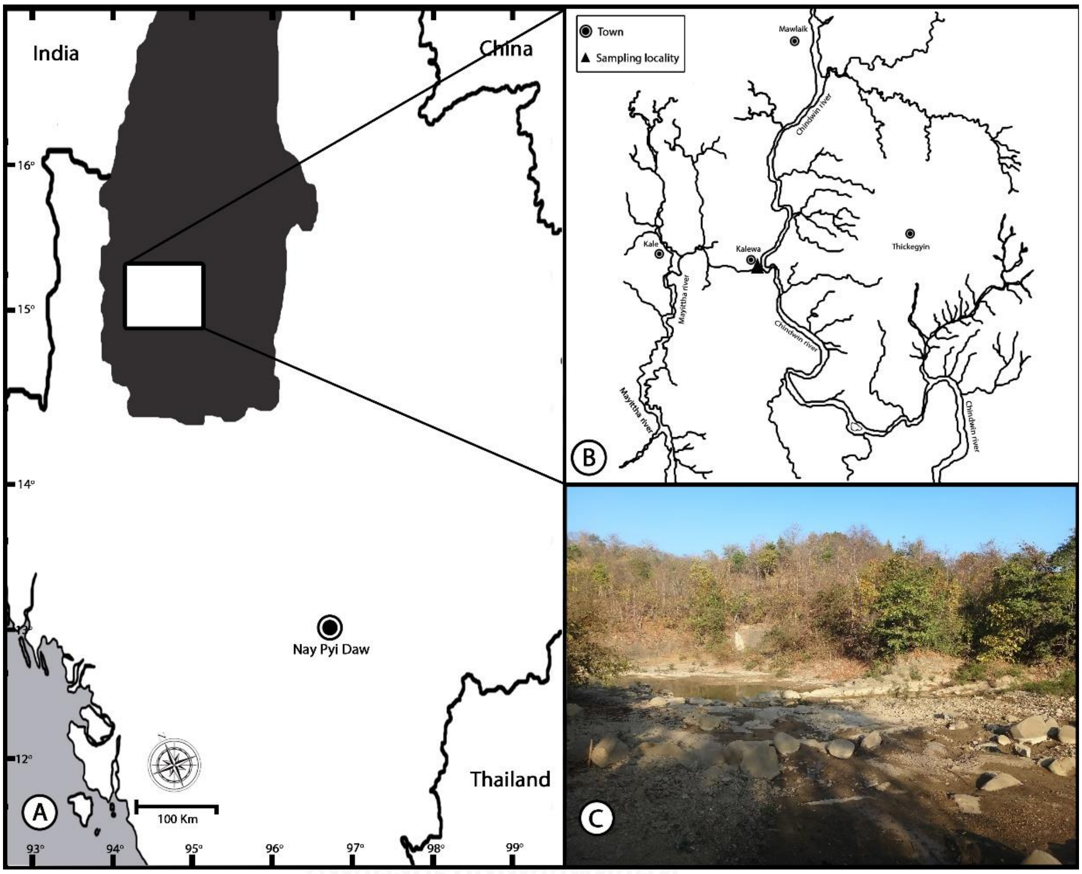


Figure 5.1 Collecting area of *Digitipes kalewaensis* n. sp.; A. Location of collection area in Myanmar. B. Collecting locality (expanded magnification). C. Habitat type.

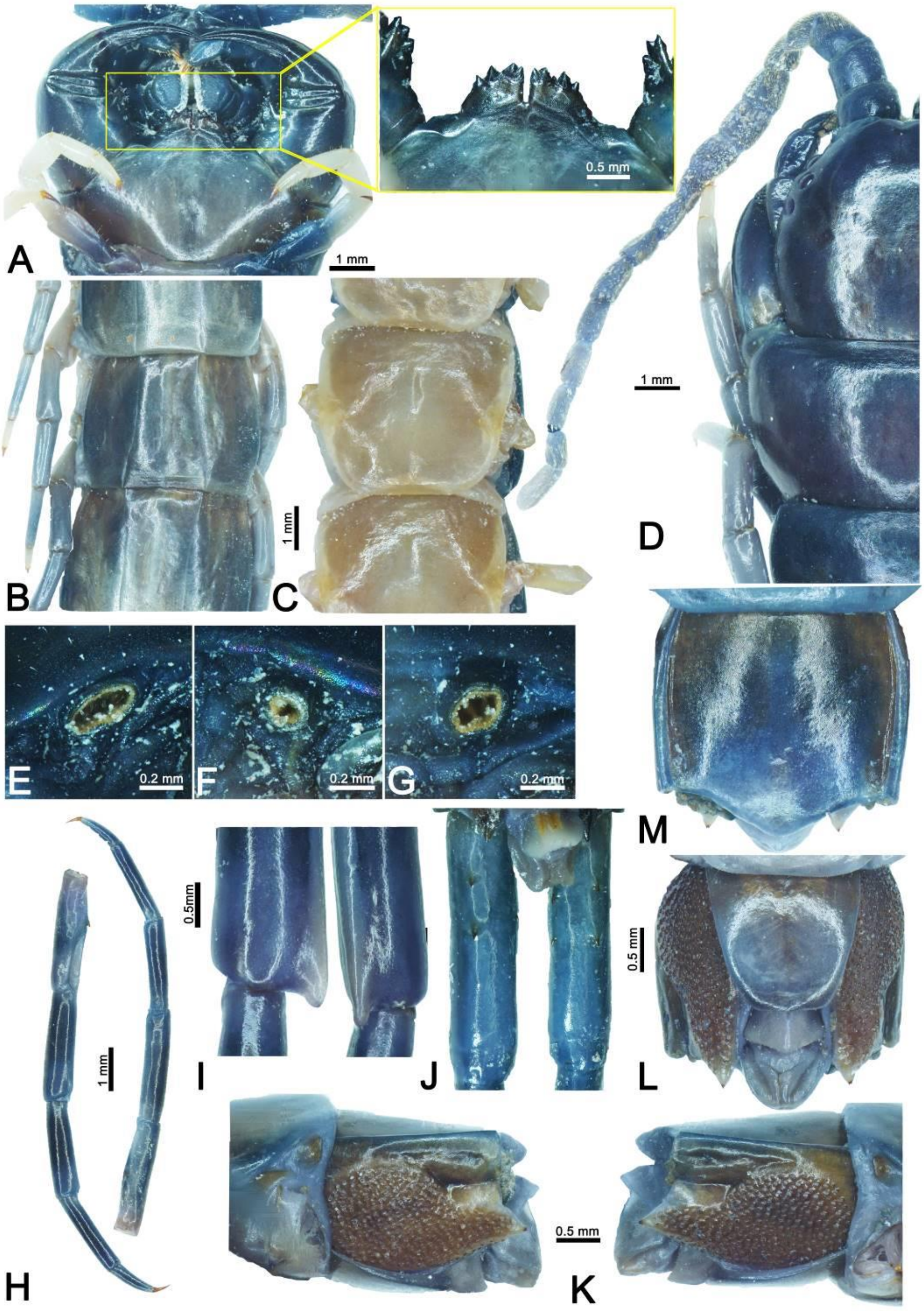


Figure 5.2 Morphological characters of *Digitipes kalewaensis* n. sp.; **A.** Forcipular coxosternite (Paratype; CUMZ 00234). **B-C.** Tergites and sternites 9–11 (Paratype; CUMZ 00241). **D**. Antenna, cephalic plate and T1 (Holotype). **E-G.** Spiracles 3, 5 and 8, respectively (Holotype). **H, J.** Ultimate legs (Paratypes; CUMZ 00234-00235). I. Projection on femur of ultimate leg in male (Holotype). **K.** Pore-field of coxopleuron (left and right; Paratype; CUMZ 00235). **L-M.** Ventral and dorsal view of ultimate leg-bearing segment (Paratype; CUMZ 00234).

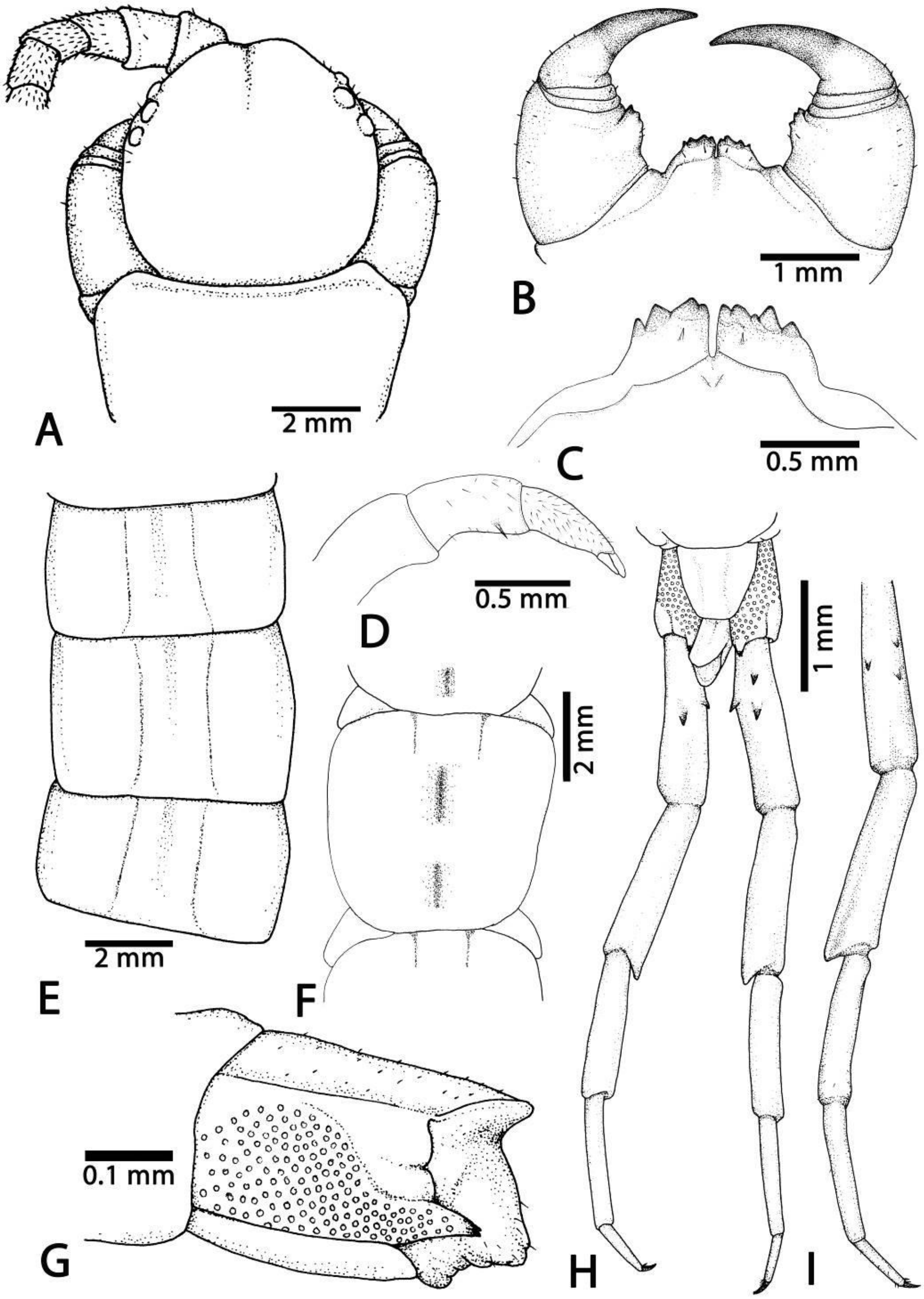


Figure 5.3 Drawings depicting variation in some morphological characters; **A.** Cephalic plate and T1 (Holotype). **B.** Forcipular segment (Holotype). **C.** Tooth-plate with five teeth on right side (Paratype; CUMZ 00234). **D.** Articles 1–3 of telopodite of second maxilla (Paratype; CUMZ 00241). **E.** Tergites 9–11 (Holotype). **F.** Sternite 10 (Paratype; CUMZ 00240). **G.** Coxopleural pore area (Holotype). **H.** Sternite of ultimate leg-bearing segment with ultimate legs (Holotype; ventral view). **I.** Left ultimate leg (Paratype; CUMZ 00234).

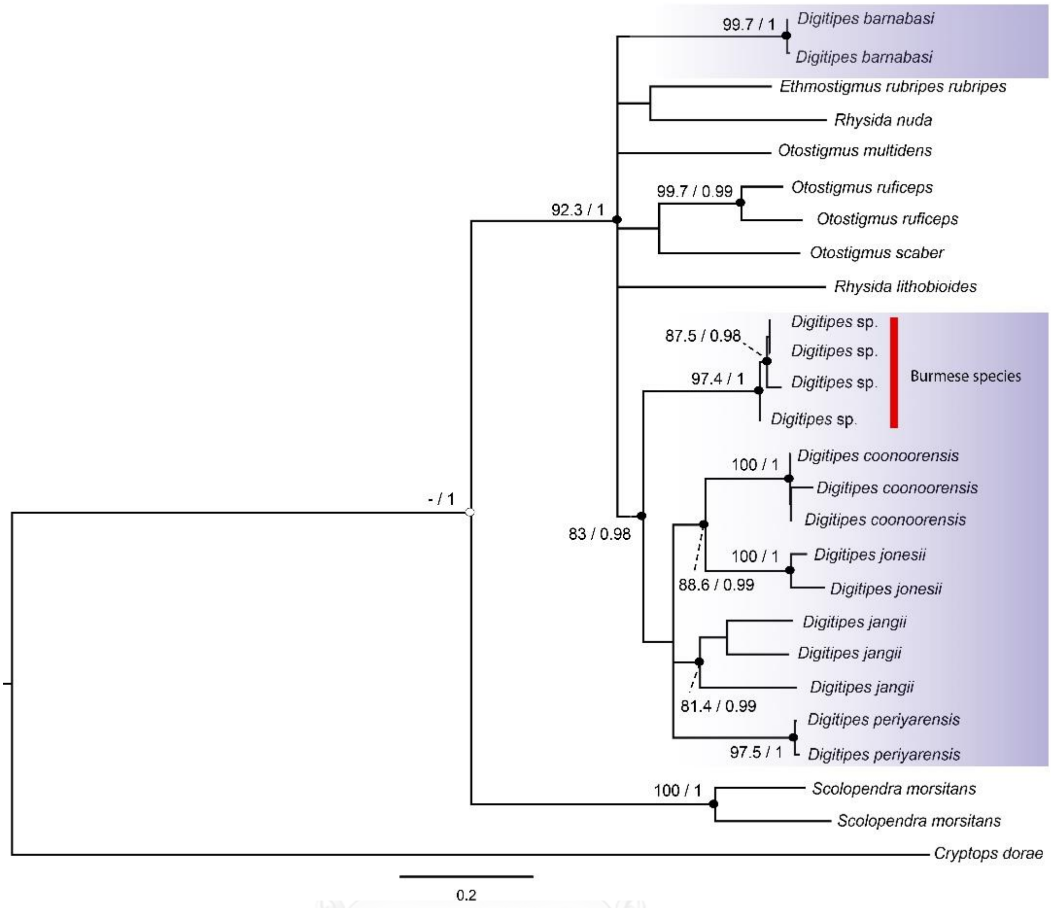
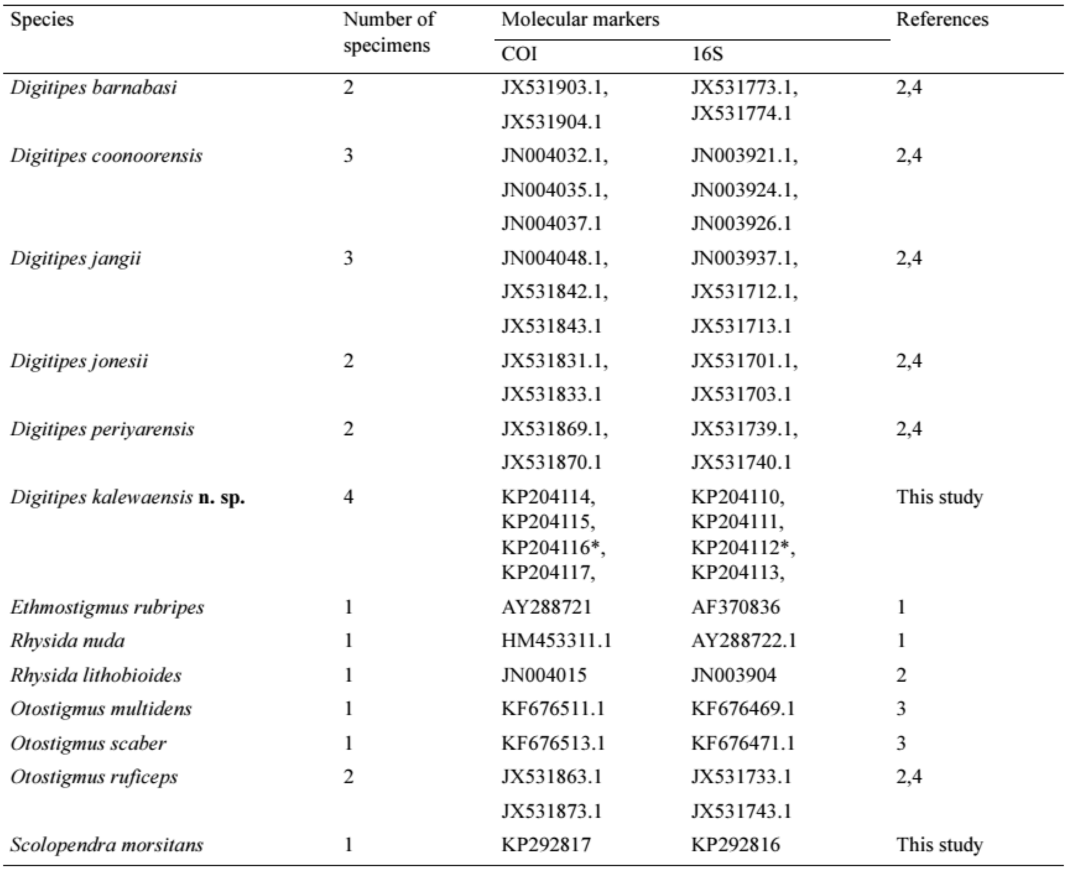


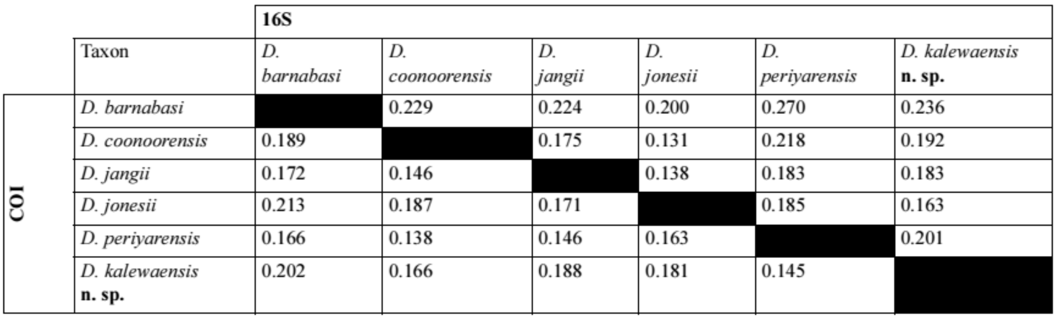
Figure 5.4 Maximum likelihood consensus tree based on combined COI and 16S sequences. Numbers at nodes are bootstrap support in maximum likelihood (ML) and posterior probabilities in Bayesian inference (BI). Black circles refer to nodes supported from both ML and BI; grey circle refers to a node supported only by ML.

Table 5.1 Accession number of all sampled taxa including outgroups. 1 = Murienne et al. (2010), 2= Joshi and Karanth (2011), 3 = Vahtera et al. (2013) and 4 = Joshi and Edgecombe (2013). “*” indicates the holotype.



Species	Number of specimens	Molecular markers		References
		COI	16S	
Digitipes barnabasi	2	JX531903.1, JX531904.1	JX531773.1, JX531774.1	2,4
Digitipes coonoorensis	3	JN004032.1, JN004035.1, JN004037.1	JN003921.1, JN003924.1, JN003926.1	2,4
Digitipes jangii	3	JN004048.1, JX531842.1, JX531843.1	JN003937.1, JX531712.1, JX531713.1	2,4
Digitipes jonesii	2	JX531831.1, JX531833.1	JX531701.1, JX531703.1	2,4
Digitipes periyarensis	2	JX531869.1, JX531870.1	JX531739.1, JX531740.1	2,4
Digitipes kalewaensis **n. sp.**	4	KP204114, KP204115, KP204116*, KP204117,	KP204110, KP204111, KP204112*, KP204113,	This study
Ethmostigmus rubripes	1	AY288721	AF370836	1
Rhysida nuda	1	HM453311.1	AY288722.1	1
Rhysida lithobioides	1	JN004015	JN003904	2
Otostigmus multidens	1	KF676511.1	KF676469.1	3
Otostigmus scaber	1	KF676513.1	KF676471.1	3
Otostigmus ruficeps	2	JX531863.1 JX531873.1	JX531733.1 JX531743.1	2,4
Scolopendra morsitans	1	KP292817	KP292816	This study

Table 5.2 Corrected mean distance among Indian-Burmese *Digitipes* members.



		16S					
	Taxon	*D. barnabasi*	*D. coonoorensis*	*D. jangii*	*D. jonesii*	*D. periyarensis*	*D. kalewaensis* **n. sp.**
COI	*D. barnabasi*		0.229	0.224	0.200	0.270	0.236
	D. coonoorensis	0.189		0.175	0.131	0.218	0.192
	D. jangii	0.172	0.146		0.138	0.183	0.183
	D. jonesii	0.213	0.187	0.171		0.185	0.163
	D. periyarensis	0.166	0.138	0.146	0.163		0.201
	D. kalewaensis **n. sp.**	0.202	0.166	0.188	0.181	0.145	

Table 5.3 Comparative analysis of taxonomic characters in all *Digitipes* members; ? indicates unavailable data in the literature. (Continued)

Characters	*D. jonesii*[4,8]	*D. periyarensis*[8]	*D. pruthii*[6]
No. of antennal articles	17/17	17/17	17/17
No. of glabrous antennal articles	3	3	3
Teeth on tooth-plates	4+4	4+4	4+4
First tergite with complete paramedian sutures	TT6–8	TT4 or 5	T8
Type of longitudinal median sulcus on cephalic plate	Posteriorly straight	Posteriorly straight	Posteriorly bifurcate
First tergite with complete margination	TT8–10 (TT7–13)	TT5 or 6	T11
Tergite surface	Smooth	Smooth	Smooth
Surface of sternites	?	?	Punctate
Shape and surface of tergite of ultimate LBS	Smooth and convex lateral margin	Smooth and convex lateral margin	Convex lateral margin
Maximum percent completeness of sternal PS	10–15%	Nearly complete (80%)	?
Shape and surface of sternite of ultimate LBS	Sides converging posteriorly	Sides converging posteriorly	Sides converging posteriorly
Arrangement of spines on coxopleural process (AP, SAP, DP, LP)	AP-2	AP-2	AP-2
	SAP-0	SAP-0	SAP-0
	DP-0	DP-0	DP-0
	LP-1 or 0	LP-0	LP-0
Length of coxopleural process	Short or moderately long	Short	Short
Pore field on coxopleuron (CP)	Not reaching margin of CP	Strongly beneath to dorsal margin of CP	Not reaching margin of CP
Prefemoral spine formula on ultimate legs	VL-3(2)	VL-3	VL-0
	VM-2(1)	VM-2(3)	VM-5
	M-0	M-0	M-0
	DM-1 (0)	DM-2	DM-0
Legs No. with two tarsal spurs	1–3 or 1–4	Absent	1–4
Legs No. with one tarsal spur	3,4 -20	Absent	5–19
Legs No. with tibial spur	1–3 or 1–4	Absent	1–4
Leg No. with femoral spur	1	Absent	1
Projection on ultimate leg femur	Bluntly conical, extending further than distal end of femur, distal part of process with small setae	?	Broad based and blunt conical process
Type locality	Thiruvananthapuram, Kerala, India	Periyar, Kerala, India	Salem, Tamil Nadu, India

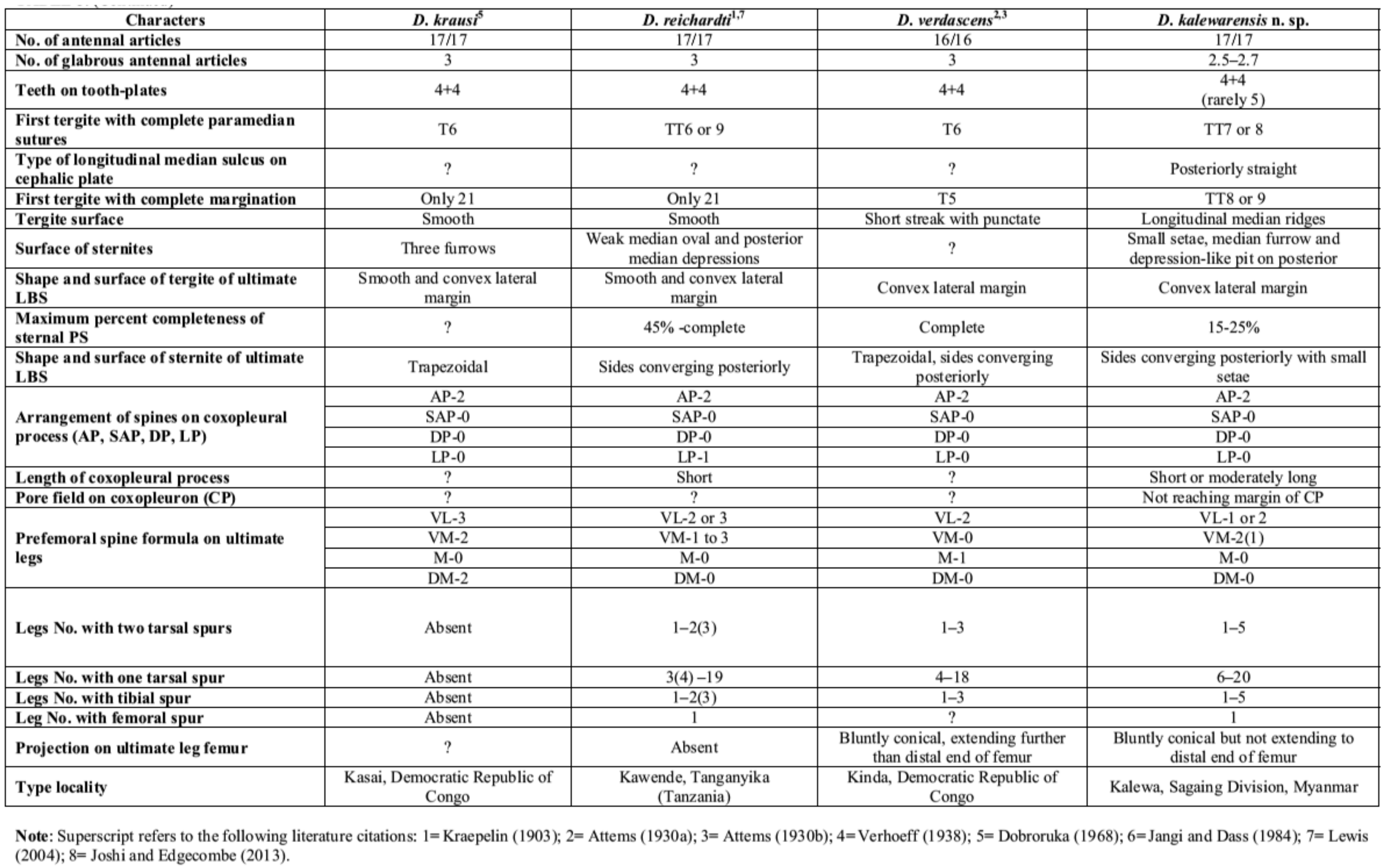
……continued on the next page

Table 5.3 Comparative analysis of taxonomic characters in all *Digitipes* members; ? indicates unavailable data in the literature. (Continued)

Characters	***D. jonesii*[4,8]**	***D. periyarensis*[8]**	***D. pruthii*[6]**
No. of antennal articles	17/17	17/17	17/17
No. of glabrous antennal articles	3	3	3
Teeth on tooth-plates	4+4	4+4	4+4
First tergite with complete paramedian sutures	TT6–8	TT4 or 5	T8
Type of longitudinal median sulcus on cephalic plate	Posteriorly straight	Posteriorly straight	Posteriorly bifurcate
First tergite with complete margination	TT8–10 (TT7–13)	TT5 or 6	T11
Tergite surface	Smooth	Smooth	Smooth
Surface of sternites	?	?	Punctate
Shape and surface of tergite of ultimate LBS	Smooth and convex lateral margin	Smooth and convex lateral margin	Convex lateral margin
Maximum percent completeness of sternal PS	10–15%	Nearly complete (80%)	?
Shape and surface of sternite of ultimate LBS	Sides converging posteriorly	Sides converging posteriorly	Sides converging posteriorly
Arrangement of spines on coxopleural process (AP, SAP, DP, LP)	AP-2	AP-2	AP-2
	SAP-0	SAP-0	SAP-0
	DP-0	DP-0	DP-0
	LP-1 or 0	LP-0	LP-0
Length of coxopleural process	Short or moderately long	Short	Short
Pore field on coxopleuron (CP)	Not reaching margin of CP	Strongly beneath to dorsal margin of CP	Not reaching margin of CP
Prefemoral spine formula on ultimate legs	VL-3(2)	VL-3	VL-0
	VM-2(1)	VM-2(3)	VM-5
	M-0	M-0	M-0
	DM-1 (0)	DM-2	DM-0
Legs No. with two tarsal spurs	1–3 or 1–4	Absent	1–4
Legs No. with one tarsal spur	3,4 -20	Absent	5–19
Legs No. with tibial spur	1–3 or 1–4	Absent	1–4
Leg No. with femoral spur	1	Absent	1
Projection on ultimate leg femur	Bluntly conical, extending further than distal end of femur, distal part of process with small setae	?	Broad based and blunt conical process
Type locality	Thiruvananthapuram, Kerala, India	Periyar, Kerala, India	Salem, Tamil Nadu, India

……continued on the next page

Table 5.3 Comparative analysis of taxonomic characters in all *Digitipes* members; ? indicates unavailable data in the literature. (Continued



Characters	***D. krausi*[5]**	***D. reichardti*[1,7]**	***D. verdascens*[2,3]**	***D. kalewarensis* n. sp.**
No. of antennal articles	17/17	17/17	16/16	17/17
No. of glabrous antennal articles	3	3	3	2.5–2.7
Teeth on tooth-plates	4+4	4+4	4+4	4+4 (rarely 5)
First tergite with complete paramedian sutures	T6	TT6 or 9	T6	TT7 or 8
Type of longitudinal median sulcus on cephalic plate	?	?	?	Posteriorly straight
First tergite with complete margination	Only 21	Only 21	T5	TT8 or 9
Tergite surface	Smooth	Smooth	Short streak with punctate	Longitudinal median ridges
Surface of sternites	Three furrows	Weak median oval and posterior median depressions	?	Small setae, median furrow and depression-like pit on posterior
Shape and surface of tergite of ultimate LBS	Smooth and convex lateral margin	Smooth and convex lateral margin	Convex lateral margin	Convex lateral margin
Maximum percent completeness of sternal PS	?	45% -complete	Complete	15-25%
Shape and surface of sternite of ultimate LBS	Trapezoidal	Sides converging posteriorly	Trapezoidal, sides converging posteriorly	Sides converging posteriorly with small setae
Arrangement of spines on coxopleural process (AP, SAP, DP, LP)	AP-2	AP-2	AP-2	AP-2
	SAP-0	SAP-0	SAP-0	SAP-0
	DP-0	DP-0	DP-0	DP-0
	LP-0	LP-1	LP-0	LP-0
Length of coxopleural process	?	Short	?	Short or moderately long
Pore field on coxopleuron (CP)	?	?	?	Not reaching margin of CP
Prefemoral spine formula on ultimate legs	VL-3	VL-2 or 3	VL-2	VL-1 or 2
	VM-2	VM-1 to 3	VM-0	VM-2(1)
	M-0	M-0	M-1	M-0
	DM-2	DM-0	DM-0	DM-0
Legs No. with two tarsal spurs	Absent	1–2(3)	1–3	1–5
Legs No. with one tarsal spur	Absent	3(4) –19	4–18	6–20
Legs No. with tibial spur	Absent	1–2(3)	1–3	1–5
Leg No. with femoral spur	Absent	1	?	1
Projection on ultimate leg femur	?	Absent	Bluntly conical, extending further than distal end of femur	Bluntly conical but not extending to distal end of femur
Type locality	Kasai, Democratic Republic of Congo	Kawende, Tanganyika (Tanzania)	Kinda, Democratic Republic of Congo	Kalewa, Sagaing Division, Myanmar

Note: Superscript refers to the following literature citations: 1= Kraepelin (1903); 2= Attems (1930a); 3= Attems (1930b); 4= Verhoeff (1938); 5= Dobroruka (1968); 6= Jangi and Dass (1984); 7= Lewis (2004); 8= Joshi and Edgecombe (2013).

Chapter 6

Systematic revision and phylogenetic reassessment of the centipede genera *Rhysida* Wood, 1862 and *Alluropus* Silvestri, 1912 (Chilopoda: Scolopendromorpha) in Southeast Asia, with further discussion of the subfamily Otostigminae

Warut Siriwut[A,B], Gregory D Edgecombe[C], Chirasak Sutcharit[B], Piyoros Tongkerd[B] and Somsak Panha[B,D]

[A]Biological Sciences Program, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand
[B]Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand
[C]Department of Earth Sciences, The Natural History Museum, London SW7 5BD, UK
[D]Corresponding author. Email: somsak.pan@chula.ac.th

Invertebrate Systematics: (in preparation)

Abstract

Phylogenetic relationships of two morphologically similar genera, *Rhysida* Wood, 1862, and *Alluropus* Silvestri, 1912, were investigated based on broad-scale taxonomic sampling together with a taxonomic revision that integrates new field collections with type and historical collections from mainland Southeast Asia and some adjacent areas such as India and Australia. Morphological revision and molecular phylogenetic results endorse the validity of seven described *Rhysida* species in Southeast Asia/Australia: *R. lithobioides* (Newport, 1845), *R. longipes* (Newport, 1845), *R. immarginata* (Porat, 1876), *R. nuda* (Newport, 1845), *R. carinulata* (Haase, 1887), *R. singaporensis* Verhoeff, 1937, and *R. polyacantha* Koch, 1985. The nominal Southeast Asian species *R. leviventer* Attems, 1953, is placed in junior subjective synonymy with *R. lithobioides*. The monotypic genus *Alluropus* is redescribed, including a revision of its type specimens from Vietnam and new records from Thailand, Laos and Cambodia. Molecular phylogeny based on three genes recovered this morphologically distinct group as nesting together with Indo-Australian *Rhysida*. Taxonomic revision reassigned *R. calcarata* Pocock, 1891, to *Alluropus* based on its morphological and molecular similarity, the differences between putative species being secondary sexual variation. Two morphologically distinct populations of *A. calcarata* **new comb.** were found distributed allopatrically in the Indochina subregion. The Vietnamese *Rhysida* species *R. marginata* Attems, 1953, is placed in junior subjective synonymy with *A. calcarata*. Phylogenetic relationships in Otostigminae remain unsettled because clades lack statistical support in several genera. Nonetheless, relationship among closely related genera such as *Alipes*+*Otostigmus* (*Parotostigmus*), *Ethmostigmus*+*Sterropristes*, *Rhysida*+*Alluropus* and *Otostigmus*+*Digitipes* are consistent with morphology, genetic composition and geographical distributions. Diversity trends in Southeast Asian Otostigminae probably refer to biotic exchange with neighbouring faunas, as has been proposed for other scolopendromorphs.

Introduction

Integration of molecular and morphological techniques has invigorated taxonomic and systematic studies for many groups of invertebrates. Molecular tools have permitted many species to be recognized as species complexes or as relict species. Sexual or colour dimorphism (Siriwut et al., 2015a), morphological plasticity (Moczek, 2010), cryptic speciation (Nantarat et al., 2014b) or introgression (Pentek-Zakar et al., 2015) can confound species delimitation when analyses draw only on traditional external morphological characters. In such instances, molecular phylogeny permits tests of classification and taxonomic identifications (Chao et al., 2011; Joshi and Karanth, 2012; Edgecombe et al., 2015), and has also used as a backbone for estimating divergence times based on geological and palaeontological calibration (Joshi and Karanth, 2011; Murienne et al., 2011). An integrative approach is especially beneficial in groups such as scolopendromorph centipedes, which are morphologically conservative but with species boundaries that are often blurred by morphological variability between populations (Edgecombe and Giribet, 2008; Edgecombe et al., 2015; Siriwut et al., 2015a; Siriwut et al., 2016).

The subfamily Otostigminae is the largest within the family Scolopendridae Pocock, 1891. It is abundant and widespread throughout tropical and subtropical regions, as is its sister group, the subfamily Scolopendrinae. Otostigminae comprises nine genera, *Alipes* Imhoff, 1854, *Rhysida* Wood, 1862, *Otostigmus* Porat, 1876, *Edentistoma* Tömösváry, 1882, *Ethmostigmus* Pocock, 1898, *Alluropus* Silvestri, 1912 *Digitipes* Attems, 1930, and *Sterropristes* Attems, 1934, and up to two hundred species have been described (Edgecombe and Bonato, 2011). They are found mostly on Gondwanian tectonic blocks such as Africa, the Indian subcontinent, some parts of Southeast Asia, and Australia. The distributions of some taxa may be limited by habitat characteristics or geographical barriers such as island archipelagos (Muadsub et al., 2012) or forest types (Vahtera and Edgecombe, 2014). Recently, phylogenetic analysis of several otostigmine genera revealed that dispersal of these animals is correlated with plate tectonic events, such as African-Indian rifting, drift and accretion during the Cretaceous-Paleogene (Joshi and Karanth, 2011). Some genera have been interpreted as endemic to Southeast Asia after taxonomic revision and intensive surveys in some remote areas (Muadsub et al., 2012), phylogenetic approaches using ecological modeling (Joshi and Karanth, 2012), and observations on unique morphological changes associated with foraging behaviour (Vahtera and Edgecombe, 2014).

