Two New Species of Cretaceous Scorpions from Burmese Amber (Arachnida: Scorpiones: Palaeoburmesebuthidae)[1]

Jorge A. Santiago-Blay[2], Michael E. Soleglad[3], Victor Fet[4], Patrick R. Craig[5], and Larry B. Smith[6]

http://www.zoobank.org/urn:lsid:zoobank.org:pub:4164C1D5-DAFF-4EA7-9011-376FC11F0443

Abstract: Two new fossil scorpion species, tentatively placed in the genus *Palaeoburmesebuthus* Lourenço, 2002 (family Palaeoburmesebuthidae Lourenço, 2015), *P. smithi* and *P. andrewrossi*, are described from Cretaceous amber (Lower Cenomanian, circa 99 Ma) of the Hukawng Valley, in northern Myanmar. This description elevates the known number of Palaeoburmesebuthidae species to 16, all from this locality and age.

Key Words: Amber, Myanmar amber, Cretaceous, scorpions, new species, *Palaeoburmesebuthus*

Introduction

Amber, or fossilized plant resinous exudate, has a broad spatiotemporal distribution (Santiago-Blay and Lambert 2007, 2017). According to Zherikhin and Ross (2000), in 1835 Brewster was first in recording amber from Burma (at least to the western world), as the country known today as Myanmar was known until 1989. Yet, mining and trading of amber from Myanmar has been taking place since, at least 100 C. E. (Poinar et al. 2006). Amber from Myanmar comes from several localities (Lambert et al. 2020, Figure 1 therein; Xuan et al. 2022, Figure 1 therein) and, at least, two botanical provenances in the northern part of the country, particularly the Hukawng Valley (Lambert et al. 2020). During the second half of the 19th century, amber from this region of northern Burma was named “Burmite”.

---

[1] Received on August 2, 2022. Accepted on November 28, 2022. Last revisions received on November 28, 2022.
[2] Department of Paleobiology, National Museum of Natural History, Washington, District of Columbia 20560 USA. E-mail: blay@si.edu .
[3] 32255 Safflower Street, Winchester, California 92596 USA. E-mail: msoleglad@gmail.com .
[4] Department of Biological Sciences, Marshall University, Huntington, West Virginia 25755-2510 USA. E-mail: fet@marshall.edu .
[5] Post Office Box 545, Monte Rio, California 95462 USA. E-mail: amberid@comcast.net .
[6] Department of Environmental Protection, Environmental Cleanup and Brownfields Program, 909 Elmerton Avenue, Harrisburg, Pennsylvania 17110 USA. Email: larrysmit@pa.gov .

DOI:10.9784/LEB10(1)SantiagoBlay.02
Electronically available on November 30, 2022. Mailed on November 30, 2022.

The geological age of Burmese amber has long been considered controversial (Cruickshank and Ko 2003). Analyzing the $^{206}Pb/^{238}U$ ratios in sediments containing zircons that surround the amber, Shi et al. (2012) estimated that the age of this amber is 100.5 ± 0.62 Ma (Lower Cenomanian, Cohen et al. 2013, 2022). However, owing to the date's variability using zircons, Mao et al. (2018) suggest that "it is plausible to generally refer to the age of Burmese amber as mid-Cretaceous, and a precise age requires further biostratigraphic and chronological studies."

As of Andrew Ross's most recent tally (Ross 2022b), "of taxa described or recorded from Kachin amber up to the end of August 2022 (excluding trace fossils and marine encrusters) are: 51 classes (or similar rank), 130 orders (or similar rank), 689 families, 1575 genera and 2390 species. This includes 8 classes, 66 orders, 612 families, 1445 genera and 2241 species of arthropods" (see also Ross 2019, 2022a). The first scorpion fossil from Burmite (the Cretaceous amber of northern Myanmar, or Burma), *Palaeoburmesebuthus grimaldii,* was described by Lourenço (2002) based on a single metasoma, or tail (AMNH). Two years later, our research team (Santiago-Blay et al. 2004a) complemented this finding by publishing data on another specimen (NHM-London), which we incorrectly assigned to the same species. At the time, we considered that the familial placement of *Palaeoburmesebuthus* was unclear. Almost simultaneously, a completely different taxon from Burmite was described, *Electrochaerilus buckleyi* (Santiago-Blay et al. 2004b) and placed in a modern family, the Chaerilidae.

About a decade later, a remarkable treasure trove of Burmite scorpions began to be described by W. R. Lourenço and his collaborators, such as A. Beigel, A. Rossi, and J. Velten, who have named as many as 37 new species of scorpions in Burmese amber belonging to seven families (5 of them new to science), 1 new subfamily, and 13 new genera (Lourenço, 2002, 2012, 2013, 2015a, 2015b, 2015c, 2015d, 2016a, 2016b, 2018a, 2018b, 2018c, 2021; Lourenço and Beigel, 2011, 2015; Lourenço and Rossi, 2017; Lourenço and Velten, 2015, 2016a, 2016b, 2016c, 2017, 2019, 2020, 2021a, 2021b, 2022; Rossi, 2015). Out of these papers on Burmite scorpions, 14 were published between 2015–2020 in a relatively new and not widely available journal, *Arachnida – Rivista Aracnologica Italiana*. Currently, the described Burmite scorpiofauna includes eight families, 14 genera, and 41 species (including two new species described in this paper) (Table 1). Besides Table 1, in the Literature Cited section of this paper, we provide a list of all these taxa at the end of the corresponding publications [inside square brackets].

Lourenço (2016b) addressed the Burmite scorpiofauna as having "buthoid" (family Palaeoburmesebuthidae) and "non-buthoid" "elements." In addition, one "buthoid" genus (*Archaeoananteroides*) was placed in the extant family Buthidae (Lourenço and Velten, 2016b). Besides our placement of the genus

Electrochaerilus in the Chaerilidae (Santiago-Blay et al., 2004b), we at this moment purposely refrain from immediate conclusions on the suprageneric placements for the other Burmite taxa, and their coordination with extant families; see also Baptista et al. (2006).

Recently, when another new Burmite fossil came to our attention, its comparison with the numerous species described by Lourenço and his collaborators was facilitated by the permission we received to cut and polish the amber as closely as possible to the specimen. This allowed us to image the specimen in considerable detail and discern many structural details. Also, we returned to our 2004 study of the "second specimen of *Palaeoburmesebuthus grimaldii*" to describe this fragmentary specimen as another new species, although we did not cut and polish the amber close to the specimen. In this paper, we provide formal descriptions of two new species.

Table 1. Burmite scorpion taxa described until the moment of this publication. Taxa are organized alphabetically within each rank. An extensive list of fossil arachnids of the world, including scorpions, is given in Dunlop et al. (2020).

Family	Subfamily	Genus	Species	References
Buthidae C. L. Koch, 1837		*Archaeoananter-oides* Lourenço in Lourenço and Velten, 2016		Lourenço and Velten (2016a)
			A. maderai Lourenço in Lourenço and Velten, 2016 [type species]	Lourenço and Velten (2016a)
Chaerilidae Pocock, 1893	Electochaeril-inae Santiago-Blay et al., 2004			Santiago-Blay et al. (2004b)
		Electrochaerilus Santiago-Blay et al., 2004		Santiago-Blay et al. (2004b)
			E. buckleyi Santiago-Blay et al., 2004 [type species]	Santiago-Blay et al. (2004b)
Chaerilobuth-idae Lourenço, 2013				Lourenço (2013)

Table 1. Continuation

		Chaerilobuthus Lourenço, 2013		Lourenço (2013)
			Ch. bautschi Lourenço in Lourenço and Velten, 2020	Lourenço and Velten (2020)
			Ch. birmanicus Lourenço in Lourenço and Velten, 2022	Lourenço in Lourenço and Velten, 2022
			Ch. brandti Lourenço, 2022 in Lourenço and Velten, 2022	Lourenço and Velten (2022a)
			Ch. bruckschi Lourenço, 2015	Lourenço (2015b)
			Ch. complexus Lourenço and Beigel, 2011	Lourenço and Beigel (2011)
			Ch. enigmaticus Lourenço, 2015	Lourenço (2015c)
			Ch. gigantosternum Lourenço, 2016	Lourenço (2016a)
			Ch. hansgeorgmuelleri Lourenço in Lourenço and Velten, 2019	Lourenço and Velten (2019)
			Ch. knodeli Lourenço, 2018	Lourenço (2018c)
			Ch. knodelorum Lourenço in Lourenço and Velten, 2015	Lourenço and Velten (2015)
			Ch. longiaculeus Lourenço, 2013 [type species]	Lourenço (2013)

Table 1. Continuation				
			Ch. meggeri Lourenço in Lourenço and Velten, 2021	Lourenço and Velten (2021b)
			Ch. schwarzi Lourenço in Lourenço and Velten, 2015	Lourenço and Velten (2015)
			Ch. serratus Lourenço, 2016	Lourenço (2016a)
		Chaeriloiurus Lourenço in Lourenço and Velten, 2020		Lourenço and Velten (2020)
			Ch. brigittemuellerae Lourenço in Lourenço and Velten, 2020 [type species]	Lourenço and Velten (2020)
Palaeoburmese-buthidae Lourenço, 2015				Lourenço (2015b; as subfamily of Archaeobuth-idae Lourenço, 2002)
		Betaburmese-buthus Lourenço in Lourenço and Beigel, 2015		Lourenço and Beigel (2015)
			B. bellus Lourenço, 2016	Lourenço (2016b)
			B. bidentatus Lourenço, 2015	Lourenço (2015a)
			B. fleissneri Lourenço in Lourenço and Velten, 2016	Lourenço and Velten (2016c)
			B. joergi Lourenço and Rossi, 2017	Lourenço and Rossi (2017)
			B. kobberti Lourenço in Lourenço and Beigel, 2015 [type species]	Lourenço and Beigel (2015)

Table 1. Continuation				
			B. larafleissnerae Lourenço in Lourenço and Velten, 2016	Lourenço and Velten (2016b)
			B. spinipedis Xuan, Cai, and Huang, 2022	Xuan, Cai, and Huang (2022)
			B. muelleri Lourenço, 2015	Lourenço (2015a)
		Palaeoburmese-buthus Lourenço, 2002		Lourenço (2002)
			P. andrewrossi **sp. n.**	This paper
			P. grimaldii Lourenço, 2002 [type species]	Lourenço (2002)
			P. longipalpis Lourenço and Rossi, 2017	Lourenço and Rossi (2017)
			P. knodeli Lourenço, 2018	Lourenço (2018a)
			P. ohlhoffi Lourenço, 2015	Lourenço (2015b)
			P. smithi **sp. n.**	This paper
		Spinoburmese-buthus Lourenço in Lourenço and Velten, 2017		Lourenço and Velten (2017)
			Spinoburmesebuthus knodelorum Lourenço, 2021	Lourenço (2021)
			S. pohli Lourenço in Lourenço and Velten, 2017 [type species]	Lourenço and Velten (2017)
Palaeoeu-scorpiidae Lourenço, 2003	Archaeo-scorpiopinae Lourenço, 2015			Lourenço (2015)

Table 1. Continuation

		Archaeo-scorpiops Lourenço, 2015		Lourenço (2015)
			A. cretacicus Lourenço, 2015 [type species]	Lourenço (2015)
		Burmesescor-piops Lourenço, 2016		Lourenço (2016a)
			B. groehni Lourenço, 2016 [type species]	Lourenço (2016a)
		Chaeriloscor-piops Lourenço in Lourenço and Velten, 2020		Lourenço and Velten (2020)
			Ch. bautschi Lourenço in Lourenço and Velten, 2020 [type species]	Lourenço and Velten (2020)
Palaeo-trilineatidae Lourenço, 2012				Lourenço (2012)
		Palaeo-trilineatus Lourenço, 2012		Lourenço (2012)
			P. ellenbergeri Lourenço, 2012 [type species]	Lourenço (2012)
Proto-ischnuridae de Carvalho and Lourenço 2001		*Cretaceo-ushormiops* Lourenço, 2018		Lourenço (2018b)
			C. knodeli Lourenço, 2018 [type species]	Lourenço (2018b)
			C. staxi Lourenço, 2022 in Lourenço and Velten 2022	Lourenço and Velten (2022b)

Table 1. Continuation				
		Cretaceousopisth-acanthus Lourenço, 2021 in Lourenço and Velten 2021	*Cretaceousopisth-acanthus smeelei* Lourenço, 2021 [type species] in Lourenço and Velten 2021	Lourenço and Velten (2021a)
Sucin-lourencoidae Rossi, 2015				Rossi (2015)
		Sucinlourencous Rossi, 2015		Rossi (2015)
			S. adrianae Rossi, 2015 [type species]	Rossi (2015)

Methods

The original specimen of *Palaeoburmesebuthus smithi* sp. n. was embedded in an oval piece of amber measuring approximately 5 cm long x 3.5 cm wide (widest part) x 1 cm thick (thickest part, Figure 1). Currently, the specimen is embedded in a parallelepipedal piece of amber measuring 9.5 x 6 x 2.5 mm.

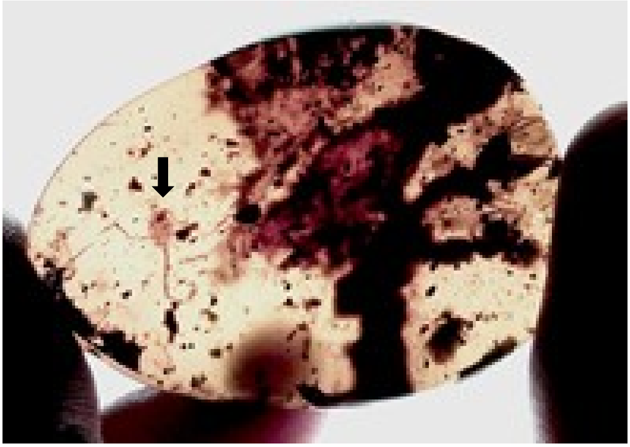


Figure 1. Original specimen of *Palaeoburmesebuthus smithi* sp. n. before cutting and polishing which took place following standard mineralogical protocols. Arrow points to the scorpion.

Scorpion anatomical nomenclature and mensuration follows Stahnke (1971) and Sissom et al. (1990), trichobothrial patterns follow Vachon (1974, 1975).

Photography of *P. smithi* **sp. n.** was performed using an Olympus DSX100 dissecting photomicroscope. The specimen was positioned as perpendicularly to the axis of view as possible while keeping illuminating conditions as consistent as possible throughout the imaging sessions. To enhance the clarity of the imaging, a drop of glycerol or of translucent jelly was placed directly on the area to be photographed and covered with a cover slip (Santiago-Blay 2008) was used. A software internal to the microscope was used stacks images.

Photography of *P. andrewrossi* **sp. n.** was performed using a dissecting microscope (Leica M420 with an Apozoom 1:6 lens to which an additional 2 x objective extension was attached), equipped with a video digital camera (lVC KY-F70BU) and a 'cold' light source. The specimen was imaged while keeping the surface closest to the scorpion covered by a drop of glycerine under a cover slip. Further cutting and polishing was avoided as this unique piece appears fragile. Photography was performed by electronically integrating images taken at slightly different focal planes using Auto-Montage (Synchroscopy, Frederick, Maryland, USA). To facilitate visualization of the structures, we have included labeled duplicates of the images when we deemed it necessary.
In all cases, images were slightly modified to improve their contrast and brightness. Scales bars are not of uniform style because different microscopes were used. Some scales bars are omitted because the specimens could not be positioned perpendicularly to the angle of the light.

Systematics

Family Palaeoburmesebuthidae Lourenço, 2015
Genus *Palaeoburmesebuthus* Lourenço, 2002

http://www.zoobank.org/urn:lsid:zoobank.org:act:4EBC1689-C09E-4763-B8F7-185698F3D31C

***Palaeoburmesebuthus smithi* Santiago-Blay, Soleglad, Craig et Fet, sp. n.**
Figures 1-21, Tables 2-3

http://www.zoobank.org/urn:lsid:zoobank.org:act:CAECDB2E-D795-4BBB-A706-400AD6CDE934

Holotype male, Private collection of Larry Smith (Harrisburg, Pennsylvania, USA, KB838, purchased on July 25, 2016); in Burmese amber (specimen described herein); Hukawng Valley, Kachin, Myanmar (Burma). A small sample of the scorpion entombed in Burmese amber was analyzed via nuclear magnetic resonance spectroscopy and given the number 1767 (Lambert et al. 2020).

Etymology. This new species is named after Larry Smith (Department of Environmental Protection, Harrisburg, Pennsylvania, USA) who kindly loaned us this specimen, and allowed further cutting and polishing of the amber piece to reveal details rarely seen in scorpions preserved in amber.

Figure 2. *Palaeoburmesebuthus smithi* sp. n. Dorsal view, pale background.

