

Basal Cyclorrhapha in Amber from the Cretaceous and Tertiary(Insecta: Diptera), and Their Relationships: Brachycera in Cretaceous Amber Part IX

Author: Grimaldi, David A.

Source: Bulletin of the American Museum of Natural History, 2018(423)
: 1-97

Published By: American Museum of Natural History

URL: <https://doi.org/10.1206/0003-0090-423.1.1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

BASAL CYCLORRHAPHA IN AMBER
FROM THE CRETACEOUS AND
TERTIARY (INSECTA: DIPTERA),
AND THEIR RELATIONSHIPS:
BRACHYCERA IN CRETACEOUS AMBER PART IX

DAVID A. GRIMALDI

*Division of Invertebrate Zoology
American Museum of Natural History, New York*

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Number 423, 97 pp., 53 figures, 5 tables

Issued October 24, 2018

Copyright © American Museum of Natural History 2018

ISSN 0003-0090

CONTENTS

Abstract.	3
Introduction.	3
Methods and Materials.	5
Systematics.	31
Lonchopteroidea.	31
Platypezidae.	37
Ironomyiidae.	58
Phoridae.	70
Syrphoidea.	84
Acknowledgments.	93
References.	94

ABSTRACT

Diverse new basal (aschizan) Cyclorrhapha fossilized in amber are described from the Tertiary and Cretaceous, and their relationships are examined with character-based phylogenetic hypotheses for each family or family group. There are 18 new species in 15 genera (11 of them new) and four families plus the Syrphoidea. Fossils are from the Early Cretaceous of Lebanon, Late Cretaceous of New Jersey (United States) and Alberta (Canada), Eocene of the eastern Baltic coast, and Miocene of the Dominican Republic, but predominantly from the mid-Cretaceous of Myanmar. Stem-group Lonchopteroidea are *Alonchoptera lebanica*, n. gen., n.sp., and *Lonchopterites burmensis*, n. sp. Platypezidae include the stem groups *Burmapeza radialis*, n. gen., n. sp., *Canadopeza biacrosticha*, n. gen., n. sp., and *Calvopeza divergens*, n. gen., n. sp. An unnamed *Microsanina* sp. is the first definitive Platypezidae in Baltic amber; *Lebanopeza azari*, n. gen., n. sp., is a stem group to the Microsaniinae and Melanderomyiinae. *Chandleromyia anomala*, n. gen., n. sp., is an anomalously derived Platypezinae from the Cretaceous, and two new species of the diverse Recent genus *Lindneromyia* are in Dominican amber (*L. neomedialis* and *L. dominicana*). Fossils of the relict family Ironomyiidae (with 3 living species from eastern Australia) include two stem-group genera with two new species each, all in Burmese amber: *Palaeopetia dorsalis* and *P. terminus*, *Proironia* (n. gen.) *gibbera* and *P. burmitica*. All other species of *Palaeopetia* are compression fossils from the Cretaceous of Asia and Eurasia. For Phoridae, a new defining feature is a stridulatum on the procoxa and profemur in both sexes, occurring in most fossil taxa where observable. New sciadocerines include *Eosciadocera pauciseta*, n. sp., a very large species in Baltic amber, and two stem groups in Burmese amber, *Prophora dimorion*, n. gen., n. sp., and a very small, undescribed taxon. *Archiphora pria* Grimaldi and Cumming in Turonian-aged New Jersey amber is transferred to *Hennigophora* Brown, based on evidence from a new specimen. Prioriphorinae (not taxonomically treated here) is a paraphyletic, Cretaceous grade to the very diverse, crown-group radiation of Euphorida that occurred in the Cenozoic. Two syrphoids occur in Burmese amber: *Prosyrrhus thompsoni*, n. gen., n. sp. (an apparent stem group to the Syrphidae), and *Aschizomyia burmensis*, n. gen., n. sp. (with more ambiguous affinities). Several immatures of undetermined family are reported, one a probable phorid larva. No definitive Schizophora are yet known from the Cretaceous.

INTRODUCTION

The Cyclorrhapha is one of the largest monophyletic groups of the Diptera, after the Brachycera and Eremoneura (more inclusive groups to which Cyclorrhapha belong), and it is certainly the most ecologically diverse group of flies. Among them are larval parasitoids and predators of other arthropods, vertebrate parasites, saprophages, mycophages, carrion feeders, leaf and stem miners, and gall formers, as well as adult predators, blood feeders, and pollinators (Marshall, 2012). Cyclorrhapha is traditionally split into two groups, one the monophyletic Schizophora, including the acalyptrates (~72 families, 60,000 named species) and calyptrates (16 families, 18,000 named species). The other group includes the paraphyletic “Aschiza,” comprised of seven families: Lonchopteridae, Opeti-

idae, Platypezidae, Ironomyiidae, Phoridae (including Sciadocerinae), Syrphidae, and Pipunculidae. Aschizans are the subject of this paper. Throughout this paper the term “aschizan” is used in an informal, adjectival sense, for two reasons. One, it is easy to use, more so than say “nonschizophoran cyclorrhaphan” (much the way “moth” is used to refer to non-papilionoid Lepidoptera), and secondly, it is more specific than “basal” Cyclorrhapha.

Cyclorrhapha is best known as the group of flies with a maggot-type larva, in which the cuticle overall is thin and hardly sclerotized; the head capsule reduced to sclerotized struts invaginated within the thorax, its hooked mandibles working in parallel to rake food substrate (Malloch, 1917; Cook, 1949; Teskey, 1981; Ferrar, 1987; Rotheray and Gilbert, 2008). The thin

cuticle and highly reduced head of maggots is probably related to the fact that Cyclorrhapha larvae generally live within the substrate they feed upon, predatory groups being the exceptions (e.g., syrphine and phorid larvae that prey on aphids). The cyclorrhaphan larva passes through only three larval instars (vs. four for other Diptera), and pupation occurs within the highly tanned cuticle of the third-instar larva. Lastly, the male terminalia are rotated 360° (circumverted), either partly (aschizans) or entirely (Schizophora) within the puparium. This twisting allows copulation while the male is dorsally mounting the female (McAlpine, 1981).

Two of the seven families of basal Cyclorrhapha are species rich: Phoridae, with approximately 4100 named species (and actual species at least 10× this number), and the intensively studied Syrphidae, or flower flies, with nearly 6000 species. Platypezidae and Pipunculidae have fewer species (250 and 1800, respectively); the Lonchopteridae and especially Opetiidae and Ironomyiidae can be considered relict, having few, geographically isolated species. Indeed, the two genera of Opetiidae could not be more distant: *Opetia* in Europe and Asia and the newly described *Puyehuemyia* in Chile (Amorim et al., 2018), their disjunction doubtless due to widespread extinction. Although Ironomyiidae is now restricted to eastern Australia, the family was widespread in Laurasia in the Cretaceous (Mostovski, 1995; McAlpine, 1973; two genera with four new species in Burmese amber are described herein). There are no Cenozoic fossils of Ironomyiidae or Lonchopteridae.

The biogeography of Ironomyiidae is similar to that of Sciadocerinae (Phoridae), which has two living species: *Sciadocera rufomaculata* White in eastern Australia and New Zealand, and *Archiphora patagonica* Schmitz in Chile. Sciadocerines were more diverse in Laurasia from the mid-Cretaceous to at least the Late Eocene (Hennig, 1964; McAlpine and Martin, 1966; Brown, 2002, 2007a; Grimaldi and Cumming, 1999; herein). This is the opposite of Euphorida, the huge radiation of modern

phorids, which had stem groups (the prioriphorines) in the mid- to Late Cretaceous, but the crown group appears to have explosively diversified in the Cenozoic (e.g., Brues, 1939; Brown 1999, 2007b, 2013).

The fossil record of Platypezidae is far richer from the Cretaceous (Zhang, 1987; Mostovski, 1995a; Grimaldi and Cumming, 1999; herein) than it is for the Cenozoic (Chandler, 2001; herein), which is why I am reporting here on species in Baltic and Dominican amber, the first definitive records of Platypezidae from these deposits. Cretaceous Platypezidae were surprisingly diverse, albeit that they are almost all stem groups, where the preservation is sufficient to tell (i.e., in amber).

In contrast to Platypezidae, the fossil records of Pipunculidae and, until now, Syrphidae have been entirely Cenozoic (e.g., Carpenter and Hull, 1939; Hull, 1945; Evenhuis, 1994 [catalog]). Two syrphoids in mid-Cretaceous Burmese amber are reported in the present paper, one an apparent stem-group syrphid. Both are the most derived flies known from the Mesozoic, suggesting that crown-group Syrphidae, and perhaps Schizophora, may be found in the Maastrichtian or even Campanian. Thus, the evolutionary history of Cyclorrhapha is one of a few basal relicts and an extraordinary radiation.

An existence of Schizophora in the Late Cretaceous has been inferred, based on Paleocene leaf mines attributed to the Agromyzidae (Winkler et al., 2010), and divergence-time models of sequence data (e.g., Wiegmann et al., 2011). Indeed, one of the main motives for the present work was to acquire detailed new data for analyzing divergence times in Cyclorrhapha, which is why this work, like past papers in the series (e.g., Grimaldi, 2016), is also devoted to flies in amber. Preservation with microscopic fidelity allows comparison to living species, and phylogenetic interpretation of extinct species, with far more precision than is possible for specimens preserved in rocks. Observation of minute structures is particularly critical for the study of cyclorrhaphans.

Divergence-time modeling relies of course on accurate understanding of relationships. In this work I am presenting cladograms with their supporting morphological characters for five families and family groupings. With the exception of one genus, *Aschizomyia*, n. gen., in the Syrphoidea, all the Cretaceous genera discussed here fit *within* or can be phylogenetically allied to a family or even more subordinate taxon. The cladograms are not quantitatively generated, though the characters were carefully assessed. Work in progress will analyze a large morphological and molecular dataset, needed for addressing relationships *among* families of aschizans, most of which are ambiguous. The most stable grouping among aschizan families seems to be Ironomyiidae + Phoridae (McAlpine, 1989; Grimaldi and Cumming, 1999; Woodley et al., 2009; Wiegmann et al. 2011; Sinclair et al., 2013; Pauli et al., 2018), although the study by Brown et al. (2015) found Ironomyiidae (Phoridae + Lonchopteridae). With the exception of McAlpine (1989), whose scheme supports a monophyletic Aschiza that includes all seven families, some studies restrict aschizan monophyly to all families except Syrphidae and Pipunculidae (which are more closely related to Schizophora) (Wiegmann et al., 2011; Pauli et al., 2018). Studies by Griffiths (1972), Sinclair and Cumming (2006), Woodley et al. (2009), and Sinclair et al. (2013), proposed more of an aschizan grade of families. As I discuss later in this work, even the Syrphidae + Pipunculidae relationship is questionable, with molecular (and some morphological) evidence supporting a closer relationship of Pipunculidae to Schizophora (Wiegmann et al., 2011; Pauli et al., 2018). The monophyly of Schizophora appears to be certain.

METHODS AND MATERIALS

Amber specimens studied for this project were trimmed, polished, studied, and photographed according the protocols described in Grimaldi (2016). Some of the more fragile, fractured pieces were embedded in the synthetic resin EpoTek 301-2, to protect the inclusions and to allow trimming for optimal observation.

Micro-CT scanning was not done, primarily because most external features were visible on the inclusions, or because inclusions in some ambers (especially Burmese) are very difficult to scan (Grimaldi, 2016).

The various amber deposits from which study specimens derived are the following:

BALTIC AMBER: Varying from Early (Ypresian) to Late Eocene (Bartonian) in age (~50–38 Ma), although most of the amber mined from Yantarnyi in Russia (the source of most of the commercial Baltic amber) is mid-Eocene (Lutetian, ~ 45 Ma) (Ritzkowski, 1997; Weitschat and Wichard, 2010). This is the largest deposit in the world of amber, preserving the most diverse assemblage of arthropods in any amber (over 3000 species in 540 families and most orders). The amber was formed by a conifer of uncertain affinity (but often attributed to Pinaceae), in a warm temperate paleoclimate (Sadowski et al., 2017).

BURMESE (MYANMAR) AMBER: Strata from the main, commercially exploited deposits in Kachin Province in northern Myanmar have been radiometrically dated to 99 Ma (Shi et al., 2012), at the boundary of the Early and Late Cretaceous (Albian-Cenomanian). This is the most prolific source in the world of Cretaceous amber, having preserved nearly 1000 species of arthropods in some 350 families and 54 orders, among an impressive array of plants, small vertebrates, and assorted invertebrates (Grimaldi and Ross, 2017). It is also the only Cretaceous amber exploited commercially, for several thousand years (Grimaldi and Ross, 2017).

CANADIAN AMBER: Source of the Canadian amber studied here is from the Campanian (Late Cretaceous) of Grassy Lake, southern Alberta, radiometrically dated to 78–79 Ma (McKellar and Wolfe, 2010). Amber from Cedar Lake, Manitoba is secondarily deposited. The amber was formed in a lagoonal, brackish paleoenvironment, probably by the extinct genus *Parataxodium*, related to bald cypress (*Taxodium*) and Chinese swamp cypress (*Glyptostrobus*) in the Cupressaceae (McKellar and Wolfe, 2010).

DOMINICAN REPUBLIC AMBER: Derives from mines in the Cordillera Septentrional in northern Dominican Republic, from strata dated as early to middle Miocene, 15–20 Ma (Iturralde-Vinent and MacPhee, 1996). It was formed under tropical conditions very similar to those today in coastal forests of the Caribbean and Central America, produced by an extinct species of tree in the living legume genus *Hymenaea* (reviewed by Penney, 2010). Most species of arthropods in the amber belong to living genera, reflecting the relatively young age. Inclusions in Dominican amber are preserved particularly well; the amber is sold commercially.

LEBANESE AMBER: This is the most prolific source of amber from the lower part of the Early Cretaceous (reviewed by Azar et al., 2010). It is found throughout the country, varying in age from Kimmeridgian (Late Jurassic) to Albion (Early Cretaceous), although insects are known only from the Cretaceous outcrops. Most of the fossiliferous amber derives from Valanginian to Aptian outcrops (130–110 Ma); the taxa preserved in this amber tend to be distinctively basal to those in other Cretaceous ambers (Grimaldi and Engel, 2005).

NEW JERSEY AMBER: From the Raritan Formation in Sayreville, Middlesex County, New Jersey, palynologically dated as Turonian (Late Cretaceous, ca. 92 Ma) (Grimaldi et al., 2000; Grimaldi and Nascimbene, 2010). This amber was formed by a tree in the Cupressaceae in a coastal environment, probably with brackish water channels.

The specimens used in this study are from the following collections:

AMNH American Museum of Natural History (Division of Invertebrate Zoology), New York. Includes Baltic, Burmese, Dominican, Lebanese, and New Jersey ambers.

AZAR Collection of Dany Azar, housed in the Museum national d’histoire naturelle, Paris. The Azar collection is the largest in the world of Lebanese amber.

CCHH Collection of Cristal and Hans Werner Hoffeins, Hamburg, Germany, which is a comprehensive collection of Baltic amber Diptera.

JZC James Zigras Collection, presently stored in the AMNH (IZ). Includes Burmese amber.

TMP Tyrell Museum of Palaeontology, Drumheller, Alberta. This institution houses a large collection of Canadian amber collected by T. Pike (Pike, 1994).

Abbreviations used in the figures are the following:

acs	acrostichal setae
alula	alula
anepm	anepimeron
anepst	anepisternum
ant tnt pit	anterior tentorial pit
antsp	anterior spiracle
apsct	apical scutellar seta
bfdsl	bifid scales
bstrsmr	basitarsomere
cib	cibarium
clvts	clavate seta
clyp	clypeus
crs	cercus
cx	coxa
dcs	dorsocentral seta
epnd	epandrium
eprect	epiproct
epst	episternum
flgmr	flagellomere
fm	femur
hal	halter
hypnd	hypandrium
hyprect	hypoproct
inl ped	inner lobe of pedicel
intfrs	interfrontal seta
invs	inner vertical seta
ktepst	katapisternum
ktg	katatergite
lab	labellum
lbrm	labrum
mcrtrc	microtrichia
md tb s	middorsal tibial seta

mr	meron
mtrsmr	metatarsomere
npls	notopleural setae
occ for	occipital foramen
ocs	ocellar seta
orbs	orbital seta
ovs	outer vertical seta
pdc1	pedicel
plp	maxillary palp
ppnl	postpronotal lobe
ppnls	postpronotal lobe seta
prsc1 dc	prescutellar dorsocentral seta
prsc1tm	prescutellum
pst s	presutural seta
pst tnt arm	posterior tentorial arm
pst tnt pit	posterior tentorial pit
pstals	postalar seta
s(x)	sternite (number)
scp	scape
sct1m	scutellum
sct1rs	scutellar setae
snsl1r fov	sensillar fovea
spnlk s	spinelike setae
sp1rals	supraalar seta
srstls	surstylus
strd	stridulatum (scraper or file)
t(x)	tergite (number)
term	terminalia
tntr	tentorium
vg	ventral groove of femur
vib	vibrissa
vn lb ep	ventral lobe of epandrium
vnfms	ventrofemoral seta
vs	vertical seta
wb	wing base

Terminology for morphological characters generally follows McAlpine (1981), including wing venation, the latter of which follows the classic Comstock-Needham system (e.g., Comstock, 1918). In the new *Manual of Afrotropical Diptera* (Kirk-Spriggs and Sinclair [eds.], 2018), the vein system of Wootton and Enos (1989) is adopted, wherein veins CuA₁, CuA₂, A₁, and A₂, and cell *cup* (e.g., McAlpine, 1981) are considered to be veins M₄, CuA, CuP, A₁,

and cell *cua*, respectively. Homology of the wing veins routinely relies on relative positions and courses, and before revising the terminology data from additional sources beside position, such as vein tracheation and development (e.g., Comstock, 1918), should ideally be taken into account. For example, recent studies have used tracheation-branching patterns in the veins of Neuroptera and Blattodea, which support established homologies and clarify some ambiguities (Breitkruz et al., 2017; Li et al., 2018). A vein tracheation study on Diptera is needed.

The presentation of fossil genera below follows how they are here classified into or allied to existing, Recent families. For Lonchopteroidea, a definition of the monogeneric family needed expanding well beyond that of *Lonchoptera*, to accommodate the fossil genera, so the superfamily was created. The concept of Platypetidae here is quite standard (i.e., Chandler, 2001), including a putative close relationship with the small family Opetiidae (but see Amorim et al., 2018, who propose a closer relationship of Opetiidae to Lonchopteridae + Phoridae). My use of Opetiidae in this work purely regards the distributions of some characters. Likewise, including fossil taxa into the definition of Ironomyiidae required expanding beyond *Ironomyia*. Monophyly of the Ironomyiidae remains unchanged, regardless of views as to its close relationship to Phoridae (e.g., Griffiths, 1972; Sinclair et al., 2013, Wiegmann et al., 2010) or somewhat more distant (e.g., Brown et al., 2015; Amorim et al., 2018). The monophyly of Phoridae has never been in dispute, as are the placements of various fossil phorids within the family, despite some disagreement as to the most closely related group to the Phoridae. For the two fossil genera that are basal “syrphoids,” *Prosyrrhus*, n. gen., and *Aschizomyia*, n. gen., I present morphological features that define the monophyly of the two families in figure 51, with relationships of the two fossil genera provided within this context.

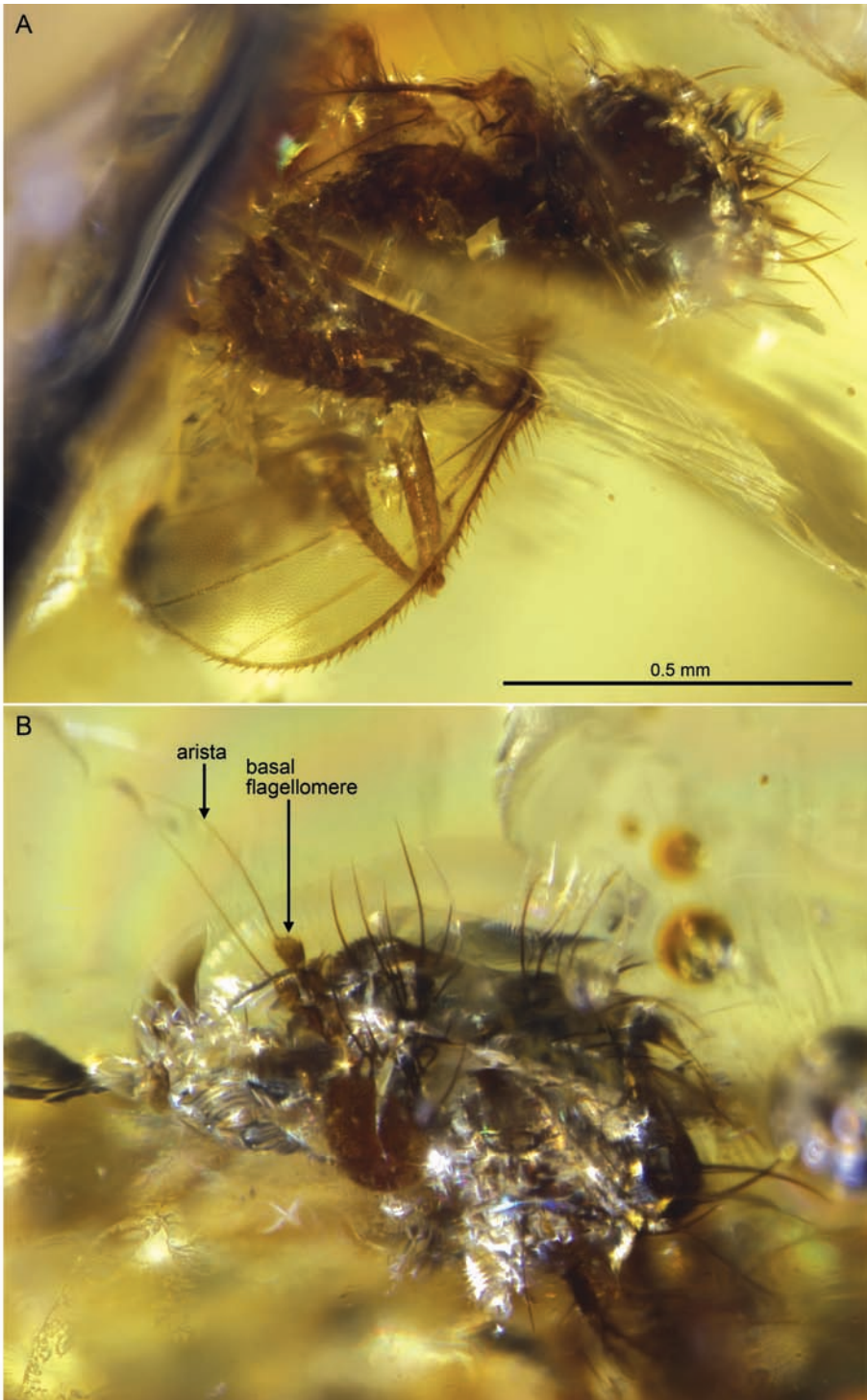


FIG. 1. *Alonchoptera lebanica*, n. gen., n. sp. (Lonchopteroidea), holotype AMNH LAE3-4, in Early Cretaceous amber from Lebanon. **A.** Dorsal view. **B.** Oblique dorsal view of head and thorax. The amber piece is permeated by many fractures.

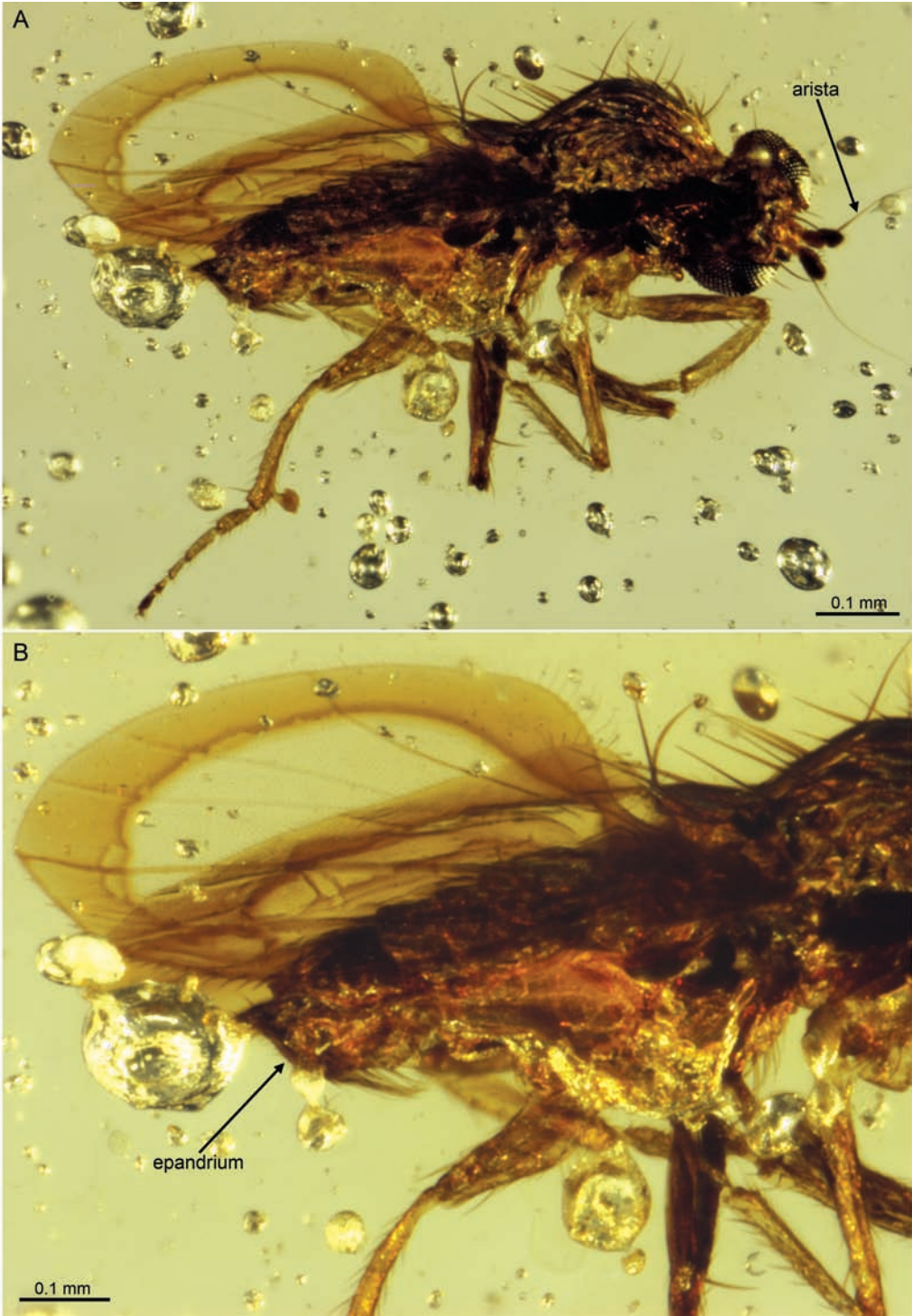


FIG. 2. *Lonchopterites burmensis*, n. sp. (Lonchopteroidea), holotype male AMNH Bu-SE15, in mid-Cretaceous amber from Myanmar. **A.** Lateral habitus. **B.** Lateral view of posterior half, with wing.

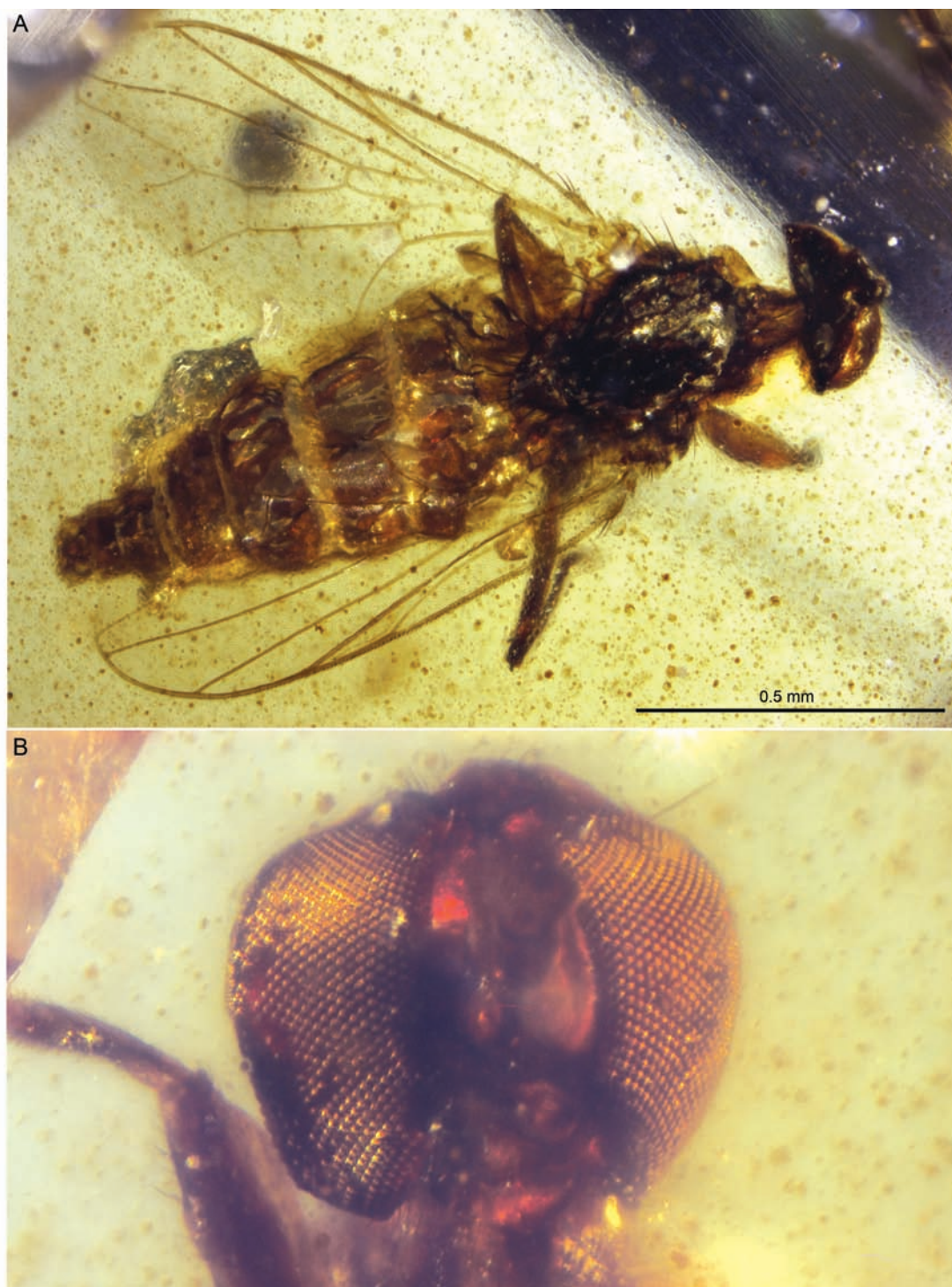


FIG. 3. *Burmapeza radialis*, n. gen., n. sp. (Platypezidae), holotype female, JZC Bu178a, in Burmese amber. **A.** Dorsal habitus. **B.** Frontal view of head.



FIG. 4. *Lebanopeza azari*, n. gen., n. sp. (Platypezidae), holotype male, Az715A, in Early Cretaceous amber from Lebanon. A, B. Dorsolateral and ventrolateral habitus. C. Detail of head and thorax. D, E. Detail of male terminalia, dorsolateral and ventrolateral views.



FIG. 5. *Microsania* sp. (Platypezidae), female, AMNH Ba502-14, in Eocene Baltic amber. A. Right lateral habitus. B. Frontal view of head.



FIG. 6. *Calvopeza divergens*, n. gen., n. sp. (Platypezidae), female holotype, AMNH Bu-SE8, in Burmese amber. A. Right lateral habitus. B. Frontal view of head. C. Lateral view of head. D. Wing. E. Mesotibiae and tarsi.



FIG. 7. *Calvopeza divergens* (Platypezidae), female paratypes in Burmese amber. A. JZC-Bu212, Dorsolateral habitus. B. Detail of head. C. Metatibiae and tarsi. D. AMNH Bu-1510.



FIG. 8. *Chandleromyia anomala*, n. gen., n. sp. (Platypezidae), male holotype in Burmese amber, AMNH Bu-KL30-27. A. Dorsolateral habitus. B. Head, ventrolateral view. C. Dorsolateral view. D. Metatarsus. E. Male terminalia, left posterolateral view.

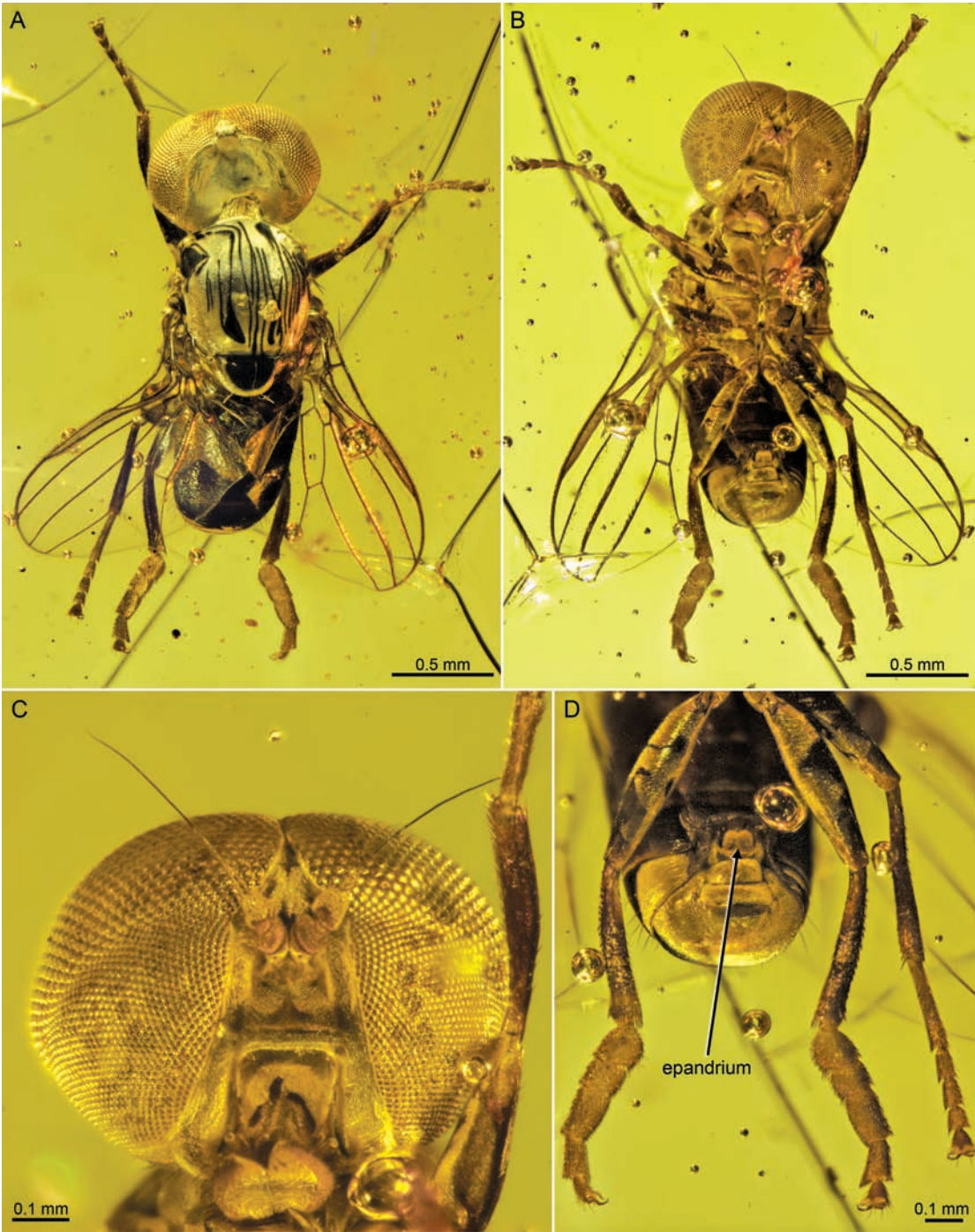


FIG. 9. *Lindneromyia neomedialis*, n. sp. (Platypezidae), male holotype in Miocene amber from the Dominican Republic, AMNH DR14-35. **A.** Dorsal habitus. **B.** Ventral habitus. **C.** Ventral view of head. **D.** Ventral view of terminalia and hind legs.

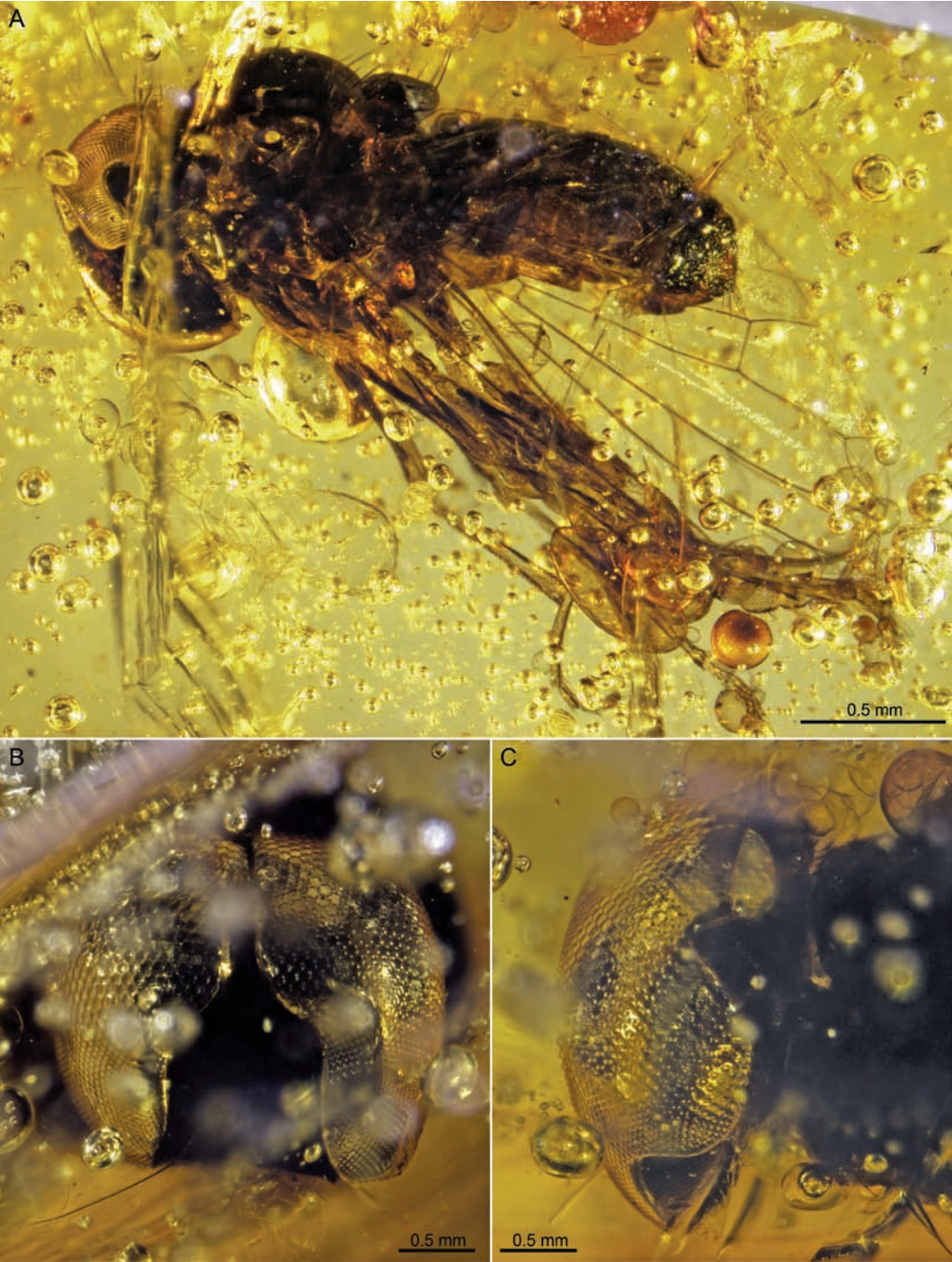


FIG. 10. *Lindneromyia dominicana*, n. sp. (Platypezidae), male holotype in Dominican amber, AMNH 14-736. A. Left lateral habitus. B. Frontal view of head. C. Lateral view of head. The eyes are largely covered with a layer of air, except for dark areas that appear, deceptively, to be emarginations.

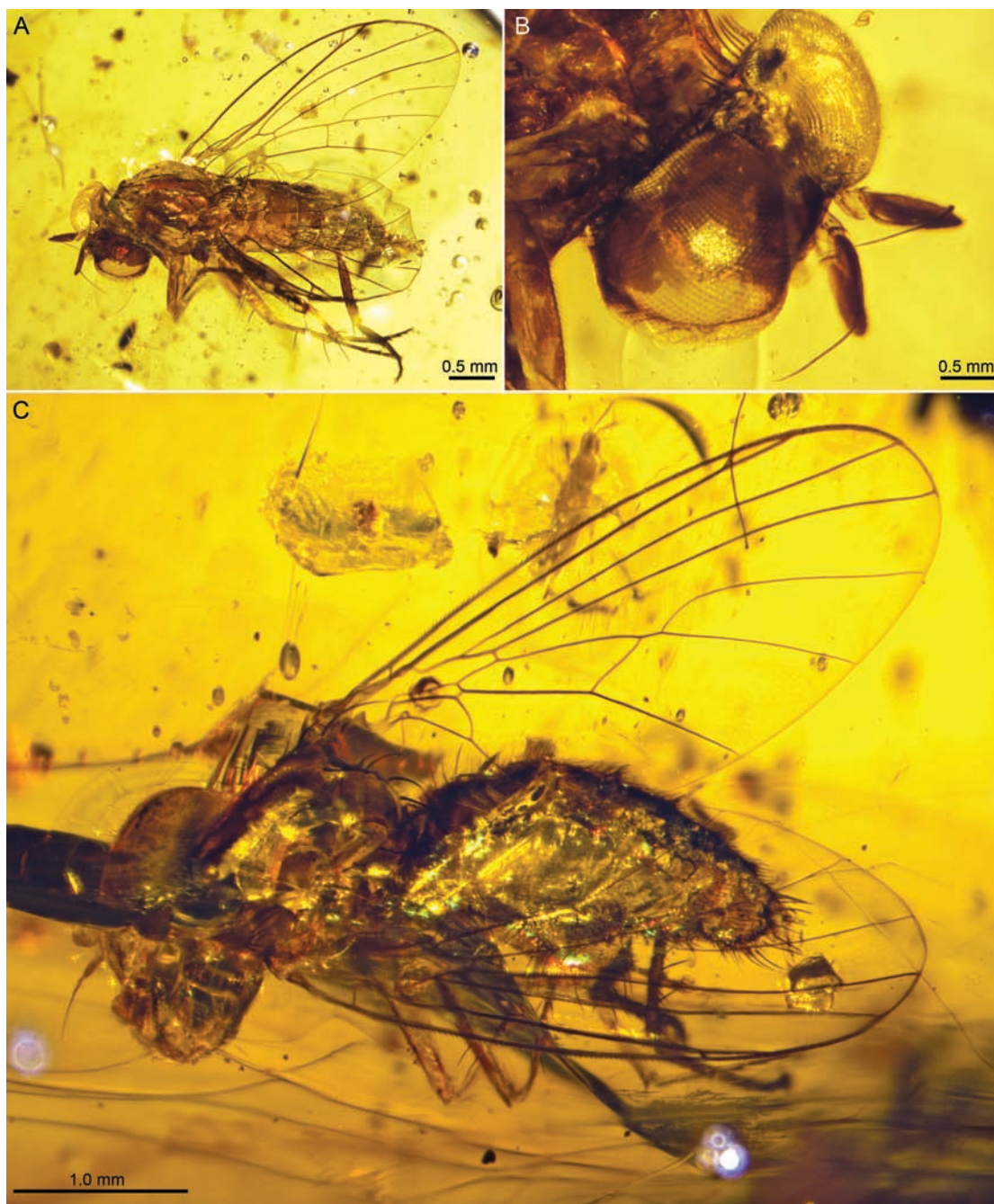


FIG. 11. *Palaeopetia dorsalis*, n. sp. (Ironomyiidae), in Burmese amber. **A, B:** Female holotype, AMNH Bu-FB34. **A.** Oblique dorsal habitus. **B.** Dorsal view of head. **C.** Paratype female, AMNH Bu-KL610.

