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Fossil Sciaroidea (Diptera) in Cretaceous Ambers, Exclusive of Cecidomyiidae, Sciaridae, and Keroplatidae

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ABSTRACT

The Recent world fauna of Sciaroidea, or fungus gnats, comprises approximately 4000 described species in eight families: Bolitophilidae, Cecidomyiidae, Diadocidiidae, Ditomyiidae, Keroplatidae, Lygistorrhinidae, Mycetophilidae, and Sciaridae. Larvae live primarily in decaying vegetation, feeding on fungal mycelia, and they can be among the most abundant insects of temperate forests. Stem-group families appeared in the Jurassic, with large Tertiary deposits being composed almost entirely of living genera, so the Cretaceous is essential for understanding the origins and diversification of Recent families. Sixty-six specimens were studied from six major deposits of Cretaceous amber, spanning 40 million years from the Early to Late Cretaceous: Lebanon (ca. 125 Ma), northern Spain (120 Ma), northern Myanmar (Burma) (ca. 105 Ma), northern Siberia (two sites, 105 and 87 Ma), New Jersey (90 Ma), and western Canada (80 Ma).

New taxa are the following: *Docidiadia burmitica* (n.gen., n.sp.) (Diadocidiidae); *Thereotricha sibirica*, (?)*T. agapa* (n.gen., n.spp.) (Sciaroidea incertae sedis); *Archaeognoriste primitiva*, *Lebanognoriste prima*, *Plesiognoriste carpenteri*, *P. zherikhini*, *Protognoriste amplicauda*, *P. goeleti*, *P. nascifoa*, *Leptognoriste davisi*, *L. microstoma* (n.gen., n.spp.) (Lygistorrhinidae). In Mycetophilidae sensu stricto: *Alavamanota burmitina*, n.sp. (Manotinae), *Neuratelia maimecha*, n.sp., *Allocotocera burmitica*, n.sp., *Pseudomanota perplexa*, n.gen., n.sp. (Sciophilinae Sciophilini); *Apolephthisa bulunensis*, n.sp., *Synapha longistyla*, n.sp., *Dziedzickia nashi*, n.sp., *Saigusaia pikei*, n.sp., *Syntemna fissurata*, n.sp., *Gregikia pallida*, n.gen., n.sp., *Gaalomyia carolinae*, n.gen., n.sp. (Sciophilinae Gnoristini); *Nedocosia exsanguis*, *N. sibirica*, *N. canadensis*, *N. novacaesarea*, n.gen., n.spp.; *Ectrepesthoneura succinimontana*, *E. swolenskyi*, n.spp.; *Izleiina mirifica*, *I. spinitibialis*, n.gen., n.spp.; *Zeliina orientalis*, *Z. occidentalis*, n.gen., n.spp.; *Temaleia birmitica*, n.gen., n.sp., *Lecadonileia parvistyla*, n.gen., n.sp.; *Disparoleia cristata*, n.gen., n.sp.; *Hemolia matilei*, *H. glabra*, n.gen., n.spp.; and *Protragoneura platycera*, n.sp. (Sciophilinae Leiini).

Relationships of the fossil genera are phylogenetically assessed with living genera. The Burmese amber fauna contains an inordinate abundance and diversity of sciaroids, perhaps because of a wetter paleoclimate in that region.

INTRODUCTION

The preservation of fossils in amber is renowned for consistently finer preservation than virtually all other modes of fossilization. Although the geological occurrence of amber begins in the Triassic, the oldest insect faunas in amber are no older than Early Cretaceous, approximately 120–130 million years ago (Ma). Nonetheless, insects in amber from the Cretaceous period (145–65 Ma) afford unparalleled insight into Mesozoic evolution. The many more preserved characters allow more accurate phylogenetic inference than is possible with compression or most other kinds of fossils, particularly for intricate organisms like insects. Detailed preservation facilitates not only reconstruction of phylogeny, but of paleoenvironments as well. In this regard, the study of extinct Diptera is essential, as Diptera usually comprise the largest proportions by individuals and species of all types of arthropods preserved in various amber deposits around the world. This paper is devoted to one particularly diverse group of flies well represented in Cretaceous amber, but which have been virtually neglected: the fungus gnats, or Sciaroidea.

The Sciaroidea is comprised of 14 families, 6 of them exclusively Mesozoic: Antefungivoridae (Middle Jurassic to Early Cretaceous; Kovalev, 1990), Archizelmiridae (Late Jurassic to Late Cretaceous; Grimaldi et al., 2003), Eoditomyiidae (Early Jurassic to Early Cretaceous; Ansorge, 1996), Mesosciophilidae (Middle Jurassic to Early Cretaceous; Kalugina and Kovalev, 1985, Blagoderov, 1993), Pleciofungivoridae (Early Jurassic to Early Cretaceous; Kovalev, 1987b), and Protopleciidae (Early Jurassic to Early Cretaceous; Blagoderov, 1996, Kovalev, 1990). No extinct families occur in the Cenozoic. The extant families of the superfamily are Bolitophilidae, Cecidomyiidae, Diadocidiidae, Ditomyiidae, Keroplatidae, Lygistorrhinidae, Mycetophilidae (s.s.), and Sciaridae, all of which but Ditomyiidae also occur in the Cretaceous. Phylogenies and comprehensive revisions of some of these families were provided by Grimaldi and Blagoderov (2001) (Lygistorrhinidae), Matile (1981a, 1990, 1997) (Keroplatidae, Sciaroidea), Munroe (1974) (Ditomyiidae), Söli (1997) (Mycetophilidae s.s), and Väisänen (1984) (Mycomyiini). There are approximately 4100 described species of Sciaroidea exclusive of the poorly studied but diverse families Cecidomyiidae and Sciaridae (Bechev, 2000). At least 10,000 and perhaps as many as 20,000–30,000 living species of Sciaroidea exist. Such diversity reflects the significance of the group in terrestrial ecosystems, particularly forests, the very habitat that produces amber.

Larvae of Sciaroidea are abundant in the sporophores of basidiomycete fungi—in decaying wood, leaf litter, and humus, where they feed on fungal mycelia. Where humus and decaying wood are particularly thick in mature forests, sciaroids are among the most abundant and diverse insects, with their larvae inhabiting 80–90% of the macrofungi in natural habitats (Yakovlev, 1988). Larval habits are not restricted, though, to mycophagy (Matile, 1997). The larvae of some genera and species of Keroplatidae are actually predators of insects they snare in their slime trails, the most famous example of which is the New Zealand ''glow-worm'', (*Arachnocampa* Edwards). Larvae of *Arachnocampa* are luminescent and suspend themselves in mucous strands from the ceilings of caves. Small midges attracted to the light become entangled in the strands, which the larvae then devour. There is even a keroplatid, *Planarivora* Hickman, whose larva is parasitic on land planarians in Tasmania (Hickman, 1964; Matile, 1981b).

The fossil record of the Sciaroidea begins in the Early Jurassic (Ansorge, 1996; Kalugina and Kovalev, 1985; Kovalev, 1987a), and by the Early Cretaceous modern families replaced older, stem-group families (Kovalev, 1987a). The Cenozoic Sciaroidea are particularly well studied, especially those in Baltic amber (approximately 270 species of Mycetophilidae, as reviewed in the catalogue of fossil Diptera [Evenhuis, 1994]). The Baltic amber sciaroid fauna, like most of the other Cenozoic faunas of these flies, is essentially modern. Prior to the work of the senior author on extensive insect Lagersätte from Asia (Blagoderov, 1995, 1997, 1998a, 1998b, 2000), there were only seven species of sciaroids known from the Cretaceous, which were placed in the Mesosciophilidae or Mycetophilidae (Kovalev, 1986, 1990; Hong, 1992; Ren et al., 1995; Jell and Duncan, 1986; Westwood, 1854). Sciaroids have been known for years to occur in the major deposits of Cretaceous ambers from Taimyr, Siberia (Zherikhin and Sukacheva, 1973; Zherikhin 1978), Burma (Zherikhin and Ross, 2000), New Jersey (Grimaldi et al., 1989), and western Canada (McAlpine and Martin, 1969; Pike, 1994). Only three species, however, were described: *Burmacrocera petiolata* Cockerell, *Sciara burmitina* Cockerell (in Burmese amber, thought at the time to be Cenozoic), and *Schlueterimyia cenomanica* Matile (in Cenomanian French amber). Since then, major new Cretaceous outcrops of amber have been discovered from northern Spain (Alonso et al., 2000), Lebanon (Azar, 2000), New Jersey (Grimaldi, 2000), and Myanmar (Grimaldi et al., 2002), which have produced significant numbers of new specimens and taxa of sciaroids. Based on study of the older collections and these newer ones, we significantly extend the known Cretaceous diversity, based on 27 genera (19 of them new) and 39 species (all of them new).

Materials and Methods

Sixty-six specimens from the Early and Late Cretaceous of six countries, and some 10 localities, were examined. We did not study inclusions of Diadocidiidae in Burmese amber from the Natural History Museum, London, since these were on loan. Adults of most extant genera of Mycetophilidae (s.s), and all species of Lygistorrhinidae were examined. Material is housed in the following institutions:

- AMNH American Museum of Natural History (Division of Invertebrate Zoology), New York, USA
- MCNA Museo de Ciencias Naturales de Álava/Arabako Natur Zientzien Museoa, Vitoria-Gasteiz, Spain
- MCZ Museum of Comparative Zoology (Department of Entomology), Harvard Cambridge, Massachusetts, USA

PIN Paleontological Institute of the Russian Academy of Sciences (Arthropoda Laboratory), Moscow, Russia
TMPD Tyrrell Museum of Palaeontology, Alberta, Canada

Specimens were derived from the following localities and formations:

Alava, Spain: The amber deposit is located on the northern slope of Sierra de Cantabria (Álava), about 30 km southeast of the city of Vitoria-Gasteiz, near the village of Peñacerrada. A comprehensive description of the amber deposit was given by Alonso et al. (2000). It was assigned to the Nograro Formation, of Aptian–middle Albian age (120–110 Ma). All of the material is housed in MCMA.

Burma (Myanmar): Historically and presently all amber from Burma derives from the northern state of Kachin. Zherikhin and Ross (2000) reviewed historical records of Burmese amber mining and locations. For many years Burmese amber was considered Cenozoic in age; however recently it has been found to be Cretaceous after the discovery of insects in it that are exclusively Cretaceous, like Serphitidae and Stigmaphronidae (Hymenoptera). A collection of approximately 1200 arthropod inclusions resides at the NHM, London, rich in types described by T.D.A. Cockerell and others. Recently, a very large, diverse collection of Burmese amber has been assembled at the AMNH from material recently excavated in Kachin, near villages close to the town of Myitkyina. This material was acquired by Leeward Capital (Calgary, Canada), who provided it to the AMNH. Study of some 3500 organisms in this collection revealed more than 20 Mesozoic insect taxa, confirming the Cretaceous age and even indicating an age of approximately Cenomanian (98–92 Ma) (Grimaldi et al., 2002). Burmese amber is by far the most prolific and diverse Cretaceous amber for Sciaroidea.

Canada: Material from *Grassy Lake*, Alberta, derives from an abandoned coal mine 8 km south and 1.6 km east of the village of Grassy Lake (Pike, 1994). This was collected by T. Pike and housed at the RTMP. This locality was previously cited as ‘‘near Medicine Hat’’ by McAlpine and Martin (1969), who deposited their material at the Canadian National Collection (CNC) of Insects and Spiders, Ottawa. The Grassy Lake amber is from the Judith River Group of the Foremost Formation, dated as Campanian (Pike, 1994; Borkent, 1995), although Grimaldi and Cumming (citing David Eberth, personal commun.) indicated the amber to be Santonian. Amber from *Cedar Lake*, Manitoba was collected by F.M. Carpenter in 1938 among beach debris (in the MCZ). Although redeposited and somewhat distant from the Grassy Lake deposit, the two deposits are thought to be contemporaneous (Borkent, 1995). An age of 85–80 myo is a reasonable estimate for Canadian amber.

Lebanon: Material studied here is from the Acra Collection (collected by Fadi and Aftim Acra near Jezzine, 30 km east of Saida, Lebanon) and the Estephan Collection (collected by Antoun Estephan, near Bcharré, northern Lebanon). Both of these collections are housed in the AMNH. Most recently, extensive collections and stratigraphic studies of Lebanese amber have been made by Azar (2000). Lebanese amber was originally reported to be Neocomian in age, pertaining to basal periods of the Early Cretaceous (Schlee and Dietrich, 1970), 145–129 Ma. A younger age of Aptian-Albian (ca. 120–110 Ma) has also been mentioned (Whalley, 1976; Zherikhin, 1978). Azar's study, which is the most comprehensive, indicates a great range of ages of Lebanese amber, from uppermost Jurassic (152 Ma) to Albian (112 Ma), but most of the deposits yielding insect inclusions are Barremian-Aptian (approximately 125 Ma). Sciaroids in Lebanese amber are the oldest known amber fossils of the superfamily.

New Jersey: Rich amber deposits from the central county of Middlesex have been known for decades, summarized by Grimaldi et al. (1989). Recently, an extraordinary outcrop was discovered in the town of Sayreville, with a smaller one being discowered in the adjacent town of East Brunswick (Grimaldi, 2000). This material has produced the oldest definitive ants, tardigrades, mushrooms, parasitiform mites, and flowers (among many others) preserved in amber. Chemical analyses of the amber and stratigraphy of the outcrops have been made. The amber occurs in the South Amboy Fire Clay of the Magothy Formation, Turonian in age

(Grimaldi, 2000). All of the New Jersey amber is deposited in the AMNH.

Siberia (Taimyr): Reviews of the arthropod fauna in the Siberian amber were provided by Zherikhin and Sukacheva (1973) and Zherikhin (1978). Sciaroidea were found at four localities, ages of which vary. Material was collected by a PIN expedition in 1973 to *Nizhnaya Agapa,* which is on the north shore of the Agapa River, 40 km downstream from Lake Ladonnakh, Yst'-Enisey depression. This material is in the Dolgan Formation, dated palynologically as Albian–Cenomanian (Saks and Ronkina, 1957). Amber from *Yantardakh* (''amber mountain'') occuring 3–5 km upstream from the mouth of the Maimecha River, Khatanga depression, in the Kheta Formation (dated as Coniacian–Santonian [Saks et al., 1959], ca. 87 myo) was collected in 1970 and 1971. A 1976 PIN expedition collected a contemporaneous material from *Bulun* (middle course of Bulun River [right tributary of Kheta River], 18 km S of post Novaya, Taimyr). Amber from *Baikura-Neru* (Taimyr Lake, Baikura-Neru Bay) contains the only incomplete specimen of Sciaroidea. Baikura-Neru, age of which is unclear, has been assigned to the Ogneva Formation (Saks et al., 1959; Aptian-Albian, 120–110 Ma), but arthropod inclusions indicate a Late Cretaceous age (Dlussky, 1987; Zherikhin and Eskov, 1999). All Siberian amber is in PIN.

Specimens originally stored in small boxes were prepared according to the method described in Nascimbene and Silverstein (2000). This involved embedding the specimen in a stable epoxy (Buehler) under vacuum. The vacuum extracts air in fine cracks, which the epoxy then permeates, thus improving visibility and fragility of the piece. Pieces were then trimmed to thin pieces, with surfaces often to within fractions of a millimeter of the inclusion, in order to optimize observation of details. Prepared in this way, pieces can be mounted on microscope slides and the inclusions observed under 100–400× magnification with a compound microscope. Specimens were measured with a digital stage micrometer mounted under a Zeiss SV8 stereoscope, and photographed using an Infinity K-2 lens attached to a Nikon D-1 camera and illuminated with focusable fiberoptic flash wands (ML-1000 from Microptics).

Morphological terminology used follows McAlpine (1981) and Söli (1997) with modification after Kovalev (Kalugina and Kovalev, 1985). To compare relative position of veins in sciaroid wings, Kovalev defined basal (from the base of Rs to the base of *r-m*), middle (from the base of *r-m* to the base of R_4), and apical (equivalent to R_5) sections in radius stem as RS1, RS2, and RS3 sections, respectively. Also, the basal (from the base of the wing to *tb*), middle (from *tb* to *r-m*), and apical (from *r-m* to the base of the M_1 and M_2 fork, equivalent to the stem of M_{1+2}) sections of media stem were defined as M1, M2, and M3 (see also figs. 80, 81). The term ''stem of M'' refers to M1, M2, and M3 sections together. The term ''base (or stem) of M_1 and M_2 fork'' refers to the point of furcation of the veins. The terms ''stem of M_1 and M_2 fork'' or ''stem of M_{1+2}'' refer to M3 section. The terms ''R_5'' and ''stem of M_{1+2}'' are used to refer to the veins themselves, and ''RS3'' and ''M3'' are used in reference to the relative length of sections. All the veins and section names are summarized in table 1, which shows comparison of the vein nomenclature used by various authors. In some cases, for the sake of stability, we preferred to use traditional vein names in descriptions of species rather than use their names based on presumed, primary homology. These veins are denoted in boldface type in the table. In the discussion of phylogeny, however, it seemed advisable to use names of veins based on homology for establishing transformation series. We used the term ''not visible'' when a structure could not be observed clearly.

SYSTEMATIC PALEONTOLOGY

SUPERFAMILY SCIAROIDEA BILLBERG, 1820

FAMILY DIADOCIDIIDAE EDWARDS, 1925

Docidiadia, new genus

DIAGNOSIS: Head round. Flagellum 14-segmented. First flagellomere length slightly more than width. Fore tibial comb absent. Wing membrane without macrotrichia. C ends beyond tip of R_5; Sc long, ends free; RS base at the middle of R_1; crossveins *r-m*,

TABLE 1
Nomenclature and Homology of Sciaroid Wing Veins According to Authors
See also figures 80 and 81.

McAlpine et al. (1981) Vockeroth (1981)	Matile (1990)	Chandler (2002)	Homology	Present paper
Sc	Sc1	Sc	Sc	Sc
sc-r	Sc2	sc-r	sc-r	Sc_2
R_1	R_1	R_1	R_1	R_1
R_{2+3}	R_4	R_4	R_{2+3}	$\mathbf{R_4}$
—	Rr	Rs	Base of Rs	RS1 section
—	—	—	Base of Rs	RS2 section
R_{4+5}	R_5	R_5	R_{4+5}	R_5 or RS3 section
MA	Arculus	—	Base of MA	MA
r-m	ta	ta	r-m	*r-m*
bm-cu	tb	tb	Base of M_{3+4}	***tb***
—	M	M	Base of MP	M1 section
—	—	—	Base of M_{1+2}	M2 section
—	—	M_{1+2}	Stem of M_{1+2}	M3 section
M_1	M_1	M_1	M_1	M_1
M_2	M_{2+3}	M_2	M_2	M_2
CuA_1	M_4+Cu1a	M_4+CuA_1	M_{3+4}	M_{3+4}
Base of CuA_1	mcu	Base of CuA_1	m-cu	*m-cu*
CuA_2	Cu1b	CuA_2	M_5	**CuA**
CuP	Cu2	CuP	CuA	**iCu**
A_1	A1	A_1	CuP	$\mathbf{A_1}$
A_2	A2	A_2	PCu	$\mathbf{A_2}$

tb, and *m-cu* in one line; M3 section and base of M fork absent; CuA strongly curved back at the apex. A short. Male 9th tergite without marginal bristles, with one large, acute, triangular medial appendage and two small lateral ones; gonostyli do not bifurcate at apex.

TYPE SPECIES: *Docidiadia burmitica*, n.sp.

ETYMOLOGY: The name is a feminine anagram of *Diadocidia*.

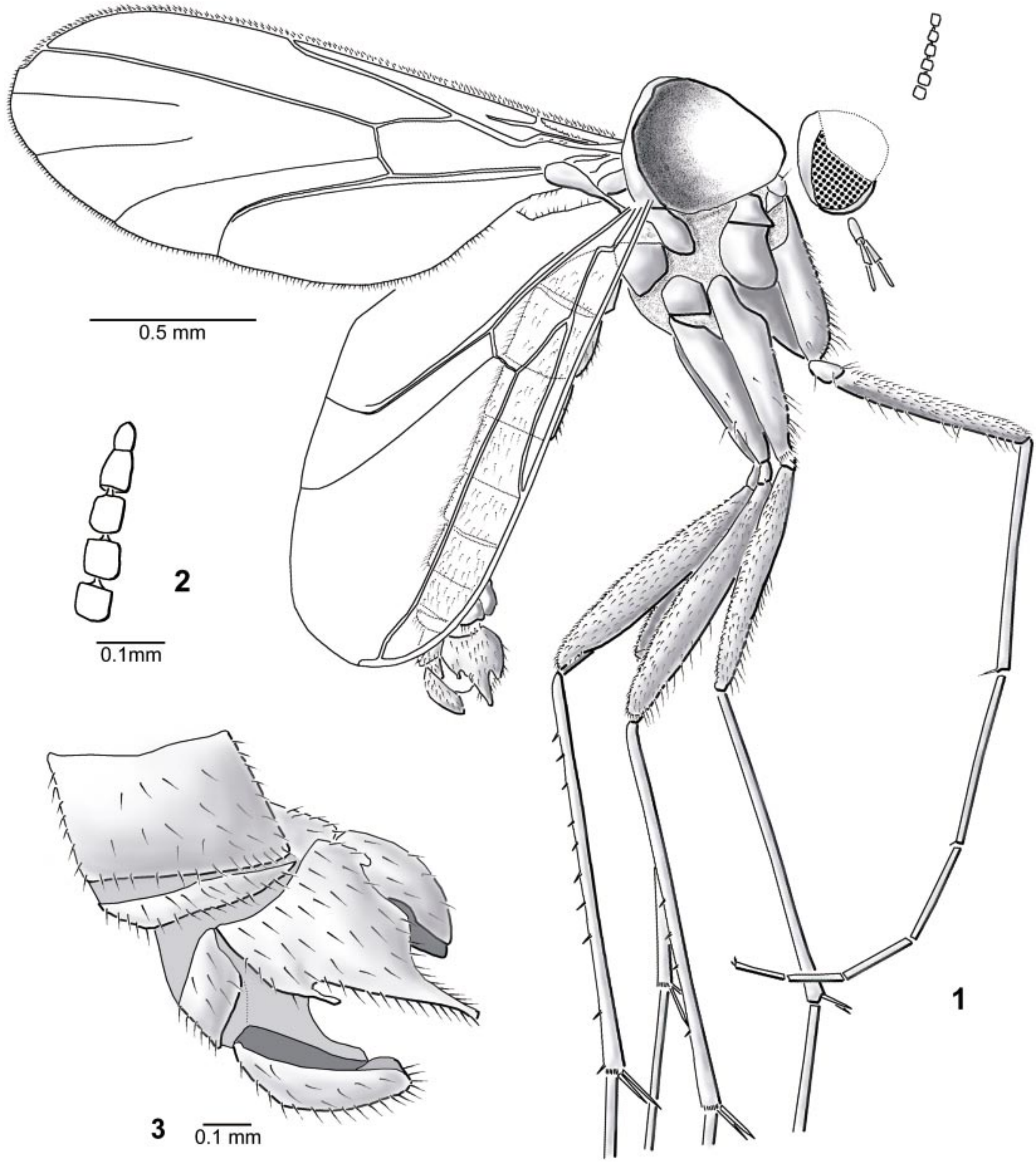
COMMENTS: The genus is close to *Diadocidia* Ruthe, but differs in having the first flagellomere short; wing membrane without macrotrichia, Sc ending free, base of RS rather distal, M3 section and base of M fork reduced; CuA curved at apex rather than with two straight sections; and male tergite IX narrow, triangular, and with two lateral appendages. *Diadocidia* consists of two subgenera and includes 10 Holarctic species (Chandler, 1994; Laštovka and Matile, 1972; Polevoi, 1996; Wu, 1995; Zaitzev, 1994) and a Neotropical one (Edwards, 1940; Papavero, 1977a), as well as undescribed Australian species (Tonnoir, 1929; Colless, 1963). One species is known from Baltic amber (Evenhuis, 1994).

Docidiadia burmitica, new species

Figures 1–3, Plate 1A

DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 1.88 mm (holotype)/1.61 (paratype); wing length = 1.61/1.55 mm. **Head.** Eyes bare, facets round. Clypeus setose. Flagellum 14-segmented; first flagellomere cylindrical, width slightly less than length; apical flagellomere twice the width. Apical flagellomere of male secondarily segmented in two parts. Scape and pedicel turbinate. Only 3 segments of palpi seen, palpomeres cylindrical, subequal in length, basal wider than the rest. **Thorax.** Scutum setose, dome-shaped, with long protruding setae. Metepisternum bare, height equal to width, shallow incision anteriorly. **Wing** membrane without macrotrichia. Costa ends beyond tip of R_5, midway between tips of R_5 and M_1. Sc ends free, slightly beyond base



Figs. 1–3. *Docidiadia burmitica*, n.sp. **1.** Holotype AMNH Bu-033. **2.** Tip of the antenna of the holotype. **3.** Male genitalia of the holotype.

of RS. R_1 setulose, R_5 with sparse setae, almost straight. R_1 short, about 0.6× wing length. M3 absent. M_1 and M_2 weakened, their bases absent. M_{3+4} weakened. **Abdomen.** Female cerci wide, subtriangular with acute ventral angle. Male tergite IX narrow, triangular with two lateral appendages. Gonocoxites short, with length about the width. Gonostyli massive, length 2.5× the length of gonocoxites, hairy, without apical teeth or spines.

MATERIAL: Holotype AMNH Bu-033, male; paratype B-002, female. Myanmar: Katchin, from amber mines near Myitkyina.

ETYMOLOGY: The species epithet is a reference to Burma, the former name of the country where the amber originates.

SCIAROIDEA INCERTAE SEDIS

Thereotricha, new genus

DIAGNOSIS: Eyes forming incomplete eye bridge, facets large, round. Ocelli three. Flagellomeres barrel-shaped, length no more than 1.5× the width. Antepronotum and proepisternum subequal, setose. Proepimeron touches episternum at the episternal suture. Anepisternum smaller than katepisternum. Anepisternal cleft distinct, narrow. Midpleural pit present. Metepisternum setose. Anterior parapsidal suture distinct. Insertion of abdomen wide. Wing membrane with or without macrotrichia. Sc short, ends free. Rs base, *r-m*, base of M_{3+4}, and CuA fork very basal. Section M2 connects *r-m* and base of M_{3+4} and CuA fork. M_{3+4} reduced.

TYPE SPECIES: *Thereotricha sibirica*, n.sp.

ETYMOLOGY: The genus name is a feminine anagram of *Heterotricha*. The name is feminine.

COMMENTS: The new genus is close to the *Heterotricha* group of genera, which have been included in the Sciaridae or Diadocidiidae. Recently, Chandler (2002) reviewed known taxa of the group and described seven more genera from all zoogeographic regions except Nearctic. These taxa seem to represent a stem group of Recent families of Sciaroidea, but monophyly of the group is not apparent. The new genus differs from all taxa of the *Heterotricha* group in having eyes with large facets, that form an eye bridge, short antennae, the scape and pedicel not differing from flagellomeres in length, palpi very short, anepisternite and katepisternite subequal, the base of RS in basal position, and *r-m* and the section of M2 subequal, where eyes and palpi demonstrate an apomorphic condition. The new genus resembles *Sciaropota* Chandler in the porrect antenna with short flagellomeres, an absence of a clearly differentiated series of scutellar bristles, large katepisternum, mesepimepon broader below, but it differs by the short Sc, long stem of M_{1+2}, and reduced M_{3+4}.

Distinct synapomorphies separate the group from other Mesozoic Sciaroidea: M1 section completely reduced; M2 section fused with *tb* in one vein meeting the base of M_{3+4}, and that oblique vein is shifted distad. The same structure of the basal veins is observed in advanced representatives of the Mesozoic family Mesosciophilidae, which are thought to represent a sister group to Mycetophilidae (Kalugina and Kovalev, 1985; Blagoderov, 1993). Similar conditions occur in the peculiar Mesozoic family Archizelmiridae (Grimaldi et al., 2003), but Archizelmiridae have crossvein *r-m* aligned with M2 + *tb* and the basal portion of M_{3+4}, forming one horizontal vein and the base of RS is shifted distad. Diadocidiidae s.str. (*Diadocidia* and *Docidiadia* n.gen.) also have these veins aligned (*r-m* through the base of M_{3+4}), but they form a vertical vein. In Mycetophilidae the combined vein M2 + *tb* lost contact with the base of M_{3+4} and meets the base of CuA or MA (arculus) (see Shcherbakov et al., 1995). Some Mycetophilidae (*Drepanocercus*, *Ectrepesthoneura*, Cretaceous *Paradzickia*, *Drepanorzeckia*, *Ekhiritus*, *Zazicia*) have the fork of M_{3+4} and CuA sessile or short-stalked, but the base of the fork is situated more basally that in Mesozoic Sciaroidea and the *Heterotricha* group. Moreover, at least in *Ectrepesthoneura* the sessile fork of M_{3+4} and CuA is secondary (see Analyses below and fig. 78). Obviously, reduction of M1 and fusion of M2 with *tb* might have originated several times in the history of Sciaroidea. Although monophyly of the group combining Recent *Heterotricha*-like taxa and Cretaceous *Thereotricha* is not proven, position of these taxa in sciaroid phylogeny should be at the base of lineages leading to Mesosoic Mesosciophilidae and Archizelmiridae and Recent Sciaridae on the one hand and higher sciaroids such as Mycetophilidae and Lygistorrhinidae on the other.

Thereotricha sibirica, new species

Figure 4, Plate 1B

DIAGNOSIS: Wing membrane without macrotrichia, RS base very basal, oblique, ~2× the length of *r-m*; M3 section long; base of M_1 and M_2 fork at level of tip of R_1; veins R_1, R_5, M_1, M_2, and CuA with long setae.

DESCRIPTION: Body length = 1.83 mm (holotype)/1.84–1.85 mm (paratypes); wing length = 1.46 mm (holotype)/1.25 mm (paratype PIN 3130/185). **Head.** Three ocelli present, equal in size, distance of lateral ocellus from median ocellus and eye margin 1.5× its diameter. Occiput with numerous small setae. Eyes large, bare, forming incomplete dorsal bridge (separated by twice the facet diameter). Scape and pedicel short, rounded. Flagellum 14-segmented, flagellomeres barrel-like, width 1.3× the length, covered by short trichia. Palpi 4-segmented. Basal segment small, bacilliform, others short, rounded; antepenultimate segment with round sensory pit dorsomedially, slightly longer than others.**Thorax.** Antepronotum with one strong seta, proepisternum with six. Proepimeron touches episternum at episternal suture. Mesonotum uniformly setose. Midpleural pit present. Katepistrnum large, expanded caudally. Ventral part of mesepimeron not very narrow, parallel-sided. Laterotergites bare, small. Metepisternum setose, with narrow anteriodorsal cleft. **Wing** membrane without macrotrichia. Costa ends beyond tip of R_5, one-third the distance between tips of R_5 and M_1. Sc very short, ends free just beyond RS base. RS base proximad, oblique, 1.5× *r-m* length. R_1, R_5, M_1, M_2, and CuA with long setae. R_1 about 0.7× wing length. RS base oblique. Crossvein *r-m* fused with *tb* and *m-cu* in one horizontal vein. M3 section 1.5× as long as fork of M_1 and M_2. M_{3+4} reduced, seen as a fold at base only. CuA ends before middle of the wing. **Legs.** Fore coxae with numerous setae on anterior and distal surfaces, mid coxae with distal rows and several setae on apical part, hind coxae with caudodistal row of setae. Fore tibia with anteroapical pit having two combs of setae. **Abdomen** setose. Eighth segment slightly shorter than preceding ones. Ninth tergite ovoid, with apical comb of short blunt setae. Gonocoxites stout, triangular in lateral view. Gonostyli small, flat, rectangular, with several apical setae.

MATERIAL: Holotype PIN 3130/183, male; paratypes, PIN 3130/182, 3130/184, 3130/185, males; all specimens in the same piece of amber. Russia: Taimyr Peninsula, Yantandarkh, coll. 1970.

ETYMOLOGY: The species epithet is in reference to Siberia, the region where the original locality is situated.

?*Thereotricha agapa*, new species

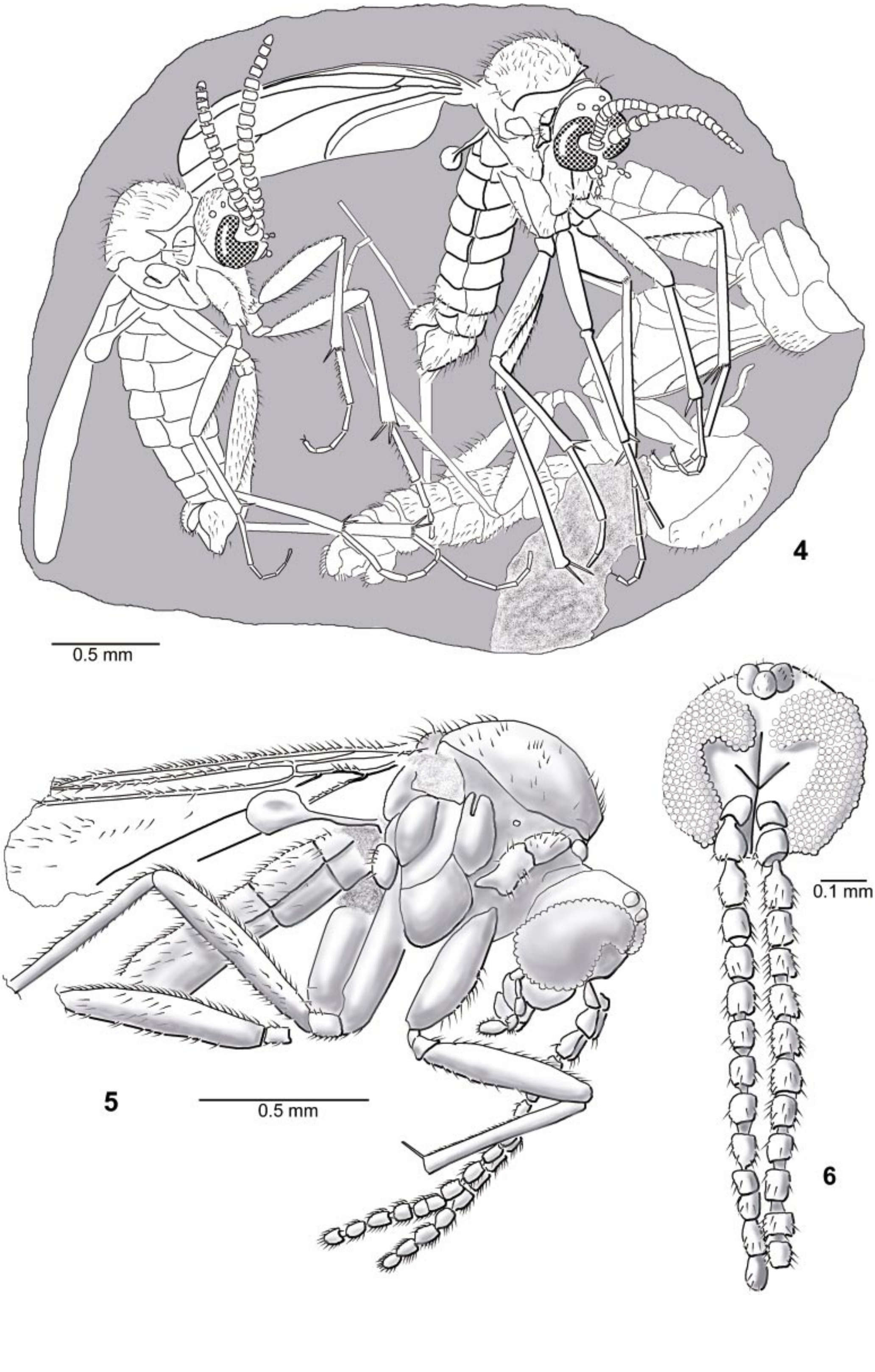
Figures 5, 6, Plate 1C

DIAGNOSIS: Three ocelli, touching. Wing membrane with scattered macrotrichia. RS base transverse, shorter than *r-m*. M_2 probably absent.

DESCRIPTION: Body length = 1.56 mm (rest, estimated length 1.87 mm); wing length 1.48 mm. Partly preserved specimen. **Head:** Occiput and vertex with straight and curved setae. Three ocelli present, each on its own mound, the latter fused by contacting edges. Eyes bare, with incomplete bridge, deeply emarginate at antennal base. Frontal furrow and keels well developed. Scape and pedicel as long as flagellomeres. Flagellum 14-segmented, flagellomeres barrel-shaped, length about 1.5× the width, with few strong setae and numerous fine trichia. Clypeus setose. Palpi 4-segmented, short. Antepenultimate palpomere with dosomedial round sensory pit. **Thorax:** Proepisternum with 3 long and and 11 shorter setae. Proepimeron touches episternum at the episternal suture, katepisternum with shallow excavation below the point. Anepisternum less than katepisternum, the latter with several trichia in lower part. Laterotergite bare, divided with katepisternum by anepimeron. Mediotergite bare. Metepisternum setose. Scutum with scattered setae. Scutellum with 6 long setae. **Wing** membrane with microtrichia and macrotrichia mostly in apical and hind area. Costa, R_1, and R_5 with long setae. Sc very short, ends free. R_1 and R_5 almost straight. RS base short, ~0.5× *r-m* length, transverse; *r-m* fused with *tb* and *m-cu*, slightly oblique. Crossvein *m-*

→

Figs. 4–6. *Thereotricha*, n.gen. **4.** *Thereotricha sibirica*, n.sp., drawing of amber piece with four embedded specimens, including holotype PIN 3130/183. **5.**? *T. agapa*, n.sp., holotype PIN 3426/256. **6.**? *T. agapa*, head of the holotype.


