

The Neuropterid Fauna of Dominican and Mexican Amber (Neuropterida: Megaloptera, Neuroptera)

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The Neuropterid Fauna of Dominican and Mexican Amber (Neuropterida: Megaloptera, Neuroptera)

MICHAEL S. ENGEL¹ AND DAVID A. GRIMALDI²

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ABSTRACT

The neuropterid fauna of early Miocene Dominican and Oligocene-Miocene Mexican amber is treated. The fauna consists entirely of Megaloptera and Neuroptera while the snakeflies (Raphidioptera) are not presently known in Tertiary ambers from the New World. Fifteen species are recognized, all in living genera and subgenera: Sialidae, *Sialis* (*Protosialis*) *casca*, new species (Dominican); Ascalaphidae, *Ululodes paleonesia*, new species (Dominican), *Amoea electrodominica*, new species (Dominican); Chrysopidae, *Chrysopa glaesaria*, new species (Dominican), *C. vetula*, new species (Dominican), *Leucochrysa* (*Nodita*) *prisca*, new species (Dominican); Coniopterygidae, *Coniopteryx antiquua*, new species (Dominican), *Spiloconis glaesaria* Meinander (Dominican), *S. oediloma*, new species (Dominican); Hemerobiidae, *Notiobiella thaumasta* Oswald (Dominican), *Symphorobius* sp. (Dominican); Mantispidae, *Dicromantispa electromexicana*, new species (Mexican), *D. moronei*, new species (Dominican); *Fero-seta prisca* Poinar, nomen emendatum (Dominican); Myrmeleontidae, *Porrerus dominicanus* Poinar and Stange (Dominican). Immature stages of Ascalaphidae (two species of *Ululodes*; Dominican), Chrysopidae (genus indet.; Dominican), and Myrmeleontidae (*P. dominicanus*?; Dominican) are reported. The neuropterid fossil record is summarized and the Dominican and Mexican amber faunas are compared to other neuropterid amber faunas. The biogeographic and paleoecological implications of the Miocene fossils are discussed. Abundance and diversity of Neuroptera in ambers appear to be related to the abundance of Sternorrhyncha, on which many neuropterans feed.

RESUMEN

Se describe la fauna de neuroptéridos encontrada en ámbar dominicano del Mioceno basal y en ámbar mexicano del Oligoceno-Mioceno. La fauna está compuesta enteramente por Megaloptera y Neuroptera, mientras que hasta la fecha no se conocen registros de Raphidioptera en yacimientos de ámbar del Terciario en el Nuevo Mundo. Se reconocen 15 especies, todas pertenecientes a géneros y subgéneros vivos en la actualidad: Sialidae, *Sialis* (*Protosialis*) *casca*, especie nueva (Dominicana); Ascalaphidae, *Ululodes paleonesia*, especie nueva (Dominicana), *Amoea electrodominica*, especie nueva (Dominicana); Chrysopidae, *Chrysopa glaesaria*, especie nueva (Dominicana), *C. vetula*, especie nueva (Dominicana), *Leucochrysa* (*Nodita*) *prisca*, especie nueva (Dominicana); Coniopterygidae, *Coniopteryx antiquua*, especie nueva (Dominicana), *Spiloconis glaesaria* Meinander (Dominicana), *S. oediloma*, especie nueva (Dominicana); Hemerobiidae, *Notiobiella thaumasta* Oswald (Dominicana), *Symphorobius* sp. (Dominicana); Mantispidae, *Dicromantispa electromexicana*, especie nueva (México), *D. moronei*, especie nueva (Dominicana); *Fero-seta prisca* Poinar, nom. emend. (Dominicana); Myrmeleontidae, *Porrerus dominicanus* Poinar y Stange (Dominicana). Se citan estadios inmaduros de Ascalaphidae (*Ululodes* spp.; Dominicana), Chrysopidae (género no determinado; Dominicana) y Myrmeleontidae (*P. dominicanus*?; Dominicana). Se comparan estas faunas extintas con otras de neuroptéridos en ámbar y se discuten las implicaciones biogeográficas y paleontológicas de los taxones tratados. La abundancia y diversidad de Neuroptera en yacimientos de ámbar parece estar relacionada con la abundancia de Stenorrhyncha, de los cuales se alimentan muchos neurópteros.

INTRODUCTION

The superorder Neuropterida comprises three distinctive orders of holometabolous insects: the Megaloptera, the Neuroptera, and the Raphidioptera. These three orders form a monophylum defined by the fusion of the third valvulae in the ovipositor, the medially divided metapostnotum, the un-

paired diverticulum of the proventriculus, and the caudally bifid mediolongitudinal suture on the first abdominal tergum (Mickoleit, 1973; Achtelig, 1975; Kristensen, 1991). Although such characters are obscure, each of the major monophyletic groups within the Neuropterida has a distinctive wing venation. Venation has allowed interpretation of fossils, and in fact the abundant record

of wing impressions in rocks gives the Neuropterida among the most extensive fossil record of all Holometabola. Together with the Coleoptera, their closest living relatives among the Holometabola (Kristensen, 1991, 1995; Hörschmeyer, 1998; Whiting et al., 1997; Carpenter and Wheeler, 1999; Wheeler et al., 2001; Grimaldi and Engel, 2005), the neuropterids are an ancient offshoot of endopterygote insects with geological histories extending back to the Early Permian (Kukulová-Peck, 1991; Carpenter, 1992; Grimaldi and Engel, 2005). Unlike the beetles, however, the neuropterid orders are not very diverse and some, like the families of Raphidioptera, are perhaps in decline globally (Aspöck, 1998; Engel, 2002a). In fact, a remarkable diversity of extinct neuropterid lineages is known from the Mesozoic and, to a lesser degree, earlier deposits (e.g., Schlüter, 1986; Carpenter, 1992; Grimaldi and Engel, 2005). Owing to the combination of their ancient age, highly apomorphic relict taxa, and numerous extinct lineages, the Neuropterida is one of those groups whereby inclusion of fossil taxa into cladistic studies is critical (Gauthier et al., 1989). It will be interesting to explore the effects of such fossil taxa on our understanding of neuropterid phylogeny at all hierarchical levels. Most neuropterid fossils, however, are compression fossils that preserve only wings or very limited, structural details. Preservation in amber, however, is unsurpassed, preserving not only the external morphology in essentially lifelike detail but often internal tissues (Grimaldi et al., 1994; Grimaldi and Engel, 2005). Amber inclusions offer a greater opportunity to make meaningful comparisons between Recent and fossil taxa as well as simultaneous cladistic analyses of paleontological and neontological data (e.g., Grimaldi and Cumming, 1999; Engel, 2001).

The most diverse neuropterid fauna in amber is from the Baltic region, which has classically received the greatest attention from systematists. There are presently 33 described species in Baltic amber (table 1). This amber is middle Eocene in age (dating reviewed in Engel, 2001; Weitschat and Wichard, 2002). Baltic amber is the largest deposit of amber in the world. It has been studied for centuries

and is the most intensively studied of amber Lagerstätte; however, very few modern studies have investigated inclusions of Neuropterida, and comprehensive revisionary work is needed. Even basic descriptive work of new species in Baltic amber is ongoing (e.g., Wichard, 1997; Engel, 1999a; Dobosz and Krseński, 2000; Wichard and Engel, 2006). Among Cretaceous ambers, the fauna of the Turonian New Jersey amber is only slightly less diverse than that of Baltic amber (table 2), particularly when accounting for the much smaller size of the deposits of the former. The only other Cretaceous amber with a significant neuropterid fauna is the Late Albian amber from Myanmar (Grimaldi et al., 2002; Engel, 2002a, 2004a, 2004b, in prep.). Other amber deposits have revealed a few other Neuropterida (table 3), principally of families well documented in the major deposits. Lastly, the Cenozoic amber deposits of North America have similarly revealed only sparse material of a few neuropterids. Previously only three species in the families Myrmeleonidae, Coniopterygidae, and Hemerobiidae have been described from Dominican amber while none has been described from Mexican amber. Herein we report on new neuropterids discovered in Dominican and Mexican amber; these include the first New World fossil of an alderfly (Sialidae) and the first green lacewings (Chrysopidae) and the first adult owlfly (Ascalaphidae) in amber. In total the fauna has now increased to 13 species distributed among seven families (table 4). The age of Dominican amber has been unfortunately confused, but it is certainly no older than Early Miocene in origin (Iturralde-Vinent and MacPhee, 1996, 1999). Mexican amber is of a similar age, originating from the Late Oligocene–Early Miocene (Langenheim, 1966).

With such a long geological duration of neuropteridan history (Permian to present), Tertiary fossils are of little phylogenetic consequence regarding higher taxa. The significance of Dominican and Mexican amber fossils lies in (1) the preservation of amber, allowing close species comparisons; (2) information for West Indian biogeography, particularly assessing any geographical extinctions; and (3) paleoecology, or taphonomic inferences provided by the taxa that are

TABLE 1
 Named Neuropterida in Baltic Amber^a

Taxa	Reference
ORDER NEUROPTERA LINNAEUS (= Planipennia)	
—Family ASCALAPHIDAE Rambur	
<i>Neadelphus protae</i> MacLeod	MacLeod, 1970
—Family BERTHOIDAE Handlirsch	
<i>Proberotha prisca</i> Krüger	Krüger, 1923
—Family CONIOPTERYGIDAE Burmeister	
<i>Archiconiocompsa prisca</i> Enderlein	Enderlein, 1910
<i>Archiconis electrica</i> Enderlein	Enderlein, 1930
<i>Coniopteryx timidus</i> (Hagen)	Pictet-Baraban & Hagen, 1856; Meinander, 1972, 1975
<i>Heminiphettia fritschi</i> Enderlein	Enderlein, 1930
<i>Hemisemidalis kulickae</i> Dobosz & Krzemiński	Dobosz & Krzemiński, 2000
<i>Hemisemidalis sharovi</i> Meinander	Meinander, 1975
—Family DILARIDAE Newman	
<i>Cascadilar eocenicus</i> Engel	Engel, 1999a
—Family HEMEROBIDAE Latreille	
<i>Hemerobites antiquus</i> Germar	Germar, 1813
<i>Prochlanius resinatus</i> (Hagen)	Pictet-Baraban & Hagen, 1856; Krüger, 1923
<i>Prophlebonema resinata</i> Krüger	Krüger, 1923
<i>Prospadobius moestus</i> (Hagen)	Pictet-Baraban & Hagen, 1856; Krüger, 1923
—Family NEVRORTHIDAE Nakahara	
<i>Rophalis relictta</i> (Hagen)	Pictet-Baraban & Hagen, 1856; Nel & Jarzembowski, 1997
—Family NYMPHIDAE Rambur	
<i>Pronymphes mengeanus</i> (Hagen)	Pictet-Baraban & Hagen, 1856; Krüger, 1923; MacLeod, 1970 [larva]
—Family OSMYLIDAE Leach	
<i>Protosmylus pictus</i> (Hagen)	Pictet-Baraban & Hagen, 1856; Krüger, 1923
—Family PSYCHOPSIDAE Handlirsch	
<i>Propsochopsis hageni</i> MacLeod	MacLeod, 1970
<i>Propsochopsis helmi</i> Krüger	Krüger, 1923
<i>Propsochopsis lapicida</i> MacLeod	MacLeod, 1970
—Family RHACHIBERTHOIDAE Tjeder	
<i>Whalfera venatrix</i> (Whalley) ^b	Whalley, 1983; Engel, 2004b
—Family SISYRIDAE Handlirsch	
<i>Sisyra</i> (?) <i>amissa</i> Hagen	Pictet-Baraban & Hagen, 1856
ORDER MEGALOPTERA LATREILLE	
—Family CORYDALIDAE Leach	
<i>Chauliodes prisca</i> Pictet	Pictet, 1854
<i>Chauliodes carsteni</i> Wichard	Wichard, 2003
—Family CORYDASIALIDAE Wichard et al.	
<i>Corydasialis inexpectatus</i> Wichard et al.	Wichard et al., 2005
—Family SIALIDAE Leach	
<i>Sialis</i> (<i>Protosialis</i>) <i>baltica</i> Wichard	Wichard, 1997
<i>Sialis</i> (<i>Protosialis</i>) <i>herrlingi</i> Wichard	Wichard, 2002
<i>Sialis</i> (<i>Protosialis</i>) <i>voigti</i> Wichard & Engel	Wichard & Engel, 2006
<i>Sialis groehni</i> Wichard	Wichard, 1997
ORDER RAPHIIDOPTERA NAVÁS ^c	
—Family INOCELLIIDAE Navás	
<i>Electrinocellia peculiaris</i> (Carpenter)	Carpenter, 1956; Engel, 1995
<i>Fibla carpenteri</i> Engel	Engel, 1995
<i>Fibla erigena</i> (Hagen)	Pictet-Baraban & Hagen, 1856; Carpenter, 1956
<i>Succinofibla aperta</i> Aspöck & Aspöck	Aspöck & Aspöck, 2004

TABLE 1
(Continued)

Taxa	Reference
—Family RAPHIDIIDAE Latreille	
<i>Raphidia baltica</i> Carpenter	Carpenter, 1956
<i>Succinoraphidia exhibiens</i> Aspöck & Aspöck	Aspöck & Aspöck, 2004

^aUndescribed immatures are recorded for Sialidae (Weidner, 1958), Raphidiidae (Berendt, 1856), Inocelliidae (Weidner, 1958), Hemerobiidae (Pictet-Baraban and Hagen, 1856), and Nevrothidae (Weitschat and Wichard, 1998, 2002).

^bThis specimen was described from “British” amber (and is therefore also listed in table 3), but this is the same as Baltic amber and is merely material from the Baltic that has washed up on the British Isles.

^cBecause Navás (1916) was the first to use the ordinal name in this form, we have attributed authorship to him even though several earlier authors had also considered the snakeflies as a distinct order (e.g., Burmeister, 1839: as Raphidiodea). Navás (1916) appears to have followed Shipley’s (1904) recommendation for a common *-ptera* ending for insect ordinal names by emending the name to Raphidioptera. Although the name Raphidioptera is somewhat meaningless in its original Greek (*raphidos*, meaning “needle”, a reference to the elongate ovipositor; and *pteron*, meaning “wing”), it is in almost universal usage for this group, and there seems to be little reason to change it back to Raphidiodea, Raphidiida, or to something more descriptive in Greek such as Ophidiodea (*ophidion*, or “snake”; *dere*, or “neck”).

preserved. The Dominican and Mexican amber faunas are relatively similar to tropical neuropterid faunas in these regions today. The fauna consists entirely of Megaloptera and Neuroptera while the snakeflies (Raphidioptera) are presently unknown in Tertiary ambers of the New World. Tertiary compression fossils of Raphidioptera are known from North America and Europe (e.g., Aspöck et

al., 1991; Nel, 1993; Engel, 2002a, 2003) and snakeflies are present in mid-Eocene ambers of Europe (Carpenter, 1956; Engel, 1995, 2002a; Weitschat and Wichard, 1998, 2002; Aspöck and Aspöck, 2004). However, on the whole the Cenozoic record of this order is insignificant and it is in the Mesozoic that a remarkable diversity of Raphidioptera from throughout the world is known (e.g., Aspöck, 1998; Grimaldi, 2000; Engel, 2002a, unpubl. data; Engel et al., 2006; Perrichot and Engel, in press).

TABLE 2

Named Neuropterida in New Jersey Amber

(from Grimaldi, 2000; Engel, 2002b: all are placed in extinct genera)

ORDER NEUROPTERA LINNAEUS

—Family BEROETHIDAE Handlirsch

Jersiberotha luzzii Grimaldi

Jersiberotha similis Grimaldi

Nascimberotha picta Grimaldi

—Family CONIOPTERYGIDAE Burmeister

Apoglaesoconis ackermani Grimaldi

Apoglaesoconis cherylae Engel

Apoglaesoconis luzzii Grimaldi

Apoglaesoconis swolenskyi Grimaldi

Glaesoconis nearctica Grimaldi

—Family MANTISPIDAE Leach

Mantispidiptera enigmatica Grimaldi

Mantispidiptera henryi Grimaldi

—Family RHACHIBEROETHIDAE Tjeder

Rhachibermissa splendida Grimaldi

ORDER RAPHIDIOPTERA NAVÁS

—Family MESORAPHIDIIDAE Martynov ^a

Mesoraphidia luzzii Grimaldi

^aAn undescribed larva of this group was also recorded.

MATERIALS AND METHODS

All measurements were made using an ocular micrometer and should be considered approximate since the optimal angle for any given metric was not always achievable owing to the uneven surface of the amber. The acronyms AMNH and MACT are used, respectively, for the American Museum of Natural History, New York, and the Morone Amber Collection, Turin, Italy.

SYSTEMATIC PALEONTOLOGY**ORDER MEGALOPTERA LATREILLE
FAMILY SIALIDAE LEACH**

The Sialidae, or alderflies, are one of two living families of Megaloptera. Sialid larvae, like those of all megalopterans, are aquatic predators, living in anything from small streams, rivers, ponds, lakes, or even phyto-

TABLE 3
 Named Neuropterida in Lebanese, Burmese, French, Siberian, Hat Creek, “British”,^a and Parisian Ambers^b
 (all are in extinct genera)

Taxa	Deposit	Reference
ORDER NEUROPTERA LINNAEUS		
—Family BEROETHIDAE Handlirsch		
<i>Banoberothes enigmatica</i> Whalley	Lebanese (Neocomian)	Whalley, 1980
<i>Microberothes macculloughi</i> Archibald and Makarkin	Hat Creek (Eocene)	Archibald & Makarkin, 2004
<i>Plesiorobius ?anadensis</i> Klimaszewski and Kevan	Canadian (Campanian)	Klimaszewski & Kevan, 1986
—Family CONIOPTERYGIDAE Burmeister		
<i>Glaesoconis cretica</i> Meinander	Siberian (Santonian)	Meinander, 1975
<i>Glaesoconis baliapteryx</i> Engel	Burmese (Albian)	Engel, 2004a
<i>Libanoconis fadiacra</i> (Whalley)	Lebanese (Neocomian)	Whalley, 1980; Engel, 2002a
<i>Phthanoconis burmitica</i> Engel	Burmese (Albian)	Engel, 2004a
<i>Libanosemidalis hammanaensis</i> Azar et al.	Lebanese (Neocomian)	Azar et al., 2000
<i>Gallosemidalis eocenica</i> Nel et al.	Parisian (Eocene)	Nel et al., 2005a
<i>Alboconis cretacica</i> Nel et al.	Lebanese (Neocomian)	Nel et al., 2005a
—Family RHACHIBEROETHIDAE Tjeder		
<i>Paraberothera acra</i> Whalley	Lebanese (Neocomian)	Whalley, 1980
<i>Retinoberothera stuermeri</i> Schlüter	French (Cenomanian)	Schlüter, 1978
<i>Eorhachiberothes burmitica</i> Engel	Burmese (Albian)	Engel, 2004b
<i>Whalfera venatrix</i> (Whalley)	“British” (Eocene)	Whalley, 1983; Engel, 2004b
<i>Alloberothera petrulevicii</i> Nel et al.	French (Cenomanian)	Nel et al., 2005b
<i>Chimerhachiberothes acrasarii</i> Nel et al.	Lebanese (Neocomian)	Nel et al., 2005b
<i>Spinoberothera mickaellacrai</i> Nel et al.	Lebanese (Neocomian)	Nel et al., 2005b
<i>Oisea celinea</i> (Nel et al.)	Parisian (Eocene)	Nel et al., 2005b
ORDER MEGALOPTERA LATREILLE		
—Family SIALIDAE Leach		
<i>Eosialis dorisi</i> Nel et al.	Parisian (Eocene)	Nel et al., 2002
ORDER RAPHDIOPTERA NAVÁS		
—Family MESORAPHIDIIDAE Martynov ^c		
<i>Nanoraphidia electroburmica</i> Engel	Burmese (Albian)	Engel, 2002a

^a“British” amber is the same as Baltic amber and is material from the Baltic that has washed up on the British Isles. These deposits are middle Eocene in age (see discussion of dating in Engel, 2001; Grimaldi and Engel, 2005).

^bAn undescribed specimen from Canadian amber has been reported as a possible berothid (McAlpine and Martin, 1969; Pike, 1995).

^cAn undescribed larva of this group was recorded by Engel (2002a), and a further account of various Cretaceous snakefly immatures is summarized by Perrichot and Engel (in press).

telmata and under stones or where dead plant material accumulates. Larvae emerge onto land to pupate in vegetation or debris. Adults are short-lived, occur along watersides, and apparently may feed on pollen and nectar, if at all. Generally little is known of adult megalopteran biology, particularly so for Sialidae.

Today the family is represented by approximately 66 living species (most in the nominate genus *Sialis*) that are distributed worldwide but are principally Holarctic with a few species in the New World tropics (*Sialis* s.l.: includes *Protosialis* and *Nipponosialis* after Whiting

[1994] and New and Theischinger [1993], respectively), South Africa (*Leptosialis*), Australia (*Austrosialis* and *Stenosialis*), and Southeast Asia (*Indosialis*). In addition, 10 extinct species have been previously proposed (table 5), almost all in Tertiary deposits. The primitive *Dobbertinia reticulata* (Handlirsch) from the Liassic of Germany is the oldest record of the family. This species is classified in its own basal subfamily, the Dobbertiniinae.

Herein we describe a new species of *Sialis* (*Protosialis*) in amber from the Dominican Republic, a group which is today unknown

TABLE 4
Neuropterida in Dominican and Mexican^a Amber

Taxa	Reference
ORDER MEGALOPTERA LATREILLE	
—Family SIALIDAE Leach	
<i>Sialis</i> (<i>Protosialis</i>) <i>casca</i> Engel & Grimaldi n.sp.	Present study
ORDER NEUROPTERA LINNAEUS	
—Family ASCALAPHIDAE Rambur	
<i>Amoea</i> <i>electrodominicana</i> Engel & Grimaldi n.sp.	Present study
<i>Ululodes</i> <i>paleonesia</i> Engel & Grimaldi n.sp. ^b	Present study
—Family CHRYSOPIDAE Schneider	
<i>Chrysopa</i> <i>glaesaria</i> Engel & Grimaldi n.sp.	Present study
<i>Chrysopa</i> <i>vetula</i> Engel & Grimaldi n.sp.	Present study
<i>Leucochrysa</i> (<i>Nodita</i>) <i>prisca</i> Engel & Grimaldi n.sp.	Present study
—Family CONIOPTERYGIDAE Burmeister ^b	
<i>Coniopteryx</i> <i>antiqua</i> Engel & Grimaldi n.sp.	Present study
<i>Spiloconis</i> <i>glaesaria</i> Meinander	Meinander, 1998a
<i>Spiloconis</i> <i>oediloma</i> Engel & Grimaldi n.sp.	Present study
—Family HEMEROBIIDAE Latreille	
<i>Notiobiella</i> <i>thaumasta</i> Oswald	Oswald, 1999
<i>Symphorobius</i> sp.	Present study
—Family MANTISPIDAE Leach	
<i>Dicromantispa</i> <i>moronei</i> Engel & Grimaldi n.sp.	Present study
<i>Dicromantispa</i> <i>electromexicana</i> Engel & Grimaldi n.sp.	Present study
<i>Feroseta</i> <i>prisca</i> Poinar	Poinar, 2006
—Family MYRMELEONTIDAE Latreille	
<i>Porrerus</i> <i>dominicanus</i> Poinar & Stange ^b	Poinar & Stange, 1996

^a*Dicromantispa electromexicana* is presently the only described neuropterid from Mexican amber.

