

Original Article

Extinct scorpion family Chaerilobuthidae from Mid-Cretaceous Burmese amber reinterpreted as subfamily of extant family Pseudochactidae (Chelicerata: Scorpiones)

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ABSTRACT

The extinct scorpion family Chaerilobuthidae Lourenço and Beigel, 2011, endemic to Burmese amber, was initially established due to its unique pedipalp trichobothrial pattern related to the Type A and Type B patterns of families Buthidae C.L. Koch, 1837 and Chaerilidae Pocock, 1893, respectively. The present contribution describes 11 new specimens, representing seven species of Chaerilobuthidae from Mid-Cretaceous Burmese amber, revealing their morphology using various imaging technologies. A revised diagnosis of *Chaerilobuthus* Lourenço and Beigel, 2011 is provided based on new morphological characters of the carapace, ocelli, chelicera, pedipalp trichobothria, coxapophyses, and leg tarsi. The other two genera of Chaerilobuthidae, *Chaeriloiurus* Lourenço, 2020 and *Serratochaerilobuthus* Lourenço, 2024, are synonymized with *Chaerilobuthus* based on a reassessment of their morphological characters and morphometric analysis, creating *Chaerilobuthus brigittemuelleriae* (Lourenço and Velten, 2020), comb. nov. and *Chaerilobuthus schmidtii* (Lourenço and Velten, 2024), comb. nov.. The systematic position of Chaerilobuthidae is clarified based on phylogenetic analyses of an updated morphological character matrix for Pseudochactidae Gromov, 1998, an extant family in Asia. Phylogenetic analysis placed Chaerilobuthidae sister to the pseudochactid subfamily Vietbocapinae Lourenço, 2012, justifying its transfer to Pseudochactidae, as Chaerilobuthinae Lourenço and Beigel, 2011, stat. nov.. This discovery confirms that Pseudochactidae date back 100 Mya and contributes to understanding the origin and evolutionary history of this relictual family.

Keywords: Burmite; scorpions; Pseudochactidae; taxonomic revision; phylogeny

INTRODUCTION

Scorpiones have a limited fossil record, with only 154 currently valid species (Dunlop *et al.* 2023). Research on Mesozoic scorpion fossils has focused on Mid-Cretaceous Burmese amber (Santiago-Blay *et al.* 2004, Lourenço 2016a, Xuan *et al.* 2023a). Compared to compression fossils, amber exquisitely preserves three-dimensional details, providing an important ‘window’ for exploring the origin, evolution, and lifestyle of arthropods during the Cretaceous period (Grimaldi *et al.* 2002). However, some morphological details of fossil scorpions have not been accurately documented due to outdated or substandard imaging methods, leading to misunderstanding of their systematic

placement (Santiago-Blay *et al.* 2004, Lourenço and Beigel 2011, Lourenço 2016a). In recent years, better preserved specimens have been investigated using advanced imaging methods, such as stereomicroscopy, fluorescent microscopy, laser confocal scanning microscopy, and micro-CT, greatly increasing knowledge of the diversity of Cretaceous scorpions (Cunningham *et al.* 2014, Fu *et al.* 2021, Xuan *et al.* 2023a, b).

The extinct family Chaerilobuthidae Lourenço and Beigel, 2011 was established based on a single specimen, *Chaerilobuthus complexus* Lourenço and Beigel, 2011, from Mid-Cretaceous Burmese amber, which exhibited similarities with both buthid and chaerilid scorpions, especially concerning

the pedipalp trichobothrial pattern. Thirteen species of *Chaerilobuthus* Lourenço and Beigel, 2011 and two monotypic genera, *Chaeriloiurus* Lourenço, 2020 and *Serratochaerilobuthus* Lourenço, 2024, were subsequently described (Lourenço 2013, 2015a, b, 2016b, 2018, Lourenço and Velten 2015, 2019, 2020, 2021, 2022, 2024a–c). Whereas the type genus, *Chaerilobuthus*, is relatively diverse morphologically, the monotypic genera *Chaeriloiurus* and *Serratochaerilobuthus* differ from *Chaerilobuthus* in rather trivial characters, e.g. the shape of the anterior carapace margin (Lourenço and Velten 2020, 2024b).

Pseudochactidae Gromov, 1998, an extant family endemic to Asia, are regarded as an important group for clarifying the basal phylogenetic relationships among Recent scorpions (Gromov 1998, Coddington et al. 2004). This family exhibits a unique trichobothrial pattern and a mixture of other characters shared by buthid and nonbuthid scorpions (Prendini et al. 2021). The first species of this family, *Pseudochactas ovchinnikovi* Gromov, 1998, found in Uzbekistan, Central Asia, attracted widespread attention (Gromov 1998, Prendini et al. 2006). Another two genera were subsequently reported from South-East Asia, *Troglokhammouanus* Lourenço, 2007 from Laos and *Vietbocap* Lourenço and Pham, 2010 from Vietnam (Lourenço 2007, 2017, Lourenço and Pham 2010). An integrative systematic revision of Pseudochactidae by Prendini et al. (2021) recognized four genera and three subfamilies: *Pseudochactas* Gromov, 1998 in Pseudochactinae Gromov, 1998; *Troglokhammouanus* in Troglokhammouaninae Lourenço, 2007; and *Vietbocap* and *Aemngvantom* Prendini et al., 2021 in Vietbocapinae Lourenço, 2012. Several hypotheses concerning the phylogenetic position of Pseudochactidae have been presented based on morphological characters (Soleglad and Fet 2003a, Coddington et al. 2004, Prendini et al. 2006). Recent phylogenomic analyses placed Pseudochactidae in the buthoid clade, sister to Chaerilidae Pocock, 1893 or Buthidae C.L. Koch, 1837 (Sharma et al. 2015, 2018, Santibáñez-López et al. 2018, 2019, 2020, 2022, Howard et al. 2019). Its phylogenetic position merits further investigation, however. Loria et al. (2022) established that Pseudochactidae originated in Eurasia and hypothesized their route of dispersal and diversification. Recently, Tang (2022) described a fifth genus, *Qianxie* Tang, 2022 from Yunnan Province, south-western China, and placed it in Troglokhammouaninae, sister to *Troglokhammouanus*, without phylogenetic analysis. No fossil species have been reported in the family, thus far.

The present contribution describes 11 new specimens of Chaerilobuthidae from Mid-Cretaceous Burmese amber and accurately documents their morphology using multiple imaging methods. The diagnoses of Chaerilobuthidae and *Chaerilobuthus* are revised, based on a morphological phylogenetic analysis that placed Chaerilobuthidae sister to the pseudochactid subfamily Vietbocapinae, justifying their transfer to Pseudochactidae, as **Chaerilobuthinae, stat. nov.** This discovery confirms that Pseudochactidae date back 100 Mya and contributes to understanding the origin and evolutionary history of this relictual family.

MATERIALS AND METHODS

Material examined

Material examined is deposited in the Nanjing Institute of Geology and Palaeontology (NIGP) at the Chinese Academy

of Sciences, Nanjing, with accession numbers 200654–200657 and 201158–201164. All specimens originate from the deposits of Noiye Bum near the Hukawng Valley in Kachin State of northern Myanmar [see locality in Xuan et al. (2022: 3, fig. 1) and Cruickshank and Ko (2003: 443, fig. 2)]. The age of Burmese amber is near the earliest Cenomanian (98.79 ± 0.62 Mya) based on radiometric zircon dating and palaeontological evidence (Shi et al. 2012, Mao et al. 2018). Amber pieces containing scorpions were trimmed using a small electric circular saw, ground with sandpaper of different grit sizes, and polished with burnishing powder to facilitate imaging.

The type material of previously described species was not examined as most specimens are in private collections. However, the published descriptions and images were carefully reviewed, allowing relevant data (measurements and discrete characters) from the type specimens to be included in the analyses so as to rigorously test their placement relative to the new material.

Microscopy and imaging

Photographs under incident and transmitted light were taken with a Zeiss Stereo Discovery V20 stereomicroscope. Widefield fluorescence photographs were taken with a Zeiss Axio Imager 2 light microscope. Confocal images were obtained with a Zeiss LSM 710 confocal laser scanning microscope (CLSM) under the 488-nm Argon laser excitation line (Fu et al. 2021). Micro-CT reconstruction was conducted using high-resolution X-ray micro-tomography (Zeiss Xradia 520 Versa) at the micro-CT laboratory of NIGP. CCD-based 0.4× and 4× objectives were used for fossil specimens of differing sizes. Scanning parameters of each specimen were as follows: NIGP 200657 (isotropic voxel size, 4.5005 µm; power, 4 W; acceleration voltage, 60 kV; exposure time, 1.5 s; projections, 2201); NIGP 201160 (isotropic voxel size, 3.982 µm; power, 4 W; acceleration voltage, 60 kV; exposure time, 1.5 s; projections, 2301); NIGP 201162 (isotropic voxel size, 3.3272 µm; power, 4 W; acceleration voltage, 60 kV; exposure time, 1 s; projections, 2301); NIGP 201163 (isotropic voxel size, 2.7015 µm; power, 3 W; acceleration voltage, 50 kV; exposure time, 2 s; projections, 2401); NIGP 201164 (isotropic voxel size, 5.9313 µm; power, 4 W; acceleration voltage, 60 kV; exposure time, 3 s; projections, 2201). Tomographic data were analysed using VGStudio MAX 3.0. Images were stacked in HELICON FOCUS 7.0 and figure plates arranged in ADOBE PHOTOSHOP 2020.

Measurements and terminology

Measurements, following Stahnke (1970), were recorded using ImageJ. General morphological terminology follows Vachon (1963), Stahnke (1970), Soleglad and Fet (2003a, b), and Prendini et al. (2021). Trichobothrial notation follows Prendini et al. (2006) and lateral ocelli terminology follows Loria and Prendini (2014). Abbreviations are as follows: mas, macroseta; ps, pedal spur; sc, spiny comb; ss, slit sensillum.

Phylogenetic analysis

In order to clarify the phylogenetic position of Chaerilobuthidae, the 11 new fossils and 16 previously described species of Chaerilobuthidae were scored into the previously published morphological character matrix of Prendini et al. (2021), updated to include *Qianxie solegladi* Tang, 2022

(Prendini *et al.*, in prep.). Four new characters (27, 77, 90, 99) were added and three characters (11, 129, 130) revised to accommodate the fossil taxa. Additionally, one previous character (30) was split into two characters (31, 32) and four previous characters (113, 114, 115, 116) were fused into two characters (118, 119). The revised matrix comprises 143 characters (Table 1, Appendix 1). Trees were rooted on the buthid, *Buthus atlantis* Pocock, 1889.

Phylogenetic analyses of the 143 morphological characters were conducted using Bayesian inference (BI) in MrBayes 3.2.7 (Ronquist *et al.* 2012) and maximum likelihood (ML) in IQTree 2.2.2.7. (Guindon *et al.* 2010). The JC69 model and gamma replacement rate were selected for analysis with BI. Two Markov chain Monte Carlo (MCMC) analyses were run simultaneously, each with one heated chain and three cold chains for determining convergence. Two million iterations were conducted, and trees sampled every 1000 generations. Analyses were stopped when the average standard deviation of split frequencies remained below 0.01. The Markov k-state (MK) model was selected for analysis with ML. ML analyses were conducted with 1000 Shimodaira–Hasegawa approximate likelihood ratio test (SH-aLRT) replicates and 1000 UFBoot2 bootstraps for all node supports.

A parsimony analysis was conducted using continuous data (22 ratios and two counts) for all chaerilobuthid taxa, in addition to the 143 discrete characters (Tables 2–4; Appendices 2, 3). A strict consensus was calculated using TNT 1.6 (Goloboff and Morales 2023). The tree was rooted on *Pseudochactas ovchinnikovi*. Most parameters were set as default in a ‘new technology search’ involving sectorial searches, tree-drifting and tree fusing. Nodal support was evaluated with a jackknife analysis.

Morphospace analysis

A principal coordinate analysis (PCA) was conducted using PAST 4.16c (Hammer *et al.* 2001) to assess the degree of morphological differentiation among the fossil taxa and their extant relatives. The first three PCA factors, explaining 94.47% of variation among the species (PCA 1: 57.38%, PCA 2: 30.87, PCA 3: 6.23), revealed the morphological disparity.

RESULTS

Phylogenetic analyses

Phylogenetic analyses with BI and ML confirmed the monophyly of the extinct family Chaerilobuthidae, and of the extant family Pseudochactidae and its troglobitic South-East Asian subfamily Vietbocapinae (Fig. 1). However, instead of placing Chaerilobuthidae sister to Buthidae or Chaerilidae, both analyses placed Chaerilobuthidae within Pseudochactidae as sister to Vietbocapinae, justifying the transfer of Chaerilobuthidae to a subfamily of Pseudochactidae, below.

Although missing data and measurement errors contributed to low nodal support, the parsimony analysis nevertheless provided insights about the placement of the new fossil specimens with respect to the type specimens of previously described species (Fig. 2).

All three phylogenetic analyses placed the monotypic chaerilobuthine genera, *Chaeriloiurus* and *Serratochaerilobuthus*, within *Chaerilobuthus*, justifying their synonymy with the latter, below.

Morphospace analyses

The morphospace analyses corroborated the phylogenetic analyses, supporting the transfer of Chaerilobuthidae to Pseudochactidae as sister-group of the extant subfamily Vietbocapinae. In the binary plot of PCA1 and PCA2, the fossil Chaerilobuthinae grouped with the extant Pseudochactidae, well separated from Buthidae and Chaerilidae along the PCA1 axis (Fig. 3A). In the binary plot of PCA1 and PCA3, Chaerilobuthinae and Pseudochactidae formed two clusters along the PCA3 axis, with Chaerilobuthinae and Vietbocapinae grouped together (Fig. 3B).

Systematic palaeontology

Order Scorpiones Koch, 1837

Family Pseudochactidae Gromov, 1998

Family Chaerilobuthinae, stat. nov.

Genus *Chaerilobuthus* Lourenço and Beigel, 2011

(Figs 4–39)

Chaerilobuthus Lourenço and Beigel, 2011: 635–639, figs 1–11. Type species: *Chaerilobuthus complexus* Lourenço and Beigel, 2011: 635–639, figs 1–11.

Chaeriloiurus Lourenço, 2020: 34–50, figs 13–22, synon. nov. Type species: *Chaeriloiurus brigittemuelleriae* Lourenço, 2020: 34–50, figs 13–22 [= *Chaerilobuthus brigittemuelleriae* (Lourenço and Velten, 2020), **comb. nov.**].

Serratochaerilobuthus Lourenço, 2024: 1–6, figs 1–12, synon. nov. Type species: *Serratochaerilobuthus schmidtii* Lourenço, 2024: 1–6, figs 1–12 [= *Chaerilobuthus schmidtii* (Lourenço and Velten, 2024), **comb. nov.**].

Diagnosis: The species of *Chaerilobuthus* share many characters with the extant family Pseudochactidae, notably: sternum pentagonal (Figs 12B, 15B, 20E, 23B, 26B, 28B, 33B, 34D, 37F); cheliceral moveable finger basal teeth absent; moveable finger ventral surface with serrula (Figs 6C, 12G, 18F, 23C, 29B, 34B, 37B); median denticle rows of pedipalp chela fingers comprising oblique subrows (Figs 13C, 15E, 29F, 33C); pedipalps with Type D trichobothrial pattern, β configuration; trichobothrium d_2 situated on femur dorsal surface, angle formed by d_1 , d_3 , and d_4 opening toward prolateral surface (Figs 7, 10, 13, 16, 21, 24, 26, 31, 35, 38); legs with prolateral and retrolateral pedal spurs present, legs III and IV with tibial spurs absent (Figs 6I–L, 7F–I, 12K, L, 15G, 18C, 20J, K, 23J, K, 29G–J, 33C, D, G, H, K, 34I–L, 37D), and telotarsi each with two rows of ventrosubmedian spinules (Figs 6J–L, 9G, I, 23J, K, 29H, J); metasomal segment V with paired ventrosubmedian carinae (Figs 5F, 9N, 20L, 33I, J, 35I); telson without subaculear tubercle (Figs 5F, 9N, 14B, 18G, 19B, 33I, J, 37I).

The extinct genus may be distinguished from other pseudochactid scorpions by the following combination of characters: carapace anterior margin sublinear, anterolateral margins entire, posterolateral margins angular, slanting, posteromedian margin slightly recurved (Figs 6A, 9A, 12A, 15A, 20B, 23A, 26A, 28A, 34A, 37A); carapace circumocular sutures absent (Figs 6A, 9A, 12A, 15A, 20B, 23A, 26A, 28A, 34A, 37A); median ocelli absent and one pair of large posterolateral major lateral ocelli present (Figs 6A, 9A, 12A, 15A, 18D, 20A, B, 23A, 26A, 28A,

Table 1. Distribution of morphological characters (1–143) used for phylogenetic analysis of Pseudochactidae Gromov, 1998, including Chaerilobuthinae Lourenço, 2011, stat. nov. Character states scored 0–5, inapplicable (–) or unknown (?). Numbers following taxon names refer to specimens in Ambrose Monell Cryocollection at the American Museum of Natural History, New York (extant taxa) and the Nanjing Institute of Geology and Palaeontology at the Chinese Academy of Sciences, Nanjing (extinct taxa). Taxon names followed by ‘HT’ (holotype) were scored from the original descriptions. Character descriptions in Appendix 1.

	1	11	21	31	41
<i>Buthus atlantis</i> 3489	0010002000	0000020000	---0000000	0000021110	1010011000
<i>Chaerilus sejnai</i> 3685	1130111101	0001101010	---1000111	0001000001	1101201201
<i>Chaerilobuthus birmanicus</i> HT	?????????1	100??0?110	---???????	2111?2????	??????????
<i>Chaerilobuthus brandti</i> HT	??????1??1	1001001110	---1100110	211103?0?0	??1??0??11
<i>Chaerilobuthus brigittemuelleri</i> HT	?????????1	2101001110	---1101110	21110210??	?????0??11
<i>Chaerilobuthus bruckschi</i> HT	??????????	100??0??10	---???????	211??2????	??????????
<i>Chaerilobuthus bruckschi</i> 201161	???????0111	1001001110	---1101110	2111021010	0111100011
<i>Chaerilobuthus bruckschi</i> 201162	???????0111	1001001110	---1101110	2111031010	0111100011
<i>Chaerilobuthus complexus</i> 200655	???????011?	1001001110	---1101110	211101?010	0111100011
<i>Chaerilobuthus complexus</i> 201160	???????0???	1001001110	---1101110	2111021010	0111100011
<i>Chaerilobuthus complexus</i> HT	???????0??1	1001001110	---1???110	211103?010	??1??0??11
<i>Chaerilobuthus enigmaticus</i> HT	??????????	???1001110	---???????	211??2????	??????????
<i>Chaerilobuthus enigmaticus</i> 201158	???????011?	100??01?1?	???1101110	???1?11010	0111100011
<i>Chaerilobuthus enigmaticus</i> 201159	??????????1	?????01110	---1101110	???101???0	011?????1?
<i>Chaerilobuthus gigantosternum</i> HT	??????????1	1001001110	---???????	211??3????	??????????
<i>Chaerilobuthus gigantosternum</i> 200654	???????111	1001001110	---1101110	2111031010	0111100011
<i>Chaerilobuthus hansgeorgmuelleri</i> HT	???????0??1	1001001?10	---1???110	21110110?0	?????0??11
<i>Chaerilobuthus hansgeorgmuelleri</i> 201164	??????????1	1001001110	---1101110	2111?11010	0111100011
<i>Chaerilobuthus knodelorum</i> HT	???????0??1	1001001?10	---????110	211102?0?0	?????0??1?
<i>Chaerilobuthus knodelorum</i> 200657	???????011?	1001001110	---1101110	2111021010	????1?0?11
<i>Chaerilobuthus longiaculeus</i> HT	??????????	??????????	??????????	??????????	??????????
<i>Chaerilobuthus meggeri</i> HT	??????????1	1001001110	---1101110	211101?0?0	??1??0??11
<i>Chaerilobuthus petersi</i> HT	??????????1	1001001110	---1101110	211103?0?0	?????1100
<i>Chaerilobuthus schmidt</i> HT	??????????1	1001001110	---1???110	211102?0?0	??1?????11
<i>Chaerilobuthus schwarzi</i> HT	???????0??1	1001001110	---1???110	211102?0??	?????????1
<i>Chaerilobuthus serratus</i> HT	??????????	1001001110	---???????	211??2????	??????????
<i>Chaerilobuthus serratus</i> 200656	???????0111	1001001110	---1101110	2111021010	0111100011
<i>Chaerilobuthus serratus</i> 201163	???????111	1001001110	---1101110	2111031010	0111100011
<i>Chaerilobuthus staxi</i> HT	??????????1	1001001?10	---1???110	211103?0?0	?????????11
<i>Pseudochactas mischi</i> HT	0002100111	0001201011	?011100110	1111011010	0111110111
<i>Pseudochactas ovchinnikovi</i> 2303A	0131100111	0001211011	0001100110	1111011010	0111110111
<i>Qianxie solegladi</i> HT	0120100111	2001211011	1011100110	0111011010	0111110111
<i>Troglokhammouanus steineri</i> 11271	1122100111	2101201011	1011100110	0000011010	0111110111
<i>Aemngvantom lao</i> 11349	0002100111	2201201111	200111-110	0000021010	0111110111
<i>Aemngvantom thamnongpaseum</i> 11351	0002100111	2201201111	200111-110	0010021010	0111110111
<i>Vietbocap canhi</i> 11270	0002100110	2212200101	212111-110	1110131010	0111110111
<i>Vietbocap canhi</i> 11348	0002100110	2212200111	212111-110	1110131010	0111110111

29A, 33A, 34A, C, 37A, C); pedipalp femoral trichobothria d_3 and d_4 situated closer to midpoint of segment (Figs 7A, 10, 13A, 16, 24A, 26D, 31, 35C, J) and d_3 – d_4 axis directed slightly away from retrodorsal carina rather than parallel to it (β configuration) (Figs 7A, 10, 13A, 16, 24A, 26D, 31, 35C, J); pectines with low tooth counts (five to eight teeth) (Figs 6D, 12B, 15D, 18I, 20G, 23F, 26B, 29C, 33B, 34G, 37H).

Additionally, two new characters, considered diagnostic for *Chaerilobuthus*, are shared with the extant pseudochactid,

Qianxie solegladi (Tang, 2022: 7, 11, [figs 10 43–46](#)): leg I maxillary lobes (coxapophyses) anterior margins with serrula (Fig. 38); leg basitarsi with pair of spinule rows distally (Figs 6I–L, 9F–I, 12H, L, 15G, 18C, 20J, K, 23K, 29G–J, 33G, H, 34I–L).

Included species: *Chaerilobuthus birmanicus* Lourenço, 2015; *Chaerilobuthus brandti* Lourenço, 2022; *Chaerilobuthus brigittemuelleri* (Lourenço and Velten, 2020), comb. nov;

Table 1. Continued

	51	61	71	81	91
<i>Buthus atlantis</i> 3489	0010001110	1100000000	1000000010	0101010110	0000000001
<i>Chaerilus sejnai</i> 3685	1101100000	1101?11001	0221200101	000002010-	1323322100
<i>Chaerilobuthus birmanicus</i> HT	?01001?001	??10?0??0	0?????1?1?	2010?0????	???????0??
<i>Chaerilobuthus brandti</i> HT	0010011001	0?10?0??0	00010?1110	2010300011	?33????0?0
<i>Chaerilobuthus brigittemuelleri</i> HT	0010011001	0?10?0??0	00010?1110	2010?000??	?33????0?0
<i>Chaerilobuthus bruckschi</i> HT	?????1100?	?????0??0	0?????1?10	201030????	?33????0??
<i>Chaerilobuthus bruckschi</i> 201161	0010011001	0?10??11??	?0010????10	??????0011	???????0?0
<i>Chaerilobuthus bruckschi</i> 201162	0010011001	0?10?01110	0001011110	2010300011	?3?????0??
<i>Chaerilobuthus complexus</i> HT	001001?001	??10?0??0	00010?1?10	2010300011	?33????0?0
<i>Chaerilobuthus complexus</i> 200655	0010011001	0?10??1?10	0001011110	2010300011	?33????020
<i>Chaerilobuthus complexus</i> 201160	0010011001	0?10?01110	0001011110	2010300011	??3????0?0
<i>Chaerilobuthus enigmaticus</i> HT	?0???1?001	0?10?0??0	0?????1?10	2010?00011	???????0?0
<i>Chaerilobuthus enigmaticus</i> 201158	0010011001	0?10?01?10	0001011110	20?0?00011	???????020
<i>Chaerilobuthus enigmaticus</i> 201159	?010011001	0?10????10	0001011110	2010300011	???????020
<i>Chaerilobuthus gigantosternum</i> HT	?010?????1	??1?0?0???	???????????	??????0011	???????0?0
<i>Chaerilobuthus gigantosternum</i> 200654	0010011001	0?10?01?10	0001011110	2010300011	???????020
<i>Chaerilobuthus hansgeorgmuelleri</i> HT	001001?001	0?10?0??0	00010?11??	201??00011	???????0?0
<i>Chaerilobuthus hansgeorgmuelleri</i> 201164	0010011001	0010?01110	0001011110	2010300011	???????020
<i>Chaerilobuthus knodelorum</i> HT	0010?11001	0?10?0??0	00010?11?0	201??00011	???????0?0
<i>Chaerilobuthus knodelorum</i> 200657	0010011001	0010??1110	0001011110	2010300011	?33????020
<i>Chaerilobuthus longiaculeus</i> HT	???????????	???????????	???????????	???????????	???????????
<i>Chaerilobuthus meggeri</i> HT	001001?001	0?1?0?0110	00010?1110	2010300???	???????0?0
<i>Chaerilobuthus petersi</i> HT	?01001?001	0?10?0??0	00010?1110	2010?00???	???????0?0
<i>Chaerilobuthus schmidt</i> HT	?010011001	0?10?0??0	00010?11?0	2010?00011	???????0?0
<i>Chaerilobuthus schwarzi</i> HT	001001100?	0?10?0??0	0001011???	?0?0?00011	???????0?0
<i>Chaerilobuthus serratus</i> HT	?010?????1	??1?0?0???	???????????	??????0011	???????0?0
<i>Chaerilobuthus serratus</i> 200656	0010011001	0010?01110	0001011110	2010300011	?33????020
<i>Chaerilobuthus serratus</i> 201163	0010011001	0?10?01110	0001011110	2010300011	?33????0?0
<i>Chaerilobuthus staxi</i> HT	001001?001	0?10?0??0	00010?11?0	2010?00???	???????0?0
<i>Pseudochactas mischi</i> HT	0020011001	0010111110	0001000010	2010101011	?334333000
<i>Pseudochactas ovchinnikovi</i> 2303A	0020011001	0010111110	0001000010	2010101011	1333333000
<i>Qianxie solegladi</i> HT	0010011001	0010111110	0111010010	2010101011	1333322020
<i>Troglokhammouanus steineri</i> 11271	0010011001	0010111110	0111110010	2010102011	1323222020
<i>Aemngvantom lao</i> 11349	0010011001	0010101110	0001010010	1020301011	0111111010
<i>Aemngvantom thamnongpaseuam</i> 11351	0010011001	0010?01110	0001010010	1020301011	?111111010
<i>Vietbocap canhi</i> 11270	0010011001	0010001110	0001010010	2010201011	0222222010
<i>Vietbocap canhi</i> 11348	0010011001	0010001110	0001010010	2010201011	0333333010

Chaerilobuthus bruckschi Lourenço, 2015; *Chaerilobuthus complexus* Lourenço and Beigel, 2011; *Chaerilobuthus enigmaticus* Lourenço, 2015; *Chaerilobuthus gigantosternum* Lourenço, 2016; *Chaerilobuthus hansgeorgmuelleri* Lourenço, 2019; *Chaerilobuthus knodelorum* Lourenço, 2018; *Chaerilobuthus longiaculeus* Lourenço, 2013; *Chaerilobuthus meggeri* Lourenço, 2021; *Chaerilobuthus petersi* Lourenço, 2024; *Chaerilobuthus schmidt* (Lourenço and Velten, 2024), comb. nov.; *Chaerilobuthus schwarzi* Lourenço, 2015; *Chaerilobuthus serratus* Lourenço, 2016; *Chaerilobuthus staxi* Lourenço, 2024.

Remarks: Results of morphological phylogenetic analysis justify the transfer of Chaerilobuthidae to Pseudochactidae, as Chaerilobuthinae, stat. nov.; the following new synonyms: *Chaeriloiurus* Lourenço, 2020 = *Chaerilobuthus* Lourenço, 2016, synonym. nov., and *Serratochaerilobuthus* Lourenço, 2024 = *Chaerilobuthus* Lourenço, 2016, synonym. nov.; and the following new combinations: *Chaerilobuthus brigittemuelleri* (Lourenço and Velten, 2020), comb. nov. and *Chaerilobuthus schmidt* (Lourenço and Velten, 2024), comb. nov..

Table 1. Continued

	101	111	121	131	141
<i>Buthus atlantis</i> 3489	- 2 0 0 - - 0 0 1 0	1 1 0 0 0 0 0 2 0 0	0 0 0 0 0 0 0 0 1 1	0 0 0 0 1 0 1 0 0 0	1 0 0
<i>Chaerilus sejnai</i> 3685	0 1 1 1 0 - 0 1 0 1	0 0 1 1 - 0 0 - 5 1	2 0 0 0 2 1 1 0 1 1	1 1 1 0 2 - 1 0 0 0	0 0 1
<i>Chaerilobuthus birmanicus</i> HT	? ? 1 ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? 0 ? ? ?	0 ? ? ? 0 ? ? 1 ? ?	? 0 1
<i>Chaerilobuthus brandti</i> HT	1 0 1 ? ? ? ? ? ? ?	? ? 0 0 ? ? ? ? 3 ?	? ? 0 ? ? 1 0 0 0 0	0 ? 1 1 ? ? ? 0 ? ?	? 0 1
<i>Chaerilobuthus brigittemuelleri</i> HT	? ? 1 ? ? ? ? ? ? ?	? ? 0 0 ? ? ? ? 4 ?	? ? 0 ? ? 1 0 0 0 0	0 ? 1 1 ? ? ? 0 ? ?	? 0 1
<i>Chaerilobuthus bruckschi</i> HT	? ? 1 ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? 1 0 0 0 0	0 ? ? ? ? ? ? 0 ? ?	? 0 1
<i>Chaerilobuthus bruckschi</i> 201161	? ? 1 2 1 1 1 ? ? ?	? ? 0 0 1 ? ? ? 4 ?	? ? 0 ? ? 1 0 0 0 0	0 ? 1 1 0 1 0 0 ? ?	? 0 1
<i>Chaerilobuthus bruckschi</i> 201162	? ? 1 2 1 1 1 ? ? ?	? ? 0 0 1 ? ? 0 4 ?	2 0 0 ? ? 1 0 0 0 0	0 ? 1 1 0 1 0 1 ? ?	? 0 1
<i>Chaerilobuthus complexus</i> HT	1 ? 1 ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? 4 ?	? ? ? ? ? 1 0 ? ? ?	0 ? ? ? 0 ? 0 0 ? ?	? 0 1
<i>Chaerilobuthus complexus</i> 200655	1 0 1 2 1 1 1 ? ? ?	? ? 0 0 1 ? ? 0 4 ?	2 0 0 ? ? 1 0 ? 0 0	? ? 1 1 ? ? ? ? ? ?	? ? ?
<i>Chaerilobuthus complexus</i> 201160	1 0 1 ? ? ? ? ? ? ?	? ? ? ? ? ? ? 0 4 ?	? ? 0 ? ? 1 0 0 0 0	0 ? 1 1 0 1 0 0 ? ?	? 0 1
<i>Chaerilobuthus enigmaticus</i> HT	1 0 1 ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? 5 ?	? ? ? ? ? 1 0 0 0 0	0 ? 1 1 0 ? ? 0 ? ?	? 0 1
<i>Chaerilobuthus enigmaticus</i> 201158	1 0 1 2 1 1 1 ? ? ?	? ? 0 0 1 ? ? 0 4 ?	? ? 0 ? ? 1 0 0 0 0	0 ? 1 1 0 ? ? 0 ? ?	? 0 1
<i>Chaerilobuthus enigmaticus</i> 201159	1 0 1 ? ? ? ? ? ? ?	? ? 0 0 1 ? ? 0 4 ?	2 0 0 ? ? 1 0 0 0 0	0 ? 1 1 0 1 0 0 ? ?	? 0 1
<i>Chaerilobuthus gigantosternum</i> HT	1 0 ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? 4 ?	? ? ? ? ? 1 0 0 ? ?	? ? ? ? 0 ? ? 0 ? ?	? 0 1
<i>Chaerilobuthus gigantosternum</i> 200654	1 0 1 2 1 1 1 ? ? ?	? ? 0 0 1 ? ? 0 4 ?	2 0 0 ? ? 1 0 0 0 0	? ? 1 1 0 1 0 ? ? ?	? ? ?
<i>Chaerilobuthus hansgeorgmuelleri</i> 201164	1 0 1 2 1 1 1 ? ? ?	? ? 0 0 1 ? ? 0 4 ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ?
<i>Chaerilobuthus hansgeorgmuelleri</i> HT	1 0 1 ? ? ? ? ? ? ?	? ? ? 0 1 ? ? ? 4 ?	? ? 0 ? ? 1 0 0 0 0	0 ? 1 1 0 ? 0 0 ? ?	? ? ?
<i>Chaerilobuthus knodorum</i> 200657	1 0 1 2 1 1 1 ? ? ?	? ? 0 0 1 ? ? 0 4 ?	2 0 0 ? ? 1 0 ? 0 0	? ? 1 1 ? ? ? ? ? ?	? ? ?
<i>Chaerilobuthus knodorum</i> HT	1 0 1 ? ? ? ? ? ? ?	? ? ? 0 1 ? ? ? 4 ?	? ? 0 ? ? 1 0 0 0 0	0 ? 1 1 0 ? ? 1 ? ?	? 0 1
<i>Chaerilobuthus longiaculeus</i> HT	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? 0 0	0 ? ? 1 1 ? 0 0 ? ?	? 0 1
<i>Chaerilobuthus megeri</i> HT	1 0 1 ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? 4 ?	? ? ? ? ? 1 0 0 0 0	0 ? 1 1 0 ? ? 0 ? ?	? 0 1
<i>Chaerilobuthus petersi</i> HT	1 0 1 ? ? ? ? ? ? ?	? ? ? 0 0 ? ? ? 2 ?	? ? 0 ? ? 1 0 0 0 0	0 ? 1 1 0 ? ? 0 ? ?	? 0 1
<i>Chaerilobuthus schmidtii</i> HT	1 0 1 ? ? ? ? ? ? ?	? ? ? 0 1 ? ? ? 4 ?	? ? 0 ? ? 1 0 0 0 0	0 ? 1 1 0 ? ? 0 ? ?	? 0 1
<i>Chaerilobuthus schwarzi</i> HT	1 0 1 ? ? ? ? ? ? ?	? ? ? 0 ? ? ? ? 4 ?	? ? ? ? ? 1 0 0 0 0	0 ? 1 1 0 ? ? 1 ? ?	? 0 1
<i>Chaerilobuthus serratus</i> 200656	1 0 1 2 1 1 1 ? ? ?	? ? 0 0 1 ? ? 0 4 ?	2 0 0 ? ? 1 0 0 0 0	0 ? 1 1 0 ? 0 1 ? ?	? 0 1
<i>Chaerilobuthus serratus</i> 201163	1 0 1 2 1 1 1 ? ? ?	? ? 0 0 1 ? ? 0 4 ?	2 0 0 ? ? 1 0 0 0 0	0 ? 1 1 0 ? ? 1 ? ?	? 0 1
<i>Chaerilobuthus staxi</i> HT	1 0 1 ? ? ? ? ? ? ?	? ? ? 0 1 ? ? ? 4 ?	? ? 0 ? ? 1 0 0 0 0	0 ? 1 1 0 ? ? 1 ? ?	? 0 1
<i>Chaerilobuthus serratus</i> HT	1 0 1 ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? 1 0 0 0 0	0 ? ? ? 0 ? 0 1 ? ?	? 0 1
<i>Pseudochactas mischi</i> HT	1 0 0 1 1 0 1 ? ? ?	? ? 0 0 1 ? 2 2 2 ?	? ? 1 ? ? 1 0 0 2 1	1 ? 1 0 0 1 0 0 ? 0	? 1 1
<i>Pseudochactas ovchinnikovi</i> 2303A	1 0 0 1 1 0 1 1 0 0	0 0 0 0 1 0 2 2 2 1	1 1 1 0 2 1 0 0 1 1	0 1 1 0 0 1 0 0 0 0	0 1 1
<i>Qianxie solegladi</i> HT	0 1 0 2 1 0 1 1 ? ?	? ? 0 0 1 0 2 2 2 ?	? ? 0 0 2 1 0 0 2 1	0 1 1 0 0 1 0 1 0 0	? 1 1
<i>Troglokhammouanus steineri</i> 11271	0 1 0 2 1 0 1 1 0 0	0 0 0 0 1 0 1 3 1 1	2 0 0 0 2 1 1 0 2 2	2 1 1 0 0 1 1 1 0 0	0 1 1
<i>Aemngvantom lao</i> 11349	1 1 1 2 1 1 1 1 0 0	0 0 0 0 1 1 2 3 1 1	2 0 0 1 1 1 0 0 2 1	2 0 1 0 0 1 1 1 0 1	0 0 1
<i>Aemngvantom thamnongpaseum</i> 11351	1 1 1 2 1 1 1 ? ? ?	? ? 0 0 1 ? 2 3 1 ?	? ? 1 ? ? 1 0 1 2 1	0 ? 1 1 0 1 0 1 ? 1	? 0 1
<i>Vietbocap canhi</i> 11270	1 1 1 2 1 1 1 1 0 0	0 0 0 0 1 0 2 1 3 1	2 0 1 0 ? 1 0 1 1 1	0 1 1 0 0 1 0 1 1 1	0 0 1
<i>Vietbocap canhi</i> 11348	1 1 1 2 1 1 1 1 0 0	0 0 0 0 1 0 2 1 3 1	2 0 1 0 ? 1 0 1 1 1	0 1 1 0 0 1 0 1 1 1	0 0 1

Chaerilobuthus bruckschi Lourenço, 2015

(Figs 4–10)

Chaerilobuthus bruckschi Lourenço, 2015: 470, 471, figs 13–18, photos 194–196.

