INSECTS FROM THE SANTANA FORMATION, LOWER CRETACEOUS, OF BRAZIL

Edited by

DAVID A. GRIMALDI

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
NUMBER 195 NEW YORK : 1990

Recent issues of the *Bulletin* may be purchased from the Museum. Lists of back issues of the *Bulletin, Novitates,* and *Anthropological Papers* published during the last five years are available free of charge. Address orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, New York 10024.

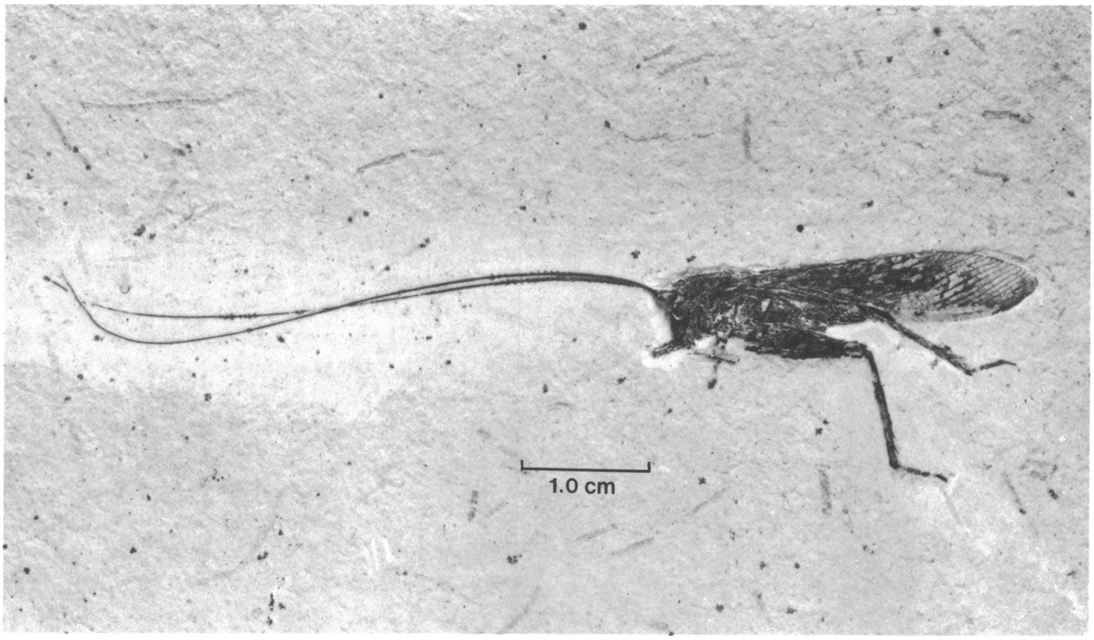
INSECTS FROM THE SANTANA FORMATION, LOWER CRETACEOUS, OF BRAZIL

Edited by
DAVID A. GRIMALDI
Assistant Curator
American Museum of Natural History

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Number 195, 191 pages, 87 figures, 3 tables
Issued August 14, 1990
Price: $20.00 a copy

Copyright © American Museum of Natural History 1990

ISSN 0003-0090



Lateral view of a tettigonioid orthopteran (Haglidae/Prophalangopsidae?) from the Santana Formation, Ceará, Brazil.

CONTENTS

Introduction. David Grimaldi and John Maisey 5

Chapter 1. Stratigraphy. John G. Maisey 15

Chapter 2. Ephemeroptera. W. P. McCafferty 20

Chapter 3. Odonata. Frank Louis Carle and Dennis C. Wighton 51

Chapter 4. Dermaptera. Edward J. Popham 69

Chapter 5. Isoptera. Kumar Krishna 76

Chapter 6. Homoptera. K. G. A. Hamilton 82

Chapter 7. Hymenoptera. D. Christopher Darling and Michael J. Sharkey 123

Chapter 8. Raphidioptera. John D. Oswald 154

Chapter 9. Diptera. David Grimaldi 164

General Index 184

Taxonomic Index 186

INTRODUCTION

DAVID GRIMALDI[1] AND JOHN MAISEY[2]

The Cretaceous Period is the most poorly represented, and thus least understood, part of the insect fossil record. This situation is changing, however, with the recent discoveries of several large deposits around the world, no doubt the largest of which is located in the northern Araripe Plateau, in the southern part of the state of Ceará, Brazil. When several large collections of Lower Cretaceous insects were assembled from this locality, it afforded an unrivaled opportunity to test the hypothesis (e.g., Carpenter, 1976) that many of the modern higher taxa of insects, such as at the family and generic levels, had originated in the Cretaceous Period.

Hennig (1981) gave a detailed account of the major deposits of Cretaceous insects, which will not be repeated here. Since then six large deposits have been found for which at least some preliminary work has been done. These are from the lower Cretaceous (also Aptian) of Victoria, Australia (Jell and Roberts, 1986), lower Cretaceous of Gansu, China (Hong, 1982), middle or late Cretaceous of Botswana (McKay and Rayner, 1986), lower Cretaceous of Mongolia (Tatarinov et al., 1986), Early Cretaceous of Lérida, Spain (Whalley and Jarzembowski, 1985), and the early Cretaceous Wealden series of England (Berriasian-Barremian) (Jarzembowski, 1984). The compression fossils most thoroughly studied thus far are in the Mongolian deposit, and the Wealden deposit is now receiving comprehensive attention by E. A. Jarzembowski. In terms of taxonomic diversity and total number of specimens, the Brazilian deposit is probably the largest in the world for Cretaceous insects.

ACKNOWLEDGMENTS AND DEPOSITION OF SPECIMENS

Without the extreme generosity of Dr. Herbert Axelrod, who made his personal collection available for study, this project would not have been possible. Several people now or formerly at the AMNH helped in the preparation, initial sorting, numbering, cataloging, and photography of specimens: Stan Blum (formerly in Vertebrate Paleontology Dept.), Greg Cavalho (Mineralogy Dept.), Darlene Judd (formerly in Entomology Dept.), and Ivy Rutzky (Vertebrate Paleontology). To Ed Jarzembowski (Brighton, U.K.), Frank Carpenter (MCZ, Harvard), and Alexander Rasnitsyn (Paleontological Institute, Moscow), who offered comments and advice, we are very grateful. We also thank our colleague Rafael G. Martins-Neto (Geosciences Institute of the University of São Paulo), who generously supplied us with reprints, manuscripts, drawings, and information of Brazilian work on the Santana fossils.

In keeping with Brazilian regulations and legal customs, holotypes and some voucher specimens have been returned to Brazil. They are deposited in the Museu de Zoologia da Universidade de São Paulo.

LOCALITY

The Araripe Plateau extends approximately 200 km east–west, along the southern borders of Ceará, northeastern Brazil. Several hundred meters of Mesozoic strata are present. There are some 300 m of Jurassic sandstones and shales, overlain by three Aptian–Albian sequences. The lowest of these is a sequence of black shales, carbonates, and evaporites. This sequence is customarily regarded as the lowest member of the Santana Formation (e.g., the "Crato Member" of authors), but da Silva (1986a) has suggested the presence of a widespread unconformity separating this sequence from the overlying sediments. The Santana Formation including this lower sequence rests locally upon basement rocks (e.g., at Rancharia). Unconformably overlying both of these sequences is a thick upper layer of reddish cross-bedded sandstone (the Exu Formation).

Although the Crato Member is widely distributed on the Araripe Plateau, the principal

---

[1] Assistant Curator, Department of Entomology, American Museum of Natural History.

[2] Curator, Department of Vertebrate Paleontology, American Museum of Natural History.

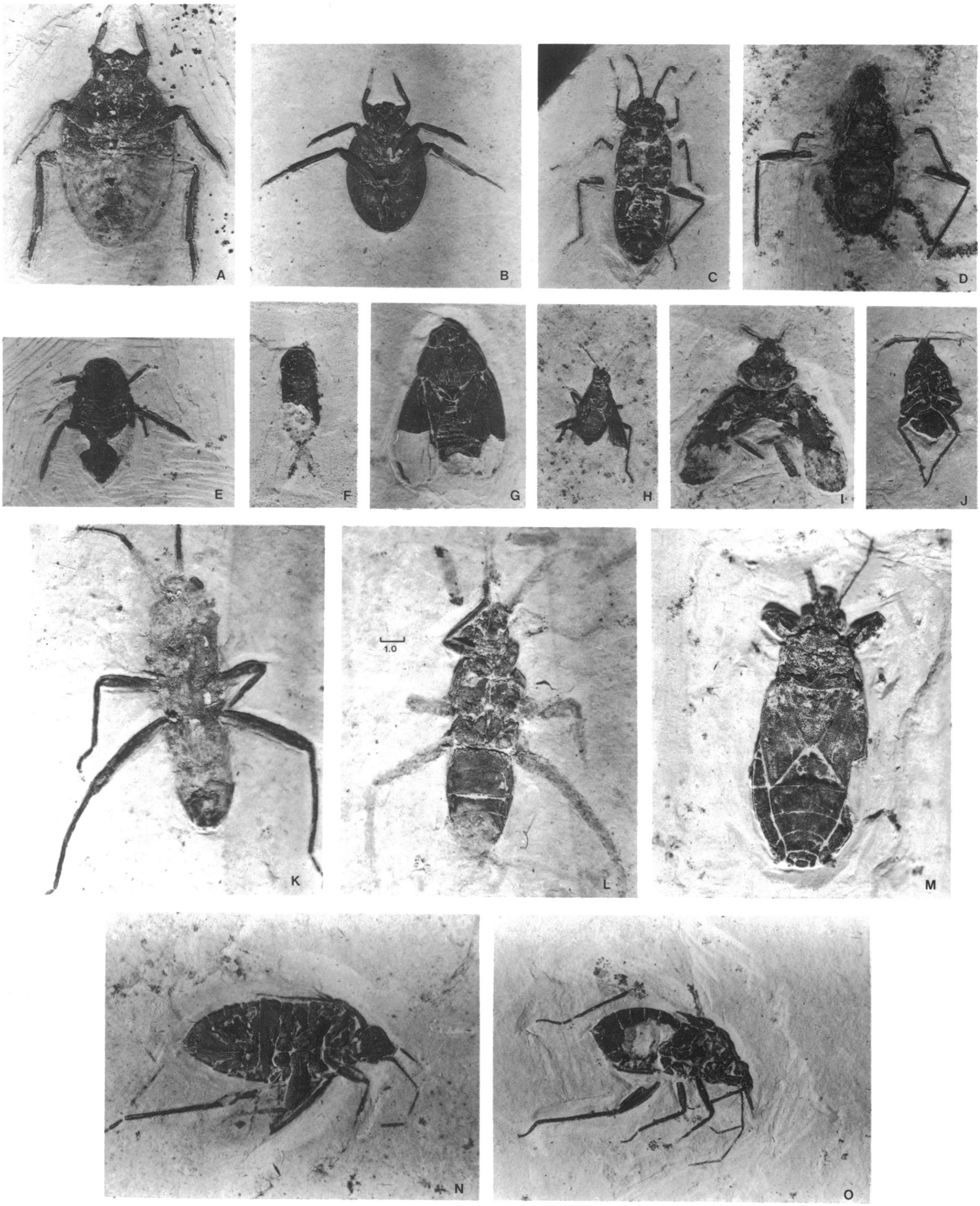


Fig. 1. Representative Heteroptera in the Santana Formation. **A, B.** Belostomatidae (both specimens ventral). **C.** Pentatomorpha (ventral). **D.** Gerromorpha? (dorsal). **E.** Naucoridae (dorsal). **F.** Corixidae (dorsal). **G.** Peloridiomorpha? (dorsal) (det. R. J. Wootton). **H.** Saldidae (dorsal). **I.** indeterminable (dorsal). **J.** indeterminable (ventral). **K, L.** Pentatomorpha (part and counterpart of same specimen, 1 shows the ventral surface). **M.** Reduviidae? (dorsal). **N.** Pentatomorpha (ventral). **O.** Cimicomorpha (ventral). Scale on L is 1.0 mm; all photos are to the same scale.

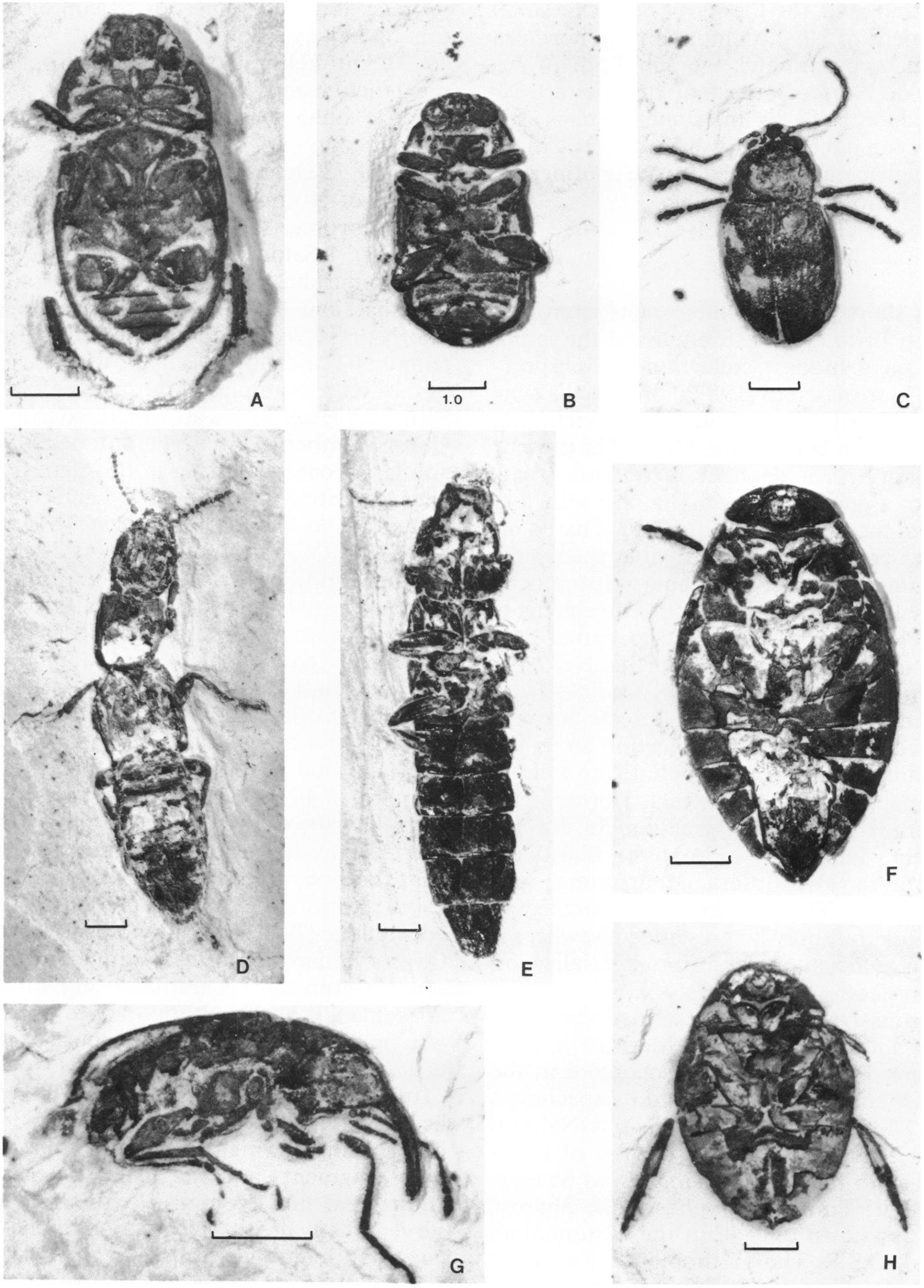


Fig. 2. Representative Coleoptera in the Santana Formation. **A, B.** Scarabaeidae: Aphodiinae?. **C.** Chrysomelidae? **D, E.** Staphylinidae. **F, H.** Dystiscidae. **G.** Curculionoidea. All scale lines are 1.0 mm.

collecting area for fossils is near the small settlement of Nova Olinda, on the northern margin, approximately 45 km ENE of Juazeiro do Norte. Here, small quarries are excavated for the flaggy limestone, which is used locally for paving and wall stone, but is increasingly being exploited for the commercial use of its fossils.

THE INSECTS

In a short paper on the insects from this deposit, Brito (1984) summarized the fauna based on a modest collection of 56 specimens. Martins-Neto (1987a) provided a synopsis of fossil insects from Brazil, including the formation being treated here. The present monograph is a detailed taxonomic treatment of a portion of the fauna, including orders not mentioned by Brito, and is based on a larger collection of identifiable specimens and numerous other fragmentary specimens. A very large collection of 3000 specimens is at the Museu de Zoologia, São Paulo, currently under study by Dr. Martins-Neto, his students, and associates.

Fourteen living orders of insects are represented in the AMNH collection from the Santana Formation, and include the following: Ephemeroptera, Odonata, Dermaptera, Isoptera, Homoptera, Hymenoptera, Raphidioptera, Diptera, Trichoptera, Blattodea, Coleoptera, Orthoptera, Neuroptera, and Heteroptera. The last six are not treated in this work, but may be presented elsewhere if there is sufficient interest from specialists on these orders.

Martins-Neto (1987a) indicated that there are, in addition, the orders Mecoptera, Lepidoptera, Plecoptera, and Psocoptera in the Crato Member, as represented by specimens in the São Paulo collection. Martins-Neto (in prep.) is describing a new species of Phasmatodea in the genus *Cretophasma* Sharov, 1968. The family Cretophasmidae Sharov, 1968, is known only from the Cenomanian of the U.S.S.R. The Trichoptera are so small and fragile that little taxonomic information can be derived from the few details which are preserved in this type of matrix, save for some details of venation and spination. Amber Trichoptera fossils apparently hold the most promise for the Cretaceous paleontology of this order (e.g., Botosaneanu and Wichard, 1983). The preliminary indications from these unstudied groups are, however, that a very diverse fauna existed, particularly for the Heteroptera.

Out of 73 Heteroptera specimens prepared, 2 were of Notonectidae, 2 Naucoridae, 10 Nepomorpha, 8 Belostomatidae (mostly nymphs), 1 Saldidae (?), 2 Reduviidae (?), 3 Cimicomorpha, 5 Lygaeiodea, 11 Pentatomorpha, and 30 (mostly incomplete and poorly preserved) undetermined Heteroptera (Randall T. Schuh, personal commun.) (see figs. la–o for examples of most of these taxa). So far, no Heteroptera are described from the Crato Member. However, a notonectid very similar to ones occurring in this deposit has been described from the lower Cretaceous of Argentina, as *Canteronecta irajae* (Mazzoni, 1982). Pinto and Ornellas (1974) described two new families (Pricecoridae and Latiscutellidae) based on two specimens from the Codo Formation of Maranhão, Brazil (stratigraphically equivalent to the Santana Formation). Only one beetle has thus far been described from the Crato Member, as a pyrochroid (*Cretaceimelittommoides cearensis* [Vulcano and Pereira, 1987]). For the Coleoptera, of 44 specimens, Roy Crowson and John Lawrence (personal commun.) identified 2 hydradephagans (apparently Dytiscidae), 2 Staphylinidae (also, L. Herman, personal commun.), a possible passalid, 1 Nitidulidae (?), 10 Curculionoidea, probably Oxycorynidae (also, E. C. Zimmerman, personal commun.), 1 Carabidae, and 11 Scarabaeoidae, probably aphodiine Scarabaeidae (see fig. 2a–h for examples of most of these taxa).

It will be difficult to treat the Blattodea because of the plethora of fossil names in the order, many of which are synonyms based on wing fragments and the like. The Santana Blattodea, however, are exquisitely preserved: many details of spination on the legs, coxae, and other ventral segments and sclerites are clear, as is the venation of fore and hind wings and even the fine setae on the cerci. One group of fossils, which are probably cockroaches, was originally believed to be Protelytroptera, an extinct order known only from the Permian (Carpenter and Kukalová, 1964). The features suggesting this were a broad head with large, round eyes; filiform antenna; the entire forewing very heavily sclerotized, punctate, and with simple dichotomous vein branching; hind wings expansive, with numerous crossveins, and with a costal stigma; and the presence of cerci (fig. 3a, g). Figure 3a–g shows representative Blattodea in the collection. Pinto and Purper (1986) described a new genus of cockroach from the Formation.

The Orthoptera in the AMNH and Brazilian collections include both Caelifera and Ensifera, with the most common being Gryllidae (about four species of Gryllinae represented in the AMNH collections [fig. 4a–c, e, f], and several species of Oecanthinae—David Nickle, personal commun.). The abundance of gryllines may be one reason why several fine specimens of cricket parasites, in the Rhopalosomatidae (Hymenoptera), were also present. Martins-Neto (1987b) described *Araripegryllus,* for *A. camposi,* and placed it in the Gryllospeculinae Gorochov. The description was based on several male forewings, which are modified for sound production and the morphology of which varies greatly among gryllid groups. A species of pygmy mole cricket (Tridactylidae) was represented by several finely preserved specimens (fig. 4d). Martins-Neto (1987c, abstract) proposed two new families of acridoids based on three species, and that author is presently treating many other acridoids. At least in the AMNH collection, it is the tettigonioids that are the common and diverse Orthoptera.

A surprising discovery was the raphidiopterans, an order not currently in the Neotropics. Martins-Neto (personal commun.) may be describing a new genus based on this species, which is possibly unwarranted given its apparent placement in *Baissoptera* (Oswald, this volume). Martins-Neto and Vulcano (1988) described three genera and one subfamily of Chrysopidae-like neuropterans: *Limaia, Araripechrysa,* and *Carirchrysa,* all in their new subfamily Limaiinae. Also, there are Ephemeroptera specimens in the deposit belonging to the Siphlonuridae (presently Holarctic, southern South America and Australia) and to the Potamanthidae (presently Holarctic and Oriental). These distributions reflect that for a Paleocene Siricidae sawfly (Hymenoptera) from Argentina (Fidalgo and Smith, 1987), since living New World siricids occur in North America. The following major taxa now have the oldest known, undisputed representative(s) in this deposit (an asterisk [*] indicates that the specimens are the only fossils known for the family): Asilidae (Diptera), Achilidae (Homoptera), *Rhopalosomatidae and Tiphiidae (Hymenoptera), and the *Oligoneuriidae, *Potamanthidae, and *Euthyplociidae (Ephemeroptera).

PRESERVATION AND PREPARATION

Besides the size and diversity of the Santana Formation insect fauna, it is the detailed preservation of the specimens, and, in such complete relief, that makes their study of interest. Ommatidia, hair fringes, setae, microtrochia on wing membranes, and the punctures and striae on various surfaces are present in many specimens, and are well defined with scanning electron microscopy (figs. 5a–l).

The following procedure was used to determine the composition of the specimens. Two insect specimens and their matrices were analyzed using automated x-ray diffraction. One specimen was ground with the matrix into a sample; the other was prepared by first dissolving the matrix in HCl and grinding up for a sample what remained as dark brown fragments. The matrix was found to be at least 99 percent carbonate (calcite, $CaCO_3$), with trace amounts of apatite and pyrolusite. The pyrolusite (a manganese oxide, MnO_4) is visible as black dendritic spots on the matrix. The fossil material itself is virtually pure geothite [iron oxide hydroxide, FeO(OH)], which shows a characteristic x-ray diffraction peak. When pulverized the fossil material forms a rust-colored powder typical of iron oxides. Touching the hot tip of a soldering iron to several samples of the pulverized material on a glass slide (under 20× magnification) produced no "ashing," which is characteristic of pure carbon. Thus, the finely preserved detail in the specimens is due to completely inorganic (mineral) replacement. The diverse faunas of fishes from the Ro-

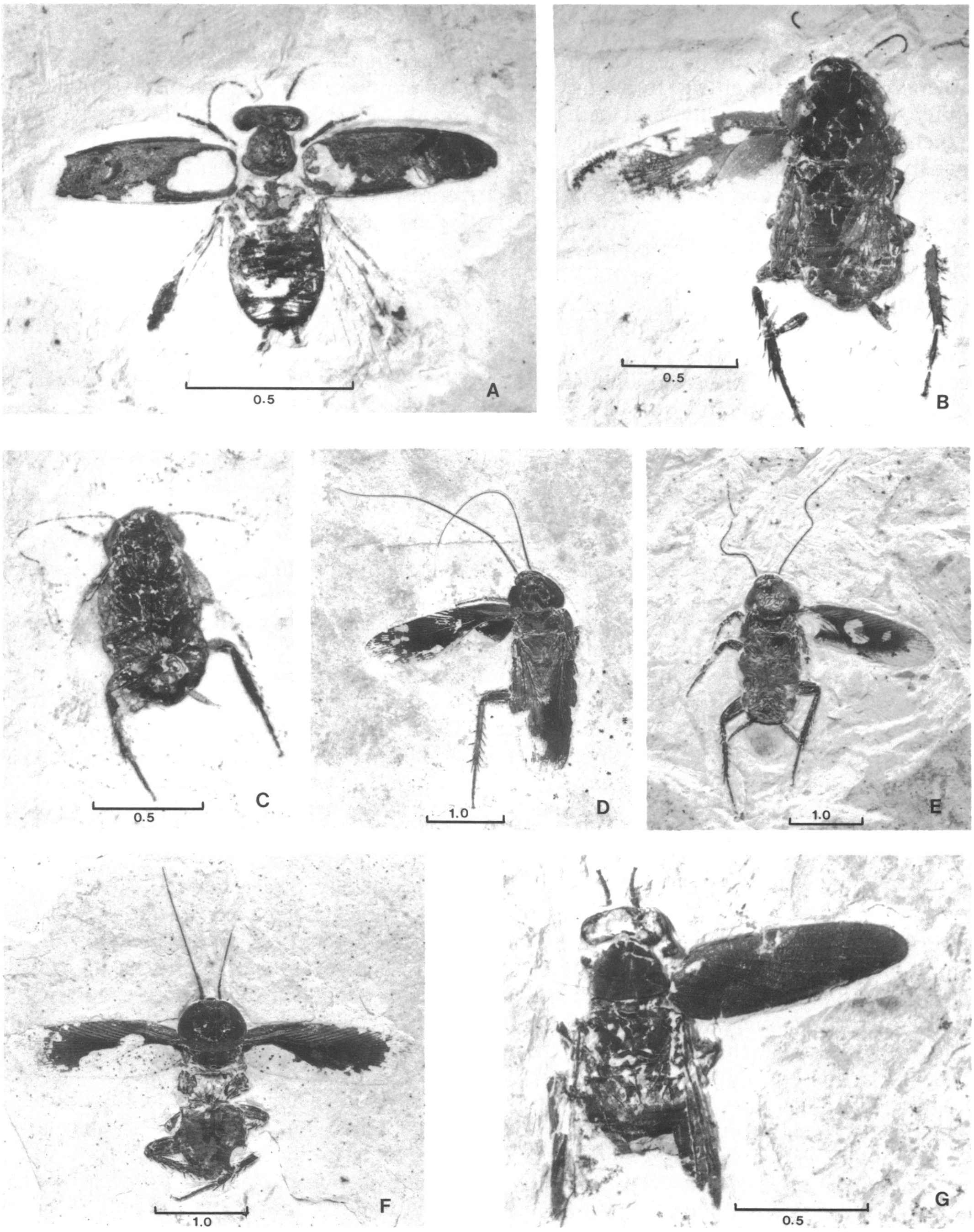


Fig. 3. Representative Blattodea in the Santana Formation. a and g show the unusual group of roaches, characterized by the elytrous forewings bearing punctation and simple, dichotomous venation. Scale lines are in cm.

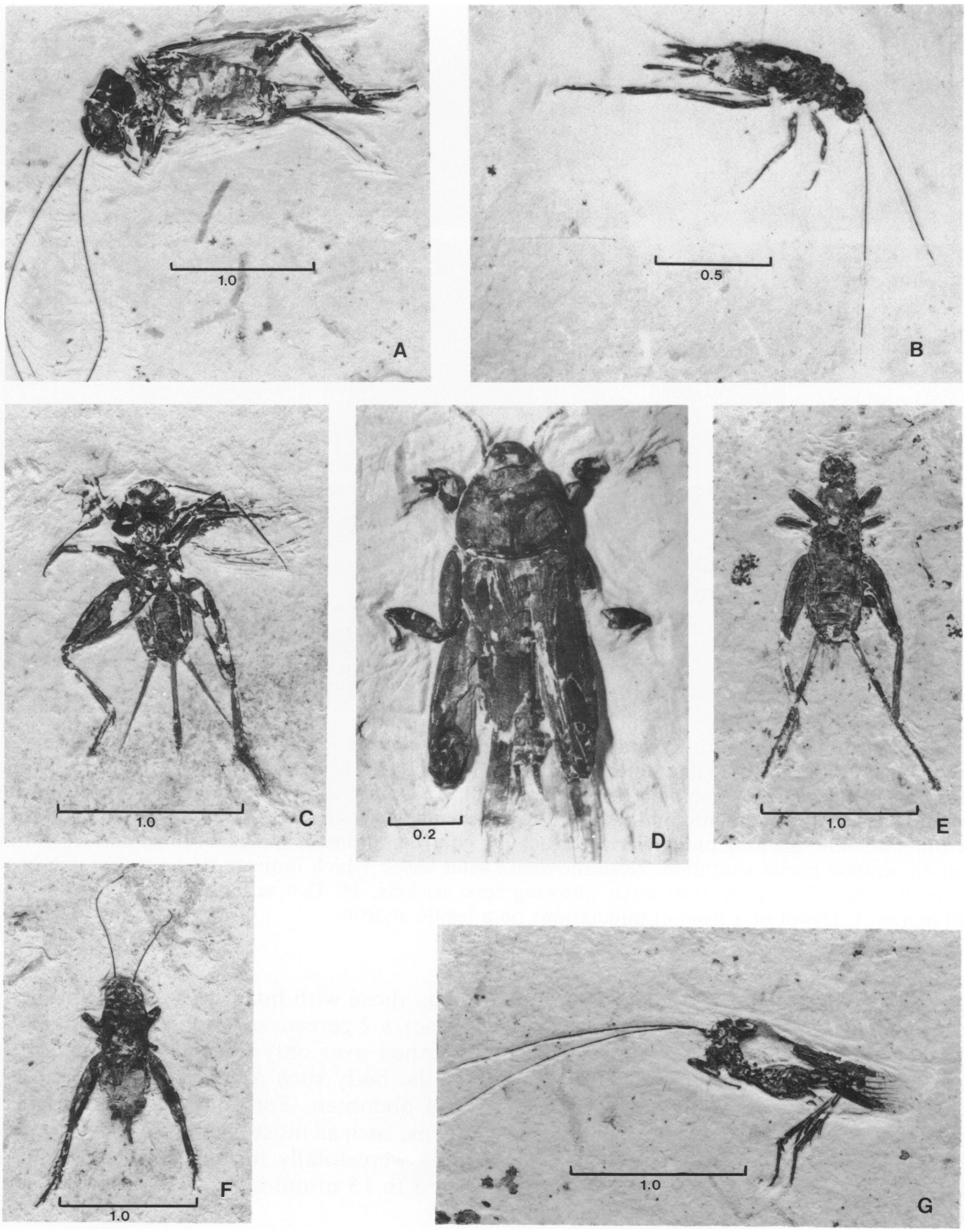


Fig. 4. Representative Orthoptera in the Santana Formation. **A–C, E, F.** Gryllinae. **D.** Tridactylidae. **G.** Unidentified Tettigonioidea.

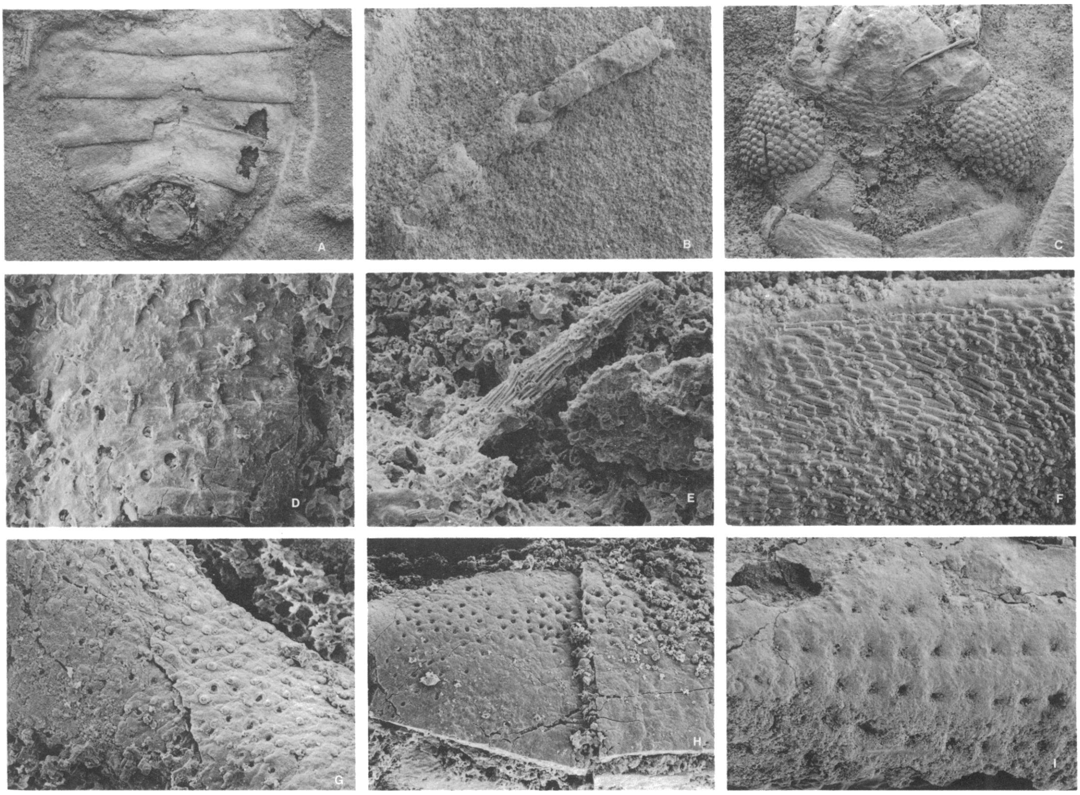


Fig. 5. Scanning electron micrographs of representative insect fossils from the Santana Formation (various magnifications). **A.** Heteropteran abdomen (ventral). **B.** Midtarsus of beetle, showing 5 tarsal segments and the second tarsomere being very small. **C.** Dorsal view of heteropteran head, showing ommatidia. **D.** Microtrichia on hind femur of heteropteran in fig. 4a and c. **E.** Detail of spine on leg of heteropteran. Note the longitudinal striae, which are common in insect spines. **F.** Inner surface of hind leg of an aquatic beetle specimen. Note the dense setal bases, which indicate that a swimming brush was on the leg. **G.** Homopteran coxa, showing setal sockets. **H.** Punctations on the clypeus of an homopteran. **I.** Detail of 4 rows of punctations on a beetle elytron.

mualdo Member of the Santana Formation (overlying the Crato Member) are also preserved in remarkable detail. Many are preserved three-dimensionally in concretions, are intact with soft tissue remains, and are composed of francolite and non-ferroancalcite (Martill, 1988).

Preparation of the fossil depended on the variable hardness of the matrix (the harder matrices having more apatite). In general, the following was found to be most reliable. Matrix was removed from around the body using various sizes of pins and microchisels (the smallest was a minuten pin mounted to a matchstick); for the very delicate specimens (e.g., those with intact wing veins and dense setae), a 2 percent solution of acetic acid was brushed over only the more robust portion of the body such as the head, thorax, legs, and abdomen. For some very solid specimens, such as most beetles and Heteroptera, they were totally immersed in the solution for 5 to 15 minutes.

PALEOENVIRONMENT

Several facts indicate that the environment in which the insects were originally fossilized was a shallow, probably eutrophic, freshwater body, at least for a part of its history. The insect fossils are always found with much more common fossils of the small (3–15 cm mean length) gonorynchiform fish, *Dastilbe,* which suggests shallow conditions. Besides the fish and insects, the limestones have yielded scorpions and spiders, a frog, and some undescribed plants. Iron and calcium precipitated out in vast quantities, which happens most favorably under high oxidation and warm conditions. The presence of a variety of plant taxa, and of a great variety of phytophagous Homoptera and Heteroptera, and the large number of Curculionoidea and Tettigonioidea, indicate a great deal of surrounding vegetation, which was perhaps emergent at the water's edge (other than a *Ranunculus,* no aquatic plants have been found). The surrounding area was probably drier than at present, as attested to by the presence of xerophilic arthropods such as Asilidae (Diptera), Myrmeleontidae (Neuroptera), and scorpions. A great deal of in situ preservation undoubtedly took place as well, as evidenced by the plethora of aquatic groups, such as the large diversity of adult and nymphal Ephemeroptera, Odonata, Heteroptera, and some Coleoptera.

The fossil evidence agrees well with da Silva's (1983, 1986a, 1986b) sedimentologically based conclusion that the Crato Member represents a lacustrine deposit that apparently formed under increasingly arid climatic conditions. Specifically, she hypothesized that the lake may well have been landlocked and fairly saline for much of its history, finally drying up to produce a sequence of gypsiferous evaporites capped in most parts by a caliche layer. There is evidence of local karstification to the southwest, suggesting a semiarid localized paleoenvironment (da Silva, 1986a).

REFERENCES

Botosaneanu, L., and W. Wichard
1983. Upper-Cretaceous Siberian and Canadian Amber Caddisflies (Insecta: Trichoptera). Bijdr. Dierkunde 53: 187–217.

Brito, I. M.
1984. Nota preliminar sobre os insetos de Fomaçao Santana, Cretaceo inferior da Chapada do Araripe, pp. 530–535. *In* An. XXXIII Congr. Brasileiro de Geol., Rio de Janeiro.

Campos, D. R. B.
1986. Primero registro fossil do Scorpionoidea na Chapada do Araripe (Cretàceo Inferior), Brasil. An. Acad. Brasileiro Cienc. 58: 135–137.

Carpenter, F. M.
1976. Geological history and evolution of the insects. Proc. XV Int. Congr. Entomol.: 63–70.

Carpenter, F. M., and J. Kukalová
1964. The structure of the Protelytroptera, with description of a new genus from Permian strata of Moravia. Psyche 71: 183–197.

da Costa Lima, A.
1950. Ninfa de efemerideo fossil do Ceará. An. Acad. Brasileira de Cienc. 22: 419–420.

Fidalgo, P., and D. R. Smith
1987. A fossil Siricidae (Hymenoptera) from Argentina. Entomol. News 98: 63–66.

Hennig, W.
1981. Insect phylogeny. Academic Press, London, 514 pp.

Hong, Y.-C.
1982. Mesozoic Fossil Insects of Jiuquan Basin in Gansu Province. Geological Publishing House, Peking, 187 pp. [in Chinese]

Jarzembowski, E. A.
1984. Early Cretaceous insects from southern England. Mod. Geol. 9: 71–93.

Jell, P. A., and J. Roberts (eds.)
1986. Plants and invertebrates from the lower Cretaceous Koonwarra fossil bed, South Gippsland, Victoria. Assoc. Australasian Paleontol. Mem. 3: 1–216.

Martins-Neto, R. G.
1987a. A paleoentomofauna Brasileira: estágio atual do conhecimento. An. X Cong. Brasileiro Paleontol., Rio de Janeiro, pp. 567–591.
1987b. Um novo género de Orthoptera (Insecta, Grylloidea) da Formaçao Santana (Cretaceo Inferior), Bacia do Araripe, nordeste do Brasil. An. X Cong. Brasileiro Paleontol., Rio de Janeiro, pp. 599–609.
1987c. Desciçao de tres generos e tres novas especies de Orthoptera (Insecta, Acridoidea) da Formaçao Santana, Bacia do Araripe (Cretaceo Inferior) nordeste do

Brasil, representando tres familias, sendo que duas novas: Archaeopneumoridae nov. fam. e Bouretidae nov. fam. An. Acad. Brasileiro Cien. 59: 444 [abstract].

Martins-Neto, R. G., and M. A. Vulcano
1988. Neuropteros (Insecta: Planipennia) da Formaçao Santana (Cretaceo Inferior), Bacia do Araripe, nordeste do Brasil. I—Família Chrysopidae. An. Acad. Brasileiro Cienc. 60: 189–201.

Martill, D. M.
1988. Preservation of fish in the Cretaceous Santana Formation of Brazil. Paleontology 31: 1–18.

Mazzoni, A. F.
1982. Notonectidae (Hemiptera, Heteroptera) de la Formacion la Cantera (Cretacio Inferior), Provincia de San Luis, Argentina. Bol. Acad. Nac. Cienc. Cordoba, Arg. 56: 259–269, 2 pls.

McKay, I. J., and R. J. Rayner
1986. Cretaceous fossil insects from Orapa, Botswana. J. Entomol. Soc. South Africa 49: 7–17.

Pinto, I. D., and L. P. de Ornellas
1974. New Cretaceous Hemiptera (Insects) from the Codó Formation—northern Brazil. An. XXVIII Congr. Brasileiro Geol. 2: 289–304.

Pinto, I. D., and I. Purper
1986. A new blattoid from the Cretaceous of Brasil. Pesquisas 18: 5–10.

Sharov, A. G.
1968. Phylogeny of the Orthopteroidea. Akad. Nauk SSSR, Trudy Paleontol. Inst. 118: 1–251.

da Silva, M. A. M. de
1983. The Araripe Basin, northeastern Brazil: regional geology and facies analysis of a Lower Cretaceous evaporitic depositional complex. Ph.D. diss., Columbia Univ., New York.
1986a. Lower Cretaceous unconformity truncating evaporite-carbonate sequence, Araripe Basin, northeastern Brazil. Rev. Brasileiro Geocienc. 16: 306–310.
1986b. Lower Cretaceous sedimentary sequences in the Basin, northeastern Brazil: a revision. Rev. Brasiliero Geocienc. 16: 311–319.

Tatarinov, L. P., et al. (eds.)
1986. Insects in the early Cretaceous ecosystems of the West Mongolia. Mockba Press, [Moscow?], 214 pp. [in Russian]

Vulcano, M. A., and F. S. Pereira
1987. Entomofauna fóssil da Chapada do Araripe, Ceará, Brasil. *Cretaceimelittommoides cearensis* gen. nov. sp. nov. (Coleoptera: Pyrochroidea). Res. Comun. X Cong. Brasiliero Paleontol., Rio de Janeiro, p. 37.

Whalley, P. E. S., and E. A. Jarzembowski
1985. Fossil insects from the lithographic limestone of Montsech (late Jurassic-early Cretaceous), Lérida Province, Spain. Bull. Br. Mus. Nat. Hist. (Geol.) 38: 381–412.

Wighton, D. C.
1987. *Gomphaeschnae obliqua* spec. nov., a new species of Gomphaeschninae from the lower Cretaceous of northeastern Brazil (Anisoptera: Aeshnidae). Odonatologica 16: 311–314.

CHAPTER 1. STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENT OF THE CRATO MEMBER (SANTANA FORMATION, LOWER CRETACEOUS OF N.E. BRAZIL)

JOHN G. MAISEY[1]

ABSTRACT

Geological data on the stratigraphy, lithological variation, and paleontological occurrences within the Lower Cretaceous sequence of the inland Araripe basin (northeastern Brazil) are reviewed. Palynological and ostracod data support an Aptian to Lower Albian age for the Santana formation, and the age of its basal Crato Member is probably Aptian. Insects, plants, and gonorynchiform fishes are among the more common fossils occurring in lacustrine laminated carbonates of the Crato Member.

INTRODUCTION

The Araripe basin today forms an elevated plateau (Chapada do Araripe), reaching altitudes of between 600 and 900 m, which extends some 200 km east-west and 70 km north-south across the southern part of the State of Ceará and into the neighboring states of Pernambuco and Piaui (north-eastern Brazil). The Araripe basin is one of a dozen or so Brazilian sedimentary basins that were active during the Cretaceous, but it differs from most in being located hundreds of kilometers away from the margin of the South American continental plate.

The Araripe plateau has long been a source of spectacular fossil vertebrates, especially fishes, turtles, crocodilians, and pterosaurs. Good specimens are abundant, and their fine state of preservation and ease of preparation (mostly using dilute organic acids) allow thorough paleontological investigation.

THE SUCCESSION WITHIN THE ARARIPE BASIN

The Araripe basin today contains approximately 700 m of a Mesozoic sedimentary sequence, thought to be of Upper Jurassic and Lower Cretaceous age. There is controversy in the literature concerning the actual age of the sediments, and considerable disagreement over how they should be subdivided stratigraphically (Small, 1913; Beurlen, 1962, 1963, 1971; L. J. Moraes et al., 1963; Braun, 1966; Silva Santos and Valença, 1968; Mabesoone and Tinoco, 1973; J. F. S. Moraes et al., 1975, 1976; Scheid et al., 1978; Oliveira et al., 1979; H. R. Lima, 1979; Silva, 1983, 1986a, 1986b).

Several issues remain controversial, but Silva's (1983, 1986a, 1986b) investigations have clarified many of the previous mysteries surrounding the Araripe basinal sequence. Silva (1986a) also provided important new evidence concerning unconformities within these sediments.

The Mesozoic sequence can be divided into two parts. The lowest of these (the Brotas group) has an unconformable relationship with the Paleozoic and Precambrian basement and also with overlying younger sediments. Generally accepted as being Jurassic in age, the rocks of the Brotas group (mostly consisting of interbedded shales and sandstones) are divided into the Alianca formation below and the Sergi formation above.

Unconformably overlying the Brotas group are Cretaceous (Aptian-Albian) sediments, termed by Silva (1986b) as the Araripe group, but known by others as the Santana formation. The latter is redefined by Silva (1986b) on the basis of important new stratigraphic data which demonstrate an intraformational unconformity (Silva, 1986a). In several earlier works, strata now included by Silva (1986) in her "Araripina formation" were regarded as the lowest member of the Santana formation (e.g., Beurlen, 1962, 1971; Mabesoone and Tinoco, 1973). It has been referred

---

[1] Curator, Department of Vertebrate Paleontology, American Museum of Natural History.

to as the Crato member by various authors, a term first coined by Beurlen (1971).

The Crato Member lies unconformably on the Brotas group, and consists of black shales overlain by laminated limestone and dolostone, algal-laminated shale, and an evaporite sequence (gypsum and anhydrite). Its upper surface is truncated by a regional disconformity, the nature of which varies across the basin. To the north and east there is a calcrete layer, comprising a calcareous and siliceous crust with chert nodules and laminae. In places the surface is slightly brecciated. Silva (1986a) found many lithological similarities with calcrete profiles described by Watts (1978) from the Quaternary of the Kalahari desert and Permo-Triassic of Scotland, and concluded that the calcrete is a caliche layer. At Barbalha, it is overlain by a 1-m-thick conglomerate, marking the local base of the Romualdo Member.

To the south and west the erosional surface at the top of the Crato Member is expressed as a paleokarst topography (e.g., in the vicinity of Rancharia-Araripina and Trindade-Ipubi). Solution cavities several meters deep are developed, some of which are connected to subsurface caverns before being infilled by muds belonging to the Romualdo Member.

The Romualdo Member forms a conspicuous series of alternating layered concretionary-calcareous shales, limestone, and sandstone. It lies unconformably on the Crato Member, and locally overlaps onto the Paleozoic and Precambrian basement (e.g., near Rancharia, 1.5 km south of Araripina).

Earlier investigators (e.g., Agassiz, 1844; Woodward, 1887, 1890, 1895, 1901; Jordan and Branner, 1908; Beurlen, 1962) believed that the sequence was of Upper Cretaceous age. Silva Santos and Valença (1968) conducted a qualitative comparison of the fossil fishes from the Araripe basin, and determined that these showed closest similarities with other Lower Cretaceous (Aptian) faunas.

This age determination has been confirmed from fossil ostracods within the Santana formation (Braun, 1966) which correlate well with those of Aptian age from the coastal Sergipe-Alagoas basin (Krommelbein, 1965a, 1965b; Krommelbein and Wenger, 1966). Palynological data, although incomplete, also confirm the age of at least part of the Araripe sequence. The upper part of the Santana formation and the overlying Exu formation have yielded pollen indicative of an Albian age (Mabesoone and Tinoco, 1973; H. R. Lima, 1978a, 1978b, 1979a, 1979b, 1980). According to Prof. G. Brenner (personal commun.), of the State University of New York (New Paltz), a Middle Albian age for the Exu formation is suggested by certain polycolpate pollen (e.g., *Galeacornea causea*). Tricolpate pollens (indicative of early angiosperms) have been recovered from both the Santana and Exu formations. Doyle et al. (1982) provided additional palynological data from a sample of the Santana formation, concluding that it contained a diverse association of angiosperm pollen characteristic of their Zone C-IX of Gabon and with the more northerly (equatorial?) palynofloras of Maranhao, the Ivory Coast, Senegal, and South Atlantic salt basins. The C-IX Zone of Doyle et al. (1982, fig. 7) falls entirely within the Upper Aptian. Unfortunately, detailed palynological data for the Crato Member have not been published, and its age remains enigmatic. It almost certainly predates the Upper Aptian, but by how much is not clear. Polycolpate pollens, like those of modern Gnetales, were reported by Mabesoone and Tinoco (1973). These are recorded as far back as the Permian, but increase rapidly in abundance and diversity from the Lower Barremian. Very tentatively, therefore, this suggests a maximum age of Lower Barremian for the Crato Member. According to Silva (1983, 1986a), however, the erosional phase leading to karstification and caliche formation may have been transitory, lasting only a few thousand years. In this case, the Crato Member is most likely of Aptian age.

The Crato Member has yielded a profoundly different suite of fossils from those of the better-known Romualdo Member overlying it. Calcareous concretions are apparently absent, and large vertebrates have not been recorded. Instead, the laminated limestones have yielded many specimens belonging to one, perhaps two, species of a small fossil gonorynchiform fish (*Dastilbe*), plus a much rarer ichthyodectoid fish (*Cladocyclus*) as well as plant and arthropod material. A small frog and a feather have also been reported (Kellner and Campos, 1986; Martins-Neto and Kellner, 1988). The plant macrofossils include possible gnetale fragments, ferns and leafy conifer fronds.

DEPOSITIONAL ENVIRONMENTS OF THE CRATO MEMBER

There is a considerable amount of lithological and paleontological data to support the view that the Crato Member is lacustrine. According to Silva (1983: 68), two lacustrine subenvironments are recognizable. One of these (represented by black shales and laminated carbonates) was probably deposited in the deeper lake center, while the other (represented by algal shales, carbonate, and evaporite) probably represents a marginal environment.

The black shale unit occurs at the base of the Crato Member, and is mostly subsurface, outcropping mainly in the northeastern part of the Araripe plateau. These shales are laminated (possibly varved), keragen-rich, and contain pyrite nodules, ostracods, and plant debris. Silva (1983: 69) found the shales to be petrographically very similar to the "oil-shales" of the Green River formation in Utah, Wyoming, and Colorado, and the East Berlin formation of the Connecticut Valley (Bradley, 1931, 1970; Eugster and Hardie, 1975; Surdam and Wolfbauer, 1975; Hubert et al., 1978). However, Silva (1983) found no evidence for subaerial exposure and suggested that the black shales of the Crato Member accumulated on a quiet, poorly oxygenated lake bed.

The laminated carbonates also outcrop in the northeast of the Araripe plateau, where they are quarried (e.g., at Barbalha). This unit varies between 10 and 50 m in thickness, and locally overlies black shales or rests directly on Paleozoic and Precambrian basement (Silva, 1983). The unit consists of calcitic to dolomitic micrites, biomicrites, and pelmicrites. Lamination is regular and parallel, but is locally cross-laminated or rippled. Darker laminae are rich in pyrite and organic matter, with lower levels of carbonates than the lighter gray or cream laminae. Bedding planes are often strewn with brownish filaments, possibly of algal origin. Here, the fish *Dastilbe* is abundant, and usually occurs singly or in twos and threes. This unit is also the one that contains the rich fossil insect assemblage reported in this monograph.

Silva (1983) found that the laminated micrite passes gradually upward into algal biomicrites and pelmicrites with many algal filaments, pellets, lumps, and mounds, numerous ostracods, and a few gastropods, pelecypods, pollen, plant remains, and possibly foraminiferans. This sequence was interpreted as representing a change from a central to marginal (shallower) lacustrine environment. There is evidence of periodic subaerial exposure (birdseye structures, desiccation cracks, etc.), diagenetic dolomitization and dedolomitization, and later diagenetic chertification.

This black shale-carbonate sequence was interpreted by Silva (1983) as a shallowing lake-center facies. However, she also recognized another continuously marginal sequence which included algal shale and calcareous algal mats overlain by tabular evaporites. The facies was recognized over a wide area near Casa de Pedra in the southeastern part of the Araripe plateau, and at Romualdo Quarry in the northeast.

The marginal shales are bioturbated and have a high organic content (mostly ostracods, algae, plant debris, molluscs, and pellets including some thought to have been produced by brine shrimp), and are strongly layered compositionally. Algal, ostracod, and plant debris layers are common, containing trapped detrital matrix. Periodic subaerial exposure is again indicated by sedimentary structures, with local development of brines (indicated by gypsum pseudomorphs) and bacterial decomposition of gypsum (indicated by gypsum pseudomorphs) and bacterial decomposition of gypsum (indicated by black coloration, pyrite nodules and grains, and associated chert and dolomite).

Tabular evaporites consist mostly of gypsum and anhydrite resting conformably on marginal algal shales and carbonates. Both primary and secondary evaporite structures have been described by Silva (1983), who regarded this deposit as having formed in a marginal sabkha-like environment. The evaporite sequence is truncated by an erosion surface, and displays karstlike solution structures, and locally evaporites are completely absent (presumably eroded away), e.g., at Barbalha.

This erosion surface marks the end of the lacustrine cycle which formed the Crato Member. Silva (1983, 1986a) considered that the subaerial interval was short-lived, although conditions evidently varied across the region even within this space of time, leading to development of karst topography in the south and west, and a caliche layer to the north and east. A generally arid and open environment is also suggested by the presence of gnetale pollen and macrofossils within the member.

REFERENCES

Agassiz, L.
1844. Sur quelques poissons fossiles du Brésil. C. R. Acad. Sci., Paris 18: 1007–1015.

Beurlen, K.
1962. A. Geologia da Chapada do Araripe. An. Acad. Brasileira Cienc. 34: 365–370.
1963. Geologia e Estratigrafia da Chapada do Araripe. XVII Congr. Brasileira. Geol., Recife, pp. 1–47.
1971. Geologie von Brasilien. Berlin: Borntraeger, 444 pp.

Bradley, W. H.
1931. Origin and microfossils of the Oil Shale of the Green River Formation of Colorado and Utah. U.S. Geol. Surv. Prof. Pap. 168: 58 pp.
1970. Green River oil shale-concept of origin extended. Geol. Soc. Am. Bull. 81: 985–1000.

Braun, O. P. G.
1966. Estratigraphia dos sedimentos da parte interior da regiao Nordeste do Brasil. Div. Geol. Mineral. D.N.P.M. 236: 76 pp.

Brito, I. M., D. de A. Campos, and R. J. Bertini
1984. Nota preliminar sobre os insetos da Formaçao Santana, Cretáceo Inferior da Chapada do Araripe. Anais. XXXII Congr. Brasileira. Geol., Rio de Janeiro, pp. 530–535.

Doyle, J. A., S. Jardiné, A. Doerenkamp
1982. *Afropollis,* a new genus of early angiosperm pollen, with notes on the Cretaeous palynostratigraphy and paleoenvironments of northern Gondwana. Bull. Centres Rech. Explor.-Prod. Elf-Aquitaise 6: 39–117.

Eugster, H. P., and L. A. Hardie
1975. Sedimentation in an ancient playa-lake complex. Geol. Soc. Am. Bull. 86: 319–334.

Hubert, J. F., A. A. Reed, W. L. Dowdall, and J. M. Gilchrist
1978. Guide to the redbeds of central Connecticut. Cont. no. 32, Dept. of Geology and Geography, Univ. Massachusetts, 129 pp.

Jordan, D. S., and J. C. Branner
1908. The Cretaceous fishes of Ceará, Brazil. Smithsonian Misc. Colln., Washington 52: 1–30.

Kellner, A. W. A., and D. de A. Campos
1986. Primeiro registro de amphibia (anura) no Cretáceo inferior da Bacia do Araripe, Nordeste do Brasil. An. Acad. Brasileira Cienc. 58: 610.

Krommelbein, K.
1965a. On "Gondwana Wealden" ostracoda from NE Brazil and West Africa. *In* West African micropalaeontology colloquium 2, Proceedings, pp. 113–119. Ibadan, Nigeria.
1965b. Preliminary remarks on some marine Cretaceous ostracods from Northeastern Brazil and West Africa. *In* West African Micropalaeontology colloquium, 2, Proceedings, pp. 119–123. Ibadan, Nigeria.

Krommelbein, K., and R. Wenger
1966. Sur quelques analogies, remarquades dans le Microfaunes Cretaceous du Gabon et du Brésil Oriental (Bahhia et Sergipe). *In* D. Reyre (ed.), Sedimentary basins of the African coasts symposium, New Delhi, 1964, Assoc. of African Geol. Surv. Paris 1966, 1st part, Atlantic Coast, pp. 193–196.

Lima, H. R. de
1979. Consideracoes sobre a subdivisao estratigráphica da Formaçáo Santana. Crétaceo do Nordeste do Brasil. Rev. Brasileira Geoc. 9: 116–121.

1978a. Palinologia da Formação Santana (Cretáceo do Nordeste do Brasil). 1. Introdução geologica e descricao sistemática dos esporos da Subturma Azonotriletes. Ameghiniana 15: 333–365.
1978b. Microfosseis da Formação Exu, Cretaceo do Nordeste do Brasil. An. XXX Congr. Brasileira Geol. 2: 965–969.
1979a. Palinologia da Formação Santana (Cretáceo do Nordeste do Brasil). II. Descriçao sistemática dos esporos da Subturma Zonotriletes e Turma Monoletes e dos polens das Turnas Saccites e Aletes. Ameghiniana 16: 27–63.
1979b. Paleontologia da Formação Santana (Cretáceo do Nordeste do Brasil): Estágio Atual de Conhecimentos. An. Acad. Brasileira. Cienc. 51: 545–556.
1980. Palinologia da Formação Santana (Cretáceo do Nordeste do Brasil). III. Descriçao sistemática dos esporos da Turma Plicates (Subturma Costates). Ameghiniana 17: 15–47.

Mabesoone, J. M., and I. M. Tinoco
1973. Palaeoecology of the Aptian Santana Formation (northeastern Brazil). Palaeogeog., Palaeoclimat., Palaeoecol. 14: 97–118.

Martins-Neto, R. G., and A. W. A. Kellner
1988. Primeiro registro de pena na Formação Santana (Crétaceo Inferior, Bacia do Araripe, Nordeste do Brasil. An. Acad. Brasileira. Cienc. 60(1): 61–68.

Moraes, J. F. S. de, C. Cheid, and J. da S. A. Santos
1975. *Projeto Santana.* Relatorio Preliminar da Etapa 1, Recife, DNPM/CPRM, 104 pp.

Moraes, J. F. S., d J. da Santos, and J. de C. Mascarenhas
1976. *Projeto Santana.* Relatorio Final da Etapa 1, Recife, DNPM/CPRM, 269 pp. (vol. 1).

Moraes, L. J., F. C. Barros, and E. Ramos
1963. Reconhecimento Fotogeslogico da Regiao Nordeste do Brasil. Div. Fm. Prod. Mineral., D.N.P.M., Folha CRATO. SB. 240. Esc. 1:250,000, Rio de Janeiro.

Oliveira, A. A. de, A. de L. F. Brito, M.E.C.M. Santos, and M. S. S. Carvalho
1979. *Projeto Chapada do Araripe.* Relatorio Final, Recife, DNPM/CPRM, 123 pp. (vol. 1).

Scheid, C., M. de B. Munis, and J. Paulino
1978. *Projeto Santana.* Relatorio final da Etapa II, Recife, DNPM/CPRM, 136 pp.

Silva, M. A. M. de
1983. The Araripe Basin, Northeastern Brazil: Regional geology and facies analysis of a Lower Cretaceous evaporitic depositional complex. Ph.D. diss., Columbia Univ., New York.
1986a. Lower Cretaceous unconformity truncating evaporite-carbonate sequence, Araripe Basin, northeastern Brazil. Rev. Brasileira. Geocienc. 16: 306–310.
1986b. Lower Cretaceous sedimentary sequences in the Basin, northeastern Brazil: a revision. Rev. Brasileira Geocienc. 16: 311–319.

Silva Santos, R. da, and J. G. Valenca
1968. Formação Santana e sua Paleoictiofauna. An. Acad. Brasileira Cienc. 40: 339–360.

Small, H.
1913. Geologia e suprimento da água subterranea no Ceará e parte do Piaui. Brasil. Insp. Obr. contra Secas, Geol. 25: 1–80.

Surdam, R. C., and C. A. Wolfbauer
1975. Green River Formation, Wyoming: a playa-lake complex. Geol. Soc. Am. Bull. 86: 335–345.

Viana, C. F.
1980. Cronoestratigraphia dos sedimentos da margem continental brasileira. Ann. XXXI Congr. Brasileira Geol., 2: 832–843.

Watts, N. L.
1978. Displacive calcite: evidence from Recent and ancient calcretes. Geology 6: 699–703.

Woodward, A. S.
1887. On the fossil teleostean fish *Rhacolepis,* Agass. Proc. Zool. Soc. London 1887: 535–542.
1890. On some Upper Cretaceous fishes of the family of Aspidorhynchidae. Proc. Zool. Soc. London 1890: 629–634.
1895. Catalogue of the fossil fishes in the British Museum (Natural History), vol. 3, xlii + 544 pp.
1901. Catalogue of fossil fishes in the British Museum (Natural History), vol. 4, xxxviii + 636 pp.

CHAPTER 2. EPHEMEROPTERA

W. P. McCafferty[1]

ABSTRACT

Fossils of 26 alate and 88 larval mayflies were studied from the Santana Formation, Lower Cretaceous, Ceará Crato, Brazil. New descriptions are as follows: larva of *Siphgondwanus occidentalis,* new genus and species (Siphlonuridae); alate forms of Siphlonuridae (?) spp. 1, 2, and 3; larva and alate form of *Colocrus indivicum,* new genus and species (Oligoneuriidae: Colocrurinae, new subfamily); alate forms of *Australiphemera revelata,* new genus and species, and *Microphemera neotropica,* new genus and species (Ephemeridae); alate form of *Pristiplocia rupestris,* new genus and species (Euthyplociidae); alate form of Ephemeroidea sp. 1; alate form of Ephemeroidea sp.; larva of Leptophlebiidae (?) sp. 1, and alate forms of Leptophlebiidae (?) spp. 2 and 3; larvae of incertae sedis spp. 1 and 2. *Protoligoneuria limai* Demoulin is redescribed from a very large series of larval specimens and is clearly a member of the Hexagenitidae rather than the Oligoneuriidae, where it was previously classified.

The study material provides the first fossils of Oligoneuriidae (as here restricted) and Euthyplociidae, and possibly Potamanthidae. Oligoneuriidae along with Coloburiscidae (new status), Isonychiidae, and Heptageniidae are recognized as the monophyletic superfamily Heptagenioidea. The higher classification is based on cladistic relationships of familial lineages. The relationships of the extinct families Hexagenitidae and Epeoromimidae are reevaluated in light of the new paleontological data. Among the Oligoneuriidae, the newly discovered extinct genus *Colocrus* is shown to be cladistically more derived than Chromarcyinae, with forewing venation intermediate between the plesiomorphic venation of Chromarcyinae and the highly specialized venation of Oligoneuriinae. The larva of *Colocrus* retains a plesiomorphic dorsal first gill similar to that of Chromarcyinae.

Although in general the mayflies studied are characteristically similar to modern schistonote forms, a majority of the lineages represented did not survive to the present in the Neotropics, either becoming entirely extinct or displaced biogeographically. Both Oligoneuriidae and Ephemeroidea apparently radiated into their major lineages by Lower Cretaceous time. Pannotes and Baetidae, however, remain unknown from the Mesozoic. Finds of Siphlonuridae, Ephemeridae, and possibly Potamanthidae in Brazil indicate previous widespread distributions for these families (extant Neotropical ephemerids being of more recent north-temperate origin). The discovery of Hexagenitidae in the Southern Hemisphere indicates a widespread Pangaean distribution for this extinct Mesozoic group. The presence of Oligoneuriidae and Euthyplociidae in West Gondwana suggests that continental vicariance in the Southern Hemisphere accounts for their present Pantropical distributions. Mayflies from the fossil site apparently include forms from both lentic and lotic aquatic habitats.

INTRODUCTION

The unearthing of larval and alate Ephemeroptera from the Santana Formation in Ceará Crato, Brazil, is a major discovery, providing the opportunity for a critical contribution to our knowledge of mayfly history. Not only are fossil ephemeropteran remains rare from the Lower Cretaceous, but prior to this they have been very poorly known from South America, with only brief accounts of a few larvae from the Lower Cretaceous of Brazil (Costa Lima, 1950; Brito, 1987) and the Eocene of Argentina (Rossi de Garcia, 1983).

As a result of this find, questions regarding the affinities of Lower Cretaceous mayflies, with either an essentially modern fauna or a more ancient one, can be resolved with more certainty. In addition, questions about biogeographic elements present in West Gondwana that, because of the connection of certain continents, may account for some present-day disjunct world distributions, can also begin to be resolved. Limited hypotheses of causal mayfly biogeography in the past have been based almost entirely on phylogenetics and other inferences from extant taxa (Edmunds, 1972, 1975; McCafferty et al., 1990). Many of these hypotheses, which have yet to be tested because of the paucity of a Southern Hemisphere fossil record, are now testable.

---

[1] Professor, Department of Entomology, Purdue University, West Lafayette, IN 47907.

Ephemeropteran paleontology has been reviewed by Tshernova (1970, 1980). Edmunds (1972) discussed fragmentary data on fossil relationships, and Landa and Soldán (1985) accounted for most extinct higher taxa in their classificatory synopsis. Sinitshenkova (1984) gave a brief account of the paleoecology of mayflies, and Hubbard (1987) has provided a useful catalog of nearly all fossils that have been referred to Ephemeroptera. For the most part, extinct families have not convincingly been placed within a phyletic scheme of extant families, and differences of opinion remain as to the superfamilial classification of several extinct families. In addition, the familial classification of many fossils requires reevaluation.

Insects from the Paleozoic that have been considered to be mayflies represent an ancient extinct fauna known mainly from northern Pangaea. However, *Triplosoba pulchella* is the only Carboniferous insect that has consistently been considered in the Ephemeroptera, and placement of a number of Carboniferous insects in the Ephemeroptera, for example, by Kukalová-Peck (1985) (Protoephemeroptera, sensu Hubbard, 1987) requires a very broad definition of the order. In my opinion, basic ephemeropteran wing venation may be highly plesiomorphic and thus several widely diverging early insect lineages could incorrectly be placed in Ephemeroptera if additional characterization is not available. Most recently, Carpenter (1987) has cast doubt on the makeup and inclusion of the Syntonopteridae in the Ephemeroptera for essentially the reasons stated above.

The extinct superfamilies Protereismatoidea and Mesephemeroidea constitute the known Permian insects that appear to be mayflies, or at least mayfly precursors, and include preschistonote larvae (McCafferty and Edmunds, 1979) with articulated wing pads (see review of Hubbard and Kukalová-Peck, 1980). Of these Paleozoic groups, only Mesoplectopteridae and Mesephemeridae continued into the Mesozoic.

Mesoplectopteron (Mesoplectopteridae) is the only known Triassic mayfly. About 18 genera of mayflies are now known from the Jurassic, all from northeastern Pangaea. These genera are currently placed in the extinct taxa Aenigmephemeridae, Epeoromimidae, Hexagenitidae, and Mesephemeridae, and the extant taxa Behningiidae, Ephemerellidae, Coloburiscinae, Leptophlebiidae (Mesonetinae), Palingeniidae, and Siphlonuridae. Of these extant groups, only Siphlonuridae in the broadest sense (e.g., Tshernova, 1967) appears to be unquestionably represented. Jurassic fossils assigned to other extant families require review. The extinct Jurassic families are all quite similar to the Siphlonuridae.

A Cretaceous mayfly fauna has only recently been documented from some fossils from Palearctic Laurasia (Tshernova, 1971; Tshernova and Sinitshenkova, 1974; Sinitshenkova, 1976, 1986), Australia (Jell and Duncan, 1986), and one from Algeria (Sinitshenkova, 1975). These include the Lower Cretaceous genera *Mesoneta* (Leptophlebiidae ?) and *Epeoromimus* (Epeoromimidae), both of which had also occurred in the Jurassic, as well as *Hexameropsis* and *Mongologenites* (Hexagenitidae), *Proameletus* and *Australurus* (Siphlonuridae), *Promirara* (Ameletopsidae ?), and *Dulcimanna* (family incertae). The new data represented herein greatly expand our knowledge of Cretaceous mayflies.

Sinitshenkova (1984) mentioned, without detail, some undescribed Brazilian fossils from the Lower Cretaceous. Those are probably referable to *Protoligoneuria limai* (Hexagenitidae), which is described in detail herein. Undescribed Australian larval fossils that were mentioned by Riek (1970) include those recently described by Jell and Duncan (1986). *Cretoneta* (Leptophlebiidae) from the Upper Cretaceous is the only other known mayfly from the Cretaceous.

Tertiary mayflies, many from Baltic amber, are much better represented (e.g., see Demoulin, 1968). The Tertiary fauna is essentially a modern one (e.g., McCafferty and Sinitshenkova, 1983; McCafferty, 1987), including both extinct and extant genera of extant families.

The Lower Cretaceous mayfly fossils from Brazil treated herein include 26 alate and 88 larval specimens, representing at least seven families. My approach in naming these fossils and assigning them to a higher classification has been a relatively conservative one. If a fossil is too incomplete to be clearly placed, then it is either not assigned a family or it is only provisionally placed in a family and not given genus and species names. Twelve additional specimens are not described or placed beyond order because of insufficient preserved detail.