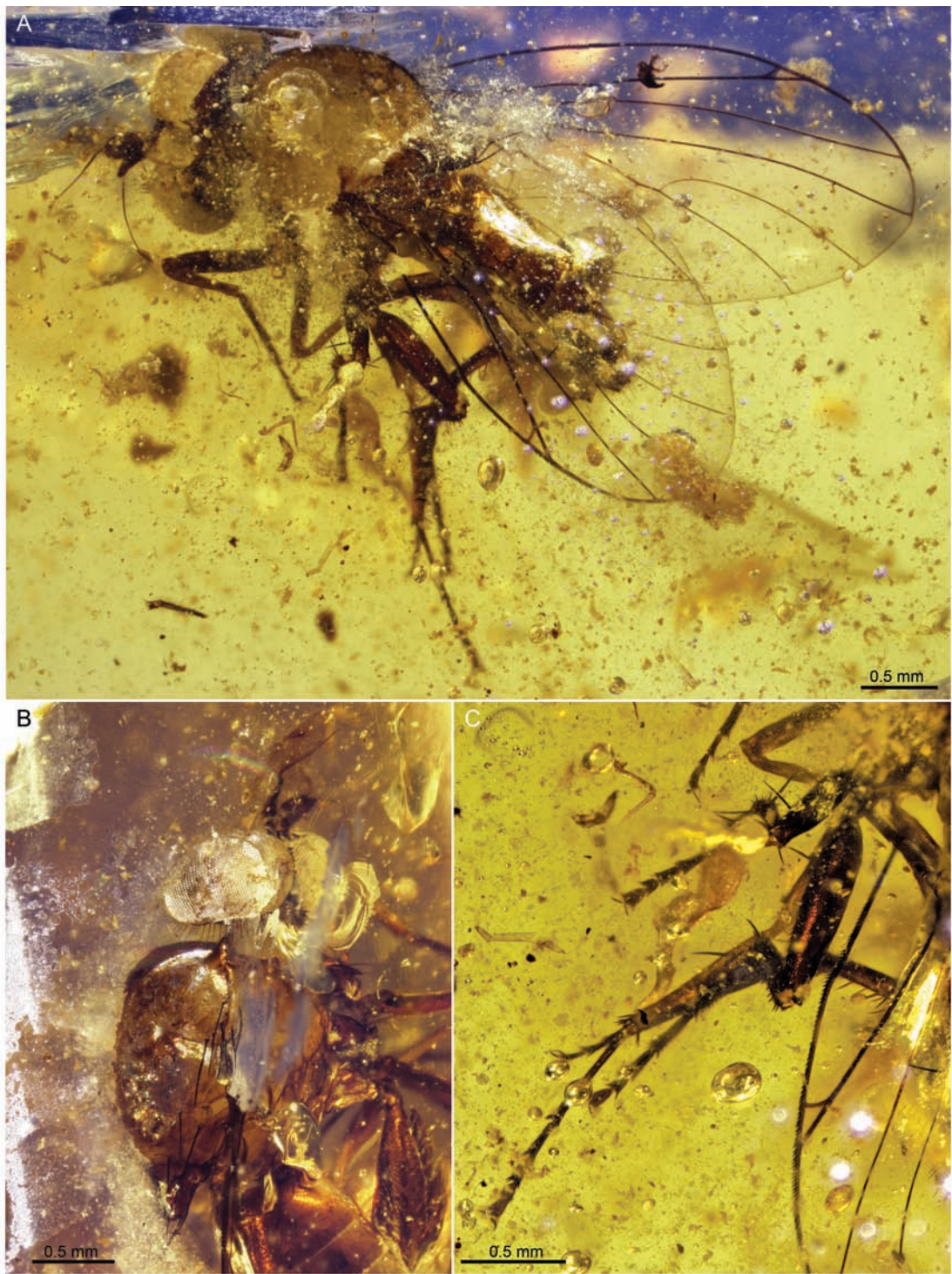


FIG. 12. *Palaeopetia terminus*, n. sp. (Ironomyiidae), holotype male in Burmese amber, AMNH Bu-SE2/6. **A.** Left lateral habitus. **B.** Right lateral view of head and thorax. **C.** Legs.

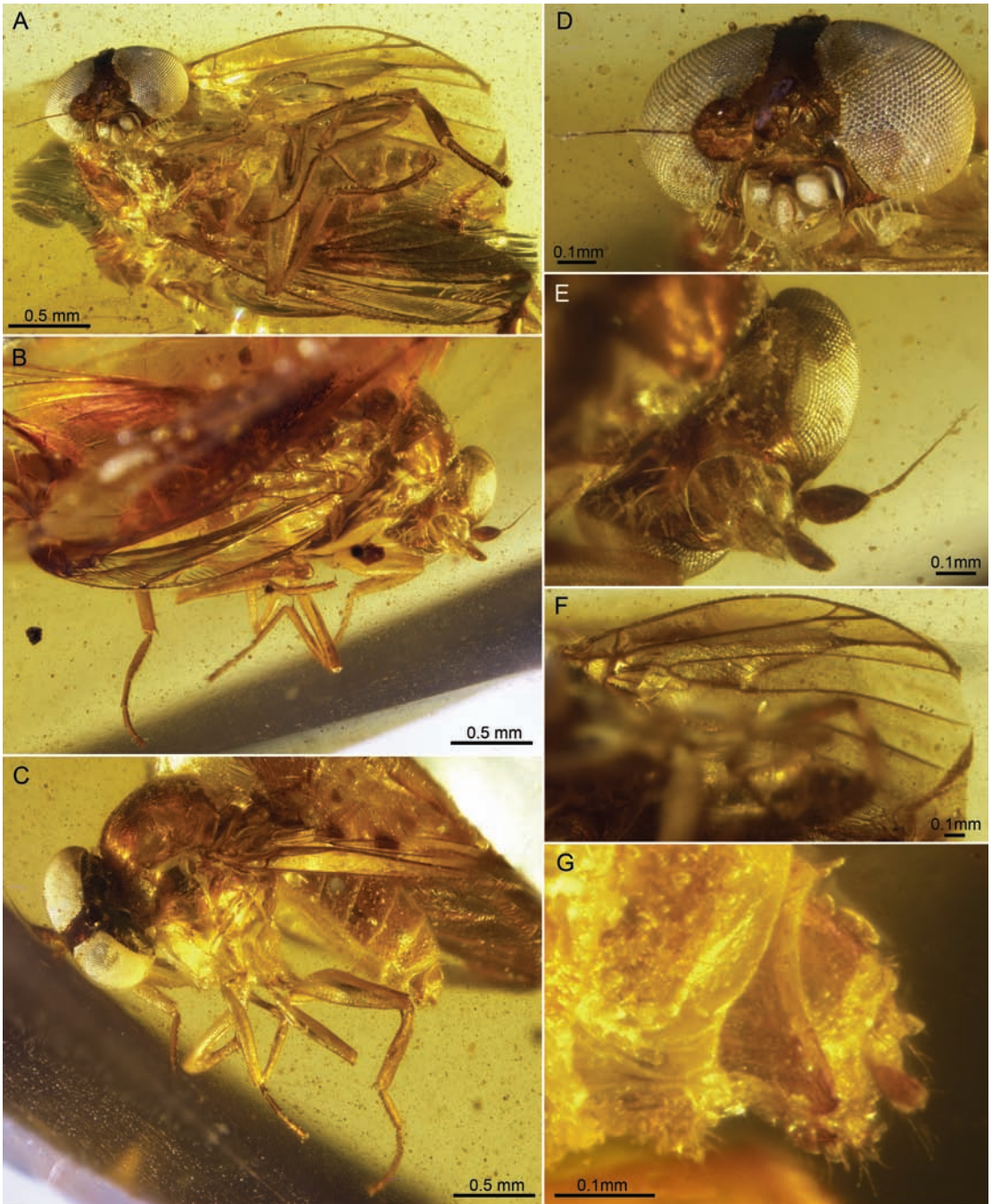


FIG. 13. *Proironia gibbera*, n. gen., n. sp. (Ironomyiidae), holotype female in Burmese amber, AMNH Bu-SE7. A–C. Habitus, in ventral (A), right lateral (B), and left lateral (C) views. D, E. Head, in frontal and ventral views, respectively. F. Wing. G. Terminalia, left lateral view.

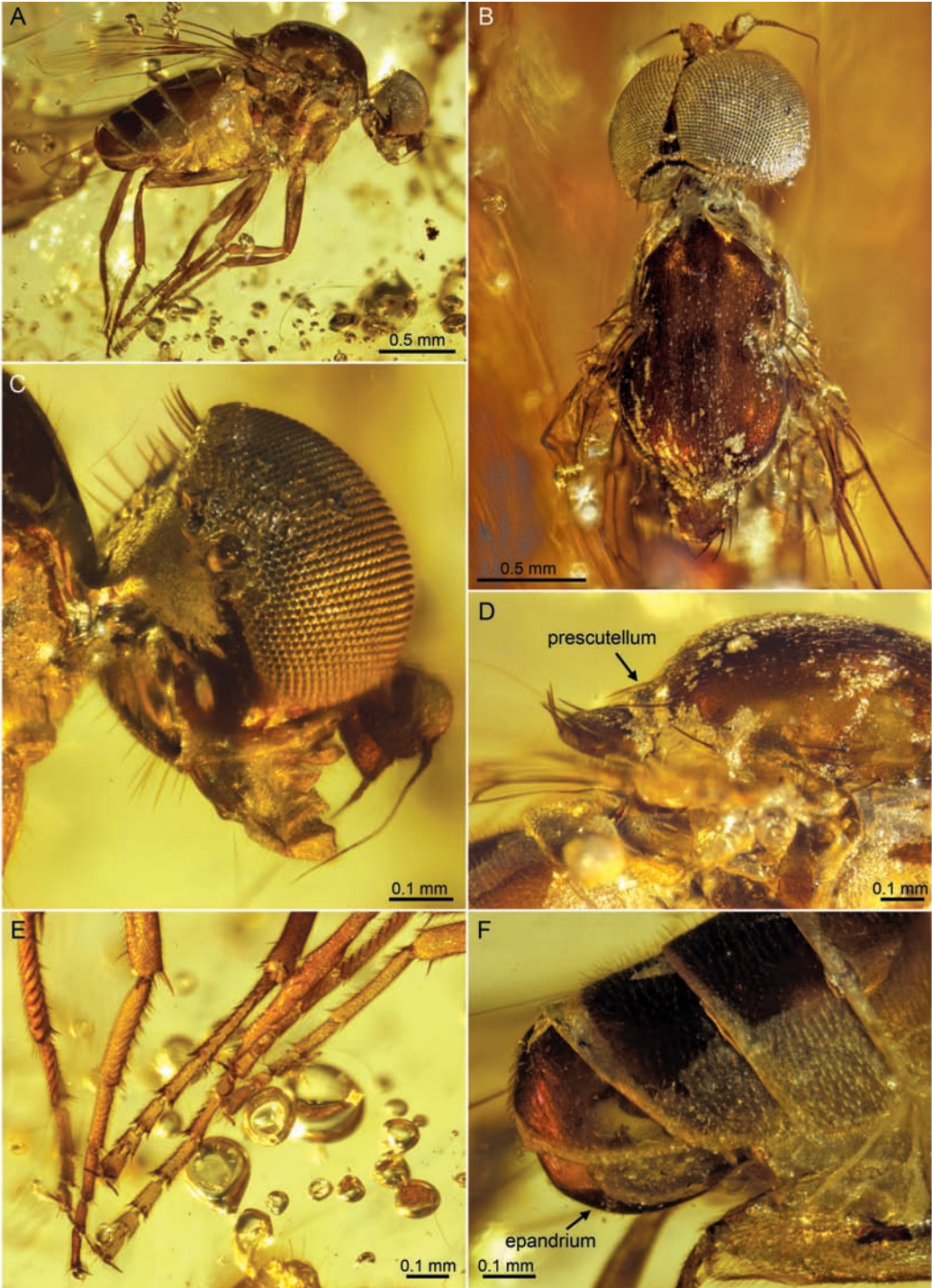


FIG. 14. *Proironia burmitica*, n. gen., n. sp. (Ironomyiidae), holotype male in Burmese amber, AMNH Bu-SE2/8. **A.** Right lateral habitus. **B.** Head and thorax, dorsal. **C.** Head, right lateral. **D.** Portion of thorax. **E.** Legs. **F.** Posterior half of abdomen.

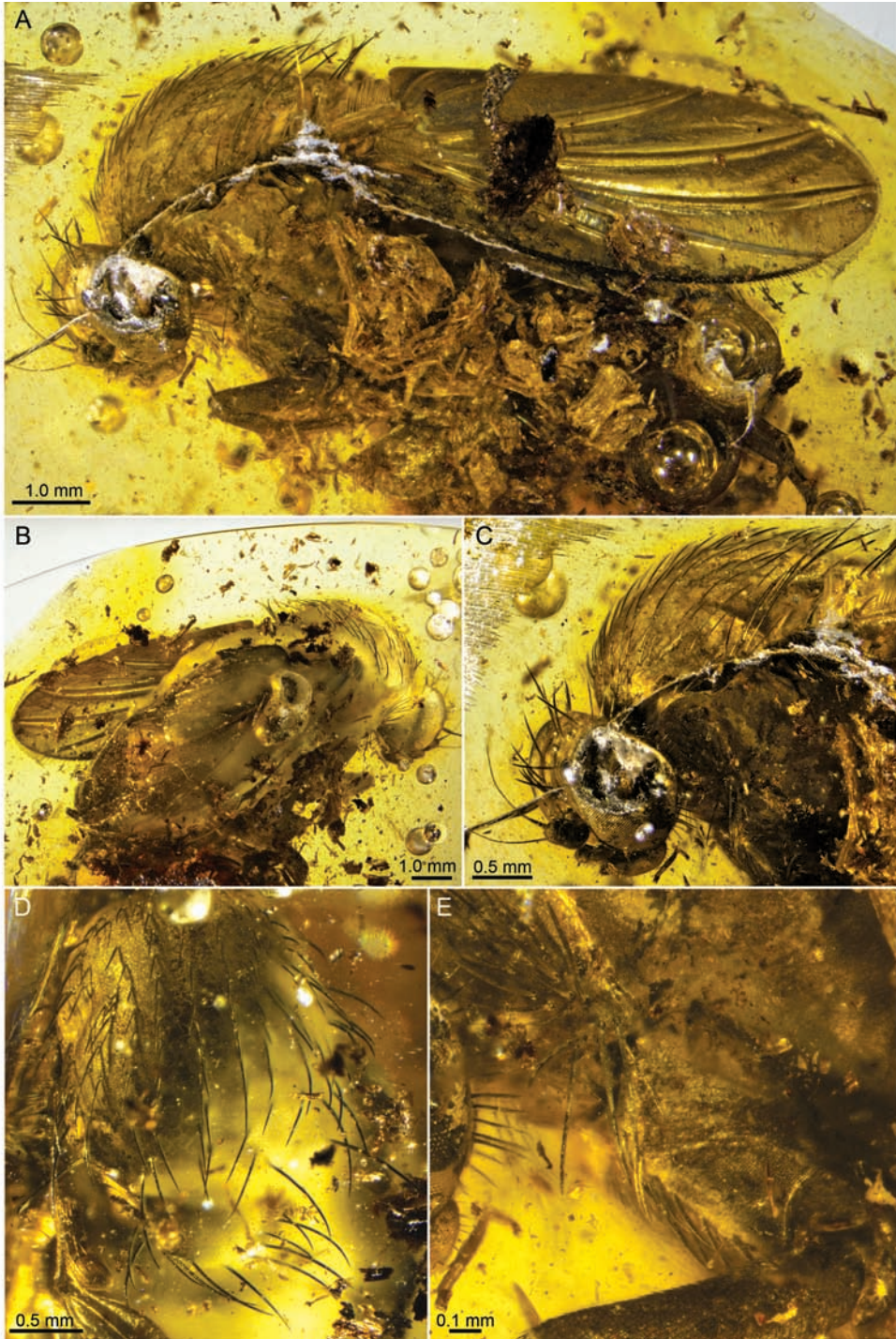


FIG. 15. *Eosciadocera setosa* Brown (Phoridae: Sciadocerinae), paratype in Baltic amber, CCHH 1358-1. **A.** Left lateral habitus; legs and pleura obscured by wood fragments. **B.** Right lateral habitus. **C.** Detail of head and anterior portion of thorax. **D.** Dorsum of thorax. **E.** Left procoxa (stridulatory file visible as a light crescent-shaped structure), and propisternum with numerous bristles.

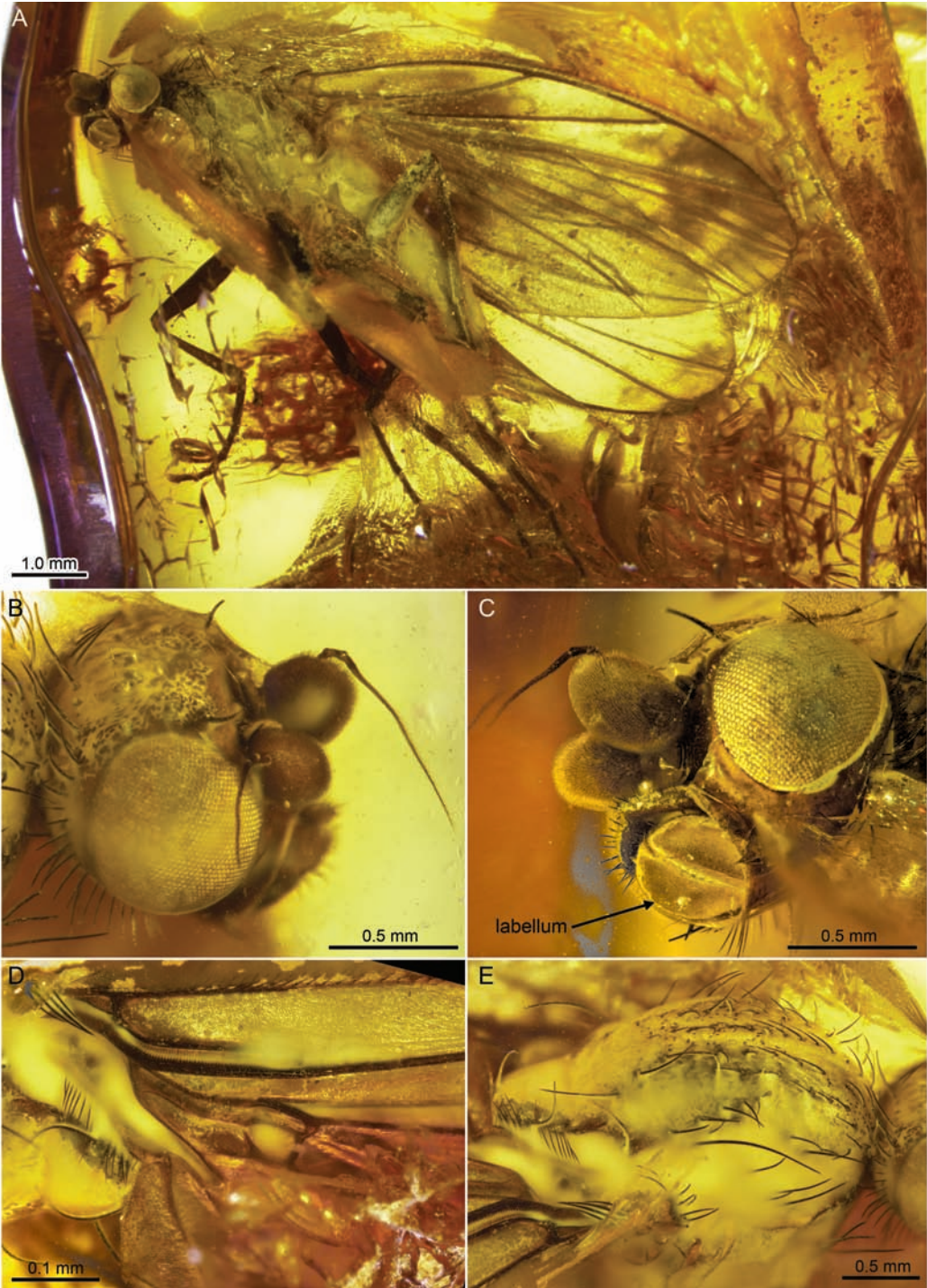


FIG. 16. *Eosciadocera pauciseta*, n. sp. (Sciadocerinae), holotype in Baltic amber, AMNH Ba-JVe565. **A.** Habitus, ventrolateral view. **B.** Head, dorsolateral view. **C.** Head, ventrolateral view. **D.** Base of wing. **E.** Thorax.

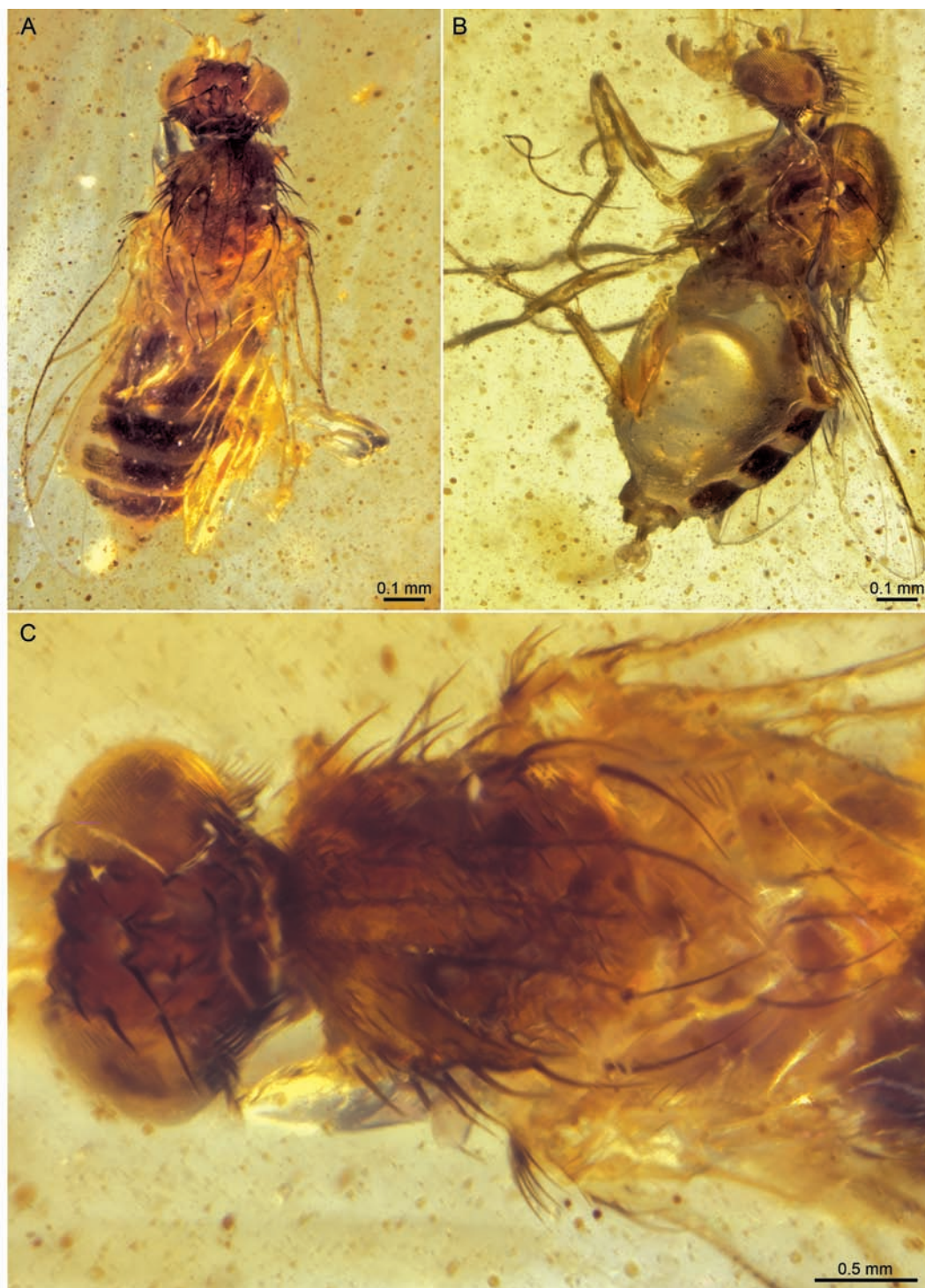


FIG. 17. *Prophora dimorion*, n. gen., n. sp. (Phoridae), paratype female in Burmese amber, JZC Bu242. A, B. Habitus, dorsal and lateral. C. Head and thorax, dorsal.

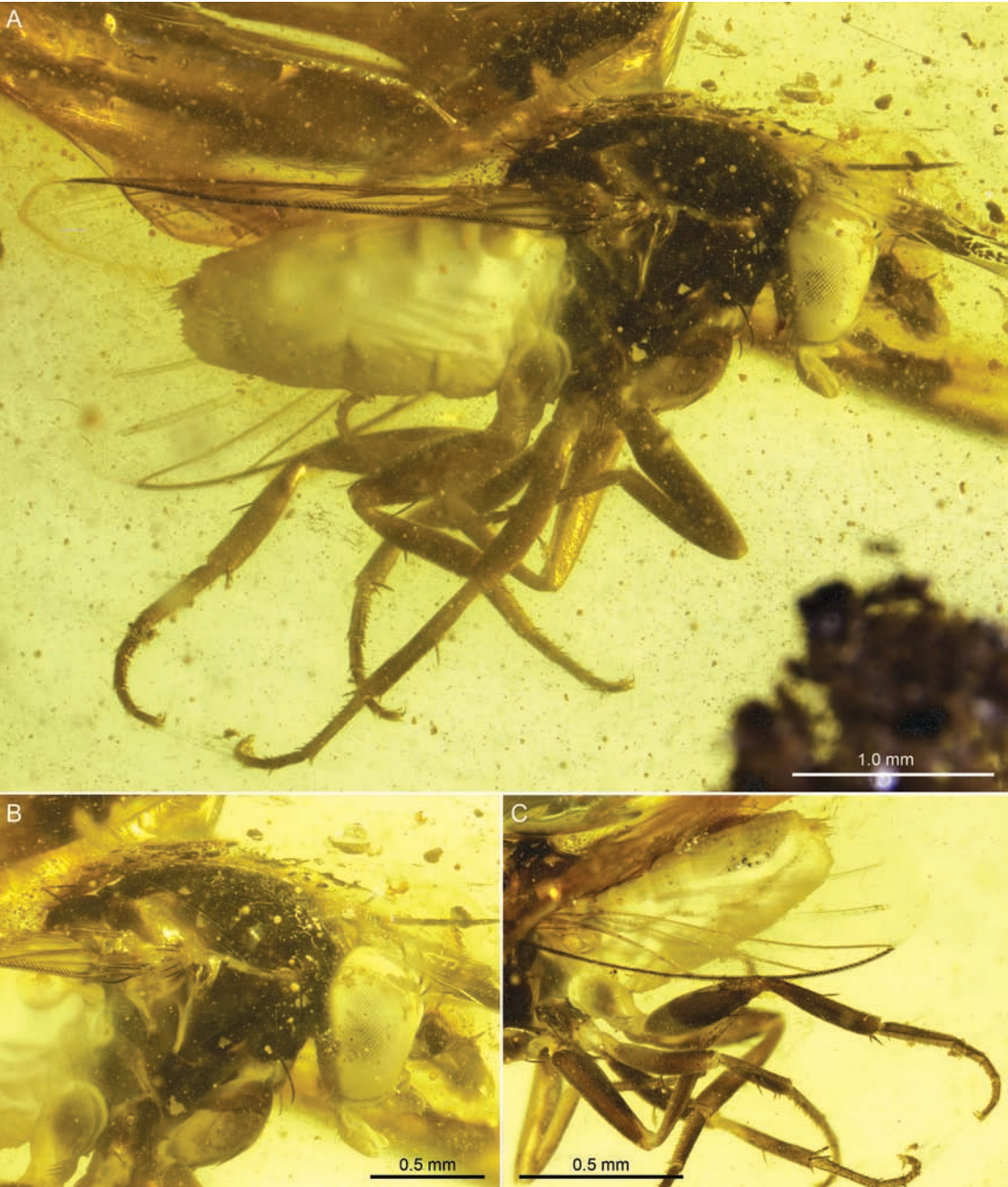


FIG. 18. *Hennigophora pria* (Grimaldi and Cumming) (Phoridae), new female specimen in Late Cretaceous amber from New Jersey, AMNH NJ-Ch1. **A.** Right lateral habitus. **B.** Head and thorax, lateral. **C.** Wing, abdomen, legs, left lateral. Legs and thorax appear to be natural coloration; light abdomen is due to milky coating.

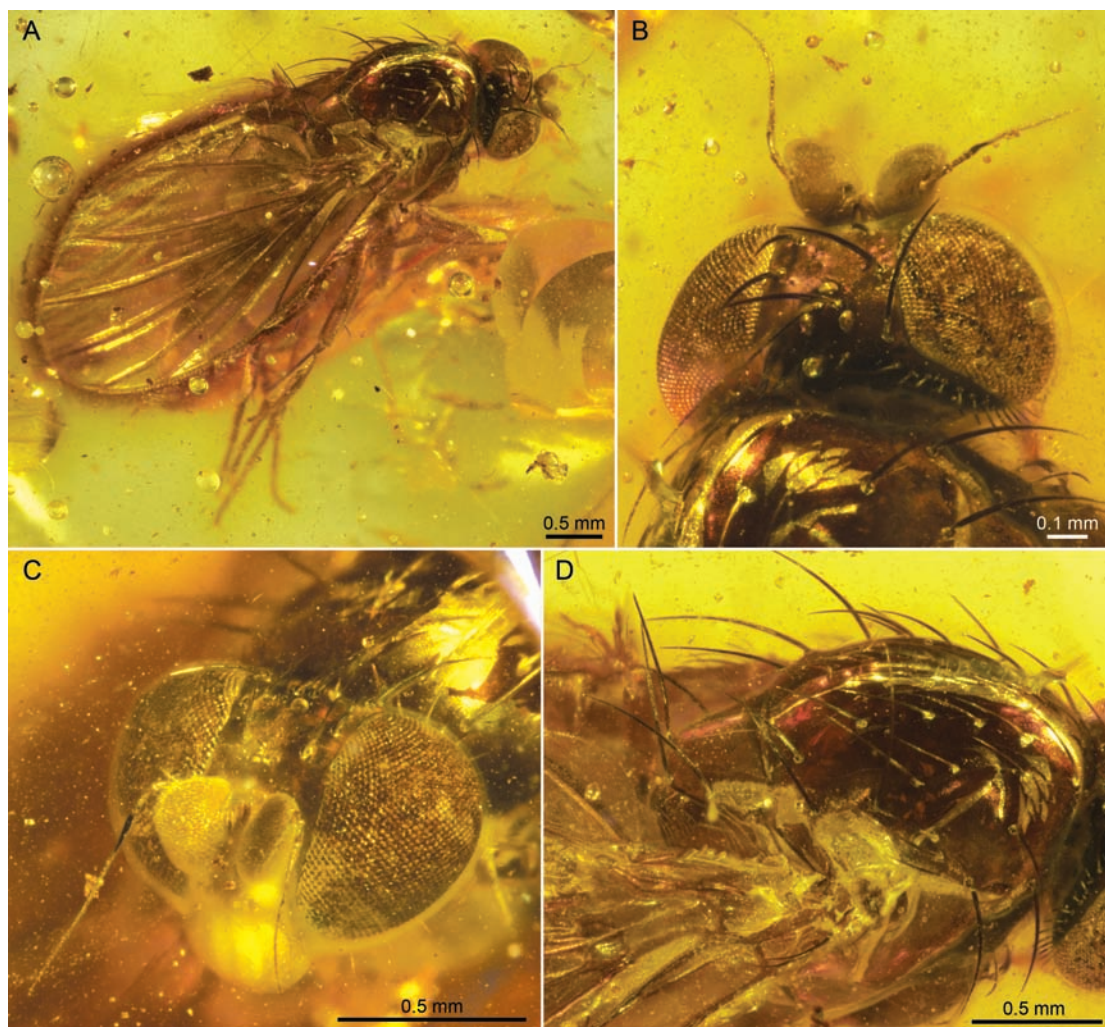


FIG. 19. *Hennigophora robusta* (Meunier) (Phoridae), male specimen in Eocene Baltic amber, AMNH Ba-JH58. **A.** Right lateral habitus. **B.** Dorsal view of head. **C.** Frontal view of head. **D.** Thorax, right lateral view.

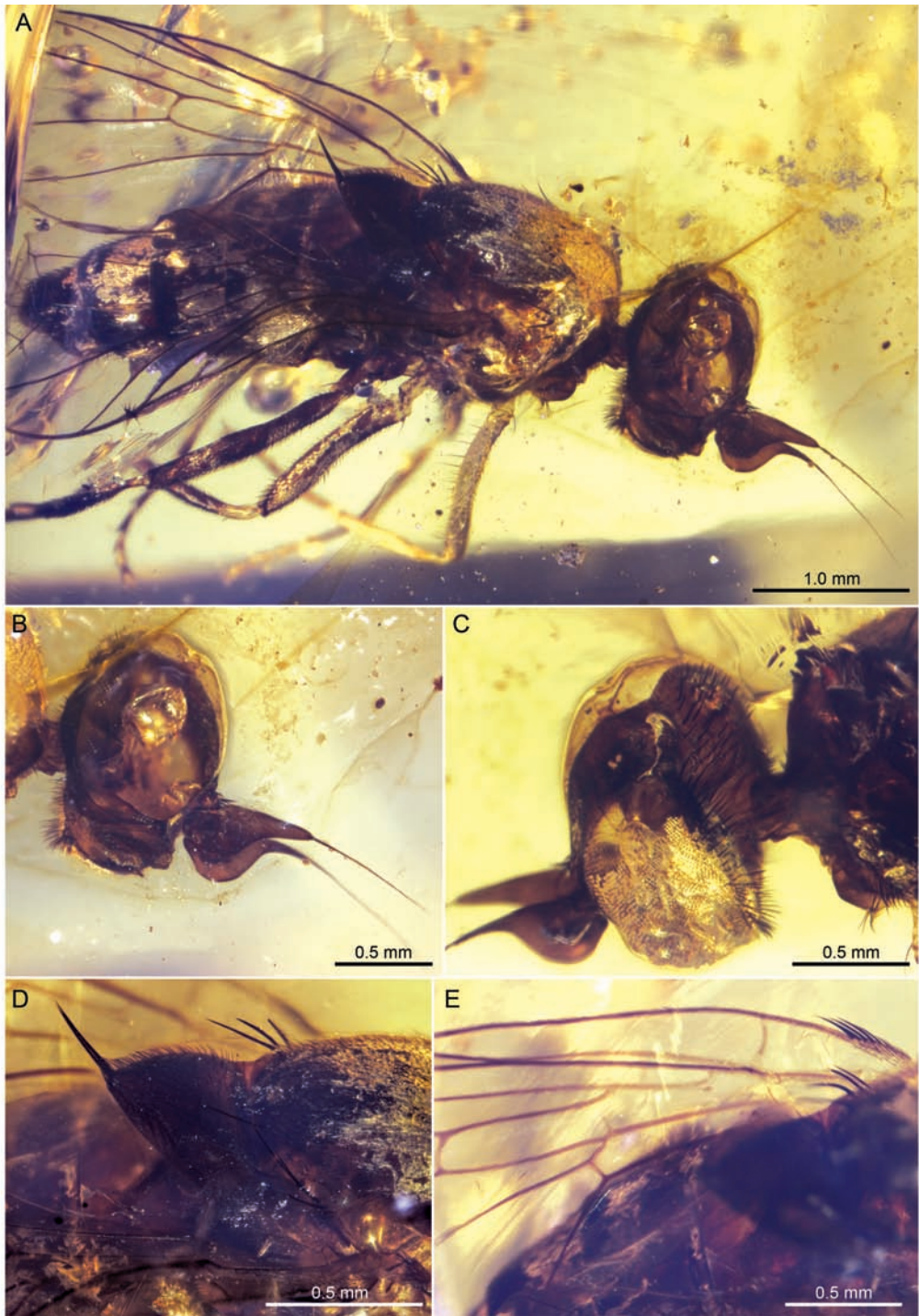


FIG. 20. *Aschizomyia burmensis*, n. gen., n. sp. (Syrphoidea), female holotype in Burmese amber, AMNH Bu-SA1 A. Habitus, dorsal lateral. B. Head, right lateral. C. Head, dorsolateral. D. Scutellum and portions of thorax. E. Basal half of wing.

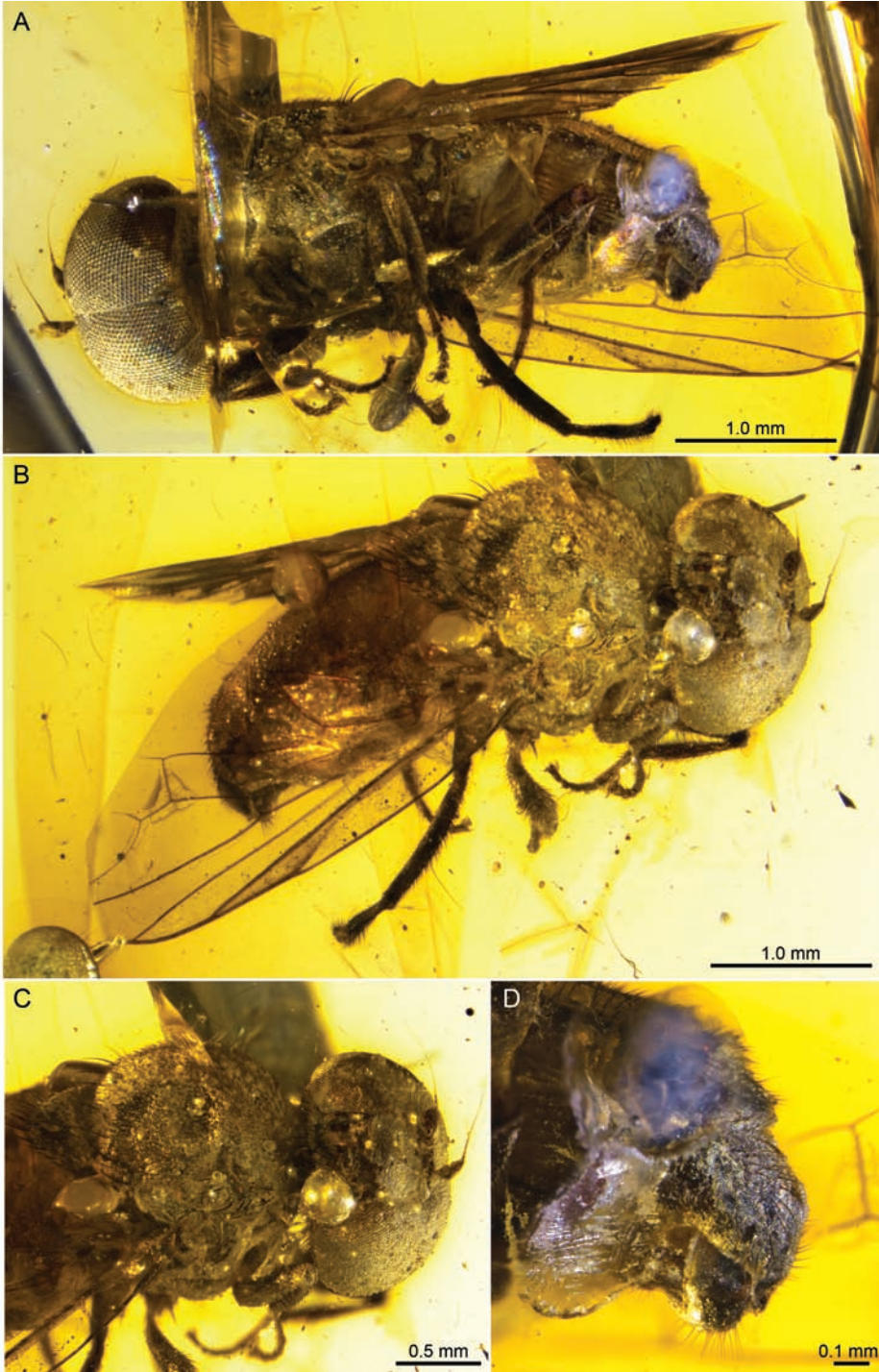


FIG. 21. *Prosyrrhus thompsoni*, n. gen., n. sp. (Syrphoidea), male holotype in Burmese amber, AMNH Bu-SE03. A. Left ventrolateral habitus. B. Right dorsolateral habitus. C. Anterior half of body. D. Detail of male terminalia, left side.



FIG. 22. Cyclorrhaphan puparium in Burmese amber, family undetermined JZC-Bu304. The large opening at the anterior end indicates the occupant had eclosed. **A.** Dorsal. **B.** Ventral.

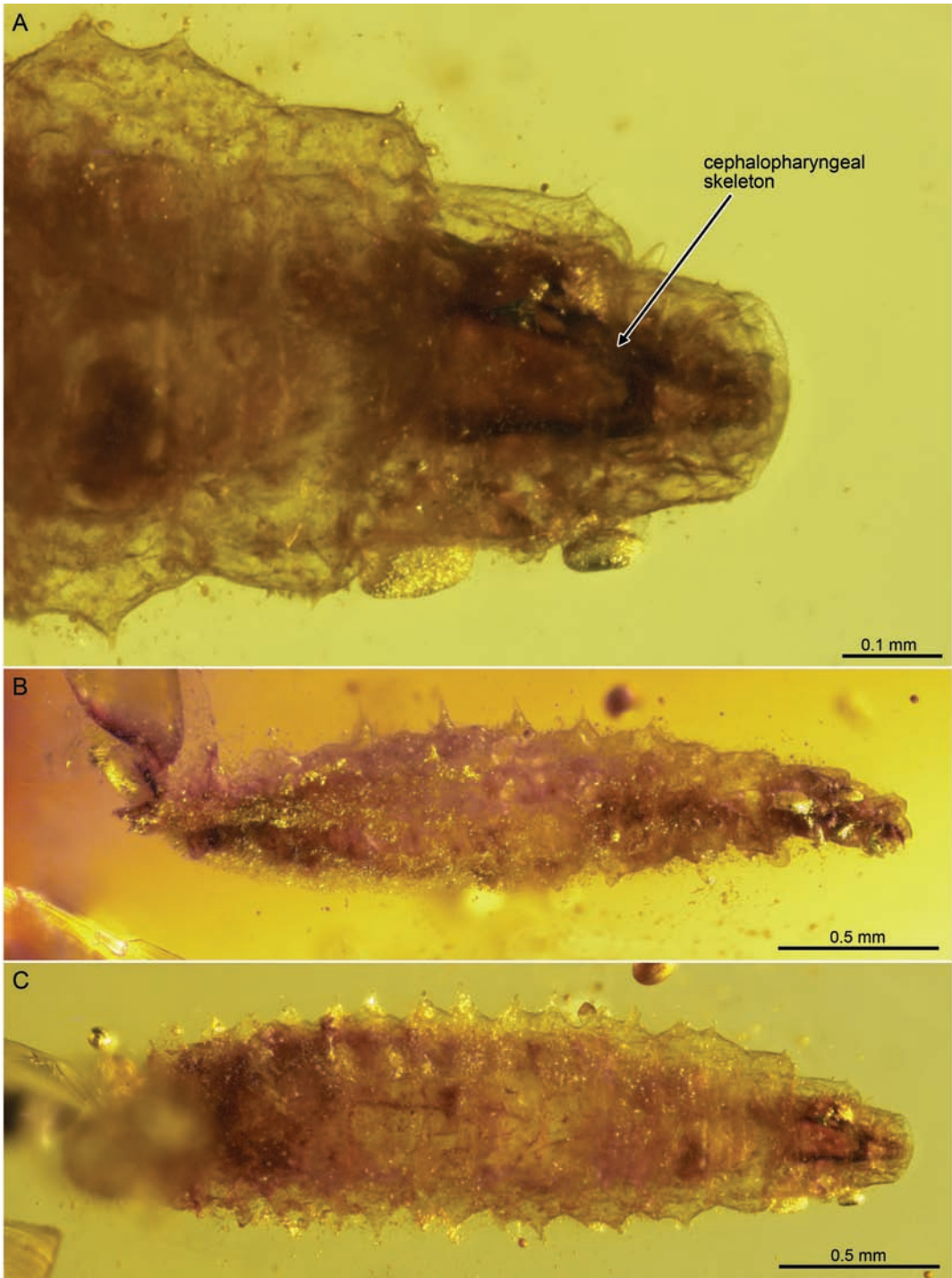


FIG. 23. Cyclorrhaphan larva in Burmese amber, probably Phoridae, AMNH Bu-1536. **A.** Anterior end, dorsal view. **B.** Left lateral habitus. **C.** Dorsal habitus.