Type material: Holotype: one juv. (sex unknown) (personal collection of KlausPeter Brucksch, Kuranda, Australia), Cretaceous (Cenomanian) burmite: **MYANMAR:** *Kachin State* (precise locality unknown).

Diagnosis: The following combination of characters is diagnostic for *C. bruckschi*: carapace anterior margin sublinear (Figs 6A, 9A); lateral ocelli markedly protruding (Figs 6A, 9A), pectines each with five or six teeth (Fig. 6D); pedipalp chela relatively slender, ratio of chela length : chela manus width less than 5 (Fig. 10); ratio of metasomal segment IV : V length less than 2 (Figs 5C, D, E, F, 9K, L, M, N); metasomal segment V dorsolateral carinae slightly serrate (Fig. 9M); telson vesicle slightly bulbous (Figs 5E, F, 9M, N), aculeus moderately long and curved, base narrow (Figs 5E, F, 9M, N).

Table 3. Measurements (mm) and counts for holotypes of described species of Chaerilobuthinae Lourenço, 2011, stat. nov., from the literature (Lourenço and Beigel 2011, Lourenço 2015a, b, 2016b, 2018, Lourenço and Velten 2019, 2020, 2022). Abbreviations as follows: Cbir = *Chaerilobuthus birmanicus* Lourenço, 2015; Cbra = *Chaerilobuthus brandti* Lourenço, 2022; Cbri = *Chaerilobuthus brigittemuelleri* (Lourenço, 2020), comb. nov.; Cbru = *Chaerilobuthus bruckschi* Lourenço, 2015; Ccom = *Chaerilobuthus complexus* Lourenço and Beigel, 2011; Ceni = *Chaerilobuthus enigmaticus* Lourenço, 2015; Cgig = *Chaerilobuthus gigantosternum* Lourenço, 2016; Chan = *Chaerilobuthus hanseorgmuelleri* Lourenço, 2019; Ckno = *Chaerilobuthus knodelorum* Lourenço, 2018.

	Cbir	Cbra	Cbri	Cbru	Ccom	Ceni	Cgig	Chan	Ckno
Carapace									
L	1.21	1.27	1.8	1.03	0.66	1.67	1	1.34	1.07
Anterior W		0.94	0.93		0.51			0.87	0.57
Posterior W	0.81	1.47	1.54		0.6			1.4	0.94
Pedipalp									
Femur L/W	1.27/0.27	1.34/0.40	1.47/0.53	-/-	0.48/0.16	-/-	0.60/0.14	1.27/0.60	0.84/0.34
Patella L/W	1.40/0.41	1.47/0.27	1.67/0.67	1.46/0.52	0.51/0.17	-/-	0.74/0.27	1.40/0.67	1.10/0.30
Chela L/W	2.07/0.61	2.21/0.27	2.53/0.67	1.87/0.34	0.80/0.14	-/-	1.34/0.34	2.14/0.87	1.40/0.40
Mesosoma									
Moveable finger L	1.07	1.47	1.47	0.93	0.54			0.94	0.84
Total L	2.67	2.54	2.2	3.11	0.94	2.67	1.47	2.54	2.1
Pectines	-/-	7/8	5/6	-/-	5/-	4/4	5/-	6/5	5/5
Metasoma									
Segment I L/W/H		0.47/0.67/-	0.73/0.93/-	0.40/0.33/-	0.11/-/-		0.34/-/-	0.47/0.74/-	0.37/0.44/-
Segment II L/W/H		0.47/0.54/-	0.80/0.93/-	0.47/0.27/-	0.14/-/-		0.34/-/-	0.60/0.74/-	0.40/0.40/-
Segment III L/W/H		0.67/0.54/-	0.93/0.87/-	0.53/0.27/-	0.20/-/0.11		0.40/0.27/-	0.74/0.80/-	0.47/0.37/-
Segment IV L/W/H		0.94/0.54/-	1.13/0.87/-	0.67/0.27/-	0.31/0.14/-		0.54/0.27/-	0.87/0.80/-	0.60/0.34/-
Segment V L/W/H		1.67/0.47/-	1.53/0.87/-	1.20/0.25/-	0.48/-/0.14		0.80/0.34/-	1.40/0.87/-	1.14/0.34/-
Total L	3.67	4.22	5.12	3.27	1.24	-	2.42	4.08	2.98
Telson									
Vesicle L					0.31				
Vesicle W		0.85	0.87	0.42	0.26			0.82	0.27
Vesicle H		0.55		0.47	0.17		0.40		
Total L	1.14	1.74	1.87	1.34	0.54	1.6	0.94	1.31	1.17

Table 4. Measurements (mm) and counts for holotypes of described species of Chaerilobuthinae Lourenço, 2011, stat. nov., and a male of the type species of Pseudochactidae Gromov, 1998 from the literature (Prendini *et al.* 2006, Lourenço 2013, 2016b, Lourenço and Velten 2015, 2021, 2024a–c). Abbreviations as follows: Clon = *Chaerilobuthus longiaculeus* Lourenço, 2013; Cmeg = *Chaerilobuthus meggeri* Lourenço, 2021; Cpet = *Chaerilobuthus petersi* Lourenço, 2024; Cschm = *Chaerilobuthus schmidtii* Lourenço, 2024; Cschw = *Chaerilobuthus schwarzi* Lourenço, 2015; Cser = *Chaerilobuthus serratus* Lourenço, 2016; Csta = *Chaerilobuthus staxi* Lourenço, 2024; Povc = *Pseudochactas ovchinnikovi* Gromov, 1998.

	Clon	Cmeg	Cpet	Cschm	Csch	Cser	Csta	Povc
Carapace	L	1.17	0.81	0.91	0.93	1.54	0.87	2.3
	Anterior W	0.77	0.42	0.57	0.57		0.59	1.4
	Posterior W	0.97	0.54	0.85	1		0.67	2.3
Pedipalp	Femur L/W	1.10/0.37	1.50	1.07	0.80/0.33	1.27/0.34	1.30	2.40/0.80
	Patella L/W	1.14/0.40	0.57/0.32	0.84/0.31	0.83/0.33	1.34/0.34	0.64/0.24	2.25/1.00
	Chela L/W	1.80/0.47	0.75/0.24	0.94/0.32	1.43/0.37	1.87/0.40	0.65/0.21	4.50/1.40
	Moveable finger L	0.9	1.08/0.17	1.51/0.41	0.77		1.20/0.17	2.5
Mesosoma	Total L	1.87	0.67	0.81	1.83	2.8	0.64	5.7
Pectines	Tooth count	-/-	5/5	10/11	6/6	-/-	5/5	11/10
Metasoma	Segment I L/W/H	0.37/0.70/-	0.21/-/0.21	0.31/0.47/-	0.30/0.40/-	0.47/0.60/-	0.24/0.27/-	1.05/1.30/1.09
	Segment II L/W/H	1.10/-/0.60	0.40/-/0.60	0.36/0.44/-	0.30/0.30/-	0.54/0.54/-	0.27/0.26/-	1.20/1.20/1.09
	Segment III L/W/H	1.10/-/0.60	0.47/-/0.57	0.43/0.44/-	0.33/0.30/-	0.67/-/0.47	0.29/0.28/-	1.30/1.20/1.04
	Segment IV L/W/H	1.20/-/0.70	0.57/-/0.53	0.57/-/0.37	0.53/-/0.30	0.94/-/0.54	0.37/0.27/-	1.70/1.10/1.00
	Segment V L/W/H	1.80/-/0.70	0.74/-/0.17	1.07/-/0.37	0.93/-/0.30	1.60/-/0.67	0.67/0.32/-	3.00/1.10/0.95
	Total L	3.18	1.82	2.74	2.39	4.22	1.84	8.25
Telson	Vesicle L	0.8						2.1
	Vesicle W						0.28	1.2
	Vesicle H	0.8	0.17	0.37	0.37	0.4		1.1
	Total L	1.5	0.77	1.14	1.07	1.74	0.78	3.15

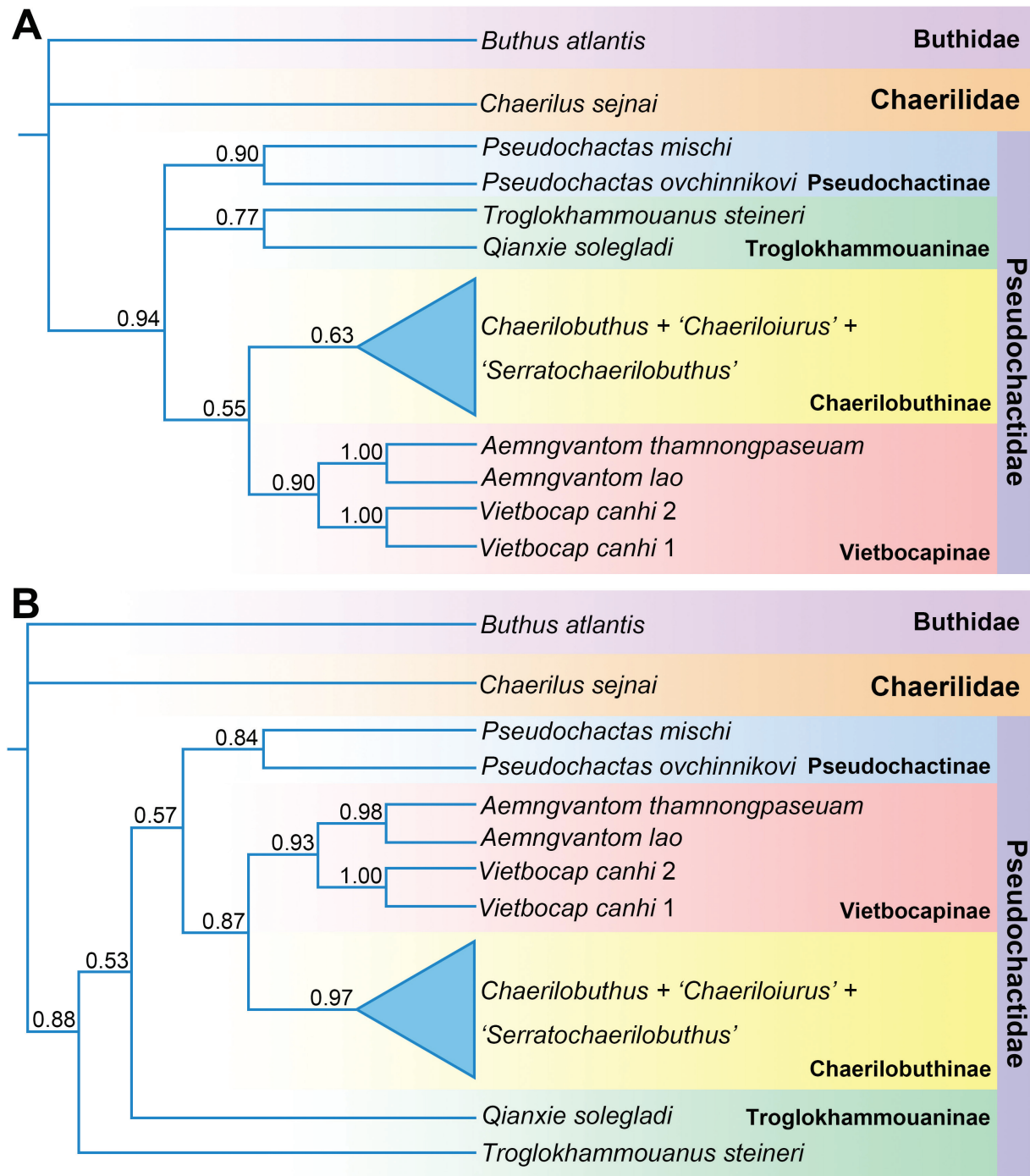


Figure 1. Phylogeny of Pseudochactidae Gromov, 1998, including Chaerilobuthinae Lourenço, 2011, stat. nov., based on Bayesian inference (A) and maximum likelihood (B). Bootstrap support values at nodes.

Description: Based on the material examined (NIGP 201161, 201162).

Carapace: Anterior margin with few, short microsetae; anteromedian depression narrow, shallow; anterosubmedial depressions absent; lateral ocular carinae absent; posteromedian and posteromarginal sulci distinct; posterior margin slightly recurved medially; surfaces almost smooth to sparsely covered by microsetae (Figs 4A, 6A, 9A). Median ocular tubercle situated anteromedially; median ocelli absent; one pair of large posterolateral major lateral ocelli present (Fig. 6A).

Coxosternal region: Surface smooth, sparsely covered in macrosetae (Fig. 5B). Sternum not visible.

Chelicerae: Fixed finger and manus, prolateral and ventral surfaces each with long, dense setae (Fig. 6B, C). Moveable finger markedly overlapping fixed finger such that cheliceral dentition partly visible; moveable finger with long dorsal distal (dd) denticle, small dorsal subdistal denticle, stout dorsal median denticle, long ventral distal (vd) denticle, and three or four small ventral accessory (va) denticles; fixed finger with long distal denticle and small subdistal denticle. Moveable finger with

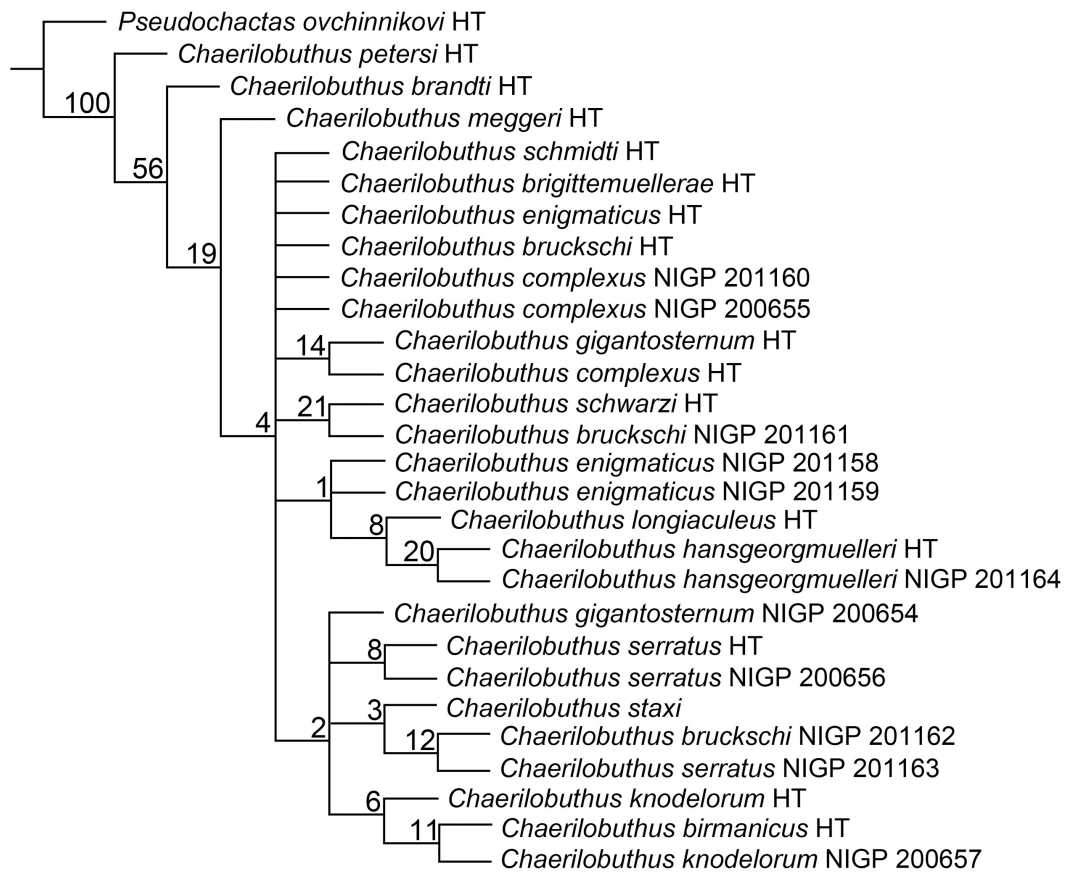


Figure 2. Phylogeny of Chaerilobuthinae Lourenço, 2011, stat. nov., inferred with parsimony. Numbers following taxon names refer to specimens in the Nanjing Institute of Geology and Palaeontology at the Chinese Academy of Sciences, Nanjing. Taxon names followed by 'HT' (holotype) were scored from the original descriptions. Jackknife support values at nodes.

prominent serrula comprising moderately long spinules in proximal three-quarters.

Pedipalps: Segments gracile (Figs 7, 10). Femur with four carinae evident; prodorsal, proventral, and retrodorsal carinae distinct, serrate; retroventral carinae smooth, costate. Patella with six carinae evident; prolateral surface, dorsoventral 'vaulted' projection ('anterior process') moderately developed with moderately developed pair of apophyses or tubercles ('patellar spurs'), each possessing one macroseta; retrodorsal, retromedian, and retroventral carinae distinct, smooth, and costate; prodorsal carina incomplete, slightly granular, and obsolete proximally. Chela relatively gracile (CL/CW = 5.83, Appendix 2); manus globose; chela with five carinae evident; digital carina distinct on fixed finger and manus; prodorsal carina moderately developed, comprising several spiniform granules; promedian carina distinct, comprising five or six prominent spiniform granules; proventral carinae obsolete, comprising few isolated granules; retroventral carina obsolete, smooth, and costate; dorsomedian, dorsal secondary, subdigital, retromedian and ventromedian carinae absent or obsolete. Chela finger dentition not visible. Trichobothrial pattern Type D, β configuration. Femur with 11 trichobothria visible, six d , two i and three e trichobothria, trichobothria d_1 , d_2 , d_4 and d_6 noticeably smaller than others ('petite'); trichobothrium e_1 situated proximal to trichobothrium d_3 ;

trichobothrium e_3 situated dorsal to trichobothrium d_6 (Figs 7A, 10). Patella with nine trichobothria visible, including three d , one i , and five e trichobothria; trichobothrium i_1 situated distal to trichobothrium d_3 (Figs 7A, 10). Chela with 12 trichobothria visible; fixed finger with two d , two e , and three i trichobothria; manus with four E and one V trichobothria; trichobothrium Et_1 situated distally on manus, almost aligned with, or proximal to, moveable finger condyle; trichobothrium eb situated on fixed finger, slightly distal to moveable finger condyle; trichobothrium esb situated medially to subdistally on fixed finger; trichobothrium V_2 situated distally on manus and near retroventral carina (Figs 7B–D, 10).

Legs: Tibia lateral and ventral surfaces each with scattered macrosetae (Figs 6I–L, 9F–I). Basitarsi each with distinct pedal spurs and pair of spinule rows, comprising c. 10 relatively long spinules, distally. Ungues moderately long, distinctly curved; dactyl pronounced, pointed.

Pectines: Three marginal lamellae and four median lamellae (Figs 6D, 9J); surface sparsely covered in macrosetae; longitudinal suture between marginal and median lamellae distinct. Fulcra absent or obsolete. Teeth rounded; distal three-quarters of each tooth occupied by sensillar field.

Genital operculum: Not visible, covered by fissures and bubbles.

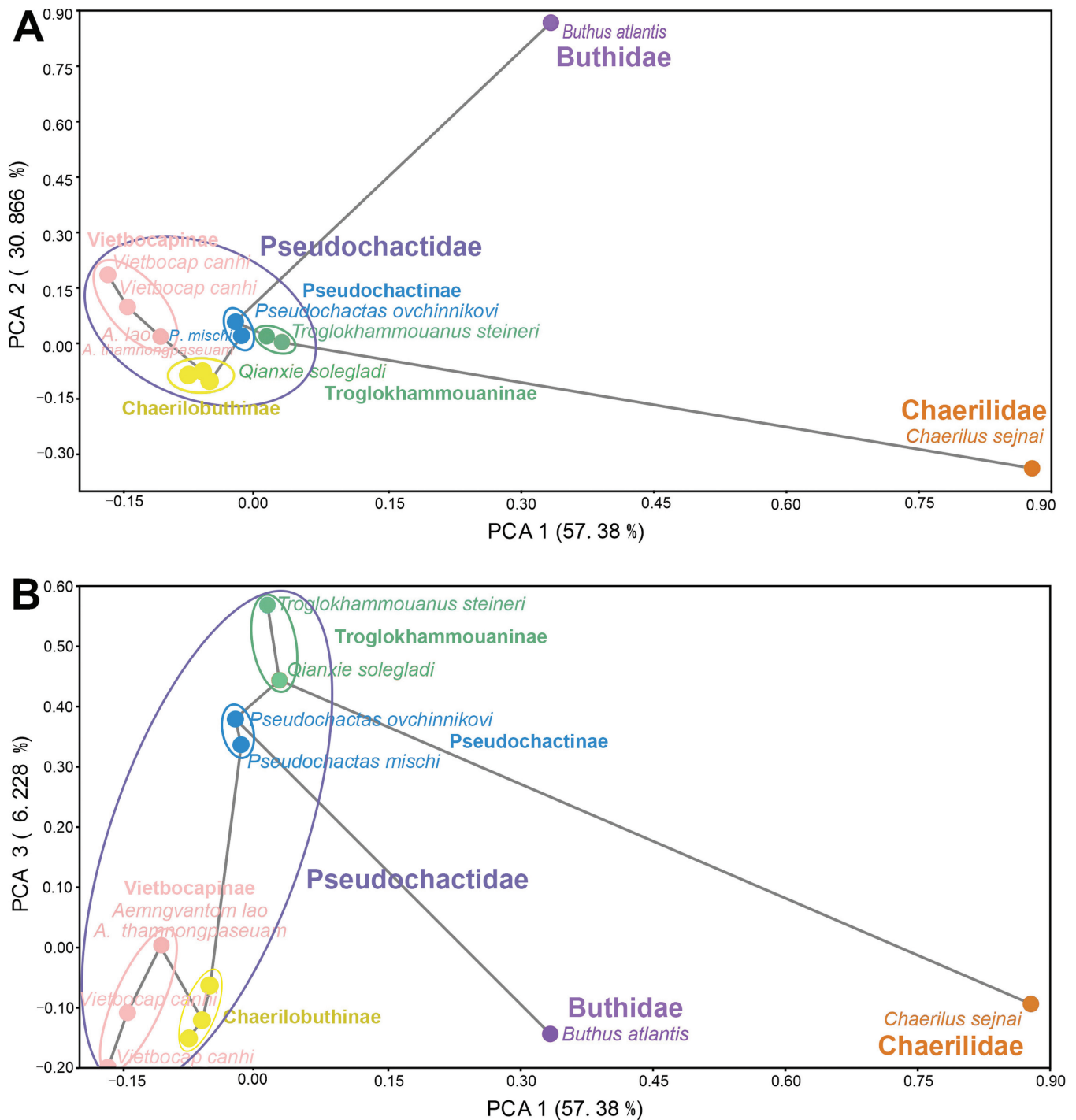


Figure 3. Morphospace analysis of family Pseudochactidae Gromov, 1998, including Chaerilobuthinae Lourenço, 2011, stat. nov. A, PCA1 × PCA2. B, PCA1 × PCA3.

Mesosoma: Pretergites surfaces almost smooth (Figs 5A, 6E, 9D); post-tergites I–VI surfaces finely granular, acarinate (Figs 5A, 6E, 9D); tergite VII surface sparsely granular with four distinct carinae (paired dorsosubmedian and dorsolateral carinae) in posterior half of segment (Fig. 6H). Sternites surfaces smooth, with scattered macrosetae; posterior margins broadly recurved; respiratory spiracles (stigmata) small, ovoid to round (Figs 6F, 9E).

Metasoma: Segments I–V progressively increasing in length, I wider than long, others longer than wide (Figs 4, 8). Segments I–V lateral and ventral surfaces each with few, short macrosetae (Figs 5C–F, 6H, 9K–N); I–IV dorsal surfaces each with distinct depression (Figs. 6H, 9K, L). Segments I–III each with six distinct carinae (paired dorsosubmedian, dorsolateral and ventrolateral carinae), IV and V each with eight distinct carinae (paired dorsosubmedian, dorsolateral, ventrolateral and



Figure 4. *Chaerilobuthus bruckschi* Lourenço, 2015, one juv. (NIGP 201161), habitus under incident light. A, dorsal aspect. B, ventral aspect. Scale bar: 1 mm.

ventrosubmedian carinae); dorsosubmedian carinae distinct on all segments, markedly serrate, and converging posteriorly; dorsolateral carinae distinct, markedly serrate on segments I–III, moderately serrate on segments IV and V; ventrolateral carinae distinct, moderately serrate on segments I–IV, weakly serrate on V; ventrosubmedian carinae absent on segments I–III, obsolete on IV, distinct, moderately serrate, and converging posteriorly on V (Figs 5C–F, 6H, 9K–N).

Telson: Dorsal surface flat; lateral and ventral surfaces relatively smooth, with several macrosetae (Figs 5E, F, 6G, 9M, N); subaculear tubercle absent; prominent, moderately long subaculear setal pair.

Material examined: **MYANMAR:** *Kachin State:* Noiye Bum near Hukawng Valley, precise locality unknown, Cretaceous (Cenomanian) burmite: 1 juv. (sex unknown), dextral pedipalp patella and chela absent (NIGP 201161), 1 juv. (sex unknown) (NIGP 201162).

Chaerilobuthus complexus Lourenço and Beigel, 2011

(Figs 11–16, 39)

Chaerilobuthus complexus Lourenço and Beigel, 2011: 635–639, figs 1–11.

Type material: Holotype: 1 juv. (sex unknown) (Senckenberg Museum, Frankfurt, Germany), Cretaceous (Cenomanian) burmite: **MYANMAR:** *Kachin State* (precise locality unknown).

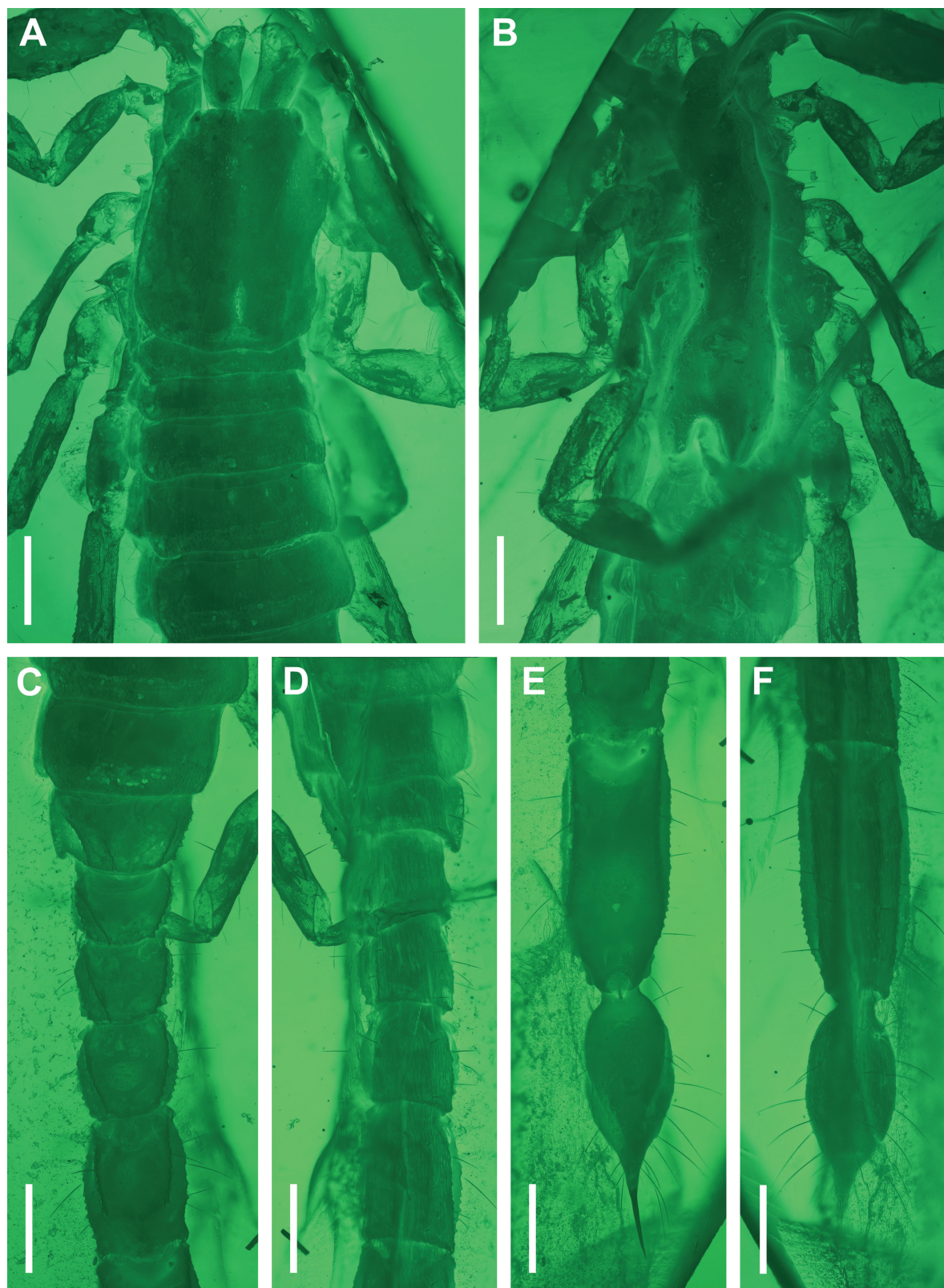


Figure 5. *Chaerilobuthus bruckschi* Lourenço, 2015, one juv. (NIGP 201161), morphology under epifluorescence. A, B, mesosoma and metasoma, dorsal and ventral aspects. C, D, metasomal segments I–IV, dorsal and ventral aspect. E, F, metasomal segment V and telson, dorsal and ventral aspects. Scale bars: 400 μm.

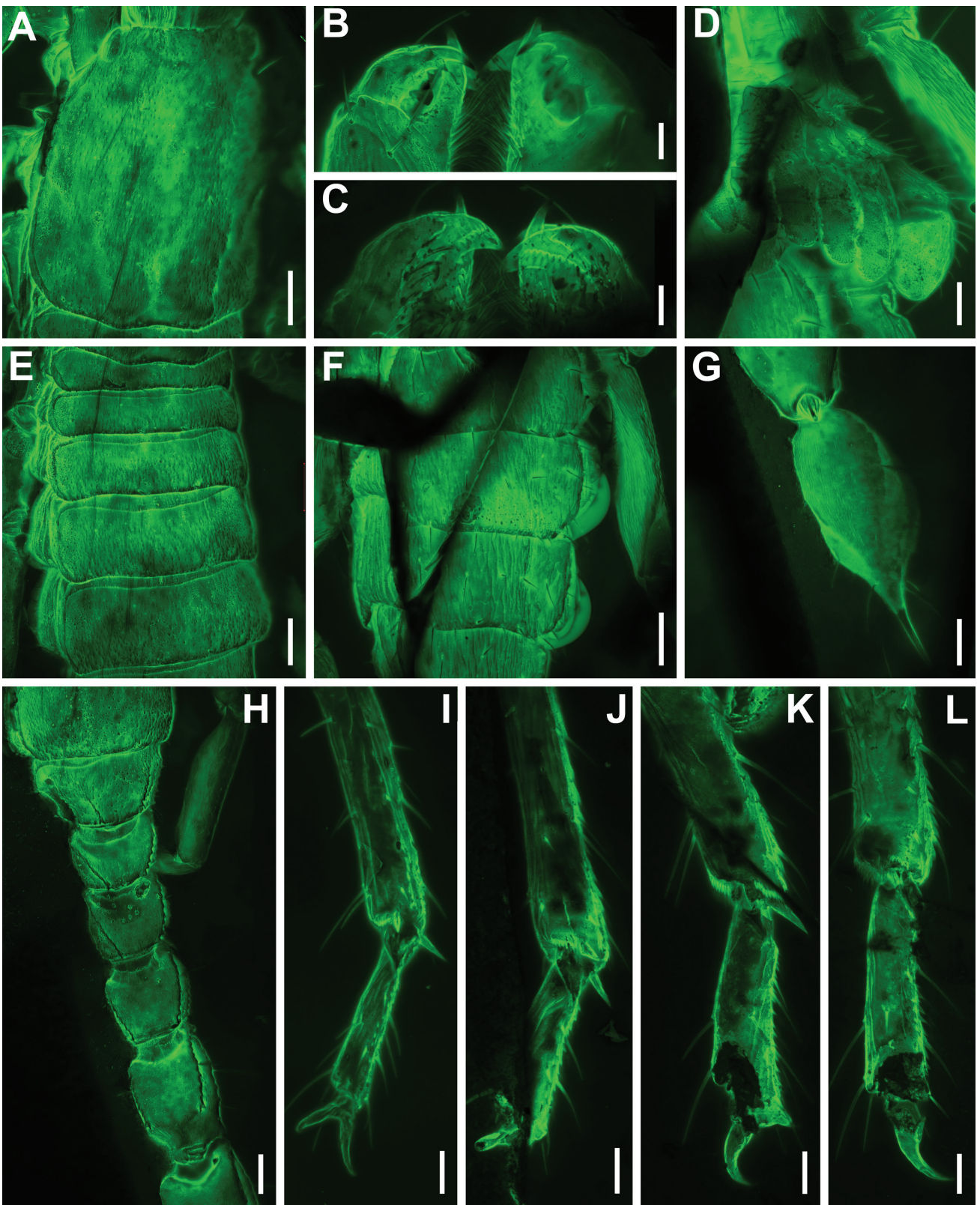


Figure 6. *Chaerilobuthus bruckschi* Lourenço, 2015, one juv. (NIGP 201161), morphology under confocal microscopy. A, carapace. B, C, chelicera, dorsal and ventral aspects. D, sinistral pecten, ventral aspect. E, tergites. F, sternites. G, telson. H, metasomal segments, dorsal aspect. I–L, legs I–IV tarsi, lateral aspect. Scale bars: 200 μm (A, E–H); 50 μm (B, C, I–L); 100 μm (D).

