

BRACHYCERAN DIPTERA IN
CRETACEOUS AMBERS AND
MESOZOIC DIVERSIFICATION
OF THE EREMONEURA

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CONTENTS

Abstract	3
Introduction	4
Materials and Methods	5
Acknowledgments	6
Systematics	6
<i>Tethepomyia</i> , Family Undetermined	6
Rhagionidae	7
Stratiomyidae	17
Hilarimorphidae	21
Scenopinidae	29
Asilidae	30
Empidoidea	31
Empidinae	32
Atelestinae	35
<i>Nemedina</i> Genus Group	37
Hybotid Lineages	50
Tachydromiinae	50
Trichopezinae	55
Microphorinae	57
Dolichopodidae	67
<i>Chimeromyia</i> , Family Undetermined	69
Platypezidae (?)	76
Ironomyiidae	79
Lonchopteridae (?)	82
Sciadoceridae	94
Phoridae	98
Larvae, Familiae Incertae Sedis	105
Phylogenetic Analysis of Cyclorrhapha	106
Discussion	110
References	117
Index	122
Color Plates	85–92

ABSTRACT

Sixty-five specimens representing 49 species in 37 genera and 12, possibly 13, families of brachycerous Diptera are described in detail. Some genera are family incertae sedis. They are preserved in Cretaceous ambers from the following areas and ages (abbreviations after each are used to designate the following origins of the ambers): Manitoba and Alberta, Canada (C) (Campanian); central New Jersey (NJ) (Turonian); and Lebanon (L) (Neocomian). All taxa described are new species and most genera are described as new, except where noted.

The new taxa and their origins are the following: *Tethepomyia thauma* (NJ), an extremely apomorphic fly of probable nematocerous affinities. In RHAGIONIDAE: *Paleochrysopilus hirsutus* (L), *Jersambromyia borodini* (NJ), *Mesobolbomyia acraei* (L); and four additional genera (3 L, 1 NJ) that are described and illustrated but not named because of incomplete preservation. STRATIOMYIDAE: a new specimen of *Cretaceogaster pygmaeus* Teskey (C) is reported, showing newly observed structures that confirm its extremely primitive position in the family; in addition, in NJ amber an additional primitive genus is described but not named, with affinities in the Pachygastrinae, Chironomyzinae, or Beridinae. HILARIMORPHIDAE: *Hilarimorphites superba*, *H. yeatesi*, and *H. longimedia*, all in NJ amber, and the only fossil hilarimorphids. SCENOPINIDAE(?): *Proratites simplex* (NJ), probably a primitive (proratine) scenopinid, which would be the only Mesozoic fossil of the family. ASILIDAE: an incomplete, unnamed specimen in NJ amber, which is one of only two Cretaceous records.

The most diverse and numerous brachycerans in Cretaceous ambers are in the EMPIDOIDEA, with new taxa as follows. EMPIDINAE: *Turonempis styx* (NJ), *Emplita casei* (NJ). ATELESTINAE: *Atelestites senectus* (L). NEMEDINA GENUS GROUP: *Cretodromia glaesa* (C); *Nemedromia campania* (C), *N. telescopica* (C), *N. turonia* (NJ); *Neoturonius asymmetrus* (NJ), *N. cretatus* (NJ), and *N. vetus* (NJ, possibly also C); *Phaetempis lebanensis* (L), which is possibly a very plesiomorphic member of this group. The *Nemedina* group today is represented by a single extant species from Hungary. TACHYDROMIINAE: *Cretoplatypalpus americanus* (C), with *Cretoplatypalpus* Kovalev previously known from a species in Cenomanian amber from northern Siberia; and *Mesoplatypalpus carpenteri* (C). TRICHOPEZINAE: *Apalocnemis canadambri* (C), which is the only species studied here belonging to an extant genus, *Apalocnemis* Philippi (previously known only from extant species widespread in distribution). MICROPHORINAE: *Micro-*

phorites similis and *M. oculus* (L), two additional species of the extinct genus *Microphorites* Hennig, known only from Lebanese amber; *Avenaphora hispida* (L); *Cretomicrophorus novemundus* (NJ), the second species in the extinct genus *Cretomicrophorus* Negrobov, originally known from Cretaceous amber of Siberia; *Archichrysotus incompletus* (NJ) and *A. manitobus* (C), the genus also previously known from Siberian amber. DOLICHOPODIDAE: *Sympycnites primaevus* (L), which is the oldest definitive dolichopodid. Three new species are described in an unusual new genus, *Chimeromyia*, known only from Lebanese amber: *C. intriguea*, *C. acuta*, and *C. reducta*. *Chimeromyia* possesses features of Empidoidea and Cyclorrhapha.

The few Cyclorrhapha in Cretaceous ambers are all very plesiomorphic. PLATYPEZIDAE: *Electrosania cretica* (NJ), the most plesiomorphic known platypezid. *Lebambromyia acraei* (L), formally unplaced to family, is a plesiomorphic phoroid closely resembling IRONOMYIIDAE (with one living species in Australia and Tasmania, and one extinct species previously described in Canadian amber). LONCHOPTERIDAE: *Lonchopterites prisca* (L) and *Lonchopteromorpha asetocella* (L), the only definitive fossils of this small, extant family. SCIADOCERIDAE: *Archiphora pria* (NJ); and *Archiscia da lebanensis* (L), the oldest fossil of the family and perhaps the most plesiomorphic phoroid. In addition, two new species are described in the Mesozoic genus *Prioriphora* McAlpine and Martin, *P. luzzii* and *P. casei* (both NJ). This is the best represented brachyceran genus in the Cretaceous, although it might be a paraphyletic taxon. Three cyclorrhaphan larvae of uncertain family identities are described, all in NJ amber; one appears similar to Sciadoceridae.

Phylogenetic significance of most of these fossils are discussed, as are certain characters of traditional importance in the higher classification of Brachycera, such as the number of arisal articles. The fossils are placed onto cladograms of the lower Brachycera, the Empidoidea, and basal Cyclorrhapha, and a chronology is proposed of the origins of brachyceran families. The Brachycera apparently originated in the Lower Jurassic, with the Asiloidea not diversifying until the Lower Cretaceous. The Eremoneura (Empidoidea + Cyclorrhapha), as expected, show later diversification, with subfamily-level radiations of empidoids in the Lower to mid-Cretaceous, and the most plesiomorphic families of Cyclorrhapha (e.g., Platypezoidea, Phoroidea, Lonchopteridae) appearing in the Lower to mid-Cretaceous. Origins and radiations of the Schizophora almost certainly are of

much more recent origin, in the mid to latest Cretaceous and especially the Cenozoic.

The diversity and detailed preservation of these

fossils contribute exceptional insight into the early evolution of the Brachycera and the Eremoneura in particular.

INTRODUCTION

The Diptera are certainly one of the most ecologically ubiquitous and significant orders of insects. The Brachycera alone constitute approximately 92 families and 60,000 species, and another 50 families and 40,000 species are in the nematoceros Diptera. The Diptera are also probably the most ecologically varied group of insects, with forms that are aquatic, leafmining, predators as adults and/or larvae, endoparasites of vertebrates, blood and hemolymph feeders, endo- and ectoparasitoids of arthropods, saprophages, carrion feeders (as larvae), cleptoparasites, and others. The exact timing is unclear, but this remarkable diversity of Brachycera has apparently developed since the Lower Jurassic, approximately 200 million years ago (Ma).

The oldest Diptera are several extinct and extant nematoceros families, from the Triassic of Australia, France, and Virginia (reviewed in Grimaldi and Fraser, 1999). *Alinka*, described by Krzeminski (1992) and believed to be the oldest brachyceran, has been placed in the extinct nematoceros family Procramptonomyiidae (Fraser et al., 1996; Grimaldi and Fraser, 1999; Shcherbakov et al., 1995). Another putative Triassic brachyceran has also been reported, based on a wing from the mid-Triassic of France (Krzeminski, 1998); commentary on these fossils is given elsewhere (Grimaldi and Fraser, 1999). Evenhuis (1994) suggested that *Crosaphis*, known at the time only as a wing from the Triassic of Australia, was a bombyliid. Not only is the venation of *Crosaphis* not brachyceran but rather mycetobiine (Anisopodidae), but recently discovered specimens with complete bodies from the Triassic of Virginia confirm their identity in or near the Mycetobiinae (Fraser et al., 1996; Grimaldi and Fraser, 1999). (The genus has formally been placed in a family of its own, the Crosaphididae.) The oldest unequivocal Brachycera do not appear until the mid and Lower Jurassic of Siberia, China, and England, including several genera of rhagionids,

Paleoplatypygus (Bombyliidae), Rhagionempididae, *Oligophryne*, and from China the unplaced genera *Mesosolva* and *Prosolva* (reviewed by Evenhuis, 1994). It is uncertain whether a definitive Triassic brachyceran will ever be found.

By far the greatest diversity of Mesozoic Brachycera are from the Jurassic, but this reflects a Cretaceous record that, until the last decade, has been poorly studied. The diverse Jurassic record is also skewed by huge deposits from the Upper Jurassic of Karatau, Kazakhstan (Rohdendorf, 1938, 1964, 1968; Ussatchev, 1968; others), and, to a slightly less extent, from the Upper Jurassic of China (Zhang, 1987, 1993; Hong, 1983; Hong and Wang, 1990). Many of these are large bodied specimens 0.5-1.0 cm in length, such as rhagionids, acrocerids, nemestrinids, and related families. Recently, Ren (1998b) proposed that long-tongued Mesozoic nemestrinids and other Brachycera indicated the existence of Jurassic angiosperms, and Grimaldi (1999) provided an evaluation of the evidence and interpretation for this hypothesis. Thus far, over 60 species of Jurassic Brachycera have been described, versus 30 from the Cretaceous, 17 of these being from Cretaceous ambers of Canada, France, and Siberia. As would be expected, the Cretaceous ambers have captured an extinct fauna of primarily tiny flies, such as empidoids.

Reports on the 17 species of Cretaceous amber brachycerans are distributed among 11 papers, as follows: Canadian amber (Brown and Pike, 1990; McAlpine, 1973; McAlpine and Martin, 1966; Teskey, 1971); Lebanese amber (Hennig, 1971); Siberian amber (Kovalev, 1974, 1978; Negrobov, 1978; Zaitsev, 1987); and French amber (Schlüter, 1978). Zherikhin and Sukacheva (1973) discussed the taphonomy and stratigraphy of the Siberian amber.

Here we present and discuss 49 new species of Brachycera from Cretaceous ambers of Canada, New Jersey, and Lebanon, which

also makes this study one of the most comprehensive in our understanding of the Mesozoic Brachycera.

Wing venation is just one source of characters for systematic placement of adult Brachycera, and diagnoses based entirely on venation usually have at least some ambiguity. Many other important features are minute, such as presence of one or two small, basal flagellomeres; position and sizes of setae on the head and thorax; and internal and external features of the genitalia (e.g., Sinclair et al., 1994; Cumming et al. 1995). Many of these nonwing characters require optical resolution on the scale of microns, for which preservation in amber is by far optimal. Thus, not only does amber preserve components of paleofaunas usually not found in even the finest-grained beds of compression fossils, but the much more complete preservation allows far more accurate phylogenetic placement of amber fossils. Here we have attempted to place the new fossils into phylogenetic schemes of the Brachycera that have been presented elsewhere (Brown, 1992; Cumming et al., 1995; Sinclair et al., 1994; Woodley, 1989; Yeates, 1994).

MATERIALS AND METHODS

Grimaldi (1992) presented some basic techniques on the preparation and study of ambers. Since then, new techniques have been developed and routinely used at the AMNH, using vibratory tumbling for preliminary preparation of New Jersey amber, and epoxy vacuum-embedding prior to water-fed trimming and polishing of the fragile, brittle Cretaceous ambers. This process is described elsewhere (Nascimbene and Silverstein, 1999).

Amber specimens came from the following sources and depositories:

CANADA: Material on loan from the Museum of Comparative Zoology (MCZ) (Harvard University) and from the Canadian National Collection of Insects and Spiders (CNC) (Centre for Eastern Oilseed and Cereal Crops, Ottawa) were collected at Cedar Lake, Manitoba. The MCZ material was collected by F. M. Carpenter in 1938 and by W. C. Legg in 1940; and the CNC material was collected by J. F. McAlpine and J.E.H. Mar-

tin, reported in 1969. The amber was not collected in situ from source deposits, but was found redeposited on shores. Borkent (1995) reviewed stratigraphy of the Canadian amber; McAlpine and Martin (1969) reviewed numerous, scattered deposits of Canadian Cretaceous amber, the most significant at the time being that from Cedar Lake. Amber collected by Pike (1995) from Grassy Lake is found in lignite from the Foremost Formation (Campanian). Potassium-argon dating of shales just above the Foremost Formation are 72–73 Ma, the youngest possible age for the Canadian amber; 73–83 Ma is therefore a reasonable approximation. Borkent stated (p. 13) that “there is limited evidence that the Cedar Lake amber also originated in Campanian deposits in Alberta . . .”, suggesting both deposits to be equivalent in age. Most recently, new dating by David Eberth (Royal Tyrell Museum) indicates the age of Canadian amber to be Santonian (76–80 Ma).

We have not yet studied the collection of three empidooids and twelve “Brachycera indeterminate” made by Pike (1995), which are housed in the Royal Tyrell Museum of Paleontology, Drumheller, Alberta. It is hoped that this will form another study, which would also provide valuable stratigraphic evidence for comparisons of the two main amber deposits.

LEBANON: Material is from the Acra and Estephan collections at the American Museum of Natural History (AMNH), and from the Staatliches Museum für Naturkunde, Stuttgart (STMN). The Acra collection and material at STMN, the latter collected by Dieter Schlee, are from Neocomian deposits near Jezzine (Schlee and Dietrich, 1970); the material collected by Antoni Estephan comes from near Beharre, which is also Neocomian, and probably contemporaneous with the deposit near Jezzine. A review of the Middle East amber deposits will be presented elsewhere, along with chemical analyses of the Lebanese, Jordanian, and Israeli ambers.

NEW JERSEY: All material described herein is from the collections of the AMNH. Grimaldi et al. (1989) provided a review of the chemistry and paleontology of New Jersey amber. The material studied here was collected by the senior author and a group of dedicated volunteers (see below) from a very

rich deposit in Sayreville, New Jersey and a less productive one in East Brunswick, New Jersey discovered in 1991. Both of these deposits stratigraphically are lignitic strata lying just above the South Amboy Fire Clay (Raritan-Magothy Formation), dated palynologically as Turonian (ca. 90–94 Ma).

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(STMN). Proper, careful study of the Cretaceous ambers would not have been possible without the help of Henry Silverstein and Paul Nascimbene. Mr. Silverstein set up the amber preparation laboratory and developed the embedding process, which Mr. Nascimbene later automated and refined. The fine pen and ink illustrations are by Ralph Idema, who rendered them from the original pencil sketches done by the authors. Tam Nguyen, Scientific Assistant at the AMNH, provided the graphics for the cladograms. Extensive library research was done by former AMNH Scientific Assistant Caroline Chaboo and by Tam Nguyen. Funding for excavations, preparation of specimens, and publication of this volume (particularly color plates) was provided by Henry Walter, trustee emeritus of the AMNH. Funds for the purchase of the Acra and Estephan collections were provided by Robert Goelet, trustee and Chairman Emeritus of the AMNH board of trustees. Lastly, insightful reviews of the manuscript were provided by Brian Brown, Peter Chandler, Bradley Sinclair, Norman Woodley, and David Yeates. We are very grateful for the generosity and assistance of these people.

SYSTEMATICS

FAMILY UNDETERMINED

TETHEPOMYIA, NEW GENUS

DIAGNOSIS: Antenna with large, cup-shaped pedicel; flagellum 1-segmented, flagellomere U-shaped; proboscis vestigial or completely lost; venation virtually lost; empodium pulvilliform; male genitalia with nematoceros condition of fused hypandrium and epandrium.

TYPE SPECIES: *T. thauma*, n.sp. In Turonian amber from Sayreville, New Jersey. Monotypic.

ETYMOLOGY: *Tethep-*, from the Greek, “to be amazed, or astonished;” and *-myia*, “fly.”

COMMENTS: In virtually every respect, this tiny fossil fly is exceptionally autapomorphic. The genitalia indicate it is not brachyceros, but the antennae are more reduced than in any other nematoceros fly. Additional autapomorphies include the vestigial/lost pro-

boscis, the virtual lack of venation, and long femora and tibiae with unusually short tarsi.

Tethepomyia thauma, new species

Figure 1

DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 1.66 mm; thorax length = 0.47; wing length = 0.94. HEAD: Nearly spherical. Eyes large, slightly bulbous, but with large postgena; no differentiation of dorsal and ventral facets. Head without any large setae, only row of small postoculars present. Antenna with large, ringlike scape; pedicel very large, cup-shaped, in which sits a single, well-preserved flagellomere that is u-shaped and setulose. At high magnification there is no indication (e.g., sockets) that distal flagellomeres were disarticulated. Oral cavity large, but not deep, no evidence of proboscis observed;

palps small, very slender, apparently 1-segmented. Back of head apparently deeply and evenly concave; thin rim on postocular margin. THORAX: Neck fairly long. Much of pleura lost in preparation of specimen. No large setae on notum. Scutellum small, without setae. Femora and tibiae of approximately equal lengths; tarsi quite short relative to tibia, with 5 tarsomeres per tarsus; total length of tarsus $0.65 \times$ length of tibia or femur. No large setae, spurs, combs, or other structures on legs. Pretarsus with small claws; empodium pulvilliform, broad. Wing narrow, diaphanous, with well-developed anal lobe, no alula. Venation virtually absent: remnants of Sc, R_1 , R_{2+3} , and Cu remain; possible remnant of pterostigma present in middle of wing near costa. No spinose setulae on costal margin. Halter well developed, with relatively large club, darkly pigmented. ABDOMEN: Long, narrow, with 6 visible segments. Apical segment with hypandrium and epandrium fused; gonocoxites short, stout; gonostyli long, opposable, with apical tooth; 3 sharp median spines (claspets?) present, which do not appear to be a trifold phallus.

TYPE: Holotype ♂, AMNH NJ-599, in amber from the Turonian of central New Jersey. Collected at White Oaks site, Sayreville, N.J., by Paul C. Nascimbene.

ETYMOLOGY: *Thauma*, from the Greek, "wonder, marvel."

FAMILY RHAGIONIDAE

PALEOCHRYSOPILUS, NEW GENUS

DIAGNOSIS: Distinguished from all living and most extinct genera by the presence of a stalk to the fork of M_1 - M_2 (usually these arise directly off the distal end of cell dm); basal section of vein M incomplete. Distinguished from *Ptiolinites* (Lower Cretaceous of Mongolia, which also has a stem to M_1 - M_2) by antennae aristate, with small basal aristonere (*Ptiolinites* has an annulated, stylate antenna).

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

ETYMOLOGY: Base referring to a large extant genus of the Rhagionidae.

Paleochrysoptilus hirsutus, new species

Figure 2

DIAGNOSIS: As for genus

DESCRIPTION: HEAD: Very fragmentary, but what appears to be frons or vertex of head is densely clothed with fine, stiff setae. Antenna with flagellomere I small, drop-shaped; flagellomeres II and III aristate/thin stylate, II very small. THORAX: Dorsal part of thorax lost, but numerous fine setae protruding from area that is probably pleural. LEGS: Fore tibia with ventral row of ca. 17 short setae; at least mid and hind tibia with apical spur; empodium setiform. WING: Long (apices extend past apex of abdomen), length = 1.71 mm; broad. Sc extended to level of r-m crossvein; R_1 setulose; no pterostigma apparent at apex of R_{2+3} ; R_{4+5} sinuous, base of R_4 - R_5 fork at same level as apex of dm cell; r-m crossvein slightly proximal to midpoint of dm cell; dm cell curved; base of vein M incomplete, evanescent to about midpoint of usual length; fork of M_1 - M_2 with a short stalk; CuA_2 and A_1 meet just before wing margin; anal lobe of wing well developed. ABDOMEN: Anteriorly broad, apically tapered very narrowly; tergites with fairly long, dense, fine setae. Cerci two-segmented.

TYPE: Holotype, ♀, AMNH L-AE89, in Lower Cretaceous amber from Lebanon, collected near Bcharre by Antoni Estephan.

Type is in a clear yellow piece of amber ($12 \times 8 \times 9$ mm), with a large piece of debris on one side. Amber is embedded in a large block of epoxy, no surface of which was trimmed into the amber (no amber surface was exposed). Most of the head and thorax of the fly are lost at the natural surface of the amber, as well as parts of the fore and mid legs. Wings are complete, with venation well displayed. The piece also contains fibrous plant material, probably remnants from bark.

ETYMOLOGY: Specific name in reference to the extensive, fine setae.

COMMENTS: See below, under discussion on Rhagionidae.

JERSAMBROMYIA, NEW GENUS

DIAGNOSIS: Distinctive for the short fork of R_4 - R_5 and long stem; base of the radial fork is considerably distal to posterior edge of cell

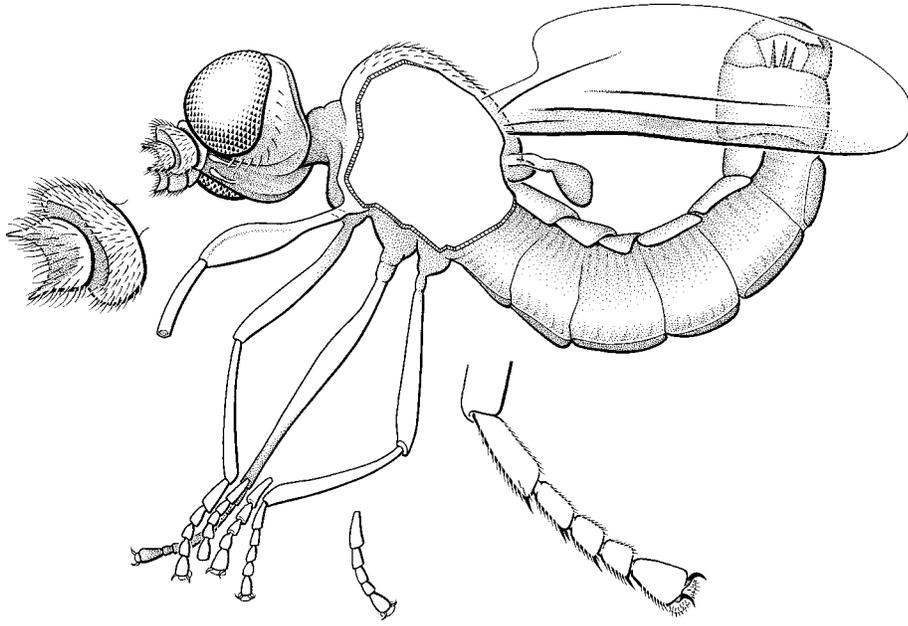


Fig. 1. Holotype of *Tethepomyia thauma* (AMNH NJ-599) in New Jersey amber, showing detail of antenna and (hind?) tarsomeres.

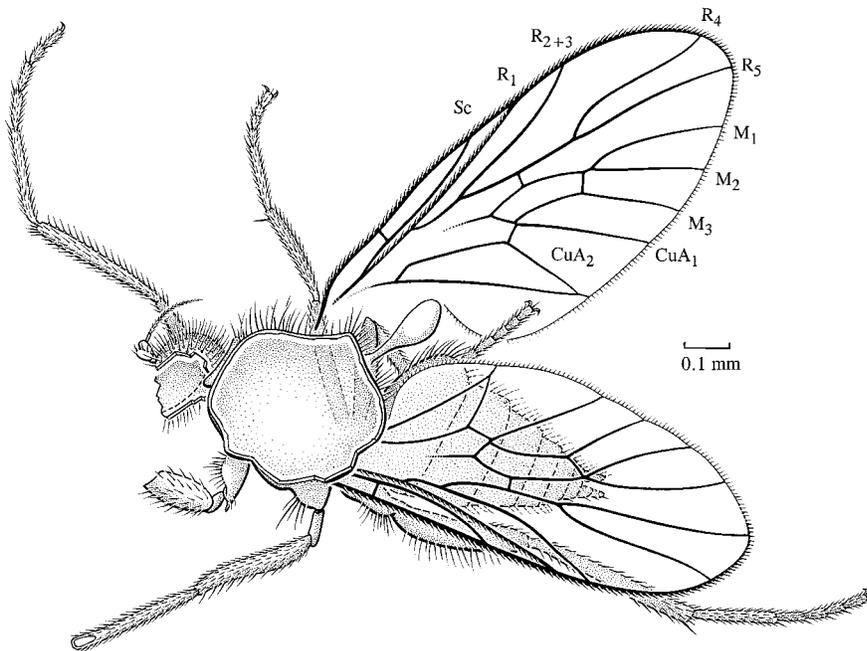


Fig. 2. Holotype of *Paleochrysopilus hirsutus* (Rhagionidae), in Lebanese amber (AMNH L-AE89).

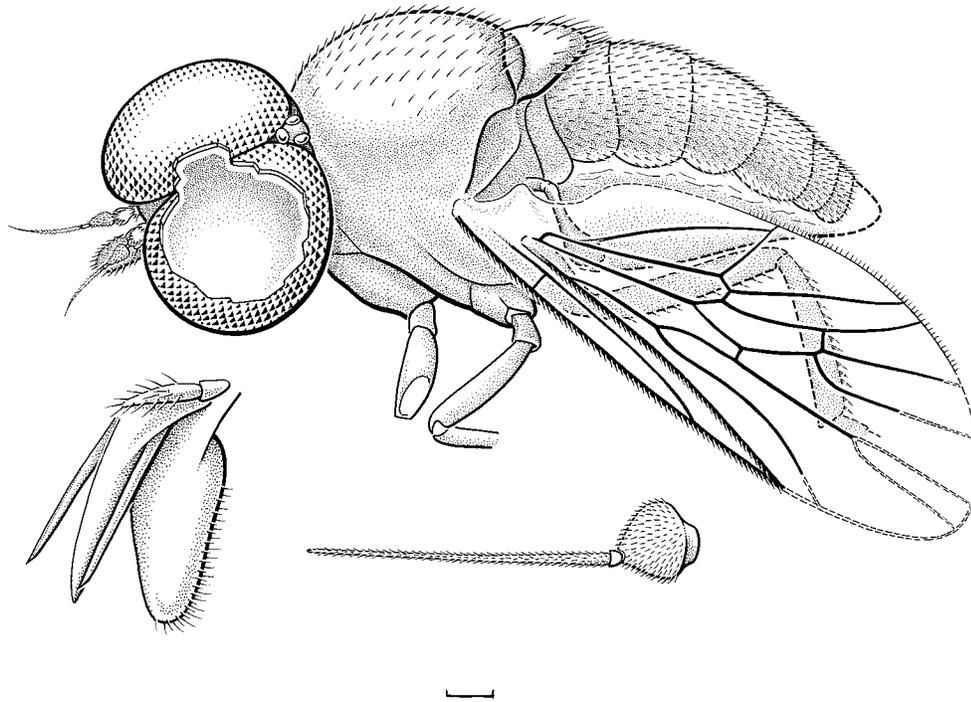


Fig. 3. Holotype of *Jersambromyia borodini* (Rhagionidae), in New Jersey amber (AMNH NJ-900).

dm; antenna with long, thin, aristate style (flagellomeres II and III), flagellomere II a very small segment.

TYPE SPECIES: *Jersambromyia borodini*, n.sp.

ETYMOLOGY: From New Jersey (source locality), *amber* (matrix), and *-myia* (Greek for fly).

***Jersambromyia borodini*, new species**

Figure 3

DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 3.50 mm; thorax length = 1.31 mm (holotype). HEAD: Eyes in male extensively holoptic, contiguous for entire length of frons; dorsal and ventral facets differentiated in size. Ocelli on low tubercle. Face bare, clypeus bulbous; proboscis protrudent. Palp two-segmented, with distal segment ca. 3× length of basal one; labrum as long as labellum, tapered to point; stylate maxillae observable, of same length as labrum. Antenna with flagellomere I a broad cone; flagellomeres II and III a long, thin style, virtually aristate; flagellom-

ere II very short, III long, with minute pubescence. THORAX: Notum with scattered, short setae and pair of larger setae (ca. twice length of others) at notal-scutellar suture. Scutellum with acute apical margin; dorsal surface sparsely setulose, with apical setae slightly longer. No pleural setae observed. Legs largely lost. Hind tibia with dorsal row of ca. 17 short spinules. WING: Apex of right one lost in holotype, complete venation reconstructed with paratype. Sc reaching to level of r-m crossvein; R₁ setulose; fork of R₄-R₅ short, base of fork distal to apex of cell dm by distance equal to 0.5 length of R₄-R₅ fork. M₁-M₂ connected directly to apex of cell dm, base of M₁ turned abruptly to meet dm; vein CuA₁ present; CuA₂ and A₁ meet just before margin of wing. ABDOMEN: Short, tapered to narrow apex, covered with short, fine, scattered setae. Genitalia not observable.

TYPES: Holotype, ♂, AMNH NJ-900, in Upper Cretaceous amber from the Turonian of New Jersey. Paratype, sex unknown, AMNH NJ-90P. Collected at the Sunrise

Landing site in East Brunswick by Paul D. Borodin, James Leggett, and Gerard Case. The fragment of amber in which the fly is preserved is one of dozens such fragments, all from a large piece (AMNH NJ-90) that was found splintered. That piece yielded a remarkable array of inclusions, including the oldest fossil mushrooms (Hibbett et al., 1995; 1997), several male ants (Grimaldi et al., 1997; Agosti et al., 1998), and many others. Both pieces with the flies were embedded in epoxy and trimmed. The holotype piece contains fractures, debris, bubbles, and most of an elaterid beetle; it was trimmed to $10 \times 6 \times 2$ mm; to observe the veins near the anal lobe it is necessary to tilt the specimen at various angles. The paratype piece has a similar composition, with no other insects in it besides the fly; it was trimmed to $10 \times 10 \times 2$ mm.

ETYMOLOGY: For Paul Borodin, one of the collectors who discovered this specimen and many other amber pieces donated to the AMNH.

COMMENTS: See below.

MESOBOLBOMYIA, NEW GENUS

DIAGNOSIS: Distinguished from all other extinct and Recent genera of Rhagionidae by the very long fork of R_4 - R_5 , where the base of fork nearly reaches r-m crossvein; by long CuA_2+A_1 ; and crossvein r-m distal to midpoint of cell dm (almost always r-m is considerably proximal to midpoint). Similar to several extinct and Recent genera by loss of M_3 (see below). Antenna with apical 2 segments aristate, basal segment very small.

TYPE SPECIES: *M. acrai*, new species.

ETYMOLOGY: From *Mesozoic*, and the extant genus which has similar venation.

Mesobolbomyia acrai, new species

Figure 4

DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 2.57 mm; thorax length = 1.01 mm; wing length = 2.32 mm. HEAD: In female eyes large, with barely any gena visible; eyes widely separated, no dorsal/ventral differentiation of facets. Frons with scattered fine setulae on anterior half; posterior half with pair of fine setae ("interfrontals") in middle, three pairs

near margin of eye ("frontal orbitals"); all proclinate; two pairs of ocellar setae. Antenna with flagellomere I nearly spherical; flagellomeres II and III aristate, II very small, III long and covered with dense, fine setulae. Palp two-segmented; segments setulose, of equal length. WING: Sc barely discernable (incomplete?); R_1 very straight, setulose, with slight pterostigma at apex; R_{2+3} slightly sinuous. Crossvein r-m just distal to midpoint of cell dm; fork of R_4 - R_5 very long, with very short stem, base of fork proximal to level of m_1 - m_2 crossvein. M_3 lost. CuA_2 meets A_1 well before wing margin.

TYPE: Holotype, ♀, AMNH-JG387/16, in amber from the Neocomian of Lebanon, collected near Jezzine by Aftim and Fadi Acra.

A complete and beautifully preserved specimen, with only the left legs and wing separated by sheared cracks in the amber. The amber itself is clear yellow; the piece was embedded in epoxy and the block trimmed to $7 \times 16 \times 16$ mm. The amber piece also contains the posterior half of a male auchenorrhynchan, and disarticulated parts of a mycetobiine. Two surfaces of the amber were trimmed and polished, for full lateral and dorsal views of the fly.

ETYMOLOGY: Patronym for the Acras, who so diligently amassed a wonderful collection of Lebanese amber fossils in the 1960's and 1970's.

COMMENTS: see below.

In addition to the three genera described above, there are four additional ones that we have chosen not to formally describe, largely because the specimens are incomplete. Minimally, a fossil taxon of Diptera should not be described without most of the wing venation preserved.

GENUS A

Figure 5

DISTINGUISHING FEATURES: Antenna with flagellomere I semicircular; flagellomeres II + III finely stylate/aristate; with flagellomere II short, approximately $0.3 \times$ length of flagellomere II. Proboscis with labium long, ca. $0.8 \times$ depth of head, very broad. Hind tibia with pair of apical spurs; cercus two-segmented, with conspicuous lateral process.

DESCRIPTION: Body Length = 3.27 mm;

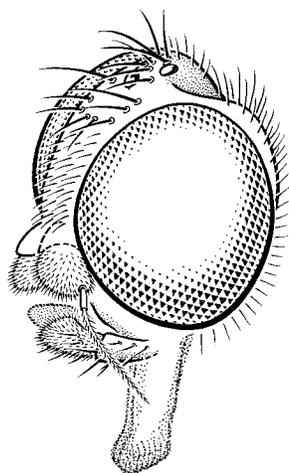
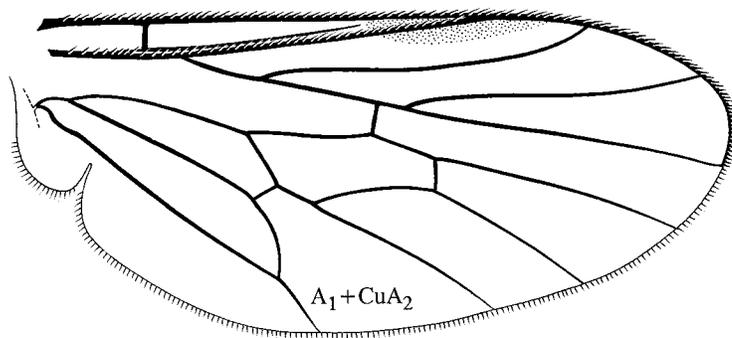


Fig. 4. Head and wing of holotype specimen of *Mesobolbomyia acrai* (Rhagionidae), in Lebanese amber (AMNH JG387/16).

wing length = 2.24 mm. HEAD: Eyes bare, large, gena $0.15\times$ depth of eye, dorsal and ventral facets undifferentiated (in female). Postocciput with group of ca. 25 fine, stiff setae. Palps two-segmented, with long, fine setae on primarily apical segment; segments of approximately equal length. Antennae with flagellomere I semicircular; flagellomeres II + III aristate; with flagellomere II short, approximately $0.3\times$ length of flagellomere II. Proboscis with labium long, ca. $0.8\times$ depth of head, very broad (difficult to ascertain width in ventral view, appears nearly equal in width to width of eye); tip of

proboscis with several stylets protruding, probably the maxillae and hypopharynx. THORAX: largely obscured, but no macrosetae present. Legs undifferentiated; at least hind tibia with pair of apical spurs. Wings incomplete, but with venation as depicted in fig. 5. ABDOMEN: apex with terminal four segments apparently telescoped; cerci bilobed, with dorsal lobe twice the size of the ventrolateral lobe.

SPECIMEN: AMNH JG99/13, in amber from the Neocomian of Lebanon, collected by Af-tim and Fadi Acra near Jezzine. The dark red amber piece, $8 \times 3 \times 3$ mm was epoxy em-

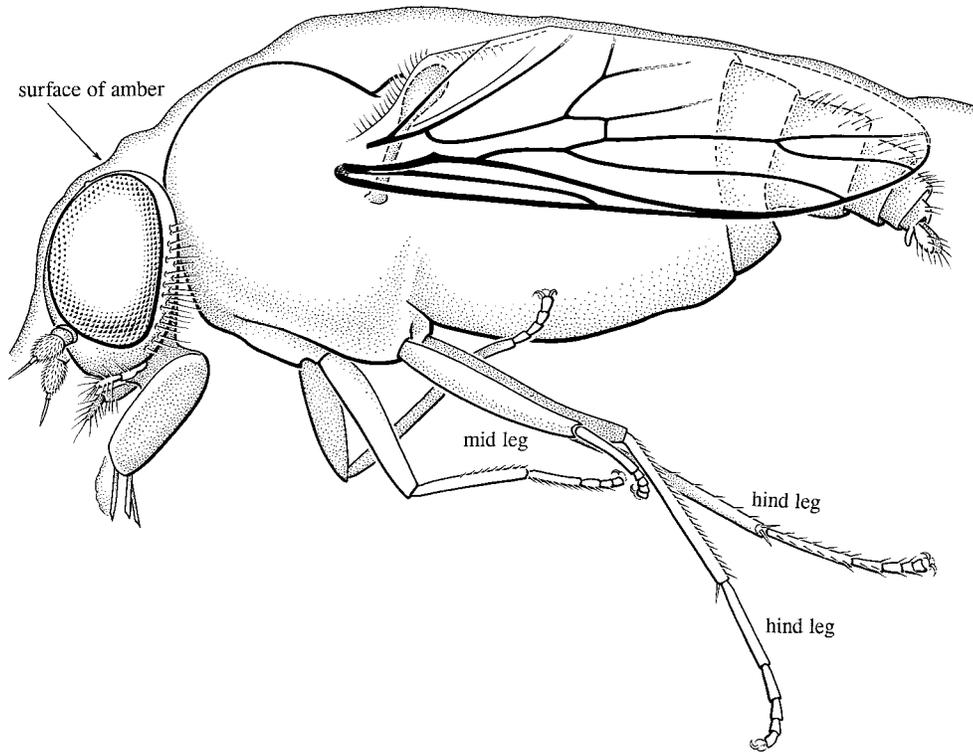


Fig. 5. Rhagionidae genus A, in Lebanese amber. AMNH JG 99/13.

bedded, then trimmed and polished close to the fly where sufficient amber existed; then it was mounted on a microscope slide with Canada Balsam and a coverslip. Dorsal surface of the fly is very close to an irregular surface of the amber; since this surface cannot be flattened and polished, dorsal view of the specimen (and most of the venation) cannot be properly observed.

COMMENTS: This specimen is very difficult to observe because of fractures in the amber, its dark red color, and its irregular surface that lies so close to the dorsal surface of the fly. The specimen requires very careful positioning, using transmitted and reflected light to see many details. Despite these difficulties, it is certain that the fly is a rhagionid, and an unusual one.

A bilobed cercus excludes the specimen from the Athericidae, Tabanidae, and Cyclorrhapha; but the lack of macrosetae on the body, aspects of the wing venation, and pair of apical tibial spurs indicates Rhagionidae.

Antennae are most like the extant genus *Bolbomyia*, and another genus, below.

GENUS B

Figure 6

DISTINGUISHING FEATURES: Eyes very large, occupying most of head (male); antenna with flagellomeres II and II stylate, thin; male genitalia symmetrical, gonopods clasping; with long, thin gonostyli and epandrial lobes.

DESCRIPTION: Total length = 1.77 mm; thorax length = 0.61 mm; wing length = 1.44 mm. **HEAD:** Large, with eyes occupying almost entire head; no cheek visible in lateral view. Eyes nearly holoptic (male), separated along length of frons by distance equal to diameter of facet; dorsal and ventral facets not differentiated; eyes surround slightly raised ocellar triangle, frons entirely covered by eyes. Antennae small, flagellomere I ovoid; flagellomeres II and III thin, about

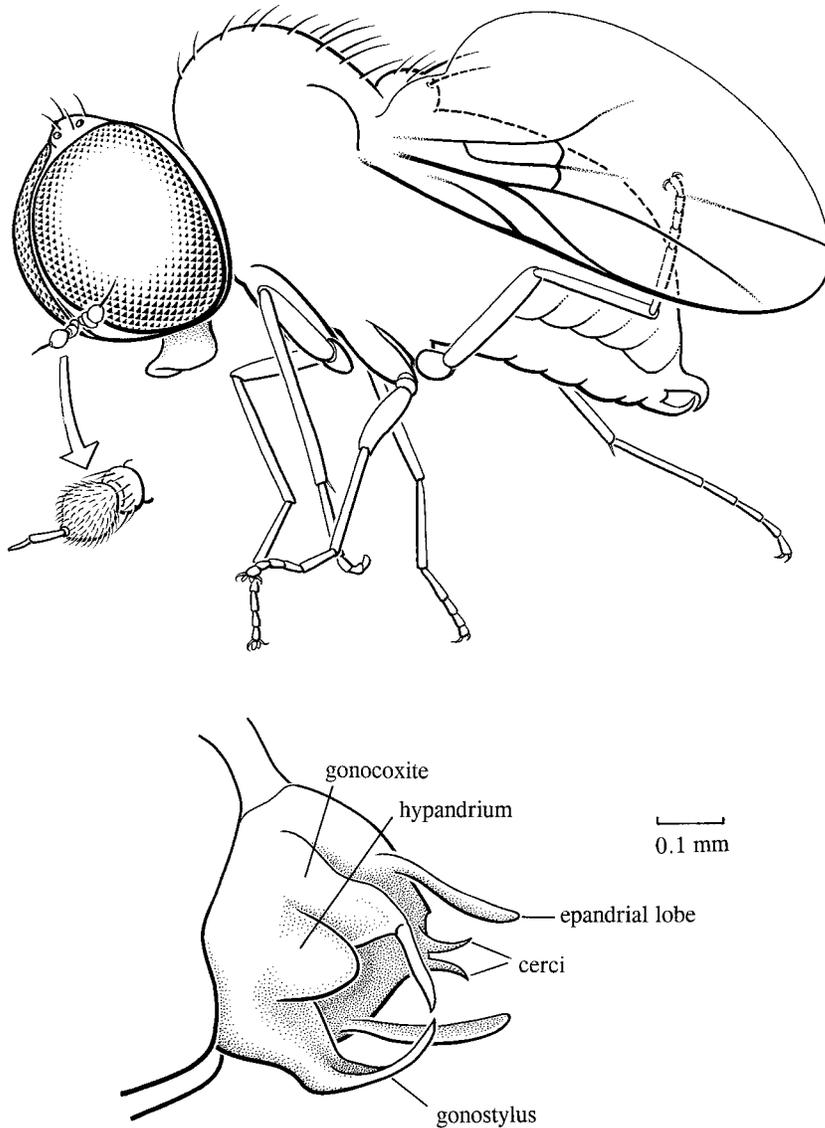


Fig. 6. Rhagionidae genus B, in New Jersey amber, also showing details of antenna and genitalia. AMNH NJ-680.

same length as flagellomere I, apical; flagellomere II 1.6 \times length of flagellomere III. Proboscis short, labellate. THORAX: Notum high and rounded, with 3 larger pairs of fine dorsocentral setae, various smaller setae; scutellum with two pairs of fine setae. Legs short, thin, without distinctive features; fore and hind tibia with apical spur. WINGS: intact, but virtually entire surface covered with layer of air and debris, so little venation is

visible: right wing shows Sc complete; R_1 short, meeting C at level of about middle of wing; R_{2+3} slightly concave; base of wing with two narrow cells (br, bm) with apical margins at same level. Existence of cell d or dm obscured. ABDOMEN: Genitalia intact and visible (fig. 6) (terminology follows Sinclair et al., 1994); symmetrical; with clasping gonopods having gonostyli that are long and thin (gonocoxites very stout); an hypandrium

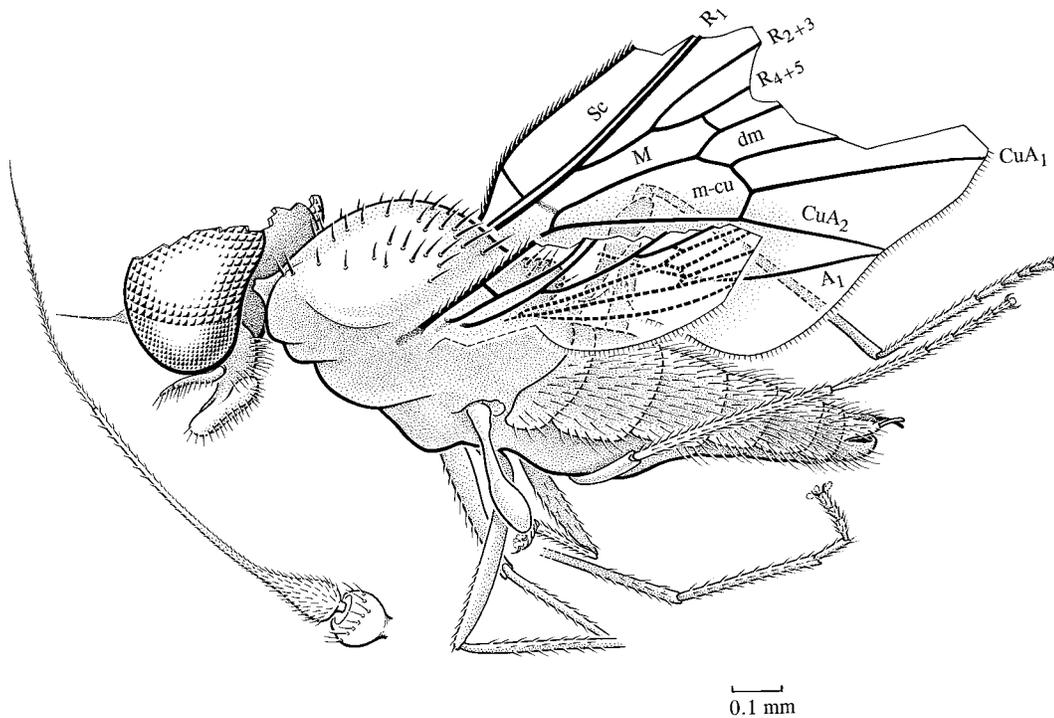


Fig. 7. Rhagionidae genus C, in Lebanese amber, with detail of antenna. AMNH L-AE131.

that appears separated from gonopods, a pair of long, narrow epandrial lobes; and small, pointed cerci that protrude beyond the posterior margin of the epandrium.

SPECIMEN: AMNH NJ-680, a unique ♂ specimen, in Cretaceous amber from the Turonian of New Jersey, collected by D. Grimaldi at the White Oaks site in Sayreville, New Jersey. Specimen is in a small, turbid yellow piece of amber, which was epoxy embedded and trimmed to a $10 \times 6 \times 3$ mm triangle.

COMMENTS: The virtual lack of venation makes it very difficult to place this specimen, but structure of the eyes, antennae, and genitalia are indicative of Rhagionidae, and probably close to *Bolbomyia*.

GENUS C

Figure 7

DISTINGUISHING FEATURES: Antenna with flagellum long, whiplike, aristate; one-, possibly two-, segmented. Notum with scattered, short, stiff spinulelike setae.

DESCRIPTION: Body length = 2.74 mm;

thorax length = 0.98 mm. **HEAD:** Male eyes large, dorsal and ventral facets greatly differentiated (dorsal facets approximately twice size of ventral ones). Vertex of head lost, so cannot determine whether specimen is (probably) holoptic. Proboscis with long, narrow labellum. Palp two-segmented, with basal segment much longer than apical one; ventral surface with fairly long, fine setae. Antenna with flagellum long, whiplike; base of flagellum bulbous, tapered to long, thin structure; one-, possibly two-segmented, if fairly abrupt constriction near middle of whip is a segment (observed under $250\times$ magnification). **THORAX:** Relatively flat, definitely not domed or arched; notum with scattered, short, stiff, spinulelike setae (posterior ones longer); similar setae sparsely scattered on scutellum. Pleural setae not observed. Legs long and thin, without distinctive setae. Empodium pulvilliform. **WING:** incompletely preserved, apparently very broad. Basal half of venation as shown in fig. 7; CuA_2 and A_1 not meeting before wing margin, but almost so; anal lobe large. **AB-**

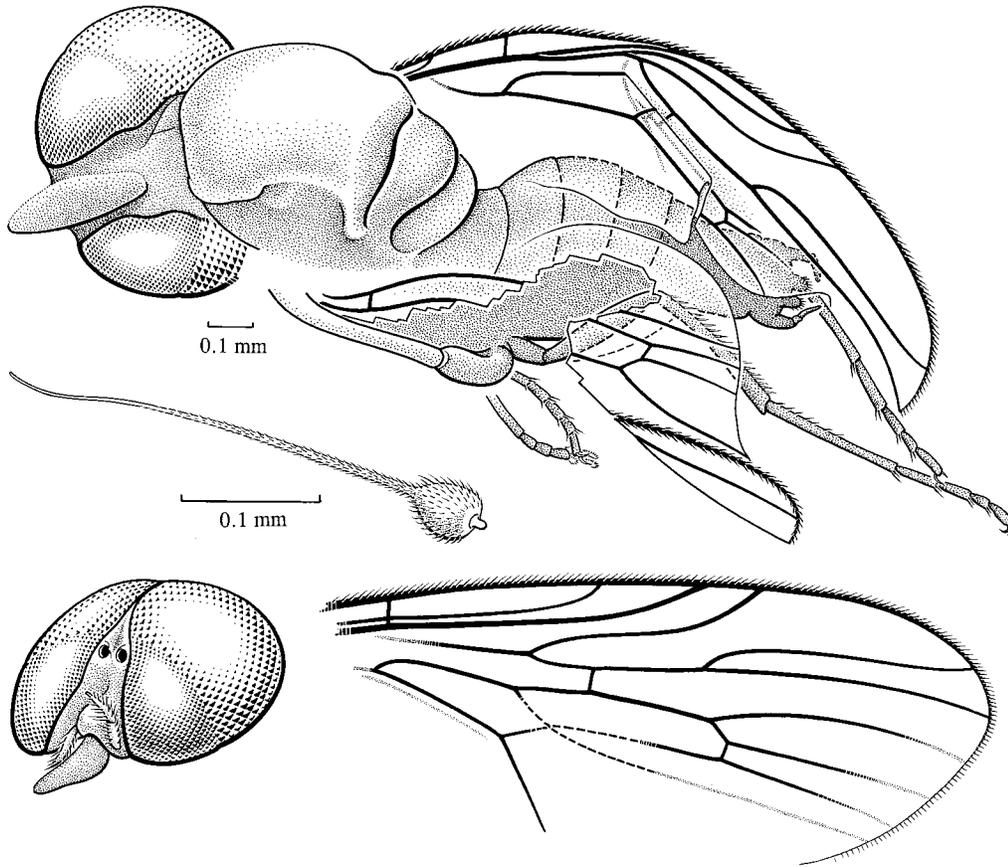


Fig. 8. Rhagionidae genus D, in Lebanese amber, with antero-ventral view of head, wing, and detail of flagellum. AMNH JS43.

DOMEN: Narrow, tapered to very narrow apex; tergites with dense, scattered, long, fine setae. Genitalia with gonostylus long, thin, projected posteriad.

SPECIMEN: ♂, AMNH L-AE131, in amber from the Neocomian of Lebanon, collected by Antoni Estephan from near Bcharre.

The amber is clear yellow, $3 \times 7 \times 8$ mm in size, embedded in an epoxy block $13 \times 12 \times 5$ mm; only one surface of the amber was partially exposed by trimming and polishing. The dorsal part of the head, apical half of the right wing, and most of the left wing were lost at the natural surface of the amber; specimen is otherwise intact. The piece also contains a female *Leptoconops* (Ceratopogonidae).

GENUS D

Figure 8

DISTINGUISHING FEATURES: Flagellum of antenna as in genus C: apparently unsegmented, with bulbous base and long fine apical portion. Differs from genus C as given below.

DESCRIPTION: Body length = 2.96 mm; thorax length = 1.11 mm. **HEAD:** Male eye large, holoptic, with dorsal and ventral facets highly differentiated (dorsal ones twice the size of ventral ones). Face narrow, margins of eye near antennal bases slightly emarginate and missing several facets. Face concave, with clypeus discrete and bulbous. Palps two-segmented, basal and apical segments of

equal lengths, both setulose. Proboscis protrudent, but details not preserved. Antennae disarticulated from specimen, but "floating" nearby specimen: flagellum one-segmented, with base bulbous, and long, thin apical portion $6\times$ length of bulbous base. THORAX: Largely obscured by poor preservation; no setae appear to have been preserved. Wings largely crumpled and torn; venation reconstructed in figure 8 from both wings. Legs with hind tibia having dorsal row of short, spinulelike setae; empodium setiform. ABDOMEN: Narrow, some parts of genitalia distinguishable; gonopods widely separated and clasping. Cerci widely separated.

SPECIMEN: ♂, AMNH JS43, in amber from the Neocomian of Lebanon, collected by Fadi and Aftim Acra near Jezzine. Specimen is virtually complete but not well preserved; left wing is largely lost; right wing crumpled, obscuring some venation. The thorax and perhaps abdomen is impregnated with a dark, granular substance; setae are lost from the body. The specimen is in a clear yellow piece of amber that is extensively fractured. It was embedded in epoxy, trimmed and polished on three sides of the amber, to $9 \times 9 \times 8$ mm.

DISCUSSION OF RHAGIONIDAE

The Rhagionidae are a group of 21 genera and about 550 species in the Recent fauna. The most recent review of living genera is by Nagatomi (1982) and most (but not all) extinct genera by Nagatomi and Yang (1998). A comparative morphological study of male genitalia of many genera of Rhagionidae is by Nagatomi (1984); he placed *Pseudoerinna* and *Glutops* in this family, but now dipterists routinely assign these to the Pelecorhynchidae. Woodley (1989) indicated that there appear to be no unambiguous synapomorphies for the Rhagionidae, and he questioned the main feature proposed by Hennig (1973): a sharp separation between the first and distal flagellomeres. Although this character certainly delineates a group of rhagionid genera, other genera, such as *Arthroceras* and *Atherimorpha*, are excluded. A bulbous clypeus, used by some dipterists to define the Rhagionidae, is actually a feature of the Tabanomorpha, sans the aberrant ge-

nus *Austroleptis*. One feature that occurs very consistently in the Rhagionidae, and very seldom in other groups (e.g., *Atherix*: Athericidae), is a base of fork R_4 - R_5 that is at the same level as the distal end of cell dm, and not distal to it. Also, vein R_5 in Rhagionidae is almost always straight, and R_4 arises from it with a sharp bend at its base, often of 90° (fig. 9). This can be proposed as a potential synapomorphy of most Rhagionidae.

There are, however, several genera placed in the Rhagionidae with an aberrant venation that have traditionally been controversial in their placement, notably *Austroleptis*, *Bolbomyia*, and *Litoleptis*. *Bolbomyia* currently comprises six species from Japan and North America; *Austroleptis* has seven species from Australia, Tasmania, and Chile; and there are six species in *Litoleptis* from Alaska, Japan, Nepal, the Philippines, and Chile. Chillcott (1963) was one of the first to discuss the missing M_3 vein in these genera, perhaps indicative of inclusion in a family other than Rhagionidae. *Austroleptis* is further aberrant by having a one-segmented cercus in the female (found also in Tabanidae + Athericidae, but plesiomorphically there are two). Sinclair et al. (1994) made the first formal attempt to locate *Bolbomyia*, which they placed as the sister group to the Athericidae + Tabanidae, based on the presence of aedeagal tines (thin, siculate structures in the sperm sac). Without explicitly discussing *Austroleptis* (which was one of the six rhagionids whose genitalia they examined), the implication is that *Austroleptis* should remain in the Rhagionidae, at least on the basis of genitalic morphology. They did suggest, however, that *Austroleptis* may be more closely related to the Xylophagomorpha simply on the basis of a record reporting them breeding in decaying wood, instead of soil (which is a general tabanomorph habitat—although at least some British *Chrysopilus* and *Rhagio* breed in decaying wood [P. Chandler, pers. comm.]). Sinclair et al. (1994) did not examine *Litoleptis* genitalia, but previous descriptions (Chillcott, 1963) indicate their male genitalia to be similar to *Bolbomyia*, with *Litoleptis* additionally autapomorphic due to loss of the dm cell and all tibial spurs (it still retains the primitive feature of a two-segmented female

cercus). In lieu of a badly needed revision of the approximately 20 species in these living genera, it is difficult to place confidence in their relationships, but a close one is likely. This discussion is germane to the present study, since there are five fossil genera sharing the feature of a loss of M_3 , one of them described above.

Fossil flies that lack M_3 are the following (fig. 10): *Pauromyia*, from the Upper Jurassic of China; *Probolbomyia*, from the Upper Jurassic of Karatau; *Paleobolbomyia*, from the mid Jurassic of Siberia (both of these are compressions); *Zarzia*, from the Upper Cretaceous (Santonian) amber of northern Siberia; and *Mesobolbomyia*, n. gen., in Lower Cretaceous amber (Neocomian) of Lebanon. *Zarzia* was described as a mythicomyiine bombyliid (Zaitzev, 1987), but Evenhuis (1994) (who reexamined the specimen) placed it in the Rhagionidae. Actually, its wing venation is very similar to *Bolbomyia*. It should be noted that there is remarkable convergence between these Tabanomorph genera and many Recent asiloid genera that also lost CuA_1 , such as *Heterotropus*, many bombyliids and scenopinids, and the Siberian amber fossil *Proplatypygus rohdendorfi*, so the error by Zaitzev is understandable. There are other venational and many nonvenational features that distinguish tabanomorphs and asiloids with this convergent wing venation. Lastly, it should be noted that *Probolbomyia* was classified in the extinct family Rhagionempididae, known entirely from 4–5 compression fossil genera from the Jurassic of central Eurasia (catalog of genera and species in Evenhuis [1994]). We agree with Kovalev (in Kalugina and Kovalev, 1985) that *Probolbomyia* and *Ussatchovia* should be retained in the Rhagionidae, sensu lato, at least provisionally. Based on much better preserved amber specimens (*Zarzia*, *Mesobolbomyia*), the Jurassic fossils are clearly not related to Empididae, as originally suggested by Nagatomi et al. (1991). Nagatomi and Yang (1998) indicated the wing venation of the extinct family Rhagionempididae to most closely resemble that of *Bolbomyia*, *Ptiolina*, *Ptiolinites*, *Spania*, and *Spaniopsis* of the Rhagionidae. Rhagionempididae (which Nagatomi makes a senior synonym of Apsilcephalidae, including the living genus *Apsil-*

ocephalus) have 3 branches off the distal end of dm cell, but Nagatomi and Yang (1998) placed *Probolbomyia* and *Ussatchovia* in this family. Both of these Jurassic genera have a thick flagellomere I with a short terminal style. It seems preferable at present to regard the living and fossil genera with loss of CuA_1 as belonging to a natural group, either within or outside the family Rhagionidae.

It is interesting to note the preponderance of fossil rhagionids with sufficient preservation that have long stylate or even aristate antennae. *Zarzia* has a long, thin, stylate antenna, and five genera of rhagionids (two of them indeterminate) in Lebanese and New Jersey amber have a long, fine apical (“aristate”) portion of the antennae, similar to *Sclerorhagio* Zhang et al. from the Upper Jurassic of China. Although there are many living species of *Chrysopilus* and some genera of Rhagionidae that have similar aristate antennae (e.g., *Solomomyia*, *Stylospania*, *Rhagina*, *Desmomyia*, *Rhagio*, some *Symphoromyia*), the rare records of short-styled taxa in the Cretaceous is intriguing.

