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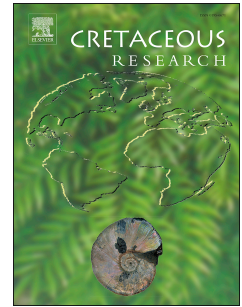
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New genera *Buserphites* and *Mesoserphites* (Hymenoptera: Serphitidae) from mid-Cretaceous amber of Myanmar.

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Abstract

Two new genera, *Burserphites* and *Mesoserphites*, belonging to the subfamily Serphitinae (Serphitidae, Hymenoptera) are described from Burmese mid-Cretaceous amber. Two new species are erected within *Burserphites* n. gen.: *B. applanatus*, and *B. myanmarensis*, and five new species are established within *Mesoserphites* n. gen.: *M. annulus*, *M. giganteus*, *M. engeli*, *M. scutatus*, and *M. viraneacapitis*. These taxa show that the family Serphitidae was highly diverse in Burmese amber, adding substantially to recent discoveries within the endemic subfamily Supraserphitinae Rasnitsyn and Ölm-Kühnle. The presence of multiple serphitid genera in Burmese amber that are unknown from other amber deposits adds support to the idea that the Western Burma Block supported a fauna with multiple endemic groups as it approached contact with mainland Asia in the latest Albian or earliest Cenomanian. Despite the growing number of species recognized from Burmese amber, most of the newly described taxa are represented by very few specimens, suggesting that we are still within the early stages of documenting the fauna, or that the collections from this region represent a broader range of time and habitats than originally thought.

Keywords: Burmese amber; Serphitoidea; taxonomy; Albian-Cenomanian; Mesozoic.

1. Introduction

The Serphitidae Brues, 1937 are a small family of extinct parasitic wasps that have been assigned to the clade Bipetiolarida Engel (2005) based on the distinctive arrangement of two petiolar segments observed in its members (see Rasnitsyn and Ölm-Kühnle, 2019b for alternative systematic interpretation). The first member of Serphitidae described was *Serphites paradoxus* Brues, 1937, and the taxon was recognized as part of its own unique family at the time of its initial description. Although recognition at the family level has varied over time (e.g., Kozlov and Rasnitsyn, 1979), this small family was widespread during the Cretaceous, ranging from the Barremian to Campanian through a series several deposits: Serphitidae are known from Lebanese, Spanish, French, Siberian, Burmese, and Canadian Cretaceous amber (Brues, 1937; Kozlov and Rasnitsyn, 1979; Engel *et al.*, 2011; McKellar and Engel, 2011; Ortega-Blanco *et al.*, 2011; Engel and Perrichot, 2014; Rasnitsyn and Ölm-Kühnle 2019a, 2019b, 2020a, 2020b). Currently, the family comprises only three subfamilies, each with a few genera: Serphitinae Brues, 1937, Microserphitinae Engel, 2015, and Supraserphitinae Rasnitsyn and Ölm-Kühnle, 2018. The Serphitidae in Burmese amber have not been studied in detail until recently, with the last three years seeing new research by Rasnitsyn and Ölm-Kühnle (2019a, 2019b, 2020a, 2020b) that has resulted in the description of five new species based on unique female specimens, and the creation of a new subfamily, Supraserphitinae, to accommodate some of these taxa. These taxa have presented characteristics of both Serphitidae and Archaeoserphitidae Engel, 2015, leading the authors to question the distinction between the families recognized within Serphitoidea Brues, 1937; however, these hypotheses remain to be tested through cladistic analyses. The presence of *Serphites* Brues, 1937 within the deposit has also been mentioned in

previous work on Burmese amber serphitids, but these specimens are currently undescribed (Rasnitsyn and Ölm-Kühnle, 2020b).

Mid-Cretaceous Burmese amber is now ranked among the richest deposits of amber, including considerable faunal and floral biodiversity, and it provides one of the best snapshots of terrestrial conditions in the Mesozoic. A particularly diverse arthropod assemblage has been described from the deposit, especially within the orders Hymenoptera, Coleoptera, and Diptera (e.g., Grimaldi *et al.*, 2002; Ross *et al.*, 2010; Ross, 2019, 2020). The deposit has also been the source of marginal marine inclusions like ammonites and ostracods (Xing *et al.*, 2018; Yu *et al.*, 2019), and taxa that are seldom preserved in Cretaceous resin, such as vertebrates and gastropods (e.g., Daza *et al.*, 2016; Xing *et al.*, 2016, 2019).

Among the serphitoid wasps, all observations indicate that the seven new species described herein belong the subfamily Serphitinae. The taxonomic features that distinguish this subfamily from others have been described at length by Engel (2015) and include possessing antennae with 6 to 8 flagellomeres. This low flagellar article count is a readily apparent characteristic of all Serphitinae, and it is shared by *Microserphites* Kozlov and Rasnitsyn, 1979 (the sole member of Microserphitinae). However, the Microserphitinae can be distinguished from Serphitinae, based on the former group possessing a pronotum that does not reach the tegula, and an indistinct pterostigma. Supraserphitinae have been described from Burmese amber, and are known exclusively from female specimens, but all available material demonstrates 10 flagellar articles. The family Archaeoserphitidae differs in that its members have 12 flagellomeres, a pronotum reaching the tegula, and a distinct pterostigma. The member of Archaeoserphitidae that was recently described from Burmese amber (i.e., *Archaeoserphites engeli* Rasnitsyn and Ölm-Kühnle, 2020a) differs from the type species of the genus and in many details of the generic

diagnosis, beyond the extent of sexual dimorphism observed elsewhere in the Serphitoidea, perhaps warranting the erection of additional taxa within the deposit.

Among the Serphitinae, the specimens described herein belong in two new genera: *Buserphites* and *Mesoserphites*. The new genus *Buserphites* can be distinguished from previously described Serphitidae based on the presence of an elongate petiolar segment (first segment is more than three times the length of the second). Meanwhile the new taxon *Mesoserphites* presents an intermingling of characteristics that have been previously attributed to the genera *Serphites* and *Aposerphites* Kozlov and Rasnitsyn, 1979. Relationships among the previously described genera of Serphitinae (*Aposerphites*, *Serphites*, and *Jubaserphites* McKellar and Engel, 2011) have not been assessed through cladistic analyses because of the low taxon sampling density that is currently available. However, it is hoped that continued work on Burmese amber exemplars will provide sufficient material to analyze Serphitidae in detail, and to assess the extent of faunal overlap or endemism that occurs in the Cretaceous deposits where they occur.

2. Material and methods

The insect inclusions in this study come from 13 specimens of mid-Cretaceous Burmese amber. Seven of these specimens come from the Royal Saskatchewan Museum collection (RSM, RSKM_P specimen numbers, Regina, SK, Canada) and contain individual serphitids, with the exception of RSKM_P3306.30, which has 3 syninclusions belonging to two different species. Five additional specimens belong to the American Museum of Natural History (AMNH, AMNH_Bu specimen numbers, New-York, NY, USA). All fossil inclusions are commercial specimens collected in the Hukawng Valley, in Myanmar's Kachin state (Grimaldi *et al.*, 2002;

Cruickshank and Ko, 2003; Ross *et al.*, 2010; Li *et al.*, 2018). Radiometric dates ($^{206}\text{Pb}/^{238}\text{U}$) obtained from zircons attached to amber pieces in this mining region have established a date for the rocks surrounding the Burmese amber deposit that is 98 ± 0.62 Ma, or latest Albian to earliest Cenomanian (Shi *et al.*, 2012); however, the amber deposit may represent a broader window of time around this time estimate (e.g., Smith and Ross, 2018, Yu *et al.*, 2019).

Amber specimens were polished to create ideal anatomical views of inclusions, and whenever necessary, specimens were supported by vacuum-injection with epoxy prior to polishing (following the technique of Nascimbene and Silverstein, 2000). Specimen photographs were taken with a Canon EOS 7D camera and EF 65 mm macro lens mounted on a Visionary Digital imaging station. The resulting series of photos taken at different levels were combined with Helicon Focus software to increase depth of field. Specimen observations were made using a Leica MZ 12.5 stereomicroscope, and an Olympus CH30 compound microscope was used for supplementary observations. All measurements were obtained with an ocular micrometre and are expressed in millimetres in the text. Whenever possible, general measurements were taken in lateral view to account for curvature of the body, and more precise measurements were taken by mounting the amber specimen in wax to obtain whatever orientation was required to create an accurate measurement.

The morphological descriptions are based on articles previously published on the superfamily Serphitoidea, as well as the larger-scale work of Goulet and Huber (1993). Harris (1979) is used to describe surface sculpturing, and our use of venation terminology is explained in Figure 1. Anatomical abbreviations include: ba., basitarsus; cx., coxa; fe., femur; fla., flagellomeres; mlt., lateral margin between tergites and sternites; msp., mesopleuron; mst., mesoscutum; mstl., mesoscutellum; mtn., metanotum; oce., ocellus; OD, ocellar diameter; ped.,

pedicel; ppd., propodeum; pro., pronotum; sca., scape; ster., sternite; ta., tarsus; ter., tergite; ti., tibia; tr., trochanter; ver., vertex. Where males and females have been attributed to the same species without direct associations (syninclusions), a section at the end of the description details differences found in the males.

3. Identification key to genera of Serphitinae

The key to the genera of Serphitidae is modified from the works of Kozlov and Rasnitsyn (1979), Ortega-Blanco *et al.* (2011), and McKellar and Engel (2011) in order to cover recent developments within the subfamily Serphitinae. Members of the subfamily Supraserphitinae are readily distinguished by their 10 flagellar articles, and are diagnosed in the works of Rasnitsyn and Ölm-Kühnle (2019a, 2019b, 2020b).

1. Flagellum with six articles; vertex with elongate, erect setae [Campanian; Canadian amber]
Jubaserphites
- Flagellum with more than six articles; vertex with short, inclined setae, or bare
2
2. Pronotum not reaching tegula; pterostigma indistinct, represented by diffuse fuscous area at apex of Sc + R; tergum with first three tergites of similar lengths [Albian–Santonian; Spanish, Siberian amber, and Burmese amber (pers. obs.)]
Microserphites

- 145 -- Pronotum reaching tegula; pterostigma distinct and sclerotized; tergum with first three
 146 tergites of different lengths.....
 147 3
 148
- 149 3. Mesoscutellum slightly convex or straight; first petiolar segment length more than three
 150 times that of second petiolar segment [Albian-Cenomanian, Burmese amber]
 151 *Buserphites* **gen. n.**
- 152 -- Mesoscutellum convex or highly convex; first petiolar segment length three times or less
 153 than that of second petiolar segment 4
 154
- 155 4. First petiolar segment length two or more times that of second petiolar segment; male
 156 antenna clubbed; lateral ocellus nearly touching or touching compound eye margin (most
 157 species), or, if ocellus widely separated, first petiolar segment nearly three times as long
 158 as second segment (*Serphites kuzminae*) [Albian-Santonian; Spanish, New Jersey,
 159 Canadian, Siberian, and Burmese amber (pers. obs.)]
 160 *Serphites*
- 161 -- First petiolar segment length less than twice that of second petiolar segment; male
 162 antenna not clavate; lateral ocellus not touching margin of compound eye
 163 5
- 164 5. Lateral ocellus nearly touching compound eye margin, separated by less than one-half
 165 ocellar diameter; clypeus dorsoventral length significantly shorter than lateral width;
 166 antennae arising near ventral margin of compound eye [Albian-Cenomanian, Burmese

amber] *Mesoserphites* **gen.**

n.

-- Lateral ocellus separated from compound eye margin by one-half ocellar diameter or more; clypeus length similar to width; antennae arise just below mid-height of compound eye [Albian–Santonian; Spanish, Siberian amber, and Burmese amber (pers. obs.)]

..... *Aposerphites*

4. Systematic palaeontology

Superfamily Serphitoidea Brues, 1937

Family Serphitidae Brues, 1937

Subfamily Serphitinae Brues 1937

Genus *Buserphites* **n. gen.**

(urn:lsid:zoobank.org:act:62611C21-654D-4E76-AC29-8FE28FC7523D)

Diagnosis. Flagellum with 7 or 8 flagellar articles; first flagellar article shortest, and flagellum broadest near midlength; lateral ocellus separated from compound eye by more than 0.5 OD (nearly touching in *Serphites*, and *Mesoserphites* n. gen.); antennae insert near anteroventral margin of compound eye; mandibles strongly curved, protuberant when closed; hind wing with 2Rs reaching 2M; mesoscutellum slightly convex or straight; first petiolar segment length more than three times that of second petiolar segment; second petiolar segment nearly cylindrical and with faint longitudinal striations.

