Diverse Orthorrhaphan Flies (Insecta: Diptera: Brachycera) in Amber from the Cretaceous of Myanmar

Brachycera in Cretaceous Amber, Part VII

David A. Grimaldi

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BRACHYCERA IN CRETACEOUS AMBER, PART VII

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ABSTRACT

A remarkable diversity of new nonempidoid orthorrhaphan flies from the mid-Cretaceous of Myanmar (Late Albian–Early Cenomanian, ca. 99 Ma) is presented, including 28 species (all but one new) in 22 genera (13 new), and at least 12 families. Two families are new; three genera are unplaced in Tabanomorpha and one unplaced within Brachycera. Comparisons are presented between the amber taxa and extensive lithified taxa from the Jurassic and Cretaceous of eastern Laurasia.

In **Stratiomyomorpha:** A new species of Zhangsolvidae has color patterns and body shape that apparently mimic Vespidae or other stinging aculeate wasps. Diverse new Xylomyidae and Stratiomyidae are described, the latter with male terminalia preserved in detail. In **Tabanomorpha:** The genus *Athericites* Mostovski et al. is synonymized with *Palaepangonius* Ren, and a new species of *Galloatherix* Nel is described in which the female proboscis is much longer than that of the male. All three genera were attributed to Athericidae, but the amber species reveal they are more basal tabanomorphs. Described are a new genus of stem-group Tabanoidea and a new species of *Cratotabanus* Martins-Neto and Kucero-Santos (Tabanidae), previously known from the Cretaceous of Brazil and New Jersey. In **Nemestrinoidea:** Three species of *Hirmoneura* Meigen are the first Nemestrinidae known from amber; one species has long cerci typical of Recent species of the genus. A new species of the Mesozoic family Rhagionemestriidae reveals this family is closely related to Acroceridae, not Xylophagidae as previously proposed. In **Archisargoidea:** A new species of Tethepomyiidae is described, the family known only in Cretaceous amber from New Jersey, Spain, and Myanmar. In **Asiloidea:** Three new species and genera of Bombyliidae are described, two of them with abdominal setal "baskets" distinctive to females of higher bombyliids. A fourth new asiloid genus is a probable stem-group bombyliid. The recently described *Pseudorhagio* Zhang et al., is transferred from Tabanomorpha to Bombyliidae. The male of a new species of *Burmapsilocephala* Gaimari and Mostovski (Apsilocephalidae) has terminalia very similar to that of *Evocoa* (Evocoidae: Recent, Chile), corroborating close relationship of the two families. In **Families incertae sedis:** A new species of *Hilarimorphites* Grimaldi and Cumming (Apystomyiidae) is described, the family known only in New Jersey and Burmese amber and the Recent fauna of California, and a sister group to either Cyclorrhapha or Eremoneura. Mysteromyiidae and Eucaudomyiidae, new families, are described, based on highly modified species with vestigial mouthparts, reduced venation, and unique specializations.

Discussion is presented on some morphological features in fossil and Recent Brachycera that have apparent phylogenetic significance but are rarely discussed. This study adds further data to the phenotypic diversity, geological history, and biogeography of a major radiation.

INTRODUCTION

This paper is a contribution to my series on the brachyceran flies preserved in amber from the Cretaceous Period, 145–66 Ma. The initial, and largest, study in the series reported 49 species in 37 genera and 13 families of orthorrhaphans (including Empidoidea) and basal Cyclorrhapha (Grimaldi and Cumming, 1999). That study was based on fly inclusions in ambers from the Campanian of western Canada (Carpenter et al., 1937; McAlpine and Martin, 1969; Pike, 1995; McKellar and Wolfe, 2010), Turonian of New Jersey (Grimaldi et al., 2000), and the Early Cretaceous (probably Valanginian to Barremian) of Lebanon (Schlee and Dietrich, 1970; Azar, 2000; Azar et al., 2010). Following that paper (Grimaldi and Cumming, 1999) was the discovery of highly fossiliferous amber from the Albian of Spain (Alonso et al., 2000; Delclòs et al., 2007; Peñalver and Delclòs, 2010), and, subsequently, additional interesting fossil Brachycera. But also around this time, in the late 1990s, mining of prolific amber deposits from northern Myanmar had resumed, yielding a great diversity of Brachycera (Grimaldi et al., 2002), subject of the present article. Prior to 2000, the only collec-

tion of Burmese amber fossils was a small, historical collection at the Natural History Museum, London, compiled in the early 20th century and largely studied by T.D.A. Cockerell (Zherikhin and Ross, 2000). The second contribution in the series (Grimaldi and Arillo, 2008) erected the family Tethepomyiidae, a group of small, reduced, very distinctive brachycerans then known in New Jersey and Spanish amber. Another family of small and enigmatic Brachycera, the Chimeromyiidae, was soon described (Grimaldi et al., 2009: part 3), occurring in Lebanese, Spanish, and Burmese ambers (Grimaldi et al., 2009). Part 4 in the series presented 13 additional species in nine families, in amber from Canada, Lebanon, Myanmar, New Jersey, and Spain (Grimaldi et al., 2011).

Since 2010 the commercial excavation of Burmese amber has exploded, yielding an unprecedented quantity and diversity of arthropods. For the Brachycera these have included thus far a new Asilidae, now known from a series of males and females (Dikow and Grimaldi, 2014: part 5), and Zhangsolvidae (also in Spanish amber), a family previously known only as lithified remains from the Early Cretaceous of China and Brazil (Arillo et al., 2015: part 6). Zhangsolvidae are particularly interesting because their long proboscis was used for feeding on nectar and pollen, and at least some of them had remarkable, whip-like antennae (Peñalver et al., 2015). The most recent discoveries are a new genus of the Eremochaetidae (Zhang et al., 2016), a rather diverse extinct family otherwise known only as compression fossils from the Jurassic to Early Cretaceous of Asia and Central Asia. An eremochaetid in amber has allowed narrowing the relationships of this interesting, probably parasitoidal family (Grimaldi and Barden, 2016 [part 8]). The present article, Part 7 , presents 28 additional species of nonempidoid orthorrhaphans in Burmese amber, belonging to at least 12 families (four genera are incertae sedis). Noteworthy is a striking new species of zhangsolvid; diverse xylomyids, stratiomyids, and bombyliids; stem-group tabanomorphs and tabanoids; the first Nemestrinidae preserved in amber; two new families of bizarre, highly modified brachycerans; and the first rhagionemestriid in amber, which clearly reveals relationships of this Mesozoic family to Acroceridae. Future articles will deal with Empidoidea and basal Cyclorrhapha.

The enormous paleodiversity in Burmese amber is no doubt largely a sampling phenomenon, a result of large-scale excavations of very rich and concentrated deposits. Although I have no modern records, according to historical records of the Geological Survey of India, between 1898 and 1940 some 83 tons of Burmese amber were mined (Chhibber, 1934). Interestingly, the amber, historically and presently, derives from a small, localized Cretaceous basin in Kachin, northern Myanmar, surrounded by extensive Quaternary sediments of the Hukawng Valley (Grimaldi and Ross, 2016). Much larger Cretaceous outcrops occur to the west but they have not been found as of yet to yield amber.

Like any Konzentrat Lagerstätte, appropriate conditions are required for production and burial of fossils. In the case of amber, the forest trees must have produced copious amounts of resin. Based on the abundant inclusions of certain leafy shoots in Burmese amber (Grimaldi and Ross, 2016), this amber was formed by a conifer, and possibly by *Metasequoia* (Taxodiaceae) or a close relative. Although modern *Metasequoia* secretes modest amounts of resin, tropical and warm temperate climates are ideal for resin production (Langenheim, 2003), and Burmese amber was formed at a low paleolatitude under wet tropical conditions (Grimaldi and Ross, 2016). Tropical conditions also contributed to the remarkable diversity of life in Burmese amber, from fungi (including mushrooms), liverworts, slime molds, ferns, various conifers, diverse angiosperm flowers and leaves, nematodes, onychophorans, snails, small lizards and frogs, feathers and even the bony remains of avialean theropods—as well as 259 families in 39 orders of arachnids, myriapods, and hexapods as of 2016 (Grimaldi and Ross, 2016), not including the Diptera reported herein. Natural catastro-

phes—hurricanes, cyclones, extreme monsoons, mudslides, forest fires, tsunamis—cause massive, widespread damage to forests that induce excessive bleeding in modern forests. Paleoforests presumably suffered the same.

Burmese amber is rounded and apparently tumbled by abrasive sediments, its surface extensively bored by pholadid bivalves (shipworms). These features indicate that the amber was redeposited into a marine environment, where it probably settled and concentrated in a shallow, near-shore basin (Grimaldi and Ross, 2016), a Cretaceous and more localized analog of the enormous deposits of Eocene Baltic amber. Thus, one of the most spectacular of the world's terrestrial Lagerstätte is a remarkable coincidence of resinous forest, catastrophe, and concentrated burial.

There have been several goals for my series on Brachycera in Cretaceous amber. First is a morphologically detailed, descriptive account of the past diversity of the group. Just as nonavian dinosaurs could hardly be predicted from a study of modern birds and crocodilians alone, there have been unexpected surprises in these Diptera: Chimeromyiidae, Eucaudomyiidae, n. fam., Mysteromyiidae, n. fam., Tethepomyiidae, Zhangsolvidae with whiplike antennae, Eremochaetidae with enormous pretarsal pads, etc. Second, and the reason for focusing on amber, is that microscopic preservation in amber allows far more informative phylogenetic inference than is generally possible with lithified insects. This was the inspiration for Willi Hennig's work on Diptera in Baltic amber (e.g., Hennig, 1965, 1967a, 1967b). Unfortunately, it was not until late in his career that Lebanese amber inclusions were collected and available for his study (Hennig, 1971, 1972; Schmidt, 2013; Dieter Schlee, personal commun. to D.A.G., 1993). I often wonder how excited Hennig would have been with the extraordinary diversity of Burmese amber flies now being uncovered. The Eremochaetidae and Rhagionemestriidae illustrate, as a few examples, how preservational fidelity reveals relationships of ambiguous, extinct taxa otherwise known only as compressions.

A third goal is to provide data for much more refined estimates and models of divergence times in Brachycera. Molecular models require calibration points by fossils, but the abundance of fossil representatives and the accuracy of their placement profoundly affects modeled estimates, as well as providing direct tests for these models. Since many Cretaceous fossil insects are stem groups to Recent taxa, the models will also require total-evidence analyses (e.g., Vea and Grimaldi, 2016), rather than a posteriori placement of fossils onto a cladogram of living taxa. Hennig believed that the geological age of a taxon should reflect its taxonomic rank (a concept with which I disagree), but it is probably universally acknowledged that divergence times are interesting for timing radiations and diversification rates, and correlating these to major geological and biotic events. Was a particular group, for example, in existence when Gondwana drifted apart, or during the Paleocene-Eocene Thermal Maximum?

Eventually, phylogenetic analyses will be made on many of the fossil Brachycera in amber, from the Cretaceous as well as Cenozoic. The analyses are in progress and already involve hundreds of morphological characters and hundreds of fossil and living species. In the meantime, I have included some discussion here on the distribution and structure of various characters that appear to have phylogenetic significance, but which have been hardly or little recognized. Such structures include transverse sulci on the abdominal tergites, metacoxal pegs, antepronotum size, thoracic macrosetae and pleura, and the small sc-r crossvein and various other venational characters. I hope to include descriptive work on Empidoidea and Cyclorrhapha in Burmese amber before the final phylogenetic analysis.

MATERIALS AND METHODS

All of the specimens reported here are in Burmese amber from the Hukawng Valley of Kachin State, northern Myanmar. The outcrops are very localized, originating from a relatively tiny area

of Cretaceous exposure at 26°15′N, 96°34′E, entirely surrounded by extensive Quaternary and Neogene exposure. The first observations of Burmese amber by Western geologists were published in the mid-19th century; Chhibber (1934) provided the most comprehensive account. Zherikhin and Ross (2000) and Ross et al. (2010) summarized history of the use of Burmese amber; Cruickshank and Ko (2003) is a modern source on the geology of Burmese amber; the latest comprehensive review is in Grimaldi and Ross (2016). The age of Burmese amber has been constrained to Late Albian–Early Cenomanian based on biostratigraphic and radioistope data. Grimaldi et al. (2002) estimated a more specific time period of Cenomanian to Turonian, based on the stratigraphic distributions of various Cretaceous insect families. Cruickshank and Ko (2003) reported an age of Late Albian (105–100 Ma) based on a *Mortoniceras* ammonite from the outcrops; this age corresponds closely to the Early Cenomanian age (99 Ma) determined by Shi et al. (2012), based on U-Pb radiometric dating of zircons in the amber sediments.

Burmese amber specimens studied here and elsewhere by the author derived either from loans or through acquisition by or donation to the AMNH. All amber was ultimately acquired commercially. Prefix initials on the specimen numbers, cited in the descriptions, indicate the proximate sources:

AMNH Bu American Museum of Natural History, Division of Invertebrate Zoology (AMNH Bu-SD, acquired from Scott Davies, American Thai, Co., Bangkok; AMNH Bu-SE, acquired from Sieghard Ellenberger, Crystal-Treasures Inc., Kassel, Germany)

JZC Bu collection of Mr. James Zigras, housed indefinitely in the Division of Invertebrate Zoology, AMNH

Authenticity of the amber is certain, based on reliability of the commercial sources and years of experience by the author with thousands of raw and prepared Burmese and other amber samples (e.g., Grimaldi et al., 2002), as well as with forgeries (Grimaldi et al., 1994). Chemistry alone can be misleading with the identification of certain amber forgeries; visual inspection is necessary (Grimaldi et al., 1994). Visual and physical features include the color, preservation of inclusions, syninclusions (debris, particles, bubbles, plant trichomes, other arthropods, etc.), UV fluorescence, hardness (e.g., when trimming and polishing), and the taxa of arthropod inclusions themselves (modern and Cenozoic taxa are easily recognizable). Indeed, among the tens of thousands of pieces of Burmese amber examined by the author none were fakes.

Preparation is the key to proper observation and photography. In all cases, pieces were received as rounded cabochens, on which flat surfaces were trimmed over (parallel to) the lateral, dorsal, frontal, and ventral surfaces of the fly body, and to the wing if possible. Trimming was done with a small, 1 mm thick diamond-edged, water-fed trim saw. Flat surfaces were carefully ground on a wet lapidary wheel using a series of Buehler wet abrasive disks: 400, 600, 800, 1200, 2400 grit, and finally alumina micropolish (Nascimbene and Silverstein, 2000). All of the pieces worked here had good integrity and were without serious fractures, so none had to be embedded in synthetic resin first. However, all will eventually be embedded in a very transparent, highly stable resin, EpoTek 301-2, to seal them against mechanical damage and environmental deterioration (Bisulca et al., 2012), the way all the AMNH amber type specimens have been conserved.

For study, a prepared sample was applied to a glass microscope slide using a small piece of dental wax and then positioned to optimize critical views. A drop of glycerine or distilled water was applied to the surface and then a glass coverslip to obscure fine scratches and minor surface imperfections. A Nikon SMZ1500 stereoscope (7.5–112×) with transmitted light base, DSRi1 digital camera, and NIS Elements software were used for photomicrography (including Z-stacking) and measurements. Gooseneck white-bal-

anced LED lighting (transmitted and reflected) used Schott KL1600, and PLC300 MikroVision units. While every effort was used to optimize preparation and lighting—essential for photomicrography—rarely does an amber piece or inclusion not have impurities, reflective fractures, dark absorbent surfaces, or something else that compromises imaging, in which case illustrations are necessary. Illustrations were made particularly of structures that are smaller, more complex, and/or critical for interpretation, such as wing venation, antenna and mouthpart structure, and terminalia. In most cases I have illustrated specimens as they are preserved; in those cases where specimens were reconstructed this is indicated. For minute structures it was often necessary to use a Leitz Wetzlar stereoscope (144×). Initial sketches for the drawings were made with a drawing apparatus for the Leitz scope (for small specimens), or a drawing tube on a Wild M1 stereomicroscope (for larger specimens). Drawing-tube sketches were made by outlining major structures and wing veins, to ensure accurate proportions, then rendering details by eye while constantly adjusting focus.

Imaging was attempted on some fly specimens in this study, and various other Burmese amber inclusions, using a General Electric Phoenix V|tome|X-S nanotube high-resolution CT scanner in the AMNH Microscopy and Imaging Facility. Unfortunately, insect inclusions in Burmese amber do not scan well, even when varying the X-ray kV, targets (tungsten or diamond), resolution, mS of slice exposures, and other parameters. In fact, CT scan quality varies greatly by the type/source deposit of amber (Dominican amber, for example, scans very well), suggesting intrinsic properties of Burmese amber are involved. In fortuitous cases good CT scans of insects in Burmese amber have been obtained (e.g., Barden and Grimaldi, 2012: figs. 2, 3; Arillo et al., 2015: fig. 11), but these are inclusions that have undergone some pyritization, which offers superior contrast to X rays.

In general, I have used the morphological terminology established in the *Manual of Nearctic Diptera* (McAlpine, 1981), including venation terms (changes in which may be established [e.g., Cu veins]), but with some modifications. The term "antennal article" was used where the identity of an article as a flagellomere was uncertain. I avoided use of "post-pedicel" since, by definition, all structures distal to the pedicel are part of the flagellum (even though each serial element may not be a flagellomere, i.e., the apical style). An emphasis has been made in diagnoses on wing venation, since venation characters are necessary for defining lithified taxa and it is essential that the Burmese taxa be compared to the diverse Jurassic and Cretaceous Diptera in rocks from Asia and Europe, not just to living taxa. In the descriptions "W/L" designates "width/length" (L/W, length/width).

SYSTEMATICS

INFRAORDER STRATIOMYOMORPHA

This group consists of three living families: Stratiomyidae (2650 species in 375 genera), Xylomyidae (143 species in 4 genera), and the small Neotropical family of large, bulky flies, the Pantophthalmidae (20 species in two genera [Val, 1976]). Monophyly of the group is well established by morphological and molecular evidence (Woodley, 1989; Yeates, 2002; Wiegmann et al., 2011). Defining features of the infraorder include a short Rs, branching off of vein R distally; loss of protibial spurs; bases of female cerci separated by tergite 10; and vein C short, ending at the tip of M_2, or between it and the tip of M_1 (except in Pantophthalmidae). The sister grouping of Xylomyidae and Stratiomyidae appears definitive, as both have three (vs. four) larval instars, the larval cuticle has calcareous "warts" (Woodley, 1989), and the antennae have well-developed sensillar foveae (Arillo et al., 2015). Many species in both families are boldly colored, usually with contrasting black and yellow markings. The fossil record is summarized below under each family. A fascinating extinct family of

the Stratiomyomorpha is the Zhangsolvidae (formerly the Cratomyiidae [Mazzarolo and Amorim, 2000]) (Arillo et al., 2015; Peñalver et al., 2015), which lived from the Early to mid-Cretaceous in Gondwana and Laurasia; a new species is described below. All Zhangsolvidae possess a long proboscis and were probably pollinators. Arillo et al. (2015) analyzed the relationships of Cretaceous and some living stratiomyomorphans, confirming the monophyly of families though the relationships among them were unresolved. Zhangsolvidae have sensillar foveae on the antenna (see Arillo et al., 2015) and vein C ending near the tip of M_1, so this family may be an extinct sister group to the Xylomyidae + Stratiomyidae.

FAMILY ZHANGSOLVIDAE

Genus *Cratomyia* Mazzarolo and Amorim

Cratomyia Mazzarolo and Amorim, 2000: 94.
Type species: *Cratomyia macrorrhyncha* Mazzarolo and Amorim, 2000, by original designation.

Emended Diagnosis: Proboscis long; wing cell m_3 long and narrow; R_4-R_5 fork short, cell cup closed, long; distinguished from other three genera of Zhangsolvidae by the presence of stem vein M_{1+2} (vs. M_1 and M_2 connected directly to cell d).

Comments: Zhangsolvidae consist of four genera and seven species (including the new species here), entirely from the Early to mid-Cretaceous: *Zhangsolva cupressa* (Zhang et al.) (compression, China), *Buccinatormyia* (two species in Spanish amber), *Linguatormyia teletacta* Grimaldi (Burmese amber), and *Cratomyia* (two others in the Crato Formation limestone of Brazil). Placement of the new Burmese amber species into *Cratomyia* is based on the very similar wing venation, since a comparison based on body structures, such as tibial spurs and antennae, was not possible. All species of the family have a long, rigid proboscis, which doubtlessly was used for probing reproductive structures of plants for pollen and nectar in the manner of many modern long-tongued flies. In fact, one of the two specimens in Spanish amber is preserved with the pollen from a Bennettitalean (Mesozoic group of gymnosperms) adhering to the body. Diverse flowers and angiosperm leaves are preserved in Burmese amber (Grimaldi and Ross, 2016), but these flies were apparently not restricted to feeding on flowers.

Cratomyia mimetica, new species

Figures 1, 2, 33

Diagnosis: Like *C. macrorrhyncha* (Crato Formation: Brazil) with short R_4-R_5 fork, long, narrow m_3 cell, and short M_{1+2} stem. Distinguished from that species by: M_1 slightly sinuous with tip slightly upturned (vs. arched downward), cell d slightly narrowed distally (vs. uniform width), cell m_3 very narrow, W/L 0.11 (vs. 0.22), anal lobe well developed. Distinguished from the other species in Burmese amber, *Linguatormyia teletacta* Grimaldi, by longer, narrower cell d, presence of M_{1+2} stem, narrower wing (W/L 0.36, vs. 0.41), much shorter basal palpomere (>5× length of apical palpomere in *Linguatormyia*); palpomeres nearly equal in length in *C. mimetica*; and by wasplike abdomen (vs. short, dorsoventrally flattened abdomen).

Description: Unique female, extraordinarily well preserved, with color patterns distinct (figs. 1, 2). Light yellowish body with bold, black markings, patterns as described below under head, thorax, abdomen. No macrosetae on body, only fine, short, decumbent setae and setulae. Rather stout-bodied fly with thorax compact, abdomen relatively large. Head width 2.16 mm, thorax length 1.88 mm, wing length 4.84 mm, abdomen length 4.49 mm. **Head:** Slightly broader than thorax, compressed/slightly flattened dorsoventrally. Dark areas include occiput, vertex, median strip on frons, around bases of antennae, most of face, at least base of proboscis (apical portion lost), at least base of antenna (apical portion lost), tips of palps. All other areas very light yellow. Frons broad, width slightly less than

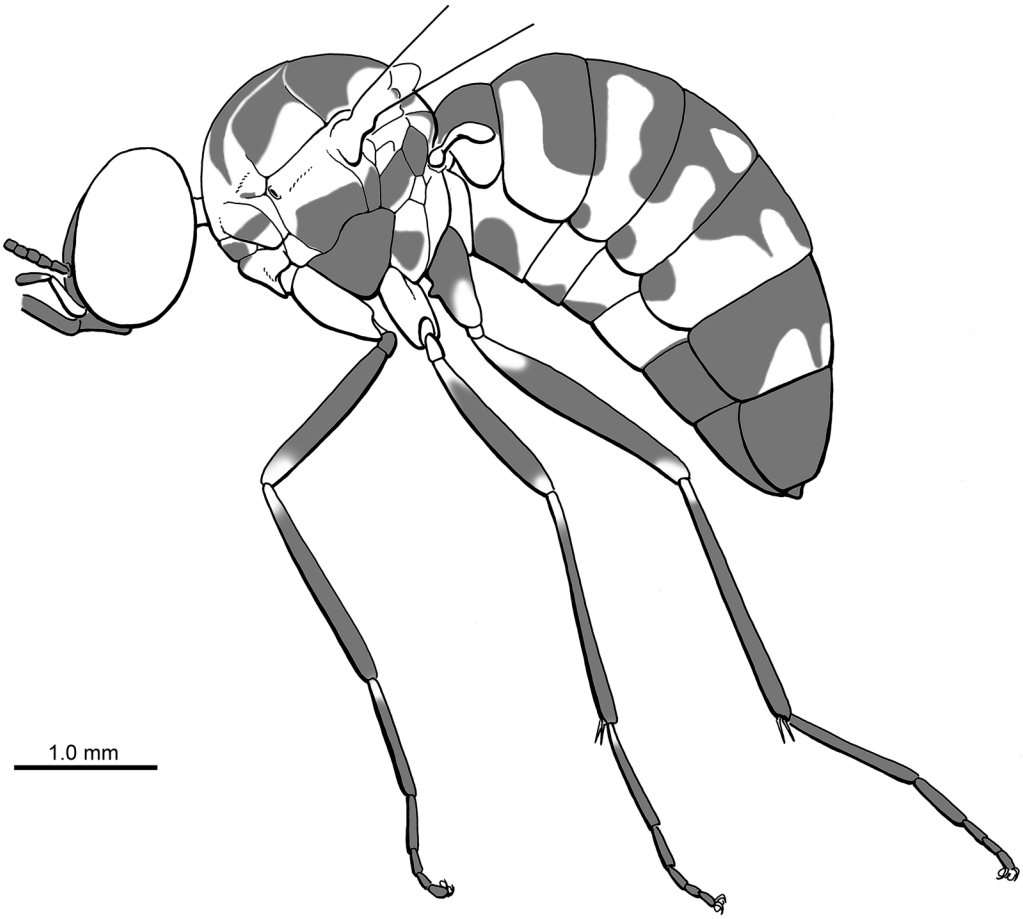

FIG. 1. *Cratomyia mimetica*, new species (Zhangsolvidae), reconstruction of lateral habitus, without wing; coloration as preserved. Based on holotype specimen, AMNH Bu-SD01.

width of eyes; flat, setulose. Ocelli light, small; on small mound slightly raised above frons, forming equilateral triangle, situated on vertex of head. Face concave, with deep paraclypeal sulci; clypeus bulbous. Hypostomal bridge complete (not interrupted medially); ventral surface of head just below mouthparts with long, fine, light setae. Occiput gently concave. Eye: Large, bare, no differentiation of facets, color light; reniform in shape dorsally (modest emargination near middle of margin with frons); broadest surface is frontally. **Antenna:** Bases close but distinctly separate, not contacting; scape, pedicel, and basal three flagellomeres preserved, all uniform in size and shape (short cylindrical), without long, fine setae. **Mouthparts:** Proboscis long, thin, projecting forward (only base preserved, most is lost at surface). Palp 2-segmented, basal palpomere slightly longer than apical one, apical palpomere slightly expanded at apex; devoid of long, fine setae. **Thorax:** Short, relatively deep, without pilosity except on laterotergite. Coloration: Black markings on middle portion of scutum, incomplete stripes lateral to this (broader posterior to transverse suture); all of katepisternum, ventral half of anepisternum, meron; all of laterotergite; portion of postpronotal lobe and preepisternum; dorsal half of metacoxa, most of legs (bases of meso- and metafemur light, as are femoral-tibial articulations). All other areas of thorax light,

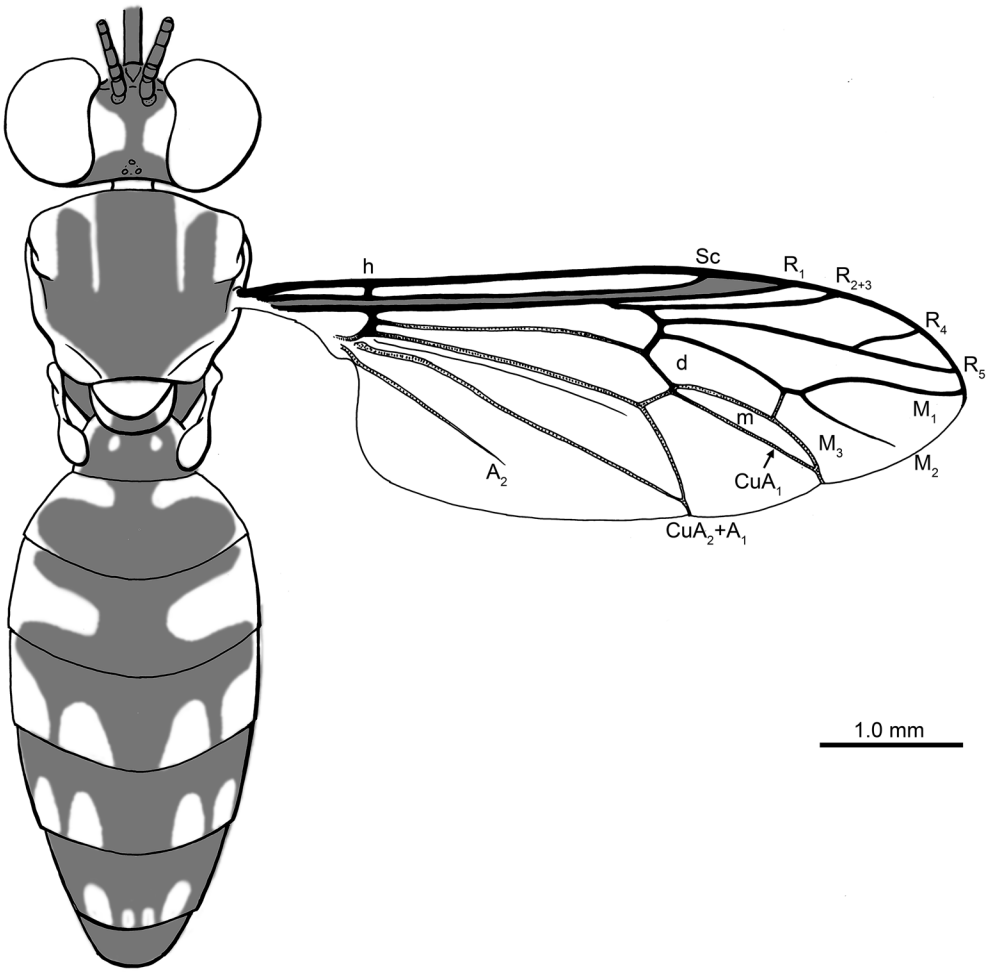

FIG. 2. *Cratomyia mimetica*, new species (Zhangsolvidae), reconstruction of dorsal habitus based on holotype. The preserved coloration pattern resembles that of stinging wasps, Vespidae.

including scutellum and halter. Scutum short, rounded in profile; transverse suture well developed but barely dorsal. Pleura largely vertical, not oblique, with ventralmost portion of katepisternum beneath level of anepimeral cleft. Antepronotum quite small; postpronotum, postpronotal lobe, and preepisternum ventrally positioned, not at anterior end of thorax. **Wing:** Relatively narrow, W/L 0.36. Veins C, R_1, R_{2+3} thick, dark; C ending at tip of M_1. Entire area between Sc and R_1 darkened, even at base. Sc complete, long, 0.62× wing length; R_1 0.76× wing length, close and parallel to Sc and R_{2+3}; R_{2+3} 0.81× wing length. Rs very short; fork of R_4-R_5 very short, 0.3× entire length of R_{4+5}. M_1 not arched, slightly sinuous, tip ending at apex of wing, M_2 distinctly incomplete; M_1 and M_2 joined to short stem (M_{1+2}) (vs. directly to cell d). Cell m_3 long, very narrow, W/L 0.11. Cells br, bm of equal length; cell cup long, closed; apex of CuA_1+A_1 meeting wing margin well past midpoint of wing (0.61× wing length). A_2 well developed, apically evanescent; anal lobe well developed, alula barely observable, upper calyp-

ter small. **Legs:** Pro- and mesocoxa light; metacoxa dorsally dark; mesocoxa only slightly closer to metacoxa than to procoxa, not contacting either one; metacoxa with well-developed knob/tubercle on anterior surface. Legs without macrosetae; with only dense, short, decumbent setae/setulae. Leg segment lengths: tibia > femur > basitarsomere > combined length of other (distal) tarsomeres. Tibial spurs 0-2-2; spurs relatively robust, shorter than apical width of tibia. Pretarsus with claws well developed, pulvilli shorter than claw; empodium pulvilliform, about same size as pulvillus. **Abdomen:** Large, length 1.3× that of head + thorax, width about equal to thorax in dorsal view, deeper than thorax in lateral view. Wasplike, with narrowed waist and apex: tergite 2 0.5× width of t3, anterior portion of t2 constricted; in lateral view t2 lower than other tergites but rounded, slightly nodelike. Markings: Tergites 2–7 with middle portions dark, t4 with dark hourglass shape, t5 and t6 with dark stripes forming light posterior spots. Dark lateral spots on tergites 4–6. Tergite 7 with 4 light spots on posterior margin; all of t8 dark. Tergites overlapping sternites laterally, abdominal pleural membrane not exposed. Sternites 3–5 with dark median area. Terminalia obscured by bubbles, largely retracted into sternite/tergite 8.

Type: Holotype, female, AMNH Bu-SD1.

Etymology: From Greek, *mimos* ("imitator, actor"), in reference to the wasplike color patterning and body shape.

Comments: Preservation of the fly is superb; the only portions lost at the surface of the amber are parts of the antennae and proboscis and apical half of the right wing. The fly is in a yellow, very clear cabochen of amber 4 × 5 × 15 mm.

This may be the earliest-known occurrence in the fossil record of aposematic mimicry, specifically of an aculeate (stinging) wasp as the model (figs. 1, 2). Diverse families of aculeates occur in Burmese amber, some of them abundant and speciose, such as ants (Formicidae) and apoids (Crabronidae and relatives). The markings on *Cratomyia mimetica,* however, strikingly resemble Vespidae, particularly of the abdomen. The constriction between abdominal segments one and two and the narrowed dark markings at the base of the abdomen (along with the light bulb of the halter) lend appearance to a wasp petiole. Further, the very dark, thick costal vein and dark membrane between Sc and R_1 must have resembled vespid wings when folded over the abdomen. Vespidae occur in Burmese amber (Perrard et al., 2016), but these are stem-group vespids and the coloration patterns of the specimens found thus far are not preserved.

FAMILY XYLOMYIDAE

This is a relatively small family of approximately 143 species as of 2016, comprising four living genera. Two of the living genera of Xylomyidae are nearly cosmopolitan, *Xylomya* Rondani and *Solva* Walker. *Arthropeina* Lindner contains six neotropical species (Fachin and Amorim, 2014); the monotypic genus *Coenomyiodes* Brunetti is from India and very poorly known. *Macroceromyx* Bigot is now synonymized with *Xylomya* and *Formosolva* James with *Solva* (Woodley, 2011). The world species were cataloged by Woodley (2011), who also discussed relationships of the genera. *Solva* and *Arthropeina* both hold the abdomen elevated and have extensive membrane on tergite 1, and are closely related (Papavero and Artigas, 1991; Woodley, 2011). *Coenomyiodes* is possibly a derived species of *Xylomya* or a sister group to *Xylomya* (Woodley, 2011). The fossil record of the family is sparse, including a species in Early Cretaceous Lebanese amber, *Cretoxyla azari* Grimaldi and Arillo, and an undescribed species possibly in this family preserved in Early Cretaceous Spanish amber (Grimaldi et al., 2011). *Xylomyia?* (sic: *Xylomya*) *shcherbakovi* Mostovski, from the Late Jurassic of Kazakhstan, is just a fragment of a wing whose identity is impossible to assess. Otherwise, all other fossils are from the Eocene: *Solva inornata* Melander and *Xylomya moratula* Cockerell from Florissant, and *Solva nana* Loew in Baltic amber. Thus, the finding of three xylomyids in

Burmese amber (described below) significantly adds to the fossil record. The two new genera differ from modern ones by possessing obvious tergal sulci and no thickened node or weak area on the short stem of vein Rs. In all *Solva* I have examined Rs is weakened only; *Arthropeina* has this stem weakened and with a thickened node; *Xylomya* has the membrane surrounding the apex of Rs thickened and yellowed. Unfortunately, none of the fossils are males, so certain genitalic features could not be assessed (e.g., enlarged male cerci, and epandrium with large lateral processes, as is found in *Xylomya*). Other differences are noted in the diagnoses, below.

Cretasolva, new genus

Diagnosis: Apical flagellomere long, slender, as in *Arthropeina*. Distinguished from *Archosolva* (also in Burmese amber) by 0-2-2 long, slender tibial spurs; wing long and slender (W/L 0.30); vein C ends at apex of M_1; Rs not thickened or weakened; vein A_1 very long, apex meeting CuA_2 at midlength of wing; cell m long and narrow, nearly reaching to wing margin (M_3+CuA_1 spur very short); tergite 1 without membranous area, transverse sulci on at least tergites 2–4.

Type Species: *Cretasolva burmitica*, new species.

Etymology: Taken directly from Cretaceous and *Solva*, but the name is not meant to imply a close relationship between it and *Solva*. The gender of the name is feminine.

Comments: See above.

Cretasolva burmitica, new species

Figures 3, 34

Diagnosis: As for genus, by monotypy.

Description: Based on unique female. Slender bodied with slender wings, legs of moderate length. Body length (excluding antennae, including cerci) 4.69 m; thorax length 1.66 mm; wing length 3.60 mm; abdomen length (including cerci) 2.50 mm. **Head:** Slightly broader than thorax, occiput slightly concave. Frons relatively broad, width slightly greater than distance between outside margins of lateral ocelli. Face concave (clypeus not observable). Eye: Relatively large, occupying most of head surface in lateral, frontal, and dorsal views. Margins with frons parallel. Eye completely bare, facets not differentiated. Ocelli slightly raised above surface of frons. **Antenna:** Submoniliform, with 8 flagellomeres evenly tapered from broad basal one to narrow apical flagellomere, apical one with minute style. Flagellomere lengths: 8 > 7 > 6 = 1 > 2–5. Scape and pedicel small; antennal sockets very close, situated in ventral half of frons. **Mouthparts:** Palps directed forward; 2-segmented, basal palpomere slender; apical one oval, nearly twice width of basal palpomere. Proboscis short, only labellum exposed; labellum large, fleshy, laterally flattened. **Thorax:** Dorsum of scutum, scutellum, portion of anepisternum with dense, very fine, setigerous punctation, denser on scutellum; no macrosetae or long pilosity. Transverse suture short, mostly lateral (pleural), with faint impression dorsolaterally. Scutellum narrow in dorsal view, longer than wide, without spines; small, short but distinct proscutellum present. Pleural sutures not easily observed in unique specimen; pleura large oblique (vs. vertical). **Wing:** Long, slender, W/L 0.30, veins well developed, most are well sclerotized, lightest ones are R_{2+3} and base of M (latter faint, not sclerotized). Minute setulae on R veins (except R_{2+3}) and M veins (except for stem), none on Cu veins. Vein C ends at apex of M_1. No pterostigma. Sc complete, ca. 0.5× wing length; R_1 0.55× wing length, close and parallel to Sc; Rs and R_{2+3} short, parallel to R_1; Rs without thickened node or weak area; fork of R_4-R_5 asymmetrical, R_4 0.66× length of R_5. Crossvein r-m close to base of cell d, M veins connected to apex of cell d; M_1, M_2 parallel; cell m long, slender, nearly reaching to wing margin (M_3+CuA_1 spur very short); crossvein m-cu present. Cell d long and narrow, W/L 0.3; cells br and bm of equal length. Vein A_1 very long, apex reaching to midlength of wing, cell cup closed. Vein A_2 short; anal lobe and alula present but small. **Legs:** Robust, of

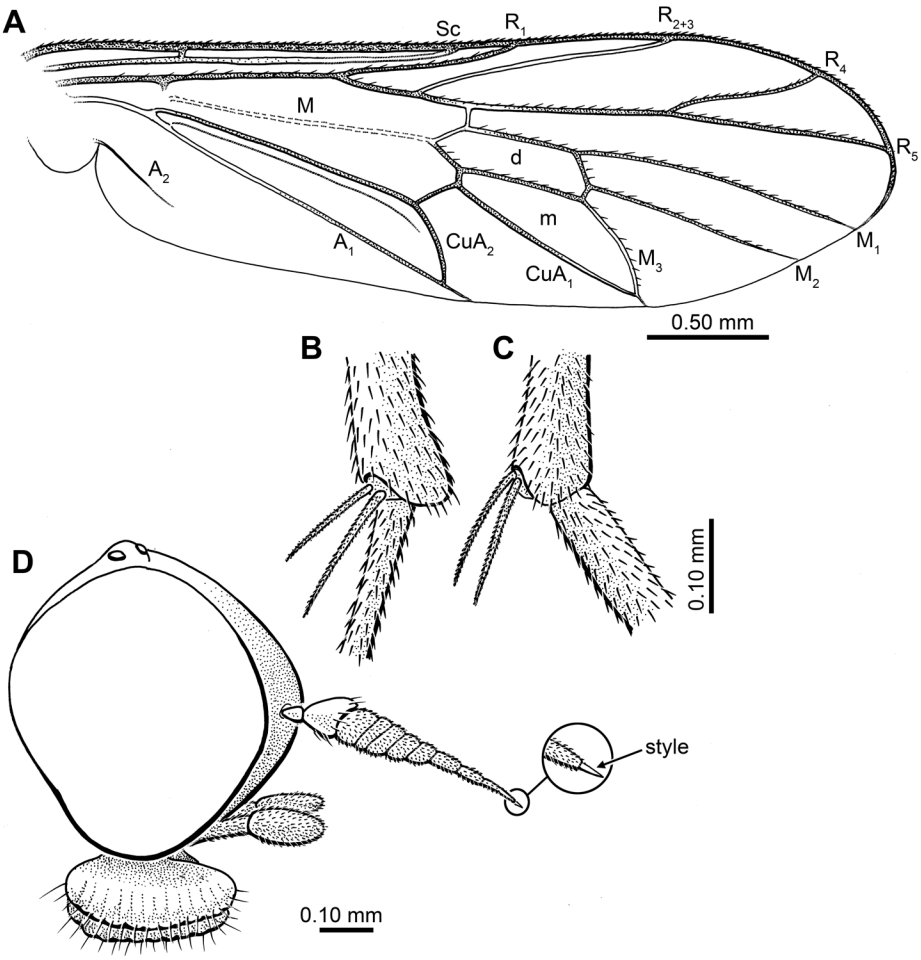

FIG. 3. *Cretasolva burmitica*, new genus and species (Xylomyidae), AMNH Bu-SE05, holotype. **A.** Wing. **B, C.** Apices of meso- and metatibia, respectively, showing spurs. **D.** Head, lateral view, with detail of antennal apex.

moderate length. Coxae robust, meso- and metacoxae meeting, distant from procoxa. Relative lengths of leg segments: Pro- and mesofemur > tibiae > basitarsomere > combined lengths tarsomeres 2–5. Metatibia > femur > basitarsomere > combined lengths tarsomeres 2–5. Tibial spurs 0-2-2; spurs long and thin, lengths ca. 1.5× apical width of tibiae. No tubercles on ventral surface of hind femur. Pretarsus with well-developed simple claws; pulvilli small, ca 0.5× length of claw; empodium pulvilliform, short and broad. **Abdomen:** Only slightly longer than thorax, thickness and width tapered to narrow apex. Seven tergites visible, basal 2 tergites fully sclerotized (no median membranous areas); tergite 1 narrow in dorsal view, width of its posterior margin ca. 0.5× that of tergite 2; tergite 2 large, nearly twice the length of tergite 3; broadest tergites t2, t3. Cerci (female) long, slender, 2-segmented, length approximately equal to length of segments 6+7, basal cercomere slightly longer than apical one; t10 small, lying between bases. Tergites 2–4 with shallow transverse sulci (possibly on t1 and t5 but not fully visible).

Type: Holotype, female, AMNH Bu-SE05.

Etymology: Derived from English *burmite,* another name for Burmese amber, and Latinized.

Comments: Specimen is in a small, irregular piece 4 × 5 × 6 mm, with the sides closely surrounding the specimen, providing most views. The fly is complete, but it lies on a weathered internal flow; body of the fly (but not the wings) has a thin, reddish covering over the exocuticle, which, along with some fine fractures, obscures some details. This reddish layer indicates initial stages of pyritization. The section with the fly was trimmed from a cabochen that also contains two small moths, one adult Cicadellidae (Auchenorrhyncha), and a spider.

Archsolva, new genus

Diagnosis: Wing broad, W/L 0.46–0.50; fork of R_4-R_5 short, nearly symmetrical; vein C ends slightly past apex of R_5 (vs. at apex of M_1); cell m short, with long vein M_3+CuA_1; tergite 1 with anterior portion membranous; tergites 1–5 with deeply impressed transverse sulci; metafemur lacking ventral denticles.

Type Species: *Archosolva biceps*, new species.

Etymology: From *archaios* (Greek, "old") (in reference to the age) and the genus *Solva*, to which the fossil appears related. The gender of the name is feminine.

Comments: Based on the short, triangular abdomen, with a thick base and narrow apex, and the membranous anterior portion of tergite one, this genus appears related to *Arthropeina* and *Solva*. However, in the fossil genus vein C ends at the apex of R_5 (vs. M_1), and it (plesiomorphically?) has deeply impressed transverse sulci.

Archosolva biceps, new species

Figures 4, 6C, 35

Diagnosis: Distinguished from *Archosolva sulcata,* n. sp., by the following: head broad frontally; metacoxa bulbous, inflated; metafemur stout; cell m relatively small, narrow; CuA_1 base connected directly to base of M_3, forming short stem as part of cell d (i.e., no crossvein m-cu).

Description: Based on unique female. Body length 4.80 mm; head width 1.14 mm; thorax length 1.74 mm; wing length 3.34 mm; abdomen length 2.61 mm (including cerci). **Head:** Short, compressed anteroposteriad, with broad anterior and posterior surfaces. Frons bare, dark, smooth. Ocelli on slightly raised mound, anterior ocellus facing forward, slightly farther from posterior ocelli than posterior ocelli are to each other. Face slightly concave, clypeus slightly raised. Occiput slightly concave. Eye: Large, occupying all of lateral surface of head in lateral view, with broad frontal surface; completely bare, facets not differentiated; inner (mesal) margins widely separated, slightly divergent anteriad, width slightly greater than distance between outer margins of ocelli. **Antenna:** Submoniliform, stout at base, evenly tapered to narrow apex, with 8 flagellomeres and minute apical style. Scape, pedicel small, slightly cone shaped; flagellomere 1 largest (broadest and longest flagellomere), flagellomeres 2–5 compact, short; flagellomere 8 slender, length approximately equal to flagellomere 1; sensillar foveae visible on basal flagellomeres. **Mouthparts:** Well developed; palps porrect, apex reaching nearly to antennal bases, basal palpomere slender, apical one laterally broad, roughly triangular, slightly longer than basal palpomere. Labellum well developed (lobes parted in type), broad, flat, subovoid, with ca. 12 pseudotracheae. **Thorax:** Scutum moderately arched, scutellum flat, both with very fine, dense, setigerous punctation; patch of fine, stiff setulae on portion of laterotergite just anterior to posterior spiracle; sparse punctation on anepisternum and katepisternum. Transverse suture deeply and discretely impressed laterally; suture shallow, short, ill defined dorsolaterally. Postpronotal lobe long and narrow in dorsal view; postpronotum well developed, immediately ventral to lobe. Scutellum broader than long, margin evenly curved in dorsal view, no spines; small proscutellum and small subscutellum present. Pleura overall oblique, ventralmost portion of katepisternum significantly posterior to level of anepisternal cleft. **Wing:** Of moderate length and width, W/L

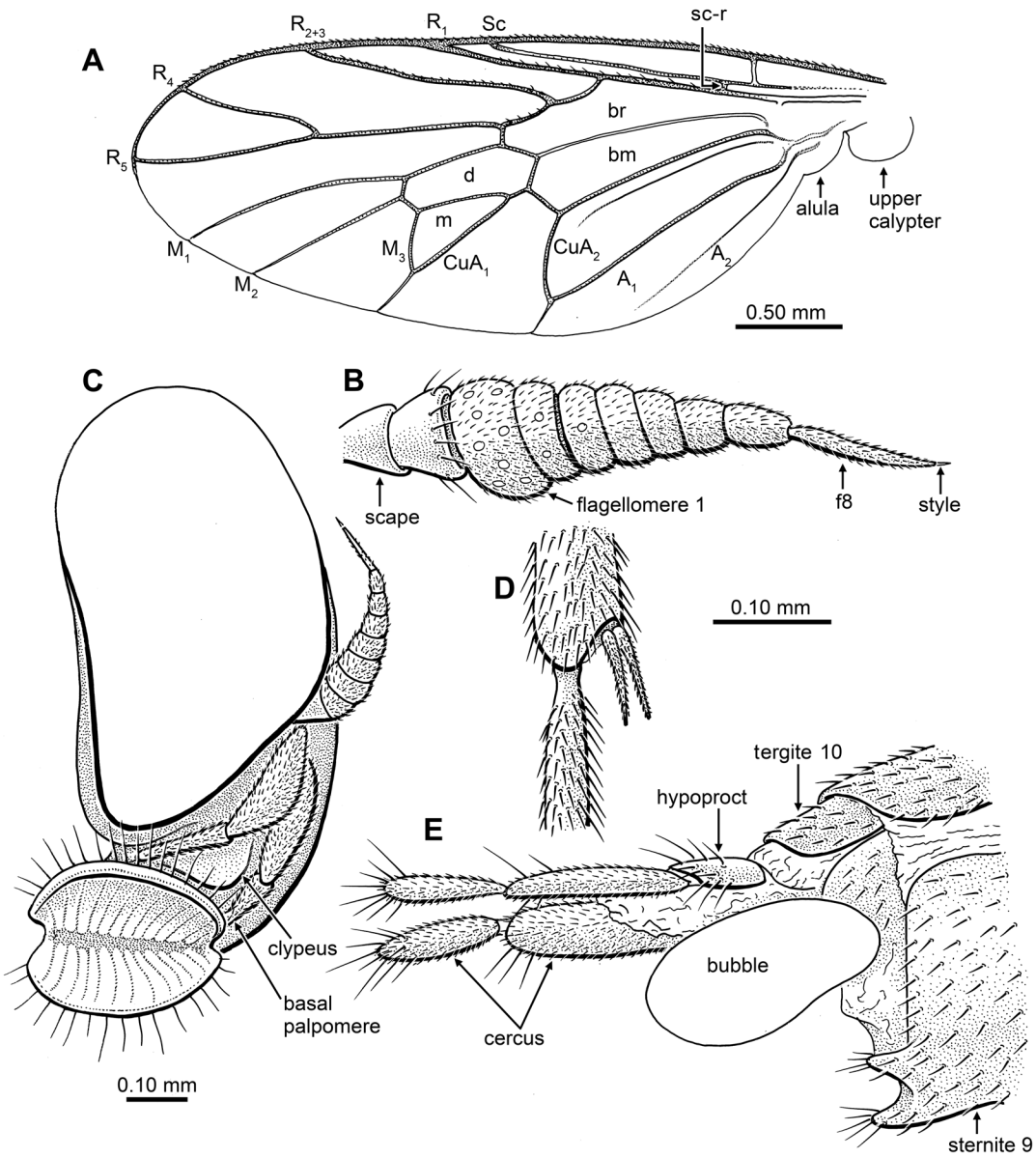

FIG. 4. *Archosolva biceps*, new genus and species (Xylomyidae), JZC Bu-257, holotype. **A.** Wing. **B.** Detail of antenna. **C.** Head, ventrolateral view. **D.** Mesotibial apex with spurs. **E.** Female terminalia, left ventrolateral view. Panels B, D, E to same scale.

0.5. All veins sclerotized, except for base of Sc (which is spectral); fine setulae only on stem of R and R_1, base of R_4-R_5 stem. C ends just past tip of R_5. Sc long, complete, 0.54× length of wing. R_1 very close and parallel to Sc; Rs short, without thickened node or weak area; R_{2+3} short and parallel to R_1; no pterostigma; fork of R_4-R_5 slightly asymmetrical, R_4 0.75× length of R_5; tip of R_5 meeting wing apex. Crossvein r-m near base of cell d; cell d slender, W/L 0.3; vein M_3 short, meeting CuA_1 well before wing margin; cell m an isosceles triangle, W/L 0.38. CuA_1 base con-

nected directly to base of M_3, forming short stem as part of cell d, lacking crossvein m-cu. Cells br, bm of equal length; cell cup closed, CuP distinct; tips of M and Cu veins distinctly tapered but meeting wing margin. A_2 well developed; anal lobe, alula, upper calypter present but narrow. **Legs:** Relatively short, robust. Pro- and mesocoxae slender, distant from each other; metacoxa swollen and inflated laterally. Metafemur significantly thicker than other two femora, without ventral spines or tubercles. Lengths of leg segments: femur > tibia > basitarsus > combined lengths basitarsomeres 2–5. Tibial spurs 0-?-2 (apices of mesotibiae lost/obscured). Pretarsus with claws well developed, simple; pulvilli slender, shorter than claws, empodium pulvilliform, smaller than pulvilli. **Abdomen:** Very broad basally, broader than thorax, evenly tapered to narrow apex; held slightly elevated. Dorsum of abdomen relatively flat; length of tergite 2 approximately equal to t3; tergite 2 fully sclerotized; tergite 1 with central depression beneath scutellum (probably membranous area). Tergites 1–5 each with deeply impressed transverse sulcus near middle of each tergite. Original color of abdomen apparently dark; tergites with dense, very fine, setigerous punctation. Tergite 9 very small, barely exposed; tergite 10 very small, transverse, not separating basal cercomeres. Cercus long, slender, length ca. equal to tergite 8 length; basal cercomere slightly longer, both segments with fine, sparse setae. Sternites 3–7 well developed (1, 2 obscured); apical margin s7 with small pair of lobes.

Types: Holotype, female, JZC Bu-257.

Etymology: From the Latin *biceps* ("two-headed" or "double-peaked"), in reference to the swollen metacoxa and metafemur.

Comments: Specimen is complete and very well preserved, only a few important features are obscured (e.g., mesotibial spurs). The fly is preserved in a piece of deep yellow amber of irregular shape, 5 × 7 × 10 mm, all surfaces flattened for most views of the fly. The piece was trimmed from a cabochen that also contains stellate trichomes, a psychodid midge, serphitid wasp, and parts of a spider. The stout metafemur and coxa suggests a relationship to *Solva* (but without ventral tubercles), and the abdomen is held slightly raised.

Archosolva sulcata, new species

Figures 5, 6D, 36

Diagnosis: Apical flagellomere long, though not slender. Distinguished from other Burmese amber xylomyids by the very broad wing (W/L 0.46), stout m cell, short R_4-R_5 fork, and the vertical fossa beneath the wing base (apparently for receiving the mesofemur).

Description: Based on unique female. Body rather stout and dorsoventrally somewhat compressed. Original coloration well preserved: face, frons, antennal flagella, occiput, scutum, and tergites light to dark brown, lobe posterior to transverses suture is darker, each trochanter with blackish-brown ventral spot; scutellum, halter, pleura, legs, sternites, and mouthparts light yellowish. Body length 4.39 mm (excluding antennae); thorax length 1.57 mm; wing length 3.22 mm; abdomen length 2.09 mm. **Head:** Broader than thorax; short, compressed anteroposteriad, broad frontally. Frons relatively narrow, width approximately equal to 4× diameter of eye facets. Face concave, clypeus small and swollen. Ocelli: only anterior one preserved. Eye: Relatively large, occupying most of head surface in lateral, frontal, and dorsal views, broadest surface is frontally. Eye completely bare, facets not differentiated. **Antenna:** Submoniliform, with 8 flagellomeres evenly tapered from broad basal one to narrow apical flagellomere, latter with minute apical style (flagellum laterally compressed in unique specimen). Flagellomere lengths: 1 > 8 > 7 > 2–6. Scape and pedicel small, narrow; antennal sockets very close, situated in ventral half of frons. **Mouthparts:** Palp 2-segmented, basal palpomere small, narrow, ringlike; apical one large, subcircular, laterally flattened. Proboscis short, only labellum exposed; labellum large, fleshy, laterally flattened. **Thorax:** Right side of thorax well preserved; left side distorted and damaged. Dorsum of scutum, scutellum, portion of anepisternum with dense,

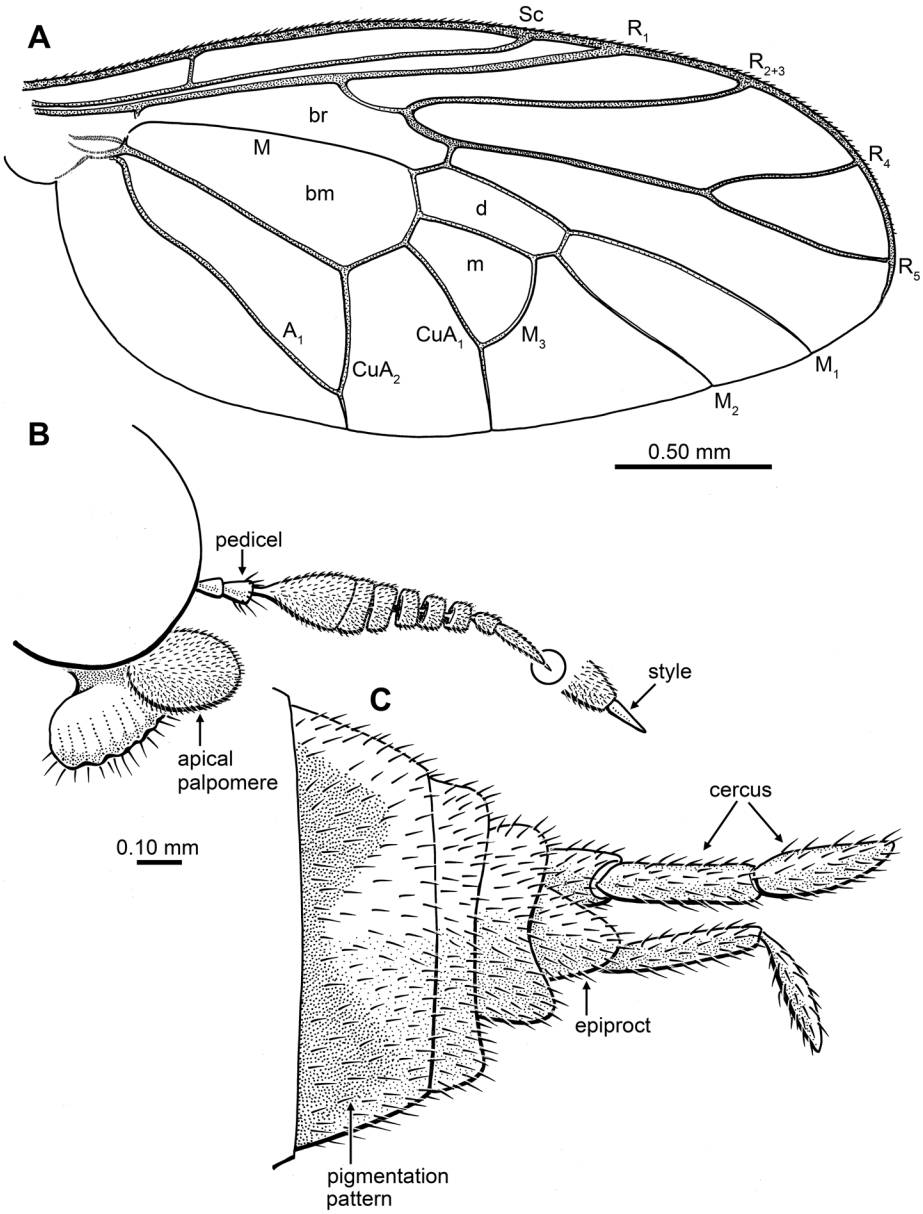

FIG. 5. *Archosolva sulcata*, new genus and species (Xylomyidae), JZC Bu-208, holotype. **A.** Wing. **B.** Anterior portion of head (lateral view), with detail of antennal tip. **C.** Female terminalia, dorsal view.

very fine, setigerous punctation; punctation sparse on pleura; no macrosetae or long pilosity; patch of longer, fine setulae on laterotergite. Transverse suture deeply impressed laterally and dorsally, curved posteriad on scutum, nearly meeting in middle. Pleura below wing base with vertical fossa, width equal to that of mesofemur (appears to have received femur). Scutellum without spines, this area of thorax poorly preserved. Pleura largely oblique (vs. vertical), with ventralmost portion of katepisternum slightly posterior to level of anepimeral cleft. **Wing:** Short, broad, W/L 0.46,

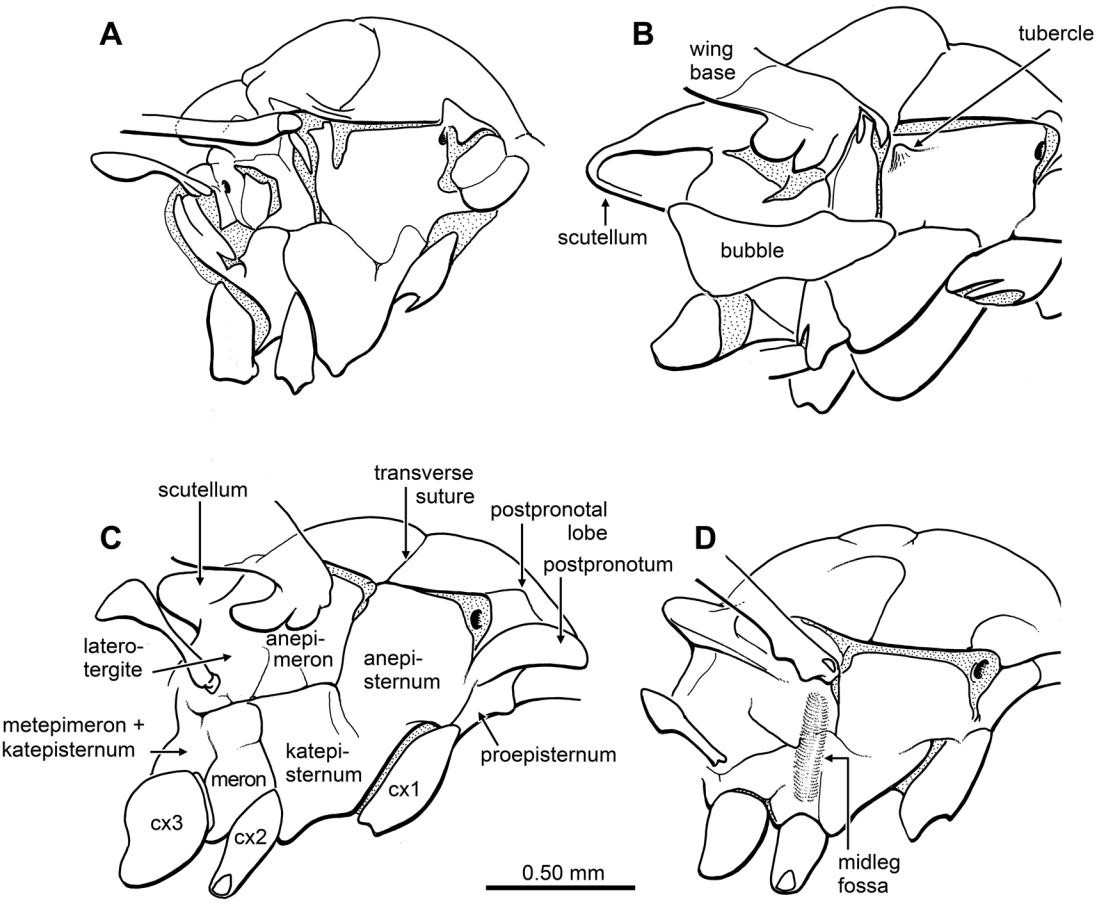

FIG. 6. Lateral views of thoraces of Burmese amber Stratiomyomorpha. **A, B.** Stratiomyidae. **C, D.** Xylomyidae. **A.** *Normyia longistyla*, new genus and species. **B.** *Narcissomyia bella*, new genus and species. View is slightly ventral. **C.** *Archosolva biceps*, holotype (note inflated metacoxa). **D.** *Archosolva sulcata*, holotype (note fossa, for apparently receiving the raised mesofemur).

veins well developed, all well sclerotized, including base of M (which is very thin); R_1 and R_{4+5} particularly thick. Minute setulae on vein R_1 only. Vein C ends slightly past apex of R_5. No pterostigma. Sc complete, ca. 0.55× wing length; R_1 0.65× wing length, close and parallel to Sc; Rs very short, less sclerotized than rest of R, without thickened node; R_{2+3} short, slightly divergent from R_1; fork of R_4-R_5 slightly asymmetrical, R_4 0.80× length of R_5; fork short, 0.38× total length of R_{4+5}. Crossvein r-m close to base of cell d, M veins connected to apex of cell d, crossvein m-cu present; M_1, M_2 parallel; cell m stout, W/L 0.63; vein M_3+CuA_1 relatively long. Cell d long and narrow, W/L 0.32; cells br and bm of equal length, bm twice the width of br. Vein A_1 meeting CuA_2, cell cup closed. Vein A_2 short; anal lobe well developed, but alula small. **Legs:** Length moderate. Coxae robust, meso- and metacoxae meeting, distant from procoxa. Relative lengths of leg segments: Femur > tibia > basitarsomere > combined lengths tarsomeres 2–5. Tibial spurs 0-2-1; spurs very thin, lengths about equal to apical width of tibiae. No spinules on ventral surface of hind femur. Pretarsus with well-developed simple claws; pulvilli small, ca 0.5× length of claw; empo-

dium pulvilliform, short and broad. **Abdomen:** Slightly longer than thorax, broad and stout at base, width tapered to narrow apex; dorsoventrally flattened; tergites not well preserved, natural margins difficult to discern, t2–5 apparently with transverse sulci; t1 apparently with membranous area. Cercus 2-segmented, basal cercomere slightly longer than apical one; t10 small, lying between bases. Sternites well developed but not meeting tergites laterally, abdominal pleural membrane well exposed.

