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New taxa and new synonymies of mid-Cretaceous Burmese amber bombyliids (Diptera: Bombyliidae) based on the collections in the Bishop Museum

Neal L. Evenhuis



Bishop Museum Press
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Cover: Holotype of *Nemomyia lamasi* Evenhuis, sp. nov. (see p. 29).

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New taxa and new synonymies of mid-Cretaceous Burmese amber bombyliids (Diptera: Bombyliidae) based on the collections in the Bishop Museum

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Abstract. Research conducted on a significant collection of Bombyliidae from mid-Cretaceous Burmese (Myanmar) amber housed in the Bishop Museum has discovered the following new taxa: *Burmobomba* **gen**. **nov**.; *Bumaso fusca* **gen**. **et sp**. **nov**.; *Electrobombylia medialis* **gen**. **nov**. **et sp**. **nov**.; *Fremo compressus* **gen**. **et sp**. **nov**.; and *Nemomyia* **gen**. **nov**.; plus, the following new species: *Burmobomba proboscidea* **sp**. **nov**.; *Burmobomba syrinx* **sp**. **nov**.; *Nemomyia burmitica* **sp**. **nov**.; *Nemomyia lamasi* **sp**. **nov**. *Similipioneeria* Ye, Yao, Shih, Ren & Wang, 2019 is found to be a junior synonym of *Pioneeria* Grimaldi, 2016 **syn**. **nov**., resulting in *Pioneeria mirantenna* (Ye, Yao, Shih, Ren & Wang), **comb**. **nov**. Endymiomyiinae, **subfam**. **nov**. is proposed for the genera *Endymiomyia* Grimaldi, *Futababombylia* Aiba *et al*. and *Burmobomba*, **gen**. **nov**. Based on additional specimens found in this study, the variability of characters in *Cretabombylia spinifera* Ye, Yao, Shih, Ren & Wang is discussed. A short analysis of pertinent characters is given, and some put in context with the impacts of various taphonomic processes. A revised key to the genera of Cretaceous amber Bombyliidae is given.

INTRODUCTION

With the recognition of Mythicomyiidae (with one fossil dating back to the mid-Jurassic and four others known from the Cretaceous) as separate from Bombyliidae, the latter being made monophyletic with the recognition of Heterotropodidae as a family [see Evenhuis (2024)]), it was not until recently that the Bombyliidae *s. str*. have been found to date back as far as the late Cenomanian Cretaceous (Grimaldi 2016, Zhang *et al*. 2016, Ye *et al*. 2019, Ngô-Muller *et al*. 2020) with an age of 98.79 mya (Shi *et al*. 2012). Recently, another genus and species of Bombyliidae was described from the slightly younger Coniacian Cretaceous (ca. 86–87 mya) Iwaki amber of Japan (Aiba *et al*. 2026).

The family is thus an ancient lineage and, being obligate nectar and pollen consumers for their developing ova, probably diversified in concert with the advent of angiosperms or gymnosperms (Zhang & Wang 2017).

Zhang *et al*. (2016) was the first to record a true bombyliid (*Pseudorhagio*) from the Cretaceous but mistakenly treated it in Tabanomorpha unplaced to family. Grimaldi (2016) noted the error of character state interpretation by Zhang *et al*. (2016) and transferred the genus to Bombyliidae. Since 2016, nine genera and ten species of Cretaceous Bombyliidae have been described, all from mid-Cretaceous Burmese amber, except one genus and species from the Cretaceous Iwaki amber of Japan (Aiba *et al*. 2026).

The five previous papers combined had described taxa based on only 12 specimens from Cretaceous amber, most singletons. Based on a significantly larger number of specimens (30, including 5 that were indeterminable and not treated taxonomically), this paper describes five new genera and seven new species, all from Burmese amber, bringing the total number of known bombyliids from Cretaceous amber to 18. Additionally, Endymiomyiinae, **subfam**. **nov**. is proposed for the genera *Endymiomyia* Grimaldi (type genus), *Futababombylia* Aiba *et al.* and *Burmobomba* Evenhuis, **gen**. **nov**. based on shared apomorphic characters of antennal article morphology. A key to the genera of Cretaceous Bombyliidae is presented, and a list of Cretaceous Bombyliidae thus far known is given with current taxonomic status. Variable characters and those impacted by taphonomic phenomena are discussed.

MATERIAL AND METHODS

All specimens studied derive from Burmese (Myanmar) amber from Hukawng Valley, Kachin State, Myanmar. Morphological terminology generally follows Cumming & Wood (2017) with some terminology following Grimaldi (2016; i.e., segments beyond the pedicel are here termed "flagellomere articles" or "articles"; and dense accumulation of apical abdominal hairs in females is termed "hair basket"). Photographic images were accomplished by obtaining a series of stacked images using a Leica M165C stereo dissecting scope via the Leica Microsystems LASX Multifocus software (v. 5.1.0.25593) and using Zerene Stacker® stacked focusing software (v. 1.04) (Zerene Systems, LLC, Richmond, Washington, USA) to align and stack-focus each final image. All type material of new species in this study derived initially from the personal collection of the author and has been deposited in the entomological collection of the Bernice Pauahi Bishop Museum, Honolulu, Hawai'i, USA (BPBM).

Abbreviations used: A_1 = anal vein; ac = acanthophorites; C = costa; bm = basal-medial cell; br = basal-radial cell; cua = anal cell; dm = discal cell; dm-m = discal-medial crossvein; M_1, M_2, M_4 = medial veins; m1, m4 = medial cells; R_1, R_{2+3}, R_3, R_4, R_5 = radial veins; r1, r4, r5 = radial cells; r-m = radial-medial crossvein; Sc = subcosta; sc = subcostal cell; sc-r = subcostal-radial crossvein; T = tergites.

SYSTEMATIC PALAEONTOLOGY

Order Diptera Linnaeus, 1758

Family Bombyliidae Latreille, 1802

KEY TO CRETACEOUS AMBER BOMBYLIIDAE

1. Antenna with some antennal articles beyond flagellomere (article 1) extremely long, thin, at least more than 8× width (Fig. 8A–D); origin of R_4 at level of end of cell dm (e.g., Figs. 5, 9A,B) ... (**Endymiomyiinae** Evenhuis, **subfam**. **nov**.) **2**

–. Antennal articles beyond flagellomere (article 1) with length of each ca. 2× width or less, or non-existent (e.g., Figs. 2A, 12B); origin of R_4 at level beyond end of cell dm (e.g., Figs. 2B, 9D,E) **4**

2. Second, third and/or fourth antennal articles much longer than wide (Figs. 8A,B); pretarsus with distinct pulvilli **3**

–. Second antennal article small (length equal to width) (Figs. 8C,D), fourth antennal article as long as flagellomere; pretarsus without evident pulvilli .... ***Burmobomba*** Evenhuis, **gen**. **nov**.

3. Hind coxa with mesal peg; vein R_4 clearly sinuous and upturned at wing margin (Fig. 9A); crossvein dm-m with spur vein (Fig. 9A) ... (Burmese amber) .... *Endymiomyia* Grimaldi

–. Hind coxa without mesal peg; vein R_4 only slightly curved toward wing margin, not distinctly sinuous (Fig. 9B); crossvein dm-m without spur vein (Fig. 9B) ... (Japanese amber) ..... *Futababombylia* Aiba *et al*.

4. Antennae separated at base by three times or more basal width of scape; vein R_{2+3} straight to wing margin ... (?Cythereinae) **5**

–. Antennae approximate at base (separated by no more than width of scape); vein R_{2+3} curved toward wing margin **6**

5. R_{2+3} branched with R_3 originating at distal end of R_2; vein A_1 sinuous .... *Nidergasia* Jouault & Nel

–. R_{2+3} not branched; vein A_1 straight to wing margin ... *Paleocytherea* Ngô-Muller & Nel

6. Antennal style placed in subapical sulcus; hind coxa with mesal peg ... (?Crocidiinae) ..... *Procrocidium* Grimaldi

–. Antennal style placed apically; hind coxa without mesal peg **7**

7. Wing with cell cua open in wing margin for width equal to length of crossvein r-m (Fig. 9C); crossvein r-m at apical 4/5 of cell dm (Fig. 9C) ..... *Nealimyia* Grimaldi

–. Wing with cell cua closed at or before wing margin, or narrowly open (if open, always less than width of crossvein r-m) (e.g., Figs. 13, 15); crossvein r-m at or before middle of cell dm (e.g., Figs. 13, 15) **8**

8. Cell cua very narrowly open at wing margin **9**

–. Cell cua clearly closed at wing margin **10**

9. Antennal flagellomere length 8–10× basal width; crossvein dm-m length subequal to last section of M_4 (Fig. 20C); proboscis shorter than length of antenna; scutum without tuberculate hairs ..... *Pseudorhagio* Zhang, Zhang & Wang

–. Antennal flagellomere length 4× basal width (Fig. 2A); crossvein dm-m length shorter than above, length 3/5 of last section of M_4 (Fig. 2C); proboscis longer than length of antenna; scutum with tuberculate hairs (Fig. 1B) ..... ***Bumaso*** Evenhuis, **gen**. **nov**.

10. Antennal flagellomere length less than 7× basal width **11**

–. Antennal flagellomere length 8–10× basal width **14**

11. Crossvein r-m slightly beyond middle of cell dm (Fig. 10C) .... ***Electrobombylia*** Evenhuis, **gen**. **nov**.

–. Crossvein r-m well before middle of cell dm (e.g., Figs. 9D–F) **12**

12. Junction of crossvein dm-m at vein M_4 at basal 1/5 of M_4 (Fig. 9E); cell cua closed at wing margin, without a petiole; dm-m crossvein sinuous .... *Pioneeria* Grimaldi

–. Junction of crossvein dm-m at vein M_4 much closer to middle of M_4 (e.g., Fig. 9D); cell cua closed before wing margin with a short petiole; dm-m crossvein sinuous or zigzagged **13**

13. Crossvein dm-m zigzagged (Fig. 9D), bent at right angles; junction of crossvein dm-m with M_4 at basal 1/4 of M_4 (Fig. 9D) ..... *Peculibombylia* Ye, Yao, Shih, Ren & Wang

–. Crossvein dm-m sinuous, not bent at sharp right angles (Fig. 9F); junction of crossvein dm-m with M_4 at basal 2/5 of M_4 (Fig. 9F) ..... *Cretabombylia* Ye, Yao, Shih, Ren & Wang

14. Crossvein dm-m zigzagged, bent at right angles (Fig. 15); junction of crossvein dm-m with M_4 at basal 1/3 of M_4 (Fig. 15) ..... ***Nemomyia*** Evenhuis, **gen**. **nov**.

–. Crossvein dm-m sinuous (Fig. 13); junction of crossvein dm-m with M_4 just before middle of M_4 (Fig. 13) ..... ***Fremo*** Evenhuis, **gen**. **nov**.

Descriptions of New Taxa

Genus *Bumaso* Evenhuis, gen. nov.

Type species: *Bumaso fusca* Evenhuis, **gen**. **et sp**. **nov**., by present designation.

Diagnosis. *Bumaso* Evenhuis, **gen**. **nov**. is closest in appearance to *Pseudorhagio* Zhang, Zhang & Wang based on the shared possession of a narrowly open cua in the wing margin; vein R_4 bent 90° and then parallel to vein R_5 for most of its length; and crossvein r-m placed at basal 1/3 of cell dm, but it can be easily separated from it by the long proboscis, longer than the antennae (much shorter than antennae in *Pseudorhagio*); the antennal flagellomere 4× basal width (8–10× basal width in *Pseudorhagio*); crossvein dm-m length 3/5 length of last section of M_4 (subequal to last section in *Pseudorhagio*); and the scutum possessing tuberculate hairs (not present in *Pseudorhagio*).

Remarks. The elongate proboscis shows some extension but the labrum (which cannot extend) length gives support to the fact the proboscis, even when fully retracted, is still longer than the antennae. However, if the proboscis is found later to have been a result of taphonomic processes, the wing and antennal characters can still easily be used to define the genus.

Etymology. The genus name derives from the Burmese “Bumaso” (Bhumasso), who are mythical spirits that inhabit the roots of trees and guard the soil (so named here to honor their protecting where the amber is mined). The name is treated as feminine.

Included species: *Bumaso fusca* Evenhuis, **sp**. **nov**.

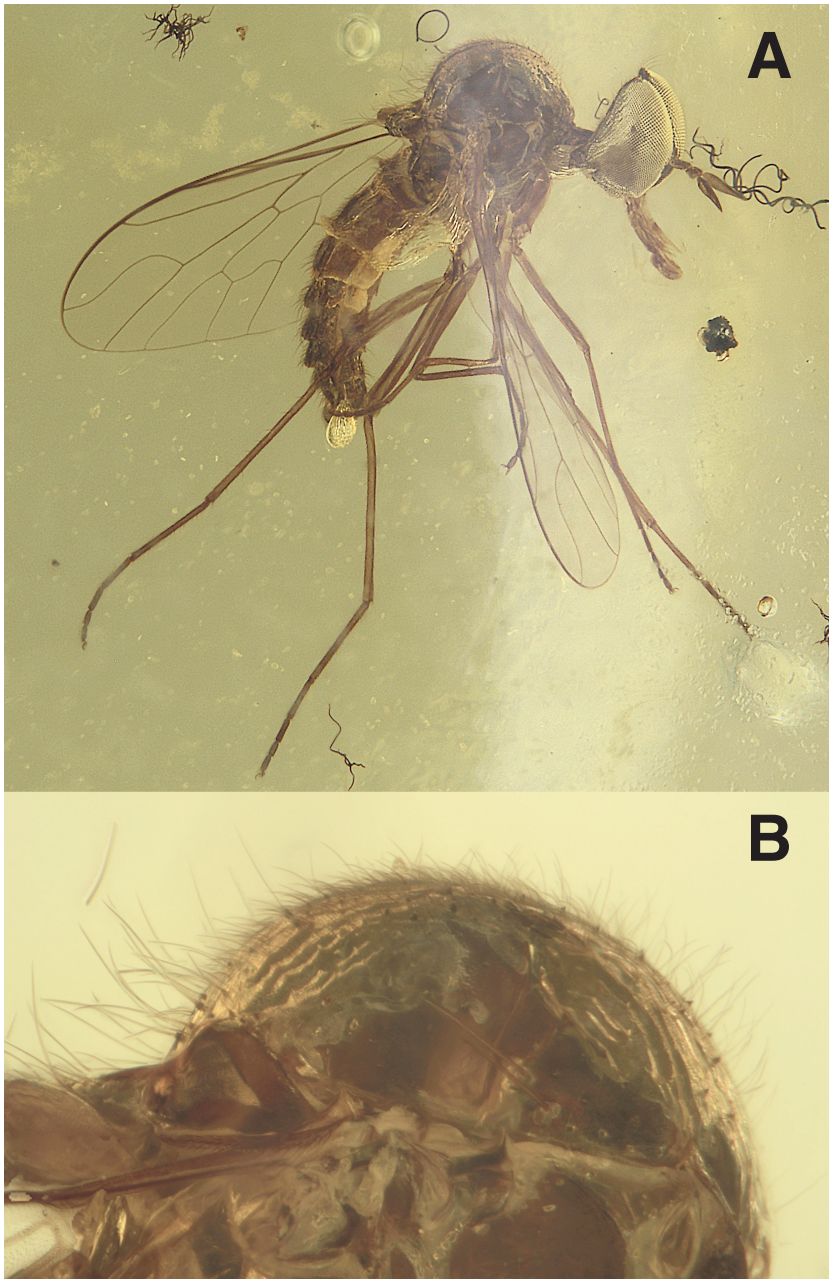


Figure 1. *Bumaso fusca* Evenhuis, sp. nov. **A**. Habitus of holotype. **B**. Detail of mesonotum showing thoracic hairs arising from basal tubercles.