New monospecific genera and their applicable species are described together since it would be impossible at this time to sort out generic vs. specific level characters. Generally, size characters may be considered specific, but not always; and whereas genitalia are usually very valuable for specific diagnosis, they are very poorly represented in these fossils. Larval mouthparts are also valuable for either specific or generic differentiation, but these too are very poorly preserved.

The adult and subimaginal stages are together referred to as alate because it is usually impossible to discriminate between the two different winged stages in these fossils. In formal descriptions of newly named taxa, alate forms are described under the heading of Adult since the structural characters described would apply to the adult even if the subimago was actually represented by the fossil(s). Body lengths that are given always exclude caudal filaments. Discussions accompanying individual descriptions include accounts of pertinent fossil records, lineage ages and relationships, classifications, and paleoecology, if possible. Concluding remarks following the taxonomic treatment concern evolution and historical biogeography as well as the paleoenvironment that are inferred from all the data presented.

ACKNOWLEDGMENTS

I wish to thank Arwin Provonsha of Purdue University for line illustrations and Dave McShaffrey of Purdue University for assistance in photographing fossils. I also thank George Edmunds, University of Utah, and Bill and Jan Peters, Florida A&M University, for their many helpful suggestions for the manuscript.

FAMILY HEXAGENITIDAE

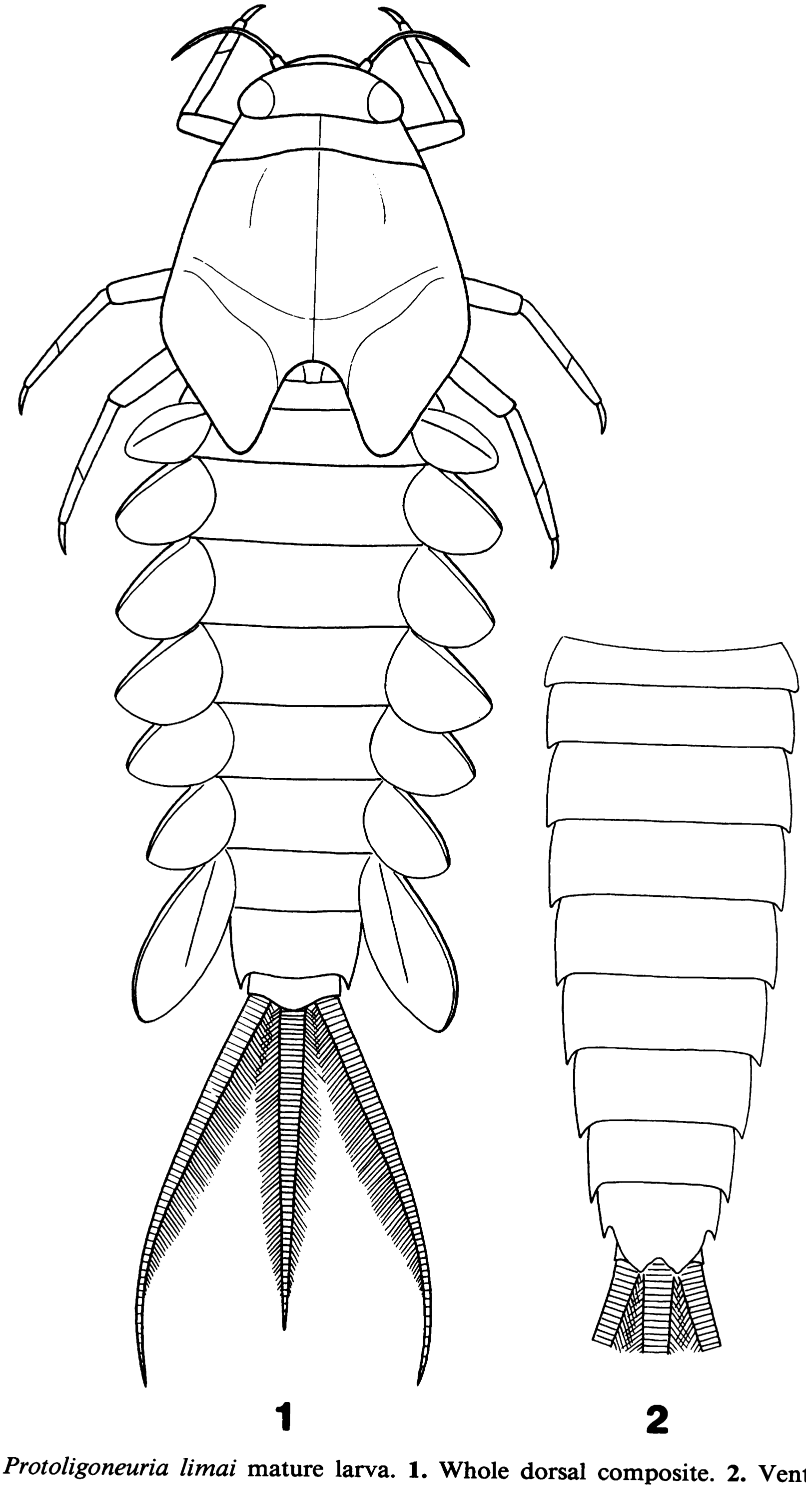
Protoligoneuria limai Demoulin

Figures 1–8

Baetidae (Siphlonurinae), Costa Lima, 1950: 419.
Protoligoneuria limai Demoulin, 1955: 271.
Palaeobaetodes costalimai Brito, 1987. NEW SYNONYM.

MATERIAL: 77 larvae: AMNH 43400–43422, 43424–43437, 43439–43452, 43454–43471, 43478, 43482, 43485–43488, and 43492–43498; 4 questionable larvae: AMNH 43438, 43483, 43490, and 43491.

DESCRIPTION: Dorsal, ventral, and lateral aspects represented; general structural details represented among various fossils except mouthparts not discernible; middle instars to mature specimens represented. Body minnowlike, fusiform, ranging from 7.0 mm to 13.4 mm long (excluding caudal filaments). Head hypognathous, shorter than broad (width nearly twice length), narrower than thorax, tapered anteriorly; discernible compound eyes relatively small, situated dorsolaterally; antennae thin and delicate, attenuated, relatively short (1.4 mm long on specimen with body 8.9 mm and head width 2.2 mm), inserted anteriorly on head capsule. Thorax widening posteriorly; all legs narrow and relatively short, becoming shorter relative to body size as individual body size increases; forelegs oriented anteriorly ventral or lateral to head, middle and hindlegs apparently oriented posterolaterally; claws single, relatively small, only slightly curved, with sharp apex, denticulation not discernible; on 10.9 mm long specimen (in millimeters): forelegs ca. 3.0 long and middle and hindlegs ca. 4.0 long, forefemur 1.0, foretibia 0.8, foretarsus 0.8, claw 0.2, middle femur 1.5, hindfemur 1.6, middle and hindtibia 1.0, middle and hindtarsus 0.8, middle and hindclaw 0.3, coxae and trochanters not clearly discernible; mature forewing pads of schistonote type, clearly divided for almost entire length, 3.4 mm long on specimen with body 11.2 mm long, somewhat abruptly narrowing along inner margin anteriorly, and subtriangular in posterior fourth. Abdomen with sharp, almost spinelike posterolateral processes on segments 1–9 (fig. 2) and with platelike gills inserted posterolaterally on segments 1–7 (no fibrilliform portion discernible) (fig. 1); gill 1 elliptical, slightly shorter than gills 2–6, with elongate rib (or possibly tracheal trunk) running slightly anterior to longitudinal midline; gills 2–6 subtriangular, all subequal, somewhat longer than corresponding segment length, with sclerotized rib running along anterior margin, rounded inner posterior portion of lamellae folded ventrally on some gills



1 **2**

Figs. 1, 2. *Protoligoneuria limai* mature larva. **1.** Whole dorsal composite. **2.** Ventral abdomen composite.

on some specimens giving unnatural appearance of straight inner margin, possible tracheation not discernible; gill 7 elliptical-elongate, strikingly longer than gills 1–6, up to nearly twice as long in large, mature specimens (in millimeters) (e.g., body = 11.1, gill 4 = 1.0, gill 7 = 1.9) but as little as 20 percent longer in small, young specimens (e.g., body = 8.5, gill 4 = 1.0, gill 7 = 1.2), with sclerotized rib running along anterior border and indication of median longitudinal tracheal trunk at least in some specimens. Caudal filaments relatively short and robust, becoming shorter relative to body as individuals become larger (e.g., body = 7.2, cerci = 4.0; body = 12.5, cerci = 4.2); median terminal filament ca. ¾ length of cerci, with dense row of long setae along entire length of both lateral borders; cerci with dense row of long setae along inner border only.

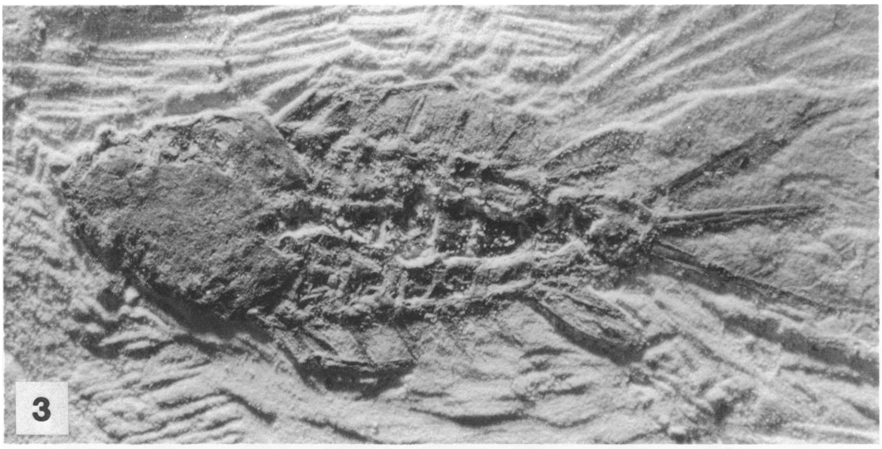
DISCUSSION: Costa Lima (1950) first reported the existence of this species with a very incomplete description of at least three fossil specimens from Ceará Crato, Brazil: Riacho do Salgado, Fazenda Santa Rosa, near Pousada Santa Fe. He did not mention the age of this material, but it undoubtedly is from the Santana Formation. The specimens which he reported on are presumably residing with the National Department of Mineral Production in Brazil. He did not name this material, but ascribed them to the family Baetidae, subfamily Siphlonurinae (presently equivalent either to the family Siphlonuridae or a complex of families including Siphlonuridae). Costa Lima's illustrations of the general facies of the body, including gill morphology and the strikingly large and elongate gill 7 (fig. 1), indicate that the AMNH materials are the same species.

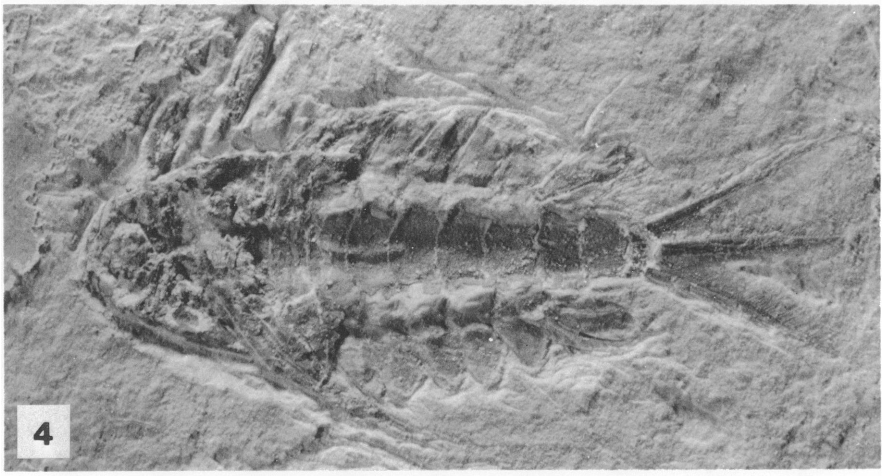
Demoulin (1955) subsequently proposed the new scientific name *Protoligoneuria limai* for these fossils based strictly on the description of Costa Lima (1950) and without designating types. Demoulin, believing Costa Lima's specimens to be members of the family Oligoneuriidae rather than Siphlonuridae, devised his generic nomen to reflect this. This family reassignment was based entirely on the known distributions of the two families (siphlonurids had been known only from southern South America, and the Holarctic and Australian realms, whereas extant oligoneuriids are common in tropical South America). As will be discussed below, his conclusion was erroneous.

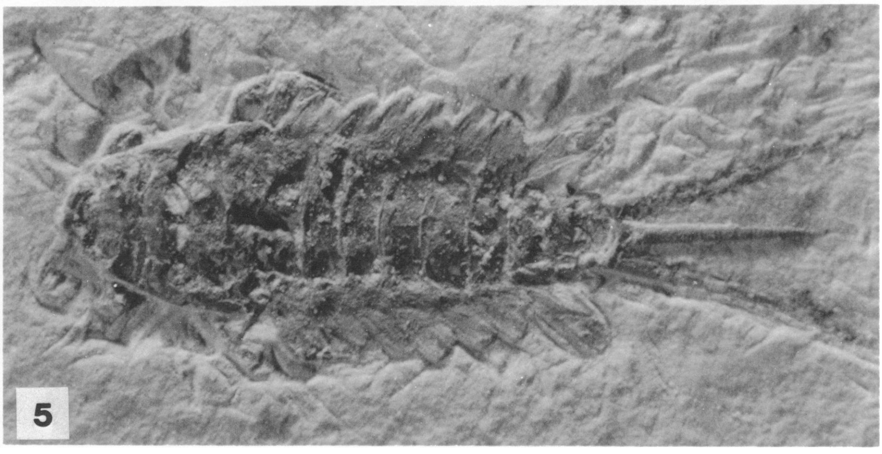
According to the International Code of Zoological Nomenclature [Art. 73b (i)], "Syntypes may include specimens . . . not seen by the author but which form the bases of previously published descriptions or illustrations upon which the author founded the new nominal species-group taxon. . . ." As such, all of Costa Lima's specimens are syntypes. Unfortunately, the existence and deposition of this material remains questionable, and even the number of specimens is not known because Costa Lima referred to the quantity of them as simply "alguns" (= some). I can only be sure that there were three specimens because he included photographs of three in his publication.

Based on additional Lower Cretaceous larvae from Ceara, Brazil, Brito (1987) renamed this species *Palaeobaetodes costalimai.* I agree that at least Brito's holotype and the two paratypes that he figured represent the same species as the Costa Lima (1950) material; however, the name *Protoligoneuria limai* must be regarded as the valid senior synonym. The latter name, although perhaps not applied under preferred circumstances by Demoulin (1955), does nevertheless meet nomenclatural regulations and therefore cannot be regarded as a nomen vanum or nomen nudum. If a neotype is deemed necessary in the future, it would best be chosen from the better preserved AMNH material.

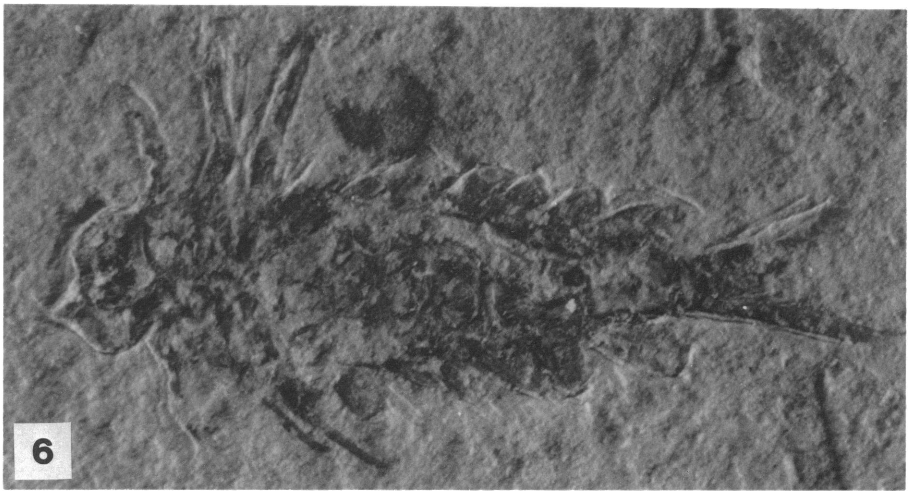
Protoligoneuria limai is clearly a minnow-like mayfly, typical of mayflies of the superfamily Baetoidea, as presently constituted, that have streamlined bodies, narrow legs, and schistonote wing pads. Its short antennae, three setaceous caudal filaments (fig. 1), and abdominal posterolateral processes furthermore suggest that it is a primitive mayfly typical of known Jurassic mayflies (Sinitshenkova, 1984), and evidently related to the Siphlonuridae or a complex of primitive families including Siphlonuridae. The lack of characteristics associated with larvae of the family Oligoneuriidae, especially forelegs with long filtering setae, precludes its inclusion in that family.



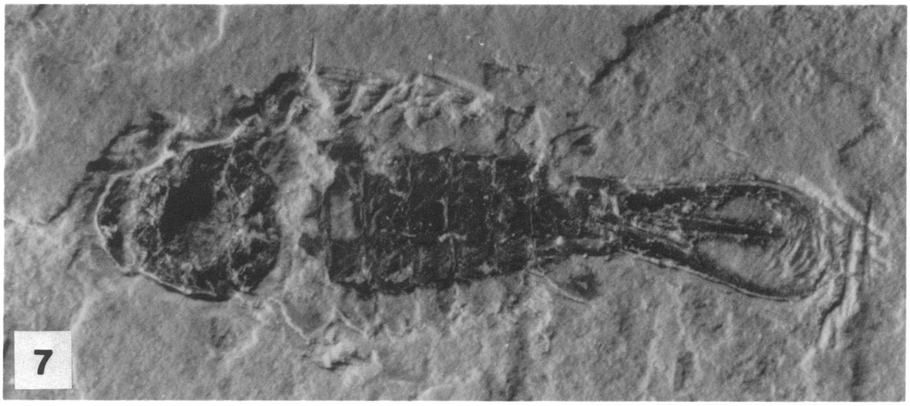




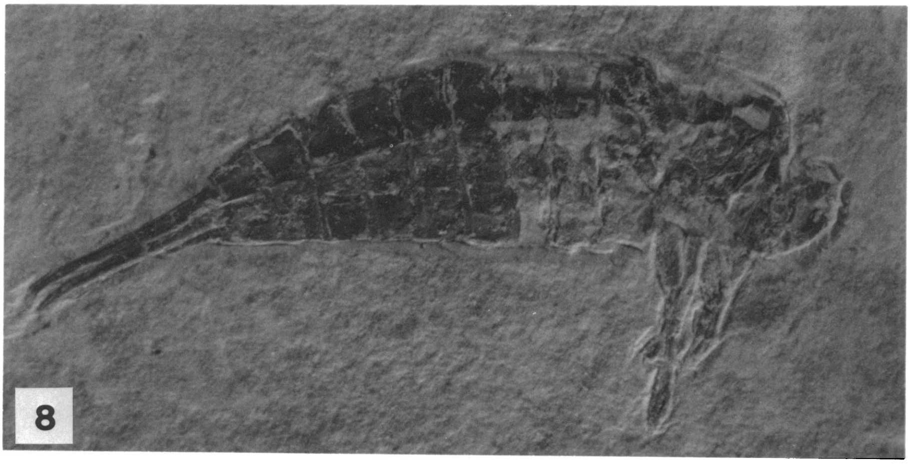
Figs. 3–5. *Protoligoneuria limai* larvae. **3.** Dorsal, middle-late instar habitus, AMNH 43455. **4.** Ventral, late instar habitus, AMNH 43469. **5.** Dorsal, middle instar habitus, AMNH 43452.



6



7



8

Figs. 6–8. *Protoligoneuria limai* larvae. **6.** Ventral, middle instar habitus, AMNH 43435. **7.** Ventral, middle instar habitus, AMNH 43415. **8.** Lateral, late instar habitus, AMNH 43418.

The Hexagenitidae are extinct but appear very closely related to the extant minnowlike mayflies, and according to Tshernova and Sinitshenkova (1974), the family is "a special extinct branch sharing a common origin with the Siphlonuridae." The genus *Ephemeropsis* from the Upper Jurassic is well represented in Palearctic Laurasia (Tshernova and Sinitshenkova, 1974) and typifies hexagenitid larvae. A minnowlike body with abdominal posterolateral processes, narrow legs, and swimming caudal filaments are found in *Ephemeropsis,* as they are in *P. limai.*

The wing venation of Hexagenitidae distinguishes that family and is a more complex type than is found in Siphlonuridae, particularly regarding the more complex cubital venation in the forewing. *Protoligoneuria* adults are unknown, and nothing can be deduced about the wings from the available larval wing pads. Edmunds (1972) has aptly pointed out that the Siphlonuridae (in its broadest sense) is a "stem group" and that fossils are difficult to assign when they may belong to Siphlonuridae or another family that is derived with it. Nevertheless, although in this case family placement would be more definitive by using adult characters, certain similarities between the larvae of *P. limai* and known larvae of Hexagenitidae strongly suggest the placement of *Protoligoneuria* in the Hexagenitidae. Such classification of larvae is not without precedent, since both *Siberiogenites* (Sinitshenkova, 1985) and *Mongologenites* (Sinitshenkova, 1986) were placed in Hexagenitidae without the benefit of associated adult fossils.

The dramatically enlarged and outspread gill 7 is perhaps the most evident similarity between *Protoligoneuria* and, for example, *Mongologenites* (Sinitshenkova, 1986) and *Ephemeropsis* (Sinitshenkova, 1975) of the Hexagenitidae. This trait could easily be interpreted as a synapomorphy. Also, the anterior rib or thickening of the gill lamellae of *Protoligoneuria* is common to at least *Hexameropsis* and *Ephemeropsis,* and this may represent a synapomorphy as well.

Protoligoneuria does differ in some detail from other genera of Hexagenitidae. Gill 7 in mature individuals appears larger relative to gill 6, than in other genera; however, *Mongologenites* gills approach the same proportionality. Other Hexagenitidae possess a somewhat apically truncate gill 7 that is more triangulate than that of *Protoligoneuria.* Also, sclerotization of gills of other Hexagenitidae is apparently present along the posterior edge of the gills. I could find no evidence of posterior sclerotization in *Protoligoneuria.*

Undescribed Brazilian fossil materials from the Lower Cretaceous that Sinitshenkova (1984) has seen and thought possibly to be *Hexameropsis* are quite probably specimens of *P. limai.* In any case, the presence of the Mesozoic mayfly family Hexagenitidae in Brazil extends the known range of the group considerably. The five previous known genera are from central or eastern Laurasia, although *Hexameropsis africana* is known from the Lower Cretaceous of Algeria, which would place it near or abutting central Laurasia. A Jurassic or older origin for the family would have accommodated a widespread Pangaean distribution that, via subsequent Lower Cretaceous vicariance, would have resulted in the disjunct distribution of *Protoligoneuria* in West Gondwana.

Certain inferences about the habit and habitat of *Protoligoneuria* can be made based on larval morphology. Larvae of fossil siphlonurids and hexagenitids, including *Protoligoneuria,* as well as several extant genera, have swimming tails. These are robust caudal filaments that possess interlocking setae on the inner borders of the cerci and lateral borders of the median terminal filament (fig. 1). In modern mayflies, swimming tails are undulated up and down along with the minnowlike abdomen to provide propulsion in swimming. This behavior is exemplified by extant *Ameletus* species. Such tails can also be used for stabilization in positively rheophilic mayflies such as current-dwelling *Isonychia* (unpublished data).

I hypothesize that the enlarged terminal abdominal gills of *Protoligoneuria* and other hexagenitids are also an adaptation for swimming. Such outspread gills would theoretically contribute additional thrust during the dorsoventral undulations of the abdomen. Anterior gill lamellae could not be undulated as such and remain relatively small. Also, extra thrust would be more important in larger individuals, and this may explain the al-

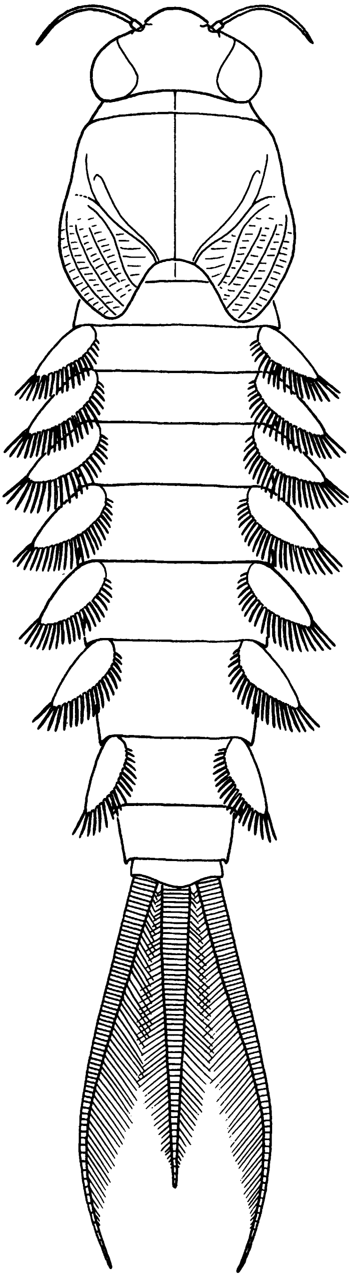


Fig. 9. *Siphgondwanus occidentalis* larva, dorsal reconstruction without legs.

lometry found in *Protoligoneuria* with regard to the disproportionately greater growth of gill 7 as larvae develop.

Well-developed swimming by mayflies is basically, but not exclusively, associated with quiet-water habitats (pools or slack edgewaters of streams as well as ponds and littoral areas of lakes). Edmunds and McCafferty (1988) gave considerable evidence showing this to be the primitive type of habitat of schistonote Ephemeroptera, although the majority of extant mayflies are adapted for current dwelling. Also, short claws (fig. 1) in extant species of primitive minnow mayflies such as Siphlonuridae are usually associated with quiet waters or habitats where they are used on solid rather than fine substrates (unpublished data).

Meshkova (1961) concluded that the presence of leaf-shaped gills, weak legs, and strongly pubescent caudal filaments of the larvae of *Ephemeropsis* indicated that they had inhabited undisturbed waters; and in fact, all other hexagenitids from Laurasia have been considered lacustrine (Sinitshenkova, 1984). It is therefore probable that *Protoligoneuria* occurred in quiet waters where larvae would swim, although a rheophilic existence cannot be entirely ruled out. Given the abundance of *Protoligoneuria* fossils, a major lentic environment, such as a lake with a considerable littoral zone, was probably present at the fossil site.

FAMILY SIPHLONURIDAE

SUBFAMILY SIPHLONURINAE (?)

Siphgondwanus occidentalis,

new genus, new species

Figures 9, 10

Type: Larva, AMNH 43404 (fig. 10).

Etymology: *Siphgondwanus* is a masculine gender nomen comprised of an arbitrary combination of letters alluding to a siphlonurid from Gondwana. The specific epithet *occidentalis* is from the Latin, meaning western. Thus the names together refer to a siphlonurid from West Gondwana (an identifiable biogeographic entity during the Lower Cretaceous that included the area now known as Brazil).

Diagnosis: The small hypognathous head with short antennae, minnowlike form of body, three short, robust tails with swimming hairs, and unique elliptical gill lamellae with posterior spinelike bristles (fig. 7) will distinguish *Siphgondwanus occidentalis.*

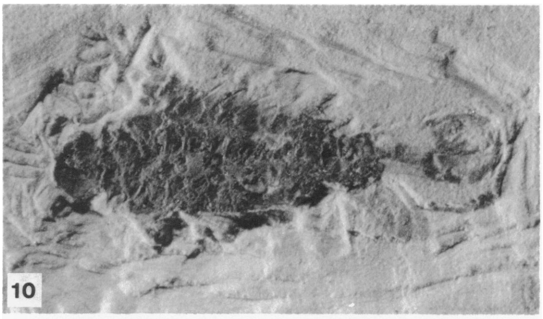
LARVA: Dorsal aspect with all legs and left abdominal gills missing, and mouthparts not discernible. Body minnowlike and 9.0 mm long. Head relatively small, broader than long but narrower than thorax, apparently hypognathous; antennae short, discernible portion very thin with length less than width of head, inserted anteriorly on head capsule. Gills (fig. 9) present on abdominal segments 1–6, presumably present on 7; gills ca. 1.0 mm long, platelike, narrow-elliptical, inserted at posterolateral corners of segments, with no fibrilliform portion or tracheation discernible, but with row of long spinelike bristles along the posterior and apical margins; gill bristles ca. 0.2 mm long. Caudal filaments relatively short and robust; cerci 4.5 mm long, with dense row of long setae along inner margin only; median terminal filament developed (3.0 mm long), with dense row of setae on lateral margins.

ADULT: Unknown.

OTHER MATERIAL EXAMINED: None.

DISCUSSION: Placement of *Siphgondwanus* in the family Siphlonuridae (in its broadest sense) is based primarily on the presence of generalized characteristics that typify the family, such as the very short antennae (compared to the usually long antennae of Baetidae), the clearly minnowlike body with swimming tails, and the sharp posterolateral processes of the abdomen that appear to be present. More importantly, however, there are no synapomorphies present in *Siphgondwanus* that would place it with any other extant or extinct family of Ephemeroptera, including Hexagenitidae. Erection of a new family for this fossil does not appear warranted at this time; nevertheless, placement in Siphlonuridae, based on plesiomorphic characteristics, certainly leaves the higher classification of *Siphgondwanus* open to future review as distinguishing apomorphies in the primitive stem groups of Ephemeroptera become better understood.

By considering Siphlonuridae in its broadest sense (e.g., McCafferty and Edmunds, 1979), the absence of synapomorphies in *Siphgondwanus* would additionally place it in the subfamily Siphlonurinae. Characters that would allow more definitive subfamilial classification are, unfortunately, not represented on the fossil. It may be noted also that the subfamilies of Siphlonuridae are progressively becoming recognized at the family level by many Ephemeroptera workers, and such revision of rank status has become almost inevitable.

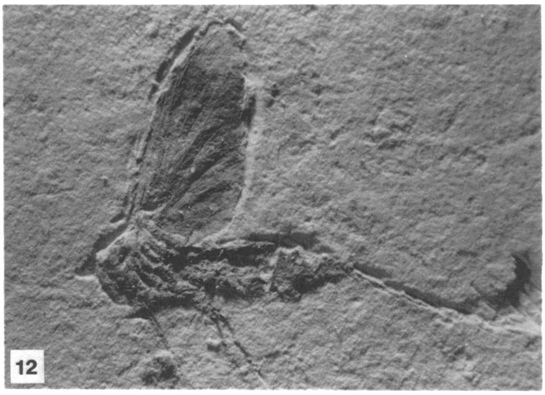


Figs. 10, 11. **10.** *Siphgondwanus occidentalis* larva, dorsal habitus, AMNH 43404 (holotype). **11.** Siphlonuridae (?) sp. 1 alate stage, dorsal habitus, AMNH 44306.

Little can be inferred about possible relationships with other siphlonurid genera because the unique gill spination of *Siphgondwanus* would appear to be an autapomorphy. Short bristles are present on the margins of some of the platelike gills of some species of the extant Holarctic siphlonurid genus *Ameletus* and are scattered over the surface of the very highly specialized gill lamellae of certain extant Coloburiscidae. The gill spination of *Siphgondwanus* (fig. 9), however, appears very different. The sharp marginal gill bristles of *Siphgondwanus* should not be confused with the unsclerotized marginal filaments associated with the gill lamellae of the Ephemeroidea.

The oldest fossils assignable to the Siphlonuridae appear to be the Jurassic genera

12



13

Figs. 12, 13. Siphlonuridae (?) spp. alate stage. **12.** Sp. 2 lateral habitus, AMNH 44313. **13.** Sp. 3 lateral habitus, AMNH 43477.

Mesobaetis (nec Baetidae) (Brauer et al., 1889), *Olgisca* (Handlirsch, 1908; Demoulin, 1970a), and *Stackelbergisca* (Tshernova, 1967). *Proameletus* (Sinitshenkova, 1976) and *Australurus* (Jell and Duncan, 1986) from the Lower Cretaceous appear to be the only other described Mesozoic genera assignable to Siphlonuridae, although the closely related families Epeoromimidae and Hexagenitidae, as well as possibly Ameletopsidae and Coloburiscidae, all of which have primitive minnowlike larvae, are also represented in the Mesozoic. Previously, fossil siphlonurids have been known mainly from the Northern Hemisphere, but also from Australia.

Extant Siphlonuridae are not known from tropical South America, although three subfamilies are amphinotic. The presence of Siphlonuridae in West Gondwana is not surprising, however, given its present Holarctic and Amphinotic distribution. Edmunds (personal commun.) considered this former existence in tropical South America to be predictable since the family crossed the equator at least twice and the most likely place was West Gondwana.

The relationships between morphology, swimming habit, and habitat are given under the discussion of *Protoligoneuria* above. Because the two genera possess similar swimming tails, the conclusions about the possible habitat of *Protoligoneuria* in Brazil also apply to *Siphgondwanus*.

SIPHLONURIDAE (?) sp. 1
Figure 11

MATERIAL: AMNH 44306, alate.

DESCRIPTION: Dorsal aspect of head, thorax, and forewing. Body length unknown. Forewing 9.0 mm, elongate-triangular; crossvenation well developed; Rs forked just basad of midlength of wing; MA fork in distal ¼ of vein; MP_2 and CuA not arched posteriorly at base; other venation not clear. Hindwings missing.

DISCUSSION: The elongate-triangular shape of the forewing, along with the very distal MA fork and relatively distal Rs fork suggest that this fossil represents a siphlonurid. Such a placement, however, must be considered tentative at the present. This fossil does not match any of the other alate Ephemeroptera fossils from Brazil.

SIPHLONURIDAE (?) sp. 2
Figure 12

MATERIAL: AMNH 44313, alate.

DESCRIPTION: Lateral aspect of female including thorax, abdomen, legs, partial caudal filaments, and forewing. Body at least 9.0 mm long (head missing). All legs well developed; foreleg subequal in length to other legs. Forewing 7.8 mm long, subtriangular; crossvenation extensive; Rs forked in basal third; MA forked in distal ¼ of vein; MP_2 and CuA not arched posteriorly at base; other venation not clear. Hindwings missing. Only one caudal filament discernible.

DISCUSSION: Again, the few characters present suggest Siphlonuridae but do not allow more than a preliminary classification.

SIPHLONURIDAE (?) sp. 3

Figure 13

MATERIAL: AMNH 43477, alate.

DESCRIPTION: Lateral aspect (?adult) (?sex) with head, thorax, abdomen, partial caudal filaments, forewing, and partial hindwing. Body 12.0 mm long. Forewing 9.2 mm long, distinctly triangular; costal, subcostal, and radial triad crossvenation well developed, other crossvenation not as well developed; marginal venation apparently developed, details not discernible, but at least some interspaces with free, short intercalaries; Rs forked in basal third, MA forked in distal third of vein, connection of MA_1, IMA, and MA_2 not discernible; MP_1 and IMP attached by crossvein near base, connection of MP_2 not discernible; CuA paralleling MP_2; other venation not clear. Hindwing at least 4.0 mm long; venation not discernible. Three caudal filaments present; median terminal filament well developed.

DISCUSSION: The apparent connecting bases of MA veins as well as MP veins is somewhat suggestive of Baetidae, but overall the wing is more typical of Siphlonuridae (certain *Siphlonurus,* e.g., have IMP and MP_2 attaching to MP_1 by crossveins only). The left cercus and median terminal filament are intact on this fossil, making it initially appear to be two-tailed. However, close examination also reveals a short broken base of the right cercus. Placement in the Siphlonuridae is tentative because the cubital region of the forewing is obscured.

FAMILY OLIGONEURIIDAE

SUBFAMILY COLOCRURINAE, NEW SUBFAMILY

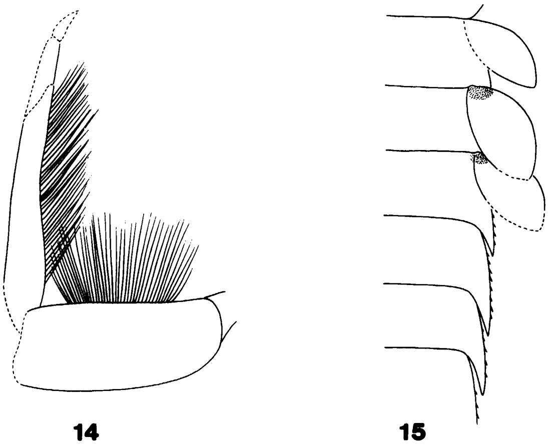
Colocrus indivicum,

new genus, new species

Figures 14–17, 19

TYPE: Larva holotype, AMNH 43484 (fig. 16). Adult paratype, AMNH 43499 (fig. 17).

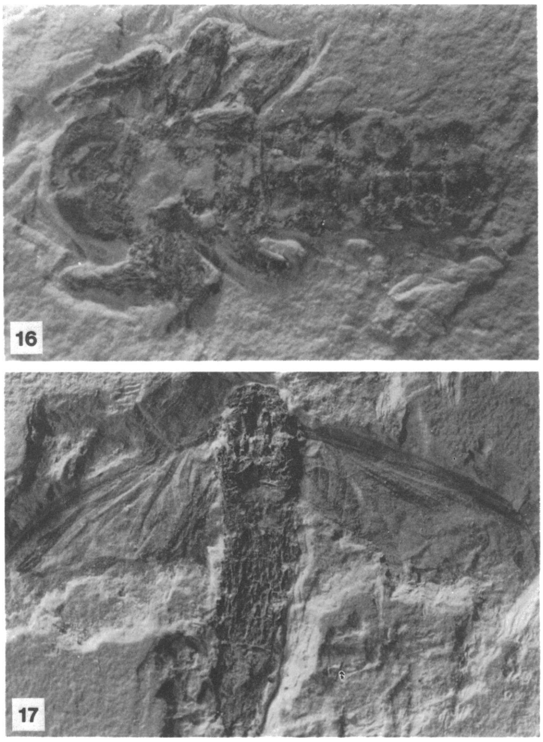
ETYMOLOGY: *Colocrus* is a neuter gender nomen from the Latin *colatus* (filter or strainer) and *crus* (leg), an allusion to the filtering sieve formed by the filtering hairs of the forelegs of the larva. The specific epithet *indivicum* is from the Latin *indivicus,* meaning indicative. It alludes to the indication of phyletic relationships that this species provides with respect to the Oligoneuriidae.



Figs. 14, 15. *Colocrus indivicum* larva, dorsal aspect. **14.** Left foreleg. **15.** Right half of partial abdomen, with gills 1–3 present, gills 4–7 missing.

DIAGNOSIS: The combination of a broadened, shortened, and rounded head capsule, filtering setae on the forelegs, broadened femora, and an abdomen with posterolateral processes and lateral elliptical gill lamellae will distinguish the larva of this taxon. The alate form is distinguishable by the lack of most intercalary veins in the forewings, crossvenation restricted to the costal and radial region, and gemination of certain major convex veins with concave veins as shown in figure 19.

LARVA: Dorsal aspect of fossil. Antennae, abdominal segments 8–10, caudal filaments, tarsi, and claws missing. Body length (from apex of head through abdominal segment 7) 10 mm. Head 3 mm wide and 2 mm long; anterior and lateral margins rounded, forming hemispherical, apparently depressed head capsule; eyes, antennae, and mouthparts not discernible. All legs with femur broad and flattened, ca. twice width of tibia; forelegs with rows of long, dense setae on inner margins of femur and tibia (fig. 14); hindlegs with coxae not apparent and therefore not abnormally overdeveloped. Abdominal segments (fig. 15) with well-developed, pointed posterolateral extensions with slightly curved inner and outer margins on at least segments



Figs. 16, 17. *Colocrus indivicum* larval and alate habitus. **16.** Larva, dorsal habitus, AMNH 43484 (holotype). **17.** Alate stage, ventral habitus, AMNH 43499 (paratype).

4–7 (other present segments not discernible in this area); abdominal segment 4 extended posteriorly at lateral margin ca. ⅙ length of segment 5, 5 and 6 extended ca. ½ length of segments 6 and 7 respectively; lateral margins of segments with short robust setae, or spurs; single, dorsal platelike gills apparent on segments 1–3 (and presumably 5–7), elliptical, as long as or slightly longer than segment length, oriented posterolaterally, and with no fibrilliform portion discernible, however, small darkened area at base of gill 2 possibly indicating presence of fibrilliform portion. Development of median terminal filament unknown.

Adult: Ventral aspect of fossil (sex?) with legs and caudal filaments missing; hindwings present but venation not discernible. Body 13.2 mm long. Head short, nearly as wide as pronotum; compound eyes apparently situated dorsolaterally, ca. ⅙ as wide as head. Forewing ca. 11.0 mm long, longitudinal veins consisting of C, Sc, R_1, Rs (giving rise to at least R_2, $?R_3$, and R_{4+5}), MA_1, MA_2, MP_1, IMP, MP_2, CuA_1, CuA_2, CuP, A_1, A_2, and A_3 (fig. 19); crossveins apparent only in costal region and distal R_1 and R_2 areas; Rs forked at ca. ⅓ distance from base; other major forks near base; cubital region with one and possibly more intercalaries; R_{4+5} and MA_1 running near each other; MA_2 and MP_1 geminating very near each other for entire length; MP_2 and CuA_1 forming close paralleling pair for entire length. CuP paralleling CuA basally and CuA_2 distally. Hindwings ca. 3.3 mm long; venation not discernible.

Other Material Examined: None.

Discussion: The Oligoneuriidae belong to a complex of families that include Coloburiscidae, Isonychiidae, Oligoneuriidae, and Heptageniidae (Edmunds et al., 1976; McCafferty and Edmunds, 1979; Landa and Soldán, 1985). These mayflies share a common siphlonurid-like ancestor (McCafferty and Edmunds, 1979) and do not appear to have given rise to any other taxa. Coloburiscidae and Isonychiidae were considered subfamilies of Siphlonuridae earlier (Edmunds et al., 1963), but, as their affinities became better known, they were recognized as subfamilies of the Oligoneuriidae by Riek (1973), McCafferty and Edmunds (1979), and Landa and Soldán (1985). Based on my cladistic analyses, I now recognize the Coloburiscidae and Isonychiidae as families separate from the Oligoneuriidae. Recognition of family status for Isonychiidae has been followed by several authors (e.g., Demoulin, 1958; Tshernova, 1970). The exact phyletic position of Coloburiscinae has not been known (McCafferty and Edmunds, 1979; Landa and Soldán, 1985), but its newly discovered earliest branched position within the complex (fig. 18) necessitates its elevation to family status: Using cladistic principles, if two or more families are recognized in this complex, Coloburiscidae must be one of them.

I also herein recognize the monophyletic grouping of the families Coloburiscidae, Isonychiidae, Oligoneuriidae, and Heptageniidae (fig. 18) to constitute a separate superfamily Heptagenioidea (nec Edmunds and Traver, 1954a). I do not agree with Tshernova (1970) that the Epeoromimidae (= *Epeoromimus* + *Foliomimus*), which is known from Jurassic and Cretaceous Palearctic larvae (Tshernova, 1969; Sinitshenkova, 1976, 1985), should be placed in the Heptagenioidea as was done by Landa and Soldán (1985) and as is suggested by its placement in Hubbard's (1987) catalog. Larvae of Epeoromimidae are basically minnowlike, have an apparent hypognathous head, lack filtering setae on the forelegs, and demonstrate no apomorphies that would associate them with the Heptagenioidea. Edmunds (1972) even suggested a placement of *Epeoromimus* in Siphlonuridae but took no formal action.

My interpretation of the sequence of derivation of familial lineages in this superfamily is shown in figure 18. It differs significantly from the scheme formerly presented by McCafferty and Edmunds (1979). My cladistic evidences for this new evolutionary hypothesis and higher classification, which are based on considerable morphology, including new cephalic characters and functional morphology of the larvae, as well as adult characters and internal anatomy, will be elaborated in another publication. Briefly, however, they indicate that ancestrally this superfamily had left the primitive quiet-water habitat of mayflies (Sinitshenkova, 1984; Edmunds and McCafferty, 1988) and invaded flowing waters where the habit of passive filter feeding of seston and the correlated well-developed filtering setae on the forelegs and mouthparts had evolved.

The earliest grade of evolution in the superfamily is represented by the Coloburiscidae, a lineage that also demonstrates a considerable number of autapomorphies. The Isonychiidae, Oligoneuriidae, and Heptageniidae share a subsequent common ancestor evidenced by several shared apomorphies. The Isonychiidae, just as the Coloburiscidae, remained ancestrally minnowlike (the general facies of Isonychiidae remain most similar to the hypothetical siphlonurine ancestor of this superfamily). Additional apomorphies are shared by Oligoneuriidae and Heptageniidae, although the Oligoneuriidae are also intermediate in numerous characteristics between the more ancestral minnowlike families and the Heptageniidae. Both Oligoneuriidae and Heptageniidae possess numerous autapomorphies, but Heptageniidae lost the ancestral passive filtering capacity and associated foreleg characteristics and became highly depressed dorsoventrally and oriented to bottom feeding in streams.

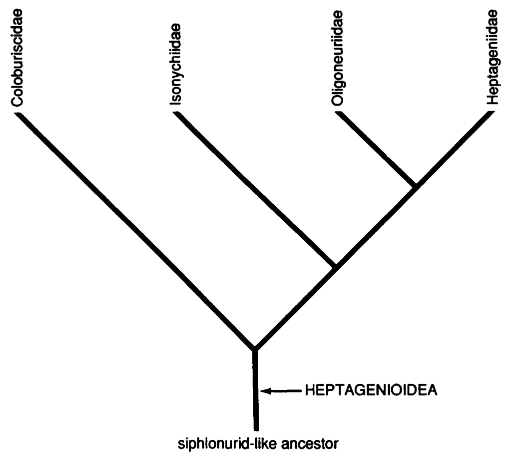
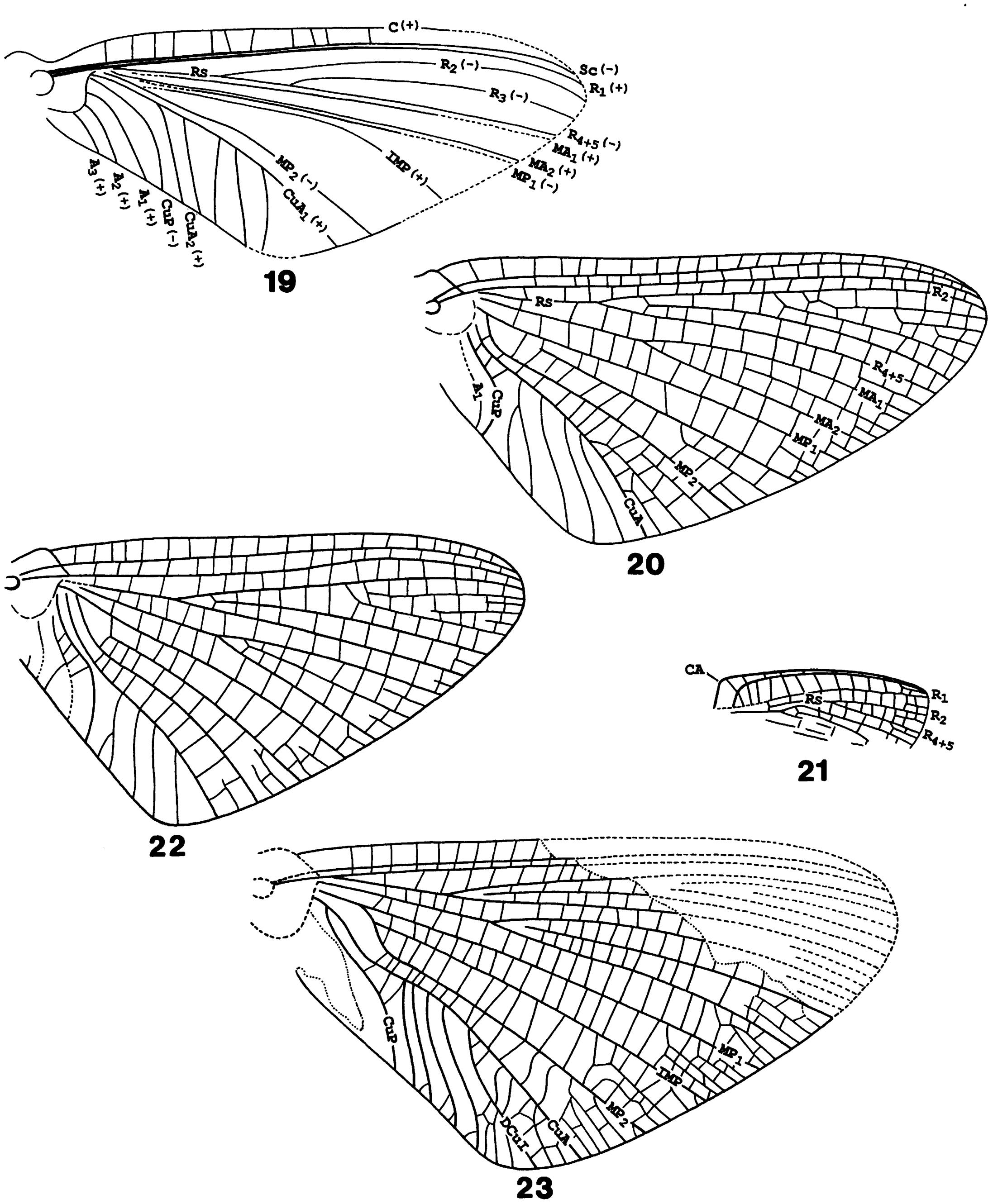


Fig. 18. Cladogram of the families of Heptagenioidea.

The larva of *Colocrus* possesses characteristics typically found in many of the Heptagenioidea that clearly place the fossil in this superfamily. The filtering forelegs (fig. 14) of *Colocrus* are similar to those found in Coloburiscidae, Isonychiidae, and Oligoneuriidae. The abdominal gills and posterolateral processes of the abdomen (fig. 15) are of a type that could be found in any of the four families, except Coloburiscidae, wherein the gills are highly modified or absent. The flattened body and femora are typical of the Heptageniidae and the more depressed forms of Oligoneuriidae. The head is most typical of Heptageniidae, but certain oligoneuriids approach the degree of flattening, shortening, and broadening seen in *Colocrus* (fig. 16). Therefore, from all available characters, the larva of *Colocrus* would be placed in the family Oligoneuriidae.

The forewings of the alate form of *Colocrus* are unique. Both intercalaries and crossvenation are reduced. Venation assignment (fig. 19) is based on alternating convexity and concavity of longitudinal veins, which are reliable landmarks for ascertaining venation in mayflies (Edmunds and Traver 1954b) and are evident in this fossil. The fact that the easily located Sc vein appears as a furrow,



Figs. 19–23. Alate stage wings. **19.** *Colocrus indivicum,* forewing reconstructed from right and left forewings, dorsal (+ = convex vein, − = concave vein). 20, 21. *Australiphemera revelata.* **20.** Forewing composite. **21.** Partial hindwing from paratype (CA = costal angulation). **22.** *Microphemera neotropica* forewing. **23.** *Pristiplocia rupestris* forewing (DCuI = distal cubital intercalary vein).

and R_1 as a ridge in this fossil clearly indicates that the ventral side of the wings is being viewed (fig. 17) (the dorsal aspect is shown in fig. 19). This follows because in the dorsal aspect these veins are always concave and convex, respectively. The venation appears to be an intermediate form between a plesiomorphic type, or wings with the full complement of basic ephemeropteran venation, and the highly reduced apomorphic type with geminating longitudinal veins that is found in the subfamily Oligoneuriinae of the Oligoneuriidae. In the oligoneuriine wing the highly geminating convex and concave longitudinal pairs of veins have the effect of flattening the wing (Edmunds, personal commun.). This is evidently an adaptation that neutralizes fluting, which is typical of ephemeropteran wings. Flattening instead allows sculling and hence highly atypical rapid forward flight.

Major intercalaries, except for IMP, are absent in *Colocrus* as they are in Oligoneuriinae, but part of the radial and cubital area of the *Colocrus* wing retains remnants of the basic ephemeropteran venation. Oligoneuriine forewings have the Rs, MA, and MP forked near the base, and R_{4+5}-MA_1, MA_2-CuA_1, and CuA_2-CuP represent the major geminated pairs of convex and concave veins. A tendency toward this gemination is clearly evident in *Colocrus,* particularly with regards to R_{4+5} and MA_1, MA_2 and MP_1, and MP_2 and CuA_1 (fig. 19). This pairing corresponds to those major geminated pairs in oligoneuriine wings (see e.g., Crass, 1947; Edmunds et al., 1976). Vein MA_1 (fig. 19) is very faint in the fossil and does not appear as either a ridge or furrow, although its position is where a convex vein would be found. Although IMP is well developed in *Colocrus,* other intercalaries are missing in the open areas between MA_1 and MA_2, MP_1 and IMP, and IMP and MP_2. The cubitoanal region of the forewing of *Colocrus* is not highly reduced as it is in Oligoneuriinae.

Because of the several shared apomorphies of the wings of *Colocrus* and Oligoneuriinae, the placement of this genus in Oligoneuriidae, as was also indicated by the larval fossil, is strongly supported. Furthermore, although the Oligoneuriinae would appear to be derived with *Colocrus* (*Colocrus* appearing to represent a transitional form), the Oligoneuriinae nevertheless possess wings that are distinctly more derived than those of *Colocrus.* Oligoneuriinae also possess a ventral gill 1 in the larval stage, whereas *Colocrus* retains a dorsal gill 1. I therefore recognize two separate subfamilies for these clades, the Oligoneuriinae and the new subfamily Colocrurinae. The new subfamily is distinct from extant oligoneuriids both by its wing venation, and by its shortened and broadened head in the larva.

It may be significant that the general appearance of the outspread wings of the fossil (fig. 17) gives an impression very similar to that of the outspread wings of dried specimens of oligoneuriine mayflies. Also, the more faint impressions of the fossil wings in comparison with the sharp image of the body may indicate that these wings retained subimaginal sheaths. Adults of modern-day oligoneuriines are known to shed the subimaginal exuviae everywhere but from the wings (Edmunds and McCafferty, 1988). The pronounced convexity and concavity of the main longitudinal veins of *Colocrus* (much more so than in other fossils studied) are also often more typical of subimaginal wings in extant specimens of mayflies.

True oligoneuriid fossils have not been known previous to this. *Protoligoneuria* is a hexagenitid, not an oligoneuriid as indicated by Demoulin (1955) (see discussion under *P. limai,* above). Other than the Lower Cretaceous Colocrurinae and six genera of Heptageniidae known from the Tertiary, the only other fossils that have been assigned to families within Heptagenioidea, sensu novum, are *Mogzonurella* larvae and *Mogzonurus* adults from the Palearctic Jurassic (Sinitshenkova, 1985), *Siphlurites* adults from the Nearctic Miocene (Cockerell, 1923); *Isonychia* larvae from the Nearctic Oligocene (Lewis, 1977); and *Cronicus* adults and subimagos from the Palearctic Eocene (Eaton, 1871). Demoulin (1970b) placed *Siphlurites* in the Isonychiinae; Demoulin (1974) placed *Cronicus* in the Coloburiscinae; and Sinitshenkova (1985) placed *Mogzonurella* and *Mogzonurus* in the Coloburiscinae. No known fossil wings of Heptagenioidea, or any other

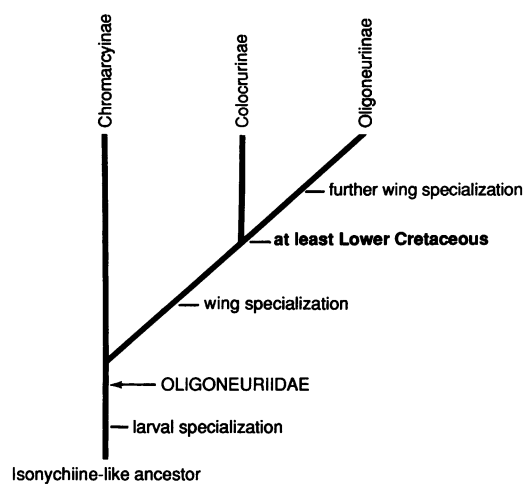


Fig. 24. Cladogram of the subfamilies of Oligoneuriidae.

Ephemeroptera for that matter, are similar to those of *Colocrus,* and no fossil mayfly larvae are similar to *Colocrus.*

McCafferty and Edmunds (1979) considered the Oriental genus *Chromarcys* to be in the subfamily Chromarcyinae of the Oligoneuriidae. Demoulin (1971) considered it in the family Chromarcyidae, believing it intermediate between the fossil family Hexagenitidae (see discussion under *Protoligoneuria,* above) and Oligoneuriidae. The genus is of considerable evolutionary interest because its larvae are typical of the Oligoneuriinae (a strong resemblance to the Neotropical *Spaniophlebia*), but its adult retains a full complement of ephemeropteran wing veins. It is therefore obviously not as derived as the Colocrurinae or Oligoneuriinae (fig. 24). Gill 1 of *Chromarcys* is dorsal, a clearly plesiomorphic trait that is also retained in *Colocrus.* All Oligoneuriinae, however, possess an apomorphic ventral gill 1.

The phyletic position of *Colocrus* (fig. 24), being more derived than *Chromarcys* and being a sister group to the Oligoneuriinae but more plesiomorphic than that group, is easily deduced based on its distinct but intermediate type of wing venation. The retention of a dorsal gill 1 as well as a highly specialized head of the larva does not falsify this deduction. It is because of this general cladistic agreement of the alate and larval fossils that I interpret them as the same species. When dealing with fossils only, this is always a somewhat subjective decision, but in this situation the association appears most probable. Considering them the same species is more prudent and conservative than describing two taxa that demonstrate the same phyletic position within the Oligoneuriidae.

Because of the monophyletic relationship of *Chromarcys, Colocrus,* and the Oligoneuriinae, I would prefer to recognize a single family with three subfamilies, which reflects an evolutionary phenocline with regard to wing venation (fig. 24). However, since Chromarcyinae represents the earliest derived group, it is a sister lineage to the common ancestor of Colocrurinae and Oligoneuriinae, and family status within a strict cladistic classification could be argued. The similarity of the larvae of Chromarcyinae to all other Oligoneuriidae generally, and the fact that its dorsal gill 1 is no longer unique in the family since Colocrurinae also possesses this character state, would support retention of *Chromarcys* in the Oligoneuriidae.

With regard to a possible relationship of Oligoneuriidae to Hexagenitidae, Tshernova and Sinitshenkova (1974) believed Hexagenitidae to be an ancestral group closely related to Siphlonuridae but not continuing beyond the Mesozoic (probably not beyond the Lower Cretaceous) nor giving rise to other modern taxa. Since the common ancestor of the Heptagenioidea was derived from a siphlonurid-like ancestor, Demoulin's (1971) phyletic conclusions about a close relationship between Hexagenitidae and Oligoneuriidae are not surprising, nor can a hypothesis that the Hexagenitidae are cladistically related to the ancestor of the Heptagenioidea be dismissed out-of-hand. However, venational characteristics of Hexagenitidae are not like those found ancestrally within the Heptagenioidea, and the larvae of Hexagenitidae were not stream-dwelling passive suspension feeders as are the larvae of plesiomorphic lineages of Heptagenioidea.

Ancestral genera of Oligoneuriidae along with the family as a whole are essentially Pantropical. The origin of the highly derived north-temperate elements of Oligoneuriinae (*Homoeoneuria* and *Oligoneurisca*) may very well have been in the Neotropics (see Mc-

Cafferty et al., 1990). Edmunds (1975) regarded the minnowlike Afrotropical genus *Elassoneuria* to be the most ancestral oligoneuriine, and he hypothesized that the family evolved on the South America-Africa-Madagascar-India land mass. The age and location of *Colocrus* add considerable credence to that hypothesis and indicate that the Oligoneuriidae originated at the latest in the Lower Cretaceous.

The biogeography and common derivation of Heptageniidae and Oligoneuriidae (fig. 18) seem to suggest that the Heptageniidae also originated in the Southern Hemisphere. The family Heptageniidae is not known from South America either as fossils or extant fauna; however, it is represented by an extant Afrotropical and Oriental fauna along with its profuse Holarctic representation.

I deduce that the habitat of *Colocrus* larvae was running water because all known coloburiscids, isonychiids, and all other oligoneuriids also possess forelegs with highly developed rows of filtering setae. Modern mayflies that possess highly developed rows of filtering setae on the forelegs passively filter seston from water and require a current to accomplish this mode of feeding (Wallace and O'Hop, 1979; Keltner and McCafferty, 1986). Virtually all heptageniids, although not necessarily filter feeders, are also stream dwellers.

FAMILY EPHEMERIDAE

Australiphemera revelata,

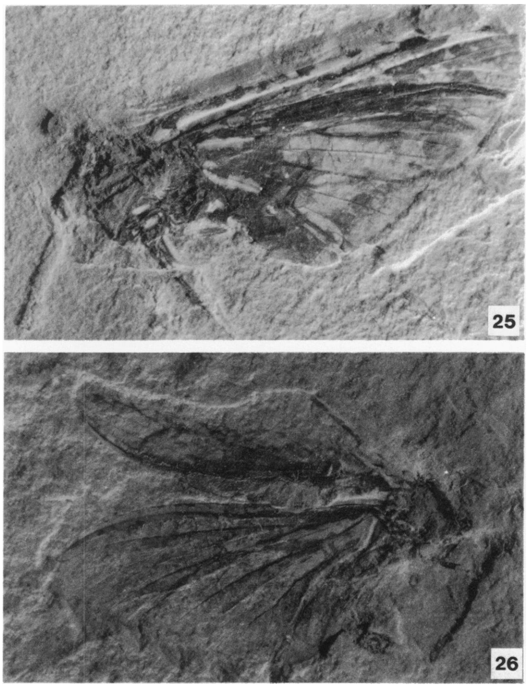
new genus, new species

Figures 20, 21, 25, 26

Types: Adult holotype, AMNH 44300 (fig. 25). Adult paratypes, AMNH 44310 (fig. 26).

Etymology: *Australiphemera* is a feminine gender nomen comprised of an arbitrary combination of letters incorporating the Latin root *australis,* meaning southern, and alluding to an ephemerid from the Southern Hemisphere. The specific epithet *revelata* is from the Latin, meaning revelatory, an illusion to the historical information that this species has revealed.

Diagnosis: This taxon can be distinguished by the following combination: relatively small, widely separated compound eyes; a typical ephemeroid forewing, and with MA forked at midlength, a relatively distinct distal arch of CuP, A_1 nearly straight, and no cubital intercalaries; and a hindwing with a well-developed costal angulation, and Rs much shorter than R_2 and R_{4+5}.



Figs. 25, 26. *Australiphemera revelata* alate stage. **25.** Lateral habitus, AMNH 44300 (holotype). **26.** Dorsal and dorsolateral habitus, AMNH 44310 (paratype).

Larva: Unknown.

Adult: Lateral and dorsal head, lateral and dorsolateral thorax, forewings and partial hindwings of fossils. Sex unknown but probably female based on small size of eyes. Body length unknown. Head ca. 2.0 mm wide, with ca. 0.5 mm diameter compound eyes widely separated and appearing lateral. Forelegs apparently well developed. Forewings (fig. 20) 11.0–11.5 mm long; crossvenation and marginal venation moderately developed; Sc visible for entire length; longitudinal veins not geminating; venation of radial triad extensive; Rs forked in basal ¼; MA fork at ca. midlength of wing; MP_2 and CuA strongly decurved at base, running singularly for entire length, not connected basally; series of forked and single veinlets attaching CuA to anal margin, distal veinlets running subpar-

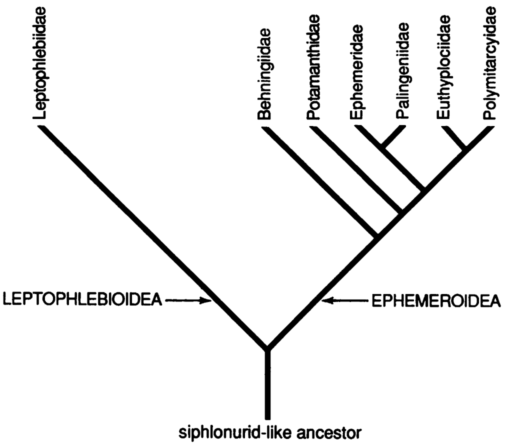


Fig. 27. Cladogram of Leptophlebioidea and Ephemeroidea.

allel to CuA, most distal veinlets ending in outer margin, at least basal veinlet forked; cubital intercalaries lacking, free cubital veinlets not apparent; CuP slightly sigmoid, strongly arching toward anal margin; A_1 nearly straight, apparently not forked, no other veins or veinlets discernible in anal area. Hindwing (fig. 21) 4.4 mm long; costal angulation well developed, anterior base of wing and costa forming near right angle; crossvenation moderately to well developed; basal attachment of R_1 apparently at wing base; Rs shorter than R_2 and R_{4+5}; posterior venation not discernible. Abdomen and caudal filaments missing.

Other Material Examined: None.

Discussion: The venational data available on the two specimens clearly indicate placement in the superfamily Ephemeroidea. Although anal venation beneath A_1 cannot be discerned, the well-developed costal crossvenation of the forewings as well as the quadrate costal arch and short Rs of the hindwing do not indicate placement in the Neoephemeridae (Caenoidea). Also on the basis of venational characteristics, which are relatively plesiomorphic within the Ephemeroidea, the ephemeroid families Behningiidae, Palingeniidae (Palingeniinae), Polymitarcyidae, and Euthyplociidae can be excluded from consideration for placement of these fossils. Unfortunately, venation in the anal region of the forewing, particularly an indication of whether A_1 is truly forked or not, which is important to differentiating the remaining families Potamanthidae and Ephemeridae, is not discernible on the fossils. In addition the costal angulation of the hindwing (fig. 21) could apply to either of these families.

Two characteristics of *Australiphemera*, however, have prompted my placement of it in the Ephemeridae. Typical of Ephemeridae and quite unlike that found in Potamanthidae, Rs of the hindwing is shorter than R_2 and R_{4+5} (a plesiomorphic trait). A Rs longer than the fork formed by R_2 and R_{4+5} is one of the distinguishing apomorphs in Potamanthidae. Also cubital veinlets in the forewing of this species are attached as is typical of Ephemeridae. Many potamanthids have some short, free veinlets that are unattached to CuA in this region of the forewing.

Placement of *Australiphemera* in the family Ephemeridae is nonetheless somewhat by default because venational characteristics of this family are plesiomorphic within the Ephemeroidea, and defining apomorphies of this family are found mainly in genitalic and larval characteristics. McCafferty (1979) showed the phyletic relationships of the Ephemeroidea, and figure 27 is adapted from this. Because of the plesiomorphic nature of the wings and lack of other data, these fossils could theoretically be represented on the cladogram anywhere along the ephemeroid line to the Ephemeridae. This species, therefore, although at present classifiable in the Ephemeridae, may actually represent a proto-Ephemeridae or possibly a proto-Potamanthidae-Ephemeridae. Moreover, the orientation of veins in the cubital region of the forewing of *Australiphemera* is somewhat suggestive of a condition intermediate between a plesiomorphic ephemeroid state (e.g., fig. 22) and that found in certain Euthyplociidae, such as *Mesoplocia.*

Fossil Ephemeridae have been found previously only from the Eocene and Oligocene of the Northern Hemisphere. The Jurassic fossil of Weyenbergh (1874) that was classified as *Ephemera* was incorrectly placed to superfamily and requires reevaluation. Tshernova (1977) described the fossil larva *Mesogenesia* from the Palearctic Upper Jurassic and placed it in the Palingeniidae. The placement of this larva was based on its possession of expanded foretibiae, possibly indicating a fossorial habit. However, the strongly developed tarsi, which appear as if they may oppose the tibiae in a chelate or raptorial fashion, are atypical of extant ephemeroid larvae. The larva described as *Archaeobehningia* (Behningiidae) from the Palearctic Upper Jurassic by Tshernova (1977) is not convincingly an ephemeroid based on the published data. Nevertheless, from the age of *Australiphemera* and the position of Behningiidae being more ancestrally derived, Behningiidae certainly could have been present prior to the Lower Cretaceous.

McCafferty and Edmunds (1979) hypothesized that the Ephemeroidea were derived from the Leptophlebiidae. It now appears, on the basis of unpublished data, that the two groups actually shared a common ancestor and that both are monophyletic (fig. 27). Tshernova (1971) placed *Cretoneta* from the Palearctic Upper Cretaceous and *Mesoneta* from the Jurassic in the subfamily Mesonetinae of the Leptophlebiidae. Hubbard and Savage (1981) believed the familial placement of *Mesoneta* to be tenuous. The family Leptophlebiidae is, however, at least as old as the Lower Cretaceous and probably older in light of the fossil Ephemeroidea reported herein (see also fossils tentatively described as leptophlebiids herein). The family Leptophlebiidae is older if *Mesogenesia* is an ephemeroid, or *Mesoneta* a leptophlebiid.

Extant Ephemeridae are nearly cosmopolitan but are poorly represented in the Neotropics (McCafferty et al., 1990) by three species of *Hexagenia*; *Ephemera* and *Afromera* are represented in the Afrotropics by a few species, and, although the genus *Ichthybotus* occurs in New Zealand, ephemerids are absent from Australia. One may assume from the presence of *Australiphemera* and other ephemeroids reported below from Brazil that some early stock was widespread (perhaps Pangaean) but became extinct later in South America. McCafferty et al. (1990) hypothesized that *Hexagenia* became distributed in South America in the Tertiary with a center of origin in North America.

Larvae of Ephemeridae burrow into soft substrates of slower reaches or depositional areas of streams and rivers as well as shallow silt bottoms of lakes and occasionally ponds. The exact consistency of the substrate and specifics of the burrow formed varies with the functional morphology of the different genera (see Keltner and McCafferty, 1986). It should be emphasized, however, that the occurrence of *Australiphemera* and other possible ephemerids from the Lower Cretaceous does not absolutely indicate that this type of burrowing habit was already evolved at that time because the plesiomorphic venational characters apparent in these fossils could have been present before this type of fossorial habit evolved. With respect to this, it should also be kept in mind that both early branched and later branched lineages in the Ephemeroidea, the Potamanthidae and Euthyplociidae, respectively (see fig. 27), as well as some Polymitarcyids, do not demonstrate true burrow-forming fossorial habit and presumably represent a more ancestral habit of sprawling or living in crevices among mixed substrate.