FAMILY STRATIOMYIDAE

GENUS *CRETACEOGASTER* TESKEY

Cretaceogaster Teskey, 1971: 1660.

DIAGNOSIS: Defined by Teskey (1971) and modified by Woodley (1986). Summarized as follows: Male eyes large, nearly holoptic; ventral ommatidia slightly smaller ($0.8\times$) than dorsal ones; flagellum conical-oval, 2-segmented, with very small terminal style; scutellum without spines, margin rounded; vein R_{4+5} with terminal fork short, ending at wing tip; r-m crossvein distal to R_{2+3} ; basal section of M lacking; 2 medial veins and CuA_1 arising from discal cell; mid tibia with 2 apical spurs; palps 2-segmented (this last character not reported in original specimen).

TYPE SPECIES: *C. pygmaeus* Teskey, 1971.

Cretaceogaster pygmaeus Teskey

Figure 11

DIAGNOSIS: As for genus.

DESCRIPTION: Provided in detail by Woodley (1986), revised on basis of new specimen as follows: Notum and eyes iridescent green (specimen must be viewed at different angles

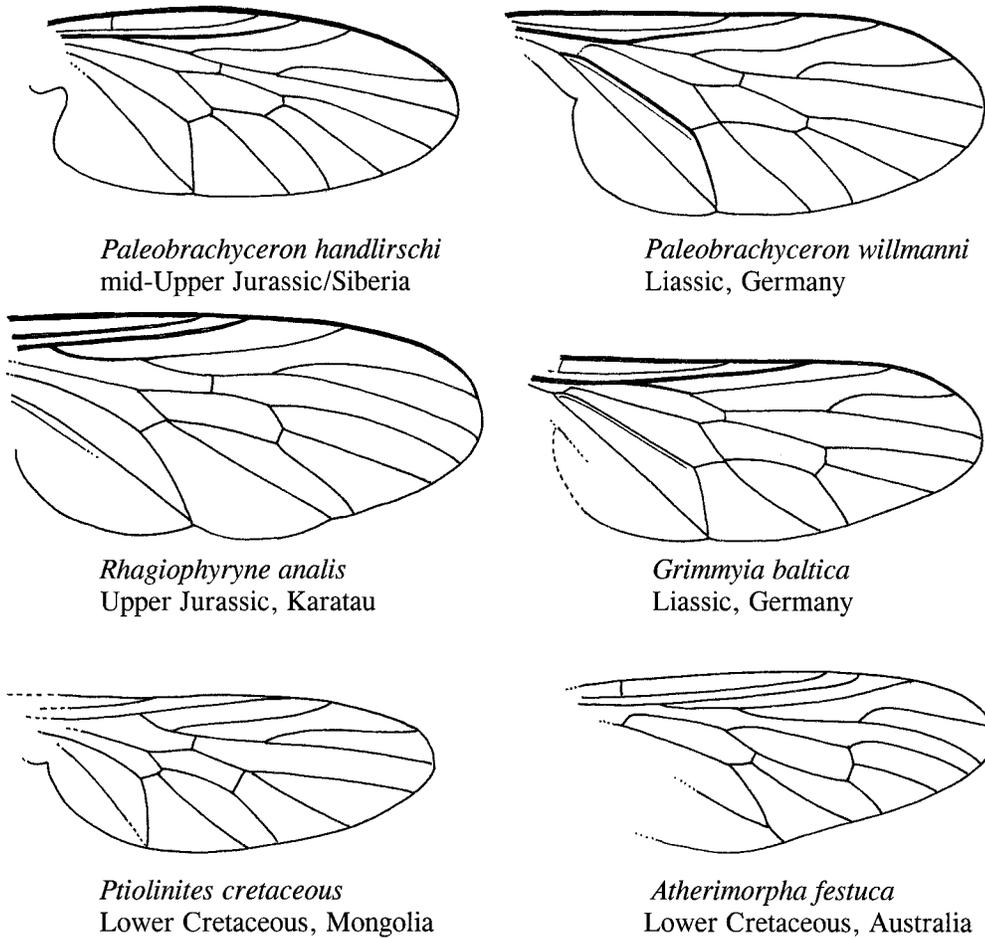


Fig. 9. Wing venation of representative genera of Mesozoic Rhagionidae.

with fiber optics to detect the iridescence); palp distinctly 2-segmented, basal segment smaller than apical one.

TYPE SPECIMEN: MCZ 6954, collected by F. M. Carpenter, in amber from Cedar Lake, Manitoba, probably Campanian in age.

ADDITIONAL MATERIAL: MCZ 6572, collected by F. M. Carpenter, in amber from Cedar Lake, Manitoba. Body length = 2.22 mm; wing length = 1.86; thorax length = 0.86. This specimen was in a piece of amber that was unprepared and prevented close observation, which probably explains why it was overlooked by F.M. Carpenter, H. Teskey, and N. Woodley. The amber piece was embedded in epoxy prior to trimming and polishing.

COMMENTS: Teskey (1971) placed this spe-

cies in the Pachygastrinae on the basis of several features, but noted that the "possible exposure of a seventh abdominal segment suggests an association with the Beridinae." Woodley (1986) re-examined the specimen and placed it into a phylogenetic scheme of the basal lineages of the Stratiomyidae. *Cretaceogaster* is actually the sister group to *Parhadrestia* (an extant genus of two poorly known species from Chile), both of which are the sister group to the rest of the Stratiomyidae.

Several characters reported by Teskey and Woodley in the original specimen could not be examined in the new specimen, namely (numbers refer to character numbers in Woodley [1986]): fusion of gonocoxites to hypandrium (1), fused parameres reduced in

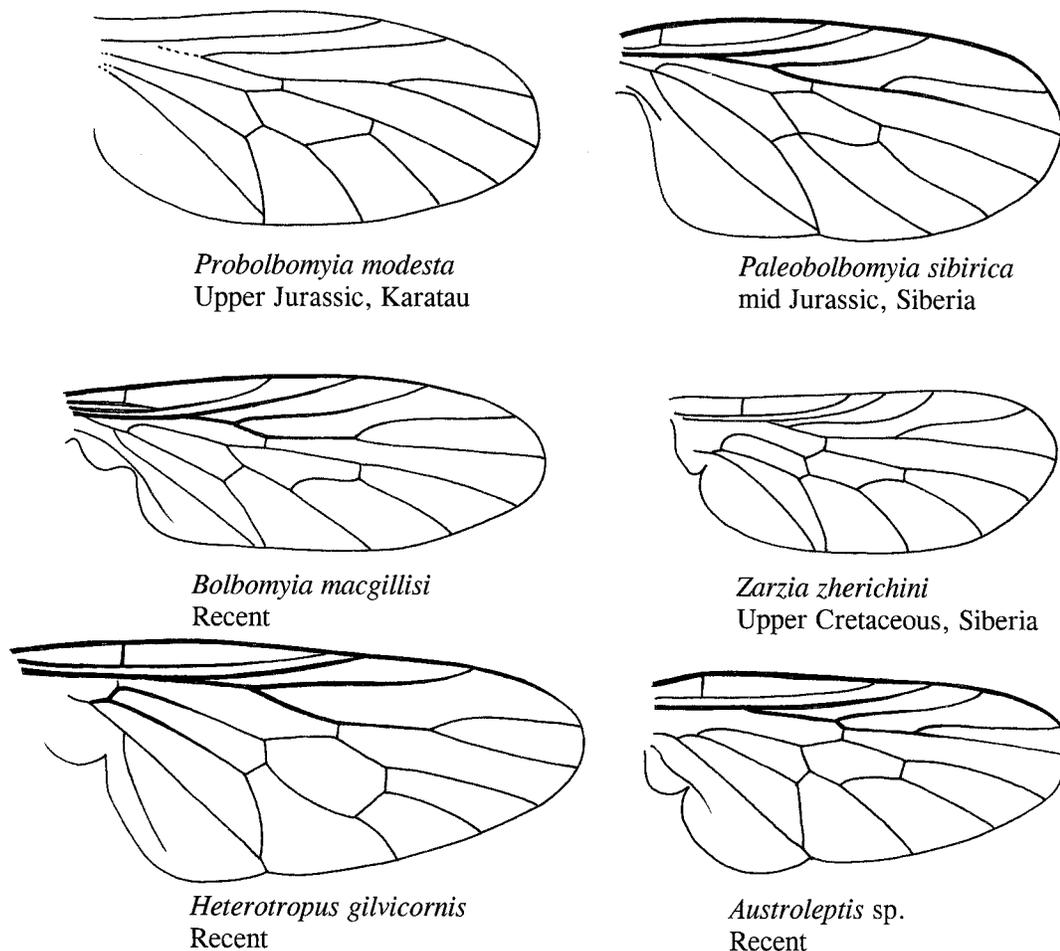


Fig. 10. Wing venation of living and Mesozoic Rhagionidae showing loss of vein CuA_1 .

size (2), male sternite VIII reduced (3), and mid tibial spurs lost (9). The apices of R_4 and R_5 are not parallel in the new specimen, contrary to Woodley (1986), although this is a very subtle feature. The new specimen confirms the following features: CuA_2 short and straight (vs. arcuate) (5), M_3 absent (7), 1 large basal and 1 small apical flagellomere (8). *Cretaceogaster* appears to be one of those enigmatic, highly primitive fossils in which no apomorphic features for the genus have yet been found, or may not occur. Features of *Cretaceogaster* plesiomorphic with regard to *Parhadrestia* are the following: antennal segmentation (8), midtibial spurs (9), and—not visible in the original specimen—two-segmented palps (6). This last character

makes *Cretaceogaster* even more plesiomorphic to *Parhadrestia* than Woodley indicated, and is further confirmation of Woodley's hypothesis of the apparent ancestral status of *Cretaceogaster*.

STRATIOMYIDAE GENUS INDET.

Figure 12

SPECIMEN: ♀, AMNH NJ-775, collected by Paul C. Nascimbene in the White Oaks site, Sayreville, New Jersey (Turonian). The specimen is poorly preserved, partially disarticulated (legs) and covered with a milky coating, and in a turbid piece of amber with particulate debris. To observe any of the crucial details, the piece had to be epoxy embedded and then trimmed extremely close to the

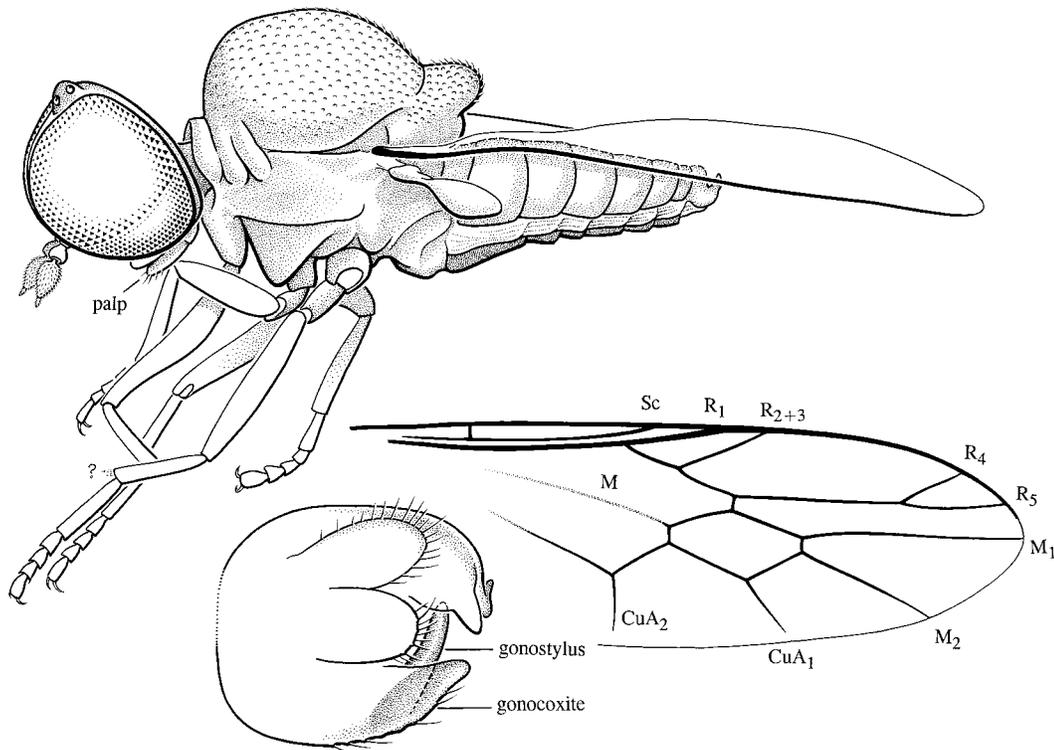


Fig. 11. *Cretaceogaster pygmaeus* (Stratiomyidae), in Canadian amber, with full view of wing and dorsal view of male genitalia. MCZ 6572.

specimen, resulting in a piece barely larger than the fly. A dorsal, left lateral, and frontal view are visible. It belongs to a genus distinct from *Cretaceogaster*.

DESCRIPTION: **HEAD:** Female, frons wide, eyes widely separated; no sutures above antennal bases present (which would separate an "upper" and "lower" frons). Antenna fusiform, with eight flagellomeres, flagellar segmentation subtle; basal flagellomere nearly 3 times the length of segments 2-7, segments 2-4 equal in length, 5 slightly shorter than 4 or 6; segment 8 (apical) narrow, stylate and equal in length to basal segment; basal flagellomere without ring of fine setulae. Palp apparently large, seen dorso-frontally as lobe protruding from oral margin. **THORAX:** Simple; scutellum apparently without any tubercles, even tiny marginal ones, but with slight rim on posterior margin; finest details difficult to discern through frothy coating. **LEGS:** With 1 apical spur on mid tibia. **WING:** Sc, R₁, R₂₊₃ very crowded;

R veins thickest; R₄ slightly sinuate, its base at midpoint of R₅; R₅ straight. Cell dm large, length 2.6× width. Apex of wing not discernable. Vein M₃ present, evanescent near wing margin. Base of vein M very weak or evanescent proximad. CuA also evanescent near wing margin. CuP slightly curved, A₁ straight, apices not discerned but trajectories indicate that they meet very close to wing margin. Anal lobe well developed, alula present. **ABDOMEN:** Existence of shallow grooves on posterior margins cannot be discerned due to frothy coating; 7, possibly 8, segments present.

COMMENTS: No apomorphic features of this interesting specimen exist that would enable one to provide a diagnosis, and therefore name it. There are, however, a number of features that allow placement of this primitive species. The subtle marginal rim of the scutellum is found in some beridines and many pachygastrines, but all other features of the fossil exclude it from the "higher"

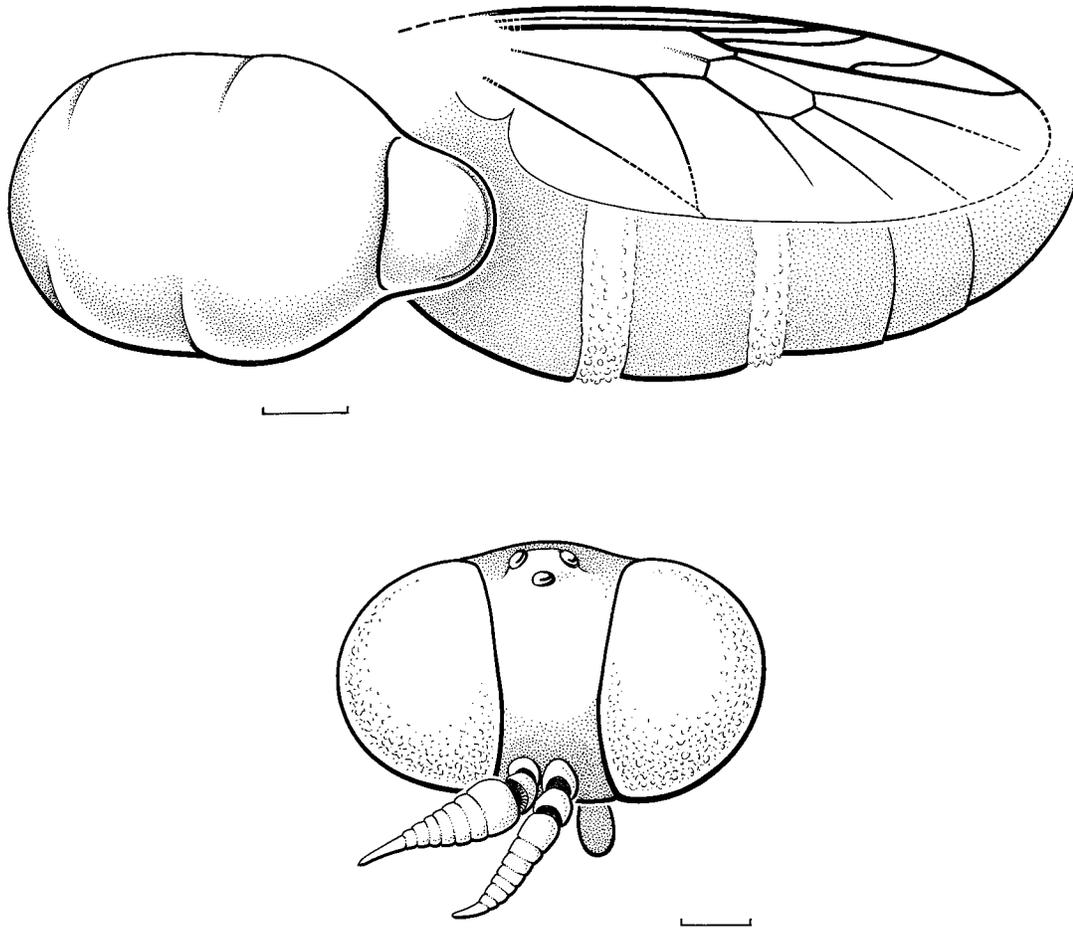


Fig. 12. Dorsal view of thorax and abdomen, frontal view of head, of stratiomyid in New Jersey amber (AMNH NJ-775).

stratiomyids, including pachygastrines. These plesiomorphic features are presence of a tibial spur, abdomen with more than 5 tergites, and veins CuP and A_1 that barely intersect before the wing margin (apomorphically they intersect well before the margin). These features suggest that the fossil is among the Parhadrestiinae, Chiromyzinae, or Beridinae.

An apparent large palp would exclude the fossil from the Chiromyzinae; and the annulate, eight-segmented flagellum is most consistent with the Beridinae. Plesiomorphic even for Beridinae, however, is a simple scutellar margin and the A and CuP veins. The fossil is perhaps slightly more derived than

Cretaceogaster, but still clearly very primitive.

This may be the oldest definitive stratiomyid—some 10–15 Ma older than *Cretaceogaster pygmaeus*—with an older record of Stratiomyidae from Lower Cretaceous limestone of Spain based only on larvae (Gomez-Palero, 1986).

FAMILY HILARIMORPHIDAE

HILARIMORPHITES, NEW GENUS

DIAGNOSIS: Antennal flagellomere with 2 segments, apical 1 small, stylate; male eyes nearly contiguous dorsally, dorsal and ventral facets undifferentiated; inner margins of eyes

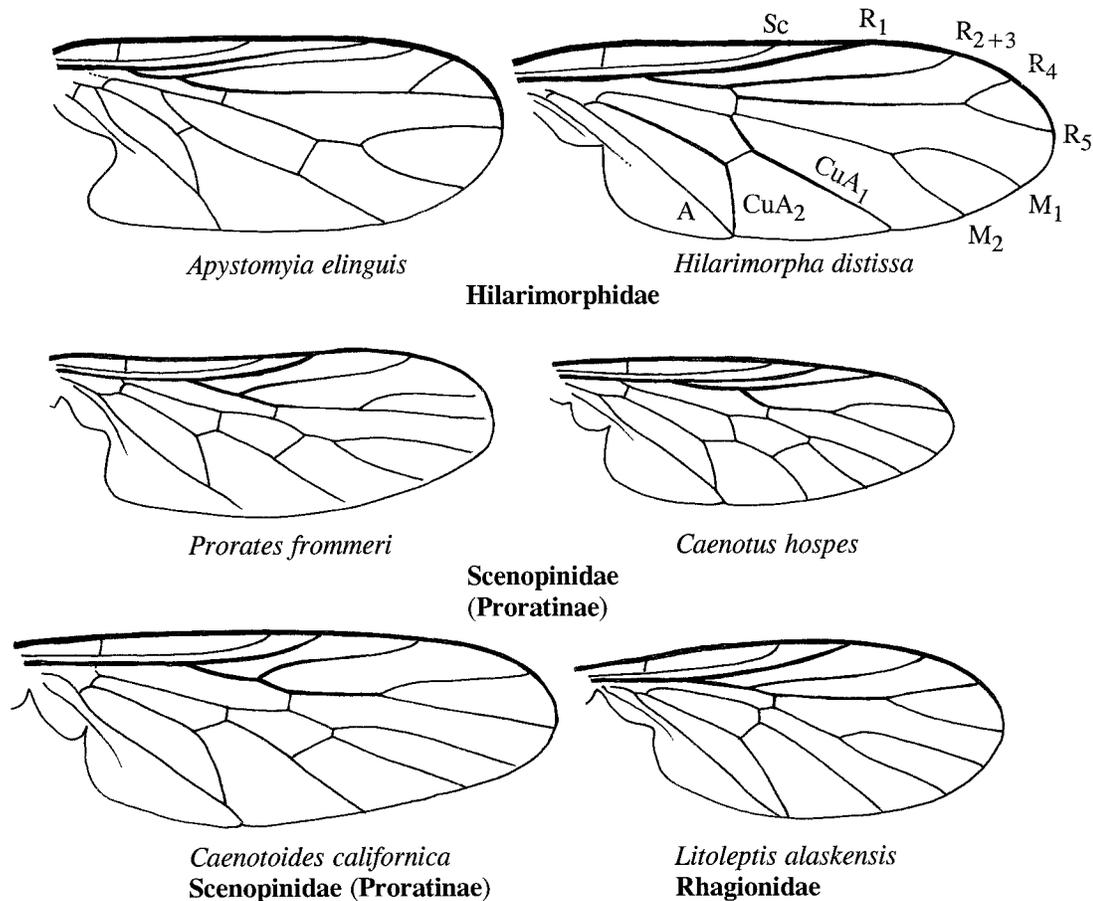


Fig. 13. Wing venation of hilarimorphids and proratine scenopinids, and *Litoleptis* (Rhagionidae) showing convergence to *Hilarimorpha*.

emarginate at level of antennal bases; cervical sclerites large, neck rather elongate; veins M_1 and M_2 , and R_4 and R_5 forked, vein M_3 absent; female without acanthophorite spines.

DESCRIPTION: Antenna small, with flagellomere I ovoid, approximately equal in size to pedicel; flagellomere II small, fingerlike and microsetulose, length equal to or slightly less than length of flagellomere I. Presence of a minute apical style undetected. Proboscis short, stout, with lobate labellum. In two male specimens (*H. superba*, n.sp.) eyes are nearly contiguous dorsally, smallest distance separated equal to less than diameter of eye facet; dorsal and ventral facets not differentiated; inner margin of eye opposite the antennal bases is emarginate. Notum arched,

with macrosetae on posterior half; gradually increased in size from small acrostichals anteriorly to setae 3 times their length; scutellum with 2 pairs of the longest setae on body (scutellum setose in *H. superba*). Anterior surface of hind coxa apparently without short peg (cf. Yeates, 1994). Hind femur of male with ventral row of ca. 20 short, stiff spines; at apical half they are arranged loosely in 2 rows. Hind tibiae with pair of small apical spurs on inside surface; male with small group of 3–4 stiff, short setae at apex of hind tibia. Pretarsus either without empodium, or empodium a very small bristle. Abdomen without pair of sensory patches seen in the Scenopinidae (cf. Yeates, 1992; Nagatomi et al., 1994).

Venation with veins Sc and R_1 long,

straight, parallel, and close to each other. Vein C ends at or near apex of R_{4+5} . Veins M_1 - M_2 forked, stem long (length approximately equal to length of fork) or short (length $0.3 \times$ length of fork); M_3 absent. Discal cell present, with apex truncate (m-cu perpendicular to M_{1+2} and CuA_1). Cell cup much longer than cell bm, apex of cup touching or nearly touching wing margin. Veins M, Cu end just before wing margin. Veins R_4 - R_5 forked, with stem long (length equal to or greater than length of fork).

Male genitalia observed only for *H. superba* (see specific description); female terminalia without acanthophorite spines.

TYPE SPECIES: *Hilarimorphites yeatesi*, n.sp.

ETYMOLOGY: *-ites*, from the Greek for "like," in reference to the similarity of this genus to the type genus of the Hilarimorphidae, as well as to *Apystomyia*.

COMMENTS: The new genus at first appeared possibly closely related to the proratine scenopinids, mostly on the basis of some wing venation characters, but it is clearly most closely related to the rare and controversial genus *Apystomyia* (Hilarimorphidae) (fig. 13). Hilarimorphid characters of the new genus are: Male eye with accentuated emargination of eye near antennal bases (Yeates, 1994); vein R_{4+5} forked with a long stem; veins M_1 - M_2 forked, with a long stem; cell cup long, with pointed apex nearly touching the wing margin (figs. 14-17). Features that *Hilarimorphites* shares with *Apystomyia* are: crossvein m-cu present; notum with macrosetae (*Hilarimorpha* has only setulae); male eyes dorsally separated very slightly (cf. figs. 38 and 39 in Yeates, 1994).

There are, however, some differences between this genus and the extant genera of the Hilarimorphidae. Notably, there is no dorsal-ventral differentiation of the eye facets in either sex of *Hilarimorphites*. Also, the distance of crossvein r-m from the basal bifurcation of M and Cu is approximately equal to the length of the crossvein; in *Hilarimorpha* r-m is generally at the level of the bifurcation (occasionally distal or proximal to this fork by a small fraction of the length of the crossvein). In *Apystomyia*, the distance that r-m is from the basal fork of M-Cu is more than twice the length of this crossvein.

TABLE 1
Summary of *Hilarimorphites* Wing Ratios
(see fig. 17)

Species	NJ-	Sex	a/b	c/d	e/c	f/g
<i>setosa</i>	495	♀	0.95^a	1.20	0.26	0.45
	60	♀	0.45	0.93	0.34	0.13
<i>yeatesi</i>	168	♀?	0.56	1.42	0.48	0.29
	314	♀	0.50	1.31	0.37	0.42
	418	♀	0.53	1.17	0.34	0.31
<i>longimedia</i>	417	♀	1.09	3.54	0.18	0.30
<i>superba</i>	673	♂	0.97	1.18	0	0.33
	772	♂	1.46	2.46	0	0.54

^a Numbers in bold are diagnostic.

We have recognized four species in this genus, all from the New Jersey amber. *Hilarimorphites superba* is the most distinctive species, the other three being distinguished largely on the basis of wing venation characters summarized below. Wing venation lengths that were made were the following (see also fig. 17):

a = R_5 , from base of fork to apex of vein.

b = stem of R_{4+5} , from r-m to base of fork of R_4 - R_5 .

c = M_1 , from base of fork to apex of vein.

d = stem of M_{1+2} , from crossvein m-cu to base of fork of M_1 - M_2 .

e = distance between level of bases of forks R_4 - R_5 and M_1 - M_2 .

f = distance from proximal end of dm cell to level of r-m crossvein.

g = greatest length of dm cell.

Ratios that were calculated were:

a/b = relative lengths of forked and stem portions of R_4 - R_5 .

c/d = relative lengths of forked and stem portions of M_1 - M_2 .

e/c = distance between bases of R and M forks relative to length of M_1 .

f/g = distance where crossvein r-m meets dm cell relative to length of dm cell.

Wing ratios are summarized in table 1.

Hilarimorphites superba, new species

Figures 14, 15

DIAGNOSIS: Large species, body length = 2.66 mm; thorax length = 0.86 mm; wing length = 2.12 mm (holotype). Notum with numerous, scattered light setae, not in longitudinal rows; scutellum with numerous se-

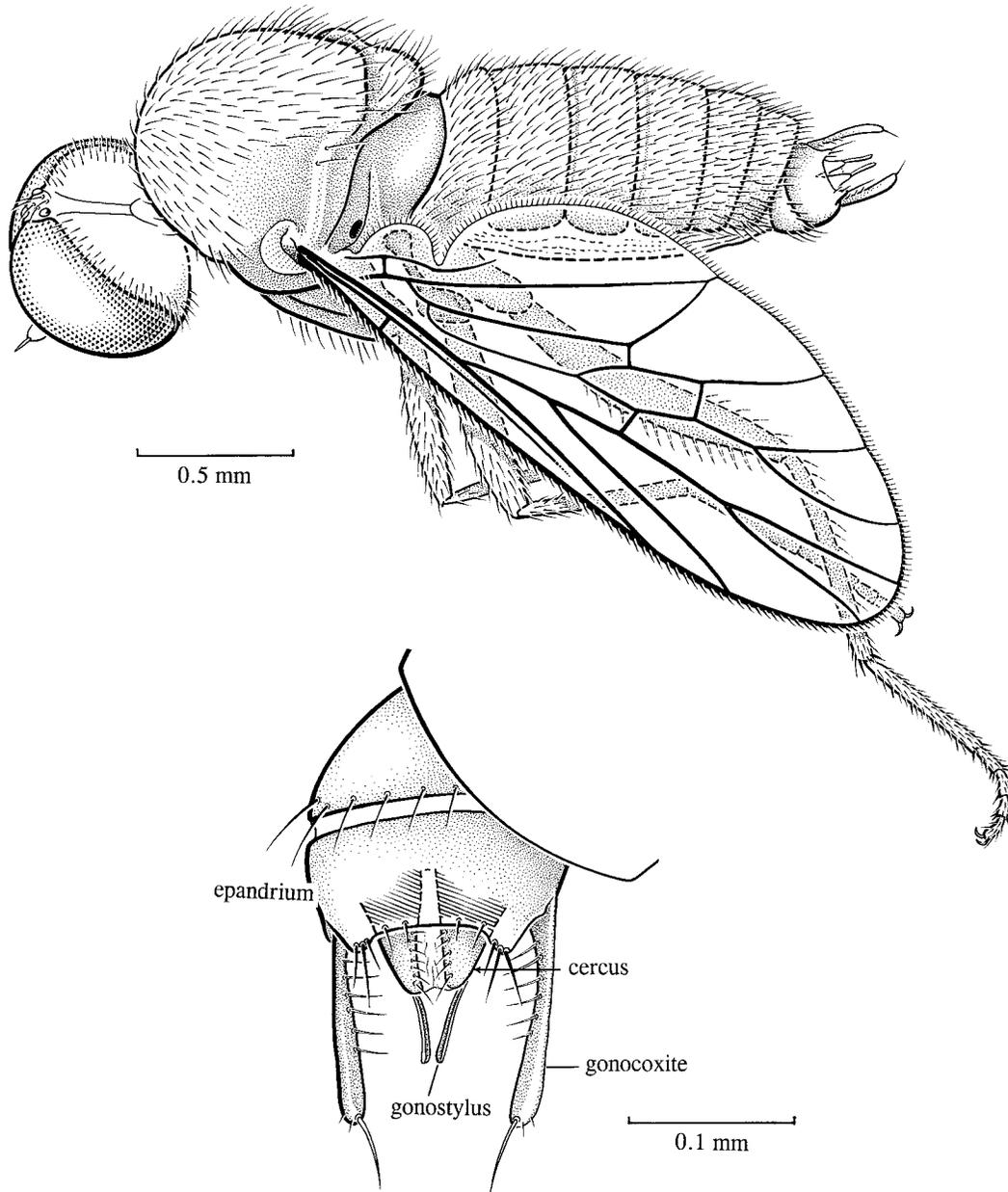


Fig. 14. Habitus and detail of male genitalia (dorsal) of holotype of *Hilarimorphites superba* (Hilarimorphidae), in New Jersey amber. AMNH NJ-772.

tae; hind femur of at least male with 2 ventral, longitudinal rows of spines. WING: Sc incomplete; R_3 slightly sinuous; M_1 slightly arched, not straight or almost so; fork of veins R_3 - R_4 equal or nearly equal to length of stem ($a/b = 1.21 [0.97-1.46]$); stem of

M_1+M_2 short ($c/d = 1.82 [1.18-2.46]$), about equal to length of forked segments of M ; dm cell long, with r-m crossvein situated near middle of cell ($f/g = 0.43 [0.33-0.54]$); veins CuA_2 and A_1 meet just before wing margin, with very short common stem. Male genita-

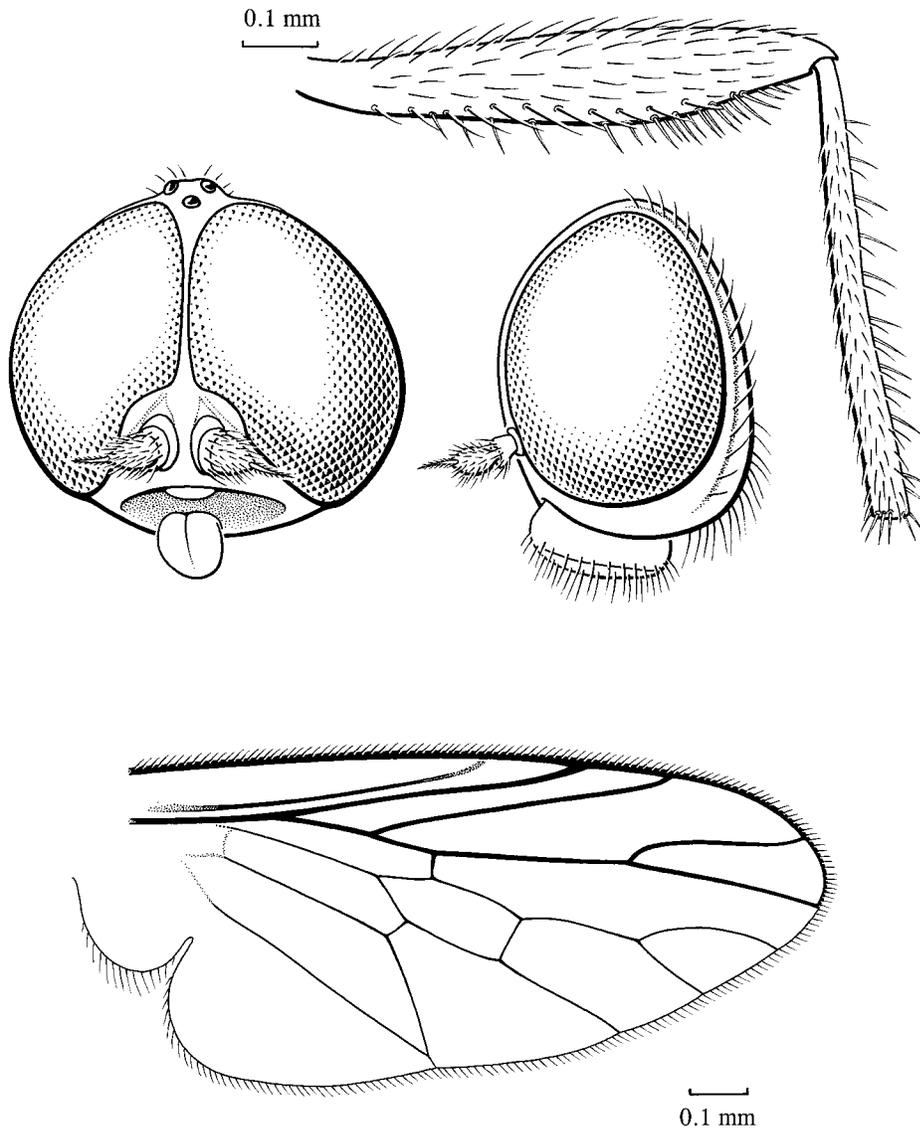


Fig. 15. Frontal and lateral views of head, wing, and hind femur plus tibia, of paratype of *Hilari-morphites superba*. AMNH NJ-673.

lia: gonocoxites long, thin, held parallel, with row of 6 stiff, fine setae on mesal surface and single large, apical seta; gonostylus thin, bare, apices almost touching. Body Length = 2.52 mm; thorax length = 0.97 mm; wing length = 2.15 mm (paratype, NJ-673).

TYPES: Holotype, ♂, AMNH NJ-772, collected by Keith Luzzi at the White Oaks site, Sayreville, New Jersey. Specimen is com-

plete and beautifully preserved in a clear yellow piece of amber 14 × 26 mm, still in its natural shape. The amber was not embedded, but the surface over the specimen was polished by the collector. The fly has small, crystalline spheres scattered over its body. Paratype, ♂, AMNH NJ-673, collected by Gene Hartstein, also from the White Oaks site. Another complete specimen in a largely

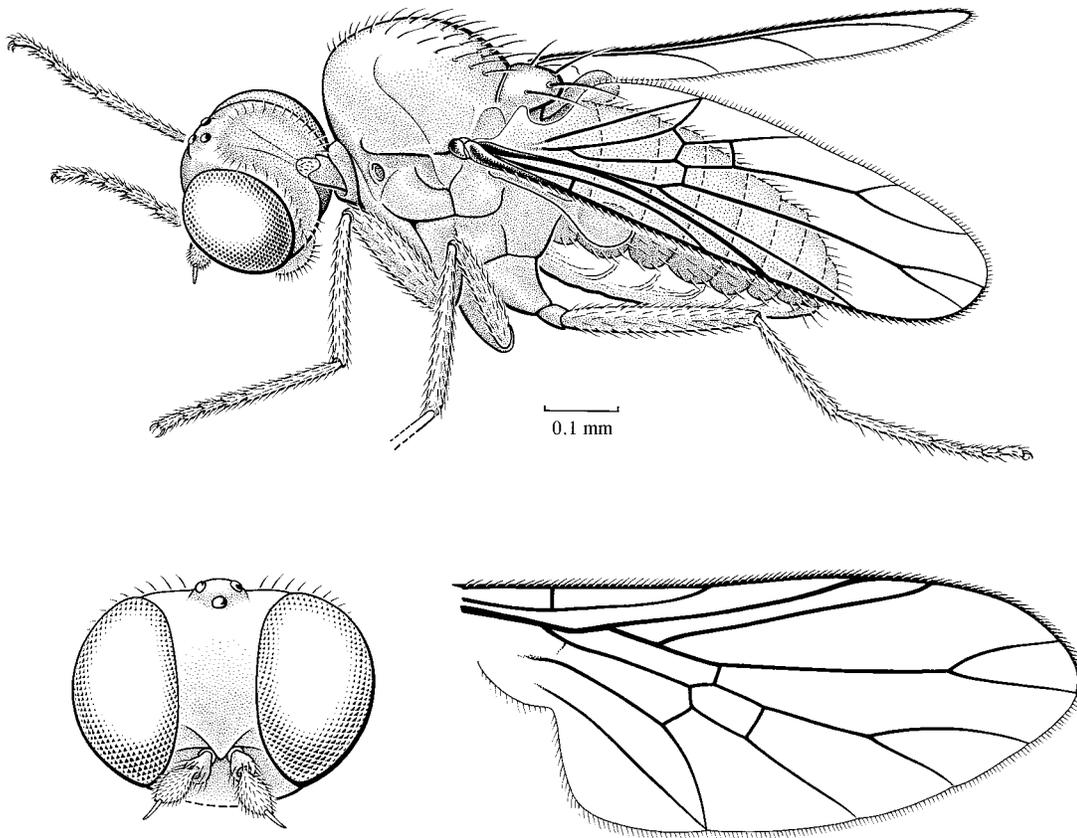


Fig. 16. Dorsolateral habitus and frontal view of head of *Hilarimorphites yeatesi* (Hilarimorphidae) holotype AMNH NJ-60, and wing of NJ-168 (paratype), in New Jersey amber.

clear yellow piece of amber, but also with a sparse suspension of dark droplets; some lateral parts of the body are obscured by bubbly froth, and bubbles obscure part of the genitalia. The specimen was embedded and trimmed, resulting in a piece of amber $6 \times 9 \times 3$ mm.

ETYMOLOGY: In reference to the large size and complete preservation of the two type specimens.

COMMENTS: Venation has many similarities to AMNH NJ-417 (*H. longimedia*, n.sp.), but with notable differences: vein C ends midway between apices of veins R_4 and R_5 ; fork of M_1 - M_2 much longer, such that stem is only about $0.35 \times$ length of forked segment; wing shorter, broader, and with the tip much more rounded in NJ-417; CuA_2 more rounded and less angulate in AMNH NJ-417.

Hilarimorphites yeatesi, new species

Figure 16

DIAGNOSIS: Notum with 2 paramedian rows acrostichal/dorsocentral setae; frons completely bare. Wing ratios: $a/b = 0.51$ (range 0.45-0.53) (vs. 0.95 or greater in other species), $e/c = 0.38$ (range 0.34-0.48) (vs. 0.34 to 0 in other species). Proportions (averages of 4 specimens): body length = 1.28 mm; thorax length = 0.44 mm; wing length = 1.07 mm.

TYPES: Holotype, ♀, AMNH NJ-60, collected by D. Grimaldi: a beautifully preserved, completely intact specimen in clear yellow amber, which was embedded and then trimmed and polished to a small, cubelike piece $7 \times 4 \times 3$ mm, for lateral, dorsal, and frontal views of the fly. Paratypes: AMNH

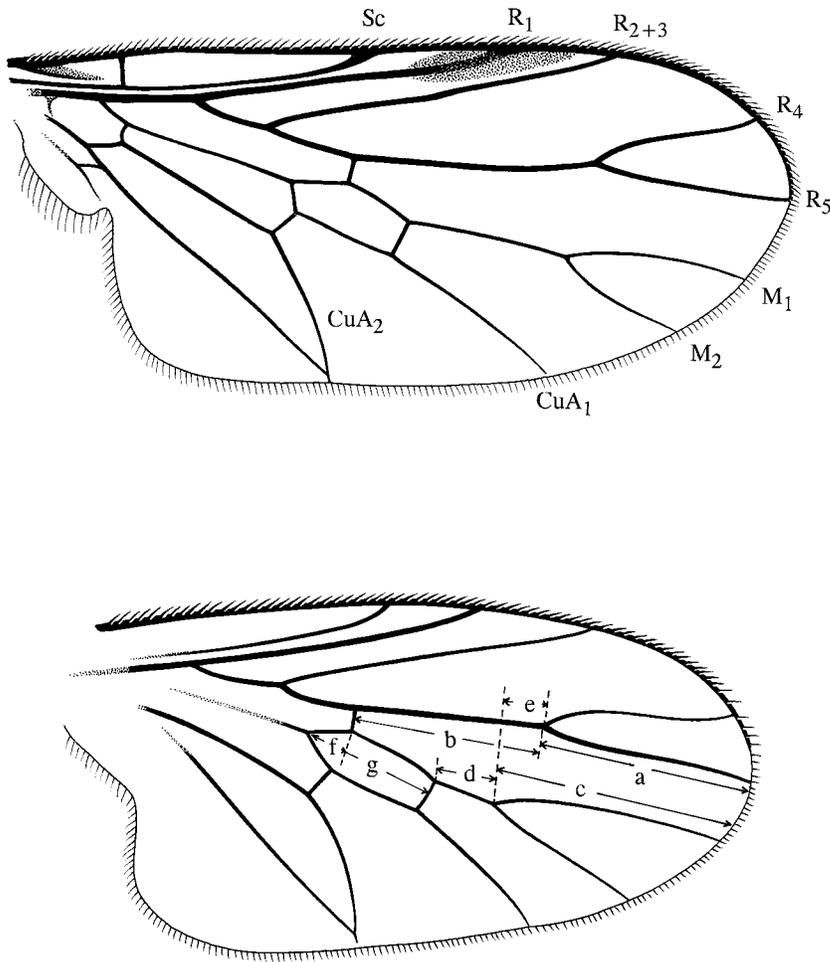


Fig. 17. Wings of *Hilarimorphites longimedia* holotype (AMNH NJ-417) above, and *H. setosa* holotype (AMNH NJ-495) below, in New Jersey amber.

NJ-168, ♂?, a beautifully preserved, complete specimen with no obscurities on surface of the fly; amber is slightly turbid, translucent yellowish (“boiled honey”), embedded and trimmed on 3 sides to $4 \times 9 \times 17$ mm; collected by Keith Luzzi (KL-11). AMNH NJ-314, ♀, a complete specimen largely obscured by frothy coating and turbidity of the amber; piece was embedded and trimmed to 1 mm. thickness to optimize view of right wing (laterally) and left wing (dorsally); collected by Keith Luzzi. AMNH NJ-418, ♀, a completely intact specimen, but body surfaces obscured somewhat by light froth coating; amber is slightly turbid (“boiled honey”), and also contains 2 male coccoids and part

of a male moth; piece was embedded and trimmed on 3 surfaces to $4 \times 7 \times 8$ mm; collected by Keith Luzzi (KL-501). All specimens are from the White Oaks site, Sayreville.

ETYMOLOGY: Patronym for David Yeates, University of Queensland and former post-doctoral fellow at the AMNH, for his work on asiloids.

Hilarimorphites longimedia, new species

Figure 17

DIAGNOSIS: Distinguished from other species by distinctively long fork of M_1 - M_2 ($c/d = 3.54$, vs. 0.93-2.46 in other species).

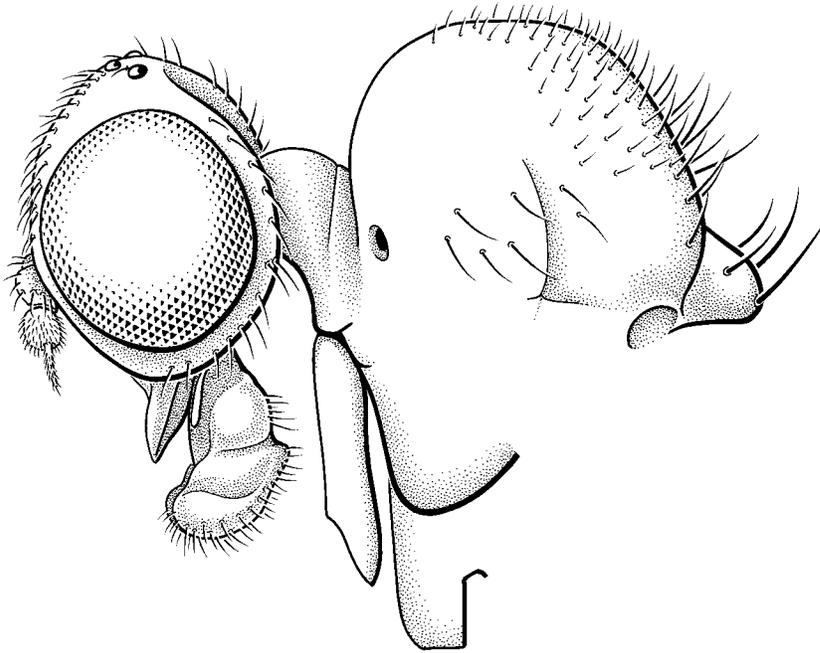


Fig. 18. Lateral view of head and thorax of *Hilarimorphites setosa* holotype (AMNH NJ-495), in New Jersey amber.

TYPE: Holotype and unique specimen, ♀, AMNH NJ-417, collected by Keith Luzzi at the White Oaks site, Sayreville. Body Length = 1.83 mm; wing length = 1.41 mm. The amber itself is very clear yellow, which was embedded and sliced to a thickness of 2 mm with flat surfaces parallel to wing surfaces (piece is 12 × 10 mm). Body of the fly is poorly preserved, most of which is covered with a milky coating and large bubble, but the entire right wing and part of the left wing are not obscured.

ETYMOLOGY: Specific name in reference to the long fork of the medial veins.

***Hilarimorphites setosa*, new species**

Figures 17, 18

DIAGNOSIS: Frons with numerous, scattered, decumbent setulae; notal and scutellar setae erect. Wing with length of R fork virtually equal to length of stem of R ($a/b = 0.95$, vs. 0.51 for *H. yeatsi*, 0.97-1.46 for *H. longimedia* and *superba*); distance between bases of R and M forks of small, $e/c = 0.26$ (vs. 0.0, 0.18, and 0.38 in other species); crossvein r-m meets cell dm near its middle,

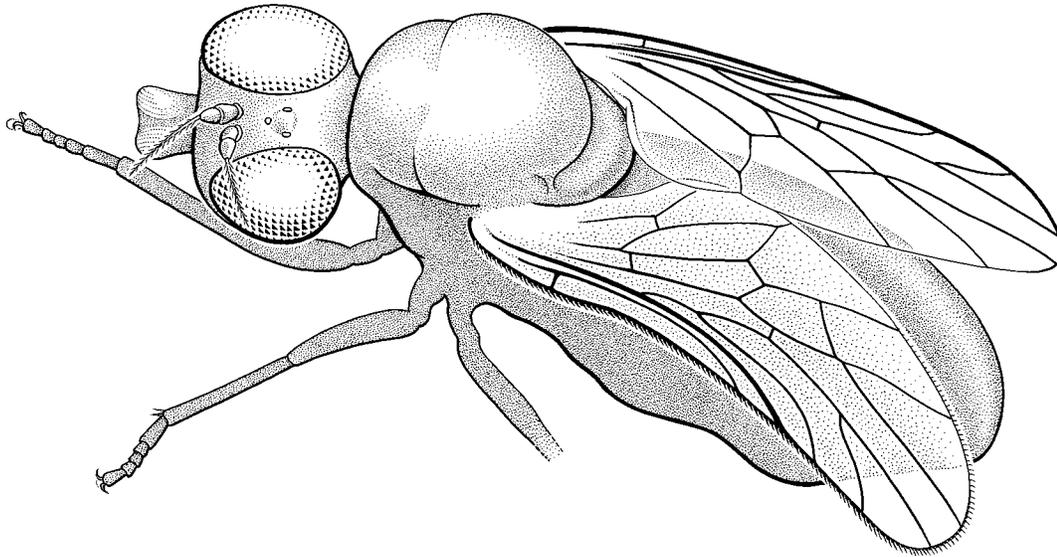
$f/g = 0.45$ (vs. 0.33, 0.38, 0.54 in other species).

TYPE: Holotype and unique specimen, ♀, AMNH NJ-495, collected by Keith Luzzi (KL-17) at White Oaks site, Sayreville, New Jersey. Body length = 1.44 mm; thorax length = 0.54 mm; wing length = 1.20 mm. Specimen is a completely intact and beautifully preserved specimen with its wings spread, in a clear yellow piece of amber. The amber piece was embedded and trimmed for a surface parallel to left lateral surface of the body and dorsally, parallel to flat surfaces of the wings.

ETYMOLOGY: Species name in reference to the setulose frons.

General Discussion of *Hilarimorphites*

Webb (1974) provided an historical review of the taxonomic placement of what was the sole genus of the family, *Hilarimorpha* Schiner; the genus contains 33 species, all but 3 of them in North America. He concluded that it was closest to the Rhagionidae. Nagatomi (1982) maintained that the family was closest to the Bombyliidae, on the basis of male genital structure. Woodley (1989), in fact, con-



—
0.1 mm

Fig. 19. Dorsal habitus of *Proratites simplex* (Scenopinidae) holotype (AMNH NJ-678), in New Jersey amber.

cluded that it would be appropriate to have *Hilarimorpha* in the Bombyliidae. Sinclair et al. (1994) placed *Hilarimorpha* in the “ther-evid clade,” of uncertain affinities, also based on male genitalic characters. It was Sinclair et al. (1994) who also were the first to propose that *Hilarimorpha* was probably most closely related to *Apystomyia* Melander. *Apystomyia* is a monotypic genus known from a few specimens collected in western North America. Formerly, *Apystomyia* was placed in the Proratinae, itself put into the Bombyliidae until Yeates (1992) transferred the proratines to the Scenopinidae. Yeates (1992, 1994) was in agreement with Nagatomi and Woodley on the phylogenetic position of the Hilarimorphidae, specifically that this family was the sister group to the Bombyliidae. Yeates also agreed with Sinclair et al. (1994) that *Apystomyia* was closely related to *Hilarimorpha*. Wiegmann et al. (1993) used *Apystomyia* and *Hilarimorpha* as asiloid outgroup taxa for polarizing eremoneuran character states, but did not indicate them as sister taxa.

The species of *Hilarimorphites* are the

only fossil hilarimorphids known, which is unexpected given what we discern as four species from the one deposit in Sayreville; although Webb (1974) found that several species of *Hilarimorpha* could be sympatric. *Paleohilarimorpha bifurcata* Meunier, in Baltic amber, was later found to be a species of *Rhagio* (Rhagionidae) (Hennig, 1967).

FAMILY SCENOPINIDAE

PRORATITES, NEW GENUS

DIAGNOSIS: Venation with some distinct features of proratines, particularly shape of discal cell, and veins M_1 - M_2 originating virtually directly off of apex of discal cell. Antenna with long apical style, with flagellomere I conical, about same size as pedicel; flagellomere II a long, thin style (virtually aris-tate), ca. 4 times length of flagellomere I.

TYPE SPECIES: *Proratites simplex*, n.sp.

ETYMOLOGY: From *Prorates*, and Greek *-ites*, for “like *Prorates*.”

Proratites simplex, new species

Figure 19

DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 3.22 mm; thorax length = 0.97 mm; wing length = 2.12 mm. HEAD: Eyes bare, not contiguous (probably a female); shortest distance between eyes (dorsally) equal to length about twice width of ocellar triangle. Antenna with long thin, apical style; pedicel and flagellomere I approximately equal in size; flagellomere I conical; flagellomere II virtually aristate, base is on apex of flagellomere I, length approximately 4× length of flagellomere I. Proboscis with well-developed labella, projects anteriorly beyond frontal margin of head for approximately one-half length of head. THORAX: Notum and scutellum devoid of macrosetae; notum noticeably arched, but not humpbacked. Legs largely obscured, but mid tibia with two apical, stout setae (not spurs). Hind leg with coxa having no peg on antero-medial surface. WINGS: Long, extending to tip of abdomen or slightly longer. Radial veins slightly upturned toward vein C. Vein C ends midway between R_4 and M_1 . Sc long, extended to level of crossvein r-m. Veins R_4+R_5 forked. Veins M_1-M_2 forked, with barely any stem to fork, base of fork connected directly to apex of cell dm. Cell dm large, irregular in shape. Veins CuA_2 and A_1 connected before wing margin, with short stem. Vein A_2 present, connected to A_1 by short crossvein. ABDOMEN: Largely obscured by milky coating.

TYPE: AMNH NJ-678, collected by Paul Nascimbene at the White Oaks site, Sayreville, New Jersey. The type is the only specimen for the species.

ETYMOLOGY: Species name in reference to the generalized features of the fly.

COMMENTS: An assignment of this fossil to the Scenopinidae is made largely on the basis of the wing venation, which is very similar to that of the proratine genera *Prorates*, *Jackhallia*, and *Caenotus* (reviewed by Nagatomi et al., 1994). Unfortunately, since the abdomen is covered with froth, the defining scenopinid feature of a pair of sensory patches on tergite II cannot be confirmed. The only fossil scenopinids are *Metatrachia pria* Yeates and Grimaldi (Miocene amber from

the Dominican Republic), and this one. *Metatrachia* is a scenopinine, this subfamily of which contains the great bulk of world species. *Proratites* provides the only Mesozoic record of the family and the only fossil record of the rare and interesting proratines.

FAMILY ASILIDAE

GENUS INDETERMINATE

Figure 20

SPECIMEN: A disarticulated and partially decomposed, partial specimen of an asilid exists in a small piece of turbid yellow amber, preserved with portions of a cockroach (AMNH NJ-558, coll. by Debra Abernathy at the White Oaks site, Sayreville, New Jersey). Remains of the asilid include most of the head, thorax, portions of some legs, and proximal quarter of the wings. Without the wing venation it is very difficult to place the specimen, and virtually impossible to diagnose the genus.

DESCRIPTION: Thorax length = 2.63 mm. The head is large; eyes with fairly large, flat, frontal surface, but no differentiation of frontal and lateral facets; eyes bare. Vertex not excavated, probably bare; ocellar triangle raised only slightly. Eyes widely separated frontally, distance between inner margin 0.28 width of head; inner margins with slight emargination just below antennal bases. Antenna with cup-shaped pedicel, drop-shaped flagellomere I, styliform terminal flagellomeres. Difficult to discern if more than one small basal stylomere present. Face with very simple mystax, composed of only 2 stouter, light-colored setae, plus several finer, slightly shorter setae. Proboscis of moderate length; hypopharynx with 3 sharp spicules on dorsal surface; palp short and bare, with two segments.

Thorax with pair of fine, stiff supra-alar setae; row of 3 fine, stiff setae on postalar callus. Notum and scutellum largely bare. Pronotum fairly large. Foreleg with tibia having approximately 6 stiff, long setae and numerous finer, shorter ones (legs very difficult to observe). Wing with small alula, but base of wing folded, obscuring bases of veins M and Cu.

COMMENTS: The only other Cretaceous asilid besides this one is *Araripogon axelrodi*

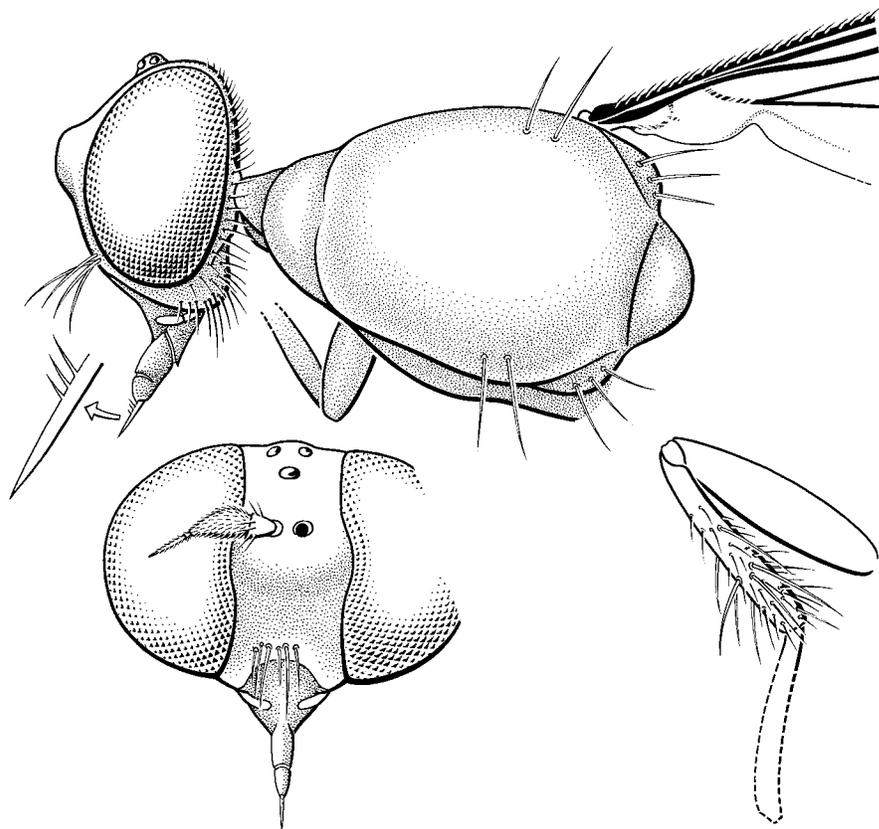


Fig. 20. Incomplete specimen of Asilidae, genus indet. (AMNH NJ-558), showing entire specimen, front of head, and left foreleg in lateral view. New Jersey amber.

