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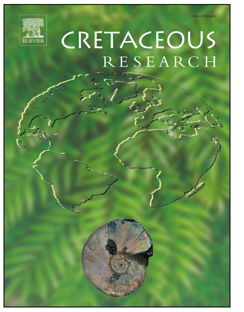

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Two new genera of Apsilocephalidae from mid-Cretaceous Burmese amber

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Abstract

Apsilocephalidae is an enigmatic dipteran family erected by Nagatomi *et al* (1991), including three extant genera and three additional extinct genera from the Eocene Baltic amber, Eocene Florissant, and mid-Cretaceous Burmese amber. We describe herein two new genera, *Myanmarpsilocephala* gen. nov. and *Irwinimyia* gen. nov., from mid-Cretaceous Burmese amber. The female genitalia of *Myanmarpsilocephala* gen. nov. and male genitalia of *Irwinimyia* gen. nov. are described and illustrated. The distribution of all Apsilocephalidae species and a key to all genera of Apsilocephalidae is provided. The described diversity of Apsilocephalidae in Burmese amber strongly suggests that apsilocephalid flies

diversified at least by the mid-Cretaceous.

Key words: Apsilocephalidae, *Myanmarpsilocephala gen. nov*, *Irwinimyia gen.nov*, Diptera, Cretaceous, Burmese amber

1. Introduction

Apsilocephalidae is one of the four asiloid families in the therevoid clade, with relationships estimated to be ((Scenopinidae + Therevidae) + (Apsilocephalidae + Evocoidae)) (Yeates, 2002; Yeates *et al.*, 2003; Winterton *et al.*, 2015; Winterton and Ware, 2015; Shin *et al.*, 2017). The Apsilocephalidae is an enigmatic group with only four described species known from three genera worldwide. Apsilocephalidae was erected as a family by Nagatomi *et al.* (1991) to include the three genera *Apsilocephala* Kröber, 1913, *Clesthentia* White, 1914 and *Clesthentiella* Nagatomi *et al.*, 1991. Winterton and Irwin (2008) described *Kaurimyia* from New Zealand and considered *Clesthentiella* Nagatomi *et al.*, 1991 a synonym of *Clesthentia* White, 1914. The extant apsilocephalid flies have a highly disjunct distribution, *Apsilocephala longistyla* Kröber, 1913 is found in the southwestern United States and Mexico; *Clesthentia aberrans* White, 1914 in Tasmania; *C. crassioccipitus* Nagatomi *et al.*, 1991 in Tasmania and *Kaurimyia thorpei* Winterton and Irwin, 2008 in New Zealand. There are still a number of undescribed species of *Apsilocephala* from North America (M. Irwin pers. comm.).

Although extant apsilocephalid flies are quite rare in collections, fossil apsilocephalids are comparatively abundant and diverse. Five fossil species have been described, from Eocene Florissant of USA, Eocene Baltic amber and mid-Cretaceous Burmese amber. Gaimari and Mostovski (2000) described the first fossil apsilocephalid fly *Burmapsilocephala cockerelli* in mid-Cretaceous Burmese amber; Hauser and Irwin (2005) transferred the Eocene Florissant species *Apsilocephala vagabunda* Cockerell, 1927 from Therevidae to Apsilocephalidae; Hauser (2007) transferred the Eocene Baltic amber species *Apsilocephala pusilla* Hennig, 1967 from

Asilidae to Apsilocephallidae; Grimaldi *et al* (2011) described the second mid-Cretaceous species and genus *Kumaromyia burmitica* Grimaldi and Hauser, 2011 from Burmese amber. Grimaldi (2016) described a new species *Burmapsilocephala evocoa* Grimaldi, 2016, and emended the diagnosis of *Burmapsilocephala*. A list of all known Apsilocephalidae and their distributions is provided in Table 1 and Fig. 1.

Herein we describe two new genera based on two new species, *Myanmarpsilocephala grimaldii* gen. *et* sp. nov. and *Irwinimyia spinosa* gen. *et* sp. nov., from mid-Cretaceous Burmese amber. The female genital structure of *M. grimaldii* sp. nov. and male genitalia structure of *I. spinosa* sp. nov. are described and illustrated. A key to the genera of Apsilocephalidae is provided.

2. Material and methods

The specimens described herein were collected from the Hukawng Valley of Kachin Province, Myanmar (locality in Kania *et al.*, 2015: their Fig. 1). The age of Burmese amber is radiometrically dated at 98.79± 0.62 Ma (earliest Cenomanian; Cohen *et al.*, 2013) based on U–Pb zircon dating of the volcanoclastic matrix (Shi *et al.*, 2012). However, the amber displays clear evidence of re-deposition, so the real age of Burmese amber can be older than enclosing rocks (Ross, 2015), hence we prefer to refer the amber age as mid-Cretaceous.