Microphemera neotropica,
new genus, new species

Figures 22, 28

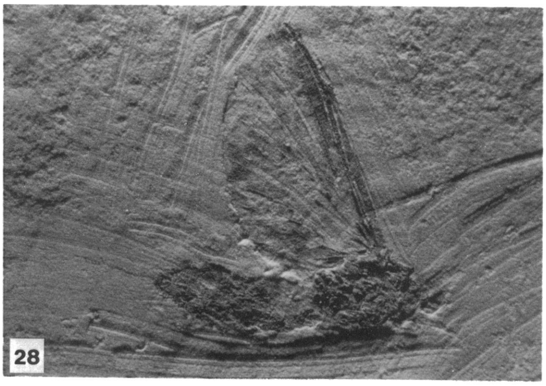
TYPE: Adult (sex?) 43301 (fig. 28).

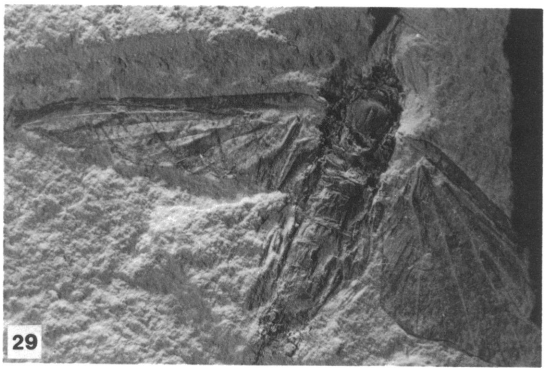
ETYMOLOGY: *Microphemera* is a feminine nomen consisting of an arbitrary combination of letters derived in part from the Greek *micros,* meaning little, and alluding to an ephemeroid genus of small size. The specific name *neotropica* is a noun in apposition and an allusion to the Neotropical distribution of the species.

DIAGNOSIS: This taxon can be distinguished by the combination of a relatively small body and wing size, in the forewing the position of the MA fork basad of midlength of the wing, the composition of the cubital intercalaries, the moderate distal arch of CuP, and A_1 that is apparently unforked and possesses only one veinlet.

LARVA: Unknown.

ADULT: Partial lateral head, lateral thorax, forewing, partial hindwing, lateral abdomen, and partial caudal filament of fossil. Sex unknown. Body 8.5 mm. Forewing 7.8 mm long; costal and other crossvenation well developed; Sc visible for entire length; longitudinal veins not geminating; venation of radial triad extensive; Rs forked in basal ¼ of wing; MA forked at ca. ⅜ distance from wing base; MP_2





Figs. 28, 29. Alate habitus. **28.** *Microphemera neotropica* lateral habitus, AMNH 44301 (holotype). **29.** *Pristiplocia rupestris* dorsal habitus, AMNH 44308 (holotype).

and CuA strongly arched posteriorly at base (based on wing dimension and distal orientation); forked basal veinlet and four distal, long, single veinlets attaching CuA to anal margin, no cubital intercalaries present, no free cubital veinlets present; CuP sigmoid and only moderately arched distally toward margin; A_1 not discernible distally but with one strong veinlet attaching it to anal margin, apparently unforked. Hindwing and caudal filaments too incomplete to describe.

OTHER MATERIAL EXAMINED: None.

DISCUSSION: Much of the discussion regarding superfamily and family placement under the genus *Australiphemera,* above, also applies to *Microphemera.* In *Microphemera* the A_1 vein (fig. 22) is visible to the distal point where it is attached to one strong veinlet, and from the space distad of this it would be difficult to envision a fork having been present. Therefore, although no hindwing evidence is available, the apparent absence of an A_1 fork leads me to place *Microphemera* in the Ephemeridae rather than the Potamanthidae.

Four short crossveins are visible in the anal area of the forewing (fig. 28). These could initially be interpreted as a series of anal veinlets, but close examination reveals that the supposed veinlets are actually costal crossveins of the underlying remnant of the hindwing, and what may have been interpreted as the A_1 is actually the costa of that hindwing. This is evidenced by the fact that this costa (supposed A_1) with its attached crossveins crosses the distal end of CuP in the forewing.

The forewing venation of *Australiphemera* and *Microphemera* is very similar (figs. 20, 22), except the MA fork is slightly more basad, and CuP is less arched distally, and the cubital veinlets are slightly shorter and more posteriorly oriented in *Microphemera.* These characteristics and the distinctly smaller size of *Microphemera* clearly distinguish the two taxa. Any suggestion that *Australiphemera* and *Microphemera* are merely dimorphic sexes of the same species is not supportable. Although some sexual size dimorphism is present in extant species of Ephemeridae, it is not exaggerated.

The history of Ephemeridae and Ephemeroidea, and the biogeography and larval habitat of extant ephemerids are treated under the discussion of *Australiphemera,* above. As a footnote, it may be of some interest that in several respects, including the reduced anal area, the forewing of *Microphemera* is reminiscent of those of the primitive extant genus *Ichthybotus,* which is the only ephemerid known from the Australian biogeographic realm, specifically New Zealand.

FAMILY EUTHYPLOCIIDAE

Pristiplocia rupestris,

new genus, new species

Figures 23, 29

TYPE: Adult (sex?) AMNH 44308 (fig. 29).

ETYMOLOGY: The feminine generic nomen *Pristiplocia* is an arbitrary combination of letters based in part on the Latin *pristinus,* meaning early or primitive, and alluding to a primitive euthyplociid. The trivial name *rupestris* is Latin, meaning "of rocks" and alluding to the fossil nature of the species.

DIAGNOSIS: This taxon is distinguishable by its size and a forewing consistent with family characteristics of Euthyplociidae as well as with a uniquely veined cubital area. This cubital area consists of an intercalary vein that originates in CuA and terminates in the outer margin and runs parallel to CuA, and other, more basal, sigmoid intercalaries subparalleling CuA and attaching CuA to the anal margin.

LARVA: Unknown.

ADULT: Dorsal aspect of fossil with head, body, and most of forewing and part of hindwing present; sexual characters not discernible but possibly female due to small head impression (small eyes). Body 13.2 mm long. Head distinctly narrower than thorax but pronotum not apparent. Forelegs developed, at least 4.0 mm long; claws, segment ratios, and other legs not discernible. Forewing (fig. 23) 13.0 mm long, with full complement of longitudinal veins and profuse crossvenation; Rs fork at ¼ distance from base; MA fork in basal ⅓ of wing, distad of Rs fork; MP_2 and CuA strongly decurved posteriorly at base; marginal areas with anastomosed short intercalaries, at least three short intercalaries in areas between MP_1 and IMP, IMP and MP_2, and MP_2 and CuA; cubital region with one distal intercalary originating on CuA and terminating in outer margin, three short somewhat reticulated marginal veinlets attaching this cubital intercalary with margin; three or four additional, more basal, long, slightly sigmoid intercalaries running diagonal from CuA to anal margin, paralleling each other and subparalleling distal cubital intercalary; CuA and CuP attached basally by three crossveins. Hindwing 4.8 mm long, with venation and shape not discernible. Caudal filaments not discernible.

OTHER MATERIAL EXAMINED: Two adults (probably males) (AMNH 44304, 44307) of questionable identity because of very incomplete wings.

DISCUSSION: *Pristiplocia* is very characteristic of present-day Euthyplociidae and would easily be keyed to that family using keys to extant mayflies. All of the characters available in the fossil agree with the family's characteristics. These include characters of the forewing (fig. 23) as follows: a basally decurved MP_2 and CuA; nongeminating longitudinal veins; an Sc visible for its entire length; a MA fork in the basal third; a cubital region with sigmoid veinlets attaching CuA to margin; no free anal veinlets at the anal margin; and very extensive crossvenation throughout the wings.

The fossil genus is very similar to extant genera in the Euthyplociinae but differs in the detail of the cubital intercalary venation of the forewing. Its venation is most similar to that of the Neotropical genus *Campylocia* (see Needham and Murphy, 1924). Both possess a cubital intercalary that originates on CuA and ends near the posterior end of the outer margin of the wing. In *Campylocia* there is sometimes a second such intercalary originating basad of the first on CuA but also paralleling CuA. From the second intercalary, or first if it is the only one, sigmoid veinlets run to the anal margin and additional similar veinlets also attach CuA to the anal margin in the more basal area. *Pristiplocia* differs from this by having very long veinlets that run almost parallel to the first cubital intercalary (fig. 23). These veinlets could thus be considered intercalaries, as I have done here. Their homology, however, is apparently with the veinlets of other euthyplociids.

Other variations in the euthyplociines include no cubital intercalaries but simply a series of parallel veinlets (such as in the Neotropical genus *Euthyplocia*) and cubital intercalaries present but not attached to CuA (such as in the Indonesian genus *Polyplocia*). The subparalleling, long veinlets (intercalaries) of *Pristiplocia* represent an additional variation.

The origin of the Euthyplociidae within the Ephemeroidea (McCafferty, 1979) (fig. 27) can now be interpreted as at least the Lower Cretaceous. No other fossils of Euthyplociidae have been known previous to this study, and fossils of its sister lineage Polymitarcyidae are known only from possible fossil burrows from the Miocene.

The family Euthyplociidae has a disjunct Pantropical distribution, including the Neotropics, Afrotropics plus Madagascar, and the tropical Orient (Indonesia and North Borneo). The discovery of *Pristiplocia* indicates that the family was probably well established

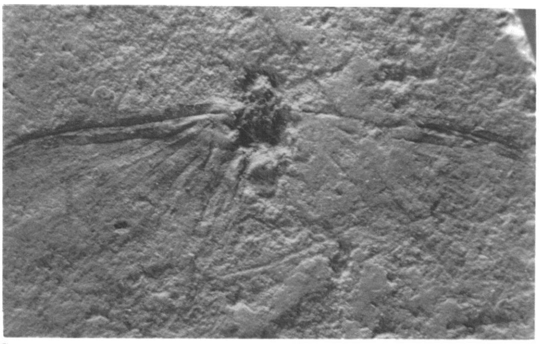


Fig. 30. Potamanthidae (?) sp. 1 alate stage, dorsal habitus, AMNH 44311.

when such disjunct areas were joined in Gondwana or southern Pangaea, and thus offers, by way of vicariance, an explanation for the present distribution of the family.

Modern euthyplociine larvae are for the most part sprawlers and always occur in running water environments. Given the close relationship of *Pristiplocia* with present-day members of the family, one may assume the presence of some stream environment at least in the vicinity of the Brazilian fossil site.

Ephemeroidea sp. 1

Figure 30

MATERIAL: AMNH 44311, alate.

DESCRIPTION: Dorsal head, thorax, partial abdomen, and partial forewings present. Sex unknown. Head 1.3 mm wide including compound eyes; eyes 0.3 mm wide in dorsal view, widely separated and laterally oriented on head. Forewing 8.5 mm long; costal crossvenation well developed; Sc visible for entire length; longitudinal veins not geminating; venation of radial triad not discernible; Rs forked in basal ¼ of wing; MA forked slightly less than midlength of wing; MP_2 and CuA arched posteriorly at base, running singularly for entire length, not connected basally; cubital region not clear; CuP sigmoid and strongly bent toward anal margin; A_1 apparently forked, with no veinlets.

DISCUSSION: This fossil is clearly an ephemeroid as per *Australiphemera* and *Microphemera,* discussed above, but has general plesiomorphic wing venation found in both the Ephemeridae and Potamanthidae. The placement to one or the other of these families is problematic. The anal area of the forewings is difficult to interpret. A_1 is evident and no veinlets can be seen. A second vein that is proximal and posterior to A_1 is nearly straight for its visible length, but is slightly curved in much the same manner as A_1. It could be interpreted as A_2, in which case an argument could be made for placing the fossil in the Ephemeridae. However, because of the space and orientation in the anal area and the proximity of the visible basal aspects of these veins, it is more reasonable to envision that they were connected basally and actually represent the two branches of a forked A_1. If their lines are reconstructed by extending them basally they form a fork very typical of the Potamanthidae.

This fossil, although also similar in size to *Microphemera* (described above), differs from it in that the A_1 anal veinlet of *Microphemera* bends in an opposite direction at its base and forms an abrupt angle with A_1 (fig. 22). The anal veinlet of *Microphemera* is thus typical of ephemerid attaching veinlets in this region and not like Potamanthidae, wherein the inner branch of A_1 follows a continuous line (no abrupt angles) with the stem of A_1, and the outer branch is most divergent from the line of the stem of A_1. The small laterally oriented eyes of the fossil, particularly if it is a male, would lend some support to the tentative potamanthid classification.

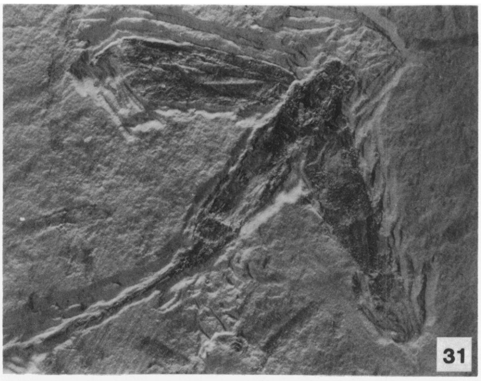
If this fossil is indeed a potamanthid, it would be the first fossil known of this family. The fossil from Baltic amber described as *Potamanthus priscus* was correctly shown to be a member of the Leptophlebiidae by Demoulin (1968). Extant Potamanthidae are restricted to the Holarctic and Oriental realms. Their larvae are stream inhabitants found in areas with mixed substrate and moderate current speed.

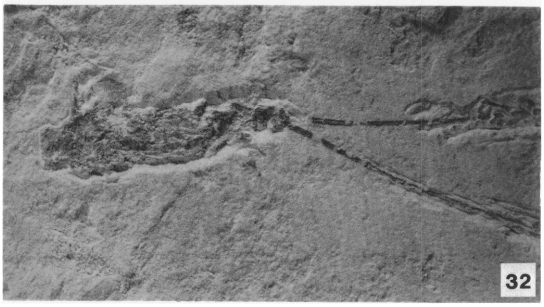
Ephemeroidea sp. 2

Figure 31

MATERIAL: AMNH 43480, alate.

DESCRIPTION: Dorsal aspect of alate fossil (? adult female) with body and partial forewings, forelegs, and caudal filaments. Body 11.1 mm long. Forewings at least 9.3 mm long; crossvenation well developed; longitudinal veins not geminating; MA forked just





Figs. 31, 32. Alate and larval habitus. **31.** Ephemeroidea sp. 2 alate stage, dorsal habitus, AMNH 43480. **32.** Leptophlebiidae (?) sp. 1 larva, dorsal habitus, AMNH 43474.

basad of midlength of wing; MP_2 and CuA strongly arched posteriorly at base; cubital and anal regions not discernible. Median terminal filament present and apparently well developed.

Discussion: Not enough characters are available on this fossil to allow even tentative identification beyond the superfamily Ephemeroidea. The ephemeroid venation of the posteriorly arched base of MP_2 and CuA and the well-developed costal crossvenation are apparent and characteristic of ephemeroid venation. The body and wing size of this specimen does not match any of the other species of ephemeroids described herein.

Leptophlebiidae (?) sp. 1

Figure 32

Material: AMNH 43474, larva.

Description: Dorsal aspect of larval fossil including head and body, left cercus, and median terminal filament; other appendages and gills missing. Body 9.2 mm long; cerci and median terminal filament at least 15 mm long. Head subquadrate, narrowing in cervical region, narrower than thorax, and possibly hypognathous. Body elongate. Setae on caudal filaments not discernible.

Discussion: The shape of the head and body along with the relatively very long caudal filaments give a strong indication that this fossil belongs in the extant family Leptophlebiidae. A number of extant genera of Leptophlebiidae give a similar overall impression and fit this general size. Unfortunately, gills, which would resolve the exact placement of this fossil, are missing. However, the narrow lanceolate-like gills common to some extant leptophlebiids, such as *Paraleptophlebia,* are easily and often broken off. No other fossil Ephemeroptera larvae from Brazil have caudal filaments approaching the relative length of those of this specimen.

An unnamed species of Leptophlebiidae (*Atalophlebia*? sp. A) from the Eocene was described from larval fossils from Argentina by Rossi de Garcia (1983). This represents the only Ephemeroptera fossil known from South America other than those treated herein.

Leptophlebiidae (?) sp. 2

Figure 33

Material: AMNH 43476, alate.

Description: Lateral aspect of fossil (? adult female) including body, forewings, and partial head and caudal filaments. Body 6.1 mm long. Forewing 5.9 mm long; not triangular, but posterior margin extensive and gradually curved; venation difficult to interpret because one forewing overlying other; crossvenation weak to moderately developed; marginal venation not discernible; Rs forked at ca. ¼ length of wing; radial triad expansive; MA forked in distal half, fork apparently symmetrical; connection of MP_2 and MP_1 near base of wing; MP_2 gradually and slightly curving toward anal margin; CuA closely paralleling MP_2; cubital and anal areas not discernible. Hindwing, if present, not discernible. Median terminal filament apparently well developed.

Discussion: The general shape of the wing, the generally weak crossvenation, the expansive radial triad taking up a large portion of the wing, and the position of the MA fork all suggest the family Leptophlebiidae. The presence of three tails would also fit this family, and the small body size might exclude it from the Siphlonuridae, a group also possessing most of these characteristics. The paucity of characteristics on the fossil precludes any reasonable assessment of relationships at this time.

The terminal area of the abdomen of the organism appears to be damaged, and thus the base of one of the caudal filaments is not in alignment with the others. The displaced caudal filament base might be interpreted as an ovipositor since ovipositorlike structures are not uncommon in certain Leptophlebiidae. The base of this structure on the abdomen, however, is too posterior for it to be an ovipositor.

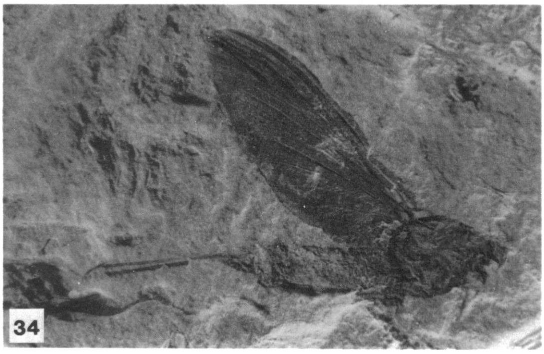
Leptophlebiidae (?) sp. 3

Figure 34

Material: AMNH 44312, alate.

Description: Lateral aspect (? adult female) with head, body, forewing, hindwing, and partial caudal filaments. Body 7.5 mm long. Forewing 7.8 mm long; crossvenation not clear; Rs forked at ca. ⅓ distance from base of wing; radial triad expansive; MA forked in distal half; MP forked near base; MP_1 intercalary present; cubital and anal area not clear. Hindwing highly reduced, 0.6 mm long; venation not discernible. Only two caudal filaments discernible.

Discussion: Again, shape of the wing, wing venation, and size of the body are highly suggestive of Leptophlebiidae. Importantly, the highly reduced hindwing is reminiscent of a number of extant Neotropical genera of Leptophlebiidae (e.g., *Thraulodes, Hagenulus, Borinquena, Careospina,* and *Neohagenulus*). The basally oriented fork of MP, however, is not as common among leptophlebiids with which I am familiar. It is relatively basal but not as basal in certain *Neohagenulus* and *Traverina.* If this is indeed a leptophlebiid, then a caudal filament is either missing or it is atypically two-tailed as, for example, the leptophlebiid genus *Careospina.*



Figs. 33, 34. Leptophlebiidae (?) spp. alate stage, lateral habitus. **33.** Sp. 2, AMNH 43476. **34.** Sp. 3, AMNH 44312.

FAMILY INCERTAE

Incertae Sedis sp. 1

Material: AMNH 43453, larva.

Description: Dorsal aspect of larval fossil with head and body, partial forelegs, and partial median terminal filament. Body 13.5 mm long; median terminal filament at least 1.0 mm long. Head flattened, slightly shorter than broad, rounded to slightly pointed anteriorly, nearly straight and subparallel laterally; compound eyes dorsal, width of one ca. ¼ head width, antennal bases dorsal, anteromedial to compound eyes. Structural details of thorax and abdomen missing; body apparently narrow-elongate. Median terminal filament very thin; cerci missing.

Incertae Sedis.sp. 2

Material: AMNH 43423, larva.

Description: Dorsal aspect of larval fossil including head, thorax, and abdomen, with left and hind femora, and left cercus and possibly partial median terminal filament intact; other appendages and structural details missing. Body 12.5 mm long; cerci at least 12.0 mm long. Head capsule rounded anteriorly, laterally subparallel, appearing longer than broad. Femora not broadened. Thorax and abdomen giving impression of stout, nonminnowlike body form; gills missing. Cerci with sparse, long setae along both inner and outer margins; median terminal filament apparently developed, marginal setae not discernible.

CONCLUDING REMARKS

New information gained from the study of the Lower Cretaceous mayflies from Ceará Crato, Brazil, directly impacts our understanding of mayfly evolution in a number of ways. It contributes to mayfly phylogeny and the augmentation of theories based primarily on extant taxa. It supplies times of origins or at least minimum ages of lineages and allows comparisons of Cretaceous fauna with modern and more ancient faunas. It also contributes West Gondwanian distributions that are of historical consequence and that allow explanations of some modern distributional patterns. Besides this, the diversity and abundance of both terrestrial and aquatic life stages of mayflies strongly suggest the habitats and paleoecology of the fossils.

The mayfly superfamily Heptagenioidea is here recognized as a monophyletic group of basically stream-dwelling larvae consisting of the families Coloburiscidae, Isonychiidae, Oligoneuriidae, and Heptageniidae. Cladistic relationships (fig. 18), which are being treated in detail elsewhere, support recognition of the families Coloburiscidae and Isonychiidae, separate from the Oligoneuriidae or Siphlonuridae. The family Oligoneuriidae, which is represented among the fossils studied, is shown to be phyletically intermediate between the suspension feeding minnowlike mayflies of the more plesiomorphic families Coloburiscidae and Isonychiidae and the bottom-feeding and flat-headed larvae of the more apomorphic family Heptageniidae.

The systematics of the family Oligoneuriidae has always been problematic (Edmunds, 1975) because of differential rates of evolution in larval and adult stages. Whereas the family is easily defined on the basis of numerous larval synapomorphies, only the genera other than *Chromarcys* demonstrate the highly specialized rapid-flight wings. Thus, a lingering question has been whether to include or exclude *Chromarcys* from the family. The newly discovered extinct genus *Colocrus* appears to be an intermediate form with regard to specialized wing venation (figs. 19, 24). The intermediate, transitional forewing of *Colocrus* further supports the proposed relationships of *Chromarcys* and Oligoneuriinae (Edmunds, 1975). It would also strengthen the case for basing family classification in this instance on the larval synapomorphies, and including the Oligoneuriinae, Colocrurinae, and Chromarcyinae in the Oligoneuriidae. Although Colocrurinae is clearly a sister lineage to the Oligoneuriinae, it does not share the apomorphic ventral gill 1 in the larval stage with Oligoneuriinae but retains the plesiomorphic dorsal condition also found in Chromarcyinae.

New minimum times of existence for several mayfly lineages are now demonstrable. The origin of the Oligoneuriidae was at least Lower Cretaceous, and the Heptageniidae could be as old as the Lower Cretaceous (fig. 18). If minimum ages are considered in relationship to the branching sequences of lineages (figs. 18, 24) then one can further infer that the origins of the Heptagenioidea and even Oligoneuriidae were actually earlier. The Heptagenioidea is derived from a siphlonurid like ancestor, and siphlonurid fossils are known from as early as the Lower or Middle Jurassic. Moreover, recently discovered *Mogzonurella* and *Mogzonurus* fossils from the Jurassic were placed in the Coloburiscinae by Sinitshenkova (1985). If this placement is correct, the common ancestor to the Heptagenioidea dates to at least the Jurassic.

Both the Ephemeridae and Euthyplociidae can now be dated to at least the Lower Cretaceous (fig. 27), based on the Brazilian fossils. Again, extrapolating from phyletic branching sequences (fig. 27), the origin of the Leptophlebioidea and the Ephemeroidea is expected to be earlier than this. This is further supported by the discovery of tentative leptophlebiids from Brazil. Finds by Tshernova (1977) of possible Behningiidae and Palingeniidae fossils from the Upper Jurassic, along with the new discoveries of Ephemeridae (or proto-Ephemeridae), Euthyplociidae, and possibly Potamanthidae from the Lower Cretaceous of Brazil indicate that the Ephemeroidea was well established and already radiated into several of its familial lineages in the Mesozoic.

Biogeographically significant discoveries include finds of taxa that may have been predicted to have been in West Gondwana because of present-day distributions and taxa that are quite unexpected. Examples of the former are *Pristiplocia* (Euthyplociidae) and *Colocrus* (Oligoneuriidae). These families have not actually been represented in the fossil record previous to this study. The family Euthyplociidae is Pantropical in distribution as is the family Oligoneuriidae, except for some highly specialized genera. Widespread Gondwanian distribution followed by vicariance associated with continental drift is therefore suggested as the underlying basis for the present-day disjunctions.

Given the relationships between the Oligoneuriidae and Heptageniidae (fig. 18), there exists a possibility of a Gondwanian origin of Heptageniidae despite the fact that the family is primarily a Holarctic group today. A place of origin still cannot be demonstrated for Heptageniidae. However, the discovery of Colocrurinae in West Gondwana in addition to a consideration of Chromarcyinae in tropical Asia, in light of these groups' relatively basal phyletic positions, adds some plausibility to an origin of Heptageniidae in the Southern Hemisphere.

The possible presence of Potamanthidae in West Gondwana was unexpected. Potamanthidae had not actually been known from the fossil record previously, and today the family is strictly Holarctic and Oriental in distribution. Unfortunately, the one alate fossil that might be in Potamanthidae is too incomplete to allow a positive identification. Nevertheless, a legitimate question remains as to why Potamanthidae is not presently represented in the Afrotropical or Neotropical realms.

The presence of two new genera of Ephemeridae in West Gondwana was somewhat unexpected because the family is poorly represented in the Neotropics today by only a few species with probable Nearctic affinities. The extinct genera, however, appear to be very primitive and may actually represent a proto-Ephemeridae-Potamanthidae group based on their plesiomorphic wing venation. It is not known whether these new genera are close relatives to *Ephemera,* which is an ancestral extant genus of Ephemeridae that is found in the Holarctic, Oriental, and Afrotropical realms but not the Neotropics.

The extinct family Hexagenitidae, although relatively well known from the Northern Hemisphere Jurassic is shown to have also existed in the Southern Hemisphere Lower Cretaceous, and to have coincided during this era with many families that have continued into the present, including the closely related Siphlonuridae.

Although the family Siphlonuridae (in its broadest sense) is not represented by extant taxa in tropical South America or Africa, Amphinotic genera are known from Transantarctic areas, including the Chilean-Patagonian area, and the group is widespread in the Holarctic. The discovery of siphlonurids from West Gondwana provides the predicted geographic link between these disjunct extant distributions of this family. Most likely, the family was widespread in Pangaea during the Jurassic. The fact that the family does not now occur in tropical areas is somewhat perplexing.

The fossil mayflies found in Brazil are distinctly advanced from Paleozoic and Triassic forms, and all, including Hexagenitidae, fall within the Schistonote grouping of modern mayflies (McCafferty and Edmunds, 1979). However, although they are characteristically typical of modern schistonotes, several of the taxa have unique combinations of morphological traits not found in extant forms. This is especially profound in the Hexagenitidae and Colocrurinae (Oligoneuriidae).

Of the higher taxa found to have existed or possibly existed in West Gondwana during the Lower Cretaceous, Hexagenitidae and Colocrurinae are now extinct, and Siphlonuridae and Potamanthidae are not now represented by extant taxa in tropical South America. Also, the Ephemeridae of Lower Cretaceous Brazil do not appear to be directly related to the few extant Neotropical species of Ephemeridae, since the latter are thought to be of Tertiary or possibly even Quarternary North American origin (McCafferty et al., 1990). This leaves only the possible Leptophlebiidae and the Euthyplociidae representing a continuous existence of connected lineages in the area since the Lower Cretaceous, although the Colocrurinae also appears to represent an ancestral branch related in origin to the modern oligoneuriines presently found in tropical South America.

From the above, and as suggested earlier, it appears that many of these mayfly groups were more widespread during the Mesozoic. In addition, there apparently was significant extinction and emigration of mayfly lineages since the Lower Cretaceous in that area of the world that includes Brazil and the present Neotropics, with only a relatively few of those lineages having possibly survived there to the present.

Pannote mayflies are an apomorphic monophyletic grouping of the extant families Ephemerellidae, Tricorythidae, Neoephemeridae, Caenidae, Baetiscidae, and Prosopistomatidae (McCafferty and Edmunds, 1979). No representatives of pannote mayflies were found in Brazil as far as I could discern. It could very well be that the pannote lineage did not originate until the Upper Cretaceous or Tertiary. The placement of certain Jurassic fossils in the Ephemerellidae by Demoulin (1954) is highly doubtful based on the remnants available. Pannote fossils are not definitely known until the Eocene and Oligocene.

The family Baetidae is a large schistonote group that is prevalent in the Neotropics as well as almost every other area of the world today. Together with the Leptophlebiidae, it demonstrates the most adaptive radiation among modern mayflies. It is of interest to me, however, that baetids were not represented in the Brazilian find. Whereas leptophlebiids are possibly as old as the Jurassic and definitely as old as the Lower Cretaceous, baetids are not known previous to the Eocene. I agree with Sinitshenkova (1985) that *Mesobaetis,* which is known from the Jurassic, should be placed in the Siphlonuridae, not the Baetidae as per Hubbard (1987).

The lack of an early fossil record could lead one to conjecture that the family Baetidae was derived more recently than the Lower Cretaceous, and much of its widespread distribution may be due to dispersal rather than continental vicariance. Alternatively, however, it may be that Mesozoic baetids simply have yet to be found. Potentially giving credence to this alternative is some indication that certain undescribed baetids in South America and Africa represent sister lineages, which theoretically could have resulted from continental drift in the Southern Hemisphere.

The presence of siphlonurid and hexagenitid larvae with swimming-adapted tails strongly suggests that a quiet-freshwater habitat was present at the fossil site in the past. This could have been a shallow lake environment, littoral ponds, or possibly even pool areas within streams, although the sheer numbers of *Protoligoneuria* larvae found would perhaps favor the suggestion of the lacustrine environment. The presence of Ephemeridae could also indicate these types of depositional habitats. The presence of a stream habitat, in addition to a lentic habitat, is supported by the presence of the filter-feeding larva of *Colocrus* that presumably would have required flowing water. Also, the presence of the alate forms of Oligoneuriidae, Euthyplociidae, and possibly Potamanthidae, the larvae of which are all obligate stream-dwelling forms, indicates that a stream environment was at least in the vicinity.

The new data here modify the general paleoecological conclusions of Sinitshenkova (1984) regarding the Mesozoic mayflies. Based on known Palearctic fossils, that author concluded that Jurassic and Lower Cretaceous mayflies were basically lacustrine. This may be generally valid for Lower and Middle Jurassic mayflies, but by the Lower Cretaceous, flowing-water mayflies, including filter feeders, had definitely evolved, as evidenced by the Gondwanian fossils. The new Brazilian data show the evolution of mayflies, from still-water forms to predominantly flowing-water forms, as had been proposed by Edmunds and McCafferty (1988), to have actually begun much earlier than the Cenozoic.

A collection of alate forms of mayflies, as in the Brazilian find, would usually be indicative of a riparian environment adjacent to a freshwater habitat. However, most of the alate mayfly fossils from Brazil, although diverse, appear to be females (at least male genitalia are not discernible), and it may therefore be primarily ovipositing females that had expired on the water and were fossilized after being washed up on bank areas or washed downstream and deposited in a lake. Such expired females of modern mayflies can be common along the shores of streams, ponds, and shallow embayments of lakes.

REFERENCES

Brauer, F., J. Redtenbacher, and L. Ganglbauer
1889. Fossile insekten aus der Juraformation Ost-Sibiriens. Mem. Acad. Imp. Sci. St. Petersbourg 36(15): 1–20.

Brito, I. M.
1987. Note preliminar sobre uma nova Êfemero do Cretaceo do Ceará (Insecta Ephemeroptera). Ann. 10th Congr. Bras. Paleontol. 2: 593–597.

Carpenter, F. M.
1987. Review of the extinct family Syntonopteridae (Order Uncertain). Psyche 94: 373–388.

Cockerell, T. D. A.
1923. A new genus of mayflies from the Miocene of Florissant, Colorado. Psyche 30: 170–172.

Costa Lima, A. da
1950. Ninfa de Efemerideo fossil do Ceará. Ann. Acad. Bras. Ciencias 22: 419–420.

Crass, R. S.
1947. The may-flies (Ephemeroptera) of Natal and Eastern Cape. Ann. Natal Mus. 11: 37–110.

Demoulin, G.
1954. Les Ephéméroptères Jurassiques du Sinkiang. Bull. Ann. Entomol. Soc. Belgique 90: 322–326.
1955. Sur une larve siphlonuridienne d'Ephémère fossile du Bresil. Bull. Ann. R. Entomol. Soc. Belgique 91: 271.
1958. Nouveau schema de classification des Archodonates et des Ephemeropteres. Bull. R. Inst. Nat. Sci. Belgique 34(27): 1–19.
1968. Deuxième contribution à la connaissance des Éphéméroptères de l'ambre Oligocène de la Baltique. Deutsche Entomol. Z. 15: 233–276.
1970a. Contribution a l'etude morphologique, systematique, et phylogenique des Ephemeropteres Jurassiques d'Europe centrale V. Hexagenitidae = Paedephemeridae (syn. nov.). Bull. R. Inst. Nat. Sci. Belgique 46(4): 1–8.
1970b. Contribution a la connaissance des Ephemeropteres du Miocene 1. *Siphlurites explanatus* Cockerell. Bull. R. Inst. Nat. Sci. Belgique 46(5): 1–4.
1971. Contribution a l'etude morphologique, systematique, et phylogenique des Ephemeropteres Jurassiques VI. L'aile postérieure des *Hexagenites* Scudder et les rapports Hexagenitidae-Chromarcyidae-Oligoneuriidae. Bull. R. Inst. Nat. Sci. Belgique 47(29): 2–10.
1974. Quatrieme contribution a la connaissance des Ephemeropteres de l'ambre Oligocene de la Baltique. Bull. R. Inst. Nat. Sci. Belgique 50(3): 1–4.

Eaton, A. E.
1871. Monograph on the Ephemeridae. Trans. Entomol. Soc. London 19: 1–164.

Edmunds, G. F., Jr.
1972. Biogeography and evolution of Ephemeroptera. Annu. Rev. Entomol. 17: 21–42.
1975. Phylogenetic biogeography of mayflies. Ann. Missouri Bot. Gard. 62: 251–263.

Edmunds, G. F., Jr., R. K. Allen, and W. L. Peters
1963. An annotated key to the nymphs of the families and subfamilies of mayflies (Ephemeroptera). Univ. Utah Biol. Ser. 8(1): 1–49.

Edmunds, G. F., Jr., S. L. Jensen, and L. Berner
1976. The mayflies of North and Central America. Minneapolis: Univ. Minn. Press.

Edmunds, G. F., Jr., and W. P. McCafferty
1988. The mayfly subimago. Annu. Rev. Entomol. 33: 509–529.

Edmunds, G. F., Jr., and J. R. Traver
1954a. An outline of reclassification of the Ephemeroptera. Proc. Entomol. Soc. Washington 56: 236–240.
1954b. The flight mechanics and evolution of the wings of Ephemeroptera, with notes on the archetype insect wing. J. Washington Acad. Sci. 44: 390–400.

Handlirsch, A.
1908. Die fossilen Insekten und die phylogenie der rezenten formen. Leipzig.

Hubbard, M. D.
1987. Ephemeroptera. Fossilium catalogus, I: Animalia, pars 129. Amstelveen, The Netherlands: Kugler Publ.

Hubbard, M. D., and J. Kukalová-Peck
1980. Permian mayfly nymphs: new taxa and

systematic characters. *In* J. F. Flannagan and K. E. Marshall (eds.), Advances in Ephemeroptera biology, pp. 19–33. New York: Plenum Press.

Hubbard, M. D., and H. M. Savage
1981. The fossil Leptophlebiidae (Ephemeroptera): a systematic and phylogenetic review. J. Paleontol. 55: 810–813.

Jell, P. A., and P. M. Duncan
1986. Invertebrates, mainly insects from the freshwater, Lower Cretaceous, Koonwarra fossil bed (Korumburra Group), South Gippsland, Victoria. Mem. Assoc. Australasian Paleontol. 3: 111–205.

Keltner, J., and W. P. McCafferty
1986. Functional morphology of burrowing in the burrowing mayflies *Hexagenia limbata* and *Pentagenia vittigera.* Zool. J. Linn. Soc. 87: 139–162.

Kukalová-Peck, J.
1985. Ephemeroid wing venation based upon new gigantic Carboniferous mayflies and basic morphology, phylogeny, and metamorphosis of pterygote insects (Insecta, Ephemerida). Can. J. Zool. 63: 933–955.

Landa, V.
1973. A contribution to the order Ephemeroptera based on comparative anatomy. Proc. 1st Internat. Conf. Ephem., Tallahassee, Fla., 1970: 155–159.

Landa, V., and T. Soldán
1985. Phylogeny and higher classification of the order Ephemeroptera: a discussion from the comparative anatomical point of view. Prague: Českoslav. Akad. Ved.

Lewis, S. E.
1977. Two new species of fossil mayflies (Ephemeroptera: Neoephemeridae and Siphlonuridae) from the Ruby River Basin (Oligocene) of southwestern Montana. Proc. Entomol. Soc. Washington 79: 583–587.

McCafferty, W. P.
1979. Evolutionary trends among the families of Ephemeroidea. Proc. 2nd Internat. Conf. Ephem., Krakow, Poland, 1975: 45–50.
1987. New fossil mayfly in amber and its relationship among extant Ephemeridae (Ephemeroptera). Ann. Entomol. Soc. Am. 80: 472–474.

McCafferty, W. P., and G. F. Edmunds, Jr.
1979. The higher classification of the Ephemeroptera and its evolutionary basis. Ann. Entomol. Soc. Am. 72: 5–12.

McCafferty, W. P., R. W. Flowers, and R. D. Waltz
1990. The biogeography of Mesoamerican mayflies. Proc. Symp. Biogeog. Mesoamerica, 1984. Tulane Univ. Biol. Ser., in press.

McCafferty, W. P., and A. V. Provonsha
1988. Revisionary notes on predaceous Heptageniidae based on larval and adult associations (Ephemeroptera). Great Lakes Entomol. 21: 15–17.

McCafferty, W. P., and N. D. Sinitshenkova
1983. *Litobrancha* from the Oligocene in eastern Asia (Ephemeroptera: Ephemeridae). Ann. Entomol. Soc. Am. 76: 205–208.

McShaffrey, D., and W. P. McCafferty
1986. Feeding behavior of *Stenacron interpunctatum* (Ephemeroptera: Heptageniidae). J. North Am. Benthol. Soc. 5: 200–210.
1988. Feeding behavior of *Rhithrogena pellucida* (Ephemeroptera: Heptageniidae). J. North Am. Benthol. Soc. 7: 87–99.

Meshkova, N. P.
1961. New data on *Ephemeropsis trisetalis* Eichwald larvae (Insekten, Ephemeroptera). Paleontol. Zh. 1961(4): 164–168. [in Russian]

Needham, J. G., and H. E. Murphy
1924. Neotropical mayflies. Bull. Lloyd Libr. 24, Entomol. Ser. 4: 1–79.

Riek, E. F.
1970. Fossil history. *In* CSIRO, The insects of Australia, 168–186. Melbourne: Melbourne Univ. Press.
1973. Classification of the Ephemeroptera. Proc. 1st Internat. Conf. Ephem., Tallahassee, Fla., 1970: 160–178.

Rossi de Garcia, E.
1983. Insectos fosiles en la formacion Ventana (Eoceno). Provincia de Neuquen. Riv. Assoc. Geol. Argentina 38: 17–23.

Sinitshenkova, N. D.
1975. Mayfly larvae of the family Hexagenitidae. Paleontol. Zh. 1975(1): 82–87. [in Russian]
1976. New early mayflies (Insecta: Ephemeroptera) from eastern Transbaykalia. Paleontol. Zh. 1976(4): 85–93. [in Russian]
1984. The Mesozoic mayflies (Ephemeroptera) with special reference to their ecology. Proc. 4th Internat. Conf. Ephem., Prague, 1983: 61–66.
1985. Jurassic mayflies (Ephemerida-Ephemeroptera) of southern Siberia and western Mongolia. Tr. Paleontol. Inst. (Moscow) 211: 11–23. [in Russian]
1986. Mayflies, Ephemerida (= Ephemerop-

tera). *In* Insects in the early Cretaceous ecosystems of the West Mongolia. 45–46. Trans. Joint Soviet-Mongolian Paleontol. Exped. 28 (Moscow) [in Russian]

Tshernova, O. A.

1967. Mayflies of a recent family in Jurassic deposits of Transbaykalia (Ephemeroptera, Siphlonuridae). Entomol. Obozr. 46: 322–326. [in Russian]

1969. New early Jurassic mayflies (Ephemeroptera, Epeoromimidae and Mesonetidae). Entomol. Obozr. 48: 153–161. [in Russian]

1970. On the classification of the fossil and recent Ephemeroptera. Entomol. Obozr. 49: 124–145. [in Russian]

1971. A mayfly (Ephemeroptera, Leptophlebiidae) from fossil resin of Cretaceous deposits in the polar regions of Siberia. Entomol. Obozr. 50: 612–618. [in Russian]

1977. Unusual new larval mayflies (Ephemeroptera: Palingeniidae, Behningiidae) from the Jura Mountain area of the Transbaykal. Paleontol. Zh. 1977(2): 91–96. [in Russian]

1980. Order Ephemerida Latreille, 1810. Tr. Paleontol. Inst. 175: 31–36. [in Russian]

Tshernova, O. A., and N. D. Sinitshenkova

1974. New fossil genus and species of the family Hexagenitidae (Ephemeroptera) from the southern European part of the USSR and its connection with recent Ephemeroptera. Entomol. Obozr. 54: 130–136. [in Russian]

Wallace, J. B., and J. O'Hop

1979. Fine particle suspension feeding capabilities of *Isonychia* spp. (Ephemeroptera: Siphlonuridae). Ann. Entomol. Soc. Am. 72: 353–357.

Weyenbergh, H.

1874. Varia zoologica et paleontologica. Period. Zool. 1: 77–109.

CHAPTER 3. ODONATA

FRANK LOUIS CARLE[1] AND DENNIS C. WIGHTON[2]

ABSTRACT

A fossil pseudostigmatid (Zygoptera) is placed in the newly established Euarchistigmatinae (for the new genus and species, *Euarchistigma atrophium*). Euarchistigmatinae is considered an extinct lentic-adapted sister group to extant pseudostigmatines with its lacustrine habitat responsible for disproportionate fossilization as compared to related groups. Platystictidae and its apparent derivative, Protoneuridae, could be derived from archaic Pseudostigmatidae through reductions, as supported by the intermediate morphology of euarchistigmatines. Euarchistigmatines inhabited lakes of the South American–African rift system, and exhibit an apomorphy unique among Odonata, that is, basal atrophy of IR_3 and its basal fusion to R_{4+5}. Three fossil protoneurids are placed in the newly established Eoprotoneurinae (for the new genus and species *Eoprotoneura hyperstigma*). Eoprotoneurines are distinguished from other protoneurids by the paucity of crossvein alignment across main veins, the distal recession of IR_3 to the first postnodal, and the well-developed pterostigmata which are distinctly larger in the hind wings.

A gomphid (Anisoptera) specimen (*Cordulagomphus tuberculatus,* n. sp.) is placed in the newly established Cordulagomphinae. In addition, *C. fenestratus,* n. sp., is described from a male wing and a nearly complete female, *C. santanensis,* n. sp., from a nymph, and *Gomphaeschna obliqua* Wighton placed in *Gomphaeschnaoides,* n. gen. Cordulagomphinae is considered an extinct lentic-adapted sister group to extant gomphids, with its lacustrine habitat responsible for disproportionate fossilization as compared to extant gomphids. Cordulagomphines also inhabited lakes of the South American–African rift system, and exhibited apomorphies which parallel aeschnine and libelluline adaptations likely related to post-Cretaceous success in lentic environments of the Northern Hemisphere.

A hind wing is described as *Wightonia araripina,* n. sp., belonging to the extinct family Aeschnidiidae comprising eight genera. The referred species establishes Aeschnidiidae in South America during the Early Cretaceous and provides further evidence which suggests an original Pangaeian distribution for the family.

A nymph, possibly in the penultimate instar, is described as *Pseudomacromia sensibilis,* n. sp., and placed in Pseudomacromiidae, new family, Aeschnidioidea new superfamily. The new species is characterized by long spinelike cerci, long ridged legs, gomphidlike prementum, petaluridlike labial palps, elevated frons, and robust elongate antennae which have the first and third segments relatively lengthened.

INTRODUCTION

The unique quality of preservation of the Santana Formation South American fossil dragonflies and damselflies has made them very valuable for paleontology. In particular, several extinct subfamilies are described, and several taxa in the deposit (e.g., *Wightonia*) extend the Cretaceous distributions of particular groups, thus indicating the relict nature of the deposit.

There are several currently available systems for naming wing veins in the Odonata. The Tillyard-Fraser system, although apparently homologically incorrect, is utilized here because of its widespread recognition and is supplemented with terms used by Needham and Westfall (1955) and Carle (1982a). Abbreviations for the systems not used are listed for comparison by Carle (1982a) and Wighton and Wilson (1986). All measurements are in millimeters (mm) and are lengths except where otherwise noted.

---

[1] Honorary Professor, Department of Entomology and Economic Zoology, Cook College, New Jersey Agricultural Experiment Station, Rutgers University, New Brunswick, New Jersey 98903.

[2] Deceased 1988; formerly: Research Associate, Laboratory for Vertebrate Paleontology, Departments of Geology and Zoology, Biological Sciences Centre, The University of Alberta, Edmonton, Alberta T6G 2E9, Canada.

ACKNOWLEDGMENTS

The authors thank George Ball and Philip Corbet for their thoughts and suggestions, Alan Lindoe for his photographic assistance, and the University of Alberta Technical Services, Ann Childs (Alberta), and Allma Edwards (AMNH) for their word processing assistance. M. L. May and M. V. H. Wilson very thoroughly reviewed the manuscript. The research was supported in part by a University of Alberta Professional Allowance to Dennis Wighton.

SYSTEMATICS

SUBORDER ZYGOPTERA

Several authors derive the Zygoptera or entire Odonata from the exceedingly narrow-winged Protozygoptera (i.e., Kennedy, 1920; Tillyard, 1928; Carpenter, 1931; Fraser, 1957). However, Carle (1982a) has shown that Protozygoptera are too specialized to be ancestral to the Odonata, and that most Mesozoic Zygoptera are referable to the broad-winged Zygoptera. One fossil Zygopteran described herein has R_{4+5} (Tillyard-Fraser notation 1938–1940)[3] originating just before the subnodus as in narrow-winged Zygoptera, and can be reasonably placed within the Pseudostigmatidae, although the Platystictidae and its possible derivative, the Protoneuridae, could be easily derived from it through reduction. It is noted that Fraser (1957) derived Platystictidae directly from Permian Protozygoptera which he classified as Zygoptera. However, extant narrow-winged Zygoptera are polyphyletic, being independently derived from broad-winged forms, *Disparocypha* from chlorocyphids, *Caliphaea* from calopterygids, *Lestoidea* and *Hemiphlebia* from amphipterygids, and pseudostigmatids+platystictids+protoneurids and coenagrionids from megapodagrionids. Although not followed herein, the family group name established by Handlirsch based on *Sieblosia* apparently has priority over Cockerell's family group name based on *Dysagrion* and Tillyard's family group name based on *Amphipteryx.*

More problematic is the origin of the unusual nymphal lifestyle of pseudostigmatines; as far as known, they are limited to phytotelmatic habitats such as small pools in epiphytic bromeliads. It is possible that the small pools and high humidity surrounding waterfalls formed the intermediate habitat as evidenced by the waterfall habitat of the morphologically similar *Thaumatoneura.* However, it is also possible that adaptation to semipermanent lacustrine environments, such as that of the fossil species described herein, may also have led to preadaptation for living in bromeliads.

FAMILY PSEUDOSTIGMATIDAE

EUARCHISTIGMATINAE, NEW SUBFAMILY

DIAGNOSIS: Crossveins not in alignment across main veins, costal braces (Cb) present; second costal brace at arculus; nodus at slightly less than ¼ wing length; pterostigma well developed and unbraced; R_1, R_2, IR_2, and R_3 strongly convergent toward posteroapical wing margin; IR_2 parallel to R_3; IR_3 atrophied basally and in forewings fused to R_{4+5}.

TYPE GENUS: *Euarchistigma,* n. gen.

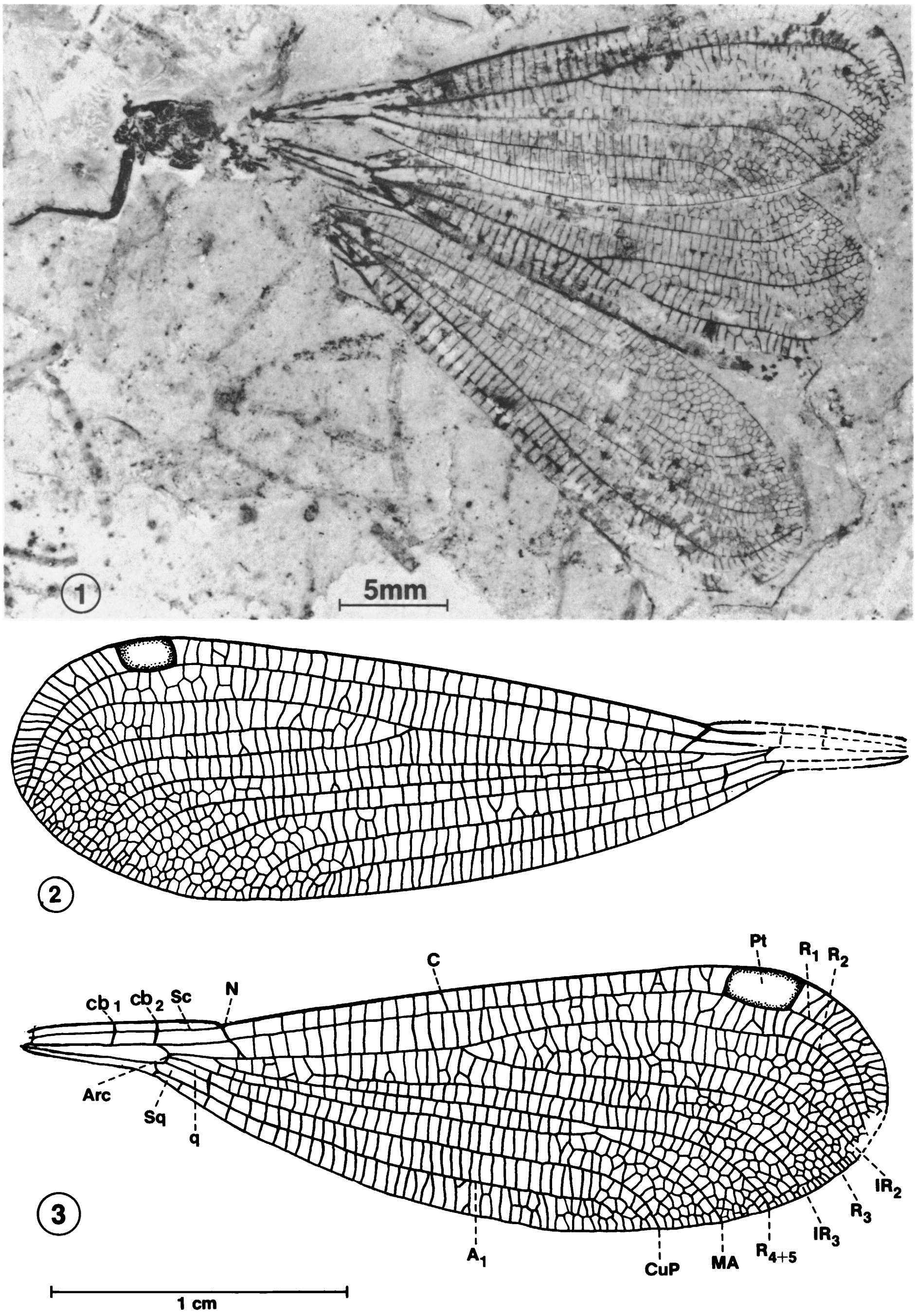
ETYMOLOGY: "Original" and "primitive" stigmatid, in reference to its relationship with basal Pseudostigmatidae.

Euarchistigma, new genus

DIAGNOSIS: Head and abdomen unknown. Thorax and legs slightly robust. Wings: R_{4+5} originating one cell before nodus; quadrangle one-celled; upper portion of discal brace nearly perpendicular to main veins, lower

---

[3] A new understanding of vein fusion and reduction, wing bracing, and wing torsion (Carle, 1982a) suggested an alternative system of wing vein homologies for the Odonata. Carle (1982a) derived the Odonata from densely veined stream-inhabiting contemporaries of the Meganisoptera. Riek and Kukalova-Peck (1983) described what are perhaps the oldest known Palaeoptera, which show exactly the vein arrangements predicted by Carle (1982a). Unfortunately, Riek and Kukalova-Peck have proposed yet another system of wing vein homologies for the Odonata by considering the base of MP to have reversed its fluting and by deriving the Odonata from the highly specialized Meganisoptera.



Figs. 1–3. *Euarchistigma atrophium,* new species, holotype AMNH 44204. **1.** Habitus. **2, 3.** Fore and hind wings, with venation terminology.

portion slightly slanted; subquadrangle one-celled; cell below subquadrangle divided in two; CuP and anal vein extended to slightly more than ⅔ wing length; 1–2 cell rows in anal field, wing petiolated to just proximal of Arc.

TYPE SPECIES: *E. atrophius,* n. sp.
ETYMOLOGY: See subfamily etymology.

Euarchistigma atrophium, new species
Figures 1–3

HOLOTYPE: AMNH 44204 part only, adult hind wings, forewing, thorax, and apparent right hind leg.

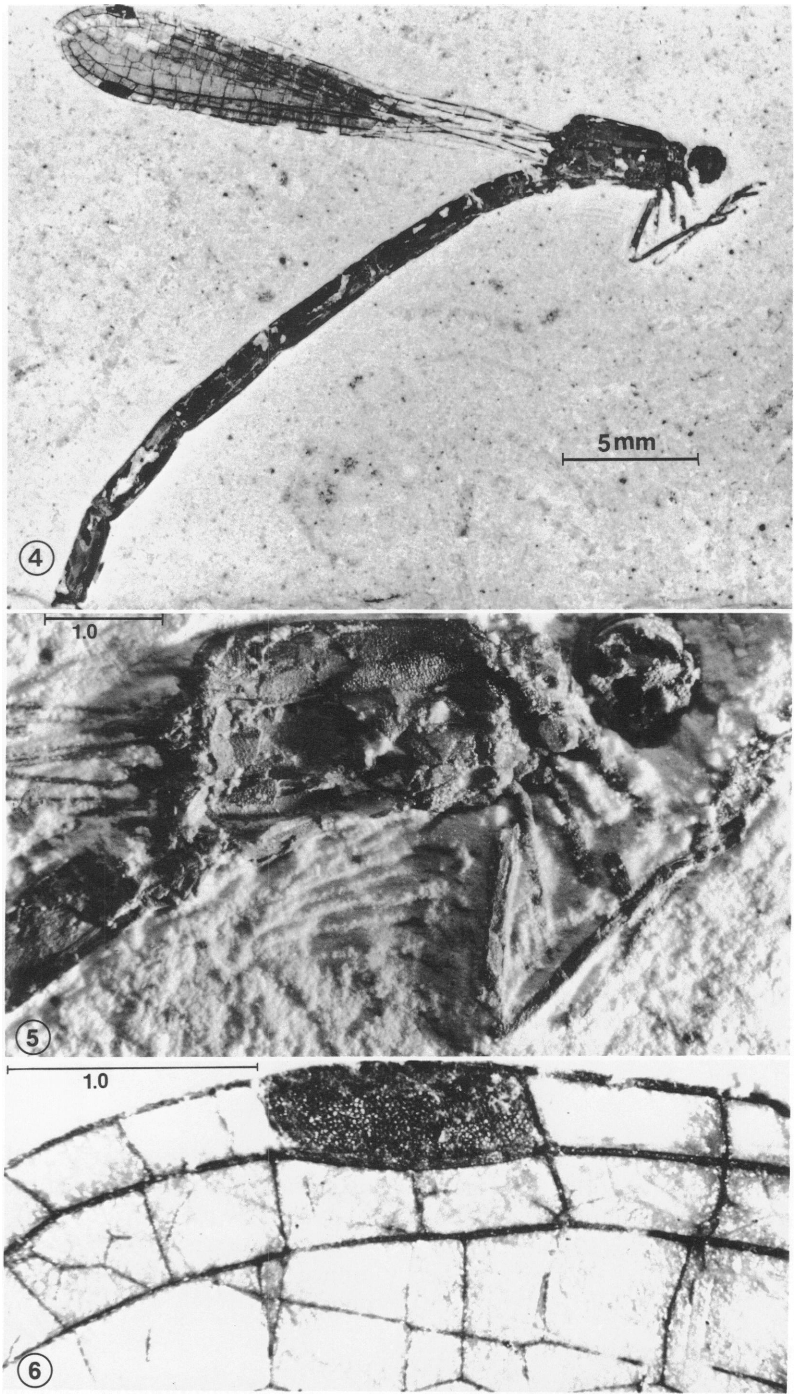
ETYMOLOGY: The specific epithet is derived from the Greek "without nourishment," referring to the basal atrophy of IR_3.

DESCRIPTION: Apparent right hind femur 3.2 × 0.6 wide, tibia 3.4, tarsi 1.8, midtibial spines separated by ca. 0.3 and ca. 0.6 long, pterothorax apparently 4.5 × 1.3 wide, distance between lateral ends of antealar carinae ca. 1.0, forewing 31.0 × 8.4 wide, hind wing 29.0 × 8.7, pterostigmata 1.7 × 1.2/2.3–2.4 × 1.2. Thorax split open along left side ca. 2.0 × 1.5 wide, apparent right hind femur relatively short. Wing membrane reddish brown, forewing with distal ⅔ of area proximal to arculus missing, right hind wing nearly complete, costal braces present without additional antenodals, nodus at 0.23/0.24 wing length, antenodal length 18.0/17.5, postnodal length 47.0/43.0, postnodal crossveins 33/31, cells beyond pterostigmata 20–21, cells below pterostigmata 7–9/6–8, cell rows below pterostigmata 2/1, origin of R_3 at 17/15–16 from base of wings, cell rows between R_2 and R_3 at level of pterostigmata 2/3, origin of IR_3 at ca. 10/8 from base of wings, CuP and A_1 separated by one cell row to near wing margin, isolated cells (2 cell rows) between A_1 and posterior wing margin 2/11.

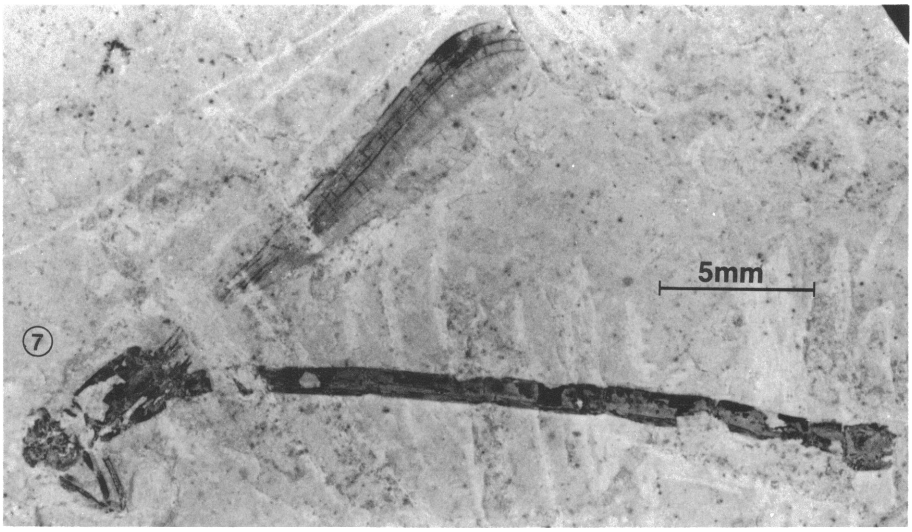
DISCUSSION: The phylogenetic position of *Euarchistigma* is somewhat uncertain. This uncertainty is due largely to the diverse outgroups made possible by the various theories of odonate origin, including the derivation of the Zygoptera from Anisozygoptera (Handlirsch, 1908), from narrow-winged Zygoptera (Kennedy, 1920), from narrow-winged Protozygoptera (Carpenter, 1931), and from unknown fossil groups related to extant broad-winged Zygoptera (Carle, 1982a). In addition, Tillyard (1928) and Fraser (1954, 1957) derived the entire Odonata from Protozygoptera.

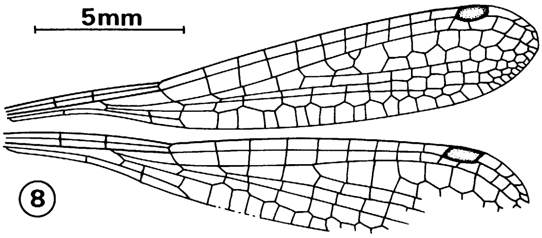
However, a few characteristics of *Euarchistigma atrophium* are so specialized that they appear apomorphic no matter what outgroup is selected. Unique within the Odonata is the basal atrophy of IR_3 and fusion with R_{4+5} (Tillyard-Fraser notation 1938–1940). The parallel arrangement of IR_2 along R_3 is found only in the Pseudostigmatidae although weakly developed in some Calopterygidae. In addition, R_1, R_2, IR_2, and R_3 are strongly convergent toward the posteroapical wing margin, a condition also developed in the Pseudostigmatidae and Platystictidae. The nodus is located at a little less than one-quarter wing length, again similar to the condition found in the Pseudostigmatidae (where it is at one-seventh to one-quarter wing length), and Platystictidae (where it is at from one-quarter to three-tenths wing length). *Euarchistigma* is also characterized by a correspondingly high number of postnodal crossveins (31–33); the corresponding numbers in the Pseudostigmatidae and Platystictidae are approximately 40 to 80+ and 15 to 25, respectively. Protoneuridae (including Platycnemididae and Isostictidae) may also be related to these groups, but the wings are so reduced that the preceding apomorphies would be lost if they had existed. Apparent plesiomorphies of *Euarchistigma* include the presence of well-developed pterostigmata, anal vein extended well beyond middle of wing, quadrangle elongate, crossveins not aligned across main veins, and most cells rectangular with the short side bordering main veins.

The phylogenetic position of *Euarchistigma* is likely near the base of the Pseudostigmatidae. However, the well-developed pterostigma and the basal atrophy and fusion of IR_3 suggest a distant relationship; therefore, Euarchistigmatinae is established for this form. *Euarchistigma* venation fills a gap between densely veined pseudostigmatids and sparsely veined platystictids, both of which share additional similarities including penile morphology, cercal shape, and general body form. The Protoneuridae may have been derived from platystictid ancestors, suggesting that the ancient megapodagronids may have given rise to the Pseudostigmatidae + Platystictidae + Protoneuridae group in the Southern Hemisphere and to the Coenagrionidae in the Northern Hemisphere, with



Figs. 4–6. *Eoprotoneura hyperstigma,* new species, holotype, AMNH 44203. **4.** Adult male, right lateral habitus. **5.** Thorax, note color pattern. **6.** Pterostigma of right hind wing.





Figs. 7, 8. *Eoprotoneura hyperstigma,* new species. **7.** AMNH 44203, adult female, left lateral habitus. **8.** Holotype wings, forewing composite and right hind wing.

megapodagrionids and lestids arising independently from amphipterygids. The latter dichotomies are based on character state polarities as proposed by Carle (1982a, 1982b).

FAMILY PROTONEURIDAE

EOPROTONEURINAE, NEW SUBFAMILY

Figures 4–8

DIAGNOSIS: Anal vein apparently absent, fused to posterior margin of wing; CuP ending just beyond discal brace, crossveins not in alignment over posterior half of wing, pterostigmata well developed subtending 2 cells.

TYPE GENUS: *Eoprotoneura,* n. gen.

ETYMOLOGY: "Dawn" protoneurid, in reference to its relationship with basal Protoneuridae.

Eoprotoneura, new genus

DIAGNOSIS: Origin of IR_3 at proximal postnodal, origin of R_{4+5} at nodus, arculus just distal to distal costal brace, CuP ended one cell beyond discal brace.

TYPE SPECIES: *Eoprotoneura hyperstigma* n. sp.

ETYMOLOGY: See subfamily etymology.

Eoprotoneura hyperstigma, new species

HOLOTYPE: AMNH 44203 (figs. 4–6), part only, lateral view of remains of an adult male including remnants of the head (in cross section), thorax, four legs, reposed overlapped wings with distinct tuberculated pterostigmas, eight abdominal segments and genital pocket and a distinctly tuberculated thoracic and abdominal cuticle. PARATYPES: AMNH 44201 (fig. 7), part only, lateral view of remains of an adult female including the head (dorsal view), thorax, three legs, reposed overlapped wings, abdomen and ovipositor. AMNH 44202 (fig. 8) part only, lateral view remains of a poorly preserved adult female including remnants of the head, thorax, leg, reposed overlapped wings, abdomen and ovipositor.

DESCRIPTION: AMNH 44203: Head ca. 1.4; thorax 4.4 × 2.4 wide; wing 18.0; costal braces present without additional antenodals, nodus at ca. 1/3 wing length, postnodal crossveins 10/8, cells beyond pterostigmata 4/5, pterostigma 1.0/1.2 × 0.4 wide, 2 cells below pterostigma, origin of R_3 10 from base of wings, cell rows between R_2 and R_3 not in alignment, origin of IR_3 at ca. 3/8 wing length at first postnodal, origin of R_{4+5} at nodus, arculus at distal costal brace, CuP fused to wing margin one cell from discal brace, A fused to posterior wing margin for entire length. Abdominal segment II 0.7, segment III 2.0, segment IV 4.1, segment V 4.4, segment VI 4.6, segment VII 0.43, segment VIII 3.5. AMNH 44201: Head 1.3, width across the eyes 2.3; labrum width 0.6; thorax 3.5 × 2.1 wide; wing ca. 16.8; pterostigma 1.1 × 0.4 wide; abdomen 25.0 × 1.0 wide, segment III 3.2, segment IV 4.0, segment V 3.9, segment VI 3.8, segment VII 3.5, segment VIII 1.3, segment IX 1.1, segment X 0.5, ovipositor 1.5. AMNH 44202: Head ca. 0.8, thorax ca. 5.0; wing ca. 17.2; pterostigma 1.2; abdomen ca. 24.5, segment IV 3.9, segment V 3.8, segment VI 3.8, segment VII 3.1, segment VIII 1.2, segment IX 1.1, segment X 1.6, ovipositor 1.8.

DISCUSSION: If *Permagrion falklandicum* Till. is considered to be a Protozygopteran based on the apparent lack of discal nodus or discal brace (Carle, 1982a), then *Eoprotoneura hyperstigma* and *Euarchistigma atrophium* represent the only fossil Coenagrioidea known from the Southern Hemisphere and the first members of the superfamily from the early Cretaceous.[4] Narrow winged Zygoptera with the discal brace perpendicular to main veins (the likely plesiomorphic condition) are also characterized by substantial reduction of CuP and reduction or loss of A, a condition well developed in *Eoprotoneura.* This condition is exhibited in many Zygoptera with Gondwanian origins including: Platystictines, Palaemnematines, Protoneurines, Caconeurines, Disparoneurines, and Isostictines. Concerning the opposite condition, Carle (1982a) has suggested that an oblique orientation of the discal brace typical of many Coenagrioidea and Lestoidea allows the preservation of CuP and A following a narrowing of the wings.

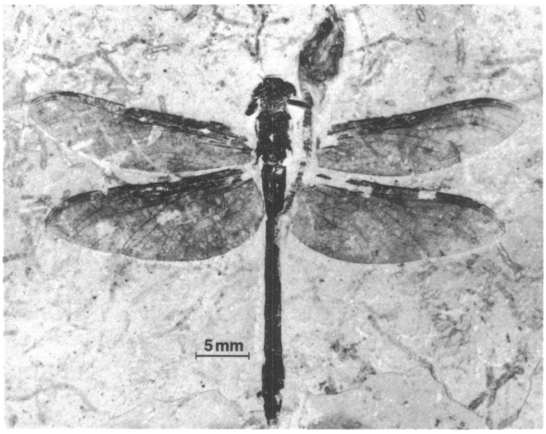
SUBORDER ANISOPTERA

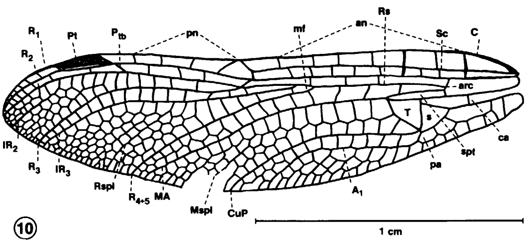
FAMILY GOMPHIDAE

Gomphids comprise the second largest and most ancient anisopteran superfamily; extant subfamilies are Hageniinae, Octogomphinae, Gomphinae, Epigomphinae, Austrogomphinae, Phyllogomphinae, Onychogomphinae, and Lindeniinae (Carle, 1986). The oldest known anisopteran, *Liassogomphus brodiei* (Buckman), is known from the Upper Liassic of England and was placed in the Gomphidae by Handlirsch (1906–1908, 1920, and 1939), although Tillyard (1925) and Carle (1982a) considered it a gomphid-like Anisozygopteran. *Govanogomphus bartheli* Schluter and Hartung (1982) is also a likely Anisozygopteran, the group being identifiable by the different orientation of the discal brace in fore and hind wings. Dimorphisms between fore and hind wings and between male and female wings of Anisopteroids have led to consid-

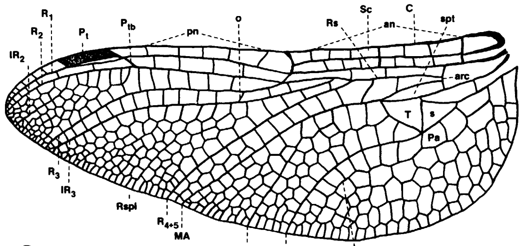
---

[4] However, an apparent megapodogrionid, *Cretacoenagrion alleni* (Jarzembowski, 1990) has been described from the early Cretaceous of England.