Diagnosis: The following combination of characters is diagnostic for *Chaerilobuthus complexus*: carapace anteromedian margin aligned with anterolateral margins (Figs 11A, 14A);

carapace anterior margin slightly depressed submedially (Figs 12A, 15A); lateral ocelli protruding (Figs 12A, 15A); sternum relatively narrow (Figs 17B, 20B); pedipalp chela

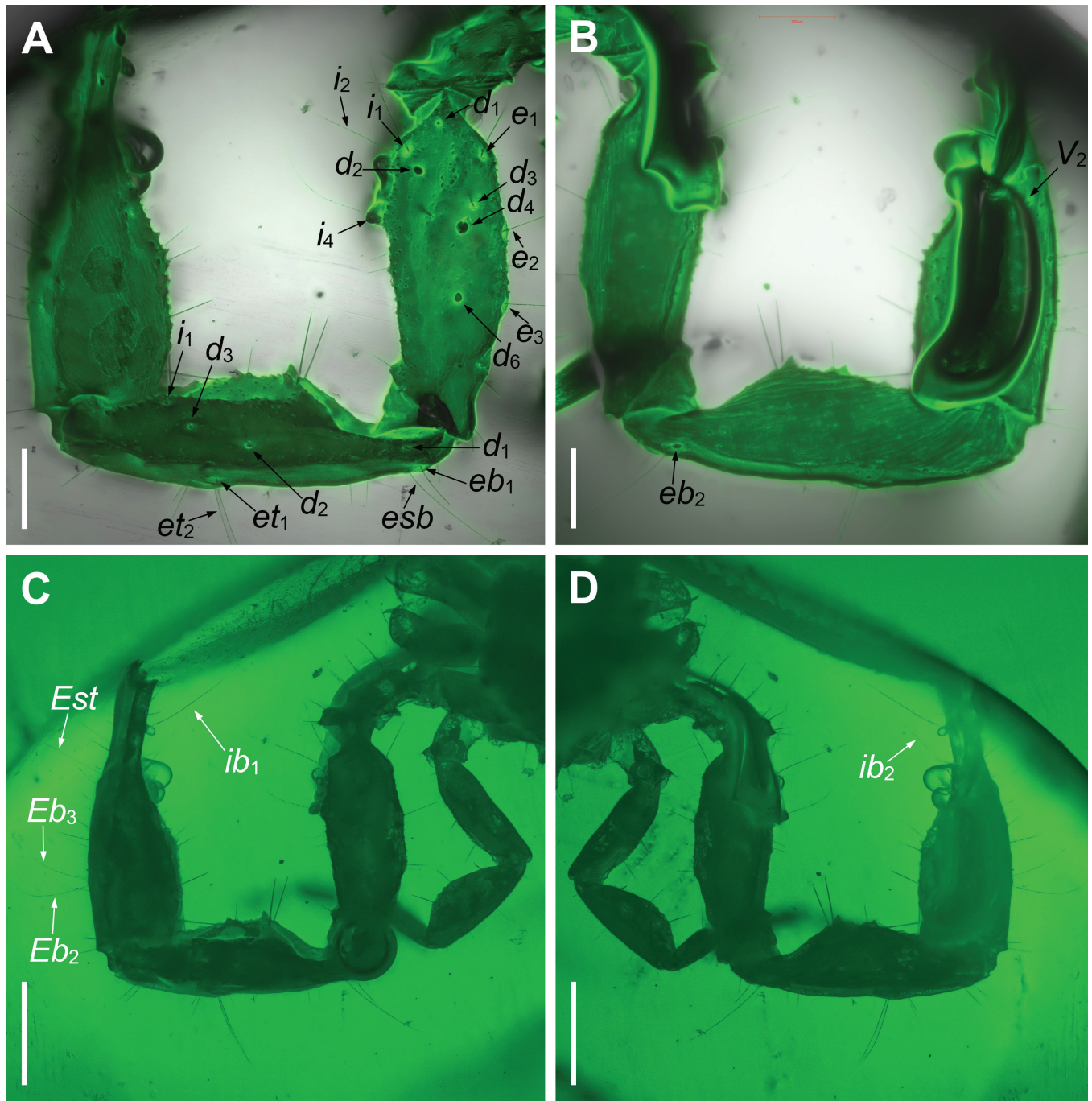


Figure 7. *Chaerilobuthus bruckschi* Lourenço, 2015, one juv. (NIGP 201161), pedipalp trichobothrial pattern under epifluorescence (A, B) and confocal microscopy (C, D). Scale bars: 200 μ m.

robust, ratio of chela length : chela manus width less than 5 (Figs 13C, 16); pedipalp chela fixed finger median denticle row comprising c. seven oblique subrows (Figs 13C, 15E); pectines each with five teeth (Figs 12B, 15D); mesosoma relatively wide, tergite VII width much greater than length (Fig 11E); metasomal segment I width much greater than length (Fig 12I, J).

Description: Based on the material examined (NIGP 200655, 201160).

Carapace: Anterior carapace margin with few, short microsetae; anteromedian depression narrow, shallow; anterosubmedial depressions absent; lateral ocular carinae absent; posteromedian and posteromarginal sulci obsolete; surfaces almost smooth to sparsely covered in microsetae (Figs 12A, 15A). Median ocular tubercle situated anteromedially; median ocelli absent; one pair of large posterolateral major lateral ocelli present.

Coxosternal region: Surface smooth, sparsely covered in macrosetae (Figs 12B, 39D). Leg I maxillary lobes

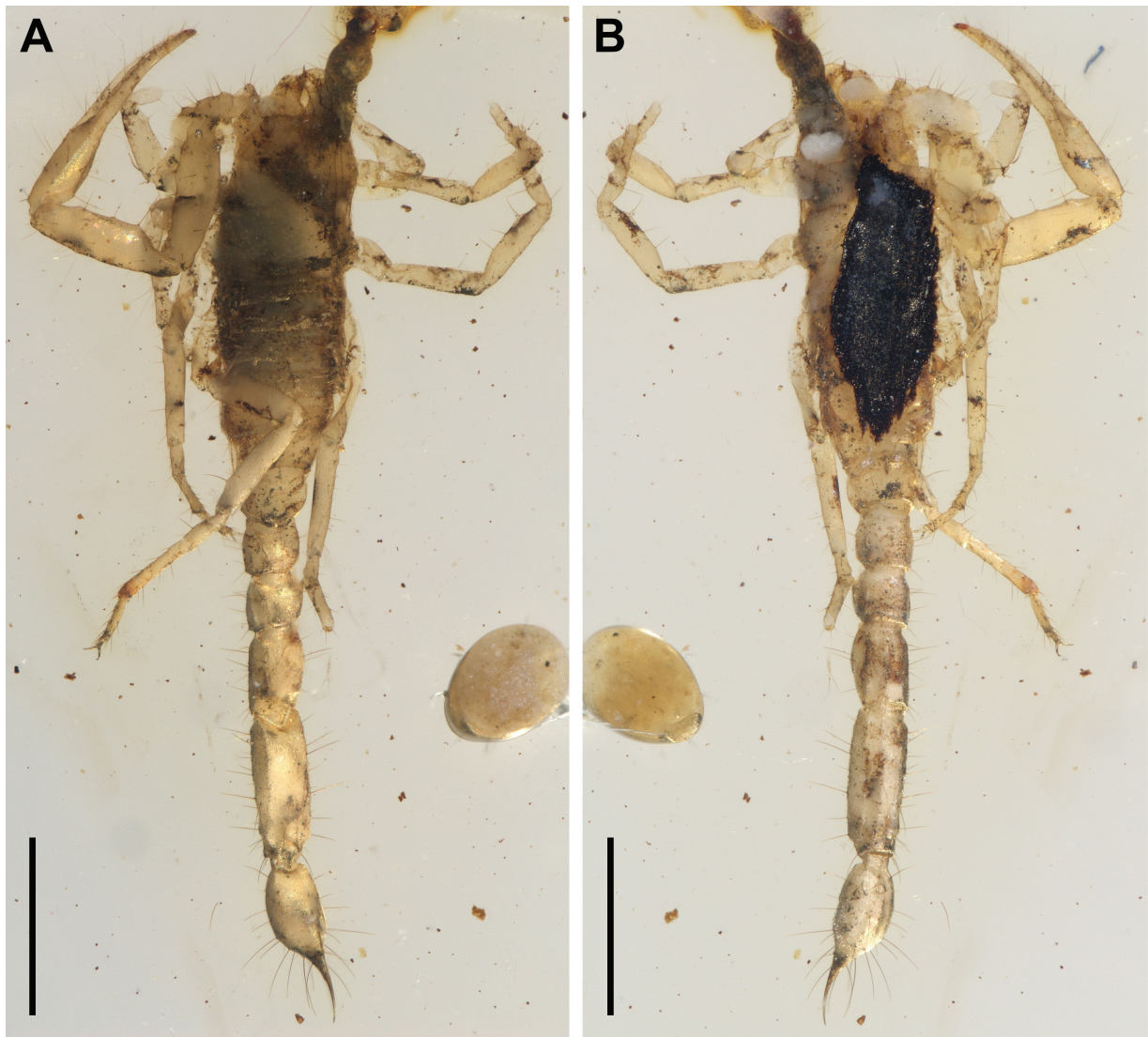


Figure 8. *Chaerilobuthus bruckschi* Lourenço, 2015, one juv. (NIGP 201162), habitus under incident light. A, dorsal aspect. B, ventral aspect. Scale bars: 1 mm.

(coxapophyses) distal margins slightly curved, dilate anteriorly and adorned with serrula comprising c. 14–16 spinules (Fig. 39D). Sternum pentagonal; lateral margins sublinear, parallel; ventral surface flat, without distinct concave region or median sulcus; posteromedian depression wide, shallow; posterior margin slightly recurved (Figs 12B, 15B).

Chelicerae: Fixed finger and manus, prolateral and ventral surfaces each with numerous long, dense macrosetae (Fig. 12C, G). Moveable finger markedly overlapping fixed finger (Fig. 12D) such that cheliceral dentition partly visible; moveable finger with long dorsal distal (dd) denticle, small dorsal subdistal denticle, stout dorsal median denticle and long ventral distal (vd) denticle; fixed finger with long distal denticle and small subdistal denticle (Figs 18E, F, 20C). Moveable finger with prominent serrula, comprising moderately long spinules in proximal three-quarters (Fig. 12C, G).

Pedipalps: Segments moderately robust; surfaces sparsely covered by short microsetae and few macrosetae (Figs 11,

13, 14, 16). Femur with three carinae evident; prodorsal and proventral carinae distinct, serrate, prodorsal carinae with small apophysis proximally (Figs 13A, 15F). Patella with four carinae evident; prolateral surface, dorsoventral ‘vaulted’ projection (‘anterior process’) distinct with prominent pair of apophyses or tubercles (‘patellar spurs’), each possessing one macroseta; retrodorsal and retroventral carinae smooth, costate (Figs 13B, 15I). Chela relatively robust; manus globose; chela with six carinae evident; digital carina incomplete, distinct on fixed finger, obsolete on manus; dorsomedian carina reduced to few granules proximally on manus; prodorsal carina distinct, comprising several strong spiniform granules; promedian and proventral carinae obsolete, each comprising few isolated granules; retroventral carina obsolete, smooth, and costate (Figs 13C, D, 15H); dorsal secondary, subdigital, retromedian and ventromedian carinae absent or obsolete. Fixed and moveable fingers median denticle rows each comprising seven oblique, slightly imbricate subrows, separated by large serrate prolateral and retrolateral

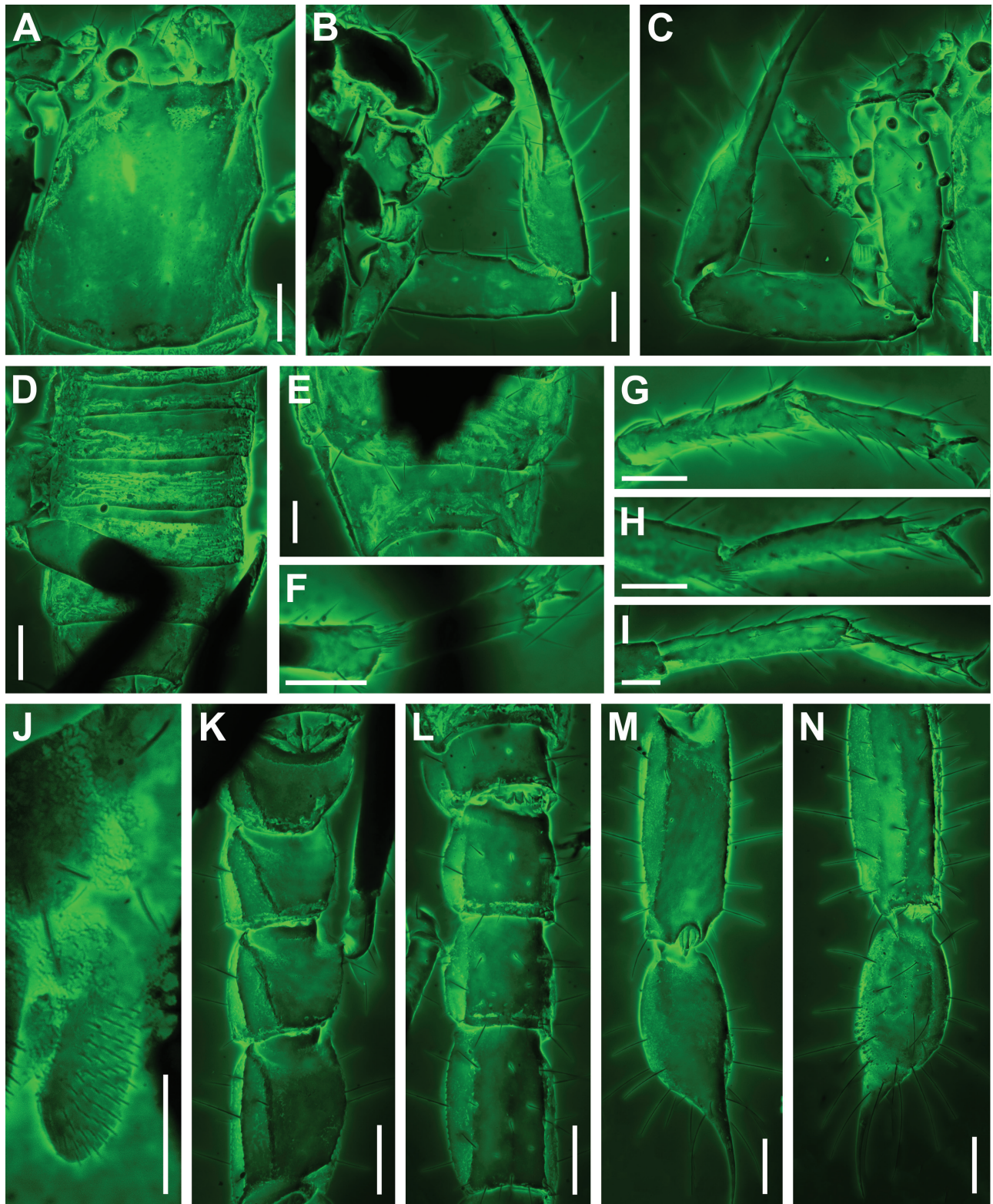


Figure 9. *Chaerilobuthus bruckschi* Lourenço, 2015, one juv. (NIGP 201162), morphology under confocal microscopy. A, carapace. B, sinistral pedipalp, ventral aspect. C, sinistral pedipalp, dorsal aspect. D, tergites. E, sternites VI and VII. F, G, leg III tarsus, dorsal and ventral aspects. H, I, leg IV tarsus, dorsal and ventral aspects. J, pectinal tooth, ventral aspect. K, L, metasomal segments I–IV, dorsal and ventral aspects. M, N, metasomal segment V and telson, dorsal and ventral aspects. Scale bars: 200 μm (A–D, K–N); 100 μm (E–I); 50 μm (J).

denticles (Figs 13C, 15E). Trichobothrial pattern Type D, β configuration. Pedipalp femur with 10 trichobothria visible, five d , two i , and three e trichobothria, trichobothria

d_1 , d_2 , d_4 , and d_6 noticeably smaller than others ('petite'); trichobothrium e_1 situated proximal to trichobothrium d_3 ; trichobothrium e_3 vertically aligned with trichobothrium

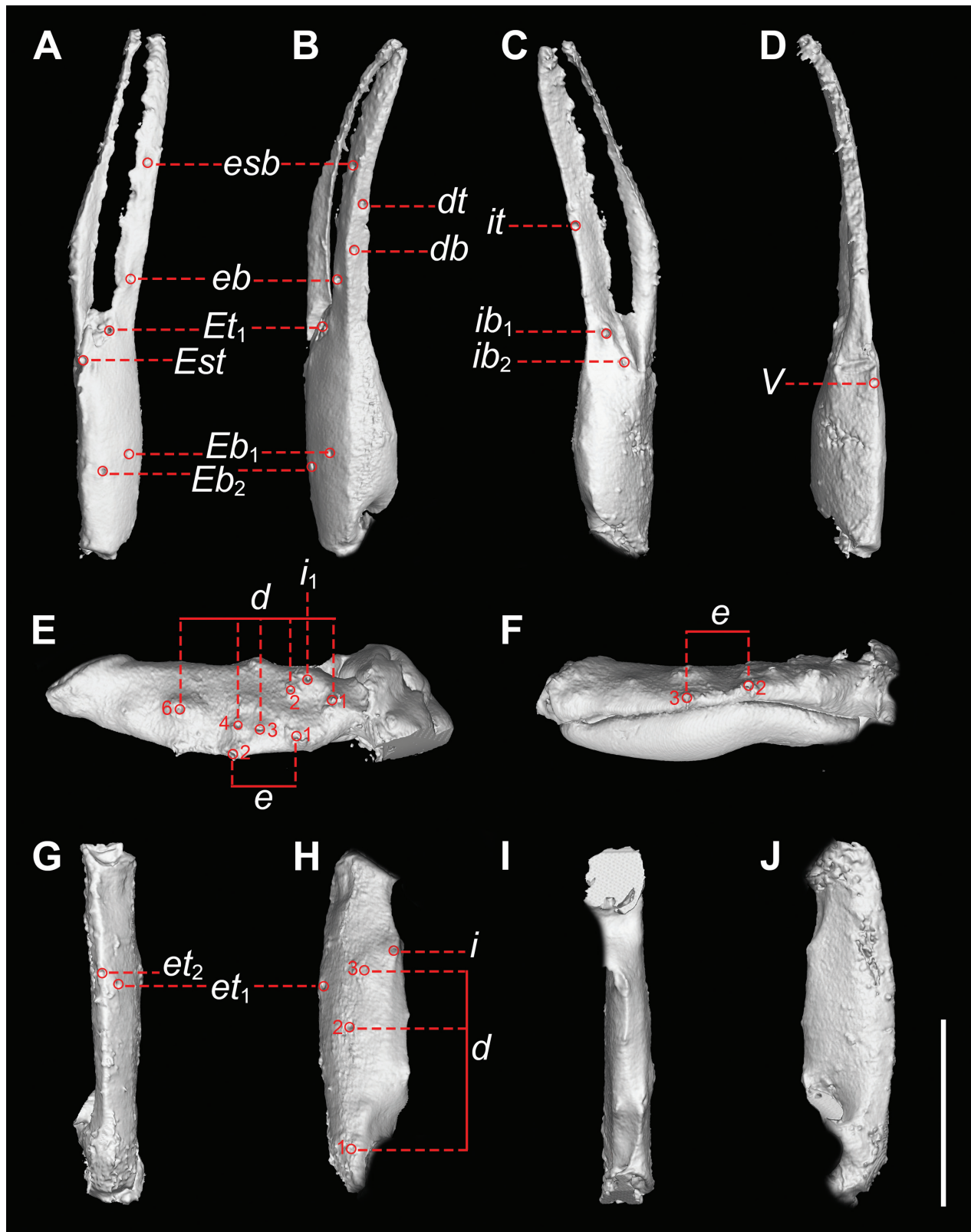


Figure 10. *Chaerilobuthus bruckschi* Lourenço, 2015, one juv. (NIGP 201162), micro-CT reconstruction of pedipalp trichobothrial pattern, dorsal, lateral and ventral aspects. A–D, chela. E, F, femur. G–J, patella. Scale bars: 500 μ m.

d_6 (Figs 13A, 16). Patella with four trichobothria visible, including three d and one i trichobothria; trichobothrium i_1 situated distal to trichobothrium d_3 (Figs 13B, 16). Chela with eight trichobothria visible; fixed finger with two d ,

two e and one i trichobothria; manus with two E and one V trichobothria; trichobothrium Et_1 situated distally on manus, almost aligned with or proximal to moveable finger condyle; trichobothrium eb situated on fixed finger, slightly

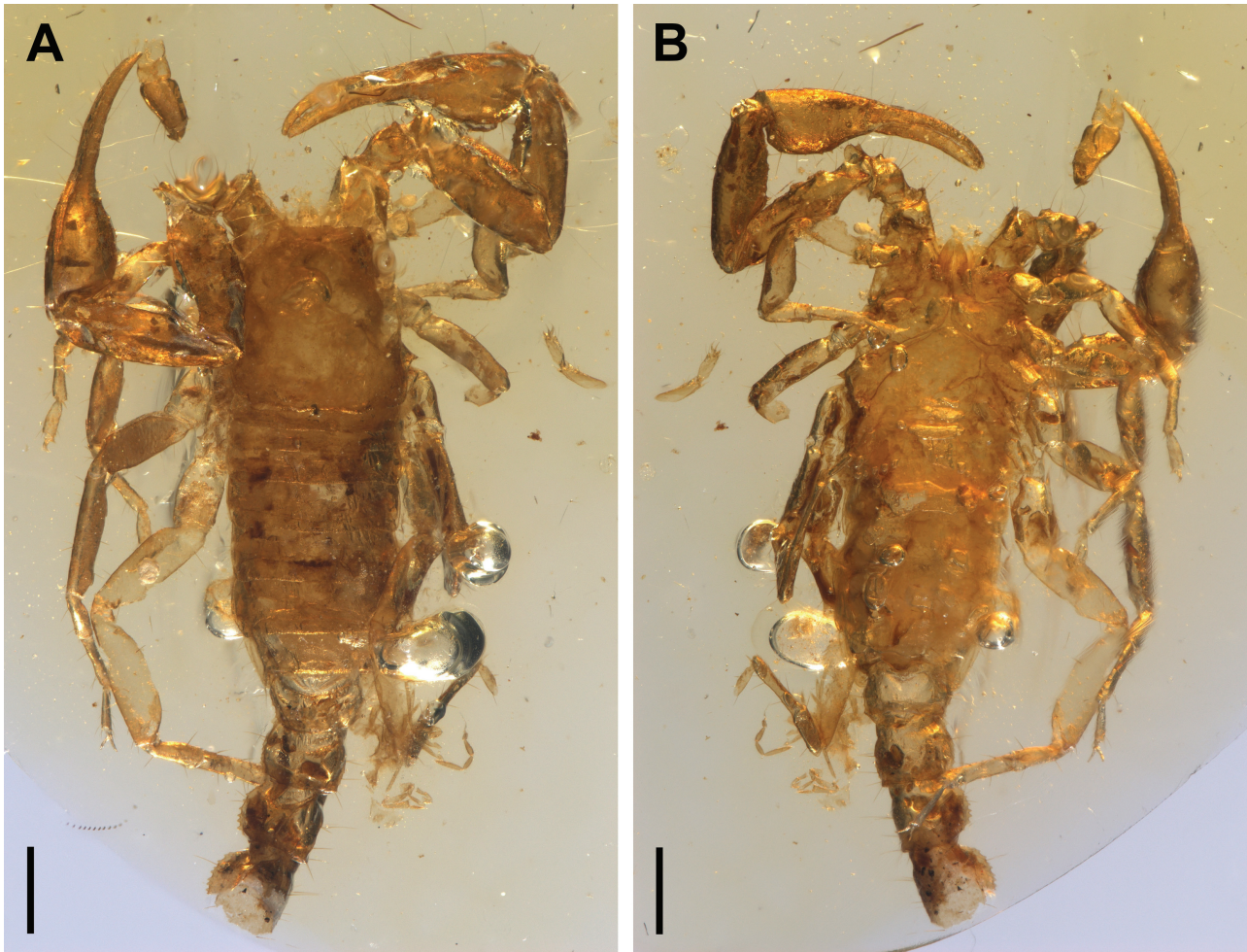


Figure 11. *Chaerilobuthus complexus* Lourenço, 2011, one juv. (NIGP 200655), habitus under incident light. A, dorsal aspect. B, ventral aspect. Scale bars: 500 μm .

distal to moveable finger condyle; trichobothrium *esb* situated medially on fixed finger; trichobothrium V_2 situated distally on manus and near retroventral carina (Figs 13C, D, 16).

Legs: Tibia lateral and ventral surfaces each with scattered macrosetae (Figs 12K, L, 15G). Basitarsi each with pair of spinule rows, comprising seven or eight relatively long spinules, distally (Figs 12H, L, 15G). Ungues moderately long, distinctly curved; dactyl pronounced, pointed (Figs 12K, L, 15G).

Pectines: Basal piece long, narrow (Figs 12B, 15D). Three marginal lamellae and four median lamellae; surface sparsely covered in macrosetae; longitudinal suture between marginal and median lamellae distinct. Fulcra absent or obsolete. Teeth rounded, distal half of each tooth occupied by sensilla field; peg sensilla very long, columnar with distinct pore.

Genital operculum: Two opercular sclerites narrow and completely separated, as long as pectinal plate (Fig. 12B).

Mesosoma: Pretergites surfaces almost smooth (Fig. 12E); post-tergites I–VI surfaces finely granular, acarinate (Fig. 12E);

tergite VII surface sparsely granular with four moderately developed carinae (paired dorsosubmedian and dorsolateral carinae) in posterior half of segment (Fig. 11A). Sternites surfaces smooth, with scattered macrosetae; posterior margins broadly recurved; respiratory spiracles (stigmata) small, ovoid, oblique (Figs 12F, 15C).

Metasoma: Segments I–III progressively increasing in length, I wider than long, others longer than wide (Fig. 12I, J). Segments I–III lateral and ventral surfaces each with few, short macrosetae; dorsal surfaces each with distinct depression. Segments I–III each with six distinct carinae (paired dorsosubmedian, dorsolateral and ventrolateral carinae); dorsosubmedian carinae distinct, markedly serrate; dorsolateral carinae distinct, moderately serrate; ventrolateral carinae obsolete on segment I, moderately developed on II and III.

Material examined: **MYANMAR:** Kachin State: Noiye Bum near Hukawng Valley, precise locality unknown, Cretaceous (Cenomanian) burmite: one juv. (sex unknown), mesosomal segments IV, V and telson absent (NIGP 200655), one juv. (sex unknown), sinistral pedipalp absent (NIGP 201160).

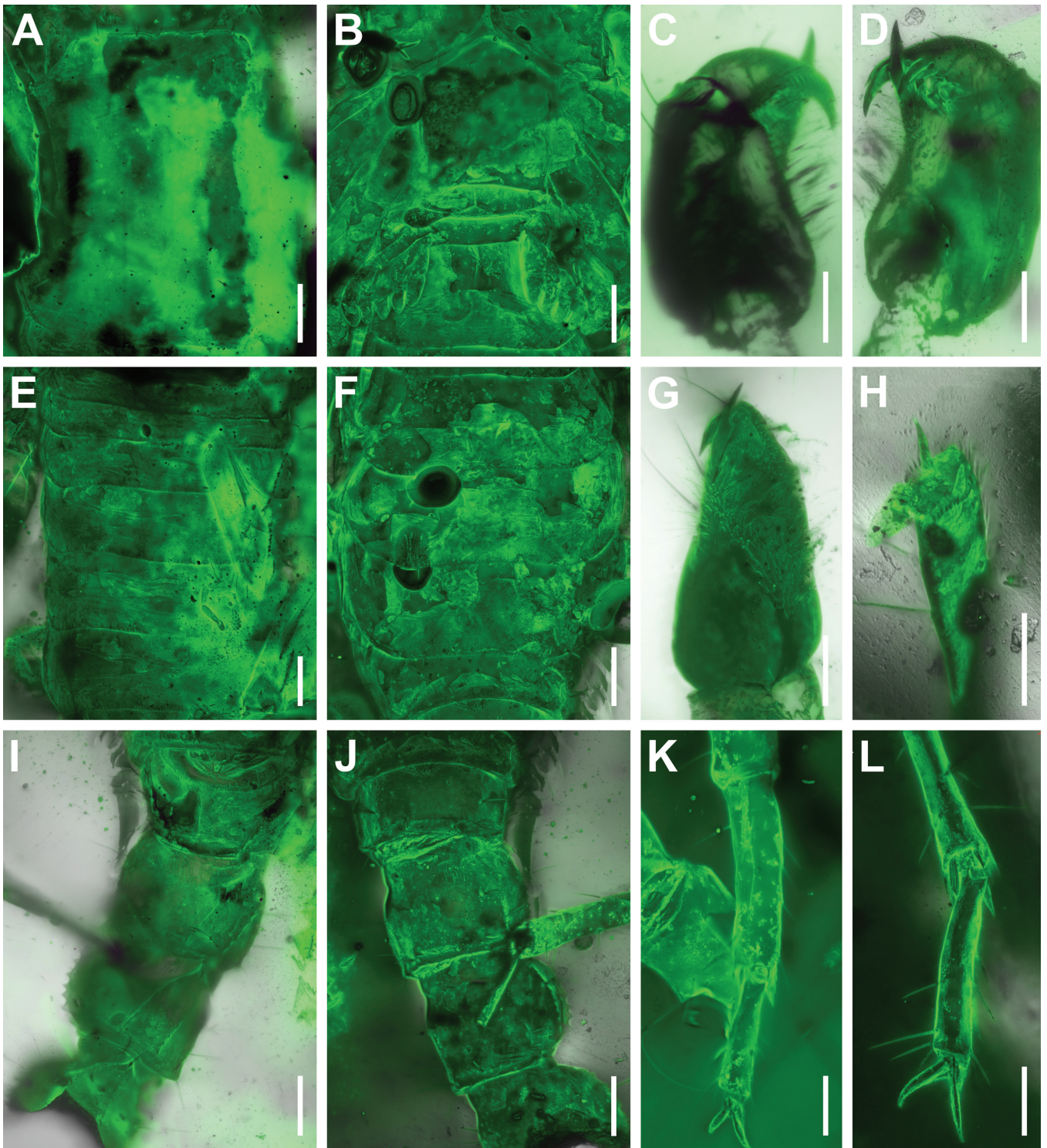


Figure 12. *Chaerilobuthus complexus* Lourenço, 2011, one juv. (NIGP 200655), morphology under confocal microscopy. A, carapace. B, sternum and pectines, ventral aspect. C, D, dextral chelicera, ventral and dorsal aspects. E, tergites. F, sternites IV–VI. G, sinistral chelicera, lateral aspect. H, leg IV basitarsus, distal paired spinule rows, lateral aspect. I, J, metasomal segments I–III, ventral and dorsal aspects. K, L, legs I and III tarsi, dorsal aspect. Scale bars: 200 μm (A, B, E, F, I, J); 100 μm (C, D, G, H, K, L).

Chaerilobuthus enigmaticus Lourenço, 2015

(Figs 17–21, 39)

Chaerilobuthus enigmaticus Lourenço, 2015: 44–48, figs 1–6.

Type material: Holotype: one juv. ♀ (personal collection of Patrick Müller, Kāshofen, Germany), Cretaceous (Cenomanian) burmite: **MYANMAR:** *Kachin State* (precise locality unknown).

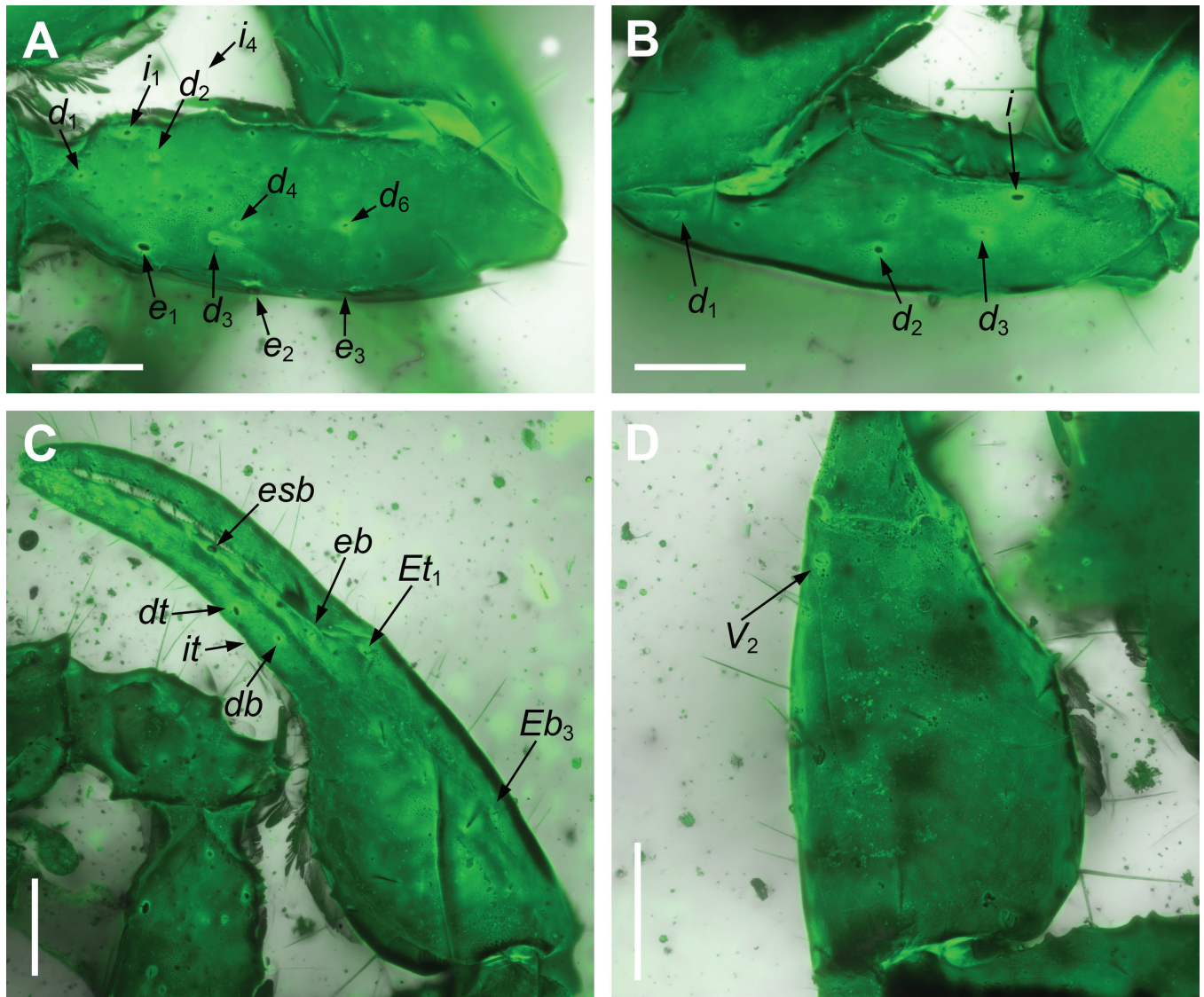


Figure 13. *Chaerilobuthus complexus* Lourenço, 2011, one juv. (NIGP 200655), pedipalp trichobothrial pattern under confocal microscopy. Scale bars: 200 μ m.

Diagnosis: The following combination of characters is diagnostic for *C. enigmaticus*: carapace anteromedian margin slightly posterior to anterolateral margins (Figs 17A and 18D); lateral ocelli not protruding, macular (Figs 18D, 20A); pedipalp chela moderately robust, manus globose, ratio of chela length : chela manus width less than 4 (Figs 18A, B, 21A); pectines each with five teeth (Figs 18I, 20F, G); ratio of metasomal segment IV : V length greater than 2 (Figs 18A, B, 20H, I, L); metasomal segment V dorsosubmedian carinae slightly serrate (Fig. 20L); telson vesicle bulbous, aculeus very short and moderately curved (Figs 18G, J, K, 19).

Description: Based on the material examined (NIGP 201158, 201159).

Carapace: Posterior width less than length ($L/PW = 1.16$, Appendix 2). Anterior margin with few, short macrosetae; anteromedian depression not visible; anterosubmedial depressions absent; lateral ocular carinae absent; posteromedian

and posteromarginal sulci obsolete; surfaces almost smooth to sparsely and finely granular (Fig. 20A, B). Median ocular tubercle situated anteromedially; median ocelli absent; one pair of large posterolateral major lateral ocelli present.

Coxosternal region: Surface smooth, sparsely covered in macrosetae (Figs 20E, 39B, C). Leg I maxillary lobes (coxapophyses) distal margins slightly curved, dilate anteriorly and adorned with serrula comprising c. 15 denticles (Fig. 39B, C). Sternum pentagonal; lateral margins sublinear, parallel; ventral surface flat, without distinct concave region or median sulcus; posteromedian depression wide, shallow (Figs 17A, 20E).