The amber pieces have been polished with sand paper with different grain sizes and with polishing power. Photographs were taken using a Zeiss Stereo Discovery V16 and Leica DFC 500 microscope systems. In most instances, incident and transmitted light were used simultaneously. In some cases, the same piece of amber is coloured differently because the two different microscope systems have different white balance and exposure. All images are digitally stacked photomicrographic composites of approximately individual focal planes obtained using the Helicon Focus 6 and Zerene Stacker software for a better illustration of the 3D structures. The line drawings and figures were prepared with CorelDraw X7. The specimens are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS). All taxonomic acts established in the present work have been registered in ZooBank (see below), together with the electronic publication LSIC: urn:lsid:zoobank.org:pub:10B71E14-DCB3-4671-B12C-9EA30CF12EE5.

3. Systematic palaeontology

Order Diptera Linnaeus, 1758

Suborder Brachycera Zetterstedt, 1842

Superfamily Asiloidea Latreille, 1802

Family Apsilocephalidae Nagatomi *et al.*, 1991

Key to genera of Apsilocephalidae

1. Cell bm with three corners distally; stylus arista-like, much longer than the length of other antennal segments combined..2

- Cell bm with four corners distally; stylus thick, length various. 3

2. Cell m_3 open; nine pairs of thoracic macrosetae present, including three pairs of notopleural setae present (Burmese amber)...............***Myanmarpsilocephala* gen. nov.**

- Cell m_3 closed and petiole; six to seven pairs thoracic macrosetae present, including one or two pairs of notopleural setae present (Burmese amber)..***Burmapsilocephala* Gaimari & Mostovski, 2000**

3. Antennal stylus elongate, much longer than basal segment of flagellum (North America, Baltic amber, Florissant shale)..........................***Apsilocephala* Kröber, 1913**

- Antennal stylus equal to or shorter than basal segment of flagellum......................4

4. Antennal stylus approximately equal length of basal segment of flagellum (apical segment greatly elongate); hind leg longer and thicker than other legs (New Zealand)...***Kaurimyia* Winterton & Irwin, 2008**

- Antennal stylus less than half the length of basal segment of flagellum; hind leg similar in size and shape to other legs..5

5. Vein M_3 straight or absent (Tasmania).............................***Clesthentia* White, 1914**

- Vein M_3 curved to join M_4 6

6. Palp one-segmented; apices of Sc and R_1 without pterostigma surrounded; fore

femur with a row of posterior setae, mid and hind femora devoid of setae……………………………………….***Kumaromyia*** **Grimaldi & Hauser, 2011**

- Palp two segmented; apices of Sc and R_1 with pterostigma surrounded; fore femur devoid of setae, mid and hind femora with short and strong ventral setae……………………………………………………...….***Irwinimyia*** **gen. nov.**

Genus *Myanmarpsilocephala* Zhang, Li, Wang and Yeates gen. nov.

(urn:lsid:zoobank.org:act:A541059F-CFA3-4F3C-B935-0D8A6E3BF601)

Derivation of name. The name is derived from the country of the type locality, Myanmar.

Type species. Myanmarpsilocephala grimaldii sp. nov. By monotypy.

Diagnosis. Body slender, thorax short and strongly arched, abdomen elongate and slender. Eyes large, dichoptic in female. Antennal scape elongate, ca. 2x length of pedicel; basal flagellomere round-triangular shaped, stylus arista-like, ca. 3x length of other segments combined. Nine pairs of thoracic macrosetae present, including three pairs of notoplural setae. M_3 and M_4 convergent apically, but cell m_3 open.

Myanmarpsilocephala grimaldii **Zhang, Li, Wang and Yeates sp. nov.**

Figs. 2−4

(urn:lsid:zoobank.org:act:AAEBC4BB-3E41-4618-9CC9-AD209CBD885F)

Derivation of name. Patronym, for David Grimaldi, from the American Museum of Natural History, New York, in recognition of his remarkable contributions to dipterology and paleontology.

Material. Holotype specimen number NIGP166977 (female) and paratype specimen number NIGP166978 (female), all stored at Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China.

Diagnosis. As for genus, by monotypy.

Description. Based on two female flies. Body length 5.8 mm, wing 4.2 mm. Head subsphaeroidal. Eyes completely bare and large, occupying most part of the head; dichoptic in female, inner margins of eyes parallel; all facets with the same diameter. Frons bare, ca. 2x length of ocellar tubercle. Ocellar tubercle slightly raised, with some short fine hairs. Face small and recessed, bare, clypeus not visible. Gena narrow, with long hairs. Occiput convex except slight concavity behind ocellar tubercle, covered with sparse strong hairs. Antennal scape and pedicel with short hairs. Scape slender, cylindrical, ca. 2x length of width; pedicel rounded, ca. 1x length of width. Length of scape, pedicel and basal flagellomere about 2:1:1. Basal flagellomere round-triangular, apex attached with long, arista-like stylus, covered with short pubescence, ca. 3x length of other three segments of antenna combined (Fig. 3B). Proboscis with fleshy labellum protruding slightly beyond oral margin, with sparse fine hairs; palp not visible (Figs. 2B, 3B).