⑩



⑪

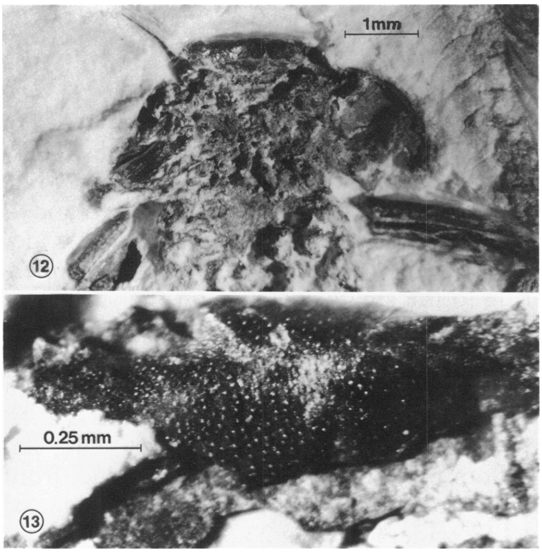
Figs. 9–11. *Cordulagomphus tuberculatus*, new species, holotype, AMNH 43256. **9.** Habitus of nearly complete adult female with fossil fish *Dastilbe* lying just under right forewing, hind wing, and abdominal segments 3 and 4. **10, 11.** Composite camera lucida drawing of fore and hind wings, with venation terminology.

erable taxonomic confusion. For example, *Turanopteron* Printkina (1968) is likely the forewing of *Oreopteron* Prin., Oreopteridae Prin. is likely the male of Asiopteridae Prin., and both are apparently synonymous with Progonaphlebiidae Tillyard (1925). The first indisputable gomphid *Nannogomphus bavaricus* Handlirsch, is known from the Upper Jurassic of Bavaria, and is referable to the Octogomphinae. Other than several large specimens from the Upper Jurassic of Europe and Asia, some of which may be referable to the Hageniinae, no additional adult gomphid fossils are known to the authors, indicating that specimens described herein are the first fossil gomphids known from the Southern Hemisphere.

The majority of extant gomphids inhabit lotic environments and are very unlikely to become fossilized. In this they resemble other relict Odonata as they also inhabit spring seeps and spring-fed rivers or streams. For example, the extant Neopetaliidae and Cordulegastridae are not known in the fossil record, but are the stem groups to lentic adapted Aeshnidae and Libellulidae, respectively, which are well represented in the fossil record.

CORDULAGOMPHINAE, NEW SUBFAMILY

Diagnosis: Small gomphids of Cretaceous Neotropics. HEAD: ligula covered by base of mouthparts; antefrons broad and low, without carina along antedorsal curvature; antefrons (vertex) lost, but shape trapezoidal as determined from adjacent areas; compound eyes widely separated dorsally; occiput rounded without transverse dorsal carina. LEGS: fore tibiae ca. 8 times longer than wide; foretibial comb with 6–7 spines. WINGS: Costal braces present; first postnodal crossvein slanted with anterior end directed proximally; pterostigmal brace present and strongly slanted; proximal edge of pterostigma angled 30–40° from R_1; pterostigma convex posteriorly and shorter than distance between costal braces; midbasal space without crossveins; arculus strongly angulated in forewings, slightly so in hind wings; sectors of arculus widely separated basally; postmedian (intermedian) crossveins 3/2; second crossvein strongly slanted and sigmoid; planates absent; supratriangle convex anteriorly, supratriangular interspace convergent toward wing margin; MA crossveins 1/1; triangles slightly closer to arculus in hind wing; triangles, supratriangles, and subtriangles without crossveins; anal loop present and 2-celled; anal field of hind wing without strong pectinate branches, anal field instead with nearly regular hexagonal cells; anal triangle present; membranule apparently vestigial. ABDOMEN: Female auricles apparently present (recognizable from changes in cuticle tex-



Figs. 12, 13. Detail on holotype of *Cordulagomphus tuberculatus.* **12.** Photograph of left antenna and dorsal surface of antefrons. **13.** Abdominal segment 2 (dorsal view).

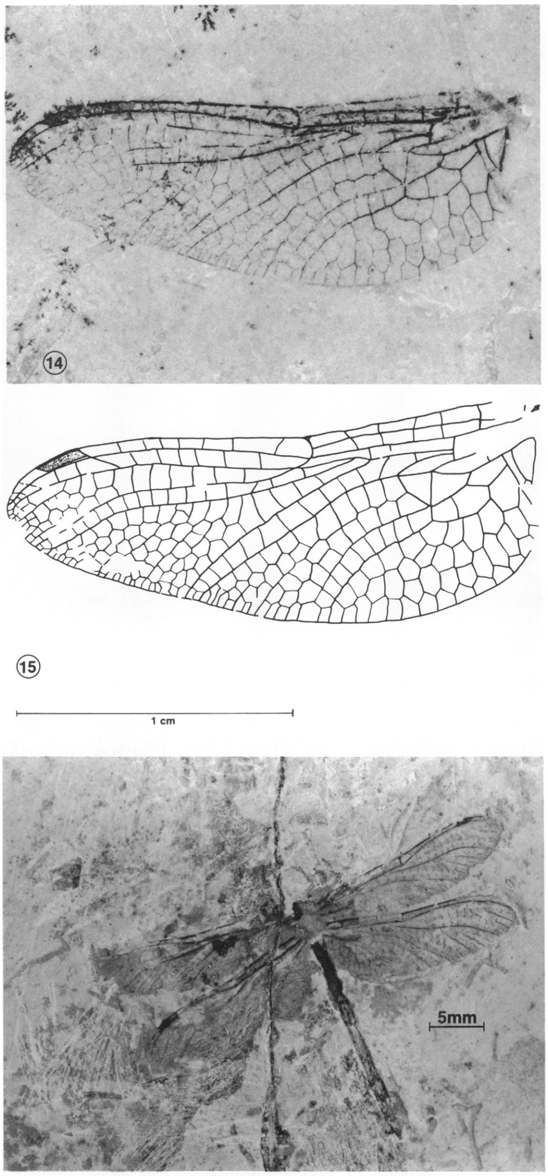
ture); dorsal, lateral, and ventral longitudinal carina absent; male epiproct likely divaricate. GENITALIA: Male genitalia unknown, female ovipositor reduced but apparently complete with metagonocoxae well developed and extended to posterior margin of segment 10.

Type Genus: *Cordulagomphus,* n. gen.

Etymology: Derived from Corduliinae and Gomphidae, referring to the corduline-like convergences in the venation of this gomphid group.

Cordulagomphus, new genus

Diagnosis: HEAD: Distance between antennal bases ca. 2.7 times length of dorsal surface of antefrons; frontal carina absent; occiput rounded, head not tumid posterior to compound eyes. WINGS: basal subcostal crossveins absent; distal costal brace of hind wing at midway between proximal costal brace and nodus; costal braces of forewing separated by twice their length; costa not curved or widened along pterostigma; pterostigmal brace present and strongly slanted; forewing arculus angulate with lower portion perpendicular to CuP, sectors of arculus separated basally by ca. ¼ length of arculus in hind wing; base of forewing distal pleat at ca. 0.52 distance between distal ends of triangle and subnodus, base of distal pleat symmetrical or slightly asymmetrical; apical planate (IR_2) extended basally to distal end of pterostigma, divergent from R_2; R_3 without posterior branch originating slightly distal to



Figs. 14–16. *Cordulagomophus fenestratus,* new species, holotype, AMNH 43262. **14.** Photograph of male hind wing. **15.** Camera lucida drawing of hind wing. **16.** AMNH 44200, habitus of nearly complete but poorly preserved adult female.

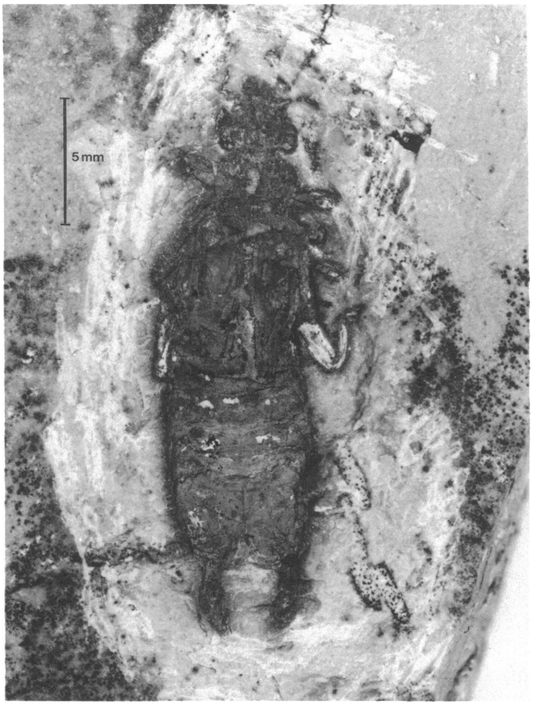


Fig. 17. *Cordulagomphus santanensis,* new species, holotype, AMNH 43258. Photograph of larva.

bridge crossvein; hind wing with 3 postmedian crossveins; anal vein angulated at proximal angle of hindwing subtriangle; CuA brace ca. ⅔ length of posterior side of forewing subtriangle, anterobasal angle of forewing triangle ca. 60°; forewing without triagonal planate; CuP and anal vein not divergent to hind wing margin; anal brace present; anal triangle ca. 1.7 times as long as wide; anal triangle not extended posteriorly to tornus; anal triangle three-celled; cells of anal triangle meet at point. ABDOMEN: Female auricles apparently present. Lateral margins of female terga 7–9 apparently not expanded, sternum 9 apparently membranous, terga 9 and 10 without medial carina, segment 10 with lateral carina apparently absent. Male epiproct likely divaricate. GENITALIA: Vulvar lamina elongate, apparently extended to at least half length of segment 9; metagonocoxae extended from middle of segment 9 to apex of segment 10.

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

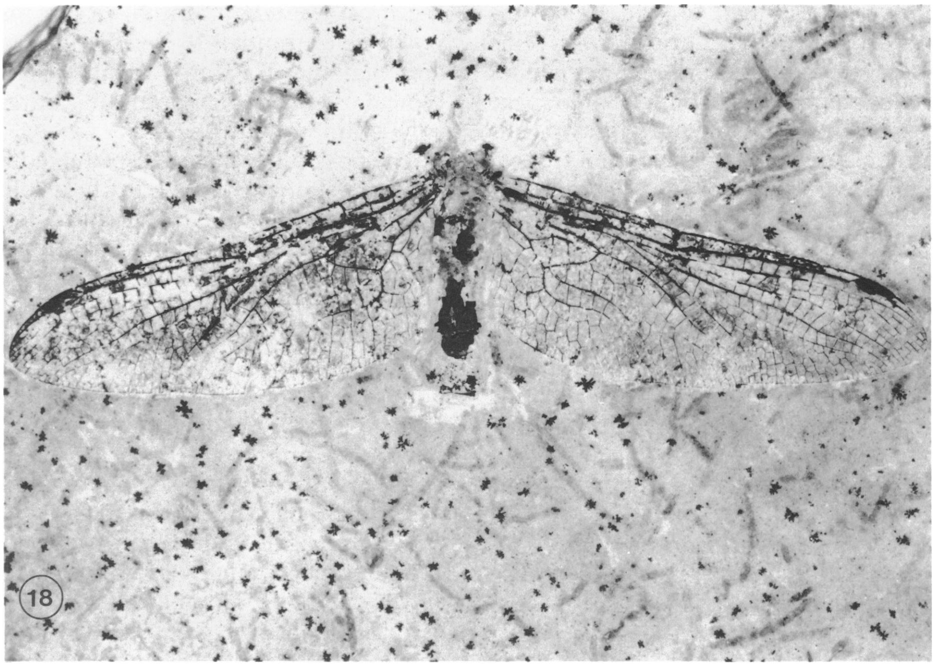
ETYMOLOGY: Same as for subfamily.

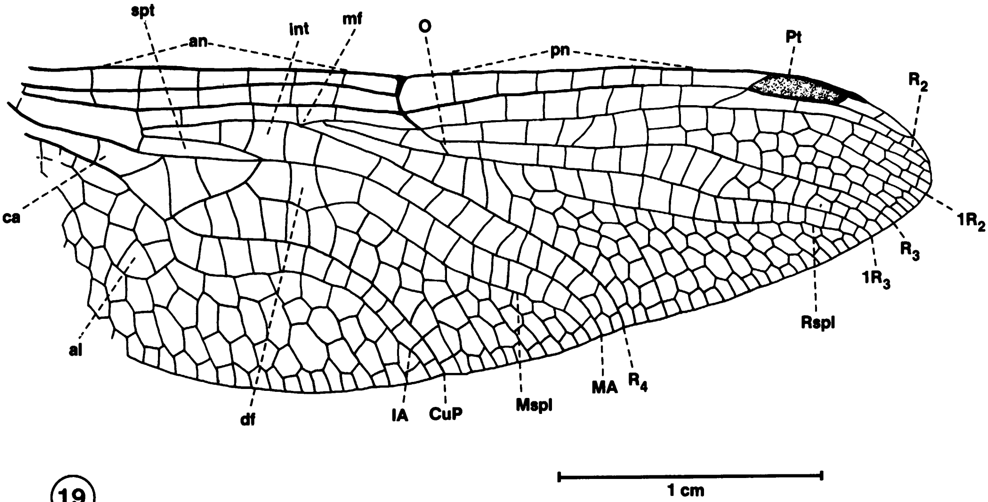
Cordulagomphus tuberculatus,
new species
Figures 9–13

HOLOTYPE: AMNH 43256 part AX-1B; adult female nearly complete, with fish *Dastilbe elongatus* lying just under right forewing, hind wing, and abdominal segments 3 and 4.

ETYMOLOGY: The specific epithet is derived from the adjective tuberculate, referring to the small swellings on the surface of abdominal segment 2.

DESCRIPTION: Total length 33.8, head 2.0 × 4.4 wide, dorsal surface of antefrons 0.5 × 2.2 wide, basal antennal ca. 0.20 × 0.18 wide, second segment ca. 0.13 × 0.06, flagellum 0.9, prothorax 1.3 × 2.5 wide, front femora 2.5, front tibiae 2.5, pterothorax 5.5 × 3.7 wide, forewing 23.3 × 6.0 wide at nodus, hind wing 22.0 × 8.0 wide at nodus, pterostigmata 2.8/2.9, abdomen including cerci 25.7, abdominal segments: I 1.2 × 2.1, II 2.1 × 2.0, III 3.9 × 1.8, IV 3.9 × 1.4, V 3.9 × 1.4, VI 3.4 × 1.5, VII 2.7 × 2.1, VIII 1.5 × 2.0, IX 1.0 × 1.8, X 1.0 × 1.4, cerci 1.0 × 0.4 wide, epiproct 0.4 × 0.9, paraprocts 0.6 × 0.4. HEAD: Dorsal surface of antefrons slightly pitched down to midline; distance between compound eyes ca. 0.8. WINGS: Venation and costa brown; pterostigma light brown; wing membrane shaded with brown, particularly along costal region; basal subcostal crossvein absent; antenodal crossveins 6–7, 9–10/7, 7–8; postnodal crossveins 4/4–5; crossveins under pterostigmata 1/1; bridge crossveins 1–2/2; supratriangular interspace with 2 cell rows toward wing margin; triangles, subtriangles, and supratriangles without crossveins; 3 cells border outer side of triangle; outer side of forewing triangle convex, outer side of hind wing triangle distinctly angulated in interior half; gaff ca. 4/9 as long as inner side of triangle; anal loop 2-celled, distal paranal cell elongate ca. 2.5 times longer than wide; anal field with 4 cell rows beyond anal loop. ABDOMEN: Brown, slightly clubbed, segments IX and X subequal in length; dorsal and lateral surface of segment II tuberculate. GENITALIA: Apparent progonocoxae extended from base of sternum VIII to middle of sternum IX (ca. 0.9 and 0.4 wide at base), where covered by base of apparent metagonocoxae, which is extend-





⑲

Figs. 18, 19. *Gomphaeschnaoides obliqua* (Wighton), holotype, AMNH 43257. **18.** Photograph of adult female hind wings. **19.** Composite camera lucida drawing of hind wing.

ed to apex of segment X (ca. 1.6 × ca. 0.8 wide at base).

Cordulagomophus fenestratus,
new species
Figures 14–16

HOLOTYPE: AMNH 43262, part only, nearly complete male hind wing.

ETYMOLOGY: The specific epithet is derived from the Latin for "having windows," referring to the alignment of antenodal crossveins, which makes the antenodal region appear as a window.

DESCRIPTION: WINGS: Hind wing 19.5 × 6.7 wide at nodus; pterostigmata ca. 2.2; membrane hyaline, with brown venation; basal subcostal crossvein absent; antenodal crossveins 5,5 and aligned, postnodal crossveins 7; pterostigma light brown; crossveins under pterostigma 1 or 2; bridge crossveins 2; triangles, subtriangles, and supratriangles without crossveins; supratriangle interspace with 1 cell row toward wing margin, two cells border outer side of triangle; outer side of hind wing triangle distinctly angulated in anterior half; gaff ca. ⅓ as long as inner side of triangle; anal fields with three cell rows beyond anal loop; anal loop 2-celled; distal paranal cell elongate, ca. 3 times longer than wide; anal triangle 3-celled, with cells meeting at point; anal wing margin smoothly curved to tornus; anal brace short, ca. 2.6.

PARATYPE: AMNH 44200, part only, dorsal view of remains of a poorly preserved adult (female), including remnants of four wings, abdomen, and terminalia.

MEASUREMENTS: Forewing ca. 19.6 × 5.4 wide at nodus; hind wing ca. 18.8 × 5.8 wide at nodus 5.8; abdomen ca. 19.4 × 1.1 wide; anal appendage ca. 1.4.

DISCUSSION: *Cordulagomphus fenestratus* can be readily separated from *C. tuberculatus* by the following characteristics: antenodal crossveins aligned, one cell row in the supratriangular interspace toward wing margin, two cells bordering the outer side of triangle, and three cell rows in the anal field.

South America is unique in its relatively large gomphid faunal component. Gomphids of the Southern Hemisphere are diverse and include Epigomphinae, Austrogomphinae, Phyllogomphinae, Lindeniinae, and a small component of Octogomphinae and Onychogomphinae (Carle, 1986). However, fossil gomphids described herein represent a sister group to extant gomphids, as evidenced by several plesiomorphies including the apparent presence of a reduced yet complete ovipositor. Yet, considerable autapomorphy exists, including a series of regular hexagonal cells in the anal field, reduction of crossveins under the pterostigma, and occasional alignment of antenodal crossveins. These apomorphies parallel Cenozoic evolution within lentic adapted Libelluloidea, suggesting cordulagomphine adaptation to lentic environments. A lentic life style is strongly supported by a gomphid nymph (fig. 17) from the Araripina Formation and the presence of the fossil fish *Dastilbe* just beneath the nearly complete specimen of *C. tuberculatus.* The juxtaposition suggests that the fish (which is the most abundant animal in the insect deposit) was stranded by a receding waterline, and that the dragonfly alighted on it (as is typical of gomphids), becoming mired in the soft sediment with the fish.

The possibility that the Cordulagomphinae represents an early stage in the evolution of more recently derived Anisoptera is unlikely because cordulagomphine venation is more specialized than that of the Cordulegastridae or Neopetaliidae. Adult synapomorphies of the higher Anisoptera not shared with cordulagomphids include the following: compound eyes approximate or contiguous dorsally, postfrons triangular in shape, antefrons raised and produced forward, second antennal segment elongate, sectors of arculus approximate or contiguous basally, medial planate present, abdomen with longitudinal carinae, and triangles of the fore and hind wings distinctly different. In the higher Libelluloidea the inner side of the forewing triangle is shifted distally, making the triangle higher than wide, whereas in the hind wing the proximal side of the triangle is shifted to near the base of the arculus. In the Aeshnoidea the forewing triangle is instead lengthened relative to the long axis of the wing so that the forewing triangle is more elongate than the hind wing triangle.

Cordulagomphus santanensis, new species

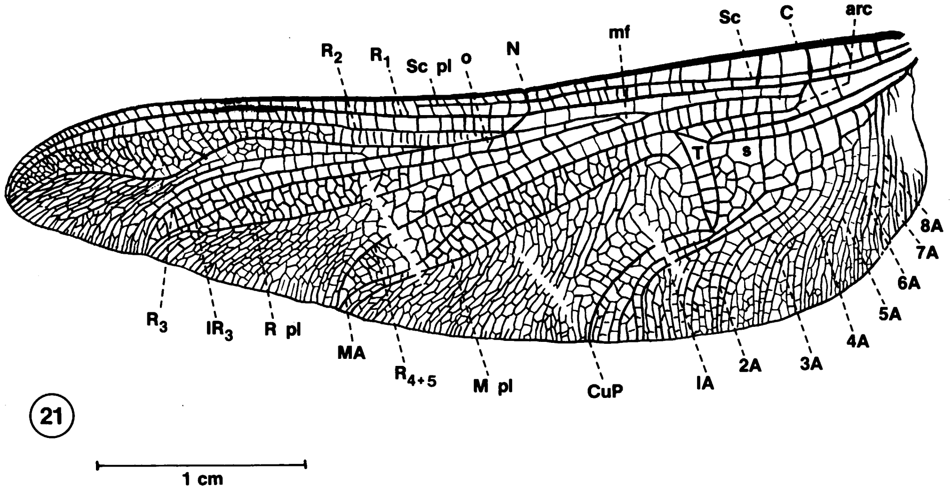
Figure 17

HOLOTYPE: AMNH 43258, nearly complete larva.

ETYMOLOGY: The specific epithet is derived from the latinized form of "Santana," a synonymous name given to the Araripina Formation.

DESCRIPTION: Ca. 23.1 total length; head relatively small, ca. 2.2 (excluding antennae) × 3.1 wide; posterolateral corners of head produced posteriorly; compound eyes small; antenna apparently of the four-segmented gomphid type with third segment spatulate, ca. 1.2 × 0.6 wide; labium short and flat; thorax ca. 5.8 × ca. 4.5 wide; wing pads ca. 5.2; hind femora somewhat flattened; abdomen flattened, without middorsal carina or well-developed lateral spines, ca. 17.4 × ca. 6.0 wide; anal appendages incomplete.

DISCUSSION: The spatulate antennae, long



Figs. 20, 21. *Wightonia araripina,* new species, holotype, AMNH 43268. **20.** Photograph of specimen. **21.** Camera lucida drawing of right hind wing, with venational terminology, ventral view.

femora, and relatively flat abdomen suggest that the nymph was a shallow burrower in soft substrates.

Gomphaeschnaoides, new genus

Figures 18, 19

Gomphaeschna obliqua Wighton, 1987: 312.

Type Species: *Gomphaeschnaoides obliqua* (Wighton).

Diagnosis: Shares several apomorphies with *Cordulagomphus,* including occasional alignment of antenodal crossveins, one crossvein under the pterostigma, pterostigmal brace strongly slanted, weakly developed pectinations of anal vein, rounded rather than elongate anal loop, distal paranal cell very wide, sectors of arculus widely separated basally, and subtriangle well developed (with proximal side not nearly perpendicular to anal

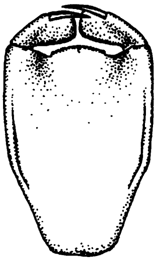


Fig. 22. *Pseudomacromia sensibilis* new species, drawing of labium, dorsal view.

vein). Three apomorphies that *Gomphaeschnaoides* shares with the higher Anisoptera are the presence of planates, the relatively proximal position of the bridge crossvein, and the anteriorly convex curvature of R_3 behind the pterostigma; however, these characteristics have evolved independently in both the Aeshnoidea and Libelluloidea, indicating that a similar trend is likely in Gomphoidea (e.g., planates apparently developed to even out stress posterior to main veins, as evidenced by the occurrence of wing failure in this area in old individuals of extant Gomphidae).

Discussion: The taxonomic position of *Gomphaeschnaoides obliqua* is problematic. Unfortunately, *G. obliqua* is only known from the hind wing of the holotype female (AMNH 43257). A definite Gomphaeschnine fossil does not occur until the Tertiary, represented by *Projagoria conjuncta* Martynov from the Northern Hemisphere, thus matching the extant distribution of the group. Three apomorphies which *Gomphaeschnaoides obliqua* share with higher Anisoptera are the presence of planates, the relatively proximal position of the bridge vein, and the anteriorly convex curvature of R_3 behind the pterostigma. However, these characteristics have evolved independently in both the Aeshnoidea and Libelluloidea, indicating that a similar trend is likely in Gomphoidea. It is also noted that planates apparently develop to even out stress posterior to main veins as evidenced by the occurrence of wing failure in this wing area in old individuals of extant Gomphidae. The proximal position of the bridge vein in *G. obliqua* as in Aeshnidae is apparently due to convergence because the bridge vein is located in an extreme distal position in the annectent Neopetaliidae. Additional fossils which preferably include the forewing of *G. obliqua* are needed to determine its true taxonomic position, but it is here placed within the Cordulagomphinae.

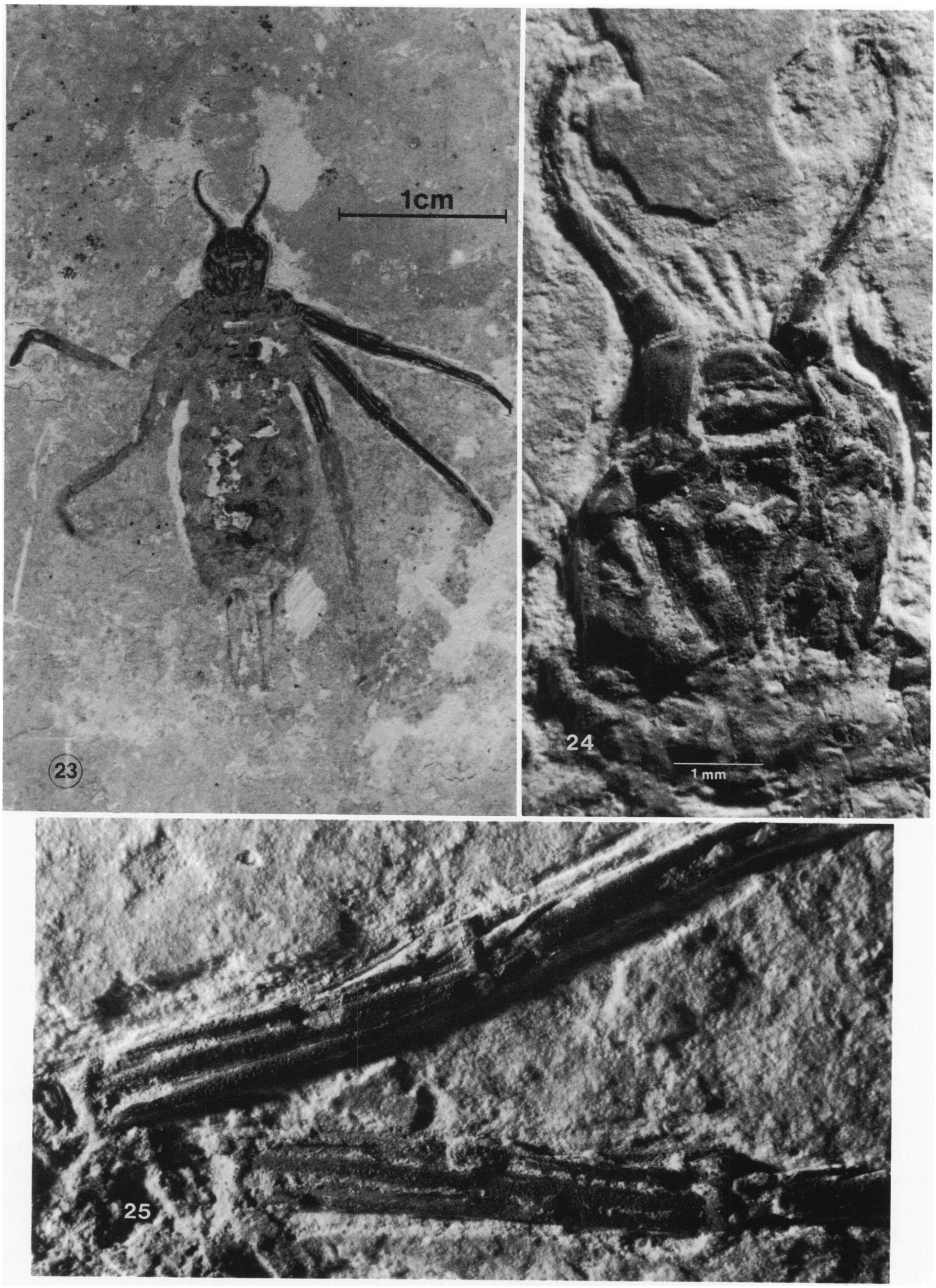
AESCHNIDIOIDEA New Superfamily

Diagnosis: Large extinct anisopterans of the upper Jurassic and lower Cretaceous, body robust, compound eyes widely separated dorsally, intercalated veins numerous, pterostigmata weak or absent, triangles longer than wide and similar in fore and hind wings, lower portion of arculus absent, discal brace located closer to nodus than to wing base, anal loop absent, ovipositor extended well beyond abdominal segment 10.

Discussion: Discovery of the well-preserved and nearly complete hind wing of *Wightonia* allows confirmation of the isolated phylogenetic position of the Aeschnididea suspected by Carle (1982a). The poorly developed arculus, nodus, and pterostigmata, and abundant intercalated veins are unique in the Anisoptera, but similar to conditions in Protodonata, suggesting that they are plesiomorphies. The transversely elongate triangles which are similar in fore and hind wings and have the distal side (upper portion of discal brace) nearer the nodus than wing base are unique to this group, suggesting an early but unfruitful attempt at triangle formation (i.e., the reduction of fluting in the discal region). The unique triangles, well-developed planates, and abundant crossveins are all likely apomorphies suggesting Aeschnidioidea to be a sister group to extant Anisoptera.

FAMILY AESCHNIDIIDAE

This extinct family was recently treated by Schlüter and Hartung (1982), who recognized seven genera: *Aeschnidium* Westwood (1854), *Urogomphus* Handlirsch (1906–1908), *Aeschnidiopsis* Tillyard (1917), *Aeschnidiella* Zalessky (1953), *Sinaeschnidia* Hong (1965), *Leptaeschnidium* Pritykina (1977), and *Aegyptidium* Schlüter and Hartung (1982). The group is fairly compact but highly specialized with a worldwide distribution, being currently unknown only in North America and Antarctica. The nymph is unknown.



Figs. 23–25. *Pseudomacromia sensibilis,* new species, holotype, AMNH 44205. **23.** Larva. **24.** Head, antennae, and tuberculated cuticle. **25.** Right metathoracic femur with longitudinal ribs.

Wightonia Carle, new genus

DIAGNOSIS: Triangle elongate, ca. 5 times as long as wide, one cell row in triangle and between sectors of arculus, one cell row between C and Sc, Scpl 8 cells long beyond nodus, IR_2 strongly undulate, MA undulate but parallel to Mpl near wing margin, RpI strongly convergent to IR_3 and R_3 at wing margin, CuP terminated at wing margin well before nodus.

TYPE SPECIES: *Wightonia araripina* n. sp.

ETYMOLOGY: Named in honor of Dennis Wighton.

Wightonia araripina, new species

Figures 20, 21

HOLOTYPE: AMNH 43268, counterpart only, complete adult right hind wing.

ETYMOLOGY: The specific epithet is derived from the name of the Araripe Plateau in which the holotype was found.

DESCRIPTION: Hind wing 46.0 × 12.0 wide at nodus; triangle ca. 5 times as high as wide and crossed by 5 subparallel crossveins; 1 row of cells between C and R_1; C and R_1 parallel and without deflection for their entire length; bridge vein near the subnodus; Scpl extending 8 cell widths beyond the nodus. In addition: 5 or 6 distinct paranal cells proximal to the subtriangle; pterostigma absent; nodus weak.

DISCUSSION: *Weightonia* is apparently most similar to *Aeschnidiopsis* Tillyard. Tillyard (1917) and Woodward (1884) could only have assumed that the holotype of *Aeschnidiopsis flindersiensis* possessed a pterostigma since that portion of the fossil is missing. Fraser (1957) went even further in his drawing of *Aeschnidiopsis flindersiensis* by illustrating a pterostigma and closed triangle and subtriangle, the area of which is also missing in the type fossil. Riek (1954) described a complete, second hind wing of *Aeschnidiopsis flindersiensis* as having a quadrangular triangle with a short, distinct crossvein closing the triangle and subtriangle, an indefinite pterostigma traversed by crossveins, and the R_1 strongly deflected down and around the pterostigma. There is no such deflection of R_1 in the area where the pterostigma would be located on the referred hind wing.

PSEUDOMACROMIIDAE, NEW FAMILY

DIAGNOSIS: Large anisopterous nymphs of Neotropical Cretaceous, antennae elongate and robust, 6-segmented, and with first and third segments relatively lengthened; prementum flat, without setae, and slightly widened distally with distal margin convex, labial palps medially truncate with well developed moveable end hook, posterior margin slightly convex; frons elevated, labrum ca. 3.5 times as wide as long, legs long with longitudinal ridges, abdomen obovate without dorsal or lateral spines, cerci elongate and slightly incurvate apically, epiproct ca. ½ length of cerci.

TYPE GENUS: *Pseudomacromia*, new genus.

ETYMOLOGY: "False" macromid, referring to this nymph's superficial resemblance to those of the Macromiidae.

Pseudomacromia, new genus

DIAGNOSIS: Same as for family.

TYPE SPECIES: *Pseudomacromia sensibilis* n. sp.

ETYMOLOGY: Same as for family.

Pseudomacromia sensibilis, new species

Figures 22–25

HOLOTYPE: AMNH 44205, part only, preserved dorsal view of remains of a larva possibly in the penultimate instar, including five legs, long robust antennae, remnants and impression of long cerci, remnants of parallel longitudinal veins, abdominal setae and tuberculated cuticle.

ETYMOLOGY: Specific epithet derived from latinized form of "capable of perceiving," to identify the nymph's potential for detecting prey by use of its large antennae.

MEASUREMENTS: Body 21.3 (excluding antennae and lateral spines); abdomen width 7.1; head 4.0 × 3.8 wide, prementum 5.4 × 3.6; thorax 4.1 × 6.1 wide; antenna 4.6, segment I 1.2 × 0.6 wide, II 0.68, III 1.4 × 0.2 wide, IV 0.7, V 0.6, VI 0.4; distance between antennal bases 1.3; prothoracic leg 13.7, femur 5.0 × 0.8 wide, tibia 6.2, tarsal segment I 0.2, II 0.6, III 1.2, pretarsal claw 0.3; mesothoracic leg 14.6, femur 5.6, tibia 6.6, tarsal segment I 0.2, II 0.83, III 1.2; metathoracic leg 18.3, femur 7.4, tibia 6.2; 9th abdominal lateral spine 5.3 × 1.0 wide; epiproct 2.0.

DESCRIPTION: Remnants of parallel wing veins (0.8 long) are visible, cases perhaps extended to abdominal segment III; head, thorax, and legs covered with distinctly tuberculated cuticle; antennae robust, curving inward, 6-segmented, without setae and longer than head; eyes rudimentary; legs robust, long, without setae; femora with 3 longitudinal ribs, each 0.2 wide; metathoracic leg extended to middle of abdominal segment VII; trochanter apparently divided; tarsi 3-segmented; 2 pretarsal claws; abdomen somewhat flattened, apparently covered with short setae; no evidence of middorsal carina; lateral abdominal spines absent, cerci very long, parallel and tapered, approximately equal to total length of last 4 abdominal segments; epiproct less than half length of lateral spines, concave.

DISCUSSION: General similarities to Macromiidae include the almost symmetrical head, small eyes, flattened-obovate abdomen, and long legs. Given the biology and habitat of extant macromiid nymphs as discussed by Corbet (1983), it is suggested that this nymph was a sprawler, perching in thick vegetation or debris near the bottom of low-energy fresh water, using its long cerci as a predator deterrent. The referred nymph is characterized by several plesiomorphic character states including a gomphidlike prementum, petaluridlike labial palps, rudimentary eyes, and large antennae. These characteristics indicate an isolated phylogenetic position within the Anisoptera and because the nymph is apparently lentic adapted it is placed within the Aeschnidioidea, the nymphs of which are unknown. However, the robust fore legs of *Urogomphus* do not match the elongate legs of this nymph.

REFERENCES

Carle, F. L.
1982a. The wing vein homologies and phylogeny of the Odonata: a continuing debate. Soc. Int. Odonatol. (Rapid Commun.) 4: 1–66.
1982b. Thoughts on the origin of insect flight. Entomol. News 93: 159–172.
1986. The classification, phylogeny, and biogeography of the Gomphidae (Anisoptera). I. Classification. Odonatologica 15(3): 275–326.
Carpenter, F. M.
1931. The lower Permian insects of Kansas. Part 2. The orders Palaeodictyoptera, Protodonata, and Odonata. Am. J. Sci. 21: 97–139.
Corbet, P. S.
1983. A Biology of dragonflies. London: Classey Ltd.
Fraser, F. C.
1954. The origin and descent of the order Odonata based on the evidence of persistent archaic characters. Trans. R. Entomol. Soc. London (B) 23: 89–94.
1957. A reclassification of the order Odonata. Sydney: R. Soc. New South Wales.
Handlirsch, A.
1906–8. Die Fossilen Insekten. Wien. Denkschr. Akad. Wiss. Wien 96: 1–82.
1907. Die fossilen Insekten und die Phylogenis der rezenten Formen. Leipzig.
1920. Kapitel 7, Palaeontologie, *In* C. Schroder, Handbuch der Entomologie 3: 117–208.
1939. Neue Untersuchungen uber die fossilen Insekten mit Erganzungen und Nachtragen sowie Ausblicken auf phylogenetische, palaeogeographische und allgemein biologische Probleme. II. Teil. Ann. Naturh. Mus. Wien 49: 1–240.
Hong, Y.
1965. A new fossil dragonfly, *Sinaeschnidia* Hong gen. nov. (Odonata, Insecta). Acta ent. sinica 14(2): 171–176.
Jarzembowski, E. A.
1990. Early Cretaceous zygopteroids of southern England, with the description of *Cretacoenagrion alleni* gen. nov., spec. nov. (Zygoptera: Coenagrionidae; "Anisozygoptera": Tarsophlebiidae, Euthemistidae). Odonatologica 29: 27–38.
Kennedy, C. H.
1920. Phylogeny of zygopterous dragonflies as based on the evidence of the penes. Ohio J. Sci. 21: 25.
Needham, J. G., and J. J. Westfall, Jr.
1955. A manual of the dragonflies of North America (Anisoptera). Berkeley: Univ. California Press.
Pritykina, L. N.
1968. Strekozy karatau (Odonata). *In* B. B. Rodendorf (ed.), Yurskie nasekomye karatau, pp. 26–55, 249, pls. 1–5 excl. Navka, Moscow. [In Russian]

1977. New dragonflies from Lower Cretaceous deposits of Transbaikalia and Mongolia. *In* Mesozoic and Cenozoic faunas, floras and biostratigraphy of Mongolia. Trans. Joint Soviet-Mongol. Palaeontol. Exped. 4: 81–96, 164. [Summary]

Riek, E. F.
1954. A second specimen of the dragon-fly *Aeschnidiopsis flindersiensis* (Woodward) from the Queensland Cretaceous. Proc. Linn. Soc. N.S.W. 79: 61–62.

Riek, E. F., and J. Kukalova-Peck
1984. A new interpretation of dragonfly wing venation based upon Early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character stages in pterygote wings. Can. J. Zool. 62: 1150–1166.

Schlüter, T., and M. Hartung
1982. *Aegyptidium aburasiensis* n. gen., n. sp. (Aeschnidiidae) and *Gondvanogomphus Bartheli* n. gen., n. sp. (Gomphidae), from the presumable lower Cretaceous deposits of southwestern Egypt (Anisoptera). Odonatologica 11(4): 297–307.

Tillyard, R. J.
1917. Mesozoic insects of Queensland. No. 2 Proc. Linn. Soc. N.S.W. 42: 676–692.
1925. The British Liassic dragonflies. Publ. Br. Mus. Fossil Insects 1: 1–38.
1928. The evolution of the order Odonata. Part 1. Introduction and early history of the order. Rec. Indian Mus. 30: 151–172.

Tillyard, R. J., and F. C. Fraser
1938–40. A reclassification of the order Odonata. Australian Zool. 9: 125–169, 195–221, 359–390.

Westwood, J. O.
1854. Contributions to fossil entomology. Proc. Geol. Soc. 10: 378–396.

Wighton, D. C.
1987. *Gomphaeschna obliqua* spec. nov., a new species of Gomphaeschninae from the Lower Cretaceous of northeastern Brazil (Anisoptera: Aeshnidae). Odonatologica 16: 311–314.

Wighton, D. C., and M. V. H. Wilson
1986. The Gomphaeschninae (Odonata: Aeshnidae): new fossil genus, reconstructed phylogeny, and geographical history. Syst. Entomol. 11: 505–522.

Woodward, H.
1884. On the wing of neuropterous insect from the Cretaceous limestone of Flinders River, North Queensland. Autralian Geol. Mag., n. ser. 1: 337–339.

CHAPTER 4. DERMAPTERA

EDWARD J. POPHAM[1]

ABSTRACT

Two fossil earwig specimens from the Lower Cretaceous of the Amazon Basin are described as *Cretolabia cearae*, n. gen. and n. sp. They are considered to belong to primitive labiid stock, because the three thoracic segments are of equal width, and, therefore, are possibly allied to the Gonolabinae. The study of this species casts doubts on the dermapteran affinities of *Protodiplatys fortis* Martynov from the Jurassic deposits of Turkestan.

INTRODUCTION

The work of Bei-Bienko (1936), Martynov (1925), Scudder (1890), Sakai (1976), Fujiyama (1985), and others shows that only about 40 species of fossil earwigs are known. The majority of these species occur in Baltic Amber and the Miocene beds of Florissant, Colorado, and Sado Island, Seki, Japan. The oldest fossil dermapteran is generally accepted as being *Protodiplatys fortis* Martynov from the Jurassic deposits of Turkestan. Two species of Labiinae are known from the Jurassic beds of southern Soviet Union, and Zhou and Chen (1983) have described one species from Zhejiang, China, of Upper Cretaceous age. The discovery of two fossil earwigs from the Cretaceous limestone of Ceará Crato in the Brazilian Amazon Basin is, therefore, of special interest. It is with the descriptions of these fossils and their affinities that this paper is primarily concerned. Martins-Neto (1990, in press) described three new genera of Pygidiocranidae from the Brazilian deposit, close to the site where these two fossil specimens were collected.

ACKNOWLEDGMENTS

I thank Mr. Alan Brindle of the Manchester Museum, England, who has also examined the specimens and confirmed the author's deductions. Mr. Brindle has also kindly enabled the author to examine a wide selection of alcohol-preserved specimens from the main dermapteran families for detailed examination.

TAXONOMY

The specimens are 7.5 and 10.0 mm in length including the cerci, which are 1.5 mm long. Both specimens have the ventral side uppermost. The general similarity between the two could indicate that they belong to the same species; there is an insufficient number of observable characters to prove otherwise. To facilitate an easy reading on the descriptions of a specimen that is lying on its back the words "left" and "right" refer to the actual insect. For example, the "left" antenna is situated on the left side of the insect. The paratype is less well preserved than the holotype, so fewer details are included in its description.

***Cretolabia,* new genus**

ETYMOLOGY: Creto- refers to the Cretaceous age and *-labia* to the labiid affinities of the genus.

DIAGNOSIS: Winged Dermaptera with a forficulid type neck, thoracic segments of equal width, and prosternum narrowed posteriorly.

TYPE SPECIES: *Cretolabia cearae,* n. sp.

***Cretolabia cearae,* new species**

Figures 1, 2

ETYMOLOGY: Specific epithet refers to the type locality, Ceará, Brazil.

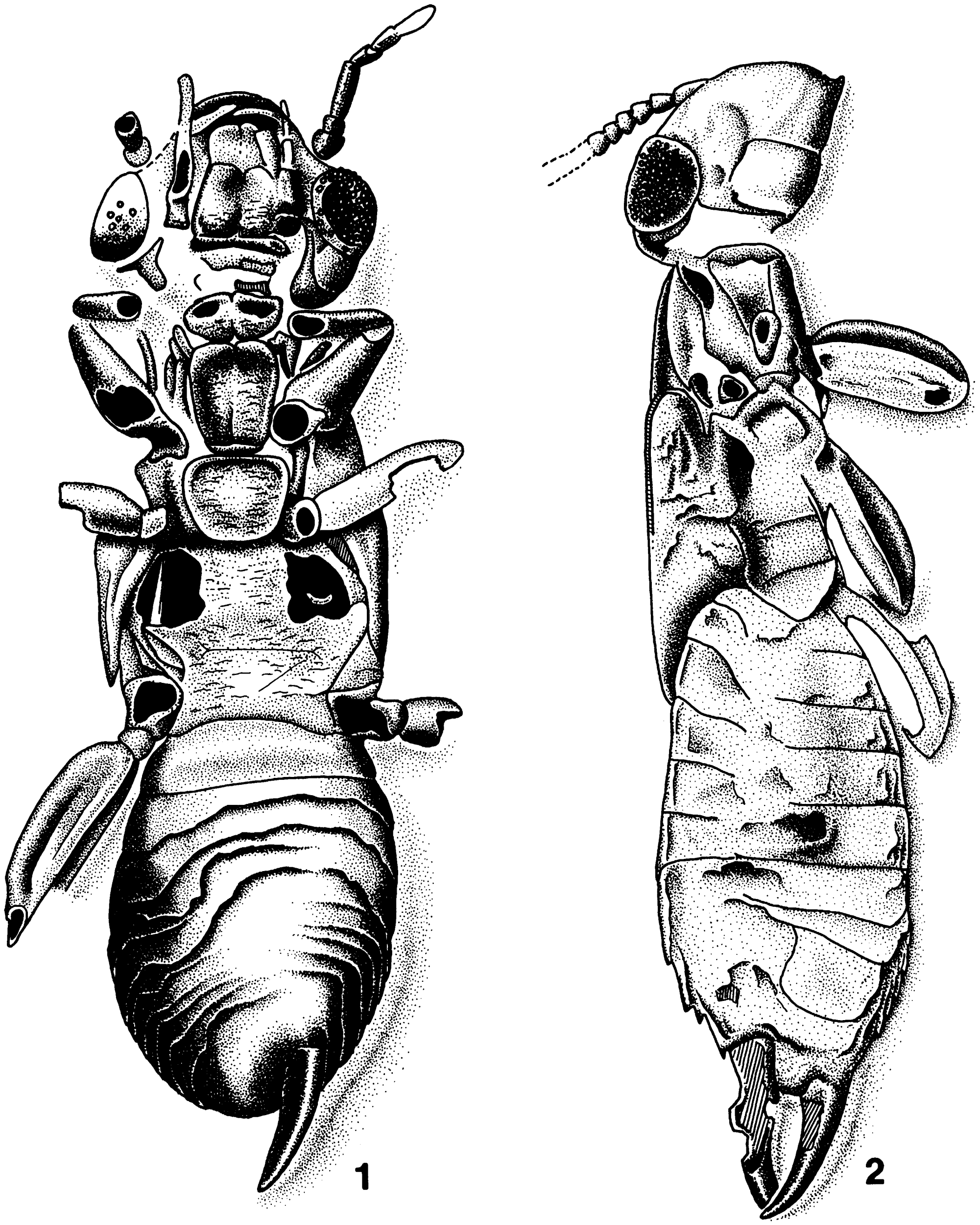
DIAGNOSIS: Abdomen ovoid; other features as in generic diagnosis.

MATERIAL: Specimen no. AMNH 43798 (holotype), AMNH 43799 (paratype).

DESCRIPTION: Holotype (fig. 1) smaller of

---

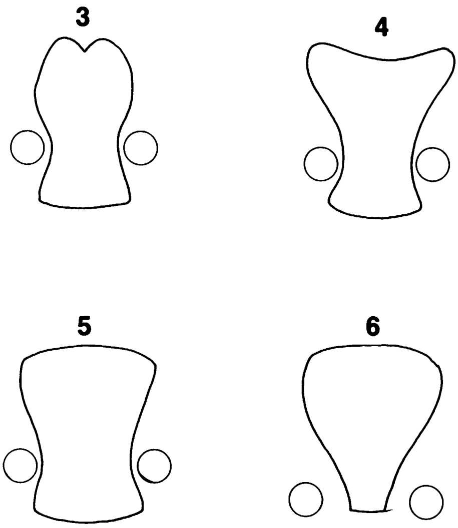
[1] Department of Biology, The University of Salford, England; Chancellor College, The University of Malawi. Presently: 26 Branch Road, Mellor Brook, Blackburn, BB2 7NU, England.



Figs. 1, 2. Habitus illustrations of *Cretolobia cearae* **1.** Holotype (AMNH 43798). **2.** Paratype (AMNH 43799).

two specimens; pale chestnut brown with no signs of any original dark pigmentation. Cuticle well preserved, with fine punctation, which indicates that specimen was sparsely covered with small setae.

Head 1 mm long, 1 mm wide, semiprognathous. Laterally, median portion of head bearing medium-size spherical eye in which many ommatidia can be seen. Left antenna with scape short and 5 cylindrical segments which are broader than long; segments 6 and 7 ellipsoidal (longer than broad). Right antenna with only a few basal segments intact. Labium visible as thin arc, and medially en-



Figs. 3–6. Prosterna of representative Dermaptera. **3.** *Cranopygia* sp. (Pygidicranidae). **4.** *Forficula auricularia* L. (Forficularidae). **5.** *Parisolabis* sp. (Parisolabidinae). **6.** *Gonolabia* sp. (Gonolabidinae).

larged between two mandibles; latter with only outer rims visible. Mandibles highly sclerotized, dark brown, in adducted position with the tip of right mandible slightly anterior to that of the left. Both maxillae situated laterally on each side of the labium. Maxilla with cardo semirectangular, supporting a broad, elongated stipes: left one with the subsidiary sclerites and associated sutures. Medially, each stipes with a crescent-shaped lacinia tapered to a minute apical tooth. Galea thin, maxillary palp 5 jointed, lateral to the left lacinia as seen. Palp segments longer than broad, tapered distally. Of the labium only mentum and submentum present; outlines of glossase apparent. Labial palps not apparent. Gular sclerite broad, articulated with postocciput. Occipital sulcus clearly visible on the left side of the head, lateral to left maxilla and posterior to compound eye.

Neck with narrow transverse anteroventral cervical sclerite, posteroventral cervical sclerite much broader, forming "forficuloid type" neck. Each ventral sclerite with a median depression, giving the appearance of left and right halves on the sclerite; this region has probably been medially indented during fossilization. Base of posterolateral cervical sclerite and a small accessory cervical sclerite visible on right side of neck. Thoracic segments of equal width, metathorax slightly longer than other segments. Prosternum large, elongated, slightly rounded anteriorly and tapered posteriorly to a straight truncated posterior margin (partially heart shaped). Epimeron visible on each side of prosternum. Right side of specimen with edge of pronotum in line with edge of elytron, indicating pronotum is as wide as pterothorax. Procoxae damaged, only circular walls visible. Left profemur flattened, with a longitudinal depression. Tibia semicylindrical, flexed anteriorly toward the midline. No tarsi preserved. Right hind femur present, but tibia seems buried in surrounding matrix.

Mesosternum squared, with rounded corners. Posteriorly on each side is a circular-shaped coxa and flattened femur. Small accessory trochantin and precoxal sclerites anterior to right mesocoxa. Side of meso- and metathorax partially covered by ventral prolongation of elytra. Metasternum large, damaged on each side immediately posterior to mesocoxae. Some leg muscles visible on right side. A small precoxal sclerite anterior to each metacoxa, trochantin narrow and posterior to sclerite. Metathoracic femur flattened, with a longitudinal furrow. Abdomen oval. First sternite large, others posterior to it damaged. Segmental junctions of sternites and tergites visible laterally. Only left cercus remains. Cercus thin, conical tapered, medially and distally.

PARATYPE (AMNH 43799; fig. 2): Anteriorly lying on its side, posteriorly slightly twisted with ventral surfaces of metathorax and abdomen exposed. Most sclerites damaged and fragmentary, with only dark brown markings indicating positions of various sclerites. Right eye oval, situated near posterior occiput, suggesting the head is only slightly prognathous (Popham, 1959). This is supported by the mouthparts directed forward and downward (details of mouthparts not discernible). Scape of right antenna missing, but six flagellomeres preserved with matrix depression indicating that distal segments were ellipsoidal. Anteroventral cervical sclerite narrow, posteroventral cervical sclerite larger. Prosternum damaged, but tapered posteriorly like that of holotype. Trochantin

Table 1
Features Used in Dermapteran Higher Classification (Fig. 7)

	Apomorphic	Plesiomorphic
1	Tarsi 3 segmented	Tarsi 5 segmented
2	Cerci segmented, but segments fused	Cercal segments separate and not fused
3	Cercal segments fused and showing segmentation	Cerci segments separate and not fused
4	Thoracic and abdominal segments slope forward	Thoracic and abdominal segments vertical
5	Forficuloid neck	Blattoid neck
6	Prothorax narrower than pterothorax	Thoracic segments of equal width
7	Wings absent	Wings present
8	Prosternum subcordate in shape	Prosternum slightly constricted near prothoracic coxae (fig. 3)
9	Abdomen dorsoventrally oval (e.g., figs. 1, 2)	Abdomen parallel sided

triangular, appears anterior to the procoxa, but other sclerites missing. Right prothoracic leg with coxa, trochantin, femur, and tibia well developed; other segments missing. Mesosternum squarish, distorted, and damaged. Midfemur, trochanter, and tibia preserved. Metasternum large, but distorted and damaged. Abdomen oval with ventral side up. Most abdominal sclerites missing but positions are clearly indicated. Right side shows junctions of sclerites; tergites appear to alternate with sternites of same segment. This characteristic feature of the Dermaptera (Forficulina) is due to the thoracic and abdominal segments slanting forward instead of being vertical as in most insects. Sternite 10 visible as a broad band, posteriorly bearing both cerci similar in shape to the one in the holotype. Right cercus slightly damaged. Between bases of the cerci is a broadly truncated pygidium distally bearing a small, narrow, brown metapygidium.

AFFINITIES OF *Cretolabia cearae*

The majority of Dermaptera fossils have been found in the Tertiary deposits of North America and Europe and closely resemble modern taxa. Only a minority of fossil species have been found in Cretaceous and Jurassic deposits. Of the new species of fossil dermapterans which Martins-Neto is describing, one shows the greatest similarity to the species here described. Although his description states that the abdomen is oval in shape—as seen in dorsal view—this claim is only supported by his figure 1B, while his figures 1A and 1C show the abdomen to be more rectangular in outline. The oval-shaped abdomen is very rare among dermapterans but occurs in the Gonolabinae. It is, therefore, likely that Martins-Neto's description for this new genus and species is based on specimens belonging to more than one species, if not genera. Further investigations should resolve this matter. The "forficuloid" type neck in *C. cearae,* in which the posteroventral cervical sclerite is substantially longer than that of the anteroventral cervical sclerite, shows that this species belongs to either the Labioidea or Forficuloidea. It does not belong to the Pygidicranoidea, which have a neck with two narrow, transverse ventral cervical sclerites (Popham, 1959, 1985). Nor does it have carcinophorid affinities. The subfamilies of the Carcinophoridae (Anisolabidae) are wingless, and show a primitive level of dermapteran organization by having the three thoracic segments of equal width, as in *Cretolabia.* Martins-Neto (1990, in press) claimed that his specimens are pygidicranids. This is mainly based on the plesiomorphic form of the antennal segments, which is not diagnostic of this taxon. The main apomorphic features, diagnostic of the pygidicranid subfamilies, are the form of the male genitalia, and of the neck, neither of which he was able to examine: the first because the male genitalia are hidden in a genital pouch and the second because the specimen was preserved with its ventral side facing downward. In contrast, it was possible to examine the necks of the specimens used in the present investigation because the insects lay partly on their left side.

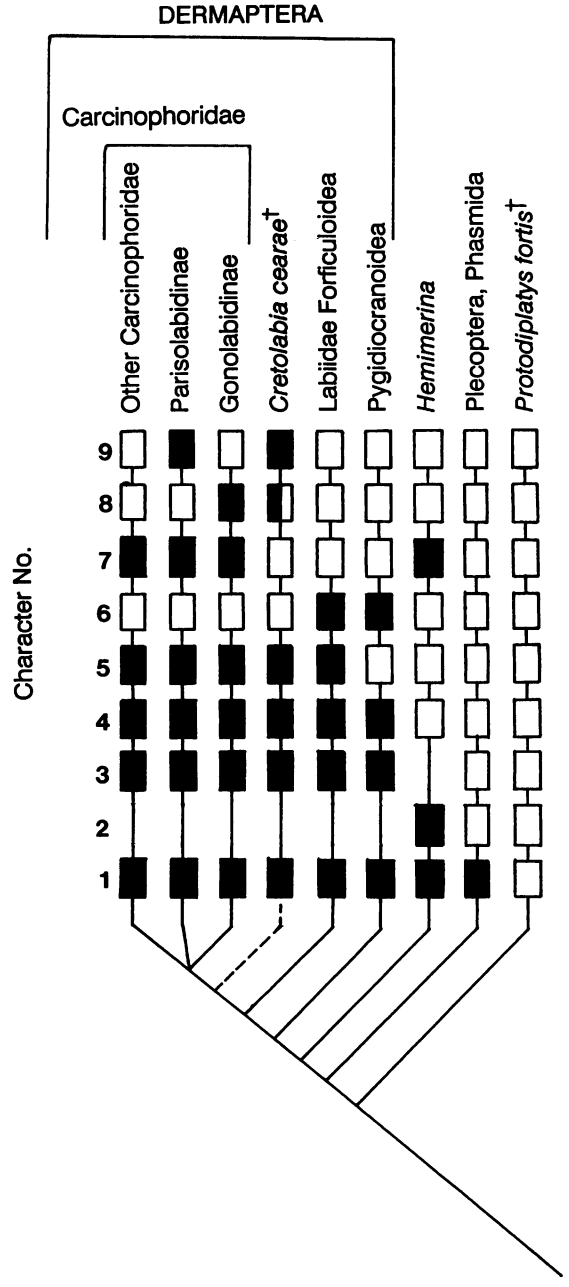


Fig. 7. Cladogram of relevant taxa indicating the systematic position of *Cretolabia cearae* (see table 1 for discussion of character numbers). ■ = plesiomorphic features; □ = apomorphic features.

Martins-Neto's suggestion that his specimens show affinities to the Echinosomatinae is unlikely in view of the absence of this subfamily in South America, while *Echinopsallus guttera* Bormans does not belong to the Echinosomatinae but to the Pyragrinae. Martins-Neto (in press, 1990) made no mention of the important monographs of Hincks (1956, 1959) on the pygidicranid subfamilies, nor did he refer to any of the works of Brindle, Popham, Sakai, or Steinmann. The absence of references to these important papers is sufficient to cast doubt on the validity of his systematic diagnoses. In the Labiidae (Spongiphoridae) and the Forficuloidea, the pterothoracic segments are larger and wider than that of the prothorax, no doubt because of the winged condition. The carcinophorid subfamilies Parisolabidinae, Brachylabinae, and Carcinophorinae each have a circumtropical distribution, suggesting that the apterous condition of these taxa was probably acquired before Gondwanaland disintegrated at the end of the Jurassic. In this scenario, it would be unlikely for *C. cearae* to be closely related to any of these subfamilies and, thus, the ovoid abdomen in *C. cearae* and of the Parisolabidinae must be due to parallel evolution.

In most dermapterans the prosternum is elongated with the bases of the coxae situated, one on either side, slightly anterior to the rear margin of the prosternum. The prosternum is usually narrowed posteriorly as far as the bases of the coxae and then slightly expanded posteriorly. This primitive type of dermapteran prosternum occurs in many subfamilies ranging from the Pygidiocraninae (fig. 3) to the Forficulinae (fig. 4) and Parisolabidinae (fig. 5). The Gonolabidinae (Carcinophoridae) are characterized by widely separated coxae and no posterior widening of the prosternum, making it somewhat heart shaped (fig. 6). The subcordate form of the prosternum of *C. cearae* would suggest affinities with the Gonolabidinae, which are known only from South America.

There is no direct evidence that *C. cearae* has affinities with the Forficuloidea, which occur predominantly in the Old World. These are mainly larger species than members of the Labiidae. The balance of evidence indicates that *Cretolabia* is a primitive Labiid, which has retained the generalized thorax form. Thus, the semicordal shape of the prosternum and the oval form of the abdomen are specializations of this genus and the presence of similar features in other earwigs is probably due to convergent evolution.

All the species described by Martins-Neto show Labiid affinities but have the three thoracic segments of equal width. This, with the evidence contained in this paper, points to the existence of a primitive group of winged Labiids in the Amazon Basin during the Lower Cretaceous. *Cretolabia cearae* is one of the few known Mesozoic fossil earwigs and shows affinities with other fossil Labiinae, like *Semenoviola obliquotruncata* Martynov and *Dermapteron incerta* Martynov from the Jurassic deposits of Turkestan. *Protodiplatys fortis,* also from Turkestan, differs from these and other earwigs in having (1) well-developed segmentation on the cerci; (2) most of the abdominal tergites situated vertically over the sternites of the same segment (though a few of the anterior tergites lie slightly anterior to the corresponding sternites), and (3) five-segmented tarsi. Handlirsch (1908) suggested that the three-segmented tarsus represented the primitive Pterygote condition and that the presence of five jointed tarsi in the Orthoptera, Dictyoptera, Isoptera, and Endopterygote orders is the derived condition. (The reduction of the tarsal joint numbers in the Hemiptera, Mallophaga, Thysanoptera, and Siphonaptera is probably associated with their relatively immobile habits.) The alternative hypothesis of Tillyard (1931) is that the Pterygota originally possessed five-jointed tarsi and that the presence of three-jointed tarsi in the Dermaptera and Plecoptera is a later reduction. Which ever view is accepted, the features of *Protodiplatys fortis* make its alleged dermapteran affinities open to doubt. When Martynov described *Protodiplatys fortis* in 1925, the Dermaptera and Blattida were regarded as being closely related taxa, but more recent work by Hennig (1953), Giles (1963), Kristensen (1975), and others has shown that this view is no longer tenable. For these reasons, the primitive nature of dermapteran organization exhibited by *Cretolabia cearae* is of special interest.

The mutual affinities of the various dermapteran taxa, including *Cretolabia cearae,* can be summarized using the following apomorphic and plesiomorphic features described in the text, in table 1, and figure 7.

DISCUSSION

The presence of fossil Labioids from the deposits of Cretaceous and late Jurassic age points to a much earlier origin of the Dermaptera than had previously been thought. Consideration of the present geographical distribution of the Labioidea supports this view. The subfamilies Parisolabidinae, Brachylabidinae, Carcinophorinae, and Labiinae are distributed from New Zealand and the eastern continental fragments of the Australasian Plate through India and the Oriental Region, Africa, to South America. This suggests that these subfamilies (including those that are apterous) were widely distributed throughout Gondwanaland before it started to disintegrate at the end of the Jurassic (Smith and Briden, 1977). Of the Pygidocranid subfamilies only the Pygidicraninae, Echinosomatinae, and Diplatyinae have circumtropical distributions in the southern continents. The absence of any Pygidicranids on the Australian Plate east of Australia is of special interest. The occurrence of the Esphaleminae in South Africa and in the southern regions of South America and of the allied Blandicinae in South Africa and Madagascar shows these taxa were present in areas as Gondwanaland was dividing in the early Cretaceous. The Labiduridae and the Forficulidae are widespread in Africa, Madagascar, and the Oriental Region but are represented by only a few genera and species in South America. This suggests that this superfamily had just reached South America before its separation from Africa. The subfamilies Allostethinae, Apachyinae, and Chelisochidae have an Afro-Oriental distribution, indicating their presence in this region of Gondwanaland by the end of the Jurassic. Many of the minor Dermapteran subfamilies are restricted to one of the southern continents, but how far they represent post-Jurassic developments is a matter for further study and investigation.

REFERENCES

Bei-Beinko, G. J.
1936. Faune del'URSS, Insectes Dermaptera.

Fujiyama, T.
1985. Early Miocene insect fauna of Seki, Sado Island, Japan, with notes on the occurrence of Cenozoic fossil insects from Sado to San-in District. Mem. Nat. Sci. Mus. (Tokyo) 1: 35–55.

Giles, E. T.
1963. The comparative external morphology and affinities of the Dermaptera. Trans. R. Entomol. Soc. London 115: 95–164.

Handlirsch, A.
1908. Die fossilen Insekten und die Phylogenie der rezenten Formen. Leipzig.

Hennig, W.
1953. Kritische Bemerkungen zum phylogenetischen System der Insekten. Beitr. Entomol. 3: 1–85.

Hincks, W. D.
1956. A systematic monograph of the Dermaptera of the world, based upon material in the British Museum (Natural History). Part one. Diplatyinae. London: British Mus.
1959. A systematic monograph of the Dermaptera of the world, based upon material in the British Museum (Natural History). Part two. Pygidicranidae excluding Diplatyinae. London: British Mus., 218 pp.

Kristenson, N. P.
1975. The phylogeny of hexapod "orders." A critical review of recent accounts. Z. Zool. Syst. Evolforsch. 13: 1–44.

Martins-Neto, R. G.
1990. (in press) Primeiro registro de Dermaptera (Insecta: Orthopteromorpha) na formacao Santana (Cretáceo Inferior), Bacia do Araripe, nodeste do Brasil. Rev. Bras. Entomol. 34.

Martynov, A.
1925. To the knowledge of fossil insects from the Jurassic beds of Turkestan. Bull. Acad. Sci. Russie 19: 572–576.

Popham, E. J.
1959. The anatomy in relation to feeding habits of *Forficula auricularia* L. and other Dermaptera. Proc. Zool. Soc. London 133: 251–300.
1985. The mutual affinities of the major earwig taxa (Insecta, Dermaptera). Z. Zool. Syst. Evolutions forsch. 23: 199–214.

Sakai, S.
1976. Dermapterorum catalogus preliminarie VIII: A basic survey for numerical taxonomy of the Arixeniidae and the Hemimeridae, the Dermaptera of the world with notes on some fossil species. Special Bulletin 8: 1–47. Tokyo: Daito Bunka Univ.

Scudder, S. H.
1890. The Tertiary insects of North America. Rep. U.S. Geol. Surv. Territories 3: 202–215.

Smith, A. G., and J. C. Briden
1977. Mesozoic and Cenozoic paleocontinental maps. Cambridge Univ. Press.

Tillyard, R. J.
1931. The evolution of the class Insecta. Pap. Proc. R. Soc. Tasmania, 1930: 1–89.

Zhou, W., and G. Chen
1983. On the discovery of a fossil insect from Zhejiang (Dermaptera). Entomotaxonomia 5: 61–62.

CHAPTER 5. ISOPTERA

KUMAR KRISHNA[1]

ABSTRACT

A new fossil species of termite, *Meiatermes araripena,* is described from the Santana limestone formations of Brazil, assigned to the Aptian to lower Albian of the Lower Cretaceous period, ca. 110 million years ago. This is the first record of the subfamily Hodotermitinae from the Neotropical region.

INTRODUCTION

Isoptera is an ancient order, regarded as the sister group to the Blattodea (cockroaches) (Hennig, 1969). The worldwide distribution of the Isoptera suggests an origin in the Paleozoic (Permian) or early Mesozoic (Triassic), before the breakup of Gondwanaland (Emerson, 1955, 1967, 1968; Emerson and Krishna, 1975). Of the approximately 70 recognized and described fossil species, however, the great majority are reported from the Cenozoic (Tertiary: Eocene and later); only three have been recorded from the Mesozoic (Cretaceous). (Because of erroneous identifications of specimens of other insect orders as Isoptera, early reports of fossil termites in Paleozoic [Permian] deposits are all incorrect.)

The first report of a fossil termite from the Cretaceous (Mesozoic) was by Emerson (1967) from the Cenomanian (early Upper Cretaceous, ca. 95 million years) of Labrador; it was described as a new subfamily, Cretatermitinae, new genus and new species, *Cretatermes carpenteri.* Since Emerson's report (1967), two additional fossils from the Cretaceous have been described: *Valditermes brenanae* by Jarzembowski (1981), a new genus and species from the Weald clay (Neocomian: (?)Hautervian, ca. 120 million years) of Surrey, England, and, more recently, *Meiatermes bertrani* by Lacasa-Ruiz and Martinez-Delclòs (1986), as a new genus and species from lithographic limestone (Neocomian: Upper Berriasian to Lower Valanginian, ca. 130 million years) from Montsec, Lleida, Spain.