^bImmatures (all reported upon herein) are recorded for Ascalaphidae, Chrysopidae, and Myrmeleontidae.

from the West Indies except for one species on the island of Cuba, that is, *Sialis* (*Protosialis*) *bifasciata* Hagen (Penny, 1977; Contreras-Ramos, 1999).

Sialis (*Protosialis*) *casca*, new species
figures 1–3

DIAGNOSIS: The orange coloration of the head and pronotum and narrowed costal area with a reduced number of costal crossveins indicate this to be a species of the subgenus *Protosialis*. For *Protosialis* species the presence of only three costal crossveins is unique while the black markings on the head are similar to that seen in *Sialis* (*Protosialis*) *flammata* (Penny) but are rounded in the fossil (not flamelike as in *S. flammata*).

DESCRIPTION: Forewing length (preserved) 7.7 mm, (estimated: from bent forewing) 8.4 mm; total body length 7.6 mm (fig. 1). Head and pronotum orange with black mark-

ings; antennae black; head with black markings along margins of eye and extending posteriorly near to posterior border of head, black extended medially but not reaching midline, borders of markings rounded (not flamelike). Apical segments of maxillary palpi with medioapical tooth. Ocelli absent. Pronotum apparently twice as wide as long, remainder of thorax dark brown. Protibia, mesofemur, mesotibia, and metatibia black, remaining leg segments whitish; fourth tarsomere bilobed. Wing membranes fuscous; veins dark brown to black; forewing with costal area distinctly narrowed just before middle of wing; three costal crossveins, distal two veins distinctly oblique (i.e., not perpendicular to C or Sc); distal r-rs crossvein meeting R_{2+3} slightly distad to R_{2+3}/R_{4+5} fork; posterior branch of R_4/R_5 separating near wing apex (i.e., distad R_2/R_3 branching); outer series of gradate crossveins confluent (figs. 2, 3). Abdomen slightly distended and bent ventrally near

TABLE 5
Named Fossil Sialidae

Taxa	Deposit	Reference
<i>Dobbertinia reticulata</i> (Handlirsch)	Jurassic, Germany	Ansorge, 2001
<i>Eosialis dorisi</i> Nel et al.	Parisian amber	Nel et al., 2002
<i>Indosialis beskonakensis</i> Nel	Miocene, Turkey	Nel, 1988a
<i>Proindosialis cantalensis</i> Nel	Miocene, France	Nel, 1988a
<i>Sialis strausi</i> Illies	Pliocene, Germany	Illies, 1967
<i>Sialis groehni</i> Wichard	Baltic amber	Wichard, 1997
<i>Sialis muratensis</i> Nel	Miocene, France	Nel, 1988a
<i>Sialis (Protosialis) baltica</i> Wichard	Baltic amber	Wichard, 1997
<i>Sialis (Protosialis) herrlingi</i> Wichard	Baltic amber	Wichard, 2002
<i>Sialis (Protosialis) casca</i> n.sp.	Dominican amber	Present study
<i>Sialis (Protosialis) voigti</i> Wichard & Engel	Baltic amber	Wichard & Engel, 2006

midpoint; apparently light brown; apex of abdomen curled under, with genitalia pointed anteriorly.

HOLOTYPE: Male; MACT-2090 (fig. 1), Miocene amber of the Dominican Republic.

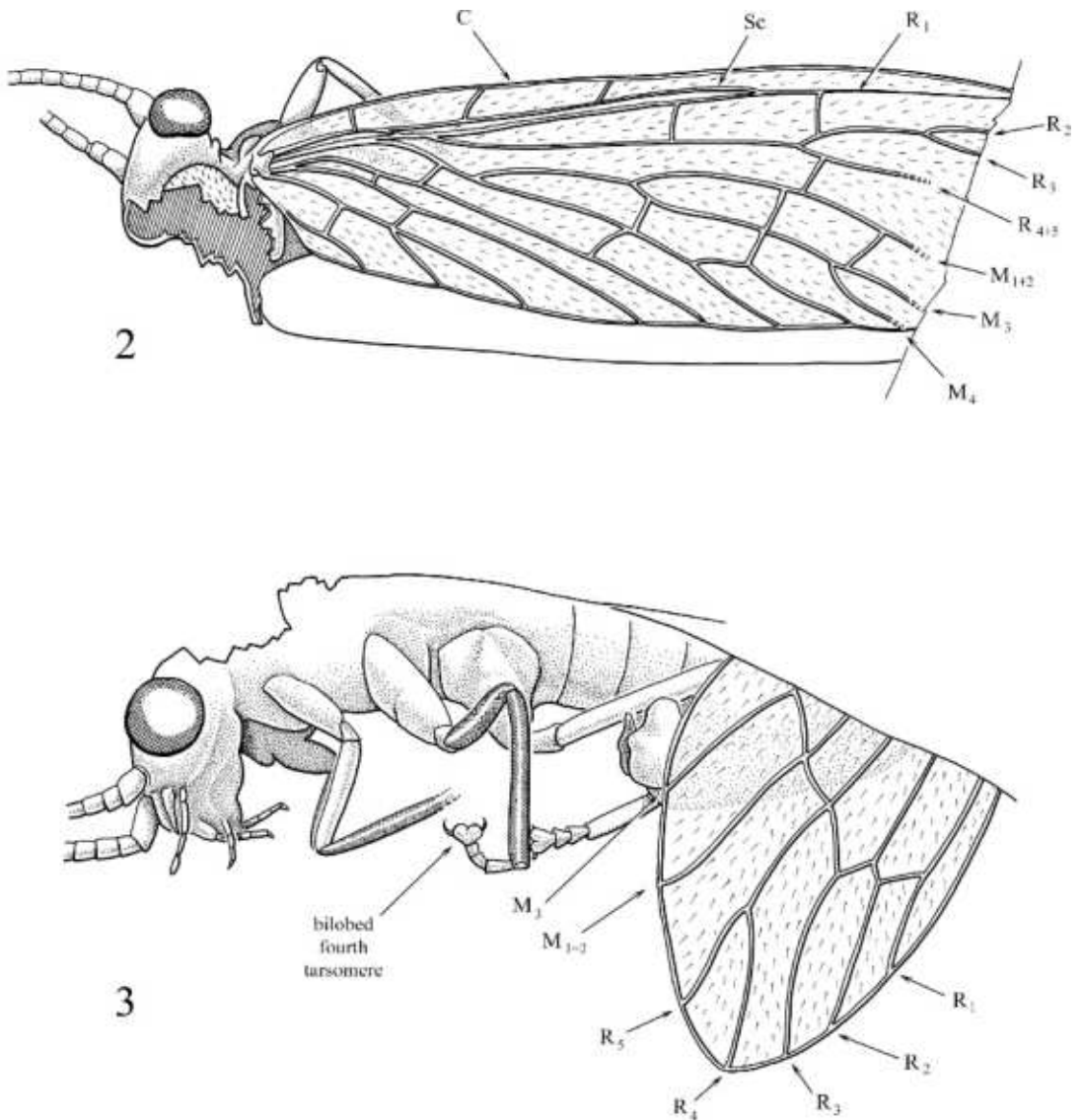
ETYMOLOGY: The specific epithet is taken from the Latin word *casca* (meaning “old”) and is a reference to the age of the specimen.

ORDER NEUROPTERA LINNAEUS
FAMILY MANTISPIDAE LEACH

The mantispids are perhaps one of the most instantly recognizable of neuropteran families and consist of approximately 400 species worldwide. Their convergent form with mantises (Mantodea) of an elongate prothorax and raptorial forelegs is remarkable. Adults tend



Fig. 1. Photomicrograph of holotype of *Sialis (Protosialis) casca*, new species (MACT-2090).



Figs. 2, 3. Holotype of *Sialis (Protosialis) casca*, new species (MACT-2090). 2. Dorsal aspect. 3. Left lateral aspect.

to be diurnal and are often found on flowers, although a few lineages are nocturnal or crepuscular. Some species are brightly colored and appear to mimic social, aculeate Hymenoptera. The most basal mantispids, the Symphrasinae, have sedentary larvae that are generalist predators found in the nests of social Hymenoptera, particularly vespids, or burrows of scarab beetle larvae. Similarly, the Calomantispinae appear to be generalist pred-

ators although the larvae of at least one studied species are ambulatory. The subfamily Drepanicinae is entirely unknown biologically. The largest subfamily, the Mantispinae and the subfamily to which the fossils described below belong, are specialized, obligate parasites of spiders, and the first-instar larva either boards a female spider and enters the egg sac as it is constructed, to feed on the eggs, or it searches directly for an egg sac. Later larval

TABLE 6
Named Fossil Mantispidae^a

Table	Deposit	Reference
<i>Climaciella? henrotayi</i> Nel	Oligocene, France	Nel, 1988b
<i>Dicromantispa electromexicana</i> n.sp.	Mexican amber	Present study
<i>Dicromantispa moronei</i> n.sp.	Dominican amber	Present study
<i>Ferosea prisca</i> Poinar	Dominican amber	Poinar, 2006
<i>Gerstaeckerella asiatica</i> Makarkin	Late Cretaceous, Kazakhstan	Makarkin, 1990
<i>Liassochyrsa stigmatica</i> Ansorge & Schülter	Early Jurassic, Germany	Ansorge & Schlüter, 1990; Wedmann & Makarkin, 2007
<i>Mesomantispa sibirica</i> Makarkin	Early Cretaceous, Siberia	Makarkin, 1996
<i>Promantispa similis</i> Panfilov	Late Jurassic, Karatau	Panfilov, 1980
<i>Prosagittalata oligocenica</i> Nel	Oligocene, France	Nel, 1988b
<i>Symphrasites eocenicus</i> Wedmann & Makarkin	Eocene, Germany	Wedmann & Makarkin, 2007
<i>Vectispa relictata</i> (Cockerell) ^b	Eocene, England	Cockerell, 1921

^aAlthough Willmann (1994) transferred the Cretaceous amber *Retinoberotha* and *Paraberotha* to Mantispidae, these are rhachiberothids. Similarly, *Whalfera venatrix* (Whalley, 1983) is excluded owing to its likely position in Rhachiberothidae (e.g., Engel, 2004b; Wedmann and Makarkin, 2007).

^bOriginally proposed in *Mantispa* and then transferred to *Promantispa* Jarzembowski (1980: nomen praeoccupatum, nec Panfilov, 1980) and finally to *Vectispa* Lambkin (1986: nomen novum pro *Promantispa* Jarzembowski, 1980).

instars are relatively immobile. Pupation occurs within the host egg sac. Adults are actively predaceous on a variety of other insect groups. Redborg (1998) has reviewed the available information on the remarkably specialized biology of Mantispidinae. Although Willmann (1990) included the Rhachiberothinae in Mantispidae, we follow Aspöck and Mansell (1994) and Aspöck et al. (2001) by considering this group as allied to the Berothidae.

The geological history of the Mantispidae has only recently begun to come together. Previously there were nine fossil species described from deposits ranging from the Early Jurassic to the Miocene (table 6: Wedmann and Makarkin, 2007), although the exact systematic position of some of these taxa is not entirely certain. Only two mantispid species had been discovered in amber until this time, but one is likely not a member of this family. *Walfera venatrix* (Whalley) was discovered in amber that had washed up on the eastern shore of Britain and presumably was derived from the Baltic amber deposits of the *blaue Erde*. The identity of *Whalfera*, however, has been questioned by many, and the genus is very likely a rhachiberothid (Aspöck and Mansell, 1994; Engel, 2004b; Grimaldi and Engel, 2005; Wedmann and Makarkin, 2007). The only other amber

mantispid is *Ferosea prisca* Poinar in Miocene Dominican amber (Poinar, 2006). Herein we report two further, definitive mantispids in Cenozoic amber from the Western Hemisphere. Spiders are common in Tertiary ambers of North America (e.g., Wunderlich, 1988; Penney, 1999), and it is therefore perhaps not surprising that their parasites would also eventually be discovered.

Dicromantispa electromexicana, new species
figures 4–8

Mantispa sp.: Engel, 2004c: 184.

Mantispa sp.: Grimaldi and Engel, 2005: 354, fig. 9.35.

DIAGNOSIS: This species is superficially similar to *Zeugomantispa minuta* (Fabricius) but differs by the more elongate pronotum that apparently lacks markings or bumps and has exceedingly sparse, minute pubescence, and by the structure of the ectoprocts. It can be separated from *D. moronei* in Dominican amber (see below) by the more elongate and unexpanded pronotum, absence of pronotal markings, major profemoral spine longer than protarsus, fewer c-sc crossveins, and smaller body size. The species can be separated from all modern *Dicromantispa* by the absence of the ventromedian lobe of the ectoproct. Such



Fig. 4. Photomicrograph of holotype male of *Dicromantispa electromexicana*, new species (CH-MP5).

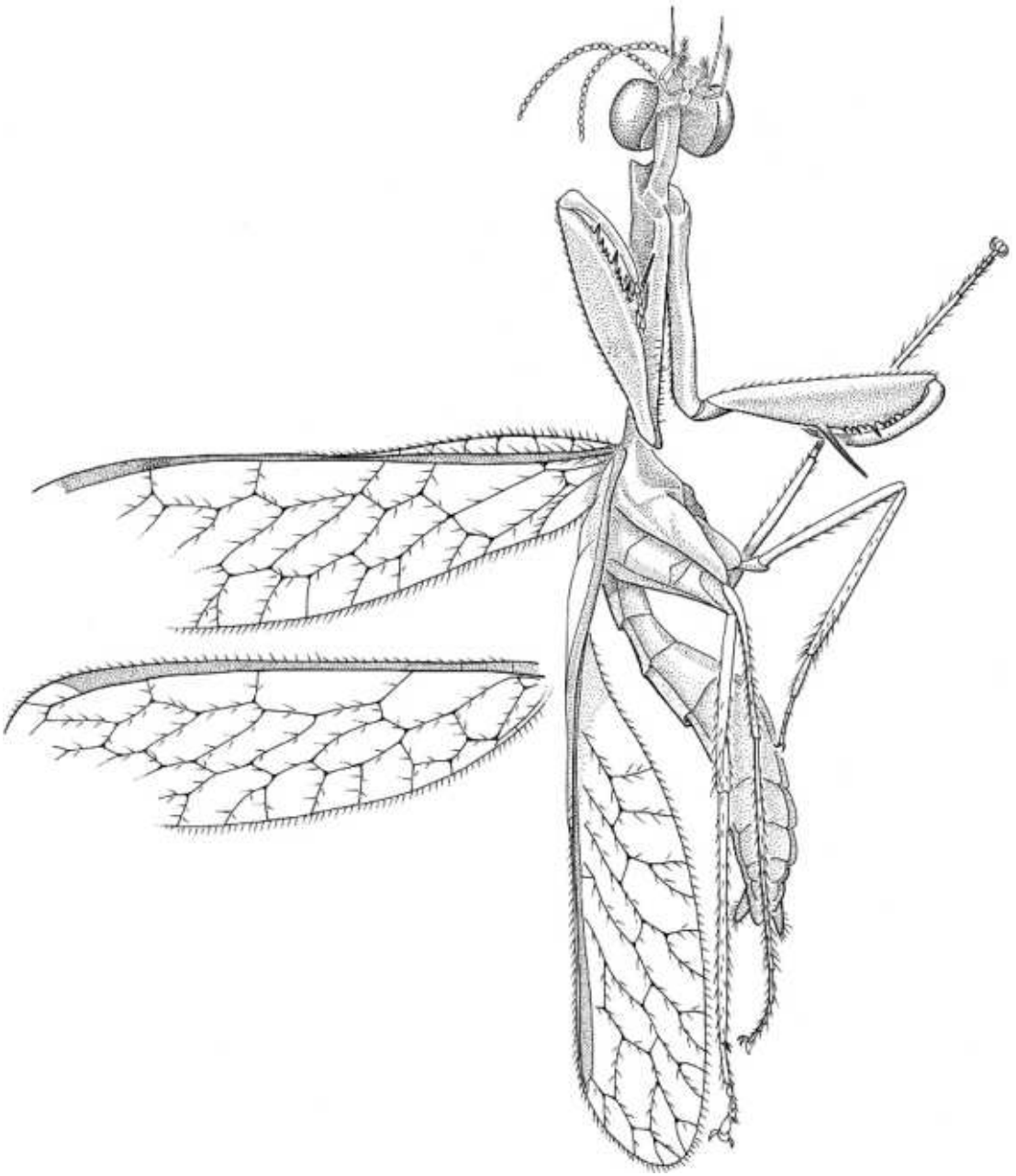
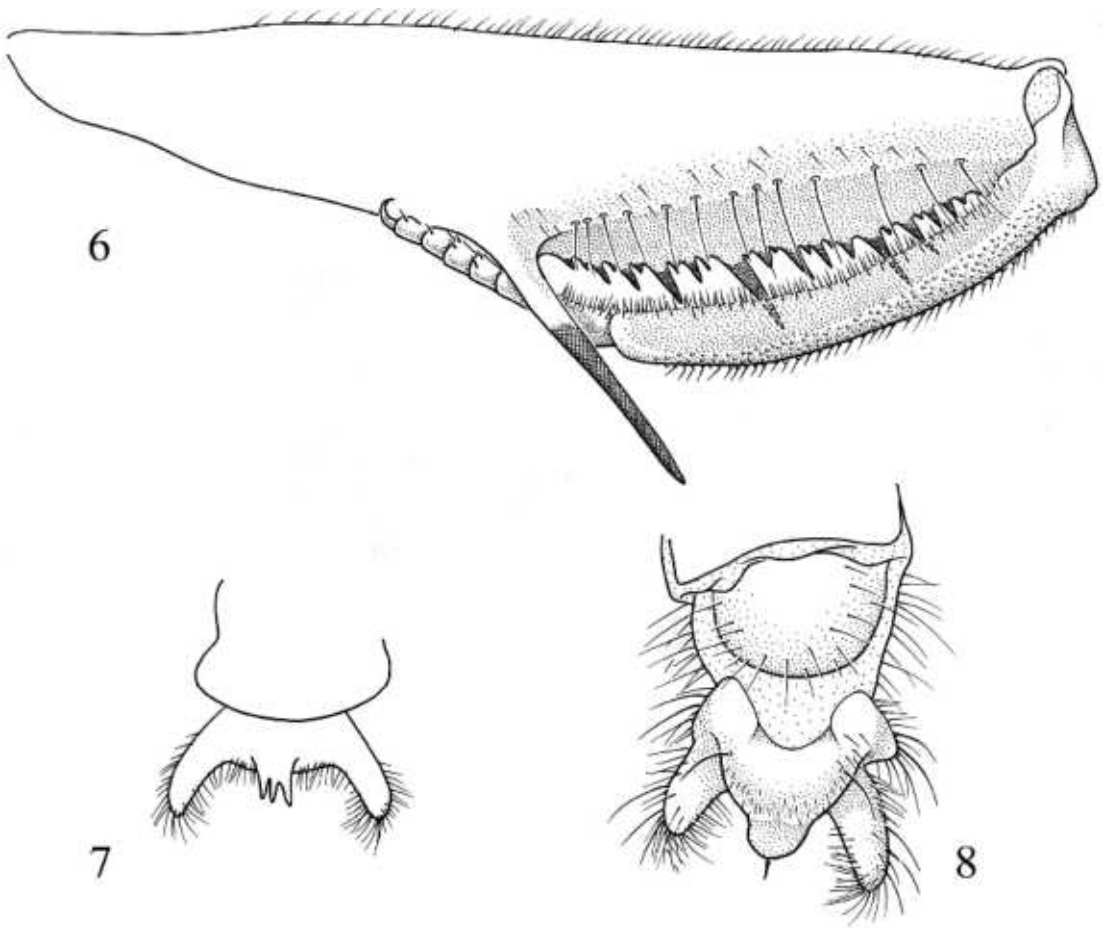


Fig. 5. Holotype male of *Dicromantispa electromexicana*, new species (CH-MP5).

a feature would appear to exclude the species from the genus. However, this feature is perhaps plesiomorphic, and in the absence of further genitalic details it seems unwarranted to establish a new genus for the species. In all other features the species best approx-

imates *Dicromantispa* among New World mantispids.

DESCRIPTION: Forewing length 7.97 mm; total body length 10.4 mm (figs. 4, 5); pronotum length 3.35 mm, width (median) 0.27 mm. Occipital margin of head absent.



Figs. 6–8. *Dicromantispa electromexicana*, new species (CH-MP5). 6. Detail of raptorial foreleg depicting profemoral spination. 7. Dorsal aspect of abdominal apex. 8. Ventral aspect of abdominal apex.

Scape, pedicel, and basal five flagellomeres piceous, remainder fuscous; 28 flagellomeres. Labial and maxillary palp segments elongate and tapering at apices. Pronotum elongate (length approx. 10 times width), not greatly expanded anteriorly; pubescence minute and extremely sparse; pronotum without markings; integument imbricate. Profemur with long, sharply pointed basal spine along inner margin, followed on outer margin by numerous short, pointed teeth intermixed with at least three intermediate length spines; basal, inner spine longest, longer than protarsus (fig. 6); integument of outer surface verrucose, otherwise imbricate. Pretarsal claws with three inner teeth except propretarsus with single claw and no arolium. Forewing longer than

abdomen; six subcostal crossveins (c-sc); pterostigma elongate, expanded apically, without markings. Hindwing with single gradate series; CuP bending sharply toward 1A; CuP separated from 1A at bend by extremely short crossvein (cup-a). Wing membrane hyaline.

Abdomen without markings; integument imbricate. Ninth sternum broadly rounded along apical margin. Ectoproct elongate and rounded with patch of dense, stiff, black setae on inner margin, without ventromedial lobe (figs. 7, 8).

HOLOTYPE: Male; AMNH CH-MP5 (fig. 4), Mexico, Chiapas, nr. Simojovel.

ETYMOLOGY: The specific epithet is a reference to the occurrence of this species in Mexican amber.

Dicromantispa moronei, new species
figures 9, 10

Mantispid sp.; Grimaldi, 1996: 93.

Mantispa sp.; Poinar and Poinar, 1999: 130, fig. 129.

Mantispa sp.; Poinar, 2006: 416.

DIAGNOSIS: Refer to diagnosis presented for *D. electromexicana* (above).