Figure 3. *Palaeoburmesebuthus smithi* sp. n. Dorsal view, dark background.

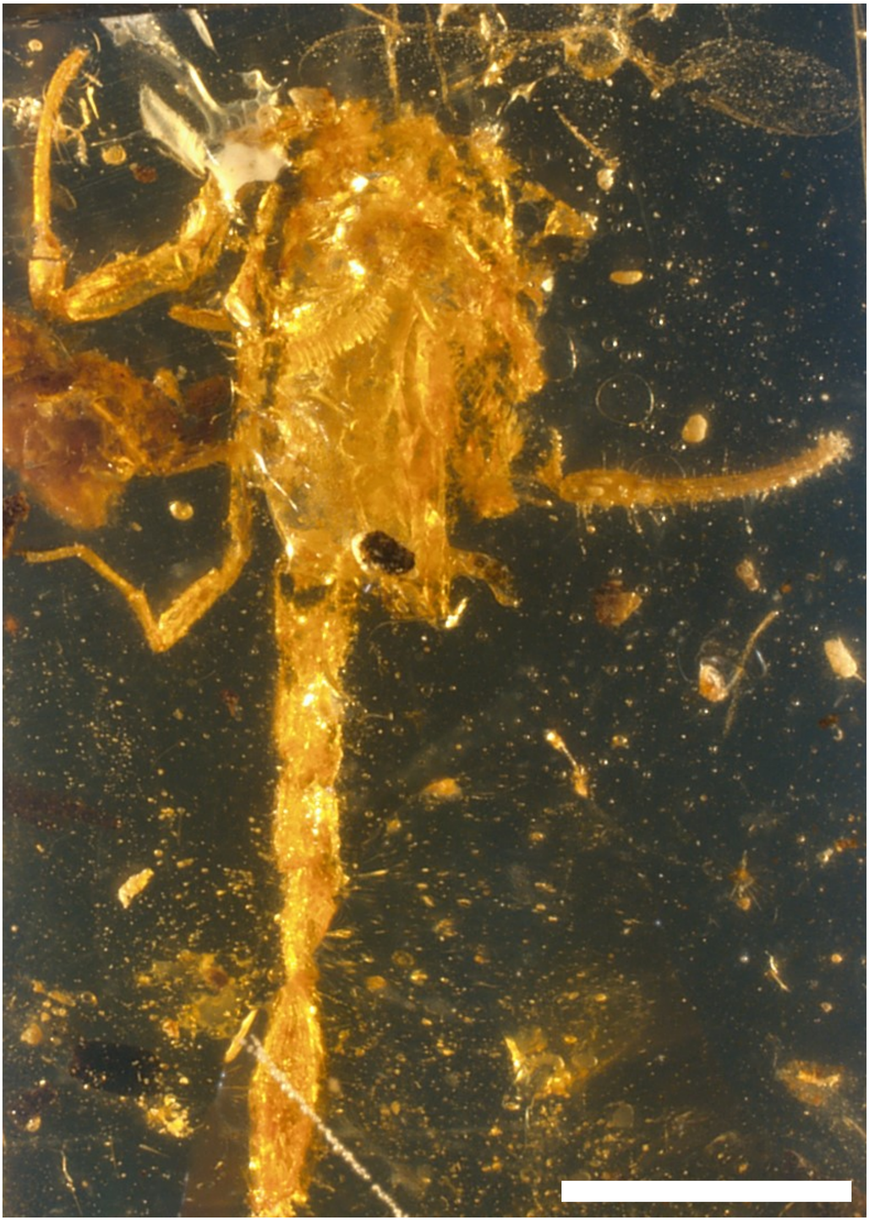


Figure 4. *Palaeoburmesebuthus smithi* sp. n. Ventral with dark background. Scale bar approximately 2 mm.

Description

The following description is based on the only known specimen, the holotype juvenile male. Measurements, in millimeters, are presented in Table 2.

Table 2. Morphometrics (mm) of the two new species herein described.

Body part	Dimension	*P. smithi* sp. n., holotype	Dimension	*P. andrewrossi* sp. n., holotype
Overall size	L	7.96		-
Carapace	L	1.13		-
Mesosoma	L	1.52		-
Metasoma + telson	L	4.18		-
Segment I	L	0.52	L/W/D	1.55/1.08/0.73
Segment II	L	0.66	L/W/D	1.55/1.13/ 0.68
Segment III	L	0.71	L/W/D	1.75/0.85/0.83
Segment IV	L	1.00	L/W/D	2.00/0.75/0.73
Segment V	L	1.29	L/W/D	2.85/0.73/ 0.75
Telson	L	1.13	L	2.83
Vesicle	L/W/D	0.37/0.2 /0.27	L/W/D	1.64 /0.59 / 0.63
Aculeus	L	0.77	L	1.51
Pedipalp	L	3.93		-
Femur	L/W	0.99/0.31		-
Patella	L/W	1.05/0.33		-
Chela	L	1.89	L	2.90
Manus (palm)	L/W	0.60 / 0.24	L/W	0.85 / 0.45
Fixed finger	L	1.29	L	2.05
Movable finger	L	1.36	L	2.40

Abbreviations: L, length; W, width; D, depth. Comment: Many structures are photographed at an angle, thus some of the measurements are only an estimate.

Diagnosis. Small patternless scorpion. Carapace without significant granulation, its anterior edge with a wide median indentation. Sternum wider than long, pentagonal. Mesosomal tergites I–VI with a raised area medially, absent in segment VII. Lateral and median carinae of tergite VII are prominent. Pedipalp extremely slender, with femur and patella more than three times longer than wide. Patella with dorsointernal (DIc), dorsomedian (DMc), and dorsoexternal (DEc) carinae. Chela slender, roughly eight times longer than wide. Both chelal fingers are more than twice as long as the palm and are approximately as long or longer than metasomal segment V. Leg IV with a well-developed tibial spur. Metasoma segment V is 2.49 times longer than segment I. Metasomal segments I and II with the dorsal, dorsolateral, and lateral carinae, segment II with the ventrolateral carina. Slight granulation present on the dorsal carinae, other carinae well developed but smooth. Telson is quite elongated, longer than all metasomal segments except for segment V. The aculeus is quite elongated. No subaculear tubercle.

Appearance. A small juvenile male specimen roughly 8 mm in length. We assume this specimen is male based on its somewhat large pectinal tooth count, relatively elongate teeth of the pecten, seemingly longer than inner margin of coxae IV. In addition, we have detected what might be a genital papilla at the base of the genital operculum. Pectinal teeth elongate, 22 teeth in the right pecten.

Coloration. Basic color is unknown due to the specimen's immersion in amber. However, darker patterns are not evident, so we can probably assume the specimen is essentially patternless.

Carapace (Figure 5). Anterior edge with a wide median indentation providing a ratio of 0.104 when its depth is compared to the carapace's length. A wide triangular depression is present on the posterior medial area of the carapace. The median eye tubercle and eyes are visible but appear to be damaged. The ocular tubercle is placed anteriorly on the carapace, its position compared to the carapace's length is 0.659, measured to posterior carapace margin. Lateral eyes are not detectable. Though the carapace's surface is somewhat rough, it appears to be devoid of any significant granulation.

Chelicerae (Figures 6 and 7). Both chelicerae are visible in the amber but the fingers curve towards the scorpion's ventral side and therefore very little is visible. Certainly, no dentition is discernible.

Sternum (Figure 8). We have isolated what is probably two-thirds of the sternum, its right side. It appears to be wider than long and pentagonal. An apical button is present distally. A posterior emargination and lateral lobes are not present. We assign this sternum to Type 1 (Soleglad and Fet 2003).

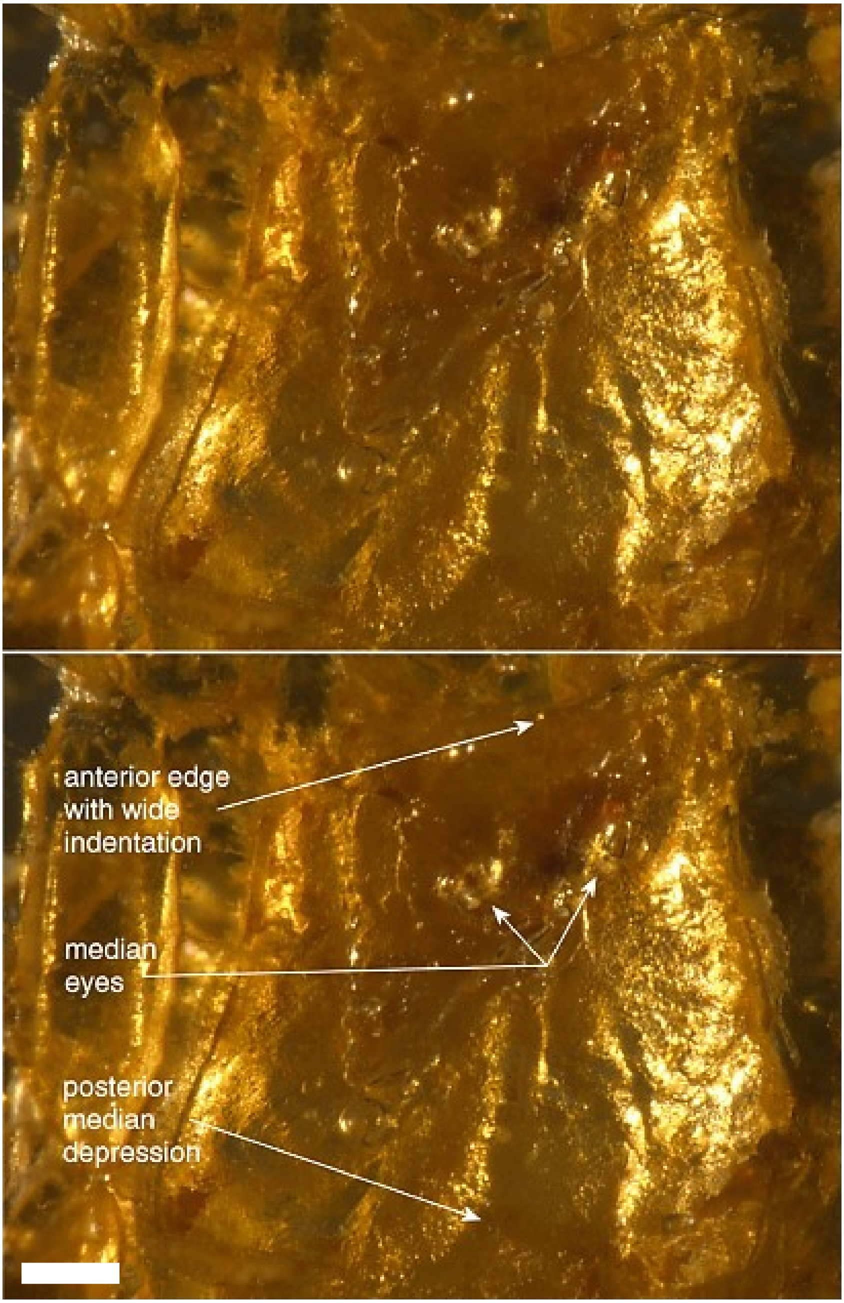


Figure 5. *Palaeoburmesebuthus smithi* sp. n. Carapace (dorsal). Scale bar approximately 200 µm.

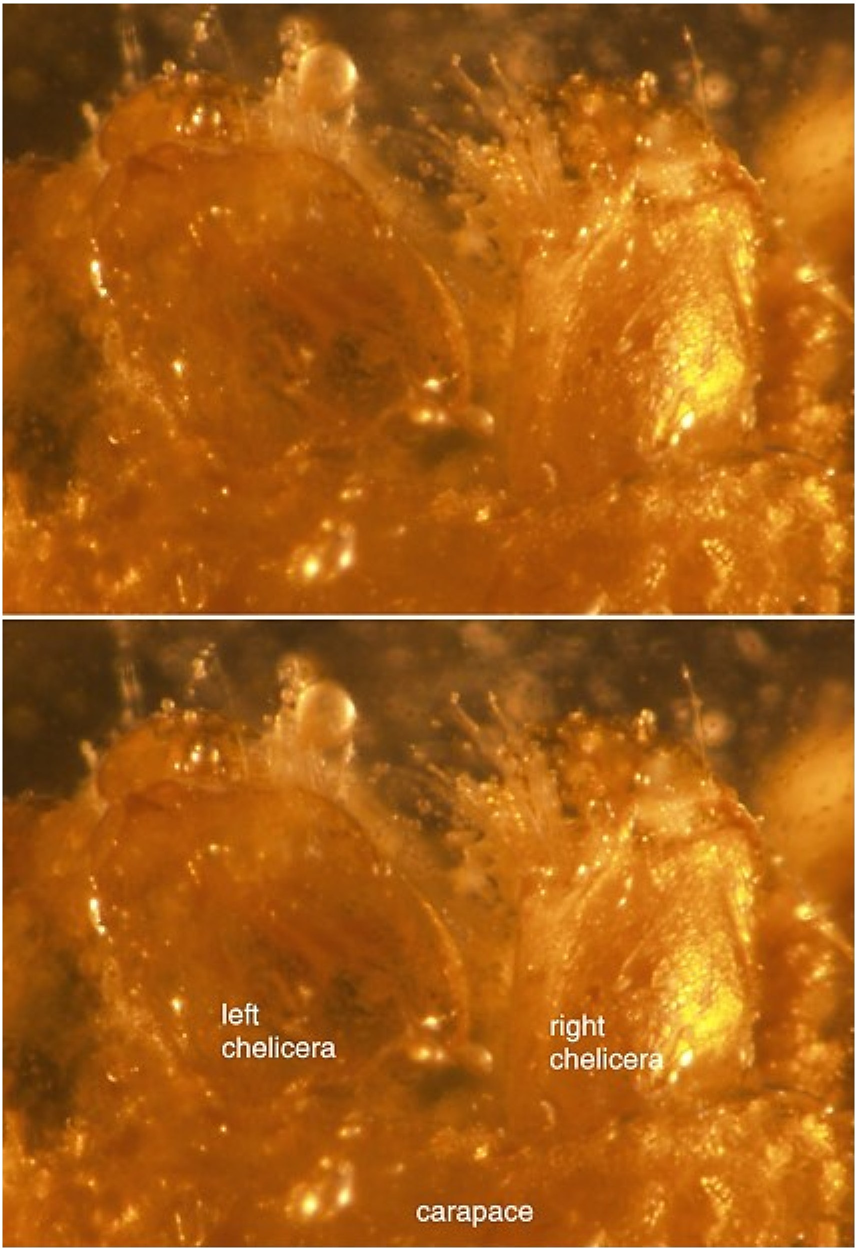


Figure 6. *Palaeoburmesebuthus smithi* sp. n. Left and right chelicerae, dorsal view.

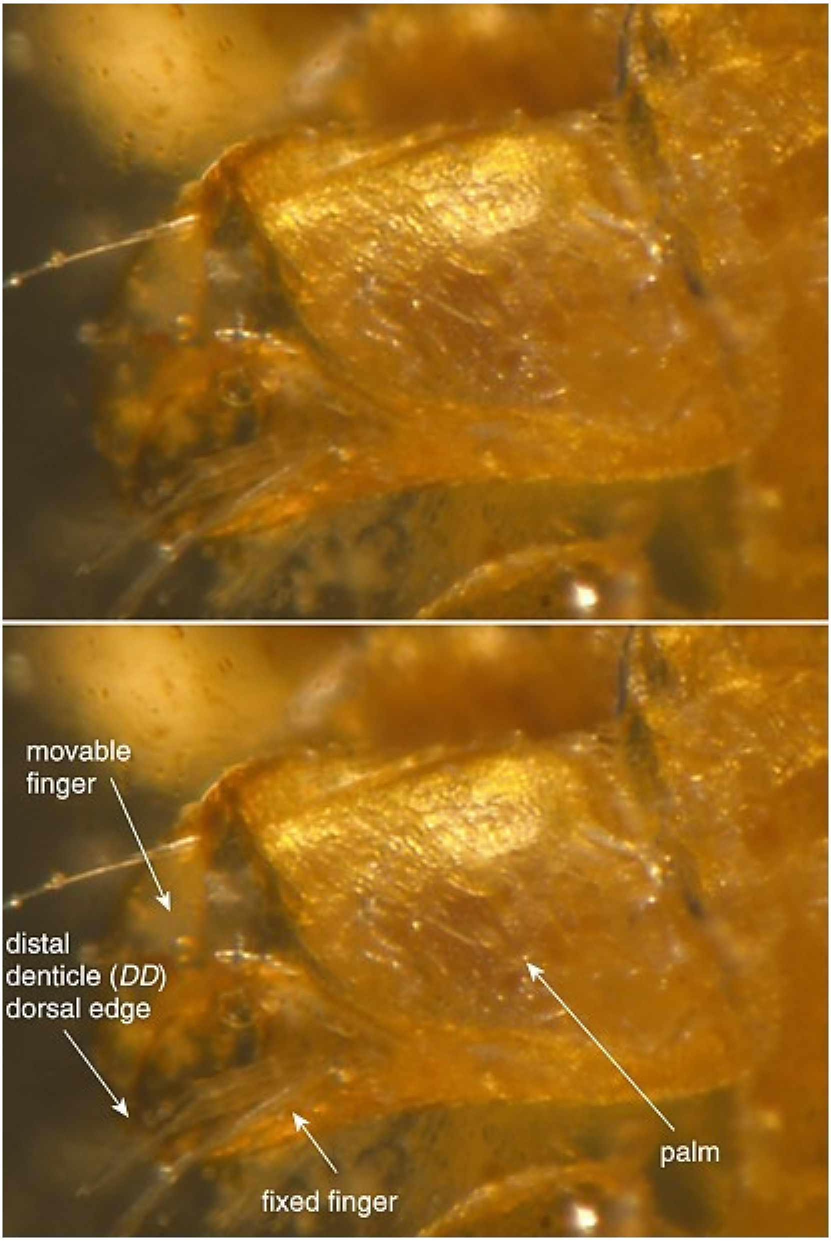


Figure 7. *Palaeoburmesebuthus smithi* sp. n. Closeup of right chelicera, dorsal view.