To date, phylogenetic relationships among the genera of Otostigminae are in question for several reasons. One is the rather artificial nature of generic diagnoses in the group, genera typically being distinguished by one or two characters that were intended to operate like an identification key rather than being necessarily being apomorphies (Vahtera et al., 2012b; Vahtera et al., 2013). Second are the relatively weakly supported and unstable relationships at many deep nodes in otostigmine phylogeny in existing molecular work (Vahtera and Edgecombe, 2014). In addition, information from local and especially regional faunas is often lacking, systematic revisionary work has not been untaken for some clades, and in many cases few specimens are available for named species (Lewis, 2000; Lewis, 2004a). A particular difficulty with taxonomic identification of these genera at the species-level is the effects of geographical variation, ontogenetic variation or sexual dimorphism, and distribution gaps (Lewis, 1978; Lewis, 1984b; Lewis, 2000; Lewis, 2003; Chagas Júnior, 2013; Joshi and Edgecombe, 2013). Previously, geographical variation has been cited as the main challenge for species delimitation in several clades within Scolopendromorpha (Jangi, 1955; Lewis, 1968; Koch, 1983a; Koch, 1983b; Koch, 1985; Lewis, 2000; Lewis, 2010d; Joshi and Edgecombe, 2013; Lewis, 2014; Siriwut et al., 2016). Several historical species were described without any data on variability between individuals or populations (Newport, 1845; Attems, 1930a; Verhoeff, 1937; Attems, 1953). Furthermore, distribution records of some species in the past included immature specimens that are not recommended for species identification of scolopendromorphs, and misidentifications can distort distribution ranges (Attems, 1953; Lewis, 2004a). Thus, without additional data on morphological variation from broad-scale sampling especially in widespread taxa, problems of species boundaries are still rife in the Otostigminae.

The genus *Rhysida* comprises nearly 40 described species (Edgecombe and Bonato, 2011), of which eight species, namely *R. lithobioides* (Newport, 1845), *R. longipes* (Newport, 1845), *R. immarginata* (Porat, 1867), *R. carinulata* (Haase, 1887), *R. calcarata* Pocock, 1891, *R. singaporiensis* Verhoeff, 1937, *R. leviventer* Attems, 1953 and *R. marginata* Attems, 1953 have been reported in mainland Southeast Asia. Another morphologically similar genus, *Alluropus* Silvestri, 1912, is a monotypic taxon, its type from Vietnam named as *A. demangei* Silvestri, 1912. Only the characteristic of a club-shaped tarsus 1 of the ultimate legs was used to distinguish *Alluropus* (see Attems, 1930a), the type species has been known from only two specimens, and the species has not been previously been revised. For these reasons, the validity of *Alluropus* and its phylogenetic position within the subfamily Otostigminae are open questions as to whether its morphological diagnosis is based on a sexually dimorphic character or an abnormality.

In this study, phylogeny of the subfamily Otostigminae is reconstructed using novel specimens from mainland Southeast Asia and most available sequences of congeneric taxa from GenBank. Phylogenetic relationships and the systematic position of *Alluropus* are investigated together with Southeast Asian *Rhysida*. Species-level taxonomy of the two genera is revised based on newly collected material and museum collections, and morphological features that may be useful diagnostic characters in these two genera are discussed. Lastly, patterns in diversity and geographical distribution of all genera in this area are investigated in light of genetic composition and relationships from a broad-scale phylogeny.

Material and methods

Taxon sampling and species identification

Specimens from museum collections and field collecting throughout mainland Southeast Asia in historic and recent surveys are used in this study. Samples were identified based on previous morphological criteria, i.e. Newport (1845), Kohlrausch (1881), Porat (1876), Verhoeff (1937), Silvestri (1912), Kraepelin (1903), Attems (1930a, 1938, 1953), Jangi and Dass (1984), Lewis (2001, 2004a, 2010d, 2014, 2015), Koch (1985), Schileyko (1992, 1995, 1998, 2007) and Joshi and Edgecombe (2013). Some available type material is revised and photographed to emend species descriptions. If not possible to examine the type material or recollect from the type locality, the closest available material from the same region is used in order to reduce the effects of geographical variation in species identification. In the case of some species that poorly known with regards to biological context such as the sexual and colour dimorphism, morphological and molecular sampling are used to evaluate states of morphological changes in some traditional characters.

Taxonomic description and distribution records of *Rhysida* and *Alluropus*

Each taxon is re-described based on a combination of taxonomic characters. Morphological terminology used in descriptions follows Bonato et al. (2010). The recent list of synonyms for both genera and each species follows Chilobase (Bonato et al. 2016). The arrangement of descriptive text is based on previous taxonomic revisions of scolopendrids, such as (Lewis, 2001, 2004b, 2010d, 2014, 2015), Schileyko (1995, 2007), Joshi and Edgecombe (2013) and Siriwut et al. (2016). Distribution records of *Rhysida* and *Alluropus* species were determined based on field sampling, museum collections, and literature from this region. Names of localities cited in descriptions were arranged according to political boundaries and were categorized into two sections as in Siriwut et al. (2016), as follows. Distribution maps for each species were drawn by compiling all records to provide more detailed comparative distribution patterns. Each locality is marked by a filled symbol to refer to data from observed material, whereas a blank symbol refers to data from the literature. All inadequately detailed localities and recorded localities for ambiguous juvenile or damaged specimens have been excluded from the distribution maps.

DNA extraction and gene amplification

DNA template was extracted from locomotory legs of 69 specimens using commercial genomic DNA extraction kits (Qaigen^{TM}). Partial sequences of cytochrome *c* oxidase subunit I (COI), 16S rRNA, and 28S rRNA were amplified following the PCR method. Amplified markers and conditions at each reaction stage are as detailed in in previous phylogenetic works on Scolopendridae (Joshi and Karanth, 2011; Vahtera et al., 2013; Siriwut et al., 2015). For the annealing stage, the setting temperature was varied in each partial gene as follows: 44–47 °C for 40 sec for COI, 39–45 °C for 40 sec for 16S, and 47–55 °C for 40 sec for 28S. The signaling and concentration of amplified PCR products were checked using 1% (w/v) agarose TBE buffer gel electrophoresis and observed under a UV Tran-simulator device after being dyed by SYBR safe reagent. DNA purification was performed to discard interference effects from primer dimer. The purified PCR products were sequenced at Macrogen, Inc. (Korea). Sequences were aligned with centipede sequences from GenBank by using the BLASTn algorithm to check the correction of amplified targets.

Phylogenetic reconstruction

Protocols for phylogenetic analysis follow (Siriwut et al., 2015a; Siriwut et al., 2015b). COI and 28S sequences were corrected under a shadow pairwise-nucleotide comparison function in Sequence Navigator (Parker, 1997) while the 16S dataset was corrected in MAFFT v7.273 (Katoh et al., 2005; Katoh and Standley, 2013). Chromatograms were used to detect erroneous sequences by pair-wise comparisons between each complimentary DNA sample. Programs for phylogenetic analyses were obtained from MOLPHY ver. 32, which includes universal parameter sets and format transformation programs such as Kakusan 4 v.4.2015 (Tanabe, 2007). Additional data preparation for some sequence files was conducted in MEGA 6 (Tamura et al., 2013a) and Mesquite (Maddison and Maddison, 2011). Kakusan 4 was used to apply standard command line and molecular parameter settings and initial testing of a DNA substitution model.

Available sequences of the subfamily Otostigminae from previous molecular studies were obtained from GenBank to combine with novel sequence data for each partial gene. Exemplars of the sister group of Otostigminae, the subfamily Scolopendrinae, were used as outgroups for rooting trees, selecting species of the both tribes, Asanadini (*Asanada*) and Scolopendrini (*Scolopendra* and *Cormocephalus*). The selection of nucleotide substitution was calculated with Jmodel test (Darriba et al., 2012) based on Neighbour-Joining tree analysis using four nucleotide sequences and nucleotide bases combined as $1^{st}+2^{nd}+3^{rd}$+non-coding codons in the CIPRES web portal. Codon positions that contained gaps or contamination were discarded. Each gene fragment was analyzed independently to find a best-fitting substitution model.

Maximum likelihood and Bayesian inference trees were computed in RAxML (Stamatakis, 2006) and MrBayes v3.2.6 (Huelsenbeck and Ronquist, 2001a) in CIPRES under default parameters. In the ML analysis, the likelihood-search was performed under 1,000 bootstrap pseudo-replicates. Bayesian inference employed 10,000,000 pseudo-replicates with random sampling function every 1,000 replicates.

The tree search was terminated after the standard deviation of portioning frequency value reached lower than 0.01. The discard function for trees was set at 50% as burn-in to decrease the effect of convergence tree topology, and a 50% majority rules consensus was used to interpret the final tree topology. Final tree topologies in both analyses were edited in FigTree. Relationships among OTUs were regarded as reasonably supported clades and support values depicted on the trees when bootstrap and posterior probability values exceeded 70% in ML or 0.95 in BI, respectively (Huelsenbeck and Hillis, 1993; Larget and Simon, 1999).

Results

Molecular phylogeny of the subfamily Otostigminae

Sixty-nine sequences from three partial genes were successfully amplified and comparatively aligned (Table 6.1). The annotation of each partial gene sequence is described in Table 2. Genetic distance of each mitochondrial DNA dataset (COI and 16S) was aligned and calculated under a K-2 parameter model with 1,000 bootstrap replicates. Interspecific variation among members of Otostigminae is between 10.5 to 25.6% for COI whereas variation in 16S is between 6.2 to 26.4%. The results of inter- and intra-specific variation of all representative taxa in the subfamily Otostigminae have been documented together with the standard deviation of each taxon sample. The substitution model selected for Maximum likelihood (ML) and Bayesian inference (BI) algorithms in tree reconstruction were GTR+CAT and GTR+I, respectively.

The phylogenetic tree found all sampled members of the subfamily Otostigminae to form a monophyletic group with outgroup rooting by four taxa in the subfamily Scolopendrinae (*Scolopendra*, *Cormocephalus* and *Asanada*). Within Otostigminae, the topology was sensitive to the algorithm used, which mainly involves a shift in the systematic position of particular genera. *Ethmostigmus*, for example, usually nested together with *Sterropristes* in ML analysis but in BI analysis this genus was nested with *Rhysida* and *Alluropus* from mainland Southeast Asia, and *Sterropristes* was isolated as the basal clade in the tree. In (Figs 6.1 and 6.2), the tree showed undetermined relationships between the genera of this subfamily, collapsing them in a polytomy (in both ML and BI). In the BI analysis (Fig. 6.1), *Sterropristes*, *Ethmostigmus*, *Alipes*, *Alluropus* and *Digitipes* are all monophyletic. Two species of *Sterropristes* have been verified with strong support, indicating the separation between *S. violaceus* and *S. metallicus*. However, phylogenetic relationships within this genus are still questionable because one specimen determined as *S. metallicus* from southern Myanmar is nested with *S. violaceus* rather than with its putative conspecifics. The phylogenetic relationship and position of the endemic genus *Edentistoma* were unstable, being allied to either *Rhysida* or to *Otostigmus* depending on which phylogenetic algorithms were used. In the case of the genus *Digitipes*, monophyly is still ambiguous because some species that have been reassigned to *Otostigmus,* namely, *O. nudus* (formerly *D. periyarensis*), are nested inside a group of the remaining members of *Digitipes*, as well as the labile position of *D. barnabasi* in the ML analysis, in which it nested with some members of *Rhysida* and *Alluropus.*

Various lineages within *Otostigmus* have undetermined relationships and are variably paraphyletic or polyphyletic, with nodes that lack strong statistical support. Old World *Otostigmus* taxa divide into seven species groups that show morphological similarity and receive clade support as follow: *spinosus-astenus* group, *multidens* group, *aculeatus* group, *sulcipes* group, *ruficeps* group, *rugulosus* group and *scaber* group. There are also three putative species that were defined as *Otostigmus* A, B and C which also nested as sister clades to those latter groups. The "*multidens"* group shows high genetic differentiation (15.2 and 13.5% intraspecific variation in COI and 16S, respectively) and the tree topology divided it into two clades. In the case of New World *Otostigmus*, the phylogenetic tree indicated that *O. spinicaudus* and *O. caraibicus* are allied to *Alipes* which is distributed in Africa, with statistical support (only in BI).

Rhysida was separated into two groups, composed of Indo-Australian species and African-Indian-Southeast Asian species, respectively. The Indo-Australian clade comprises four described species, *R. singaporensis*, *R. carinulata, R. nuda* and *R. polyacantha*, while *R. immarginata* (a former subspecies of *R. nuda*) was nested with other remaining taxa. *R. longipes* and *R. lithobioides* resemble each other closely and are widespread throughout Indian Oceanic territory, some parts of Africa, and mainland Southeast Asia. The monotypic genus *Alluropus* is nested together with Indo-Australian *Rhysida* with statistical support only in the BI analysis. Within

Alluropus (Fig. 6.1: clade A), two main clades with strong support both in ML and BI analyses have clear geographical signal: the genus consists of an Indochina clade (Fig. 1:clade B) and a Tenessarim clade (Fig. 6.1: clade C). In the BI analysis, each *Alluropus* clade represented composite populations of two morphotypes of *A. calcarata* whereas the ML tree (Fig. 6.2) showed that the Tenessarim clade only comprises morphotype 2. These two morphotypes depicted 10.5% and 7.2% interspecific variation in COI and 16S, respectively.

Species diversity of mainland Southeast Asia Otostigminae

In total, 948 collected specimens from Thailand and some neighbouring countries were classified and categorized into five genera as follow: 10 species in *Otostigmus*, two species in *Sterropristes*, two species in *Digitipes*, four species in *Rhysida*, and one species in *Alluropus.* Twenty morphologically distinct species were detected by identification based on previous taxonomic studies of Otostigminae, of which four unknown putative species have been found. Morphological comparison based on traditional taxonomic characters such as the appearance of paramedian and median sutures on the sternites, the appearance of keels and spines on tergites, the presence of a median furrow on the tergite of the ultimate leg-bearing segment, number of teeth on the tooth-plates, numbers of spines on the coxopleural process, and number of legs with tarsal and tibial spurs. Moreover, some species also exhibit secondary sexual characters on the ultimate legs of males, providing taxonomic information at the genus- or species-levels. This pertains to *Digitipes*, *Alluropus* and some species of *Otostigmus.*

Rhysida and *Alluropus* are the second and third most abundant genera in this area. In this study, 507 specimens were found and identified as belonging to these two genera. They exhibited morphological similarity and sympatric distributions in some areas. We provide further information in order to emend the diagnoses of the genera and species description based on the re-examination of some type material of described species as follow: *R. lithobioides*, *R. immarginata*, *R. leviventer*, *R. marginata* and *Alluropus calcarata.* The systematic revision of these two genera was conducted in order to verify the taxonomic validity and delimit boundaries between some species following results from examination of types and additional specimens and molecular phylogeny of three partial genes. The descriptions in this study are mainly based on mainland Southeast Asia species but also give some discussion of closely related *Rhysida* species from India, Indo-Australia and other part of Southeast Asia. A taxonomic key to Southeast Asian *Rhysida* and *Alluropus* is provided as follows:

Taxonomic key to genera and species of *Rhysida* and *Alluropus* in SE-Asia

1. Incomplete paramedian sutures on sternites, leg 1 with prefemoral spur, tarsus 1 of ultimate legs club-shaped…..…..….***Alluropus calcarata* (Pocock, 1891)**
   Complete paramedian sutures on sternites, leg 1 without prefemoral spur, tarsus 1 of ultimate legs long and slender in male…...***Rhysida* Wood, 1860 (2)**
2. Most tergites with margination……..…………………………………………….**3**
   Tergites without margination except tergite of ultimate leg-bearing segment………..………………………......……..***R. immarginata* Porat, 1867**
3. Coxopleural process extremely long……...…..…***R. monticola* (Pocock, 1891)**
   Coxopleural process short or moderately long…………………...…………....**4**
4. Posterior tergites with keels and spinulation, tooth-plates usually with >5 teeth, two tarsal and tibial spur on legs 1-18……………..………..……..…**5**
   Posterior tergites smooth, tooth-plate with 3 to 4 teeth on each side, two tarsal and tibial spur present only on anterior legs………………………….……..…**6**
5. Coxopleural process bearing 0-3 dorsal, 1-2 lateral spines....……......................
   ……………………………………………….…………..***R. carinulata* Haase, 1887**
   Coxopleural process bearing 1 subapical and 1 lateral spine…….……………..
   ……………………………………...……..***R. singaporensis* Verhoeff, 1937**
6. Coxopleural process bearing 1 subapical and 1 lateral spines, tooth-plate with 4 to 5 teeth, two tarsal spurs on legs 1-11 ….…. ***R. longipes* (Newport, 1845)**
   Coxopleural process with 0-1 lateral spines and subapical spine absent, tooth-plate with 3 to 4 teeth, two tarsal spurs on legs 1-5………..………………..……
   …………………......................…...……..……***R. lithobioides* (Newport, 1845)**

Systematics

Family Scolopendridae Leach, 1816

Subfamily Otostigminae Krapelin, 1903

Genus *Rhysida* Wood, 1862

Synonyms

Branchiostoma Newport, 1845
Ethmophorus Pocock, 1891
Ptychotrema Peters, 1855
Trematoptychus Peters, 1862

Type species. *Rhysida lithobioides* (Newport, 1845)

Diagnosis. Variable length up to 11-12 cm. 16-22 antennal articles, basal 3 to 4 glabrous dorsally. Cephalic plate without paramedian sutures on posterior part. Coxosternite smooth, without median suture. Each tooth-plate usually with 4-7 teeth. T1 overlapping cephalic plate, without transverse suture. Incomplete paramedian sutures on sternites. Coxopleural process with two apical and one subapical spines, lateral and dorsal spines present or absent. Legs with femoral, tibial and tarsal spurs. Ten pairs of oval spiracles on segments 3, 5, 7, 8, 10, 12, 14, 16, 18 and 20. Genital segments 1 and 2 well developed, sternite of genital segment 1 round and convex posteriorly, with median suture. Gonopods present in male.

***Rhysida lithobioides* (Newport, 1845)**

Figs 6.3, 6.4

Brachiostoma lithobioides Newport, 1845: 411. Kohlrausch, 1881: 67. Haase, 1887: 84

Rhysida lithobioides Kraepelin, 1903: 150, fig. 93. Attems, 1930: 187, figs 232-234. Jangi and Dass, 1984: 48, fig. 50. Lewis, 2001: 44-45.

Rhysida lithobioides abessynica Attems, 1930: 187, fig. 233

Rhysida lithobioides paucidens Pocock, 1897: 188, fig. 234. Jangi and Dass, 1984: 48 Lewis, 1996: 146, fig. 12

Rhysida lithobioides trispinosus Jangi and Dass, 1984: 48, figs 93-100.
Rhysida lithobioides kumaonensis Khanna, 1994: 338, figs 8-14.
Rhysida lithobioides shivalikensis Khanna, 1994: 312, figs 1-5.
Rhysida leviventer Attems, 1953: 147 **Syn. nov.**

Type locality: China

Material examined: Holotype. OMNH-MYRI 009, one dried spm., labeled " Branchiostoma lithobioides Newpt", China. Type material defined as *R. lithobioides abessynica.* NHMW Inv. No. 1591, seven spms., unknown locality, with label "Typus", leg. Roret, 1907. NHMW Inv. No. 2058, one syntype spm. of *R. leviventer*, Xieng Khouang, Laos, leg.-don. Dawidoff C., det. Attems.

Diagnosis. 16-18 antennal articles, 3 basal articles glabrous dorsally. 3-4 teeth on tooth-plate. Tergites with paramedian sutures from TT4-7, margination starting from TT9. Sternites with paramedian sutures extending 10-35% length of sternite. Coxopleural process with 2 apical and 0-1 lateral and absent dorsal spines. Ultimate leg prefemora with 1-3 VL, 1-3 VM, 0-2 M, 1-2 DM and 0-1 corner spines. Two tarsal spurs on legs 1-5 (1-18), one tarsal spur on legs 6(19)-20. Tibial spur on legs 1-4(5). Leg 1 with femoral spur.

Composite description (Holotype in parenthesis). Body length ranges from 33-65 (44) mm. Colour in both live and preserved material greenish-brown. Antenna pale grey or yellowish. Cephalic plate and ultimate leg-bearing segment orange brown or yellowish. Forcipular segment orange. Locomotory legs pale grey, light blue on distal part. Cephalic plate without small, fine setae. Anterior median part of cephalic plate with short, straight sulcus without bifurcation posteriorly.

Antenna with 16-19 articles (7, in damaged condition), basal 3 articles glabrous dorsally; 3 articles glabrous ventrally. Antenna reaches to TT5 or 6. Forcipular trochanteroprefemoral process bearing one apical and two lateral teeth. Tooth-plate wider than long, with 4-5 (4) main teeth, separated into two groups, two inner and two outer; basal part with a clear, fine seta on each side. Coxosternite with median diastema reaching to base of tooth-plate, basal part of tooth-plate with curved sutures extending laterally subparallel to margin of coxosternite. Angulation of basal sutures ca 130º-135º.

Tergites 1 to 3 overlapping posterior part of foregoing tergite. Paramedian sutures complete from TT(4)-5; margination starting on TT8(9)-14 (17 in one spm. of NHMW Inv.No. 1591). Tergite of ultimate leg-bearing segment usually without median furrow on posterior part (furrow present in one specimen). Sternites with short paramedian sutures on anterior part, extending 10-35% length of sternite. Sternite of ultimate leg-bearing segment with sides converging posteriorly, posterior margin slightly concave.

Coxopleural process moderately long, with two apical spines; lateral and dorsal spines absent. Dense pore field covering whole area of coxopleuron except on ventro-distal part of coxopleural process, pore-free area reaching to 10-30 % the distance to margin of sternite of ultimate leg-bearing segment. On lateral side of coxopleura, dense pore area not covered by lateral margin of tergite of ultimate leg-bearing segment. Ultimate legs long and slender with ratio of ultimate leg articles as follow; 0.5:1 between tarsus 1 and tarsus 2, 0.8: 1 between tarsus 2 and tibia, 0.9:1 between tibia and femur and 0.8:1 between femur and prefemur. Prefemoral spines of ultimate leg: 1 (2 to 3) VL, 1 (2 to 3) VM, 0 (2) M, 1-2 (3) DM and 0-1 corner spines.

Legs without short setae; legs 1 to 5 usually with two tarsal spurs, subsequent legs to leg 20 with one tarsal spur. Tibial spurs on leg 1-5 (only left side in legs 2-4 of holotype) and femoral spur on leg 1. Two accessory spurs and pretarsal claw present on all legs.

Remark According to previous taxonomic studies of this type species, *R. lithobioides* comprises six subspecies; *R. l. lithobioides*, *R. l. abessynica*, *R. l. paucidens*, *R. l. trispinosus*, *R. l. kumaonensis* and *R. l. shivalikensis*. The nominotypical subspecies of *R. lithobioides* was reported from China whereas the five latter subspecies were reported from African and Indian territories. Only *R. l. lithobioides* exhibited a morphological difference from the other subspecies in its number of legs with one and two tarsal spurs (legs 1-5 with one tarsal spur and subsequently with two in the holotype of *R. l. lithobioides* whereas the other subspecies show legs 1-18 with two tarsal spurs and subsequently with one) and appearances of a lateral spine on the coxopleural process only in *R. l. lithobioides.* The taxonomic comparison of six subspecies is given in Table 6.3. However, without further molecular sequences and additional materials of those previously described subspecies, the morphological concordance between these subspecies makes it questionable as to whether they depict geographical variation or cryptic species. Moreover, *R. lithobioides* s. l. is also morphologically identical to an Indo-Chinese *Rhysida* species, *R. leviventer* from Xieng Khauang, central Laos, with respect to the incomplete paramedian sutures on the sternites, the arrangement of spines on the coxopleural process, and the number of legs with tarsal and tibial spurs. For this reason, *R. leviventer* is now synonymized under *R. lithobioides.*

Distribution The exact distribution range of this species is still unknown. The type specimen was collected from an unspecified locality in China. Attems (1930) stated that this species may also probably be found in Burma. Further distribution records are in northeastern Africa (Lewis, 2001) and India (Jangi and Dass, 1984; Khanna, 1994). The summary of its distribution is as follows: **Africa**. Somalia, Ethiopia. **India**. Pondicherry, Tamil Nadu, Maharashtra, Uttra Pradesh: Terai. **Southeast Asia**. Burma?, Laos. **East Asia** China.

***Rhysida longipes* (Newport, 1845)**

Figs 6.5B, 6.6-6.7

Rhysida longipes—Pocock, 1891: 418, 1895: 23, pl. 2, fig. 11. Kraepelin. 1903: 148, fig. 91. Chamberlin, 1920: 19. Attems, 1930: 193. Jangi and Dass, 1984:48, fig. 50. González-Sponga 2002: 59, pl. 8. Schileyko, 1995: 74, 1998: 269, 2007: 82. Lewis, 2002: 86, figs 11-14. Tran et al., 2013: 227.

Synonyms

Brachiostoma longipes Newport, 1845: 411. Gervais, 1847: 249. Kohlrausch, 1881: 22. Haase, 1887: 83, pl. 5, fig. 86.

Branchiostoma affine Kohlrausch, 1878: 22 Kraepelin, 1903: 148

Branchiostoma gracile Kohlrausch, 1878: 21 Kraepelin, 1903: 148

Branchiostoma longipes rotundatum Haase, 1887: 83. Kraepelin, 1903: 148.

Otostigmus simplex Chamberlin 1913: 75. Attems, 1930: 153. Schileyko, 1998: 269, 2001: 432. Lewis, 2002: 1690, figs. 8-11.

Rhysida longipes brevicornis Takakuwa , 1934: 224, Chao, 2008.

Type locality: Not designed

Material examined: Thailand CUMZ 00422, seven spms., Mueang, Mae Hong Son (N 19°21'51", E 97°58'59"). CUMZ 00423, six spms., Ban Rom-Mai, Mueang, Mae Hong Son (N 19°18'26.1", E 97°57'51.6"). CUMZ 00424, seven spms., Chulalongkorn University, Bangkok (N 13°44'19", E 100°31'49"). CUMZ 00425, four spms., Black Ant Resort, Mae Sariang, Mae Hong Son (N 18° 9'50.6", E 97°55'53.4"). CUMZ 00426, one spm., Victory Monument, Bangkok (N 13°45'41", E 100°32'26"). CUMZ 00427, one spm., Wat Pa Ban Yai, Mueang, Mae Hong Son (N 19°17'55.2", E 97°59'12.5"). **Malaysia** CUMZ 00428, 21 spms, Sugai Siput Utara, Perak, Malaysia (N 4°45'38.4", E 101°7'3.8"). CUMZ 00429, 12 spms, Gunung Datok, Ipoh, Perak, Malaysia (N 4°46'55.4", E 101°7'14"). CUMZ 00430, two spms, Kampung S. Ramasamy, Perak, Malaysia (N 4°46'55.4", E 101°7'14"). CUMZ 00431, 12 spms., Bukit Merah, Perak, Malaysia (N 5°2'14.5", E 100°39'13.3"). **Myanmar** CUMZ 00432, one spm., PK-2, Bahin Village, Myaing, Makway (N 21°43'40",E 94°43'14").

Diagnosis 16-18 antennal articles, 3 basal articles glabrous dorsally. 4-5 teeth on tooth-plate. Tergites with paramedian sutures from TT4-6, margination starting from TT 8-11. Paramedian sutures extending 10-15% length of sternites. Coxopleural process with 3-4 apical and 0-1 lateral spines. Ultimate leg prefemora with blackish thorn-like spines, including 3-4 VL, 2-3 VM, 0-1M and 1-2 DM and 2-5 corner spines. Two tarsal spurs on legs 1-8(11), one tarsal spur on legs 9-19. Tibial spur on legs 1-4. Leg 1 with femoral spur.

Composite description Body length ranges from 22-73 mm. Body colour in both live and preserved material greenish-brown. Antenna pale grey or blue. Cephalic plate, first tergite and ultimate leg-bearing segment orange brown or yellowish. Forcipular segment orange. Most locomotory legs yellowish with light blue on latero-distal part of each article. Cephalic plate without small, fine setae. Anterior median part of cephalic plate with short, straight sulcus without bifurcation posteriorly.

Antenna with 16-18 articles, basal 3 articles glabrous dorsally; 2.8 articles glabrous ventrally. Antenna reaches to T3-4. Forcipular trochanteroprefemoral process bearing one apical and two or three lateral teeth. Tooth-plate wider than long, with 4-5 main teeth on each side, separated into two groups, two or three inner and two outer; basal part with a clear, fine seta on each side or without. Interior part of article 2 of telopodite of second maxilla with a fine pigmented spine. Coxosternite without median suture, coxosternal median diastema reaching to base of tooth-plate, basal part of tooth-plate with curved sutures extending laterally subparallel to margin of coxosternite. Angulation of basal sutures ca 130º-135º.

TT1-3 overlapping posterior part of cephalic plate or foregoing tergite. Tergites with paramedian sutures complete from TT5-8; margination starting on TT8-11. Tergite of ultimate leg-bearing segment without median furrow on posterior part. Sternites with short paramedian sutures on anterior part, extending 10-20% length of sternite. Surface of sternites with or without circular depression on postero-median part. Sternite of ultimate leg-bearing segment with sides converging posteriorly, posterior margin slightly concave.

Coxopleural process long, with two apical, one subapical, one lateral spine, without dorsal spine. Dense pore field covering entire area of coxopleuron except on ventro-distal part of coxopleural process, pore-free area reaching to 80-100% the distance to margin of sternite of ultimate leg-bearing segment. On lateral side of coxopleura, dense pore area not covered by lateral margin of tergite of ultimate leg-bearing segment. Ultimate legs long and slender with ratio of articles as follow; 1:1.9 between tarsus 1 and tarsus 2, 1.9:2.1 between tarsus 2 and tibia, 2.1:2.4 between tibia and femur and 2.4:2.7 between femur and prefemur. Prefemoral spines of ultimate leg: VL-3 to 4, VM-2 to 3, M- 0 to 1, DM- 1 and 1 corner spines.

Legs with short setae on anterior segments; legs 1 to 7 (8) usually with two tarsal spurs (occasionally, two tarsal spurs on only one side), subsequent legs to leg 19 (18 in in one specimen) with one tarsal spur. One tibial and femoral spur on legs 1-3 or 4 in equal frequency (5 in one specimen). Two accessory spurs and pretarsal claw present on all legs. Pretarsus and tarsus 2 of ultimate legs without small setae.

Remarks In the most recent revisions, *R. longipes* consist of three nominal subspecies: *R. longipes longipes*, *R. longipes simplicolor* Chamberlin, 1920, and *R. longipes malayanicus* Verhoeff, 1937. The distinction between these three subspecies is based on the number of spines on the coxopleural process and the number of legs with tarsal spurs. In addition, Attems (1930) proposed *R. l. l.* var. *sinhalana* based on the four glabrous antennal articles in specimens from Sri Lanka. We examined additional material from Sri Lanka in the NHMW and NHMUK and confirm that this unique morphological characteristic is presented only in this local population. In this study, a high genetic divergence is observed between sampled populations from Southeast Asia and India. Genetic distance ranges from 11-14% variation within species, which is higher than found in other *Rhysida* species (1-5% in *R. immarginata* and *R. singaporensis*). This result may suggest the further investigation of each morphological subspecies using morphological and molecular taxonomy is needed to clarify this subspecies complex. In addition, Koch (1985) and Lewis (2002) pointed out the morphological similarity between *R. longipes* and *R. nuda*. The present phylogenetic analysis supports the distinction between *R. longipes* from India, Burma, Thailand and the Malay Peninsula and Australian *R. nuda.* The tree topology placed *R. longipes* as sister taxon to other Indian species (*R. lithobioides* and *R. immarginata*) whereas *R. nuda* grouped with other Indo-Australian species. For this reason, former taxonomic ambiguity between *R. longipes* and *R. nuda* is clearly resolved.

Distribution A widespread species occurring throughout tropical mainland and island faunas. The native distribution is difficult to determine because it is synanthropic in several countries. The current distribution record of this species is as follows: **Southeast Asia.** Myanmar; Thailand; Malay Peninsula. **Indian Ocean**. India: Tamil Nadu, Goa, Madhya Pradesh, Maharashtra, Mysore; Sri Lanka. **Africa**. West and east territories: Madagascar, Seychelles, Mauritius. **Central and South America.** Mexico.

Rhysida immarginata (Porat, 1867)

Figs 6.5A, 6.8-6.10

Rhysida immarginata Porat, 1867: 24, Kraepelin, 1903: 143. Attems, 1930:190

Synonyms

Brachiostoma immarginatum Porat, 1867: 24. Meinert, 1886 : 118

Brachiostoma indicum Kohlrausch, 1881: 67.

Brachiostoma subspinosum Tömösvary, 1885: 653

Brachiostoma immarginatum celebense Haase, 1887: 85, pl.5, figs 89-90.

Type locality: Manila [Philippines]

Material examined: Syntype: NHRS-KASI 00000044, two spms. Manila, 1853, Col. Kinberg, det. C. U. v. Porat.

Additional materials. Thailand CUMZ 00433, four spms., Wat Tha Li Phong, Chiang Yai, Nakhon Si Thammarat (N 8°5’14”, E 100°7’55”). CUMZ 00434, one spm., Wat Tham Khao Chin, Mueang, Satun (N 6°38’32”, E 100°5’15”). CUMZ 00435, three spms., Wat Tham Phung Chang, Mueang, Phang Nga (N 8°26’34”, E 98°30’57”). CUMZ 00436, 10 spms., Chulachomklao Royal Military Academy Monument, Kra Buri, Ranong (N 10°29’37”, E 98°54’35”). CUMZ 00437, 11 spms., Wat Sala Luang Bon, Ranot, Songkhla (N 7°50’46”, E 100°21’10”). CUMZ 00438, two spms., Wat Tham Phannara, Nakhon Si Thammarat (N 8°25’19”, E 99°22’47”). **Malaysia** CUMZ 00439, seven spms., Gunung Mesah, Guping, Perak (N 4°24’57.9”, E 101°11’14.6”). CUMZ 00440, 35 spms., paddy field, Kedah (N 6°12’2”, E 100°21’59”). CUMZ 00441, two spms., ice factory near Batu Madu, Gua Musang, Kelantan (N 4°52’14”, E 101°57’36”). CUMZ 00442, two spms., Klinik Desa, Kampong Panit Luar, Kedah (N 6°12’30”, E 100°16’22”). CUMZ 00443, one spm., Sungai Terong, Perak (N 4°38’21.8”, E 100°42’50”). **Laos** CUMZ 00444, two spms., Ban Nam Noen, Hua Mueang, Houaphan (N 20°35’24”, E 101°3’17”). **Undetermined** CUMZ 00445, four spms., unknown locality.

Diagnosis 16-18 antennal articles, 3 basal articles glabrous dorsally. 3-4 teeth on tooth-plate. Tergites with paramedian sutures from TT4-7, only tergite of ultimate leg-bearing segment marginated. Paramedian sutures extending 10-15% length of sternites. Coxopleural process with 2 apical and 1 subapical spines. Ultimate leg prefemora with 3-4 VL, 2-3 VM, 0-1M and 1-2 DM and 2-5 corner spines. Two tarsal spurs on legs 1-8(11-13), one tarsal spur on legs 9-19. Tibial spur on legs 1-4. Leg 1 with femoral spur.

Composite description Maximum body length to 19-81 mm (45 and 46 mm. in syntypes). Body colour in live material black-green sequined. Antenna pale grey or yellowish. Forcipular segment yellowish. Most locomotory legs reddish orange. Cephalic plate without small, fine setae. Anterior median part of cephalic plate with short, straight sulcus without bifurcation posteriorly.

Antenna with 17-20 (19-20) articles, basal 3 articles glabrous dorsally; 2.8 articles glabrous ventrally. Antenna reaches backward to TT4-5. Forcipular trochanteroprefemoral process bearing one apical and two or three lateral teeth. Tooth-plate wider than long, with four or five main teeth on each side, separated into two groups, two inner and two outer; basal part with a clear, fine seta on each side or without. Interior part of article 2 of second maxilla with a fine pigmented spine. Coxosternite without median suture, median diastema reaching to base of tooth-plate, basal part of tooth-plate with curved sutures extending laterally subparallel to margin of coxosternite. Angulation of basal sutures ca 100º-110º.

Tergites 1 to 3 overlapping posterior part of foregoing tergite. Paramedian sutures complete from TT4(5)-6; margination only on T21. Tergite of ultimate leg-bearing segment without median depression on posterior part. Sternites with short paramedian sutures on anterior part, extending 10-15% length of sternite. Surface of sternites with or without circular depression on postero-median part. Sternite of ultimate leg-bearing segment with sides converging posteriorly, posterior margin slightly concave.

Coxopleural process moderately long, with two apical and one subapical spine(s); lateral and dorsal spine absent. Dense pore field covering entire area of coxopleuron, pore-free area reaching to 50-100% the distance to margin of sternite of ultimate leg-bearing segment. On lateral side of coxopleura, dense pore area not covered by lateral margin of tergite of ultimate leg-bearing segment. Ultimate legs long and slender with ratio of articles as follow: 0.5:1 between tarsus 1 and tarsus 2, 0.8:1 between tarsus 2 and tibia, 0.8:1 between tibia and femur and 0.9:1 between femur and prefemur. Prefemoral spines of ultimate leg: 1-2 VL, 0-1 VM, 1 DM and 2-5 corner spines.

Legs with short setae on anterior segments; legs 1 to 13 usually with two tarsal spurs (atypically, two tarsal spurs on legs 15-16: NHMUK, Mandalay), subsequent legs to leg 19 with one tarsal spur. One tibial and femoral spur on legs 1-2 in equal frequency (leg 5 in one specimen). Two accessory spurs and pretarsal claw present on all legs. Pretarsi and tarsi 1 and 2 without small setae.

Remarks A diagnostic character of this species is the lack of tergite margination. This species was previously recognized as a subspecies of the Australian species *R. nuda immarginata.* However, previous taxonomic revision has argued that they are in fact different species. In this study, the molecular phylogeny supports their separation, indicating a closer relationship between *R. immarginata* and Indian *Rhysida* than with Australian species. This relationship may correlate to the plate tectonic history of the Indian subcontinent, as proposed by molecular dating of Indian scolopendromorphs (Joshi and Karanth, 2010). However, a broad-scale phylogeographic study of this species would be useful to verify taxonomic validity of specimens bearing the name *R. immarginata* from the African and Neotropical regions.