Type: Holotype, female, JZC Bu-208.

Etymology: In reference to the thoracic sulcus, which apparently accomodates the mesofemur when it is raised.

Comments: Specimen is in a small, irregular piece 3 × 5 × 10 mm, with the sides closely surrounding the specimen, providing most views. The fly is virtually complete, portions of the left side (head, thorax) are lost or damaged, and some parts have been distorted by compression. The section with the fly was trimmed from a cabochen that also contains several thrips (Thysanoptera). The area around and including tergite 1 is poorly preserved, but judging from the lack of setae in this area (which cover other tergites and a portion of tergite 1), it appears that a substantial portion of tergite 1 is membranous. The abdomen is held slightly raised.

FAMILY STRATIOMYIDAE

Soldier flies are conspicuous, found on flowers or in large numbers at breeding sites, and well represented on all vegetated continents. Woodley (2001) provided a world catalog of the species and genera and their classification, and an analysis of subfamily relationships based on morphology. His phylogeny proposed the following relationships: Parhadrestiinae (Chiromyzinae (Beridinae (Antissinae + *Exodontha* + Clade 4))). Clade 4, what I am calling "higher" stratiomyids here, includes the remaining, familiar, and generally speciose subfamilies like Pachygastrinae, Hermetiinae, Sarginae, etc. Parhadrestiinae are highly relict, with two species from Chile (Woodley, 1986); Chiromyzinae consist of 14 genera from Central and South America, and Australia; Beridinae consist of 33 world genera, which have been monographed (Woodley, 1995). The study by Brammer and von Dohlen (2007), a molecular-phylogenetic analysis based on two gene regions, agrees in many respects with the conclusions of Woodley (2001), particularly about relationships of the basal subfamilies. Its main finding was that Chrysochlorinae appear quite polyphyletic, which is corroborated by their morphological analysis (Brammer and von Dohlen, 2010). The molecular study estimated the following divergence times: basal subfamilies diverging in the Early to mid-Cretaceous, and subfamilies of higher stratiomyids in the Late Cretaceous (66–80 Ma). As of yet there is no direct evidence for higher stratiomyids in the Cretaceous, though divergence of basal subfamilies during this period is likely. Higher stratiomyids are diverse by the Paleogene (Evenhuis, 1994), and modern genera by the Miocene (e.g., Grund and Hauser, 2005; Coty and Nel, 2013).

The morphological analysis by Arillo et al. (2015) found that Cretaceous stratiomyids were all basal taxa, possibly stem groups to living Stratiomyidae, though there was no resolution of relationships. Indeed, Cretaceous Stratiomyidae are distinctly plesiomorphic to all living taxa in the family with the exception of *Parhadrestia* James. This is generally true for wing venation, and where preserved (i.e., taxa in amber) for characters of the body.

Plesiomorphic venational features of the Cretaceous genera (*Cretaceogaster* Teskey, *Lysistrata* Arillo and Grimaldi, *Montsecia* Mostovski and Delclòs, *Normyia,* n. gen., *Narcissomyia,* n. gen.) include the following:

1. R_{2+3} branches off of Rs near the middle of the segment between R_1 and r-m. In Beridinae the base of R_{2+3} is very near, opposite, or even distal to r-m (this last state is common in higher stratiomyids).

2. R_{2+3} is mostly parallel to R_1, only slightly converging with it, whereas in Beridinae the apex of R_{2+3} is abruptly turned costad, and in higher stratiomyids it is often just a short

transverse vein between C and Rs. Chiromyzinae have a long, sloping R_{2+3}.

3. R_4 is quite long in *Parhadrestia* and the Cretaceous genera, except for *Cretaceogaster* where it is short and the R_4-R_5 fork highly asymmetrical as in Beridinae. In higher stratiomyids R_4 is often very short and crossveinlike. R_4 is lost in Chiromyzinae. Measuring R_4 relative to the length of R_{4+5}-R_5, from where it forks with R_{2+3} to the tip of R_5, R_4 is merely 0.13–0.31 this other segment in Beridinae (mean 0.17), in *Cretaceogaster* 0.26, in other Cretaceous genera and in *Parhadrestia* 0.33–0.55.

4. In all stratiomyids vein C ends at the apex of R_5 or slightly beyond. In *Parhadrestia*, Chiromyzinae, Beridinae, and Cretaceous genera R_5 and C extend closer to the wing tip.

5. The same taxa (above) also have two M veins instead of three (some beridines have three M veins, but these are usually abbreviated). Higher stratiomyids have three M veins.

6. In higher stratiomyids cell d is small, especially in length (L/W 0.8–1.6 [mean 1.3]). Cell d L/W in *Parhadrestia* and *Cretaceogaster* is 1.8 and 1.64, respectively. In Beridinae, Chiromyzinae, and Cretaceous genera cell d L/W is always greater than 2.0, sometimes significantly so (e.g., *Narcissomyia* 3.2, *Lysistrata* 3.4) (the exception is *Normyia telescopica*, n. sp., which is 1.75).

Important features of the body in the Cretaceous genera are the following:

1. Antennae never reduced, generally with eight flagellomeres that are tapered apically. *Lysistrata* apparently has seven flagellomeres, but this may be a preservational artifact.

2. Scutellar spines do not occur in Cretaceous stratiomyids, as is the condition in *Parhadrestia* and Chiromyzinae. Beridinae have scutellar spines, with the exception of two genera that are significantly subordinate within the subfamily, *Allognosta* and *Microhadrestia*, so this is clearly a loss. Higher stratiomyids have scutellar spines.

3. The amber fossils provide insight into an interesting character system, namely the transverse tergal grooves or sulci on the abdomen, which generally occur on tergites 2 through 5 or 6. This feature has been used to define the monophyly of the Beridinae, but the grooves also occur in *Parhadrestia*, some Chiromyzinae, all the Cretaceous species in which the abdomen is visible, as well as in the xylomyids in Burmese amber. I am inclined to think that transverse tergal sulci is a synapomorphy of Xylomyidae + Stratiomyidae, which was lost in modern Xylomyidae and higher Stratiomyidae.

4. Lastly, in the few male stratiomyids preserved in Cretaceous amber (including well-preserved ones reported below), the male genitalia are very similar to that of Beridinae and *Parhadrestia* (Woodley, 1995): gonocoxa stout (sometimes with mesal tubercle or spine); gonostylus stout, also often with one or more spines, as in the new Burmese amber genera *Normyia* and *Narcissomyia*. Whether the gonocoxites are fused or not to the hypandrium was not observable.

Gegantoberies liaoningensis Huang and Lin (2007), from the Early Cretaceous Yixian Formation of China, is misassigned: it is definitely not in the Stratiomyidae, and probably not even in the Stratiomyomorpha, given the very long stem of vein Rs that forks from R_1 near its base. With the diversity and fine preservation of Stratiomyidae in Burmese amber, these fossils provide a unique window into the early history of the family.

Normyia, new genus

Diagnosis: Antenna with 8 flagellomeres, tapered apicad; eyes bare, holoptic in male; palp 2-segmented; no scutellar spines; tibial spurs 0-1-0 or 0-2-0; abdominal tergites 2–6 each with deeply impressed transverse sulci; thorax deep in lateral view; katepisternum pendulous, ventralmost portion nearly reaching to level of mesocoxal apex. R_{2+3} gradually converging toward

apex of R_1 (not meeting); R_4 slightly sinuous, long (its length relative to length of $R_{4\text{-}5}$, from where it branches from Rs to tip of R_5) 0.43–0.55 (vs. <0.20, as in Beridinae); cell d large; M_3 absent; gonostylus with apical and subapical (medial) spines.

Type Species: *Normyia woodleyi*, new species.

Etymology: Patronym for Norman Woodley, USDA–Systematic Entomology Laboratory, in recognition of his outstanding contributions to the systematics of Stratiomyidae and Diptera in general. The gender of the name is feminine.

Comments: See above.

Normyia woodleyi, new species

Figures 7, 37–39

Diagnosis: Based on male and female. Basal and apical flagellomeres (1, 8) short, <2× lengths of adjacent flagellomeres (2, 7); R_5 turned slightly upward; cell d large, L/W 2.14 (vs. 1.75–2.0); mesotibia with 1 stout spur; terminal abdominal segments of female not telescoping.

Description: Male holotype, paratype. Body length 2.31, 2.56 mm (respectively), thorax length 0.98, 1.01 mm; wing length 1.59, 2.02 mm; abdomen length 0.93, 1.20 mm. Female paratype: body length 2.85, thorax length 1.01 mm, wing length 1.94 mm, abdomen length 1.48 mm. **Head:** Large, significantly broader than thorax, approximately hemispherical in shape with occiput dark, flat to slightly recessed, with virtually no setae. Ocelli on raised tubercle, with anterior ocellus directed forward, posterior ocelli directed laterally. Eye: Male: Large, holoptic, occupying nearly all of nonoccipital portion of head; facets with dorsoventral differentiation, dorsal ones ca. 2× diameter of ventral ones, a discrete transverse separation between the two. Eyes completely bare; medial/inner margins meeting just anterior to ocellar triangle, strongly diverging just above antennae, slightly emarginate near antennal bases, inner margins ventrally slightly divergent posteriad; essentially no cheek exposed. Female: Frons widely separated, lateral margins parallel. **Antenna:** With 8 flagellomeres, submoniliform, tapered in width apically; flagellomeres 1 and 8 longest, flagellomere 1 width 5× that of flagellomere 8; no apical stylus; all flagellomeres with sensillar foveae; scape funnel shaped, pedicel flask shaped, with apical whorl of setae, length of antenna 0.35 mm; antennal sockets very close, possibly touching medially. **Mouthparts:** Clypeus and palps small, recessed into shallow concavity of face, face is fully ventral; clypeus small, narrow, triangular; labrum short; palps small, light, 2-segmented, basal palpomere slightly longer and narrower than apical one, palp overall slightly shorter than clypeus. Labellum well developed, fleshy, exposed well beyond oral margin. **Thorax:** Relatively short, deep in lateral view, dark (notum probably somewhat metallic, given tiny blue-green reflections from cuticle). Scutum and scutellum with very fine, setigerous punctation; setulae very fine, short. Antepronotum very well developed; postpronotum large, joined to lateral margins of antepronotum; postpronotal lobe narrow, triangular; anterior third of scutum with pair of very faint paramedian sulci. Transverse suture very well developed, deeply impressed, inner apices converging posteromedially; suture forming rounded lobelike portion of scutum posteriorly. Small proscutellum present; scutellum narrow, length slightly less than width, no spines. Posterior portion of anepisternum large, bulging; katepisternum ventrally extended, nearly pendulous, with ventral margin nearly at same level as ventral margin of mesocoxa; medial margins of both katepisterna meeting ventrally. **Wing:** W/L 0.37. Sc complete, long, 0.5× wing length; C ends slightly past tip of R_5. R and R_1 close and parallel to Sc, diverging slightly at apices. Rs very short, 0.25× length of R_1; R_{2+3} slightly shorter than R_1, convergent, apices of veins nearly touching; fork of R_4-R_5 long, base of fork only slightly distal to level of cell d apex; R_4 sinuous, R_5 straight, tip slightly upturned, ending before wing tip. Faint pterostigma between Sc, R_1, and R_{2+3}, r-m crossvein at middle of cell d; base of M between cells br and bm very faint, not tubular or at all sclerotized. M_1 faintly curved; apices of M_1, M_2, CuA_1 tapered and evanescent, not meeting wing mar-

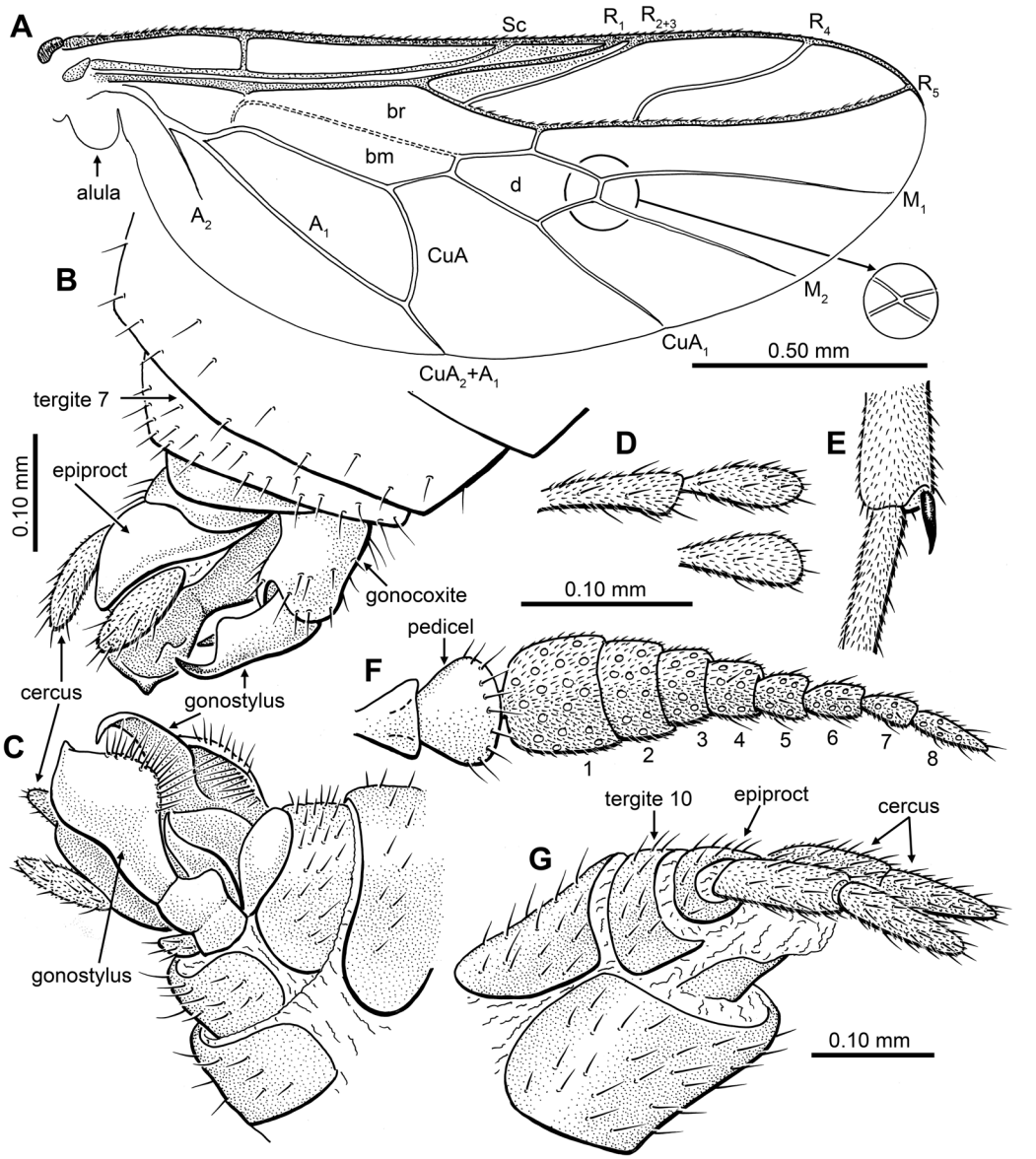

FIG. 7. *Normyia woodleyi*, new genus and species (Stratiomyidae). **A–F**: Holotype male, AMNH Bu-SE04b. **G**: Paratype female, JZC Bu-001. **A.** Wing. **B.** Male terminalia, oblique dorsal view. **C.** Male terminalia, oblique ventral view. **D.** Palp, holotype (above), female paratype (below). **E.** Mesotibial apex with spur. **F**. Antenna. **G.** Female terminalia, posterolateral view. Panels C–E to same scale.

gin; bases of M_1 and M_2 either meeting truncate apex of cell d separately (e.g., left wing of holotype), or cell d apex pointed and joined to bases of R_4 and R_5 into an "X" (i.e., right wing of holotype). Cell d small, W/L 0.43; cell br longer than bm, both cells narrow. CuA_2 arched, meeting A_1 well before wing margin. Anal lobe slender; A_2 short and extremely faint; alula small. **Legs:** Relatively short, covered with fine setulae, tibial spurs 0-1-0, length of mesotibial spur slightly shorter

than width of tibial apex, distal half of spur heavily sclerotized. Length of femur > tibia > basitarsomere = combined lengths of tarsomeres 2–5. Empodium pulvilliform; empodium and pulvilli small, significantly shorter than pretarsal claws. **Abdomen:** Broad, relatively short, moderately flattened dorsoventrally. Tergites 1–5 each with transverse furrow impressed near posterior margins, furrows deepest on tergites 2–4, furrow lengths ca. 0.8× tergite width; 7 tergites exposed (7th very small) in male, 10 in female. Sternites 1–7 well developed (if an 8th, then not visible). **Male Terminalia:** Well developed, exposed. Gonocoxa simple, short, cylindrical, fully articulating with gonostylus; gonostylus somewhat scoop shaped, broad in lateral view, with slightly hooked apical spine; smaller preapical median spine. Proctiger small, approximately triangular (apex narrow), cercus 1-segmented, ovoid, lateral to epiproct. **Female Terminalia:** Cercus 2-segmented, segments approximately equal in length, basal cercomere slightly thicker; terminalia not telescoping. Sternite 10 possibly present.

Types: Holotype, male, AMNH Bu-SE04B. Paratype male, AMNH Bu-SE04A; paratype female, JZC Bu-001.

Etymology: Patronym, for dipterist Norman Woodley.

Comments: The holotype and paratype, AMNH Bu-SE4A, B are very well-preserved males from the same piece, originally a cabochen 12 × 8 × 7 mm, which are now separated into small polished cubes each 6 × 5 × 3 mm. The paratype is partial (lost left side of thorax and head), but the internal clearing better resolves some sutures. The male holotype is complete and superbly preserved; there is a mycetophilid syninclusion.

Normyia telescopica, new species

Figures 8, 40

Diagnosis: Larger than *N. woodleyi*; female tergites 6–10 telescoping (vs. not), spurs 0-2-0 (vs. 0-1-0); basal flagellomere about twice the length as in *N. woodleyi*, or ca. 4× length of flagellomere 2; wing shorter and broader, tip of R_5 ends at tip of wing (vs. before), cell d shorter (L/W 1.75 vs. ≥2.0). Mesotibia with 2 subequal spurs (vs. 1), one is 0.7× length of other.

Description: Based on female. Body length 5.60 mm; antenna length 0.74 mm; thorax length 1.66 mm; wing length 2.87 mm; abdomen length (everted) 3.38 mm. **Head:** Broader than thorax, slightly flattened anteroposteriad; occiput greatly recessed, occipital foramen and its perimeter deeply recessed, such that antepronotum nearly entirely recessed. Eye: Female: Large, dichoptic, occupying much of frontal, dorsal, ventral, and all of lateral surfaces of head; frons well exposed; no differentiation of facets; eyes completely bare; medial/inner margins slightly divergent dorsal to ventrally; small emargination near antennal base. Ocelli on low tubercle, ocelli obscured. **Antenna:** Projecting forward; with 8 flagellomeres, submoniliform, flagellomeres tapered in width apically; flagellomere 1 width 4× that of flagellomere 8; flagellomere lengths relative to segment 1: 1.0 : 0.25 (2) : 0.25 (3) : 0.25 (4) : 0.20 (5) : 0.17 (6): 0.26 (7): 0.46 (8); no apical stylus; all flagellomeres with sensillar foveae; scape and pedicel funnel shaped; length of antenna 0.68 mm; antennal sockets appear contiguous. **Mouthparts:** Face receding, clypeus not fully visible, mouthparts well exposed beyond oral margin; palp 2-segmented, basal palpomere slightly longer and narrower than apical one. Labellum well developed, large, length approximately equal to length of head. **Thorax:** Apparently all dark, perhaps originally black, with very little punctation and setulae. Antepronotum well developed, largely recessed into occipital concavity; postpronotum not substantially enlarged; postpronotal lobe narrow, lateral; pair of short, very faint paramedian sulci on anterior portion of scutum, posteriorly ending in transverse suture. Transverse suture well developed, moderately impressed, dorsal portion curved posteromediad. Proscutellum well developed; scutellum longer than wide, no spines. Posterior portion of anepisternum slightly bulging; katepisternum ventrally extended, not quite pendulous, medial margins of both katepisterna meeting on venter of thorax.

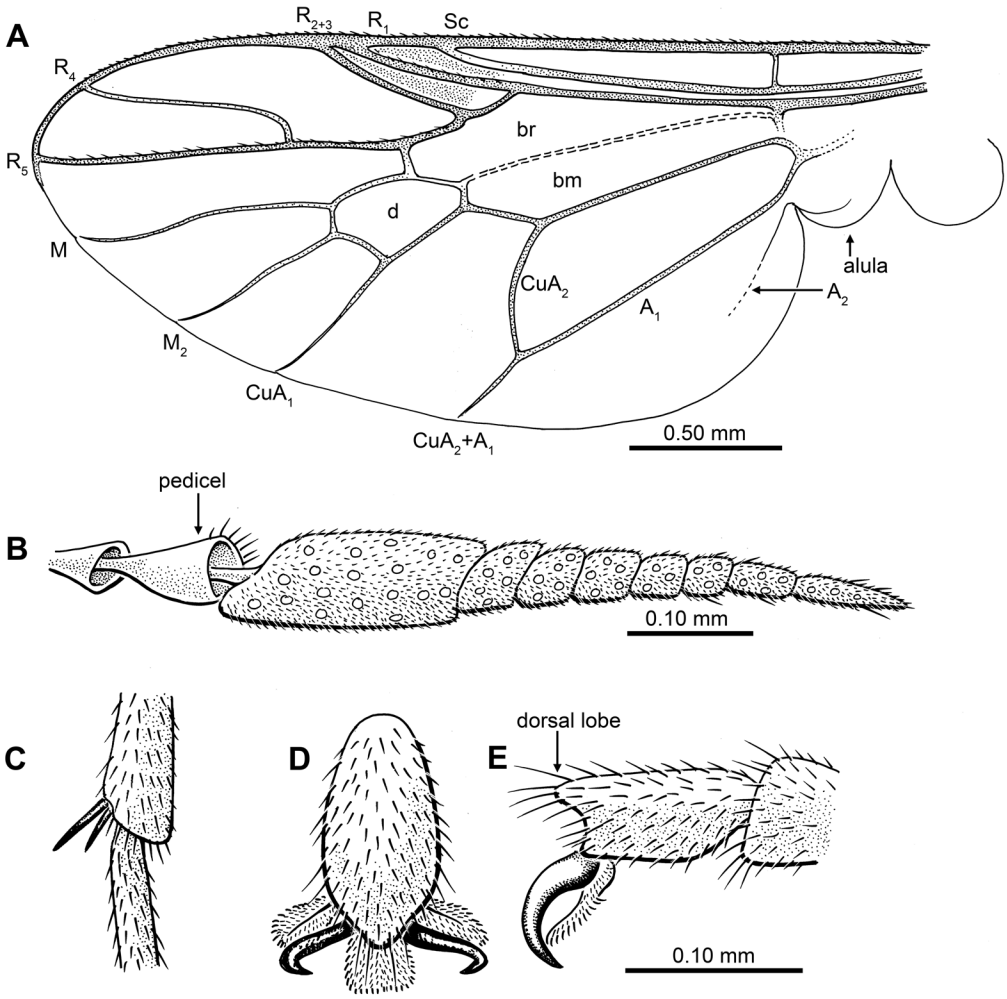

FIG. 8. *Normyia telescopica*, new genus and species (Stratiomyidae), JZC Bu-104, holotype. **A.** Wing. **B.** Antenna. **C.** Mesotibial apex, with spurs. **D.** Apical tarsomere with pretarsal structures, dorsal view. **E.** Apical tarsomere with pretarsal structures, lateral view.

Wing: Wing short and broad, W/L 0.42. Sc complete, slightly longer than half wing length; C ends slightly past tip of R_5. R and R_1 close and parallel to Sc, diverging slightly at apices. Stem of Rs very short, 0.3× length of R_1; R_{2+3} slightly shorter than R_1, convergent, apices of veins very close at wing margin; fork of R_4-R_5 long, base of fork only slightly distal to level of cell d apex; R_4 diverges from stem at right angle, then slightly divergent from stem of $R_{4\text{-}5}$, R_5 straight even to tip, ending at apex of wing. Pterostigma between apex of Sc and R_1, and between R_1 and R_{2+3}, r-m crossvein slightly proximal to middle of cell d; base of M between cells br and bm very faint, not tubular or at all sclerotized. M_1 faintly curved; apices of M_1, M_2, CuA_1 tapered and evanescent, not meeting wing margin or barely so; bases of M_1 and M_2 meeting truncate apex of cell d separately (e.g., left wing of holotype). Cell d small; cell br longer than bm, both cells narrow. CuA_2 arched, meeting A_1 well before wing margin. Anal lobe well developed; A_2 short, faint; alula

and upper calypter well developed. **Legs:** Robust, femur significantly longer than other segments, apices of femora with long ventral slit near articulation with tibia. Tibial spurs 0-2-0, mesal one of mesotibial pair 0.7× size of lateral one, lateral spur slightly shorter than width of tibial apex, distal portions of spurs heavily sclerotized. Leg segment lengths: femur > tibia > tarsus, basitarsomere = combined lengths of tarsomeres 2–5. Dististarsomere with produced apicodorsal lobe; empodium pulvilliform; pulvilli slightly shorter than pretarsal claws. **Abdomen:** Female: large, anteriorly broad, moderately dorsoventrally flattened. Tergites 1–5 each with transverse furrow impressed near middle of tergite, furrows deepest on tergites 2–4, furrow lengths ca. 0.8–0.9× tergite width. **Male Terminalia:** unknown. **Female Terminalia:** Segments 6–10 telescoping (at least partially), apically tapered, with substantial intersegmental membrane. Sternites well developed. Cerci sheared off at amber surface (e.g., segmentation not visible).

Types: Holotype, female, JZC Bu-104.

Etymology: The species name is derived from the New Latin *telescopicus* (literally, "far-seeing"), but used here as a feminine adjective in reference to the telescoping posterior segments of the female abdomen.

Comments: The unique specimen was trimmed and polished into a small, irregular polygonal piece 8 × 5 × 4 mm, to maximize views of various structures. It was separated from a cabochen of amber that also contains a female *Parapolycentropus* scorpion fly.

Normyia longistyli, new species

Figures 6A, 9, 41

Diagnosis: Readily distinguished from other stratiomyids in Burmese amber by the long, thin apical flagellomere (length > than combined lengths of flagellomeres 6 + 7), and by vein M tubular (vs. nebulous) between cells br and bm; other features include 0-1-0 tibial spurs, R_{2+3} long, parallel to (vs. converging with) R_1 as in *Narcissimyia,* but *N. longistyli* with wing broader and cell d shorter; R_4+R_4-R_5 straight (vs. upturned), apex of R_5 ending before wing tip. Terminal abdominal segments of female not telescoping.

Description: Based on female. Body length 3.46 mm; thorax length 1.08 mm; wing length 2.07 mm; abdomen length 1.83 mm. **Head:** Female only: Large, significantly broader than thorax, slightly compressed dorsoventrally; frons dark, inner margins of eyes widely separated, by distance slightly greater than outside margins of lateral/posterior ocelli; occiput dark, slightly concave, occipital foramen relatively large; occiput dark, with fine setulae only. Face and oral region entirely ventral. Eye: Female: Large, dichoptic, occupying all of lateral surface of head, much of dorsal, frontal, ventral surfaces; facets not differentiated. Eyes completely bare; inner margins bordering frons parallel, very small emargination near antennal bases; inner margins bordering face subparallel; no cheek exposed laterally. Ocelli on raised tubercle, with anterior ocellus directed forward, posterior ocelli directed laterally. **Antenna:** Projecting forward, with 8 flagellomeres, submoniliform, evenly tapered in width apicad; flagellomere 1 width 6× that of flagellomere 8; apex without stylus but with fine setae; all flagellomeres with sensillar foveae; scape and pedicel funnel shaped, scape shorter, pedicel with apical whorl of setae, length of antenna 0.50 mm; lengths of flagellomeres relative to flagellomere 1: 1.0 (1) : 0.30 (2) : 0.20 (3): 0.25 (4) : 0.36 (5) : 0.40 (6) : 0.40 (7) : 1.10 (8); antennal sockets very close, touching medially. **Mouthparts:** Labrum not visible, clypeus relatively flat, narrow, bounded laterally by fracturelike sutures; palps light, 2-segmented, apical palpomere clavate, basal one cylindrical. Labellum well developed, fleshy, and membranous, with 18–20 pseudotracheae on each lobe. **Thorax:** Deep, scutum moderately arched in lateral view. Scutum, scutellum, pleura apparently all dark, but probably iridescent-metallic originally (judging from spectral highlights). Scutum and scutellum evenly, densely, and very finely punctate; each punctation with fine setula; small

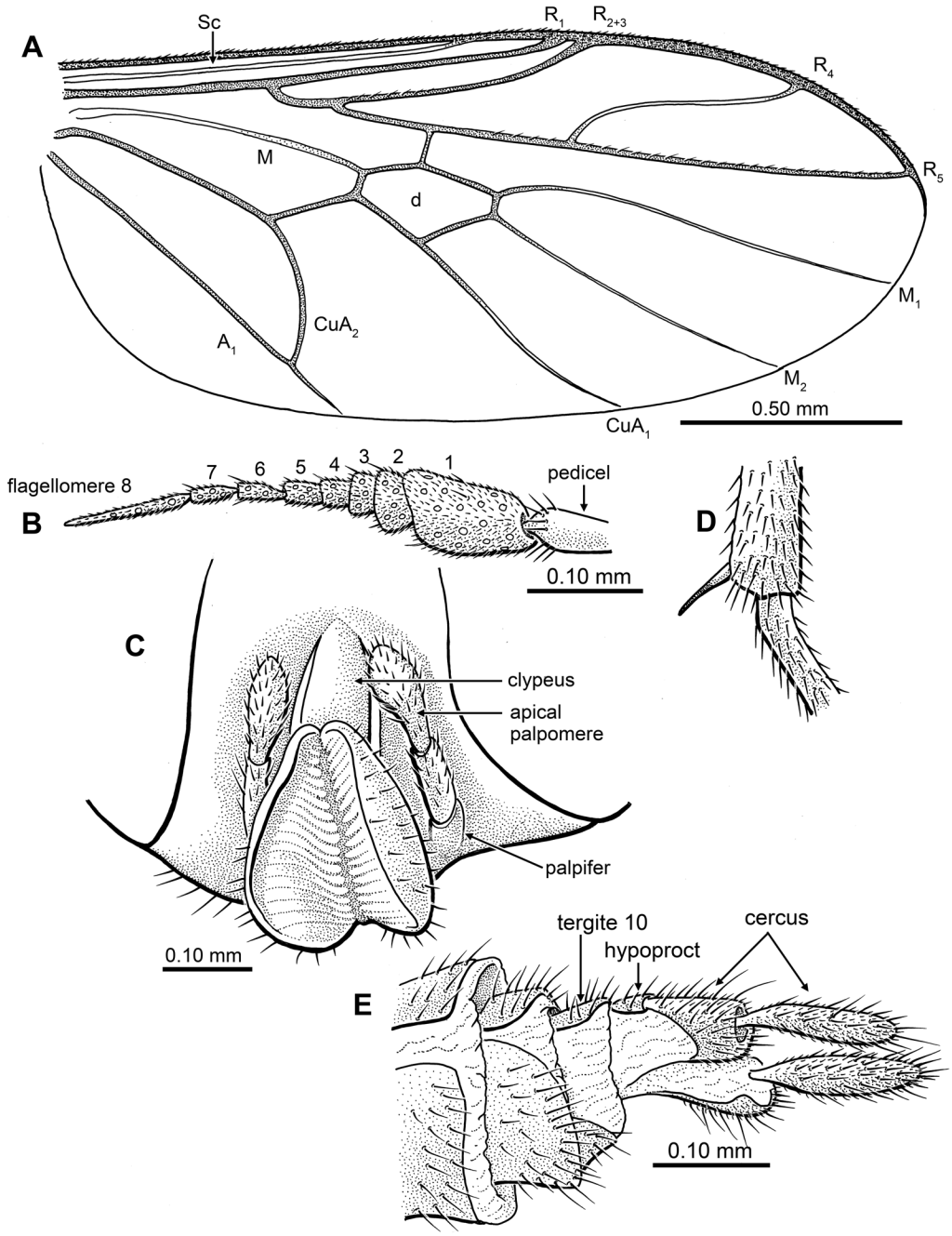

FIG. 9. *Normyia longistyli*, new genus and species (Stratiomyidae), AMNH Bu-SE021, holotype. **A.** Wing, reconstructed. **B.** Antenna. **C.** Anterior portion of head, ventrofrontal view. **D.** Female terminalia, ventrolateral view.

sparse punctate area on katepisternum. Antepronotum very well developed, but short, without fine, stiff setae; anterior end of antepronotum apparently fitting over collarlike ledge on dorsal margin of occipital foramen. Postpronotum well developed, edges discrete, bordering posterolateral margin of antepronotum; postpronotal lobe small, posterior portion slightly protuberant; anteroparamedian sulci not present on scutum. Transverse suture well developed, deeply impressed, inner apices converging medially; sutures forming pair of low, rounded lobelike portions of scutum posteriorly. Small, narrow, lenticular proscutellum present; scutellum narrow, length approximately equal to width, no spines. Posterior portion of anepisternum slightly protuberant; katepisternum ventrally extended, moderately pendulous, ventral margin ending at middle of mesocoxa; medial margins of katepisterna meeting ventrally. **Wing:** Relatively broad. Sc complete, long, apex meets C at level of crossvein r-m; C ends slightly past tip of R_5. R and R_1 close and parallel to Sc, first two converging slightly at apex, nearly touching where they meet C. Rs very short, 0.24× length of R_1; R_{2+3} is 0.84× length of R_1; fork of R_4-R_5 long, length of R_4 0.69× that of R_5, base of fork distal to level of cell d apex; R_4 very slightly sinuous, curved primarily at base (not perpendicular to R_5), R_5 virtually straight, tip ending before wing tip. Faint pterostigmatic area very faint; base of vein M between cells br and bm fine but tubular. M_1 very faintly curved; apices of M_1, M_2, CuA_1 tapered and evanescent, barely meeting wing margin; bases of M_1 and M_2 meeting truncate apex of cell d separately. Cell d short, W/L 0.50; cell br longer than bm, both cells narrow. CuA_2 very arched, meeting A_1 well before wing margin. Anal lobe well developed; anal veins, alula not visible. **Legs:** Robust, covered with fine setulae, tibial spurs 0-1-0; mesotibial spur straight, slightly shorter than width of tibial apex, apical half of spur well sclerotized. Lengths of leg segments: femur > tibia > tarsus, basitarsomere > combined lengths of tarsomeres 2–5. Tarsomere 5 with dorsal apex extended into small lobe; empodium pulvilliform, empodium and pulvilli slender, significantly shorter than pretarsal claws. **Abdomen:** Anteriorly broad, flattened dorsoventrally. Tergite 1 broadest, tergites evenly tapered in width distad. Tergites 2–6 each with transverse furrow impressed near posterior margins, furrows deepest on tergites 2–5 (faint on tergite 6), furrow lengths ca. 0.9× tergite width; 9 tergites exposed. **Female Terminalia:** Cercus 2-segmented, segments approximately equal in length; basal cercomere thicker, cylindrical; segments 6–8 probably telescoping, at least moderately.

Types: Holotype, male AMNH Bu-SE021.

Etymology: From the Latin *stilus* (noun, a pointed instrument), in reference to the long apical flagellomere.

Comments: The wing venation needed significant reconstruction since both wings are lying immediately over each other and overlapping. The fly was trimmed to 6 × 5 × 3 mm piece, from a cabochen containing an orthopteran hind leg; the amber contains a light suspension of fine particles.

***Narcissomyia*, new genus**

Diagnosis: Antenna with 8 flagellomeres, tapered apicad, most longer than wide; eyes bare, holoptic in male; palp 2-segmented; no scutellar spines; tibial spurs 0-1-0, mesotibial spurs long, slender, apex slightly hooked; Abdominal tergites 2–6 each with deeply impressed transverse sulcus; thorax deep in lateral view; wing slender W/L 0.34, Rs branching from R slightly basal to level of CuA_2 (vs. apical to this), cell d long (L/W 3.2 vs. ≤ 2.5 in almost all other stratiomyids); CuA_2 strongly arched; R_4 long, forking from R_{4+5} at level of m_1-m_2 crossvein. Male: gonostylus with 3 apical spines, gonocoxa with strongly curved basal-medial spine. Female terminalia not telescoping, cerci slender.

Type Species: *Narcissomyia bella*, new species.

Etymology: After the beautiful mythological youth of Greek mythology, Narcissus, in reference to the exquisite preservation of the holotype male, plus *myia*, Greek for "fly."

***Narcissomyia bella*,** new species

Figures 6B, 10, 42

Diagnosis: As for genus, by monotypy.

Description: Male holotype, female paratype (respectively): antenna length 0.70, (not measured); body length 4.17, 4.83 mm; thorax length 1.68, 148 mm; wing length 3.49, 3.07 mm; abdomen length 2.09, 2.49 mm. **Head:** Large, significantly broader than thorax, with extensive dorsal surface, somewhat flattened dorsoventrally; occiput surfaces behind eyes bulging slightly, central half of occiput surrounding occipital foramen concave; occiput dark, with fine setulae only. Eye: Male: very large, holoptic, occupying nearly all of nonoccipital portion of head; facets with dorsoventral differentiation, dorsal ones ca. 2× diameter of ventral ones, a discrete transverse separation between the two. Eyes completely bare; medial/inner margins meeting from anterior end of ocellar triangle to just dorsal to antennal bases, strongly divergent just above antennae, slightly emarginate near antennal bases and with small, dark callosity within emargination; inner margins of eyes ventrally strongly divergent posteriad; very little cheek exposed laterally. Female: Eyes dichoptic, with significant amount of frons exposed, no differentiation of facets. Ocelli on raised tubercle, with anterior ocellus directed forward, posterior ocelli directed laterally. **Antenna:** Projecting forward, with 8 flagellomeres, submoniliform, evenly tapered in width apically; flagellomere 1 width 4.5× that of flagellomere 8; no apical stylus; all flagellomeres with sensillar foveae; scape and pedicel funnel shaped, latter with apical whorl of setae, length of antenna 0.60 mm; lengths of flagellomeres relative to flagellomere 1: 1.0 (1) : 0.44 (2) : 0.40 (3): 0.44 (4) : 0.38 (5) : 0.44 (6) : 0.32 (7) : 0.48 (8); antennal sockets very close, possibly touching medially. **Mouthparts:** Face fully ventral, steeply receded posteriad, moderately concave; clypeus and labrum not visible in either specimen, apparently quite small; palps light, 2-segmented, apical palpomere significantly broader than distal one in lateral view (laterally flattened). Labellum well developed, fleshy and membranous, exposed well beyond oral margin. **Thorax:** Scutum, scutellum, pleura apparently all dark; scutum and scutellum evenly, densely, and very finely pimplate; each pimple with fine setula; small sparse pimplate areas on katepisternum and anepisternum. Antepronotum very well developed, with very fine, stiff setae laterally; postpronotum well developed, pimplate, largely separate from lateral margins of antepronotum; postpronotal lobe narrow, triangular, posterior end slightly protuberant; anteroparamedian sulci not present on scutum. Transverse suture very well developed, deeply impressed, inner apices converging posteromedially; sutures forming pair of rounded lobelike portions of scutum posteriorly. Small proscutellum present, but well developed, discrete; scutellum narrow, length greater than width, no spines. Posterior portion of anepisternum large, protuberant portion pointed; katepisternum ventrally extended but not pendulous, ventral margin ending at middle of mesocoxa; medial margins of both katepisterna meeting ventrally. Postnotum a narrow tongue lying between lateral lobes of tergite 1. **Wing:** Relatively long and slender, linear, W/L 0.34. Sc complete, long, 0.47× wing length; C ends slightly past tip of R_5. R and R_1 close and parallel to Sc, diverging slightly at apices. Stem of Rs very short, 0.21× length of R_1; R_{2+3} and R_1 of equal length, R_{2+3} convergent with R_1 only at apex, apices of veins very close at C; fork of R_4-R_5 long, base of fork slightly distal to level of cell d apex; R_4 not sinuous, curved primarily at base (not perpendicular to R_5), R_5 entirely straight, tip ending before wing tip. Faint pterostigma between Sc and R_1, and apices of R_1 and R_{2+3}, r-m crossvein slightly basal to middle of cell; base of M between cells br and bm very faint, not tubular or at all sclerotized. M_1 very faintly curved; apices of M_1, M_2, CuA_1 tapered and evanescent, barely meeting wing margin; bases of M_1 and M_2 meeting truncate apex of cell d separately (e.g., left wing of holotype), though width of cell apex varying significantly. Cell d fairly long, W/L 0.33; cell br longer than bm,

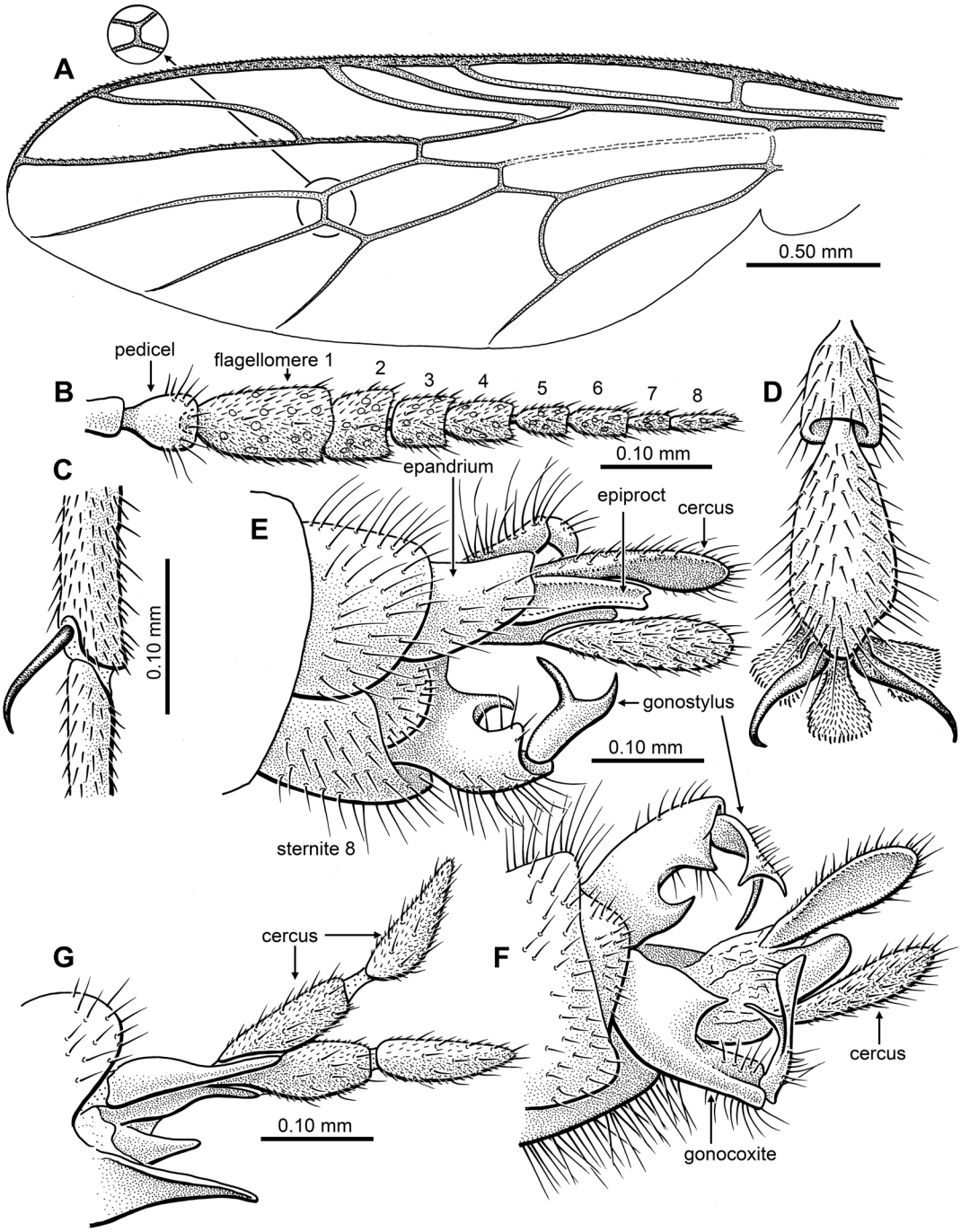

FIG. 10. *Narcissomyia bella*, new genus and species (Stratiomyidae). **A–F**: AMNH Bu-SE3/1, holotype male. **G**: AMNH Bu-Pk01, paratype female. **A.** Wing. **B.** Antenna. **C.** Mesotibial apex, showing spur. **D.** Tarsomeres 4, 5, dorsal view, with pretarsal structures. **E.** Male terminalia, dorsolateral view. **F.** Male terminalia, ventrolateral view. **G.** Female terminalia, left lateral view. Panels C, D to same scale.

both cells narrow. CuA_2 very arched, meeting A_1 well before wing margin. Anal lobe slender; A_2 not present/visible; alula small. **Legs:** Robust, covered with fine setulae, tibial spurs 0-1-0; mesotibial spur long, narrow, apically slightly hooked, length slightly greater than width of tibial apex, spur well sclerotized. Lengths of length segments: femur > tibia > basitarsomere > combined lengths of tarsomeres 2–5. Tarsomere 5 with dorsal apex extended into small lobe; empodium pulvilliform, slightly broader than pulvilli; empodium and pulvilli slightly shorter than pretarsal claws. **Abdomen:** Broad, flattened dorsoventrally. Tergites 2–5 each with transverse furrow impressed near posterior margins, furrows deepest on tergites 2–4, furrow lengths ca. 0.9× tergite width; 9 tergites exposed in male and female. **Male Terminalia:** Well developed, mostly exposed. Gonocoxa short, broad, fully articulating with gonostylus, having hooklike spine on mesal margin; gonostylus with three large spines, two distally and one medial. Epiproct narrow, tonguelike, lying between bases of cerci; cercus 1-segmented in male, ovoid, lateral to epiproct. **Female Terminalia:** Cercus 2-segmented, segments approximately equal in length, basal cercomere slightly thicker, apical cercomere with acute apex; terminalia not telescoping. Sternite 10 possibly present.

Types: Holotype, male AMNH Bu-SE3/1. Paratype female AMNH Bu-Pk1.

Etymology: From the feminine form of the Latin adjective, *bellus* ("beautiful"), for the beautiful preservation of the holotype.

Comments: The holotype is in a thin piece slabbed to 5 mm thickness (14 × 8 mm dimensions), surfaces parallel to the lateral sides and wing of the fly. The amber has superb clarity and contains only some plant trichomes. The fly is complete and preservation excellent. Paratype female is in a cabochen 12 × 10 × 5 mm with some small bubbles; a flattened surface was made over the left side of the fly, the right side is close to surface of the cabochen (so could not be flattened). The fly is complete, though slightly crumpled; scutum has metallic-reflective highlights.

INFRAORDER TABANOMORPHA

This is a monophyletic group of some 5300 species in five extant families. Although there is a diverse fossil record of tabanomorphs that extends into the Jurassic and Cretaceous, there are no extinct families. Jurassic and Cretaceous fossils attributed to the Rhagionidae are very diverse, but many of them are taxonomically problematic. As a result, I have generally avoided the Rhagionidae in Burmese amber for this study, with the exception of four taxa that have some similarities to Athericidae and to spaniine rhagionids, but which I have left incertae sedis within Tabanomorpha.

In Tabanomorpha the small, relict families Pelecorhynchidae (50 species) and Oreoleptidae (1 species) have no fossil record. Pelecorhynchidae contains two or three genera and 51 species: *Glutops* Burgess (11 species: Holarctic), *Pelecorhynchus* Macquart (38 species: Australia and Tasmania [Mackerras and Fuller, 1942], Chile [Llanos et al., 2015]), and *Pseudoerinna* Shiraki (2 species: Asia, sometimes put into Rhagionidae). These are generally stout, pilose flies, inhabiting xeric areas where they feed from flowers. The monotypic *Oreoleptis* Zloty et al. (Oreoleptidae) is known only from western North America, where it has been reared from larvae living in cold streams in the Cascade Mountains in Washington and the Rocky Mountains in Alberta (Zloty et al., 2005). *Oreoleptis* larvae have prolegs that are even longer than those in athericid larvae (Zloty et al., 2005). *Qiyia jurassica*, from the Daohugou beds (Middle Jurassic of Inner Mongolia, China (Chen et al., 2014), is known entirely as larvae. It was placed in Athericidae based on its seven pairs of crocheted prolegs and long anal tubercles, although it uniquely possesses a median, radial structure on the ventral side of the thorax, interpreted as a sucker used for putatively parasitizing the salamanders that are abundant in this deposit (Chen et al., 2014). The larvae of all tabanomorphs, where their diet is definitely known, are predaceous, and have features that

partly define the group, including the possession of a poison canal on the larval mandible. Other defining features, in the adult, include an inflated or bulbous clypeal region laterally bounded by deep paraclypeal sulci and by a cercus with a ventral lobe in the female.

Relationships among families of the "tabanoid" group are well established: Pelecorhynchidae (Oreoleptidae (Athericidae + Tabanidae)), based on morphological and molecular studies (Hennig, 1973; Stuckenberg, 1973; Nagatomi, 1977; Woodley, 1989; Zloty et al., 2005; Kerr, 2010; Wiegmann et al., 2011). Rhagionidae in its modern sense (Kerr, 2010) are the sister group to the Tabanoidea, and Vermileonidae are either a sister group to Rhagionidae or to Rhagionidae and all other tabanomorphs (Woodley, 1989; Kerr, 2010; Zloty et al., 2005; Wiegmann et al., 2011). The phylogenetic position of Vermileonidae has traditionally been ambiguous.

The sister-group relationship of Athericidae + Tabanidae is very well supported (Stuckenberg, 1973; Woodley, 1989; Kerr, 2010; Wiegmann et al., 2011). Defining morphological features include a "scale" (small, flattened lobe) immediately posterior to the hind thoracic spiracle; tergite 1 divided along the midline; a compact, dorsoventrally flattened abdomen; a 1-segmented cercus; R_4-R_5 often widely divergent and encompassing the wing tip, with R_4 sinuous; and a small proscutellum present (although this also occurs in Pelecorhynchidae, but not in *Oreoleptis*). Further, the epandrium is enlarged and elongate in both families (Stuckenberg, 1973), males have aedeagal tines, and the female labrum has a dorsoproximal process (Nagatomi and Soroida, 1985).

Tabanomorpha is notorious for the hematophagous females of most species of Tabanidae, many Athericidae, and some Rhagionidae (reviewed by Nagatomi and Soroida, 1985; Kerr, 2010). Based on relationships it appears that hematophagy arose twice in tabanomorphs: once in Tabanidae + Athericidae, and again in the closely related, relatively derived rhagionid genera *Symphoromyia* Frauenfeld (Holarctic: 36 species) and *Spaniopsis* White (Australia: 7 species) (Kerr, 2010). In hematophagous tabanomorphs the mandibles, hypopharynx, and laciniae are approximately equal in length to the labrum, instead of shorter (Nagatomi and Soroida, 1985), as well as having the tips of the mandibles finely serrate.

Striking new stem-group tabanomorphs and Tabanidae are described from mid-Cretaceous Burmese amber, below. Based on the long mandibles with serrate tips in the females of *Atherhagiox simulans*, n. gen., n. sp., and *Galloatherix completus*, n. sp., these species appear to have been hematophagous. Features of many of the fossils are revealing about the chronology of characters that partly define Athericidae and Tabanidae, such as 1-segmented cerci and a postmetaspiracular scale.

STEM-GROUP TABANOMORPHS

Three genera discussed here have some similarities with Athericidae, *Atherhagiox,* n. gen., *Galloatherix* Nel, and *Palaepangonius* Ren. I am placing them as incertae sedis within Tabanomorpha since they lack too many of the features of Athericidae and appear to be quite basal.

Athericidae are a modest-sized family of approximately 90 living species in nine genera. It was not until the paper by Stuckenberg (1973) that the family was erected, the living genera traditionally having been grouped into Rhagionidae. Three of the living genera are essentially Holarctic (with a few species in Africa) (*Atherix* Meigen, *Atrichops* Verrall, *Ibisia* Rondani); one genus is Asian (*Asuragina* Yang and Nagatomi); three others are in the southern areas of Africa (*Pachybates* Bezzi, *Trichantha* Stuckenberg) or South America (*Xeritha* Stuckenberg). *Suragina* Walker are the largest and most cosmopolitan genus, with about 40 species. *Dasyomma* Macquart, with about 30 species, have a classic austral distribution that includes Australia, Tasmania, as well as Chile and Argentina (the South American species revised by Coscarón and Coscarón, 1995) and Bolivia (Woodley, 2007). *Dasyomma* species are striking, black and orange/yellow, and in at least several of them the

coloration in strongly sexually dimorphic (Woodley, 2007). The genus is further significant since it lacks the suprametacoxal pit distinctive to Athericidae, and has an antenna with an ovoid basal flagellomere and apical style (vs. reniform with dorsal attachment) (Stuckenberg, 1973). Without question, *Dasyomma* are the living sister group to all other extant athericids (Stuckenberg, 1973; Nagatomi, 1984; Woodley, 2007). As in all athericids, in *Dasyomma* the antennal style is aristalike and the tips of wing veins R_1 and R_{2+3} fuse, meet, or nearly so.

The resemblance of *Atherhagiox*, *Galloatherix*, and *Palaepangonius* to Athericidae is based on the following features: basal flagellomere reniform, with remainder of flagellum an aristalike style; R_{2+3} converging toward tip of R_1; and R_4-R_5 fork with tips of these veins encompassing the tip of the wing. These features, however, also occur in spaniine Rhagionidae (Kerr, 2010), where R_{2+3} is often short, sinuous, and approximating R_1. *Symphoromyia* Frauenfeld has a flagellum very similar to these fossil genera. In fact, these fossils lack features that define Tabanoidea (Tabanidae + Athericidae): cerci are 2-segmented (vs. 1), abdomen is not dorsoventrally flattened, and actually telescoping in *Atherhagiox*; and where observable (i.e., *Atherhagiox*, *Galloatherix*), a suprametacoxal pit and post-metaspiracular scale are absent. Tergite 1 (e.g., divided or not) is generally too obscured to determine in the fossils. Tibial spurs are equivocal in diagnostic value here; in the fossil genera tibial spurs are 1-2-2, or in *Atherhagiox* 0-2-1 (vs. 0-2-2 in Athericidae). Two features that the fossil genera share with Athericidae and Tabanidae rather than Rhagionidae are the shape and position of the palps and a deeply incised basicosta. Palps are arched and converge frontally in Tabanoidea, versus being straight and parallel to the flanks of the proboscis in Rhagionidae. Lastly, the tibiae of the fossils, or at the least the metatibiae, bear a dorsolongitudinal row of fine, dark spinules. Such spinules occur in Rhagionidae, not Athericidae. Collective evidence indicates, therefore, that *Atherhagiox*, *Galloatherix*, and *Palaepangonius* may be closer to spaniine rhagionids than to Athericidae.

Compared to Rhagionidae, the geological record of Athericidae is modest. Eight genera have been described thus far, with only three genera and four species from the Tertiary. Generic status of compression fossil species of *Atherix* and *Atrichops* in Miocene and Eocene shales (Evenhuis, 1994) will need to be evaluated. Stuckenberg (1973) described two species of *Succinatherix* in Eocene Baltic amber, the genus purportedly related to *Ibisia*. Other species in Baltic amber originally described as athericids were eventually found to be in the rhagionid genus *Symphoromyia* (reviewed by Stuckenberg, 1973). The first described Cretaceous athericid is *Palaepangonius eupterus* Ren, from the Early Cretaceous Yixian Formation of China, originally placed in Tabanidae (Ren, 1998a, 1998b) but subsequently transferred to Athericidae by Zhang (2012) on the basis of venation. Mostovski et al. (2003) described five additional Early Cretaceous species, placed in *Athericites* Mostovski et al., and attributed to Athericidae but known just from lithified wings. These two Cretaceous genera are synonymized, below. Another putative athericid from the Cretaceous of China is *Sinocretomyia miniscule* J.-F. Zhang, from the Laiyang Formation (Zhang, 2012), which plesiomorphically has an ovoid (vs. reniform) basal flagellomere with apical style, as in *Dasyomma*. *Galloatherix incompletus* Nel et al. is known from an isolated wing (fig. 11D) in late Early Cretaceous amber from France (Nel et al., 2014). A species in Burmese amber described here is placed into *Galloatherix* based on the very similar wing venation. Lastly, a species from the Late Jurassic of Australia, *Notoatherix antiqua* Oberprieler and Yeates (2014), also known only from an isolated wing, has the characteristic near fusion of the tips of veins R_1 and R_{2+3}, but this genus uniquely has an unforked vein R_{4+5}. The unusual Jurassic larva, *Qiyia jurassica* Chen et al. (2014), discussed above, is attributed to the Athericidae, but this remains to be conclusively

established. Despite the abundance of these larvae in the Daohugou beds, corresponding adults that are unambiguously athericids from the same deposits have yet to be recognized.