SUPERFAMILY LONCHOPTEROIDEA

This is a group comprised of the monogeneric Recent family Lonchopteridae (*Lonchoptera* Meigen) plus four stem-group Cretaceous fossils in three extinct genera, discussed below and in Grimaldi and Cumming (1999): *Lonchopterites* Grimaldi and Cumming, *Lonchopteromorpha* Grimaldi and Cumming, and *Alonchoptera*, n. gen. The approximately 55 described species of *Lonchoptera* are gracile, yellowish to grayish, pollinose flies of moderate size. Interestingly, there are no definitive Tertiary fossils of Lonchopteridae (Evenhuis, 1994), even from the prolific Baltic amber and Florissant and Green River shale deposits, which would be immediately recognizable based on wings. The only fossils are four species from the mid-Cretaceous Burmese amber and Early Cretaceous Lebanese amber, all of which are minute flies slightly longer than one millimeter, substantially smaller than living species. A suite of features, many of them concerning the wing, indicates the close relationship of these Cretaceous genera to Lonchopteridae (fig. 24, table 1), such as:

- (1) long setae on head, including a pair of large interfrontal reclinate setae positioned very close to anterior margin of frons;
- (2) base of arista generally slightly dorsal to the apex of the basal flagellomere;
- (3) pair of large vibrissae present, although none of the fossils have the row of large, protruding setae on the oral margin;
- (4) males are dichoptic, although this is known for the fossils with certainty only in *Lonchopterites burmensis*, n. sp. (the sex is uncertain for *Lonchopteromorpha asetocella* Grimaldi and Cumming);
- (5) vein R_1 very short;
- (6) loss of crossvein dm-cu; crossvein br-m is either very small (*Lonchopteromorpha*) or absent (all other genera);
- (7) basal wing cells bm and cup are very small;
- (8) veins M_1 and M_2 form a long fork, branches of which diverge only slightly;

(9) vein C has long spinules, although most of the fossils lack the row of lateral setae on vein C.

Some of these apomorphic features, and those in table 1, are shared with Phoridae and/or Opetiidae and Platypezidae, such as the interfrontals, dichoptic male eyes and several of the vein features. Whether these characters are synapomorphic for these families will require a comprehensive phylogenetic study (see below). The fossil lonchopteroids lack some of the synapomorphies of *Lonchoptera* (e.g., setulose R and M veins; pointed wing tip), thus indicating their stem-group nature. Rather than redefining the concept of *Lonchoptera* or Lonchopteridae as more inclusive and less specific, I feel it is best to leave the three fossil genera as incertae sedis within a superfamily Lonchopteroidea (fig. 24).

The family Lonchopteridae has traditionally been accorded an isolated but uncertain position at or near the base of the Cyclorrhapha, as either near the Phoroidea (McAlpine, 1989; Woodley et al., 2009), or closer to the base of the entire Cyclorrhapha (Griffiths, 1972; Hennig, 1976; Wiegmann et al., 2010). Early Cretaceous lonchopteroids indicate that the lineage clearly diverged early in the history of Cyclorrhapha.

Alonchoptera, new genus

DIAGNOSIS: Distinguished from all living and extinct lonchopterids by the very broad, nonlanceolate wing (width $0.60\times$ length); vein C with very long spinules, R_{4+5} ending slightly beyond wing apex; arista situated apically on flagellomere I; setae on dorsum of head and thorax very long and fine; setation of head most similar to that of *Lonchopterites* (also in Lebanese amber).

TYPE SPECIES: *A. lebanica*, new species.

ETYMOLOGY: A-, from the Greek, "without," or "devoid of," and stem base from the only genus of Lonchopteridae, *Lonchoptera* ("spear winged"); in reference to the broadly rounded (versus lanceolate) wing shape.

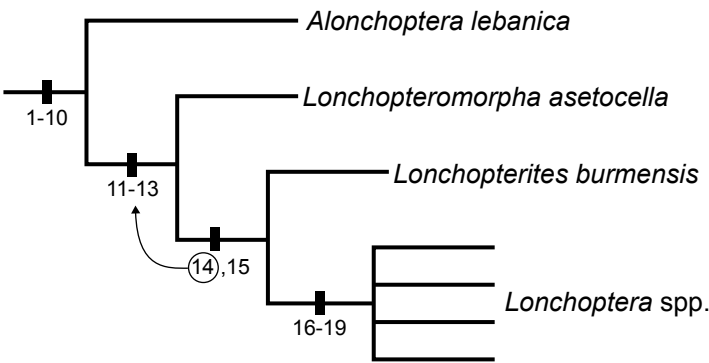


FIG. 24. Cladogram of fossil and Recent (Lonchoptera) Lonchopteroidea. Numbers refer to synapomorphies in table 1. Position of character 14 is equivocal.

TABLE 1
Characters in the cladogram for Lonchopteroidea (fig. 24)

1. Anal lobe, alula, vein A absent to highly reduced.
2. Crossvein dm-cu absent (lost).
3. Vein C with long spinules.
4. Veins M ₁ , M ₂ form long fork, diverging only slightly.
5. Cells bm, cup very small.
6. Vein R ₁ short.
7. Vein Sc very short.
8. Vibrissa present, large.
9. Large pair reclinate interfrontal setae present, usually very close to anterior margin of frons.
10. Large orbital and vertical setae present.
11. Vein R ₄₊₅ ends at wing tip.
12. Wing tip slightly to acutely pointed.
13. Arista situated preapically on basal flagellomere.
14. Male eyes dichoptic.
15. Crossvein br-m absent.
16. Veins R (at least) and usually M veins setulose.
17. Setae on oral margin large, protruding.
18. Venation sexually dimorphic: veins CuA ₂ and A ₁ joined to CuA ₁ in female.
19. Wing lanceolate/fusiform in shape, with base as well as tip narrowed.

COMMENTS: Despite the broad wing with a rounded (vs. pointed) apex, numerous features indicate a close relationship of this genus with Lonchopteridae. These features include: long costal spinules, short R₁, loss of crossvein dm-cu, short cell cup; no anal lobe or alula; long setae on the head and thorax; two pairs of scutellar setae, with the apical pair upright and cruciate. Unfortunately, the presence of interfrontals (normally located just above the antennae) and long cheek setae cannot be confirmed since fractures obscure these portions of the head.

Alonchoptera lebanica, new species

Figures 1, 25

DIAGNOSIS: As for the genus, by monotypy.

DESCRIPTION: A very small fly, body length ca. 1.9 mm; wing 0.40 mm. **Head:** Eyes well separated, red (color preserved), subcircular in lateral view, bare of micropubescence, no dorsoventral differentiation of facets (only female known). Frons: Without median furrow; inclinate/proclinate interfrontals, if present, not observable due to fractures. Ocellar setae long,

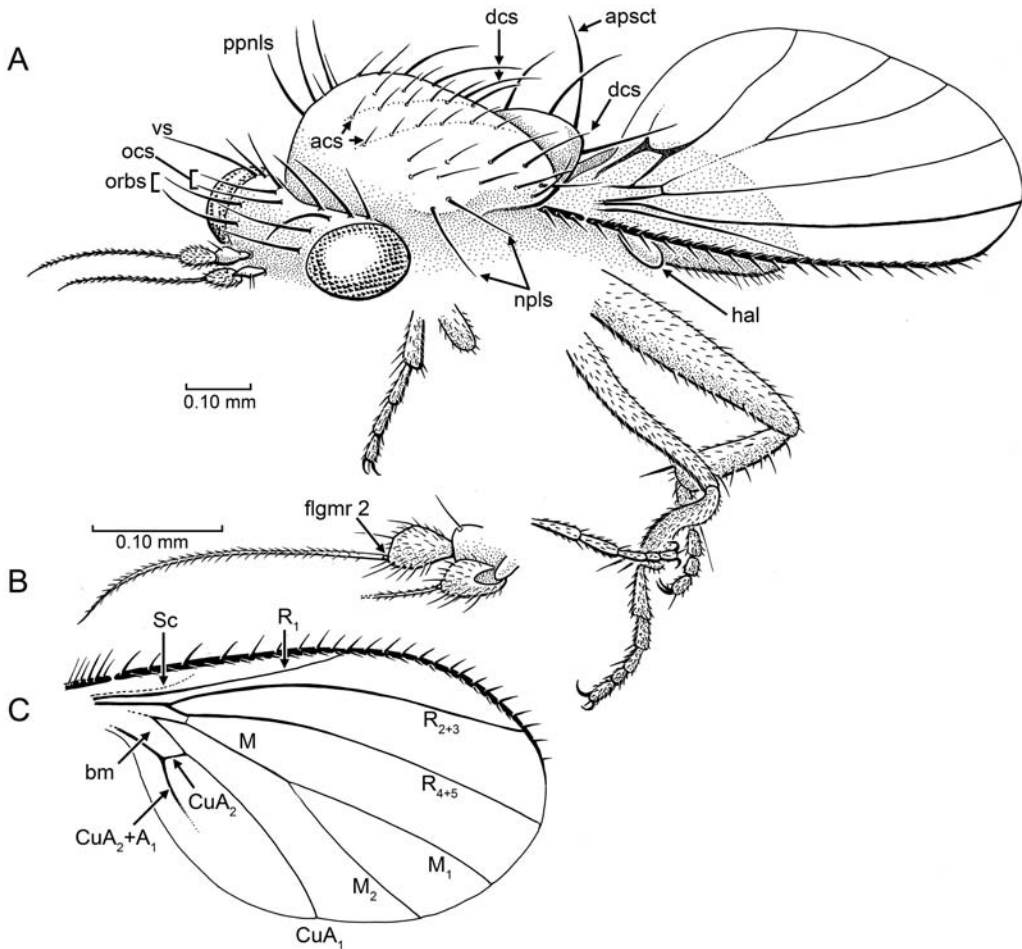


FIG. 25. *Alonchoptera lebanica*, n. gen., n. sp. (Lonchopteroidea), holotype AMNH LAE3-4, in Early Cretaceous amber from Lebanon. A. Fronto-lateral habitus (missing portions are obscured by fractures). B. Antenna. C. Wing.

fine, upright, parallel. Two pairs of long fronto-orbital setae present, upright (barely reclinate). Pair of inner and pair of outer vertical setae present; inner verticals inclinate; outer verticals prolaterocline; outer verticals longest setae on head; two inclinate setae lateral to outer vertical. No large postoccipital setae visible. Oral margin obscured, including presence/absence of oral/cheek setae. **Antenna:** Scape not observable, pedicel with single dorsal seta, conus appears to be absent (some visibility through cuticle); basal flagellomere short, length ca. 1.3×

width, setose (more so ventrally); base of arista situated terminally on basal flagellomere; basal aristomere(s) either absent or very small and unobservable; apical aristomere long, slightly more than 2× length of rest of antenna; arista setulose, length of fine branches of arista 34× greatest diameter of trunk of arista. **Mouthparts:** (completely obscured). **Thorax:** Short, broad, with numerous long setae. Acrostichals well developed, in 2 rows of 6 setae each. Dorsocentrals in two paramedian rows, two long prescutellar dcs in each row. Two supraalar

setae, 2 postalar setae; 2 long notopleural setae; presence/absence of proscutellum not determinable; scutellum with two pairs setae; apical pair long, crossed for about half their length. **Wing:** Short, broad, broadly rounded at apex; hyaline (no infusate or darkened areas) (cannot discern microtrichia). C with row of 5–6 longer prehumeral setae; vein C with row of long, spinelike setae, C ends after apex R_{2+3} ; Sc very faint, appears incomplete; very short (ends at approximately level of br-m crossvein). R_1 short, length approximately half that of wing; tip of R_{4+5} ends approximately at wing apex. Cells br and bm small; crossvein br-m very short, very close to base of wing; M_1 - M_2 forked, branches end on trailing edge of wing; cell cup absent; anal lobe highly reduced, alula apparently absent. **Legs:** Relatively long, with some longer setae. **Abdomen:** Hardly visible in unique specimen.

SPECIMENS EXAMINED: Holotype, Female, AMNH LAEIII-4, coll. Antoni Estephan, near Bcharré, Lebanon (Early Cretaceous). In the AMNH. Specimen is complete but obscured in many parts by numerous internal fractures in the amber, despite having been vacuum embedded in EpoTek resin.

ETYMOLOGY: In reference to the country of origin.

Genus *Lonchopterites* Grimaldi and Cumming

Lonchopterites Grimaldi and Cumming, 1999:

82. Type species: *L. prisca* Grimaldi and Cumming, 1999 (Lebanese amber).

DIAGNOSIS: (slightly revised, in italics): Antenna with arisal base situated terminally (*L. prisca* Grimaldi and Cumming) or *slightly dorsally* (*L. burmensis*, n. sp.); arista 2-articled, basal one minute, ringlike. Head with large pair of reclinate interfrontals; large pair of laterocline fronto-orbitals; ocellar setae large, *inside* (*L. prisca*) or *outside of triangle* (*L. burmensis*, n. sp.). Wing apex faintly pointed; vein C with large spinules; R_{4+5} ending at tip of wing; R_{2+3} and R_{4+5} divergent at base of wing; M_1 and M_2 diverge

near middle of wing; crossveins r-m and dm-cu lacking; anal lobe present, but small; *anal vein short, incomplete*. The genus is defined largely on the basis of features that are symplesiomorphic for the Lonchopteroidea.

TYPE SPECIES: *L. prisca* Grimaldi and Cumming.

Lonchopterites burmensis, new species

Figures 2, 26

DIAGNOSIS: Distinguished from the type species by the ocellar setae lying outside of the ocellar triangle; lack of inner vertical setae; base of arista slightly dorsal to apex of basal flagellomere (vs. on apex); face with smaller pair of setae lateral to vibrissae; vein R_1 slightly shorter ($0.28\times$ wing length, vs. $0.40\times$). Based on unique male specimen.

DESCRIPTION: **Head:** [(Seen largely in just dorsal view), total width ca. 280 μm . Eyes of male dichoptic, widely separated (150 μm near middle of frons); mesal margins diverging posteriorad; dorsoventral facets undifferentiated; eye completely bare, fine setae lacking. Frons: Broad, without median furrow; pair of well-developed inclinate interfrontals present, bases very close to bases of antennae; distance between interfrontals approximately equal to that of ocellars. One pair of fronto-orbital setae present, slightly laterocline and reclinate; setal base very close to inner margin of eye. Interfrontal, fronto-orbital, and ocellar seta approximately equal in length. Ocellar setae reclinate and slightly laterocline, bases situated lateral to anterior ocellus, not within ocellar triangle. Inner vertical setae apparently lacking; outer vertical setae laterocline, length ca. $1.3\times$ that of fronto-orbital. Postocellar setae lacking. Row of 3–4 stiff, inclinate postoccipital setae present on each side. Pair of large, projecting facial vibrissae present; vibrissae slightly larger than orbitals; slightly smaller seta lateral to vibrissa. **Antenna:** Porrect; scape small, cylindrical, bare; pedicel slightly conical, asymmetrical, distal rim with fine setulae (especially mesal

margin), pedicel without conus (visible through cleared cuticle); basal flagellomere short, slightly asymmetrical and short, with fine setulae; base of arista situated slightly dorsal to apex of basal flagellomere; arista with two articles, basal one minute and ringlike, arista overall long and virtually bare, very faintly microsetulose, length ca. 220 μm (base of antenna 100 μm). **Mouthparts:** not visible; oral margin protruding slightly. **Thorax:** Fairly long, ca. 0.50 mm, ca. 0.30 mm at deepest portion; dorsally (scutum) bristly, flattened posteriad; subscutellum and anatergite not exposed. Acrostichals and dorsocentrals long, suberect, in rows extending entire length of scutum; acrostichals in two rows of 9–10 setae each (anterior setae thicker); row of slightly longer dorsocentrals lateral to this, posterior dorsocentrals more than 2 $\times$ length of anterior ones. Pleural area obscured, sutures not visible, devoid of setae. Postpronotal lobe with 3 fine, long setae; notopleural area with 2 long, fine setae. Prescutellum absent; apex of scutellum slightly upraised; two pairs of scutellar setae, one apical pair (upright and cruciate), one subapical pair. **Wing:** Fairly slender, width 0.42 $\times$ the length, length 0.85 mm, apex slightly pointed; overall faintly fuscous, membrane entirely covered with minute microtrichia; no pterostigma. No setae on any veins except C; large prehumeral costal seta absent. Costal vein terminating at apex of R_{4+5} , having row of ca. 25 long spinules on leading edge, no setae or spinules on lateral surface. Sc short, apically evanescent. R_1 very short, 0.28 $\times$ the wing length; R_{2+3} slightly sinuate, 0.82 $\times$ length of wing; R_{4+5} ends at pointed apex of wing, this vein distinctly thicker than others; M veins very faint, forked, length of fork 0.52 $\times$ length of wing, stem of fork very faint, grading basally to nebulous; CuA_1 complete, reaching wing margin, slightly curved; cell bm not apparent, cell cup faint (M margin nebulous); vein A_1 present but incomplete. Crossvein br-m, bm-cu, and dm-cu absent; anal lobe present but small, with marginal fringe of ca. 12 fine, long setae; alula absent. **Legs:** Male protarsomeres lacking denticles; metatarsomeres lacking rows of pali-

sade setae; pulvillus well developed, empodium setiform; metabasitarsomere slightly expanded in width, broader than any other tarsomeres, slightly shorter than metatarsomere 2. Apex of tibia with pair of short, stout, curved, spinelike setae on ventral margin; dorsal margin with erect, fine preapical seta. **Abdomen:** Abdominal muscle plaques apparently absent; spiracles not observable; six large tergites visible (including epandrium); segmentation of basal tergites not visible. **Male Terminalia:** Well developed, ventroflexed; cercus terminal; epandrium tucked ventrally, with comb of ca. 10 fine setae on medial margin; two rows of setae forming basketlike structure; surstylus not visible (possibly absent). Phallus short, terminal, spinelike. **Female Terminalia:** Unknown.

SPECIMENS EXAMINED: Holotype, male, AMNH Bu-SE15, from mid-Cretaceous of northern Myanmar, Kachin Province. Deposited in AMNH. In excellent condition.

ETYMOLOGY: In reference to the source country.

FAMILY LONCHOPTERIDAE

Genus *Lonchoptera* Meigen

Lonchoptera Meigen, 1803: 30.

DIAGNOSIS: Very distinctive gracile, bristly, yellowish to grayish pollinose flies with lanceolate wings and having the following derived features: Male dichoptic; bristles on head long and thick, including long pair of reclinate interfrontals situated very close to anterior margin of frons; vibrissa large, gena with row of 4–5 large, protruding setae; arista preapically dorsal; thorax elongate and shallow, with scutum flattened posteriorly and scutellum near middle of notum, postscutellum very exposed (see Morphology section above for details); tibiae with bristles; male protarsus with ventral denticles. Pretarsus with empodium putatively absent (Klymko and Marshall,

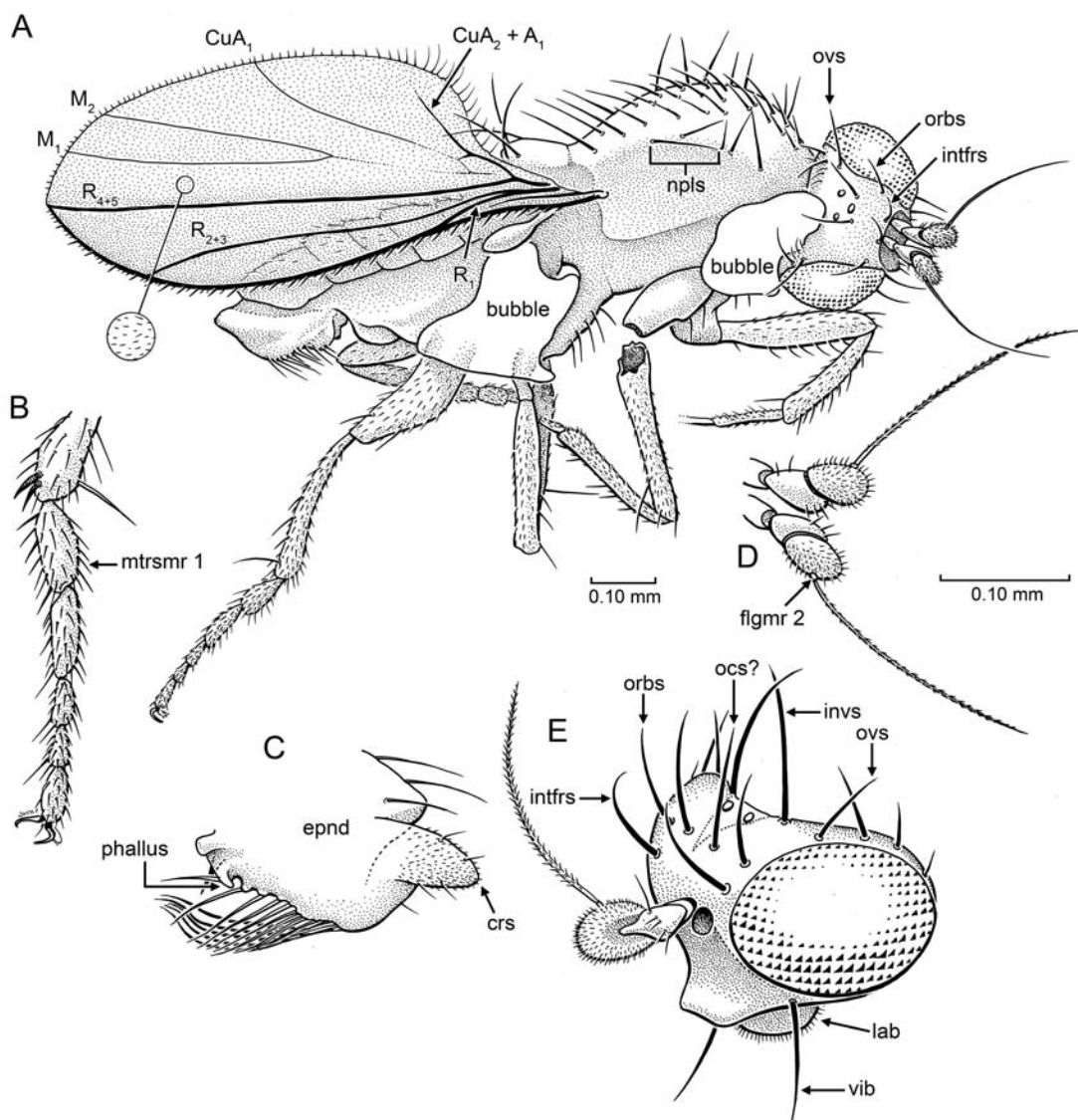


FIG. 26. *Lonchopterites burmensis*, n. sp. (Lonchopteroidea), in mid-Cretaceous amber from Myanmar. A–D. holotype male AMNH Bu-SE15. A. Lateral habitus. B. Right metatarsus. C. Terminalia, left lateral view. D. Antennae, dorsal view. E. Head, paratype JZC Bu-1578.

2008) (SEMs I've made of *L. bifurcata* indicate the empodium may be highly reduced). Wing narrow, lanceolate, apex narrowly pointed, most veins with row of large setulae (except usually R_{2+3}); R_{2+3} – R_{4+5} converge very close to wing tip; R_1 very short; venation dimorphic, with female having A_1 + CuA_2 looped and api-

cally meeting CuA_1 ; crossveins dm-cu and r-m absent. Abdomen with tergites I and II fused; spermathecae unsclerotized; surstyli absent.

TYPE SPECIES: *L. lutea* Panzer, 1809, by subsequent designation.

COMMENTS: Taxonomy on the approximately 70+ species in the genus has been by

regional treatments (Systema dipteriorum, 2013). The genus is probably native to the Palearctic, Oriental, Afrotropical, and Nearctic regions, the presence of *Lonchoptera bifurcata* (Fallén) in Australia and South America almost certainly representing introductions (Klymko and Marshall, 2008). The distribution of most native species is boreal, restricted to higher latitudes and higher altitudes for more southerly occurrences.

Lonchoptera bifurcata is very common in disturbed habitats throughout the world, particularly grassy, open, even landscaped areas. The species has particular significance in being one of few parthenogenetic Cyclorrhapha. Amongst over 2500 Nearctic specimens examined by Klymko and Marshall (2008), for example, all were females, suggestive of obligate parthenogenesis in North America; the seven known males are all European records, where parthenogenesis is obviously facultative though sex is very rare. The mechanism of parthenogenesis was reported by Stalker (1956) and Ochman et al. (1980) (under the junior synonymic name *L. dubia* Curran). Stalker identified four clones based on karyotypes and Ochman et al. (1980) identified nine in the Rochester, New York, area based on isozymes, so some of the chromosomally defined clones have surely diverged by further point mutations. It would be interesting to use DNA sequences to identify further clonal diversity and to determine whether the North American clones are monophyletic. *Lonchoptera bifurcata* is diploid ($2n = 4$), and its parthenogenesis is considered a result of chromosomal abnormalities, reflected by the fact that approximately 25% of the eggs do not develop (Stalker, 1956). Interestingly, the other species of *Lonchoptera* (all bisexual) that have been examined have metaphase $2n = 6$. These obligately bisexual species are more restricted in distribution and habits; larvae where known are saprophagous, and some species are associated with seepages (reviewed in Klymko and Marshall, 2008).

FAMILY PLATYPEZIDAE

Platyppezidae is a small family of only about 250 Recent species worldwide, most of which are quite rare, represented in museum collections by only a few specimens. In an intensive survey of a montane tropical forest in Costa Rica, for example, among the 100,000 or so specimens processed and more than 4200 fly species found, none were Platyppezidae (Brown et al., 2018; Borkent et al., 2018). Systematics of the group is well established, with major contributions to the world fauna by E.L. Kessel and by P.J. Chandler (e.g., Chandler, 1994; 2001). Chandler (2001) presented a comprehensive phylogenetic scheme for the genera based on adult and larval morphology and reviewed the biology and natural history of Platyppezidae in detail. Those genera whose hosts are known mostly breed in fleshy macrofungi, especially mushrooms; *Agathomyia* forms galls in bracket fungi. Larvae are stout, broad, somewhat flattened, with each segment usually having pairs of tubercles (lateral pairs can be annulated, fringed, or otherwise elaborate in some taxa). Males are holoptic, have a larger anal lobe, and they swarm, which is how many species are found. The striking color patterns—commonly with iridescent, reflective patches on a velvety black or brown cuticle—are clearly used for signaling while swarming.

As presently recognized (Chandler, 2001) there are four subfamilies: the basal Microsaniinae plus Melanderomyiinae, and two sister groups that comprise most of the species, Calomyiinae + Platyppezinae. The Palearctic genus *Opetia* Meigen is now placed in a separate family, Opetiidae, along with the recently discovered Chilean genus *Puyehuemysia* Amorim et al. (2018). Within Microsaniinae, the worldwide genus *Microsania* Zetterstedt is well known for being attracted to smoke (reviewed in Chandler, 2001; see also Klocke et al., 2011), although the breeding sites of these flies remain unknown. Melanderomyiinae is monotypic, consisting of *Melanderomyia kahli* Kessel from eastern North America, which breeds in stinkhorn fungi (Phal-

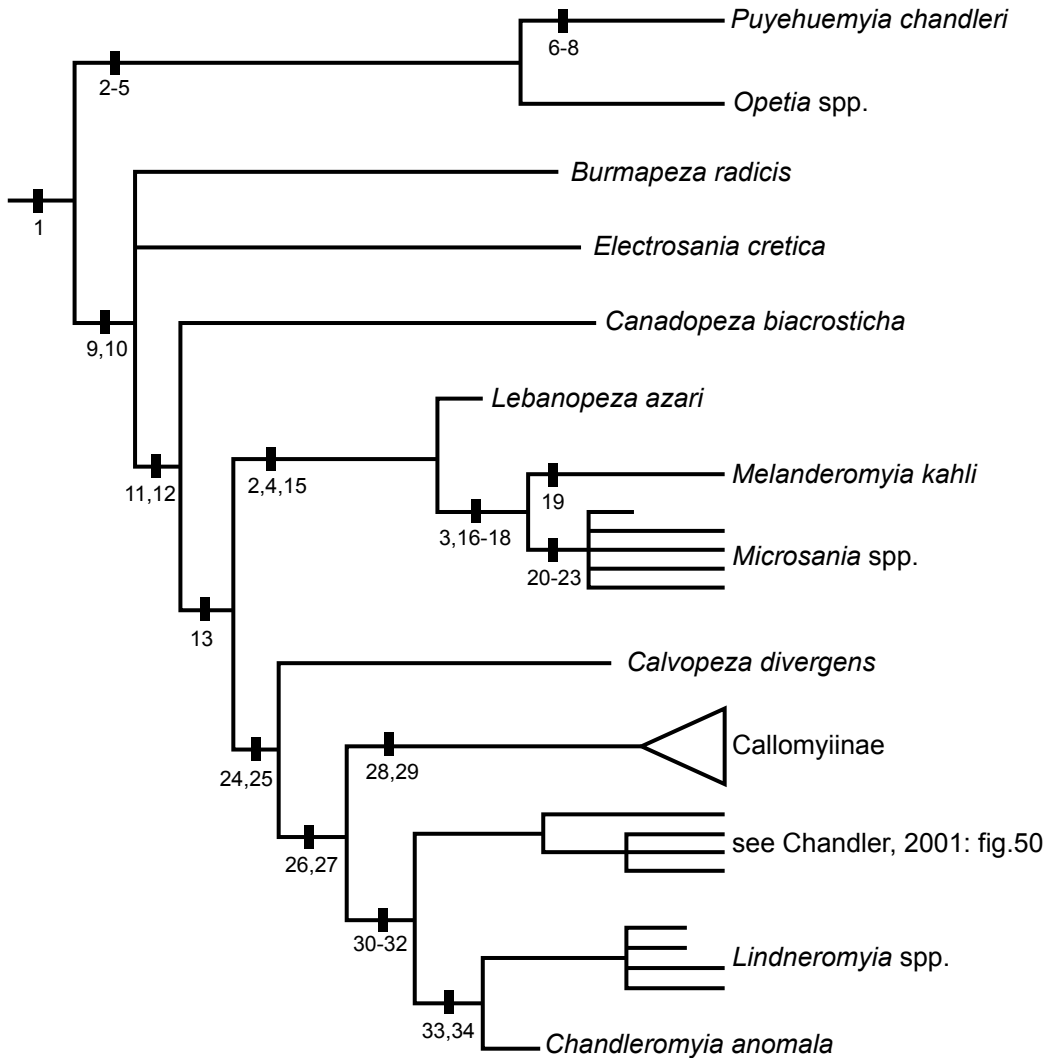


FIG. 27. Cladogram of fossil and some Recent taxa of Platypezidae. Numbers refer to synapomorphies in table 2. For characters within Callomyiinae and Platypezinae, see Chandler, 2001.

laes). Chandler (2001) proposed six morphological characters to link *Microsania* and *Melanderomyia*; the molecular phylogeny of Tkoč et al. (2017) proposed that *Melanderomyia* is the sister group to Callomyiinae plus Platypezinae. In most other respects, though, the phylogenetic relationships in both studies agree.

Although Platypezidae are uncommon as fossils, there appears to be a significant, extinct phylogenetic diversity of these flies, especially from

the Cretaceous. In fact, Mostovski (1995a) reported a surprising diversity and abundance of compression-fossil Platypezidae from several Cretaceous sites in Eurasia, most specimens of which I have restudied (these are housed in the Paleontological Institute, Moscow). Zhang (1987) described compression-fossil Platypezidae from China (originally reported as Jurassic, now known to be Early Cretaceous). As Mostovski (1995b) mentioned—which I can confirm here for several

TABLE 2
Characters in the cladogram for Platypezidae (fig. 27)

1. Wing shapes sexually dimorphic, male with large anal lobe.
2. Sc vein short, less than 0.3× wing length.
3. Cell cup very small, barely extended beyond apex of cell bm.
4. Anal lobe of female very narrow.
5. Crossvein dm-cu (cell dm) absent.
6. Aristal portion of antenna thick, 3-articled.
7. Terminal segment of female abdomen piercing.
8. Eyes setulose.
9. Vein C not circumambient, ends at apex of M ₁ .
10. Length of fork of M ₁ -M ₂ less than or equal to length of stem.
11. Acrostichals reduced to 0, 1, or 2 rows.
12. Proscutellum lost.
13. Acrostichals reduced to uniserial row or lost entirely, dorsocentrals in pair of graded rows.
14. Vein R ₁ relatively short.
15. M veins reduced (bases or branches lost, or weakly developed).
16. Basal flagellomere short, stout, subcircular or reniform.
17. Clypeus inflated, face bulging in females.
18. Setae on anal lobe and alula flattened.
19. M not forked (vein M ₂ lost).
20. Sclerotized portion of vein C ends at apex of R ₁ , thick, with large spinules.
21. M ₁ basally incomplete.
22. Pterostigma present, large, between Sc and R ₁ and distal to apex of R ₁ .
23. Metabasitarsomere 1-2 or 3 expanded, tarsomere 1 longest on leg.
24. More than one metatarsomere expanded in both sexes.
25. Small, dark, sclerotized, bifid scales on tarsi and portions of tibiae (first reported by Comstock and Comstock, 1904 [p. 474: fig. 579], contra Tkoč et al., 2016).
26. Crossvein dm-cu close to wing margin, separated by distance ≤2× length of dm-cu, often much closer) (cell dm-cu very long).
27. CuA2 straight, forming side of slender, acute triangle of cell cup.
28. Male profemur with posteroventral oxhorn seta.
29. Male metafemur with large posteroventral seta near base.
30. Metabasitarsomere short, less than length of 2+3+4.
31. Acrostichals absent.
32. Female without fronto-orbital or interfrontal setae.
33. Third metatarsomere longer than first.
34. Gena, parafacial areas bare.

in amber (i.e., *Paleopetia* Zhang)—some of Zhang’s genera are in fact Ironomyiidae, not Platypezidae. The typical preservation in these compression fossils is of isolated wings, so venation is the primary source of characters, but in exceptional circumstances there are also preserved wing microtrichia and some body features (e.g., flattened hind tarsomeres, personal obs.). Unfortunately, critical details are never preserved of acrostichals, dorsocentrals, genitalia, bifid scales and other small structures of the legs, etc., so interpretation of these compression fossils is quite limited. Until now the only platypezid in amber from the Cretaceous (Turonian: New Jersey) has

been *Electrosania cretica* Grimaldi and Cumming (1999). Chandler (2001) suggested that *Electrosania* might be an opetiid based on the numerous acrostichals (its single basal aristomere is also unique for the family), but in the cladogram of basal platypezids presented here (fig. 27), *Electrosania* is one of two basalmost stem group genera for the family. In the present work I am reporting four additional platypezid genera and species from the Cretaceous, all in amber.

Surprisingly, fossil Platypezidae have been even rarer in the Tertiary, despite the richer deposits from this geological era. Cockerell (1909, 1911) described two platypezids from the

late Eocene shales of Green River and Florissant, and the only platypezid described from the vast deposits of Baltic amber is the controversial *Oppenheimiella baltica* (Meunier), of uncertain family placement since the original description is ambiguous and the type lost. *Microsania* is newly reported herein from Baltic amber, along with two species of *Lindneromyia* in Miocene amber from the Dominican Republic.

A phylogenetic hypothesis of relationships for some extinct and basal extant genera of Platypezidae is presented in figure 27, based on 54 morphological characters (see table 2). Fossils in the phylogeny are represented only by genera preserved in amber. There is a grade of Cretaceous genera basal to Callomyiinae and Platypezinae, as well as three Cenozoic fossils in living genera (*Microsania* in Baltic amber, and two species of *Lindneromyia* in Dominican amber). Further, a stem-group genus to *Melanderomyia* + *Microsania* occurs in Early Cretaceous amber from Lebanon. The most surprising discovery is a crown-group platypezine in Burmese amber, *Chandleromyia*, n. gen.

Burmapeza, new genus

DIAGNOSIS: (female only). Acrostichals numerous, scattered, not in rows; prescutellum present, scutellum setulose; wing membrane entirely covered with microtrichia; M_1 - M_2 fork short, asymmetrical; apices M_2 , CuA_1 , A_1 + CuA_2 incomplete; crossvein dm-cu $2.5\times$ its length from wing margin. Tibiae and tarsi without bifid scales. Basal flagellomere subcircular, arista dorsal.

TYPE SPECIES: *B. radialis*, new species.

ETYMOLOGY: Referring to the country of origin, and *-peza* ("foot"), a common suffix for genera of Platypezinae.

COMMENTS: Like *Electrosania* in New Jersey amber, this is a basal, stem-group genus of Platypezidae (fig. 27), based on the numerous, scattered acrostichals; retention of a prescutellum; absence of dark, bifid scales on the legs; and metatarsi unmodified. It is placed in Platypezidae based on the C vein ending at the tip of M_1 (vs.

being circumambient) and the short M_1 - M_2 fork. The short, subcircular basal flagellomere is unusual, though not unique in Platypezidae. *Melanderomyia* and *Microsania* also have a short basiflagellomere (though usually reniform); the dorsal arista in *Burmapeza*, however, is unique within the family, a feature commonly seen in Syrphidae, Platypezidae, Phoridae, and Schizophora. *Burmapeza* can be clearly excluded from any of those cyclorrhaphan groups, and the antennal structure is considered here to be convergent.

Burmapeza radialis, new species

Figures 3, 28

DIAGNOSIS: As for genus, by monotypy.

DESCRIPTION: (female only). **Head:** Somewhat flattened anteroposteriad, with broad frontal surface. Eyes bare, occupying all of lateral surface, well separated, no differentiation of facets. Median furrow of frons, interfrontal and fronto-orbital setae not observable (due to preservation); three pairs of small, stout ocellar setae present; row short, stout, postocular setae present near posterior margin of eye. Vibrissa, genal setae absent. **Antenna:** Scape not visible, apical rim of pedicel with fine setae; arista dorsal; basal flagellomere short, laterally flattened, subcircular in lateral view; three aristomeres present, basal two minute, apical aristomere length $1.5\times$ that of basal flagellomere, with minute micropubescent. **Mouthparts:** Palp well developed, clavate; labellum barely visible.

Thorax: Scutum relatively flat dorsally. Acrostichals numerous, very fine, not in rows; 3 pairs prescutellar setae (lateralmost pair the dorsocentrals), graded row of dorsocentrals absent; 1 supraalar, 3–4 notopleurals present. Prescutellum present; scutellum relatively large, setulose on dorsal surface, posterior rim with 4 setae and smaller setulae. **Wing:** Relatively broad, short, width $0.5\times$ the length; membrane entirely covered with dense microtrichia, even in cells. Two prehumeral costal setae present; vein C with 2 long rows of thick setulae that grade to fine setu-

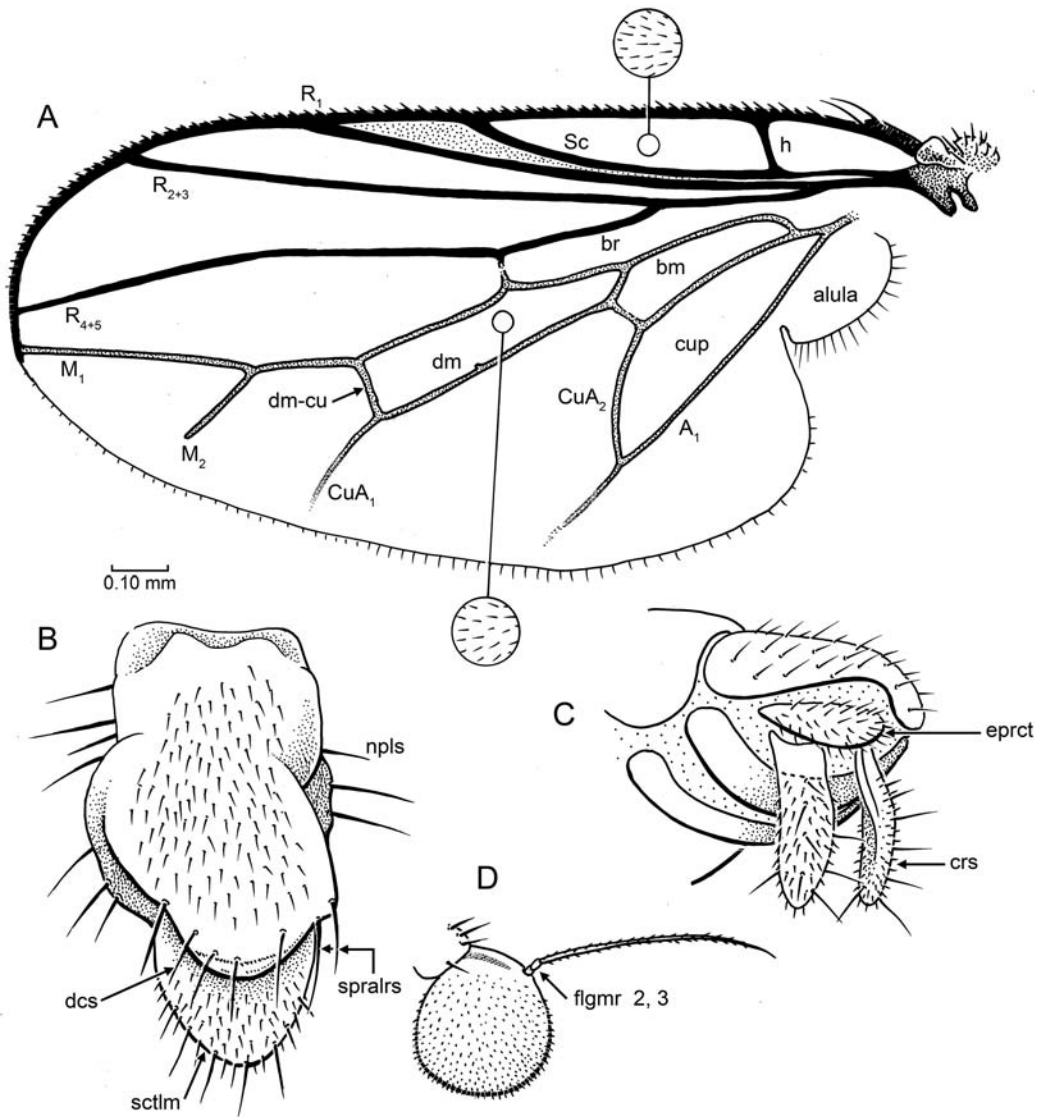


FIG. 28. *Burmapeza radialis*, n. gen., n. sp. (Platypetidae), holotype female, JZC Bu178a, in Burmese amber. A. Wing. B. Thorax, dorsal, as preserved (slightly distorted by preservation). C. Female terminalia. D. Antenna, lateral.

lae apicad; C terminates at apex of M_1 . Pterostigma absent; slight tint between Sc and R_1 . Sc long, terminates near middle of wing; R_1 long, runs very close to Sc at base. R_{4+5} terminates at tip of wing, slightly deflexed in middle posteriad. Cells rm and bm complete; crossvein dm-cu $2.5\times$ its length from wing margin; M_1 - M_2 fork asymmetrical (M_1 branch longer, complete),

apex of M_2 abruptly incomplete; tips of CuA_1 , CuA_2 + A_1 incomplete (gradually faded). Cell cup large, CuA_2 curved. Anal lobe and alula well developed. **Legs:** Relatively unmodified, generalized. Femora stoutest and longest podomeres, especially metafemur; metatibia slightly curved femorad, with apical circlet of 5 stout, short setae. Legs without dark, bifid scales on tibiae or

tarsi; with fine setulae only. Hind tarsomeres not expanded/flattened; tarsomere lengths $1 > 2 > 3 > 4 = 5$. Pulvilli and empodium not observable.

Abdomen: Relatively long, slightly flattened dorsoventrally; tergites well developed (8 visible), with fine setae; tergite 7 with 2 pairs of slightly longer setae; sternites well developed but not very visible. Cercus slender, elongate, ventroflexed.

SPECIMENS EXAMINED: Holotype, female, JZC Bu178a, the better preserved of two specimens in the same piece of amber. The other specimen (178b) is partial (sex uncertain), and is designated as a paratype. The species description is taken mostly from the holotype, but features of the head were derived from the paratype because it is better preserved.

ETYMOLOGY: From Latin ("of the root"), in reference to the basal phylogenetic position of the genus and type species within Platypezidae.

Canadopeza, new genus

DIAGNOSIS: (female only). Acrostichals in 2 even rows; 1 large pair dorsocentrals; M forked, slightly asymmetrical, M_2 very faint, almost spectral; cell dm short, dm-cu less than half the distance between M-Cu fork and wing margin; CuA_2 curved; microtrichia over entire surface of wing; legs without dark, bifid scales; metatarsus not inflated. With the exception of the spectral M_2 vein, these features are plesiomorphic for the Platypezidae.

TYPE SPECIES: *C. biacrosticha* new species.

ETYMOLOGY: Derived from Canada, the country of origin, and *-peza* (foot), a common suffix in the generic names of Platypezidae.

COMMENTS: The new genus occupies a basal position in Platypezidae (fig. 27), based on the biserial (vs. uniserial) acrostichals, lack of bifid scales on the legs, metatarsus not flattened and expanded, the short dm cell, and vein CuA_2 curved. It is interesting to note that the two Cretaceous genera known from Laurasia (Canada, New Jersey) are very basal stem groups, along with *Burmapeza*, n. gen. Otherwise, other Creta-

ceous genera, in amber from Lebanon and Myanmar, have a more derived position (fig. 27). It is possible that more basal taxa were sustained longer into the Cretaceous at higher paleolatitudes, or were relegated to higher latitudes, similar to what is seen today with *Microsania*, *Melanderomyia*, and *Platypezina*.