Distribution Widespread species likely to be pan-tropical based on occurrence in both Old World and New World territories. Taxonomic review of Australian *Rhysida* (Koch, 1985) indicated that most extra-Australian records of *R. nuda*, a native Australian species, seem to actually refer to *R. immarginata*. The extensive range of its distribution remains questionable. In this study, populations are most abundant in the Thai-Malay Peninsula. The distribution of *R. immarginata* in mainland Southeast Asia is as follows: Myanmar, Thailand, Laos, Vietnam, Malaysia (Peninsular).

***Rhysida singaporensis* Verhoeff, 1937**

Figs 6.5C, 6.11-6.12

Rhysida singaporensis Verhoeff, 1937: 218. Wang and Tang, 1965: 448. Lewis, 2001: 48, figs 100-103. Decker, 2013: 18.

Type locality: Bukit Timah, Singapore
Material examined: Topotypes CUMZ 00446, three spms, Bukit Timah, Singapore (N 1°20’39”, E 103°46’46”)

Diagnosis 19-21 antennal articles, 3 basal articles glabrous dorsally. 5-7 teeth on tooth-plate. Tergites with paramedian sutures from TT2-3, tergite margination from TT7-9, median keel present on TT10-20. Scattered spinulation present on surface of TT13-21. Paramedian sutures extending 10-25% length of sternites. Coxopleural process with 2 apical and 0-1 subapical and one lateral spines. Ultimate leg prefemora: 0-1 VL, 0-1 VM, 0-2 M and 1-2 DM and 0-1 corner spines. Two tarsal spurs on legs 1-18, one tarsal spur on legs 19-20. Tibial spur on legs 1-3. Leg 1 with femoral spur.

Composite description Maximum body length up to 73-89 mm. Body colour in both live and preserved material greenish-brown. Antenna pale grey or blue. Cephalic plate, T1 and ultimate leg-bearing segment orange brown or yellowish. Forcipular segment orange. Most locomotory legs yellowish with light blue on latero-distal part of each article. Cephalic plate without small, fine setae. Anterior median part of cephalic plate with short, straight sulcus without bifurcation posteriorly.

Antenna with (17)19-21 articles, basal 3 articles glabrous dorsally; 2.8 articles glabrous ventrally. Antenna reaches to TT4-5. Forcipular trochanteroprefemoral process bearing one apical and two or six lateral teeth. Tooth-plates wider than long, with 5-7(8) teeth on each side, separated into two groups, three to four inner and two to three outer; basal part with a clear, fine seta on each side or without. Interior part of article 2 of telopodite of second maxilla with a fine pigmented spine. Coxosternite without median suture, median diastema reaching to base of tooth-plate, basal part of tooth-plate with curved sutures extending laterally subparallel to margin of coxosternite. Angulation of basal sutures ca 100º-110º.

Cephalic plate without transverse suture. TT1 and 2 overlapping posterior part of foregoing tergite. Tergites with paramedian sutures complete from TT2-3; margination starting on TT7-9. Tergites on posterior half of body with median keels and small spines. Tergite of ultimate leg-bearing segment without median furrow on posterior part. Sternites with short paramedian sutures on anterior part, extending 10-25% length of sternite. Surface of sternites without depression. Sternite of ultimate leg-bearing segment with sides converging posteriorly, posterior margin slightly concave.

Coxopleural process long, with two apical, one or absent subapical, one lateral spines and dorsal spine absent. Dense pore field covering entire area of coxopleuron except on ventro-distal part of coxopleural process, pore-free area reaching to 40-60% the distance to margin of sternite of ultimate leg-bearing segment. On lateral side of coxopleura, dense-pore area not covered by lateral margin of tergite of ultimate leg-bearing segment. Ultimate legs long and slender with ratio of articles as follow: 0.6:1 between tarsus 1 and tarsus 2, 0.9:1 between tarsus 2 and tibia, 0.9:1 between tibia and femur and 1:1 between femur and prefemur. Prefemoral spines of ultimate leg: 1 VL, 0-1 VM, 0-2 M, 1 DM and 0-1 corner spines.

Legs without short setae on anterior segments; legs 1 to 18 with two tarsal spurs, subsequent legs to leg 20 with one tarsal spur. One tibial spur on legs 1-2(3). Only leg 1 with femoral spurs. Two accessory spurs and pretarsal claw on all legs. Tarsus 1 and tarsus 2 of ultimate legs without small setae.

Remarks This species has been reported from only the type locality, Bukit Timah, Singapore. However, another *Rhysida* species, *R. carinulata*, has been reported as nearly overlapping with it in Southeast Asia. One specimen previously described as *R. rugulosa* Pocock, 1894, from Sumatra (NHMUK 1896.10.6.12; Holotype) is morphologically similar to *R. singaporensis*. Flower (1901) identified *Rhysida* specimens from Bukit Timah, Singapore, as *R. carinulata* (subsequently designated as the type locality of *R. singaporensis* by Verhoeff in 1937). Recently. re-examination of Flower’s collection indicated that this species is properly referred to *R. singaporensis*. Moreover, the phylogenetic tree indicated that *R. singaporensis* was grouped with *R.* cf. *carinulata* from Sulawesi. However, the genetic distance in the COI dataset (19.8% genetic divergence) suggests differentiation between these two closely related species. The shared characters of these two species seem to be the scattered spinulation on tergite surfaces, which has not been reported in other *Rhysida* species.

Distribution This insular species is probably distributed in the Malay Archipelago, as recent records of it are restricted to Southeast Asia. Khanna (1984) recorded one specimen of *R. carinulata* from West Himalaya, Uttra Pradesh, India. Because of a lack of a description of this specimen, the taxonomic validity of this related species to *R. singaporensis* in mainland Asia is ambiguous. The distribution of this species is as follows: Singapore; Bukit Timah. Indonesia; Sumatra: Damau.

Genus *Alluropus* Silvestri, 1912

Type species *Alluropus demangii* Silvestri, 1912 (by monotypy)

Diagnosis. Length up to 11-12 cm. 16-22 antennal articles, basal 3 glabrous dorsally. Cephalic plate without paramedian sutures on posterior part. Coxosternite smooth, without median suture. Each tooth-plate usually with 4 teeth. T1 overlapping cephalic plate, without transverse suture. Complete paramedian sutures on sternites. Coxopleural process with two apical and one subapical spines, one lateral and one dorsal spines. Legs with femoral, tibial and tarsal spurs. Prefemoral spur present on leg 1. Ultimate legs with male secondary sexual characters, such as club-like structure of tarsus 1 and dorsomedian projection on prefemur. Ten pairs of oval spiracles on segments 3, 5, 7, 8, 10, 12, 14, 16, 18 and 20. Genital segments 1 and 2 well developed, sternite of genital segment 1 round and convex posteriorly, with median suture.

Distribution. This monotypic genus is distributed throughout mainland Southeast Asia except for Myanmar.

Alluropus calcarata (Pocock 1891) Comb. nov.

Figures 6.14-6.21

Rhysida calcarata Pocock, 1891: 61. Kraepelin, 1903: 146. Attems, 1930: 191, 1938: 338. Schileyko, 1998: 268, 2001: 441, 2007: 83.

Alluropus demangei Silvestri, 1912: 44, fig. 1. Attems, 1930: 198. Schileyko, 2007: 92. Tran et al. 2013: 221 **Syn. nov.**

Rhysida marginata Attems, 1953: 148. Schileyko, 2007: 92. Tran et al., 2013: 227. **Syn. nov.**

Type locality: Cambodia

Material examined: Specimens defined as morphotype 1. Thailand CUMZ 00447, three spms., Tha Khantho, Kalasin (N 16°50’6.1”, E 103°16’32”). CUMZ 00448, twelve spms., Wat Tha Thung Na Rit Tha Ram, Sai Yok Kanchanaburi (N 14°29’48”, E 98°50’23”). CUMZ 00449, three spms., Wat Tham Phonhom Lok, Sai Yok Kanchanaburi (N 14°6’4”, E 99°13’37”). CUMZ 00450, one spm., Kui Buri, Prachuap Khiri Khan (N 13°3’59”, E 99°40’49”). CUMZ 00451, one spm., Wat Khlong Wan, Mueang, Prachuap Khiri Khan (N 11°45’30”, E 99°44’5”). CUMZ 00452, one spm., Ban Nong Hua Phon, Kaset Wisai, Roi Et (N 15°41’51”, E 103°34’48”). CUMZ 00453, four spms., Wat Tham Welu Wan, Dan Chang, Suphan Buri (N 14°57’14”, E 99°38’54”). CUMZ 00454, two spms, Huai Hong Khrai, Chiang Mai (N 18°51’2”, E 99°13’27”). CUMZ 00467, one spm., Wat Tham Namphu, Nong Chang, Uthai Thani (N 15°26’44”, E 99°35’19”). CUMZ 00455, two spms., Wat Pa Bua Kaeo, Thong Pha Phum, Kanchanaburi (N 14°37’33”, E 98°40’40”). CUMZ 00456, two spms., from Wat Tham Khao Phrachan, Khao Chakan, Sa Kaeo (N 13°34’42”, E 102°5’34”). CUMZ 00457, two spms., Phupha Lom, Mueang, Loei (N 17°33’16”, E 101°52’7”). CUMZ 00458, Wat Tha Khanun, Thong Pha Phum, Kanchanaburi (N 14°4’34”, E 98°38’10”). CUMZ 00459, two spms., Nong Bo, Bonbue, Maha Sara Khram (N 16°1’51”, E 103°7’5”). CUMZ 00460, one spm., Khon Kaen University, Khon Kaen (N 16°28’23”, E 102°49’4”). CUMZ 00461, one spm., Khao Cha Ang Oan, Bo Thong, Chon Buri (N 13°12’1”, E 101°34’56”). CUMZ 00462, one spm., Lai Nan, Wiang Sa, Nan (N 18°49’0.1”, E 100°46’23”). CUMZ 00463, one spm., Tham Khao Kriap, Surat Thani (N 9°49’1”, E 99°2’16”). CUMZ 00464, one spm., Lam Ta Khong, Mueang, Nakhon Ratchasima (N 14°50’36”, E 101°34’2”). CUMZ 00465, eight spms., Wat Khao Isan Thep Prathan, Pak Tho, Ratchaburi (N 13°23’7”, E 99°46’25”). CUMZ 00466, six spms., Wat Pa Sai Mun, Sai Mun, Yasothon (N 15°56’30”, E 104°12’6”). CUMZ 00467, six spms., Wat Tham Namphu, Nong Chang, Uthai Thani (N 15°21’4”, E 99°41’0.1”). **Laos** CUMZ 00468, two spms., Hin Thoep Bridge, Nam Lik , Wang Wiang, Vientiane (N 18°54’43”, E 102°26’33”). CUMZ 00468, one spm., Ban Sop Hun, Mueang Ngoi, Luang Phra Bang (N 20°34’31”, E 102°36’21”). CUMZ 00469, two spms., Wat Phrachao Sing Kham Chai Ram, Nong Bua, Mueang La, Oudomxay (N 19°53’24”, E 102°8’13”). CUMZ 00470, one spm., Hot Spring Resort, Ban Nam-Hom, Xieang Khuang (N 19°29’25”, E 103°15’48”). CUMZ 00471, two spms., Ban Pa Oi, Mueang Huai Sai , Bokeo (N 20°16’44”, E 100°24’50”). CUMZ 00472, four spms., Wat Ban U, Luang Phra Bang (N 19°55’54”, E 102°12’40”). CUMZ 00473, three spms., Luang Phra Bang (N 19°50’37”, E 102°13’8”).

Specimens defined as morphotype 2. Thailand. CUMZ 00474, one spm., Tham Pha Nang Khoi, Rong Kwang, Phrae (N 18°22’8”, E 100°21’13”). CUMZ 00475, one spm., Thong Pha Phum, Kanchanaburi. CUMZ 00476, two spms., Black Ant Resort, Ban Kat, Mae Sariang, Mae Hong Son (N 18°9’50.6”, E 97°55’53.4”). CUMZ 00477, six spms., Phop Phra, Tak (N 16°30’36.5”, E 98°42’7.2”). CUMZ 00478, two spms., Tham Pha Mon, Pang Mapha, Mae Hong Son (N 19°30’43”, E 98°16’41.6”). CUMZ 00479, two spms., Mae La Noi, Mae Hong Son (N 18°32’4.4”, E 97°56’68”). CUMZ 00480, four spms., Wang Chao Waterfall, Tak (N 16°47’52.8”, E 99°9’5.3”). CUMZ 00481, two spms., Tha Song Yang, Tak (N 17°26’16.4”, E 98°3’28.2”). CUMZ 00482, one spm., Pang Mapha, Mae Hong Son (N 19°31’11.1”, E 98°15’35.5”). CUMZ 00483, six spms., Wat Mae Long, Mae Chaem, Chiang Mai (N 18°13’50.8”, E 98°26’25”). CUMZ XXXX, 10 spms., Wang Chao, Tak (N 16°47’52.8”, E 99°9’5.3”). CUMZ 00484, two spms., Wat Tham Luang, Don Sak, Surat Thani (N 9°9’16”, E 99°28’14”). CUMZ 00485, three spms., Wat Don Chedi, Phop Phra, Tak (N 16°30’9”, E 98°42’25.1”). CUMZ 00486, seven spms., Wat Tham Si Wilai, Chaloemphrakiat, Saraburi (N 14°42’46”, E 100°51’59”). CUMZ 00487, three spms., Suan Nakhon Si Khuean Khan, Phra Pradaeng, Samut Prakan (N 13°41’50”, E 100°33’50”). CUMZ 00488, two spms., Khao Phanom Wang, Kanchanadit, Surat Thani (N 9°5’31”, E 99°36’21”). CUMZ 00489, seven spms., Pai, Mae Hong Son (N 19°22’15.1”, E 98°25’50.9”). CUMZ 00490, one spm., Wat Phra That Sae Saeng, Phu Phiang, Nan (N 18°45’31”, E 100°47’27”). CUMZ 00491, one spm., Khao Yoi, Phetchaburi (N 12°50’12”, E 99°56’44”). CUMZ 00492, four spms., Mae Sariang, Mae Hong Son (N 18°12’36.2”, E 97°56’16”). CUMZ 00493, 11 spms., Chiang Kham, Phayao (N 19°27’49”, E 100°19’26”). CUMZ 00494, three spms., Ban Tha Song Yang, Tha Song Yang, Tak (N 17°26’16.4”, E 98°3’28.2”). CUMZ 00495, one spm., Ban Ta Puean Lakhue Kho, Mo Kro, Umphang, Tak (N 16°11’49”, E 98°52’45”). CUMZ 00496, six spms., Wat Tham Pidok, Nakhi, Prachin Buri (N 14°8’58”, E 101°48’46”). CUMZ 00497, one spm., Wat Tham Chiang Dao, Chiang Dao, Chiang Mai (N 19°23’40”, E 98°55’44”). CUMZ 00498, three spms., Suan Hin Maharat, Long, Phrae (N 18°9’11”, E 99°59’13”). CUMZ 00499, three spms., Wat Huai Yot, Mae Chaem, Chiang Mai (N 18°16’44.9”, E 98°22’48.1”). CUMZ 00500, one spm., Mueang, Sa Kaeo (N 13°19’45”, E 102°3’28”). CUMZ 00501, 18 spms., Wat Thung Baen, Mae Sariang, Mae Hong Son (N 18°6’42.6”, E 97°54’59.9”). CUMZ 00502, one spms., Mae Taeng, Chiang Mai (N 19°6’9.4”, E 98°49’6.4”). CUMZ 00503, two spms., Tham Pha Tha Phon, Noen Maprang, Phitsanulok (N 16°30’36”, E 100°39’39”). CUMZ 00504, two spms., Wat Pa Ban Mai, Mueang, Mae Hong Son (N 19°17’55.2”, E 97°59’12.5”). CUMZ 00505, six spm., Khun Yuam, Mae Hong Son (N 18°48’21.3”, E 97°55’53.4”). CUMZ 00506, seven spms., Tha Song Yang, Tak (N 17°33’58.9”, E 97°54’42.9”). CUMZ 00507, five spms., Wat Mae Tan Nuea, Tha Song Yang, Tak (N 17°13’49”, E 98°13’45.7”). CUMZ 00508, 24 spms., Wat Pa Khane Chue, Mae La Mat, Tak (N 17°2’54.2”, E 98°29’16.4”). CUMZ 00509, 28 spms., Mae Chaem, Chiang Mai (N 18°28’49”, E 98°22’36”). CUMZ 00510, 13 spms., Mae La Mat, Tak (N 16°58’54”, E 98°31’35”). CUMZ 00511, five spms., Mueang, Mae Hong Son (N 19°18’26.1”, E 97°57’51.6”). CUMZ 00512, 11 spms., Ban Pa Mum, Mae Chaem, Chiang Mai (N 18°28’46”, E 98°22’56”). CUMZ 00513, 11 spms., Mae Taeng, Chiang Mai (N 19°11’56”, E 98°53’8”). CUMZ 00514, nine spms., Khao Phanom Wang, Kanchanadit, Surat Thani (N 9°5’31”, E 99°36’17”). CUMZ 00515, 18 spms., Phop Phra, Tak (N 16°30’36.5”, E 98°42’7.2”).

Diagnosis 16-22 antennal articles, basal 3 glabrous dorsally. Tooth-plate usually with 4 teeth. T1 overlapping cephalic plate. Complete paramedian sutures on sternites. Coxopleural process with two apical and one subapical spines, lateral and dorsal spines. Legs with femoral, tibial and tarsal spurs. Prefemoral spur present on legs 1.

Tarsi of ultimate legs with male secondary sexual characters, such as club-like structure and tarsus 1 flattened in male. Prefemora of ultimate leg flattened dorsally.

Description. Body length ranges from 23-52 mm. Body colour in both live and freshly preserved material dark blue. Antenna pale grey or blue. Cephalic plate, T1 and ultimate leg-bearing segment orange brown or yellowish. Forcipular segment orange. Most locomotory legs yellowish with light blue on latero-distal part of each article. Ultimate legs and last two or three pairs of legs dark blue with pale yellowish on posterior part of each article. Cephalic plate without small, fine setae. Anterior median part of cephalic plate with short, straight sulcus without bifurcation posteriorly.

Antenna with 18-21 articles, basal 3 articles glabrous dorsally; 2.8 articles glabrous ventrally. Antenna reaches to T3-4. Forcipular trochanteroprefemoral process bearing one apical and two to four lateral teeth. Coxosternal tooth-plate wider than long, with four main teeth each sides, separated into two groups, two inner and two outer; basal part with a clear, fine seta on each side or without. Interior part of article 2 of telopodite of second maxilla with a fine pigmented spine. Coxosternite without median suture, median diastema reaching to base of tooth-plate, basal part of tooth-plate with curved sutures extending laterally subparallel to margin of coxosternite. Angulation of basal sutures ca 115º-120º.

TT1 and 2 overlapping posterior part of foregoing tergite. Tergites with paramedian sutures complete from T3; margination starting on TT9-12. Tergite of ultimate leg-bearing segment without median furrow on posterior part. Sternites with complete paramedian sutures. Surface of sternites without circular depression. Sternite of ultimate leg-bearing segment with sides converging posteriorly, posterior margin slightly concave.

Coxopleural process long, with two apical, one subapical, one lateral and dorsal spines. Dense pore field covering entire area of coxopleuron except on ventro-distal part of coxopleural process, pore-free area reaching to 60-100% the distance to margin of sternite of ultimate leg-bearing segment. On lateral side of coxopleura, dense pore area not covered by lateral margin of tergite of ultimate leg-bearing segment. Ultimate legs long and slender with ratio of articles as follow: 0.3:1 between tarsus 1 and tarsus 2, 1.5:1 between tarsus 2 and tibia, 1.1:1 between tibia and femur and 0.5:1 between femur and prefemur. Prefemoral spines of ultimate leg: VL-4 to 6, VM-3 to 4, M- 0 to 6 and DM- 2 to 4 spines and postero-dorsal part with well-developed process bearing 3 to 7 CS spines.

Legs with short, dense setae on ventral side; legs 1 to 17 usually with two tarsal spurs (16 in one specimen), subsequent legs to leg 19 (20 on one side in one specimen) with one tarsal spur. One tibial spur on legs 1-3 (4 in one specimen). Prefemoral and femoral spurs on leg 1. Two accessory spurs and pretarsal claw on all legs. Femur and tibia of ultimate leg club-shaped, with median sulcus on dorsal side. Tarsus 2 of ultimate legs flattened laterally, distal part extended to cover the articulation between tarsus 2 and tarsus 1. Tarsus 1 flatter than tarsus 2. Pretarsus with accessory spurs.

Remarks The original description is based on two syntype specimens of *A. demangei* from Phu-Lay, Vietnam, housed in Genoa, Italy (Fig. 6.15). Pocock (1981) described a new Cambodian *Rhysida*, namely *R. calcarata*, based on three specimens (Figs. 6.17-6.19), with a note that one of them probably depicts female characters of this species (flattened femora of the ultimate leg). The original description also indicated characteristics of *Alluropus*, such as complete paramedian sutures on the sternites and a prefemoral process on the ultimate legs, not reported in other Southeast Asian *Rhysida* such as *R. longipes*. In this study, we re-examine the Indochinese *Rhysida* species, namely *R. marginata* Attems, 1953 based on syntype species in the NHMW collection. The revised description of the syntypes is as follows:

***Rhysida marginata* Attems, 1953**

Figure 6.13

Type locality: Ca Mau, Vietnam

Material examined: Syntype. NHMW Inv. No. 2059, one spm., Camau (Cochinchina), leg. and don. Dawidoff, det. Attems.

Composite description Body length 21 mm. Body colour in preserved material entirely pale yellowish. Cephalic plate without small, fine setae.

Anterior median part of cephalic plate with short, straight sulcus without bifurcation posteriorly.

Antenna with 18 and 21 articles on left and right sides, respectively, basal 3 articles glabrous dorsally. Forcipular trochanteroprefemoral process bearing one apical and two lateral teeth. Tooth-plate wider than long, with four main teeth, separated into two groups, two inner and two outer; basal part with a clear, fine seta on each side or without. Interior part of article 2 of second maxilla with a fine pigmented spine. Coxosternite without median suture, median diastema reaching to base of tooth-plate, basal part of tooth-plate with curved sutures extending laterally subparallel to margin of coxosternite. Angulation of basal sutures ca 155º-165º.

Tergites with paramedian sutures complete from T2; margination starting on T12. Tergite of ultimate leg-bearing segment without median furrow on posterior part. Sternites with complete paramedian sutures on anterior part. Sternite of ultimate leg-bearing segment with sides converging posteriorly, posterior margin slightly concave.

Coxopleural process long, with two apical, one subapical, one lateral spines and dorsal spine absent. Dense pore field covering entire area of coxopleuron except on ventro-distal part of coxopleural process, pore-free area reaching to 80% the distance to margin of sternite of ultimate leg-bearing segment. On lateral side of coxopleura, dense pore area not covered by lateral margin of tergite of ultimate leg-bearing segment. Ultimate legs long and slender with ratio of articles as follow: 0.3:1 between tarsus 1 and tarsus 2, 0.8:1 between tarsus 2 and tibia, 0.9:1 between tibia and femur and 0.9:1 between femur and prefemur. Ultimate leg prefemoral spine: 4-5 VL, 2-3 VM, 3 M, 2-3 DM and 3 CS spines.

Legs with short setae on anterior segments; legs 1 to 8 with two tarsal spurs , subsequent legs to leg 19 with one tarsal spur. One tibial spur on legs 1-2. Femoral spur only on leg 1. Two accessory spurs and pretarsal claw on all legs. Pretarsus and tarsus 2 of ultimate legs with small setae.

This *Rhysida* species was described from a juvenile specimen collected from southern Vietnam. It displays some morphological similarity with *R. leviventer* sensu Attems, 1953 (=*R. lithobioides*), which was collected from northeastern Laos. However, *R. marginata* shows complete paramedian sutures while *R. leviventer* has only short paramedian sutures on the anterior part of the sternites. This *Rhysida* species is similar to the genus *Alluropus*, which is also reported from Vietnam in all respects. For this reason, we presently regard *R. marginata* as a junior synonym of *A. calcarata.*

In our phylogenetic analysis, specimens from eastern and northeastern Thailand previously determined as *R. calcarata* group together with specimens exhibiting typical *Alluropus* characters (such as the club-shaped tarsus of the ultimate legs). The phylogenetic tree combined these two nominal species together in both ML and BI. For this reason, *R. calcarata* is here transferred to *Alluropus*. The specific epithet of the previous name *Alluropus* "*demangei* Silvestri, 1912" was replaced by "*calcarata* Pocock, 1891", and thus *A. demangei* Silvestri, 1912 is a junior subjective synonym of *A. calcarata* (Pocock, 1891).

With regards to phylogenetic relationships with other genera of Otostigminae, the BI tree nested *A. calcarata* with four Indo-Australian species of *Rhysida*, namely *R. singaporensis*, *R. carinulata*, *R. nuda* and *R. polyacantha,* whereas in the ML tree these two groups clustered with one Indian *Digitipes* but without significant support. *A. calcarata* exhibits two morphologically distinct populations. Morphotype 1 shows taxonomic compatibility with the type specimens of this species. The diagnostic characters of *Alluropus* are presented only in this morphotype. A short description of the other morphotype of *A. calcarata* (Morphotype 2) is given below:

> Antenna with 18-21 articles, basal 3 articles glabrous dorsally; 2.8 articles glabrous ventrally. Forcipular trochanteroprefemoral process bearing one apical and two to four lateral teeth. Tooth-plate wider than long, with four main teeth on each side. Coxosternite without median suture
>
> Paramedian sutures on tergites complete from T3; margination starting on TT9-12. Tergite of ultimate leg-bearing segment without median furrow on posterior part. Sternites with complete paramedian sutures. Surface of sternites

without circular depression. Sternite of ultimate leg-bearing segment with sides converging posteriorly, posterior margin slightly concave.

Coxopleural process moderately long, with two apical, one subapical, one lateral and dorsal spines. Ultimate legs long and slender. Prefemoral spines of ultimate leg: 4-6 VL, 3-4 VM, 0-6 M and 2-4 DM and 3-7 CS spines, without prefemoral process.

Legs with short, dense setae on ventral side; legs 1 to 17 usually with two tarsal spurs (legs 1 to 16 in one specimen), subsequent legs to leg 19 (20 on one side in one specimen) with one tarsal spur. One tibial spur on legs 1-3 (4 in one specimen). Prefemoral and femoral spurs on leg 1. Two accessory spurs and pretarsal claw on all legs. Prefemur and femur of ultimate leg flattened dorsally. Tarsus 1 and 2 of ultimate legs slender.

The separation of these two morphotypes as different species is questionable because the morphological identification and molecular result of determined species in both morphotype are incongruent. The mixing of specimens of morphotypes 1 and 2 was found in two main clades. Genetic variation between these two morphotypes depicted a lower value in the COI and 16S datasets, respectively. For this reason, we treat the two morphologically distinct populations as variation within *A. calcarata.*

Distribution This species is widely distributed in the Indochina subregion and some parts of the Thai-Malay Peninsula. The currently known distribution (including locality records of *R. calcarata*) from previous and recent field collecting is as follows: Thailand (entirely), Laos (entirely), Vietnam: Ca Mau, Cambodia (probably entirely), Malaysia.

Discussion

Phylogenetic relationship of the subfamily Otostigminae

Scattering of putative congeneric species within Otostiminae has been recorded in some phylogenetic studies over the past decade, either based on morphology or molecular datasets only (Edgecombe, 2008a, b; Koch et al., 2009; Murienne et al., 2010; Joshi and Karanth, 2011) or their combination (Vahtera et al., 2013; Vahtera and Edgecombe, 2014). In this study, a more broadly sampled phylogenetic tree still depicted unresolved relationships among generic members, as in previous results from broad-scale phylogeny of the order Scolopendromorpha (Vahtera, 2013). *Otostigmus* and *Rhysida* in particular represent groups for which congeners are divided into two or more groups. Genetic composition evaluated from pairwise sequence alignment indicated high genetic variation both between and within species. This result may shed light on species boundaries as has been done in other scolopendromorphs such as in the family Cryptopidae (Vahtera et al., 2012a) or the subfamily Scolopendrinae (Vahtera et al., 2013; Siriwut et al., 2015a).

The scattering of *Otostigmus* OTUs can be observed in the trees from both BI and ML analyses. Clades are nonetheless compatible with species identification based on morphology. Two New World *Otostigmus* species, *O. caraibicus* and *O. spinicaudus*, depicted a close relationship with an African endemic genus *Alipes*. This clade is retrieved in both BI and ML analyses although only in BI does it have statistical support. This relationship was also reported in previous cladistic study based on combination of morphology and molecular datasets using parsimony methods (Vahtera and Edgecombe, 2014), although available sequences of representative species from the Neotropical and African faunas is still limited. In the case of Old World *Otostigmus*, at least seven representative species groups were recognized from BI and ML trees. Each species clade may share some diagnostic morphological characters that can be used for species delimitation and defining shared diagnostic characters of sister taxa. In the case of *O. multidens*, its OTUs were split into two groups, one that nested with *rugulosus* and *scaber* groups and a second group that settled among other *Otostigmus*. This species group exhibited a greater number of teeth on the tooth-plates than in other *Otostigmus* (>6 teeth on each side versus 3-4 in most other species). A *spinosus-astenus* group is composed of Indo-Australian taxa that resemble each other morphologically but can be diagnosed by the presence of dorsal-lateral spines on the prefemur of leg 20 only in *O. spinosus*. Moreover, male *O. spinosus* was also reported to exhibit a lateral projection on tarsus 2 of the ultimate legs, regarded as a secondary sexual character of this species. This additional feature seems useful for distinguishing these two sympatric species. Recently, a taxonomic revision of the *rugulosus* species group assigned 11 described species, making this the largest group within the genus (Lewis, 2010). In this study, *O. rugulosus* specimens formed a monophyletic group that clustered with *O. scaber*. However, the relationship between these two sister groups is still unresolved. In the case of the remaining species groups, the Indian-Malaysian species *O. ruficeps* and *O. sulcipes* were regarded as valid species that are genetically distinct from other *Otostigmus* species, consistent with results from recent taxonomic revisions of both (Joshi and Edgecombe, 2013; Lewis, 2015). The last described species group clustered *O. aculeatus* and *O. politus*, two species reported originally from throughout tropical-temperate Asia. They share the characteristic of complete paramedian sutures on the sternites, a trait that rarely occurs in *Otostigmus*. In this study, there are three putative groups from mainland Southeast Asia that show morphological distinctness and possess characteristics of *Otostigmus*. Because available specimens for observation are limited, the proposal of new species for these three morphological groups is provisional, but at least the molecular phylogeny also indicated that they are genetically distinct.

The African-Indian endemic genus *Digitipes* is thought to be closely related to *Otostigmus* based on morphological characteristics. Only male secondary characters can be used for generic justification. Attems (1930) originally limited the distribution of this genus to the Afrotropics. Later, a further six new species were reported from India (Jangi and Dass, 1984). Recently, molecular phylogenetics and ecological niche modelling have been used to predict their diversity and distribution patterns (Joshi and Karanth, 2012). These results indicated that in Peninsular India this genus may be specific to western montane regions. Taxonomic revision of Indian *Digitipes* after molecular investigation also verified the taxonomic validity of previous described species and also explored further new species from this area drawing on information from molecular and morphological examination. An even broader distribution of this genus has been indicated by recent systematic study of Burmese species (Siriwut et al. 2015b). This phylogenetic result indicated shared biodiversity between the Indian and Burmese faunas. In this study, all members of *Digitipes* grouped together with moderate support (with 72% bootstrap support in ML and 0.94 posterior probability in BI). However, the relationships of this genus are still contentious because of the insertion of *O. nudus* (previously regarded as *D. periyarensis* Joshi and Edgecombe,

2013) within the clade of *Digitipes*. This *Otostigmus* species was described from India and nested together with other *Digitipes* species in previous molecular analyses. It was named as *D. periyaresis* based on two female specimens from Kerala, western India. Later, Lewis (2015) synonymized this species under *O. nudus* Pocock, 1890 according to their morphological identity. In this study, the tree topology still indicates that this *Otostigmus* consistently nests inside *Digitipes* in both ML and BI analyses. Furthermore, the survey from the southern part of Thailand and Myanmar also indicated another morphological type which shows a genetic alliance to *D. kalewaensis* from the western part of Myanmar. This finding may suggest the distribution of this genus may extend further southwards to peninsular mainland Southeast Asia, where it would be sympatric with other members of Otostigminae.

Recently, the endemic genus *Edentistoma* has been investigated using both morphological and molecular observations in order to explore its evolutionary position within Otostigminae. Results from initial morphological cladistic analysis indicated that this enigmatic taxon was likely to be an ally of another endemic Southeast Asia genus, *Sterropristes* (Schileyko, 1992; Schileyko and Pavlinov, 1997). Later, phylogenetic reconstruction adding molecular sequences contradicted that relationship by nesting *Edentistoma* together with *Otostigmus* or *Rhysida* depending on the method used for tree construction (Vahtera and Edgecombe, 2014). In this study, *Edentistoma* remains inconsistently nested either with *Otostigmus* or *Rhysida* depending on the chosen methods.

The peninsular Southeast Asian genus *Sterropristes*, identified by its uniquely serrate forcipular tarsungula, was placed as sister group to all other Otostigminae in both BI and ML analyses. A variable position of it and *Ethmostigmus* nested together as a basal clade within Otostigminae has been observed in the ML analysis with acceptable support. In recent revisions, only three described species of *Sterropristes* were reported from Southeast Asia (Muadsub et al., 2012). According to this latest revision, these species resemble each other closely morphologically, the differences amounting to the number of legs with two tarsal spurs and which podomeres of the ultimate legs are convex ventrally. In this study, the mainland and insular species, *S. metallicus* and *S. violaceus*, have been verified as distinct species. Previous hypotheses of relationship for this genus have been proposed by Verhoeff (1937), who assigned *Sterropristes* (=*Malaccolabis* Verhoeff, 1937) to a subfamily Sterropristinae. Later, tribes Ethmostigmini and Arrhabdotini were proposed in a new classification hypothesis for Scolopendromorpha based on the presence of spiracles on particular trunk segments and numbers of trunk segments (Schileyko, 1992). In this classification, *Sterropristes* was placed in the tribe Arrhabdotini together with *Edentistoma* (after Attems, 1930) but only morphological cladistics supported this hypothesis (Edgecombe, 2008a; Koch et al., 2009; Vahtera et al., 2012b). The combination of morphology and molecular data indicated that *Sterropristes* was separated out of sister clade of *Edentistoma*, similar to our study. These two genera exhibited morphological similarity in lacking a trochanteroprefemoral process on the forcipular segment and having enlarged tooth-plates. This result may validate the subfamily Sterropristinae or even tribe Ethmostigmini. However, representative OTUs of *Sterropristes*, *Ethmostigmus* and *Edentistoma* are limited. Consequently, the evolutionary relationships and phylogenetic position of these three genera is still ambiguous.

Phylogeny and taxonomic reassessment of *Alluropus* and *Rhysida*

Previously, the genera *Alluropus* and *Rhysida* were assigned to the tribe Otostigmini, which groups these two genera together with *Alipes*, *Digitipes*, *Otostigmus* and *Ethmostigmus* (Attems, 1930). Later, the occurrence of a spiracle on segment 7 was used to assign *Ethmostigmus*, *Rhysida* and *Alluropus* to a tribe Ethmostigmini (Schileyko, 1992). However, the taxonomic value of spiracle position and its appearance on particular trunk segments has been debated because of its variable presence and marked degree of homoplasy across Scolopendromorpha (Di et al., 2010). In this study, phylogenetic tree yielded a clade gathering all *Alluropus* specimens, and its sister clade was composed of Indo-Australian *Rhysida* species, namely *R. singaporensis*, *R. nuda*, *R. carinulata* and *R. polyacantha*. This broader clade received statistical support only in the BI analysis whereas in the ML tree, the *Rhysida*-*Alluropus* clade was unresolved and was allied to *D. barnabasi*. However, the monophyly of *Alluropus* OTUs has been confirmed by both methods. This result permits the distinction of this monotypic genus from other genera of Otostigminae, especially from *Rhysida*. *Alluropus*, originally described from two male specimens that exhibited secondary sexual characters on the tarsus of the ultimate legs (Silvestri, 1912; Attems, 1930a). On the contrary, the female of *Alluropus* shows morphological identity with some Southeast Asian species until now referred to *Rhysida*, such as *R. lithobioides* and *R. marginata*. It seems that these two sympatric genera are difficult to determine based only on morphology when the number of observed specimens is limited or only immature stages are available. The misidentification problem is most acute in the case of two historical species from these two genera, "*A. demangei*" (described from male specimens) and *R. calcarata* (described from female and immature specimens), but now treated as a single species, *A. calcarata*.

In this study, the re-investigation of types and examination of additional specimens of several species of these two genera suggested further characters that may be useful for diagnosis. Three candidate characters - the presence or absence of paramedian sutures on the sternites, the number of spines on the coxopleural process, and the presence of prefemoral spurs on leg 1 - are proposed in this study because they are restricted to these two genera and are conserved at the species level. Complete paramedian sutures on the sternites occur consistently in *Alluropus* whereas they are incomplete in all Southeast Asian *Rhysida* species. In the case of arrangements of spines on the coxopleural process, *Rhysida* usually presents two apical, a subapical and a lateral spine whereas a dorsal spine has been reported in all *Alluropus* specimens. Even more reliable is the appearance of prefemoral spurs on leg 1, which is restricted to *Alluropus* and supports the reassignment of *R. calcarata* to *Alluropus* (consistent with their molecular grouping). This character still remains visible on one individual of the syntypes (subsequent specimens have lost most of their legs).

Variation in some taxonomic characters

Centipedes in the subfamily Otostigminae are currently known to depict morphological variability in several taxonomic characters, which has caused problems for species identification. Lewis (1978) documented the extent of morphological variation in taxonomic characters that seems to be related to some geographical populations. Isolation mechanisms have been discussed with reference to morphological changes associated with mating behaviour or changes due to developmental stage (Lewis, 1984b). However, some genera in the Otostigminae show similarities in some traditional taxonomic characters of scolopendromorphs as a whole, such as the spinulation on the ultimate leg prefemur and number of glabrous antennal articles. This situation of this subfamily may particularly support the assumption of species isolation based on stages of development. In this study, the variation of ten traditional taxonomic characters is discussed in order to confirm their taxonomic potential for generic or species identification of this subfamily.