Grimaldi, from Aptian limestone of the Santana Formation, Ceará, Brazil. Otherwise, Asilidae are fairly well represented in Tertiary deposits, particularly in Oligocene shales of Florissant, Colorado; Eocene deposits of the Green River Formation, Wyoming; and Miocene and Oligo/Eocene amber of the Dominican Republic and Baltic region.

The New Jersey amber specimen, with its flat frontal surface of the eyes, virtually straight margin on the vertex, small alula, and especially the mystax with only several stiff setae, all appear to be plesiomorphic traits reminiscent of leptogastrines. In Leptogastrinae there is no alula nor anal lobe on the wing, which is probably apomorphic (i.e., a loss), since this feature is convergent in some other flies with a gracile body. Unfortunately, most of the wing and all of the abdomen is lost—which are structures needed

to confirm whether the fossil is a leptogastrine or close. In addition, the halteres appear to have not been preserved, which would have been useful since leptogastrines have very long halteres.

SECTION EREMONEURA SUPERFAMILY EMPIDOIDEA

The higher classification of the Empidoidea and ranking of the major included lineages has been in a state of flux in recent years. Chvála (1983) divided the group into five families, but precise recognition and ranking of these groups remains contested (see Cumming et al., 1995; Sinclair, 1995; Woodley, 1989). Although the classification presented here reflects this uncertainty, it attempts to recognize the major subgroups in the Empidoidea, including the Trichopezinae

(sensu Sinclair, 1995) and an additional lineage referred to here as the *Nemedina* genus group. The classification is based primarily on analyses by Sinclair et al. (1994), Cumming et al. (1995), Sinclair (1995). The Ocydromiinae + Hybotinae + Tachydromiinae lineage (= Hybotidae sensu Chvála, 1983) is referred to here simply as the hybotid lineage, and the paraphyletic Microphorinae is subdivided into the Microphorini and Parthalassiini to more adequately treat the many Cretaceous fossils found in this group.

The family Protempididae was proposed by Ussatchev (1968) for the single fossil specimen *Protempis antennata* Ussatchev from Upper Jurassic shales of Kazakhstan. This fossil has been considered the earliest known member of the Empidoidea based on plesiomorphic characters of the wing (Chvála, 1983). However, it is also similar in many respects to the Rhagionempididae and Hilarimorphidae, and its exact placement within the Asiloidea + Eremoneura lineage (including the recent addition of *Protempis minuta*, *Helempis yixianensis*, and *Helempis eucalla* described by Ren [1998a]) still needs to be determined.

SUBFAMILY EMPIDINAE

The only known Mesozoic member of this lineage was described by Waters (1989) from the early Cretaceous of Botswana, as *Empis orapaensis*.

TURONEMPIS, NEW GENUS

DIAGNOSIS: Antennal scape and pedicel large, pedicel drop-shaped; arista with 3 articles, apically situated; mouthparts moderately long, labellum fleshy; palps pointed, projecting; acrostichal and dorsocentral setae differentiated, with 2 rows of 6 acrostichals; fore basitarsus not expanded. Wing broad; costal vein ends between apices of veins R₅ and M₁; apex of R₁ with light pterostigma; R₄₊₅ with wide apical fork; Sc apically evanescent; cell dm large; CuA₂ slightly recurved, A₁ branching off cup cell close to apex (not near middle); anal lobe large.

TYPE SPECIES: *Turonempis styx*, n.sp., in Turonian (mid Cretaceous) amber from Sayreville, New Jersey. Monotypic.

ETYMOLOGY: From Turonian (age of amber

deposit), and *-empis*, a typical suffix for empidid names based on the type genus.

Turonempis styx, new species

Figure 21

DIAGNOSIS: As for genus.

DESCRIPTION: Thorax length = 0.68 mm; wing length = 1.86 mm; total length = 2.21 mm. HEAD: Largely obscured by milky coating, *Hilara*-like in shape, apparently dichoptic. Projecting through coating is large pair of laterocline ocellar setae and row of typical postoculars; no other setae apparent on head. Bases of antennae very close together, almost touching; scape and pedicel large, pedicel drop-shaped. Arista barely dorso-preapical, with 3 articles: basal 2 articles small, both slightly less than 0.3× length of apical article, basal article twice length of second article; apical aristomere with fine microtrichia. Clypeus slightly bulging; mouthparts moderately long, labellum fleshy; palps pointed, projecting. THORAX: Acrostichal and dorsocentral setae differentiated, with 2 rows of 6 acrostichals each; 6 setae in each row of dorsocentrals, posterior pair of dorsocentrals twice length of anterior pairs, next anteriormost pair slightly smaller than posterior pair. Two notopleural, 3 supraalar, 3 laterotergal setae present. Scutellum broad, with 2 pairs of setae, apical pair cruciate for one-half their length. Legs unmodified, with fore basitarsus not expanded. WING: Costal vein ends midway between apices of veins R and M; Sc apically evanescent; R₁ straight, meets costa near midpoint of wing's length; R₂₊₃ straight; R₄₊₅ with wide apical fork, R₅ branch 0.4× length of trunk of R₄₊₅; cell dm large, truncate apically, length nearly equal to length of apical section of M₁, width 0.28 width of wing; veins M₁, M₂, and CuA₁ branching off apex of dm cell; CuA₁ not quite reaching margin of wing; bm cell slightly longer and wider than cup cell; CuA₂ slightly recurved, A₁ very straight, incomplete, branching off cell cup near its apex, not more basally; anal lobe large. ABDOMEN: short, extended to middle of vein M₁, largely obscured.

TYPE: Holotype (probably ♀) and only known specimen, AMNH NJ-520 (KL-541), in Turonian amber from Sayreville, New Jer-

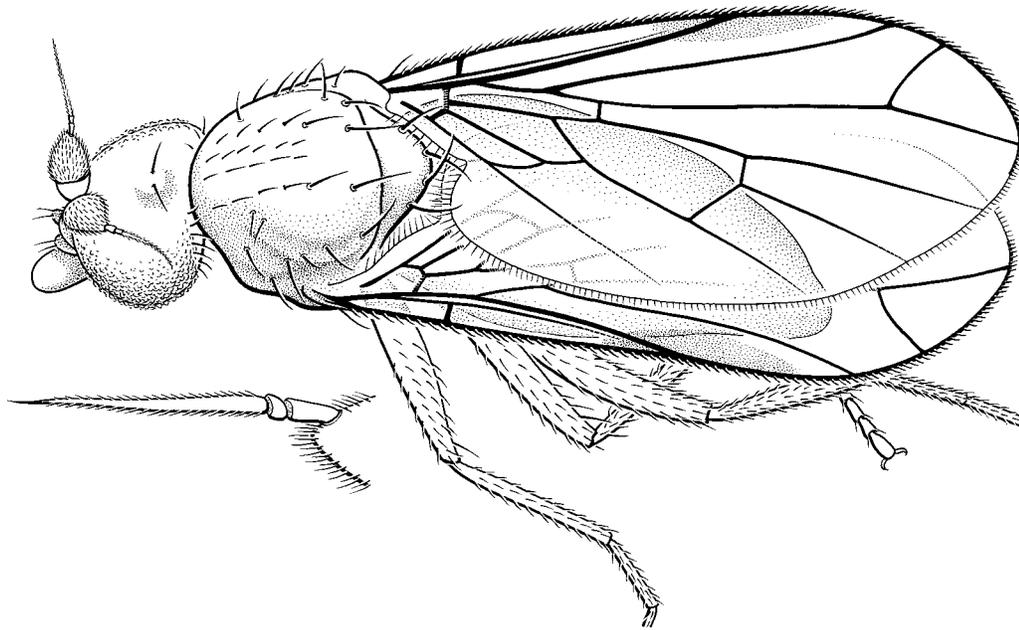


Fig. 21. *Turonempis styx* (Empididae) holotype, AMNH NJ-520, in New Jersey amber, with detail of arista.

sey (White Oaks site). Specimen is complete, but the head and thorax are largely covered with a milky coating.

ETYMOLOGY: From the name of the mythical river of the underworld.

COMMENTS: Most of the distinctive systematic characters are on the anterior part of the head and the wing venation. Wing shape and venation are very similar to some extant genera of Empidini. Similarities with these taxa include the large anal lobe, recurved CuA_2 , evanescent Sc , costa ending between R_5 and M_1 , and the wide shape of the R_{4+5} fork. The venation of *Turonempis* is most similar to the extant empidine genus *Sphicosa* Philippi, but the dm cell in *Turonempis* is longer. In addition, the shape of the antenna, including a relatively elongate arista with 3 articles, distinguishes *Turonempis* from *Sphicosa* and other Empidini.

EMPLITA, NEW GENUS

DIAGNOSIS: Antenna with apical arista, article 2 with minute terminal style; proboscis $0.7\times$ depth of eye, suspended vertically under head; legs unmodified. Wing with Sc incomplete; R_4+R_5 narrowly forked; cell dm

long, veins M_1 and M_2 connecting to dorsoapical corner of dm ; cells bm , cup short, of equal lengths, CuA_2 only slightly recurved; anal lobe present but small, anal vein virtually absent. Female terminalia apparently telescopic, without acanthoporphorite spines.

TYPE SPECIES: *Emplita casei*, n.sp. Monotypic.

ETYMOLOGY: From *Empis* (type genus of Empididae) and *litos*, Greek for "simple," "plain" (in reference to a basic morphology).

Emplita casei, new species

Figure 22

DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 2.09 mm; wing length = 1.72mm; thorax length = 0.56 mm. HEAD: Subspherical. Frons bare, with short, scattered ocellar setulae; ocellar triangle barely raised. Eyes bare, widely separated, nearly circular in lateral view. Face bare, without setulae. Gena very narrow, division between it and face by frontoclypeal suture not discerned. Clypeus not discerned. Mouthparts fairly elongate, suspended verti-

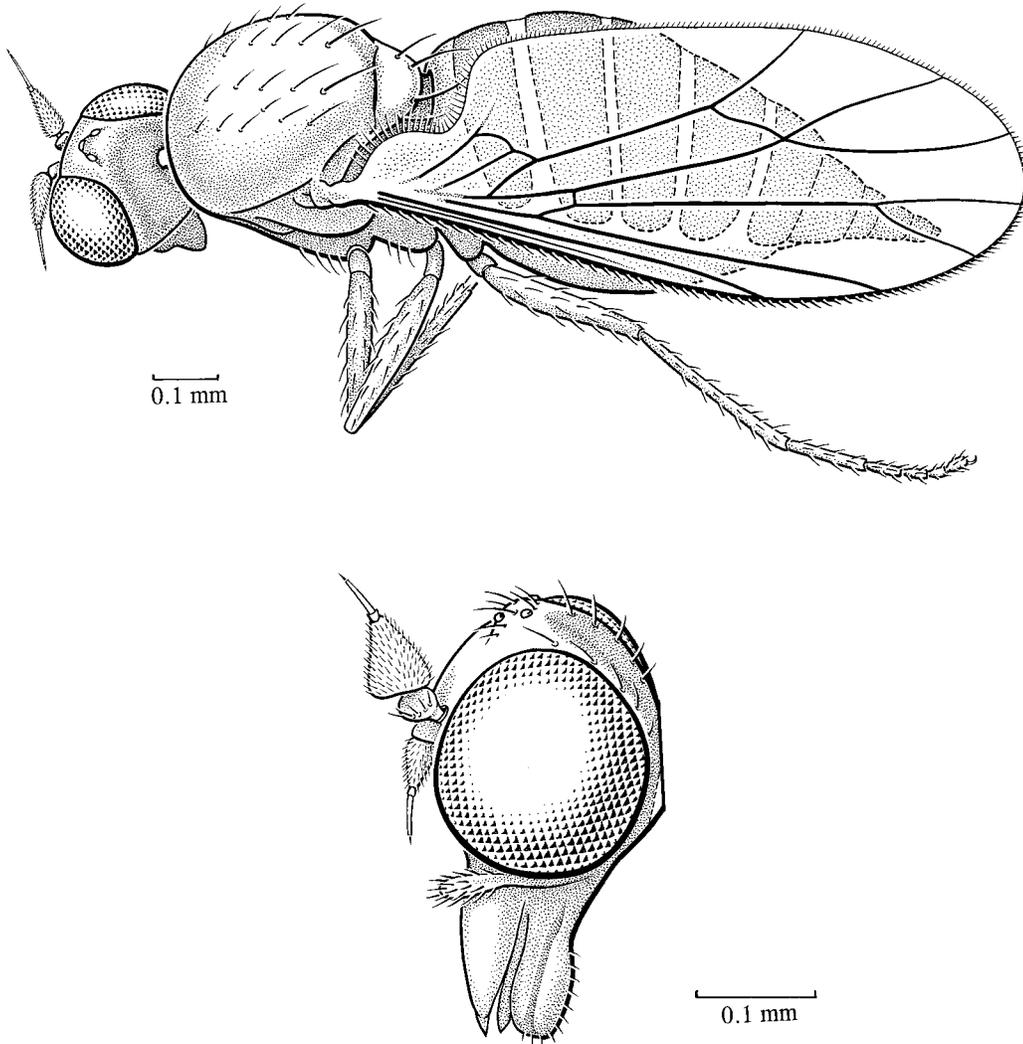


Fig. 22. *Emplita casei* (Empididae) holotype, with lateral view of head. AMNH NJ-200, in New Jersey amber.

cally beneath head. Proboscis stout, $0.7\times$ diameter of eye, suspended vertically beneath head; covered with milky coating, so mouthpart components not clearly distinguishable, but labrum appears large, its length equal to length of proboscis. Palp linear, setulose, free. Antenna: pedicel spherical; first flagellomere triangular in lateral view; arista apical, with 2 articles ($0.65\times$ length of flagellomere I); arista article 2 with minute terminal style. THORAX: Notum simple, not arched; with two paramedian rows dorsocentrals, no acrostichals. Five setae in each dor-

socentral row, posterior two setae in each row longest. Scutellum with two pairs of setae. Pleural setae either absent or not discerned. Pretarsus with empodium either absent or very small/setiform (but definitely not pulvilliform). Legs simple, without distinctive setae. Foreleg tarsomere lengths not discerned. WING: Completely hyaline, without infuscation or spots. C ends between apices of veins R_5 and M_1 ; Sc apically evanescent; R_1 very straight, close and parallel to C; R_{2+3} also very straight and parallel to C; branches of R_4+R_5 fork divergent, but relatively nar-

row and not bell-shaped; veins M_1 and M_2 forked, base of fork arising directly off anteroapical corner of dm cell (no stem to M_1 - M_2); cell dm narrow, produced apically; CuA_1 reaching wing margin; CuA_2 short and only slightly recurved; anal lobe small but present, alula present, anal vein virtually absent. ABDOMEN: Tergites bare or virtually so (setae not discerned). Terminal segments of female apparently telescoping, without acanthophorite spines. Female tX and details of cercus not discerned, except that cerci are lobate and unsclerotized.

TYPE: Holotype, ♀, AMNH NJ-200, collected at the White Oaks site in Sayreville, New Jersey, by G.R. Case. Specimen is in a clear, light-yellow piece of amber that was epoxy-embedded, then trimmed on three sides to observe dorsal and lateral views of the fly (amber piece is $3 \times 5 \times 7$ mm; epoxy block is $3 \times 7 \times 9$ mm). Specimen is complete, but obscured by a few bubbles near the surface of the amber; also, venation at the base of the wing and details of the antenna are very faintly preserved and must be observed with a compound scope (160–200 \times magnification) and reflected light.

ETYMOLOGY: For the collector of the specimen, Gerard R. Case.

COMMENTS: Features of the wing, such as the very slightly recurved CuA_2 , R_{4+5} fork, evanescent Sc, and costa ending between R_5 and M_1 , are most similar to extant members of the Empidinae. The head, mouthparts, and antennal shape of *Emplita* are most similar to the tribe Hilarini, but the R_{4+5} fork (although narrow) is not bell-shaped like most hilarines, and no member of this tribe has M_1 and M_2 arising off the anteroapical corner of cell dm. The costa of *Emplita* ending between R_5 and M_1 is most similar to the condition found in the Empidini, but the narrow shape of the R_{4+5} fork is unlike other members of the tribe. Unfortunately the details of the setation of the postnotum (setae present in Empidini versus absent in Hilarini) are not apparent on the fossil specimen.

SUBFAMILY ATELESTINAE
ATELESTITES, NEW GENUS

DIAGNOSIS: Antenna elongate; flagellomere I linear; arista apical; hind tibia not dilated. Wing with Sc incomplete; R_{4+5} not forked;

large dm cell with veins M_1 , M_2 and CuA_1 branching separately off apex of dm cell; cell cup long, with acute outer angle; anal vein (A_1 reaching wing margin; anal lobe large. Male genitalia with large deeply emarginate epandrium that overlaps hypandrium apically; subapical surstyli; apex of phallus appearing tripartite.

TYPE SPECIES: *Atelestites senectus*, n.sp. Monotypic.

ETYMOLOGY: From *Atelestus* (an extant genus of Empididae) and *-ites*, Greek for "like," in reference to the similarity of the two genera.

Atelestites senectus, new species

Figure 23

DIAGNOSIS: As for genus.

DESCRIPTION: Total length = 1.61 mm.; thorax length = 0.41 mm; wing length = 1.18 mm. Complete male specimens, with genitalia intact. HEAD: Large, virtually spherical, with eyes in male very large and occupying virtually entire head, surrounding ocellar triangle (cheek and frons not exposed). Eyes holoptic, meet from near anterior ocellus to probably bases of antennae (this latter area difficult to observe closely); dorsal facets approximately twice the size of ventral ones. Antenna aristate; basal flagellomere (I) conical; flagellomere II is the shape of an elongate drop; flagellomere III linear, 2.2 \times length of flagellomere II; arista apical, apparently with 1 article. Proboscis not observed due to depth of amber. THORAX: Notum small, with scattered acrostichals, single pair of dorsocentral setae; 3 notopleural setae; scutellum with 2 pairs of setae, apical pair pointed dorsad (perhaps a preservational artifact). Legs long, particularly femur and tibia; without distinctive modifications; hind tibia not dilated. WING: Broad; vein C ends midway between veins M_1 and M_2 ; Sc apically evanescent; crossvein h well developed, located at level of basal-most branching of veins M and Cu; apices of veins R_{2+3} and R_{4+5} encompass apex of wing, vein R_{4+5} not forked; large dm cell present, longer than free branches of M_1 , M_2 , and CuA_1 ; cells bm and cup large, the latter 1.6 \times length of bm; cell cup particularly large and wide, with vein CuA_2 curved abruptly

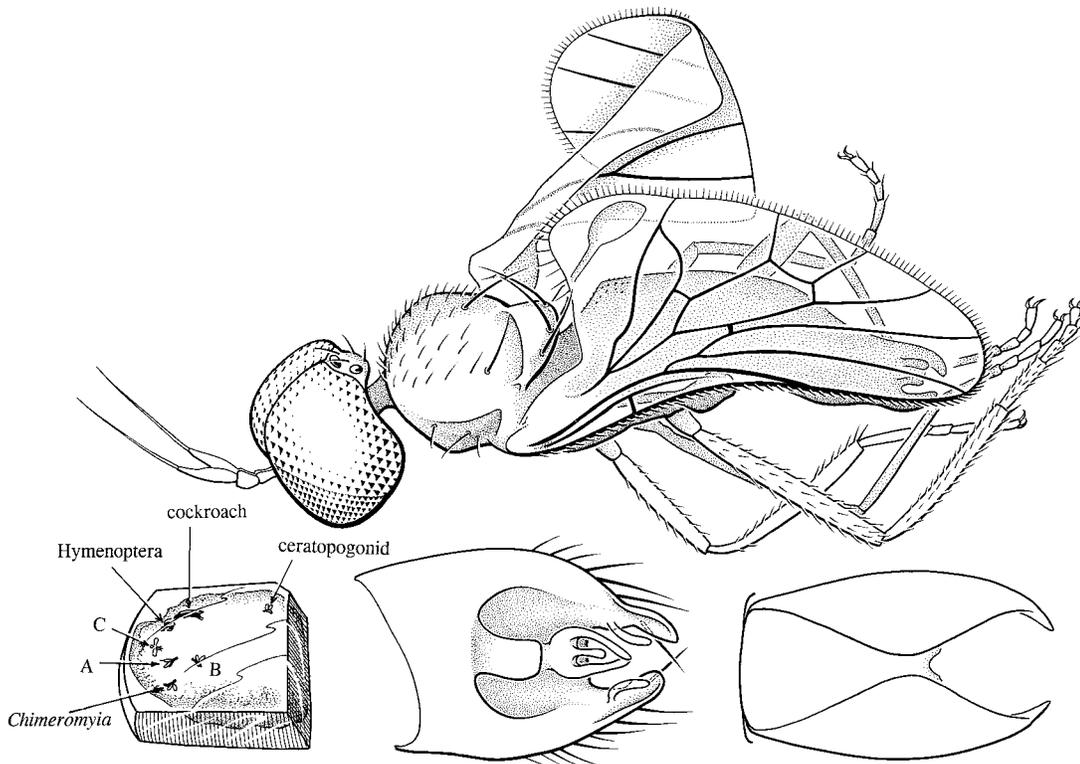


Fig. 23. Entire specimen and dorsal and ventral views of male genitalia of *Atelestites senectus* (Empididae), AMNH L-AE72, in Lebanese amber. Piece shows location of specimens (arrows).

and meeting vein A_1 three-fourths of the way toward margin; vein A_1 complete to wing margin; vein A_2 either not developed or not discerned; anal lobe large, well developed; alula not developed. Halter on a long, thin stalk, approx. $0.3\times$ length of wing. ABDOMEN: Long and thin, apex reaching nearly to apex of wing. Male genitalia of specimen B displayed best: with large, deeply emarginate epandrium overlapping hypandrium apically; surstyli subapical, cerci difficult to see, discernable as dorsal lobe(s) covering base of phallus; apex of phallus with lateral processes (appearing tripartite).

TYPE: Holotype, ♂, AMNH L-AE72 (specimen A), in Lebanese amber from Neocomian (Lower Cretaceous), collected by Antoni Estephan in northern Lebanon, Bcharre. Piece AMNH L-AE72 has 7 insect inclusions: a ceratopogonid, roach, probable parasitoid wasp, sciadocerid (*Archisciada*, below), and 3 empidoids (fig. 23). Two of the empidoids, labelled here A and B, belong

to the same taxon; specimen C is a different taxon, based on the lack of a large anal lobe, a much shorter anal cell (if present – depth of the amber obscures views), and the antenna and male genitalia are different. Unfortunately, the amber cannot be cut and polished to optimize views of specimen C, since this would destroy valuable inclusions surrounding it.

ETYMOLOGY: From the Latin, for “old,” “aged,” in reference to the age of this Lower Cretaceous species.

COMMENTS: This species is the earliest known and most plesiomorphic member of the subfamily Atelestinae. Plesiomorphies for the subfamily include the presence of a dm cell (observed in the extant genera *Meghyperus* Loew and *Acarteroptera* Collin) that emits three separate veins (M_1 , M_2 and CuA_1), and a hind tibia that is not dilated. However, *Atelestites senectus* has the apex of the phallus appearing tripartite, similar to the other extant genus in the subfamily, *Atelestus*

Walker. It is likely that the specimens in AMNH L-AE101 also belong to *Atelestites* and possibly *senectus*, based on the structure of the antenna and wing (the latter with some subtle differences). These additional specimens are females.

NEMEDINA GENUS GROUP

This lineage is represented by the extant genus *Nemedina* Chandler, known until recently from a single species *N. almirabilis* Chandler, based on a unique female from Hungary. Chandler (1981) placed *Nemedina* as incertae sedis within the Empidoidea primarily because the genus has a single spermatheca, lacks a fore tibial gland, and has peculiar wing venation (apex of cell br modified through inclusion of a short vertical Rs and recurrent r-m with radial and medial veins closely approximated, in conjunction with the R_{4+5} unforked, and the bm and dm cells absent). Sinclair and Arnaud (1998) recently described a similar second species of *Nemedina* from a copulating pair in Baltic amber. Based on this Baltic amber inclusion, the male of *Nemedina* is now known to be holoptic and has symmetrical unrotated genitalia as predicted by Chandler (1981). With the discovery of the additional fossil genera described below it is likely that this entire empidoid lineage will eventually require ranking at the subfamily level. The lineage was apparently more diverse in the Cretaceous.

NEMEDROMIA, NEW GENUS

DIAGNOSIS: Eyes holoptic in male, dichoptic in female; antenna with terminal to slightly subapical arista. Wing with costal vein ending at M_{1+2} ; Sc incomplete; R_{4+5} not forked; cells bm and dm absent (bm-cu and dm-cu veins absent); apex of cell br formed by short vertical Rs and recurrent r-m with the radial and medial veins closely approximated; CuA_1 arising from cell br; cell cup long, with acute outer angle; anal vein (A_1 nearly reaching wing margin; anal lobe small but distinct. Male genitalia with forked or Y-shaped protuberances; terminal segments of female elongate and telescoping, without acanthophorite spines.

TYPE SPECIES: *Nemedromia campania*, n.sp.

ETYMOLOGY: Derived from *Nemedina* (an extant genus of Empidoidea) and *-dromia* (Greek for runner), a common suffix of empidid genera.

COMMENTS: *Nemedromia* resembles the extant genus *Nemedina* in the form of the wing, but differs from that genus in the smaller anal lobe, the lack of crossvein h, CuA_1 arising from cell br rather than the apex of the anal cell (cup), and the less truncate anal cell with CuA_2 abruptly curved. In addition, the female terminalia of *Nemedromia* are elongate and telescoping, not more or less truncate with broad cerci as in *Nemedina*. *Nemedromia* appears to contain at least three species from Turonian and Campanian ambers.

Nemedromia campania, new species

Figure 24

DIAGNOSIS: Differs from *N. telescopica* n.sp. and *N. turonia* n.sp. in the broader wing, vein R_{4+5} slightly curved upwards towards costa, less arched CuA_2 , more pointed basal flagellomere, and the Y-shaped protuberance of the male genitalia.

DESCRIPTION: Thorax Length = 0.35 mm (CAS 1091A), 0.59 (MCZ 6907); body length = 1.01 mm (CAS 1091A), 1.48 (MCZ 6907); wing length = 0.91 mm (CAS 1091A), 1.25 (MCZ 6907). HEAD: Eyes holoptic in male, meeting for short distance; no apparent differentiation of dorsal and ventral facets. Ocelli large, 3–4 times the diameter of an eye facet. Antenna aristate, with arista terminal; flagellomere I drop-shaped, setulose, with long seta on dorso-apical surface; flagellomere II small, length approximately 3× width; flagellomere III long, aristate, with numerous fine setulae with lengths approximately 3× width of segment. Proboscis not visible. THORAX: With numerous acrostichal and dorsocentral setulae, irregularly arranged; pair of small notopleural setae; one supra-alar seta; pair of dorsocentral setae; two pairs of scutellar setae, apical pair cruciate and nearly twice length of anterior pair. WING: Apex broadly rounded, with anal lobe small but distinct; costal vein ending at M_{1+2} ; Sc apically evanescent; R_{4+5} not forked, curved slightly upwards towards costa; cells bm and dm absent; apex of cell br

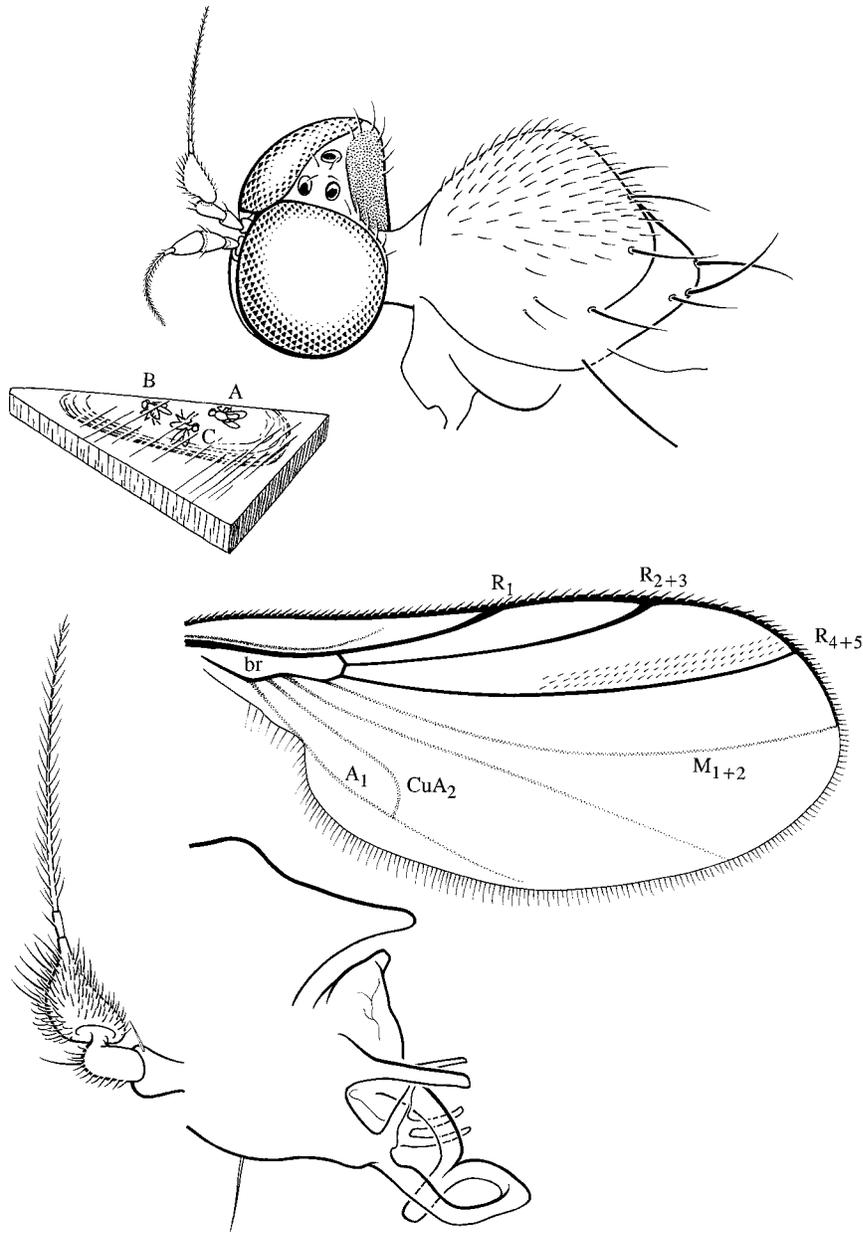


Fig. 24. *Nemedromia campania* (Empididae), with piece showing position of specimen; anterior half of specimen; wing; and details of antenna and genitalia. In Canadian amber (CAS-1091A [CNC]).

formed by short vertical Rs and recurrent r-m with the radial and medial veins closely approximated; CuA₁ arising from cell br; cell cup long, with acute outer angle; anal vein (A₁) evanescent towards wing margin; radial veins and costa darkest, other veins light.

Wing membrane with microtrichia in longitudinal rows; posterior margin with long fine setulae, alternating with shorter setulae. ABDOMEN: Male genitalia with protruding Y-shaped filament.

TYPE: Holotype, ♂, CNC CAS1091A, in

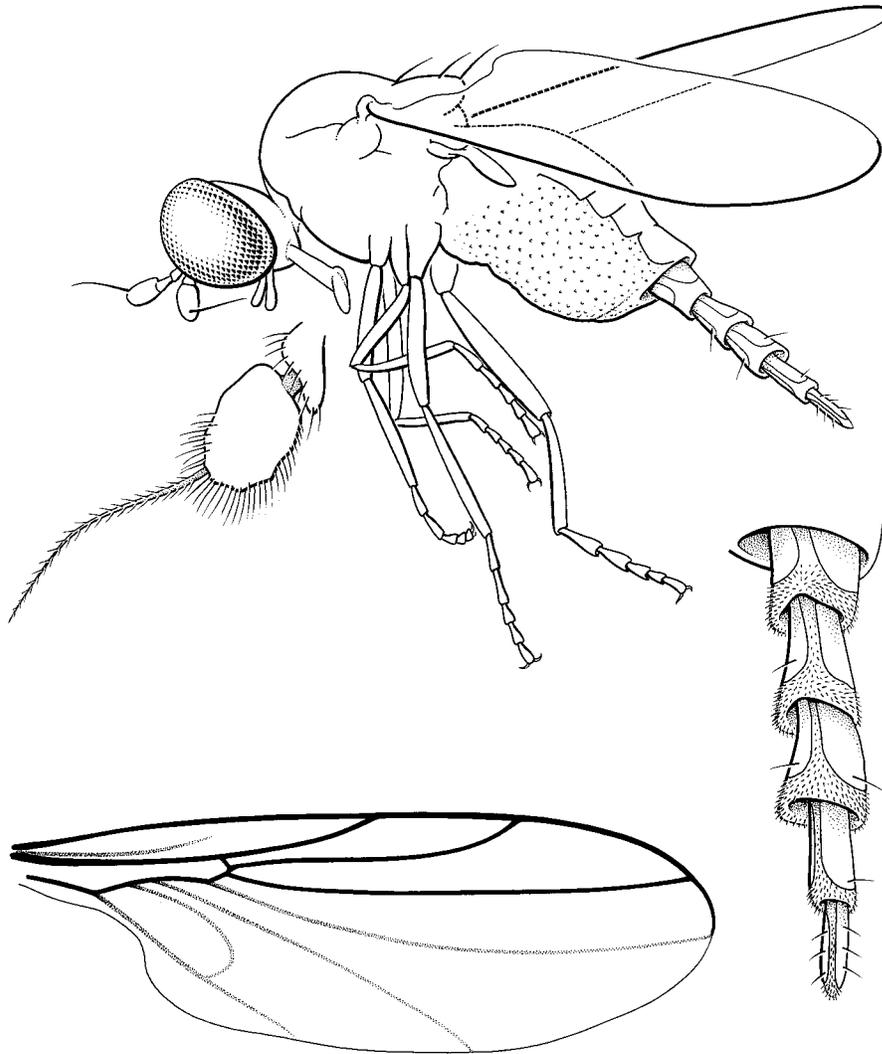


Fig. 25. *Nemedromia telescopica* (Empididae). Lateral habitus, wing, and details of antenna and posterior abdominal segments. In Canadian amber (CAS-920 [CNC]).

Campanian amber from Cedar Lake, Manitoba, collected by J.F. McAlpine. In Canadian National Collection of Insects, Ottawa. Another specimen, MCZ 6907 (not figured), appears to be the same species as CNC CAS1091A.

ETYMOLOGY: Species name in reference to Campanian, the age of the amber deposit in which it was found.

COMMENTS: There are three specimens of *Nemedina*-like flies in piece CAS 1091, which we have labelled A, B, and C (fig. 24).

The genitalia on specimen 1091A are exposed, but some details are obscured due to some distortion of the specimen.

Nemedromia telescopica, new species

Figure 25

DIAGNOSIS: Differs from *N. campania*, n.sp. in the narrower wing, straighter vein R_{4+5} , more strongly arched CuA_2 , and ovoid-shaped basal flagellomere. *Nemedromia telescopica* differs from *N. turonia* n.sp. by the

more closely approximated bases of veins R_{2+3} and R_{4+5} , and the more subapically positioned arista.

DESCRIPTION: Body Length = 1.28 mm; thorax length = 0.38 mm; wing length = 0.87 mm. HEAD: Eyes large, occupying virtually all of head in lateral view (no gena exposed; postgena is obvious); dichoptic (female). Long, slender palps apparent; proboscis fairly long and slender, length $0.7\times$ height of head. Antenna with pedicel scoop-shaped; distal 2 flagellomeres aristate, subapical (dorsally); flagellomere I ovoid, with long, fine setae on apical half; flagellomere II probably present and tiny, but not observed; flagellomere III aristate, with basal half noticeably thicker than apical half, having very fine setulae. THORAX: With few apparent setae: pair of short dorsocentral setae near scutellum; scutellum with 2 pairs of setae. WING: Apex linear and slightly pointed, not broadly rounded; anal lobe small but distinct; costal vein ending at M_{1+2} ; Sc apically evanescent; R_{4+5} not forked, nearly straight; cells bm and dm absent; apex of cell br formed by very short vertical Rs and recurrent r-m with the radial and medial veins closely approximated; CuA_1 arising from cell br; cell cup moderately long, with curved apex formed by strongly arched CuA_2 ; anal vein (A_1 nearly reaching wing margin; radial veins and costa darkest, other veins light. ABDOMEN: Short, stout, but with terminal segments narrow and telescoping, consisting of 4 abdominal segments plus terminal cerci.

TYPE: Holotype, ♀, CNC CAS920, in Campanian amber from Cedar Lake, Manitoba or Medicine Hat, Alberta (not specified), collected by J.F. McAlpine. In Canadian National Collection of Insects, Ottawa.

ETYMOLOGY: In reference to the distinctive telescoping ovipositor of this species.

Nemedromia turonia, new species

Figure 26

DIAGNOSIS: Differs from *N. telescopica* n.sp. by the separated bases of veins R_{2+3} and R_{4+5} , and the apically positioned arista. *Nemedromia turonia* differs from *N. campania* n.sp. in the narrower wing, straighter vein R_{4+5} , more strongly arched CuA_2 , and ovoid-shaped basal flagellomere.

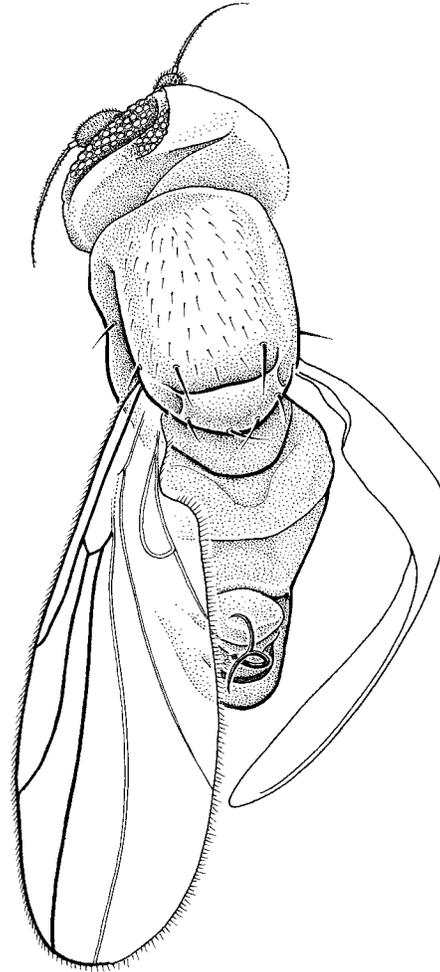


Fig. 26. *Nemedromia turonia* (Empididae). Dorsal habitus of NJ-132, in New Jersey amber.

DESCRIPTION: Body length = 0.72 mm; thorax length = 0.28 mm; wing length = 0.70 mm. HEAD: Eyes apparently holoptic in male. Antenna aristate, with arista terminal; flagellomere I ovoid; flagellomere II small; flagellomere III long aristate with numerous fine setulae. Proboscis not visible. THORAX: With numerous acrostichal and dorsocentral setulae irregularly arranged; one notopleural seta; one supra-alar seta; pair of dorsocentral setae; two pairs of scutellar setae; apical pair cruciate. WING: Apex linear and slightly rounded; anal lobe small but distinct; costal vein ending at M_{1+2} ; Sc not apparent; R_{4+5} not forked, nearly straight; cell

bm and dm absent; apex of cell br formed by short vertical Rs and recurrent r-m with the radial and medial veins closely approximated; CuA_1 arising from cell br; cell cup moderately long, with curved apex formed by strongly arched CuA_2 ; anal vein (A_1) reaching wing margin; radial veins and costa darkest. ABDOMEN: Male genitalia with forked protuberance.

TYPE: Holotype, ♂, AMNH NJ-132, in Turonian amber from White Oaks site, Sayreville, New Jersey, collected by D. Grimaldi.

ETYMOLOGY: Species name in reference to Turonian, the age of the amber deposit in which it was found.

PROLATOMYIA, NEW GENUS

DIAGNOSIS: Head lengthened; eyes narrowly dichoptic in female; antenna with apical arista; proboscis short, projected forward from posterior region of head; thorax long and narrow; hind femur and tibia thickened. Wing narrow; costal vein ending near M_{1+2} ; Sc not observed; R_{4+5} not forked; cells bm and dm absent (bm-cu and dm-cu veins absent); apex of cell br formed by short vertical Rs and recurrent r-m with the radial and medial veins closely approximated; CuA_1 arising from cell br; cell cup open apically with CuA_2 incomplete; anal vein (A_1) evanescent towards wing margin; anal lobe indistinct. Female terminalia greatly lengthened and telescoping, without acanthophorite spines; ultimate segment including cerci approximately twice length of penultimate segment.

TYPE SPECIES: *Prolatomyia elongata*, n.sp. Monotypic.

ETYMOLOGY: From *prolato*, for elongate; and *myia*, for fly, in reference to the extremely lengthened form of this fossil genus.

Prolatomyia elongata, new species

Figure 27

DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 1.89 mm; thorax length = 0.49 mm; wing length = 1.05 mm. HEAD: Lengthened; eyes narrowly dichoptic in female; single row of postocular setae. Antenna aristate, with arista apical; flagellomere I drop-shaped, setulose; flagellomere II not observed; flagellomere III long aristate with numerous fine setulae. Pro-

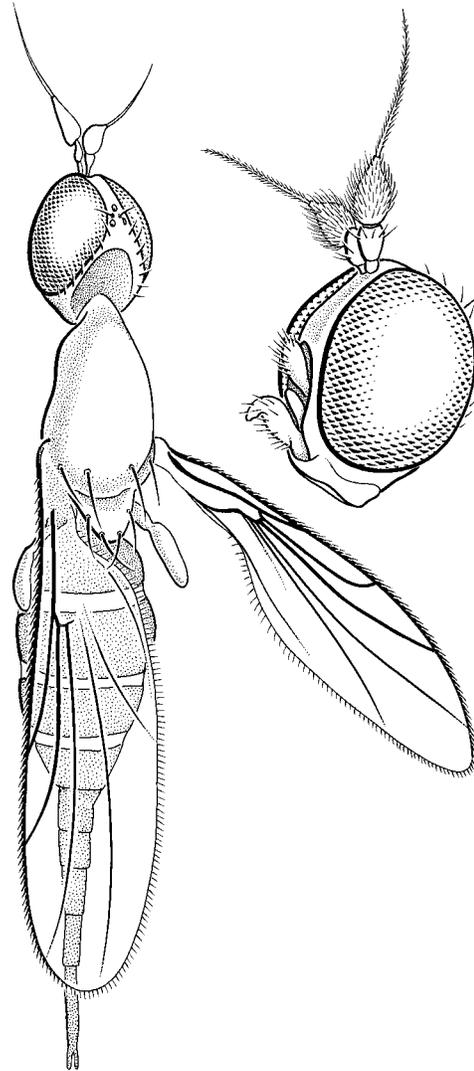


Fig. 27. *Prolatomyia elongata* (Empididae), in Canadian amber (MCZ 6906).

boscis short, projected forward from back of head; palps paddle-shaped, setulose. THORAX: long and narrow, with few apparent setae: one supra-alar seta; pair of dorsocentral setae; two pairs of scutellar setae; apical pair cruciate. Hind femur and tibia thickened. WING: Linear and narrow with apex slightly pointed; anal lobe indistinct; costal vein ending near M_{1+2} ; Sc not apparent; R_{4+5} not forked; cells bm and dm absent; apex of cell br formed by short vertical Rs and recurrent r-m with the radial and medial veins closely

approximated; CuA_1 arising from cell br; cell cup open apically with CuA_2 incomplete; anal vein (A_1) evanescent towards wing margin; radial veins and costa darkest. ABDOMEN: Lengthened; terminal segments of female elongate and narrow, telescoping, without acanthophorite spines; ultimate segment including cerci approximately twice length of penultimate segment.

TYPE: Holotype, ♀, MCZ 6906, in amber from Cedar Lake, Manitoba, collected by F. M. Carpenter, coll.

ETYMOLOGY: Species name in reference to the distinctive, elongate form of this species.

COMMENTS: The wing venation of *Prolatomia elongata* is most similar to that seen in *Nemedromia*, but vein CuA_2 is incomplete so that cell cup remains open apically. The lengthened head, thorax and abdomen easily distinguish this species from other members of the *Nemedina* genus group lineage.

CRETODROMIA, NEW GENUS

DIAGNOSIS: Eyes very large, extensively holoptic in males, dorsal and ventral facets differentiated; antenna with subapical (dorsal) arista; notum strongly humpbacked. Wing with venation reduced; costal vein ending just past M_{1+2} ; Sc incomplete; R_{4+5} not forked; cells bm, dm and cup absent (veins bm-cu, dm-cu, CuA_2 and A_1 absent); apex of cell br formed by short vertical Rs and recurrent r-m with the radial and medial veins closely approximated; CuA_1 arising from base of cell br, nearly reaching wing margin; anal lobe present but small. Male genitalia small, symmetrical and unrotated; epandrium deeply emarginate, medially divided, without articulated surstyli; cerci simple, lobate; hypandrium apparently small; phallus with terminal filament.

TYPE SPECIES: *Cretodromia glaesa*, n.sp. Monotypic. Known only from upper Cretaceous amber of Cedar Lake, Manitoba.

ETYMOLOGY: Derived from Cretaceous and *-dromia* (related to Greek for "runner"), a common suffix of empidid genera.

Cretodromia glaesa, new species

Figure 28

DIAGNOSIS: As for genus.

DESCRIPTION: Total length = 1.75 mm; tho-

rax length = 0.53 mm; wing length = 1.36 mm. HEAD: Large, hemispherical in shape. Eyes very large, occupying nearly entire frontal and lateral part of head; extensively holoptic, for nearly entire length of frons from antennal emargination to anterior ocellus; eyes bare, dorsal and ventral facets very strongly differentiated, dorsal facets $2.5\times$ diameter of ventral facets (same size as ocelli). Inner margin of eye with emargination around bases of antennae. Ocellar triangle on shallow tubercle, with 2 short pairs of setae. Occipital setae not apparent. Antennae with scape very small; pedicel small, cup-shaped; flagellum aristate, with flagellomere I suboval, arista subapical and somewhat dorsal; arista short, ca. $1.8\times$ length of flagellomere I; arista with 2 articles, basal article of arista small. Proboscis not observed. THORAX: Largely dark brown, including legs. Notum very strongly arched, humpbacked; with sparse, short, scattered setae. One pair of fine, erect dorsocentrals present; scutellum with single, apical pair setae; transverse suture laterally very wide, with 3 short notopleural setae just anterior to suture. Legs slender, with only mid tibia unusually long; foretibia with "dimple" near proximal end. Hind femur with dorsal surface having 2 longitudinal rows 12–13 short, spinelike setae; hind tibia slightly thickened, with ventral row ca. 20 short, stiff setae; hind tarsi slightly expanded. WING: Long and moderately narrow, width 0.38 the length; anal lobe small but distinct; venation reduced; costal vein ending just past M_{1+2} ; Sc apically evanescent; R_{2+3} curved upward, R_{4+5} (not forked) and M_{1+2} straight; cells bm, dm, and cup absent (veins bm-cu, dm-cu, CuA_2 and A_1 absent); apex of cell br formed by short vertical Rs and slightly recurrent r-m, with the radial and medial veins closely approximated; CuA_1 arising from base of cell br, nearly reaching wing margin. Halter with very long, thin stem. ABDOMEN: Long and slender, with dark sclerites; tergites with sparse vestiture of short, stiff setae. Male genitalia small, symmetrical, and unrotated; epandrium deeply emarginate, dorsomedially divided, without articulated surstyli; cerci lobate; hypandrium apparently small; phallus with narrow terminal filament.

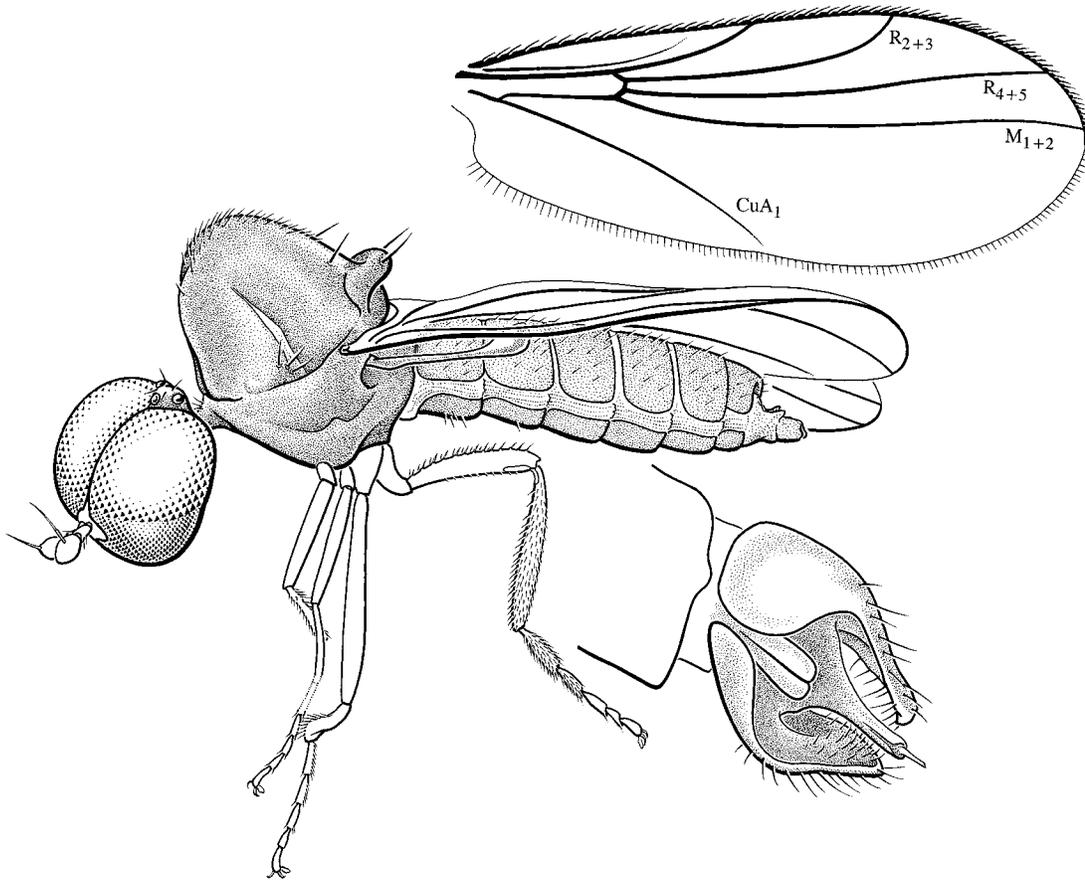


Fig. 28. *Cretodromia glaesa* (Empididae) holotype (MCZ 7097), with wing, and detail of genitalia (dorsal view). Canadian amber.

TYPE: Holotype, ♂, MCZ 7097, in amber from Cedar Lake, Manitoba; collected by F. M. Carpenter.

ETYMOLOGY: From the Latin, *glaesum* (or "amber"), in reference to the fossilization medium.

COMMENTS: *Cretodromia glaesa* is distinguished from other members of the *Nemedina* genus-group lineage by the lack of an anal (cup) cell, including the complete absence of veins CuA_2 and A_1 . In general habitus *Cretodromia glaesa* resembles the male of *Nemedina* described by Sinclair and Arnaud (1998), although the arista is more dorsal, the notum is more strongly arched, and the anal area of the wing (including venation) is much more reduced in *Cretodromia* than *Nemedina*.

NEOTURONIUS, NEW GENUS

DIAGNOSIS: Eyes dichoptic in male and female; antenna with apical arista; proboscis relatively short. Wing with costal vein ending at M_{1+2} ; Sc complete, or apically evanescent; R_{4+5} not forked; cell dm absent (dm-cu vein absent); apex of cell br formed by short, nearly vertical Rs and recurrent r-m, with the radial and medial veins closely approximated; cell bm long and narrow, nearly vertically directed; CuA_1 arising from cell bm; cell cup of moderate length, subequal to length of cell bm, truncate apically; anal vein (A_1 nearly reaching wing margin; anal lobe of small to moderate size. Male genitalia asymmetrical.

TYPE SPECIES: *Neoturonius asymmetricus*, n.sp.

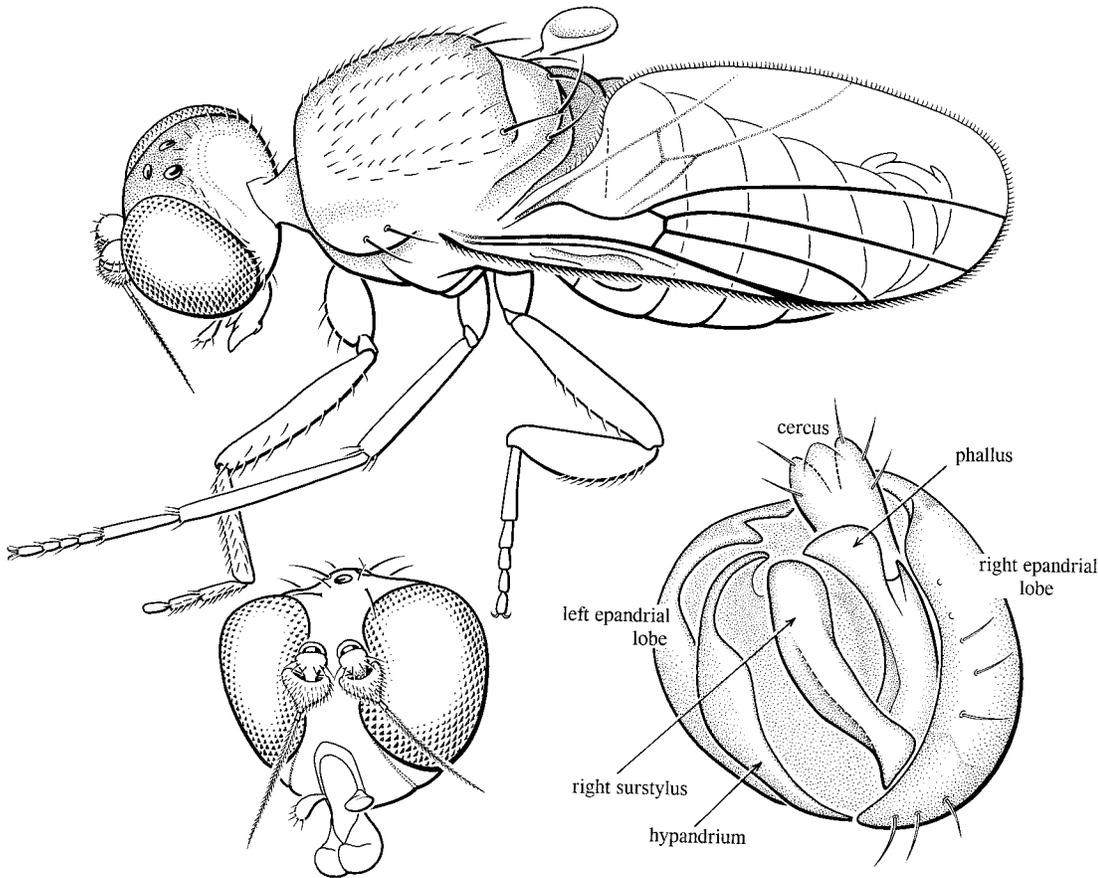


Fig. 29. *Neoturonius asymmetricus* (Empididae). Dorsolateral habitus, frontal view of head, and detail of genitalia (posterior view) of AMNH NJ-90N, in New Jersey amber.

ETYMOLOGY: In reference to the North American origin and age (Turonian) of the amber deposits containing the three included species.

COMMENTS: *Neoturonius* most closely resembles the fossil species *Burmitempis halteralis* described by Cockerell (1917b) from Burmese amber (originally believed to be as young as Miocene, now generally believed to be upper Cretaceous). Both have similar wing venation, including the modified apex of cell br with a short vertical Rs and recurrent r-m (characteristic of the *Nemedina* genus group lineage), in conjunction with a long narrow vertically directed cell bm and truncate anal (cup) cell. However, based on Cockerell's description, *Neoturonius* and *Burmitempis* appear to differ in number of

important respects, including the shape of the anal cell, size of the anal lobe, shape of the antenna, length of the halter, and configuration of the male genitalia. *Burmitempis* has been questionably placed in the Empididae (see Evenhuis, 1994), but appears to belong to the *Nemedina* genus group on the basis of its *Neoturonius*-like wing venation. *Neoturonius* contains at least three species from Turonian amber of New Jersey, and possibly a fourth from Campanian amber of Canada.

Neoturonius asymmetricus, new species

Figure 29

DIAGNOSIS: Differs from *N. cretatus*, n.sp. and *N. vetus*, n.sp. in the more vertically directed vein Rs and the lack of numerous stiff

tarsal setulae on at least the mid legs. Also distinguished from *N. cretatus* n.sp. by an incomplete vein Sc, and from *N. vetus* n.sp. by the lack of a vestige of vein A₂.

DESCRIPTION: Body length = 1.26 mm; thorax length = 0.42 mm; wing length = 0.83 mm. **HEAD:** Male head dichoptic, dorsal and ventral margins of eyes distantly separated. Eyes bare; dorsal and ventral facets undifferentiated in size; frontal margins of eyes slightly emarginate around bases of antennae. Palps and proboscis relatively small. Antenna aristate, with arista apical. Pedicel with base large, narrowed apically. Flagellomere I cordate, microsetulose, broader than pedicel; very small flagellomere II connected to tip of flagellomere I; flagellomere III long, fine, microsetulose. **THORAX:** Notum with acrostichal and dorsocentral setulae arranged in 6 even rows. Pair of short dorsocentral setae present, located near scutellum; scutellum with two pairs of short setae, posterior/apical pair cruciate. Thorax also with pair of notopleural setae on each side. Legs rather stout, with hind tibia slightly crassate. At least midleg with apices of all segments having 2 pairs of setae. Foretibia without gland at base. **WING:** Apex broadly rounded with anal lobe of moderate size; costal vein ending at M₁₊₂; Sc apically evanescent; R₄₊₅ not forked; cell dm absent; apex of cell br formed by short vertical Rs and recurrent r-m, with the radial and medial veins closely approximated; cell bm long and narrow, nearly vertically directed; CuA₁ arising from cell bm; cell cup of moderate length, slightly shorter than length of cell bm, truncate apically; anal vein (A₁) nearly reaching wing margin; cubital and anal veins light, other veins dark. Halter of moderate length, without elongate stem. **ABDOMEN:** Male genitalia asymmetrical, not or barely rotated (artificially displaced); cerci lobate; phallus short; right surstylus digitiform, clasping against hypandrium.

TYPE: Holotype, ♂, AMNH NJ-90N, collected by James Leggett, Paul Borodin, and Gerard Case at the Sunrise Landing Site, East Brunswick, New Jersey. This large piece of amber contained approximately 40 inclusions, including two small specimens of the oldest fossil mushrooms (Hibbett et al., 1995, 1997).