***Bumaso fusca* Evenhuis, gen. et sp. nov.**

(Figs. 1–3)

Diagnosis. As for genus.

Material examined. Holotype ♂ (BPBMENT 0000081295) from Hukawng Valley, Burma. The type specimen is embedded in a golden cabochon measuring 16 × 13 × 3 mm with no syninclusions, but considerable debris.

Description. **Male** (Fig. 1A). Lengths: body: 3.5 mm; wing: 3.0 mm. Head higher than wide, tear-drop shaped in lateral view; eyes holoptic, large, bare, occupying all of lateral, much of dorsal and ventral surfaces of head; ocelli small; ocellar tubercle slightly raised on vertex, small; frons not evident; face absent below antennae, oral margin touching antenna bases; occiput not produced posteriorly in lateral view, slightly concave in caudal view, with row of postocular hairs from ocellar tubercle to basal one-third of posterior margin of eye; antennal sockets approximate; antenna (Fig. 2A) with scape cylindrical, about 1.5× width, with sparse erect short hairs dorsally; pedicel subcylindrical, slightly tapering at apex, without apical ring of hairs; with two antennal articles: flagellomere linear-lanceolate, article 2 tiny, as wide as long, minute stylus apically; proboscis projecting anteroventrally beyond oral margin for length longer than antenna; labrum long, stiff, pointed, ca. 7/8 length of proboscis; labellum ellipsoid, length 1/3 of proboscis; palpi not visible.

Thorax black, strongly humpbacked in lateral view; antepronotum well developed; cervical sclerites with sparse hairs; scutum with fine hairs, some hairs with tuberculate bases on anterior, postalar, and lateral surfaces; long hairs in prescutellar area; scutellum narrow, triangular with long hairs dorsally and posteriorly; notopleural area with three macrochaetae; pleura bare; halter stem and knob brownish orange.

Legs long, thin, femora devoid of vestiture; hind tibia with sparse minute bristles on posterior surface; tibial spur formula 0-2-0; basitarsus long, as long as combined length of remaining tarsomeres; claws small, pulvilli 3/4 length of claws; empodium setiform.

Wing (Fig. 2B,C) subhyaline with dark brown veins; costa circumambient, thickest up to end of R_4; Sc complete, ending in costa at level slightly beyond level of crossvein r-m; crossvein sc-r present; R_1 straight, ending in costa at level slightly beyond level of end of cell dm; R_{2+3} originating at midpoint of Rs between R_1 and crossvein r-m, slightly curved upward at wing margin; R_4 curved 90° after origin, sinuous to wing margin; cell

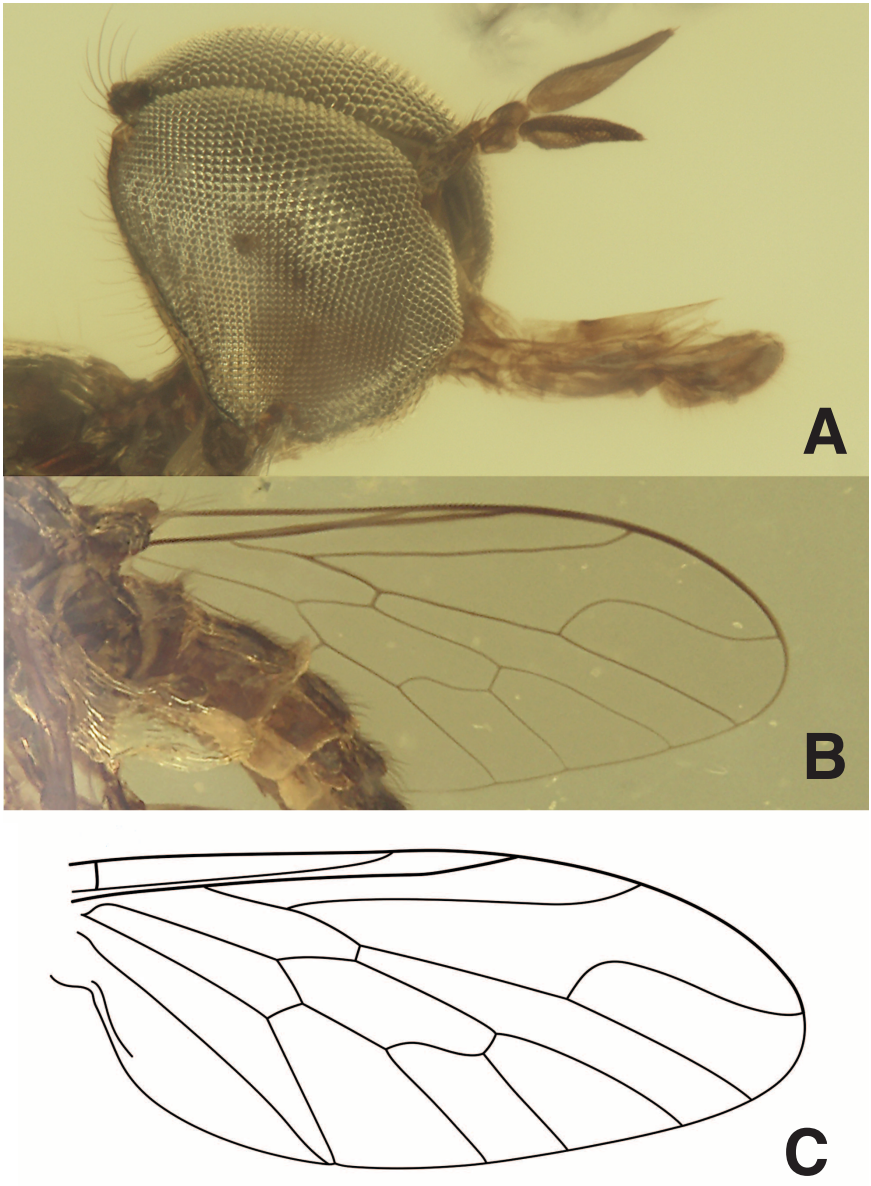


Figure 2. *Bumaso fusca* Evenhuis, sp. nov. **A**. Head and antennae, lateral view. **B**. Photo of right wing. **C**. Illustration of wing.

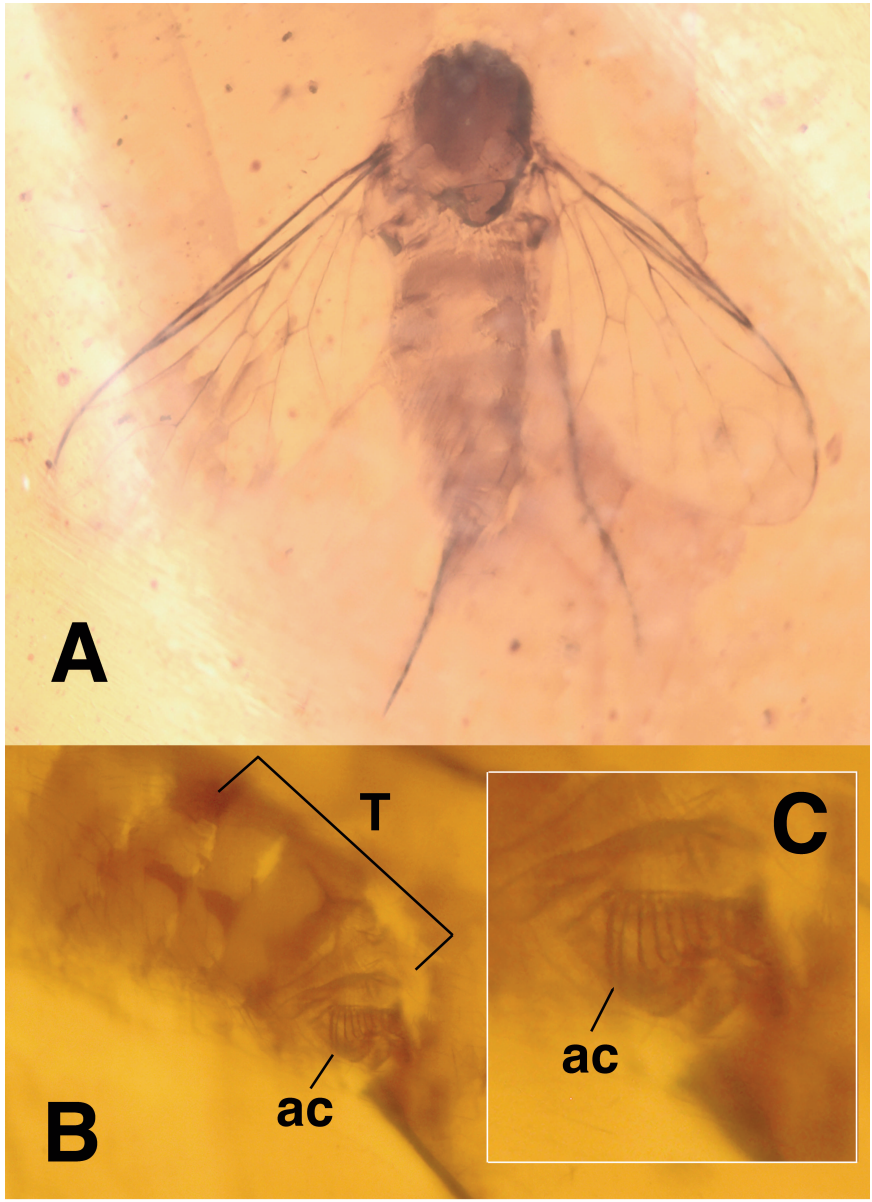


Figure 3. *Bumaso* sp. **A**. Habitus of female specimen. **B**. Apex of abdomen showing acanthophorite spines. **C**. Detail of acanthophorite spines.

r5 parallel sided at wing margin; cell br slightly longer than cell bm; crossvein r-m at basal 1/3 of cell dm; vein closing apex of cell dm perpendicular to vein M_1; veins M_1 and M_2 diverging at wing margin; veins M_2 and M_4 parallel; crossvein dm-m sinuous, junction of M_4 and crossvein dm-m at basal 2/5 of M_4; cell cua narrowly open at wing margin for width less than crossvein r-m; anal lobe narrow, width less than width of cell m4.

Abdomen slender, no wider than thorax in dorsal view, with vestiture of fine setae along posterior margin of tergites; genitalia rotated 45°; epandrium subquadrate, cerci exserted; gonocoxa obscured by a bubble.

Female. Unknown.

Etymology. The specific name derives from the Latin *fusca* [= dark]; referring to the general dark color of the specimen.

Remarks. A female (BPBMENT 0000081296) fitting the characters of this genus (based mainly on the wing venation) is left as *Bumaso* sp. as it is too damaged with the head missing as well as the bottom half of the thorax and most of the abdomen, and legs; parts of two legs are near the body but detached from it. It is shown in Fig. 3A. A ventral view of the abdominal tip (Fig. 3B) shows acanthophorite spines (8 with curved tips) (Fig. 3C), but no evidence of a developed "hair basket".

Genus *Burmobomba* Evenhuis, gen. nov.

Type species: *Burmobomba syrinx* Evenhuis, **sp**. **nov**., by present designation.

Diagnosis. *Burmobomba* Evenhuis, **gen**. **nov**. differs from all other Cretaceous bombyliids by the apparent lack of pulvilli (although micro-vestiges obscured by resin refraction cannot be entirely ruled out); the relatively small second and third flagellar articles and an elongated fourth antennal article; all others possess small to microscopic antennal articles or a different combination of tiny and elongated antennal articles distal to flagellomere article 1. In addition, vein sc-r is absent, which is present in most other Cretaceous bombyliids (although it was noted as indiscernible in *Nidergasia* Jouault & Nel and *Futababombylia* Aiba *et al*.). The modification of the apical segments of the female abdomen into a tubular/telescoping ovipositor appears to be fairly unique among bombyliids (see below under "Remarks" for further comments).

Remarks. The apparent lack of pulvilli is unique in Bombyliidae (all other taxa have pulvilli). The phylogenetically related Mythicomyiidae and Hilarimorphidae harbor species that also lack pulvilli. However, rather than being of phylogenetic significance, I treat this as an independent loss of this feature in this genus.

This genus is also unique among most Bombyliidae by females possessing an elongated ovipositor: in some specimens, this ovipositor is sclerotized and tubular, in others it is telescoping and appears to be flattened. This modification is obviously related to its mode of oviposition at or near potential hosts for immatures (assuming they are predators or parasitoids as are extant Bombyliidae). It is also related to two other Cretaceous genera that have elongated antennal articles and cell cua closed away from the wing margin by a stalk (*Endymiomyia* Grimaldi and *Futababombylia* Aiba *et al*.). Grimaldi (2016) conservatively placed his *Endymiomyia* as a possible stem-group to Bombyliidae, primarily because the antennae did not conform to other Bombyliidae. Unfortunately, the only known specimen of *Endymiomyia* (*E. quadra*) is a male, so it is not known what the female ovipositor looks like. The only specimen of *Futababombylia* (*F. kishini*) is a female, and the terminal segments of the abdomen were described as possibly having a hair basket and acanthophorite spines. As the synapomorphies of elongated antennal articles beyond the flagellomere and origin of vein R_4 at the level of the closing crossvein of cell dm clusters all three genera into one clade and places them separate from all other subfamilies of Bombyliidae, I here propose they be placed in the subfamily Endymiomyiinae, **subfam**. **nov**. with *Endymiomyia* Grimaldi, 2016 as its type genus.

The finding here of two species of *Burmobomba* with two different configurations of antennal articles and two distinct types of ovipositor may warrant the creation of two separate genera. However, I keep them as one until further research can be done to ascertain the status of each.

Etymology. The genus name derives from *Burmo* (from Burma) + *bomba* (shortened from “bombyliid”). The name is treated as feminine.

Included species: *Burmobomba proboscidea* Evenhuis, **sp**. **nov**.; *B. syrinx* Evenhuis, **sp**. **nov**.

***Burmobomba proboscidea* Evenhuis, sp. nov.**

(Figs. 4–5, 8A)

Diagnosis. Easily separated from the only congener, *B. syrinx*, by the longer proboscis, extending at least to the middle of the antennae (only the labellum exposed in *B. syrinx*), the flagellomere linear-lanceolate, length ca. 6× greatest width (flagellomere more conical and length ca. 3× greatest width in *B. syrinx*), the third antennal article short, as long as wide (longer, length 3× width in *B. syrinx*), and the telescoping terminal abdominal segments with long acanthophorites (ovipositor) (these segments sclerotized and tubular and without apparent acanthophorites in *B. syrinx*).

Material examined. Holotype ♀ (BPBMENT 0000081195) and 3♀ paratypes (BPBMENT 0000081289, -0000081291, -0000081194) from Hukawng Valley, Burma. The holotype specimen is embedded in a yellowish cabochon measuring 20 × 14 × 6 mm. Syninclusions: one small nematoceran, one ?cecidomyiid, and one small hymenopteran.

Description. **Female** (features not visible in holotype are taken from paratypes) (Fig. 4A). Lengths of type: body: 2.8 mm; wing: 2.5 mm. Head bean shaped in lateral view; eyes holoptic, large, bare, no differentiation of facets, posterior eye margin slightly sinuous; occiput not evident in lateral view, slightly concave in caudal view, occipital fringe minute laterally, not evident dorsally; frons and face not evident; antennal sockets approximate; antenna (Figs. 5A, 8A) with scape long, cylindrical, about 3× width, black; pedicel black, subcylindrical (length ca. 1.5× width); flagellomere linear-lanceolate, ca. 6× greatest width, with articles 2 and 3 small, length ca. equal to width, article 4 long, thin, 4/5 length of flagellomere; apical style minute; proboscis projecting beyond oral margin for length of antenna; labrum long, stiff, pointed, length ca. 3/4 that of proboscis; labellum large, ellipsoid, length 2/3 of proboscis; palpi not visible.