Antenna

The antenna provides some of the most historically long-used diagnostic characters in previous taxonomic studies of Scolopendromorpha (Attems, 1930a). Recently, morphological characters such as sensilla distribution and number of glabrous articles have been reviewed with respect to their use in centipede classification (Lewis, 2000). In the case of variability among members of Otostigminae, these characters usually showed a narrow range of variation or were constant between congeners as follows: *Otostigmus* (2 to 4 glabrous articles), *Rhysida* (3 to 4), *Alluropus* (3), *Ethmostigmus* (3 to 4), *Sterropristes*, *Edentistoma* (5), *Alipes* (2 to 3), *Digitipes* (2 to 3). This situation contrasts with the other scolopendrid subfamily, Scolopendrinae, which instead shows a broad range of variation even between congeneric species, e.g. three to nine glabrous articles in *Scolopendra* (Siriwut, et al. 2016). In this study, we found that variation of this character may be specific to particular local populations (see remarks on *R. longipes* for example). It seems that even when this variation occurs in a narrow range, it may contain taxonomic signal that may be associated with cryptic speciation.

Forcipular segment

This character is highly variable among genera in this subfamily, from lacking tooth-plates in *Edentistoma*, serrate transangular tooth-plates in *Sterropristes*, to thick and robust tooth-plates in *Ethmostigmus*. This extreme modification may suggest adaptations of animals living under various ecological and geographical types. Some biological remarks reveal an association between morphological changes and distribution pattern or even behaviours, such as the arboreal species, *Edentistoma octosulcatum*, found in lowland riverine forest in Sarawak, Borneo, which consumes some sympatric millipedes (Lewis, 1982a; Vahtera and Edgecombe, 2014).

Ethmostigmus, which includes the largest-sized centipedes in this subfamily, is usually found in evergreen and savanna areas in Africa (Lewis, 1972a). Specialized modifications are useful for determining taxonomic boundaries in the group.

Paramedian sutures on sternites

This particular character was mainly used to identify some species within *Otostigmus*. Because of the rare occurrence of complete sutures in that genus, this character is highly valuable for species delimitation. However, some species that were assigned to different morphological groups share this characteristic, such as *O. aculeatus* and *O. politus* Karsch, 1881 as indicated in this phylogenetic study. Another taxonomic example has been documented in this study between *Alluropus* and *Rhysida*. *Alluropus* specimens have complete or nearly complete (>80%) sutures on the sternites whereas most *Rhysida* in Southeast Asia have only short paramedian sutures on the anterior part of sternites. This observation provides a distinguishing character between these two closely related genera.

Tergite margination

The tergites of scolopendromorphs usually exhibit margination, starting from various segments. It was also regarded as a key diagnostic character of some genera and species of Scolopendrinae such as *Campylostigmus* Ribaut, 1923, *Asanada* Meinert, 1886 and *Arthrorhabdus*, Pocock , 1891. This character has been predicted to show a particular relationship to developmental stages (Lewis, 2000). Among Otostigminae, several species lack margination on tergites 1 to 20, as is the case for *R. immarginata*, *Otostigmus* (*Parotostigmus*) and three African species of *Digitpes*. This may suggest that this character is a plesiomorphic trait throughout Scolopendromorpha and when it occurred it may not result from ontogenetic variation of each individual like other morphological variation such as number of antennal articles, spines on the ultimate leg prefemur, and colouration pattern (Lewis, 1968; Siriwut et al., 2015a).

Median suture and depressions on tergites and sternites

The appearance of these characters is most typically presented in *Otostigmus*. In Southeast Asia, it is especially clear on the tergites of *O. scaber* Porat, 1876. In contrast, there are several species that have median sutures or depression on the sternites, e.g. *O. sulcipes* Verhoeff, 1937 and *O. geophilinus* Hasse, 1887. Some

Digitipes species also show some linear depression on sternites which similarly have distinct patterns (Siriwut et al., 2015b). This kind of depression starts from the anterior to middle parts of the trunk and rapidly decreases posteriorly. In New World *Otostigmus*, some species were reported to exhibit a median suture on the sternite of the ultimate leg-bearing segment, as is the case for *O. insignis* (Attems, 1930a).

Number of legs with tarsal and tibial spurs

Legs with tarsal and tibial spurs have high taxonomic value for identification of all members of this subfamily. However, there are problems in using this variable character to determine some closely related species because of overlapping ratios between species. It is also hypothesized that this character may change depending on individual or geographical variations in some Scolopendromorpha (Jangi, 1955; Lewis, 1968; Jangi and Dass, 1984; Lewis, 2000). In this study, we observe this character to be valuable for species delimitation but according to the phylogenetic result of genus *Alluropus* that morphologically discordant with genetic composition. It may suggested that to using the presence ratio of these characteristic is ambiguity and may depend on character state relied to evolution lineage of each group.

Prefemoral spurs on leg 1

In this study, leg 1 prefemoral spur has been proposed as an additional key character for *Alluropus* because it is present in all specimens in both morphological types of the type species but has not been reported from any other member of Otostigminae. However, there is still some ambiguity with respect to this character because a specimen of *R. immarginata* from Singapore (NHMUK; general collection) also showed this character on one side.

Number of spines on the coxopleural process

In Otostigminae, the ultimate leg-bearing segment either possesses or lacks a coxopleural process. When absent (e.g. *Sterropristes*), the coxopleuron is usually rounded, without a spine on the distal-posterior part, whereas when present, the coxopleural process bears variable numbers of spines that have been used to delimit several species in this subfamily. However, some particular species such as *Otostigmus* (*Parotostigmus*) *gemmifer* Attems, 1928 also lack spines on this process. The length of the coxopleural process also varies from moderate length (in *Otostigmus*, *Rhysida*, *Digitipes* and *Alluropus*) to long and robust (in *Ethmostigmus*).

Shape, length and number of spines on the coxopleural process were predicted to be recognition factors during courtship and mating (Heymons, 1901; Brunhuber, 1970; Lewis, 1981). In this study, the number of spines on the coxopleural process between *Rhysida* and *Alluropus* is similar, but Indo-Austrian *Rhysida*, the sister clade of *Alluropus*, lack the dorsal spine on the coxopleural process. It seems that this character shows some taxonomic value, supporting prior usage of it for diagnoses.

Keel formation and spinulation on tergite surfaces

Within the Otostigminae, keels and spinulation were found to be developed disorderly. In the case of keels, these typically occur on posterior tergites. Lewis (2000) suggested that the number of segments that present keels on the tergites may vary according to developmental stage. On some occasions, keels are present on anterior tergites, i.e. in *O. scaber* and *O. insularis*, in which tergites with keels start from TT3 or 6. In the case of spinulation, some taxonomic observations are available (Koch, 1985; Lewis, 2010d). In this study, spinulation was not restricted to tergites but it was also presented on the prefemur of locomotory legs in some *Otostigmus* species. This morphological characteristic is also reported in some New World *Otostigmus* (Chagas-Jr., 2012). Moreover, our examination of some *Rhysida* and *Ethmostigmus* also confirmed the assumption that this character is shared between genera. *Rhysida singaporensis*, *R. carinulata* and *E. platycephalus* exhibited spinulation on the tergites. In the case of the two species of *Rhysida*, a relationship between these insular taxa is indicated by this character, which is supported by them forming a clade in our phylogenetic tree. *Ethmostigmus platycephalus* Newport, 1845, previously was recognized as subspecies of *E. rubripes* Brandt, 1840. After taxonomic revision of *Ethmostigmus* based on historical collection in Vienna, *E. platycephalus* has been elevated to species level. The spinulation on tergites is quite useful for separation these two *Ethmostigmus* species.

Morphological variation of ultimate legs

The uniqueness and high variability of the ultimate legs has been reported in this subfamily. This character shows variable shapes and sizes which is documented functionally in different roles such as stridulation (*Alipes*), pincer-like or hood-like structure for defense (*Sterropristes* and *Alluropus*), and short thickness (*Edentistoma*). Moreover, secondary sexual characters are also observed to be specific to this pair of legs. Several species were reported to demonstrate this kind of morphological change that can be quite useful for species identification, as in a pair of tubular processes in males of *Otostigmus* (*Parotostigmus*), a femoral process in males of *Digitipes*, and a club-like shape of tarsus 1 in *Alluropus.* Previous taxonomic observation on taxonomic characters in Scolopendromorpha (Lewis, 2000; Chao, 2008; Kronmüller, 2012; Siriwut et al., 2014) suggested that this morphological sex character shows taxonomic value which is congruent with the results of both morphological and molecular analyses in this study.

Species diversity and distribution trends of Southeast Asian Otostigminae

According to the present and previous taxonomic and phylogenetic studies, Southeast Asia probably contains the highest centipede diversity, especially in the subfamily Otostigminae. This region has been recognized as a giant jigsaw puzzle because of it geological composition (Metcalfe, 1998, 2002, 2011). Geographical richness in both barriers and corridors seems to have affected many kinds of animals, including centipedes (Woodruff, 2003; de Bruyn et al., 2004; Woodruff and Turner, 2009b; Siriwut et al., 2015a). Although the habitat preference of Otostigminae is often associated with anthropogenic areas, some genera are predicted to be endemics according to their distributional ranges and abundance in natural habitat. Molecular study of *Scolopendra*, which belongs to the sister subfamily of Otostiminae, revealed that genetic diversity of mainland Southeast Asia fauna can be divided into three sub-regions: India-Burma, Indochina and the Malay Peninsula. In the case of Otostigminae, the relationship among members of this subfamily remain quite ambiguous but at least the data from morphology and distribution may show some taxonomic signal for species group recognition, e.g. *Rhysida* being divided into two geographical groups, Indo-Australian and Indian-Burmese, respectively. In *Otostigmus*, the most diversified genus in this region, some species contain two genetically distinct populations that correlated to geographical distribution as refers in determined specimen of *O. multidens*. The monotypic genus *Alluropus*, now known to be dispersed along Indochina and the Thai-Malay Peninsula, can be presented as an example showing the discordance between morphological, genetic and distribution data.

As indicated by the phylogenetic tree, the genetic divergence between/within members of Otostigminae is greater than in other Scolopendridae. The phylogeography of the genus *Scolopendra* in several regions revealed the correlation between geographical barriers and geological events that seems to have affected genetic divergence of these animals (Siriwut et al., 2015a). In this study, four unknown putative species were recognized by both morphological and molecular comparisons. This may indicate that the true regional diversity of this subfamily is still underestimated. For this reason, further studies on taxonomy and phylogeny are needed in order to provide more data to detect diversification. Comprehensive field surveys in several parts of Southeast Asia are required in order to investigate the morphological variation that seems to be associated with geographical distribution, as suggested in previous taxonomic studies (Schileyko, 2007; Siriwut et al., 2014; Siriwut et al., 2015b, 2016). The result may provide further understanding about speciation mechanisms in this centipede group.

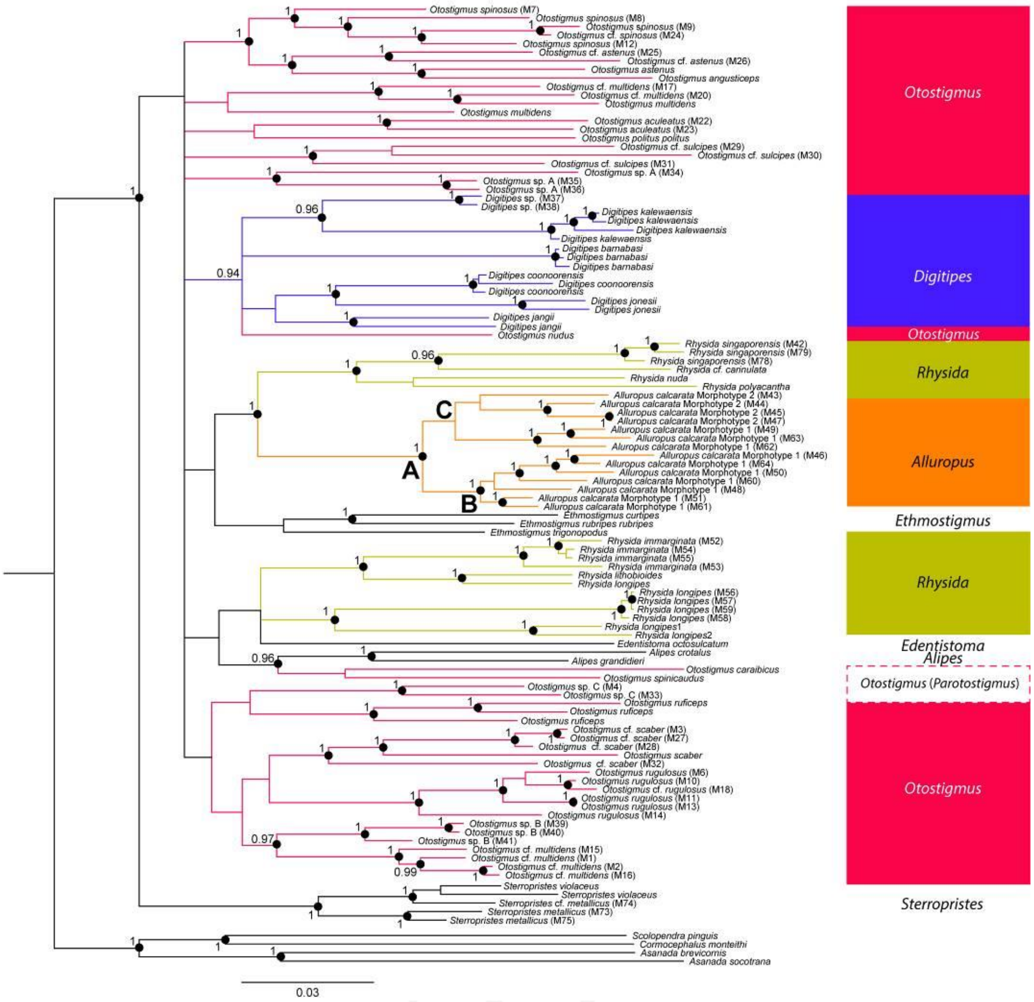


Figure 6.1 Phylogenetic tree for the subfamily Otostigminae obtained from Bayesian inference; black circles indicate node support (>0.95 posterior probability).

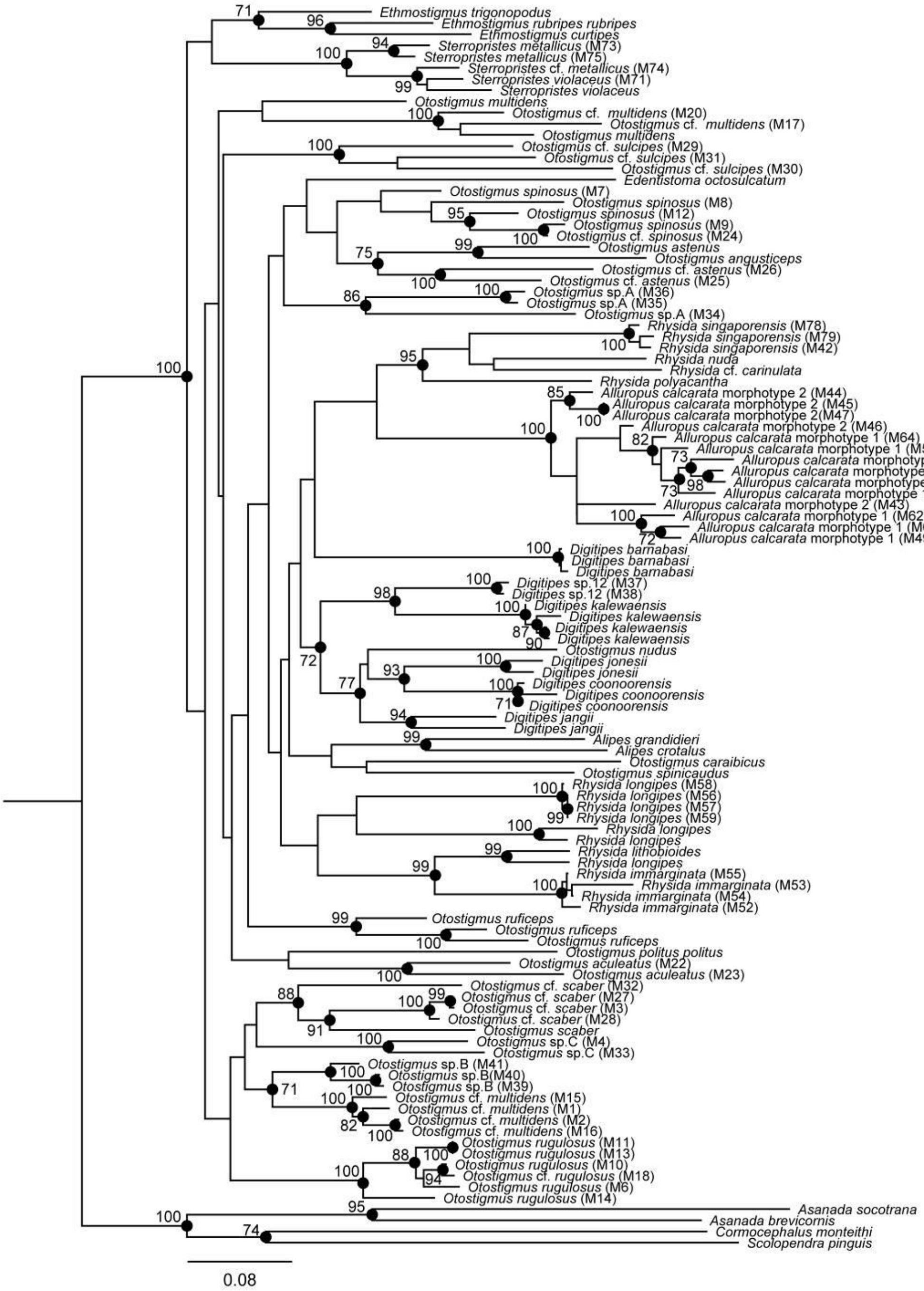


Figure 6.2 Maximum likelihood tree for the subfamily Otostigminae obtained from RAxML using GTR+CAT model; black circles indicate node support (>70% bootstrap value)**.**

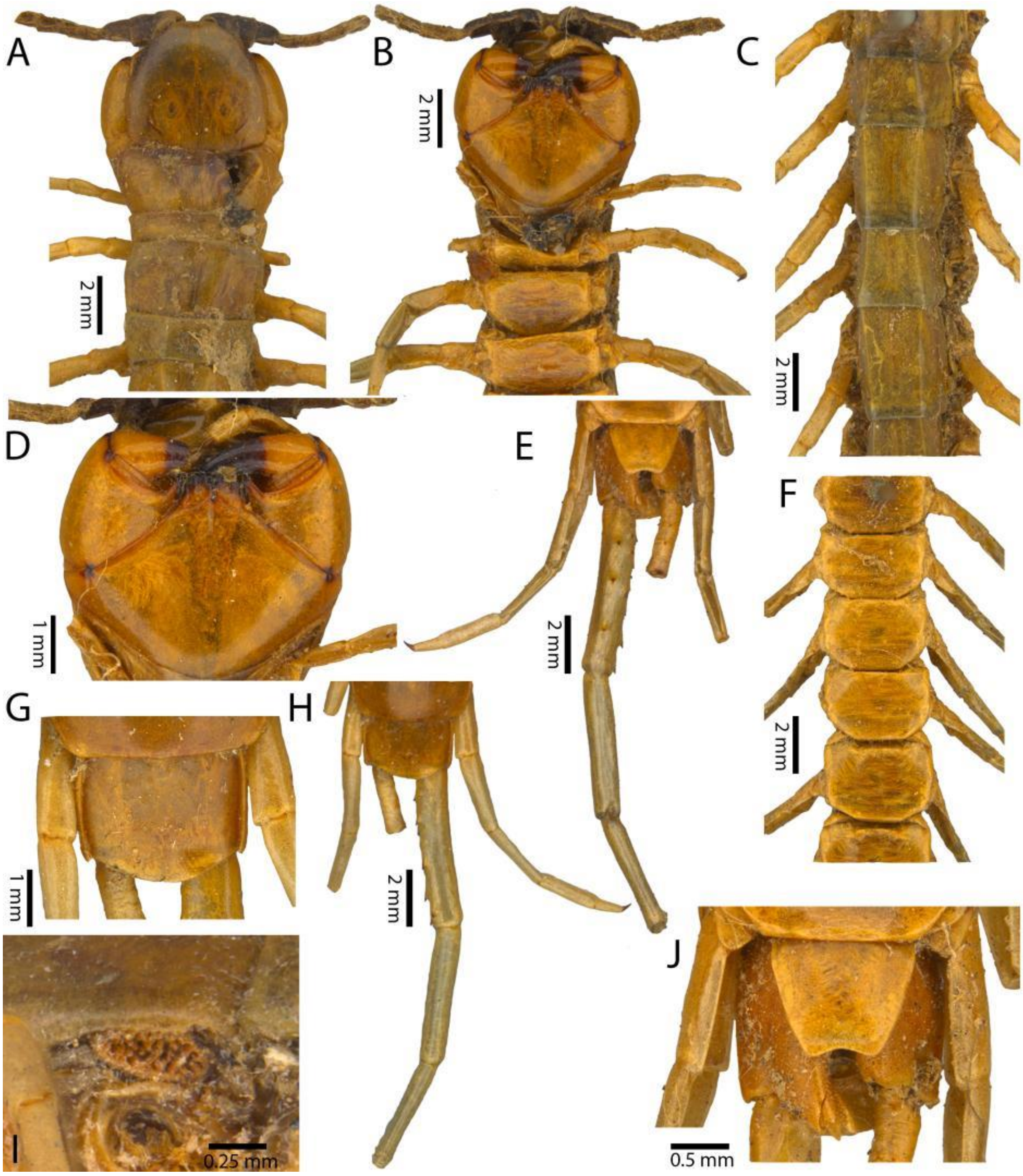


Figure 6.3 Holotype of *Rhysida lithobioides* (Newport, 1845): **A** Cephalic plate and tergites1-4 **B** Forcipular segment and sternites 1-4 **C** Tergites 8-13 **D** Forcipular segment **E** Sternite of ultimate leg-bearing segment, legs 20 and ultimate legs **F** Sternites 8-13 **G** Tergite of ultimate leg-bearing segment **H** Tergite of ultimate leg-bearing segment, legs 20 and ultimate legs **I** Spiracle 3 **J** Sternite of ultimate leg-bearing segment and coxopleura.

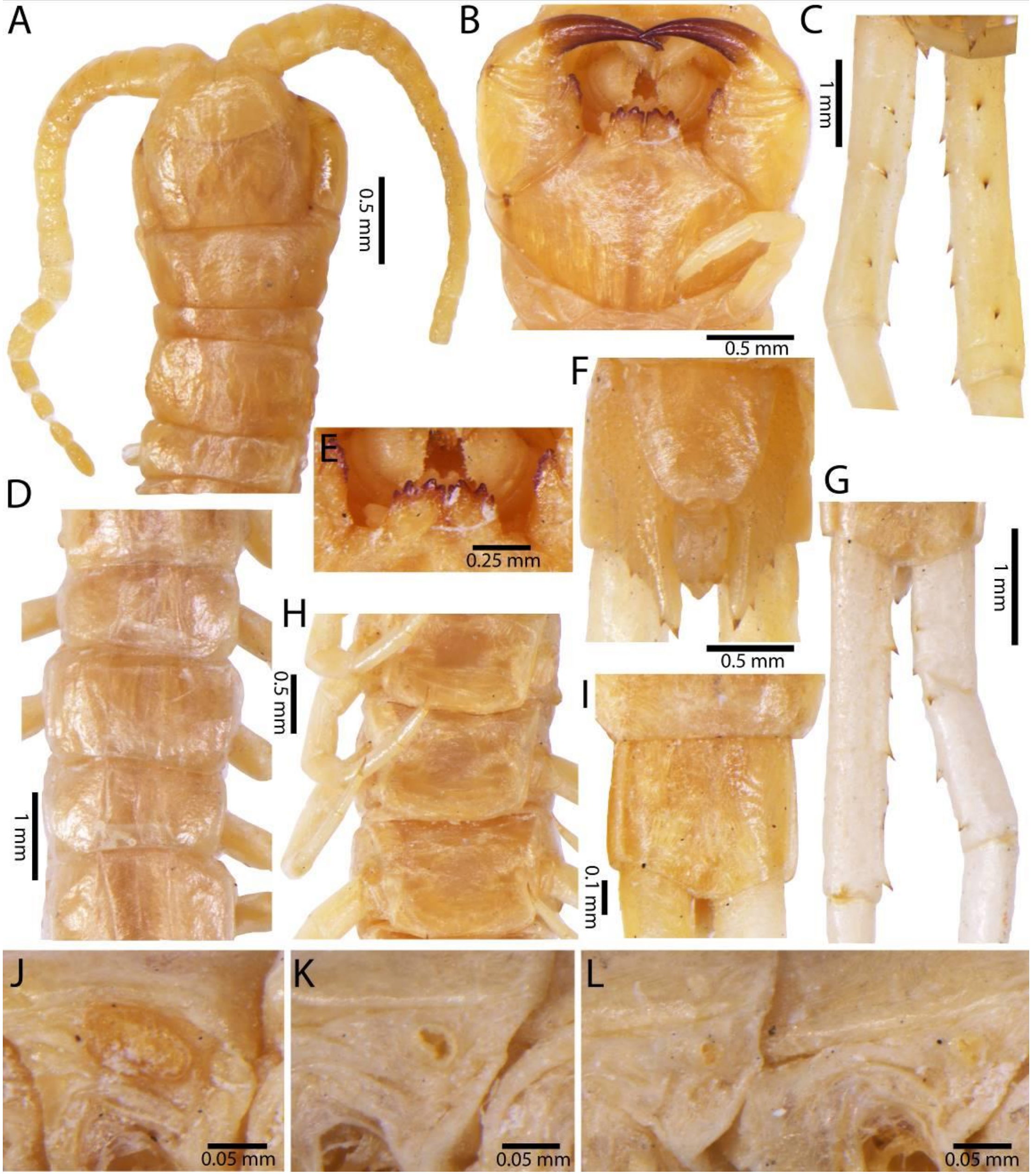


Figure 6.4 Holotype of *Rhysida leviventer* Attems, 1953: **A** Cephalic plate and tergites1-4 **B** Forcipular segment and leg 1 **C** Ventral view of ultimate leg prefemora **D** Tergites 9-13 **E** Tooth-plates **F** Sternite of ultimate leg-bearing segment and coxopleura **G** Dorsal view of ultimate leg prefemora **H** Sternites 9-11 **I** Tergite of ultimate leg-bearing segment **J-L** Spiracles 3, 5 and 7-8.

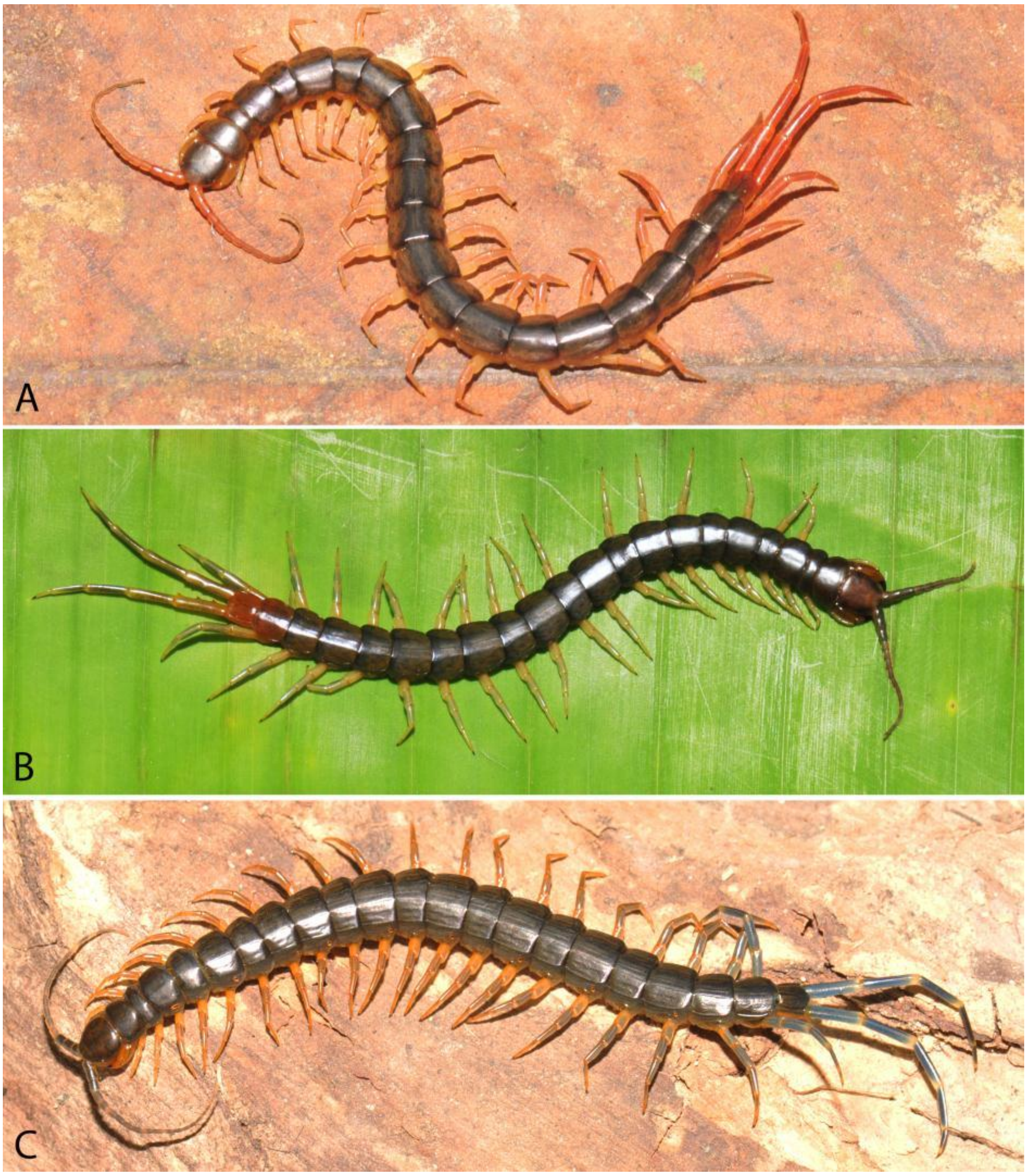


Figure 6.5 Live habitus specimens of some *Rhysida* species in mainland Southeast Asia: **A** *Rhysida immarginata* (Porat, 1876) **B** *Rhysida longipes* (Newport, 1845) **C** *Rhysida singaporensis* Verhoeff, 1937.

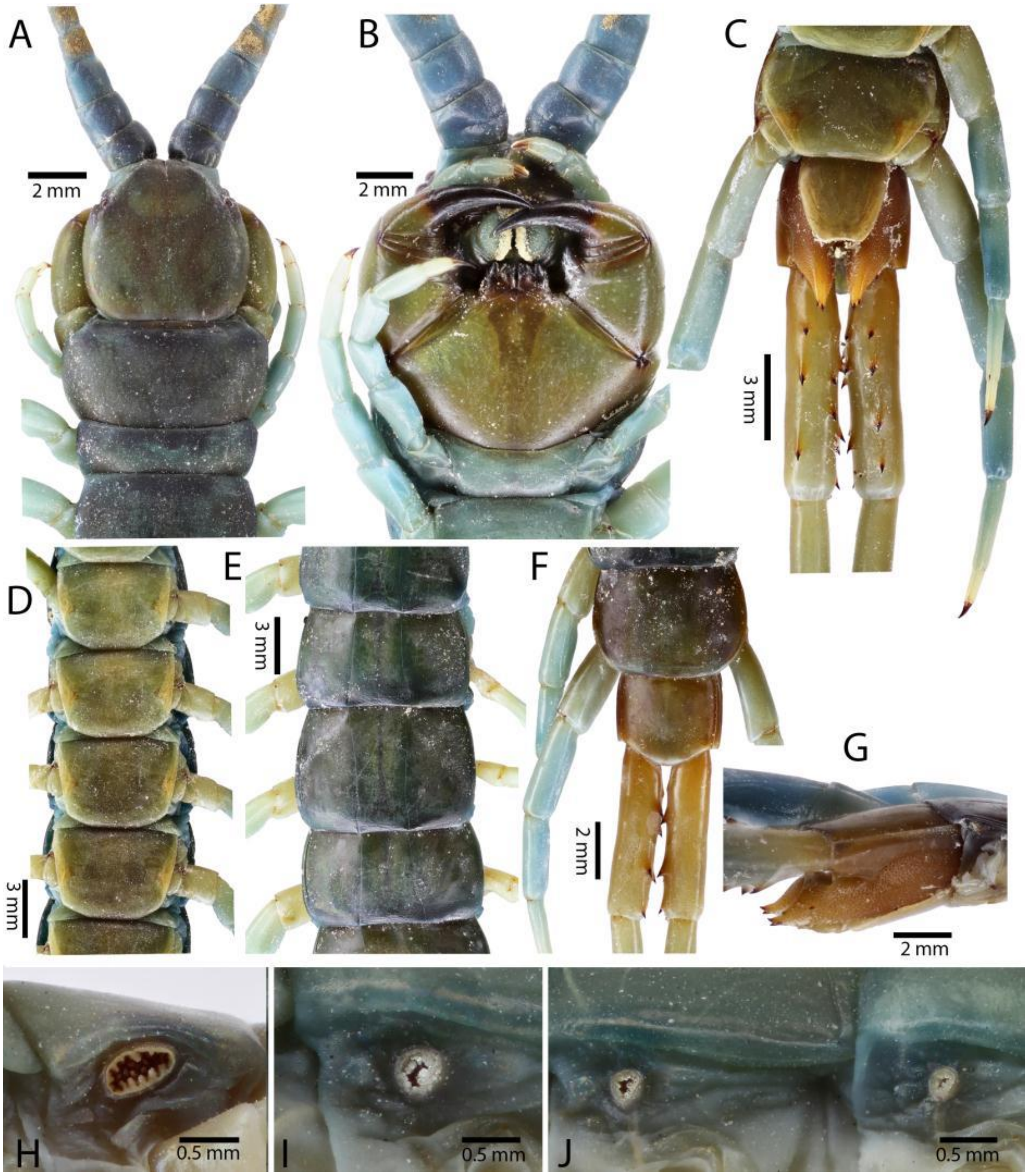


Figure 6.6 Morphological characters of *Rhysida longipes* (Newport, 1845): **A** Cephalic plate and tergites 1-3 **B** Forcipular segment, sternites 1-2 and legs 1-2 **C** Sternite of ultimate leg-bearing segment, coxopleura, ultimate leg prefemora and legs 19-20 **D** Sternites 9-12 **E** Tergites 9-11 **F** Tergite of ultimate leg-bearing segment and ultimate leg prefemora **G** Coxopleuron **H-J** Spiracles 3, 5 and 7-8.

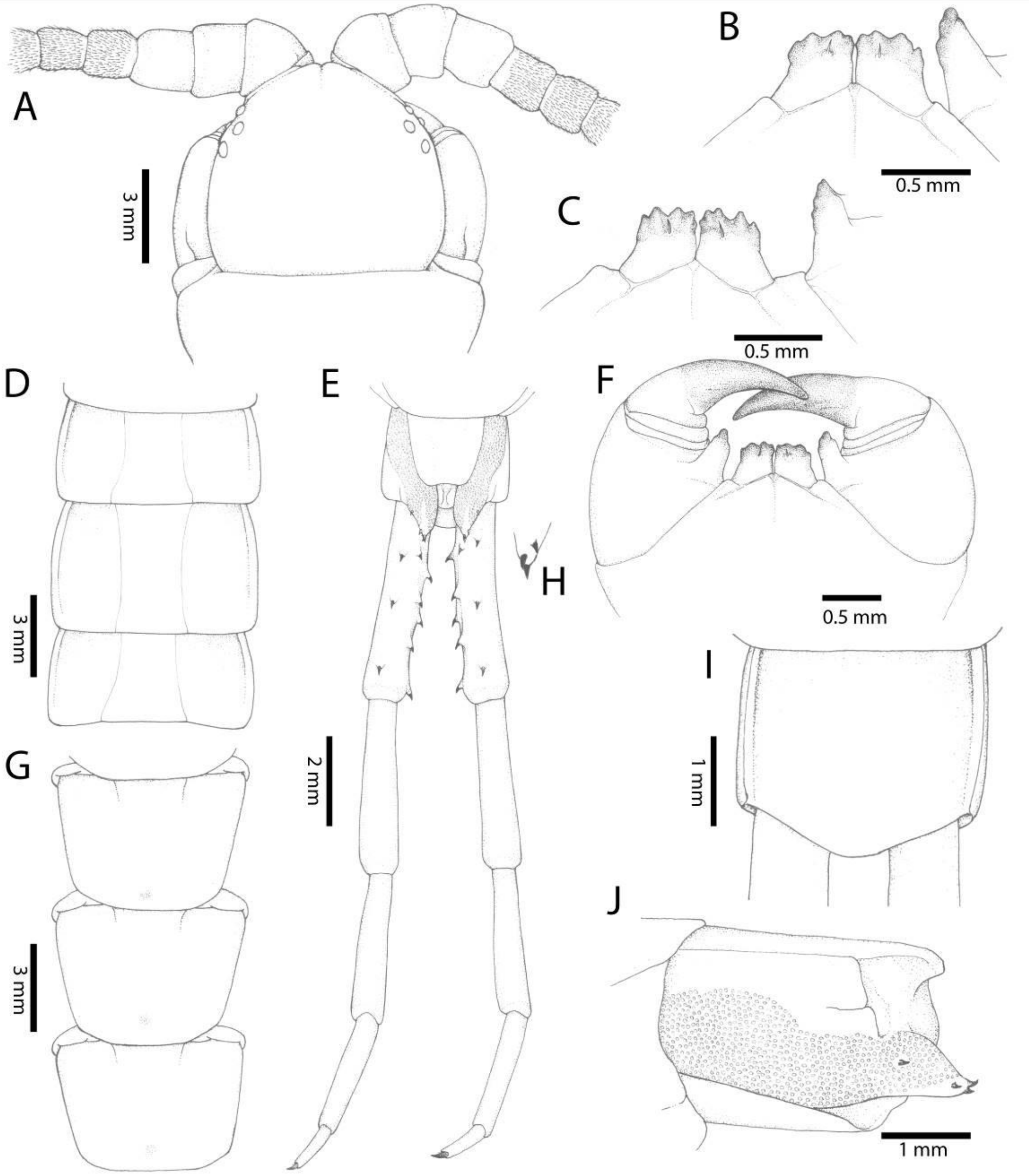


Figure 6.7 Morphological variation of *Rhysida longipes* (Newport, 1845): **A** Cephalic plate and glabrous antennal articles **B-C** Variation in teeth on tooth-plates **D** Tergites 9-11 **E** Sternite of ultimate leg-bearing segment, coxopleura and ultimate legs **F** Forcipular segment **G** Sternites 9-11 **H** Spines on distal part of coxopleural process **I** Tergite of ultimate leg-bearing segment **J** Coxopleuron.