In addition, a few undescribed fossil termites have been reported or recorded from the Cretaceous: in Lebanese amber (Aptian to Necomian, ca. 110–130 million years) (Acra et al., 1972; Schlee and Dietrich, 1970; Schlee, 1972; Schlee and Glöckner, 1978); in Siberian Senonian amber (ca. 80 million years) (Zherikhin and Sukatsheva, 1973); and in French Cenomanian amber (ca. 100 million years) (Schlüter, 1975, 1978). These undescribed fossils await further study, identification, and placement in proper taxa.

The new species described in this paper is the fourth fossil termite to be described from the Cretaceous Period and the first record of the subfamily Hodotermitinae from the Neotropical region.

ACKNOWLEDGMENTS

The author wishes to thank Ms. Peling Fong and Ms. Joan Whelan of the Interdepartmental Laboratory, American Museum of Natural History, for their help in the operation of the scanning electron microscope.

FAMILY HODOTERMITIDAE[2]

SUBFAMILY HODOTERMITINAE

Meiatermes araripena, new species

Figures 1–3
Table 1

IMAGO (figs. 1–3): Total body length without wings small, about 8.0 mm. Head small,

---

[1] Research Associate, Department of Entomology, American Museum of Natural History; Professor of Biology, City College, City University of New York.

[2] The family Hodotermitidae is considered by Snyder (1949), Emerson (1967, 1968), and Krishna (1970) to include the subfamilies Termopsinae, Porotermitinae, Stolotermitinae, Cretatermitinae, and Hodotermitinae. Grassé (1949) and some other authors have divided the

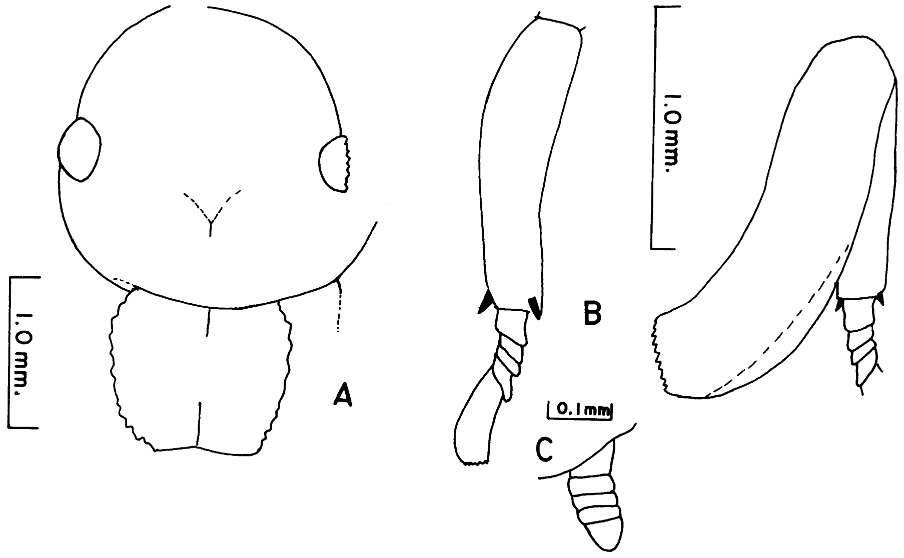


Fig. 1. A–C. *Meiatermes araripena*. **A.** Partial head and pronotum of imago (no. 43903) in dorsal view. **B.** Forelegs of imago (no. 43903), with five tarsal segments. **C.** Cercus of imago (no. 43901).

roundish, Y-suture faintly visible (figs. 1A, 2A, B). Eyes small, semicircular, protruding slightly beyond head capsule (figs. 1A, 2A, B), not concave in front as in *Archotermopsis wroughtini* (Desneux) (Emerson, 1933). Ocelli absent. Antenna with only 3 segments preserved; first long, second and third subequal. Pronotum not preserved in holotype; in specimens 43901 and 43903, partially preserved, appears as wide as head, front margin widely concave. Legs not preserved in holotype; foretibia in specimen 43903 with at least 2 apical tibial spurs clearly visible; tarsi with 5 segments clearly visible (figs. 1B, 2C) (in the fossil genus *Termopsis,* 5-segmented; in *Archotermopsis* and other extant genera of Termopsinae, imperfectly 5-segmented [Emerson, 1933]; in the fossil genus *Ulmeriella* of Hodotermitinae, apparently 5-segmented [Emerson, 1968]; in all other extant genera of Porotermitinae, Stolotermitinae, and Hodotermitinae, 4-segmented). Cerci in specimen 43901 not completely visible, but probably with 5 segments (fig. 1C). Fore and hind wing membrane with reticulations (archidictyon) between veins. Forewing scale in holotype partially preserved, detached from wing; costal border distinctly convex (in *Ulmeriella* straight or faintly convex); humeral suture not clearly visible in specimen 43901, but apparently straight (fig. 3), as in *Porotermes* and *Stolotermes.* Forewing (fig. 3) with region between costal margin and main branch of Rs very wide apically, about 0.60 mm, much wider than in *Cretatermes*; R_1 faintly visible in holotype; Rs prominent, with 5 or 6 superior branches, 2 or 3 inferior branches, and some secondary branches fanning out to occupy most of the apical area (fig. 3), typical of Hodotermitinae; M joining Rs in basal fifth of wing; Cu with two branches preserved. Hind wing (fig. 3) with Rs similar to forewing, occupying a wide area in the apical region; Sc, R_1, R_{2+3} clearly preserved in holotype; M joining Rs in basal fifth; vein visible below M, not clear whether a branch of M or of Cu.

SPECIMENS: Number 43902 (holotype) imago, with damaged head in dorsal view in relief and fragments of middle and apical region of fore and hind wing; 43901 (paratype) com-

---

family Hodotermitidae into two: Termopsidae, the dampwood dwellers, to include the subfamilies Termopsinae, Porotermitinae, Stolotermitinae, and ?Cretatermitinae; and Hodotermitidae, the harvesters, to include only the subfamily Hodotermitinae. In this paper, the family Hodotermitidae is treated sensu Snyder, Emerson, and Krishna.

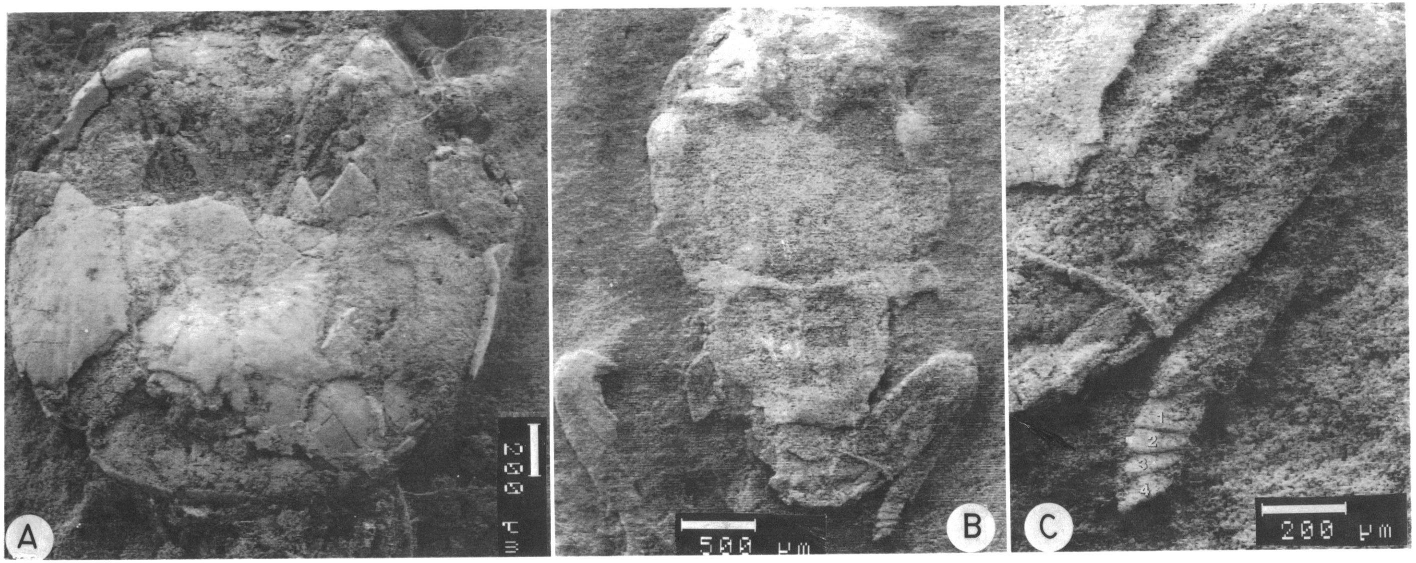


Fig. 2. A–C. *Meiatermes araripena*, SEM electronic digital images of uncoated specimens (low kV [1.0]). **A.** Head of holotype (no. 43902) in dorsal view. **B.** Head, pronotum, and legs of imago (no. 43903) in dorsal view. **C.** Foreleg of imago (no. 43903), showing four tarsal segments (fifth not preserved).

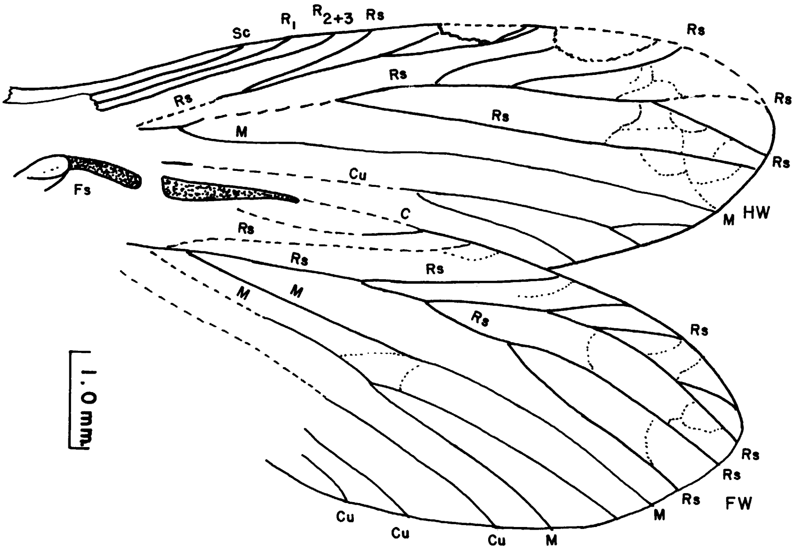


Fig. 3. *Meiatermes araripena.* Fore and hind wing of holotype (no. 43902). C, costal margin of forewing; Fs, forewing scale; FW, forewing; HW, hind wing.

plete imago with wing fragments in dorsal view in relief, left legs folded, and cerci visible; 43903 (paratype) imago head and pronotum in dorsal view in relief, left and right foreleg with tibia and tarsal segments, middle or hind leg, and fragments of middle portion of wings.

ETYMOLOGY: This species is named after the Araripe Plateau, where it was collected.

DISCUSSION: Unquestionably, *Meiatermes araripena,* n. sp. belongs to the Hodotermitidae, as it has a combination of preserved characters—the absence of ocelli and the presence of five-segmented tarsi and five-segmented cerci—that are unique to this family. There are other characteristics that distinguish the Hodotermitidae, such as the imago mandible dentition, which, in the primitive genera of the Hodotermitidae (*Archotermopsis, Stolotermes, Ulmeriella*) is, in fact, even more primitive than that of the Mastotermitidae and similar to the blattoid dentition, but, unfortunately, none of these characteristics are preserved in these specimens.

The new species has characteristics which clearly place it in the subfamily Hodotermitinae—a wide area occupied by the radial sector in the outer fourth and inferior branches reaching the inner margin of the wing—and not in any of the other subfamilies of the Hodotermitidae: Termopsinae, Stolotermitinae, Porotermitinae, or Cretatermitinae.

Even though in the Termopsinae, the fossil genus *Termopsis* clearly has five-segmented tarsi and the extant genera *Archotermopsis, Zootermopsis,* and *Hodotermopsis* have imperfectly five-segmented tarsi, the wing venation of this subfamily is very different from that of Hodotermitinae. Also, in Termopsinae, the wings are much longer than those of the new species, the area occupied by the radial sector is proportionately narrower, the radial sector runs parallel to the costal margin, and, in the middle portion of the wing, the median is closer to the cubitis than to the radial sector.

In both the Porotermitinae and Stolotermitinae, in contrast to the new species, the tarsi are four-segmented, the radial sector runs close and almost parallel to the costal margin throughout the length of the wing, its superior branches are not secondarily branched, and a few weak inferior branches reach the inner border of the wing below the median vein.

This new species does not belong to the Cretatermitinae, a subfamily created by Emerson (1967) for his new genus *Cretatermes,* because in the new species the field occupied by the radial sector is much wider both in the fore and the hind wing, the radial sector has more branches, and the median vein branches out of the radial sector closer to the basal third of the wing in both the fore and the hind wing.

Jarzembowski (1981) described the genus *Valditermes* and placed it in the Cretatermitinae (Hodotermitidae). However, in 1984 he described the hind wing of *Valditermes brenanae* as possessing an anal lobe and lacking a humeral suture, characteristics that distinguish the family Mastotermitidae. Further, his figure 16 (1984: 76) shows that in the forewing, the area occupied by the radial sector is narrow apically, more like that of Mastotermitidae than the Cretatermitinae or Hodotermitinae of the Hodotermitidae. Also, in figure 2 (1981: 92) as diagrammed by Jarzembowski, the basal inner margin of the hind wing is angular, as in Mastotermitidae, further suggesting the presence of an anal fold. Though I have not examined the specimens, on the basis of these characters, I suggest that the genus *Valditermes* be transferred from the Cretatermitinae of the family Hodotermitidae to the family Mastotermitidae.

Although this new species certainly belongs to the Hodotermitinae (Hodotermitidae), it is difficult, due to the fragmentary nature of the specimens, to assign it with absolute certainty to any known genus of the subfamily. It definitely does not belong to the extant genera *Hodotermes, Microhodotermes,* or *Anacanthotermes* because the imagoes of these genera are much larger than that of the new species, the wings are narrower in proportion to their length, and the tarsi are four-segmented. In some respects—size, wing length, and wing venation—the new species resembles some of the species included in the fossil genus *Ulmeriella,* from the Oligocene to Pliocene of Europe and North America, but *Ulmeriella* differs in having a sinuate humeral suture, lenticular eyes (as in *Archotermopsis*), a pronotum narrower than its head, and a wing narrower in proportion to its length.

The Cretaceous, monotypic, fossil genus *Meiatermes* was described for the species *bertrani* in 1986 by Lacasa-Ruiz and Martinez-Delclòs, who placed it in the Hodotermitinae. In many respects, the new species has the characteristics of *Meiatermes*: a circular head, semicircular eyes, a pronotum as wide as its head, a humeral suture almost straight, wings proportionately wide relative to length, and branching patterns of the radial sector. Even though there are some differences in the wing venation, such as the median joining the radial sector in the forewing in *Meiatermes,* because of the fragmentary nature of the material (the mandible dentition and the basal portion of the wing are not available for comparison), I hesitate to erect a new genus for this species. Therefore, I am tentatively placing this new species in the genus *Meiatermes. Meiatermes bertrani* Lacasa-Ruiz and Martinez-Delclòs differs from *Meiatermes araripena,* new species, in having a longer and wider forewing (length 8.21–11.15 mm, width 3–3.60 mm) and the median vein not joined to the radial sector. Further, *M. bertrani* is reported from Spain and from an older geological deposit.

Even though termites are predominantly tropical in distribution, most of the species of the family Hodotermitidae are temperate or warm-temperate; relatively few (6 living species out of 50 living and fossil species) are tropical. *Meiatermes araripena* is the first fossil species of this family from the tropics. The other species of this genus, *M. bertrani,* is warm temperate.

Table 1
Measurements (in millimeters) of Three Fragmentary Imagoes of *Meiatermes araripena,* new species

	43902 (holotype)	43903	43901
Total length without wings	7.70[a]	8.00	7.70
Length of head	1.90	2.00	2.00
Width of head	1.90	2.00	1.90[a]
Diameter of eye	0.42	0.40	—
Width of pronotum	—	1.60	1.60
Median length of pronotum	—	0.75	0.60
Length of foretibia	—	1.13	—
Length of forewing scale	—	—	0.09
Length of forewing without scale	—	7.50[a]	—
Width of forewing	2.80	2.75	—
Length of hind wing without scale	7.60[a]	—	—
Width of hind wing	2.50	—	—

[a] Measurement approximate.

REFERENCES

Acra, A., R. Milki, and F. Acra
1972. The occurrence of amber in Lebanon. Abstr. Reunion Sci. Assoc. Av. Sci., Beirut 4: 76–77 (UNESCO).

Emerson, A. E.
1933. A revision of the genera of fossil and recent Termopsinae (Isoptera). Univ. California Publ. Ent. 6: 165–196.
1955. Geographical origins and dispersions of termite genera. Fieldiana: Zool. 37: 465–521.
1967. Cretaceous insects from Labrador 3. A new genus and species of termite (Isoptera: Hodotermitidae). Psyche 74: 276–289.
1968. A revision of the fossil genus *Ulmeriella* (Isoptera, Hodotermitidae, Hodotermitinae). Am. Mus. Novitates 2332: 22 pp.

Emerson, A. E., and K. Krishna
1975. The termite family Serritermitidae (Isoptera). Am. Mus. Novitates 2570: 31 pp.

Grassé, P.-P.
1949. Ordre des isoptères ou termites. *In* P.-P. Grassé, Traité de zoologie 9: 408–544. Paris: Masson et Cie.

Hennig, W.
1969. Die Stammesgeschichte der Insekten. Frankfurt: A.M. Kramer.

Jarzembowski, E. A.
1981. An early Cretaceous termite from southern England (Isoptera: Hodotermitidae). Syst. Entomol. 6: 91–96.
1984. Early Cretaceous insects from southern England. Mod. Geol. 9: 71–93.

Krishna, K.
1970. Taxonomy, phylogeny, and distribution of termites. *In* K. Krishna and Frances M. Weesner (eds.), Biology of termites 2: 127–152. New York and London: Academic Press.

Lacasa-Ruiz, A., and X. Martinez-Delclòs
1986. *Meiatermes*: Nuevo genero fosil de insecto Isoptero (Hodotermitidae) de las calizas Neocomienses del Montsec (Provincia de Lèrida, España). Lleida: Institut d'Estudis Ilerdencs.

Schlee, D.
1972. Bernstein aus dem Libanon. Kosmos 68: 460–463.

Schlee, D., and H.-G. Dietrich
1970. Insektenführender Bernstein aus der Unterkreide des Libanon. Neues Jahrb. Geol. Palaeont., Monatshefte 1970: 40–50.

Schlee, D., and W. Glöckner
1978. Bernstein. Stuttgarter Beitr. Naturk., ser. C, 8: 1–72.

Schlüter, T.
1975. Nachweis verschiedener Insecta-Ordines in einem mittelkretazischen Harz Nordwestfrankreichs. 1(2): 151–161.
1978. Zur Systematik und Palökologie harzkonservierter Arthropoda einer Taphozönose aus dem Cenomanium von NW-Frankreich. Berl. Geowiss. Abh., ser. A, 9: 1–150.

Snyder, T.
1949. Catalog of the termites (Isoptera) of the world. Smithsonian Misc. Coll. 112: 1–490.

Zherikhin, V. V., and I. D. Sukatsheva
1973. Cretaceous insect-bearing "amber" (retinite) from northern Siberia. 24th Ann. Rep. on Lectures in Memory of N. A. Kolodovsky (April, 1971), pp. 3–48. Leningrad: Nauka.

CHAPTER 6. HOMOPTERA

K. G. A. HAMILTON[1]

ABSTRACT

Ninety-seven specimens of Homoptera (AMNH 43328, 43600–4, 43607–33, 43635–6, 43638–68, 43670–90, 43692–6, 43711–3, 43760–1, 44105) from the Santana Formation, Lower Cretaceous of Brazil are known. Nearly half (43) are Cicadellidae belonging to 3 new genera and 11 new species, 8 of which are described. Six specimens, belonging to 2 new genera and 3 new species, are Jascopidae. Three specimens (including one nymph) are described as a new genus and species of Cicadoprosbolidae. A single specimen of a primitive cercopoid is described as a new family, CERCOPIONIDAE. One specimen of a new genus of Aleyrodoidea is tentatively assigned to the family Boreoscytidae; it is a member of the Fulgoromorpha rather than Sternorrhyncha. A new genus of 2 species represents the earliest record of Achilidae, and 1 specimen represents a possible cixiid. The remaining 36 specimens belong to a new family, LALACIDAE. They are assigned to 24 species in 8 genera, of which 15 species and 7 genera are described as new. The previously described genera of Cretaceous Homoptera are listed by superfamily, and compared to these newly discovered fossils. A possible case of parasitism by Dryinidae is reported.

INTRODUCTION

Mesozoic Homoptera are known mainly from isolated, often fragmentary, tegmina. These have a low information content. From these alone it is possible to state with certainty only a few principles, notably that the primitive Homopterous tegmen had a "Y-vein" on the clavus, 4-branched media, and Sc short or absent.

Recent discoveries of nearly complete fossils of Homoptera are greatly enhancing our understanding of the origins and evolution of the suborder. A few specimens have been preserved in Cretaceous amber (Hamilton, 1971; Fennah, 1987). Several important Mesozoic fossiliferous beds in Asia (Bekker-Migdisova, 1985; Shcherbakov, 1986) and Australia (Jell and Duncan, 1986) are notable. The specimens from Santana limestone, described below, are the best-preserved Mesozoic Homopterous fossils known and represent the richest known of such faunas.

ACKNOWLEDGMENTS

The specimens examined in this study were prepared by D. Judd and D. A. Grimaldi. Photographs were taken by B. W. Lukey and printed by D. Andrews of Biographics, Agriculture Canada. The assistance of F. M. Carpenter in securing obscure papers on fossil Homoptera is also gratefully acknowledged. All measurements are in millimeters.

MEMBRACOIDEA

The following genera include the earliest definite records of Cicadellidae, apparently belonging to its most primitive subfamilies (for phylogeny, see Hamilton, 1983). One genus displays characters thought to be ancestral for the family Cicadellidae as a whole. The others show a wide variety of modern head and leg characters, which suggests adaptation to various lifestyles similar to those existing in the family today. Two additional genera are apparently members of the extinct Jascopidae, which are thought to be ancestral to the modern Membracoidea (Hamilton, 1971).

JASCOPIDAE

PARACARSONINI, NEW TRIBE

DIAGNOSIS: Coronal margin overlapping eyes. Two included genera.

Paracarsonus, new genus

Figures 1–3, 85–86

ETYMOLOGY: From *para,* near and *Carsonus,* a primitive leafhopper genus (Bathysmatophorini). Gender: masculine.

---

[1] Research Entomologist, Biosystematics Research Centre, Agriculture Canada, Research Branch, Ottawa, Canada K1A OC6.

TYPE SPECIES: *Paracarsonus aphrodoides,* n. sp.

DIAGNOSIS: Coronal margin carinate.

DESCRIPTION: Head with declivous crown separated from face by carinate edge. Ocelli between eyes, 3 diameters distant from hind margin of crown, 2 diameters from eyes. Antennal ledges small but distinct. Frons strongly inflated, deeper in lateral aspect than genae. Lora ovoid, not as long as clypellus. Genal lobes absent, exposing broad procoxales (= "proepimera"). Rostrum moderately long, extending to hind coxae. Tegmen short, punctate, 2 anteapical cells and 7 apical cells, venation carinate, M 2-branched, the 2nd briefly united to Cu_1. Hind tibia stout, very short, scarcely longer than femur, with a few setae on outer edge without enlarged bases, and large setal bases in apical pecten as in Cercopidae. Hind basitarsus very stout, longer than other 2 tarsomeres together. Claws small. Abdominal segments 4–8 of similar size, basal segments much narrower; ovipositor distinctly exceeding pygofers.

PLACEMENT: The development of the head gives members of this genus a superficial resemblance to members of the cicadellid tribe Aphrodini, but this is not supported by any critical characters. The deep frons and ocelli on the crown between the eyes suggest a relationship to the Cicadellinae, but these are plesiomorphs merely showing the primitive nature of these insects. Its placement in the Jascopidae is based on the very short hind tibiae with prominent apical pecten, the enlarged hind basitarsomeres, and small claws. The tegminal venation is similar to those of Mongolian "Cicadelloidea" (Shcherbakov, 1986) in having the 2nd branch of M united to Cu_1.

Paracarsonus aphrodoides, new species
Figures 1–3, 85–86

ETYMOLOGY: From *Aphrodes,* a leafhopper genus and *-oides,* similar to.

DIAGNOSIS: Only species in genus; carinate coronal edge unique in Cretaceous Homopterous fauna.

MATERIAL: *Holotype:* male, AMNH 43668, a well-preserved lateral compression lacking most of legs on right side, and middle leg on left side; genitalia concealed by tegmen (fig. 1). *Paratypes:* 2♂, 1♀: male, AMNH 43650, a ventral compression with "scalped" frons and left tegmen spread; detail poorly preserved (fig. 85); male, AMNH 43713, a ventral compression lifted completely off the matrix, leaving a dorsal impression; face well preserved (fig. 2); legs incomplete, hindwing veins barely indicated (fig. 3); female, AMNH 43671, a ventrolateral compression, both crushed and damaged, rostrum and ovipositor well preserved (fig. 86).

MEASUREMENTS: Length to tip of abdomen, male = 4.5–5.1 (type = 4.8), female = 5.7; length of crown = 0.7; median length of pronotum = 0.8; hind tibia = 1.2–1.5; hind basitarsus = 0.6–0.7.

Platyjassites, new genus
Figures 4–6, 84

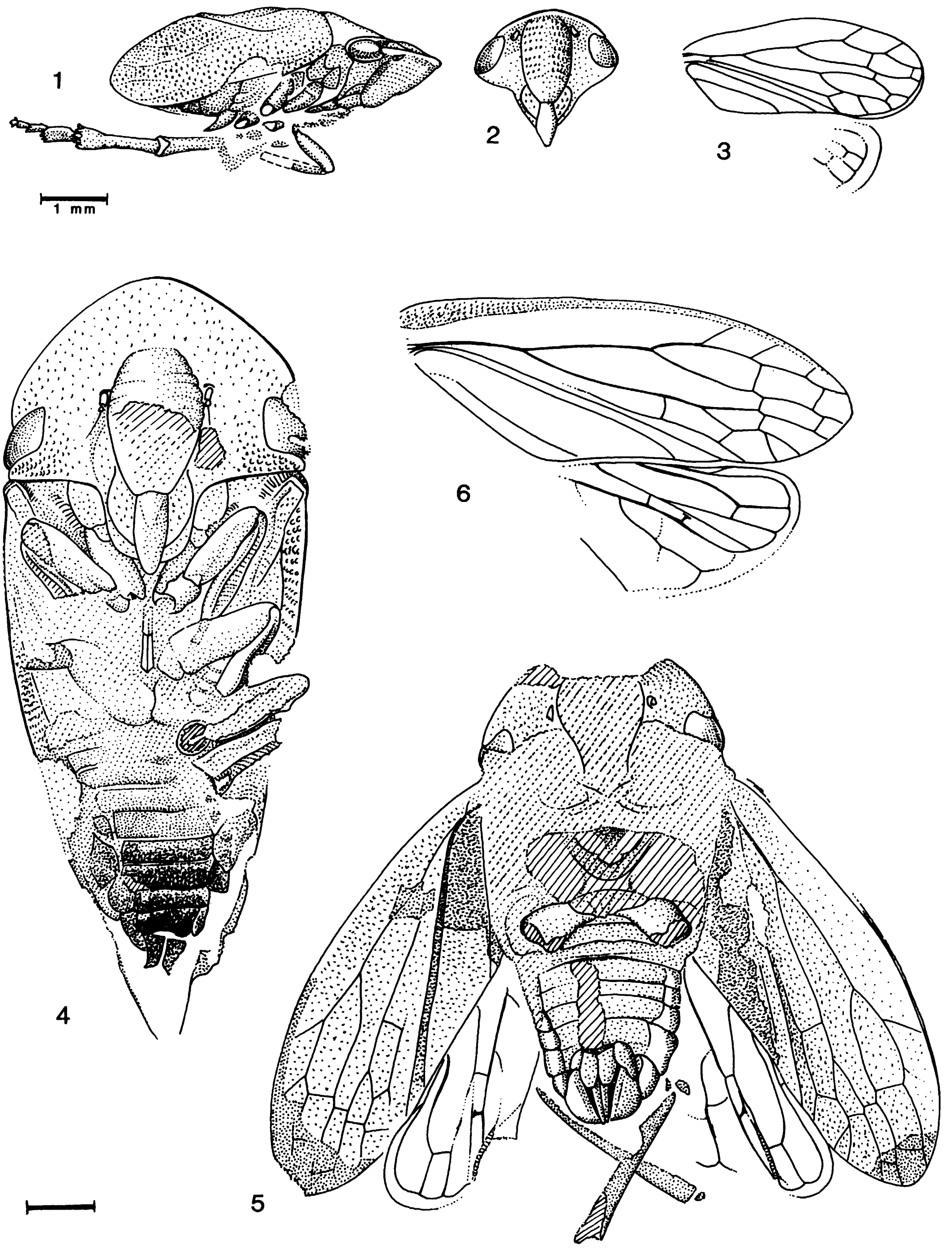
ETYMOLOGY: From *platy,* flat; *Jassid,* leafhopper; *-ites,* petrified. Gender: masculine.

TYPE SPECIES: *Platyjassites inflatifrons,* n. sp.

DIAGNOSIS: Large, strongly flattened head with prominent frons.

DESCRIPTION: Head enormously enlarged, foliaceously extending before eyes. Antennal ledges absent. Frons inflated, one-third as wide as face. Lora ovoid, as long as clypellus. Genae pitted and deeply excavated, exposing broad but short procoxales. Rostrum small, extending between middle coxae. Tegmen strongly pitted throughout, 2 anteapical cells, venation with a few supernumerary crossveins before tips. Tibiae short and longitudinally carinate, setae absent or small. Claws and hind tarsi unknown. Abdominal segments 1–8 of similar size, pregenital segment with rounded outer lobes; subgenital plates tapered, apically truncate, valve transverse; ovipositor very short, scarcely exceeding rounded pygofers.

PLACEMENT: Members of this genus are strikingly similar to those of *Petalocephala* Stål, but with the frons much larger and the coronal margin extending before the eyes, as in *Platyjassus* Evans (a member of the unrelated Scarinae). Its venation and coronal margin suggest it is related to *Paracarsonus.* Alternatively, it might be an anomalous member of the Ledrinae. The imperfectly preserved legs prevent its being definitely



Figs. 1–6. Jascopidae. **1,** *Paracarsonus aphrodoides,* n. sp. holotype, AMNH 43668; **2,** face of paratype, AMNH 43713; **3,** same, venation; **4,** *Platyjassites inflatifrons,* n. sp. holotype, AMNH 43693; **5,** ?*Platyjassites* sp., AMNH 43635; **6,** same, venation.

placed in either the Cicadellidae or the Jascopidae.

Platyjassites inflatifrons, new species

Figure 4

ETYMOLOGY: *inflatio*, swelling; *frons*, part of the head.

DIAGNOSIS: Frons more than ⅓ width of head.

MATERIAL: *Holotype:* male, AMNH 43693, a well-preserved ventral compression lacking most tarsi, legs on right side, and "knee" joint of hind leg (fig. 4); tegmina too deeply embedded to distinguish venation.

MEASUREMENTS: Length to tip of abdomen = 11.1; head = 4.0 wide, 4.3 long.

DISCUSSION: This specimen is better preserved than the only other one known. The second specimen, a female, is smaller than the male, presents a less inflated frons, and likely represents a separate species.

Platyjassites sp.

Figures 5, 6, 84

MATERIAL: Female, AMNH 43635, ventral compression with "scalped" frons, clypellus, genae, thorax and legs; tip of head also missing; dorsum exposed from scutellum to base of ovipositor (fig. 84); tegmina spread, showing venation of all wings (figs. 5, 6).

MEASUREMENTS: Length from preserved part of head to wing tips = 8.2; head = 3.7 wide.

CICADELLIDAE

SUBFAMILY CICADELLINAE

DIAGNOSIS: Members of the subfamily Cicadellinae are characterized by their slender body and greatly inflated frons that holds the powerful cibarial dilator muscles needed for feeding on xylem fluids. The following fossil forms are more primitive than any known Cicadellinae, and are assigned to a new tribe.

PROERRHOMINI, NEW TRIBE (MONOBASIC)

Proerrhomus, new genus

Figures 7–9, 81–83

ETYMOLOGY: *pro*, before; *Errhomus*, a primitive leafhopper genus (Bathysmatophorini). Gender: masculine.

TYPE SPECIES: *Proerrhomus rugosus*, n. sp.

DIAGNOSIS: Combination of ocelli between eyes on crown, and thin antennal ledges.

DESCRIPTION: Head with declivous crown indistinctly separated from face. Ocelli between eyes, 3–4 diameters distant from hind margin of crown, 2 diameters from eyes. Antennal ledges thin but not carinate. Frons strongly inflated, deeper in lateral aspect than genae. Lora narrow, as long as clypellus. Rostrum short, extending between forecoxae. Tegmen strongly pitted, venation without crossveins before tips. Foretibia with a row of prominent setae on apical half. Hind tibia stout, 50 percent longer than femur, with well-separated longitudinal rows of setae (those on outer edge about as long as thickness of tibia), without enlarged setal bases. Hind basitarsus about as long as distitarsus, 50 percent longer than second tarsomere, with prominent "heel," plantar setae small. Claws short and broad. Abdominal segments 4–8 of similar size, basal segments much narrower; ovipositor scarcely exceeding pygofers.

PLACEMENT: Members of this genus are superficially similar to long-winged forms of the Bathysmatophorini, but have the ocelli placed further back on the crown (as in Cicadellini and Cercopoidea) and the tegmen heavily pitted, as in Ledrinae. One specimen, tentatively assigned to this genus, has the mesonotal sutures exposed, and these form the narrow "prescutum" characteristic of Ulopinae, Ledrinae, and Iassinae (Hamilton, 1983). All these characters are likely to be plesiomorphic for the family as a whole. Placement in any modern tribe is therefore unlikely, although it can be assigned to the subfamily Cicadellinae sensu lato with confidence.

Proerrhomus rugosus, new species

Figure 7

ETYMOLOGY: *rugosus*, pitted.

DIAGNOSIS: Crown longer than 1.0 mm; tegminal venation without reticulations.

MATERIAL: *Holotype:* female, AMNH 43612, a well-preserved lateral compression lacking tegminal tips, most of fore and middle legs (except right foreleg), left femur, tibial pectens, and eighth sternite (Hamilton, in press: fig. 9).

MEASUREMENTS: Length to tip of abdomen = 10.0; length of crown = 1.6; median length of pronotum = 1.2; hind basitarsus = 0.9.

DISCUSSION: This is the best-preserved of 4 specimens referable to this genus.

?*Proerrhomus* sp. A

Figures 8, 9, 81, 83

MATERIAL: Male, AMNH 43613, dorsal compression with upper surface of pronotum, scutellum, clavi and tegminal tips "scalped," exposing mesonotum, abdomen, hind tibia, and tips of hind wings (figs. 9, 83); male(?), AMNH 43630, lateral compression with poorly preserved pronotum and wings; genitalia missing; abdominal sclerites on far side visible due to "scalping"; fore and middle legs largely missing (figs. 8, 81).

MEASUREMENTS: Length to hind wing tips = 8.4; length of crown = 0.8; head across eyes = 1.9; median length of pronotum = 1.6; hind basitarsus = 0.6.

DISCUSSION: The specimens listed here may belong to a single species, with crown shorter than 1.0 and body length less than 10.0, but they are too poorly preserved to warrant description.

?*Proerrhomus* sp. B

Figure 82

MATERIAL: Sex unknown, AMNH 43696, ventral compression with body "scalped"; eyes and antennal pits well preserved; tegmina represented by narrow strips showing reticulations (fig. 82).

MEASUREMENTS: Length to wing tips = 10.7; head across eyes = 2.5.

DISCUSSION: The body length greater than 10.0 and reticulate tegmina are distinctive, but this specimen is too poorly preserved to warrant description.

SUBFAMILY MYERSLOPIINAE

DIAGNOSIS: This subfamily, like the Cicadellinae, has a greatly enlarged frons, but the body form is squat and beetlelike. Modern members of the Myerslopiinae are flightless, curiously deformed insects that live in surface soil in Southern Hemisphere countries. Fossils here assigned to this subfamily are the more normal form for leafhoppers and are probably primitive members of this ancient lineage.

OVOJASSINI, NEW TRIBE (MONOBASIC)

Ovojassus, new genus

Figures 10–12, 87–88

ETYMOLOGY: *ovus*, egg [shape]; *Jassus*, leafhopper genus, type of Jassidae. Gender: masculine.

TYPE SPECIES: *Ovojassus concavifer*, n. sp.

DIAGNOSIS: Combination of ovoid shape and strongly inflated frons.

DESCRIPTION: head without defined crown. Ocelli between eyes, 2–3 diameters distant from hind margin of crown, 2 diameters from eyes. Antennal ledges bulbous, distinct. Frons strongly inflated, deeper in lateral aspect than genae. Lora narrow, longer than clypellus. Genal lobes absent, exposing short, broad procoxales. Rostrum short, extending between forecoxae. Tegmen short, venation carinate but not clearly preserved. Hind tibia stout, short, 100 percent longer than femur, with well-separated longitudinal rows of setae, macrosetae on outer edge about as long as thickness of tibia, mounted on enlarged setal bases. Hind basitarsus about as long as other 2 tarsomeres together, with prominent "heel"; plantar setae not evident. Claws small and broad. Abdominal segments 4–8 of similar size, basal segments much narrower; ovipositor slightly exceeding pygofers.

PLACEMENT: This genus is probably allied to *Hallex* n. gen., differing significantly in the small claws and robust hind tibia.

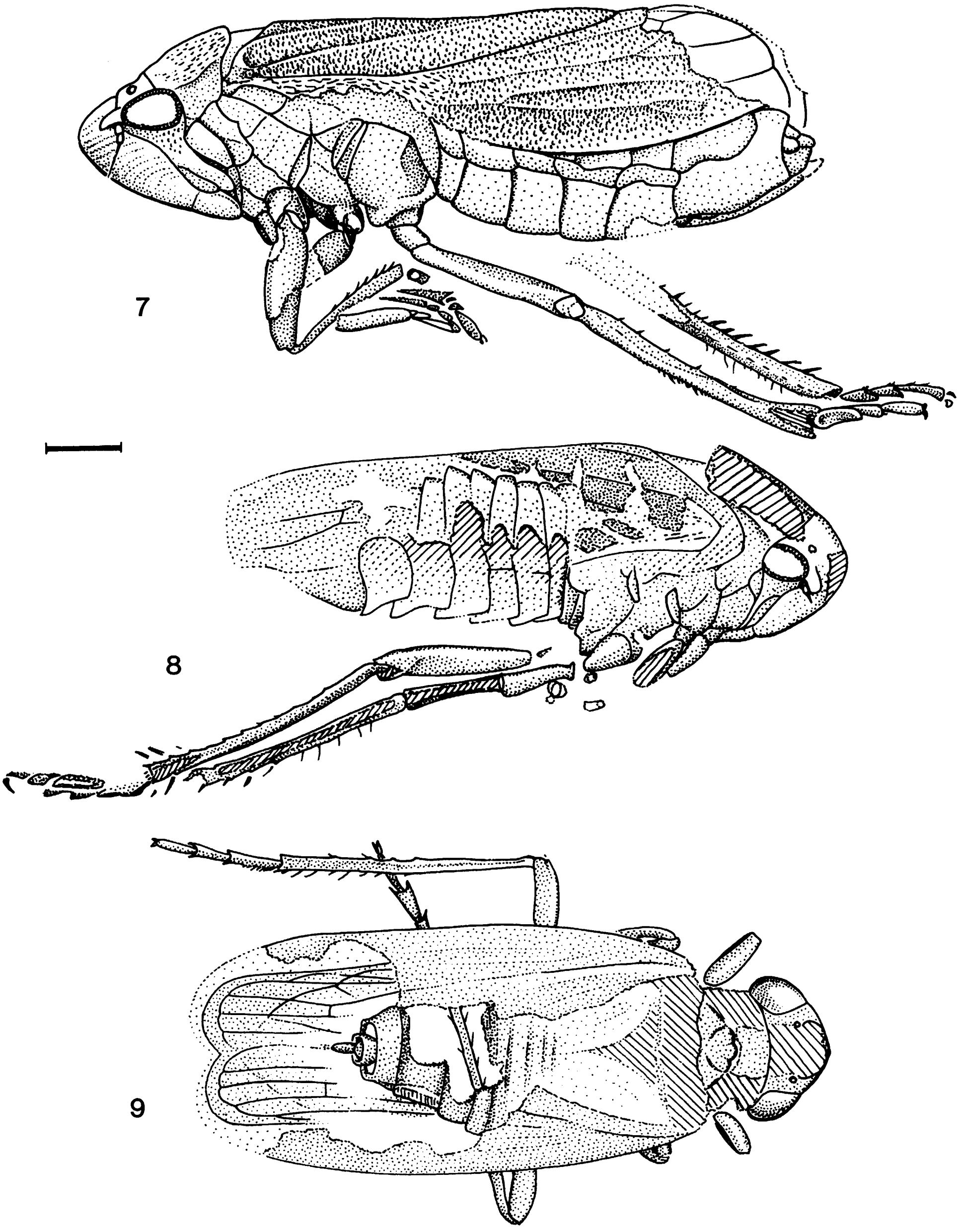
Ovojassus concavifer, new species

Figures 10, 87

ETYMOLOGY: *concavus*, hollow; *-fer*, bearing.

DIAGNOSIS: Body more than 4.0 mm; female pregenital sternite deeply notched.

MATERIAL: *Holotype:* female, AMNH 43660, a ventrolateral compression lacking most of legs, hind leg and forefemur on left side preserved (tarsal detail lost); tegminal tips missing; apex of frons cracked due to slight flattening; seventh sternite exposed, left side intact, deeply and broadly excavated nearly to base (fig. 10). *Paratypes:* 1♂, 2♀: female, AMNH 43663, a ventrolateral



Figs. 7–9. *Proerrhomus* spp., Cicadellidae. **7**, *P. rugosus,* n. sp. holotype, AMNH 43612; **8**, ?*Proerrhomus* sp. A, AMNH 43630; **9**, ?*Proerrhomus* sp. B, AMNH 43613.

compression; body "scalped" and legs damaged; female, AMNH 43664, a lateral compression; tegmen and body "scalped"; head and hind legs well preserved (fig. 87); male, AMNH 43672, a lateral compression; eye, frons, and tegmen tip "scalped"; detail poorly preserved.

MEASUREMENTS: Length, male = 4.8, female = 5.3–5.5 (type, to tip of abdomen = 4.9); length of crown = 0.5–0.6; median length of pronotum = 1.0; hind tibia = 1.9–2.3; hind basitarsus = 0.5–0.6.

Ovojassus minor, new species

Figures 11, 12, 88

ETYMOLOGY: *minor*, smaller.

DIAGNOSIS: Body less than 4.0 mm; pregenital sternite of female toothed.

MATERIAL: *Holotype:* female, AMNH 43652, a ventrolateral compression lacking most of legs, hind leg and forefemur on left side preserved (tarsal detail apparent only on right hind leg, fig. 12); tegminal tips missing; crown bulged due to flattening (fig. 88); seventh sternite clearly exposed, prominently toothed at middle (fig. 11).

MEASUREMENTS: Length = 3.4; length of crown = 0.3; median length of pronotum = 0.6; hind tibia = 1.3; hind basitarsus = 0.3.

DISCUSSION: The hind tibia was damaged during handling before and after photography.

HALLICINI, NEW TRIBE (MONOBASIC)

Hallex, new genus

Figures 13–27, 89–103

ETYMOLOGY: *hallex*, big toe. Gender: masculine.

DIAGNOSIS: Tarsal claws half length of hind basitarsomere; hind tibia flattened.

TYPE SPECIES: *Hallex xestocephalus*, n. sp.

DESCRIPTION: Head without defined crown. Ocelli between eyes, 2 diameters distant from hind margin of crown, 2–3 diameters from eyes. Antennal ledges weak but distinct. Frons strongly inflated, deeper in lateral aspect than genae. Lora narrow, longer than clypellus. Gena lobes absent, exposing short, broad procoxales. Rostrum short, extending between forecoxae. Tegmen short, 2 anteapical and 4–5 apical cells in typical leafhopper orientation, hind wing tip with M and Cu forked once each, connected by crossvein, together with R forming 3 apical cells. Hind tibia flattened, moderately long, 50 percent longer than femur, with 2 apparent longitudinal rows of setae, macrosetae on outer edge longer than thickness of tibia but shorter than its width, mounted on slightly enlarged setal bases. Hind basitarsus about as long as apical tarsomere, second tarsomere much shorter; basitarsus with inconspicuous "heel," plantar setae large (also present on fore basitarsus); fine hairs on apical tarsomere. Claws fingerlike and broad (figs. 13–18). Abdominal segments 3–7 of similar size, basal segments much narrower; ovipositor slightly exceeding pygofers.

PLACEMENT: This genus is probably allied to *Ovojassus*, differing significantly in the long claws and flattened hind tibia.

DISCUSSION: This one genus represents over one-third of the total collection (37 specimens) and has 6 known species, separable by body length and proportions of the head, femora, and tarsi. There are slight differences in venation, but these appear to occur within a species rather than between species.

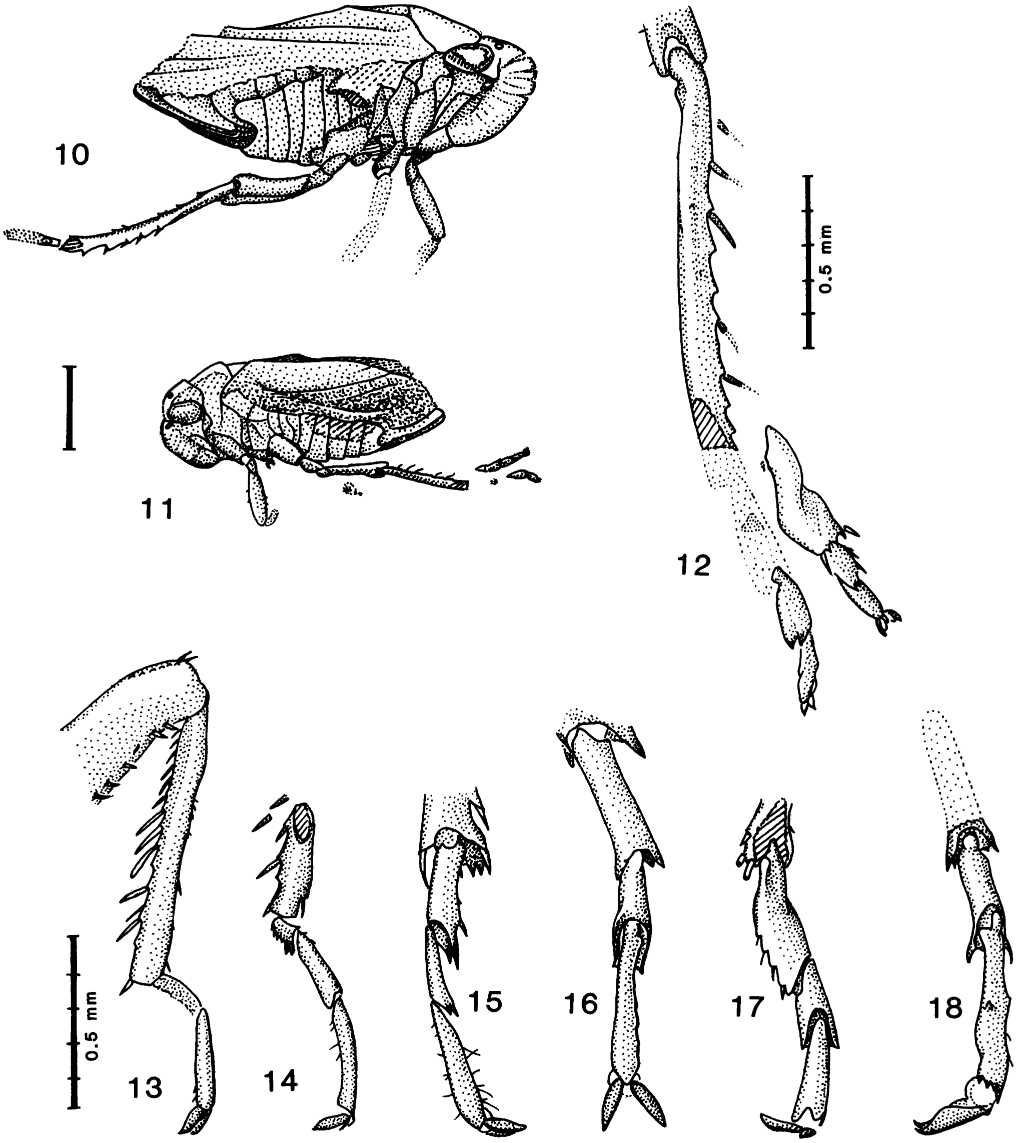
Hallex xestocephalus, new species

Figures 13–15, 19, 24, 89–94

ETYMOLOGY: *Xestocephalus*, a leafhopper genus (Aphrodini).

DIAGNOSIS: Body almost as small as in *H. brevipes*, n. sp., length of male less than 5.0 mm, of female less than 6.0 mm, but with tegmen three times as long as broad, and hind distitarsi longer than 0.3 mm.

MATERIAL: *Holotype:* female, AMNH 43656, a dorsolateral compression lacking most of middle and tegminal tips; antennal ledge and foremargin of eye chipped (fig. 19); seventh sternite visible in oblique view, conically produced, tip excavated as V-shaped notch. *Paratypes:* 5♂, 11♀: female, AMNH 43642, a ventral compression, with wings spread; specimen damaged; male, AMNH 43646, a ventral compression; wings scarcely indicated; detail poorly preserved; male, AMNH 43648, a dorsolateral compression without abdomen and wings beyond thorax, but clearly showing a natural posture of the hind legs (figs. 24, 89); male, AMNH 43651, a ventral compression with wings spread, hind wings poorly preserved; right hind leg mostly missing (fig. 90); male, AMNH 43653, a dorsolateral compression; tegmina slightly crushed, tips missing, but head and legs well preserved (fig. 91); female, AMNH 43654, a lateral compression; frons missing; detail poorly preserved; male, AMNH 43655, a lateral compression; left legs (except hind tibia)



Figs. 10–12. *Ovojassus* spp. **10,** *O. concavifer,* n. sp. holotype, AMNH 43660; **11,** *O. minor,* n. sp. holotype, AMNH 43652; **12,** same, hind tibia and tarsi.

Figs. 13–18. Tarsi of *Hallex* spp. **13-15,** fore, middle, and hind tarsi of *H. xestocephalus,* n. sp. holotype, AMNH 43656; **16,** hind tarsus of *Hallex gracilior,* n. sp. holotype, AMNH 43640; **17,** of *H. brevipes,* n. sp. holotype, AMNH 43645; **18,** same, of *H. gongrogony,* n. sp. holotype, AMNH 43644.

and tarsi of middle and hind legs missing; female, AMNH 43657, a lateral compression; legs crushed; head well preserved (fig. 27); female, AMNH 43658, a lateral compression; head, pronotum, and tegmina crushed; female, AMNH 43659, a dorsolateral compression, somewhat crushed; left femur and tibia broken; other legs mostly concealed by body (fig. 92); female, AMNH 43661, a lateral compression; detail poorly preserved; female, AMNH 43662, a lateral compression, with head crushed; only tips of hind legs preserved (fig. 93); female, AMNH 43670, a lateral compression, in poor condition; female, AMNH 43674, a lateral compression; detail very poorly preserved; female, AMNH 43675, a dorsal compression; head crushed; right wings spread; tip of left wings and abdomen "scalped," exposing cast of genitalia; 7th sternite damaged on midline (fig. 94); female, AMNH 43760, a dorsal compression with tegmina spread; body "scalped"; legs folded under body.

MEASUREMENTS: Length, male = 4.6–4.8, female = 5.0 (type)–5.6 (5.3 ± 0.1); crown length = 0.4–0.5, width = 1.0–1.1; median length of pronotum = 0.7–0.8; tegmen three times as long as broad; hind tibia = 1.9–2.3; hind distitarsus = 0.4–0.5.

DISCUSSION: This is the most common Homoptera from this fossil bed.

Hallex gongrogony, new species

Figures 18, 22, 25, 95–97

ETYMOLOGY: *gongros*, swelling; *gony*, knee.

DIAGNOSIS: Body as large as in *H. gracilior* n. sp., length of male more than 5.0 mm, of female more than 5.9 mm, but tegmen three times as long as wide.

MATERIAL: *Holotype:* male, AMNH 43644, a dorsal compression with left side of head and most of thorax "scalped," right tegmen extended (hind wing not apparent), fore and middle legs under specimen, and tegminal tips and genital segment missing (fig. 95). *Paratypes:* 2♂, 3♀: male, AMNH 43328, a dorsal compression; only left tegmen well preserved; female, AMNH 43641, a dorsal compression with tegmina spread; only left tegmen well preserved; female, AMNH 43666, a ventrolateral compression lacking tegminal tips; tegmen crushed; right hind femur missing (fig. 96); female, AMNH 43667, a lateral compression lacking tip of left tegmen and abdomen; only head well preserved (fig. 97); male, AMNH 43673, a lateral compression; body "scalped"; legs fragmented.

MEASUREMENTS: Length, male = 5.6–5.8(type), female = 6.0–6.6; crown length = 0.4, width = 0.9–1.0; median length of pronotum = 1.0–1.1; tegmen three times as long as broad; hind tibia = 2.4–2.6; hind distitarsus = 0.5–0.6.

DISCUSSION: This species has the largest femoral apex in the genus.

Hallex brevipes, new species

Figures 17, 20, 98, 99

ETYMOLOGY: *brevis*, short; *pes*, foot.

DIAGNOSIS: Body smaller than in *H. xestocephalus* n. sp., length of female less than 5.0 mm; with tegmen 2.5 times as long as broad, and hind distitarsus shorter than 0.4 mm.

MATERIAL: *Holotype:* female, AMNH 43645, a ventral compression with center of frons "scalped," tegmina extended (tip of left hind wing visible, fig. 20), middle legs and abdominal sternites missing (fig. 98). *Paratypes:* 2 females: AMNH 43639, a dorsal compression, with right wings spread; detail poorly preserved (fig. 99); AMNH 43647, a ventral compression, with wings spread; detail poorly preserved.

MEASUREMENTS: Length, female = 4.6–4.7 (type); crown length = 0.5, width = 1.1; median length of pronotum = 0.9; tegmen 2.5 times as long as broad; hind tibia = 1.8–2.1; hind distitarsus = 0.3.

DISCUSSION: This species has the shortest tegmina and distitarsi in the genus (fig. 17).

Hallex laticeps, new species

Figure 100

ETYMOLOGY: *latus*, wide; *ceps*, head.

DIAGNOSIS: Crown wider than 1.1 mm; tegmen four times as long as broad.

MATERIAL: *Holotype:* sex unknown, AMNH 43711, a dorsal compression, wings and most of legs concealed by tegmina, right femoral apex and tarsus exposed (1 femoral macroseta broken off, glued next to femur, fig. 100).

MEASUREMENTS: Length = 5.5; crown length = 0.3, width = 1.4; median length of pronotum = 1.0; tegmen four times as long as broad; hind distitarsus = 0.4.

Hallex gracilior, new species

Figures 16, 21, 23, 101–103

ETYMOLOGY: *gracilis*, slender; *-ior*, more.

DIAGNOSIS: Crown less than 1.1 mm wide; tegmen four times as long as broad.

MATERIAL: *Holotype:* male, AMNH 43640, a dorsal compression with center of crown and clavi "scalped," tegmina extended (tips of hind wings visible), legs except hind tarsi concealed (figs. 21, 101). *Paratypes:* 4♂, 2♀: male, AMNH 43638, a dorsal compression; left middle and right hind leg (except tarsi) well preserved; male, AMNH 43643, a dorsal compression; legs folded under body; tegmina spread and fragmented; pygofer scalped; detail poorly preserved; male, AMNH 43649, a dorsal compression; base of right tegmen and hind tibia well preserved (fig. 102); female, AMNH 43676, a crushed dorsal compression with wings spread; only base of corium and hind tibiae well preserved (fig. 103); female, AMNH 43694, a ventral compression lacking tarsi, head well preserved (fig. 23); lifted off matrix, exposing dorsal impression of tegminal venation; male (?), AMNH 43711, a dorsal compression, poorly preserved.

MEASUREMENTS: Length, male = 5.2–5.6 (type 5.5), female = 6.1–6.2; crown length = 0.3–0.5, width = 1.0; median length of pronotum = 0.8; tegmen four times as long as wide; hind tibia = 2.6–2.8; hind distitarsus = 0.5.

Hallex sp.

MATERIAL: Male, AMNH 43712, a dorsal compression; center of crown, wing tips and abdomen (except genitalia) "scalped"; details poorly preserved.

MEASUREMENTS: Length = 6.4; crown length = 0.8, width = 1.0; tegmen 3.5 times as long as wide.

DISCUSSION: The crown is distinctive, more than 0.5 mm long, but this specimen is too poorly preserved to warrant description.

CICADOIDEA: CICADOPROSBOLIDAE

The Cicadoprosbolidae is a Mesozoic family that encompasses the following genera: *Cicadoprosbole* Bekker-Migdisova, 1946 (Lower Jurassic), *Hylaeoneura* Lameere and Severin, 1897 (Upper Cretaceous), *Kisylia* Martynov, 1937 (Jurassic), *Leptoprosbole* Riek, 1976 (Upper Triassic), *Mesodiphthera* Tillyard, 1919 (Upper Triassic), *Paraprosbole* Whalley, 1985 (Liassic), *Shuraboprosbole* Bekker-Migdisova, 1949a (Mesozoic), and *Turutanovia* Bekker-Migdisova, 1949a (Mesozoic). The family was formerly known only by tegmina intermediate between Cicadidae and Prosbolidae, possibly allied to the Tettigarctidae, but with a large costal cell on the tegmen and a very small marginal membrane (appendix) on all the wings.

Architettix, new genus

Figures 28–31, 104, 105

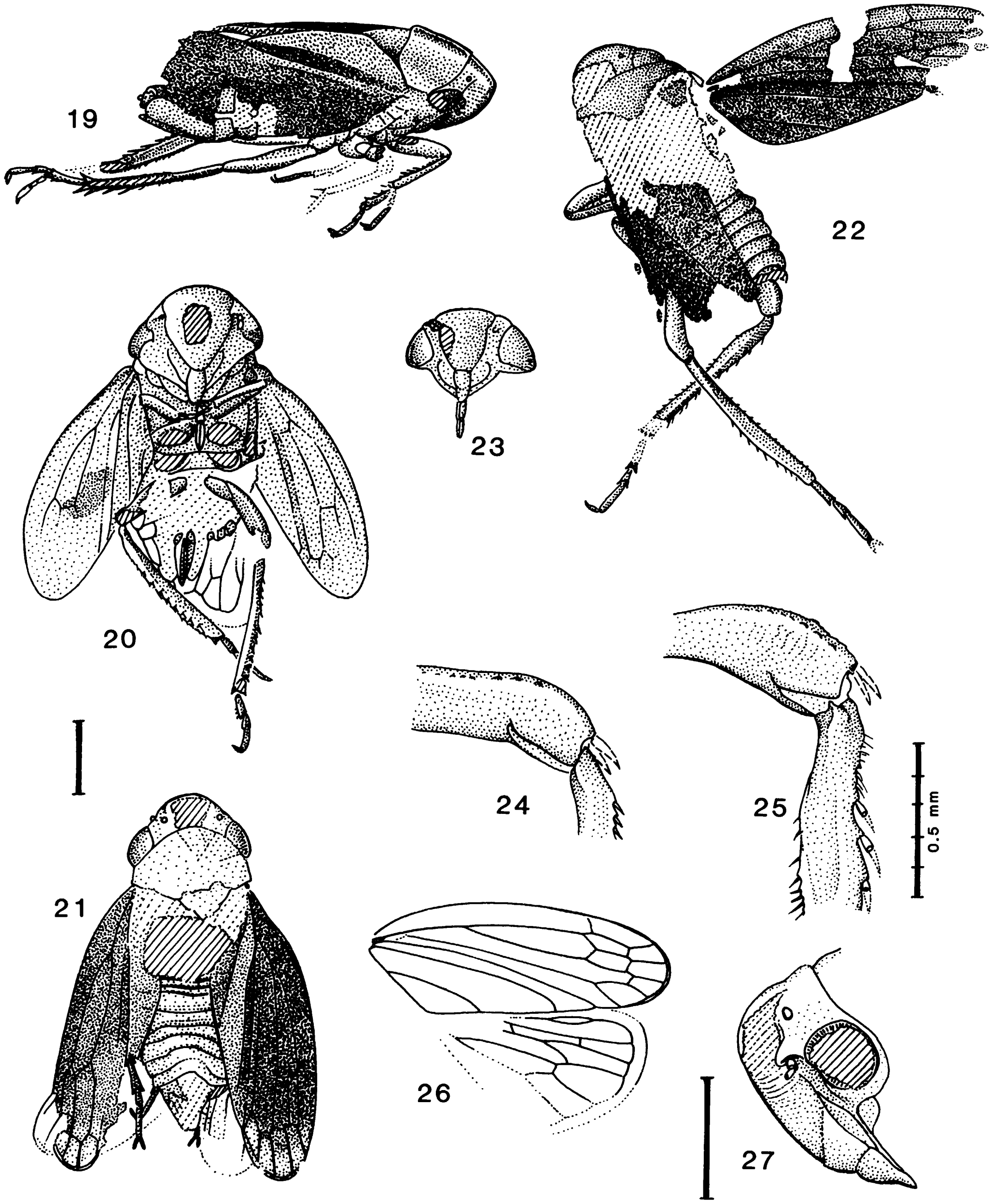
ETYMOLOGY: *archon,* patriarch; *tettix,* cicada. Gender: feminine.

DIAGNOSIS: Costal crossveins simplified; M_{3+4} unbranched; nodal line present.

TYPE SPECIES: *Architettix compacta,* n. sp.

DESCRIPTION: Head with inflated, declivous crown indistinctly separated from face. Median ocellus near tylus; lateral ocelli large, between eyes, 2–3 diameters distant from hind margin of crown, close to eyes. Antennal ledges bulbous, ventrally excavated. Frons strongly inflated, as deep in lateral aspect as genae. Lora large, longer than clypellus. Rostrum long, extending beyond hind coxae nearly to apex of hind femora. Pronotum long, pitted; mesonotum broadly exposed. Tegmen strongly pitted on costal cell, membranous beyond fork of M, traversed by weak nodal line, with 2 anteapical and 8 apical cells (M_{3+4} unbranched). Forefemur 50 percent thicker than hind femur, unarmed. Hind tibia slender, more than twice as long as femur, with 1 prominent spine on outer edge, apex with more than 3 setae set on enlarged setal bases. Hind basitarsus about as long as distitarsus, 50 percent longer than second tarsomere, without prominent "heel"; plantar setae large and biserrate on basal 2 tarsomeres, fine on distotarsus. Claws and pulvillae well developed, as in Cercopoidea. Abdominal segments 4–8 of similar size, basal segments much narrower, sterna 1 and 2 concealed; ovipositor exserted, scarcely exceeding pygofers.

PLACEMENT: This genus has Cicadoprosbolid wings, although with somewhat reduced venation. The body shows an interesting mixture of cicadoid and cicadellid characters. The cicadellid-like tarsi exclude them from any extant cicadoid family.



Figs. 19–27. *Hallex* spp. **19,** *H. xestocephalus* holotype; **20,** *H. brevipes,* holotype; **21,** *H. gracilior* holotype; **22,** *H. gongrogony* holotype; **23,** face of *H. gracilior* paratype, AMNH 43694; **24,** apex of femur of *H. xestocephalus* paratype, AMNH 43648 (femoral macrosetae from AMNH 43711); **25,** same, of *H. gongrogony* holotype; **26,** venation of *Hallex* spp. (composite); **27,** head of *H. xestocephalus* paratype, AMNH 43657.

Architettix compacta, new species

Figures 28–31, 104, 105

ETYMOLOGY: *compacta,* thick.

DIAGNOSIS: The only species in the genus (see generic diagnosis).

MATERIAL: *Holotype:* male, AMNH 43690, a ventrolateral compression with center of frons, clypellus, and abdomen "scalped" (fig. 28), 1 tegmen detached, basal portions of middle and hind legs on left side and all but fragments on right side missing (Hamilton, in press: fig. 12). *Paratypes:* female, AMNH 43600–1, 2 halves of a lateral compression split through length of body, external head features determinable by location of apodemes (fig. 104), pronotum, mesonotum, and coxae all that can be determined of thorax, abdomen strongly flattened, showing sclerites clearly on right half (fig. 29); nymph (?), AMNH 43683, lateral compression showing little detail except of head (pronotal fragment removed to show vertex, fig. 105) and fore and hind legs, except tarsi; possible male genitalia exposed (fig. 30).

MEASUREMENTS: Length, male = ca. 13.6, female = 14.7, nymph = 8.1; vertex length = 0.9–1.2; median length of pronotum = 3.0–3.9; hind tibia = 3.7–4.1; hind basitarsus = 0.9.

CERCOPOIDEA

Members of the cercopoidea are characterized by the tegmen with a prominent ventral flange near the base ("Sc" of authors), R 3-branched and M 2-branched, often richly provided with tiny cells apically, and with the hind wing M unbranched. Only a single representative is known from Santana limestone.

CERCOPIONIDAE, NEW FAMILY

DIAGNOSIS: One specimen of a new genus from the Brazilian bed cannot be assigned to any family, modern or extinct. This specimen has the hindwing M vein not connected to other veins by crossvenation. It is tentatively grouped with *Mesojassula* Evans (1956) which is based on an unassociated hind wing with similar venation. *Sinocercopis* Hong (1982) may belong to this family, but the venation is too inaccurately illustrated to make this certain.

Cercopion, new genus

Figures 32, 33

ETYMOLOGY: *cercos,* tail; *pion,* rich. Gender: feminine.

DIAGNOSIS: Hind wing with crossvein between branches of R; otherwise as in *Mesojassula,* but probably narrower.

TYPE SPECIES: *Cercopion reticulata,* n. sp.

DESCRIPTION: Head scarcely produced, tylus short; ocelli between eyes, separated by 2 diameters from hind margin of crown and eyes. Pronotum longer than crown. Tegmen deeply grooved on basal third near first longitudinal vein (S + M), reticulate apically, M apparently unbranched. Hind wing with narrow appendix and nearly parallel, unbranched veins, first 2 possibly connected by a crossvein (fig. 33). Fore and hind femora similar width before apex.

PLACEMENT: The tegmen is similar to that of modern Cercopidae as it shows the characteristic deep groove of the tegmen in the neighborhood of the first longitudinal vein (S + M), which is the dorsal expression of a large ventral flange that clips the tegmen against the pleuron when the wings are folded. The hindwing has M unbranched, also a cercopoid character. The ocelli, set far back from the tylus, and the lack of crossveins joining M on the hind wing to adjacent veins, exclude it from all extant families of Cercopoidea.

Cercopion reticulata, new species

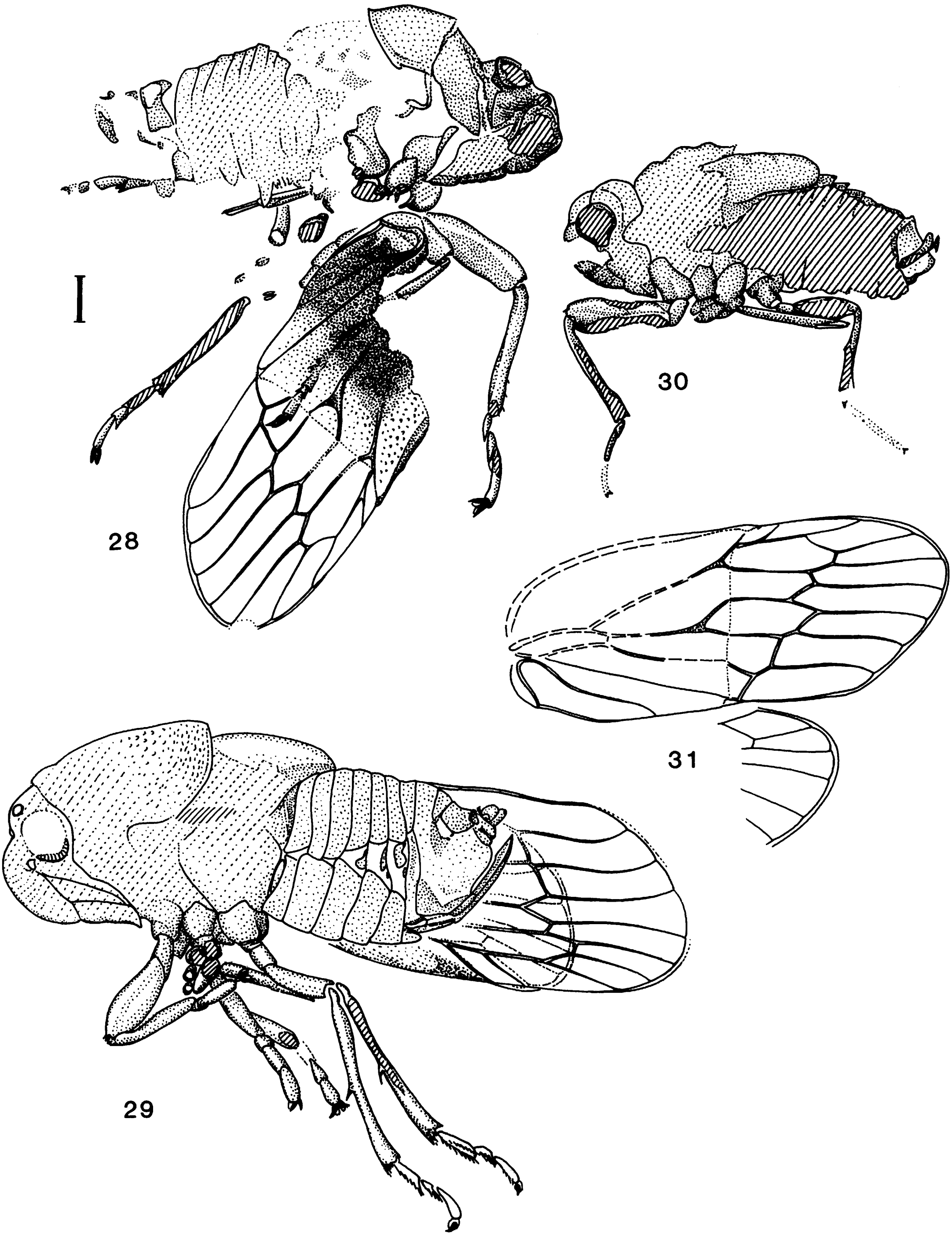
Figures 32, 33

ETYMOLOGY: *reticulata,* netlike.