Chelicerae: Fixed finger and manus, prolateral and ventral surfaces each with numerous long, dense macrosetae (Fig. 18E, F). Chelical dentition partly visible, moveable finger with long dorsal distal (dd) denticle, small dorsal subdistal denticle, stout dorsal median denticle, long ventral distal (vd) denticle and four or five small ventral accessory (va) denticles; fixed finger with

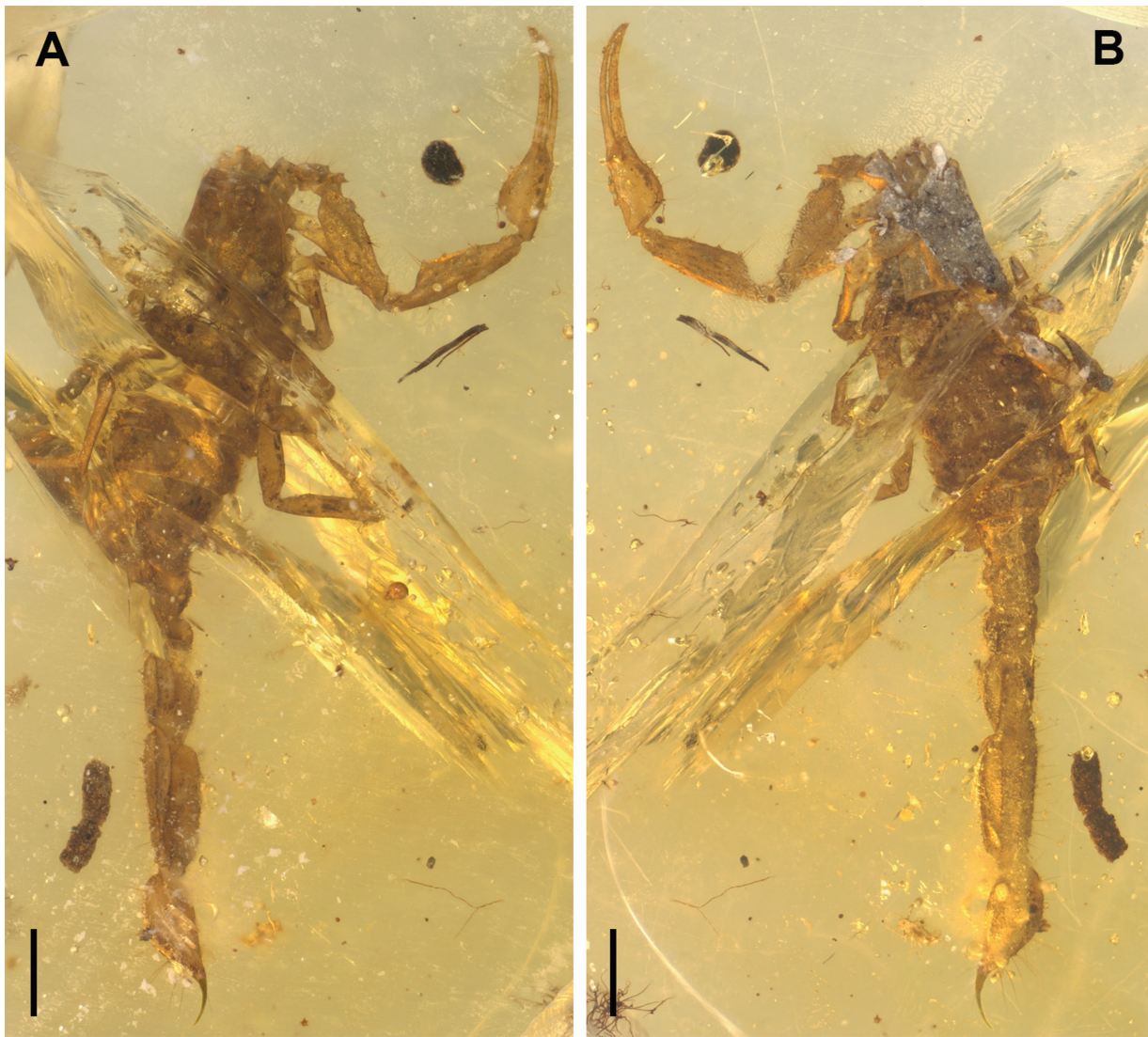


Figure 14. *Chaerilobuthus complexus* Lourenço, 2011, one juv. (NIGP 201160), habitus under incident light. A, dorsal aspect. B, ventral aspect. Scale bars: 1 mm.

long distal denticle and small subdistal denticle (Figs 18E, F, 20C). Moveable finger with prominent serrula comprising long spinules in proximal three-quarters (Fig. 18F).

Pedipalps: Segments moderately robust; surfaces sparsely covered by short microsetae and few macrosetae (Figs 18A, B, 21A). Femur with four carinae evident; prodorsal and proventral carinae distinct, serrate; retrodorsal and retroventral carinae smooth, costate (Figs 18A, 21A, C). Patella with five carinae evident; prodorsal carina obsolete, comprising several tubercles; prolateral surface, dorsoventral 'vaulted' projection ('anterior process') distinct with prominent pair of apophyses or tubercles ('patellar spurs'), each possessing one macroseta; retrodorsal and retroventral carinae smooth, costate (Figs 18A, B, 21A, D). Chela relatively robust (CL/CW = 3.22 or 3.55, Appendix 2); manus globose; chela with six carinae evident; digital carina complete, distinct, granular medially, becoming costate proximally and distally; dorsomedian carina reduced to few granules at base of fixed finger, becoming obsolete proximally on manus; prodorsal carina

distinct, comprising several prominent spiniform granules; promedian and proventral carinae obsolete, each comprising few isolated granules; retroventral carina obsolete; dorsal secondary, subdigital, retromedian and ventromedian carinae absent or obsolete (Figs 18A, B, 21A, B, E, F). Only fixed finger distal denticle subrows visible, oblique, slightly imbricate and separated by large serrate prolateral and retrolateral denticles (Fig. 21A). Trichobothrial pattern Type D, β configuration. Femur with three trichobothria visible: two *d* and one *i* trichobothria (Fig. 21C). Patella with six trichobothria visible, including three *d*, one *i*, and two *e* trichobothria; trichobothrium *i*₁ situated distal to trichobothrium *d*₃ (Fig. 21A, D). Chela with 10 trichobothria visible; fixed finger with two *d* and one *i* trichobothria; manus with four *E* and one *V* trichobothria; trichobothrium *Et*₁ situated distally on manus, almost aligned with or proximal to moveable finger condyle; trichobothrium *eb* situated on fixed finger, slightly distal to moveable finger condyle; trichobothrium *esb* situated medially on fixed finger; trichobothrium *V*₂ situated distally on manus and near retroventral carina.

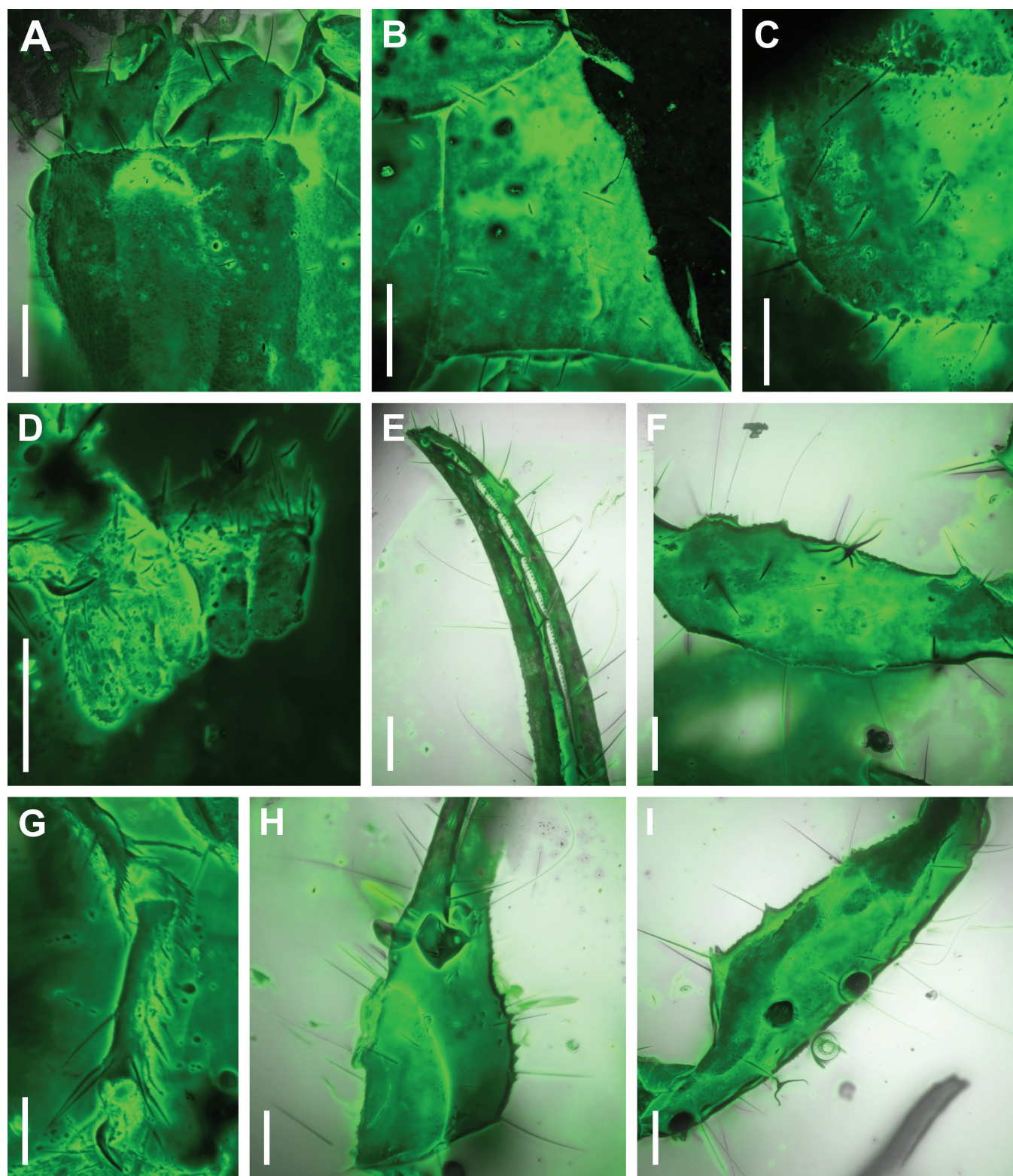


Figure 15. *Chaerilobuthus complexus* Lourenço, 2011, one juv. (NIGP 201160), morphology under confocal microscopy. A, lateral ocelli. B, sternum. C, respiratory spiracle. D, dextral pecten, ventral aspect. E, pedipalp chela fingers, lateral aspect. F, dextral pedipalp femur, dorsal aspect. G, leg III tarsus, lateral aspect. H, dextral pedipalp chela manus, ventral aspect. I, dextral pedipalp patella, ventral aspect. Scale bars: 200 μ m.

Legs: Tibia lateral and ventral surfaces each with scattered macrosetae (Fig. 18C, 20J, K). Basitarsi each with pair of spinule rows, comprising c. 10 relatively long spinules, distally. Telotarsi

each with slightly irregular pair of ventrosubmedian spinule rows, comprising relatively long spinules. Ungues moderately long, distinctly curved; dactyl pronounced, pointed.

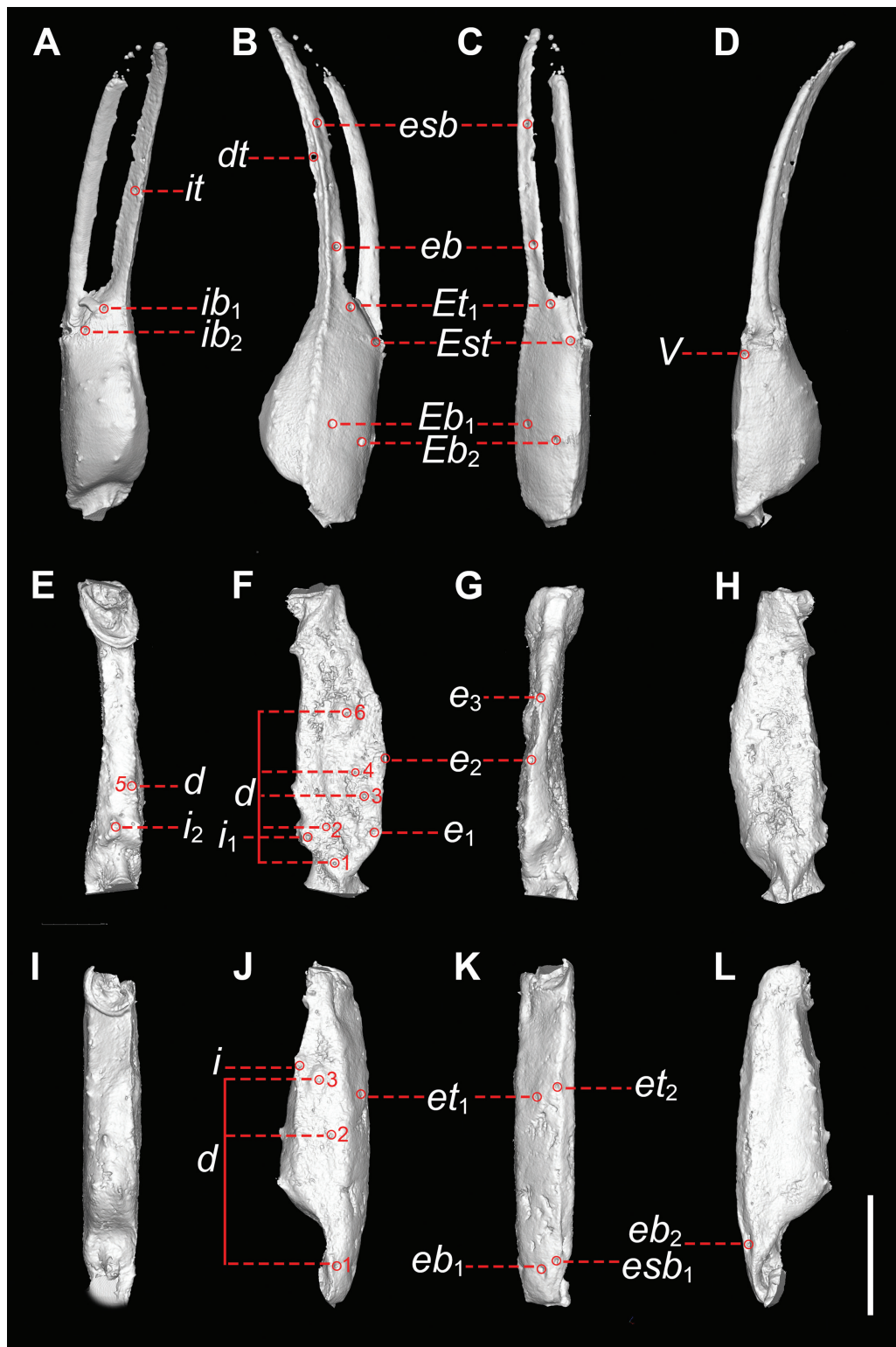


Figure 16. *Chaerilobuthus complexus* Lourenço, 2011, one juv. (NIGP 201160), micro-CT reconstruction of pedipalp trichobothrial pattern, dorsal, lateral and ventral aspects. A–D, chela. E–H, femur. I–L, patella. Scale bars: 500 μ m.

Pectines: Basal piece long, narrow (Fig. 20F). Three marginal lamellae and four median lamellae; surface sparsely covered in macrosetae; longitudinal suture between marginal and median lamellae distinct (Figs 18I, 20G). Fulcra absent or obsolete. Teeth rounded, distal three-quarters of each tooth occupied by sensillar field; peg sensilla very long, columnar (Fig. 20G).

Genital operculum: Two opercular sclerites narrow and completely separated, as long as pectinal plate; surfaces with several microsetae (Fig. 20E).

Mesosoma: Pretergites surfaces almost smooth (Fig. 19A); post-tergites I–VI surfaces finely granular, acarinate (Fig. 19A); tergite

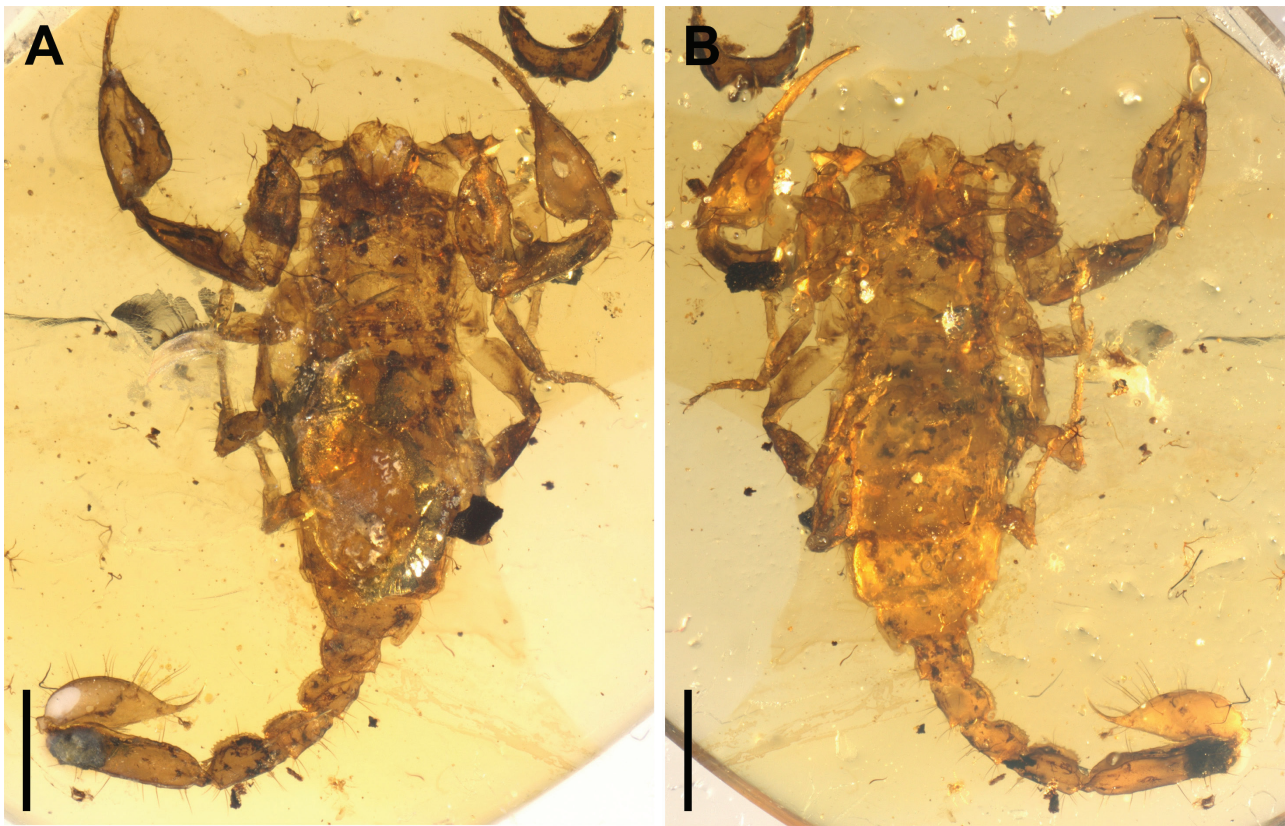


Figure 17. *Chaerilobuthus enigmaticus* Lourenço, 2015, one juv. (NIGP 201158), habitus under incident light. A, dorsal aspect. B, ventral aspect. Scale bars: 1 mm.

VII surface sparsely granular, with four slightly serrate carinae (paired dorsosubmedian and dorsolateral carinae) in posterior half of segment (Fig. 20H). Sternites surfaces smooth, with scattered macrosetae; posterior margins broadly recurved; respiratory spiracles small, ovoid, oblique (Figs 18H, 20D).

Metasoma: Segments I–V progressively increasing in length, I wider than long, others longer than wide (Fig. 18J, K, 20H, I, L). Segments I–V lateral and ventral surfaces each with few, short macrosetae (Fig. 18J, K, 20H, I, L); I–IV dorsal surfaces each with distinct depression (Figs. 18K, 20H). Segment I with six distinct carinae (paired dorsosubmedian, dorsolateral, and ventrolateral carinae), segments II–V each with eight distinct carinae (paired dorsosubmedian, dorsolateral, ventrolateral, and ventrosubmedian carinae); dorsosubmedian carinae distinct on all segments, markedly serrate on II–IV, moderately serrate, converging posteriorly on I and V; dorsolateral carinae distinct, moderately serrate on segments I, II and V, slightly serrate on III and IV; ventrolateral carinae distinct, moderately serrate on segments I–IV, markedly serrate on segment V; ventrosubmedian carinae absent on segment I, obsolete on II and III, distinct, moderately serrate on IV and V, and converging posteriorly on V (Fig. 18J, K, 20H, I, L).

Telson: Vesicle bulbous; dorsal surface flat; lateral and ventral surfaces relatively smooth with several macrosetae; (Figs 18G, 19A, B); subaculear tubercle absent; prominent subaculear setal pair, moderately long. Aculeus short, shallowly curved; base narrow, less than one-third vesicle width.

Material examined: **MYANMAR:** Kachin State: Noiye Bum near Hukawng Valley, precise locality unknown, Cretaceous (Cenomanian) burmite: two juv. (sex unknown) (NIGP 201158, 201159).

Chaerilobuthus gigantosternum Lourenço, 2016

(Figs 22–24)

Chaerilobuthus gigantosternum Lourenço, 2016: 68–72, figs 12, 13, 15, 16.

Type material: Holotype: one juv. (sex unknown) (Geologisch-Paläontologisches Institut, University of Hamburg, Germany: 11037-1 GPIH4566), Cretaceous (Cenomanian) burmite: **MYANMAR:** Kachin State (precise locality unknown).

Diagnosis: The following combination of characters is diagnostic for *C. gigantosternum*: carapace relatively long ($L/Pw = 1.25$); carapace anteromedian margin slightly convex and anterosubmedian margin slightly concave (Figs 22A, 23A); carapace posterior margin linear; lateral ocelli not protruding, macular (Fig. 23A); sternum relatively wide; cheliceral moveable finger with distinct serrula; pedipalp chela slender, manus elongate, with ratio of chela length : chela manus width greater than 4 (Fig. 24); pectines relatively large, each with five teeth (Fig. 23F); ratio of metasomal segment IV : V length less than 2 (Fig. 23H, I).

Description: Based on the material examined (NIGP 200654).

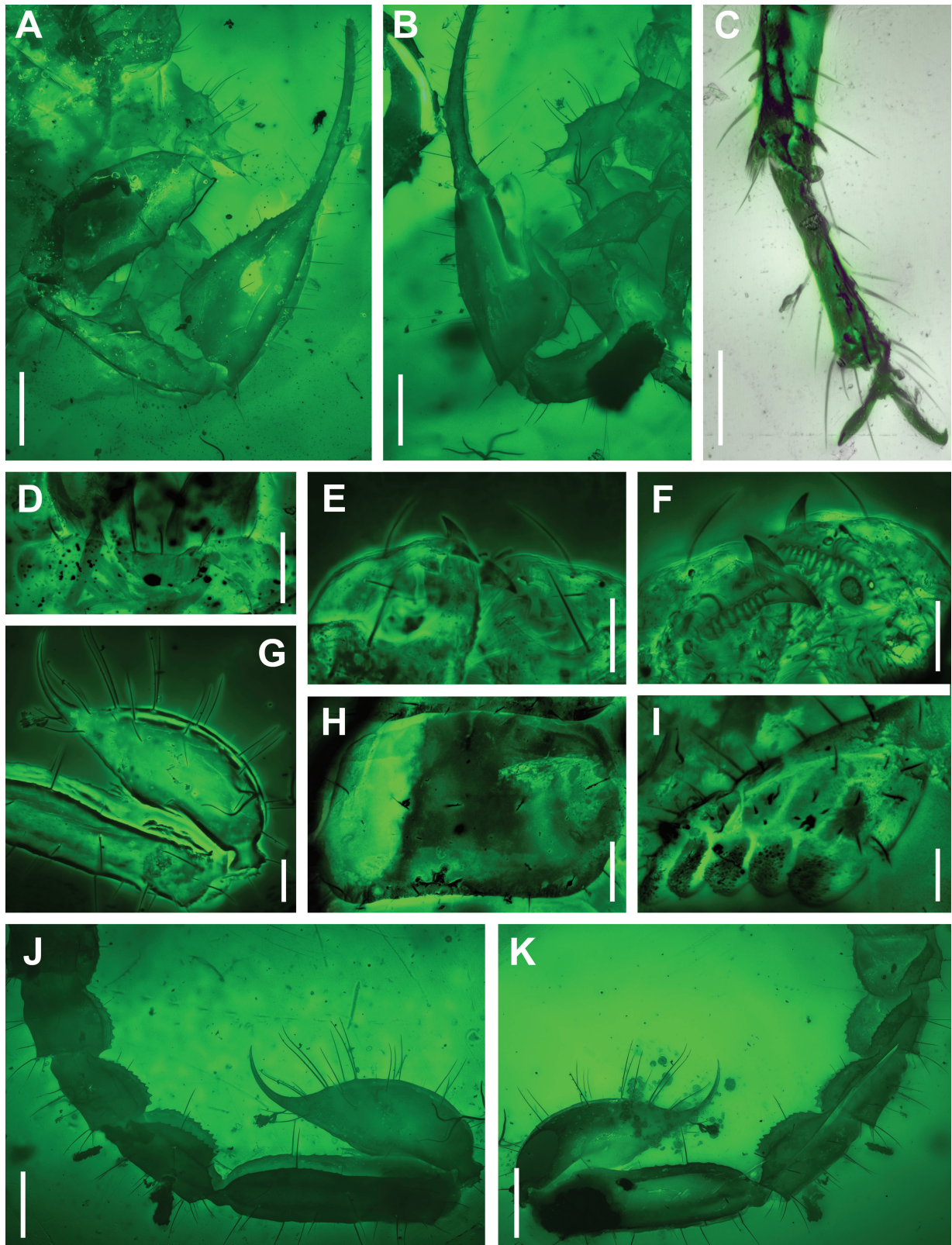


Figure 18. *Chaerilobuthus enigmaticus* Lourenço, 2015, one juv. (NIGP 201158), morphology under epifluorescence (A, B, J, K) and confocal microscopy (C–I). A, B, dextral pedipalp, dorsal and ventral aspects. C, leg II tarsus, ventral aspect. D, lateral ocelli. E, F, cheliceral fingers, dorsal and ventral aspects. G, telson, lateral aspect. H, sternite V. I, dextral pecten, ventral aspect. J, K, metasoma and telson, lateral aspect. Scale bars: 400 μm (A, B, J, K); 100 μm (C, E, F); 200 μm (D, G, H, I).

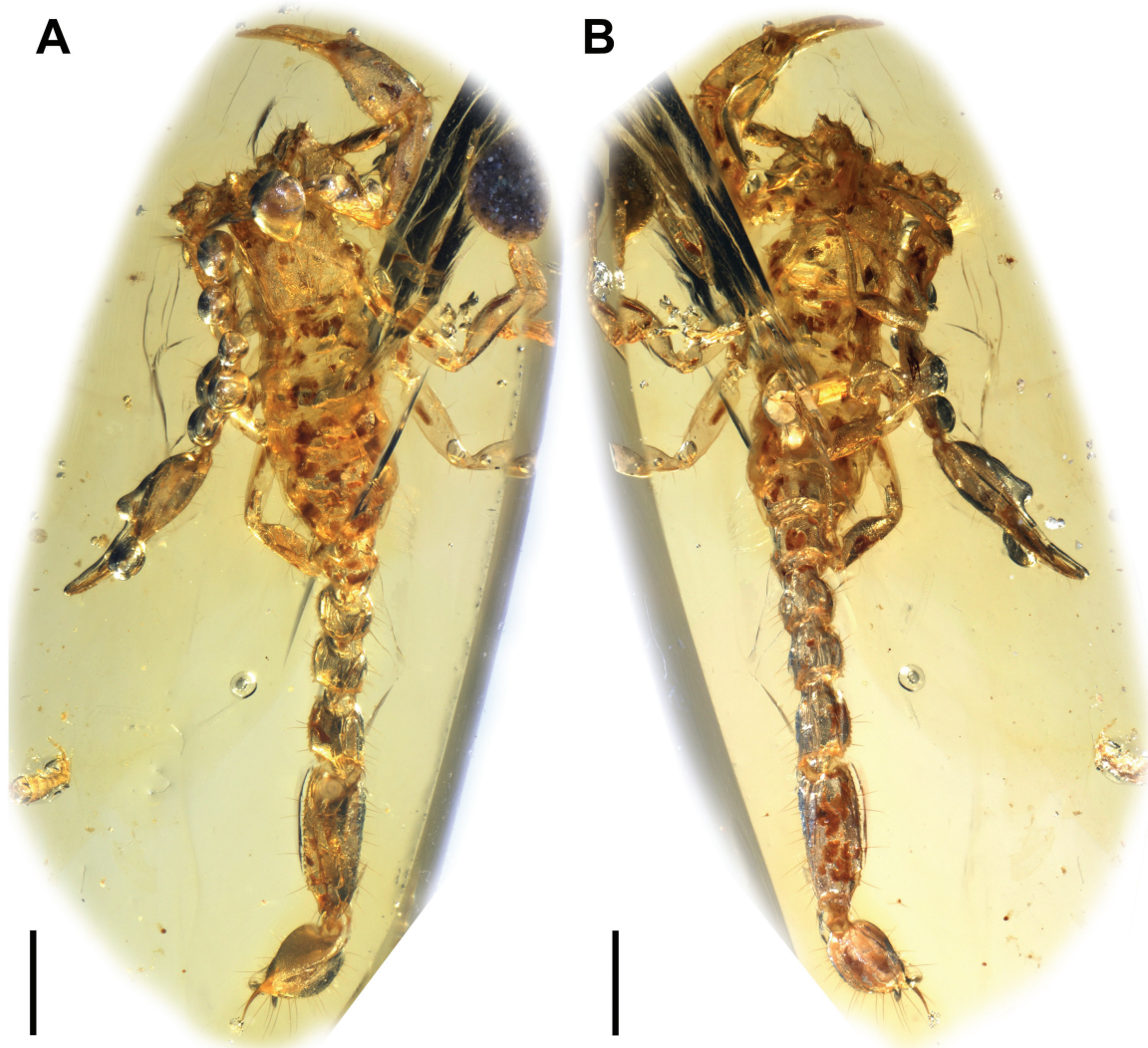


Figure 19. *Chaerilobuthus enigmaticus* Lourenço, 2015, one juv. (NIGP 201159), habitus under incident light. A, dorsal aspect. B, ventral aspect. Scale bars: 1 mm.

Carapace: Anterior margin of carapace with few, short microsetae; anteromedian depression not visible; anterosubmedial depressions absent; lateral ocular carinae distinct; posteromedian and posteromarginal sulci not distinct; surfaces almost smooth to sparsely and finely granular (Fig. 23A). Median ocular tubercle situated anteromedially; median ocelli absent; one pair of large posterolateral major lateral ocelli present.

Coxosternal region: Surface smooth, sparsely covered in few macrosetae (Fig. 23B). Distal margins of leg I maxillary lobes (coxapophyses) slightly curved and dilate anteriorly, adorned with serrula comprising c. 13 spiny denticles. Sternum pentagonal; lateral margins sublinear, parallel, ventral surface flat, without distinct concave region or median sulcus; posteromedian depression wide, shallow.

Chelicerae: Fixed finger and manus, prolateral and ventral surfaces each with numerous macrosetae. Cheliceral dentition partly visible, moveable finger strongly overlapping fixed finger; moveable finger with long dorsal distal (dd) denticle, small dorsal subdistal

denticle, stout dorsal median denticle and long ventral distal (vd) denticle; fixed finger with long distal denticle. Moveable finger with prominent serrula, comprising c. 10 long spinules and extending almost entire length of ventral surface (Fig. 23C).

Pedipalps: Segments gracile (Figs 22, 23). Femur with three carinae evident; prodorsal, proventral and retrodorsal carinae distinct, smooth and costate. Patella with three carinae evident; retroventral carinae distinct, smooth and costate; prolateral surface, dorsoventral ‘vaulted’ projection (‘anterior process’) distinct, with obsolete pair of apophyses or tubercles (‘patellar spurs’), each possessing one macroseta. Chela relatively slender ($CL/CW = 4.37$, Appendix 2); manus elongate; chela with three carinae evident; digital carina complete, distinct, granular medially, becoming costate proximally and distally; prodorsal carina distinct, smooth; retroventral carina obsolete, smooth and costate; other carinae absent or obsolete. Chela finger dentition not visible. Trichobothrial pattern Type D, β configuration (Fig. 24). Femur with 10 trichobothria visible, five d , three e , and two i trichobothria, trichobothrium e_1 situated proximal

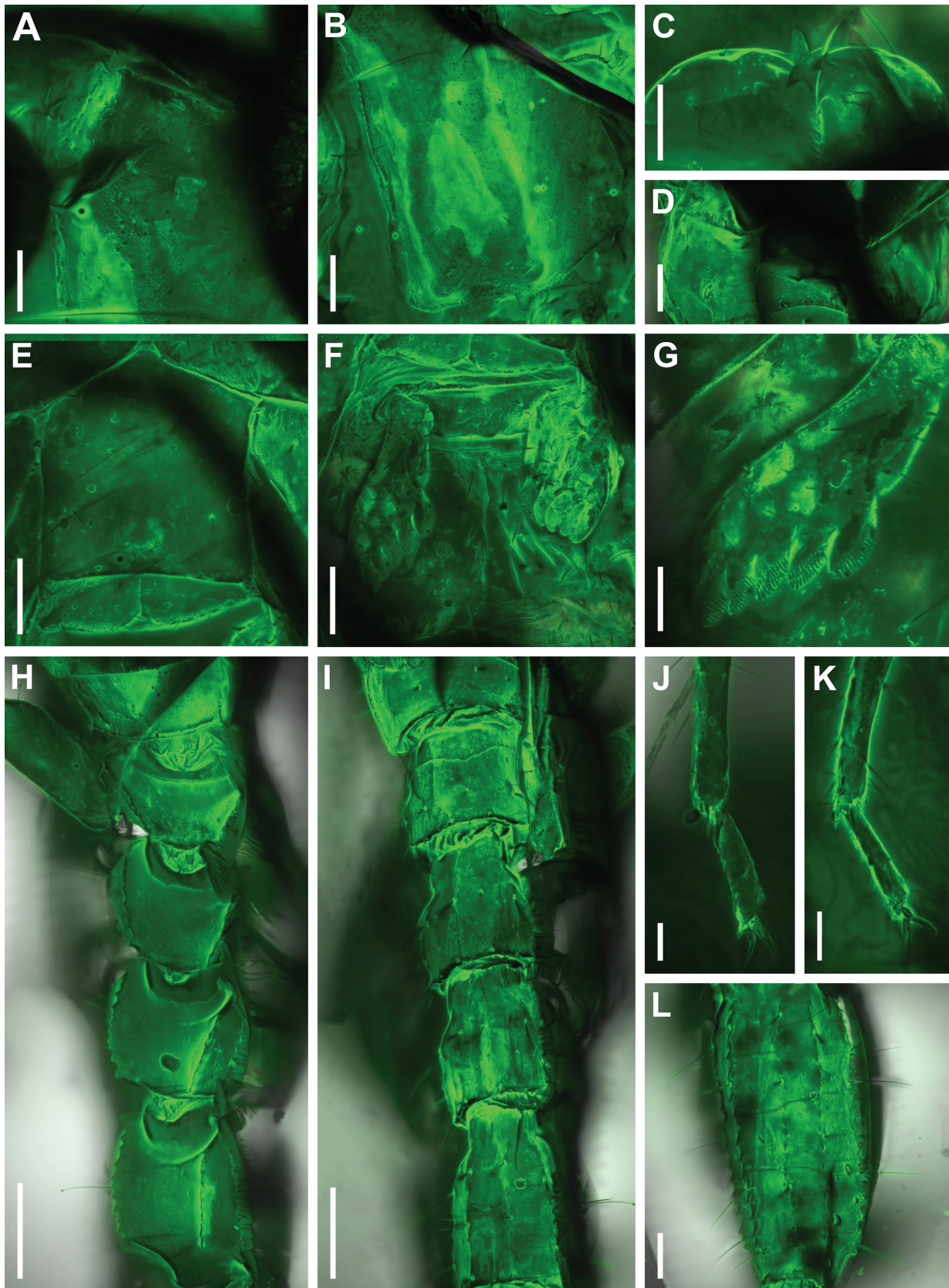


Figure 20. *Chaerilobuthus enigmaticus* Lourenço, 2015, one juv. (NIGP 201159), morphology under confocal microscopy. A, lateral ocelli. B, carapace. C, cheliceral fingers, dorsal aspect. D, respiratory spiracle. E, sternum and genital operculum. F, pectinal plate, pectines and sternite III, ventral aspect. G, dextral pecten, ventral aspect. H, I, metasomal segments I–IV, dorsal and ventral aspects. J, K, legs I and II tarsi, lateral aspect. L, metasomal segment V, ventral aspect. Scale bars: 100 μ m (A, C, G, J, K); 200 μ m (B, D, E, F, L); 400 μ m (H, I).