DESCRIPTION: Forewing length 14.5 mm; total body length 17.7 mm (fig. 9); pronotum length 7.7 mm, width (median) 0.6 mm, width (anterior) 1.3 mm. Occipital margin of head absent. Antenna light brown; 29 flagellomeres; F2–28 each wider than long; F1 longer than wide and slightly longer than combined lengths of F2–3; F29 conical. Labial and maxillary palp segments elongate and tapering at apices. Pronotum elongate (length approx. seven times maximum width), greatly expanded anteriorly; pubescence minute and extremely sparse; pronotum with light brown stripes along lateral posterior thirds; integument imbricate. Profemur with long, sharply pointed basal spine along inner margin, followed on outer margin by numerous short, pointed teeth intermixed with at least five intermediate length spines; basal, inner spine longest, slightly shorter than protarsus (fig. 10); integument of outer surface verrucose, otherwise imbricate. Pretarsal claws with three inner teeth except propretarsus with single claw and no arolium. Forewing longer than abdomen; seven subcostal crossveins (c-sc); pterostigma elongate, expanded apically, without markings. Hindwing with single gradate series; CuP bending sharply toward 1A; CuP separated from 1A at bend by extremely short crossvein (cup-a). Wing membrane hyaline.

Abdomen distended, apparently without markings.

HOLOTYPE: Female; MACT-432 (fig. 9), Miocene amber of the Dominican Republic.

ETYMOLOGY: The specific epithet is a patronymic honoring Dott. Ettore Morone, Turin, Italy.

Feroseta prisca Poinar, nomen emendatum

Feroseta prisca Poinar, 2006: 412.

COMMENTS: This species was only recently described from Miocene amber of the

Dominican Republic. We have not had the privilege of examining the holotype, as it resides in a private collection, but the description and published sketches of the specimen demonstrate that it is not conspecific with the taxa we have established herein. The species was placed in a new genus, the validity of which seems somewhat dubious. We have not been able to further investigate the placement of this species, and it is hoped that future students of the Mantispidae will be able provide greater clarity on the affinity of this fossil. The construction of the generic name, *Feroseta*, indicates a feminine gender and the specific epithet, therefore, must be emended to *prisca*.

FAMILY CONIOPTERYGIDAE BURMEISTER

The dustywings, family Coniopterygidae, perhaps occupy a relatively basal position among planipennian families owing to the retention of a well-developed and projecting labrum in the larva (Withycombe, 1924), although it has also been suggested that the family is more derived and allied to the Sisyridae and the Berothidae + Mantispidae + Dilaridae + Rhachiberothidae clade (e.g., Aspöck, 1992; Aspöck et al., 2001). There are approximately 460 living species presently recognized in the family (e.g., Meinander, 1972, 1990, 1995, 1998b; Sziraki, 1994, 1997; and various other supplements), which is distributed worldwide. Dustywings are relatively plant-specific and occur on conifers and deciduous trees or bushes. Adults and larvae are generalist predators, feeding on aphids, coccids, and mites, among other minute organisms.

At present, 16 fossil and two subfossil species of Coniopterygidae have been described (table 7), with the oldest being two species from the Late Jurassic of Eurasia. The fossil species were reviewed by Meinander (1975) with additions by Whalley (1980), Meinander (1998a), Grimaldi (2000), and Engel (2002b, 2004a). Until now only a single described species occurred in Dominican amber (Meinander, 1998a). Here we describe two new species: one of the genus *Coniopteryx* and the other of *Spiloconis*. Today *Coniopteryx* is distributed worldwide, and at least two species occur in the West Indies (Dominican



Fig. 9. Photomicrograph of holotype of *Dicromantispa moronei*, new species (MACT-432).

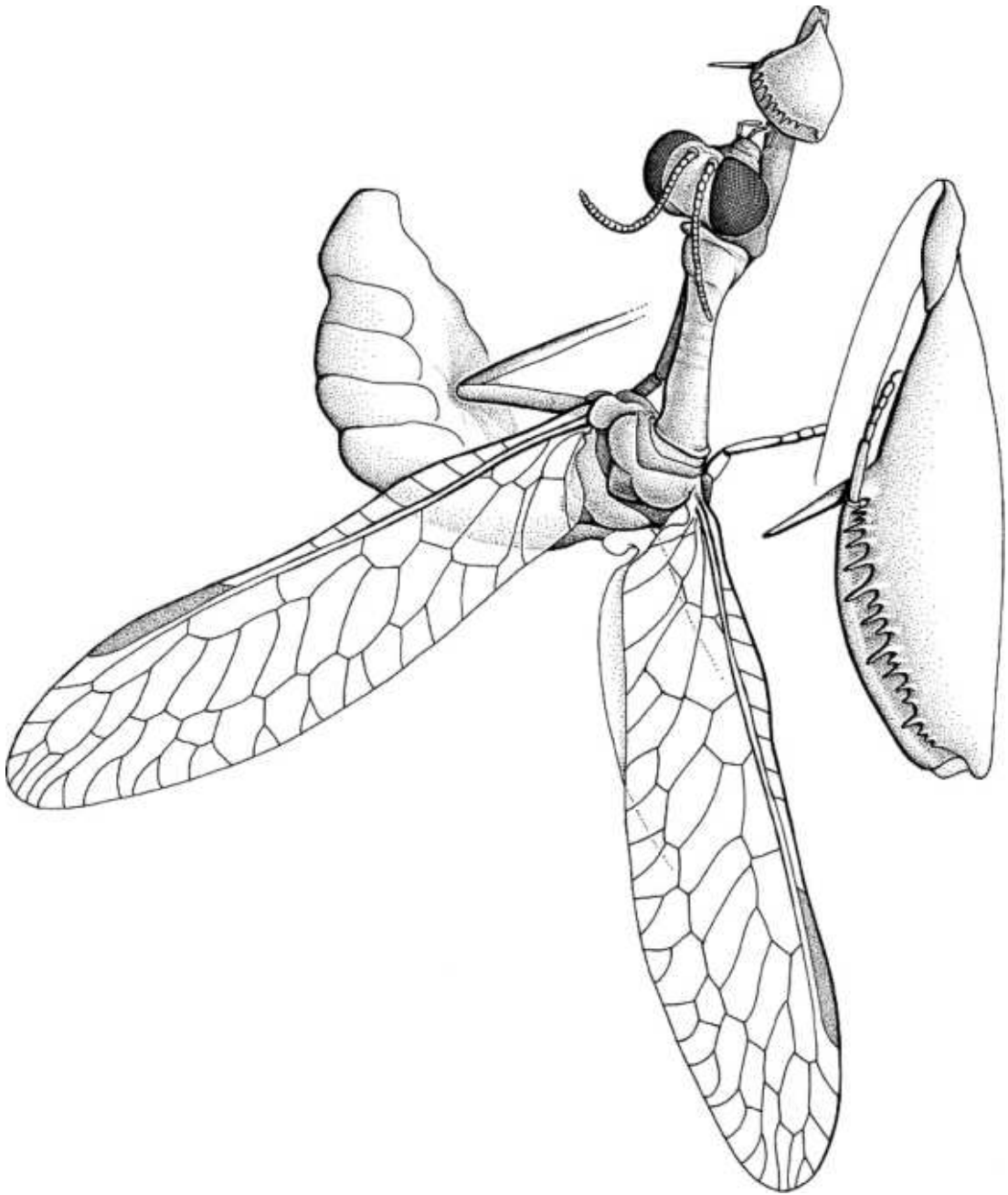


Fig. 10. Holotype of *Dicromantispa moronei*, new species (MACT-432), with details of foreleg enlarged.

Republic). The two species of apparently the genus *Spiloconis* would represent a remarkable extinction for the West Indian fauna, owing to the restricted presence of this genus to south-

east Asia, Australia, and some Oceanic Pacific Islands. However, the monophyly of *Spiloconis* is uncertain and may be an artifact of unresolved specific relationships.

TABLE 7
Named Fossil Coniopterygidae^a

Taxa	Deposit	Reference
<i>Alboconis cretacea</i> Nel et al.	Lebanese (Neocomian)	Nel et al., 2005a
<i>Apoglaesoconis ackermanni</i> Grimaldi	New Jersey amber	Grimaldi, 2000
<i>Apoglaesoconis cherylae</i> Engel	New Jersey amber	Engel, 2002b
<i>Apoglaesoconis luzzii</i> Grimaldi	New Jersey amber	Grimaldi, 2000
<i>Apoglaesoconis swolenskyi</i> Grimaldi	New Jersey amber	Grimaldi, 2000
<i>Archiconiocompsa prisca</i> Enderlein	Baltic amber	Enderlein, 1910
<i>Archiconis electrica</i> Enderlein	Baltic amber	Enderlein, 1930
<i>Coniopteryx antiquua</i> n.sp.	Dominican amber	Present study
<i>Coniopteryx enderleini</i> Meunier ^b	African copal	Meunier, 1910a
<i>Coniopteryx timidus</i> (Hagen)	Baltic amber	Pictet-Baraban & Hagen, 1856; Meinander, 1972, 1975
<i>Gallosemidalis eocenica</i> Nel et al.	Parisian (Eocene)	Nel et al., 2005a
<i>Glaesoconis balipteryx</i> Engel	Burmese amber	Engel, 2004a
<i>Glaesoconis cretica</i> Meinander	Siberian amber	Meinander, 1975
<i>Glaesoconis nearctica</i> Grimaldi	New Jersey amber	Grimaldi, 2000
<i>Heminipheta fritschi</i> Enderlein	Baltic amber	Enderlein, 1930
<i>Hemisemidalis kulickae</i> Dobosz & Krzemiński	Baltic amber	Dobosz & Krzemiński, 2000
<i>Hemisemidalis sharovi</i> Meinander	Baltic amber	Meinander, 1975
<i>Juracoconiopteryx zherichini</i> Meinander	Jurassic, Kazakhstan	Meinander, 1975
<i>Libanoconis fadiacra</i> (Whalley)	Lebanese amber	Whalley, 1980; Engel, 2002b
<i>Pararchiconis quievreuxi</i> Nel	Oligocene, France	Nel, 1990
<i>Phthanoconis burmitica</i> Engel	Burmese amber	Engel, 2004a
<i>Semidalis copalina</i> Meunier ^b	Malagasy copal	Meunier, 1910b
<i>Spiloconis glaesaria</i> Meinander	Dominican amber	Meinander, 1998a
<i>Spiloconis oediloma</i> n.sp.	Dominican amber	Present study

^aAnsorge (1996) transferred the Liassic fossil *Archiconiopteryx liasina* (Handlirsch, 1906; Enderlein, 1909) to a separate family, Archiconiopterygidae, in the Hemiptera.

^bThe two subfossil species described from copal (*Coniopteryx enderleini* and *Semidalis copalina*) are likely synonymous with extant species.

Coniopteryx antiquua, new species
figures 11–16

DIAGNOSIS: Body lacking typical scalelike setae, basal flagellomeres wider than long, and wing membranes hyaline.

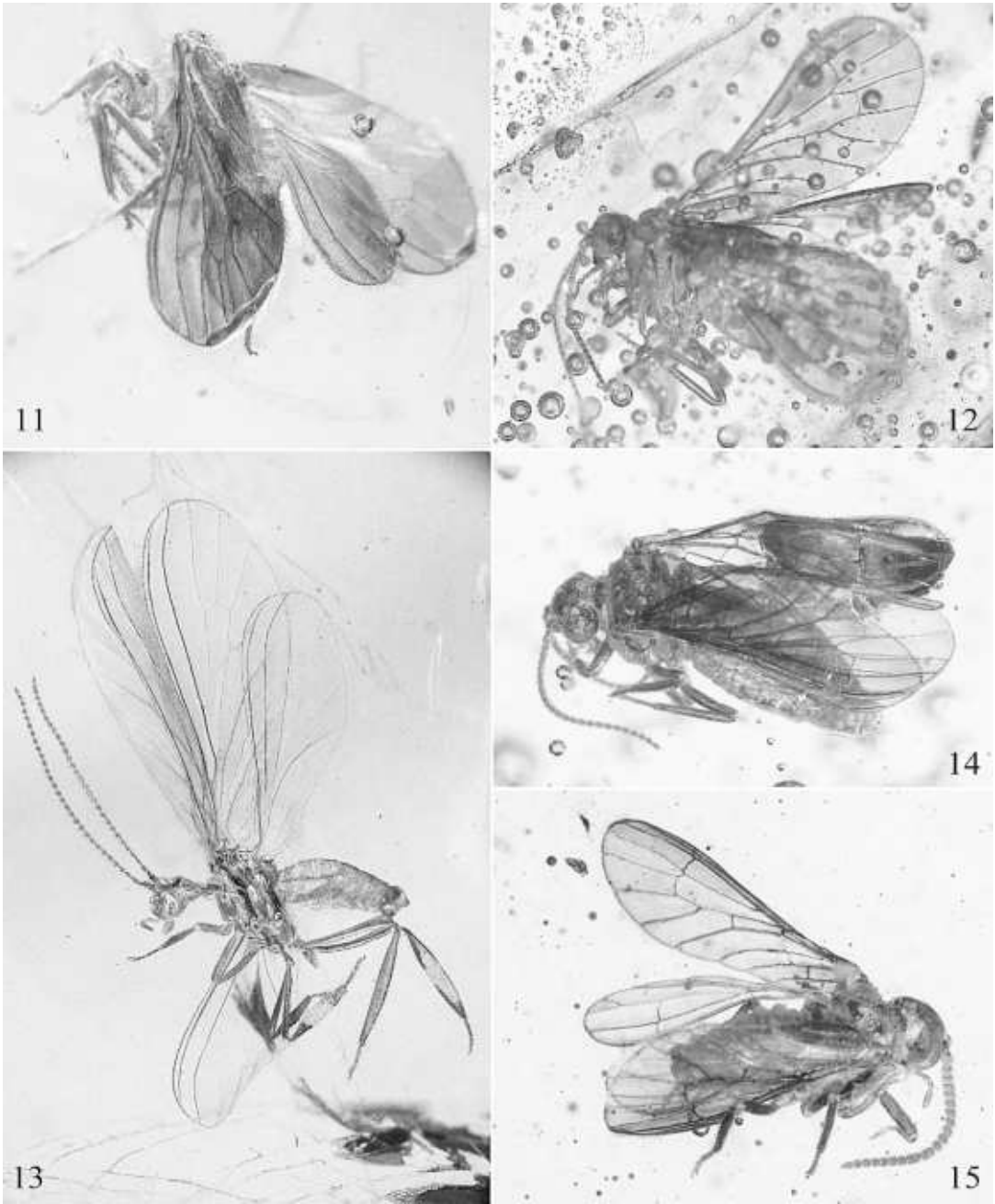
DESCRIPTION: Total body length 1.05 (1.05–1.77) mm; forewing length 1.48 (1.41–2.01) mm. Maxillary palpus normal, i.e., third segment slightly longer than broad. Frons slightly swollen between and above antennae, without hook. Antennae with whorls of setae, some as long as flagellomere width; basal flagellar articles wider than long, progressively becoming as wide as long. Integument pale brown, antennae concolorous. Body with sparse, minute setae, without scalelike setae; legs with scattered short setae, mostly on

tibiae. Wing membrane hyaline; veins pale brown.

HOLOTYPE: Male; AMNH DR-14-25 (fig. 11), Miocene amber of the Dominican Republic, northern mines.

PARATYPES: Female; AMNH DR-10-14 (fig. 14), Miocene amber of the Dominican Republic. AMNH DR-14-268 (fig. 12), Miocene amber of the Dominican Republic. AMNH DR-10-15 (fig. 15), Miocene amber of the Dominican Republic. AMNH DR-14-853 (fig. 13), Miocene amber of the Dominican Republic. MACT-2966 (fig. 16), Miocene amber of the Dominican Republic. MACT-2760, Miocene amber of the Dominican Republic.

ETYMOLOGY: The specific epithet is taken from Latin *antiquus* and is a reference to the antiquity of the species.



Figs. 11–15. *Coniopteryx antiquua*, new species. 11. Holotype (DR-14-25). 12. Paratype female (DR-014-268). 13. Paratype male (DR-14-853). 14. Paratype (DR-10-14). 15. Paratype (DR-10-15).



Fig. 16. Paratype of *Coniopteryx antiquua*, new species (MACT-2966).

Spiloconis glaesaria Meinander
figures 17, 18

Spiloconis glaesaria Meinander, 1998a: 33.

DIAGNOSIS: A larger species with forewing length 2.33–2.35 mm and body size 2.00–2.05 mm (latter metrics from holotype). Basalmost flagellomere similar to following segments, not distinctly swollen by comparison. Crossvein r-rs meeting stem of Rs slightly before R_{2+3}/R_{4+5} fork.

HOLOTYPE: Female; AMNH DR-10-59 (fig. 17), Miocene amber of the Dominican Republic.

NEW MATERIAL: Female; AMNH DR-14-1094 (fig. 18), Miocene amber of the Dominican Republic.

COMMENTS: Since this species was described a second female has been identified in the collection of the AMNH (refer to Meinander [1998a] for a description of the species). The second specimen reported herein agrees with the holotype except in the position of the distalmost seta on M being apicad of the junction of the basal rs-m and cua-m crossveins.

Spiloconis oediloma, new species
figures 19, 20

DIAGNOSIS: This species differs from *S. glaesaria* by the smaller forewing length and body size (fig. 19), the swollen basal flagello-

mere that is distinctly larger than the following segments, and the r-rs crossvein distad to the fork of Rs (thereby meeting R_{2+3}) (fig. 20).

DESCRIPTION: Forewing length 1.85 mm; total body length 1.38 mm. Compound eyes not reduced, more than one-half of head height; gena only slightly narrower than compound eye in lateral view (the gena is considerably more narrow than the compound eye in *S. glaesaria*); head brown. Antenna 23-segmented, uniformly dark brown; scape twice as long as broad; basal flagellomere distinctly larger than following flagellomeres; segments with two whorls of setae. Thorax dark brown; legs light brown. Forewing with dark markings faint but as described for *S. glaesaria*; distal setae on M near junction of basal rs-m and cua-m crossveins; basal rs-m crossvein shortly beyond R/Rs fork; distal rs-m on R_{4+5} ; sc-r crossvein confluent with r-rs crossvein, r-rs distad fork or Rs and meeting R_{2+3} (fig. 20).

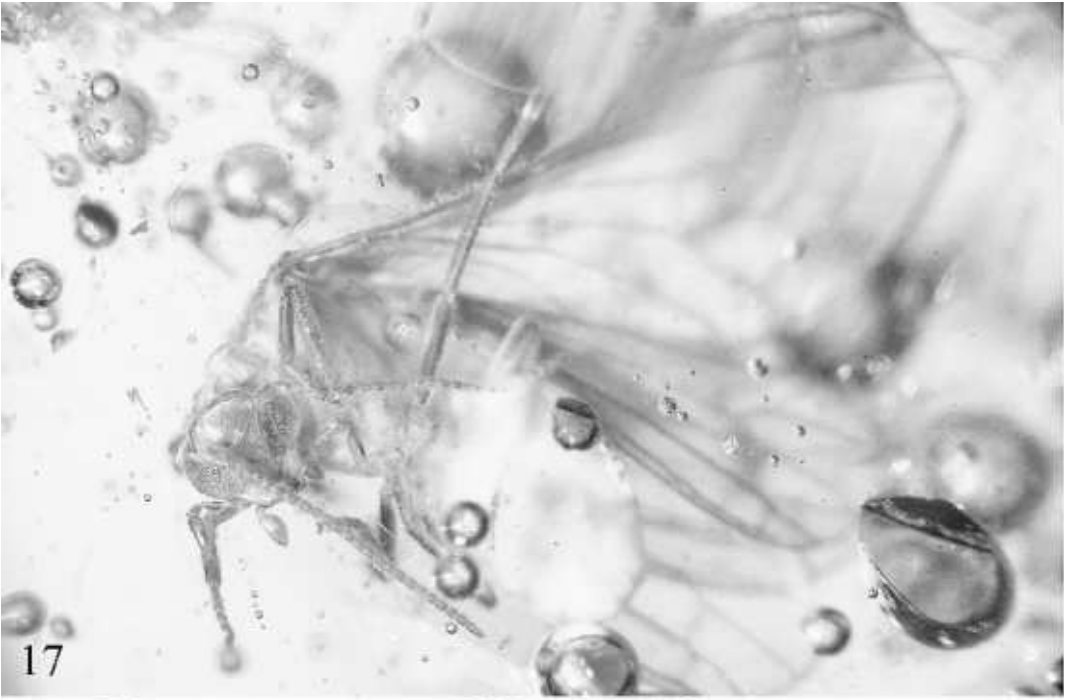
HOLOTYPE: AMNH DR-14-1097 (fig. 19), Miocene amber of the Dominican Republic.

ETYMOLOGY: The specific epithet is derived from the Greek word *oidaleos* (meaning “swollen”) and is a reference to the enlarged basal flagellar segment.

FAMILY HEMEROBIIIDAE LATREILLE

The family Hemerobiidae, the brown lacewings, consists of approximately 560 species distributed throughout the world. Species occur on vegetation as both adults and larvae, presumably owing to the occurrence of their principle prey (e.g., Sternorrhyncha) in these habitats. Larvae are predaceous and while adults are presumed to be as well, little information is available on their feeding habits. Some adults have been discovered eating honeydew.

Brown lacewings are not common in the fossil record (table 8), and a confident identity for those described in Baltic amber has yet to be achieved. The oldest hemerobiid is presently a single species from the Jurassic of Kazakhstan and shares at least a few synapomorphies typical of Tertiary and recent hemerobiids (Oswald, 1993). Presently there are two species known in Dominican amber, one of which (*Notiobiella thaumasta* Oswald) appears to be more common than other Dominican neuropterid fossils.



Figs. 17, 18. *Spiloconis glaesaria* Meinander. 17. Holotype (DR-10-59). 18. Newly discovered female (DR-14-1094).



Fig. 19. Photomicrograph of holotype of *Spiloconis oediloma*, new species (DR-14-1097).