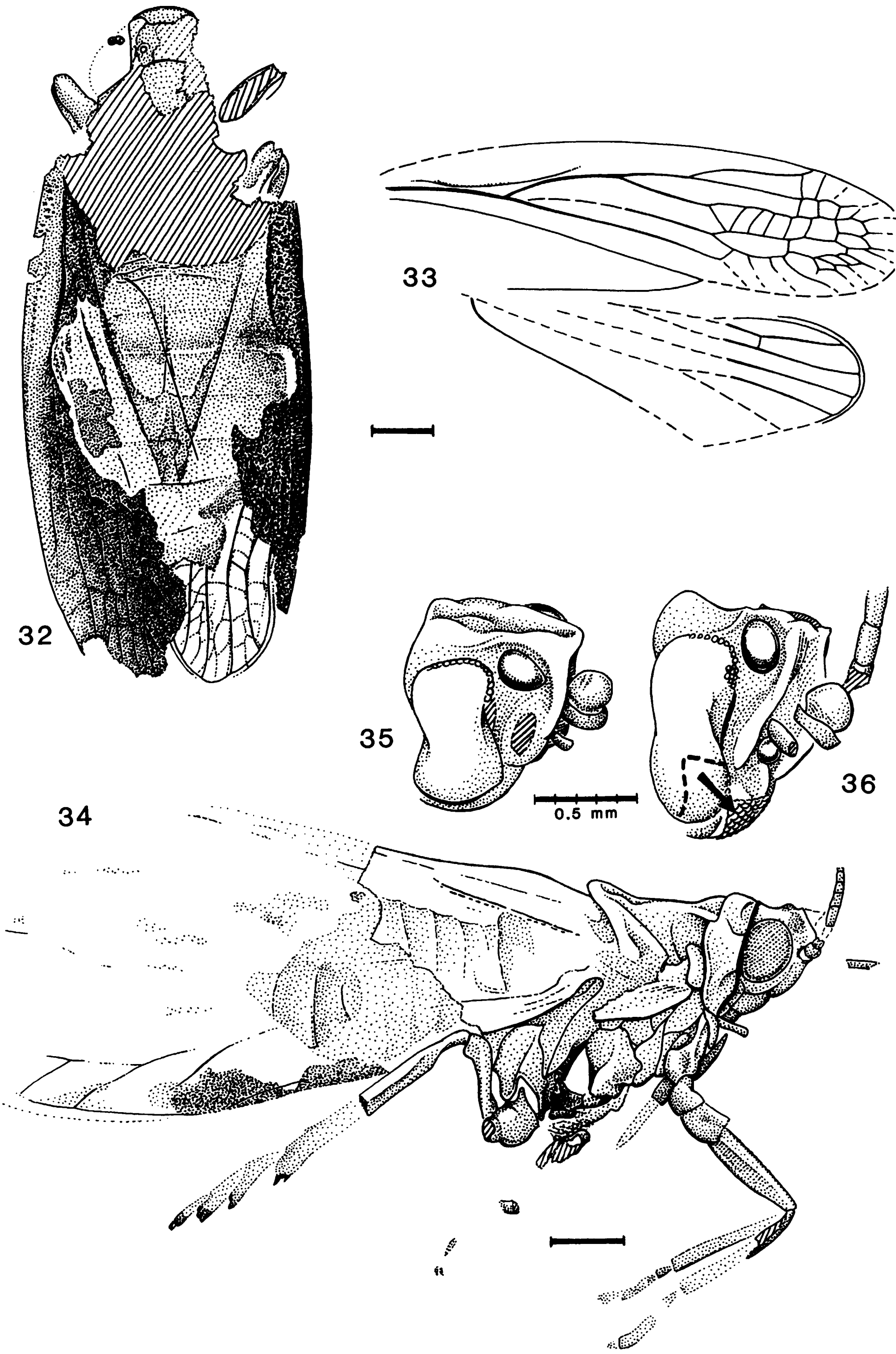
DIAGNOSIS: The only species in the genus (see generic diagnosis).

MATERIAL: *Holotype:* male, AMNH 43695, a dorsal compression lacking eyes; thorax "scalped"; clavus and adjacent parts of corium crushed; tegminal tips torn, exposing right hind wing tip; legs mostly concealed beneath body (fig. 32).

MEASUREMENTS: Length = 10.8; vertex length = 0.8; forefemur = 1.2.



Figs. 28–31. *Architettix compacta,* n. sp., Cicadoprosbolidae. **28,** Holotype, AMNH 43690; **29,** paratype, composite of AMNH 43600 + 43601; **30,** paratype nymph, AMNH 43683; **31,** venation (restored).



Figs. 32–36. *Cercopion reticulata,* n. sp., Cercopoidea. **32,** Holotype, AMNH 43695; **33,** venation (restored). 34–36. *Megaleurodes megocellata,* n. sp., Aleyrodoidea. **34,** Holotype, AMNH 43608, showing cast of left side of head; **35,** head of same, dorsolateral; **36,** same, ventrolateral, showing displacement of a section of eye surface.

ALEYRODOIDEA: BOREOSCYTIDAE?

A single fossil with poorly preserved wings appears to be an Aleyrodoid. However, it has 3-segmented tarsi and therefore cannot be assigned to any modern family. This specimen is tentatively assigned to the Boreoscytidae (Bekker-Migdisova, 1949b) which was based on unassociated Permian forewings which have similar costal crossveins and shape.

Megaleurodes, new genus

Figures 34–36

ETYMOLOGY: *megas,* great; *Aleurodes,* whitefly genus. Gender: feminine.

DIAGNOSIS: Only aleyrodoid with tegulae and 3-segmented tarsi.

TYPE SPECIES: *Megaleurodes megocellata,* n. sp.

DESCRIPTION: Head triangular in lateral aspect; crown concave between parallel ridges; frons scarcely projecting beyond genae; antennae large, scape broad and short, pedicel bulbous, more than 4 cylindrical, narrower segments forming flagellum; antennal ledges forming vertical carinae from tip of head to frons; eye constricted at middle; lateral ocelli before upper corners of eyes, very large; median ocellus half as large, at apex of frons between lateral carinae; clypellus and lora short, strongly depressed; rostrum broad, extending as far as middle coxae. Pronotum short and collarlike, broadly exposing mesonotum. Tegulae large, bean-shaped. Tegmen triangular, clavi linear, costa with strong crossveins near wing tip, clavus with 1 vein paralleling claval suture. Forelegs simple, unarmed; hind femur short, narrow, with prominent apex; hind tibia stout, more than twice as long as femur, with 1 lateral spur and several apical spines; hind tarsi 3-segmented, tarsomeres of slightly diminishing length, basal tarsomeres with wide ventral pectens.

PLACEMENT: The facial carinae, collarlike pronotum, large tegulae, and 3-segmented tarsi with broad pectens are distinctive fulgoroid characters. On the other hand, the divided eye, position of the ocelli, large antennae, and depressed face with large rostrum not pinned between forecoxae are distinctive characters of the Aleyrodoidea. From this combination of characters, it seems certain than whiteflies are a sister group of the Fulgoroidea and not Sternorrhyncha, as has been supposed. The Jurassic Fulgoridiidae, which have elongate, multiarticulate antennae and fulgoroid-like heads and bodies (Bode, 1953), are likely the common ancestor of both superfamilies.

Megaleurodes megocellata, new species

Figures 34–36

ETYMOLOGY: *megas,* great; *ocellata,* having little eyes [ocelli].

DIAGNOSIS: The only species in the genus (see generic diagnosis).

MATERIAL: *Holotype:* female(?), AMNH 43608, a lateral compression with head twisted to right (fig. 35), left eye nearly flat and circular (fig. 34), right eye strongly bean shaped; left antenna detached, in front of face over median ocellus (fig. 36), right antenna represented only by 2 flagellomeres beyond lateral carinae; middle legs missing; tarsi indicated by casts; all but base of right tegmen, basal half of right hind wing, and fragment of abdominal wall "scalped"; venation of left wings obscure except near tip of costa (fig. 34).

MEASUREMENTS: Length = 11.5; vertex length = 0.7; median length of pronotum = 0.8; hind tibia = 3.2; hind basitarsus = 1.0.

FULGOROIDEA

The Fulgoroidea form the second largest group of the Lower Cretaceous fauna in number of specimens, and show the greatest diversity in genera and species. Modern families represent only a small part of this ancient fauna. There is one genus of Achilidae and one specimen of a possible Cixiidae represented in Santana limestone. The majority of the Fulgoroidea belong to an extinct family that is closest to Cixiidae on the basis of retained plesiomorphs. Its apomorphic characters link the Delphacidae, Meenoplidae, Kinnaridae, and Cixiidae.

ACHILIDAE

Acixiites, new genus

Figures 37–42, 107–109

ETYMOLOGY: *Achilidae* + *Cixiidae,* fulgoroid families; *-ites,* petrified. Gender: feminine.

TYPE SPECIES: *Acixiites immodesta,* n. sp.

DIAGNOSIS: Venation simple; tegmen without crossvein on ampliated lobe behind Cu.

DESCRIPTION: Dorsoventrally compressed; head with narrow to broad crown without areas defined by carinae. Antennae below eyes. Rostrum long, extending beyond hind coxae nearly to apex of hind femora. Pronotum short, collarlike, with diverging carinae as in *Delphacodes* Fieber; mesonotum broadly exposed, without carinae. Tegmen lacking appendix; first 2 veins (R and M) each dichotomously 4-branched, third (Cu) 2-branched; crossveins numerous, variously arranged; ampliated lobe behind Cu as in Derbidae, but with spurious extension of claval suture as in Achilidae. Hind tibia slender, twice as long as femur, unarmed, apical pecten with more than 6 spines. Hind basitarsus about as long as others together; pectens on basal 2 tarsomeres with 9 or 10 spines. Abdominal segments 3–8 of similar size, basal segments much narrower; male anal tube (tergite 10) broad and flattened.

PLACEMENT: The dorsoventral compression and spurious extension of the claval suture onto the broadly overlapping tegminal tips place this genus in the Achilidae. The generalized venation appears more primitive than any known in modern genera. The venation resembles that of primitive Derbidae, but the elongate rostrum excludes the genus from that family. The general resemblance to Cixiidae is entirely due to primitive characters.

Acixiites immodesta, new species

Figures 37, 38, 40, 41, 107

ETYMOLOGY: *im-*, not; *modesta,* modest.

DIAGNOSIS: Crown less than 0.5 mm wide; tegminal crossveins few.

MATERIAL: *Holotype:* male, AMNH 43679, a dorsal compression with tegmina spread, exposing abdomen, a portion of a distorted hind wing and the apex of a hind tibia (Hamilton, in press: fig. 15); fore and middle legs concealed beneath body; genitalic capsule twisted dorsad, anal tube directed cephalad (fig. 37). *Paratypes:* 3♂: AMNH 43632, a dorsal compression lacking tegminal tips, exposing extreme apex of hind wing and genitalic capsule as in holotype (figs. 38, 107); AMNH 43678, ventral compression with wings spread, in poor condition; AMNH 43761, dorsal compression showing little detail except of hind tarsi (fig. 40) and wing tips; possible male genitalia exposed.

MEASUREMENTS: Length = 6.4 (type); body = 4.1–4.4; crown width at apex = 0.3–0.4; hind basitarsus = 0.6.

Acixiites costalis, new species

Figures 39, 42, 108, 109

ETYMOLOGY: *costalis,* costal [of the tegmen].

DIAGNOSIS: Crown more than 0.5 mm wide; tegminal crossveins numerous.

MATERIAL: *Holotype:* female, AMNH 43633, a dorsal compression with tegmina spread, exposing body and portions of hind wings; fore and middle legs concealed; abdomen "scalped," exposing hind legs, claws missing (fig. 108); a trace of a short ovipositor scarcely longer than pygofers (fig. 39). *Paratype:* male, AMNH 43636, a dorsal compression lacking tegminal tips, exposing genitalic capsule; head damaged during preparation (fig. 109).

MEASUREMENTS: Length = ca. 7.0; body of male = 5.3, female = 6.5; crown width at apex = 0.6; hind basitarsus = 0.7.

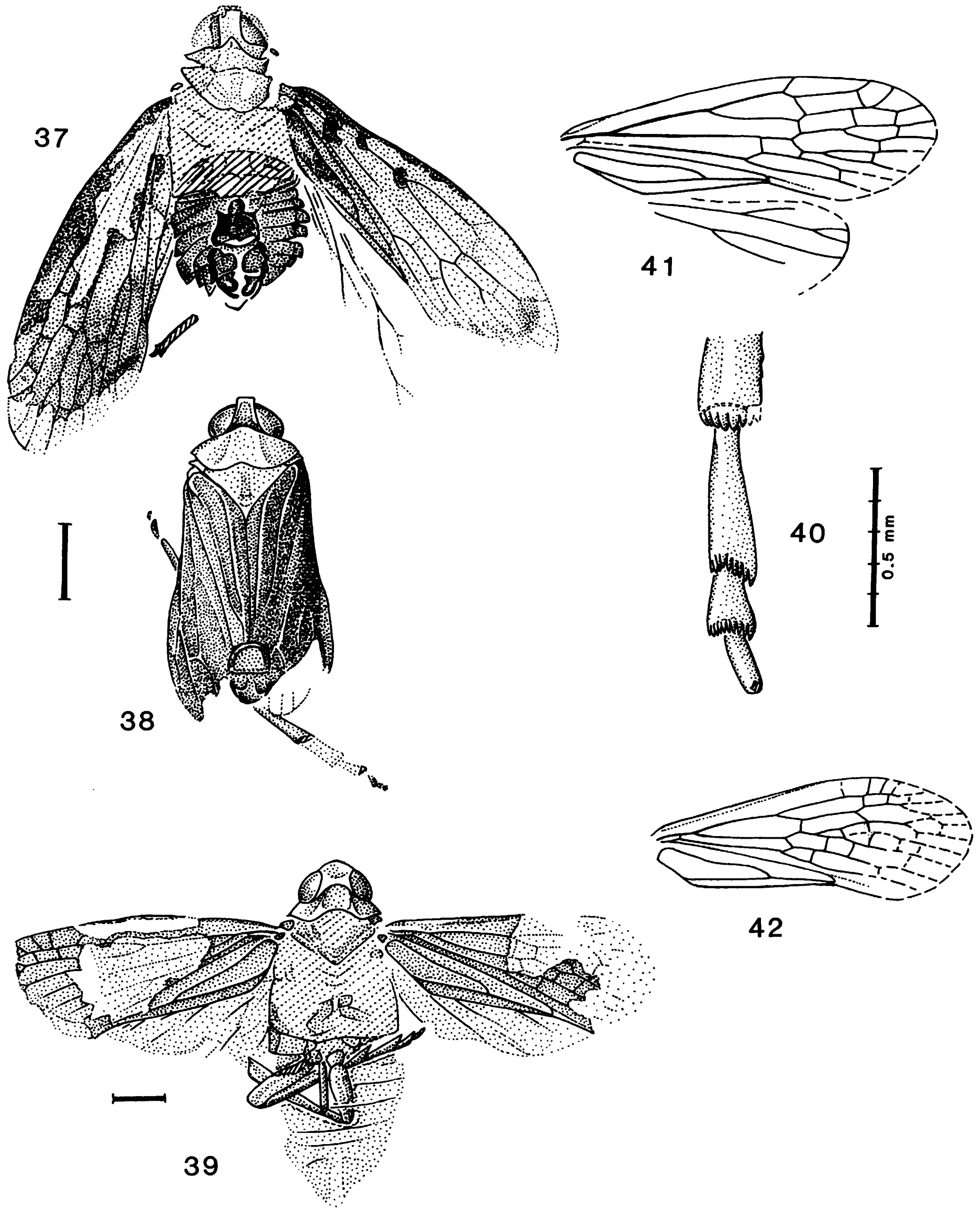
CIXIIDAE?

Genus unknown

Figure 106

MATERIAL: Male(?), AMNH 43692, a dorsal compression of a very large insect with tectiform wings, lacking head and pronotum, and with most of body and wings "scalped"; venation of hind wings obscure; hind tarsomeres excavated from matrix and attached, inverted, beside specimen (fig. 106).

MEASUREMENTS: Length = 25.5; hind basitarsus = 3.1; second tarsomere = 1.9.



Figs. 37–42. *Acixiites* spp., Achilidae. **37,** *A. immodesta,* n. sp. holotype, AMNH 43679; **38,** paratype of same, AMNH 43632; **39,** *A. costalis,* n. sp. holotype, AMNH 43633; **40,** hind tibial and tarsal pectens of paratype of *immodesta,* AMNH 43761; 41, tegminal venation of holotype of *immodesta* (reconstructed); **42,** same, of *costalis* (reconstructed).

PLACEMENT: The hind tarsus is similar to those of modern Cixiinae. No other critical diagnostic characters can be distinguished from this specimen despite its huge size for a cixiid.

LALACIDAE, NEW FAMILY

Figures 43–80, 110–133

TYPE GENUS: *Lalax,* new genus.

DIAGNOSIS: Heads narrow, bearing intermediate carinae (similar to those of some Delphacidae) defining a pair of shallow pits near apex of crown (figs. 52, 68, 73) and sometimes a median pit as well (figs. 50, 53). Median ocellus close to frons, as in Cixiidae. Tegmina held tectiform, often steeply so; reinforced margin beyond ambient vein (appendix) narrow, broadest on costa, with sclerous striations as in Kinnaridae and Meenoplidae; stigma absent or an extension of thickened margin. Appendix narrow on hind wing. Venation similar to that of modern Kinnaridae, with long r-m crossveins on both wing pairs, but usually with more veinal branchings (figs. 56, 58, 65, 69, 74, 75). Hind tarsi resemble those of some Meenoplidae, but basal pair of tarsomeres (and sometimes also tibia) of hind leg with pectens bearing movable setae (similar to pectens of Cicadellidae). Ovipositor short, strongly curved, sword-shaped with rounded tip. Three subfamilies.

PROTODELPHACINAE, NEW SUBFAMILY

DIAGNOSIS: Delphacid-like insects with large antennae (figs. 43–45), generalized venation (fig. 46), and pectens on tibia and both basal tarsomeres similar, with 12–14 short macrosetae set on narrow, elongate bases (fig. 47). One included tribe and genus.

PROTODELPHACINI, NEW TRIBE

Protodelphax, new genus

Figures 43–47, 110–114

ETYMOLOGY: *protos,* first; *Delphax,* a planthopper genus. Gender: masculine.

DIAGNOSIS: Antennal scape elongate; tibial and tarsal pectens with 12–14 macrosetae.

TYPE SPECIES: *Protodelphax miles,* n. sp.

DESCRIPTION: Head strongly laterally compressed, facial carinae parallel as far as clypellus. Antennae with scape elongate, emarginate on dorsal margin of tip, set before lower angle of notched eyes. Rostrum moderately long, exceeding middle coxae. Pronotum short, collarlike, without carinae; mesonotum not large, without carinae. Tegmen with 5 or 6 anteapical and 8–12 apical cells; appendix narrow except at stigma (fig. 46). Hind wing with 8 apical cells formed by crossveins between all main veins as far as Cu_2; most veins parallel and evenly spaced. Hind tibia stout, 50 percent longer than femur, armed with 3 or 4 minute spines on outer edge, apical pecten with 14 spines. Hind basitarsus 50 percent longer than others; pectens on basal 2 tarsomeres with 14 and 12 spines. Abdominal segments 3–8 short, basal segments much narrower; sternites of female telescoped next to base of ovipositor; male genital segment elongate, bearing short claspers; ovipositor curved dorsad, round-tipped, not exceeding pygofers.

PLACEMENT: The elongate antennae and telescoped abdominal sternites suggest a relationship to the Delphacidae. If this is a real relationship, then it is likely that the Delphacid hind tibial spurs are derived from the macrosetation of the tibial pecten.

Protodelphax miles, new species

Figures 43, 47

ETYMOLOGY: *miles,* soldier.

DIAGNOSIS: Length greater than 8.0 mm; face less than 2.0 mm long.

MATERIAL: *Holotype:* female, AMNH 43624, a lateral compression with left tegmen twisted, exposing abdomen and a portion of right hind wing; left hind leg, right fore and middle tarsi, and right hind femur missing (fig. 43).

MEASUREMENTS: Length = 8.3; body length = 4.8; face = 1.8; antenna = 0.9; hind basitarsus = 0.6.

DISCUSSION: The face of this species is two times as long as the antennae, the smallest head of any species in the genus.

Protodelphax macroceps, new species

Figures 44, 110

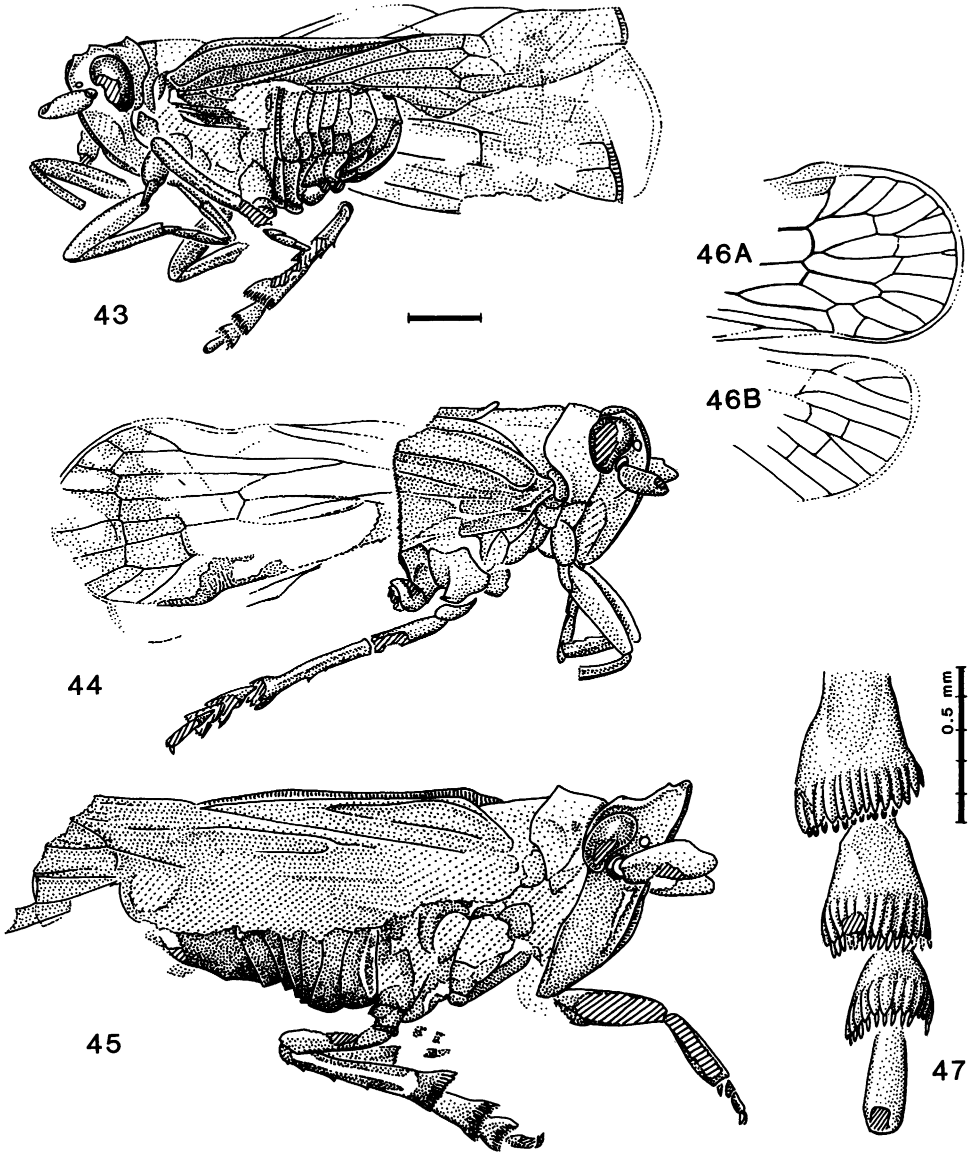
ETYMOLOGY: *macros,* long; *ceps,* head.

DIAGNOSIS: Length greater than 8.0 mm; face more than 2.0 mm long.

MATERIAL: *Holotype*: sex unknown, AMNH 43681, a lateral compression broken away behind hind coxae, exposing wings on far side; left hind leg, right middle leg, and fore and middle tarsi missing (fig. 110).

MEASUREMENTS: Length = 8.1; face = 2.2; antenna = 0.7; hind basitarsus = 0.8.

DISCUSSION: The face of this species is three times as long as the antennae. This is proportionately the longest head of any species in the genus.



Figs. 43–47. *Protodelphax* spp. **43,** *P. miles* n. sp. holotype, AMNH 43624; **44,** *P. macroceps,* n. sp. holotype, AMNH 43681; **45,** *P. rhinion,* n. sp. holotype, AMNH 43622; **46,** *Protodelphax* sp., venation (A from AMNH 43686, B from AMNH 43665); **47,** hind tibial and tarsal pectens of *P. miles* holotype.

Protodelphax rhinion, new species
Figures 45, 113

Etymology: *rhinos,* snout; *-ion,* having the nature of.

Diagnosis: Head with an apical hornlike process.

Material: *Holotype:* male, AMNH 43622, a lateral compression with costa and wing tips broken away, exposing abdominal sternites; right antennal scape damaged on lower margin; right legs and left middle leg missing (fig. 113).

Measurements: Length = 9.7; length of body = 7.7; face = 3.1; antenna = 1.2; hind basitarsus = 0.8.

Discussion: This species has the tip of the head distinctly produced.

Protodelphax chamus, new species
Figures 111, 112

ETYMOLOGY: *chamai,* dwarf.

DIAGNOSIS: Length less than 6.0 mm.

MATERIAL: *Holotype:* female, AMNH 43621, a lateral compression with wings poorly preserved; only tip of right hind leg preserved (fig. 112). *Paratype:* female, AMNH 43620, a lateral compression with crushed head and missing wing tips (fig. 111).

MEASUREMENTS: Length = 5.9; length of body = 3.9–4.0; face = 1.9; antenna = 0.7; hind basitarsus = 0.6.

DISCUSSION: This is the smallest species in the genus.

Protodelphax sp.
Figures 46, 114

MATERIAL: Male, AMNH 43665, a lateral compression split lengthwise showing large antennae and hind wing tip (fig. 46B); tegminal tips missing.

Male, AMNH 43686, a lateral compression with body "scalped"; antennae incomplete (fig. 114); tegminal tips well preserved (fig. 46A).

MEASUREMENTS: Length = 6.7 (AMNH 43665 to tips of hind wings = 6.4); length of body = 4.5–4.7; face = 1.8–2.0; antennae of AMNH 43665 = 1.0; basitarsus = 0.6.

DISCUSSION: These specimens appear to have the proportionately largest antennae in the genus, more than 1/7 the length of the body. They may be the same species, but are too poorly preserved to be described.

ANCORALINAE, NEW SUBFAMILY

DIAGNOSIS: Robust insects with veins prominently raised on upper surface of tegmen, and pectens on tibia and both basal tarsomeres with 10–15 narrow, elongate spine bases; small macrosetae set on tarsal pectens; hind basitarsus with concave plantar surface (fig. 54). Two included genera, distinctive enough to represent separate tribes.

ANCORALINI, NEW TRIBE

Ancorale, new genus
Figures 48–51, 115–118

ETYMOLOGY: *ancorale,* cable. Gender: neuter.

TYPE SPECIES: *Ancorale flaccidum,* n. sp.

DIAGNOSIS: Tegminal veins numerous, with helical ridges.

DESCRIPTION: Head moderately broad; median ocellus present; facial carinae diverging toward frons (fig. 49). Antennae small and globular. Rostrum short, extending between middle coxae. Pronotum short, collarlike, with diverging carinae meeting hind margin; mesonotum large, with median groove. Tegmen with very numerous, close-packed, prominent veins clearly showing helical tracheal reinforcements; appendix narrow. Hind wing tip with similar dense venation (fig. 48). Hind tibia stout, twice as long as femur, unarmed, apical pecten with 13 spines. Hind tarsomeres of similar lengths, distotarsus very slender; pecten on basitarsus with 10 spines; second tarsomere almost as wide, but pecten not preserved. Male genital segment elongate, bearing short claspers; ovipositor scarcely exceeding short pygofers.

PLACEMENT: The venation is unique in the family. Similar veinal proliferation without strong crossveins is known only in higher Fulgoroidea (e.g., *Phylloscelis*). Jurassic *Ricaniites* Handlirsch (1908) has rows of crossveins before the apex.

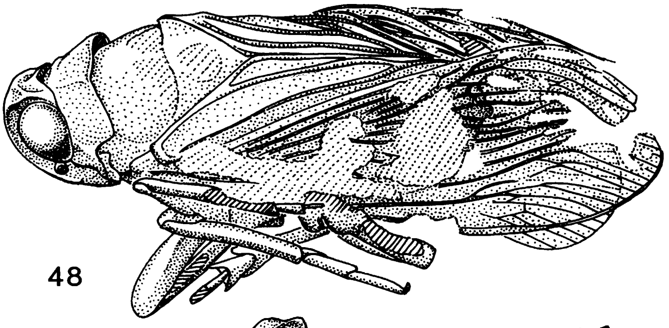
Ancorale flaccidum, new species
Figures 48, 49, 115–117

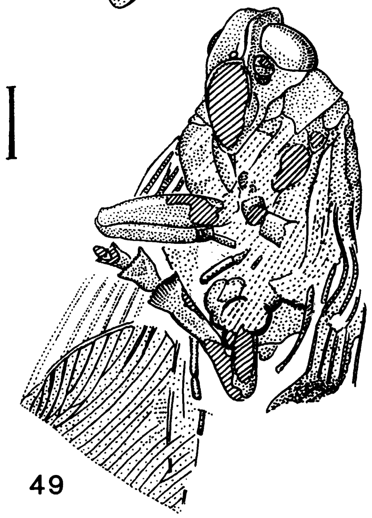
ETYMOLOGY: *flaccidum,* drooping.

DIAGNOSIS: Length of body between 6.0 and 7.0 mm.

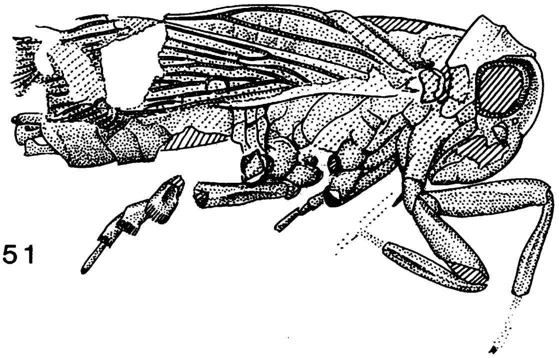
MATERIAL: *Holotype:* female, AMNH 43609, a dorsolateral compression with pronotum disjointed, exposing underlying mesonotum (fig. 48); tegmina pressed against body; legs doubled under body. *Paratypes:* 3 ♂: AMNH 43626, a ventral compression with right tegmen spread, pleated at tip, rest of specimen poorly preserved (fig. 116); AMNH 43680, a lateral compression showing venation just behind abdomen; details poorly preserved (fig. 115); male(?), AMNH 43682, a ventrolateral compression with right tegmen folded over at tip, right foreleg and left hind leg lacking tip of tarsi, other legs and wings absent; abdomen missing (fig. 49); fragments of overburden retaining veins were glued below specimen (fig. 117).

MEASUREMENTS: Length, male = 8.4–8.5,


48


49


50


51

Figs. 48–51. *Ancorale* spp. **48,** *A. flaccidum,* n. sp. holotype, AMNH 43609; **49,** paratype of same, AMNH 43682; **50,** *Ancorale* sp., AMNH 43677; **51,** *A. aschemon,* n. sp. holotype, AMNH 43625.

female = 9.3; length of body 6.5–6.7; crown at apex = 0.3; hind basitarsus = 0.7.

DISCUSSION: The tegmina are usually crumpled, folded, or twisted, suggesting that the wings were unusually flaccid despite the large number of veins. This, however, may be an artifact of preservation. The well-preserved bodies indicate that they were not teneral.

Ancorale aschemon, new species

Figure 51

ETYMOLOGY: *aschemon,* misshapen.

DIAGNOSIS: Length of body more than 7.0 mm.

MATERIAL: *Holotype:* male, AMNH 43625, a lateral compression showing distinctly inflated frons (fig. 51); base of abdomen damaged, foretarsi, middle legs, parts of hind femora, and tegminal tips missing.

MEASUREMENTS: Length of body = 7.4; crown at apex = 0.3; hind basitarsus = 0.7.

DISCUSSION: The inflated frons of this specimen may be an artifact of preservation.

Ancorale sp.

Figures 50, 118

Male, AMNH 43627, a dorsal compression; head, thorax, and anal tube "scalped"; details poorly preserved.

Male, AMNH 43677, a dorsal compression with tegminal tips poorly preserved, legs folded under body (figs. 50, 118).

MEASUREMENTS: Length = 7.5; length of body 5.8; crown at apex 0.4.

DISCUSSION: If both specimens belong to the same species, this is the smallest species in its genus, with body less than 6.0 mm. They are too poorly preserved to warrant description.

KINNAROCIXIINI, NEW TRIBE

Kinnarocixius, new genus

Figures 52–57, 119, 120

ETYMOLOGY: *Kinnara* + *Cixius,* two fulgoroid genera. Gender: masculine.

TYPE SPECIES: *Kinnarocixius quassus,* n. sp.

DIAGNOSIS: Tegminal veins strongly convex; tibial and tarsal pectens with 15 spine bases each.

DESCRIPTION: Head scarcely produced, long, eyes well separated. Pronotum and mesonotum without carinae. Tegmen with strongly convex veins forming 5 or 6 anteapical and 9–11 apical cells; base of outer anteapical cell (crossvein r-m) long; appendix narrow except on costa where it forms a bulla. Hind wing with 6 apical cells; discal crossvein r-m long (fig. 56). Hind tibia stout, armed with at least 1 spine on outer edge, apical pecten with 15 spines. Hind tarsomeres of diminishing size; pectens on basal 2 tarsomeres each with 15 spines set with stout setae (fig. 54).

PLACEMENT: The prominent tegminal veins and characteristic hind tarsi indicate that this genus is allied to *Ancorale.* In other respects it seems to be a generalized member of the Lalacidae.

Kinnarocixius quassus, new species

Figures 52–55, 119, 133

ETYMOLOGY: *quassus,* shattered.

DIAGNOSIS: Tegminal Rs 3-branched, M symmetrically branched; hind wing without triangular discal cell.

MATERIAL: *Holotype:* male, AMNH 43617, a dorsolateral compression with left tegmen raised and folded over at tip; hind margin of pronotum damaged; foretarsi, middle legs, and base of right hind tibia missing (fig. 52); right hind tarsus and apex of tibia removed from matrix and attached, inverted, beside specimen (fig. 119). *Paratype:* male, AMNH 44105, a dorsal compression with wings partly spread, abdomen scalped (fig. 53), detail poor except on head and tegminal tips (fig. 133).

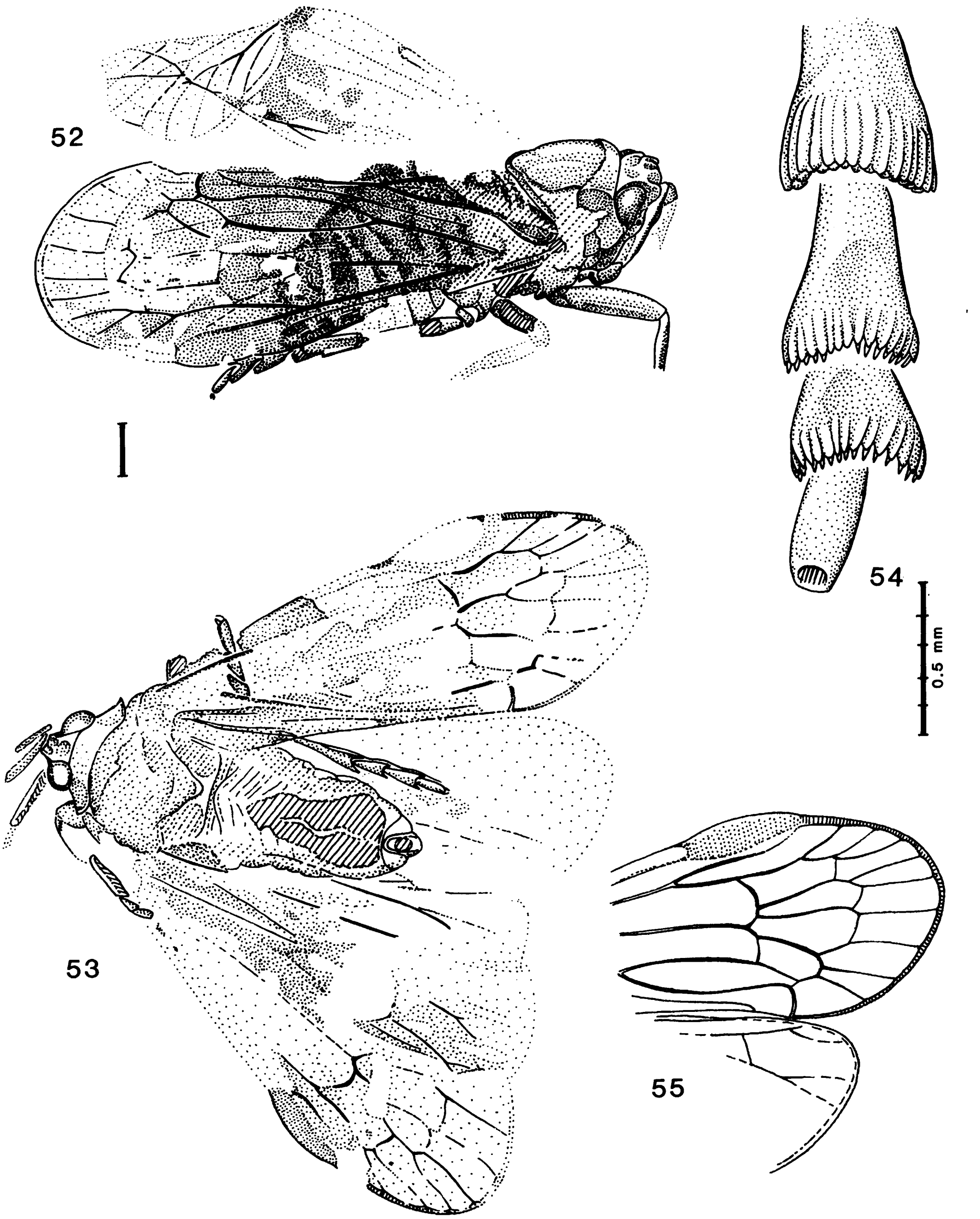
MEASUREMENTS: Length = 12.7 (type)–13.1; crown at apex = 0.4–0.5; length of tegmen = 11.2–11.4; hind basitarsus = 0.8–0.9.

DISCUSSION: The venation at the tips of all four tegmina show considerable differences. The reconstructed venation (fig. 55) shows an intermediate condition.

?*Kinnarocixius* sp.

Figures 56, 57, 120

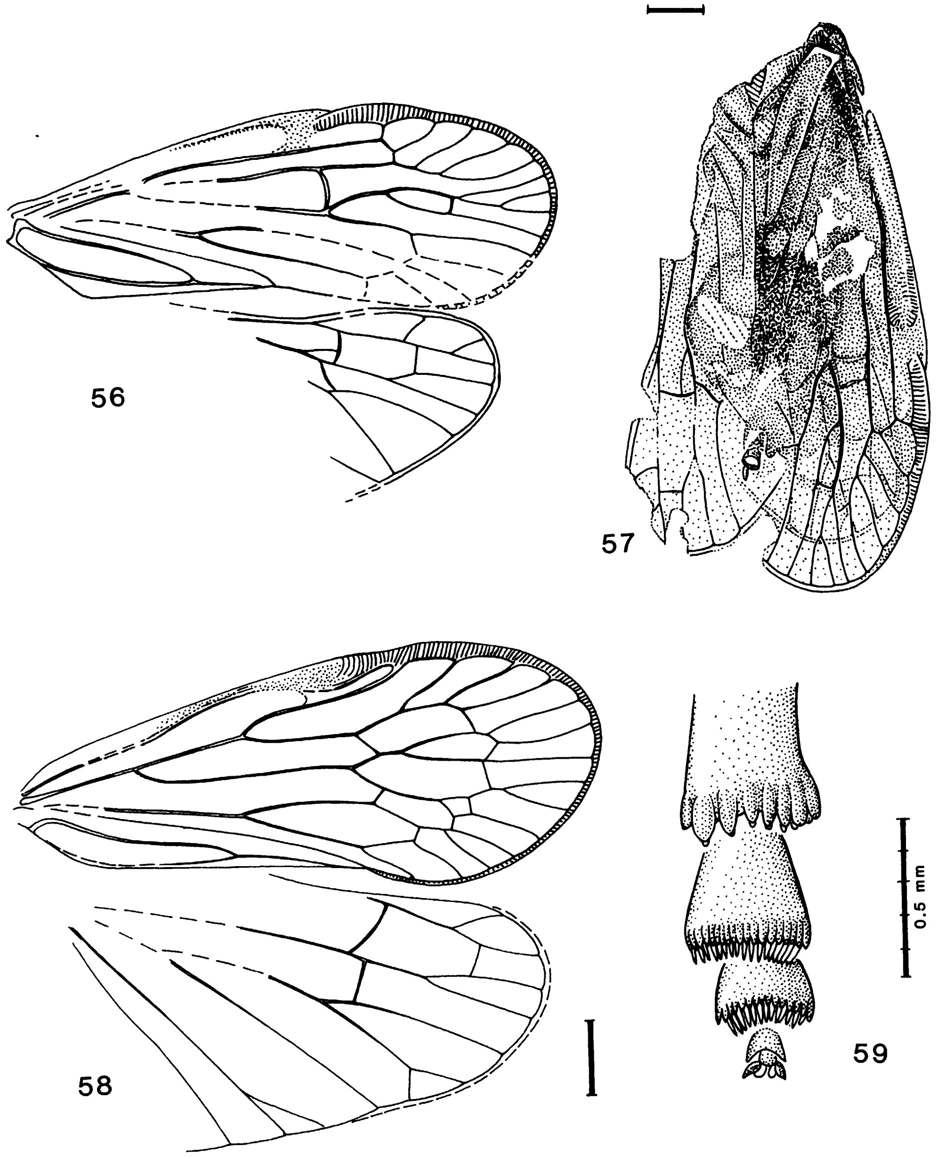
MATERIAL: Male, AMNH 43614, a dorsal compression of a right tegmen and hind wings on a badly crushed, headless and limbless trunk (fig. 120).



Figs. 52–55. *Kinnarocixius quassus*, n. sp. **52**, Holotype, AMNH 43617; **53**, paratype, AMNH 44105; **54**, hind tibial and tarsal pectens of holotype; **55**, venation (reconstructed).

Measurements: Length of tegmen = 10.4 mm.

Discussion: The venation of this specimen bears obvious similarities to that of the other specimens assigned to this genus (fig. 57). Its salient differences are as follows: tegmen with substigmal cell small, Rs 4-branched instead of 3-branched, stem of Rs longer, M asymmetrically branched; hind wing with small, triangular discal cell adjacent to r-m (fig. 56).



Figs. 56–59. *Kinnarocixius* sp., AMNH 43614, reconstructed venation and fossil. 58–59. *Lalax mutabilis,* n. sp. **58,** reconstructed venation; **59,** hind tibial and tarsal pectens of AMNH 43615.

The specimen is in too poor condition to warrant description.

LALACINAE, NEW SUBFAMILY

DIAGNOSIS: Dictyopharid-like insects with prominent appendix on costal margin, long r-m crossvein on hind wing (figs. 58, 65, 69, 74, 75), short, deeply channeled hind tibiae with pectens reduced to 6–8 large spines with at most a trace of setae at tips, and tarsal pectens contrastingly densely packed, usually with prominent setae (figs. 59, 66, 70). Five included genera in 2 tribes.

LALACINI, NEW TRIBE

DIAGNOSIS: Hind tibial pecten with 6–8 short spines. Two included genera.

Lalax, new genus

Figures 58–62, 127, 128

ETYMOLOGY: *lalax,* a croaker. Gender: masculine.

TYPE SPECIES: *Lalax mutabilis,* n. sp.

DIAGNOSIS: The only fulgoroid with a strongly inflated frons.

DESCRIPTION: Head narrow; carinae ending at upper margin of bulbous, protruding frons. Antennae rather slender, set before notched lower angle of eyes. Rostrum not long, extending between middle coxae. Pronotum short, collarlike, with carinae paralleling hind margin; mesonotum moderately large, without carinae. Tegmen delicate, similar to that of *Vulcanoia* but with cubital veins meeting margin transversely, and few supernumerary veinal branchings defining 5 anteapical and 13 apical cells; appendix narrow, widest on costa, with well-defined stigmal area (fig. 58). Hind wing nearly as long as tegmen, with simple venation. Fore and hind femora of similar length. Hind tibia short and slender, 50 percent longer than femur, unarmed, apical pecten with 8 stout spines tipped by minute, stout setae (fig. 59). Hind basitarsus as long as other tarsomeres together; pectens on basal 2 tarsomeres with 19 and 15 spines set with long setae. Abdomen short and rounded, segments 3–8 of similar lengths, basal segments narrower.

PLACEMENT: The hind tibial pecten has more and smaller spines than those of the Carpopodini, but they are arranged in a transverse row as in that tribe.

Lalax mutabilis, new species

Figures 58–62, 127, 128

ETYMOLOGY: *mutabilis,* changeable.

DIAGNOSIS: Body length between 9.0 and 11.0 mm; crown rounded.

MATERIAL: *Holotype:* male, AMNH 43685, a lateral compression with right wings dragged downward; metathorax and abdominal sterna "scalped"; only fragments of legs on one side of body preserved (fig. 60). *Paratypes:* 1♂, 2♀: female, AMNH 43615, a lateral compression with abdomen and 1 hind wing dragged downward (fig. 128); a bulbous sac overlaps the tegminal base (fig. 62) which may represent parasitism by a dryinid; female, AMNH 43618, a lateral compression in poor condition; male, AMNH 43684, a lateral compression in similar condition to holotype, but with genitalia poorly preserved, frons missing (figs. 61, 127).

MEASUREMENTS: Length, male = 9.3 (type)–9.5, female = 10.3–10.6; body length, male = 5.6–5.8, female = 8.2; median length of pronotum = 0.6–0.7; hind tibia = 1.7–1.8; hind basitarsus = 0.6.

DISCUSSION: The venation usually differs somewhat on opposite sides of the same insect, most noticeably on the hind wing tips (figs. 60–62).

Lalax sp.

MATERIAL: Male(?), AMNH 43628, a lateral compression; detail poorly preserved.

MEASUREMENTS: Length = 7.5; pronotum = 0.5; hind basitarsus = 0.8.

DISCUSSION: This is the smallest species in the genus, with length less than 9.0 mm. Its crown is distinctively pointed, but it is too poorly preserved to warrant description.

Patulopes, new genus

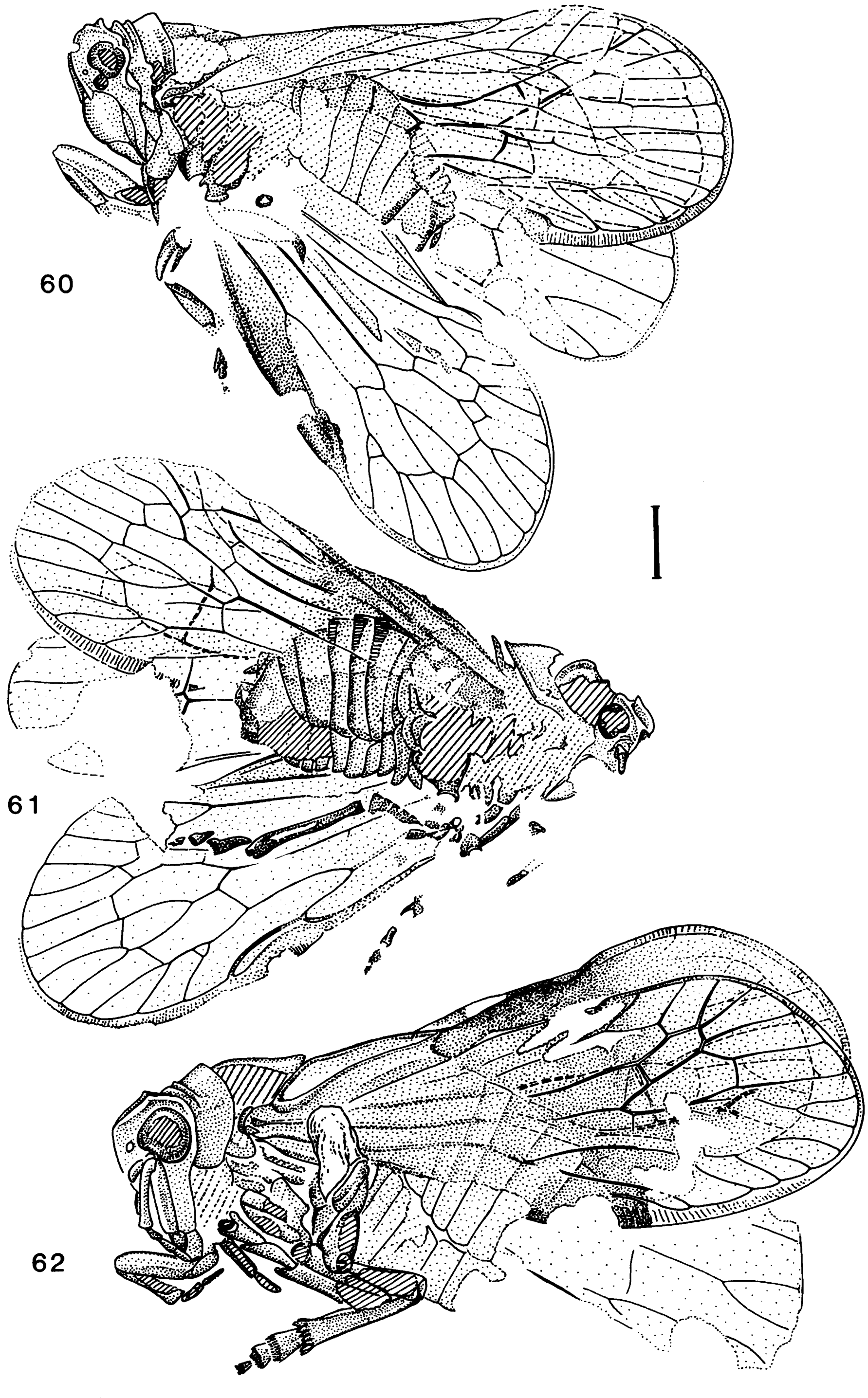
Figures 63–66, 131, 132

ETYMOLOGY: *patulus,* broad, spread out; *pes,* foot. Gender: feminine.

TYPE SPECIES: *Patulopes setosa,* n. sp.

DIAGNOSIS: Pectens on basal 2 tarsomeres broadly flared, with 23 and 18 macrosetae.

DESCRIPTION: Head narrow; short carinae ending at upper margin of frons. Antennae rather slender, set above curved carinae below front of eyes. Rostrum long, extending between hind coxae. Pronotum very short, almost divided behind eye, with carinae diverging toward hind margin; mesonotum moderately large, without carinae. Tegmen slender, with simple venation defining 1 anteapical and 10 or 11 apical cells; appendix narrow, widest on costa, with poorly defined stigmal area (fig. 65). Hind wing nearly as long as tegmen, with simple venation. Fore and hind femora of similar length. Hind tibia short and stout, 50 percent longer than femur, unarmed, apical pecten oblique, with 6 very short spines lacking setae (fig. 66). Hind tarsomeres of diminishing length; basitarsus with concave plantar area; pectens on basal 2 tarsomeres broadly flared, with 23 and 18 spines set with long setae. Abdomen short, segments



Figs. 60–62. *Lalax mutabilis,* n. sp. **60,** Holotype, AMNH 43685; **61,** paratype, AMNH 43684; **62,** paratype, AMNH 43615.

3–8 of similar lengths, basal segments narrower; ovipositor weakly curved dorsad, apex bluntly pointed.

PLACEMENT: The hind tibia only 50 percent longer than the femur, and the small antennae show its affinities to *Lalax*.

Patulopes setosa, new species
Figures 64, 66

ETYMOLOGY: *setosa,* bristly.

DIAGNOSIS: Tegminal veins indistinct, outlined in setae.

MATERIAL: *Holotype:* female, AMNH 43623, a lateral compression with left facial carina broken, exposing median ocellus (fig. 64); left wings damaged, exposing abdomen; tegminal veins obscure, outlined in setae; only fore and hind legs on one side of body preserved.

MEASUREMENTS: Length = 9.2; body length = 6.0; median length of pronotum = 0.5; hind tibia = 1.8; hind basitarsus = 0.8.

Patulopes myndoides, new species
Figures 63, 65, 131, 132

ETYMOLOGY: *Mynda,* a fulgoroid genus; *-oides,* like.

DIAGNOSIS: Tegminal veins distinct.

MATERIAL: *Holotype:* male, AMNH 43631, a lateral compression with costal margin broken (fig. 63), abdomen poorly preserved (fig. 131). *Paratype:* female, AMNH 43629, a lateral compression showing venation (fig. 65); rest of body very poorly preserved (fig. 132).

MEASUREMENTS: Length, male = 8.2, female = 8.8; body length, male = 5.6, female = 6.3; median length of pronotum = 0.5; hind tibia = 1.6; hind basitarsus = 0.7.

?*Patulopes* sp.

MATERIAL: Male(?), AMNH 43610, a lateral compression with head missing; details poorly preserved.

MEASUREMENTS: Length, excluding head = 7.2 mm.

DISCUSSION: this specimen is tentatively associated with *Patulopes* due to its oblique tibial pecten. Its broad tegmen with complex venation is distinctive, but the specimen is too poorly preserved to warrant description.

CARPOPODINI, NEW TRIBE

DIAGNOSIS: Hind tibial pecten with 6 large spines. Three included genera.

Carpopodus, new genus
Figures 67–70, 121, 122

ETYMOLOGY: *carpus,* wrist; *podos,* foot. Gender: masculine.

TYPE SPECIES: *Carpopodus difficilis,* n. sp.

DIAGNOSIS: Foretibia 0.7 times or more length of face; tibial pecten with 6 prominent spines; basal tarsomere pectens of 16 and 22 setae.

DESCRIPTION: Head strongly laterally compressed, facial carinae parallel as far as ocelli, flaring to end near midlength of clypellus (fig. 68). Antennae of usual fulgoroid shape, set before lower angle of eyes. Rostrum moderately long, extending to hind coxae. Pronotum short, collar-like, with carinae paralleling hind margin; mesonotum large, without carinae. Tegmen with all corial veins ramifying, number of crossveins variable; appendix narrow except on costa (fig. 69); most veins parallel and evenly spaced. Forefemora twice as long as hind femora. Hind tibia short and stout, twice as long as femur, laterally unarmed, deeply channeled, apical pecten with 6 fingerlike spines bearing tiny, rounded setae at tips (fig. 70). Hind basitarsus slightly longer than second tarsomere, 50 percent longer than distitarsomere; pectens on basal 2 tarsomeres with 16 and 22 spines set with short setae. Abdominal segments 2–8 of similar lengths, basal segment much narrower; ovipositor weakly curved, round-tipped, exceeding short pygofers.

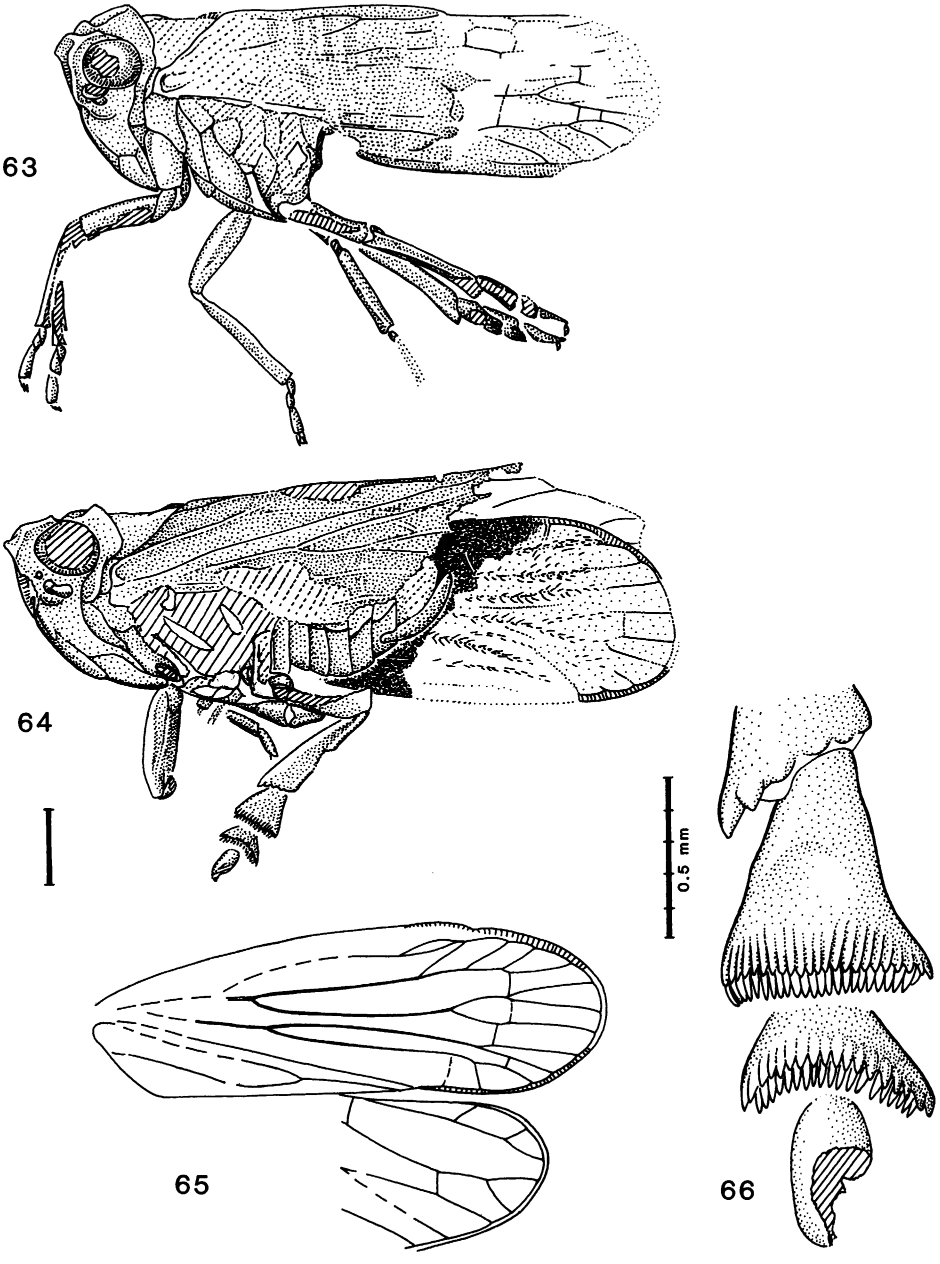
PLACEMENT: The hind legs are distinctive of the Carpopodini. The numerous branches of the tegminal veins and the long forefemora distinguish it from the other genera in the tribe.

Carpopodus difficilis, new species
Figures 67, 69, 70

ETYMOLOGY: *difficilis,* troublesome.

DIAGNOSIS: Forefemur 0.8 times face length; venation not reticulate.

MATERIAL: *Holotype:* female, AMNH 43604, a lateral compression with costal margin, clypellus and lower end of right facial

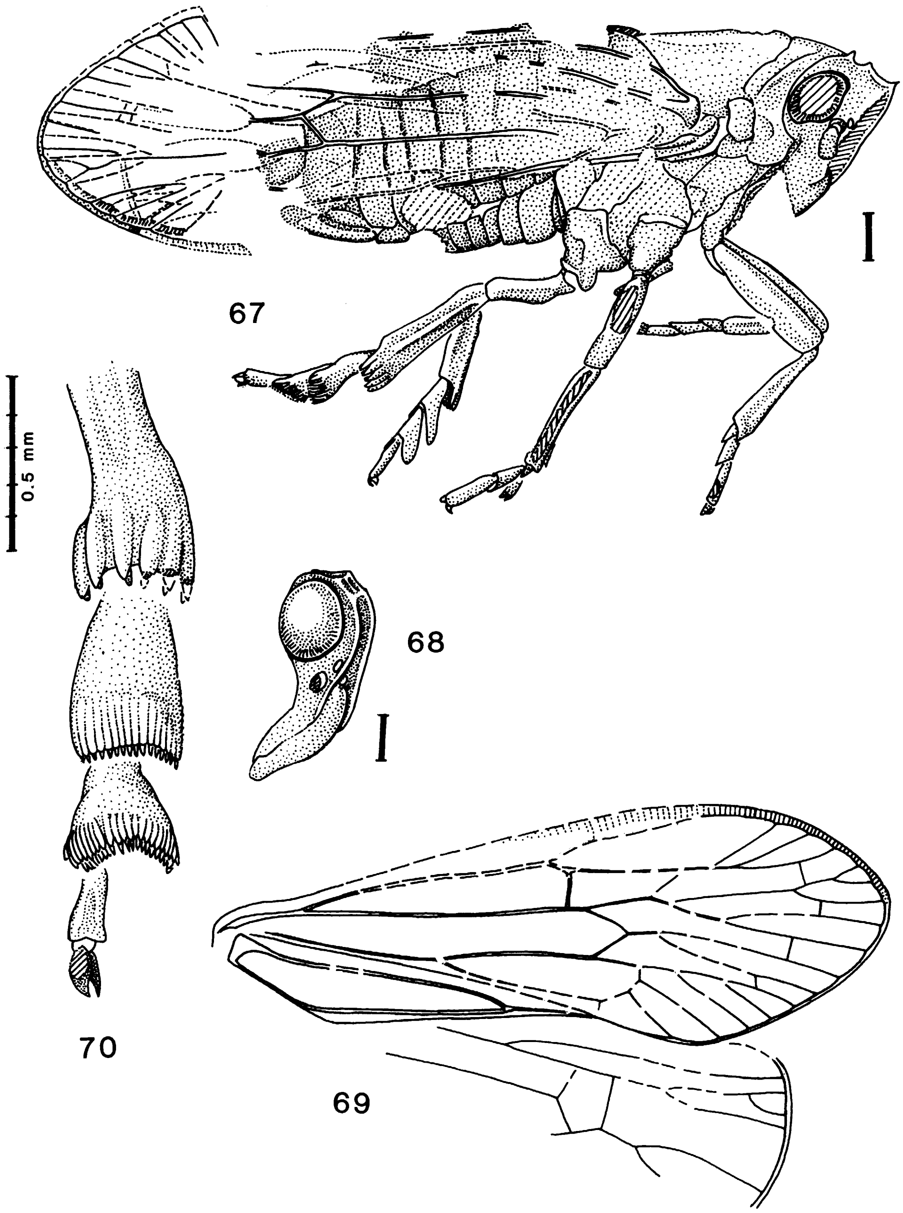


Figs. 63–66. *Patulopes* spp. **63,** *P. myndoides,* n. sp. holotype, AMNH 43631; **64,** *P. setosa,* n. sp. holotype, AMNH 43623; **65,** venation of AMNH 43629; **66,** hind tibial and tarsal pectens of holotype.

carina damaged; left middle leg and left hind femur deep in matrix.

MEASUREMENTS: Length = 17.6; body length = 13.7; face = 4.0; median length of pronotum = 1.2; forefemur = 3.2; hind basitarsus = 1.4.

DISCUSSION: Because all four wings are superimposed in this fossil (fig. 67), and the venation is complex, great difficulty attended the identification of the exact veinal branching pattern. The reconstruction of the venation (fig. 69) is therefore tentative.



Figs. 67–70. *Carpopodus* spp. **67,** *C. difficilis,* n. sp. holotype, AMNH 43604; **68,** head of *Carpopodus* sp. B, AMNH 43619, anterolateral aspect; **69,** venation (reconstructed); **70,** hind tibial and tarsal pectens of AMNH 43604.

Carpopodus sp. A
Figure 121

MATERIAL: sex unknown, AMNH 43602, a poorly preserved lateral compression lacking frons and clypellus, bases of legs and tegmina, and most of abdomen; reticulate venation apparent beyond body (fig. 121).

MEASUREMENTS: Length = 18.5; face = 3.4; median length of pronotum = 1.0; forefemur = 3.0; hind basitarsus = 1.4.

DISCUSSION: This fossil resembles *C. diffi-*

cilis, but has reticulate venation and a longer forefemur, 0.9 times face length. It is too poorly preserved to warrant description.

Carpopodus sp. B

Figures 68, 122

DIAGNOSIS: Forefemur 0.7 times face length.

MATERIAL: Sex unknown, AMNH 43619, a lateral compression with wings, hind legs, and abdomen missing (fig. 122). Face well preserved, in anterolateral view showing median ocellus (fig. 68).

MEASUREMENTS: Face = 2.7; forefemur = 1.9.

Discussion: This fossil is placed in *Carpopodus* by the large size of the forefemora, although its body is much smaller than that of its congeners. It is too poorly preserved to warrant description.

Psestocixius, new genus

Figures 71–75, 123, 125

ETYMOLOGY: *psestos,* scraped; *Cixius,* a fulgoroid genus. Gender: masculine.

DIAGNOSIS: Appendix wide on costa; tarsi and pectens similar to those of *Carpopodus.*

TYPE SPECIES: *Psestocixius fuscus,* n. sp.

DESCRIPTION: head laterally compressed at tip, facial carinae diverging as far as midlength of clypellus (fig. 73). Antennae of usual fulgoroid shape, set below eyes. Rostrum long, extending between hind coxae. Pronotum short, collarlike, with weak, divergent carinae not reaching hind margin; mesonotum moderately large, without carinae. Tegmen broad at tip, superficially resembling those of *Cixius,* with a few supernumerary veinal branchings defining 12 or 13 apical cells; appendix prominent, widest on costa (figs. 74, 75). Forefemora 50 percent longer than hind femora. Hind tibia short and stout, twice as long as femur, armed with 2 small spines on outer edge; tarsi and pectens similar to those of *Carpopodus* (fig. 70), with an indeterminate but large number of tarsal spines. Abdomen as in *Carpopodus.*

PLACEMENT: The hind legs are distinctive of the Carpopodini. The broad wing tips and prominent tegminal appendix distinguish it from the other genera in the tribe.

Psestocixius fuscus, new species

Figures 71, 74, 123

ETYMOLOGY: *fuscus,* dusky.

DIAGNOSIS: Tegmina embrowned (heavily sclerotized?).

MATERIAL: *Holotype:* male, AMNH 43616, a lateral compression with right hind femur concealed by body, left middle and left hind leg missing (fig. 71). *Paratype:* male, AMNH 43687, a lateral compression with head and legs poorly preserved, wing tips well defined (fig. 123).

MEASUREMENTS: Length = 11.3–11.6 (type); body length = 8.2–8.3; median length of pronotum = 0.7–0.8; hind basitarsus = 1.0–1.2.

Psestocixius delphax, new species

Figures 72, 73, 125

ETYMOLOGY: *delphax,* young pig.

DIAGNOSIS: Tip of head prolonged into distinctive "snout."

MATERIAL: *Holotype*: male, AMNH 43607, a lateral compression with abdomen poorly indicated, left legs concealed by body (fig. 125); face well preserved, showing median ocellus in oblique view (fig. 73).

MEASUREMENTS: Length = 10.4; median length of pronotum = 0.6; hind tibia = 2.3; hind basitarsus = 1.0.