Etymology. The new genus name is a combination of the Latin adjective *bu-* meaning “large, huge, great”, which refers to the proportion between the first petiolar segment length and the second segment, combined with *-serphites*, a common suffix for Serphitidae, based on the type species; the name is masculine.

Type species. *Buserphites applanatus* **gen. et sp. n.**

Included species. Two species in Albian-Cenomanian Burmese amber: *B. applanatus* **gen. et sp. n.**, and *B. myanmarensis* **gen. et sp. n.**

Remarks. If members of this genus attained very small body sizes (with reduced venation), they may be difficult to distinguish from species of *Microserphites*.

***Buserphites applanatus* gen. et sp. n.**

(urn:lsid:zoobank.org:act:F2928524-EDDF-46BB-8519-A3321326F9B2)

Material examined. Holotype AMNH_Bu-1512 (female). Polished amber piece including support epoxy, one of three amber pieces cut from larger amber sample, with dimensions of 11.6 mm x 5.2 mm x 2.7 mm; amber is yellow with flow lines and with high particulate content.

Etymology. New species name refers to mesosoma-shape, using the Latin adjective *applanatus*, which means “flattened”.

Type locality. Hukawng Valley, Kachin State, in Myanmar, near Tanai Village (on Ledo Road 105 km NW of Myitkyna), Myanmar, Upper Cretaceous.

Diagnosis. New species is generally similar to other species of *Buserphites* (*B. myanmarensis*), but differs in following combination of characters: compound eye occupying approximately one-

half of head in lateral view; ocelli almost forming equilateral triangle (possibility affected by antero-posterior taphonomic head compression); lateral ocelli separated from compound eye margin by 1 OD, ovate; antennae with 8 flagellomeres (in female); scape somewhat globose, not reaching vertex, and approximately 2.7 times longer than its greatest width; mandibles deeply divided, with elongate, pointed teeth; right mandible with 3 teeth, middle tooth shortest, ventral tooth longer and thinner than others, and with broad base; left mandible with 2 teeth, slender throughout lengths, with ventral tooth significantly longer than dorsal tooth; transition between dorsal surface and declivity on propodeum rounded, convex; forewing with nebulous C and highly sclerotized pterostigma; pterostigma with globose, triangular posterior expansion of fuscous area adjacent to r-rs and Rs veins; Sc+R not contacting 1Rs; 1Rs forming bulbous prestigmal expansion, not truncated before contact with pterostigma; M+Cu broad and fuscous apically, becoming spectral; 1m-cu as wide as Cu, width extending, after reaching 2M; 3M relatively straight; Cu shorter than combined 1M and 1Rs, and terminates in CuP; vein A with distal portions slender, spectral, bearing row of thickened, long, inclined microtrichia; hind wing with only anterior vein visible (Sc+R); metasoma with gaster as long as mesosoma; first petiolar segment about 3.2 times length of second segment.

Description. Total body length ~1.86 mm; mesosoma ~0.68 mm in length; forewing ~0.94 mm long and ~0.43 mm wide; hind wing ~0.68 mm long, ~0.34 mm wide; metasoma ~0.73 mm long; gaster ~0.50 mm long (Fig. 2).

Head: appears wider than long, but is taphonomically compressed; compound eye with rounded margins and apparently globose (also taphonomically compressed), bearing numerous erect, fine setae; gena gently inflated, bearing numerous semi-erect, fine setae; median ocellus slightly

larger than lateral ocellus (greater in diameter), and separated from lateral ocellus by 1 OD; lateral ocellus ovate, and separated from compound eye by 1 OD; antenna with 8 flagellar articles that are weakly clavate and broadest near midlength of flagellum; antennae compressed antero-posteriorly; flagellar articles approximately: 18, 32, 43, 47, 47, 51, 49, and 56 μm in length; scape approximately 85 μm long and 32 μm wide; pedicel approximately 55 μm long; first flagellar article semi-clavate and shortest; subsequent flagellar articles flattened and club-shaped; apical flagellar article longest and terminating in rounded point; pedicel clavate and relatively short, narrower than flagellar articles. Maxillary palpus nearly as long as mandible, terminating in long, slender palpomere; labial palpus apparently 3-segmented, with terminal palpomere spear-shaped, highly inflated, and with acute point.

Mesosoma: dorsoventrally compressed, dark and without clear surface structure visible; mesoscutum with punctuate surface structure, and without notauli visible; mesoscutellum flattened, sunken compared to mesoscutum; propodeum moderately convex, apparently with foveolate-rugulose surface structure.

Wings: orientation and curvature of wings renders observation difficult. Forewing with pterostigma shaped like equilateral triangle, with half of anterior margin more deeply pigmented; pterostigma with convex anterior margin (vein R), slightly concave basal margin (1r-rs), and nearly straight apical margin (2r-rs); R fuscous; nebulous 2Rs extending adbasally from pterostigma, forming long prestigmal expansion, and apparently reaching 2M; 3Rs nebulous, extending apically from pterostigma, short, relatively straight, and reaching near wing apex; 1R tubular, fuscous, not extending beyond pterostigma; nebulous C and tubular Sc+R, both equal in width, veins nearly straight, and separated by wide costal cell; costal cell base and apex equal in width, little more than two times width of C vein; Sc+R and C complete to base of wing; tubular,

curved M, equal to Sc+R in width; Sc+R tubular, not fusing apically with bulbous 1Rs; M+Cu contacting Sc+R midway through its length; 2M thinner basally than apically, reaching wing margin apically and reaching 2Rs basally; 2M with straight basal section; Cu equal to 1M in width, and terminating in CuA; CuA tubular, slender, highly curved posteriad basally (withinapical one-third of posterior wing margin), straight and reaching posterior wing margin apically. Vein A with distal portions slender, spectral, and bearing row of thicker, long, inclined microtrichia.

Legs: slightly compressed, long; base of legs covered by inclined setae; trochanters extremely short, especially protrochanter, which superficially appears absent; profemur comparatively long, metafemur slightly shorter than others and significantly broader; tibiae very long; tibial spur formula 1-2-2, with protibial spur curved, fine, and long, while meso- and metatibial spurs are relatively straight and slightly shorter; basitarsus shorter than cumulative length of other tarsomeres; tarsomeres I and IV longer than II and III, and III is shortest tarsomere; pretarsus long, with short and simple claws.

Metasoma: with combined length of petiolar segments slightly less than two-thirds of gastral length; first petiolar segment markedly long, cylindrical; surface of first petiolar segment with numerous, prominent, longitudinal carinae separated by fossulate sulci; second petiolar segment broader than first petiolar segment, but with surface details difficult to observe, apparently cylindrical with faint longitudinal striations; gaster compressed ventrodorsally, dark and without clear surface structure visible; gaster ovate in dorsal view; tergum with six apparent tergites, with first tergite longer than second, and bearing fine punctures and minute, inclined setae; first three tergites comprise less than half of gastral length; sternum with four apparent sternites, with first sternite longer than second; lateral margins between tergites and sternites appear to have well-

developed laterotergites, visible as bulbous carina with five segments. Female genitalia with paramere clavate, apex moderately expanded.

Buserphites myanmarensis gen. et sp. n.

(urn:lsid:zoobank.org:act:4141CD5B-1A6C-4A9C-B99E-6708C144BA73)

Material examined. Holotype RSKM_P3306.61 (probable female). Polished amber piece including support epoxy, with dimensions of 8.6 mm x 7.9 mm x 4.7 mm; amber is orange with multiple, darkly oxidized flow lines.

Etymology. Species name refers to country of origin, Myanmar.

Type locality. Hukawng Valley, Kachin State, in Myanmar, upper Albian-lowermost Cenomanian.

Diagnosis. New species similar to other species of *Buserphites*, but differs in following combination of characters: compound eye occupying approximately one-third of head in lateral view; ocelli forming isosceles triangle; lateral ocelli separated from compound eye margin by 0.5 OD, ovate, canted posterolaterally, and separated by 4 OD from median ocellus; antennae (female) with 7 flagellomeres; scape approximately four times longer than its greatest width; mandibles deeply divided, with pointed, stout, elongate, and highly curved teeth, and bearing relatively long setae on both outer and inner surfaces of teeth; right mandible apparently bears three teeth, with dorsal and middle teeth diminutive, and ventral tooth most prominent, long and slender; left mandible appears to have two teeth and narrow base; mesosoma with transcutellar

furrow bearing two broad foveae medially, and with finer punctures laterally; transition between dorsal surface and declivity on propodeum marked by strong lateral protuberance; forewing with pterostigma weakly sclerotized and tubular C vein; pterostigma with wide, long, tubular posterior expansion of fuscous area adjacent to r-rs crossvein and Rs vein; Sc+R contacting 1Rs and forming bulbous prestigmal expansion, slightly truncated before contact with pterostigma; M+Cu spectral; 1m-cu may be present, but spectral; 3M sinuous; Cu length equal to that of 1M and 1Rs combined; Cu not terminating in CuP; vein A apparently absent; legs with trochanters long and globose, with two longitudinal carinae; basitarsus slightly shorter than cumulative length of other tarsomeres; metasoma with gaster slightly longer than mesosoma; first petiolar segment comparatively long, about 3.4 times length of second segment; first tergite extending ventrally, partially enclosing second petiolar segment.

Description. Total body length ~1.97 mm; mesosoma ~0.70 mm in length; forewing ~1.21 mm long, and ~0.30 mm wide; hind wing ~0.42 mm long, and ~0.10 mm wide; metasoma ~1.09 mm in length; gaster ~0.75 mm long (Fig. 3).

Head: wider than long; compound eye teardrop-shaped, slightly globose posteriorly, with relatively straight margin adjacent to gena, and bearing numerous, erect, fine setae; gena flattened, with areolate-rugulose surface structure; frons straight, and not sunken relative to compound eyes; vertex mounded between lateral ocelli with few punctations; median ocellus same size as lateral ocellus, and separated from lateral ocellus by 3 OD; antenna 9-segmented, and weakly clavate; scape approximately 136 μ m long and 33 μ m wide, scape length approximately four times its greatest width; pedicel approximately 67 μ m long, pear-shaped, and slightly longer than third flagellar article; flagellar articles with flattened posterior edge, and

measuring approximately: 50, 55, 64, 61, 59, 61, and 90 μm in length; first flagellar article semi-clavate and shortest; second flagellar article clavate; subsequent flagellar articles chalice-like and equant; apical flagellar article elongate, and terminating in acute point. Maxillary palpus apparently shorter than mandible, four-segmented, and geniculate between second and third palpomeres, terminal palpomere longest, with acute point.

Mesosoma: with pronotum steeply sloping anteriorly, almost concealed by mesoscutum in dorsal view, and with tiny foveate surface structure; mesoscutum highly convex, shield-shaped, with lateral margins angular, with tiny foveate surface structure, and with notauli; notauli broad, shallow, and difficult to observe, apparently with curved line of fovea in sulcus; notauli converging posteriorly, forming broad V-shape, which is pointed near anterior margin of mesoscutellum; mesoscutellum flattened, sunken compared to mesoscutum, with areolate-rugulose surface structure anteriorly and foveate-reticulate posteriorly, with fine carina separating mesoscutellum from propodeum; metanotum present as very fine lip posterior to mesoscutellum; propodeum slightly convex, situated well ventral to metanotum, with broad foveate surface structure, and with strong posteriorly sloping declivity.