ETYMOLOGY: Name refers to the asymmetrical male genitalia of this species.

COMMENTS: The lack of numerous stiff tarsal setulae on the mid and hind legs of this specimen is possibly a feature associated with males of *Neoturonius*; however, the holotype of *N. cretatus* n.sp. could be a male specimen (gender obscured by milky coating, see below) that possesses short stiff tarsal setulae on the mid leg.

Neoturonius cretatus, new species

Figure 30

DIAGNOSIS: Incompletely preserved specimen, with most of head and body covered with a thick, milky coating. Legs are well preserved and distinctive: mid tarsal segments 1-3 with apical half brownish, slightly expanded, covered with numerous short, stiff setulae in regular rows. Hind legs with femur having small row of 4-5 short, stiff setulae on ventral surface; hind tibiae crassate. Also distinguished from *N. asymmetricus* and *N. vetus* on basis of having a complete vein Sc.

DESCRIPTION: Body length = 1.41 mm; thorax length = 0.45 mm; wing length = 0.84 mm. **HEAD:** Largely obscured by milky coating and loss at surface of amber. Antenna aristate; arista probably apical. **THORAX:** Obscured by milky coating, but with short scutellar setae protruding (pair of cruciate apicals and short pair of subapicals); dorsocentrals/acrostichals not observed. Legs largely dark brown, with proximal halves of some tarsal segments light colored; mid tarsal segments 1-3 with apices slightly expanded, covered with rows of numerous short, stiff setulae. Fore tibia without gland. Hind legs with femur having short row of 4-5 short, stiff setulae on ventral surface; tibiae crassate. **WING:** Apex rounded with anal lobe of moderate size; costal vein ending at M₁₊₂; Sc complete; R₄₊₅ not forked; cell dm absent; apex of cell br formed by short, nearly vertical Rs and recurrent r-m, with the radial and medial veins closely approximated; cell bm long and narrow, nearly vertically directed; CuA₁ arising from cell bm; cell cup of moderate length, subequal to length of cell bm, truncate apically; anal vein (A₁) nearly reaching wing margin; cubital and anal veins light, other veins dark. **ABDOMEN:** Largely obscured by thick milky coating.

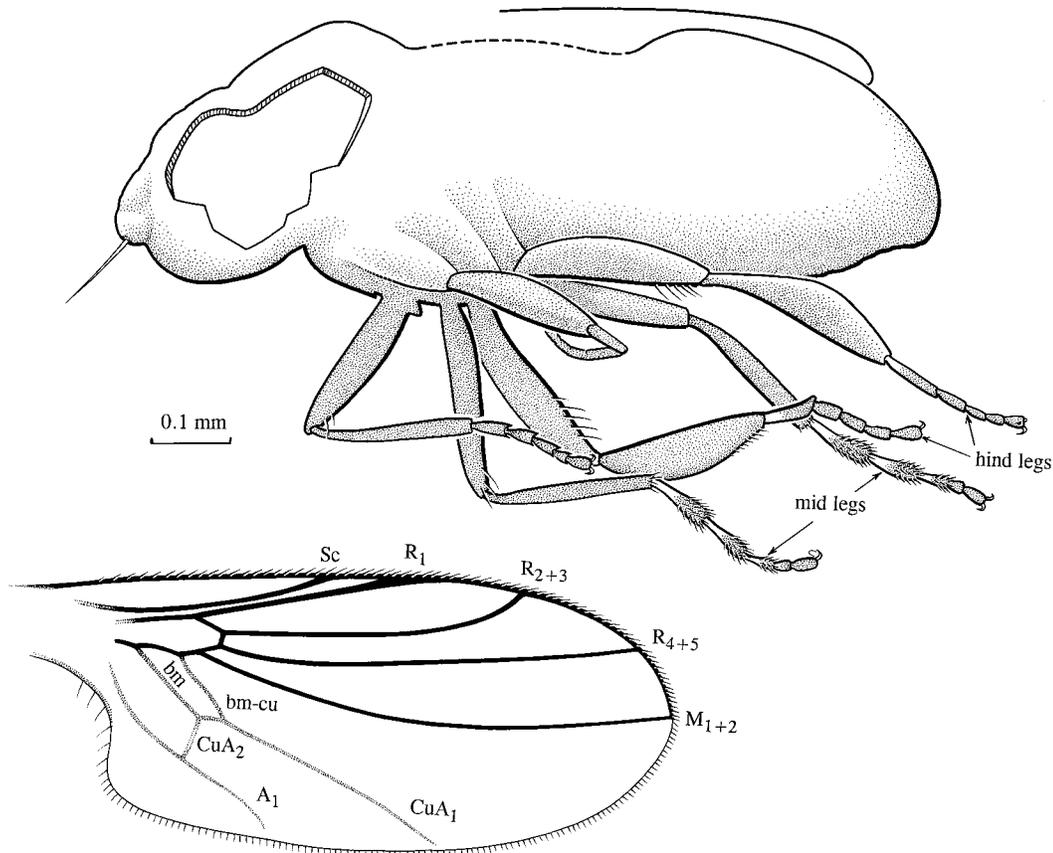


Fig. 30. *Neoturonius cretatus* (Empididae). Wing and entire specimen of AMNH NJ-679, in New Jersey amber. Body is largely covered with a milky coating, except for the legs.

TYPE: Holotype, sex indeterminate, AMNH NJ-679, collected by Keith Luzzi at the White Oaks site, Sayreville, New Jersey.

ETYMOLOGY: In reference to the Cretaceous age of this species.

COMMENTS: Because the abdomen of this specimen is largely shrouded under a coating, the sex cannot be determined with certainty. Since there is not a pointed, long apex of the abdomen (as in PN660), the specimen is likely a male. This species is closely related to *Neoturonius vetus* n.sp., on the basis of tarsal modification, but differences in the tarsi are indicative of different species.

Neoturonius vetus, new species

Figure 31

DIAGNOSIS: Distinguished from *N. asymmetricus* n.sp. and *N. cretatus* n.sp. primarily

on the basis of the apical brushes of setulae on the fore and mid tarsomeres.

DESCRIPTION: Body length = 1.15 mm; thorax length = 0.36 mm; wing length = 0.85 mm. **HEAD:** Partially obscured by milky coating. Female head dichoptic. Proboscis short. Antenna aristate; arista apical to subapical. **THORAX:** Notum with acrostichal and dorsocentral setulae arranged in several even rows. Pair of short dorsocentral setae present, located near scutellum; scutellum with two pairs of short setae, posterior/apical pair cruciate. Legs with apical halves of fore and mid tarsomeres covered in brush of short setulae. Fore tibia without gland. Hind femur without ventral row of 4–5 stiff setae; hind tibia not crassate. **WING:** Apex rounded with anal lobe of small to moderate size; costal vein ending at M_{1+2} ; Sc apically

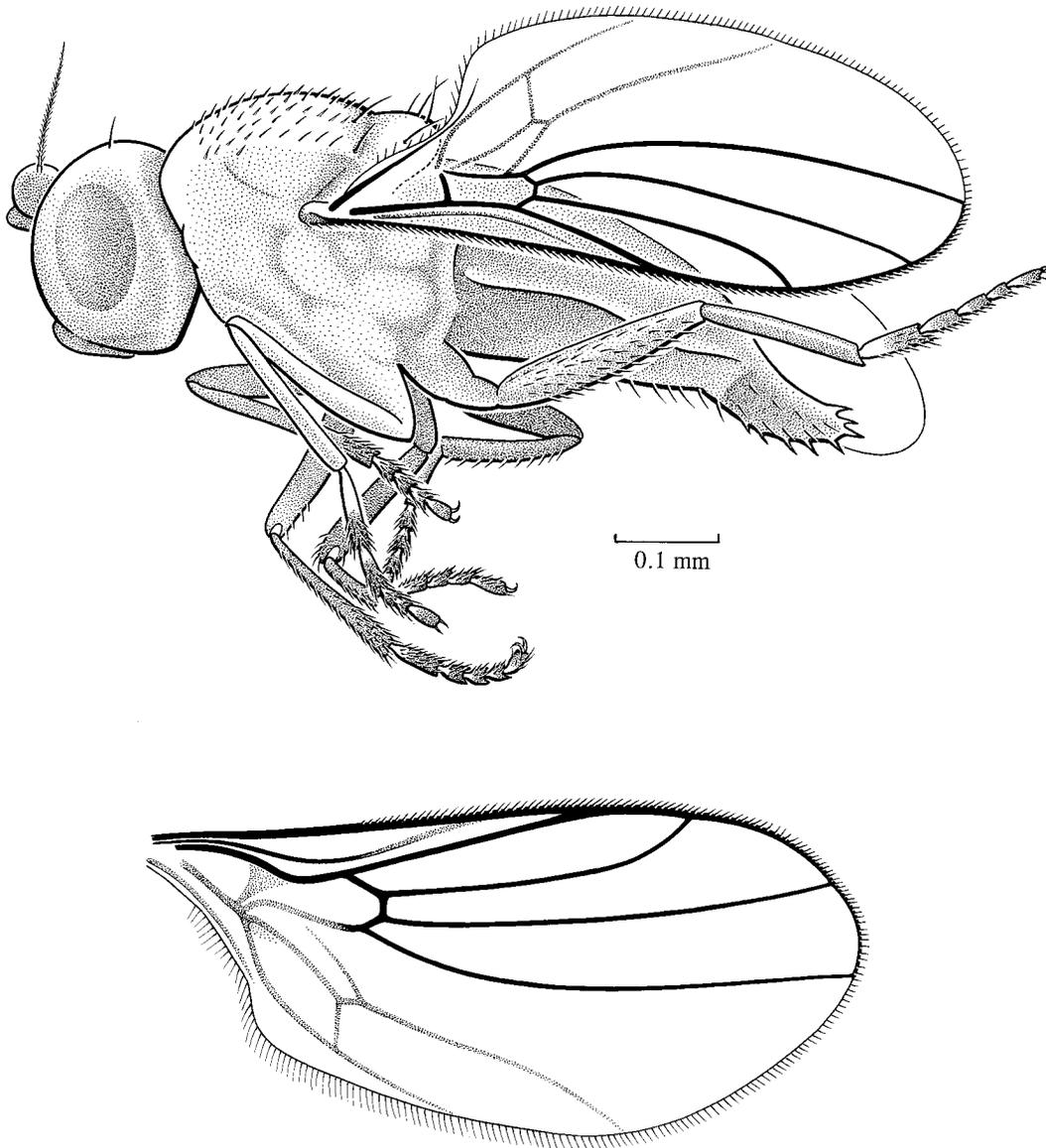


Fig. 31. *Neoturonius vetus* (Empididae). Lateral habitus of AMNH NJ-774, in New Jersey amber. Wing is of CAS 984 (CNC), in Canadian amber and possibly conspecific with *N. vetus*.

evanescent; R_{4+5} not forked; cell dm absent; apex of cell br formed by nearly vertical Rs and recurrent r-m, with the radial and medial veins closely approximated; cell bm long and narrow, nearly vertically directed; CuA_1 arising from cell bm; cell cup of moderate length, subequal to length of cell bm, truncate apically; anal vein (A_1) nearly reaching wing margin; vestige of A_2 present along

wing base; cubital and anal veins light, other veins dark. ABDOMEN: Ovipositor partly obscured by thick milky coating.

TYPE: Holotype, ♀, AMNH NJ-774, collected by Paul C. Nascimbene at the White Oaks site, Sayreville, New Jersey.

ETYMOLOGY: From Latin for "old," in reference to the age of this Upper Cretaceous species.

COMMENTS: It is possible that the very similar, incomplete specimen CAS 984 found in younger, Campanian amber from Canada belongs to this species; however, the wing (fig. 31) is somewhat broader and the anal lobe is smaller.

PHAETEMPIS, NEW GENUS

DIAGNOSIS: Eyes holoptic in male, with dorsal and ventral facets differentiated, dichoptic in female; antenna with short apical arista; proboscis short; notum slightly humped. Wing with costal vein ending at M_{1+2} ; Sc incomplete; R_{4+5} not forked; cell dm absent (dm-cu vein absent); Rs base horizontal; apex of cell br formed by short vertical apex of Rs, and recurrent r-m, with the radial and medial veins closely approximated; M_{1+2} bent upward in middle; cell bm long and narrow, nearly vertically directed; CuA_1 arising from cell bm, nearly reaching wing margin; cell cup of moderate length, subequal to length of cell bm, truncate apically; anal vein (A_1) incomplete; anal lobe large. Male genitalia symmetrical, unrotated; epandrium deeply emarginate, long, bearing marginal row of 5 spinelike setae; cerci small, projected dorsally; hypandrium inconspicuous; phallus appearing biarticulated. Female terminalia without acanthophorites, ending in long pointed cerci.

TYPE SPECIES: *Phaetempis lebanensis*, n.sp. Monotypic.

ETYMOLOGY: Derived from a common suffix for empidid genera, and from Phaeton, of Greek mythology. Unable to control the horses that carried the chariot of his father, the Sun, through the heavens, Phaeton was struck dead by Zeus's thunderbolt, and his body fell into the mythical river Eridanus (probably the Po in northern Italy). Phaeton's sisters wept for him on the banks, and their clothes turned to bark, their feet became rooted, and their tears hardened into droplets of amber.

COMMENTS: In many respects the wing venation of *Phaetempis* resembles that of *Neoturonius*. However, unlike *Neoturonius* and other members of the *Nemedina* group lineage, the apex of cell br (although similarly modified) is more plesiomorphic, with the base of vein Rs positioned horizontally rather than more vertically. *Phaetempis* is also rel-

atively plesiomorphic in retaining cell bm (also in *Neoturonius*), suggesting that if the genus belongs to the *Nemedina* genus group it may be the most basal member of the lineage.

Phaetempis lebanensis, new species

Figures 32, 33

DIAGNOSIS: As for genus.

DESCRIPTION: Total length = 1.80 mm (holotype), 1.60 (paratype); thorax length = 0.51 mm (holotype), 0.56 (paratype); wing length = 1.17 mm (holotype), 1.18 (paratype). HEAD: Rounded, particularly in male. Female with eyes greatly separated; frons with row of 3 fine, short setae near margin of eye. Male eyes holoptic for most of length of frons; dorsal and ventral facets differentiated, dorsal facets approximately twice diameter of ventral ones. Male eyes occupy most of lateral space of head, gena very narrow. Ocelli in both sexes on small tubercle, with pair of small ocellar setae. Antennae with pedicel subspherical; flagellomere I drop-shaped; arista apical, 2-articled, basal aristomere 0.25× length of apical aristomere, arista slightly shorter than length of flagellomere I. Oral margin in male extended deeply dorsad, to base of antennae. Proboscis small, all but labellum largely retracted into oral cavity. THORAX: Notum slightly humpbacked, with pair of short rows of acrostichals (5 per row); no large dorsocentrals, 8–9 setulae per row of dorsocentrals. Row of 4 notopleural setae present. Scutellum with 4 marginal setae, upright and of equal length. Legs slender, unmodified (without tibial gland or raptorial structures). Hind femur in male with dorsal row of ca. 10 fine, stiff setae. WING: Moderately broad, tapered towards apex, with anal lobe large; costal vein ending at M_{1+2} ; Sc apically evanescent; R_{4+5} not forked; cell dm absent; Rs base horizontal; apex of cell br formed by short vertical apex of Rs, and recurrent r-m, with the radial and medial veins closely approximated; M_{1+2} bent upward in middle, where M_2 would diverge if present; cell bm long and narrow, nearly vertically directed; CuA_1 arising from cell bm, incomplete but nearly reaching wing margin (longer in male); cell cup of moderate length, subequal to length of cell bm, trun-

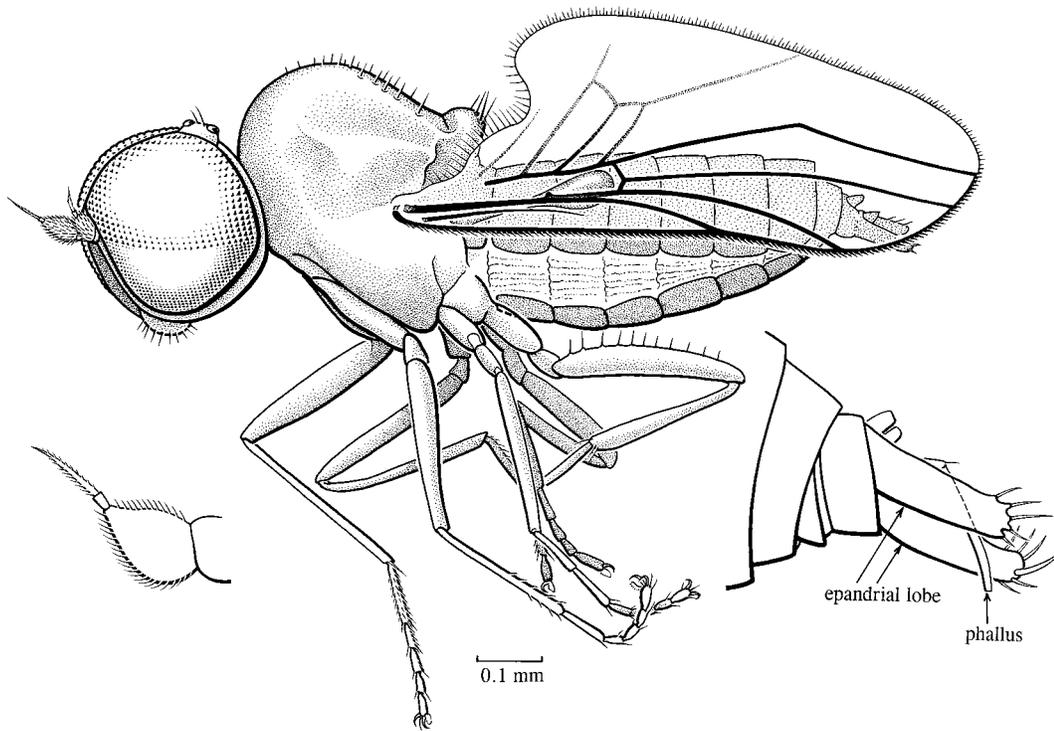


Fig. 32. *Phaetempis lebanensis* (Empididae) holotype (AMNH L-AE13), with detail of antenna and male genitalia (lateral view). Lebanese amber.

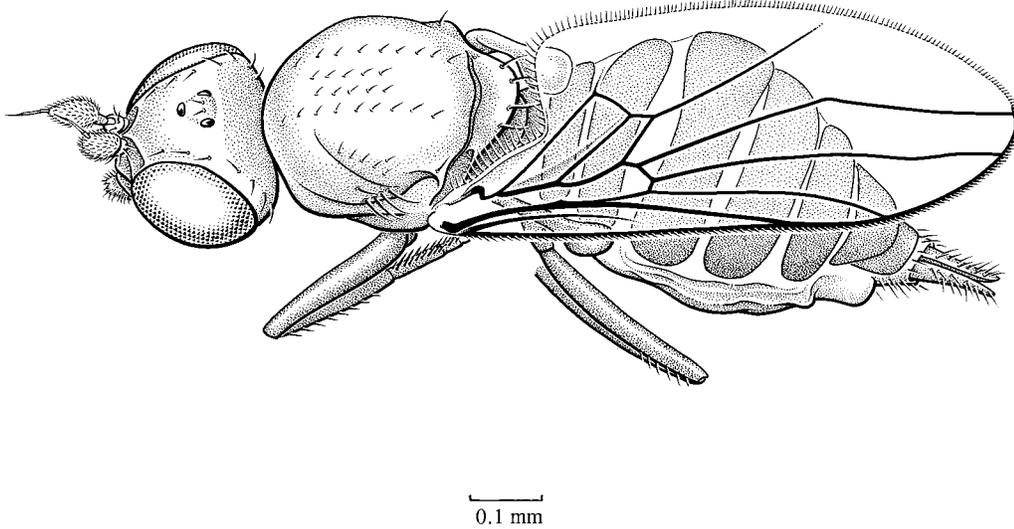


Fig. 33. *Phaetempis lebanensis* (Empididae) paratype (BM Pal. PI II454). Lebanese amber.

cate apically; anal vein (A_1) incomplete and short; vestige of A_2 present. ABDOMEN: Fairly long and slender, apex extended to apex of wing or nearly so. Male genitalia symmetrical, unrotated; epandrium deeply emarginate, lengthened posteriorly, bearing marginal row of 5 spinelike setae; cerci small, projected dorsally; hypandrium inconspicuous; phallus appearing biarticulated, with long terminal filament. Female terminalia without acanthoporphite spines; ending in long pointed cerci.

TYPES: Holotype, ♂, AMNH L-AE13, in Neocomian amber from near Bcharre, northern Lebanon, collected by Antoni Estephan. Paratype, ♀, BM Pal. PI II454, in Lebanese amber from near Jezzine, Aftim and Fadi Acra coll. (JS-276-G/3); paratype in Dept. Palaeontology, Natural History Museum, London.

ETYMOLOGY: Referring to Lebanon, source of the amber.

COMMENTS: The NHM specimen is the one which is referred to by Poinar (1992) as a chloropid and "the oldest known representative of the schizophoran (muscid)[sic] Diptera" (p. 184). Poinar cited a 1981 report on the Acra collection of Lebanese amber, written by P.E.S. Whalley of the NHM and which had actually never been published. This is an example of how a serious error becomes propagated without careful study of the specimen.

HYBOTID LINEAGE

GENUS *TRICHINITES* HENNIG

Trichinites Hennig, 1970: 7. Monotypic, by original designation.

DIAGNOSIS (extracted from Hennig, 1970): Arista longer than flagellomere I, with 2 (possibly 3) articles; fore tibial gland absent; notum with 4 irregular rows of acrostichal and dorsocentral setulae, 2 pairs of larger dorsocentral setae; wing with costal vein ending beyond apex of M_1 ; Sc incomplete; R_{4+5} not forked; dm cell with veins M_1 , M_2 and CuA_1 branching separately off apex of dm cell, reaching wing margin; cell cup moderately long, subequal to length of cell bm, truncate apically; anal vein (A_1) reaching wing margin; anal lobe large; terminal segments of female telescoping, without acanthoporphite spines, cerci long.

TYPE SPECIES: *Trichinites cretaceus* Hennig. Holotype and only known specimen is a female in Neocomian amber from near Jezzine, Lebanon, in the Staatliches Museum für Naturkunde, Stuttgart (no number for the specimen was provided). We did not examine this specimen.

COMMENTS: *Trichinites* was considered by Hennig (1970) to belong to the stem group of the hybotid lineage, primarily because of similar apomorphies in the wing venation (e.g., abbreviated C, incomplete Sc, and R_{4+5} unforked), and the lack of the fore tibial gland (found in all members of the hybotid lineage proper). Interestingly, the length and shape of the anal (cup) cell in the most basal *Nemedina* group genera, *Phaetempis* and *Neoturoni*, and the earliest known hybotine genus, *Pseudoacarterus* (Waters, 1989), resembles that observed in *Trichinites*, suggesting that this is the plesiomorphic form of the anal cell in the Empidoidea (see discussion in Hennig, 1970; Chvála, 1983).

SUBFAMILY TACHYDROMIINAE

GENUS *CRETOPLATYPALPUS* KOVALEV

Cretoplatypalpus Kovalev, 1978: 72 (original, Russian version), p. 351 (English translation). Monotypic.

DIAGNOSIS: Extracted from Kovalev's description: Eyes bare, dichoptic in both sexes; inner margin of eyes emarginate at bases of antennae; antenna aristate, with flagellomere I "flattened, pointed-pyriform" (drop-shaped), arista apical and 2-segmented; proboscis projecting ventrad. Prosternum free; propleuron narrow; acrostichal and dorsocentral setae undifferentiated, but with several larger, prescutellar setae; scutellum with 3 pairs setae. Mid femur with single, longitudinal row of spinelike setae on ventral surface. Wing with Sc incomplete; anal vein faint but present; anal cell closed.

TYPE SPECIES: *C. archaeus* Kovalev. Known from male and females in two amber pieces (PIN 3426/206 and 3426/208) from Ust'-Yenisey, on the right bank of the Nizhnyaya River, some 40 km below its source, western part of the Taymyr peninsula, northern Siberia. This deposit is reported as the Dolganian Formation, and understood to be upper Cenomanian in age, making this species the oldest tachydromiine.

Cretoplatypalpus americanus, new species

Figure 34

DIAGNOSIS: Differs from *C. archaeus* by the following features: flagellomere I drop shaped, bilaterally symmetrical; posterior pair of ocellar setae slightly longer than (vs. $0.5\times$ length of) anterior pair; emargination of eyes at base of antennae rounded (vs. wedge-shaped); wing narrower (width $0.37\times$ the length, vs. $0.42\times$ in *archaeus*), with anal lobe present; R_{2+3} longer, reaching closer to wing tip; R_{2+3} , R_{4+5} and M_{1+2} straight and virtually parallel; br and bm cells of equal width (cell br $0.5\times$ width of bm in *archaeus*); CuA_1 evanescent just before wing margin (vs. complete); m-cu nearly perpendicular to longitudinal veins (vs. acute); A_1 present, directed toward tip of CuA_1 but evanescent very close to wing margin. Male genitalia: in *americanus* the cerci are smaller, epandrium not divided as deeply, apices of surstyli not toothlike.

DESCRIPTION: Body length = 1.59 mm; thorax length = 0.51 mm; wing length = 1.48 mm. HEAD: Rounded. Eyes bare, narrowly dichoptic in male (female unknown), width of separation $0.3\times$ width of median ocellus; inner margins at bases of antennae emarginate (semi-circular). Two pairs ocellar setae present, posterior ones slightly longer than anterior ones; numerous fine, stiff, erect setae on vertex. Antenna aristate; pedicel cup-shaped, with ring of fine setae on apical margin; flagellomere I elongate, drop-shaped, bilaterally symmetrical, with slightly longer setulae on ventral surface; arista 2-articled, basal segment very small, length of arista $1.7\times$ length of flagellomere I. Proboscis well developed, projecting ventrad, length of exposed portion $0.7\times$ height of eye; palp long and thin, length $0.5\times$ length of exposed portion of proboscis, with long setae on dorsal surface. THORAX: Setae on notum without differentiated acrostichals and dorsocentrals (setae scattered); mid femur with ventral row of spinelike setae; scutellum with 3 pairs of marginal setae. Sternal area of thorax not observable. WING: Narrow, width $0.37\times$ the length; costal vein reaching to apex of M_{1+2} ; Sc evanescent, but nearly reaching C; position of crossvein h at midpoint of cell br; R_1 straight, meeting C at $0.6\times$ length of wing;

R_{2+3} , R_{4+5} and M_{1+2} straight and virtually parallel (R_{2+3} slightly upturned apically); bases of R_{4+5} and M_{1+2} connected to distal wall (r-m) of cell br; br and bm cells of equal width; M_{3+4} evanescent just before wing margin; m-cu nearly perpendicular to longitudinal veins, not slightly acute to them; anal lobe well developed, A_1 present, directed toward tip of M_{3+4} but evanescent very close to wing margin. ABDOMEN: Male genitalia: Rotated 45° ; cerci small, fused, unsclerotized; epandrium divided dorsally about one-half length of epandrium; apices of surstyli not toothlike.

TYPE: Holotype, ♂, MCZ 6914, in amber of Campanian age from Cedar Lake, Manitoba, collected by W. C. Legg.

ETYMOLOGY: In reference to North American.

COMMENTS: Kovalev (1978) discussed the systematic position of *Cretoplatypalpus*, particularly with respect to *Archiplatypalpus* (in slightly younger Siberian amber), and the plesiomorphic, extant tachydromiine genera *Platypalpus* Macquart and *Symballophthalmus* Becker. Earlier (1974) he discussed the position of *Archiplatypalpus* as the most basal lineage in the tribe Tachydromiini, exclusive of *Symballophthalmus*. In his 1978 paper he hypothesized *Cretoplatypalpus* as being even more primitive than *Symballophthalmus*, and representing the ground plan of the tribe.

Despite the apparently older age of the Siberian *Cretoplatypalpus*, there are features of the American species that are plesiomorphic to the Siberian one, in particular the presence of an anal lobe and more distinct anal vein. Unfortunately, the prosternum cannot be observed in the Canadian amber specimen, but it is probably free. Kovalev used the age of the Mesozoic fossils to polarize the character states in scutellar seta numbers, with 3 pairs being plesiomorphic and 2 pairs apomorphic (see discussion below, under *Mesoplatypalpus*).

The genus *Electrocyrtoma* Cockerell (1917a; monotypic: *burmanica* Cock.), known from Burmese amber of presumed lower Tertiary to upper Cretaceous age, apparently is related to this group of Mesozoic genera of tachydromiines. *Electrocyrtoma* possesses 7 or more scutellar setae.

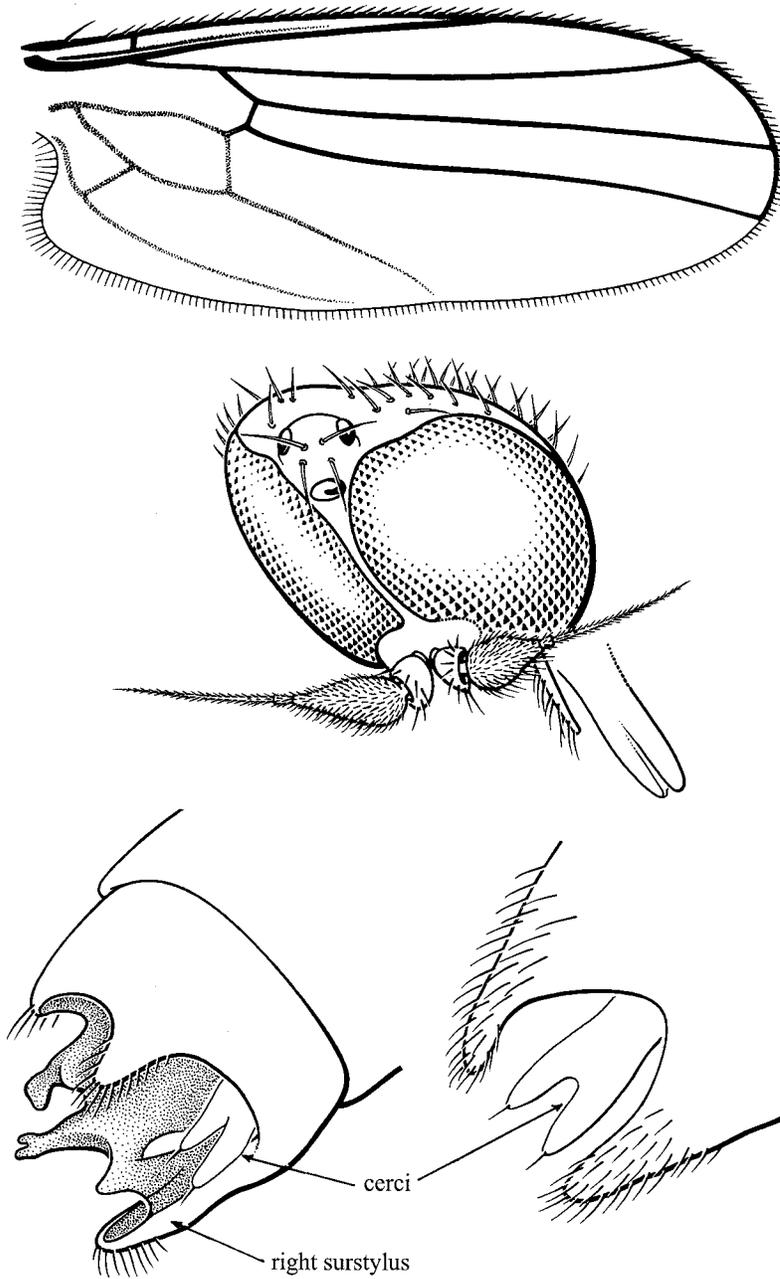


Fig. 34. *Cretoplatypalpus americanus* (Empididae) holotype (MCZ 6914), showing dorsolateral view of head, wing, and details of genitalia. In Canadian amber.

GENUS *ARCHIPLATYPALPUS* KOVALEV

Archiplatypalpus Kovalev, 1974: 84 (original, Russian version), p. 196 (English translation version).

DIAGNOSIS: Extracted from Kovalev (1974) as: Eyes bare, holoptic [a principal character subsequently used to distinguish *Archiplatypalpus* from *Cretoplatypalpus*], with emargination at bases of antennae; two pairs of ocellar setae; vertical setae hardly distinguishable from other occipital setae; probasisternum free; acrostichals and dorso-centrals not differentiated; mid femur with single longitudinal row of spinelike setae on ventral surface; scutellum with 2 pairs setae.

TYPE SPECIES: *A. cretaceus* Kovalev, known from two male specimens in a piece of amber (PIN 3130/15) from Yantardakh ("amber mountain"), mouth of Maimecha River, eastern part of the Taymyr Peninsula, northern Siberia. This deposit is the Kheta suite, dated as Coniacian to lower Santonian.

COMMENTS: This genus is known only from the type species in Siberian amber.

MESOPLATYPALPUS, NEW GENUS

DIAGNOSIS: Distinguished from other genera of Tachydromiinae (including Cretaceous genera *Cretoplatypalpus* and *Archiplatypalpus*) by C ending just slightly past apex of R_{4+5} ; reduced anal lobe without veins A_1 or CuA_2 present (cell cup absent); eyes narrowly dichoptic in female; scutellum with 8 setae.

TYPE SPECIES: *Mesoplatypalpus carpenteri*, n.sp. Monotypic. From upper Cretaceous amber of Cedar Lake, Manitoba.

ETYMOLOGY: Referring to Mesozoic, with a suffix common to other Cretaceous genera of the subfamily.

Mesoplatypalpus carpenteri, new species

Figure 35

DIAGNOSIS: As for genus.

DESCRIPTION: Body length: 2.01 mm; thorax length = 0.62 mm; wing length = 1.41 mm; HEAD: Rounded. Eyes bare, large, with virtually no exposed gena; posterior margin slightly emarginate; narrowly dichoptic (known only for female). Antenna aristate; flagellomere I a long, irregular triangle, length $1.5\times$ greatest width, ventral margin

slightly irregular; two articulated arista, basal aristomere very short, apical aristomere only slightly longer than flagellomere I and with minute microtrichia. Setae on head either dislodged, or most originally absent, including ocellars. Proboscis projecting ventrad, exposed portion $0.65\times$ height of eye. THORAX: Notum dome-shaped, but not hump-backed, with acrostichal/dorsocentral setae on posterior half. Row of 4 short, stiff supralar setae present. Scutellum with 4 pairs short setae. Legs relatively short and unmodified, forelegs longest; none of the legs raptorial. Foretibia slightly thicker than fore femur, with dorsal surface having row of ca. 20 short, stiff setae; slight indentation on apical half of dorsal surface possibly indicates presence of tibial gland. WING: C ending just slightly past apex of R_{4+5} ; Sc evanescent, incomplete for apical eighth of its length; R_1 meets C at approximately midpoint of wing, pterostigma absent; R_{2+3} straight, not curved; veins R_{4+5} and M_{1+2} originating directly off apex of br cell, both veins slightly convergent at apex of wing, not divergent nor slightly upturned; br and bm cell of approximately equal length, bm cell twice the width of br cell; CuA_1 evanescent, not quite reaching margin of wing; anal lobe reduced, veins A_1 and CuA_2 absent. ABDOMEN: Six standard tergites visible in female, seventh ring-like, with oviscapt long and pointed.

TYPE: Holotype, ♀, MCZ 6911, in amber from Cedar Lake, Manitoba, collected by W. C. Legg.

ETYMOLOGY: Patronym, for the late Frank M. Carpenter, professor at the Museum of Comparative Zoology for nearly 65 years; in recognition of his status as dean of American paleoentomology and his pioneering efforts in the study of Canadian amber.

COMMENTS: *Mesoplatypalpus carpenteri* exhibits an apparent plesiomorphic number of scutellar bristles (8) like other Mesozoic tachydromiine genera (6–7) and the primitive extant tachydromiine genus *Symballophthalminus* (6). Based on outgroup comparison with several groups of Ocydromiinae (particularly the similar tribe Oedaleini), 6–8 scutellar bristles would appear to be the plesiomorphic number for the Tachydromiinae. Unlike these basal tachydromiine genera, however, *Me-*

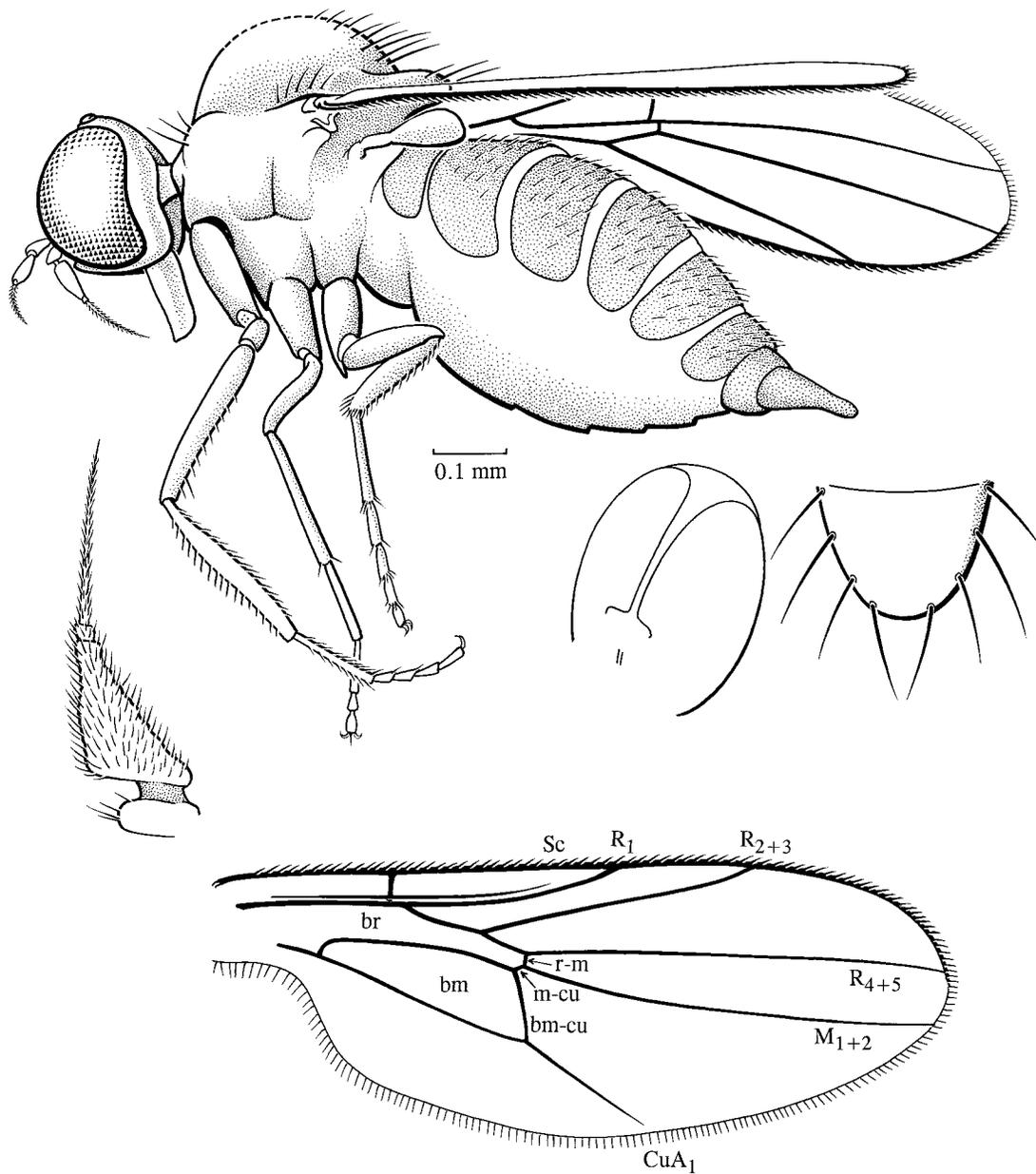


Fig. 35. *Mesoplatypalpus carpenteri* (Empididae) holotype (MCZ 6911), with detail of antenna, oblique frontal view of head, dorsal view of scutellum, and wing. In Canadian amber.

soplatypalpus has a more derived wing that completely lacks an anal (cup) cell. Unfortunately, it is not known whether the prosternum of *Mesoplatypalpus* is free (plesiomorphic) or is fused to the proepimeron (derived), which would help resolve whether the

genus is related to one of the basal genera, or more closely related to other members of the tribe Tachydromiini, such as *Platypalpus*, *Charadrodromia* Melander, *Dysaletria* Loew, *Tachypeza* Meigen, *Tachydromia* Meigen, and *Tachyempis* Melander.

SUBFAMILY TRICHOPEZINAE
GENUS *APALOCNEMIS* PHILIPPI

Apalocnemis Philippi, 1865: 752. By original designation.

DIAGNOSIS: Antenna aristate; flagellomere I short, arista apical and long; eye completely bare; proboscis length variable, sometimes sexually dimorphic and shorter in male, perpendicular in female. Wing with Sc apically evanescent; R_{4+5} forked; dm cell with veins M_1 , M_2 and CuA_1 branching separately off apex of dm cell; cell bm and cup short, subequal in length, with CuA_2 recurved; anal vein (A_1) evanescent; anal lobe large. Female terminalia with acanthophorites; female cercus pointed, upright.

TYPE SPECIES: *Apalocnemis obscura* Philippi, 1865. By monotypy. An extant species from Chile.

Apalocnemis canadambris, new species

Figure 36

DIAGNOSIS: Fits broadly into either of Collin's (1933) *Apalocnemis* groups C or D, which are separated from each other (pp. 74–75) primarily on the basis of male mouthparts. *Apalocnemis canadambris* differs from the extant species in these groups by possessing a shorter, more truncate acanthophorous ovipositor.

DESCRIPTION: Total length = 1.76 mm.; thorax length = 0.59 mm; wing length = 1.83 mm. Body largely dark brown, legs light colored. HEAD: Rounded. Eyes bare, large, occupying most of lateral part of head (gena virtually gone), with slight emargination on inner margins around bases of antennae. Antenna with long, terminal arista; flagellomere I subtriangular, with long fine setulae on ventral surface; arista 2-articled, basal article short ($0.35\times$ length of flagellomere I), apical article $3.5\times$ length of flagellomere I, with microtrichia slightly longer than thickest width of aristal trunk. Face bare; oral margin of face slightly projecting, with small median point flanked by two other points. Proboscis thick, length approximately equal to diameter of eye, with distinct labelum having long, fine setae; labrum large, apparently convex, hypopharynx also apparent and equal to full length of proboscis. Head setae: pair of long, lateroreclinate ocellars;

proclinate postocellars; and series of verticals, postverticals, and postoculars. Head distinctly distant from thorax, on long neck [preservational artifact?]. THORAX: Notum strongly hump-backed, with numerous long acrostichal and dorsocentral setae; antepnotum with row of fine setae; anterior face of notum with pair of short, stiff setae pointed directly forward; postpronotal lobe with very long, upright seta; anepimeron with row of 3 stiff setae, directly below wing base; scutellum with two pairs setae, apical pair cruciate. Legs long, slender, bristly. Empodium either lost or very small and setiform. Foreleg: coxa with ventral row of 4 setae, tibia with 2 dorsal and preapical ventral setae; tarsomere 2 twice length of distal tarsomeres. Midleg: tibia with 3 dorsal setae, 3 preapical setae. Hindleg: femur slightly thickened (width twice that of tibia), with dorsal row of ca. 12 setae (length of longest one equal to width of femur), ventral row of shorter setae; tibia with dorsal row ca. 15 short, stiff setae, lateral setulae in 2 longitudinal rows. WING: Relatively broad, width $0.4\times$ length. All veins bare (without setulae). Costal vein obscure beyond apex of R. Sc evanescent, not reaching C. R_1 straight, meets C at midpoint of wing, no pterostigma at apex of this vein. R_{2+3} virtually straight; base of R where R_{2+3} branches off is slightly thickened, this trunk much thinner basally. R_{4+5} deeply forked; branch of R_5 ending in apex of wing, this branch $0.75\times$ length of main trunk of R_{4+5} , with branches divergent. Cell dm narrow; length $0.6\times$ that of distal section of M_1 ; width of cell $0.25\times$ length. Cells bm and cup of equal length, vein CuA_2 curved. Anal veins absent; anal lobe large. ABDOMEN: Relatively short, extended (in female) to about midlength of wing. Female terminalia short, truncate; tergite VII with a few large setae along posterior margin; tergite VIII short; tX larger, with row of 8 acanthophorite spines on inner and posterior margin. Cercus small, with nipple-shaped apex and subapical seta. Sternite X small, just ventral to cercus, with 3–4 setae on posterior margin.

TYPE: Holotype (and only known specimen), a superbly preserved ♀, MCZ 6908, in amber from Cedar Lake, Manitoba, W. C. Legg collector.

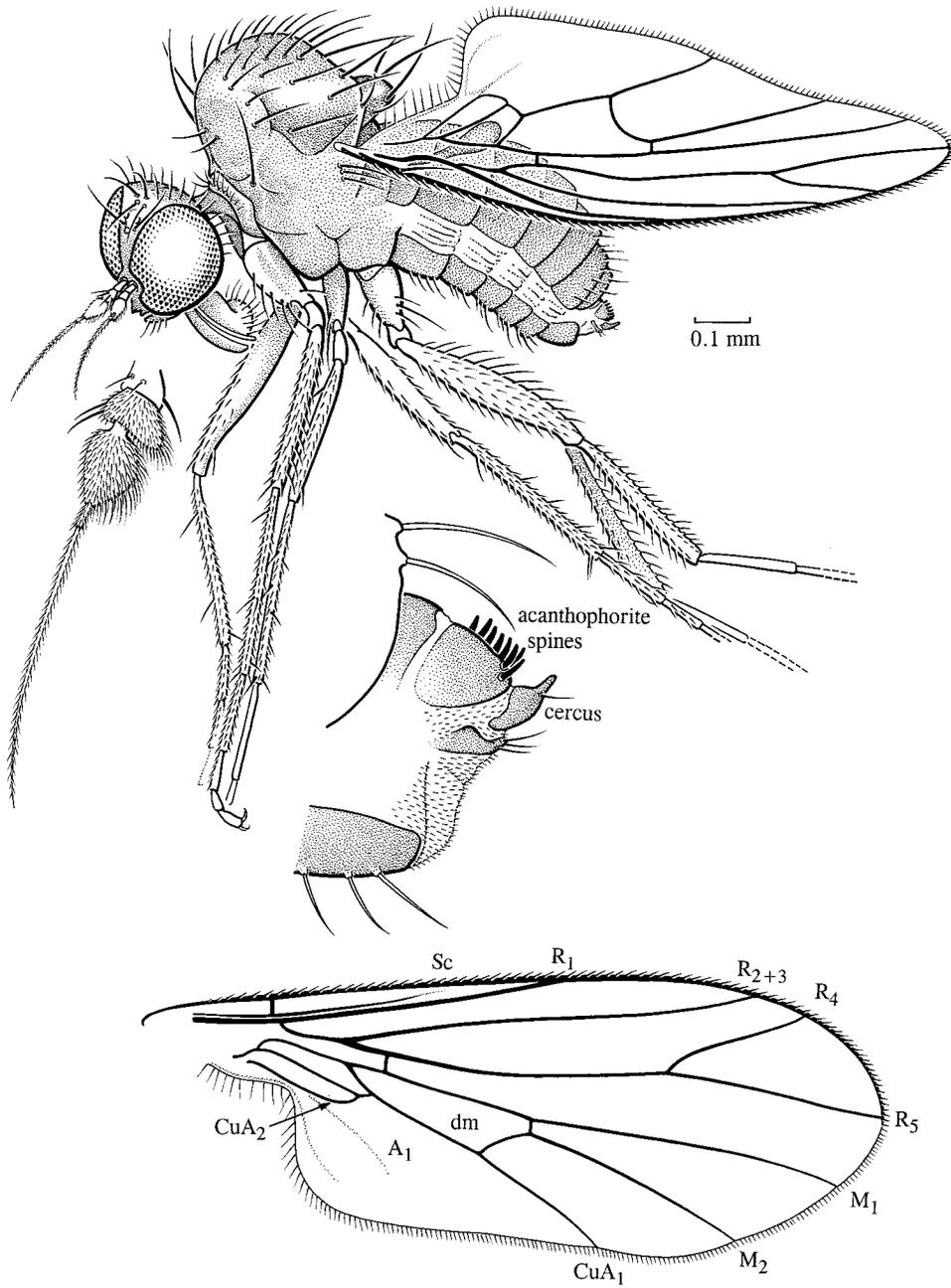


Fig. 36. *Apalocnemis canadambri* (Empididae) holotype, with detail of antenna, wing, and female genitalia (lateral view). MCZ 6908, in Canadian amber.

ETYMOLOGY: The name combines Canada and amber.

COMMENTS: *Apalocnemis* is one of the most basal lineages of the subfamily Trichopezinae (Sinclair, 1995), so it should not seem too surprising to find a Cretaceous representative of this extant genus. The truncate form of the ovipositor in *A. canadambri* is presumably plesiomorphic for the genus.

SUBFAMILY MICROPHORINAE

TRIBE MICROPHORINI

GENUS *MICROPHORITES* HENNIG

Microphorites Hennig, 1971: 16. By original designation.

DIAGNOSIS: Extracted from Hennig, as follows: Distinguished from *Microphor* Macquart and *Schistostoma* Becker by the small, rounded anal lobe of wing; from *Microphorella* Becker and *Parathalassius* Mik by antennae located near the middle of anterior margins of the eyes, arista 2-articled, bm-cu crossvein complete, and eye bare. Except for the small anal lobe, these features are inclusive of the ground plan of the Empidoidea, and illustrate the plesiomorphic nature of this genus. Hennig (1971) hypothesized *Microphorites* to be close to the ground plan of the Microphorinae.

TYPE SPECIES: *M. extinctus* Hennig. Holotype and only known specimen is a female in Lebanese amber, no. 32/59 in the Staatliches Museum für Naturkunde, Stuttgart.

COMMENTS: The condition of the male terminalia of *Microphorites* is presumed to be rotated and lateroflexed to the right like all other microphorines and dolichopodids (Cumming et al., 1995). This is verified by the discovery of the male of *Microphorites oculus*, n.sp., described below, assuming this species (with only partially visible wings) is assigned to the correct genus (see comments in description below).

Sinclair (1995) hypothesized the presence of acanthophorite spines in the ground plan of female microphorine terminalia, given their presence in *Schistostoma*, *Parathalassius*, *Microphorella*, and outgroup taxa including Dolichopodidae. Based on examination of new material of *Microphorites similis*, n.sp. described below, where the type and only specimen has the terminalia slightly extruded), obvious acanthophorite spines ap-

pear absent, as Hennig (1971) indicated for the damaged abdomen of *M. extinctus*. However, acanthophorite spines are represented in the extant genus *Microphor* by slender setae arranged in a pattern indicative of their reduction (see Sinclair, 1995, p. 718). This form of reduction may be the condition in *Microphorites*. Well-developed acanthophorite spines are also present in *Archichrysotus manitobus*, n.sp., described below. All other microphorines discussed here are males.

The three species assigned to *Microphorites* are all from Neocomian amber of Lebanon.

Microphorites similis, new species

Figure 37

DIAGNOSIS: Similar in most respects to *Microphorites extinctus*, differing as follows: Flagellomere I slightly shorter (length $1.7\times$ greatest width, vs. $1.9\times$ in *M. extinctus*); costal vein ends at apex of R_{4+5} (vs. circumambient in *M. extinctus*); dm-cu not arched, but angulate; bm and cup cells smaller, m-cu crossvein much shorter; vertical base of M_2 slightly longer; notopleural setae not differentiated from acrostichals/dorsocentrals. Differs from *M. oculus*, n.sp. primarily in the shorter and less abruptly tapered flagellomere I.

DESCRIPTION: Body length = 1.42 mm; thorax length = 0.63 mm; wing length = 1.23 mm. Known only from female holotype. HEAD: Hemispherical; eyes bare, large, deep, with virtually no gena exposed. Antenna aristate, arista apical; pedicel cup-shaped, with marginal ring of fine setae; flagellomere I drop-shaped, proximal end bulbous, tapered apically to narrow point, ventral surface with long fine setulae; arista with small basal article, apical article long and fine, with fine microtrichia having lengths approximately equal to width of arista trunk; arista $2\times$ length of basal flagellomere. Palp projecting beyond oral margin; proboscis largely visible, with fairly long labellum, hypopharynx and labrum visible laterally, clypeus not visible. Postgena extensively haired. THORAX: Notum moderately arched; acrostichal and dorsocentral setae differentiated, with two median rows acrostichals (ca. 6 setae per row); ca. 6 dorsocentral setae per row, posteriormost setae longest, then next most pos-

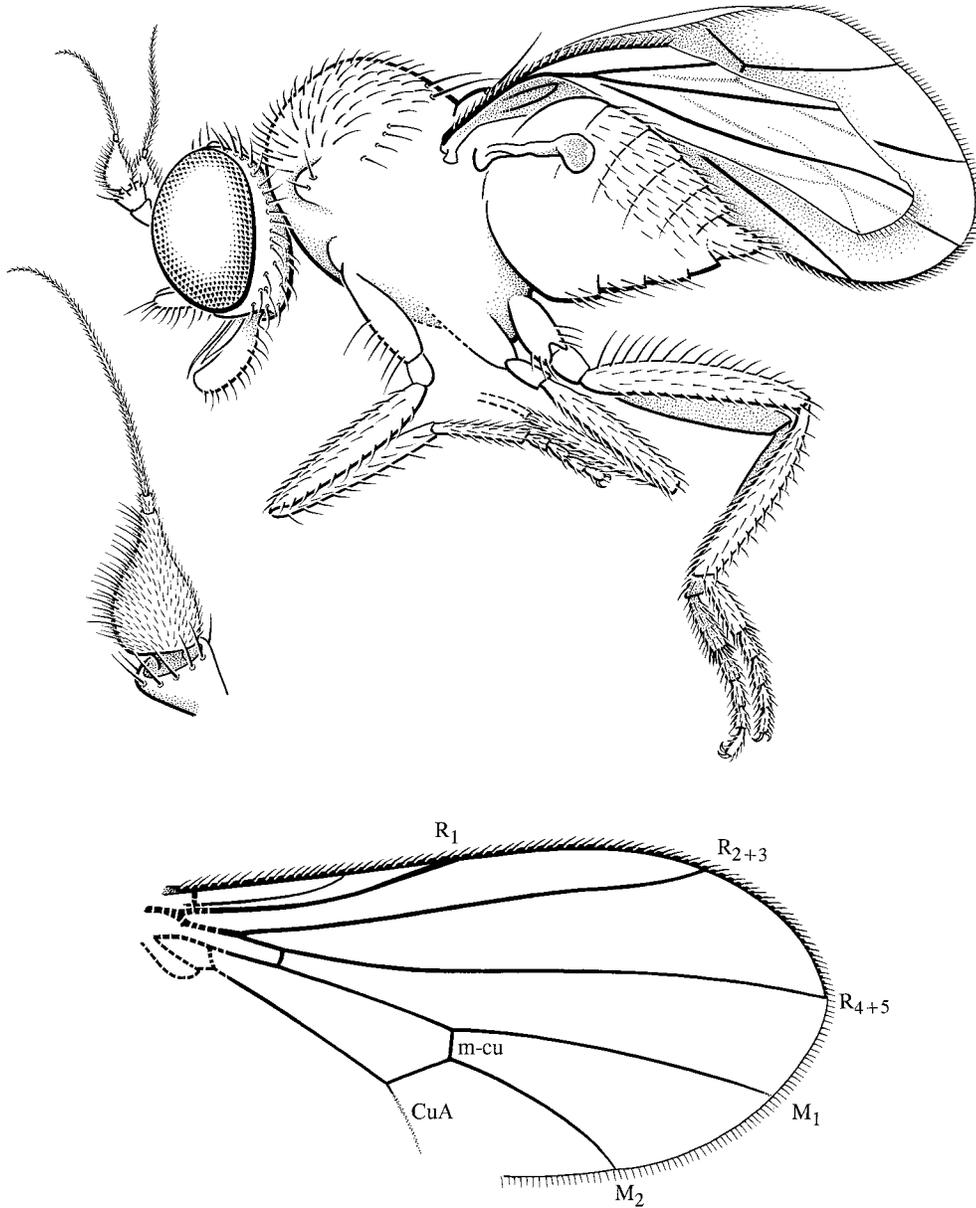


Fig. 37. *Microphorites similis* (Empididae: Microphorinae) holotype (AMNH JS424), with detail of antenna and wing. Lebanese amber.

terior dorsocentrals, with remaining anterior dorsocentrals shortest. Scutellum with two pairs of setae; apical pair longer, tips nearly crossing. Legs of moderate length, somewhat bristly; hind femur with dorsal row ca. 15 setae, longest setae proximally, lengths gradually shorter distad, longest setae equal in

length to width of femur. Hind basitarsus with apical-medial comb of 6 stout, short setae. WING: Very similar to *M. extinctus*, with differences as noted above; anal lobe margin not discerned. ABDOMEN: Short, about $0.5 \times$ wing length, tapered to apical point; acanthophorite spines absent.

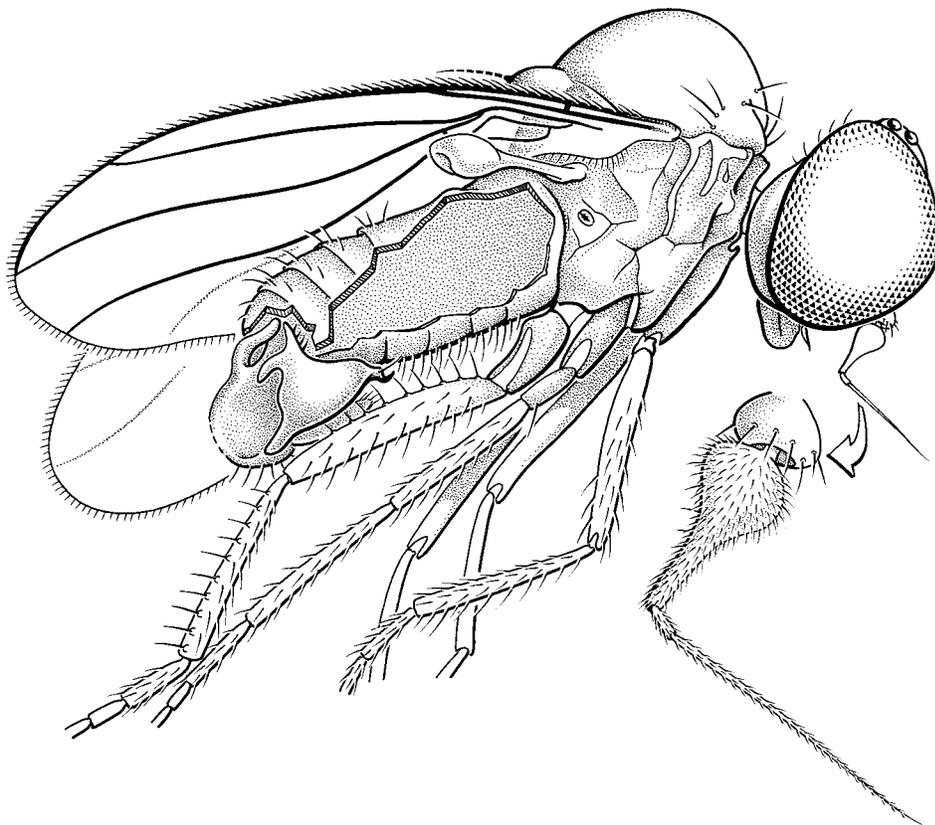


Fig. 38. *Microphorites oculeus* (Empidoidea: Microphorinae) holotype (AMNH JS445), with detail of antenna. Lebanese amber.