Canadopeza biacrosticha, new species

Figure 29

DIAGNOSIS: As for genus, by monotypy.

DESCRIPTION: (Female only). **Head:** Eyes (partially collapsed in unique specimen) female dichoptic, eyes well separated (face and frons broad), bare, no facet differentiation or emargination of eye edges. Median furrow of frons (presence/absence) not observable; at least 2 pairs short, fine fronto-orbital setae present (fracture obscures observation of anterior portion of frons); no vertical setae; postocular setae very fine, short. Ocelli slightly raised; triangle with 1 pair short, stout, upright setae. Vibrissa, genal setae absent; occiput without large setae, circlet of fine setulae around cervical connection. **Antenna:** Scape setulose; pedicel about same length as basal flagellomere, with setulae on apical rim; arista terminal; basal flagellomere small, short and conical; 3 aristomeres, basal 2 minute (basalmost one longer), apical aristomere fine, with micropubescence. **Mouthparts:** Clypeus narrow; palp of moderate size, protruding beyond oral margin. Labellum well developed, with ~7 pseudotracheae on each lobe.

Thorax: Scutum rounded but not arched. Acrostichals in 2 even rows of ~20 setae; short, decumbent, stiff. One pair of large, prescutellar dorsocentrals present, row of ~15 small, even-sized ones anterior to each; 2 rows of short, fine lateral scutal setae on each side. One short postalar seta; no supraalars; 3 short, fine notopleural setae (middle one longest). Prescutellum absent; scutellum side, short, with row of 4 pairs of setae (middle ones largest). **Wing:** Relatively short and broad, appears entirely hyaline (any infuscation

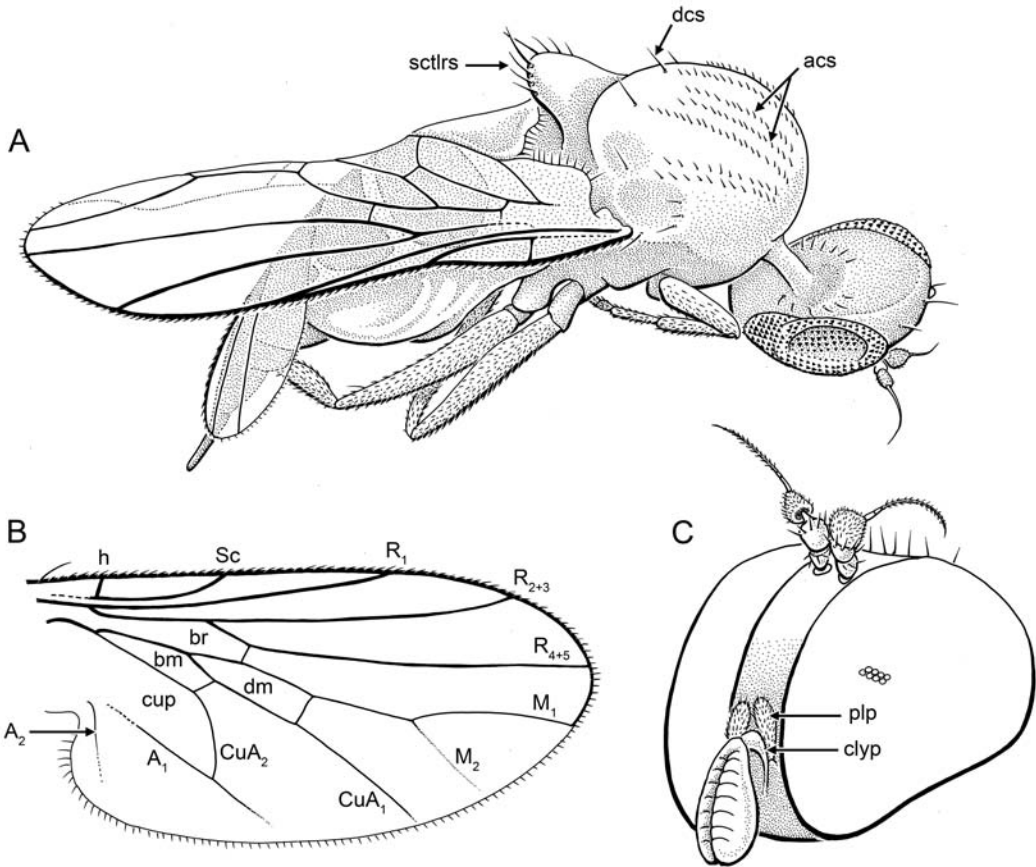


FIG. 29. *Canadopeza biacrosticha*, n. gen., n. sp. (Platypezidae), holotype female, RTMP 96.9.2, in Late Cretaceous amber from Canada. **A.** Dorsolateral habitus, as preserved. **B.** Wing, reconstructed. **C.** Head, oblique frontal view.

on costal edge unapparent); membrane entirely covered with microtrichia (even on sc cell). One prehumeral costal seta present; C terminates at apex of M₁, C with well-developed spinules. Sc relatively short, apex near level of r-m vein, R₁ short, 0.6× length of wing; Sc and R₁ divergent, not parallel; pterostigma absent. Apex R₂₊₃ slightly upturned; R₄₊₅ ends near wing tip; R veins thicker than others; cells rm and bm complete; crossvein dm-cu near middle between fork of M+CuA₁ and wing apex (cell dm short). M₁₊₂ forked, slightly asymmetrical, M₂ very faint (almost spectral). Vein CuA₂ curved (not straight); cell cup large, longer than terminal vein; anal lobe well developed, alula not observ-

able. **Legs:** Lacking macrosetae, except for stout ventroapical spur on mesotibia. No dark, bifid scales on legs. Basitarsomeres of all legs equal to or slightly longer than combined length of distal tarsomeres; no metatarsomeres flattened or expanded. Puvilli well developed; empodium not observable, probably minute.

Abdomen: Tergites and sternites well developed, apparently without macrosetae. **Female Terminalia:** Four apical segments telescoping, approximately equal in length; cerci simple, with pair of dark hypoproct lobes protruding at base ventrally.

SPECIMENS EXAMINED: Holotype, female, RTMP 96,9.26. Deposited in the Royal Tyrell

Museum of Paleontology, Drumheller, Alberta, Canada. The specimen is complete and in good condition, although flows and fractures within the amber prevent observation of some structures.

ETYMOLOGY: In reference to the two rows of acrostichal setae.

Lebanopeza, new genus

DIAGNOSIS: (male only). Eyes holoptic, dorsal facets larger; small prescutellum present; acrostichals in short uniserial row; wing with microtrichia over entire surface; C ends at apex of R_{4+5} (vs. M_1); crossvein dm-cu (cell dm) absent, CuP curved; M entirely spectral, branches of M_1 - M_2 fork virtually symmetrical; dark bifid scales lacking on legs; metatarsomeres not expanded; male terminalia lateroflexed to right. Except for the lack of crossvein dm-cu and the faint M vein, all these features appear plesiomorphic for the Platypezidae.

TYPE SPECIES: *L. azari*, new species.

ETYMOLOGY: From Lebanon, the country of origin, and *-peza* (foot), a common suffix for generic names in the Platypezidae.

COMMENTS: *Lebanopeza* appears to be an extinct stem group to *Microsania* + *Melanderomyia* (fig. 27). It lacks at least four features that define these two extant genera (chars. 3, 16, 17, 18; table 2), but shares with them the loss of crossvein dm-cu (cell dm), a distinctly shortened Sc vein and somewhat shortened R_1 , and reduction in the medial veins. In *Melanderomyia* M_2 is lost; in *Microsania* the base of M_1 is lost; in *Lebanopeza* the entire stem and fork of M_1 - M_2 is extremely faint and unsclerotized.

The wing of *Lebanopeza* is similar to *Mauritulus sopes* Mostovski, preserved as a compression (along with portions of the body) in shale from the Early Cretaceous of Eurasia (Mostovski, 1995a). Both genera have a slender wing; membrane densely covered with microtrichia; R_1 straight, relatively short; C definitely (*Lebanopeza*) or apparently (*Mauritulus*) ending at the apex of R_{4+5} ; M_1 - M_2 fork nearly symmetrical;

and crossvein dm-cu (cell dm) absent. *Lebanopeza* differs from *Mauritulus* by having a shorter Sc cell ($0.3\times$ wing length, vs. $0.45\times$), cell cup with apical stem of CuP+ A_1 (in *Mauritulus* these veins join virtually at the wing margin), and in having no metatarsomeres expanded (in *Mauritulus* the basitarsomere is slightly expanded).

Lebanopeza azari, new species

Figures 4, 30

DIAGNOSIS: As for genus, by monotypy.

DESCRIPTION: (male only). Entire body appears blackish, possibly velvety. **Head:** Eyes large (partially collapsed in unique specimen), bare, holoptic for ~ 10 facets; dorsal facets $2\times$ or more the diameter of ventral ones. Ocellar triangle on tubercle, with minute pair of upright setae; small triangle of frons exposed just above antennae (bare of setulae, median furrow not apparent); interfrontal and fronto-orbital setae not observable; postocular setae appear to be minute; vibrissa absent. **Antenna:** Scape not observable; pedicel short, funnel shaped; arista terminal; basal flagellomere drop shaped; 3 arisotomeres, 2 basal ones small, ringlike, apical arisotomere fine, length $\sim 1.5\times$ that of rest of flagellum, with micropubescence. **Mouthparts:** Small, entirely recessed into depressed oral cavity, cavity occupies almost all of face; palp not visible, possibly minute. Labellum short, fully opened and flat, with ~ 5 pseudotracheae per lobe.

Thorax: Scutum short, arched, black (probably velvety), the few setae are short, thick, stiff. Acrostichals in uniserial row of 4 minute setulae; dorsocentrals in graded row of 4–5 setae (posterior one largest), anterior dc about same size as acrostichals. No supraalar seta; 1 short, stout postalar; 3 stout notopleural setae just anterior to transverse suture, slightly longer than dorsocentrals. Prescutellum present but small; scutellum short, with single pair of short apical setae. **Wing:** Relatively slender, length $2.8\times$ the width; with slight infuscation in Sc cell and between Sc and R_1 ; membrane entirely covered with micro-

trichia (including all cells); pterostigma absent. No prehumeral setae on C; vein C terminates at apex of R_{4+5} ; C with row longer, stout setae interspersed among numerous setulae. Sc short, $0.3\times$ length of wing; R_1 $0.7\times$ wing length. Radial veins heavily sclerotized; medial veins virtually unsclerotized, faint. R_{4+5} ends at wing tip; cells rm and bm nearly equal in size; crossvein dm (cell dm) absent. M_1 - M_2 fork present, veins slightly divergent, almost symmetrical; length of fork approximately equal to that of stem. Cell cup large, significantly longer than terminal vein; CuP curved; A_2 very short, apically evanescent; anal lobe well developed; alula shallow, with long setae (not flattened). Halter bulb black, large, length equal to that of stem. **Legs:** Dark, relatively short, slender. Protibia equal to length of profemur; meso- and metatibia shorter than respective femur. Mesotibia with pair of short, stout apical spurs, one $2\times$ length of other. Tibiae and tarsi with setulae, short stout ones at apex of some podomeres. Dark, bifid scales absent from all podomeres. Metabasitarsomeres not expanded. Pulvilli well developed; empodium not observable (probably minute, setiform).

Abdomen: Short, stout, about same length as thorax; 8 well-developed tergites visible, enfolded laterally, with scattered, fine setae; sternites not observable. **Male Terminalia:** Apical three tergites (7, 8, and 9 [epandrium]) lateroflexed 90° to right; epandrium capsulelike; surstylus digitiform, curved, suspended ventrally; cercus small, broad; postgonites with visible portion flanking phallus; phallus curved.

SPECIMENS EXAMINED: Holotype, male, Az 715A, in the Museum national d'Histoire naturelle, Paris. The fly is complete, preserved in a tiny chip of amber that is mounted in balsam on a microscope slide.

ETYMOLOGY: Patronym for Dany Azar, for his work on Lebanese amber.

Genus *Microsania* Zetterstedt

DIAGNOSIS: Male holoptic, female dichoptic; female frons with well-developed orbitals and

pair of interfrontals (latter sometimes present or visible in male); postoculars long, occiput setose. Face protruding (clypeus bulging) in female; basal flagellomere oval to subcircular; arista micropubescent. Acrostichals present, uniserial; dorsocentrals in two uniserial rows. Thorax short, deep; scutum in lateral view arched. Metabasitarsomere and tarsomere 2 (sometimes 3) laterally flattened, expanded; tarsomere 1 is longest of metatarsomeres; legs without dark, bifid scales. Wing with Sc, R_1 sclerotized, short, latter slightly over $0.5\times$ length of wing. Pterostigma large, between entire R_1 and Sc and extends apically past R_1 . Base of M_1 incomplete; wing with membrane entirely microtrichose. Cell cup small; crossvein dm-cu absent. Alula with flattened setae; male abdomen with longer setae, terminalia curled under abdomen.

COMMENTS: This is a global genus of some 23 named extant species: 5 Australia + New Zealand, 4 Asia, 2 Pacific Islands (Vanuatu, Fiji), 2 Africa, 8 Palearctic, and 2 New World. The North American specimens are in serious need of revision (there are more than just two species), and I have also seen new species from Mexico, Peru, and Chile. Species are rather uniform externally (males are best separated using genitalia), and females of some species cannot be distinguished with certainty (e.g., Chandler, 2001).

The female specimen in Baltic amber described below is the first fossil of the genus, and it is remarkably similar to modern species. A detailed comparison of the females of world species is needed to determine whether there are features of this fossil that allow diagnosing it as a species. In the meantime, I am deferring formally naming it, just noting the impressive morphological stasis of *Microsania* from the Eocene to the present. Surprisingly, this is also the only definitive platypezid known in Baltic amber (though an undescribed opetiid is known), despite the centuries of collecting and studying Baltic amber insects in Europe. Interestingly, the amber piece resided for more than a century in an old collection of darkened, crazed Baltic amber insect inclusions at the AMNH, which was purchased from Ward's Scien-

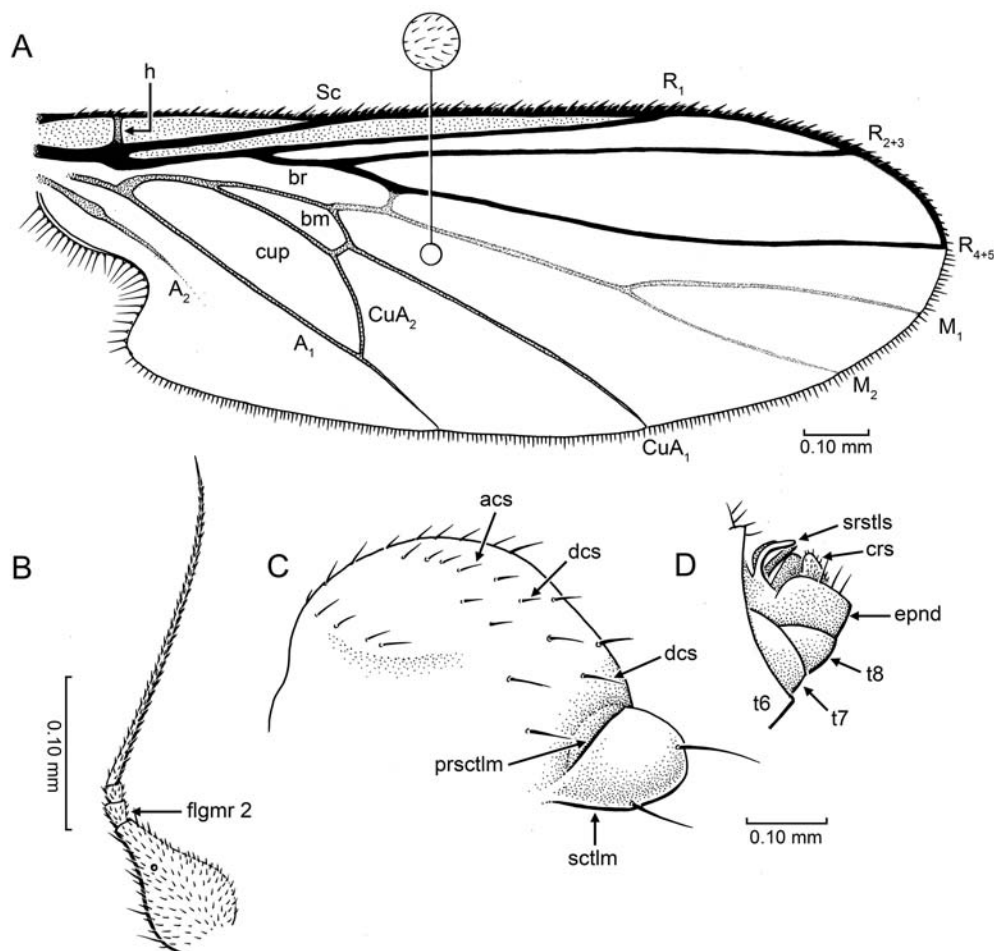


FIG. 30. *Lebanopeza azari*, n. gen., n. sp. (Platypezidae), holotype male, Az715A, in Early Cretaceous amber from Lebanon. A. Wing. B. Antenna. C. Dorsal portion of thorax. D. Male terminalia, left lateral view.

tific Establishment in Rochester, New York, in the early 1900s. It was originally labelled as an empidid. The deteriorated surfaces were removed, better revealing the fly. The fly is partially coated with a milky exudate, typical of the preservation of insects in Baltic amber.

Microsania sp.

Figures 5, 31

SUMMARY: Complete female in Baltic amber; with typical array of *Microsania* characters (see generic diagnosis above). Additional details

include the following: M, Cu veins with minute gap between apices and wing margin; bm cell and vein CuA2 appear incomplete (the former possibly an artifact of preservation); 2 pairs fronto-orbital setae, anterior pair inclinate, posterior pair latero-proclinate; strong pair of interfrontals present; pair of long, fine presutural setae (probably dorsocentrals) present; prescutellum appears present.

DESCRIPTION: Head: Eyes bare, red; dichoptic. Frons with faint median furrow on anterior half; pair of interfrontals present, well developed, proclinate; 2 pairs of fronto-orbitals, anterior pair inclinate, slightly more posterior pair latero-

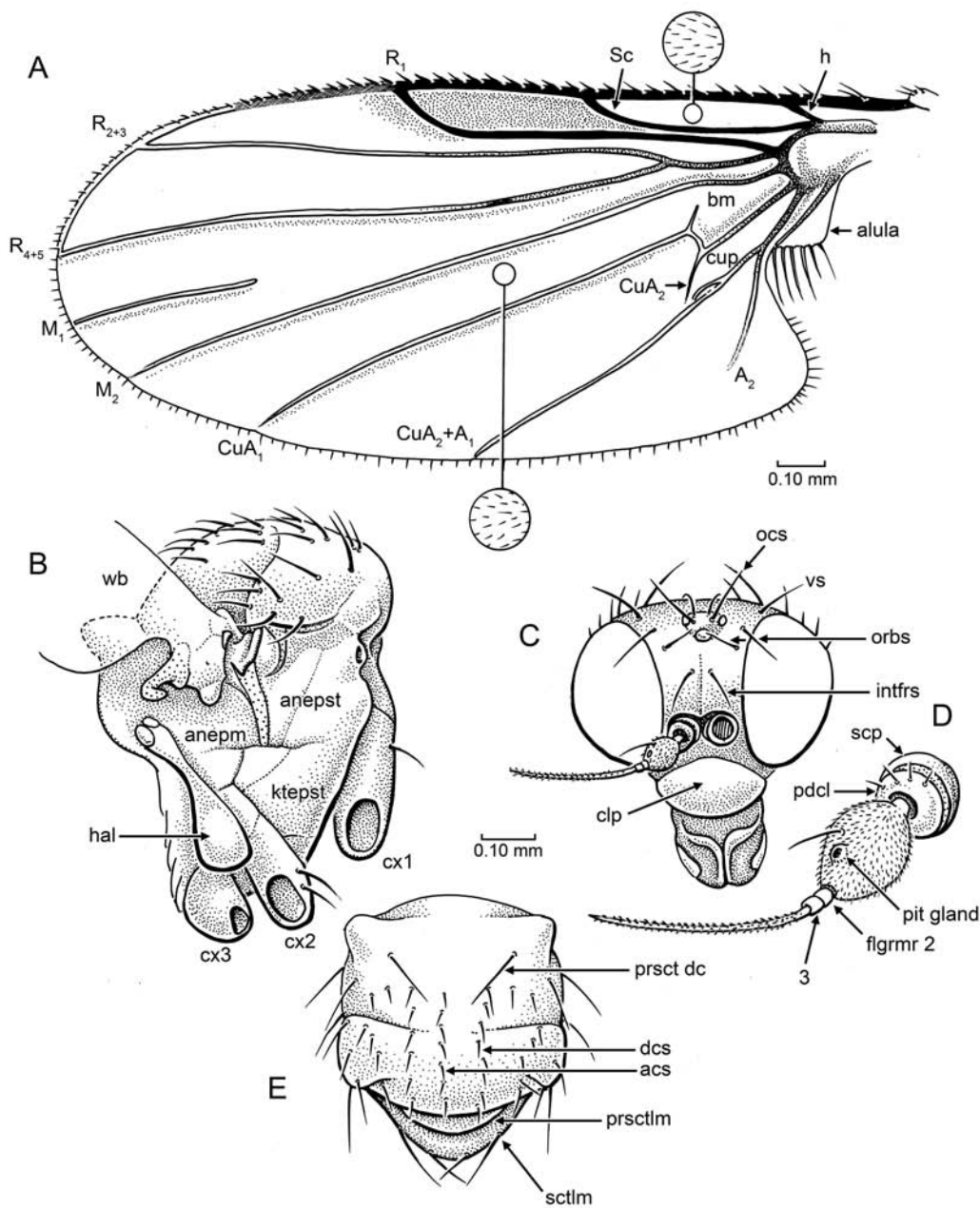


FIG. 31. *Microsania* sp. (Platypezidae), female, AMNH Ba502-14, in Eocene Baltic amber. A. Wing. B. Thorax, lateral view. C. Head, frontal. D. Antenna. E. Thorax, dorsal.

proclinate. Pair of ocellar setae present, long, divergent, smaller pair posteriad. Laterocline pair of outer verticals present; inclinate pair of inner verticals, plus other setae on vertex; post-occipital setae well developed.

Clypeus (face) bulging; vibrissa, genal setae absent. Proboscis relatively broad but short. **Antenna:** Scape and pedicel short, ringlike; pedicel with setulae; arista terminal, basal flagellomere ovoid, with sensory/glandular pit and seta on dorsal surface; basal aristomere minute, short; apical aristomere long, not particularly fine, micropubescent.

Thorax: Short, deep in lateral view, rounded and slightly arched. Acrostichals uniserial, ~7 in row; dorsocentrals in pair of rows, ~7–8 setae each row, anteriormost pair long, fine, ~3× length of posterior dcs, ~5 scattered setae lateral to dcs. 1 large supraalar seta; 1 large postalar; 6 scattered notopleural setae. Anepisternum, katapisternum, anepimeron bare. Scutellum short, broad; with two pairs setae, apical pair cruciate; prescutellum present. **Wing:** Relatively elongate, length 2.3× width; darkened between Sc and R₁, with darkened area extending past apex of R₁; membrane entirely covered with well-developed microtrichia. Vein C with spinules, longer on portion from apex of R₁ to base; C terminates at apex of R₄₊₅, portion between terminus and apex of R₁ hardly sclerotized. Sc about half the length of R₁; R₄₊₅ terminates at apex of wing. Cell rm absent; cell bm open apically (bm-cu appears incomplete), crossvein dm-cu (cell dm) absent. M₁ basally incomplete; M₂ complete; between apices of M and Cu veins and wing margin with a minute gap. CuA₂ short, apically incomplete(?), cell cup small, possibly open; A₁ apically evanescent; anal lobe well developed, alula with long flattened setae. **Legs:** Coxa laterally attached to thorax; length of femur ≈ tibia on all legs; all podomeres setulose. Largest setae on legs stout, spine like; 2 on dorsal surface mesotibia (at 0.3× length of tibia, plus preapically); 1 dorsally on metatibia and metabasitarsomere, both preapical. Setae and setulae on all tibiae and tarsi in longitudinal rows. Mesotibia and tarsus with 2 ventral, seamlike rows of stout, short setulae. Metatarso-

meres 1 and 2 with transverse rows setulae. Claws and pulvilli well developed. Metabasitarsomere barely expanded in lateral view. **Abdomen:** Abdomen relatively short, stout, distinctly shorter than wings; 8 well-developed tergites, 6 well-developed sternites visible. Tergites with short, scattered setae (no macrosetae), sparser on sternites; sternites nearly equal in size to tergites on same segment. Pleural membrane wrinkled and exposed between lateral margins of abdominal sclerites. Cerci small, 1-segmented, suboval.

SPECIMEN EXAMINED: Female, AMNH Ba-502-14, in Eocene Baltic amber. Specimen is complete and well preserved (the eyes have even retained a reddish color), but portions of the cuticle are obscured by a milky coating.

COMMENTS: I chose not to name this fossil because I could find no diagnostic characters to separate it from extant species, one reason being it is a female.

Calvopeza, new genus

DIAGNOSIS: (female only). Macrosetae absent from head, thorax, and abdomen (some fine setae/setulae on legs); fine, minute acrostichals present in 2–3 irregular, short rows. Scutum strongly arched; palp large, long. Vein M₁ arched strongly away from M₂; membrane of wing mostly with microtrichia, except in basal cells; A₁+CuA₂ apically incomplete, A₂ spectral. Tibiae and tarsi with dark bifid scales; metatarsomeres 1–4 slightly flattened and expanded.

TYPE SPECIES: *C. divergens*, new species.

ETYMOLOGY: From *calvus* (L., “naked, bare”), in reference to the virtual lack of setae on the head and body, and *-peza*, a common suffix in genera of Platypezidae. The genus name is feminine.

Calvopeza divergens, new species

Figures 6, 7, 32

DIAGNOSIS: As for genus, by monotypy.

DESCRIPTION: (female only). **Head:** Broader than long, but slightly narrower than thorax. **Eyes:**

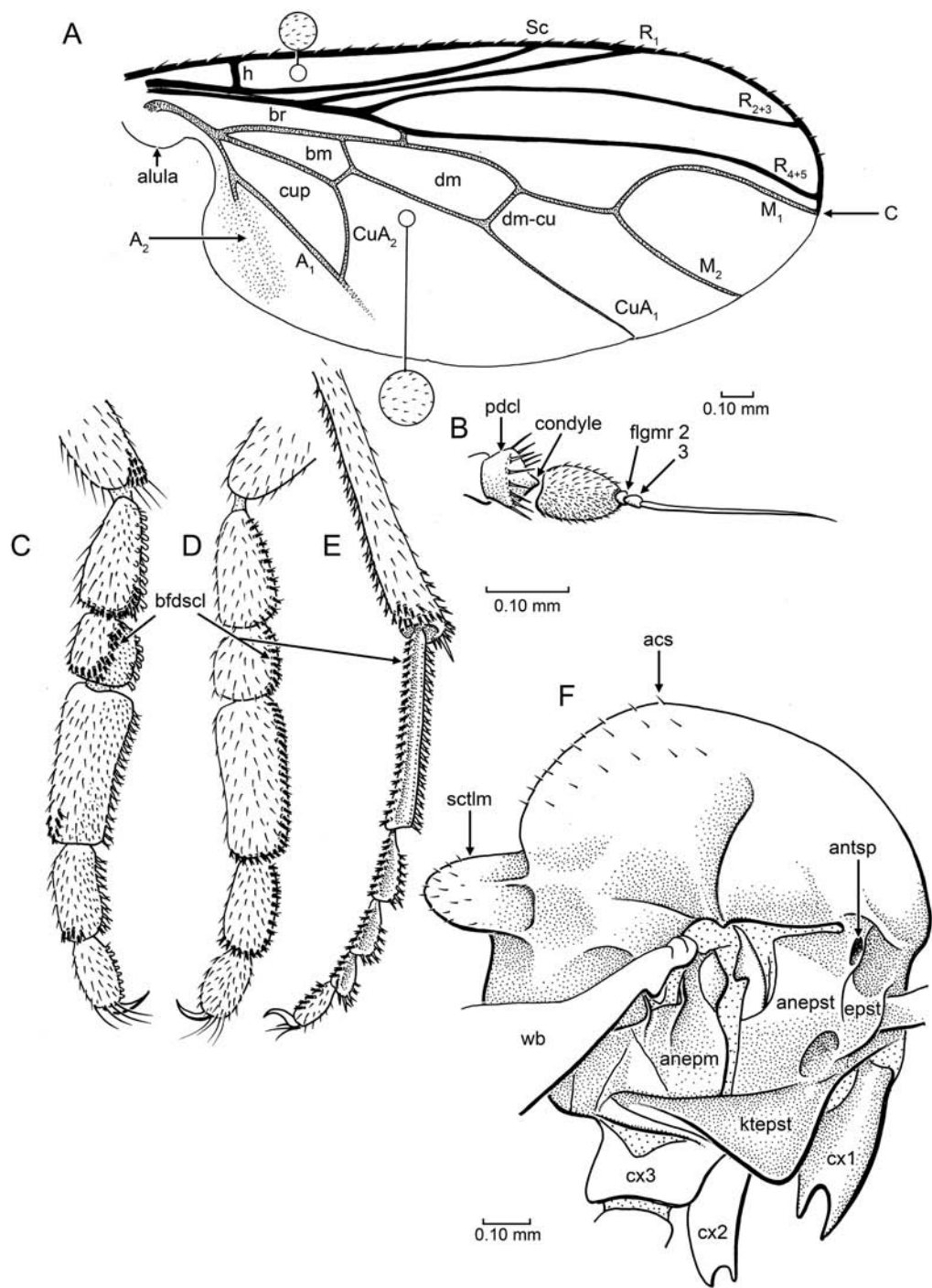


FIG. 32. *Calvopeza divergens*, n. gen., n. sp. (Platypezidae), in Burmese amber. A, C, D, F. Female holotype, AMNH Bu-SE8. B, E. Female paratype, JZC Bu-212. A. Wing. B. Antenna. C, D. Hind leg, lateral and mesal, respectively. E. Mid leg, mesal. F. Thorax, lateral.

Bare, as preserved silvery, no emargination, large (occupying nearly entire lateral surface of head); no differentiation of facets. Frons without median furrow; with few, scattered fine setulae; no interfrontal, fronto-orbital, vertical, or ocellar setae; frons margins slightly divergent dorsad. Ocelli on low tubercle. Postocular setae reduced to a few fine setulae. Oral margin slightly concave; face flat, vibrissa and genal setae absent. **Antenna:** Scape small; pedicel ringlike, with distal rim of fine setulae, apex short, conical; arista apical; basal flagellomere ovoid; two minute basal aristomeres present, basalmost one smaller; apical aristomere bare, hardly longer than rest of antenna. **Mouthparts:** Clypeus short, much broader than long; palp large, oblong, flat, light, without setae (with just setulae and microtrichia); labellum well developed, laterally flattened when closed, with fine setulae on ventral surface.

Thorax: Scutum strongly arched, neck positioned low (slightly below level of scutellum); transverse suture short, restricted to vertical-lateral portion of scutum. Acrostichals extremely fine, short, in 2–3 irregular short rows; no thoracic macrosetae (e.g., dorsocentrals, supraalars, postalars, notopleurals, scutellars). Anepisternum relatively large, katapisternum small; prescutellum absent; thorax deep in lateral view; scutellum relatively small, roughly triangular in dorsal view.

Wing: Entirely clear (no tinting, even between Sc and R₁); pterostigma absent; membrane with fine microtrichia except in cells cup, br and base of bm. Vein C with fine setulae only, lacking thick spinules; C terminates at apex of M₁; Sc and R₁ long, closely adjacent. R veins without setulae or spinules, more sclerotized than other veins. Cell rm narrow, long, bm shorter than cup; crossvein br-m very short; dm-cu distant from wing margin by 3.5× its length (cell dm short); cup large, CuA₂ slightly arched, A₂ spectral. Anal lobe well developed, alula small. **Legs:** Very slender; coxae relatively short; metafemur slightly longer than pro- and mesofemur; bare except for dark bifid scales on tarsi and portions of tibiae, long row of extremely fine setae on dorsum of profemur (lengths about equal to femur width).

Dark, bifid scales: row on lateral edge of pro- and mesotibia, plus encircling apex of tibia; 2–3 irregular rows on metatibia; on ventral surface of pro- and mesotarsomeres 1–4. Metatarsus slightly inflated and flattened laterally, tarsomere 2 shortest, tarsomere 3 longest, with 2 ventral rows of bifid setae.

Abdomen: Relatively short, stout; eight tergites visible, 2–4 largest ones; pleural membrane extensive (tergites and sternites not meeting laterally); tergites completely bare of setae or setulae; sternites small, subcircular to almost square, each extensively isolated by membrane, 7 visible. **Female Terminalia:** Cercus 1-segmented, digitiform, setulose, hypoproct well developed (~ 0.5× length of cercus).

SPECIMENS EXAMINED: Holotype, female, AMNH BuSE-8. Paratypes JZC Bu212 (female), AMNH Bu-1510. All in Burmese amber. All are completely intact, though the holotype is particularly well preserved.

ETYMOLOGY: The species name refers to the widely divergent M veins.

Chandleromyia, new genus

DIAGNOSIS: (male only). Eyes extensively holoptic; gena bare, occiput with very fine, scattered short setae; clypeus a broad triangle; palp minute; arista bare; acrostichals entirely absent, only 1 pair of (short, prescutellar) dorsocentrals; 1 short pair of scutellars; 4–5 notopleurals. Wing entirely covered with dense microtrichia; M not forked (M₂ lost), dm-cu close to wing margin; CuP slightly curved. Tibiae and tarsi with bifid scales. Metatarsomeres 1–4 flattened, expanded; tarsomere 2 shortest, with blunt spine; tarsomere 3 with clavate seta. Abdomen short, broad; male tergite 7 narrow, tubular.

TYPE SPECIES: *C. anomala*, n. sp.

ETYMOLOGY: For Peter J. Chandler, in recognition of his work on global Platypzeidae, and on Diptera in general. The genus name is feminine.

COMMENTS: This genus is extremely similar phenetically, and apparently close phylogenetically, to *Lindneromyia neomedialis*, n. sp., in

Dominican amber, described below. This is based on the squared oral margin, minute palps; face, gena, arista bare; complete lack of acrostichals, one (short, prescutellar) pair of dorsocentral setae; one short pair of scutellars; no supraalars, one short postalar; loss of vein M_2 ; r-m crossvein near level of cell Sc apex; and thick, stiff, spinelike setae on posterior margin of tergite 6 lacking. *Chandleromyia* differs from *L. neomedialis* based on the setose occiput (completely bare in *Lindneromyia*); 4–5 notopleurals (vs. 2); wing membrane entirely with dense microtrichia (vs. partially covered with minute, faint ones); cell dm long, with dm-cu close to wing margin (vs. cell short, vein near middle of wing); vein M_1 deflexed (vs. almost straight); vein CuP curved (vs. straight); spine and clavate seta on metatarsomeres 2 and 3, respectively (vs. without); male tergite 7 narrow, tubular (vs. short, much broader than long, inserted into emargination of tergite 6).

Though separated by approximately 80 million years, the two flies appear closely related. There is no question about the provenance of the two specimens; AMNH DR14-35 was acquired in the 1990s in the Dominican Republic by me; AMNH Bu-KL30-27 was acquired from Myanmar. With a derived platypezine in the mid-Cretaceous, this greatly extends the age of crown-group Platypezidae (fig. 27).

Chandleromyia anomala, new species

Figures 8, 33

DIAGNOSIS: As for genus, by monotypy.

DESCRIPTION: (male only). **Head:** Large, broader than thorax. Eyes bare, large, holoptic for ~30 facets (virtually entire length of frons except short segment above antennae). Dorsal facets (~70% of eye) large, 2× diameter of ventral facets. Frontal margins of eyes emarginate around bases of antennae, margins slightly divergent ventral to this. Median furrow of frons, interfrontal, fronto-orbital setae (presence/absence) not observable. Face entirely bare. Ocelli on tubercle, with pair of short posterior

setae (length shorter than diameter of ocellus). Vertical setae absent; postoculars minute, except for short row of 4–5 short, thick setae on dorsal portion. Occiput with fine, short, scattered, light setae (lengths ca. equal to diameter of large eye facets); occipital setae do not extend to gena. Vibrissa, genal setae absent. **Antenna:** Scape small, barely exposed, apparently bare; pedicel small, conical, with apical circlet of setulae; arista terminal; basal flagellomere small, tapered, with incised portion mesally; two small basal aristomeres (lengths ~3× the diameter); apical aristomere long, fine, bare of any micropubescence. **Mouthparts:** Oral margin squared; clypeus a broad triangle; labrum broad, apex pointed and sclerotized; labellar lobes deeply separated anteriorly, ~0.65× lobe length; palp very small.

Thorax: Scutum convexed but not arched, flatter anteriorly. Acrostichals completely absent, even minute ones. Only 1 pair of dorsocentrals present, short, prescutellar, no smaller, graded dorsocentrals present. Supraalar setae absent; 4–5 stout notopleural setae present (4 on one side of specimen, 5 on other side); anepisternum and kat-episternum bare. One pair of short, stiff postalar setae present. Prescutellum absent. Scutellum with one pair of apical setae only; setae short, stout. **Wing:** Length/width 2.4; hyaline, except for faint tint between Sc and R_1 . Membrane microtrichia well developed over entire surface of wing, even in cell Sc. Two prehumeral costal setae at base of C; C with spinules, end near apex of R_{2+3} . Sc relatively short, apex slightly beyond level of crossvein r-m; R_1 straight, bare, length 0.72× the wing length; bases of Sc and R_1 close, divergent for apical half. Pterostigma absent. Vein R_{4+5} ends at wing tip; cells rm and dm closed; crossvein br-m slightly basal to level of Sc apex; crossvein dm-cu close to wing margin, separated from margin 0.75× its length. M not forked (M_2 lost); M_1 bent in middle, deflected anteriorly. Tip of CuA_1 incomplete; cell cup longer than vein at apex, cell not extremely acute or narrow; CuP slightly curved, not straight; $CuP+A_1$ tip incomplete. **Legs:** All femora without macrosetae, spines or tubercles. Dark bifid scales on all tibiae and tarsi: scattered

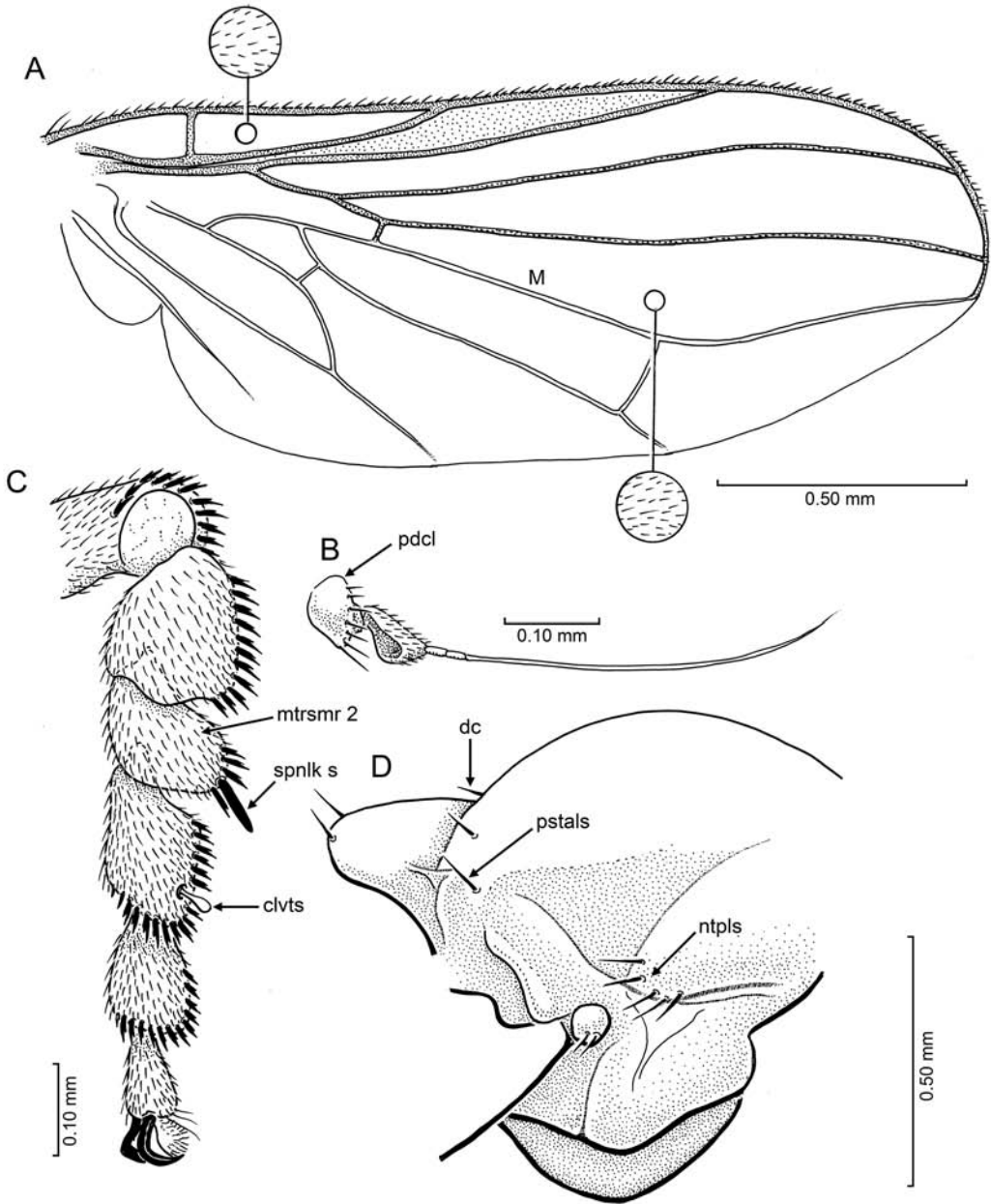


FIG. 33. *Chandleromyia anomala*, n. gen., n. sp. (Platypezidae), male holotype in Burmese amber, AMNH Bu-KL30-27. **A.** Wing. **B.** Antenna. **C.** Metatarsus, lateral. **D.** Thorax, lateral.

on partial, lateral surface of tibiae, encircling ventral portion of tibial apex; in dense lateral row on tarsi. Metatarsomeres 1–4 flattened laterally, expanded; tarsomere 2 with blunt spine on latero-apical corner; tarsomere 3 with small, light, clavate seta preapically near row of bifid scales. Mesotibia with 2 ventroapical spurs, large one mesally (its length ca. diameter of tibia). Pulvilli well developed; empodium not observable (probably minute, setiform).

Abdomen: Tergites without macrosetae or setulae; 8 tergites visible; anterior 6 broad (1–4 broadest); tergite 7 narrow, longer than wide, tubular, ventroflexed (presumably circumverted); epandrium small, capsular. Male genitalia not observable (preservation insufficient). Sternites well developed, but lateral margins do not meet tergites (pleural membrane exposed).

SPECIMENS EXAMINED: Holotype, male, AMNH Bu-KL30-27, in Burmese amber. The fly is extremely well preserved, complete, though some details are obscured (e.g., small structures of the genitalia).

ETYMOLOGY: In reference to the anomalously early appearance of a platypezine in the mid-Cretaceous.

Lindneromyia Kessel

Lindneromyia Kessel, 1965a: 1. Type species *L. africana* Kessel.

Symmetricella Kessel, 1965b: 235. Synonymy by Chandler (1989).

Plesioclythia Kessel and Maggioncalda, 1968: 58. Synonymy by Chandler (1989)

Penesymmetria Kessel and Maggioncalda, 1968: 63. Synonymy by Chandler (1989).

DIAGNOSIS: Predominantly black, velvety; ocellars and postorbital setae short; female without fronto-orbital setae; occipital setae present, not extending to gena. Dorsocentral setae short, uniserial (prescutellar pair largest); 3–5 strong notopleurals; 1 strong postalar; 2–3 pairs scutellars. Male femora without large setae; mesotibia with 2 apical spurs; metatarsomeres 1 to 3 or 4 laterally

flattened and expanded, length of tarsomere $3 \geq 1$, metabasitarsomere short. Wing with minute, extremely faint microtrichia, absent from most/all costal cells; costal edge generally slightly convex proximal to tip of Sc; M usually forked (simple [M_2 lost] in 3 extant species), fork short. Crossvein dm-cu less than twice its length from wing margin, usually much less; length of cell cup equal to or generally less than length of apical vein.