Wings: difficult to observe due to orientation and curvature. Forewing with pterostigma shaped like equilateral triangle, with weakly sclerotized and slightly concave basal margin (1r-rs), convex anterior margin (R), slightly concave basal margin (1r-rs), and nearly straight apical margin (2r-rs); pterostigma with wide, long, tubular, posterior expansion of fuscous area adjacent to r-rs and Rs veins; 2Rs extending adbasally from pterostigma, forming slender, long expansion, and apparently reaching 2M; 3Rs extending apically from pterostigma, slightly curved (convex anteriorly), short, and nearly reaching wing anterior margin apically; 1R tubular, fuscous, not extending beyond pterostigma; tubular C and tubular Sc+R, both equal in width and nearly

straight, separated by wide costal cell; costal cell base and apex equal in width, slightly more than two times width of C vein; Sc+R and C extending basally to reach wing margin; 1M tubular, equal to Sc+R in width, relatively straight; M+Cu contacting Sc+R midway through its length; Cu equal to 1M+1Rs in width, and terminating in CuA; CuA tubular, slender, slightly curved posteriad basally, straight apically, and reaching posterior wing margin apically. Hind wing difficult to observe; basal wing with anterior (probable Sc+R) and posterior (probable A) vein, but both appear to fade quickly adapically.

Legs: covered by numerous, inclined, fine, short setae; mesocoxa ovate, and metacoxa elongate with strong longitudinal depression in basal half of ventral surface; pro- and meso-trochanter slightly bell-shaped while metatrochanter ovate with protuberance in middle; femora short, and broad, especially in apical area, which is laterally compressed; tarsi longer than corresponding femora; all tibiae flared apically; pro- and mesotibiae laterally compressed, metatibia swollen apically; protibia with two carinae extending longitudinally along dorsal surface; protibia with single apical spur that is straight and as long as tibial apex is wide; mesotibia with two apical spurs, anterior spur length approximately equal to apical tibial width, posterior spur approximately double this length; metatibia with two short, robust spurs that appear to be shorter than apical width of metatibia; pro- and metabasitarsus slightly shorter than cumulative length of other tarsomeres, while mesobasitarsus shorter than cumulative length of other tarsomeres; tarsomeres I and IV longer than II and III, and III is shortest tarsomere

Metasoma: with combined length of petiolar segments slightly less than two-thirds of gastral length; first petiolar segment comparatively shorter, about 3.4 times length of second; first petiolar segment with fine longitudinal carinae, and expanded posteriorly, with concave ventral margin; second petiolar segment, difficult to observe, apparently cylindrical with faint

longitudinal striations, segment may be slightly inset into dorsal margin of first petiolar segment; gaster in dorsal view teardrop-shaped, and in lateral view it appears slightly flattened dorsally and convex ventrally; tergum with six apparent segments, with second tergite longest, and first tergite extensively overlapping second petiolar segment (forming hood-like cover), with patch of foveate integument; other tergites with punctured surface structure, and second tergite with transverse row of fovea along posterior margin; sternum with four apparent (visible) segments, with second sternite longest; lateral margin between tergites and sternites apparently separated by carina that extends posteriorly from lateral margins of tergite 1. Genitalia not everted, but apex of ovipositor visible; very short ovipositor sheath appears to be protruding from distal end of metasoma (probable female specimen).

Genus *Mesoserphites* n. gen.

(urn:lsid:zoobank.org:act:0B5A649F-9A39-465E-BEC9-71FA4023FE59)

Etymology. The new genus name is a combination of the Latin adjective *meso* meaning “middle” refers to the mixture of characters between the genera *Serphites* and *Aposerphites*, combined with *-serphites* a common suffix for Serphitidae; the name is masculine.

Diagnosis. Lateral ocellus nearly touching or touching compound eye margin; clypeus inclined and dorsoventrally short; antennae insert near anteroventral margin of compound eye; mandibles overlap when closed, non-protuberant; pronotum reaching tegula and pterostigma distinct; first petiolar segment less than 2 times length of second segment; gaster with different lengths between first three terga, which cover more than half of gastral length.

397 *Type species. Mesoserphites annulus* **gen. et sp. n.**

398 *Included species.* Five new species in Burmese Albian-Cenomanian amber described herein: *M.*

399 *viraneacapitis*, *M. engeli*, *M. giganteus*, *M. annulus*, and *M. scutatus*.

400

401 Key to species of *Mesoserphites* **n. gen.**

402

403 1. Head slightly longer than wide; first petiolar segment length less than 1.5 times length of
 404 second petiolar segment; first petiolar segment rimmed anteriorly; first petiolar segment
 405 with ring-like expansion posteriorly; first petiolar segment without hamulus
 406 anterodorsally [Albian-Cenomanian, Myanmar] *M.*
 407 *viraneacapitis* **n. sp.**

408 -- Head as long as wide, or wider than long; first petiolar segment length more than 1.5
 409 times that of second petiolar segment; first petiolar segment not rimmed anteriorly; first
 410 petiolar segment without ring-shaped posterior expansion; first petiolar segment with
 411 hamulus anterodorsally
 412 2

413

414 2. Gaster longer than mesosoma; second petiolar segment with broad hook-like projection
 415 posteroventrally; sulcus near transscutal line shallow and weakly developed [Albian-
 416 Cenomanian, Myanmar] *M. engeli* **n.**
 417 **sp.**

418 -- Gaster shorter than mesosoma; second petiolar segment without broad hook-like
 419 projection posteroventrally; sulcus along transscutal line broad and well-developed
 420 3

- 421
- 422 3. Tarsi slightly shorter than corresponding femora; total body length more than 3 mm;
- 423 second petiolar segment without ring-like expansion posteriorly [Albian-Cenomanian,
- 424 Myanmar] *M.*
- 425 *giganteus* **n. sp.**
- 426 -- Tarsi as long as or longer than corresponding femora; total body length less than 2.5 mm;
- 427 second petiolar segment with ring-like expansion posteriorly
- 428 4
- 429
- 430 4. Mesocoxa with two central longitudinal carinae on lateral surface; second petiolar
- 431 segment cylindrical with broad ring-like expansion posteriorly; total body length less
- 432 than 1 mm [Albian-Cenomanian, Myanmar] *M.*
- 433 *annulus* **n. sp.**
- 434 -- Mesocoxa without two central longitudinal carinae on lateral surface; second petiolar
- 435 segment cylindrical with narrow collar posteriorly; total body length less than 2 mm
- 436 [Albian-Cenomanian, Myanmar] *M. scutatus* **n.**
- 437 **sp.**

438

439

440 *Mesoserphites annulus* gen. et sp. n.

441 (urn:lsid:zoobank.org:act:BA204CB5-3BB8-41A0-B3E5-C754358F51E0)

442

Material examined. Holotype RSKM_P3306.60 (male). Polished amber piece including support epoxy, one of four amber pieces cut from original block, with dimensions of 17.1 mm x 10.0 mm x 6.9 mm; amber is clear yellow-orange and flow lines indicate runnel on one side of piece.

Etymology. The new species name refers to the ring-like expansion present near the posterior margin of the second petiolar segment. It is based on the Latin word for “ring or circle”, *annulus*; name is masculine.

Type locality. Hukawng Valley, Kachin State, in Myanmar, upper Albian-lowermost Cenomanian.

Diagnosis. Unique characters of the new species that distinguish it from congeners include: scape approximately 1.6 times longer than its greatest width; tarsi as long as corresponding femora; pronounced lateral sulcus between tergites and sternites, which may overarch laterotergites (narrow carina present in *M. giganteus*, and *M. viraneacapitis*); second petiolar segment with slender, ring-like posterior margin (not present in all other *Mesoserphites*). Differential characters include: total body length ~2.1 mm; head wider than long; compound eye occupying approximately two-thirds of head in lateral view; ocelli forming weakly isosceles triangle; right mandible with three teeth progressively elongated ventrally, with gap between ventral and middle tooth; left mandible with two broad-based teeth, and with ventral tooth slightly more robust and elongate; gaster significantly shorter than mesosoma; sternum with six visible segments; first petiolar segment shorter, about 1.7 times length of second segment; first petiolar segment without globose, ring-like posterior part, and not rimmed anteriorly; first petiolar segment with hamulus anterodorsally.

Description. Total body length ~2.10 mm; mesosoma ~1.05 mm in length; forewing ~1.03 mm long, and ~0.52 mm wide; hind wing ~0.58 mm long, and ~0.21 mm wide; metasoma ~0.83 mm in length; gaster ~0.43 mm long (Fig. 4).

Head: wider than long; in lateral view, compound eye rounded and globose, bearing numerous, small, erect, fine setae; frons straight, slightly sunken; vertex with scabrous surface structure (possibly due to taphonomic deformation), and highly mounded between lateral ocelli; gena moderately inflated laterally, with punctured surface structure, and bearing suberect, short, fine setae; gena moderately inflated near vertex; median ocellus apparently twice size of lateral ocellus, and separated from lateral ocellus by 4 OD; lateral ocelli nearly touching compound eye margin, and separated by 5 OD; antenna 9-segmented, and clavate; flagellar articles measuring approximately: 80, 61, 57, 62, 69, 66, and 113 μm ; pedicel measuring approximately 82 μm ; scape measuring approximately 137 μm long and 86 μm wide; first flagellar article longest and bell-shaped semi-clavate; subsequent flagellar articles nearly square in outline, with rounded-edge; apical flagellar article terminates in rounded, blunt point; pedicel slightly longer than first flagellar article. Mandibles robust and deeply divided, with elongate and pointed teeth; right mandible with teeth that progressively diminish in size dorsally, with ventral tooth longest and slender, and middle tooth broader; left mandible with long and curved teeth; maxillary palpus four-segmented, and geniculate between second and third palpomere, with terminal palpomere forming elongate, acute point; maxillary palpus significantly longer than labial palpus, but only three-quarters of length of mandible.

Mesosoma: has mesoscutum with areolate-rugulose to minutely colliculate surface structure; mesoscutellum with areolate-rugose surface structure; mesopleuron flattened in ventral half, with row of fovea in external outline, and swollen in dorsal half with rugulose-lacunose surface

structure; metanotum with scrobiculate surface structure (transverse row of shallow foveae separated by strong carinae); propodeum with rugulose surface structure.

Wings: forewing with pterostigma shaped like equilateral triangle, with 1rs-r curved and 2rs-r straight; pterostigma with slender and long, posterior expansion of fuscous area adjacent to r-rs and Rs; 2Rs nebulous, extending straight adbasally from pterostigma, vein long but expanding, and fading before reaching M; 3Rs extending apically from pterostigma, forming curved expansion and reaching anterior wing margin apically; C nebulous, straight and broad; costal cell wider apically, with width approximately three times that of C, and narrower basally (slightly more than one width of C); tubular 1M slightly wider than tubular Sc+R; Sc+R, straight, fusing apically with bulbous 1Rs, and truncated in contact with pterostigma; Sc+R basally reaching C before bend; M+Cu spectral, curved and reaching 1M and Cu apically; 2M distally nebulous and straight; 1m-cu spectral; Cu relatively straight and terminating in CuP and CuA; CuA nebulous, basally straight, fuscous, and broad, then curving posteriad, thinning gradually to reach wing apex; CuP fading before reaching A; A nearly straight and tubular. Hind wing lanceolate; nebulous Sc+R nearly straight; R wider than Sc+R, with three hamuli; Rs crossvein spectral and fading rapidly basally.

Legs: moderately robust; pro- and mesotrochanter long and bell-shaped, while metatrochanter slightly longer and more clavate; protibia with two, long, straight spurs; calcar bifid near apex; metatibia with one straight apical spur, which is finer and shorter than mesotibial spur; metatibia wider than mesotibia apically, also with rows of spines near apex, which become elongate (almost equal to length of spur) near posteroventral margin; basitarsus with sparse, semi-erect setae; meso- and metabasitarsus as long as other tarsomeres' combined length, while probasitarsus shorter; tarsomeres I and II longer than III and IV, and III smallest tarsomere; pro-

and mesopretarsi with claws as long as arolium, while metapretarsus with finer and shorter claws.

Metasoma: with gaster more ovate than teardrop-shaped in ventral view; gaster bare, swollen anterodorsally, and straight ventrally in lateral view; tergum with five segments visible, first slightly longer than second; length of petiolar segments equal to gastral length; first petiolar segment cylindrical, with few, prominent, longitudinal carinae, and with fossulate, wide, deep, sulci between, approximately one on each edge; first petiolar segment slightly wider anteriorly, with pronounced anterior lip on dorsalmost margin; second petiolar segment cylindrical with punctures. Male genitalia with parameres clavate, apex moderately expended; penis valves gently swollen posteriorly.