The first amber hemerobiid discovered was of the Notiobiellinae and the nominate genus, in particular. The genus *Notiobiella* is widely distributed with species occurring in South and Central America, Africa, southeast Asia, Australia, and scattered Pacific islands. Of the approximately 36 described species, two occur today in the West Indies, and the fossil *N.*

thaumasta is apparently most closely related to *N. israeli* from Cuba and Hispaniola (Oswald, 1999). The second species is a new species of the Sympherobiinae. The species described below falls readily into the Sympherobiinae and *Sympherobius* except for one character (presence/absence of 4m-cu: see Comments below under the species). *Sympherobius* is

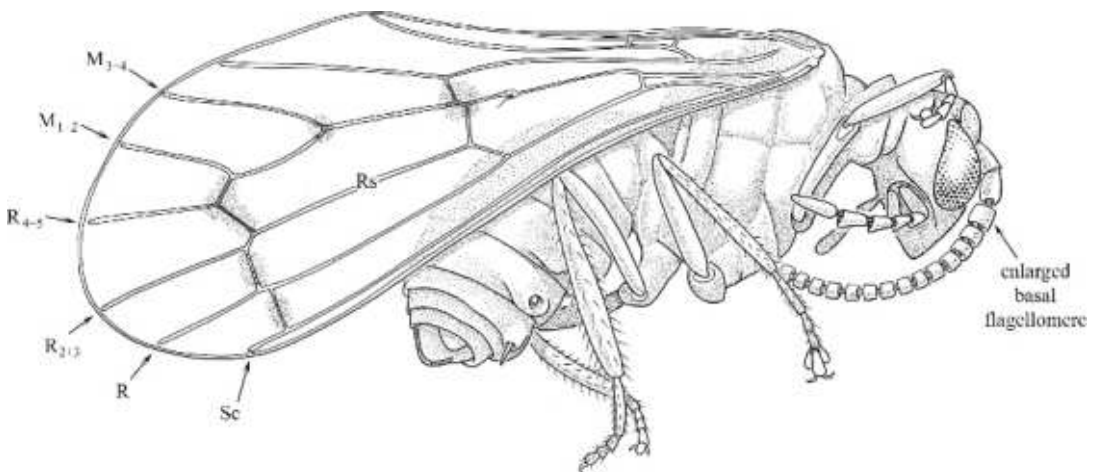


Fig. 20. Holotype of *Spiloconis oediloma*, new species (DR-14-1097).

TABLE 8
Named Fossil Hemerobiidae^a
 (an unnamed species of *Symphorobius* is reported herein in Dominican amber)

Taxa	Deposit	Reference
<i>Bothromicromus lachlani</i> Scudder	British Columbia	Scudder, 1878
<i>Cretomerobius disjunctus</i> Ponomarenko	Cretaceous, Mongolia	Ponomarenko, 1992
<i>Cretomerobius wehri</i> Makarkin et al.	Eocene, Washington	Makarkin et al., 2003
<i>Drepanopteryx oedobia</i> Makarkin	Miocene, Caucasus	Makarkin, 1991
<i>Drepanopteryx ramosa</i> Makarkin	Miocene, Caucasus	Makarkin, 1991
<i>Hemerobites antiquus</i> Germar	Baltic amber	Germar, 1813
<i>Hemerobius incertus</i> Makarkin	Miocene, Caucasus	Makarkin, 1991
<i>Hemerobius prohumulinus</i> Makarkin	Miocene, Caucasus	Makarkin, 1991
<i>Hemerobius tinctus</i> Jarzembowski	Eocene, England	Jarzembowski, 1980
<i>Megalomus caucasicus</i> Makarkin	Miocene, Caucasus	Makarkin, 1991
<i>Megalomus densistriatus</i> Henriksen	Eocene, Denmark	Henriksen, 1922
<i>Megalomus sikhotesensis</i> Makarkin	Miocene, Caucasus	Makarkin, 1991
<i>Notiobiella thaumasta</i> Oswald	Dominican amber	Oswald, 1999
<i>Prochlanius resinatus</i> (Hagen)	Baltic amber	Pictet-Baraban & Hagen, 1856; Krüger, 1923
<i>Promegalomus anomalus</i> Panfilov ^b	Jurassic, Kazakhstan	Panfilov, 1980
<i>Prophlebonema resinata</i> Krüger	Baltic amber	Krüger, 1923
<i>Prospadobius moestus</i> (Hagen)	Baltic amber	Pictet-Baraban & Hagen, 1856; Krüger, 1923
<i>Wesmaelius mathewesi</i> Makarkin et al.	Eocene, Canada	Makarkin et al., 2003

^a*Mesohemerobius jeholensis* Ping (1928), from the Cretaceous of China, was removed from Hemerobiidae and considered as Neuroptera incertae sedis by Makarkin et al. (2003).

^bOriginally placed in its own family, Promegalomidae, but transferred to Hemerobiidae by Oswald (1993) through synonymy of the junior family.

widely distributed in tropical regions of North and South America and temperate regions of the former two continents as well as Africa, Asia, and Europe. Like *Notiobiella*, only two living species, *Symphorobius insulanus* Banks and *S. zelenyi* Alayo, are distributed in the West Indies, both on the island of Cuba (Alayo, 1968; Oswald, 1988).

Morphological terminology follows that of Oswald (1993).

Notiobiella thaumasta Oswald
 figures 21–25

Notiobiella thaumasta Oswald, 1999 [2000]: 298.

HOLOTYPE: Male; AMNH DR-14-1124 (fig. 25), Miocene amber of the Dominican Republic.

PARATYPES: Female; AMNH DR-14-1124, Miocene amber of the Dominican Republic. Female; AMNH DR-14-1129, Miocene amber of the Dominican Republic. Female; AMNH DR-SH-18, Miocene amber of the Dominican Republic.

NEW MATERIAL: MACT-3397 (fig. 21), Miocene amber of the Dominican Republic.

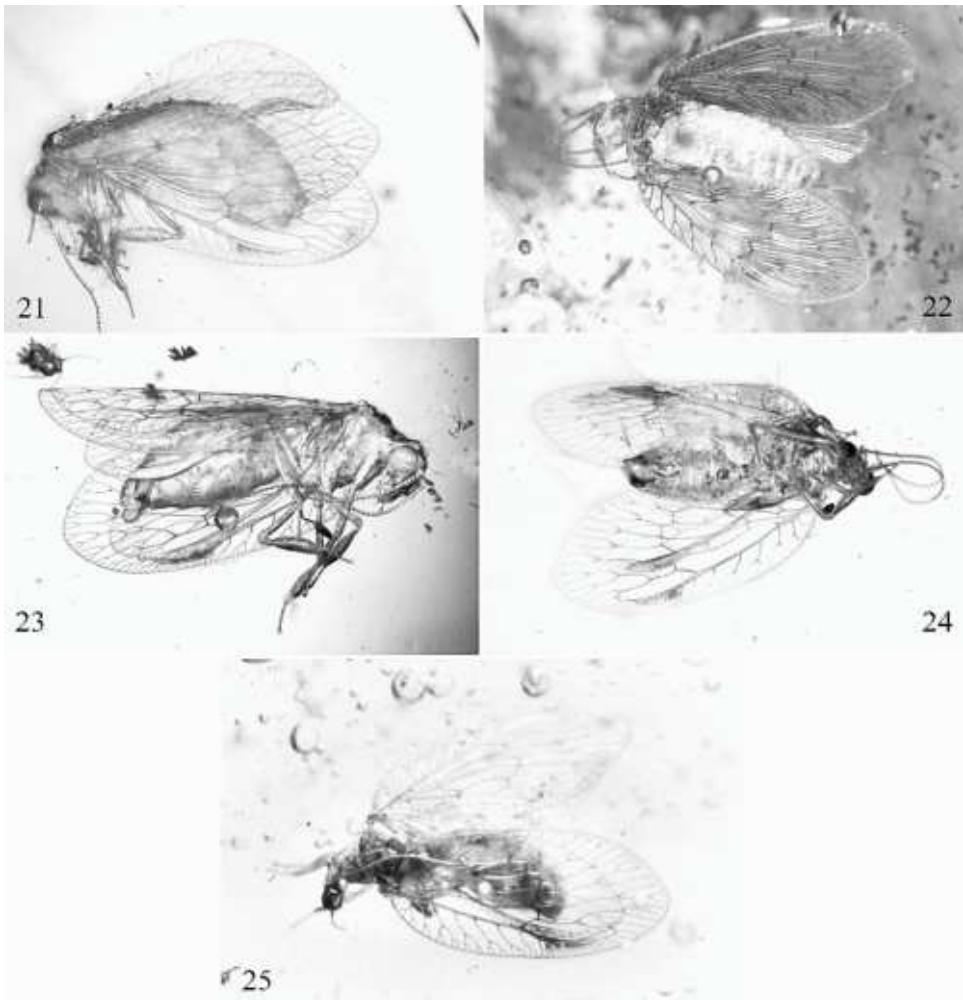
MACT-2972 (fig. 22), Miocene amber of the Dominican Republic. MACT-3240 (fig. 23), Miocene amber of the Dominican Republic. MACT-3241, Miocene amber of the Dominican Republic. MACT-2965 (fig. 24), Miocene amber of the Dominican Republic. MACT-1092, Miocene amber of the Dominican Republic.

COMMENTS: This species was recently described on the basis of a single male and three female specimens. The new material does not alter the concept of the species, and therefore the description of Oswald (1999) is not repeated or emended here.

Symphorobius sp.

DIAGNOSIS: The species is unique within the genus for the plesiomorphic retention of crossvein 4m-cu (absent in all Recent *Symphorobius*), the presence of the distal radial crossvein ($r_{2+3-r_{4+5}}$), and the unpatterned wings.

DESCRIPTION: Total body length 2.52 mm; forewing length 2.53 mm. Integument light brown; flagellum concolorous; 42 flagello-



Figs. 21–25. Photomicrographs of *Notiobiella thaumata* Oswald. 21. MACT-3397. 22. MACT-2972. 23. MACT-3240. 24. MACT-2965. 25. Holotype (DR-14-1124).

meres (observed for left antenna; right antenna damaged slightly beyond midpoint). Wing membrane hyaline; longitudinal veins and crossveins light brown. Forewing with proximal humeral trace strongly recurrent, trichosores present on humeral margin, humeral veinlets simple; costal space broad; Sc widely separated from R along its entire length; 2sc-r absent; two prestigmal radial sectors, posterior radial sector with a single branch proximad midpoint; four interrarial crossveins comprising outer gradate series, outer gradates alternating in position (not stepped in a single direction); proximal radial crossvein ($r_{1+2+3-r_{4+5}}$) absent; distal radial crossvein ($r_{2+3-r_{4+5}}$)

present; two r-m crossveins (i.e., 2r-m and 3r-m), 4r-m absent; 3im present, 4im absent; 4m-cu present; CuA branching distad 2m-cu, next branch confluent with 3m-cu; CuP simple, not forked proximad 2cua-cup. Setae generally pale brown, minute, and sparse except on wings setae more elongate and numerous and at abdominal apex setae elongate. Terminalia not visible.

MATERIAL: Private collection of J.M. Pérez, Miocene amber of the Dominican Republic.

COMMENTS: Owing to the uncertain final repository of the only known specimen (which resides in the collection of a dealer who

intends to sell it), we have avoided describing this species as new until such time as new material is discovered or the specimen is deposited in a more permanent collection, preferably that of a museum.

The fossil can be easily assigned to the Sympherobiinae based on the following combination of characters in the forewing: proximal humeral trace recurrent (strongly so in the fossil), trichosores present on humeral margin, broad costal space, 2sc-r absent, two prestigmal radial sectors, posterior radial sector branching proximad its midpoint, 4r-m absent, and CuP simple, not forked proximad 2cua-cup. Within the sympherobiines, the fossil is apparently sister to living *Sympherobius* and is placed basal within this genus. Although the fossil lacks one of the four synapomorphies of the genus (i.e., apomorphic loss of forewing 4m-cu), we have placed the species here rather than erect a monotypic genus sister to *Sympherobius* based upon a single character (moreover, a single *plesiomorphic* character!). Both *Nomerobius* and *Neosympherobius* plesiomorphically retain 4m-cu (as well as 4im in the forewing, which is absent in the fossil). The fossil can be immediately excluded from both of these genera as follows: absence of 4im in forewing (present in *Nomerobius* and *Neosympherobius*), presence of outer gradates (absent in *Neosympherobius*), four outer gradates alternating in position (stepped in a single direction in *Nomerobius*). Until a cladistic study of the world *Sympherobius* fauna is completed, it is not possible to definitively determine whether the fossil is indeed sister to the remainder of the genus, but the loss of 4m-cu would apparently be a good synapomorphy of Recent *Sympherobius*, as it was originally hypothesized by Oswald (1993). However, note that the fossil is not without some similarity to the principally eastern United States species *S. amicus* (Fitch) and *S. umbratus* (Banks), all of which are unique among *Sympherobius* for the presence of a distal radial crossvein, this being either a plesiomorphy or the secondary reacquisition of this feature (as hypothesized by Oswald [1988] for the two living species). It is certainly plausible that this character is a plesiomorphy for the fossil and a synapomorphy for the two

living species rather than a character uniting all three taxa (i.e., if the fossil is indeed basal while *S. amicus* and *S. umbratus* are more derived, as other characters would suggest). Such determination will await a cladistic analysis for all *Sympherobius*.

FAMILY CHRYSOPIDAE SCHNEIDER

Larvae are active, generalist predators. Some species rapidly cover themselves with debris (held in place by long, curved setae), which may include remains of their prey. Most species are arboreal. Adults are commonly predators although some lineages are specialized to feed on honeydew and harbor symbiotic yeasts, presumably to facilitate digestion.

Although a veritable plethora of chrysopid fossils have been previously described or reported on (e.g., Adams, 1967; Carpenter, 1935; Cockerell, 1909, 1914; Handlirsch, 1908; Handschin, 1937; Makarkin, 1991, 1994; Martins-Neto and Vulcano, 1989c; Martynov, 1927; Nel and Henrotay, 1994; Nel and Séméria, 1986; Panfilov, 1980; Peñalver et al., 1995; Ren and Guo, 1996; Schlüter, 1982; Scudder, 1890; Séméria and Nel, 1990; Statz, 1936; Willmann and Brooks, 1991), none has been discovered in amber until now. Fossils recognizable as Chrysopidae (albeit of an extinct, plesiomorphic subfamily) are known as far back as the Late Jurassic. The wing terminology of Brooks and Barnard (1990) is used for the three chrysopine fossils described herein to facilitate comparison with their monograph on the world fauna of living Chrysopidae.

The genera *Chrysopa* and *Chrysoperla* are separated mostly by behavior and minutiae of the terminalia. However, there are some minor differences of wing venation that distinguish these two genera. Both of the fossils considered below fall within the *Chrysopa* class of wing venation and are therefore considered to be of this genus.

Chrysopa? glaesaria, new species figures 26, 27

Chrysopa sp.: Grimaldi and Engel, 2005: 351, fig. 9.30.

DIAGNOSIS: This species differs most notably from *C. vetula*, also in Dominican amber,

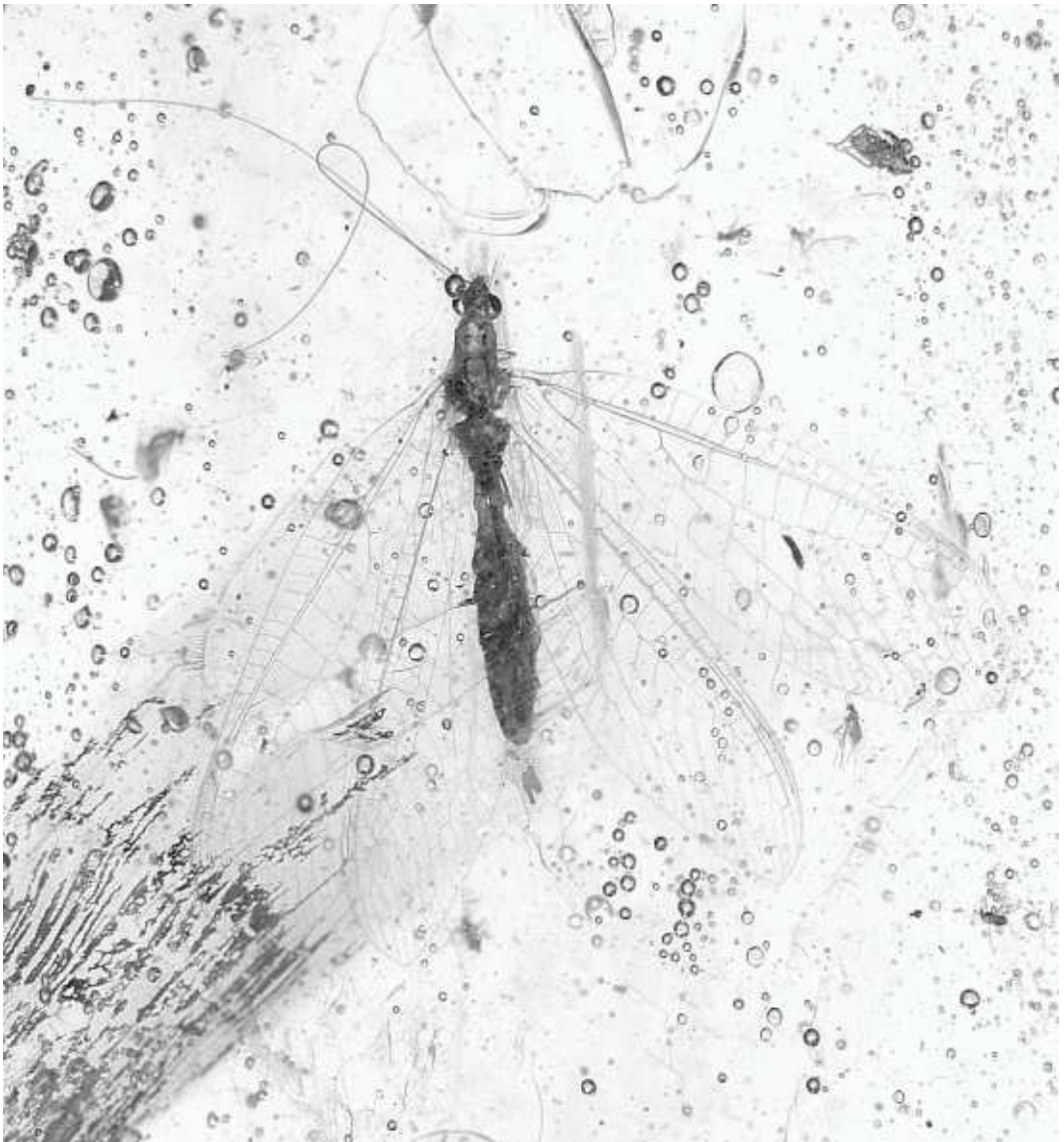


Fig. 26. Photomicrograph of *Chrysopa glaesaria*, new species (MACT-1221).

by the submedian longitudinal stripes on the pronotum and larger size. Other differences are presented in the following description.

DESCRIPTION: Forewing length 16 mm; total body length 12.1 mm; pronotum length 1.0 mm, width 1.25 mm. Integument generally golden with faint green highlights except when indicated below; integument faintly imbricate. Palpi tapering at apices; labrum emarginate; lateral quarters of clypeus black; scapes close

together with black on inner surfaces; flagellum about as long as forewing.

Pronotum with two narrow, longitudinal stripes of dark brown on either side of midline, lateral margins not marked, slightly wider than long, anterior margin broadly rounded; meso- and metathoracic pleura dark brown, mesothorax with narrow, longitudinal stripes of dark brown on either side of midline, laterally unmarked.

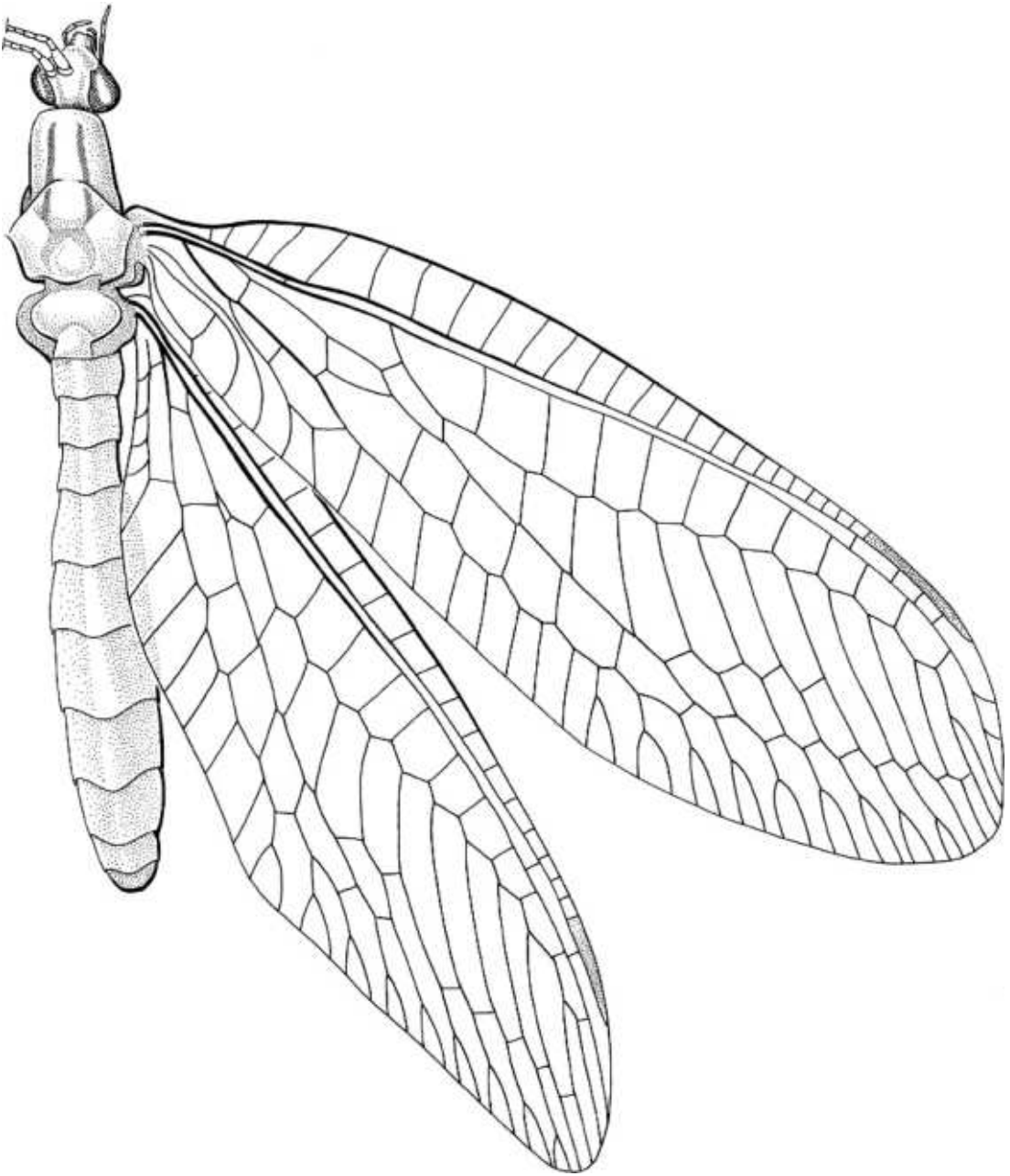


Fig. 27. Holotype of *Chrysopa glaesaria*, new species (MACT-1221).