Thorax black, mesonotum convex, but not strongly arched, as wide as head, with minute hairs and sparse tomentum and scales dorsally; cervical area not visible because head is appressed closely to thorax; pleura bare; macrochaetae not visible (broken off?); halter with stem and knob light brown.

Legs long, thin, femora devoid of vestiture; mid and hind tibiae with 2 rows of minute bristles along entire length; tibial spur formula 0-2-0; fore and mid basitarsi long, as long as combined length of remaining tarsomeres, with bristles as on tibiae; claws tiny, pulvilli not visible; empodium setiform.

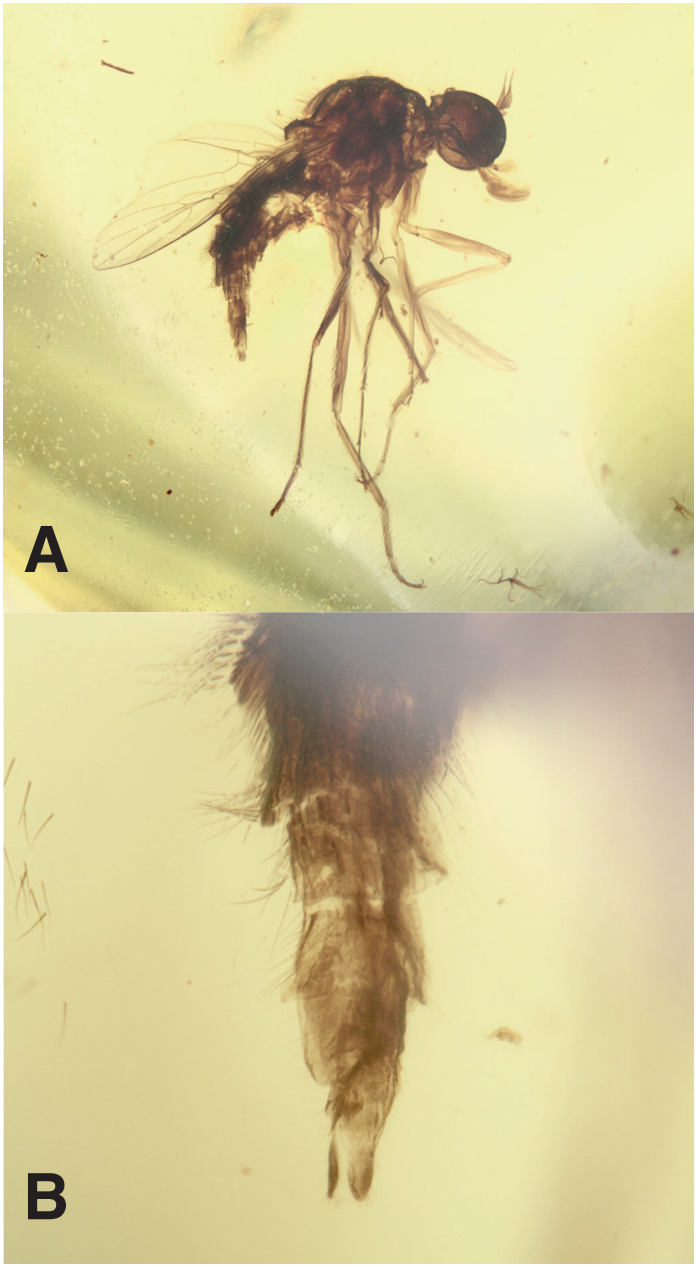


Figure 4. *Burmobomba proboscidea* Evenhuis, sp. nov. **A**. Habitus of holotype. **B**. Apical portion of abdominal segments showing telescoping abdomen.

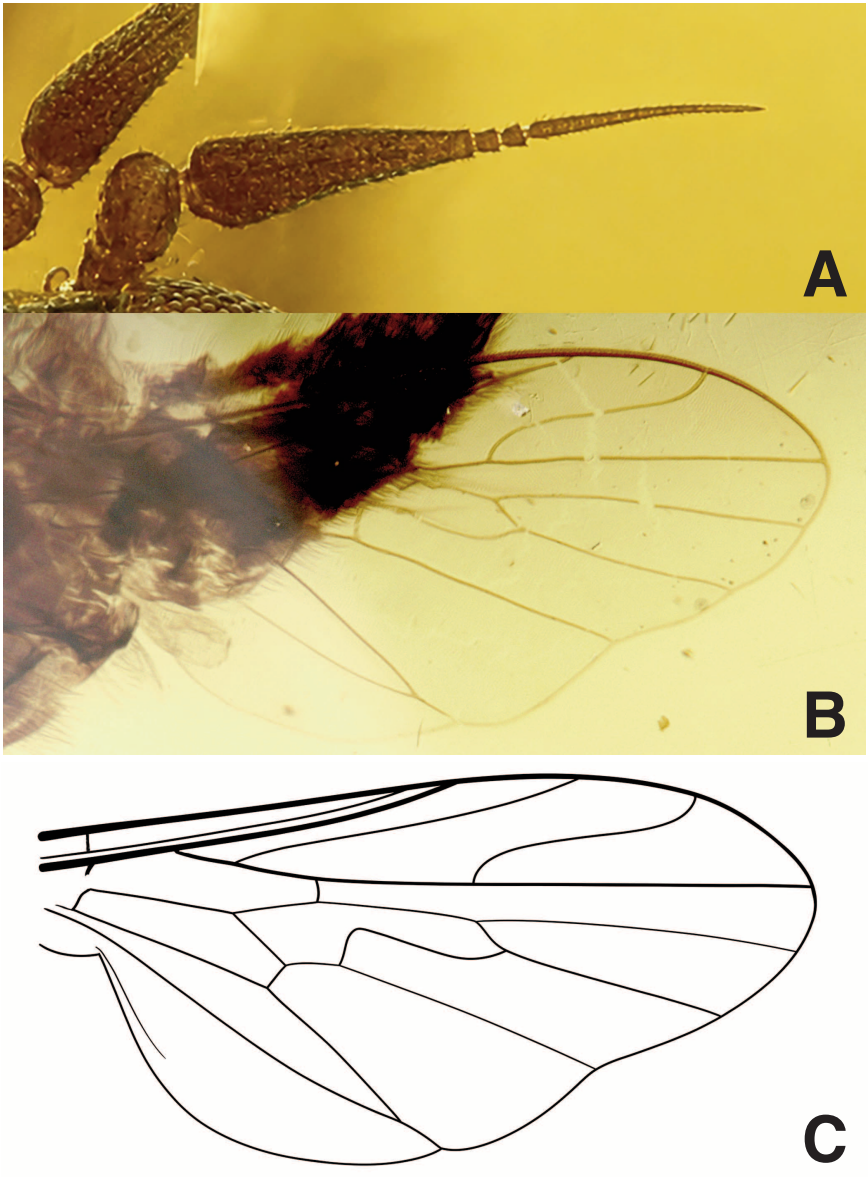


Figure 5. *Burmobomba proboscidea* Evenhuis, sp. nov. **A**. Antenna. **B**. Photo of right wing. **C**. Illustration of wing.

Wing (Fig. 5B,C) subhyaline with dark brown veins; infuscation present at end of cell sc and into apex of cell r1; costa circumambient, thickest up to end of R_4; Sc complete, ending in costa at level of crossvein r-m; crossvein sc-r present; R_1 straight, ending in costa at level slightly before level of end of cell dm; R_{2+3} originating at midpoint of Rs between R_1 and crossvein r-m, straight to wing margin; R_4 sinuous, angled ca. 40° toward wing margin, originating at level of vein closing cell dm; cell r5 parallel sided at wing margin; cell br distinctly longer than cell bm; crossvein r-m at basal 1/3 of cell dm; vein closing apex of cell dm angled, not perpendicular to vein M_1; veins M_1 and M_2 almost parallel, only slightly diverging at wing margin; veins M_2 and M_4 parallel; crossvein dm-m bent 90° off of vein M_4, sinuous to vein M_2; junction of M_4 and crossvein dm-m at basal 1/4 of M_4; cell cua closed at wing margin by a long petiole; anal lobe narrow, width less than width of cell m4.

Abdomen slender, no wider than thorax in dorsal view, without vestiture of fine, decumbent setae, but fine black hairs at posterior margin of tergites; last segments of abdomen (ovipositor?) telescoping (Fig. 4B), without a sclerotized tubular structure; acanthophorites well developed, paddle-shaped and apically projecting, without spines.

Male. Unknown.

Remarks. The telescoping abdomen and bare acanthophorites is reminiscent of that found in *Lordotus* Loew (see Hall & Evenhuis 1982: 211, fig. 170, for *L. gibbus*), which uses its paddle-shaped acanthophorites as blades probing into the soil where it oviposits eggs.

Etymology. The species name derives from the Latin *proboscis*; referring to the characteristic proboscis of this species, extending well beyond the oral margin.

Burmobomba syrinx **Evenhuis**, **sp**. **nov**.

(Figs. 6–7, 8B)

Diagnosis. Easily separated from the only congener, *B. proboscidea*, by the short proboscis, with only the labellum exposed (as long as antennae in *B. proboscidea*), the flagellomere linear-conical, length ca. 3× greatest width (flagellomere more linear and length ca. 6× greatest width in *B. proboscidea*), the third antennal article long, ca. 3× width (short, length equal to width in *B. proboscidea*), and the tubular ovipositor (these apical abdominal segments telescoping in *B. proboscidea*).

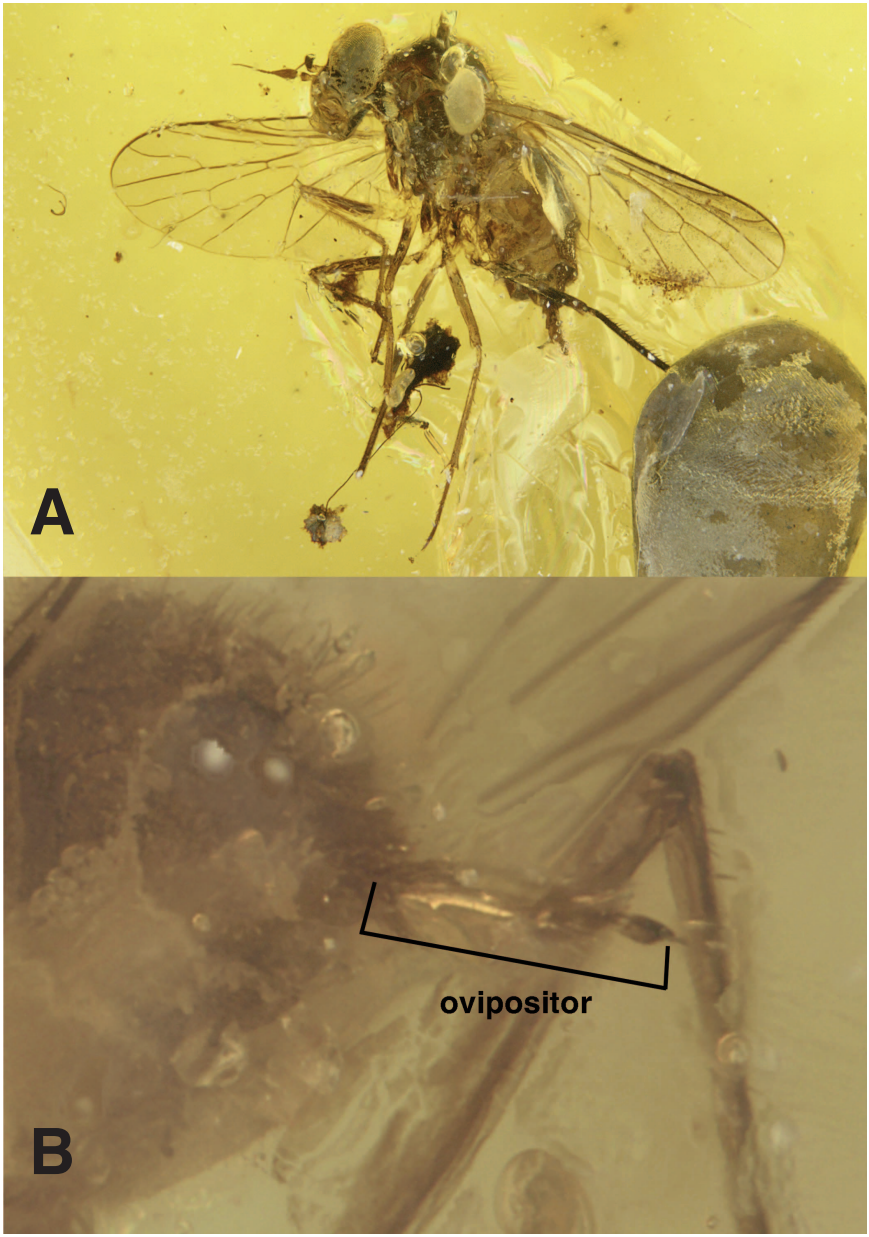


Figure 6. *Burmobomba syrinx* Evenhuis, sp. nov. **A**. Habitus of holotype. **B**. Apical portion of abdomen showing tubular ovipositor.

Material examined. Holotype ♂ (BPBMENT 0000081292) and 4♀ paratypes (BPBMENT 0000081289, -0000081290, 0000081193, 0000081299) from Hukawng Valley, Burma. The holotype specimen is embedded in a reddish-orange cabochon measuring 16 × 9 × 2 mm with no syninclusions.

Description. **Male** (Fig. 6A). Lengths: body: 3.1 mm; wing: 3.0 mm. Head bean shaped in lateral view; eyes holoptic, large, bare, no differentiation of facets, posterior eye margin slightly sinuous; occiput not evident in lateral view, slightly concave in caudal view, occipital fringe minute laterally, not evident dorsally; frons and face not evident; antennal sockets approximate; antenna (Figs. 7A, 8B) with scape long, cylindrical, about 3× width, yellow; pedicel yellow, brown apically, subcylindrical, slightly flared and with ring of stiff hairs apically (length ca. 1.5× width in paratype); flagellomere linear-conical, ca. 3× greatest width, with article 2 small, length ca. equal to width, article 3 ca. 3× width, article 4 long, thin, as long as flagellomere; apical style minute; proboscis short, only labellum projecting beyond oral margin; labellum large, rounded, length 7/8 of proboscis; palpi not visible.

Thorax black, mesonotum convex, but not strongly arched, as wide as head, with minute hairs and sparse tomentum and scales dorsally; cervical area not visible because head is appressed closely to thorax; pleura bare; macrochaetae present as 1 notopleural, 3 prealar and fine hairs on postalar callus. Halter with stem and knob light brown.

Legs long, thin, femora devoid of vestiture; hind tibia with sparse minute bristles on posterior surface; tibial spur formula 0-2-0; basitarsus long, as long as combined length of remaining tarsomeres; claws large (2× length of those in female), pulvilli not visible; empodium setiform.