4
0.5 mm
5
0.5 mm
6
0.1 mm

cu twice the length of *r-m*. M_2 probably absent. M_{3+4} absent. M_1 straight, weak.

MATERIAL: Holotype PIN 3426/256, sex unknown. Russia, Taimyr Peninsula, Nizhnyaya Agapa, coll. 1973.

ETYMOLOGY: The species is an epithet in reference to the locality, the Nizhnyaya Agapa River.

COMMENTS: Structure of ocelli and a transverse RS base are apparent characters of generic level, distinguishing the species from *T. sibirica*, but incomplete preservation of the specimen from Nizhnyaya Agapa does not allow description of a new genus. Both species share such synapomorphies as an incomplete eye bridge, proepimeron apex at the episternal suture, setose metepisternum, and M_{3+4} reduced. Until more specimens of this peculiar group will be found and phylogenetic analysis is done we prefer to keep the species in this genus.

FAMILY LYGISTORRHINIDAE EDWARDS, 1925

DIAGNOSIS: Eyes round; pedicel bears bristles apically; mouthparts reduced and form proboscis in some genera; Anepimeron fused to katepisternum; Sc very short; R_1 short; stem of M and M_{1+2} fork base absent; *r-m* aligned with tb; M2 + *tb* subhorizontal; hind coxae short, hind tibiae and tarsi swollen; metepisternum with deep anterodorsal cleft; gonostyli of simple shape (presumably reversed in *Plesiognoriste* and *Protognoriste*).

Archaeognoriste, new genus

DIAGNOSIS: Palpi long, three-segmented, mouthparts reduced. Base of RS present, crossvein *r-m* distinct. All the coxae approximately equal in length. Hind tibiae slightly swollen. Gonostyli with long inner process.

TYPE SPECIES: *Archaeognoriste primitiva*, n.sp.

ETYMOLOGY: The name is a combination of *archaeos* (Greek αρχαίος, or ancient) and the genus name *Gnoriste*. The name is feminine.

Archaeognoriste primitiva, new species

Figures 7, 8, Plate 1D

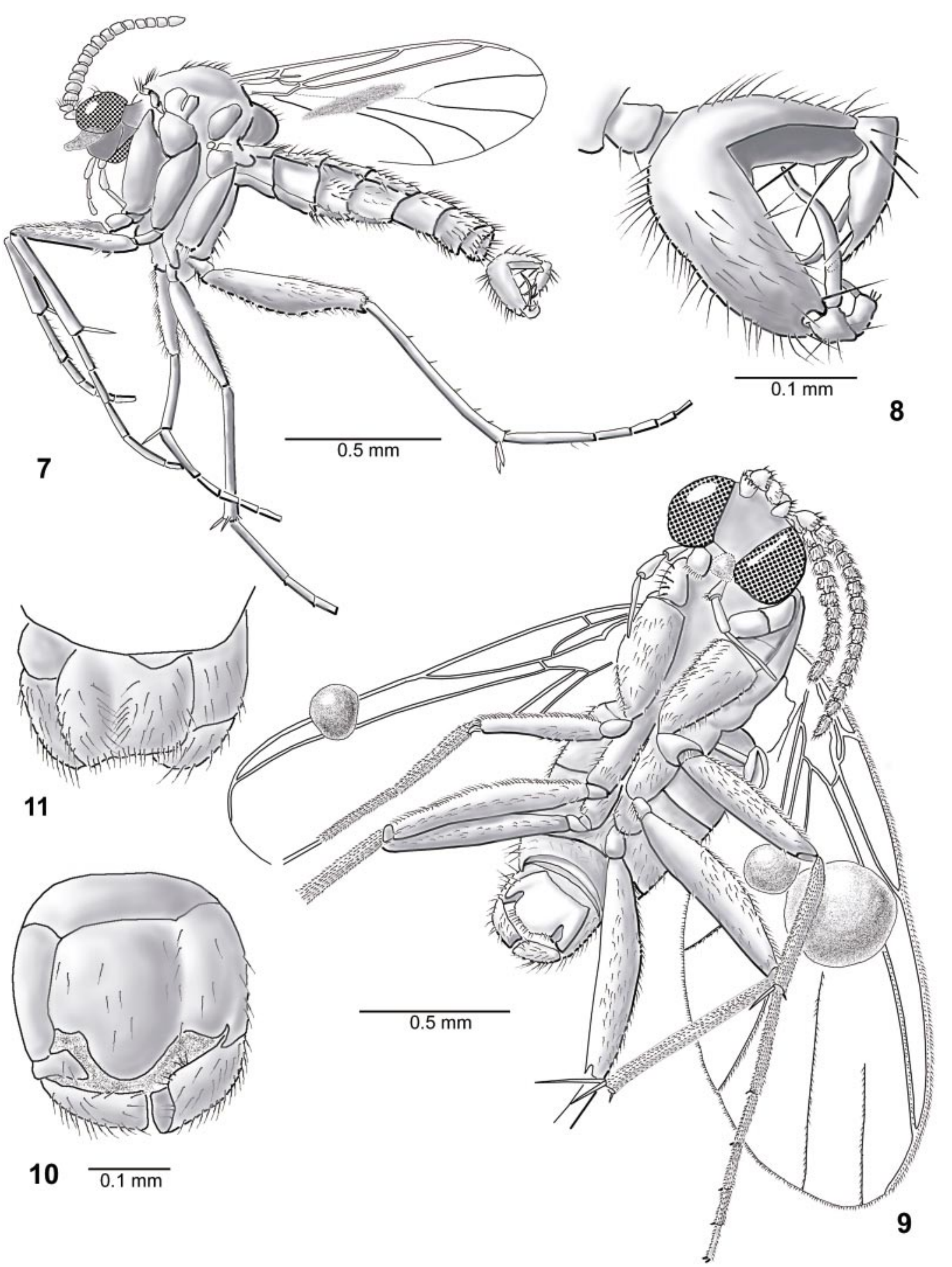
DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 1.58 mm (holotype)/1.47–1.61 mm (paratypes); wing length = 0.98/0.95–1.10 mm. **Head:** Posterior surface flat, with scattered setulae. Frons membranous. Eyes large, hairy. Ocelli not seen. Scape and pedicel slightly wider than flagellomeres, subconical. Flagellum 14-segmented, flagellomeres cylindrical, width about equal to length. Palpi 3-segmented, segments cylindrical. Penultimate segment about 0.75× the length of apical one and 2× the length of antepenultimate. **Thorax:** Scutum irregularly covered with short setae and bearing long lateral and acrostichal setae. Scutellum with two pairs of long setae and several short ones. Antepronotum and preepisternum with 6–8 long setae. Anepisternal suture declines posteriorly. Anepisternum with small cleft. Mediotergite setose, laterotergites bare. Dorsal edge of mesepimeron protruding toward laterotergite. Metepisternum with deep cleft, height more than width. **Wing** membrane without macrotrichia. C not reaching wing tip, ends one-fourth distance between tips of R_5 and M_1. All veins bear setae. Sc very short, free. R_1 about 0.6× the length of wing. RS base distinct, at the level of Sc tip. Crossvein *r-m* fused with *tb*, oblique. Stem of M and base of M_1 and M_2 fork absent. M_{3+4} base very weak. M and CuA veins weak. **Legs:** Fore coxae densely setose, mid and hind coxae with setae on apical half, all coxae about equal in size. Tibial and tarsal trichia not in rows. **Abdomen** setose, with exception of 1st and 2nd sternites. Seventh sternite short, 8th small and retractable. Ninth tergite small, rectangular, with well-developed, short, one-segmented cerci apically. Gonocoxites straight. Gonostyli saberlike, thinner to apex, with one apical and one very long curved basal processes.

MATERIAL: Holotype AMNH Bu-1539, male; paratypes AMNH Bu-412a and Bu-412b, 2 males in the same piece, Bu-485, Bu-693, males. Myanmar: Katchin, from amber mines near Myitkyina.

ETYMOLOGY: The species epithet is from Latin *primitivus* meaning ''the first *or* earliest of its kind'' and is a reference to the basal position of the species within Lygistorrhinidae.

COMMENTS: Venation of the species is almost identical to *Palaeognoriste* sp. (Grimaldi and Blagoderov, 2001: figs. 5a, 6a), with bases of RS and *r-m* somewhat reduced



Figs. 7–11. *Archaeognoriste*, n.gen. and *Lebanognoriste*, n.gen. **7.** *A. primitiva*, n.sp., holotype AMNH Bu-1539 **8.** *A. primitiva*, male genitalia. **9.** *L. prima*, n.sp. holotype AMNH JG268/1. **10.** *L. prima*, male genitalia dorsally. **11.** *L. prima*, male genitalia ventrally.

and shifted proximally. Characters such as reduced palpi, membranous frons, the wing venation, simplified genitalic structure, and a large metepisternum (presumably plesiomorphic) with deep anteriodorsal cleft obviously refer the species to the Lygistorrhinidae, but compared to more derived species the new species has many plesiomorphies: presence of RS base and a distinct *r-m*, unmodified legs, and gonostyli with long processes.

Lebanognoriste, new genus

DIAGNOSIS: Wing membrane without macrotrichia, R_1 short, crossvein *r-m* fused with base of M_{3+4}, fork of M_{3+4} and CuA not sessile; preapical palpomere attached at the tip of antepreapical, inner mid and hind tibial spurs longer than outer ones.

TYPE SPECIES: *Lebanognoriste prima*, n.sp.

ETYMOLOGY: The name is a combination of Lebanon, source country of the amber, and the genus name *Gnoriste*. The name is feminine.

COMMENTS: *Lebanognoriste* together with *Archaeognoriste* form the most basal group of Lygistorrhinidae. Synapomorphies such as rather long fore coxae; short vein R_1; short, transverse RS1 section; reduced base of the M_1 and M_2 fork; and crossvein *r-m* shifted proximally and aligned to M2 + *tb* fused vein, which is oblique or longitudinal and shifted proximally, undoubtedly ally these two genera with the lygistorrhinids (see also Analyses). Both genera lack autapomorphies, and comparison to recent representatives of the family indicates various plesiomorphies.

Lebanognoriste prima, new species

Figures 9–11, Plate 1E

DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 1.53 mm; wing length = 1.64 mm. **Head:** Postocciput flat, with several strong setae behind eye margin. Eyes setose. Ocelli not visible. Scape and pedicel twice as wide as flagellomeres, scape with one and pedicel with two apical rows of setae. Flagellum with 14 cylindrical segments, covered by hairs as long as 1/2 flagellomere diameter. Face setulose. Only three apical segments of palpi visible; antepenultimate and penultimate knoblike; apical long, slender, straight, its length approximately the combined length of preceding two palpomeres. **Thorax:** Mesonotum with few long lateral and scattered shorter setae. Anterior parapsidal suture distinct. Scutellum with 6 long setae and sparse short ones. Laterotergites and mediotergite bare. **Wing** membrane without macrotrichia, microtrichia not arranged in rows. All longitudinal veins with setae. Costa ends far beyond tip of R_5. Humeral cross-vein transverse. R_1 short, about 0.4× wing length. Sc short, ends in R at middle of *r-m*. R_5 slightly curved caudally. M_1 slightly curved forward at tip. M fork base and M stem absent. Crossvein *r-m* short, oblique, fused with base of M_{3+4}. M_{3+4} and CuA stem short, but distinct. M_{3+4} almost straight, CuA curved gently back. **Legs:** Fore tibiae with simple anteroapical depressed area bearing one row of short bristles. Mid tibia with inner spur 1.5× as long as outer one, inner hind tibia spur 1.3× as long as outer one. Tibial setulae in distinct rows. Tibial spurs 2–3× the tibial diameter. Tarsal claw with one tooth. **Abdomen** short, setose, with 7 visible segments. Genitalia rounded, rotated at 180°. Gonocoxites massive, fused ventrally. Gonostyli hemicylindrical, slightly curved, shovel-like at apex. Ninth tergite length equals the width, with two deep lateral incisions.

MATERIAL: Holotype AMNH JG268/1, male. Lebanon: near Jezzine, coll. Aftim and Fadi Acra.

ETYMOLOGY: The species epithet is a Latin word *primus* meaning ‘‘first’’ and is a reference to the oldest find of the family in the fossil record.

Plesiognoriste, new genus

DIAGNOSIS: Wing membrane without macrotrichia. Palpi short, two-segmented. Face wide, about one-third of head width. Eyes of male relatively small, setose. Proboscis not distended. Laterotergites bare. All veins with setae. R_5 runs very close to R_1. RS base absent. M_2 absent. M_{3+4} and CuA fork short. Middle and hind tibiae spurs almost equal in length. Tibial setulae forming more or less regular rows apically.

TYPE SPECIES: *Plesiognoriste carpenteri*, n.sp.

ETYMOLOGY: The genus name is a combination of *plesion* (Greek πλησίον, or neighbor) and the genus name *Gnoriste*. The name is feminine.

COMMENTS: See under *Protognoriste*.

Plesiognoriste carpenteri, new species

Figures 12, 13, Plate 1F

DIAGNOSIS: Apical palpal segment curved, bulbous; flagellomeres longer than wide, anepisternite with small dorsal cleft; M_{3+4} gently curved, M_{3+4} and CuA stem weakened, fore and hind tibiae and hind femora broadened.

DESCRIPTION: Body length = 1.32 mm; wing length = 1.27 mm. **Head:** Antennae inserted near middle of head. Scape cylindrical; pedicel subconical, apex wide with oblique margin. Flagellum 14-segmented, flagellomeres cylindrical, length of each twice the width, covered with setulae as long as flagellomere diameter. Face wide, pentangular, setose. Frons and occiput uniformly setulose. Three ocelli present, equal in size, distance from middle to lateral ocelli the same length as from lateral ocellus to eye margin (distance of lateral ocellus from eye margin equal to diameter of ocellus). Eyes setose, slightly emarginate at antennal bases. Palpi with two visible segments; apical segment slightly curved, bulbous, setulose; basal one with a few short setae. **Thorax:** Scutum with long lateral and dorsocentral setae. Scutellum with 6 long setae. Antepronotum setose, divided from proepisternum by a distinct suture. Anepisternum with small dorsal cleft. Mediotergite bare. Laterotergite not fully visible. **Wing** membrane without macrotrichia; microtrichia not arranged in regular rows. Costa ends slightly beyond tip of R_5. All veins bear setae. Sc very short, ends free, humeral cross-vein almost transverse. R_1 about 0.6× wing length. RS base absent. R_5 runs very close to R_1, virtually straight; base weak, so that vein invisible proximal to Sc tip. M_1 weak, originates midway between tips of R_1 and R_5. M_2 and stem of M absent. M_{3+4} curved gently. CuA has distinct kink at base of M_{3+4}. M_{3+4} and CuA stem weak. **Legs** rather short and stout. Fore coxae with long bristles on anterior edge. Fore tibia widened. Hind coxae equal in length to middle ones, but broader, with scattered setae. Hind femora swollen, without ventral spines. Hind tibiae with apical comb of setae. Tarsal claw with one tooth. **Abdomen** shorter than wings, setose. Gonocoxites quadrate, flat, setose, with dorsal protruding appendage. Gonostyli simple, length ~3× the width, apically with two black inner spines and outer comb of short setae.

MATERIAL: Holotype MCZC 6927, male. Canada: Manitoba, Cedar Lake, coll. F.M. Carpenter.

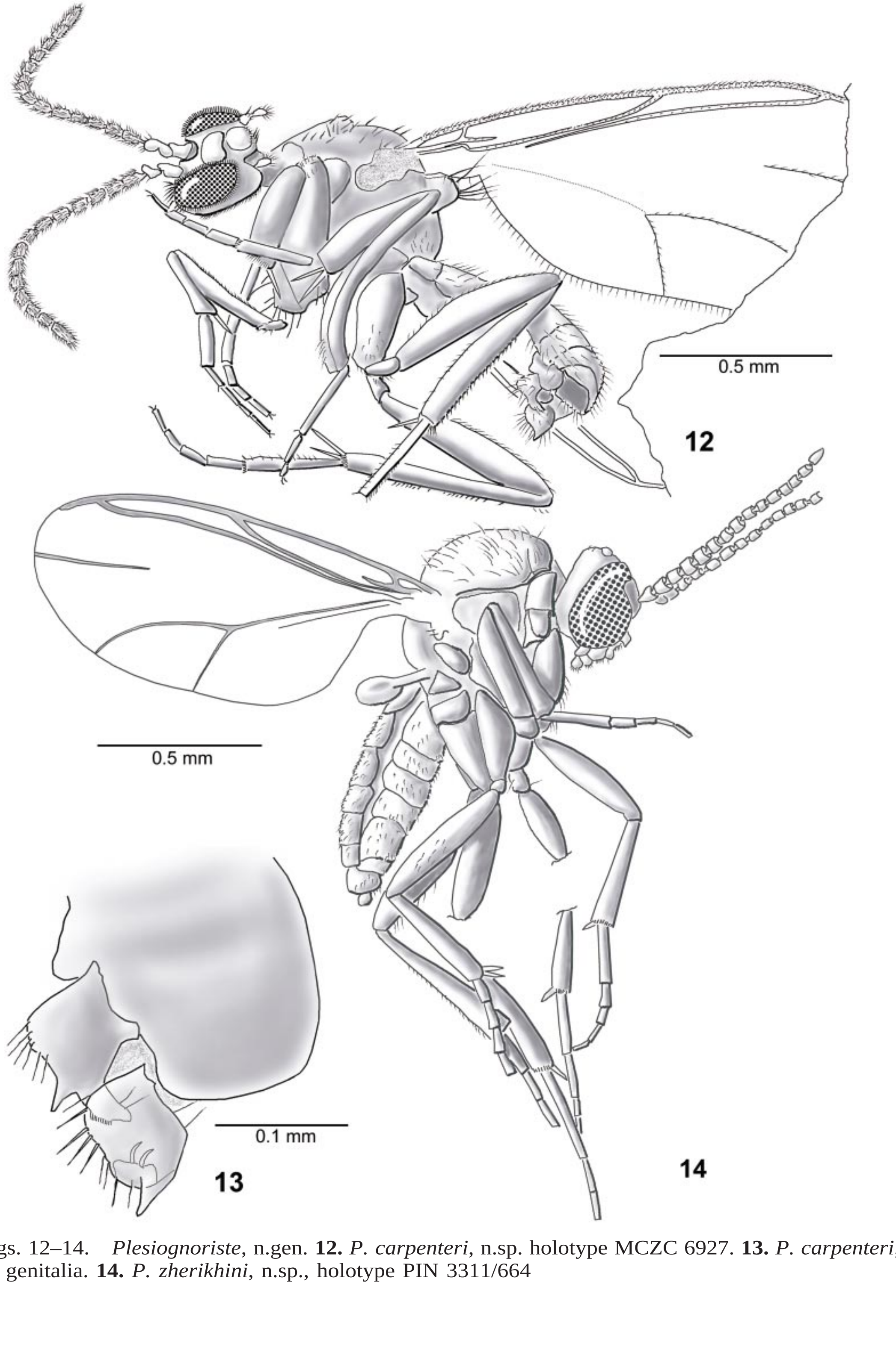
ETYMOLOGY: The species epithet is a patronym for the late Professor Frank Carpenter of the MCZ, who collected this and many others Canadian amber specimens.

Plesiognoriste zherikhini, new species

Figure 14, Plate 2A

DIAGNOSIS: Scape and pedicel not enlarged, flagellomeres short, eyes form incomplete bridge, apical palpal segment rounded, M_{3+4} strongly curved, legs not modified.

DESCRIPTION: Body length = 1.40 mm; wing length = 1.22 mm. **Head:** Postocciput flat. Antennae inserted near middle of face. Scape and pedicel not enlarged, widths equal to width of average flagellomere. Flagellum 14-segmented, flagellomeres cylindrical, width about equal to length, setulose. Frons setose. Eyes setulose, emarginate at antennal bases, forming lobes toward middle of head 4–5 facets wide, but dorsal bridge incomplete, separated by distance more than 4× facet diameter. Ocelli three, equal in size to the distance from middle to lateral ocelli, twice the length as from lateral ocellus to eye margin (distance of lateral ocellus from eye margin equal to diameter of ocellus). Face setose. Palpi short, only 2 visible, rounded segments, with numerous hairs. Clypeus bare. **Thorax:** Scutum with long lateral, dorsocentral, and acrostichal setae. Scutellum with 6 long setae. Anterior parapsidal suture distinct. Suture between antepronotum and proepisternum oblique. Proepimeron touches mesepisternum at anepisternal suture. Anepisternal cleft narrow, oblique. Mediotergite and laterotergites bare. Metepisternum touches katepisternum. **Wing** membrane without macrotrichia, with scattered microtrichia. All veins setose.



Figs. 12–14. *Plesiognoriste*, n.gen. **12.** *P. carpenteri*, n.sp. holotype MCZC 6927. **13.** *P. carpenteri*, male genitalia. **14.** *P. zherikhini*, n.sp., holotype PIN 3311/664

Costa ends beyond tip of R_5, one-third the length between tips of R_5 and M_1. Sc very short, ends free. R_1 short, about 0.5 wing length. R_5 about 0.85× wing length, curved slightly, runs very close to R_1. M_1 confined to apical third of wing. RS base, M_1 and stem of M absent. Crossvein *r-m* fused with R_5, horizontal, fused with CuA base. CuA base weak. Base of M_{3+4} and CuA fork at level of tip of R_1. M_{3+4} curved and well rounded. CuA with two straight segments forming obtuse angle. **Legs:** Coxae almost equal in length. Hind coxae bare at base. Fore tibia distally with apical hemispherical anteroapical depression with comb of fine setae. Tarsal claw without teeth. **Abdomen** shorter than wings, with 7 visible segments, setose. Sixth and 7th segments twice as short as 5th, 8th retracted. Cerci one-segmented.

MATERIAL: Holotype PIN 3311/664, female. Russia: Taimyr Peninsula, Yantardakh, coll. 1971.

ETYMOLOGY: The species epithet is a patronym in honor of the late Dr. Vladimir Zherikhin of the Paleontological Institute in Moscow, prominent paleoentomologist, who collected the specimen.

Protognoriste, new genus

DIAGNOSIS: Wing membrane without macrotrichia, occiput without row of strong setae. Palpi short. Eyes bare. Face wide. Stem of M and M_2 absent. RS base distinct. Crossvein *r-m* meets M_{3+4} and CuA stem. CuA gently curved. Abdomen insertion broad. Fore tibiae shorter than femora.

TYPE SPECIES: *Protognoriste amplicauda*, n.sp.

ETYMOLOGY: The name is a combination of *protos* (Greek πρώτος, or first) and the genus name *Gnoriste*. The name is feminine.

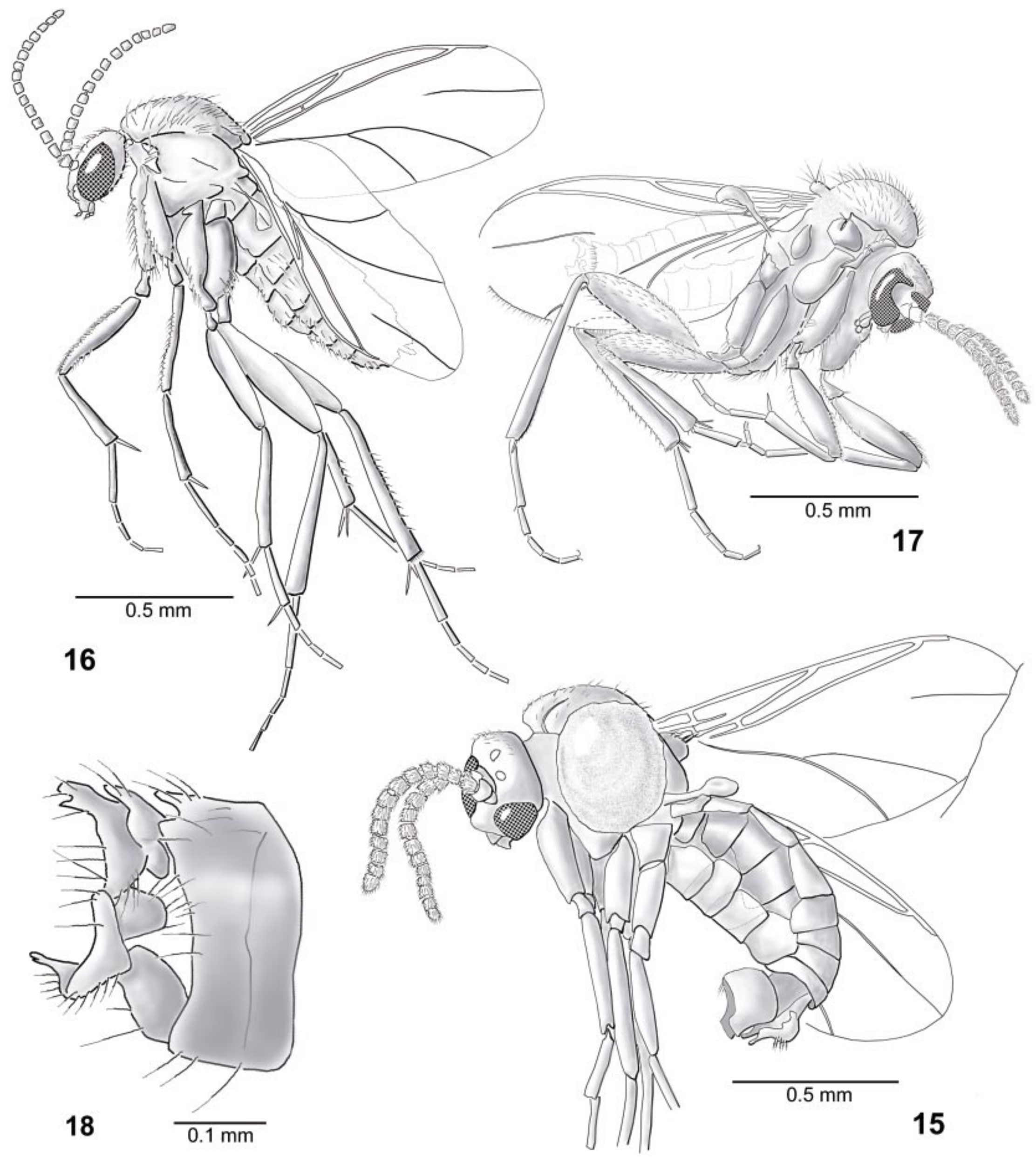
COMMENTS: The following apomorphic characters refer the genera *Plesiognoriste* and *Protognoriste* to the Lygistorrhinidae: short palpi; small dorsal cleft of anepisternum; anepisternum and metepimeron not divided by laterotergite (possibly plesiomorphic); short, incomplete Sc; short R_1; RS base and M stem reduced; *r-m* horizontal and fused with R_5; hind coxa smaller and broader than mid coxa; abdomen insertion narrow; cerci simple. Face wide, with three ocelli, situated almost in straight line, suggestive of Manotinae, but structures of palpi, katepisternum and metepimeron, and absence of strong setae, show no apomorphies with respect to that subfamily. Eye size, face width, vein vestiture, tibial spurs of equal size, and complicated shape of the gonostyli are more primitive conditions than occur in Recent lygistorrhinids, although some features of venation and gonostyli are apomorphic. The short fork of M_{3+4} and CuA and absence of a long proboscis are most similar to the genus *Seguyola* Matile. It is possible that these two genera should be treated as a separate subfamily of Lygistorrhinidae. We prefer to expand the definition of the family to include newly described taxa.

Protognoriste amplicauda, new species

Figure 15, Plate 2B

DIAGNOSIS: R_1 length 3× that of *r-m*. Gonocoxite massive. Gonostyli straight, flattened dorsoventrally.

DESCRIPTION: Body length = 1.25 mm; wing length = 1.11 mm. **Head:** Eyes setulose, setae very short. Ocelli three, equal, almost in straight line, distance of lateral ocellus from eye margin equal to distance from mid ocellus to lateral one. Vertex and frons setose. Scape very small. Pedicel spherical, obscure. Flagellum 14-segmented, flagellomeres cylindrical, lengths about equal to widths, setose. Palpi short, 3-segmented, apical segment rounded, penultimate cylindrical, length 2× the width. Face wide, quadrate. **Thorax:** Scutum with lateral, dorsocentral and acrostichal setae. Scutellum with several long setae. Mediotergite with short trichia. Metepisternum with anterodorsal cleft, height about equal to width. **Wing** membrane without macrotrichia. Costa ends beyond tip of R_5, at 1/6 the length between tips of R_5 and M_1. Sc short, ends free at the level of RS base. Humeral cross-vein transverse. R_1 short, about 0.4× wing length. R_5 about 0.8× wing length, almost straight. RS base very short, transverse. Crossvein *r-m* horizontal, meets M_{3+4} and CuA stem, its length 3× less than R_1 length. M_1 almost straight, weakened at base. M_2 and M stem absent. Base of M_{3+4} and CuA fork between



Figs. 15–18. *Protognoriste*, n.gen. **15.** *P. amplicauda*, n.sp., holotype PIN 3426/257. **16.** *P. goeleti*, n.sp., holotype AMNH Bu-406. **17.** *P. nascifoa*, n.sp., holotype AMNH Bu-434. **18.** *P. nascifoa*, male genitalia.

levels of RS base and R_1 tip. CuA and M_{3+4} curved caudally. **Legs:** Coxae almost equal in length, hind coxae bare. Tibial setulae in distinct rows. Tibiae, especially fore, short. Tarsal claw with small obtuse tooth. **Abdomen** as long as wing, with 8 segments, setose. Eighth segment short, retracted. Gonocoxite massive. Gonostyli straight, flattened dorsoventrally.

MATERIAL: Holotype PIN 3426/257, male. Russia: Taimyr Peninsula, Nizhnyaya Agapa, coll. 1973.

ETYMOLOGY: The species epithet is derived from Latin words *amplus* meaning ''large, distinguished'' and *cauda* meaning ''tail'' in reference to large terminalia of the species.

Protognoriste goeleti, new species

Figure 16, Plate 2C

DIAGNOSIS: R_1 length 1.8× that of *r-m.*

DESCRIPTION: Body length = 1.21 mm; wing length = 0.95 mm. **Head:** ovate, height ~1.5× width in profile. Occiput and postgena densely setose. Antennae attached below the middle of the head. Scape and pedicel subconical, wider than flagellum. Flagellomeres cylindrical, length 1.1–1.5× the width. Eyes setose, ovate, without incision, facets round, close. Clypeus bare. Two palpomeres seen: basal one ovate, length 2× the width, apical round, 4× shorter than basal. **Thorax:** Scutum irregularly setose. Anterior parapsidal suture distinct. Scutellum small. Anepisternum with several setae. Proepimeron touches mesepisternum at anepisternal suture. Anepisternum with deep cleft in the middle. Laterotergite shifted dorsocaudally, so that metepisternum contacts katepisternum for some distance, not in a point. Laterotergites and metepisternum with short hairs. Mediotergite short. Meron at mid coxae large. **Wing** membrane with microtrichia not arranged in rows. Costa ends beyond tip of R_5, at one-fourth length between tips of R_5 and M_1. Sc very short, ends free. Humeral cross-vein oblique. R_1 short, about 0.4× wing length. RS base short, transverse. R_5 about 0.8× wing length, almost straight. M_1 slightly sigmoid, confined to apical third of wing, ends at tip of wing. Stem of M and M_2 absent. Crossvein *r-m* horizontal, very weak, meets M_{3+4} and CuA stem, its length 1.2× more than length of R_1. M_{3+4} and CuA fork 1.7× stem length, its base between levels of RS base and tip of R_1. M_{3+4} and CuA curved gently. **Legs:** Fore tibia 1.25× shorter than fore femora. Tibial and tarsal setulae not in rows. Hind tibia with 15 dorsal bristles. Tibial spurs 2× the diameter of tibia. Hind tibiae with apical comb of short setae. Fore coxae with dense anterior setae, mid and hind coxae with setae in apical part, hind coxae without posterior setae. **Abdomen** insertion broad. Abdomen shorter than wings. Cerci with large basal and small round apical segments.

MATERIAL: Holotype AMNH Bu-406, female. Myanmar: Katchin, from amber mines near Myitkyina.

ETYMOLOGY: The species epithet in honor of Mr. Robert Goelet, for his generosity in funding purchase of specimens and the authors' work.

Protognoriste nascifoa, new species

Figures 17, 18, Plate 2D

DIAGNOSIS: RS base and the base of the M_{3+4} and CuA fork very basally. R_1 length 4× *r-m.*

DESCRIPTION: Body length = 1.09 mm; wing length = 1.05 mm. **Head:** Occiput and frons setose. Pedicel and scape wider than flagellomeres. Flagellum 14-segmented, flagellomeres cylindrical, length about equal to width. Face wide, quadrate. Clypeus setose, palpi 2-segmented, basal palpomere swollen, apical one very small. Eyes with incision, forming incomplete eye bridge (possibly artifact, face deformed). **Thorax:** Proepimeron contacts katepisternum. Anepisternum width 1.5× height, with distinct cleft posteriorly. Laterotergites, mediotergite and metepisternum with very short trichia. Scutum with numerous erect setae. Metepisternum with long anteriodorsal process touching katepisternum. **Wing:** Sc very short, free. Costa produced beyond R_5 one-third distance between R_5 and M_1 apices. RS base situated proximally, faint, oblique. R_1 length 4× that of *r-m.* Crossvein *r-m* weak, 4× shorter than R_1. M_1 originates at distal third of wing, curved at base. Base of the M_{3+4} and CuA fork at the level of RS base. **Legs:** Hind coxae shorter than mid ones. Fore coxae with long anterior setae, mid and hind ones with apical setae. Tibial setulae not in rows except apical half of hind tibiae. Hind tibiae long, swollen somewat at apex, with dorsal row of bristles and apical comb of setae. Tibial spur length 1.0–1.3× tibial diameter. **Abdomen** setose, segments short. Genital complex wider than long. Gonocoxites fused. Gonostyli with one outer and two inner lobes.

MATERIAL: Holotype AMNH Bu-434, male. Myanmar: Katchin, from amber mines near Myitkyina.

ETYMOLOGY: The species epithet derived from U.S. National Science Foundation, a generous sponsor of this and other fossil insect research at the AMNH.

Leptognoriste, new genus

DIAGNOSIS: Palpi short, 4-segmented. Mouthparts form short proboscis or reduced. Laterotergites and mediotergite setose. Wing membrane with macrotrichia. Sc long, ends at C. Costa produced beyond R_5, not reaching wing apex. M_1 absent. M_2 reduced at the base. RS base transverse. M_{3+4} and CuA fork stalked. Hind coxae shorter than fore and mid ones. Male genitalia simple.

TYPE SPECIES: *Leptognoriste davisi*, n.sp.

ETYMOLOGY: The name is a combination of *leptos* (Greek λεπτόσ, or thin, lean) and the genus name *Gnoriste*. The new name is feminine.

Leptognoriste davisi, new species

Figures 19–22, Plate 2E

DIAGNOSIS: The base of M_{3+4} and CuA fork at level of base of RS. Mouthparts form short proboscis. M_1 reaching wing margin. Ninth tergite small, longer than wider, rectangular.

DESCRIPTION: Body length = 1.94 mm (holotype)/1.69 mm (paratype); wing length = 1.26 mm (holotype)/1.27 mm (paratype). **Head** round with protruding ocelli. Ocelli in triangle, lateral separated from medial by ocellus diameter and from eye margin by 2 ocellus diameters. Eyes large, rounded, with light emargination, with large facets. Clypeus narrow, triangular, setose. Palpi 4-segmented, palpomere length ratio 1:2:2:3. Apical palpomere attached preapically. Short proboscis, one-half head height. **Wing** length equal to abdomen length. Sc produced slightly beyond RS base. R_1 length 1.2× *r-m*. M_2 originates in distal half of wing. Base of M_{3+4} and CuA fork at level of RS base. Macrotrichia numerous in basal part of wing. **Thorax:** Scutum with long lateral, dorsocentral and acrostichal and shorter irregular setae. Anterior parapsidal suture distinct. Antepronotum and proepisternum setose. Anepisternum wider than its height. Proepimeron touches katepisternum slightly below anepisternal suture. Mesepisternum with long anterodorsal process, touching anepisternum. Laterotergites with row of long setae. Mediotergite irregularly setose with short setae. **Legs:** Coxae with relatively short setae. Hind tibiae with bristles in dorsal row, 1.5× longer than femora. **Abdomen** setose, except first sternite. Abdomen insertion very narrow. Tergite 8 shorter than sternite. Tergite 9 narrow, rectangular with numerous setae at apex. Gonocoxites rather slender. Gonostyli slightly curved.

MATERIAL: Holotype AMNH Bu-126a, male; paratype AMNH Bu-126b, male, in the same piece. Myanmar: Katchin, from amber mines near Myitkyina.