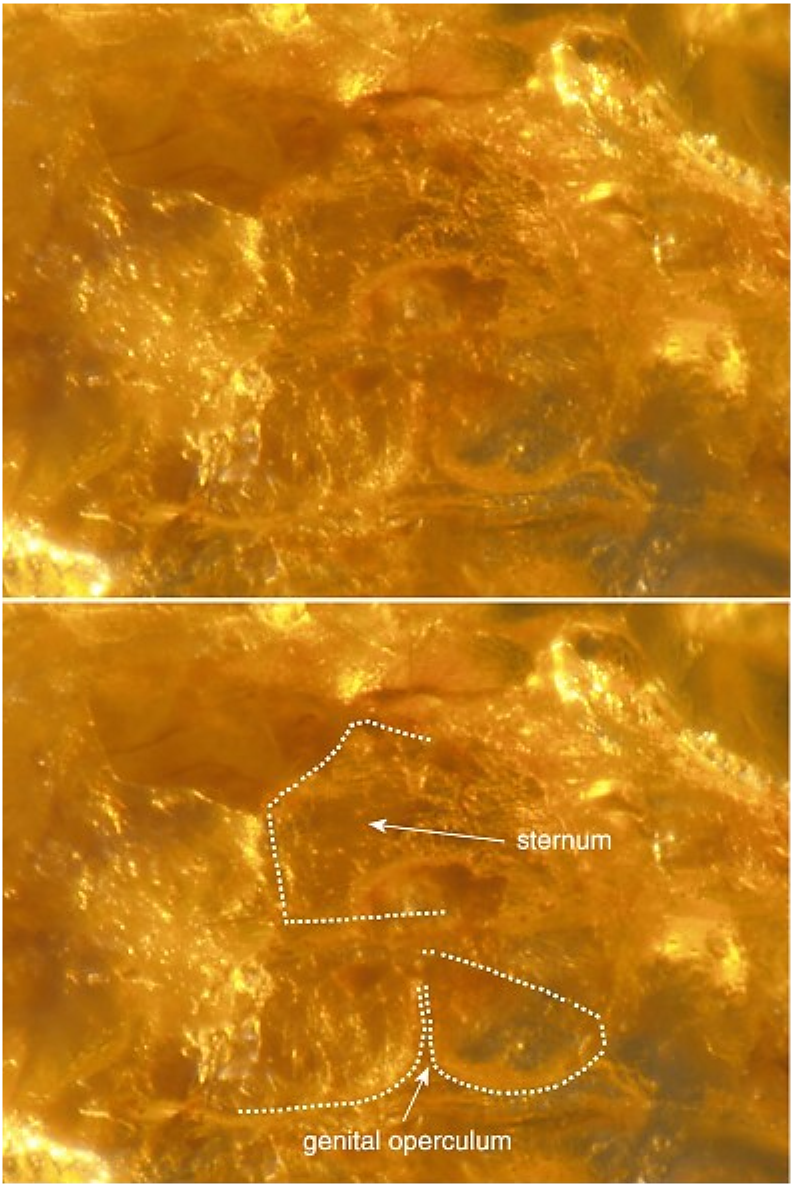


Figure 8. *Palaeoburmesebuthus smithi* sp. n. Closeup of the sternopectinal area. Sternopectinal area showing partial sternum and genital opercula (partially indicated with dotted line). A single genital papilla is also suggested, but this is tentative at best based on the faintness of the possible substructure.

Mesosoma (Figure 9): Tergites I–VII are reasonably visible. Tergites I–VI exhibit a raised area medially though absent in segment VII. Surface is somewhat rough, subtle small granulation is visible in some areas. Lateral and median carinae of tergite VII are prominent, left lateral carina is delicately granulate, right lateral carina not visible. Sternites are severely damaged, stigmata not visible.

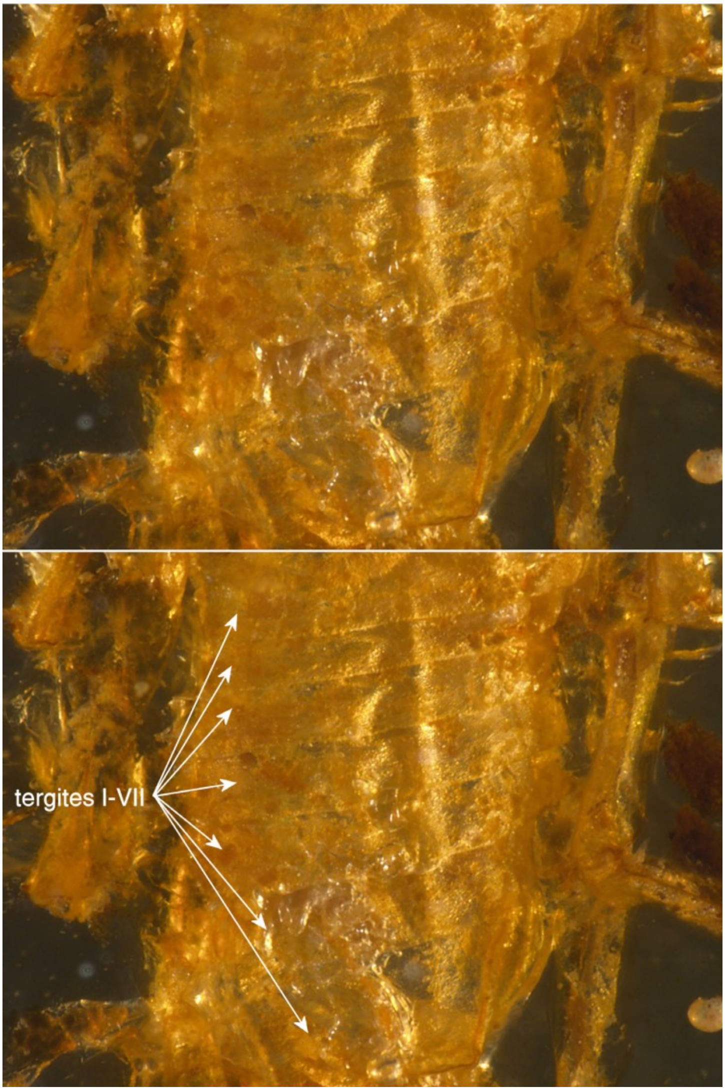


Figure 9. *Palaeoburmesebuthus smithi* sp. n. Dorsal view of mesosoma showing seven tergites, labelled on the bottom panel.

Genital operculum (Figures 8 and 10). The sclerites are partially visible, especially the left sclerite which is wider than long. Proximally the two sclerites are partially separated exhibiting a rounded separation. Visible in this separation is a small projection which may be one of the two genital papillae.

Pectines (Figures 10-11). Both pectines are damaged, especially the left pecten. Only the pectinal teeth are discernible, other sclerites such as the anterior and middle lamellae, or fulcra are not detectable. The pectinal teeth are somewhat elongate, roughly 6.5 times longer than wide. We report 22 teeth in the right pecten but some of the mid-distal tines may be questionable. Individual teeth show a thin ridge traversing the length of the tooth, possibly delineating the sensorial area.

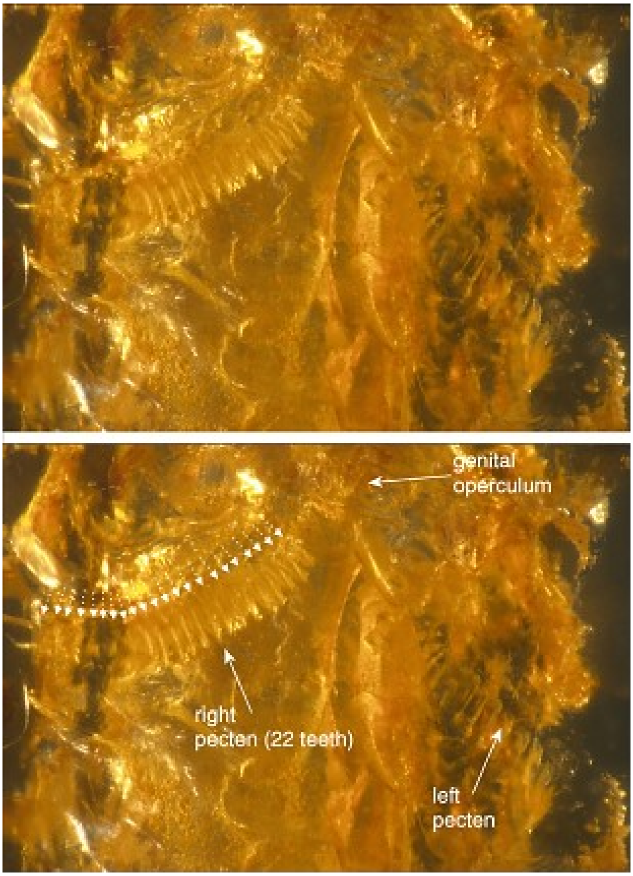


Figure 10. *Palaeoburmesebuthus smithi* sp. n. Overall view of ventral region showing genital operculum and pectines. Arrowheads point to individual pectinal teeth. Right pecten showing 22 teeth.

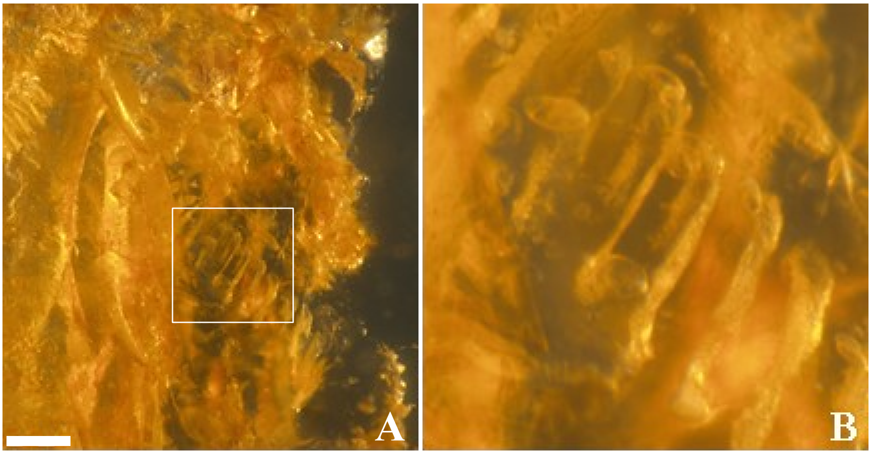


Figure 11. *Palaeoburmesebuthus smithi* sp. n. A. Close-up of part of right pecten. Scale bar approximately 200 µm. B. Close-up of insert in A. Note detail of peg sensillar area preserved on the ventral aspect of pecten teeth.

Pedipalps (Figures 12 and 13). The overall appearance and structure of the right pedipalp is visible in the amber. Pedipalp quite slender, the femur and patella are more than three times longer than wide. The chela is quite slender, roughly eight times longer than wide. Both chelal fingers are more than twice the length of the palm and approximately as long or longer than metasomal segment V. Femur. Only the dorsal surface provides information of the carinae showing dorsointernal (DIc) and dorsoexternal (DEc) carinae, which appear to be modestly granulated. Patella: Only the dorsal surface provides information of the carinae showing dorsointernal (DIc), dorsomedian (DMc), and dorsoexternal (DEc) carinae. These carinae appear to be rough to smooth. Chelal carinae: Carinae are not detectable, but this could be due to the cloudiness of the amber. Chelal finger dentition: The fingers are closed so no clear dentition is visible, except for the distal denticles of the fingertips, and possibly slightly enlarged outer denticles (OD) occurring between median denticle row terminations.

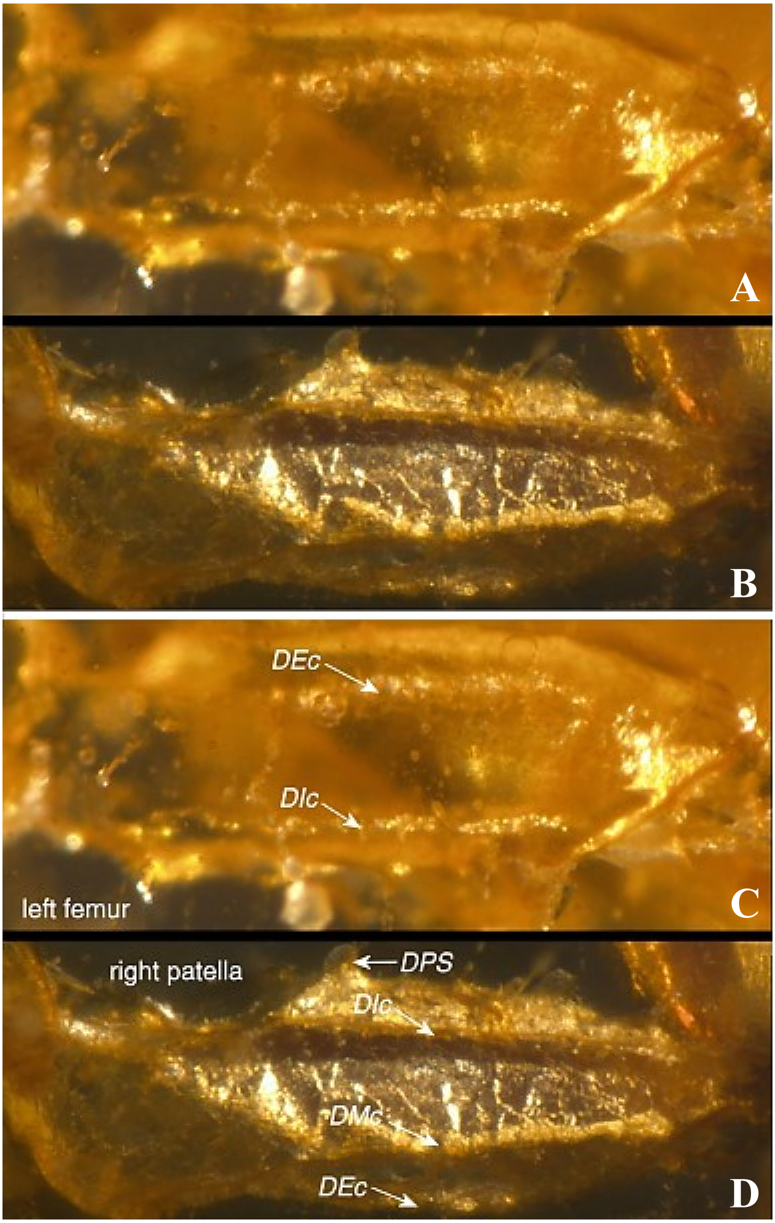


Figure 12. *Palaeoburmesebuthus smithi* sp. n. A and C. Left pedipalp femur, dorsal view. B and D. Right pedipalp patella, dorsal view. *DPS* = dorsal patellar spur, *DIc* = dorsointernal carina, *DMc* = dorsomedian carina, and *DEc* = dorsoexternal carina.