Mesoserphites giganteus gen. et sp. n.

(urn:lsid:zoobank.org:act:A596C263-1C97-485A-99A0-3C41E07E4641)

Material examined. Holotype RSKM_P3306.63 (female); paratype AMNH_BU 667 (male). RSKM_P3306.63 is polished amber piece including support epoxy, one of four amber pieces cut from original amber specimen, with dimensions of 21.0 mm x 15.3 mm x 8.4 mm; amber is clear yellow-orange with multiple layers. AMNH_BU 667 is polished amber piece embedded in support epoxy with dimensions of 11.1 mm x 7.7 mm x 4.3mm; amber is clear yellow-orange with multiple layers and minor particulate content.

Etymology. The new species name refers to total body length, which is greatest of all known Serphitidae. Epithet based on Latin word for “gigantic”, *giganteus*.

Type locality. Hukawng Valley, Kachin State, in Myanmar, upper Albian-lowermost Cenomanian.

Diagnosis. Unique characters for new species include: total body size more than 3.46 mm (significantly shorter in all other *Mesoserphites*); combined length of petiolar segments relatively long, three-quarters of gastral length (although apex of gaster is not preserved); tarsi shorter than corresponding femora; broad and deeply impressed sulcus near transscutal line interrupted by raised areas posterior to notauli. Differential characters that separate new species from other members of *Mesoserphites* include: head wider than long; ocelli forming weakly isosceles triangle; compound eye occupying approximately one-third of head in lateral view; scape approximately 2.2 times longer than its greatest width; right mandible with three teeth; left mandible with two teeth; mesoscutellum convex; gaster apparently much shorter than mesosoma in length; first petiolar segment comparatively short, about 1.9 times length of second segment; first petiolar segment without globose, ring-like posterior part, and not rimmed anteriorly; first petiolar segment with hamulus anterodorsally.

Description. Holotype total body length more than ~3.46 mm (specimen incomplete with posterior metasoma missing); mesosoma ~1.76 mm in length; forewing ~0.94 mm long (incomplete), and ~0.53 mm wide; hind wing ~0.96 mm long (incomplete), and ~0.34 mm wide; metasoma ~1.44 mm in length; gaster ~0.79 mm long (incomplete) (Figs. 5–6).

Head: globose; gena slightly inflated; vertex highly mounded between lateral ocelli; frons broadly concave; ocelli apparently forming isosceles triangular; median ocellus appears equal in size to lateral ocellus, and separated from lateral ocellus by 2 OD; lateral ocelli rounded and

nearly touching compound eye margin, separated by 4 OD; antenna 10-segmented and proportionally short; flagellar articles measuring approximately: 106, 94, 101, 93, 99, 97, 87, and 105 μm ; pedicel measuring approximately 151 μm ; scape measuring approximately 333 μm long and 155 μm wide; first flagellar and apical flagellar articles longest and equal in length; flagellum flattened along posterior margin, and slightly serrated along anterior margin; first flagellar article clavate or rounded anteriorly, and subsequent flagellar articles chalice-shaped; apical flagellar article bud-shaped, and terminating in acute point; pedicel pear-shaped, and approximately one-quarter length of scape; torulus slender, curved, and well-defined. Mandibles deeply divided, with elongate and pointed teeth on robust mouthparts; right mandible with middle tooth shorter than two others, ventral tooth longer and wider than dorsal tooth; left mandible with ventral tooth much wider and longer than dorsal tooth; maxillary and labial palpi not clearly visible, terminal maxillary palpomere broad and flattened, with acute point.

Mesosoma: has pronotum with costate surface structure; mesoscutum and mesoscutellum, shield-shaped, and highly convex; mesoscutum with coriaceous surface structure between curved notauli; notauli forming V-shape which comes to point near anterior margin of mesoscutum; mesoscutellum with middle part (between wings) forming transverse mounded strip, with anterior row of foveate-reticulate sculpture then foveate surface structure; mesoscutellum slightly concave adjacent to transverse raised strip, with confused rugulose surface structure; mesopleuron nearly triangular, with row of fovea on anterior and posterior margins, and broadly notched on posterodorsal margin; metanotum dorsally broad, concave, and with rugulose surface structure; propodeum convex, with alveolate-rugulose surface structure separated by high carinae.

Wings: with incomplete preservation. Forewing without triangular pterostigma visible, missing apical two-thirds; 1rs-r convex; C nebulous, straight; Sc+R tubular not reaching C basally; Sc+R, slightly curved; Sc+R reaching bulbous 1Rs before contact with pterostigma; M+1Rs tubular, basal abscissa as wide as Sc+R; 2M curved in contact with 1m-cu and spectral, highly slender; M+Cu slender tubular, broader apically than basally, not reaching Sc+R basally, and broader than M basally, slightly curved; Cu (basal abscissa) straight, as wide as 1M, terminating in CuP; CuA (distal abscissa) spectral; A tubular, short, slender, and fading midway toward base of wing. Hind wing with Sc+R tubular, broader, relatively straight, and reaching Rs; Rs (basal abscissa) nebulous, short, and straight; R tubular, as wide as Sc+R, slightly curved, and terminating in bulbous expansion with three hamuli.

Legs: covered by semi-erect setae; procoxa equal in length and width, while mesocoxa slightly longer than wide and metacoxa elongate; protrochanter bell-shaped, with meso- and metatrochanter rectangular; femurs spindle-shaped; pro- and mesotibia elongate bell-shaped, and metatibia bulbous posteroapically with numerous, long, semi-erect, broad setae; pro- and mesotibia with two spurs, with posterior spur longer and more slender than anterior spur, and without metatibial spur apparent; metabasitarsus significantly longer than cumulative length of other tarsomeres; pretarsus long with broad arolium between two simple, long, broad claws.

Metasoma: with gaster flattened ventrally and swollen dorsally (in lateral view); preservation is incomplete, but two terga and three sterna are perceptible; lateral margins between tergites and sternites without broad separation, difficult to observe boundaries; first petiolar segment shorter in length, longitudinally carinate, with row of fovea between carina, and with notched anterodorsal edge; second petiolar segment quadrangular, slightly curved dorsally and with two straight edges between corners ventrally.

Male: paratype AMNH_BU 667 does not have genitalia exposed externally, but it is very similar in overall appearance to holotype specimen. As with other males in *Mesoserphites*, it possesses seven flagellar articles and appears to be smaller than corresponding female. Highly curved preservation position within surrounding amber gives male more pronounced ‘hunch-backed’ appearance which may not be representative; posture also complicates measurements, male apparently with ~2.31 mm total body length, ~354 µm head length, ~875 µm mesosomal length, ~521 µm petiolar length, ~563 µm gastral length. Darker preservational colour of cuticle, combined with bubbles adhering to surface of mesosoma, highlight coarser surface sculpture of punctures on mesoscutum.

Mesoserphites engeli gen. et sp. n.

(urn:lsid:zoobank.org:act:49CE3893-D002-43D9-B7CC-A51959EE9821)

Material examined. Holotype RSKM_P3306.62 (female); paratype AMNH_Bu 1356 (male). Holotype within polished amber piece including support epoxy, one of two amber pieces cut from original block with dimensions of 10.3 mm x 9.3 mm x 4.4 mm; amber is clear yellow with flow lines delimiting runnel around specimens. Paratype within 12.8 mm x 16.9 mm x 5.9 mm block of epoxy embedded amber, and very well preserved with partially everted genitalia.

Etymology. The new species name is a patronym for Dr. Michael Engel, in recognition of his substantial contributions to the Serphitidae.

Type locality. Hukawng Valley, Kachin State, in Myanmar, upper Albian-lowermost Cenomanian.

Diagnosis. Unique characters for species include: ocelli clearly forming equilateral triangle (isosceles triangle in all other *Mesoserphites* spp.); head as long as wide or slightly transverse (elongate in *M. viraneacapitis*, and more transverse in all other *Mesoserphites* spp.); mesoscutum without visible notauli, highly convex, and in lateral view appearing somewhat mounded, lacking pronounced sulcus along transscutal line; second petiolar segment with hamulus posteroventrally (without hamulus posteroventrally in all other *Mesoserphites* spp.). Differential characters for new species include: total body length ~1.96 mm; compound eye relatively large, occupying approximately two-thirds of head in lateral view; lateral ocelli ovate, separated from compound eye margin by less than 0.5 OD (nearly touching compound eye margin), and canted posterolaterally, with lateral edge recessed into vertex; scape approximately 4.7 times longer than its greatest width; combined length of petiolar segments relatively short, equal to one-third of gastral length; sternum with four visible segments; first petiolar segment proportionally longer, about 1.9 times length of second segment; first petiolar segment without globose, ring-like posterior part, and not rimmed anteriorly; first petiolar segment with hamulus anterodorsally; gaster slightly longer than mesosoma.

Description. Total body length ~1.96 mm; mesosoma ~0.69 mm in length; forewing approximately 0.94 mm long (incomplete), and ~0.34 mm wide; hind wing ~0.72 mm long, and ~0.18 mm wide; metasoma ~0.96 mm in length; gaster ~0.66 mm long (Fig. 7).

Head: with compound eye globose and rounded in lateral view, bearing minute, erect, fine setae; gena moderately inflated; head with slight taphonomic distortion in holotype, width 1.2 times length (proportion closer to 1.3 in male paratype) vertex slightly mounded between lateral ocelli and with posterior margin rounded; frons slightly convex; median ocellus slightly smaller than lateral ocellus, and separated from lateral ocellus by approximately 3 OD; antenna 10-segmented; flagellar articles measuring approximately: 75, 42, 40, 54, 52, 57, 58, and 83 μm ; pedicel measuring approximately 70 μm ; scape measuring approximately 164 μm long and 35 μm wide; first flagellar article bell-shaped; subsequent flagellar articles appear shorter and nearly chalice-like; apical flagellar article terminates in rounded acute point; pedicel pear-shaped, approximately two-fifths of length of scape, and broader than first flagellar article. Mandibles deeply divided with elongate, pointed teeth; details of closed mandibles not clearly distinguishable; right mandible apparently with three stout teeth visible in holotype, teeth progressively diminishing in size dorsally; left mandible apparently with two teeth visible in holotype; maxillary palpus apparently as long as mandible, or perhaps longer than mandible, four-segmented, and geniculate between second and third palpomere, with terminal palpomere slender, long, and with acute point; labial palpus approximately half length of maxillary palpus, apparently three-segmented and geniculate between first and second palpomere, with terminal palpomere possessing highly inflated acute point.

Mesosoma: dark and without clear surface structure visible; mesoscutellum slightly convex dorsally; mesopleuron bud-shaped, rounded along dorsal margin; metanotum convex, sunken deeply in mesosoma; propodeum with many scabrous surface mounds.

Wings: not completely preserved. Forewing with triangular pterostigma equilateral in shape, and with slender, elongate, posterior expansion of fuscous area adjacent to r-rs and Rs; C nebulous

and Sc+R tubular; Sc+ R fusing apically with bulbous 1Rs+1M, equal to width of adjacent costal cell; 1Rs+1M and Sc + R both dark and truncated in contact with pterostigma; 3Rs dark and narrow tubular, basal curved towards anterior part of wing.

Legs: with moderately dense cover of fine setae; procoxa rounded, length and width equal, while meso- and metacoxa longer than wide, and with two longitudinal carinae on lateral surface equidistant from each other and from external margins of coxa; trochanters equal in length, and appear laterally compressed; profemur shorter and wider than meso- and metafemur; tarsi longer than corresponding femora; tibial spur formula 1-2-2, with protibial spur slightly longer than meso- and metatibial spurs; probasitarsus equal to cumulative length of other tarsomeres; pro- and metatarsomeres I, II and IV subequal in length and longer than mesotarsomeres; pretarsus with short arolium, and long, thin claws.

Metasoma: gaster more ovate than teardrop-shaped, with punctured surface structure in dorsal view; gaster slightly flattened ventrally in lateral view; tergum apparently with five segments, with first tergite longer than second; second petiolar segment somewhat rectangular (ventrally and dorsally straight) with hook-like posteroventral lip. Genitalia not everted, but apex of ovipositor sheathe appears to be protruding from distal end of metasoma, probable female specimen.