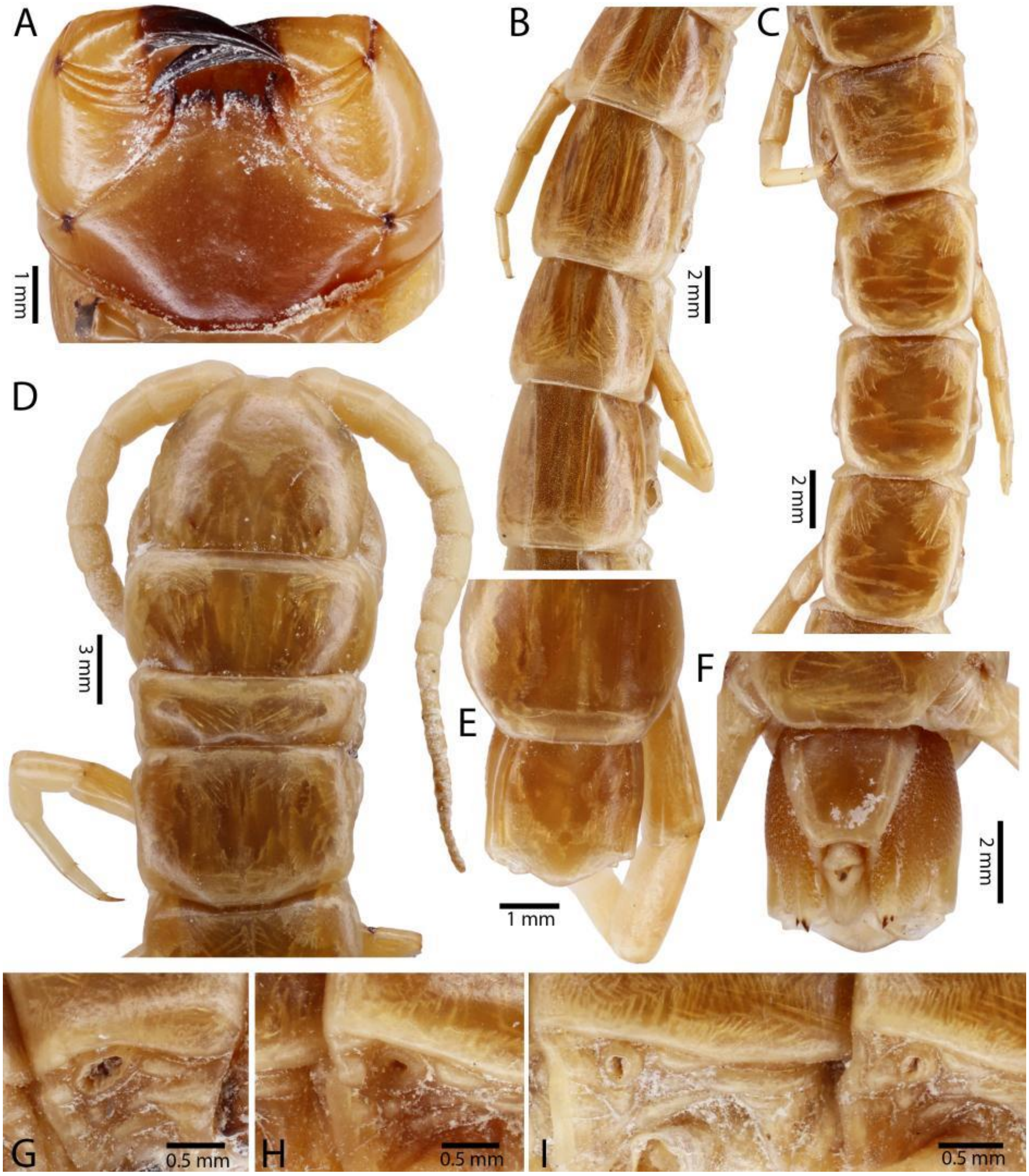


Figure 6.8 Syntype 1 of *Rhysida immarginata* (Porat, 1876): **A** Forcipular segment **B** Tergites 9-12 **C** Sternites 11-13 **D** Cephalic plate, antenna and tergites 1-3 **E-F** Tergite and sternite of ultimate leg-bearing segment **G-I** Spiracles 3, 5, 7 and 8.

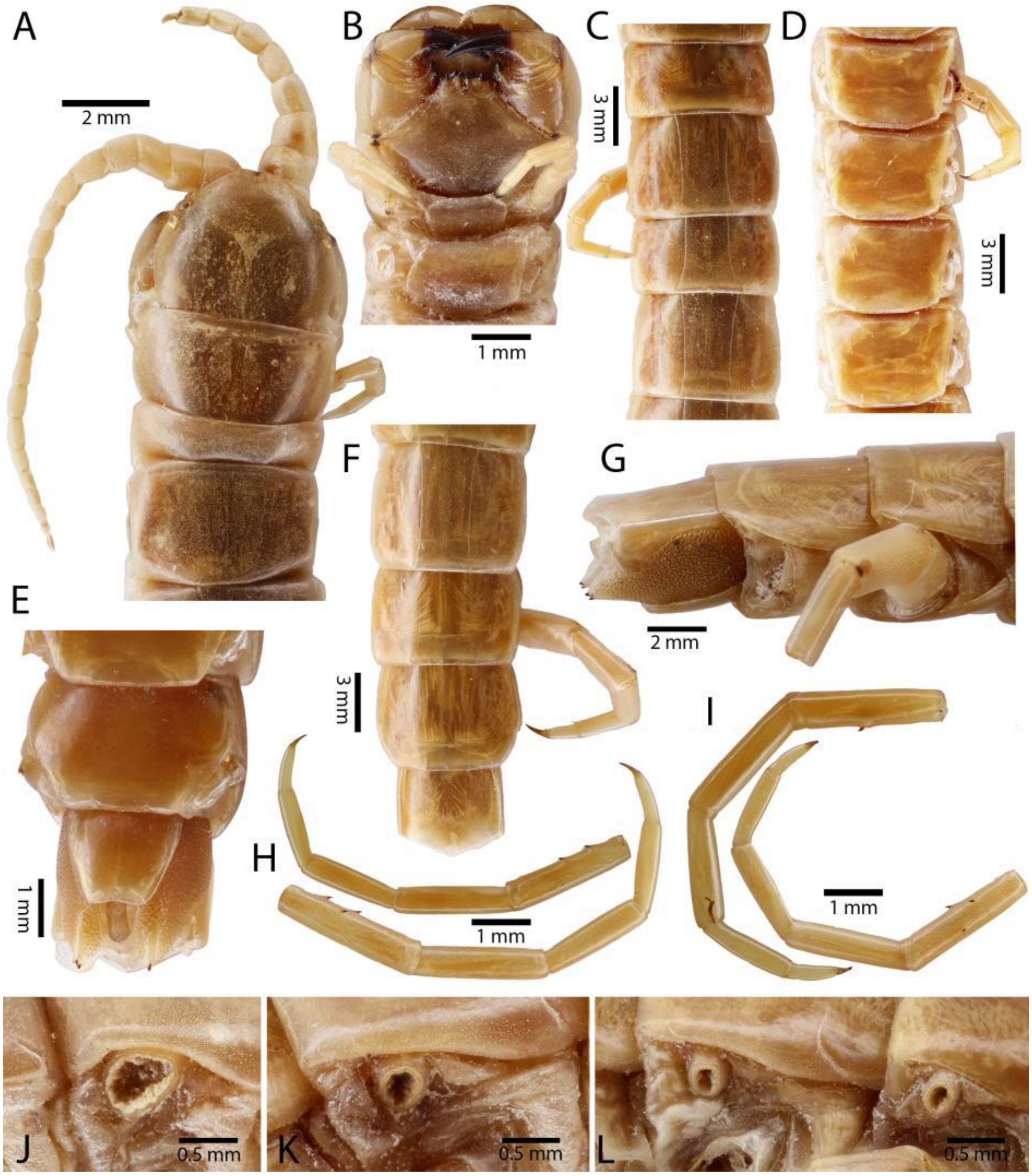


Figure 6.9 Syntype 2 and ultimate legs (loose in tube) of *Rhysida immarginata* (Porat, 1876): **A** Cephalic plate, antenna and tergites 1-3 **B** Forcipular segment, sternites 1-2 and legs 1-2 **C** Tergites 9-12 **D** Sternites 10-13 **E** Sternite 20, sternite of ultimate leg-bearing segment and coxopleura **F** Tergites 18-20 and tergite of ultimate leg-bearing segment and legs 19 **G** Coxopleuron and segments 19-20 **H-I** Ultimate legs **J-L** Spiracles 3, 5 and 7-8.

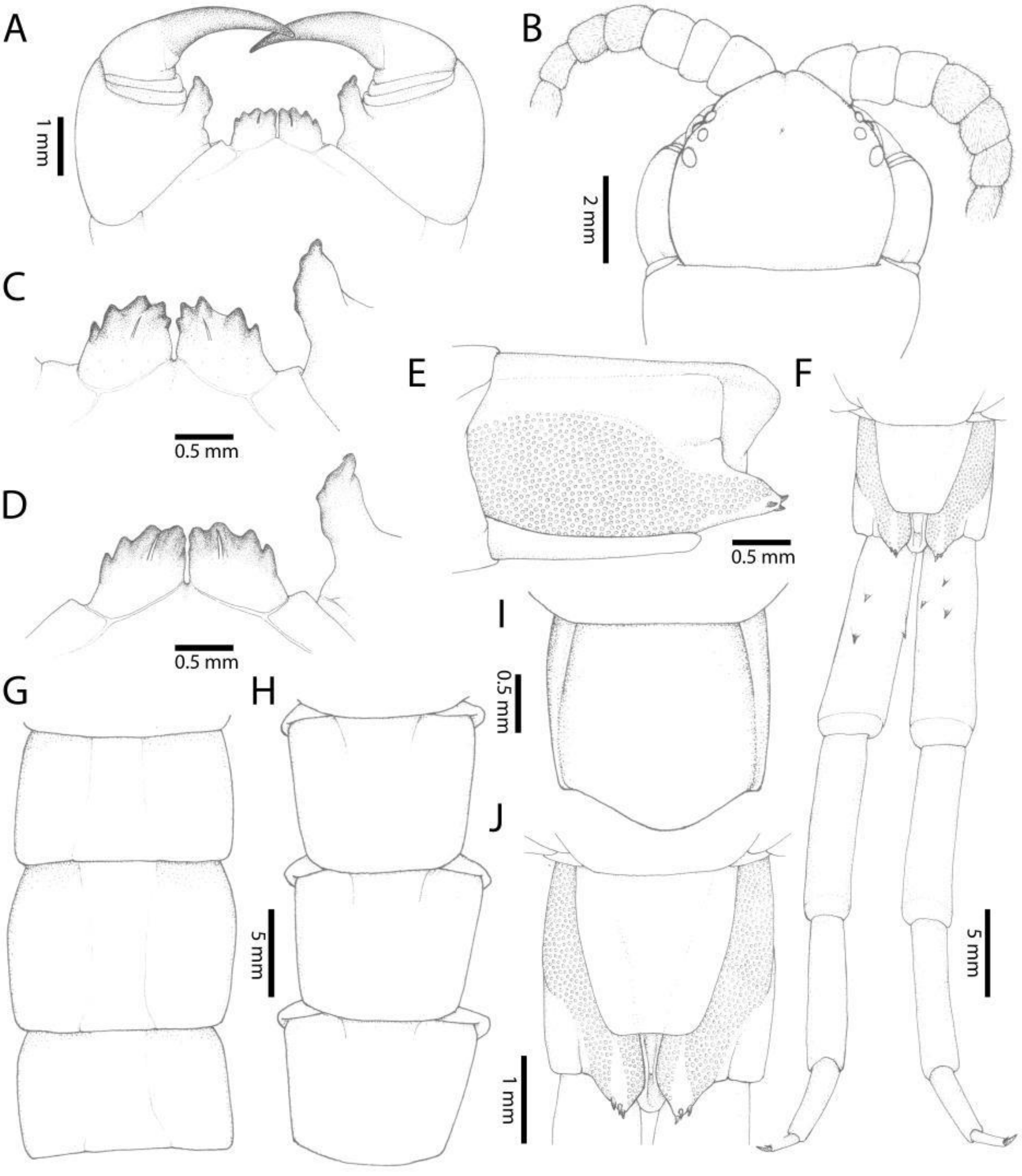


Figure 6.10 Morphological variation of *Rhysida immarginata* (Porat, 1876): **A** Forcipular segment **B** Cephalic plate and glabrous antennal articles **C-D** Variation in teeth on tooth-plates **E** Coxopleuron **F** Sternite of ultimate leg-bearing segment, coxopleura and ultimate legs **G** Tergites and sternites 9-11 **I** Tergite of ultimate leg-bearing segment **J** Sternite of ultimate leg-bearing segment and coxopleura.

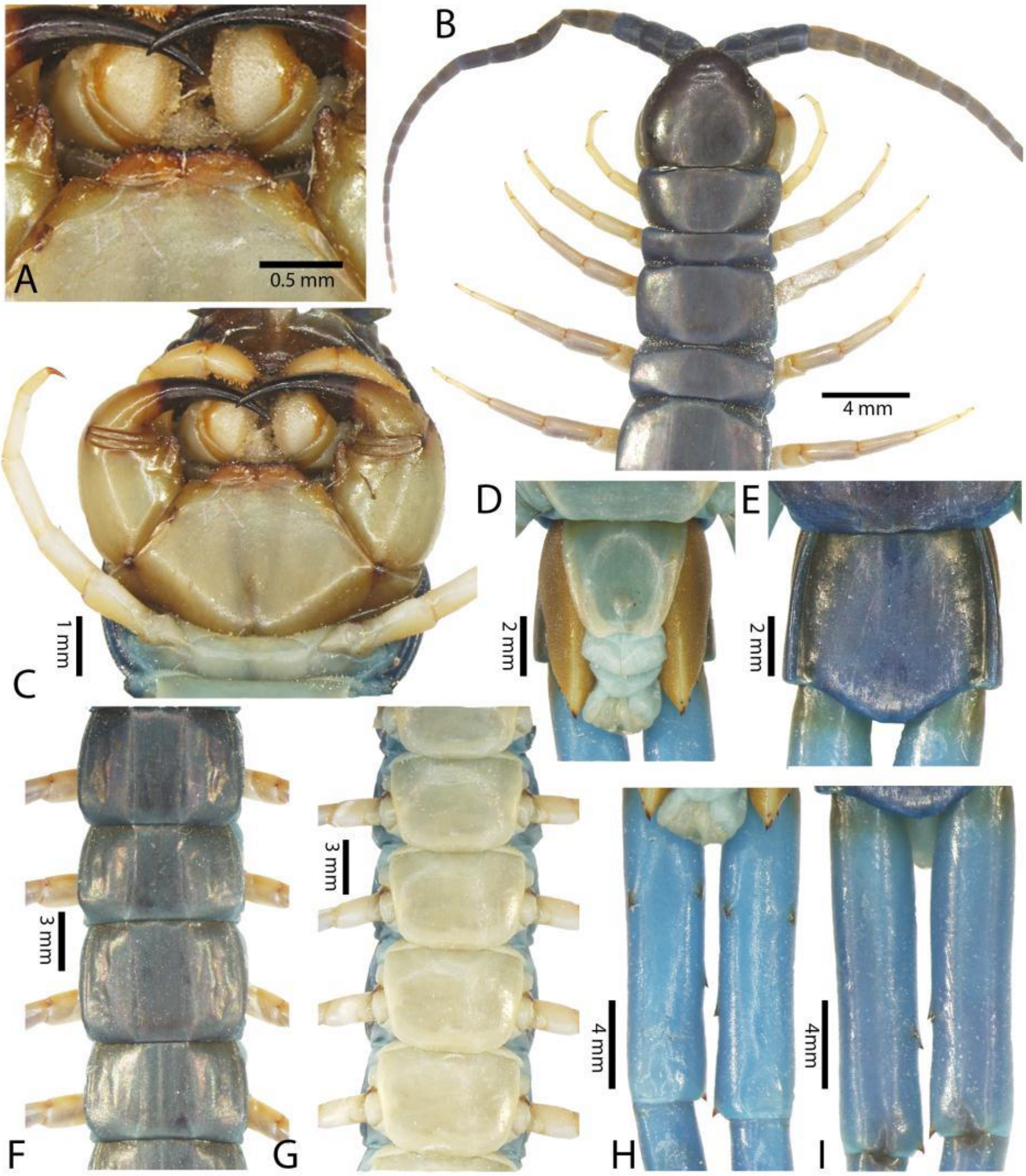


Figure 6.11 Morphological characters of *Rhysida singaporensis* Verhoeff, 1937 (topotypes): **A** Tooth-plates **B** Cephalic plate, antenna and tergites 1-5 **C** Forcipular segment, sternites and legs 1 **D-E** Sternite and tergite of ultimate leg-bearing segment **F-G** Tergites and sternites 10-13 **H-I** Ventral and dorsal views of ultimate leg prefemora.

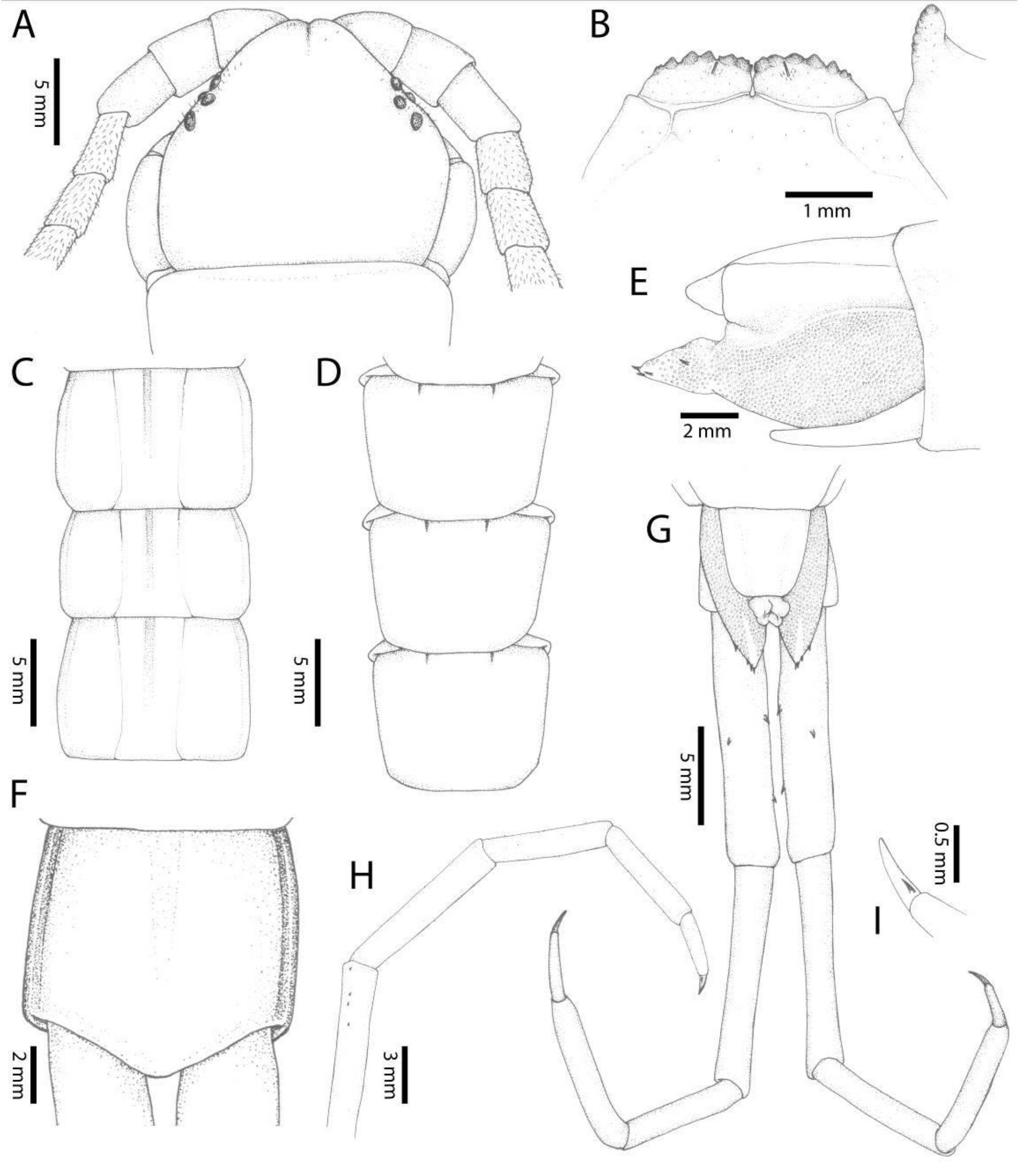


Figure 6.12 Morphological variation of *Rhysida singaporensis* Verhoeff, 1937 (topotypes): **A** Cephalic plate and glabrous antennal articles **B** Tooth-plates **C**-**D** Tergites and sternite 9-11 **E** Coxopleuron **F** Sternite of ultimate leg-bearing segment **G** Sternite of ultimate leg-bearing segment, coxopleura and ultimate legs **H** Lateral view of right ultimate leg.

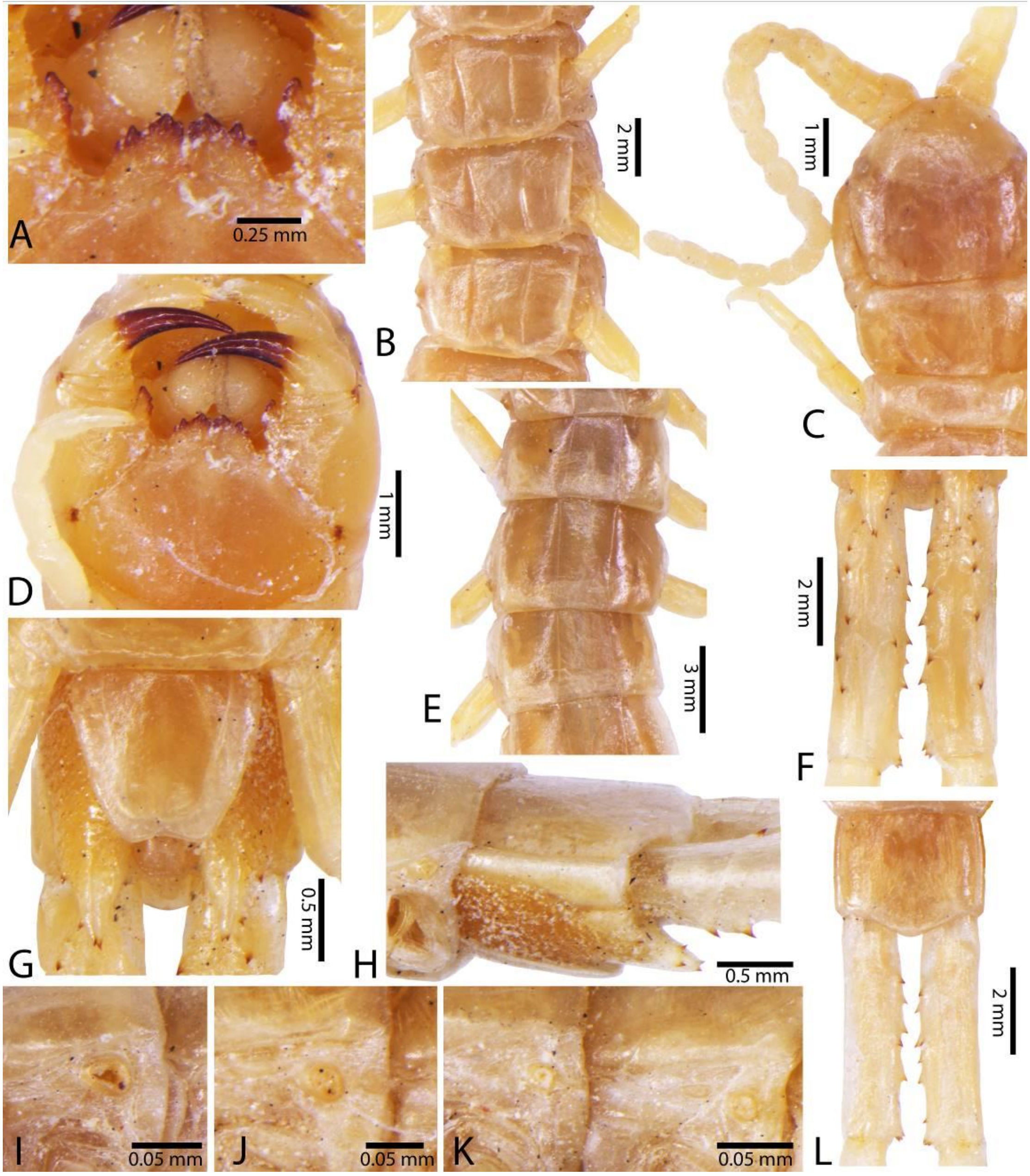


Figure 6.13 Holotype of *Rhysida marginata* Attems, 1953: **A** Tooth-plates **B** Sternites 9-11 **C** Cephalic plate, antenna, tergites1-3 and legs 2 **D** Forcipular segment **E** Tergites 9-11 **F** Ventral view of ultimate leg prefemora **G** Sternite of ultimate leg-bearing segment and coxopleura **H** Coxopleuron **I-K** Spiracles 3, 5 and 7-8 **L** Tergite of ultimate leg-bearing segment and ultimate leg prefemora.

Figure 6.14 Live habitus specimens of *Alluropus calcarata* (Pocock, 1891); **A** Adult male (morphotype 1) **B** Adult female (morphotype 1) **C** lateral view of ultimate legs displaying male secondary sexual characters **D** Female coiling with brood**.**

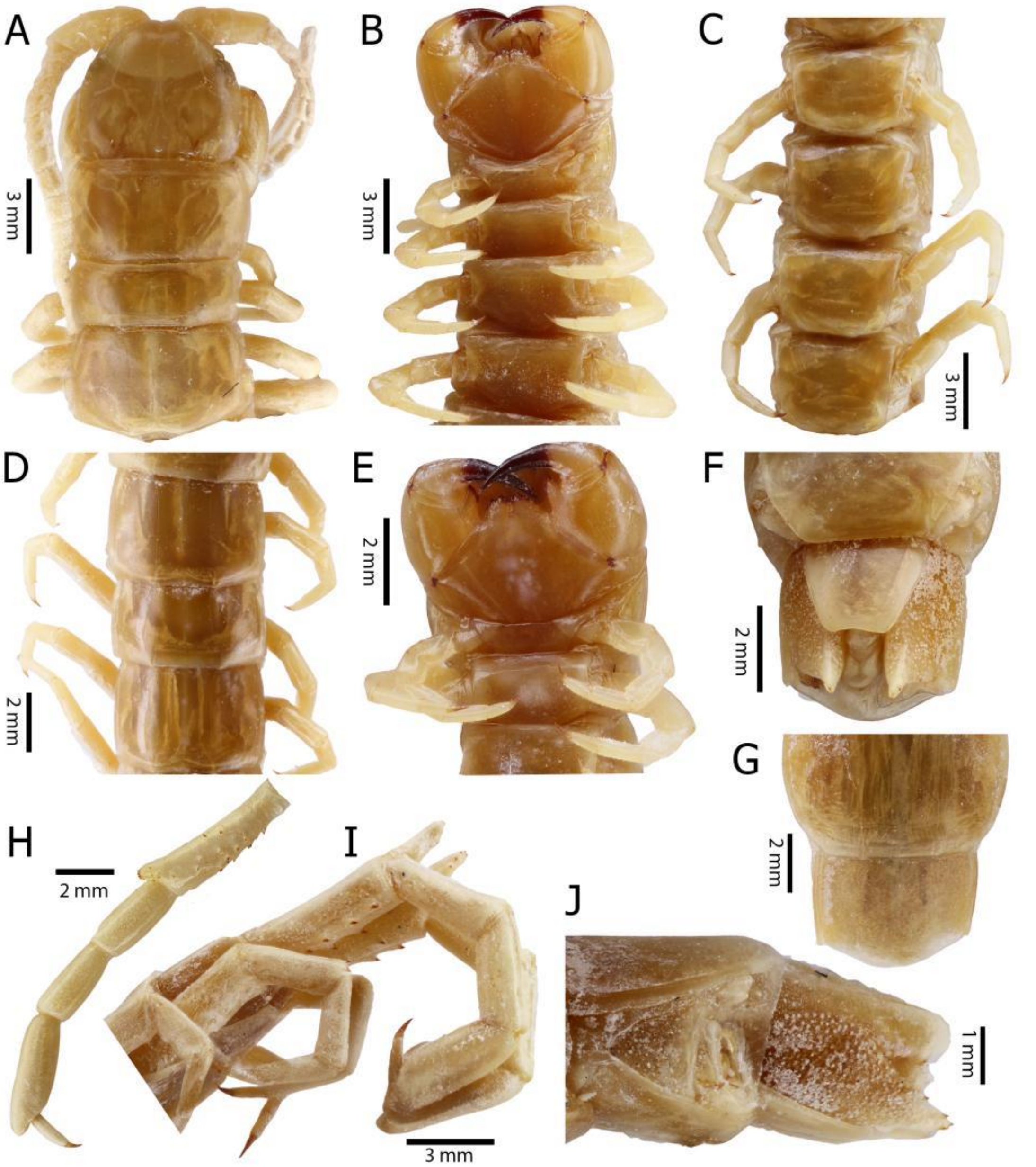


Figure 6.15 Syntypes specimens of *A. calcarata* "*Alluropus demangei* Silvestri, 1912": **A** Cephalic plate, antenna and tergites 1-3 **B** Forcipular segment and sternites 1-5 **C-D** Sternites and tergites 9-11 **E** Forcipular segment and sternites 1-2 **F** Sternite of ultimate leg-bearing segment and coxopleura **G** Tergite of ultimate leg-bearing segment **H** Ultimate leg **I** Lateral view of legs 20 and ultimate legs **J** Coxopleuron**.**

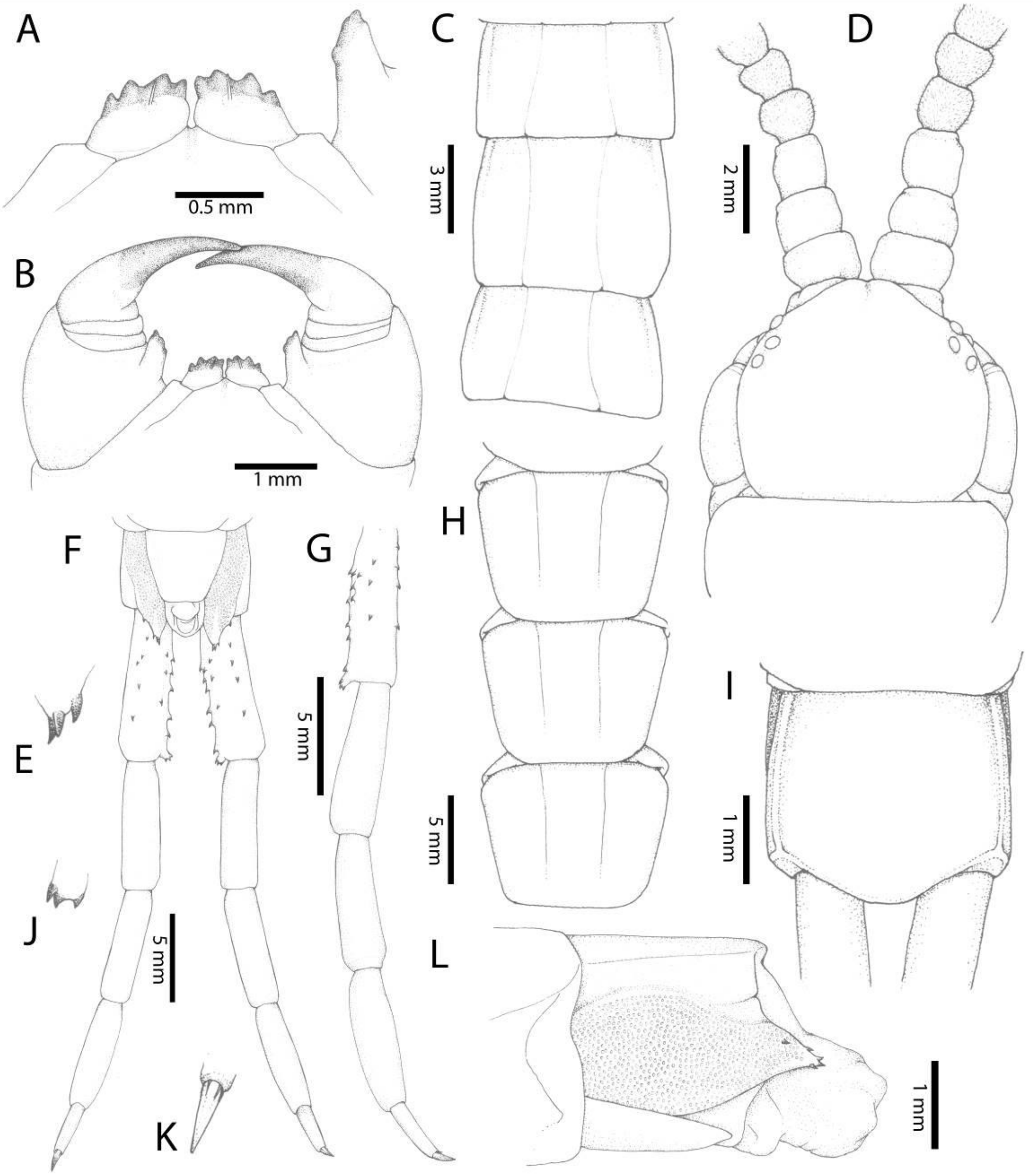


Figure 6.16 Morphological variation in morphotype 1 of *Alluropus calcarata* (Pocock, 1891); **A** Tooth-plates **B** Forcipular segment **C** Tergites 9-11 **D** Cephalic plate and glabrous antennal articles **E** Spines on coxopleural process **F** Sternite of ultimate leg-bearing segment, coxopleura and ultimate legs **G** Lateral view of ultimate leg (female) **H** Sternites 9-11 **I** Tergite of ultimate leg-bearing segment **J** Spines on prefemoral process on ultimate legs **K** Pretarsus with two accessory spurs **L** Coxopleuron**.**

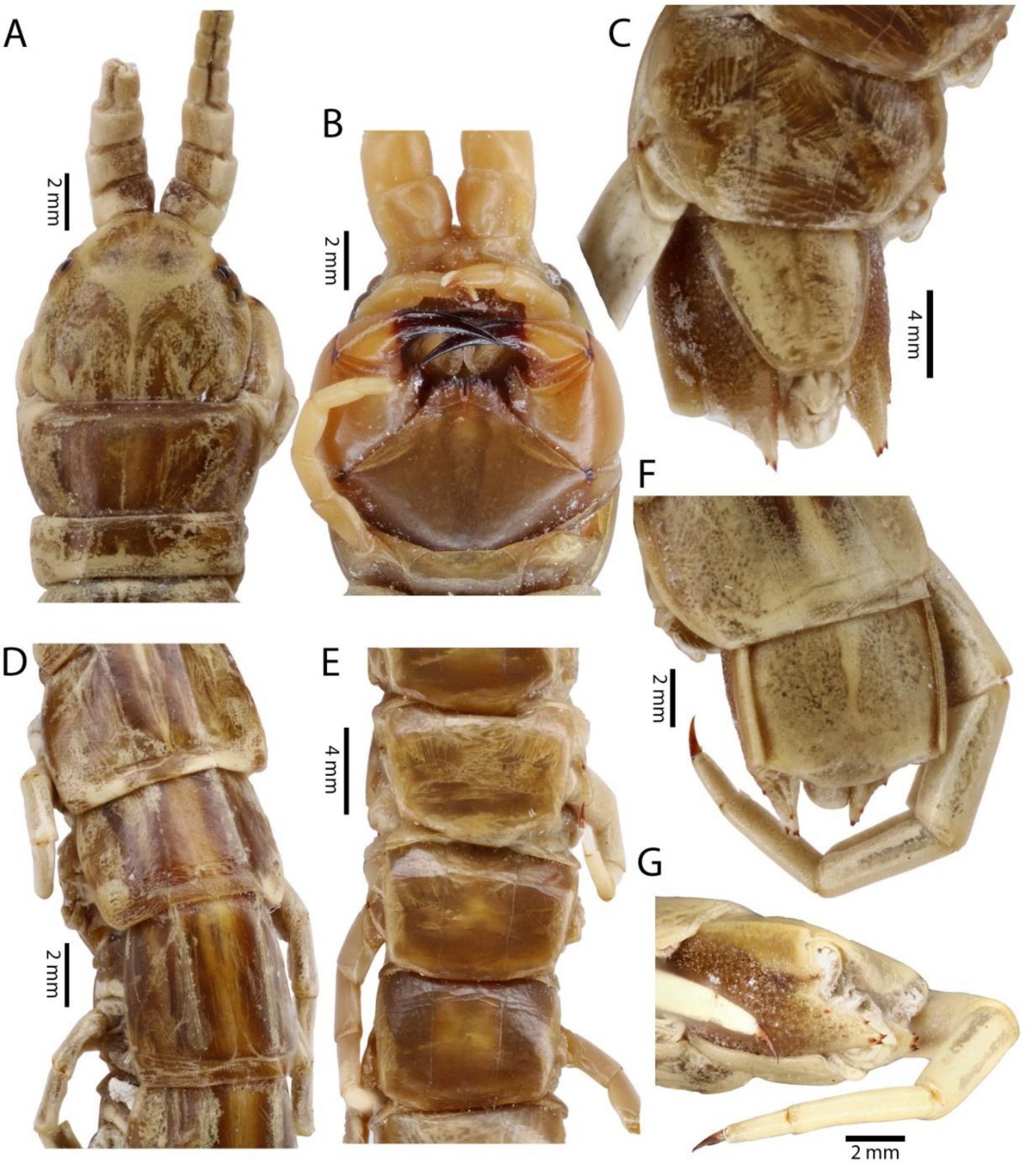


Figure 6.17 Syntype specimen 1 of *Alluropus calcarata* (Pocock, 1891) [previously designated type of *R. calcarata*]: **A** Cephalic plate **B** Forcipular segment **C** Sternite 20 and sternite of ultimate leg-bearing segment **D-E** Tergites and sternites 8-10 **G** Coxopleuron**.**