Thorax mostly bare of hairs, with only very sparse setulae on scutum and coxae, except scutum and postalar callosity with some hairs. Bristle-like macrosetae as follows: 1 postpronotal; 3 notopleural; 1 suparaalar; 1 postalar; 2 dorsocentral; 1 scutellar (apical). Scutum strongly arched, dorsum of scutellum slightly below that of scutum, scutellum small with some fine hairs on posterior margin, no proscutellum present, subscutellum present (Fig. 2C). Halter fusiform, apically pointed (Fig. 2E).

Wing 4.3 mm long, 1.4 mm wide, hyaline; tip of Sc reaching nearly to middle of wing; tip of R_1 slightly beyond middle of wing. Crossvein sc-r present. R_1 and R_2 almost straight and nearly parallel; R_4 arising half way from the base of R_{4+5}; R_4 strongly curved on basal half and slightly sinuous apically, nearly parallel to R_5; tip of R_5 ending at apex of wing. Crossvein r-m located in the middle of cell d, cell br much longer than cell bm, cell bm with three corners apically. Vein R_5, M_1 and M_2 nearly parallel. Vein M_3 slightly curved to M_4, but cell m_3 open. Cell cu closed with a short petiole. A_1 short and apically evanescent. Anal lobe well developed, alula and upper calypter not developed (Figs. 2D, 3A).

Legs. Metacoxa with well-developed peg on anterior surface (Fig. 2F). Femora without setae, tibiae and tarsi with sparse setae. Apical spurs absent. Pulvilli slender, slightly shorter than claw; empodium bristleform, as long as claw.

Abdomen elongate and slender, nearly cylindrical. Tergites 1 to 3 covered with hairs, tergites 4 to 7 with tiny fine hairs.

Terminalia (female): tergite 8 simple, without long hairs. Tergites 9+10 with ca. 8 short acanthophorite spines on each half, posterolaterally with a cluster of ca. 4 long strong setae. Cerci small, shallow, lying between acanthophorite spines, as seen in posterior view (Figs. 3C−D and Figs. 4B−D).

Genus *Irwinimyia* Zhang, Li, Wang and Yeates gen. nov.

(urn:lsid:zoobank.org:act:C59E8172-662E-40EA-9FB4-40971500E04E)

Derivation of name. Patronym, for Michael E. Irwin, Arizona State University, Tucson, in recognition of his remarkable contributions to dipterology and collection development.

Type species. Irwin spinosa sp. nov. By monotypy.

Diagnosis. Body stout. Eyes large, bare. Scape very slender, width ca. half of pedicel; apical segment of stylus long, ca. 1/2 length of basal flagellomere. Palp two-segmented. Eight pairs of thoracic macrosetae present. Mid and hind femora with ventral setae; hind coxa with small knob on anterior surface. Wing with C ending between apices of R_5 and M_1; apices of Sc and R_1 with pterostigma surrounding apices; crossvein r-m located on basal half of cell d, cell br much longer than cell bm; M_3 curved to join M_4, cell m_3 closed and petioled; R_4 and R_5 divergent, not parallel for any part of their lengths.

***Irwinimyia spinosa* Zhang, Li, Wang and Yeates sp. nov.**

(urn:lsid:zoobank.org:act:991DDAC6-B055-4EBB-8585-742EDAE68893)

Figs. 5−6.

Derivation of name. This name refers to the ventral setae on mid and hind femora.

Material. Holotype specimen number NIGP166979 (male), stored at Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China.

Diagnosis. As for genus, by monotypy.

Description. Based on a male fly. Body length 4.2 mm; wing length 3.7 mm.

Head hemispherical. Eyes completely bare and large, occupying most of the head; holoptic in male; all facets with the same diameter. Medial margins of eyes meeting from ocellar triangle to just above bases of antennae, frons small and bare. Ocellar tubercle slightly raised, with some short fine hairs. Face small and recessed, bare, clypeus flat. Gena narrow, with long hairs. Postgena well developed, with long hairs. Occiput flat, covered with sparse strong hairs (Fig. 5B).