Forewing oval and broad, longer than abdomen, with sparse setae except along margins; 22 costal crossveins (c-sc); costal area narrows progressively toward apex; Sc and R deviate slightly near apex, Sc joins C at apex; R straight, not sinuous; single sc-r

crossvein toward wing base (vein *bsc*), four sc-r crossveins below pterostigma; pterostigma elongate and unmarked; cell *m1* much smaller than *m2* (as typical for *Chrysopa*, while in *Plesiochrysa* these cells are closer in size); cell *im* ovate, broad, first rs-m crossvein meets *im*

subapically; no radial crossvein (r-m) basal to origin of Rs, radial crossveins straight; cell *c1* shorter than *c2*; cell *dec* narrowly open along posterior wing margin; six closed cells between PsM and PsC; two gradate series, inner gradate series incomplete, anterior gradates absent, gradates parallel; 1A forked (fig. 27). Hindwing with two gradate series. Wing membrane hyaline; veins light brown.

Abdomen apparently with basal bands of dark brown on terga; eighth and ninth terga not fused; sternum two without stridulatory apparatus; callus cerci rounded.

HOLOTYPE: Female; MACT-1221 (figs. 26–27), Miocene amber of the Dominican Republic.

ETYMOLOGY: The specific epithet is derived from the Latin word *glaesarius*, meaning “of amber”.

Chrysopa? vetula, new species

figures 28–31

DIAGNOSIS: Refer to diagnosis presented for *C. glaesaria* (above).

DESCRIPTION: Forewing length 9.7 mm; total body length 7.6 mm; pronotum length 0.7 mm, width 0.75 mm. Integument generally golden with faint green highlights except when indicated below; integument strongly imbricate. Palpi tapering at apices; labrum emarginate; lateralmost borders of clypeus black; scapes close together with black on inner and outer surfaces; flagellum about as long as forewing.

Pronotum with two narrow, longitudinal stripes of dark brown on lateral borders, slightly wider than long, anterior margin broadly rounded; meso- and metathoracic pleura apparently light brown, mesothorax with narrow, longitudinal stripes of dark brown on anterolateral margins.

Forewing oval and broad, longer than abdomen, with sparse setae; 18 costal crossveins (c-sc); costal area narrows progressively toward apex; Sc and R deviate slightly near apex, Sc joins C at apex; R straight, not sinuous; single sc-r crossvein toward wing base (vein *bsc*), three sc-r crossveins below pterostigma; pterostigma elongate and unmarked; cell *m1* much smaller than *m2*; cell *im* ovate, relatively narrow, first rs-m crossvein meets *im*

subapically; no radial crossvein (r-m) basal to origin of Rs, radial crossveins straight; cell *c1* shorter than *c2*; cell *dec* narrowly open along posterior wing margin; six closed cells between PsM and PsC; two gradate series, inner gradate series incomplete, anterior gradates absent, gradates parallel; 1A forked. Hindwing with two gradate series. Wing membrane hyaline; veins light brown.

Abdomen apparently light brown, somewhat distended; eighth and ninth terga apparently not fused; sternum two without stridulatory apparatus.

HOLOTYPE: Female; MACT-1246 (fig. 28), Miocene amber of the Dominican Republic.

ETYMOLOGY: The specific epithet is derived from the Latin word *vetus* (meaning “old”).

Leucochrysa (Nodita) prisca, new species

figures 32, 33

DIAGNOSIS: A relatively small species of *Leucochrysa* (at a forewing length of 10.5 mm) lacking the red or brown markings of the head.

DESCRIPTION: Forewing length 10.5 mm; total body length 6.6 mm; pronotum length 0.63 mm, width 0.73 mm. Head apparently light brown, antennae uniformly light brown, face darker brown below level of antennae, markings apparently absent; integument apparently imbricate. Palpi tapering at apices; labrum emarginate; flagellum about as long as forewing.

Pronotum apparently unmarked, slightly longer than wide, anterior margin broadly rounded; remainder of body apparently light brown, perhaps with metallic highlights.

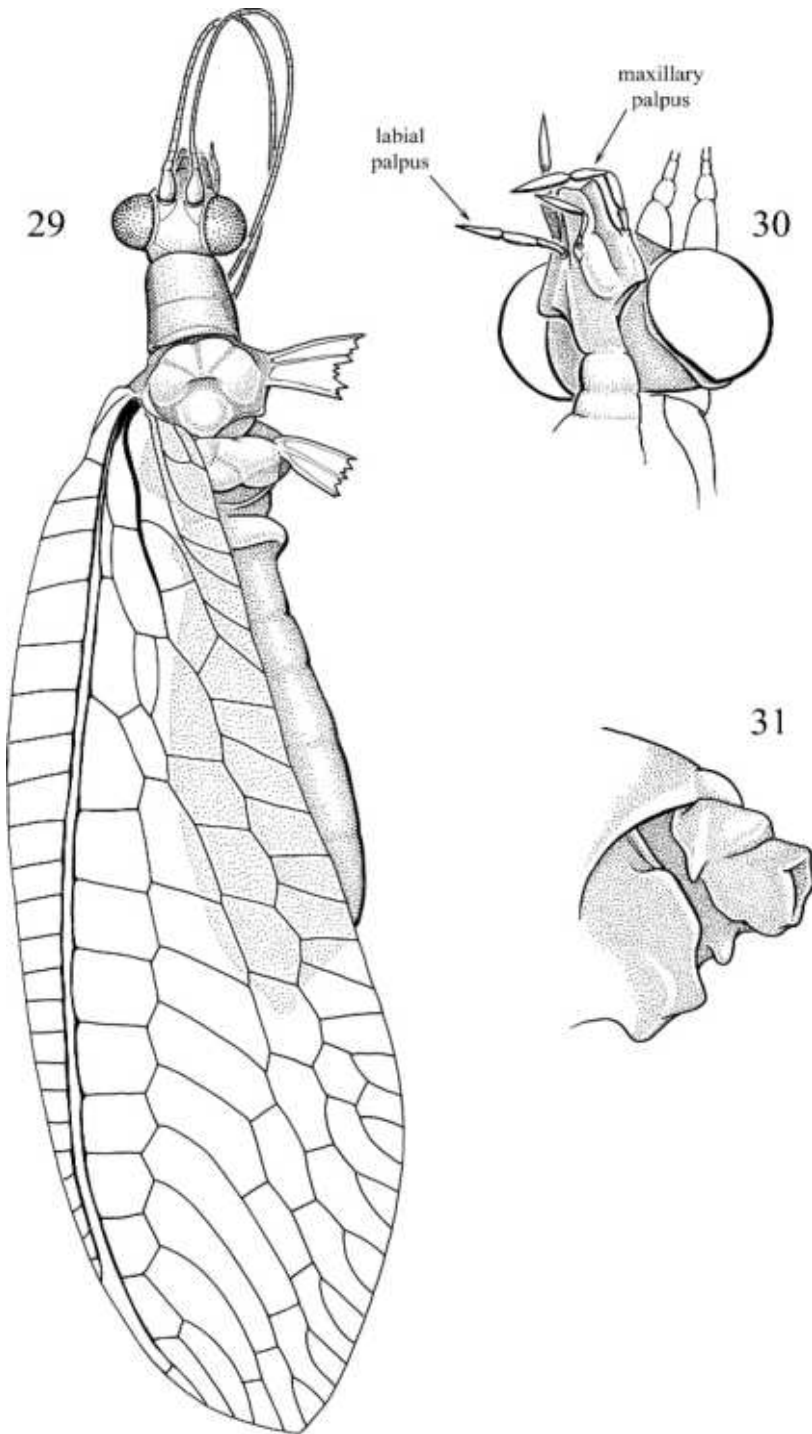
Forewing oval and narrow, longer than abdomen, with sparse setae except along margins; 16 costal crossveins (c-sc); costal area narrows progressively toward apex; Sc and R deviate slightly near apex, Sc joins C at apex; R straight, not sinuous; single sc-r crossvein toward wing base (vein *bsc*), three sc-r crossveins below pterostigma; pterostigma elongate and marked with faint clouds of smoky brown; cell *m1* much smaller than *m2*; cell *im* ovate, broad, first rs-m crossvein meets *im* subapically; no radial crossvein (r-m) basal to origin of Rs, radial crossveins straight; cell *c1* as long as *c2*; cell *dec* narrowly open along



Fig. 28. Photomicrograph of holotype of *Chrysopa vetula*, new species (MACT-1246).

posterior wing margin, longitudinally divided anteriorly to form small cell *c*₃; six closed cells between PsM and PsC; two gradate series, inner gradate series complete, gradates paral-

lel; 1A forked (fig. 33). Hindwing with two gradate series. Wing membranes hyaline; major longitudinal veins light brown, although darkened at points where crossveins



Figs. 29–31. Holotype of *Chrysopa vetula*, new species (MACT-1246). 29. Dorsal habitus of body and left forewing. 30. Ventral aspect of head. 31. Abdominal apex.

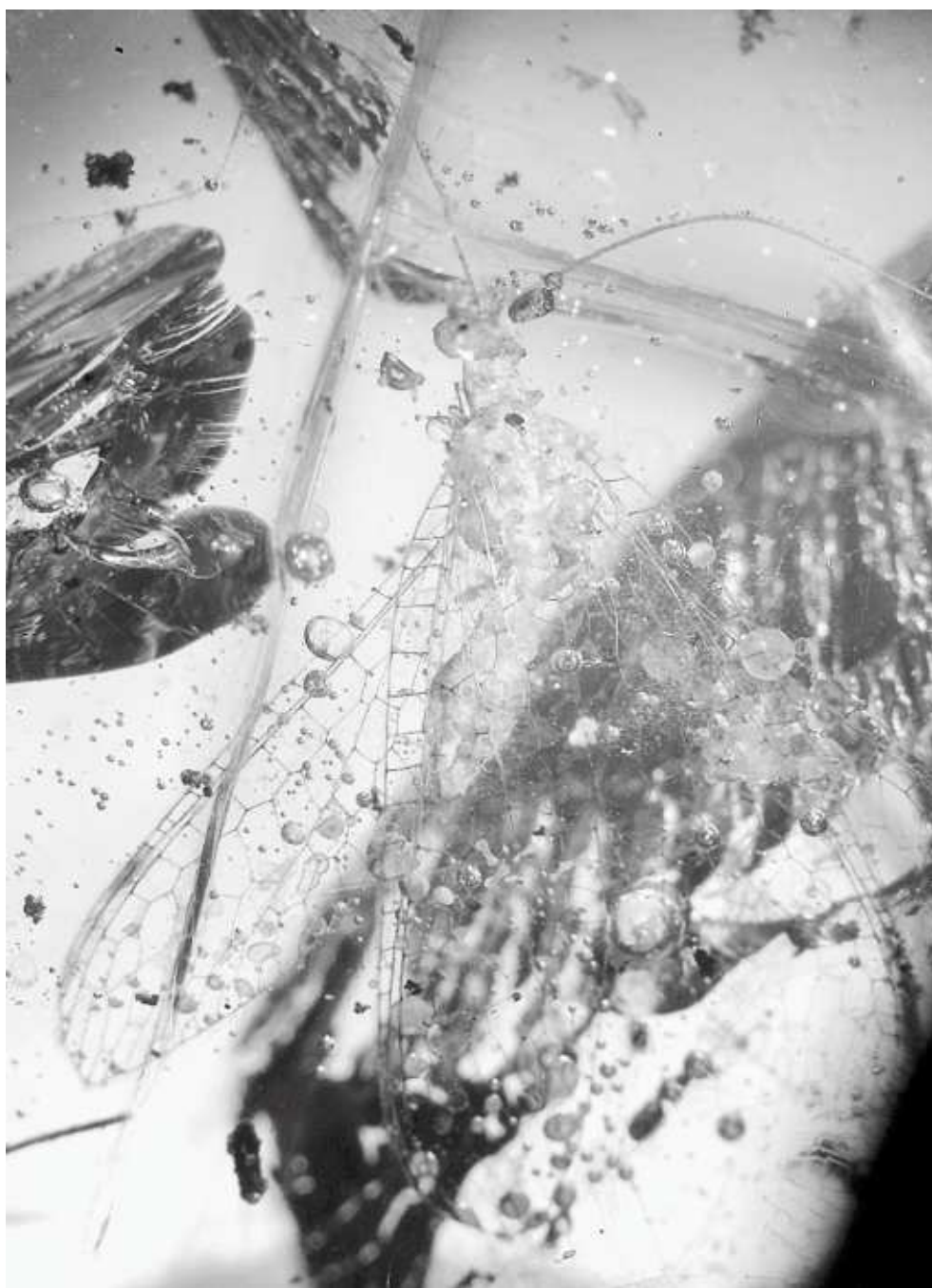


Fig. 32. Photomicrograph of holotype of *Leucochrysa (Nodita) prisca*, new species (MACT-544).

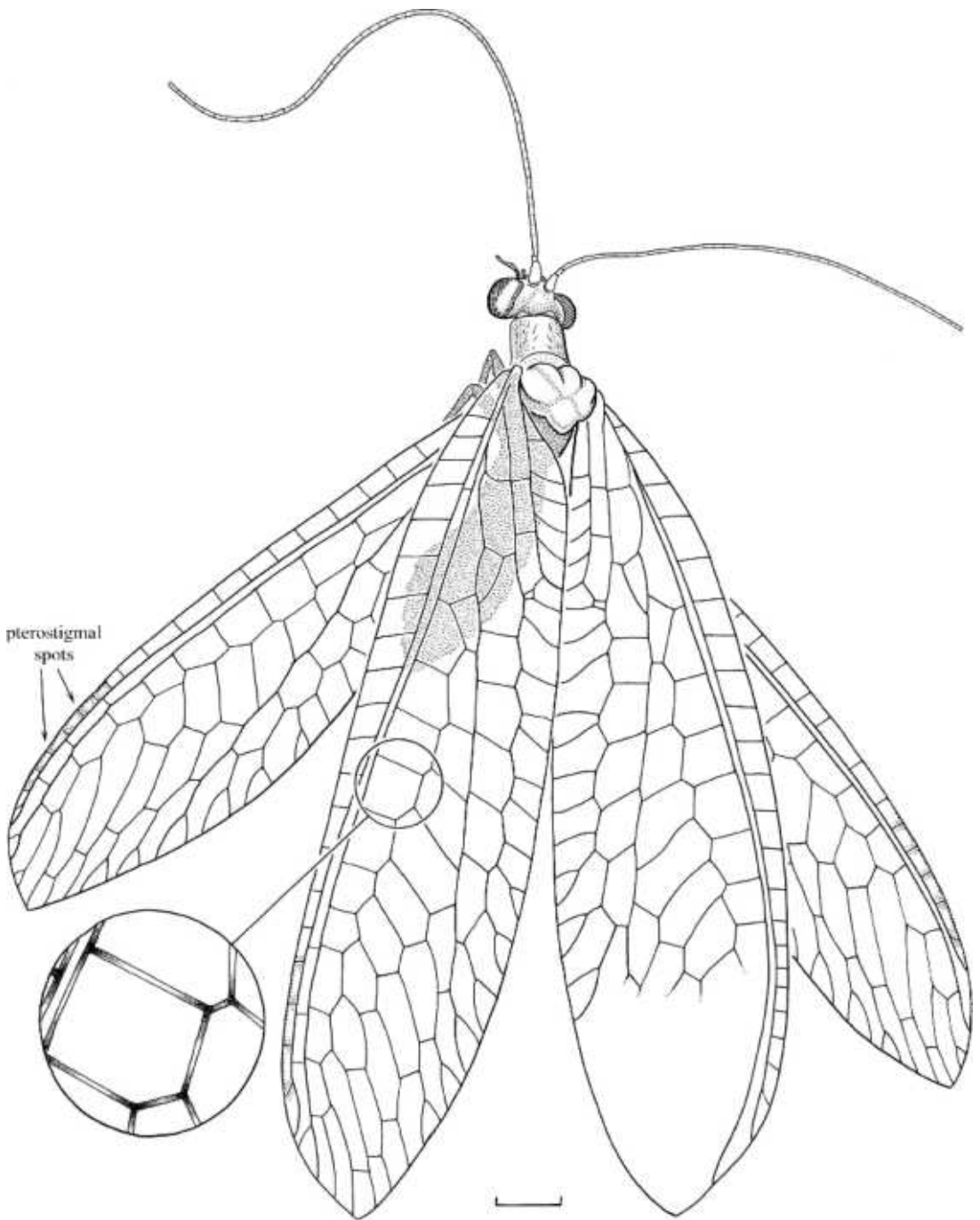


Fig. 33. Dorsal habitus of holotype of *Leucochrysa (Nodita) prisca*, new species (MACT-544).

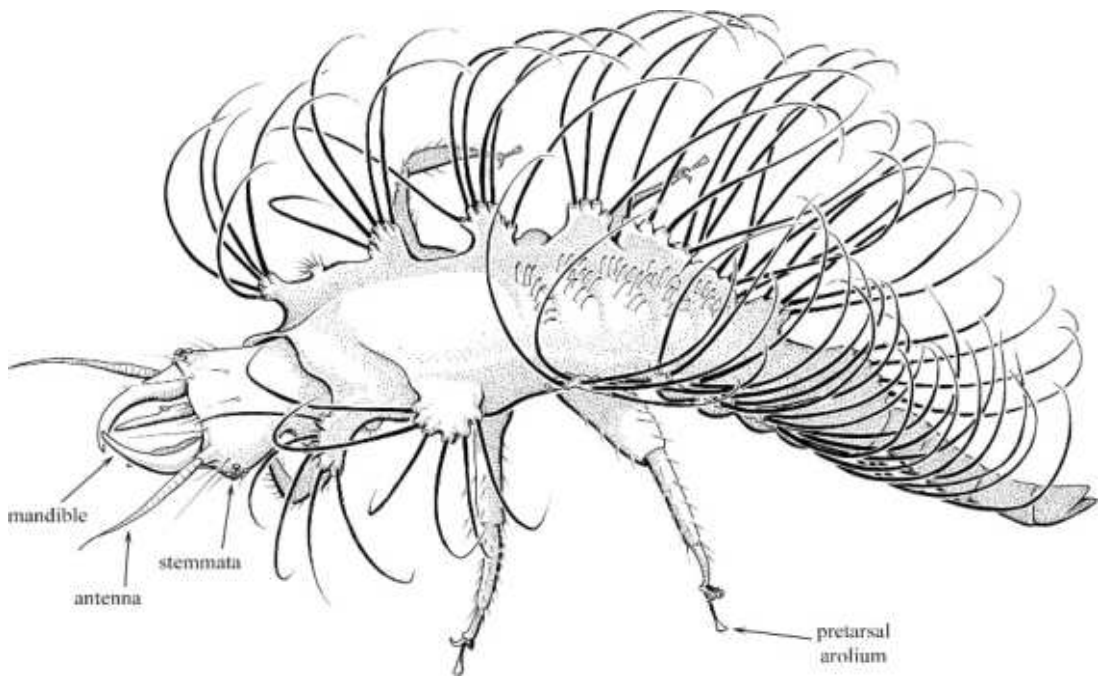


Fig. 34. Oblique dorsal habitus of immature chrysopid (DR-10-1454).

form; crossveins distinctly darker than longitudinal veins, darker where two or more veins meet each other.

Abdomen uniformly colored; sternum two without stridulatory apparatus.

HOLOTYPE: Female; MACT-544 (fig. 32), Miocene amber of the Dominican Republic.

ETYMOLOGY: The specific epithet is taken from the Latin word *priscus* (meaning “old”).

Chrysopidae larva

figure 34

Chrysopidae larva: Grimaldi and Engel, 2005: 352, fig. 9.31.

COMMENTS: Integument reddish-brown throughout, without apparent markings and largely lacking microtrichiae. Head distinctly flattened and roughly quadrate, slightly longer than wide; antennae longer than mandibles and slightly longer than head capsule; mandibles nearly as long as head capsule; mandibles simple, without dentition. Lateral tubercles on thorax and abdominal segments I–VII well developed (fig. 34), tubercles spherical and nodulate at apices at setal origins; prothoracic

segment with secondary, smaller, lateral tubercles posterior to main lateral tubercles, secondary tubercles with short, simple, erect setae; main lateral tubercles of each segment with 4–6 simple, greatly elongate setae forming a dorsal space or corbicula for the accumulation of debris on the dorsal surface of the thorax and abdomen. Thoracic and abdominal dorsa relatively flattened except slightly upcurved and flared dorsolaterally to form dorsal corbicula; dorsum without setae except metathoracic and first four abdominal segments with short, erect, setae with spatulate apices medially (fig. 34). Abdomen tapering in width to relatively narrow apical segment; apical segment tapered to rough point at apex.

MATERIAL: Larva; AMNH DR-10-1454 (fig. 34), Miocene amber of the Dominican Republic.

COMMENTS: Like modern chrysopid larvae, the fossil exhibits the flattened dorsum and elongate, curved, lateral setae designed to form a dorsal corbicula. The larva fills the corbicula with debris so as to disguise itself not only from predators but from prey (the so-called “sheep in wolf’s clothing”). Given the distribution of this behavior and such mor-

phological adaptations across the diversity of chrysopids, it is not surprising to find a larva exhibiting this suite of features as long ago as the Miocene. Indeed, such design and behavior may stretch back into the Cretaceous.

FAMILY MYRMELEONTIDAE LATREILLE

The antlions are notable predators, familiar for the conical pits constructed by larvae of some species. Larvae dwell in the ground or on trees and it seems that eggs are laid singly, sometimes scattered in dry soil or sand. Most larvae are subterranean and some construct conical pits that are used as traps for prey. The larva lies buried at the bottom of the pit with only the open jaws protruding. In other groups, the larvae burrow freely in sand, and move under the sand or on the surface at night. Still others appear to live on trees and closely resemble bark. Larvae can often be found under overhangs where they are protected from rain. Adults are typically predatory although some are known to feed on pollen.

Several fossils of the family are known as compressions from the Early Cretaceous of Brazil and China (e.g., Martins-Neto, 1990, 1992; Martins-Neto and Vulcano, 1989a, 1989b). Many of these species have been assigned to a variety of new, extinct subfamilies but the validity of these requires careful reevaluation (e.g., the Araripeneurinae is a synonym of Palparinae). The only other Cretaceous records of the antlions are the fossils *Samsonoleon fragmentus* Ponomarenko from Israel (Lower Cretaceous; Dobruskina et al., 1997) and *Palaeoleon ferrogeneticus* Rice from Labrador (Upper Cretaceous; Rice, 1969), both sometimes placed in a separate family, Palaeoleontidae (e.g., Dobruskina et al., 1997; Martins-Neto, 2000). Additionally, Whalley (1980) reported an incomplete, unnamed specimen of a putative myrmeleontid in Lebanese amber but we have not been able to confirm its identity. Aside from the fossils discussed below, *Dendroleon septemmontanus* Statz is the only compression of a myrmeleontine from the Tertiary (Statz, 1936). Only a single, definitive myrmeleontid species is known in amber from any deposit, this being the recently described *Porrerus dominicanus* from Dominican amber (Poinar and Stange,

1996). Below we make minor corrections to the original description, present new figures of the holotype, and report on additional specimens.