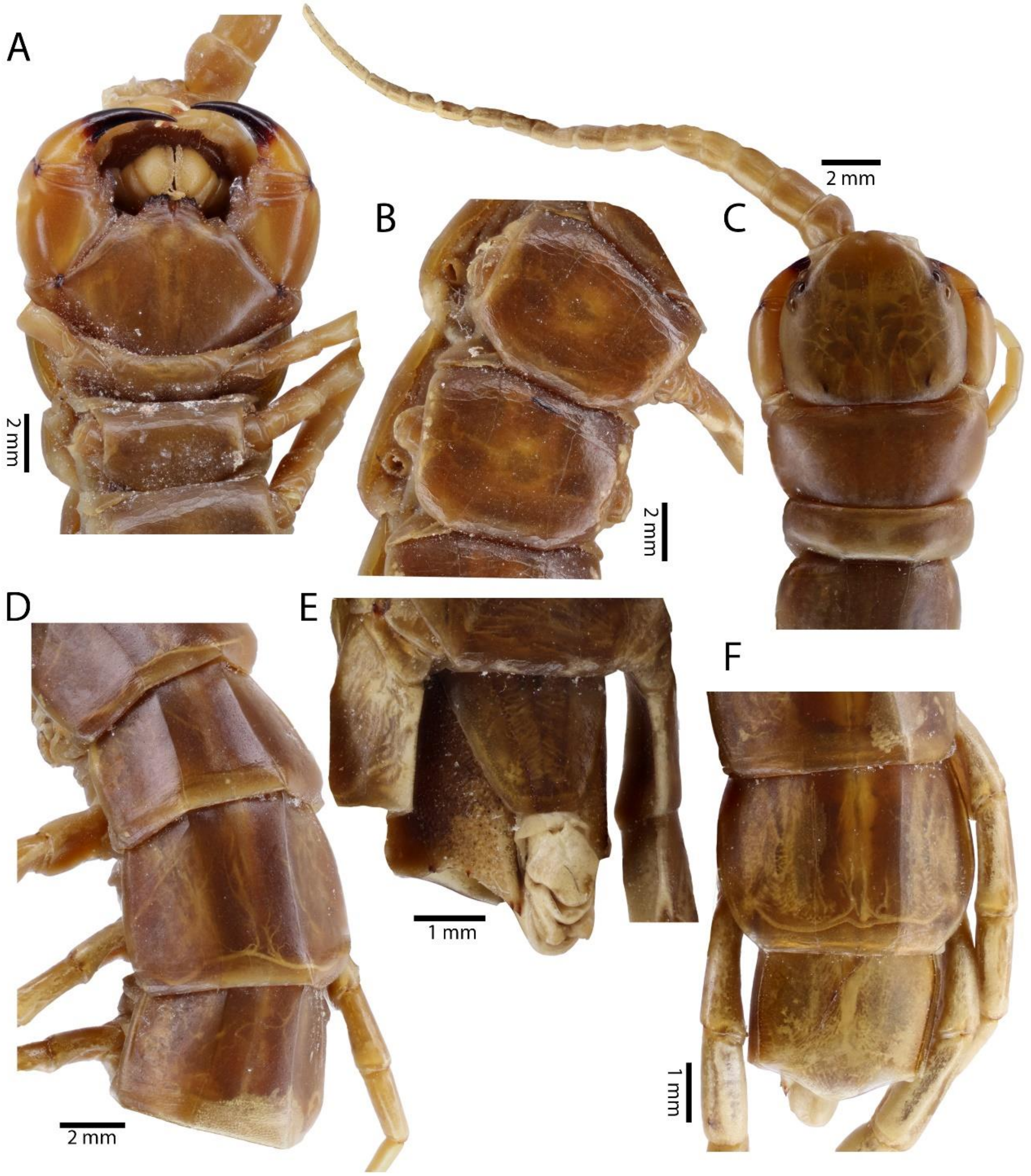


Figure 6.18 Syntype specimen 2 of *Alluropus calcarata* (Pocock, 1891) [previously designated type of *R. calcarata*]; **A** Forcipular segment **B** Sternites 7-8 **C** Cephalic plate and left antenna **D** Sternites 7-9 **E** Sternite of ultimate leg-bearing segment, coxopleuron and female genital segments **F** Tergite 20 and tergite of ultimate leg-bearing segment**.**

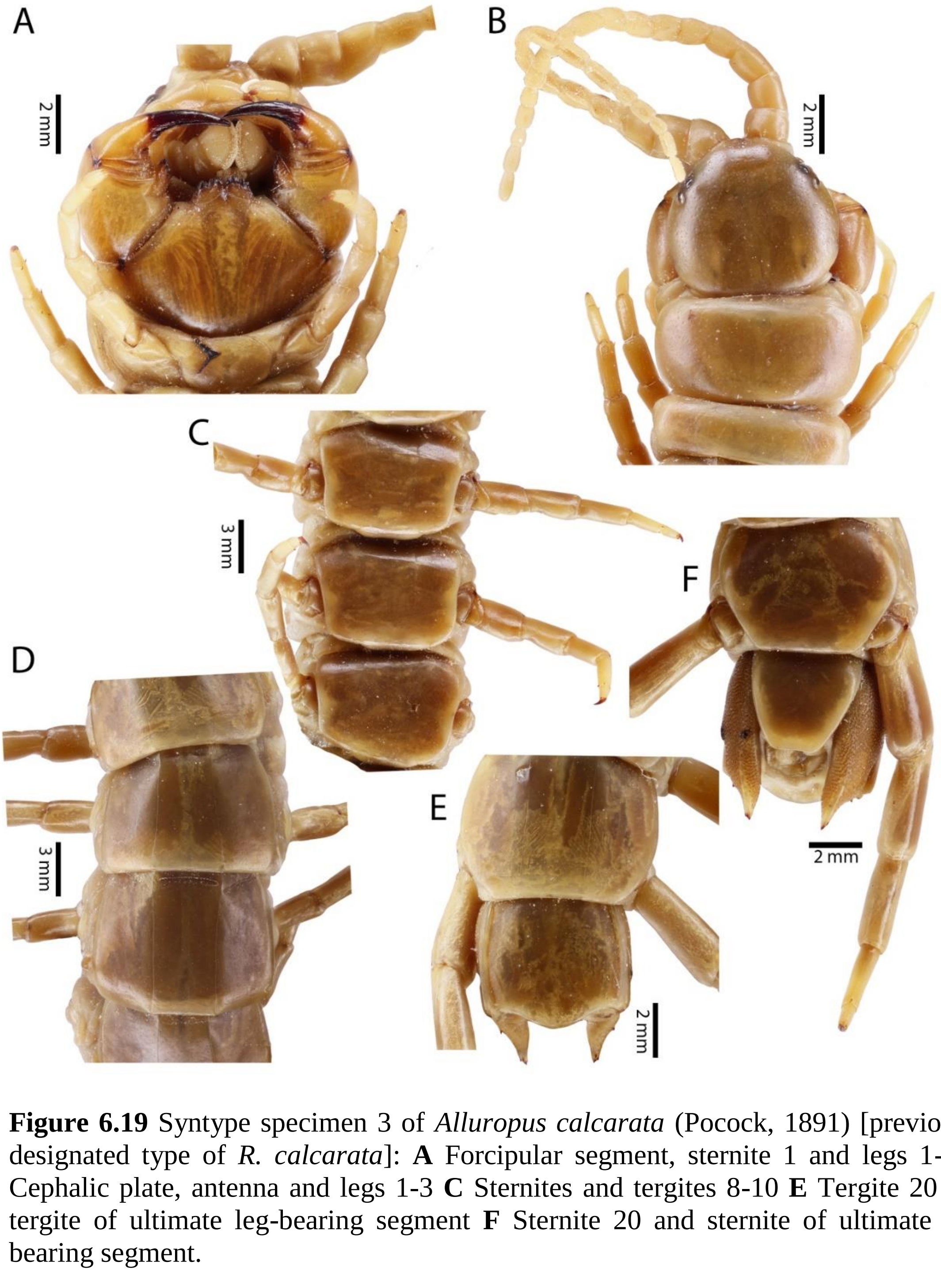


Figure 6.19 Syntype specimen 3 of *Alluropus calcarata* (Pocock, 1891) [previously designated type of *R. calcarata*]: **A** Forcipular segment, sternite 1 and legs 1-2 **B** Cephalic plate, antenna and legs 1-3 **C** Sternites and tergites 8-10 **E** Tergite 20 and tergite of ultimate leg-bearing segment **F** Sternite 20 and sternite of ultimate leg-bearing segment.

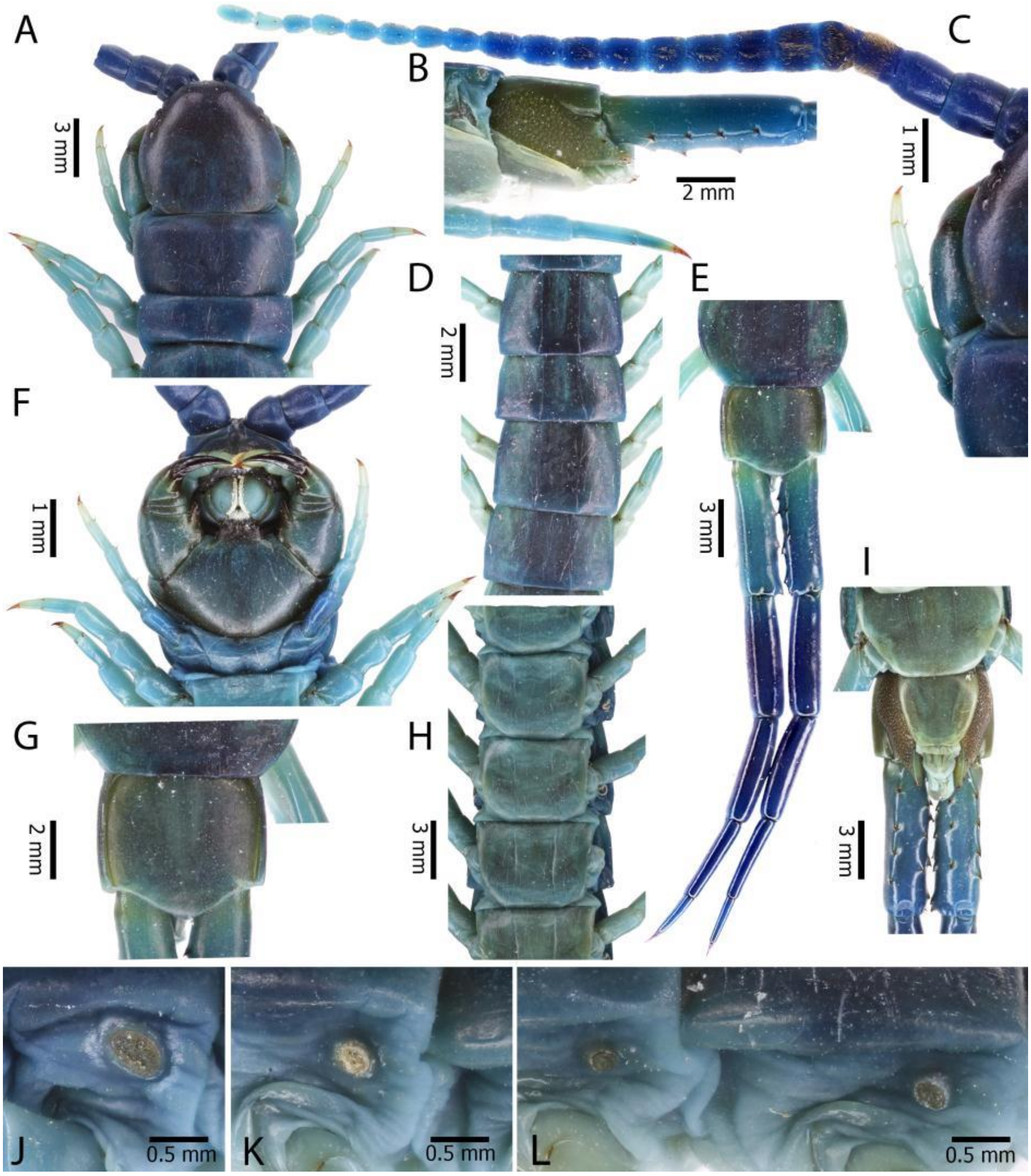


Figure 6.20 Morphological characters of morphotype 2 in *Alluropus calcarata* (Pocock, 1891): **A** Cephalic plate, antenna and legs 1-2 **B** Coxopleuron **C** Cephalic plate and antenna **D** Tergites 9-12 **E** Tergite 20 and tergite of ultimate leg-bearing segment **F** Forcipular segment, sternites 1-2 and legs 1-3 **G** Tergite of ultimate leg-bearing segment **H** Sternites 7-10 **I** Tergite 20 and tergite of ultimate leg-bearing segment **J-L** Spiracles 3, 5 and 7-8**.**

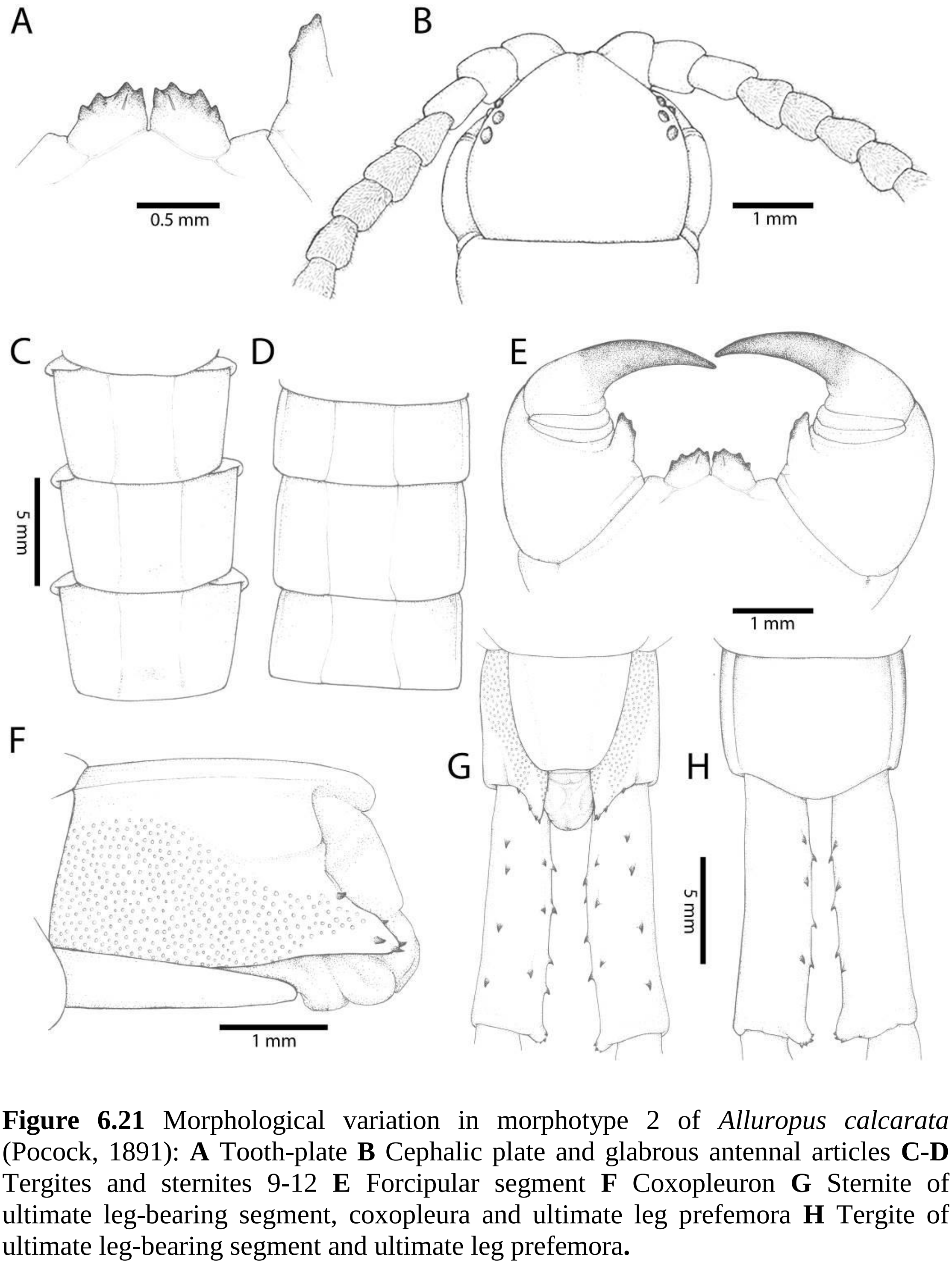


Figure 6.21 Morphological variation in morphotype 2 of *Alluropus calcarata* (Pocock, 1891): **A** Tooth-plate **B** Cephalic plate and glabrous antennal articles **C-D** Tergites and sternites 9-12 **E** Forcipular segment **F** Coxopleuron **G** Sternite of ultimate leg-bearing segment, coxopleura and ultimate leg prefemora **H** Tergite of ultimate leg-bearing segment and ultimate leg prefemora**.**

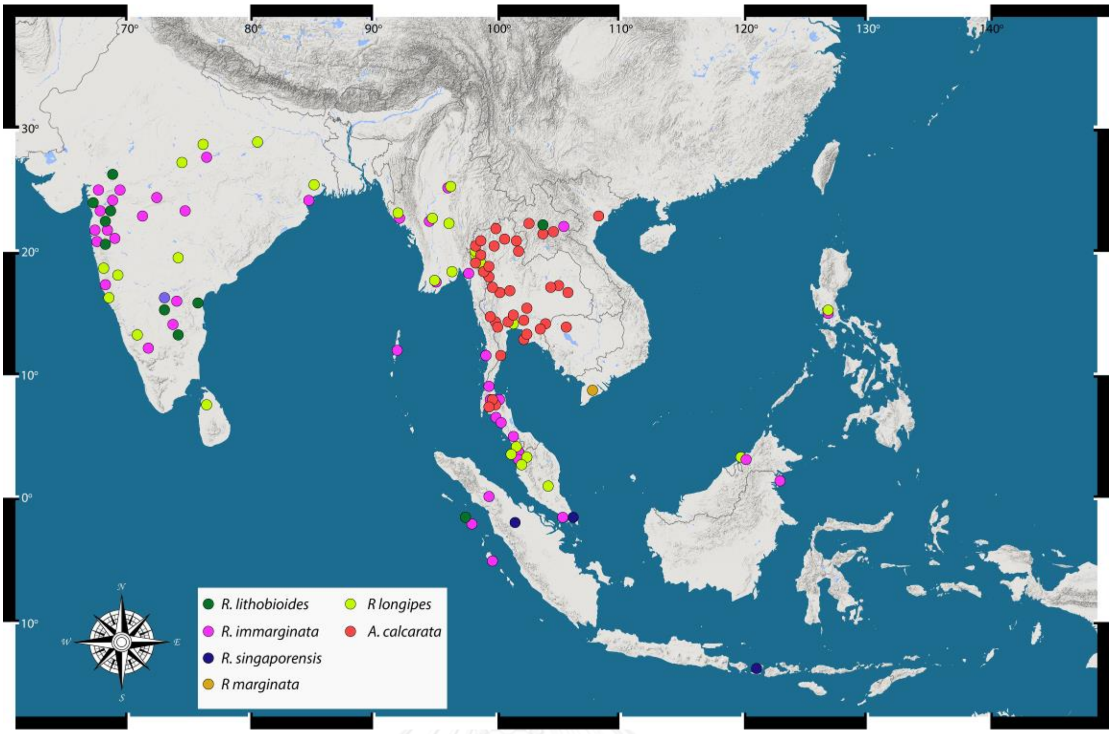


Figure 6.22 Distribution record of some *Rhyida* and *Alluropus calcarata* based on data from previous literature and the present study.

Table 6.1 Collections used in molecular phylogenetic analysis

Sampling No	Locality
M1	Khao nui Park, Rattaphum, Songkhla, Thailand
M2	Gua Ikan, Kelantan, Malaysia
M3	Ban Pak Bak, Mueang Ngoi, Luang Phrabang, Laos
M4	Wat Tham Yai, Tha Chana, Chumporn, Thailand
M5	Wat Nong Bo Charoen Tham, Nam Yuen, Ubon Ratchathani, Thailand
M8	Thung Khai Botanical Garden, Yantakhao, Trang, Thailand
M7	Ban na ka som, Attapue, Laos
M9	Nai Phlao Baech, Khanom, Nakhon Si Thammarat, Thailand
M6	Wat Chakkachan, Chum Ta Bong, Nakhon Sawan, Thailand
M12	Khao nui Park, Rattaphum, Songkhla, Thailand
M10	Tham Krasae, Sai Yok, Kanchanaburi, Thailand
M11	Wat Phra That Chae Haeo, Phu Phiang, Nan, Thailand
M13	Mae Taeng, Chiang Mai, Thailand
M14	Makok Waterfall, Chanthaburi, Thailand
M15	Ban Na San, Surat Thani, Thailand

Table 6.1 Collections used in molecular phylogenetic analysis (Continued)

Sampling No	Locality
M16	Gua Musang, Kelantan, Malaysia
M17	Taphome Stone Castle, Siem Reap, Cambodia
M18	Wat Welu Wan, Dan Chang, Suphanburi, Thailand
M19	Ban Nong Hua Non, Kasetwisai Roi Et, Thailand
M20	Pan Faen, Mae Taeng, Chiang Mai, Thailand
M21	Wat Nikhom Kaset, Man Yai, Mukdahan, Thailand
M22	Wat Phra-Ong Thom, Siam Riep, Cambodia
M23	Ban Pha Wong, Mueang Yommarat, Huaphan, Laos
M24	Khao Kha, Sichon, Nakhon Si Thammarat, Thailand
M25	Tham Mi Ka Ram Mae Taeng Chiang Mai, Thailand
M26	Ban Sop Laos, Huaphan, Laos
M27	Ban Sop Hun, Mueang Ngoi, Luang Phrabang, Laos
M28	Wat Ban Hu, Luang Phrabang, Laos
M29	Huai Hong Khrai, Chiang Mai, Thailand
M30	Laos-China borders, Luang Namtha, Laos

Table 6.1 Collections used in molecular phylogenetic analysis (Continued)

Sampling No	Locality
M31	Phra Cave, Ban Namyen, Myanmar
M32	Mae Cham, Chiang Mai, Thailand
M33	Phra Cave, Ban Namyen, Myanmar
M34	Phra Cave, Ban Namyen, Myanmar
M35, M36	Dhamatat Cave, Moulmein, Myanmar
M37, M38	Phra Cave, Ban Namyen, Myanmar
M39, M40	Phra Cave, Ban Namyen, Myanmar
M41	Myeik Archipelago, Myeik, Myanmar
M42, M78, M79	Bukit Timah, Singapore
M52	Chulachomklao Royal Military Academy Monument, Kra Buri, Ranong
M53	Gunung Mesah, Gu Ping, Perak, Malaysia
M54	Wat Sala Luang Bon, Ranot, Songkhla, Thailand
M55	Ban Nam Noen, Hua Mueang, Huaphan, Laos
M56	Chulalongkorn University, Bangkok, Thailand

Table 6.1 Collections used in molecular phylogenetic analysis (Continued)

Sampling No	Locality
M57	Ulukinta, Indian Temple, Perak, Malaysia
M58	Black Ant Resort, Mae Sa Rieang, Mae Hong Son, Thailand
M59	PK-2, Bahin village, Burma
M60	Tha Khantho, Kalasin, Thailand
M61	Huai Hong Khrai, Chiang Mai, Thailand
M62	Wat Khlong Wan, Mueang, Prachuap Khiri Khan, Thailand
M63	Wat Tha Thung Na Rittha Ram, Sai Yok, Kanchanaburi, Thailand
M64	Hotspring Resort, Ban Nam Hom, Xieng Khouang, Laos
M48	Viengsa, Nan, Thailand
M49	Wat Pa Buakaeow, Thong Phapume, Kanchanaburi, Thailand
M50	Wat Tam Khao Prachan, Khao Chakun, Sra Kaeo, Thailand
M51	Wat Pa Sai Mun, Sai Mun, Yasothon, Thailand
M43	Wat Pa Kanejue, Mae La Mat, Tak, Thailand
M44	Phapadaeng, Samut Prakarn, Thailand

Table 6.1 Collections used in molecular phylogenetic analysis (Continued)

Sampling No	Locality
M45	Wat Thammapidok, Na Ke, Prachin Buri, Thailand
M46	Than Pha Ta Phon, Neun Ma Phange, Pitsanulok, Thailand
M47	Wat Tham Luang, Donsak, Surat Thani, Thailand
M67	Lan Sang Waterfall, Mueang, Tak, Thailand
M71	Surin Island, Phang Nga, Thailand
M72	Penang Hill, Penang, Malaysia
M73	Phra Cave, Myanmar
M75	Klong Jak Waterfall, Koh Lanta, Krabi, Thailand
M76	Nakasom, Attapue, Laos
M77	Mae Cham, Chiang Mai, Thailand
M45	Wat Thammapidok, Na Ke, Prachin Buri, Thailand

Table 6.2 Sequence annotation for three molecular markers (COI, 16S and 28S rRNA)

Genetic markers	Length	Variable site	Conserved site	Informative site
COI	543	259	284	234
16S	425	269	156	238
28S	317	88	229	61

Table 6.3 Morphological comparison in some taxonomic characters of *R. lithobioides* subspecies. Abbreviation: PS, paramedian sutures; AP, apical spine; SAP, subapical spine; LP, lateral spine; L, left side; R, right side; ?, insufficient data. References: [1] Attems, 1930, [2] Jangi and Dass, 1984, [3] Khanna, 1994, [4] This study

Character	***R. l. lithobioides*[1, 4]** **(Holotype)**	***R. l. abessynica*[1, 4]**	***R. l. paucidens*[1]**	***R. l. trispinosus*[2]**	***R. l. kumaonensis*[3]**	***R. l. shivalikensis*[3]**
Tergites with PS starting	T 4	TT 4-6	T 4	T 3	TT 5-6	T4
Tergite margination starting	T 9	T 4	T13	T 13	T 18	T (17, 18) 19
Percentage of PS on sternite	10%	10-35%	Short on anterior in original	Short on anterior in original	? (absent in original)	? (not visible in original)
Sternite of ultimate leg-bearing segment with median depression	absent	absent	present	present	present	present
Number of spine on coxopleural process	AP: ? SAP: ? LP:1	AP: 2	AP: 2 SAP: 1	AP: 3	AP: 3	AP: 3
Prefemoral spine on ultimate legs	VL: 2-3 VM: 2-3 M: 0-2 DM: 3-2 CS: 1	VL: 1-3 VM: 1-2 M: 1-2 DM: 1-2	VL: 1 VM: 1 DM: 1-2	VL: 2 VM: 1 DM: 1	VL: 2 VM: 2 M: 1	VL: 2 VM: 1 M: 1
Legs with two tarsal spurs	1-5	1-(11)18	1-18	1-18	1-18	1-16
Legs with one tarsal spurs	6-17 (missing legs 18-20)	(14)16-20	19-20	19-20	19	17-20
Legs with tibial spurs	1-2R,3L,4L (missing legs 2-4 one side)	1-5	1	1	?	1
Legs with femoral spurs	1	1	1	1	?	1

Chapter 7

Discussion and Conclusion

Taxonomy and systematics of Scolopendromorpha in mainland Southeast Asia have until now been poorly known and available biodiversity data were scattered, with the only modern comprehensive works on taxonomy having been done from Vietnam (Schileyko, 1992, 1995, 2007; Tran et al., 2013) and some parts of Thailand (Muadsub et al., 2012). Recently, knowledge of species records in Thailand from biodiversity databases (Bonato et al., 2016) and previous surveys recorded only nine species of Scolopendromorpha in Thailand (Haase, 1887a; Flower, 1901; Sinclair, 1901; Attems, 1930a). In this study, comprehensive surveys conducted throughout Thailand and some adjacent areas reveal substantially more species diversity than previously known. Twenty-four species have been reviewed, including taxonomic revision with available type materials. In order to confirm their validity, morphological comparison and molecular phylogeny have been combined for taxonomic investigation, as is now becoming increasingly used in taxonomic and systematic studies (Edgecombe and Giribet, 2008; Joshi and Edgecombe, 2013; Vahtera and Edgecombe, 2014). Based on this integrative approach, twenty-four species have been validated. They were classified into two families, Scolopendridae and Cryptopidae. Scolopendridae comprises nine genera distributed mainly in anthropogenic areas, the most striking group being the genus *Scolopendra*. They have been reported as synanthropic in all tropical regions (Lewis, 1981; Lawrence, 1984) and exhibit enormous body size, reaching up to 25 cm for native Asian species, i.e. *Scolopendra dehaani* (Flower, 1901).

The occurrence records of several centipede groups from this study suggest the habitat preferences of each species. For example, specimens of *Scolopendra* were collected in various habitat types such as anthropogenic areas, agricultural areas, and some primary forest on the mainland and on islands. According to its diversity, *Scolopendra* in mainland Southeast Asia can be divided into three groups according to habitat characteristics. *Scolopendra dehaani* is recognized as a highly adaptable species, found throughout this region but especially in anthropogenic zones.

Secondly, *S. pinguis*, *S. calcarata*, *S. japonica*, *S. dawydoffi* and *S. cataracta* are likely to be montane species due to their distributions being delimited specifically along mountain areas and often found living in high humidity sites such as near waterfalls, small streams, and near river banks. The third group is composed of two widespread species, *S. morsitans* and *S. subspinipes*. Previous records suggest these species are introductions to the region (Shelley et al., 2005). In this study, it is demonstrated that *S. morsitans* in mainland Southeast Asia is restricted in its distribution to the coastal forest and some populations that live in dipterocarp forest of the northern and eastern regions. In the case of the historically long-recorded species *S. subspinipes,* it is shown that accurately-identified records are confined to islands. After broad specimen sampling in museum collections, most specimen records were found to have a scattered distribution on islands throughout Southeast Asia, as indicated in previous insular faunal studies (Haase, 1887a; Pocock, 1889, 1894; Attems, 1898, 1907, 1909; Attems, 1914a, b, c, 1915, 1927, 1930b; Attems, 1938, 1953). During field survey, only one specimen of *S. subspinipes* was found from Singapore. Previous taxonomic studies in Vietnam also report this species to be distributed along the coastal area and northern territory. It may be concluded that habitat preference of *Scolopendra* may be associated with specific aspects of their biology, as previously suggested for several centipede groups (Lewis, 1968, 1972b, 1982b, 1984a), and might be linked to the diversity of this genus in this area.

Morphological examination of *Scolopendra* suggested four morphological groups, the *subspinipes*, *cingulata*, *pinguis+calcarata* and *morsitans* groups, respectively. This morphological classification conforms to several previous taxonomic studies (Kraepelin, 1903; Attems, 1930a). Taxonomic survey from both morphology and molecular data of *S. subspinipes* sensu Attems, 1930, either validated or synonymized several former subspecies of *S. subspinipes* (Chao, 2008; Lewis, 2010b; Chao et al., 2011; Kronmüller, 2012). In this study, this taxonomic emendation was confirmed apart from the possible resurrection of some synonyms, such as *S. subspinipes piceoflava* (=*S. subspinipes*), based on potential morphological diagnosibility after type specimen re-examination. Diversity trends of the genus *Scolopendra* seem to further suggest that species richness in this region involves faunal transition with neighbouring regions such as India and China. In other genera of Scolopendridae, taxonomic reviews likewise verified the validity of several recorded species. The most diverse group is the subfamily Otostigminae, which is composed of several morphologically distinct genera such as *Sterropristes* and *Alluropus*. The endemic genus *Sterropristes* was reviewed again after previous suggestions that each species in this group shows a narrow distribution range. In this study, we provide additional distribution records of two species that result in wider distributions than previously known (Attems, 1934; Verhoeff, 1937; Muadsub et al., 2012).

In the case of the monotypic genus *Alluropus*, taxonomic validity has been revised in light of close affinity to species until now classified in another genus, *Rhysida*. The club-shape and elongated prefemoral process of the ultimate legs were discovered to be male secondary sexual characters. Some taxonomic characters such as number of spines on the coxopleural process, the complete paramedian sutures on sternites, and the occurrence of a prefemoral spur on leg 1 were proposed as additional diagnostic characters of *Alluropus.* The distribution of *Alluropus* seems to be sympatric with some widespread species of *Rhysida* such as *R. immarginata* and *R. longipes*. The morphological survey of *Alluropus* specimens indicated two morphological types that have disjunct geographical distributions. They are mainly distributed along the central part and the margin of the Korat Plateau in the northeastern part of Thailand. However, molecular analysis indicated that these two morphologically distinct groups are not phylogenetically distinct (specimens of one morphotype are nested within clades mostly composed of the other morphotype) and they are thus interpreted as geographical variation within a single species.

Otostigmus were classified into six morphological species groups; *O. spinosus+O. astenus, O. scaber, O. aculeatus, O. sulcipes, O. rugulosus* and *O. multidens.* Previous revision of *Otostigmus* species indicated that there are nine species groups delimited based on morphological characters (Attems, 1930a; Lewis, 2010d), but these groupings had not been tested phylogenetically. In this study, some species groups were confirmed by molecular phylogeny. *Otostigmus multidens* and *O. rugulosus* are the most abundant centipede species in this region. Interestingly, there are other two species that show narrowly distributed populations based on geography: *O. scaber* and *O. spinosus*. A similar pattern in their distributions was found in this study, corresponding to the separation of populations into two groups that inhabit the Thai-Malay Peninsula and the Indochina sub-region, respectively. This geographical distribution may also be observed in several other animal taxa in this area (Emerson et al., 2000; Stuart et al., 2006; Muadsub and Pinkaew, 2014; Yodthong et al., 2015). The hypothesis of the Sunda shelf during sea-level fluctuations has often been used as supporting evidence for a land bridge between these two sub-regions (Woodruff, 2010; Hanebuth et al., 2011; Lambeck et al., 2014; Niedermeyer et al., 2014).

The problem of species identification based on traditional morphological characters has been documented. The isolation mechanisms of scolopendrids have long been debated in many tropical groups (Lewis, 2003). As previously suggested, geographical variation is likely to be the main challenge for accurate species delimitation in this centipede group (Lewis, 1968, 1978, 2000; Lewis, 2003; Edgecombe, 2007). From this reason, some traditional taxonomic characters previously used to identify species of Scolopendromorpha have been carefully documented to evaluate their taxonomic potential. From such morphological surveys, it can be shown that some taxonomic characters such as the number of glabrous antennal articles, the occurrence of paramedian and median sutures on the tergites and sternites, the number of spines on the coxopleural process, and the spine formula of the ultimate leg prefemora varied between different centipede groups or even within populations. Nonetheless, species boundaries can be recognized from each of these characters, especially in particular genera, i.e. *Scolopendra*, *Otostigmus* and *Rhysida*. From these traditional characters, variability that can be attributed to geographical variation has been found at different taxonomic levels. It seems that exclusive reliance on meristic characters that contain variation is difficult to sustain for taxonomic identification. In the past, some taxonomists also reported some shape characteristics in descriptions, such as the shapes of the cephalic plate, coxosternite, tergites and sternites, and the tergite and sternite of the ultimate leg-bearing segment in particular. However, no analyses had been conducted to determine whether this kind of variation was either adequate for species identification within Scolopendromorpha or was just variation between individuals.

Morphometric analysis has recently been implemented in centipede taxonomy (Lopez Gutierrez et al., 2011; Simaiakis et al., 2011). Some described species have been proposed based on the non-overlapping ratios of some taxonomic characters (Zhang and Wang, 1999). Geometric morphometrics has been used in this study to investigate shape variation of three conserved characters in *Scolopendra*: the cephalic plate, coxosternite, and the tergite of the ultimate leg-bearing segment. Results of this study indicated that these characters can determine species boundary within a set of sampled specimens of this genus. The shape variation from the tergite of the ultimate leg-bearing segment in particular showed a high degree of accuracy compared to the other characters. It may confirm that such shape variation tests are useful for species delimitation in several other morphologically conservative groups that lack appropriate characters for diagnosis. Morphological survey of several body systems in centipedes that have not been widely used in taxonomy have shown that they can provide additional taxonomic characters (Müller and Meyer-Rochow, 2006a; Müller and Meyer-Rochow, 2006b; Edgecombe, 2008a, b; Koch et al., 2009; Vahtera et al., 2012b). For this reason, further study on this kind of topic is needed to clarify taxonomic problems of centipedes in this region.

Molecular phylogenetics is now considered to be the one of powerful tools for taxonomic clarification, having been applied to varied systematic problems in Scolopendromorpha and other centipedes (Joshi and Karanth, 2011; Vahtera et al., 2012a, 2013; Vahtera and Edgecombe, 2014). In this study, every collected species of the family Scolopendridae has been sequenced. Three standard molecular markers for centipede phylogenetics, cytochrome *c* oxidase subunit I (COI), 16S rRNA and 28S rRNA, were partially amplified. As in the widely-accepted classification scheme, phylogenetic reconstruction of the family Scolopendridae recovered two fundamental groups that correspond to taxonomic classification, Scolopendrinae and Otostigminae. In Scolopendrinae, *Scolopendra* was divided into four groups that are compatible with previous hypotheses based on morphology. A new species, namely *Scolopendra cataracta* Siriwut, Edgecombe and Panha, 2016, was described based on specimens from Laos, Thailand and Vietnam. This new species belongs to the *subspinipes* group, which can be diagnosed by the characteristic of long and slender ultimate legs and is also supported by a phylogenetic tree that nested this species together with *S. subspinipes* (from Singapore, Indonesia and Caribbean islands) and *S. dehaani* (from mainland Southeast Asia). Two species groups within *Scolopendra* seem to indicate native distributions in this region, the *cingulata* group and *pinguis+calcarata* group, respectively. The *cingulata* group can be identified by the characteristic of robust and thick ultimate legs. This species group is composed of native Indochinese species, these being *S. dawydoffi* and three widespread tropical-temperate species, *S. japonica*, *S. multidens* and *S. cingulata*. The *pinguis+calcarata* group on the other hand exhibited a narrow distribution along the west-north territory of Thailand, the northern part of Laos, and Vietnam. This group is also probably distributed further to the Burmese-Chinese mountain range. In the case of other genera in the subfamily Scolopendrinae, they are resolved as monophyletic and the sister clade to *Scolopendra*.