Genus *Palaepangonius* Ren

Palaepangonius Ren, 1998b: 66. Type species: *Palaepangonius eupterus* Ren, Yixian Formation (Early Cretaceous), Beipiao, Liaoning Province, China.

Athericites Mostovski, Jarzembowski, and Coram, 2003: 165. Type species: *Athericites gordoni* Mostovski, Jarzembowski and Coram. NEW SYNONYMY.

Palaepangonius zazicola (Mostovski, Jarzembowski, and Coram), 2003: 166. Zaza Formation, Baissa, Siberia. NEW COMBINATION.

Palaepangonius kensmithi (Mostovski, Jarzembowski, and Coram), 2003: 166. Weald Clay, Surrey, England. NEW COMBINATION.

Palaepangonius gordoni (Mostovski, Jarzembowski, and Coram), 2003: 167. Weald Clay, Surrey, England. NEW COMBINATION.

Palaepangonius finchi (Mostovski, Jarzembowski, and Coram), 2003: 167. Weald Clay, Surrey, England. NEW COMBINATION.

Palaepangonius sellwoodi (Mostovski, Jarzembowski, and Coram), 2003: 168. Purbeck Limestone, Dorset, England. NEW COMBINATION.

Emended Diagnosis: Revised from Ren (1998a) and Mostovski et al. (2003): Proboscis (known for two species) significantly longer than head, projecting forward, labellum small; hind tibia with one or two spurs. Basicosta well developed, deeply incised; apex of R_{2+3} converging toward apex of R_1, pterostigma between apices of these two veins dark, well developed; fork of R_4 and R_5 long, diverging acutely at level of apex of cell d, tips of veins encompassing wing tip; M_3 and CuA_1 slightly convergent; CuA_2 and A_1 convergent but not meeting before wing margin.

Comments: Zhang (2012) originally indicated that *Athericites* is a junior synonym of *Palaepangonius*, with which I concur, but that author did not officially synonymize the two genera. The wing venation of *P. eupterus*, as preserved or drawn by Ren (1998a), shows in the holotype the tip of vein R_5 ending at the apex of the left wing, which appears to be a preservational artifact; R_4 and R_5 encompass the apex in the right wing, interpreted by Ren (1998a) as the natural condition. Unfortunately, the species described by Mostovski et al. (2003) do not have bodies, so the existence of a proboscis cannot presently be confirmed. The main distinction between the two Cretaceous genera from eastern Asia is that in *Sinocretomyia* crossvein r-m and the base of CuA_1 are near the middle of cell d (instead of basally in *Palaepangonius*) (fig. 11). In both genera the basal flagellomere is ovoid with an apical attachment of the style.

In *Palaepangonius eupterus* the proboscis is long, which, along with placement of this species in Tabanidae, prompted Ren (1998b) to interpret this fly as a pollinator of Jurassic angiosperms, for which there is no direct (i.e., pollen) evidence. Various *Scaptia* and other living pangoniines with long proboscides are effective pollinators (Arroyo et al., 1982). It was later determined that the Yixian Formation is Early Cretaceous in age, not Jurassic (Swisher et al., 2002), and also that some other Jurassic-Cretaceous insects with long proboscides (including Brachycera) fed on nectar and pollen from extinct Bennettitales and other gymnosperms (Ren et al., 2009; Peñalver et al., 2015). Thus, inferences about paleodiets can be misleading when based entirely on modern analogs.

Palaepangonius glossa, new species

Figures 11A, 43

Diagnosis: Wing long and narrow, W/L 0.30, similar to *P. sellwoodi* (Mostovski et al.). Costa just distal to basicosta thickened (as in Tabanidae): R_{2+3} short, ending very near apex of R_1 but not meeting it; R_{4+5} nearly linear (not sinuous),

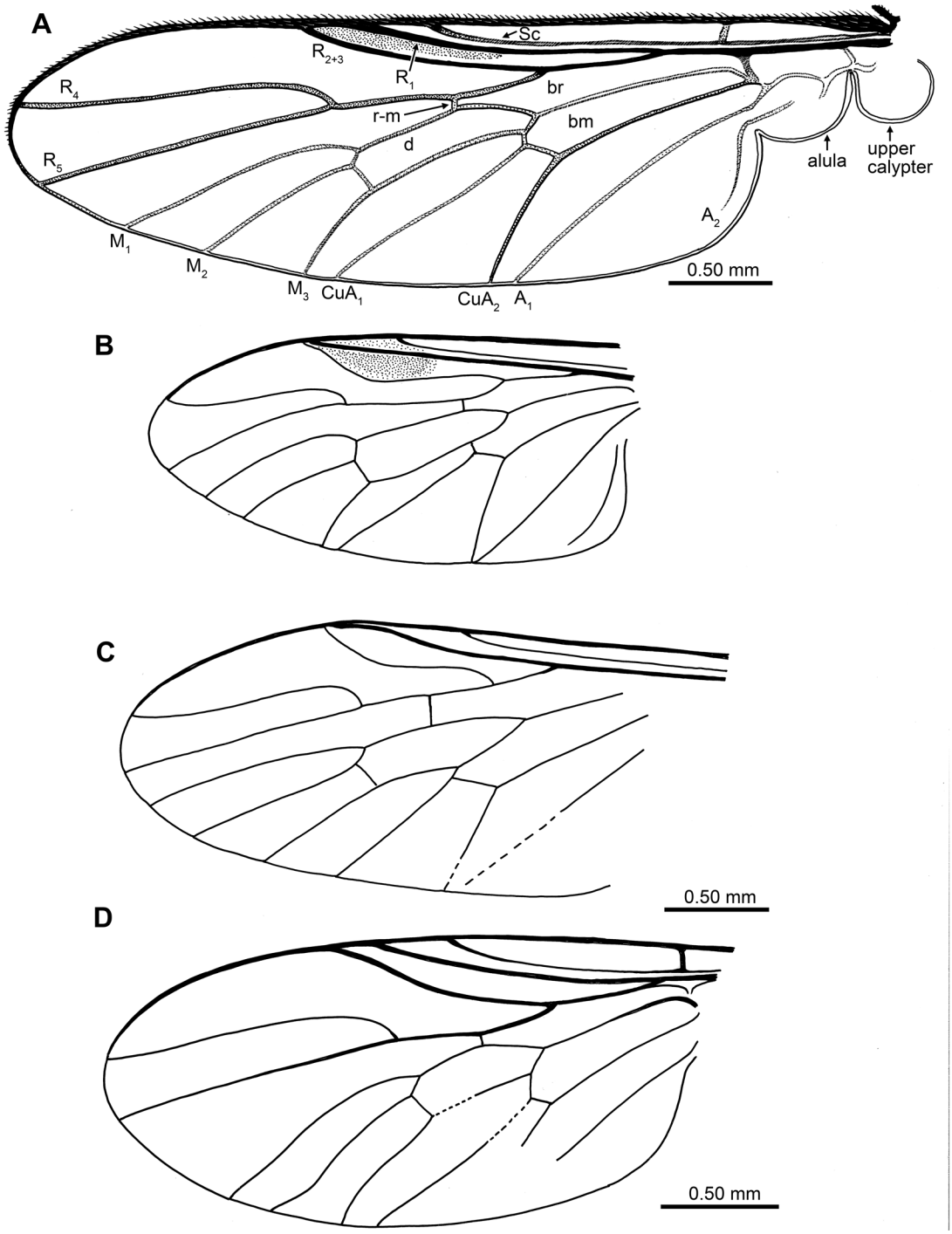

FIG. 11. Wings of assorted genera of Cretaceous Tabanomorpha. **A.** *Palaepangonius glossa*, new species, JZC Bu-248. **B.** *Athericites kensmithi* (ex: Mostovski et al., 2003). **C.** *Sinocretomyia miniscule* (ex: J.-F. Zhang, 2012). **D.** *Galloatherix incompletus* (ex: Nel et al., 2014). Not to the same scale.

close and parallel to Sc (as in *P. sellwoodi*); basal cells like those of *P. gordoni* (fig. 11). Differs from *P. eupterus* by the longer cell br, and by vein R_4 not sinuous and diverging from stem more acutely.

Description: Based on female. Body length 4.83 mm; thorax length 1.34 mm; abdomen length 2.93 mm; wing length 4.49 mm; proboscis length 1.67 mm. **Head:** Eyes large, dichoptic, in dorsal and lateral view with occiput visible posteriorly. No differentiation of facets. Eye bare, inner margins slightly divergent from vertex to antennae, virtually parallel. Frons essentially bare, with minute and very sparse setulae. Frons, ocellar tubercle, occiput black. Ocelli on low tubercle, with short, stiff setae. Occiput with short, stiff, scattered setae. Frontal region of head obscured by clumps of dense fungal mycelia. Postgena with some long, fine erect, light setae. **Antenna:** On low tubercle; scape small, ringlike; pedicel cylindrical; basal flagellomere subcircular, not reniform. Distal portion of antennal flagellum aristate, with fine pubescence; fine setalike stylus present. **Mouthparts:** Proboscis long, ca. 1.9× length of head, labellum long and slender, 0.37× length of entire proboscis. Palp 0.25× length of proboscis; slender (shape obscured); palps in frontal view converging, with tips meeting medially over proboscis. Mandibles-laciniae-labrum enfolded within labium (not visible). **Thorax:** Coated in milky layer, but most details visible. Dorsum appears dark through milkiness, with short, sparse, erect setae. Notopleural area with slightly thicker, stiff, short setae. Anepimeron and katepisternum with short, erect setae; other pleurites bare. Area around metathoracic spiracle and above metacoxa is obscured. Scutellum with fine, short setae on disk; longer ones on margin. Proscutellum appears to be present. **Wing:** Narrow and long, W/L 0.30. Sc long, 0.5× length of wing; R_1 slightly longer, with thickened apex; R_{2+3} slightly upturned, converging toward but not meeting apex of R_1. Fork of $R_{4\text{-}5}$ at same level as apex of cell d; tips of R_4 and R_5 straddling apex of wing, but veins only moderately divergent. Cell d narrow, slightly curved; veins M_1, M_2, M_3 present, first two slightly sinuous. Veins M_3 and CuA_1 slightly convergent. Cell br longer than cell bm. Cell cup open, veins CuP and A_1 not meeting. **Legs:** Long and slender. Tibial spurs 1-?-2, spurs long, lengths 1.5× (pro) to 2.0× (metathoracic) the apical width of respective tibia. Femora with no macrosetae or with very few, fine ones. Tibiae and tarsi setulose, without rows of short, black spinulelike setae on dorsal or ventral margins. Protarsi obscured. Hind coxa with anterior surface obscured. **Abdomen:** Partially preserved, segmentation obscured. Tergite 1 not visible. Sternites well developed. Female cerci 2-segmented, basal segment mostly obscured, apical segment cordate.

Type(s): Holotype, female, JZC Bu-248.

Etymology: Directly from the Greek, *glossa* ("tongue"), treated as a feminine noun in apposition

Comments: Unfortunately, critical areas of the thorax are obscured in the fossil, i.e., the metathoracic pleural area and tergite one (i.e, medially divided or not). The fly occurred in an ovoid cabochen originally 33 × 15 × 12 mm, lying at one end, and then separated. A flat surface was polished over the thorax and head plus wing. There are internal flows within the piece, with a suspension of particulate debris, trichomes, sand grains, and a beaded lacewing (Neuroptera: Berothidae).

Atherhagiox, new genus

Diagnosis: Differs from living and extinct athericids by having base of fork of R_{4+5} significantly proximal to level of apex of cell d (i.e., cell d is quite long). Further, veins M_1 and M_2 sinuous as in *Galloatherix*; like this genus and *Sinocretomyia* and *Palaepangonius*, R_{2+3} also sinuous, but its apex not in contact with apex of R_1. *Atherhagiox* further differs from *Sinocretomyia* by the reniform (vs. ovoid) basal flagellomere.

Type Species: *Atherhagiox ambiguum*, new species.

Etymology: The generic name is a combination of the two names of type genera of Athericidae and Rhagionidae—*Atherix* and *Rhagio*—and

refers to the hybrid set of characters of the new genus. The gender of the name is neuter.

Comments: *Atherhagiox* have similarities with certain Rhagionidae, and the boundaries between this family and Athericidae have historically been vague. Like the rhagionid genus *Symphoromyia*, the new genus has a reniform basal flagellomere with an aristalike terminal section of the flagellum and a sinuous R_{2+3}; both genera also have 0-2-1 tibial spurs. Other similarities are plesiomorphic: a vein R_{2+3} that does not converge with or approximate the apex of R_1; suprametacoxal pit (found in all athericids except *Dasyomma*) is lacking; cerci 2-segmented, and female terminalia telescoping. However, like athericids and unlike rhagionids, *Atherhagiox* have a deeply excised, lappetlike basicosta and arched palps. Mandibles are present in the female (these are absent in most Rhagionidae with the exception of *Symphoromyia*).

Atherhagiox ambiguum, new species

Figures 12B, C, D; 44

Diagnosis: Very similar to *A. simulans*, n. sp. (also known only as a female), except that *A. ambigua* has: smaller body size (3.5 mm, vs. 4.0); basal flagellomere more narrow; wing with vein Sc shorter; base of R_4 perpendicular (vs. acute) to stem of $R_{4\text{-}5}$; cells br and bm shorter (in *A. ambigua* cell bm is 0.24× length of wing, in *A. simulans* it is 0.34×); cell cup closed; CuA_2 and A_1 meeting just before wing margin (vs. at wing margin); $R_{4\text{-}5}$ more sinuous than in *A. simulans*.

Description: Based on female. Body length 3.52 mm; thorax length 0.90 mm; abdomen length 2.15 mm; wing length 2.81 mm. **Head:** Eyes large, dichoptic, bare, no dorsal-ventral differentiation of facets; dorsal margins of eyes extending above margin of head vertex; in lateral view eye occupying entire lateral surface (occiput not visible). Inner margins of eyes dorsally convergent toward level of antennae, then divergent ventrally. Ocelli on large, well-defined tubercle. Frons bare, no setae/setulae. Face with bulging clypeus, laterally bordered by deep sulci between clypeus and parafacial plates. **Antenna:** Aristate. Base membranous; scape and pedicel lengths approximately equal, dorsal portion of scape longer than ventral portion, without bristlelike setae; pedicel bean shaped, attachment slightly dorsal, with 2–3 stiff setae on ventrodistal margin; basal flagellomere reniform, its attachment to pedicel dorsal; apical portion of flagellum aristate, length 3× that of basal flagellomere, with microscopic pubescence, no minute apical style apparent. **Mouthparts:** Proboscis length ca. 1.5× that of head; labellum long, 0.7× length of theca, with fine setae on ventral surface. Labrum long, same length as lacinia + mandibles; tip of mandible with several minute teeth/serrations. Palps long, slender, gently curved (dorsally convex); 2-segmented, basal segment 0.3× length of distal segment; apical segment tapered distad. In frontal view palps closely flanking proboscis. **Thorax:** Dorsum and portion of pleura (anepisternum, anepimeron, katatergite, meron) dark brown. Scutum dorsally with fine, short, erect setae; longer, thicker setae at middle of scutum, along margins and on disk of scutellum, 9–10 on notopleural area. Postpronotal lobe with fine, light setae. No pubescence or setae on pleurites. Proscutellum present, very narrow. No post-metathoracic spiracular scale or suprametacoxal pit present. **Wing:** Short, broad, hyaline except for small pterostigmatic area over distal half of R_{2+3}. Minute setulae on dorsal surface at base of R-R_1. Vein C with very small, fine spinules to wing tip; basicosta well developed; tip of Sc reaches to 0.4× length of wing; R_1 runs very close to Sc, length 0.6× that of wing; R_{2+3} sinuous, apex not converging with apex of R_1; cells br and bm of nearly equal length; cell d long, narrow, slightly arched; apices of R_4 and R_5 barely encompass wing tip; R_4 branches from stem of $R_{4\text{-}5}$ very proximal to apex of cell d. Veins M_1, M_2, M_3 present, first two slightly sinuous. Veins M_3 and CuA_1 virtually parallel; cell cup closed, elongate, and narrow, CuP and A_1 meeting just before wing margin; vein A_2 present, nearly complete. Anal lobe well developed; alula well developed, approximately same size as upper calypter. Halter knob evenly

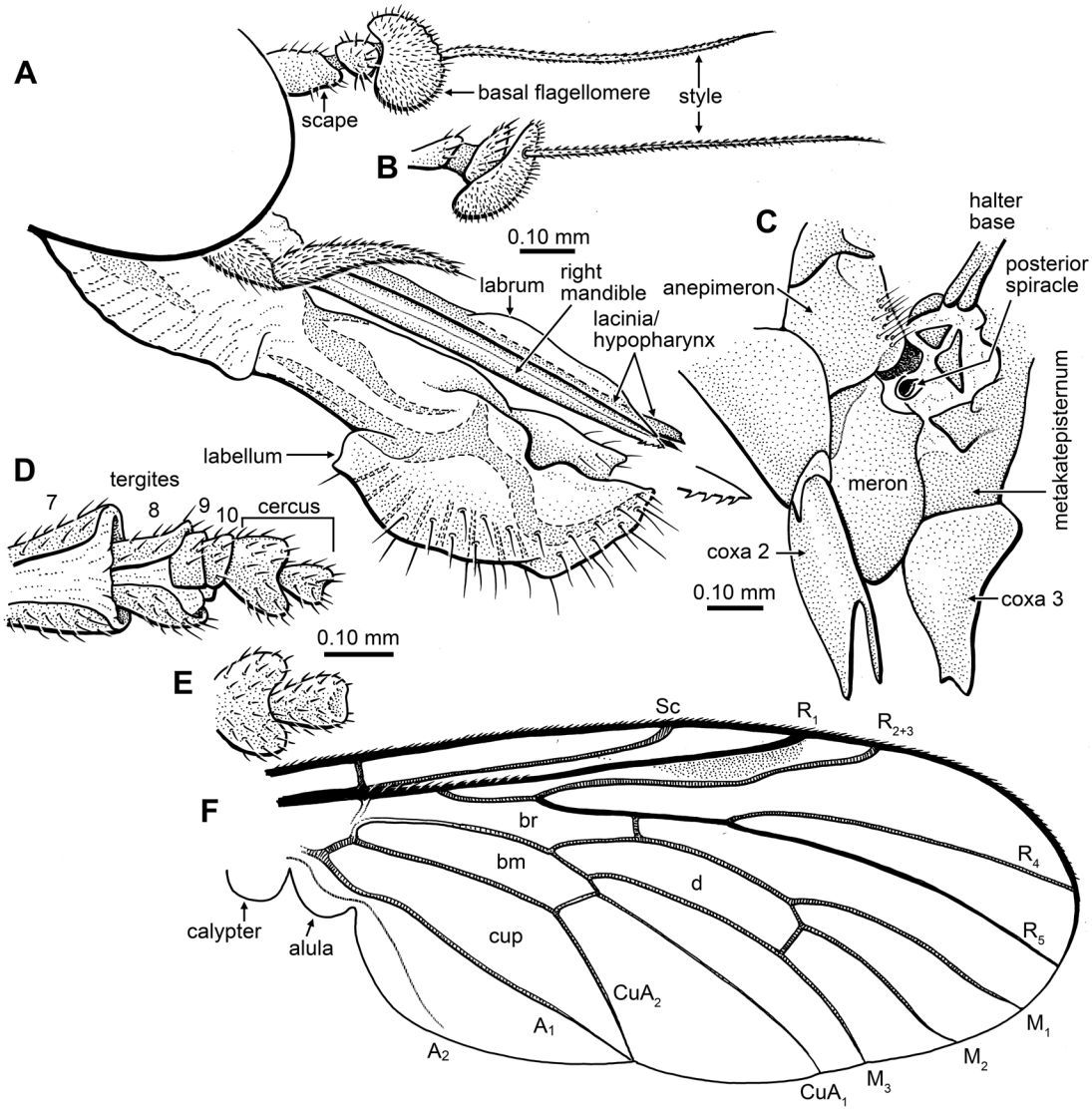

FIG. 12. *Atherhagiox,* new genus (stem-group Tabanomorpha). **A, E, F**: ***A. simulans***, new species, JZC Bu-288, holotype. **B, C, D**: *A. ambiguum*, new species, AMNH Bu-SE2/3, holotype. **A.** Lateral view of mouthparts, anterior part of head, and antenna. **B.** Antenna. **C.** Posteroventral portion of thorax, lateral view. **D.** Female terminalia, lateral view. **E.** Female cercus. **F.** Wing, upper surface.

drop shaped, symmetrical; dorsal and ventral portions brown with color pattern having discrete margins. **Legs:** Long, slender; largely yellowish grading to brown on tarsi. Pro- and mesofemur without macrosetae; metafemur with ventral row of very fine setae. Tibial spurs 0-2-1, middle spurs of equal length. All tarsi with ventral row of short, black, spinulelike setae; metatibia with dense dorsal row of spinules. Pretarsal structures small, empodium pulvilliform. Mesocoxa with dense setae; metacoxa without anterior knob. **Abdomen (female)**: Not dorsoventrally flattened, terminal segments tapering and telescoping; pleural membrane between tergites and sternites 2–4 broad;

spiracles in membrane, one for each of segments 2–4. Tergite 1 obscured (cannot determine if medially divided); tergites 2–4 large, 5–10 appear to be telescoping, significantly narrower than preceding segments. Tergites dark brown, heavily setulose; sternites light brown, well developed, with fine, sparse setulae. Dorsal portion of tergite 10 obscured (medial division not observable). Cerci 2-segmented, basal segment cordate in lateral view, ventral lobe slightly more extended; apical cercomere with small emargination on posterior margin.

Types: Holotype, female, AMNH Bu-SE2/3.

Etymology: The species name is from the Latin ("ambiguous"), and refers to the apparent relationships of *Atherhagiox* to Rhagionidae and/or Athericidae.

Comments: See above, under Tabanomorpha and genus. The fly is in a thin slab 3 mm thick, with two large, flat, parallel surfaces 12 × 13 mm, optimizing views of wings and sides of body. The fly is complete and the amber has superb clarity. The piece also contains some plant trichomes and bubbles.

Atherhagiox simulans, new species

Figures 12A, E, F; 45

Diagnosis: Very similar to *A. ambiguum*, n. sp., described above, with diagnositic differences as given for that species.

Description: Based on female. Body length 4.08 mm; thorax length 1.27 mm; abdomen length 2.12 mm; wing length 3.26 mm; proboscis length 0.80 mm. **Head:** Eyes large, dichoptic, bare, no dorsal-ventral differention. Frons bare, no setae/setulae. Face with bulging clypeus, laterally bordered by deep sulci between clypeus and parafacial plates. **Antenna:** Aristate. Base membranous; scape slightly longer than pedicel, scape without bristlelike setae; pedicel nearly spherical, with ring of small, stiff setae; basal flagellomere reniform, its attachment to pedicel apparently in center; apical portion of flagellum aristate, length 4× that of longest axis of basal flagellomere, with microscopic pubescence, no minute apical style apparent. **Mouthparts:** Proboscis length slightly greater than that of head; labellum long, 0.5× length of theca, with fine setae on ventral surface. Labrum long, same length as lacinia + mandible; tip of mandible with several minute teeth/serrations. Palps long, 0.4× length of proboscis, significantly wider at base and tapered to narrow apex, gently curved (dorsally convex); 2-segmented, basal segment 0.3× length of distal segment. **Thorax:** Scutum dorsally with fine, short, erect setae; longer, thicker setae at middle of scutum, along margins, on disk of scutellum, and in notopleural area. Postpronotal lobe with fine, light setae. No pubescence or setae on pleurites. **Wing:** Short, broad, W/L 0.42, hyaline except for small pterostigmatic area between distal halves of R_1 and R_{2+3}. Minute setulae on dorsal surface at base of R-R_1. Vein C with very small, fine spinules to wing tip. Basicosta not observable. Tip of Sc reaches to 0.5× length of wing; R_1 runs very close to Sc, length 0.6× that of wing; R_{2+3} sinuous (apparent kink in R_{2+3} appears preservational), length ca. 0.7× wing length, apex of R_{2+3} not converging with apex of R_1; cells br and bm of nearly equal length; cell d long, narrow, slightly arched; apices of R_4 and R_5 barely encompass wing tip; R_4 branches from stem of $R_{4\text{-}5}$ very proximal to apex of cell d (near middle of cell d). Veins M_1, M_2, and M_3 present, first two slightly sinuous. Veins M_3 and CuA_1 parallel; cell cup virtually closed, elongate and narrow, CuP and A_1 nearly meeting at wing margin; vein A_2 present, nearly complete but apically evanescent. Anal lobe well developed; alula shallow, smaller than upper calypter. **Legs:** Long, slender. Pro- and mesofemur without macrosetae; metafemur with ventral row of very fine setae. Tibial spurs 0-2-1, middle spurs of equal length. All tarsi with ventral row of short, black, spinulelike setae; metatibia with dense dorsal row of spinules. Pretarsal structures small, empodium pulvilliform. Mesocoxa with dense setae; anterior surface of metacoxa not observable. **Abdomen (female):** Not dorsoventrally flattened, terminal segments tapering and tele-

scoping; pleural membrane between tergites and sternites 2–4 broad; tergite 1 obscured (cannot determine if medially divided); tergites 2–4 large, 5–10 appear to be telescoping, significantly narrower than preceding segments. Tergites heavily setulose; sternites light brown, well developed, with fine, sparse setulae. Dorsal portion of tergite 10 obscured (medial division not observable). Cerci 2-segmented, basal segment cordate in lateral view, ventral and dorsal lobes symmetrical; apical cercomere with faint emargination on posterior margin.

Type: Holotype, female, JZC Bu-288.

Etymology: In reference to the similarity between this species and the type species of the genus.

Comments: The unique specimen is not very well preserved, much of the cuticle of the body crumpled and softened, making sutures and small sclerites difficult to observe (e.g., proscutellum, tergite 1, metaspiracular area). However, the right wing is very well preserved (the left wing is distorted); the proboscis is cleared, distended, and most of the mouthparts are separated (fig. 12A), allowing observation of fine details of these structures.

Genus *Galloatherix* Nel et al.

Galloatherix Nel, de Ploëg, and Perrichot, 2014: 592.

Type Species: *Galloatherix incompletus* Nel, de Ploëg, and Perrichot, 2014: 592. An isolated wing in Late Albian–Early Cenomanian amber from near Archingeay, Charentes-Maritime, France.

Emended Diagnosis: Nel et al. (2014) diagnosed *Galloatherix* based on the following wing vein features: R_{2+3} sinuous, apex close to (but not contacting) apex of R_1; cell m_3 not present (tips of M_3 and CuA_1 distant, each meeting wing margin); cell br only slightly longer than cell bm; veins M_1, M_2, and M_3 longer than discal cell. To this diagnosis can provisionally be added: sexual dimorphism in mouthparts, proboscis of female ca. 2.5× the length of that in male; palp slender, digitiform; flagellomere 1 reniform; post-metathoracic spiracle scale and suprametacoxal pit absent; proscutellum present; with 1-2-2 long tibial spurs; cerci 2-segmented.

Comments: The wing venation of *G. completus,* n. sp., and *G. incompletus* from the Cretaceous of France are very similar, with diagnostic species differences as noted below. Additional features based on nonwing characters were added to the generic diagnosis, above, but must be considered provisional until specimens of *G. incompletus* are found that have the body.

***Galloatherix completus*,** new species

Figures 13, 46

Diagnosis: Distinguished from *G. incompletus* Nel et al. by the wing of *G. completus* having vein R_{2+3} less sinuous; cell d slightly longer, veins M_1, M_2, and M_3 shorter (fig. 11D).

Description: Based on male and female. Male (paratype), female holotype, respectively: body length 3.64, 4.79 mm; thorax length 1.24 mm, (female not measured); abdomen length 1.83, 2,59 mm; wing length 2.48, 4.17 mm; proboscis length 0.52, 1.46 mm. FEMALE: **Head:** Eyes large, somewhat anteroposteriorly flattened, frontal surface broad; in lateral view occiput not visible posteriorly. Facets not differentiated; eye almost bare, with sparse, very fine, short setulae. Medial margins distant along frons, nearly parallel, width approximately equal to distance between outside margins of antennal bases. Frons with fine, short, sparse setulae (appears to have transverse striae, but these are probably artifactual). Ocelli on low tubercle; vertex with short, stiff setae. Occiput not visible. Face with large, bulbous clypeus; clypeus bare, roughly pear shaped, with broad, more bulbous end dorsally; clypeus bordered laterally by extensive membranous area and then more laterally by deep grooves/sulci. **Antenna:** Basal 3 segments short, compact; apical antennal article aristate. Antennal base with small, shelflike lobe dorsally; scape cylindrical, with deeply incised lateral and medial areas;

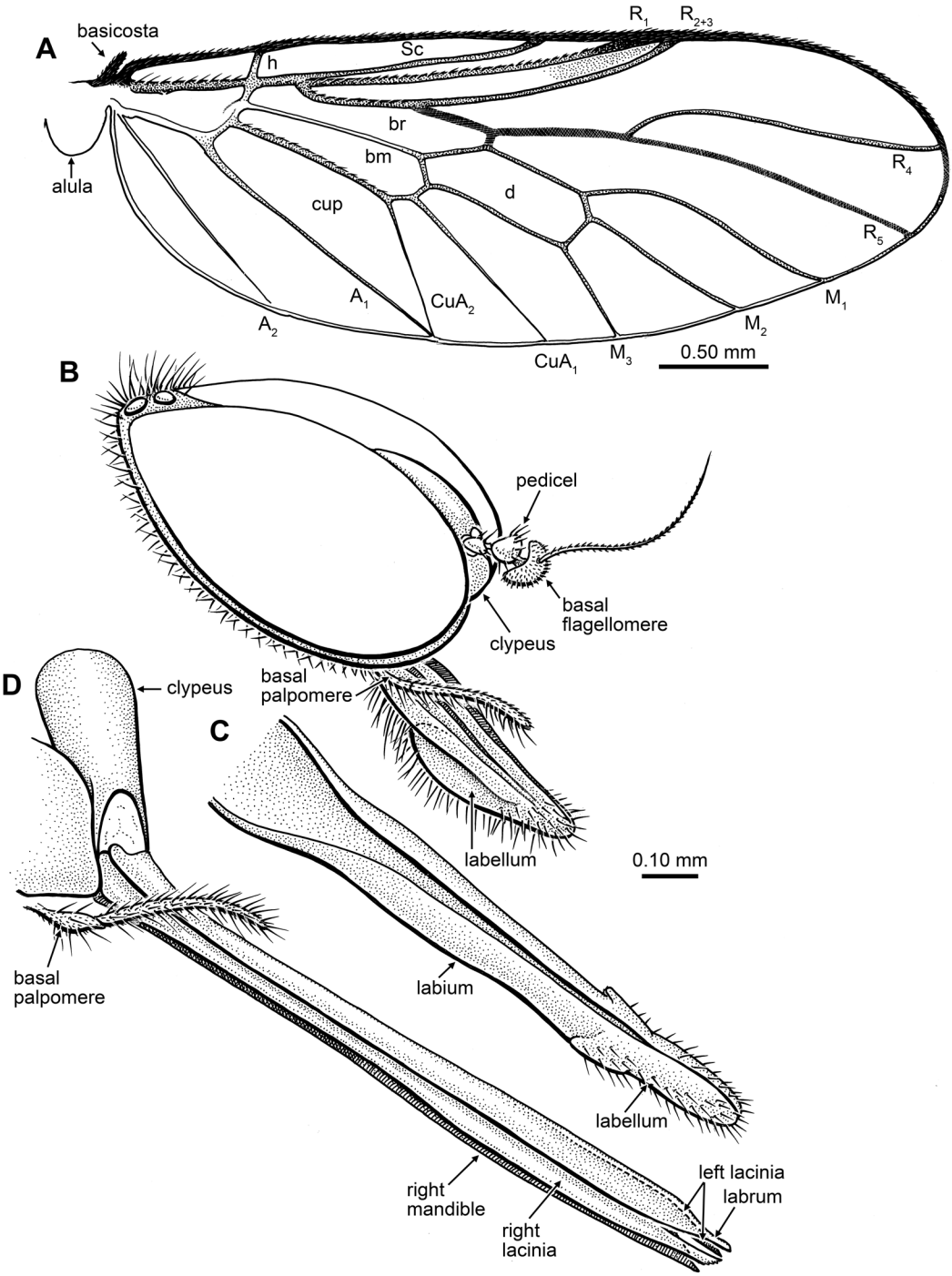

FIG. 13. *Galloatherix completus*, new species (stem-group Tabanomorpha), AMNH Bu-SE2/5a. **A, C, D.** Female holotype, AMNH Bu-SE2/5a. **B.** Male paratype, AMNH Bu-SE2/5b. **A.** Wing. **B.** Male head, oblique lateral view. **C, D**: Female mouthparts, with labium and labellum separated from remainder. Panels B–D to the same scale.

pedicel short, squat, apical surface conforming to proximal surface of flagellomere 1; scape and pedicel with short, stiff setae. Flagellomere 1 reniform, connected to pedicel at middle of flagellomere. Apical flagellar article long, fine, aristalike, with minute pubescence. Presence of minute apical style not observable. **Mouthparts:** Proboscis long, fortuitously separated from labium and labellum in holotype specimen. Proboscis significantly longer than head depth: depth of head 1.0 mm, length of exposed part of proboscis 1.46 mm (labium slightly shorter). Labium broad and shallow basally, apically narrowed to (at labellum) 0.5× basal width; dorsal longitudinal groove not separate on labellum, gradually separated and widened basad; labium bare of setae; labellum with fine, stiff setae. Labellum 0.2× length of theca. Mandibles present, flat, long, swordlike, tips sharp but not finely serrate; lacinia slightly thinner than mandible, flattened and swordlike, tip sharp and with minute serrations. Labrum long and slender. Palp long, slender, gently curved (dorsally convex), slightly tapered in thickness distad; 2-segmented, basal segment short, 0.37× length of distal segment; apical segment with short, stiff setae on dorsal and ventral surfaces. **Thorax:** Right side of holotype preserved as hollow impression within interior of amber piece, revealing details; left side and scutellar area entirely lost. Dorsum of mesonotum with short, stiff, erect setae; notopleural area with slightly longer setae; pleurites entirely bare. **Wing:** Moderately long and slender, W/L 0.37, hyaline except for small pterostigmatic area between apices of veins R_1 and R_{2+3}; 1–3 rows of minute setulae/microtrichia on dorsal surfaces of bases of R_1 and Rs and stem of Cu; longest setulae at stem of vein R + Sc. Basicosta a slender, deeply excised lappet. Vein C circumambient, significantly thinned at apex of wing, with very fine stiff setulae. Sc 0.53× length of wing; R_1 0.63× length of wing; R_{2+3} not sinuous, apex of R_{2+3} converging toward and very close to apex of R_1, but not meeting; stem of R_{4-5} thickest vein after C; fork of R_{4+5} arising slightly distal to distal end of cell d. Cell d straight, not curved; length of d greater than veins M_2 and M_3, shorter than M_1; M_1 slightly sinuous. Cell br 1.45× length of cell bm; apices of M_3 and CuA_1 distant, not converging, meet wing margin; apices of CuP and A_1 not preserved (cannot determine whether forming cup cell). Anal lobe present but small, alula well developed but more shallow than upper calypter, upper calypter subcircular. **Legs:** Long, slender. Femora setulose, especially dorsally. Ventral surface of profemur with minute tubercle near middle, bearing 4–5 long, fine, stiff setae that point distad. Tibiae and tarsi with dense vestiture of setulae. Tibial spurs 1-2-2, long, lengths greater than apical widths of respective tibiae. Dorsal surface of metatibia and ventral surface of all basitarsi with short, stout spinulelike setae. Empodium pulvilliform, broader than pulvilli. **Abdomen:** Not dorsoventrally flattened, with large membrane between tergites and sternites. Sternites large, bare. Tergites with vestiture of dense, short, erect, and decumbent setae. Cerci 2-segmented, shape of basal segment not observable.

MALE: Very similar to female with differences as follows: **Head:** Anteroposteriorly flattened, with eyes fully frontal and occupying nearly entire frontal surface of head. Eyes holoptic in middle portion of frons, medial margins divergent ventrally and dorsally. Facets differentiated in size: inner half-diameter of eye with larger facets, grading laterally to smallest facets laterally; lateralmost facets with diameter ca. 0.5× that of medial facets. Frons dorsal to antennae with short, fine pubescence. Ocelli large, on low tubercle; tubercle with thick stiff, stout setae. Occiput with thick, short, stiff setae. Clypeus small, bulbous, with deep sulci laterally (no membranous areas); bare. **Antenna:** Flagellomere 1 connected to pedicel near dorsal end of flagellomere (vs. at middle). **Mouthparts:** Proboscis short, length slightly greater than 0.5× depth of head capsule; labellum equivalent in size to that of female. Palp more slender than in female, digitiform, even in width throughout (not apically tapered); with stiff setae on ventral surface only. **Thorax:** Well preserved in male, including color pattern. Mesono-

tum largely dull brown, with pair of light, incomplete, paramedian stripes thickened in width along transverse suture and at base of stripe. Notum dorsally with dense vestiture of thick, decumbent setulae, longer, finer setae laterally (on supraalar region, scutellar margin). **Legs:** Hind femur with ventral row of long, fine, erect setae on distal half. **Abdomen:** Moderately dorsoventrally flattened; tergites and sternites broad, pleural membrane between them not exposed. Tergites with denser, longer setae than in female.

Types: Holotype, female, AMNH Bu-SE2/5a. Paratype, male, in same piece as female, AMNH Bu-SE2/5b.

Etymology: Named as a contrast to the type species, *G. incompletus*, which is known only as a wing; *G. completus* is known from the bodies of both sexes as well as wings.

Comments: Fortuitously, the male and female are preserved in the same piece of amber, a flattened, ovoid, clear yellow piece 23 × 11 × 3 mm. Conspecificity of the two individuals is reflected by the matching wing venation, the detailed structure of the antenna and palp, and other aspects of the general morphology. In fact, the two individuals were probably in copula just prior to capture in amber since the abdominal tips of the flies oppose each other very closely (fig. 46) (the male terminalia were ground off at the surface of the amber prior to acquisition; female terminalia are intact and not coupled). What is most striking is the sexual dimorphism in the length of the proboscis, with that of the female nearly three times that of the male. I am unaware of any living tabanomorphs where there is such dramatic sexual dimorphism in mouthparts.

FAMILY TABANIDAE

Females of most species of tabanids are hematophagous with notoriously painful or irritating "bites," wherein skin is punctured with knifelike serrated mandibles. Some species, such as the long-proboscid pangoniines, feed on flower nectar and pollen. The species-level taxonomy of tabanids is quite advanced, no doubt due to their conspicuous habits, medical significance, and their large, robust size. There are approximately 4450 species. The family is unquestionably monophyletic.

The traditional subfamily and tribal classification of Tabanidae (e.g., Mackerras, 1954, 1955) has been challenged recently by the molecular study of Morita et al. (2016), which was based on four genes (one mitochondrial, three nuclear). Pangoniinae, long thought to be the basalmost tabanids, appears to be a monophyletic sister group to all other tabanids (Morita et al., 2016). Pangoniines plesiomorphically have eight free flagellomeres (vs. four, the others being fused), and an undivided ninth tergite in both sexes; the subfamily apomorphically has bifid gonostyli.

Tabanidae have a significant fossil record. Evenhuis (1994) listed seven Tertiary genera (all extant) with 14 species (several of these nomina nuda). It was not until 1994 that the first definitive Cretaceous tabanid was described, *Cratotabanus stenomyomorphus* (Martins-Neto and Kucera-Santos, 1994). Since then five additional Cretaceous species have been described: *Eopangonius pletus* Ren (Ren, 1998a) (Early Cretaceous: Yixian Formation, China), *Baissomyia redita* Mostovski et al. (2003) (Early Cretaceous: Zaza Formation, Russia) (placement uncertain); *Eotabanoid lordi* Mostovski et al. (2003) (Early Cretaceous: Purbeck Group, England), *Cratotabanus newjerseyensis* Grimaldi (Grimaldi et al., 2011) (Late Cretaceous: Raritan Formation, New Jersey), *Laiyangitabanus formosus* J.-F. Zhang (2012) (Early Cretaceous: Laiyang Formation, China). *Palaeopangonius eupterus* Ren (Ren, 1998a) was transferred to Athericidae (Zhang, 2012; herein, above), but the position of this genus is ambiguous (above). The great majority of tabanid fossils are compressions, although two of the three Cretaceous species of *Cratotabanus* occur in amber, *C. newjerseyensis* and *C. asiaticus*, n. sp. (below). There are at least six described tabanid species in Tertiary amber (all in living genera or tribes), from the Miocene from the Dominican Republic and Mexico and Eocene of Baltic region (Evenhuis, 1994; Trojan, 2002; Strelow et al., 2013). I have seen several additional (undescribed) species in Tertiary ambers.

Tabanipriscus, new genus

Diagnosis: Wing broad in middle (W/L = 0.41), significantly tapered apicad; anterior edge not straight, slightly convex; basicosta deeply incised, base of C thick; fork of R_{4+5} long, base diverging near level of cell d apex (vs. significantly distad); face with pair of small, rugose callosities; antenna with at least 7 (probably 8) free flagellomeres, tapered apicad; cerci 2-segmented.

Type Species: *Tabanipriscus transitivus*, new species.

Etymology: Taken from the root and type genus name for Tabanidae (*Tabanus*), and *priscus* (Latin, "first"), in reference to the plesiomorphic nature of this genus. The gender of the name is masculine.

Comments: This is not a species of Tabanidae as currently defined for modern and Tertiary species. It is possible that *Tabanipriscus* is actually a stem group to Athericidae + Tabanidae. Features of the fossil that are plesiomorphic for Tabanidae include: anterior edge of wing not straight, slightly convex; preserved portion of R_4 only very slightly sinuous; R_4-R_5 fork not widely divergent (though still apparently encompassing tip of wing), fork longer than in any living Tabanidae, 2 cercomeres. Placement in/near Tabanidae is based on the deeply incised basicosta, very thick base of C, head shape, a pair of facial callosities, mouthpart structure; the broad, dorsoventrally flattened abdomen, and the lack of a peg/knob on the anterior surface of the hind coxa (which all tabanids lack, but which athericids, some pelecorhynchids, and *Oreoleptis* possess). Pleural metathoracic area of the unique specimen is unfortunately not visible.

Tabanipriscus transitivus, new species

Figures 14, 47

Diagnosis: As for genus, by monotypy.

Description: Based on unique female. Body length ca. 8.92 mm; antennal length 4.15 mm; wing length 6.45 mm; abdomen length 4.15 mm. **Head:** Very rounded, occiput flattened (slightly concave); eyes large, dichoptic, completely bare, no differentiation of facets, eyes occupy entire lateral surface of head and much of frontal surface. Frons bare, without callosities; very narrow, width ca. equal to 6× diameter of eye facet, margins virtually parallel. Ocelli large, on shallow mound. **Antenna:** Sockets extensively membranous. Scape somewhat cylindrical, ventral surface proximally extended, distally with stiff, short setae; pedicel goblet shaped, with apical ring of short, stiff setae. Flagellum with at least 7 (probably 8) articulating flagellomeres; basal flagellomere broader than all other antennomeres; flagellomeres gradually decrease in width apicad, apical one 0.25× width of basal one. Minute terminal stylus appears to be present. Clypeus not particularly bulging, except for pair of rugose lobes/callosities below antennal bases, and small lobe at base of clypeus. Lateral margins of clypeus forming ridge just medial to deep parafacial sulci. Cheek near base of mouthparts with membranous areas. Occiput and postgena with fine erect setae. **Mouthparts:** Palp 2-segmented; basal segment more slender and cylindrical, with dense, stiff, fine setae; apical palp larger, slightly arched (dorsally convex), with dense microtrichia and some thick setulae (apical portions lost); palps held above proboscis, convergent apicad. Apex of proboscis lost, but clearly short; labium short, with long, fine, stiff setae; labellum large, fleshy; laciniae and mandibles partially exposed. **Thorax:** Dorsally light, ochre; devoid of macrosetae, with vestiture of fine, short setulae; fine macrosetae on prepisternum, preepimeron, and anepimeron; prescutellum present; scutellum (deformed in unique specimen), dark (blackish brown), with short pilosity (subscutellar area obscured). Metaspiracular and supra-metacoxal areas obscured. **Wing:** Largely hyaline, except for pterostigmatic area around apex of R_1; minute microtrichia over entire wing membrane. Wing broad in middle (W/L = 0.41), significantly tapered apicad, anterior edge not straight, slightly convex. Basicosta deeply incised, slender, lappet-like; C circumambient, base very thick, with fine, stiff setae; tips of wings lost. Crossvein h very

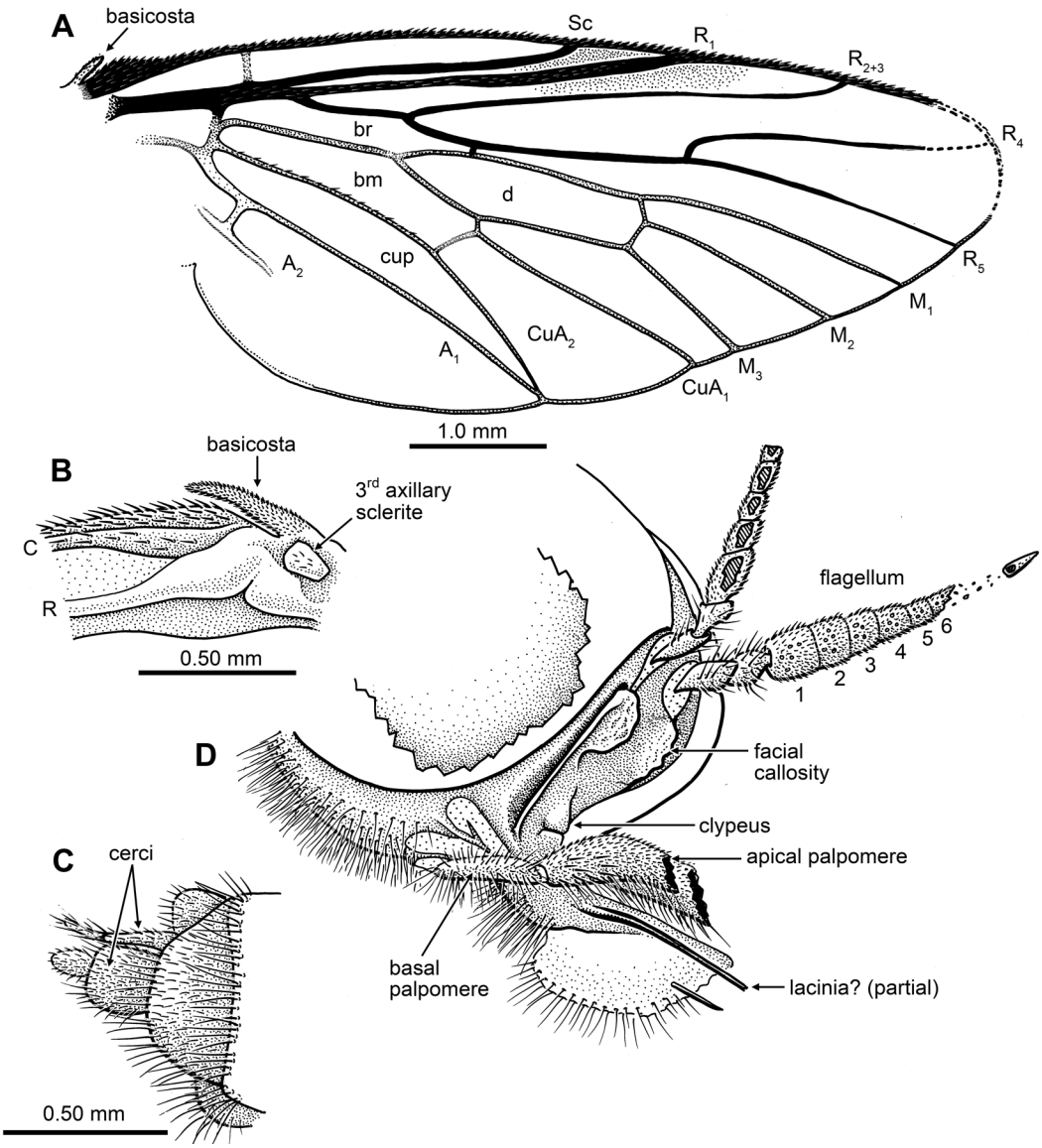

FIG. 14. *Tabanipriscus transitivus* (stem-group Tabanidae), new genus and species, holotype AMNH Bu SE2/10. **A.** Wing. **B.** Base of costal region of left wing, dorsal view. **C.** Female terminalia, oblique left lateral view. **D.** Head, right frontolateral view, as preserved. Panels C, D to same scale.

faint; Sc straight, upturned only at tip, length 0.5× wing length; R_1 very close to Sc, length 0.65×; stem of R and base of R_1 with 2–3 rows microtrichia on dorsal surface, diminished to 1 row apicad; apex of R_1 significantly thickened. Fork of R_{4+5} long, base diverging near level of cell d apex (vs. significantly distad); R_4 and R_5 moderately divergent, tips of both probably straddling wing apex (based on course of R_4); preserved portion of R_4 only very slightly sinuous. Cell bm slightly longer and broader than cell br; cell d straight (not arched), narrow (W/L 0.22); vein M_1 slightly longer than cell d, veins M_2, M_3 shorter; M veins very slightly divergent;

M_3 and CuA_1 slightly convergent; stem of CuA with row of microtrichia on dorsal surface. Cell cup present, tips of CuA_2 and A_1 meeting just before wing margin; vein A_2 present, short. Anal lobe well developed, alula present but shallow, basalmost area of wing obscured (e.g., presence/absence of calypters). **Legs:** Dark brown, with dense vestiture of short, stiff setulae (especially on tibiae and tarsi); coxae with long, fine pilosity, metacoxa without peg on anterior surface; tibial spurs 0-2-2, middle spurs longest; empodium pulvilliform. **Abdomen:** Broad, dorsoventrally flattened; lateral margins of tergites and sternites meeting laterally; (middle portion of tergite 1 obscured); tergites and sternites with dense, short pilosity. Cerci 2-segmented, basal segment symmetrical, ca. twice the size of apical segment. Tergite 9 not visible.

Type(s): Holotype, female, AMNH Bu-SE2/10.

Etymology: From the Latin *transitivus* ("transitional"), in reference to the phylogenetically intermediate morphology of this tabanomorphan.

Comments: The holotype is in a dark amber-colored piece 15 × 17 × 6 mm, which also contains fragments of small arthropods, frass pellets, a small fragment of bark, and twisted spider webbing. The fly is moderately well preserved, missing only portion of the right eye (an optic lobe is visible), tips of the palps, proboscis, and wings, and distal segments of the hind legs. The thorax and abdomen are somewhat crumpled and deformed, obscuring some critical features such as the metaspiracular, suprametacoxal, and subscutellar areas, as well as tergite one.

Genus *Cratotabanus* Martins-Neto and Kucera-Santos

Cratotabanus Martins-Neto and Kucera-Santos, 1994: 291.

Cratotabanus: Grimaldi et al., 2011 (revised diagnosis).

Emended Diagnosis: Modified and updated from Grimaldi et al. (2011) based on new material in Burmese amber: M_1 (and sometimes M_2 and M_3) long, length(s) about equal to that of cell d (vs. significantly shorter in modern genera); R_5 only slightly deviated from path of stem vein R_{4+5}. Further, in *C. asiaticus*, n. sp., postmetaspiracular scale lacking; female cercus 2-segmented; tergite 1 divided, tergite 10 undivided. Differs from *Laiyangitabanus* (monotypic: *formosus*) based on venational characters: in *Cratotabanus* wing apex more acute; R_{2+3} straight (vs. slightly sinuous), R_4-R_5 fork larger, more asymmetrical (i.e., R_4 significantly longer, quite sinuous), cell d slightly narrower, r-m very close to base of cell d (vs. at approximately basal third of cell) (fig. 16).

Type Species: *Cratotabanus stenomyomorphus* Martins-Neto and Kucera-Santos, in limestone from the Crato Formation (Aptian) of Brazil.

Comments: There is no question about the tabanid identity of *Cratotabanus*, based on the observation of new details in this amber specimen. *Cratotabanus newjerseyensis*, also in Cretaceous amber (Turonian: New Jersey), was largely obscured. Although *Cratotabanus asiaticus* plesiomorphically lacks a developed postmetaspiracular scale, has a 2-segmented cercus, and tergite 10 is undivided, this species possesses the typical tabanid wing venation and head shape, and it has a large basal calypter and divided first tergite. These features cast significant light on the sequence of character evolution in tabanoids. Paleogeographic records of *Cratotabanus* are very similar to that of the Cretaceous family Zhangsolvidae (Stratiomyomorpha) (above; Arillo et al., 2015): both taxa are known from the Crato Formation of Brazil and in Burmese amber, and in adjacent areas of Laurasia (*Cratotabanus* in New Jersey amber and Zhangsolvidae in Spanish amber); Zhangsolvidae is further known from the Cretaceous of China.

Cratotabanus asiaticus, new species

Figures 15, 48

Diagnosis: Separated from *C. newjerseyensis* by *C. asiaticus* having the following: larger body (12.5 mm); apices of veins Sc and R_1 gradually meeting C, not upturned; R_4 significantly less

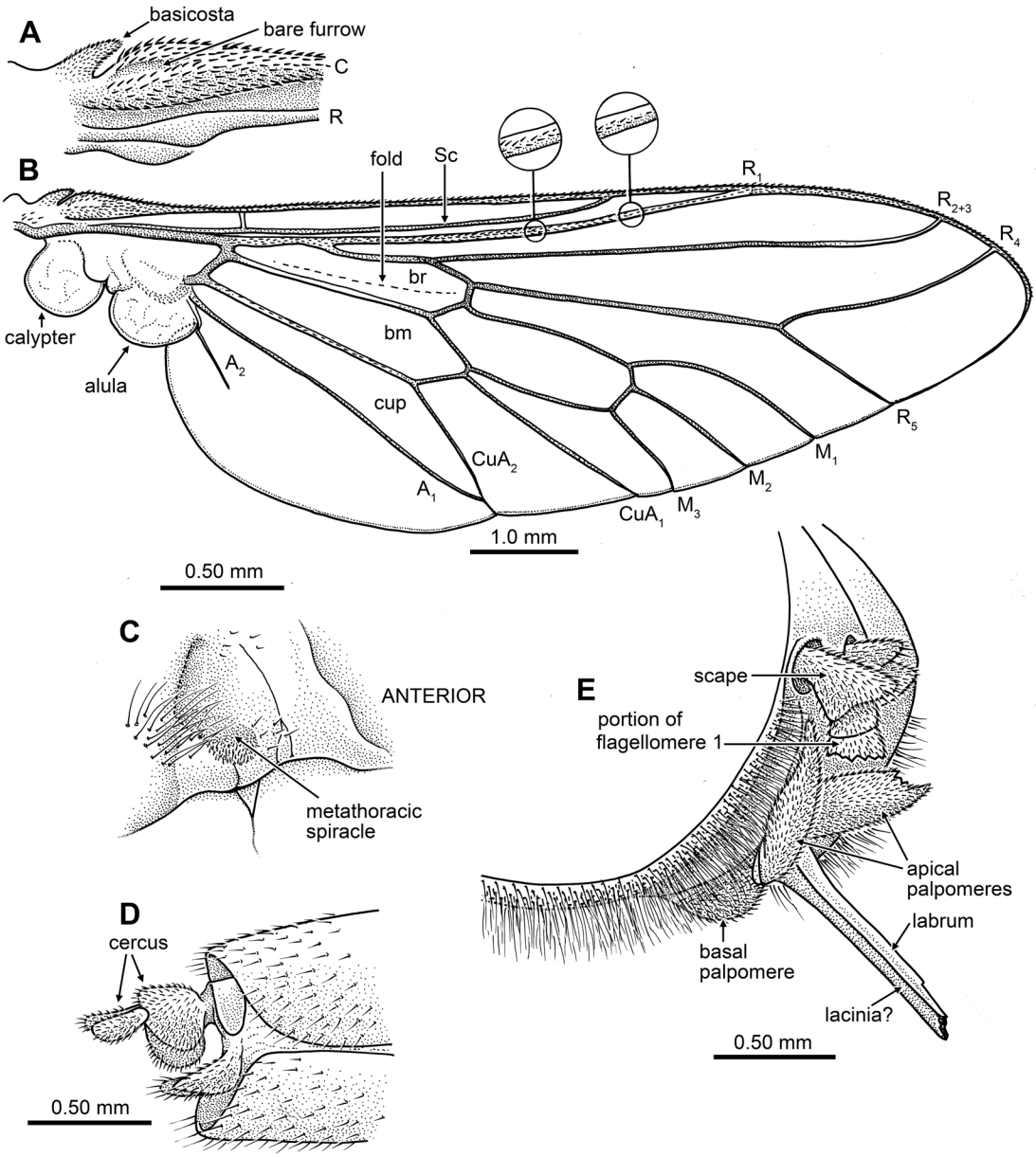

FIG. 15. *Cratotabanus asiaticus* (Tabanidae), new species, holotype AMNH Bu-SE3/2. **A.** Base of costal region of right wing, dorsal view. **B.** Wing, dorsal view, with details of setulose R_1. **C.** Area surrounding metathoracic spiracle. Note absence of postspiracular scale. **D.** Female terminalia, right lateral view. **E.** Anterior portion of head, as preserved. Apical portions of the antennae have been lost, as have the apical portion and labium + labellum of the proboscis.

sinuous; M_1 more arched; apex of bm more acute; cell cup closed (i.e., A_1+CuA_2 joined before wing margin); A_2 shorter, terminating abruptly; cell d slightly shorter. Distinguished from *C. stenomyomorphus* by having much longer vein R_1, apex extended well beyond level of cell d apex (vs. at same level). Venation otherwise very similar to that of *C. stenomyomorphus* (cf. fig. 16).

Description: Based on unique female. Body length 11.87 mm; wing length 8.75 mm; thorax length 4.22 mm; abdomen length 6.58 mm. **Head:** Hemispherical, with frontal half very rounded, posterior half/occiput slightly concave; eyes very large, dichoptic, completely bare, no differentiation of facets, eyes occupy nearly entire preoccipital portion of head. Frons bare, without callosities; with very small central ridge; very narrow, width ca. equal to 4× diameter of eye facet, margins virtually parallel. Ocelli large, on virtually no mound. Minute supraantennal lobe between antennal bases. **Antenna:** Lost past 3rd article. Antennal sockets and pedicel hardly exposed. Pedicel slightly funnel shaped, with very few stiff, short apical setae; only fragment of basal flagellomere preserved. Clypeus hidden by palps, not observable; deep parafacial sulcus present. Cheek, occiput, and postgena with dense, fine pilosity. **Mouthparts:** Palp 2-segmented; basal segment robust but shorter than apical segment; both palpomeres with dense, fine setae (no macrosetae); apical palp slightly arched (dorsally convex); positions of palps distorted, resting position not observable. Most of proboscis lost, remaining portions are bases apparently of labrum and perhaps laciniae or mandibles. **Thorax:** Dorsally light brown, pleural area mostly dark brown; scutum and scutellum devoid of macrosetae, with vestiture of extremely small, fine, decumbent setulae. Fine, long, whitish pilosity on supraalar region, ventrolateral portions of scutellum, and pleuron. Prescutellum and subscutellum present. Postmetaspiracular scale absent or possibly very small. **Wing:** Largely hyaline, except for very narrow pterostigmatic at apex of R_1; minute microtrichia over entire wing membrane. Wing long and slender (W/L = 0.33), apex acutely narrowed; anterior edge straight. Basicosta deeply incised, wider at base, lappet-like; C circumambient, base very thick, with fine, stiff setae, C abruptly narrowed at wing tip. Crossvein h faint; Sc straight, gradually meeting C, not upturned at tip, length 0.55× wing length; R_1 very close to Sc, length 0.70× that of wing; stem of R and entire length of R_1 with 2–3 rows of microtrichia on dorsal surface, diminished to 1 row on apex of R_1. Fork of R_{4+5} short, base diverging far distal to level of cell d apex; R_4 and R_5 very divergent, asymmetrical (R_4 longer), tips of both encompassing much of wing apex; R_4 slightly sinuous. Cell bm slightly longer and broader than cell br; cell d straight (not arched), narrow (W/L 0.28); vein M_1 same length as cell d, veins M_2, M_3 shorter; M veins slightly divergent; M_3 and CuA_1 convergent; stem of CuA with row of microtrichia on dorsal surface. Cell cup present, tips of CuA_2 and A_1 meeting before wing margin; vein A_2 present, short, with abrupt end. Anal lobe well developed, alula rounded and short; upper and lower calypters present, lower calypter large, subcircular. **Legs:** With dense vestiture of very short setulae (especially on tibiae and tarsi); coxae with fine, sparse pilosity, metacoxa without peg on anterior surface; tibial spurs 0-2-2; empodium pulvilliform, apically broader than pulvilli. **Abdomen:** Not particularly dorsoventrally flattened; tergites and sternites wide, with lateral margins almost meeting laterally; tergite 1 medially divided; tergites and sternites with dense, very short pilosty. Cerci 2-segmented, basal segment symmetrical, ca. twice the size of apical segment. Tergite 9 apparently not divided medially.

Types: Holotype, female, AMNH Bu-SE3/2.