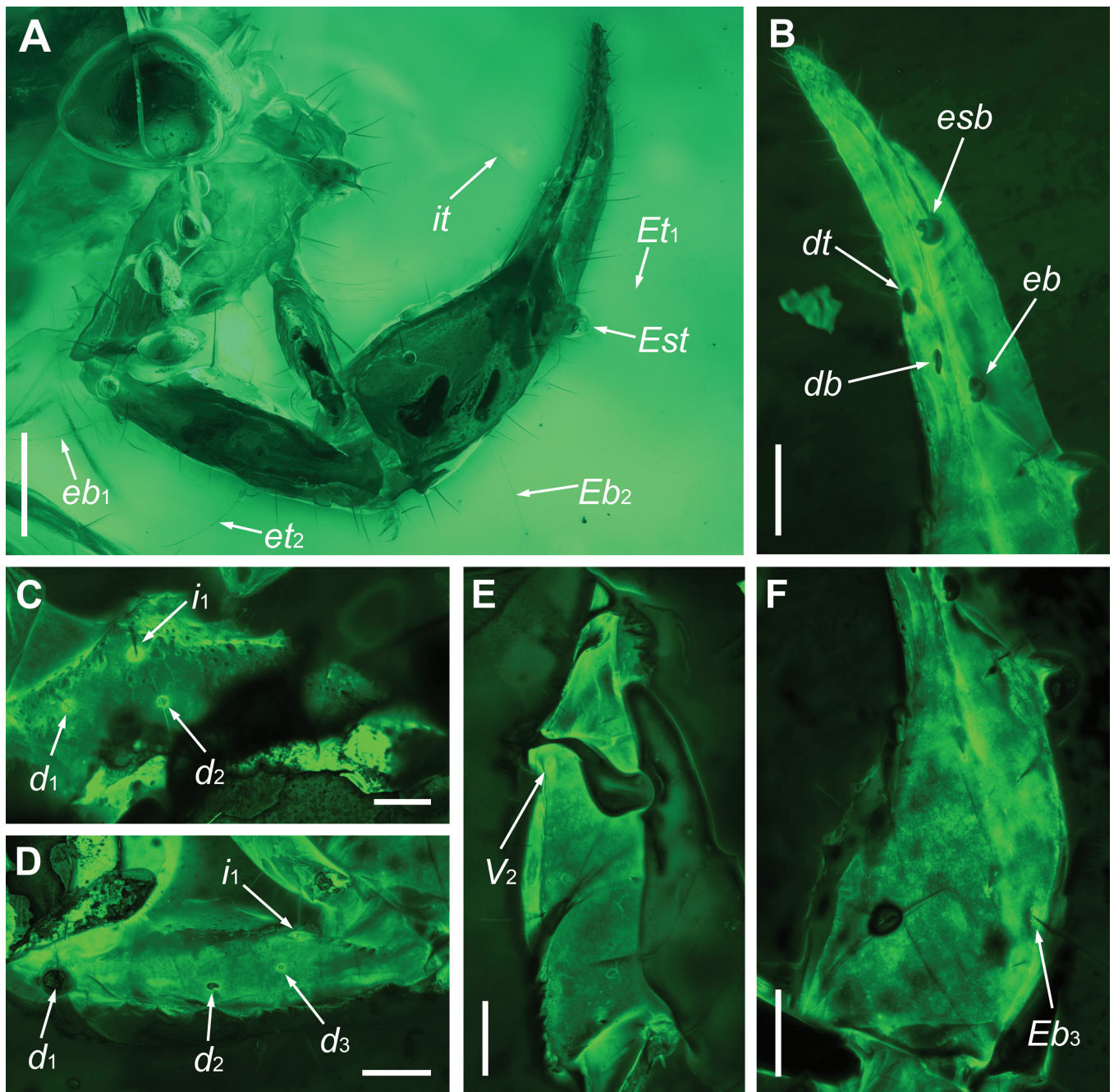


Figure 21. *Chaerilobuthus enigmaticus* Lourenço, 2015, one juv. (NIGP 201159), pedipalp trichobothrial pattern under epifluorescence (A) and confocal microscopy (B–F). Scale bars: 400 μ m (A); 200 μ m (B–F).

to trichobothrium d_3 ; trichobothrium e_3 situated dorsal to trichobothrium d_6 . Patella with eight trichobothria visible, including three d , one i , and four e trichobothria; trichobothrium i_1 situated distal to trichobothrium d_3 . Chela with 12 trichobothria visible; fixed finger with two d , two e , and three i trichobothria; manus with four E and one V trichobothria; trichobothrium Et_1 situated distally on manus, almost aligned with or proximal to moveable finger condyle; trichobothrium eb situated on fixed finger, slightly distal to moveable finger condyle; trichobothrium esb situated medially on fixed finger; trichobothrium V_2 situated distally on manus and near retroventral carina.

Legs: Tibial lateral and ventral surfaces each with scattered macrosetae (Fig. 23J, K). Basitarsi each with pair of spinule rows, comprising c. 12 relatively long spinules, distally. Telotarsi each with slightly irregular pair of ventrosulmedian spinule rows, comprising relatively long spinules. Ungues moderately long, distinctly curved; dactyl pronounced, pointed.

Pectines: Basal piece not visible. Three marginal lamellae and four median lamellae; surface sparsely covered in macrosetae; longitudinal suture between marginal and median lamellae distinct (Fig. 23E, F). Fulcra absent or obsolete. Teeth rounded, distal

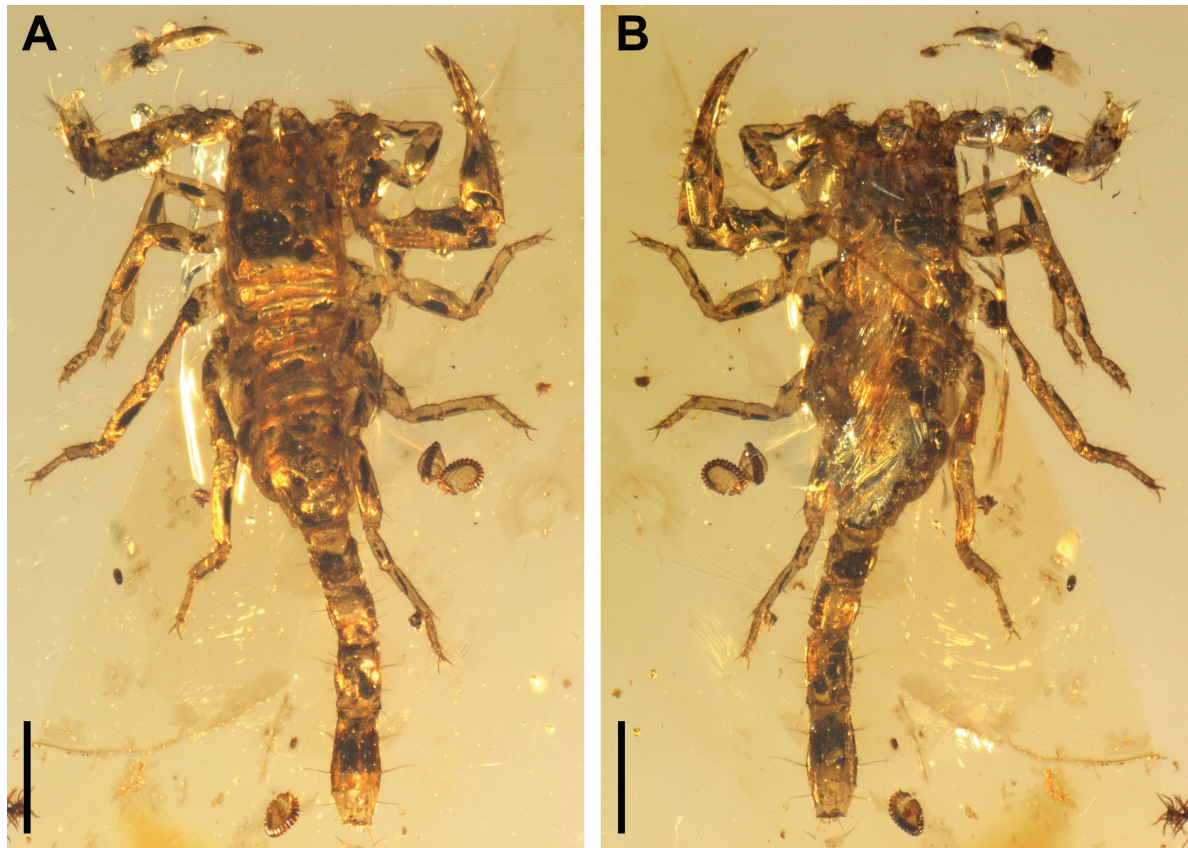


Figure 22. *Chaerilobuthus gigantosternum* Lourenço, 2016, one juv. (NIGP 200654), habitus under incident light. A, dorsal aspect. B, ventral aspect. Scale bars: 1 mm.

three-quarters of each tooth occupied by sensillar field; peg sensilla very long and columnar.

Genital operculum: Opercular sclerites not visible.

Mesosoma: Pretergites surfaces almost smooth (Fig. 23D); posttergites I–VI surfaces finely granular, acarinate (Fig. 23D); tergite VII surface sparsely granular with four carinae (paired dorsosubmedian and dorsolateral carinae) in posterior half of segment (Fig. 23D). Sternites surfaces smooth, with scattered macrosetae; respiratory spiracles (stigmata) small, ovoid to round (Fig. 23E).

Metasoma: Segments I–V progressively increasing in length, I wider than long, others longer than wide (Fig. 23H, I). Segments I–V lateral and ventral surfaces each with few, short macrosetae; I–IV dorsal surfaces each with distinct depression. Segments I–III each with six distinct carinae (paired dorsosubmedian, dorsolateral, and ventrolateral carinae), IV and V each with eight distinct carinae (paired dorsosubmedian, dorsolateral, ventrolateral, and ventrosubmedian carinae); dorsosubmedian and dorsolateral carinae distinct, slightly serrate; ventrolateral carinae distinct, costate-granular; ventrosubmedian carinae obsolete.

Material examined: **MYANMAR:** *Kachin State:* Noiye Bum near Hukawng Valley, precise locality unknown, Cretaceous (Cenomanian) burmite: first instar juv. (sex unknown) (NIGP

200654). Hypothesized to be in first instar based on small size and weak development of carinae and sulci.

Chaerilobuthus hansgeorgmuelleri Lourenço, 2019

(Figs 25–26, 39)

Chaerilobuthus hansgeorgmuelleri Lourenço, 2019 in Lourenço and Velten, 2019: 2–10, figs 1–8.

Type material: Holotype: one juv. ♀ (personal collection of Hans-Georg Müller, Gelsenkirchen, Germany), Cretaceous (Cenomanian) burmite: **MYANMAR:** *Kachin State* (precise locality unknown).

Diagnosis: The following combination of characters is diagnostic for *C. hansgeorgmuelleri*: carapace length less than posterior width (Fig. 26A); carapace anterior margin slightly depressed submedially (Fig. 26A); lateral ocelli protruding (Fig. 26A); sternum relatively wide (Fig. 26B); pectines each with five teeth (Fig. 26B); pedipalp patella trichobothrium *i* aligned with trichobothrium *d*₃ (Fig. 26F); pedipalp chela robust, manus globose, ratio of chela length : chela manus width less than 3 (Fig. 26C).

Description: Based on the material examined (NIGP 201164).

Carapace: Length less than posterior width ($L/PW = 0.94$). Anteromedian depression narrow, shallow; anterosubmedial

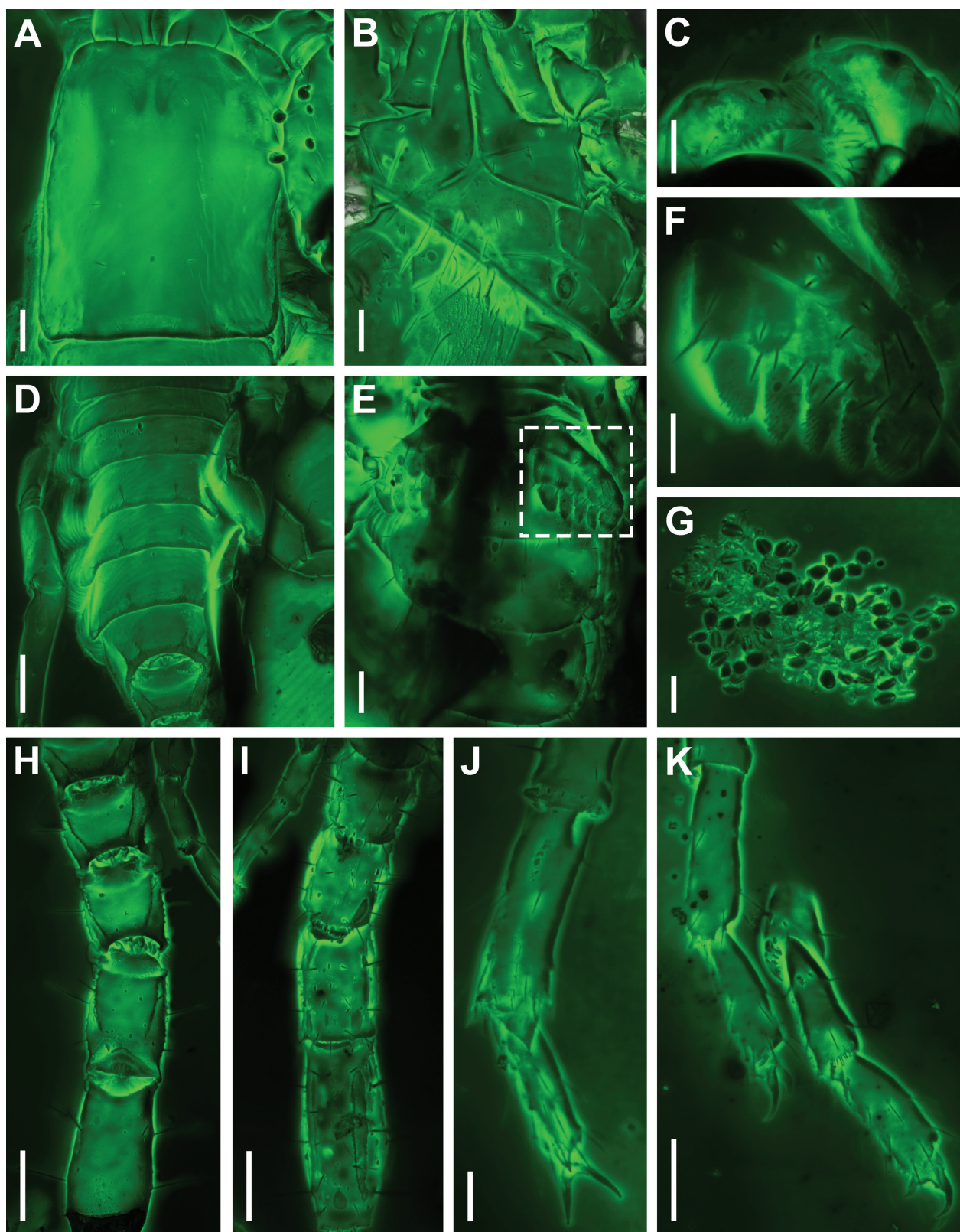


Figure 23. *Chaerilobuthus gigantosternum* Lourenço, 2016, one juv. (NIGP 200654), morphology under confocal microscopy. A, carapace. B, coxosternal region. C, chelicera, ventral aspect. D, tergites. E, pectines and sternites, ventral aspect. F, sinistral pecten, ventral aspect. G, pollen around scorpion. H, I, metasomal segments I–IV, dorsal and ventral aspects. J, dextral leg II tarsus, ventral aspect. K, sinistral legs I and II tarsi, lateral aspect. Scale bars: 100 μm (A, B, E, K); 50 μm (C, F, G, J); 200 μm (D, H, I).

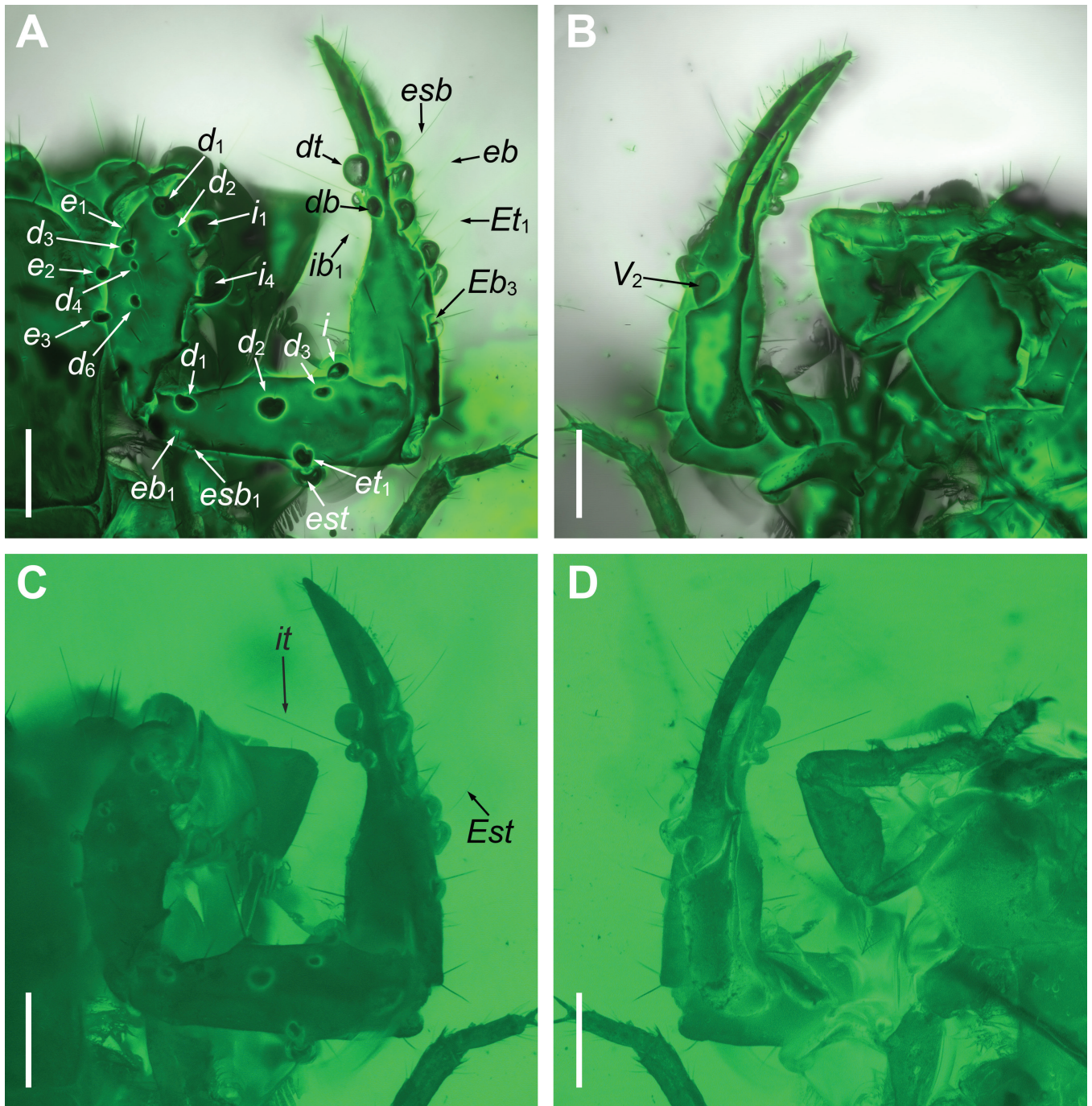


Figure 24. *Chaerilobuthus gigantosternum* Lourenço, 2016, one juv. (NIGP 200654), pedipalp trichobothrial pattern under confocal microscopy (A, B) and epifluorescence (C, D). Scale bars: 200 μ m.

depressions absent; lateral ocular carinae absent; posteromedian and posteromarginal sulci distinct; surfaces almost smooth to sparsely and finely granular (Fig. 26A). Median ocular tubercle situated anteromedially; median ocelli absent; one pair of large posterolateral major lateral ocelli present.

Coxosternal region: Surface smooth, sparsely covered in macrosetae (Figs 25B, 39G). Leg I maxillary lobes (coxapophyses) distal margins slightly curved, dilate anteriorly and adorned with serrula comprising c. 15–25 denticles (Fig. 39G). Sternum broad, pentagonal; lateral margins sublinear,

parallel; ventral surface flat, without distinct concave region or median sulcus; posteromedian depression wide, shallow (Fig. 26B).

Chelicerae: Fixed finger and manus, prolateral and ventral surfaces each with numerous long, dense macrosetae (Fig. 25A). Cheliceral dentition not clearly visible.

Pedipalps: Segments moderately robust; surfaces sparsely covered by short microsetae (Fig. 25A). Femur with three carinae evident; dorsal surface with several coarse granules; prodorsal and proventral

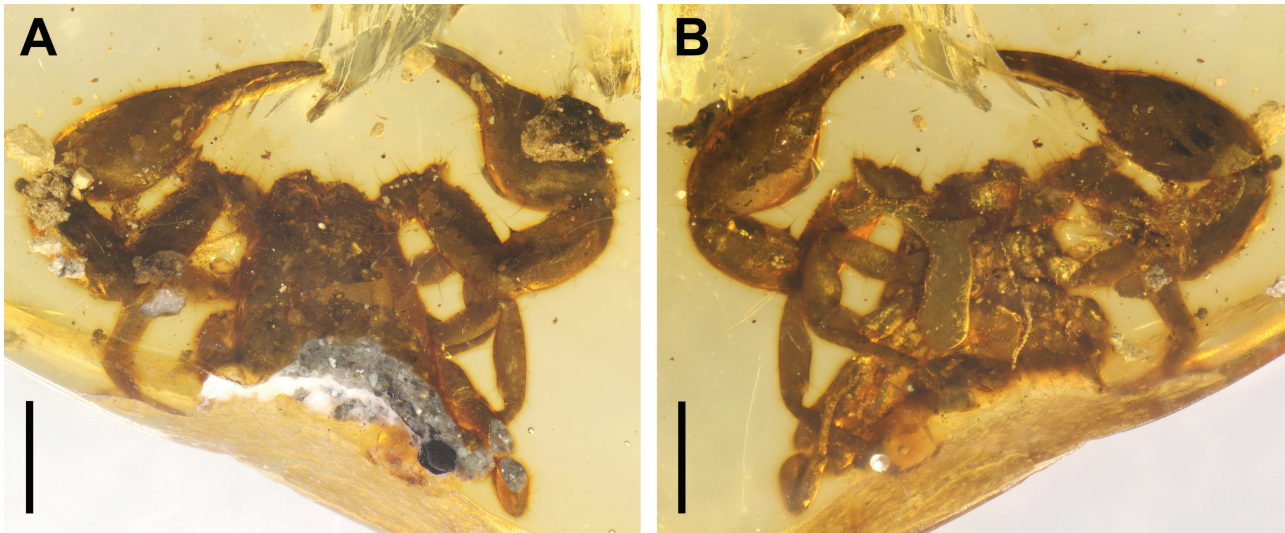


Figure 25. *Chaerilobuthus hansgeorgmuelleri* Lourenço, 2019, one subad. (NIGP 201164), habitus under incident light. A, dorsal aspect. B, ventral aspect. Scale bars: 1 mm.

carinae distinct, serrate; retrodorsal carinae distinct, smooth, and costate (Fig. 26D). Patella with five carinae evident; prodorsal carina distinct, costate-granular; prolateral surface, dorsoventral 'vaulted' projection ('anterior process') distinct with moderately developed pair of apophyses or tubercles ('patellar spurs'), each possessing one macroseta; retrodorsal and retroventral carinae smooth, costate (Figs 25B, 26F). Chela relatively robust (CL/CW = 2.62, Appendix 2); manus globose; chela with six carinae evident; digital carina complete, distinct; dorsomedian carina moderately distinct, costate at base of fixed finger to medially on manus, becoming obsolete proximally on manus; prodorsal carina distinct, comprising several prominent spiniform granules, promedian and proventral carinae obsolete, each comprising few isolated granules; retroventral carina obsolete; dorsal secondary, subdigital, retromedian, and ventromedian carinae absent or obsolete (Figs 25A, B, 26C). Chela finger dentition not visible. Trichobothrial pattern Type D, β configuration. Femur with 11 trichobothria, five *d*, three *i*, and three *e* trichobothria; trichobothrium *e*₁ situated proximal to trichobothrium *d*₃; trichobothrium *e*₃ situated dorsal to trichobothrium *d*₆ (Fig. 26D). Patella with 10 trichobothria, including three *d*, one *i*, and two *e* trichobothria; trichobothrium *i*₁ aligned with trichobothrium *d*₃ (Fig. 26F). Chela with 12 trichobothria; fixed finger with two *d*, three *i*, and two *e* trichobothria; manus with four *e* and one *v* trichobothria; trichobothrium *Et*₁ situated distally on manus, almost aligned with, or proximal to, moveable finger condyle; trichobothrium *eb* situated on fixed finger, slightly distal to moveable finger condyle; trichobothrium *esb* situated medially on fixed finger; trichobothrium *V*₂ situated distally on manus and near retroventral carina (Fig. 26C).

Pectines: Basal piece not visible (Fig. 26B). Three marginal lamellae and four median lamellae; longitudinal suture between marginal and median lamellae distinct. Fulcra absent or obsolete. Teeth rounded, peg sensilla not visible.

Genital operculum: Two opercular sclerites narrow and completely separated (Fig. 26B).

Material examined: **MYANMAR:** Kachin State: Noiije Bum near Hukawng Valley, precise locality unknown, Cretaceous (Cenomanian) burmite: one subad. (sex unknown), mesosoma and metasoma absent (NIGP 201164).

Chaerilobuthus knodelorum Lourenço, 2018

(Figs 27–31, 39)

Chaerilobuthus knodelorum Lourenço, 2018: 2, 3, figs 1–12.

Type material: Holotype: one juv. (sex unknown) (personal collection of KlausPeter Brucksch, Kuranda, Australia), Cretaceous (Cenomanian) burmite: **MYANMAR:** Kachin State (precise locality unknown).

Diagnosis: The following combination of characters is diagnostic for *C. knodelorum*: carapace anterior margin sublinear (Figs 28A, 29A); lateral ocelli not protruding, macular (Fig. 29A); cheliceral finger ventral surface with serrula extending almost entire length (Fig. 29B); pedipalp chela relatively wide, ratio of chela length : width less than 4 (Figs 28C, F, 29E); leg telotarsi ventrosubmedian rows with very long spinules (Fig. 29G, H, J); pectinal lamellae relatively wide, pectines each with five, relatively large teeth (Fig. 29C); mesosoma long, ratio of mesosoma : carapace length greater than 2.5.

Description: Based on the material examined (NIGP 200657).

Carapace: Anterior margin with few, short microsetae; anteromedian depression narrow, shallow; anterosubmedian depressions absent (Fig. 28A); lateral ocular carinae absent; posteromedian and posteromarginal sulci distinct (Fig. 30A); posterior margin slightly recurved medially (Figs 28A, 29A); surfaces almost smooth to sparsely and finely granular (Figs. 28A). Median ocular tubercle situated anteromedially; median ocelli absent; one pair of large posterolateral major lateral ocelli present.

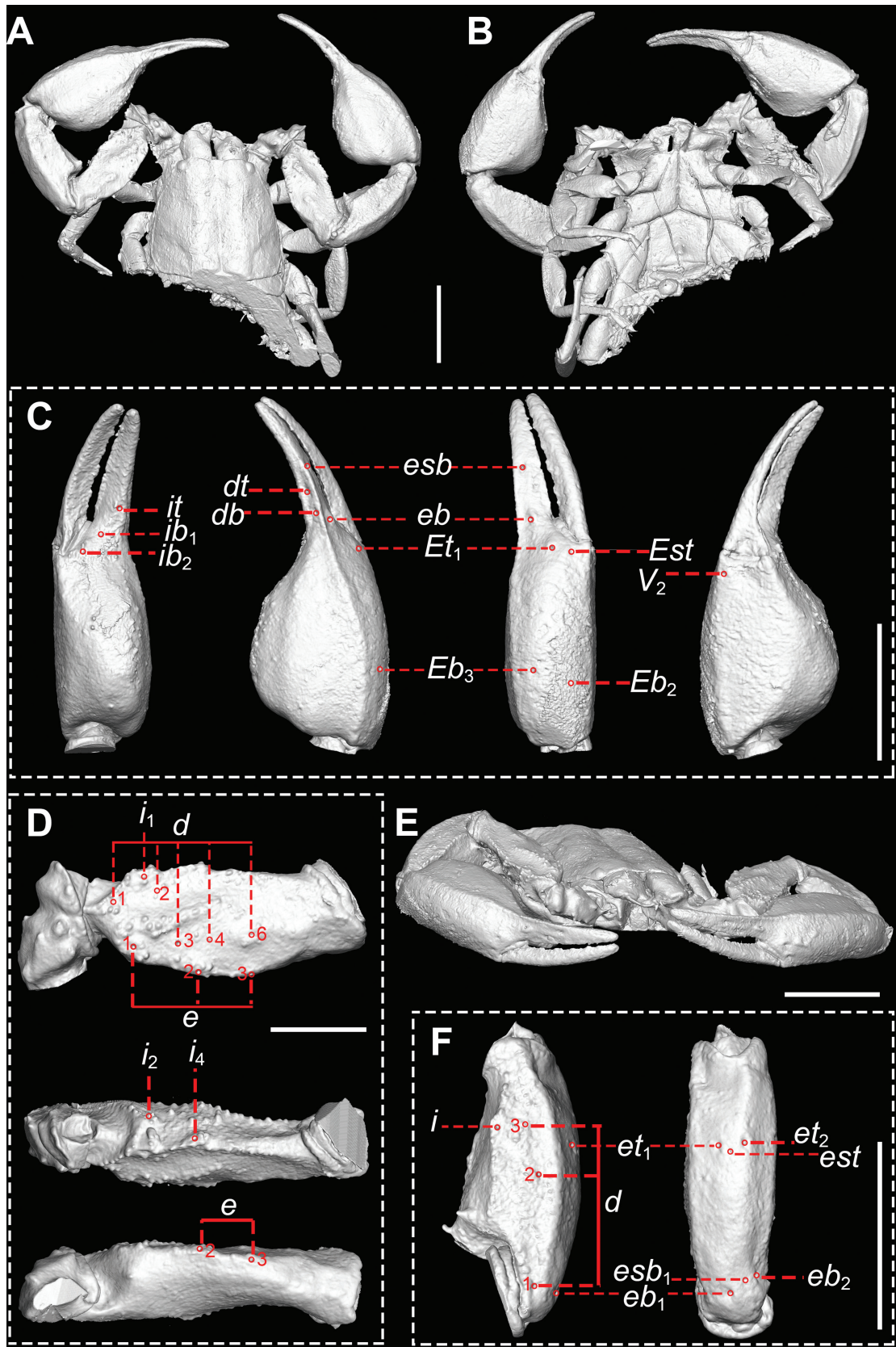


Figure 26. *Chaerilobuthus hansgeorgmuelleri* Lourenço, 2019, one subad. (NIGP 201164), micro-CT reconstruction. A, B, E, carapace, dorsal, ventral, and frontal aspects. C, D, F, pedipalp trichobothrial pattern, chela, femur, and patella, dorsal, ventral, and lateral aspects. Scale bars: 1 mm (A, C, E, F); 500 μ m (D).

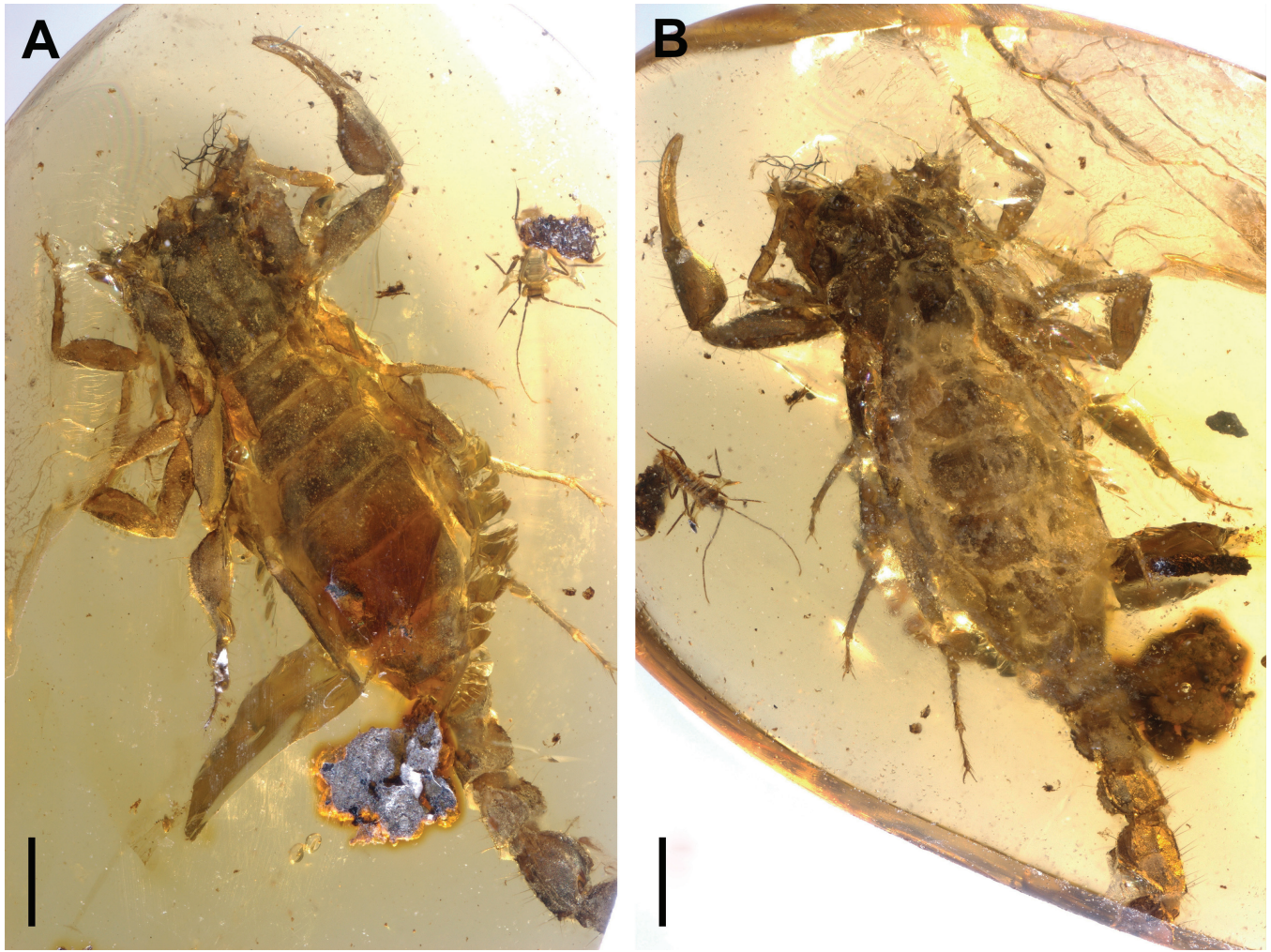


Figure 27. *Chaerilobuthus knodelorum* Lourenço, 2018, one juv. (NIGP 200657), habitus under incident light. A, dorsal aspect. B, ventral aspect. Scale bars: 1 mm.

Coxosternal region: Surface smooth, sparsely covered in macrosetae (Fig. 28B). Leg I maxillary lobes (coxapophyses) distal margins slightly curved and dilate anteriorly, adorned with serrula (Fig. 39E). Sternum pentagonal; lateral margins sublinear, parallel; posterior margin slightly recurved; ventral surface flat, without distinct concave region or median sulcus; posteromedian depression relatively wide, shallow (Fig. 30B).

Chelicerae: Cheliceral dentition partly visible; moveable finger with long dorsal distal (dd) denticle, small dorsal subdistal denticle, stout dorsal median denticle and long ventral distal (vd) denticle; fixed finger with long distal denticle and small subdistal denticle (Fig. 28A). Moveable finger with prominent serrula, comprising moderately long spinules and extending almost entire length of ventral surface (Fig. 29B).