ETYMOLOGY: The species epithet is a patronym for Mr. Jim Davis, who supplied the AMNH with fossiliferous amber from Myanmar.

Leptognoriste microstoma, new species

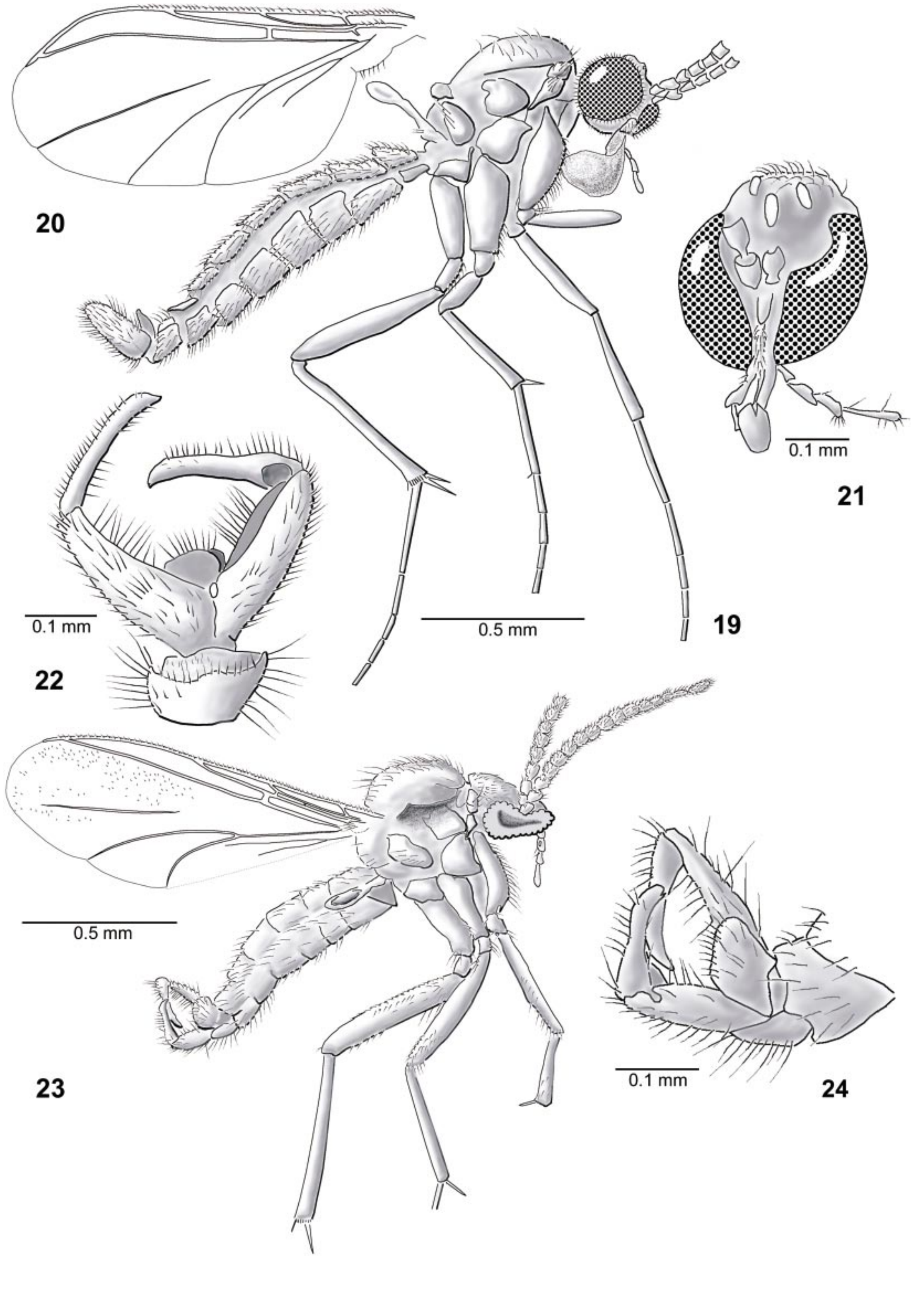
Figures 23, 24, Plate 2F

DIAGNOSIS: Mouthparts reduced. R_1 shorter than *r-m*. M_2 weak at apex. Base of M_{3+4} and CuA fork beyond the level of RS base. Male 8th tergite wider than long, rounded.

DESCRIPTION: Body length = 1.33 mm; wing length = 1.24 mm. **Head:** Occiput with long setae. Pedicel slightly wider then scape and flagellum, flagellomeres barrel-shaped, as long as wide. Palpi 4-segmented, palpomere length ratio 1:2:2:3.5. **Thorax:** Scutum with long lateral, acrostichal, and dorsocentral setae and short setae between rows. Proepimeron touches katepisternum below the episternal suture. Anepisternum width about equal to height. Laterotergites with long setae. Mediotergite with several long setae ventrally. Mesepisternum with long anterodorsal process, touching anepisternum. **Wing** length

→

Figs. 19–24. *Leptognoriste*, n.gen. **19.** *L. davisi*, n.sp., holotype AMNH Bu-126a. **20.** *L. davisi*, wing of the holotype. **21.** *L. davisi*, head of the holotype. **22.** *L. davisi*, male genitalia of the holotype. **23.** *L. microstoma*, n.sp., holotype AMNH Bu-429. **24.** *L. microstoma*, male genitalia.


20
0.1 mm
21
0.1 mm
0.5 mm
19
22
0.5 mm
23
0.1 mm
24

1.5× the abdomen length. R_1 slightly shorter than *r-m*. Macrotrichia in basal part of wing absent. M_2 weak at apex. Base of M_{3+4} and CuA fork beyond the level of RS base. **Legs:** Fore coxae with dense long anterior setae, mid and hind ones with apical. Hind tibiae without dorsal bristles, only slightly longer than femora. **Abdomen.** Tergite 9 wider than long, rounded on apex. Sternite I bare. Gonostyli curved at apex.

MATERIAL: Holotype AMNH Bu-429. Myanmar: Katchin, from amber mines near Myitkyina.

ETYMOLOGY: The species epithet is a combination of *micros* (Greek μικροζ, or small) and *stoma* (Greek στόμα, or mouth), in reference to the reduced mouthparts.

FAMILY MYCETOPHILIDAE NEWMAN, 1834

SUBFAMILY MANOTINAE EDWARDS, 1925

Alavamanota Blagoderov and Arillo, 2002

Alavamanota Blagoderov and Arillo, 2002: 34.

DIAGNOSIS: Antepronotum and proepisternum completely divided; mediotergite and laterotergites bare; wing membrane with or without macrotrichia; R_1 relatively short, length of R_1 about the length of *r-m*; R_4 present; M_{3+4} and CuA fork with stem.

TYPE SPECIES: *Alavamanota hispanica* Blagoderov and Arillo, 2002.

COMMENTS: Closest to the recent genus *Manota* Williston, 1896, distinguished by having the fourth palpomere attached preapically but very close to the apex of the third; two crossveins instead of one between R_1 and R_5 (RS1 and R_4); tibial trichia irregularly arranged; sternite 9 separate; sternite 8 without 4 strong protuberances bearing long setae; and the basal segment of each cercus small.

***Alavamanota burmitina*, new species**

Figure 25, Plate 3A

DIAGNOSIS: Flagellum compressed dorsoventrally; mesonotum with long lateral setae; wing membrane with macrotrichia; length of small radial cell 6× width; base of M_1 and M3 section weak; tibial setulae arranged in rows.

DESCRIPTION: Body length = 2.50 mm (holotype)/1.62–2.5 mm (paratypes); wing length = 1.69 mm (holotype)/1.08–1.85 mm (paratypes). **Head:** Postocciput with row of long protruding setae behind eye margin. Eyes slightly emarginate, densely setose, setae length 2× facet diameter. Facets round, densely set. Three ocelli in triangle, close to each other. Frons and face setulose. Antennae inserted above middle of head. Scape and pedicel subconical, with apical setae. Flagellum 14-segmented, flagellomeres compressed, widths 1.2–2× length, apical one conical. Texture of flagellomeres polygonlike. Only 3 segments of palpi visible, antepenultimate and penultimate with strong setae; penultimate 2.5× as long as preceding one, ovate; apical segment 1.7× length of penultimate one, narrow. **Thorax:** Scutum uniformly densely setose with short setae, bearing long lateral and posterior setae. Anterior parapsidal suture distinct. Suture between antepronotum and proepisternum complete, both segments uniform and covered with bristles. Scutellum with long setae. Anepisternum wider than higher, with wide dorsal cleft. Anepisternal suture declines posteriorly. Katepisternum setose ventrally. Mediotergite and laterotergites bare. Metepisternum with several light hairs posteroventrally. **Wing** membrane with macrotrichia; microtrichia not arranged in rows. Costa ends slightly beyond the tip of R_5, C and R_5 run very close to each other in apical part. R_1, R_5, *r-m*, M_1, and M_2 with setae ventrally and dorsally. Sc very short, ends free. Humeral vein oblique. R_1 about equal to length of *r-m*. Ratio of *r-m* and RS2 section is 1: 1.4. Base of M_1 and M_2 fork at the level of R_4. Small radial cell with length 6× width. Crossvein *r-m* horizontal, fused to *tb*, meets MA. M_{3+4} and CuA fork long, but not sessile. CuA curved caudally. **Legs.** Hind coxae bear apical only, not posterior setae. Tibial spur lengths ca. 4× tibial diameter. Tibial trichia in rows. **Abdomen** setose, with 6 visible segments. Gonocoxites fused, lighter then abdomen, setose, swollen. Gonostyli not seen.

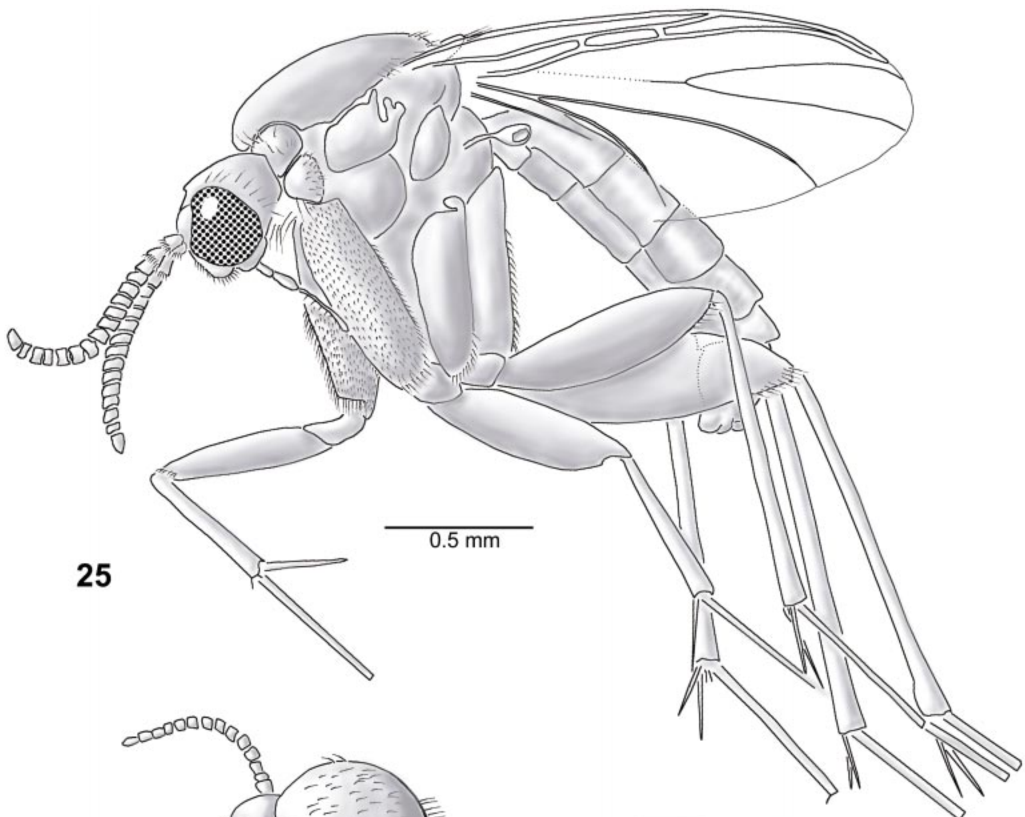
MATERIAL: Holotype AMNH Bu-1271, male; paratypes AMNH Bu-428a, Bu 279a, males. Myanmar: Katchin, from amber mines near Myitkyina.

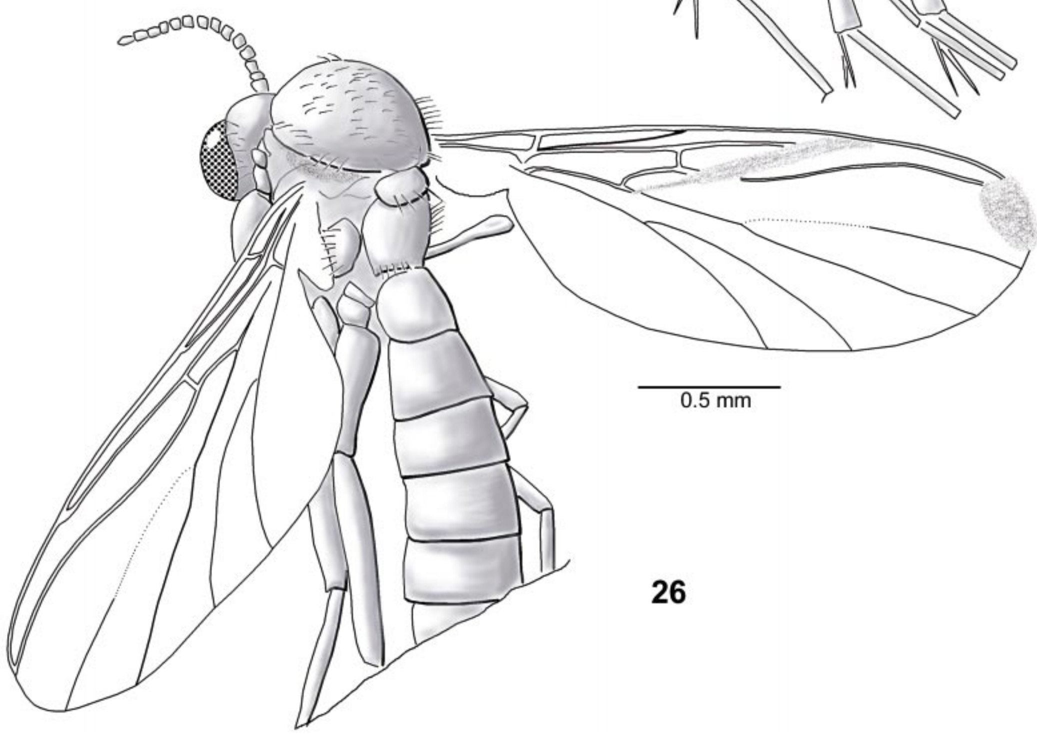
SUBFAMILY SCIOPHILINAE WINNERTZ, 1863

TRIBE SCIOPHILINI WINNERTZ, 1863

Neuratelia Rondani, 1856

Neuratelia Rondani, 1856: 195.
Anaclinia Winnertz, 1863:770.





Figs. 25, 26. *Alavamanota* and *Neuratelia*. **25.** *A. burmitina*, n.sp., holotype AMNH Bu-1271. **26.** *N. maimecha*, n.sp., holotype PIN 3311/661.

Proanaclinia Meunier, 1904:145.
Odontopoda Aldrich, 1897: 187.

DIAGNOSIS: As given by Vockeroth (1972): Tibiae with distinct bristles, length of tibial spurs twice the tibia diameter; anepisternum, mesepimeron, and metepisternum bare; wing membrane with macrotrichia; sternite 8 of male large; gonocoxites partly or completely fused ventrally, gonostyli complex, subdivided or with elaborate processes.

TYPE SPECIES: *Mycetophila nemoralis* Meigen, 1818: 256 (orig. des.).

COMMENTS: Two species of the genus were described from Baltic amber (Meunier, 1904)

Neuratelia maimecha, new species

Figure 26, Plate 3B

DIAGNOSIS: Sc short, ends before RS base; length of RS1 section 2.5× that of crossvein *r-m*; base of M_{3+4} and CuA fork at the middle of *r-m*; mediotergite with sparse, fine trichia.

DESCRIPTION: Body length = 2.11 mm (rest); wing length = 2.05 mm. **Head:** Flagellum 14-segmented, flagellomeres cylindrical, with length about equal to width. Scape and pedicel rounded. Mouthparts form proboscis slightly shorter than head height. Palpi 4-segmented, basal and antepenultimate segments oval, penultimate and apical segment bacilliform, apical slightly longer and narrower than penultimate, length ratio 1:3:4:5.5. **Thorax:** Scutum with numerous, short, scattered setae and long lateral ones. Antepronotum with three setae, proepisternum with five. Anepisternum bare, with deep cleft in posterior part. Anepisternal suture declines posteriorly. Metepisternum quadrate, touching katepisternum. Laterotergites with several setae, mediotergite with sparse, fine trichia caudally. **Wing** membrane with microtrichia and few macrotrichia. Costa ends beyond tip of R_5. Sc meets C just before RS base. Sc_2 absent. Longitudinal veins with setae. M_{3+4} and CuA base slightly distad of M3 base. **Legs:** Tibiae with distinct bristles. Fore tibia longer than first tarsomere.

MATERIAL: Holotype PIN 3311/661, end of abdomen not preserved, sex unknown. Russia: Taimyr Peninsula, Yantardakh, coll. 1971.

ETYMOLOGY: Species epithet is derived from the Maimecha river on the Taimyr Peninsula, Siberia, where the amber deposit is located.

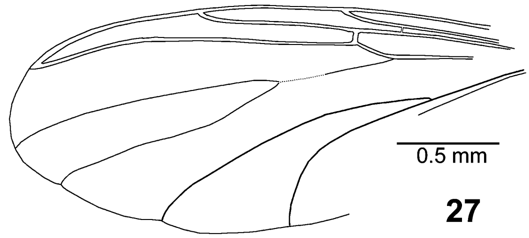


Fig. 27. *Allocotocera burmitica*, n.sp., holotype AMNH B-056, reconstruction of wing venation.

Allocotocera Mik, 1886

Eurycera Dziedzicki, 1885:166.
Allocotocera Mik, 1886: 102.
Euryceras Marshall, 1896: 291.

DIAGNOSIS: Laterotergites and mediotergite setose. Wing membrane with macrotrichia and with or without microtrichia. Sc_2 preapical or medial. Base of M_{3+4} and CuA fork before the base of the fork of M_1 and M_2.

TYPE SPECIES: *Eurycera flava* Dziedzicki, 1885: 167 [= *pulchella* (Curtis, 1837)] (by monotypy).

COMMENTS: Another fossil species occurs in Lower Cretaceous Spanish amber (Blagoderov and Arillo, 2002).

Allocotocera burmitica, new species

Figure 27, Plate 3C

DIAGNOSIS: Wing membrane with macro- and microtrichia. Segment M3 2.5× length of *r-m*, 0.3× that of M fork. Sc ends at level of RS base; Sc2 in the apical one-fourth of Sc, distal to midpoint of Sc.

DESCRIPTION: Body length = 2.86 mm; wing length = 2.46 mm. **Head:** Flagellum 14-segmented, thickened to apex. Flagellomeres almost equal in length, length of the first one 2× its width, apical one 5× its width. Scape and pedicel subconical, with small apical setae, 2× wider than flagellomeres. Eyes pubescent. Two palpomeres seen, cylindrical, length ca. 4× the width. **Thorax:** Scutum irregularly covered with short setae and with strong, long lateral setae. Antepronotum with long setae. Scutellum with two pairs of long setae and several more short ones. Laterotergites and mediotergite with setae. Metepisternum with two short setae posteroventrally.

Wing membrane clear, with macro- and microtrichia. Costa ends at tip of R_5. Sc meets C beyond RS base. Sc_2 at level of base of section M3. Section of RS1 transverse. R_1 rather short, about 0.7× wing length. R_5 curved caudally, not reaching wing apex. Crossvein *r-m* approximately 2.5× as long as section RS1 and 2.5× length of section M3. Fork of M_1 and M_2 3.3× as long as section M3. Base of M_{3+4} and CuA fork slightly before base of section M3. **Legs:** Hind coxae with long posterior setae. Fore tibiae longer than first tarsomere. Cerci 1-segmented, 2× as long as 8th tergite, setose.

MATERIAL: Holotype AMNH B-056, female. Myanmar: Katchin, from amber mines near Myitkyina.

ETYMOLOGY: The species epithet is a reference to the country of origin of the amber.

COMMENTS: The species is very close to *A. xavieri*, but differs in having a shorter Sc vein and a longer M_1 and M_2 fork.

Pseudomanota, new genus

DIAGNOSIS: Infraorbital setae absent. Three palpomeres, penultimate one with long thin apical appendage. Antepronotum wide. Proepisternum rodlike. Laterotergites and mediotergite bare. Sc short, free. Wing membrane with macrotrichia. Base of M_1 and M_2 fork reduced. M_1 reaches wing margin before wing apex. M_{3+4} free at the base. Gonostyli simple, slightly curved.

TYPE SPECIES: *Pseudomanota perplexa* n.sp.

ETYMOLOGY: The genus name is a combination of *pseudos* (Greek ψεῦδοσ, or a lie, a fraud) and the genus name *Manota*. The name is feminine.

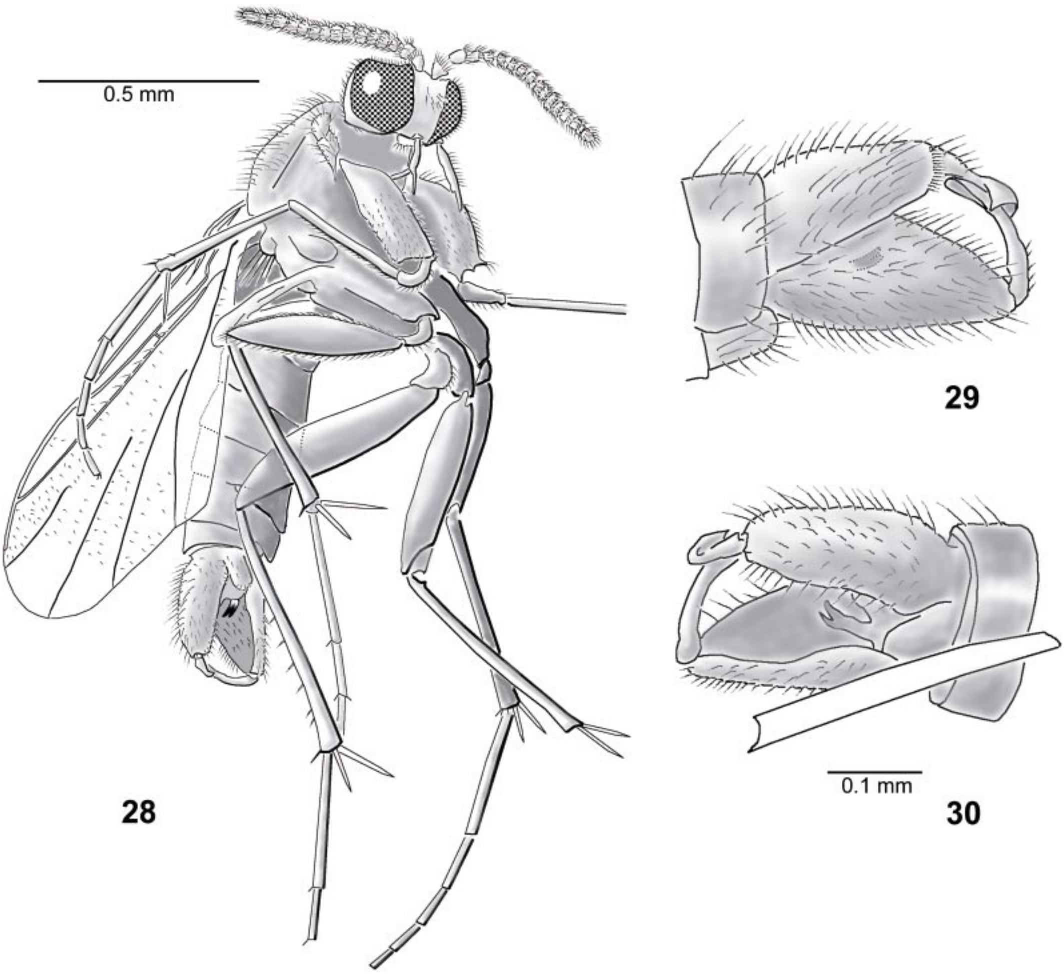
COMMENTS: Some structures, especially the wide quadrate face, long and flexible apical palpomere, short Sc and R_1, horizontal *r-m,* and reduced venation are like Manotinae. Also, unlike typical Sciophilinae, the new genus has laterotergites and especially the mediotergite bare. Nevertheless, the genus is attributed to the subfamily Sciophilinae based on a long, rodlike proepimeron, the rather distal position of humeral vein, and long and slender gonocoxites (which are not known for any manotines). Within Sciophilinae the new genus might be close to the *Azana* group of genera (Matile, 1998), demonstrating reduction of median veins. All of the genera in the group have reduced venation, with CuA simple and not forming a fork with M_{3+4}. Matile (1998) supposed that M_{3+4} in this group was reduced completely, while the fork of M_1 and M_2 lost its base. Jugding on the position of vein apices, at least *Paratrizygia, Neoaphelomera,* and *Neotrizygia* may have lost M_2, and an incomplete vein between M_1 and CuA may be homologous to M_{3+4}. The new species has venation more primitive than the genera in the *Azana* group, preserving all the longitudinal veins, although without bases.

Pseudomanota perplexa, new species

Figures 28–30, Plate 3D

DIAGNOSIS: As for the genus.

DESCRIPTION: Body length = 1.44 mm; wing length = 1.07 mm. **Head:** Eyes large, setulose, with large facets. Occiput and postgena setose, without erect bristles. Ocelli not seen. Antennae attached above middle of head. Frons, face and clypeus setose. Pedicel subconical. Flagellum 14-segmented, slightly thicker toward apex; flagellomeres cylindrical, width 1–1.5× length. Three palpomeres seen, basal one heart-shaped, penultimate one with long thin apical appendage about one-third its length, apical one long and slender. **Thorax:** Antepronotum and proepisternum wide, completely divided, setose. Proepimeron narrow, rodlike. Scutum with lateral, acrostichal, and dorsocentral setae with bare strips in between. Anterior parapsidal suture distinct. Anepisternal suture declines posteriorly. Anepisternum with wide cleft. Metepisternum with long, narrow anterodorsal process touching laterotergite. Laterotergites and mediotergite bare. **Wing** membrane with macrotrichia and microtrichia. Humeral vein slightly distad of MA. Costa extends to R_5 apex at two-thirds distance between tips of R_5 and M_1, not reaching wing apex. Length of R_1 is 0.6× wing length. Small radial cell length 5× width. M_1 originates at apical one-third of wing, reaching wing margin before wing apex. M_2 originates at apical



Figs. 28–30. *Pseudomanota perplexa*, n.sp. **28.** Holotype AMNH Bu-599a. **29.** Male genitalia dorsally. **30.** Male genitalia ventrally.

half of wing. M_{3+4} free at the base. M_1, M_2, M_{3+4}, and CuA apices weak. **Legs:** Tibial setulae not arranged in rows except on apex of mid and hind tibiae. Tibial spurs ca. 3.5× tibia diameter. Hind tibia with a dorsal row of bristles. **Abdomen** setose, with 6 segments visible. Genital complex as long as 4th–6th segments combined, rotated 180°. Tergite 9 small, apex round, covering basal part of gonocoxites only. Aedeagus with two teeth apically. Gonocoxites separated, massive, setose. Gonostyli simple, sticklike, slightly curved, apically flat, shovel-like.

MATERIAL: Holotype AMNH Bu-599a, male. Myanmar: Katchin, from amber mines near Myitkyina.

ETYMOLOGY: The species epithet is from the Latin word *perplexus*, meaning ''muddled, intricate'', in reference to the intriguing combination of sciophiline and manotine characters.

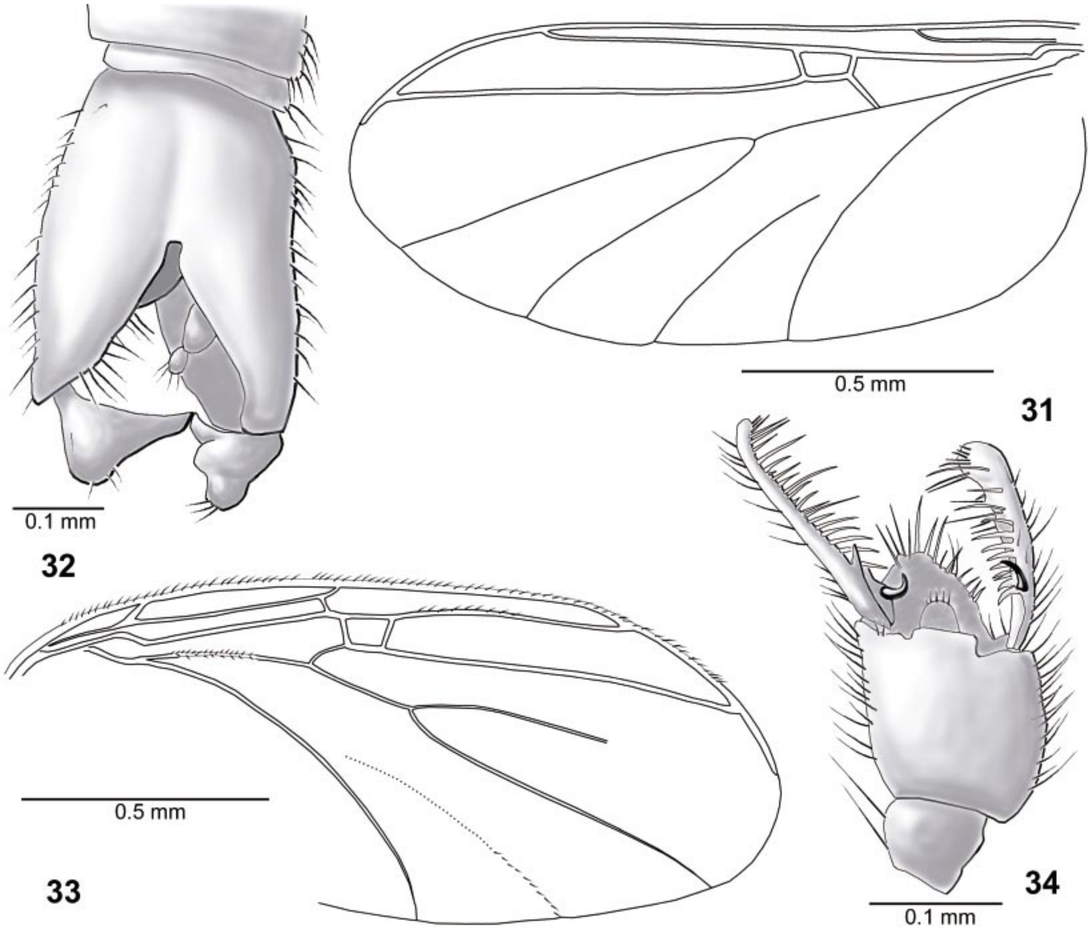
TRIBE GNORISTINI EDWARDS, 1925

Apolephthisa Grzegorgzek, 1885

Apolephthisa Grzegorgzek, 1885: 205.

DIAGNOSIS: Mediotergite bare; laterotergites setose; Sc meets C; R_4 present; base of M_{3+4} distad of *r-m*, faint; M2 several times longer than *r-m*.

TYPE SPECIES: *A. rara* Grzegorgzek, 1885:



Figs. 31–34. *Apolephthisa* and *Synapha*. **31.** *A. bulunensis*, n.sp., holotype PIN 3963/4, reconstruction of wing venation. **32.** Male genitalia. **33.** *S. longistyla*, n.sp., holotype MCZC 6944, reconstruction of wing venation. **34.** Male genitalia.

206 (by monotypy) [= *subincana* (Curtis, 1837) (*Sciophila*)]

COMMENTS: This genus is widely distributed in the Holarctic but is of low diversity, including only one described Palaearctic and one undescribed Nearctic species (Vockeroth, 1981). *Apolephthisa mesozoica* is described from the Lower Cretaceous of Mongolia (Blagoderov, 1998a), and one undescribed specimen is known from Palaeocene Sakhalin amber (Blagoderov, in prep.).

Apolephthisa bulunensis, new species

Figures 31, 32, Plate 3E

DIAGNOSIS: Sc short, ends before RS base. Gonostyli with distinct rounded apical lobe and long inner process.

DESCRIPTION: Body length = 2.24 mm; wing length = 1.46 mm. **Head:** Eyes slightly emarginate near antennal base. Flagellum with 14 cylindrical flagellomeres, covered by trichia equal to 0.5× flagellomere diameter. Palpi rather long; antepenultimate segment oval, broadened; penultimate and apical segments long and slender, together equal to fore coxa in length; apical segment slightly clubbed at apex, with several short setae. Palpomere length ratio 1:2:4. **Thorax:** Scutum with lateral, dorsocentral, and acrostichal rows of short setae. Mediotergite bare. **Wing:** Veins R_1, R_5, M_1, and M_2 with setae. Sc meets C before RS base. R_5 almost straight. Costa ends beyond tip of R_5 one-fifth the distance between tips of R_5 and M_1.

M_1, M_2, and M stem weak. Base of M_{3+4} absent. **Legs:** Hind coxae without posterior setae. **Abdomen** setose, with 7 visible segments, 8th one small and retracted. Gonocoxites long, stout, thinner apically. Gonostyli with rounded apical lobe, bearing dorsoventral row of bristles and long inner process, ending in a short spur.

MATERIAL: Holotype PIN 3963/4, male. Russia: Taimyr Peninsula, Bulun, coll. 1976.

ETYMOLOGY: The species epithet is toponymic.

COMMENTS: Given the current low diversity of the genus, it would seem highly improbable for three fossil species to occur unless the genus was more diverse and abundant in the past.

Synapha Meigen, 1818

Synapha Meigen, 1818: 227.
Sinapha Rondani, 1856: 196, misspelling.
Empalia Winnertz, 1863: 762.

DIAGNOSIS: As given by Freeman (1951): Setae on stems and forks of both M and Cu present, flagellomere lengths not more than width, Sc long, penultimate palpomere shorter than apical and antepenultimate ones, laterotergites bare or setose, midtibial organ present.

TYPE SPECIES: *S. fasciata* Meigen, 1818 (by monotypy).

COMMENTS: About 25 extant species of *Synapha* are known from all biogeographic regions. Two fossil species of the genus were described from Eocene Baltic amber (Meunier, 1904) and the Lower Cretaceous of Montsec, Spain (Blagoderov and Martínez-Delclós, 2001). The related genus *Austrosynapha* Tonnoir, 1929 has 23 species from South America, which were cataloged by Papavero (1977b); 7 occur in New Zealand (Tonnoir and Edwards, 1927) and one is from Australia (Tonnoir, 1929).

Synapha longistyla, new species

Figures 33, 34, Plate 3F

DIAGNOSIS: Distinguished from living and fossil members by the structure of genitalia, having gonostyli very long and with numerous inner spurs.

DESCRIPTION: Body length = 2.15 mm; wing length = 1.58 mm. **Head** round. Eyes large, rounded, with round facets. Flagellum 14-segmented, flagellomeres cylindrical, length of each about 1.5× its width. Two palpomeres seen. Penultimate 0.7× length of apical one, which is slender and flexible. **Thorax:** Scutum irregularly setose. Mediotergite and laterotergites bare. **Wing:** R_1 and R_5 almost straight, with setae, remaining veins bare, except apex of M_{3+4}, a few setae present on M_2 and CuA_1 dorsally. Length ratio of sections RS1, RS2, and RS3 is 1:1.4: 13. Crossvein *r-m* slightly sigmoid, its length 2× length of M3 section. Base of M_{3+4} absent, the vein originates at level of M3 midpoint. CuA and M_{3+4} gently curved caudally. **Legs:** Midtibial organ absent. **Abdomen** with 6 visible segments, 7th and 8th segments small and retractable. Gonocoxites fused. Gonostyli long, straight, with numerous stiff spines arranged in rows on inner surface and several dark, curved ones at base.

MATERIAL: Holotype MCZC 6944, male, Canada: Manitoba, Cedar Lake.

ETYMOLOGY: The species epithet refers to the long gonostyli of the species.

COMMENTS: This species lacks distinct synapomorphies of *Synapha* (i.e., midtibial sensory organ and short gonostyli) as well as strong setae on the medial and cubital forks. The fossil has moderately long flagellomeres and subequal palpomeres, considered to be synapomorphies of *Austrosynapha* (see table 2). Long, slender gonostyli, which are characteristic for *Austrosynapha* and many other Mesozoic fungus gnats, is considered to be plesiomorphic. Most likely, the new species together with the Lower Cretaceous *S. rubiesensis* Blagoderov and Martínez-Delclós, 2001 represent a *Synapha*-*Austrosynapha* stem group, although monophyly of the group and included genera is still to be established. Matile (1991) noted that *Synapha* was probably polyphyletic. The definition of both genera is vague, and often characters of different subgroups overlap. For example, species of *A.* (*Paraaustrosynapha*) Duret have short flagellomeres, while species of *A.* (*Neoaustrosynapha*) Duret retain some macrotrichia on the medial fork (Duret, 1980).