Etymology: "From Asia," in reference to the continent of origin, in contrast to the other two species of the genus from the Cretaceous of South and North America.

SUPERFAMILY NEMESTRINOIDEA

Nemestrinidae are homeodactylus brachycerans. Woodley (1989) placed them with Acro-

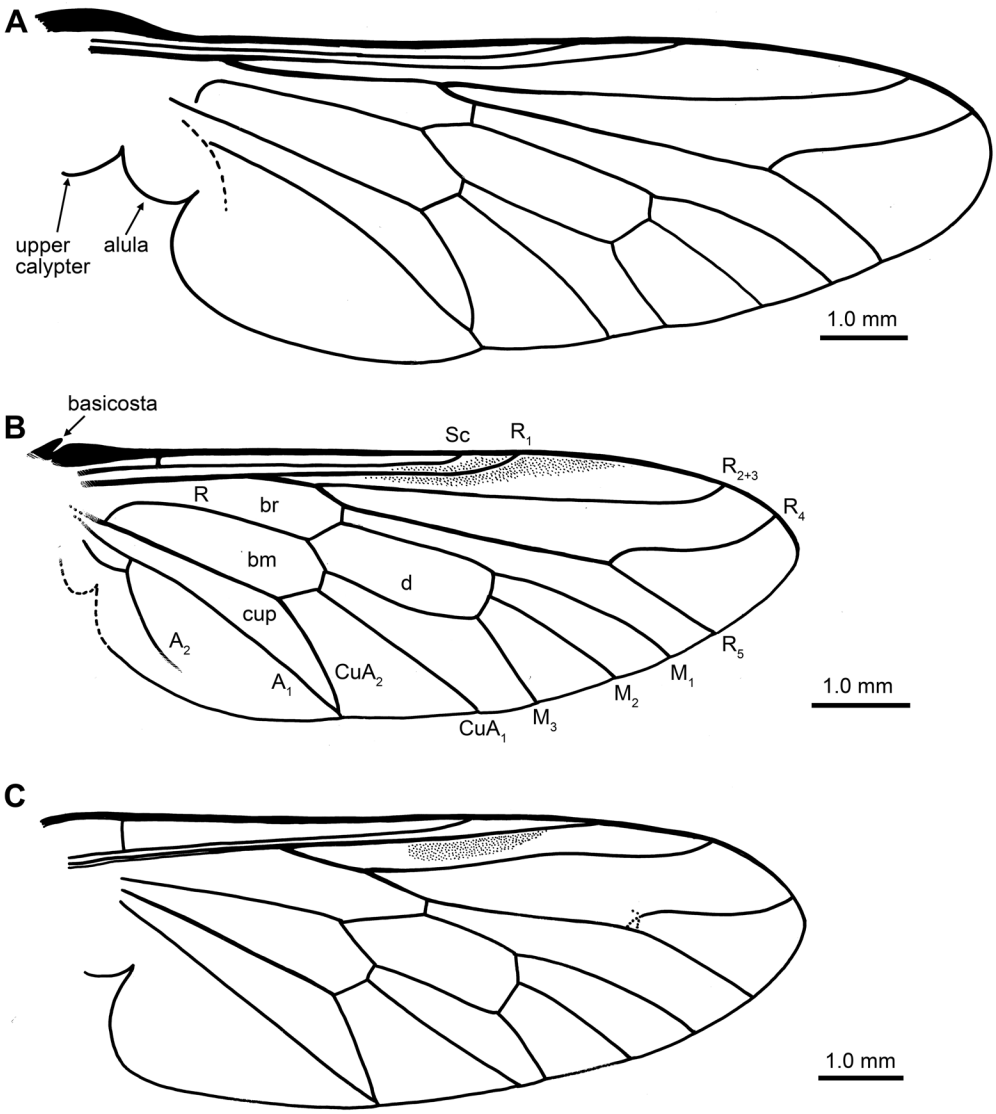

FIG. 16. Wings of assorted Cretaceous Tabanidae. **A.** *Cratotabanus stenomyomorphus* (ex: Martins-Neto and Kucera-Santos, 1994). **B.** *Cratotabanus newjerseyensis* (ex: Grimaldi et al., 2011). **C.** *Laiyangtabanus formosus* (ex: J.-F. Zhang, 2012). At slightly different scales.

ceridae into Nemestrinoidea, on the basis of parasitoidal larvae with planidia. Nemestrinoidea were hypothesized as the sister group to the rest of the Muscomorpha (Asiloidea + Eremoneura) by virtue of the reduced number of cercomeres and flagellomeres and loss of tibial spurs. This grouping has been used here, and by this morphological definition Rhagionemestriidae even appears to be an extinct (Mesozoic) transitional group between these two families. Yeates' (2002) morphological analysis indicated that Nemestrinidae was the sister group to Acroceridae + Heterodactyla, which also makes sense. Some recent molecular evidence supports an Acroceridae + Nemestrinidae grouping (Winterton et al.,

2007), but another study (Wiegmann et al., 2011) suggests a Nemestrinidae + Xylophagidae sister grouping, which I am unable to reconcile morphologically given the major differences in wing venation, tibial spurs, antennal and cercomere segmentation, and great disparity in genital morphology.

FAMILY NEMESTRINIDAE

The family of "tangled-vein" flies is distinctive and relict, with only 250 world species in 23 genera, but in some areas they are ecologically vital. The group has an extensive fossil record. These flies are immediately recognized by the diagonal vein, in which obliquely aligned through the wing are portions or the entireties of veins Rs, base of R_{4+5}, crossvein r-m, portions of M_{1-3}, and CuA_1. Nemestrinids have one cercomere, a pulvilliform empodium, two palpomeres, no tibial spurs, and primitively four flagellar articles (often reduced to one or two), the apical 1–3 articles formed into a slender stylate portion of the antenna. The proboscis varies from vestigial (e.g., *Trichopsidea* Westwood) to extraordinarily long (e.g., *Moegistorrhynchus* Macquart). Bernardi (1973) monographed the world genera, though the family would benefit from an updated, comprehensive phylogenetic analysis.

Life histories of very few species are known, and all are larval parasitoids with a first instar planidial larva (Clausen, 1940; York and Prescott, 1952; Prescott, 1960; Greathead, 1958; Bernardi, 1973). Adults either don't feed or, in ones with developed labella, they are anthophilic, feeding on flower nectar and pollen. The group occurs in xeric regions of the world, particularly deserts and Mediterranean biomes: southern South America, southern Africa, Australia; eastern Africa, the Middle East, central Asia, and western North America (Bernardi, 1973). The only tropical area with significant numbers of species is southern Asia from India to Japan and Indonesia, but this includes just about 17 species of Cyclopsideinae, in the genera *Ceyloniola* Strand (1 sp.), *Nycterimyia* Lichtwardt (9 spp.) and *Nycterimorpha* Lichtwardt (6 spp.). South Africa, by contrast, has 43 species of Nemestrinidae (Barraclough, 2006). Here, about a dozen long-tongued nemestrinids form five guilds of monolectic to oligolectic pollinators, which collectively pollinate some 170 species of flowering plants in the Western and Northern Cape regions, particularly ones with long, narrow corolla tubes (Goldblatt and Manning, 2000; Manning and Goldblatt, 1996, 1997). The most remarkable of these guilds involves three species of the genus *Moegistorrhynchus* Macquart, endemic to the Western and Northern capes, which have a proboscis 90–100 mm in length—more than 3.5 times the length of the body. Like most pollinating flies, nemestrinids have exceptional flight ability, with stationary hovering required to guide the proboscis into the long, narrow corollas. Coalescence of apical wing veins, with numerous cross veins, appears to be correlated with hovering ability and length of the proboscis.

Nemestrinidae have one of the best fossil records among orthorrhaphous Brachycera, some 25 species in 13 genera from the Late Jurassic to Late Eocene. Isolated lithified wings are fortunately easily recognizable as Nemestrinidae by the diagonal vein. Bequaert and Carpenter (1936) reexamined the late Eocene species from Florissant described by Scudder and Cockerell; Evenhuis (1994) cataloged the fossil species up to 1992; Mostovski (1998) treated the Late Jurassic species from Karatau, including revisions of the taxa described by Rohdendorf; Mostovski and Martínez-Delclòs (1999) treated a diverse paleofauna from the Early Cretaceous of Spain and described further taxa from Eurasia; Ansorge and Mostovski (2000) listed all taxa known to that time. Additional taxa have been described from the Late Jurassic (Zhang et al., 2008) and Early Cretaceous (Ren, 1998a) of China.

The three species (two new) of *Hirmoneura* reported here are the first Nemestrinidae known from amber.

Genus *Hirmoneura* Meigen

Hirmoneura Meigen, 1820: 132; Bernardi, 1973 (synonyms and major subsequent citations).

Diagnosis (adapted and modified from Bernardi, 1973): Head broad, hemispherical; proboscis small, barely visible past oral margin; basal flagellomere drop shaped, with three slender, apical flagellar articles forming stylus, apical article longest and fine; venation with few or generally no apical radial and medial cells; cell cup absent; hypandrium (male) highly reduced or lost; female cerci long, tapered, apically pointed.

Type Species: *Hirmoneura obscura* (Wiedemann), Recent.

Comments: *Hirmoneura* are one of the three largest genera in the Nemestrinidae after *Trichophthalma* Westwood and *Nemestrinus* Latreille. It contains approximately 50 described living species distributed nearly equally between Old and New worlds (Bernardi, 1973). The venation of this genus and the two largest ones (above) are very similar and generalized, with the least amount of vein coalescence among nemestrinid genera; these genera also share similarities in antennal structure and a distinctive modification of the ocelli, where the anterior ocellus is separated considerably anterior to the posterior ones and on a separate mound. These three genera are probably closely related, though phylogenetic work is needed to test this. Interestingly, in the one Burmese amber specimen in which the dorsum of the head is visible, the ocelli are unmodified, no doubt plesiomorphically. The female cerci of *Hirmoneura caudoprima,* however, are extended into a long, tapered, pointed oviscapt, like many of the modern species of the genus. All three of the Burmese amber species also lack the dense, long pilosity of modern species. Monophyly of modern *Hirmoneura* is supported by a hypandrium in the male that is small or usually lost, unknown for the fossil taxa. There are three species of *Hirmoneura* based on compression fossils from the Early Cretaceous of Spain and Siberia (Mostovski and Delclòs, 2000); these have a closed cell cup. The genus is also recorded from the Cenozoic (Wedmann, 2007). Otherwise, the venation of Cretaceous *Hirmoneura* is remarkably similar to modern species, but this may just be a plesiomorphic resemblance, as the ocelli of the amber *Hirmoneura* suggests these three species to be stem groups. The recent venation terminology is used here rather than that in Bernardi's (1973) work, with differences as follows: R_{3+4} (vs. R_4 in Bernardi), M_3+CuA_1 (vs. M_3+M_4), CuA_2 (vs. Cu_1).

Hirmoneura caudiprima, new species

Figures 17A, 18A–C, 49A–D

Diagnosis: Very similar to modern *Hirmoneura* species in wing venation (including lack of cell cup) and by the female cerci modified into a long, sclerotized, swordlike oviscapt; differing from all modern species by body lacking pilosity and by having ocellar triangle unmodified (in living species the anterior ocellus is significantly anterior to the posterior ones and there are two separate mounds). Differs from the other two new species of *Hirmoneura* in Burmese amber by the longer oviscapt and venation differences (given in diagnoses below). *Hirmoneura richterae* Mostovski et al. and *H. elenae* Mostovski et al., Early Cretaceous compression fossils from Spain and Siberia, respectively, possess cell cup.

Description: Based on female. Body length 9.98 mm (including cerci); thorax length 2.88 mm; wing length 8.77 mm; abdomen length 6.02 mm (including cerci). **Head:** Hemispherical in dorsal view, slightly flattened in lateral view, width equal to greatest width of thorax. Eyes very large, occupying virtually all of hemispherical anterior portion of head; occiput flat or slightly concave. Eye completely bare, no differentiation of facets, barely dichoptic. Frons present but extremely narrow, width at level of ocelli only 4–5× diameter of facets; inner margins of eyes gradually converging anteriad to width about equal to facet diameter. Ocelli present, small, forming equilateral triangle; anterior ocellus not on separate mound from posterior ones. **Antenna:** Distal portion slender and stylate, 6 antennal arti-

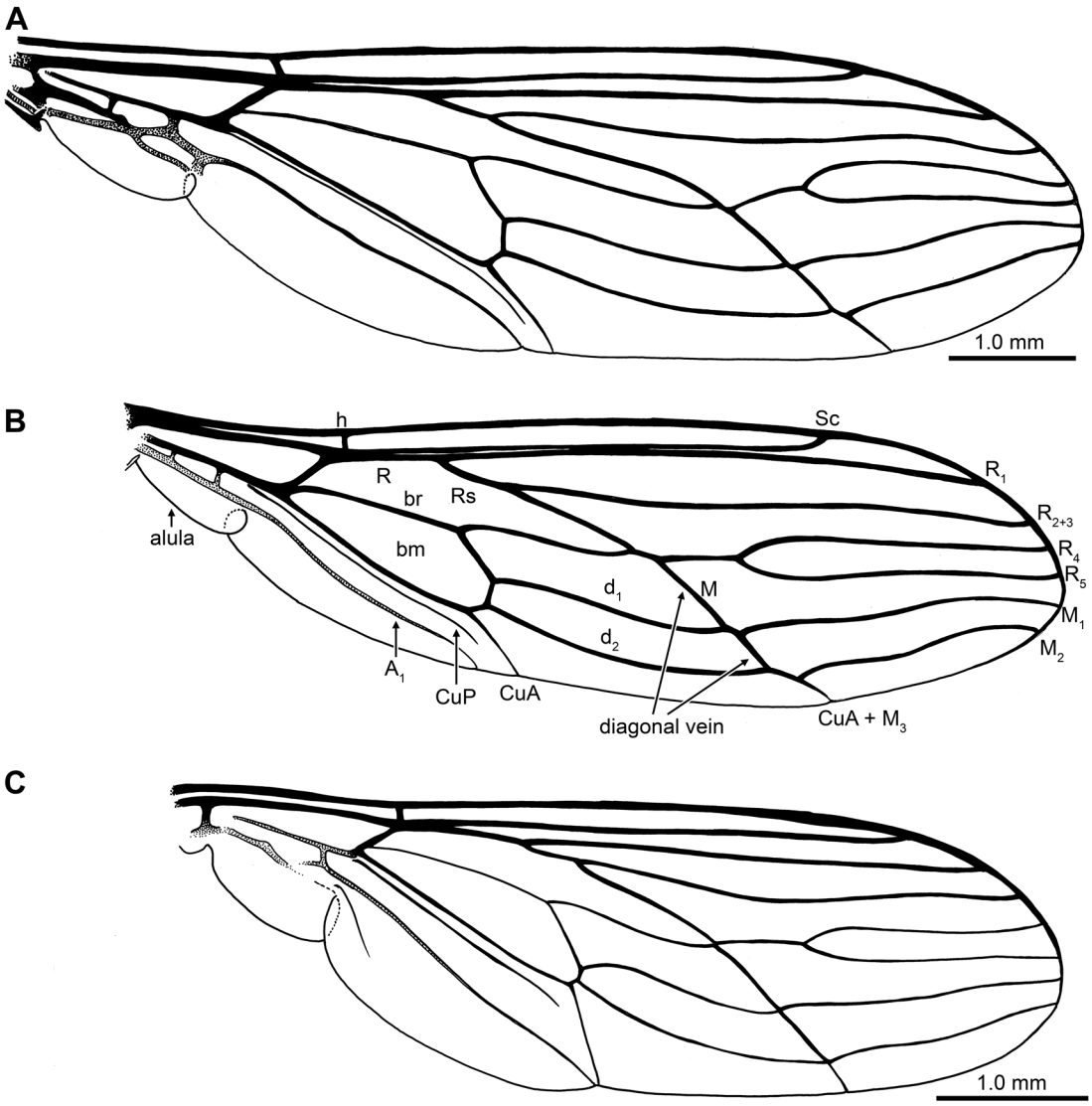

FIG. 17. Wings of three species of *Hirmoneura* Meigen (Nemestrinidae) in Burmese amber. **A.** *Hirmoneura caudiprima* new species, holotype, AMNH Bu-SE17. **B.** *Hirmoneura zigrasi*, new species, holotype, JZC Bu-169. **C.** *Hirmoneura* aff. *richterae* Mostovski and Martínez-Delclòs, HP-B-6084.

cles present: cylindrical scape, shorter pedicel; drop-shaped flagellomere 1; and stylate portion comprised of short basal flagellomeres (2 and 3) and longer apical one (flagellomere 4). Lengths of antennal articles: apical article (f4) > scape = flagellomere 1 > pedicel > f2 = f3. **Mouthparts:** Small, barely protruding beyond margins of oral cavity, elements mostly not observable. **Thorax:** Robust, dorsally flattened, with very short fine setae, slightly longer on scutellum. Body without long, dense, fine pilosity. Scutum with pair of very shallow, faint, paramedian grooves on anterior half, to level of transverse suture. Postalar wall protuberant, forming calli. **Wing:** Long, slender, W/L 0.29, anterior and posterior margins almost parallel; membrane entirely hyaline, microtrichia not visi-

ble (either absent or microscopic). Sc 0.78× length of wing, gradually meets C, apex not upturned. Vein h opposite MA. R_1 very close and parallel to Sc, virtually straight; apices of veins R_1, R_2, R_{3+4}, R_5 slightly convergent apicad, diagonal vein well formed, running through distal third of wing; no apical radial-medial cells present. Cell br long, 1.56× length of cell bm, more slender. Cell cup absent (CuA_2 apices do not meet A_1 before wing margin). CuP well defined, anal lobe virtually absent; alula present but shallow. A_2 not extended beyond distal incision of alula. **Legs:** Long, slender. Mesocoxa much closer to ipsilateral metacoxa that to procoxa; coxae moderately pilose; hind coxa without knob on anterior surface. Femora slightly wider than respective tibiae; virtually bare; tibiae and tarsi with short, decumbent setae. Hind leg: femur 1.9 mm, tibia 3.1 mm, tarsus 2.3 mm. Basitarsus longer than respective tarsomeres 2–5 combined. Claws large, empodium pulvilliform, slightly larger than empodia. No tibial spurs. **Abdomen:** Dorsoventrally slightly compressed, relatively small, length 1.25× that of thorax; abdomen greatly tapered in width apicad, tergite 7 0.12× width of tergite 1. Tergites and sternites well developed, edges meeting laterally. Female cerci long, sclerotized, tapered into apical point, forming swordlike oviscapt. Distal margin of female sternite 9 medially emarginate, forming two small lateral lobes.

Type: Holotype, female, AMNH Bu-SE17.

Etymology: From the Latin, meaning "first tail," in reference to the long, ovipositor-like cerci of the species, the earliest occurrence of this feature in the genus.

Comments: Bernardi (1974) demonstrated that substantial intraspecific variation in the venation occurs in *Neorhynchocephalus* species (which also exists in other nemestrinids), but most of this variation occurs in the branching patterns of the apical portions of the R and M veins. The venation differences diagnosed among the three species here involve basal veins.

The fly is in a piece of translucent amber that retains its natural outline, 30 × 20 mm, slabbed to 8 mm thickness and polished over surfaces that expose each side of the fly and a wing. The fly is missing only the distal half of the left wing and some leg segments. Syninclusions are a mite and small adult mayfly (Ephemeroptera: Baetidae).

Hirmoneura zigrasi, new species

Figures 17B, 49E–G

Diagnosis: Differs from *H. caudoprima* by: smaller size, wing length 7.5 mm (vs. 8.7 mm), female cerci short; and various details of venation: cell br shorter (0.36 length of wing, vs. 0.51), diagonal vein near middle of wing (vs. more distal), apices of longitudinal veins slightly less convergent; forked portion of $R_{3\text{-}5}$ slightly longer (0.34× length of wing, vs. 0.26×); veins comprising diagonal vein are less aligned; cells d1 and d2 slightly shorter. Much larger in body size than *H.* aff. *richterae* in Burmese amber, cell cup not closed.

Description: Based on partial female specimen that is missing head, right ventrolateral portion of thorax, and most of legs except left meso- and metafemora. Thorax + abdomen length 8.5 mm (including cerci), thorax length 3.07 mm, wing length 7.5 mm; abdomen length 5.54 mm. **Head:** Lost at surface of amber with exception of thin sliver of posterior margin of left eye and margin of bordering occiput; no pilosity on preserved facets. **Thorax:** Robust, slightly dorsally flattened, with very short fine setae; small tufts of fine, light pilosity in supraalar region, otherwise body without long, dense, fine pilosity. Scutum with pair of very shallow, faint, paramedian grooves on anterior half, to level of transverse suture; transverse sutures deep, extend medially for 2/3 width of scutum. Postalar walls protuberant, forming calli. **Wing:** Long, slender, W/L 0.30, anterior and posterior margins almost parallel; membrane entirely hyaline, microtrichia on membrane extremely fine. Sc 0.73× length of wing, gradually meets C, apex slightly upturned. Vein h slightly apical to level of MA. R_1 very close and parallel to Sc, virtually straight; apices of veins R_1, R_2, R_{3+4}, R_5 virtually parallel, hardly convergent apicad.

Diagonal vein well formed, running through middle of wing, with several small crossveins; no apical radial-medial cells present. Cell br long, 1.53× length of cell bm, more slender than bm. Cell cup not closed (CuA_2 apex does not meet A_1 before wing margin). CuP well defined, anal lobe virtually absent; alula present but shallow. A_2 not apparent. **Legs:** (Largely lost in unique specimen). **Abdomen:** Slightly compressed dorsoventrally, length 1.75× that of thorax; abdomen tapered in width apicad, tergite 0.21× width of tergite 1. Tergites and sternites well developed, edges meeting laterally. Female cerci slightly elongate, length ca. 2.2× width, not developed into swordlike oviscapt. Distal margin of female sternite 9 with two small paramedian lobes with fine setae.

Types: Holotype, female, JZC Bu-169.

Etymology: Patronym for James Zigras, for his generosity over the years in making a wide array of Burmese amber species available for study.

Comments: A partial specimen missing the structures described above; the remaining portions are hollowed and cleared (improving resolution of sutures, etc.), but the amber is translucent and obscures some details.

Hirmoneura aff. *richterae* Mostovski and Delclòs

Figures 17C, 18D, 50

Emended Diagnosis: A very small species, body length 6.01 mm, wing length 6.02 mm. Venation essentially identical to that of *H. richterae* (Early Cretaceous, Montsec, Catalonia, Spain) in vein branching patterns and proportions. Both species have female cerci slightly elongate (length ca. 3.3× basal width) and tapered to apical point. The only difference between the two species is size, *richterae* being larger (10.3 mm wing length), which by itself I do not consider diagnostic.

Description (based on present, amber specimen): Based on female. Among smallest known nemestrinids, head length 0.91 mm; head width 1.73 mm; body length 6.01 mm; thorax length 1.69 mm; wing length 6.02 mm; abdomen length 3.12 mm. **Head:** Hemispherical in dorsoventral views, slightly flattened in lateral view, width slightly larger than greatest width of thorax. Eyes very large, occupying virtually all of hemispherical anterior portion of head; occiput slightly concave. Eye completely bare, no pilosity; no differentiation of facets. Dorsum of head barely observable, inner margins of eyes almost meeting in middle of frons; ocellar area not visible. Clypeus bulbous, black, slightly oval in shape; laterally flanked by deep paraclypeal pits. Genae are black, setose, rounded lobes facing mediad, forming deep notch posterior to labellum. **Antenna:** Portion distal to basal flagellomere lost; scape short, slightly shorter than pedicel; flagellomere 1 incompletely preserved but seemingly drop shaped. **Mouthparts:** Well preserved, though portion of labellum lost at surface. Proboscis short, apex barely extending past ventral surfaces of eyes. Palps long, slender, digitiform, not tapered apicad; projecting forward over paraclypeal sulci; basal palpal segment slightly longer than distal segment; tips dark, most of palp yellowish; palp with fine, erect setae. Proboscis very short, only labellar lobes visible at oral cavity; color light. **Thorax:** Robust, dorsally flattened, length 2.4 mm, with very short fine setae. Body without long, dense, fine pilosity; small tufts of short pilosity on subalar area. Postalar walls protuberant, forming calli. **Wing:** Slender, W/L 0.33, anterior and posterior margins almost parallel; membrane entirely hyaline, microtrichia very fine, covering entire membrane of wing. Sc 0.80× length of wing, gradually meets C, apex not upturned. Vein h opposite MA. R_1 very close and parallel to Sc, virtually straight; apices of veins R_1, R_2, R_{3+4}, and R_5 virtually parallel. Diagonal vein well formed, running through middle of wing in straight line (no crossveins); no apical radial-medial cells present. Cell br 1.41× length of cell bm, more slender. Cell cup almost closed, apices of CuA_2 and A_1 virtually meeting before wing margin. CuP well defined; anal lobe virtually absent;

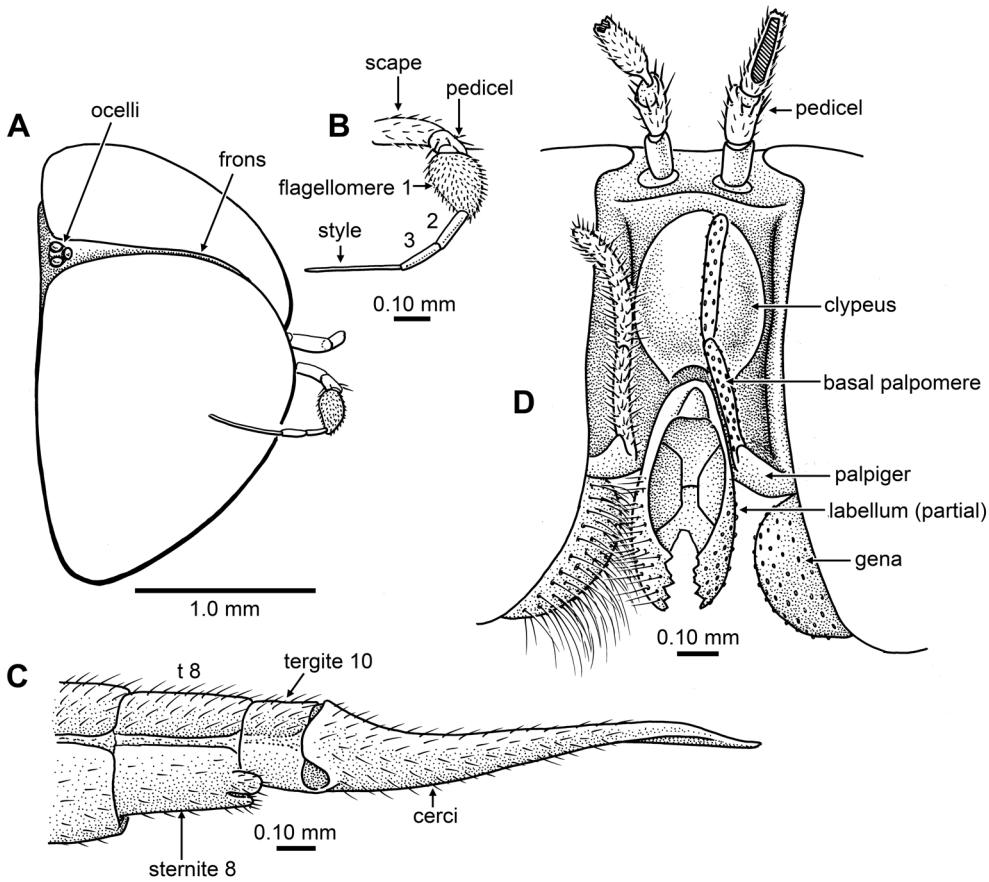

FIG. 18. Details of *Hirmoneura* spp. in Burmese amber. **A–C.** *Hirmoneura caudiprima*, holotype AMNH Bu-SE17. **D.** *Hirmoneura* aff. *richterae*, HP-B-6084. **A.** Head, oblique dorsal view. **B.** Antenna, dorsolateral view (as preserved). **C.** Female terminalia, left lateral view. **D.** Face and mouthparts, ventral view.

alula present but shallow. A_2 extended beyond distal incision of alula, apex evanescent. **Legs:** Prolegs and distal portions of mesothoracic legs lost; metathoracic legs slender. Mesocoxa much closer to ipsilateral metacoxa than to procoxa; metacoxa with short, sparse pilosity on mesal surface, no knob on anterior surface. Metafemur with sparse, short pilosity on ventral surface, slightly wider than metatibia; tibia and tarsi with short, dense, decumbent setae; metabasitarsus longer than respective tarsomeres 2–5 combined. Claws large, empodium pulvilliform. No meso- or metatibial spurs. **Abdomen:** Dorsoventrally compressed, relatively short and broad, width 0.65× the length; abdomen suboval in dorsolateral views, not tapered in width apicad. Tergites and sternites well developed, edges meeting laterally. Female cerci relatively short, length ca. 3.3× basal width, not heavily sclerotized, tapered into apical point but not forming oviscapt. Distal margin of female sternite 9 not visible.

Specimen: Female, HP-B-6084, in collection of Di-Ying Huang, Institute of Geology and Palaeontology, Nanjing, China.

Comments: The unique specimen lies within a dark piece of amber 18 × 14 × 3 mm, which also contains two phlebotomine psychodids, a cecidomyiid, and a mite. The fly is missing only portions of the legs and apices of antennae; the

dorsum is obscured by several layers of particles, debris, and sand grains.

FAMILY RHAGIONEMESTRIIDAE

This is a small extinct family from the Late Jurassic to Early Cretaceous, comprised of six genera and nine species. Proposals are not supported here that the unusual living genera *Exeretonevra* and *Heterostomus* be placed in this family (e.g., Mostovksi and Martínez-Delclòs, 2000; Nel, 2010), or conversely, that Rhagionemestriidae should be placed in Xylophagidae (Jarzembowski and Mostovski, 2000). *Exeretonevra* larvae indicate that this genus is in the Xylophagidae (Palmer and Yeates, 2000), a placement confirmed by molecular evidence (Wiegmann et al., 2011). *Heterostomus* appear to be in the Tabanomorpha based on adult and pupal morphology (Coscarón et al., 2013). Lastly, the discovery of a species of rhagionemestriid in Burmese amber, described below, indicates a relationship distant from Xylophagidae.

Critical structures of *Jurassinemestrinus eurekus,* n. sp., reveal that this family is without question closely related to Acroceridae. This is based on the following synapomorphies: hemispherical head comprised mostly of the eyes; hind margin of eye with slight emargination, fine transverse line through middle of eye; antenna small, with simple, stylate terminal article, reduced number of antennal articles (1-segmented in Acroceridae, 2-segmented in *J. eurekus*); tergal mounds (found in some but not all Acroceridae); wing membrane glassy (devoid of microtrichia), and wrinkled; distinctive lack of a transverse scutal suture; and structure of the male genitalia.

There are four genera and four species of Late Jurassic Rhagionemestriidae, all from Central Asia and China (fig. 20): *Rhagionemestrius rapidus* Ussatochov (Karbastau Formation, Kazakhstan), *Nagatomukha karabas* Mostovski and Martínez-Delclòs (2000), *Sinonemestrius tuanwangensis* Hong and Wang (Laiyang, China), *Jurassinemestrinus orientalis* J.-F. Zhang (Daohughou Formation, Inner Mongolia, China) (Ussatchov, 1968; Mostovski and Martínez-Delclòs, 2000; J.-F. Zhang, 2010). Early Cretaceous Rhagionemestriidae include *Iberomusca kakoeima* Mostovski and Martínez-Delclòs and *I. ponomarenkoi* Mostovski and Martínez-Delclòs, 2000 (Las Hoyas Formation, Spain), *Sinonemestrius akirai* Jarzembowski and Mostovski (Weald Clay, England), *Sinomusca mostovskii* Nel (Yixian Formation, China), and the species in Burmese amber (herein). The group was widespread in eastern Laurasia in the Late Mesozoic.

Genus *Jurassinemestrinus* J.-F. Zhang

Jurassinemestrinus Zhang, 2010: 313.

Emended Diagnosis: Very similar to *Sinomusca* Nel (monotypic: *S. mostovskii* Nel, Yixian Formation, Liaoning Province, China) by head large, hemispherical; eyes holoptic or nearly so, occupying nearly entire head; antennae small; body compact; R_1 long, R_{2+3} slightly to distinctly sinuous; forks of R_{4+5} and M veins short; cell bm very long. *Sinomusca*, however, has a much longer cell d and consequently much shorter br cell (br 0.66× length of bm cell, vs. equal length in *Jurassinemestrinus*). Zhang (2010) provided diagnostic differences in venation between *Jurassinemestrinus* and the more generalized genera of Rhagionemestriidae.

Type Species: *Jurassinemestrinus orientalis* J.-F. Zhang, 2010. By monotypy. From Daohugou Formation of Inner Mongolia, China (mid-early Late Jurassic [Callovian–Early Oxfordian]).

Jurassinemestrinus eurema, new species

Figures 19, 51

Diagnosis: Very similar to *J. orientalis* Zhang based on the elongate br and bm cells, short stem of M_{1+2}, presence of a closed cell cup (with A_1 and CuA_2 meeting just before wing margin). *J. eurema*, however, has: R_{2+3} much more sinuous (as in *Sinomusca*), cell br much thicker, and the stem of R_{4+5} much more arched. It differs from *J.*

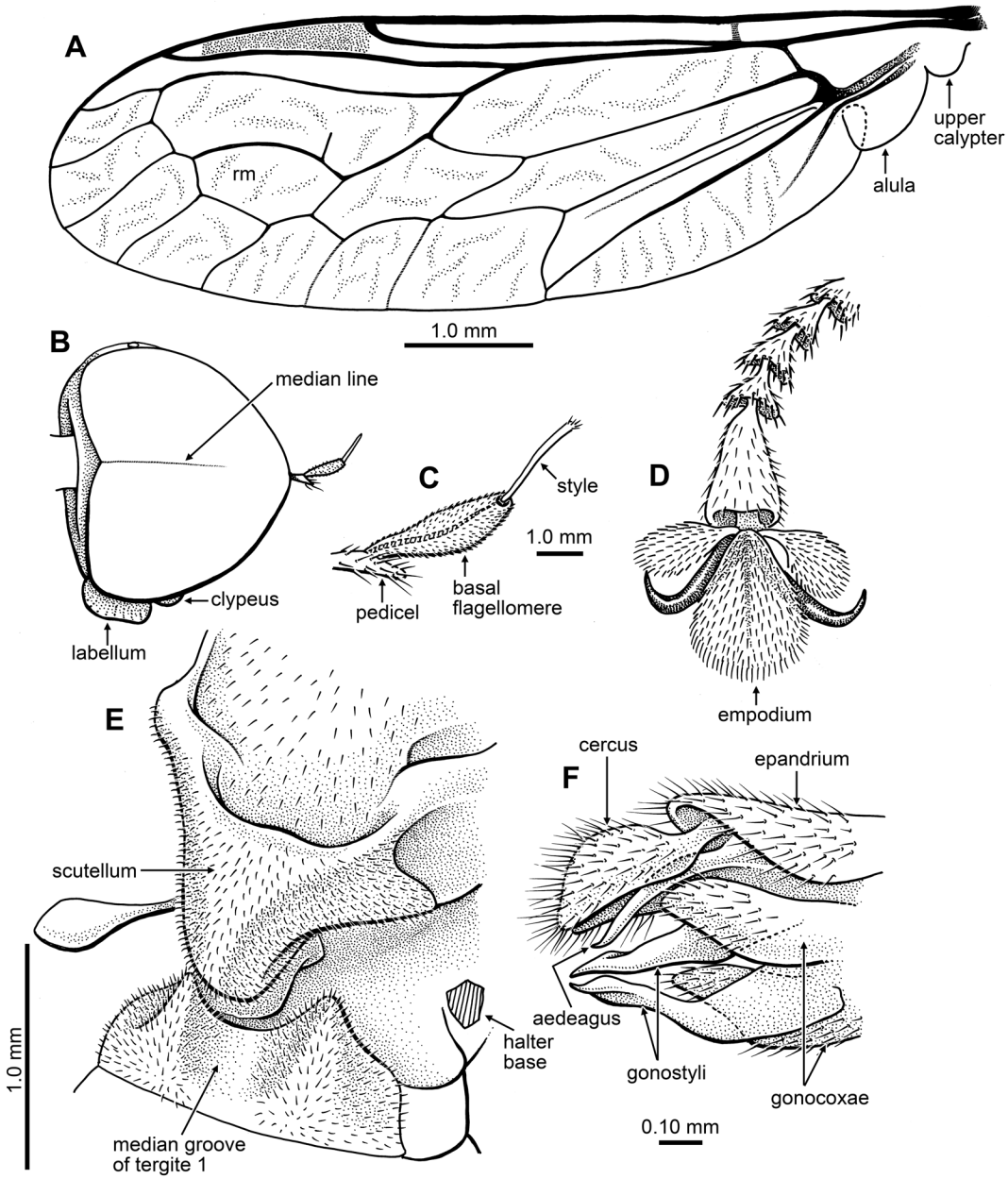

FIG. 19. *Jurassinemestrinus eurema* (Rhagionemestriidae), new species, holotype AMNH Bu-SE3/3. **A.** Wing. **B.** Head, right lateral view. **C.** Antenna, lateral view. **D.** Left protarsus, ventral view. **E.** Posterior portion of thorax and anterior portion of abdomen, oblique dorsal view, showing shapes of scutellum and groove on tergite 1. **F.** Male terminalia, oblique right lateral view. Panels C, D to same scale.

orientalis and *Sinomusca mostovksii* most distinctively by the presence of an r-r crossvein (between the apices of R_{2+3} and R_4) and an r-m crossvein (between the stem of R_{4+5} and base of M_1), thus forming two subapical cells. These two crossveins are considered minor (species-level) modifications, often seen in orthorrhaphans as a bracing mechanism for the wing tip during flight.

Description: Based on male. Large fly, 8.88 mm body length; thorax length 3.01 mm; abdomen length 4.50 mm; wing length 7.09 mm. **Head:** Very large, length 1.9 mm; hemispherical, pipunculidlike (especially in lateral view); depth of head slightly greater than that of thorax. Eyes occupy virtually all of head, dorsally, frontally, ventrally. Cheeks and parafacial plates not present, these spaces occupied by eyes. Eyes holoptic for 0.85× length of frons; fully bare, no pilosity; no differentiation (e.g., dorsoventral) of facets. Posterior margin of eyes with small, V-shaped emargination connected to fine line dividing dorsal and ventral halves of eye; line extends to about middle of eye. Frontal margins of eyes (between antenna and proboscis) separated by very narrow width equal to diameter of facets. Ocelli well developed, in very narrow triangle between eye margins, width ca. 5× eye facet diameter; posterior ocelli facing opposite (laterad), anterior ocellus facing anteriad; very narrow longitudinal ridge posterior to ocelli. Occiput dark, without pilosity; deeply and virtually entirely concave. **Antenna:** Very small, length 0.7 mm. Scape barely exposed, pedicel scoop shaped (ventral margin longer), flagellomere 1 largest article, oblong, slightly longer than apical article; apical article stylate, digitiform, apex blunt, with minute microtrichia and without minute apical stylus. **Mouthparts:** Small; slightly exposed beyond margins of eyes; labellum well developed, laterally very compressed. Palps present, laterally compressed, segmentation obscure. Clypeus very small, slightly exposed above labellum. **Thorax:** Robust, devoid of long pilosity, dorsally with minute setae, no macrosetae; cuticle color appears to be dark yellow to orange. Transverse scutal suture absent. Anterior spiracle large, slitlike, vertical; posterior spiracle surrounded by membrane. Anepisternum, anepimeron, katepisternum well defined. Scutellum in dorsal view a narrow triangle, apex very narrow and laterally compressed. No pre- or postscutellum present. Bases of procoxae far anterior to mesocoxae; meso- and metacoxae nearly in contact. **Wing:** Long and fairly narrow; anterior and posterior edges nearly parallel. Wing hyaline, except for heavily sclerotized pterostigma between apices of Sc and R_1; edges of pterostigma discrete. Wing membrane glassy, devoid of microtrichia; with coarse, shallow, irregular furrows (not fine, parallel pleating). Sc and R_1 long, apex of latter reaching to 0.8× length of wing. R_1 slightly sinuous. R_{2+3} very sinuous; apical portions of R_{2+3}, R_4, R_5, M_1, M_2, and M_3 very short. Uniquely with r-r crossvein (between the apices of R_{2+3} and R_4) and r-m crossvein (between stem of R_{4+5} and base of M_1), thus forming two subapical cells (rr, rm); base of R_{4+5} stem with short, incomplete vein projecting into cell rr (this vein shorter in right wing). Cell br same length as cell bm, bm much thicker. Cell dm an irregular hexagon. Cell cup closed (CuA_2 and A_1 meet shortly before wing margin), CuA_2 short, slightly sinuous; A_2 present as short vein apically evanescent into anal region. Anal lobe very small, alula well developed, upper calypter present but small, lower calypter absent. Tegula well developed. Halter with narrow stem, knob darker. **Legs:** Slender, without macrosetae, with dense vestiture of fine microsetae on tibiae and tarsi. No tibial spurs. Tarsi and apices of tibiae darker than rest of legs. Procoxae long, adpressed to sternum, medial margins mostly in contact; meso- and metacoxa small; metacoxa without knob on anterior surface. Femur length longer than that of respective tibia. Pro- and mesobasitarsomeres short, lengths of each about equal to that of respective tarsomeres 2+3+4; metabasitarsomere length equal to combined length of metatarsomeres 2–5. All tarsomeres 2–4 funnel shaped, with apical ring of setulae; apical tarsomere large, broad, length equal to combined length of tarsomeres 2–4. Pretarsal structures large; claws large, simple; empodium pulvilliform,

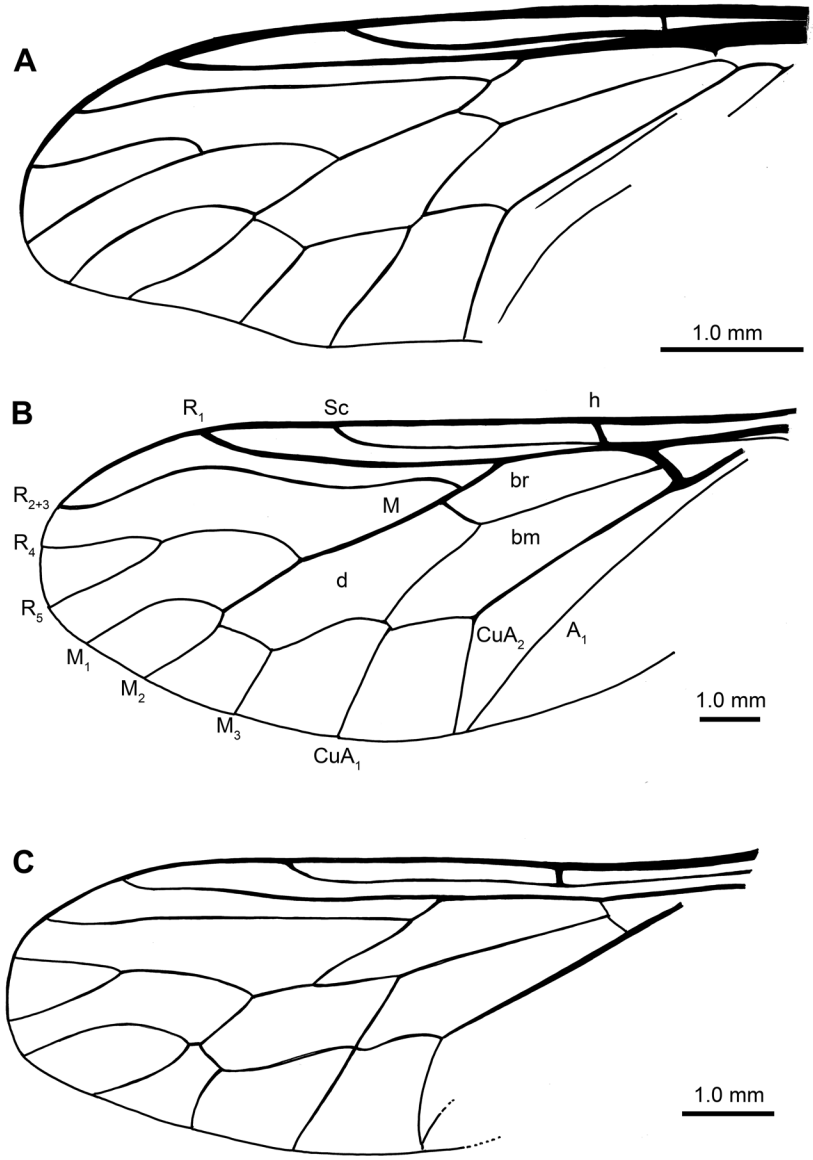

FIG. 20. Wings of assorted genera of Rhagionemestriidae. **A.** *Nagatomukha karabas* (ex: Mostovski and Martínez-Delclòs, 2000). **B.** *Sinomusca mostovskii* (ex: Nel, 2010). **C.** *Jurassinemestrius orientalis* (ex: J.-F. Zhang, 2010). Not to the same scale.

larger than pulvilli; all lobes slightly longer than claws. **Abdomen:** Relatively large, broad, dorsoventrally flattened. Width greater than width of head or thorax. Tergites and sternites all wide, lateral margins in contact (pleural membrane not exposed or very small, or both); without pilosity or macrosetae, with minute, stiff setulae. Tergite 1 with pair of paramedian lobes, forming depression/groove for reception of narrow scutellar apex. Posterior margins of tergites 2–4 raised, forming slight transverse mounds (best seen in lateral view). Sternite 7 small, triangular. **Male Terminalia:** Small, projected posteriad, well exposed. Epandrium a small, flat, unspecialized

tergite; cerci 1-segmented, setose, laterally compressed, ventral margin flat; aedeagus exposed terminally beneath cerci, apex pointed, not extending beyond apex of cerci; gonostylus well developed, sclerotized, base broad, apex curled mediad with tip pointed; gonocoxa a simple setose lobe at base of gonostylus, overlapping its base. **Female Terminalia:** Unknown.

Type: Holotype, Male AMNH Bu-SE3/3.

Etymology: From the Greek, *eurema* (a noun in apposition), "that which is found unexpectedly."In reference to the revealing nature provided by this species on the relationships of Rhagionemestriidae.

Comments: The type and unique specimen is superbly preserved and entirely complete in a light yellow, almost fully transparent (slightly turbid) prism-shaped piece of amber, 22 mm length × 8–10 mm on each side.

SUPERFAMILY ARCHISARGOIDEA

This is a Late Mesozoic (Middle Jurassic to mid-Cretaceous) group of four families, 27 genera, and about 70 species, recently reviewed by Grimaldi and Barden (2016). The families include Archisargidae, Eremochaetidae, Kovalevisargidae, and Tethepomyiidae. With the exception of one tethepomyiid in New Jersey amber (Grimaldi and Cumming, 1999), and one archisargid from Australia (Oberprieler and Yeates, 2012), all others are from the Jurassic and Cretaceous of Asia and Europe. This is probably the largest monophyletic group of Brachycera that is extinct. Defining features include a spherical head with large eyes, compact thorax; many have a long, cylindrical abdomen; and the venation of some groups is quite distinctive. The outstanding defining feature, however, are the female terminalia, produced into a pointed, aculeate structure. Besides having an unnecessarily complex taxonomic history, the relationships of archisargoids have been very vague since all except Tethepomyiidae and one recently discovered eremochaetid are lithified fossils, most of them just wings (reviewed by Grimaldi and Barden, 2016). Tethepomyiidae, discussed below, are tiny and reduced, and have revealed little on the close relatives of archisargoids. The discovery of *Zhenia xiai* (Eremochaetidae) in Burmese amber (Zhang et al., 2016) is exciting, because preservation is so revealing about relationships. Based on *Zhenia*, archisargoids are not closely related to Stratiomyomorpha as is often stated (Zhang et al., 2016), but rather to Nemestrinoidea or Muscomorpha. The aculeate cerci of *Zhenia* were probably used for parasitoidism, but the most remarkable feature of the fly is the enormous pulvilli and empodium (the former misinterpreted as the claws by Zhang et al., 2016; the claws are actually vestigial). These enormous pads probably adapted the fly to seizing hosts.

FAMILY TETHEPOMYIIDAE

This is a small monophyletic family of five species in two genera, known only in Cretaceous amber from New Jersey, Spain, and Myanmar (Grimaldi and Cumming, 1999; Grimaldi and Arillo, 2008; Grimaldi et al., 2011). The genus *Tethepomyia* (diagnosis presented below) consists of four species, one each from New Jersey and Spain, and now two from Myanmar. The highly reduced wing venation of these species has obscured relationships. Fortunately, *Tethepomima holomma* Grimaldi and Arillo, in Spanish amber, plesiomorphically retains the branching pattern of the major R veins (R_1, R_{2+3}, R_{4+5}, which are all unbranched), M (which has no branches), and CuA_1-CuA_2 is forked apically. Further, there are two small basal cells (br, bm), but no discal cell, and the male genitalia are relatively generalized for Brachycera (well developed gonocoxa and gonostylus, epandrium small and dorsal). The presence of thoracic macrosetae would indicate a close relationship with Eremoneura, but the purported presence of a small tibial spur on each leg would contradict this (indicating a more basal placement). The empodium structure was not reported, so the pretarsi and tibial apices of the unique speci-

men of *Tethepomima holomma* need to be very carefully reexamined. Lastly, the discovery of a female tethepomyiid, *Tethepomyia zigrasi* Grimaldi in Burmese amber, revealed that this group is probably within or at least closely related to the Mesozoic group Archisargoidea, which is defined largely by the piercing, aculeate female cerci (Grimaldi and Barden, 2016) (see above). In *T. zigrasi*, the cerci are not only piercing and aculeate, they are hooked ventrally, and apparently pinch against a small, spined sternal lobe (fig. 52C). With little question, these tiny flies were parasitoids, just as the Eremochaetidae and other archisargoids appear to have been (Zhang et al., 2016; Grimaldi and Barden, 2016). The eremochaetid in Burmese amber lacks tibial spurs, has a 1-segmented cercus and palp, and a single styluslike article on the flagellum (plus a tiny apical style), indicating placement of the Eremochaetidae near the Muscomorpha, but it has a very large pulvilliform empodium. *Tethepomyia coxa*, n. sp., has either a setiform or highly reduced empodium.

Genus *Tethepomyia* Grimaldi and Cumming

Tethepomyia Grimaldi and Cumming, 1999: 6.

Emended Diagnosis: Minute flies with body length ca. 1.5 mm; head hemispherical, eyes large (holoptic in males, occupying most of head); antennal flagellum reduced to U-shaped article (known for three species); mouthparts reduced, where observed; thorax short and compact; legs without tibial spurs, tarsal segments (including basitarsomere) short, compact; empodium either minute or setiform; wing short, broad, venation highly reduced to vestige of R-R_1, sometimes with vestiges of Rs, M, Cu (forked in some species), and/or A. Abdomen slender, cylindrical; male genitalia relatively generalized, female with cerci modified into piercing oviscapt hooked ventrad (seen only in *T. zigrasi*).

Type Species: *Tethepomyia thauma* Grimaldi and Cumming, 1999. New Jersey amber.

***Tethepomyia coxa*, new species**

Figures 21, 53

Diagnosis: Distinguished from other species in the genus by the greatest reduction in wing venation, no vestige of Rs or Cu remaining. Further distinguished from *T. zigrasi* (also in Burmese amber, known as female) by that species having very hunched scutum and retaining vestiges of Cu and A; from *T. buruhandi* (Spanish amber), which retains vestige of Cu; and from *T. thauma* (New Jersey amber), which retains vestige of Rs and the male genitalia are not dorsoflexed.

Description: Based on male. A minute fly, 1.52 mm body length; thorax length 0.43 mm; abdomen length 0.79 mm; wing length 1.12 mm. Head large, hemispherical (male), thorax compact, abdomen slender, wing short with highly reduced venation, body devoid of setae/setulae, with just sparse microtrichia in areas. **Head:** Oblong, with very large holoptic eyes. Eye in lateral view occupies all of lateral surface; also occupies most of dorsal, frontal, and much of ventral surfaces of heads. Eye bare, facets differentiated dorsoventrally: ventral facets ca. 0.7× diameter of dorsal ones; dividing line slightly below middle of eye. Ocelli on raised tubercle on vertex of head. Face, proboscis, mouthparts, antenna obscured by crystalline coating. Occiput concave. **Thorax:** Compact, short; flattened dorsally, depth shallow in lateral view; dorsal surfaces of scutum and scutellum in same plane. Antepronotum short. Scutum with faint paramedian sulci on anterior part of scutum. Postpronotal lobe flattened, slightly projecting, ledgelike. Notopleural suture wide, membrane very exposed; anepisternal-anepimeral cleft wide, membrane very exposed; anepimeron small, isolated by membrane (much of pleura obscured). Katepisternum small, shallow, ventral portion at same level as dorsal portion of mesocoxa. No proscutellum; scutellum short, broad; mediotergite (subscutellum?) bulging, very visible dorsally; metanotum articulating with metakatepisternum, latter pointed posteriorly. **Wing:** Highly reduced venation, short and broad,

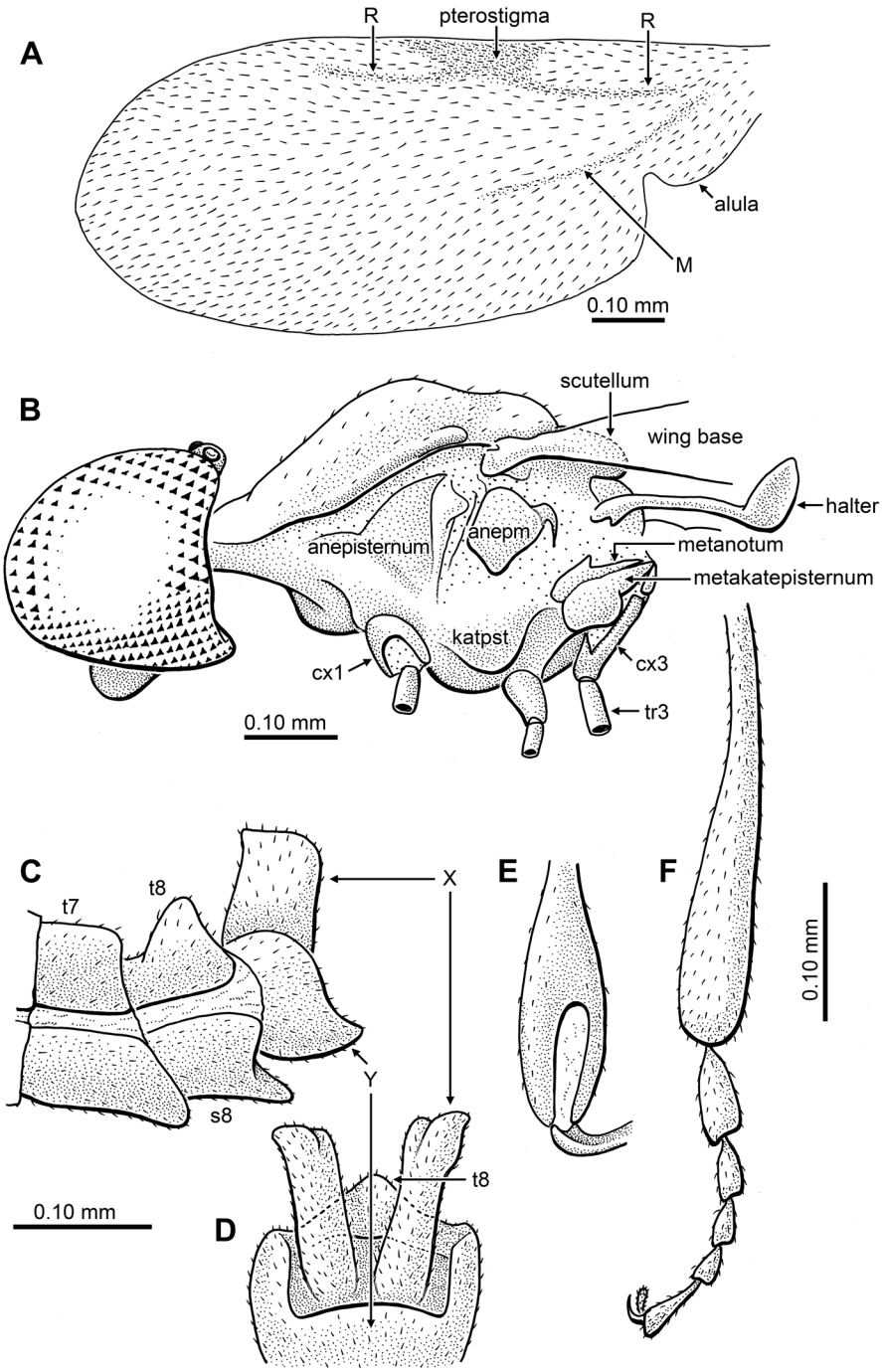

FIG. 21. *Tethepomyia coxa* (Tethepomyiidae), new species, holotype AMNH Bu-SE10. **A.** Wing. **B.** Head and thorax, left lateral view. **C.** Male terminalia, left lateral view. **D.** Male terminalia, posteroventral view. **E.** Metafemur, ventral view, showing long notch at the femoral-tibial joint. **F**. Metatibia and tarsi, lateral view. Abbreviations: **anepm,** anepimeron; **cx,** coxa; **katpst,** katepisternum; **tr,** trochanter. **X,** either cerci or surstyli; **Y,** either sternite 9 or epandrium (see text).

W/L 0.42. Vein C lost. Incomplete, faint vestiges of only R and M stems (no branches) remain, as nebulous infuscation with slightly denser microtrichia; M reaching to about middle of wing. Very faint pterostigma between middle of R and anterior edge of wing. Wing entirely with dense microtrichia, slightly finer and denser on pterostigma and veins. Anal lobe present. **Legs:** Relatively short. All coxae well separated, short; metacoxa distinctly separated from mesocoxa, articulating with metakatepisternum. No metacoxal tubercle. Trochanters well developed. Meso- and metafemora expanded apically, especially latter. All femora with long, wide, ventral "notch" (femoral-tibial articulation) on distal half. Tibiae expanded apically, especially metatibia, slightly curved (as if to fit against ventral surface of femur). No tibial spurs, bristles, or setae. Basitarsomere very short, length approximately equal to that of tarsomeres 2+3. Leg segment lengths: tibia > femur > tarsus. Pretarsus: claws well developed; pulvilli ca. 0.5× length of claws; empodium not observable (either minute or setiform). **Abdomen:** Slender, cylindrical, slightly longer than length of head + thorax. Tergites and sternites well developed; 8 tergites visible, t1 small, t2–7 large, t8 a small dorsal lobe. Male genitalia dorsoflexed, with large pair of dorsal lobes ("X" in fig. 21C, D) articulating basally within ventral sclerite ("Y" in fig. 21C, D); lobe pair (X) and ventral sclerite (Y) either cerci and sternite 9, respectively, or—if eremoneuran—surstyli and epandrium, respectively.

Type: Holotype, male, AMNH Bu-SE10.

Etymology: Taken directly from *coxa*, and used as a noun in apposition, in reference to the unusual configuration of the metacoxa with the metanotum and metakatepisternum.

Comments: The holoytpe is in a tiny, square chip of amber 5 × 5 × 1.5 mm piece of amber, trimmed from a large, deep-colored cabochen 21 × 30 × 16 mm, which also contains an empidoid fly and Coleoptera. Without new imaging of the other *Tethepomyia* species, it is uncertain whether the unusual thoracic morphology *of T. coxa* is unique to the genus or not. The metacoxa is shifted posterodorsad, such that it articulates with the metakatepisternum. This coxa is also elongate and has a deep dorsolateral excision. The holotype of *T. coxa* certainly has the best thoracic preservation among the five known specimens of the family. Unfortunately, portions of the head are obscured, so details of the antenna and mouthparts are not visible.

SUPERFAMILY ASILOIDEA

This group contains approximately 8100 described species in eight or nine living families. The position of the small Holarctic family Hilarimorphidae has been ambiguous (Trautwein et al., 2010), including it being the sister group to the Bombyliidae (Woodley, 1989; Yeates, 1994), or to the Eremoneura (Yeates, 2002). The proposal that Hilarimorphidae is a sister group to the Acroceridae (Wiegmann et al., 2011) is morphologically anomalous, possibly a result of these two being basal families. Other than Hilarimorphidae, which is a cool temperate group, Asiloidea are by far most diverse and abundant in xeric regions, from deserts and chaparral to Mediterraean biomes, where they are important pollinators. Anthophilous species with long mouthparts occur in Bombyliidae, Mydidae, Apioceridae, and Scenopinidae.