In Otostigminae, the relationship between/within genera remains poorly resolved. In terms of well-supported nodes, a polytomy is observed between genera apart from the genus *Alluropus*, which is robustly monophyletic. The molecular phylogeny also indicated that *Alluropus* shows a close relationship with the genus *Rhysida*, and in particular with an Indo-Australian species group. The tree topology also clarified taxonomic ambiguity for some *Rhysida* species such as *R. longipes, R. nuda* and *R. singaporensis* by demonstrating that they are distinct species based on their measures of genetic divergence. The genus *Otostigmus* splits into two major groups that have weakly supported interrelationships. Presently, morphology is the most effective tool for interpreting the relationship within each of these clades. In spite of this ambiguity, the relationship of each clade that contains more than one species can be discussed with regards to their likely native distributions, such as Indo-Australian, Indian-Burmese and Asian tropical-temperate species. Moreover, the relationship between *Otostigmus* and *Digitipes* is still questionable, although at least all recently revised species of *Digitipes* were grouped together with one *Otostigmus* species that was previously attributed to *Digitipes*. In the case of the genus *Sterropristes,* this study supports previous taxonomic identification (Muadsub et al., 2012) that the Thai-Malay peninsula has two morphologically and genetically distinct species, *Sterropristes violaceus* and *S. metallicus*. In the overall phylogeny of Otostigminae, four putative undescribed/unnamed species were found from recently collected specimens. The possible genera that these unknown species should belong to are *Otostigmus* and *Digitipes*. It seems that several members of these two genera might require further taxonomic and systematic studies to clarify and identify the undetermined species that are found in this region.

As previously suggested, geographical distribution may affect morphological changes in several centipede genera. Southeast Asia can be seen as a giant faunal puzzle that contains several kinds of geological characteristics such as limestone karst, special dry zones, highlands or plateaus, and island archipelagos. This area is also recognized for having the potential to infer migration in both land and aerial taxa (Woodruff and Turner, 2009b; de Bruyn et al., 2014). In this study, we provide evidence for land bridges and migration routes of some centipede species based upon their distribution records and genetic composition at the within-population level. For example, two widespread *Scolopendra* species, *S. dehaani* and *S. morsitans*, were reported living in anthropogenic areas such that their distribution patterns seem to be affected by passive dispersal (Shelley et al., 2005). However, their genetic composition still shows a relationship to geographical barriers in this region such as the Korat Plateau and Isthmus of Kra. In the case of native species, *S. pinguis* and *S. calcarata* reveal high genetic divergence, and their phylogenetic clade composition shows geographic relationships between local populations in each sub-region along the Thai-Laos border area.

For this reason, further small-scale phylogeographic study of native species is needed. The boundaries of genetic exchange between different geographical populations may suggest further context of evolutionary history of the centipedes in this region. This assumption was supported by phylogeographic results that have been done in other centipede orders such as Scutigeromorpha (Giribet and Edgecombe, 2013) Lithobiomorpha (Giribet and Edgecombe, 2006) and Craterostigmomorpha (Edgecombe and Giribet, 2008; Giribet et al., 2009). The divergence rates of morphology and DNA sequences may not be equivalent at each taxonomic level, as witnessed by the partly incompatible pattern of relationship between morphological identification and genetic discrimination among members of Otostigminae. This result contrasts with phylogenetic results for Scolopendrinae, in which species delimitation based on external morphology, geometric morphometrics and molecular phylogenetics/divergence is highly congruent. However, molecular methods may show some signal for speciation events, as has been proposed for various scolopendromorph groups distributed in the Mediterranean and South Pacific areas (Murienne et al., 2011; Simaiakis et al., 2012).

In this study, brooding and feeding behaviour of five scolopendromorph genera, namely *Scolopendra*, *Cormocephalus*, *Rhysida*, *Alluropus* and *Otostigmus*, were observed in natural and captive conditions. The duration of the brooding and mating seasons may be divided into two periods. The first of these starts during the end of summer until early in the rainy season (May-July) and the second is in mid-winter until early summer (November-March). In first duration, *Otostigmus*, *Rhysida*, *Alluropus* and *Cormocephalus* have been recorded displaying these behaviours. Six *Otostigmus*, two *Rhysida*, two *Alluropus* and one *Cormocephalus* broods were found in natural habitats. Only *Scolopendra* seems to exhibit this behaviour during the second period. These observations improve our fundamental knowledge that the duration of the reproductive season of these regional species may differ compared with other centipede faunas. The feeding ability of *S. dehaani* was also observed during field surveys in the southern part of Thailand. The animals show high body flexibility during approach to the prey (the snail-eating snake, *Pareas carinatus*). Segments of the centipede body can twist nearly 360 degrees when snatching the prey. This observation exposes the potential of feeding mechanisms and prey size in *Scolopendra* to be adaptations for hunting varied kinds of prey. This observation may suggest why populations of this species are especially dense in several areas of this region.

In conclusion, a comprehensive field-based, integrative approach to taxonomy and systematics has expanded the species diversity of centipedes in Thailand and some adjacent countries, which had not been revised since the past century. Several species that exhibit regional and local endemism can potentially be used to improve fundamental knowledge and further applications. Molecular phylogeny of these primitive arthropods supported the hypothesis that faunal composition is often related to geological characteristics and paleo-events such as the Isthmus of Kra and Sunda shelf during sea-level fluctuation. New discoveries of several morphologically and genetically distinct species, whether they show clear separation or still contain taxonomic ambiguity (e.g. incipient species), may stimulate further comprehensive survey at a local scale. Lastly, biological and ecological notes from this study may inform the assumption that these evolutionarily ancient animals can adapt themselves to living under various natural pressures.

Investigations aimed at further understanding of scolopendromoph diversity in Southeast Asia should address systematic problems such as species boundaries, the species delimitation process and evolutionary history. As suggested previously, research conducted by using recent available data and additional novel techniques seems to be useful for testing various classification and identification hypotheses as well as determining the effects of geographical barriers and paleoenvironment events on diversification processes. Moreover, the comparative result of this study indicated that endemic and widespread species exhibit characteristics of cryptic and allopatric speciation processes. The phylogenetic relationships of some parts of Scolopendromorpha may be further clarified based on adding more gene markers, using either partial sequences (such as 18S and EF-1 alpha, widely surveyed in other groups of arthropods) or at a broader genomic level (such as entire mitochondrial genomes). The integration of molecular systematics, classical taxonomy and some fundamental biological studies to assess species delimitation, ecological niches and population structure deserves special attention. Further analyses of the DNA barcoding region of all recorded species seems to be an interesting approach to collect and reserve genetic data that may give us some valuable information for further applications, such as pharmaceutical and traditional drug medicines, toxin and biochemical substances, bio-indicators and bio-control, and also benefits to biodiversity inventory and conservation projects in Southeast Asia.

REFERENCES

Akkari, N., Stoev, P., and Lewis, J.G.E. 2008. The scolopendromorph centipedes (Chilopoda, Scolopendromorpha) of Tunisia: Taxonomy, distribution and habitats. ZooKeys 3: 77-102.

Ali, J.R., and Aitchison, J.C. 2008. Gondwana to Asia: Plate tectonics, paleogeography and the biological connectivity of the Indian sub–continent from the Middle Jurassic through latest Eocene (166–35 Ma). Earth–Science Reviews 88: 144-166.

Attems, C. 1897. Myriopoden. Ergebnisse der Hamburger Magalhaensischen Sammelreise 1892/93: 1-8.

Attems, C. 1898. Myriopoden. In: Semon R. (ed.), Zoologische Forschungsreise in Australien und dem Malayischen Archipel. Fünfter Band: Systematik, Tiergeographie, Anatomie wirbelloser Tiere. Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena 8: 505-516.

Attems, C. 1901. Dr. Brauer's Myriopoden-Ausbeute auf den Seychellen in Jahre 1895. Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere 13: 133-171.

Attems, C. 1903. Beiträge zur Myriopodenkunde. Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere 18: 63-154.

Attems, C. 1907. Javanische Myriopoden gesammelt von Direktor K. Kraepelin im Jahre 1903. Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 24 (Beiheft 2): 77-142.

Attems, C. 1909. Die Myriopoden der Vega-Expedition. Arkiv för Zoologi 5: 84.

Attems, C. 1914a. Die indo-australischen Myriopoden. Archiv für Naturgeschichte 80A: 1-398.

Attems, C. 1914b. Myriopoden von Neu-Guinea, gesammelt während der Expedition 1903. – Résultats de l'expédition scientifique Néerlandaise à la Nouvelle-Guinée. Vol V. Zoologie. Nova Guinea 5: 567-587.

Attems, C. 1914c. Zur Fauna von Nord-Neuguinea. Nach den Sammlungen von Dr. P. N. van Kampen und K. Gjellerup aus den Jahren 1910 und 1911. Myriopoden. Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere 37: 379-384.

Attems, C. 1915. Myriopoden von Neu-Guinea II. Gesammelt während der Expeditionen 1904-1909. – Résultats de l'expédition scientifique Néerlandaise à la Nouvelle-Guinée. Nova Guinea, Zoologie 13: 1-38.

Attems, C. 1927. Myriopoden von Ambon und anderen Inseln der Banda-See. Zoölogische mededeelingen 10: 61-70.

Attems, C. 1928. Neue Scolopendriden der Museen Wien und Hamburg. Zoologischer Anzeiger 78: 279-309.

Attems, C. 1930a. Myriapoda 2. Scolopendromorpha. Berlin: Walter de Gruyter.

Attems, C. 1930b. Myriopoden der Kleinen Sunda-Inseln, gesammelt von der Expedition Dr. Rensch. Mitteilungen aus dem Zoologischen Museum in Berlin 16: 117-184.

Attems, C. 1930c. Scolopendromorpha du Congo Belge. Revue de Zoologie et de Botanique Africaines 19: 287-294.

Attems, C. 1932. Résultats Scientifiques du Voyage aux Indes Orientales Néerlandaises. Mémoires du Musée Royal d'Histoire Naturelle de Belgique. Mémoires du Musée Royal d'Histoire Naturelle de Belgique, Hors Série 3 12: 1-34.

Attems, C. 1934. Neue Myriopoden des Museums Basel. Verhandlungen der naturforschenden Gesellschaft in Basel 45: 43-62.

Attems, C. 1938. Die von Dr. C. Dawydoff in französisch-Indochina gesammelten Myriopoden. Mémoires du Muséum National d'Histoire Naturelle 6: 187-353.

Attems, C. 1953. Myriopoden von Indochina. Expedition von Dr. C. Dawydoff (1938-1939). Mémoires du Muséum National d'Histoire Naturelle Paris, Série A 5: 133-230.

Bird, M.I., Taylor, D., and Hunt, C. 2005. Palaeoenvironments of insular Southeast Asia during the Last Glacial Period: A savanna corridor in Sundaland? Quaternary Science Reviews 24: 2228.

Blanchard, E. 1829. Insectes. In Guérin-Menéville, F.E. (ed.), Iconographie du règne animal de G. Cuvier : ou, Représentation d'après nature de l'une des espèces les plus et souvent non encore figurées de chaque genre d'animaux, pp. Paris.

Bollman, C. 1889. Myriopoda in the scientific results of explorations by the U.S. Fish Commission Steamer 'Albatross. Proceedings of the United States National Museum 12: 211-216.

Bolton, S.J., Macleod, N., and Edgecombe, G.D. 2009. Geometric approaches to the taxonomic analysis of centipede gonopods (Chilopoda: Scutigeromorpha). Zoological Journal of the Linnean Society 156: 239-259.

Bonato, L., et al. 2016. ChiloBase 2.0 - A World Catalogue of Centipedes (Chilopoda). [Online]. Available from: http://chilobase.biologia.unipd.it.

Bonato, L., et al. 2010. A common terminology for the external anatomy of centipedes (Chilopoda). ZooKeys 69: 17-51.

Bonato, L., and Minelli, A. 2002. Parental care in *Dicellophilus carniolensis* (C.L. Koch, 1847): new behavioural evidence with implication for the higher phylogeny of centipedes (Chilopoda). Zoological Anzeiger 241: 193-198.

Bookstein, F.L. 1996. Applying landmark methods to biological outline data. Image Fusion and Shape Variability 79 - 87.

Bookstein, F.L. 1997. Landmark methods for forms without landmarks: Morphometrics of group differences in outline shape. Medical Image Analysis 1: 225-243.

Brandt, J.F. 1840. Observations sur les espèces qui composent la genre *Scolopendra* suivies des caractères des espèces qui se trouvent dans le Museum zoologique de l'Académie des Sciences de St. -Pétersbourg et de quelques coups d'oeil sur leur distribution géographique. Bulletin Scientifique, Académie Imperiale des Sciences de Saint Pétersbourg 7: 148-160.

Brandt, J.F. 1841. Remarques Générales sur l'Ordre des Insectes Myriapodes. Bulletin Scientifique publié par l'Académie Impériale des Sciences de Saint-Pétersbourg 7: 293-328.

Brena, C., and Akam, M. 2012. The embryonic development of the centipede *Strigamia maritima*. Developmental Biology 363: 290-307.

Brölemann, H.W. 1902a. Myriapodes des Musée de São Paolo. Revista do Museu Paulista 5: 35-237.

Brölemann, H.W. 1902b. Myriapodes du Musée de Saõ Paulo. Revista do Museo Paulista 5: 35-237.

Brölemann, H.W. 1912. The Myriapoda in the Australian Museum. Part I. - Chilopoda. Records of the Australian Museum 9: 37-75.

Brown, R.M., and Stuart, B.I. 2012. Patterns of biodiversity discovery through time: an historical analysis of amphibian species discoveriesin the Southeast Asian mainland and adjacent island archipelagos. In Gower, D.J., et al. (ed.), Biotic Evolution and Environmental Change in Southeast Asia, pp. 349-389. Cambridge: Cambridge University Press.

Brunhuber, B.S. 1970. Egg laying, maternal care and development of young in the scolopendromorph centipede *Cormocephalus anceps anceps* Porat. Journal of the Linnean Society of London 49: 49-59.

Bücherl, W. 1946. Novidades sistematicas na ordem Scolopendromorpha. Memórias do Instituto Butantan 19: 135-158.

Bücherl, W. 1971. Venomous Chilopods or Centipeds. In n.p. (ed.), Invertebrates, pp. New York, London: Academic Press.

Butler, A.G. 1876. Preliminary notice of new species of Arachnida and Myriapod from Rodriguez. Annals and Magazine of Natural History ser. 4 17: 439-446.

Cannon, C.H., Morley, R.J., and Bush, A.B.G. 2009. The current refugial rainforests of Sundaland are unrepresentative of their biogeographic past and highly vulnerable to disturbance. Proceedings of the National Academy of Sciences 106: 11188-11193.

Chagas Júnior, A. 2012. The centipede genus *Otostigmus* Porat in Brazil: Description of three new species from the Atlantic Forest; a summary and an identification key to the Brazilian species of this genus (Chilopoda, Scolopendromorpha, Scolopendridae, Otostigminae). Zootaxa 3280: 1-28.

Chagas Júnior, A. 2013. A redescription of *Rhysida celeris* (Humbert & Saussure, 1870), with a proposal of eight new synonyms (Scolopendromorpha, Scolopendridae, Otostigminae). ZooKeys 258: 17-29.

Chagas Júnior, A., Chaparro, E., Jiménez, S.G., Triana, H.D.T., Flórez D., E., and Seoane, J.C.S. 2014. The centipedes (Arthropoda, Myriapoda, Chilopoda) from Colombia: Part I. Scutigeromorpha and Scolopendromorpha. Zootaxa 3779: 133–156.

Chagas Júnior, A., Knysak, I., and Guizze, S.P.G. 2007. Revalidation of the subgenus *Dactylotergitius* Verhoeff, and redescription of *Otostigmus* (*D.*) *caudatus* Brölemann and *Otostigmus* (*D.*) *cavalcantii* Bücherl (Scolopendromorpha : Scolopendridae : Otostigminae). Zootaxa 1639: 57-67.

Chamberlin, R.V. 1912. New North American chilopods and diplopods. Annals of the Entomological Society of America 5: 141-172.

Chamberlin, R.V. 1918. The Chilopoda and Diplopoda of the West Indies. Bulletin of the Museum of Comparative Zoology 62: 151-262.

Chamberlin, R.V. 1920a. The Myriapoda of the Australian Region. Bulletin of the Museum of Comparative Zoology 64: 1-269.

Chamberlin, R.V. 1920b. On some new myriopods collected in India in 1916 by C. A. Kofoid. University of California, Publications in Zoology 19: 389-402.

Chamberlin, R.V. 1921. New Chilopoda and Diplopoda from the East Indian Region. Annals and Magazine of Natural History, ser. 9 7: 50-87.

Chamberlin, R.V. 1922. The Centipedes of Central America. Proceedings of the U.S. National Museum 60: 1-22.

Chamberlin, R.V. 1939. On a collection of chilopods from the East Indies. Bulletin of the University of Utah 29: 1-15.

Chamberlin, R.V. 1944. Some chilopods from the Indo-Australian Archipelago. Notulae Naturae 147: 1-14.

Chamberlin, R.V., and Wang, Y.-H.M. 1952. Some records and descriptions of chilopods from Japan and other oriental areas. Proceedings of the Biological Society of Washington 65: 177-186.

Chao, J.-L. 2008. Scolopendromorpha (Chilopoda) of Taiwan. Saarbrücken, Germany: VDM Verlag Dr. Müller Aktiengesellschaft & Co. KG.

Chao, J.-L., Hsu, H., Nguyen, D., and Chang, H. 2011. DNA barcoding for the identification and taxonomy of Scolopendromorpha centipedes from Taiwan, Vietnam, Japan and China. in 15th International Congress of Myriapodology. pp. 23. Womens College, University of Queensland, Brisbane Australia.

Chao, J.L.C., and Wen, H. 2003. The scolopendromorph centipedes (Chilopoda) of Taiwan. African Invertebrates 44: 1-11.

Chen, G., and Hare, M. 2011. Cryptic diversity and comparative phylogeography of the estuarine copepod *Acartia tonsa* on the US Atlantic coast. Molecular Ecology 20: 2425 - 2441.

Chia, O.K.S., and Ng, P.K.L. 2006. The freshwater crabs of Sulawesi, with descriptions of two new genera and four new species (Crustacea: Decapoda: Brachyura: Parathelphusidae). Raffles Bulletin of Zoology 54: 381.

Chin-Baarstad, A., Klug, H., and Lindstrom, K. 2009. Should you eat your offspring else does? Effect of an egg predator on filial cannibalism in the sand goby. Animal Behaviour 78: 203-208.

Clouse, R.M., and Giribet, G. 2010. When Thailand was an island—the phylogeny and biogeography of mite harvestmen (Opiliones, Cyphophthalmi, Stylocellidae) in Southeast Asia. Journal of Biogeography 37: 1114-1130.

Daday, J. 1889. A Magyar nemzeti muzeum indegenföldi Myriopodái - Myriapoda extranea musaei nationalis hungarici. Természentrajzi Füzetek 12: 115-156.

Daday, J. 1891. A Heidelbergi egyeten zooligiai gyüjtemenyenek idegenföldi myriapodai (Myriopoda extranea collectionis zoologicae Universitatis Heidelbergensis). Természetrajzi Füzetek 14: 135-154.

Daday, J. 1893. Uj vagy kevesse ismert idegenföldi Myriapodak a Magyar Nemzeti Muzeum allattari gyüjtemenyeben - Myriapoda extranea nova vel minus cognita in collectione Musaei Hungarici (in Hungarian, with Latin descriptions). Matematikai és Eermészettudományi Ertesíto 12: 2-6.

Darriba, D., Taboada, G.L., Doallo, R., and Posada, D. 2012. jModelTest 2: More models, new heuristics and parallel computing. Nature Methods 9: 772.

Davis, B.L., and Baker, R.J. 1974. Morphometrics, evolution, and cytotaxonomy of mainland bats of the genus *Macrotus* (Chiroptera: Phyllostomatidae). Systematic Zoology 23: 26-39.

de Bruyn, M., Nugroho, E., Hossain, M.M., Wilson, J.C., and Mather, P.B. 2004. Phylogeographic evidence for the existence of an ancient biogeographic barrier: the Isthmus of Kra Seaway. Heredity 94: 370-378.

de Bruyn, M., et al. 2014. Borneo and Indochina are major evolutionary hotspots for Southeast Asian biodiversity. Systematic Biology 63: 879-901.

Decker, P. 2010. Contributions to the Myriapod fauna of Thailand - New records of millipedes and centipedes from Thailand (Myriapoda: Diplopoda, Chilopoda). Schubartiana 4: 23-34.

Decker, P. 2013. Annotated checklist of the millipedes (Diplopoda) and centipedes (Chilopoda) of Singapore. Raffles Museum of Biodiversity Research: [Electronic version].

Demange, J.M., and Richard, J. 1969. Morphologie de l'appareil génital mâle des Scolopendromorphes et son importance en systématique (Myriapodes Chilopodes). Bulletin du Muséum national d'Histoire naturelle 40: 968-983.

Di, Z., Cao, Z., Wu, Y., Yin, S., Edgecombe, G.D., and Li, W. 2010. Discovery of the centipede family Plutoniumidae (Chilopoda) in Asia: a new species of *Theatops* from China, and the taxonomic value of spiracle distributions in Scolopendromorpha. Zootaxa 2667: 51-63.

Dobroruka, L. 1968. Myriapoda-Chilopoda aus der Sammlung des Musée Royal de l’Afrique Centrale. Revue de Zoologie et de Botanique Africaines 78: 3–4, 201–215.

Dohle, W. 1985. Phylogenetic pathways in the Chilopoda. in Proceedings of the 6th International Congress of Myriapodology. pp. 55-66. Amsterdam. Bijdragen tot de Dierkunde.

Dryden, I., and Mardia, K. 1998. Statistical shape analysis.

Dunn, C.W., Hejnol, A., Matus, D.Q., Pang, K., and Browne, W.E. 2008. Broad phylogenomic sampling improves resolution of the animal tree of life. Nature 452: 745.

Edgar, R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32: 1792-7.

Edgecombe, G.D. 2007. Centipede systematics: progress and problems. In Zhang, Z.Q. and Shear, W.A. (ed.), Linnaeus Tercentenary: Progress in invertebrate taxonomy, pp. 1-766. Zootaxa.

Edgecombe, G.D., and Bonato, L. 2011. Chilopoda – Taxonomic overview, Scolopendromorpha. In Minelli, A. (ed.), Treatise on Zoology - Anatomy, Taxonomy, Biology. The Myriapoda, pp. 538. Brill.

Edgecombe, G.D., Bonato, L., and Giribet, G. 2010. Brooding in *Mecistocephalus togensis* (Geophilomorpha: Placodesmata) and the evolution of parental care in centipedes (Chilopoda). International Journal of Myriapodology 3: 139-144.

Edgecombe, G.D., and Giribet, G. 2007. Evolutionary biology of centipedes (Myriapoda: Chilopoda). Annual Reviews of Entomology 52: 70-151.

Edgecombe, G.D., and Giribet, G. 2008. A New Zealand species of the trans-Tasman centipede order Craterostigmomorpha (Arthropoda : Chilopoda) corroborated by molecular evidence. Invertebrate Systematics 22: 1 - 15.

Edgecombe, G.D., and Giribet, G. 2009. Phylogenetics of scutigeromorph centipedes (Myriapoda: Chilopoda) with implications for species delimitation and historical biogeography of the Australian and New Caledonian faunas. Cladistics 25: 406-427.

Edgecombe, G.D., Giribet, G., and Wheeler, W.C. 2002. Phylogeny of Henicopidae (Chilopoda: Lithobiomorpha): a combined analysis of morphology and five molecular loci. Systematic Entomology 27: 31–64.

Edgecombe, G.D., Vahtera, V., Giribet, G., and Kaunisto, P. 2015. Species limits and phylogeography of Newportia (Scolopendromorpha) and implications for widespread morphospecies. ZooKeys 510: 65-77.

Edgecombe, G.D.K., M. 2008a. The contribution of preoral chamber and foregut morphology to the phylogenetics of Scolopendromorpha (Chilopoda). in Proceedings of the 14th International Congress of Myriapodology. pp. 295-318. Görlitz, Germany. Soil Organisms.

Edgecombe, G.D.K., M. 2008b. Phylogeny of scolopendromorph centipedes (Chilopoda): morphological analysis featuring characters from the peristomatic area. Cladistics 24: 872-901.

Emerson, S.B., Inger, R.F., and Iskandar, D. 2000. Molecular systematics and biogeography of the fanged frogs of Southeast Asia. Molecular Phylogenetic and Evolution 16: 131-42.

Ernst, A., Rosenberg, J., and Hilken, G. 2009. Structure and distribution of antennal sensilla in the centipede *Cryptops hortensis* (Donovan, 1810) (Chilopoda, Scolopendromorpha). Soil Organisms 81: 399-411.

Fernández, R., Edgecombe, G.D., and Giribet, G. 2016. Exploring phylogenetic relationships within Myriapoda and the effects of matrix composition and occupancy on phylogenomic reconstruction. Systematic Biology [Accepted].

Field, K.G., Olsen, G.J., Lane, D.J., Giovannoni, S.J., and Ghiselin, M.T. 1988. Molecular phylogeny of the animal kingdom. Science 239: 748.

Flower, S.S. 1901. Notes on the millipedes, centipedes, scorpions, etc., of the Malay Peninsula and Siam. Journal of the Straits Branch of the Royal Asiatic Society 36: 1-48.

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

Fung, H.T., Lam, S.K., and Wong, O.F. 2011. Centipede bite victims: A review of patients presenting the two emergency departments in Hong Kong. Hong Kong Medical Journal 17: 381-385.

Gervais, P. 1837. Études pour servir á l' histoire nat. des Myriap. Annales des Sciences naturelles, série 2. n.p.

Gervais, P. 1847. Myriapodes. In Walckenaer, C.A. and Gervais, F.L.P. (ed.), Histoire naturelle des Insectes Aptères, Tome 4., pp. 1-57, 210-623. Librairie Encyclopédique de Roret, Paris.

Giribet, G., Carranza, S., Riutort, M., Baguna, J., and Ribera, C. 1999. Internal phylogeny of the Chilopoda (Myriapoda, Arthropoda) using complete 18S rDNA and partial 28S rDNA sequences. Philosophical Transactions B 254: 215-222.

Giribet, G., Cuéllar, A.G., and Edgecombe, G.D. 2009. Further use of molecular data in studying biogeographic patterns within the centipede genus *Craterostigmus*: the case for a monophyletic New Zealand species. Soil Organisms 81: 557-563.

Giribet, G., and Edgecombe, G.D. 2006. The importance of looking at small-scale patterns when inferring Gondwanan biogeography: a case study of the centipede *Paralamyctes* (Chilopoda, Lithobiomorpha, Henicopidae). Biological Journal of the Linnean Society 89: 65-78.

Giribet, G., and Edgecombe, G.D. 2012. Reevaluating the arthropod tree of life. Annual Review of Entomology 57: 167.

Giribet, G., and Edgecombe, G.D. 2013. Stable phylogenetic patterns in scutigeromorph centipedes (Myriapoda : Chilopoda : Scutigeromorpha): dating the diversification of an ancient lineage of terrestrial arthropods. Invertebrate Systematics 27: 485-501.

González-Sponga, M.A. 2002. Miriápodos de Venezuela. Descripción de siete nuevas especies del género *Rhysida* y redescripción de *Rhysida longipes* Newport, 1845 (Chilopoda: Scolopendridae). Aula Y Ambiente 2: 49-60.

Goodall, C. 1991. Procrustes methods in the statistical analysis of shape. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 53: 285-239.

Gorog, A.J., Sinaga, M.H., and Engstrom, M.D. 2004. Vicariance or dispersal? Historical biogeography of three Sunda shelf murine rodents (*Maxomys surifer*, *Leopoldamys sabanus* and *Maxomys whiteheadi*). Biological Journal of the Linnean Society 81: 91-109.

Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W., and Gascuel, O. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Systematic Biology 59: 307-21.

Guindon, S., and Gascuel, O. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Systematic Biology 52: 696–704.

Haase, E. 1887a. Die Indisch-Australischen Myriopoden. 1. Chilopoden. Abhandlungen und Berichte des Königlichen zoologischen und anthropologisch-ethnographischen Museum zu Dresden 4: 1-118.

Haase, E. 1887b. Die Indisch-Australischen Myriopoden. 1. Chilopoden. Abhandlungen und Berichte des Königlichen zoologischen und anthropologisch-ethnographischen Museum zu Dresden, 4: 1-118.

Hanebuth, T., Stattegger, K., and Grootes, P.M. 2000. Rapid flooding of the Sunda Shelf: A late-glacial sea-level record. Science 288: 1033-1035.

Hanebuth, T.J.J., Stattegger, K., and Bojanowski, A. 2009. Termination of the Last Glacial Maximum sea-level lowstand: the Sunda-Shelf data revisited. Global Planet Change 66: 76.

Hanebuth, T.J.J., Voris, H.K., Yokoyama, Y., Saito, Y., and Okuno, J.i. 2011. Formation and fate of sedimentary depocentres on Southeast Asia's Sunda Shelf over the past sea-level cycle and biogeographic implications. Earth-Science Reviews 104: 92-110.

Heiser, M., and Schmitt, T. 2013. Tracking the boundary between the Palaearctic and the Oriental region: New insights from dragonflies and damselflies (Odonata). Journal of Biogeography 40: 2047-2058.

Heymons, R. 1901. Die Entwicklungsgeschichte der Scolopender. Zoologica 13: 1-244.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., and Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965-1978.

Horton, B.P., Gibbard, P.L., Mine, G.M., Morley, R.J., Purintavaragul, C., and Stargardt, J.M. 2005. Holocene sea levels and palaeoenvironments, Malay-Thai Peninsula, Southeast Asia. The Holocene 15: 1199-1213.

Huelsenbeck, J., and Ronquist, F. 2001a. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17: 754 - 755.

Huelsenbeck, J.P., and Hillis, D.M. 1993. Success of phylogenetic methods in the four taxon case. Systematic Biology 42: 247-264.

Huelsenbeck, J.P., and Ronquist, F. 2001b. MrBayes: Bayesian inference of phylogeny. Bioinformatics 17: 754-755.

Humbert, A., and Saussure, H. 1870. de Myriapoda nova Americana. Series 2. Revue et Magasin de Zoologie 22: 202-205.

Iorio, E. 2003. Morphologie externe des appareils génitaux mâle et femelle de la famille Scolopendridae (Chilopoda, Scolopendromorpha). Bulletin de Phyllie 16: 10-16.

Jangi, B.S. 1955. Some aspects of the morphology of the centipede *Scolopendra morsitans* Linn. Annals and Magazine of Natural History, Ser. 12 8: 597-607.

Jangi, B.S. 1959. Further notes on the taxonomy of the centipede *Scolopendra morsitans* Linnaeus (Scolopendridae). Entomological News 70: 253-257.

Jangi, B.S., and Dass, C.M. 1984. Scolopendridae of the Deccan. Journal of Scientific and Industrial Research 43: 27-54.

Jobb, G., von Haeseler, A., and Strimmer, K. 2004. TREEFINDER: a powerful graphical analysis environment for molecular phylogenetics. BMC Evolutionary Biology 4: 18.

Joshi, J., and Edgecombe, G.D. 2013. Revision of the scolopendrid centipede *Digitipes* Attems, 1930, from India (Chilopoda: Scolopendromorpha): reconciling molecular and morphological estimates of species diversity. Zootaxa 3626: 99-145.

Joshi, J., and Karanth, K.P. 2011. Cretaceous-Tertiary diversification among select scolopendrid centipedes of South India. Molecular Phylogenetics and Evolution 60: 287-294.

Joshi, J., and Karanth, K.P. 2012. Coalescent methods in conjunction with niche modelling reveals cryptic diversity among centipedes in the Western Ghats of South India. PLoS ONE 7: e42225.

Katoh, K., Kuma, K., Toh, H., and Miyata, T. 2005. MAFFT version 5: improvement in accuracy of multiple sequence alignment. Nucleic Acids Research 33: 511-518.

Katoh, K., and Standley, D.M. 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Biology and Evolution 30: 772-780.

Khanna, V. 1994. Centipede fauna of NE States, India (Chilopoda: Scolopendromorpha). Records of the Zoological Survey of India 94: 459-472.

Khanna, V. 2001. A check-list of the Indian species of the centipedes (Chilopoda: Scolopendromorpha). Annals of Forestry 9: 199-219.

Kimura, M. 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16: 111-120.

Klingenberg, C.P. 2011. MorphoJ: an integrated software package for geometric morphometrics. Molecular Ecology Resources 11: 353-357.

Klug, H., and Lindstrom, H. 2008. Hurry-up and hatch: selective filial cannibalism of slower developing eggs. Biology Letters 4: 160-162.

Koch, C.L. 1847. System der Myriapoden mit den Verzeichnissen und Berichtigungen zu Deutschlands Crustaceen, Myriapoden und Arachniden. Kritische Revision der Insectenfaune Deutschlands, III, Bändchen, Regensburg. 1-196.

Koch, L. 1878. Japanesische Arachniden und Myriapoden. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 27: 785-795.

Koch, L.E. 1982. Taxonomy of the centipede *Scolopendra laeta* Haase (Chilopoda: Scolopendridae) in Australia. Zoological Journal of the Linnean Society 76: 125-140.

Koch, L.E. 1983a. Morphological characters of Australian scolopendrid centipedes, and the taxonomy and distribution of *Scolopendra morsitans* L. (Chilopoda: Scolopendridae: Scolopendrinae). Australian Journal of Zoology 31: 79-91.

Koch, L.E. 1983b. Revision of the Australian centipedes of the genus *Cormocephalus* Newport (Chilopoda: Scolopendridae: Scolopendrinae). Australian Journal of Zoology 31: 799-833.

Koch, L.E. 1985. The taxonomy of Australian centipedes of the genus *Rhysida* Wood (Chilopoda: Scolopendridae: Otostigminae). Journal of Natural History 19: 205-214.

Koch, M., Parschke, S., and Edgecombe, G.D. 2009. Phylogenetic implications of gizzard morphology in scolopendromorph centipede (Chilopoda). Zoologica Scripta 38: 269-288.

Koh, L.P., et al. 2013. Biodiversity State and Trends in Southeast Asia. In Levin, S. (ed.), Encyclopedia of Biodiversity, pp. 509-527. Academic Press.

Kohlrausch, E. 1878. Beiträge zur Kenntnis der Scolopendriden. Inaugural-Dissertation, Marburg,

Kohlrausch, E. 1881. Gattungen und Arten der Scolopendriden. Archiv für Naturgeschichte 47: 50-132.

Kraepelin, K. 1903. Revision der Scolopendriden. Jahrbuch der Hamburgischen wissenschaftlichen Anstalten 20: 1-276.

Kraepelin, K. 1904. Catalogue des Scolopoendrides des collections du Muséum d’Histoire Naturelle de Paris (Collection du Muséum determinée par M. Le Professor Karl Kraepelin, et collection H. W. Brölemman). Bulletin de Muséum d’Histore naturelle Paris 1904: 243-253, 316-325.

Kraus, O. 1957. Eine kleine Myriapoden-Ausbeute aus Katanga (Belgisch Congo). Revue de Zoologie et de Botanique Africaines 55: 396–404.

Kronmüller, C. 2009. A new species of Scolopender from the Philippines (Chilopoda: Scolopendridae). Arthropoda 17: 48-51.

Kronmüller, C. 2010. *Scolopendra antananarivoensis* spec. nov. – a new species of *Scolopendra* Linnaeus, 1758 related to *Scolopendra morsitans* Linnaeus, 1758 from Madagascar (Myriapoda, Chilopoda, Scolopendridae). Spixiana 33: 281-288.

Kronmüller, C. 2012. Review of the subspecies of *Scolopendra subspinipes* Leach, 1815 with the new description of the South Chinese member of the genus *Scolopendra* Linnaeus, 1758 named *Scolopendra hainanum* spec. nov. Spixiana 35: 19-27.

Kronmüller, C., and Lewis, J.G.E. 2015. On the function of the ultimate legs of some Scolopendridae (Chilopoda, Scolopendromorpha). ZooKeys 510: 269-278.

Laakmann, S., Gerdts, G., Erler, R., Knebelsberger, T., Martinez Arbizu, P., and Raupach, M. 2013. Comparison of molecular species identification for North Sea calanoid copepods (Crustacea) using proteome fingerprints and DNA sequences. Molecular Ecology and Resources 13: 862 - 876.

Lambeck, K., and Chappell, J. 2001. Sea level change through the last glacial cycle. Science 292: 679-86.

Lambeck, K., Rouby, H., Purcell, A., Sun, Y., and Sambridge, M. 2014. Sea level and global ice volumes from the Last Glacial Maximum to the Holocene. Proceedings of the U.S. National Academy of Sciences 111: 15296-15303.

Lanfear, R., Calcott, B., Ho, S.Y., and Guindon, S. 2012. Partitionfinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29: 1695-701.

Langkilde, T., and Boronow, K.E. 2012. Hot boys are blue: Temperature-dependent color change in male eastern fence lizards. Journal of Herpetology 46: 461-465.

Larget, B., and Simon, D.L. 1999. Markov chain Monte Carlo algorithms for the Bayesian analysis of phylogenetic trees. Molecular Biology and Evolution 16: 750-759.

Latreille, M. 1829. Les Myriapodes. In Cuvier, P.M.L. (ed.), Règne Animal, pp. 326-339. Paris.

Latzel, R. 1892. Note sur quelques Myriapodes de Tahiti. Bulletin de la Société Zoologique de France 17: 185–186.

Lawrence, R.F. 1947. Some observations on the post-embryonic development of the Natal forest centipede, *Cormocephalus multispinus* (Kraep.). Annals of the Natal Museum 11: 139-156.

Lawrence, R.F. 1984. The centipedes and millipedes of Southern Africa. n.p.

Leach, W.E. 1816. A tabular view of the external characters of four classes of animals, which Linné arranged under Insecta; with the distribution of the genera composing three of these classes into orders and descriptions of several new genera. Transactions of the Linnean Society of London 11: 306-400.

Lewis, J.G.E. 1968. The variation of the centipede *Scolopendra amazonica* in Africa. Zoological Journal of the Linnean Society 48: 49-57.

Lewis, J.G.E. 1972a. The life histories and distribution of the centipedes *Rhysida nuda togoensis* and *Ethmostigmus trigonopodus* (Scolopendromorpha, Scolopendridae) in Nigeria. Journal of Zoology 167: 399-414.