Dziedzickia Johannsen, 1909

Hertwigia Dziedzicki, 1885: 166 (preocc. Schmidt, 1880).

TABLE 2
Comparison of *Synapha, Austrosynapha,* and *A. longistyla* n.sp.

Character	*Synapha*	*Austrosynapha*	*Synapha longistyla*
Macrotrichia on stems and branches of M and Cu forks	Present	Absent	Some macrotrichia present on M stem and branches
Sc	Long	Short	Long
Flagellomeres lengh	Equal to or less than width	2–4× the width	1.5× longer than wide
Penultimate palpomere	Shorter than apical and antepenultimate one	Last three palpomeres subequal	Apical palpomere 1.5× the length of penultimate one
Setae on laterotergites	Absent or present	Absent	Absent
Midtibial organ	Present	Absent	Absent
Gonostyli	Short	Long and slender as a rule	Very long

Dziedzickia Johannsen, 1909: 44.

DIAGNOSIS: After Freeman (1951): Eyes emarginate at level of antennae; 3 ocelli in a straight line; laterotergal hairs present or absent; wing membrane without macrotrichia; Sc ending at R before or beyond base of RS, Sc_1 may be present as a short stump; base of M_{3+4} and CuA fork considerably basal to M_1 and M_2 fork; R_4 may be present or absent.

TYPE SPECIES: *Hertwigia marginata* Dziedzicki, 1885: 165 (by monotypy).

COMMENTS: About 50 extant species of the genus are described, mostly from the New World, especially South America, with several species from Holarctic and Afrotropics. Four species are known from Baltic amber (Meunier, 1917a, 1917b, 1922) and one from the Oligocene of Rott (Statz, 1944). Some authors (Chandler, 1999; Hutson, 1979; Matile, 1992; Vockeroth, 1980) noted that the genus in present definition was plausibly polyphyletic since some of the species belong to other gnoristine genera, such as *Syntemna* Winnertz, 1863 and *Hadroneura* Lundström, 1906.

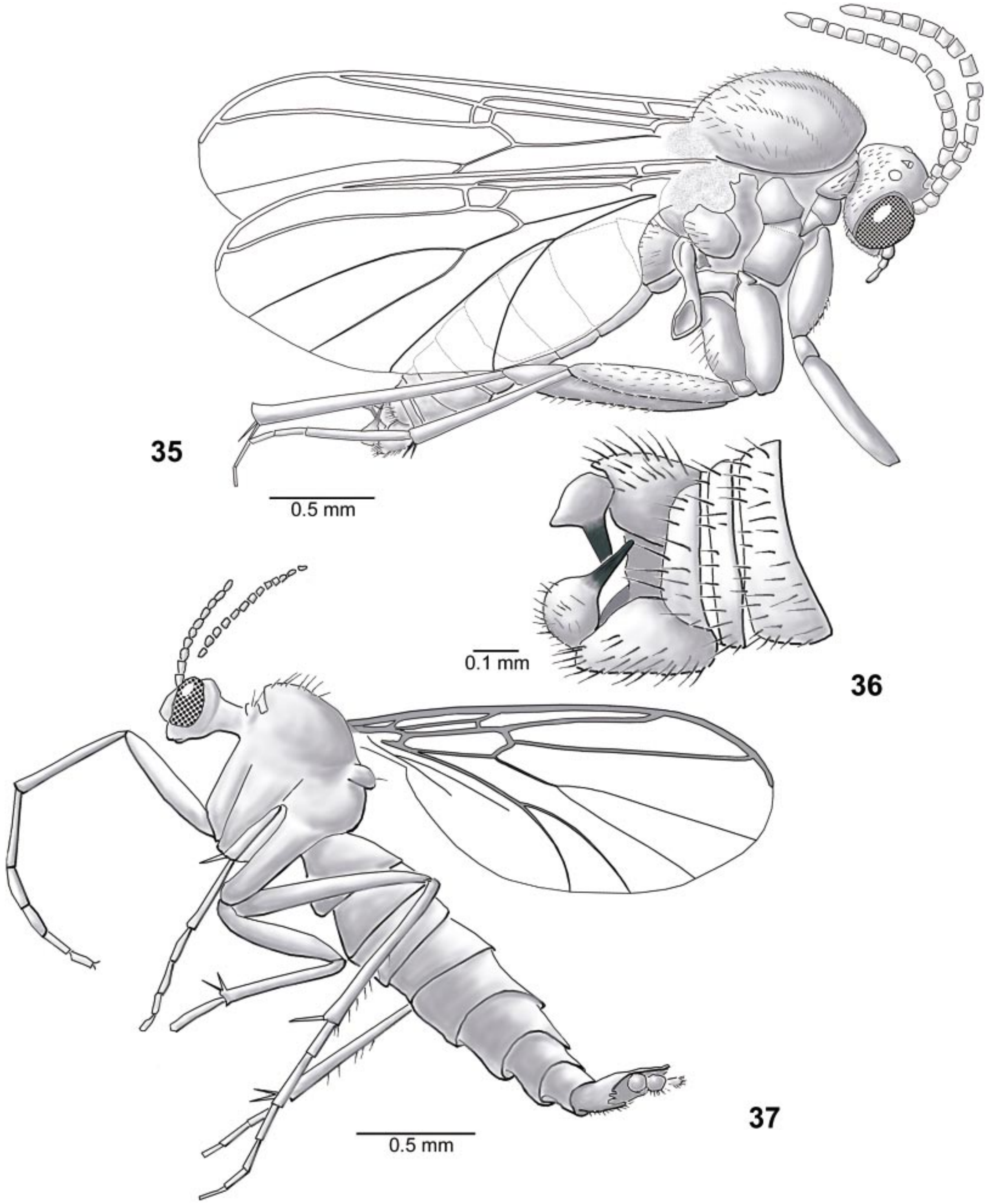
Dziedzickia nashi, new species

Figures 35, 36, Plate 4A

DIAGNOSIS: Laterotergites setose. Forked veins without setae. Tergite 9 short. Gonocoxites simple. Gonostyli with strong inner process.

DESCRIPTION: Body length = 2.96 mm (holotype)/2.92–3.37 mm (paratypes); wing length = 2.50 mm (holotype)/2.28–3.32 mm (paratypes). Brown gnats, thorax dark brown, occiput greyish brown, tibiae and tarsi yellowish. **Head:** Eyes large, bare, slightly emarginate; three ocelli in line. Median ocellus slightly sunken, distance from middle to lateral ocellus and from lateral one to eye margin ~1.5× ocellus diameter. Scape and pedicel shorter than flagellomeres, bare. Flagellomeres cylindrical, length ~1.5× width, length of apical one ~2× the width. Three palpomeres seen, short, gradually thinner toward apex. Mouthparts less than one-fourth height of head. **Thorax:** Mesonotum very convex, with dorsocentral, acrostichal, and lateral setae well developed. Antepronotum and laterotergite setose, other sclerites bare. Proepimeron thick, short, touches katepisternum. Anepisternal suture declines posteriorly. **Wing** membrane without macrotrichia. Sc ends at R_1 beyond RS base. Sc_1 absent. RS1, RS2, and RS3 ratio 1:1.2–1.3:11–15. M3 length 2× that of *r-m* crossvein. Base of M_{1+2} fork at level of R_4. Base of M_{3+4} and CuA fork before base of *r-m*. **Abdomen** setose, 7th segment 2× shorter than 6th. **Male**: Gonocoxites massive, bristly, separated ventrally by deep cleft. Ninth tergite short, transverse, covers only base of gonocoxites. Gonostyli with a strong, thin, dark process pointed inward. **Female** with cerci 2-segmented. Basal segment 2.5× apical one, cylindrical. Apical segment rounded.

MATERIAL: Holotype AMNH NJ-117a, male. Paratypes: AMNH NJ-117b, c, e, m, females, NJ-117d, g, h, males, NJ-117f (wing), all in the same piece of amber. USA: New Jersey, Sayerville, coll. P. Nascimbene. See figure 38 for a map of syninclusions.



Figs. 35–37. *Dziedzickia* and *Saigusaia*. **35.** *D. nashi*, n.sp., holotype AMNH NJ-117a. **36.** Male genitalia of the holotype. **37.** *Saigusaia pikei*, n.sp., holotype TMPD P79.15.7.21

ETYMOLOGY: The species epithet is patronymic for Mr. Paul Nascimbene, who collected the piece and who has diligently prepared numerous amber specimens for the AMNH.

COMMENTS: Differs from all other species by the structure of male genitalia. A thorough comparision will be possible only after revision of the genus.

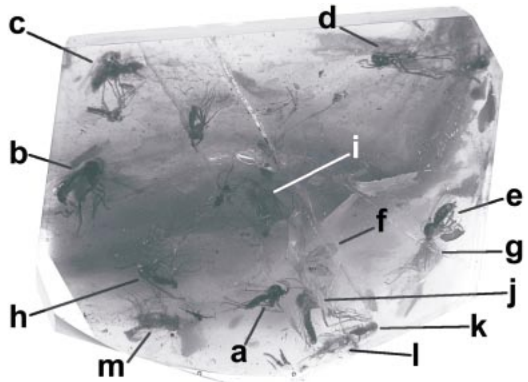


Fig. 38. Map of AMNH NJ-117 syninclusion.

Saigusaia Vockeroth, 1980

Saigusaia Vockeroth, 1980: 541.

DIAGNOSIS: As given by Vockeroth (1980): Face weakly sclerotized, bare; laterotergites bare; metepisternum with short fine hairs; prosternum bare; sternites of abdomen with median fold line. Male with tergite 7 and sternite 7 haired; subequal in length, two-thirds length of segment 6; tergite 9 not fused with gonocoxites. Female with sternite 8 deeply emarginate posteriorly.

TYPE SPECIES: *Boletina cincta* Johannsen, 1912: 270 (by original designation).

COMMENTS: Three species of the genus are known from Eastern North America, Europe and Japan (Khonsu), and Taiwan and Nepal.

Saigusaia pikei, new species

Figure 37, Plate 4B

DIAGNOSIS: Distinguished from the living species by Sc long, meeting C just before RS base.

DESCRIPTION (see also table 3): Body length = 2.84 mm, wing length = 1.80 mm. **Head:** Ocelli three, each slightly raised, very close. Eyes pubescent. Vertex and clypeus setulose. Flagellum 14-segmented, flagellomeres cylindrical, with length slightly greater than width. Mouthparts form short proboscis, length is one-half the head height. Only three palpal segments seen: antepenultimate segment swollen, penultimate and apical ones narrower, bacilliform. Length ratio 1:1.7:2.7. **Thorax:** Antepronotum with two long setae. Scutum with strong, curved lateral, dorsocentral and acrostichal setae. Mediotergite and laterotergites bare. Scutellum with 5 pairs of rather short setae. Metepisternum with two long setae dorsally. **Wing:** Costa ends beyond tip of R_5, one-third distance between tips of R_5 and M_1. Stem of R, R_1 and R_5 with rows of dorsal and ventral setae. R_1 and R_5 straight. Sc meets C just before RS base. Sc_2 apical, proximal to base of M3. Crossvein *r-m* 1.5× length of RS1 and 0.3× length of M3 section. Fork of M_1 and M_2 2.7× length of M3. M_1 and M_2 fork campanulate, veins straight, with a few ventral setae apically. Base of M_{3+4} and CuA fork proximal to base of M_1 and M_2 fork, M_{3+4} and

TABLE 3
Comparison of *Boletina, Saigusaia,* and *Saigusaia pikei* n.sp.

Character	*Saigusaia*	*Boletina*	*Saigusaia pikei*
Face	Weakly sclerotized, bare	Strongly sclerotized, setose	Bare (sclerotization cannot be determined)
Laterotergites	Bare	Bare or setose	Bare
Termination of Sc	Proximal to level of *r-m* base	At or distal to level of *r-m* base	Distal to level of *r-m* base
Metepisternum	With short trichia	Bare	With fine trichia
Prosternum	Bare	Setose or bare	?
Sternite 1	Bare	Sternite 1 setose	Sternite 1 bare
Medial fold-line on sternites 2 to 7	Present	Present or absent	?
Posterior margin of ♀ sternite 8	Deeply emarginated	Entire or emarginated	Emarginated
Sternite 8 anterior to emargination	Medially membranous	Not membranous	Membranous

CuA curved caudally. **Legs:** Tibial bristles 2× tibial diameter. Tarsal claw with one tooth. **Abdomen:** Sternite 8 with two triangular, rounded, caudal lobes covered by long setae. Cerci two-segmented. Basal segment large and broad, apical one 0.5× the length and 0.5× the width of basal one; both setose.

MATERIAL: Holotype TMPD P79.15.7.21, female. Canada: Alberta, Grassy Lake, coll. T. Pike.

ETYMOLOGY: The species epithet is patronymic for Dr. T. Pike, who collected the specimen.

COMMENTS: This species has almost all the features of *Saigusaia* (table 3, see also Vockeroth, 1980), so despite the long Sc vein its placement in the genus is virtually certain.

Syntemna Winnertz, 1863

Syntemna Winnertz, 1863: 767.

DIAGNOSIS: Mediotergite bare; laterotergites setose; wing membrane with macrotrichia; Sc meets R; radial cell very small, subquadrate; base of M_{3+4} and CuA fork proximal to base of M_1 and M_2 fork; segment 7 of abdomen reduced.

TYPE SPECIES: *S. morosa* Winnertz, 1863: 767, by monotypy.

COMMENTS: About 20 extant species are known from the Holarctic (Zaitzev, 1994), with an additional 12 species described from Baltic amber (Meunier, 1904, 1917a, 1922) and 4 from the Lower and Upper Cretaceous of northeast Asia (Blagoderov, 1995, 1998a, 2000).

Syntemna fissurata, new species

Figures 39, 40, Plate 4C

DIAGNOSIS: Sc ends at R at the base of RS; R_4 present; crossvein *r-m* 0.5× length of M3 section; base of fork of M_{3+4} and CuA proximal to the base of M_1 and M_2 fork.

DESCRIPTION: Body length = 3.06 mm, wing length = 2.28 mm. **Head** not fully visible. Flagellum 14-segmented, flagellomeres barrel-shaped, length of each 1.5× the width, setose, length of setae about equal to flagellomere width. **Thorax:** Scutum with strong, long setae in lateral, dorsocentral, and acrostichal rows, with short setulae. Antepronotum, proepisternum, laterotergites, and mediotergite setose. **Wing** membrane with microtrichia and short macrotrichia. Costa ends beyond the tip of R_5, one-fourth distance between tips of R_5 and M_1. Sc meets R just before base of RS. Sections of RS1 and RS2 equal and 1.5× length of *r-m*. Crossvein *r-m* 0.5× length of M3 section. Fork of M_1 and M_2 3.5× length of its stem (M3). Base of fork of M_{3+4} and CuA proximal to the base of M2 section. **Legs:** Inner surface of mid tibia with fissurelike sensory pit in apical third. Tarsal claws with two short teeth at the base. **Abdomen** setose, with 7 visible segments, 7th one very small. Cerci 2-segmented, basal segment roundish, with numerous long trichia; apical segment bacilliform, with length twice the width, bare. Lateral lobes of 8th sternite setulose.

MATERIAL: Holotype TMPD P83.15.3.8, female. Canada: Alberta, Grassy Lake, coll. T. Pike

ETYMOLOGY: The species epithet is the Latin word *fissures*, meaning ''full of cracks'', in reference to the state of preservation of the specimen.

COMMENTS: The new species differs from all other known Mesozoic species in having section M3 long, at least twice the length of crossvein *r-m*.

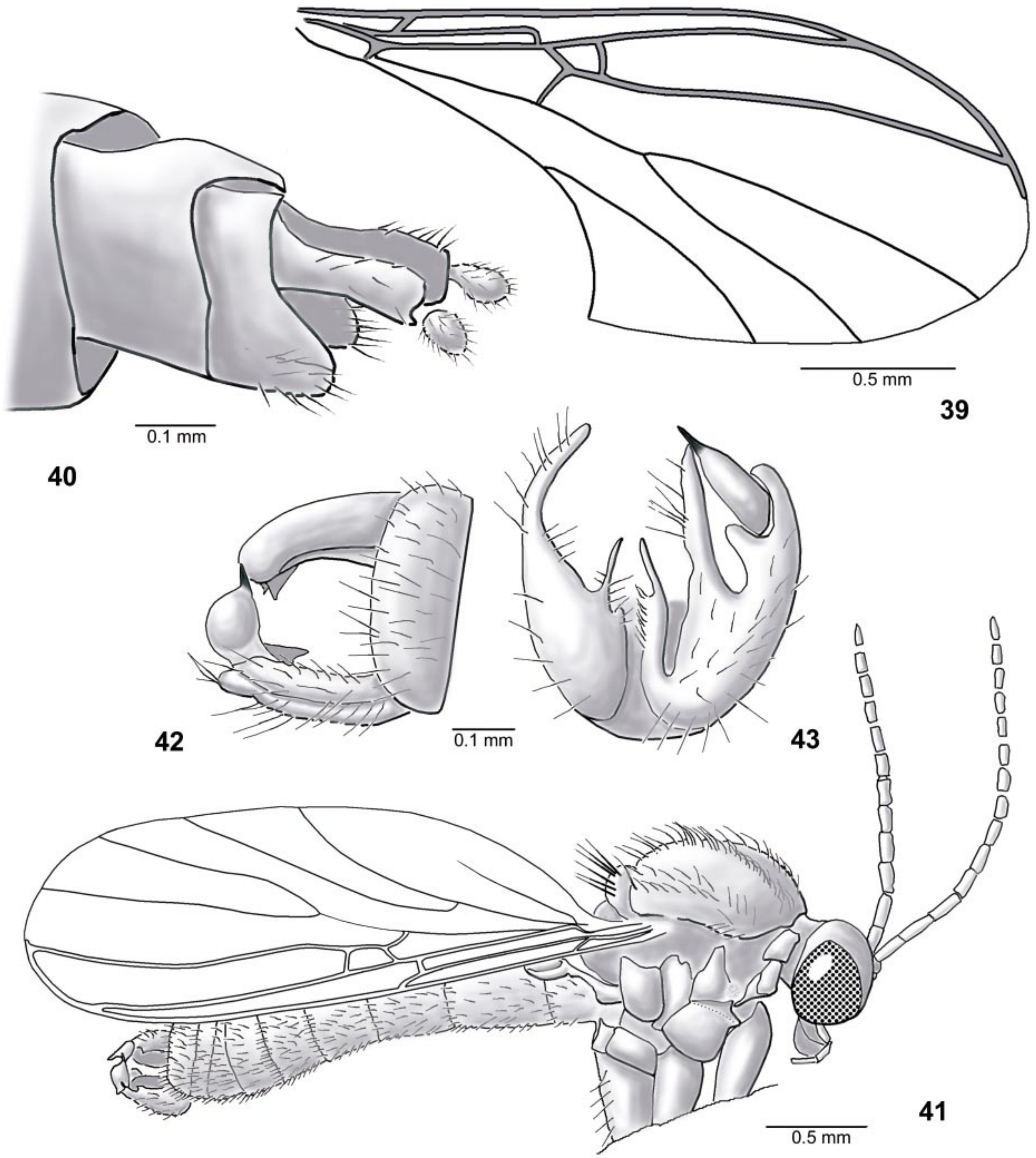
Gregikia, new genus

DIAGNOSIS: Costa virtually ends at the apex of R_5. Sc bare. Sc_2 apical. Section M2 setose. R_5 not reaching wing apex. M3 weak. Acrostichal setae absent. Tergite 9 short. Gonostyli well developed.

TYPE SPECIES: *Gregikia pallida*, n.sp.

ETYMOLOGY: The name is derived from some letters commonly used in names of genera in this complex. The name is feminine.

COMMENTS: The genus is very similar to *Palaecomoptera* Blagoderov, 1997, five species of which were described from the Lower Cretaceous of Transbaikalia and Mongolia (Blagoderov, 1997, 1998a), as well as to three monotypic genera: *Grzegorzekia* Edwards, *Creagdhuhia* Chandler, and *Phoenikiella* Chandler. It is distinguished from *Palaecomoptera* by R_5 not reaching wing apex, costa not produced after R_5 apex, and base of fork of M_1 and M_2 weak. The genus dif-



Figs. 39–43. *Syntemna* and *Gregikia*. **39.** *S. fissurata*, n.sp., holotype TMPD P83.15.3.8, left wing. **40.** Female genitalia of the holotype. **41.** *G. pallida*, n.sp., holotype AMNH NJ 117j. **42.** Male genitalia dorsally. **43.** Male genitalia ventrally.

fers from *Grzegorzekia*, *Creagdhuhia*, and *Phoenikiella* by a short apical palpomere, absence of acrostichal setae, weak M stem and base of fork of M_1 and M_2, absence of setae on A, from *Grzegorzekia* also by having Sc bare. Gonocoxites of the new genus also have two lobes as in the last three genera, but the gonostyli are better developed. This state is undoubtedly more plesiomorphic than the highly modified genital complex of *Grzegorzekia*, *Creagdhuhia* and *Phoenikiella*. Species of *Palaecomoptera* have gonostyli developed as well, but some (*P. shcherbakovi*, *P. lukashevichae*) have tergite 9 large, fully covering the gonocoxites.

Gregikia pallida, new species

Figures 41–43, Plate 4D

DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 3.77 mm (holotype)/3.09–3.65 mm (paratypes); wing length = 3.26 mm (holotype)/2.36–3.76 mm (paratypes). **Head:** Vertex setose. Scape and pedicel small. Flagellum 14-segmented. Flagellomeres cylindrical, length 2× the width, covered by trichia, length of trichia about one-half flagellomere width. Only three segments of palpi visible; segments short, nearly cylindrical, combined length slightly less then head height. **Thorax:** Scutum with erect setae, arranged in rows with wide bare strips between them, acrostichal setae absent. Antepronotum and proepisternum setose. Proepimeron touches mesepisternum at anepisternal suture. Scutellum with four pairs of setae. Anepimeron very narrow ventrally, so that laterotergite touches katepisternum. Katepisternum larger than anepisternum. Mediotergite, laterotergites, and metepisternum bare. **Wing:** Costa ends slightly beyond tip of R_5. Sc meets C at level of RS base. R stem, R_1, R_5, and distal parts of M_1 and M_2 with setae. R_5 not reaching wing apex. Section RS1 oblique. R_4 transverse. Ratios of lengths of RS1, RS2, and RS3 is 1:1.5:12–15. Length of crossvein *r-m* about equal to RS1 and 0.25× M3 section. M_1 subparallel to R_5; veins M_1, M_2, M_{3+4}, and CuA divergent. Base of fork of M_{3+4} and CuA proximal to M3 base. M_{3+4} and CuA curved gently. M_1, M_2, M_{3+4}, and CuA with a few setae on apical part. **Legs:** Hind coxae with long dorsolateral setae. Mid tibiae without sensory pit. Tarsal claw with one basal tooth. **Abdomen** densely setose. Segments 7 and 8 short, about one-half length of segment 6. Tergite 9 short, does not cover gonocoxites. Gonocoxites densely setose, with long, slim apical and basal lobes, pointed caudally and bearing numerous inner setae. Gonostyli ovate, bare, with strong dark apical processes.

MATERIAL: Holotype AMNH NJ 117j, male. Paratypes: AMNH NJ 117i, male (see fig. 74 for the scheme of syninclusions), coll. P. Nascimbene; AMNH NJ 871a and NJ 871b, sex unknown, coll. K. Luzzi. USA: New Jersey, Sayreville.

ETYMOLOGY: The species epithet is a Latin word *pallidus* meaning ''pale'' in reference to state of preservation of the specimen.

Gaalomyia, new genus

DIAGNOSIS: Palpi 3-segmented, short. Scutum with long lateral, dorsocentral, and acrostichal setae. Laterotergites bare. Sc ends at R. Base of fork of M_{3+4} and CuA at the level of *r-m* base. M3 section approximately equal to *r-m*. Gonostyli simple.

TYPE SPECIES: *Gaalomyia carolinae*, n.sp.

ETYMOLOGY: The name is a feminine anagram of the genus name *Aglaomyia*.

COMMENTS: The new genus differs form *Aglaomyia* Vockeroth in having acrostichal setae present, palpi short, Sc ending at R basally of posterior fork, and 7th abdominal segment well developed. *Palaeodocosia* Meunier has palpi 4-segmented, vein Sc shorter, and the base of fork M_{3+4} and CuA more proximal. *Pseudalysiinia* Tonnoir has palpi 4-segmented and incrassate, with no bristles on the thorax and legs, and tibial spurs short. The genus may be close to *Ipsaneusidalys* Blagoderov, 1998, especially *I. longipennis*, but the latter differs in having long fork of M_{3+4} and CuA and M3 section, and R_5 is sinuous. Preservation of *I. longipennis* seems to be insufficient to decide if both species are congeneric.

Gaalomyia carolinae, new species

Figure 44, Plate 4E

DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 2.68 mm;

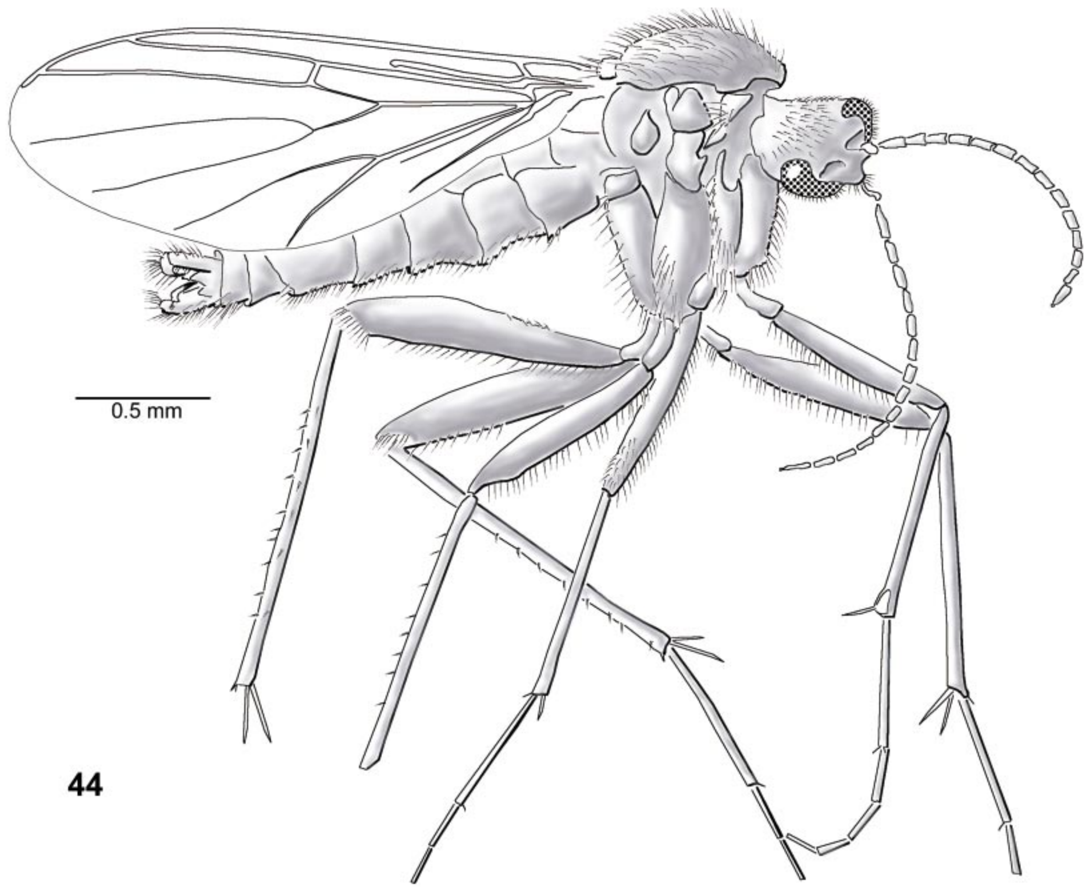


Fig. 44. *Gaalomyia carolinae*, n.sp., holotype AMNH Bu-390.

wing length = 2.34 mm. **Head:** Occiput and frons densely setose. Eyes large, with round facets, slightly emarginate, setulose. Ocelli absent. Scape and pedicel rounded, flagellum 14-segmented, filiform. Length of 1st and apical flagellomeres 2.5× width, with others 2× width. Palpi 3-segmented, palpomeres equal in length and subsequently narrower to apex. Length of penultimate one 1.5× width, apical one 3× width. Clypeus setose. **Thorax:** Scutum with long lateral, dorsocentral, and acrostichal setae. Proepimeron touches katepisternum at shallow incision. Katepisternum larger than anepisternum. Anepisternal suture horizontal. Antepronotum and proepisternum with long setae, other thoracic sclerites bare. **Wing** membrane without microtrichia. R, R_1, R_5, and M_1 with dorsal setae. Sc ends at R at the level of base of *r-m*. R_1 and R_5 straight. Crossvein *r-m* equal to M3 section. Length of fork of M_1 and M_2 4× M3 section. M_1 and M_2 not reaching wing margin. **Legs:** Fore and mid coxae densely setose, hind coxae with long posterolateral setae. Femora with ventral row of setae. Tibial spurs 2–2.3× tibial diameter. **Abdomen** densely setose. Sternite I bare. Eighth tergite short, length 0.5× 7th tergite. Tergite IX reniform, width 3× length. Gonocoxites slender, length 3.5× width, widely separated. Gonostyli saberlike, curved inside.

MATERIAL: Holotype AMNH Bu-390, male. Myanmar: Katchin, from amber mines near Myitkyina.

ETYMOLOGY: The species epithet is a patronym honoring our friend and colleague Caroline S. Chaboo, specialist on chrysomelid beetles.

TRIBE LEIINI EDWARDS, 1925

Nedocosia, new genus

DIAGNOSIS: Three ocelli, lateral ones do not contact eye margin. Sc merges with R. R_1 2–3× length of *r-m*. Veins of median and cubital forks lightly sclerotized. Base of M_{3+4} and CuA fork lies between levels of base of *r-m* and M_1–M_2 fork. Tibial bristles absent.

TYPE SPECIES: *Nedocosia exsangius*, n.sp.

ETYMOLOGY: The genus name is derived from the prefix *ne-*, ‘‘negation’’, and the genus *Docosia*. The name is feminine.

COMMENTS: This genus is most similar to *Docosia* Winnertz, 1863, which consists of 25 extant Palaearctic, 15 Nearctic, and 2 Neotropical species (Zaitzev, 1994). Seven species of *Docosia* are known from Baltic amber (Meunier, 1904, 1916, 1922, 1923) and one from the Oligocene shales of Rott, Germany (Statz, 1944). The new genus differs by having lateral ocelli not touching the eye margins (undoubtedly plesiomorphic), and by the lack of strong tibial bristles. Differences in sclerotization of anterior veins (Sc, R, R_5) and posterior veins (forks) in the new genus are not as great as in *Docosia* species. Two species of *Docosia* described from the Lower Cretaceous of Transbaikalia (Blagoderov, 1995) may also belong to the new genus, in fact showing affinities to *N. novacaesarea*.

Nedocosia exsanguis, new species

Figures 45, 46, Plate 4F

DIAGNOSIS: Sc meets R before level of base of *r-m*. Laterotergites bare. Cerci with two combs of dark setae. Apices of gonostyli sharp, curved inward at right angle.

DESCRIPTION: Body length = 1.29 mm; wing length = 0.67 mm (rest). **Head** oval, with rounded occiput, occiput and frons with scattered setae. Ocelli three, lateral one about its own diameter from eye margin and two diameters from medial ocellus. Eyes slightly emarginate, with round facets and short interfacetal trichia. Scape subconical, pedicel cylindrical. Flagellum 14-segmented, flagellomeres of hexagonal surface texture, cylindrical, lengths about equal to width. Face and clypeus setose. **Thorax:** Scutum with setae in lateral, dorsocentral, and acrostichal rows. Antepronotum with 4 long and several shorter setae. Proepimeron very small, touches katepisternum at incision. Laterotergites and mediotergite bare. Metepisternum broader than high. **Wing:** Sc meets R before M3 base. Costa ends beyond tip of R_5, more than one-half length between tips of R_5 and M_1. Crossvein *r-m* 0.37× length of R_1, and 0.6× length of M3 section. Base of fork of M_{3+4} and CuA between levels of bases of M3 section and M_1 and M_2 fork. M_{3+4} very weak. M_1 and M_2 fork campanulate. Longitudinal veins with setae, except Sc. **Legs**: Fore coxae with anterior setae, mid coxa with apical setae. Fore leg with first tarsomere 2× longer than second and 0.55× length of tibia. **Abdomen:** Tergites setose, sternites bare. Cerci with two comblike rows of black bristles. Apices of gonostyli sharp, squarish, curved inward.

MATERIAL: Holotype PIN 3130/193, male. Russia: Taimyr Peninsula, Yantardakh, coll. 1970.

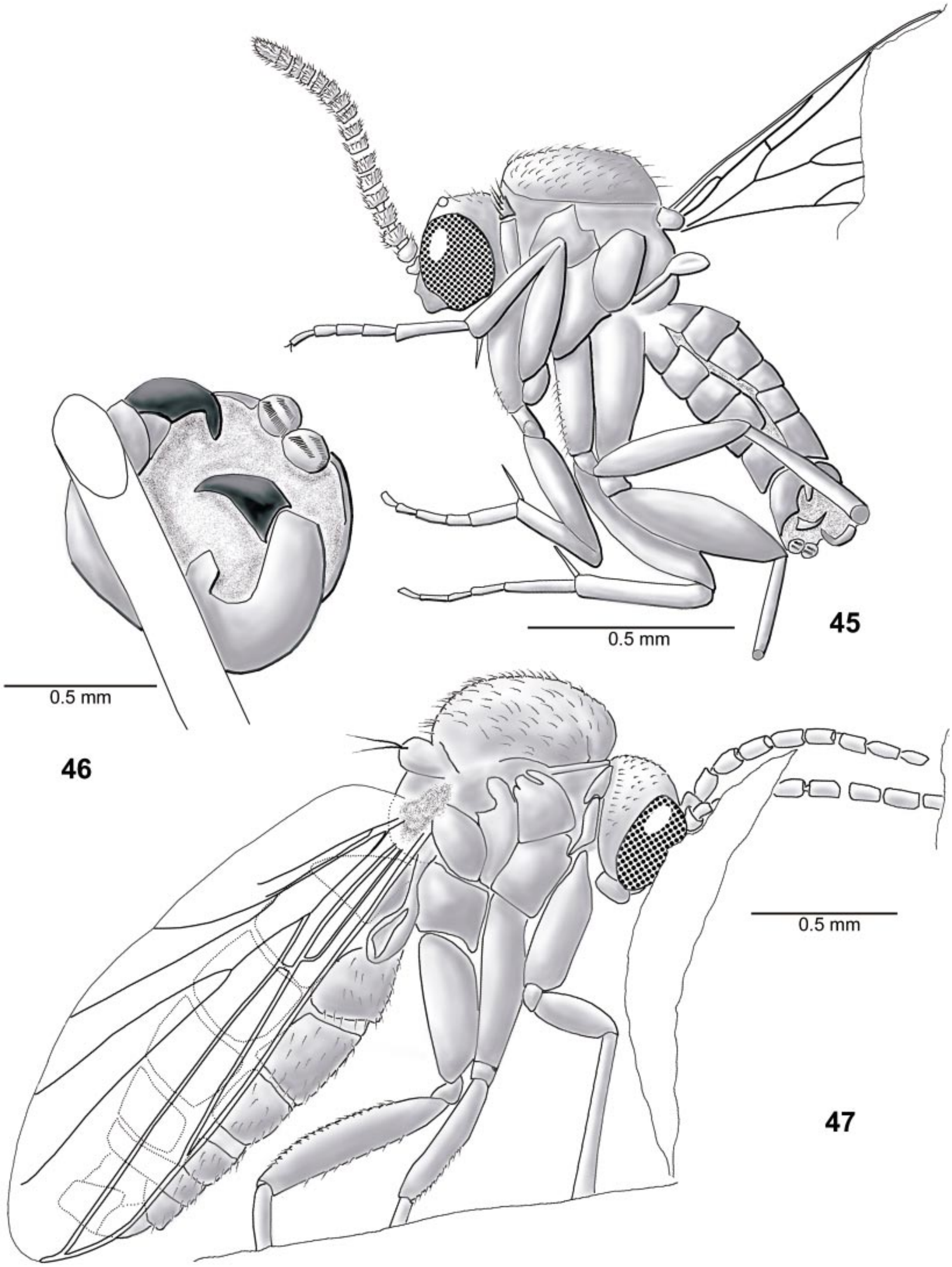
ETYMOLOGY: Latin, meaning pale or bloodless, referring to the pale color of the specimen.

Nedocosia sibirica, new species

Plate 5A

DIAGNOSIS: Sc meets R at the level of the base of the stem of M_{1+2}. Laterotergites setose. Anterior edge of fore coxa bare. Hind legs stout.