Antennal scape and pedicel with short hairs. Scape slender and very thin, cylindrical, ca. 2x length of width, and width ca. half of pedicel; pedicel rounded, ca. 1x length of width. Length of scape, pedicel and basal flagellomere about 1.2:1:3. Basal flagellomere long, drop-shaped; second flagellomere annular, stylus longer, about half length compared to basal flagellomere (Figs. 5B and 6A). Proboscis short, labellum fleshy and slightly beyond oral margin, with sparse fine hairs; palp clavate with long ventral hairs, two-segmented, ca. 0.75 length of proboscis (Fig. 6B).

Thoracic scutum and scutellum densely covered with fine setulae. Bristlelike macrosetae as follows: 0 postpronotal; 3 notopleural; 1 suparaalar; 1 postalar; 2 dorsocentrals (posterior half); 1 scutellar (apical). Scutum strongly arched, dorsum of scutellum slightly below that of scutum, no proscutellum or subscutellum present. Pleura mostly bare, except proepisternum and antepisternum covered with fine hairs.

Wing 4 mm long, 1.2 mm wide, tip of Sc reaching nearly to middle of wing; tip of R_1 reaching slightly beyond middle of wing. Crossvein sc-r absent. Apices of Sc and R_1 with pterostigma surrounding. Apex of cell R_1 and R_2 straight and nearly parallel; R_4 arising over half way from the base of R_{4+5}; R_4 arising at right angle and slightly sinuous apically, curved anteriorly; tip of R_5 ending at apex of wing. Crossvein r-m located on basal half of cell d, cell br much longer than cell bm, cell bm with four corners apically. Apex of R_5 slightly curved forward, M_1 and M_2 nearly parallel. Vein M_3 strongly curved to join M_4, cell m_3 and cu closed and petiolate. A_1 not visible. Anal lobe well developed, alula and upper calypter not developed (Fig. 5C).

Legs. Metacoxa with well-developed peg on anterior face. Fore femur without setae; mid femur with two short ventral setae on apical half; hind femur with a row of short ventral setae, setae denser on apical half (Fig. 6D). Tibiae and tarsae with sparse setae. Apical spurs absent. Pulvilli slender, slightly shorter than claw; empodium bristleform, just over half length of claw.

Abdomen 2.4 mm long (excluding genitalia), 0.8 mm wide, taper apically. Tergites and sternites covered with hairs. Terminalia (male): projecteing posterially, slightly flexed dorsally. Epandrium arched over gonocoxites, deeply divided distally; acinacifoliate cercus and thin hypandrium projecting between epandrium lobes. Gonocoxite setose, entirely free from epandrium and hypandrium, slightly longer than gonostylus; gonostylus apex slender, handle-shaped, rounded apically; gonocoxite and gonostylus articulating in horizontal plane. Phallus projecting posterodorsally, only middle part visible between epandium and gonocoxite (Figs. 5D, 6E).

4. Discussion

The main diagnostic characters of Apsilocephalidae are antenna with basal flagellum rounded-triangular, with an apical stylus; thorax convex; mesoscutum and scutellum with setae; vein R_5 ending at or close to apex of wing; surstyli of male epandrium present (Nagatomi *et al.*, 1991; Hauser, 2007; Winterton and Irwin, 2008).

Myanmarpsilocephala gen. nov. is similar to *Burmapsilocephala* Gaimari and Mostovski, 2000 in having the cell bm with three corners distally and stylus arista-like, much longer than the length of other antennal segments combined. It differs from *Burmapsilocephala* in having the antennal scape elongate, ca. 2x length of pedicel (vs. subequal); cell m3 open (vs. closed); Proboscis short with fleshy labellum (vs. slightly longer and not appear to be fleshy); nine pairs of thoracic macrosetae present, including three pairs of notoplural setae (vs. six and two). All except these two Apsilocephalidae genera have three distal corners of cell bm, and the character of three distal corners of bm occurs in combination with a long antennal stylus and only in the extinct species from Burmese amber. The open m_3 cell is only found in the new genus *Myanmarpsilocephala*, and this character is an apomorphy of the genus.

Irwinimyia gen. nov. is similar to *Kumaromyia*, but can be easily distinguished by a two-segmented palp (vs. one-segmented in *Irwinimyia*); the pilosity of both the thorax and abdomen (vs. pleura devoid of fine or bristle-like setae); wing with Sc complete and pterostigma surrounding apices of Sc and R_1 (vs. without); crossvein r-m located on basal half of cell d (vs. base), br much longer than bm (vs. nearly as long as); mid and hind femur with short and strong ventral setae (vs. bare).

The enigmatic family Apsilocephalidae has an extant distribution in western north America and Australasia. The distribution of extinct species in the Palaearctic and Nearctic regions indicates that the extant distribution is a reduced relictual one. The fossil record indicates that the family Apsilocephalidae was diverse at genus and species level and widely distributed in the mid-Cretaceous, pushing the origin of this family back, much earlier than 100 million years ago. Consistent with this implication, molecular divergence time estimation suggests the family originated in the early Cretaceous (Wiegmann *et al*., 2011).