Porrerus dominicanus Poinar and Stange figures 35–41

Porrerus dominicanus Poinar and Stange, 1996: 384.

HOLOTYPE: Female; MACT-1220 (figs. 35, 36), Miocene amber of the Dominican Republic, La Toca mine (formerly in the Work Collection, Oregon).

NEW MATERIAL: Female; MACT-1170 (figs. 37, 38), Miocene amber of the Dominican Republic. Female; MACT-1414, Miocene amber of the Dominican Republic. Female; MACT-3496 (figs. 39–41), Miocene amber of the Dominican Republic.

COMMENTS: This species was recently described on the basis of a single female (fig. 35, 36). The original description requires some alteration and is emended here. The number of presectoral crossveins reported by Poinar and Stange (1996) is in error not only by comparison with the two new specimens but also with the holotype. The basalmost crossvein has become almost entirely cleared as a product of preservation and was apparently overlooked by these authors. Thus, the number of presectoral crossveins must be increased by one (to five). The other two specimens reported below agree with the holotype. Some minor variations exist between the specimens merely in the number of crossveins (by one or two). The complete fore- and hind wing venation of *P. dominicanus* is depicted in figures 39 and 40, while figure 41 depicts the hindleg spination of the species.

Porrerus dominicanus? [Larva] figures 42, 43

Porrerus larva: Grimaldi and Engel, 2005: 346, fig. 9.20.

DESCRIPTION: Head length 1.2 mm; anterior width 0.8 mm; posterior width 0.46 mm; total body length 4.5 mm. Head, pronotum, and legs more strongly sclerotized than remainder of body. Head elongate and trapezoidal, anterior width approximately 1.75

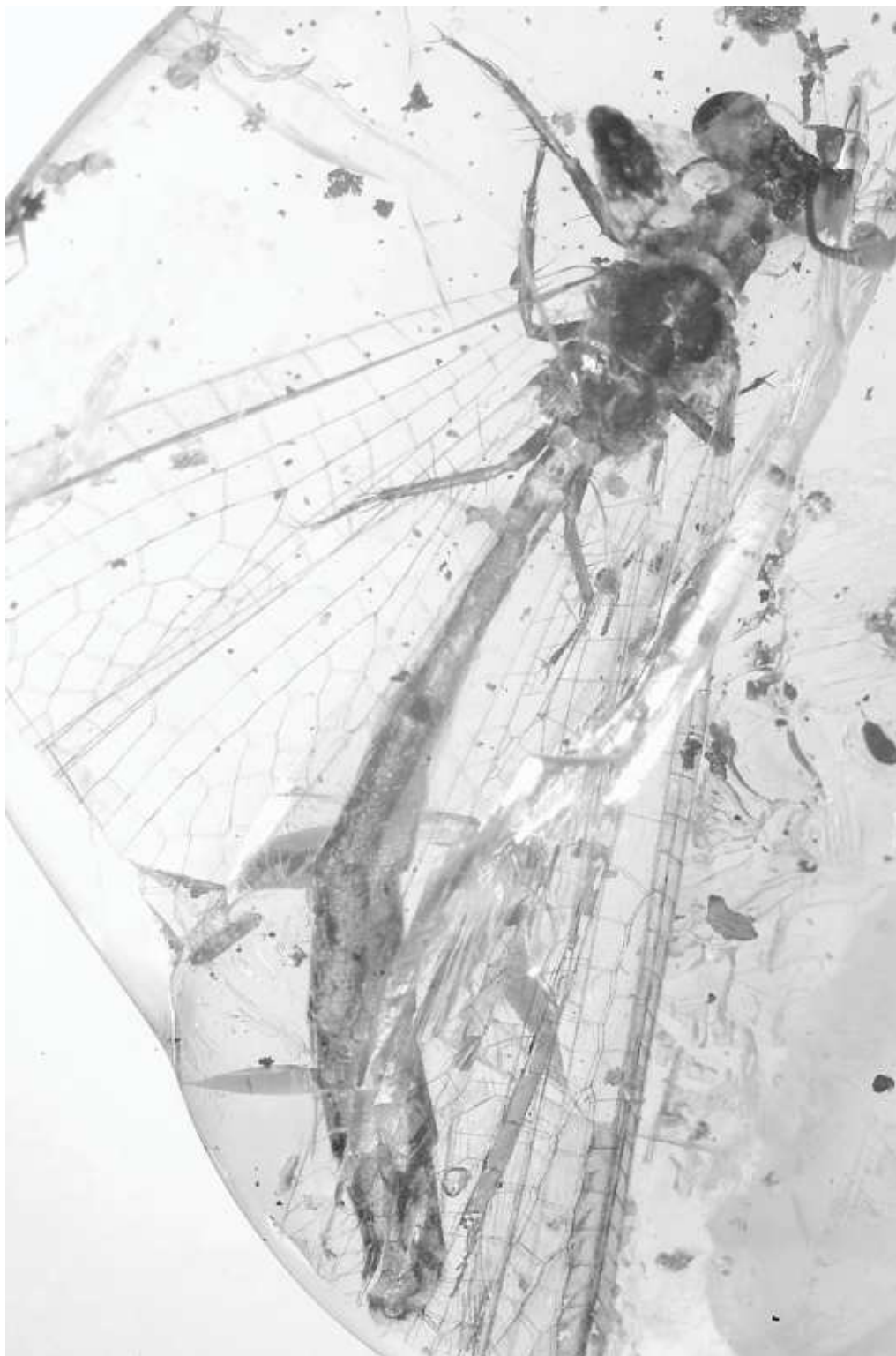


Fig. 35. Ventral photomicrograph of holotype of *Porrerus dominicanus* Stange and Poinar (MACT-1220).

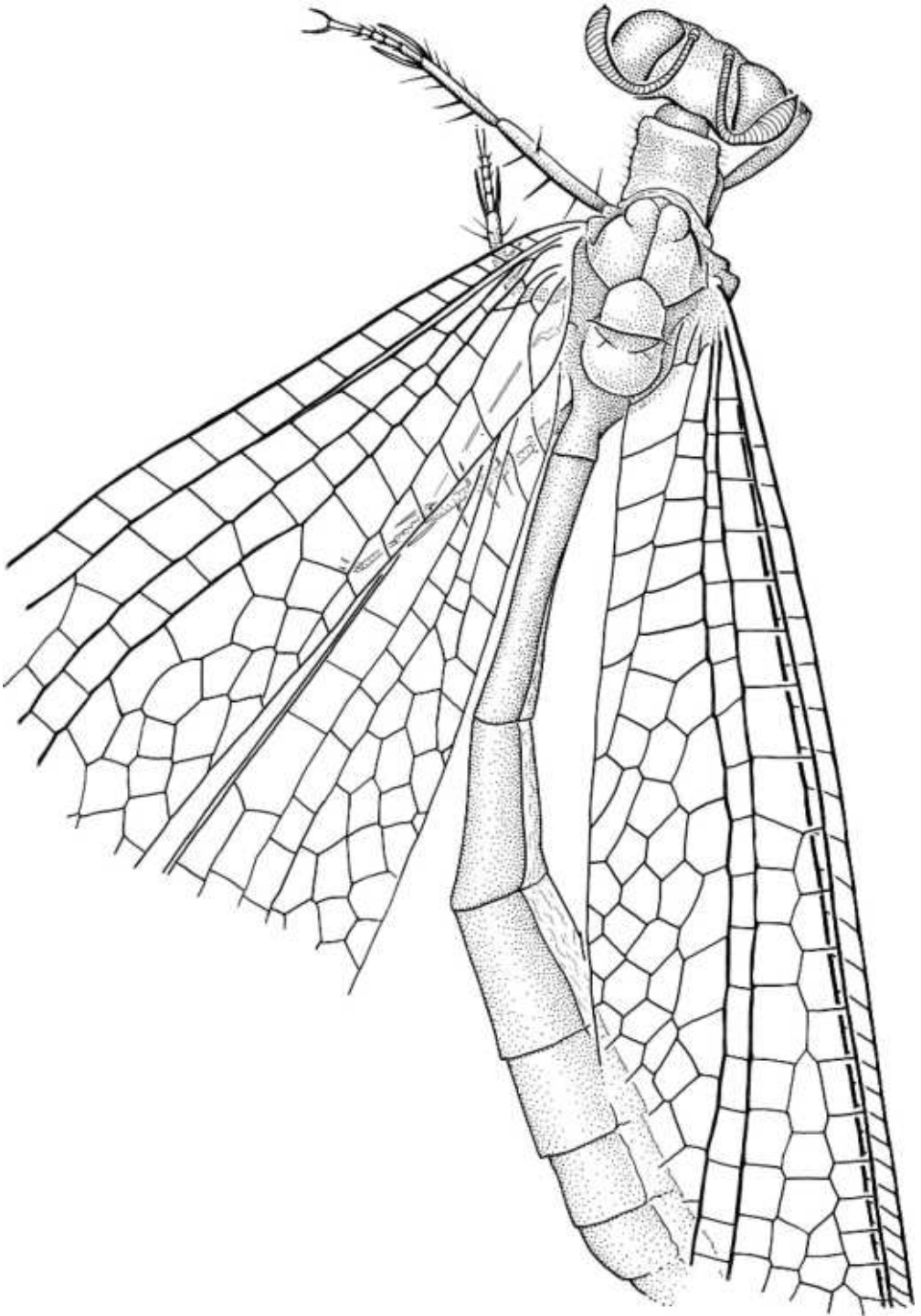


Fig. 36. Dorsal habitus of holotype of *Porrerus dominicanus* Stange and Poinar (MACT-1220).



Fig. 37. Ventral photomicrograph of *Porrerus dominicanus* Stange and Poinar (MACT-1170).

times posterior width; without dolichasters; with numerous, scattered, elongate, black setae; dorsum of head very gently convex along posterior two-thirds, anteriorly between

mandibles strongly concave; venter of head relatively flat. Mandibles slightly upturned, longer than head, widely separated (separated by approximately 3.75 times basal mandibular

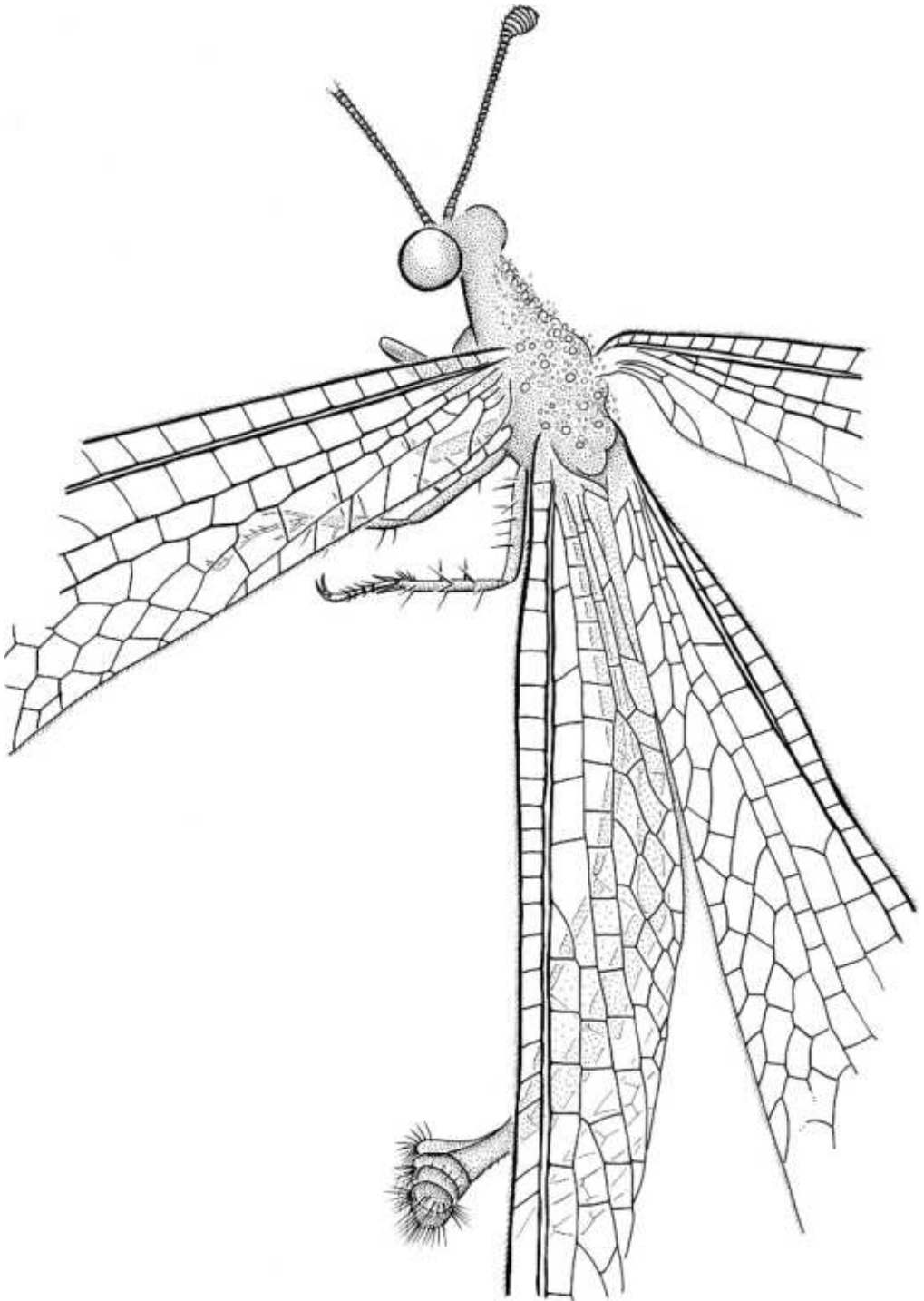
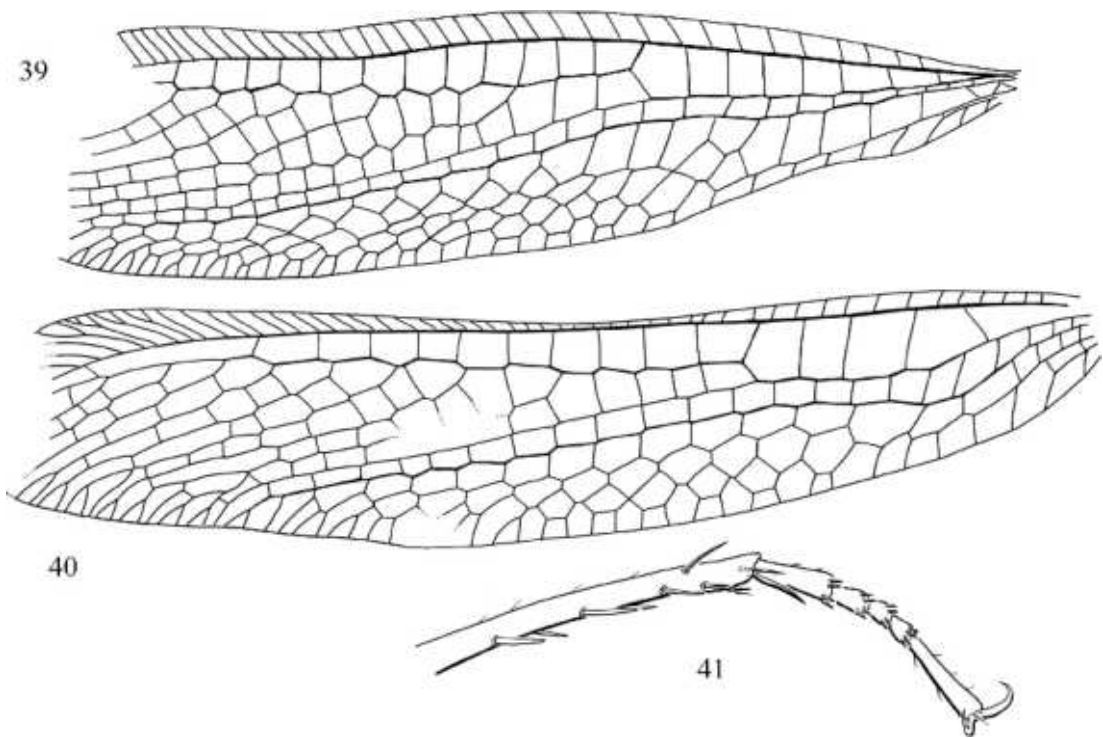


Fig. 38. Dorsal habitus of *Porrerus dominicanus* Stange and Poinar (MACT-1170).



Figs. 39–41. Wing venation and leg spination of *Porrerus dominicanus* Stange and Poinar (MACT-3496). 39. Forewing. 40. Hind wing. 41. Leg spination.

width); three teeth, first tooth situated about at midpoint of mandible, teeth progressively longer toward mandible apex, parallel; setae on outer margin of mandible longer than greatest width of mandible; fringe of appressed setae along outer basal margin of mandible. Labial palpus about as long as basal mandibular width. Ocular tubercle present, short (i.e., not prominent), cylindrical, without dolichasters. Antennal tubercle positioned close to ocular tubercle, separated by less than width, without dolichasters; apparently 18 antennal segments. Pronotum quadrangular, apparently about as wide as long. Mesothoracic spiracle sessile, situated between tubercles. Claws elongate and relatively straight, simple; legs with elongate, black setae, longer than leg width. Meso- and metathoracic and abdominal segments with transverse rows of elongate, black setae, such setae not borne on tubercles; more dense, shorter setae situated as a patch medially between meso- and metathoracic segments, such setae not arranged in rows. Body without

scoli, with paired lateral tubercles each bearing numerous elongate setae. Eighth sternum with pair of small, submedian teeth near posterior margin; ninth sternum with numerous stout setae, without bladelike digging setae, with some shorter, stout setae borne on a common base near posterior margin and slightly upturned.

MATERIAL: Larva; MACT-1282 (figs. 42, 43), Miocene amber of the Dominican Republic. The specimen is preserved along with a scelionid wasp, a mite, a beetle larva, and a collembolan.

COMMENTS: The specimen is clearly an immature of the tribe Myrmeleontini as is evidenced by the combination of elongate mandibles, elongate mandibular setae, sessile mesothoracic spiracle, presence of submedian teeth on S8, and absence of bladelike digging setae on S9. Immatures of myrmeleontines are relatively homogeneous and characters separating the genera are presently not well defined. For this reason, confident assignment of this specimen to any genus of

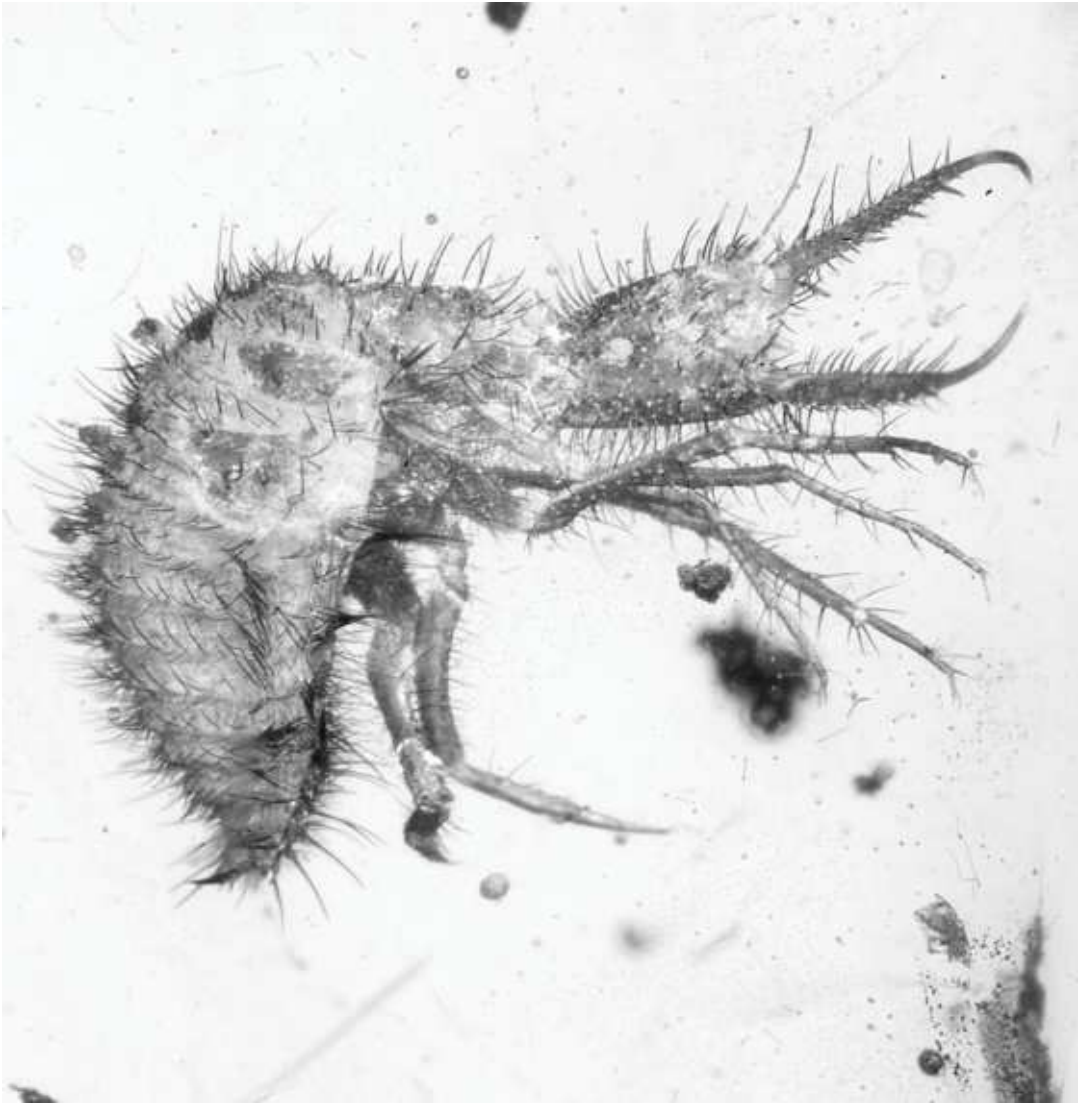


Fig. 42. Photomicrograph of immature of *Porrerus dominicanus* Stange and Poinar (MACT-1282).

Myrmeleontini is tenuous but the presence of several adults of *Porrerus* (see above) is suggestive that this may be an immature of the same species. We have therefore tentatively assigned this immature to *P. dominicanus*.

FAMILY ASCALAPHIDAE RAMBUR

The owlflies, family Ascalaphidae, consist of approximately 430 species. The family is most diverse in both xeric and mountainous regions of the subtropics or tropics. Owlflies

species are frequently large and some groups appear to represent a conglomeration of features from other orders of insects, overall sharing a superficial habitus with dragonflies. Female ascalaphids lay eggs in clusters on twigs or grass stems. The first-instar larvae aggregate at twig apices into a defensive ring. The larvae eventually disperse to live solitarily in the litter or on trees where they are generalist predators.