The consensus on asiloid relationships is the following: Hilarimorphidae + Bombyliidae; Asilidae + Mydidae + Apioceridae (Woodley, 1989; Yeates and Irwin, 1996; Dikow, 2009; Yeates, 2002; Wiegmann et al., 2011); and the "therevoid" clade, comprised of Apsilocephalidae + Evocoidae + Therevidae + Scenopinidae (Yeates, 2002; Wiegmann et al., 2011; Winterton and Ware, 2015). The earliest definitive fossils of asiloids occur in the Cretaceous, with Asilidae and Mydidae in the Aptian-aged Crato limestone of Brazil (Grimaldi, 1990; Wilkommen and Grimaldi, 2007); additional Asilidae occur in Burmese and New Jersey amber (Dikow and Grimaldi, 2014). Apsilocephalidae and Bombyliidae occur in Burmese amber (Gaimari and Mostovski, 2000; Grimaldi et al., 2011; herein), and a putative Scenopinidae was

reported in New Jersey amber (Grimaldi and Cumming, 1999), but which needs to be restudied. Evocoidae have no fossil record (but see below, under *Burmapsilocephala,* n. sp.), and definitive fossil Therevidae are only Tertiary (Metz and Irwin, 2000; Hauser and Irwin, 2005). Most asiloid families are well represented as lithified remains and amber inclusions from the Tertiary (Evenhuis, 1994).

A small, long-proboscid fly in Early Cretaceous Lebanese amber, *Cretahilarimorpha* Myskowiak et al. has been assigned to Hilarimorphidae (Myskowiak et al., 2016). This is a very unusual fly. On the one hand, its venation is easily derivable from extant Hilarimorphidae, with long br-bm cells, no discal cell, and a short, asymmetrical R_4-R_5 fork. Vein R_{2+3} is very short, nearly meeting the apex of R_1, which makes the venation also resemble that of Chimeromyiidae, a small family of tiny flies in Cretaceous amber (Grimaldi et al., 2009). Chimeromyiidae, however, are eremoneurans, and *Cretahilarimorpha* is far more basal. Unlike *Hilarimorpha*, *Cretahilarimorpha* has a short costal vein, as in Stratiomyidae, but the most significant structure is the antenna. The antenna in the fossil is robust, with eight large, tapering flagellomeres, as seen in stratiomyomorphans and tabanomorphans. I am unaware of any Muscomorpha, including Asiloidea and Nemestrinoidea, that has such a primitive antennal structure. Hilarimorphid antennae are short, with three flagellomeres (the apical two forming a small, thin, styluslike portion). The empodium of *Cretahilarimorpha* is apparently reduced (Myskowiak et al., 2016), but it is uncertain whether it is setiform. The long, projecting proboscis is autapomorphic and not revealing of relationships. Given this situation, I am hesitant to include *Cretahilarimorpha* in Asiloidea or Muscomorpha.

Molecular models and biogeography support a Late Mesozoic diversification of asiloids. Basal, subfamily-level divergences of Therevidae and Scenopinidae are estimated to be Cretaceous (Winteron et al., 2015; Winterton and Ware, 2015). A relatively derived phylogenetic position of *Burmapogon* in Burmese amber (Dikow and Grimaldi, 2014) indicates that basal divergences of Asilidae must extend at least to the Early Cretaceous, perhaps Late Jurassic. The relationships of the subgenera of *Apiocera* and genera of megasceline Mydidae are biogeographically congruent: western North America (South Africa (Australia + southern South America)) (Yeates and Irwin, 1996). Interestingly, the Apsilocephalidae and Evocoidae, which are likely sister groups, share a similar disjunct distribution (but not including Africa). The *Apiocera* and mydid taxon-area relationships were interpreted as Pangean in origin, 160–180 Ma (Yeates and Irwin, 1996), which I consider as probably too old, but a topic that lends additional significance to the asiloids in Burmese amber.

Comments on the small crossvein sc-r are worthwhile here, particularly since the vein is present in many of the fossil bombyliids described below. Crossvein sc-r is widespread in Asilidae and occurs in many Bombyliidae (e.g., *Apolysis*, *Crocidium*, *Paracosmus*, *Phthiria*, etc.), some Nemestrinidae (e.g., *Neorhynchocephalus*), in the Mesozoic family Eremochaetidae (Grimaldi and Barden, 2016), and Evocoidae. It is widespread in the Syrphidae, though not in the Pipunculidae or aschizan Cyclorrhapha. It could be argued that the crossvein is developed multiple times in assorted lineages (e.g., associated with hovering flight), but it may be diagnostic for the Muscomorpha and lost multiple times in more derived groups.

FAMILY BOMBYLIIDAE

This is a large, heterogeneous family of asiloid flies that are ecologically important as larval parasitoids and adult pollinators, especially in Mediterranean biomes. They range from minute, empidoidlike Mythicomyiinae (sometimes placed in their own family), to very large, striking Anthracinae with bold color patterns. Hull (1973) monographed the world genera, comprised of some 4500 species, and summarized the biology, morphology, fossils, and zoogeography. Beeflies are efficient pollinators of diverse

herbaceous angiosperms (e.g., Grimaldi, 1988; Herrera, 1988; Pentadinous and Ellis, 1993; Goldblatt and Manning, 2000; Kastinger and Weber, 2001; Larsen et al., 2001; Orford et al., 2015). They feed on nectar as well as pollen, many of them using a long proboscis to probe flowers; others have short proboscides. They are excellent hoverers. Yeates (1994) comprehensively analyzed the morphology and phylogeny of the 15 or so subfamilies, pruning the family of enigmatic genera traditionally placed in it, such as *Caenotus* and *Prorates* (now in Scenopinidae) and *Apystomyia* (in Apystomyiidae) (Yeates, 1992). Bombyliidae is at the base of the Asiloidea, as either sister group to the Hilarimorphidae—and this pair as sister group to all other asiloids (Yeates, 1994)—or itself as sister group to all other asiloids (Woodley, 1989; Yeates, 2002; Wiegmann et al., 2011), or even as sister group to all other heterodactylan flies (Trautwein et al., 2010). The world species are cataloged (Evenhuis and Greathead, 1999, 2003).

The Tertiary fossil record of Bombyliidae is quite diverse, particularly as lithified remains in the larger shale deposits. The fossil record was reviewed by Hull (1973) and Evenhuis (1994); more recent reports include Nel and de Plöeg (2004); Nel (2006); Wedmann and Yeates (2008). There is a substantial diversity of beeflies in Tertiary amber, including Cylleniinae in Baltic amber (Hennig, 1966), and some 17 species of Mythicomyiinae in Miocene Dominican amber and Eocene ambers from Europe (Baltic, Bitterfeld, Rovno, Oise) (Evenhuis, 2002, 2013). One of the few Cretaceous reports of beeflies is *Microburmyia* Grimaldi, a putative stem-group mythicomyiine in amber from Burma (Grimaldi et al., 2011). The four new Bombyliidae described here are, thus, important new records, especially since these are phylogenetically more derived than *Microburmyia*.

Nealimyia, new genus

Diagnosis: Notum arched, head far below dorsum of scutum; antenna with one flagellomere, plus minute apical style; face concave; proboscis very short, only labellum exposed. Two notopleural macrosetae. Wing slender, sc-r crossvein present, R_4-R_5 fork virtually symmetrical, apices of CuA_2 and A_1 highly convergent but not meeting; anal lobe narrow. Tergites 7, 8 with very thick, long, fine setae forming setose basket at apex of abdomen.

Type Species: *Nealimyia evenhuisi*, new species. Monotypic. In Burmese amber.

Etymology: Patronym, for Neal Evenhuis, Bishop Museum, Honolulu, in recognition of his contributions to dipterology and the systematics of Bombyliidae. The gender of the name is feminine.

Comments: The venation is most similar in basic proportions to the crocidiine genera *Crocidium* Loew (from Africa) and *Desmatomyia* Williston (from the Nearctic Region), and the thick setal "basket" is quite similar to that in the latter genus.

Nealimyia evenhuisi, new species

Figures 22, 54

Diagnosis: As for genus, by monotypy.

Description: Based on female. Hunchbacked fly, with large, arched scutum; head attached to thorax just above procoxae, top of head far below top of scutum. Cuticle of fly dark, true color not discernable. Body length 5.05 mm; thorax length 1.95 mm; abdomen length 2.46 mm; wing length 3.96 mm. **Head:** Slightly hemispherical, with large eyes. Eye (female) occupying all of lateral and most of frontal surfaces of head, not extended to posterior (occipital) region of head. Eye completely bare, no differentiation of facets; posterior margin simple, not emarginate, no transverse line through middle of eye. In lateral view dorsal portion of occiput protruding; ventral portion of eye broader, more rounded than dorsally; eye occupying ventrolateral surface of head (no cheek exposed). Female eyes well separated, lateral margins of frons slightly convergent dorsally, almost parallel; frons bare, no pilosity or pubescence. Ocelli well developed, level with vertex of head (not on mound). Face including clypeus sloped steeply into head, beginning just below antennal bases to deep pit just above pro-

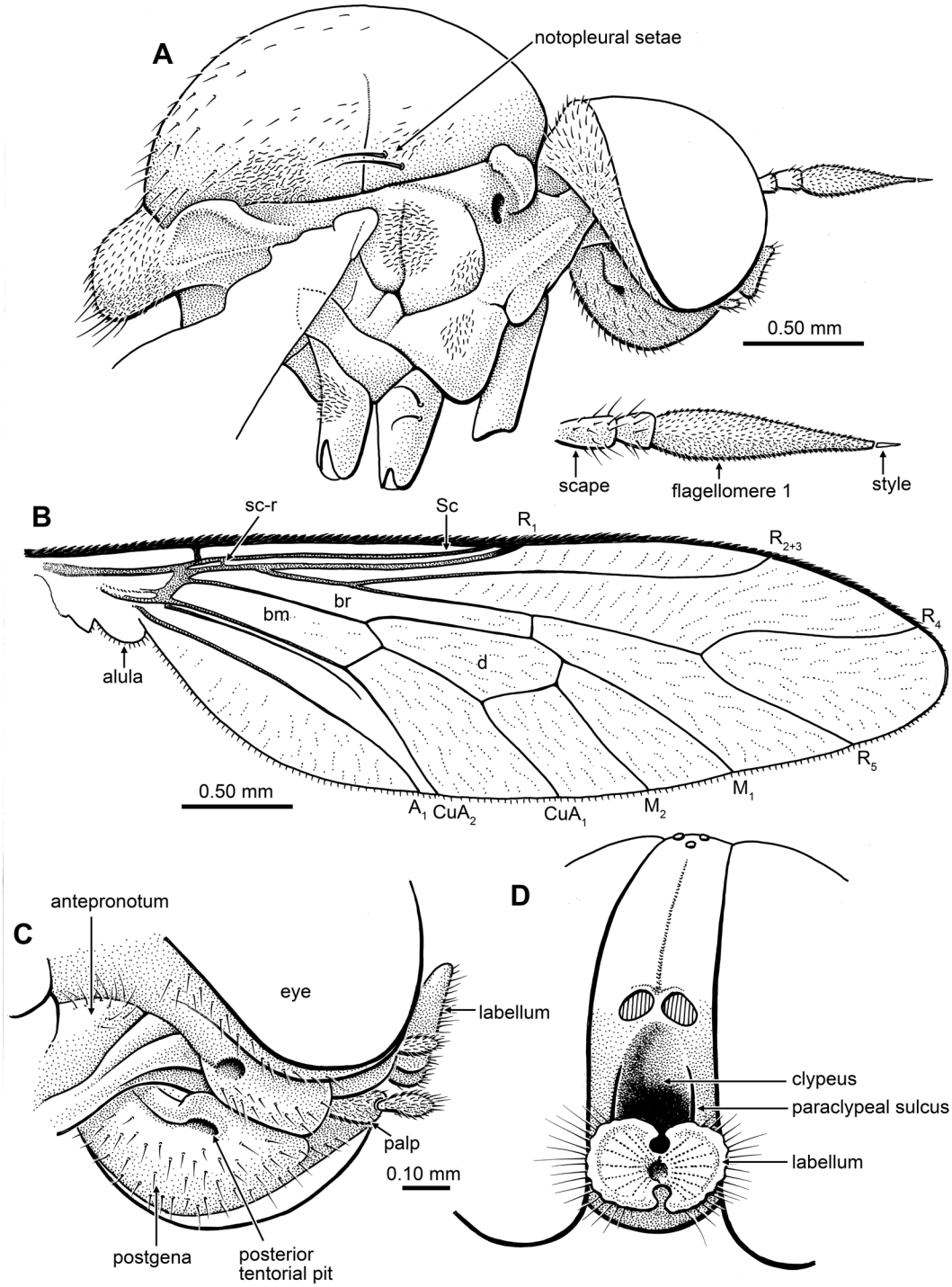

FIG. 22. *Nealimyia evenhuisi* (Bombyliidae), new genus and species, holotype, AMNH Bu-SE2/7. **A.** Head and thorax, right lateral view, with detail of antenna. **B.** Wing. **C.** Detail of head, oblique ventral view of anterior portion. **D.** Detail of head, frontal view (only antennal sockets shown).

boscis. Occiput and postgena partially recessed, but without broad, hemispherical concavity as in Anthracinae. Postgena with median longitudinal suture just below occipital foramen; posterior tentorial pits lateral to suture, just below ventral margin of occipital foramen; foramen apparently not constricted or divided into two; occiput protruding well beyond dorsal margin of eye, setose. Occipital pocket, occipital apodeme apparently absent. Dorsal portion of occiput with median sulcus. **Antenna:** Insertions (sockets) subcircular, very close, located just above facial depression; antennae held forward. Scape narrow at base, slightly wider distally, slightly longer than pedicel; pedicel slightly broadened distally; flagellum long, slender, drop shaped, unsegmented, tapered to narrow width, with minute apical style at tip (seen in left antenna, tip of right one lost). **Mouthparts:** Proboscis short, only labellum exposed frontally and laterally; labellum well developed, opened in holotype exposing broad, flat pseudotracheal surface; labellar lobe ear shaped, with ca. 8 pseudotracheae and fringe of fine, stiff setae on lateral rim. Labium very short, barely visible ventrally. Palp very short, not extending beyond labellum, basal palpomere slightly larger than apical one, apex of palp (i.e., pit) not observable. Lacinia and labrum not visible. **Thorax:** Large, deep, hunched; scutum large, deep, arched; transverse suture well developed. Scutum without macrosetae (bristles), largest setae are fine, short, stiff ones anterior to scutellum; most of scutum with very small, fine setulae; patches of golden, fine, sparse pilosity on supraalar and notopleural regions, portions of katepisternum and anepisternum, and posterior surface of metacoxa. Notopleural suture well developed, completely anteroposterially transverse through thorax. Neck with long antepronotum and lateral cervical sclerites, located just above base of procoxa. Katepisternum relatively small; meron and anepisternum large, well defined; postalar wall dorsally protruding as shallow ledge, ventrally recessed. No proscutellum; scutellum relatively small compared to scutum, dorsal surface entirely with setulae, longer ones on posterior margin; no subscutellum; postnotum short. **Wing:** Long, slender, W/L 0.29; entirely hyaline, no pterostigma or other infuscation; membrane very faintly and finely wrinkled, with fine microtrichia. Basicosta small, not lappetlike; vein C circumambient, crossvein h heavily sclerotized; Sc 0.48× length of wing, complete; R_1 very close to and parallel to Sc, almost fused apically; faint sc-r crossvein present. R_{2+3} 0.78× wing length, tip upturned; R_4-R_5 forked, tips of fork encompassing wing tip, R_4 slightly sinuous and longer than R_5. Cell d large, r-m near apex of cell; two branches of M present (M_1, M_2); CuA_1 arising preapically from cell d. Cell br much longer (1.56×) than cell bm; stem of M heavily sclerotized. CuA_2 and A_1 meeting wing margin separately (cell cup open); anal lobe and alula narrow; upper calypter very small. **Legs:** Slender. Procoxa ca. 2× length of meso- and metacoxae. Femora with short, decumbent setae only. Lengths of femora: metafemur > meso > profemur. Tibia slightly longer than respective femur; protibia without macrosetae; mesotibia with dorsolongitudinal row of eight stiff, short setae; metatibia with dorsolongitudinal and ventrolongitudinal row of 8–6 setae, respectively. Tibial spurs 0-1-0; mesotibial spur slightly longer than apical width of tibia. Basitarsus longer than combined distal tarsomeres. Claws well developed, simple; empodium setiform; pulvilli are short pads, shorter than claws. **Abdomen (female):** Significantly more slender than thorax in dorsal view, slightly longer than thorax. Tergite 1 simple, not divided; tergites 2–7 little differentiated in size, all with dense vestiture of small, decumbent setae. **Terminalia (female):** Posterior margin of tergite 7 and sternite 7 (possibly t8 + s8, which are recessed within 7) with long, dense brush of fine, golden setae, forming a thick "basket." Presence/absence of acanthophorite spines not observable.

Type: Holotype, female, AMNH Bu-SE2/7.

Etymology: Patronym for Neal Evenhuis, dipterist, bombyliid specialist, colleague.

Comments: The fly lies in a slabbed portion of a runnel, 13 × 9 × 4 mm, which also contains

some internal flow surfaces and a light suspension of very fine bubbles and particles. The fly is complete and very well preserved.

Pioneeria, new genus

Diagnosis: Antenna subcylindrical, with three flagellomeres (2 apical ones short), plus minute apical style. Proboscis short but labium exposed; neck long, with stiff setae dorsally, long pilosity laterally. Four notopleural, one supraalar macrosetae; mesotibia with two spurs. Wing slender, sc-r crossvein present, cell br only slightly longer than bm; R_4 moderately sinuous, slightly longer than R_5; cell d narrow, long; cell cup closed (CuA_2 and A_1 meeting at wing margin); A_2 well developed, terminating abruptly; anal lobe well developed. Terminalia unknown. Distinguished from *Pseudorhagio* Q.-Q. Zhang et al. (Zhang et al., 2016) as discussed below under Comments.

Type Species: *Pioneeria bombylia*, new species.

Etymology: From the English *pioneer*, originally from Old French, *paonier* ("foot soldier"). In reference to the early appearance of this fossil for the family Bombyliidae. The gender of the name is feminine.

Comments: The antenna is unique within Bombyliidae, possessing a subcylindrical flagellum with two short apical articles. Another distinctive feature is the two (vs. one) mesotibial spurs. Unfortunately, the terminalia were lost at the surface of the amber.

Pseudorhagio zhangi Q.-Q. Zhang, J.-F. Zhang, and Wang was recently described in Burmese amber, placed in Tabanomorpha family incerta sedis because it has such unusual features for that infraorder (Zhang et al., 2016). Disparate features include the following: R_4 strongly curved at base and very sinuous; scutum very arched, such that the neck and dorsum of the head are well below the dorsum of the scutum; crossvein m-cu is very sinuous; flagellum is long, stylate and 1-articled; there are two M veins; spurs 0-2-0; and the female abdomen has a thick brush of fine setae on the terminal segments.

Indeed, *Pseudorhagio* is unusual for Tabanomorpha, because it is actually an asiloid, specifically in the Bombyliidae. In fact, it bears important similarities to *Pioneeria*, such as two long mesotibial spurs, a hunchbacked scutum, the antennal structure (the fine sutures between the apical two flagellar in *Pioneeria* are very subtle, and may have been missed by Zhang et al.; these authors did not mention the minute apical style, which appears to be present in their fig. 2B). The thick apical brush on the abdomen confirms placement in the Bombyliidae. The only structure in contradiction with an asiloid placement is that the empodium in *Pseudorhagio* is described as pulvilliform, although in their figure 4A there does not seem to be three pretarsal lobes (only two), so this feature also needs to be independently confirmed. *Pioneeria* differs from *Pseudorhagio* by the following: R_4 much less sinuous; wing more slender; scutum with five macrosetae on each side, fringe of long setae on scutellum and posterolateral portion of scutum (vs. without); neck long and setose.

Pioneeria bombylia, new species

Figures 23, 55

Diagnosis: As for genus, by monotypy.

Description: Based on probable female. Thorax length 2.92 mm; head width 1.74 mm; head length 0.88 mm; wing length 6.44 mm. **Head:** Roughly hemispherical in shape, anterior half convex, posterior half flattened and concave. Eye large, bare, no differentiation of facets; eye occupying all of lateral, much of dorsal and ventral surfaces of head; posterior edge of eye not emarginate; eye without fine transverse line through middle; no emargination near antennal base. Ocelli present, but small; ocellar triangle small, barely raised above surface of vertex. Frons (female?) well developed, width 0.16× that of head, lateral margins diverging slightly anteriad. Face and clypeus steeply recessed into oral cavity immediately ventral to antennal bases, forming ceiling to proboscis. Postgena deeply sunken, forming deep concavity into which neck

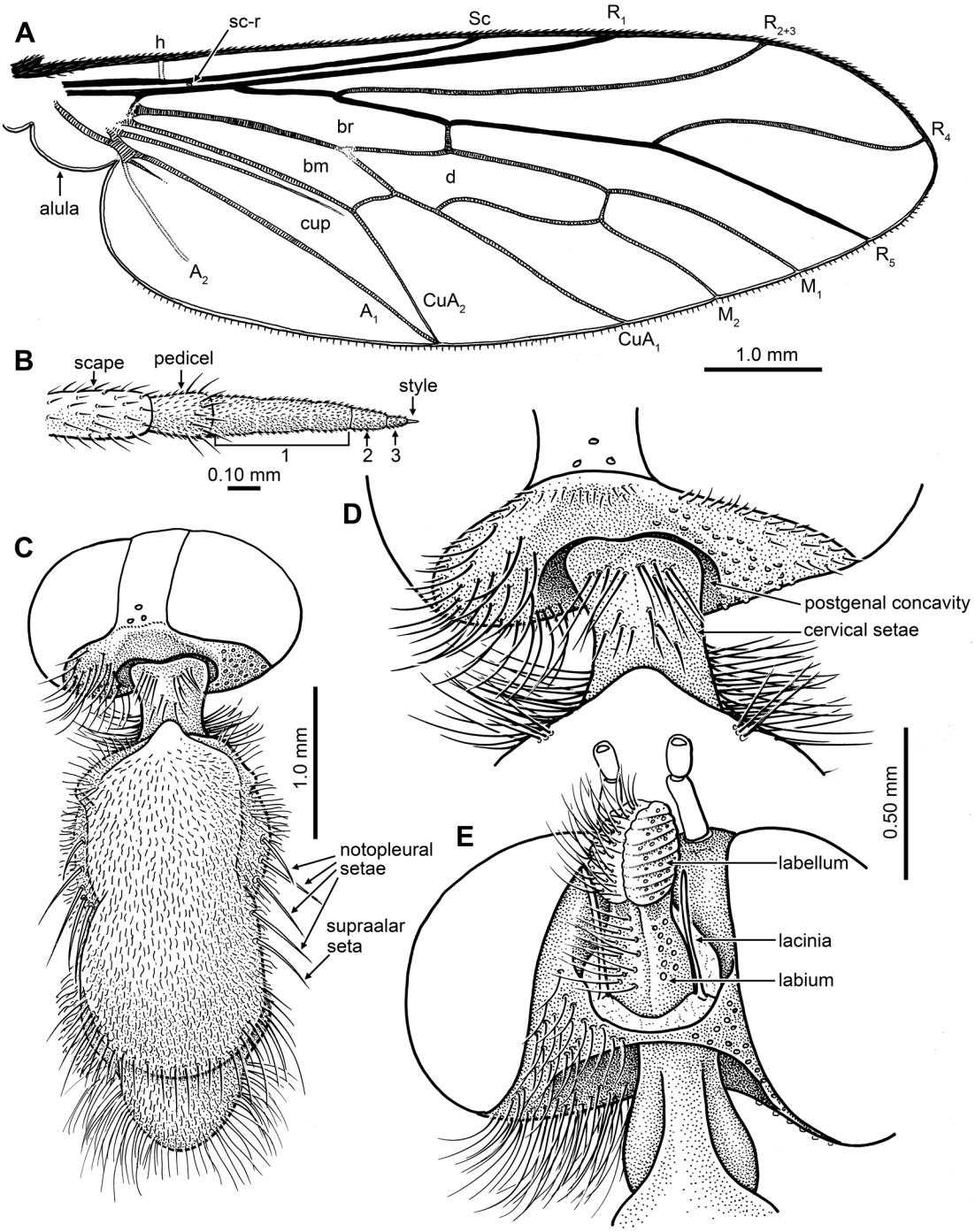

FIG. 23. *Pioneeria bombylia* (Bombyliidae), new genus and species, holotype, AMNH Bu-SE2/9. **A.** Wing. **B.** Antenna, lateral view. **C.** Head and thorax, dorsal view. **D.** Detail of cervical area, showing setation and pilosity. **E.** Detail of ventral portion of head, with mouthparts.

inserts; postgena rimmed by pilosity of fine, long, golden setae. Gena pilose, with brush of long, fine setae. Occiput slightly concave posterior to frons, slightly bulging posterior to eyes. Occipital foramen not visible. **Antenna:** Cylindrical, apically tapered. Scape cylindrical, 2× length of pedicel; pedicel very slightly wider at apex, with apical ring of fine setae; flagellum with 3 definite articles, basal article 2× length of distal articles combined, with faint appearance of vestigial segments; 3rd flagellar article half the size of 2nd; minute stylus present, apical. **Mouthparts:** Proboscis short, projecting forward, prelabellar portion recessed into oral cavity; labellum exposed, projecting beyond frontal surface of eyes. Labium short, broad, width 0.7× the length, with long, fine pilosity. Lacinia long, laterally flanking labium; tip blunt, reaching to middle of labellum. Labellar lobes rounded, fleshy, setose, with 8 pseudotracheae. **Thorax:** Relatively long and narrow in dorsal view, narrower than head. Neck long, dorsally with long, fine, stiff setae; 2 paramedian groups of 6–7 longer setae anteriorly, 4–5 shorter setae near middle of neck; cervical setae point backward; neck laterally with brush of fine, long, golden setae sticking out laterally. Most of scutum and pleura covered with fine, golden pilosity; pilosity longer on pleural, notopleural, supraalar areas, posterior margin of scutum, postpronotal lobes, and posterolateral margin of scutellum. Notopleural area with 4 thick, whitish macrosetae (bristles), 1 such macroseta on supraalar area. Laterotergite/anatergite with long, fine pilosity. Transverse suture short, entirely vertical on lateral surface of scutum; scutum pinched in near middle at transverse suture. **Wing:** Slender, W/L 0.35. Basicosta light, well developed; C circumambient, black proximally, greatly thinned posterior to R_4 apex. Crossvein h faint; small, faint crossvein sc-r present. Sc complete, sclerotized, apex ending at midwing length. R-R_1 thickest, most heavily sclerotized vein, length 0.65× that of wing; faint pterostigmatic area between apical third of R_1 and C. R_{2+3} upturned at apex, fork of R_{4+5} asymmetrical, branch of R_4 longer and sinuous, apices encompassing wing tip. Branches of M_1 and M short, attached to apex of cell d; Y-juncture of M_1-M_2 weakened; CuA_1 attached near base of cell d; cells br and bm nearly equal in length; apices of CuA_2 and A_1 meet at wing margin (cup closed); vein A_2 present, but nebulous; anal lobe well developed; alula shallow; upper calypter well developed. **Legs:** Bases of all coxae closely situated, coxae suspended beneath thorax (not projecting forward or laterally). All coxae with brush of fine, long, golden setae, on anterior surface of procoxa, lateral surfaces of meso- and metacoxae. Femora with fine, decumbent setae, length metafemur > meso > profemur. Mesotibia with dorsolongitudinal row of 5 short, spinelike setae, 3 such setae ventrally; protibia without spinelike setae [metatibia and metatarsus lost]. Tibial spurs 0-2-?. Basitarsomere slightly longer than distal tarsomeres combined. Pretarsal structures small, pulvilli small, empodium setiform. **Abdomen:** Slender, no wider than thorax in dorsal view. 7 tergites preserved, tergites ≥ 8 lost at surface of amber. Tergites 2–7 with dense vestiture of fine, decumbent setae; tergites wrapped laterally, lateral margins of tergites and sternites nearly meeting; tergite 1 with long pubescence. Sternites well developed. **Terminalia:** Lost at surface of amber.

Type: Holotype, sex unknown (probably female), AMNH Bu-SE2/9.

Etymology: Taken from the stem of the name Bombyliidae.

Comments: The fly is in a dark piece of amber retaining its natural oval outline, 15 × 32 mm, slabbed to 5 mm thickness. Surface of the amber is reddish, with a reddish coating over the fly (nascent pyritization), but the amber has excellent clarity. Apex of the abdomen and some tarsi were lost at the surface of the amber. Syninclusions are a thrips (Thysanoptera) and Ceratopogonidae (Diptera).

Procrocidium, new genus

Diagnosis: Small bodied, without long pilosity; antenna with one flagellomere, plus minute

subapical style. Three notopleural, one supraalar seta present. Wing short, relatively broad, apex rounded; fork of R_4-R_5 nearly symmetrical, vein R_4 only slightly sinuous; cells br and bm nearly equal in length (vs. br much longer), crossvein sc-r present, r-m crossvein near base of cell d (vs. distal); CuA_2 very long, converging with but not meeting CuA_1 toward wing margin, A_1 apparently lost. Mesotibia with long apical spur; metacoxa with well-developed anterior peg; acanthophorite spines present; thick brush of fine setae on tergites 7 and 8, but sand chamber not well developed.

Type Species: *Procrocidium minutum*, new species.

Etymology: In reference to the apparent relationships of the fossil to the subfamily Crocidiinae, with the prefix denoting some generalized features as well. The gender of the name is neuter.

Comments: The genus is phylogenetically intermediate among subfamilies of Bombyliidae, sensu Yeates (1994), probably close to Crocidiinae. On the one hand, it possesses acanthophorite spines (node 41 in Yeates, 1994), which are not found in the basal grade of subfamilies Mythicomyiinae, Oligodraninae, Usiinae, Toxophorinae, and Lordotinae. Also, tergites 9 and 10 are separate, unlike the fused condition in the first three of these subfamilies. The new genus has a dense brush of fine setae on tergite 8, but sternite 8 is not invaginated into a sand chamber (node 42 in Yeates, 1994), which partly defines the "higher beeflies," the larger, more typical, pilose species. The dense brush of fine setae on the apical tergites of female bombyliids is, according to Yeates (1994) closely associated with the development of a sand chamber, a pouch formed from the invagination of sternite 8 and tergite 8 in which eggs are coated with sand grains. The brush occurs in *Nealimyia*, *Pseudorhagio*, and *Procrodium* (apex of the female abdomen is not preserved in the unique specimen of *Pioneeria*, but I predict this genus has the brush).

Plesiomorphic features of *Procrodium* include cells br and bm nearly equal in length (vs. br much longer); vein R_4 not strongly sinuous (generally S-shaped in higher beeflies); crossvein r-m connected to cell d near its base (instead of in distal half of cell d). These features, plus a virtual lack of pilosity, a flagellum structure similar to that of *Oligodranes* and *Usia*, and a sinuous dm-cu crossvein like that in *Pseudamictus*, indicate that the new genus is an amalgam of plesiomorphic and apomorphic features that will need a quantitative analysis. Probably most revealing is that the genus has a long mesotibial spur and well-developed metacoxal peg, like the subfamily Crocidiinae (Yeates, 1994). *Crocidium* also have a small sc-r crossvein.

Procrocidium minutum, new species

Figures 24, 56

Diagnosis: As for genus, by monotypy.

Description: Based on female. Small, compact fly, thorax length 1.21 mm., wing length 2.83 mm. **Head:** Apparently hemispherical (based on portions preserved), width slightly greater than thorax. Eye: Occupying lateral, much of frontal and dorsal surfaces; bare; no differentiation of facets; no emargination of posterior or anterior margins; dorsomedial margins widely separated, parallel. Frons completely bare, dark, cuticle apparently dark; width nearly 2× that between outside margins of antennal bases. Ocelli on vertex of head, barely raised above frons surface, with ca. 8 small, stiff, erect setae in triangle. Face not preserved. Occiput setose, barely recessed (not strongly concave); occipital foramen large, pear shaped (vs. 8-shaped), apparently invaginated sleevelike into posterior third of head. Anterior and posterior apodemes well developed (visible through exposed and cleared walls). Occiput laterally with thick, stiff, short setae. **Antenna:** Small, short; scape cylindrical, pedicel subspherical, with single preapical whorl of minute setulae; 1 (basal) flagellomere present, elongate drop shaped, having minute, subapical stylus; antennal article lengths; basal flagellomere > scape > pedicel. **Mouthparts:** Not preserved. **Thorax:** Broad, apparently rather short (poste-

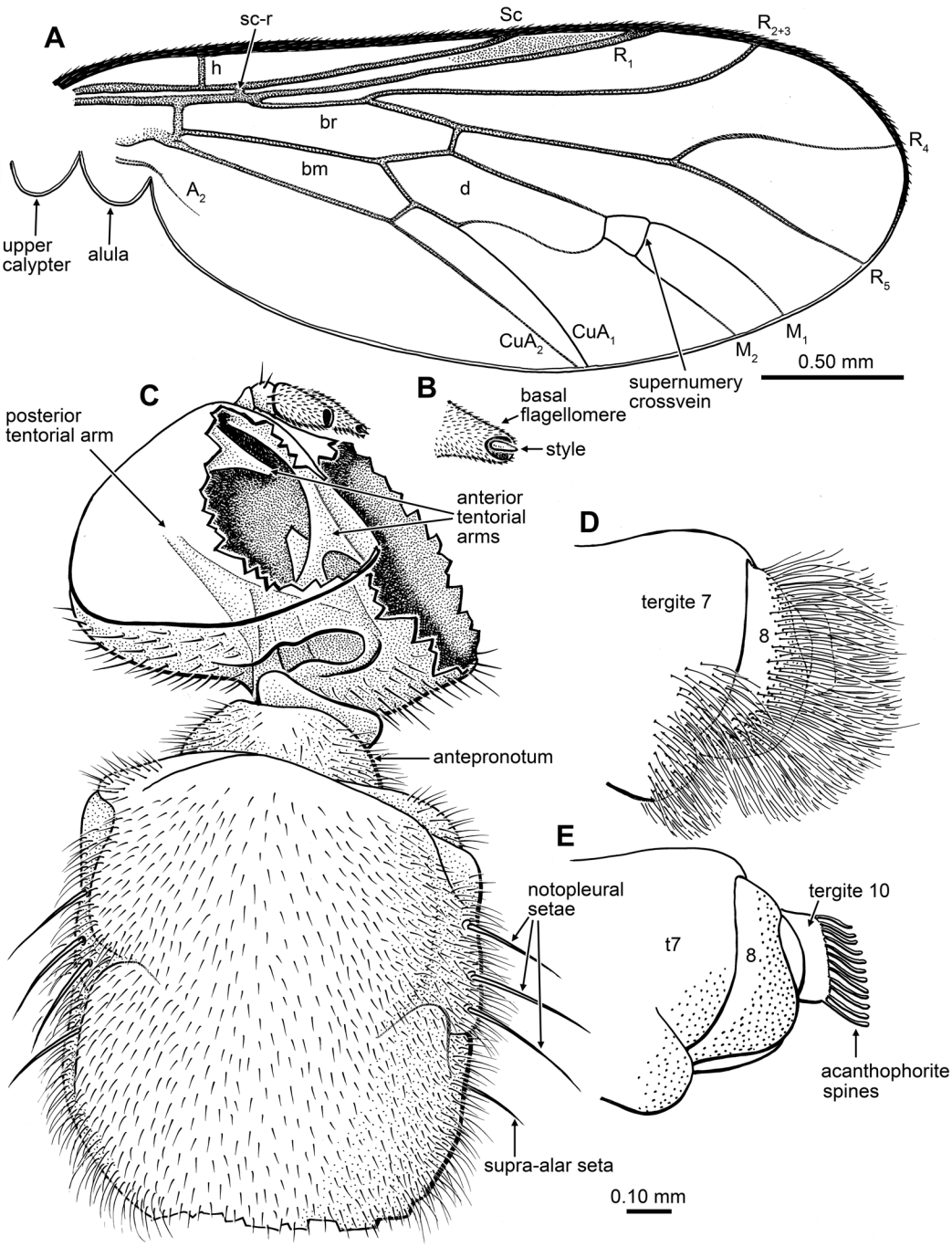

FIG. 24. *Procrocidum minutum* (Bombyliidae), new genus and species, holotype, JZC Bu-098. **A.** Wing. **B.** Detail of tip of antenna, showing minute apical style. **C.** Head and thorax, dorsal view, as preserved (head is tilted to show right lateral view). Portions of the head wall are lost, revealing the tentorial arms. **D.** Female terminalia, left lateral view, with pilosity intact. **E.** Female terminalia, left lateral view, with pilosity removed and showing acanthophorite spines. Panels C–E to same scale.

rior portion lost). Dorsum of scutum very high, dome shaped, raised well above dorsum of antepronotum; antepronotum in approximately middle of thoracic depth as seen in lateral view. Antepronotum very well developed, laterally setose, width ca. 0.50× that of scutum; length of antepronotum 0.27× the width. Lateral cervical sclerites very large, posterior portion bulging. Scutum with very short, decumbent setulae; setulae on posterolateral portions of scutum longer. Transverse suture well developed, dorsally with apex pointed posteriad. Notopleural area just above notopleural suture with row of 3 long, stiff macrosetae; 1 such macroseta on supraalar area; all macrosetae whitish. **Wing:** C thick, circumambient, abruptly tapered in width midway between apices of R_4 and R_5; basicosta very small; crossvein sc-r present. Crossvein h long, lightly sclerotized; Sc reaching slightly past level of middle of wing; R_1 ca. 0.70× length of wing, apex gradually tapered to C, faint pterostigma between apices of Sc and R_1. R_1 thick; R_{2+3} slightly upturned apically. Fork of R_4-R_5 nearly symmetrical, R_4 slightly sinuous. Crossvein r-m very basal, at 0.27× length of cell d from its base. Cells br and bm nearly equal in length. M_1 and M_2 nearly parallel; m-cu strongly sinuous. Tips of CuA_1 and CuA_2 nearly meeting at wing margin. A_2 fairly long, apically evanescent. Alula small, upper calypter well developed. Anal lobe shallow. **Legs:** Hind coxa with well-developed peg on anterior surface. Mesotibia with long apical spur. Basitarsomere slightly longer than combined length of distitarsomeres. Pretarsus with small pulvilli, shorter than claws; empodium setiform, minute. **Abdomen:** Very partial. **Terminalia (female):** Tergite 8 apparently without dorsal apodome on anterior margin, or so short as to be unnoticeable, definitely not tongue shaped; ventrolateral portion of t7 with very fine, blond setae, shorter than setae on tergite 8. Tergites 9 and 10 separate (cannot determine whether 9 and 10 with dorsal connection); tergite 8 with dense brush of long, fine, blond setae on distal half and ventral portion. Tergite 10 narrow, with ca. 12 long acanthophorite spines on each half, spines slightly sinuous, widened apically and increased in length ventrad; spines in two even rows on posterolateral margins, dorsomedial separation between lateral rows. Sternite 8 not appearing invaginated (e.g., no sand chamber). Cerci small, shallow, lying between acanthophorites, as seen in posterior view.

Type: Holotype, female, JZC Bu-098.

Etymology: In reference to the small size of the holotype.

Comments: Specimen is in a small, irregularly cubic, clear yellow piece of amber 4 × 6 × 7 mm, cut from a cabochen 15 mm diameter, the entire piece of which contains no other insect inclusions. The fly is partial and portions are disarticulated (fig. 56), but sufficiently preserved to diagnose, in fact exposing some critical features. Head is still attached to the thorax, but the ventral portion (including the mouthparts) has decayed away. The wings are fully intact and connected to the thorax, but portions are folded; the venation required some reconstruction. Posterior portion of the thorax (scutum, scutellum) has decayed away. Portions and entireties of five legs are preserved, one is disarticulated at the base. The abdomen is largely decayed away, with tergites 1–3 remaining; apex of the abdomen (including the terminalia) is disarticulated from the rest of the abdomen and partially cleared, lying under the outstretched left wing near the head (fig. 56).

Endymiomyia, new genus

Diagnosis (male): Holoptic, thorax short and compact, abdomen long, cylindrical; wing long, linear, very slender, apex narrow. Veins R_5 and stem of R_{4+5} straight, tip of R_5 ending at apex of wing; R_4, R_5, M_1, and M_2 almost parallel; crossvein sc-r present. Cells br and bm equal length; cell d very long, short spur of M_3 present; cell cup closed; anal lobe and A_2 well developed; upper calypter small, with inflated bulla. Proboscis short; antenna with stylate flagellum, 4 flagellar articles, basal flagellomere drop shaped, others forming slender stylus; fine terminal style

present. Mesocoxa with one spur; metacoxa with well-developed peg. Gonocoxa small; phallus with long (parameral?) sheath.

Type Species: *Endymiomyia quadra*, new species.

Etymology: Derived from Endymion of Greek mythology, a youth so beautiful that Selene, the moon, purportedly cast him into perpetual sleep so that she could lie with him; and *myia*, Greek for "fly." In reference to the gender, lovely preservation, and age of the holotype. The gender of the name is feminine.

Comments: See below, under species description.

Endymiomyia quadra, new species

Figures 25, 57

Diagnosis: As for genus, by monotypy.

Description: Based on male. Body length 6.58 mm; thorax length 1.67 mm; head width 1.64 mm; wing length 6.52 mm; abdomen length 3.87 mm; abdomen width (at base) 0.48 mm. Dorsum of thorax and abdomen dark, color not discernable. **Head (male):** Large, broader than thorax, dorsoventrally slightly flattened. Eyes very large, holoptic for most of length of frons, bare; facets on frontal surface ca. 2× diameter of surrounding facets; presence/absence of median transverse line through eye not observable (eyes partially decayed); posterior margin of eye (preserved portion) not emarginate; frontal margins divergent above antennae and ventrad, very slight emargination around base of antenna; eye partially occupying ventral surface of head (gena). Ocelli small, ocellar triangle small, slightly raised; lateral ocelli touching inner margins of eyes. Antennae inserted near middle of front of head, antennal sockets nearly contiguous, touching inner margins of eyes. Clypeus very small, faintly convex; oral cavity not sunken above proboscis (only ventral to proboscis). Gena well developed, setose, with fine light setae; hypostomal bridge complete; postgena concave, posterior tentorial pits visible; shape of dorsal portion of occipital foramen not visible (e.g., constricted/bisected); occiput not fully visible but apparently not concave. **Antenna:** Stylate, with 4-articled flagellum; antenna held forward. Scape small, short, cylindrical; pedicel slightly larger, apex slightly expanded and with whorl of setulae; basal flagellomere drop shaped, apically tapered to narrow stem; flagellum articles 2, 3, and 4 forming slender stylus, articles 2 and 3 nearly equal in size, article 4 longer than 2+3; very fine, minute style at apex of antenna. **Mouthparts:** Short, tip of proboscis protruding slightly beyond frontal surface of head, labellum small (obscure). Palp very slender, digitiform, 2-segmented, segments approximately equal length, apical segment slightly expanded; both palpomeres with ventral brush of long, fine, light setae; palp setae nearly as long as palp. Palpal pit present, preapically on lateral surface. Labrum fine, narrow, tubelike, lateral margins almost/actually meeting ventrally; length of labrum equal to that of proboscis. Laciniae not visible. Labium short, setose, visible in ventral view. **Thorax:** Short, compact, dorsally somewhat flattened. Scutum and scutellum very dark, with sparse vestiture of very fine, golden setae, longest setae on posterior portion of scutum, margins of scutellum, laterally on thorax. Notopleural area with 3 stiff, black, bristlelike macrosetae just anterior to transverse suture; 1 slightly thinner such seta on supraalar area. Pleura largely obscured by fractures, but katepisternum large, deep, separating procoxae from mesocoxae. Katepisternum, anepimeron, meron bare. Proscutellum and postscutellum absent. Scutellum triangular in dorsal view. **Wing:** Very long, slender, significantly tapered apically. Vein C circumambient, but abruptly narrowed past apex of R_5; C thick, black on anterior edge; basicosta small, not deeply incised or lappetlike. Crossvein h long, sclerotized, slightly distal to level of arculus; crossvein sc-r present, very short. Sc long, complete, 0.64× length of wing. R veins thick, sclerotized (except R_4 and apex of R_{2+3}); R_1 parallel and very close to Sc, slender pterostigma surrounding apex; R_{2+3} significantly tapered apicad into thin vein, preapically faintly

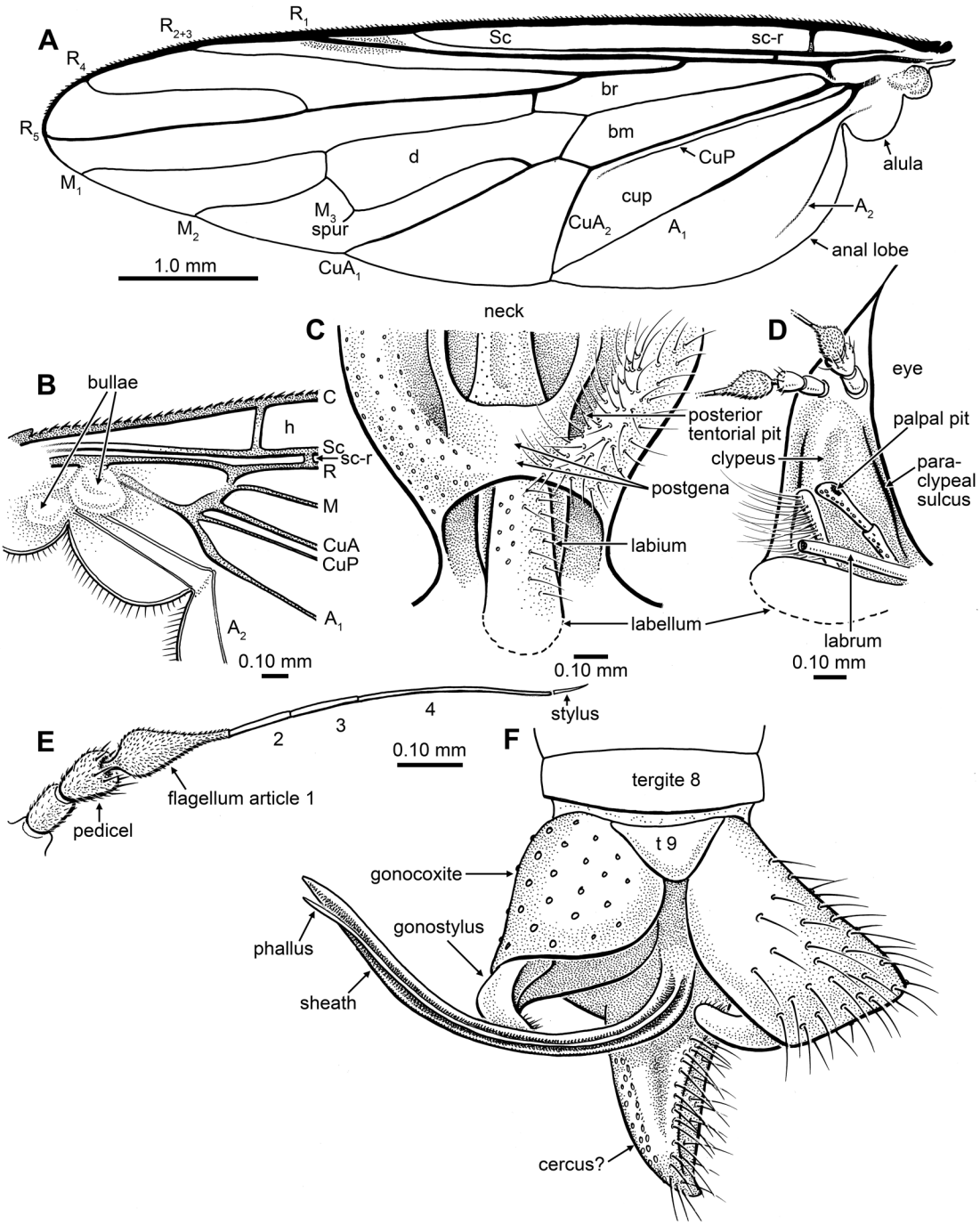

FIG. 25. *Endymiomyia quadra* (stem-group Bombyliidae?), new genus and species, holotype JZC Bu-209. **A.** Wing, dorsal view. **B.** Detail of wing base, dorsal view. **C.** Detail of anterior portion of head, ventral view. **D.** Face, with antennae and mouthparts, oblique frontal view. **E.** Detail of antenna, lateral view. **F.** Male terminalia, dorsal view. Panels E, F to same scale.

sinuous, tip of R_{2+3} reaches to 0.83× wing length. R_5 and Rs thick, virtually straight and in line. Base of R_4 forks nearly perpendicular from R_5, tip of R_4 upturned; tip of R_5 ending at wing tip. Cells br and bm of equal length. Crossvein r-m near base of cell d; cell d very long. M veins thin; M_2 slightly sinuous, short; short spur of M_3 present, attached to apex of cell d (occurs in both wings). CuA thick, sclerotized, CuP present as sclerotized, tubular vein, ending at level of cell bm apex. A_1 and CuA_1 fuse just before wing margin (cell cup closed). A_2 present, long, apically evanescent. Anal lobe and alula well developed; upper calypter small. Dorsal surface of wing base between stems of M+Cu and A_2 with small, crescentic bulla; smaller, rounded bulla at base of upper calypter. Halter knob broad, dark; stem light, slender, long. **Legs:** Long, slender, dark. Procoxa long, slender, well separated from meso- and metacoxae. Legs mostly preserved in unique specimen, but all except hind ones detached from body, jumbled; tips of hind tibiae lost. Tibial spurs 0-1-?. Metacoxal pegs present on anterior surface, well developed. Pretarsus with claws well developed, empodium setiform, stiff and bristlelike; pulvilli slender, crescent shaped, slightly longer than claws. **Abdomen:** In male, very slender, nearly cylindrical; tergites and sternites well developed, dark, lateral edges nearly meet. Tergite 1 very short, tergites 2–4 nearly equal in length (base of tergite 2 slightly swollen); tergite 9 small, triangular, lying at bases of gonocoxae. Tergites with long, fine, erect, light setae; setae longest and most dense on lateral surfaces of tergites 1–5, especially tergite 2 (setae here are longer than width of tergite). **Terminalia (male):** Tergite 8 short, transverse; tergite 9 small, triangular, lying between bases of gonocoxae. Gonocoxae large, broad, setose, scoop shaped (mesal surface concave); gonostylus small, subapical, lobate. Phallus very thin, long, stylate, lying in broader, flattened sheath; phallus longer than gonocoxa + gonostylus. Large setose lobe(s) (cerci?) ventral to phallus, with basal furrow into which phallus base lies; apex of lobe(s) pointed.

Type: Holotype, male, JZC Bu-209. The specimen is in a small cubic piece of amber trimmed from a larger cabochen-shaped piece that contains a cucujoid beetle, a small beetle of undetermined family, a psychodid midge, and a suspension of wood particles. The fly is virtually complete, except that the hind legs distal to the apices of the tibiae are lost at the surface, and although three other legs are preserved they are detached and lying near the body. Also, the ventral halves of the eyes have decayed away. Otherwise, the specimen is very well preserved, with venation fully exposed and much of the genitalia visible.

Etymology: Latin for "square," used as a noun in apposition, in reference to the 4-articled flagellum that is unique amongst Heterodactyla.

Comments: By virtue of the setiform empodium and a process of elimination, this striking species is not a nemestrinid, acrocerid, or eremoneuran, but appears most consistent with Asiloidea. Another feature supporting this placement is the presence of bristlelike macrosetae on the thorax, which is a feature of Asiloidea + Eremoneura. Within Bombyliidae I have observed the presence of notopleural and supraalar macrosetae in *Cyllenia*, *Henica*, *Nomalonia*, *Peringueyimyia*, and some bombyliines, but not in more basal beeflies (e.g., phthriines, usiines). The macrosetae occur in the three genera of Bombyliidae described herein, as well as *Endymiomyia*. The fossil has very well-developed metacoxal pegs, which, albeit widespread in orthorraphans, occur among Asiloidea in Apsilocephalidae (including *Burmapsilocephala*, see below), *Hilarimorpha* (Hilarimorphidae), the basal bombyliid genus *Oligodranes*, and the (rather phylogenetically intermediate) bombyliid subfamily Crocidiinae (Yeates, 1994). I am tentatively placing *Endymiomyia* in Bombyliidae, even though the flagellum has four articles. In all Heterodactyla (Bombyliidae + Asiloidea + Eremoneura) the flagellum has three articles, so this is clearly plesiomorphic. Also, *Endymiomyia* lacks the depression/fossa on the dorsal wall of the oral cavity, which in all modern bombyliids (and the three Cretaceous genera above) extends up the face; this fossa accommodates the proboscis that

projects forward in bombyliids. *Endymiomyia* has a vestigial spur of M_3, the vein of which is completely lost in all other bombyliids except for various genera and species in the derived subfamily Anthracinae.

FAMILY APSILOCEPHALIDAE

This is a small, highly relict family with three genera and four species in the extant fauna that have widely disjunct distributions: *Apsilocephala longistyla* Kröber in the southwestern United States and Mexico; *Clesthentia aberrans* White, in New Zealand, *C. crassioccipitus* (Nagatomi et al.) in Tasmania; and *Kaurimyia thorpei* Winterton and Irwin in New Zealand. *Clesthentiella* Nagatomi et al. were synonymized under *Clesthentia* by Winteron and Irwin (2008). Cretaceous fossils include *Burmapsilocephala cockerelli* Gaimari and Mostovski in Cretaceous Burmese amber (see below), and a new species of *Burmapsilocephala* described below, also in Burmese amber. Tertiary species are *Apsilocephala vagabonda* (Cockerell), in Late Eocene shale from Florissant, Colorado (originally described in *Rueppellia* [Therevidae], transferred by Hauser and Irwin, 2005); and *Apsilocephala pusilla* (Hennig) in Eocene Baltic amber (originally described as "*Psilocephala*" [Therevidae] and transferred to Apsilocephalidae by Hauser, 2007). *Apsilocephala pusilla* is the most common therevoid fly in Baltic amber. Gaimari and Mostovski (2000) mentioned an undescribed species of *Apsilocephala* in Baltic amber. The therevoid fly *Kumaromyia burmitica* Grimaldi and Hauser in Burmese amber was considered a possible apsilocephalid (Grimaldi et al., 2010) and this identity was adopted elsewhere (Winterton and Ware, 2015[).

Apsilocephalidae is in the therevoid clade of Asiloidea, the family first erected by Nagatomi et al. (1991a). Later, however, Nagatomi and Yang (1998) synonymized Apsilocephalidae under the Mesozoic family Rhagionempididae, a change that has never been adopted by other dipterists. Placement of *Apsilocephala* within the therevoid clade has been confirmed by several phylogenetic studies, possibly as the sister group to Therevidae (Yeates et al., 2003; Trautwein et al., 2010), although evidence is strong that it is closely related to the monotypic Chilean family Evocoidae (Wiegmann et al., 2011; Winterton and Ware, 2015; Winterton et al., 2016).

Genus *Burmapsilocephala* Gaimari and Mostovski

Burmapsilocephala Gaimari and Mostovski, 2000: 43.

Emended Diagnosis: Separated from the extant genus *Apsilocephala* by the fossil genus having a longer aristalike terminal article of the flagellum; one postpronotal macroseta (vs. none); scutellum with one pair of macrosetae (vs. two); vein R_5 ends near or at the wing tip (vs. ventrally); dorsocentral setae lacking.

Type Species: *Burmapsilocephala cockerelli* Gaimari and Mostovski, 2000. In Burmese amber.

Comments: The genus was described by Gaimari and Mostovski (2000) on the basis of a well-preserved female specimen in the Burmese amber collection of the Natural History Museum, London. As discussed by them, the body is very similar to that of *Apsilocephala longistyla*, with differences as noted in the diagnosis above, although *Burmapsilocephala* are considerably more gracile than the common *Apsilocephala pusilla* in Baltic amber. Also, the male genitalia of a new species of *Burmapsilocephala*, described below, bear little resemblance to that of the living species *A. longistyla* or *A. pusilla* in Baltic amber (which are quite similar). The male genitalia of living *Apsilocephala* (possibly several species) have been thoroughly studied, with descriptions and illustrations provided by Nagatomi et al. (1991b), Sinclair et al. (1994), and Yeates (1994). The male genitalia of *Burmapsilocephala* are considerably simpler than in *Apsilocephala*, the former lacking the pair of large bristles on the gonocoxa; the large "apical coiled tube" (Nagatomi et al., 1991b) (phallus) is not apparent; the gonocoxae and gonostyli are free and articulating (not fused to epandrium); epandrium (tergite

9) is not simple and entire but rather fully separated medially; cerci are small lobes between the epandrial lobes and gonocoxae. Indeed, the bisected epandrium and small cercal lobes are very similar to the condition in another relict, long-legged gracile asiloid, *Evocoa* (Evocoidae) (Yeates et al., 2003). *Evocoa*, however, have a substantially different wing from that of *Apsilocephala* and *Burmapsilocephala*, with *Evocoa* having lost M_3 and cell m3, cell cup is open (CuP and A_1 are not even convergent), and the wing base is petiolate. Interestingly, Evocoidae and Apsilocephalidae are probably living sister groups, so the genitalic resemblance is probably based on close relationship of the two families.

***Burmapsilocephala evocoa*,** new species

Figures 26A–C, 58

Diagnosis: Distinguished from *B. cockerelli* (fig. 26D) also in Burmese amber, by possession of 14 thoracic macrosetae (vs. 12) as follows: 1 pair of notopleural setae (vs. 2), 2 pairs supraalars (vs. 1), 2 pairs postalars (vs. 1); notopleural setae distinctly shorter than in *cockerelli*; R_5 ending at wing tip (vs. posterior to it), crossvein r-m at middle of cell d (vs. in basal third); A_2 and anal lobe more developed (possibly sexually dimorphic).

Description: Based on male. A slender, delicate, gracile fly with long, slender legs and abdomen. Body length 4.38 mm; thorax length 1.00 mm; abdomen length 2.87 mm; wing length ca. 2.90 mm; hind leg length 4.57 mm. **Head:** Dorsal surface flattened, broad. Eyes completely bare (no interfacetal setulae), holoptic in male, occupying most of head dorsally, frontally, laterally; medial margins of eyes meeting from ocellar triangle to just above bases of antennae, small portion of frons exposed; anteromedian margins of eyes slightly emarginate around bases of antennae; facets on dorsal surfaces ca. 2× diameter of ventral and lateralmost facets. Ocelli on small, low tubercle on posterodorsal margin of head capsule, with several stiff setulae in triangle. Face, including clypeus, deeply recessed, clypeus not visible. **Antenna:** Basal three segments stout, approximately equal in length; scape short, cylindrical; pedicel scoop shaped (longer setulae ventrally). Basal flagellomere asymmetrically drop shaped, attached dorsally to ventral apex of scape. Terminal article of antenna aristalike; long, flagellate, with short pubescence, length of article approximately equal to length of head. Occiput behind posterior margin of eyes with fringe of long, stiff, very fine setae. **Mouthparts:** Proboscis short, slightly flattened laterally, only labellum visible beyond oral margin; palp and number of pseudotracheae not visible. **Thorax:** Virtually bare of setulae, with only very sparse setulae on scutum and coxae. Bristlelike macrosetae as follows: 1 pair scutellars (apical), 1 postpronotal; 1 notopleural; 2 supraalars, 2 postalars. Scutum slightly arched, dorsum of scutellum slightly below that of scutum, scutellum small, no proscutellum present. Tranverse suture short, S-shaped, fully lateral. **Wing:** Slender, middle portion of wing obscured due to preservation and folding. Tip of Sc reaching nearly to middle of wing; tip of R_1 slightly beyond middle of wing. R_1 and R_{2+3} very straight, nearly parallel; R_4-R_5 forked, base of fork slightly distal to level of apex of cell d; R_4 slightly sinuous, tip of R_5 ending at apex of wing. Crossvein rm at middle of cell d. Cell br significantly longer than cell bm. Cells m3 and cup present (CuA_1 + A_1 meeting before wing apex). A_2 well developed but apically evanescent; anal lobe well developed, alula and upper calypter not developed. **Legs:** Metacoxa with well-developed knob on posterior surface. All tibiae with dorsal and ventral longitudinal rows of short, erect macrosetae (lengths of setae approximately equal to width of tibia), as follows: protibia with 2 dorsal, 2 ventral setae; mesotibia with 3 dorsal, 5 ventral; metatibia with 8–10 dorsal, 5–6 ventral setae. Apices of tibiae with circlet of approximately 4 small setae. Tibial spurs absent. Leg segment lengths: tibia > femur > tarsomere 1 > tarsomere 2 > 3 > 4 = 5. Tarsomeres 1–4 on all legs with circlets of minute setae. Pulvilli slender, slightly shorter than claw; empodium tiny, bristleform. **Abdomen:** Long, slender, nearly cylindrical. Eight tergites exposed; lateral margins

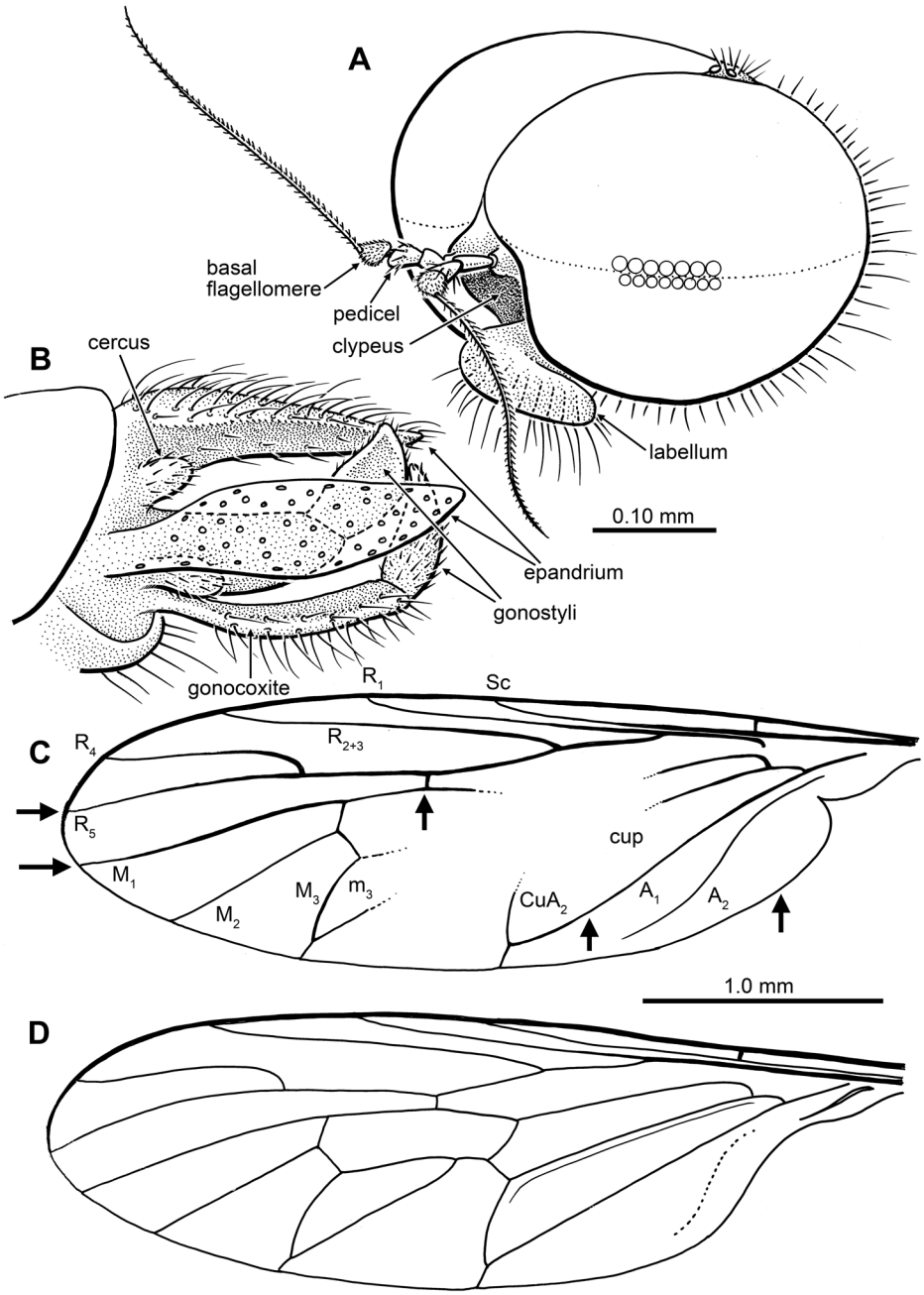

FIG. 26. *Burmapsilocephala* spp. (Apsilocephalidae) in Burmese amber. **A–C.** *Burmapsilocephala evocoa*, new species. **D.** *B. cockerelli* Gaimari and Mostovski (ex: Gaimari and Mostovski, 2000). **A.** Head, oblique frontal view. **B.** Male terminalia, oblique lateral view. **C.** Wing of *B. evocoa* (portion are not fully observable). Arrows indicate diagnostic venational differences. **D.** Wing of *B. cockerelli*. Panels A, B to same scale.

of tergites and sternites meeting. **Terminalia (male):** Projected posteriad, not flexed dorsad or ventrad. Epandrium apparently widely divided into pair of flat, setose lobes dorsally. Pair of small, setose lobes between epandrium and gonocoxae, probably the cerci. Gonocoxae setose, entirely free from epandrium and hypandrium, longer than gonostyli; gonostyli with only microtrichia (no setae), slightly pointed apically, without teeth; gonocoxae and gonostyli apparently articulating in oblique plane. Aedeagus not visible.