Wing (Fig. 7B) subhyaline with dark brown veins; costa circumambient, thickest just before end of R_4; infuscation present at end of cell sc and into apex of cell r1; Sc complete, ending in costa at level of crossvein r-m and curved upward; crossvein sc-r present; R_1 straight, ending in costa at level slightly before level of end of cell dm; R_{2+3} originating at midpoint of Rs between R_1 and crossvein r-m, straight to wing margin; R_4 sinuous, angled ca. 40° toward wing margin, originating at level of vein closing cell dm; cell r5 almost parallel sided at wing margin, slightly wider than at base; cell br distinctly longer than cell bm; crossvein r-m at basal 1/3 of cell dm; vein closing apex of cell dm perpendicular to vein M_1; veins M_1 and M_2 almost parallel, only slightly diverging at extreme ends at wing margin; veins M_2 and M_4 parallel; crossvein dm-m bent 90° off of vein M_4, sinuous to vein M_2; junc-

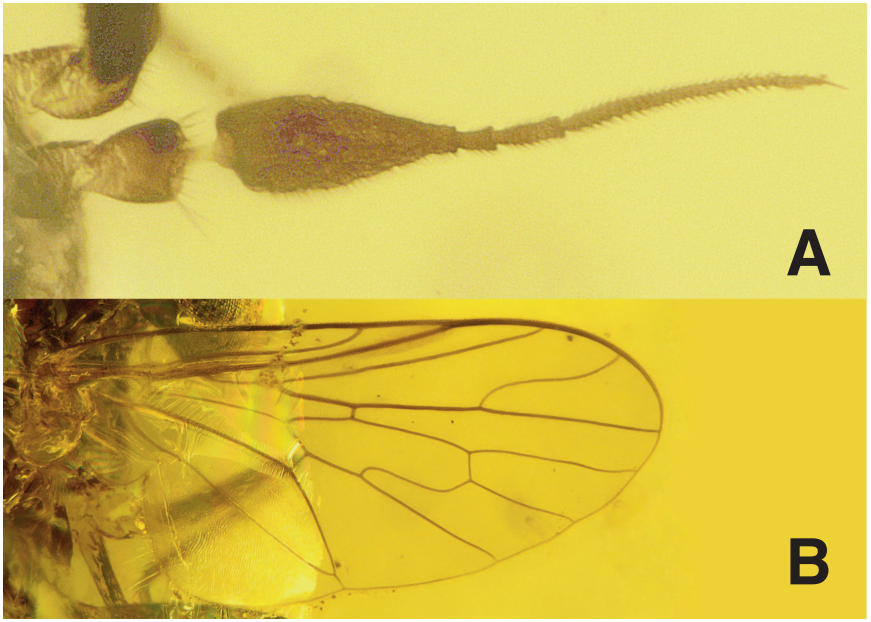


Figure 7. *Burmobomba syrinx* Evenhuis, sp. nov. **A**. Antenna. **B**. Photo of right wing.

tion of M_4 and crossvein dm-m at basal 1/3 of M_4; cell cua closed at wing margin by a long petiole; anal lobe broad, width subequal to that of widest part of cell m4.

Abdomen slender, no wider than thorax in dorsal view, without vestiture of fine, decumbent setae, but fine black hairs at posterior margin of tergites; genitalia not rotated; epandrium oblong-conical; cerci not evident; gonocoxae hemispherical, gonostylus small, rounded.

Female. As in male except as follows: Lengths: body: 2.0–3.0 mm; wing: 1.8–2.8 mm. head wider than thorax; eyes dichoptic, frons width 3× that of ocellar tubercle, parallel-sided to antennal bases; all antennal segments black; abdomen with segments II–IV wider than thorax, tapering sharply to apex; last segment with sclerotized ovipositor appearing tubular (Fig. 6B).

Remarks. The female ovipositor consists of segments VII–X, with some specimens having this structure partially retracted into the abdomen with only last two segments visible.

Etymology. The species name derives from the Greek σῦριγξ (*syrinx*), a "pipe"; referring to the tubular shape of the female ovipositor.

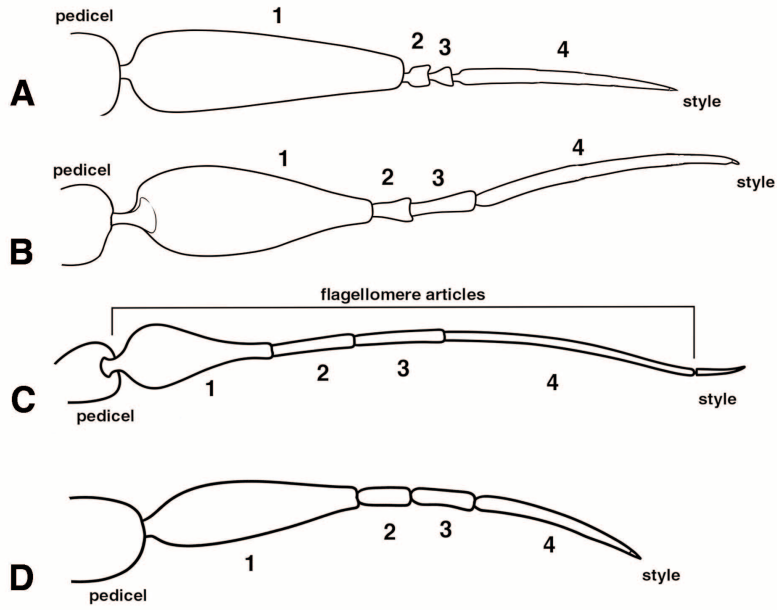


Figure 8. Endymiomyiinae, antennae, schematic, with vestiture removed, showing configuration of flagellomere articles. **A**. *Burmobomba proboscidea* Evenhuis, sp. nov. **B**. *Burmobomba syrinx*, sp. nov. **C**. *Endymiomyia quadra* Grimaldi (redrawn from Grimaldi 2016). **D**. *Futababombylia kishini* Aiba, Inose & Watanabe, 2026 (redrawn from Aiba *et al*. 2026). Numbers = antennal article numbers.

Genus *Electrobombylia* Evenhuis, gen. nov.

Type species: *Electrobombylia medialis* Evenhuis, **gen**. **et sp**. **nov**., by present designation.

Diagnosis. Closest in appearance to *Pseudorhagio* Zhang, Zhang & Wang but differs from it by the placement of the crossvein r-m just beyond the middle of cell dm (this crossvein at basal 1/3 of cell dm in *Pseudorhagio*).

Etymology. The name derives from the Latin *electro* [= amber] + the suffix -*bombylia* in keeping with other Cretaceous fossil bee fly generic names.

Included species: *Electrobombylia medialis* Evenhuis, **sp**. **nov**.

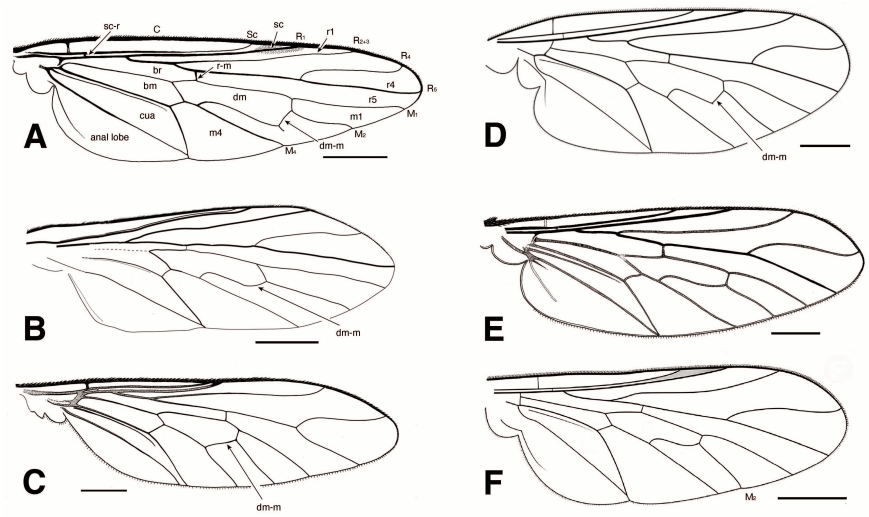


Figure 9. Wings of previously described Cretaceous Bombyliidae. **A**. *Endymiomyia quadra* Grimaldi (redrawn from Grimaldi 2016; wing texture excluded). Scale bar: 1.0 mm. **B**. *Futababombylia kishini* Aiba, Inose & Watanabe, 2026 (redrawn from Aiba *et al*. 2026, including reconstruction to put the basal portion together with the apical portion that is cut in the original illustration). Scale bar: 0.5 mm. **C**. *Nealimyia evenhuisi* Grimaldi, 2016 (redrawn from Grimaldi 2016). Scale bar: 0.5 mm. **D**. *Peculibombylia relictivena* Ye, Yao, Shih, Ren & Wang, 2019 (redrawn from Ye *et al.* 2019). Scale bar: 0.5 mm. **E**. *Pioneeria bombylia* Grimaldi, 2016 (redrawn from Grimaldi 2016). Scale bar: 1.0 mm. **F**. *Cretabombylia spinifera* Ye, Yao, Shih, Ren & Wang, 2019 (redrawn from Ye *et al*. 2019). Scale bar: 0.5 mm.

Electrobombylia medialis **Evenhuis**, **gen**. **et sp**. **nov**.

(Figs. 10–11)

Diagnosis. As for genus.

Material examined. Holotype ♂ (BPBMENT 0000081183) from Hukawng Valley, Kachin State, northern Burma in a small piece of golden amber cabochon measuring 11 × 9 × 3 mm. Syninclusions: a small beetle.

Description. **Male** (Fig. 10A). Lengths: body: 4.8 mm; wing: 4.5 mm. Head higher than wide, tear-drop shaped in lateral view (Fig. 11A); eyes holoptic, large, bare, occupying all of lateral and much of dorsal surfaces of head; ocelli small; ocellar tubercle clearly raised on vertex, small; frons a small triangle above antennal sockets; face absent below antennae, oral margin touching antenna bases; occiput not produced posteriorly in lateral view,

slightly concave in caudal view, with row of sparse, fine postocular hairs; antennal sockets approximate; antenna (Fig. 11A) with scape long, cylindrical, about 3.5× width; pedicel subglobular, length subequal to width; with two antennal articles; flagellomere linear-lanceolate, article 2 as wide as long, minute stylus apically; proboscis contained within oralgenal cup; labellum rounded, 1/2 length of proboscis; palpi not visible.

Thorax black, convex but not strongly arched in lateral view; antepronotum well developed; scutum with minute hairs, longer hairs on scutellum; scutellum subtriangular, rounded apically, with long hairs dorsally and posteriorly; macrochaetae: 2 notopleural, 2 prealar, fine hairs on postalar callus; pleura bare; halter stem and knob paddle shaped, pale brown.

Legs long, thin, femora devoid of vestiture; hind tibia with sparse minute bristles on posterior surface; tibial spur formula 0-2-0; basitarsus long, as long as combined length of remaining tarsomeres; claws small, pulvilli 3/4 length of claws; empodium setiform.

Wing (Fig. 10B–C) [apex of right wing cut off by surface of amber piece] subhyaline with dark brown veins; costa circumambient, thickest up to end of R_4; Sc complete, ending in costa at level well beyond level of crossvein r-m; crossvein sc-r present; R_1 straight, ending in costa at level slightly beyond level of end of cell dm; R_{2+3} originating at midpoint of Rs between R_1 and crossvein r-m, curved upward on apical 1/4; R_4 curved 40° after origin, then fairly straight to wing margin; cell r5 parallel sided at wing margin with both veins R_5 and M_1 curved downward; cell br distinctly longer than cell bm; crossvein r-m slightly beyond middle of cell dm; vein closing apex of cell dm very small, perpendicular to vein M_1; veins M_1 and M_2 markedly diverging at wing margin; veins M_2 and M_4 converging slightly; crossvein dm-m sinuous, junction of M_4 and crossvein dm-m at basal 2/5 of M_4; cell cua closed at wing margin by a minute petiole; anal lobe broad, as wide as cell m4 at its widest point.

Abdomen slender, slightly clubbed apically due to genital capsule, no wider than thorax in dorsal view, with vestiture of fine setae along posterior margin of tergites; genitalia rotated 90°; epandrium with deep medial notch, cerci exserted (Fig. 11B).

Female. Unknown.

Etymology. The specific epithet derives from the Latin *medialis* [= in the middle]; referring to the characteristic placement of the r-m crossvein just beyond the middle of cell dm.

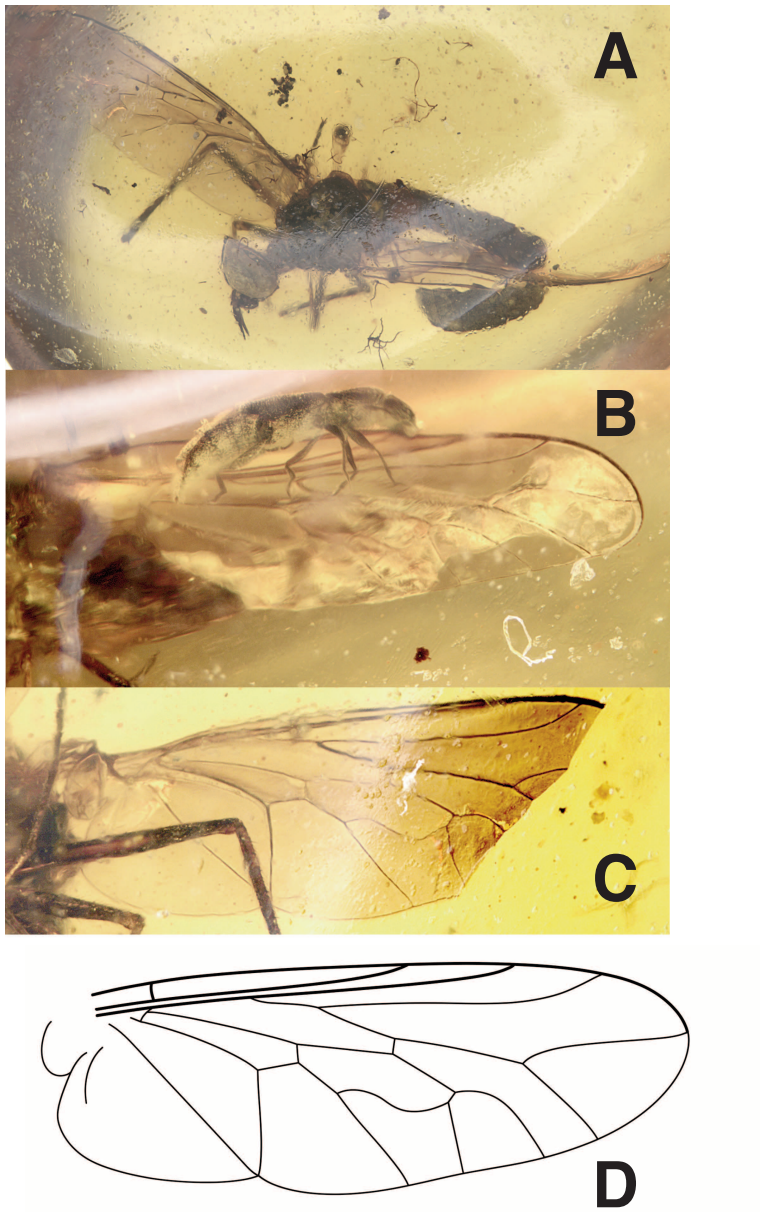


Figure 10. *Electrobombylia medialis* Evenhuis, sp. nov. **A**. Habitus of holotype. **B**. Left wing. **C**. Right wing. **D**. Reconstruction of wing based on left and right wings viewed at different angles including those that could not be photographed.