The geological record of Ascalaphidae is exceedingly sparse with four definitive ascala-

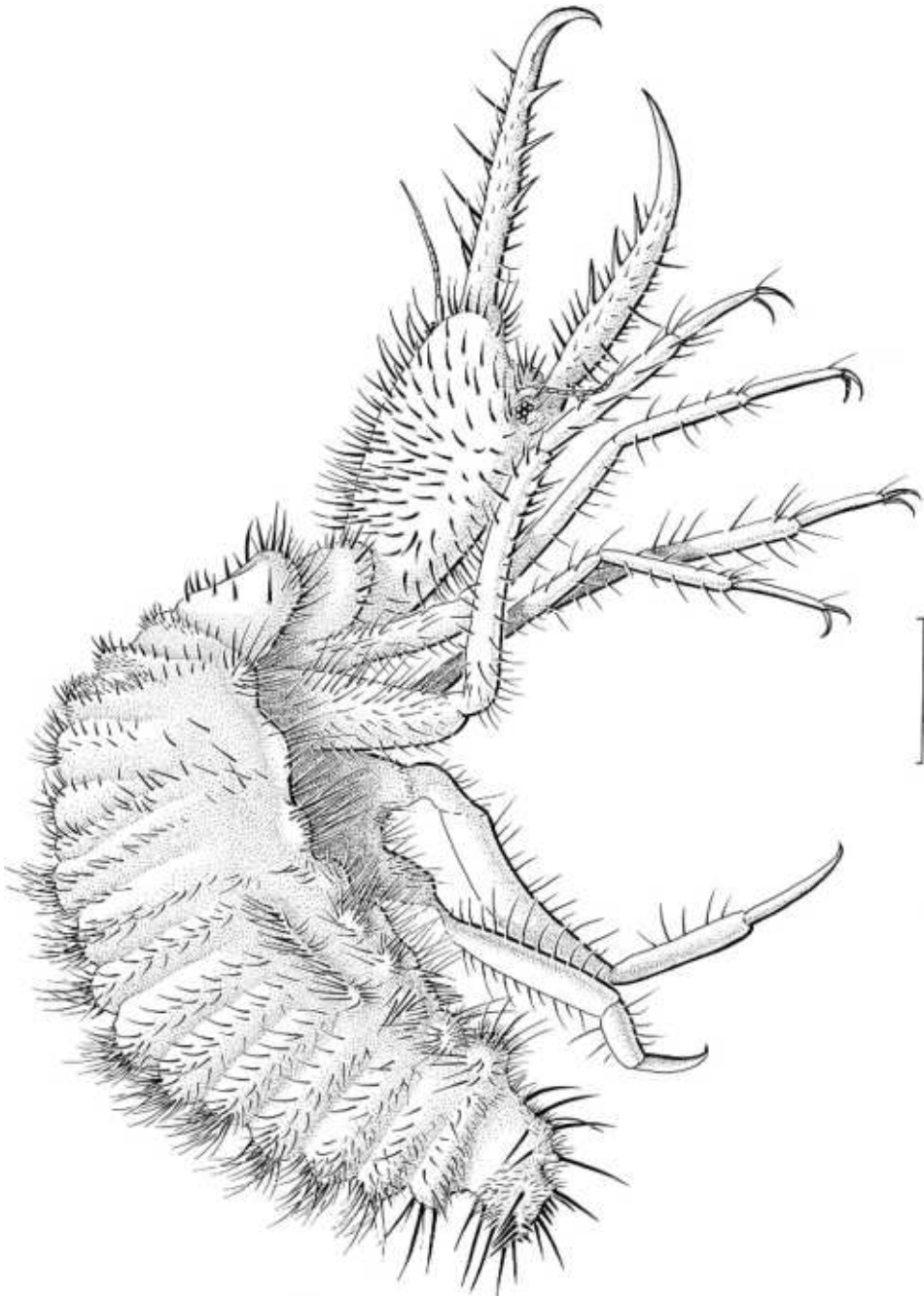


Fig. 43. Habitus of immature of *Porrerus dominicanus* Stange and Poinar (MACT-1282).

phids previously proposed from Tertiary compression fossils in Europe and the Russian Far East, one species known only from the larva in Baltic amber, as well as one

species dubiously assigned Lower Cretaceous fossil (table 9). Herein we describe the first adult ascalaphids in amber as well as larvae of two species of the genus *Uluodes*.

TABLE 9
Named Fossil Ascalaphidae^a

Taxa	Deposit	Reference
<i>Amoeba electrodominicana</i> n.sp.	Dominican amber	Present study
<i>Ascalopteryx oligocenicus</i> Nel	Oligocene, France	Nel, 1990
<i>Borgia proavus</i> (Hagen)	Oligocene, Germany	Hagen, 1858; Navás, 1913
<i>Mesascalaphus yangi</i> Ren et al.	Late Jurassic, China	Ren et al., 1995
<i>Neadelphus protae</i> MacLeod ^b	Baltic amber	MacLeod, 1970 [larva]
<i>Proshupalacsa biamoensis</i> Markarkin	Oligo-Miocene, Russian Far East	Makarkin, 1998
<i>Ricartus edwardsi</i> (Oustalet)	Oligocene, France	Oustalet, 1870; Navás, 1913
<i>Ululodes paleonesia</i> n.sp. ^b	Dominican amber	Present study [+larva]

^aThe Early Cretaceous fossil *Cratopteryx robertosantosi* Martins-Neto and Vulcano (1989a) is only questionably assigned to the Ascalaphidae and is therefore not listed here.

^b*Neadelphus* is known only from the larva whereas *Ululodes paleonesia* is known from both adults and larvae.

Interestingly, the fossil species are representative of two of the three known subfamilies: Ascalaphinae (*Ululodes paleonesia*, new species) and Haplogleniinae (*Amoeba electrodominica*, new species).

Amoeba electrodominicana, new species
figure 44

Ululodes adult: Grimaldi and Engel, 2005: 347, fig. 9.23.

DIAGNOSIS: Like modern *Amoeba*, this species exhibits the absence of wing pigmentation (excluding the pterostigma) otherwise found in all other Haplogleniinae. The fossil species has more elongate antennae (longer than the forewing), lacks integumental markings, and has CuA relatively straight to the wing margin (fig. 44) (more strongly arched posteriorly in modern species).

DESCRIPTION: Total body length 21 mm; forewing length 23 mm. Integument light brown, without apparent maculations. Head longer than wide; compound eyes not divided; antenna arising near lower tangent of compound eyes; antenna elongate, longer than body or wings; scape and pedicel with elongate setae, setae nearly as long as scape; antennal articles each distinctly longer than wide except those of antennal club wider than long, with a few setae near apex of each article; antennal club composed of nine articles. Fore- and hind wings of equal length and approximately equivalent shape; pterostigma of fore- and hind wing formed of dark pigmented spot near wing apex where Sc meets R (fig. 44) and

composed of several closed cells, remainder of wing membranes hyaline; veins black; forewing M and CuA relatively straight to wing margin, weakly arching posteriorly at extreme apex; forewing axillary angle obtuse, nearly orthogonal, not produced; hind wing CuP not arched posteriorly, instead running parallel to 1A; 2A absent; hind wing without anal lobe. Body relatively densely pubescent, setae simple and dark brown; those setae of femora and tibiae elongate and more stout (fig. 44); pretarsal claws long, thin, and simple; abdominal apex with dense, stiff, short, black setae.

HOLOTYPE: Male; AMNH, no accession number (fig. 44), Miocene amber of the Dominican Republic.

ETYMOLOGY: The specific epithet is a reference to the occurrence of this species in Dominican amber.

Ululodes paleonesia, new species
figures 45, 46

DIAGNOSIS: The new species is noteworthy for the combination of the elongate antennae (longer than the forewing), pterostigma of forewing darkly pigmented and enlarged, and hyaline wing membranes. The species closely resembles the modern *U. macleayana* (Guilding) but differs by the more elongate antennae and the distinctly narrower area of the wing posterior to CuA (fig. 46) (maximal width of posterior area distinctly less than width of area anterior to CuA at same point while in *U. macleayana* the posterior area is broader than the anterior area).

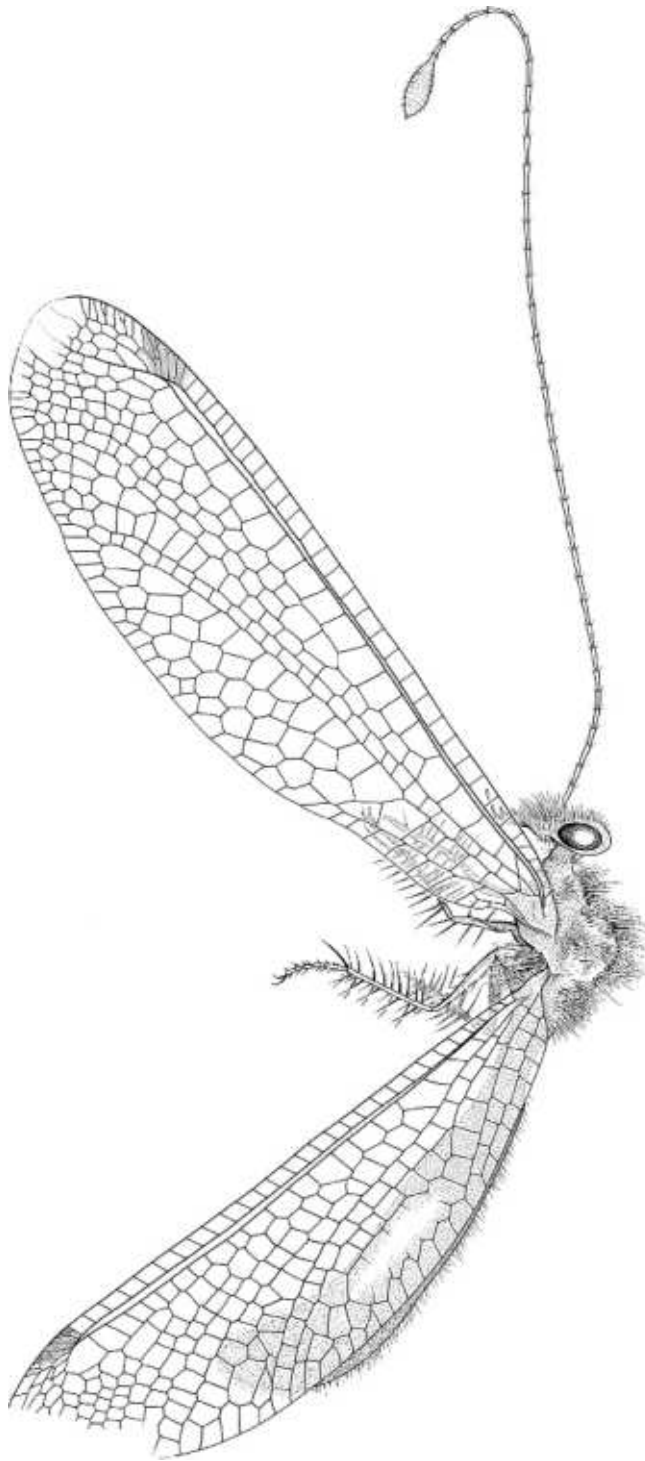


Fig. 44. Lateral habitus of holotype of *Amoea electrodominicana*, new species (no accession number).

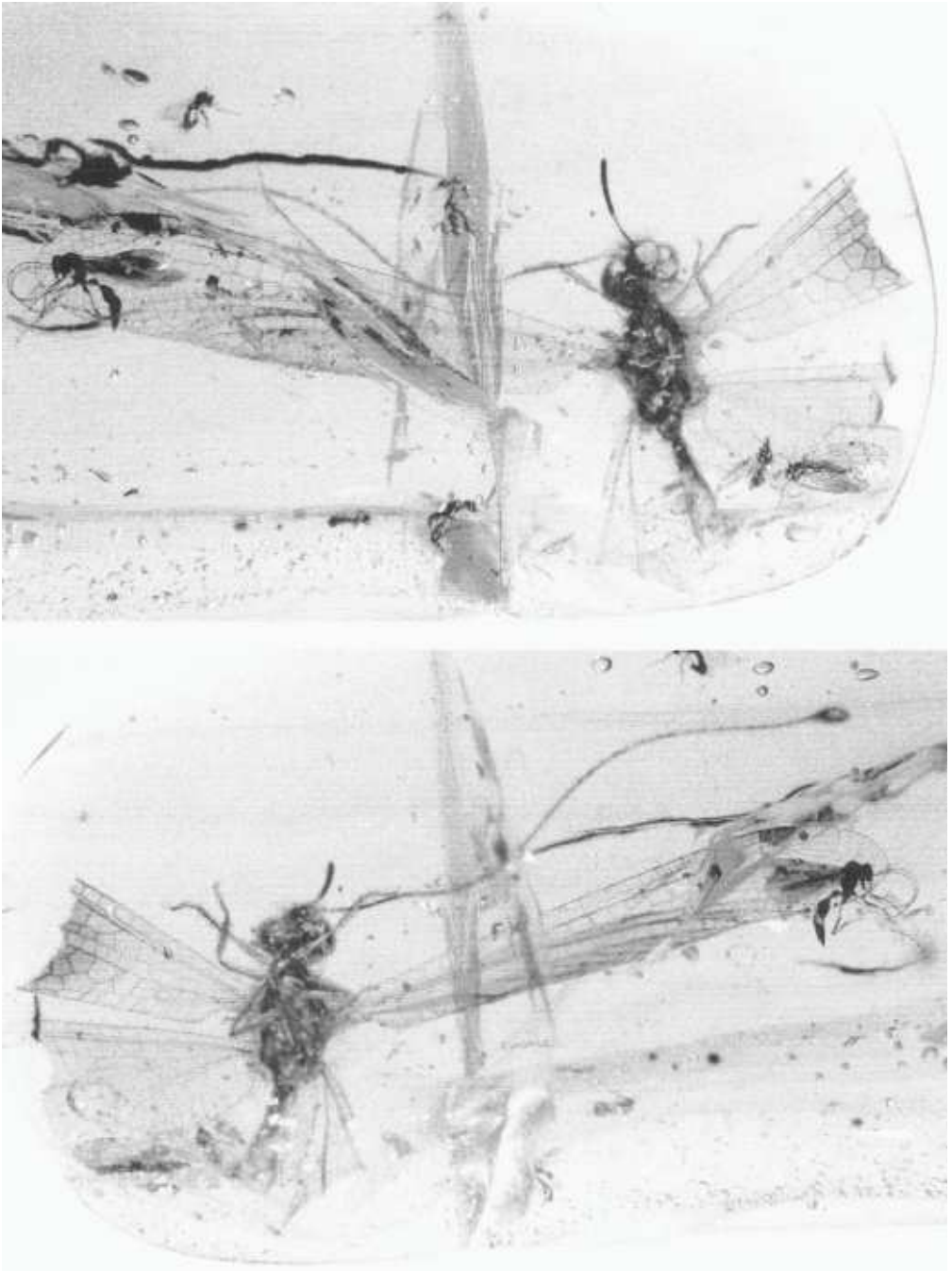


Fig. 45. Photomicrograph (dorsal above, ventral below) of holotype of *Ululodes paleonesia*, new species (MACT-3546).

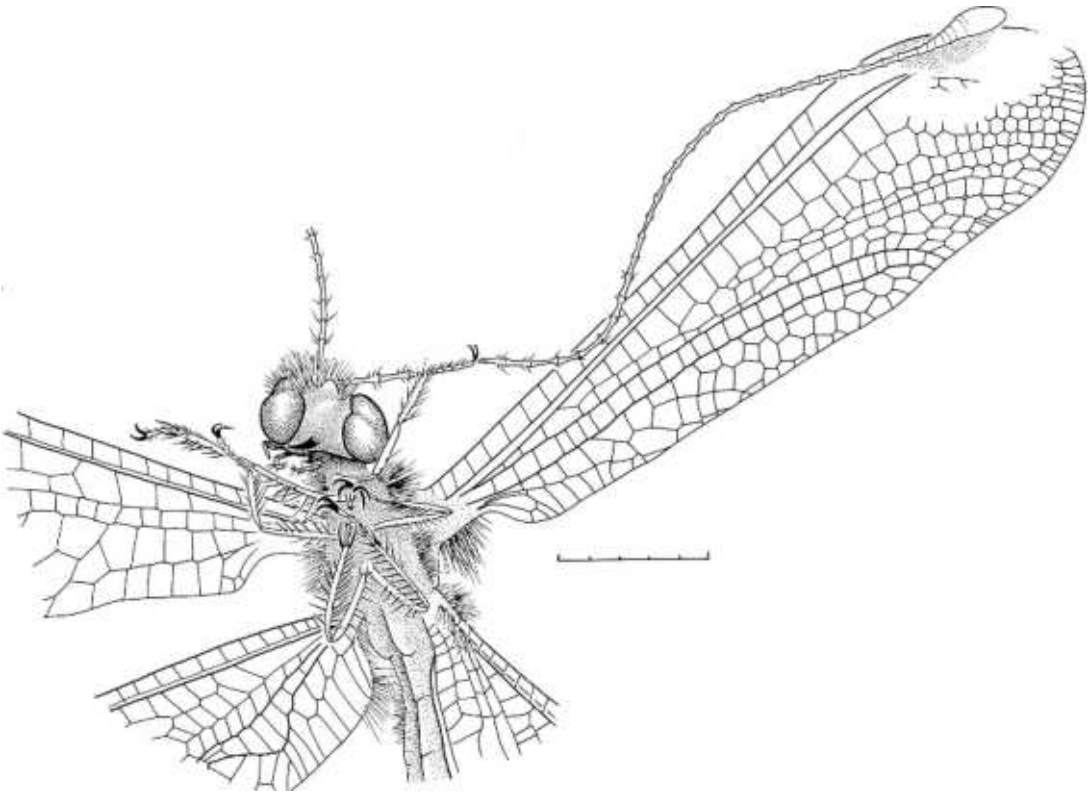


Fig. 46. Ventral habitus of holotype of *Ululodes paleonesia*, new species (MACT-3546).

DESCRIPTION: Length as preserved approximately 13 mm (only preserved from head through portion of abdominal segment IV: figs. 45, 46); forewing length 22 mm. Integument light brown, without apparent maculations. Head about as long as wide; compound eyes distinctly divided horizontally near midpoint; antenna arising near midpoint of head length; antenna elongate, longer than forewing; scape, pedicel, flagellar articles with simple, erect setae near apices; flagellar articles each distinctly longer than wide (approximately twice as long as wide) except those of antennal club wider than long. Pterostigma of forewing formed of darkly pigmented spot near wing apex where Sc meets R and composed of several closed cells (fig. 46), remainder of wing membrane hyaline; membrane of preserved portion of hind wings hyaline (figs. 45, 46); veins of both wings black; maximal width of posterior area of wing posterior to CuA less than width of area anterior to CuA at same point in forewing;

hind wing CuP distinctly arched posteriorly toward its apex (fig. 46); 2A absent; hind wing without anal lobe. Body relatively densely pubescent, setae simple and dark brown; those setae of femora and tibiae of medium length, long but shorter than those of thorax; pretarsal claws long, thin, and simple; abdominal apex with dense, stiff, short, black setae.

HOLOTYPE: MACT-3546 (fig. 45), Miocene amber of the Dominican Republic.

ETYMOLOGY: The specific epithet is a combination of the Greek words *palaios* (meaning "ancient") and *nesos* (meaning "island") and is a reference to the Miocene, island habitat of this species.

Ululodes sp. 1 [Larvae]
figures 47–49

DESCRIPTION: **Third instar?:** Body length (exclusive of mandibles) 5.9 mm; head capsule length 1.5 mm; head capsule width 1.8 mm.



Fig. 47. Photomicrograph of immature of *Ululodes* sp. 1 (MACT-1200).

Head, pronotum, and mandibles dark brown; remainder of body brown. Head quadrate, slightly wider than long, dorsoventrally flattened. Posterolateral margins weakly cordate. Labral margin narrow and strongly bilobed with a single wide notch at midline; labral

lobes bulbous. Dorsum of head weakly convex medially and laterally; ventral surface convex with excavated anterolateral margins to permit retraction of jaws beneath ocular tubercle. Surface integument granulose, covered with scattered clumps of particulate debris. Ocular

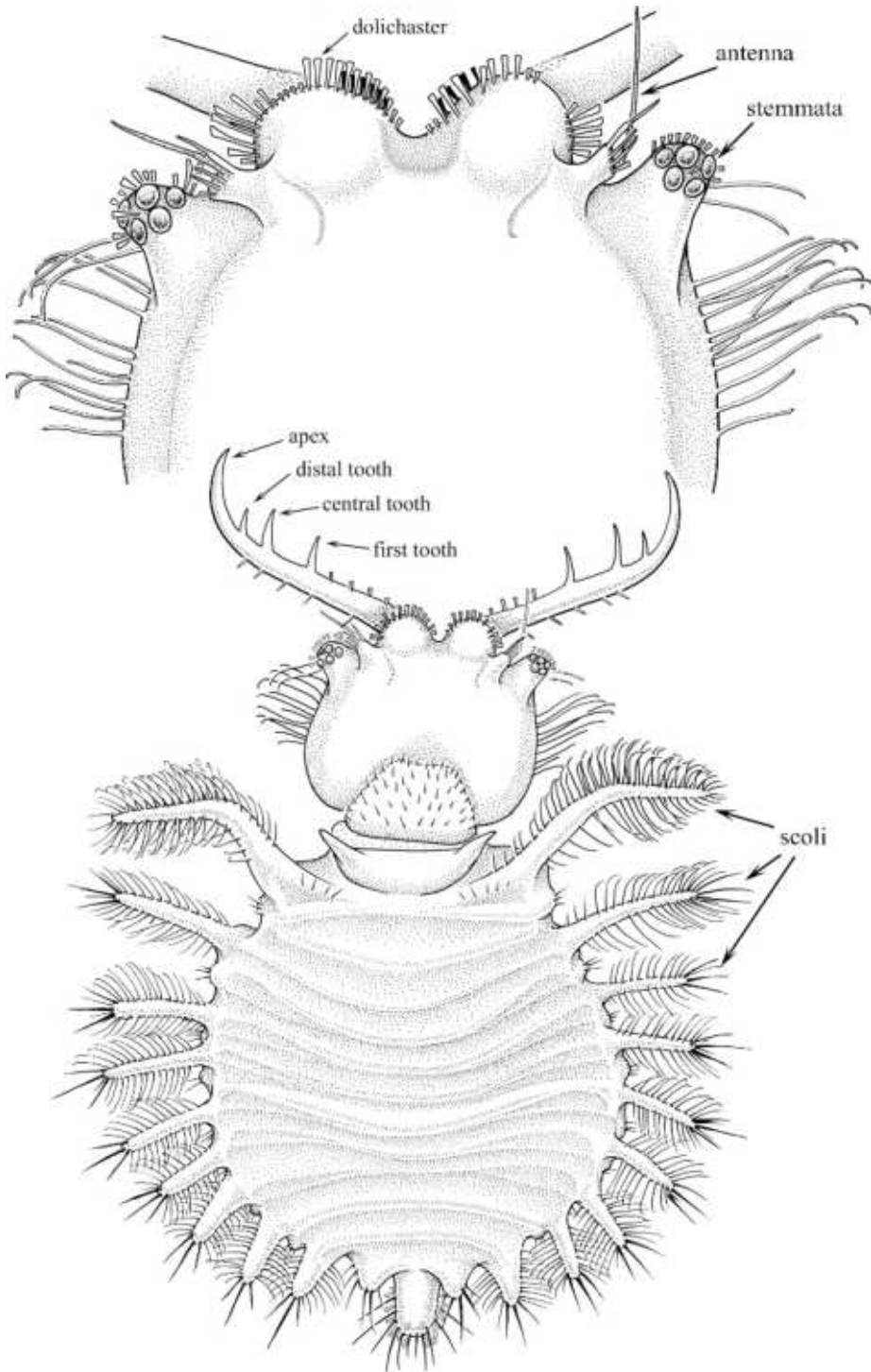


Fig. 48. Habitus of immature of *Uhlodes* sp. 1 (MACT-1200), with details of head enlarged.