5. Conclusion

The discovery of two new well preserved apsilocephalid species *Myanmarpsilocephala grimaldii* and *Irwinimyia spinosa* increases the diversity of Apsilocephalidae in mid-Cretaceous Burmese amber. The origin of this family should be much earlier than 100 million years ago. Our findings also further illuminate the relictual nature of the extant distribution of Apsilocephalidae.

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Figure Captions

Fig. 1. Distribution of extant and fossil Apsilocephalidae worldwide. Regions filled with red colour represent distribution of extant species; △ triangles represent Eocene records; ☆ star represents Cretaceous records.

Fig. 2. *Myanmarpsilocephala grimaldii* sp. nov., holotype NIGP166977. A, photograph of lateral features, scale bar represents 2 mm; B, photograph of head in ventral view, scale bar represents 0.2 mm; C, photograph of head and thorax in lateral view, scale bar represents 0.5 mm; D, photograph of wing, scale bar represents 0.5 mm; E, photograph of haltere, scale bar represents 0.2 mm; F, photograph of hind coxa, scale bar represents 0.2 mm.

Fig. 3. *Myanmarpsilocephala grimaldii* sp. nov., holotype NIGP166977. A, drawing of wing, scale bar represents 0.5 mm; B, drawing of antenna, scale bar represents 0.2 mm; C, photograph of genitalia in lateral view, scale bar represents 0.2 mm; D, drawing of genitalia in lateral view, scale bar represents 0.2 mm.

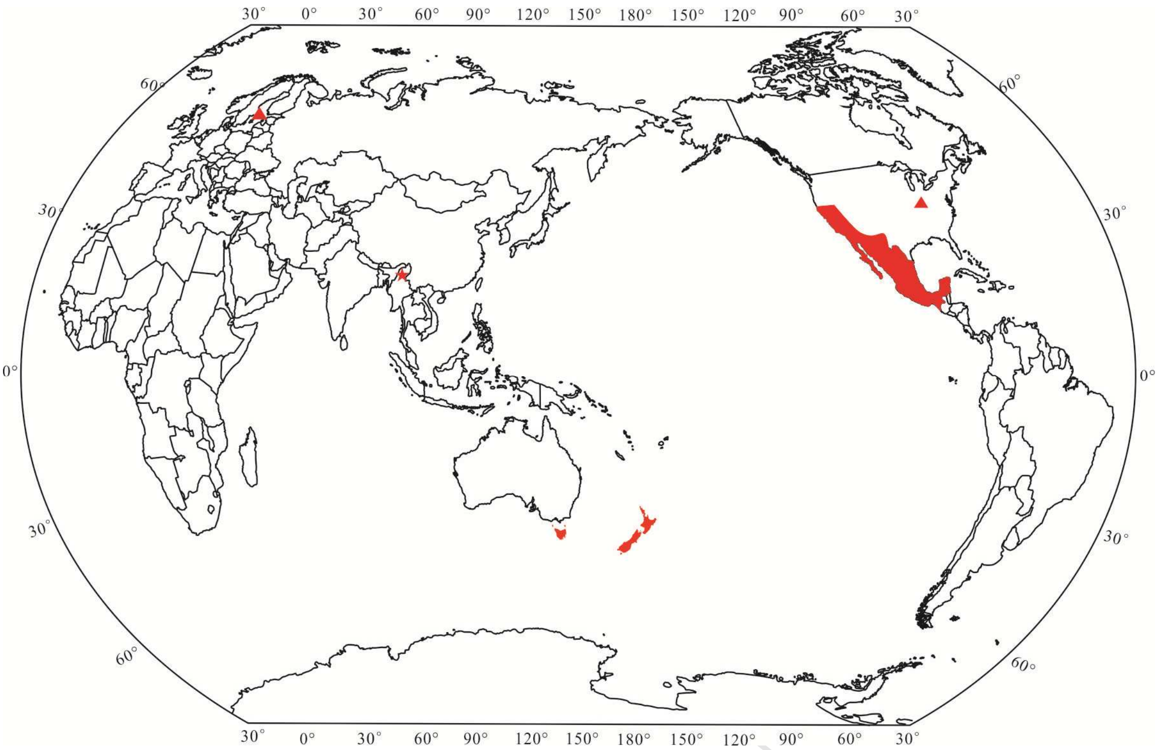
Fig. 4. *Myanmarpsilocephala grimaldii* sp. nov., paratype NIGP166978. A, photograph of dorsal features, scale bar represents 1 mm; B, photograph of genitalia in dorsal view, scale bar represents 0.1 mm; C, photograph of genitalia in ventral view, scale bar represents 0.1 mm; D, drawing of genitalia in dorsal view, scale bar represents 0.1 mm.