Lindneromyia neomedialis, new species

Figures 9, 34

DIAGNOSIS: (male only). Vein M unforked (M_2 lost), R_{4+5} and M_1 slightly sinuous; gena completely and occiput virtually bare; metatarsomeres 1–4 flattened, expanded, basitarsomeres short, tarsomere 3 longest; acrostichals completely absent; only 1 (short) pair dorsocentrals and scutellars present; 2 notopleurals; wing membrane with very faint, minute microtrichia over about half of wing (mostly posteriorly); male abdominal segments 7–8 inserted into deep emargination of posterior portion of tergite 6.

DESCRIPTION: (male only). **Head:** Large, broader than thorax. Eyes bare, large, occupying all of lateral portion and much of frontal surface of head; holoptic in male from just above antennae to anterior ocellus (~15 facets); dorsal facets about 2× diameter of ventral ones. Median furrow of frons, interfrontal setae, orbitals, verticals (presence/absence) not observable. Ocelli on tubercle; setae absent, 6 minute setulae present. Postocular setae minute, in short row along posterodorsal margin of eye; occiput otherwise bare. Vibrissa, genal setae absent. **Antenna:** Slight oval depression on face beneath each antenna. Scape small, bare; pedicel cup shaped, with 4–5 setulae on rim; arista terminal; basal flagellomere short, roughly drop shaped but without slender apical extension. Arista with two minute, ringlike articles at base; basal aristomere long, fine, bare (not micropubescent). **Mouthparts:** Oral margin and clypeus squared; clypeus thin. Palp small, with apex truncate (possibly with a pore). Labellum

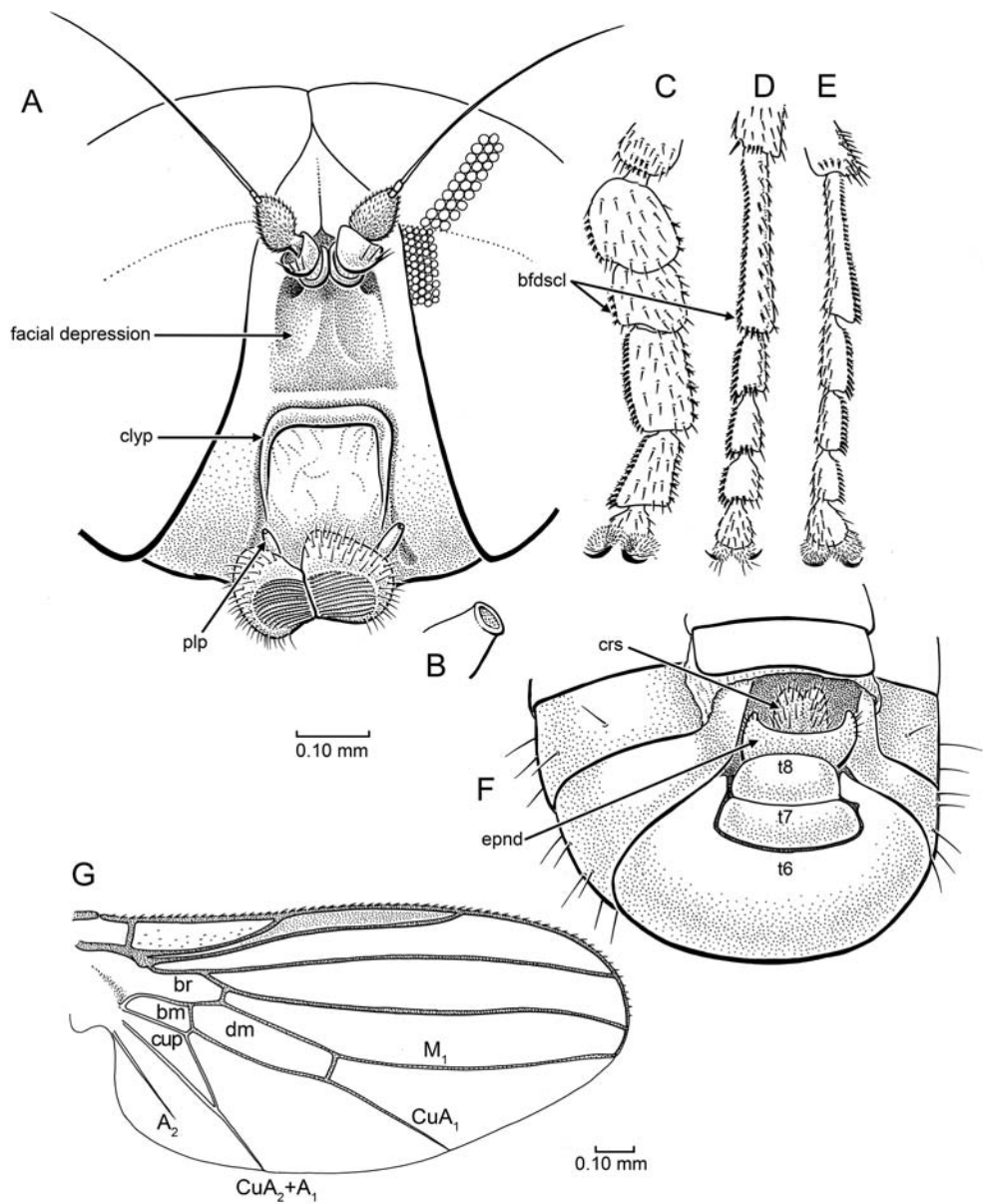


FIG. 34. *Lindneromyia neomedialis*, n. sp. (Platypetidae), male holotype in Miocene amber from the Dominican Republic, AMNH DR14-35. A. Head, frontal view. B. Tip of palp. C, D, E. Tarsi: hind, mid, and fore (respectively). F. Apex of abdomen, ventral. G. Wing (slightly reconstructed at base).

(opened) broad, with ~10 pseudotracheae; labrum not observable.

Thorax: Scutum rounded but not arched; curvature greater on anterior portion; scutum and scutellum appear black, perhaps velvety. Acrostichals absent; only one pair of (short, prescutellar, inclinate) dorsocentrals present (smaller graded dcs completely absent). Supralar setae absent; 1 short postalar; 2 short notopleurals; anepisternum and katepisternum bare. Prescutellum absent. Scutellum with only one pair of small preapical setae, divergent. **Wing:** Length/width 2.0, hyaline except for faint tint between Sc and R_1 . Membrane with faint, minute, barely detectable microtrichia over about half the (posterior portion of) wing, including much of cell Sc. No veins with setulae or spinules; prehumeral costal seta very small; vein C with spinules to slightly past apex of R_{2+3} ; C terminates at apex of M_1 . Sc relatively short, close to R_1 ; pterostigma absent. R_{2+3} almost straight, R_{4+5} and M_1 slightly sinuous, convergent at wing tip; R_{4+5} ends near wing tip; cells br, bm closed. Crossvein dm-cu short, distant from wing margin, $5\times$ its length from wing margin (vs. ca. $0.5\text{--}3\times$). M unforked (M_2 lost), without abrupt bend in M_1 . CuA_1 relatively straight; cell cup pointed, CuP straight (not curved); anal lobe and alula well developed. Halter knob large, dark, bulbous, length ~ equal to that of stem. **Legs:** Relatively short; all femora without macrosetae, spines or tubercles. Tarsomeres 1–4 flattened, expanded; tarsomere 3 longest, 1 is broadest. All tarsomeres with posteroventral, seamlike row of dark, bifid scales; more such scales scattered over dorsum of metatarsomeres; 2 sparse rows of scales dorsally on meso- and metatibia. Mesotibia with single, short ventroapical spur, length less than diameter of tibial apex. Pulvilli well developed; empodium setiform.

Abdomen: Dark; relatively short, as preserved only slightly longer than thorax. Tergites well developed, wrap laterally, contact lateral margins of sternites (which are also well developed). Abdomen laterally with fine, erect setae; dorsally with few or no setae (probably velvety black);

terminal tergites without large, spinelike setae. Six tergites visible dorsally, 2 small ones ventrally (tergites 7 and 8) (plus epandrium), all three ventroflexed (presumably completely circumverted), recessed in deep emargination on posterior portion of tergite 6. Cerci light, appear fused at bases. Posterior margin tergite 6 without thick, stiff setae; epandrium crescentic.

SPECIMENS EXAMINED: Holotype, male, AMNH DR14-35, from mines near Santiago, Dominican Republic (Miocene). Specimen is complete and has excellent preservation, although the surface of the amber is crazed.

ETYMOLOGY: *Neo-*, referring to New World; and *-medialis*, referring to the medial vein, as this is the only New World species of the genus thus far with a simple medial vein.

COMMENTS: *Lindneromyia* is the largest genus of the family, and the predominant one in the tropics. Three species in the genus have a simple medial vein: *L. africana* Kessel (from Kenya, type species of the genus), *L. fonsecai* Chandler (from Australia), and *L. kesseli* Bowden (from South Africa). *Lindneromyia neo-medialis* significantly differs from these three species based on the single pair of dorsocentrals (vs. in two rows) and scutellars (vs. 2–3 pairs); lack of stiff setae on tergite 6 (which is widespread in Platypezidae); and the very distinctive, short dm-cu crossvein distant from the wing margin (vs. very close to the margin). *Lindneromyia fonsecai* has a very abrupt bend in M_1 (some individuals retain a spur of M_2). *Lindneromyia africana* is reported to lack the small basal aristomeres (which would be very unusual, perhaps an observational error), and the basal flagellomere is setose (not just with microtrichia); dm-cu is extremely close to the wing margin ($\sim 0.3\times$ crossvein length), and R_1 is quite long (terminating at level of CuA_1 apex). Despite these differences I am hesitant to accord a separate generic status to the fossil, especially since the external male terminalia agree so closely with *Lindneromyia* (e.g., Chandler, 1994; Chandler, 2001). Also, many of the distinctive features of *L. neomedialis* are autapomorphic losses.

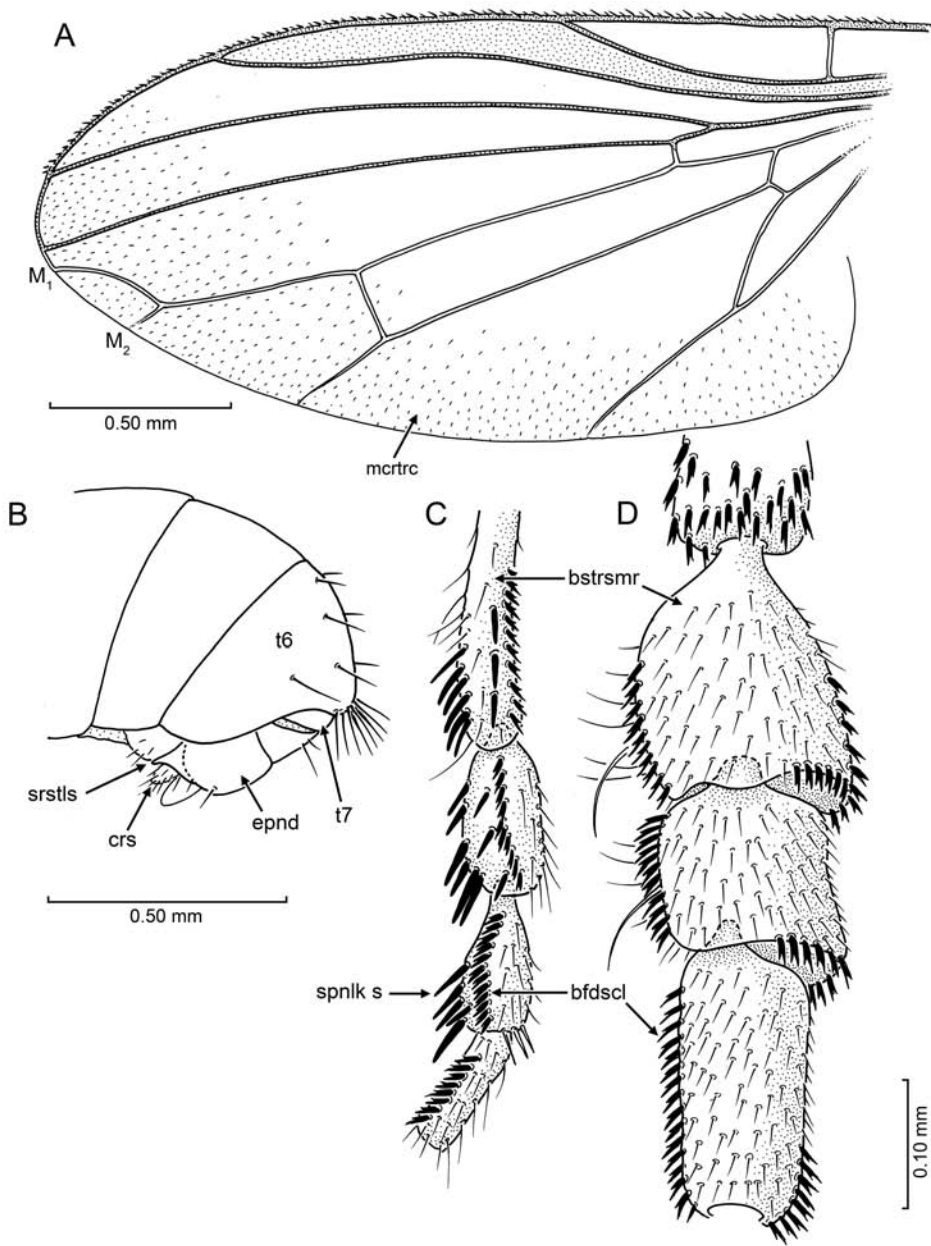


FIG. 35. *Lindneromyia dominicana*, n. sp. (Platypozidae), male holotype in Dominican amber, AMNH 14-736. A. Wing. B. Apex of abdomen, left lateral. C. Protarsomeres 1-4. D. Metatarsomeres 1-3, lateral.

Lindneromyia neomedialis differs from *Metaclythia* (monotypic: *currani* Kessel, known from Ontario, Canada, and Wisconsin, United States), which also has a simple M vein, based on the following: Cell dm short (vs. long), gena bare (vs. setose); single pair of dorsocentrals (vs. in graded row); scutellars in single pair (vs. two); 2 (vs. 4) notopleurals; tergite 6 lacking spinelike setae (vs. with 2 pairs).

Lindneromyia dominicana, new species

Figures 10, 35

DIAGNOSIS: (male only). Distinguished from the other species in Dominican amber, *L. neomedialis*, by 2 uniserial rows of dcs (vs. only 1 pair [prescutellar] dcs); 2 pairs of scutellars (vs. 1 pair); tergite 6 with 3 pairs of stiff, spinelike setae on posterior margin (vs. none); metatarsomeres 1, 2 with seta adjacent to lateral seam of bifid scales (vs. no setae); M forked; crossvein dm-cu $\sim 1.3\times$ its length from wing margin (vs. >3).

DESCRIPTION: (male only). **Head:** Width greater than thorax. Eye very large, holoptic for ~ 15 facets, bare, dorsal facets $2\times$ diameter of ventral ones; frontal margins emarginate around bases of antennae. (Silvery layer of air covers most surfaces of eyes, portions near some margins not being covered, giving appearance of emarginations on posterior and dorsal margins, but entirely an artifact). Frons mostly not observable; small triangle exposed above antennae. Ocelli on low tubercle, setae not observable. Occiput with well-developed setae; gena and postgena bare. **Antenna:** Entirely black like face, possibly velvety; basal 3 segments small, basal flagellomere roughly ovoid, with narrow tip (no slender extension); 3 aristomeres, basal 3 minute, apical aristomere long, thin, completely bare. **Mouthparts** short, almost entirely recessed into oral cavity (details not observable).

Thorax: Scutum rounded but not arched; scutum and scutellum appear black (possibly velvety). Acrostichals absent. Dorsocentrals in 2 uniserial rows ~ 10 dcs each; prescutellar longest

dc, twice length of adjacent dc; remaining dcs very small. No supraalar setae, 3 notopleurals; 1 postalar. Scutellum with 2 pairs marginal setae; apical pair twice the length of anterior pair; both pairs upright. **Wing:** Fairly short and broad, length/width 0.50. Membrane mostly bare, portions of posterior and apical margins with very fine, faint microtrichia; costal cells entirely bare. Prehumeral C seta very near wing base. Vein C ends at apex of M_1 ; with fine spinules, ending at apex R_{2+3} . Sc, R_1 close and parallel in basal half, membrane between them tinted; pterostigma absent; Sc $\sim 0.45\times$ wing length, R_1 $0.70\times$ wing length. R_{2+3} terminates just before wing tip; R_{4+5} at wing tip. M branched, asymmetrical, M_1 twice the length of M_2 . Crossvein br-m at level of $0.65\times$ Sc length; dm-cu $1.3\times$ its length from wing margin, cell dm long. Vein CuP very slightly curved; A_1 not observable; cell cup relatively short, slightly longer than apical vein. Anal lobe well developed; alula not observable. **Legs:** Femora without macrosetae, spines, or tubercles. Tibiae: Long ventral row/seam bifid scales present, shorter dorsal row; presence/absence mesotibial spurs not observable; apex of mesotibia and much of metatarsomeres with thick, dark setae (lengths almost equal to tarsal width). Tarsi: pro- and mesotarsus with biserial ventral rows of bifid scales (mesal row thickest); metatarsomeres 1–4 laterally flattened, expanded, widths $1 > 2 > 3 > 4 > 5$; lengths $3 > 1 > 2 > 4 > 5$.

Abdomen: Slightly longer than thorax, wings extended well beyond apex of abdomen. Six large tergites dorsally, 3 small tergites tucked ventrally (tergites 7 and 8 very short); epandrium (tergite 9) about same length as tergite 6. Tergites 1 and 2 with numerous long, fine setae laterally; middle portions of tergites 1 and 2 and others with very sparse, short setulae. Tergite 6 with 3–4 stiff, long, thick setae on posterior margin. Sternites: Only 3 large ones visible. **Male terminalia:** Epandrium with a few, very small scattered setulae, U-shaped in posterior view; surstylus well developed, triangular, articulates with (but not connected to) epandrium. Cerci ovoid, setulose. Other details not visible.

SPECIMEN EXAMINED: Holotype, Male, AMNH DR-14-736, in amber from the Dominican Republic (Early Miocene). The fly is entirely preserved, but a layer of bubbles in the amber on the right side is very close to the specimen; left lateral and dorsal views are best observed. Portions of eyes have a silvery layer of air. The fly may have been velvety black, as it reflects very little light. The amber piece was embedded in synthetic resin and trimmed close to the fly for optimal observation.

ETYMOLOGY: Referring to the Dominican Republic, the country of origin.

Platypezidae, genus and species undetermined

Figure 36

SUMMARY: Partial male specimen in Lebanese amber, missing most of head, some of thorax, all of legs and abdomen; wing entirely preserved. Eye with dorsoventral differentiation of facets; thorax with at least 2 pairs prescutellar dorsocentrals (presence/absence acrostichals and serial dorsocentrals not observable); wing with Sc very long, R_{4+5} terminating at apex of wing; M forked, slightly asymmetrical; dm-cu distant from wing margin by $4\times$ its length; cell cup short, acute, length slightly less than length of apical vein. Microtrichia not observable.

DESCRIPTION: (male only). **Head:** Eye with facets dorsoventrally differentiated (dorsal ones larger); dorsal margins lost, not observable. Occiput apparently bare. **Antenna:** Scape bare and pedicel lost, flagellum detached but close to body; basal flagellomere roughly triangular, with deep medial emargination; arista terminal, basal two aristomeres (flagellomeres 2 and 3) small, tubular; apical aristomere fine, longer, entirely bare. **Thorax:** much of it lost at surface and in amber. Acrostichals not observable; 2 pairs prescutellar dorsocentrals present, presence/absence of serial dorsocentrals not observable. Supraalar, postalar, notopleural setae not observable; 1 (pair?) scutellar setae preserved; prescutellum absent. **Wing:** Relatively short, broad, length/

width 1.9. Tinting between Sc and R_1 not observable; pterostigma absent. Termination of vein C not observable (wing tip and posterior edge lost at surface of amber), C with spinules. Vein Sc long, $0.55\times$ length of wing; R_1 close and parallel to Sc, diverging at apex; R_{4+5} ending at wing tip. Crossvein r-m short, at level of middle of Sc. M forked, slightly asymmetrical, length M_1 slightly greater than stem of M (from dm-cu). Cells rm and bm complete. Crossvein dm-cu relatively short, distant from apparent margin of wing by $\sim 4\times$ its length. Cell cup slender, acute, slightly shorter than apical vein; CuA_2 straight, not curved; anal lobe large (folded in specimen), alula well developed.

SPECIMENS EXAMINED: AMNH JG79/76, in Acra Collection of Lebanese amber (Early Cretaceous) at the American Museum of Natural History.

COMMENTS: The specimen is one of only two Platypezidae known from Early Cretaceous amber of Lebanon, making these among the oldest Platypezidae. The specimen is not formally named here because the only significant diagnostic characters involve the wing venation. Most of the head, much of the thorax, all legs and the entire abdomen are lost. Absence of data on acrostichals, dorsocentrals, and leg characters (e.g., bifid scales, metatarsomeres) results in too much uncertainty regarding placement. Distinctive features of the wing venation are the very long Sc vein and dm-cu distant from the apparent margin of the wing.

FAMILY IRONOMYIIDAE

DIAGNOSIS: Relatively stout-bodied flies; male frons very narrow to partially holoptic, no differentiation of facets; eyes bare. Flagellomere 1 in some species cordate to reniform, basal margin deeply emarginate; in some Cretaceous species with deep basal seam. Arista apical to preapical, micropubescent to bare, 3-articled (with 2 small, ringlike basal articles); palp 1-segmented; vibrissa absent. Prescutellum present, lenticular; scutellum with 8 marginal setae (median ones

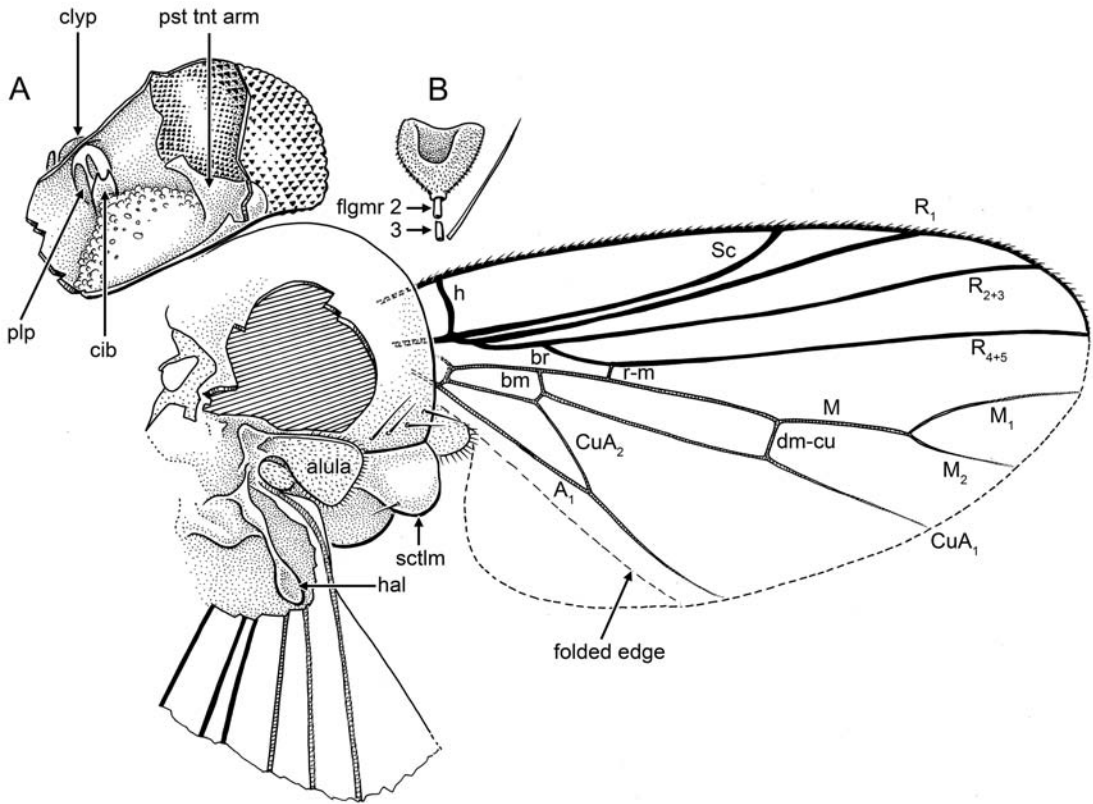


FIG. 36. Platypezidae indet., male in Early Cretaceous amber from Lebanon, AMNH JG 79/76. **A.** Entire body, as preserved, showing exposed internal structure of head. **B.** Detached antenna, as preserved.

longest), dorsal surface with or without small setae. Wing membrane glassy, entirely or largely without microtrichia; faint stigma between apices of Sc and R_1 ; Sc free at base and apex, fused with R_1 for most of its length. Sc long, ca. $0.50\text{--}0.65\times$ length of wing; R_{4+5} ends at wing tip; C ends at tip of R_{4+5} ; A present, incomplete.

COMMENTS: This diagnosis was made more inclusive in order to accommodate the Cretaceous fossils, the family definition previously applying just to the Recent type genus. There is one living genus of the family, *Ironomyia* White (in eastern Australia, below), and five fossil genera, all from the Cretaceous (Early [Berriasian] to Late [Santonian]): *Cretonomyia* J.F. McAlpine (McAlpine, 1973), *Eridomyia* Mostovski and *Hermatomyia* Mostovski (Mostovski, 1995), *Palaeopetia* Zhang (Mostovski, 1995, herein) and *Proironia* in Bur-

mese amber (herein). With the exception of *Cretonomyia*, all the fossils are from central and eastern Asia. Interestingly, there is no fossil ironomyiid known from the Cenozoic, despite the wealth of insect fossils from this period. Perhaps by this time the occurrence of ironomyiids had already contracted into Australia.

The compression fossils seem to be well placed in this family, based on the unique condition whereby Sc and R_1 are fused for all but their base and apices, although in all of them veins M_1 and M_2 are plesiomorphically forked, with a stem attached to the apex of cell d (instead of each directly attached to d). Other plesiomorphic features of *Palaeopetia* are discussed below, based on my new observations of specimens in Burmese amber. *Cretonomyia pristina*, in Late Cretaceous amber from western Canada, is a

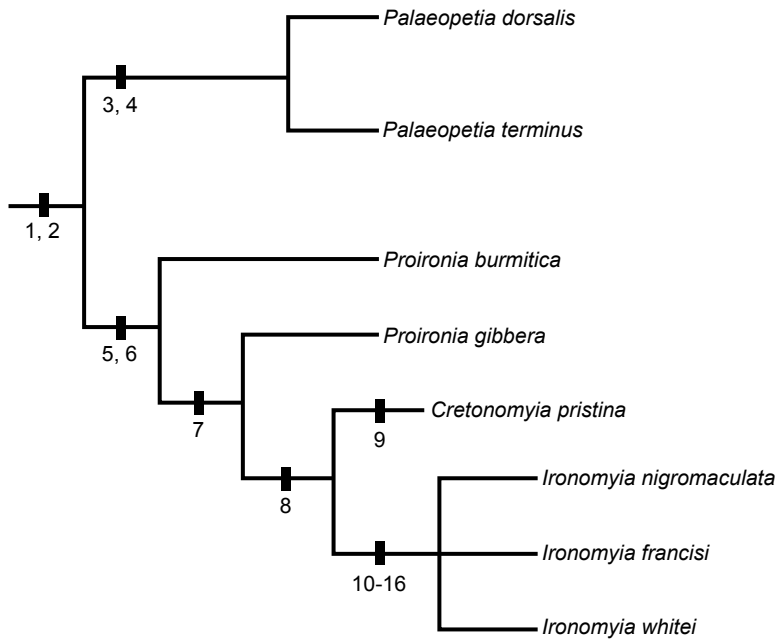


FIG. 37. Cladogram of amber fossil and Recent Ironomyiidae. Numbers on cladogram refer to synapomorphies given in table 3.

TABLE 3
Characters in the cladogram for Ironomyiidae (fig. 37)

1. Vein Sc joined to R ₁ in middle, with both veins free basally and apically.
2. Labellum small, width barely greater than width of prementum.
3. Legs (especially tibiae) with large, long, stout setae that are nearly perpendicular to longitudinal axis of leg segment.
4. Basal flagellomere with groovelike seam on lateral and mesal surfaces.
5. Wing membrane entirely devoid of microtrichia, even at wing margins.
6. Antennal pedicel with fingerlike lobes extended into basal flagellomere, one on mesal and one on lateral surface.
7. Cell d apically acute (position of crossvein dm-cu is acute to veins it connects).
8. Veins M ₁ and M ₂ connected directly to cell d (no stem).
9. Fusion of veins Sc and R ₁ short, less than 0.4× vein lengths (vs. >0.6×).
10. Eyes not holoptic or dorsally touching in males.
11. Veins R ₂₊₃ and R ₄₊₅ very close, nearly parallel.
12. Anal lobe of wing well developed, protruding.
13. Acrostichal setae on mesoscutum reduced to two rows (vs. abundant and scattered).
14. Dorsocentral setae small, reduced.
15. Proboscis slender, rigid, extended well beyond oral margin; labrum long.
16. Thorax and abdomen with dark, bold, sexually dimorphic markings of velvety black and silvery pruinescence.

definitive ironomyiid, its pedicel even with the fingerlike lobe extending into flagellomere one (on medial and lateral surfaces), and a short cup cell, as in *Ironomyia*. It differs from *Ironomyia* by the following, mostly plesiomorphic features: Proboscis shorter, labellum broader; postvertical setae more strongly developed; 3 (vs. 2) notopleural setae; fore- and midtibiae with preapical dorsal seta; wing with Sc fused with R_1 for only a short segment, cell dm apparently stout (though not well preserved in the unique fossil).

McAlpine (2008) disputed that *Lebambromyia acrai* Grimaldi and Cumming, in Early Cretaceous amber from Lebanon, was an ironomyiid. Indeed, it has many plesiomorphic features: Sc parallel and very close to but not fused with R_1 (though sclerotized between them), vein dm-cu not oblique; cell cup relatively large; wing membrane with microtrichia; M_{1+2} unforked; flagellomere 1 with deep emargination, but cordate, and without fingerlike lobe of pedicel. Upcoming phylogenetic work will determine whether *Lebambromyia* is a very primitive stem group to Ironomyiidae, as previously suggested (Grimaldi and Cumming, 1999).

Relationships of *Ironomyia* to other basal Cyclorrhapha have been extensively discussed, the consensus being that it is a close relative to the Phoridae sensu lato (including Sciadocerinae) (Griffiths, 1972; Sinclair et al., 2013; Wiegmann et al., 2011), although Brown et al. (2015) hypothesized an Ironomyiidae + (Lonchopteridae + Phoridae) relationship, and McAlpine (2008) was equivocal but seemed to favor a close relationship of Ironomyiidae with Eumuscomorpha (Syrphidae + Pipunculidae + Schizophora). An ongoing study of mine will further explore the relationships of Ironomyiidae to other families. Given the extralimital fossils of ironomyiids in the northern hemisphere, the phylogenetically basal position of the family among Cyclorrhapha, and the very restricted distribution of the three Recent species, *Ironomyia* is clearly a highly relict genus.

A cladogram of relationships of the three genera of Ironomyiidae preserved in amber (all from the Cretaceous), plus the living genus, is presented in figure 37. It is based on 16 morphologi-

cal characters, listed in table 3. Results are discussed under the respective genera.

Ironomyia White

Ironomyia White, 1916: 216. Type species *I.*

nigromaculata White, 1916; J.F. McAlpine, 1967 (as family); D.K. McAlpine, 2008 (revision of *Ironomyia* species).

DIAGNOSIS: (based on McAlpine and Martin, 1966; J.F. McAlpine, 1967; D.K. McAlpine, 2008, with modifications): Relatively stout flies with dark, bold velvety markings that contrast with pruinulent silvery and gray areas; patterns sexually dimorphic. **Head:** Antennal pedicel with fingerlike lobe inserted into deep, notchlike emargination of flagellomere 1 (flagellomere 1 strongly reniform, with two “sacculi” [McAlpine, 2008], i.e., sensory pits). Proboscis relatively long and slender, labellum small. **Thorax:** Dorsocentral setae small, reduced in number; acrostichals in two rows. **Wing:** R_{2+3} and R_{4+5} close, parallel, slightly sinuous; cell d apically acute, with strongly oblique dm-cu; cell cup relatively short; anal lobe well developed. **Abdomen and Terminalia:** Tergites 1 and 2 partially fused (separated via sulcus only, no intersegmental membrane [D.K. McAlpine, 2008]); sternites well developed. Male terminalia circumverted 360°, symmetrical, ventroflexed; surstyli well developed, not fused to epandrium; postgonites absent (as in Phoridae), sternite 8 fused to epandrium, phallapodeme articulated (Sinclair et al., 2013). Female terminalia telescoping, with long membranous section posterior to segment 7; three spermathecae.

TYPE SPECIES: *I. nigromaculata* White.

COMMENTS: There are three species of *Ironomyia*, all Recent, the other two species besides the type being *I. francisi* D.K. McAlpine and *I. whitei* D.K. McAlpine. The genus is distributed in eastern Australia from Queensland to Tasmania (McAlpine, 2008). According to McAlpine (2008) these flies are uncommon, usually found on tree trunks, sometimes attracted to lights. Their life histories are unknown.

Palaeopetia Zhang

Palaeopetia Zhang, 1987: 595.

Sinolestia Hong and Wang, 1988 (synonymy by Mostovski, 1995). Type species *S. lata* (Hong and Wang).

DIAGNOSIS: Vein Sc fused to R_1 for most of their lengths; pterostigma (between apices of Sc and R_1) well sclerotized; M_1 - M_2 forked, with short stem connected to apex of cell d; crossvein dm-cu perpendicular to longitudinal veins (not oblique). As seen in at least the two species in Burmese amber: pedicel without fingerlike lobe; flagellomere 1 with distinctive seam on lateral and mesal surfaces; wing membrane largely glassy, with microtrichia only at trailing margin of wing; acrostichals numerous, scattered, as in *Cretonomyia* (not in 2 rows as in *Ironomyia*); scutellar setae larger than in *Ironomyia*; thorax with 4 notopleural, 1 large pair dorsocentral, 1-2 large postalar setae; midleg with large stiff setae, 1 on femur, 3-5 on tibia.

TYPE SPECIES: *P. laiyangensis* Zhang, 1987. Early Cretaceous, China (compression).

COMMENTS: There are nine species of *Palaeopetia* described thus far, all of them compressions from the Cretaceous. Besides the type species the others are the following: *P. lata* (Hong and Wang) (Early Cretaceous, China); *P. tertia* Mostovski, *P. volacris* Most., *P. longisaetigera* Most., *P. mina* Most., *P. commemorabilis* Most., *P. armata* Most., *P. bellula* Most., *P. asaetigera* Most. (Cretaceous of Eurasia and Siberia). These species were diagnosed largely on the basis of subtle differences in wing vein proportions (Mostovski, 1995b), nonetheless suggestive of significant past diversity of ironomyiids. I have examined some of the specimens described by Mostovski (1995b), including all of the types.

The amber species reveal the plesiomorphic nature of the genus, which appears to be a sister group to all other fossil and living ironomyiids based on the antennal structure and retention of some microtrichia on the wing membrane (fig. 37). Even though *Palaeopetia dorsalis*, n. sp., and

P. terminus, n. sp., are known only from opposite sexes, it is very doubtful that the species differences are sexually dimorphic, given especially the positions of the arista, setation of the thorax, and microtrichial patterns on the wing.

Palaeopetia dorsalis, new species

Figures 11; 38A, B, E, H; 39, 40B

DIAGNOSIS: Differs from *P. terminus*, n. sp., also in Burmese amber, by smaller size, wing shorter and broader (L/W 1.77, vs 1.89), with microtrichia covering more of the wing membrane; arista situated dorso-preapically (vs. terminal); 1 (vs. 2) postalar seta; posteriormost notopleural seta slightly longer than others (vs. 2× the size); anteriormost scutellar seta nearly equal in size to adjacent one (vs. 0.3× the size); hind tibia with dorsal row of 3 strong setae (vs. 6, alternating with smaller, thick setae).

The Burmese amber species of *Palaeopetia* can be separated from all the compression-fossil species by the following venational differences: apical separation of Sc and R_1 ca. 0.5× their length (i.e., these two veins fused for greater distances in the amber species); cell cup is slightly shorter and wider, the apex less acute.

DESCRIPTION (based on unique female): **Head:** Eyes large, occupying most of dorsal and lateral portions of head, female dichoptic; eye bare, no differentiation of facets. Female frons: relatively narrow, sides parallel, width approximately equal to distance between outer margins of posterior ocelli; frons glabrous, without setae, possibly without setulae (obscure); presence/absence of median furrow obscure. Ocelli well developed, raised above frons but not tuberculate; no ocellar setae; 2 short postocellars present. Occiput broad, gently and largely concave, lateral and dorsal margin near eye and vertex rimmed on each side with ca. 25 stout, stiff, flattened setae, lengths 6-8× diameter of eye facet. Occipital foramen very large, width ca. 0.3× occiput width. No vibrissa or genal setae. **Antenna:** Scape subcylindrical, short, with

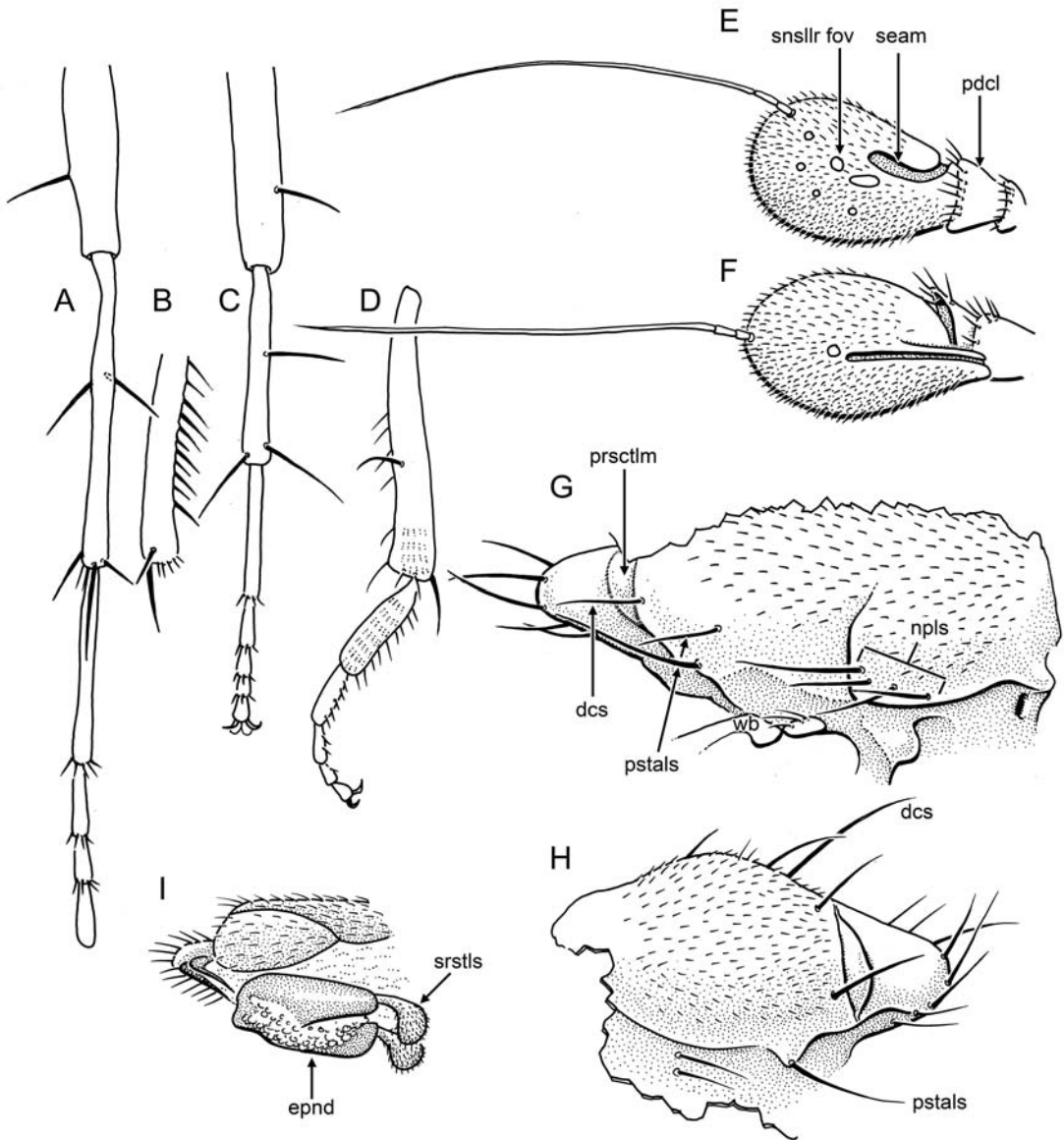


FIG. 38. *Palaeopetia* n. spp. (Ironomyiidae) in Burmese amber. **A, B, E, H.** *P. dorsalis*, holotype male, AMNH Bu-FB34. **C, D, F, G, I.** *P. terminus*, holotype male, AMNH Bu-SE2/6. **A, C.** Midlegs. **B, D.** Portions of hind leg. **E, F.** antenna, lateral. **G, H.** Thorax, as preserved. **I.** Male terminalia, ventrolateral view.

transverse row of 3 stout, black setulae dorsally; pedicel very short, rimlike, dorsal margin with row of 5–6 stout, short setae. Basal flagellomere large, laterally flattened, roughly drop shaped, with long groove-like seam on inner (mesal) surface, shorter seam on lateral surface, plus some

apparent foveae (sacculi, sensu McAlpine, 2008). Arista bare; attachment dorsal-preapical, slightly lateral (not on dorsal edge), 3-articled, basal 2 articles small; total arista length 2.5× that of basal flagellomere. **Mouthparts:** Short, barely protruding beyond oral margin; palp 1-seg-

mented, extended slightly past labellum; labellum small, prementum and clypeus not observable. **Thorax:** Brown, notum slightly convex (not dome shaped) in lateral view. Acrostichals numerous, fine, evenly scattered on notum (not in rows). One pair of dorsocentral setae, stout, close to scutellum, length ca. equal to that of apical scutellar setae; distance between dorsocentrals slightly greater than length of dorsocentral. Prescutellum well developed, lenticular, width almost equal to that of scutellum base. Scutellum with 4 pairs stout marginal setae, increasing in length apicad, apical pair upturned and slightly cruciate; dorsal surface of scutellum without fine setulae. One very long postalar seta, length ca. $1.8\times$ the dorsocentral. Notopleural setae in row of four (entirely preserved on right side). No pleural setae present; prosternum not observable. **Wing:** Membrane entirely hyaline, no markings or infusate areas; microtrichia absent except at wing margin between tips of R_{2+3} and CuA_2+A_1 . Wing short, broad, L/W 1.77 (from tip of wing to level of crossvein h). Vein C ends at tip of R_{4+5} . Sc long, joined to R_1 for $0.65\times$ its length, separated at base and at apex, membrane slightly darkened between apical fork of Sc and R_1 . Stem of Rs short, fork of R_{2+3} - R_{4+5} long, apices of Rs veins straddling tip of wing. Crossvein br-m very short, cell d present, L/W 3.6, apically truncate (not acute) (dm-cu perpendicular to M_2 and CuA_1). Basal cells bm and cup closed; cell cup triangular; vein CuA_2+A_1 complete, reaching wing margin; A_2 present, incomplete, anal lobe very shallow. **Legs:** Metafemur and metatibia slightly longer and thicker than in other two pairs of legs. Basitarsomere on all legs approximately equal in length to remaining, distal tarsomeres. All coxae with 2 setae (ventral on fore- and midlegs, dorsal on hind legs). Pro- and metafemur without setae; mesofemur with long, stout seta on anterior surface, $\frac{1}{3}$ from femur apex. Protibia with short middorsal seta, 2 apical setae (lengths ca. equal to width of tibia). Mesotibia with 4 long setae: 2 midlength (anterior and posterior surfaces), 2 apical. Metatibia with 2 stout, long, lat-

eral setae, row of 4 shorter fine ones on dorsal edge; 1 large ventroapical seta plus several smaller ones. Metabasitarsomere slightly expanded. Pretarsal claws well developed, strongly curved; pulvilli well developed, slightly shorter than claw; empodium not visible (probably small and setiform). **Abdomen (female):** Length ca. equal to that of head + thorax, width slightly greater than thorax; tapered apicad. Eight well-developed tergites visible, none with macrosetae, covered overall with decumbent setulae, no apparent color/pruinescence patterns; tergites extend laterally over pleural membrane. Sternites well developed, broad, lateral margins nearly touching tergites, 7 sternites visible (first one probably small, hidden). **Female Terminalia:** Largely membranous; terminal sternite (8?) divided medially into 2 small oval sclerites; hypoproct well developed, apically pointed; cerci well developed, 1-segmented, cercus broad, with apical half darkly pigmented. Spermathecae not visible.

SPECIMENS EXAMINED: Holotype, female, AMNH Bu-FB34, in Burmese amber. In good condition, largely well preserved except for loss/damage of portions of thorax.