Type: Holotype, male, AMNH Bu-SE2/4.

Etymology: Taken directly from the name of the type genus of Evocoidae, to which this fossil seems related.

GENERA AND FAMILIES INCERTAE SEDIS

Gracilomyia, new genus

Diagnosis: Body slender, wing slender (W/L 3.0) with narrow apex; antennal flagellum stylate, with four articles, middle two (2, 3) short and small; neck long, antepronotum large; thorax without macrosetae. Vein C circumambient; Sc, R_1, R_{2+3} very long; sc-r crossvein lacking; R_4-R_5 forked; M_3 absent; cell d large, cup cell open; anal lobe absent; tibial spurs 1-2-2; metacoxal peg present; cercus with two segments.

Type Species: *Gracilomyia wit*, n. sp.

Etymology: Combination taken directly from gracile (Latin, *gracilis*, "slender, thin"), and *myia* (Greek, "fly"), in reference to the body shape. The gender of the name is feminine.

Comments: Placement of the genus is ambiguous, partly because the pretarsal structure is not obvious. If heterodactylan, a flagellum reduced to four articles would be consistent with placement in the Muscomorpha (Nemestrinoidea + Asiloidea + Eremoneura). However, the tibial spurs and two cercal segments indicate that the genus, at best, is a stem group to Muscomorpha. Alternatively, if homeodactylan, the genus is possibly related to the Rhagionidae, some of which (i.e., *Arthroteles*, *Atherimorpha*) have a 4-articled, stylate flagellum with apical setae. This placement would also be more consistent with the tibial spurs and cercal segmentation. Inconsistent with a placement in or near Rhagionidae are: anal lobe and alula narrow; apices of CuA_2 and A_1 distant (cell cup open); fork of R_4-R_5 very short; and antepronotum large. Two M veins occur in both Rhagionidae (e.g., *Austroleptis* Hardy, *Bolbomyia* Loew, *Spaniopsis* White) and various heterodactylans. Resolving the placement of *Gracilomyia* will require additional specimens.

Gracilomyia wit, new species

Figures 27, 59

Diagnosis: As for genus, by monotypy.

Description: Based on unique female. A relatively large, slender, and elongate fly with long, slender legs. Body length 7.51 mm; thorax length 2.58 mm; thorax width 1.00 mm; abdomen length 3.77 mm; wing length 4.81 mm; antennal length 0.61 mm. **Head:** Subspherical, slightly compressed dorsoventrally, slightly broader than thorax. Frons dark, bare; ocellar triangle slightly raised above frons, ocelli forming equilateral triangle, anterior ocellus facing forward. Face, beneath antennal insertions, short. Occiput convex. Eye: Large, completely bare, no differentiation of facets; in lateral view eye occupying most of head, occiput slightly exposed posteriorly; in dorsal view eyes widely separated, ca. 2× width of ocellar triangle. **Antenna:** Stylate, with 4 flagellar articles. Bases of antennae close, touching. Scape and pedicel small, shorter and narrower than basal flagellomere; flagellomere 1 cylindrical, with ca. 0.3× the length; flagellomere 2, 3 minute, 3 is short, ringlike; flagellomere 4 long, slender, stylate (*not* aristate or flagellate), longer than rest of antenna, apex with 2–3 fine, stiff setulae, no minute apical style. **Mouthparts:** Labellum large, flattened laterally (number of pseudotracheae not observable); number of palpomeres not observable (presumably 2), apical palpomere fairly broad in lateral view. Other mouthparts, clypeus not

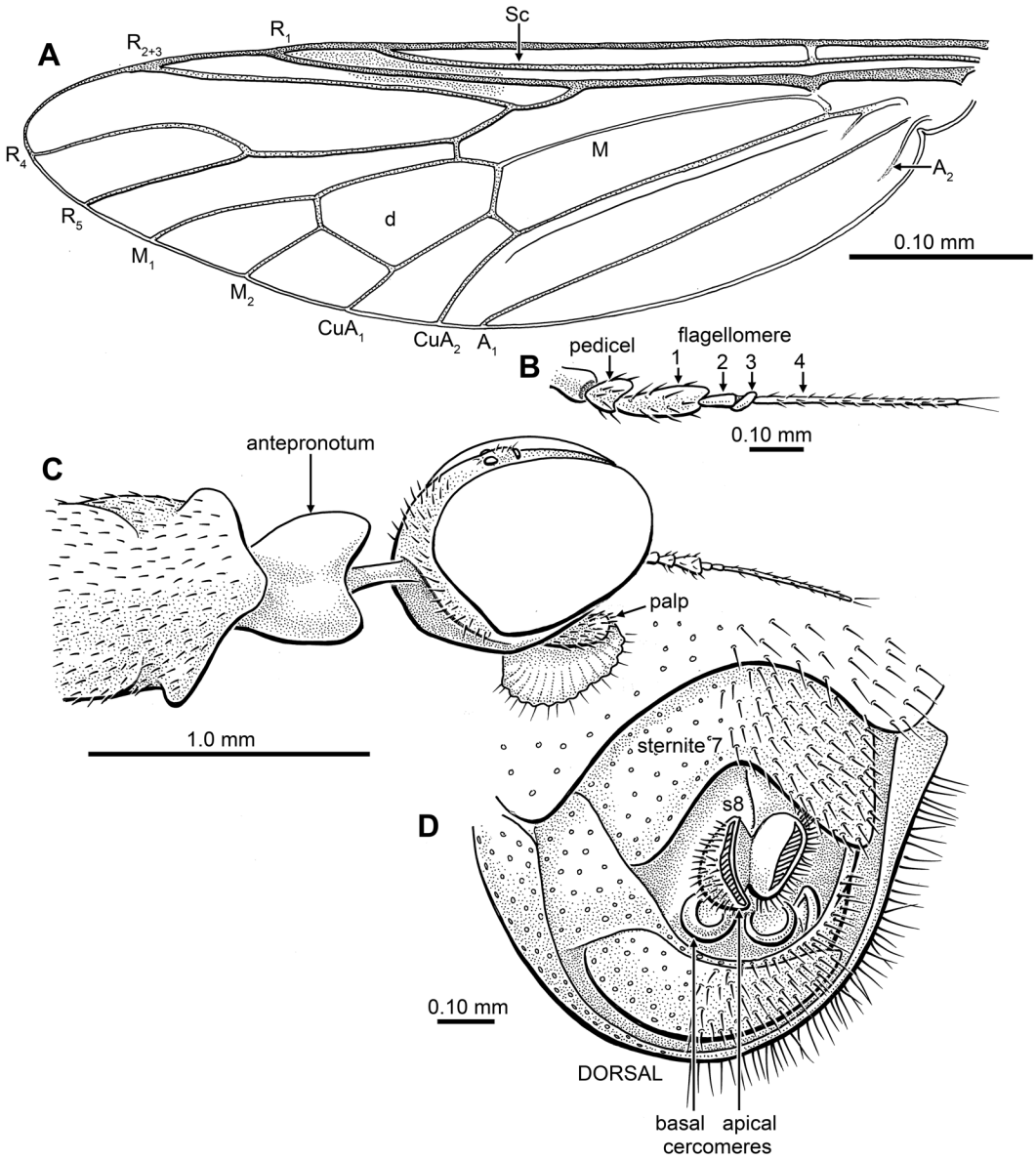

FIG. 27. *Gracilomyia wit*, new genus and species (unplaced to family), AMNH Bu-SE14, holotype. **A.** Wing. **B.** Antenna. **C.** Head and anterior portion of thorax, dorsal view. **D.** Female terminalia, posterior view. The apices of distal cercomeres were lost at surface of the amber.

observable (if clypeus bulging, then very slightly). **Thorax:** Narrow in dorsal view, slightly narrower than abdomen; deep in lateral view, not oblique (ventralmost point of katepisternum is beneath level of anepisternal cleft). Antepronotum very large, collarlike, glabrous, dorsally shielding long, thin neck. Postpronotal lobes moderately projecting laterally. Scutum and scutellum with fine, short, decumbent setulae; thorax without macrosetae or long pilosity; scutellum longer than wide, no spines; proscutellum very small. **Wing:** Long, slender, W/L

0.30, apex narrow, not rounded; vein C circumambient. Sc long, 0.6× wing length; R_1 long, 0.73× wing length; Sc and R_1 close, parallel; presence/absence sc-r not observable; faint pterostigma between apices of R_1 and Sc. Rs short; R_{2+3} close and parallel to R_1; fork of R_{4+5} relatively short, slightly asymmetrical (R_4 slightly longer and more curved), length of fork equal to length of R_{4+5} stem; apex of R_4 distinctively ending at tip of wing. Cell d large, broad, crossvein r-m near base of cell. Two short M veins present, M_1 and M_2, lengths less than length of cell d. A_1 very short, complete, meets wing margin at midlength of wing; A_2 very short. Anal lobe and alula very narrow. **Legs:** Coxae slender; mesocoxa contacting thorax just at its base, largely free from katepisternum and meron; metacoxa well separated from mesocoxa, with well-developed knob in middle of anterior surface. Leg segments: femur = tibia > basitarsomere > combined length of other tarsomeres. Tibial spurs 1-2-2; all tibial spurs fine; protibial spur short (length less than width of tibia); lengths of meso- and metatibial spurs slightly greater than width of tibia. Legs without macrosetae. Pretarsi lost or largely obscured, pulvilli appear to be present; empodium ambiguous (either lost, very small, or setiform). **Abdomen:** Longer than thorax and head combined. Tergites well developed, 9 tergites visible, with short, fine, decumbent setae; tergite 1–8 wrapping laterally and overlapping with lateral margins of sternites (which are also large, well developed), no lateral membrane exposed. Sternites 1, 2 narrower than segment 3 in dorsal view (ca. 0.7× the width); 0.5× depth of segment 3 in lateral view—almost petiolate. Tergite 9 small, almost enclosed by tergite 8. Apex of abdomen opening ventrally. Cercus 2-segmented, apical halves of apical cercomeres shaved off at amber surface; basal cercomere small, ringlike, sclerotized, enclosed by tergite 9, ventral portion does not appear to have small lobe.

Types: Holotype, female, AMNH Bu-SE14.

Etymology: Acronym for "what is this?" Treated as a noun in apposition.

Comments: Piece containing the holotype is 5 × 9 × 13 mm, trimmed from a larger cabochen, with flattened surfaces for viewing the dorsal and left lateral surfaces close to the fly. The amber has a thick suspension of fine bubbles, which, along with some fine circular fractures around portions of the head and thorax, obscure some structures. Of the three tarsi that are preserved, two are curled toward the body, obscuring the pretarsi. Only the left protarsus is visible (dorsally), and light must be repeatedly moved to obtain views of the pretarsus. It is likely that the empodium is not pulvilliform. The fly is virtually complete; apices of four legs and portion of the distal cercomeres were lost at the surface of the amber.

MYSTEROMYIIDAE, NEW FAMILY

Diagnosis: As for genus, below.

Type Genus: *Mysteromyia*, new genus. Monogeneric.

Comments: This new species, genus, and family is probably a noncyclorrhaphan eremoneuran, based on the lack of tibial spurs, the setiform empodium, 1-segmented cercus, and antennal flagellum with three articles. However, there is no evidence that *Mysteromyia* is an empidoid. Although the plumose "arista" is similar to certain acalyptrates, as in various ephydroids and Periscelididae, there is no doubt that this fly is not even a cyclorrhaphan, the convergence in wing venation with Phoridae notwithstanding. It lacks a lunule (this area of the head is very well preserved), and there are no macrosetae anywhere on the body, nor even sockets from dislodged setae. The apical two articles of the antennal flagellum are situated terminally (vs. dorsally) on flagellomere 1. Also, each branch of the plumose arista has a socket, indicating that each is probably a seta on the antennal stylus (in schizophorans a plumose arista has unsocketed, true branches). There are 10 well-defined abdominal tergites (vs. 8), albeit the terminal one highly reduced. The highly costalized wing venation has an overall similarity to that of Phoridae—but only superficially. Phoridae differ

by the following: Sc is very short and usually incomplete, R_1 much shorter, R_{2+3} either entirely fused to R_{4+5} or separated only as a small apical fork (collectively, Rs); entire Rs usually very short, half or less of wing length; basal cells not configured as in *Mysteromyia*; M and CuA veins readily apparent and even sclerotized; alula is small and commonly spinose. Clearly, costalization is convergent in the two families, and other than the loss of abdominal sternites there are no derived features in common.

***Mysteromyia*,** new genus

Diagnosis: Head and frons broad, eyes widely separated; ptilinal suture/lunule absent. Clypeus minute, mouthparts highly vestigial/absent. Antenna with three postpedicel articles: large flagellomere 1, small flagellomere 2; apical article a large, plumose "arista," terminally situated on flagellomere 2, branches of "arista" with socketed bases. Anterior part of scutum with three large, oblong tubercles; ventrum of thorax extensively membranous. Veins R_1 and R_{2+3} highly costalized; posterior R, M, and Cu veins faint and parallel; Sc complete, R_1 and R_{2+3} not fused, R_{4+5} free, cell cup complete but small; no pterostigma; alula and upper calypter well developed. Body devoid of macrosetae. Empodium setiform; tibial spurs lacking. Sternites lost; minute acanthophorite spines possibly present; female cercus 1-segmented.

Type Species: *Mysteromyia plumosa*, new species.

Etymology: From the Greek, Latinized as *mysterium* ("mystery"), for the mysterious relationships of this bizarre fly. The gender of the name is feminine.

Comments: See above for family.

***Mysteromyia plumosa*,** new species

Figures 28, 29, 60

Diagnosis: As for genus, by monotypy.

Description: Based on female. Body length 3.48 mm; head width 1.06 mm, head length 0.38 mm; thorax width 0.67 mm, thorax length 0.79 mm; abdomen length 2.27 mm; wing length 2.00 mm. **Head:** Broad (due to broadened frons and facial area), distance between inner margins of eyes slightly greater than 2× frontal width of eyes; width of head greater than greatest width of thorax. Head cuticle brown, appears finely wrinkled (probably preservational). Eyes bulging, with very fine, sparse setulae; no differentiation of facets (e.g., frontally or dorsoventrally). Eye semicircular in lateral view, occiput very exposed; height of eye occupies entire dorsoventral height of head. Inner frontal margin of eye gently emarginate at level slightly above antennae. Head devoid of macrosetae. Ocelli absent, though anterior one possibly present as porelike vestige near center of frons; frons with fine vertical line between central pore and face. Frons and frontoorbital plate well defined by suture. No lunule/ptilinal suture present above antennal bases. Face very small, with very small triangular clypeus between antennal bases. **Antenna:** Bases separated by width equal to diameter of scape. Scape and pedicel very short, ringlike. Flagellum: Flagellomere 1 thickest antennal article, bulbous, asymmetrical, setulose, with small nipplelike lobe on anteroapical margin; flagellomere 2 small, asymmetrical, situated at apex of flagellomere 1 (vs. dorsally); flagellomere 3 a plumose "arista" with long, dense, dorsal and ventral branches, with ca. 20 dorsal and 20 ventral branches, longest branches at base (lengths ca. 0.5× length of aristal trunk), branches tapered in length apicad; base of each branch socketed. Gena slightly bulbous, setulose. **Mouthparts:** Proboscis and palps completely absent, mouth present as small figure-eight-shaped pit on head venter, with 2 small sclerites within. Occiput bulging, central portion of occiput concave, to which cervical area is attached. **Thorax:** Slightly longer than broad, no macrosetae. Dorsally: Mostly light brown, virtually bare, with very sparse setulae/microsetae in small areas. Postpronotal lobes small, widely separated. Anterior part of scutum with 3 large, oblong, high tubercles/calli, an anteromedian one and two postero-

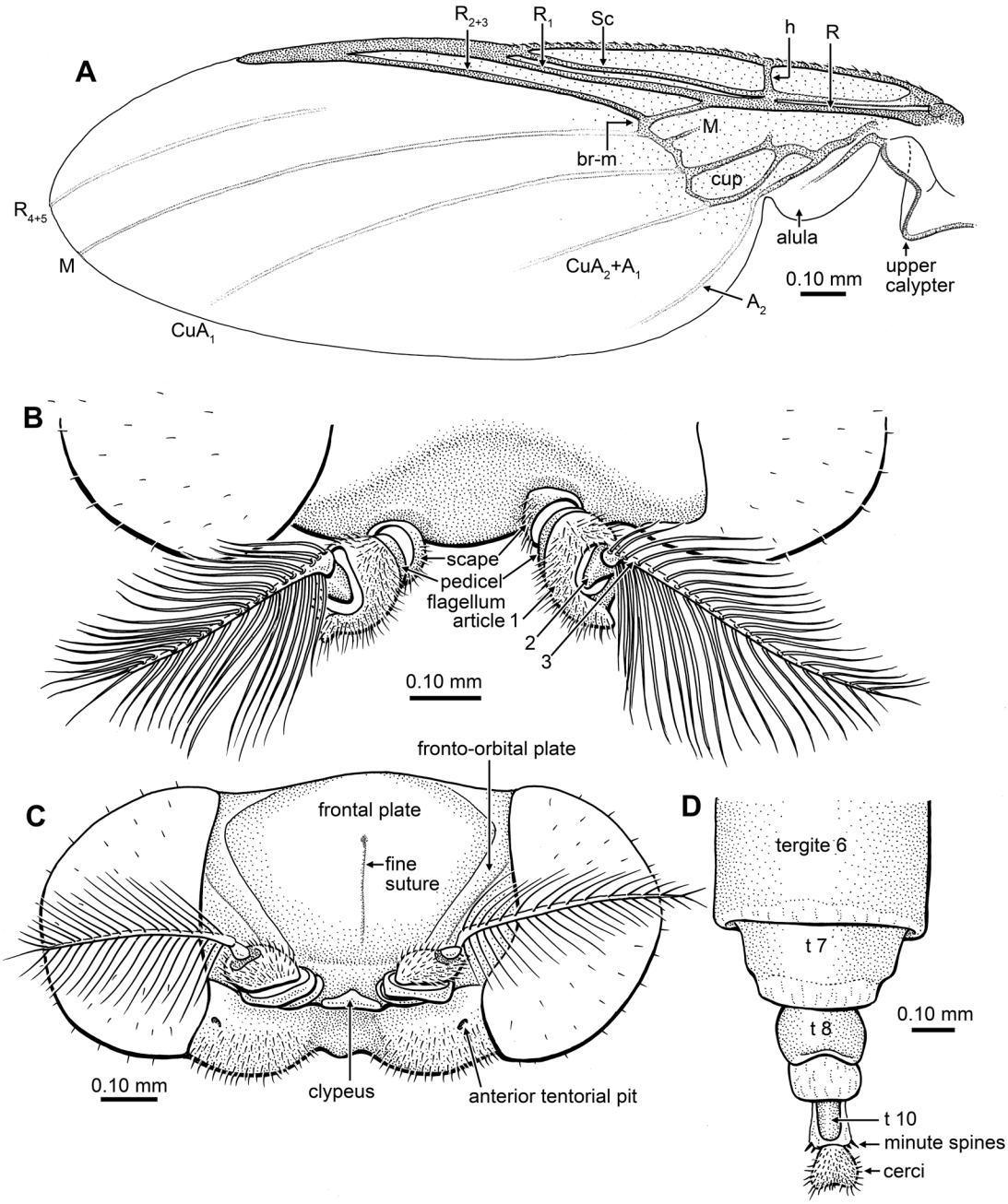

FIG. 28. *Mysteromyia plumosa*, new genus and species (Mysteromyiidae, new family), holotype JZC Bu-1817a. **A.** Wing, dorsal surface. **B.** Frontal portion of head, with antennae, dorsofrontal view. **C.** Head, frontal view. **D.** Female terminalia, dorsal view.

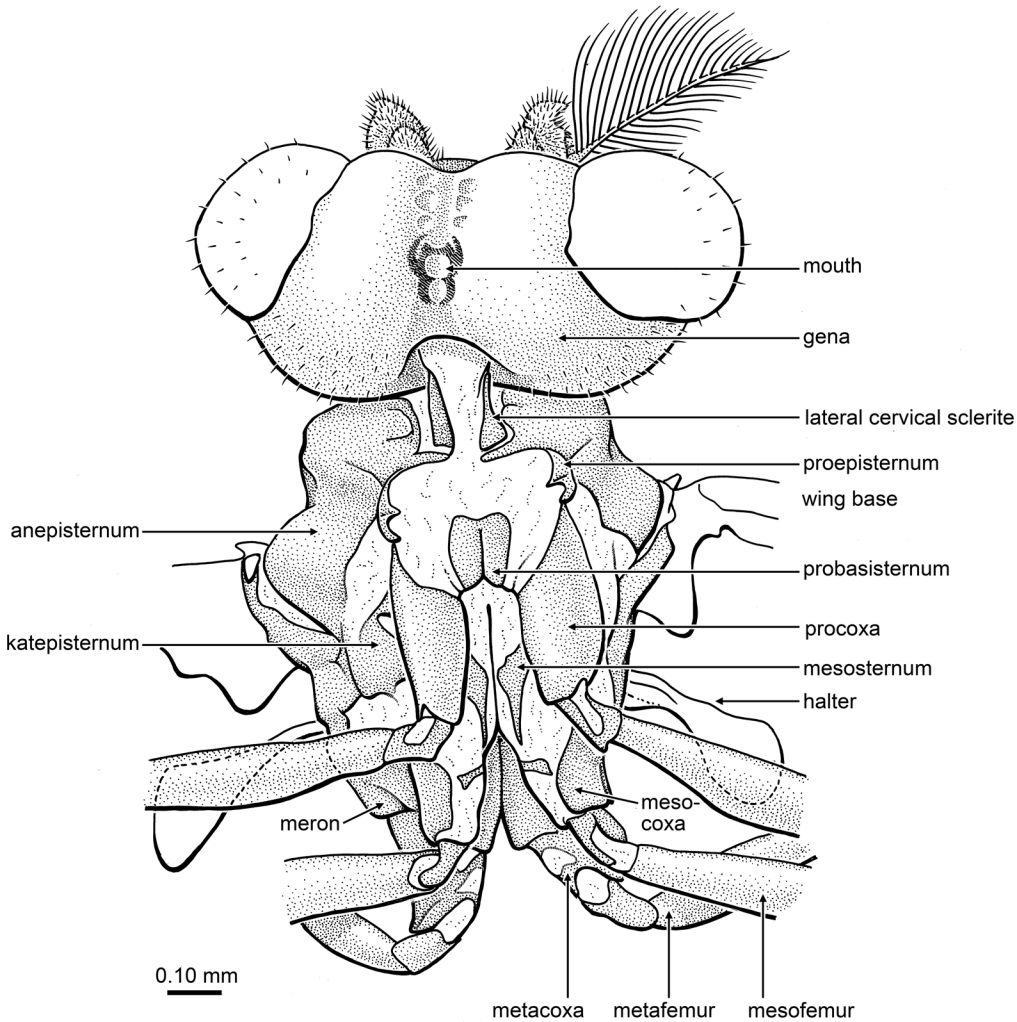

FIG. 29. *Mysteromyia plumosa*, JZC Bu-1817a. Ventral view of head and thorax, showing loss of mouthparts and significant reduction of ventral sclerites.

paramedian ones. Transverse suture very short, virtually longitudinal (not transverse); supraalar lobe expanded into pointed lobe in dorsal view. Dorsum of thorax flattened, such that scutellum situated almost entirely dorsally. Scutellum pentagonal in shape; no proscutellum; postnotum broad, fully exposed dorsally. Ventrally: extensively membranous. Ventral cervical sclerite long, slender, isolated in membrane. Anepisternum bulging laterad. Proepisternum a small, narrow sclerite, prosternum a small, central sclerite. Area between procoxae and proepisterna broadly membranous. Katepisternum small, anterior portion membranous. Meso- and metasternites small, surrounded by extensive membrane, as is medial-ventral surface of mesocoxa. **Wing:** Ovoid, with dramatically costalized radial veins; membrane and veins posterior to costalized veins very faint. Wing W/L 0.35. Costa without spinules; Sc complete, long, 0.48× length of wing; R_1 meets C immediately after apex of Sc; C+R_1 ends 0.80× length of wing along anterior margin, where apex of R_{2+3} meets C+R_1; Rs extremely short. C, Sc, R_1, Rs, R_{2+3}, and basal

crossveins r-m and m-cu tubular and sclerotized; C+R and R_{2+3} thickest and most heavily sclerotized. Membrane without microtrichia, except for faint, minute microtrichia in basal veins M, cup, Sc, and R. Veins R_{4+5}, M, CuA_1, CuA_2+A_1, and A_2 extremely faint, not tubular or sclerotized, simple (unforked). R_{4+5} basally incomplete; CuA_2+A_1 and A_2 apically incomplete. Alula and upper calypter well developed; lower calypter not present. **Legs:** Slender, darker brown than rest of body. No macrosetae; no tibial spurs. Coxae well developed, ones in each pair well separated; mesocoxa and metacoxa with ventromedial surfaces membranous; no metacoxal pegs. Profemur equal to length of protibia; meso- and metafemur shorter than meso- and metatibia. Tibiae with apical, semicirclet of stiff microsetae; tarsi long, basitarsomeres longer than remaining (distal) tarsomeres combined. Claws well developed, empodium setiform and minute; pulvilli small, slender lobes. **Abdomen (female):** Slender, longer than head and thorax combined. Tergites brown, virtually glabrous. Tergite 1 highly reduced, a very narrow transverse band/strap; tergite 2 larger, largest tergite is 3; tergite 6 longest; tergite 7 short, tergite 8 small, slightly reniform; tergite 9 apparently lacking; tergite 10 a small, slender sclerite. Presence/absence of abdominal muscle plaques uncertain. Sternites lost, venter of abdomen completely membranous. **Male Terminalia:** Unknown. **Female Terminalia:** Segment 10 membranous, apical margin with minute spines (acanthophorite spines?); cerci fused, 1-segmented.

Type: Holotype, female, JZC Bu-1817a.

Etymology: In reference to the plumose structure of the apical antennal article.

Comments: With the exception perhaps of certain apterous, inquiline Phoridae, *Mysteromyia* is one of the most remarkable flies I've seen, living or extinct. A host of highly derived features make this an unmistakable taxon: the plumose "arista" (with socketed branches), loss of mouthparts, loss of abdominal sternites, reduction in thoracic sternites; the extreme, phoridlike costalization of the wing; and the three large scutal tubercles (similar to what is seen in Trichoptera). This fly is definitely not a Cyclorrhaphan but may be an eremoneuran.

The fly was embedded within a cabochen originally 21 × 13 × 8 mm, along with the remains of an orthopteran (head, antennae), a beautifully preserved alate termite (Kalotermitidae), an empidoid fly, and a Collembolan. The piece was sectioned into four pieces, with the fly in a cubed section 6 × 7 × 3 mm, along with a pselaphid beetle. The fly is complete and beautifully preserved.

EUCAUDOMYIIDAE, NEW FAMILY

Type Genus: *Eucaudomyia,* new genus. Monotypic. In Burmese amber.

Diagnosis: Head small relative to thorax, spherical, eyes occupying anterior three-quarters of head; antenna small, with single postpedicel article, situated frontally (not dorsally or ventrally); body short, very broad (especially thorax), scutellum very small. Wing with highly reduced venation (Rs simple, M vestigial, unbranched) all longitudinal veins apically evanescent; anal lobe highly reduced; tibiae without apical spurs, empodium padlike. Female terminalia developed into long, slender, jackknifed oviscapt comprised of tubular segments VII and VIII, and long, slender, valvelike cerci and hypoproct. Known only from females.

***Eucaudomyia*, new genus**

Type Species: *Eucadomyia longicerci* n. sp.

Diagnosis: As for family, monogeneric.

Etymology: *Eu-* (Greek, "well"), *cauda* (Latin, "tail, appendage"), *myia* (Greek, "fly"), the "well-tailed fly," in reference to the unique oviscapt and how it contrasts with the short, broad body. The gender of the name is feminine.

Comments: This taxon could possibly be placed in Archisargoidea, but the antennae are inserted frontally (vs. dorsally in Archisargoidea), and the venation is too reduced to discern homologies with typical archisargoids. Like

archisargoids, *Eucaudomyia* have a subspherical head with large eyes; no macrosetae on the body or tibial spines; a small antenna with a 1-articled postpedicel; and cerci that are modified into an oviscapt. The oviscapt in typical archisargoids, however, has a bulbous base and is abruptly narrowed to a sharp tip; in *Eucaudomyia* the cerci are long, valvelike structures dorsally closed by a long epiproct, the apex not particularly sharp.

Eucaudomyia have some features in common with Tethepomyiidae, especially *Tethepomyia*: large eyes; a pair of incomplete, paramedian longitudinal furrows on the mesonotum; short, consolidated tarsi (including the basitarsomeres), vestigial mouthparts (where observable, though these are less reduced in *Tethepomyia*), the reduced venation, and structure of the oviscapt (the female of *Tethepomima* is unknown). In both groups all longitudinal veins are apically evanescent (except in *Tethepomima*); veins R_1 and Rs are thick and sclerotized, but simple (unbranched) in *Tethepomyia* and *Eucaudomyia* (2-branched in *Tethepomima*); vein M is simple in all three genera; veins CuA, CuP, and A are present. *Tethepomyia zigrasi* has a reduced anal lobe, like *Eucaudomyia*, though the other three species of tethepomyiids have a well-developed anal lobe. Another difference between tethepomyiids and *Eucaudomyia* is vein CuA with an apical fork in the former (though not visible for *T. thauma*).

The only tethepomyiid where the female is known is *Tethepomyia zigrasi* (fig. 52). Its oviscapt is a pointed, grasping structure that is curved ventrally (fig. 52C), but there are some modifications in common with *Eucaudomyia*. Both species have abdominal segment VII modified into a funnellike shape, and segment VIII (called "syntergosternite VIII" for *Tethepomyia* in Grimaldi et al., 2011) is tubular. The apical segment of the oviscapt in *T. zigrasi* was interpreted as "syntergosternite IX" in Grimaldi et al. (2011), but this structure is probably comprised of the fused cerci (unfused but elongate in *Eucaudomyia*). *Tethepomyia* were probably parasitoids (Grimaldi et al., 2011), but the structure of *Eucaudomyia*'s oviscapt indicates this species probably was not a parasitoid. In *Eucaudomyia* the cerci are not particularly sharp, sclerotized, or needle shaped. It may have oviposited into soil or in crevices in bark.

***Eucaudomyia longicerci*,** new species

Figures 30, 31, 61–63

Diagnosis: As for genus, by monotypy.

Description: Based on female. Holotype, paratype respectively: body length 5.33, 5.51 mm; wing length 2.38, 2.90 mm; thorax length 0.72, (not measured) mm; thorax width 1.18, (not measured) mm; head width 0.73, (not measured) mm; midleg length 1.87, (not measured) mm; abdomen length (including cerci) (not measured), 3.77 mm; length of cerci + telescoping abdominal segments 2.62, (not measured) mm. **Head:** Subspherical, relatively small in proportion to thorax; eye large, mouthparts vestigial. Eye bare, no interfacetal setulae; no differentiation of facets in female (male unknown); frontal and dorsal margins of eyes close but not touching, separated by distance ca. 3–4× diameter of eye facet; eyes occupying most of head (especially dorsally and ventrally); gena large and exposed. Ocelli present, well developed; ocellar triangle darkly pigmented, close to posterior margin of head capsule. Face very narrow, width 3–4× diameter of eye facets, with prominent vertical carina/ridge near the middle. **Antenna:** With insertions on opposite sides of carina (not on carina edge); antenna short, 0.10 mm length; slender, 0.01 mm thickness, apparently bare (with possible exception of apical setulae); 2-segmented, with short ringlike basal segment (presumably pedicel), and slender, slightly clavate-digitate postpedicel article (flagellum). **Mouthparts**: Highly vestigial, lacking labellum, theca, and maxillary palps; mouth opening present as a small subcircular ostiole (diameter ca. 0.05 mm). Anterodorsal to mouth opening is a tongue-shaped sclerite, possibly the clypeus. Posteroventral to the mouth opening is small, broad

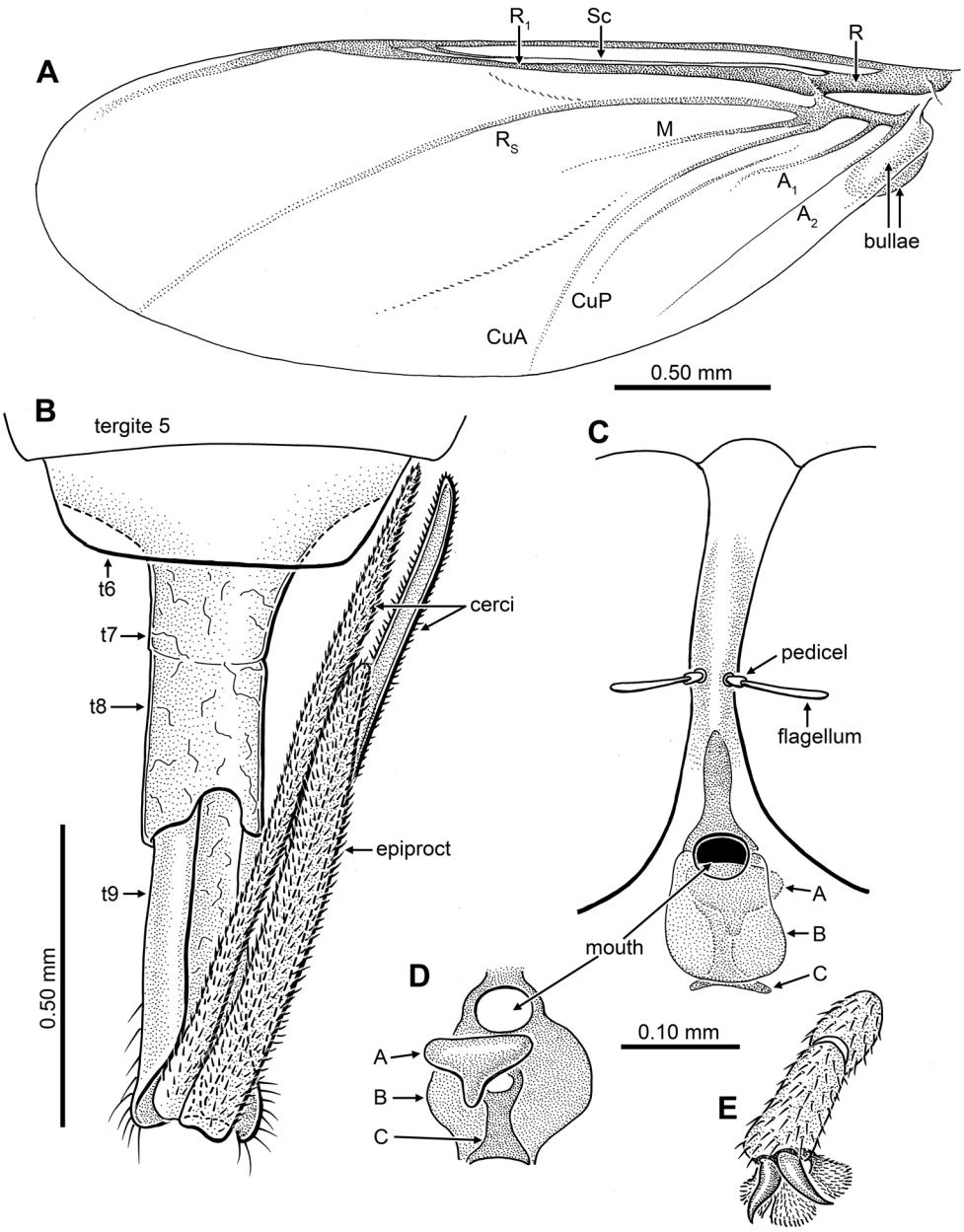

FIG. 30. *Eucaudomyia longicerci*, new genus and species (Eucaudomyiidae, new family), holotype JZC Bu-241. **A.** Wing. **B.** Female terminalia, ventral view. **C.** Anterior portion of head (frontal view), with antenna and vestigial mouthparts. **D.** Mouthparts, interior view (specimen was cleared). **E.** Apical tarsomeres and pretarsus. Panels C–E to same scale.

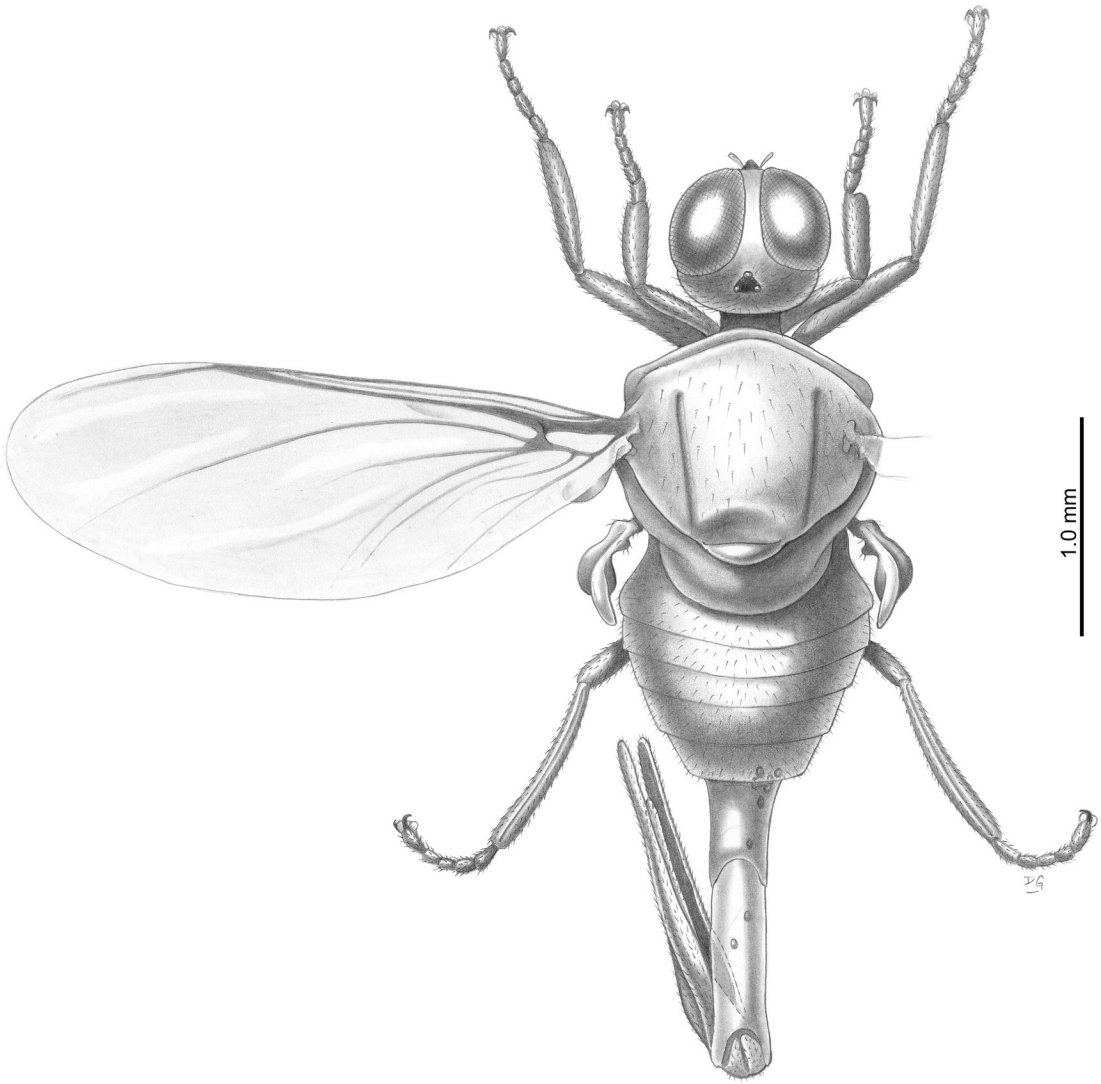

FIG. 31. *Eucaudomyia longicerci*, new genus and species, reconstruction of female dorsal habitus, based on holotype and paratype. The small circular structures within the base of the abdomen must be eggs (seen in paratype specimen).

sclerite, 0.1 × 0.1 mm, probably the labium (though if internal as it appears, possibly the ventral floor of the cibarium); attached to this sclerite is a small, hourglass-shaped one, possibly the dorsal keel of cibarium. A small, heavily sclerotized, free sclerite internally, bearing a nipplelike lobe, which is possibly a vestigial cibarium. **Thorax:** Very broad, width 1.7× width of head; without macrosetae, with only fine, sparse/scattered setulae. Insertion of cervical area ventral, not anterior. Dorsum of mesonotum slightly humped, with steep, slightly concave incline meeting scutellum; notum with pair of paramedian, shallow, incomplete furrows extending from posterior margin of notum to ca. 0.8× length of notum (not reaching anterior margin). Pronotum a broad, very thin collar. Scutellum a very small, posterior lobe. Pleuron not visible.

Sternal region well preserved and visible in JZC Bu-241: katepisterna virtually form a ventral floor of the thorax (very little exposed laterally); proepimeron large, triangular, about half the size of katepisternum; sutures between katepispternum, proepimeron, anepisternum and anepimeron forming large, symmetrical X (fig. 62E). Thoracic phragmas highly reduced. Coxal articulations of both legs in each pair nearly touching; distance between ipsilateral pro- and mesocoxae approximately equal to diameter of articulation; distance between ipsilateral meso- and metacoxae twice this diameter. **Legs:** Without large setae or spines, only fine decumbent setulae. Coxae thick, slightly crassate; trochanters ca. 0.3× width of coxa; femur slightly longer than synpodal tibia; no apical tibial spurs; tarsus short, ca. 0.5× length of tibia; basitarsomere short (even metathoracic ones), slightly longer than other tarsomeres. Individual tarsomere lengths: 1 > 2 = 5 > 3 > 4. Pretarsus with padlike empodium and pulvillus, pads relatively small, barely extending beyond claws; claws well developed (no preapical teeth), stout, thick at base. **Wing:** Simple, apically rounded; venation highly reduced. Vein C present only for one-half length of wing along C margin, without spinules; Sc thin, complete, slightly shorter than C (obscured in furrow between C and R_1). R_1 thick, sclerotized, slightly thicker where it meets C, diverging apically slightly away from wing margin. Rs simple, no branches, arched, running near middle of wing, apically evanescent. Vein M a short, basal spur <0.20× wing length. CuA arched, virtually complete, apically evanescent; CuP present near and parallel to CuA. Anal lobe essentially absent. Dense, fine microtrichia over entire membrane. Halter short, thick, with long ovoid apical knob; knob 0.6× entire length of halter, with narrow apex and longitudinal fold; small lobe on posterior margin of stem. **Abdomen:** Anterior portion (segments 1 to 6) short, broad in female (male unknown); greatest width (at tergite 2) approximately equal to width of thorax, tapered posteriad. Length of tergites 1 to 6 0.9× the greatest width of abdomen; width of segment 6 0.6× that of segment 2. Oviscapt very long, comprised of segments 7, 8 (possibly a 9th segment), cerci, and epiproct. Length of oviscapt 3.1× length of abdomen, 1.12× length of rest of body. Oviscapt: segment 7 funnel shaped at base, tubular apically, with notch on dorsal margin, length 0.6 mm (including section telescoped into segment 6), glabrous; segment 8 tubular and glabrous, also with dorsoapical notch, length 1.1 mm (including section telescoped into segment 7); cerci developed into pair of long, digitate, valvelike lobes (length 1.6 mm) flexed ventrally under segments 7 and 8 (elbow pivot between cerci and apex of segment 8), inner surfaces of cerci concave, dorsal surface closed by elongate epiproct (length 1.3 mm). Oviscapt apparently not any more sclerotized than rest of abdomen; cerci with fine, decumbent setulae (not glabrous); apices of cerci not particularly pointed, "valves" separated. Eggs (seen in paratype): small, ovoid, length 0.1 mm, width 0.05 mm, matured at least 15 at one time, passed through at least segment 8 (and probably through cercal "valves").

Types: Holotype, female, JZC Bu-241. Paratype, female, Di-Ying Huang collection, Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Etymology: Latinized version from Greek, meaning "of the long cerci," treated as a noun in apposition; in reference to the elongate cerci in the female.

Comments: The holotype is a small, trimmed, polished piece 8 × 7 × 2 mm with a suspension of fine bubbles; fly is fully exposed dorsally and ventrally, with a frontal view of the head. The dorsum of the thorax and head are decayed away, but these tagmata are cleared, better exposing sutures, minute and internal structures such as the vestigial mouthparts. The paratype specimen is in an oblong piece 17 × 8 × 5 mm, which appears to be a segment of a runnel. Preservation of the paratype is fair to good: thoracic dorsum is visible, left side partially decayed, the head dorsoventrally compressed, ocellar triangle fully visible. Dorsum of abdomen and oviscapt are fully visible; much of the ventrum is obscured by

a layer of air over the surface and by compression; mouthparts and sternites are entirely obscured. Legs and wings are mostly visible.

FAMILY APYSTOMYIIDAE

The dipterist Mario Bezzi (1868–1927) is said to have called *Sciadocera rufomaculata* White "the most wonderful fly in the world" (Oldroyd, 1964: 167), because it is an amalgam of characters from various groups of Eremoneura. Actually, the species is well established as a close relative to the rest of the Phoridae. Title to "the most wonderful fly" could be owned by *Apystomyia elinguis* Melander, for its highly relict nature (the only surviving species of the family, restricted to a few localities in California), and for its phylogenetic position as sister group to either the Cyclorrhapha (Trautwein et al., 2010; Wiegmann et al., 2011), or to the Eremoneura (Empidoidea + Cyclorrhapha) (Sinclair et al., 2013). The extraordinarily relict nature of this fly is further revealed by Late Mesozoic relatives *Hilarimorphites* (in New Jersey and Burmese amber [Grimaldi and Cumming, 1999; Grimaldi et al., 2011; herein]) and *Apystomimus zaitzevi* Mostovski (preserved as lithified remains from the Late Jurassic of Kazakhstan). Morphologically, the grouping of the fossils into Apystomyiidae appears certain, so clearly the family was widespread at least in the Late Mesozoic. It is very interesting that *Hilarimorphites* have not yet been found in Canadian, French, Lebanese, or Spanish Cretaceous ambers. The absence of apystomyiid fossils from the Cenozoic may reflect that by the Eocene they were already highly restricted or quite rare.

Genus *Hilarimorphites* Grimaldi and Cumming

Emended Diagnosis: Small, dark flies known thus far only in Cretaceous amber from New Jersey and Myanmar; antennal flagellum 2- (New Jersey amber species) or 3-segmented (Burmese amber), apical flagellar article or two stylate; male nearly holoptic; dorsocentral and scutellar macrosetae present, sometimes acrostichals; tibial spurs absent, empodium setiform; metacoxal peg present; R_4-R_5 fork short, cell d present, M_1-M_2 forked, M_3 absent; cell cup closed or nearly so. Female cercus 1-segmented; male body very setose, with enlarged anal lobe and alula.

Type Species: *Hilarimorphites yeatsi* Grimaldi and Cumming, in New Jersey amber.

Comments: Species in the genus are the following: in New Jersey amber: *Hilarimorphites superba* Grimaldi and Cumming, *H. yeatsi* Grimaldi and Cumming, *H. setosa* Grimaldi and Cumming, and *H. longimedia* Grimaldi and Cumming; in Burmese amber: *H. burmanica* Grimaldi and Cumming, and the distinctive new species described below.

***Hilarimorphites cummingi*,** new species

Figures 32, 64

Diagnosis: Distinctly differs from other species in the genus by the very short, almost nonexistent stem vein M_{1+2}; the short, closed cup cell with a long CuA_2 + A_1 vein; and the apices of veins M_1, M_2, CuA_1, and CuA_2+A_1 evanescent and incomplete. Other details are given under Comments.

Description: Based on female. A small, robust, entirely dark-bodied fly with very sparse setae and setulae and relatively short wings. Body length 2.13 mm; thorax length 0.61 mm; abdomen length 1.32 mm; wing length 1.14 mm; antenna length 0.23 mm. **Head:** Approximately hemispherical, with largest surface of eyes frontally. In lateral view significant occipital surface exposed behind eye. Eye entirely bare, no differentiation of facets; inner (medial) margins bordering frons well separated, margins parallel; no emargination near antennal base. Occiput with lateral portions bulging, central portion concave dorsally but not ventrally; with very sparse, minute, fine setulae; pairs of small, very short, stiff setae flanking ocellar triangle just posterior to eye margin. Frons glabrous, dark; ocellar triangle slightly raised above frons surface, on vertex of head. **Antenna:** Scape very short, ringlike;

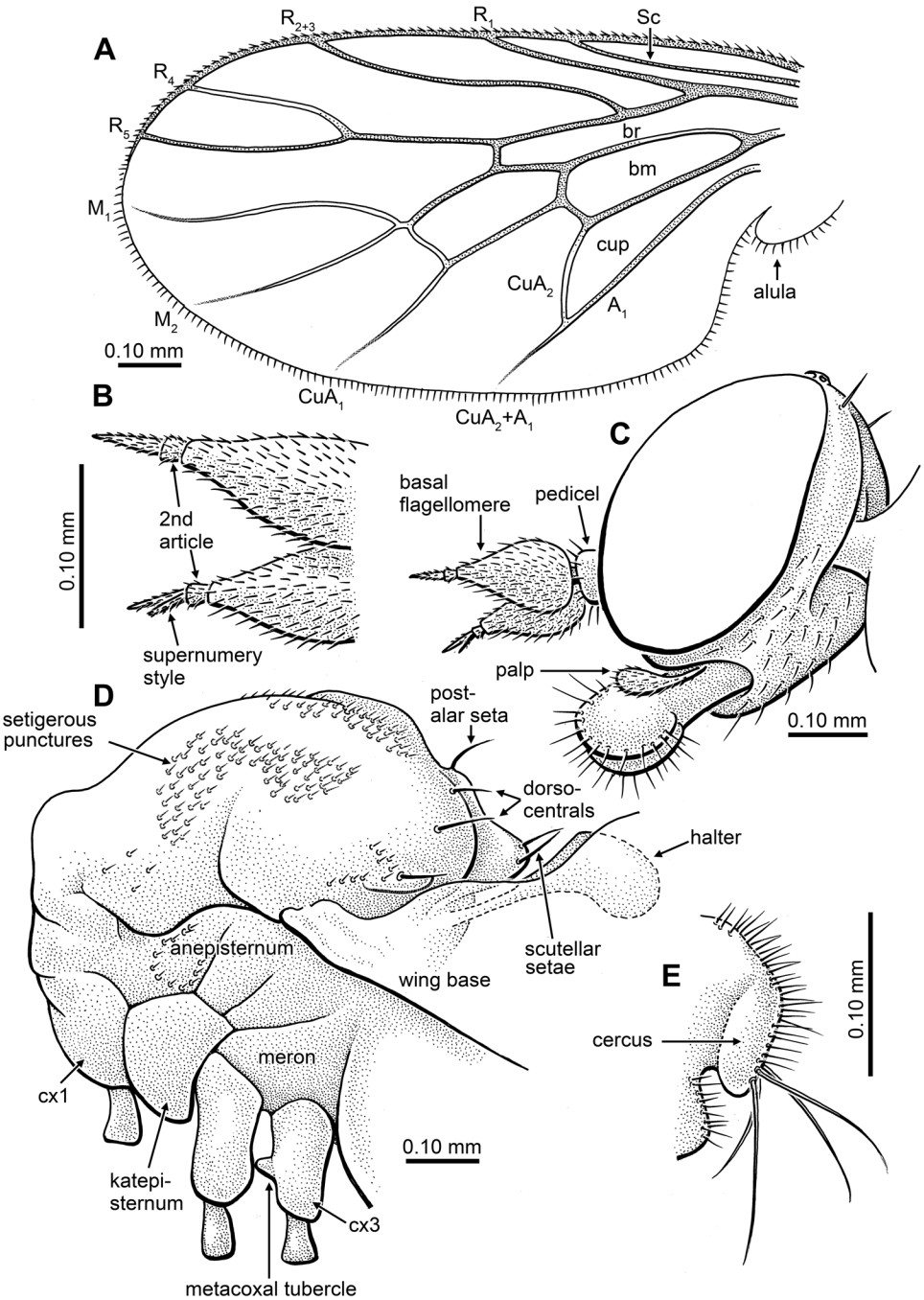

FIG. 32. *Hilarimorphites cummingi*, new species (Apystomyiidae), JZC Bu-177, holotype. **A.** Wing. **B.** Apices of antennae, detail. **C.** Head, oblique left lateral view. **D.** Thorax, dorsolateral view. **E.** Female terminalia, left lateral view.

pedicel slightly longer and thicker, with circlet of fine setae; basal flagellomere largest antennal article, drop shaped in lateral view, with small 2-articled stylus; 2nd article of flagellum (basal article of stylus) very small, ringlike; 3rd (apical) flagellum article 3× length of 2nd, greatly tapered apicad (right antenna with stylus teratological, having a duplicated apical article). All flagellar articles with microtrichia, vestiture slightly longer on ventral surface of flagellomere 1. **Mouthparts:** Short, labellum rounded (with lobes closed), having fine setae on outer surface. Labium very short, exposed; palp short, clavate, 1-segmented. No other mouthparts exposed. **Thorax:** Relatively short, compact, notum barely arched. Scutum with median, glabrous strip, bordered laterally by setulose patches. One pair short, stiff, stout dorsocentral setae present, just anterior to scutellum; scutellum with pair of short, apical setae that nearly cross at apices (size equal to dorsocentrals); one seta on each supraalar ridge, slightly larger than others. No prescutellum present; scutellum short, apex slightly tilted upward. No notopleural setae present. Pleura orientation essentially vertical, not oblique. Antepronotum short; postpronotal lobes small; katepisternum narrow, vertical. **Wing:** Short, broad, W/L ca. 0.52 (base obscured), apex reaching to abdominal segment 5. Vein Sc short, ends slightly past tip of R_5; Sc complete, but thin, ca. 0.3× length of wing; R_1 short, ca. 0.5× wing length, close and parallel to Sc; no pterostigma; R_{2+3} very slightly sinuous; basal R veins very thick, fork of R_4-R_5 thinner and lighter, stem vein R_{4+5}, slightly shorter than fork of R_4-R_5; R_4-R_5 fork slightly divergent, nearly symmetrical. Cell br slightly thinner and longer than cell bm; cell d fairly large, W/L 0.3, situated near center of wing. Veins M_1, M_2, CuA_1, and CuA_2+A_1 with apices evanescent, incomplete (not reaching wing margin); M_1 slightly sinuous; stem vein M_{1+2} very short, these veins almost connected directly to cell d; M_3 absent; cell cup short, closed, with long CuA_2+A_1 vein. Anal lobe well developed; alula narrow. **Legs:** Coxae contact thorax at bases only, suspended, with several fine setae on anterior faces. Metacoxa with well-developed peg/tubercle on anterior surface. Leg segment lengths (all pairs): tibia > femur > basitarsomere = tarsomeres 2–5. No tibial spurs. Pretarsus with empodium setiform; pulvilli rather small, significantly shorter than claws. **Abdomen:** Relatively long, slender, longer than thorax + head (including antennae), does not appear to be telescoping. Eight large tergites; sternites well developed; tergites 2, 3 largest, all with fine, short, erect and decumbent setulae. Cercus rather small, dorsoapical, setulose, with two pairs of long setae.

Type: Holotype, female, JZC Bu-177.

Etymology: Patronym for Jeff Cumming, Canadian National Collection of Insects, Agriculture Canada, Ottawa, for his outstanding contributions to the morphology and systematics of Diptera.

Comments: The very short stem of M_{1+2} of *H. cummingi* is unique among all fossil apystomyiids, including *Apystomimus*, as are the evanescent, incomplete apices of the M and CuA veins. The long vein CuA_2+A_1 is also unique; in all other fossils these veins meet just before or at the wing apex, or (in *H. burmanica*) not at all. It is interesting that the four species of *Hilarimorphites* in New Jersey amber have a 2-articled flagellum; the ones in Burmese amber have it 3-articled (i.e., a 2-articled stylus). In *H. burmanica* the second flagellar article is long, with a minute apical article; in *H. cummingi* the second article is short and ringlike. The venation of *H. cummingi* is actually quite similar to that of *Proratites simplex* Grimaldi and Cumming, in New Jersey amber, originally assigned to Scenopinidae (Proratinae), although that assignment is questionable. The two species differ since *Proratites* has a long, stylate flagellar article, lacks thoracic setae, and has various venational differences (larger cell d, M and Cu veins complete, shorter CuA_2+A_1 vein, asymmetrical R_4-R_5 fork). This new species adds further evidence to the past diversity and relict nature of Apystomyiidae.