Male: paratype specimen is very similar to female holotype; male differences include having seven flagellar articles, with first article slightly shorter than apical article; maxillary palpus as long as mandible; head slightly transverse; first petiolar segment 2.1 times length of second, as opposed to 1.9 times in type specimen; total body length ~ 1.4 mm. Parameres exposed in paratype are clavate with two terminal setae that are elongate and erect; small, mound-like projections anterior to parameres bear five, erect, apical setae, but details of region are unclear.

Mesoserphites scutatus gen. et sp. n.

(urn:lsid:zoobank.org:act:DF1E1F2C-3C8B-497E-9607-93651773B394)

Material examined. Holotype RSKM_P3306.30a (female, wings partially folded and obscured); paratypes RSKM_P3306.30b (male), RSKM_P3306.30c (partial, probably female based on size), AMNH_BU 676 (female weathered specimen with exposed ovipositor apex). RSKM_P3306.30a and RSKM_P3306.30b within polished amber piece including support epoxy, one of three amber pieces cut from original block, with dimensions of 10.4 mm x 7.6 mm x 6.5 mm; amber is orange with high particulate content. RSKM_P3306.30c in polished amber piece including support epoxy, one of three amber pieces cut from original block, with dimensions of 10.4 mm x 7.6 mm x 6.5 mm; amber is orange with high particulate content; specimens preserved alongside syninclusion of *M. viraneacapitis* (RSKM_P3306.30d). AMNH_BU 676 is one of three pieces cut from larger amber sample, embedded in epoxy block with dimensions of 6.3 mm x 6.4 mm x 2.3 mm.

Etymology. The new species name refers to mesosoma-shape, which is inflated and shield-shaped, using the Latin adjective *scutatus*, which means “shield-shaped”.

Type locality. Hukawng Valley, Kachin State, in Myanmar, upper Albian-lowermost Cenomanian.

Diagnosis. Unique characters for the new species include: broad transcutellar furrow separating mesoscutum from mesoscutellum and isolating distinctive shield-shaped mesoscutellum; first petiolar segment with posterior margin notched dorsally to accept part of second segment (not present in other *Mesoserphites* spp.). Differential characters include: head wider than long; compound eye occupying approximately one-half of head in lateral view; lateral ocellus removed from margin of compound eye by 0.5 OD; left mandible with two large teeth, more robust and broad-based than teeth on right mandible; right mandible with three large teeth diminishing in size dorsally, and with dorsal and middle tooth closely spaced; antenna with eight flagellar articles, and first article is longest, slightly longer than pedicel; tarsi significantly longer than corresponding femora; gaster slightly shorter than mesosoma; sternum with six visible segments; first petiolar segment relatively short, about 1.6 to 1.8 times length of second segment; first petiolar segment without globose or ring-like posterior part, and not rimmed anteriorly first petiolar segment with hamulus anterodorsally.

Description. Female holotype RSKM_P3306.30a, with total body length ~1.96 mm; mesosoma ~0.67 mm in length; metasoma ~0.93 mm in length; gaster ~0.65 mm long. Male paratype RSKM_P3306.30c slightly more gracile, with total body length ~1.92 mm (angled within amber); mesosoma ~0.65 mm in length; metasoma ~0.94 mm in length; gaster ~0.62 mm long (Fig. 8).

Head: in female holotype globose in lateral view, with rounded compound eye; gena broad and slightly inflated; ocelli not clearly visible in holotype, apparently forming isosecles triangle with gentle mounding between ocelli; antenna 10-segmented in female, unknown in male; scape approximately 133 μ m long and 61 μ m wide; pedicel ~82 μ m long and swollen apically,

significantly broader than basal flagellar article; flagellar articles measure approximately 97, 66, 51, 41, 46, 46, 51, and 56 μm in length, and become gradually broader from pedicel to flagellomere six, then taper to acutely pointed apical flagellomere; flagellomere seven with inclined stiff setae apically; left mandible bearing two broad-based teeth, plus diminutive dorsal tooth, and bearing long setae; right mandible with three broad-based teeth that gradually increase in length ventrally in series; maxillary palpus four-segmented and geniculate at midlength, palpus approximately two-thirds of mandibular length; labial palpus either three- or four-segmented, and approximately half of length of mandible.

Male: paratype similar to female but missing some details, with left side of head missing; gena slightly inflated; antennae missing; mandibles deeply divided, with left mandible bearing two broad-based teeth, plus diminutive dorsal tooth, and bearing long setae; right mandible not distinguishable.

Mesosoma: with pronotum convex, with punctured surface structure; pronotum with row of fovea surrounding external edges; mesoscutum highly convex, shield-shaped, with row of fovea on anterior margin; notauli appear strongly curved and removed from lateral margins of mesoscutum; mesoscutellum with scrobiculate surface structure anteriorly, and with rugose surface structure posteriorly, separated from mesoscutum by broad transverse sulcus along transscutal line; mesopleuron bud-shaped, flattened dorsally, with posterodorsal margin bearing broad row of fovea; metanotum with scrobiculate surface structure, and apparently seven depressions; propodeum convex with scabrous surface structure.

Wings: folded and incomplete in female holotype, with many details only visible in partial wings (missing apices) preserved in male paratype —details provided here are based predominantly on paratype, but appear consistent in holotype. Forewing with C nebulous, and costal cell very wide,

width approximately five times that of nebulous Sc+R; Sc+R as wide as 1M, nebulous adbasally; Sc+R fused apically with bulbous 1Rs, and truncated in contact with pterostigma; 2M faintly pigmented, broad, fuscous basally, but fading rapidly towards apex; Cu slightly concave.

Legs: covered by inclined setae; procoxa length and width equal, mesocoxa more ovate and metacoxa elongate; procoxa with two central longitudinal carina on lateral surface equidistant from each other and from external margins of coxa; pro- and mesotranter longer and broader than metatrochanter; pro- and mesofemur shorter and narrower than metafemur; metafemur with longitudinal depression on posterior surface; probasitarsus longer than, and metabasitarsus as long as cumulative length of other tarsomeres; tarsomeres I and IV longer than II and III, and III is smallest tarsomere; pretarsus with short arolium between two long, simple claws.

Metasoma: with combined length of petiolar segments equal to one-half of gastral length; gaster covered with fine punctures and minute, erect setae; gaster in lateral view convex dorsally, and nearly straight ventrally; tergum with five apparent tergites, and with second tergite longest, slightly longer than first tergite; sternum without clear surface structure visible; lateral margins between tergites and sternites difficult to observe; first petiolar segment nearly cylindrical, and slightly curved, with anterodorsal expansion/pronounced anterodorsal lip; surface of first petiolar segment with few, prominent, longitudinal carinae separated by fossulate sulci; second petiolar segment bulbous, with flattened dorsal surface. Apex of ovipositor sheath appears to be protruding from distal end of metasoma, holotype probably female.

Remarks. Specimen AMNH_BU 676 is smaller than other female exemplars, with a total body length of approximately 1.75 mm; and it has moderately dense, suberect setae on the first and second petiolar segments, with setae lengths equal to about half of the adjacent petiolar width. These differences may suggest that the specimen belongs to a different species, but there is

limited evidence to support this—the specimen exhibits significant taphonomic distortion and weathering which may affect apparent dimensions, and highlight setae that are more subtle in other representatives.

Mesoserphites viraneacapitis gen. et sp. n.

(urn:lsid:zoobank.org:act:BB62F301-6CBF-4124-995A-DB0BBDE62F0E)

Material examined. Holotype RSKM_P3306.30d (male); paratype AMNH_BU 312 (male). Holotype in polished amber piece including support epoxy, one of three amber pieces cut from original block, with dimensions 10.4 mm x 7.6 mm x 6.5 mm; amber is orange with high particulate content; preserved alongside syninclusions of *M. scutatus* (RSKM_P3306.30a–c). Paratype in epoxy-embedded amber piece polished to dimensions of 10.9 mm x 11.4 mm x 4.3 mm; amber is pale orange, clear, with prominent flow lines.

Etymology. The new species name refers to the head-shape which is similar to the mask of the fictional character “Spider-Man”; it is a combination of the Latin noun *vir-* meaning “man” combined with *aranea* meaning “spider”, and *capitis* for the head-shape.

Type locality. Hukawng Valley, Kachin State, in Myanmar, upper Albian-lowermost Cenomanian.

Diagnosis. Unique characters among *Mesoserphites* species include: head longer than wide (equant in *M. engeli* and transverse in all other *Mesoserphites*); frons straight and sunken compared to eye, and highly slender (not sunken, and wider in all other *Mesoserphites* spp.);

clypeus subvertical (inclined in all other *Mesoserphites* spp.) and mandibles with relatively low anterior projection when closed; mesoscutellum flattened (convex in all other *Mesoserphites* spp.); first petiolar segment relatively short, about 1.4 times length of second segment; first petiolar segment with globose ring-like posterior part and apparently rimmed anteriorly (not ring-like posterior part and not rimmed anteriorly in all other *Mesoserphites* spp.); first petiolar segment without hamulus anterodorsally (with hamulus anterodorsally in all other *Mesoserphites* spp.). Compared to other *Mesoserphites* species, new species has differential characters that include: total body length ~1.85 mm; compound eye occupying approximately one-third of head in lateral view; ocelli forming weakly isosceles triangle; left mandible with two long teeth; scape approximately 3.1 times longer than its greatest width; gaster slightly longer than mesosoma; combined length of petiolar segments slightly less than two-thirds of gastral length; sternum with five visible segments.

Description. Total body length ~1.85 mm; mesosoma ~0.58 mm in length; forewing approximately 1.13 mm long, and ~0.55 mm wide; hind wing ~0.78 mm long, and ~0.19 mm wide; metasoma ~0.95 mm in length; gaster ~0.60 mm long (Fig. 9).

Head: with compound eye forming high teardrop-shape, globose eyes bearing numerous, erect, fine setae; gena more inflated, especially near compound eye ventral margin and moderately inflated near vertex; median ocellus markedly larger than lateral ocelli; lateral ocelli nearly touching compound eye margin, weakly rounded, canted posterolaterally; antenna 9-segmented; flagellar articles measuring approximately: 89, 73, 75, 67, 73, 59, and 78 μm ; pedicel measuring approximately 78 μm ; scape measuring approximately 188 μm long and 60 μm wide; first flagellar article clavate; second flagellar article shorter, clavate, and following articles almost

830 rectangular in outline; apical flagellar article terminates in acute point; pedicel elongate, pear-
831 shaped, and approximately one-fifth length of scape; scape length equal to height of compound
832 eye. Mandible closed, and bearing numerous, long, erect, fine setae; left mandible apparently
833 with two very long, pointed teeth, with dorsal tooth thinner than ventral tooth; right mandible not
834 clearly visible; maxillary palpus geniculate and terminating in slender and long rounded point,
835 only apical two segments visible, but palpus significantly shorter than mandible.

836 Mesosoma: without clear surface structure visible; mesoscutum, convex and slightly shield-
837 shaped, with punctate-reticulate surface structure; mesoscutellum with scabrous surface
838 structure; propodeum relatively straight, with scabrous surface structure.

839 Wings: forewing with equilateral triangle-shaped pterostigma, with 1rs-r and 2rs-r curved while
840 R is straight; pterostigma with globose, triangular, posterior expansion of fuscous area adjacent
841 to r-rs and Rs; 2Rs nebulous, extending adbasally from pterostigma, forming long, straight
842 expansion reaching 2M (or seems to pass between 2M and 1m-cu crossvein and fading before
843 Cu); 3Rs straight, extending apically from pterostigma, expanding and reaching anterior wing
844 margin apically; C nebulous, straight, with basal curvature; costal cell wider apically, with width
845 approximately three times that of C, and narrower basally, less than half as wide as C; tubular
846 1M wider than Sc+R; tubular Sc+R, fusing apically with bulbous 1Rs, and truncated in contact
847 with pterostigma; Sc+R basally reaching C before bend; M+Cu spectral, reaching apically 1M
848 and Cu in lowest point, straight; 2M fuscous and straight; 1m-cu crossvein slightly broader than
849 2M; Cu curved and terminating in CuP and CuA distally; CuA straight, fuscous, and wider
850 basally, then curved and gradually thinning to wing apex; CuP fading before reaching A; A
851 slightly curved and tubular. Hind wing lanceolate; nebulous Sc+R relatively straight; R wider

than Sc+R, with three hamuli; Rs crossvein spectral and fading rapidly; posterior margin of wing has small nebulous patch that may represent A, with patches erect setae along vein.