TYPE: Holotype, ♀, AMNH JS424, in amber from near Jezzine, Lebanon (Neocomian), Aftim and Fadi Acra, collectors. A complete and superbly preserved specimen. Critical views of the base of the wing must be observed from a frontal and partially from a dorsal view.

ETYMOLOGY: Name means "similar," in reference to the species' close similarity to *Microphorites extinctus*.

***Microphorites oculeus*, new species**

Figure 38

DIAGNOSIS: Distinguished from *M. extinctus* and *M. similis*, n.sp. primarily on the basis of the longer and more abruptly tapered flagellomere I.

DESCRIPTION: Body length = 1.52 mm; thorax length = 0.51 mm; wing length = 1.33 mm; Known only from male holotype.

HEAD: Large, nearly spherical. Eyes bare, occupying most of head; gena not present; eyes holoptic for most of frons, dorsal and ventral facets not differentiated. Antenna aristate; pedicel cuplike, with apical-marginal ring of fine setulae; flagellomere I abruptly tapered, with base bulbous, apical half long and slender, length of flagellomere I $2.0\times$ greatest width, without especially long setulae on ventral or dorsal surfaces; length of basal aristomere $3.5\times$ the width; arista nearly $2.0\times$ length of flagellomere I. Proboscis apparently quite small (retracted?), with only part of labellum and labrum exposed beyond oral margin. THORAX: Moderately domed; most of notal setae apparently sheared off, but with short row of 3 fairly long notopleural setae remaining, along with several long setae on anterior surface of notum. Legs fairly long and slender. Hind leg with femur and

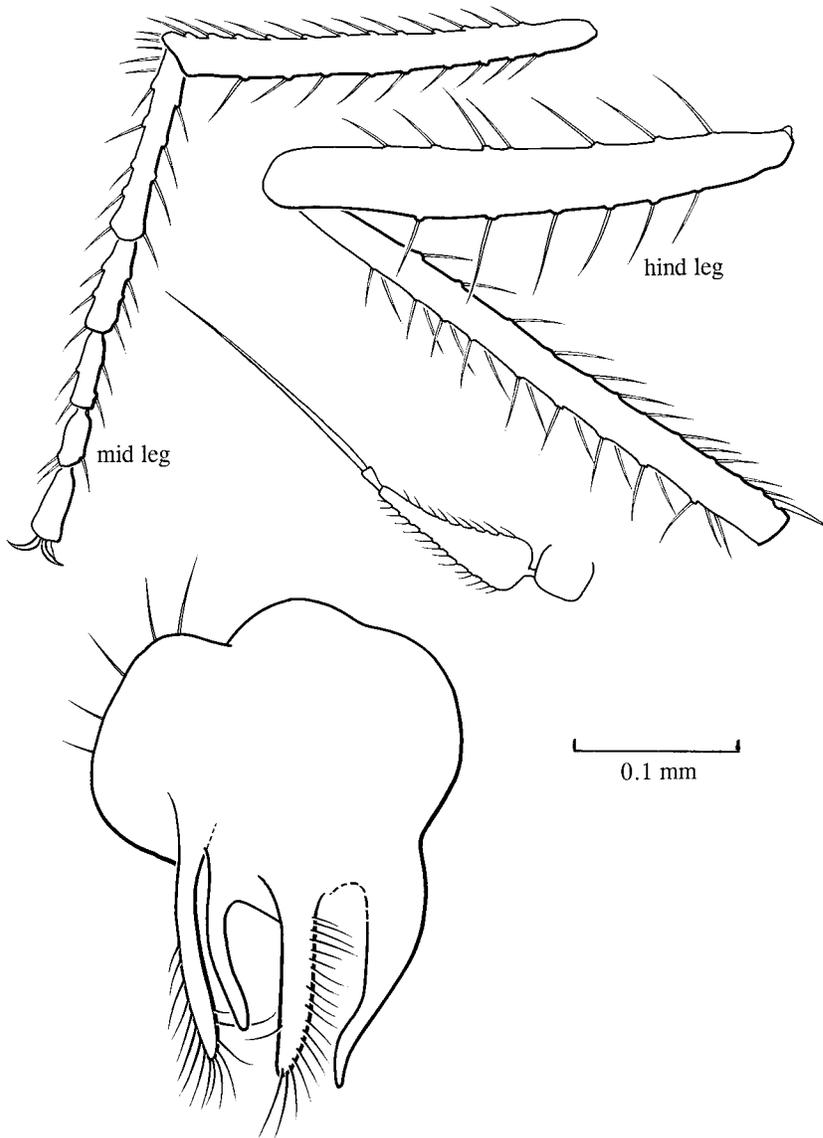


Fig. 39. *Microphorites?* sp. (Empidoidea: Microphorinae), AMNH JG78/23, showing details of fore and mid legs, antenna, and male genitalia (posterior view). Lebanese amber.

tibia having dorsal rows of fine, stiff, erect setae. WING: Not entirely visible, particularly for basal and cubital/anal areas; costal vein ending at apex of R_{4+5} ; M_1 and M_2 present; basal cells, anal cell and dm cell not observable; bm-cu crossvein apparently complete. ABDOMEN: Pregenital segments of abdomen of moderate length; total length approximately $0.5\times$ length of wing. Hypo-

pygium large, rotated and lateroflexed to right (disarticulated in type); posteroventral margin setose; left lamella with acute ventral lobe, apex of lobe with slightly hooked tooth.

TYPE: Holotype, ♂, AMNH JS445, in amber from near Jezzine, Lebanon (Neocomian), collected by Aftim and Fadi Acra.

ETYMOLOGY: From Latin, "full of eyes," or "having many eyes."

COMMENTS: Although critical details of the wing are not apparent in this fossil specimen, the arrangement of the discernable venation (particularly the apparent complete bm-cu crossvein, and the orientation of M_2 which hints at the presence of cell dm) suggests that the venation is probably similar to that in *M. extinctus* and *M. similis*, n.sp. In addition, the distinctive setation on the hind leg of *M. oculus*, n.sp. is very similar to that seen in *M. similis*, as is the costa ending at R_{4+5} , indicating that both could perhaps belong to the same species. However, differences exhibited in the shape of flagellomere I appear to fall beyond the range of sexually dimorphic variation seen in the Microphorinae.

Another male specimen in Lebanese amber, AMNH JG 78/23 (fig. 39), may belong to this species, on the basis of the hind leg setation and length of flagellomere I. However, the wings are poorly preserved, among other features, and the venation is undecipherable. The hypopygium of AMNH JG 78/23 does not appear similar to the hypopygium of *M. oculus*, although both have a distinctive row of setae along the posteroventral margin.

AVENAPHORA, NEW GENUS

DIAGNOSIS: Eyes bare, broadly dichoptic in male; antenna with 2-articled arista; frons with 3 pairs of frontal-orbital setae, anterior pair inclinate. Wing with costal vein ending at R_{4+5} ; R_1 short; cell dm absent (dm-cu vein absent); M_{1+2} forked; cell bm slender, bm-cu vein complete; cell cup narrow, subequal to length of cell bm, truncate apically; anal vein (A_1) present, extended midway to wing margin; anal lobe of moderate size. Male genitalia rotated and lateroflexed to right, nearly symmetrical; cercus enlarged.

TYPE SPECIES: *Avenaphora hispida*, n.sp. Monotypic. In Neocomian amber from Lebanon.

ETYMOLOGY: Named derived from Greek for "without"; Latin, "vein"; and *-phora*, a common suffix for generic names of microphorines.

Avenaphora hispida, new species

Figure 40

DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 1.16 mm;

thorax length = 0.53 mm; wing length = 0.96 mm. Known only from male holotype. HEAD: Relatively broad, slightly broader than thorax. Eye bare. Male frons wide, margins of eyes diverging dramatically posteriad; frons with 3 pairs of frontal-orbital setae, anterior pair inclinate and slightly cruciate, middle and posterior pairs reclinate; pair of small ocellar setae; pair of cruciate postocellars, pair of latero-clinate outer verticals. Antenna with cuplike pedicel, distal margin with ring of fine setulae; flagellomere I drop-shaped, ventral surface with longer setulae; arista with 2 articles (suture between aristomeres difficult to discern), basal article slightly thicker and bare, ca. $0.2\times$ width of distal article; distal article whiplike, with numerous microtrichia slightly longer than width of aristal trunk; total length of arista slightly more than $3\times$ length of flagellomere I. Proboscis not easily discerned, apparently quite small and/or largely retracted into oral cavity. THORAX: Notum hardly arched; dorsocentral and acrostichal setae differentiated; acrostichals in 2 median rows, about 6 setae per row; dorsocentrals slightly larger, 5 per row, posterior pair of dorsocentrals twice length of anterior 3 pairs. One supra-alar, 1 postpronotal, 2 pairs of scutellar setae. Scutellar setae longer than posteriormost dorsocentrals, almost upright; apical scutellars cruciate. Legs of moderate length, bristly. Forelegs: femur with 2–3 long ventral setae, basitarsomere with ventral comb of fine, short setae. Midlegs: trochanter appears unusually long, tibia with 3 apical and 1 preapical seta. Hind legs: femur slightly stouter than others, midtibia with ventral surface having pair of preapical setae and opposing pair of setae at midlength, basitarsus with pair of ventro-apical setae. WING: Relatively short, broad, length $2.4\times$ greatest width, anal lobe of moderate size, alula absent. Costa extended to apex of R_{4+5} ; Sc very difficult to discern; R_1 short, extended to $0.4\times$ length of wing, no pterostigma; R_{2+3} and R_{4+5} nearly straight; r-m crossvein very short, cell dm absent; M_{1+2} forked, both veins not quite reaching wing margin; CuA_1 well developed; cells bm and cup slender, of subequal length; bm-cu vein complete, apex of CuA_2 not looped into cell bm; vein A_1 extended to midway between cell cup and wing margin. ABDOMEN: Rel-

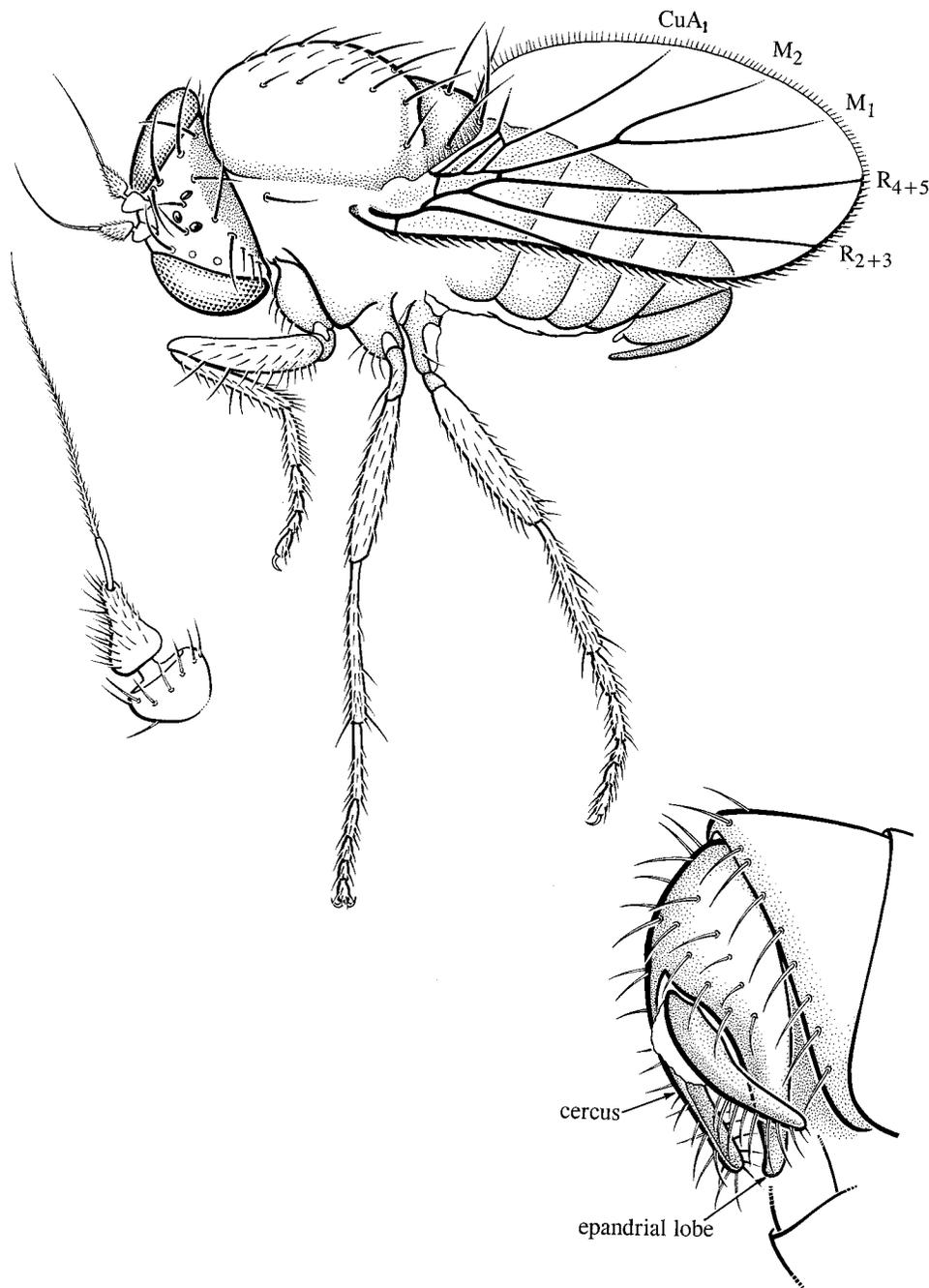


Fig. 40. *Avenaphora hispida* (Empidoidea: Microphorinae) holotype (AMNH L-AE24), with details of antenna (lateral view) and male genitalia (ventrolateral view). Lebanese amber.

atively short and stout, $0.6\times$ length of wing. Hypopygium fairly large, rotated and lateroflexed to right, nearly symmetrical; epan-drium with pair of long apical lobes; cercus long and pendulous, with marginal fringe of long, fine setulae.

TYPE: Holotype, ♂, AMNH L-AE24, in amber from Bcharre, northern Lebanon, collected by Antoni Estephan.

ETYMOLOGY: Species name from Latin, "bristly," or "shaggy," for the setae on the frons and legs.

COMMENTS: This species exhibits an interesting mosaic of features. Significant plesiomorphies include the 2-articled arista, bare eyes, presence of M_2 , bm-cu vein complete, cell cup truncate apically, anal vein extended midway to wing margin, and a moderately large anal lobe, which places *Avenaphora* in the paraphyletic tribe Microphorini. However, this fossil species is relatively apomorphic in the dichoptic condition of the male, loss of cell dm (dm-cu absent), and the form of the hypopygium, which is relatively symmetrical with a large epan-drium, inconspicuous hypandrium, and enlarged cercus. These apomorphies (excluding the loss of cell dm) suggest that *Avenaphora* has closer affinities to the Dolichopodidae and/or Parathalassiini.

SUBFAMILY MICROPHORINAE

TRIBE PARATHALASSIINI

GENUS *CRETOMICROPHORUS* NEGROBOV

Cretomicrophorus Negrobov, 1978: 82.

DIAGNOSIS: Extracted from Negrobov: Distinguished from *Microphor* and *Schistostoma* by "lack of a separate clypeus and the less developed anal lobe of the wing. . . distinguished from the Recent *Microphorella* Becker and *Parathalassius* Mik by bare eyes" (p. 222 of English translation). Negrobov further distinguished *Cretomicrophorus* from *Microphorites* in Lebanese amber by the former having "position of the antennae on the apical third of the head, the open posterior cells, the arrangement of the veins on the wing and the scutal chaetotaxy" (p. 222 of English translation). *Cretomicrophorus* primarily differs in wing venation from *Microphorites* by the incomplete bm-cu vein. It also differs from *Microphorites* and

other members of the Microphorini (*Microphor*, *Schistostoma*, *Avenaphora*) in the single articulated arista.

TYPE SPECIES: *C. rohdendorfi* Negrobov, 1978. Not examined.

COMMENTS: In addition to genera discussed by Negrobov (1978), *Cretomicrophorus* differs from the extant parathalassiine genera *Plesiothalassius* Ulrich and *Amphithalassius* Ulrich by its more primitive, bare eyes. *Cretomicrophorus* appears to be closer to the ground plan of the Parathalassiini than do either of these plesiomorphic genera.

Cretomicrophorus novemundus,

new species

Figure 41

DIAGNOSIS: Differs from *C. rohdendorfi* by the new species having: flagellomere I slightly longer and more tapered; thorax apparently not metallic green (iridescence is not always preserved); 6 (vs. 8) pairs of dorsocentral setae; 4 pairs (vs. 6) acrostichals; scutellum with only long, apical pair of setae, no pair of smaller, anterior ones; wing with stigma; medial wing vein shorter, length ca. same length as free branches of CuA_1 , M_1 , and M_2 ; wing cells bm, cup, and br longer; humeral crossvein at same level as basal branches of R_1 , not anterior to them; mid tibia without 2 pairs of (opposing) setae; hypopygium much larger.

DESCRIPTION: Known only from male specimen. Thorax length = 0.75 mm; wing length = 2.01 mm; total length not measurable. HEAD: Very difficult to observe front of head, based on collapse of structure and position of specimen in amber. Eye bare. Antenna with long basal flagellomere, base bulbous and apically tapered very gradually to point, length nearly $3\times$ greatest width (vs. $2\times$ in *C. rohdendorfi*); arista with single article; arista slightly longer than flagellomere I. THORAX: Notum collapsed, but setae well preserved, showing 8 pairs dorsocentral setae, with posterior pair approximately twice the length of more anterior ones; penultimate pair of dorsocentrals only slightly longer than more anterior pairs. Two rows of acrostichal setulae present, with 4 setulae per row. Scutellum with only apical pair of setae, length of setae greater than posterior pair of

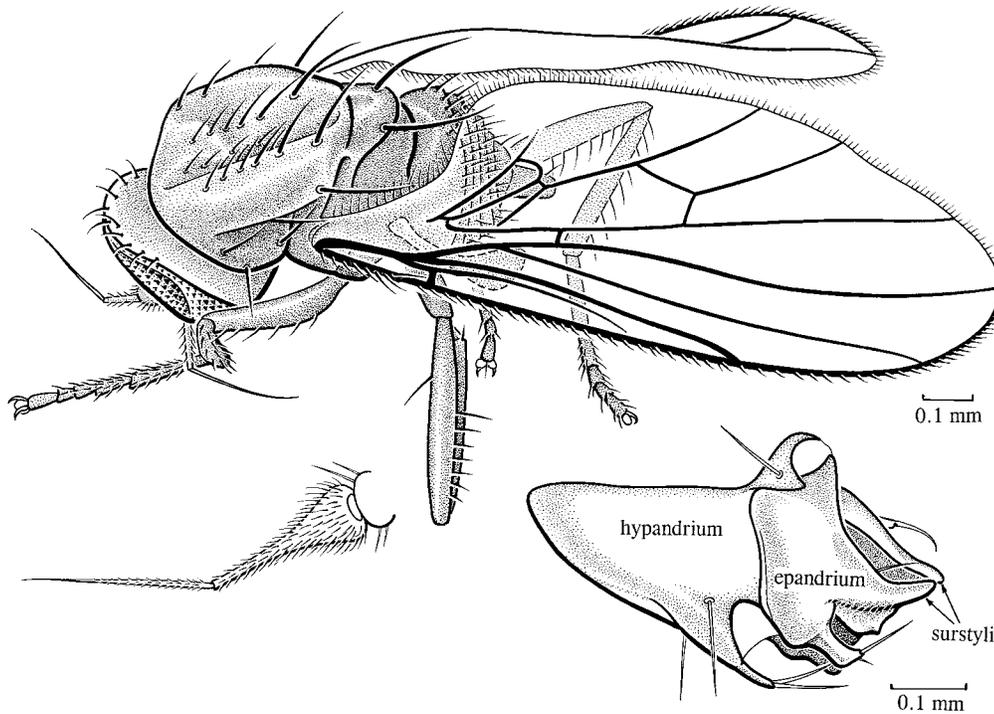


Fig. 41. *Cretomicrophorus novemundus* (Empididae: Microphorinae) holotype (AMNH NJ-635), with details of antenna and disarticulated male genitalia. In New Jersey amber.

dorsocentrals. One long supra-alar seta; one long notopleural, one long anepisternal, 2 long anepimeral setae present. Legs of moderate length, relatively unmodified. Mid and hind femora (at least for male) with ventral row of stiff setae (lengths about equal to width of femur); hind tibia with dorsal row of 8–10 stiff setae. WING: Anal lobe of moderate size; alula absent. Costal vein extended to very slightly beyond apex of R_{4+5} ; Sc incomplete, almost reaching C; apex of R_1 surrounded by pterostigma; short r-m crossvein present, perpendicular to longitudinal veins; cell dm present, M_2 equidistant between CuA_1 and M_1 ; bm-cu crossvein incomplete (not quite contacting base of M_1); cell cup with small spur of anal vein (A_1). ABDOMEN: Male pregenital segments short, length of first segment approximately equal to lengths of apical segments combined; segment 7 peduncular, apparently attaching internally to a large genital capsule. Genital capsule detached from body of specimen, somewhat disarticulated. Hypopygium

with hypandrium having pair of pointed ventral lobes, lobe with apical pair stiff setae; epandrium with pair of appendages bearing stiff, apical seta, and pair of large, lobate surstyli.

ETYMOLOGY: Name derived from Latin for “New World.”

TYPE: Holotype, ♂, AMNH NJ-635, in Turonian amber from Sayreville, New Jersey (White Oaks site), collected by Gerard R. Case.

COMMENTS: In the form of the larger anal lobe, *C. novemundus* n.sp. appears more plesiomorphic than the younger *C. rohdendorfi* in Siberian amber. A significant difference between the two species is in the size of the male hypopygium. Negrobov (1978) described the hypopygium of *C. rohdendorfi* as a tiny oval sclerite with its apex tucked into abdominal tergite 5. Given the disarticulation of the large hypopygium from the narrow peduncle of *C. novemundus*, the holotype and only known specimen of *C. rohdendorfi*

should be rechecked to determine if part of its hypopygium is missing.

GENUS *ARCHICHRYOTOSUS* NEGROBOV

Archichrysotus Negrobov, 1978: 84 (original, Russian version), pg. 223 (English translation).

DIAGNOSIS: As defined by Negrobov (1978), distinguished from other Microphorinae by two, rather than three, veins connected to discal cell (vein M_2 lost).

TYPE SPECIES: *A. hennigi* Negrobov. Other species: *A. minor* Negrobov. Both in Coniacian/Santonian amber from Taymyr, Siberia. Neither species was examined by us.

COMMENTS: *Archichrysotus* was placed in the Microphorinae by Negrobov (1978), but was treated as a dolichopodid by Chvála (1981, 1983) primarily because of the loss of vein M_2 (a homoplasious feature within the Empidoidea, occurring within Atelestinae and "Hybotidae"). The somewhat similar *Retinitus nervosus* Negrobov, described from the Upper Cretaceous of Siberia, was tentatively placed in the Dolichopodidae by Negrobov (1978). Both genera possess an arista with a single article and are therefore probably best classified together within the Parathalassini following Evenhuis (1994), although *Retinitus* has the Sc fused to R_1 as in the Dolichopodidae.

Archichrysotus incompletus, new species

Figure 42

DIAGNOSIS: Distinguished from *Archichrysotus hennigi* and *A. minor* by single pair of scutellar setae (anterior pair lost); only posterior two pairs of dorsocentrals distinguishable in size from acrostichals; pair of frontal-orbital setae; and by incomplete anterior crossvein bm-cu (forming one wall of cell bm).

DESCRIPTION: Body length = 1.32 mm; thorax length = 0.59 mm; wing length = 1.37 mm. HEAD: Little discernable, since most features cloaked in layer of milky froth. Pair of frontal orbital setae present, slightly proclinate and inclinate; ocellar setae fine, widely divergent. Details of eyes not observable, but clearly widely separated by frons. Antennae not well preserved, only right flagellomere I intact; aristomeres lost; flagellomere I drop-shaped, with bulbous base,

most similar in shape to *A. hennigi*. THORAX: Notum hardly arched; with two median rows acrostichals; two lateral rows dorsocentrals; two posterior pairs of dorsocentrals longer than acrostichals and other dorsocentrals. Pair of postpronotal setae; two notopleurals; one supra-alar; scutellum with only apical pair, long setae. Legs of moderate length, with setae slightly thicker and denser than is typical, giving slightly bristly appearance. WING: Sc complete, very close to R_1 ; costal vein extended to apex of R_{4+5} ; no pterostigma; R_{2+3} and R_{4+5} virtually straight; M_1 , CuA_1 , and A_1 not quite reaching wing margin; vein M_2 lost; posterior crossvein dm-cu long and straight, slightly less than perpendicular to longitudinal veins; anterior crossvein bm-cu, where it forms one side to cell bm, incomplete; cell cup slightly wider than bm; A_1 incomplete, extended beyond half-way to wing margin; A_2 present on postero-basal margin of wing, with slight spur of vein into anal lobe. Anal lobe slightly reduced; alula absent. ABDOMEN: Short, slightly less than one-half length of wing. Sex of holotype and only specimen probably male, based on rounded terminal segment (details obscured by milky coating).

TYPE: Holotype, AMNH NJ-169, in Turonian amber from Sayreville, New Jersey (White Oaks site), Keith Luzzi, collector. The specimen is snagged on several strands of spider silk, which may account for its slight decomposition and disarticulation.

ETYMOLOGY: Name refers to the incomplete bm-cu crossvein.

COMMENTS: The incomplete crossvein bm-cu observed in *A. incompletus* (but not the other three species of *Archichrysotus*) is the condition shared with all other Parathalassini. This suggests that the incomplete crossvein is plesiomorphic in *Archichrysotus*, and exhibits a reversal to the complete condition within the genus.

Archichrysotus manitobus, new species

Figure 43

DIAGNOSIS: Distinguished from other species of the genus by the longer Sc (extended nearly to level of dm-cu) and R_1 (ends past midpoint of wing); C ending between apices of R_{2+3} and R_{4+5} ; relatively short bm and cup cells, with proximal end of cup not acutely

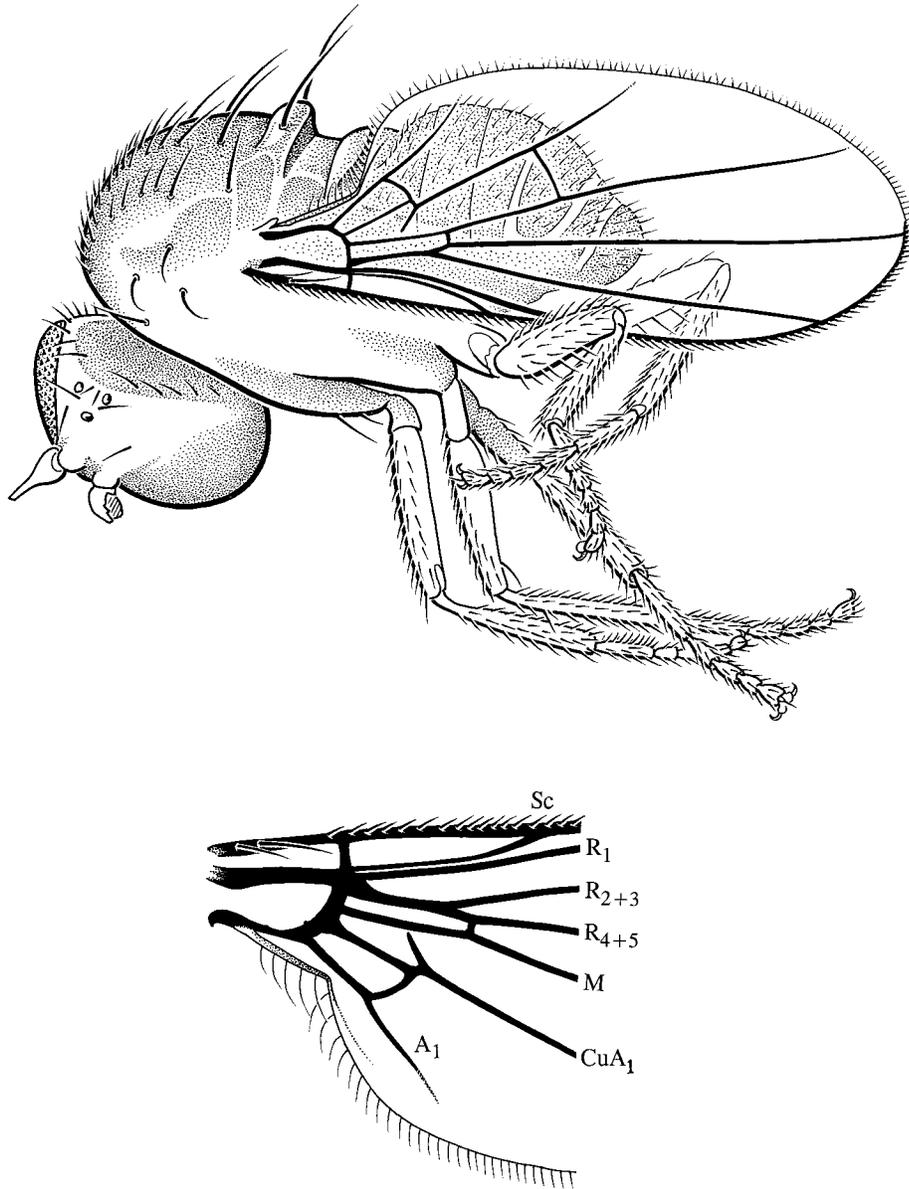


Fig. 42. *Archichrysotus incompletus* (Microphorinae) holotype (AMNH NJ-169), with detail of base of wing. New Jersey amber.

tapered. Distinguished from *A. hennigi* and *A. minor* by longer arista ($2.2\times$ length of flagellomere I, vs. $0.8-1.2\times$ in other species).

DESCRIPTION: Body length = 1.78 mm; thorax length = 0.60 mm; wing length = 1.85 mm. HEAD: In frontal view with face and frons wide, width ca. $0.4\times$ width of

head. Eyes bare, dorsal and ventral facets undifferentiated; slight emargination of facial margins of eyes at level of antennae. Proboscis obscured. No frontal-orbital setae; pair of large, divergent ocellar setae; small verticals and postverticals. Antennae with terminal arista; flagellomere I drop-shaped,

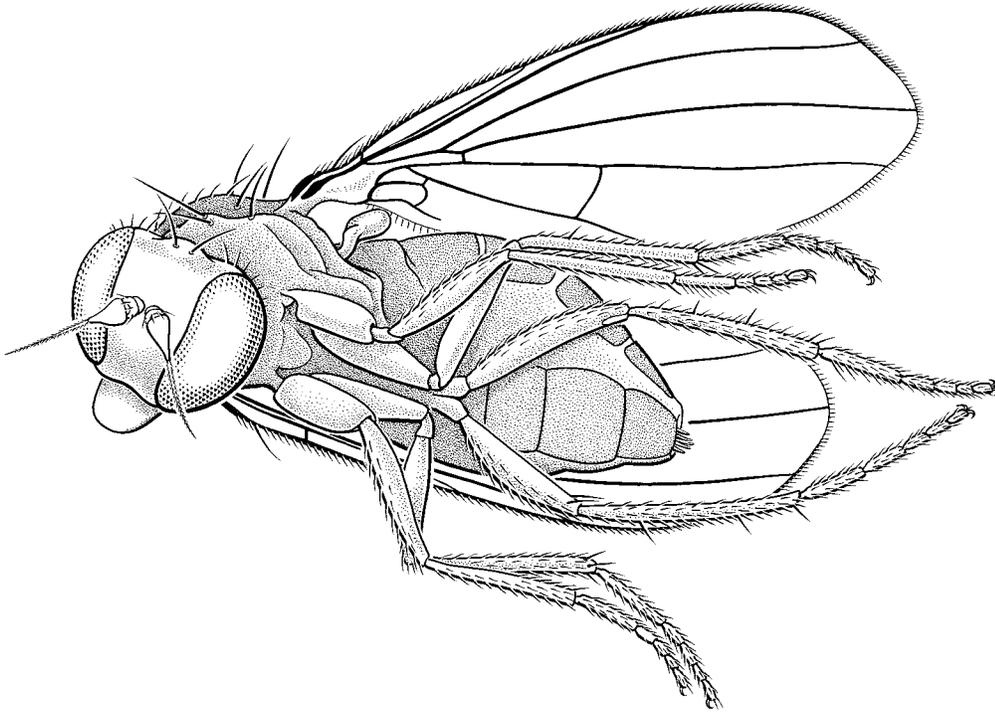


Fig. 43. *Archichrysotus manitobus* (Microphorinae) holotype (MCZ 7096). Canadian amber.

with bulbous proximal end; arista with single article, relatively long, $2.2\times$ length of flagellomere I; base of arista not observable in detail (backlighting not possible). THORAX: Dorsal surface not observable. Postpronotal lobe with two long setae; two notopleurals; one supra-alar. Legs of moderate length and setation. WING: C ending between apices of R_{2+3} and R_{4+5} ; Sc long, complete, extended nearly to level of crossvein m-cu; R_1 long, extended past midpoint of wing; basal cells bm and cup relatively short; bm-cu crossvein complete; proximal end of cup rounded, not acutely; A_1 short. ABDOMEN: Of moderate length. Sternites well developed; 5 acanthophorite spines visible.

TYPE: Holotype, ♀, MCZ 7096, in amber from Cedar Lake, Manitoba, collected by W. C. Legg.

ETYMOLOGY: From Manitoba, source of the amber.

COMMENTS: The wing of this fine specimen was also illustrated by Hennig (1970: fig. 16), but he did not formally describe the specimen.

FAMILY DOLICHOPODIDAE

SYMPYCNITES, NEW GENUS

DIAGNOSIS: Head long, with insertion of neck high on head; female dichoptic; eye micropubescent ventrally; antennal scape without row of dorsal setae; flagellomere I triangular; arista dorsal with two articles; mid and hind femur with preapical bristles; hind basitarsus without dorsal setae. Wing with costal vein ending at M_1 ; Sc fused to R_1 ; long bm+dm cell with veins M_1 and CuA_1 (M_2 absent). Female terminalia with acanthophorite spines and spinose cerci.

TYPE SPECIES: *Sympycnites primaevus*, n.sp. Monotypic.

ETYMOLOGY: From *Sympycnus* (an extant genus of Dolichopodidae), and *-ites*, Greek for "like," in reference to similarity of the two genera.

Sympycnites primaevus, new species

Figure 44

DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 3.48 mm;

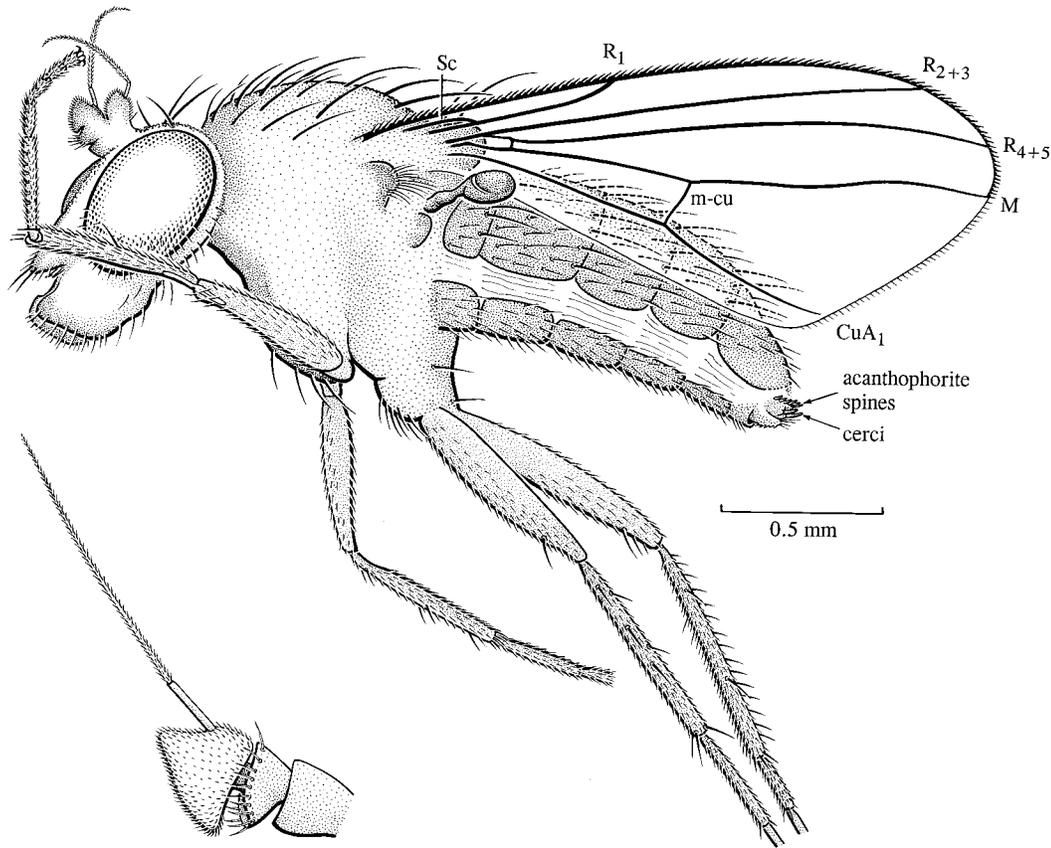


Fig. 44. Dolichopodidae, *Sympycnites primaevus*, AMNH L-AE133. In Lebanese amber.

thorax length = 1.11 mm; wing length = 2.71 mm. HEAD: Insertion of neck high on head; eyes widely separated, $1.5\times$ higher than wide in lateral view, micropubescent ventrally. Frons with single pair proclinate, fronto-orbital setae, about $0.5\times$ length of ocellars; ocellar setae upright, slightly reclinate, with bases very close. Mouthparts largely obscured by milky coating, but palps protrudent, pointed, setulose, with pair of stiff setae at apex; labellum apparently large and broad; pair of tiny epipharyngeal blades seen protruding just beneath palps. Antenna inserted high on head, near upper quarter of eye; scape without dorsal setae; pedicel cup-shaped; flagellomere I triangular in lateral view, apex pointed, with very short setulae; arista with two segments, basal segment bare, small, apical segment microsetulose, $5\times$ length of basal segment. THORAX: Metallic brown green, largely obscured by milky

froth, through which large, stiff notal setae protrude. Two paramedian rows dorsocentrals present, lengths of setae increasing from anterior to posterior, with 6–7 setae per row; two rows acrostichals present with 4–5 setae, situated on anterior half of notum. Scutellum with two pairs of large setae. Pleura largely coated, no setae protruding. Legs dark brown, with large setae along lengths of all tibia (see fig. 44), mid and hind femora with large preapical seta on ventral surface; mid tibia with three large apical setae; hind tibia with row of 15 stiff setae on dorsal surface (length equal to width of tibia); hind basitarsus without dorsal setae. WING: Hyaline; C ending at apex of M_1 ; Sc curved downward and fused to R_1 just proximal to midpoint of R_1 ; R_1 short, meets C at approx. $0.4\times$ length of wing; veins R_{2+3} and R_{4+5} straight, both unbranched; r-m short, basal; M unbranched, with slight kink near middle between dm-cu

and apex of vein; crossvein dm-cu long; CuA_1 nearly straight, probably not reaching margin of wing. Anal region of wing obscured by folding. Halter dark brown. Dark, setose lobe present at base of wing. ABDOMEN: Tergites dark brown, slightly metallic, setose. Female terminalia with transverse row of approximately 8 small acanthopore spines; cerci spinose.

TYPE: Holotype, ♀, AMNH L-AE133, in amber from near Bcharre, northern Lebanon (Neocomian), collected by Antoni Estephan. The clear yellow piece of amber also contained two nymphal aphids (Aphidoidea), all specimens of which were separated after epoxy embedding and trimming with a thin diamond saw. The piece of amber with the dolichopodid is now $14 \times 9 \times 1.5$ mm (the epoxy block of same thickness but slightly larger other dimensions). Thinness of the preparation served to optimize lateral views of the fly (especially venation) in a highly fractured piece of amber. The fly is complete, but most of the head and thorax are covered with a milky coating through which setae protrude.

ETYMOLOGY: From the Latin for "young," in reference to the unexpectedly old age of this Lower Cretaceous specimen.

COMMENTS: Despite its great age, *Sympycnites primaevus* is surprisingly similar to the extant but very generalized genus *Sympycnus* Loew. However, *Sympycnites* is even more plesiomorphic in retaining anterior biserial acrostichals and lacking an anterior dorsal setal serration on the fore tibia.

Extant Dolichopodidae are diverse and abundant, with approximately 150 genera and 5000 species, found primarily in moist, vegetated regions. The oldest definitive dolichopodid known until now was *Prosystemus zherikhini* Negrobov, from amber of Sakhalin Island, far eastern Russia and apparently Paleocene in age. Dolichopodids are very abundant in Miocene amber from the Dominican Republic (some 15 genera and 30 species, D. Grimaldi, unpubl.), and in the Eocene/Oligocene Baltic amber there are 21 genera and 70 species. (The Baltic amber Dolichopodidae were described almost entirely by F. Meunier and are nomenclaturally chaotic. See Evenhuis [1994] for many nomenclatural changes). By the Lower Cenozoic, modern

genera of Dolichopodidae were certainly in existence, which is evidence independent from and consistent with the fossil we describe here that indicates Dolichopodidae existed in the Cretaceous.

It is indeed strange that a definitive Cretaceous dolichopodid has not been found until now, and that it occurs in such an ancient amber as Lebanese. A Cretaceous existence of these flies could be predicted by the presence in Lebanese and other Cretaceous ambers of a diverse array of Microphorinae, which is either the sister group to the dolichopodids or an assemblage paraphyletic with respect to the dolichopodids. Evenhuis (1994) mentioned several Cretaceous records, one in Canadian amber mentioned by McAlpine and Martin (1969), and another in Siberian amber, mentioned by Zherikhin and Sukacheva (1973). We have seen all of the Canadian amber specimens reported by McAlpine and Martin, as well as ones from the MCZ, and since we have seen no dolichopodids, the original report probably refers to a microphorine, such as *Archichrysotus manitobus*, n.sp. The Siberian amber report probably refers to the specimen later described by Negrobov as *Retinitus*.

SECTION EREMONEURA FAMILY INDETERMINATE

CHIMEROMYIA, NEW GENUS

DIAGNOSIS: Antenna aristate, with arista situated dorsally on flagellomere I (two species) or apically (one species); arista with 3 articles, including 2 short basal articles and long apical one; pair of thick setae present on face near middle of oral margin (vibrissae?); frons without frontal orbital setae, two pairs of ocellar setae; notum with single, median row of acrostichals; venation distinct: Sc incomplete, R_{2+3} short, R_4 - R_5 forked; M_2 incomplete at both ends or lost; r-m and m-cu veins in line, forming large basal cell; anal veins and anal lobe lost. Abdominal muscle plaques apparently present (Stoffolano et al., 1988) (observed only for holotype specimen of *C. intriguea*). Male genitalia symmetrical, apparently rotated 180° (dorsoflexed) (as seen in AMNH L-AE38); terminal segments of female possibly telescoping (as seen in AMNH L-AE43).

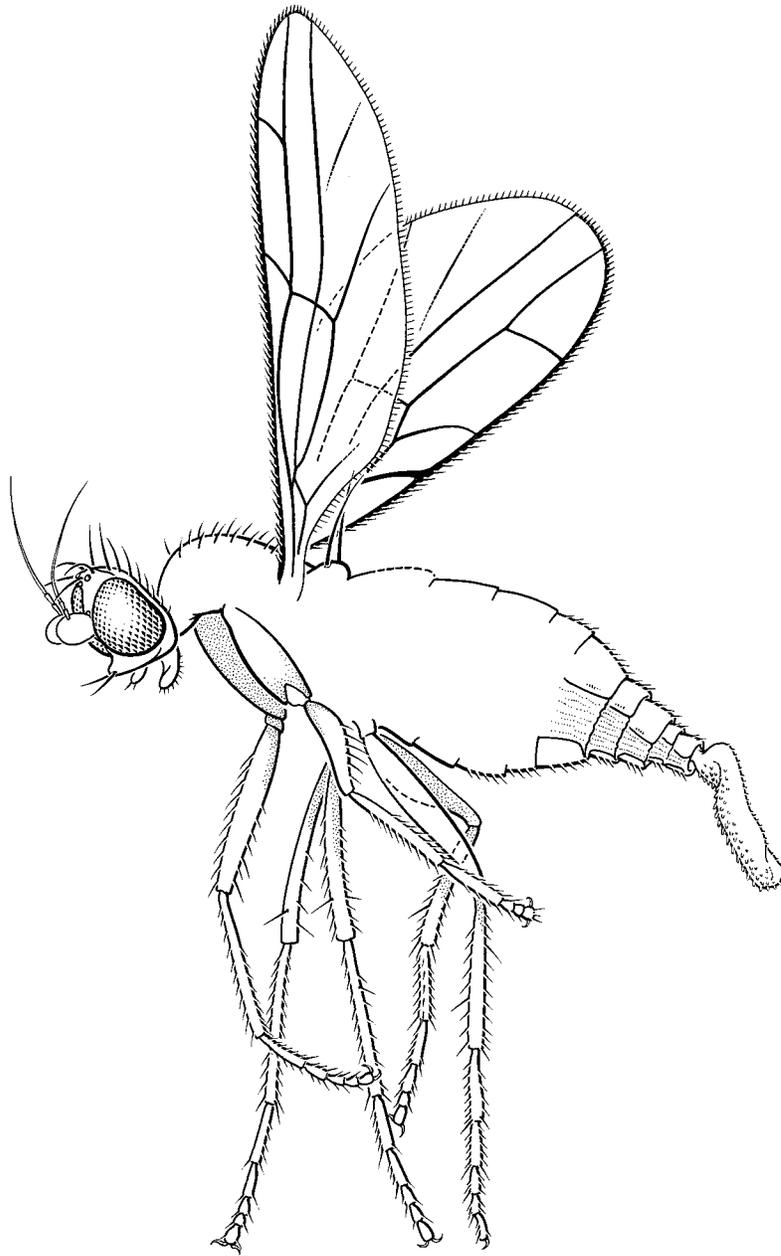


Fig. 45. *Chimeromyia intriguea* (Empidoidea? Eremoneura indet.) holotype (AMNH L-AE43). Lebanese amber

TYPE SPECIES: *Chimeromyia intriguea*, n.sp., in Neocomian amber from near Jezzine and Bcharre, Lebanon.

ETYMOLOGY: In reference to the traits of the genus that combine features of empidooids

and Cyclorrhapha, and its various autapomorphies.

COMMENTS: Hennig (1970) reported on, but did not formally describe, an incomplete specimen of an apparent specimen of *Chi-*

meromyia. That specimen is in the Stuttgart Museum (no. C54/1). He placed it with almost certainty in the Cyclorrhapha on the basis of the three aristomeres. That specimen has the arista situated apically on flagellomere I, as in *Chimeromyia reducta*, n.sp. Unlike *C. reducta*, however, C54/1 has longer ocellar setae and three pairs of vertical setae (vs. two pairs), similar to what is found in *C. intriguea* and *C. acuta*, n.spp. The Stuttgart specimen differs autapomorphically from the AMNH specimens by a very prominent ocellar tubercle and slight emargination of the inner margin of the eye just above the antennal bases. Otherwise, the lack of frontal setae and two pairs of ocellar setae—the latter Hennig believed to be unique in all the Diptera (they actually occur in *Cretoplatypalpus*)—clearly indicate the Stuttgart specimen belongs in the new genus *Chimeromyia*. Hennig mentioned the absence of genal setae or vibrissae, but all our specimens have a very prominent, distinctive pair in the middle near the oral margin. In lieu of re-examining the Stuttgart specimen, it is possible that these unusual “vibrissae” were disarticulated from the specimen during preservation. Hennig also mentioned the plesiomorphic absence of a ptilinum, which we have also not been able to detect in our specimens. Unfortunately, the Stuttgart specimen lacks wings, which is probably why Hennig did not formally name the specimen. We are pleased to fulfill Hennig’s “. . .hope that more extensive collecting will bring to light further Cyclorrhapha [in Lebanese amber]” (p. 1970). It is possible he would have been as perplexed as we are by the nature of the complete beast.

The chimeric, empidoid/cyclorrhaphan nature of the genus can be summarized as follows. Empidoid characters of *Chimeromyia* are: forked R_4 - R_5 ; dorsoflexed male genitalia; large br-bm cells, with opposing r-m and m-m crossveins (as in some Tachydromiinae, like *Megagrapha*); Sc incomplete (also as in many tachydromiines). Muscle plaques are extremely difficult to discern in the crumpled abdomens of specimens merely 0.7–1.5 mm long, but on the last 3 tergites of the holotype of *C. intriguea*, muscle plaques were observed under 400 \times magnification using a compound microscope and intense, fiber op-

tic reflected light. The undescribed species of *Chimeromyia* in the Stuttgart Museum has slightly emarginate inner margins of the eyes near the antennae, as in tachydromiines.

Cyclorrhaphan characters are: 3-articled arista (lacking in the most primitive living Cyclorrhaphan, *Opetia*, but also found in some empidoids); dorsal arista (occurs in two of the three species; this feature occurs in some tachydromiine empidids, like *Stilpon*); bristly legs and large vertical setae, as seen in Phoridae; short R_1 and R_{2+3} (as in Phoridae); pair of strong oral setae, the apparent vibrissae.

Like some empidoids and primitive Cyclorrhapha (e.g., Platypezoidea/ primitive Phoridae), the acrostichals are in a single, median row; frons is without large setae.

Chimeromyia intriguea, new species

Figures 45–47

DIAGNOSIS: Distinguished from *C. reducta* by *intriguea* having: flagellomere I with arista situated dorsally; posterior pair of ocellars equal in length to anterior pair; long pair of inner verticals present, slightly longer than ocellars; scutellum with single pair long, upright setae; wing venation with R_{2+3} turned abruptly costad, base of M extended proximally past veins r-m and m-m, an incomplete vein M_2 present, costa with heavy spinules. Distinguished from *C. acuta* and *C. reducta* by *intriguea* having flagellomere I rounded in shape, not pointed.

DESCRIPTION: Total length = 1.16 mm (holotype)/1.19 (paratype); thorax length = 0.31 mm/0.33; wing length = 0.99/0.89 mm. HEAD: Higher than long. Eye bare, unknown if male holoptic or with dorsal and ventral facets differentiated (only females known). Eye slightly reniform to drop shaped, with slight indentation on posterior margin (AMNH L-AE43) or with dorsal “tip” (AMNH L-AE118). Proboscis protrudent from oral margin, but small. Oral margin of face protrudent, with pair of thick, stiff setae on anterior tip, setae very close together, possibly the vibrissae (true vibrissae are usually situated just anterior to the cheeks). Frons fairly broad, without setae or setulae. Antenna aristate, with ovoid flagellomere I; arista dorsal to dorsolateral, with 3 aristo-

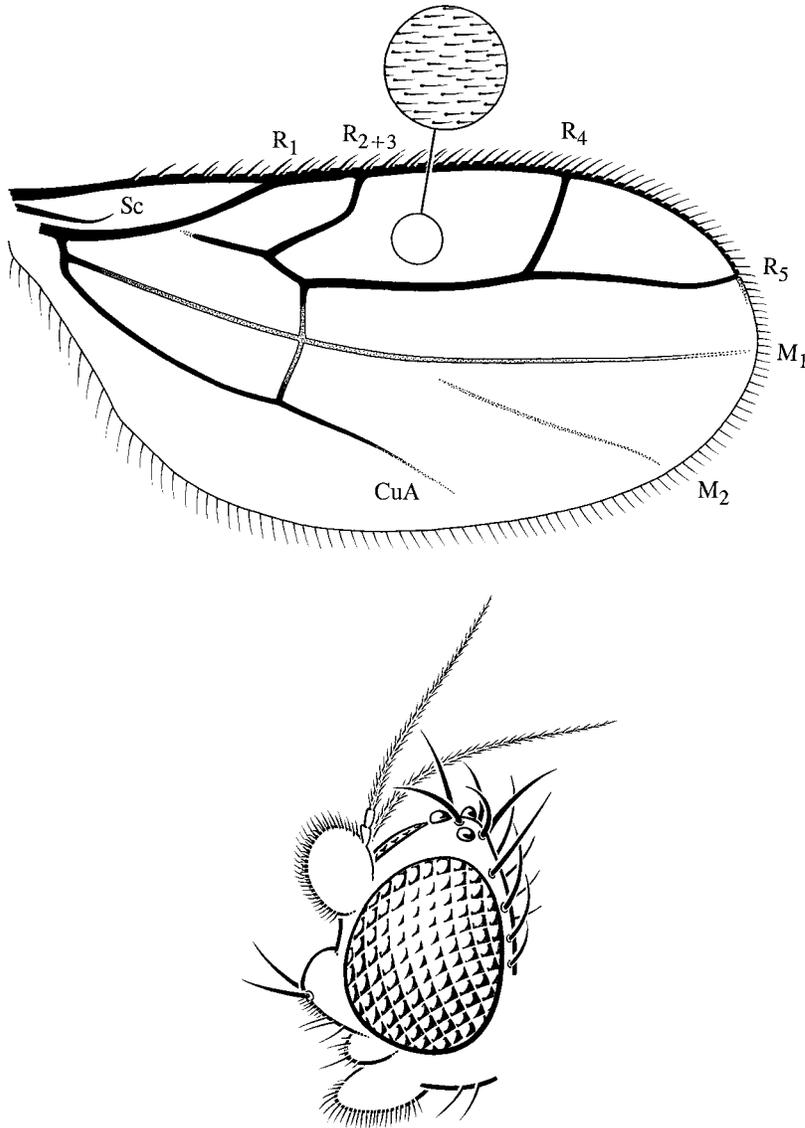


Fig. 46. *Chimeromyia intriguea* holotype (AMNH L-AE43), detail of wing and lateral view of head.

meres; basal two aristomeres small, of approximately equal size; apical flagellomere long, with short pubescence. Ocelli and ocellar setae on slight tubercle; two pairs of long ocellar setae present. Pair of long, convergent inner vertical setae; outer verticals about $0.5\times$ the length, approximately same size as postoculars. THORAX: Elongate, shallow, with anterior coxa quite long. Notum with single, median row of acrostichal setulae; pair of paramedian rows of dorsocentrals, the

most posterior pair of dorsocentrals twice the length of others. One long notopleural and one postpronotal seta present. No setae on pleura. Scutellum with single pair of (apical) setae, long and upright, slightly cruciate. Legs bristly: forelegs with femur having ventral row long setae, two rows shorter setae on tibia; midlegs with femur having ventral preapical setae, tibia having preapical setae on dorsal and ventral surfaces; hind legs with tibia having dorsal seta proximal to midpoint,

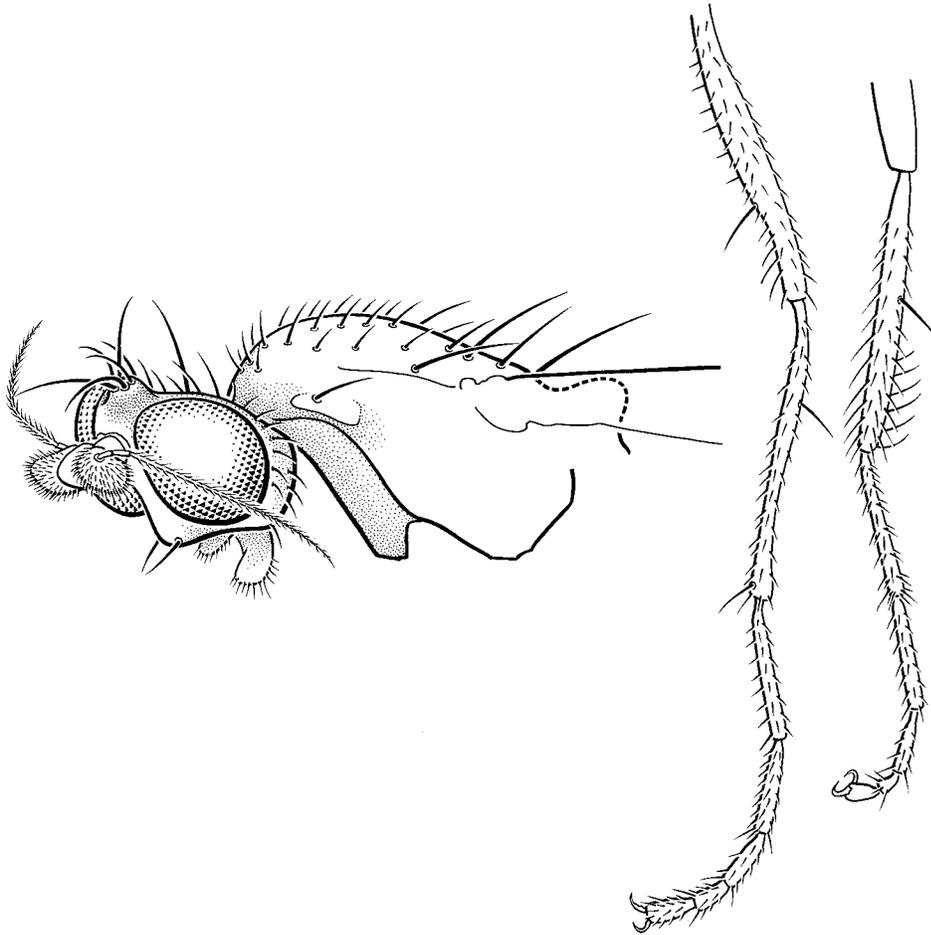


Fig. 47. *Chimeromyia intriguea* paratype (AMNH L-AE118), thorax plus head, detail of mid (above) and hind (below) legs. Lebanese amber.

ventral preapical seta, and row of about 6 curved setae on apical half dorsal surface. WING: short, apex broadly rounded, base narrow; costal vein with heavy spinules to slightly past R_4 , no breaks near where Sc would meet costa, costa extended to apex of M_1 ; crossvein h not apparent. Sc incomplete, evanescent at one-third length of R_1 ; R_1 short, $0.33\times$ length of wing. Base of R incomplete; R_{2+3} short, kinked in middle, abruptly meeting costa; R_4 - R_5 forked, branch of R_5 $0.38\times$ length of wing. Radial veins most heavily sclerotized; medial veins lightly sclerotized. M_1 parallel to main trunk of R, diverging from Cu near apex of Sc. Veins r-m and m-m virtually in line, forming equal sized br and bm cells, with trunk of M bi-

secting two cells. Vein M_2 very light, incomplete at both ends. CuA incomplete. No trace of anal veins; anal lobe not present, with long, fine setae on posterior margin. ABDOMEN: Known only for females, with apical three segments apparently telescoping; with eversible, spiculed membrane.