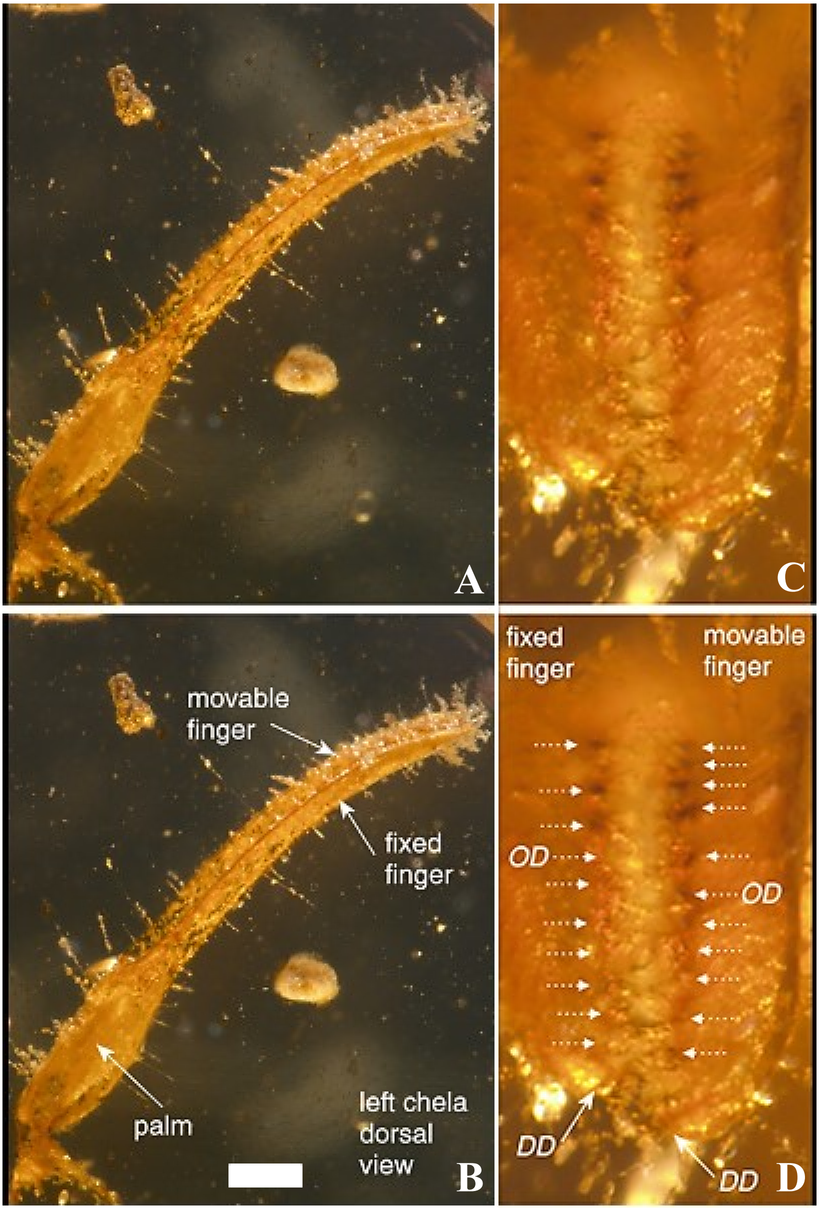


Figure 13. *Palaeoburmesebuthus smithi* sp. n. A and B. Left pedipalp chela, dorsal view. Scale bar approximately 200 µm. C and D. Close-up of chelal finger terminus showing dentition, external view. DD = distal denticle, OD = outer denticle.

Trichobothrial patterns (Figures 14-16). Due to the cloudiness of the amber and the specimen's small size, only 12 potential trichobothria could be isolated (femur: i_{1-3}; patella: *i*, et_1; chela: Eb_1, Eb_2, *Est*, *esb*, *est*, *eb*, *db*). These were identified solely by long thin setal bristles projections. None were identified using areola.

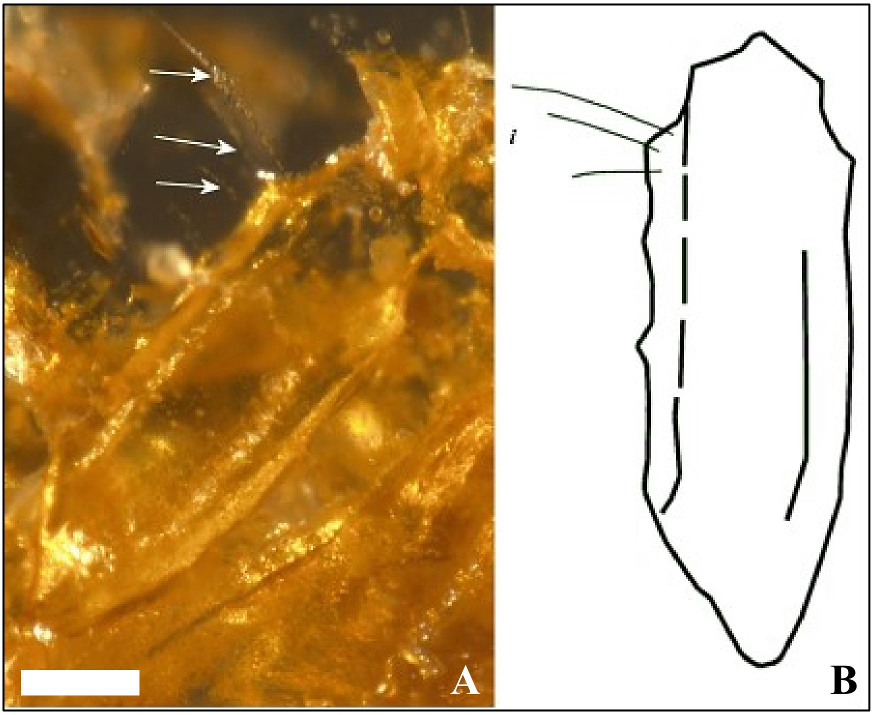


Figure 14. *Palaeoburmesebuthus smithi* sp. n. Left pedipalp femur, dorsal view. A. Potential trichobothria are based solely on long thin setae (arrows) protruding from the internal side. The areolae (or base) of the trichobothrial setae are based on hypothesized positions that are consistent with their suggested labels. B. Interpretation of panel A. The *i* refers to internal trichobothria. Scale bar approximately 200µm.

Legs (Figure 17-18). Leg IV definitely exhibits a well-developed tibial spur. This leg also shows pedal spurs, a unguicular spine, and ungues. However, smaller more delicate spination and/or setation is not visible.

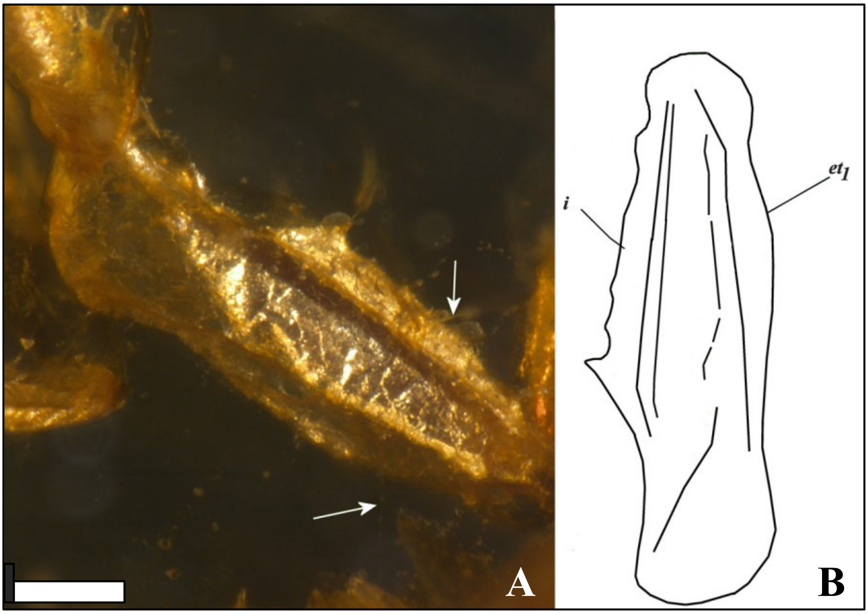


Figure 15. *Palaeoburmesebuthus smithi* sp. n. A. Right pedipalp patella, dorsal view. B. Interpretation of panel A. Potential trichobothria are based solely on long thin setae (arrows) protruding from the internal and external sides. The areolae (or base) of the trichobothrial setae are based on hypothesized positions that are consistent with their suggested labels. The *i* refers to internal trichobothrium; et_1 refers to the external terminal trichobothrium 1. Scale bar approximately 200µm.

Metasoma (Figures 19-20): Metasoma is somewhat slender though individual segment widths were not measurable due to their twisting in the amber. Segment V is 2.49 times longer than segment I. Carinal structure is partially visible on segments I and II exhibiting the dorsal, dorsolateral, and lateral carinae on segments I and II, and the ventrolateral on segment II. Slight granulation is visible on the dorsal carinae, the other carinae visible appear to be well developed but smooth.

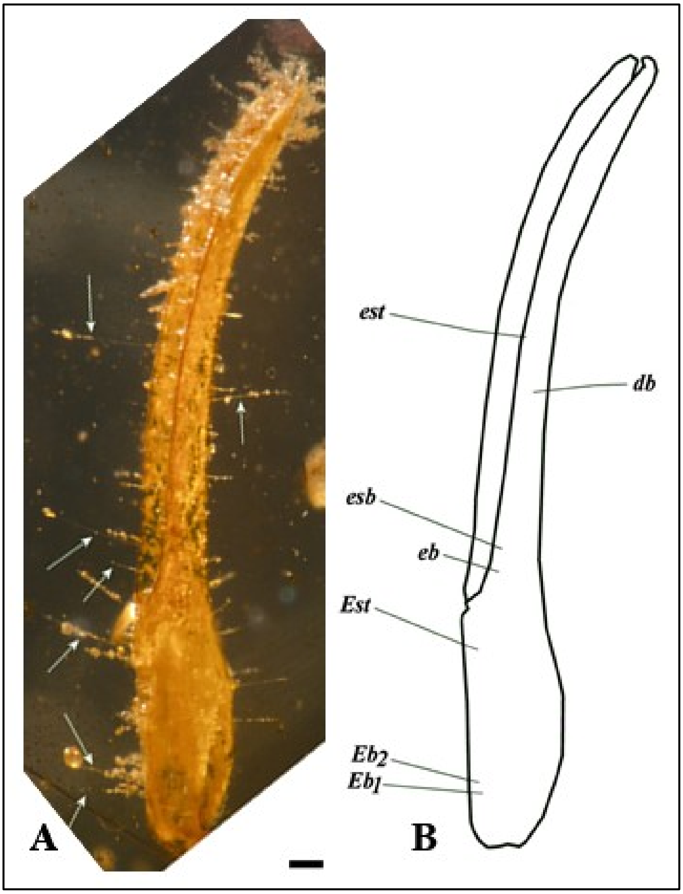


Figure 16. *Palaeoburmesebuthus smithi* sp. n. Left chela (dorsal view). A. Photo. B. Interpretation of panel A. Potential trichobothria are based solely on long thin setae (arrows on A) protruding from the internal and external sides. The areolae (or base) of the trichobothrial setae are based on hypothesized positions that are consistent with their suggested labels. Scale line approximately 100 µm

Telson (Figure 21). Telson is quite elongated, longer than all metasomal segments except for segment V, which is only 1.143 times longer. The aculeus is quite elongated, accounting for 67.7% of the telson's length. There is no apparent subaculear tubercle present, just a small projecting area where the elongated subaculear setal pair originates. The vesicle appears to be somewhat rough in texture, but no obvious granulation is present. A vesicular tab is visible at the base of the vesicle. Several elongated setae project from the vesicle's ventral surface and a couple of elongated setae project from the base of the aculeus.

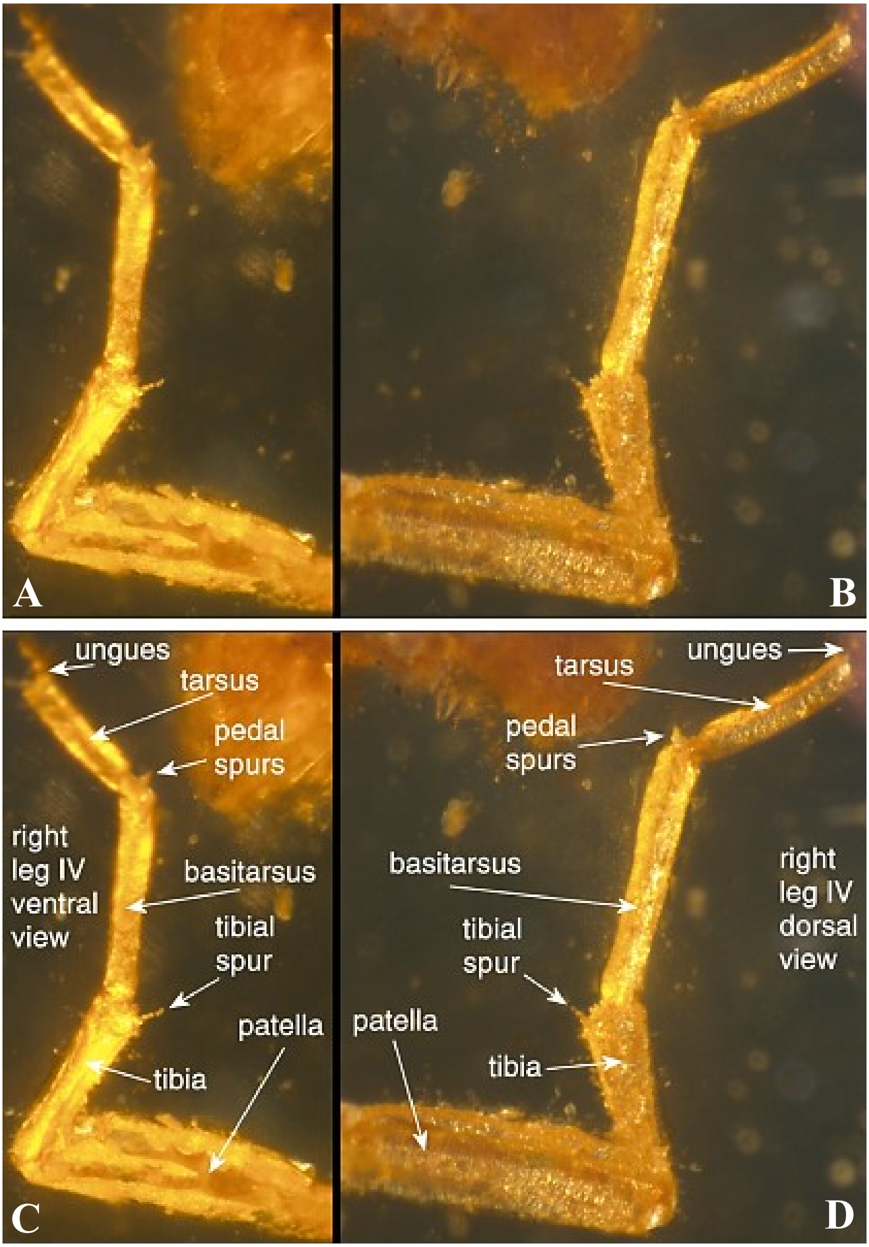


Figure 17. *Palaeoburmesebuthus smithi* sp. n. Right leg IV. A and C. Ventral view. B and D. Dorsal view.

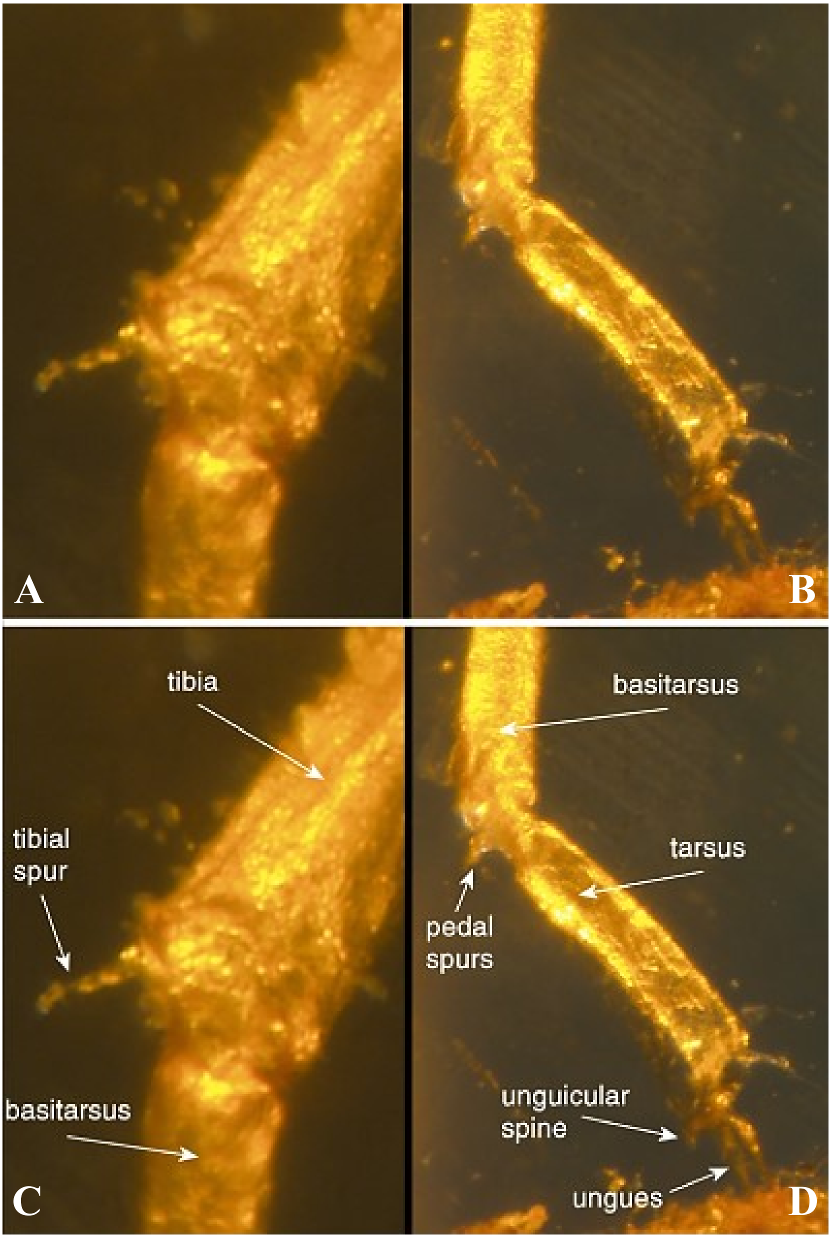


Figure 18. *Palaeoburmesebuthus smithi* sp. n. Close-ups of right leg IV. A and C. Tibia, tibial spur, and basitarsus. B and D. Basitarsus, pedal spurs, tarsus, unguicular spine, and the ungues.