Fig. 5. *Irwinimyia spinosa* sp. nov., holotype NIGP166979. A, photograph of lateral features, scale bar represents 1 mm; B, photograph of head in lateral view, scale bar represents 0.2 mm; C, photograph of wing, scale bar represents 0.5 mm; D, photograph of genitalia in lateral view, scale bar represents 0.1 mm.

Fig. 6. *Irwinimyia spinosa* sp. nov., holotype NIGP166979. A, drawing of antenna, scale bar represents 0.1 mm; B, drawing of palp, scale bar represents 0.1 mm; C, photograph of hind tibia, scale bar represents 0.2 mm; D, drawing of hind tibia; E, drawing of genitalia in lateral view, scale bar represents 0.1 mm.

Table 1. An updated list of all known Apsilocephalidae.

Genus	Species	Locality	Geological age
Apsiocephala Kröber, 1914	*A. longistyla* Kröber, 1914	Southwest of US and Mexico	Extant
	A. pusilla Hennig, 1967	Baltic amber	Eocene
	A. vagabunda Hauser and Irwin, 2005	Florissant, USA	Eocene
Burmapsilocephala Mostovski, 2000	*B. cockerelli* Gaimari and Mostovski, 2000	Burmese amber	mid-Cretaceous
	B. evocoa Grimaldi, 2016	Burmese amber	mid-Cretaceous
Clesthentia White, 1914	*C. aberrans* White, 1914	Tasmania, Australia	Extant
	C. crassioccipitus Nagatomi et al., 1991	Tasmania, Australia	Extant
Irwinimyia **gen. nov.**	*I. spinosa* **sp. nov.**	Burmese amber	mid-Cretaceous
Kaurimyia Winterton and Irwin, 2008	*K. thorpei* Winterton and Irwin, 2008	New Zealand	Extant
Kumaromyia Grimaldi and Hauser, 2011	K. burmitica Grimaldi and Hauser, 2011	Burmese amber	mid-Cretaceous