Legs: moderately robust and covered by numerous, inclined, fine setae; procoxa and mesocoxa slightly longer than wide, and metacoxa elongate; protrochanter slightly shorter than mesotrochanter and both are bell-shaped, while metatrochanter is elongate and globose; metafemur with shallow and broad central depression; pro- and mesofemur more slender than metafemur; profemur with rounded expansion on posterior surface; tibial spur formula 1-2-2, with protibial spur fine and long, and meso- and metatibial spurs shorter; protibia shorter than meso- and metatibia; basitarsus shorter than cumulative length of other tarsomeres; pretarsus short, with heart-shaped arolium, and broad, long claws.

Metasoma: gaster covered with fine punctures and minute, semi-erect setae, ovate in dorsal view, convex dorsally, and straight ventrally in lateral view; tergum with five segments, first tergite longer than second; lateral margins between tergites and sternites difficult to distinguish, only visible as fine line; first petiolar segment somewhat cylindrical, with anterior width slightly greater than two-thirds of posterior width; first petiolar segment with numerous, fine carinae separated by fine fossulae; second petiolar segment bulbous, with slightly flattened dorsal surface. Male genitalia with parameres semi-clavate, apex moderately expanded; penis valves gently swollen basally, and moderately separated.

Remarks. Paratype specimen AMNH_BU 312 differs from the holotype in having a head that appears slightly transverse, as well as a body that appears more gracile, smaller (~1.63 mm in total body length), and more setose. However, most of these differences can be attributed to taphonomic distortion, because the specimen has shrivelled in the surrounding amber and developed a wrinkled cuticle, as well as dark cuticle preservation highlighting translucent

structures like setae. Observations of the paratype are limited to only one side, due to cracks and syninclusions in the surrounding amber, but it is more parsimonious to consider this specimen part of the *M. viraneacapitis* series, than a unique exemplar of a different species.

In general, *M. viraneacapitis* displays some characteristics of Supraserphitinae, including the subvertical clypeus and petiolar segments that are closer to being even (first segment is only 1.4 times length of second). However, the seven flagellar articles preclude the *M. viraneacapitis* males described here from being the unknown male form of *Supraserphites*, which would presumably have nine flagellar articles.

5. Discussion

Discovery of the two new genera *Buserphites* and *Mesoserphites* extends the diversity of the family Serphitidae and builds upon the known diversity in Burmese mid-Cretaceous amber. Despite the large number of serphitids that are commercially available from this deposit, the diversity of these specimens seems to outstrip the samples that are currently available within the AMNH and RSKM collections. Most of the new species discovered are only known from a unique specimen (singleton), or very small specimen sets within museum collections. This may lead to taxonomic uncertainty, and a lack of connection between males and females of each species, until larger sample sets are described. Taxonomic uncertainty is exacerbated in our study because many of the specimens in Burmese amber have undergone weak compression or taphonomic shrivelling. This cuticle deformation varies between specimens, but it appears to be more significant in small-bodied taxa, such as some of the species described herein. Distortion is noticeable on cuticle surface structures within some specimens, so we have tried to emphasize large-scale structural differences and specify regions of uncertainty within our descriptions.

Many of the new species proposed herein have both female and male specimens assigned to them. These associations are difficult to support in cases where the sexes are not found as syninclusions. Consequently, future work and large sample sets may show that some of these specimens belong to unrecognized species, instead of being sexually dimorphic forms within the species proposed here. In previous work on Upper Cretaceous serphitid wasps (e.g., McKellar and Engel, 2010), males appear to have seven flagellar articles while females possess eight, and males appear to be slightly smaller or more gracile than their female counterparts. For the time being, and with the limited sample set that is available, we have refrained from erecting additional species in all cases where these features were the main differences between specimens.

The new species within *Buserphites* **n. gen.** clearly differ from all known Serphitoidea in having: a flagellum with seven or eight segments (six-segmented in *Jubaserphites*, eleven-segmented in *Supraserphites*, and twelve-segmented in Archeoserphitidae); a lateral ocellus that is separated from the compound eye by 0.5 OD (nearly touching compound eye in *Serphites*, and *Mesoserphites* **n. gen.**); a pronotum that extends to reach the tegula, and a pterostigma that is distinct (pronotum not reaching tegula, and forewing with pterostigma indistinct in *Microserphites*); a first petiolar segment that is 3.4 times the length of the second segment (two times or less in *Mesoserphites* **n. gen.**, *Aposerphites*, and *Microserphites*, or between two and three times in *Serphites*); and a second petiolar segment with faint longitudinal striations (apparently unique in Serphitoidea). The new species within *Mesoserphites* **n. gen.** can be distinguished from other Serphitoidea based on having the following combination of characteristics: a flagellum with seven or eight articles (six articles in *Jubaserphites*, and ten articles in *Supraserphites*); the lateral ocellus nearly touching the compound eye (separated from

eye by 1 OD in *Aposerphites*, and separated from eye by 0.5 OD in *Buserphites* **n. gen.**); a pronotum that reaches the tegula, and a pterostigma that is distinct (pronotum not reaching tegula, and the forewing with pterostigma indistinct in *Microserphites*); a first petiolar segment that is less than two times the length of the second segment (more than two times in *Serphites*, 3.4 times in *Buserphites* **n. gen.**); and a gaster with different lengths between first three terga (first three terga similar in length in *Aposerphites*). An extensive cladistic analysis of Serphitoidea will be necessary to fully test the limits and relationships of these genera, and to determine which characteristics are phylogenetically informative or autapomorphies that may refine our diagnoses. However, with the pace of recent work on this deposit, and the large number of terminal taxa that still need to be described, this type of analysis would be better performed after a preliminary account of all serphitoids has been completed.

The two new genera reported here have not been found in other Cretaceous amber deposits, despite the fact that Serphitoidea have been one of the most extensively studied groups of Hymenoptera in these assemblages. It remains unclear whether the Burmese amber assemblage's important taxonomic and morphological diversity is most probably a consequence of a particular palaeoenvironment, time averaging as a result of sampling multiple strata in the Hukawng Valley, or palaeogeographic constraints that existed prior to the mid-Cretaceous in Myanmar. The palaeoenvironment for this region during the Cretaceous was more tropical than it is today, with average temperatures between 32 and 55°C south of 40°N latitude (Spicer *et al.*, 1996; Grimaldi *et al.*, 2002). In general, the Cretaceous was a hothouse interval with extensive tropical belts. It seems that Burmese amber captured one of the most diverse terrestrial assemblages in the Cretaceous, because it combined a large amount of resin production with a diverse tropical fauna, and not because it represents an unusual coastal habitat (e.g., Xing *et al.*,

2018; Yu *et al.*, 2019) conditions. Although many taxa are shared between Myanmar and other Cretaceous sites (Grimaldi *et al.*, 2002; Ross, 2019, 2020), or make a case for faunal exchange between the Burmese amber forest and Asia (e.g., Oliveira *et al.*, 2016; Fu *et al.*, 2019), recent research has suggested that groups such as Hymenoptera show substantial endemism. Eight families of wasps are known solely from Burmese amber, and within Serphitidae the subfamily Supraserphitinae is also restricted to this deposit (Zhang *et al.*, 2018; Rasnitsyn and Ölm-Kühnle 2018, 2019a, 2019b). This points toward the development of endemic groups as the Western Burma Block drifted toward its contact with Asia during the Cretaceous (Liu *et al.*, 2016). The new findings among Serphitidae reported herein seem to add further support to this pattern of endemism at the genus-level; however, additional data are required from Asia to fully understand the timing and direction of faunal exchanges in the region. Additional work will also be required on the geology surrounding Burmese amber, to determine whether our impressions of this assemblage are being shaped by a significantly longer depositional time or broader range of depositional environments than other Cretaceous amber deposits with lower serphitid diversity.

6. Conclusions

This study expands the known diversity of the family Serphitidae in Burmese amber, through the discovery of 7 new species, leading to the definition of two new genera. These new genera seem to be endemic to the amber deposit, much like members of the recently described subfamily Supraserphitinae. Moreover, this deposit appears to have preserved members of the small family Serphitidae in large numbers and with greater diversity than the other Cretaceous amber deposits where this family has been recovered. It is unclear whether this is a result of greater diversity and abundance of serphitids in the Burmese amber forest, or if it is merely a result of the deposit

being commercially mined on such a large scale. The presence of many singleton species within our study seems to point toward diversity, as opposed to specimen availability, being the dominant factor in this deposit. Overall, Burmese amber now contains the most species from the family, with 12 species reported (including the studies of Rasnitsyn and Ölm-Kühnle, 2019a, 2019b, 2020a, 2020b). Additionally, preliminary work on existing museum collections suggests that Burmese amber contains many additional new species within the family Serphitidae that await description.

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Figure Captions.

Fig. 1. (A) General serphitid wasp wing terminology. (B) General serphid wasp anatomical terminology, based on the drawing of *M. engeli* **gen. et sp. n.** Abbreviations of veins: A, Anal; C, Costal; Cu, Cubital; CuA, Cubital apical; CuP, Cubital posterior; 1M, Median 1 (basal); 2M, Median 2 (apical); M+Cu, between Median 1 and Cubital; 1m+cu, between Median 1 and 2, and Cubital; R, Radial; 1Rs, Radial zone 1; 2Rs, Radial zone 2; 3Rs, Radial zone 3; 1r-rs, costal cell margin + pterostigma basal vein + pterostigma expansion; 2r-rs, pterostigma apical margin; Sc, Subcostal. Abbreviations of anatomy: ba., basitarsus; cx., coxa; fe., femur; fla., flagellomeres; mlt., lateral margin between tergites and sternites; msp., mesopleuron; mst., mesoscutum; mstl., mesoscutellum; mtn., metanotum; oce., ocellus; ped., pedicel; ppd., propodeum; pro., pronotum; sca., scape; ster., sternite; ta., tarsus; ter., tergite; ti., tibia; tr., trochanter; ver., vertex.

Fig. 2. *Buserphites applanatus* **gen. et sp. n.** holotype AMNH_Bu-1512 (probable female). (A) Lateroventral habitus view. (B) Specimen illustration showing venation. (C) Laterodorsal habitus view, arrow indicating right mandible. (D) Posterodorsal habitus view, , arrow indicating left mandible. Scale bars 1 mm in (A–D).

Fig. 3. *Buserphites myanmarensis* **gen. et sp. n.** holotype RSKM_P3306.61 (probable female). (A) Dorsal habitus view. (B) Specimen illustration showing venation and cuticular sculpture. (C) Lateral habitus view, partly masked by high particulate content in amber. (D) Ventral habitus

view, arrow indicating posterior extent of tergite 1 on ventral surface of gaster. Scale bars 1 mm in (A–D).

Fig. 4. *Mesoserphites annulus* **gen. et sp. n.** holotype RSKM_P3306.60 (male).

(A) Posterodorsal habitus view. (B) Specimen illustration showing venation and cuticular sculpture. (C) Detailed view of gaster and wing venation in A, arrow indicates posterior extent of tergite 1 on ventral surface of gaster. (D) Anterolateral habitus view. (E) Predominantly ventral habitus view, arrows indicate muscle tissue preserved within legs. (F) Predominantly dorsal habitus view, partly obscured by drying lines in amber. Scale bars 1 mm in (A, B, D–F), 0.25 mm in (C).

Fig. 5. *Mesoserphites giganteus* **gen. et sp. n.** holotype RSKM_P3306.63 (female).

(A) Dorsolateral habitus view. (B) Specimen illustration showing venation and cuticular sculpture. (C) Posterodorsal habitus view, showing surface of gaster truncated by polished edge of amber piece and infilled by clay minerals (arrow), and details of propodeal sculpture. (D) Lateral habitus view of body and ventral view of head. (E) Detailed view of wing venation and dorsal mesosomal sculpture from A. Scale bars 1 mm in (A–D), 0.25 mm in (E).