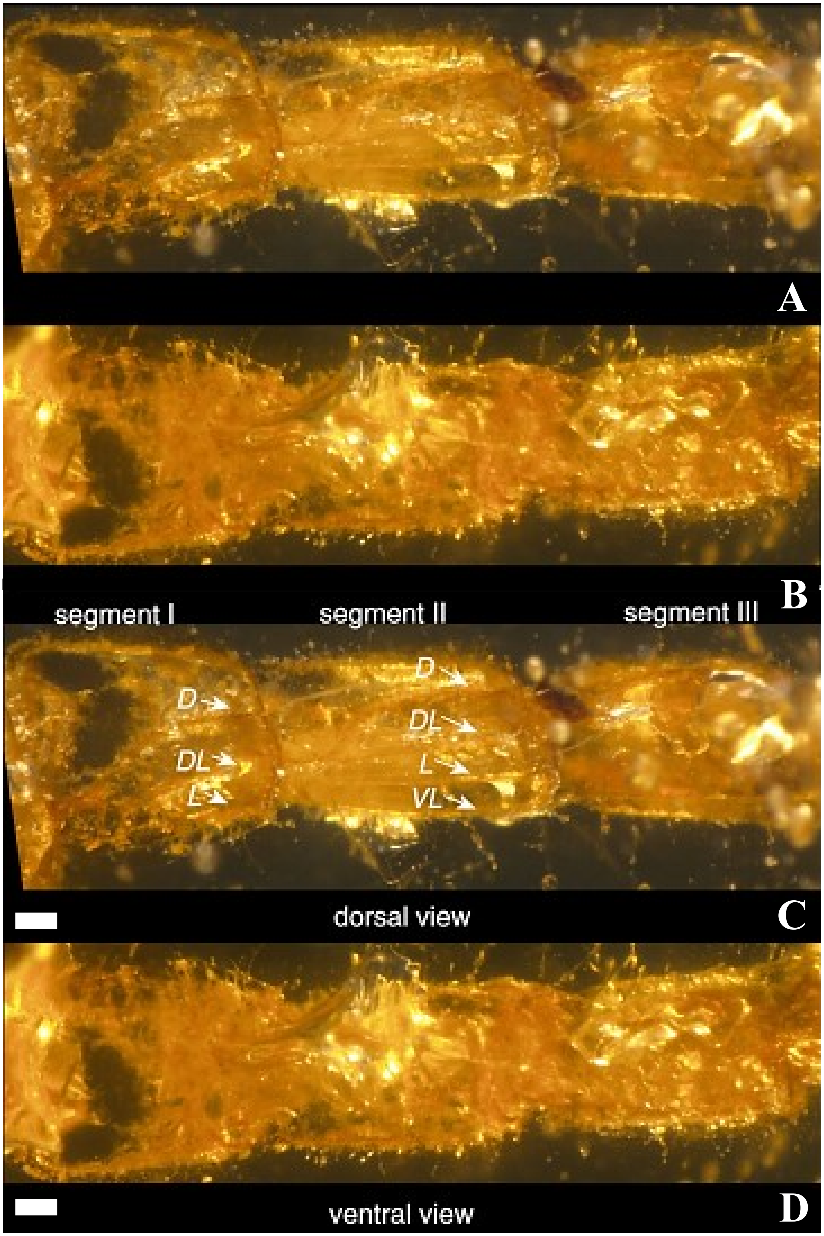


Figure 19. *Palaeoburmesebuthus smithi* sp. n. Metasomal segments I-III. A and C. Dorsal view. B and D. Ventral view. D = dorsal carina, DL = dorsal lateral carina, L = lateral carina, and VL = ventrolateral carina. Note that segments rotate slightly from segment I to III. Scale bars approximately 100µm.

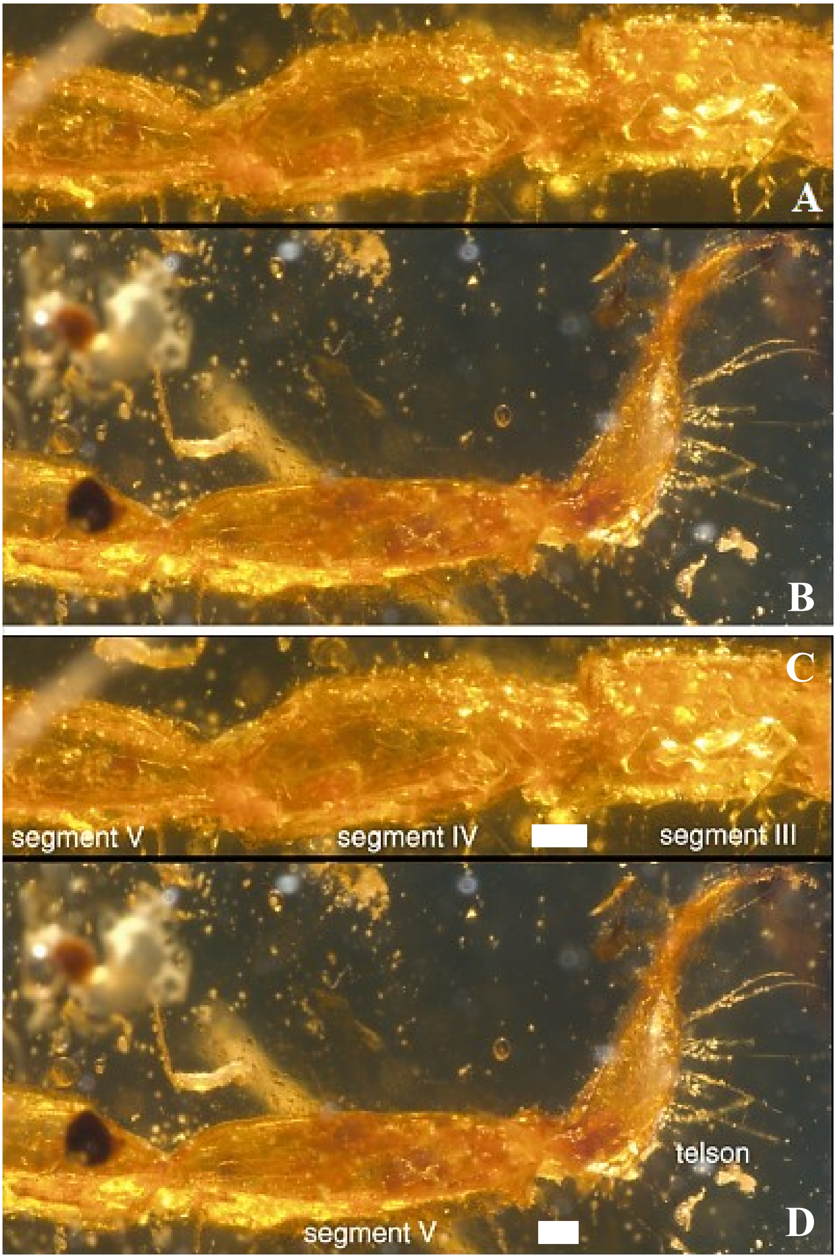


Figure 20. *Palaeoburmesebuthus smithi* sp. n. Metasomal segments and telson. A and C. Lateral view of III-V. B and D. Lateral view of the distal portion of IV, V, and telson. Scale bars approximately 100µm.

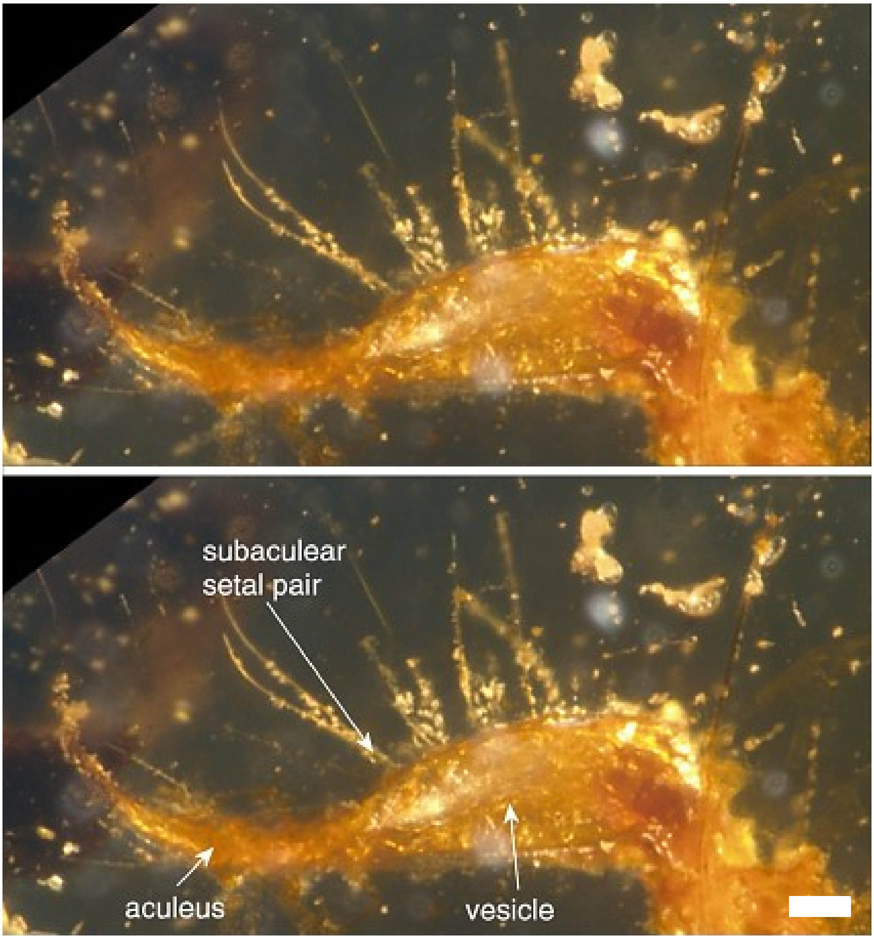


Figure 21. *Palaeoburmesebuthus smithi* sp. n. Telson, lateral view. Scale bar approximately 100 µm.

Comments. We must stress here that, due to the specimen's very small size and the cloudiness of the amber, it is extremely difficult to definitely identify small important taxonomic characters. All descriptions presented below including the measurements (Table 1) are estimates only. For example, the specimen is not positioned in the amber such that proper measurements can be obtained, its mesosoma and pedipalps are angled and the metasoma is twisted at segment IV. We have conservatively identified what might be trichobothria by concentrating only on long thin bristles projecting from the pedipalp. We cannot with assurance identify individual trichobothria by its areola. Even the relatively large pectinal tooth count is based only on the right pecten and some of the mid-distal teeth are estimates only.

Important taxonomic characters that are observed with some confidence is the telson lacking a subaculear tubercle, the presence of a tibial spur on leg IV, and the presence of the dorsomedian (DMc) carina on the pedipalp patella, only known for the parvorder Buthida. Important taxonomic characters, which are *not* observable on this fossil, are the dentition of the cheliceral and chelal fingers, shape of the stigma, carination of the metasoma, details of the sternopectinal area, in particularly the maxillary lobes, and more observable trichobothria, a major character in scorpion systematics.

Further characters for potential lower-level placement includes the absence of a subaculear tubercle on the telson, the large number of pectinal teeth (22), and the extreme slenderness of the pedipalp chela.

Palaeoburmesebuthus andrewrossi
Santiago-Blay, Soleglad, Fet, Craig, et Smith sp. n.

Figures 22-29, Tables 2-3

http://www.zoobank.org/urn:lsid:zoobank.org:act:E2C3A713-C2F7-448A-BD69-B6F495774A8A

Holotype. Natural History Museum (London, England, UK), In. 20174 in Burmese amber (specimen described herein); Hukawng Valley, Kachin, Myanmar (Burma).

Unidentified scorpion: Ross 1998:36, Figure 100; Ross and York 2000:14; Rasnitsyn and Ross 2000:24; Grimaldi et al. 2002, 10 (in part), 28 (in part).

Palaeoburmesebuthus grimaldii Lourenço, 2002 (misidentification): Santiago-Blay et al., 2004a: 148-150, Figures 1-2; Plate 4, Figures 6-12.

Etymology. This new species is named after Dr. Andrew J. Ross (currently, Principal Curator of Palaeobiology, Department of Natural Sciences, National Museums Scotland, Edinburgh, Scotland, UK) who in 2004 kindly loaned us this amber specimen, information on which we have published at that time without describing it as a new species (Santiago-Blay et al., 2004a).

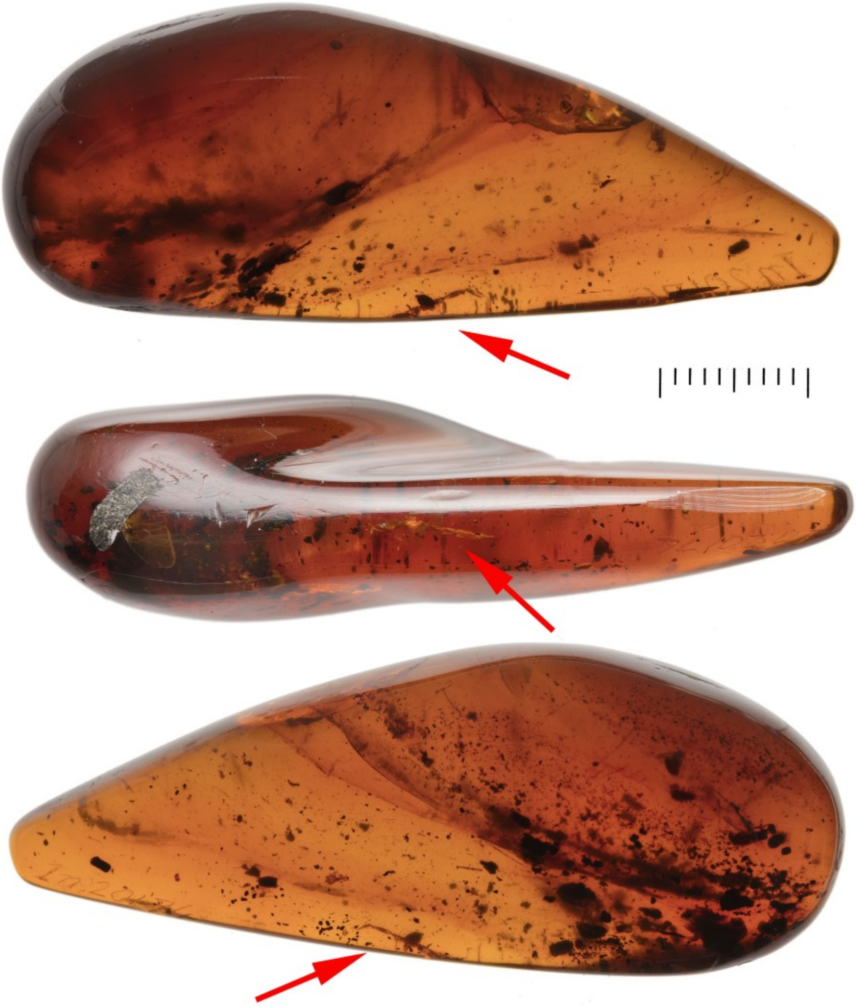


Figure 22. Overall views of the amber specimen, *Palaeoburmesebuthus andrewrossi* sp. n. Scale represents 1 cm.