DESCRIPTION: Body length = 2.37 mm, wing length = 1.82 mm. **Head:** Occiput and frons setose. Ocelli three, equal in size; distance of median to lateral ocellus and from lateral ocellus to eye margin equal to twice their diameter. Eye with slight incision at antennal bases. Antennae short, only 10 flagellomeres preserved; flagellomeres cylindrical, widths 1.1–1.5× lengths. Face triangular, setose, clypeus ovate, bare. Palpi 5-segmented, short, antepenultimate segment swollen, with medial sensory pit on inner surface. Apical palpomere shorter than penultimate one, both slender, with sparse setulae. Length ratio 1: 3:3:5:5. **Thorax:** Mesonotum with short trichia and setae of various sizes; setae arranged in 5 rows. Antepronotum with three setae; proepisternum with two on lower part. Scutellum with two very long setae and two smaller ones. Laterotergites with a few tri-



Figs. 45–47. *Nedocosia* n.gen. **45.** *N. exsanguis,* n.sp., holotype PIN 3130/193. **46.** Male genitalia. **47.** *N. novacaesarea,* n.sp., holotype AMNH NJ-117k.

chia in lower part. Mediotergite bare. **Wing:** Sc meets R at the level of the base of the stem of M_{1+2}. R_1 twice the length of *r-m*. R_5 curved slightly back. C ends far beyond tip of R_5, but does not reach wing apex. Stem of R, R_1, and R_5 with setae. **Legs:** Anterior edge of fore coxae without setae. Fore tibiae with semicircular anteroapical depressed area, covered with numerous small trichia. Mid tibial spur length 2.5× apical diameter of tibia, hind tibial spur 1.5× diameter. Hind legs stout, longer than mid legs. First fore tarsomere 2.5× longer than second and 0.67× length of tibia. Cerci simple.

MATERIAL: Holotype PIN 3311/665, female. Russia: Taimyr Peninsula, Yantardakh, coll. 1971.

ETYMOLOGY: The species epithet is a reference to the region of origin of the amber.

***Nedocosia canadensis*, new species**

Plate 5B

DIAGNOSIS: Sc meets R before level of base of the stem of M_{1+2}. R_1 2.5× length of *r-m*. M_{3+4} and CuA fork at the level of *r-m*. M3 section shorter than *r-m* crossvein. Laterotergites and mediotergite bare.

DESCRIPTION: Body length = 1.50 mm (preserved part). **Head:** Occiput with setae of different length. Ocelli not seen. Eyes with round facets, setulose. Scape small, pedicel subconical. Flagellum 14-segmented, flagellomeres cylindrical, lengths equal to widths, densely covered by trichia no longer than half width of basal flagellomere. Three segments of palpi seen, combined length equal to head height. **Thorax:** Scutum uniformly setose with long and short setae. Antepronotum with two very long setae and several short ones. Laterotergites and mediotergite bare. **Wing:** Sc meets R before level of base of the stem of M_{1+2}. R_1 2.5× length of *r-m*. Crossvein *r-m* 1.3× length of M3 section. Base of fork of M_{3+4}–CuA proximal to base of fork of M_1–M_2.

MATERIAL: Holotype MCZC 6897, incomplete specimen, sex unknown. Canada: Manitoba, Cedar Lake, coll. F. M. Carpenter.

ETYMOLOGY: The species epithet is a reference to the country of origin of the amber.

***Nedocosia novacaesarea*, new species**

Figure 47, Plate 5C

DIAGNOSIS: Flagellum 11-segmented. Sc long, ends at R between RS and *r-m* bases. Base of M_{3+4} and CuA fork at level of *r-m*. Fore leg with tibia equal to femur or slightly longer.

DESCRIPTION: Body length = 2.34 mm (holotype)/2.88 mm (paratype); wing length = 1.75 mm (holotype)/2.20 mm (paratype). **Head:** Three ocelli in line, distances between median and lateral ones, and between lateral and eye margin, are equal. Face rectangular, bare. Clypeus bare. Scape and pedicel rounded, shorter than flagellomeres. Flagellum 11-segmented, flagellomeres cylindrical, with lengths 2× width. Two palpomeres seen, apical one 2× length of basal. **Thoracic** sclerites bare. Scutum with long lateral setae and numerous short ones, not arranged in rows. Proepimeron small, fits in shallow incision on katepisternum. Anepisternal suture declines backward. Metepisternum touches anepimeron. Meron large. **Wing:** Costa ends beyond tip of R_5, more than one-third length between tips of R_5 and M_1. Sc long, ends at R between RS and *r-m* bases. Length of R_1 2.5–3× that of *r-m*, M3 section twice that of *r-m*. Length of fork of M_1 and M_2 2.5–3× M3 section. Base of fork of M_{3+4} and CuA at level of *r-m* base. **Legs:** Fore coxae with short anterior setae, hind coxae with long posterolateral setae. Fore leg with tibia equal to femur. Tibial spurs 1.2–1.5× tibial diameter. **Abomen** setose. Seventh segment very narrow. Gonocoxites massive, with apices blunt.

MATERIAL: Holotype AMNH NJ-117k, male; paratype NJ-117l, male in the same piece. USA: New Jersey, Sayreville, coll. P. Nascimbene.

ETYMOLOGY: The species epithet is derived from Latin *Nova Caesarea* meaning ‘‘New Jersey’’ and is a reference to the state of origin of the amber.

COMMENTS: The species is similar in venation to *Docosia baisae* Blagoderov, 1998 and *D. zaza* Blagoderov, 1998, by proximal position of the forked base of M_{3+4} and CuA, but differs from the latter species in having Sc long and M3 section short.

Ectrepesthoneura Enderlein, 1911

Willistoniella Meunier, 1904: 74 (preoccupied by Mik, 1895).
Meunieria Johannsen, 1909: 87 (preoccupied by Kieffer, 1904).
Ectrepesthoneura Enderlein, 1911: 115.

DIAGNOSIS: As given by Chandler (1980): Lateral ocelli remote from eye margin; laterotergites bare; Sc ending in R before base of RS; R_4 present; R_1 short, at most twice as long as *r-m*; R_5 straight; C prolonged well beyond tip of R_5; veins of medial and cubital sectors weak and faint; posterior fork sessile. Males with ''sensory pit'' near the base of mid tibia; hind tibial comb absent.

TYPE SPECIES: *Tetragoneura hirta* Winnertz, 1846: 19 (orig. designation)

COMMENTS: There are about 10 extant species from the Holarctic region. The genus is very close to *Tetragoneura* Winnertz (about 100 widespread living species) and is sometimes included in it or treated within the tribe Gnoristini (Tuomikoski, 1966; Vaisanen, 1986). There are two fossil species described from Baltic amber (Meunier, 1904) and the Oligocene of Rott, Germany (Statz, 1944). Chandler (1999) suggested that *Ectrepesthoneura* was paraphyletic.

Ectrepesthoneura succinimontana, new species

Figures 48, 49, Plate 5D

DIAGNOSIS: Fore tibiae slightly shorter than fore femur. Section M3 and bases of M_1 and M_2 very weak. Length of small radial cell twice the width.

DESCRIPTION: Body length = 2.39 mm; wing length = 2.02 mm. **Head:** Occiput and frons with short curved setae. Ocelli three, distance of lateral one to eye margin more than twice the ocellus diameter. Scape subconical, pedicel rounded, width twice flagellomere width. Eleven segments of flagellum preserved, flagellomeres cylindrical, with length about equal to width. Face setose. Palpi 4-segmented; 1st palpomere very small; antepenultimate one oval, its length twice the width, with medial sensory pit; penultimate one with length 3× width, attached to the second one preapically; apical segment long and slender. Clypeus triangular, setose. **Thorax:** Scutum with numerous long setae mostly curved forward and shorter ones curved back, arranged in rows. Antepronotum with 3 long setae. Scutellum with two pairs of long setae. Other thoracic sclerites bare. **Wing:** All longitudinal veins with short setae. Sc meets R proximal to base of M3. Length ratio of sections RS1, RS2, and RS3 is 1:2:13. RS1 transverse, 0.3× length of *r-m*. Crossvein *r-m* 0.7× length of R_1 and 0.5× length of M3 section. Costa ends beyond tip of R_5, one-third distance between tips of R_5 and M_1. Section M3 and M_1 and M_2 bases very weak. **Legs:** Fore coxae with numerous anteromedial setae, hind coxae with posterolateral setae. Fore and mid tibiae slightly shorter than fore femora. Mid and hind tibiae and tarsi with rows of black bristles. Tibial spurs 1.5–2× tibial diameter. Tarsal claw with one long tooth. **Abdomen** setose. Eighth sternite almost triangular. Cerci 2-segmented, basal segment stick-shaped, with length twice the width, extends beyond 8th sternite; apical one discoidal, attached at the apex of the basal one, 2.2× shorter. Dorsal border of 8th sternite (gonocoxite 8 of Martinsen and Söli, 2000) straight.

MATERIAL: Holotype PIN 3311/662, male. Russia: Taimyr Peninsula, Yantardakh, coll. 1971.

ETYMOLOGY: From Latin *succinum* meaning ''amber'' and *montanus* meaning ''mountainous''. *Yantardakh* means ''amber mountain'' in Dolgan language.

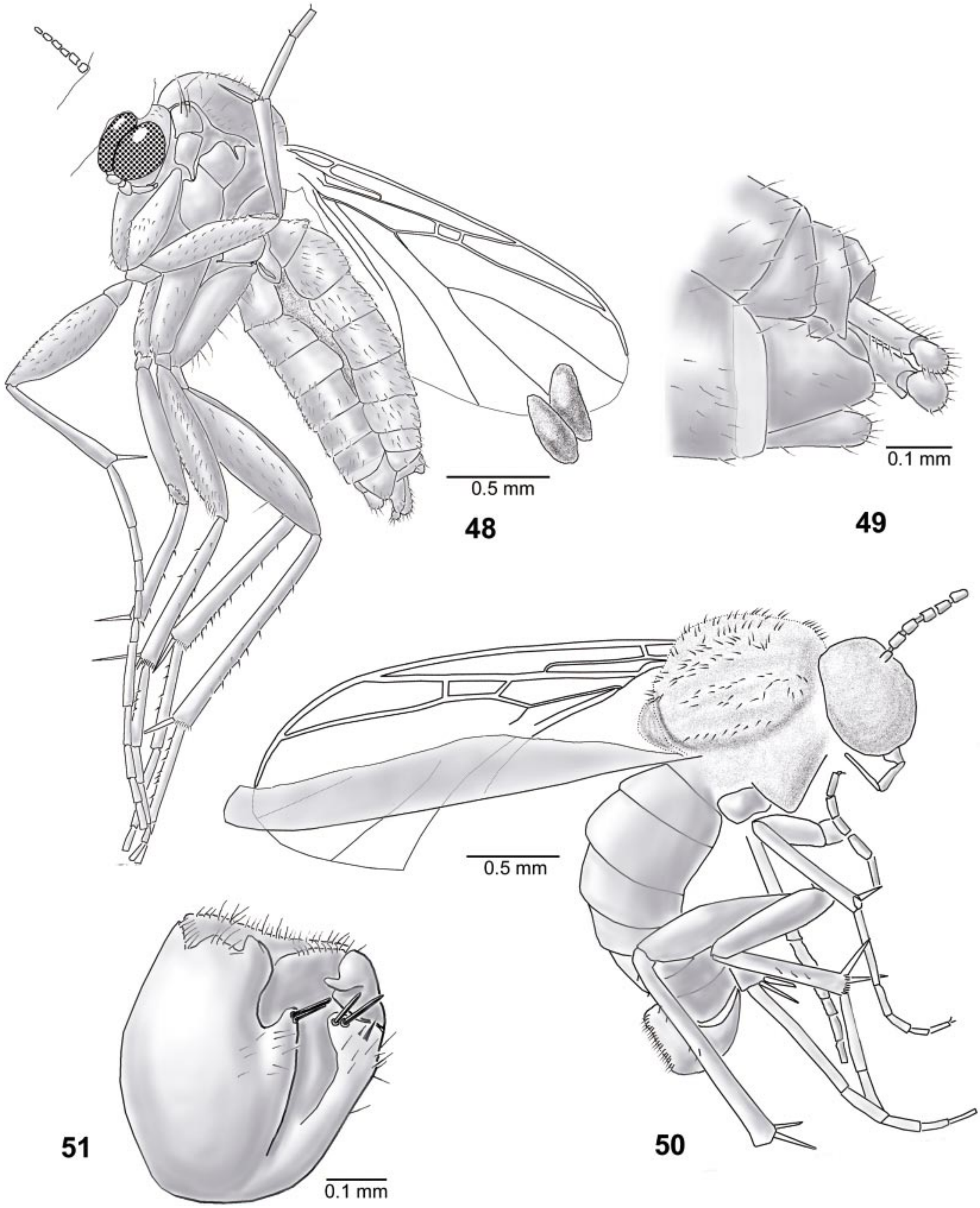
COMMENTS: Comparision with recent species is difficult, because nongenital characters used for distinguishing species have been considered to be unreliable for this genus (Martinsen and Söli, 2000). For species where the female genitalia are known the new species is most similar to *E. hirta* Winnertz.

Ectrepesthoneura swolenskyi, new species

Figures 50, 51, Plate 5E

DIAGNOSIS: Sc long, meets R just before base of M3. Small radial cell relatively long. Gonocoxites with triangular ventral appendages bearing 2 long, dark apical spurs.

DESCRIPTION: Body length = 2.71 mm; wing length = 2.46 mm. **Head:** Ocelli three, from lateral ocellus to eye margin twice ocellus diameter. Flagellomeres cylindrical, length 1.5× width. Three palpomeres seen,



Figs. 48–51. *Ectrepesthoneura* End. **48.** *E. succinimontana*, n.sp., holotype PIN 3311/662. **49.** Female genitalia. **50.** *E. swolenskyi*, n.sp., holotype AMNH NJ-824. **51.** Male genitalia.

apical one slender, length ratio 1:2:3.5. **Thorax:** Antepronotum with 2 setae, proepisternum with 4. Scutum with setae curved forward, lateral setae very long. **Wing:** All longitudinal veins except Sc with short setae. Costa ends beyond tip of R_5, one-half distance between tips of R_5 and M_1. Sc meets R just before M3 base. Length of R_1 2.2× that of *r-m*. Length of M3 2.7× that of *r-m*. Ratios of lengths of sections RS1, RS2, and RS3 1:2.3:7. RS1 oblique, 0.58× length of *r-m*. M3, M_1, and M_2 weak, M_1 slightly curved forward. M_{3+4} and CuA curved gently caudad. **Legs:** Fore and mid tibiae longer than femora. Mid tibia with anterolateral, posterolateral, and posteromedial rows of short bristles, hind tibia with two rows of posterior setae. Basal third of mid tibia with large, dark, narrow sensory pit. Tibial spurs 1.3–1.7× tibial diameter. **Abdomen.** Ninth tergite large, conceals gonocoxites and gonostyli almost completely; caudal edge straight, without medial cleft. Ninth tergite straight caudally, without cleft, with numerous curved setae apically. Gonocoxites with triangular ventral appendages bearing 2 long, dark apical spurs. Gonostyli short, pointed, curved S-like.

MATERIAL: Holotype AMNH NJ 824, male. USA: New Jersey, Sayreville; coll. S. Swolensky, 1997–1998 (mentioned in Grimaldi, 2000: fig. 48h).

ETYMOLOGY: The species epithet is patronymic for the late Steve Swolensky, who collected the specimen.

COMMENTS: The new species differs from other species of the genus in the structure of male genitalia, especially by ventral appendages of gonocoxites bearing dark sclerotized spurs.

Izleiina, new genus

DIAGNOSIS: Facets round. Lateral ocelli not touching eye margins. Clypeus setose. Sc meets C just beyond level of base of M3; Sc_2 absent. Length of R_1 2× that of *r-m*. Section M3, and fork of M_1 and M_2–M_{3+4} reduced; CuA weakened. M_{3+4} interrupted at base.

TYPE SPECIES: *Izleiina mirifica*, n.sp.

ETYMOLOGY: Name is derived from the tribe Leiini.

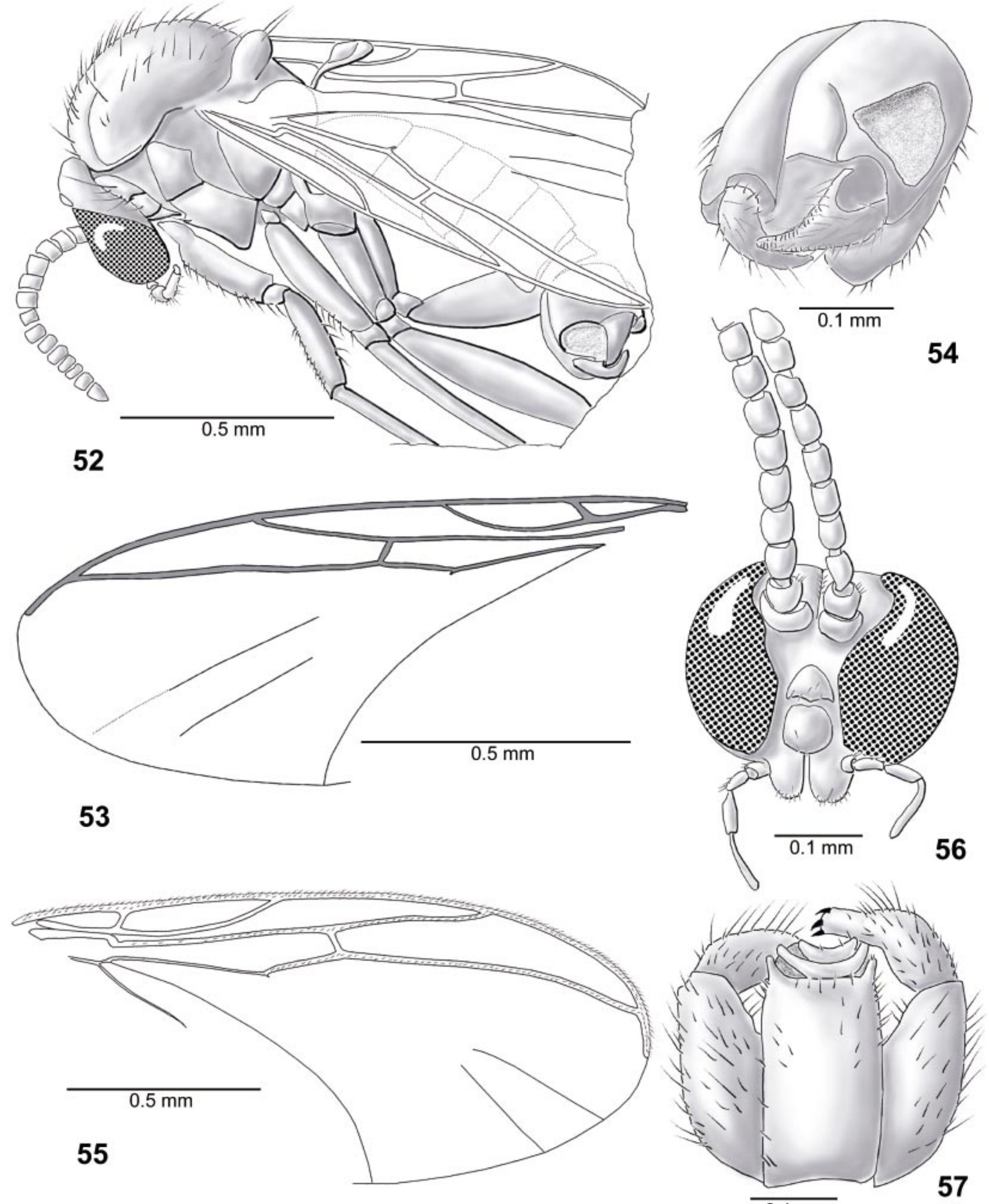
COMMENTS: We assume that in the new genus vein M_1 is entirely reduced. As a rule, in most leiine genera, vein M_1 reaches the wing margin at or even before the wing apex. They have retained a complete vein that is homologous to CuA based on the length and shape of the vein, and which is strongly curved back and ends at the level of RS1, as in most Leiini. The new genus differs from *Neoclastobasis* Ostroverchova by the lateral ocelli touching eye margins, and from *Clastobasis* Skuse and *Neoclastobasis* by C ending beyond the tip of R_5, and by the presence of the base of M_{3+4}. Having R_1 relatively long and Sc ending at C makes the genus similar to *Rondaniella* Johannsen and *Indoleia* Edwards, but differs from them by reduction of the veins in the medial sector. Such a reduction also occurs in other leiine genera, for example *Novakia* Strobl and *Sigmoleia* Tonnoir and Edwards, but they have Sc very short and free. Species of *Cycloneura* Marshall and *Paracycloneura* Tonnoir and Edwards also have M unbranched and M_{3+4} free or reduced at the base, the anepisternum large, metepisternum narrow like *Izleiina*, but they differ strongly in the shape of CuA, by having M_2 long, Sc short and free, and by the presence of strong tibial bristles.

Izleiina mirifica, new species

Figures 52–54, Plate 5F

DIAGNOSIS: Apical palpomere short. Tibiae without bristles. Gonostyli conical, curved inward.

DESCRIPTION: Body length = 1.44 mm, wing length = 1.23 mm. **Head:** Ocelli three, distance from eye margin equal to two ocellus diameters; distance between each other equal to one diameter. Flagellum 14-segmented, flagellomeres cylindrical, lengths about equal to widths, covered by setulae no longer than one-half flagellomere width. Palpi 4-segmented, three basal segments baciliform, apical one short and rounded. Occiput, frons, face, and clypeus with short setulae. **Thorax:** Prescutum and anterior parapsidal suture distinct. Antepronotum with 6 setae, proepisternum with two. Scutum arched. Scutellar setae in rows. Scutellum with two pairs of long setae. Cavity on anterior edge of katepisternum shallow. Laterotergites and mediotergite bare. **Wing:** Sc



Figs. 52–57. *Izleiina*, n.gen. **52.** *I. mirifica*, n.sp., holotype PIN 3130/187. **53.** Reconstruction of wing venation. **54.** Male genitalia. **55.** *I. spinitibialis*, n.sp., holotype AMNH NJ-346, reconstruction of wing venation. **56.** Head. **57.** Male genitalia.

meets C just beyond level of base of M3. C ends far beyond apex of R_5. R_1, R_5, and *r-m* with setae. R_1 length 2× that of *r-m*. R_5 straight. Length of crossvein *r-m* 0.5× length of section M3. M3 weak, can be seen only by absence of microtrichia on wing membrane. M_{3+4} and CuA fork base proximal to the base of *r-m*. M_{3+4} interrupted at base, not reaching wing margin. **Legs:** Fore coxae with anterior setae, mid coxae with lateroapical ones. Tibiae without bristles. **Genitalia:** Gonocoxites massive, fused. Gonostyli hornlike and slightly curved, with long setae, colored lighter than gonocoxites.

MATERIAL: Holotype PIN 3130/187, male. Russia: Taimyr Peninsula, Yantardakh, coll. 1970.

ETYMOLOGY: The species epithet is a Latin word *mirificus* meaning ''amazing'' in reference to unusual combination of characters. The name is feminine.

Izleiina spinitibialis, new species

Figures 55–57, Plate 6A

DIAGNOSIS: Tibiae with bristles. Gonostyli cylindrical, length 2.5× the width, with 3 dark teeth at the apex

DESCRIPTION: Body length = 2.07 mm; wing length = 1.65 mm. **Head:** Ocelli three, almost in a straight line. Lateral ocelli distant by two diameters from medial ocellus and their own diameter from eye margin. Frontal furrow distinct. Eyes emarginate at antennal base, bare. Frons bare. Face setose. Scape and pedicel without strong setae, rounded, wider than flagellomeres. Eight flagellomeres seen, cylindrical in shape, lengths 1.5× width. Clypeus rounded, setulose. Palpi 4-segmented, basal segment rounded, antepenultimate and penultimate one bacilliform with lengths 3–4× width; apical palpomere long. **Thorax:** Scutellum with 4 long setae. Laterotergites and mediotergite bare. **Wing:** Sc long, meets C at level of M3 base. R_1 straight, 2× length of *r-m*. R, R_1, R_5, and *r-m* with a dorsal row of setae. Crossvein *r-m* almost horizontal. R_5 curved caudally. C ends beyond tip of R_5. M_2 and M_{3+4} weak. Base of CuA weak. CuA curved caudally, not sigmoid. **Legs:** Tibiae with bristles. **Abdomen:** Genitalia covered by long setae. Ninth tergite rectangular, length 2.3× the width. Gonocoxites slightly swollen. Gonostyli almost straight, length 2.5× width, with 3 dark teeth at the apex.

MATERIAL: Holotype AMNH NJ-346, male. USA: New Jersey, Sayreville, coll. Y. Goldman, 1995.

ETYMOLOGY: The species epithet is derived from Latin *spina*, meaning ''spine'', and *tibia*, meaning ''leg''.

Zeliinia, new genus

DIAGNOSIS: Close to *Izleiina* n.gen., but differs in having palpi long, Sc free, M_1 reduced at base, M_2 absent, and base of posterior fork proximally with *r-m* touching the base of M_{3+4}. Setulae on flagellomeres arranged in rings.

TYPE SPECIES: *Zeliinia orientalis*, n.sp.

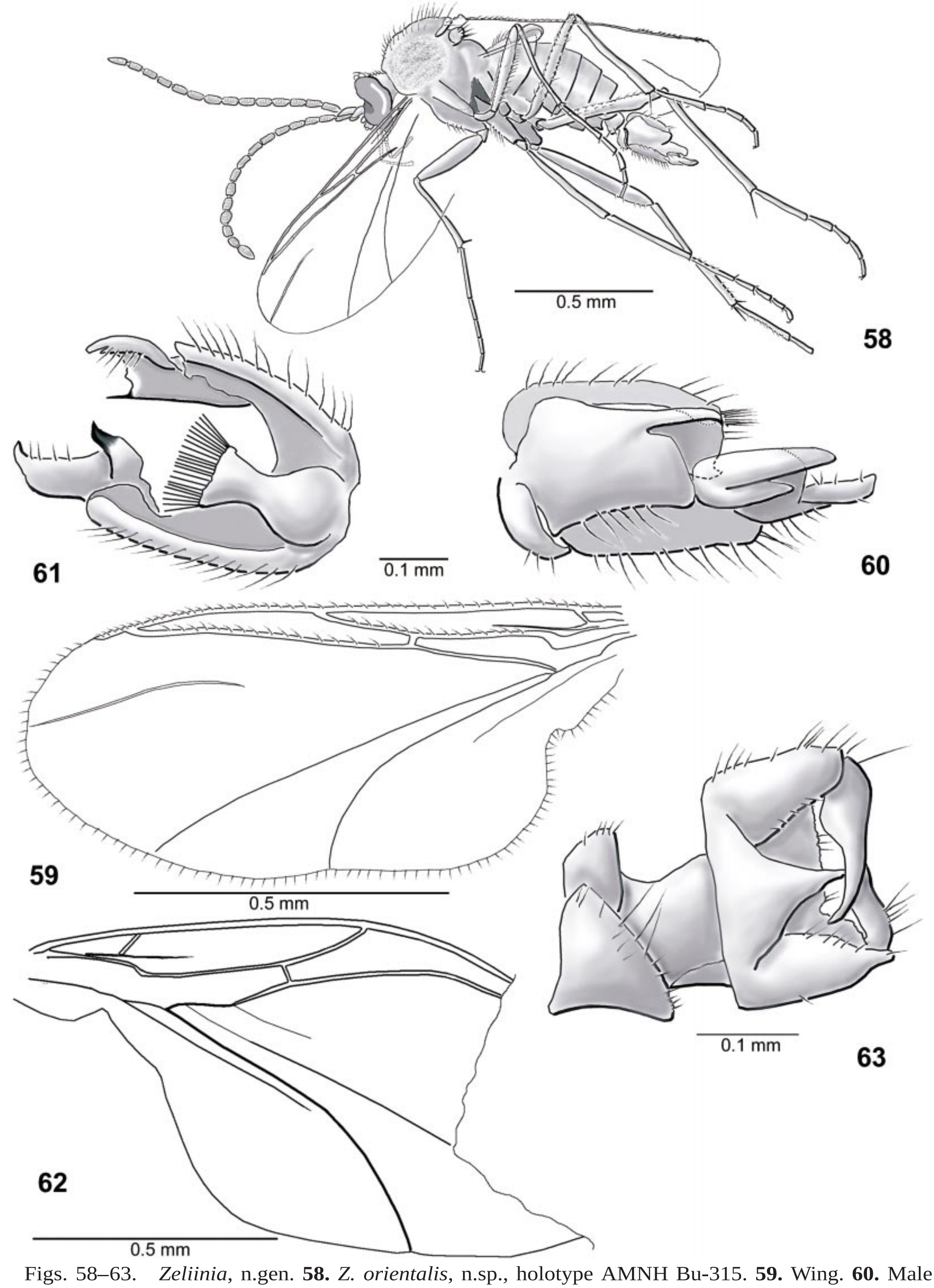
ETYMOLOGY: The genus name is an anagram for *Izleiina*. The name is feminine.

Zeliinia orientalis, new species

Figures 58–61, Plate 6B

DIAGNOSIS: Genitalia longer than wide; gonostyli bilobate. Tergite 9 obovate, with numerous setae at apex.

DESCRIPTION: Male. Body length = 1.25 mm; wing length = 1.07 mm. **Head:** Ocelli three, close to each other. Eyes strongly incised, forming incomplete bridge. Pedicel slightly wider than scape and flagellum; 14 cylindrical flagellomeres with length 2× width. Three palpomeres seen, sticklike, length ratio 1:1.3:2. **Thorax:** Scutum with long lateral, dorsocentral, and acrostichal setae. Katepisternum larger than anepisternum, proepimeron touches katpisternum at small excavation. Antepronotum and proepimeron setose. Laterotergites and mediotergite bare. **Wing:** Costa slightly produced beyond apex of R_5. Sc free, ends at the middle of *r-m*. R_1 and R_5 with long dorsal and ventral setae. Crossvein *r-m* forming one vein with *tb* and M2 section, equal to 1.5× length of R_1. Length of R_5 2.8× R_1. Base of M3 faint. M_1 ends at wing apex, base curved posteriorly. Base of M_{3+4} and CuA fork contact *r-m*. **Legs:** Tibial setulae irregular. Tibia II with apical comb of setae. Tibial spurs 1–1.5× tibial diameter, spur formula 1:1:1. **Abdomen** setose, 7th and 8th segments short, narrow, retractable. Genital complex large,



Figs. 58–63. *Zeliinia*, n.gen. **58.** *Z. orientalis*, n.sp., holotype AMNH Bu-315. **59.** Wing. **60.** Male genitalia laterally. **61.** Male genitalia dorsally. **62.** *Z. occidentalis*, n.sp., holotype MCZC 6943. **63.** Male genitalia.

length equal to 4th–8th segments combined. Ninth tergite fiddle-shaped, with two apical combs of dark setae. Gonocoxites rectangular in lateral view. Gonostyli bilobate.

MATERIAL: Holotype AMNH Bu-315, male. Myanmar: Katchin, from amber mines near Myitkyina.

ETYMOLOGY: The species epithet is a Latin word *orientalis*, meaning ''eastern'', referring to origin of the amber.

Zeliinia occidentalis, new species

Figures 62, 63, Plate 6C

DIAGNOSIS: Clypeus with long setae; mediotergite and laterotergites bare, wing membrane without macrotrichia, Sc short, ends free, R_1 short, 1.5× longer than *r-m,* ends proximally at tip of CuA. Genital complex wider than long; gonostyli unilobate.

DESCRIPTION: Body length = 1.79 mm; wing length = 1.22 mm. **Head:** Eyes bare, forming dorsal bridge, possibly incomplete (vertex and occiput not fully seen due to deformation). Scape and pedicel short, rounded. Flagellum 14-segmented, flagellomeres equal in length, apical flagellomeres more narrow than basal ones, with length about twice the length of pedicel, covered with short microtrichia. First flagellomere length 1.6× width, preapical is 2.5× width. Clypeus setose. Three visible palpal segments, two basal ones about equal in length; apical palpomere long and slender, about twice the length of the penultimate. **Thorax:** Antepronotum with two setae, proepisternum with one. Scutum with long lateral, dorsocentral, and acrostichal setae. Scutellum with 4 pairs of long setae. Katepisternum larger than anepisternum. Metepisternum small, quadrate, bare. Mediotergite and laterotergites bare. **Wing** membrane without macrotrichia. R, R_1, and R_5 setulose. Sc short, ends free. R_1 1.5 length of *r-m,* R_5 more than 4.5× length of *r-m.* Crossveins *r-m, tb,* and *m-cu* fused into one oblique vein, with distinct kink at the base of the stem of M_{1+2} (M3 section). Stem of M_{1+2} and base of M_{3+4} weak. M apparently without fork. M_{3+4} and CuA curved gently caudad. **Legs:** Femora with ventral row of long setae. Coxae relatively short, fore coxa as long as mid and hind ones. Mid and hind tibiae with short bristles. Tibial spurs 1.2–1.5× tibial diameter. Tarsal claws with very small tooth. **Abdomen** densely setose, with long setae. Genitalia rectangular, width 1.6× length. Gonocoxites stout, gonostyli simple, pointed, with inner surface slightly curved apically.

MATERIAL: Holotype MCZC 6943, male. Canada: Manitoba, Cedar Lake, coll. F.M. Carpenter.

ETYMOLOGY: The species epithet is Latin meaning ''western'', referring to origin of the amber

COMMENTS: *Z. occidentalis* differs from the type species in the structure of genitalia, and although it possesses the same arrangement of flagellar setulae and venation pattern, both species may not be congeneric.

Temaleia, new genus

DIAGNOSIS: Wing membrane with macrotrichia; Sc long, meets C before base of M3 section; C ends at tip of R_5; M3 section 3× length of *r-m*; M_{3+4} not interrupted at the base; tibial setulae irregular; tibial bristles absent; abdominal segment 6 not reduced; 7th and 8th segments telescopic.

TYPE SPECIES: *Temaleia birmitica,* n.sp.

ETYMOLOGY: The genus name is a feminine anagram of *Metaleia.*

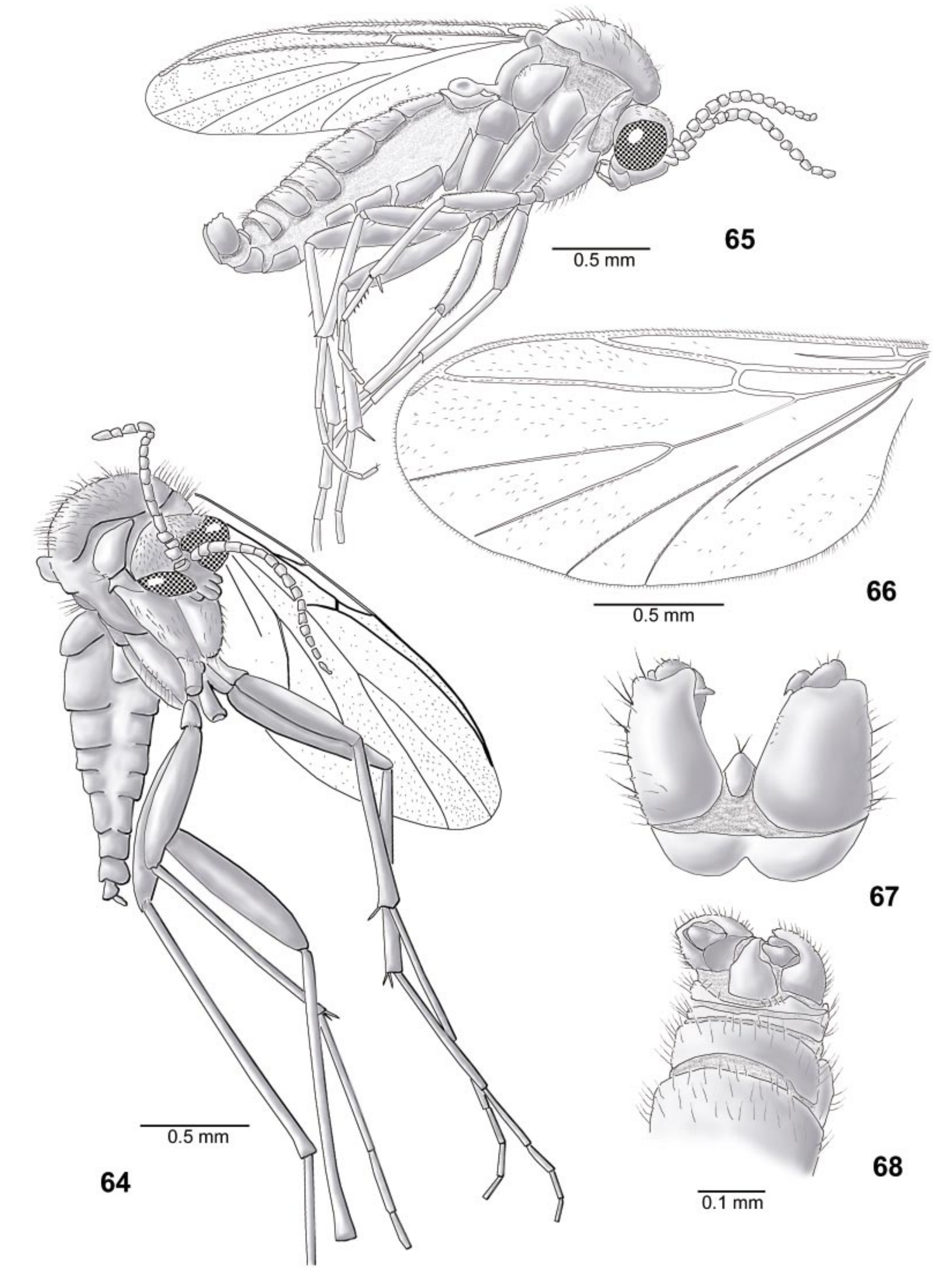
COMMENTS: The genera *Clastobasis* Skuse, 1896, *Neoclastobasis* Ostroverchova, 1970, and *Metaleia* Baxter, 1994 have M_{3+4} interrupted at the base and/or CuA sinuous. The genus *Sticholeia* Söli, 1996, besides having extremely long cerci and other details of the male terminalia, differs by having a short M3 section.