Lewis, J.G.E. 1972b. The population density and biomass of the centipede *Scolopendra amazonica* (Bucherl) (Scolopendromorpha: Scolopendridae) in Sahel savana in Nigeria. Entomologist's Monthly Magazine 108: 16-18.

Lewis, J.G.E. 1978. Variation in tropical scolopendrid centipedes: problems for the taxonomist. Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg 21: 51-54.

Lewis, J.G.E. 1981. The Biology of Centipedes. Cambridge, UK: Cambridge University Press.

Lewis, J.G.E. 1982a. Observations on the morphology and habits of the bizarre Borneo centipede *Arrhabdotus octosulcatus* (Tomosvary), (Chilopoda, Scolopendromorpha). Entomologist's Monthly Magazine 117: 245-248.

Lewis, J.G.E. 1982b. The scolopendrid centipedes of the Oxford University 1932 Sarawak Expedition. Journal of Natural History 16: 389-397.

Lewis, J.G.E. 1984a. The Myriapoda of the Gunung Mulu National Park. The Sarawak Museum Journal 30: 35-51.

Lewis, J.G.E. 1984b. Possible species isolation mechanisms in some scolopendrid centipedes (Chilopoda; Scolopendridae). in Proceedings of the 6th International Congress of Myriapodology. pp. 125-130. Bijdragen tot de Dierkunde.

Lewis, J.G.E. 1986. The genus *Trachycormocephalus* a junior synonym of *Scolopendra*, with remarks on the validity of other genera of the tribe Scolopendrini (Chilopoda: Scolopendromorpha). Journal of Natural History 20: 1083-1087.

Lewis, J.G.E. 2000. Variation in three centipede species genus *Otostigmus* and it bearing on species discrimination (Chilopoda; Scolopendromorpha; Scolopendridae). Journal of Natural History 34: 433-448.

Lewis, J.G.E. 2001. The scolopendrid centipedes in the collection of the National Museum of Natural History in Sofia (Chilopoda: Scolopendromorpha: Scolopendridae). Historia Naturalis Bulgarica 13: 5-51.

Lewis, J.G.E. 2002. The scolopendromorph centipedes of Mauritius and Rodrigues and their adjacent islets (Chilopoda: Scolopendromorpha) – Results of the Himalaya-Expeditions of J. Martens. Journal of Natural History 36: 79-106.

Lewis, J.G.E. 2003. The problems involved in the characterisation of scolopendromorph species (Chilopoda: Scolopendromorpha). African Invertebrates 44: 61-69.

Lewis, J.G.E. 2004a. Notes on the type specimens of three species of *Otostigmus* described from Indo-China by Carl Attems (Chilopoda: Scolopendromorpha: Scolopendridae). Annalen des Naturhistorischen Museums in Wien, Serie B 105B: 27-33.

Lewis, J.G.E. 2004b. Redescription and reassignment of the type material of the African centipedes *Otostigmus reichardti* Kraepelin and *Otostigmus tanganjikus* Verhoeff, with remarks on the genera *Digitipes* Attems, *Otostigmus* Porat and *Rhysida* Wood (Chilopoda: Scolopendromorpha). African Invertebrates 45: 279-286.

Lewis, J.G.E. 2007. Scolopendromorph centipedes from Seychelles with a review of previous records (Chilopoda: Scolopendromorpha). Phelsuma 15: 8-25.

Lewis, J.G.E. 2010a. Field observations on three scolopendrid centipedes from Mauritius and Rodrigues (Indian Ocean) (Chilopoda: Scolopendromorpha). International Journal of Myriapodology 3: 123-137.

Lewis, J.G.E. 2010b. A key and annotated list of the *Scolopendra* species of the Old World with a reappraisal of Arthrorhabdus (Chilopoda: Scolopendromorpha: Scolopendridae). International Journal of Myriapodology 83-122.

Lewis, J.G.E. 2010c. Order Scolopendromorpha Pocock, 1895. In Gerlach, J. and Marusik, Y. (ed.), Arachnida and Myriapoda of the Seychelles Islands, pp. 435. Manchester: Siri Scientific Press.

Lewis, J.G.E. 2010d. A revision of the *rugulosus* group of *Otostigmus* subgenus *Otostigmus* Porat, 1876 (Chilopoda: Scolopendromorpha: Scolopendridae). Zootaxa 2579: 1-29.

Lewis, J.G.E. 2014. A review of the *orientalis* group of the *Otostigmus* subgenus *Otostigmus* Porat, 1876 (Chilopoda: Scolopendromorpha: Scolopendridae). Zootaxa 3889: 388-413.

Lewis, J.G.E. 2015. On Verhoeff's *Otostigmus* subgenus *Malaccopleurus*, the *nudus* group of *Otostigmus* subgenus *Otostigmus* Porat, 1876, and *Digitipes* Attems, 1930, with a description of the foetus stadium larva in *O. sulcipes* Verhoeff, 1937, (Chilopoda: Scolopendromorpha: Scolopendridae). Zootaxa 4039: 225-248.

Lewis, J.G.E., and Daszak, P. 1966. On centipedes collected on the Raleigh International Expedition to Mauritius and Rodrigues 1993, with a description of a new species of *Scolopendra* (Scolopendromorpha; Scolopendridae). Journal of Natural History 30: 293-297.

Lewis, J.G.E., Minelli, A., and Shelley, R.M. 2006. Taxonomic and nomenclatural notes on scolopendrid centipedes (Chilopoda: Scolopendromorpha: Scolopendridae). Zootaxa 1155: 35-40.

Linnaeus, C. 1758. Systema Naturae. Editio Decima. Salvius, Holmiae.

Lohman, D.J., et al. 2011. Biogeography of the Indo-Australian Archipelago. Annual Review of Ecology, Evolution, and Systematics 42: 205-226.

Lohmann, G. 1983. Eigenshape analysis of microfossils: a general morphometric procedure for describing changes in shape. Mathematical Geology 15: 659 - 672.

Lopez Gutierrez, B., MacLeod, N., and Edgecombe, G.D. 2011. Detecting taxonomic signal in an under-utilised character system: Geometric morphometrics of the forcipular coxae of Scutigeromorpha (Chilopoda). ZooKeys 156: 49-66.

Lourenço, W., and Pham, D. 2015. A remarkable new species of *Alloscorpiops* Vachon, 1980 from a cave in Vietnam (Scorpiones, Euscorpiidae, Scorpiopinae). ZooKeys 500: 73-82.

Lourie, S.A., and Vincent, A.C.J. 2004. A marine fish follows Wallace's Line: the phylogeography of the three-spot seahorse (*Hippocampus trimaculatus*, Syngnathidae, Teleostei) in Southeast Asia. Biogeography 31: 1975-1985.

Lovatt Smith, P.F., Stokes, R.B., Bristow, C., and Carter, A. 1996. Mid-Cretaceous inversion in the Northern Khorat Plateau of Lao PDR and Thailand. Geological Society, London, Special Publications 106: 233-247.

Lucas, H. 1853. Essai sur les animaux articulés qui habitent l'ile de Crète. Revue et Magasin de Zoologie Pure et Appliquée 5: 418-424, 461-468, 514-531, 565-576.

Lukoschek, V., Osterhage, J.L., Karns, D.R., Murphy, J.C., and Voris, H.K. 2011. Phylogeography of the Mekong mud snake (*Enhydris subtaeniata*): The biogeographic importance of dynamic river drainages and fluctuating sea levels for semiaquatic taxa in Indochina. Ecology and Evolution 1: 330-42.

Luo, S.J., et al. 2014. Sympatric Asian felid phylogeography reveals a major Indochinese-Sundaic divergence. Molecular Ecology 23: 2072-92.

Machado, G. 2000. Maternal care in the neotropical centipede *Otosigmus scabricauda* (Chilopoda: Scolopendromorpha). Entomological News 111: 250-254.

Maddison, W.P., and Maddison, D.R. 2011. Mesquite: a modular system for evolutionary analysis. Version 2.75. [Online]. Available from: http://mesquiteproject.org

Mahalanobis, P.C. 1936. On the generalised distance in statistics. Proceedings of the National Institute of Sciences of India 2: 49-55.

Meinert, F.V.A. 1886. Myriapoda Musei Cantabrigensis, Mass. Part I. Chilopoda. Proceedings of the American Philosophical Society 1885: 161-233.

Menezes, R.S.T., Brady, S.G., Carvalho, A.F., Del Lama, M.A., and Costa, M.A. 2015. Molecular phylogeny and historical biogeography of the neotropical swarm-founding social wasp genus *Synoeca* (Hymenoptera: Vespidae). PLoS ONE 10: e0119151.

Metcalfe, I. 1998. Palaeozoic and Mesozic geological evolution of the SE Asian region: multidisciplinary constraints and the implications for biogeography. In Hall, R. and Holloway, J.D. (ed.), Biogeography and Geological Evolution of SE Asia, pp. 25–41. Leiden: Backhuys.

Metcalfe, I. 2002. Permian tectonic framework and palaeogeography of SE Asia. Journal of Asian Earth Sciences 20: 551-566.

Metcalfe, I. 2011. Tectonic framework and Phanerozoic evolution of Sundaland. Gondwana Research 19: 3-21.

Metcalfe, I. 2013. Gondwana dispersion and Asian accretion: Tectonic and palaeogeographic evolution of eastern Tethys. Journal of Asian Earth Sciences 66: 1-33.

Mitić, B., Antić, D., Ilic, B., Makarov, S., Lučić, L., and Ćurčić, B. 2012. Parental care in *Cryptops hortensis* (Donovan) (Chilopoda: Scolopendromorpha) from Serbia, the Balkan Peninsula. Archives of Biological Sciences, Belgrade 64: 1117–1121.

Miyosi, Y. 1955. Chilopoda and Diplopoda from Aoga-shima, Izu Island. Miscellaneous Reports of the Research Institute for Natural Resources, Tokyo 38: 150-153.

Moczek, A.P. 2010. Phenotypic plasticity and diversity in insects. Philosophical Transactions of the Royal Society of London. Series B 365: 593-603.

Monge-Najera, J. 1995. Phylogeny, biogeography and reproductive trends in the Onychophora. Zoological Journal of the Linnean Society 114: 21-60.

Monod, L., and Prendini, L. 2015. Evidence for Eurogondwana: the roles of dispersal, extinction and vicariance in the evolution and biogeography of Indo-Pacific Hormuridae (Scorpiones: Scorpionoidea). Cladistics 31: 71-111.

Morgan, J.A.T., et al. 2002. A phylogeny of planorbid snails, with implications for the evolution of *Schistosoma* parasites. Molecular Phylogenetics and Evolution 25: 477-488.

Morley, C.K. 2012. Late Cretaceous–Early Palaeogene tectonic development of SE Asia. Earth-Science Reviews 115: 37-75.

Mosimann, J. 1979. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. Journal of the American Statistical Association 63: 930-978.

Moyle, R.G., et al. 2011. Diversification of an endemic Southeast Asian genus: Phylogenetic relationships of the spiderhunters (Nectariniidae: Arachnothera). The Auk 128: 777-788.

Muadsub, S., and Pinkaew, N. 2014. *Sirindhornia* Pinkaew and Muadsub (Lepidoptera: Tortricidae), a new enarmoniine genus from Thailand. Zootaxa 3869: 53-63.

Muadsub, S., Sutcharit, C., Pimvichai, P., Enghoff, H., Edgecombe, G.D., and Panha, S. 2012. Revision of the rare centipede genus *Sterropristes* Attems, 1934, with description of a new species from Thailand (Chilopoda: Scolopendromorpha: Scolopendridae). Zootaxa 3484: 35-52.

Müller, C.H.G., and Meyer-Rochow, V.B. 2006a. Fine structural description of the lateral ocellus of *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda: Craterostigmomorpha) and phylogenetic considerations. Journal of Morphology 267: 850-865.

Müller, C.H.G., and Meyer-Rochow, V.B. 2006b. Fine structural organization of the lateral ocelli in two species of *Scolopendra* (Chilopoda: Pleurostigmophora): an evolutionary evaluation. Zoomorphology 125: 13-26.

Murienne, J., Daniels, S.R., Buckley, T.R., Mayer, G., and Giribet, G. 2013. A living fossil tale of Pangaean biogeography. Proceedings of the Royal Society of London B: Biological Sciences 281.

Murienne, J., Edgecombe, G., and Giribet, G. 2011. Comparative phylogeography of the centipedes *Cryptops pictus* and *C. niuensis* (Chilopoda) in New Caledonia, Fiji and Vanuatu. Organisms Diversity & Evolution 11: 61-74.

Murienne, J., Edgecombe, G.D., and Giribet, G. 2010. Including secondary structure, fossils and molecular dating in the centipede tree of life. Molecular Phylogenetics and Evolution 57: 301-313.

Nantarat, N., Tongkerd, P., Sutcharit, C., Wade, C.M., Naggs, F., and Panha, S. 2014a. Phylogenetic relationships of the operculate land snail genus *Cyclophorus* Montfort, 1810 in Thailand. Molecular Phylogenetics and Evolution 70: 99-111.

Nantarat, N., Wade, C.M., Jeratthitikul, E., Sutcharit, C., and Panha, S. 2014b. Molecular evidence for cryptic speciation in the *Cyclophorus fulguratus* (Pfeiffer, 1854) species complex (Caenogastropoda: Cyclophoridae) with description of new species. PLoS ONE 9: e109785.

Newport, G. 1844a. [Conclusion of the monograph on the Myriapoda Chilopoda]. Proceedings of the Linnean Society of London 1: 191-197.

Newport, G. 1844b. A list of the species of Myriapoda order Chilopoda contained in the cabinets of the British Museum with synoptic descriptions of forty-seven new species. Annals and Magazine of Natural History 13: 94-101.

Newport, G. 1845. Monograph of the class Myriapoda order Chilopoda; with observations on the general arrangement of the Articulata. Transactions of the Linnean Society of London 19: 265-302, 349-439.

Niedermeyer, E.M., Sessions, A.L., Feakins, S.J., and Mohtadi, M. 2014. Hydroclimate of the western Indo-Pacific Warm Pool during the past 24,000 years. Proceedings of the National Academy of Sciences 111: 9402-9406.

Nishikawa, K., et al. 2012. Molecular phylogeny and biogeography of caecilians from Southeast Asia (Amphibia, Gymnophiona, Ichthyophiidae), with special reference to high cryptic species diversity in Sundaland. Molecular Phylogenetics and Evolution 63: 714-23.

Oeyen, J.P., Funke, S., Böhme, W., and Wesener, T. 2014. The evolutionary history of the rediscovered austrian population of the giant centipede *Scolopendra cingulata* Latreille 1829 (Chilopoda, Scolopendromorpha). PLoS ONE 9: e108650.

Ohler, A., and Grosjean, S. 2005. Color pattern and call variation in *Kalophrynus* from south-east Asia. Herpetozoa 18: 99-106.

Outlaw, D.C., and Voelker, G. 2008. Pliocene climatic change in insular Southeast Asia as an engine of diversification in *Ficedula flycatchers*. Journal of Biogeography 35: 739-752.

Parker, S.R. 1997. Sequence Navigator: Multiple sequence alignment software. Methods in Molecular Biology 70: 54-145.

Pemberton, R.W. 1999. Insects and other arthropods used as drugs in Korean traditional medicine. Journal of Ethnopharmacology 65: 207-216.

Pentek-Zakar, E., Oleksa, A., Borowik, T., and Kusza, S. 2015. Population structure of honey bees in the Carpathian Basin (Hungary) confirms introgression from surrounding subspecies. Ecology and Evolution 5: 5456-5467.

Perez, S., Bernal, V., and Gonzalez, P. 2006. Differences among sliding semi-landmark methods in geometric morphometrics, with an application to human craniofacial and dental variation. Journal of Anatomy 208: 769 - 784.

Peters, W. 1855. Über die Myriapoden im allgemeinen und insbesondere über die in Mossambique beobachteten Arten dieser Familie. Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin 14: 75-85.

Peters, W. 1862. Insecten und Myriapoden Trans.). In n.p. (Ed.),^(Eds.), Naturwiss. Reise nach Mossambique, 1842-48 ausgeführt Zoology V (ed., Vol. 5, pp. 1-556). Berlin. (Reprinted from.

Pimvichai, P., Enghoff, H., and Panha, S. 2014. Molecular phylogeny of the *Thyropygus allevatus* group of giant millipedes and some closely related groups. Molecular Phylogenetics and Evolution 71: 170-183.

Pocock, R.I. 1889. Report on the myriapods of the Mergui Archipelago. Journal of the Linnean Society of London 21: 287-302.

Pocock, R.I. 1890. Report upon a small collection of scorpions and centipedes sent from Madras by Mr. Edgar Thurston, of the Government Central Museum. Annals and Magazine of Natural History, ser. 6 5: 236-244.

Pocock, R.I. 1891a. List of the Arachnida and "Myriopoda" obtained in Funafuti by Prof. W.J. Sollas and Mr. Stanley Gardiner, and in Rotuma by Mr. Stanley Gardiner. Annals and Magazine of Natural History, Series 7 1: 321–329.

Pocock, R.I. 1891b. Notes on the synonymy of some species of Scolopendridae with descriptions of new genera and species of the group. Annals and Magazine of Natural History 7: 51-58.

Pocock, R.I. 1891c. On the Myriopoda of Burma. Part 2. Report upon the Chilopoda collected by Sig. L. Fea and Mr. E. W. Oates. Annali del Museo Civico di Storia Naturale Giacomo Doria 30: 401–432.

Pocock, R.I. 1892. Supplementary Notes on the Arachnida and Myriapods of the Mergui Archipelago: with description of some New Species from Siam and Malaysia. Journal of the Linnean Society of London 24: 316-326.

Pocock, R.I. 1894. Chilopoda, Symphyla and Diplopoda from the Malay Archipelago. In Weber, M. (ed.), Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien, III, pp. 307-404. Leiden: Brill.

Pocock, R.I. 1895. Chilopoda and Diplopoda. Biologia Centrli-Americana 14: 1-217.

Pocock, R.I. 1898. List of the Arachnida and "Myriopoda" obtained in Funafuti by Prof. W. J. Sollas and Mr. Stanley Gardiner, and in Rotuma by Mr. Stanley Gardiner. Annals and Magazine of Natural History, ser. 7 1: 321-329.

Porat, C. 1876. Om några exotiska myriopoder. Bihang till Kongliga Svenska Vetenskaps-Akademien Handlingar 4: 1-48.

Posada, D. 2008. jModelTest: Phylogenetic model averaging. Molecular Biology and Evolution 25: 1253 - 1256.

Prendini, L., Weygoldt, P., and Wheeler, W.C. 2005. Systematics of the *Damon variagatus* group of African whip spiders (Chelicerata: Amblypygi): evidence from behaviour, morphology and DNA. Organisms, Diversity & Evolution 5: 203-236.

Prunescu, C.-C. 1965. Contribution à l'étude de l'évolution des Chilopodes. Revue Roumaine de Biologie, Série de Zoologie 10: 89-102.

Puillandre, N., Cruaud, C., and Kantor, Y.I. 2010. Cryptic species in *Gemmuloborsonia* (Gastropoda: Conoidea). Journal of Molluscan Studies 76: 11-23.

Purcell, S., and Tekanene, M. 2006. Ontogenetic changes in colouration and morphology of white teatfish, *Holothuria fuscogilva*, juveniles in Kiribati. SPC Beche-de-mer Information Bulletin 23: 29-31.

Quek, S.P., Davies, S.J., Ashton, P.S., Itino, T., and Pierce, N.E. 2007. The geography of diversification in mutualistic ants: a gene's-eye view into the Neogene history of Sundaland rain forests. Molecular Ecology 16: 2045.

Racey, A. 2009. Mesozoic red bed sequences from SE Asia and the significance of the Khorat Group of NE Thailand. Geological Society, London, Special Publications 315: 41-67.

Radl, R.C. 1992. Brood care in *Scolopendra cingulata* Latreille (Chilopoda: Scolopendromorpha). Naturwissenschaftlich-medizinischer Vereins in Innsbruck Supplement 10: 123-127.

Remington, C.L. 1950. The bite and habits of a giant centipede (*Scolopendra subspinipes*) in the Philippine Islands. The American Journal of Tropical Medicine and Hygiene 1: 453.

Ribaut, H. 1912. Chilopodes in: Voyage de Dr. Merton aux iles Kei et Aru. Abhandlungen der Senckenbergischen naturforschenden Gesellschaft 34.

Ribaut, H. 1923. Chilopodes de la Nouvelle-Calédonie et des îtes Loyalty. Berlin.

Rohlf, F. 1999. Shape statistics: Procrustes superimpostions and tangent spaces. Journal of Classification 16: 197 - 223.

Rohlf, F. 2001. TpsDig(c), v 1.31. Free software.

Rohlf, F. 2002. tps software series.

Ronquist, F., et al. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539-542.

Rudman, W.B. 1991. Purpose in pattern: the evolution of colour in chromodorid nudibranchs. Journal of Molluscan Studies 57: 5-21.

Rust, J., et al. 2010. Biogeographic and evolutionary implications of a diverse paleobiota in amber from the early Eocene of India. Proceedings of the U.S. National Academy of Sciences 107: 18360-18365.

Schileyko, A.A. 1992. Scolopenders of Viet-Nam and some aspects of the system of Scolopendromorpha (Chilopoda Epimorpha). Part 1. Arthropoda Selecta 1: 5-19.

Schileyko, A.A. 1995. The scolopendromorph centipedes of Vietnam (Chilopoda: Scolopendromorpha). Part 2. Arthropoda Selecta 4: 73-87.

Schileyko, A.A. 1998. Some Chilopoda from Sa Pa and Muong Cha, North Vietnam. Biological diversity of Vietnam. Biological diversity of Vietnam. Data on zoological and botanical studies in Fansipan Mountains (North Vietnam). 262-270.

Schileyko, A.A. 2001. New data on chilopod centipedes of Vietnam. Biological Diversity of Vietnam. Data on zoological and botanical studies in Vu Quang National Park (Ha Tinh Province, Vietnam). 417-445.

Schileyko, A.A. 2007. The scolopendromorph centipedes (Chilopoda) of Vietnam, with contributions to the faunas of Cambodia and Laos. Part 3. Arthropoda Selecta 16: 71-95.

Schileyko, A.A., and Pavlinov, I.J. 1997. A cladistic analysis of the order Scolopendromorpha (Chilopoda). – In: Enghoff, H. (ed.): Many-legged animals - A collection of papers on Myriapoda and Onychophora. Entomologica Scandinavica Supplement 51: 33-40.

Schileyko, A.A., and Stagl, V. 2004. The collection of scolopendromorph centipedes (Chilopoda) in the Natural History Museum in Vienna: a critical re-evaluation of former taxonomic identifications. Annalen des Naturhistorischen Museums in Wien, Series B 105B: 67-137.

Schilthuizen, M. 2013. Rapid, habitat-related evolution of land snail colour morphs on reclaimed land. Heredity 110: 247-252.

Schwendinger, P., and Giribet, G. 2005. The systematics of south–east Asian genus Fangensis Rambla (Opiliones: Cyphophthalmi: Stylocellidae). Invertebrate Systematics 19: 297-323.

Shear, W.A., and Bonamo, P.M. 1988. Devonobiomorpha, a new order of centipeds (Chilopoda) from the Middle Devonian of Gilboa, New York State, USA, and the phylogeny of centiped orders. American Museum Novitates 2927: 1-30.

Sheets, H.D., Kim, K., and Mitchell, C.E. 2004. A combined landmark and outline-based approach to ontogenetic shape change in the Ordovician trilobite *Triarthrus becki*. Morphometrics: applications in biology and paleontology 67-82.

Shelley, R.M. 2000. The centipede order Scolopendromorpha in the Hawaiian Islands (Chilopoda). Bishop Museum Occasional Papers 64: 39-48.

Shelley, R.M. 2005. A Synopsis of the North American Centipedes of the order Scolopendromorpha (Chilopoda). Martinsville, Virginia, USA: Virginia Museum of Natural History.

Shelley, R.M. 2006. A chronological catalog of the New World species of *Scolopendra* L., 1758 (Chilopoda: Scolopendromorpha: Scolopendridae). Zootaxa 1253: 1-50.

Shelley, R.M., Edwards, G.B., and Chagas Júnior., A. 2005. Introduction of the centipede *Scolopendra morsitans* L., 1758, into northeastern Florida, the first authentic North American record, and a review of its global occurrences (Scolopendromorpha: Scolopendridae: Scolopendrinae). Entomological News 116: 39-58.

Shinohara, K. 1949. Notes on Centipedes collected by Mr. Fajiyama in Hachijo Island. Acta Arachnologica 11: 80-85.

Shinohara, K. 1961. Survey of the Chilopoda and Diplopoda of Manazuru Seashore, Kanagarwa Prefecture, Japan. Science Report of the Yokosuka City Museum 6: 75-82.

Silvestri, F. 1894. Chilopodi e Diplopodi della Papuasi. Annali del Museo Civico di Storia Naturale di Genova, serie 2 14: 619-659.

Silvestri, F. 1895. I Chilopodi ed i Diplopodi di Sumatra e delle isole Nias, Engano e Mentavei. Annali del Museo Civico di Storia Naturale di Genova, serie 2 14: 707-760.

Silvestri, F. 1912. Descrizione di un novo genere di Scolopendridae (Chilopoda) del Tonkino. Bollettino del Laboratorio di Zoologia Generale e Agraria della Reale Scuola Superiore d' Agricoltura in Portici 6: 43-44.

Simaiakis, S.M., Dimopoulou, A., Mitrakos, A., Mylonas, M., and Parmakelis, A. 2012. The evolutionary history of the Mediterranean centipede *Scolopendra cingulata* (Latreille, 1829) (Chilopoda: Scolopendridae) across the Aegean archipelago. Biological Journal of the Linnean Society 105: 507-521.

Simaiakis, S.M., Giokas, S., and Korsós, Z. 2011. Morphometric and meristic diversity of the species *Scolopendra cingulata* Latreille, 1829 (Chilopoda: Scolopendridae) in the Mediterranean region. Zoologischer Anzeiger 250: 67-79.

Sinclair, F.G. 1901. On the myriapods collected during the "Skeat Expedition", to the Malay Peninsula 1899-1900. Proceedings of the Zoological Society of London 1901: 505-533.

Siriwut, W., Edgecombe, G.D., Sutcharit, C., and Panha, S. 2014. Brooding behaviour of the centipede *Otostigmus spinosus* Porat, 1876 (Chilopoda: Scolopendromorpha: Scolopendridae) and its morphological variability in Thailand. Raffles Bulletin of Zoology 62: 339-351.

Siriwut, W., Edgecombe, G.D., Sutcharit, C., and Panha, S. 2015a. The centipede genus *Scolopendra* in mainland Southeast Asia: Molecular phylogenetics, geometric morphometrics and external morphology as tools for species delimitation. PLoS ONE 10: e0139182.

Siriwut, W., Edgecombe, G.D., Sutcharit, C., Tongkerd, P., and Panha, S. 2015b. First record of the African-Indian centipede genus *Digitipes* Attems, 1930 (Scolopendromorpha: Otostigminae) from Myanmar, and the systematic position of a new species based on molecular phylogenetics. Zootaxa 3931: 71-87.

Siriwut, W., Edgecombe, G.D., Sutcharit, C., Tongkerd, P., and Panha, S. 2016. A taxonomic review of the centipede genus *Scolopendra* Linnaeus, 1758 (Scolopendromorpha, Scolopendridae) in mainland Southeast Asia, with description of a new species from Laos. ZooKeys 590: 1-124.

Stamatakis, A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22: 2688 - 2690.

Stuart-Fox, D., Whiting, M.J., and Moussalli, A. 2006. Camouflage and colour change: Antipredator responses to bird and snake predators across multiple populations in a dwarf chameleon. Biological Journal of the Linnean Society 88: 437-446.

Stuart, B.L., Inger, R.F., and Voris, H.K. 2006. High level of cryptic species diversity revealed by sympatric lineages of Southeast Asian forest frogs. Biology Letters 2: 470-474.

Takakuwa, Y. 1935. Über drei neue Arten der Chilopoden aus Formosa und Marshallinseln. Transactions of the Natural History Society of Formosa 24: 221-225.

Takakuwa, Y. 1936. Zwei Brachygeophilus-Arten und eine Pleurogeophilus-Art aus Japan. Transactions of the Sapporo Natural History Society 14: 143-147.

Takakuwa, Y. 1942a. Die Myriopoden von Formosa, Philippinien, u. s. w. . Transactions of the Natural History Society of Formosa 32: 359-367.

Takakuwa, Y. 1942b. Myriapoda of the Micronesia (in Japanese with German description). Kagaku-Nanyo (Micronesian Science) 5: 14-44.

Takakuwa, Y. 1942c. Myriapods of several local areas. Acta Arachnologica 7: 39-42 (in Japanaese).

Takakuwa, Y. 1943. Verbreitung der Chilopoden und Diplopoden in Japan. Nihon-Seibutsu-Chiri-Gakkai-kaiho / Bulletin of the Biogeographical Society of Japan 13: 147-213.

Takakuwa, Y. 1947. Class Chilopoda (in Japanese). In Unknown (ed.), Encyclopedia of Animals of Japan, pp. 930-940. Tokyo: Acta Forestalia Fennica.

Takano, M. 2001. Myriapods of the Institute for Nature Study in Tokyo (in Japanese). Miscellaneous reports of the National Park for Nature Study 33: 219-227.

Takashima, H. 1949. The General View of Japanese Myriapods. Acta arachnologica 11: 8-25.

Takashima, H., and Shinohàra, K. 1952. The centipede-fauna of the Tokyo District. Acta Arachnologica 13: 3-17.

Tamura, K., Stecher, G., Peterson, D., Filipski, A., and Kumar, S. 2013a. MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0 Molecular Biology and Evolution 30: 2725-2729.

Tamura, K., Stecher, G., Peterson, D., Filipski, A., and Kumar, S. 2013b. MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. Molecular Biology and Evolution 30: 2725–2729.

Tanabe, A.S. 2007. Kakusan: A computer program to automate the selection of a nucleotide substitution model and the configuration of a mixed model on multilocus data. Molecular Ecology Resources 77: 962-964.

Thoma, M., Kranz-baltensperger, Y., Kropf, C., Graber, W., Nentwig, W., and Frick, H. 2014. The new Southeast Asian goblin spider genus *Aposphragisma* (Araneae, Oonopidae): diversity and phylogeny. Zootaxa 3798: 1-86.

Tömösváry, Ö. 1882. A Myriopodák osztályának egy új alakja Borneo szigetérol [A new form of the class Myriapoda from the island of Borneo]. Természetrajzi Füzetek 5: 229-230.

Tömösváry, Ö. 1885. Myriapoda a Joanne Xanthus in Asia orientali collecta. Ennumeravit speciesque novas descripsit. Természentrajzi Füzetek 9: 63-72.

Tran, B.T.T., Le, S.X., and Nguyen, A.D. 2013. An annotated checklist of centipedes (Chilopoda) of Vietnam. Zootaxa 3722: 219-244.

Undheim, E.A.B., Fry, B.G., and King, G.F. 2015. Centipede venom: Recent discoveries and current state of knowledge. Toxins 7: 679-704.

Vahtera, V., and Edgecombe, G.D. 2014. First molecular data and the phylogenetic position of the millipede-like centipede *Edentistoma octosulcatum* Tömösvary, 1882 (Chilopoda: Scolopendromorpha: Scolopendridae). PLoS ONE 9: e112461.

Vahtera, V., Edgecombe, G.D., and Giribet, G. 2012a. Evolution of blindness in scolopendromorph centipedes (Chilopoda: Scolopendromorpha): insight from an expanded sampling of molecular data. Cladistics 28: 4-20.

Vahtera, V., Edgecombe, G.D., and Giribet, G. 2012b. Spiracle structure in scolopendromorph centipedes (Chilopoda: Scolopendromorpha) and its contribution to phylogenetic. Zoomorphology 131: 225-248.

Vahtera, V., Edgecombe, G.D., and Giribet, G. 2013. Phylogenetics of scolopendromorph centipedes: Can denser taxon sampling improve an artificial classification? Invertebrate Systematics 27: 578-602.

Vanhooydonck, B., Herrel, A., Gabela, A.N.A., and Podos, J. 2009. Wing shape variation in the medium ground finch (*Geospiza fortis*): an ecomorphological approach. Biological Journal of the Linnean Society 98: 129-138.

Varón, A., Vinh, L.S., and Wheeler, W.C. 2010. POY version 4: Phylogenetic analysis using dynamic homologies. Cladistics 26: 72-85.

Verhoeff, K.W. 1892. Bearbeitung der von A. F. Moller auf der Insel St. Thomé gesammelten Chilopoden und Diplopoden. Berliner Entomologische Zeitschrift 37: 193-202.

Verhoeff, K.W. 1937. Chilopoden aus Malacca, nach den Objecten des Raffles Museum in Singapore. Bulletin of the Raffles Museum 13: 198–270.

Verhoeff, K.W. 1938. Chilopoden-Studien, zur Kenntnis der Epimorphen. Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere 71: 339–388.

Voris, H.K. 2000. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. Journal of Biogeography 27: 1153-1167.

Wang, D. 1951. The Myriapoda of the Philippine Islands. Department of Invertebrate Zoology Edward Brothers Inc, University of Utah.

Wang Yu-Hsi, M. 1955a. A preliminary report on Myriapoda and Arachnida of Lan Yu Islets (Botel Tobago), China. Quarterly Journal of the Taiwan Museum 8: 195-201.

Wang Yu-Hsi, M. 1955b. Records of myriapods on Formosa with description of new species. Quarterly Journal of the Taiwan Museum 8.

Wang Yu-Hsi, M. 1956. Records of Myriapods on Formosa with description of new species (2). Quarterly Journal of the Taiwan Museum 9: 155-159.

Wang Yu-Hsi, M. 1957. Records of myriapods on Taiwan Islands (3) - Pescadore Islets, Kao-Yung, Pingtung, Changhua and Taipei. Quarterly Journal of the Taiwan Museum 10: 23-29.

Wang Yu-Hsi, M. 1962. Serica Im: The Chilopoda of the Philippine Islands (A Revision of the Myriapoda of the Philippine Islands Part 2). Quarterly Journal of the Taiwan Museum 15: 79-106.

Wang Yu-Hsi, M. 1965. The centipeds of Malay Archipelago and south sea islands: Singapore, Sarawak and Sumatra. Quarterly Journal of the Taiwan Museum 18: 443-452.

Wang Yu-Hsi, M. 1967a. Millipedes and centipedes from Bukit Timah, Singapore, Cameron Highlands, Malaysia. Quarterly Journal of the Taiwan Museum 20: 393-398.

Wang Yu-Hsi, M. 1967b. Records on millipedes and centipedes from Brunei and from the Philippines. Quarterly Journal of the Taiwan Museum 20: 391-392.

Wang Yu-Hsi, M., and Tang, M.C. 1965. Serica IR The millipedes of Malay Archipelago and South Sea Islands Singapore, Sarawak and Sumatra. Quarterly Journal of the Taiwan Museum 18: 399-441.

Wilson, D., Heinsohn, R., and Endler, J.A. 2007. The adaptive significance of ontogenetic colour change in a tropical python. Biology Letters 3: 40-43.

Wirote, A. 2001. Thai Romanization (Version 1.5.2). Retrieved from http://pioneer.chula.ac.th/~awirote/resources/thai-romanization.html

Wood, H.C. 1861. Descriptions of new species of *Scolopendra* in the collection of the Academy. Proceedings of the Academy of natural Science of Philadelphia 10-15.

Wood, H.C. 1862. On the Chilopoda of North America, with a catalogue of all the specimens in the collections of the Smithsonian Institution. Journal of the Academy of Natural Sciences of Philadelphia 5: 2-52.

Woodruff, D. 2010. Biogeography and conservation in Southeast Asia: how 2.7 million years of repeated environmental fluctuations affect today’s patterns and the future of the remaining refugial-phase biodiversity. Biodiversity and Conservation 19: 919-941.

Woodruff, D.S. 2003. Neogene marine transgressions, palaeogeography and biogeographic transitions on the Thai–Malay Peninsula. Journal of Biogeography 30: 551-567.

Woodruff, D.S., and Turner, L.M. 2009a. The Indochinese-Sundaic zoogeographic transition: a description and analysis of terrestrial mammal species distributions. Biogeography 36: 803.

Woodruff, D.S., and Turner, L.M. 2009b. The Indochinese–Sundaic zoogeographic transition: a description and analysis of terrestrial mammal species distributions. Journal of Biogeography 36: 803-821.

Würmli, M. 1972. Chilopoda von Sumba und Flores. I. Scolopendromorpha. Verhandlungen der naturforschenden Gesellschaft in Basel 82: 88-104.

Würmli, M. 1975. Systematische Kriterien in der Gruppe von *Scolopendra morsitans* Linné, 1758 (Chilopoda: Scolopendromorpha: Scolopendridae). Deutsche Entomologische Zeitschrift 22: 201-206.

Xiong, B., and Kocher, T.D. 1991. Comparison of mitochondrial DNA sequences of seven morphospecies of black flies (Diptera: Simuliidae). Genome 34: 306-311.

Yodthong, S., S., C.D., Prasankok, P., and Aowphol, A. 2015. Phylogenetic Patterns of the Southeast Asian Tree Frog *Chiromantis hansenae* in Thailand. Asian Herpetological Research 5: 18.

Zeh, D.W., and Smith, R.L. 1985. Parental investment by terrestrial arthropods. American Zoologist 25: 785-805.

Zhan, S., et al. 2014. The genetics of monarch butterfly migration and warning colouration. Nature 514: 317-321.

Zhang, C. 1992. Scolopendra. Chinese Journal of Zoology 27: 8-11.

Zhang, C., and Wang, K. 1999. A new centipede *Scolopendra negrocapitis* sp. nov. from Hubei Province, China (Chilopoda: Scolopendromorpha: Scolopendridae). Acta Zootaxonomica Sinica 24: 136-137.

APPENDIX

VITA

Warut Siriwut was born on 13th October 1988 in Kanchanaburi province, west Thailand. He received the Bachelor of Science in Biology with second class honours from Khon Kaen University. He started Ph.D. studies under the supervision of Prof. Dr. Somsak Panha and Dr.Gregory D. Edgecombe in Biological Sciences Program, Faculty of Science, Chulalongkorn University since 2012. During Ph.D. study, he honorably received grant fellowships from The Royal Golden Jubilee Ph.D. Program under Thailand Research Fund and One Years Ph.D. placement by Newton-RGJ Co-Funding.