Description

(after Santiago-Blay et al., 2004a)

The following description is based on the only known type specimen, the holotype (fragmented, sex non identifiable). Measurements are presented in Table 2.

Diagnosis. Small scorpion (fragmented), without patterning. Chela very slender. Leg III (?) with tibial spur. Leg tarsus with two delicate rows of ventral spinules. Stigmata circular. Metasoma with dorsal carinae on segments I-IV, dorsolaterals on I-II, laterals on I, ventrolaterals of I-II, and one ventromedian on II. Metasomal segment V with dorsolaterals, ventrolaterals, and one ventromedian carinae. Telson elongated, without subaculear tooth; aculeus as long as vesicle.

Appearance. Amber inclusion containing five detached fragments of a single scorpion: metasoma with three mesosomal segments (one of them complete); right pedipalp chela to which the distal portion of the right patella is attached; and three leg fragments. Carapace, most of mesosoma, and most of appendages are absent.

Basic color. Pale yellow, with no patterning.

Carapace, chelicerae, sternum, pectines, genital operculum. Unknown.

Pedipalps (Figure 23). Right chela and extreme distal aspect of its attached patella are present. For the chela, dorsoexternal and ventroexternal views are available. Chela very slender with short palm; fingers long and thin, distal denticles forming subtle hooks as typical of recent scorpions with slender fingers; except for distal denticles, finger dentition not visible. Carinal structures of chelal palm not visible; internal aspect conspicuously protrudes forming a somewhat wide palm at that point. Trichobothria (Figure 20): Only six external trichobothria are visible under stated criteria (see Methods, above): two basal trichobothria located on external aspect of palm, tentatively identified as Eb_1 and Eb_2; one trichobothrium on external distal half aspect of palm with areola, tentatively identified as *Est;* one trichobothrium on extreme distal aspect of palm with areola is tentatively designated as Et_1; one trichobothrium on base of fixed finger with areola, tentatively identified as *eb:* and one long seta on distal aspect of fixed finger, pointing in an external direction, tentatively identified as *et.* Shorter setae present may represent additional trichobothria but are excluded here from consideration based on the criteria stated in Methods, above. Other setation: There is a distinct seta protruding from the extreme internal aspect of the palm; numerous short setae are evident on the extreme fingertips; additional various sized setae are found on exterior aspect of movable finger.

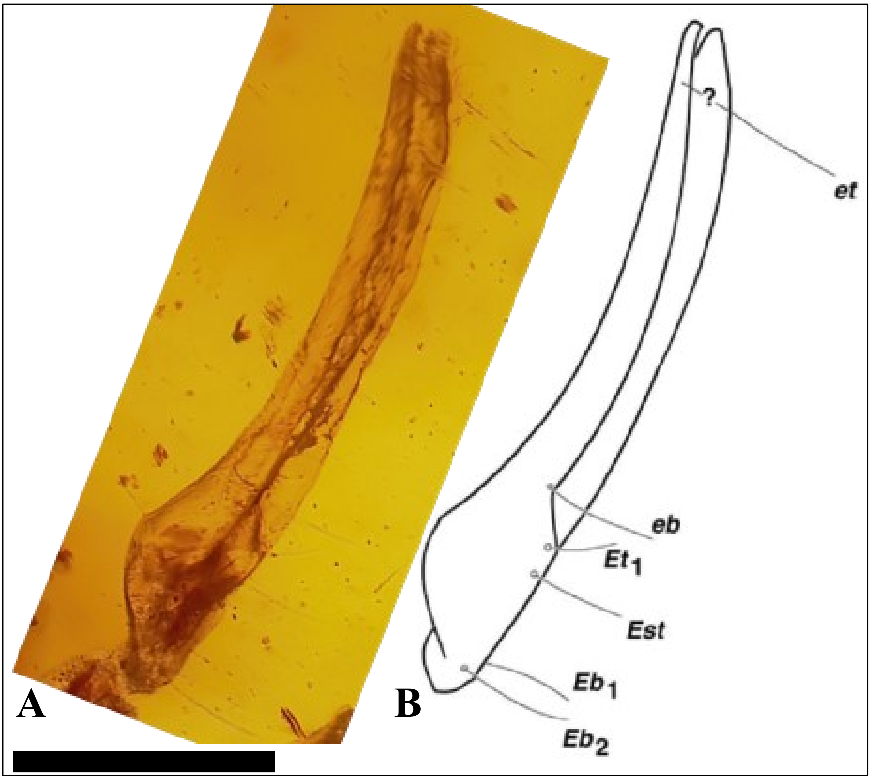
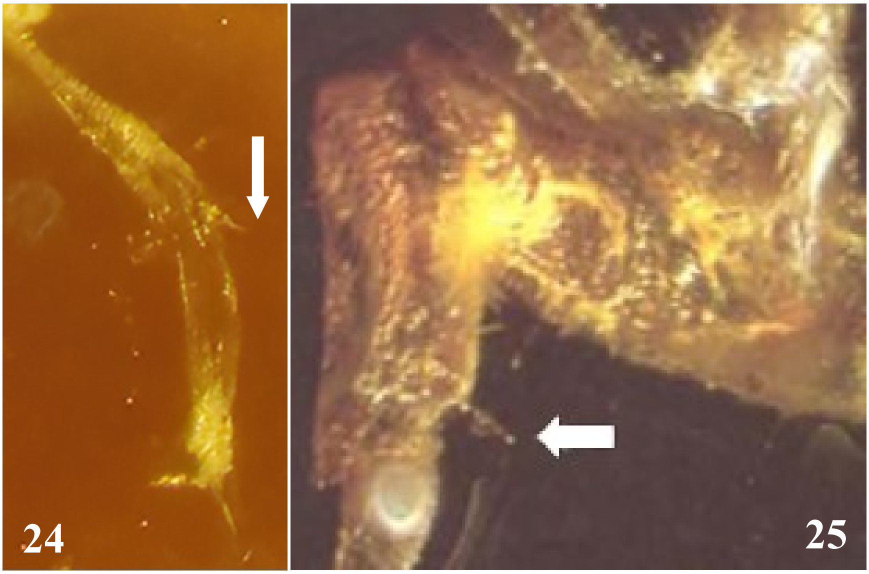


Figure 23. *Palaeoburmesebuthus andrewrossi* sp. n. Right pedipalp chela, with visible trichobothria, dorsoexternal aspect. A. Photo. B. Interpretation of panel A. Potential trichobothria are based solely on long thin setae (arrows on A) protruding from the internal and external sides. The areolae (or base) of the trichobothrial setae are based on hypothesized positions that are consistent with their suggested labels. Figure 23 modified from Santiago-Blay et al. (2004a). Scale bar approximately 1 mm.

Legs (Figures 24-25). Three leg fragments are present. Fragment 1 (Figure 24): a terminal leg portion which includes the epitarsus, unguicular spine, tarsus (= telotarsus), two pedal spurs, and a partial protarsus (= basitarsus); epitarsus (the ungues), long and thin, splayed in position with possible evidence of an unguicular spine at their base; tarsus exhibits two delicate rows of ventral spinules (areolae were not visible so we assumed that these are spinules, not setae); and two pedal spurs are evident between tarsus and partial protarsus. Leg pair designation of Fragment 1 is unknown. Fragment 2 (Figure 25): a leg portion which includes a tibia, possible tibial spur (arrow), and a partial patella; the tibia is somewhat short and thick, well developed tibial spur protrudes from tibial distal edge; patella portion is quite rounded (as all patellae seen in Recent scorpions).

We conclude that Fragment 2 is either from legs III or IV since tibial spurs are only known from these two leg pairs, leg III is our best guess due to thickness and stockiness of tibia (i.e., leg IV usually much longer and thinner than leg III). Fragment 3 (unfigured): Found disjointed from the Fragment 2 patella-tibia leg portion, appears to be a partial femur and connecting trochanter. The trochanter is quite robust. Fragment 3 could belong to the same leg as Fragment 2.



Figures 24 and 25. *Palaeoburmesebuthus andrewrossi* sp. n. 24. Leg fragment, showing tibia with a possible tibial spur (arrow), and patella (partial and angled in view). 25. Leg showing epitarsus, tarsus with two ventral rows of delicate spinules (black arrow with white border), pedal spur (white arrow) and protarsus (partial).

Mesosoma (Figures 26). Tergites: present but not visible due to positioning of the specimen. Sternites: Sternites III (small portion), IV (4/5 posterior-left portion) and V (complete) are visible. Sternite III: two setae and one stigma (= spiracle) are visible on this small portion. Sternite IV: two circular stigmata are visible on this segment; three setae are situated on anterior edge. Sternite V: two pairs of delicately crenulate carinae are present, the left pair clearly visible; two small setae visible on posterior aspect of outer carinae; lateral edges equipped with small serrations.

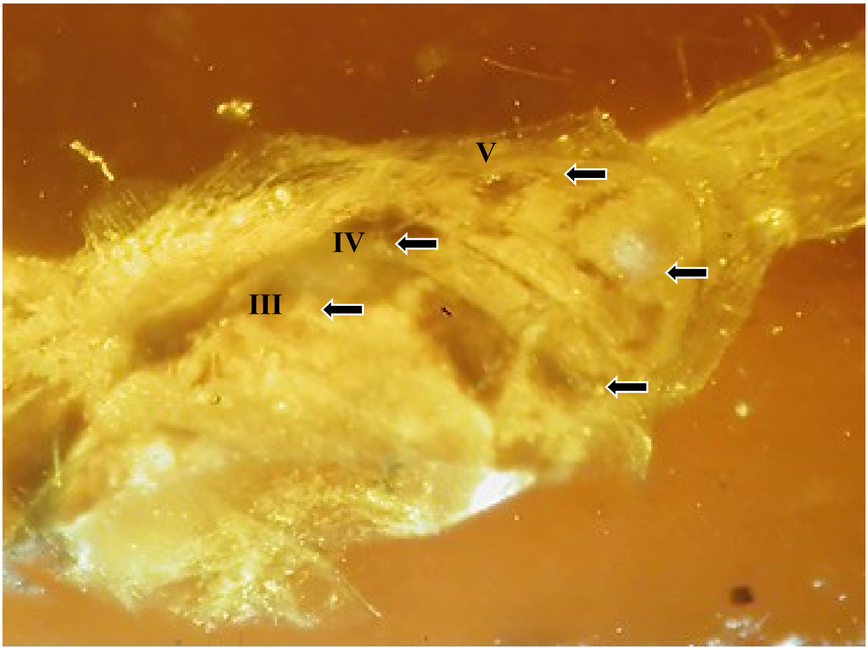


Figure 26. *Palaeoburmesebuthus andrewrossi* sp. n. Ventral aspect of mesosoma, showing sternite V with two pairs of carinae, sternite IV (almost complete) with two stigmata, and sternite III (in part) with one stigma. All visible stigmata are pointed to by arrows.

Metasoma (Figures 27-29). Seen in dorsal and right lateral views. Segments I-IV. Carinae: dorsal pair on I-IV, delicate crenulation visible on segments I-II; dorsolateral pair on I-II (right aspect better seen than left on III-IV); delicate crenulation on segments I-II: lateral carina on I (right aspect only); ventrolateral of segments I-II (right aspect only); ventromedian on segments II (right aspect only). Setation: two lateral pairs (one pair per side) on segment IV; three ventral pairs on II-IV (only two visible on III but placement implies three pairs). Segment V. Carinae: one dorsolateral pair; one inferior lateral (right aspect only); one inferior median. Setation: five pairs of lateral setae (one seta per side) visible; five pairs of conspicuously long (as depth of metasoma V) and thick ventrals emanating from somewhat protruding tubercles. Metasoma V ventral aspect not visible but lateral view of segment V implies that inferior median carina is singular because setal pairs are closely set, presumably straddling a single carina. Similarly, inferior median carinal pairs assumed to be present on segments I-IV (although only visible on segment II). In summary, ten carinae are found on segment I, eight on segments II-IV and five on segment V.

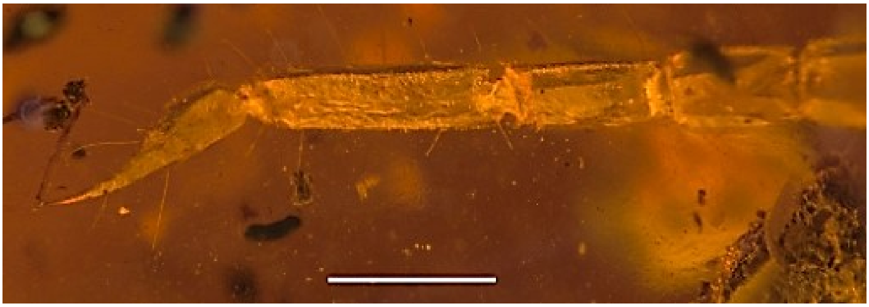
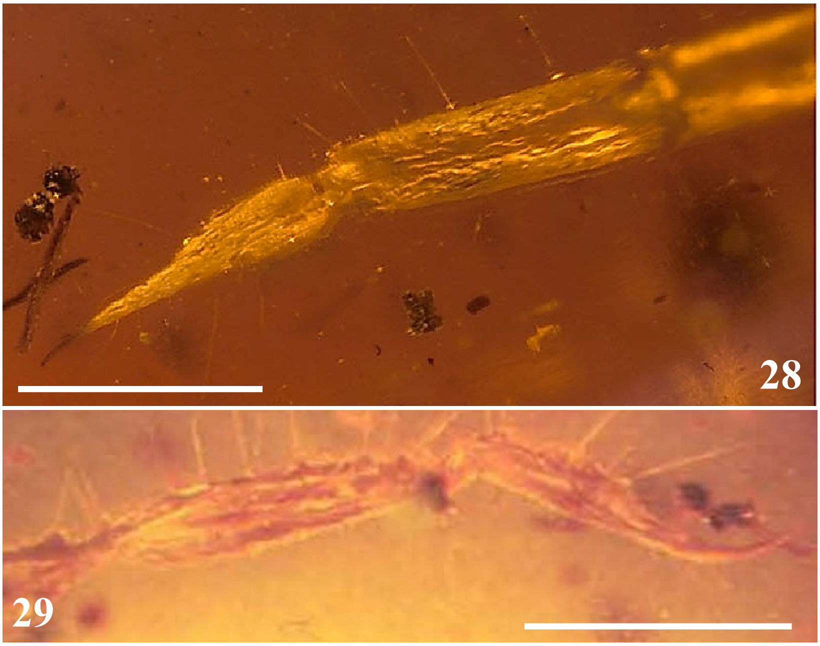


Figure 27. *Palaeoburmesebuthus andrewrossi* sp. n. Dorsal view of metasomal segments II-V and telson (dorsolateral). Scale bar approximately 2 mm.

Telson (Figures 27-29). Elongated, relatively flat, lacking a subaculear tooth; aculeus as long or longer than vesicle; vesicle-aculeus juncture not distinct, base of aculeus relatively thick, slightly thinner than vesicle at that point. Carinae: vesicle equipped dorsolaterally with two carinal pairs. Setation: two long setae at aculeus-vesicle juncture; four setae at midpoint of vesicle; two or three setae on base of vesicle.



Figures 28-29. *Palaeoburmesebuthus andrewrossi* sp. n. Metasomal segments IV (distal aspect), metasomal segment V, and telson. 28. Dorsal view. 29. Lateral view. Scale bar approximately 2 mm.

Discussion

As we assigned the two new species we describe herein to the genus *Palaeoburmesebuthus* Lourenço, 2002 (Palaeoburmesebuthidae), it was not our goal, or a feasible task, to analyze all type specimens across the genus and the family. Our two new species, which are tentatively placed in *Palaeoburmesebuthus*, differ from all four known species of *Palaeoburmesebuthus* and all eight known species of *Betaburmesebuthus*. We defaulted on the genus that was described first until the delineation of both genera is clarified based on their type species. Clearly, this is not a standard practice in describing extant taxa, when the authors commonly rely on the data published by others. At the same time, not all available publications on Burmite amber scorpions provide exhaustive comparative data. Because the preservation in amber often does not render all the diagnostic characteristics available, the keys to the most fossil taxa provided by Lourenço and collaborators are necessarily based on fragmentary data. Unfortunately, most of the papers by Lourenço and collaborators lack detailed photographs. Hence, we cautiously relied on the line drawings therein provided, and on the information gleaned from the descriptions.