Temaleia birmitica, new species

Figure 64, Plate 6D

DIAGNOSIS: As for the genus.

DESCRIPTION: Body length = 2.17 mm (holotype)/2.03–2.38 mm (paratype); wing length = 1.96 mm (holotype)/1.50–2.07 mm (paratype). **Head:** Pedicel rounded, length about equal to width. Flagellum 14-segmented; flagellomere length about twice the width. Eyes large, densely setose. Occiput covered with numerous short setae. Clypeus setose. Palpi 3-segmented, very short, palpomeres with length about equal to width. Labella longer than palpi. **Thorax:** Scutum



Figs. 64–68. *Temaleia* and *Lecadoniella*. **64.** *T. birmitica*, n.sp., holotype AMNH Bu-483a. **65.** *L. parvistyla*, n.sp., holotype MCZC 6941. **66.** Wing. **67.** Male genitalia ventrally. **68.** Male genitalia dorsally.

irregularly covered with short setae and with long lateral, dorsocentral, and acrostichal setae. Scutellum with three pairs of long bristles. Laterotergites and mediotergite with several protruding bristles. **Wing** membrane with microtrichia and macrotrichia, located mostly in distal half of wing. Costa ends at tip of R_5, not reaching wing apex. Sc long, meets C before base of M3. Sc_2 apical. R_1 very short, 1.5× length of *r-m*. M3 section 3× length of *r-m*. M_1 meets wing edge at wing apex. M_1 and M_2 fork 2.5× as long as M3 section. Base of M_{3+4} and CuA fork at level of M3 base. M_{3+4} and CuA curved gently caudad. **Legs:** Fore coxae with anterior and anterolateral setae. Mid coxa with lateroapical setae, hind one with posteroapical setae. Tibial spurs short, no longer than maximum tibial diameter. Tibial and tarsal bristles absent. Tibial setulae irregular. **Abdomen** pubescent, with 7 visible segments, 8th small and retracted. Ninth tergite large, oval. **Female:** Cerci one-segmented, bacilliform, setose. **Male:** Gonocoxites and gonostyli long, slender, bacilliform. Gonostyli slightly curved inside at apex, saberlike.

MATERIAL: Holotype AMNH Bu-483a, female; paratypes AMNH Bu-060, male, Bu-054, male. Myanmar: Katchin, from amber mines near Myitkyina.

ETYMOLOGY: The species epithet is a reference to Burma, the former name of the country where the amber originates.

Lecadonileia, new genus

DIAGNOSIS: Palpi reduced, laterotergites setose; wing membrane with macrotrichia; Sc free, Sc_2 absent; M_{3+4} interrupted at base, M_{3+4} and CuA curved gently caudad, 9th tergite small or fused with synsclerite; gonocoxites widely separated.

TYPE SPECIES: *Lecadonileia parvistyla*, n.sp.

ETYMOLOGY: The genus name is a feminine anagram of the *Caledonileia* Matile, 1993.

COMMENTS: The genus is close to the genus *Caledonileia*, from which it differs in number and position of ocelli, number of palpomeres, setation of scutum, and in having Sc long, the radial cell wide, M3 long, and gonostyli unilobate (Matile, 1993). The genus differs from *Megophthalmidia* Dziedzicki in having M_{3+4} interrupted at the base and the fork of M_1 and M_2 not shifted anteriorly, so that M_1 reaches the wing margin beyond the wing apex.

Lecadonileia parvistyla, new species

Figures 65–68, Plate 6E

DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 2.24 mm, wing length = 2.05 mm. **Head:** Vertex setose. Ocelli three, lateral one twice its diameter from eye margin. Frons bare, face with tiny trichia. Scape small, roundish. Pedicel rounded, with dorsal setae, wider than flagellomeres. Flagellum 14-segmented, cylindrical, flagellomere length equal to width. Palpi 4-segmented. Basal palpomere very short, apical three subequal, lengths 2.5–3× their width. Clypeus setose. **Thorax:** Scutum irregularly setose. Antepronotum with 4 setae, proepisternum with 5. Ventral process of proepimeron just opposite anapleural suture. Anepisternum with distinct oblique cleft. Anepimeron very narrow ventrally. Laterotergites setose. Mediotergite bare. **Wing** membrane with macrotrichia. Costa ends beyond tip of R_5, at one-fourth length between tips of R_5 and M_1. R_1 and R_5 with two rows of setae; R stem, *r-m*, M_1, M_2, M_{3+4}, and CuA with one row. Sc ends free at the level of the base of M3 section. R_1 equal to M3 section and 2.5× length of *r-m*. Fork of M_1 and M_2 1.8× length of M3. M_{3+4} base absent, vein begins at level of RS base. **Legs:** Fore coxae with numerous setae on anterior and lateral surfaces. Mid coxae with setae on apical half. Hind coxae with posterolateral row of setae. Tibial bristles short. Fore tibiae with 3 apical bristles; mid one with 2 anterior and 6 apical bristles; hind tibia with 4–6 bristles in anterior, anteroventral, and anterodorsal rows and several apical bristles. Anteroapical depression on fore tibiae well developed, with single row of short setae. Tarsal claws without teeth. **Abdomen** setose. Eighth and 9th segments very short and retracted. Gonocoxites semicylindrical, widely separated at base. Gonostyli small, with one apical appendage turned medially.

MATERIAL: Holotype MCZC 6941, male.

Canada: Manitoba, Cedar Lake, coll. F.M. Carpenter.

ETYMOLOGY: The species epithet is a combination of the Latin word *parvus*, meaning ‘‘small’’, and *stylus*, meaning ‘‘spike, stem, pen’’, in reference to simple small gonostyli of the species.

Disparoleia, new genus

DIAGNOSIS: Ocelli absent; anepisternum with very short setae and trichia; mediotergite and laterotergites bare; wing membrane with micro- and macrotrichia; Sc ends at C; *r-m* 2× length of R_1, M3 base at basal one-sixth of wing, M3 weak, M_2 absent.

TYPE SPECIES: *Disparoleia cristata*, n.sp.

ETYMOLOGY: The genus name is a combination of the Latin word *dispar*, meaning ‘‘unequal, unlike’’, and the genus *Leia*, in reference to the distinctiveness of the new genus. The name is feminine.

COMMENTS: The genus differs from all Recent Leiini in the unique combination of such characters as absence of ocelli, very long *r-m* with the proximal position of the base of M3, and reduction of veins in the medial sector. It differs from *Novakia* Ströbl in having the base of RS distinct, M_2 absent, and Sc ending at C. It differs from *Zeliinia*, n. gen. in having flagellomeres of smooth texture, ocelli absent, vein M_1 and M3 section present though weak, and fork of M_{3+4} and CuA long but not sessile.

Disparoleia cristata, new species

Figures 69, Plate 7A

DIAGNOSIS: As for genus.

DESCRIPTION: Female. Body length = 2.73 mm, wing length = 2.08 mm. **Head:** Vertex with group of long erect setae. Scape and pedicel wider than flagellum. Flagellum 14-segmented, flagellate, flagellomeres longer and narrower apicad. Eyes setose, slightly emarginate at antennal base. Ocelli absent. Clypeus setose. Palpi 3-segmented, 1st palpomere short, 2nd longer, cut obliquely, 3rd longer than length of 1st and 2nd, narrow. **Thorax:** Scutum with lateral and dorsocentral rows of long setae and short irregular setae. Scutellum with numerous short setae. Antepronotum with long curved setae and several short ones. Anepisternum with 4 light short setae in upper part and very fine hairs at lower apical part. Proepimeron touches katepisternum slightly ventral to anepisternal suture. Mediotergite and laterotergites bare. Metepisternum large, with dorsal margin wider than ventral one. **Wing** membrane with microtrichia and short macrotrichia. Costa ends beyond tip of R_5, at one-third length between tips of R_5 and M_1. Humeral vein located beyond the MA. Sc short, ends at C before level of M3 base, apex faint. R_1 very short, *r-m* 3× length of R_5. Median veins weak. M_1, base of M_1 and M3 very weak. Base of M3 very proximal, slightly distal to apex of Sc. Crossvein *r-m* 3× length of M2 section, M3 section 3.5× that of M2. Base of M_{3+4} and CuA fork slightly distal to level of base of M3 section. R, R_1, R_5, M_{3+4}, and CuA with setae dorsally and ventrally. **Leg:** Tibial spur formula 1:2:2. Spurs long, 4–5× tibia diameter. Mid and hind tibiae with bristles. Empodium absent; tarsal claws with one tooth. **Abdomen:** Tergites of abdomen setose. Seventh tergite 1.5× shorter than 6th, 8th is very short. Cerci 2-segmented, slightly shorter than 6th and 7th segments together. Apical segment round, basal one bacilliform, 2.5× apical.

MATERIAL: Holotype AMNH B-0125, female. Myanmar: Katchin, from amber mines near Myitkyina.

ETYMOLOGY: The species epithet is Latin word *cristatus*, meaning ‘‘tufted, plumed’’, in reference to the group of setae on the vertex.

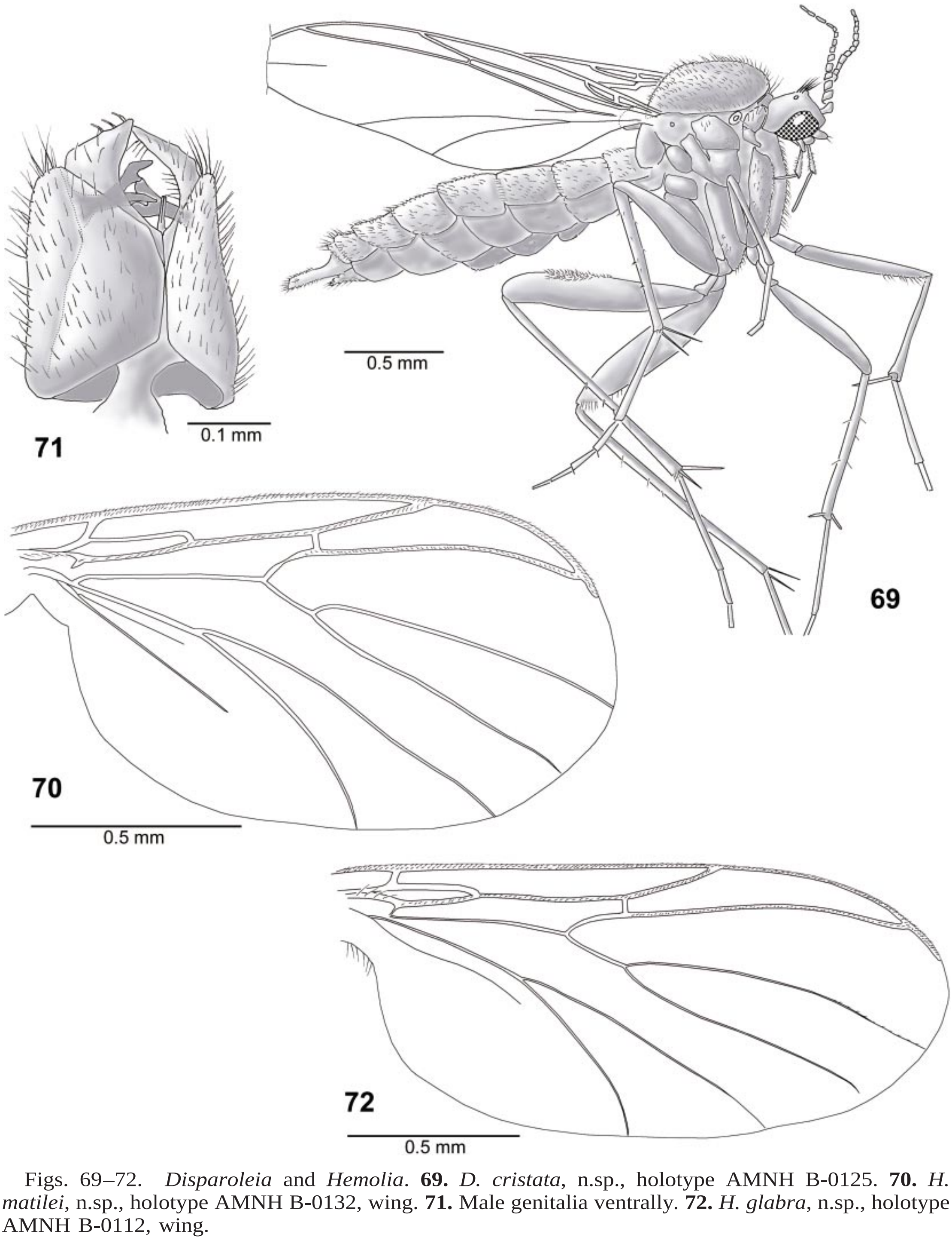
Hemolia, new genus

DIAGNOSIS: Three ocelli in straight line, middle one small, lateral ones not touching eye margin; wing membrane without macrotrichia; Sc short, ends at R; R_1 short, no more than 2× length of *r-m*; *r-m* short, oblique; M3 short; tibial setae in rows, mid and hind tibiae with inner spurs longer than outer one.

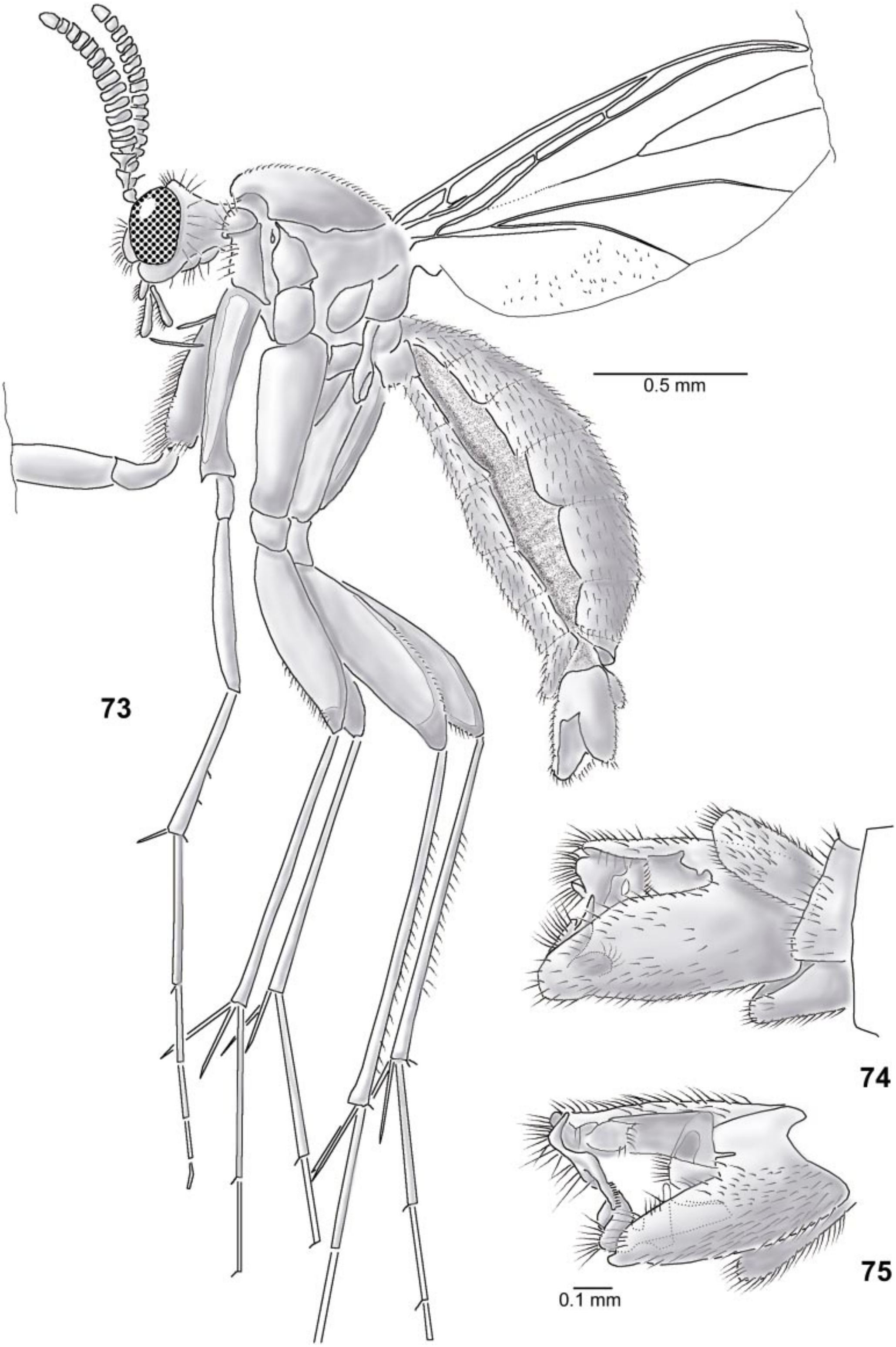
TYPE SPECIES: *Hemolia matilei*, n.sp.

ETYMOLOGY: The genus name is a feminine anagram of *Mohelia* Matile, 1978.

COMMENTS: The genus is close to *Mohelia* in the structure of the ocelli, and wing venation, and it differs in tibial spur length and details of male genitalia structure. It differs from *Mohelia* in having setae on the mediotergite, tibial setae in rows, mid and hind



Figs. 69–72. *Disparoleia* and *Hemolia*. **69.** *D. cristata*, n.sp., holotype AMNH B-0125. **70.** *H. matilei*, n.sp., holotype AMNH B-0132, wing. **71.** Male genitalia ventrally. **72.** *H. glabra*, n.sp., holotype AMNH B-0112, wing.



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tibiae with inner spurs longer rather than the outer ones, and C ending close to the tip of R_5; Sc is longer, R_1 longer than *r-m*; and M3 is short.

Hemolia matilei, new species

Figures 70, 71, Plate 7B

DIAGNOSIS: Scutum densely setose; laterotergites setose; Sc rather long, ends at the level of M_{3+4} and CuA fork base.

DESCRIPTION: Body length = 2.19 mm (holotype)/2.39 mm (paratype); wing length 1.49 mm (holotype)/2.21 mm (paratype). **Head:** Eyes setose. Occiput and frons densely setose. Three ocelli in straight line, middle one small; lateral one separated from eye margin by its own diameter. Flagellum 14-segmented, flagellomeres cylindrical; length of flagellomeres about equal to their width. Clypeus setose. Palpi 4-segmented, basal segment small, penultimate and apical ones situated preapically, antepenultimate with round sensory pit on inner surface. **Thorax:** Scutum with long setae not arranged in distinct rows. Laterotergites with long setae. Scutellum protruding, with 6 pairs of long setae. Antepronotun and proepisternum with long setae. **Wing** rather wide, membrane without macrotrichia. Costa ends beyond tip of R_5 at one-fifth length between tips of R_5 and M_1. Sc ends in R at the level of M_{3+4} and CuA fork base. R, R_1, and R_5 with setae dorsally. R_1 length 1.8× length of *r-m*. Crossvein *r-m* about the length of M3, with constriction in the middle. Length of M_1 and M_2 fork 5.3× length of M3. **Legs:** Tibial setae in rows. Tibial spur formula 1:2:2; mid and hind tibial spurs differ in length: inner spur 1.7× outer one. Fore leg basitarsomere shorter than tibia. **Abdomen** setose, with 6 visible segments, 7th and 8th ones small and retractable. Gonocoxites divided by complete suture ventrally. **Male:** Gonostyli large, triangular, flat, with inner, bilobed appendage. Aedeagus bilobate. **Female:** Eighth sternites triangular; 10th sternite with 4 dark, thick, wavy, blunt setae. Cerci 2-segmented, rounded, flat; apical segment 0.24× basal one, semicircular.

MATERIAL: Holotype AMNH B-0132, male; paratype AMNH B-0133a, female. Myanmar: Katchin, from amber mines near Myitkyina.

ETYMOLOGY: The species epithet is a patronym in honor of the late Professor Loïc Matile, a world authority on Sciaroidea, who was also very generous and helpful to both authors.

Hemolia glabra, new species

Figure 72, Plate 7C

DIAGNOSIS: Laterotergites bare; scutum almost bare, dark and shining, Sc meets R well before the level of base of M_{3+4} and CuA fork.

DESCRIPTION: Body length = 3.16 mm; wing length = 2.05 mm. **Head:** Occiput with short setae. Three ocelli in line, of the same size, distant from each other and from eye margin by two ocellus diameters. Eyes large, setose. Pedicel with round sensory organ. Flagellum 14-segmented, apical segment conical, secondarily divided. **Thorax:** Scutum almost bare; dark, shiny. Anterior parapsidal suture distinct. Scutellum and laterotergites bare. Mediotergite with a few fine setae anteroventrally. Mid and hind tibiae with inner spurs 1.5× longer than outer ones. **Wing** membrane without macrotrichia. Humeral vein at the level of MA. Costa ends beyond tip of R_5, at one-third the length between tips of R_5 and M_1. Sc short, ends at R. R_1 1.3× the length of *r-m*. Length of M3 about equal to length of *r-m*. Length of M_1 and M_2 fork 4.3× the length of M3. Base of M_{3+4} and CuA fork between tip of Sc and M3 base. **Legs:** Coxae without setae. Hind tibiae with posterior bristles. **Abdomen** with scattered setae. Cerci 2-segmented, apical segment conical, basal one cylindrical, 3× length of apical one. Gonocoxites 8 long, narrow, slightly curved, with long setae.

MATERIAL: Holotype AMNH B-0112, fe-

←

Figs. 73–75. *Protragoneura platycera*, n.sp. **73.** Holotype AMNH Bu-135. **74.** Male genitalia laterodorsally. **75.** Male genitalia lateroventrally.

male. Myanmar: Katchin, from amber mines near Myitkyina.

ETYMOLOGY: The species epithet is Latin for ''hairless, smooth'', in reference to the absence of thoracic setae and setulae.

Protragoneura, new genus

DIAGNOSIS: Small, dark gnats with antennae shorter than thorax, flagellomeres shorter than wide. Mesonotum densely covered with short trichia, with or without a few setae laterally. Sc short, free. Costa is not produced beyond the tip of R_5, which is long, curved, and almost reaching the tip of M_1. Fork of M_1 and M_2 shifted anteriorly, M_1 ends before wing apex. Base of M_{3+4} and CuA fork at the level of base of M3, in basal one-sixth of wing. M3 length about equal to that of M_1 and M_2 fork.

TYPE SPECIES: *Protragoneura platycera*, n.sp.

ETYMOLOGY: The genus name is a combination of the prefix *pro*- (Greek προ-, beforehand) and *Tetragoneura*. The name is feminine.

COMMENTS: Closest to *Tetragoneura* Winnertz, 1846, about 100 extant species of which are known from the Holarctic (17 spp.), Neotropical (ca. 60 spp.), and Australasian (23 spp.) regions. The new genus differs in having C not extended beyond the tip of R_5, RS2 section (small radial cell) long, and base of M_{3+4} and CuA fork very basal; M_1 and M_2 fork shifted anteriorly. Setation of mesonotum is also distinctive and separates the new genus from *Tetragoneura*.

Protragoneura platycera, new species

Figures 73–75, Plate 7D

DIAGNOSIS: As for genus.

DESCRIPTION: Body length = 2.49 mm (holotype)/2.39 mm (paratype); wing length = 1.63 mm (holotype)/1.93 mm (paratype). **Head** ovate, with row of long erect setae behind eye margin. Scape and pedicel subconical, with numerous apical setae, both black. Flagellum compressed laterally, flagellomeres transverse, widths 1.5–2.5× length, densely covered with short trichia. Clypeus setose. Three palpomeres seen; antepenultimate one swollen, obovate, length 2× width. Penultimate one attached to antepenultimate palpomere preapically; length 4× width, knoblike. Apical palpomere long and narrow. Length ratio 1:1.7:2.5. **Thorax:** Scutum densely covered with short erect trichia, bearing some setae laterally. Antepronotum and proepisternum with long strong setae. Anepisternum with deep cleft. Katepisternum without distinct excavation on anterior margin. Laterotergites, mediotergite bare. Metepisternum with few short trichia ventrally. **Wing** membrane with macrotrichia in distal and posterior part. Sc extremely short, free. All longitudinal veins except R base with setae. M3 reduced, can be traced by setae only. M_1 base reduced. Base of M_{3+4} and CuA fork weakened. Small radial cell length 7× width. Halters dark, with few short setae. **Legs:** Coxae and femora dark, densely setose, tibiae and tarsi yellowish. Hind tibiae with numerous posterior bristles. Tibial spurs 4× tibial diameter. **Abdomen** with 6 visible segments, 7th and 8th very short, retracted. Tergite 9 oval, short, covering the base of gonocoxites. Gonocoxites fused at base, massive, narrowing to apex in distal half. Gonostyli with long ventral lobe bearing a comb of short, knoblike setae; a somewhat shorter, dorsal, bare lobe and internal wide lobe with a row of curved bristles.

MATERIAL: Holotype AMNH Bu-135, male; paratype AMNH Bu-1076, male. Myanmar: Katchin, from amber mines near Myitkyina.

ETYMOLOGY: The species epithet is derived from *platy* (Greek πλάτυς, broad) and *cerus* (Greek κέρας, horn), in reference to the compressed antennae.

ANALYSES

LYGISTORRHINIDAE AND THE *HETEROTRICHA* GROUP

Figure 76

Forty-two morphological characters were coded for all known Mesozoic Lygistorrhinidae, *Palaeognoriste* sp. from Baltic amber, and exemplar species of all living genera of the family. The genera *Bolitophila*, *Chiletricha*, *Drepanocercus*, and *Paratinia* were used as outgroups. In previous studies Mycetophilidae was suggested to be a sister group to the Lygistorrhinidae, while Bolitophilidae was the sister group to those fami-

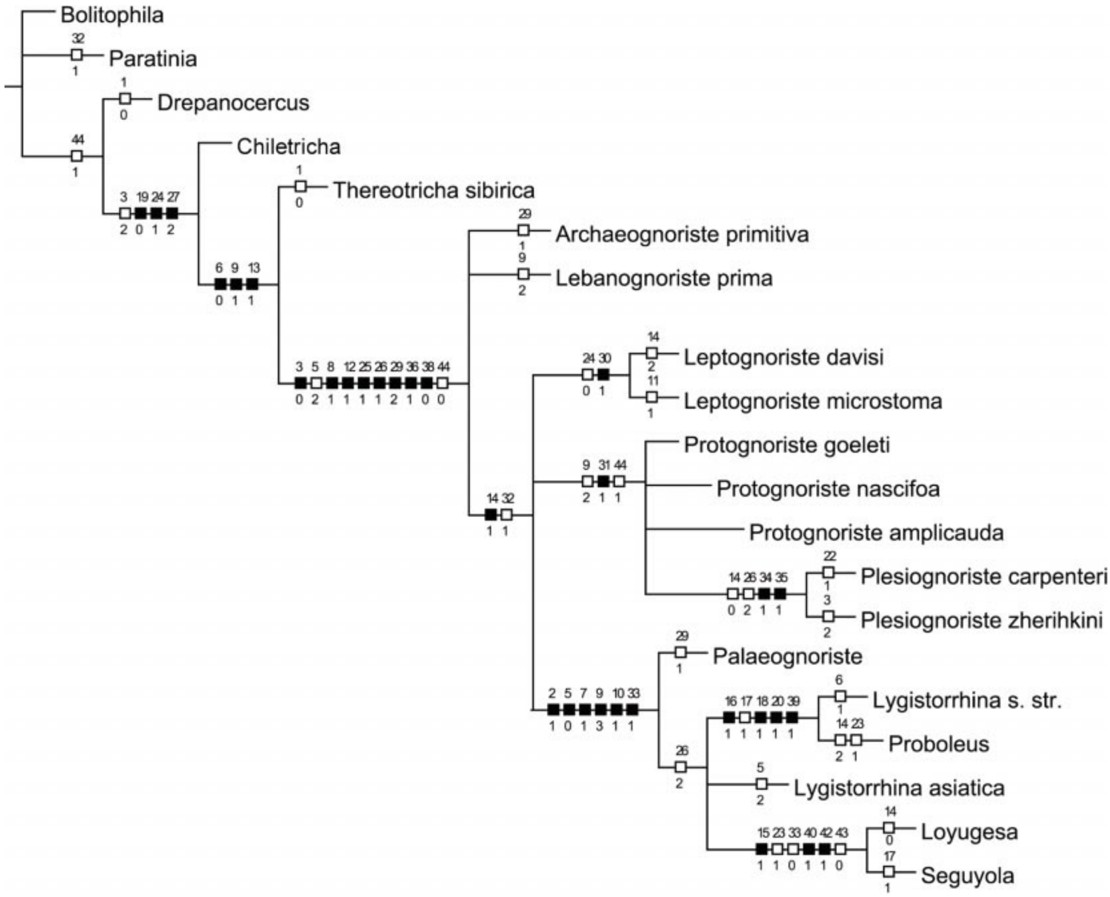

Fig. 76. Phylogeny of Lygistorrhinidae based on cladistic analisys of data presented in table 4 (length 84, CI 0.65, RI 0.81). ■ unreversed changes; □ homoplastic character transitions. The character number is indicated above the branch and the state change is indicated below. *Bolitophila*, *Paratinia*, *Drepanocercus*, *Chiletricha* and *Thereotricha* are the outgroup.

lies plus Sciaridae (Matile, 1990, 1997; Söli, 1997). The position of the *Heterotricha* group is disputed, showing affinities with Diadocidiidae, Sciaridae, and Mycetophilidae, as well as the extinct families Archizelmiridae and Mesosciophilidae (Grimaldi et al., 2003). A data matrix used for cladistic analysis is presented in table 4. Character descriptions are provided in table 5. Analysis of the data matrix using Winnona, (version 2.0; Goloboff, 1999) resulted in four trees of length 83, CI of 0.66, and RI of 0.82. The strict consensus of the trees is shown on figure 76.

A previous cladistic analysis of Lygistorrhinidae (Grimaldi and Blagoderov, 2001) included as the only fossil *Palaeognoriste*, considered a sister group to all living lygistorrhinids. The present analysis yielded the same topology for Recent genera: basal position of ‘‘*L. asiatica*’’, and sister-group relationships between *Seguyola-Loyugesa* and *Lygistorrhina* (with *Probolaeus* as a subgenus of *Lygistorrhina*). The Cretaceous genera *Archaeognoriste* and *Lebanognoriste* are at the base of the lygistorrhine clade and represent a basal, paraphyletic stem group. While having superficial similarity with the *Heterotricha* group of genera in venation pattern, they show strong apomorphies of Lygistorrhinidae in the structure of transverse veins, antennae, thorax, and male genitalia (characters 3, 8, 12, 25, 26, 29, 36, 38, 44). The other Cretaceous genera *Plesiog-*

TABLE 4
Data Matrix for Analysis of Lygistorrhinidae
Character descriptions presented in table 5.

	11111111112222222222333333333344444
	12345678901234567890123456789012345678901234
Bolitophila hybrida (Meigen, 1904)	10101100000000000020000000000000000000--0--00
Paratinia sp.	10101100000000000020100000110001000011-0--00
Drepanocercus ensifer Vockeroth, 1980	00101100000000000020100000110000000011-0---1
Chiletricha seminuda (Freeman, 1951)	10211100001000000000100100210000000011-0---1
†*Thereotricha sibirica* n.sp.	00201000102010000000110100210000000011-0---1
†*Archaeognoriste primitiva* n.sp.	10012001101110000000010111211000000110-0--10
†*Lebanognoriste prima* n.sp.	??01200120???00000??000111212000000110-0--10
†*Leptognoriste davisi* n.sp.	00012001102?12000010200011212101000110-0--10
†*Leptognoriste microstoma* n.sp.	??0120011011?11000010200011212101000110-0--10
†*Protognoriste amplicauda* n.sp.	10012001202?11000?10200111212011000110-0---1
†*Protognoriste goeleti* n.sp.	??012001202?11000010200111212011000110-0---1
†*Protognoriste nascifoa* n.sp.	??012001202?11000010200111212011000110-0---1
†*Plesiognoriste carpenteri* n.sp.	10012001202??0000?10210112212011011110-0---1
†*Plesiognoriste zherikhini* n.sp.	10212001202?10000?10200112212011011110-0---1
†*Palaeognoriste* sp.	11010011312111000020210111211000-100110000010
Lygistorrhina asiatica Senior-White, 1922	01012011312111000020210112212000-100110001010
Lygistorrhina s.str.	11010111312111011111210112212000-100110101010
Probolaeus sp.	11010011312112011111211111221200-100110101010
Loyugesa khuati Grimaldi and Blagoderov, 2001	-1010011312110100020211112212001000110011100
Seguyola sp.	-1010011312111101020211112212001000110011100

noriste, *Protognoriste*, and *Leptognoriste* occupy intermediate positions between primitive and recent lygistorrhinids. Interestingly, although these genera do not form a monophyletic entity, all species have only one vein in the medial fork preserved. The independent loss of a median vein in various Mesozoic lygistorrhinids suggests rapid radiation of the family in the beginning of its history, followed by replacement of Mesozoic groups by recent ones.

MYCETOPHILIDAE S.S.

Figures 77–79

Sixty-one characters were coded for 38 species representing three main lineages of Cretaceous fungus gnats: Sciophilinae (including 3 recent and 3 fossil species), Leiinae (3 recent and 13 fossil species), and Gnoristinae (9 recent and 7 fossil species). *Macrocera* and *Bolitophila* were used as outgroups. A data matrix used for cladistic analysis is presented in table 6. Character descriptions are provided in table 7.

Winnona (version 2.0; Goloboff, 1999) was used to search for the most parsimonious tree (MPT). An heuristic search (tree bisection-reconnection), cutting trees up to four points, yielded eight MPTs of length 311, CI of 0.21 and RI of 0.51. The low indices of the trees are due to the very homoplastic dataset, reflected by numerous cases of independent occurrence of structures. The strict consensus of these MPTs (fig. 77a) is an unresolved bush for Gnoristinae, with Leiinae paraphyletic with respect to Sciophilinae. Such an unexpected result can be explained by including in the parsimony analysis two peculiar fossil genera, *Lecadonileia* and *Disparoleia*, which share some characters (5, 10, 17, 18) with Sciophilinae. Nonetheless, in all the analyses conducted, *Lecadonileia* and *Disparoleia* nested within Leiinae, having synapomorphies with other genera of the subfamily (e.g., characters 12, 29, 47, 50, 51, 52). Due to taxon sampling and the limited number of characters used, the most parsimonious result hypothesized synapomorphies of Sciophilinae as reversals. The alternative, when characters 5, 10, 17, and 18 appear independently in different clades, is less parsimonious by two steps (see below). In-

TABLE 5
Characters Used in Cladistic Analysis of Lygistorrhinidae
All characters are nonadditive.