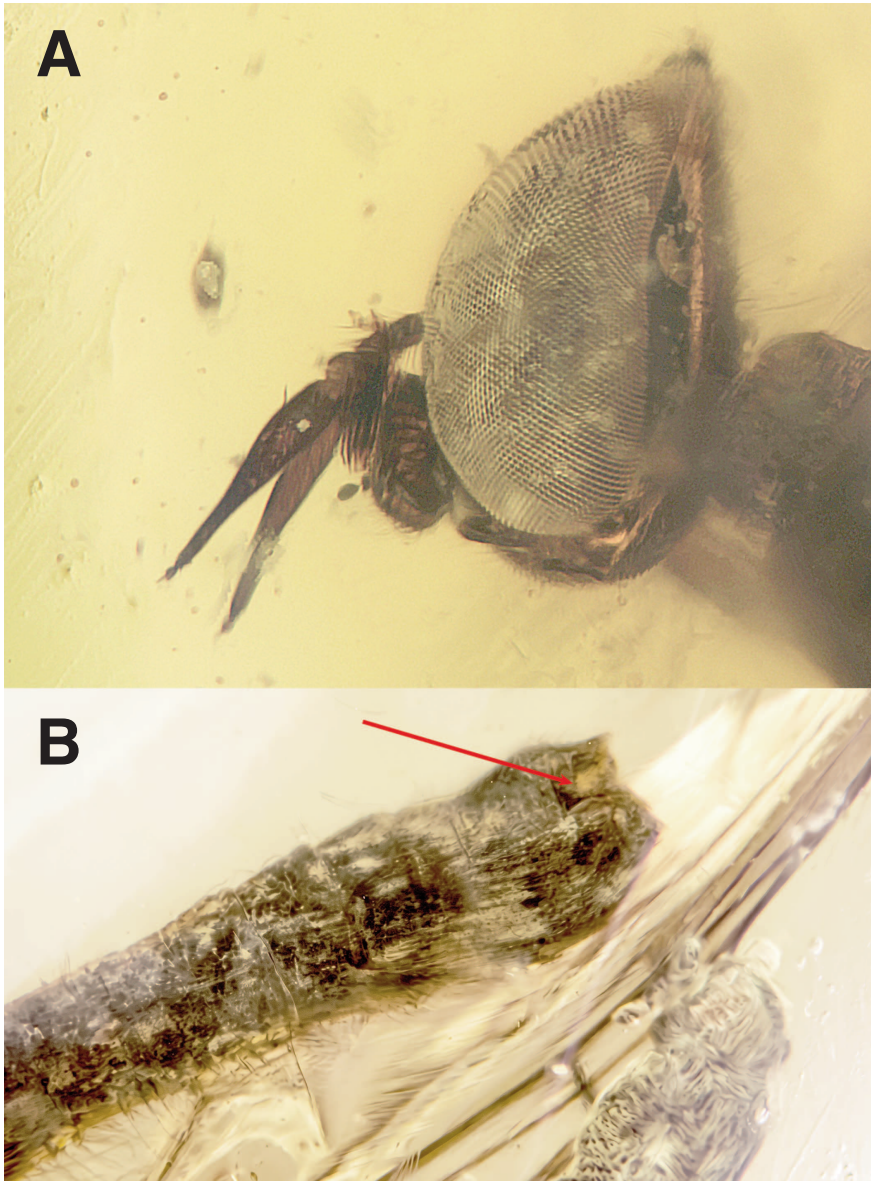


Figure 11. *Electrobombylia medialis* Evenhuis, sp. nov. **A**. Head and antenna, lateral view. **B**. Apex of abdomen and genitalic capsule. Arrow points to deeply incised epandrium.

Genus *Fremo* Evenhuis, gen. nov.

Type species: *Fremo compressus* Evenhuis, **gen. et sp. nov.**, by present designation.

Diagnosis. Closest in appearance to *Nemomyia* Evenhuis, **gen. nov.** by the shared character state of a long, thin antennal flagellomere (length about 8× basal width) but can be separated from it by the sinuous crossvein dm-m (zigzagged in *Nemomyia*) and the junction of crossvein dm-m placed just before the middle of M_4 (placement of dm-m at basal 1/3 of M_4 in *Nemomyia*).

Etymology. The name *Fremo* is an arbitrary combination of letters and is treated as masculine.

Included species: *Fremo compressus* Evenhuis, **sp. nov.**

***Fremo compressus* Evenhuis, gen. et sp. nov.**

(Figs. 12–13)

Diagnosis. As for genus.

Material examined. Holotype ♀ (BPBMENT 0000081286) from Hukawng Valley, Kachin State, northern Burma in a cloudy piece of golden amber cabochon measuring 22 × 12 × 7 mm. Syninclusions: none.

Description. **Female** (Fig. 12A). Lengths: body: 5.8 mm; wing: 5.8 mm. Head wider than thorax in dorsal view (Fig. 12B), globular; eyes dichoptic, bare, no differentiation of facets; ocelli small; ocellar tubercle barely raised above surface of vertex; frons width slightly more than width between lateral ocelli; postgena concave; gena occiput slightly convex, with paired bullae medially; occipital fringe with sparse stiff hairs; antennal sockets slightly separated; antenna (Fig. 12B) with scape cylindrical, 4× length of pedicel; pedicel cylindrical, longer than wide; flagellum with 3 articles: flagellomere linear, length 8× basal width, article 2 tiny, length subequal to width, article 3 cylindrical, length ca. 2× width, minute style apically; proboscis short, prelabellar portion recessed into oral cavity; labellum rounded, slightly projecting beyond oral margin.

Thorax black, laterally compressed, rather long and narrow in dorsal view, narrower than head; cervical area long, dorsally with few long, fine (hardly visible) stiff setae; most of scutum and pleura covered with fine pilosity; macrochaetae: 2 notopleural; 1 prealar, postalar not discernible; pleura bare; halter with stem pale brown, knob dark brown.

Legs long, thin, devoid of vestiture; tibial spur formula 0-2-0; basitarsus long, as long as combined length of remaining tarsomeres; claws small, pulvilli 3/4 length of claws; empodium setiform.

Wing (Fig. 13) subhyaline with dark brown veins; costa circumambient, thickest up to end of CuA; Sc complete, ending in costa at level of crossvein r-m; crossvein sc-r present; R_1 fairly straight, ending in costa at level slightly before level of end of cell dm; R_{2+3} originating at midpoint of Rs between R_1 and crossvein r-m, curved slightly upward at wing margin; R_4 curved 90° after origin, then sinuous to wing margin; cell r5 slightly parallel sided at wing margin with veins R_5 and M_1 slightly diverging; cell br equal in length to cell bm; crossvein r-m at basal 1/3 of cell dm; vein closing apex of cell dm not perpendicular to vein M_1; veins M_1 and M_2 slightly diverging at wing margin; veins M_2 and M_4 parallel; crossvein dm-m sinuous, junction of M_4 and crossvein dm-m just before middle of M_4; cell cua closed at wing margin by a minute petiole; anal lobe narrow, much narrower than cell m4 at its widest point.

Abdomen narrow, tapering to apex, no wider than thorax in dorsal view, vestiture of tergites and apex of abdomen not discernible.

Etymology. The specific name derives from the Latin *compressus*, referring to the laterally compressed thorax and abdomen.

Genus *Nemomyia* Evenhuis, gen. nov.

Type species: *Nemomyia lamasi* Evenhuis, **sp**. **nov**., by present designation.

Diagnosis. Closest in appearance to *Fremo* Evenhuis, gen. nov. by the long, thin antennal flagellomere (length more 8× or more basal width) but can be separated from it by the zigzagged crossvein dm-m (sinuous in *Fremo*) and the junction of crossvein dm-m placed at the basal 1/3 of M_4 (placement of dm-m just before the middle of M_4 in *Fremo*).

Etymology. The genus epithet derives from the Greek *νέμος* [*nemos*] [= "forest, wood, sacred grove"] + *μυῖα* [*myia*] [= fly]; referring to the amber matrix originally deriving from the resins of ancient conifers such as Araucariaceae.

Included species: *Nemomyia burmitica* Evenhuis, **sp**. **nov**.; *N. lamasi* Evenhuis, **sp**. **nov**.

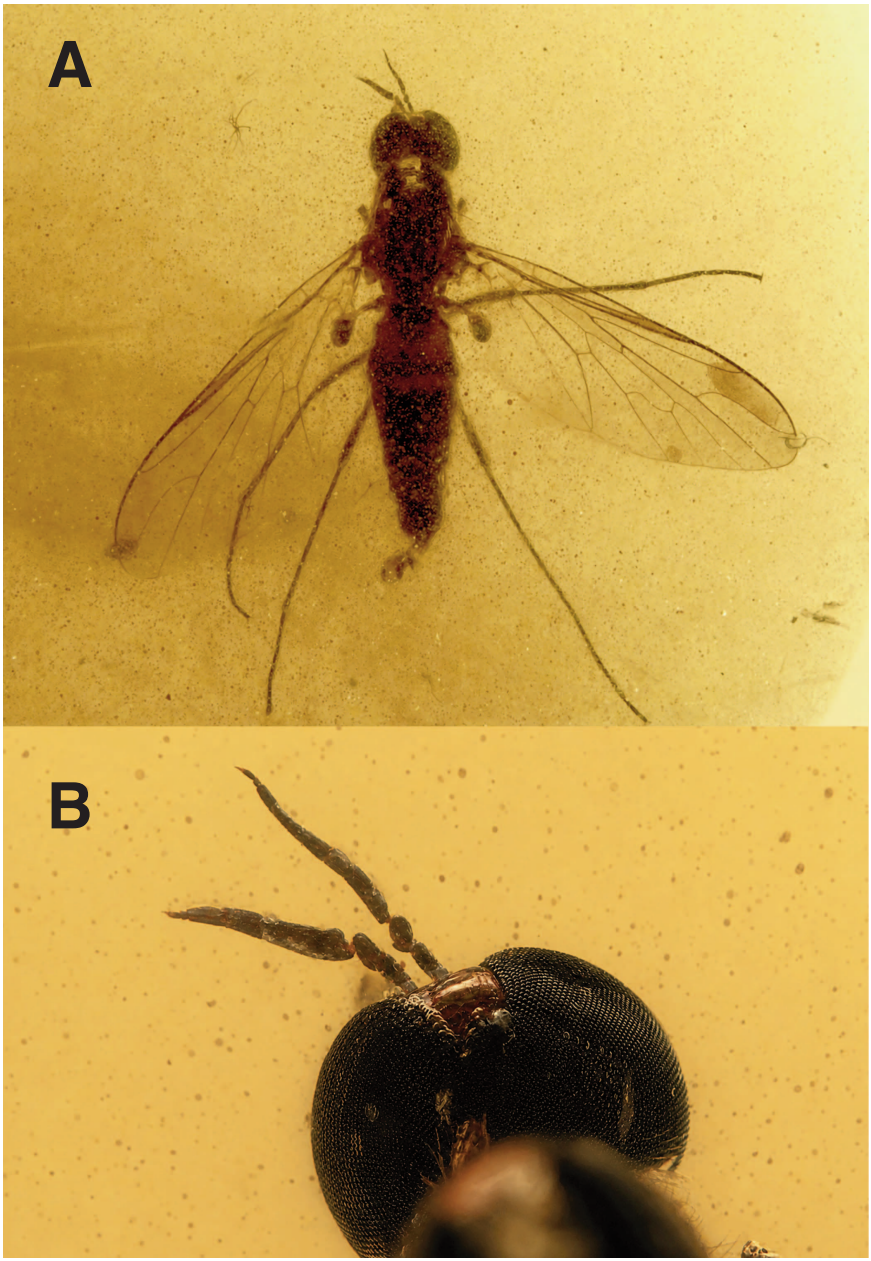


Figure 12. *Fremo compressus* Evenhuis, sp. nov. **A**. Habitus of holotype. **B**. Head and antenna, dorsal view.

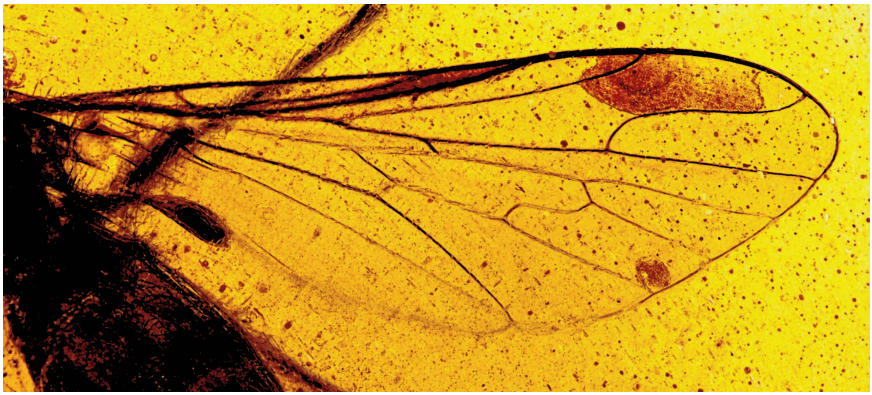


Figure 13. *Fremo compressus* Evenhuis, sp. nov., photo of wing.

***Nemomyia burmitica* Evenhuis, sp. nov.**

(Figs. 14–15)

Diagnosis. Easily separated from the only other species in the genus (*N. lamasi*) by the black lateral margin of the mesonotum (white in *N. lamasi*); end of vein R_{2+3} at level of origin of R_4 (this vein ending well beyond origin of R_4 in *N. lamasi*), and vein M_2 angled toward M_4 (veins M_1, M_2 and M_4 all parallel to each other in *N. lamasi*).

Material examined. Holotype ♂ (BPBMENT 0000081297) from Hukawng Valley, Burma. The holotype is embedded in a small golden cabochon measuring 16.0 × 10.0 × 2.3 mm. Syninclusions: a small beetle.

Description. **Male** (Fig. 14A). Lengths: body: 4.0 mm; wing: 4.0 mm. Head (Fig. 14B) slightly wider than thorax in dorsal view, eyes large, holoptic above antennae for length of 12 ommatidia, diverging at ocellar tubercle and above antennal sockets; ocelli small; ocellar tubercle narrow, distinctly raised above surface of vertex; frons triangular; face absent; occiput concave in dorsal view; antennal sockets approximate; antenna (Fig. 14B) with scape cylindrical, about 2.5× width; pedicel cylindrical, ca. 1.5× width; flagellum with 3 articles; flagellomere long, thin, linear, length ca. 10× basal width; articles 2 and 3 tiny, length equal to width; minute stylus barely visible apically; proboscis short, only labellum exposed beyond oral margin.