TYPES: Holotype, ♀, AMNH L-AE43, in Neocomian amber from northern Lebanon, collected by Antoni Estephan from near Bcharre. Paratypes: ♀, AMNH L-AE118, ibid; and ♀, AMNH L-AE134a, ibid. Holotype is in a piece of vacuum-embedded, clear yellow amber, and is completely intact and well displayed. L-AE118 and L-AE134a are also embedded and in clear yellow pieces of amber; L-AE118 does not have the wings

fully observable, although the head and thorax are quite visible. In the amber piece with L-AE134 are also two small elateroid beetles (L-AE134b, c); venation of the fly is fully observable and the body complete, but the head and other parts of the body are badly compressed.

ETYMOLOGY: Name derived from late Latin, from *intrico*, to "entangle" or "perplex," referring to the unusual morphology.

Chimeromyia acuta, new species

Figure 48

DIAGNOSIS: Very similar to *C. intriguea* in virtually all aspects, except that *C. acuta* has a larger flagellomere I with an acute ventral margin, with longer setulae on ventral margin; also, frons is wider and eyes are a more narrow ovoid.

DESCRIPTION: Body length = 0.69 mm; thorax length = 0.26 mm; wing length = 0.64 mm. Features as given in diagnosis and for description of *C. intriguea*. Male genitalia well preserved, dorsoflexed. Cerci broad and flat, with terminal fringe of long setulae. Epandrium with 2 pairs of ventral lobes, a shorter posterior pair and anterior pair about twice length of posterior ones and with apical hook. Surstylus simple, fingerlike, with approximately 3 long apical setulae; hypandrium with pair of long apical lobes extended approximately to apices of longer epandrial lobes.

TYPE: Holotype and only known specimen, ♂: AMNH L-AE38, in Neocomian amber from northern Lebanon, collected near Bcharre by Antoni Estephan. The preparation is a 12 × 4 × 2 mm piece of epoxy with the sliver of amber within, containing the completely preserved fly. Detail of the antennae and genitalia must be observed with transmitted and reflected fiber optic light using a compound microscope.

ETYMOLOGY: Name refers to the shape of flagellomere I.

Chimeromyia reducta

Figure 49

DIAGNOSIS: Distinguished from *C. intriguea* and *C. acuta* by *reducta* having: flagellomere I slightly pointed, with arista situated apically; arista shorter; ocellar setae

short, posterior pair 0.5× length of anterior pair; vertical setae short, with inner pair 0.5× length of posterior pair; scutellum with two pairs of setae; wing venation with R₂₊₃ gradually meeting costa, base of M non-existent proximally past veins r-m and m-m, no vein M₂ present (not even incomplete); costa with short, fine, stiff setae.

DESCRIPTION: Body length = 1.16 mm (holotype)/1.50 (paratype); thorax length = 0.34 mm/0.48; wing length = 1.02/1.07 mm. HEAD: With wide frons, particularly dorsally where width is 2.2× width of anterior margin. Eye bare, unknown if male holoptic or with dorsal and ventral facets differentiated (only females known). Eye shape unknown (eyes collapsed in AMNH L-JS97, covered with milky coating in JS204). Oral margin of face with pair of thick, stiff setae on anterior tip, setae very close together. Frons without setae or setulae. Antenna aristate, with flagellomere I slightly drop-shaped, the apex narrow; arista apical, with 3 aristomeres; basal two aristomeres small, of approximately equal size; apical flagellomere only about 1.5× length of flagellomere I, with microscopic pubescence. Ocelli and ocellar setae barely raised above frons; two pairs of short ocellar setae present, anterior pair 2× length of posterior pair. Pair of minute, convergent inner vertical setae present (lengths about same as posterior ocellars); outer verticals about 2× the length. THORAX: Notum with single, median row of acrostichal setulae; pair of paramedian rows of six dorsocentrals, most posterior pair of dorsocentrals apparently longer than others based only on socket size (setae were lost). One long notopleural and one postpronotal seta present. No setae on pleura. Scutellum with two pairs of setae; short anterior setae, lengths of posterior ones unknown (setae lost). WING: short, apex broadly rounded, but posterior margin not observable. Costal vein with sparse, fine, stiff setulae to nearly R₅, no breaks near where Sc would meet costa, costa extended to apex of M₁; veins h and Sc not observable. R₁ of moderate length, 0.42× length of wing. Base of R complete; R₂₊₃ gradually meeting costa; R₄-R₅ forked, branch of R₅ 0.20× length of wing. Radial and medial veins all lightly sclerotized. M₁ parallel to main trunk of R. Veins r-m and

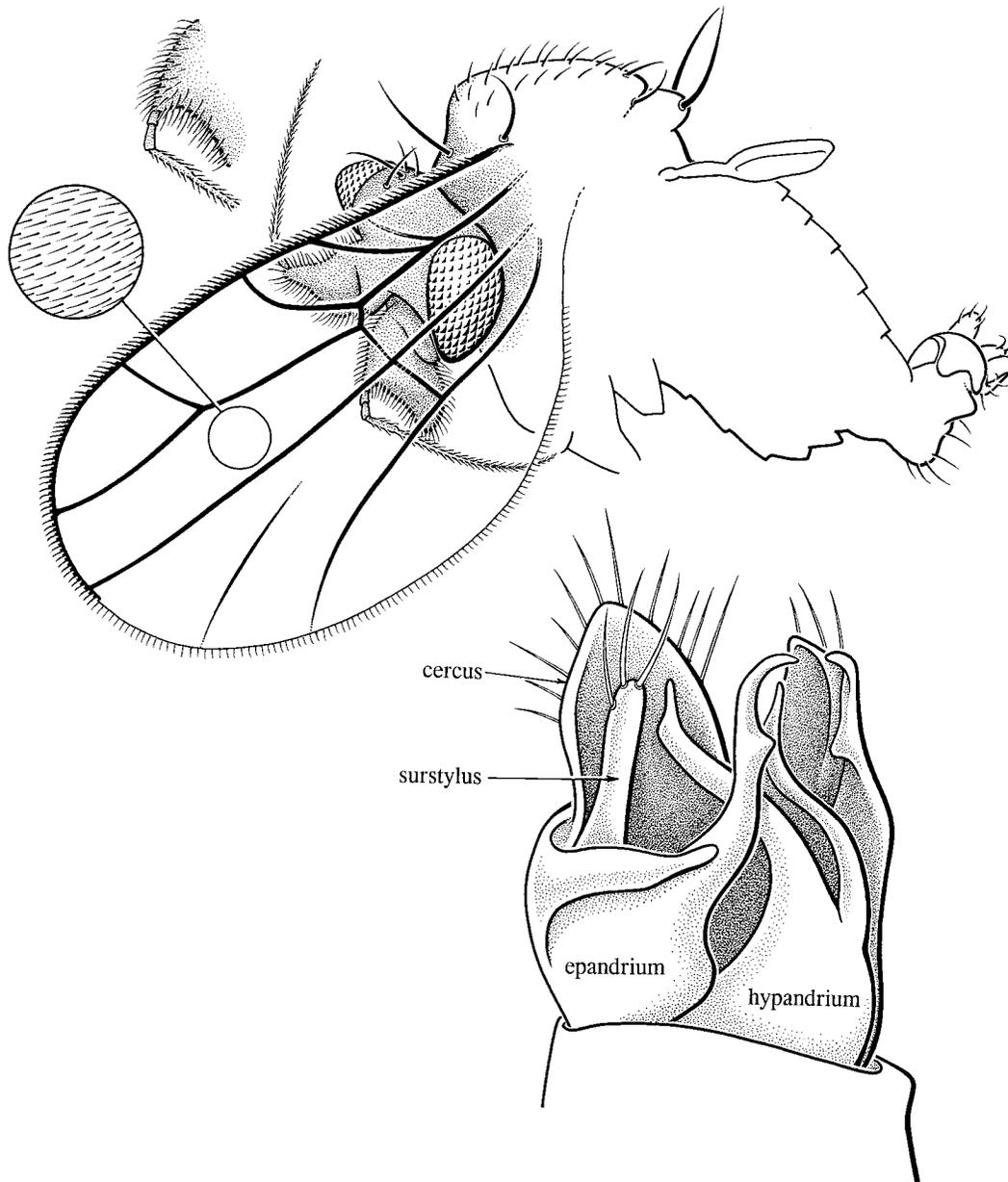


Fig. 48. *Chimeromyia acuta* holotype (AMNH L-AE38), complete specimen, with detail of dense wing microtrichia, base of arista, and genitalia (posterolateral view). Lebanese amber.

m-m connect at M, forming large br-bm cell (vein M does not pass between br-bm). M_2 lost. Total length of CuA and existence of anal veins not observable. ABDOMEN: Known only for females, with apical three segments apparently telescoping.

TYPES: Holotype: ♀, AMNH L-JS97 (Acra

Collection), in Neocomian amber from Lebanon, collected by Aftim and Fadi Acra from near Jezzine. Paratype: ♀, AMNH L-JS204 (Acra Collection), *ibid.* The paratype has most of the wing obscured, but is referable to this species on the basis of the setation. Unfortunately, the body of the paratype is

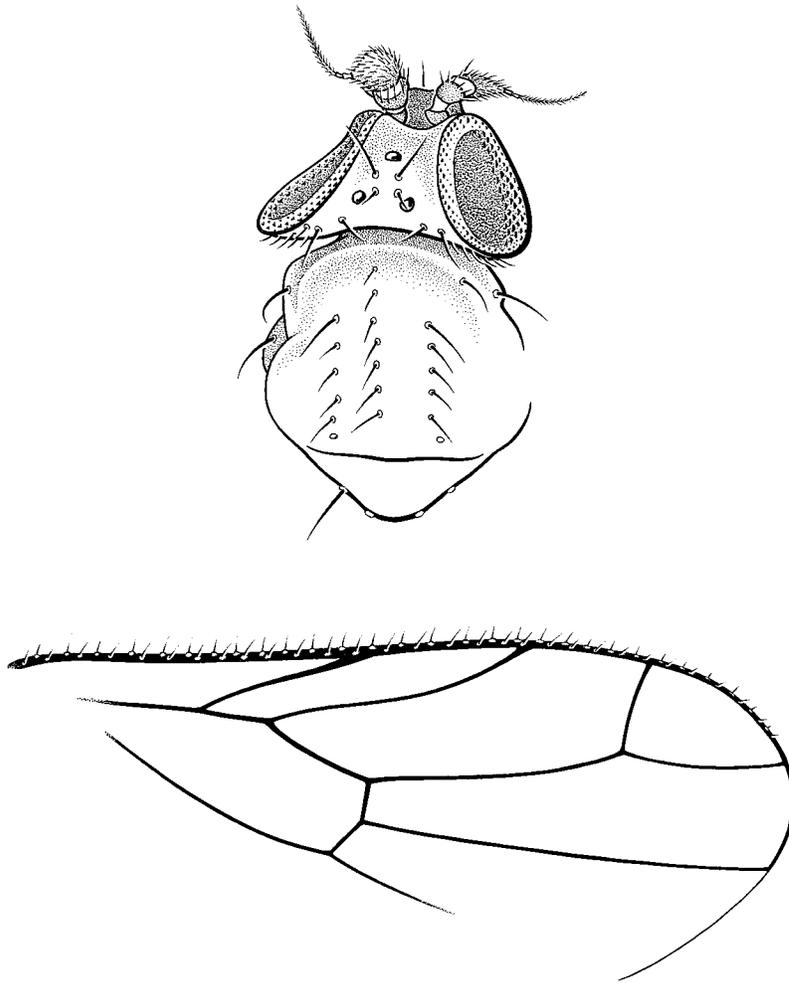


Fig. 49. *Chimeromyia reducta* holotype (AMNH L-JS97), dorsal view of head and thorax (eyes collapsed) and visible portion of wing. Lebanese amber.

largely covered with a milky coating, through which the setae protrude. Both specimens were vacuum-embedded in epoxy.

ETYMOLOGY: In reference to the reduced size of the setae and wing venation.

SECTION EREMONEURA
SUBSECTION CYCLORRHAPHA
FAMILY PLATYPEZIDAE (?)

ELECTROSANIA, *NEW GENUS*

DIAGNOSIS: Mouthparts small; antenna aristate; arista terminal, with two flagellomeres; pair of dorsocentral setae present; acrostichal setulae numerous and irregularly ar-

ranged, not in a single row; wing with cell dm present, large; vein M_{1+2} forked, with posterior fork extended in line with base of M vein, anterior fork turned abruptly anteroapically and more than twice the length of posterior fork; r-m crossvein considerably distant from crossvein m-cu, nearly in middle of vein M; cell cup large; calypter present.

Venation similar to *Proplatypeza* Mostovsky, from the Lower Cretaceous of Baissa, Buryatiya, and Lake Bon Tsagan, Mongolia, but differs from *Proplatypeza* by having longer fork of M_1 ; m-cu crossvein not slanted; crossvein r-m considerably distal to basal m-cu (instead of opposite each other); and much

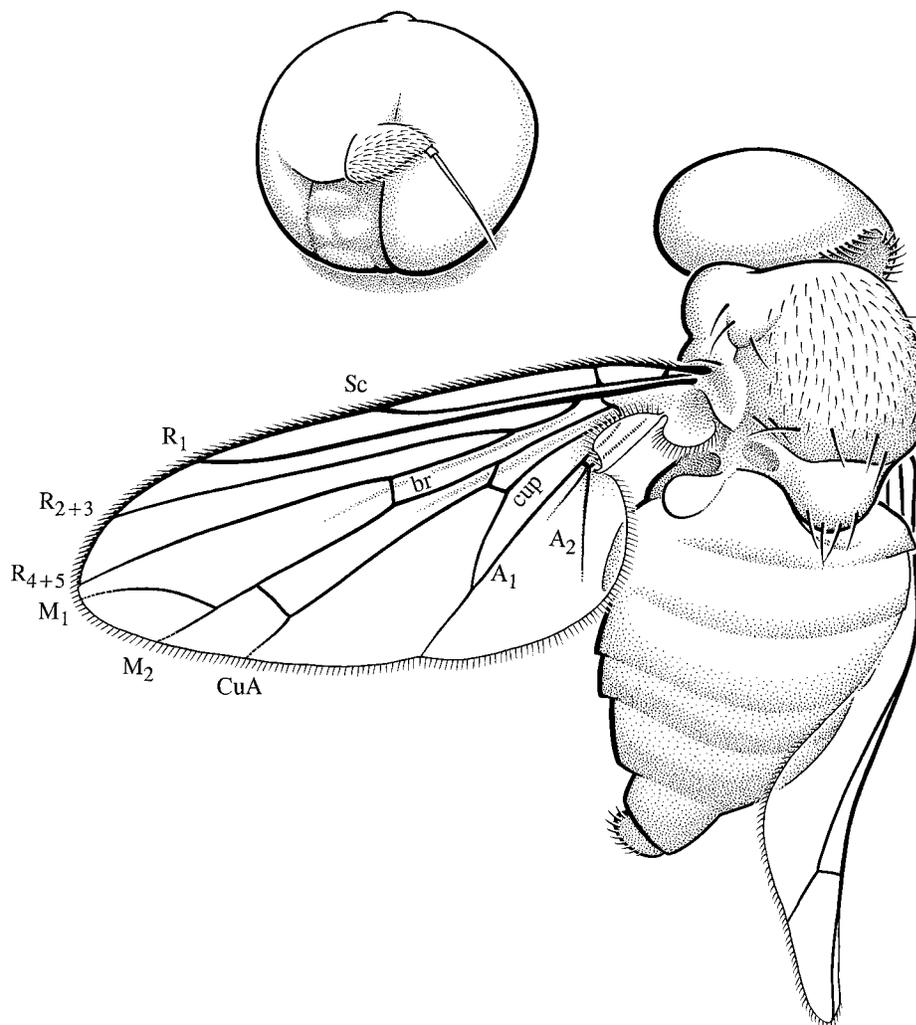


Fig. 50. *Electrosania cretica* (Platypezoidea) holotype (AMNH NJ-518a), also with front of head. Head and body are largely covered with a milky coating. In New Jersey amber.

longer R_1 . Also, *Electrosania* has no enlarged hind basitarsomeres.

TYPE SPECIES: *E. cretica*, n.sp. Known only from mid Cretaceous (Turonian) amber of New Jersey.

ETYMOLOGY: *Electro-*, referring to the Greek for "amber"; and *-sania*, an ending for a modern, primitive genus of platypezids, *Microsania*.

Electrosania cretica, new species

Figure 50

DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 3.45 mm;

thorax length = 1.29 mm; wing length = 3.18 mm. Body largely covered with milky coating, obscuring many details of head and body. HEAD: Eyes apparently large, hemispherical, no gena appears present; apparently not holoptic (but sex of specimen is ambiguous, preserved portions of terminalia are suggestive of female) Mouthparts small, barely protruding. No large setae protruding though milkiess on head; left antenna protrudes through milkiess, revealing a roughly conical flagellomere I, flagellomeres II+III aristate, situated apically on flagellomere I. Two aristomeres present; basal one minute,

length approximately equal to width; apical aristomere slightly longer than flagellomere I, completely bare. THORAX: With notum evenly covered with numerous, fine, irregularly spaced acrostichals. Three setae on postpronotal lobe; three, closely situated supra-alar setae; pair of short dorsocentral setae, close to center of notum and near scutellum. Scutellum with two pairs of short setae. Legs undifferentiated (no broadening of basal tarsomeres on hind legs). WING: Venation well preserved. Vein C not circumambient, ends at apex of R_{4+5} or possibly M_1 , but this structure at tip of wing not perfectly observable; Sc complete, no breaks in C at h or Sc; veins R_1 , R_{2+3} , and R_{4+5} virtually straight, unbranched; crossvein r-m distant from m-cu by four times length of r-m, r-m nearly in middle of M; vein M with apical fork (M_{1+2}), posterior branch of fork in line with stem of M; anterior branch 2.7× longer than posterior branch and turned abruptly costad, apex nearly touching apex of vein R_{4+5} . Crossvein dm-cu considerably apicad, distance from margin of wing equal to length of crossvein. Cell cup large, nearly twice length of cell bm; length cup nearly three times length of distal portion of vein A_1 . A_2 straight, well developed, but not reaching wing margin. Anal lobe, alula, and calypter well developed. Membrane of wing with fine microtrichia. ABDOMEN: Largely concealed by milky coating; terminalia appear small, suggestive of female.

TYPE: Holotype, AMNH NJ-518a (KL-454a), collected by Keith Luzzi at White Oak Pits, Sayreville, New Jersey. The fly is in a piece of amber that was originally cylindrical, then was embedded and sliced lengthwise for an oblique dorsal view of the fly and a full view of the wing. Typical of New Jersey amber, the core layers of cylindrical pieces have the densest suspension of particles.

ETYMOLOGY: Referring to Cretaceous.

COMMENTS: The wing venation of *Electrosania* is most similar to that of the aschizous Cyclorrhapha, particularly cell dm, the forked M_{1+2} , and the arrangement of cells br, bm, and cup. *Electrosania* can be excluded from the Syrphidae due to the lack of a spurious vein through r-m (which occurs in most syrphids, except, e.g., some *Graptomyza* and *Paragodon*) and lack of an sc-r crossvein.

Pipunculids have an autapomorphic wing venation (plus other features), and the lack of a geniculate proboscis and fusion/near fusion of R_{2+3} and R_{4+5} also excludes the fossil from the Conopidae. The large calypter and especially the shape of the forked M_{1+2} vein is indicative of the Platypezidae, the latter character being strikingly similar to that of some of the more derived, extant genera like *Polyporivora*, *Plesioclythia*, and *Calotarsa*. A distinctively long cup cell in the fossil is also seen in *Polyporivora*. On the other hand, there are two features of *Electrosania* distinctly plesiomorphic to all known extant genera of platypezids: a two-segmented arista, and numerous scattered acrostichals (vs. single row, or no acrostichals). While all Cyclorrhapha and some empidoids have three aristomeres, two aristomeres in *Electrosania* is possibly the primitive state, not a loss of one segment, which would be most consistent with the plesiomorphic acrostichals. The arista and acrostichals would make *Electrosania* the most plesiomorphic platypezid.

There have been several genera of brachycerans described in the Platypezidae based on compression fossils from the Upper Jurassic of China described by Zhang (1987) and Hong and Wang (1988). Mostovski (1996a) synonymized *Sinolesta* Hong and Wang with *Palaeopetia* Zhang, and the latter genus transferred to the Ironomyiidae on the basis of the largely fused Sc and R_1 (but see below). The other genera of purported platypezids from the Jurassic of China—*Mesopetia*, *Lithopetia*, and *Pseudopetia*—are only questionably platypezids, or not a platypezid at all, although Evenhuis (1994) included these in platypezids in the world catalog of fossil flies. The venation of *Mesopetia* and apparently *Lithopetia* (not as well preserved as the former) are unlike any living platypezid based on the very long M_{1+2} fork, which has symmetrical branches and barely any stem; also, there are no other diagnostic features preserved other than venation. The venation of *Pseudopetia* is not preserved well enough as drawn by Zhang to show any apomorphic features, and the annulate style on its antenna would also exclude this genus from the Cyclorrhapha: it is perhaps a rhaigionid.

Mostovsky (1995) described five genera

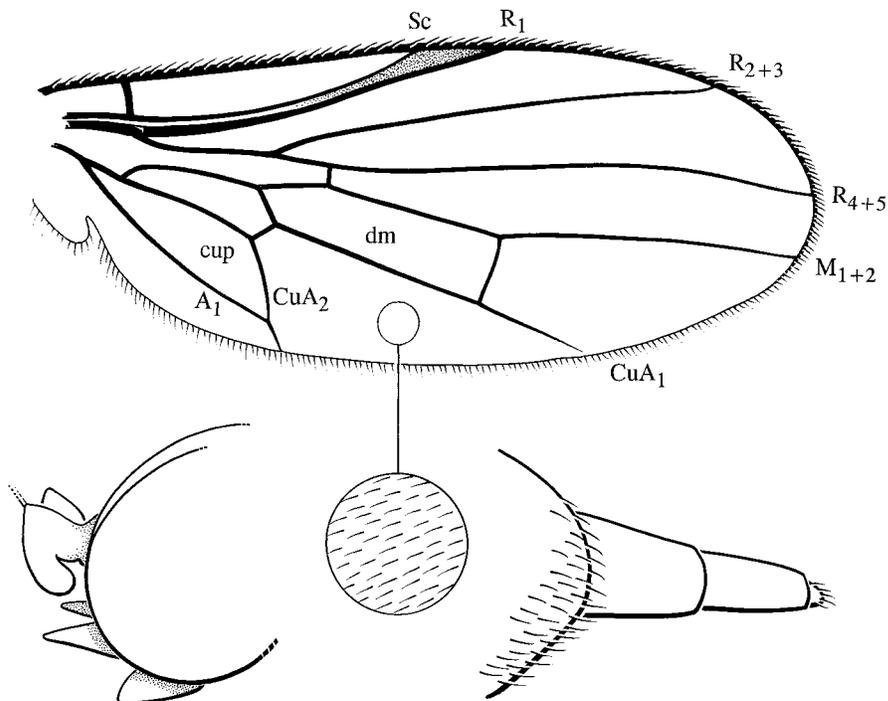


Fig. 51. *Lebambromyia acrai* (Phoridae, near Ironomyiidae) holotype (AMNH JG85/8), showing details of wing, lateral view of head, and terminalia. Lebanese amber.

and 11 species of Platypezidae from the Lower Cretaceous of Baissa, Buryatiya; Cenomanian of Ten'kinskiy, Magadan; and Barremian-Aptian of Lake Bon-Tsagan, Mongolia. Venation of these genera is consistent with modern platypezids, and for Mostovskiy's taxa *Maritulus sospes*, *Parnasos firmipes*, and a lesser extent, *Proplatypeza parva* and *P. amabilis*, the preserved hind tarsi show a broadened basitarsomere. Even though critical details of acrostichals and number of aristomeres are not preserved in the fossils, it is likely that these are platypezids.

FAMILY IRONOMYIIDAE

LEBAMBROMYIA, NEW GENUS

DIAGNOSIS: First flagellomere cordate in lateral view, having pointed apex and rounded ventral lobe; palps pointed; arista terminal, with 3 articles, including two small basal ones; frons with numerous small, stiff setulae, no macrosetae; proboscis small, retracted into oral cavity.

Wing with Sc and R₁ very close, particularly in middle, but not coalesced; area between Sc and R₁ largely sclerotized; vein C extended to slightly beyond apex of M₁₊₂; veins R₂₊₃ and R₄₊₅ nearly straight, not curved; vein CuA₁ absent, m-m vein perpendicular (not oblique) to veins M₁ and M₂; cell cup long, 1.6× length cell bm, base of cup extended proximad well past base of cell bm and distad nearly to wing margin; no trace of vein A₂. Anal lobe of wing very small; alula small. Female terminalia telescoping.

TYPE SPECIES: *L. acrai*, new species, in Neocomian amber from near Jezzine, Lebanon.

ETYMOLOGY: Derived from Lebanon and amber (source and matrix of the fossil) and Greek, *-myia*, a common suffix for fly.

Lebambromyia acrai, new species

Figures 51, 52

DIAGNOSIS: As for genus.

DESCRIPTION: Thorax length = 0.93 mm (holotype)/0.94 (paratype); wing length =

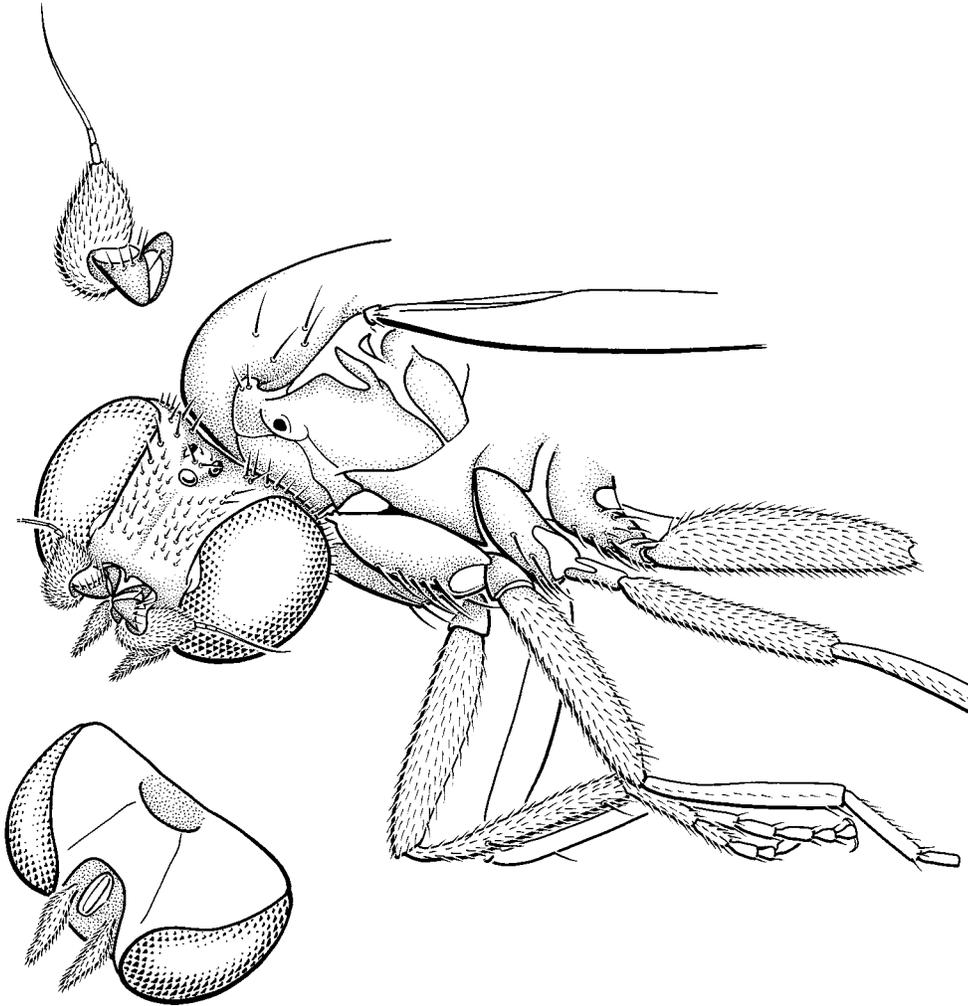


Fig. 52. *Lebambromyia acrai* paratype (AMNH JG292/1), showing entire specimen, detail of antenna, and ventral view of head. Lebanese amber.

1.88 mm (holotype). Based on two specimens, one (holotype, AMNH JG 85/8) with wing venation completely preserved; other specimen (paratype, AMNH JG 292/1) without preserved venation but structure of antennae and palps indicates conspecificity with AMNH JG 85/8. HEAD: Eyes large, occupying entire lateral surface of head (no gena exposed); eye bare, dorsal and ventral facets not differentiated; inner margins of eyes at anterior surface of frons with small areas where 7–8 facets are missing. Antennae very distinctive: pedicel asymmetrically conical, with row of small setae on apical mar-

gin, without thin lobes on inner or outer surfaces; flagellomere I cordate in lateral view, with broadly rounded ventral lobe and narrow apical tip; arista terminal, bare, with three aristomeres, two basal ones short and of equal size; total length of arista 1.2× length of flagellomere I. Palps jutting forward, slender, pointed. Proboscis small, labellum largely retracted within oral cavity. Frons broad, with ca. 25 small, stiff, scattered setulae, including median pair and two posterolateral pairs of slightly thickened ones; pair of small divergent ocellar setae; no postocellar setae; short, stiff vertical and

postvertical setae. THORAX and legs relatively unmodified (fig. 52), postpronotal lobe with two small setae; four small notopleural setae present; katapisternum and other pleural sclerites without setae. WING with membrane having microtrichia, venation well preserved: vein C extended to slightly beyond apex of vein M_{1+2} ; no breaks in C near h or apex of Sc; Sc very close to R_1 , particularly near middle, then slightly divergent apically; area between Sc and R_1 largely sclerotized; veins R_{2+3} and R_{4+5} nearly straight, not curved; basal fork of R_1 and $R_{2,5}$ at level of crossvein h, not considerably distal to h; distance of crossvein r-m from fork of R_{2+3} and R_{4+5} slightly more than twice length of r-m (vs. equal to length of r-m or slightly greater); veins M_1 and M_2 complete, vein CuA_1 not present. Cell dm very long, crossvein m_1-m_2 perpendicular to M veins, not oblique. Cell cup very long, acute; length $1.6\times$ length cell bm, base of cup extended proximad well past base of cell bm and distad nearly to wing margin; no trace of vein A_2 present. Anal lobe of wing barely developed, small alula present. ABDOMEN of AMNH JG85/8 (♀) with apex preserved, showing two long, presumably telescoping segments and a smaller terminal segment (possibly retracted). Without acanthophorite spines at apex.

TYPES: Holotype, ♀, AMNH JG 85/8 (Acra Collection, in AMNH), consisting of two pieces of deep orange amber, each embedded in epoxy and polished separately. One half contains the head, thorax, and left wing; the other half contains the right wing, legs, and abdomen. Body is covered with a milky coating, but the wing is well preserved and reveals most of the diagnostic features.

Paratype, sex unknown, AMNH JG292/1 (Acra Collection, in AMNH), is in a yellowish, highly fractured piece of amber with the head, thorax, legs and basal portions of the wings and abdomen preserved. No milky coating occurs on the specimen, with details of the head, pleura, and legs extremely well preserved, but wing venation barely observable.

ETYMOLOGY: Name derives from patronym, in recognition of Aftim and Fadi Acra, who assembled an important collection of fossils in the Lower Cretaceous amber from

Lebanon. A portion of this collection of which now resides in the AMNH.

COMMENTS: *Lebambromyia* is at the base of or perhaps even the sister group to the entire Phoridae (sensu Brown [1992]: Ironomyiidae + Phoridae + Sciadoceridae). There are two genera of ironomyiids: the living *Ironomyia nigromaculata* White, from Tasmania and New South Wales, Australia (see McAlpine, 1966 for comparative morphology of this species); and *Cretonomyia pristina* McAlpine, in Campanian amber from Cedar Lake, Manitoba (McAlpine, 1973).

Lebambromyia seems to share several distinctive features with the two genera of ironomyiids: structure of basal antennomeres, setation of the frons, and especially the structure of veins Sc and R_1 . In *I. nigromaculata* and *C. pristina* the pedicel has a fingerlike lobe on the medial and lateral surfaces; *Lebambromyia* has no such lobes (plesiomorphically), but flagellomere I is instead cordate and with a pronounced ventral lobe, so the basal antennal segments are clearly not homologous. In all three taxa the frons has scattered, short, stiff setulae, which is actually probably plesiomorphic given a similar condition in the platypezids. Lastly, in *I. nigromaculata* and *C. pristina* the Sc is largely or briefly fused with vein R_1 , and the space between where they diverge apically is sclerotized (McAlpine, 1973 did not mention this latter character, but re-examination of type no. 12920 in the CNC indicates this region is slightly sclerotized—sometimes pterostigmas and other such sclerotized areas on membranes are not well preserved in amber fossils). This appears to be the only feature that *Lebambromyia* shares with ironomyiids that is possibly (but not definitively) apomorphic.

Brown (1992) indicated that since Sc and R_1 are fused in sciadocerids and phorids, the partial fusion seen in ironomyiids is symplesiomorphic. In fact, Brown (1992) discussed that only a “tentative” synapomorphy links the two ironomyiid genera, the structure of the antennal pedicel—in our view, a very distinctive and probably reliable synapomorphy. Another apparent synapomorphy of ironomyiids is the sclerotization between the divergent, apical portions of Sc and R_1 . If

this were the plesiomorphic groundplan of the Phoroidea, one would expect the apical part of Sc+R₁ in phorids and sciadocerids to be greatly thickened, which it is not. Also, the vein that connects M₁₊₂ and CuA₁ (labelled as vein M₃₊₄ in McAlpine [1966; 1973]) is oblique and curved: the plesiomorphic condition is definitely as is seen in *Lebambromyia* and platypezids, namely perpendicular to M and CuA veins.

With the exception of the sclerotization between veins Sc and R₁, the venation of *Lebambromyia* is very similar to that of some of the plesiomorphic platypezids, like *Calomyia*, *Bertamyia*, and *Agathomyia*. Some of these plesiomorphic platypezids, in fact, even have Sc and R₁ very close together and with a sclerotized pterostigmal area; but the latter generally surrounds the apex of R₁ and is confined between R₁ and Sc only in a few platypezid genera, nor does this area have the degree of sclerotization seen in ironomyiids. *Lebambromyia* even has microtrichia of standard size on the wing membrane, plesiomorphic to the situation seen in platypezids and ironomyiids where the microtrichia are microscopic and make the wing membrane appear glassy.

Mostovsky (1996a) described 19 new species and 2 new genera of brachyceran flies from Lower and Upper Cretaceous sediments of Siberia and Mongolia, which he placed in the Ironomyiidae. Without explicitly stating so, these assignments were apparently made on the basis of wing venation, since all the fossils have Sc and R₁ apparently coalesced, except for an apical fork in which there is often sclerotization (limited resolution in rock fossils makes the coalescence of veins Sc and R in these fossils a feature of probability, not certainty. Even in *Lebambromyia* preserved in amber, close scrutiny is required to see through the sclerotization that Sc and R are very close but not coalesced). Unfortunately, and expected for compression fossils, details of the basal antennomeres are not preserved in these Eurasian Mesozoic flies. Also, very unusual is that all species have M₁ and M₂ forked, unlike ironomyiids, with both branches symmetrical. The more derived genera of Platypezidae have forked M₁-M₂ veins, but these veins are nearly always asymmetrical, with the costalmost branch be-

ing longer and curved upward. Thus, the fossils described by Mostovsky (1996a) should only tentatively be considered Ironomyiidae.

FAMILY LONCHOPTERIDAE (?)

LONCHOPTERITES, NEW GENUS

DIAGNOSIS: Antenna with terminal arista, arista with two articles (possibly three, if a small basal one is obscure). Head with large, thick setae, including pair of vibrissae, pair of thin anterofrontals, pair of thicker posterofrontals (slightly laterocline), pair of large ocellars, postverticals, and two pairs of verticals. Legs with conspicuous setae on tibia, especially anterior surface and apex. Wing with apex moderately pointed; costal vein spinulose; vein R₄₊₅ ending at narrow apex of wing; R₂₊₃ and R₄₊₅ divergent at very base of wing; fork of M₁-M₂ near middle of wing, r-m crossvein not apparent (presumably close to base of wing); cubital area largely obscured, but well developed anal lobe present.

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

ETYMOLOGY: From Greek, for "like *Lonchoptera*," referring to the type genus of the Lonchopteridae.

Lonchopterites prisca, new species

Figure 53

DIAGNOSIS: As for generic diagnosis.

DESCRIPTION: Body length = 1.11 mm; thorax length = 0.37 mm; wing length = 0.94 mm. HEAD: Antenna with flagellomere triangular, laterally flattened; arista terminal, with two segments (possibly three, if a small basal one is obscure); apical segment of arista micropubescent. Head with large, thick setae, on slight tubercles. Setae include pair of proclinate vibrissae, pair of thin anterofrontals (anterodorsocline), pair of thicker posterofrontals (laterocline), pair of large ocellars (projected upward and divergent), postverticals (cruciate for about 0.25× their total length), and two pairs of verticals (ipsilateral verticals cruciate for 0.6× their total length). All setae on head of nearly same length. Eyes large, bare, without differentiated facets. Cheek narrow (depth is 0.35× depth of eye); face tall, with very slight carina. THORAX: Full, dorsal view of notum not possible, but

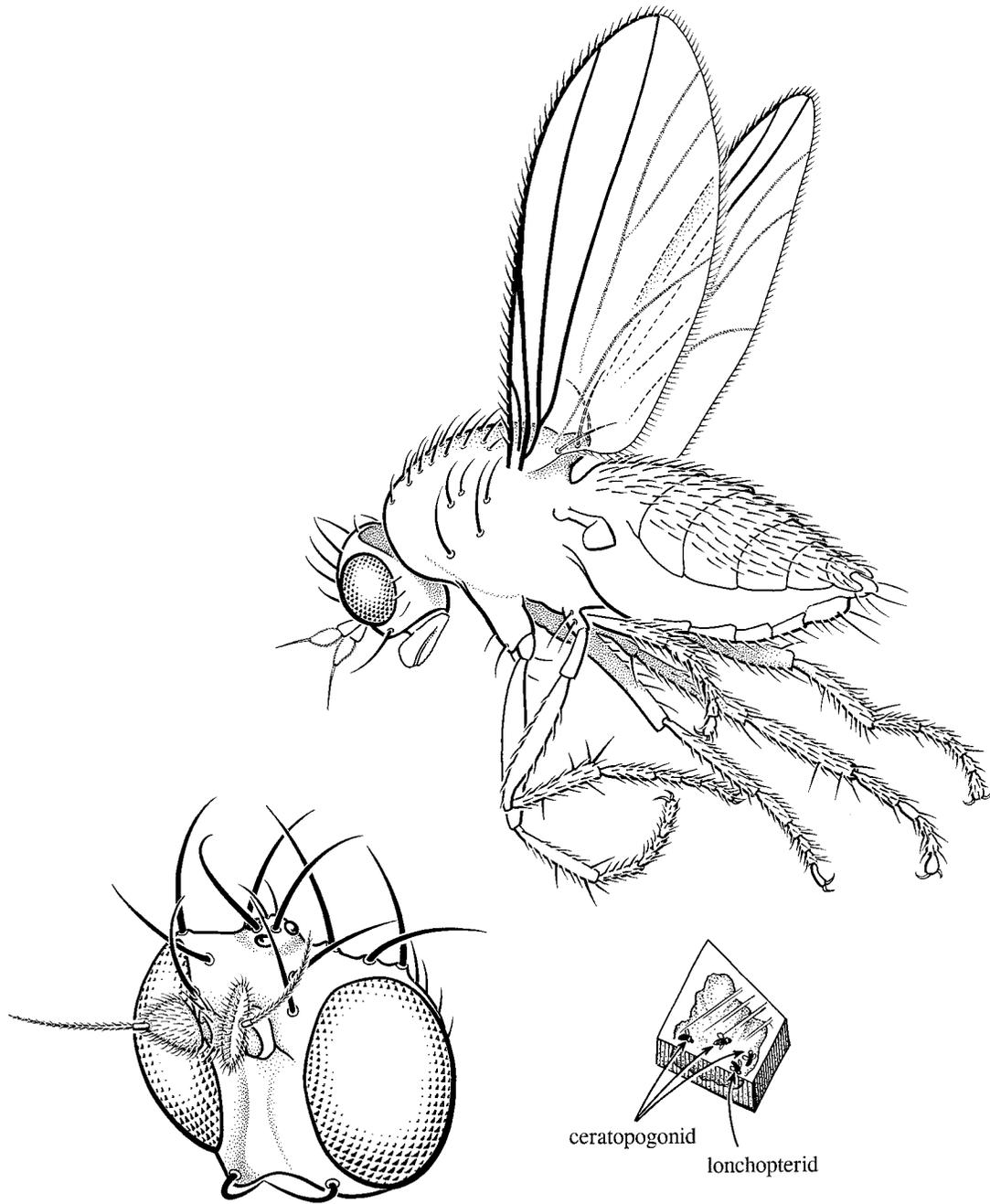


Fig. 53. *Lonchopterites prisca* (Lonchopteridae) holotype (AMNH L-AE79), with detail of head (frontal view), and embedded amber piece showing position of specimens. Lebanese amber.

what appear to be short dorsocentrals or large acrostichals are present; two pairs of scutellar setae present, apical pair cruciate for $0.5\times$ their length. Largest setae on thorax are pair of notopleurals, and three anepisternal setae (twice length of notopleurals). Legs bristly; forefemur with ventral row of long setae (setal length about equal to width of femur); tibiae with conspicuous setae, especially on anterior surface and apex; apices of tarsomeres with conspicuous setae. WING: Moderately broad, length $2.4\times$ width; with apex moderately pointed; costal vein spinulose, ending at apex of vein R_{4+5} . Vein R_{4+5} terminating in narrow apex of wing; R_{2+3} and R_{4+5} divergent at very base of wing; fork of M_1-M_2 near middle of wing, r-m crossvein not apparent (presumably close to base of wing); cubital area largely obscured, but well developed anal lobe present. Only female known; abdomen of generalized structure, with small pair of terminal cerci closely adpressed to apex of abdomen.

TYPE: AMNH L-AE79, in amber from the Neocomian of northern Lebanon, near Bcharre, collected by Antoni Estephan. The clear yellow amber piece is embedded in epoxy, and also contains two female and one male *Leptoconops* (Ceratopogonidae). The lonchopterid is complete and well preserved, although parts of the thorax are obscured by fractures. A full lateral view of the body and frontal view of the head was made possible by cutting and trimming the specimen parallel and close to those surfaces of the fly. Some parts of the venation are seen best in the right wing, although only the left wing is fully illustrated.

ETYMOLOGY: From Latin, for "old" or "ancient."

COMMENTS: The basal portions of M, Cu, and anal region of the wing cannot be observed clearly, so it will be difficult to confirm if the fossil possesses certain synapomorphies of modern lonchopterids (e.g., very short CuA_2 , small bm and cup cells). Nonetheless, the fossil is rather striking in that the only apparent fossils of the Lonchopteridae would be found in such rare and ancient amber instead of, say, the much more abundant Baltic amber (Hennig, 1973). The modern fauna of Lonchopteridae is modest, with only about 35 described species, the greatest diversity cen-

tered in southeast Asia (Saigusa, 1975). Moreover, the family appears to be of special phylogenetic significance, being a primitive member of the Phoroidea (sensu Cumming et al., 1995) or Phoroidea (sensu Brown, 1992).

Some characteristics of *Lonchopterites* are similar to the living, relict genus *Opetia* (Opetiidae). Even though AMNH L-AE79 is a female, its venation is similar to that of male *Opetia*, specifically the lengths and positions of radial and medial forks, and the course of CuA_1 . Also, the apparent 2-segmented arista in *Lonchopterites* is similar to the situation in *Opetia*, which also has (plesiomorphically) a terminal arista. However, *Lonchopterites* is probably a very plesiomorphic member of the Lonchopteridae (see phylogenetic analysis, below), based on the following characters. Venation: Costa heavily spinulose; veins R_1 and Sc are short (although the former is slightly longer than in any living species), fork of veins R_{2+3} and R_{4+5} are very deep, near the base of the wing (vein R_{2+3} in the fossil plesiomorphically does not curve toward R_{4+5}); R_{4+5} longitudinally bisects the wing near the middle, ending in a pointed apex. The wing apex is moderately pointed, but shape of the wing is not lanceolate as in modern species; the fossil plesiomorphically possesses a well-developed anal lobe (entirely lost in modern species). The fossil plesiomorphically does not have a circumambient costal vein, but C ends at the apex of R_{4+5} .

Overall the fossil has a bristly body like modern lonchopterids, although the setae on the head are more developed than those on the thorax. As in modern lonchopterids, the vibrissae are well developed, and orbital setae are long and thick. Unlike modern lonchopterids there are two pairs of frontal-orbital setae in the fossil, which is a situation also seen in the Canadian amber fossil phorid, *Sciadophora bostoni*. Also similar to modern lonchopterids are the very long, upright ocellar setae. Lastly, the primitive nature of the fossil is also revealed by structure of the antenna: arista is plesiomorphically terminal/apical (not subapical as in modern species), and two aristomeres appear to be present—although this latter feature is somewhat uncertain because of preservation.

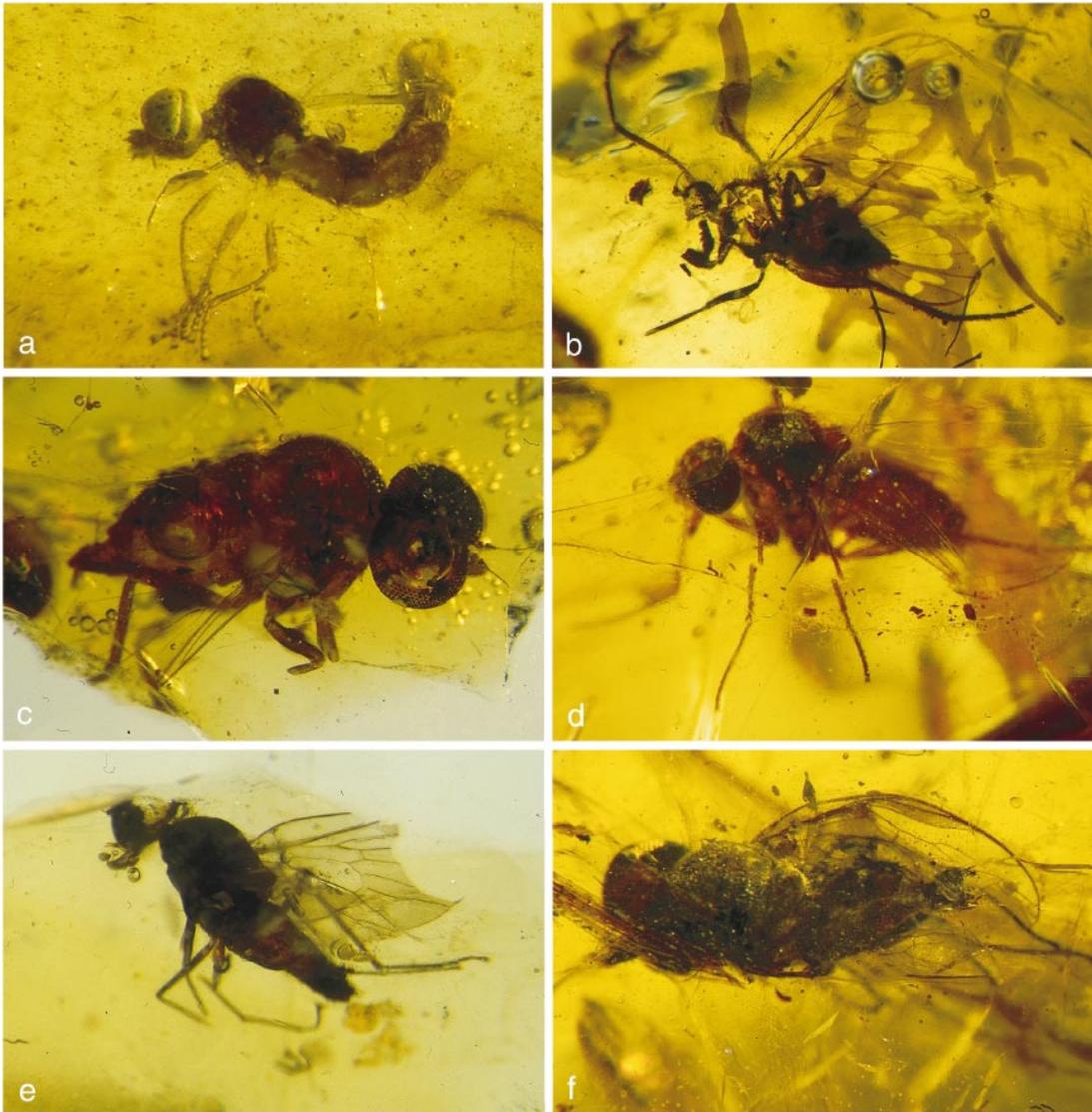


Plate 1. Family indet. (a) and Rhagionidae. b, d–f: Lebanese amber; a, c: New Jersey. **a.** *Tethepomyia thauma*, holotype (AMNH NJ-599). **b.** *Paleochrysopilus hirsutus*, holotype (AMNH L-AE89). **c.** *Jersambromyia borodini*, holotype (AMNH NJ-900). **d.** *Mesobolbomyia acrai*, holotype (AMNH JG 387/16). **e.** Rhagionidae genus C (AMNH L-AE131). **f.** Rhagionidae genus D (AMNH JS43).

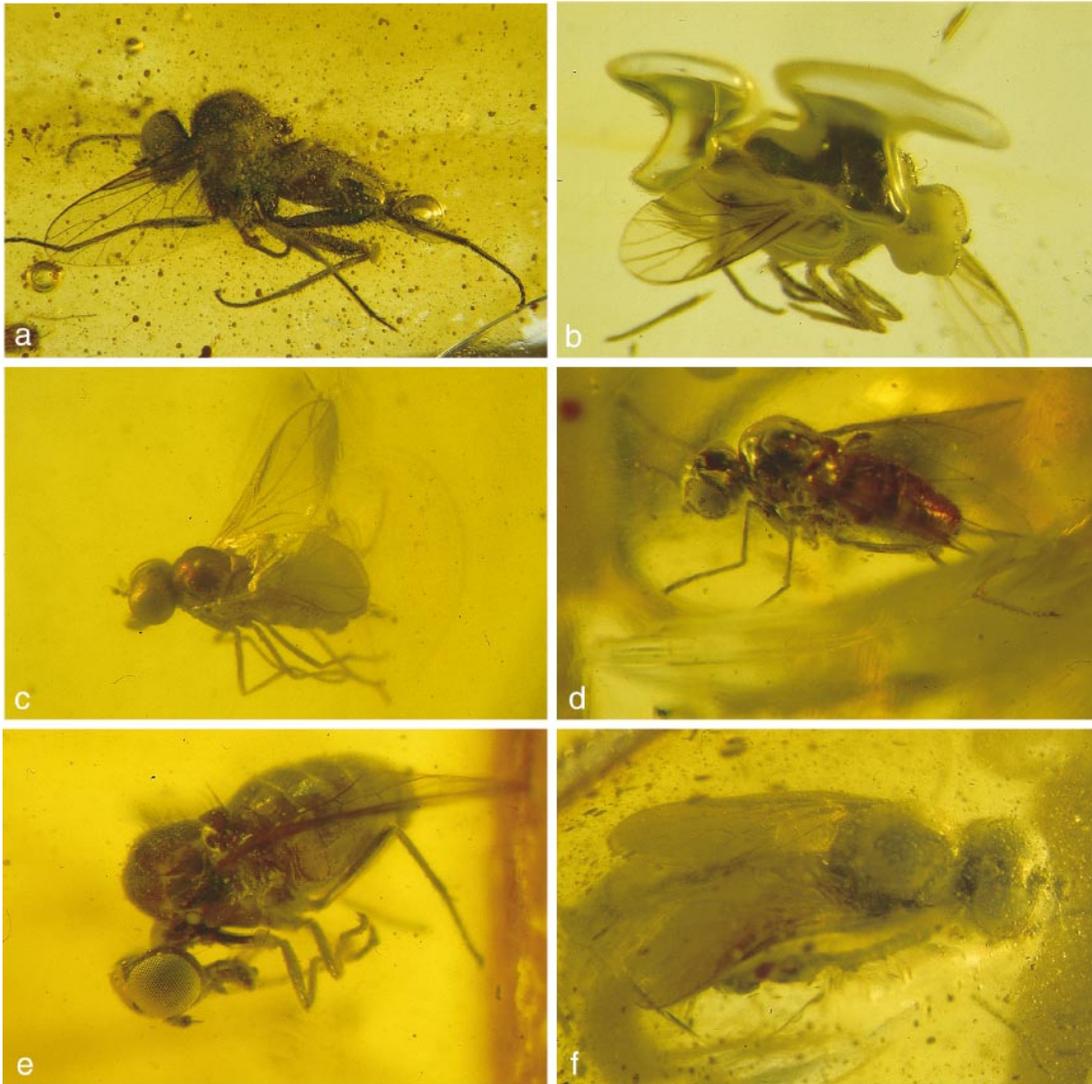


Plate 2. Asiloidea in New Jersey amber. **a.** *Hilarimorphites superba* (Hilarimorphidae), paratype (AMNH NJ-673). **b.** *H. longimedia*, holotype (AMNH NJ-417). **c.** *H. yeatesi*, paratype (AMNH NJ-168). **d.** *H. yeatesi*, paratype. **e.** *H. setosa*, holotype (AMNH NJ-495). **f.** *Proratites simplex* (Scenopinidae?), holotype (AMNH NJ-678).

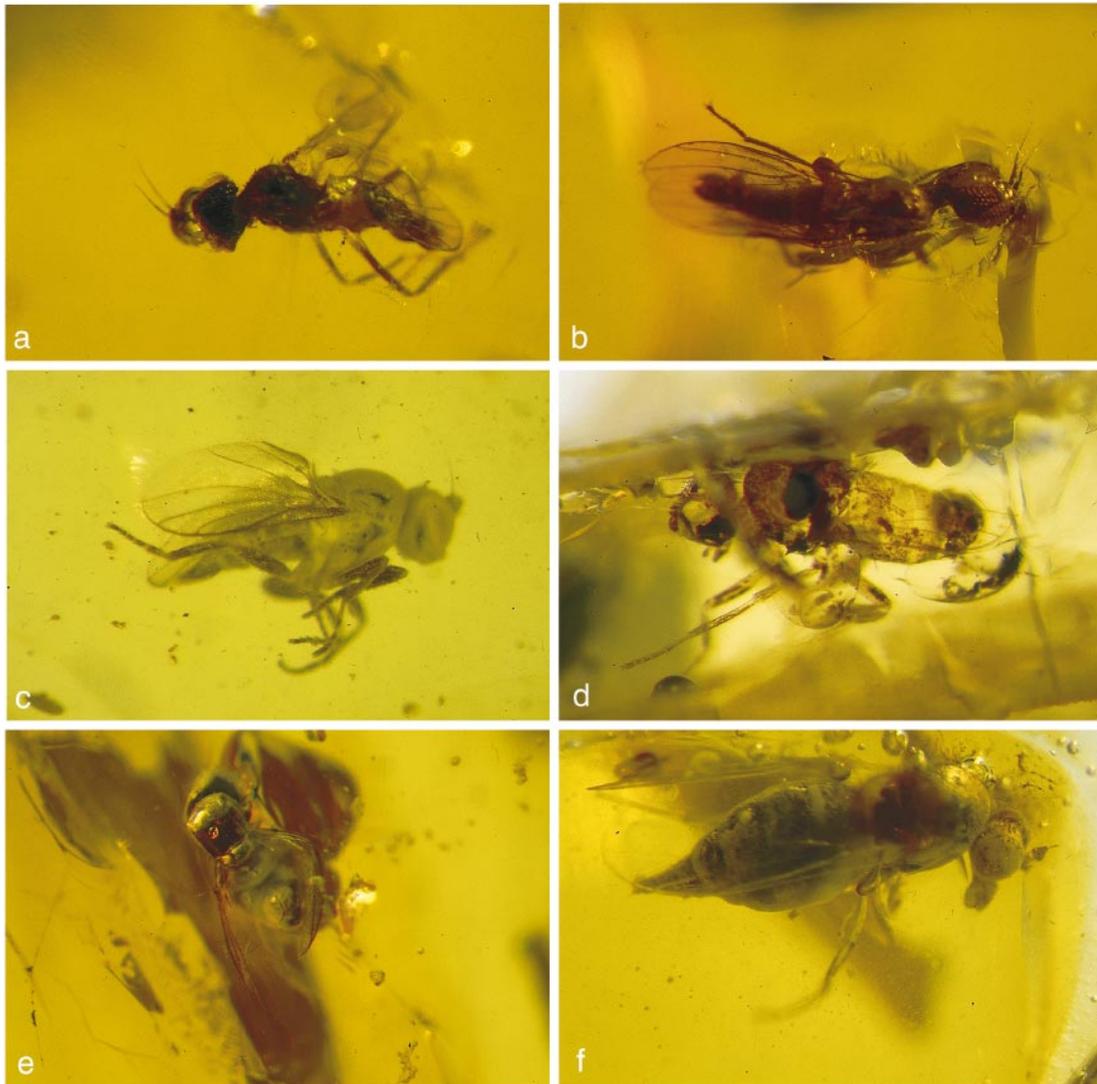


Plate 3. Empidoidea: a, b: Lebanese amber; c–f: New Jersey. **a.** *Atelestites senectus*, holotype (AMNH L-AE72). **b.** *Atelestites senectus*, paratype (AMNH L-AE72A). **c.** *Neoturonius vetus*, holotype (AMNH NJ-774). **d.** *Neoturonius asymmetrus*, holotype (AMNH NJ-90N). **e.** *Nemedromia turonia*, holotype (AMNH NJ-132). **f.** *Emplita casei*, holotype (AMNH NJ-200).