1. Position of ocelli: in triangle (0); in line (1)
2. Median ocellus: normal (0); reduced or absent (1)
3. Compound eyes: no incision (0); slight emargination (1); extreme emargination (2)
4. Gena: present (0); absent, mouthparts somewhat inverted (1)
5. Scape and pedicel: cylindrical (0); rounded (1); turbinate (2)
6. Scape and pedicel: longer than 1st flagellomere (0); shorter than 1st flagellomere (1)
7. Dorsal bristles on flagellomere: absent (0); present (1)
8. Pedicel: bears hairs or bare (0); bears bristles apically (1)
9. Number of palpomeres: 5 (0); 4 (1); 3 or 2 (2); 1 (3)
10. Proboscis consists of 5 long parts: no (0); yes (1)
11. Proepimeron: contacts episternum ventral to episternal suture (0); contacts episternum slightly ventral to suture (1); contacts episternum at suture (2)
12. Anepimeron: free (0); fused to katepisternum (1)
13. Metepisternum: without dorsal incision (0); with dorsal incision (1)
14. Laterotergite: bare (0); setae latero-ventral (1); row of setae (2); trichia (3)
15. Scutum: normal (0); dome-shaped (1)
16. Laterotergite: normal (0); flap-like (1)
17. Scutum: normal position (0); well anterior to fore coxa (1)
18. Hind coxa: simple (0); with proximal concavity (1)
19. Anterodorsal angle of metepisternum: closer to ventral surface than is posteriodorsal angle (0); closer to dorsal surface than is posteriodorsal angle (1); at the same level (2)
20. Metepisternum: normal (0); extends dorsally above lower level of laterotergite (1)
21. Coxae: about equal (0); fore shorter than others (1); fore longer (2)
22. Hind femur and tibia: normal (0); long and inflated (1)
23. Mid tibia: with 2 spurs (0); with 1 spur (1)
24. Costa runs after R_5: just a little (0); a lot (1)
25. R1: long (0); short, ~1/2 wing length (1)
26. RS1: oblique (0); transverse, short (1); reduced or absent (2)
27. R2+3: short, distally (0); short, proximally (1); absent (2)
28. M1 section: present(0); absent (1)
29. M_1 and M_2 fork base: normal (0); reduced (1); absent (2)
30. M_1 vein: present (0); absent (1)
31. M_2 vein: present (0); absent (1)
32. M_{3+4} and CuA fork base: sessile, distal (0); sessile, basal (1); distal (2)
33. M_{3+4} and CuA fork base: complete (0); reduced (1)
34. CuA: curved evenly (0); kinked (1)
35. R_1 and R_5: distant (0); closed (1)
36. *r-m*: distad of *tb* (0); aligned with *tb* (1)
37. *tb* and M2: independent (0); fused to one line (1)
38. *tb*+M2: subvertical or reduced (0); subhorizontal (1)
39. Palpi length: nearly equal to labella length (0); palpi shorter than labella (1)
40. Antennae: with 14 flagellomeres (0); with 12 flagellomeres (1)
41. Anal cell: present (0); greatly reduced or absent (1)
42. Tergite IX: with tuft of dense, spicule-like setae (0); with fine scattered setae (1)
43. Gonostyli: stout, W:L ratio 2–2.5× (0); slender, W:L ratio 3.5–5× (1)
44. Gonostyli: simple, cylindrical (0); complex shape (1)

terestingly, analyzing the dataset with WinXpiwe (version 1.3; Goloboff, 1997), a program intended for analysis of homoplastic data (see Goloboff, 1993), yields a topology with Sciophilinae and Leiinae each as monophyletic (fig. 77b). The same result occurs when *Lecadonileia* and *Disparoleia* are excluded from the analysis.

Since the monophyly of Sciophilinae and Leiinae is strongly supported (Söli, 1997), the final analysis was conducted in Winnona with Sciophilinae and Leiinae constrained as monophyletic. It resulted in 11 trees of length 313 (only two steps longer than the MPTs found), CI of 0.24 and RI of 0.58. The strict consensus tree (fig. 78) of length 333, CI of 0.22 and RI of 0.54 again indicates Gnoristinae as basal and paraphyletic to Sciophilinae and Leiinae. All the fossil species assigned to extant genera except *Synapha longistyla* form monophyletic clades with recent species. *Pseudomanota* is closely allied with *Paratrizygia* and probably represents a stem group to the *Azana* group of genera (Matile, 1998). *Drepanocercus* and *Gregikia* are at the base of mycetophilids. *Tetragoneura* and *Ectrepesthoneura* should be classified in Leiinae, not Gnoristinae, as was suggested by Väisänen (1986). On the other hand, his conclusion about *Syntemna*, traditionally placed in Sciophilinae, is probably right, for on the cladogram it is nested within Gnoristinae.

In general, including fossils into an anal-

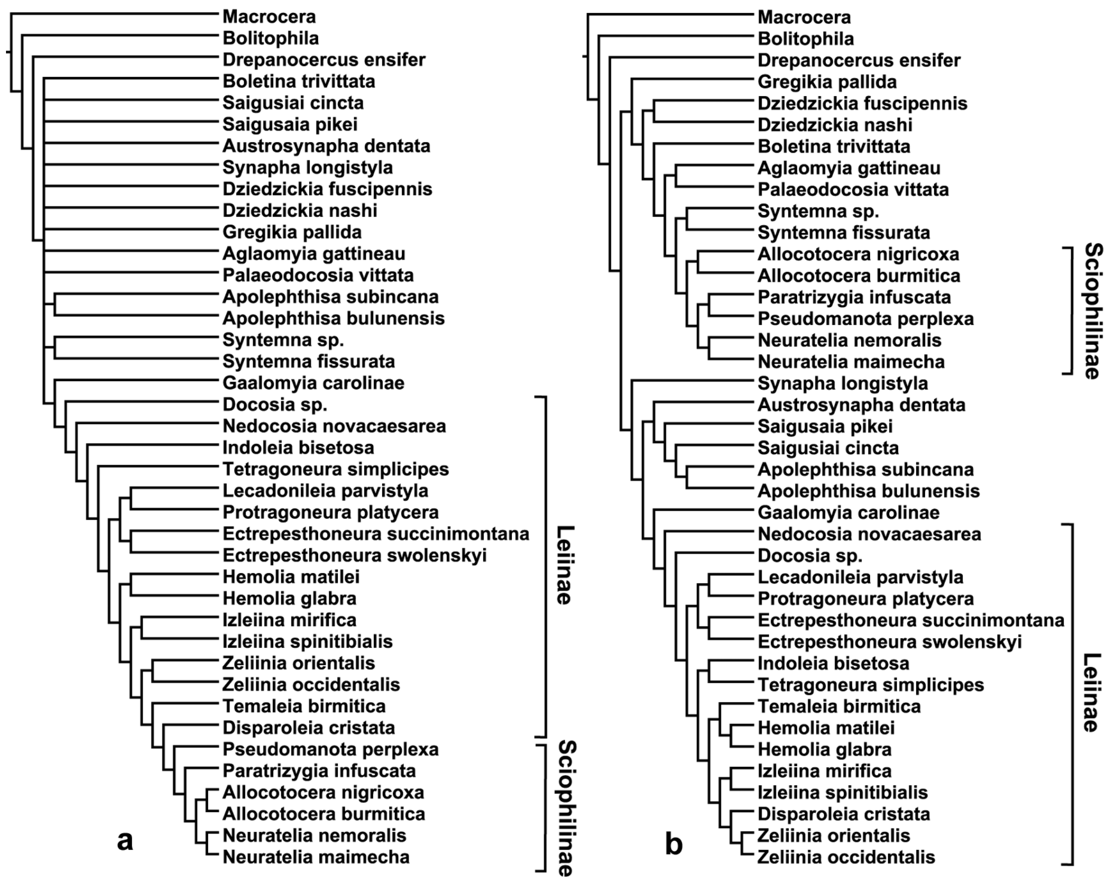

Fig. 77. Unconstrained cladistic analyses of Mycetophilidae using Winnona (a) and WinXpiwe (b). **a.** Strict consensus tree of eight equally parsimonious trees (length 359, CI 0.21, RI 0.51). **b.** Fittest tree (total fit = 3056.9, concavity 3).

ysis dramatically affects results (fig. 79). To a large extent this effect is a result of exellent preservation in amber, which has preserved characters virtually completely. The topology of the MPTs is particularly affected, probably due to extensive homoplasy. Homoplasious characters in plesiomorphic fossils not only decrease resolution and increase length of the tree but make taxon definitions diffuse. Nonetheless, including fossils in a cladistic analysis has proven to be extremely useful (Gauthier et al., 1988), and this study is an another example of that. First, fossils are the only way to establish existence and position of entirely extinct lineages, like Mesozoic lygistorrhinids or leiines from Burmese amber. Secondly, they allow the identification of stem groups for extant lineages. Basal taxa have a fundamental influence on topology. This is especially true for ancient groups that had a rapid initial diversification, where unusual combinations of characters occur.

DISCUSSION

PHYLOGENY

A systematic review of Bibionomorpha and Sciaroidea was not the purpose of this work and is well beyond the scope of our project. We concur with the composition and evolutionary history of the infraorder as established by Shcherbakov et al. (1995), and also grant that fossils afford unique insight into sciaroid phylogeny.

The traditional nomenclature of venation

TABLE 6

Data Matrix for Analysis of Gnoristinae, Sciophilinae, and Leiinae

Character descriptions presented in table 7.

	11111111112222222222333333333344444444445555555555666
	1234567890123456789012345678901234567890123456789012345678901
Macrocera nebulosa Coquillett, 1901	210000001000100000000000100130-000000010100000010000100000000000
Bolitophila hibrida (Meigen, 1904)	0000000000000000000000001010000010000000100212011020010000000
Drepanocercus ensifer Vockeroth,1980	0000000110000000000110102111030010001010001010000200000000000
†*Gregikia pallida* n.sp.	0000000110110000000000?02?0100100?0?1?1001111100120000000000
Dziedzickia fuscipennis (Coquillett, 1905)	0001000110010001001000002001001000001010001011001200000000000
†*Dziedzickia nashi* n.sp.	0001000110010100001000002001001000001010001011000200000000000
Boletina trivittata (Meigen, 1818)	000100011001000000000001031110210000101-1011010011000000000100
†*Synapha longistyla* n.sp.	0110000110010000000000002001021010000000010130?000200000000000
†*Gaalomyia carolinae* n.sp.	00010001100000000010000031010110000101 0-2000100002001000000000
Aglaomyia gattineau Vockeroth, 1980	1011000100100000000000003001001000000000-2011000011100000000100
Palaeodocosia vittata (Coquillett, 1901)	1011000110110100001000003001001000000101-2010110001000000000100
Austrosynapha dentata Freeman, 1951	0110000110010000000000003001021000010 10-2010110002001000000000
Saigusaia cincta (Johannsen, 1912)	0010000110010001000000003111011000011 11-2012110002001000000100
†*Saigusaia pikei* n.sp.	0010000110010001000000003011021000010 10-20101?0002001000000000
Syntemna sp.	1011000110010100101011102101011000000101110001100010010000000 0
†*Syntemna fissurata* n.sp.	?011?0011?010100101001102101011000000101110100200 0?00001000000
Apolephthisa subincana (Curtis, 1837)	1010000110010101000110102121011010011110001200000200100000100
†*Apolephthisa bulunensis* n.sp.	1010?001100?0?0?0001101021?1011010011110111 01?000200100000000
Paratrizygia infuscata Freeman, 1951	1011100111000110110111103121011111 1--11-0110200112010001000 10
†*Pseudomanota perplexa* n.sp.	1011111111100000112111112121011110001110111011011211000000010
Allocotocera nigricoxa Freeman, 1951	111110011100111111011110311101100110101-1002000012100000000000
†*Allocotocera burmitica* n.sp.	1111?0011?00011111011110311101100110101-10020?0012100000000000
Neuratelia nemoralis (Meigen, 1818)	111110011100011011011010313101110001111-1002010011000000000010
†*Neuratelia maimecha* n.sp.	111110011100011011011010313101110001111-11?2010011?000000000 10
Docosia sp.	001100111000000000010000130011110000111 1-1011001000011000000000
†*Nedocosia novacaesarea* n.sp.	001101011000000000010001031011110000111 1-1010011010011100000000
Indoleia bisetosa (Edwards, 1928)	1010010110100100000100113121101 0-010101-1012011110111000 00100
Tetragoneura simplicipes Freeman, 1951	001101111000000000020000130211110000010 1-2112011101011000000000
†*Lecadonileia parvistyla* n.sp.	011111111100010010200111312111101111111-1013021001210000000000
†*Protragoneura platycera* n.sp.	0011001110000001102001112121101001111110211302111221000000000
†*Ectrepesthoneura succinimontana* n.sp.	0101010110000000001110112101130001111110210001110101000000001
†*Ectrepesthoneura swolenskyi* n.sp.	???1010110?0000000100011210113000111111021001?11010?001000001
†*Disparoleia cristata* n.sp.	011100111110100011000111312111110000000-21110011021110000001 0
†*Temaleia birmitica* n.sp.	001101011000011010000011312111100000000-21000011122101000000 0
†*Hemolia matilei* n.sp.	001101011000010000100001310110100000000-20130011110100000001 00
†*Hemolia glabra* n.sp.	001101011000001000100011310110100000000-201310100?110000001 0-
†*Zeliinia orientalis* n.sp.	011101011000000000200011312113110000000-11101?111221000012-10
†*Zeliinia occidentalis* n.sp.	011101011000000000200011312113010000000-21101?111221000110010
†*Izleiina mirifica* n.sp.	0011010110000000000000001131211-111000000-1110111-01?101010??10
†*Isleiina spinitibialis* n.sp.	0011010110??00000000000001131211-111000000-11101?1-010?000100010

in Sciariodea is controversial and somewhat misleading. Fortunately, early fossils provide a strong basis for vein homology (Rasnitsyn, 1980; Shcherbakov et al., 1995), since they show intermediate conditions. The short vein of the radial sector is usually thought to be R_4 (Chandler, 2002). There are four veins in the radial sector of the dipteran ground plan. All representatives of Bibionomorpha s.l. (including Axymyiiformia and Anisopodiformia of Shcherbakov et al., 1995) have no more than three radial veins posterior to R_1, which can be interpreted as R_2, R_3, and R_{4+5} or R_{2+3}, R_4, and R_5 according to the authors' concepts of vein homology. We prefer the second scheme, assuming that a long vein

TABLE 7

Characters Used in Cladistic Analysis of Gnoristinae, Sciophilinae, and Leiinae

All characters are nonadditive.

1. Scape and pedicel: subequal (0); scape larger than pedicel (1); scape much larger than pedicel
2. Flagellum: as wide as pedicel (0); narrower than pedicel (1)
3. Pedicel: bare (0); setose (1)
4. Face: bare (0); setose (1)
5. Lower margin of face: straight or polygonal (0); evenly concave (1)
6. Head and thorax connection: narrow (0); head flat behind; (1)
7. Antennal attachment: normal, face small (0); above the middle of the head (1)
8. Antepronotum: bare (0); setose (1)
9. Proepisternum: bare (0); setose (1)
10. Proepimeron: normal (0); narrow, rod-like (1)
11. Katepisternum: height more than width (0); height nearly equal to width (1)
12. Secondary episternal suture: absent (0); present (1)
13. Anepisternum: bare (0); setose (1)
14. Laterotergites: bare (0); setose (1)
15. Megiotergite: bare (0); setose (1)
16. Metepisternum: bare (0); setose (1)
17. Wing membrane vestiture: with microtrichia (0); with micro- and macrotrichia (1)
18. Sc base: bare (0); setose (1)
19. Sc: long, ends at C (0); ends at R (1); short, free (2)
20. Sc ventrally: bare (0); setose (1)
21. Sc dorsally: bare (0); setose (1)
22. Humeral vein: located proximal to MA (0); distal to MA (1)
23. R_1 ventrally: bare (0); setose (1)
24. R_1 to wing length: long, ca. 0.7–0.8× (0); short, less than 0.6× (1)
25. R_{2+3}: free (0); distally (1); proximally (2); absent (3)
26. R_5 ventrally: bare (0); setose (1)
27. Sc_2: apical (0); paramedial (1); absent (2); basal (3)
28. *tb*: transverse, free (0); fused to M2, horizontal (1)
29. *r-m*: oblique, short (0); longitudional, long(1)
30. M_{3+4} and CuA fork base: basally of *r-m* base (0); at *r-m* level (1); distally (2); at the base of wing (3)
31. M2:(*tb*) runs into M_{3+4} (*m-cu*) (0); M_{3+4} and CuA stem (1)
32. Vein M_1: complete (0); reduced basally (1)
33. Vein M_{3+4}: complete (0); reduced basally(1)
34. Section M2 ventrally: bare (0); setose (1)
35. Section M2 dorsally: bare (0); setose (1)
36. Vein M_1 ventrally: bare (0); setose (1)
37. Vein M_1 dorsally: bare (0); setose(1)
38. Vein M_{3+4} ventrally: bare (0); setose (1)
39. Vein M_{3+4} dorsally: bare (0); setose (1)
40. Section RS2: longer than RS1 (0); shorther than RS1 (1)
41. Sc apex: beyond RS base (0); before RS base (1); before *r-m* base (2)
42. Section M3: normal (0); weak or reduced (1)
43. 7th abdominal segment: normal (0); reduced (1)
44. Scutum vestiture: 5 rows of setae (0); acrostichal setae absent(1); acrostichal and dorsocentral setae absent (2); lateral, acrostichal and dorsocentral setae absent (3)
45. Short irregular setae on scutum: present (0); absent (1)
46. Anepisternal suture: horizontal (0); declines posteriorly (1); declines anteriorly (2)
47. Vein R_1 ratio to *r-m*: long, more than 3× *r-m* (0); short, ca. 0.3–3× *r-m* (1)
48. Vein M_1 reaching wing margin: beyond wing apex (0); at or before wing apex (1)
49. Costa: produced beyond R5 tip for a long distance (0); just a little (1)
50. Palpi: 5-segmented (0); 4-segmented (1); 3-segmented (2)
51. Tibial spurs: normal, 2–3× the tibia diameter (0); long, 3.5–4× (1); short, 1–1.5× (2)
52. Incision on katepisternum at the proepimerone apex: absent (0); present (1)
53. Sternite I of abdomen: setose (0); bare (1)
54. Tibial bristles: present (0); absent (1)
55. Sensory pit on mid tibia: absent (0); present (1)
56. Vein M_1: present at least apically (0); reduced completely (1)
57. Vein M_2: present at least apically (0); reduced completely (1)
58. Tibial spurs: 1:2:2 (0); 1:1:2 (1); 1:1:1 (2)
59. Outer and inner tibial spurs: the same length (0); of different length (1)
60. M fork base: normal (0); reduced (1)
61. Long setae on scutum: curved backward (0); curved forward (1)

(R_4) is less likely to be atrophied and lost than is a shorter vein (R_2).

Basal Bibionomorpha (Procramptonomyiidae, Protorrhyphidae) have crossvein *r-m* situated between the bases of R_{2+3} and R_4. The earliest Bibionomorpha have two opposing tendencies in the transformation of radial veins. In one group (for example, Triassic *Yala*), the base of the forks of radial veins are shifted basally, so bases of the second (R_{2+3}) and the third (R_4) radial veins are very close, and the veins may originate even before the base of *r-m* crossvein. These veins are parallel and close to each other along the whole length, which makes fusion of these veins more likely. The fusion is completed,

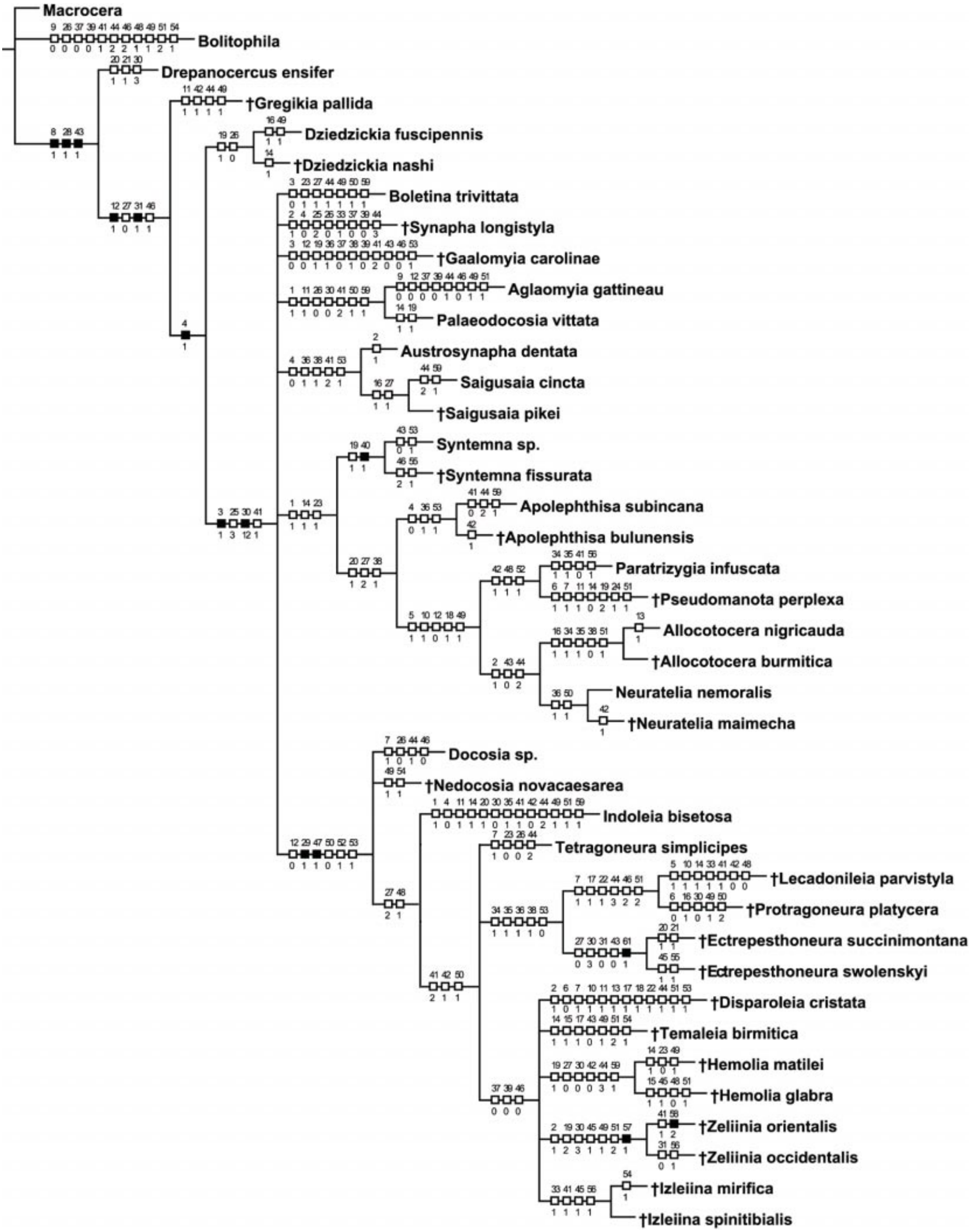

Fig. 78. Phylogeny of Mycetophilidae based on cladistic analysis of data presented in table 6 (length 342, CI 0.22, RI 0.53). ■ unreversed changes; □ homoplastic character transitions. The character number is indicated above the branch and the state change is indicated below. *Macrocera* and *Bolitophila* are the outgroups.

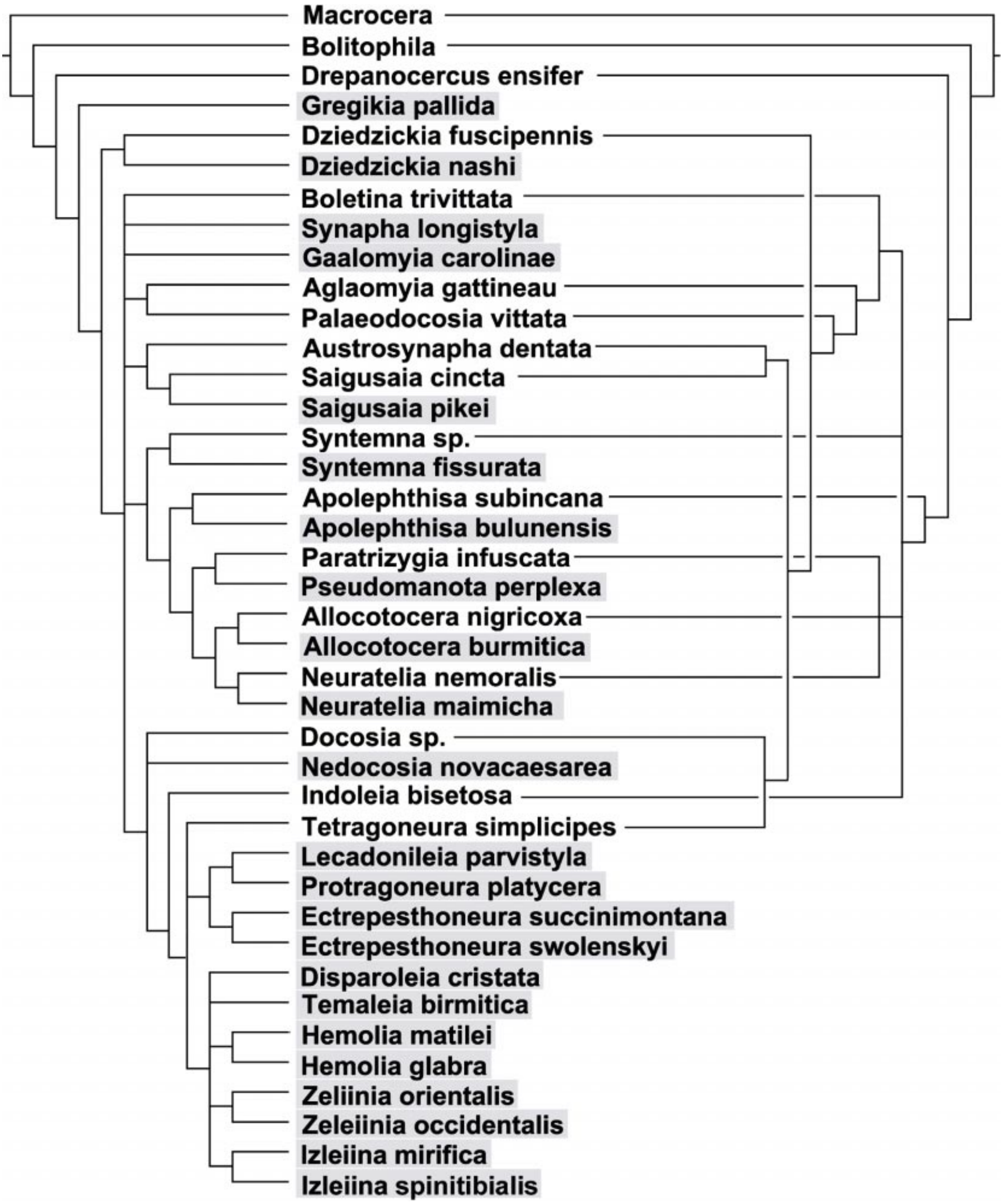

Fig. 79. Comparison of topologies of trees for fossil and recent species (right) and recent species only (left). Tree on the right is the same as on figure 77. Tree on the left is a strict consensus of 6 MPT (length 157, CI 0.40, RI 0.43).

for example, in Pachyneuridae (where veins are fused basally) and Cramptonomyiidae (apically). Thus, a fore fork in the radial sector of Pachyneuridae, Axymyiidae, and Perissommatidae should be considered as R_{2+3} + R_4.

The other group of Bibionomorpha has a distal shifting of the bases of these forks, accompanied by shortening and reduction of R_4 (e.g., *Alinka*, or an undescribed Protorrhyphidae from the Upper Triassic of North America) and shifting of the base of R_{2+3} close to the base of *r-m* (*Complecia*, *Eoditomyia*) or beyond it (*Alinka*, *Eomycetophila*). Protopleciidae, a presumed ancestor of Sciaroidea, has only one long intermediate vein in its radial sector originating distad of the base of crossvein *r-m*. Having evidence of distal shifting of the base of the radial veins in the earliest history of the Bibionomorpha, and considering that R_4 as a shorter vein is more likely be reduced than a long R_{2+3}, we prefer to homologize an intermediate vein in the radial sector of Sciaroidea with R_{2+3}. A transformation series would thus include: from two long veins (in Procramptonomyiidae, Protorhyphidae, and Paraxymyiidae [Paraxymyiinae]), to one long and one short vein (Paraxymyiidae [Eomycetophilinae] and Eodytomyiidae), to one long vein proximad (*Crosaphis*) or distad of *r-m* (Protopleciidae, Pleciofungivoridae, Bolitophilidae, Ditomyiidae, and Keroplatidae), to finally a short crossvein joining R_1 or absent (all other Sciaroidea) (figs. 80, 81).

The posterior fork of Sciaroidea wings is sometimes denoted as CuA_1 and CuA_2 or M_4 + CuA_1 and CuA_2. However, the fore vein in the posterior fork is undoubtedly a remnant of the posterior vein in medial sector, namely M_4 (fig. 80). With reduction of the discal cell and M_3 (Heterorhyphidae, Paraxymyiidae) and basal displacement of *tb* and M stem (Mesosciophilidae, *Heterotricha* group, Mycetophilidae), M_4 lost contact with the base of M. Vein homology in Diptera was thoroughly discussed by Shcherbakov et al. (1995).

The monophyly of Sciaroidea is supported by several synapomorphies (Matile, 1997), including loss of vein R_4, abbreviation of the costa at the apex of the wing, long coxae, and narrow insertion of the abdomen (reversed in Sciaridae). The last character (Matile, 1990: 386; 1997: 300) was proposed presumably to separate conditions observed in Sciaridae and some representatives of the *Heterotricha* group, when the mesothoracic phragma is greatly enlarged and strongly projected into the abdomen. Actually, the narrow insertion of the abdomen, coupled with reduced phagma, is limited to Mycetophilidae, Keroplatidae, and Lygistorrhinidae, and apparently developed independently. Other Sciaroidea have a phragma that is somewhat developed, though not projecting deeply into the abdomen (Chandler, 2002). Chandler (2002) hypothesized that a large phragma protruding into the abdomen may be a synapomorphy of Sciaridae and the *Heterotricha* group (except *Pterogymnus* and *Sciaropota*). Unfortunately, the structure of the phagma is rarely seen on fossil specimens, even ones in amber, so in most cases we can only speculate on it. That is why this undoubtedly important phylogenetic character was not included in the analyses. However, it is clear that at least in Lygistorrhinidae, acquiition of a narrow insertion of the abdomen and reduced phragma was not a brief event: early representatives have the plesiomorphic condition (*Lebanognoriste*, *Protognoriste*, *Plesiognoriste*) as well as the apomorphic one (*Archaeognoriste*, *Leptognoriste*). It is possible that the two latter genera constitute a monophyletic group with recent Lygistorrhinidae.

Reduction of the stem of M (section M1 of Kovalev [Kalugina and Kovalev, 1985]), proposed as a synapomorphy of Sciaroidea, actually occurred independently many times in the history of the group. This section is present in Protopleciidae, Pleciofungivoridae, Bolitophilidae, some Mesosciophilidae, and Keroplatidae. If we accept the reduction of the section M1 as a synapomorphy of Sciaroidea, the superfamily becames polyphyletic or leads to an assumption of loss and numerous independent restorations of the vein, which is highly improbable. Other synapomorphies mentioned above combine recent families of Sciaroidea (Ditomyiidae, Diadocidiidae, Keroplatidae, Bolitophilidae, Mycetophilidae, Lygistorrhinidae, Sciaridae) with several extinct families (Antefungivoridae, Archizelmiridae, Eoditomyiidae, Me-

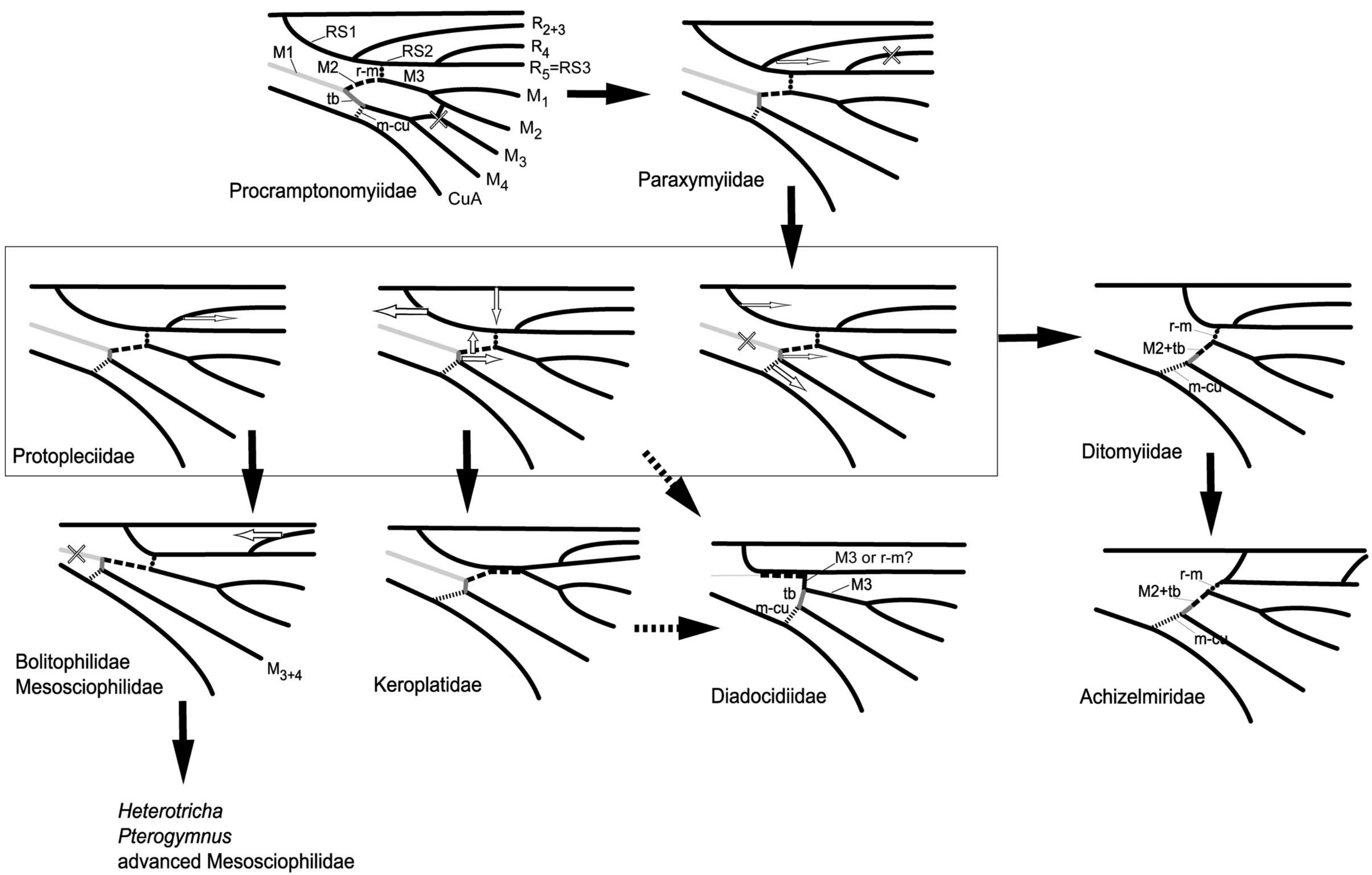

Fig. 80. Scheme of wing venation of different taxa of Bibionomorpha and possible ways of vien transformation.

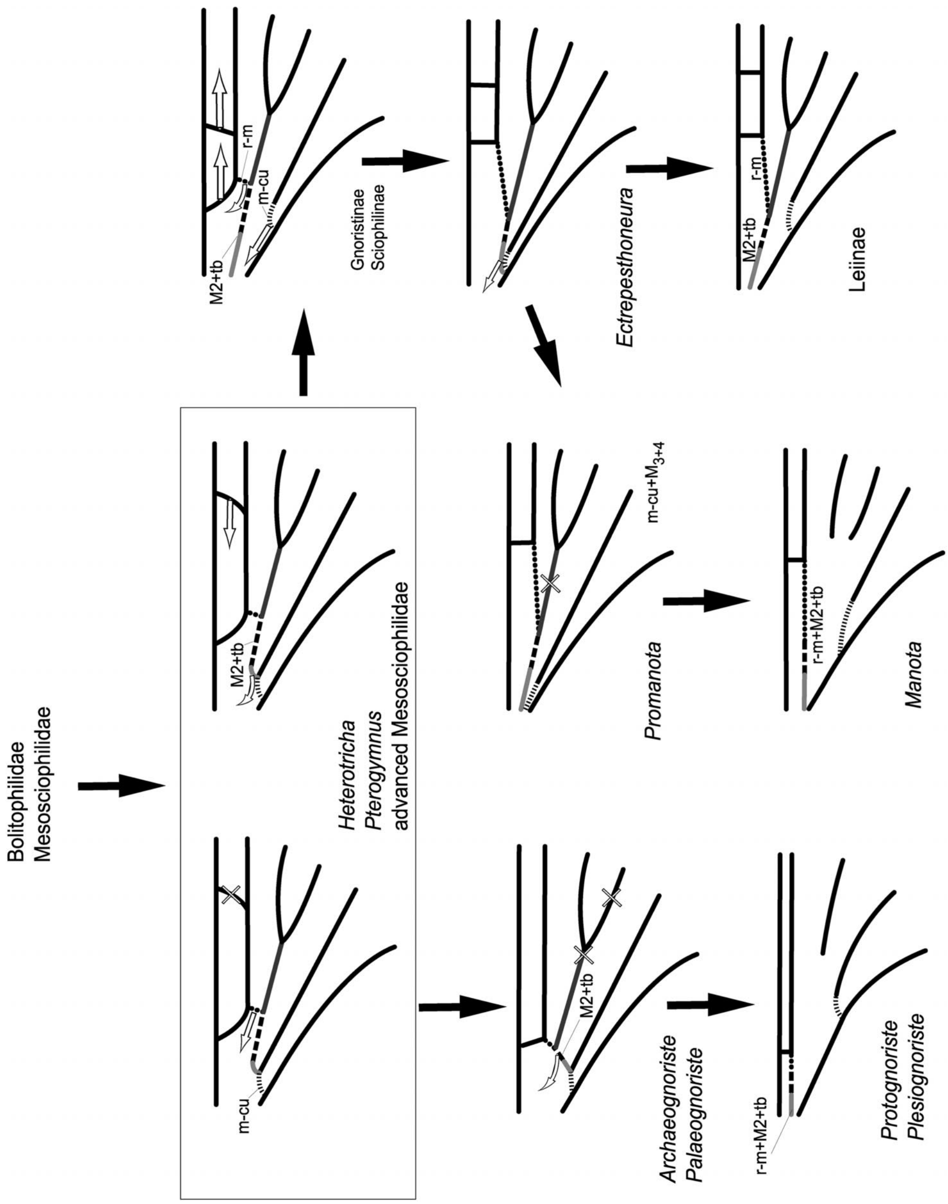

Fig. 81. Scheme of wing venation (continued).

sosciophilidae, Pleciofungivoridae, and Protopleciidae) into one monophyletic group with Cecidomyiidae, probably, as a sister group to all others.