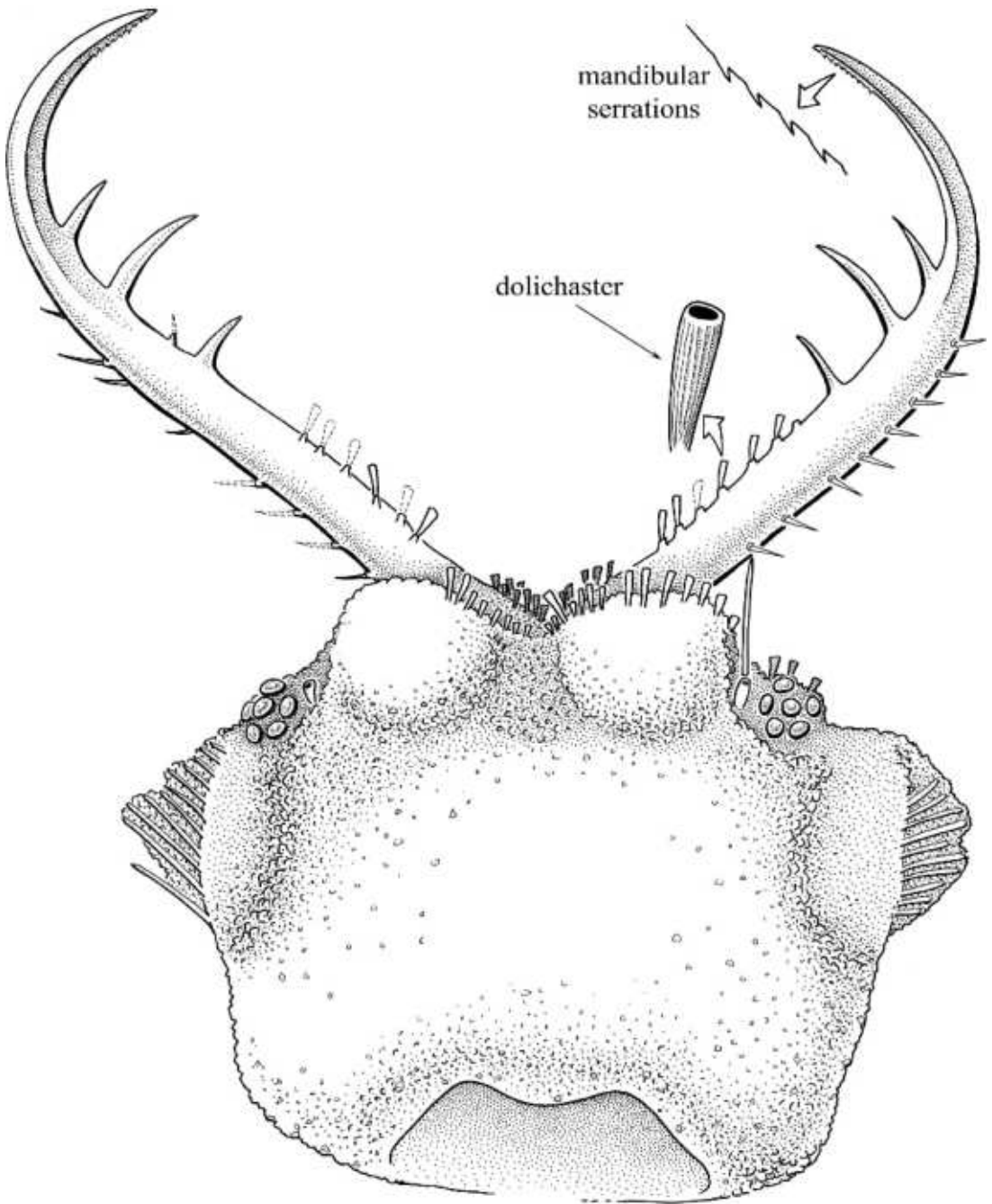


Fig. 49. Details of head of *Ululodes* sp. 1 immature (DR-10-2010).

tubercles prominent although not particularly enlarged; slightly cylindrical, not tapered distally or flattened; all five stemmata similar in size. Antennal tubercles prominent, cylin-

dric, nearly one-half length of ocular tubercle, well separated from latter by approximately length of antennal tubercle. Jaws slightly falcate and with slight upward tilt,

tapering at apices, much longer than head capsule. First tooth of mandible situated approximately at midpoint; central tooth at about midpoint between first tooth and apex; central tooth longer than other two teeth and slightly curved; distal tooth smaller than preceding two teeth and situated at midpoint between apex and central tooth.

Body ovoid in outline. Pronotum small, sclerotized, slightly convex, trapezoidal, about twice as wide as long, without scoli or tubercles but with short, stiff setae pointed anteriorly. Remainder of body lightly sclerotized. Lateral margins of meso- and metathoracic and abdominal segments except ninth and tenth with prolonged, unflattened, finger-like, setose scoli, 10 pairs in total and decreased in length posteriorly. Each mesothoracic scoli as long as head capsule or nearly so, inclined forward basally and reflexed posteriorly at about its midpoint. Metathoracic scoli two-thirds as long as mesothoracic scoli; not reflexed. Remaining eight pairs of abdominal scoli straight, shorter than thoracic scoli. Pairs of vestigial scoli present, positioned behind and slightly ventrad elongate scoli on meso- and metathorax.

Dense, double fringe of long serrate setae present on lateral margins of head and peripherally on all scoli. Single row of shorter, distally flared, serrate dolichasters closely set along entire anterior labral margin. Ocular tubercle with still shorter, tightly packed dolichasters, with two elongate, subequal setae projecting posteriorly from posterior margin. Antennal tubercle bearing a group of three long dolichasters. Two pairs of stout, toothlike digging setae present on posterior border of ninth abdominal segment; dolichasters present along margin of apical abdominal segment.

MATERIAL: Larva; MACT-1200 (figs. 47, 48), Miocene amber of the Dominican Republic. Larval head; AMNH DR-10-2010 (fig. 49), Miocene amber of the Dominican Republic.

COMMENTS: This larva can be confidently assigned to the genus *Uluodes* based on the excellent descriptive work of living ascalaphid immatures by Henry (1976). The absence of pronotal tubercles, presence of 10 scoli, and reflexed mesothoracic scoli, among many other characters (Henry, 1976), are all in-

dicative of the genus *Uluodes*. Although tempted to do so, we have not assigned this fossil immature to the species *U. paleonesia* despite the presence of an adult of this species in the same deposit. Given that two diagnosable species of larval *Uluodes* can be recognized (see *Uluodes* sp. 2 below) it is entirely unknown to which, if any, the adult might belong. The behavior of ascalaphid larvae mentioned above perhaps accounts for the entrapment of this immature in resin and preservation in amber.

Uluodes sp. 2 [Larva]
figures 50, 51

Uluodes larva: Grimaldi and Engel, 2005: 348, fig. 9.24.

DESCRIPTION: Third instar?: As described for *Uluodes* sp. 1 except as follows: Body length (exclusive of mandibles) ca. 4 mm (difficult to ascertain as body is bent: fig. 50); head capsule length 0.9 mm; head capsule width 1.2 mm. Labral lobes bulbous but broader and less prominent than in *Uluodes* sp. 1. Head and pronotum more densely covered by setae; those elongate setae on lateral margins of head distinctly more numerous and dense (fig. 51). First tooth of mandible situated well beyond midpoint; first tooth slightly shorter than immediately following, central tooth, these each longer than distal tooth (fig. 51). Dolichasters of mandible proximal to first tooth more numerous than in *Uluodes* sp. 1 (cf. figures 48, 49, and 51).

MATERIAL: Larva; MACT-3550 (figs. 50, 51), Miocene amber of the Dominican Republic.

COMMENTS: Refer to those comments provided for the larva of *Uluodes* sp. 1.

DISCUSSION

PALEOECOLOGY

Many of the neuropterans in Dominican and Mexican amber were predacious as larvae and/or as adults on other arthropods that probably frequented trunks of the amber-producing *Hymenaea* trees. Adult Mantispidae are generalized predators, much like their dictyopteran analogs, the mantises

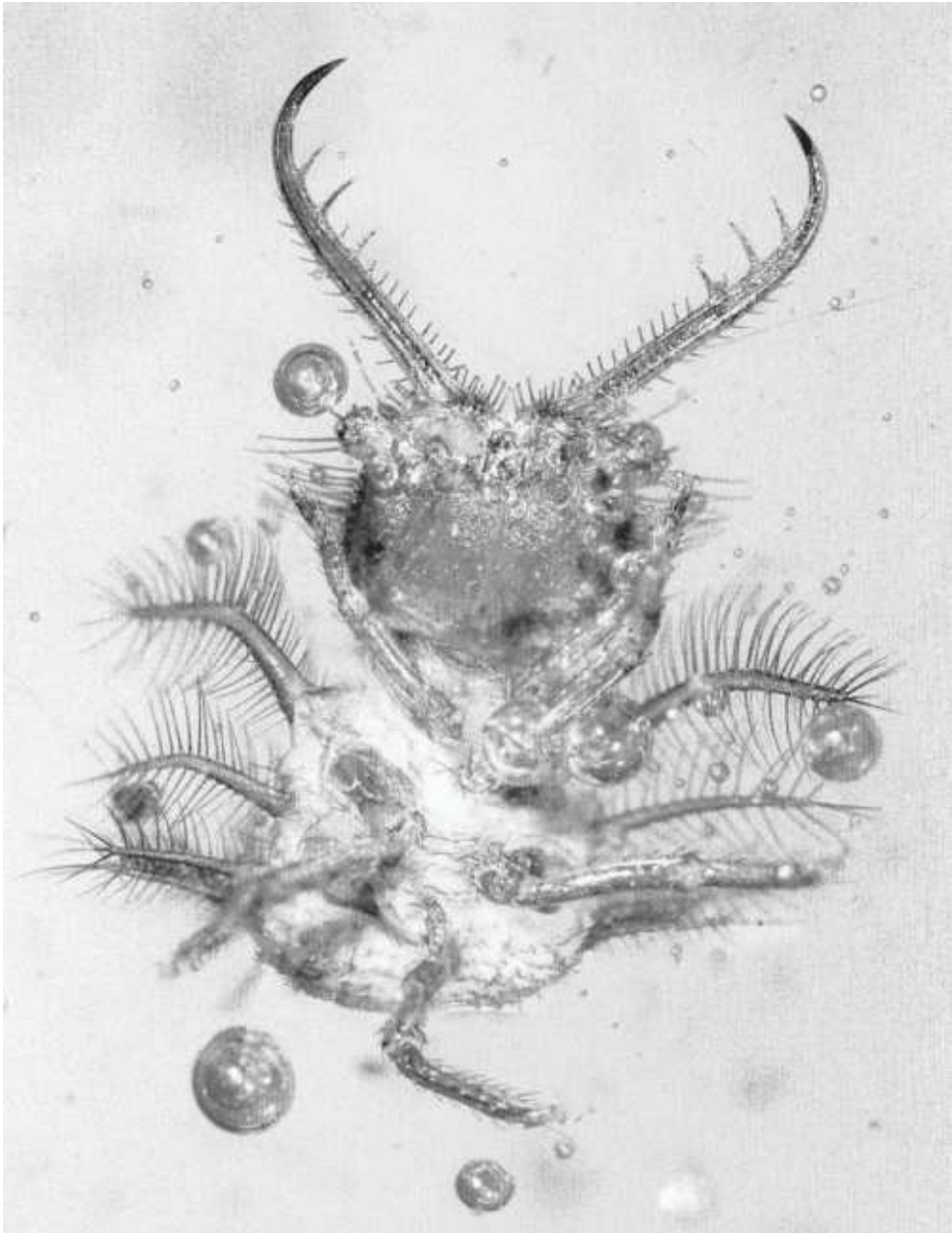


Fig. 50. Photomicrograph of immature of *Ululodes* sp. 2 (MACT-3550).

(Mantodea). Larvae of some mantispids (i.e., *Plega* and other symphrasines) are terrestrial predators of larval social aculeates and of scarab larvae. Other larvae, including those of *Dicromantispa*, are parasitoids of spiders, and there is an abundance and considerable diversity of spiders preserved in both Dominican

and Mexican amber (Wunderlich, 1988; Penney, 1999). Larval Myrmeleontoidea are morphologically highly specialized predators that are quite generalized in their types of prey. Although the pit-constructing “ant-lions” are known best, this behavior occurs mostly in Myrmeleontinae. Larvae of some

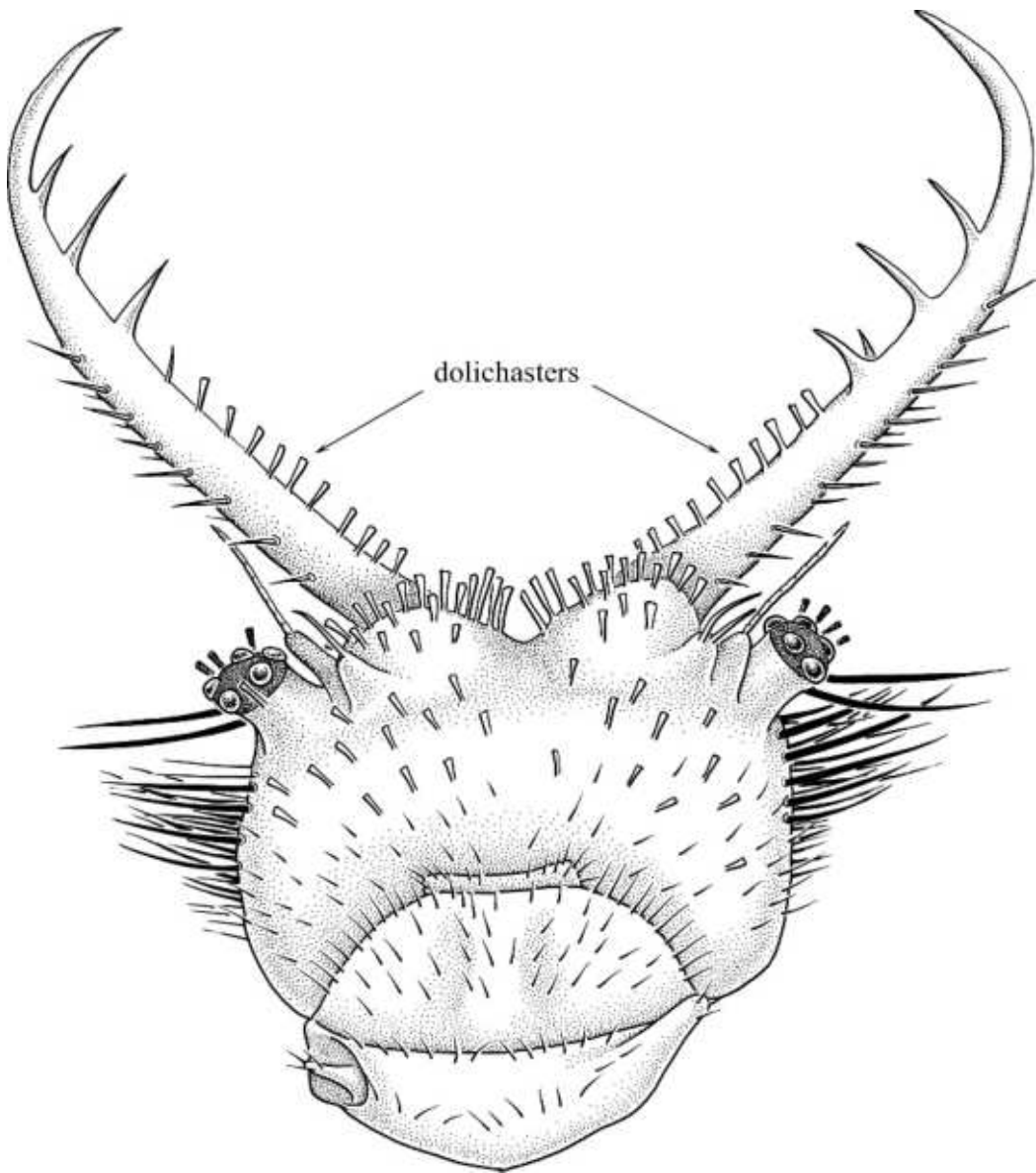


Fig. 51. Details of head of *Ululodes* sp. 2 immature (MACT-3550).

myrmeleontids are roaming predators on tree trunks, which no doubt was the habit of MACT-1282. Larvae of many ascalaphids are ambush predators on tree trunks, to which they are superbly adapted with their very flat bodies that they camouflage with bits of lichen and other debris. Adult ascalaphids often perch on tree trunks, and some are even known to roost each day on hanging branches and vines.

Adult and larval Hemerobiidae, Chrysopidae, and Coniopterygidae tend to be most prevalent where there are dense aggregations of sedentary or sessile Sternorrhyncha, on which they extensively feed. Hemerobiidae are more prevalent in forested areas, in contrast to Chrysopidae, which prefer more open areas. This may account for the slightly greater ease of locating hemerobiids in Dominican amber, although the larger size of chrysopids may

bias against their fossilization in amber. Chrysopidae and Coniopterygidae are particularly well adapted to feeding amongst aggregations of aphids, psyllids, whiteflies, and scale insects (Sternorrhyncha). Larval and adult coniopterygids have a covering of flocculent wax over the body, which no doubt disguises them among their prey (many of which also produce wax in abundance). Larval chrysopids camouflage themselves by placing debris, even the husks of their victims, amongst their long hairs (fig. 34) (Eisner et al., 1978; Eisner and Silberglied, 1988).

Oddly, sternorrhynchans of all groups are rare in Dominican amber, comprising less than 1% of all inclusions (Grimaldi, unpubl. data), which probably reflects the distinctly broad-leaved tropical forests in which Dominican and Mexican ambers were produced. In contrast, sternorrhynchans are among the most abundant inclusions in middle Eocene Baltic amber (Aphidoidea: 23% of all inclusions; Larsson, 1978), Campanian-aged Canadian amber (Aphidoidea: 22% of all inclusions; McAlpine and Martin, 1969), and Turonian-aged amber from New Jersey (Coccoidea: 10% of all inclusions; Grimaldi et al., 2000; Koteja, 2000). All of these amber deposits were produced in warm temperate or subtropical coniferous forests. The abundance of Coccoidea in New Jersey amber probably explains the abundance and diversity of Neuropterida in that amber (table 2), particularly regarding the fact that the amount of New Jersey amber excavated is a tiny fraction of that mined in the Dominican Republic or the Baltic region. The New Jersey amber fauna includes several bizarre mantispids, a larval and adult psychopsid, larval and adult mesoraphidiids, and a significant diversity and abundance of berothids and coniopterygids (with the latter two groups being significant coccoid predators). The Baltic amber fauna (table 1) is comprised thus far of 19 species in 10 families of Neuroptera—the most diverse of any amber deposit. While this may reflect the enormous quantities of Baltic amber collected over centuries, it is also probably a reflection of the abundant sternorrhynchan fauna in that amber. Neuropterida are rare in all ambers but appear to be less so (particularly for Neuroptera) for those deposits with

a significant abundance of sternorrhynchan prey.

AGE OF FAUNA AND BIOGEOGRAPHY

Without question, the neuropterid fauna of Dominican and Mexican amber is very similar to the modern fauna of Mesoamerican tropical forests. While the age of Dominican amber has been unnecessarily confused as being Miocene to even Eocene in age (see critique in Grimaldi, 1995a), all critical evidence indicates that it is early Miocene in age (Iturralde-Vinent and MacPhee, 1996, 1999). This conclusion is congruent with the mostly modern character of the biological inclusions in Dominican amber (e.g., Grimaldi, 1995b, for flies; Engel, 1999b, 2001, for bees).

There is an interesting mixture of biogeographic elements among the Neuropterida in Dominican amber. Taxa that have a predominantly Holarctic distribution are *Sialis* and *Chrysopa*. Neotropical taxa are represented by *Leucochrysa* (also Nearctic), *Porrerus*, *Ululodes* (also southern Nearctic), and *Symphorobius* (also Nearctic). The most interesting biogeographic connection is the presence of two species of *Spiloconis*, a group today found only in Madagascar, Southeast Asia, and Australia. Old World extinctions in Dominican amber are well documented: *Valeseguya* woodgnats (Diptera: Anisopodidae; Grimaldi, 1991) and *Mastotermes* termites (Isoptera: Mastotermitidae; Krishna and Emerson, 1983; Krishna and Grimaldi, 1991), both presently in Australia; certain species of *Ogcodes* (Diptera: Acroceridae; Grimaldi, 1995b) in Africa and Asia; and *Leptomyrme* from the Indo-Australian region (e.g., Baroni Urbani, 1980) as well as some other kinds of ants principally restricted to the Eastern Hemisphere (e.g., Brandão et al., 1999). The interpretation and concomitant implications of these extinctions, however, depend on monophyletic taxa. Unrecognized paraphyly of particular groups can mislead reconstructions by implying a significant biogeographic extinction when, in fact, modern counterparts, living in the same general region as the fossils under question, are classified in a separate supraspecific group that merely represents a monophyletic derivative of

the same lineage. The extinction of *Spiloconis* in the New World seems, for the time being, well founded. The reduced, essentially internalized, male terminalia typical of *Spiloconis* species is apomorphic for the Aleuropteryginae, thereby supporting the monophyly of the genus. Although male terminalia are unknown for the *Spiloconis* fossils discussed herein, the observable apomorphic traits in the fossils are known only in species of *Spiloconis* among aleuropterygines and support the conclusion that the fossils belong to this lineage. Factors that might have led to the localized decline and eventual loss of this genus in the Western Hemisphere remain elusive.

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