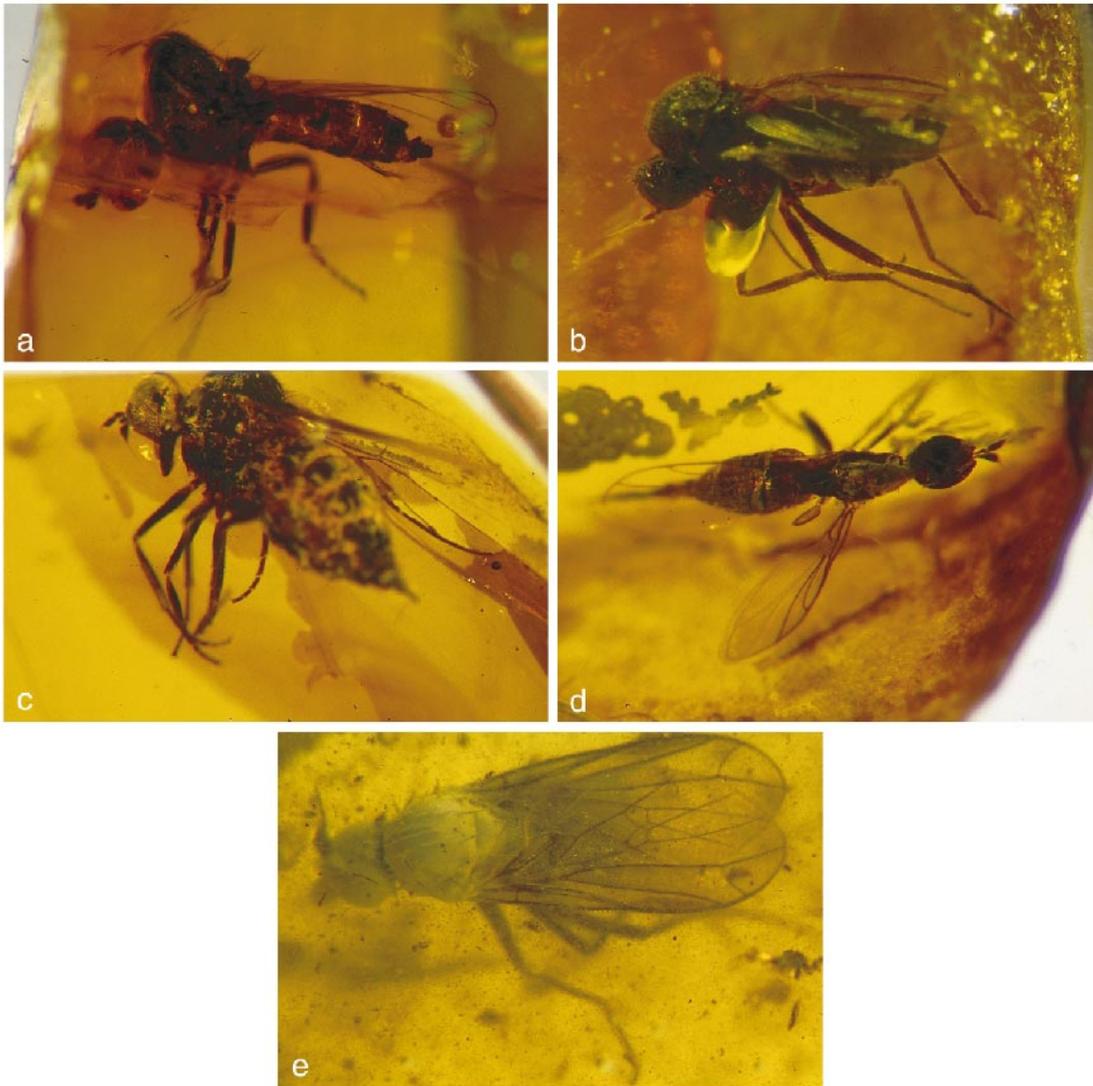


Plate 4. Empidoidea: a–d: Canadian amber; e: New Jersey. **a.** *Cretodromia glaesa*, holotype (MCZ 7097). **b.** *Cretoplatypalpus americana*, holotype (MCZ 6914). **c.** *Mesoplatypalpus carpenteri*, holotype (MCZ 6911). **d.** *Prolatomyia elongata*, holotype (MCZ 6906). **e.** *Turonempis styx*, holotype (AMNH NJ-520).



Plate 5. Empidoidea (a–d) and Eremoneura incertae sedis (e, f), in Lebanese (a, b, d–f) and Canadian (c) ambers. **a.** *Phaetempis lebanensis*, holotype (AMNH L-AE13). **b.** *P. lebanensis*, paratype (BM Pal. PI II 454). **c.** *Apalocnemis canadambra* (Empididae), holotype (MCZ 6908). **d.** *Sympycnites primaevus* (Dolichopodidae), holotype (AMNH L-AE133). **e.** *Chimeromyia acuta*, holotype (AMNH L-AE38). **f.** *Chimeromyia intriguea*, holotype (AMNH L-AE43).

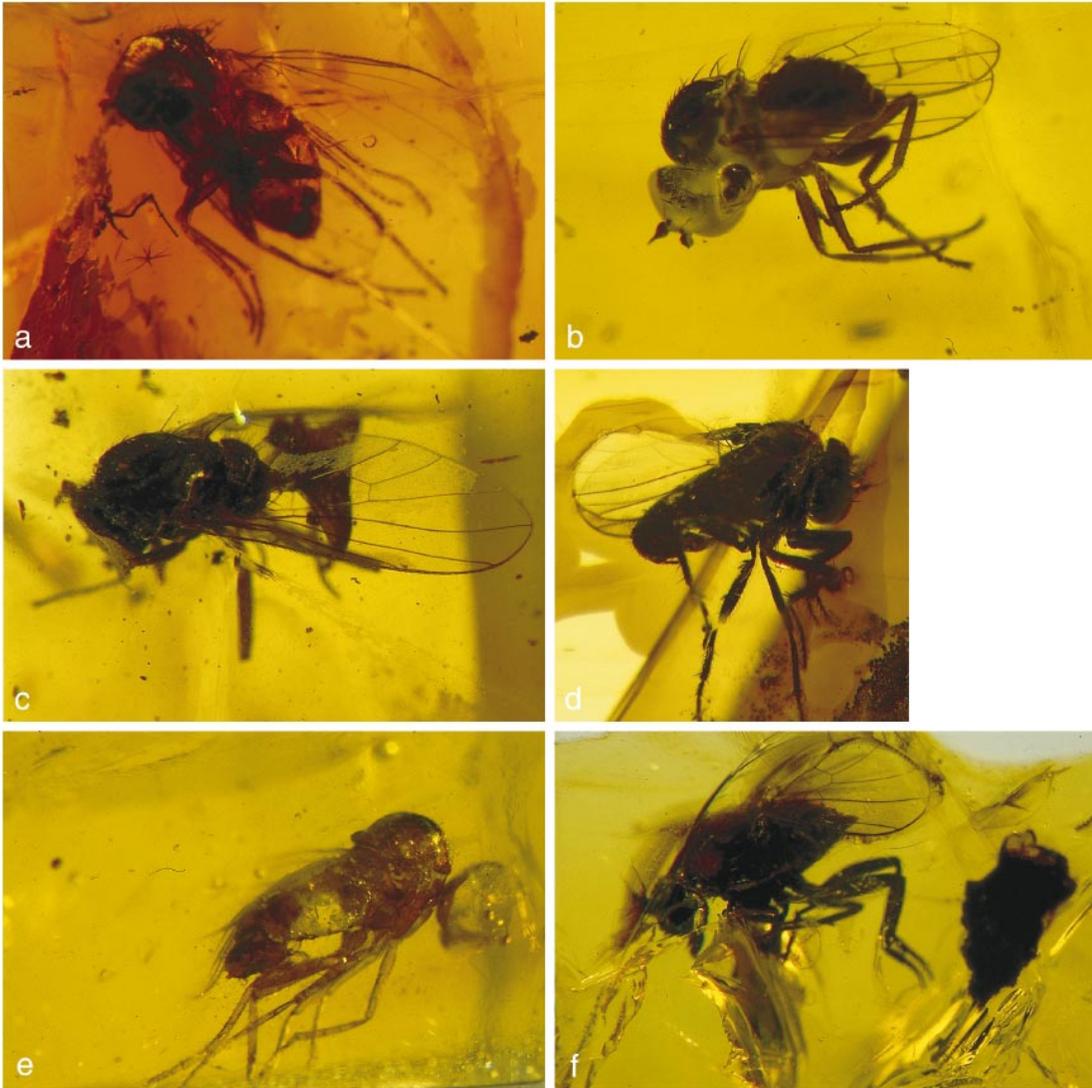


Plate 6. Empidoidea: Microphorinae, in Canadian (a), Lebanese (d–f), and New Jersey (b, c) ambers. **a.** *Archichrysotus manitobus*, holotype (MCZ 7096). **b.** *Archichrysotus incompletus*, holotype (AMNH NJ-169). **c.** *Cretomicrophorus novemundus*, holotype (AMNH NJ-635). **d.** *Avenaphora hispida*, holotype (AMNH L-AE24). **e.** *Microphorites oculus*, holotype (AMNH JS445). **f.** *Microphorites similis*, holotype (AMNH JS424).

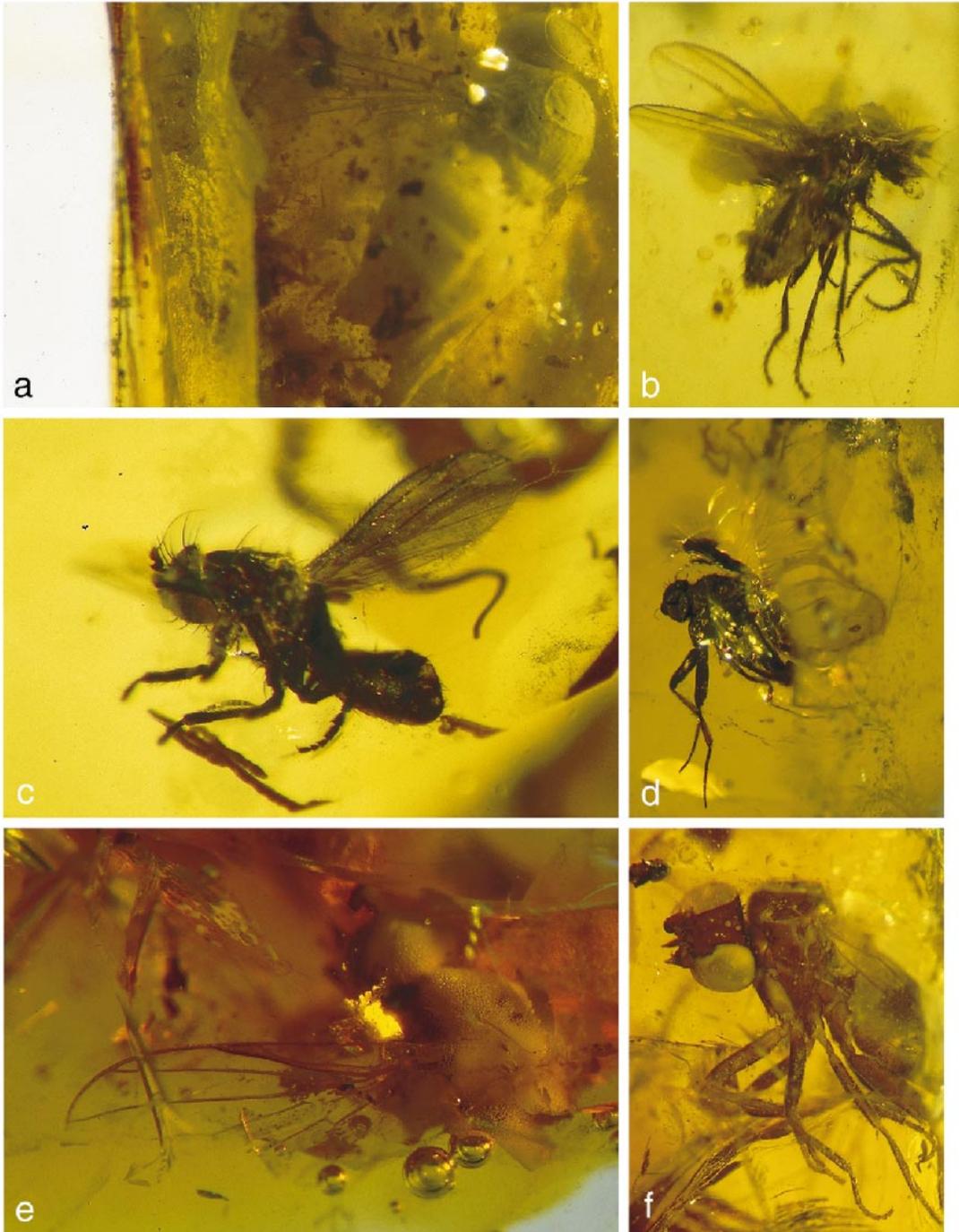


Plate 7. Cyclorrhapha, in New Jersey (a) and Lebanese (b–f) ambers. **a.** *Electrosania cretica* (?Platypezidae), holotype (AMNH NJ-518a). **b.** *Lonchopterites prisca* (?Lonchopteridae), holotype (AMNH L-AE79). **c.** *Lonchopteromorpha asetocella* (?Lonchopteridae), holotype (AMNH L-AE132). **d.** *Archisciada lebanensis* (Sciadoceridae), holotype (AMNH L-AE72). **e.** *Lebambromyia acrai* (?Ironomyiidae), holotype (AMNH JG85/8). **f.** *L. acrai*, paratype (AMNH JG292/1).



Plate 8. Cyclorrhapha in New Jersey amber. a-d: Phoroidea; e, f: larvae, familia indet. **a.** *Archiphora pria* (Sciadoceridae), holotype (AMNH NJ-773). **b.** *Prioriphora casei* (Phoridae), holotype (AMNH NJ-230a). **c.** *Prioriphora luzzii*, holotype (AMNH NJ-281). **d.** *P. luzzii*, paratype (AMNH NJ-519). **e.** Larva (AMNH NJ-628). **f.** Larva (AMNH NJ-280).

LONCHOPTEROMORPHA,
NEW GENUS

DIAGNOSIS: Arista dorso-subapical, 2-articled; interfrontal setae present; pair of vibrissae and series of strong subvibrissal setae present. WING: narrowed apically, not rounded or pointed; M_1 - M_2 deeply forked; CuA_2 short, curved and meeting base of CuA_1 , CuA_1 straight, evanescent (not reaching wing margin); anal vein short, evanescent, anal lobe absent.

TYPE SPECIES: *L. asetocella*, n.sp.

ETYMOLOGY: Meaning "in the form of *Lonchopter*[a]."

***Lonchopteromorpha asetocella*,**
new species

Figure 54

DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 1.08 mm; thorax length = 0.43 mm; wing length = 0.87 mm. HEAD: Frons wide and flat, bristly, with nearly full complement of following pairs of long setae: inclinate inner verticals, lateroocellate outer verticals; two pairs of frontal-orbitals, both slightly reclino-lateroocellate, one pair slightly posteromedial to other; reclinate interfrontals. No ocellar or postocellar setae present. All setae on frons approximately of equal lengths. Eyes sunken in unique specimen, so difficult to discern if pubescent. Antenna: pedicel scoop-shaped, with marginal row of spinules on distal half; flagellomere I somewhat hemispherical, with longer setulae on ventral surface; arista 2-articled, long, slightly more than 3 times length of flagellomere I; basal arisal segment short, its length 2.5× the width; long apical aristomere microsetulose, length of setulae slightly longer than greatest width of arisal trunk. Frontal view of head obscured, but oral margin and/or clypeus apparently protrudent. Pair of vibrissae present, subtended by row of setae along gena decreased in size posteriad. THORAX: Thorax apparently flat, especially anteriorly and above procoxae, much deeper above meso- and metacoxae. Dorsal surface obscured by air bubble, with at least two pairs of dorsocentrals. 3-4 long notopleural setae; 1 slightly shorter supraalar seta; pleura apparently without setae. Legs bristly; fore and mid tibiae (hind tibiae

lost and obscured) with stiff, long middorsal seta; hind tarsomeres stout, basitarsomere more so. WING: infusate, graded to hyaline towards posterior margin; narrowed apically, but not rounded or pointed; C with row of thick spinules that end at apex of R_{2+3} , C ends at apex of M_1 ; Sc incomplete (but this area somewhat obscured in unique specimen); R_1 short, 0.28 length of wing; R_{2+3} and R_{4+5} straight and virtually parallel, apex of R_{4+5} ending just about at apex of wing; very short r-m crossvein apparently present at base of wing; M_1 - M_2 deeply forked, forked section nearly 0.5× length of wing; CuA_2 short, curved, and meeting base of CuA_1 , CuA_1 straight and evanescent; anal vein short, evanescent, with short cu-a crossvein; small cup cell apparently melanized; anal lobe absent; posterproximal margin of wing with row of 10 longer setae. ABDOMEN: without distinctive features; features of (male?) genitalia not apparent in unique specimen.

TYPE: Holotype, (♂?) AMNH L-AE132, in amber from the Neocomian of Lebanon, collected by Antoni Estephan from near Bcharre. Amber is very clear, light yellow, was epoxy-embedded, trimmed and polished to a thin slab 11 × 9 × 2 mm which optimizes lateral view of the fly.

ETYMOLOGY: Name from Greek for *a-* ("without"); Latin *-set-* (for "hair"); and *-ocella* ("little eye"), referring to the absence of ocellar setae.

COMMENTS: This is another lonchopterid-like fly similar to *Lonchopterites*, a distinctly primitive taxon in Lebanese amber. *Lonchopteromorpha* differs from this other genus by the following: dorsal arista, interfrontals present, absence of ocellars and postverticals, presence of subvibrissal setae, slightly stouter hind tarsomeres, wing infusate and apex slightly less acute, R_1 and R_{2+3} slightly shorter, fork of M_1 slightly longer, CuA_1 straight (not slightly curved), and no anal lobe is present on the wing.

Lonchopteromorpha is more derived, and presumably more closely related to modern lonchopterids, on basis of the interfrontal setae, a dorsal arista, structure of the pedicel and first flagellomere, presence of subvibrissal setae, and loss of an anal lobe on the wing. Basal venation of *Lonchopterites* is ob-

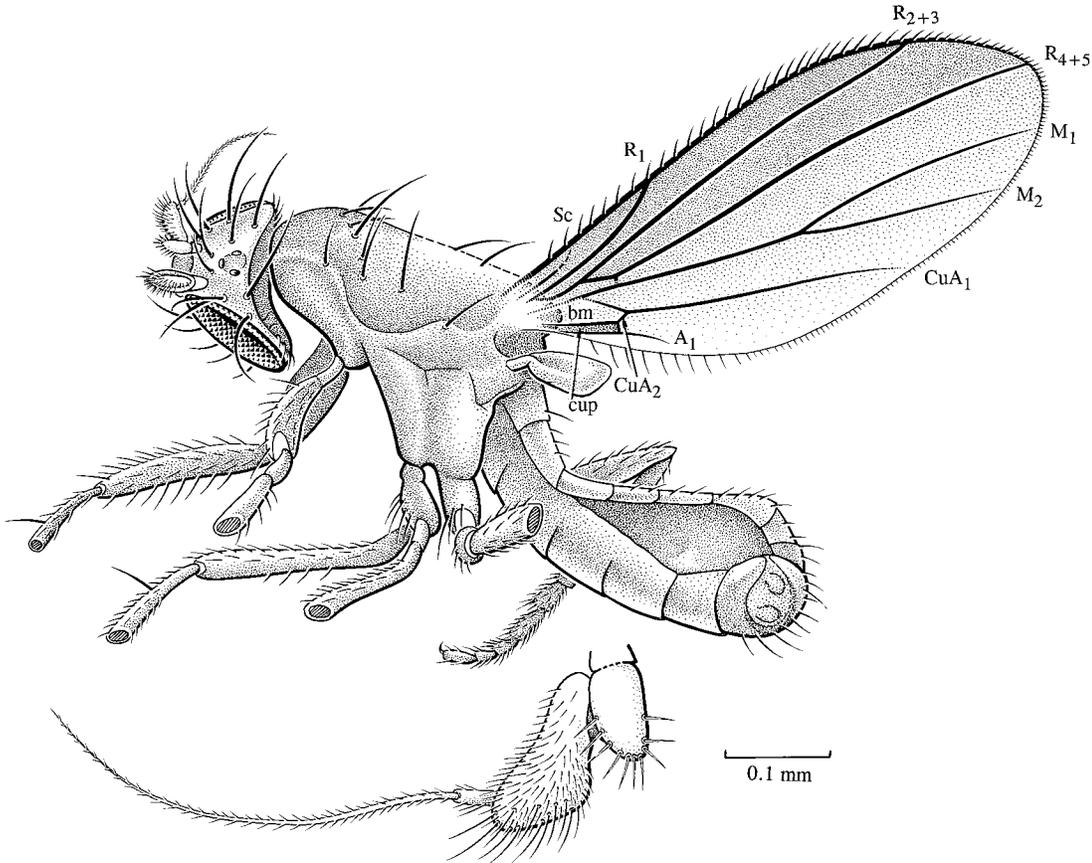


Fig. 54. *Lonchopteromorpha asetocella* (Lonchopteridae) holotype (AMNH L-AE132), complete specimen and detail of antenna. Lebanese amber.

scure, but in *Lonchopteromorpha* the configurations of the small br and bm cells are similar to modern lonchopterids, as is presence of a small cup cell. The small, evanescent vein that is at the posterobasal corner of the wing, which we are calling the anal vein, is probably homologous to the vein termed $A_1 + CuA_2$. Although the phylogenetic analysis of *Cyclorrhapha* (below, and see fig. 62) indicates this genus and *Lonchopterites* to be plesiomorphically separated from living lonchopterids, apparent relationships appear to be: *Lonchopterites* (*Lonchopteromorpha* + living Lonchopteridae).

FAMILY SCIADOCERIDAE

ARCHISCIADA, NEW GENUS

DIAGNOSIS: Antenna with dorsal, 3-articled arista; orbital setae small, stiff, with two

pairs of frontal-orbitals on dorsal half of frons; legs robust, fore coxae approximately twice size of mid and hind coxae; tibial setulae in longitudinal rows; vein C terminates at apex of M_1 ; R_1 long, $0.42 \times$ length of wing; R, M, Cu veins converge in basal fifth of wing, only apparent crossveins are very short, faint $m_1 - m_2$ and m-cu crossveins opposite each other; $A_1 + CuA$ faint but length well developed, nearly reaching wing margin; A_2 also faint but long, curved, evanescent and nearly reaching to apex of $A_1 + CuA_2$. Mid and hind tibiae with middorsal seta.

TYPE SPECIES: *Archisciada lebanensis*, n.sp.

ETYMOLOGY: *Archi*, refers to the fossils' antiquity (Lebanese amber), and *-sciada*, from Sciadoceridae.

Archisciada lebanensis, new species

Figure 55

DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 1.24 mm; thorax length = 0.54 mm; wing length = 1.45 mm. HEAD: Relatively small, eye relatively large, with barely any cheek visible. No dorsal/ventral differentiation of eye facets. No oral setae/vibrissae apparent. Antenna with flagellomere of moderate size; arista situated dorsally, with 3 aristomeres (two of them small and basal), terminal aristomere micropubescent. Orbital setae short, stiff, with two pairs of frontal-orbitals (located on dorsal half of front), pair of ocellars, pair of verticals. THORAX: Without any apparent, large setae on notum or pleura; notum with scattered acrostichals of standard size. Forelegs robust, with coxae twice the size of mid coxae; forefemur thick, with apex having 4 short setae; tibia $0.8\times$ length of femur, widened apically and with setulae in longitudinal rows. Mid and hind tibia with a single mid-dorsal seta, apices of tibiae with small comb of 5–6 short setae. Tarsi slender. WING: Large, broad, width nearly $0.5\times$ the length. Crossvein h apparent, but Sc not apparent (either due to faintness or coalescence with R_1), C extended to apex of M_1 (not R_{4+5}); R_1 long, $0.42\times$ length of wing; R, M, Cu veins converge in basal fifth of wing, with no crossveins except where longitudinal veins converge. Only apparent crossveins are very short, faint m_1 - m_2 and m-cu crossveins opposite each other. Vein A_1 +Cu A_2 faint but length well developed, nearly reaching wing margin; A_2 also faint but long, curved, evanescent and nearly reaching to apex of A_1 +Cu A_2 . Anal lobe large. ABDOMEN: Small, considerably tapered apicad. Male genitalia with epandrium large, slightly asymmetrical; cerci small, thin. Known only from a single male.

TYPE: Holotype, ♂, in amber piece AMNH L-AE72, from the Neocomian of northern Lebanon, near Bcharre, collected by Antoni Estephan.

This piece of amber is rather large and also contains portions of a hymenopteran, roach, a ceratopogonid, and three epidoids. Because of the other inclusions it is difficult to prepare the piece any further for optimal

observation of the sciadocerid. The specimen is complete but portions of the thorax are obscured by fractures and the distal two-thirds of the wings lie under an irregular surface. Since the wing is also very close to the surface of the amber, it is virtually impossible to further prepare the specimen. To follow the paths of veins, many of which are very faint (particularly the bases of the longitudinal veins), the piece must be illuminated with transmitted and reflected light and gradually and constantly tilted in different directions.

ETYMOLOGY: Referring to Lebanon, country of the amber's origin.

COMMENTS: Unfortunately, definitive characters of modern sciadocerids and relatives cannot be confirmed in the fossil, such as 2 (vs. 3) long, unsclerotized spermathecae. The fact that Sc is not observable could be due to it being faint or coalesced with R_1 (the latter a synapomorphy of Phoroidea). Lastly, the most definitive sciadocerid synapomorphy of the fossil is the male genitalia: the epandrium is large, and tilting the amber piece for various views indicates asymmetry of the genitalia. Otherwise, the fossil possesses characters of the Phoroidea, particularly the branching of the medial and cubital veins at the base of the wing and the lack of posterior crossveins. The small bm and bcu cells cannot be detected in the fossil because this region of the wing is somewhat obscure. *Archisciada* could be considered as the most plesiomorphic known phoroid on the basis of the following: size of male flagellomere I unmodified (not particularly large, as in sciadocerids); vein C plesiomorphically extended beyond apex of R_{4+5} to apex of M_1 ; fork of veins M_1 and M_2 very basal, at same level as basal forking of R; vein A_2 long, with anal lobe of wing well developed.

Archisciada lebanensis probably represents the sister group to the living, austral genera *Archiphora* and *Sciadocera*, but also possesses features close to the sister group of the living and other fossil Phoroidea. Since Brown (1992) placed the Canadian Cretaceous genera described by McAlpine and Martin (1966)—*Sciadophora* and *Prioriphora*—in the Phoridae, *Archisciada* is one of only two Cretaceous fossil sciadocerids. *Archiphora robusta* (Meunier) 1917, in Baltic

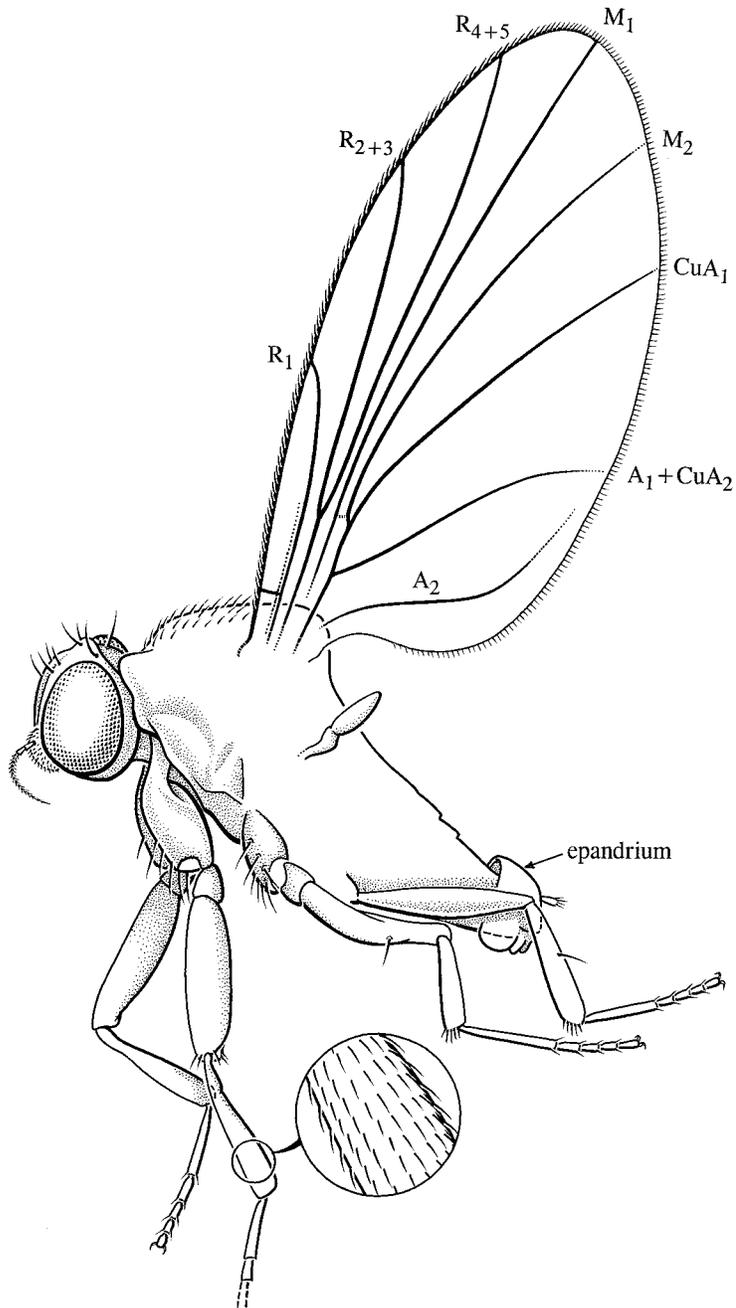


Fig. 55. *Archisciada lebanensis* (Sciadoceridae) holotype (AMNH L-AE72). Lebanese amber.

amber, is another fossil sciadocerid, with another species of *Archiphora* described from Cretaceous amber, below.

GENUS *ARCHIPHORA*

Archiphora Schmitz, 1929: 9. By original designation.

DIAGNOSIS: According to Brown (1992), features shared with the other genus of Sciadoceridae (*Sciadocera*) are an enlarged flagellomere I, empodia absent, vas deferentia not forming a common sperm duct, and asymmetrical male genitalia. Brown, citing Hennig (1964), diagnosed the differences between the two genera by *Archiphora* having an anal lobe that was markedly reduced. He also corrected the illustration of *Archiphora patagonica* venation in McAlpine and Martin (1966) to indicate an incomplete base or stem of the M vein. The sciadocerids are venationally distinct from the plesiomorphic, Cretaceous phorids by the former having CuA₂ lost or reduced (cell cup lost) and the base of M₁-M₂ seemingly shifted forward.

TYPE SPECIES: *Archiphora patagonica* (Schmitz), 1929. The other species in this genus is *A. robusta* (Meunier), in Baltic amber.

Archiphora pria, new species

Figure 56

DIAGNOSIS: Distinguished from *Archiphora patagonica* and *A. robusta* by the larger anal lobe of the wing (plesiomorphic); a complete base of vein M, which turns down and meets the base of CuA (plesiomorphic); forebasitarsus expanded, ovate (apomorphic). Distinguished from *A. robusta* additionally by veins CuA and A being divergent, not parallel (plesiomorphic).

DESCRIPTION: Body of specimen is largely covered with a thick, milky coating, except for legs and wings; the coating obscures many details, but setae still protrude. Body length = 2.59 mm; thorax length = 1.16 mm; wing length = 1.96 mm. **HEAD:** Arista dorsal, basal segmentation obscured; mouthparts largely obscured; frons with very short setae, including three pairs interfrontals, two (frontal-orbital?) pairs posterior to these; ocellar/postvertical setae either very short or largely absent; presence of median furrow on frons obscured. **THORAX:** Dorsal surface of

notum without any setae protruding through coating except for pair of prescutellar (acrosutichal?) setae either very small or absent; only thoracic macrosetae are notopleurals and two pairs of scutellars. Presence of proscutellum not discernable. **LEGS:** Tibiae and tarsi with very fine, dense setulae in longitudinal rows. Forebasitarsus distinctly expanded and thicker than other tarsomeres, nearly oval; mid and hind femora with preapical seta; mid tibia with long apical seta, length nearly twice width of tibia; hind tibia with preapical and apical setae. **WING:** C ending at apex of R₄₊₅, proximal to apex of wing; Sc fused to R₁ in basal third of R₁; R₂₊₃ about midway between R₁ and R₄₊₅. Radial veins thickest; M, Cu, A veins light. Veins M₁-M₂ deeply forked, with distinct stem (stem not evanescent nor particularly weak); area between apices of M₁ and M₂ posterior to apex of wing, this area does not encompass apex of wing; small, elongate cup cell present; short r-m and m-cu crossveins present, virtually in line. Cu evanescent near margin of wing; simple, unbranched; A reaching wing margin; anal lobe well developed, small alula present. **ABDOMEN:** Poorly preserved, obscure.

TYPE: Holotype and only known specimen, AMNH NJ-773, in a clear yellow piece of amber that was epoxy embedded and trimmed for maximal views of wing, legs, and head. Sex is unknown. Collected by Keith Luzzi at the White Oaks site, Sayreville, New Jersey (Turonian).

ETYMOLOGY: Name is from Latin, for "former," or "earlier," in reference to the oldest representative of the genus.

COMMENTS: Brown (1992) discussed the relationships of the Cretaceous amber phorids and the sciadocerids. Unfortunately, some of the characters he uses cannot be distinguished in this fossil, particularly of the terminalia. An enlarged male flagellomere I is also difficult to ascertain, since sex of the New Jersey amber fossil is unknown. The specimen was carefully prepared to produce a flat surface of the amber parallel and very close to the flat surface of the wing, so the presence of the base of vein M is unequivocal. This feature and the large anal lobe indicate this species to be more primitive than

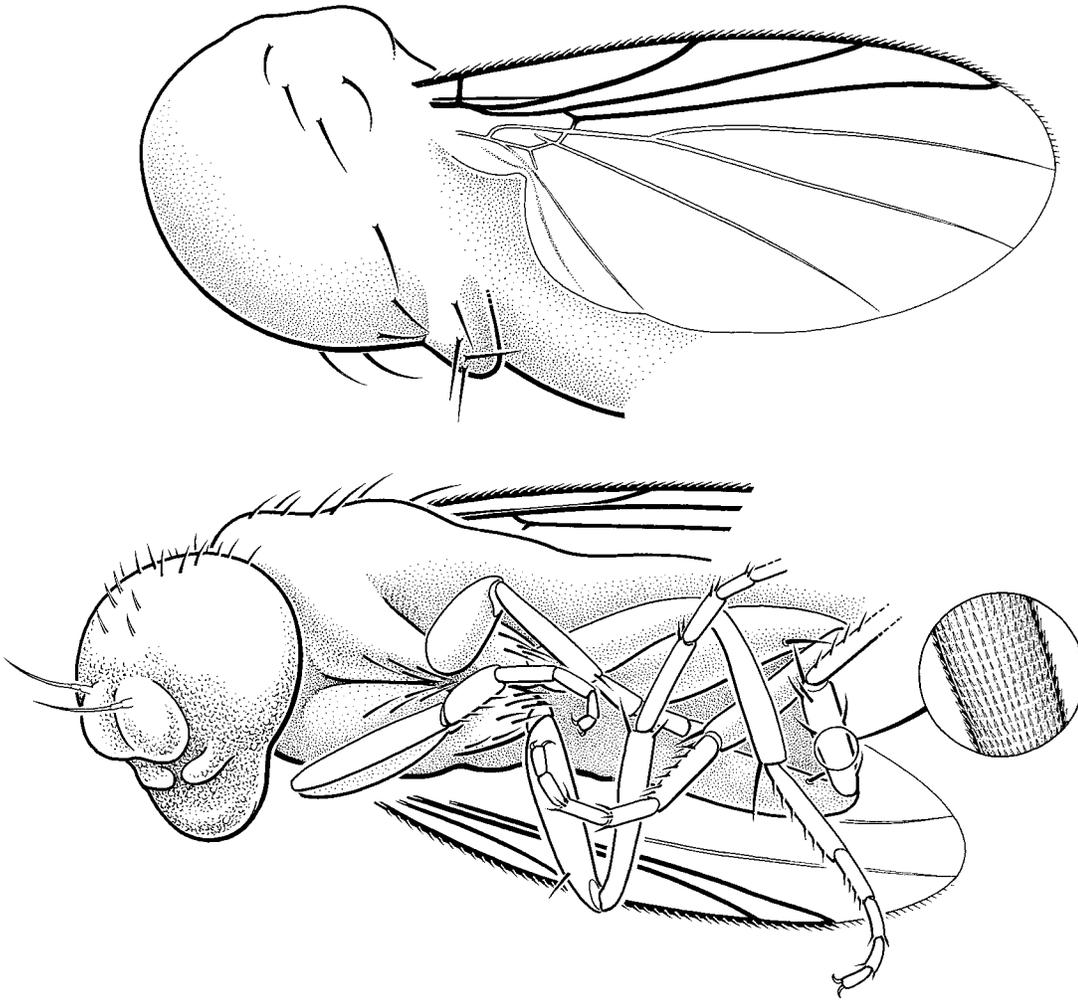


Fig. 56. *Archiphora pria* (Sciadoceridae) holotype, in New Jersey amber (AMNH NJ-773).

Sciadocera or the other species of *Archiphora*, but not as primitive as *Archisciada*.

FAMILY PHORIDAE

GENUS *PRIORIPHORA*

Prioriphora McAlpine and Martin, 1966: 532.

DIAGNOSIS: Emended by Brown and Pike (1990) and Brown (1992) to include only features at the family level: "Sc wing vein distally fused to R_1 . Fork of wing veins R_{2+3} and R_{4+5} long, much longer than that of living Phoridae. Base of wing vein M_1 and M_2 reduced or absent. Wing cell cup absent.

Proscutellum absent" (Brown and Pike, 1990: 846).

TYPE SPECIES: *P. canadambra* McAlpine and Martin, 1966, in upper Cretaceous (Campanian) amber from Cedar Lake, Manitoba. Type in CNC (no. 9127).

INCLUDED SPECIES: Seven species, including two new species described below, type species and the following: In Campanian amber from Medicine Hat, Alberta: *P. intermedia*, *P. longiscostalis*, and *P. setifemoralis* (Brown and Pike, 1990). Also, *Prioriphora polyanka* Mostovsky (1996b), in Santonian amber from Yantardakh, Taymyr, Siberia.

Prioriphora luzzii, new species

Figure 57

DIAGNOSIS: Distinguished from other species of the genus primarily on basis of wing venation and chaetotaxy of head: costal vein very short (costal ratio $0.45 \times$ length of wing), stem of R_{2+3} and R_{4+5} $0.16 \times$ length of R apical to r-m crossvein. Setae on frons distinctly shorter than in other species of genus (where known), with pair of anterior frontal-orbitals (interfrontals?) just anterior to midline, pair of posterior frontal-orbitals posterolateral to these and at mid line; 2 pairs of verticals, with "inner" vertical actually lateral and slightly posterior to ipsilateral outer vertical, and one-half the length.

DESCRIPTION: Body length = 1.81 mm (holotype)/2.07 (paratype); thorax length = 0.52 mm (holotype)/0.74 (paratype); wing length = 1.12 mm (holotype only). HEAD: Setae on frons distinctly short, with pair of anterior frontal-orbitals (interfrontals?) just anterior to midline, pair of posterior frontal-orbitals posterolateral to these and at mid line; 2 pairs of verticals, with "inner" vertical actually lateral and slightly posterior to ipsilateral outer vertical, and one-half the length. Pair of ocellar setae present, parallel and slightly reclinate; no postverticals present. Frontal orbitals/ interfrontals, ocellars are of equivalent length; "outer" verticals slightly longer. Frons with ca. 30 setulae scattered over entire surface, with a fine median furrow that becomes evanescent towards ocellar triangle. Eyes bare, rather narrow in frontal view. Antenna with flagellomere I virtually spherical, arista situated dorsally. Arista with two short basal segments of equal length, base of third aristomere thickened. Labellum small, labium broad and troughlike (distinctly wider than width of clypeus or labellum); palp with long apical seta. THORAX: Notum with single, median row acrostichal setulae, extending nearly entire length of notum; pair of paramedian rows of acrostichals just anterior to prescutellar dorsocentral setae, rows of similar length, scattered acrostichals flanking paramedian row, on anterior half of notum. Fine setulae in longitudinal rows on all tibiae and tarsi. Mid femur with seta at mid length, no such seta on hind femur. Mid and hind tibiae with 1 seta at mid length, foretibia

without middle seta. Fore and hind tibia with 1 long, 1 short apical seta ("spur"). WING: With very short costal vein, ratio $0.45 \times$ length of wing. Row of stout spinules along entire length of C. Sc converging with R_1 at 0.65 length of R_1 . No cell dm present or vestige thereof. Stem of R_{2+3} and R_{4+5} comparatively long, $0.16 \times$ length of R apical to r-m crossvein. R_{2+3} and R_{4+5} close, nearly parallel for their entire length, hardly divergent. Basal stem of M_1 - M_2 very light, but present (best seen in paratype, AMNH NJ-519). Terminalia well preserved in AMNH NJ-510, showing pair of moderately long cerci having long, fine median setae pointed mediad, with small basal and apical lobes on inner surface.

TYPES: Holotype: ♀, AMNH NJ-281, collected by Keith Luzzi at White Oaks site, Sayreville, New Jersey. Paratype: AMNH NJ-519, collected by Keith Luzzi also at White Oaks. Both specimens are in transparent yellow amber pieces that were vacuum-embedded with epoxy for specific trimming. Holotype is in excellent condition, with the amber polished flat for a complete view of the right side of the body and front of the head. Paratype is largely covered with a milky froth, through which the larger setae and setulae protrude, and the basal veins of the wing are particularly well preserved and observable.

ETYMOLOGY: Patronym for Keith Luzzi, collector of this and many other wonderful New Jersey amber specimens.

Prioriphora casei, new species

Figures 58, 59

DIAGNOSIS: Distinguished from other species of genus by the large, nearly rectangular scutellum; wing with large anal lobe and well developed anal vein; broad head, with eyes wide in frontal view (width of frons relative to width of head = 0.41); anterior frontal orbital setae situated in middle of frons, posterior frontal orbitals slightly posterolateral to these; inner and outer verticals of nearly equal length.

DESCRIPTION: Body length = 1.95 mm; thorax length = 0.78 mm; wing length = 1.48 mm. An exceptionally well preserved specimen with even color patterns preserved for some parts: flagellomere I dark, palps

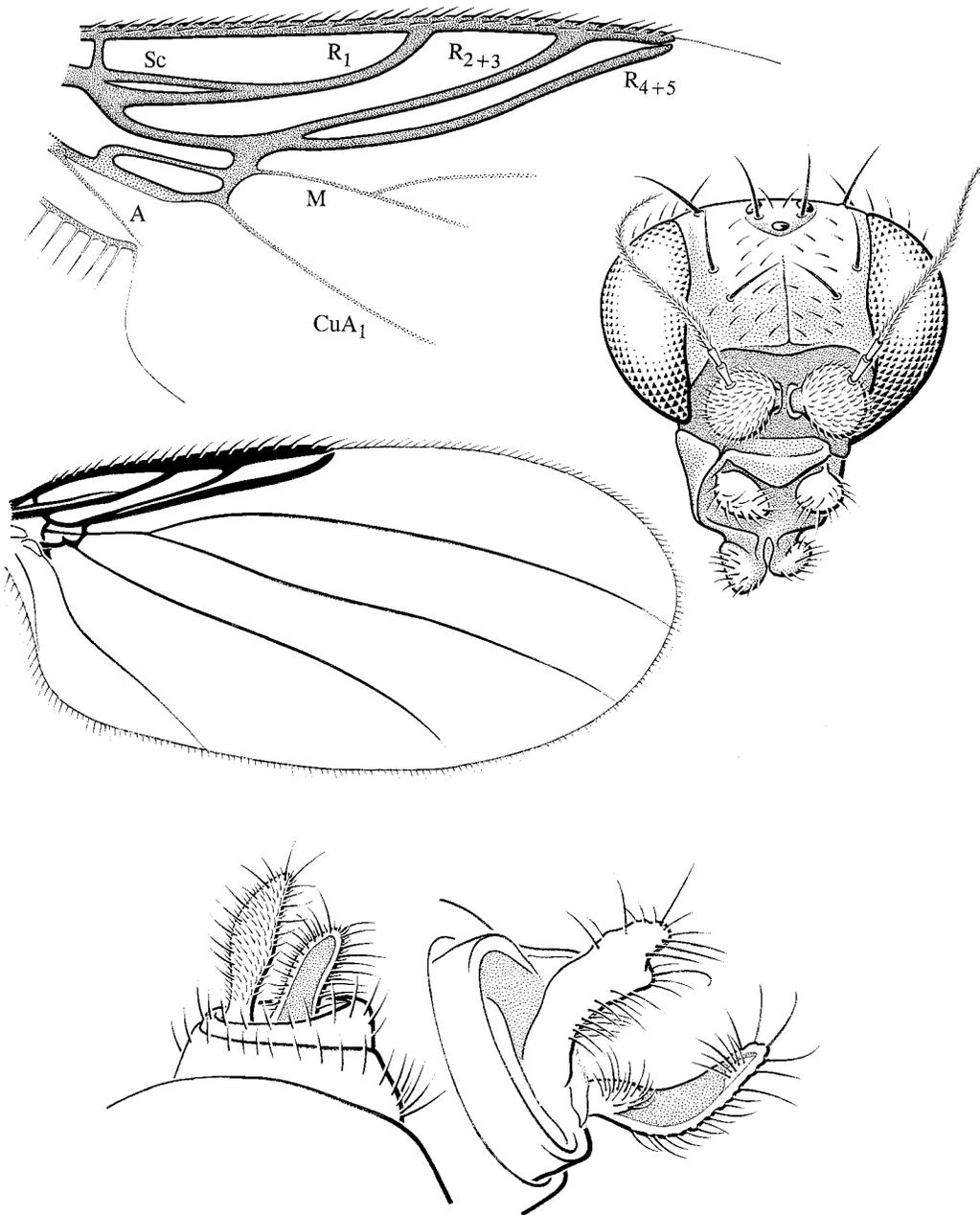


Fig. 57. *Prioriphora luzzii* (Phoridae) holotype (AMNH NJ-281), showing wing, frontal view of head, and details of female terminalia; also, base of wing of paratype specimen, AMNH NJ-519. New Jersey amber.

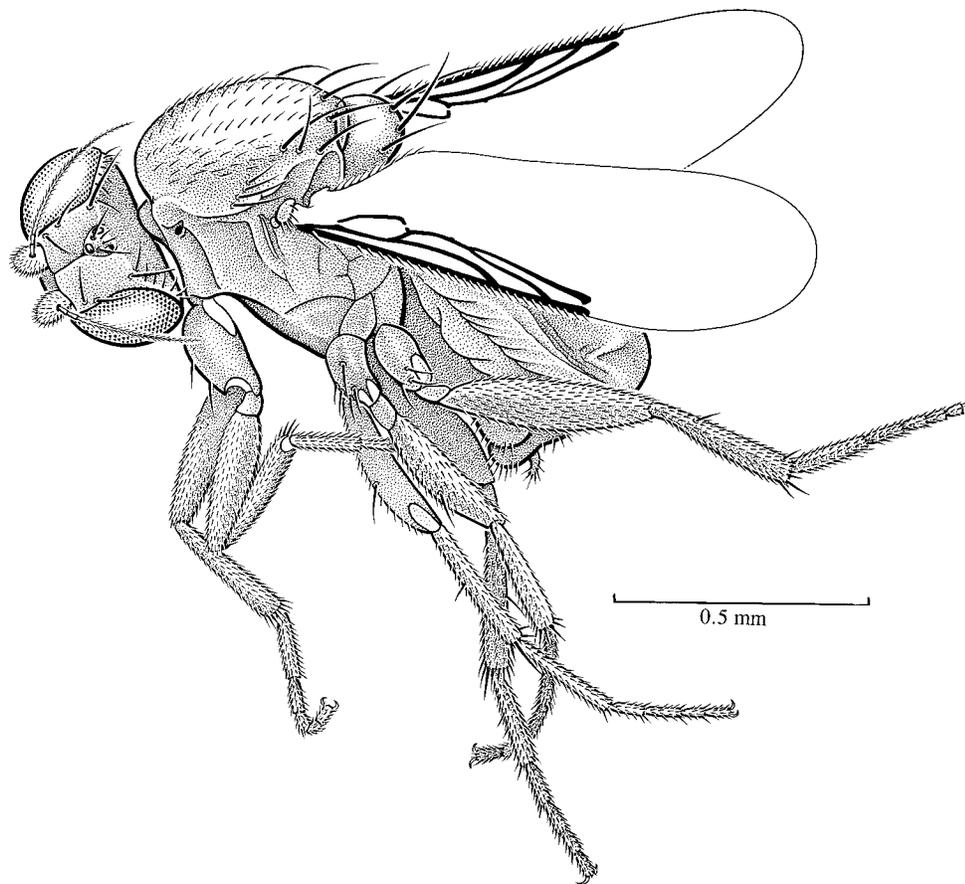


Fig. 58. *Prioriphora casei* (Phoridae) holotype (AMNH NJ-230A), complete specimen. New Jersey amber.

brown, frons with velvety black, lateral patches, eyes red. HEAD: Broad, with eyes wide in frontal view, width of frons relative to width of head = 0.41 (vs. 0.33 in *P. canadensis*, which has a very narrow frons and eyes of moderate size, and 0.52 in *P. luzzii*). Face very short, with clypeus nearly reaching ventral margin of scapes. Palp with apical seta. Eyes red, facets undifferentiated, eyes spaced far apart. Antenna with flagellomere I hemispherical, having minute setulae; arista situated dorsally; two basal aristomeres short, of equal length; third aristomere long, with base slightly thickened and overall with microscopic pubescence. Frons with two pairs of frontal orbital setae, of moderate and approximately equal lengths. Anterior frontal orbital situated at midline of frons by dis-

tance equal to length of seta; posterior frontal orbitals slightly posterolateral to anterior ones. Patch of velvety black pigmentation on lateral margins of frons; group of ca. 30 setulae on anteromedian part of frons. Complete frontal furrow present along midline of frons, extended to ocellar triangle. Ocellar setae upright and slightly divergent, of approximately same length as frontal orbitals. Inner verticals medial to outer verticals, ipsilateral verticals divergent. THORAX: Notum with single, median row acrostichal setulae, extended nearly entire length of notum; pair of paramedian rows acrostichals just anterior to dorsocentrals, length of these rows similar to median one; scattered acrostichals flanking paramedian row on anterior half of notum. Row of 4 notopleural setae present.

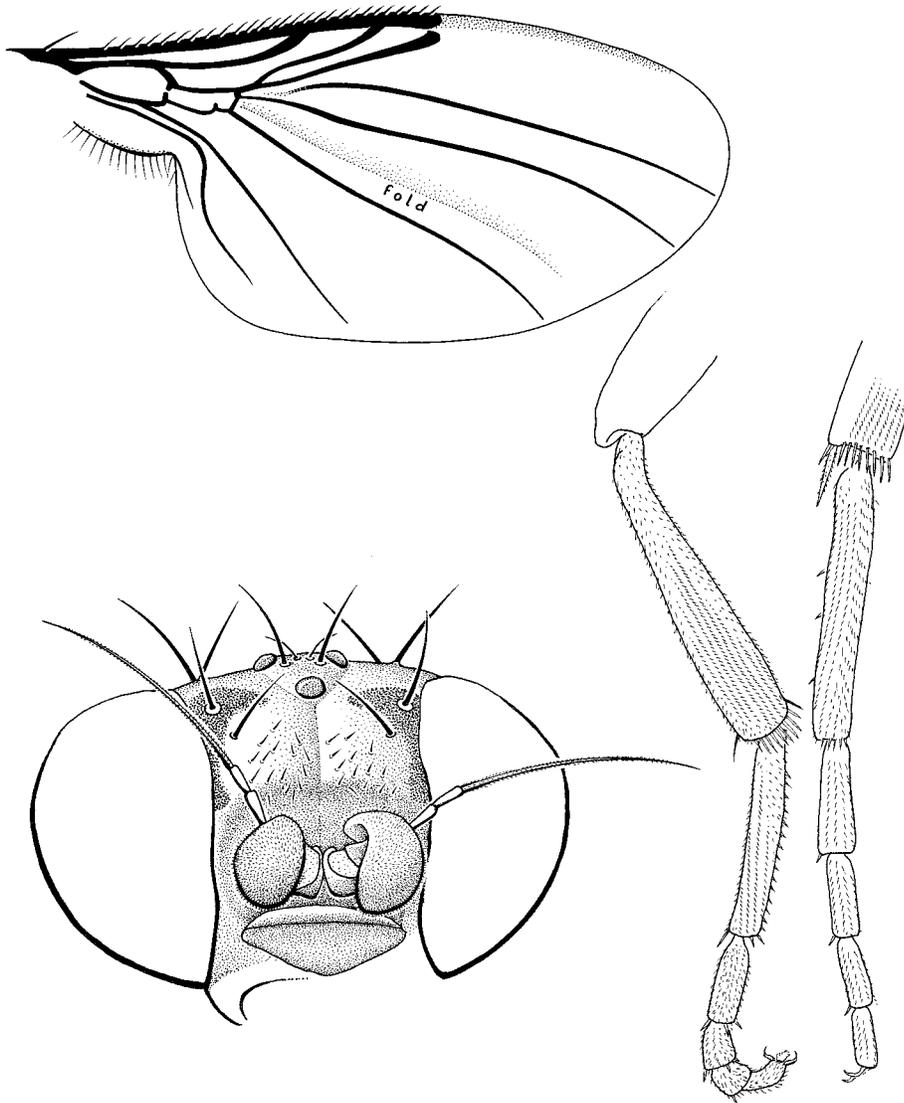


Fig. 59. *Prioriphora casei* holotype, with wing, legs, and frontal view of head.

Scutellum large, nearly equal to width of notum, rectangular, with two pairs setae. Mid femur with seta present at mid length, no such seta on hind femur. Hind tibia with 2 dorsal setae, 1 just proximal to midpoint, other near distal end, apical one ca. $0.5\times$ size of other. Mid tibia with 1 seta at mid length. WING: With costal vein $0.58\times$ wing length; anal lobe large, with veins A_1+CuA_2 and A_2 well developed.

ETYMOLOGY: Patronym for Gerard R.

Case, in recognition of his untiring efforts in the collection of New Jersey amber.

TYPE: Holotype, ♀, AMNH NJ-230A, collected by Gerard R. Case at the White Oaks site, Sayreville, New Jersey. This is a beautifully preserved specimen that is completely intact. The amber is very transparent yellow, it was vacuum embedded in epoxy, and the piece trimmed close to the fly to obtain full views of the left side of the body, front of the head, and dorsally (wing).

TABLE 2
Summary of Diagnostic Characters in *Prioriphora* (Phoridae)

Species	Deposit/age	Costal ratio	Notopleurals	Interfrontals	Anal lobe
<i>canadambra</i>	Manitoba Campanian	0.55	7	long, close, anterior, reclinate	small
<i>intermedia</i>	Alberta Campanian	0.72	3	short, close near middle, reclinate	small
<i>longicostalis</i>	Alberta Campanian	0.80	?	?	small
<i>setifemoralis</i>	Alberta Campanian	0.90	?	?	?
<i>polyanka</i>	Taymyr Santonian	0.55	4	long, close anterior, reclinate	large
<i>casei</i>	New Jersey Turonian	0.58	4	long, apart near middle, inclinate	large
<i>luzzii</i>	New Jersey Turonian	0.45	4	short, apart near middle, inclinate	moderate

General Discussion of *Prioriphora*:

Interpretation of these flies is made possible by the phylogenetic framework of Phoridae, particularly Phoridae, presented by Brown (1992). Brown hypothesized the following relationships: Sciadoceridae (*Sciadophora* (*Prioriphora* (living Phoridae))). The clade of *Prioriphora* + living Phoridae are linked by loss of the proscutellum—a small, lenticular sclerite anterior to the scutellum. *Sciadophora*, considered the most plesiomorphic phorid, is linked to *Prioriphora* + living Phoridae on the basis of CuA_2 lost or reduced, and the base of M_1 - M_2 shifted forward, appearing to arise from Rs. This latter character, however, does not apply to *Prioriphora luzzii*, and given the apparent lack of synapomorphies to diagnose *Prioriphora*, it appears very likely that this “genus” is a paraphyletic grade between sciadocerids and the more derived, modern phorids. Table 2 summarizes main diagnostic features of the described species of *Prioriphora*.

It had been suggested by one of us elsewhere (Grimaldi, 1989) that *Sciadophora* belonged to the Sciadoceridae—in accordance with the original placement of McAlpine and Martin (1966)—and that *Prioriphora* belonged in the Phoridae. Although the latter placement was corroborated by Brown (1992) and Brown and Pike (1990), they re-

examined the types of both these genera (monotypic at the time) and found inaccuracies in the original descriptions that confirmed the placement of *Sciadophora* in the Phoridae as well. For example, the costa in *Prioriphora* is actually longer than is shown in the original illustration, and the radial veins not so thick. In reality, the wings of *Sciadophora* are very similar to those of *Prioriphora*, but other features (female terminalia, proscutellum, and anepisternal setae) allow separation of the genera.