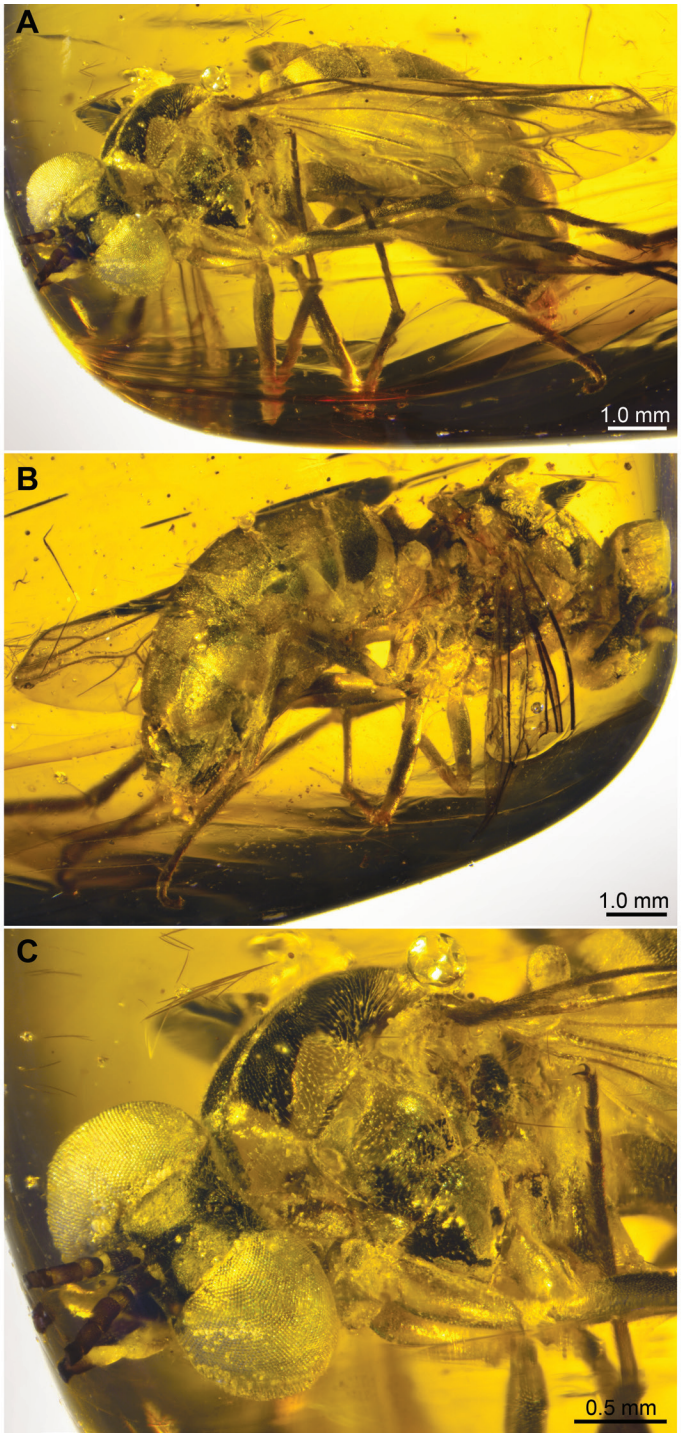

FIG. 33. *Cratomyia mimetica*, new species (Zhangsolvidae), holotype AMNH Bu-SE01. **A.** Left habitus. **B.** Right habitus. **C.** Head and thorax.

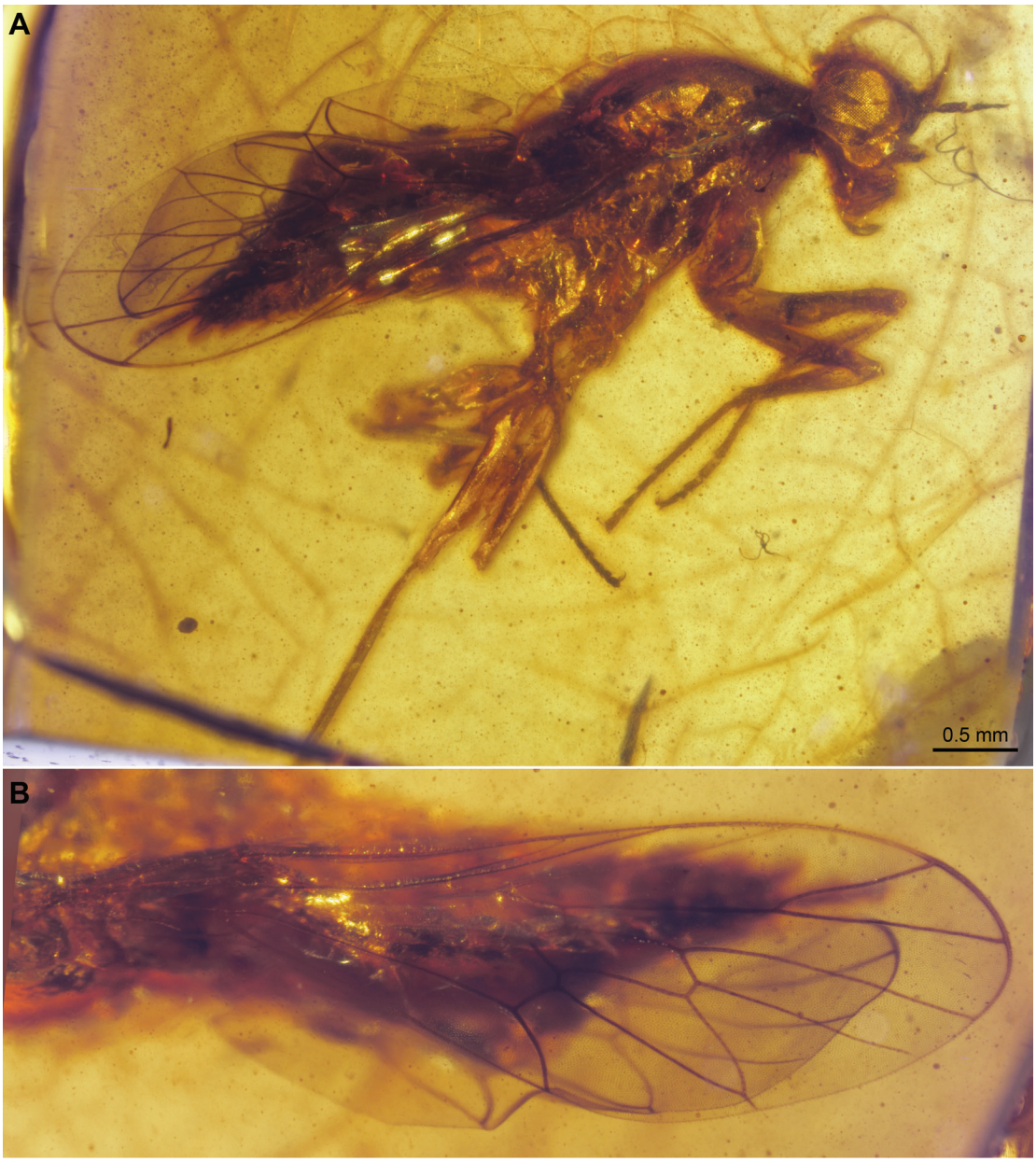

FIG. 34. *Cretosolva burmitica*, new genus and species, holotype AMNH Bu-SE005 **A.** Right habitus. **B.** Right wing.

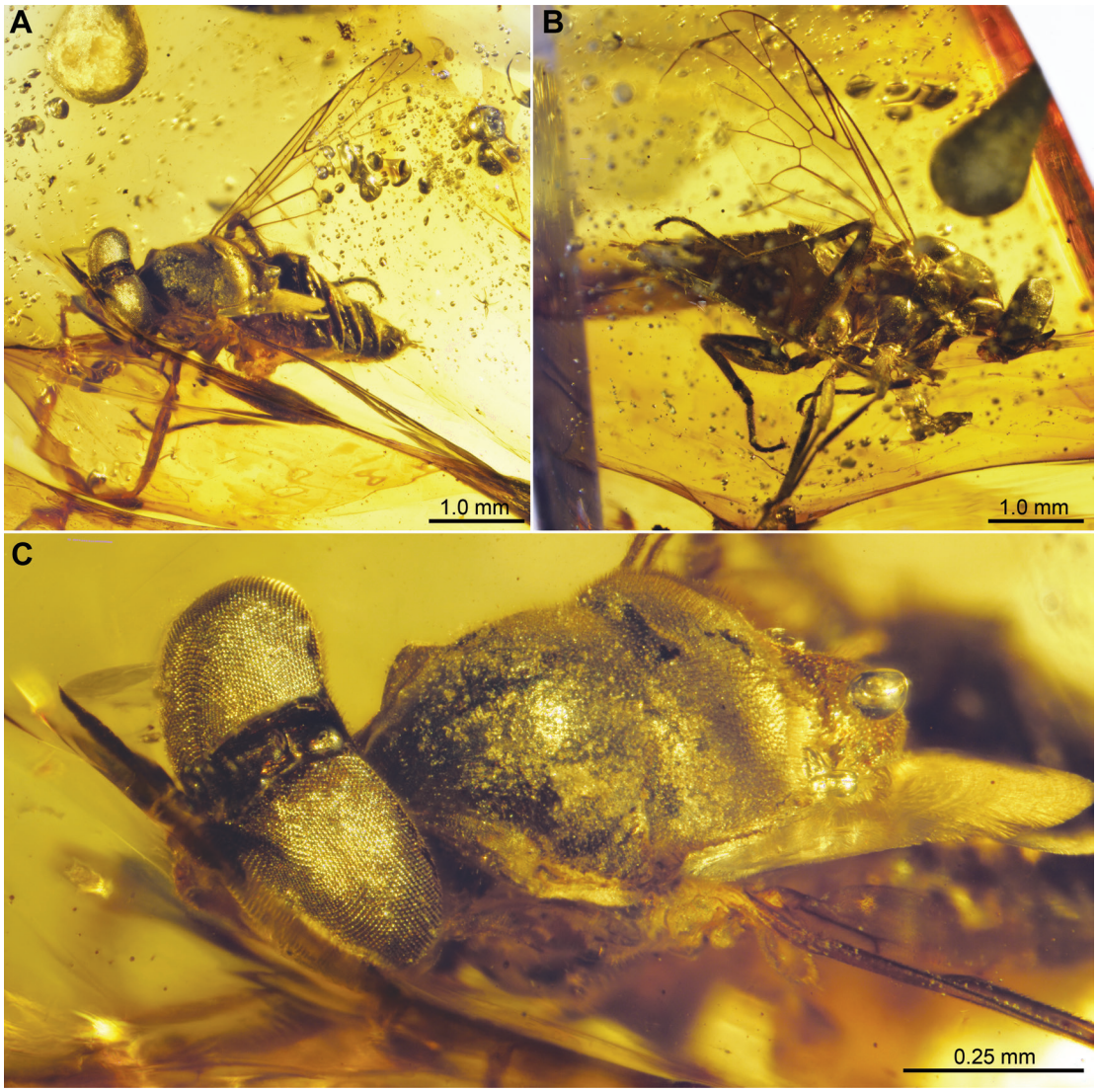

FIG. 35. *Archosolva biceps*, new genus and species (Xylomyidae), holotype JZC Bu-257. **A.** Dorsofrontal view of habitus. **B.** Habitus, right lateral view. **C.** Head and thorax, oblique dorsal view.

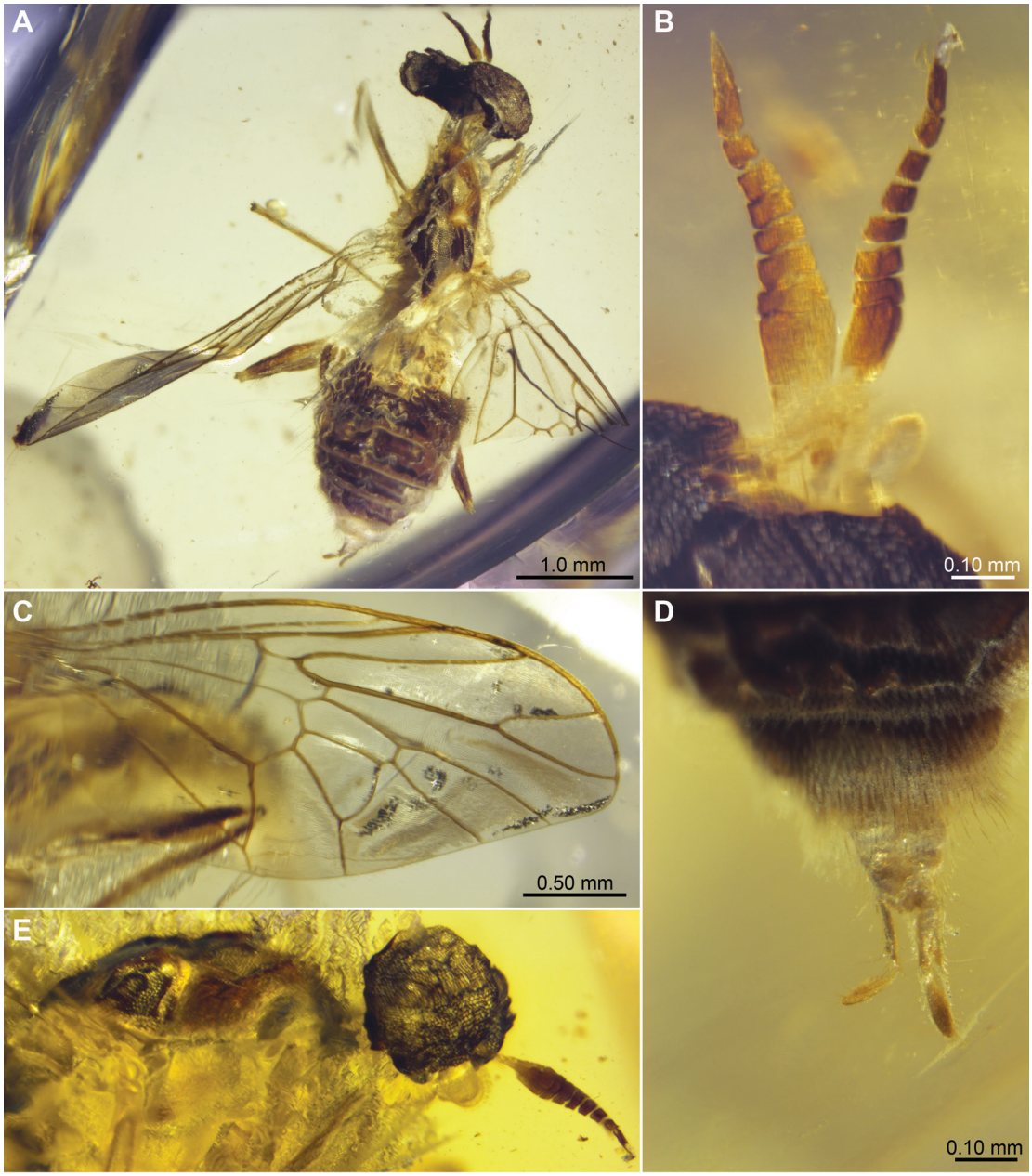

FIG. 36. *Archosolva sulcata*, new genus and species (Xylomyidae), holotype JZC Bu-208. **A.** Habitus, dorsal view. **B.** Antennae, dorsal view. **C.** Left wing. **D.** Terminalia, dorsal view. **E.** Head and thorax, right lateral view.

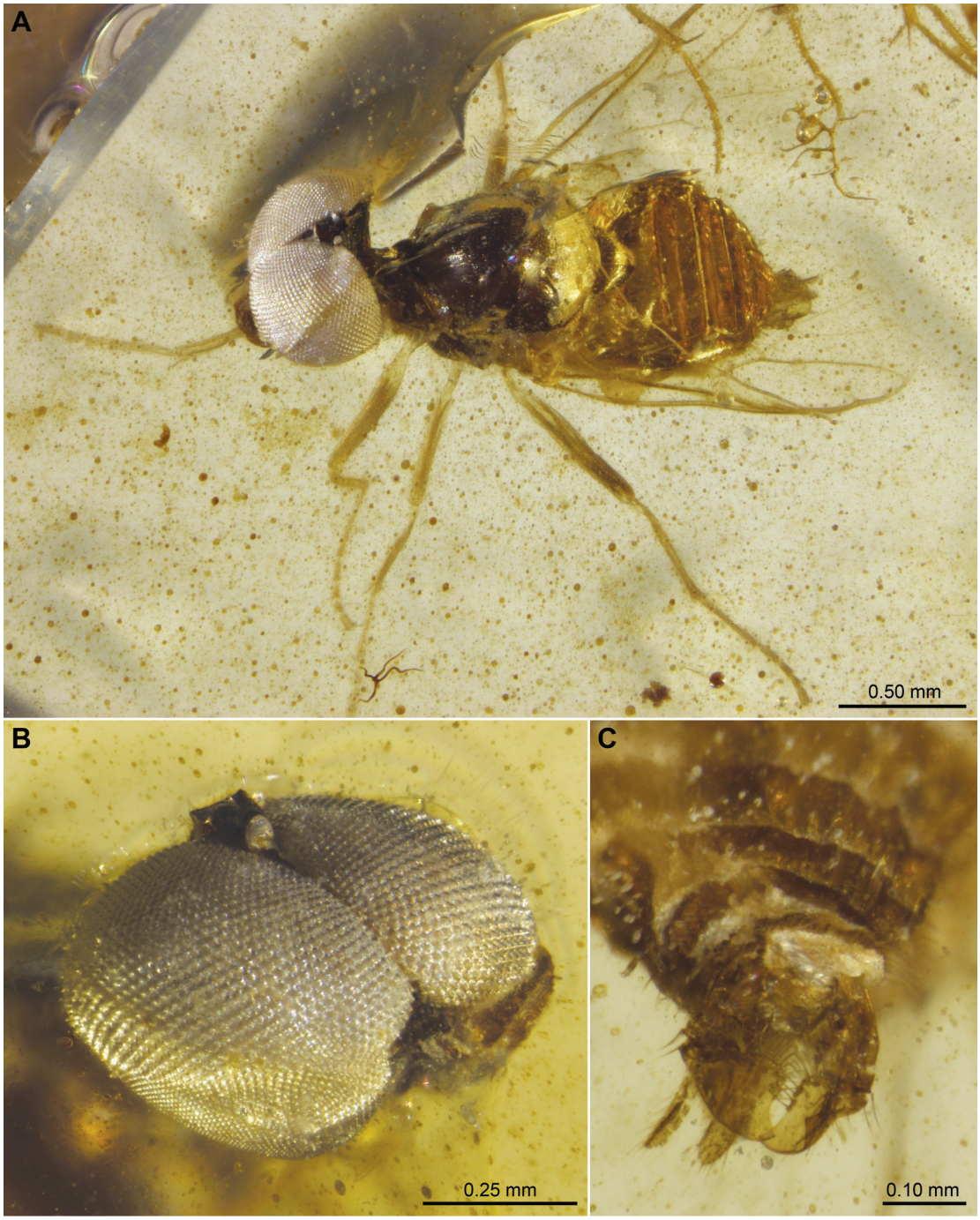

FIG. 37. *Normyia woodleyi*, new genus and species (Stratiomyidae), holotype male AMNH Bu-SE004b. **A.** Habitus, dorsal. **B.** Head, oblique dorsal view. **C.** Terminalia, posteroventral view.

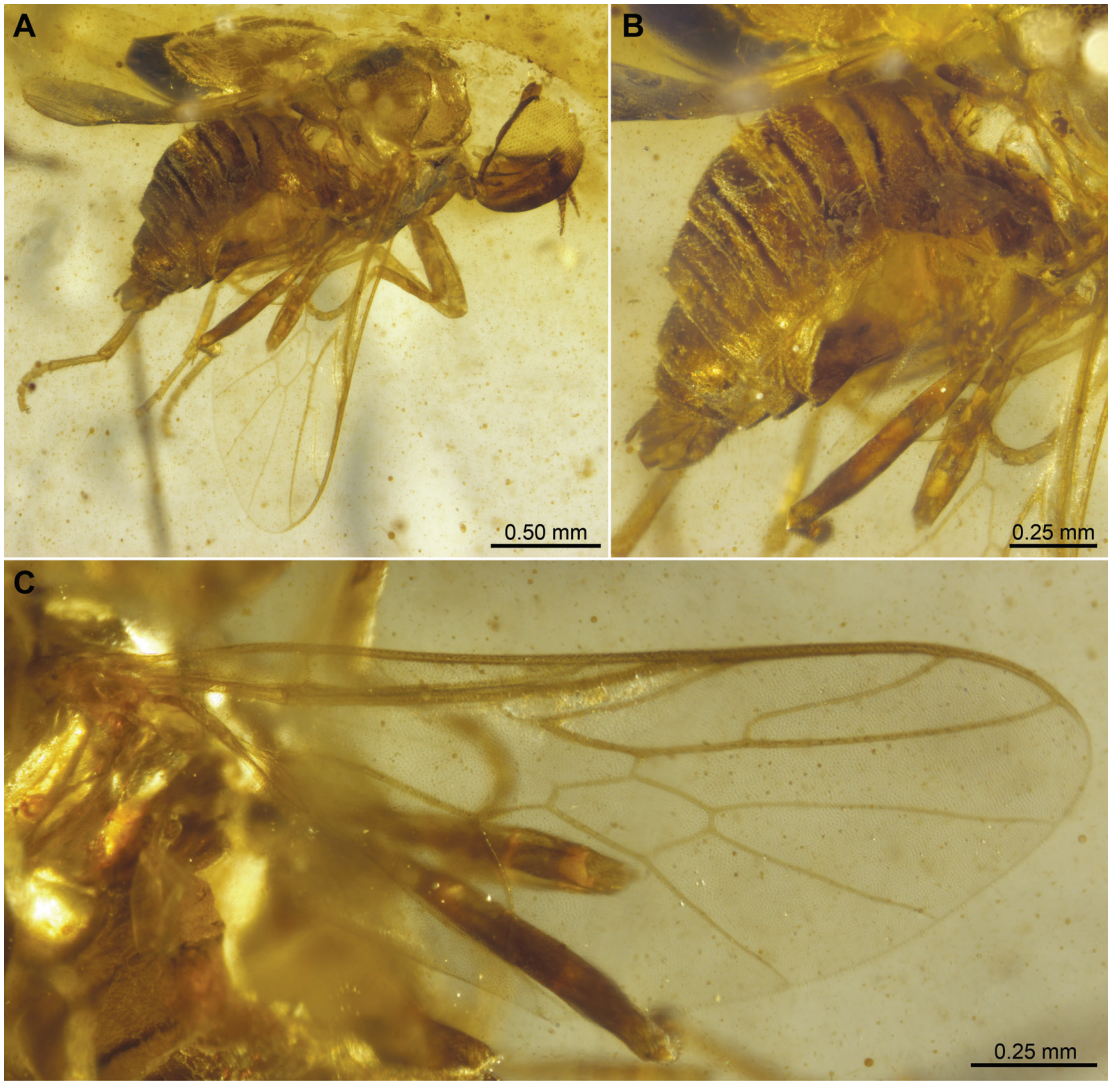

FIG. 38. *Normyia woodleyi*, paratype male AMNH Bu-SE004a. **A.** Habitus, right lateral view. **B.** Detail of abdomen, showing deeply impressed tergal sulci. **C.** Right wing.

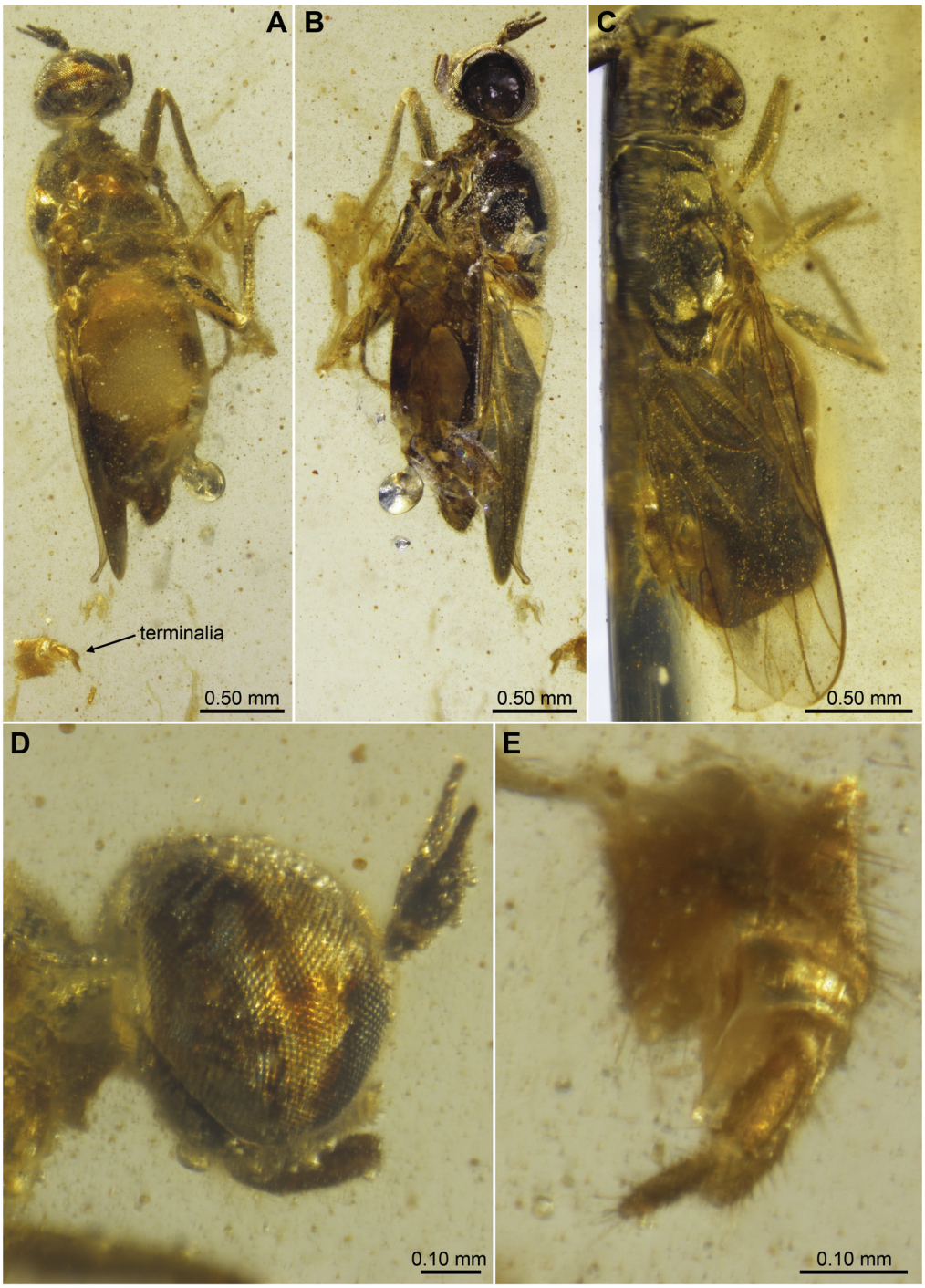

FIG. 39. *Normyia woodleyi*, paratype female JZC Bu-001. **A.** Habitus, right lateral. **B.** Habitus, left lateral. **C.** Habitus, dorsal. **D.** Head, right lateral. **E.** Terminalia, oblique left lateral.

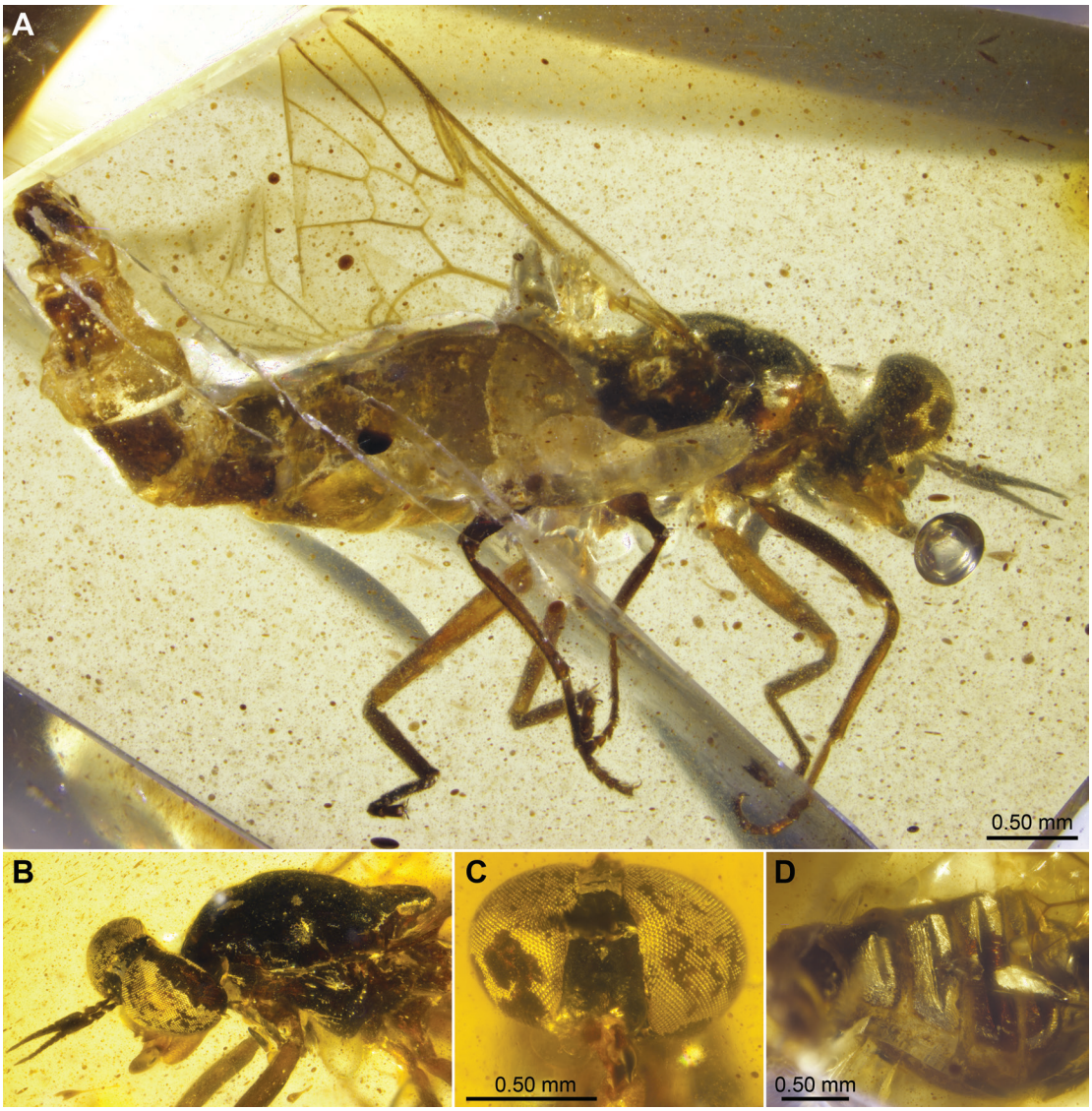

FIG. 40. *Normyia telescopica*, new genus and species (Stratiomyidae), holotype JZC Bu-104 **A.** Habitus, right lateral. **B.** Head and thorax. **C.** Head, frontal view. **D.** Portion of abdomen, showing deeply impressed tergal sulci.

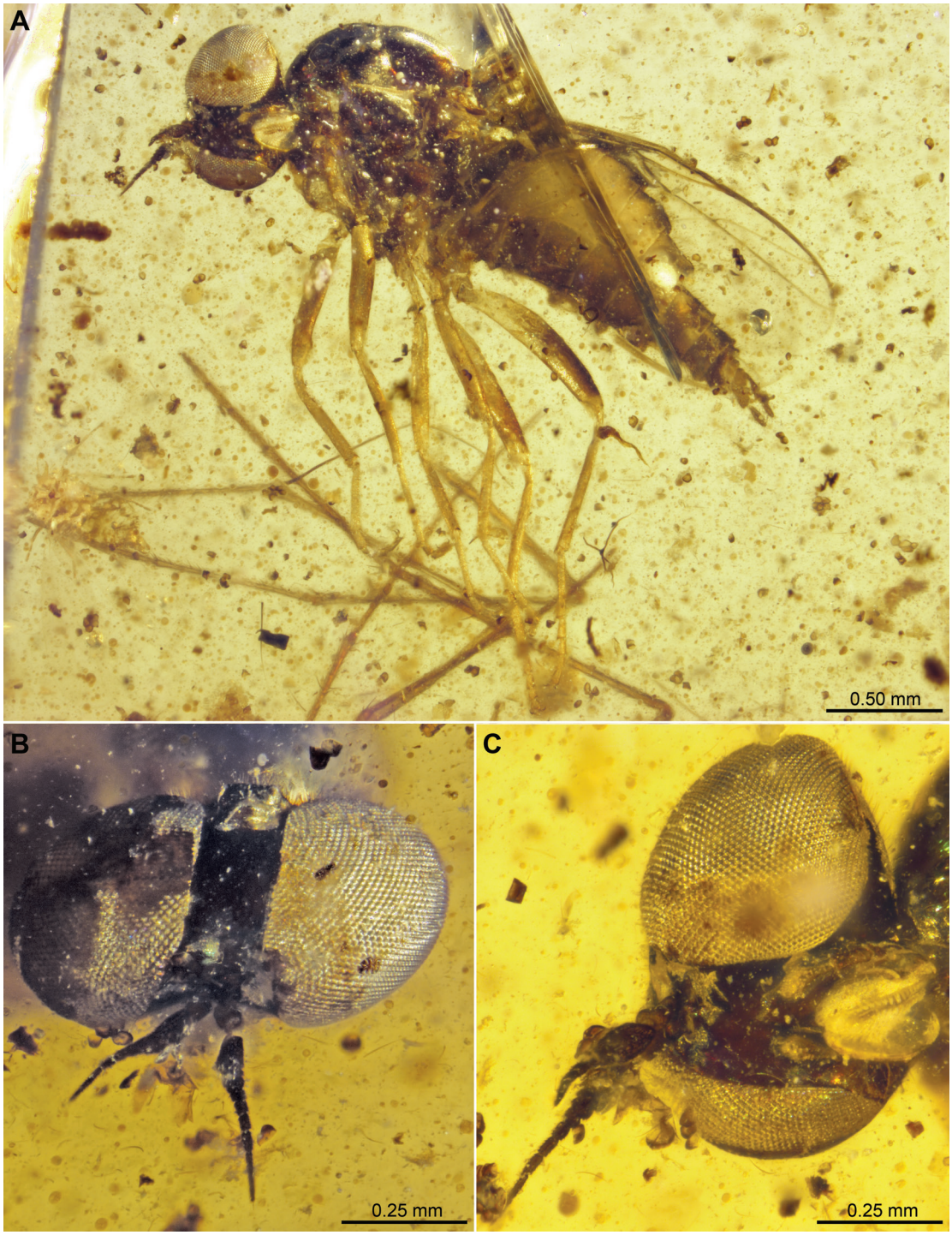

FIG. 41. *Normyia longistyli*, new genus and species (Stratiomyidae), holotype AMNH Bu-SE21. **A.** Habitus, left lateral view. **B.** Head, dorsal view. **C.** Head, ventral view.

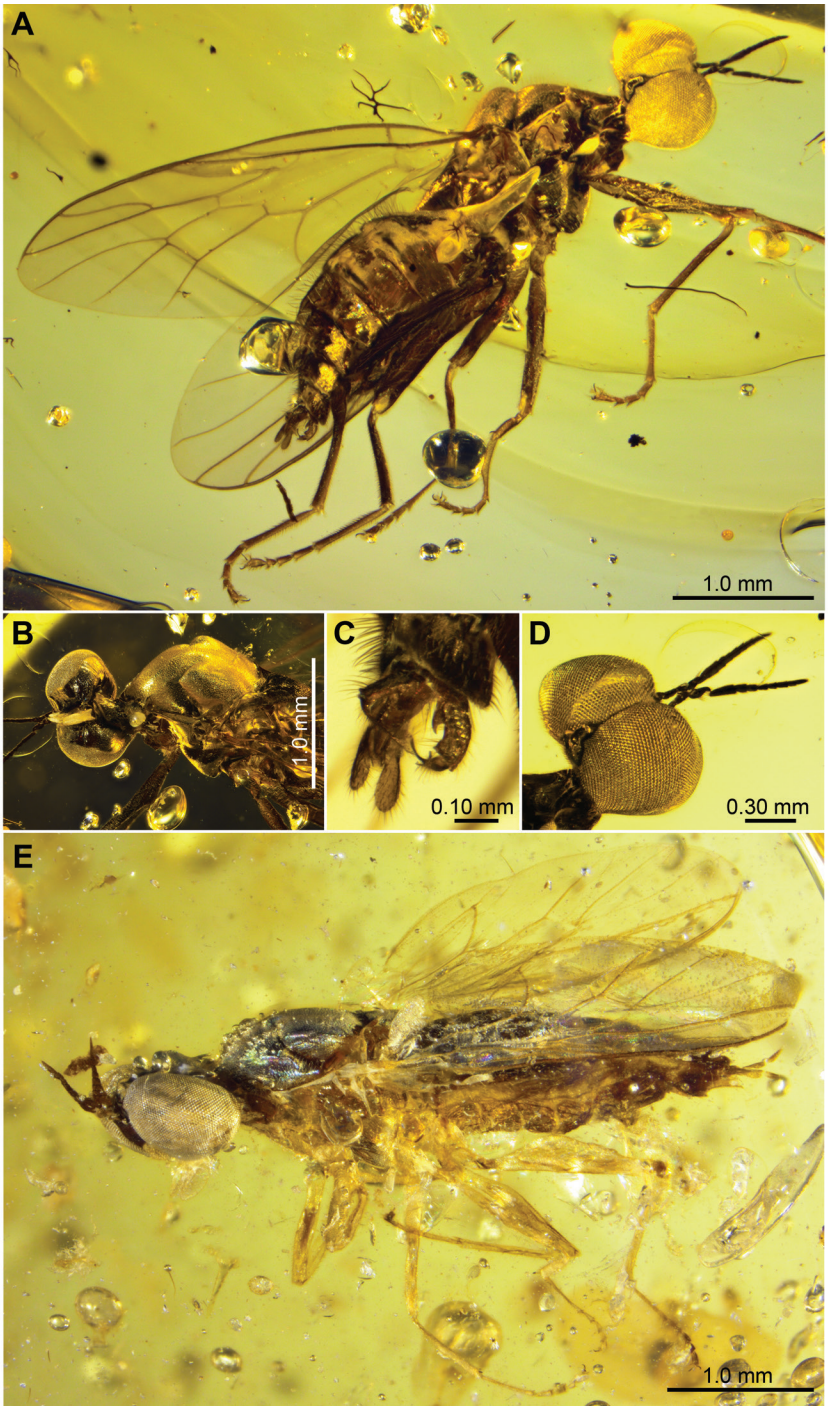

FIG. 42. *Narcissomyia bella*, new genus and species (Stratiomyidae). Holotype male AMNH Bu-SE3/1 (A–D), paratype female AMNH Bu-Pk1 (E). **A.** Habitus, right lateral view. **B.** Thorax and head, dorsal view (head is turned to expose ventral view). **C.** Male genitalia, oblique ventral view. **D.** Head, dorsal view. **E.** Habitus of female, left lateral.

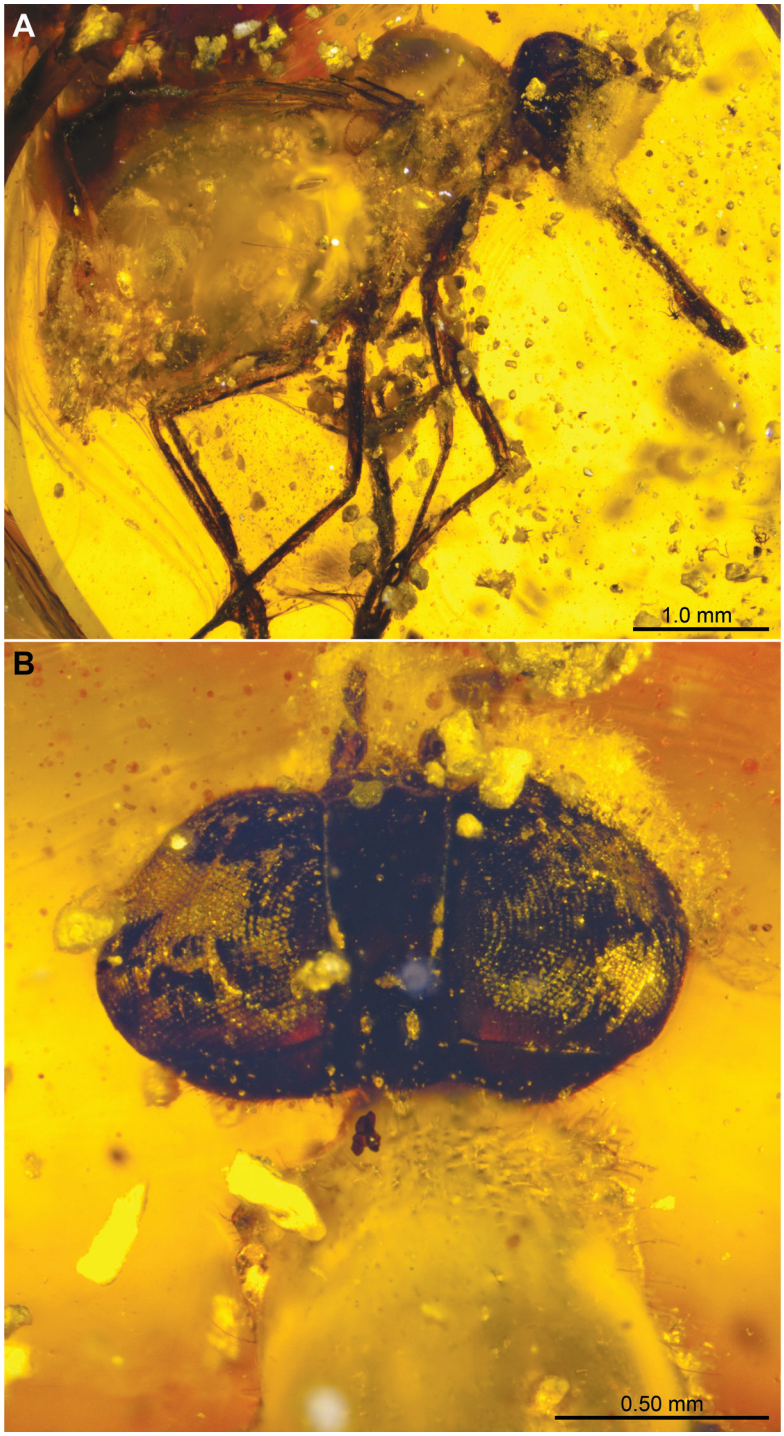

FIG. 43. *Palaepangonius glossa*, new species (stem-group Tabanomorpha), holotype JZC Bu-248. **A.** Habitus, right lateral. **B.** Head, dorsal view.

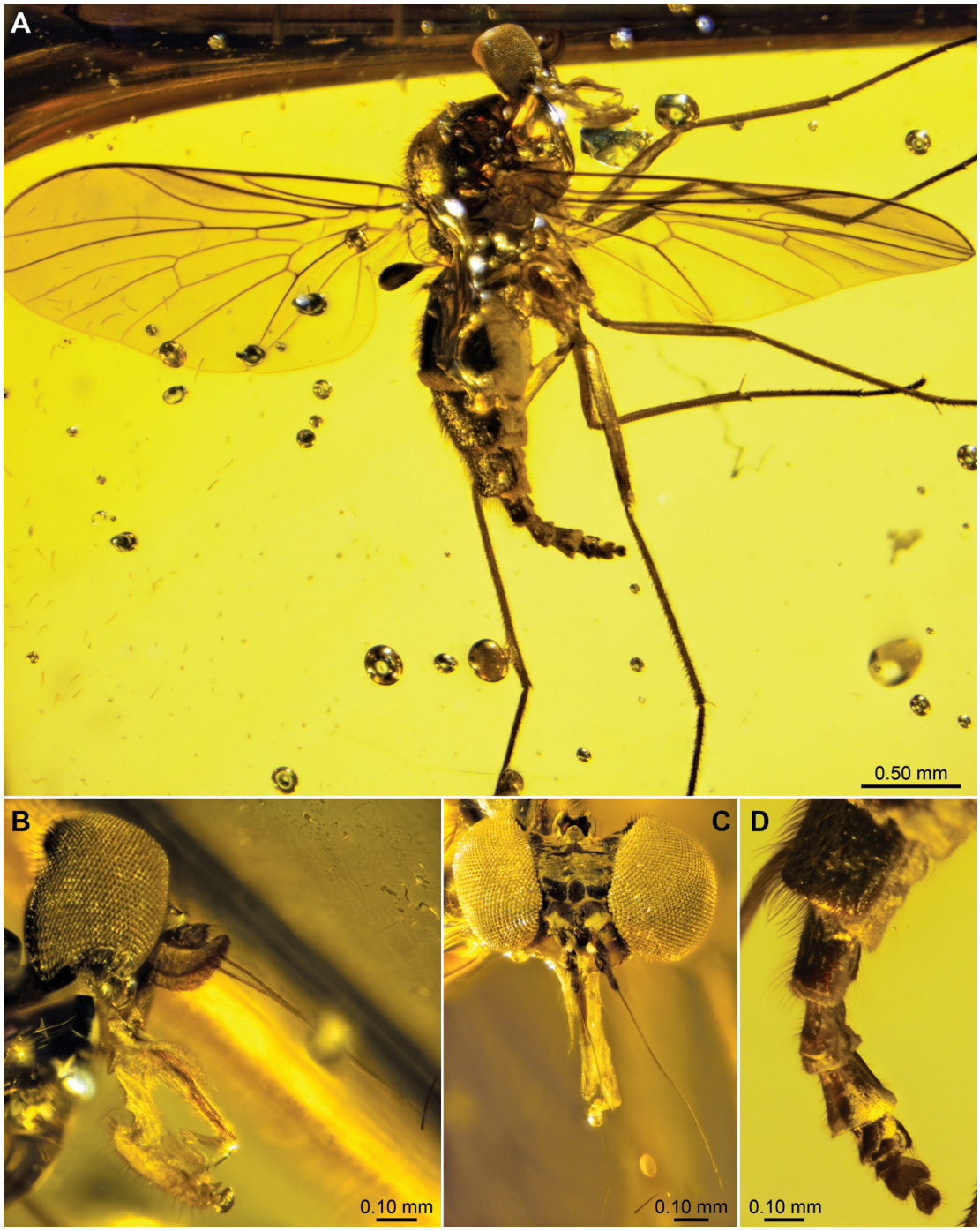

FIG. 44. *Atherhagiox ambiguum*, new genus and species (stem-group Tabanomorpha), holotype AMNH Bu-SE2/3. **A.** Habitus, dorsolateral view. **B.** Head, right lateral. **C.** Head, frontal. **D.** Female terminalia, dorsolateral.

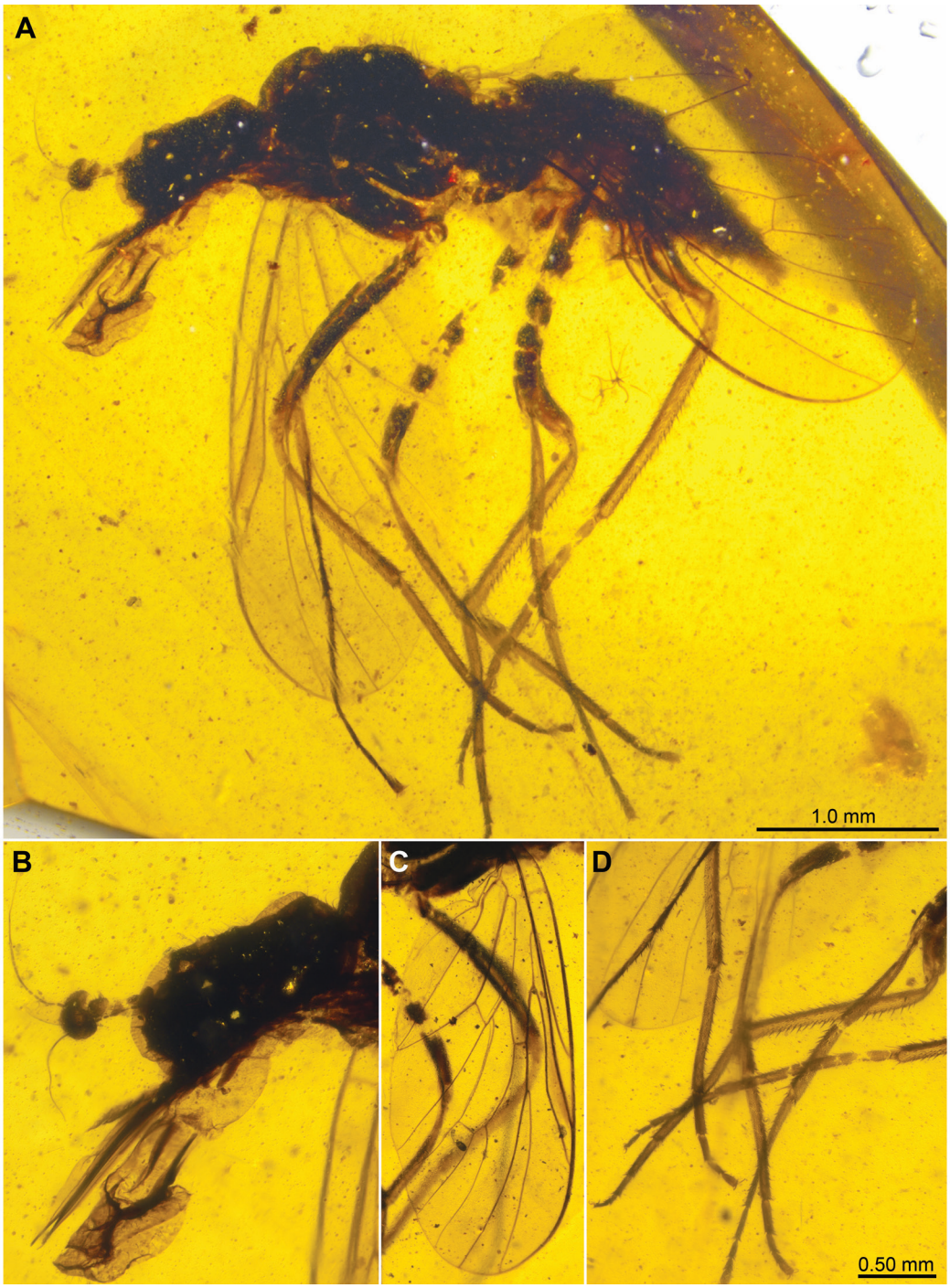

FIG. 45. *Atherhagiox simulans*, new genus and species, holotype JZC Bu-288. **A.** Habitus, left lateral. **B.** Head, left lateral. **C.** Right wing. **D.** Legs.

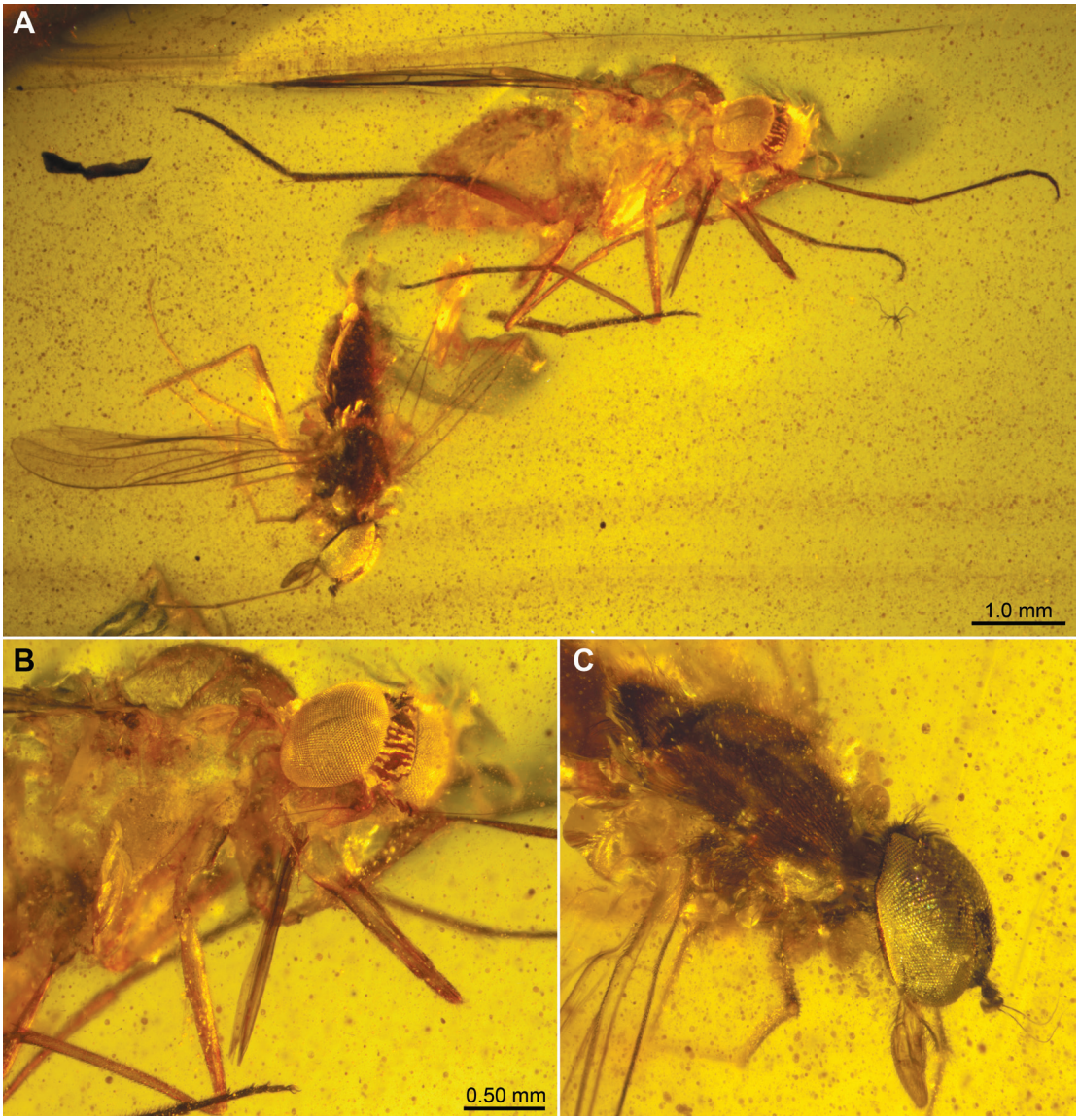

FIG. 46. *Galloatherix completus*, new species (stem-group Tabanomorpha), female holotype and male paratype AMNH Bu-SE2/5a, b. **A.** Habitus of female (above) and male (below), shown as preserved (in or near copula). **B.** Head and thorax of female holotype, frontolateral view. **C.** Head and thorax of male paratype, lateral view.

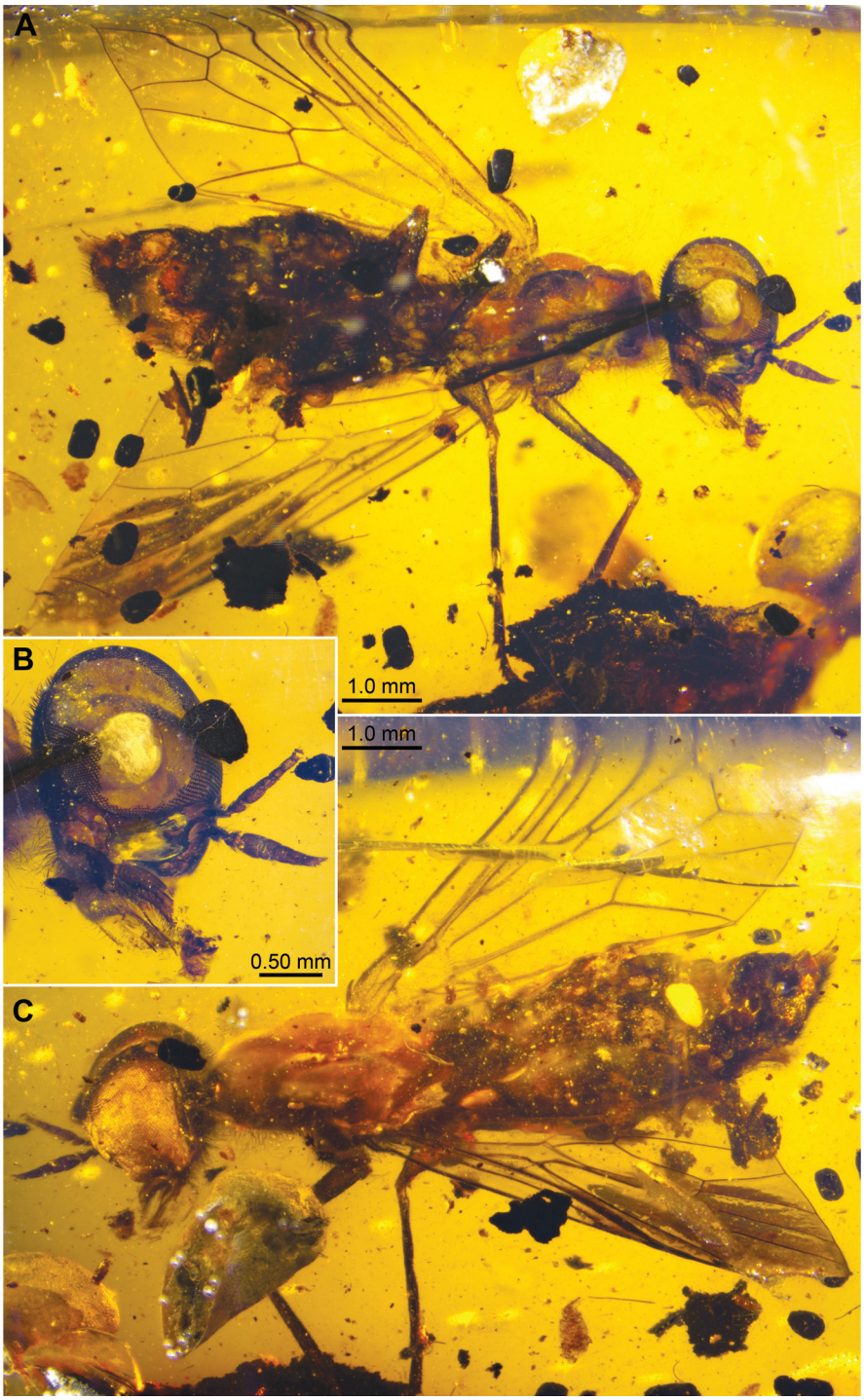

FIG. 47. *Tabanipriscus transitivus*, new genus and species (stem-group Tabanidae), holotype female, AMNH Bu-SE2/10. **A.** Habitus, ventrolateral view. **B.** Head, right lateral view. **C.** Habitus, dorsolateral view.

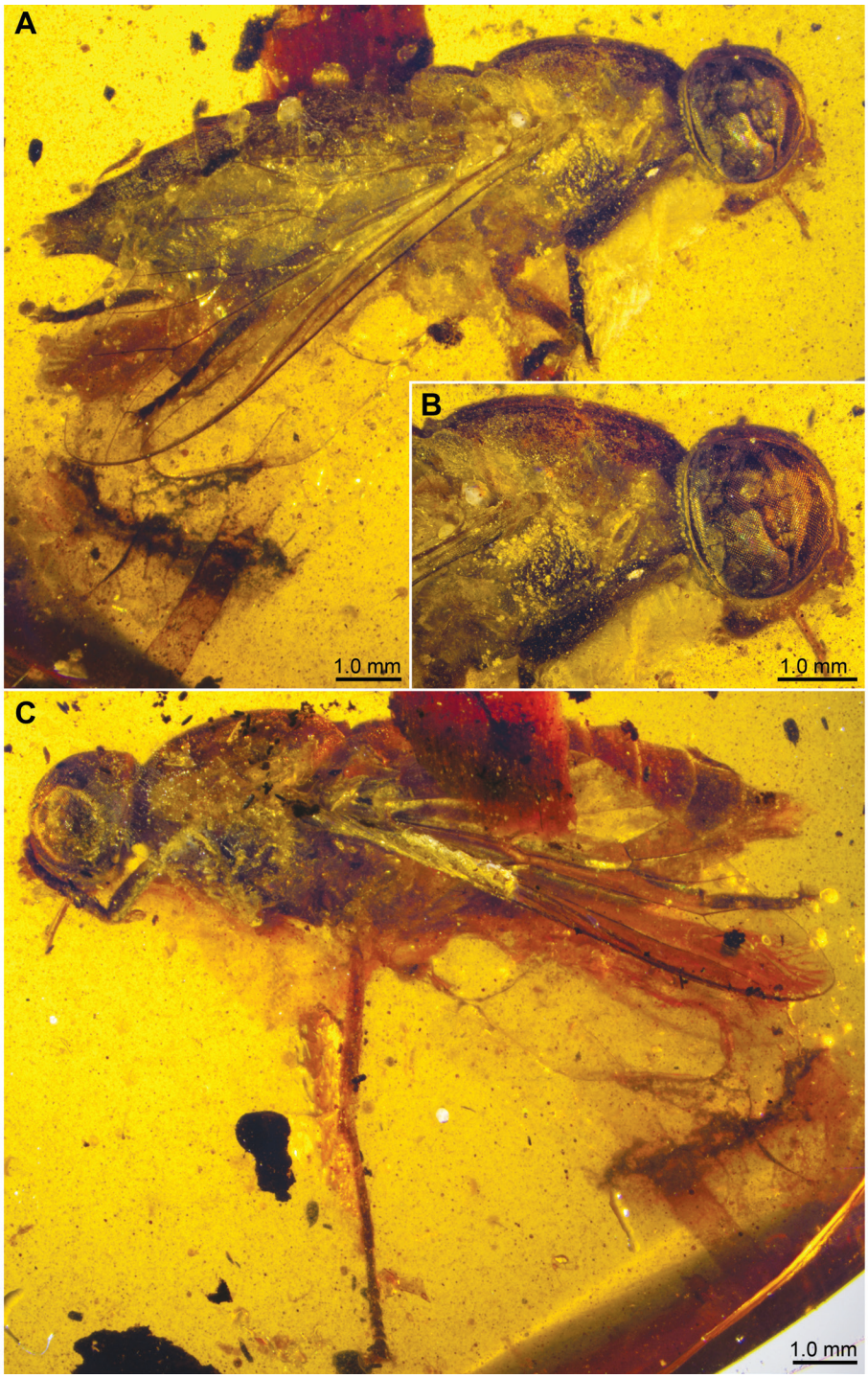

FIG. 48. *Cratotabanus asiaticus*, new species (Tabanidae), holotype female, AMNH Bu-SE3/2. **A.** Habitus, right lateral. **B.** Detail of head and thorax, right lateral. **C.** Habitus, left lateral.