Pedipalps: Segments gracile; surfaces finely granular (Fig. 27). Femur with three carinae evident; prodorsal carina distinct, markedly serrate; retrodorsal carina distinct, slightly serrate; proventral carina smooth, costate (Figs 28F, 31). Patella with six carinae evident; prolateral surface, dorsoventral ‘vaulted’

projection (‘anterior process’) distinct with obsolete pair of apophyses or tubercles (‘patellar spurs’), each possessing one macroseta; retrodorsal, retromedian, and retroventral carinae distinct, smooth and costate; prodorsal carina obsolete (Figs 29D, 31). Chela relatively robust ($CL/CW = 3.75$, Appendix 2); manus globose; chela with five carinae evident; digital carina incomplete, distinct on fixed finger, obsolete on manus; prodorsal carina distinct, markedly serrate; promedian carina distinct, comprising several prominent spiniform granules distally; retroventral carina obsolete, smooth and costate (Figs 28C, F, 29E, 31); dorsomedian, dorsal secondary, subdigital, proventral, retromedian and ventromedian carinae absent or obsolete. Fixed and moveable fingers median denticle rows visible distally, each comprising oblique, slightly imbricate subrows of c. 13 small denticles, separated by large serrate prolateral and retrolateral denticles (Fig. 29F). Trichobothrial pattern Type D, β configuration (Fig. 31). Pedipalp femur with four trichobothria visible, two d and two e trichobothria. Patella with nine trichobothria visible, including two d , one i , and six e trichobothria; trichobothrium i_1 situated distal to trichobothrium d_3 . Chela with 11 trichobothria visible; fixed finger with one d , two e , and

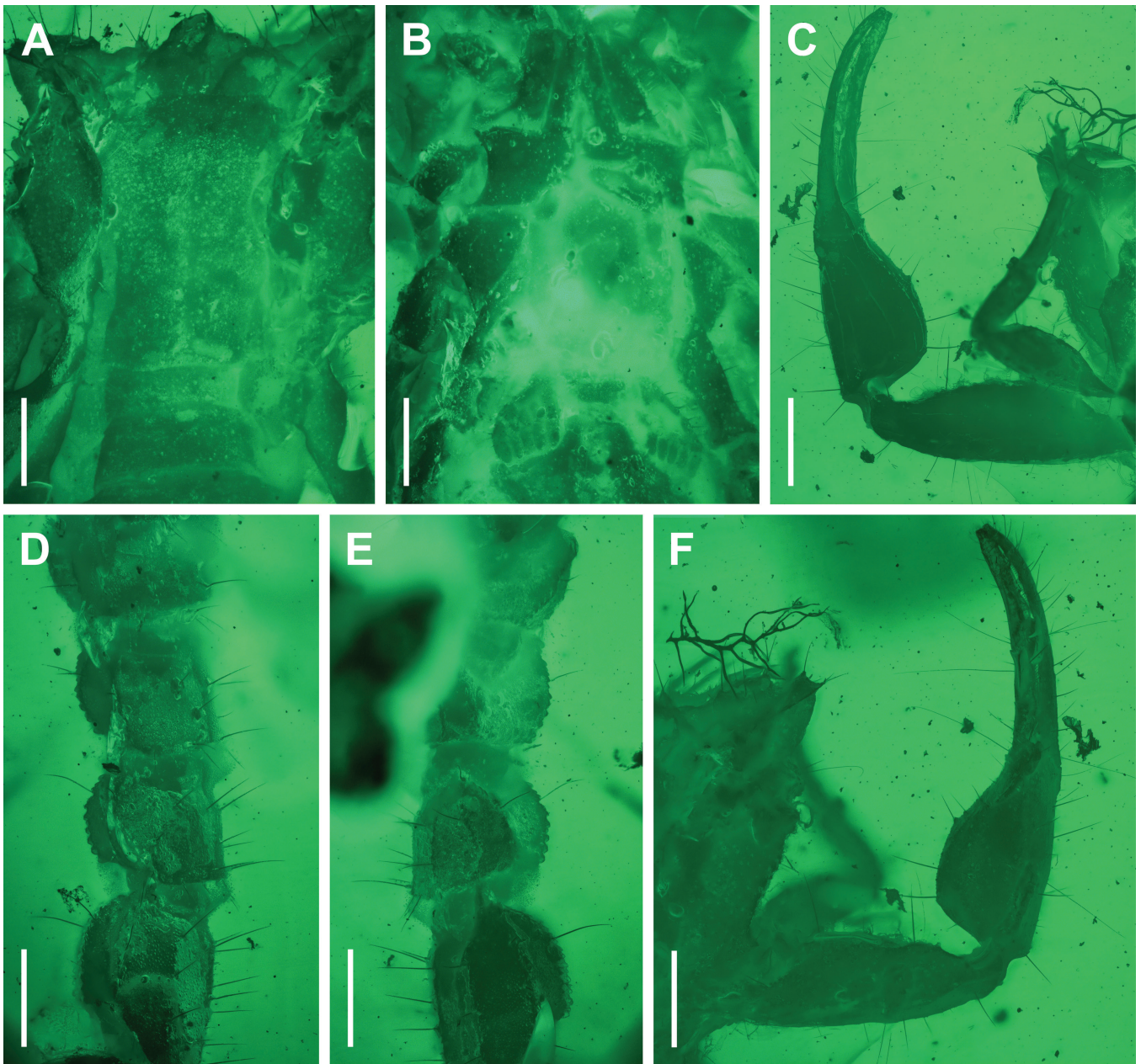


Figure 28. *Chaerilobuthus knodelorum* Lourenço, 2018, one juv. (NIGP 200657), morphology under epifluorescence. A, carapace and tergites I–III. B, coxosternal region and pectines, ventral aspect. C, F, dextral pedipalp, ventral and dorsal aspects. D, E, metasomal segments I–IV, lateral aspect. Scale bars: 500 μ m.

three *i* trichobothria; manus with four *E* and one *V* trichobothria; trichobothrium *Et*₁ situated distally on manus, almost aligned with or proximal to moveable finger condyle; trichobothrium *eb* situated on fixed finger, slightly distal to moveable finger condyle; trichobothrium *esb* situated submedially to slightly distally on fixed finger; trichobothrium *V*₂ situated distally on manus and near retroventral carina.

Legs: Tibia lateral and ventral surfaces each with scattered macrosetae (Fig. 29H–J). Basitarsi each with prominent pedal spurs (Fig. 29G–J) and pair of spinule rows, each comprising c. 10 relatively long spinules, distally (Fig. 29G–J). Ungues

moderately long, distinctly curved; dactyl pronounced, pointed (Fig. 29H–J).

Pectines: Pectines very short, not extending beyond coxa of leg IV (Fig. 29C, 30B). Three marginal lamellae and four median lamellae; surface sparsely covered in macrosetae; longitudinal suture between marginal and median lamellae distinct. Fulcra absent or obsolete. Teeth elongate, distal three-quarters of each tooth occupied by sensillar field.

Genital operculum: Two opercular sclerites relatively wide, as long as pectinal plate, and completely separated (Figs 28B, 30).

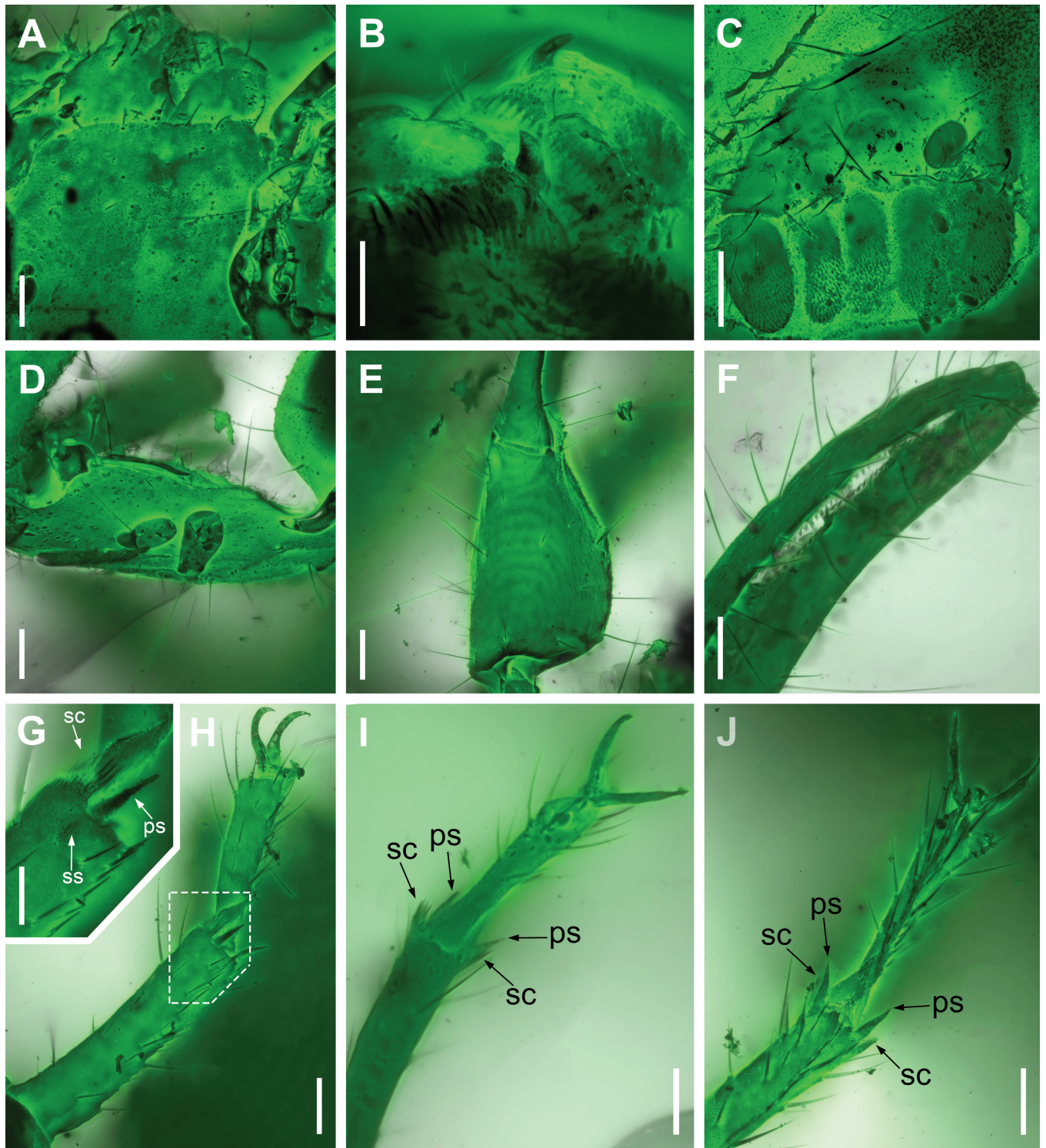


Figure 29. *Chaerilobuthus knodelorum* Lourenço, 2018, one juv. (NIGP 200657), morphology under confocal microscopy. A, lateral ocelli. B, chelicera, ventral aspect. C, dextral pecten, ventral aspect. D, dextral pedipalp patella, dorsal aspect. E, dextral pedipalp chela manus, ventral aspect. F, dextral chela fingers, lateral aspect. G, leg I, basitarsus, distal end, lateral aspect. H–J, legs I–III tarsi, lateral, dorsal, and ventral aspects. Scale bars: 200 μm (A, D, E); 100 μm (B, C, F, H–I); 50 μm (G).

Mesosoma: Pretergites surfaces almost smooth; post-tergites I–VI surfaces finely granular, acarinate (Figs 27A, 28A); sinistral dorsosubmedian and dorsolateral carinae of tergite VII visible (Fig. 27A). Sternites surfaces smooth, with scattered macrosetae; posterior margin of sternite I broadly recurved (Fig. 27B); respiratory spiracles (stigmata) not visible.

Metasoma: Segments I–IV progressively increasing in length, I wider than long, others longer than wide (Figs 27A, B, 28D, E). Segments I–IV lateral and ventral surfaces each with few, short macrosetae; dorsalsurfaces each with distinct depression. Segments I and II each with six distinct carinae (paired dorsosubmedian, dorsolateral, and ventrolateral carinae), III and IV each with eight



Figure 30. *Chaerilobuthus knodelorum* Lourenço, 2018, one juv. (NIGP 200657), micro-CT reconstruction. A, dorsal aspect. B, ventral aspect. Scale bars: 1 mm.

distinct carinae (paired dorsosubmedian, dorsolateral, ventrolateral, and ventrosubmedian carinae); dorsosubmedian carinae distinct, crenulate, and converging posteriorly on segments I–IV; dorsolateral carinae distinct, slightly serrate on segments I–III, moderately serrate on IV; ventrolateral carinae distinct, slightly serrate on segments I–IV; ventrosubmedian carinae absent on segments I and II, obsolete on III and IV.

Remarks: The specimen examined possesses a relatively small pair of pectines, unlike the larger pectines of the holotype specimen, suggesting that it may be female.

Material examined: **MYANMAR:** *Kachin State:* Noije Bum near Hukawng Valley, precise locality unknown, Cretaceous (Cenomanian) burmite: one juv. [♀?], metasomal segment IV and telson absent (NIGP 200657).

Chaerilobuthus serratus Lourenço, 2016

(Figs 32–39)

Chaerilobuthus serratus Lourenço, 2016: 72–74, figs 14, 17–19.

Type material: Holotype: one juv. (sex unknown) (Geologisch-Paläontologisches Institut, University of Hamburg, Germany: 11037-2 GPIH4567), Cretaceous (Cenomanian) burmite: **MYANMAR:** *Kachin State* (precise locality unknown).

Diagnosis: The following combination of characters is diagnostic for *C. serratus*: carapace anteromedian margin aligned with anterolateral margins (Figs 33A, 34A, 37A); lateral ocelli not protruding, macular (Figs 34A, C, 37C); pedipalp chela slender,

ratio of chela length : chela manus width greater than 4 (Figs 35A, E, 38); pectines each with five teeth (Figs 34G, 37H); ratio of metasomal segment IV : segment V length less than 2 (Figs 33I, J, 37G); metasomal segment V dorsosubmedian carinae distinctly serrate (Fig. 32I, J); telson vesicle slightly elongated, not bulbous, aculeus relatively long and moderately curved, base narrow (Figs 33I, J, 37I).

Description: Based on the material examined (NIGP 200656, 201163).

Carapace: Posterior width less than length ($L/PW = 1.19$ or 1.24 , Appendix 2). Anteromedian depression narrow, shallow; anterosubmedian depressions absent; lateral ocular carinae distinct; posteromedian and posteromarginal sulci distinct; surfaces almost smooth to sparsely and finely granular (Figs 32A, 33A, 34A, 37A). Median ocular tubercle situated anteromedially; median ocelli absent; one pair of large posterolateral major lateral ocelli present.

Coxosternal region: Surface smooth, sparsely covered in macrosetae (Figs 33B, 34D, 37F). Leg I maxillary lobes (coxapophyses) distal margins not rounded, slightly dilated anteriorly and adorned with serrula comprising 13 or 14 denticles (Fig. 39A). Sternum pentagonal; lateral margins sublinear, parallel; ventral surface flat, without distinct concave region or median sulcus; posteromedian depression wide, shallow (Figs 32B, 33B, 34D, 37F).

Chelicerae: Fixed finger and manus, prolateral and ventral surfaces each with numerous long, dense macrosetae (Figs 34B,

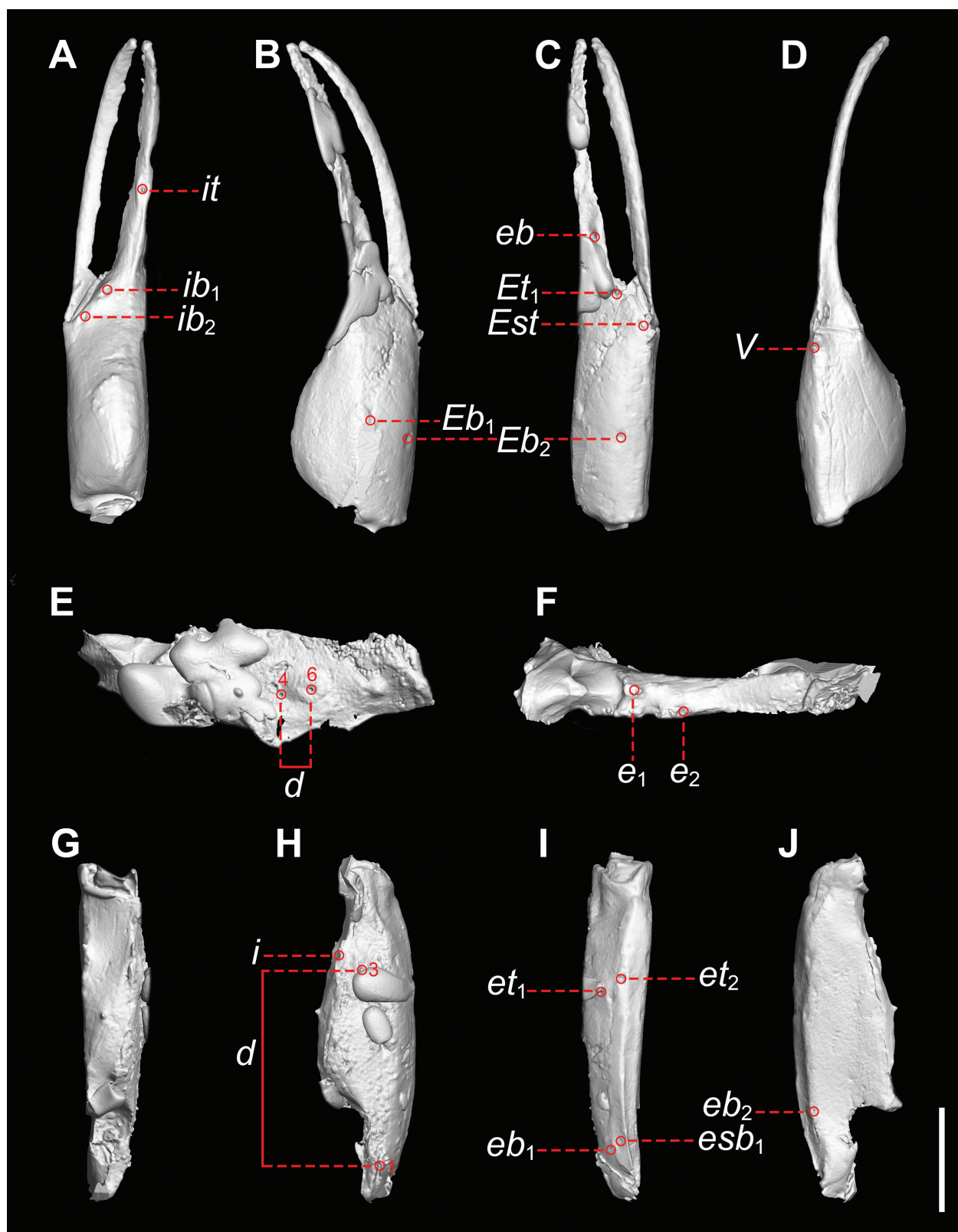


Figure 31. *Chaerilobuthus knodelorum* Lourenço, 2018, one juv. (NIGP 200657), micro-CT reconstruction of pedipalp trichobothrial pattern, dorsal, lateral and ventral aspects. A–D, chela. E, F, femur. G–J, patella. Scale bars: 600 μ m.

37B). Cheliceral dentition partly visible, moveable finger with long dorsal distal (dd) denticle, long ventral distal (vd) denticle, and three or four small ventral accessory (va) denticles;

fixed finger with long distal denticle. Moveable finger with prominent serrula, comprising short spinules in proximal two-thirds.

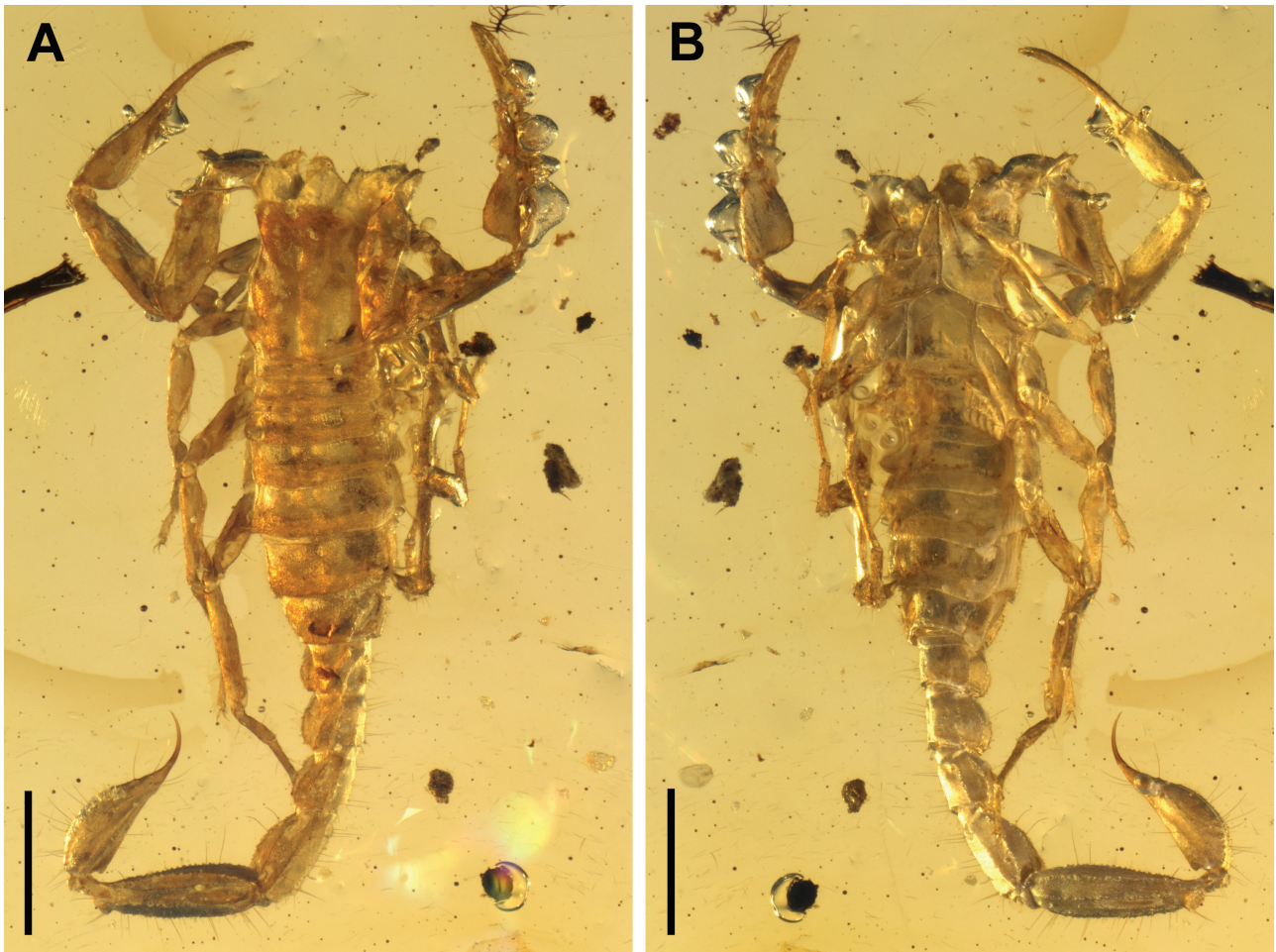


Figure 32. *Chaerilobuthus serratus* Lourenço, 2016, one juv. (NIGP 200656), habitus under incident light. A, dorsal aspect. B, ventral aspect. Scale bars: 1 mm.

Pedipalps: Segments gracile; surfaces sparsely covered by short microsetae and few macrosetae (Figs 35A, E, 38B, E). Femur with four carinae evident; prodorsal and proventral carinae obsolete, crenulate; retrodorsal and retroventral carinae smooth, costate; ventral surface sparsely and finely granular (Figs 35C, G, I, J, 38A, F, I). Patella with five carinae evident; prodorsal carina obsolete, comprising several tubercles; prolateral surface, dorsoventral ‘vaulted’ projection (‘anterior process’) moderately developed with prominent pair of apophyses or tubercles (‘patellar spurs’), each possessing one macroseta; retrodorsal and retroventral carinae smooth, costate (Figs 35A, D, E, H, 38C, G, J). Chela relatively slender ($CL/CW = 4.94\text{--}5$, Appendix 2); manus globose; chela with six carinae evident; digital carina complete, distinct, granular medially, becoming costate proximally and distally; dorsomedian carina reduced to few granules at base of fixed finger, becoming obsolete proximally on manus; prodorsal, promedian, and proventral carinae obsolete, each comprising few isolated granules; retroventral carina distinct, disjunct proximally; dorsal secondary, subdigital, retromedian, and ventromedian carinae absent or obsolete (Figs 35A, B, E, F, 38D, H, K). Chela finger dentition partly visible, fixed and moveable fingers median denticle rows each comprising oblique, slightly

imbricate subrows of c. 12 denticles (first subrow with five denticles), separated by large, serrate prolateral and retrolateral denticles (Fig. 33C). Trichobothrial pattern Type D, β configuration (Figs 35, 38). Femur with 10 trichobothria, four d , three i , and three e trichobothria; trichobothria d_1 , d_2 , d_4 , and d_6 noticeably smaller than others (‘petite’); trichobothrium e_1 situated proximal to trichobothrium d_3 ; trichobothrium e_3 situated dorsal to trichobothrium d_6 (Fig. 35A, C, E, G, I, J). Patella with 10 trichobothria, including three d , one i , and six e trichobothria; trichobothrium i_1 situated distal to trichobothrium d_3 (Fig. 35A, D, E, H). Chela with 12 trichobothria; fixed finger with three i , two e , and two d trichobothria; manus with four E and one V trichobothria; trichobothrium Et_1 situated distally on manus, almost aligned with or proximal to moveable finger condyle; trichobothrium eb situated on fixed finger, slightly distal to moveable finger condyle; trichobothrium esb situated medially on fixed finger; trichobothrium V_2 situated distally on manus near retroventral carina; macroseta situated medially on manus and near retroventral carina (Fig. 35A, B, E, F).

Legs: Tibia lateral and ventral surfaces each with scattered macrosetae (Figs 33D, G, H, K, 37D). Basitarsi each with pair

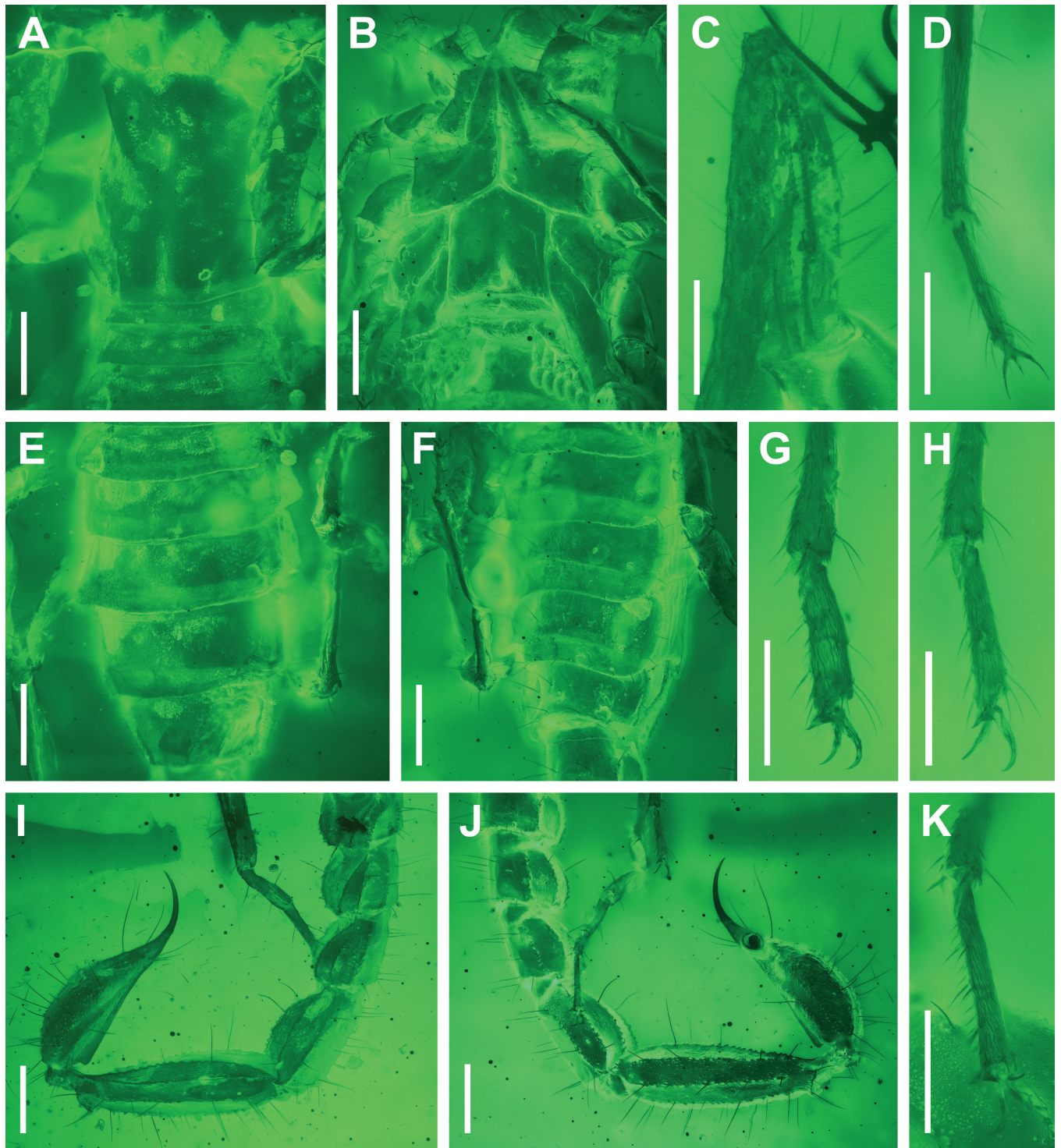


Figure 33. *Chaerilobuthus serratus* Lourenço, 2016, 1 juv. (NIGP 200656), morphology under epifluorescence. A, carapace and tergites I–III. B, coxosternal region and pectines, ventral aspect. C, pedipalp chela denticle rows, dorsal aspect. D, leg I tarsus, dorsal aspect. E, tergites III–VII. F, sternites III–VII. G, leg II tarsus, lateral aspect. H, leg III tarsus, lateral aspect. I, J, metasoma and telson, lateral aspect. Scale bars: 400 μm (A, B, E, F, I, J); 200 μm (C, D, G, H, K).

of spinule rows, comprising 10–13 relatively short spinules, distally (Fig. 34I–L). Telotarsi each with slightly irregular pair of ventrosubmedian spinule rows, comprising relatively long spinules (Fig. 33K, L). Ungues moderately long, distinctly curved; dactyl pronounced, pointed (Figs 34I–L, 37D).

Pectines: Basal piece long, narrow with shallow median sulcus (Figs 33B, 34D, 37H). Three marginal lamellae and four median lamellae; surface sparsely covered in macrosetae; longitudinal suture between marginal and median lamellae distinct (Figs 33B, 34G, 37H). Fulcra absent or obsolete.

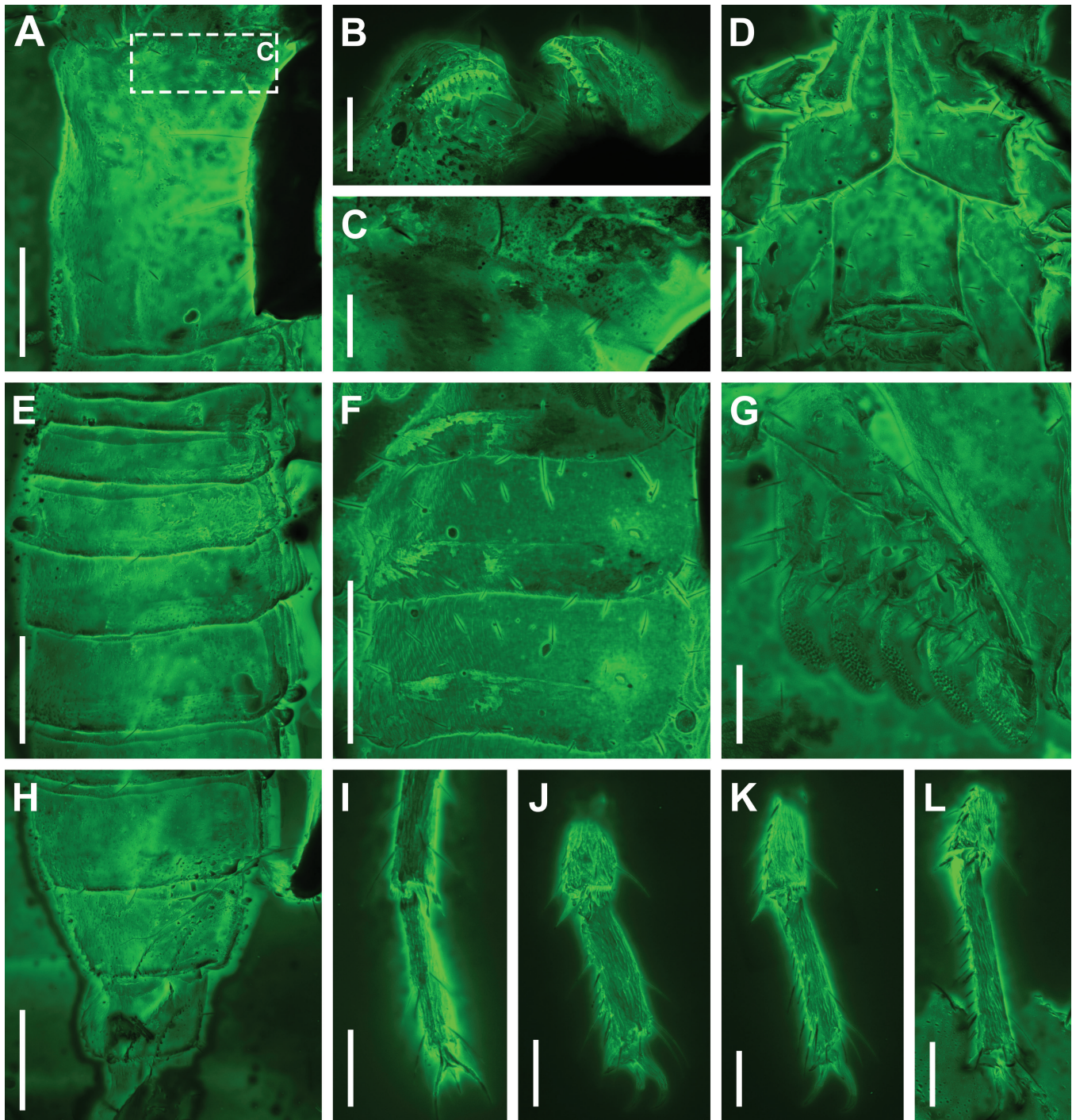


Figure 34. *Chaerilobuthus serratus* Lourenço, 2016, one juv. (NIGP 200656), morphology under confocal microscopy. A, carapace. B, chelicera, ventral aspect. C, lateral ocelli. D, sternum and genital operculum. E, tergites I–V. F, sternites III–V. G, sinistral pecten, ventral aspect. H, tergites VI, VII, and metasomal segment I, dorsal aspect. I–L, pedipalp chela fingers dentition, lateral aspect. Scale bars: 400 μm (A, D, E, F, H); 100 μm (B, C, G, I–L); 200 μm (M).

Teeth rounded, distal three-quarters of each tooth occupied by sensillar field; peg sensilla relatively long, columnar (Fig. 34G, 37H).

Genital operculum: Two opercular sclerites narrow and completely separated, as long as pectinal plate (Figs 33B, 34D, 37F).

Mesosoma: Pretergites surfaces almost smooth (Figs 33A, E, 37E); post-tergites I–VI surfaces finely granular, acarinate (Fig. 34E, 37E); tergite VII surface sparsely granular with four serrate carinae (paired dorsosubmedian and dorsolateral carinae) in posterior half of segment (Fig. 34H). Sternites surfaces smooth, with scattered macrosetae; posterior margins broadly recurved (Figs 33F, 34F); respiratory spiracles (stigmata) small, ovoid to round (Fig. 34F).