Assigning our two new species to "buthoids" versus "non-buthoids" (a vernacular terminology loosely applied in literature (see Baptista et al., 2006; Lourenço, 2016b) was a rather straightforward decision. Among several new families described from Burmite by Lourenço and collaborators, our new taxa clearly belong to the family Palaeoburmesebuthidae. This conclusion is based on general configuration of pedipalps, telson, metasomal carination, and (albeit fragmentary) trichobothrial patterns. The new taxa do not match the monotypic genus *Spinoburmesebuthus* Lourenço and Velten, 2017, which has peculiar spinoid morphosculpture on the pedipalp, lacking in both of our specimens. The only remaining two genera in this family are *Palaeoburmesebuthus* Lourenço, 2002 and *Betaburmesebuthus* Lourenço and Beigel, 2015.

A key provided by Lourenço (2016b) stated that the difference between these two genera was the so-called *alpha*- vs. *beta*-configuration of femoral trichobothria (Vachon, 1975). This character was the reason for naming *Betaburmesebuthus* in the first place since its type species, *B. kobberti*, had an observable *beta*-configuration (Lourenço and Beigel, 2015) as opposed to *alpha*-configuration first observed for the genus *Palaeoburmesebuthus* in previously described *P. ohlhoffi* (Lourenço, 2015d).

This femoral configuration, however, is *not* known for the type species of the genus *Palaeoburmesebuthus, P. grimaldii* Lourenço, 2002, which is known *only* from a partial metasoma (segments III-V and telson), not the most taxonomically informative part of scorpion anatomy. The only remarkable feature of *P. grimaldii* was its elongated telson, with length/depth ratio 5.62. This rivals most known ratios in extant parvorder Buthida (or family Buthidae). Graeme Lowe (personal communication to V. Fet 2021) kindly provided us with his unpublished data, which indicate that the most elongated telsons in extant Buthidae (length/depth ratio above 4.5) are found only in the males of some species of *Ananteris* and *Reddyanus*. This metric varies with sex and age of an animal; adult males usually have more elongated telsons, a major mark of sexual dimorphism in scorpions. One should be further cautious applying any morphometric conclusions to amber fossils, most of which are juvenile specimens.

When we (Santiago-Blay et al., 2004a) published our "second specimen of *Palaeoburmesebuthus grimaldii*", with its telson length/depth ratio 4.49, no other Burmite scorpions were known. When Lourenço (2015d) described the second species of *Palaeoburmesebuthus, P. ohlhoffi*, he followed the same logic as we did (Santiago-Blay et al., 2004a) on assigning a new 'buthoid' to the only then known genus known at that time. The telson length/depth ratio of *P. ohlhoffi*, however, is 9.29. The trichobothrial *alpha*-configuration was reported for *P. ohlhoffi* but not for the type species, which is known only from a partial metasoma, therefore, one cannot know whether these species are congeneric. A trichobothrial *alpha*-configuration was reported for two more described *Palaeoburmesebuthus* species; of these, telson length/depth ratio is known only for *P. knodeli* where it is 4.18.

At the same time, Lourenço and Beigel (2015) erected the genus *Betaburmesebuthus,* based solely on the trichobothrial *beta*-configuration, as the genus name attests. Its type species *Betaburmesebuthus kobberti* had telson length/depth ratio 4.90. Other six species described in this genus have telson length/depth ratio from 3.94 to 4.76 (Table 3). A trichobothrial *beta*-configuration was reported for all described species of *Betaburmesebuthus*, but usually it is represented only by line drawings rather than an actual photo.

Another important character, which in extant scorpions is usually fixed at genus level, is the presence of tibial spurs on legs III and IV, a plesiomorphic condition in extant Buthidae. The tibial spurs III-IV are present, when this part of the leg is observable, in *Palaeoburmesebuthus* (two species) but variable in *Betaburmesebuthus* (present in three species, absent or reduced in three other species). Notably, tibial spurs III-IV are not observable in the type species of *Palaeoburmesebuthus* (*P. grimaldii*), known only from a partial metasoma, and are absent in the type species of *Betaburmesebuthus* (*B. kobberti*). This furthers a suspicion that both *Palaeoburmesebuthus* and *Betaburmesebuthus* could include more than one genus. The exact delineation of these two genera, in our opinion, is currently impossible.

Table 3. Comparative morphology of 13 species of *Palaeoburmesebuthus* and *Betaburmesebuthus*. Table 1 in Xuan et al. (2022) include a useful comparison of character states for the eight described species of *Betaburmesebuthus* as well las *Spinoburmesebuthis pohli*.

Taxon	Femoral trichobothrial pattern alpha or beta	Tibial spur III	Tibial spur IV	Sub aculear tubercle	DPS
Palaeoburmesebuthus					
P. grimaldii	n/a	n/a	n/a	n/a	n/a
P. knodeli	alpha	yes	yes	yes	no
P. longipalpis	alpha	n/a	n/a	n/a	n/a
P. ohlhoffi	alpha	yes	yes	no	no
P. smithi **sp. n.**	n/a	n/a	yes	no	yes
P. andrewrossi **sp. n.**	n/a	yes	n/a	no	n/a
Betaburmesebuthus					
B. bellus	beta	yes	yes	no	reduced
B. bidentatus	beta	?no	?no	n/a	yes, double
B. fleissneri	beta	yes	yes	no	yes
B. joergi	beta	yes	yes	no	no
B. kobberti	beta	no	no	reduced	yes
B. larafleissnerae	beta	no	reduced	no	reduced
B. muelleri	beta	n/a	reduced	no	reduced
B. spinipedis	beta	n/a	reduced	reduced	1 strong, 3 spinoid

Abbreviations: DPS = dorsal patellar spur, n/a = not available.

Table 3. Continuation.

Taxon	PTC right-left	Spiracles	MetV L / MetIV L	MetV L / Tel L
Palaeoburmesebuthus				
P. grimaldii	n/a	n/a	1.53	1.22
P. knodeli	21-20	oval to slit-like	1.56	1.99
P. longipalpis	n/a	n/a	n/a	n/a
P. ohlhoffi	n/a	n/a	1.45	0.61
P. smithi **sp. n.**	22-n/a	round	1.29	1.14
P. andrewrossi **sp. n.**	n/a	n/a	1.43	1.01
Betaburmesebuthus				
B. bellus	18-17	slit-like	1.46	1.14
B. bidentatus	n/a	n/a	n/a	n/a
B. fleissneri	20-21	oval to round	1.42	1.07
B. joergi	18-18	oval	1.50	1.11
B. kobberti	20-20	round	1.34	1.00
B. larafleissnerae	17-18	oval	1.45	1.04
B. muelleri	14-15	round	1.31	1.04
B. spinipedis	16-16	oval to slit-like	1.53	1.12

Abbreviation: PTC = pecten teeth count.

Table 3. Continuation.

Taxon	Telson L/D	Chela L/W	Total Length
Palaeoburmesebuthus			
P. grimaldii	5.62	n/a	~9-10
P. knodeli	4.18	n/a	11.23
P. longipalpis	n/a	12.74	~10-11
P. ohlhoffi	9.29	6.65	12.28
P. smithi **sp. n.**	4.16	7.99	7.96
P. andrewrossi **sp. n.**	4.49	6.44	n/a
Betaburmesebuthus			
B. bellus	3.97	6.59	11.80
B. bidentatus	n/a	7.38	~18-19
B. fleissneri	4.76	6.82	11.37
B. joergi	4.10	4.86	17.65
B. kobberti	4.90	6.29	10.41
B. larafleissnerae	4.18	5.68	12.29
B. muelleri	3.94	5.12	9.36
B. spinipedis	4.00	6.9[a]	11.54

[a] Estimated from illustrations in Xuan et al. (2022).

Diagnostic morphological features of all 13 species are listed in Table 3. Although for many listed taxa (including the two new species) the information is fragmentary, unique combinations of characters are sufficient to distinguish our new taxa from other 11 species.

For *P. smithi* **sp. n.**, its diagnostic features are the presence of tibial spur IV; absence of subaculear tubercle; presence of DPS; 22 pectinal teeth; round spiracles; and a unique combination of morphometric ratios for metasoma and pedipalp chela. Telson length to depth ratio is 4.16, which is close to 4.18 in *P. knodeli;* however, *P. smithi* **sp. n.** differs from *P. knodeli* by other morphometric ratios, absence of subaculear tubercle, presence of DPS, and round spiracles. Chela length to width ratio is 7.99, which exceeds that in all known species except *P. longipalpis* where it is 12.74.

For *P. andrewrossi* **sp. n.,** its diagnostic features are the presence of tibial spur III; absence of subaculear tubercle; and a unique combination of morphometric ratios for metasoma and pedipalp chela. Telson length to depth ratio is 4.49, and chela length to width ratio is 6.44, a combination which differs from all other known species.

Recommendations

We emphasize that a study of Burmite amber scorpions - as any fossils – is inherently limited either by often fragmentary nature of inclusions, or precluded observation of morphological features, or both. Although we do not intend to be prescriptive, we suggest describing new fossil taxa based on specimens whose remnants are likely taxonomically informative at the intended rank, particularly when other specimens for a particular deposit are known. For instance, a metasoma (or tail) most likely documents the presence of a scorpion, and it is unlikely, by itself, to be useful to diagnose a species. Furthermore, we recognize that describing new taxa in groups of organisms that are rare in the fossil record, such as scorpions in Burmite, eventually will demand a comparative study of all Burmite fossil scorpions. Although we do not advocate the banning of private collections from the taxonomic endeavor, all specimens, whether deposited in a private collection or in a more traditional museum, should be available for scientific examination by other scholars (e.g., Selden et al. 2005). Such studies should be facilitated by newer imaging methods, such as microCT (also known as microtomography or micro computed tomography, e.g., Peris et al. 2022), epifluorescence microscopy (e.g., Singh et al. 2021), and other imaging techniques as those greatly facilitate character observation. In our descriptions provided in this paper, we attempted to report exhaustively list both observable and non-observable diagnostic features, as was done in our previous works on amber scorpions (Santiago-Blay et al., 2004a, 2004b; Baptista et al., 2006).

Disclaimer

The authors are aware of the fact that Burmese amber is often mined under harsh working conditions in the current Myanmar government (Haug et al. 2020a, 2020b; Anonymous 2022 and references therein; for a somewhat different point of view, see Poinar and Ellenberger 2020). It is our conscious decision not to ignore or boycott Burmite research, but instead to contribute to it and to attract the international research community attention to the political reality.

Acknowledgements

We thank Dr. Andrew J. Ross (formerly at the Natural History Museum, London, currently at the National Museums Scotland, Edinburgh, Scotland, UK) for the loan of the *B. andrewrossi* NHM specimen for our previous study (Santiago-Blay et al. 2004a). We are profoundly grateful to Richard Greene (National Museum of Natural History, Smithsonian Institution Libraries, Smithsonian Institution, Washington, District of Columbia, USA) who made it possible for us to rapidly access the articles published in *Arachnida - Rivista Aracnologica Italiana* up to 2020. Tim Rose, Tim Gooding (both at the Department of Mineral Sciences, Smithsonian Institution, Washington, District of Columbia, USA) and Steffi Valdeig assisted JASB in the polishing of the specimen of *P. smithi* **sp. n.** Andrew Hasselman (Washington, DC) and S. Valdeig assisted coauthor JASB in imaging *P. smithi* **sp. n.**

Claire Mellish (Natural History Museum, herein abbreviated NHM, London, England, UK) facilitated the photographic requests and other communications pertaining to *P. andrewrossi* **sp. n.** Harry Taylor (Photographer, NHM) produced exquisite images of the type of *P. andrewrossi* **sp. n.** deposited at NHM (Figure 22), all images of *P. andrewrossi* **sp. n.** are copyrighted by the Natural History Museum, London, England, UK).

VF is greatly thankful to Dr. Paul Selden (formerly of University of Kansas, Lawrence, Kansas, USA) for his long-term advice and help on fossil scorpions and other arachnids. We thank Graeme Lowe (Auckland, New Zealand) for his detailed comments and review. Five additional colleagues reviewed this paper and made constructive suggestions towards its improvement.

Literature Cited

Anonymous. 2022. Myanmar Amber. *Ethics Unwrapped*. McCombs School of Business. The University of Texas at Austin. Austin, Texas, USA. https://ethicsunwrapped.utexas.edu/case-study/myanmar-amber

Baptista, C. J., J. A. Santiago-Blay, M. E. Soleglad, and V. Fet. 2006. The Cretaceous scorpion genus, *Archaeobuthus*, revisited (Scorpiones: Archaeobuthidae). *Euscorpius* 35:1-40. https://doi.org/10.18590/euscorpius.2006.vol2006.iss35.1

Cohen, K. M., S. C. Finney, P. L. Gibbard, and J.-X. Fan (2013, updated), The ICS International Chronostratigraphic Chart. *Episodes* 36:199-204. https://doi.org/10.18814/epiiugs/2013/v36i3/002

Cohen, K. M., D. A. T. Harper, P. L. Gibbard, and N. Car. 2022. *International Chronostratigraphic Chart*. v 2022/02. International Commission on Stratigraphy. https://stratigraphy.org/news/143

Cruickshank, R. D. and K. Ko. 2003. Geology of an amber locality in the Hukawng Valley, Northern Myanmar. *Journal of Asian Earth Sciences* 21:441-455. https://doi.org/10.1016/S1367-9120(02)00044-5

Dunlop, J. A., D. Penney, and D. Jekel, with additional contributions from L. I. Anderson, C. Bartel, S. J. Braddy, J. C. Lamsdell, P. A. Selden, and O. E. Tetlie. 2020. A summary list of fossil spiders and their relatives. https://wsc.nmbe.ch/resources/fossils/Fossils20.5.pdf . *In* Dunlop, J. A., D. Penney, and D. Jekel. 2022. *World Spider Catalog.* Version 23.5. Natural History Museum Bern. Online at http://wsc.nmbe.ch , doi: 10.24436/2. Accessed on July 10, 2022.

Grimaldi, D. A., M. S. Engel and P. C. Nascimbene. 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates* 3361:1-71. https://doi.org/10.1206/0003-0082(2002)361<0001:FCAFMB>2.0.CO;2

Haug, C., J. W. F. Reumer, J. T. Haug, A. Arillo, D. Audo, D. Azar, V. Baranov, R. Beutel, S. Charbonnier, R. Feldmann, C. Foth, R. H. B. Fraaije, R. Gašparič, D. E. Greenwalt, M. Hyžný, J. W. M. Jagt, E. A. Jagt-Yazykova, E. Jarzembowski, H. Kerp, A. G. Kirejtshuk, C. Klug, D. S. Kopylov, U. Kotthoff, J. Kriwet, L. Kunzmann, R. C. McKellar, A. Nel, A. Nützel, V. Perrichot, A. Pint, O. Rauhut, J. W. Schneider, F. R. Schram, G. Schweigert, P. A. Selden, J. Szwedo, B. W. M. van Bakel, T. van Eldijk, F. J. Vega, B. Wang, and M. Reich. 2020a. Comment on the letter of the Society of Vertebrate Paleontology (SVP) dated April 21, 2020 regarding "Fossils from conflict zones and reproducibility of fossil-based scientific data": the importance of private collections. *Paläontologische Zeitschrift* 94:413-429. https://doi.org/10.1007/s12542-020-00522-x

Haug, J. T., D. Azar, A. Ross, J. Szwedo, B. Wang, A. Arillo, V. Baranov, J. Bechteler, R. Beutel, V. Blagoderov, X. Delclòs, J. Dunlop, K. Feldberg, R. Feldmann, C. Foth, R. H. B. Fraaije, A. Gehler, D. Harms, L. Hedenäs, M. Hyžný, J. W. M. Jagt, E. A. Jagt-Yazykova, E. Jarzembowski, H. Kerp, P. K. Khine, A. G. Kirejtshuk, C. Klug, D. S. Kopylov, U. Kotthoff, J. Kriwet, R. C. McKellar, A. Nel, C. Neumann, A. Nützel, E. Peñalver, V. Perrichot, A. Pint, E. Ragazzi, L. Regalado, M. Reich, J. Rikkinen, E.-M. Sadowski, A. R. Schmidt, H. Schneider, F. R. Schram, G. Schweigert, P. A. Selden, L. J. Seyfullah, M. M. Solórzano-Kraemer, J. D. Stilwell, B. W. M. van Bakel, F. J. Vega, Y.-D. Wang, L.-D. Xing, and C. Haug. 2020b. Comment on the letter of the Society of Vertebrate Paleontology (SVP) dated April 21, 2020 regarding "Fossils from conflict zones and reproducibility of fossil-based scientific data": Myanmar amber. *Paläontologische Zeitschrift* 94:431-437. https://doi.org/10.1007/s12542-020-00524-9

Lambert, J. B., J. M. Karlberg, N. R. Muppala, T. A. Contreras, Y. Wu, and J. A. Santiago-Blay. 2020. A new molecular type of amber for Burma (Myanmar). *Life: The Excitement of Biology* 7(4):197-212. https://blaypublishers.files.wordpress.com/2020/02/lambert_et_al_new_burmite_amber-1.pdf

Lourenço, W. R. 2001. A remarkable scorpion fossil from the amber of Lebanon. Implications for the phylogeny of Buthoidea. *Comptes Rendus de l'Académie des Sciences*, Paris 332:641-646. https://doi.org/10.1016/S1251-8050(01)01583-X . [*Archaeobuthus estephani* gen. n., sp. n.]