Thorax slender in dorsal view, in lateral view with anterior portion sloping to highest point at caudal 2/3; scutum with fine scattered hairs, long hairs in prescutellar area and on

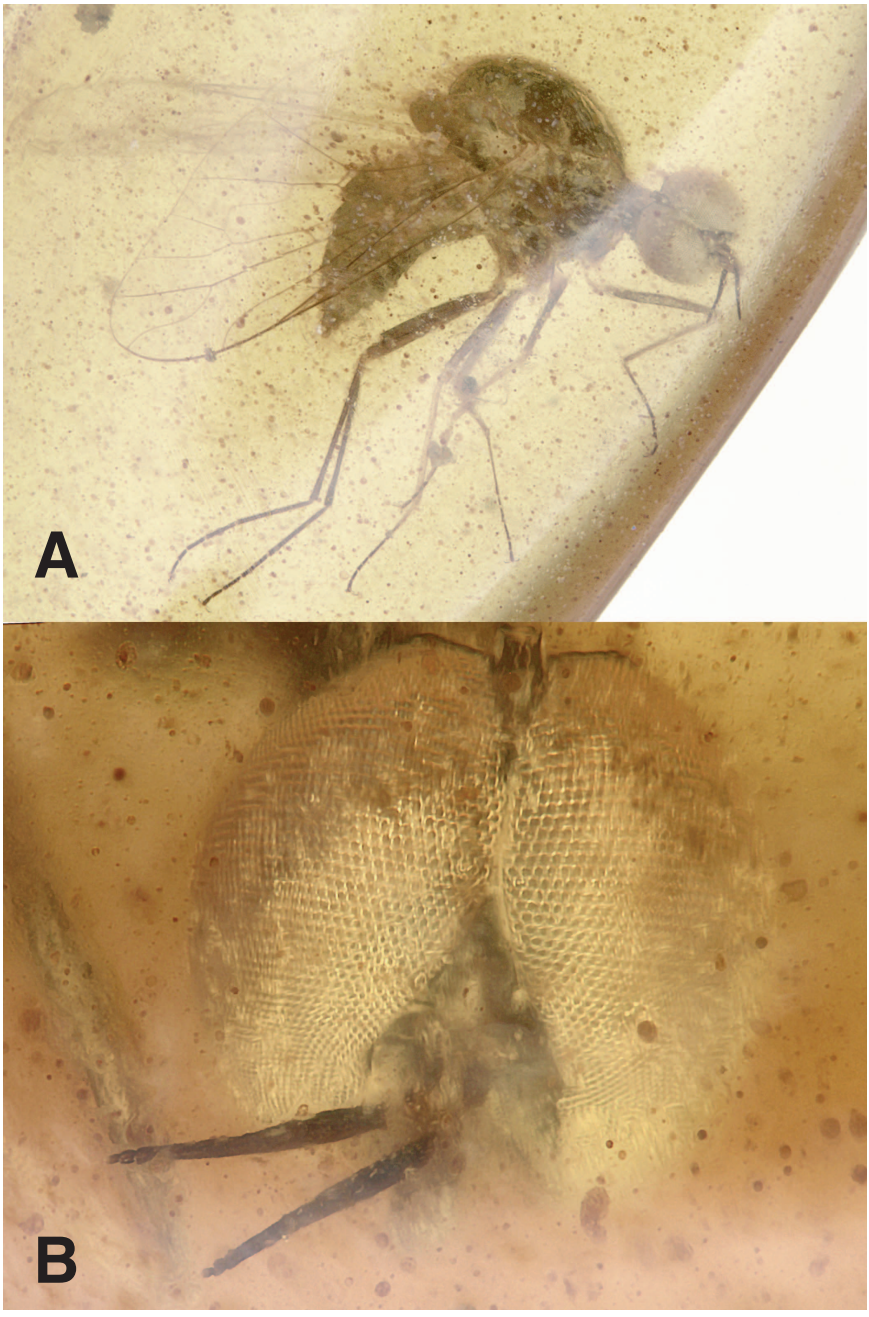


Figure 14. *Nemomyia burmitica* Evenhuis, sp. nov. **A**. Habitus of holotype. **B**. Head and antenna, dorsal view.

scutellum; macrochaetae not evident; scutellum hemispherical; antepronotum well-developed; halter with stem and knob dark brown.

Legs long, thin, devoid of vestiture; tibial spur formula 0-2-0; basitarsus long, as long as combined length of remaining tarsomeres; claws large, pulvilli 3/4 length of claws; empodium setiform.

Wing (Fig. 15) subhyaline with dark brown veins; costa circumambient, thickest up to end of R_4; Sc complete, ending in costa at level slightly beyond level of crossvein r-m; crossvein sc-r present; R_1 straight, ending in costa at level of end of cell dm; R_{2+3} originating at midpoint of Rs between R_1 and crossvein r-m, distinctly curved upward at wing margin, ending in costa at level of origin of R_4; R_4 curved 45° after origin, sinuous to wing margin; cell r5 parallel sided at wing margin; cell br longer than cell bm; crossvein r-m just before middle of cell dm; vein closing apex of cell dm angled, not perpendicular to vein M_1; veins M_1 and M_2 clearly diverging at wing margin; veins M_2 and M_4 converging at wing margin; crossvein dm-m zigzagged, curved 90° from cell m4 and curved 90° again at base of M_2; junction of M_4 and crossvein dm-m at basal 1/3 of M_4; cell cua closed at wing margin; anal lobe broad, as wide as cell m4 at its widest point.

Abdomen in lateral view tapered to small apex; as wide as thorax in dorsal view, with vestiture of scattered hairs on posterior margin of tergites; genitalia not rotated, epandrium elongate-conical; gonocoxae not visible.

Female. Unknown.

Nemomyia lamasi **Evenhuis**, **sp**. **nov**.

(Figs. 16–17)

Diagnosis. Easily separated from the only other species in the genus (*N. burmitica*) by the white lateral margin of the mesonotum (black in *N. burmitica*), end of vein R_{2+3} at level well beyond origin of R_4 (this vein ending at origin of R_4 in *N. burmitica*), and veins M_1, M_2 and M_4 being relatively parallel to each other toward the wing margin (vein M_2 clearly angled toward M_4 in *N. burmitica*).

Material examined. Holotype ♀ (BPBMENT 0000081285) from Hukawng Valley, Burma. The type specimen is embedded in a cloudy orange cabochon measuring 31 × 25 × 5 mm. Syninclusions: a heteropteran husk, small spider, a psocid, and bits of dirt.

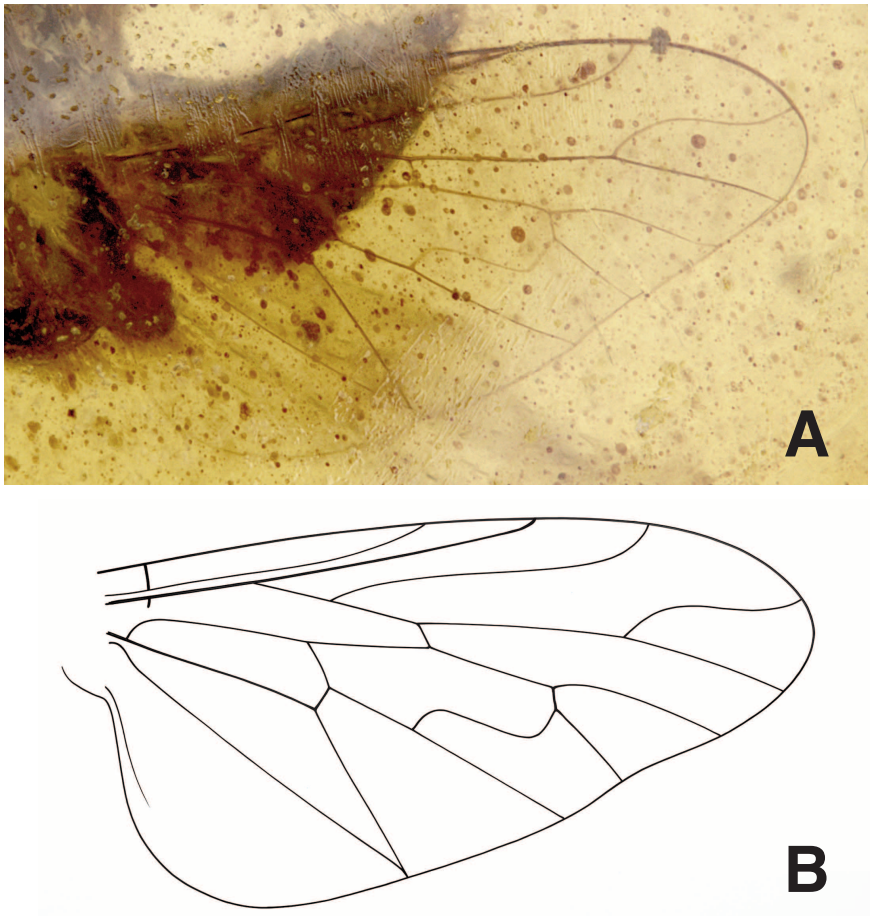


Figure 15. *Nemomyia burmitica* Evenhuis, sp. nov. **A**. Photo of wing. **B**. Illustration of wing.

Description. **Female** (Fig. 16A). Lengths: body: 5.0 mm; wing: 4.7 mm. Head (Fig. 16B) slightly wider than thorax in dorsal view, eyes dichoptic; frons width 3× width of ocellar tubercle; ocelli small; ocellar tubercle narrow, slightly raised above surface of vertex; face absent; occiput slightly convex, with single row of occipital hairs placed internally on occiput, not along edge; antennal sockets approximate; antenna (Fig. 16B) with scape cylindrical, about 2.5× width; pedicel cylindrical, ca. 1.5× width; flagellum with 2 articles; flagellomere long, thin, linear, length ca. 10× basal width; antennal article 2 tiny, length equal to width; with minute stylus apically; proboscis short, only labellum exposed beyond oral margin; palpus exposed, two segmented, apical segment 1/4 length of basal segment.

Thorax slender in dorsal view, in lateral view less convex than in *N. burmitica*, black dorsally with broad band of pale yellow laterally; scutum with fine scattered hairs, uniformly distributed, without longer hairs in prescutellar area or on scutellum; macrochaetae not evident; scutellum hemispherical; antepronotum well-developed; halter with stem and knob dark brown.

Legs long, thin, devoid of vestiture; tibial spur formula 0-2-0; basitarsus long, as long as combined length of remaining tarsomeres [hind tarsi cut off at surface of amber]; claws small (1/2 size of those in *N. burmitica*), pulvilli 3/4 length of claws; empodium setiform.

Wing (Fig. 17A,B) subhyaline with dark brown veins; costa circumambient, thickest just beyond end of R_4; Sc complete, ending in costa at level slightly beyond level of crossvein r-m; crossvein sc-r present; R_1 straight, ending in costa at level just beyond end of cell dm; R_{2+3} originating at midpoint of Rs between R_1 and crossvein r-m, slightly curved upward at wing margin, ending in costa well beyond level of origin of R_4; R_4 curved 45° after origin, slightly curved to wing margin; cell r5 parallel sided at wing margin; cell br longer than cell bm; crossvein r-m at basal 2/5 of cell dm; vein closing apex of cell dm angled, not perpendicular to vein M_1; veins M_1 and M_2 slightly diverging at wing margin; veins M_2 and M_4 parallel; crossvein dm-m zigzagged, curved 90° from m4 and curved 90° again at base of M_2; junction of M_4 and crossvein dm-m at basal 1/3 of M_4; cell cua closed at wing margin with short petiole; anal lobe broad, as wide as cell m4 at its widest point.

Abdomen in lateral view slightly tapered to apex; as wide as thorax in dorsal view, slightly compressed dorsoventrally, with stiff hairs on posterior margin of tergites; apex with dense patch of hairs (?sand chamber) but no acanthophorites discernible.

Male. Unknown.

Remarks. While the stark color variation of the lateral mesonotum could potentially be interpreted as a secondary sexual dimorphism (as seen in certain extant bombyliids exhibiting predominantly dark males and patterned dark and pale-colored females), the fundamental differences in wing venation (R_{2+3} length, crossvein r-m position, and medial vein trajectories) provide definitive evidence that *Nemomyia burmitica* and *N. lamasi* represent two distinct species.

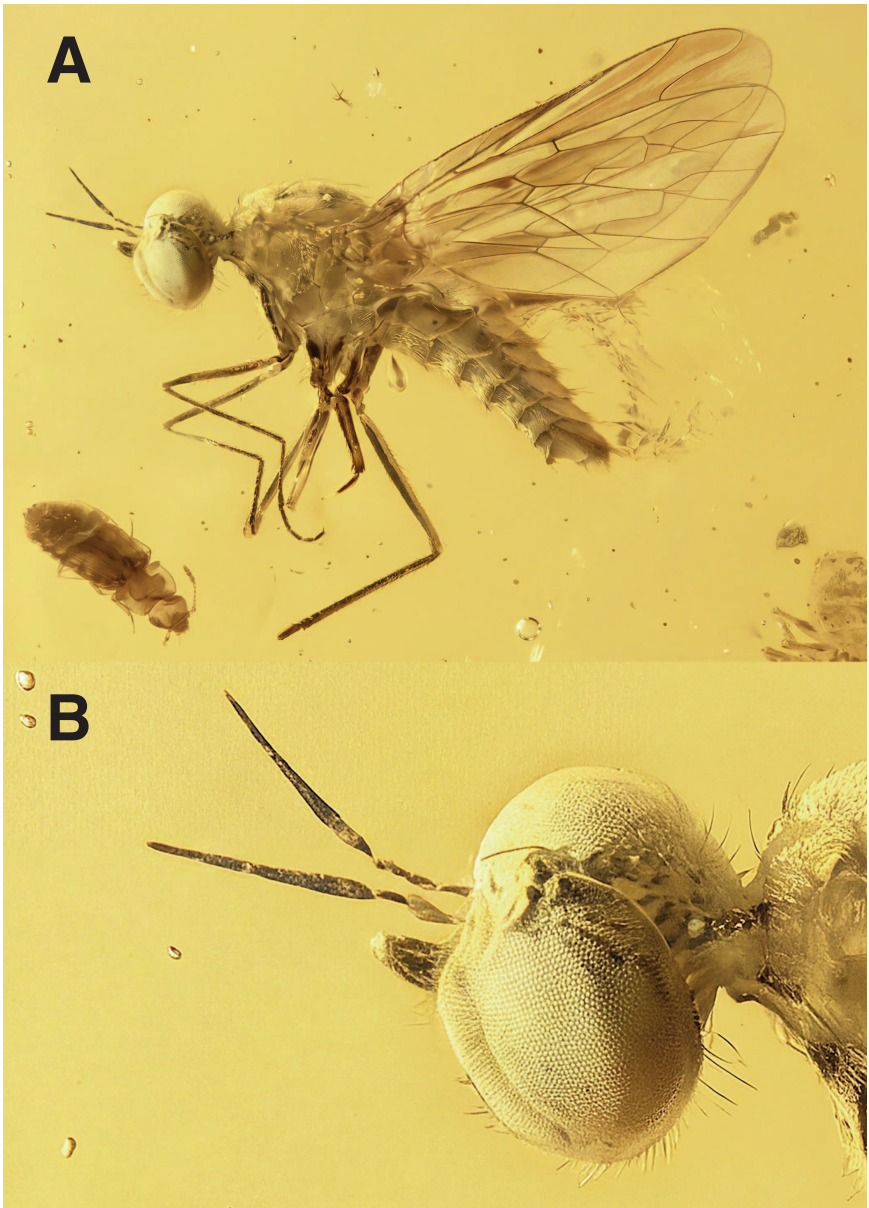


Figure 16. *Nemomyia lamasi* Evenhuis, sp. nov. **A**. Habitus of holotype. **B**. Head and antenna, dorsal view.



Figure 17. *Nemomyia lamasi* Evenhuis, sp. nov. **A**. Photo of wings. **B**. Illustration of left wing.

Etymology. The specific name honors my colleague, Dr. Carlos Lamas, for his contributions to Neotropical dipterology.

NOTES ON DESCRIBED SPECIES

Genus *Cretabombylia* Ye, Yao, Shih, Ren & Wang

Cretabombylia Ye, Yao, Shih, Ren & Wang, 2019: 8. Type species: *Cretabombylia spinifera* Ye, Yao, Shih, Ren & Wang, 2019, by original designation.

Diagnosis. Most similar to *Peculibombylia* Ye, Yao, Shih, Ren & Wang by the shared character states of crossvein r-m just before middle of cell dm and cell cua closed before the wing margin by a short petiole, but can be separated from it by the sinuous crossvein dm-m without a spur vein (sharply zigzagged and with a spur vein in *Peculibombylia*) and the junction of crossvein dm-m with vein M_4 is at the basal 2/5 of M_4 (this junction is at the basal 1/4 in *Peculibombylia*).

Included species: *Cretabombylia spinifera* Ye, Yao, Shih, Ren & Wang, 2019.

***Cretabombylia spinifera* Ye, Yao, Shih, Ren & Wang**

(Fig. 18)

Cretabombylia spinifera Ye, Yao, Shih, Ren & Wang, 2019: 8.