Several characters seen in the two species described here are of potential phylogenetic significance, in particular the median furrow: a fine suture along the longitudinal midline of the frons. Brown (1992) discussed the distribution of this feature, indicating it is present in some platypezids, and that an incomplete anterior furrow occurs in *Ironomyia*, *Lonchoptera*, and *Archiphora*, but was absent from *Sciadocera* and Cretaceous fossil phorid genera,” although the preservation of the fossils may preclude its observation” (p. 20). The furrow is distinctly present in *Prioriphora luzzii*, *P. casei*, and Mostovsky (1996b) indicates it is also present in *P. polyanka*. It is likely to be present in all *Prioriphora*. This finding is significant since Brown (1992) considered a complete furrow to be “neomorphic” in the ground plan of

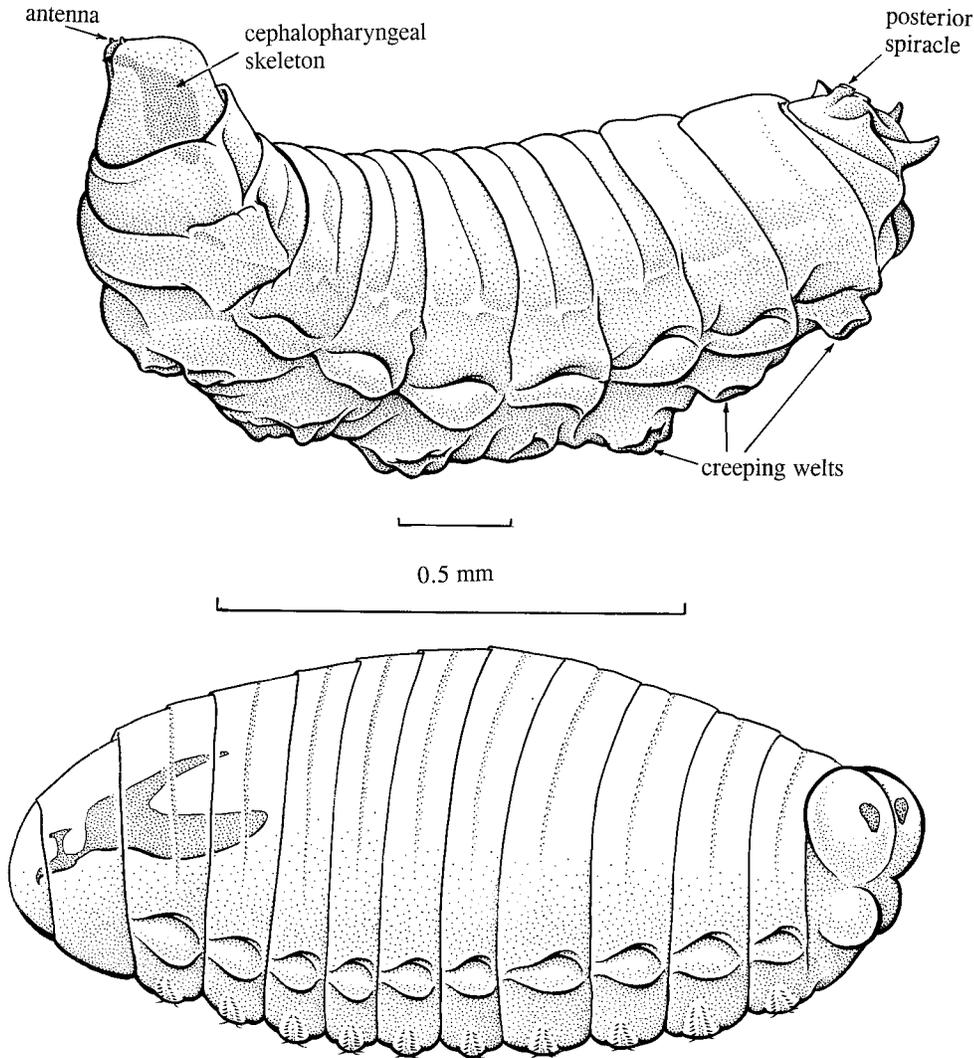


Fig. 60. Larvae of *Eremoneura* in New Jersey amber. NJ-628 (above), NJ-574 (below).

the Phoridae. Given that the furrow occurs in the most primitive phorids (the Cretaceous taxa), several extant genera of primitive phorids and several derived, extant genera, it appears that this structure is in the ground-plan of the Phoridae.

Prioriphora—whatever its formal taxonomic status—is the best represented brachyceran in Cretaceous amber, being known from ambers of Canada, New Jersey, and Siberia, and the oldest known specimen being an undescribed form from Cenomanian amber of Spain (A. Arillo, personal commun. to

DG, 1998). Clearly, the primitive phorids were widespread throughout Laurasia, and probably globally (given the paucity of Gondwanan Cretaceous amber deposits, and the present austral distribution of sciadocerids). Grimaldi (1989) described a *Metopina* from New Jersey Cretaceous amber of unknown age; elsewhere it was discussed that this amber specimen is probably uppermost Cretaceous in age (Grimaldi, 1999). Thus, it seems that only primitive phorids occur in the Cretaceous, and the radiations of modern genera did not take place until the Tertiary.

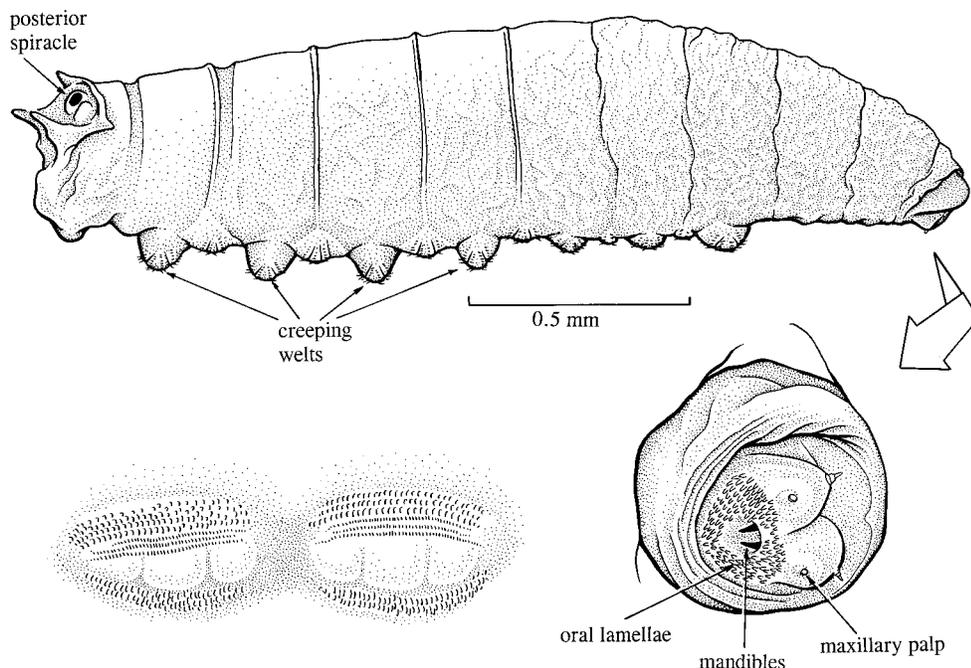


Fig. 61. Cyclorrhaphan larva in New Jersey amber (AMNH NJ-280), with details of head and fourth creeping welt.

LARVAE, FAMILIAE INCERTAE SEDIS

Figures 60, 61

Three larvae were found in amber from the White Oaks site in Sayreville, New Jersey. On the basis of complete lack of any head capsule sclerotization, and structure of mouthparts (mandibles) and cephalopharyngeal skeleton, all three are clearly cyclorrhaphans. Unfortunately, other apomorphic characters of Cyclorrhapha or more inclusive groups (as summarized in McAlpine, 1989) were not observable. These include: ring gland present, main ganglia fused, and larval development involving three instars (absence of a fourth instar is not observable in fossils). McAlpine (1989) also mentioned that "aschizous" Cyclorrhapha have the hypopharyngeal and tentoropharyngeal sclerites fused. Although the internal, cephalopharyngeal skeleton is visible in specimens AMNH NJ-628 and NJ-574, details of it are not visible.

These are the oldest definitive cyclorrhaphan larvae.

AMNH NJ-628 (fig. 60). Collected by Paul C. Nascimbene. Amber is a clear yellow, with

a suspension of coarse debris particles and fragments of wood/bark. Larva is very well preserved, stout, and thick: 3.90 mm long. Dorsal surface of the larva is curved concavely. HEAD: Almost conical, with pair of nipplelike antennae very close together; oral cavity small, with few/sparse lamellae; antennae, maxillary palps, mouth cavity close and crowded. Mouthhooks and cephalopharyngeal skeleton appear thick, but details not observable. BODY: Dorsal and lateral surfaces without any tubercles; smooth. Abdominal segments 1–7 each with creeping welts divided into pair of ovate, low, pseudopods. Whitish cloud surrounding posterior end obscures details, such as of the posterior spiracles, but two pairs of tubercles are apparent: a smaller anterolateral pair, and larger midlateral pair.

Similarity in the posterior tubercles indicates a possible relationship with NJ-280, but the different head structures also indicate distinctly separate taxa. The stout shape, with body curved dorsally, 7 pairs of small pseudopods, and posterior tubercles, are very similar to *Sciadocera rufomaculata* (Sciadoceridae) (Ferrari, 1987).

AMNH NJ-574 (fig. 60): Collected by Keith Luzzi. The amber is a small, clear yellow-orange piece also containing a male chironomid. The piece is a fragment from a "stream" of amber 4 mm diameter, 7 mm long. Larva is 1.53 mm long. Unfortunately, the larva is bloated, and filled with water or other clear liquid (in which there is also a shifting air bubble). Bloated distortion of the body obscures details of the posterior end and head. Cephalopharyngeal skeleton present, entirely internal. Cuticle of body entirely smooth; without pseudopods or dorsal/lateral tubercles. Posterior end with two broad, hemispherical lobes that meet medially; spiracular plates located in ventromedial region of the lobes. Cuticle is clear enough to see a well-preserved cephalopharyngeal skeleton: mandibles small; dorsal cornuas large; hypopharyngeal sclerite long, but impossible to detect whether it is fused to tentoropharyngeal sclerite.

AMNH NJ-280 (fig. 61): Collected by Keith Luzzi. Specimen in a clear yellow piece of amber; larva is 3.28 mm long. The amber contains particulate debris, 7 chironomids (one with a mite attached to the abdomen).

The larva is in excellent condition and is completely distended. HEAD: No sclerotization, with pair of small, nipplelike maxillary palps and dorsally with similar pair of antennae. Mouthhooks protrude slightly from oral cavity; simple, without numerous teeth or serrations, as in many phorids. Small lamellae arranged irregularly (not in rows) surround mouth cavity. BODY: Cuticle very finely rugose, but is perhaps a preservational effect. Dorsal and lateral parts of segments without tubercles (as occur in many platyphezids and most phorids). Creeping welts on abdominal segments 1–7 divided into pair of oval, raised tubercles ("pseudopods"). Posterior end with pair of spiracular plates very close together, large, suggesting larva to be third instar (spiracular slits not observable). Pair of smaller dorsolateral tubercles present, plus pair of larger midlateral tubercles. No fine hairs surround spiracular plates.

Paired abdominal "pseudopods" appear sporadically in Eremoneura: in *Eristalis*, some Empididae, and for the Schizophora, in *Aulacigaster*, *Cladochaeta*, *Ephydra*, *Leucopis*, and *Sepedon*. The shape of the larva is typical of Cyclorrhapha; not as long, narrow, and tubular as many empidoids.

PHYLOGENETIC ANALYSIS OF CYCLORRHAPHA

A numerical cladistic analysis was performed on the basal Cyclorrhapha, because the primitive, Cretaceous genera had more characters that were unpredicted than other taxa in this study. These characters, in particular, are the number of arisal articles or arisomeres, a circumambient costal vein, and presence of a vibrissa. The analysis was also done to quantify the effects of fossil taxa on a phylogeny of living families and the effects of reversing the polarity on an ambiguous character, the arisomere number.

The matrix was derived from Cumming et al. (1995), using characters listed in table 5 (matrix in table 6). In addition, nine Cretaceous amber eremoneuran genera were also scored: *Archiphora*, *Archisciada*, *Chimeromyia*, *Electrosania*, *Lebambromyia*, *Lonchopterites*, *Lonchopteromorpha*, *Prioriphora*, and *Sciadophora*. This resulted in 11 terminal fossil taxa, since all three spe-

cies of *Chimeromyia* were individually coded. Our reason was that the genus is polymorphic for several important characters, such as the arista being terminal or subapical. Polymorphisms, in addition, add unnecessary ambiguity to a cladistic analysis, when resolution is easily made by scoring subordinate taxa (Nixon and Davis, 1991; Nixon, 1996). Analyses used the programs Hennig86 (Farris, 1988), Nona (Goloboff, 1996a), Phast (Goloboff, 1996b), and Dada (Nixon, 1995). Dada was used to edit and submit the matrix to other programs. The matrix was first run in Hennig86 using successive weighting, searches for multiple trees made with branch swapping (mhennig* then bb*), then supplemented with the autospin feature of Dada, which randomly shuffles the order of taxa in a matrix before the analysis. Bremer support values (Bremer, 1988) were calculated using Phast.

A complete matrix was constructed using both fossil and living taxa, and two versions of this matrix were run: **A**, where three aristomeres was scored as apomorphic for the Cyclorrhapha; and **B**, where three aristomeres was scored as plesiomorphic. To test the effects of fossil taxa on a phylogeny of recent taxa, matrices A and B were stripped of fossil taxa, and two additional matrices analyzed: **C**, living taxa with three aristomeres as apomorphic for the Cyclorrhapha; and **D**, where three aristomeres are plesiomorphic. Asiloids were used as the outgroup comparison, and a monophyletic Empidoidea was included among the families and genera of basal Cyclorrhapha.

RESULTS: No difference occurred in the tree statistics for matrices A and B (length = 32, CI = 65, RI = 82); there were minor differences in topology of the two consensus cladograms (see fig. 62), in particular the position of *Chimeromyia* and the resolution of phoroid relationships. Cladograms resulting from matrices C and D were identical in topology, and only slightly different statistically (C: L = 25, CI = 73, RI = 82; D: L = 26, CI = 68, RI = 77). The polarity of the aristomere number character has little effect on the higher relationships of living Cyclorrhapha, but a more significant effect when fossils are incorporated. For both matrices A and B, *Chimeromyia* was a basal eremoneuran, but not a cyclorrhaphan; the extinct genus *Lebambromyia* was grouped with the Ironomyiidae; and Phoroidea was monophyletic (unresolved in matrix A, resolved in B). Hierarchy of the living taxa was unaffected by adding fossil taxa to the analysis, which could simply mean that present hypotheses of relationships are well supported on the basis of accurately homologized characters. (Conversely, if a fossil has a substantial effect on the phylogeny of modern taxa, one reason could be that the phylogenetic hypothesis was unstable or poorly justified to begin with. This possibility would need to be explored on a character-by-character evaluation. See general discussion, below).

Of most significance is that *Electrosania*, from the Cretaceous of New Jersey, does not group with the Platypezidae; and *Lonchopterites* and *Lonchopteromorpha*, from the Lower Cretaceous of Lebanon, do not group with the Lonchopteridae. The most parsimonious arrangement of synapomorphies used in the matrix indicates these are very basal cyclorrhaphans perhaps deserving of separate new families. But, as we discussed earlier under Lonchopteridae, there are characters not included in the matrix that may group these genera with the Lonchopteridae and the Platypezidae (e.g., from wing venation). Also, we do not believe it is prudent to construct major new taxa, like families, without use of important character systems, such as from male genitalia.

Parsimoniously, there is equal justification for two alternative hypotheses of aristomere evolution (mapped onto cladograms in fig. 62). **1.** There are two origins of three aristomeres in Eremoneura, occurring in *Chimeromyia* and in Platypezidae + all other Cyclorrhapha. (There are a few empidooids with three aristomeres, but these are obvious convergences; the empidooid groundplan is undoubtedly two aristomeres). **2.** Alternatively, there is a single origin of the two-articled arista in the Eremoneura, and a reversal of this character to the plesiomorphic three-articled condition in Platypezidae + all other Cyclorrhapha. While numerical cladistics has exposed the problem, resolution may lie in scrutiny of the character itself. Given the propensity of arisal flagella to arise independently in Rhagionidae, Vermilionidae, Stratiomyidae, and other groups, it might be a similar situation in the lower Eremoneura. Presumably, such convergence would be revealed by a detailed comparative study of the eremoneuran antenna.

It would appear highly improbable that, by chance alone, four Cretaceous eremoneuran genera would have aristomere numbers contrary to what is expected on the basis of living taxa. It could be argued, in fact, that the three definitive Cretaceous amber Cyclorrhapha genera that possess the *Opetia*-like ground plan of two aristomeres (*Electrosania*, *Lonchopterites*, and *Lonchopteromorpha*) is additional evidence for the derived status of three aristomeres in all other cyclorrhaphans. Although Cretaceous amber cyclorrhaphans did not have substantial effect on the phylogenetic hierarchy of living families, they do represent new and important basal taxa; they have also contributed valuable insight into character evolution, itself affecting the entire phylogenetic scheme of living + fossil Eremoneura.

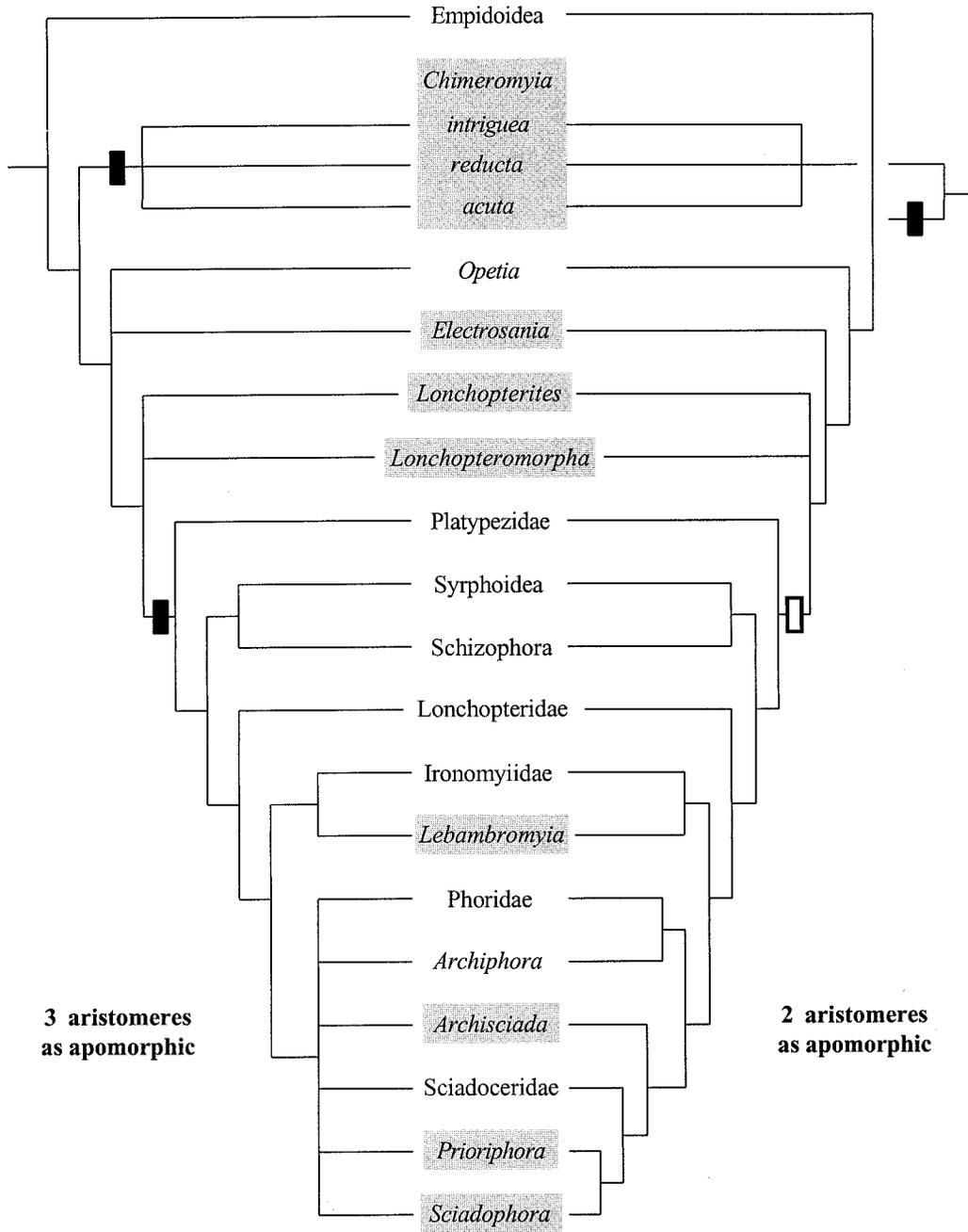


Fig. 62. Cladograms of extinct, Cretaceous (in shaded areas) and living groups of basal Cyclorhapha, based on matrix in table 6 and analysis discussed in text. Left, analysis with 3 aristomeres coded as apomorphic; right, analysis with 2 aristomeres as apomorphic. See text for statistics.

DISCUSSION

The fossil record provides at least six insights into evolution: **1.** Existence of extinct species and lineages (e.g., ornithischian dinosaurs). **2.** Periods, episodes, and patterns of extinctions (e.g., the end Permian and the K-T extinctions). **3.** Exclusive data for refuting or supporting hypotheses of vicariance biogeography. **4.** Exclusive data on the ages of lineages. Although fossils can provide only minimum ages, in a phylogenetic context and with sufficient records a chronology can be reconstructed. **5.** Possible effects on phylogenetic hypotheses, which is a topic that is debated (Patterson, 1981; Donoghue et al., 1989). **6.** Revising the sequence of appearance ["ontogeny"] of synapomorphies (Patterson, 1981).

With regard to the Brachycera we report here in Cretaceous ambers, conclusions can be made for each of these points.

1. All species and most (92%) genera of Brachycera in Cretaceous ambers are extinct. There are, in fact, some exceptionally unusual extinct taxa from the Cretaceous, such as *Tethepomyia* and *Chimeromyia*.

2. The stratigraphic sampling of the fossil deposits studied here, and for the Brachycera as a whole, is far too coarse to reveal any patterns of extinctions (e.g., sudden extinctions at the end of the Cretaceous). Fossils from this study did reveal, however, that certain groups were more diverse than presently exist, such as the *Nemedina* group. Presently, the *Nemedina* group (Empidoidea) is known from a single species from Hungary, but at least 3–4 genera (depending on the position of *Phaetempis lebanensis*) and 7–8 species occurred in the Cretaceous.

3. Biogeography: The minimum ages provided by our new records give compelling evidence that the distributions of lower Brachycera, including higher taxa of empidoidea and basal Cyclorrhapha, could have been affected by Cretaceous continental drift. Conversely, the Cretaceous ages may refute any Cenozoic-based biogeographic hypotheses. Moreover, a significant extinction from the Northern Hemisphere is *Archiphora* in New Jersey amber (presently in southern South America, also known in Eocene Baltic amber). Grimaldi (1992) discussed the con-

straints and implications of biogeographic extinctions on vicariant hypotheses.

4. Significant new data are now available to reconstruct the chronology of brachyceran evolution, discussed in detail below. By interpreting the fossils in a phylogenetic context with modern taxa, we have been able to find that the appearance of various taxa in the fossil record roughly correlates with their phylogenetic relationships, as was independently concluded by Mostovski (1998) based more on compression-fossil Diptera.

5. Phylogenetic effects of fossils. The relatively simple phylogenetic analysis in this study indicates that fossil taxa had little effect on the topology of living Cyclorrhaphan families (fig. 62). This would seem to support Patterson's (1981) conclusion that "... it is rare, perhaps unknown, for fossils to overthrow theories of relationship based on Recent forms," a view recently espoused by Brown (1992) regarding phoroids in Cretaceous ambers. Actually, as discussed above, the polarity of aristomere number affects a phylogeny of living + extinct taxa (but not of living taxa alone). Also, it seems likely that the presence of two aristomeres is the plesiomorphic condition for the Cyclorrhapha, based on a rather improbable frequency of the condition in the otherwise primitive Cretaceous genera *Electrosania*, *Lonchopterites*, and *Lonchopteromorpha*. In this situation, just one character has an apparently significant impact on phylogenetic relationships of basal Cyclorrhapha. In a similar study on basal relationships of ants, also using several genera in Cretaceous amber, the phylogenetic effects of fossils on a topology of living taxa is substantial (Grimaldi et al., 1997).

There are fundamental phylogenetic effects, as well, by adding stem-group taxa from early fossils, such as *Cretaceogaster*, *Electrosania*, *Lonchopterites*, and *Lonchopteromorpha*. *Prioriphora* is an excellent example of a stem-group, since it is an extensive grade of eight known species over a 30–40 million-year period, representing a paraphyletic assemblage at the base of the living Phoridae. The major problem, however, is more a technical one than semantic or definitional, which is: to what extent are stem-

TABLE 3
Characters on Cladogram in Figure 63

-
1. Female cercus with well-developed lateral process (two-segmented)
 2. Bulbous clypeus
 3. Loss of vein CuA₁ (M₃?)
 4. Female cercus one-segmented
 5. R₄-R₅ encompasses wing tip
 6. aristate/stylate flagellum (perhaps ground plan of Tabanomorpha)
 7. R₂₊₃ short
 8. Lower calypter large
 9. Tibial spurs lost (midtibial ones reappear in some bombyliids)
 10. Flagellum with four or fewer segments
 11. Diagonal vein present
 12. Loss of male tergite 10
 13. Fine pleating of wings (plus many other autapomorphies for Acroceridae)
 14. Margins of eyes near antennae broadly emarginate
 15. Sensory patches on tergite II
 16. Facial mystax
 17. Mouthparts with reduced labellae, long hypopharynx (plus many other autapomorphies for Asilidae)
-

group, fossil taxa ancestral and truly lacking in features apomorphic for the living "crown" group; or does their preservation not allow observation of sufficient characters to make this determination?

Similarly, the debate on the phylogenetic significance of fossils in general is to some extent tautological. First, cladistics (as a method) and fossils (taxa) are not comparable nor exclusive to each other. Patterson's essay was a reaction against the Simpsonian tradition, wherein fossils supposedly provide the best or only evidence of evolutionary relationships. It is now clearly understood that fossils are treated just like any other taxon in a phylogenetic analysis, and as such, can contribute significantly to phylogenetic relationships (Donoghue et al., 1989; Novacek, 1992). (Interestingly, Patterson [1981] supported his argument with various examples where fossils apparently had little or no impact on phylogenetic relationships, including the amniotes and the mammals. Patterson is resoundingly refuted in these examples by Gauthier's analyses of fossil and living amniotes [reviewed in Donoghue et al., 1989] and Novacek's [1992] reassessment of fossil and living mammals. Examples of Cretaceous amber ants and flies can be added to

this). Patterson (1981) made the reverse claim as well: living taxa have had substantial effects on our interpretation and classification of fossils. Famous examples he cites are *Latimeria* (a coelacanth fish) and *Metasequoia* (a taxodiaceous tree): both genera discovered merely 60 years ago to be extant and belonging to groups with extensive Mesozoic fossil records. The choana—a soft, funnel-like lining of the nasal cavity—in *Latimeria*, for example, apparently altered views on the relationships of coelacanths to other fishes. This reasoning, too, is tautological.

Phylogenies and schemes of evolutionary relationships, concerning fish, insects, or otherwise, have been part of the neontological tradition since Haeckel's time, and formalized much later by Willi Hennig. This tradition, plus the fact that living taxa have a vastly larger array of preserved characters, is why living taxa are usually the starting point for phylogenetic reconstruction. Hennig (1981) stated, "[phylogenetic trees] must actually be available before we can begin to interpret the fossils" (p. 11). More modern, numerical phylogenetic methods incorporate the fossils into a matrix with living taxa. As a result, the effects of missing characters in a phylogenetic analysis are now known to be very substantial, which weakens the application of the parsimony criterion, or the fundamental basis of cladistics (Nixon, 1996). Simulation studies by Wheeler (1992) indicate that the number of characters in a cladistic analysis is most responsible for its resolution, and the number of taxa most important for its accuracy. In a recent study of living and fossil ants (Grimaldi et al., 1997), taxa that were missing more than 70% of the full complement of characters (e.g., poorly preserved compression fossils) had the greatest effects on topology of cladograms. Indeed, missing characters in a phylogenetic analysis even produce different results depending on the algorithm being used (Platnick et al., 1991). These points have been thoroughly discussed by Novacek (1992), who also pointed out that to test any special significance of adding fossils to a phylogenetic analysis, such an analysis must be compared against one where there are random additions of living, in-group taxa.

TABLE 4
Characters on Cladogram in Figure 64

1. Wing with cell cup closed apically or absent
2. Adult palpus one-segmented
3. Male genitalia with epandrium deeply emarginate or modified laterally as surstyli
4. Wing with R_{4+5} unbranched
5. Male genitalia circumverted 360° and folded under abdomen
6. Antenna with 3-articled arista
7. Prosternum fused to proepimeron
8. CuA_2 recurved, acutely joined to A_1 with cell cup subequal or shorter than cell bm
9. Male genitalia with surstyli positioned subapically on inner margin of epandrium
10. Cell br with modified apex, including short vertical R and recurrent $r-m$, and with radial and medial veins closely approximated
11. Fore tibia with gland
12. Male genitalia rotated to the right
13. Cell dm absent
14. Female with sternite 8 articulated or fused with tergite 8
15. Female cercus heavily sclerotized and pointed at apex
16. Female cercus arched dorsally and held upright
17. Female tergite 7 with fringe of setae along posterior margin
18. Male genitalia lateroflexed to the right
19. Bm-cu abbreviated or absent
20. Antenna with one-articled arista
21. Sc often fused to R_1 or absent

TABLE 5
Characters on Cladogram in Figure 65

1. Wing with cell cup closed apically or absent
2. Adult palpus one-segmented
3. Male genitalia with epandrium deeply emarginate or modified laterally as surstyli
4. Wing with R_{4+5} unbranched
5. Male genitalia circumverted 360° and folded under abdomen
6. Antenna with three-articled arista
7. Wing membrane bare or with minute microtrichia ("glassy")
8. Wing with costal vein ending at R_{4+5} or M_1 (not circumambient)
9. Acrostichal and dorsocentral setae differentiated
10. Antennal pedicel with thumblike condyle inserted into first flagellomere
11. Male eyes dichoptic
12. Sc and R_1 very close or fused
13. Wing with area between Sc and R_1 sclerotized
14. Wing with stigmatic sclerotization absent; dm-cu shifted basad; M_1 - M_2 fork shifted basad
15. Antenna with dorsal arista
16. Male genitalia asymmetrically enlarged on left side
17. Wing with radial veins thickened; anal lobe reduced
18. Male antenna with flagellomere I enlarged; empodia absent
19. Wing with CuA_2 lost/reduced; base of M_1 - M_2 shifted forward
20. Ptilinum present
21. Abdominal muscle plaques absent

Clearly, including taxa that have many missing characters (i.e., fossils) into a phylogenetic analysis that is based on taxa with a full complement, will inevitably result in an *apparent* lesser significance of fossils. The issue, again, is not entirely a conceptual one, but also technical: how to physically extract as many characters as possible from early fossils. This is why we concentrated our study on flies preserved in Cretaceous ambers, instead of compression fossils. If our study were based on compression fossils, pivotal characters like aristemere numbers, circumambient costal vein, presence of vibrissae, and others, would certainly have not been preserved, and the phylogenetic significance of the fossils probably diminished.

6. Patterson (1981), corroborated by Donoghue et al. (1989), stated that fossils serve to "contribute new combinations of characters, which sometimes contradict ontogenetic sequence" (p. 219). Early fossils are also more likely to have plesiomorphic features

that can corroborate presumed ground plans. Five examples among others from our study show how fossil taxa have contributed significant information on character evolution. (1) *Mesobolbomyia* and *Zarzia* indicate that the distinctive, short, annulate style of *Bolbomyia* (Eocene to extant), although seemingly plesiomorphic, is probably derived from a long, thin flagellum. Moreover, the *Bolbomyia*-type of antenna was derived after the loss of vein CuA_1 . (2) *Electrosania* shows that certain venational features distinctive to platypezids (asymmetrical fork of M_{1+2}) were derived prior to apomorphic conditions of the acrostichals. *Electrosania* plesiomorphically has acrostichals that are numerous and scattered. (3) *Lebambromyia* has veins Sc and R_1 very close, with sclerotization between them, indicating that these features were derived prior to loss of microtrichia on the wing membrane, or other ironomyiid/phoridean apomorphies. (4) *Lonchopterites* had well-developed head setae, short

TABLE 6
Data Matrix for Living and Fossil Cyclorrhapha
Coded for 3 *Aristomer*s as Apomorphic
(character 6)

Outgroup	00000000000000000000
Empidoidea	11100000000000000000
<i>Opetia</i>	11111000000000000001
Platyezidae	11111111000000000001
Lonchoteridae	11111100111000000001
Ironomyiidae	11111101011110000001
Sciadoceridae	11111101111101110101
Phoridae	111111011111010010101
Syrphoidea	11111101010000100001
Schizophora	11111101110000100001
<i>Chim. intriguea</i>	111001010?1000000000
<i>Chim. reducta</i>	111001010?1000000000
<i>Chim. acuta</i>	111001010?10001000000
<i>Electrosania</i>	11?1?0010?0000?0000?
<i>Lebambromyia</i>	11?1?1010?11100?0000?
<i>Lonchopterites</i>	11?1?0011?0000?00001
<i>Lonchopteromorpha</i>	11?1?0011?0000?00001
<i>Archisciada</i>	111111011?11011100001
<i>Archiphora</i>	1111?1011?11011?0010?
<i>Prioriphora</i>	1111?1011?11011?11001
<i>Sciadophora</i>	1111?1011?11011?11101

Sc and R₁ veins, a very deep fork of veins R₂₊₃ and R₄₊₅ (among other apomorphic features), but not the lanceolate wing distinctive to modern lonchopterids, indicating that wing shape evolved after many structures on the body. (5) *Prioriphora* demonstrates that “costalization” of the wing veins appeared prior to the loss of the median furrow on the frons.

Chronology of Brachyceran Evolution

Hennig’s belief was that the chronology of appearance of fossils in the geological record should (eventually) mirror the order of lineages on cladograms: absolute ages must reflect relative relationships. This is why he consistently discusses fossils in his treatment of insect phylogeny (Hennig, 1981) and why he arduously monographed Diptera fossils in Baltic (e.g., Hennig, 1965) and Cretaceous ambers (Hennig, 1970, 1971, 1972). Eventually, with the cumulative description of sufficient fossils, the dates of minimum age provided by fossils can be extrapolated to accurate estimates of the actual, or absolute, age. Hennig (1981: 11) stressed, “. . . the [phylogenetic] tree is always defective in *one* respect: it does not show when the [diver-

gence] events took place. . . . This can only be done by studying the fossils themselves. . . .” Although understanding phylogenetic relationships is sine qua non for any evolutionary study, it is not necessarily sufficient. Chronology provides another important dimension. More recently, work by Norrell and Novacek (1992a, 1992b) found frequent, statistically significant correlations between cladistic rank of various amniote taxa, and their stratigraphic rank. For many of the correlations that were not particularly strong, cladistic relationships of the group or stratigraphy of fossils were poorly known. This helps to confirm the validity of Hennig’s approach. Brachyceran relationships and appearance in the fossil record also appear to be roughly correlated.

Figures 63–65 are cladograms of the lower Brachycera, Empidoidea, and Cyclorrhapha, respectively, which show the geological time scale, the phylogenetic and geological positions of the fossils (in circled letters), and current diversity. There is also a selection of pertinent apomorphies (numbers with solid or half-solid rectangles), characters of internal genitalia and others not observable in fossils being excluded. The cladograms represent consenses from several sources, and no attempt was made here to derive new characters and matrices nor resolve ambiguous and disputed relationships. The basic pattern that was expected is apparent: the lower Brachycera through to the Asiloidea have the oldest fossil record; the asiloids have a record that is slightly younger (no older than Cretaceous) than other lower Brachycera; the Empidoidea show slightly earlier diversification than the Cyclorrhapha, with the latter having a fossil record that is entirely Cretaceous and younger.

“Lower” Brachycera: Cladistic relationships used in figure 63 are derived from Woodley (1989), Sinclair et al. (1994), and Yeates (1994). The diagram includes all significant, interpretable fossils, not just ones in amber. With the exception of some asiloids from the Jurassic of Karatau, the oldest records are most consistent among the tabanomorpha. Strangely, no Mesozoic tabanid is yet to be found, despite their modern predilection for habitats that would favor fossilization (e.g., swamps). The Rhagionidae are

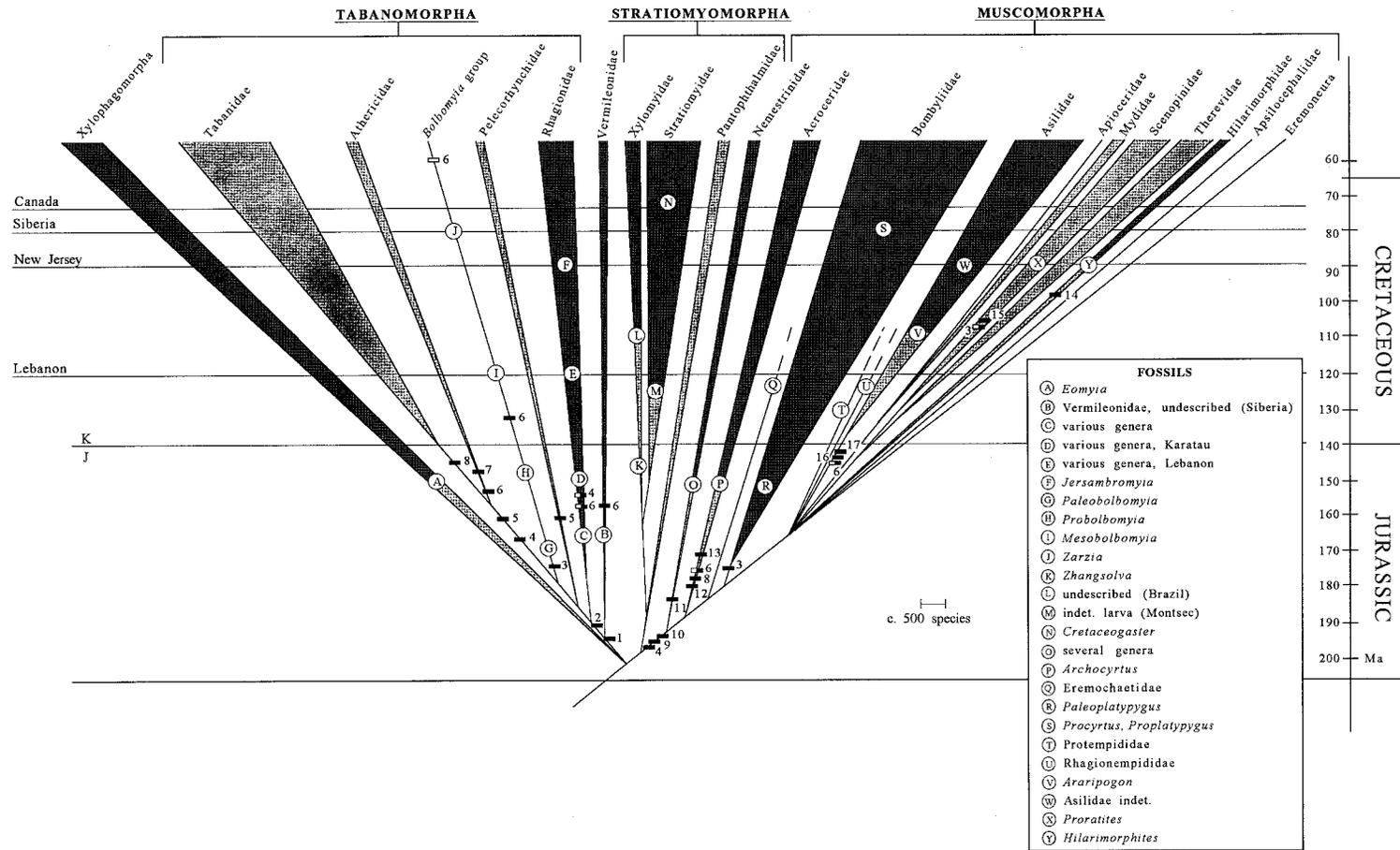


Fig. 63. Phylogenetic tree of lower Brachycera, superimposed on geological time scale. Circled letters = fossils (see inset table); numbers = apomorphic characters visible in most fossils (see table 3). See text for explanation of cladogram. Widths of clades approximate numbers of extant species. Dark shading = minimum ages established by oldest fossils; light shading = inferred ages.

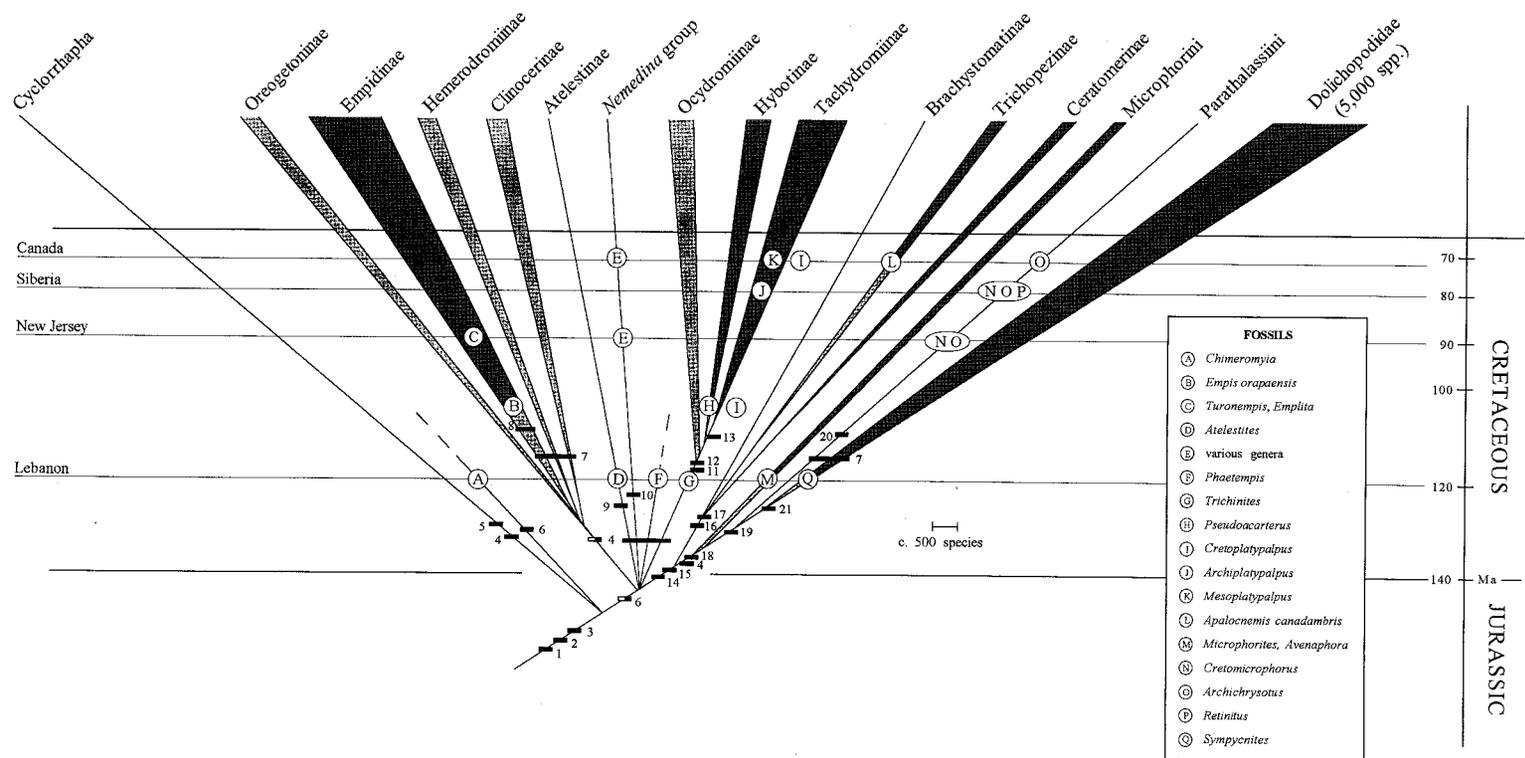


Fig. 64. Phylogenetic tree of Empidoidea, superimposed on geological time scale. See figure 63 legend for explanation and table 4 for relevant characters.

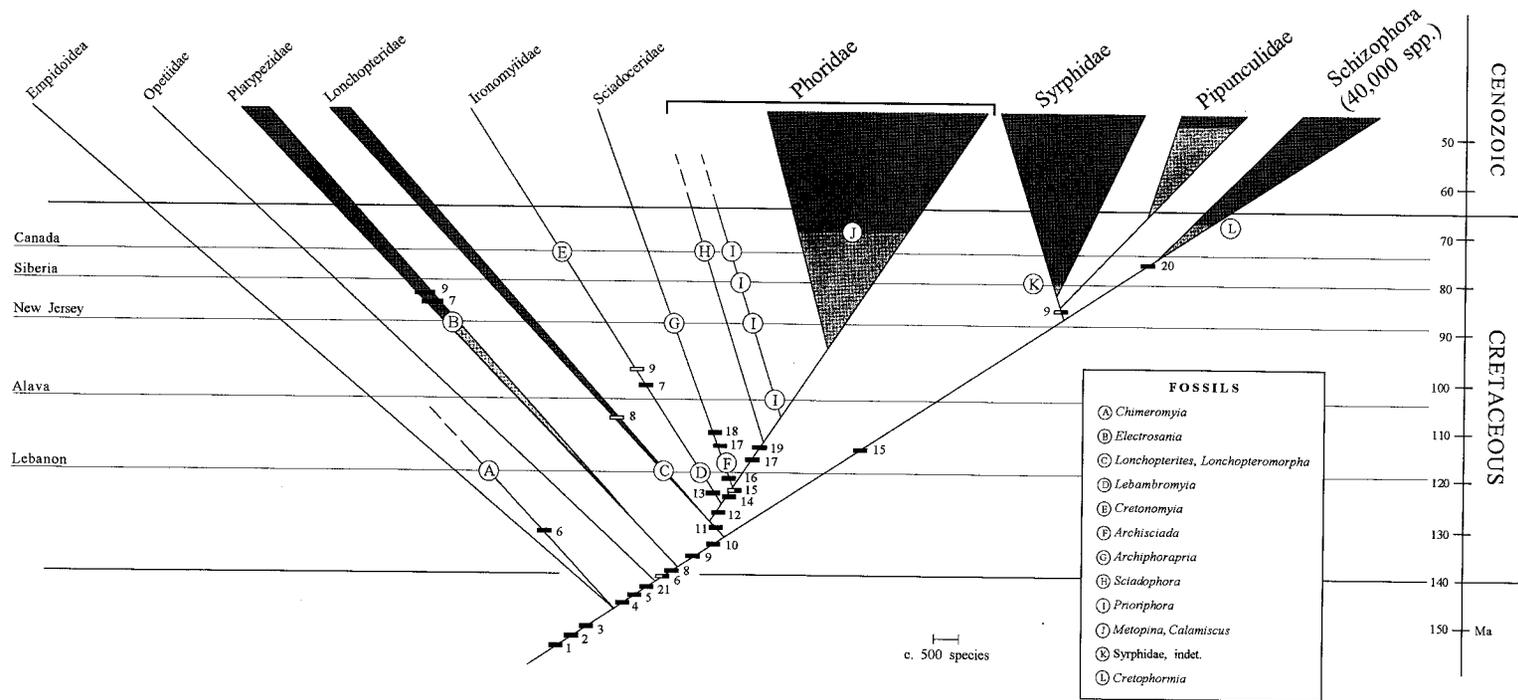


Fig. 65. Phylogenetic tree of Cyclorrhapha, superimposed on geological time scale. See fig. 63 legend for explanation and table 5 for relevant characters.

possibly paraphyletic (see text); genera apparently related on the basis of a lost vein CuA_1 , including the unusual living genus *Bolbomyia*, appear to have a very long fossil record. In fact, the extinct diversity of this lineage is relatively high compared to other families, indicating the group to be presently relict. The few species and disjunct distributions of *Bolbomyia*-like genera would also reflect a relict status. The “higher” asiloids have a relatively young fossil record, the oldest being an asilid from the Aptian of Brazil, and therevids with an entirely Cenozoic record. The basal diversification of the the Brachycera took place in the Lower Jurassic, ca. 200 Ma. Elsewhere (Grimaldi, 1999) the argument is presented that the radiation of particular families with anthophilous species, such as Stratiomyidae, Bombyliidae, Scenopinidae, and Acroceridae, diversified in the mid Cretaceous. Indeed, the Mesozoic fossils of all these families are very primitive.

Figure 64 is based on phylogenetic relationships presented by Cumming et al. (1995). This is the only section that seems to show little or no correlation of cladistic rank with stratigraphic appearance. If the fossil data is examined on a finer scale, however, the Cretaceous empidoids frequently represent primitive members for their respective taxa. For example, *Atelestites* (L. Cretaceous) is the most primitive atelestine; *Phaetempis* (L. Cretaceous) is probably the most primitive member of the *Nemedina* group, which includes Upper Cretaceous, Eocene, and modern taxa; *Trichinites* (L. Cretaceous) appears to be the stem group to the hybotid lineage; and the Cretaceous tachydromiine genera are plesiomorphic to the living genera, on the basis of scutellar seta number. One group within the empidoids that apparently defies the correlation of cladistic-stratigraphic rank is the microphorine-dolichopodid lineage. This may be due to unresolved paraphyly of the microphorines and the sister group of the dolichopodids, but also to an unexpectedly early fossil dolichopodid (*Sympycnites*). The fossil record of these small flies, so dependent upon amber for recognizable preservation, may simply be too sparse in the Lower Cretaceous in order to discern cladistic-age correlations.

The cladogram of Cyclorrhapha in figure 65 is derived from Cumming et al. (1995) and Brown (1992), and shows the best correlation between cladistic rank and age, probably because phylogenetic relationships are the best understood. Clearly, the basal diversification of the Cyclorrhapha occurs in the Lower Cretaceous, and it is doubtful that this group extended into the Jurassic. *Chimero-myia* is included in figure 65 simply because of its “hybrid” combination of features, some of them empidoid, others cyclorrhaphan. The oldest definitive Cyclorrhapha are *Lebambromyia*, Ionchopterids, and *Archisciada*, from Lebanese amber, and the apparent Platypezidae described by Mostovski from the Lower Cretaceous of Eurasia (the Jurassic “platypezids” and lower Cretaceous “ironomyiids” described by Hong and Mostovski, respectively, are of uncertain relationships). The Lebanese amber taxa are all exceptionally primitive at the family level. Even *Electrosania*, in younger New Jersey amber, is probably a very primitive member of the Platypezidae. With the exception of a *Metopina* in Cretaceous amber from New Jersey, all Cretaceous phorids are very primitive (it was discussed elsewhere that the report of a Cretaceous *Metopina* and even a milichiid in New Jersey amber [Grimaldi et al., 1989] is probably from uppermost Cretaceous, ca. 65 Ma [Grimaldi, 1999]). The Phoroidea/Phoridae, in fact, show one of the best clade-age rank correlations: earliest appearances of *Archisciada* (*Archiphora* (*Sciadophora* + *Prioriphora* (modern Phoridae)))) are Neocomian (Turonian (Aptian? (Maastrichtian?))). Even within *Archiphora*, the relationships of *A. pria* (*robusta* + *patagonica*) correlates with the ages of Turonian (Eocene + extant).

The earliest known schizophoran is *Cretophormia* McAlpine, based on a mineralized, 3-dimensional fossil of puparia in 70 Ma sediments from Alberta, Canada (McAlpine, 1970). However, the first abundant fossil evidence for the Schizophora is the Eocene Baltic amber (Hennig, 1965), which contains a great diversity of “acalyprates” and some muscoids that are consistently primitive at generic levels. The Schizophoran radiations therefore are largely Cenozoic.

A Paleoecological Consideration

Definitive calyprates do not appear until the Cenozoic, since the only Cretaceous record, *Cretophormia* (originally placed in the Calliphoridae), has a family-level relationship that is uncertain in the Schizophora. This group is probably the most ecologically significant decomposer of carrion: they are often the first insects to arrive at a carcass, their egg-to-adult development time is between 11–20 days, and individual females lay hundreds of eggs (Smith, 1986). Infestation of carcasses by muscoid larvae leads to its putrefaction and invasion by other insects, such as by beetles. The probable ab-

sence of muscoids in the Cretaceous raises the question of how carrion was decomposed. With ponderous sauropods and other dinosaurs grazing the Cretaceous plains, and giant carnosuars preying on them, surely there were massive carcasses available: a situation ideal for carrion-breeding cyclorrhaphans such as the modern sarcophagids and calliphorids. It is possible that there existed in the Cretaceous ecological systems analogous to modern African savannas, where bones litter the landscape because carrion is quickly consumed by small vertebrate scavengers.

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INDEX OF TAXONOMIC NAMES

Page of original citation in bold, page(s) with figures in italics.

- Acarteroptera*, 36
Agathomyia, 82
Apalocnemis canadambri n.sp., **55**, 56, 89
Apalocnemis, 55, 109
 Apsilocephalidae, 17
Apsilocephalus, 17
Apystomyia, 29
Araripogon axelrodi, 30
Archichrysotus hennigi, 65
Archichrysotus incompletus n.sp., **65**, 66, 90
Archichrysotus manitobus n.sp., **65**, 67, 90
Archichrysotus minor, 65
Archichrysotus, **65**
Archiphora patagonica, 97
Archiphora pria n.sp., **97**, 92, 98
Archiphora robusta, 95
Archiphora, 95, **97**, 106, 109, 112, 116
Archiplatypalpus, 51, **53**
Archisciada lebanensis n.sp., **95**, 91, 96
Archisciada n.gen., **94**, 106, 112, 116
Arthroceras, 16
 Asilidae, 30–31, 31
 Atelestinae, 35–37
Atelestites, n.gen., **35**, 116
Atelestites senectus n.sp., **35**, 36, 87
Atelestus, 36, 37
Atherimorpha, 16
Austroleptis, 16
Avenaphora hispida n.sp., **61**, 62, 90
Avenaphora n.gen., **61**
- Bertamyia*, 82
Bolbomyia, 16
Burmitempis halteralis, 44
- Calomyia*, 82
Calotarsa, 78
Charadrodromia, 54
Chimeromyia acuta n.sp., **74**, 75, 89
Chimeromyia intriguea n.sp., 70, **71**, 72, 73, 89
Chimeromyia n.gen., **69**, 106–109, 112
Chimeromyia reducta, **74**, 76
Chrysopilus, 16, 17
Cretaceogaster pygmaeus, **17**, 20
Cretaceogaster, 17, 109
Cretodromia glaesa n.sp., **42**, 43, 88
Cretodromia n.gen., **42**
Cretomicrophorus novemundus n.sp., **63**, 64, 90
Cretomicrophorus rohdendorfi, 64
Cretomicrophorus, **63**
- Cretonomyia pristina*, 81
Cretophormia, 117
Cretoplatypalpus americanus n.sp. **51**, 52, 88
Cretoplatypalpus, 50
 Cyclorrhapha, 76–108
- Desmomyia*, 17
 Dolichopodidae, 67–69
Dysaletria, 54
- Electrocyrtoma burmanica*, 51
Electrosania cretica n.sp., **77**, 77, 91
Electrosania n.gen., 76, 106–108, 111, 112, 116
 Empidinae, 32–35
 Empidoidea, 31–69
Empis orapaensis, 32
Emplita casei n.sp., **33**, 34, 87
Emplita n.gen., **33**
Eremoneura, 31–108
- Glutops*, 16
- Helempis eucalla*, 32
Helempis yixianensis, 32
Hilarimorpha, 28–29
 Hilarimorphidae, 21–29, 22
Hilarimorphites longimedia n.sp., **27**, 27, 86
Hilarimorphites n.gen., **21**, 28
Hilarimorphites setosa n.sp., **28**, 27, 28, 86
Hilarimorphites superba n.sp., **23**, 24, 25, 86
Hilarimorphites yeatsi n.sp., **26**, 26, 86
 Hybotid lineage, 50
- Ironomyia nigromaculata*, 81
 Ironomyiidae, 79–82
- Jersambromyia borodini* n.sp., **9**, 9, 85
Jersambromyia, n.gen., **7**
- Lebambromyia acrai* n.sp., **79**, 79, 80, 91
Lebambromyia n.gen., **79**, 106–108, 111, 112, 116
Lithopetia, 78
Litoleptis, 16
 Lonchopteridae, 82–84, 93–94
Lonchopterites n.gen., **82**
Lonchopterites prisca n.sp., **82**, 83, 91, 106–109, 112
Lonchopteromorpha asetocella, **93**, 91, 94
Lonchopteromorpha n.gen., **93**, 106–109, 112

- Maritulus sospes*, 79
Meghyperus, 36
Mesobolbomyia acraei n.sp., **10**, 11, 85
Mesobolbomyia n.gen., **10**, 111
Mesopetia, 78
Mesoplatypalpus carpenteri n.sp., **53**, 54, 88
Mesoplatypalpus n.gen., **53**
Metopina, 104
Microphor, 57
Microphorella, 57
Microphorinae, 57–67
Microphorini, 57–63
Microphorites extinctus, 57
Microphorites oculus n.sp., **59**, 59, 90
Microphorites similis n.sp., **57**, 58, 90
Microphorites n.sp., 60, 61
Microphorites, **57**
- Nemedina alamirabilis*, 37
Nemedina genus group, **37**–50, 109, 116
Nemedromia campania n.sp., **37**, 38
Nemedromia n.gen., **37**
Nemedromia telescopica n.sp., **39**, 39
Nemedromia turonia n.sp., **40**, 40
Neoturionius vetus n.sp., **46**, 47, 87
Neoturionius asymmetricus n.sp., **44**, 44, 87
Neoturionius cretatus n.sp., **45**, 46
Neoturionius n.gen., **43**
- Opetia*, 84
- Palaeopetia*, 78
Paleobolbomyia, 17
Paleochrysopilus hirsutus n.sp., **7**, 8, 85
Paleochrysopilus n.gen., **7**
Paleohilarimorpha bifurcata, 29
Parathalassiini, 63–67
Parathalassius, 57
Parnasos amabilis, 79
Parnasos parva, 79
Pauromyia, 17
Phaetempis lebanensis n.sp., **48**, 49, 89, 109
Phaetempis n.gen., **48**
Platypalpus, 51, 54
Platypezidae, 76–79
Plesioclythia, 78
Polyporivora, 78
Prioriphora canadambra, 98, 103
Prioriphora casei n.sp., **99**, 92, 101, 102, 103
Prioriphora intermedia, 103
Prioriphora luzzii n.sp., **99**, 92, 100, 103
Prioriphora polyanka, 103
Prioriphora setifemoralis, 103
- Prioriphora*, **98**, 103–104, 106, 108–110, 112, 116
Probolbomyia, 17
Prolatomyia elongata n.sp., **41**, 88
Prolatonmyia n.gen., **41**
Proplatypygus rohdendorfi, 17
Proplatypygus, 17
Proratinae, 29
Proratites n.gen., **29**
Proratites simplex n.sp. **30**, 29, 86
Prosystemus zherikhini, 69
Protempis antennata, 32
Protempis minuta, 32
Pseudoerrina, 16
Pseudopetia, 78
Ptiolina, 17
Ptiolinites, 17
- Retinitus nervosus*, 65
Rhagina, 17
Rhagio, 16, 17
Rhagionidae genus A, **10**, 12
Rhagionidae genus B, **12**, 13
Rhagionidae genus C, **14**, 14, 85
Rhagionidae genus D, **15**, 15, 85
Rhagionidae, 7–17, 18, 19
- Scenopinidae, 29–30
Schistostoma, 57
Sciadocera rufomaculata, 105
Sciadocera, 95, 103, 105
Sciadoceridae, 94–98
Sciadophora bostoni, 84
Sciadophora, 106, 108, 112, 116
Sclerorhagio, 17
Sinolesta, 78
Solomomyia, 17
Spania, 17
Spaniopsis, 17
Sphicosa, 33
Stratiomyidae 17–21
Stratiomyidae genus indet., **19**, 21
Stylospania, 17
Symballophthalmus, 51, 53
Symphoromyia, 17
Sympycnites n.gen., **67**
Sympycnites primaevus n.sp., **67**, 68, 89
Sympycnus, 69
- Tachydromia*, 54
Tachydromiinae, 50–54
Tachyempis, 54
Tachypeza, 54

Tethepomyia n.gen., **6**, 109

Tethepomyia thauma n.sp., **6**, 8, 85

Trichinites cretaceus, **50**

Trichinites, **50**

Trichopezinae., 55–57

Turonempis n.gen., **32**

Turonempis styx, **32**, 33, 88

Ussatchovia, 17

Zarzia, 17, 11