Vulcanoia Martins-Neto

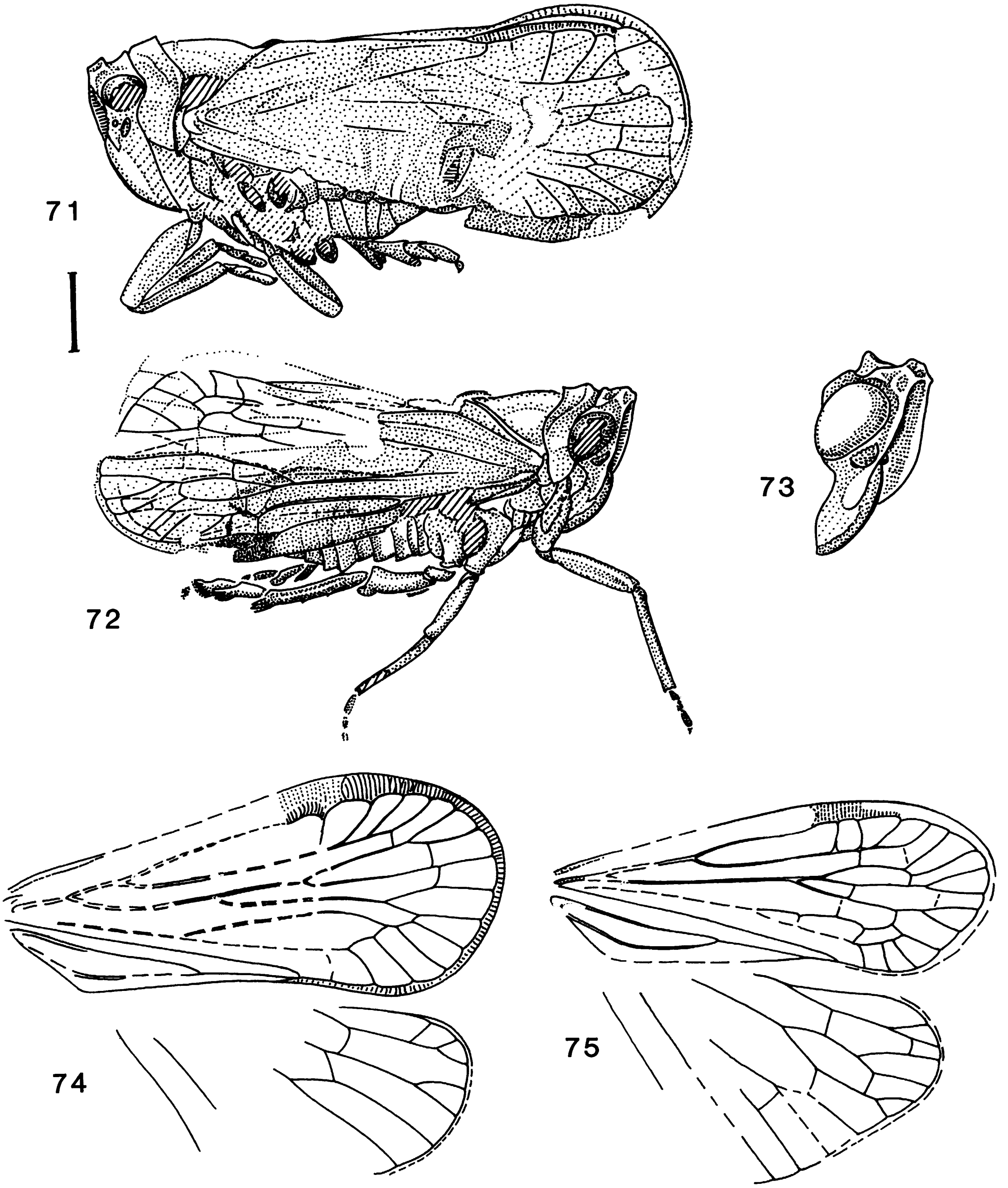
Figures 76–80, 124, 126, 129, 130

Vulcanoia Martins-Neto, 1988: 313.

DIAGNOSIS: Four cubital veins meet anal edge of tegmen nearly vertically.

TYPE SPECIES: *Vulcanoia membranosa* Martins-Neto, 1988.

DESCRIPTION: Head laterally compressed, facial carinae parallel as far as clypellus (fig. 79). Antennae of usual fulgoroid shape, set below eyes. Rostrum extending to hind coxae. Pronotum longer than crown, without carinae; mesonotum large, without carinae. Tegmen broad at tip, superficially resembling that of *Cixius,* with first branch of R thicker than other veins, short and curved toward stigmal area on costal margin; M and Cu with numerous branchings defining 10 or 11 apical cells, with cubital cells nearly perpendicular to wing edge (figs. 78, 80); appendix as in



Figs. 71–75. *Psestocixius* spp. **71,** *P. fuscus,* n. sp. holotype, AMNH 43616; **72,** *P. delphax,* n. sp. holotype, AMNH 43607; **73,** head of AMNH 43607, anterolateral aspect; **74,** venation of *P. fuscus* paratype, AMNH 43687; **75,** same, of *P. delphax.*

Lalax (fig. 58). Forefemora slightly longer than hind femora. Hind tibia short and stout, 50 percent longer than femur, unarmed; tarsi and pectens similar to those of *Carpopodus* (fig. 70), with an indeterminate but large number of tarsal spines. Abdomen as in *Carpopodus.*

Placement: The hind legs are distinctive of the Carpopodini. The broad wing tips and cubital branches meeting the costa nearly vertically distinguish it from the other genera in the tribe.

Vulcanoia apicalis, new species

Figures 76–78, 126

Etymology: *apicalis,* apical.

Diagnosis: Numerous cells confined to apical ¼ of hind wing.

Material: *Holotype:* female, AMNH 43603, a lateral compression with facial carinae pressed together (fig. 77) and body "scalped"; clypellus, left front leg, both middle legs, left hind femur and upper part of tibia missing (fig. 126); cells confined to apex of tegmen (fig. 78).

Measurements: Length = 15.7; body length = 11.1; median length of pronotum = 1.1; tegmen = 12.8; hind tibia = 2.9; hind basitarsus = 1.3.

Discussion: The tegmen of this specimen appears to be narrower than that of other members of the genus, and the pronotum is much longer. It may prove to belong to an as yet unrecognized genus.

Vulcanoia acuceps, new species

Figures 79, 129, 130

Etymology: *acus,* pin [point]; *ceps,* head.

Diagnosis: Hindwing tip with nearly symmetrical venation.

Material: *Holotype*: male, AMNH 43689, a lateral compression with "scalped" eye and body; only fragments of legs preserved (figs. 79, 129). *Paratype*: female, AMNH 43688, a lateral compression with face missing; details poorly preserved; possibly an ovipositor tip present (fig. 130).

Measurements: Length, male = 11.6, female = 13.5; body length, male = 8.8, female = 10.1; tegmen = ca. 10.5; hind tibia = 1.8–2.2; hind basitarsus = 0.8.

Discussion: This and the previous species have fewer branches of M in the tegmen, a longer r-m crossvein in the hindwing, and are larger than the type species of the genus.

Vulcanoia sp.

Figure 124

Material: Male, AMNH 43611, a lateral compression; clypellus, tegmen, and base of left hind leg missing; details poorly preserved (fig. 124).

Measurements: Length = 11.9; tegmen = 9.9; hind tibia = 2.0; hind basitarsus = 1.0.

Discussion: This specimen may represent a male of *V. apicalis,* but is almost 4 mm smaller.

OTHER CRETACEOUS FOSSIL HOMOPTERA

Homoptera as amber inclusions from the Upper Cretaceous can be placed in extant superfamilies, although they often represent extinct families, and none represent modern genera. In addition to those listed below, Canadian amber has undescribed genera represented by adults of small Cicadellidae, Psyllidae, and Cixiidae and nymphs of cicadellidae and various fulgoroids.

Aphidoidea: *Alloambria* Richards (1966), *Amberaphis* Richards (1966), *Aniferella* Richards (1966), *Antonaphis* Kononova (1977), *Canadaphis* Essig (*in* Carpenter et al., 1937), *Jantardakhia* Kononova (1975), *Juraphis* Shaposhnikov (1979), *Jurocallis* Shaposhnikov (1979), *Khatangaphis* Kononova (1975), *Palaeoaphis* Richards (1966), *Palaeoforda* Kononova (1977), *Pseudambria* Richards (1966), *Retinaphis* Kononova (1975), *Shaposhnikovia* Kononova (1976), *Tajmyraphis* Kononova (1975), *Tajmyrella* Kononova (1976).

Coccoidea: *Electrococcus* Beardsley (1969).

Membracoidea: *Jascopus* Hamilton (1971).

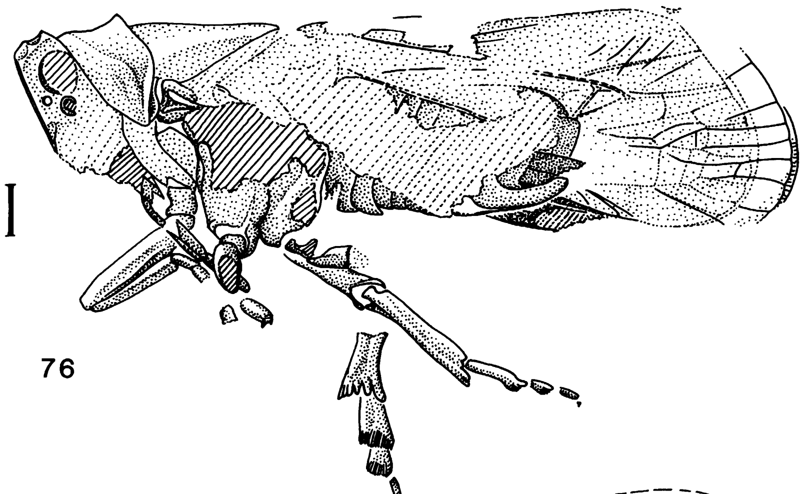
A few Lower Cretaceous Homoptera are known from amber. These represent the following superfamilies and genera:

Aphidoidea: *Annulaphis* Shaposhnikov, 1979, *Ellinaphis* Shaposhnikov, 1979, *Oviparosiphum* Shaposhnikov, 1979.

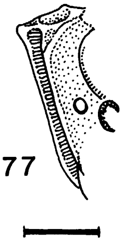
Aleyrodidae: *Bernaea* Schlee, 1970, *Heidea* Schlee, 1970.

Fulgoroidea: *Mundopoides* Fennah, 1987.

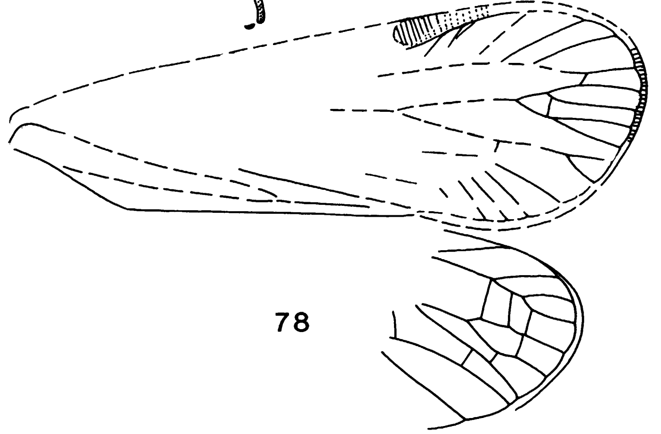
Rock fossils from the Upper Cretaceous are few in number. *Hylaeoneura lignei* Lameere and Severin (1897) is a cicadoprosbolid, related to *Architettix. Mesojassoides gigantea* Oman (1937) is a possible cicadellid, although it is associated with a detached clavus with a Y-vein. *Netutela annunciator* Emeljanov (1983) is a dictyopharid. *Petrop-*



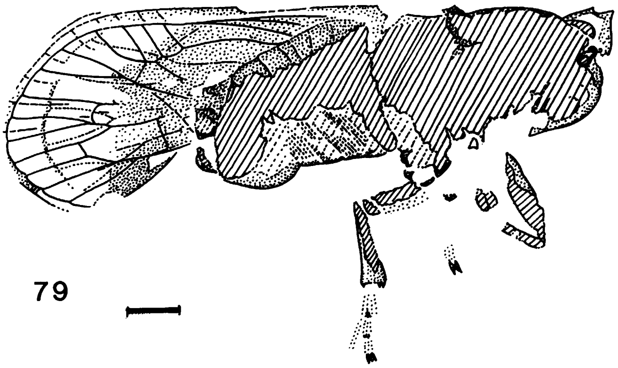
76



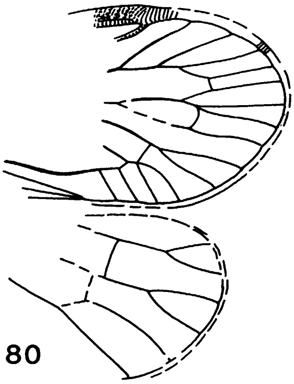
77



78

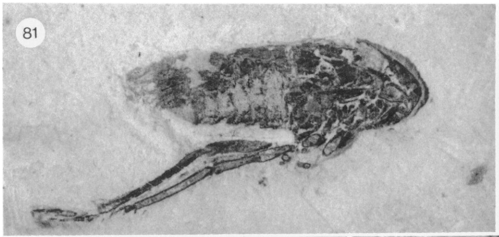


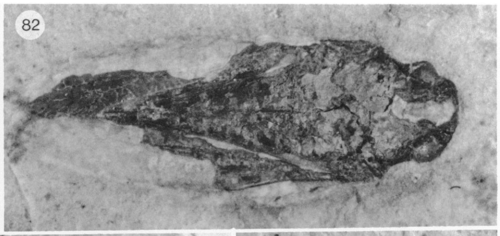
79

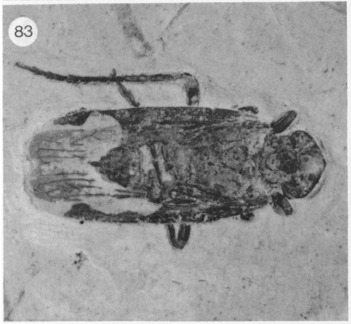


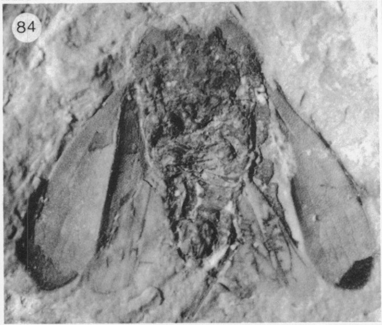
80

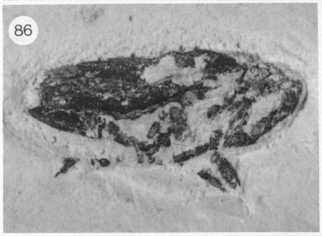
Figs. 76–80. *Vulcanoia* spp. **76,** *V. apicalis,* n. sp. holotype, AMNH 43603; **77,** face of same, anterolateral aspect; **78,** reconstructed venation of same; **79,** *L. acuceps,* n. sp. holotype, AMNH 43689; **80,** venation of same.

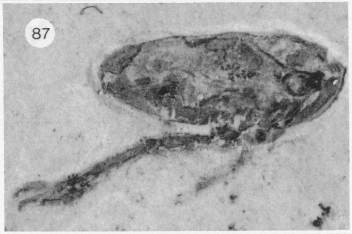


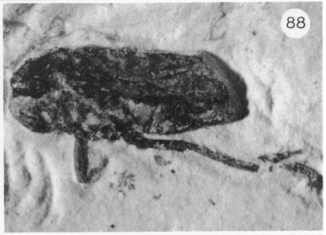


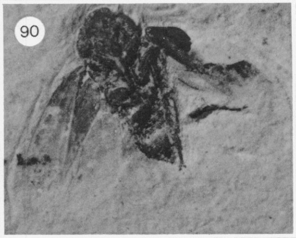


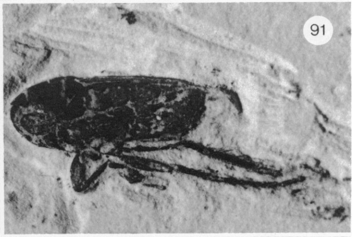


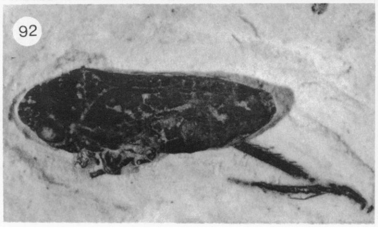


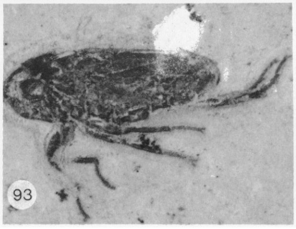


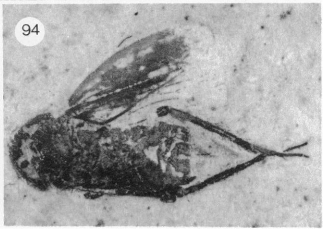












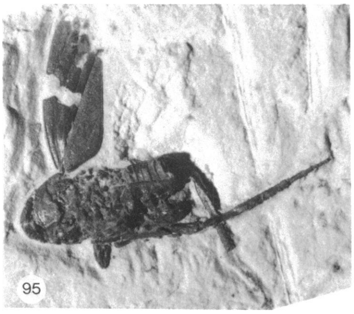
Figs. 81–83. *Proerrhomus* spp. **81,** sp. A, AMNH 43630; **82,** sp. B, AMNH 43696; **83,** sp. A, AMNH 43613.

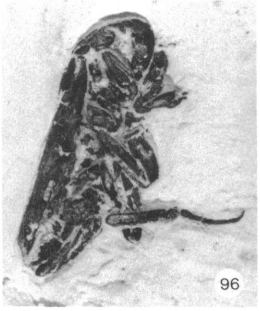
Fig. 84. *Platyjassites* sp., AMNH 43635.

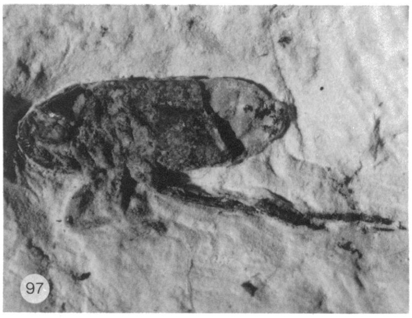
Figs. 85, 86. *Paracarsonus aphrodoides* paratypes. **85,** AMNH 43650; **86,** AMNH 43671.

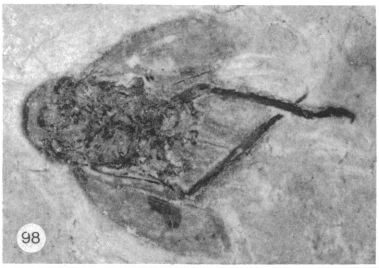
Figs. 87, 88. *Ovojassus* spp. **87,** *O. concavifer* paratype, AMNH 43664; **88,** *O. minor* holotype.

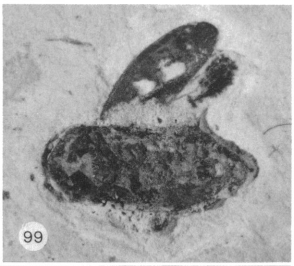
Figs. 89–94. *Hallex xestocephalus,* paratypes. **89,** AMNH 43648; **90,** AMNH 43651; **91,** AMNH 43653; **92,** AMNH 43659; **93,** AMNH 43662; **94,** AMNH 43675.

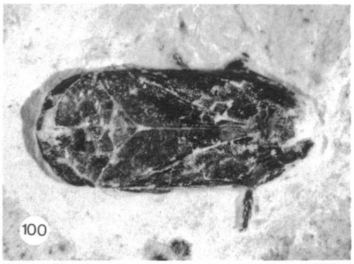


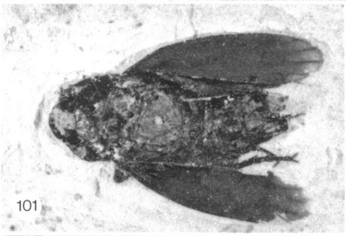


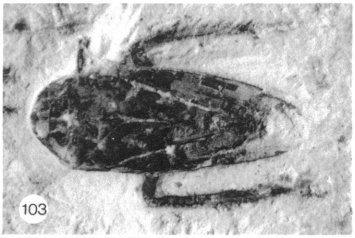


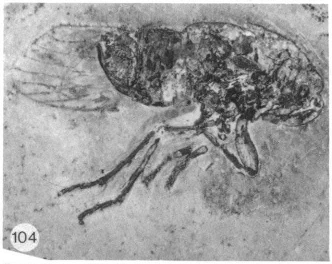


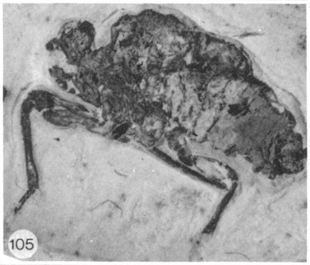


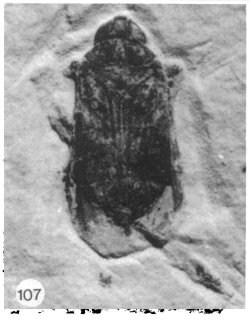


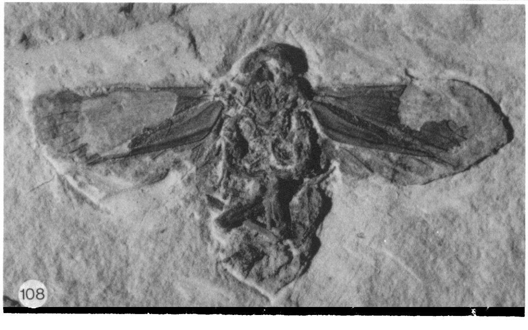


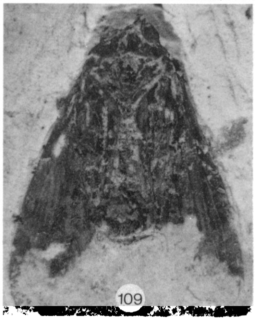










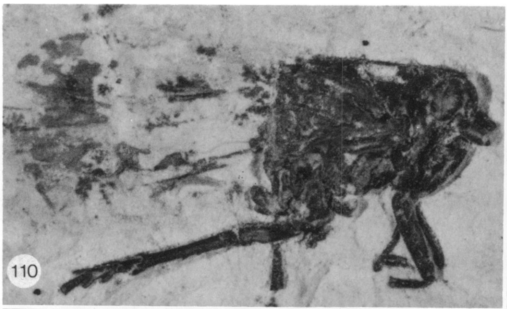


Figs. 95–103. *Hallex* spp. **95,** *H. gongrogony* holotype; **96,** paratype of same, AMNH 43666; **97,** same, AMNH 43667; **98,** *H. brevipes* holotype; **99,** paratype of same, AMNH 43639; **100,** *H. laticeps* holotype; **101,** *H. gracilior* holotype; 102, paratype of same, AMNH 43649; **103,** same, AMNH 43676.

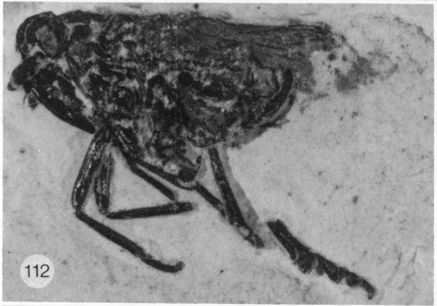
Figs. 104, 105. *Architettix compacta* paratypes. **104,** AMNH 43601; **105,** AMNH 43683.

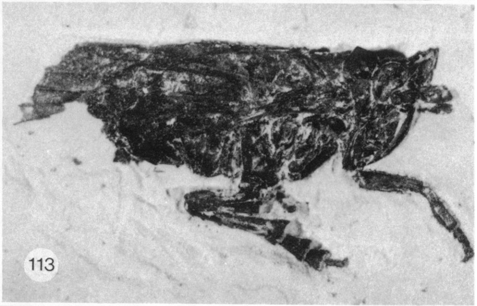
Fig. 106. Cixiidae, genus unknown, AMNH 43692.

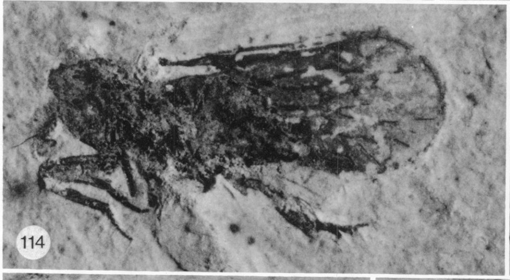
Figs. 107–109. *Acixiites* spp. **107,** *A. immodesta* paratype, AMNH 43632; **108,** *A. costalis* holotype; **109,** paratype of same, AMNH 43636.

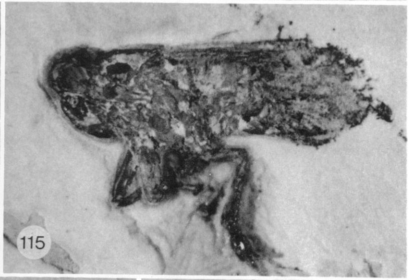

110

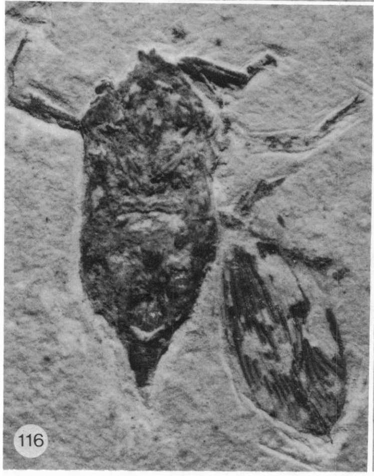

111


112

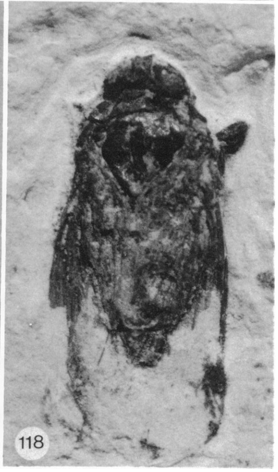

113


114


115

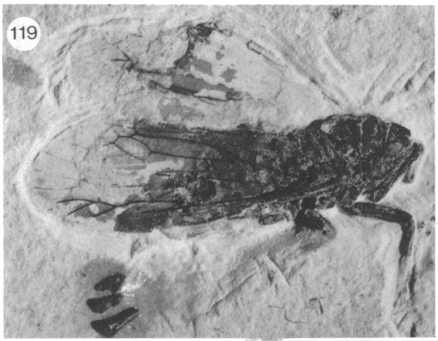

116

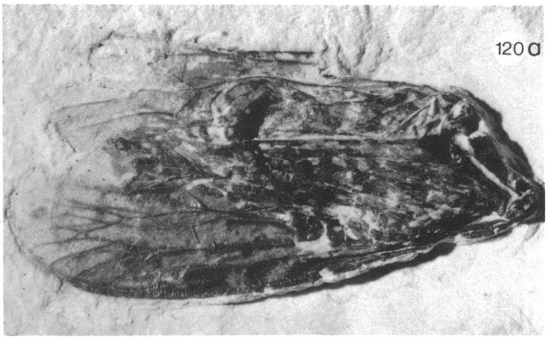

117

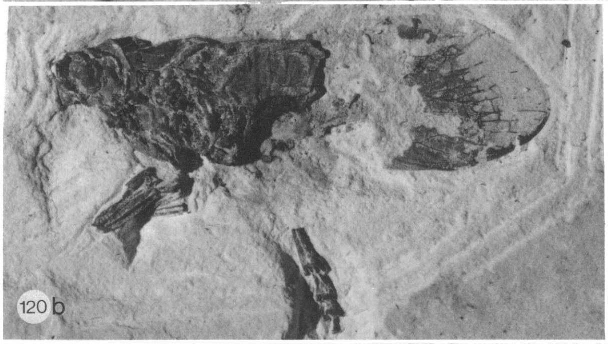

118

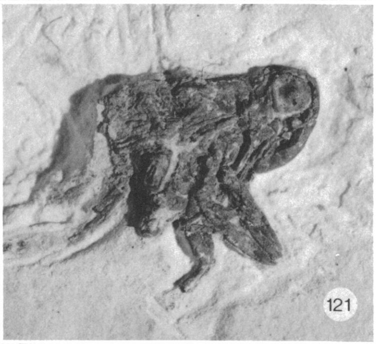
Figs. 110–114. *Protodelphax* spp. **110,** *P. macroceps* holotype; **111,** *P. chamus* paratype, AMNH 43620; **112,** same, holotype; **113,** *P. rhinion* holotype; **114,** *Protodelphax* sp., AMNH 43686.

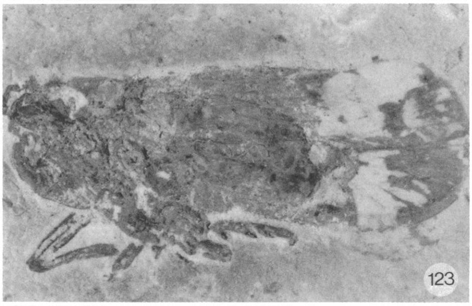
Figs. 115–118. *Ancorale* spp. **115,** *A. flaccidum* paratype, AMNH 43680; **116,** same, AMNH 43626; **117,** same, AMNH 43682; **118,** *Ancorale* sp., AMNH 43677.

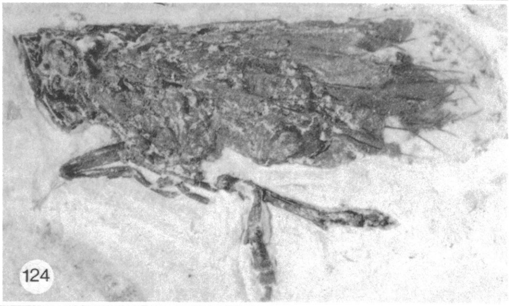


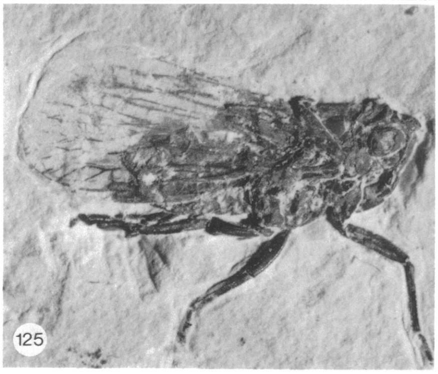


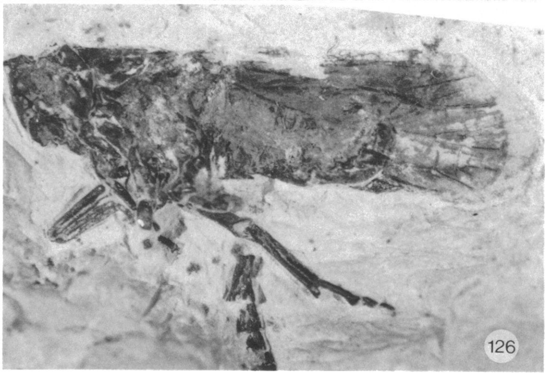




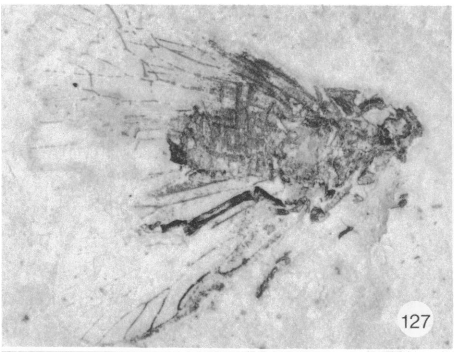


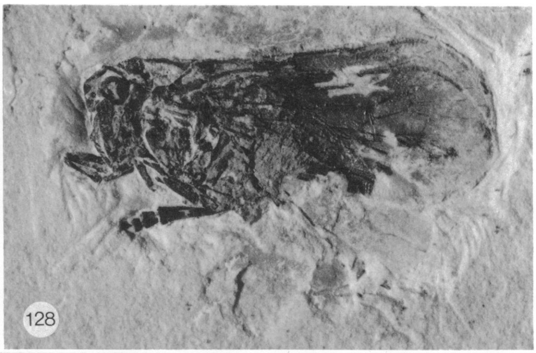


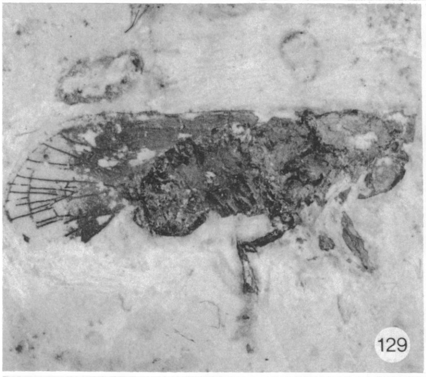


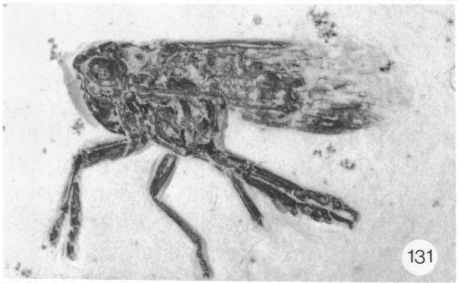


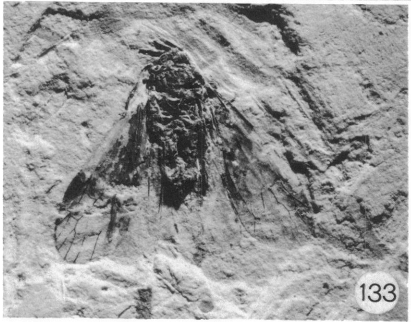
Figs. 119, 120. *Kinnarocixius* spp. **119,** *K. quassus* holotype; **120,** *Kinnarocixius* sp., AMNH 43614.
Figs. 121, 122. *Carpopodus* spp. **121,** sp. A, AMNH 43602; **122,** sp. B, AMNH 43619.
Figs. 123, 125. *Psestocixius* spp. **123,** *P. fuscus* paratype, AMNH 43687; **125,** *P. delphax* holotype.
Figs. 124, 126. *Vulcanoia* spp. **124,** *V.* sp. A, AMNH 43611; **126,** *V. apicalis* holotype.











Figs. 127, 128. *Lalax* spp. **127,** *L. mutabilis* paratype, AMNH 43684; **128,** same, AMNH 43615.
Figs. 129, 130. *Vulcanoia acuceps* n. sp. **129,** holotype; **130,** paratype, AMNH 43688.
Figs. 131, 132. *Patulopes* spp. **131,** *P. myndoides* holotype; **132,** paratype of same, AMNH 43629.
Fig. 133. *Kinnarocixius quassus* paratype, AMNH 44105.

teron mirandum Cockerell (1912), formerly thought to be an Homopteran, is actually a Trichopteran.

Rock fossils of Homoptera from the Lower Cretaceous include *Mesojassula marginata* Evans (1956), a disassociated hind wing of a cercopoid, and several genera of Palaeontinidae: *Wonnacottella* Whalley and Jarzembowski (1985), *Montsecocossus* Gomez-Pallerola (1984), and *Ilerdocossus* Gomez-Pallerola (1984).

A number of Homoptera were recently recorded from Lower Cretaceous Australian mudstone (Jell and Duncan, 1986). Most of these are poorly preserved, many of them nymphs. They superficially resemble leafhoppers, but have the hind tarsi of Jascopidae, a family resembling leafhoppers. One appears to have a flat face like Idiocerini, but this is an artifact as the head is badly crushed. The only well-preserved adult was tentatively placed in the Cixiidae, but the photograph accompanying the record shows clearly a relative of the Triassic tegmen *Mesodipthera prosboloides* Tillyard (1922). This fossil is a cicadomorphan, but would be incorrectly placed in *Mesodipthera,* which is a genus of Cicadoprosbolidae.

Several Lower Cretaceous cicadomorphs were recently described from Mongolia (Shcherbakov, 1986). One is the hind wing of a cicadoprosbolid, possibly related to *Architettix* but with longer apical cells. The others are leafhopperlike insects with MP fused to Cu_1 for a short distance, and are probably members of the Jascopidae.

PHYLOGENETIC CONCLUSIONS

The Cretaceous fossils described here fit in well with the previously discovered Homopterous fossils, and help form a simplified picture of the evolution of the suborder.

Undoubted members of Homoptera are first known from the Permian. The oldest of these are similar in having generalized venation and bodies; they probably represent the ancestral stock from which the three modern lineages (Fulgoromorpha, Psyllomorpha, and Cicadomorpha) diverged. Toward the end of the Permian several now extinct superfamilies are clearly defined: Palaeontinoidea, Dysmorphoptiloidea, and Pincombeoidea. The last-named of these may represent the stem group of the Psyllomorpha, but this is by no means certain.

Triassic Homoptera largely belong to Permian superfamilies, but additional superfamilies are represented by a few genera. One of these is Aphidoidea (*Triassoaphis* Evans, 1956). The representatives of the other superfamilies probably belong to the stem group of the Cicadomorpha: Cicadoidea (Cicadoprosbolidae: *Mesodipthera*), Cercopoidea (Archijassidae, Chiliocyclidae), and Ipsvicioidea (Ipsviciidae, Serpentivenidae, Granulidae).

The Jurassic fauna shows a flowering of the Palaeontinoidea, and a lesser development of the Cicadoprosbolidae, with a corresponding decline of other, older lineages. If *Cercopidium hahnii* Westwood (1854) is an Ipsvicioid, as seems likely, then it is the only one known from the Jurassic. Other Ipsvicioids are known only from the Triassic.

During the Jurassic there appears for the first time Tettigarctidae (*Liassocicada* Bode, 1953), Membracoidea (Jascopidae and Procercopidae), Psylloidea (*Liadopsylla* Handlirsch, 1921), and two possible Fulgoroidea (*Cixius petrinus* Fennah, 1961 and *Ricaniites* Handlirsch, 1908). Jurassic Homoptera fossils also show a rich endowment of Fulgoridiidae. These insects have been mistakenly considered to belong to the Fulgoroidea, but they have long, multiarticulate antennae (Bode, 1953) and the legs do not fossilize well, possibly because they were slender and delicate. They apparently represent the stem group of the Fulgoroidea + Aleyrodoidea, and their heads are certainly much like that of the aleyrodoid described herein.

The Cretaceous period completed the transition from the archaic Homopterous fauna to the establishment of the ancient lineages of the modern fauna. By the lower Cretaceous, the Permian families had dwindled to a single representative, the highly successful and distinctive Palaeontinidae. Only three genera of this family are known from the Jurassic/Cretaceous boundary, and these are not known from more recent deposits despite their large size and distinctive venation. The primitive families of Fulgoromorpha and Cicadomorpha from the Triassic and Jurassic continue through the Cretaceous, gradually being replaced by modern ones: Achilidae, Cixiidae, and Cicadellidae in the Lower Cretaceous, Dictyopharidae by the Upper Cretaceous. Other fulgoroid families, Cicadidae and Membracidae are known only from the Tertiary.

Early Homoptera had small cibarial chambers (judging by the size of the overlying frons) and must have fed on undifferentiated cells such as parenchymal cells of roots. This feeding strategy is still reflected in Coleorrhyncha, which feed on mosses, Cixiidae which attack roots, and Achilidae and Derbidae which are fungal feeders. Development of a simple mesenteric filtering device, as represented by that of Aphidoidea and Psylloidea, permitted them to feed on plant sap, but the lower nutrition level of xylem and other readily accessible cells must have encouraged low-energy strategies such as plant parasitism. The developed of an efficient filter chamber in Cicadomorpha permitted large insects to develop on xylem fluids which were probably readily accessible in the plants of their day. Angiosperms, with sizable phloem tubes near the surface of the stems, offered a high-energy source to all Homoptera. This resulted in the great radiation of aphids, scales, leafhoppers, whiteflies, and fulgoroids. Which plants these utilized first cannot be guessed at, for modern diets appear to be derived from Tertiary ecological associations.

REFERENCES

Beardsley, J. W.
1969. A new fossil scale insect (Homoptera: Coccoidea) from Canadian amber. Psyche 76: 270–279.

Bekker-Migdisova, Ye. E.
1946. Contributions to the knowledge of the comparative morphology of the recent and Permian Homoptera. Acad. Sci. Bull. URSS (Ser. Biol.) 1946: 741–766.
1949a. The Mesozoic Homoptera of Middle Asia. Trav. Inst. Paléozool. Acad. Sci. URSS 22: 68 pp.
1949b. The new Permian family Boreoscytidae and questions on the phylogeny of the ancestors of Homoptera. Trudy Paleont. Inst. Akad. Nauk 20: 171–182. [in Russian]
1985. Fossil insects of the Psyllomorpha. Moscow: Nauka, 93 pp.

Bode, A.
1953. Die Insektenfauna des ostniedersâchsischen Oberen Lias. Palaeontographica, Stuttgart (A) 103(1–4): 1–375.

Carpenter, F. M. et al.
1937. Insects and arachnids from Canadian amber. Univ. Toronto Stud., Geol. Ser. 40: 7–55.

Cockerell, T. D. A.
1912. The oldest American homopterous insect. Can. Entomol. 44: 93–95.

Emeljanov, A. F.
1983. Dictyopharidae from the Cretaceous deposits on the Taymyr Peninsula (Insecta, Homoptera). Paleontol. J. 17: 77–82.

Evans, J. W.
1956. Mesozoic and Palaeozoic Homoptera. Australian J. Zool. 4: 165–254.

Fennah, R. G.
1961. The occurrence of a Cixiine Fulgoroid (Homoptera) in the Weald clay. Ann. Mag. Nat. Hist., ser. 13, 4: 161–163.
1987. A new genus and species of Cixiidae (Homoptera: Fulgoroidea) from Lower Cretaceous amber. J. Nat. Hist. 21: 1237–1240.

Gomez-Pallerola, J. E.
1984. Nuevos paleontinidos del yocrimento infracretacico de la 'Pedrera de Meia' (Lerida). Bol. Geol. Min. 95: 301–309.

Hamilton, K. G. A.
1971. A remarkable fossil Homopteran from Canadian Cretaceous amber representing a new family. Can. Entomol. 103: 943–946.
1983. Classification, morphology and phylogeny of the family Cicadellidae (Rhynchota: Homoptera). *In* W. J. Knight et al. (eds.), Proceedings of the 1st international workshop on leafhoppers and planthoppers of economic importance, London, 4–7 Oct. 1982: 15–37. London: Commonwealth Institute of Entomology.

Handlirsch, A.
1921. Palaeontologie. *In* Schroeder's Handbuch der Entomologie 3(6): 209–306.

Hong, Y. -c.
1982. Mesozoic fossil insects of Jinquan Basin in Gansu Province. Beijing: Geological Publishing House. [in Chinese]

Jell, P. A., and P. M. Duncan
1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra fossil bed (Korumburra group), South Gippsland, Victoria. *In* P. A. Jell and J. Roberts (eds.), Plants and invertebrates from the Lower Cretaceous Koonwarra fossil bed, South Gippsland, Victoria. Assoc. Australian Palaeontol. Mem. 3: 111–202. Sydney.
Kononova, E. L.
1975. A new aphid family (Homoptera, Aphidinea) from the Upper Cretaceous of the Taymyr. Entomol. Rev. 56: 60–68.
1976. Extinct aphid families (Homoptera, Aphidinea) of the late Cretaceous. Paleontol. J. 10: 352–360.
1977. New aphid species (Homoptera, Aphidinea) from Upper Cretaceous deposits of the Taymyr. Entomol. Rev. 56: 72–80.
Lameere, A., and G. Severin
1897. Les insectes de Bernissart. Ann. Soc. Entomol. Belgique 41: 35–38.
Martins-Neto, R. G.
1988. A new fossil insect (Homoptera, Cixiidae) from the Santana Formation (Lower Cretaceous), Araripe Basin, northeast Brazil. Interciencia 13: 313–316.
Martynov, A.
1937. Liassic insects from Shurab and Kisyl-Kiya, Ferghana. Trav. Inst. Palaeont. Acad. Sci. URSS 7: 232 pp.
Oman, P. W.
1937. Fossil Hemiptera from the Fox Hills sandstone (Cretaceous) of Colorado. J. Paleontol. 1: 38.
Richards, W. R.
1966. Systematics of fossil aphids from Canadian amber (Homoptera: Aphididae). Can. Entomol. 98: 746–760.
Riek, E. F.
1976. A new collection of insects from the Upper Triassic of South Africa. Ann. Natal Mus. 22: 791–820.
Schlee, D.
1970. Insekten fossilien aus der unteren Keide, 1. Verwandt Schaftsforschung an fossilen und rezenten Aleyrodina (Insecta, Hemiptera). Stuttg. Beitr. Naturk. 213: 1–72.
Shaposhnikov, G. Kh.
1979. Late Jurassic and Early Cretaceous aphids. Paleontol. J. 13: 449–461.
Shcherbakov, D. E.
1986. Cicadina (=Auchenorrhyncha). *In* A. P. Rasnitsyn (ed.), Insects in the Early Cretaceous ecosystems of West Mongolia. 28: 47–50. Moscow: Nauka.
Tillyard, R. J.
1919. Mesozoic insects of Queensland, no. 7. Hemiptera Homoptera; with a note on the phylogeny of the suborder. Proc. Linn. Soc. N.S.W. 44: 857–896.
1922. Mesozoic insects of Queensland, no. 9. Orthoptera, and additions to the Protorthoptera, Odonata, Hemiptera and Planipennia. Proc. Linn. Soc. N.S.W. 47: 447–470.
Westwood, J. O.
1854. Contributions to fossil entomology. Q. J. Geol. Soc. London 10: 378–396.
Whalley, P. E. S.
1985. The systematics and palaeogeography of the lower Jurassic insects of Dorset, England. Bull. Br. Mus. (Nat. Hist.), Geol. 39: 107–189.
Whalley, P. E. S., and E. A. Jarzembowski
1985. Fossil insects from the lithographic limestone of Montsech (Late Jurassic—Early Cretaceous), Lérida Province, Spain. Bull. Br. Mus. (Nat. Hist.), Geol. 38: 381–412.

CHAPTER 7. ORDER HYMENOPTERA

D. CHRISTOPHER DARLING[1] AND MICHAEL J. SHARKEY[2]

ABSTRACT

The discovery of Southern Hemisphere fossils has in many ways revitalized the study of the insect fauna of the Cretaceous. There are, however, only a few localities in Chile, Australia (Queensland, Victoria), and South Africa (McKay and Rayner, 1986); Hymenoptera fossils have been reported only from the Koonwarra fossil bed in Australia (Jell and Duncan, 1986). The Santana Formation of Brazil is the first fossil locality for Cretaceous Hymenoptera in the Southern Hemisphere of the New World. Although only 17 specimens are available for study, this locality has yielded several interesting finds. For Symphyta, there is the first fossil representative of Syntexinae (Anaxyelidae); this family is represented in the recent fauna by a single Nearctic species. For the parasitic Hymenoptera, there is an ephialtitid that extends the range of this taxon from the Jurassic into the Cretaceous. And for Aculeata, the stinging wasps, there is a tiphiid, that extends the age of this family by about 70 million years, from the Oligocene to the Lower Cretaceous, and the first fossil representative of the Rhopalosomatidae. All are described and named here.

INTRODUCTION

Our understanding of the Hymenoptera from the Cretaceous has expanded dramatically in the past 30 years. In 1973, Evans tabulated the known genera of Aculeata (12) and noted that it seemed incredible that it was only 16 years since the first description of a Cretaceous aculeate wasp (Sharov, 1957). The past 15 years have been even more remarkable. Table 1 lists 45 genera of Cretaceous aculeates, 37 if the tentative synonymy in the Formicidae is followed (Wilson, 1987). The number of described genera of aculeates has more than doubled but, more importantly, the number of family-level taxa has increased from 7 to 14. The figures for the Parasitica and Symphyta are even more dramatic. All but one of the 28 Cretaceous genera of Symphyta have been recorded in the past 25 years and the number of genera of parasitic Hymenoptera has increased from 13 to 65 in the last 30 years. To some extent, this apparent increase in diversity is due to the recognition of paraphyletic taxa and imprecise generic limits but this does not negate the fact that we now know considerably more about the Hymenoptera fauna of the Cretaceous. Studies of the rich fossil localities of the Transbaikalia region of the U.S.S.R. by Dr. A. P. Rasnitsyn and his collaborators at the Paleontological Institute in Moscow have not only increased our knowledge of Cretaceous Hymenoptera but have also provided an explicit (albeit controversial) outline of the evolution and diversification of Hymenoptera (Rasnitsyn, 1980a; 1988a, but see Carpenter 1986).

Illustrations were prepared after viewing the specimens both under normal and oblique illumination, and with and without wetting using 95 percent ethanol. Solid lines denote actual wing veins and distinct impressions made by veins; broken lines represent extrapolations. Nomenclature for the venation follows Ross (1936), with minor variations. The taxonomic accounts for Symphyta and parasitic Hymenoptera are the primary responsibility of MJS, the Aculeata is the primary responsibility of DCD.

ACKNOWLEDGMENTS

Dr. A. P. Rasnitsyn (Palaeontological Institute, Moscow) was extremely cooperative in discussing the placement of these fossils

---

[1] Associate Curator, Department of Entomology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6; Assistant Professor, Department of Zoology, University of Toronto.

[2] Research Scientist, Biosystematics Research Centre, Agriculture Canada, K.W. Neatby Bldg., Ottawa, Canada K1A 0C6.

TABLE 1
Known Cretaceous Hymenoptera. Classification following Rasnitsyn, 1988a.
(R = sedimentary rock, A = amber) by
A. Rasnitsyn, Paleontological Institute, Moscow

Taxa	A/R	Source	Reference
Incertae Sedis			
Mesosirex (1 sp.)	R	Hebei, China	Hong 1984a (REVISED POSITION)
"*Paroryssus*" (1 sp.) (misident.)	R	Hebei, China	Lin 1976 (REVISED POSITION)
SUBORDER SIRICINA (SYMPHYTA)			
Incertae Sedis			
Sinanxyela (1 sp.)	R	Inner Mongolia, China	Hong 1982b (REVISED POSITION)
XYELOMORPHA			
Xyelidae			
Eoxyela (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1965, 1969
Spathoxyela (2 spp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1965, 1969 Krassilov & Rasnitsyn 1982
Xyela (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1965
Angaridyela (3 spp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1968, 1969
Baissoxyela (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1969
Gigantoxyela (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1969
Chaetoxyela (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1969
Ceroxyela (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1969
Xyelites (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1969
Uroxyela (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1969
Anthoxyela (2 spp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1977 Krassilov & Rasnitsyn 1982
TENTHREDINOMORPHA			
Xyelotomidae			
Undatoma (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1977
Protenthredo (1 sp.)	R	Inner Mongolia, China	Hong 1982a (REVISED POSITION)
? *Protenthredo* (1 sp.)	R	Inner Mongolia, China	Hong 1982a (REVISED POSITION)
Tenthredinidae			
Palaeathalia (1 sp.)	R	Shandong, China	Zhang 1985
Tenthredinoidea Incertae Sedis			
Vitimilarva (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1969
? *Nematus* (1 sp.)	R	Schlan, Bohemia	Handlirsch 1908
SIRICOMORPHA			
Praesiricidae			
Praesirex (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1968, 1983a
Xyelydontes (1 sp.)	R	Mongolia	Rasnitsyn 1983a
Sepulcidae			
Ghilarella (1 sp.)	R	Mongolia	Rasnitsyn 1988b
Trematothorax (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1988b
Thoracotrema (2 spp.)	R	Magadan, U.S.S.R.; Mongolia	Rasnitsyn 1988b
? "*Euryxyela*" (1 sp.) (nom. preocc.)	R	Hebei, China	Hong 1984a (REVISED POSITION)
Cephidae			
Mesocephus (2 spp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1968, 1969
	R	Mongolia	Rasnitsyn 1988b

TABLE 1—(*Continued*)

Taxa	A/R	Source	Reference
Anaxyelidae			
Prosyntexis (1 sp.)	R	Ceará, Brazil	this study
Dolichostigma (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1968, 1969
Kempendaja (1 sp.)	R	Yakutsk, Siberia, U.S.S.R.	Rasnitsyn 1968, 1969
Siricidae			
Sinosirex (1 sp.)	R	Hebei, China	Hong 1975
SUBORDER VESPINA (APOCRITA)			
Incertae Sedis			
Cephenopsis (1 sp.)	R	Hebei, China	Hong 1984a (REVISED POSITION)
Longhuaia (1 sp.)	R	Hebei, China	Hong 1984a (REVISED POSITION)
Polychorella (1 sp.)	R	Shandong, China	Zhang 1985 (REVISED POSITION)
Mesomutilla (1 sp.)	R	Shandong, China	Zhang 1985 (REVISED POSITION)
Family indet.	R	Lérida, Spain	Whalley & Jarzembowski 1985
	R	West Mongolia	Rasnitsyn 1986b
ORUSSOMORPHA			
Orussidae			
Mesorussus (1 sp.)	A	Taymyr, Siberia	Rasnitsyn 1977
EPHIALTITOMORPHA			
Ephialtitidae			
Ephialtites (1 sp.)	R	Lérida, Spain	Meunier 1903 Whalley & Jarzembowski 1985
Karataus (1 sp.)	R	Ceará, Brazil	this study
EVANIOMORPHA			
Megalyridae			
Cleistogaster (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1975
Neocleistogaster (3 spp.)	R	West Mongolia	Rasnitsyn 1986b
Cretodinapsis (1 sp.)	R	Transcaucasian, U.S.S.R.	Rasnitsyn 1977
Stemmogaster (1 sp.)	R	Shandong, China	Zhang 1985
Trigonalidae			
Darbigonalus (1 sp.)	R	West Mongolia	Rasnitsyn 1986b
Cretogonalys (1 sp.)	R	Taymyr, U.S.S.R.	Rasnitsyn 1977
Ichneumonomima (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1975, 1980b
Maimetshidae			
Maimetsha (1 sp.)	A	Taymyr, Siberia	Rasnitsyn 1975
Stigmaphronidae			
Stigmaphron (1 sp.)	A	Taymyr, Siberia	Kozlov 1975
Elasmomorpha (1 sp.)	A	Taymyr, Siberia	Kozlov 1975
Hippocoon (1 sp.)	A	Taymyr, Siberia	Kozlov 1975
Allocotidus (1 sp.)	A	Kuk Inlet, Alaska	Muesebeck 1963 Kozlov 1975
Megaspilidae			
Prolagynodes (1 sp.)	A	Taymyr, Siberia	Alekseev & Rasnitsyn 1981
? *Lygocerus* (1 sp.)	A	Cedar Lake, Canada	Brues 1937
Conostigmus (2 spp.)	A	Cedar Lake, Canada	Brues 1937
	A	Taymyr, Siberia	Alekseev & Rasnitsyn 1981
Praeaulacidae			
Cretocleistogaster (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1975, 1988a
Westratia (1 sp.)	R	Australia	Jell & Duncan 1986 (REVISED POSITION)

TABLE 1—(*Continued*)

Taxa	A/R	Source	Reference
Gasteruptiidae			
Manlaya (9 spp.)	R	South-East & West Mongolia	Rasnitsyn 1980b, 1986b
Kotujella (1 sp.)	A	Taymyr, Siberia	Rasnitsyn 1975, 1980b
Baissa (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1975, 1980b
Cretevaniidae			
Cretevania (3 spp.)	A	Taymyr, Siberia	Rasnitsyn 1975
Genus indet.	R	Wealden Beds, England	Jarzembowski 1984
PROCTOTRUPOMORPHA			
Mesoserphidae			
Mesoserphus (1 sp.)	R	West Mongolia	Rasnitsyn 1986b
Genus indet.	R	Ceará, Brazil	this study
Heloridae			
Gurvanhelorus (1 sp.)	R	West Mongolia	Rasnitsyn 1986b
Pelecinidae			
Iscopinus (1 sp.)	R	Transbaikalia, U.S.S.R.	Kozlov 1974
Proctotrupidae			
Gurvanotrupes (1 sp.)	R	West Mongolia	Rasnitsyn 1986b
Protoprocto (1 sp.)	R	Ceará, Brazil	this study
Oligoneuroides (1 sp.)	R	Shandong, China	Zhang 1985 (REVISED POSITION)
Genus indet.	R	Australia	Jell & Duncan 1986
Austroniidae			
Trupochalcis (1 sp.)	A	Taymyr, Siberia	Kozlov 1975
Diapriidae			
Cretacoformica (1 sp.)	R	Australia	Jell & Duncan 1986 (REVISED POSITION)
Ismarinae indet.	A	France	Schlüter 1978
Scelionidae			
Baryconus (1 sp.)	A	Cedar Lake, Canada	Brues 1937
Proteroscelio (1 sp.)	A	Cedar Lake, Canada	Brues 1937
Cenomanoscelio (1 sp.)	A	Besonnais, France	Schlüter 1978
Genus indet.	A	France	Schlüter 1978
Serphitidae			
Microserphites (1 sp.)	A	Taymyr, Siberia	Kozlov & Rasnitsyn 1979
Aposerphites (1 sp.)	A	Taymyr, Siberia	Kozlov & Rasnitsyn 1979
Serphites (2 spp.)	A	Cedar Lake, Canada	Brues 1937
	A	Taymyr, Siberia	Kozlov & Rasnitsyn 1979
Archaeocynipidae			
Archaeocynips (2 spp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn & Kovalev 1988
Dahurocynips (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn & Kovalev 1988
Cynipidae			
Protimaspis (1 sp.)	A	Cedar Lake, Canada	Kinsey 1937
Mymarommatidae			
Palaeomymar (3 spp.)	A	Taymyr, Siberia	Kozlov & Rasnitsyn 1979
Archaeromma (2 spp.)	A	Cedar Lake, Canada	Brues 1937
	A	Medicine Hat, Canada	Yoshimoto 1975
Galloromma (1 sp.)	A	Besonnais, France	Schlüter 1978
Mymaridae			
Triadomerus (1 sp.)	A	Cedar Lake, Canada	Yoshimoto 1975
Carpenteriana (1 sp.)	A	Cedar Lake, Canada	Yoshimoto 1975
Protooctonus (1 sp.)	A	Cedar Lake, Canada	Yoshimoto 1975
Macalpinia (1 sp.)	A	Medicine Hat, Canada	Yoshimoto 1975
Tetracampidae			
Baeomorpha (4 spp.)	A	Cedar Lake, Canada	Brues 1937
	A	Medicine Hat, Canada	Yoshimoto 1975

TABLE 1—(*Continued*)

Taxa	A/R	Source	Reference
Distylopus (1 sp.)	A	Cedar Lake, Canada	Yoshimoto 1975
Bouceklytus (1 sp.)	A	Cedar Lake, Canada	Yoshimoto 1975
Trichogrammatidae			
Enneagmus (1 sp.)	A	Cedar Lake, Canada	Yoshimoto 1975
ICHNEUMONOMORPHA			
Praeichneumonidae			
Praeichneumon (1 sp.)	R	Mongolia	Rasnitsyn 1983b
Eoichneumonidae			
Eoichneumon (1 sp.)	R	Australia	Jell & Duncan 1986 Rasnitsyn & Sharkey 1988
Baissobracon (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn & Sharkey 1988
Cretobraconus (7 spp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn & Sharkey 1988
Archobraconus (6 spp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn & Sharkey 1988
Ichneumonidae			
Tanychorella (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1975
Tanychora (2 spp.)	R	Transbaikalia, U.S.S.R.; Central Mongolia	Townes 1973a
Catachora (1 sp.)	A	Taymyr, Siberia	Townes 1973b
Urotryphon (1 sp.)	A	Taymyr, Siberia	Townes 1973b
Eubaeus (1 sp.)	A	Taymyr, Siberia	Townes 1973b
Genus indet.	R	Lérida, Spain	Whalley & Jarzembowski 1985
Braconidae			
Eobraconus (1 sp.)	R	Mongolia	Rasnitsyn 1983b, 1985
Diospilus (1 sp.)	A	Cedar Lake, Canada	Brues 1937
Pygostolus (1 sp.)	A	Cedar Lake, Canada	Brues 1937
Neoblacus (1 sp.)	A	Cedar Lake, Canada	Brues 1937
		VESPOMORPHA (ACULEATA)	
CHRYSIDOIDEA			
Dryinidae			
Baissobius (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1975, 1980a
Cretodryinus (1 sp.)	A	Taymyr, Siberia	Ponomarenko 1975
Laberius (1 sp.)	A	Taymyr, USSR	Ponomarenko 1981
Richardsidryinus (1 sp.)	A	Medicine Hat, Canada	Ponomarenko 1981 Olmi 1984
Avodryinus (1 sp.)	A	Medicine Hat, Canada	Ponomarenko 1981
? Bethylidae			
Cretabythus (1 sp.)	A	Taymyr, Siberia	Evans 1973 Rasnitsyn 1988a
Bethylidae			
Archaepyris (1 sp.)	A	Taymyr, Siberia	Evans 1973
Celonophamia (1 sp.)	A	Taymyr, Siberia	Evans 1973
Chrysididae			
Procleptes (1 sp.)	A	Cedar Lake, Canada	Evans 1969
Hypocleptes (1 sp.)	A	Taymyr, Siberia	Evans 1973
Protamisega (1 sp.)	A	Taymyr, Siberia	Evans 1973
APOIDEA			
? Baissodidae			
Baissodes (2 spp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1975
? *Baissodes* (1 sp.)	R	West Mongolia	Rasnitsyn 1986b
Oryctobaissodes (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1975
Trichobaissodes (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1975, 1977
Vitimosphex (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1975
Genus indet.	R	Wealden Beds, England	Jarzembowski 1984

TABLE 1—(*Continued*)

Taxa	A/R	Source	Reference
Sphecidae			
Archisphex (1 sp.)	R	Tunbridge, England	Evans 1969
Cretosphex (3 spp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1975
	R	Ceará, Brazil	this study
Angarosphex (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1975
? *Angarosphex* (1 sp.)	R	West Mongolia	Rasnitsyn 1986b
Lisponema (1 sp.)	A	Cedar Lake, Canada	Evans 1969
Pittoecus (1 sp.)	A	Taymyr, Siberia	Evans 1973
Gallosphex (1 sp.)	A	Beonnais, France	Schlüter 1978
Mataeosphex (1 sp.)	R	Shandong, China	Zhang 1985 (REVISED POSITION)
Shandongodes (2 spp.)	R	Shandong, China	Zhang 1985 (REVISED POSITION)
? *Palaeapis* (1 sp.)	R	Shandong, China	Hong 1984b (REVISED POSITION)
Genus indet.	R	Wealden Beds, England	Jarzembowski 1984
Apidae			
Trigona (1 sp.)	A	New Jersey, U.S.A.	Michener & Grimaldi 1988a, b
? *Celliforma* (2 spp.)	R	Utah, USA; Uruguay	Zeuner & Manning 1976
POMPILOIDEA			
Pompilidae			
Pompilopterus (1 sp.)	R	Transbaikalia, U.S.S.R.	Rasnitsyn 1975
Rhopalosomatidae			
Mesorhopalosoma (1 sp.)	R	Ceará, Brazil	this study
SCOLIOIDEA			
Tiphiidae			
Architiphia (1 sp.)	R	Ceará, Brazil	this study
Mutillidae			
? *Cretavus* (1 sp.)	R	Siberia	Sharov 1957 Rasnitsyn 1980a
Falsiformicidae			
Falsiformica (1 sp.)	A	Taymyr, Siberia	Rasnitsyn 1975
Taimyrisphex (1 sp.)	A	Taymyr, Siberia	Evans 1973 Rasnitsyn 1980a
FORMICOIDEA[a]			
Armaniidae			
Armania (1 sp.)	R	Magadan, U.S.S.R.	Dlussky 1983 Dlussky & Fedoseeva 1988
Pseudoarmania (2 spp.)	R	Magadan, U.S.S.R.	Dlussky 1983 Dlussky & Fedoseeva 1988
Armaniella (1 sp.)	R	Magadan, U.S.S.R.	Dlussky 1983 Dlussky & Fedoseeva 1988
Archaeopone (2 spp.)	R	Southern Kazakstan	Dlussky 1975, 1983
Poneropterus (1 sp.)	R	Magadan, U.S.S.R.	Dlussky 1983 Dlussky & Fedoseeva 1988
Dolichomyrma (2 spp.)	R	Southern Kazakstan	Dlussky 1975, 1983 Dlussky & Fedoseeva 1988
? *Cretopone* (1 sp.)	R	Southern Kazakstan	Dlussky 1975, 1983 Dlussky & Fedoseeva 1988
? *Petropone* (1 sp.)	R	Southern Kazakstan	Dlussky 1975, 1983 Dlussky & Fedoseeva 1988

TABLE 1—(*Continued*)

Taxa	A/R	Source	Reference
Sphecomyrmidae			
Sphecomyrma (2 spp.)	A	New Jersey, U.S.A.	Wilson et al. 1967
	A	Medicine Hat, Canada	Wilson 1985
Cretomyrma (2 spp.)	A	Taymyr, Siberia	Dlussky 1975, 1987 Dlussky & Fedoseeva 1988
Palaeomyrmex (1 sp.)	A	Taymyr, Siberia	Dlussky 1975, 1987 Dlussky & Fedoseeva 1988
? *Baikuris* (2 spp.)	A	Taymyr, Siberia	Dlussky 1987 Dlussky & Fedoseeva 1988
VESPOIDEA			
Vespidae			
Curiosivespa (2 spp.)	R	Southern Kazakstan	Rasnitsyn 1975

[a] See Wilson, 1987, for alternative classification and tentative synonymy.

during his brief visit to Ottawa in 1988. He also assisted in assembling the literature. A longer collaboration that would have enabled him to coauthor this contribution would have improved it in many ways; he is responsible for much that is right with the paper. The authors assume full responsibility for any shortcomings. This paper also benefited from the careful study and subsequent drawings executed by Patricia Stephens (Royal Ontario Museum). David Rudkin and Alan McColl (Royal Ontario Museum) assisted with the photographic plates. Assistance with the manuscript was provided by Roslyn Darling and Julie Thomson-Delaney. Comments provided by J. M. Carpenter and A. S. Menke were useful in illustrating some of the difficulties in trying to incorporate fossils into classifications derived mainly from extant species.

TAXONOMIC ACCOUNTS

SUBORDER SYMPHYTA

FAMILY ANAXYELIDAE: SUBFAMILY SYNTEXINAE

Prosyntexis Sharkey, new genus

ETYMOLOGY: The generic name reflects the close relationship to *Syntexis.*

DIAGNOSIS: 1r-m crossvein of forewing absent; 2R1 cell of forewing wider basally than apically; RS + M of forewing reaching 1m-cu crossvein; 3R1 cell closed; 1M cell long and four-sided; cu-a crossvein only slightly postfurcal.

TYPE SPECIES: *Prosyntexis gouleti* Sharkey, new species.

DISCUSSION: This genus is remarkably close to *Syntexis* which is known from one extant Nearctic species, *Syntexis libocedrii* Rohwer. One synapomorphic character state of the two genera is the shape of the 2R1 cell of the forewing which is wider basally than apically. *Prosyntexis* can be distinguished from *Syntexis* in the following characters: 3R1 cell of forewing closed, M and Cu of forewing reaching wing margin, 1M cell long and four-sided instead of five-sided.

Prosyntexis gouleti Sharkey, new species

Figure 1

ETYMOLOGY: Named after Henri Goulet in recognition of his research on the systematics of Symphyta.

TYPE MATERIAL: Holotype female; AMNH 43270 (dorsal aspect; body except forewings in poor condition).

DESCRIPTION: Length 12.8 mm. Forewing length 10.0 mm; costal cell relatively narrow and apparently widening apically; 1Cu about half length of 1M; M + Cu and 1Cu veins almost forming a straight line; 3r-m and apex of stigma equidistant from wing base. Ovipositor length about 1.7 mm.

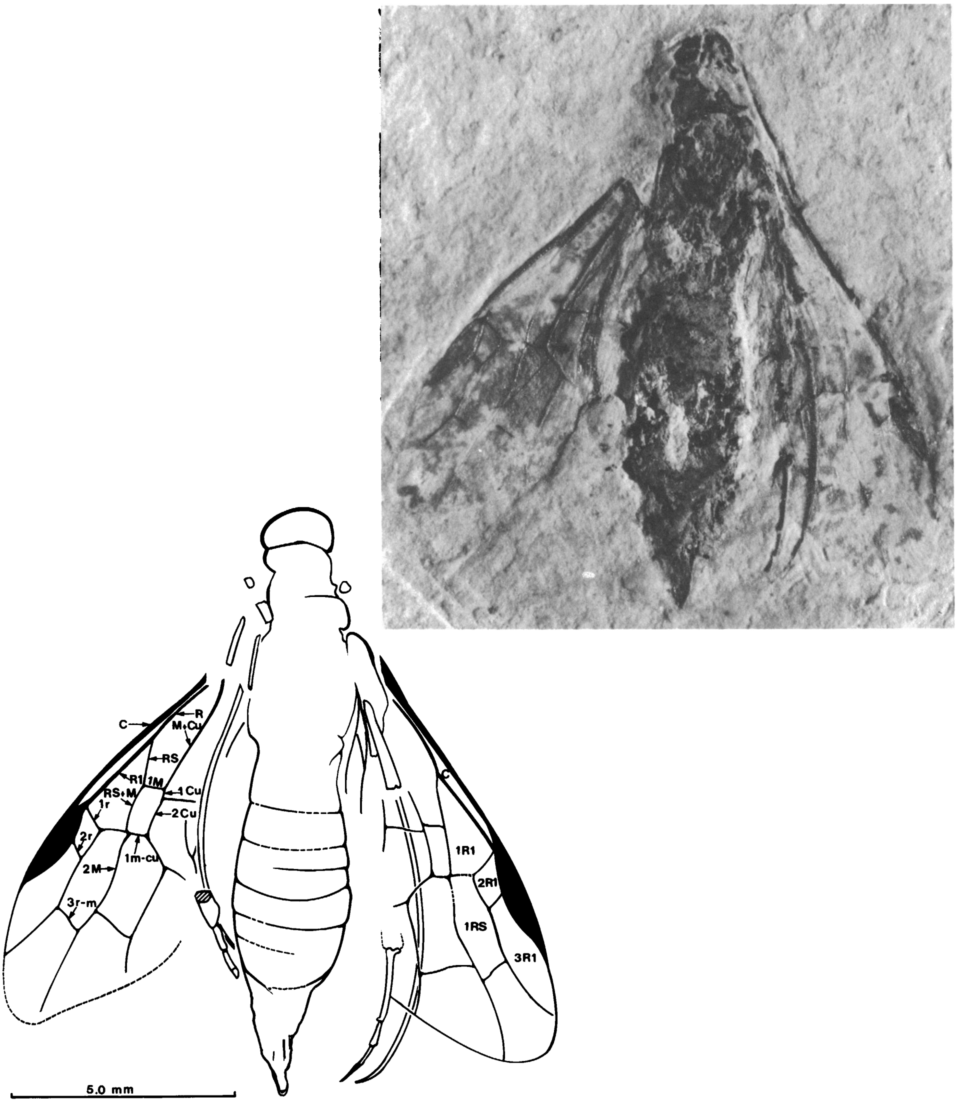


Fig. 1. *Prosyntexis gouleti* (Anaxyelidae), holotype (AMNH 43270). Cells labeled on right wing, veins labeled on left wing.