Material examined. 1♂ (BPBMENT 0000081293) from Hukawng Valley, Kachin State, northern Burma; 3♂, same data (BPBMENT 0000081294, 0000081309, 0000081310) in the same piece of amber; 1♀. same data (BPBMENT 0000081198)

Remarks. Five additional specimens of this species have been examined in this study (4♂, 1♀) and there appears to be some variation in a few characters, although all key out to *Cretabombylia* and match the salient characters of *C. spinifera*. Four specimens (BPBMENT 0000081293, 81294, 81309, and 81310) have what appears to be a longer proboscis than that of the type of *C. spinifera*. However, the proboscis is actually the same length as a proboscis when projecting anteroventrally (as happens when probing flowers). When at rest the proboscis lies within the oralgenal cup with only the labellum projecting in lateral view. A fifth specimen, a female (BPBMENT 0000081198) has only a single antennal article, otherwise fits the characters of *C. spinifera*. A short description of characters of the male that differ from the female are given below:

Male. Eyes holoptic, as wide as thorax; occiput slightly convex, appressed tightly to thorax so antepronotum and cervical sclerites not visible; postgena long pilose; antennae with single article; proboscis with labellum 1/2 length of proboscis, ellipsoid; thorax with prescutellar area and scutellum long pilose, fine hairs and a few tuberculate setae elsewhere dorsally; with three notopleural macrochaetae; no pre-alar macrochaetae; post-alar callus with short fine hairs; abdomen with genitalia not rotated; epandrium thin in lateral view, gonocoxa crescent-shaped with thin gonostylus.

The single female examined also has a single antennal article (Fig. 18A), but otherwise fits the characters of this species (there is some telescoping due to taphonomic maturation, but otherwise the antennal characters fit). The occiput looks concave from a dorsal view, but this is most likely due to partial collapse during taphonomic maturation. Examination of the apex of the abdomen does not show any acanthophorite spines. The original description by Ye *et al.* (2019) mentions these, but the image (their fig. 4G) shows instead

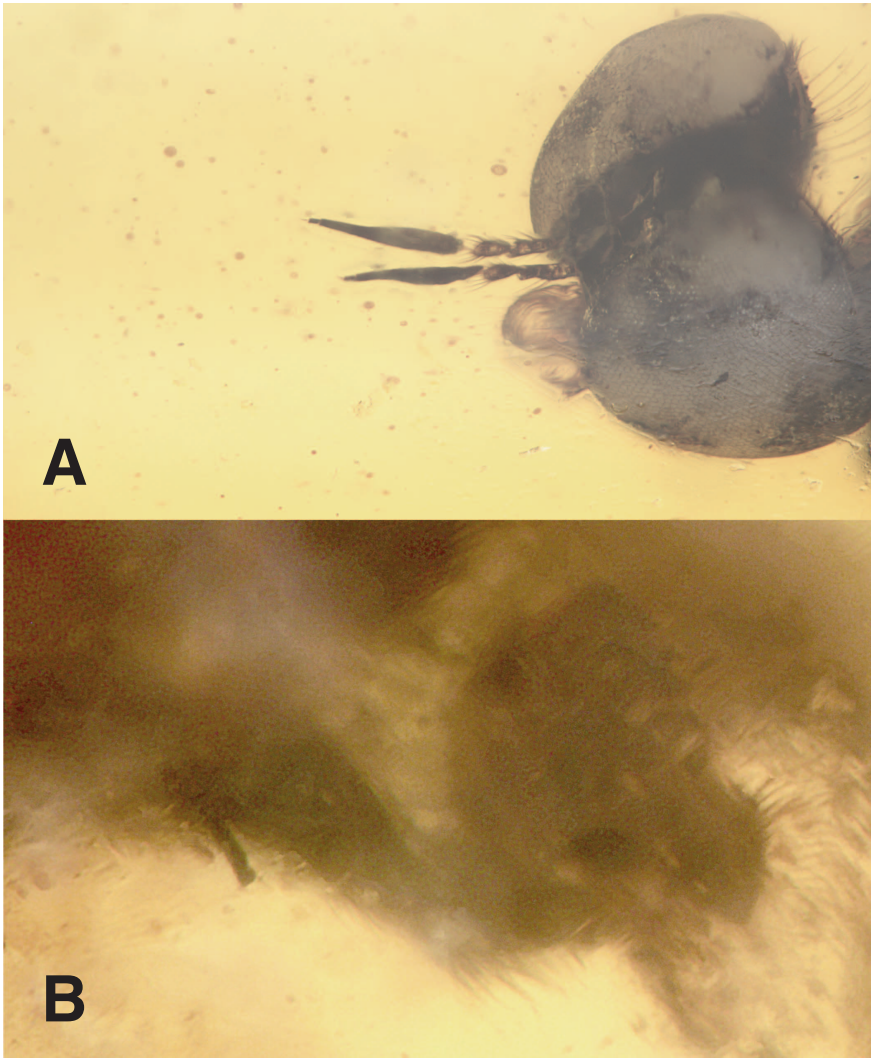


Figure 18. *Cretabombylia spinifera* Ye, Yao, Shih, Ren & Wang, 2019. **A**. Head and antenna. **B**. Terminal abdominal segments of female abdomen showing hairs at apex.

what I see as some short stiff hairs and not true acanthophorite spines. The specimen examined in this study has those same short stiff hairs and also a few long hairs on the apical segments (not many and certainly not dense) (Fig. 18B) but the latter is not what I would call a true “hair basket” (see below for further remarks on this terminology).

Pseudorhagio Zhang, Zhang & Wang

Pseudorhagio Zhang, Zhang & Wang, 2016: 3. Type species: *Pseudorhagio zhangi* Zhang, Zhang & Wang, 2016, by original designation.

Diagnosis. Closest to *Bumaso*, **gen**. **nov**. due to the shared character state of an open cell cua in the wing margin, but it can be separated from it by the longer antennal flagellomere 8–10× basal width (4× basal width in *Bumaso*), and the scutum without tuberculate hairs (tuberculate hairs anteriorly and laterally in *Bumaso*).

Included species. *Pseudorhagio zhangi* Zhang, Zhang & Wang, 2016.

Pseudorhagio zhangi Zhang, Zhang & Wang
(Figs. 19–20)

Pseudorhagio zhangi Zhang, Zhang & Wang, 2016: 3.

Material examined. 1♀ (BPBMENT 0000081300) from Hukawng Valley, Kachin State, northern Burma.

Remarks. One specimen (Fig. 19A) was identified in this study with wing venation (Fig. 20B,C) and antennae (Fig. 20A) that fits the characters of *Pseudorhagio zhangi* and is a female. It is unfortunately in a cloudy piece of amber with a considerable amount of debris making examination of many features difficult. There appears to be a dense accumulation of hairs at the apex of the abdomen (Fig. 19B), but it is difficult to ascertain for sure if this is a true sand chamber, and whether or not acanthophorite spines are present. Coincidentally, the posture of this specimen in the amber piece is very similar to the holotype (Zhang *et al.* 2016: fig. 1A) and has the same abdominal constriction at segments III–VI as shown in that figure.

New Taxonomic Status

Genus *Pioneeria* Grimaldi

Pioneeria Grimaldi, 2016: 67. Type species: *Pioneeria bombylia* Grimaldi, 2016, by original designation.

Similipioneeria Ye, Yao, Shih, Ren & Wang, 2019: 6. Type species: *Similipioneeria mirantenna* Ye, Yao, Shih, Ren & Wang, 2019, by original designation, **syn**. **nov**.

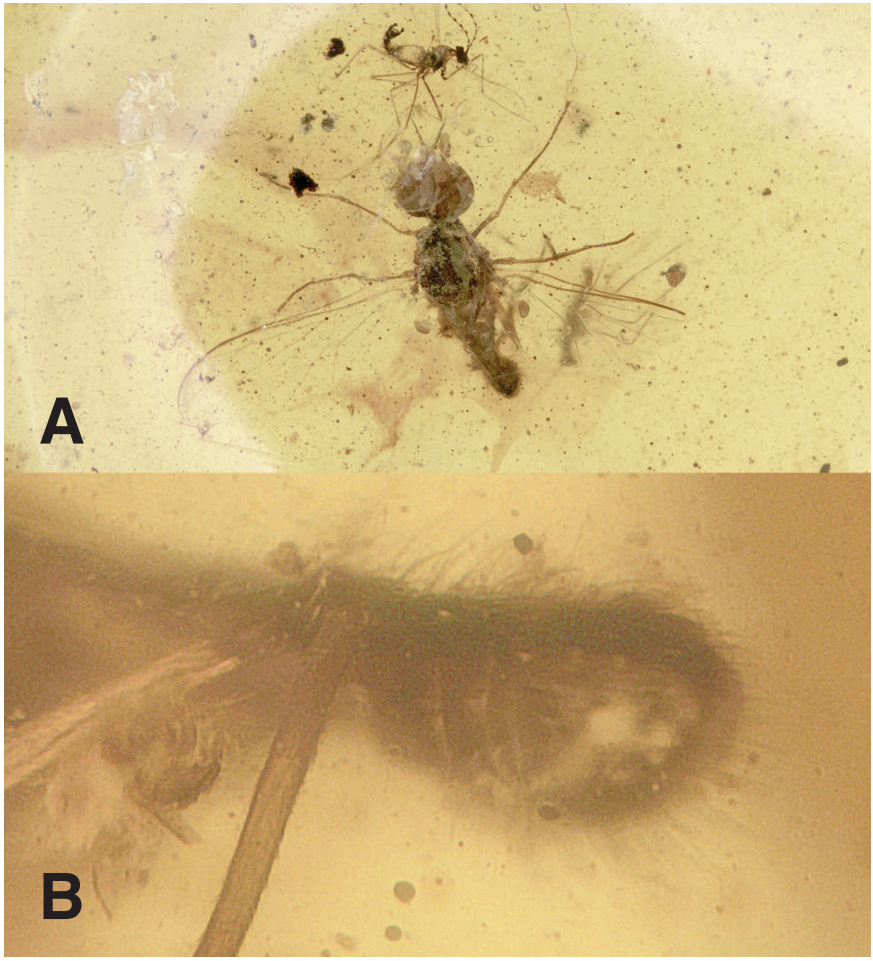


Figure 19. *Pseudorhagio zhangi* Zhang, Zhang & Wang. **A**. Habitus. **B**. Terminal abdominal segments of female abdomen showing hairs at apex.

Revised diagnosis. Head with antennal sockets approximate, separation subequal to or less than the width of the scape; scape cylindrical; pedicel subglobular to subcylindrical; flagellomere linear, tapering slightly to apex, length more than 4× basal width; flagellomere articles beyond article 1 varying in number (excluding the minute hyaline apical stylar segment) from one to three; proboscis exserted slightly beyond oral margin, with large labellae. Thorax with notopleural and supra-alar macrosetae present. Wing (Fig. 9E) with sc-r crossvein present; crossvein r-m at basal 1/3 of discal cell making cell br and cell bm

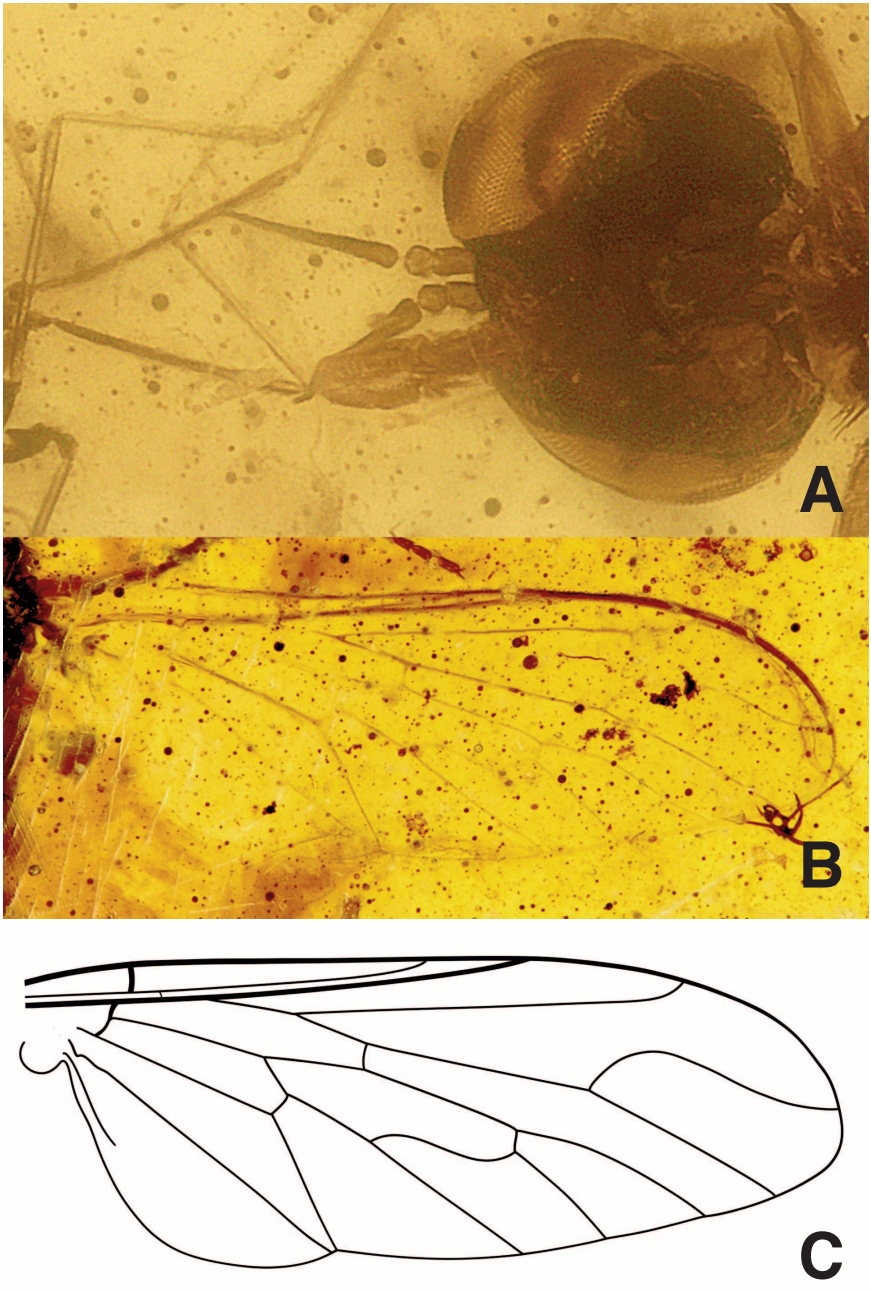


Figure 20. *Pseudorhagio zhangi* Zhang, Zhang & Wang. **A**. Head and antennae. **B**. Photo of wing. **C**. Illustration of wing.

subequal in length; R_{2+3} gently curving upward toward wing margin; R_4 slightly to moderately sinuous; veins R_5, M_1, M_2, and M_4 (M_3 of Ye *et al*. 2019) generally parallel to each other; crossvein dm-m (m-m of Ye *et al*. 2019) sinuous; junction of crossvein dm-m and M_4 at basal 1/5; cell cua closed at wing margin, without a distinct petiole.

Grimaldi (2016) reviewed the first true Cretaceous bombyliids, all from Burmese amber: *Nealimyia*, *Pioneeria*, and *Procrocidium*; with *Endymiomyia* proposed as a possible stem group bombyliid; and transferred *Pseudorhagio* Zhang, Zhang & Wang, 2016 from Tabanomorpha to Bombyliidae. A few years later, Ye *et al*. (2019) proposed three more new genera of bombyliids, also from Burmese amber: *Similipioneeria*, *Cretabombylia*, and *Peculibombylia*. *Pioneeria* has been previously separated from all other Cretaceous bombyliids by the pilose cervical area but, although thought to be an unusual phenomenon, this character state of cervical vestiture is not treated here as a character of phylogenetic significance as it is found to varying degrees in other taxa of Cretaceous bombyliids. Other more robust characters have been found in this study to distinguish *Pioneeria* from other Cretaceous bombyliids.

Nealimyia is easily separated from all other Cretaceous bombyliids by the placement of the crossvein r-m at the apical 4/5 of cell dm and the cell cua open in the wing margin (Fig. 9C). *Procrocidium* is separated from all other Cretaceous bombyliids by the antennal style inserted into a subapical sulcus of the antennal flagellomere.