Fig. 6. *Mesoserphites giganteus* **gen. et sp. n.** paratype AMNH_BU 667 (male).

(A) Predominantly ventral habitus view of curled specimen. (B) Specimen illustration demarcating body regions in A. (C) Predominantly dorsal habitus view, highlighting details of mesosomal sculpture. (D) Lateral habitus view. Scale bars 1 mm in (A–D).

Fig. 7. *Mesoserphites engeli* gen. et sp. n. specimens.

RSKM_P3306.62 (female) holotype (A–F): Dorsolateral habitus view (A). Specimen illustration showing venation and body segmentation (B). Oblique anterior view of head, arrow indicates outer margin of closed mandibles (C). Detailed dorsal view of head in A, arrow indicates lateral ocellus (D). Detailed view of mesosomal dorsal surface in A (E). Ventrolateral habitus view (F). AMNH_Bu 1356 (male) paratype (G–I): Dorsal habitus view with wings bent over body, and wing from nearby aphidoid syninclusion (arrow) (G). Ventral habitus view, with inset of gastral apex (H). Lateral habitus view through significant overlying amber (I). Scale bars 1 mm in (A, B, F–I), 0.25 mm in (C–E).

Fig. 8. *Mesoserphites scutatus* gen. et sp. n. specimens.

RSKM_P3306.30a (female) holotype (A,B): Ventrolateral habitus view with wings folded over specimen and obscured, horizontal arrow indicates right mandible, vertical arrow marks left mandible (A). Dorsolateral habitus view through thick overlying amber (B). RSKM_P3306.30b (male) paratype (C, D): Dorsolateral habitus view, with wings truncated by polished surface of amber piece near their midlengths, and head truncated on left side (C). Specimen illustration highlighting surface sculpture (D). RSKM_P3306.30c (partial, probable female based on size)

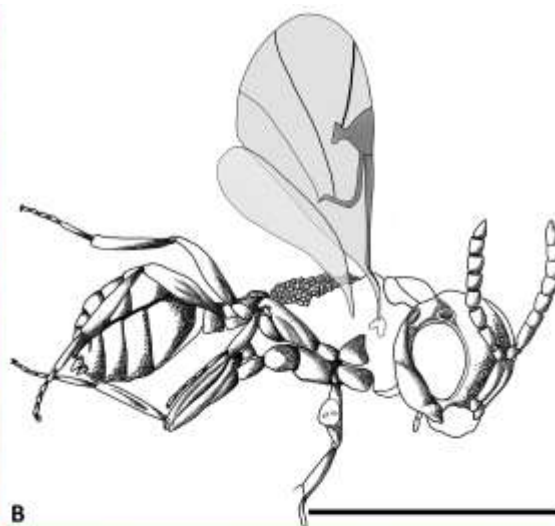
paratype (E): Anterior view of head, body missing beyond middle of mesosoma, arrow marks right mandible. AMNH_BU 676 (female) paratype (F): Dorsolateral habitus view of weathered specimen with exposed ovipositor apex (arrow). Scale bars 1 mm in (A–D, F), 0.25 mm in (E).

Fig. 9. *Mesoserphites viraneacapitis* **gen. et sp. n.** specimens.

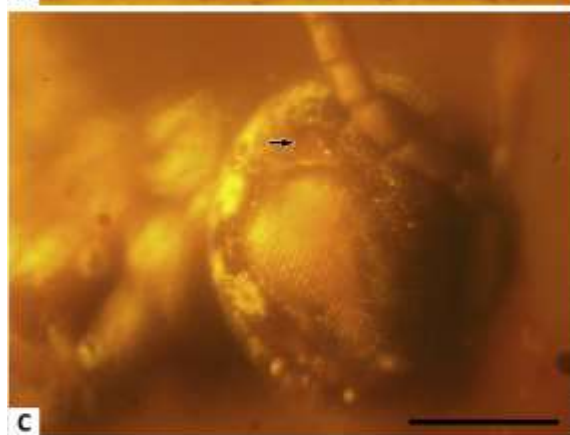
RSKM_P3306.30d (male) holotype (A–D): Ventrolateral habitus view (A). Specimen illustration showing venation and cuticular sculpture (B). Detailed view of head in A, with lateral ocellus marked by arrow (C). Posterodorsal habitus view. AMNH_BU 312 (male) paratype (E, F): Lateral habitus view (E). Specimen illustration outlining body regions and venation (F). Scale bars 1 mm in (A, B, D–F), 0.25 mm in (C).



A



B



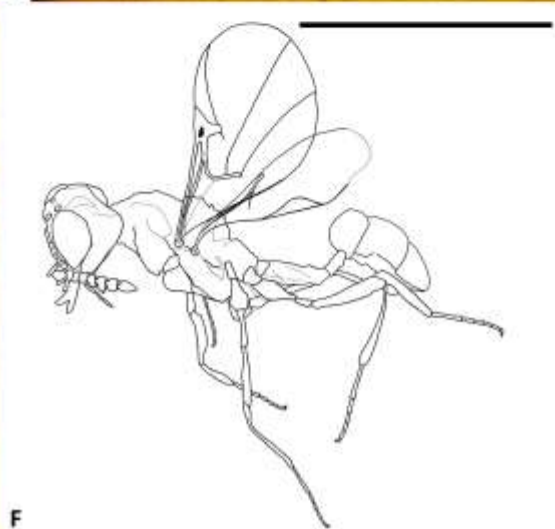
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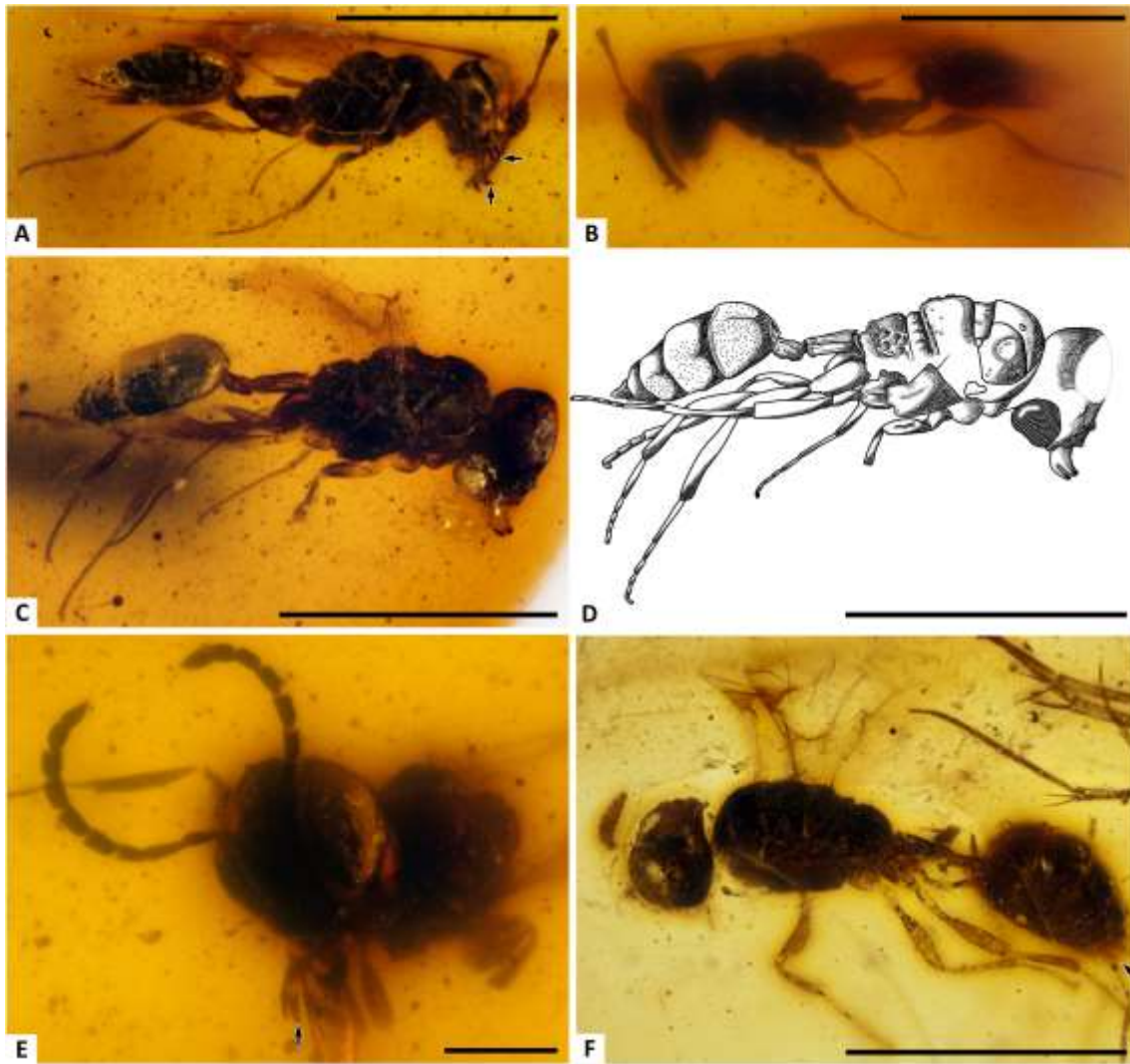
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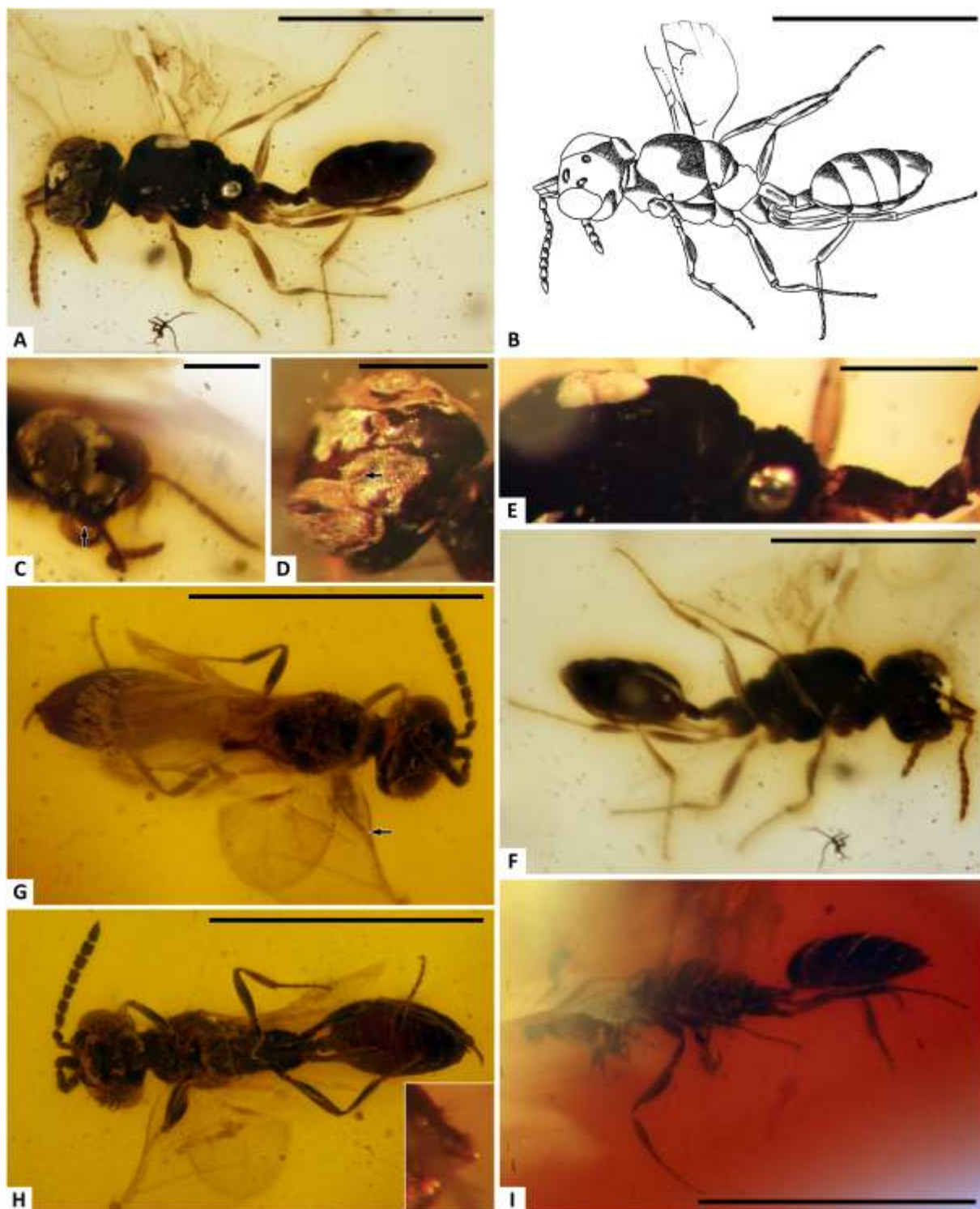