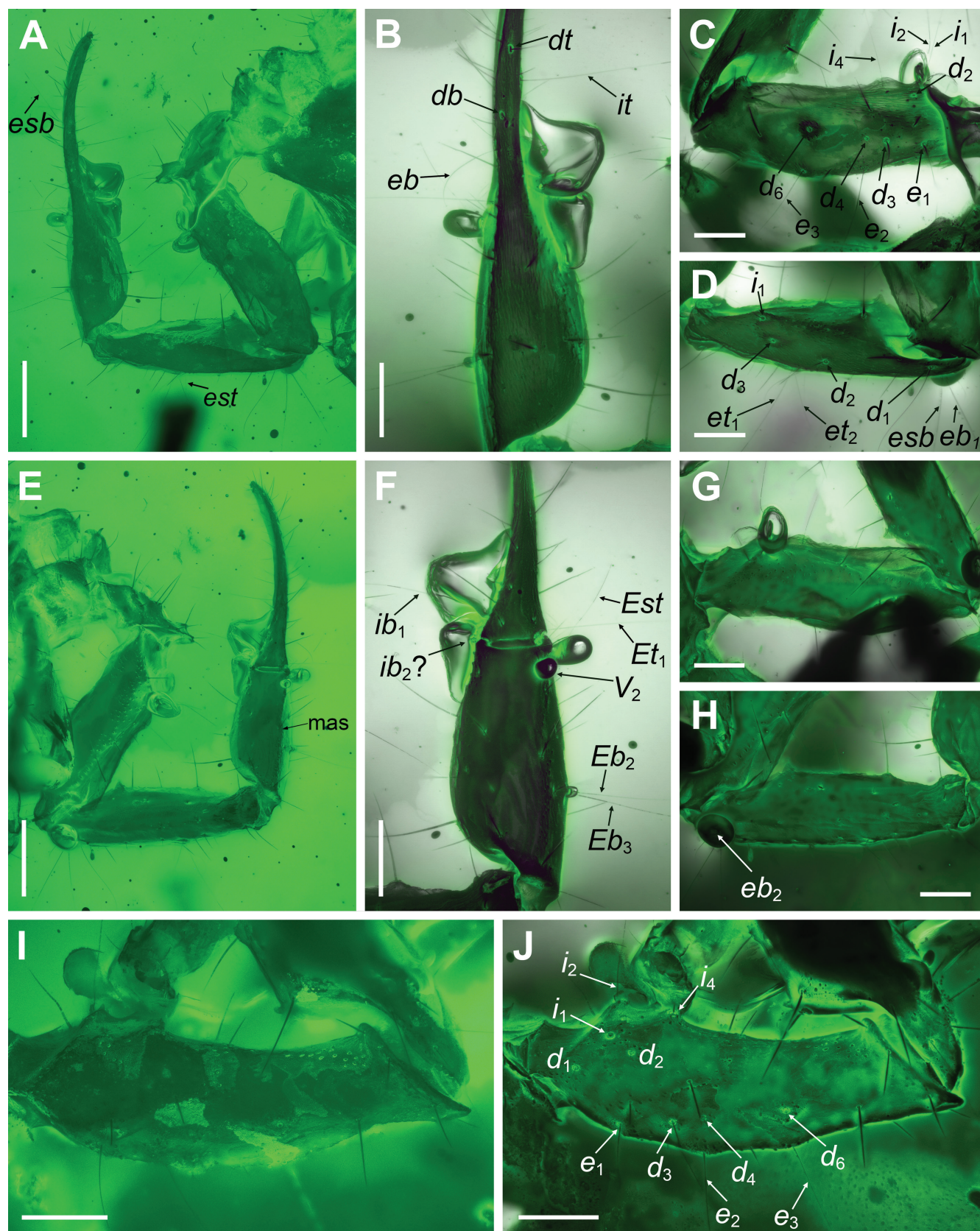


Figure 35. *Chaerilobuthus serratus* Lourenço, 2016, one juv. (NIGP 200656), pedipalp trichobothrial pattern under confocal microscopy (B–D, F–H, J) and epifluorescence (A, E, I). A–D, sinistral pedipalp, dorsal aspect. E–H, sinistral pedipalp, ventral aspect. I, J, dextral femur, dorsal aspect. Scale bars: 400 μ m (A, E); 200 μ m (B–D, F–J).

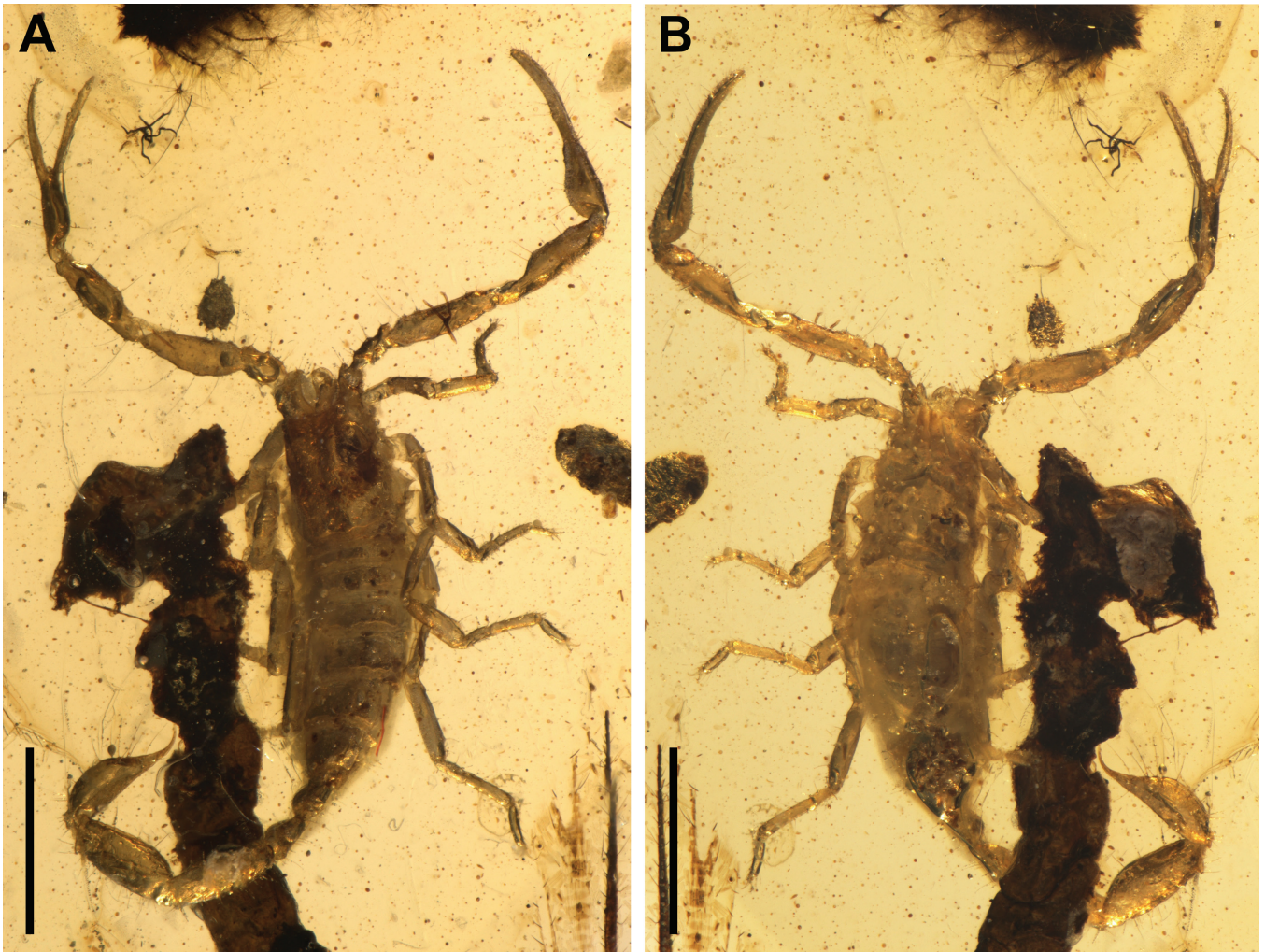


Figure 36. *Chaerilobuthus serratus* Lourenço, 2016, one juv. (NIGP 201163), habitus under incident light. A, dorsal aspect. B, ventral aspect. Scale bars: 1 mm.

Metasoma: Segments I–V progressively increasing in length, I wider than long, others longer than wide (Figs 33I, J, 34H, 37G). Segments I–V lateral and ventral surfaces each with few, short macrosetae; I–III dorsal surfaces each with distinct depression. Segment I with six distinct carinae (paired dorsosubmedian, dorsolateral, and ventrolateral carinae), segments II–V each with eight distinct carinae (paired dorsosubmedian, dorsolateral, ventrolateral, and ventrosubmedian carinae); dorsosubmedian carinae distinct on all segments, serrate throughout length, converging posteriorly; dorsolateral carinae distinct, serrate on segments I–III, smooth, costate on IV and V; ventrolateral carinae obsolete on segments I and II, distinct, slightly granular on III–V; ventrosubmedian carinae absent on segment I, obsolete on II and III, distinct, serrate on IV and V.

Telson: Vesicle elongate; dorsal surface relatively smooth; lateral and ventral surfaces finely and densely granular; (Figs 33I, J, 37I); ventral surface with several macrosetae; subaculear tubercle absent; prominent subaculear setal pair. Aculeus moderately long, shallowly curved; base moderately wide, less than half vesicle width.

Material examined: **MYANMAR:** Kachin State: Noiye Bum near Hukawng Valley, precise locality unknown, Cretaceous (Cenomanian) burmite: two juv. (sex unknown) (NIGP 200656, 201163).

DISCUSSION

Systematics

The phylogenetic analyses and morphospace analyses presented herein support a sister-group relationship between the extinct subfamily Chaerilobuthinae, stat. nov., and the extant subfamily Vietbocapinae, an eyeless, troglobitic clade occurring in South-East Asia (Figs 1, 3). This result is supported by several morphological characters, including the absence of median ocelli, the vestigial or absent circumocular sutures, and the absence of tibial spurs on legs III and IV. Interestingly, the shape of the pedipalps is more variable among Chaerilobuthinae than Vietbocapinae, suggesting that Chaerilobuthinae may have occupied a greater range of ecological niches (see below).

The 11 specimens described and illustrated herein were tentatively assigned to seven of the 16 species of *Chaerilobuthus*

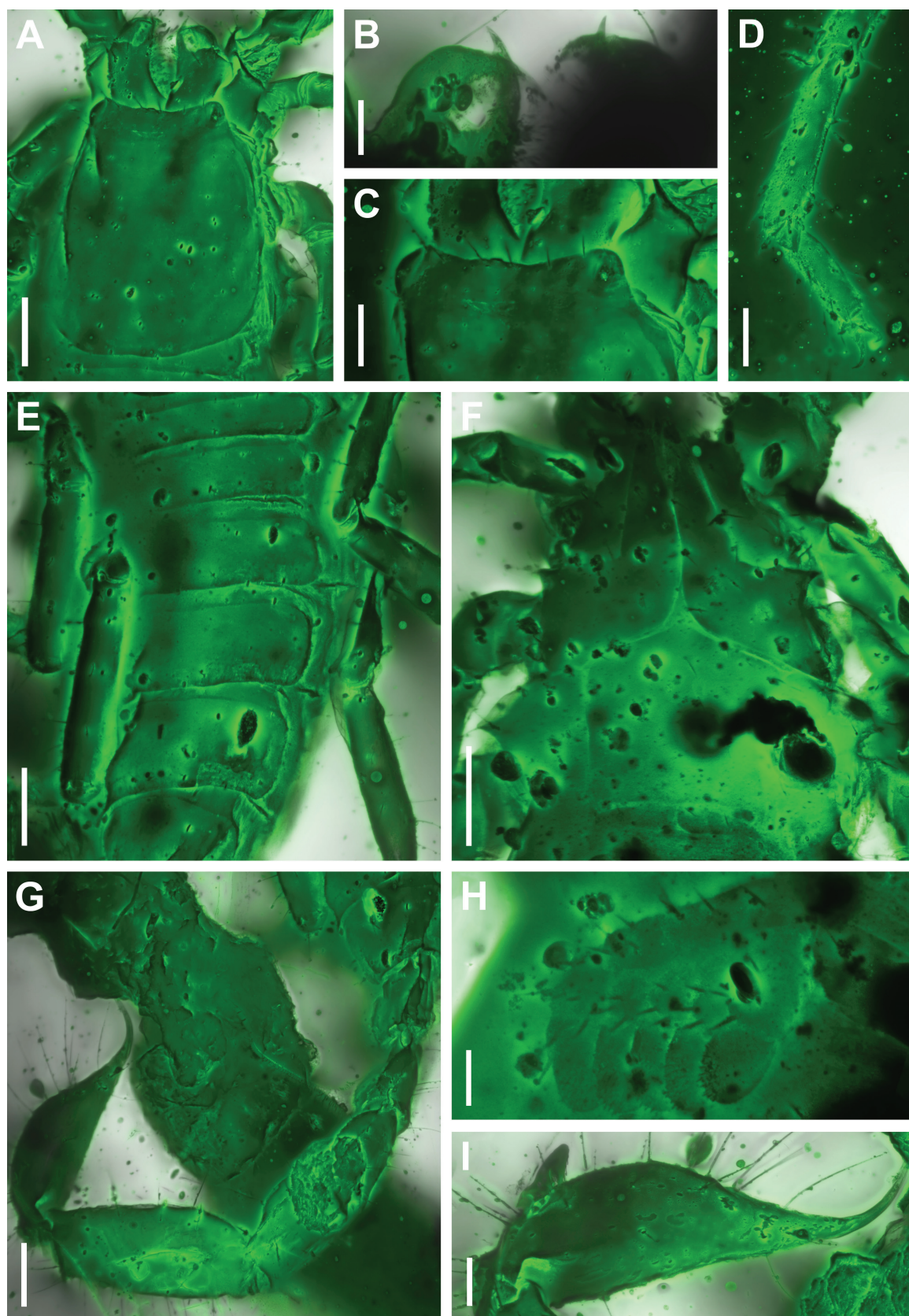


Figure 37. *Chaerilobuthus serratus* Lourenço, 2016, one juv. (NIGP 201163), morphology under confocal microscopy. A, carapace. B, chelicera, dorsal aspect. C, lateral ocelli. D, leg III tarsus, lateral aspect. E, tergites. F, coxosternal region. G, metasoma and telson, lateral aspect. H, pectines, ventral aspect. I, telson, lateral aspect. Scale bars: 200 µm (A, E–G); 50 µm (B, H); 100 µm (C, D, I).

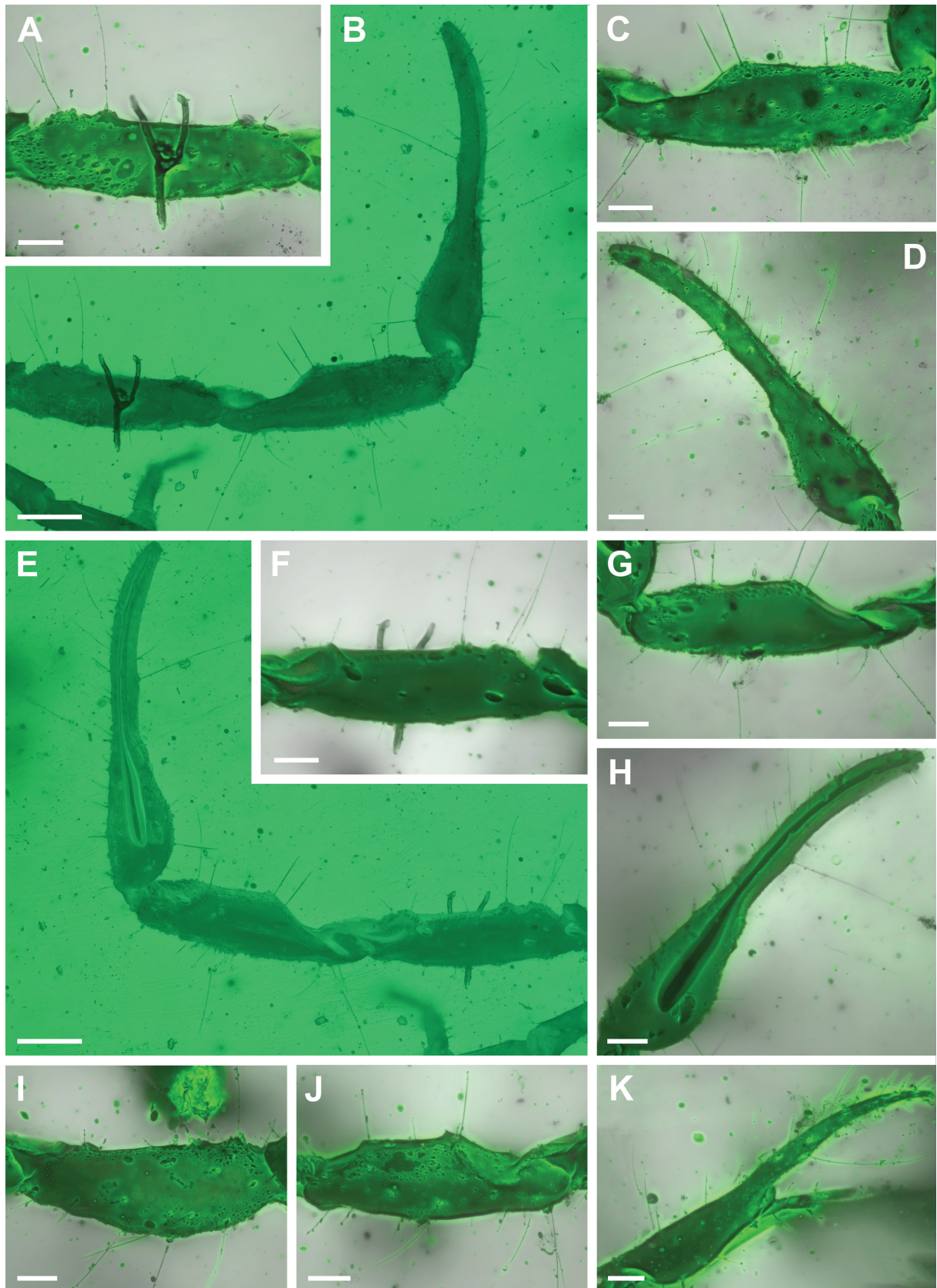


Figure 38. *Chaerilobuthus serratus* Lourenço, 2016, one juv. (NIGP 201163), pedipalp trichobothrial pattern under confocal microscopy (A, C, D, F, G, H, I–K) and epifluorescence (B, E). Scale bars: 100 μm (A, C, D, F–K); 200 μm (B, E).

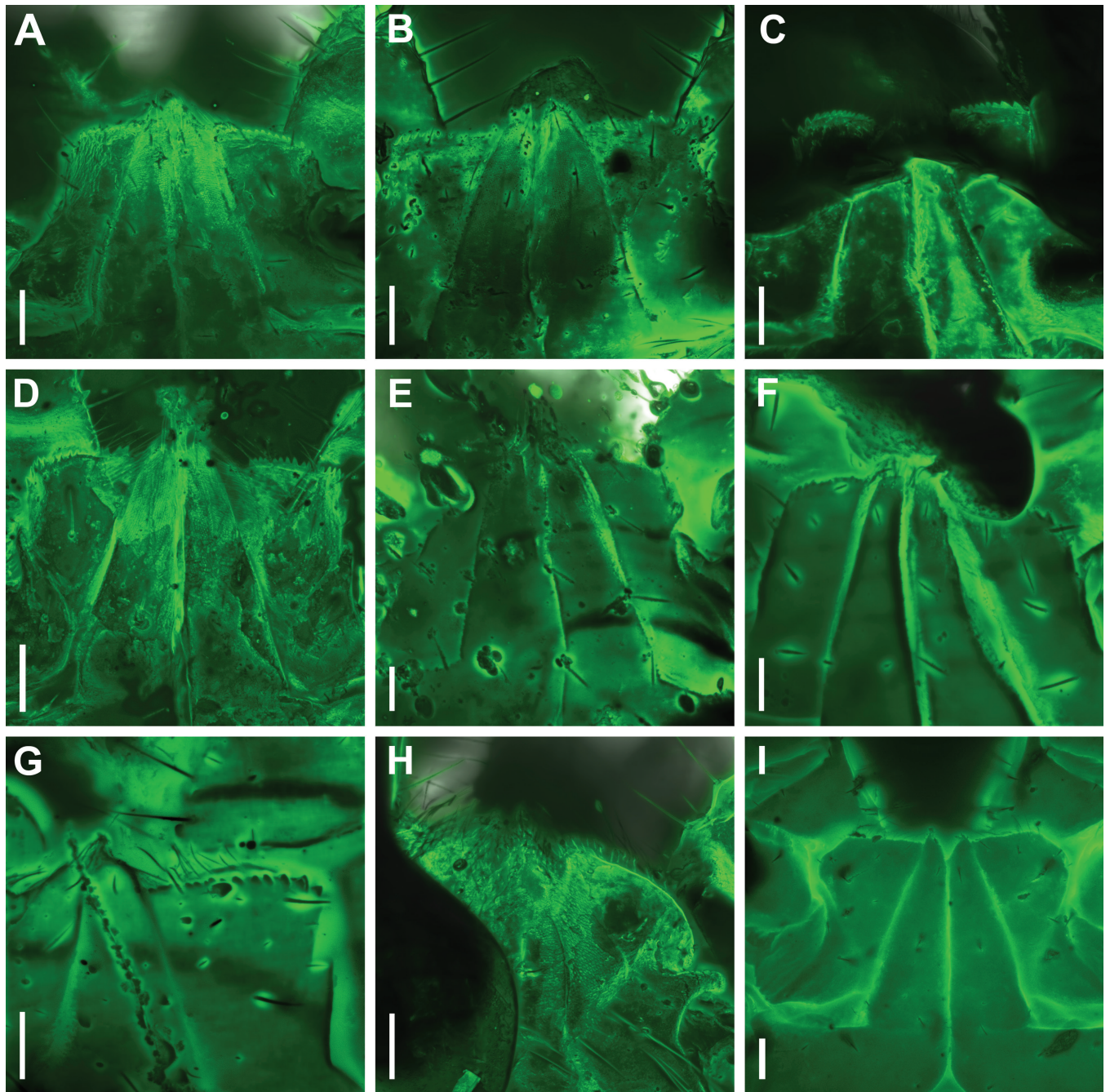


Figure 39. Scorpion taxa illustrating presence or absence of serrula on maxillary lobes (coxapophyses) of legs I and II under confocal microscopy. A, *Chaerilobuthus serratus* Lourenço, 2016, one juv. (NIGP 200656). B, *Chaerilobuthus enigmaticus* Lourenço, 2015, one juv. (NIGP 201158). C, *Chaerilobuthus enigmaticus* Lourenço, 2015, one juv. (NIGP 201159). D, *Chaerilobuthus complexus* Lourenço, 2011, one juv. (NIGP 200655). E, *Chaerilobuthus knodelorum* Lourenço, 2018, one juv. (NIGP 200657). F, *Chaerilobuthus gigantosternum* Lourenço, 2016, one juv. (NIGP 200654). G, *Chaerilobuthus hansgeorgmuelleri* Lourenço, 2019, one subad. (NIGP 201164). H, *Betaburmesebuthus bellus* Lourenço 2016, one juv. (NIGP 200649). I, *Chaerilus* sp., one juv. (NIGP 180155). Scale bars: 100 μ m (A–E, G–I); 50 μ m (F).

described to date, based on phylogenetic analysis (Fig. 2). However, most of the type specimens on which these species were based are immature, probably resulting in unreliable diagnoses. For example, the shape of the carapace, sternum, and pedipalps are known to vary during scorpion development (Sissom 1990, Soleglad and Fet 2003a, Kovářik et al. 2015). Some of the described species may also be invalid because the putative diagnostic differences between them are inconsistent. Examples

include *C. bruckschi* and *C. enigmaticus*, as well as *C. knodelorum* and *C. schwarzi* (Lourenço 2015a, b, 2018, Lourenço and Velten 2015). Other species, such as *C. birmanicus* and *C. longiaculeus*, were based on extremely incomplete and/or deformed specimens (Lourenço 2013, 2015a), in which few if any diagnostic characters can be reliably discerned.

Two monotypic genera were unsupported by the evidence available. *Chaeriloiurus brigittemuelleriae*, type species

of *Chaeriloiurus*, closely resembles species of *Chaerilobuthus*. The only putative diagnostic difference between these two genera is the allegedly convex anteromedian margin of the carapace (Lourenço and Velten 2020), a character known to vary intragenerically, including in *Chaerilobuthus*. Additionally, the image of the carapace of the holotype of *C. brigittemuellerae* in the original description is unclear, casting doubt on the accuracy of the corresponding illustration. Based on a lack of evidence justifying its recognition as a distinct genus (Fig. 2), *C. brigittemuellerae* is transferred to *Chaerilobuthus*, resulting in *Chaerilobuthus brigittemuellerae* (Lourenço and Velten, 2020), comb. nov.

Another monotypic genus, *Serratochaerilobuthus*, was recently established (Lourenço and Velten 2024b). However, the five putative diagnostic characters of its type species, *S. schmidtii*, are also shared by various species of *Chaerilobuthus*. Seven or eight denticle subrows in the median denticle row of the pedipalp chela fixed finger is a diagnostic character of *Chaerilobuthus* overlooked by previous authors (Figs 13C, 15E, 29F, 33C). A prominent apophysis on the prolateral surface of the pedipalp patella is observed in *C. meggeri* (Lourenço and Velten 2021: 3, figs 9, 10). The unguis of the telotarsi, described as long and sharp, are indistinguishable from those of other species of *Chaerilobuthus*, such as *C. complexus* (Lourenço and Beigel 2011: 3, figs 1, 2), *C. knodelorum* (Lourenço 2018: 7, 8, figs 5, 8; Figs 27, 29H–J), and *C. schwarzi* (Lourenço and Velten 2015: 3, fig. 1). Prominent spiniform granules on the metasomal carinae are also observed in *C. meggeri* (Lourenço and Velten 2021: 4, fig. 14) and *C. schwarzi* (Lourenço and Velten 2015: 5, fig. 15). An alleged additional trichobothrium on the ventral surface of the pedipalp chela, unsupported by photographic evidence, is probably a misinterpreted macro- or microseta. Based on a lack of evidence justifying its recognition as a distinct genus (Fig. 2), *S. schmidtii* is transferred to *Chaerilobuthus*, resulting in *Chaerilobuthus schmidtii* (Lourenço and Velten, 2024b), comb. nov.

Morphology

Trichobothrial patterns are among the most informative morphological characters for scorpion systematics (Vachon 1974, Sissom 1990, Prendini 2000, Prendini and Wheeler 2005). Despite the many specimens of Chaerilobuthinae reported by previous authors (Lourenço and Beigel 2011, Lourenço 2015a, b, 2018, Lourenço and Velten 2015, 2019, 2020, 2021, 2022), the trichobothrial pattern of the subfamily was not explicitly defined. By applying modern imaging methods, such as confocal laser scanning microscopy, the present study accurately documented the trichobothrial pattern of these extinct scorpions, revealing that it conforms largely to the Type D pattern, previously restricted to the extant Pseudochactidae, and comprising a total of 33 trichobothria: 11 trichobothria on the pedipalp femur (d_1 – d_4 , d_6 , i_2 , i_4 , e_1 – e_3), 10 trichobothria on the patella (d_1 – d_3 , i_1 , eb_1 , eb_2 , esb_1 , est , et_1 , et_2), and 12 trichobothria on the chela (db , dt , ib_1 , ib_2 , it , eb , esb , Eb_2 , Eb_3 , Est , Et_1 , V_2). Previous researchers erroneously concluded that two V trichobothria occur on the chela manus of chaerilobuthine scorpions by mistaking a macroseta for a V trichobothrium (Lourenço and Beigel 2011, Lourenço 2015b, 2018, Lourenço and Velten 2015, 2019, 2020, 2021, 2022). Compared to the basic Type D pattern observed

in extant pseudochactid scorpions, however, chaerilobuthine scorpions lack the femoral trichobothrium d_5 and the chelal trichobothrium Eb_1 (Figs 7, 10, 13, 16, 21, 24, 26, 31, 35, 38). Additionally, femoral trichobothria d_3 and d_4 are situated closer to the midpoint of the segment and the d_3 – d_4 axis is directed slightly away from the retrodorsal carina rather than parallel to it as in extant pseudochactid scorpions (Figs 7A, 10, 13A, 16, 24A, 26D, 31, 35C, J).

Previous researchers claimed that some species of *Chaerilobuthus* bear very small median ocelli (Lourenço 2018, Lourenço and Velten 2019, 2024a) but failed to provide clear evidence to substantiate this assertion. Based on the present investigation, the absence of median ocelli is a stable diagnostic character of *Chaerilobuthus*, suggesting that the median ocelli allegedly observed in some species of the genus may be granules on the carapace or impurities in the amber.

Previous studies also reported one to three pairs of minute lateral ocelli in some species of *Chaerilobuthus* (Lourenço and Beigel 2011, Lourenço 2018, Lourenço and Velten 2015, 2019, 2022), again without supporting evidence. However, as illustrated by all 11 specimens documented herein, as well as *C. meggeri* (Lourenço and Velten 2021), a single pair of large lateral ocelli appears to be a reliable diagnostic character of *Chaerilobuthus*.

Two interesting new characters were discovered in the present study, i.e. a serrula along the anterior margin of the maxillary lobes (coxapophyses) of leg I and a pair of spinule rows at the distal ends of the leg basitarsi (Figs 6I–L, 9F–I, 12H, L, 15G, 18C, 20J, K, 23K, 29G–J, 33G, H, 34I–L, 39). The serrula, a comb-like row of tiny denticles or modified setae around the mouthparts, occurs in several arachnid orders. This structure occurs along the anterior margin of the coxal endite and serves a masticatory function in most spiders (Staveley 1866, Maddison and Hedin 2003, Jocqué and Dippenaar-Schoeman 2006), whereas it occurs on the ventral surface of the cheliceral moveable finger and acts as a cleaning organ in pseudoscorpions (Hoff 1949, Cowles 2018), schizomids (Rowland 1975), and whip spiders (Garwood *et al.* 2017). A serrula has also been documented on the ventral surface of the cheliceral moveable finger of various scorpion taxa (Graham and Fet 2006) but was not previously reported along the anterior margin of the coxal endite. This is the first time a serrula was observed on the maxillary lobes (coxapophyses) in scorpions, making it a diagnostic feature of *Chaerilobuthus* that distinguishes it from other genera in Burmese amber, such as *Betaburmesobuthus* Lourenço, 2015 (Fig. 39H) and *Chaerilus* Simon, 1877 (Fig. 39I). Interestingly, this structure was also illustrated (although not described) in images accompanying the description of the extant pseudochactid, *Qianxie* (Tang 2022: 7, fig. 10), and its presence has since been verified on the maxillary lobes of several other extant pseudochactid scorpions. A prominent serrula, resembling the structure observed in *Qianxie* and Chaerilobuthinae, also occurs in *Troglokhammouanus*, but the serrula is vestigial in *Aemngvantom* and *Vietbocap*, and absent in *Pseudochactas* (Prendini *et al.*, in prep.).

Another intriguing structure is the pair of spinule combs situated along the distal edge of the leg basitarsi, dorsal to the pedal spurs and slit sensilla (Figs 6I–L, 9F–I, 12H, L, 15G, 18C, 20J, K, 23K, 29G–J, 33G, H, 34I–L). This structure, observed in all

Chaerilobuthus specimens examined during the present study, resembles the ‘rosette-like structure’ described in the extant iurid scorpion, *Calchas* Birula, 1899 (Fet et al. 2009: 28, Benli et al. 2013: 27–29).

Ecology, evolution, and biogeography

The palaeoenvironment during the depositional period of Burmese amber is considered to have been a tropical rain-forest near an estuary or gulf (Smith and Ross 2016, Bolotov et al. 2021), with many specialized, autochthonous species (Grimaldi et al. 2002). The presence of pollen and sporangia preserved together with scorpions in Burmese amber, including Chaerilobuthinae, suggest that these Cretaceous scorpions were epigean (Figs 22, 23G). This observation must be reconciled with the apparent troglomorphy of *Chaerilobuthus*, e.g. the absence of median ocelli (Prendini et al. 2021). It is hypothesized that *Chaerilobuthus* were endogean/humicolous like the extant species of *Troglotayosicus* Lourenço, 1981 which also lack median ocelli but possess lateral ocelli and do not exhibit other pronounced troglomorphy. Most specimens of *Troglotayosicus* were collected from leaf litter, except *Troglotayosicus vachoni* Lourenço, 1981, collected inside a cave (Lourenço 1981, Botero-Trujillo and Francke 2009, Botero-Trujillo et al. 2012, 2017, Sánchez-Vialas et al. 2020, Moreno-González et al. 2024).

Recent palaeogeographical reconstructions suggest that Pseudochactidae originated in the Tajik–North Pamir plate of Eurasia during the Carboniferous and subsequently dispersed to South-East Asia, consistent with the ‘Out of Eurasia’ hypothesis (Loria et al. 2022). According to Loria et al. (2022), pseudochactids dispersed from the Tajik block via the South China and North China plates to the West Burma block during the Triassic and Jurassic periods. Another possibility, however, is that pseudochactids originated in Gondwanaland, from which the West Burma block, where the Burmese amber mine is located, was apparently derived (Matthews et al. 2016, Metcalfe 2017). Palaeomagnetic reconstructions suggest that this plate was isolated near the equator in the Tethys Ocean during the Mid-Cretaceous (Westerweel et al. 2019) and several studies of Burmese amber arthropods and plants suggest Gondwanan affinities (Poinar 2018, Wriedt et al. 2021, Chitimia-Dobler et al. 2023, Wood and Wunderlich 2023). This alternative hypothesis, which requires further testing, implies that pseudochactids were transported to Asia during the Cretaceous via the West Burma Block, and subsequently migrated into South-East Asia and, ultimately, Central Asia while gradually becoming extinct elsewhere in former Gondwana.

CONCLUSION

The present study examined 11 *Chaerilobuthus* specimens from Mid-Cretaceous Burmese amber using multiple imaging methods. The examination revealed many new characters concerning the carapace, ocelli, chelicerae, pedipalp trichobothria, coxosternal region, and leg tarsi, allowing the diagnostic characters of the genus to be revised and the specimens to be assigned to seven described species. The specimens were measured and scored into a morphological character matrix that was analysed to test their phylogenetic positions. Phylogenetic

analyses placed Chaerilobuthidae sister to the extant subfamily Vietbocapinae of Pseudochactidae, rather than to Buthidae or Chaerilidae, justifying their transfer to Pseudochactidae, as Chaerilobuthinae, stat. nov. The discovery of the first fossil records of Pseudochactidae confirms that the family dates back 100 Mya and contributes to understanding its origin and evolutionary history.

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CONFLICT OF INTEREST

There is no conflict of interest between the authors of the publication.

DATA AVAILABILITY

The data on which this study is based are provided in the text.

APPENDICES

APPENDIX 1

Morphological characters and character states used for phylogenetic analysis Pseudochactidae Gromov, 1998, including Chaerilobuthinae Lourenço, 2011, stat. nov. Character states scored 0–5, inapplicable (–), or unknown (?). Terminology, including trichobothrial homology, follows Prendini et al. (2006). Characters corresponding to lists of Lamoral (1980), Stockwell (1989), Prendini (2000), Soleglad and Sissom (2001), Soleglad and Fet (2001), Soleglad and Fet (2003b: table 4), Soleglad and Fet (2003b: table 5), Prendini (2004), Prendini et al. (2021: appendices 2 and 3), and Prendini et al. (in prep.) denoted, respectively, by abbreviations L80, S89, P00, S&S01, S&F01, S&F03.4, S&F03.5, P04, PEA21, and PEA25, followed by the corresponding number. Character matrix in Table 1.

COLORATION AND INFUSCATION

1. Tegument base coloration: yellowish (0); brown (1); unknown (?). [PEA21/1, PEA25/1]
2. Carapace infuscation: absent (immaculate) (0); present (1); unknown (?). [PEA21/2, PEA25/2]
3. Mesosomal tergites infuscation: absent (immaculate) (0); median stripe and pair of lateral bands (1); paired submedian and sublateral stripes (2); entirely or mostly (anterior two-thirds) infusate (3); unknown (?). [PEA21/3, PEA25/3]
4. Legs, femoral and patellar surfaces, infuscation: prolateral and retrolateral surfaces infusate (0); prolateral surfaces infusate, retrolateral surfaces immaculate (2); prolateral

and retrolateral surfaces immaculate (2); unknown (?). [PEA21/4, PEA25/4] Prendini *et al.* (in prep.) revised the original character (PEA21/1) to the current version (PEA25/4).