The new genera proposed by Ye *et al*. (2019) are all very similar to each other and were separated primarily by the number of antennal stylar segments beyond the flagellomere. In examining specimens during this study, this character has been found to be highly plastic in Cretaceous fossil bombyliids. Although possibly being of species-level significance (a second specimen of *Cretabombylia spinifera* examined here differs in the number of antennal flagellar articles beyond the flagellomere), it is generally not of generic significance in many extant bombyliids and can vary from 1 to 4 segments in just the genus *Bombylius* (cf. Hall & Evenhuis 1980*)*. Given this interpretation of antennal article variability, I have compared the descriptions of *Similipioneeria* and *Pioneeria* and have concluded that, aside from the antennal flagellomere segmentation and cervical pilosity, the two have virtually the same character states used to define each genus (e.g., head characters and wing venation), and are in fact synonymous; I therefore here synonymize *Similipioneeria* under *Pioneeria*, **syn**. **nov**.

The character states that Grimaldi (2016) gave to separate *Pioneeria* from *Pseudorhagio* (degree of sinuosity of R_4; number of notopleural macrochaetae; posterior scutellar margin vestiture) are found here to be variable among species and not significant in separating Cretaceous bombyliids. More robust character states across Cretaceous bombyliids found in this study are in the wing venation. In *Pseudorhagio* and *Bumaso* Evenhuis, **gen**. **nov**. cell cua is narrowly open in the wing margin; in all species of *Pioneeria* it is closed at the wing margin. Also, the junction of crossvein dm-m with M_4 is at the basal 1/5 in *Pioneeria* whereas it is at the basal 2/5 (just before the middle) in *Pseudorhagio* and *Bumaso* Evenhuis, **gen**. **nov**.

Included species. *Pioneeria bombylia* Grimaldi, 2016; *Pioneeria mirantenna* (Ye, Yao, Shih, Ren & Wang, 2019), **comb**. **nov**.

NOTES ON CHARACTERS

Below I discuss the conditions of character states seen in some Cretaceous amber bombyliids and attempt to clarify what may be causing certain interpretations by previous authors. I also put into context how certain structures may have become deformed due to taphonomic processes of fossilized amber.

Flagellomere and segmentation

I follow Grimaldi (2016) in using his terminology for antennal segmentation. I agree with him that all segments after the pedicel are the "flagellum", but as to what is an actual segment of the flagellum or of the style is indeterminable in many of the fossils examined here, so "flagellomere article" is used for those segments apical to pedicel and before the apical or subapical style (with the segment directly after the pedicel termed "flagellomere" or "article 1"). Although sometimes considerable weight has been put on the number of these antennal articles in genera by previous workers of Cretaceous Bombyliidae, my experience with extant Bombyliidae shows this character to be extremely variable among taxa (the genus *Bombylius*, in which species can possess anywhere from 1 to 4 antennal articles before the minute apical style). Given this significant intra-generic variability, I do not consider the absolute count of antennal articles to be a stable generic indicator in these ancient lineages. Instead, taxonomic limits should be defined by more robust character suites, such as wing venation and head architecture.

This plastic interpretation directly informs the synonymy of *Similipioneeria* under *Pioneeria* proposed herein. Aside from minor antennal article counts and cervical pilosity (the latter of which can vary considerably due to taphonomic wear), *Similipioneeria* shares a structural character suite that is used to define *Pioneeria*—most notably the placement of the crossvein r-m at the basal 1/3 of the discal cell and the placement of crossvein dm-m at the extreme basal 1/5 of M_4. Splitting genera on highly plastic antennal segment numbers while ignoring identical wing venation suites obscures more clear generic relationships.

Flagellomere (article 1) shape

Ye *et al.* (2019) used the shape of the base of the flagellomere (article 1) having a petiole as a unique character in Bombyliidae, and described the genus *Cretabombylia* saying its possession of this as a unique defining character. In reality, this is a normal shape of a flagellomere in many Diptera where the flagellomere inserts into an apical socket of the pedicel. See e.g., McAlpine (2011: 122, figs. 19, 21; for the apical socket of the pedicel and 2011: 126, figs. 27, 28 for a typical flagellomere shape with a basal petiole that inserts into the pedicel socket). Under normal preservation, these antennal segments are tightly appressed to each other, concealing the basal petiole. Where the petiole is clearly exposed in these fossils, I hypothesize that it is not an autapomorphic structural novelty, but rather a taphonomic artifact resulting from post-mortem telescoping and matrix shearing during the resin's thermal maturation phase (see also below under *Taphonomic Processes of Morphological Features*).

Proboscis

In Cretaceous amber bombyliids examined here, the proboscis is a small tubular structure with a stiff labrum, stiff labium, and large, fleshy labellae. The apparent length of the proboscis can vary in some bombyliids by virtue of extending the labium and hypopharynx from inside the oralgenal cup. Note that the proboscis in many Cretaceous genera is held within a large oralgenal cup at rest, exposing only the labellum. However, when the proboscis is extended downward for feeding, its full length becomes visible and it may appear "long", when in fact it is structurally identical to a resting proboscis tucked into the oralgenal cavity.

Where no mechanical extension or taphonomic stretching is evident, proboscis length remains a highly reliable character to separate taxa. Crucially, true structural proboscis length can be verified when it correlates with independent, non-oral morphological characters. For example, while it might be argued that the long proboscis defining *Bumaso,* **gen**. **nov**. is merely a taphonomically stretched *Pseudorhagio*, the validity of *Bumaso* as a separate genus is corroborated by a comparatively shorter flagellomere (4× basal width vs. 8–10× in *Pseudorhagio*) and the presence of unique tuberculate scutal hairs that are entirely absent in the latter genus.

Thoracic vestiture

Macrochaetae

Previous descriptions of new taxa of Cretaceous amber bombyliids have heavily weighted the number and placement of notopleural and supra-alar macrochaetae (thickened bristles originating from sockets with a narrow, raised rim found on the lateral portions of the mesothorax). This does not seem to be a useful generic character since many of the specimens examined either retain these macrochaetae (an unusual state of preservation) or, far more commonly, have had them sheared off, leaving only the empty structural sockets. Extant bombyliids are easily denuded of setae and macrochaetae when handled roughly; similarly, Cretaceous bombyliids trapped in sticky resin would be highly susceptible to losing these macrochaetae due to initial struggles or subsequent matrix movement during diagenesis.

Tuberculate setae

A few taxa of Cretaceous amber bombyliids are shown to have fine thoracic setae arising from minute tubercles (i.e., *Bumaso fusca*). These are not seen in many extant bombyliids. Some species of the extant genus *Thevenetimyia* Bigot have such thoracic tubercles, but not as origins of vestiture, and are not related to the amber bombyliids researched in this study.

Pterostigma

In actuality, a true pterostigma is an area along the costal border of the wing that has undergone sclerotization and darkening. The area often termed "pterostigma" in Cretaceous amber bombyliids is instead only infuscation consisting of darkened pigmentation of a small area where a true pterostigma occurs in other orders of insects. This may be an artefact of preservation in resin as its presence is not consistent among multiple specimens of the same species, and even between the left and right wings of a single individual.

Pulvilli

The pretarsus in all extant Bombyliidae has pulvilli. It is however not present in some taxa of the related families Mythicomyiidae and Hilarimorphidae; as well as in some Asilidae. It is therefore plausible that pulvilli were independently lost in the genus *Burmobomba*. Because pulvilli can be extremely minute in basal bombyliid lineages (see Yeates 1994), there is an inherent risk that current optical limitations or resin refraction might obscure micro-vestiges. While I treat them here as absent based on close examination, future advanced imaging will be required to definitively confirm whether micro-vestiges of the pulvilli are present in these fossils.

Male genitalic rotation

I have documented any male genitalic rotation observed in the specimens examined in this study to aid future comparative work. However, as Yeates (1994) demonstrated, genitalic rotation has evolved independently multiple times across Asiloidea and particularly within the Bombyliidae. In addition, determining whether such rotation in fossils was facultative (occurring only during copulation) or obligate (rotating permanently immediately following eclosion) remains impossible. Furthermore, taphonomic twisting of the abdominal apex during plastic resin flow can also easily mimic true biological rotation, necessitating a highly conservative taxonomic approach to this character.

Sand chamber [***"hair basket" of Grimaldi*** (***2016***)]

Grimaldi (2016) conservatively introduced the descriptive term "hair basket" to define accumulations of specialized hairs at the apex of the female abdomen in certain fossil taxa. I adopt this terminology here for ambiguous cases where a true, highly organized sand chamber cannot be definitively demonstrated. The presence of unspecialized apical abdominal hairs is common and phylogenetically uninformative across Asiloidea. However, dense mats of hairs originating specifically from tergite 8 and sternite 8 (see Yeates 1994: 122, fig. 437) in the presence of true acanthophorite spines are of significant phylogenetic interest, signaling a specialized hovering oviposition behavior. These true sand chambers (the *Sandkammer* of Schremmer 1964) are present in modern Bombyliinae, Cythereinae, Lomatiinae, and Anthracinae.

Acanthophorite spines

These spines originate off of modifications of tergite 10 (or a fusion of tergite 9+10) in the female genitalia, which in some asiloids has divided into paired lateral sclerites called acanthophorites. Yeates (1994) discussed these spines in connection with their presence or absence in asiloids and their putative phylogenetic significance. Their function is related directly to ovipositional behavior, where those taxa having a sand chamber use the spines to gather sand into a sand chamber (surrounded by a dense mat of hairs or tergites and sternites) for coating eggs during oviposition to prevent their desiccation. Other extant taxa retain the spines but lack dense hair mats or a true sand chamber; in these cases, the spines are used to excavate small pits in the substrate for egg deposition (e.g., certain *Aphoebantus* spp., pers. observ.).

Several taxa examined in this study, which were described by previous authors as bearing "acanthophorite spines", lack an associated "hair basket". Closer inspection suggests these structures may not represent true heavily sclerotized spines, but rather unthickened, stiff apical hairs. They may represent a plesiomorphic, transitional state that predated the evolution of robust digging or sand-gathering spines. Modern taxa that oviposit eggs directly onto substrates without excavation (e.g., *Cyx* Evenhuis, *Systropus* Wiedemann, *Geron* Meigen, and *Toxophora* Meigen, pers. observ.) lack these spines entirely. Current phylogenetic frameworks indicate that the absence of these spines is plesiomorphic (as seen in basal clades like Oligodraninae, Usiinae, and Toxophorinae), whereas true acanthophorite spines represent a more derived apomorphy.

Taphonomic processes impacting morphological features

Several specimens of Cretaceous amber bee flies described in previous literature, as well as multiple individuals evaluated in this study, exhibit pronounced post-mortem deformation, compression, and elongation. These distortions are concentrated in the head capsule, antennal segments, and proboscis. It is critical to recognize that these distorted structures are not autapomorphic or synapomorphic novelties, but are instead entirely taphonomic and diagenetic artefacts.

The morphological deformities observed here—marked by a severe dorsoventral or lateral deflation of the head capsule (e.g., see Aiba *et al.* 2026, fig. 2B for an example of likely head deformation), the unnatural exposure and telescoping of internal antennal petioles, and the excessive stretching of the proboscis—reflect exoskeletal resistance to decay

and subsequent geological compaction (Martínez-Delclòs *et al.* 2004). Unlike the heavily sclerotized thoracic box, which protects flight musculature and resists environmental pressures, the significantly thinner head capsule and its slender appendages are uniquely susceptible to post-mortem mechanical forces.

Following initial entrapment in the mid-Cretaceous resin, the rapid autolysis and microbial decomposition of internal cephalic tissues (the brain, optic lobes, and large muscle masses) would rapidly transform the head capsule into an unsupported, hollow chitinous shell. Similarly, the delicate membranous rings connecting the antennal flagellomeres and the internal connective tissues of the mouthparts would decay completely long before the surrounding resin achieved full polymerization.

As the Kachin amber matrix underwent long-term polymerization and subsequent thermal maturation, it was subjected to intense geological pressure and slow, directional plastic flow. Deprived of internal structural support, the hollow head capsules could collapse under this pressure. Simultaneously, the viscous, fluid-like movement of the shifting resin would drag the loosened, unanchored antennal segments outward along the plane of resin flow, producing a "telescoped" or elongated appearance (see particularly Fig. 21, which also has a collapsed head capsule) and an artificial extension of the proboscis. The pristine structural integrity maintained by the heavily reinforced thoracic sclerites across these same specimens helps support this taphonomic interpretation. Consequently, striking modifications of the head shape, occiput, and antennae in these fossils must be evaluated with extreme caution and are treated here as products of post-mortem plastic deformation rather than true evolutionary transformations.

CHECKLIST OF CRETACEOUS BOMBYLIIDAE

Subfamily Endymiomyiinae, **subfam**. **nov**.

Genus ***Endymiomyia*** Grimaldi, 2016

Endymiomyia quadra Grimaldi, 2016

Genus ***Burmobomba*** Evenhuis, **gen**. **nov**.

Burmobomba proboscidea Evenhuis, **sp**. **nov**.

Burmobomba syrinx Evenhuis, **sp**. **nov**.

Genus ***Futababombylia*** Aiba, Inose & Watanabe, 2026

Futababombylia kishini Aiba, Inose & Watanabe, 2026



Figure 21. *Burmobomba proboscidea* Evenhuis, sp. nov. Paratype female (BPBMENT 0000081194), showing collapse of head and telescoping of antennal segments due to taphonomic processes. Numbers refer to flagellomere articles.

?Subfamily Cythereinae

Genus ***Paleocytherea*** Ngô-Muller & Nel, 2020

Paleocytherea pouilloni Ngô-Muller & Nel, 2020

Genus ***Nidergasia*** Jouault & Nel, 2020

Nidergasia neraudeaui Jouault & Nel, 2020

Subfamily nr. **Crocidiinae**

Genus ***Procrocidium*** Grimaldi, 2016

Procrocidium minutum Grimaldi, 2016

Subfamily *Incertae Sedis*

Genus ***Bumaso*** Evenhuis, **gen**. **nov**.

Bumaso fusca Evenhuis, **sp**. **nov**.

Genus ***Cretabombylia*** Ye, Yao, Shih, Ren & Wang, 2019

Cretabombylia spinifera Ye, Yao, Shih, Ren & Wang, 2019

Genus ***Electrobombylia*** Evenhuis, **gen**. **nov**.

Electrobombylia medialis Evenhuis, **sp**. **nov**.

Genus ***Fremo*** Evenhuis, **gen**. **nov**.

Fremo compressus Evenhuis, **sp**. **nov**.

Genus ***Nealimyia*** Grimaldi, 2016

Nealimyia evenhuisi Grimaldi, 2016

Genus ***Nemomyia*** Evenhuis, **gen**. **nov**.

Nemomyia burmitica Evenhuis, **sp**. **nov**.

Nemomyia lamasi Evenhuis, **sp**. **nov**.

Genus ***Peculibombylia*** Ye, Yao, Shih, Ren & Wang, 2019

Peculibombylia relictivena Ye, Yao, Shih, Ren & Wang, 2019

Genus ***Pioneeria*** Grimaldi, 2016

Similipioneeria Ye, Yao, Shih, Ren & Wang, 2019, **syn**. **nov**.

Pioneeria bombylia Grimaldi, 2016

Pioneeria mirantenna (Ye, Yao, Shih, Ren & Wang, 2019), **comb**. **nov**.

Genus ***Pseudorhagio*** Zhang, Zhang & Wang, 2016

Pseudorhagio zhangi Zhang, Zhang & Wang, 2016

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USE OF AI

Gemini AI® was used to check the manuscript for inconsistencies of usage and typographical errors. No generative AI was used in the production of this paper or images.

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