E



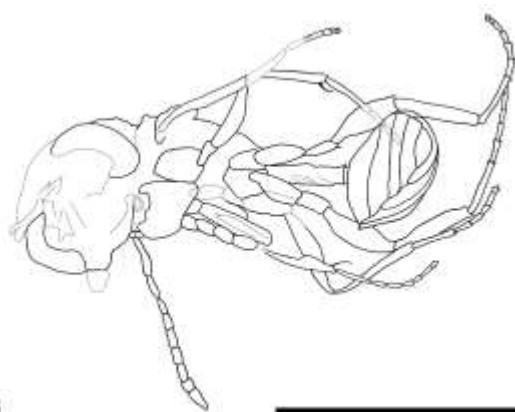
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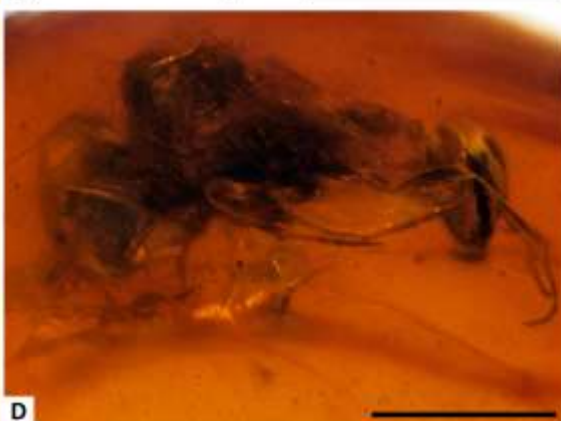
A



B



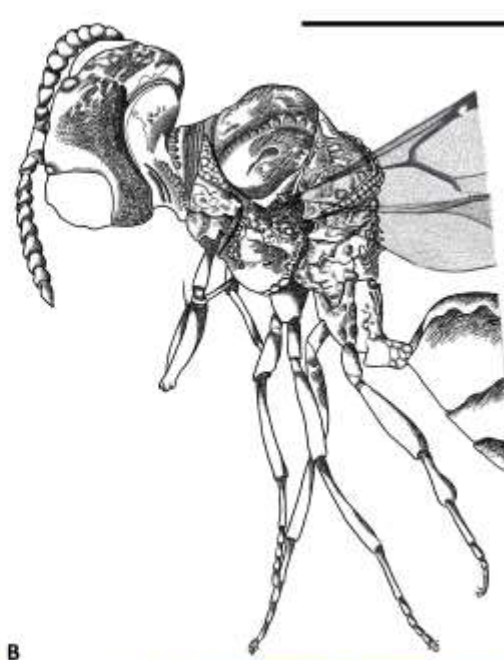
C



D



A



B



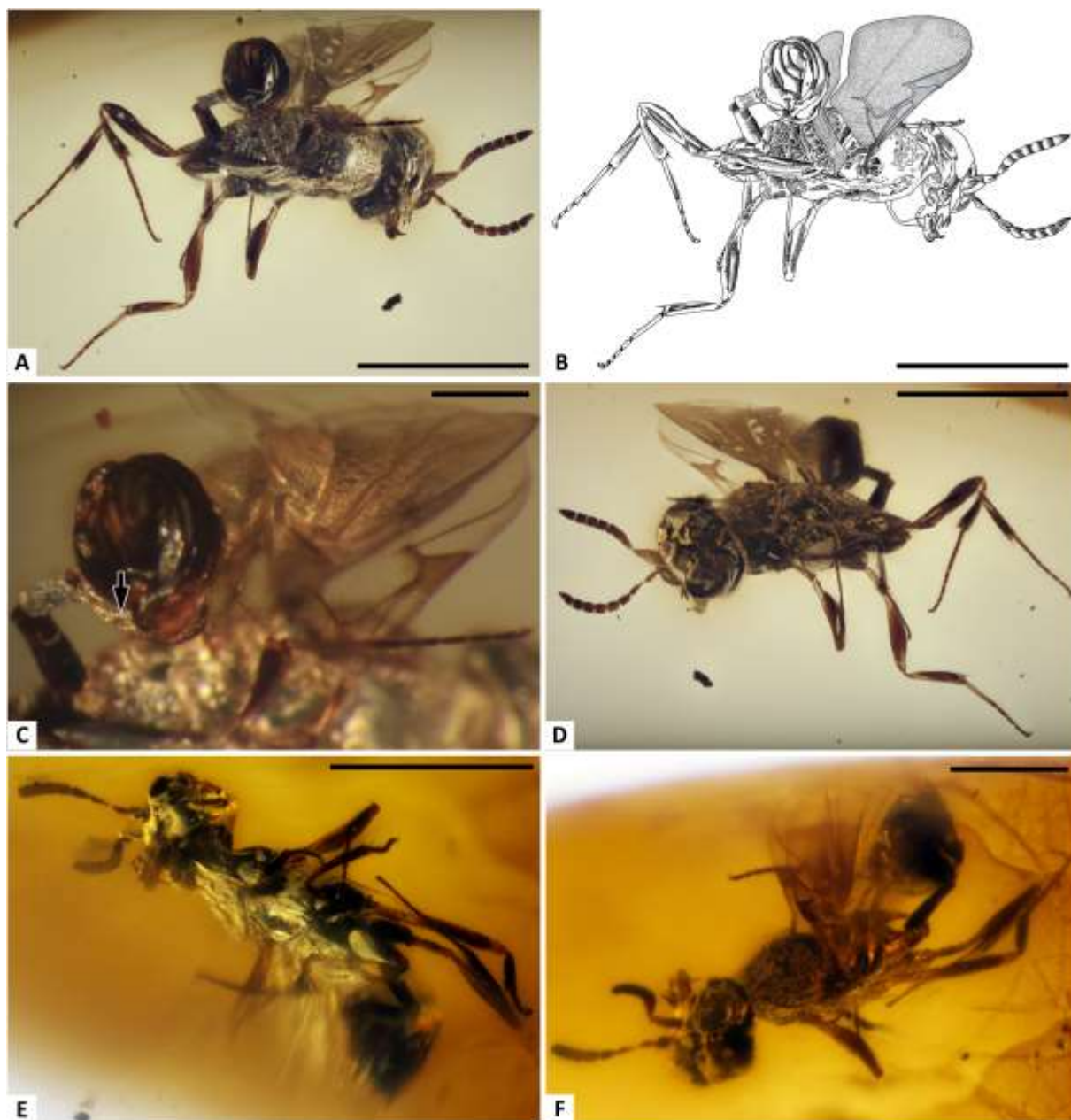
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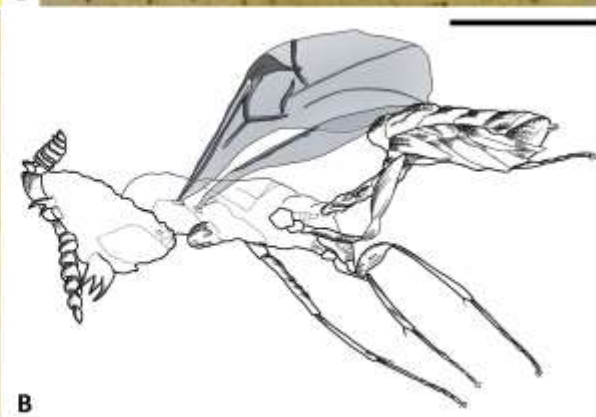
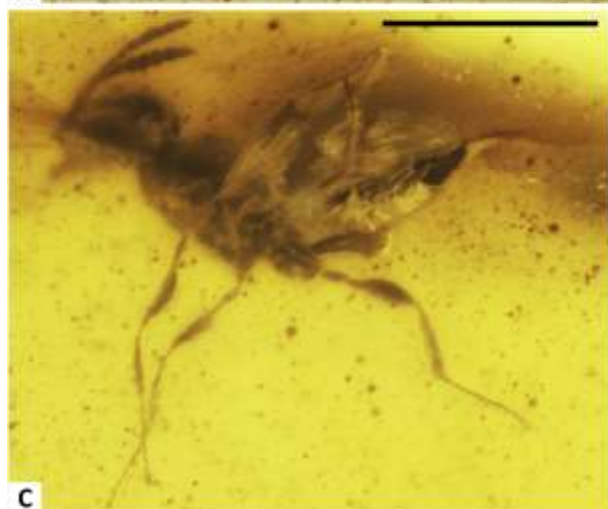
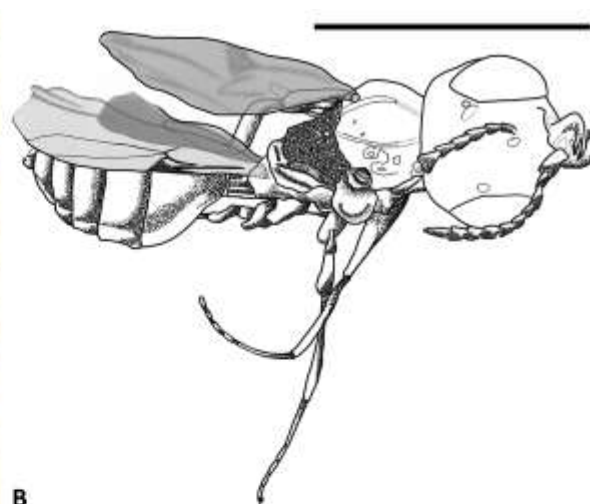


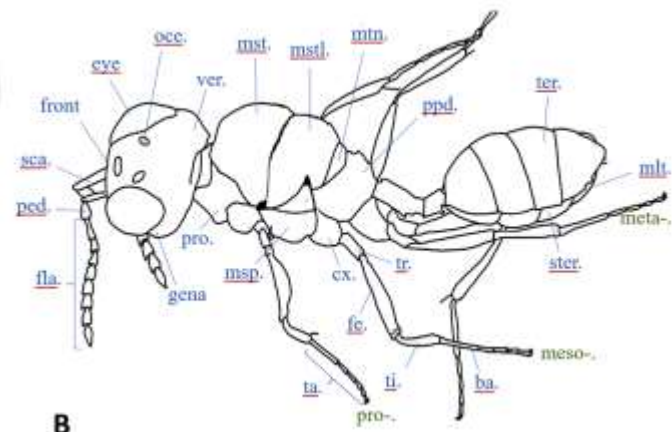
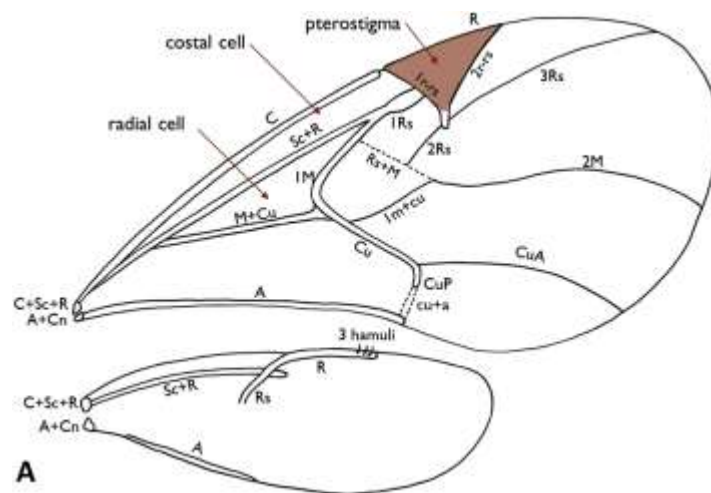
D



E







Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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