ETYMOLOGY: In reference to position of the arista on the basal flagellomere.

Palaeopetia terminus, new species

Figures 12; 38C, D, F, G, I; 40A

DIAGNOSIS: Distinguished from *P. dorsalis*, n. sp., as given in the diagnosis above.

DESCRIPTION: Very similar to *P. dorsalis* with the exception of the following features: **Head:** Antenna with arista terminal, not dorsal-preapical. Male eyes large, holoptic for length of approximately 8 facets; ocellar triangle and small portion of frons exposed; no differentiation of facets; ocelli on low tubercle, close together. **Thorax:** Posteriormost notopleural seta very long and robust, ca. $2\times$ the length and width of other notopleurals; 2 (vs. 1) postalar setae (anterior one finer). Transverse suture well developed.

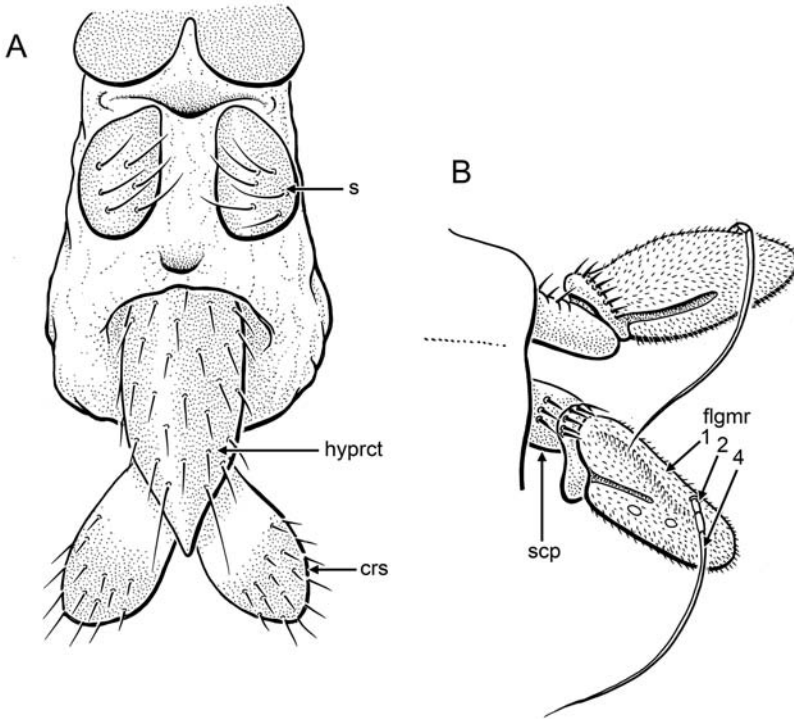


FIG. 39. *Palaeopetia dorsalis*, n. sp. (Ironomyiidae) in Burmese amber, holotype female AMNH Bu-FB34. **A.** Female terminalia, ventral view. **B.** Antennae, oblique dorsal view.

Anteriormost scutellar seta very small, length less than $0.3\times$ that of adjacent scutellar seta (vs. approximately equal in size). **Legs:** Hind tibia with dorsal row of 6 stout, slightly curved setae, alternating with smaller stout setae. **Wing:** As drawn: longer, L/W 1.89 (vs. 1.77), from tip to level of crossvein h. M_1 slightly more arched; microtrichia confined to wing margin. **Terminalia:** Epandrium glabrous, brown, apparently heavily sclerotized; laterally flattened (clamlike), with fine setae on inner edge; surstylus pendulous, setulose, curved and clavate, apparently articulating with ventrolateral portion of epandrium (not fused). Aedeagus and paraphallic structures not observable.

SPECIMENS EXAMINED: Holotype, male, AMNH Bu-SE2/6, in Burmese amber. In excellent condition.

ETYMOLOGY: In reference to the position of the arista on the basal flagellomere.

Proironia, new genus

DIAGNOSIS: Eyes virtually touching dorsally in male; antennal pedicel with fingerlike lobes extended into basal flagellomere on mesal and lateral surface; wing with membrane entirely glassy (no microtrichia); veins M_1 and M_2 with short to long stem (not connected directly to cell d); anal lobe of wing shallow; acrostichals numerous and scattered, not in rows.

TYPE SPECIES: *P. gibbera*, new species.

ETYMOLOGY: *Pro-* (first), and *-ironia* (from *Ironomyia*), in reference to the stem-group position of this extinct genus relative to *Ironomyia*. The genus name is feminine.

COMMENTS: The new genus is a stem group; it does not appear to have any features that are apomorphic with respect to *Ironomyia* and *Cretonomyia* (fig. 37). It seems preferable to have a separate genus for these two species, rather than

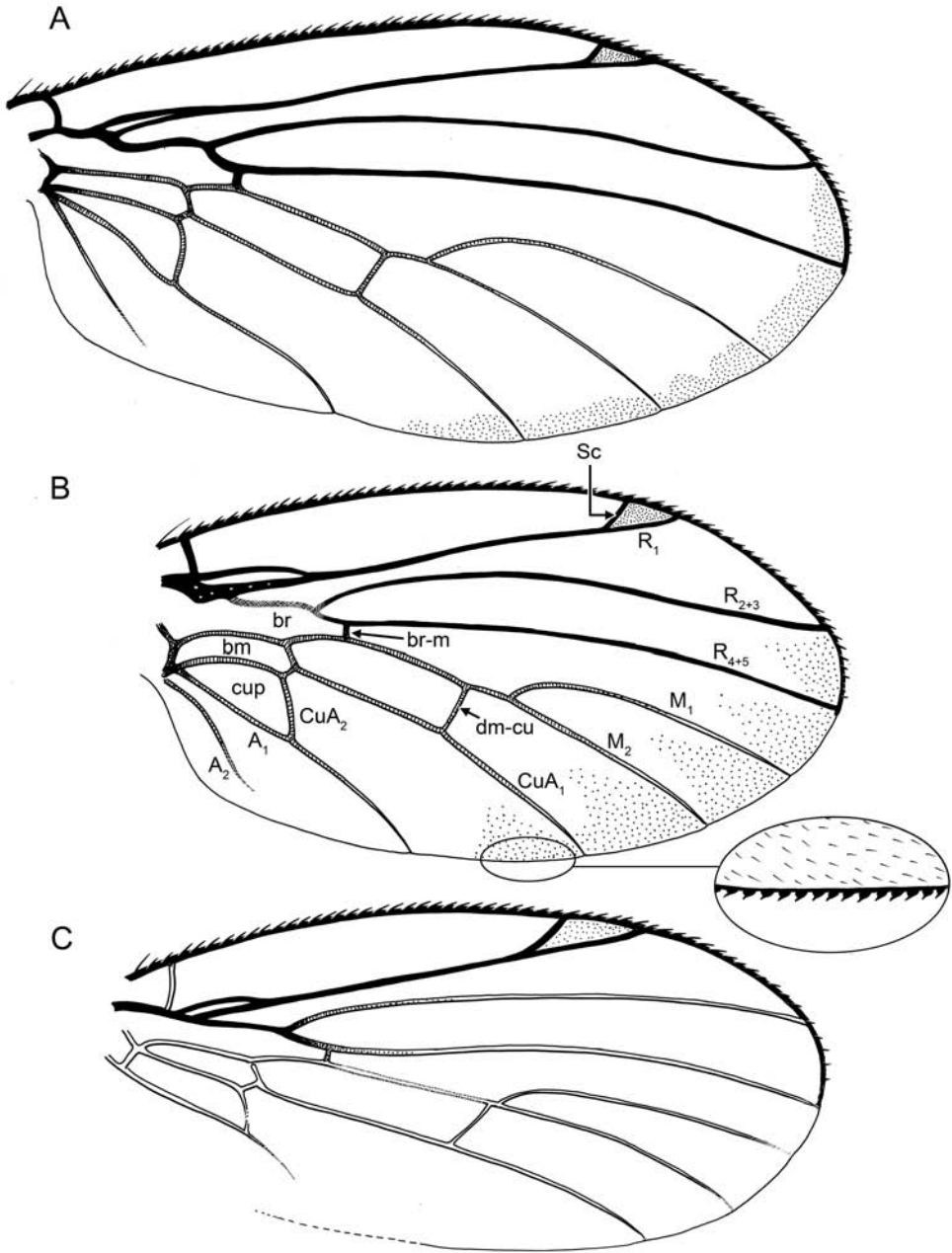


FIG. 40. Wings of fossil Ironomyiidae in Burmese amber. **A.** *Palaeopetia terminus*, AMNH Bu-SE2/6. **B.** *Palaeopetia dorsalis*, AMNH Bu-FB34. **C.** *Proironia gibbera*, AMNH Bu-SE7.

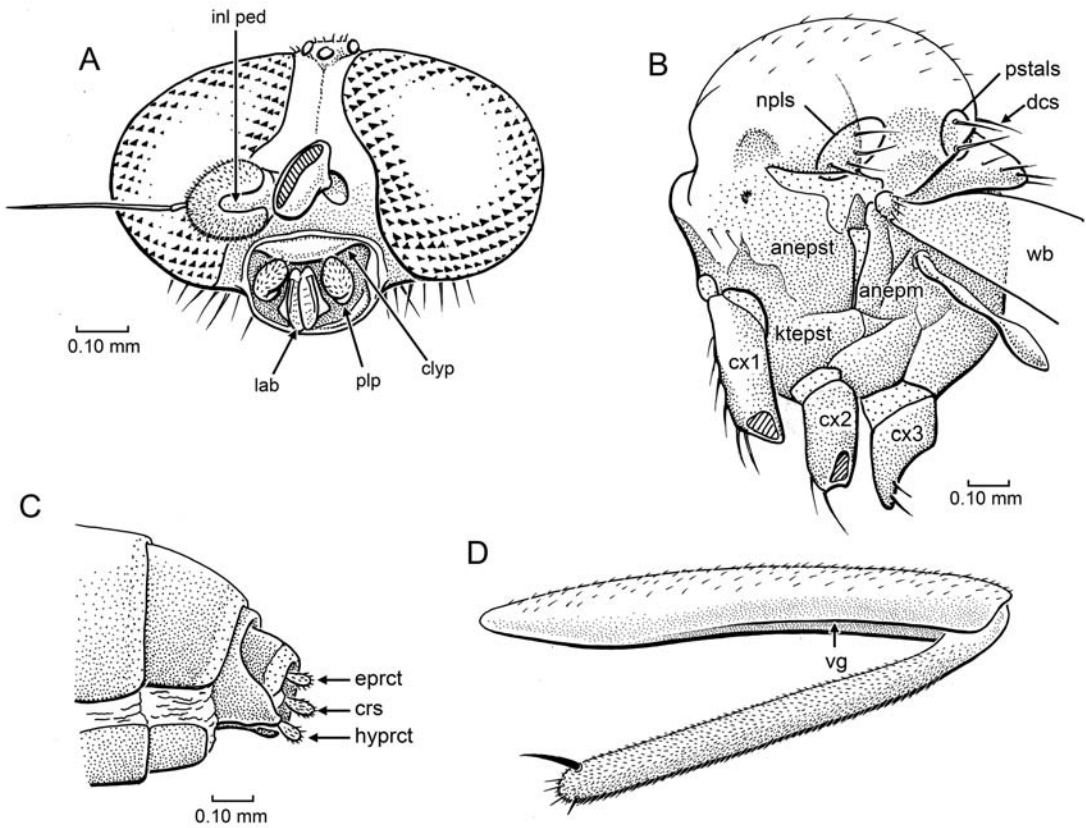


FIG. 41. *Proironia gibbera*, n. gen., n. sp. (Ironomyiidae), holotype female in Burmese amber, AMNH Bu-SE7. **A.** Frontal view of head. **B.** Left lateral view of thorax. **C.** Abdominal apex. **D.** Proleg: femur and tibia, lateral view.

expand the definition of the extant genus *Ironomyia*, which is quite apomorphic. Also, despite the list of differences between the two species, given in the diagnosis immediately below, they are actually quite similar. The most significant differences appear to be the orientation of cross-vein dm-cu and length of M_1 - M_2 stem.

***Proironia gibbera*, new species**

Figures 13, 41

DIAGNOSIS: Differs from the other species of the genus, also in Burmese amber, by the following: Head broader, concavity of occiput not nearly as deep; pedicel lobe long, more fingerlike, extended $>0.5\times$ the length of basal flagellomere

(vs. less than this, lobe more triangular); notopleural, postalar setae shorter; thorax deeper, scutum more dome shaped (vs. slightly flattened on top); pro- and mesocoxae not setose (vs. with dense, fine setae); mesofemur with longitudinal groove, nearly length of femur (vs. without); wing with costal edge convex (vs. flat), apical fork of Sc- R_1 larger; apex of wing broadly rounded (vs. acute); fork of M_1 - M_2 with very short stem; crossvein dm-cu oblique to M_2 and CuA₁ (vs. perpendicular).

DESCRIPTION: Head: Rather broad, depth/width 0.66. Occiput near posterior margin of eyes rimmed with row of stiff, whitish setae. **Eyes:** Bare, fully separated in female by distance slightly greater than outside width of lateral ocelli; no differentiation of facets. **Frons:** Dark

brown, largely bare, with a few fine, scattered, minute setulae; lateral margins parallel, modest emarginations around bases of antennae; median furrow present, faint; no ocellar, postocellar or frontal setae present. Face below antennae relatively short; oral cavity exposed anteriorly; clypeus broad but narrow; oral margin rimmed by protruding membrane. Vibrissa absent. **Antenna:** Bases very close, oval; scape very small, conical; pedicel with fingerlike lobe inserted into lateral and mesal surfaces of basal flagellomere; basal flagellomere subcircular, laterally flattened; arista terminal, with 1 or 2 small basal articles (not clearly observed); arista bare. **Mouthparts:** Compact, not protruding beyond level of basal flagellomeres. Palp small, globular, light in color; labellum small, laterally flattened, extended slightly beyond level of palps. **Thorax:** Very deep, depth ca. $1.1 \times$ the length; scutum arched, almost hemispherical in profile. Scutum with scattered, very fine, decumbent setulae (barely visible); one pair of dorsocentral setae, short, stout, very close to anterior margin of scutellum; scutellum with 4 pairs of short, stout setae; 4 notopleural setae, located just above pleural cleft and anterior to transverse suture; 2 postalar setae; prescutellum well developed, lenticular. **Wing:** Relatively broad, width/length 0.51, apex broadly rounded, anterior (costal) edge convex (not flat); membrane entirely glassy, no microtrichia (even near wing margin). Vein C ends at apex of R_{4+5} . Sc long, fused to R_1 for $0.62 \times$ its length, both veins free at base and apex. R_{2+3} and R_{4+5} long, nearly parallel; crossvein br-m very short; cell d long and narrow (L/W 5.55), apex acute (crossvein dm-cu oblique). M_1 and M_2 joined at base by very short stem connecting to cell d; cell cup narrow, apex acute. A_1 , A_2 , anal lobe and alula not entirely visible.

Legs: Slender. All coxae with a few, fine, light setae; femora without macrosetae. Protibia with thick, short, preapical seta on mesal surface, ca. 10 short transverse, ctenidial-like rows of fine setae, apical row long and comblike; tarsomeres 1–4 with short ctenidial combs. Mesofemur with narrow but well-defined longitudinal groove on

ventral surface (nearly length of femur), to which tibia must fit against. Mesotibia with minute, spurlike lobe on ventral surface, spurlike ventroapical sea; tarsomeres 1–4 with short rows transverse ctenidia. Metatarsus same as mesotarsus. Pretarsus with claws well developed, pulvilli slightly shorter than claws; empodium setiform.

Abdomen: Relatively short, tapered apicad; with fine, short, scattered setulae on tergites and sternites, no macrosetae. Eight tergites and 7 sternites visible, well developed, narrow pleural membrane exposed. Dorsal margin of tergite 7 very short, hidden beneath posterior margin of tergite 6. Cercus 1-segmented. **Female Terminalia:** Largely retracted, not visible.

SPECIMENS EXAMINED: Holotype, female, AMNH Bu-SE07, in Burmese amber. In excellent condition.

ETYMOLOGY: From Latin *gibber* (L., “hunched”).

Proironia burmitica, new species

Figures 14, 42

DIAGNOSIS: Distinguished from its congener as given in the diagnosis above.

DESCRIPTION: **Head:** Depth/width 0.92. Occiput near posterior margin of eyes rimmed with row of stiff, whitish setae that point backward. **Eyes:** Bare; meeting dorsally (or virtually so) for distance ca. 8 facets; no differentiation of facets; medial edges emarginate around eyes. **Frons:** A barely exposed sliver, dark brown; faint median furrow present on dorsal sliver of frons; medial edges emarginate around antennae; no ocellar, postocellar, or frontal setae present. Ocellar triangle raised; lateral/posterior ocelli closer to each other than to anterior ocellus. Face below antennae very short; oral cavity partly exposed anteriorly; clypeus narrow, Ω -shaped; oral margin not rimmed by protruding membrane. Vibrissa absent. **Antenna:** Bases very close, scape small, short and funnel shaped; pedicel with triangular lobe inserted into lateral and mesal surfaces of basal flagellomere, lobe

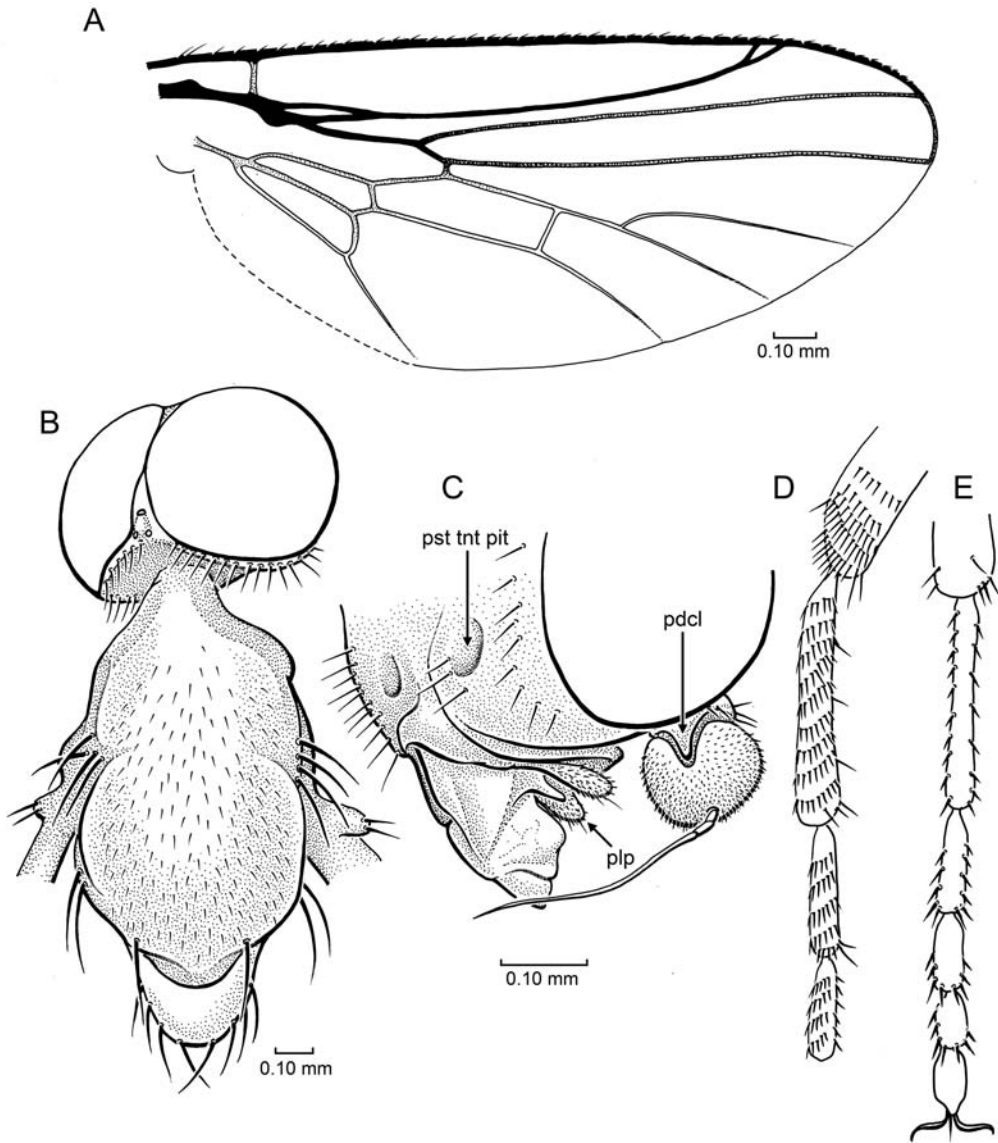


FIG. 42. *Proironia burmitica*, n. gen., n. sp. (Ironomyiidae), holotype male in Burmese amber, AMNH Bu-SE2/8. **A.** Wing. **B.** Dorsum of head and thorax. **C.** Oblique posterior view of head. **D.** Hind leg, mesal view (not showing tarsomeres 4 and 5). **E.** Midtarsus, dorsal view.

not quite $0.5\times$ length of basal flagellomere; basal flagellomere subcircular, laterally flattened, dorsal third light, ventral $2/3$ darker, brown; arista terminal, with 2 small basal articles, length of each article ca. $2\times$ its width; arista bare. **Mouthparts:** Compact, not protruding beyond level of basal flagellomeres (as preserved). Palp small,

globular, light in color; labellum small, laterally flattened, extended slightly beyond level of palps. Occiput dark brown, dorsal portion deeply concave. **Thorax:** Depth ca. $0.95\times$ the length; scutum convex in profile, slightly flattened on top. Scutum with scattered, very fine, very decumbent setulae (most visible laterally).

One pair of dorsocentral setae present, stout and short, length slightly less than length of scutellum; very close to anterior margin of scutellum. Scutellum with 4 pairs of short, stout setae, apical pair upright with tips crossing; 4 stout, stiff notopleural setae, located just above pleural cleft and anterior to transverse suture; 2 postalar setae; prescutellum well developed, lenticular.

Wing: Width/length 0.48, apex slightly acute, anterior (costal) edge virtually flat; membrane entirely glassy, no microtrichia (even near wing margin). Vein C ends at apex of R_{4+5} . Sc long, fused to R_1 for $0.77\times$ its length, both veins free at base and apex. R_{2+3} and R_{4+5} long, nearly parallel; crossvein br-m very short, cell d L/W 3.0, apex square (crossvein dm-cu perpendicular to longitudinal veins); M_1 and M_2 joined at base by stem connecting to cell d, stem $0.21\times$ length of stem + fork; cell cup narrow, apex acute. A_1 , A_2 , anal lobe and alula not entirely visible. **Legs:** Slender, brown, pro- and mesocoxae with sparse brush of ca. 10 fine, long setae ventrally (metacoxa bare); femora without macrosetae. Protibia with thick, short, preapical seta on dorsal surface, ca. 8 short, transverse, ctenidial-like rows of fine setulae, tarsomeres 1–4 with short ctenidial combs. Mesofemur without longitudinal groove on ventral surface. Mesotarsomeres 1–4 with 2 longitudinal rows small, stout setae on ventral surface. Metatarsus same as protarsus. Pretarsi with claws well developed, pulvilli shorter than claws; empodium setiform, fine and projecting. **Abdomen (Male):** Relatively short, base thick; with fine, short, erect, pilelike setulae on tergites, no macrosetae. Tergites large, covering most of lateral surface of abdomen; dark brown. Six well-developed tergites visible (sternites not exposed); narrow pleural membrane exposed. Epandrium large, bulbous, ventroflexed, tucked under tergite 7. **Male Terminalia:** Not exposed.

SPECIMENS EXAMINED: Holotype, male, AMNH Bu-Se2/8, in Burmese amber. Complete, very well preserved.

ETYMOLOGY: In reference to *burmite*, a common term for Burmese amber.

FAMILY PHORIDAE, SENSU LATO

DIAGNOSIS: Wing: Vein Sc fused to R_1 except at base (i.e., fused at apex as well); R veins thick, sclerotized (others tubular, transparent to spectral); cell dm minute and at base of wing (sciadocerines) or lost (Euphorida), cell cup very small and basal (open apically, CuA_2 incomplete); pterostigma absent, anal lobe reduced; C ends at apex of R_{4+5} , R_{4+5} well before wing tip; $CuA-CuP$ interrupted at base. Both sexes with stridulum on proleg: base of profemur with scalelike teeth (the scraper) on the inner (mesal surface); outer surface of procoxa with longer, filelike rows, scales, or microtrichia (the file, or plectrum). Ocellar setae large, upright; male genitalia asymmetrical.

COMMENTS: The family concept above includes the Sciadocerinae, following Brown (2007a) and Brown et al. (2015). A hypothesis of relationships of the genera of sciadocerines and subfamilies of living (crown-group) and stem-group Euphorida is presented in figure 43, based on 36 morphological characters (table 4). Some of these characters were used in Brown (2007a) and Brown et al. (2015); others are newly presented here or reinterpreted. For example, Brown (2007a) partly defined all living and extinct Sciadocerinae on the basis of asymmetrical male genitalia, a feature that I consider a ground-plan character of the entire Phoridae (contra Nakayama, 2012), since all male Cretaceous stem-group Euphorida (prioriphorines) that I have examined have this feature as well, as do many extant Euphorida.

The species and ecological diversity of Euphorida is enormous. The approximately 4100 described species (about the 15th dipteran family in species number) represents perhaps 10% of the actual diversity. For example, in an intensive survey of the Diptera species in a Costa Rican forest, Phoridae was the second most diverse family (with 407 species), after Cecidomyiidae (Borkent et al., 2018; Brown et al., 2018). They are usually the most abundant brachyceran family in Malaise traps. Propelled by large, flattened coxae and femora, the stout-bodied phorids scuttle among

spaces in substrates with quick, zigzag movements. Since the wings are folded tightly over the dorsum of the body, they pervade the interstices of leaf litter and nests and galleries of other insects. These are the beetles of the Diptera.

There is little doubt that Phoridae is also the most ecologically diverse family of flies (reviewed by Disney, 1994). Breeding substrates and hosts include carrion, feces, and dead and dying insects and snails; the refuse, provisions, and brood of social insect nests; in myriad fungi (even highly toxic *Amanitas*), in necrotic fruits and vegetation, and as parasitoids and parasites of a wide array of animals (slugs, terrestrial snails, spider egg sacs, millipedes, beetles, aphids and scale insects, ants, termites, bees, some caterpillars, and grasshoppers). A few species are highly polyphagous, most are very specialized in diet. *Myriophora*, for example, are attracted to wounded or stressed millipedes by the scent of pungent defensive secretions, into which the flies lay their eggs. A recent monograph on this genus (Hash and Brown, 2015) delimited 65 New World species, 57 of them newly described. Species of *Apocephalus* ("ant-decapitating" flies) are well-known as parasitoids of ants: at the La Selva Biological Station in Costa Rica 127 species of the genus were identified; many species in this genus are restricted to certain species of ant hosts (Brown and Feener, 1995). Inquiline phorids in particular can have dramatic sexual dimorphism, with the female being brachypterous or apterous, microphthalmic or even eyeless (Disney, 1994).

When and how did such spectacular diversity arise? Based on characters 1–4 in table 4, the species *Archisciada lebanensis* (Grimaldi and Cumming, 1999), in Early Cretaceous amber from Lebanon, ~125 Ma, appears to be a very basal stem group to the Phoridae (fig. 43). All other Cretaceous, true Phoridae are either sciadocerines or prioriphorines (fig. 43), the oldest of which occurs in amber from the Albian (~105 Ma) of Álava, Spain, and Charentes-Maritime, France (Arillo and Mostovski, 1999; Solorzano-Kraemer et al., 2011). Prioriphorines are fairly

abundant in Burmese amber, with perhaps 6–7 species; these will be described in a separate paper by other authors. They also occur in Late Cretaceous amber from New Jersey, Siberia, and Alberta (Brown and Pike, 1990; Mostovski, 1999; Grimaldi and Cumming, 1999; review in Brown, 2007a), and are morphologically rather uniform. By the Eocene, modern subfamilies and even genera appeared, though the generic identities of Baltic amber species described by Brues (1939) and other early authors are being revised (e.g., Brown, 1999, 2007b). In Miocene Dominican and Mexican amber all phorids are modern genera, including the first appearance of the massive genus *Megaselia*. Thus, the evolutionary history of the Euphorida appears to have been entirely within the Cenozoic, with a caveat that the latest Cretaceous (Maastrichtian) is poorly known. As such, the Euphorida is one of the most extraordinary radiations of the past 66 Ma, second only to the Schizophora.

THE STRIDULATUM: Both sexes of the two living sciadocerines, and several genera of Euphorida that were examined (*Dohrniphora* sp., *Diplonevra* sp., *Megaselia* sp.) have a file-and-scraper system—or stridulum—on their forelegs (figs. 44, 45). The file is on the apex of the coxa on the outer (lateral) surface, and the scraper is on the inside (mesal) surface of the femur, at the base. Apparently, when the femur is folded against the coxa the file and scraper must rub over each other, creating a faint rasping sound. Phorids probably fold the forelegs repeatedly and very quickly while standing or running on four legs. I did not observe any sexual dimorphism in the stridulum in *Sciadocera*, specimens of *Archiphora* being too few to tell.

In *Sciadocera* (fig. 45) the scraper consists of 10–14 coarse, scalelike teeth on the inner surface of the profemur, near the base, the proximal end of which approaches the dorsal surface of the femur, its distal end angled and receding away from the femur base and approaching the ventral margin. The scraper lies approximately in the middle to near the distal edge of a slightly recessed area on the femur that lacks setae (but

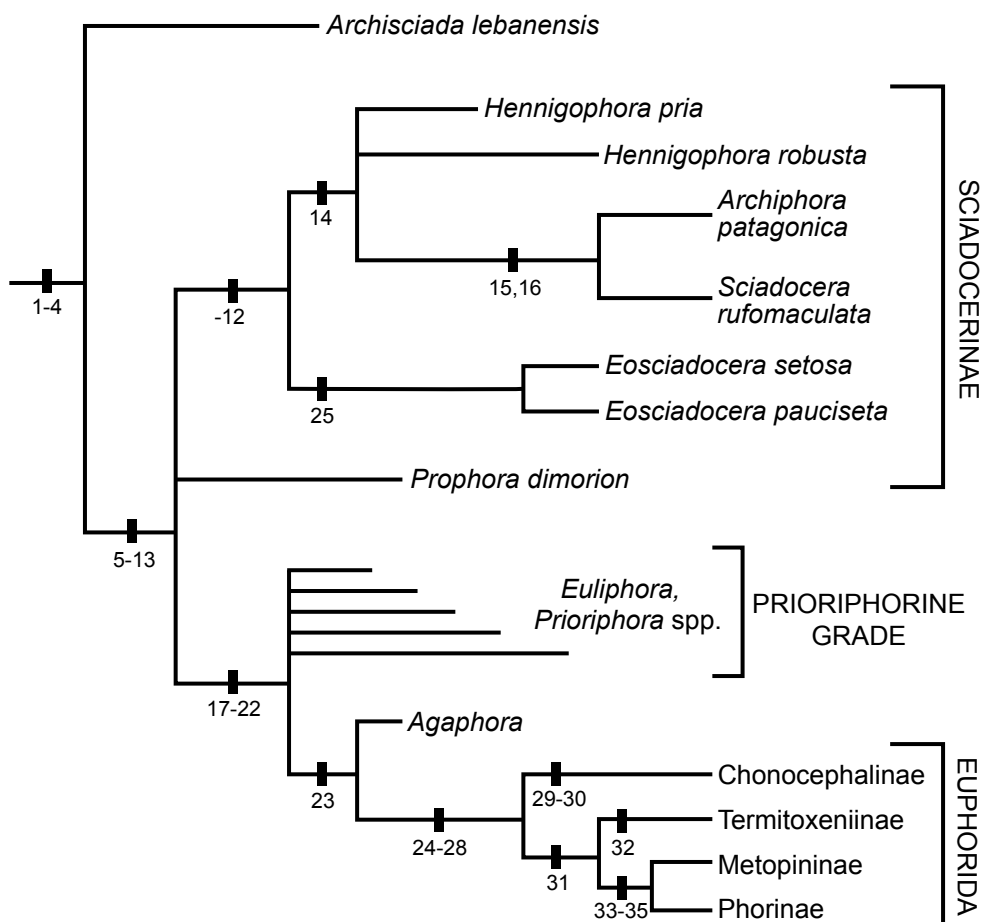


FIG. 43. Cladogram of fossil and Recent subfamilies of Phoridae, including Sciadocerinae. Numbers on cladogram refer to synapomorphies given in table 4.

has microtrichia). The “teeth” of the scraper look like minute carinae under light microscopy; under SEM these are scalelike, with the receding ends abruptly tapered to a fine point. The scraper scales gradually increase in size distad, though the apical one is small. The length of each scale is approximately 30 μm , that of the carinalike portion ca. 18 μm , the pointed tip ca. 6 μm . Each carina has a shallow, microscopic groove along the edge. Scraper scales are spaced approximately 15 μm (measured base to base from adjacent ones). Due to the rarity of *Archiphora* specimens I used an uncoated specimen for SEM, which did not image well (fig. 44). Thus, detailed structure of the scraper in that species was not observed.

The file was observed in both living sciadocerine species under SEM. In both, the file consists of more than 100 short, filelike ridges in a row that arches from the pointed lobe of the coxal apex to well around the curved distal articulation of the coxa. The file ridges are parallel to each other, the distal end of each having a minute microtrichia. In *Sciadocera* each file ridge is approximately 7 μm in length; in *Archiphora* 5 μm . The file ridges are considerably more packed in *Archiphora*, approximately 1.4 μm between adjacent ridges, versus 6 μm in *Sciadocera*. I counted approximately 110 file ridges in *Sciadocera*; there are considerably more than this in *Archiphora*.

TABLE 4
Characters in the cladogram for Phoridae sensu lato (fig. 43)

1. Cell dm minute and at base of wing (sciadocerines) or lost (Euphorida).
2. Pterostigma lost.
3. R ₄₊₅ ends well before wing tip.
4. Male genitalia (epandrium, epandrial lobes, surstyli, periphallic appendages) slightly to significantly asymmetrical.
5. Anal lobe of wing reduced.
6. Cell cup very small and basal (open apically, CuA ₂ incomplete).
7. Vein C ends at apex of R ₄₊₅ .
8. Sc fused to R ₁ except at base (i.e., fused at apex as well).
9. CuA, CuP interrupted at base.
10. R veins thick, sclerotized; others tubular, transparent to spectral.
11. Pair of large ocellar setae, upright (parallel or divergent), not proclinate.
12. Frons with median groove/sulcus (absent in sciadocerines and lost in various modern euphorids).
13. Stridulatum on proleg in both sexes: scraper on profemur, file on procoxa.
14. Empodium absent or highly reduced/minute.
15. Stem of M ₁ and M ₂ lost/spectral.
16. Male flagellomere 1 enlarged.
17. All sternites lost in both sexes.
18. Tip of R ₄₊₅ not fused to C, with fine separation.
19. Cell bm lost (i.e., open basally).
20. Cell cup lost (i.e., vein CuA ₂ lost).
21. M ₁ ending at or before wing tip (vs. beyond).
22. R veins highly costalized, ≤0.7× wing length.
23. Base of M ₂ appears attached to stem of Rs.
24. Proscutellum lost.
25. Fork of Rs veins very short, near apex.
26. Anterior interfrontals present, very close together near median sulcus.
27. Ocellar setae either lost or shifted posteriad, to level between posterior ocelli, or even behind this level (e.g., like postocellars).
28. Pair of preocellar present (“upper interfrontal setae”: Peterson, 1986).
29. Meron and epimeron fused.
30. Male frons greatly narrowed ventrally.
31. Base of M ₁ appears attached to R ₄₊₅ .
32. Postpronotal macroseta absent (lost).
33. Dorsum of scutum with only dense, short, scattered setae (macrosetae only on margins).
34. Thoracic macrosetae feathered.
35. Hind femur and coxa flat posteriorly.

The femoral scraper was clearly observed in several fossils: *Eosciadocera* (both Baltic amber species), *Hennigophora robusta*, *Hennigophora pria* in New Jersey amber, and *Prophora dimorion*, n. gen., n. sp., in Burmese amber. In all of these it is a curved line. I was unable to observe a stridulatum in prioriphorines, mainly because these flies are so minute that approximately 200× magnification through the amber would be necessary. Providing that the coxa and femur are sufficiently separated, the scraper or file thus exposed, a magnification of ≥100× with high-resolution optics is needed for the larger taxa (like sciadocerines), as well as a smooth, pol-

ished amber surface. Scrapers on the above fossils were observed with several good research microscopes (Nikon, Leitz, Wild). Bright lighting is also critical, preferably raking across the scales of the scraper.

A stridulatum similar to that of sciadocerines, with rows of ridges and scales, occurs in several euphorid genera, such as *Latiborophaga* (data courtesy of Brian Brown, Natural History Museum of Los Angeles). In three euphorid genera I examined—*Dorniphora perplexa*, *Diplonevra* sp., and *Megaselia* sp.—the scales of the scraper are irregularly arranged in a small, bare patch (also at the base of the

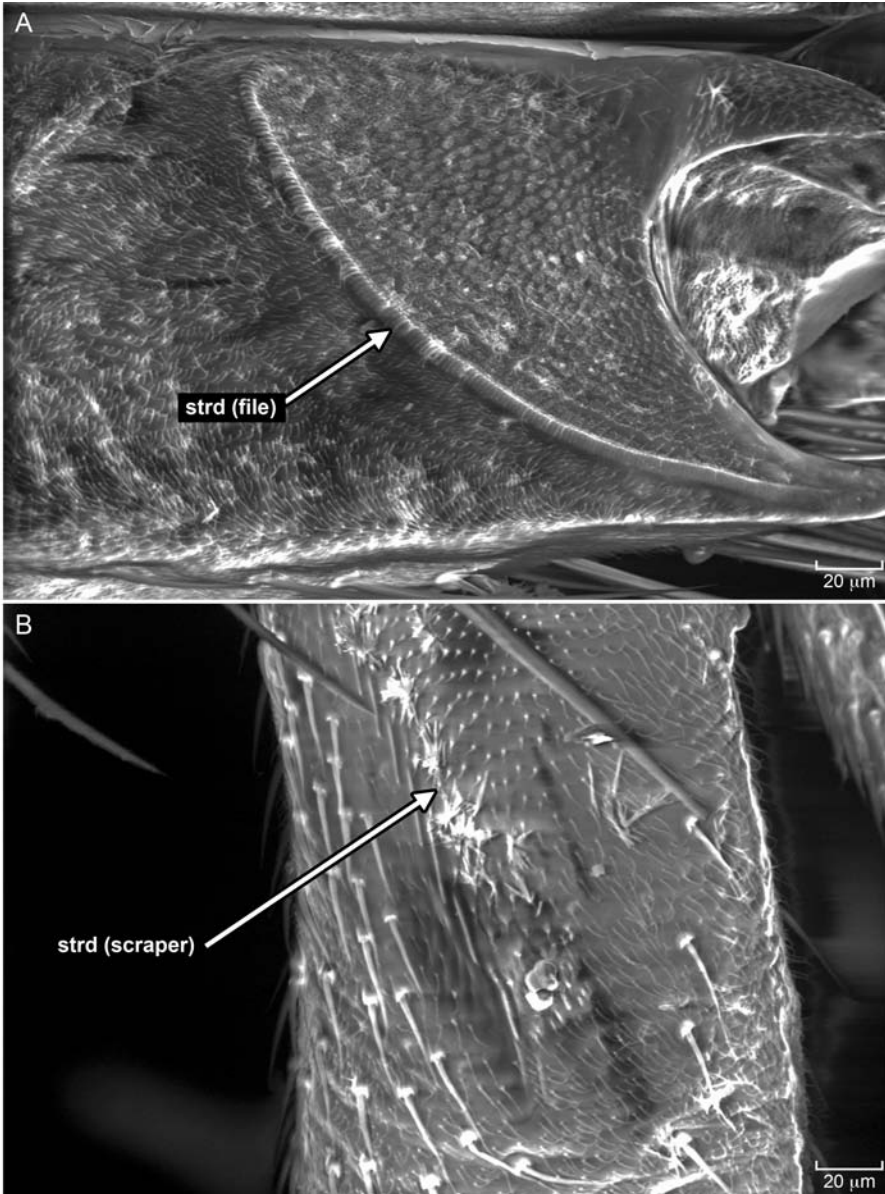


FIG. 44. Scanning electron micrographs of the stridulum of *Archiphora patagonica* (Phoridae: Sciadocerinae), uncoated specimen. A. Procoxa, showing file. B. Proximal end of profemur, showing scraper.

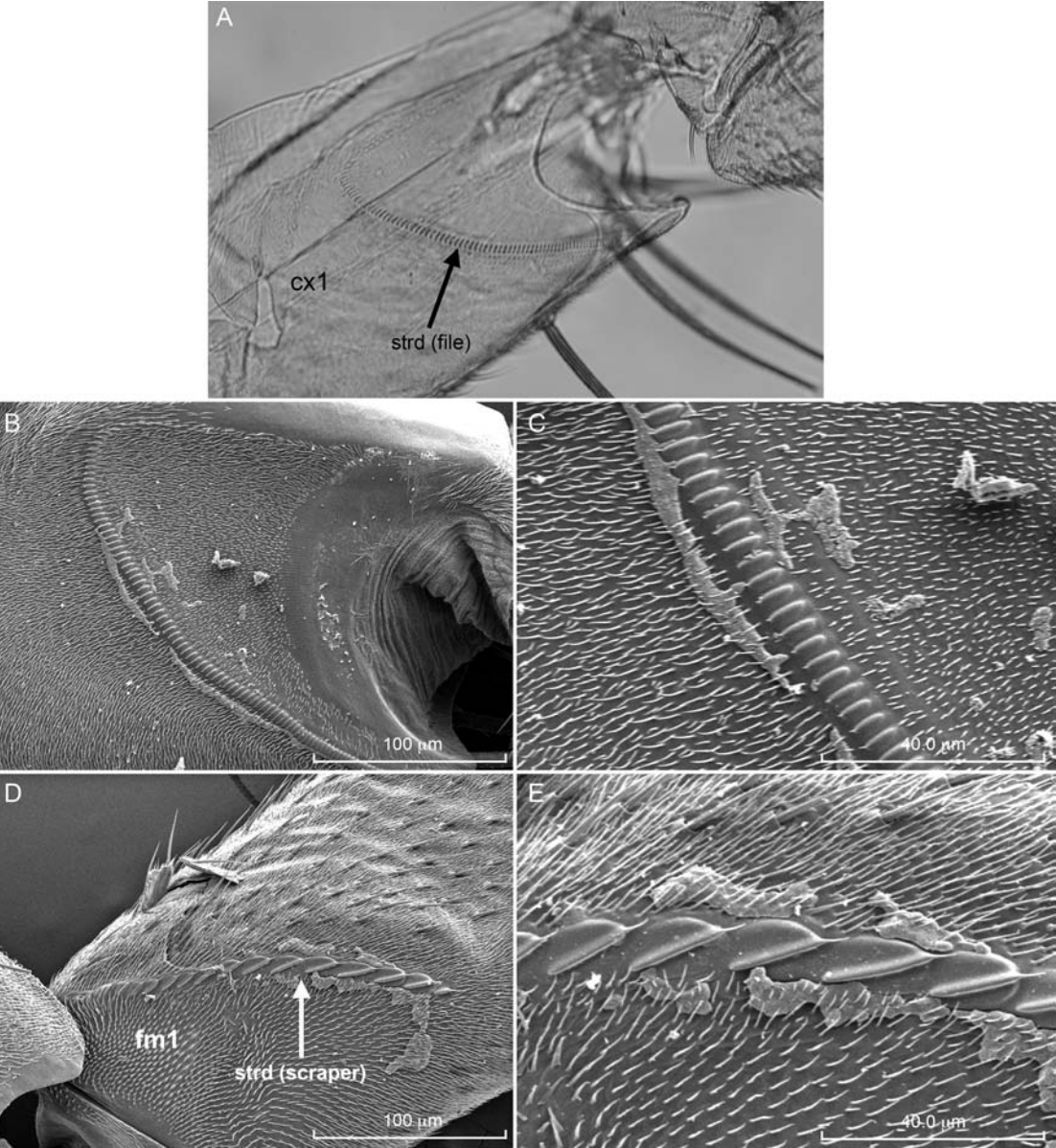


FIG. 45. Stridulum of *Sciadocera rufomaculata* (Phoridae: Sciadocerinae). **A.** photomicrograph; **B–E.** scanning electron micrographs. **A.** Procoxa, showing file. **B.** Procoxa, with file. **C.** Detail of file in **B.** **D.** Distal end of profemur showing scraper. **E.** Detail of scraper scales in **D.**

femur), not in a curved row. In *Dohrniphora* and *Diplonevra* the “file” or plectrum consists of very fine, parallel striae occupying most of the lateral surface of the coxa, appearing almost like a fingerprint. In *Megaselia*, the plectrum consists of rows of fine microtrichia, some of them scales. Clearly, the stridulatum in Phoridae has been modified into various forms, which will require a separate comparative study (do modifications conform to major phorid lineages?). Nonetheless, it is probably safe to assume that the proleg stridulatum is another synapomorphy for the distinctive, monophyletic Phoridae.