The phylogeny of recent families of Sciaroidea was proposed by Matile (1990, 1997) based on imaginal and preimaginal characters, to which extinct groups could be added. Ditomyiidae has been proposed as a sister group to all other living Sciaroidea except Cecidomyiidae; however, no Ditomyiidae are known in the fossil record before the Eocene (Evenhuis, 1994). *Eoditomyia primitiva* Ansorge from the Lias of Germany possibly represents a stem-group ditomyiid (Ansorge, 1996). The presence of R_4 in Eoditomyiidae may be evidence for an independent origin of Ditomyiidae from Paraxymyiidae, which would make Sciaroidea polyphyletic. In any case, discovery of *Eoditomyia* allows us to propose a Mesozoic, possible Jurassic, origin of true, crown-group Ditomyiidae, despite the absence of fossils.

Matile (1997) provided the only synapomorphy for Diadocidiidae + Keroplatidae, which is the absence or closure of larval abdominal spiracles. Chandler (2002) argued that the abdominal spiracles may be secondarily lost in *Diadocidia* due to the tube-living habit of larvae. The other putative synapomorphy of Diadocidiidae + Keroplatidae might be the proximal position of the base of RS with respect to *tb*. The same condition is observed in *Australosymmerus*, but this genus is not considered as basal (Munroe, 1974). All other groups of Sciaroidea have (at least in the ground plan) crossvein *tb* proximal to or at the level of the base of RS. The vertical alignment of veins *r-m*, M2, and *tb* in Diadocidiidae and Ditomyiidae, though similar in shape, probably appeared independently. Rigidity of the wing is provided by a long R_1 in Ditomyiidae and by the lengthened base of RS in Diadocidiidae. Thus, crossvein *r-m* was pulled basad with the base of RS in Diadocidiidae, while in Ditomyiidae crossveins *r-m*, *tb*, and *m-cu* were pulled distad together with the base of RS.

Bolitophilidae are represented by only one genus in the Recent fauna. Another genus—*Mangas* Kovalev—was described from the Lower Cretaceous of Mongolia, and close relatives were reported from the Lower Cretaceous of Transbaikalia (Kovalev, 1986). Chandler (2002) doubted that the position of *Mangas* was within Bolitophilidae, although he admitted another undescribed but figured specimen could belong to the family. He wrote (2002: 136) ‘‘There is nothing to indicate that it is not allied to *Heterotricha*’’. One of us (V.B.) had the opportunity to study the type of *M. exilis* in the collection of PIN. Despite obscure venation, Kovalev’s drawing seems to be accurate and some characters are apparent: long curved base of RS is situated distally, not basally; *r-m* is vertical, not oblique; section M2 (not *tb*, as noted on Chandler’s fig. 92) is long and longitudinal (not oblique), although not apparent basally due to preservation; and there is a short section M3 (M_{1+2} stem) (it is much shorter than M_1 and M_2 fork and almost the same length as visible part of section M2). This combination of characters is not known in the *Heterotricha* group (where the base of Rs and crossvein *r-m* are not shifted distally, and section M2 is much shorter than section M3), but it is characteristic of Bolitophilidae. Bolitophilidae and the *Heterotricha* group are a relicts of Mesozoic sciaroids like Protopleciidae and Pleciofungivoridae, though the relationships between bolitophilids and genera allied to *Heterotricha* are not perfectly apparent.

Mycetophilidae and Lygistorrhinidae are sister groups when only Recent taxa are analyzed. Including fossils in the analysis indicates an independent origin of Bolitophilidae, Mycetophilidae, Lygistorrhinidae, and possibly Sciaridae from within the Mesosciophilidae-*Pterogymnus*-*Heterotricha* complex. All these recent families as well as extinct Archizelmiridae share synapomorphies, which are also found in Mesosciophilidae and *Heterotricha* group. *Pterogymnus* Freeman is probably related to Mesosciophilidae (Chandler, 2002). One of the *Heterotricha*-like genera, *Sciaropota* Chandler, 2002, shows an alliance with an archizelmirid genus, *Archimelzira* from New Jersey amber (Grimaldi et al., 2003), and probably should be included in Archizelmiridae. Relationships within the *Heterotricha* group cannot be resolved easily because of the extensively paraphyletic nature of this complex.

Taphonomy and Biogeography

Sciaroidea today are most abundant and diverse in moist to wet temperate forests of the Holarctic and south temperate (e.g., Austral) regions—wherever thick humus and fungal mycelia are abundant. Although sciaroids are diverse in tropical forests, they are diffuse in numbers there. Among taxa known in the Cretaceous, Leiinae and Lygistorrhinidae are better represented in the tropics than Gnoristinae, which are common in temperate regions but scarce in tropical forests.

The most striking aspect of the Cretaceous amber faunas is the one in Burmese amber. Of all insect inclusions in other Cretaceous ambers, sciaroids comprise 1% or less in each deposit: For example, Taymyr 12 sciaroids/3450 inclusions; Canada 5/1281; Lebanon 2/600, 2/917, 15/1258 (all of the latter are archizelmirids); and New Jersey 17/1800. Of all insects in Burmese amber, by contrast, 5% of them are sciaroids. This is a proportion very similar to that found in Baltic and Dominican ambers. The proportions of Baltic amber sciaroids have been grossly overestimated based on museum collections (which are highly biased) at 15–20%. Based on crude Baltic amber samples analyzed by PIN at the mine sites in Kaliningrad in 1992, sciaroids (without Sciaridae) comprise 4% of all insect inclusions. The proportion of Mycetophilidae in Dominican amber based on unbiased samples is 3.3% of all insect inclusions (data of D.G.). Among Cretaceous deposits the Burmese sciaroid fauna is most similar to Early Cretaceous orictocenoses of Baisa and Bon Tsagan (Lower Cretaceous of Transbaikalia and Mongolia), which have 1.9% and 1.3%, respectively, of their entire insect faunas comprised of sciaroids. The Taimyr, New Jersey, and Canadian amber sciaroid faunas seem the most similar to each other.

The Burmese amber sciaroid fauna probably reflects a particularly wet paleoenvironment, although not necessarily warmer than the other Cretaceous deposits. Based on a large, new assemblage of more than 3000 insect inclusions in Burmese amber, Grimaldi et al. (2002) concluded that Burmese amber reflected the most tropical environment among all Cretaceous amber deposits. Sciaroids present conflicting evidence. On the one hand, sciaroids in Burmese amber were abundant, as in temperate forests. However, no species is particularly abundant, and Leiinae and Lygistorrhinidae are quite diverse, as would be found in tropical forests today.

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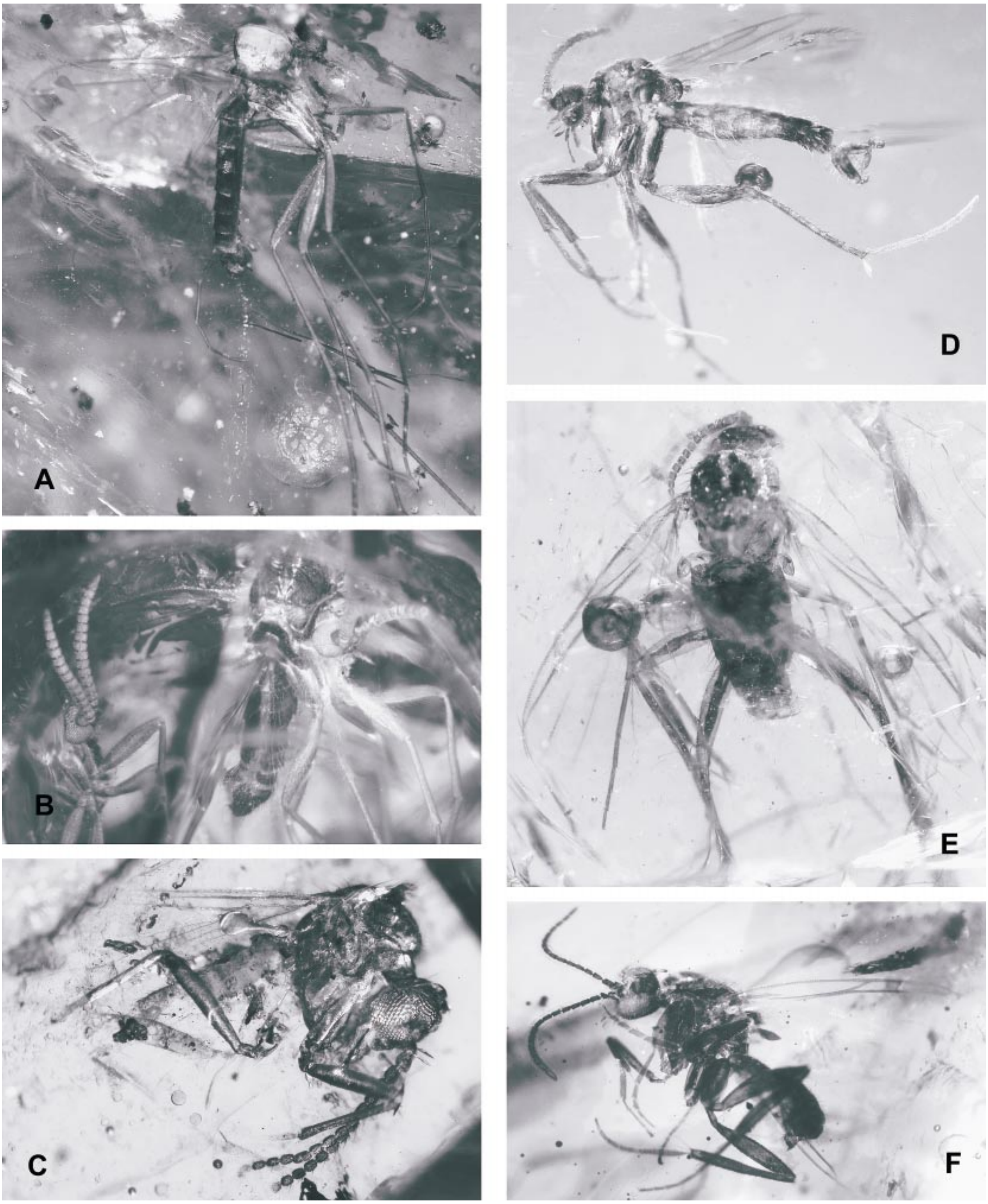

Plate 1. Families Diadocidiidae and Lygistorrhinidae. **A.** *Docidiadia burmitica* Blagoderov and Grimaldi, holotype AMNH Bu-033. **B.** *Thereotricha sibirica* Blagoderov and Grimaldi, holotype PIN 3130/183. **C.**? *T. agapa* Blagoderov and Grimaldi, holotype PIN 3426/256. **D.** *Archaeognoriste primitiva* Blagoderov and Grimaldi, holotype AMNH Bu-1539. **E.** *Lebanognoriste prima* Blagoderov and Grimaldi, holotype AMNH JG268/1. **F.** *Plesiognoriste carpenteri* Blagoderov and Grimaldi, holotype MCZC 6927.

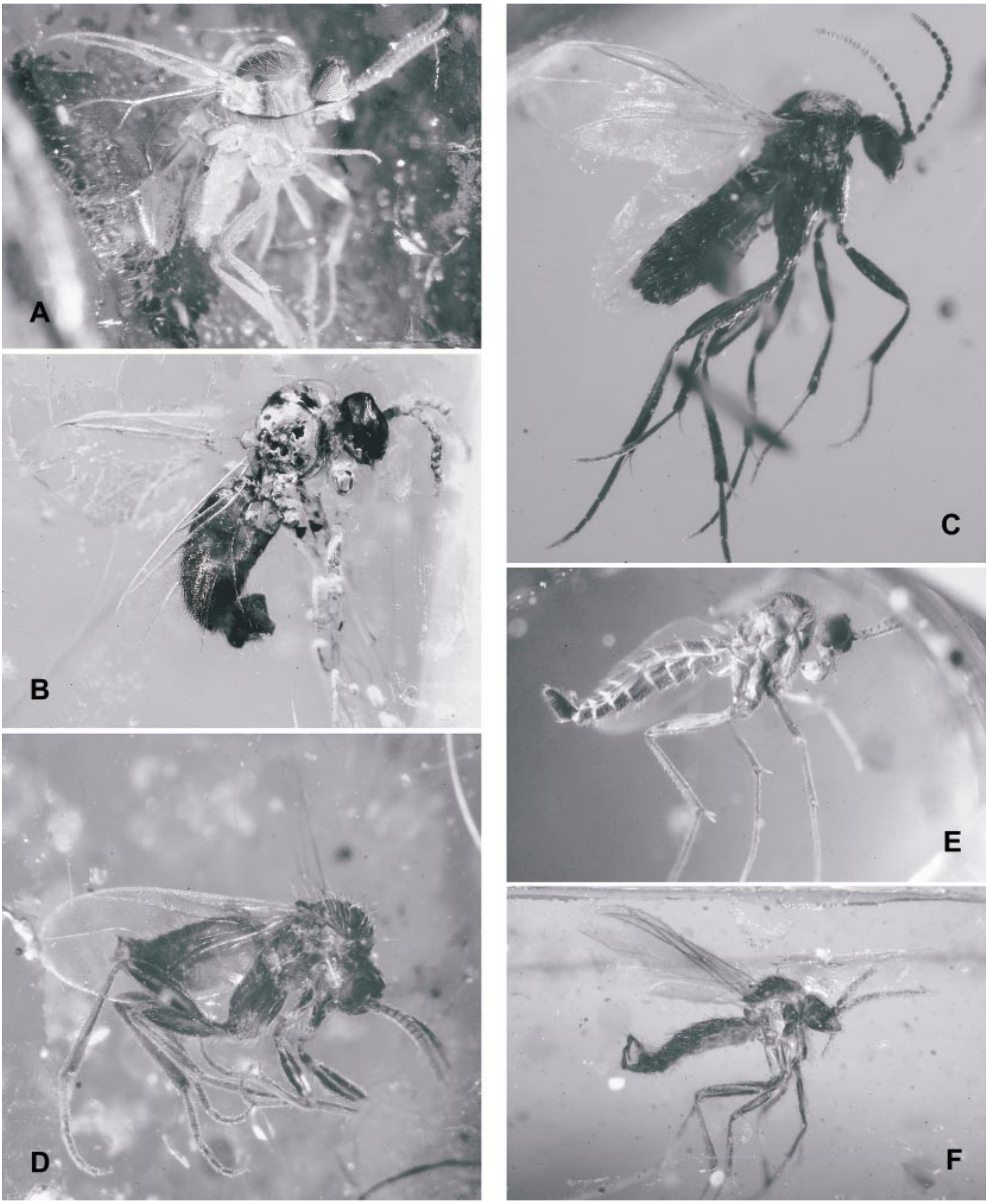

Plate 2. Family Lygistorrhinidae. **A.** *Plesiognoriste zherikhini* Blagoderov and Grimaldi, holotype PIN 3311/664. **B.** *Protognoriste amplicauda* Blagoderov and Grimaldi, holotype PIN 3426/257. **C.** *P. goeleti* Blagoderov and Grimaldi, holotype AMNH Bu-406. **D.** *P. nascifoa* Blagoderov and Grimaldi, holotype AMNH Bu-43. **E.** *Leptognoriste davisi* Blagoderov and Grimaldi, holotype AMNH Bu-126a. **F.** *L. microstoma* Blagoderov and Grimaldi, holotype AMNH Bu-429.

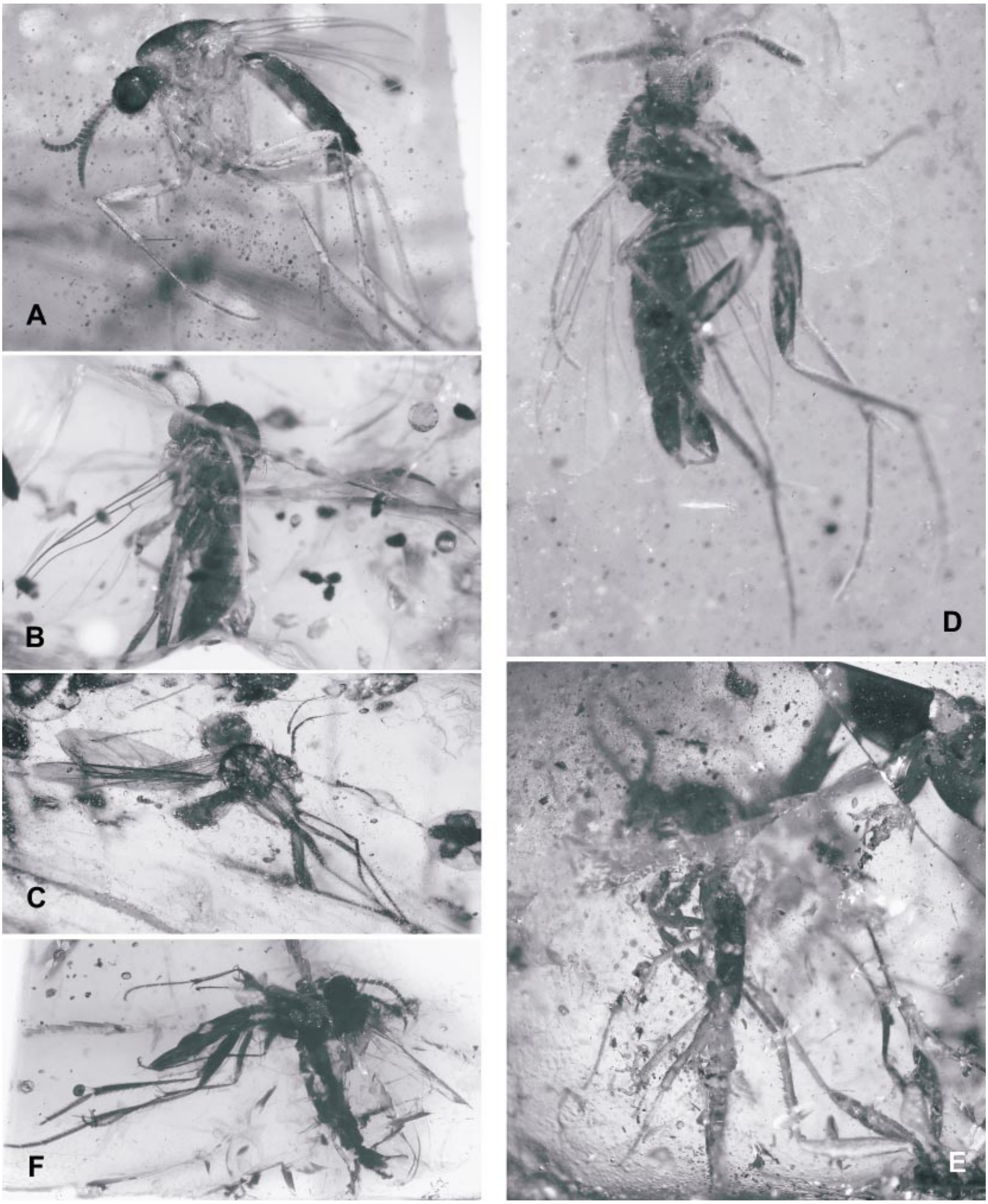

Plate 3. Family Mycetophilidae: Manotinae, Sciophilini, Gnoristini. **A.** *Alavamanota burmitina* Blagoderov and Grimaldi, holotype AMNH Bu-1271, **B.** *Neuratelia maimecha* Blagoderov and Grimaldi, holotype PIN 3311/661. **C.** *Allocotocera burmitica* Blagoderov and Grimaldi, holotype AMNH B-056. **D.** *Pseudomanota perplexa* Blagoderov and Grimaldi, holotype AMNH Bu-599a. **E.** *Apolephthisa bulunensis* Blagoderov and Grimaldi, holotype PIN 3963/4. **F.** *Synapha longistyla* Blagoderov and Grimaldi, holotype MCZC 6944.

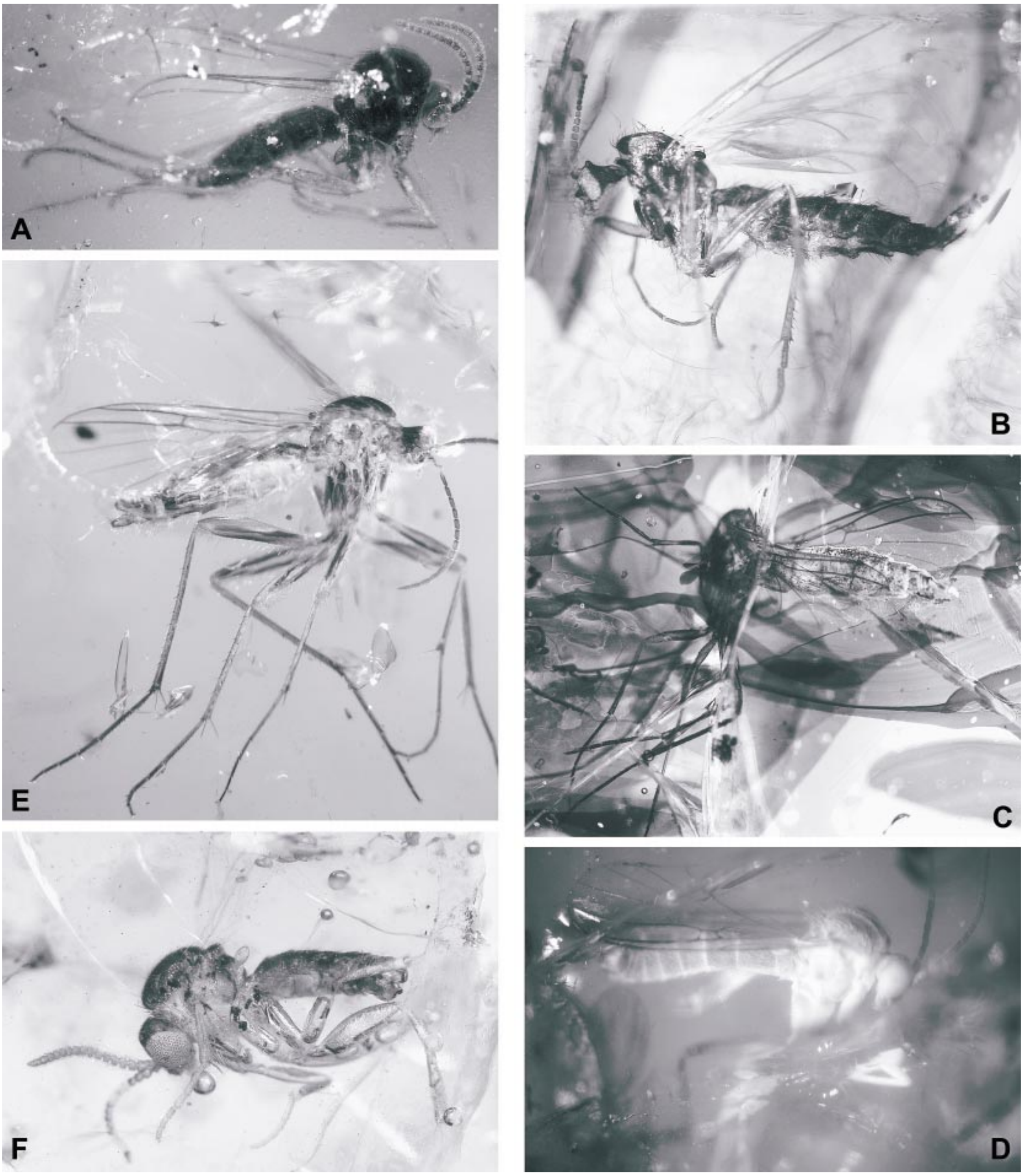

Plate 4. Family Mycetophilidae: Gnoristini and Leiini. **A.** *Dziedzickia nashi* Blagoderov and Grimaldi, holotype AMNH NJ-117a. **B.** *Saigusaia pikei* Blagoderov and Grimaldi, holotype TMPD P79.15.7.21. **C.** *Syntemna fissurata* Blagoderov and Grimaldi, holotype TMPD P83.15.3.8. **D.** *Gregikia pallida* Blagoderov and Grimaldi, holotype AMNH NJ 117j. **E.** *Gaalomyia carolinae* Blagoderov and Grimaldi, holotype AMNH Bu-390. **F.** *Nedocosia exsanguis* Blagoderov and Grimaldi, holotype PIN 3130/193.

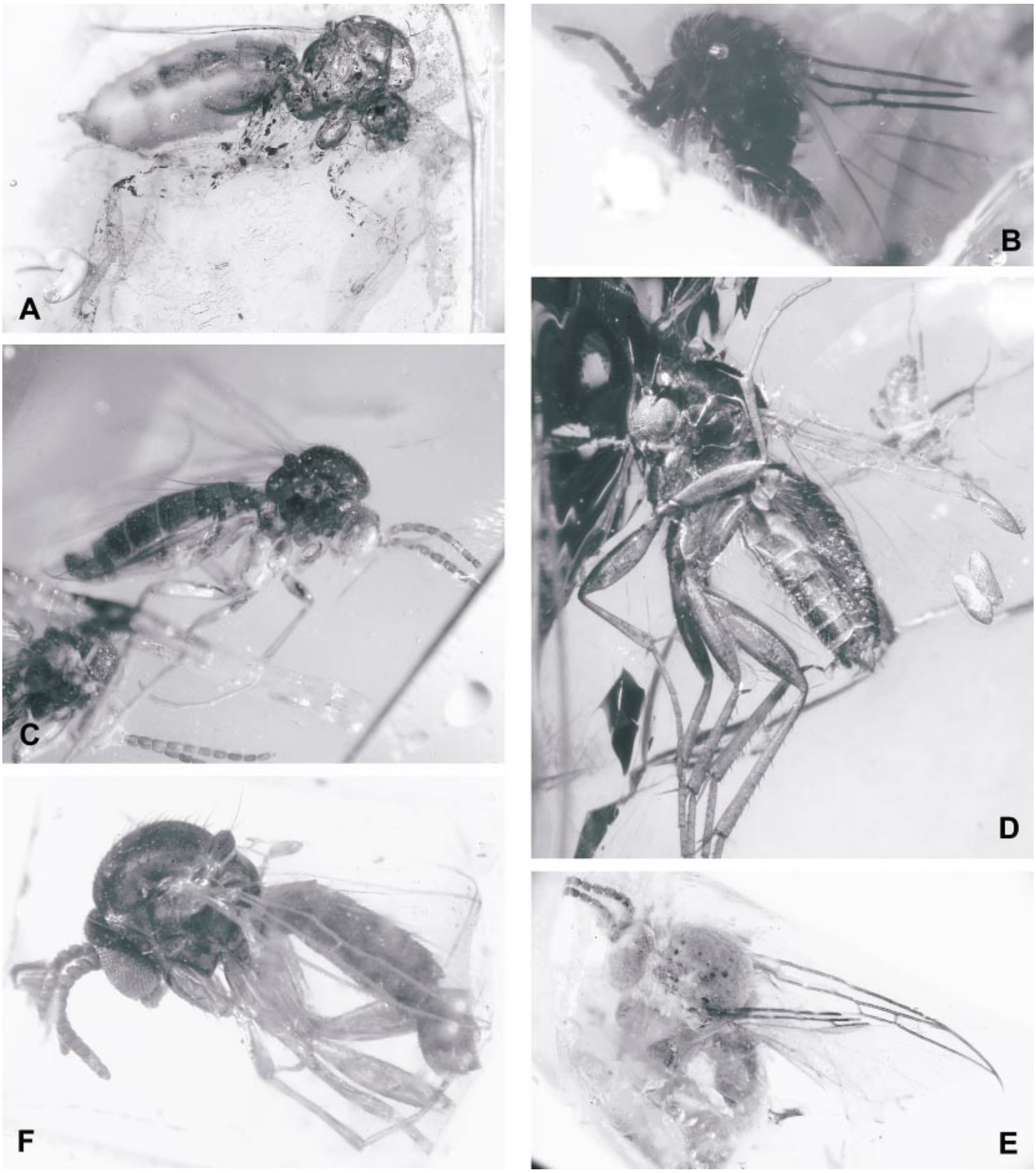

Plate 5. Family Mycetophilidae: Leiini. **A.** *Nedocosia sibirica* Blagoderov and Grimaldi, holotype PIN 3311/665. **B.** *N. canadensis* Blagoderov and Grimaldi, holotype MCZC 6897. **C.** *N. novacaesarea* Blagoderov and Grimaldi, holotype AMNH NJ-117k. **D.** *Ectrepesthoneura succinimontana* Blagoderov and Grimaldi, holotype PIN 3311/662. **E.** *E. swolenskyi* Blagoderov and Grimaldi, holotype AMNH NJ-824. **F.** *Izleiina mirifica* Blagoderov and Grimaldi, holotype PIN 3130/187.

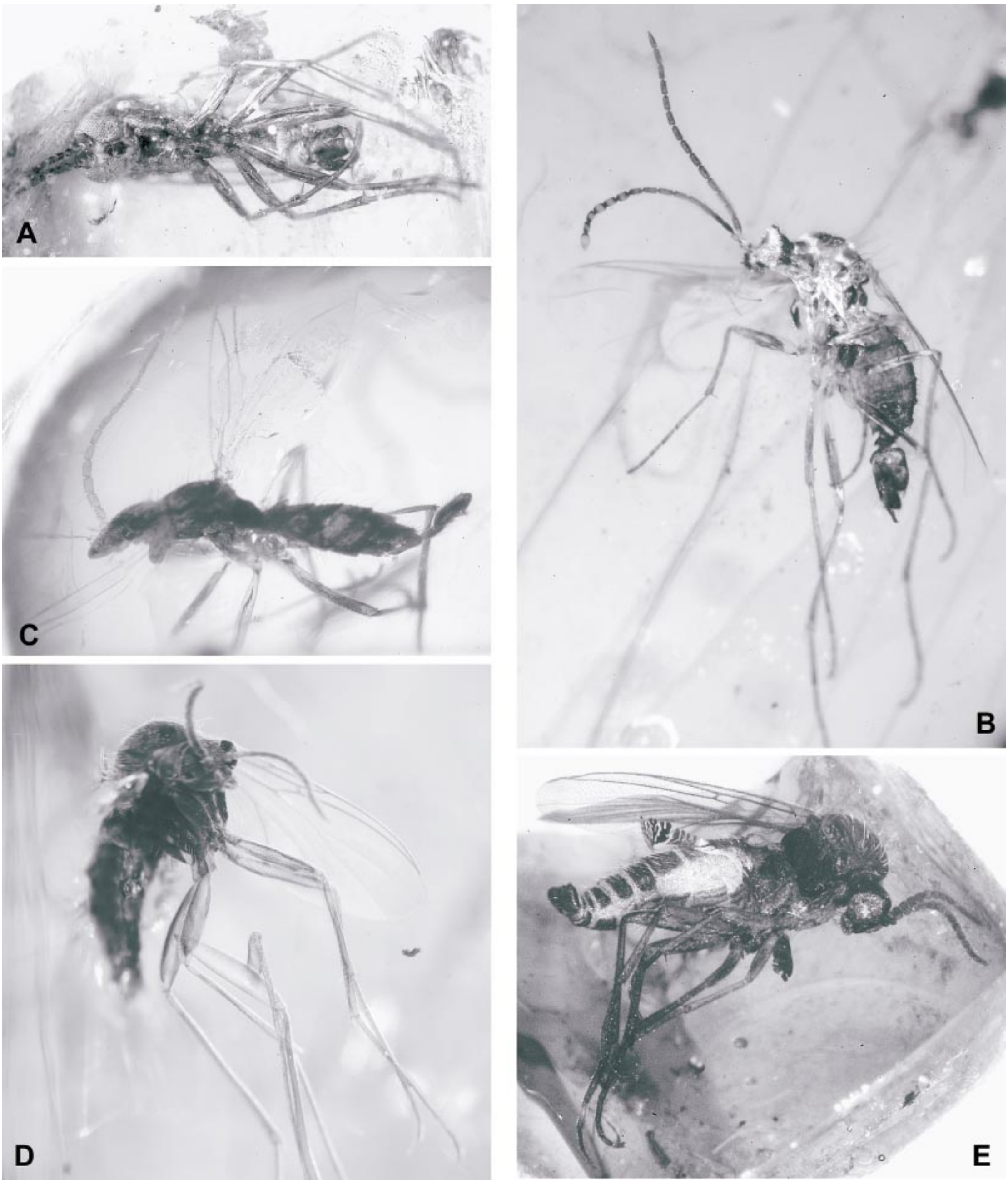

Plate 6. Family Mycetophilidae: Leiini. **A.** *I. spinitibialis* Blagoderov and Grimaldi, holotype AMNH NJ-346. **B.** *Zeliinia orientalis* Blagoderov and Grimaldi, holotype AMNH Bu-315. **C.** *Z. occidentalis* Blagoderov and Grimaldi, holotype MCZC 6943. **D.** *Temaleia birmitica* Blagoderov and Grimaldi, holotype AMNH Bu-483a. **E.** *Lecadonileia parvistyla* Blagoderov and Grimaldi, holotype MCZC 6941.

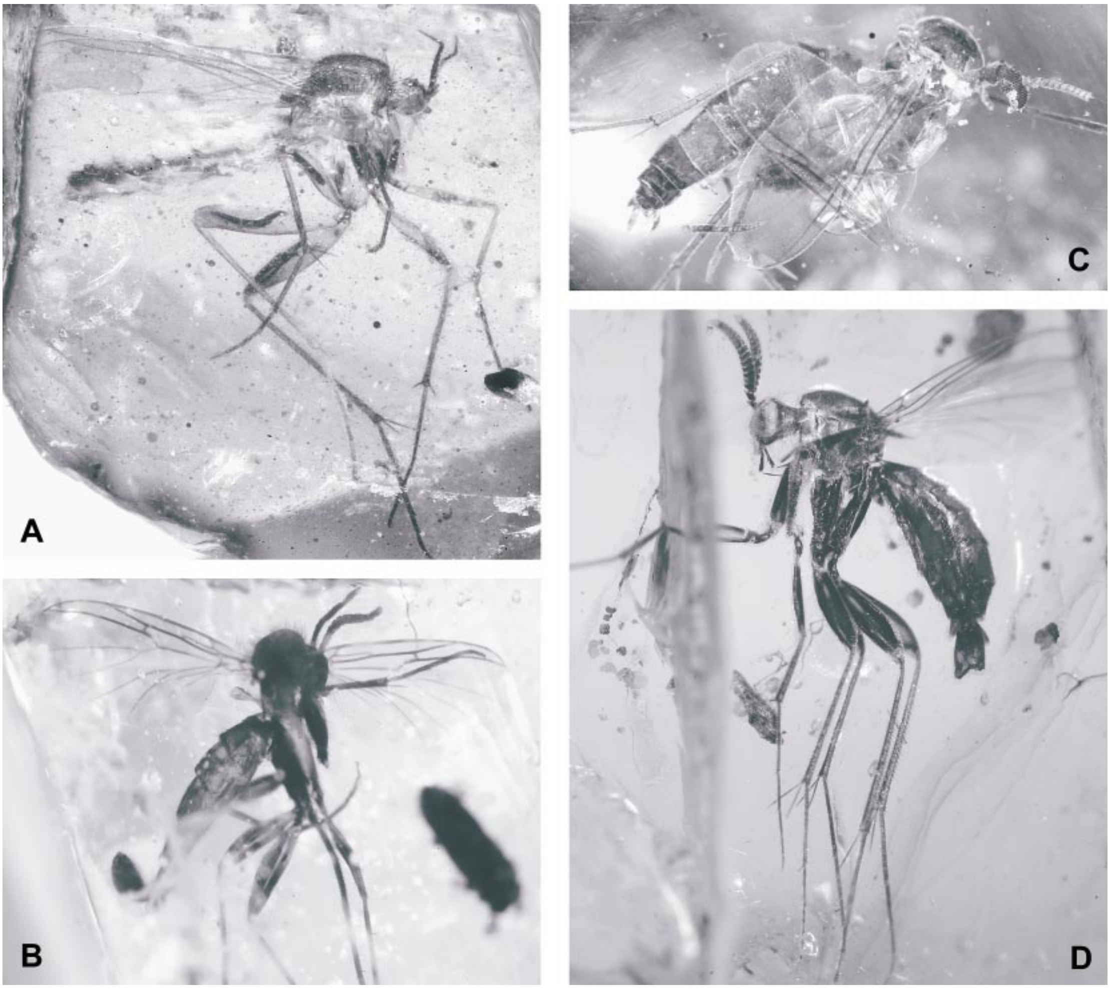

Plate 7. Family Mycetophilidae: Leiini. **A.** *Disparoleia cristata* Blagoderov and Grimaldi, holotype AMNH B-0125. **B.** *Hemolia matilei* Blagoderov and Grimaldi, holotype AMNH B-0132. **C.** *H. glabra* Blagoderov and Grimaldi, holotype AMNH B-0112. **D.** *Protragoneura platycera* Blagoderov and Grimaldi, holotype AMNH Bu-135.