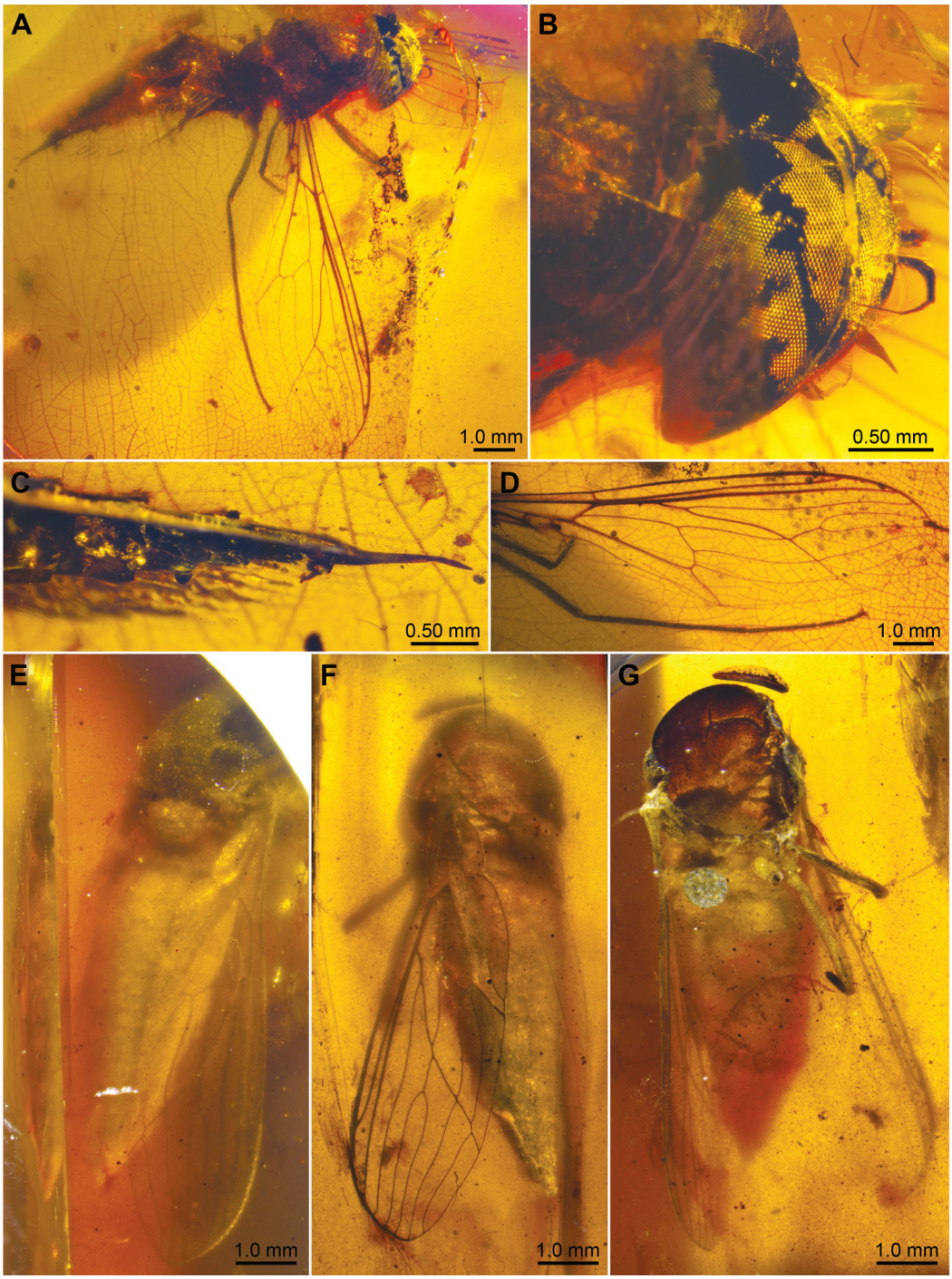

FIG. 49. *Hirmoneura* spp. (Nemestrinidae). **A–D.** *Hirmoneura caudiprima*, new species, holotype female, AMNH Bu-SE17. **E–G.** *Hirmoneura zigrasi*, new species, holotype female, JZC Bu-169. **A.** Habitus, dorsolateral. **B.** Head, dorsolateral. **C.** Female terminalia, showing long cerci. **D.** Right wing. **E.** Habitus, dorsal. **F.** Habitus, left lateral. **G.** Habitus, ventral.

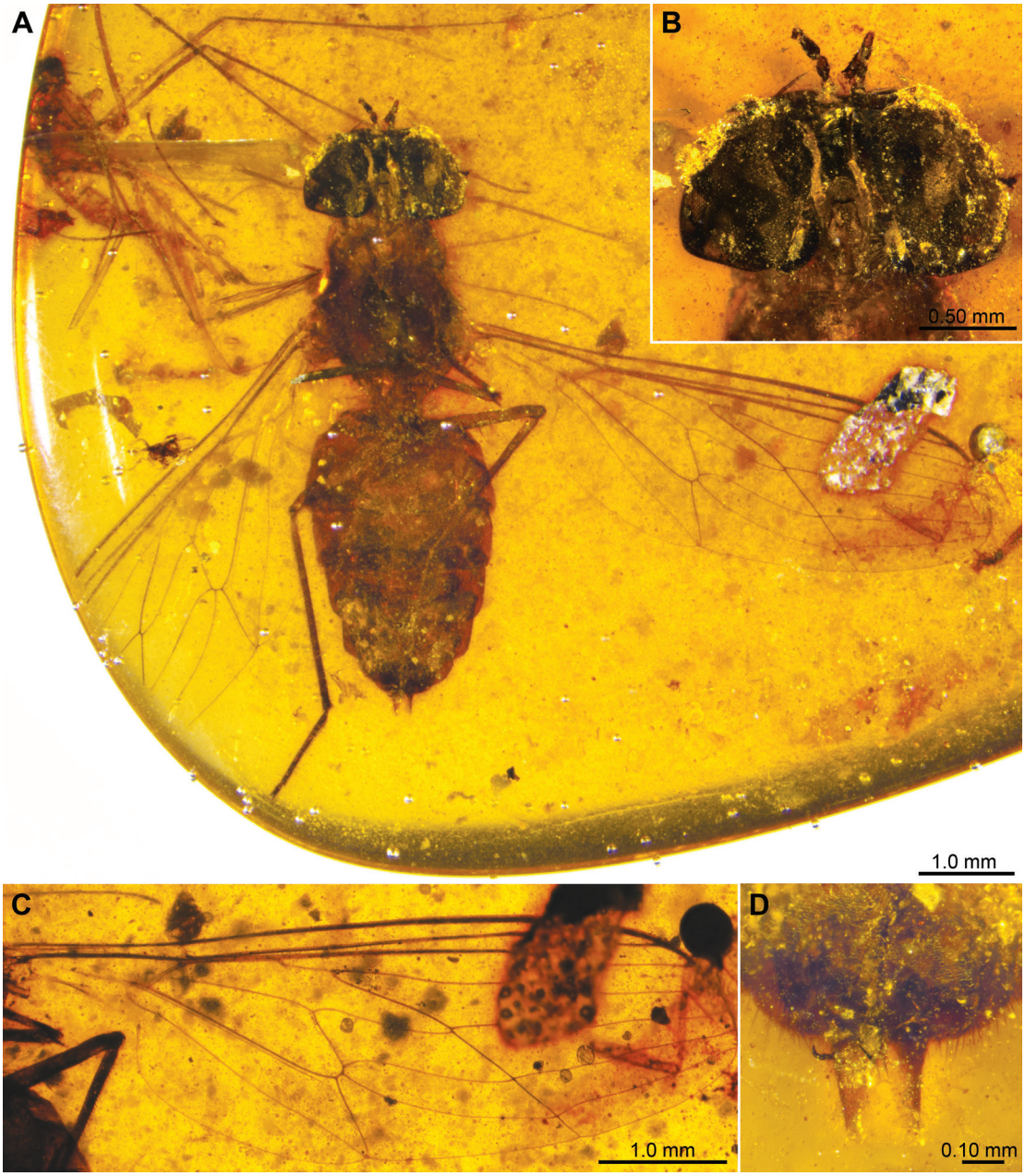

FIG. 50. *Hirmoneura* aff. *richterae* Mostovksi et al. (Nemestrinidae), HP-B-6084. **A.** Habitus, ventral view. **B.** Head, ventral. **C.** Left wing. **D.** Terminalia, ventral.

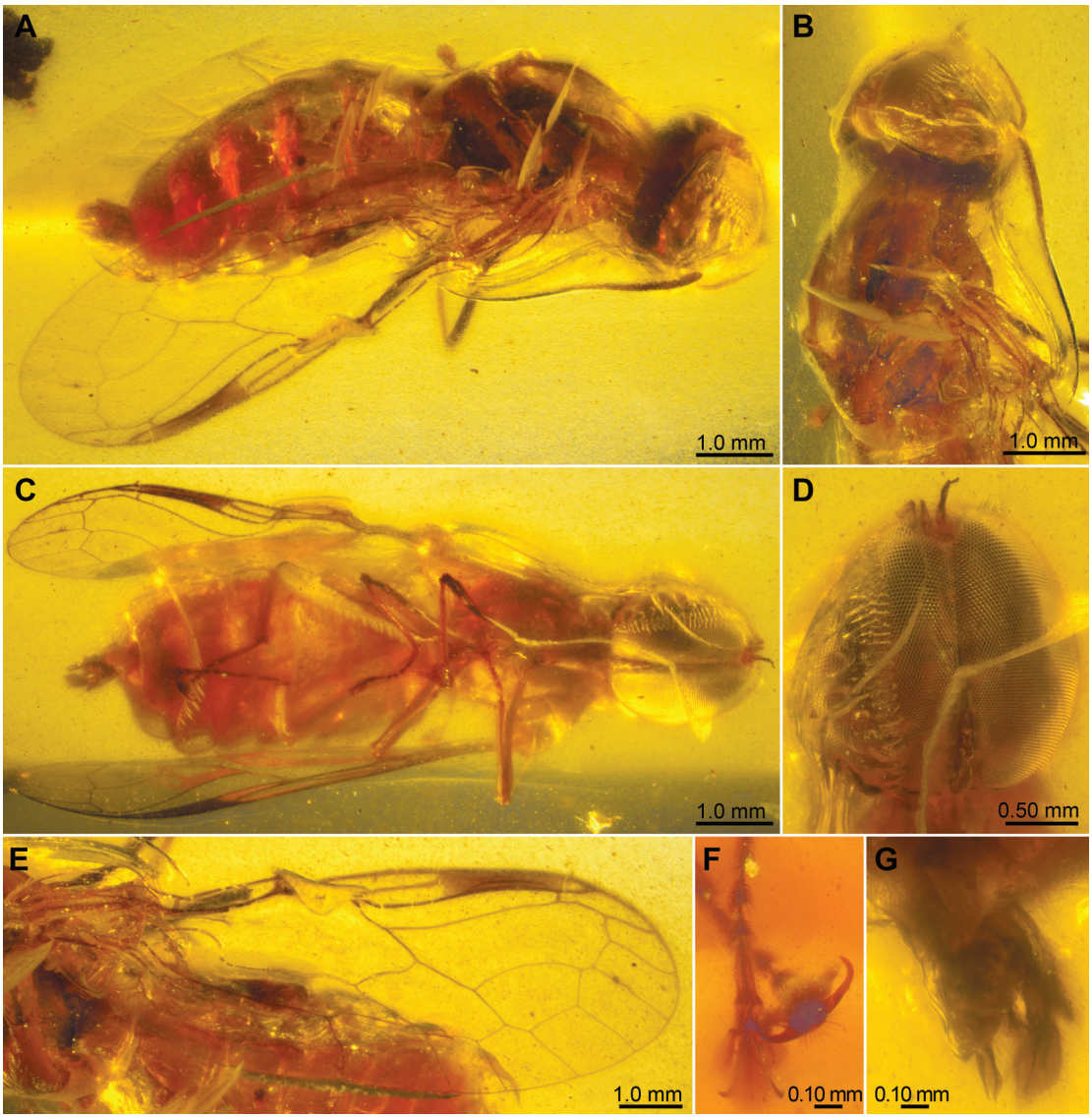

FIG. 51. *Jurassinemestrinus eurema*, new species (Rhagionemestriidae), holotype AMNH Bu-SE3/3. **A.** Habitus, right lateral. **B.** Head and thorax, right lateral. **C.** Habitus, ventral. **D.** Head, ventral. **E.** Right wing. **F.** Tarsi. **G.** Male terminalia.

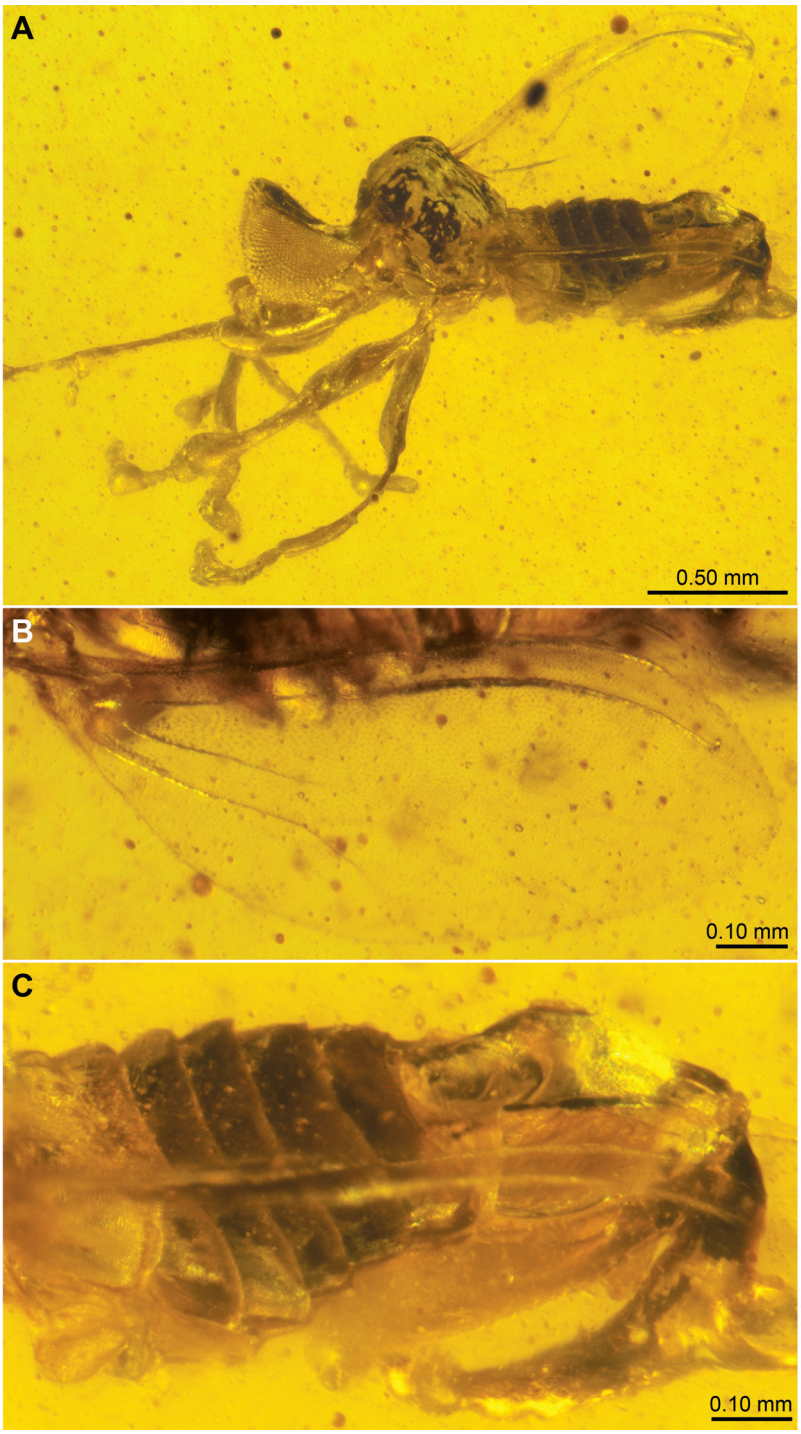

FIG. 52. *Tethepomyia zigrasi* Grimaldi, 2011 (Tethepomyiidae), in Burmese amber. Female holotype, JZC Bu. **A.** Habitus, left lateral view. **B.** Left wing. **C.** Abdomen and terminalia, left lateral, showing hooked cerci.

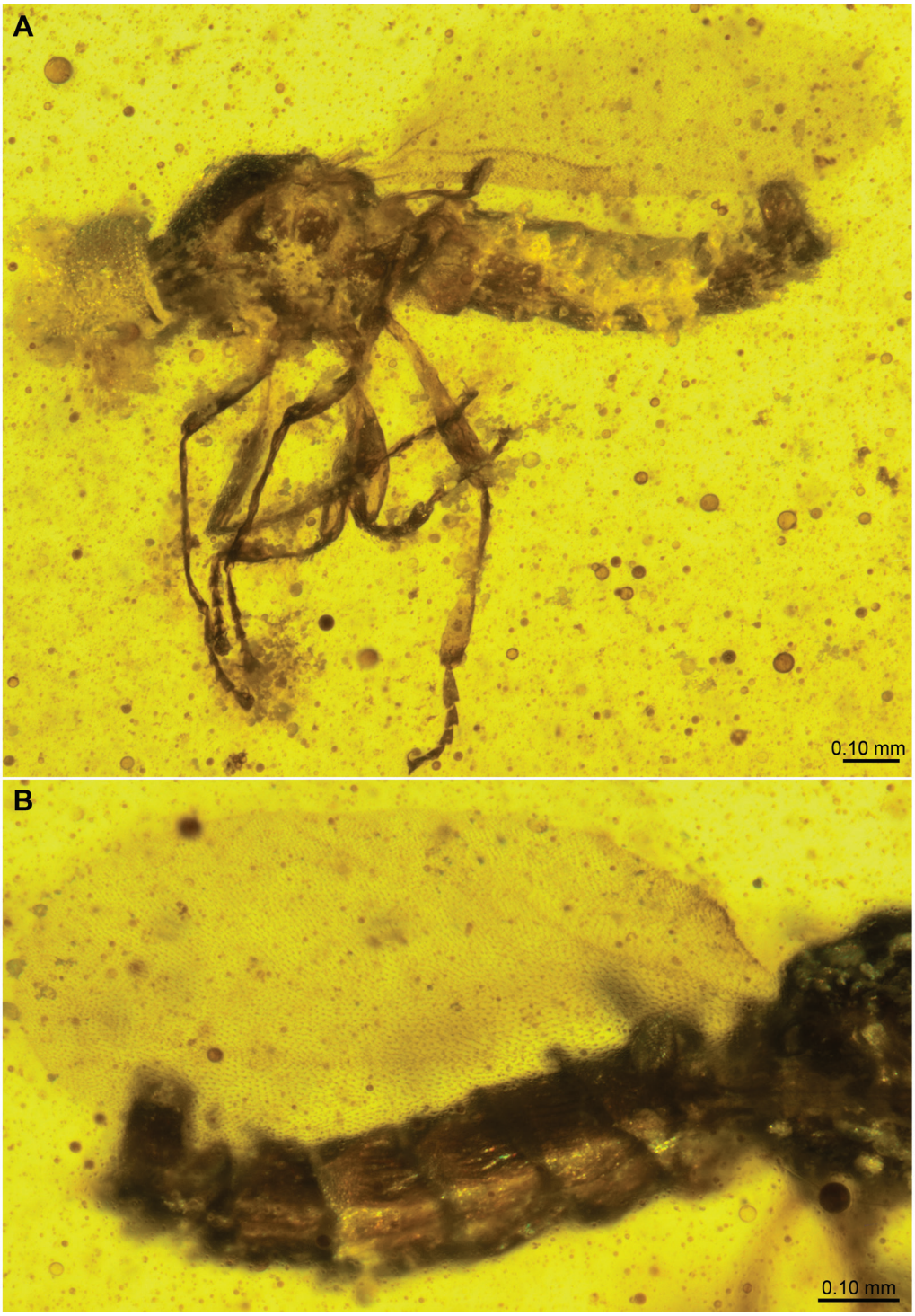

FIG. 53. *Tethepomyia coxa*, new species (Tethepomyiidae), holotype AMNH Bu-SE10. **A.** Habitus, left lateral. **B.** Detail of wing and abdomen, showing density of microtrichia on wing membrane.

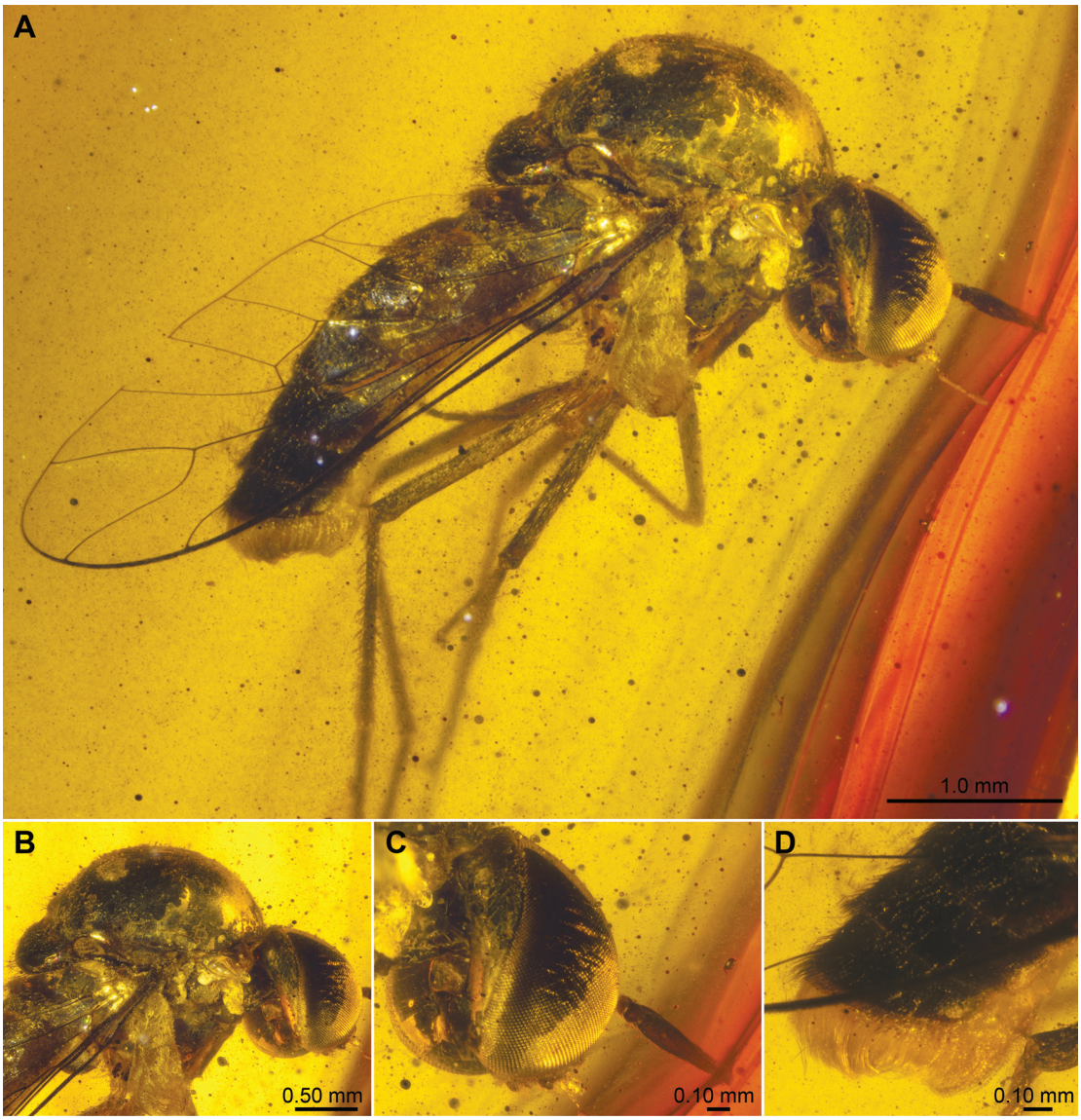

FIG. 54. *Nealimyia evenhuisi*, new genus and species (Bombyliidae), holotype, AMNH Bu-SE2/7. **A.** Habitus, right lateral. **B.** Head and thorax, right lateral. **C.** Head, right lateral. **D.** Terminalia, right lateral, showing dense brush of fine setae.

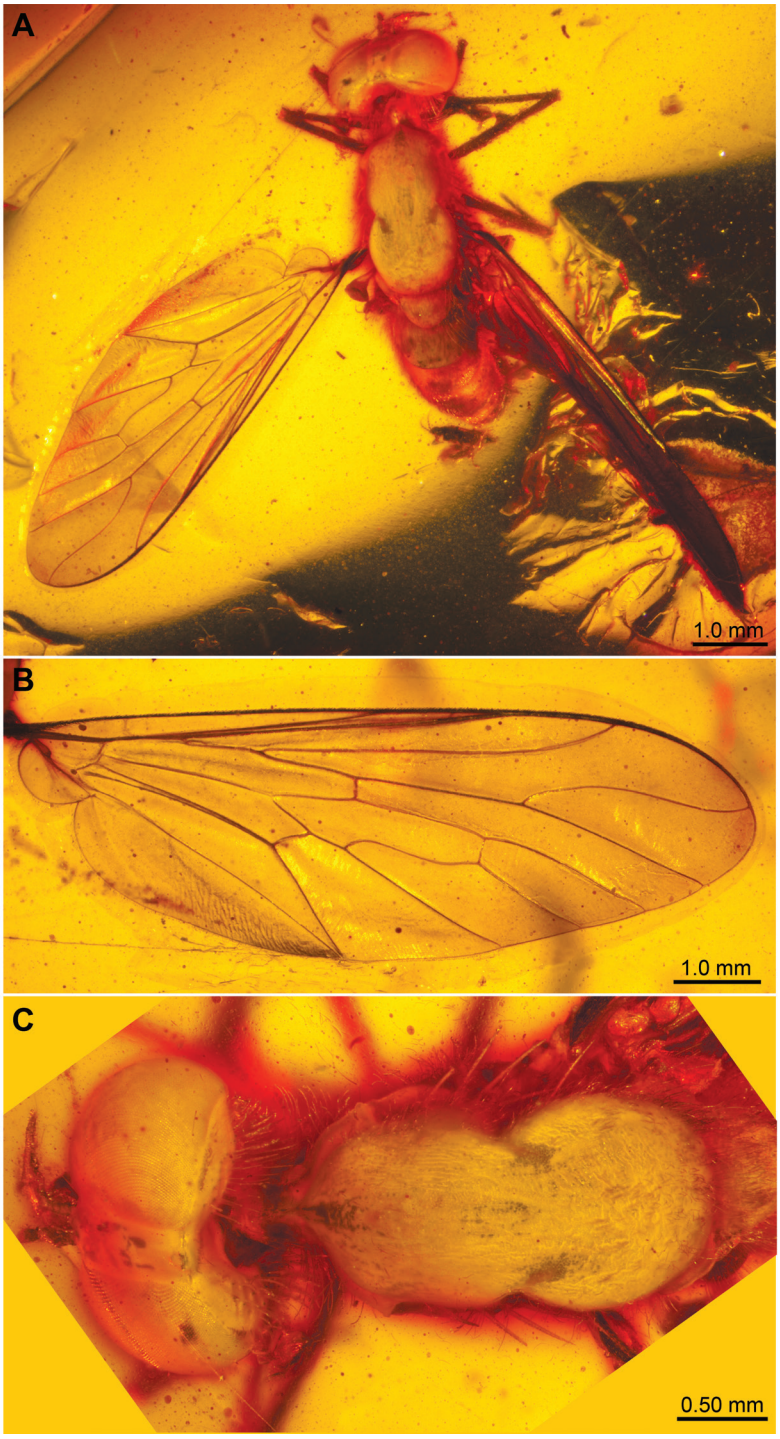

FIG. 55. *Pioneeria bombylia*, new genus and species (Bombyliidae), holotype AMNH Bu-SE2/9. **A.** Habitus, dorsal. **B.** Left wing. **C.** Head and thorax, dorsal view.

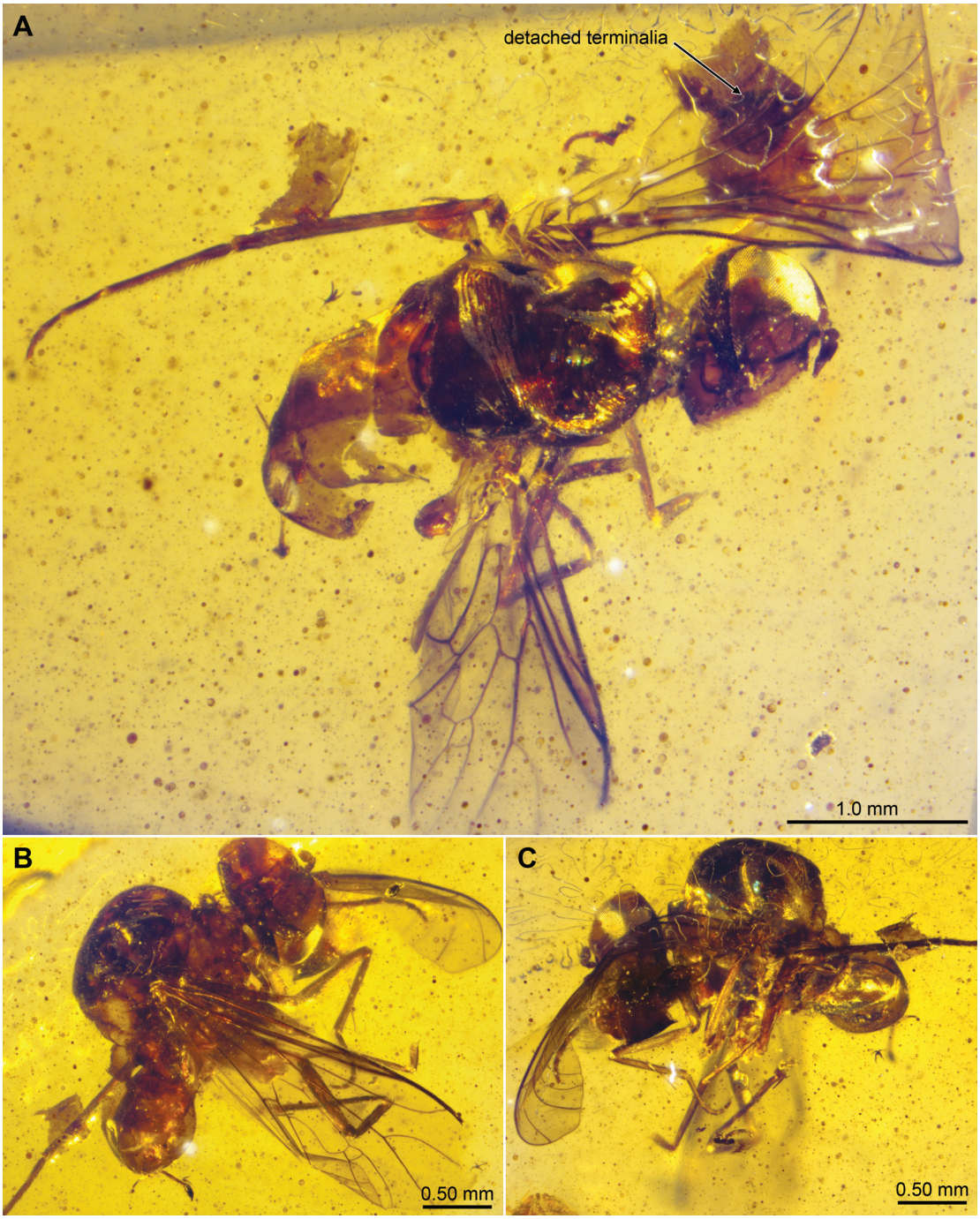

FIG. 56. *Procrocidium minutum*, new genus and species (Bombyliidae), holotype JZC Bu-098. **A.** Habitus, dorsal view, location of detached terminalia is indicated. **B.** Habitus, oblique right lateral view. **C.** Habitus, left lateral view.

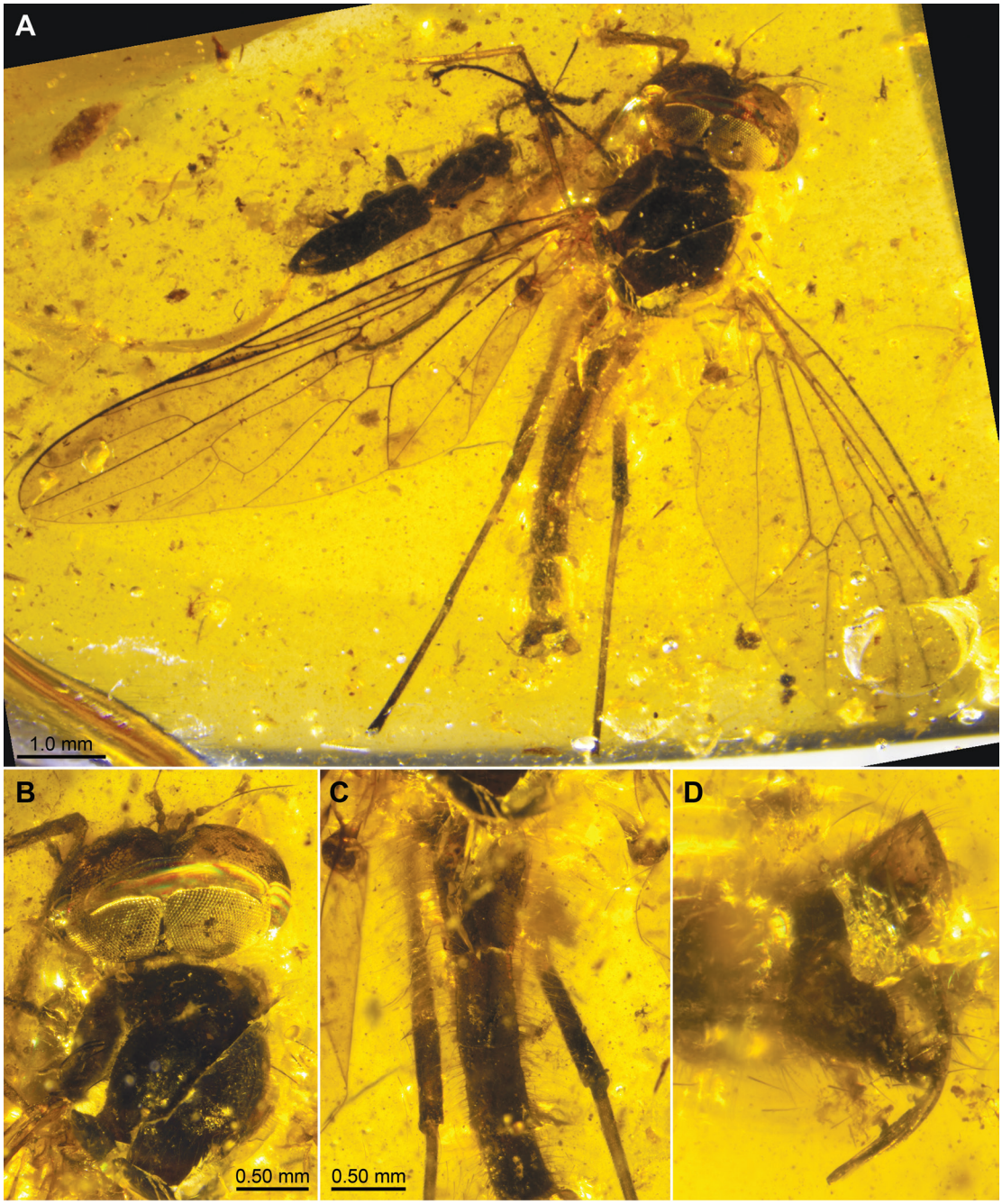

FIG. 57. *Endymiomyia quadra*, new genus and species (stem-group Bombyliidae), holotype JZC Bu-209. **A.** Habitus, dorsal view. **B.** Head and thorax, dorsal view. **C.** Base of abdomen, showing long lateral pilosity. **D.** Male terminalia, dorsal.

FIG. 58. *Burmapsilocephala evocoa*, new species (Apsilocephalidae), holotype AMNH Bu-SE2/4. **A.** Habitus, left lateral. **B.** Head and thorax, left lateral.

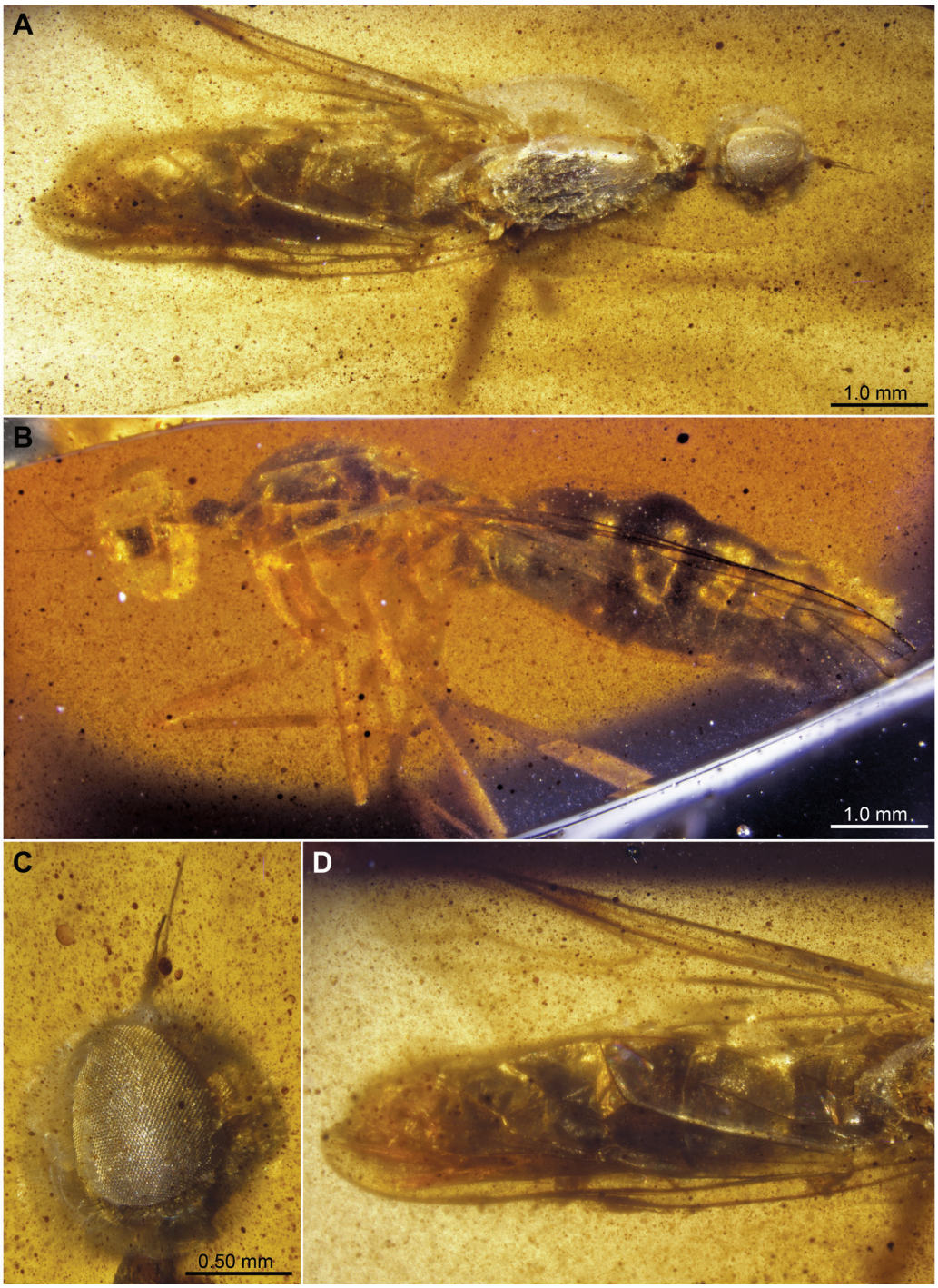

FIG. 59. *Gracilomyia wit*, new genus and species (unplaced to family), holotype AMNH Bu-SE14. **A.** Habitus, dorsal. **B.** Habitus, lateral. **C.** Head, left lateral. **D.** Abdomen and wings, dorsal.

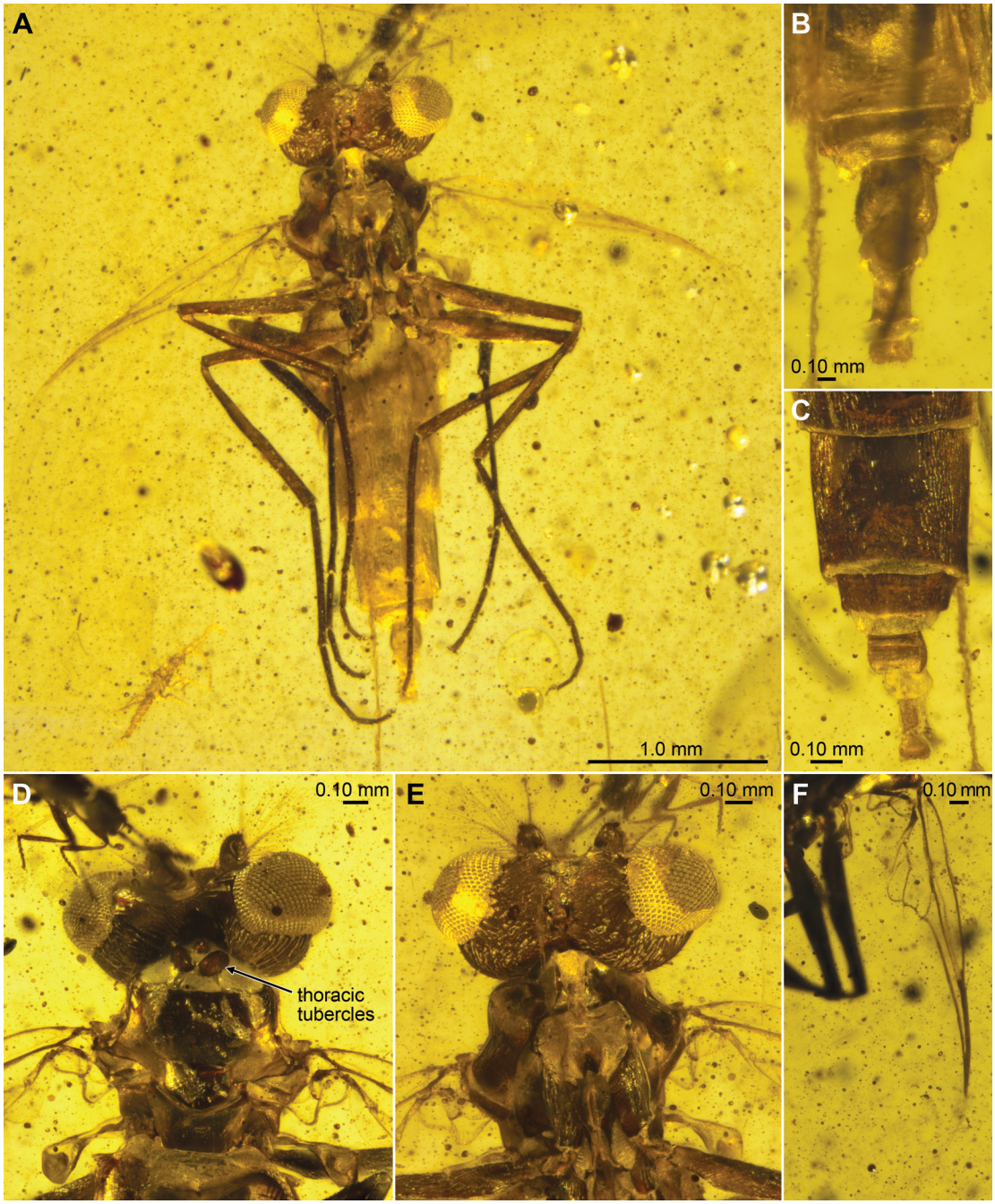

FIG. 60. *Mysteromyia plumosa*, new genus and species (Mysteromyiidae, new family), holotype JZC Bu-1817a. **A.** Habitus, ventral. **B.** Terminalia, ventral. **C.** Terminalia, dorsal. **D.** Head and thorax, dorsal, showing tubercles. **E.** Head and thorax, ventral. **F.** Right wing.

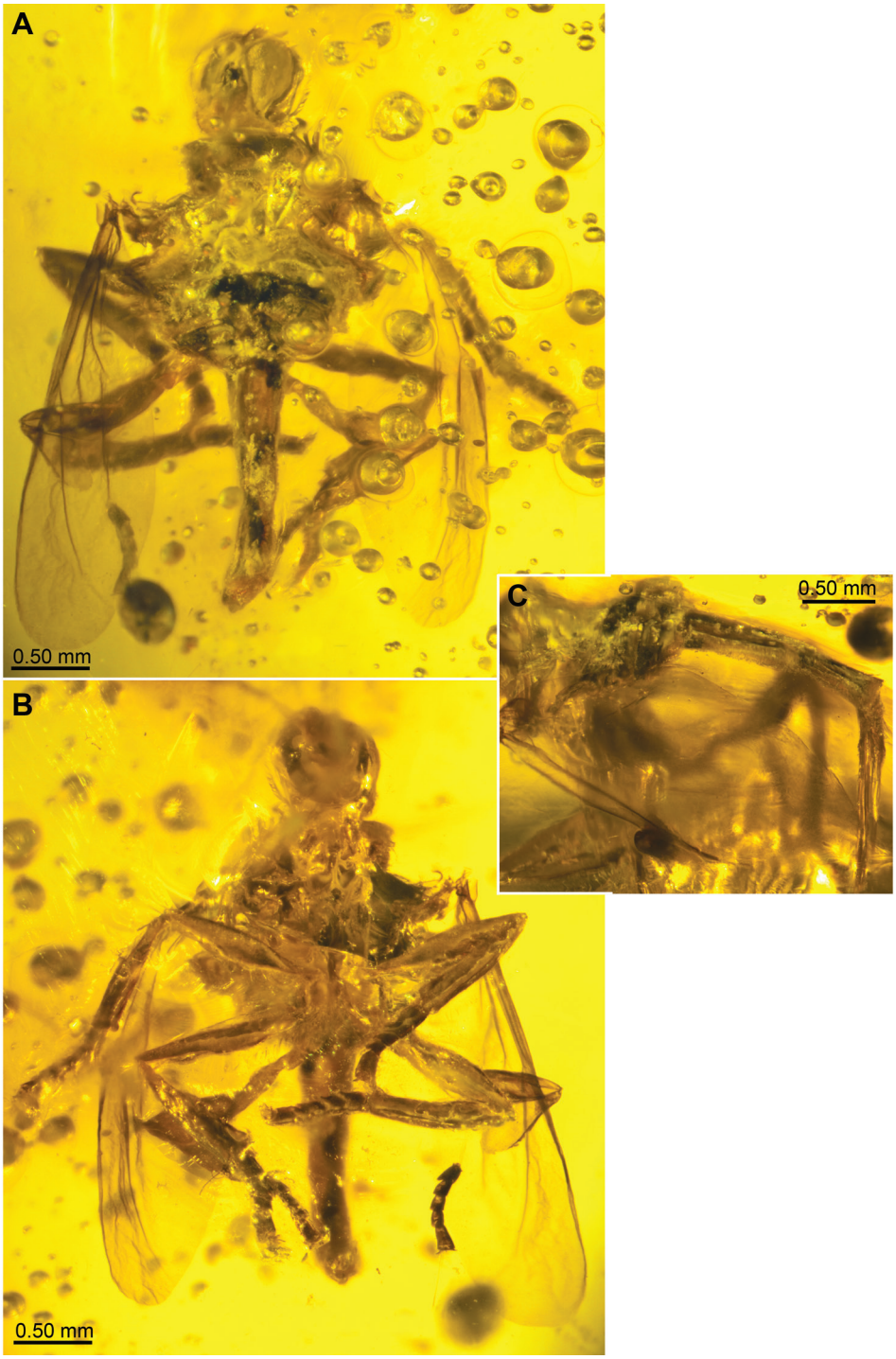

FIG. 61. *Eucaudomyia longicerci*, new genus and species (Eucaudomyia, new family), paratype Huang coll., IGP, Nanjing. **A.** Habitus, dorsal. **B.** Habitus, ventral. **C.** Abdomen with telescoping abdomen and long cerci, left lateral.

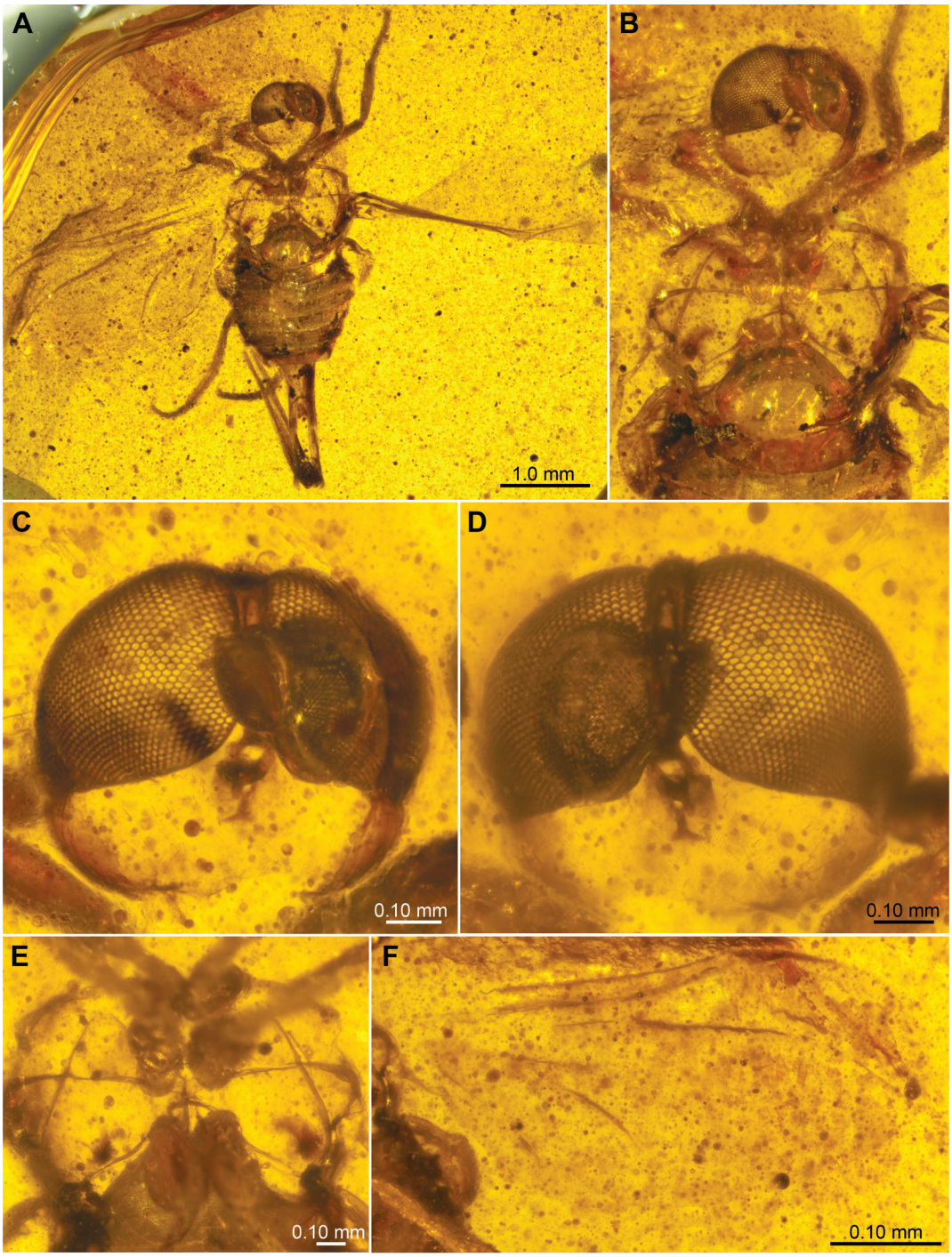

FIG. 62. *Eucaudomyia longicerci*, holotype JZC Bu-241. **A.** Habitus, dorsal. The head and thorax are cleared. **B.** Head and thorax, dorsal. **C.** Head, ventral. **D.** Head, dorsal. **E.** Thorax, ventral, showing peculiar arrangement of sternites and pleurites. **F.** Left wing.

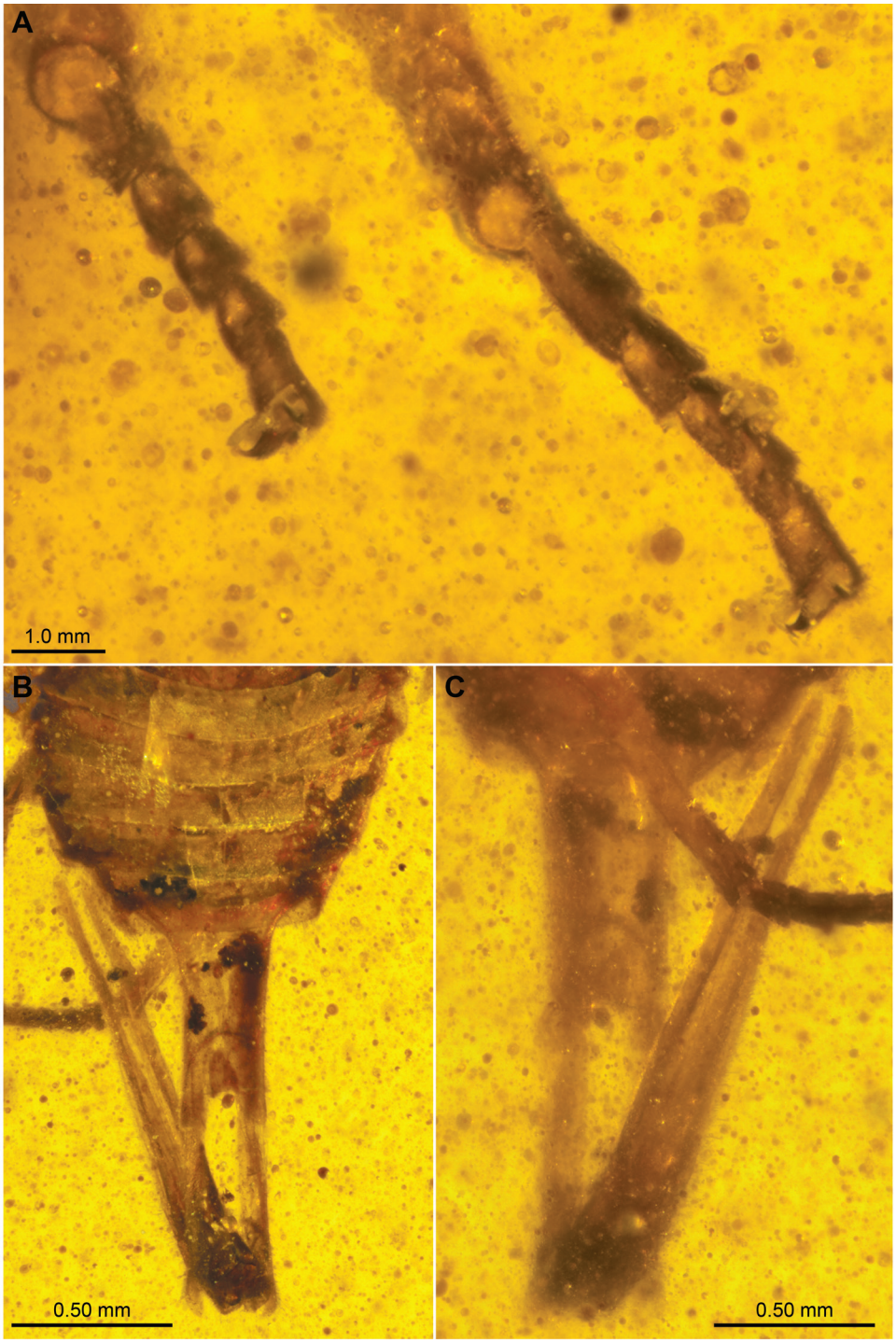

FIG. 63. *Eucaudomyia longicerci*, holotype. **A.** Tarsi. **B.** Abdomen, dorsal. **C.** Telescoping portion of abdomen and cerci, ventral.

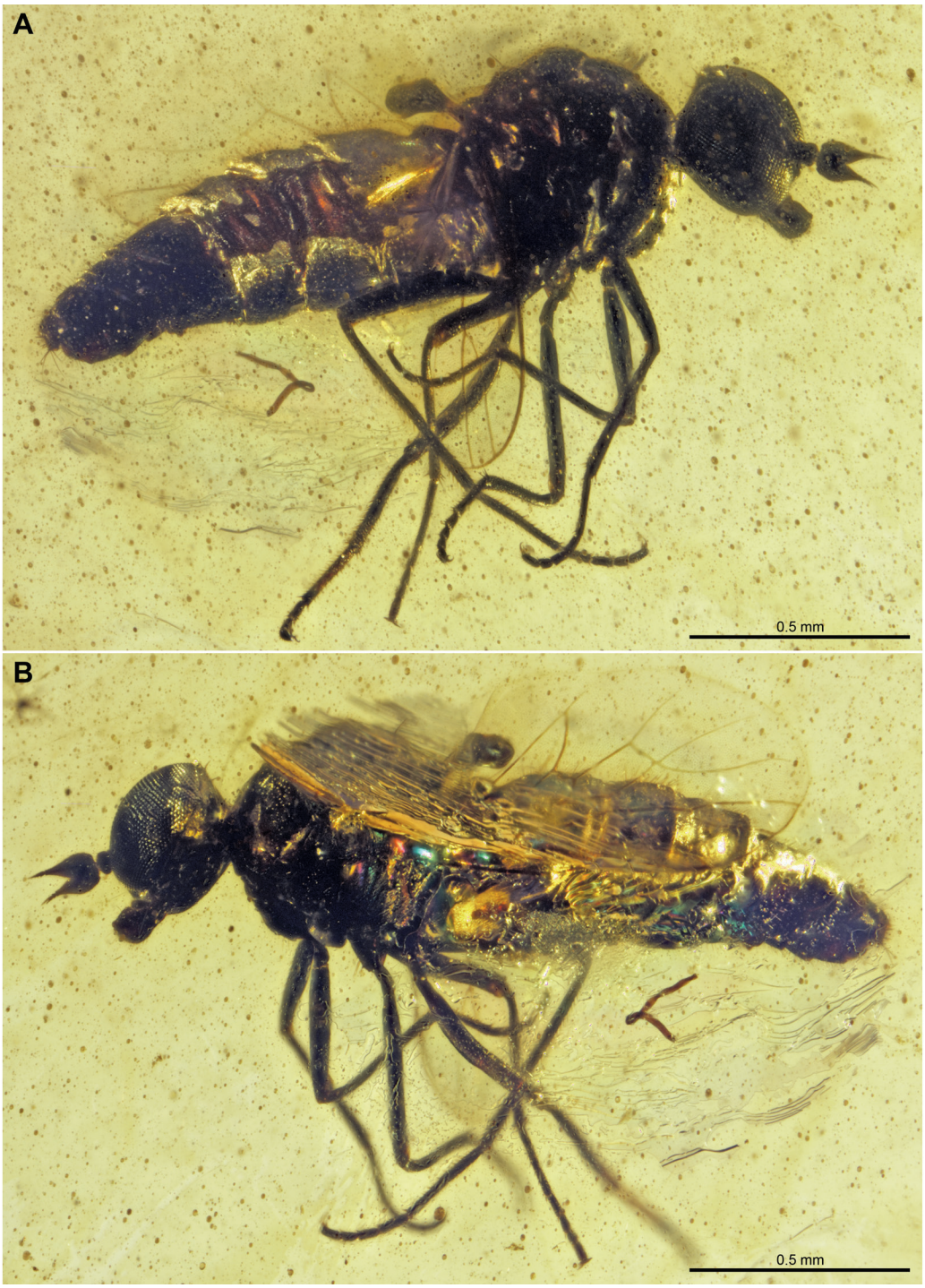

FIG. 64. *Hilarimorphites cummingi*, new species (Apystomyiidae), holotype JZC Bu-177. **A.** Habitus, right lateral. **B.** Habitus, left lateral.

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On the cover: Holotype specimen (male) of *Burmapsilocephala evocoa*, new species (Apsilocephalidae), in Burmese amber.