Lourenço, W. R. 2002. The first scorpion fossil from the Cretaceous amber of Myanmar (Burma). New implications for the phylogeny of Buthoidea. *Comptes Rendus Palevol* 1:97-101. https://doi.org/10.1016/S1631-0683(02)00017-9 [*Palaeoburmesebuthus grimaldii* gen. n., sp. n.]

Lourenço, W. R. 2012. About the scorpion fossils from the Cretaceous amber of Myanmar (Burma) with the descriptions of a new family, genus and species. *Acta Biológica Paranaense* (Curitiba, Brasil) 41(3-4):5-87. [Palaeotrilineatidae fam. n., *Palaeotrilineatus ellenbergeri* gen. n., sp. n.]

Lourenço, W. R. 2013. A new species of *Chaerilobuthus* Lourenço & Beigel, 2011 from Cretaceous Burmese amber (Scorpiones: Chaerilobuthidae). *Acta Biológica Paranaense* (Curitiba, Brasil) 42(1-2):1-5. https://doi.org/10.5380/abpr.v42i1-4.35095 [*Chaerilobuthus longiaculeus* sp. n.]

Lourenço, W. R. 2015a. A new contribution to the knowledge of Cretaceous Burmese amber scorpions with the description of two new species of *Betaburmesebuthus* Lourenço, 2015 (Scorpiones: Archaeobuthidae: Palaeoburmesebuthinae). *Arachnida – Rivista Aracnologica Italiana* 3:27-36. [*Betaburmesebuthus bidentatus* sp. n., *Betaburmesebuthus muelleri* sp. n.]

Lourenço, W. R. 2015b. A new subfamily, genus and species of fossil scorpions from Cretaceous Burmese amber (Scorpiones: Palaeoeuscorpiidae). *Beiträge zur Araneologie* 9:457-464 [*Archaeoscorpiops cretacicus* gen. n., sp. n.]

Lourenço, W. R. 2015c. An unusual new species of *Chaerilobuthus* Lourenço & Beigel, 2011 (Scorpiones: Chaerilobuthidae) from the Cretaceous amber of Myanmar (Burma). *Arachnida – Rivista Aracnologica Italiana* 5:44-48. [*Chaerilobuthus enigmaticus* sp. n.]

Lourenço, W. R. 2015d. Clarification of the familiar status of the genus *Palaeoburmesebuthus* Lourenço, 2002 from Cretaceous Burmese amber (Scorpiones: Archaeobuthidae: Palaeoburmesebuthinae). *Beiträge zur Araneologie* 9:465-475. [Palaeoburmesebuthinae subfam. n.; *Palaeoburmesebuthus ohlhoffi* sp. n., *Chaerilobuthus birmanicus sp. n., bruckschi* sp. n.]

Lourenço, W. R. 2016a. A new genus and three new species of scorpions from Cretaceous Burmese amber (Scorpiones: Chaerilobuthidae: Palaeoeuscorpiidae). *Arthropoda Selecta* 25(1):67-74.

https://doi.org/10.15298/arthsel.25.1.06 [*Burmesescorpiops groehni* gen. n., sp. n., *Chaerilobuthus gigantosternum* sp. n., *Chaerilobuthus serratus* sp. n.]

Lourenco, W. R. 2016b. A preliminary synopsis on amber scorpions with special reference to Burmite species: an extraordinary development of our knowledge in only 20 years. *ZooKeys* 600:75-87. https://doi.org/10.3897/zookeys.600.8913 [*Betaburmesebuthus bellus* sp. n.]

Lourenço, W. R. 2018a. A further new species of *Palaeoburmesebuthus* Lourenco, 2002 (Scorpiones: Palaeoburmesebuthidae) from Burmite. *Revista Iberica de Aracnologia* 32:51-54. [*Palaeoburmesebuthus knodeli* sp. n.]

Lourenço, W. R. 2018b. A new remarkable scorpion genus and species from Cretaceous Burmese amber (Scorpiones: Protoischnuridae). *Arachnida – Rivista Aracnologica Italiana* 18:2-14. [*Cretaceoushormiops knodeli* gen. n., sp. n.]

Lourenço, W. R. 2018c. Further data on the genus *Chaerilobuthus* Lourenco *et* Beigel, 2011 (Scorpiones: Chaerilobuthidae) from Cretaceous Burmite and description of a new species. *Arachnida – Rivista Aracnologica Italiana* 19:2-13. [*Chaerilobuthus knodelorum* sp. n.]

Lourenço, W. R. 2021. Further comments on the elements of the family Palaeoburmesebuthidae Lourenço, 2015 with description of a new species of *Spinoburmesebuthus* Lourenço, 2017 from Early Cretaceous Burmite amber (Scorpiones). *Faunitaxys* 9(17):1-6. [*Spinoburmesebuthus knodelorum* sp. n.]

Lourenço, W. R. and A. Beigel. 2011. A new scorpion fossil from the Cretaceous amber of Myanmar (Burma). New phylogenetic implications. *Comptes Rendus Palevol* 10:635-639. https://doi.org/10.1016/j.crpv.2011.08.001 [Chaerilobuthidae fam. n.; *Chaerilobuthus complexus* gen. n., sp. n.]

Lourenço, W. R. and A. Beigel. 2015. A new genus and species of Palaeoburmesebuthinae Lourenço, 2015 (Scorpiones: Archaeobuthidae) from Cretaceous amber of Myanmar. *Beiträge zur Araneologie* 9:476-480. [*Betaburmesebuthus kobberti* gen. n., sp. n.]

Lourenço, W. R. and A. Rossi. 2017. Two more new species of Burmese amber scorpions of the family Palaeoburmesebuthidae Lourenço, 2015 (Scorpiones). *Arachnida – Rivista Aracnologica Italiana* 13:11-21. [*Palaeoburmesebuthus longipalpis* sp. n., *Betaburmesebuthus joergi* sp. n.]

Lourenço, W. R. and J. Velten. 2015. Another new species of *Chaerilobuthus* Lourenço & Beigel, 2011 (Scorpiones: Chaerilobuthidae) from the Cretaceous amber of Myanmar (Burma). *Arachnida – Rivista Aracnologica Italiana* 5:2-8. [*Chaerilobuthus schwarzi* sp. n.]

Lourenço, W. R. and J. Velten. 2016a. A new genus and species of fossil scorpion from Burmese Cretaceous amber (Scorpiones: Buthoidea: Buthidae). *Arachnida – Rivista Aracnologica Italiana* 10:2-9. [*Archaeoananteroides maderai* gen. n., sp. n.]

Lourenço, W. R. and J. Velten. 2016b. A sixth new species of Cretaceous Burmese amber scorpion of the genus *Betaburmesebuthus* Lourenço, 2015 (Scorpiones: Palaeoburmesebuthidae). *Arachnida – Rivista Aracnologica Italiana* 10:10-17. [*Betaburmesebuthus larafleissnerae* sp. n.]

Lourenço, W. R. and J. Velten. 2016c. One more new species of *Betaburmesebuthus* Lourenço, 2015 (Scorpiones: Palaeoburmesebuthinae) from Cretaceous burmite. *Arachnida – Rivista Aracnologica Italiana* 6:4-11. [*Betaburmesebuthus fleissneri* sp. n.]

Lourenço, W. R. and J. Velten. 2017. One more new genus and species of fossil scorpion from Burmese Cretaceous amber belonging to the family Palaeoburmesebuthidae (Scorpiones). *Arachnida – Rivista Aracnologica Italiana* 13:2-10. [*Spinoburmesebuthus pohli* gen. n., sp. n.]

Lourenço, W. R. and J. Velten. 2019. One more contribution to the knowledge of Cretaceous Burmese amber scorpions: description of one new species of *Chaerilobuthus* Lourenco *et* Beigel, 2011 (Scorpiones: Chaerilobuthidae). *Arachnida – Rivista Aracnologica Italiana* 25:2-10 [*Chaerilobuthus hansgeorgmuelleri* sp. n.]

Lourenço, W. R. and J. Velten. 2020. A new contribution to the knowledge of Cretaceous Burmese amber scorpions with the descriptions of two new genera and two new species (Scorpiones: Chaerilobuthidae; Palaeoeuscorpiidae: Archaeoscorpiopinae). *Arachnida – Rivista Aracnologica Italiana* 28:34-50 [*Chaeriloscorpiops bautschi* gen. n., sp. n.; *Chaeriloiurus brigittemuellerae* gen. n., sp. n.]

Lourenço, W. R. and J. Velten. 2021a. One more new genus and species of scorpion from Early Cretaceous Burmese amber (Scorpiones: Protoischnuridae). *Faunitaxys* 9(14):1-5. [*Cretaceousopisthacanthus* Lourenço gen. n., *Cretaceousopisthacanthus smeelei* sp. n.]

Lourenço, W. R. and J. Velten. 2021b. Early Cretaceous Burmite fossils of the genus *Chaerilobuthus* Lourenço & Beigel, 2011 (Scorpiones: Chaerilobuthidae) and description of a particular new species. *Faunitaxys* 9(30):1-5. [*Chaerilobuthus meggeri* sp. n.]

Lourenço, W. R. and J. Velten. 2022a. The remarkable variability of the genus *Chaerilobuthus* Lourenço & Beigel, 2011 (Scorpiones: Chaerilobuthidae) and description of a new species from Early Cretaceous Burmite. *Faunitaxys* 10(10):1-6. [*Chaerilobuthus brandti* sp. n.]

Lourenço, W. R. and J. Velten. 2022b. A second new species for the genus *Cretaceoushormiops* Lourenço, 2018 from Cretaceous Burmite (Scorpiones: Protoischnuridae). *Faunitaxys* 10(43):1-5. [*Cretaceoushormiops staxi* sp. n.]

Mao, Y., K. Liang, Y. Su, J. Li, X. Rao, H. Zhang, F. Xia, Y. Fu, C. Cai, and D. Huang. 2018. Various amberground marine animals on Burmese amber with discussions on its age. *Palaeoentomology* 1(1):91-103. https://doi.org/10.11646/palaeoentomology.1.1.11

Peris, D., B. Mähler, and J. Kolibáč. 2022. Review of the family Thanerocleridae (Coleoptera: Cleroidea) and the description of *Thanerosus* gen. nov. from Cretaceous amber using micro-CT scanning. *Insects* 13:438. 14 pp. https://doi.org/10.3390/insects13050438

Poinar Jr., G. O., R. Buckley, and A. Brown. 2006. The secrets of Burmese amber. *Mid-America Paleontology Society Digest* 29(3):20-29.

Poinar, G. and S. Ellenberger. 2020. Burmese amber fossils, mining, sales and profits. *Geoconservation Research* 3(1):12-16. https://doi.org/10.30486/GCR.2020.1900981.1018

Rasnitsyn, A. P. and A. J. Ross. 2000. A preliminary list of arthropod families present in the Burmese amber collection at The Natural History Museum, London. *Bulletin of The Natural History Museum, Geology Series* 56:21-24.

Ross, A. J. 1998. *Amber, the Natural Time Capsule.* The Natural History Museum. London, England, UK. 73 pp.

Ross, A. J. 2019. Burmese (Myanmar) amber checklist and bibliography 2018. *Palaeoentomology* 2(1):22-84. https://doi.org/10.11646/palaeoentomology.2.1.5

Ross, A. J. 202b2. Supplement to the Burmese (Myanmar) amber checklist and bibliography, 2021. *Palaeoentomology* 5(1):27-45. https://doi.org/10.11646/palaeoentomology.5.1.4

Ross, A. J. 2022b. Burmese (Myanmar) amber taxa, on-line supplement v.2022.1. 33 pp. https://www.nms.ac.uk/media/1166967/burmese-amber-taxa-v2022_1.pdf , http://www.nms.ac.uk/explore/stories/natural-world/burmese-amber/

Ross, A. J. and P. V. York. 2000. A list of type and figured specimens of insects and other inclusions in Burmese amber. *Bulletin of the Natural History Museum, Geology Series* 56:11-20.

Rossi, A. 2015. A new family, genus and species of scorpion from burmite of Myanmar (Scorpiones: Sucinlourencoidae). *Arachnida – Rivista Aracnologica Italiana* 1:3-21. [Sucinlourencoidae fam. n.; *Sucinlourencous adrianae* gen. n., sp. n.]

Santiago-Blay, J. A. 2008. Lubricating jelly helps improve image clarity of inclusions entombed in amber. *Annales de la Société Entomologique de France (Nouvelle Série)* 44(2):209-210. http://dx.doi.org/10.1080/00379271.2008.10697557

Santiago-Blay, J. A., V. Fet, M. E. Soleglad, and P. R. Craig. 2004a. The second Cretaceous scorpion specimen from Burmese amber (Arachnida: Scorpiones). *Journal of Systematic Palaeontology* 2(2):100 (some figures), 147-152. https://doi.org/10.1017/S1477201904001221

Santiago-Blay, J. A., V. Fet, M. E. Soleglad, and S. R. Anderson. 2004b. A new genus and subfamily of scorpions from Lower Cretaceous Burmese amber (Scorpiones: Chaerilidae). *Revista Ibérica de Aracnología* 9:3-14 [Electochaerilinae; *Electrochaerilus buckley* gen. n., sp. n.].

Santiago-Blay, J. A. and J. B. Lambert. 2007. Amber's botanical origins revealed. Large collections of the substances exuded by trees today may help to track backward from amber samples to the ancient plants that produced them. *American Scientist* 95(2):150-157.

https://www.jstor.org/stable/27858931 . Reprinted, with permission, as: Aux sources de l'ambre. *Pour la Science* (Paris, France) 356:70-75. https://doi.org/10.1511/2007.64.1020

Santiago-Blay, J. A. and J. B. Lambert. 2017. Plant exudates and amber: their origin and uses. *Arnoldia* 75(1):2-13. https://repository.si.edu/bitstream/handle/10088/33180/2017%20Santiago-Blay%20and%20Lambert%20Arnoldia.pdf?sequence=1&isAllowed=y

Selden, P. A., J. A. Corronca, and M. A. Hünicken. 2005. The true identity of the supposed giant fossil spider Megarachne. *Biology Letters* 1:44–48. https://doi.org/10.1098/rsbl.2004.0272

Shi, G., D. A. Grimaldi, G. E. Harlow, J. Wang, M. Yang, W. Lei, Q. Li, and X. Li. 2012. Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Research* 37:155-163. https://doi.org/10.1016/j.cretres.2012.03.014

Singh, H., W. S. Judd, B. Samant, P. Agnihotri1, D. A. Grimaldi, and S. R. Manchester. 2021. Flowers of Apocynaceae in amber from the early Eocene of India. *American Journal of Botany* 108(5):883-892. https://doi:10.1002/ajb2.1651

Sissom, W. D., G. A. Polis, and D. D. Watt. 1990. Field and laboratory methods. pp. 445-461 *in* Polis, G. A. (Editor). *Biology of Scorpions.* Stanford University Press. Stanford, California, USA. 587 pp.

Soleglad, M. E. and V. Fet. 2003. The scorpion sternum: structure and phylogeny (Scorpiones: Orthosterni). *Euscorpius* 5:1-34. https://doi.org/10.18590/euscorpius.2003.vol2003.iss5.1

Stahnke, H. L. 1971. Scorpion nomenclature and mensuration. *Entomological News* 81:297-316.

Vachon, M. 1974. Études des caractères utilisés pour classer les familles et les genres des scorpions (Arachnides). 1. La trichobothriotaxie en arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez les Scorpions. *Bulletin du Muséum national d'Histoire naturelle* 3e série 140 (Zoologie 104):857–958.

Vachon, M. 1975. Sur l'utilisation de la trichobothriotaxie du bras des pédipalpes des Scorpions (Arachnides) dans le classement des genres de la famille des Buthidae Simon. *Comptes Rendus de l'Academie des Sciences, Paris*, D 281:1597-1599.

Xuan, Q., C. Cai, and D. Huang. 2022. A new Palaeoburmesebuthidae scorpion from mid-Cretaceous Burmese amber (Arachnida: Scorpiones: Buthoidea). *Cretaceous Research* 134. 105165. https://doi.org/10.1016/j.cretres.2022.105165 [*Betaburmesebuthus spinipedis* sp. n.]

Zherikhin, V. V. and A. J. Ross. 2000. A review of the history, geology and age of Burmese amber (Burmite). *Bulletin of the Natural History Museum, Geology* 56(1):3-10.