SUBFAMILY SCIADOCERINAE

DIAGNOSIS: Pretarsus with empodium either minute or completely lost. Acrostichals long, in 1–3 rows (except *Ulrichophora*). Plesiomorphic features include: cells cup and bm present (closed); frons without median sulcus; tip of R_{4+5} fully fused to C; sternites fully developed in both sexes.

COMMENTS: There are two living sister species of Sciadocerinae, *Archiphora patagonica* Schmitz in Chile and *Sciadocera rufomaculata* White in Australia and New Zealand. Their close relationship is indicated by characters 14 and 15 (table 4): stem of M_1 – M_2 lost or spectral, and the basal flagellomere is enlarged in males (it is much larger in *Archiphora*). A Baltic amber (Eocene) species was transferred to its own genus, *Hennigophora robusta* (Meunier), by Brown (2007a), into which I am also transferring *Archiphora pria* Grimaldi and Cumming (see below). Two other genera of sciadocerines occur in Baltic amber: *Ulrichophora* Brown (monotypic: *lobata*), and *Eosciadocera* Hong (two species). I have not examined *Ulrichophora*, but the fly has some distinctive features, the most striking being the numerous acrostichals not arranged into one or a few rows (Brown, 2007a). *Eosciadocera setosa* and *E. pauciseta*, n. sp., are striking because of their large size, nearly 7 mm in body length.

Hennigophora Brown

Hennigophora Brown, 2007a: 8. Type species *Archiphora robusta* (Meunier) (Baltic amber, fig. 19).

DIAGNOSIS: (From Brown, 2007a, with modifications in parentheses): Basal flagellomere of male relatively small (little differentiated from female); frons large, with frontal setae as in *Archiphora patagonica* (which has 1 pair interfrontal setae, 1 pair orbitals) (fig. 46B); scutum with large setae consisting of 1 median acrostichal row and 1 dorsocentral row on each side (fig. 19); stem of M_1 and M_2 well developed (tubular, but not sclerotized; fig. 46B); anal lobe small; empodium absent; (stridulatum present); male terminalia with separate surstylus on left side.

COMMENTS: Brown (2007a) placed *Hennigophora robusta*, *Ulrichophora lobata*, and “*Archiphora pria*” in a polytomy with *Archiphora patagonica* and *Sciadocera rufomaculata*. Based on the discovery of a new specimen of *A. pria*, which is better preserved than the original specimen/holotype (AMNH NJ-773), I am transferring this species to *Hennigophora*, though this is essentially based on plesiomorphic resemblance.

Hennigophora pria (Grimaldi and Cumming),
new combination

Figures 18, 46C, 47A

Archiphora pria Grimaldi and Cumming, 1999: 97.

SUMMARY: The original (holotype) specimen of *H. pria* is covered with a milky coating that obscures many surface details, critically the acrostichals, as well as the presence/absence of a median furrow on the frons, and terminalia, though portions of larger macrosetae protrude through the coating. A new specimen in New Jersey amber, AMNH NJ-Ch1, has some critical features that are better preserved, but this specimen lost the left side of the head and thorax before or during fossilization, and the abdomen has a thin milky coating. A few acrostichals can be seen in

left profile, which appear to be in one (or possibly several) rows and are significantly smaller than those in *H. robusta* (whose acrostichals are about as large as the flanking dorsocentrals; fig. 19). Male genitalic structure cannot be compared to *H. robusta* since this specimen is female. Most importantly, the stridulatum is present in AMNH NJ-Ch1, with a scraper very visible on the mesal surface of the right profemur, and a file on the lateral surface of the left procoxa. The location, arc, and length of the stridulatum are just as in living sciadocerines, but the number and structure of ridges and teeth are not visible. A stridulatum was also observed in *H. robusta* based on a file on the right procoxa of a male specimen, AMNH Ba-JH58 (fig. 19) (this specimen also lacks a median furrow on the frons).

Hennigophora pria is similar to *H. robusta* in venation (proportions and lengths of main veins, a tubular stem of M; fig. 47A, B), setation of legs; and a broad frons (judging from the preserved right half in AMNH NJ-Ch1). It differs from *H. robusta* by having a pair of reclinate interfrontals, near the frontal margin of the frons (vs. absent); also, setae are shorter, especially the acrostichals, supraalars, postalars, and scutellars. In agreement with Brown (2007a), *Archiphora* should be restricted to the sole living species.

Eosciadocera Hong

Eosciadocera Hong, 1981: 140. Type species *E. helodis* Hong, 1981 (Fushun amber).

DIAGNOSIS: (from Brown, 2002, with modifications) Largest phorids, body lengths 6–7 mm; with many very large, bristlelike setae; frons narrow; 1–4 pairs frontal setae; size of basal flagellomere with little or no sexual dimorphism. Acrostichals, dorsocentrals, postoculars (even setae on tegula) large, thick macrosetae; proepisternum very bristled (10–20 setae). Branches of M_1 and M_2 tubular, not sclerotized; these veins not completely connected. Wing membrane with dense microtrichia overall; proleg stridulatum present; frontal sulcus absent.

TYPE SPECIES: *E. helodis* Hong, in Early Eocene amber from Fushun, China. Unfortunately, the collection of Fushun amber insects studied by Hong is lost, including the types, and additional specimens of *Eosciadocera* have not been found in new excavations of Fushun amber (Wang et al., 2014). It is necessary to rely on the original description.

COMMENTS: There are now three species of *Eosciadocera*: *E. helodis* in Fushun amber, *E. setosa* Brown in Baltic amber (fig. 15), and *E. pauciseta*, n. sp., also in Baltic amber (fig. 16). The flies are extraordinarily large and bristly, almost like calyptrates, and apparently very rare in Baltic amber. Brown (2002) expressed some doubt about the sciadocerine position of the genus, but later included *Eosciadocera* in this subfamily (Brown, 2007a). Courtesy of Christel Hoffeins, who loaned the paratype of *E. setosa* (CCHH 1358-1; fig. 15), I was able to observe the stridulatum in this species. There are considerable differences between the two Baltic amber *Eosciadocera* species (listed in the diagnosis below), but I am placing the new species in this genus given the striking similarities between the two, such as the uniquely large size and numerous, large macrosetae.

Eosciadocera pauciseta, new species

Figures 16, 47D; 49A, D, E

DIAGNOSIS: Similar to *Eosciadocera setosa*, also in Baltic amber, by the very large body size (6–7 mm), protibia with only a ventroapical macroseta; one large pair of vertical setae; pair of small (divergent) postocellar setae; basal flagellomere subspherical; 1 to several rows of large acrostichals; proepisternum with many large setae; and anepisternum without large setae. Proleg with stridulatum. Differs from *E. setosa* by the following: two (vs. four) pairs fronto-orbital setae; frons broad, greater than $\frac{1}{2}$ head width (vs. $\frac{1}{4}$); palp relatively large, flat, with stout black setae on distal margin (vs. small, fine setae); proscutellum absent (vs. present); notopleurals 4 (vs.

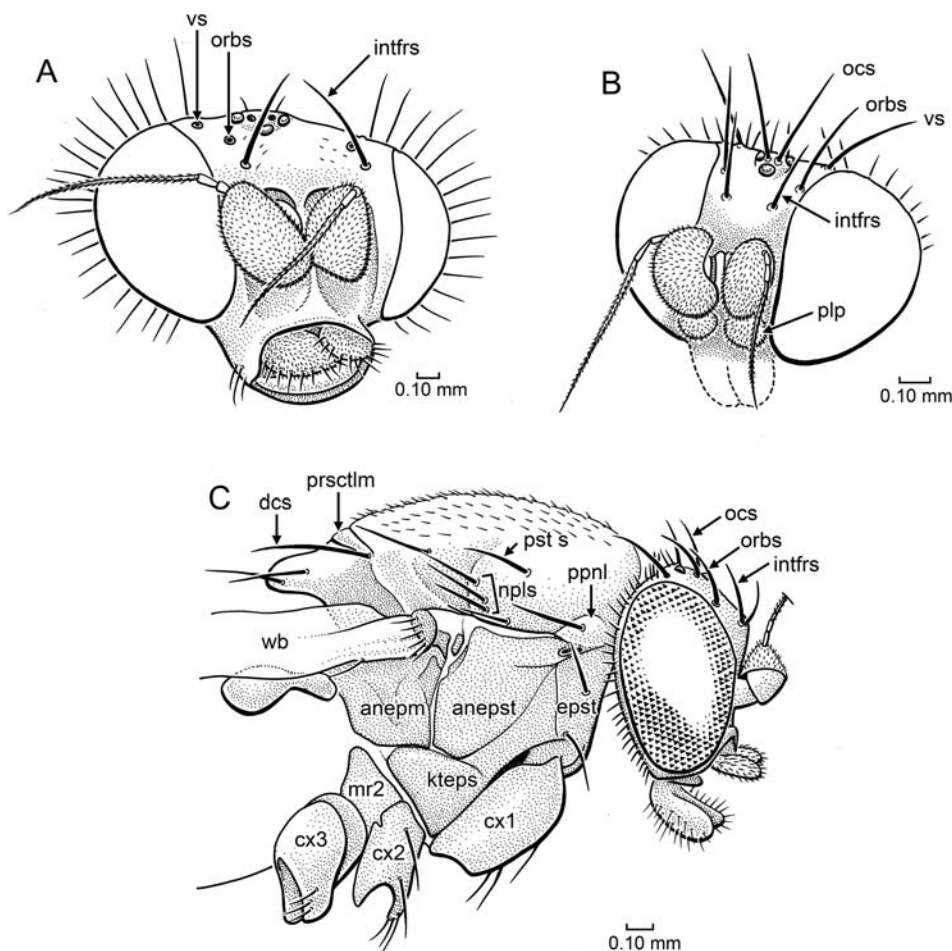


FIG. 46. Sciadocerinae in Eocene Baltic amber (A, B) and Late Cretaceous amber from New Jersey (C). **A.** *Eosciadocera pauciseta*, AMNH Ba-Je565, frontal view of head. **B.** *Hennigophora robusta*, AMNH Ba-JH58, oblique frontal view of head. **C.** *Hennigophora pria*, AMNH NJ-Ch1, lateral view of head and thorax.

5–8); scutellars in two pairs (vs. 5–6 pairs); meta-femur without macrosetae (vs. 5–6 long ones).

DESCRIPTION: Large, ca. 6.7 mm body length; color appears brownish overall, with thick, black macrosetae. **Head:** Eyes well separated, bare, no differentiation of facets, no emarginations. Frons without median sulcus, broad (ca. $0.65\times$ width of head), length (from anterior ocellus to anterior margin) shorter than width. Ocellar triangle approximately in middle of dorsum of head (including frons). Frontal setae: two pairs fronto-orbitals (posterior pair lost, but sockets visible),

situated near middle of frons length; ipsilateral fronto-orbitals separated by distance ca. $5\times$ diameter of fronto-orbital seta socket. Supra-antennal interfrontals possibly absent (or just lost in specimen). One pair of vertical setae present (setae lost, but sockets visible), situated midway between posterior fronto-orbital and row of postocular occipital setae. Ocellar setae: 1 pair (lost, but sockets visible, apparently large); post-ocellars minute, fine, length slightly greater than diameter of ocellus, located between posterior ocelli. Occiput just behind posterior margins of

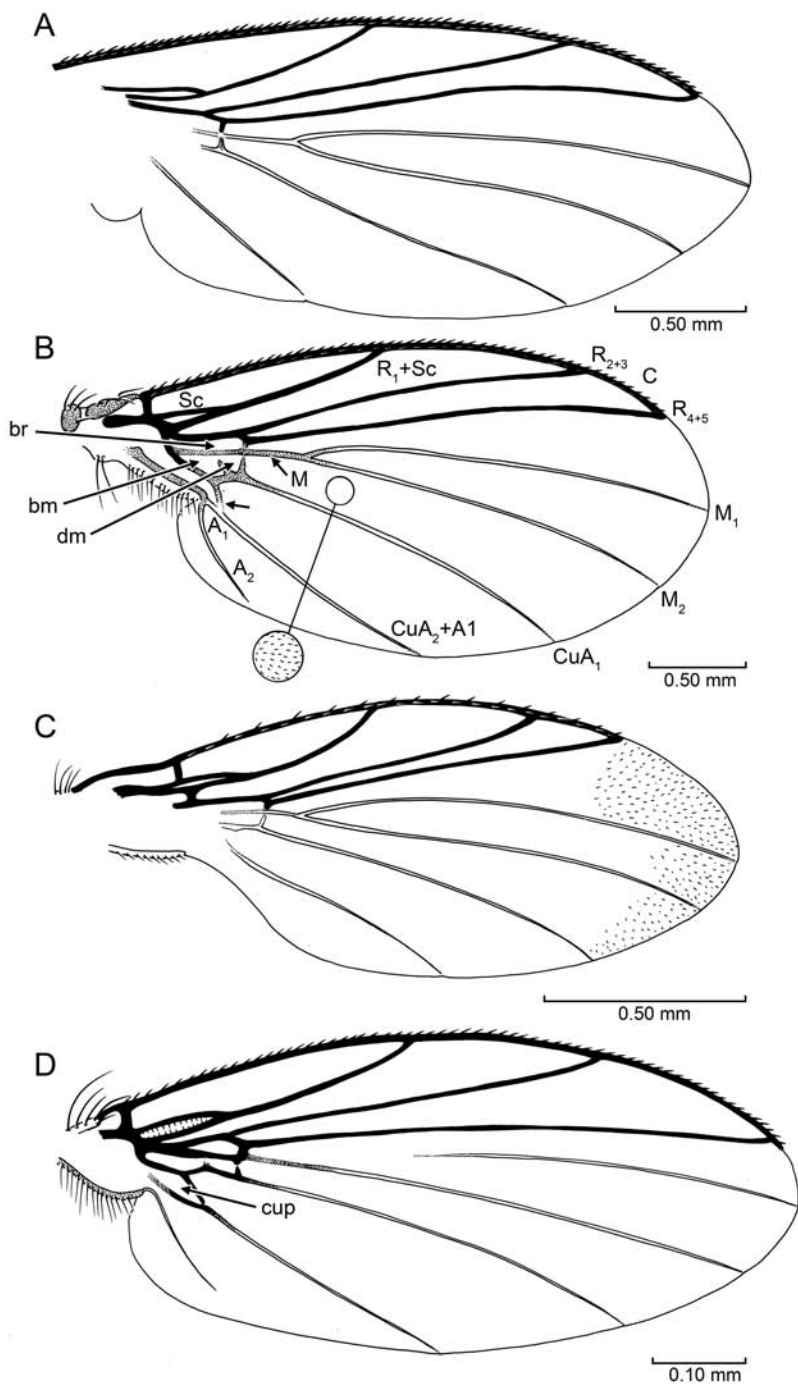


FIG. 47. Wings of Sciadocerinae preserved in Eocene Baltic amber (B, D), and Cretaceous ambers (A, C), to different scales. **A.** *Hennigophora pria* in New Jersey amber, AMNH NJ-Ch1. **B.** *Hennigophora robusta* in Baltic amber, AMNH Ba-JH51. **C.** *Prophora dimorion* in Burmese amber, JZC Bu242. **D.** *Eosciadocera pauciseta* in Baltic amber, AMNH Ba-JVe565.

eye with 19–20 long, stout postocular setae; 7–8 additional large occipital setae mesal to this row. Face deeply concave, with very thin vertical carina, flanked by pair of recessed areas (fossae) for antennae. Vibrissa absent. **Antenna:** Scape very narrow, ringlike, no setae; pedicel short, conical, no setae. Basal flagellomere subspherical (length slightly greater than width), covered with short, velvetlike pile. Arista dorsal; 3-merous, basal two articles short (lengths ca. $2\times$ their widths). arista micropubescent. **Mouthparts:** Oral margin protruding, such that oral cavity faces forward, surrounded by short sleeve. Palp large, flattened, distal margin with thick, short setae. Labellum fully recessed into oral cavity (as preserved); opened lobes nearly forming circle, pseudotracheae not visible, though minute microtrichia are.

Thorax: Heavily bristled; scutum gently arched; proscutellum absent or very reduced; prosternum large, fully exposed, bare. Acrostichals large, in even central row of ~ 10 setae; row of ~ 10 dorsocentral setae lateral to acrostichals (setae in both rows about same size). Other thoracic setae: 1 large postpronotal; oblique row of 6 supraalar (1 very large); 1 large postalar; 4 large, presutural notopleurals; 6–7 large proepisternals (rest of pleuron without setae). One pair of large dorsocentrals, sockets slightly lateral to line formed by outer row of acrostichals; 2 pairs of large scutellars (lengths very similar), apical scutellars very close. **Wing:** Very long, ca. 8 mm, nearly twice length of abdomen. Membrane of wing clear, no infuscation, entirely covered with microtrichia. Tegula bristly, with 7–8 thick setae; basicosta with row of 4 large setae; vein h thick; Sc thick, fused to R_1 at $0.30\times$ length of R_1 ; C with 2 rows thick spinules, vein ends at apex of R_{4+5} ; R_{2+3} ends midway between apices of R_1 and R_{4+5} . Vein R_{4+5} ends well before apex of wing, fully fused to C. Base of M_1 lost, evanescent, apex of M_1 ending at wing tip; M_2 complete, including base. Cu veins complete; anal vein present, incomplete. Cell r-m complete (closed basally); cell dm slightly opened basally and distally; cell cup present, apex of

CuA_2 not fused to A_1 . Alula small, with fringe of 10–12 stiff, nonfeathered setae. **Legs:** Pretarsi with curved bristle near where empodium would be (as in *Ironomyia*); tarsomeres 1–4 with hair seam on mesal surface, 2 longitudinal rows of dark, small, spinulelike setae ventrally. Foreleg: Coxa heavily setose overall, with >30 thick, large macrosetae; femur without macrosetae; stridulatum present, “scraper” exposed on bare, light patch at base of inner surface of right fore femur, with about 12 minute ridges; tibia with only ventroapical macroseta, no others. Midleg: coxa setose, ca. 10 setae; femur without macrosetae; tibia with 2 middorsal setae, 4 apical ones. Hind leg: coxa with a few fine setae; femur with single ventrolateral macroseta; tibia with pair of middorsal macrosetae, plus 4 apical ones. **Abdomen** (female): Sternites well developed; apical segment with longer, thicker setae; pair of long, fine setae just above cerci (on epiproct?); cerci short, pointed downward, setose.

SPECIMENS EXAMINED: Holotype, female, AMNH Ba-JVe565, in Eocene Baltic amber. The specimen is complete, but portions of it are covered in milky coating or are obscured by fractures.

ETYMOLOGY: From Latin *paucus* (“few”), in reference to its fewer setae compared to *setosa*.

SUBFAMILY INDETERMINATE

Prophora, new genus

DIAGNOSIS: Proleg stridulatum present (seen in holotype specimen only); frons with well-developed median sulcus, one pair of fronto-orbital setae in both sexes; one pair of interfrontals in male, 3 pairs in female; one pair of verticals in male, two pairs in female; basal flagellomere not sexually dimorphic in size; one pair of dorsocentrals, two pairs of scutellars present; sternites well developed in male, lost in female except for terminal two sternites (7 and 8); lacking wing-vein characters of Euphorida (i.e., chars. 19–24 in table 4, fig. 43).

TYPE SPECIES: *P. dimorion*, n. sp.

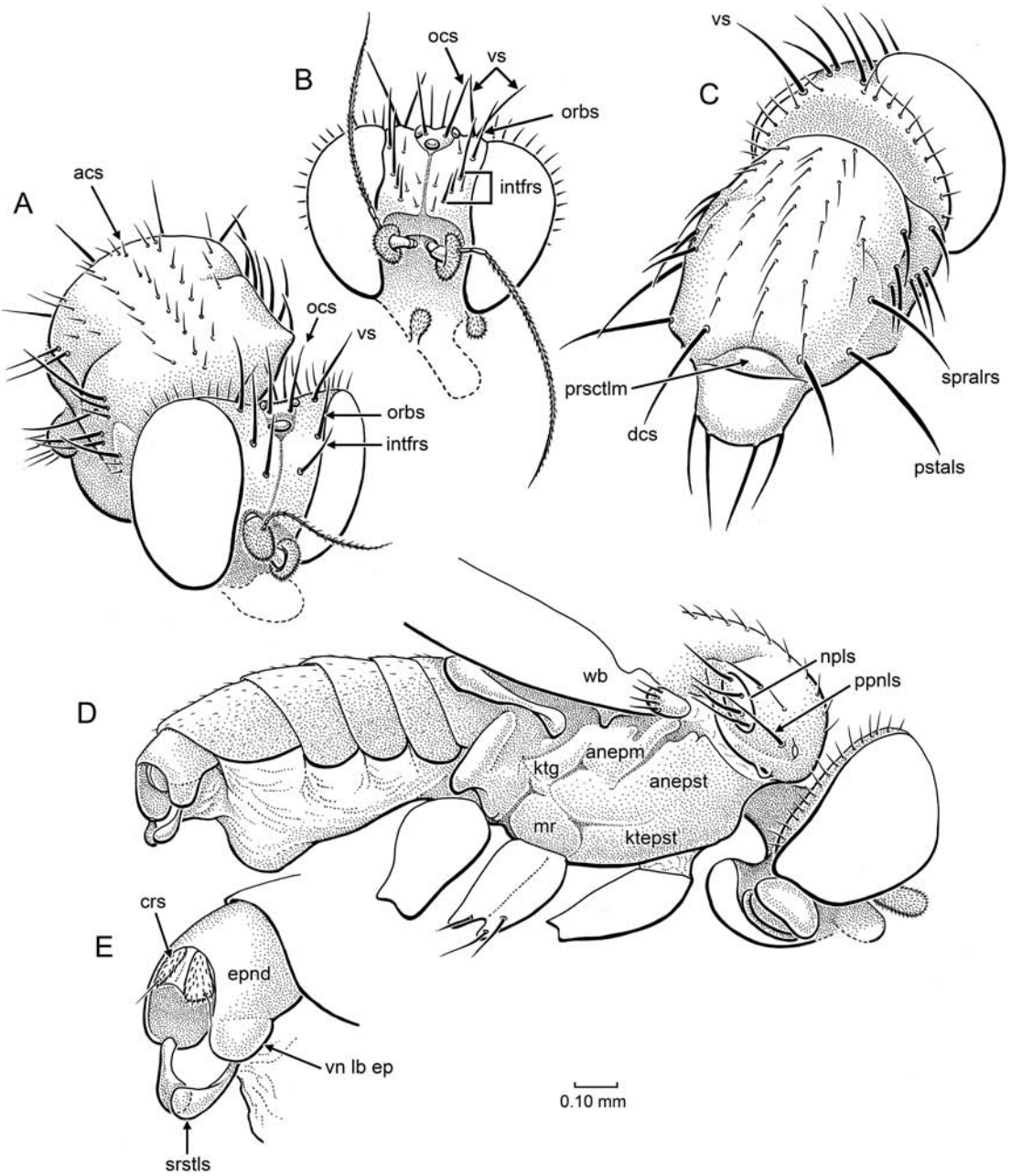


FIG. 48. *Prophora dimorion*, n. gen., n. sp., in Burmese amber. **A, C–E.** Holotype male, AMNH Bu8783; **B.** paratype female, JZC 242. **A.** Head and thorax, oblique frontal view (male). **B.** Head, frontal view (female). **C.** Head and thorax, oblique posterior view. **D.** Body, lateral view. **E.** Male terminalia, right lateral view.

ETYMOLOGY: *Pro-* (“first, before”), and *-phora*, common suffix for generic names in the Phoridae. The name is feminine.

COMMENTS: The possession of a sulcus on the frons and great reduction in female sternites (which occur in stem-group and many crown-group Euphorida), but more generalized venation of the Sciadocerinae, makes the phylogenetic position of this genus apparently close to the basal fork of the two lineages.

Prophora dimorion, new species

Figures 17, 47C, 48

DIAGNOSIS: As for genus, by monotypy.

DESCRIPTION: Based on both sexes. Body length 1.8 mm; setae not feathered. **Head:** Eyes large, well separated even in male, occupying entire lateral portions of head; bare, no differentiation of facets; margins entire. Frons: Parallel sided, with well-developed median sulcus. Frontal setae: 1 large pair of fronto-orbital setae in both sexes, midway between interfrontals and verticals; 1 large pair of reclinate interfrontals in male, 3 pairs in female (anterior two pairs smaller); 1 large pair of vertical setae in male (2 pairs in female); 1 large pair of upright ocellar setae (sockets in middle of triangle) in both sexes; postocellars ca. 0.65× length of ocellars, slightly divergent. No vibrissa. Occiput near posterior margin of eye with row of fine setae, decreasing in size ventrad. **Antenna:** Scape very thin, ring-like; pedicel small, conical, inserted into basal flagellomere on mesal surface of flagellomere; basal flagellomere small, short ovoid; arista dorsally situated, 3-articled, basal 2 articles very short; terminal article of arista long (greater than width of head), micropubescent. Mouthparts not fully observable. **Thorax:** Short, stout, dorsum gently to moderately arched. Proscutellum present, well developed, lenticular, prosternum large, exposed, bare. Setae: 1 central row of ca. 10 long, fine acrostichals; row of similar setae on each side of acrostichals, anterior to dorsocentrals, shorter row lateral to these; all setae in rows decreasing

in length anteriorly. One large pair of dorsocentrals present; 1 large supraalar; 1 large postalar; 1 large postpronotal; row of 4 large, presutural notopleurals; 2 pairs of large scutellars (apical pair slightly longer). Pleuron without setae. **Wing:** Very similar in shape and vein proportions to *Hennigophora robusta*; membrane with microtrichia at posterior margin only. C with short spinules, widely spaced (distance between each greater than length of spinule). Tegula with row 4 strong setae on posterior margin, basicosta with 4 setae; details of wing base with poor visibility due to preservation (e.g., development of M stem, basal cells). R_{4+5} relatively short; anal lobe relatively well developed (as in *Hennigophora*); alular setae long, not feathered. **Legs:** All pretarsi with empodium either absent or so reduced as to be unobservable at 200×; tarsomeres 1–4 with setulae in longitudinal rows, hair seam on mesal surface. Foreleg: coxa with minute, fine setulae overall; row of 6 large setae on ventrodistal margin; coxa widely separated, by distance approximately equal to thickness of coxa. Femur: Stridulatum present (as seen in male holotype: 11 scalelike teeth of scraper observed on left profemur; file not observable; no large setae on profemur. Protibia without large setae. Mid- and hindlegs: coxa with several large setae on posterior margin; femur without large setae; tibia with 1 large ventroapical seta, several smaller ones partially encircling tibial apex. **Abdomen:** Tergites well developed in both sexes; at least 3–4 large anterior sternites present in male (more posterior ones obscured), female with all but two terminal sternites (7 and 8) lost. **Male Terminalia:** Epandrium exposed, well developed, with ventral lobe (has broad attachment); surstylus articulating with lobes (not fused), clavate, pendulous. Ventral epandrial lobes, surstyli, periphallal appendages asymmetrical. **Female Terminalia:** Largely obscured; abdominal segments 7 and 8 much smaller than anterior ones, terminalia do not appear telescoped; hypoproct well developed.

SPECIMENS EXAMINED: Holotype, male, AMNH Bu8783; paratype, female, JZC Bu242, both in Burmese amber, well preserved, complete.

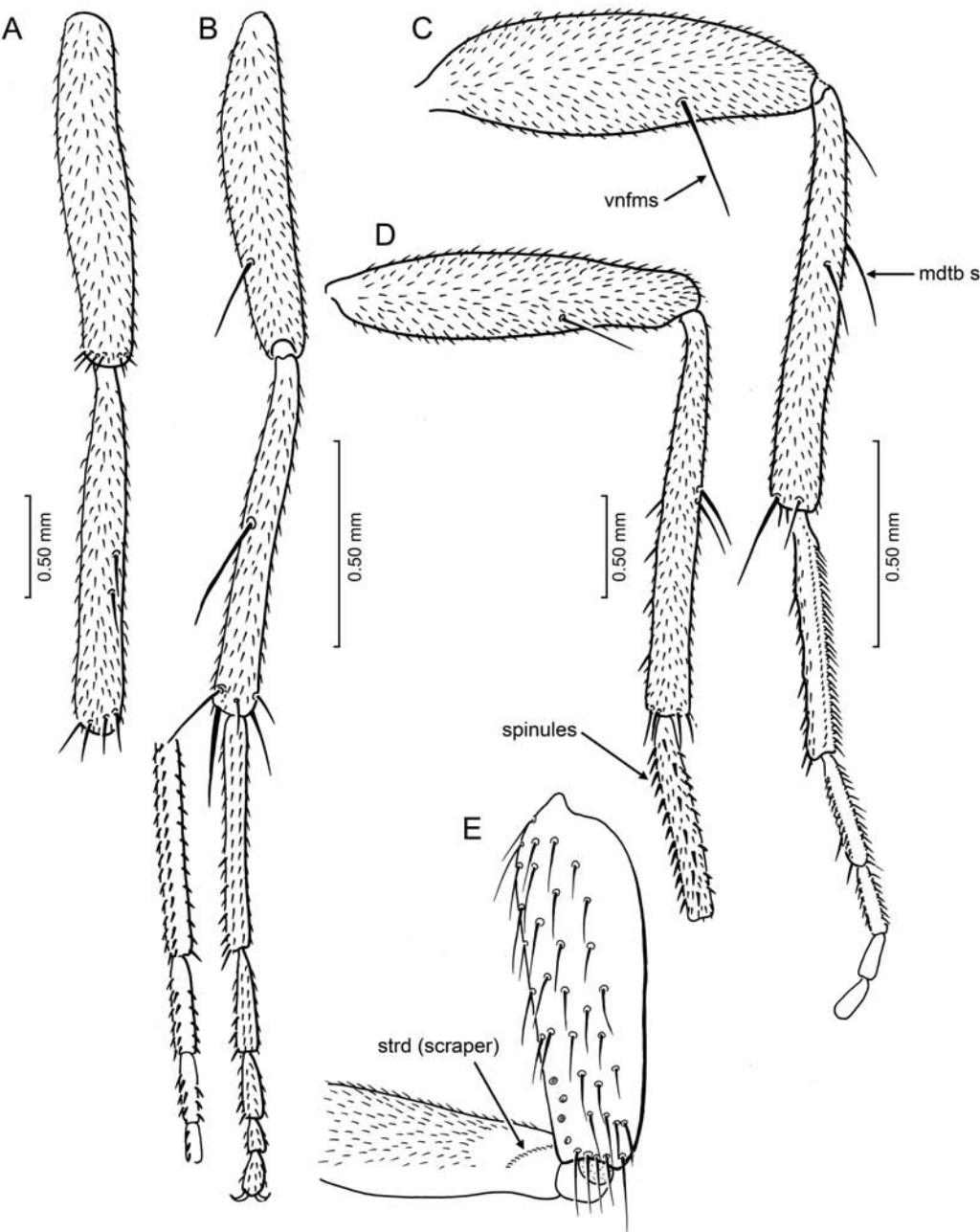


FIG. 49. Legs of Sciadocerinae in Baltic amber, showing large bristlelike macrosetae. **A, B.** Midleg; **C, D.** hind leg. **A.** *Eosciadocera pauciseta*, femur and tibia, AMNH Ba-JVe565. **B.** *Hennigophora robusta*, AMNH Ba-JH58. **C.** *Eosciadocera pauciseta*, femur, tibia, basitarsomere. **D.** *Hennigophora robusta*, entire leg. **E.** Base of proleg (coxa and base of femur) of *Eosciadocera pauciseta*, showing position of exposed scraper of the stridulum.

ETYMOLOGY: From Greek, *di-* (“two”) and *morion* (“parts” in genitive plural) in reference to sexual dimorphism of the head setation.

COMMENTS: Differences between the holotype male and paratype female are attributed to sexual dimorphism, otherwise the two specimens are very similar: body size and proportions, identical setation of the thorax, proportions of the wing veins, even the widely spaced costal spinules. Differences are the frontal setation, with the female having 2 additional pairs of small interfrontals (vs. 1 pair in the male), and a pair of inner verticals. Also, the female has only two small sternites (7 and 8); the male has well developed ones. Head setation is sexually dimorphic in living sciadocerines; likewise for the development of abdominal sternites in some basal Euphorida.

Sciadocerinae indet.

Figure 50

SUMMARY: A unique male specimen (AMNH Bu-1376) of a minute species (~1.7 mm body length), which is not being formally described since critical structures are not visible (i.e., arrangement of frontal setae, palp size, empodium, presence/absence of stridulatum, base of M vein). This species is like *Prophora dimorion* in *appearing* to have a frontal sulcus (this is barely visible), acrostichals in single row, 1 pair of large dorsocentral setae (vs graded row), 2 pairs of scutellars, presence of proscutellum, and few leg macrosetae. It differs from *Prophora* by significantly smaller size; head with finer, shorter frontal setae; 2 (vs. 3–4) pairs of notopleural setae; scutellar setae upright (vs. posterocline); no postalars (vs. 1); microtrichiae completely absent from wing membrane (vs. with some at apex); base of M appears spectral, though not fully visible (vs. present, tubular, though not sclerotized). Further, the male abdomen and genitalia are substantially different: in Bu-1376 segments 6–7 with constriction between them, tergite 7 bulbous, epandrium asymmetrical (vs. symmetrical in *Prophora*); male terminalia very asymmetrical, surstyli apparently absent or so

small as to not be visible (vs. symmetrical, with pendulous surstyli).

GENERAL DESCRIPTION: Body short, length ~1.7 mm total length, broad, with relatively few setae. Head about same width as thorax. Antenna with arista dorsal, preapical. Head setae barely visible, appears to have 1 small pair of supraantennal interfrontals; 1 large pair of orbitals; 1 pair of ocellars; 1 pair of verticals; postoculars relatively short. Scutum arched, short; 1 short row ~6 acrostichals; 7–8 dorsocentral setae, not graded (1 large pair of prescutellar dorsocentrals; other dorsocentrals small, about same size as acrostichals). Two long notopleural setae, 1 supraalar, no postalars. Proscutellum present, narrow; scutellum short, wide, with 2 long, upright pairs of setae. Pleural region not visible. Wing short, broad (L/W 1.7), venation very similar to that of *Hennigophora robusta*, except that base of M appears spectral, not tubular; membrane devoid of microtrichia. Abdomen very short and broad at anterior end, width of segments 2 and 3 about same as thorax; abdomen tapered in width to segment 6 (= 0.25× width of segment 2), forming constriction between segments 6 and 7. Tergite 7 slightly asymmetrical, larger than tergite 6; tergite 9 (epandrium) well developed on right side; terminalia asymmetrical, shifted mostly to right (component structures not discernable); surstylus not apparent. Legs with very few macrosetae; mesotibia with apical pair of long, spurlike setae.

The specimen is largely complete, but some legs and segments are disarticulated. It is in a dark piece of amber that also contains a layer of sand grains, stellate trichomes, and particulate debris. A piece of bark or plant fragment lies under the fly; this and the sand grains prevent viewing the front of the head, prolegs, and some other areas.

“SYRPHOIDEA”

This is traditionally a superfamily that includes the two families Syrphidae and Pipunculidae, which share a significant number of morphological features. These include, for example, highly asymmetrical preepandrial sclerites;

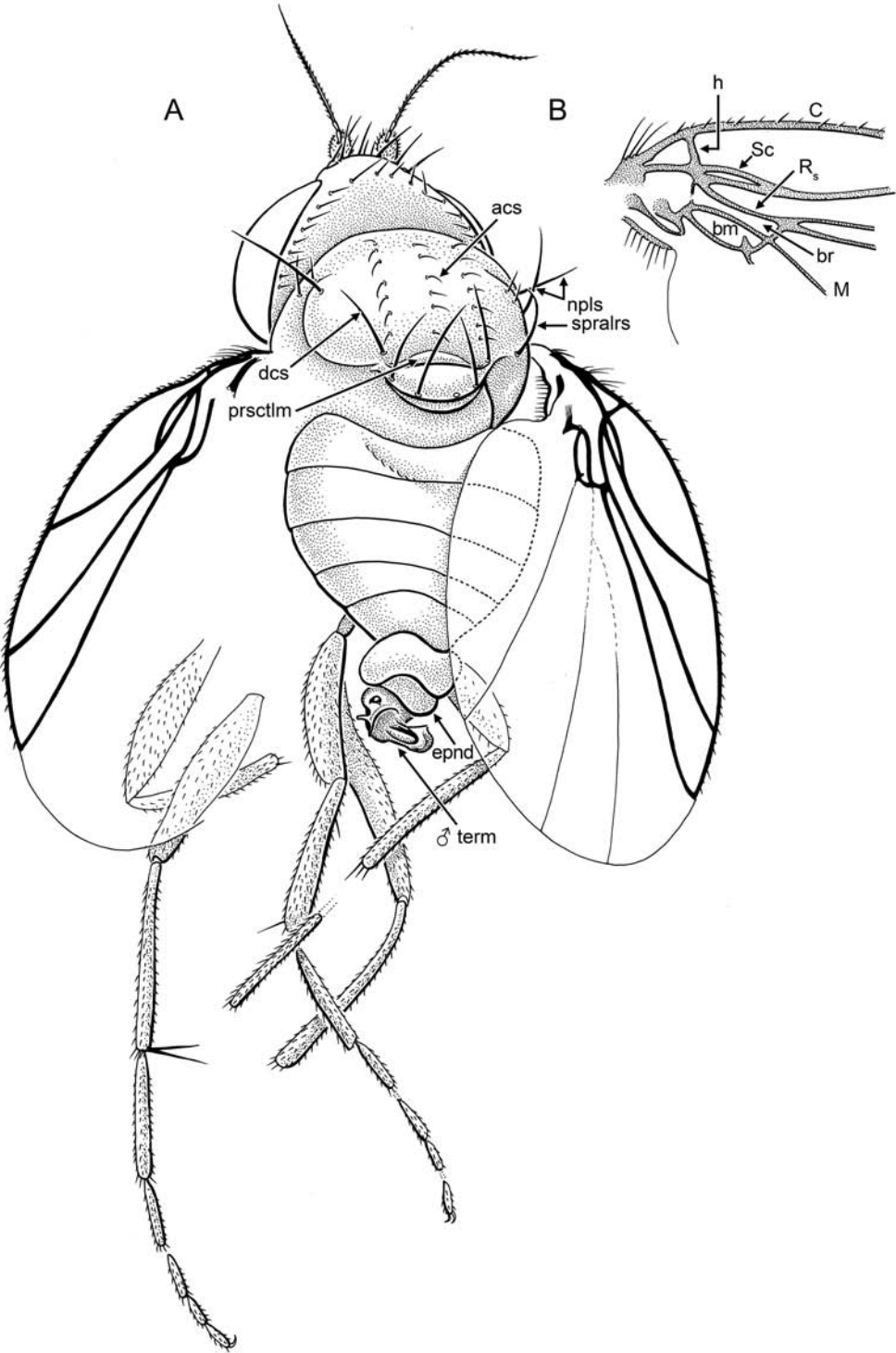


FIG. 50. Minute, undescribed Sciadocerinae (Phoridae) in Burmese amber AMNH Bu-1376. A. Dorsal habitus, as preserved (some podomeres are disarticulated; portions of wing and body obscured). B. Detail of wing base.

cell cup large (much longer than its terminal vein); loss of vein M_2 , although this appears to be convergent (discussed below); and body with few to no macrosetae (if present, these usually are on the lateral portions of the thorax). Most molecular and some morphological evidence, however, indicates that Syrphoidea is not a natural group, with the Pipunculidae more closely related to the Schizophora (Wiegmann et al., 2011; Tachi, 2014; Pauli et al., 2018). Both of these families are clearly monophyletic, whose crown-group fossils are entirely from the Cenozoic.

Syrphidae are well-known, comprising approximately 6000 species in 200 genera of usually larger, boldly patterned pollinators that are excellent hoverers. The head is typically large, hemispherical, with large eyes (males holoptic or nearly so), occiput concave; thorax short and broad; abdomen varying from short to long, commonly dorsoventrally depressed. Diagnostic characters are summarized in the cladogram in figure 51 and table 5 (numbers 5–15), many of them venational: frons without macrosetae; male sternite 8 large, bulbous, terminal; wing cell bm long, 0.3 to 0.5× wing length; apex CuA_1 incomplete, not reaching wing margin; cell cup large, much longer than its terminal vein; vein C ends at apex of R_{4+5} (vs. M_1); alula large, well developed; $sc-r$ crossvein present; spur vein through $br-m$; apex M_1 curved upward to fuse with R_{4+5} preapically; M_2 lost. The thorax usually has only fine, pilelike setae; if bristlelike macrosetae occur they are on the pleura or near the scutellum.

Many fossil Syrphidae have similarities to living genera, where it can be determined (i.e., preserved in amber), but generic placements need to be “critically re-examined” (Vockeroth and Thompson, 1987: 718). This will be a large undertaking, since there are approximately 40 genera and 90 species of fossil Syrphidae known, nearly half of them in Baltic amber (Meunier, 1902, 1907; Hull, 1945), the others are largely compressions from the Eocene Florissant and Green River formations (e.g., Scudder, 1878; Evenhuis, 1994; Hull 1945, 1960). Fortunately, higher-level relationships in Syr-

phidae are well explored (Skevington and Yeates, 2000; Ståhl et al., 2003; Mengual et al., 2008; Young et al., 2016; Pauli et al., 2018). The subfamily of ant inquilines Microdontinae is the sister group to the other subfamilies; Eristalinae appears to be paraphyletic (Young et al., 2016; Pauli et al., 2018) with respect to the Pipizinae + Syrphinae (each of which is monophyletic).

Recent Pipunculidae have approximately 1800 species in 21 living genera, and are immediately recognizable for the huge eyes that occupy most of the head. Like Syrphidae they have a short, stout thorax and are excellent hoverers, but are commonly found in tall grass and dense vegetation in search of their hosts, which are female Tipulidae (for *Nephrocerus*) or auchenorrhynchans (all others). Diagnostic characters are summarized in figure 51 and table 5 (chars. 9, 15, 18–21), which include besides the huge eyes: wing slender, alula absent, anal lobe very reduced (wing nearly petiolate); M_2 lost (at most a spur of M_1); claws and pulvilli very large; female with piercing ovipositor. The last two of these are clearly related to how the female grabs the host and injects it with eggs. Interestingly, the larva apparently has just 2 instars. Male segments 6 and 7 and posteriad are twisted left, and segment 8 is a syntergosternite that is a large, bulbous structure at the apex of the abdomen. There are 8 genera and 16 species of fossil Pipunculidae, all of them from the Cenozoic (summary in Archibald et al., 2014), the oldest from the Early Eocene Okanagan Highlands of British Columbia, Canada. Kehlmaier et al. (2014) separated the two fossil species of *Metanephrocerus* in Baltic amber, plus the living species of *Protonephrocerus* (from Chile) into Protonephrocerinae, separate from Nephrocerinae (e.g., Rafael and Meyer, 1992).

Two fossil genera of syrphoids in Burmese amber are described here: *Prosyrphus*, which appears to be a stem-group Syrphidae, and *Aschizomyia*, which has an ambiguous position among syrphoids (fig. 51; table 5).

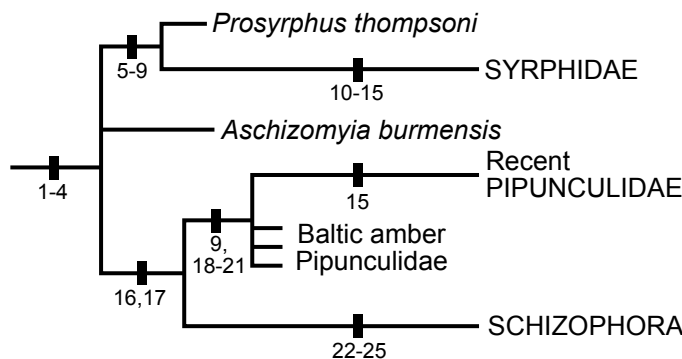


FIG. 51. Cladogram of Cretaceous and Recent families of syrphoids in relation to the Schizophora. Numbers on cladogram refer to synapomorphies given in table 5.