CHELICERAE

5. Cheliceral fixed finger, ventral surface, teeth or denticles: two major teeth (0); four or five small denticles (ventral accessory denticles) (1); unknown (?). [S&S01/8, S&F03.5/45, P04/1, PEA21/5, PEA25/5]
6. Cheliceral fixed finger, median and basal teeth, fusion: fused into bicuspid ('conjoined on trunk') (0); separate (1); unknown (?). [S&S01/9, S&F03.5/44, PEA21/6, PEA25/6]
7. Cheliceral moveable finger, dorsal margin, basal teeth: absent (0); one (1); two (2); unknown (?). [S89/33, S&S01/2, S&F03.5/40, PEA21/7, PEA25/7]
8. Cheliceral moveable finger, ventral margin, teeth or denticles: two large, subequal median teeth (0); four or five ventral accessory denticles (crenulate margin) (1); unknown (?). [S89/34–36, S&S01/4, S&F03.5/42, 43, PEA21/8, PEA25/8]
9. Cheliceral moveable finger, ventral margin, serrula: absent (0); present (1); unknown (?). [S89/34–36, S&S01/4, S&F03.5/42, 43, PEA21/9, PEA25/9]

CARAPACE

10. Carapace posterior width, relative to length: posterior width greater than length (0); posterior width similar to or less than length (1); unknown (?). [PEA21/10, PEA25/10]
11. Carapace anteromedian margin, alignment relative to anterolateral margins: anteromedian margin recessed, posterior to anterolateral margins (0); anteromedian margin aligned with anterolateral margins (1); anteromedian margin protruding, anterior to anterolateral margins (2); unknown (?). [PEA21/11, PEA25/11]
12. Carapace anteromedian margin, curvature: sublinear (0); convex (procurved) (1); shallowly concave (re-curved) (2); unknown (?). [PEA21/12, PEA25/12]
13. Carapace anterolateral margins: entire (0); with pronounced incision lateral to lateral ocelli (rostrrolateral incision) (1); unknown (?). [PEA21/13, PEA25/13]
14. Carapace anteromedian depression, dimensions: broad, deep (0); narrow, shallow (1); narrow, deep (2); unknown (?). [PEA21/14, PEA25/14]
15. Carapace anterosubmedial depressions, medial to lateral ocelli: absent (0); vestigial (1); well developed (2); unknown (?). [PEA21/15, PEA25/15]
16. Carapace anterosubmedial lyriform carinae, vertical development and macrosculpture: absent (0); obsolete, granular (1); pronounced, costate-granular (2); unknown (?). [PEA21/16, PEA25/16]
17. Carapace median ocular tubercle (or eyeless surface representing ocular tubercle), distance from anterior margin relative to carapace length: medial (0); anteromedial (1); unknown (?). [PEA21/17, PEA25/17]
18. Carapace median ocelli: present (0); absent (1); unknown (?). [PEA21/18, PEA25/18]
19. Carapace interocular sulcus (regardless of presence or absence of median ocelli), depth: deep (0); shallow (1); unknown (?). [PEA21/19, PEA25/19]
20. Carapace circumocular sutures: absent (0); present (1); unknown (?). [PEA21/20, PEA25/20]
21. Carapace circumocular sutures, development: complete, connected posteriorly (post-ocular) (0); complete, disconnected posteriorly (1); partial (disconnected) (2); unknown (?); inapplicable (-). [PEA21/21, PEA25/21]
22. Carapace circumocular triangle (regardless of presence or absence of median ocelli), shape: subtriangular (broad V-shape), median ocular curvatures present (0); parallel-sided (U-shape), median ocular curvatures absent (1); unknown (?); inapplicable (-). [PEA21/22, PEA25/22]
23. Carapace circumocular sulci, posterior margin, distance from anterior margin relative to carapace length: anteromedial (0); medial (1); posteromedial (2); unknown (?); inapplicable (-). [PEA21/23, PEA25/23]
24. Carapace lateral ocelli, anterolateral major (ALMa) ocelli: present (0); absent (1); unknown (?). [PEA21/24, PEA25/24]
25. Carapace lateral ocelli, mediolateral major (MLMa) ocelli: present (0); absent (1); unknown (?). [PEA21/25, PEA25/25]
26. Carapace lateral ocelli, posterolateral major (PLMa) ocelli: present (0); absent (1); unknown (?). [PEA21/26, PEA25/26]
27. Carapace lateral ocelli, posterolateral major (PLMa) ocelli, size: small (0); large (1); unknown (?). This new character was added in the present study.
28. Carapace lateral ocelli, anterodorsal minor (ADMi) ocelli: present (0); absent (1); unknown (?). [PEA21/27, PEA25/27]
29. Carapace lateral ocelli, posterodorsal minor (PDMi) ocelli: present (0); absent (1); unknown (?). [PEA21/28, PEA25/28]
30. Carapace lateral eyespot: absent (0); present (1); unknown (?). [PEA21/29, PEA25/29]
31. Carapace circumocular surfaces: mostly granular (0); mostly smooth except for sparse granulation near anterior carapace margin (1); entirely smooth (2); unknown (?). [PEA21/30, PEA25/30] Prendini *et al.* (in prep.) split the original character (PEA21/30) to create PEA25/30 and 31. State 2 was added for the fossil taxa in the present study.
32. Carapace anterolateral and posteromedian surfaces: mostly granular (0); smooth (1); unknown (?). [PEA21/30, PEA25/31] Prendini *et al.* (in prep.) split the original character (PEA21/30) to create PEA25/30 and 31.
33. Carapace mediolateral surfaces, macrosculpture: granular (0); smooth (1); unknown (?). [PEA21/31, PEA25/32]

34. Carapace posterolateral margins, curvature: gently curved (0); angular, slanting (1); unknown (?). [PEA21/32, PEA25/33]
35. Carapace posteromedian margin, curvature: shallowly concave (recurved) (0); sublinear to shallowly convex (procurved) (1); unknown (?). [PEA21/33, PEA25/34]

PEDIPALPS

36. Pedipalps shape: segments very robust, chela manus in-crassate (0); segments moderately robust, chela manus globose (1); segments gracile, chela manus globose (2); segments gracile, chela manus elongate (3); unknown (?). [PEA21/34, PEA25/35]
37. Pedipalp femur trichobothrium i_2 : absent (0); present (1); unknown (?). [Prendini et al. (2006) preferred hypothesis, PEA21/35, PEA25/36]
38. Pedipalp femur petite trichobothrium i_3 : absent (0); present (1); unknown (?). [Prendini et al. (2006) preferred hypothesis, PEA21/36, PEA25/37]
39. Pedipalp femur petite trichobothrium i_4 : absent (0); present (1); unknown (?). [Prendini et al. (2006) preferred hypothesis, PEA21/37, PEA25/38]
40. Pedipalp femur prodorsal carina, longitudinal development: complete (0); partial (1); unknown (?). [PEA21/38, PEA25/39]
41. Pedipalp femur trichobothrium d_1 , size: petite (0); full size (1); unknown (?). [Prendini et al. (2006) preferred hypothesis, PEA21/39, PEA25/40]
42. Pedipalp femur trichobothria d_1 and i_{1-4} , relative alignment: d_1 aligned with or distal to i_{1-4} (0); d_1 proximal to i_{1-4} (1); unknown (?). [S&S01/38, S&F03.5/5, PEA21/40, PEA25/41]
43. Pedipalp femur petite trichobothrium d_2 : absent (0); present (1); unknown (?). [Prendini et al. (2006) preferred hypothesis, PEA21/41, PEA25/42]
44. Pedipalp femur trichobothrium d_3 , size: petite (0); full size (1); unknown (?). [Prendini et al. (2006) preferred hypothesis, PEA21/42, PEA25/43]
45. Pedipalp femur trichobothrium d_4 , size: absent (0); petite (1); full size (2); unknown (?). [Prendini et al. (2006) preferred hypothesis, PEA21/43, PEA25/44]. States 1 and 2 were accidentally swapped in the original character (PEA21/43). Prendini et al. (in prep.) corrected it to the current version (PEA25/44).
46. Pedipalp femur trichobothrium d_5 : absent (0); present (1); unknown (?). [Prendini et al. (2006) preferred hypothesis, PEA21/44, PEA25/45]
47. Pedipalp femur trichobothrium d_6 , size: petite (0); full size (1); unknown (?). [Prendini et al. (2006) preferred hypothesis, PEA21/45, PEA25/46]
48. Pedipalp femur trichobothria d_3 and d_4 alignment relative to retrodorsal carina: d_4 prolateral to d_3 such that d_3-d_4 directed away from retrodorsal carina (beta configuration) (0); d_3 and d_4 in same axis, such that d_3-d_4 parallel to retrodorsal carina (1); d_4 retrolateral to d_3 such that d_3-d_4 directed toward retrodorsal carina (alpha configuration) (2); unknown (?). [S&F03.5/3, P04/11, PEA21/46, PEA25/47]
49. Pedipalp femur retrodorsal carina, vertical development: absent or obsolete (0); present, distinct (1); unknown (?). [PEA21/47, PEA25/48]
50. Pedipalp femur trichobothrium e_3 : absent (0); present (1); unknown (?). [Prendini et al. (2006) preferred hypothesis, PEA21/48, PEA25/49]
51. Pedipalp femur trichobothrium e_4 : absent (0); present (1); unknown (?). [S&F01/62, S&F03.4/62, PEA21/49, PEA25/50]
52. Pedipalp patella promedian carina ('dorsal patellar spur carina'): present (0); absent (1); unknown (?). [S&F03.5/94 (part), PEA21/50, PEA25/51]
53. Pedipalp patella prolateral surface, dorsoventral projection ('anterior process'): absent (0); moderate (1); pronounced (2); unknown (?). [P00/18, S&S01/16, 17, S&F03.5/97, 98, PEA21/51, PEA25/52]
54. Pedipalp patella prolateral surface, dorsoventral projection, pair of spiniform granules proximally (dorsal and ventral 'patellar spurs' situated proximally on dorsal and ventral prolateral carinae, respectively): present (0); absent (1); unknown (?). [P00/18, S&S01/16, 17, S&F03.5/97, 98, PEA21/52, PEA25/53]
55. Pedipalp patella trichobothrium i_2 : absent (0); present (1); unknown (?). [S&F01/28, S&F03.4/28, PEA21/53, PEA25/54]
56. Pedipalp patella dorsomedian carina: present (0); absent (1); unknown (?). [S&F03.5/95, PEA21/54, PEA25/55]
57. Pedipalp patella trichobothrium d_3 : absent (0); present (1); unknown (?). [S&F01/31, S&F03.4/31, PEA21/55, PEA25/56]
58. Pedipalp patella trichobothrium d_4 : absent (0); present (1); unknown (?). [S&F01/32, S&F03.4/32, PEA21/56, PEA25/57]
59. Pedipalp patella petite trichobothrium d_5 : absent (0); present (1); unknown (?). [S&F01/33, S&F03.4/33, PEA21/57, PEA25/58]
60. Pedipalp patella retromedian carina: present (0); absent (1); unknown (?). [PEA21/58, PEA25/59]
61. Pedipalp patella trichobothrium em_1 : absent (0); present (1); unknown (?). [S&F01/41, S&F03.4/41, PEA21/59, PEA25/60]
62. Pedipalp patella trichobothrium est , size: petite (0); full size (1); unknown (?). [S&F01/43, S&F03.4/43, PEA21/60, PEA25/61]
63. Pedipalp patella ventromedian carina: present (0); absent (1); unknown (?). [PEA21/61, PEA25/62]
64. Pedipalp patella trichobothria v_1 , v_2 , and v_3 : absent (0); present (1); unknown (?). [S&F01/47-49, S&F03.4/47-49, PEA21/62, PEA25/63]
65. Pedipalp chela manus prolateral dorsal carina (σ), longitudinal development: absent or obsolete (0); complete (1); unknown (?). [PEA21/63, PEA25/64]
66. Pedipalp chela manus prolateral ventral carina (σ , φ), longitudinal development: absent or obsolete (0); complete (1); unknown (?). [PEA21/64, PEA25/65]

67. Pedipalp chela manus trichobothrium ib_1 : absent (0); present (1); unknown (?). [S&F01/1, S&F03.4/1, PEA21/65, PEA25/66]
68. Pedipalp chela manus petite trichobothrium ib_2 : absent (0); present (1); unknown (?). [Prendini *et al.* (2006) preferred hypothesis, PEA21/66, PEA25/67]
69. Pedipalp chela fixed finger trichobothrium it_1 (*it* situated at base of fixed finger): absent (0); present (1); unknown (?). [S89/70–72, P00/47, S&S01/40, S&F03.5/11, 14, PEA21/67, PEA25/68]
70. Pedipalp chela fixed finger trichobothrium it_2 (*it* situated in proximal third of fixed finger): absent (0); present (1); unknown (?). [S89/70–72, P00/47, S&S01/40, S&F03.5/11, 14, PEA21/68, PEA25/69]
71. Pedipalp chela fixed finger trichobothrium it_3 (*it* situated distally on finger): absent (0); present (1); unknown (?). [S89/70–72, P00/47, S&S01/40, S&F03.5/11, 14, PEA21/69, PEA25/70]
72. Pedipalp chela manus dorsomedian carina, longitudinal development: absent or obsolete (0); vestigial (1); complete (2); unknown (?). [PEA21/70, PEA25/71]
73. Pedipalp chela manus dorsal secondary and subdigital carinae, longitudinal development: absent or obsolete (0); vestigial (1); complete (2); unknown (?). [PEA21/71, PEA25/72]
74. Pedipalp chela manus digital carina, longitudinal development: absent or obsolete (0); complete (1); unknown (?). [PEA21/72, PEA25/73]
75. Pedipalp chela manus retromedian carina, longitudinal development: absent or obsolete (0); partial (1); complete (2); unknown (?). [PEA21/73, PEA25/74]
76. Pedipalp chela manus secondary accessory and retroventral carinae, fusion: entire (0); incomplete, slight disjunction evident in proximal third (1); unknown (?). [PEA21/74, PEA25/75]
77. Pedipalp chela manus trichobothrium Eb_1 : present (0); absent (1); unknown (?). This character was newly added in the present study.
78. Pedipalp chela manus trichobothrium Eb_3 , size: petite (0); full size (1); unknown (?). [Prendini *et al.* (2006) preferred hypothesis, PEA21/75, PEA25/76]
79. Pedipalp chela manus trichobothrium Est_1 (*Est* situated distal on chela manus): absent (0); present (1); unknown (?). [S89/86, PEA21/76, PEA25/77]
80. Pedipalp chela manus trichobothrium Est_2 (*Est* situated proximal to moveable finger condyle): absent (0); present (1); unknown (?). [S89/86, PEA21/77, PEA25/78]
81. Pedipalp chela manus/fixed finger trichobothrium Et_1 (in Pseudochactidae, and positionally homologous trichobothrium eb in Buthidae and Chaerilidae), position: situated proximally on fixed finger (0); situated on fixed finger, slightly distal to moveable finger condyle (1); situated distally on manus, aligned with or proximal to moveable finger condyle (2); unknown (?). [PEA21/78, PEA25/79]
82. Pedipalp chela manus petite trichobothrium Et_4 : absent (0); present (1); unknown (?). [S&F01/21, S&F03.4/21, PEA21/79, PEA25/80]
83. Pedipalp chela trichobothrium eb (not positionally homologous with eb in Buthidae and Chaerilidae), position: absent (0); present, situated on fixed finger, slightly distal to moveable finger condyle (1); present, situated in proximal third of fixed finger, distal to basalmost retrolateral denticle of median denticle row (2); unknown (?). [PEA21/80, PEA25/81]
84. Pedipalp chela fixed finger petite trichobothrium esb_1 (esb situated in proximal quarter of fixed finger, between second and third most proximal retrolateral denticles of median denticle row): absent (0); present (1); unknown (?). [Prendini *et al.* (2006) preferred hypothesis, PEA21/81, PEA25/82]
85. Pedipalp chela fixed finger trichobothrium esb_2 (in Pseudochactidae, not positionally homologous with esb in Buthidae and Chaerilidae), position: absent (0); situated in proximal third of fixed finger, approximately aligned with proximal retrolateral denticle of median denticle row (1); situated in proximal third of fixed finger, between first and second most proximal retrolateral denticles of median denticle row (2); situated approximately midway on fixed finger, between second and third most proximal retrolateral denticles of median denticle row (3); unknown (?). [PEA21/82, PEA25/83]
86. Pedipalp chela fixed finger trichobothria est and et , position: absent (0); situated medially on finger (1); situated distally on finger (2); unknown (?). [Prendini *et al.* (2006) preferred hypothesis, PEA21/83, PEA25/84]
87. Pedipalp chela manus ventromedian carina, longitudinal development: absent or obsolete (0); vestigial (1); partial (2); unknown (?). [PEA21/84, PEA25/85]
88. Pedipalp chela manus V_1 : absent (0); present (1); unknown (?). [Prendini *et al.* (2006) preferred hypothesis, PEA21/85, PEA25/86]
89. Pedipalp chela manus V_2 : absent (0); present (1); unknown (?). [Prendini *et al.* (2006) preferred hypothesis, PEA21/86, PEA25/87]
90. Pedipalp chela manus V_2 , position: medial (0); near retroventral carina (1); unknown (?); inapplicable (-). [PEA25/88] This character was newly added by Prendini *et al.* (in prep.).
91. Pedipalp chela fixed and moveable fingers, shape lateral aspect (adult ♂): sublinear, similar to adult ♀ (0); sinuous, sexually dimorphic (1); unknown (?). [PEA21/87, PEA25/89]
92. Pedipalp chela fixed finger, median denticle rows, number of subrows: 11 (0); 10 (1); 8 (2); 7 (3); unknown (?). [PEA21/88, PEA25/90]
93. Pedipalp chela moveable finger, median denticle rows, number of subrows: 11 or 12 (0); 10 (1); 8 (2); 7 (3); unknown (?). [PEA21/89, PEA25/91]
94. Pedipalp chela fixed finger, median denticle rows, number of prolateral denticles: 11 (0); 10 (1); 8 (2); 7 (3); 6 (4); unknown (?). [PEA21/90, PEA25/92]
95. Pedipalp chela moveable finger, median denticle rows, number of prolateral denticles: 11 or 12 (0); 10 (1); 8 (2); 7 (3); unknown (?). [PEA21/91, PEA25/93]

96. Pedipalp chela fixed finger, median denticle rows, number of retrolateral denticles: 11 or 12 (0); 9 (1); 7 (2); 6 (3); unknown (?). [PEA21/92, PEA25/94]
97. Pedipalp chela moveable finger, median denticle rows, number of retrolateral denticles: 12 (0); 9 (1); 7 (2); 6 (3); unknown (?). [PEA21/93, PEA25/95]

COXOSTERNUM

98. Leg I, maxillary lobes (coxapophyses), distal edges, shape: unexpanded (non-spatulate) (0); distinctly expanded (spatulate) (1); unknown (?). [L80/5, S&S01/68, S&F03.5/70, PEA21/94, PEA25/96]
99. Leg I, maxillary lobes (coxapophyses), anterior margins, serrula: absent (0); vestigial, few serrations restricted to anterolateral margins (1); distinct, extensive serrations along anterior and lateral margins (2); unknown (?). [PEA25/97] This character was newly added by Prendini *et al.* (in prep.).
100. Sternum shape: pentagonal (0); subtriangular (1); unknown (?). [L80/3, 18, S89/28, P00/9, S&S01/69, S&F03.5/64, PEA21/95, PEA25/98]
101. Sternum lateral margins, curvature: curved medially (0); sublinear (1); unknown (?); inapplicable (-). [PEA21/96, PEA25/99]
102. Sternum ventral surface: flat/planar ('no concave region, minimal outer ridge') (0); shallowly concave ('marginal concave region, minimal outer ridge') (1); markedly concave ('well-developed concave region and outer ridge') (2); unknown (?). [L80/3, 18, S89/28, P00/9, S&S01/69, S&F03.5/64, PEA21/97, PEA25/100]

LEGS

103. Legs III and IV, tibial spurs: present (0); absent (1); unknown (?). [S89/89, S&F03.5/59, P04/15, PEA21/98, PEA25/101]
104. Legs I–IV basitarsi and telotarsi, spinules: absent (0); short (1); long (2); unknown (?). [PEA21/99, PEA25/102]
105. Legs I–IV telotarsi, spinule rows: single ventromedian row (0); paired ventrosubmedian rows (1); unknown (?); inapplicable (-). [L80/9, S89/93, 94, 97, P00/68, 70, S&S01/83, 84, 88, 89, S&F03.5/57, 58, PEA21/100, PEA25/103]
106. Legs I–IV telotarsi, paired ventrosubmedian rows of spinules: regular (0); slightly irregular (1); unknown (?); inapplicable (-). [PEA21/101, PEA25/104]
107. Legs I–IV telotarsi, ventrosubmedian rows of (socketed) macrosetae: present (0); absent (1); unknown (?). [L80/9, S89/93, 94, 97, P00/68, 70, S&S01/83, 84, 88, 89, S&F03.5/57, 58, PEA21/102, PEA25/105]

GENITAL OPERCULUM

108. Genital papillae (♂), length relative to genital opercula: inconspicuous (0); conspicuously visible

along entire length of opercula (1); unknown (?). [S&S01/72, S&F03.5/81, PEA21/103, PEA25/106]

REPRODUCTIVE ANATOMY

109. Paraxial organ, accessory glands: absent (0); present (1); unknown (?). [S89/113, PEA21/104, PEA25/107]
110. Hemispermaphore, basal lobe: present (0); absent (1); unknown (?). [S89/112, PEA21/105, PEA25/108]
111. Hemispermaphore, *pars recta*: absent (Chaerilidae, Pseudochactidae) (0); present (Buthidae) (1); unknown (?). [L80/2 (part), S89/110, 111, P00/82, S&S01/74, S&F03.5/73, PEA21/106, PEA25/109]
112. Ovariuterus, number of 'cells' in ovariuterine net (reticulate mesh): six (0); eight (1); unknown (?). [S89/102, S&F03.5/100, PEA21/107, PEA25/110]

PECTINES

113. Pectines, marginal lamellae, fusion: three (0); two (fusion of proximal and medial marginal lamellae) (1); unknown (?). [PEA21/108, PEA25/111]
114. Pectines, marginal and median lamellae, fusion: separate, longitudinal suture between marginal and median lamellae present (0); fused, longitudinal suture between marginal and median lamellae absent (1); unknown (?). [PEA21/109, PEA25/112]
115. Pectines, median lamellae, fusion and number: variously fused, many fewer than pectinal teeth (0); separate, similar number to pectinal teeth (1); unknown (?); inapplicable (-). [PEA21/110, PEA25/113]
116. Pectines, proximal median lamella (scape), angle (♂): acute (0); obtuse (1); unknown (?). [PEA21/111, PEA25/114]
117. Pectines, fulcra: moderate to large (0); small (1); very small (vestigial) (2); unknown (?). [PEA21/112, PEA25/115]
118. Pectines, median lamellae, count: 4 (0); 5–8 (1); 9–10 (2); 11–15 (3); unknown (?); inapplicable (-). [PEA21/113, 114, PEA25/116] Prendini *et al.* (in prep.) fused the original male and female characters (PEA21/113, 114) into a single unisex character (PEA25/116) to minimize the effect of missing entries.
119. Pectines, tooth count: >20 (0); 13–16 (1); 9–12 (2); 7 or 8 (3); 5 or 6 (4); 3 or 4 (5); unknown (?). [PEA21/115, 116, PEA25/117] Prendini *et al.* (in prep.) fused the original male and female characters (PEA21/115, 116) into a single unisex character (PEA25/117) to minimize the effect of missing entries.
120. Pectinal teeth, peg sensillae, sockets: papillate (0); smooth (1); unknown (?). [PEA21/117, PEA25/118]
121. Pectinal teeth, peg sensillae, length and shape: short, barely protruding from sensilla socket, stout, subcylindrical basally, flattened and truncate distally (0); intermediate, protruding from sensilla socket stout, flattened and truncate distally (1); long, protruding from sensilla socket, cylindrical, tubular or bottle-shaped, and rounded distally (2); unknown (?). [PEA21/118, PEA25/119]

122. Pectinal teeth, peg sensilla, laterodistal processes: absent (0); present (1); unknown (?). [PEA21/119, PEA25/120]

TERGITES

123. Post-tergites I–VI surfaces, macrosculpture: granular (0); smooth or nearly so (1); unknown (?). [PEA21/120, PEA25/121]

STERNITES

124. Sternites VI and VII, ventral surface, macrosculpture (♂): smooth (0); granular (1); unknown (?) [PEA21/121, PEA25/122]
125. Sternite VII, ventral surface, ventrosubmedian and ventrolateral carinae (adult ♂): well developed, costate (0); obsolete, granular (1); absent (2); unknown (?). [PEA21/122, PEA25/123]
126. Sternites III–VI, respiratory spiracles (stigmata), shape: long, slit-like (0); small, circular or oval (1); unknown (?). [L80/20 (part), S&F03.5/101, PEA21/123, PEA25/124]

METASOMA

127. Metasomal segments I–IV, dorsosubmedian and dorsolateral carinae, posterior granules size relative to preceding granules: similar (0); markedly larger and spiniform (1); unknown (?). [PEA21/124, PEA25/125]
128. Metasomal segment V, dorsolateral carinae, vertical development: distinct (0); obsolete (1); unknown (?). [PEA21/125, PEA25/126]
129. Metasomal segments I and II, median lateral carinae, longitudinal development: absent or obsolete (segments I and II) (0); complete (segment I), partial, becoming obsolete anteriorly (segment II) (1); complete (segments I and II) (2); unknown (?). [PEA21/126, PEA25/127] The states in previous versions of this character were revised to accommodate a third state observed in the fossil taxa.
130. Metasomal segments III and IV, median lateral carinae, longitudinal development: absent or obsolete (segments III and IV) (0); partial, becoming obsolete anteriorly (segment III), vestigial or absent (segment IV) (1); complete (segments III and IV) (2); unknown (?). [PEA21/127, PEA25/128] The states in previous versions of this character were re-

vised to accommodate a third state observed in the fossil taxa.

131. Metasomal segment V, median lateral carinae, longitudinal development: absent or obsolete (0); partial (1); complete (2); unknown (?). [S&F03.5/86, PEA21/128, PEA25/129]
132. Metasomal segment I, ventrosubmedian carinae (♂): distinct (0); absent or obsolete (1); unknown (?). [PEA21/129, PEA25/130]
133. Metasomal segment I, ventrosubmedian carinae, vertical development: distinct (0); absent or obsolete (1); unknown (?). [PEA21/130, PEA25/131]
134. Metasomal segments II–IV, ventrosubmedian carinae, vertical development: distinct (0); absent or obsolete (1); unknown (?). [PEA21/131, PEA25/132]
135. Metasomal segment V, ventrosubmedian carinae, longitudinal development: complete (0); partial (1); absent (2); unknown (?). [S&F03.5/84, PEA21/132, PEA25/133]
136. Metasomal segment V, ventrosubmedian carinae, posterior orientation: diverging (0); converging (1); unknown (?); inapplicable (-). [S&F03.5/84, PEA21/133, PEA25/134]
137. Metasomal segment V, ventromedian carina, vertical development: absent or obsolete (0); distinct (1); unknown (?). [PEA21/134, PEA25/135]

TELSON

138. Telson vesicle, shape: globose (0); elongate (1); unknown (?). [PEA21/135, PEA25/136]
139. Telson vesicle surfaces, macrosculpture (♂): lateral and ventral surfaces with granular carinae (0); lateral and ventral surfaces smooth or nearly so (1); unknown (?). [PEA21/136, PEA25/137]
140. Telson vesicle surfaces, macrosculpture (♀): lateral and ventral surfaces with granular carinae (0); lateral and ventral surfaces smooth or nearly so (1); unknown (?). [PEA21/137, PEA25/138]
141. Telson vesicle, venom gland epithelium walls, folding: simple, unfolded (0); complex, folded (1); unknown (?). [S89/137, P00/113, S&S01/14, S&F03.5/99, PEA21/138, PEA25/139]
142. Telson subaculear tubercle: absent (0); obsolete, very small bump (1); unknown (?). [PEA21/139, PEA25/140]
143. Telson aculeus, length and shape: long, deeply curved (0); short, shallowly curved (1); unknown (?). [PEA21/140, PEA25/141]

APPENDIX 2

Ratios and counts for 11 new specimens of Chaerilobuthinae Lourenço, 2011, stat. nov., in the collections of the Nanjing Institute of Geology and Palaeontology (NGIP 200654–200657, 201158–201164) used in parsimony analysis. Abbreviations as follows: Cbru = *Chaerilobuthus bruckschi*

Lourenço, 2015; Ccom = *Chaerilobuthus complexus* Lourenço and Beigel, 2011; Ceni = *Chaerilobuthus enigmaticus* Lourenço, 2015; Cgig = *Chaerilobuthus gigantosternum* Lourenço, 2016; Chan = *Chaerilobuthus hansgeorgmuelleri* Lourenço, 2019; Ckno = *Chaerilobuthus knodelorum* Lourenço, 2018; Cser = *Chaerilobuthus serratus* Lourenço, 2016.

	Cbru	Cbru	Ccom	Ccom	Ceni	Ceni	Cgig	Chan	Ckno	Cser	Cser
	201161	201162	200655	201160	201158	201159	200654	201164	200657	200656	201163
Carapace anterior W : L	0.52	0.49			0.60		0.58	0.63		0.61	0.52
Carapace posterior W : L	0.88	0.87				0.86	0.80	1.06		0.84	0.81
Carapace L : mesosoma L	0.53	0.83	0.70		0.48	0.54	0.65		0.39	0.58	0.51
Pedipalp femur W : L		0.30	0.29	0.31	0.39	0.40	0.38	0.39	0.36	0.32	0.27
Pedipalp patella W : L	0.30	0.28	0.29	0.27	0.32	0.31	0.33	0.40	0.28	0.26	0.26
Pedipalp chela manus W : chela L		0.17	0.28	0.21	0.28	0.31	0.23	0.38	0.27	0.20	0.20
Pedipalp moveable finger L : chela L		0.66	0.61	0.63	0.52	0.56	0.61	0.51	0.61	0.59	0.66
Mesosoma L : metasoma L	0.75	0.49			0.82	0.69	0.71			0.66	0.74
Metasomal segment I W : L	1.41	1.32	1.89	1.53		1.51	1.20		1.27		
Metasomal segment II W : L	1.26	1.06		1.22		1.15	1.10				
Metasomal segment III W : L	1.22	1.03		1.05		1.08	0.92				
Metasomal segment IV W : L	0.79	0.68		0.64		0.80	0.60				
Metasomal segment V W : L	0.45	0.36		0.39		0.41					
Metasomal segment I : segment II L	0.91	0.90	0.84	0.83	0.78	0.80	0.95		0.95	0.97	1.00
Metasomal segment II : segment III L	0.95	0.97	0.74	0.93	0.91	0.96	0.81		0.83	0.90	0.92
Metasomal segment III : segment IV L	0.64	0.68		0.62	0.71	0.74	0.74		0.71	0.58	0.68
Metasomal segment IV : segment V L	0.53	0.55		0.58	0.47	0.48	0.66			0.60	0.58
Metasomal segment V : telson L	0.90	0.91		0.92	0.96	1.10				0.88	0.87
Metasomal segment V : telson vesicle W	1.20	0.94									
Telson vesicle W : telson L	0.34	0.35									
Telson vesicle H : telson L					0.32	0.44				0.28	0.29
Telson L : mesosoma L	0.45	0.42		0.43	0.44	0.37				0.44	0.43
Pectinal tooth count (sinistral)	6		5	5	5	5	5	5	5	5	5
Pectinal teeth (dextral)			5	5	5	5	5	5	5	5	5

APPENDIX 3

Ratios and counts for holotypes of described species of Chaerilobuthinae Lourenço, 2011, stat. nov., and a male of the type species of Pseudochactidae Gromov, 1998 from the literature (Prendini *et al.* 2006, Lourenço and Beigel 2011, Lourenço 2013, 2015a, b, 2016b, 2018, Lourenço and Velten 2015, 2019, 2020, 2021, 2022) used in parsimony analysis. Abbreviations as follows: Cbir = *Chaerilobuthus birmanicus* Lourenço, 2015; Cbra = *Chaerilobuthus brandti* Lourenço, 2022; Cbri = *Chaerilobuthus brigittemuelleri* (Lourenço, 2020), comb. nov.; Cbru = *Chaerilobuthus bruckschi* Lourenço,

2015; Ccom = *Chaerilobuthus complexus* Lourenço and Beigel, 2011; Ceni = *Chaerilobuthus enigmaticus* Lourenço, 2015; Cgig = *Chaerilobuthus gigantosternum* Lourenço, 2016; Chan = *Chaerilobuthus hansgeorgmuelleri* Lourenço, 2019; Ckno = *Chaerilobuthus knodelorum* Lourenço, 2018; Clon = *Chaerilobuthus longiaculeus* Lourenço, 2013; Cmeg = *Chaerilobuthus meggeri* Lourenço, 2021; Cpet = *Chaerilobuthus petersi* Lourenço, 2024; Cschm = *Chaerilobuthus schmidtii* Lourenço, 2024; Cschw = *Chaerilobuthus schwarzi* Lourenço, 2015; Cser = *Chaerilobuthus serratus* Lourenço, 2016; Csta = *Chaerilobuthus staxi* Lourenço, 2024; Povc = *Pseudochactas ovchinnikovi* Gromov, 1998.

	Cbir	Cbra	Cbri	Cbru	Ccom	Ceni	Cgig	Chan	Ckno	Clon	Cmeg	Cpet	Cschm	Cschw	Cser	Csta	Povc
Carapace anterior W : L	0.67	0.74	0.52		0.77			0.65	0.53		0.66	0.52	0.55	0.61		0.66	0.61
Carapace posterior W : L		1.16	0.86		0.91			1.04	0.88		0.83	0.52	0.63	1.08		0.68	1.00
Carapace L : mesosoma L	0.45	0.50	0.82	0.33	0.70	0.63	0.68	0.53	0.51		0.63	0.67	0.93	0.51	0.55	0.77	0.40
Pedipalp femur W : L	0.21	0.30	0.36		0.33		0.23	0.47	0.40		0.34	0.56	0.37	0.41	0.27	0.38	0.33
Pedipalp patella W : L	0.29	0.18	0.40	0.36	0.33		0.36	0.48	0.27		0.35	0.32	0.34	0.40	0.25	0.32	0.44
Pedipalp chela manus W : chela L	0.29	0.12	0.26	0.18	0.18		0.25	0.41	0.29		0.26	0.16	0.27	0.26	0.21	0.14	0.31
Pedipalp moveable finger L : chela L	0.52	0.67	0.58	0.50	0.68			0.44	0.60		0.50	0.62	0.54	0.54		0.53	0.56
Mesosoma L : metasoma L	0.73	0.60	0.43	0.95	0.76		0.61	0.62	0.70		0.59	0.86	0.60	0.77	0.66	0.72	0.69
Metasomal segment I W : L		1.43	1.27	0.83				1.57	1.19		1.89		1.52	1.33	1.28	1.13	1.24
Metasomal segment II W : L		1.15	1.16	0.57				1.23	1.00				1.22	1.00	1.00	0.96	1.00
Metasomal segment III W : L		0.81	0.94	0.51			0.68	1.08	0.79				1.02	0.91	-	0.97	0.92
Metasomal segment IV W : L		0.57	0.77	0.40	0.45		0.50	0.92	0.57							0.73	0.65
Metasomal segment V W : L		0.28	0.57	0.21			0.43	0.62	0.30							0.48	0.37
Metasomal segment I : segment II L		1.00	0.91	0.85	0.79		1.00	0.78	0.93		0.93	0.91	0.86	1.00	0.87	0.89	0.88
Metasomal segment II : segment III L		0.70	0.86	0.89	0.70		0.85	0.81	0.85	1.00	0.85	0.85	0.84	0.91	0.81	0.93	0.92
Metasomal segment III : segment IV L		0.71	0.82	0.79	0.65		0.74	0.85	0.78	0.92	0.82	0.73	0.75	0.62	0.71	0.78	0.76
Metasomal segment IV : segment V L		0.56	0.74	0.56	0.65		0.68	0.62	0.53	0.67	0.42	0.50	0.53	0.57	0.59	0.55	0.57
Metasomal segment V : telson L		0.96	0.82	0.90	0.89		0.85	1.07	0.97	1.20	1.05	0.96	0.94	0.87	0.92	0.86	0.95
Metasomal segment V : telson vesicle W		0.55	1.00	0.60				1.06	1.26							1.14	0.92
Telson vesicle W : telson L		0.49	0.47	0.31	0.48			0.63	0.23							0.36	0.38
Telson vesicle H : telson L		0.32		0.35	0.31		0.43			0.53	0.42	0.22	0.32	0.35	0.23		0.35
Telson L : metasoma L		0.31	0.41	0.37	0.41	0.44	0.39	0.32	0.39		0.41	0.42	0.42	0.45	0.41	0.42	0.38
Pectinal tooth count (sinistral)	0.31	0.41	0.37	0.41	0.44	5	5	6	5	7	7	10	5	6	5	5	11
Pectinal teeth (dextral)		8	6	6	4	4	4	5	5	6	6	11	5	6	5	5	10

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