Myanmarpsilocephala **gen. nov.**	*M. grimaldii* **sp. nov.**	Burmese amber	mid-Cretaceous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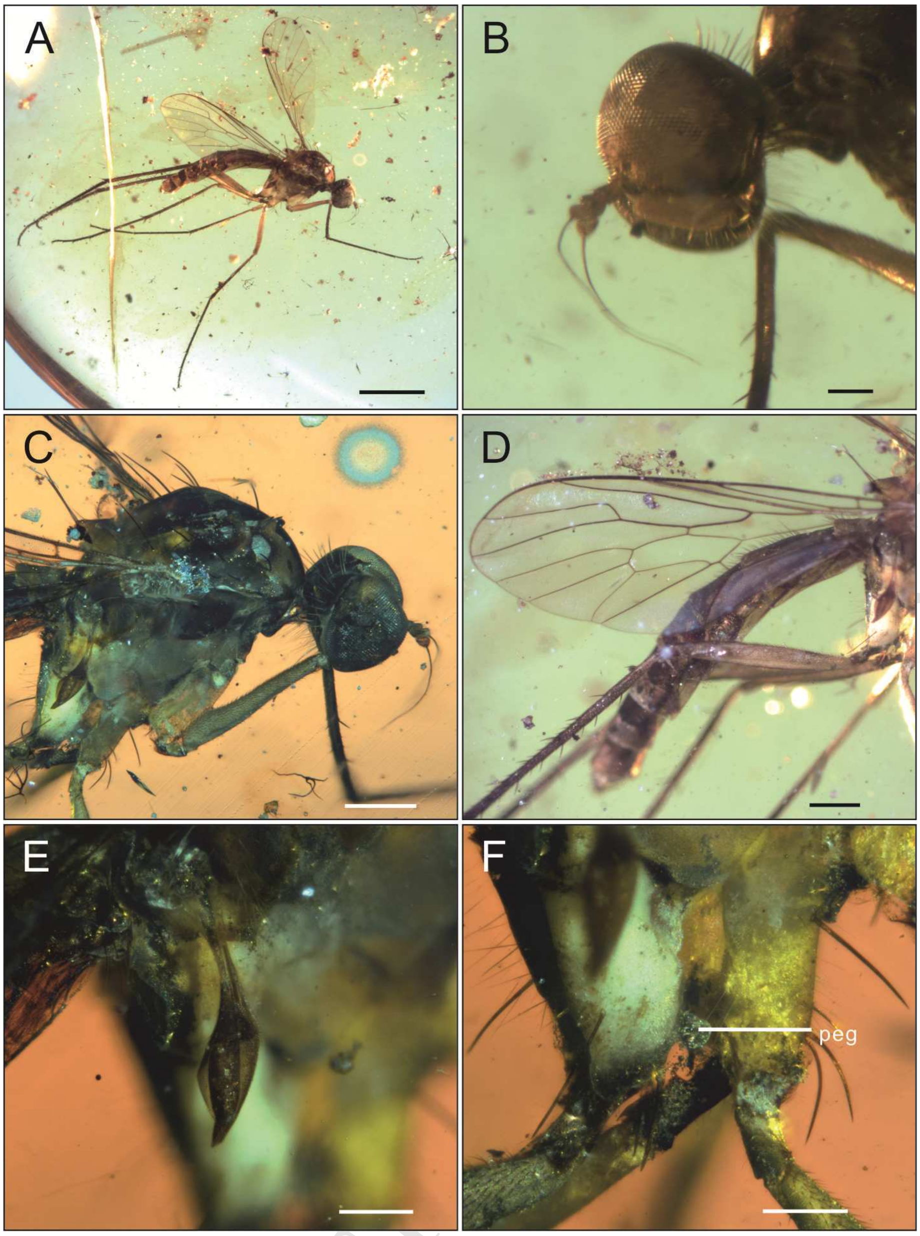
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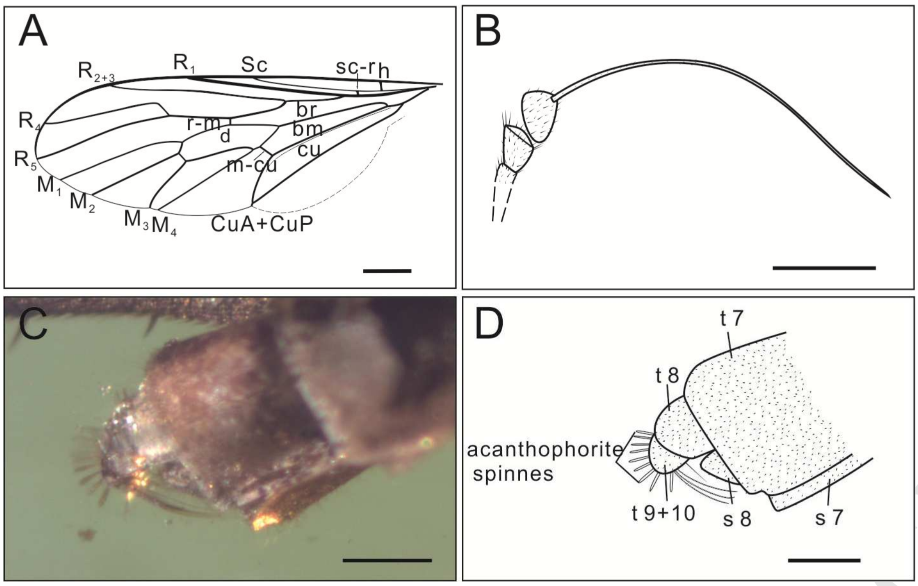
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R5
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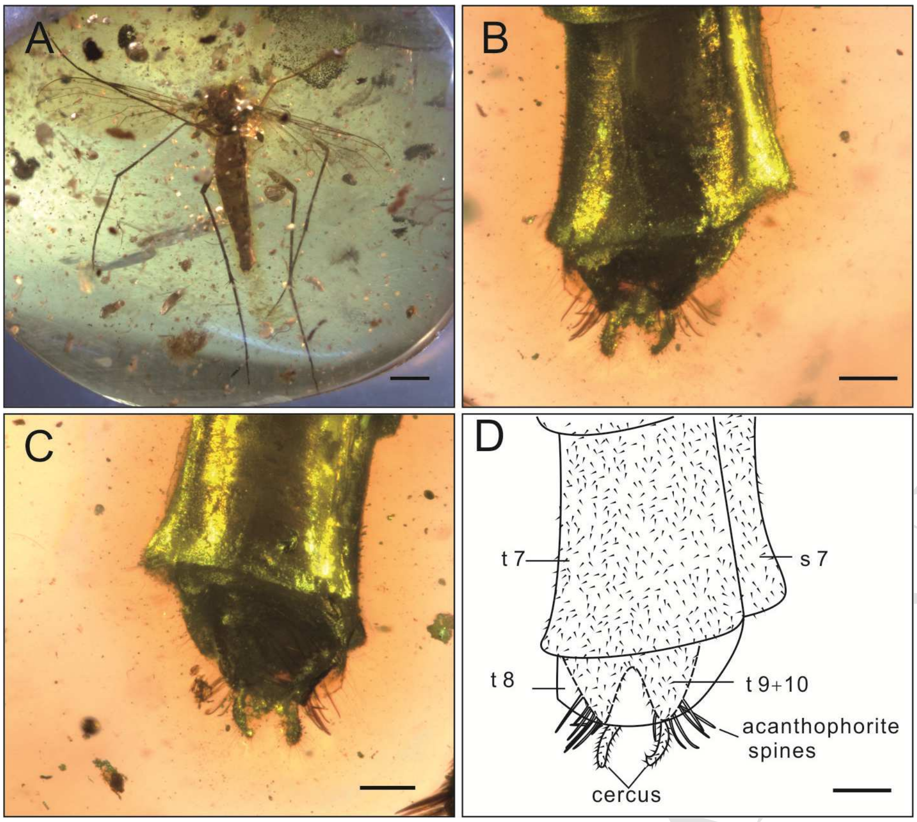
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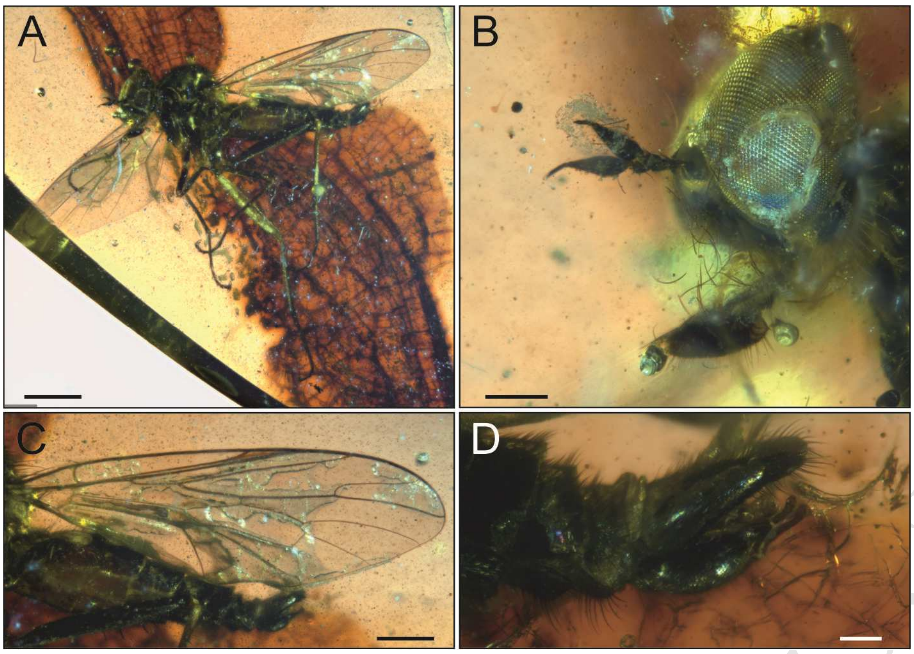
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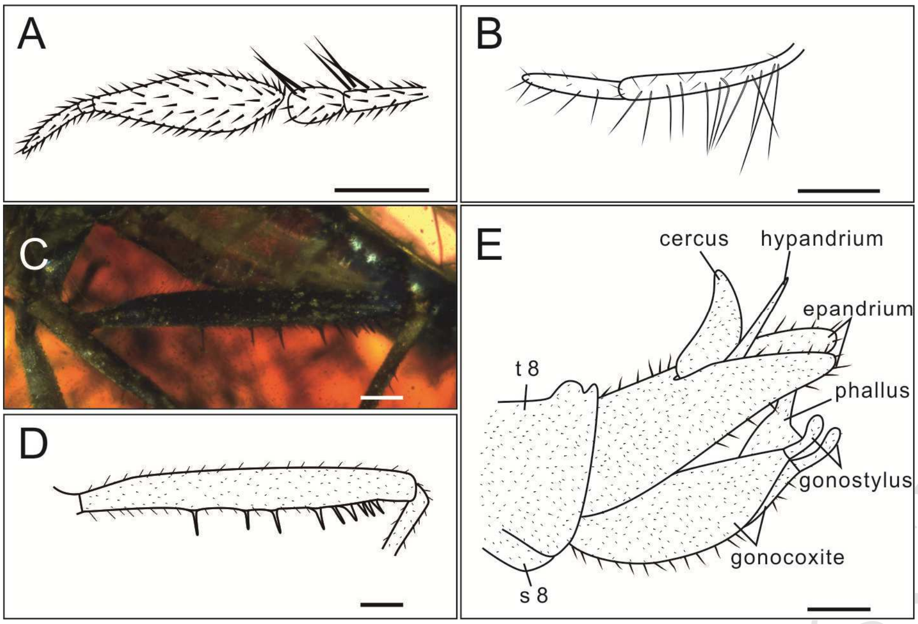
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D
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