TABLE 5
Characters in the cladogram for syrphoids and Schizophora (fig. 51)

1. Arista dorsal (also occurs in some Phoridae).
2. Crossvein br-m generally far distal to level of Sc apex.
3. Male postabdominal (>6) segments asymmetrical, especially sternite 7, displacing epandrium to right side (secondarily symmetrical in some Schizophora, e.g., Ephydroidea + Calyptrata).
4. Phallapodeme (male) articulated (Sinclair et al., 2013).
5. Loss of macrosetae on frons (indeterminate for Pipunculidae).
6. Male sternite 8 large, terminal, bulbous, asymmetrical.
7. Wing cell bm $\frac{1}{2}$ to $\frac{1}{3}$ length of wing.
8. Apex of CuA ₁ incomplete, not reaching wing margin.
9. Wing cell cup large, much longer than terminal vein (occurs in Syrphidae and Pipunculidae).
10. Vein C ends at apex of R ₄₊₅ (vs. M ₁).
11. Alula large, well developed.
12. Crossvein sc-r present, well developed.
13. Spurious vein present, through br-m.
14. Vein M ₁ curved upward to meet R ₄₊₅ preapically.
15. M ₂ lost (at most a spur on curvature of M ₁); convergently developed in Pipunculidae.
16. Thorax with metepimeron and tergite 1 articulating (Tachi, 2014).
17. Male with syntergosternite 8 (fused with male syntergosternite 7 in some).
18. Head very large, hemispherical to subspherical, mostly eyes, holoptic or nearly so in both sexes; occiput deeply recessed; face very narrow.
19. Claws and pulvilli very large.
20. Wing slender, petiolate; alula absent, anal lobe very narrow.
21. Female with piercing oviscapt (endoparasitoids of Auchenorrhyncha, Tipulidae).
22. Circumversion of male genitalia completed within puparium.
23. Frons with frontal vittae desclerotized, differentiating fronto-orbital plates and ocellar triangle.
24. Well-developed ocellar, postocellar, 2 pairs vertical macrosetae.
25. Ptilinum present, externally with ptilinal fissure.

Prosyrphus, new genus

DIAGNOSIS: (male only). Extensively holoptic; arista dorsal; mouthparts small, clypeus minute; scutum and scutellum with numerous scattered setulae, two pairs of prescutellar dorsocentral setae, notopleural setae, four pairs of scutellar setae. Vein r-m at level of Sc apex; M with short apical fork, M_1 not connected to R_{4+5} ; dm and cup cells very large; alula small; spurious vein and sc-r lacking; male abdominal segments 6–8 very asymmetrical, epanandrium to left side, sternite 8 terminal and bulbous.

TYPE SPECIES: *P. thompsoni*, n. sp.

ETYMOLOGY: From Latin *pro-* (“first, before”), in reference to the stem-group position of the fossil among Syrphidae.

COMMENTS: *Prosyrphus* is a stem-group Syrphidae (fig. 51). It has a large cell bm ($\sim\frac{1}{3}$ length of wing), apex of CuA_1 incomplete (not reaching the wing margin), cell cup large, and male genitalia that are very asymmetrical with a bulbous, terminal sternite 8 (among other genitalic features). Based on the unique male, features of the frons (e.g., lack of macrosetae) cannot be determined. Moreover, the body is stout and short; wing shape broad and apically tapered, the body overall with few macrosetae, and the mesal surface of the pedicel has a tonguelike lobe inserted into the basal flagellomere, features consistent with many modern syrphids.

Prosyrphus lacks synapomorphies of crown-group Syrphidae, namely: a large alula, sc-r and spurious veins, M_1 curved upward to meet R_{4+5} preapically; M_2 lost (or at most a spur on the curvature of M_1). Kovalev (1979) reported a fragmentary specimen of a syrphid or syrphoid in Late Cretaceous Siberian amber, but the characters are too few for a definitive attribution, and it may no longer be available for study since many of the Siberian amber specimens at the Paleontological Institute in Moscow have disintegrated. Otherwise, *Prosyrphus* appears to be the most derived dipteran known from the Mesozoic, although I predict that syrphids more

derived than *Prosyrphus* will eventually be found in the Late Cretaceous, especially in the Maastrichtian and Campanian.

Prosyrphus thompsoni, new species

Figures 21, 52

DIAGNOSIS: As for genus, by monotypy.

DESCRIPTION: (male only). Body stout, compact. **Head:** Broad, slightly broader than thorax, faintly compressed dorsoventrally. Eye completely bare of setulae; large, occupying all of dorsal and lateral surfaces and much of venter; dorsal facets slightly larger than ventral ones, no discrete dividing line; male holoptic for entire length of frons. Frons obscured (presence/absence of median furrow, interfrontal and fronto-orbital setae not determinable). Ocelli on low tubercle, with two small pairs of stiff ocellar setae. Vertical setae absent; postocular setae fine, small; occiput faintly concave, with scattered fine setulae. Face relatively broad, $\sim 0.3\times$ width of head; bare, slightly swollen in middle; anterior tentorial pits deep, vertical and slitlike, close to eye margin. Oral cavity small, entirely ventral; vibrissa and genal setae absent. **Antenna:** Scape small, bare, slightly asymmetrical; pedicel asymmetrical, with tonguelike lobe inserted into mesal surface of basal flagellomere; arista dorsal; basal flagellomere reniform; arista with two minute articles at base, apical article long, flagellate, tapered to very fine apex, completely bare of micropubescence. **Mouthparts:** Clypeus minute; oval; isolated, not articulating with labrum; palp small, slender; proboscis, small, short, slender; labrum slender; labellum small, arely wider than rest of proboscis.

Thorax: Short, broad, deep in lateral view; scutum rounded but not arched. Acrostichals numerous, scattered, not in rows. Dorsocentral macrosetae present, in 2 prescutellar pairs, none in serial rows. Macrosetae: 2 supraalar; 5 notopleural; 4 pairs of scutellars, longest ones near center, disk of scutellum with setulae. **Wing:** Broad, length/width 2.0, tapered apicad; hyaline,

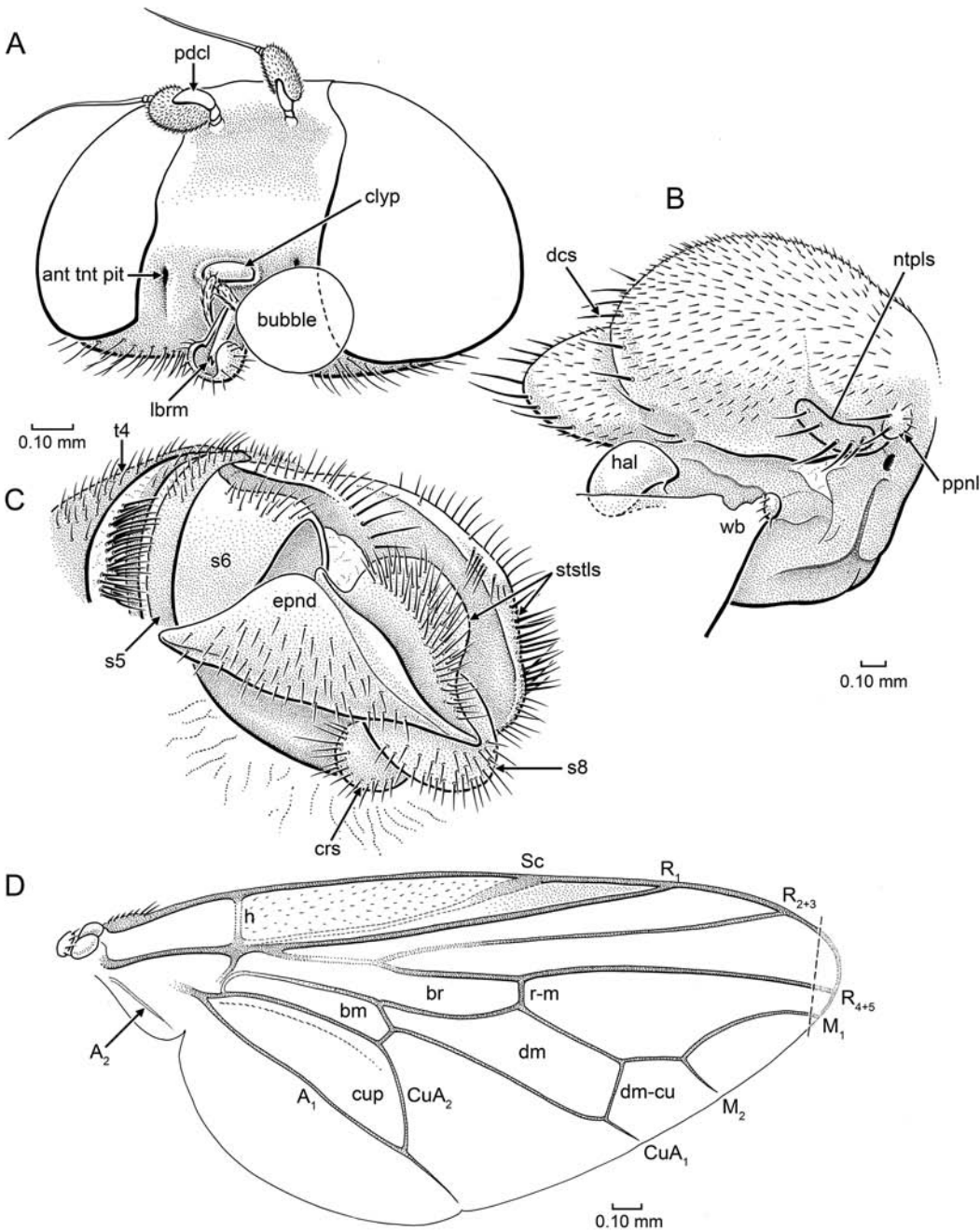


FIG. 52. *Prosyrrhus thompsoni*, n. gen., n. sp. (Syrphoidea), male holotype in Burmese amber, AMNH Bu-SE03. A. Head, ventral view. B. Thorax, dorsolateral view. C. Male terminalia, left ventrolateral view. D. Wing.

slightly darkened between apices of Sc and R_1 ; membrane with dense, very fine microtrichia, less dense in cell Sc; pterostigma absent. Prehumeral costal seta(e) small, large macrosetae absent; vein C with minute spinules; end of C not visible (wing tips lost at surface of amber); Sc long, $\sim 0.6 \times$ length of wing; R_1 long, running close to base of Sc, slightly diverging apicad; sc-r appears absent; R_{2+3} straight, base weak; R_{4+5} straight; spurious vein absent; cell dm large, cleaver shaped; cell rm long, r-m at same level as apex of Sc; cell bm narrow; crossvein dm-cu close to wing margin, separated by distance $\frac{3}{4}$ length of dm-cu; M_1 - M_2 forked, tip of M_1 not reaching wing margin; tip of CuA_1 not reaching wing margin; CuA_2 curved, A_1 straight; cell cup large, much longer than apical vein; anal lobe large, alula relatively small. Halter stem slender. **Legs:** Setose, relatively short, slender; femora longer than respective tibia, profemur with ventral row ~ 7 long setae, setal lengths about equal to femur width. Mesotibia with short, stout ventroapical spur. Basitarsomeres longest of all tarsomeres; pulvillus $\sim 0.7 \times$ length of claw; empodium not observable (perhaps minute); claw $\sim 0.5 \times$ length of tarsomere 5.

Abdomen: Short, stout; anterior 4 tergites large, with short, scattered setulae, laterally curved but not contacting sternites (pleural membrane exposed). Five large sternites visible, anterior and posterior margins in contact; with short, scattered setulae. **Male Terminalia:** Segments 6, 7, and 8 asymmetrical, ventroflexed; sternites 5 and 6 exposed dorsally; sternite 8 bulbous, terminal; epandrium triangular, shifted to left; surstyli large, heavily setose; cerci symmetrical, setose, hidden beneath sternite 8, point forward.

Female Terminalia: unknown.

SPECIMENS EXAMINED: Holotype, male AMNH Bu-SE03 The specimen is in beautiful condition, very well preserved, and virtually complete (missing only the tips of the wings).

ETYMOLOGY: Patronym for F.C. Thompson, for his many contributions to the systematics of Syrphidae and Diptera in general.

Aschizomyia, new genus

DIAGNOSIS: Head lacking macrosetae, female frons pubescent; ptilinal suture absent; basal flagellomere large, tapered asymmetrically to apical point (which bears arista); scutum with numerous scattered setulae (none in rows); thorax with one pair of dorsocentral setae, one pair of of scutellars, three postalars, four notopleurals, no supraalars. Vein Sc long; apices of R_{4+5} and M_1 converge closely at wing tip but do not meet; M forked, with very short stem; cells dm and cup very large. Metatibia with ventral pair short, stout apical spurs.

TYPE SPECIES: *A. burmensis*, n. sp.

ETYMOLOGY: Derived directly from *Aschiza*, and *-myia* (Greek, "fly"). The genus name is feminine.

COMMENTS: The phylogenetic position of the genus is equivocal (fig. 51), having features of Syrphidae and Pipunculidae but decidedly more primitive than the crown group of either. Syrphid features include a short sc-r crossvein, apex of CuA_1 incomplete, the exposed female frons being pubescent (the head lacking any macrosetae), and the alula is well developed. *Aschizomyia* plesiomorphically has a small cell bm; C ends at the apex of M_1 (instead of R_{4+5}); M is forked, and M_1 does not join R_{4+5} preapically. The venation is very similar to that of *Protonephrocercus*, but *Aschizomyia* lacks all the features of the head, female terminalia, and pretarsi that characterize Pipunculidae. The large cup cell occurs in both Syrphidae and Pipunculidae, possibly convergently. It is difficult to discern whether the arista is dorsally or apically situated on the basal flagellomere, since it occurs at the apex of a narrow, pointed lobe and the flagellomere is asymmetrical, with an extensive, emarginate ventral margin. I have chosen to depict *Aschizomyia*, preliminarily, in a basal trichotomy with Syrphidae and Pipunculidae + Schizophora because of the equivocal morphological evidence. The lack of a ptilinum indicates that *Aschizomyia* is not a schizophoran, though the possibility remains that it is a stem-group one.

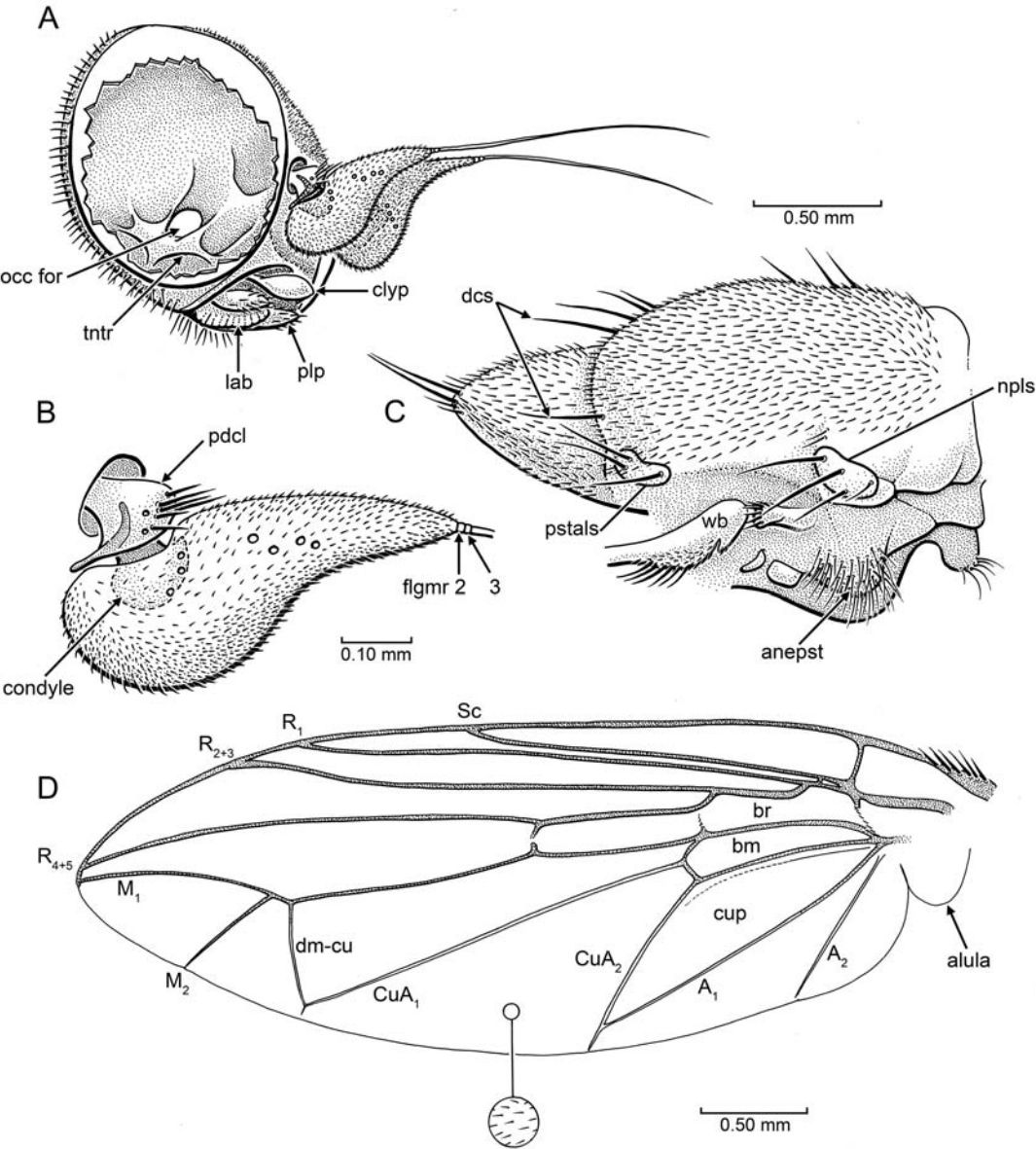


FIG. 53. *Aschizomyia burmensis*, n. gen., n. sp. (Syrphoidea), female holotype in Burmese amber, AMNH Bu-SA1 **A.** Head, lateral view as preserved, showing internal structures. **B.** Antenna, lateral view. **C.** Thorax, dorsolateral view. **D.** Wing.

Aschizomyia burmensis, new species

Figures 20, 53

DIAGNOSIS: As for genus, by monotypy.
DESCRIPTION: (female only). **Head:** Hemispherical. Eye large, bare of setulae (portion of

right eye missing); occupying all of lateral surface of head (cheek not exposed), margins flanking frons are parallel. Frons well developed, width slightly less than face; with fine, short pubescence only; no macrosetae on head (e.g., no interfrontals, ocellars, orbitals, verticals, or

vibrissae). Occiput densely setose, with thick, short setae overall; occiput slightly swollen laterally, centrally deeply recessed. Oral margin slightly protruding dorsally. Ptilinum lacking. **Antenna:** Scape hidden (probably minute); pedicel asymmetrical, with ventral lobe; dorsoapical portion with stiff setae, having rounded condylelike "conus" inserted into base of flagellomere 1 (cuticle is cleared). Basal flagellomere large, laterally flattened, apex tapered and pointed; asymmetrically drop shaped in lateral view; arista attached to pointed apex. Arista with 2 minute basal articles; apical article long, fine, flagellate, bare (no micropubescence visible). **Mouthparts:** Clypeus protruding; narrow U-shaped, articulating with but not fused to oral margin. Palp relatively large, apex pointed, slightly longer than labellum; labellum flat, as preserved largely recessed into oral cavity and between palps; labrum not observable.

Thorax: Relatively flattened dorsally, not particularly deep. Prosternum (very exposed) cordate, entirely free, unconnected to surrounding sclerites. Scutum and scutellum covered in dense, short setulae (these thicker and longer on scutellum, especially lateral margins) (rows of acrostichals absent). Transverse suture very short, far anterior, just above notopleural setae. Thorax with following large macrosetae: 1 pair of large, prescutellar dorsocentrals; row of 3 postalar setae (posteriormost one very thick); row of 4 notopleural setae (posterior 2 largest, thickest; anterior one $\sim 0.5\times$ size of others); anepisternum with dense, fine pilosity; katapisternum bare. Prescutellum absent; scutellum triangular in dorsal view, apex pointed, with pair of large, thick scutellar setae. **Wing:** Relatively slender, length $2.5\times$ the width, apex narrow (not broadly rounded); no infuscation or darkening of membrane, even between Sc and R_1 ; membrane with fine microtrichia over entire surface. Row of 5 prehumeral costal setae; vein C with fine setulae (without thick/coarse spinules), C ends at tip of M_1 . Sc relatively long, slightly greater than $0.5\times$ length of wing; R_1 close and parallel to Sc, ends closer to apex of R_{2+3} ; crossvein sc-r present,

close to level of crossvein h. Apex R_{2+3} slightly divergent from apex of R_{4+5} ; apices of R_{4+5} and M_1 converge closely at wing tip but do not meet. Cell dm very large; cell br long, slender, with small, incomplete, spurlike crossvein near base of CuA_1 . Crossvein dr-m weakened in middle; no trace of spurious vein present; cell dm very large, crossvein dm-cu very close to wing margin. M_1 - M_2 fork present, with very short stem attached to apex of cell dm. Apex CuA_1 incomplete (not reaching wing margin); cell cup large, with short apical vein; anal lobe present, small; A_2 present, complete; alula well developed. Halter relatively small.

Legs: Of moderate length and width. Pro- and mesocoxae short, mostly integrated into pleura; metacoxa slightly longer, suspended and largely free from pleura; pro- and mesocoxae with setae on distal margin. All podomeres setulose, with longer setae on some portions; profemur with irregular, ventral row 10–12 longer, fine setae; mesofemur with longer setulae on distal half. Tibial spurs 0-2-0, mesotibial spurs ventroapical, short, stout; apex of metatibia slightly swollen; basitarsomere length equal to length of tarsomeres 2+3 on all legs; claws large, pulvilli relatively small (≤ 0.5 length of claws); empodium setiform.

Abdomen: As preserved, dorsoventrally flattened; 6 tergites exposed, 1–4 large, all covered with dense, short, decumbent setulae (as on scutum); 6 sternites present, 1–4 large, well developed, width $\sim 0.7\times$ width of abdomen. Pleural membrane exposed between lateral margins of sternites and ventral margins of tergites. Spiracles in membrane, close to margin of tergite. **Male Terminalia:** Unknown. **Female Terminalia:** Very simple; terminal segments apparently not telescoping; cercus small, oval, simple, 1-segmented.

SPECIMENS EXAMINED: Holotype, female, AMNH Bu-SA1. The specimen is very well preserved, missing only the right eye and the tips of the left wing and metatarsi.

ETYMOLOGY: In reference to the country of origin.

CYCLORRHAPHA Undetermined

(Immatures)

Figures 22, 23

A cyclorrhaphan larva in Burmese amber, AMNH Bu-1536, is well preserved, complete, and has many structures preserved in detail. Length is ~2.5 mm, body relatively slender. Body is visible dorsally and ventrally, though debris adhering ventrally obscures some details (e.g., creeping welts). Cuticle somewhat cleared, partially revealing cephalopharyngeal skeleton. Cephalopharyngeal skeleton (CPS) with dorsal and ventral cornus well developed, appear fully sclerotized, extend posteriorly to level of suture between segments 2 and 3. CPS dorsally with narrowly U-shaped epipharyngeal sclerite, which has multiple fine perforations. Mandibles appear simple, apparently lacking multiple small teeth on ventral margin or on broad lateral surfaces at base (as are found, for example, in *Megaselia* [Phoridae]). Body: Anterior two segments distinctly narrower than other, posterior segments. Apical structures of anterior spiracles not visible, not everted (though internal tracheal trunk visible). Dorsal and lateral portions segments 3–11 with short, stout, erect, exocuticular tubercles (each broadly conical with minute apical process); each segment with transverse row of eight such tubercles, bilaterally symmetrical, lateral ones pointing outward, dorsal ones pointing upward. Apical segment with ventralmost pair of tubercles small, very close; flanked by pair of larger, pointed tubercles, both pairs pointing backward; 2 lateral pairs present (one pair is dorsolateral), pointed laterad. Posterior spiracles not visible (this area obscured).

The body shape plus the presence and structure of transverse rows of tubercles is most similar to larvae in the Phoridae, though a well-developed, perforated epipharyngeal sclerite occurs in only some phorids (Ferrar, 1987). Phoridae have diverse mandible structure, some

with heavily dentate mandibles, others lacking teeth. AMNH Bu-1536 is possibly the larva of either a prioriphorine (which are diverse and relatively common in Burmese amber), or one of the sciadocerines taxonomically treated here as adults. Three Cyclorrhapha larvae were reported in Late Cretaceous amber from New Jersey (Grimaldi and Cumming, 1999), all quite different from each other and from larva Bu-1536.

A small puparium in Burmese amber, JZC Bu304 (1.4 mm body length), is typically cyclorrhaphan. It has a flattened ventral surface, rounded dorsal surface, and large opercular area (the adult had eclosed). There are no features of the puparium diagnostic of particular families, such as spines or a pair of everted anterior spiracles.

ACKNOWLEDGMENTS

I am indebted to various people and sources of support for the completion of this work. Generous sponsorship was provided by U.S. National Science Foundation grant OPUS DEB-1556502. People who loaned critical specimens for study are Dany Azar, Christel and Hans Hoffeins, Alexandr Rasnitsyn, and James Zigras. People who generously donated specimens to the AMNH are Scott Anderson, Keith Luzzi, and Steven Chomicki. Sieghard Ellenberger, Jens von Holt, and Jurgen Velten provided valuable specimens of Baltic and Burmese amber specimens for purchase. I am also very grateful for all the expert assistance by people at the AMNH: Paul Nascimbene, with preparation of amber specimens; Steve Thurston, for preparation of plates; Andrew Smith, of the MIF lab for SEM imaging; and Mary Knight, Scientific Publications, editor par excellence. Brian Brown and Dalton de Souza Amorim provided expert reviews of the manuscript; Brian, in fact, checked for and informed me of the presence of a stridulum in Euphorida. I am very grateful for these reviews even though some of my conclusions may differ with them.

REFERENCES

- Amorim, D.S., V.C. Silva, and B.V. Brown. 2018. *Puye-huemyia chandleri*, gen. nov., sp. nov. (Diptera: Opetiidae): remnant of a Cretaceous biota in Chile. *American Museum Novitates* 3892: 1–27.
- Archibald, S.B., C. Kehlmaier, and R.W. Mathewes. 2014. Early Eocene big headed flies (Diptera: Pipunculidae) from the Okanagan Highlands, western North America. *Canadian Entomologist* 146: 429–443.
- Arillo, A., and M.B. Mostovski. 1999. A new genus of Prioriphorinae (Diptera, Phoridae) from the Lower Cretaceous amber of Álava (Spain). *Studia Dipterologica* 6: 251–255.
- Azar, D., R. Gèze, and F. Acra. 2010. Lebanese amber. In D. Penney (editor), *Biodiversity of fossils in amber from the major world deposits*: 271–298. Manchester UK: Siri Scientific Press.
- Borkent, A., et al. 2018. Remarkable fly (Diptera) diversity in a patch of Costa Rican cloud forest: why inventory is a vital science. *Zootaxa* 4402 (1): 53–90.
- Breitkreuz, L.C.V., S.L. Winterton, and M.S. Engel. 2017. Wing tracheation in Chrysopidae and other Neuropterida (Insecta): a resolution of the confusion about vein fusion. *American Museum Novitates* 3890: 1–44.
- Brown, B.V. 1999. Re-evaluation of the fossil Phoridae (Diptera). *Journal of Natural History* 33: 1561–1573.
- Brown, B.V. 2002. A new primitive phorid (Diptera: Phoridae) from Baltic amber. *Studia Dipterologica* 8 (2001): 553–556.
- Brown, B.V. 2004. A new Baltic amber *Triphleba* Rondani with greatly enlarged palpi (Diptera: Phoridae). *Studia Dipterologica* 11: 549–552.
- Brown, B.V. 2007a. A further new genus of primitive phorid fly (Diptera: Phoridae) from Baltic amber and its phylogenetic implications. *Contributions in Science, Natural History Museum of Los Angeles County* 513: 1–14.
- Brown, B.V. 2007b. Novel character states in fossil species of modern phorid genera (Diptera: Phoridae). *Studia Dipterologica* 14: 107–116.
- Brown, B.V. 2009. An enigmatic new genus and species of phorid fly from Baltic amber. *Studia dipterologica* 16 (1/2): 43–46.
- Brown, B.V. 2013. A new species of *Anevrina* from Baltic amber (Diptera: Phoridae). *Annals of the Entomological Society of America* 106: 310–312.
- Brown, B.V., and D.H. Feener, Jr. 1995. Efficiency of two mass sampling methods for sampling phorid flies (Diptera: Phoridae) in a tropical biodiversity survey. *Contributions in Science, Natural History Museum of Los Angeles Co.* 459: 1–10.
- Brown, B.V., and E.M. Pike. 1990. Three new fossil phorid flies (Diptera: Phoridae) from Canadian Late Cretaceous amber. *Canadian Journal of Earth Sciences* 27: 845–848.
- Brown, B.V., D. de Souza Amorim, and G.A. Kung. 2015. New morphological characters for classifying Phoridae (Diptera) from the structure of the thorax. *Zoological Journal of the Linnean Society* 173: 424–485.
- Brown, B.V. et al. 2018. Comprehensive inventory of true flies (Diptera) at a tropical site. *Communications Biology* (8 pp.). [doi:10.1038/s42003-018-0022-x]
- Brues, C.T. 1939. Fossil Phoridae in Baltic amber. *Bulletin of the Museum of Comparative Zoology, Harvard University* 85: 413–36.
- Carpenter, F.M., and F.M. Hull. 1939. The fossil Pipunculidae. *Bernstein-Forschungen* 4: 8–17.
- Chandler, P.J. 1989. Superfamily Platypezoidea. 46. Family Platypezidae. In N.L. Evenhuis (editors), *Catalogue of the Diptera of the Australasian and Oceanian regions*: 420–421. Honolulu: Bishop Museum Press.
- Chandler, P.J. 1994. The Oriental and Australasian species of Platypezidae (Diptera). *Invertebrate Systematics* 8: 351–434.
- Chandler, P.J. 2001. The flat-footed flies (Diptera: Opetiidae and Platypezidae) of Europe. *Fauna Entomologica Scandinavica* 36: 1–276. Leiden: Brill.
- Cockerell, T.D.A. 1909. Descriptions of Tertiary insects. Part V. Some new Diptera. *American Journal of Science* 27: 53–58.
- Cockerell, T.D.A. 1911. Fossil insects from Florissant, Colorado [3]. *Bulletin of the American Museum of Natural History* 30 (6): 71–82.
- Comstock, J.H. 1918. *The wings of insects*. Ithaca, NY: Comstock Publishing Co.
- Comstock, J.H., and A.B. Comstock. 1904. *A manual for the study of insects*. Ithaca NY: Comstock Publishing Company, 4th ed.
- Cook, E.F. 1949. The evolution of the head in the larvae of the Diptera. *Microentomology* 14: 1–57.
- Disney, H. 1994. *Scuttle flies: the Phoridae*. Springer Science & Business Media.
- Evenhuis, N.L. 1994. *Catalogue of the fossil flies of the world (Insecta: Diptera)*. Leiden: Backhuys Publishers.
- Ferrar, P. 1987. *A guide to the breeding habits and immature stages of Diptera Cyclorrhapha*. Entomograph 8, vols. 1 and 2. Leiden: E.J. Brill.

- Griffiths, G.C. 1972. The phylogenetic classification of Diptera Cyclorrhapha, with special reference to the structure of the male postabdomen. Series Entomologica, 8. The Hague: Dr. W. Junk, N.V.
- Grimaldi, D.A. 2016. Diverse orthorrhaphan flies (Insecta: Diptera: Brachycera) in amber from the Cretaceous of Myanmar: Brachycera in Cretaceous amber, Part VII. Bulletin of the American Museum of Natural History 408: 1–131.
- Grimaldi, D.A., and J.M. Cumming. 1999. Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. Bulletin of the American Museum of Natural History 239: 1–124.
- Grimaldi, D.[A.], and M.S. Engel. 2005. Evolution of the insects. Cambridge: Cambridge University Press, xv+755 pp.
- Grimaldi, D.A. and P.C. Nascimbene. 2010. Raritan (New Jersey) amber. In D. Penney (editor), Biodiversity of fossils in amber from the major world deposits: 167–191. Manchester UK: Siri Scientific Press.
- Grimaldi, D.A., and A. Ross. 2017. Extraordinary Lagerstätten in amber, with particular reference to the Cretaceous of Burma. In N.C. Fraser and H.-D. Sues (editors), Terrestrial conservation Lagerstätten, windows into the evolution of life on land: 287–342. Edinburgh: Dunedin Press.
- Grimaldi, D.[A.], A. Shedrinsky, and T.P. Wampler. 2000. A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey. In D. Grimaldi (editor), Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey: 1–76. Leiden: Backhuys Publishers, viii+498 pp.
- Hash, J.M., and B.V. Brown. 2015. Revision of the New World species of the millipede-parasitic genus *Myriophora* Brown (Diptera: Phoridae). Zootaxa 4035: 1–79.
- Hennig, W. 1964. Dipteren-Familie Sciadoceridae im baltischen Bernstein (Diptera: Cyclorhapha Aschiza). Stuttgarter Beiträge zur Naturkunde 127: 1–10.
- Hennig, W. 1976. Das Hypopygium von *Lonchoptera lutea* Panzer und die phylogenetischen Verwandtschaftsbeziehungen der Cyclorrhapha (Diptera). Stuttgarter Beiträge zur Naturkunde 283: 1–63.
- Hong, Y.-c. 1981. Eocene fossil Diptera Insecta in amber of Fushun coalfield. Geological Publishing House, Beijing vi+166 pp. [in Chinese]
- Hull, F.M. 1945. A revisional study of the fossil Syrphidae. Bulletin of the Museum of Comparative Zoology 95: 251–355.
- Hull, F.M. 1960. A new genus and four new species of fossil Diptera from Montana and Colorado. Contributions to the Museum of Paleontology, University of Michigan 15: 269–279.
- Iturralde-Vincent, M.A., and R.D.E. MacPhee. 1996. Age and paleogeographical origin of Dominican amber. Science 273: 1850–1852.
- Kehlmaier, C., M. Dierick, and J.H. Skevington. 2014. Micro-CT studies of amber inclusions reveal internal genitalic features of big-headed flies, enabling a systematic placement of *Metanephrocerus* Aczél, 1948 (Insecta: Diptera: Pipunculidae). Arthropod Systematics and Phylogeny 72: 23–36.
- Kessel, E.L. 1965a. *Lindneromyia*, a new genus of flat-footed flies, and the descriptions of two new species of Platypezidae from Africa (Diptera). Stuttgarter Beiträge zur Naturkunde 143: 1–6.
- Kessel, E.L. 1965b. *Symmetricella*, a new genus of Platypezidae from Peru (Diptera). Wasmann Journal of Biology 23: 235–239.
- Kessel, E.L., and E.A. Maggioncalda. 1968. A revision of the genera of Platypezidae, with the descriptions of five new genera and considerations of phylogeny, circumversion and hypopygia (Diptera). Wasmann Journal of Biology 26: 33–106.
- Kirk-Spriggs, A., and B.J. Sinclair (editors). 2018. Manual of Afrotropical Diptera, vols. 1–2. Pretoria: South African National Biodiversity Institute.
- Klocke, D., A. Schmitz, and H. Schmitz. 2011. Fire-adaptation in *Hypocerides nearcticus* Borgmeier and *Anabarhynchus hyalipennis hyalipennis* Macquart and new notes about the Australian “smoke fly” *Microsania australis* Collart (Diptera: Phoridae, Therevidae and Platypezidae). Open Entomology Journal 5: 10–14.
- Klymko, J., and S.A. Marshall. 2008. Review of the Nearctic Lonchopteridae (Diptera), including descriptions of three new species. Canadian Entomologist 140: 649–673.
- Li, X.-R., Y.-H. Zheng, C.-C. Wang, Z.-Q. Wang. 2018. Old method not old-fashioned: parallelism between wing venation and wing-pad tracheation of cockroaches and a revision of terminology. Zoomorphology. [doi.org/10.1007/s00435-018-0419-6]
- Malloch, J.R. 1917. A preliminary classification of Diptera, exclusive of Pupipara, based upon larval and pupal characters, with keys to imagines in certain families. Part 1. Illinois Natural History Survey Bulletin 12 (3): 161–409.
- Marshall, S.A. 2012. Flies, the natural history and diversity of Diptera. Buffalo, NY: Firefly Books.

- McAlpine, D.K. 2008. New extant species of ironic flies (Diptera: Ironomyiidae) with notes on ironomyiid morphology and relationships. *Proceedings of the Linnean Society of New South Wales* 129: 17–38.
- McAlpine, J.F. 1967. A detailed study of Ironomyiidae (Diptera: Phoroidea). *Canadian Entomologist* 99 (3): 225–236.
- McAlpine, J.F. 1973. A fossil ironomyiid fly from Canadian amber (Diptera: Ironomyiidae). *Canadian Entomologist* 105: 105–111.
- McAlpine, J.F. 1981. Morphology and terminology – adults. In J.F. McAlpine et al. (editors), *Manual of Nearctic Diptera*, vol. 1: 9–63. Research Branch Agriculture Canada monograph 27. Ottawa: NRC Research Press.
- McAlpine, J.F. 1989. Phylogeny and classification of the Muscomorpha. In J.F. McAlpine and D.M. Wood (editors), *Manual of Nearctic Diptera*, vol. 3: 1397–1518. Research Branch Agriculture Canada monograph 32. Ottawa: NRC Research Press.
- McAlpine, J.F., and J.E.H. Martin. 1966. Systematics of Sciadoceridae and relatives with descriptions of two new genera and species from Canadian amber and erection of family Ironomyiidae (Diptera: Phoroidea). *Canadian Entomologist* 98: 527–544.
- McKellar, R.C., and A.P. Wolfe. 2010. Canadian amber. In D. Penney (editor), *Biodiversity of fossils in amber from the major world deposits*: 96–113. Manchester, UK: Siri Scientific Press.
- Mengual, X., G. Ståhls, and S. Rojo. 2008. First phylogeny of predatory flower flies (Diptera, Syrphidae, Syrphinae) using mitochondrial COI and nuclear 28S rRNA genes: conflict and congruence with the current tribal classification. *Cladistics* 24: 543–562.
- Meunier, F. 1902. Description de quelques diptères de l'ambre. *Annales de la Société Scientifique de Bruxelles (Mem.)* 26: 96–104.
- Meunier, F. 1907. Beiträge zur Syrphiden-Fauna des Bernsteins. *Jahrbuch der Königlich Preussischen Geologisches Landesanstalt und Bergakademie* 24: 201–210.
- Mostovski, M., 1995a. New representatives of Platypozidae (Diptera) from the Mesozoic, and main directions in the evolution of the family. *Paleontologicheskii Zhurnal* 2: 106–118.
- Mostovski, M.B. 1995b. New taxa of ironomyiid flies (Diptera, Phoromorpha, Ironomyiidae) from Cretaceous deposits of Siberia and Mongolia. *Paleontologicheskii Zhurnal* 4: 86–103.
- Mostovski, M. 1999. Curious Phoridae (Insecta, Diptera) found mainly in Cretaceous ambers. *Estudios del Museo Ciencias Naturales de Álava* 14 (Espec. 2): 231–243.
- Nakayama, H. 2012. Complex asymmetric male genitalia of *Anevrina* Lioy (Diptera: Phoridae). *Arthropod Structure and Development* 41: 35–49.
- Ochman, H., B. Stille, M. Niklasson, R.K. Selander, and A.R. Templeton. 1980. Evolution of clonal diversity in the parthenogenetic fly *Lonchoptera dubia*. *Evolution* 34: 539–547.
- Pauli, T., et al. 2018. New data, same story: phylogenomics does not support Syrphoidea (Diptera: Syrphidae Pipunculidae). *Systematic Entomology* 43: 447–459.
- Penney, D. 2010. Dominican amber. In *Biodiversity of fossils in amber from the major world deposits*: 23–166. Manchester, UK: Siri Scientific Press.
- Pike, E.M. 1994. Historical changes in insect community structure as indicated by hexapods of Upper Cretaceous Alberta (Grassy Lake) amber. *Canadian Entomologist* 126: 695–702.
- Rafael, J.A., and M. de Meyer. 1992. Generic classification of the family Pipunculidae (Diptera): a cladistic analysis. *Journal of Natural History* 26: 637–658.
- Ritzkowski, S. 1997. Das geologische Alter der bernsteinführenden Sedimente in Sambia (Bezirk Kaliningrad), bei Bitterfeld (Sachsen-Anhalt) und bei Helmstedt (SE-Niedersachsen). In *Investigations into amber. Proceedings of the International Interdisciplinary Symposium: Baltic amber and other fossil resins*: 2–6. Gdansk Poland: Archaeological Museum in Gdansk: Museum of the Earth, Polish Academy of Sciences.
- Rotheray, G.E., and F. Gilbert. 2008. Phylogenetic relationships and the larval head of the lower Cyclorhapha (Diptera). *Zoological Journal of the Linnean Society* 153: 287–323.
- Sadowski, E.-M., A.R. Schmidt, L.J. Seyfullah, and L. Kunzmann. 2017. Conifers of the 'Baltic amber forest' and their palaeoecological significance. *Stapfia* 106: 1–73.
- Scudder, S.H. 1878. The fossil insects of the Green River shales. *Bulletin of the U.S. Geological and Geographic Terrestrial Survey* 4: 747–776.
- Shi, G., et al. 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* 37: 155–163.
- Sinclair, B.J., J.M. Cumming, and S.E. Brooks. 2013. Male terminalia of Diptera (Insecta): a review of evolutionary trends, homology and phylogenetic implications. *Insect Systematics and Evolution* 44: 373–415.

- Skevington, J.H., and D.K. Yeates. 2000. Phylogeny of the Syrphoidea (Diptera) inferred from mtDNA sequences and morphology with particular reference to classification of the Pipunculidae (Diptera). *Molecular Phylogenetics and Evolution* 16: 212–224.
- Solorzano-Kraemer, M.M., V. Perrichot, B.V. Brown, P. Tafforeau, and C. Soriano. 2011. A new species of the Cretaceous genus *Prioriphora* (Diptera: Phoridae) in French amber. *Systematic Entomology* 36: 581–588.
- Ståhls, G., H. Hipa, G. Rotheray, J. Muona, and F. Gilbert. 2003. Phylogeny of Syrphidae (Diptera) inferred from combined analysis of molecular and morphological characters. *Systematic Entomology* 28: 433–450.
- Stalker, H.D. 1956. On the evolution of parthenogenesis in *Lonchoptera* (Diptera). *Evolution* 10: 345–359.
- Systema dipterorum. 2013. Online resource (www.diptera.org), version 1.5, last updated 13 June 2013.
- Tachi, T. 2014. Homology of the metapleuron of Cyclo-rrhapha, with discussion of the paraphyly of Syrphoidea (Diptera: Aschiza). *Insect Systematics and Evolution* 45: 395–414.
- Teskey, H.J. 1981. Morphology and terminology – larvae. In J.F. McAlpine et al. (editors), *Manual of Nearctic Diptera*, vol. 1: 65–88. Research Branch Agriculture Canada monograph 27. Ottawa: NRC Research Press.
- Tkoč, M., A. Tóthová, G. Ståhls, P.J. Chandler, and J. Vaňhara. 2017. Molecular phylogeny of flat-footed flies (Diptera: Platypezidae): main clades supported by new morphological evidence. *Zoologica Scripta* 46: 429–444.
- Vockeroth, J.R., and F.C. Thompson. 1987. Chapter 52, Syrphidae. In J.F. McAlpine et al. (editors), *Manual of Nearctic Diptera*, vol. 2: 713–743. Research Branch Agriculture Canada monograph no. 28. Ottawa: NRC Research Press.
- Wang, B., et al. 2014. A diverse paleobiota in Early Eocene Fushun amber from China. *Current Biology* 24: 1606–1610.
- Weitschat, W., and W. Wichard. 2010. Baltic amber. In D. Penney (editor), *Biodiversity of fossils in amber from the major world deposits: 80–115*. Manchester, UK: Siri Scientific Press.
- White, A. 1916. The Diptera-Brachycera of Tasmania, Part III. Families Asilidae, Bombyliidae, Empidae, Dolichopodidae, and Phoridae. *Papers and Proceedings of the Royal Society* 1916: 148–266.
- Wiegmann, B.M., et al. 2011. Episodic radiations in the fly tree of life. *Proceedings of the National Academy of Sciences of the United States of America* 108 (14): 5690–5695.
- Winkler, I.S., C.C. Labandeira, T. Wappler, and P. Wilf. 2010. Distinguishing Agromyzidae (Diptera) leaf mines in the fossil record: new taxa from the Paleogene of North America and Germany and their evolutionary implications. *Journal of Paleontology* 84: 935–954.
- Woodley, N.E., A. Borkent, and T.A. Wheeler 2009. Phylogeny of the Diptera. In B.V. Brown et al. (editors), *Manual of Central American Diptera*, vol. 1: 74–94. NRC Research Press, Ottawa.
- Wootton, R.J., and A.R. Enos. 1989. The implications of function on the origin and homologies of the dipterous wing. *Systematic Entomology* 14: 507–520.
- Young, A.D., et al. 2016. Anchored enrichment dataset for true flies (order Diptera) reveals insights into the phylogeny of flower flies (family Syrphidae). *BMC Evolutionary Biology* 16: 143.
- Zhang, J.-F. 1987. Four new genera of Platypezidae. *Acta Palaeontologica Sinica* 26: 595–603.