SUBORDER APOCRITA

FAMILY EPHIALTITIDAE

Karataus Rasnitsyn, 1977

DIAGNOSIS: Costal cell of forewing present; forewing with more than 10 closed cells; crenulae present apically on metasomal terga 1 and 2; ovipositor long, abdomen constricted between first and second segments.

Karataus kourios Sharkey, new species

Figures 2, 3

ETYMOLOGY: Kourios is Greek for "youthful" and is a reference to this species as the most recent or youngest member of the Ephialtitidae.

TYPE MATERIAL: Holotype female; AMNH 43269 (mostly dorsal aspect, body except

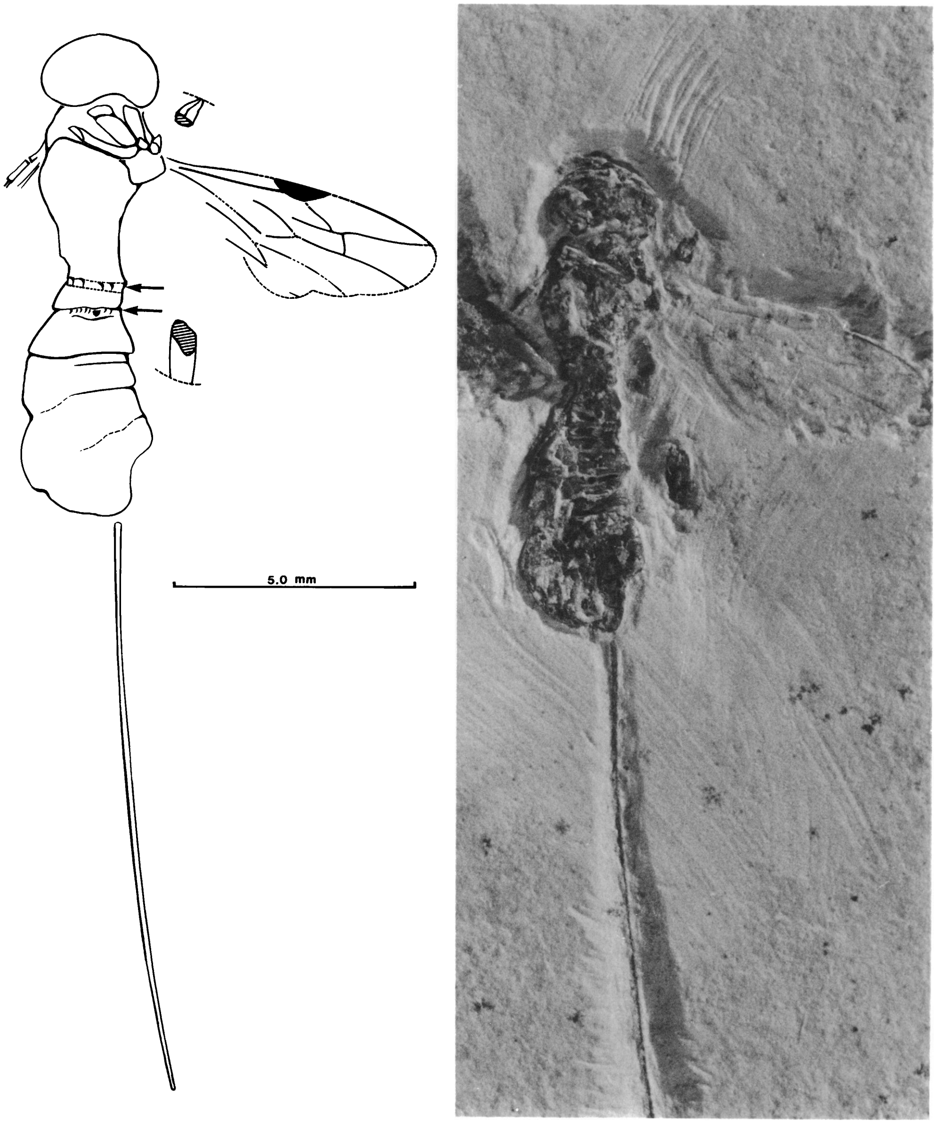


Fig. 2. *Karataus kourios* (Ephialtitidae), holotype (AMNH 43269). Arrows indicate crenulae on metasomal terga 2 and 3.

forewings in poor condition). Paratype female; AMNH 43268.

DESCRIPTION: Length including ovipositor 10.0 mm; head large; forewing length 11.0 mm; costal cell of forewing rather long and narrow, stigma conspicuous; hind coxa large; hind femur 2.2 mm; ovipositor length 12.0 mm.

DISCUSSION: This species is a rather typical ephialtitid, as evidenced by the long ovipositor, large body size, and weak constriction of metasomal segment 2. This fossil represents the most recent specimen known; additional specimens are known only from the Jurassic. The specimen is referred to the genus *Karataus* based on the large hind coxa

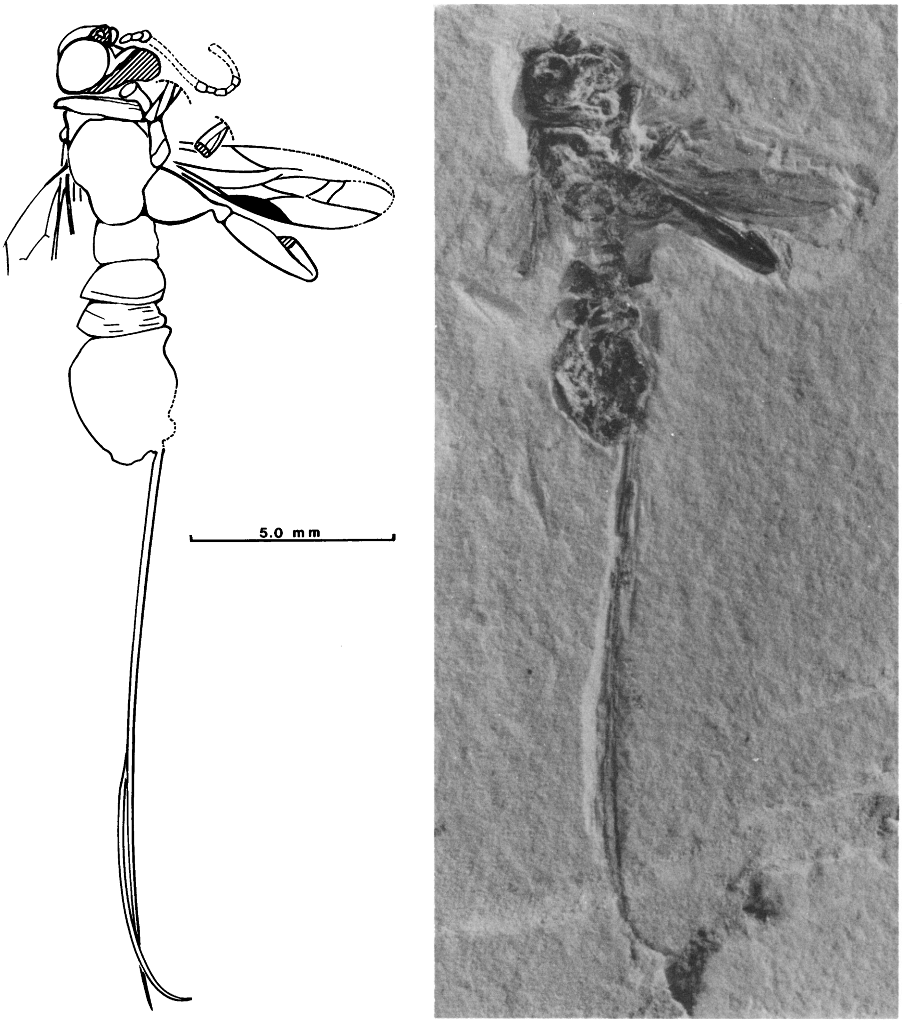


Fig. 3. *Karataus kourios* (Ephialtitidae), paratype (AMNH 43263).

and crenulae apically on metasomal terga 2 and 3 (Rasnitsyn, personal commun.). This species differs from others in the genus in that the hind femur is not greatly incrassate.

FAMILY PROCTOTRUPIDAE(?)

Protoprocto Sharkey, new genus

Etymology: The name *Protoprocto* is derived from the Greek for "first" and is a reference to the relative age of this lineage. Gender masculine.

Diagnosis: Pronotum elongate, triangular; forewing with veins moderately sclerotized; 1M vein strongly curved apically; 1M cell quadrate; RS vein extending distinctly beyond stigma; metasoma spindle shaped; ovipositor sheaths short and robust.

Type species: *Protoprocto asodes* Sharkey, new species.

Discussion: It is rather difficult to place this species within the Proctotrupoidea; the venation of most families is very similar. The shape of the metasoma, which tapers sharply apically, and the short robust ovipositor sheaths are the most convincing characters for placing this taxon in the Proctotrupidae. The elongate pronotum is similar to the con-

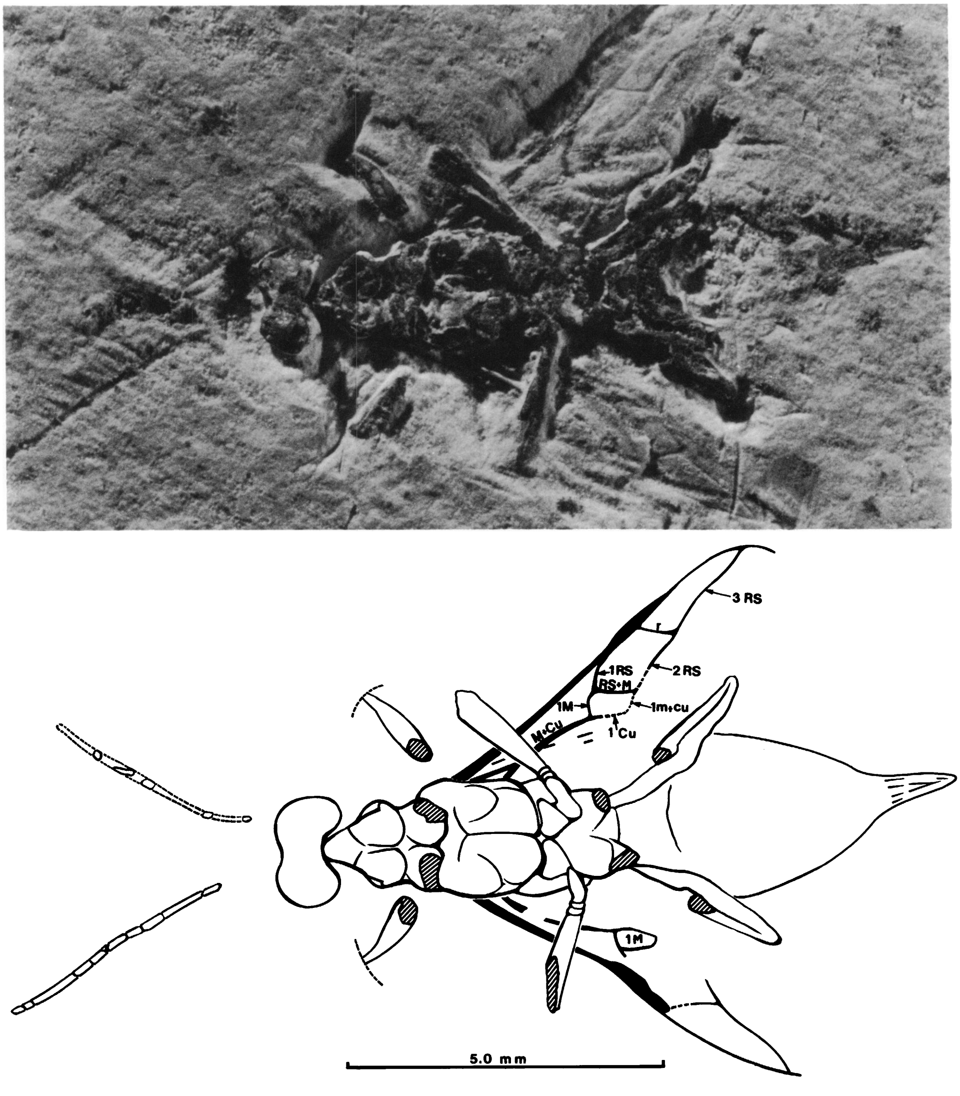


Fig. 4. *Protoprocto asodes* (Proctotrupidae?), holotype (AMNH 44101).

dition found in the Roproniidae; however the metasoma is petiolate in roproniids.

Protoprocto asodes Sharkey, new species

Figure 4

ETYMOLOGY: The specific epithet is from the Greek for "muddy or slimy" and is a reference to the likely condition of the holotype millions of years ago.

TYPE MATERIAL: Holotype female; AMNH 44101 (ventral aspect: condition good).

DESCRIPTION: Length 9.2 mm. Head quadrate, wider than long. 1M vein about as long as 1RS, both veins curved, especially 1M; 1M cell quadrate with 1M vein slightly longer than 1m-cu; 3RS vein 1.8 length of 2RS. 3RS almost reaching wing apex. Midfemur length 0.2 mm. Metasoma sessile, ovipositor length 0.8 mm.

FAMILY MESOSERPHIDAE

Figure 5

MATERIAL: AMNH 43272 (dorsal aspect, body condition good, wing condition poor).

DESCRIPTION: Length 3.8 mm. Head slight-

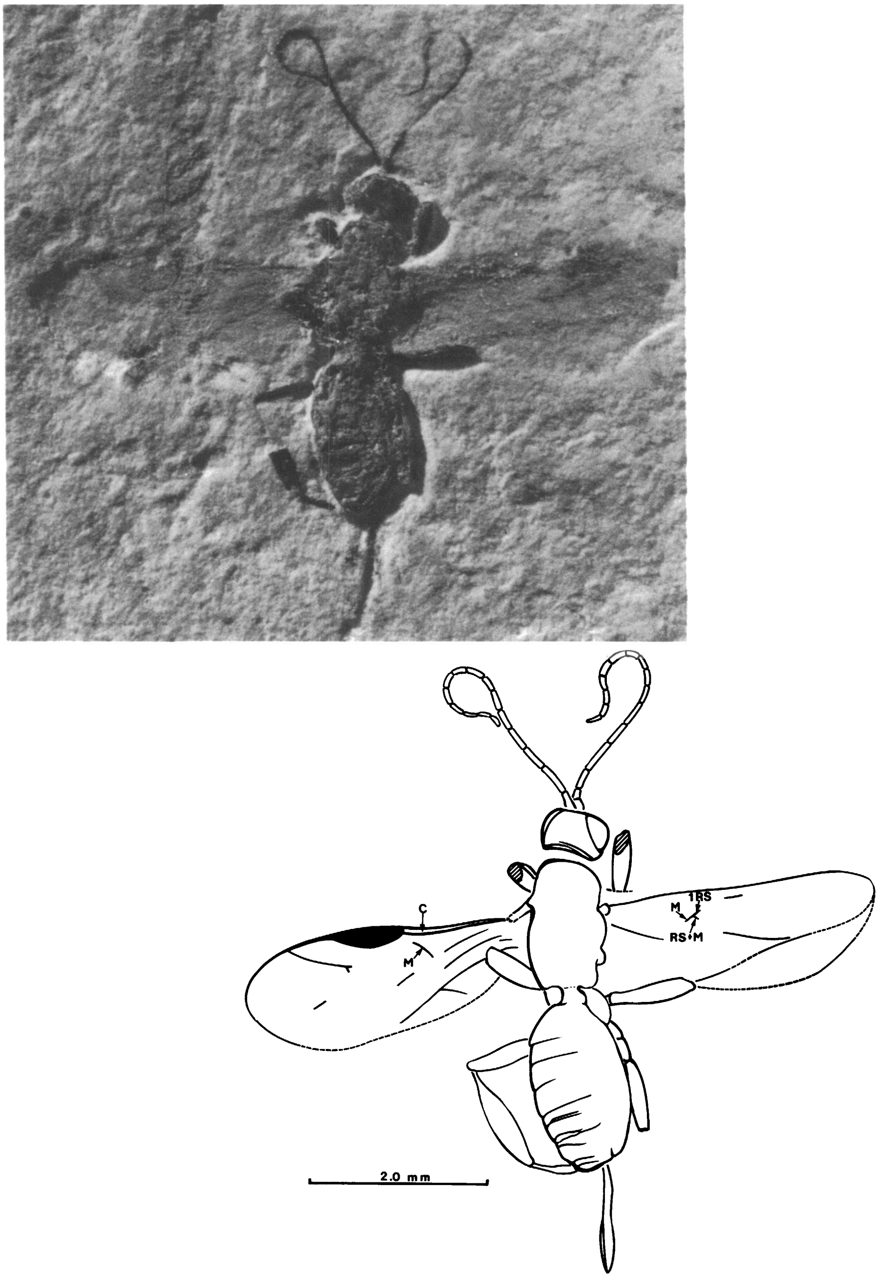


Fig. 5. Mesoserphidae (AMNH 43272).

ly wider than long, antenna with 12-segmented flagellum. Forewing length 3.0 mm; costal cell present; stigma present; basal vein (M + RS) curving weakly toward stigma; cell 1M small, vein 1RS longer than 1M. Hind tibia incrassate. Metasomal terga mostly of equal length; length of ovipositor sheath 1.0 mm, slightly swollen apically.

DISCUSSION: This is an interesting specimen as it does not fit easily in any existing taxon. I hesitate to describe a new family for it due to its poor state of preservation and lack of important venational characters. Placement in the Proctotrupoidea is more or less by default, but also because of the small 1M cell of the forewing, i.e., 1RS long relative to the length of 1M. Aculeata is rejected because of the long ovipositor and Ichneumonomorpha is rejected because of the presence of a costal cell. The specimen could belong to the Megalyridae (Evaniomorpha) as it has a 12-segmented flagellum and a rather transverse quadrate pronotum. The main reason that I doubt this placement is that vein 1M of the forewing is more distal than that of any extant megalyrid (Shaw, 1988). Among Proctotrupoidea, this species falls most easily within the concept of the Mesoserphinae, which as presently defined is paraphyletic. Again this decision is more or less by default because the specimen does not show synapomorphies to allow for its placement in any other proctotrupoid family.

SUBORDER ACULEATA

FAMILY TIPHIDAE:
SUBFAMILY ANTHOBOSCINAE(?)

Architiphia Darling, new genus

ETYMOLOGY: The name *Architiphia* is derived from the Greek for "ancient" and is a reference to the genus as the most ancient Tiphiidae. Gender feminine.

DIAGNOSIS: Antenna tightly curled; posterior genual plates absent; wing venation complete; forewing with marginal cell appendiculate, vein cu-a interstitial or slightly postfurcal, and Cu extended to wing margin.

DESCRIPTION: Antenna tightly curled, structure of antennal socket not discernible. Mesosoma with laminate mesosternal plates that overlap base of midcoxa; legs long, spines present at least on mid and hind tibia; femora moderately stout, lacking posterior genual plates; hind tibial spur almost as long as basitarsomere; basitarsomere very long, subequal in length to tarsomeres 2–4; tarsomeres with (whirls of ?) large spines at apices and smaller spines medially; hind tarsal claws with indication of small inner tooth. Forewing with 10 closed cells; costal cell present; major longitudinal veins (R1, M, Cu1) not reaching wing margin; wing margin without evidence of microtrichiae; stigma large and prominent; basal vein (M + RS) slightly oblique, joining R distinctly before stigma, the first abscissa of RS shorter than distance from R1 to stigma; 2r crossvein arising apically from stigma, distal to midpont; marginal cell (2 + 3R1) lanceolate, not rounded at wing margin, and not far removed from wing tip, slightly appendiculate (i.e., vein R1 extended beyond apex of cell); RS vein straight between RS + M and 2r, 2r much shorter than length of RS between RS + M and 2r; 3 submarginal cells (1R1, 1RS, 1RS2) becoming wider toward wing apex; crossveins 2r-m and 3r-m arched toward base and apex of wing respectively; 3 discoidal cells (1M, 2M, 2Cu); 1 M elongate, 1m-cu long and sinusoidal, reaching M much closer to 2r-m than to RS; 2m-cu reaching M near midpoint between 2r-m and 3r-m; cu-a interstitial or slightly postfurcal to fork of M + Cu. Hindwing with 3 closed cells; RS and M extended beyond 2r-m; submedian cell (R + 1R1) elongate; Cu long, extended to wing margin; cu-a distinctly postfurcal to fork of M + Cu; A2 absent. Metasoma without elongate petiole; with 5 visible sterna.

TYPE SPECIES: *Architiphia rasnitsyni* Darling, new species.

DISCUSSION: The classification of *Architiphia* as a member of the Tiphiidae is rather straightforward and greatly facilitated by the recent review of the fossil Tiphiidae (Rasnitsyn, 1986a). This species meets all the diagnostic characters mentioned by Rasnitsyn (1986a), namely strongly fossorial legs with mid and hind tibiae thick and spiny, plesiomorphic wing venation (10 closed cells in the forewing, without the distal reduction in venation characteristic of Scoliidae), and laminate mesosternal plates.

Subfamilial placement is more problematic, primarily because of the absence of the anterior surface of the head; the nature of the antennal insertion is not known. The Anthoboscinae are generally regarded as the most plesiomorphic subfamily in the Tiphiidae (sensu Brothers, 1975). Pate (1947) stated that "Anthoboscinae are without question the most generalized extant Tiphiidae." Plesiomorphic characters for the Tiphiidae include the following (Brothers, 1975): sexual dimorphism slight, both females and males fully winged; antennal sockets with simple reflexed rims, not overlain with tubercles; tegula short, not completely covering the axillary sclerites of forewing; males with hypopygium simple, not unciform; and wing venation complete (cf. females in the Tiphiinae and Myziniinae among the subfamilies with alate females). Posterior genual plates are laminate lobes on the lower posterior margin of the apex of the hind femora. These are strongly developed in female anthoboscines and are one-half or more the length of the femora in extant species (Pate, 1947). These are clearly absent in *Architiphia rasnitsyni* (figs. 6, 8). Rasnitsyn (1986a) noted that for all females in the Anthoboscinae that he has studied the antenna are tightly curled. Tightly curled antenna are present in *Architiphia rasnitsyni* (fig. 6), but this character is also found in extant members of other tiphiid subfamilies, e.g., the Tiphiinae.

Referral of *Architiphia* to the present concept of the Anthoboscinae assumes that tubercles covering the antennal sockets are absent and *Architiphia* would become the first anthoboscine that lacks genual plates. I hesitate to burden the higher classification with additional subfamilies for extinct taxa and have therefore referred *Architiphia* to the Anthoboscinae with a query.

There are two genera of fossil Tiphiidae described, both from the Oligocene: *Lithotiphia* Cockerell and *Geotiphia* Cockerell. Both genera were referred to the subfamily Myzininae, based primarily on the presence of tubercles covering the antennal sockets (Rasnitsyn, 1986a). *Architiphia* can be distinguished from *Lithotiphia* by two characters of the forewing venation: position of vein cu-a (postfurcal versus antifurcal) and the presence of a free section of Cu in *Architiphia*. *Architiphia* can be distinguished from *Geotiphia* primarily on the structure of the antenna (tightly curled versus straight or variously bent) and wing venation; the marginal cell of *Geotiphia* is not appendiculate, with the apex removed from the wing margin (see Rasnitsyn, 1986a, his figs. 2–7).

Architiphia greatly increases the minimal age of the family Tiphiidae, from the Oligocene to the Lower Cretaceous, by about 70 million years, from 35 to about 105 mybp. The implications of this finding for the phylogeny of the Aculeata are unclear, but certainly a greater age must be granted to the Tiphiidae.

Architiphia rasnitsyni Darling, new species

Figures 6–9

ETYMOLOGY: This species is named for Dr. A. P. Rasnitsyn, in recognition of his work on fossil Tiphiidae and in appreciation for his assistance with this project.

TYPE MATERIAL: Holotype female; AMNH 43265 (ventral aspect: in good condition, except anterior surface of head missing).

DESCRIPTION: Length about 16 mm. In habitus robust, with distinct punctures evident on mesosternum, coxae, and metasomal sterna. Head subcircular in anterior aspect, about as wide as mesosoma; eye almost extended to base of mandible, malar space small; clypeus slightly produced; mandible spatulate (teeth may or may not be present). Forewing length about 11 mm; stigma length about 4 times maximum width; marginal cell length about 4 times maximum width. Hindwing length about 6 mm.

FAMILY RHOPALOSOMATIDAE

Mesorhopalosoma Darling, new genus

ETYMOLOGY: A reference to the Mesozoic occurrence of the Rhopalosomatidae. The gender is neuter.

DIAGNOSIS: Costal cell reduced; forewing with 2r-m and 2m-cu present; and hindwing with 2r-m crossvein in basal portion of wing.

DESCRIPTION: Legs not fossorial, femora and tibiae long, not expanded medially, without strong spines, tarsi expanded in female. Forewing with 9 closed cells, without dense microtrichiae; costal cell very narrow, C and R very closely associated; stigma linear; basal vein (M + RS) oblique, joining R just before stigma, the first abscissa of RS longer than distance from R1 to stigma; 2r arising apically from stigma, distal to midpoint; marginal cell (2 + 3R1) lanceolate, not rounded at wing margin, very long, and not far removed from wing apex; RS strongly curved between RS + M and 2r, 1r absent, 2r much

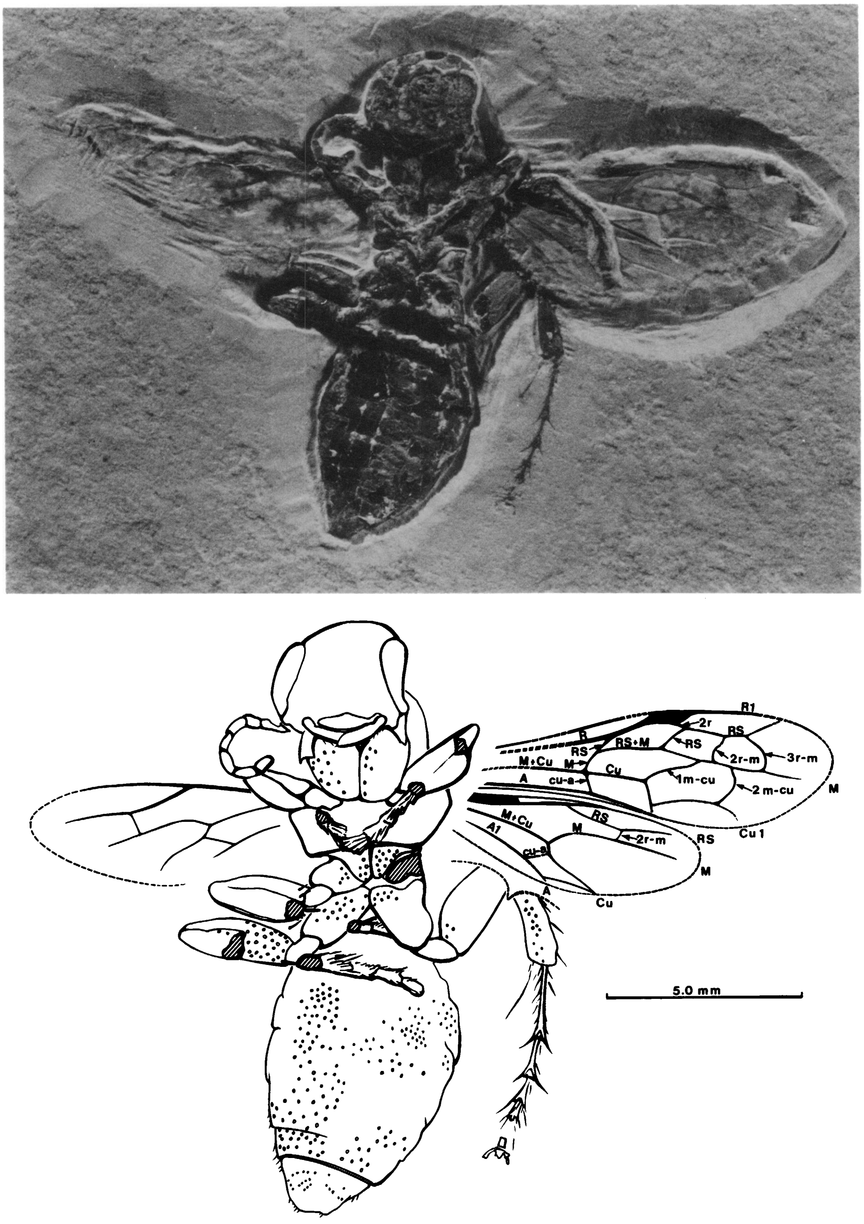
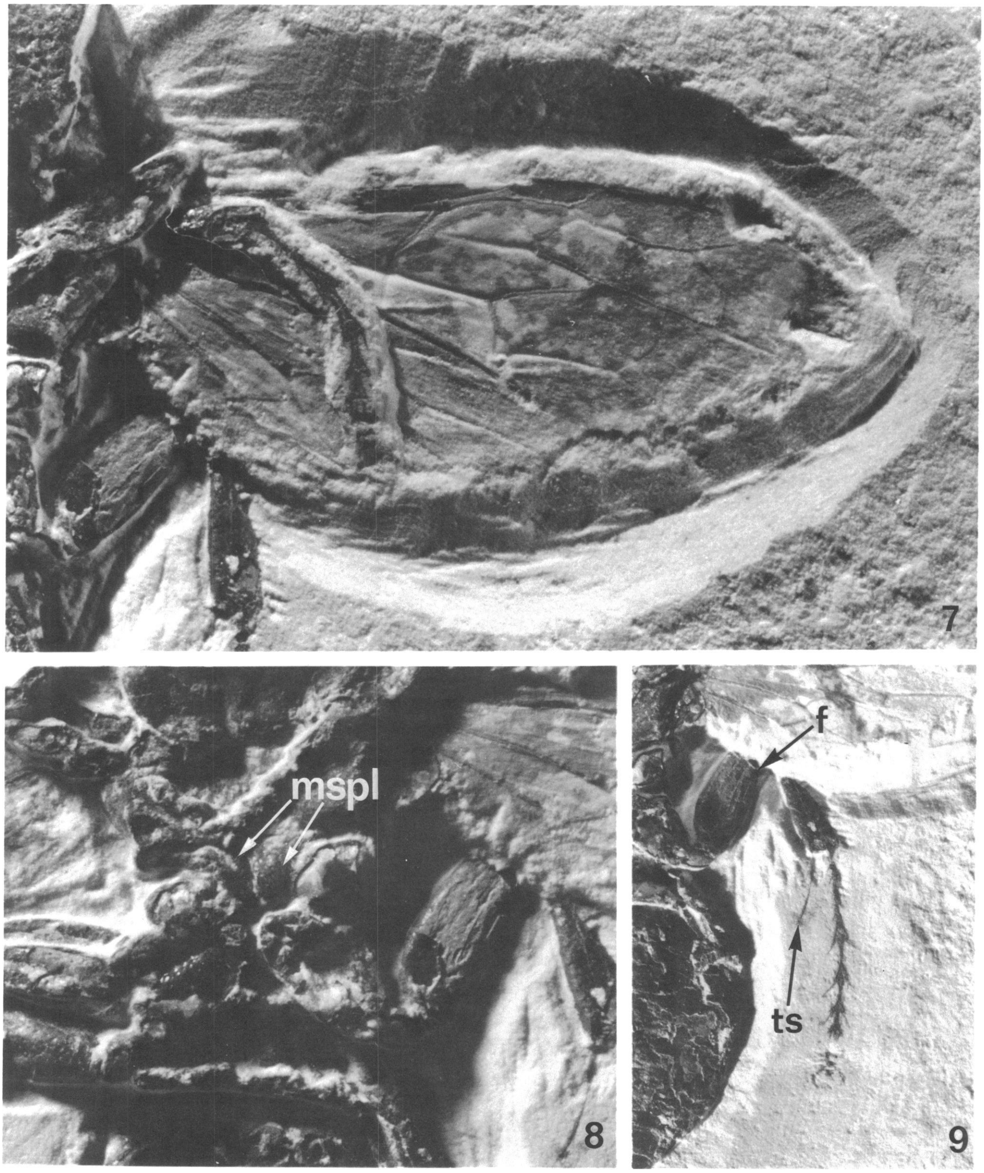


Fig. 6. *Architiphia rasnitsyni* (Tiphiidae), holotype (AMNH 43265), habitus. Mesothoracic tarsus not drawn.

shorter than length of RS between RS + M and 2r; 3 submarginal cells (1R1, 1RS, 1RS2); 2r-m and 3r-m vertical, not strongly angled, 2r-m nearly straight, 3r-m sinuous; M between 2r-m and 3r-m, equal to length of RS between 2r-m and 3r-m; 3 discoidal cells (1M, 2M, 2Cu); 1M elongate; 1m-cu long, entering second submarginal cell much closer to 2r-m than RS; 2m-cu sinusoidal, entering third submarginal cell at midpoint between 2r-m and 3 r-m; cu-a interstitial with fork of M + Cu. Hindwing with 2 closed cells; RS, M, and Cu veins not extended to wing margin; submedian cell (R + 1R1) short, 2r-m in basal



Figs. 7–9. *Architiphia rasnitsyni* (Tiphiidae), holotype (AMNH 43265), detail **7.** Forewing and mesothoracic tarsus (subsequently detached from specimen). **8.** Ventral region of mesothorax; mspl, mesosternal plates. **9.** Hindleg; f, femur; ts, tibial spur.

half of wing, near fork of M + Cu; cu-a strongly angled, interstitial to fork of M + Cu; A2 vein absent. Metasoma with distinct petiole, first metasomal segment distinctly separated from remaining segments (gaster); gaster long, subequal in length to rest of body.

TYPE SPECIES: *Mesorhopalosma cearae* Darling, new species.

DISCUSSION: This genus is referred to the family Rhopalosomatidae primarily on the basis of the reduced costal cell. The costal cell is narrower than the width of the radius and much narrower than in other extant aculeate families but not as reduced as in extant species of Rhopalosomatidae. In *Rhopalosoma* and *Liosphex* the costal cell is only indicated distad. The hindwing venation is also consistent with the placement as a rhopalosomatid; crossvein 2r-m is positioned in the basal half of the wing, very near the fork of M + Cu. A basal placement of 2r-m is reported as a groundplan character only for the Formicidae (Brown and Nutting, 1950). The more common condition in the Aculeata has this crossvein in the distal third of the wing, as exhibited by the Pompilidae, suggested as the sister group of the Rhopalosomatidae (Brothers, 1975, but see Day, 1988). The inferred structure of the metasoma is also consistent with placement as Rhopalosomatidae or Formicidae. Female *Rhopalosoma* and *Liosphex* have very wide tarsi, weakly concave beneath with dense setae. The tarsi only slightly expanded in *Mesorhopalosoma* (fig. 13), but this character is not universal in the family (Townes, 1977).

Characters of the forewing venation argue against the referral of these fossils to the Formicidae. In all ants, only a single r-m crossvein is present and 2m-cu is absent (Brown and Nutting, 1950). The holotype of *M. cearae* shows clearly the presence of two r-m crossveins and 2m-cu (fig. 10). There are substantial differences in wing venation between the fossil and the current concept of the Rhopalosomatidae, based both on a comparison of extant genera (*Liosphex* and *Rhopalosoma*) and the characterization of the groundplan of the family provided by Brothers (1975): namely, forewing 2r-m and 2m-cu present versus both crossveins absent (the position of 2m-cu is indicated by a fold and short wing stubs in female *Rhopalosoma nearcticum* Brues); forewing cu-a interstitial to M + Cu versus distinctly postfurcal, by a distance at least equal to length of cu-a; hindwing C extended nearly to wing margin versus reduced distally; and hindwing cu-a interstitial to M + Cu versus antifurcal. The character states of the fossil are best regarded as plesiomorphic based on outgroup comparison with the Pompilidae. This genus is plesiomorphic relative to Rhopalosomatidae and Formicidae, the extant families which share the apomorphic configuration of the hindwing with the fossils. A conservative approach to higher taxa and nomenclature is appropriate given the plesiomorphic characters of this species. It seems counter productive to erect a higher taxa and the only other available option, short of the purgatory associated with incertae sedis, is to assign the genus to the family with which it shares a putative synapomorphy. This genus is therefore referred to the Rhopalosomatidae on the basis of the reduced costal cell.

This is the first fossil representative in the Rhopalosomatidae. Where known, rhopalosomatids are parasites of crickets (Townes, 1977) and crickets are a major component of the insect fauna of the Santana formation (Grimaldi, this volume).

Mesorhopalosoma cearae Darling, new species

Figures 10, 11, 13, 14

ETYMOLOGY: The specific epithet is a noun in the genitive case, derived from the type locality, Ceará, Brazil.

TYPE MATERIAL: Holotype (female?); AMNH 43266 (ventral aspect: wings in good condition). Paratype (female?); AMNH 44103 (lateral aspect: rather poorly preserved, but wing venation discernible). In the description, the holotype is referred to by the notation HT, the paratype, PT.

ADDITIONAL MATERIAL: Two additional specimens may be representative of this species but are not included in the type material because the wing venation is not adequately preserved: AMNH 43276 (fig. 13; dorsolateral aspect: legs and metasoma preserved) and AMNH 44109 (fig. 14; dorsal aspect).

DESCRIPTION: Length, 11[PT]–16[HT] mm. In habitus slender, without distinct punctures. Head subcircular, narrower than mesosoma; eye large, extended to oral cavity; ocelli large [HT]; clypeus produced in lateral view [PT]. Forewing length, about 7[PT]–11[HT] mm; stigma linear, length about 5 times maximum width; length of marginal cell about 5.5 times the maximum width. Hindwing length, 5[PT]–8[HT] mm.

DISCUSSION: The additional specimens are only tentatively referred to this species, based primarily on the similarity in the structure of the metasoma. AMNH 43276 has the tarsi somewhat expanded (most noticeable on the hindleg, fig. 13), as is characteristic for the Rhopalosomatidae. AMNH 44109 is also suggestive of this family because of the very large (maxillary?) palpi (fig. 14). Another possibility is that these two specimens are ants (Formicidae). Ponerine ants have a similar structure of the metasoma and are known from the Late Cretaceous (table 1).

FAMILY SPHECIDAE

?*Cretosphex* Rasnitsyn, 1975

There is considerable uncertainty concerning the taxonomy of a number of genera of Cretaceous aculeates, namely *Archisphex, Angarosphex, Vitimosphex,* and *Cretosphex.* These genera have all been considered, at one time or another, to be related to Apoidea (as Sphecoidea). The family-level taxa Sphecidae, Angarosphecidae, and Baissodidae have been used for various combinations of these genera. The most recent treatments refer *Angarosphex* to the Sphecidae with a query (Rasnitsyn, 1975) and *Vitimosphex* and *Archisphex* to the Baissodidae with a query (Rasnitsyn, 1986b). The affinities of these three genera are uncertain. Rasnitsyn (1975) originally considered *Angarosphex* as representing a new family of "? Scolioidea" (Angarosphecidae) and *Cretosphex* as a "? Sphecoidea." In 1980 he suggested that both genera, and *Archisphex,* could be included in the subfamily Ampulicinae of Sphecidae but suggested that further study would probably indicate that these genera represent a distinct family. Lomholdt (1982) stated emphatically that these are not ampulicines, and he apparently supports the placement of these genera as Sphecidae-Pemphredoninae. This view was first suggested for *Archisphex,* if only tentatively, by Evans (1969) and later by Bohart and Menke (1976: 31). But as Evans cautioned, there are generalized members of other subfamilies of Sphecidae (he mentions Nyssoninae and Sphecinae) that have very similar venation. Nyssoninae typically have vein 2m-cu entering the second submarginal cell (Bohart and Menke, 1976) which is consistent with *Archisphex* but not *Angorasphex* and *Cretosphex.*

The taxonomy is further complicated because unequivocal diagnoses have not been presented for these genera and it is not possible to assign specimens to genera with certainty. A conservative taxonomic approach is taken here and the Santana fossils are assigned to the Cretaceous genus with the most similar wing venation, i.e., *Cretosphex.* The following diagnosis will distinguish *Cretosphex* (including the type species, *C. incertus* Rasnitsyn, and the Santana fossils) from the three other Cretaceous genera (figs. 12, 17, 18 and fig. 122 of Rasnitsyn 1975; cf. fig. 125 (*Angarosphex*), fig. 139 (*Vitimosphex*) of Rasnitsyn [1975], and fig. 1 of Evans [1969] (*Archisphex*)): 1r present at least as short veins stubs; cu-a crossvein interstitial with fork of M + Cu; 3r-m vein angled toward apex of wing; 2m-cu interstitial with 2r-m; hindwing cu-a crossvein distinctly postfurcal of fork of M + Cu.

Cretosphex is most similar to *Angarosphex* Rasnitsyn; in both genera 1r is represented by a distinct stub and 1m-cu is interstitial with the RS (Rasnitsyn, 1975; figs. 125 and 122). In *Archisphex,* 1r is absent and in 2m-cu is curved strongly toward the wing base and enters the second submarginal cell. Vein 1r is also absent in *Vitimosphex.*

Two new species of *Cretosphex* are here recognized and formally described. These two species are essentially identical in wing venation, but differ considerably in size, and in other morphological characters (see Diagnosis). It is possible that this variation is related to body size and/or that a single sexually dimorphic species is present. Both new species differ from *C. incertus* by having 2r-m and 3r-m divergent (figs. 17, 18) versus parallel (Rasnitsyn, 1975; fig. 122).

Cretosphex parvus Darling, new species

Figures 15–17

ETYMOLOGY: From the Latin for "little," a reference to the smaller size of this species relative to its sympatric congener.

TYPE MATERIAL: Holotype female; AMNH 43264 (ventral aspect: legs and wings excellent). Paratype; AMNH 44106 (dorsal aspect: head, wings poorly preserved). Paratype; AMNH 44104 (dorsal aspect?: only metasoma adequately preserved, wings crumpled). The description is a composite of the three fossils and reference is made to individual specimens where necessary.

DIAGNOSIS: Length about 10 mm; wings not densely hairy; marginal cell shorter, length

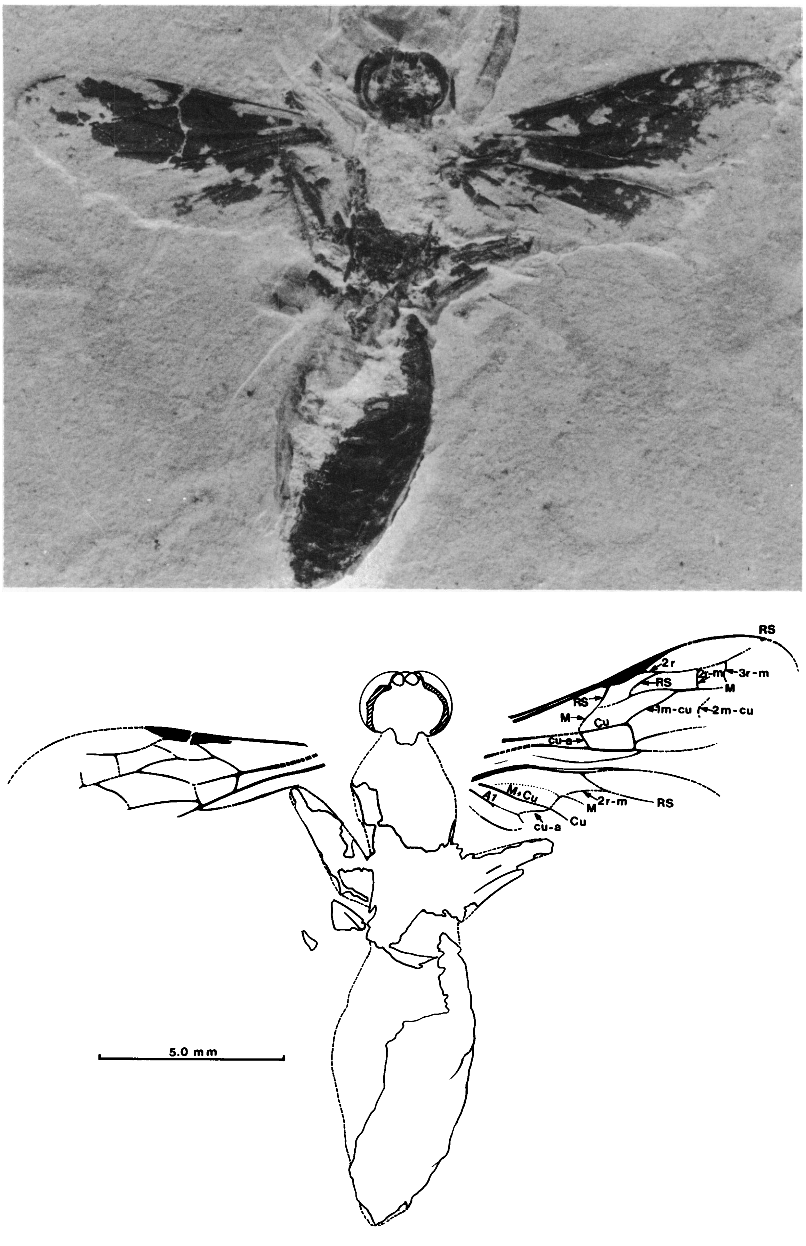
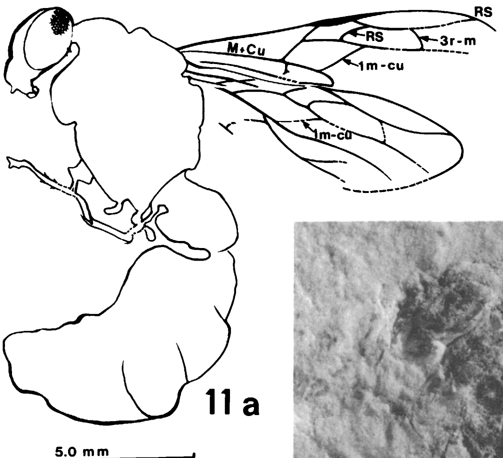


Fig. 10. *Mesorhopalosoma cearae* (Rhopalosomatidae), holotype (AMNH 43266).

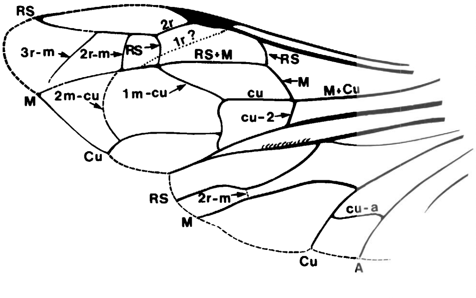
less than 5 times maximum width; femora narrower and tarsi shorter than in *C. magnus*.

DESCRIPTION: Length about 10 mm. In habitus robust, without evidence of distinct punctures. Head (excl. 44104) transverse in dorsal view, width about twice maximum length. Mesosoma (43264) with hind femur spindle shaped, length about 4 times maximum width; hind tibia slender, with distinct peglike spines on outer surface; tarsi slender, without strong spines, basitarsi not wider than distal tarsomeres. Forewing (43264, 44106) length about 5 mm, with 10 closed cells, without dense microtrichiae; costal cell present; major longitudinal veins (R1, M, Cu1) probably almost reaching wing margin; stigma lin-



11 a

11 b

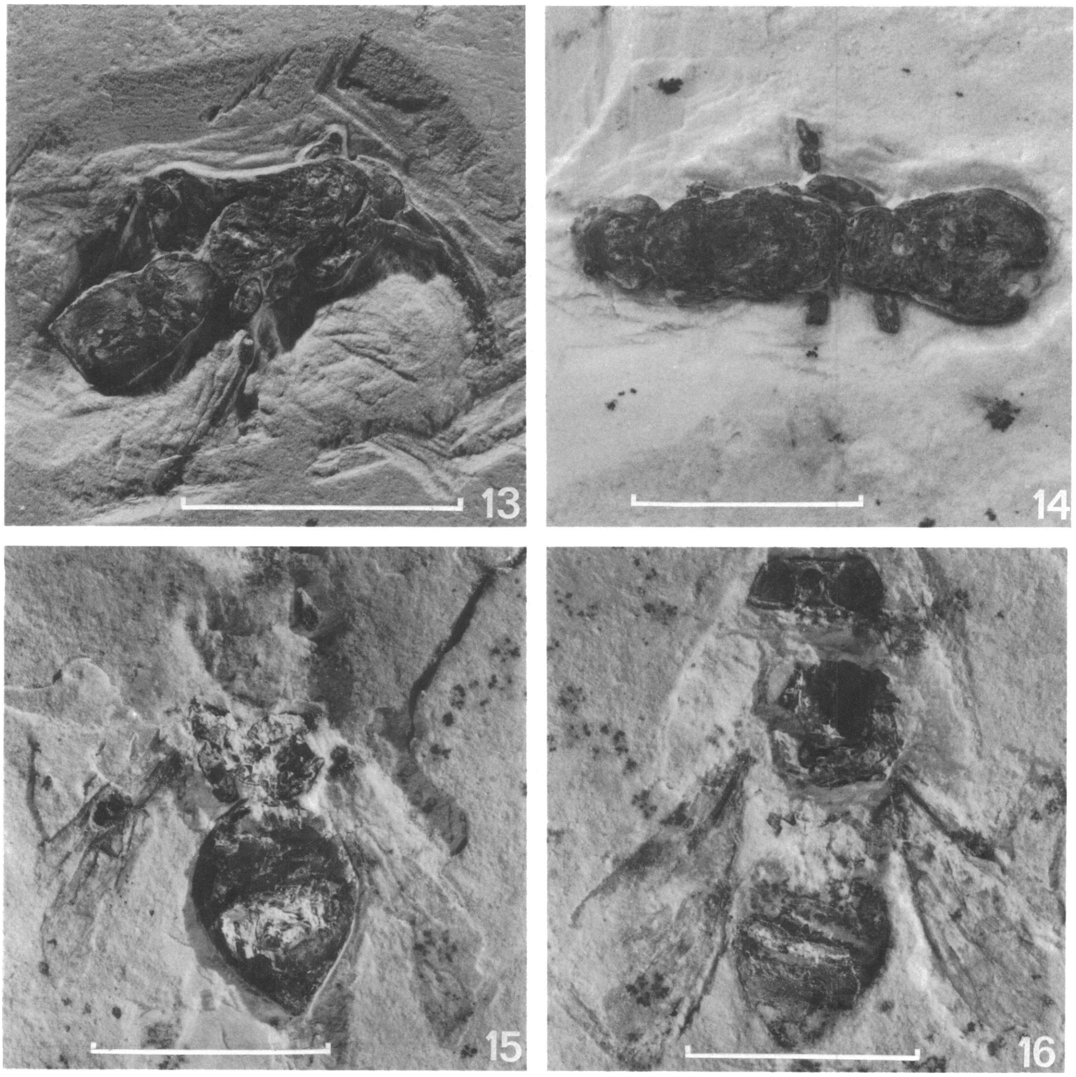


12 a

12 b

Figs. 11, 12. **11.** *Mesorhopalosoma cearae* (Rhopalosomatidae), paratype (AMNH 44103). **12.** *Cretosphex magnus* (Sphecidae), paratype (AMNH 43267).

ear, length about 4.5 maximum width; basal vein (M + RS) slightly oblique, joining R before stigma, the first abscissa of RS shorter than distance from R1 to stigma; 2r arising apically from stigma, distal to midpont; marginal cell (2 + 3R1) lanceolate, not rounded at wing margin, length 3.5 (43264) to 4.8 (44106) maximum width, and not far removed from wing tip, appendiculate (i.e., R1 extended beyond apex of cell); RS slightly curved between RS + M and 2r, 1r indicated by short vein stubs on stigma and RS (only 43264), 2r subequal to length of RS between RS + M and 2r; 3 submarginal cells (1R1, 1RS, 1RS2); 2r-m and 3r-m rather straight, not strongly arched, 2r-m nearly vertical, 3r-m strongly angled, M between 2r-m and 3r-m fully twice the length of RS between 2r-m



Figs. 13–16. **13, 14.** Rhopalosomatidae? (AMNH 43276 and 44109). **15, 16.** *Cretosphex parvus* (Sphecidae), paratypes (AMNH 44104 and 44106). Scale lines, 5 mm.

and 3r-m; 3 discoidal cells (1M, 2M, 2Cu); 1M elongate, 1m-cu long and sinusoidal, interstitial with RS; 2m-cu interstitial with 2r-m; cu-a interstitial with fork of M + Cu (vein not evident in 44100). Hindwing (43264) length about 5.5 mm, with 4 closed cells. Hamuli dispersed along wing margin distal to fork of R and RS (44104 only); RS and M extended beyond 2r-m, nearly reaching wing margin (?); submedian cell (R + 1R1) elongate, narrowed apically; cu-a distinctly postfurcal to fork of M + Cu; A2 not indicated. Metasoma broadly oval, without elongate petiole; cuticle preserved in 44104, sculpture finely imbricate, without distinct punctures.

Cretosphex magnus Darling, new species

Figures 12, 18

ETYMOLOGY: From the Latin for "large," a reference to the larger size of this species relative to its sympatric congener.

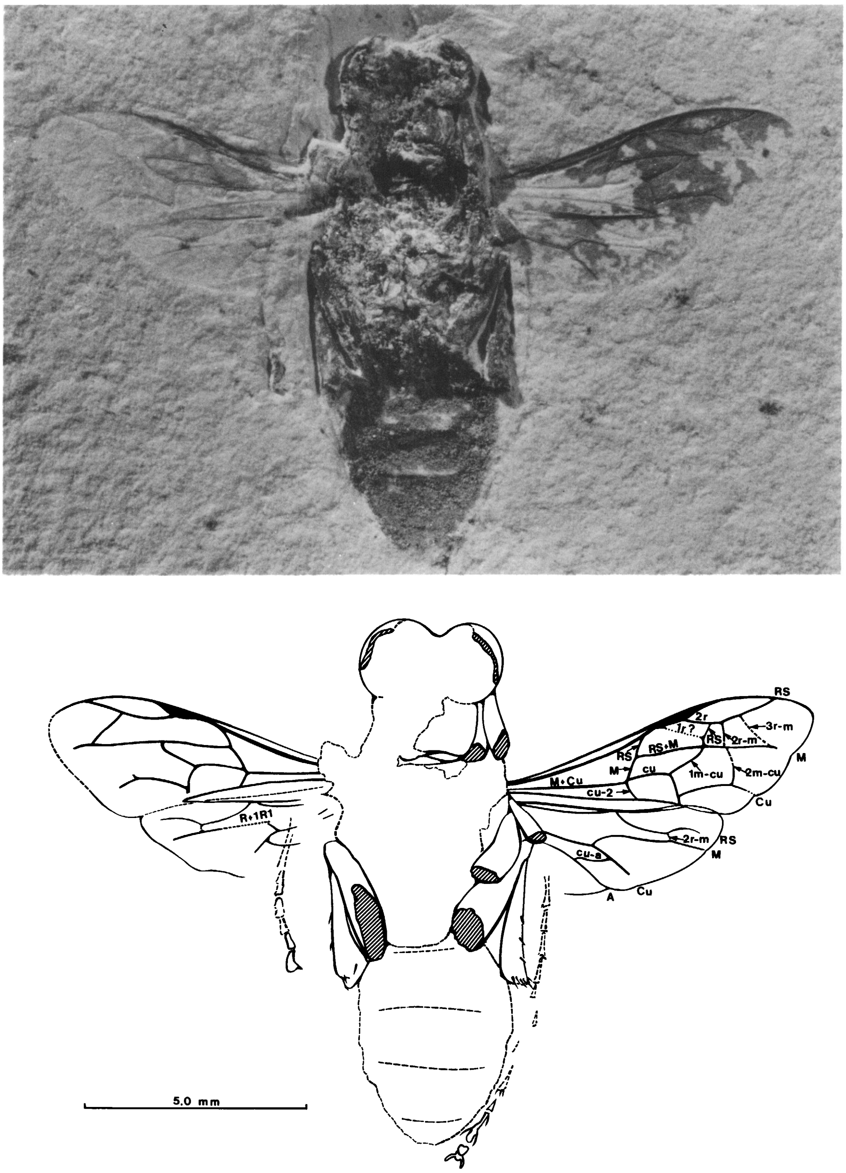


Fig. 17. *Cretosphex parvus* (Sphecidae), holotype (AMNH 43264).

TYPE MATERIAL: Holotype female; AMNH 44107 (ventral aspect: in good condition, except distal metasomal segments missing). Paratype; AMNH 43267 (dorsal aspect?: legs and wings excellent). The description is a composite of both fossils and reference is made to specific specimens where necessary.

DIAGNOSIS: Length about 15 mm; wings densely hairy; marginal cell longer, length greater than 5 times maximum width; femora more robust and tarsi longer than in *C. parvus*.

DESCRIPTION: Length about 15 mm. In habitus robust, without evidence of distinct punctures. Head transverse in dorsal view, width about twice maximum length; antenna bent, not tightly curled, with flagellomeres 3–6 (?) about 2.4 times as long as wide (44107). Mesosoma (44107) with mesosternum having rounded reflexed plates, without lobe overlapping coxa; legs (incl. 43267) with hind coxa large, about one-half length of hind femur; hind femur strongly spindle shaped, length about 2.5 maximum width; hind tibia slender, with distinct peglike spines on outer surface; tarsi long and slender, without strong spines, basitarsus not wider than distal tarsomeres, but extremely long, length twice tarsomere 2, lengths of tarsomeres 1–5 as 156:78:53:40:73 (43267) and 174:85:71:35:77. Forewing length about 7 mm, with 10 closed cells, with dense microtrichiae; costal cell present; major longitudinal veins (R1, M, Cu1) probably almost reaching wing margin; stigma linear, length about 4 times the maximum width; basal vein (M + RS) slightly oblique, joining R before stigma, the first abscissa of RS shorter than distance from R1 to stigma; 2r arising apically from stigma, distal to midpoint; marginal cell (2 + 3R1) lanceolate, not rounded at wing margin, very long, length 5.0 (44107) to 6.3 (43267) times the maximum width, and not far removed from wing tip, appendiculate (i.e., R1 extended beyond apex of cell); RS slightly curved between RS + M and 2r, 1r indicated by fold and short vein stubs on stigma and RS (only 44107), 2r subequal to length of RS between RS + M and 2r; 3 submarginal cells (1R1, 1RS, 1RS2); 2r-m and 3r-m rather straight, not strongly arched, 2r-m slightly angled, 3r-m strongly angled, M between 2r-m and 3r-m fully twice the length of RS between 2r-m and 3r-m; 3 discoidal cells (1M, 2M, 2Cu); 1M elongate, 1m-cu long and sinusoidal, interstitial with RS; 2m-cu interstitial with 2r-m; cu-a interstitial with fork of M + Cu. Hindwing length, about 5.5 mm, with 4 closed cells, microtrichiae not nearly as dense as on forewing. Hamuli dispersed along wing margin distal to fork of R and RS (43267); RS and M extended beyond 2r-m, nearly reaching wing margin; submedian cell (R + 1R1) elongate, narrowed apically; cu-a distinctly postfurcal to fork of M + Cu; A2 present (44107). Metasoma (44107) broadly oval, without elongate petiole, with 6 (?) sterna, posterior 3 indicated by rows of long setae; cuticle preserved laterally on sternite 3, sculpture distinctly alveolate, without distinct punctures.

DISCUSSION: Only through a process of elimination similar to that of Evans (1969), is it possible to place these fossils in Apoidea. It should be noted that the characteristic structure of the pronotum is not evident in the fossils, and few other characters will unequivocally identify the superfamily Apoidea (Sphecidae s.l. + Apidae s.l.). Lomholdt (1982) listed three synapomorphies for this clade derived from the structure of the metasoma, including the enlargement of the metapostnotum to form the propodeal triangle (Brothers, 1976). The assessment of all of these characters requires more detailed preservation than is usually possible with mineral replacement fossils. Brothers (1975) noted that "both the anal [A2] and jugal [A3] veins are retained in the sphecid group and the anal vein [A2] only is retained in the apid group." Although they are plesiomorphies, the presence of A2 would seem to be diagnostic for Apoidea, and A3 for Sphecidae.

It is also extremely difficult to assign an apoid fossil to either Sphecidae or Apidae (or Larridae, if a classification is adopted that restricts Sphecidae to the subfamilies Sphecinae and Ampulicinae; see Lomholdt 1982). Traditionally, Mesozoic apoids were assigned to Sphecidae largely on the basis of a circular argument, involving the "coevolution" of bees and angiosperms (e.g., Burnham, 1978). The recent discovery of a highly derived stingless bee (*Trigona prisca* Michener) from the Upper Cretaceous amber of New Jersey (Michener and Grimaldi, 1988a, b) indicates that considerable care must be taken in assigning Mesozoic fossils to either Apidae or Sphecidae. There appear to be no diagnostic differences in wing venation and the traditional differentiae, plumose hairs and expanded hind basitarsus, are either unlikely to be preserved in mineral replacement fossils or subtle. Brothers (1975) noted that plesiomorphic sphecids can be distinguished from plesiomorphic apids by the structure of the hindwings: A3 present versus absent; costa extended beyond fork of RS versus reduced distally. In addition, the presence of a calcar on the hind tibia has been used to distinguish apids from sphecids (Lanham, 1960); however Lomholdt (1982) noted that some prim-

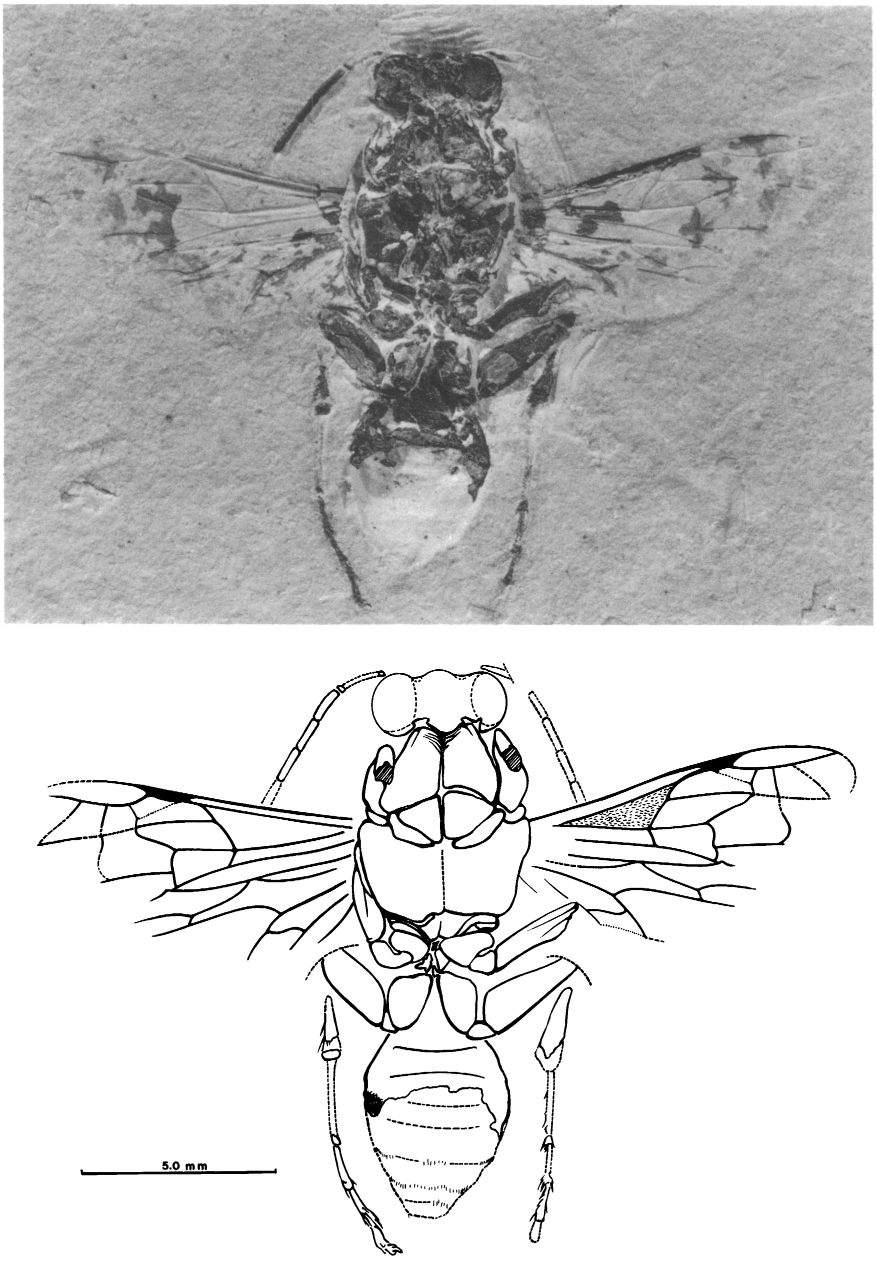


Fig. 18. *Cretosphex magnus* (Sphecidae), holotype (AMNH 44107).

itive bees possess this calcar, but he did not provide examples or references.

These fossils can only tentatively be referred to Sphecidae. There is no indication that the hind basitarsus is expanded in the fossils, and the basitarsi are rather well preserved in two of the five fossils. There is also a clear indication of 1r, either as distinct vein stubs between RS and the stigma or as a fold (figs. 12, 17, 18). Remnants of this vein are found in at least some Ampulicinae and Astatinae (Bohart and Menke, 1976; their fig. 11E, *Austrotoma,* their fig. 56, *Dryudella* sp.) and Sphecinae (*Sphex ichneumoneus, Sceli-*

phron cementarium). The spinose hind tibia also argues against these being bees in the traditional sense.

It is difficult to refer these fossils to any subfamily of Sphecidae with any certainty. The forewing is consistent with those of the Sphecinae; the venation is very similar to that of *Stangeella* (Bohart and Menke, 1976; their fig. 18A), except that the marginal cell is appendiculate in the fossils. It is also appendiculate in other genera of Sphecinae (e.g., *Chalybion, Trigonopsis*). However, all sphecines have a cylindrical petiole, and this structure is not clearly indicated in the fossils. The venation of the hindwing is inconsistent with that of Sphecinae; the media diverges before not after cu-a (Bohart and Menke, 1976). This orientation of the cu-a crossvein is consistent with referral to the subfamilies Pemphredoninae, Ampulicinae, or Astatinae. The Upper Cretaceous sphecids *Lisponema* and *Pittoecus* were assigned to the Pemphredoninae by Evans (1973); at least one of the genera (*Lisponema*) has the enlarged stigma characteristic of this subfamily. However, the Ceará fossils cannot be regarded as Pemphredoninae: the stigma is not enlarged, and a cu-a in the forewing is interstitial (antifurcal in Pemphredoninae). The Ampulicinae can be excluded on the basis of habitus; the fossils do not have an elongate body with long slender appendages. In sum, Astatinae may not be a bad selection. As noted by Bohart and Menke, this subfamily "retains many characters of the archaic sphecid stock." However, the marginal cell is truncate apically in Astatinae.

FAMILY SPHECIDAE: SUBFAMILY AMPULICINAE(?)

Figure 19

MATERIAL: AMNH 44108 female? (ventral aspect: wings, antenna, and legs poorly preserved).

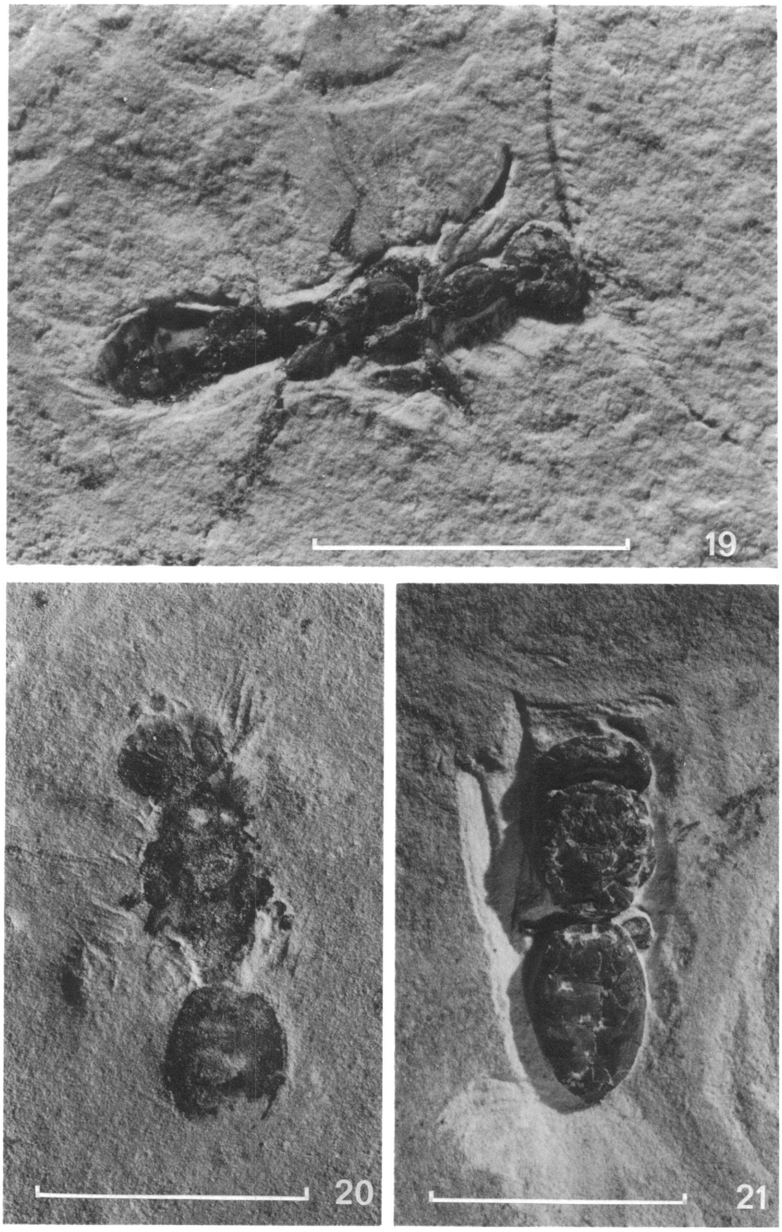
DESCRIPTION: Length about 7 mm. In habitus gracile, distinctly petiolate. Head: spherical, about as wide as mesosoma, eye rather large and bulging; antenna very long and narrow, almost equal to total body length (approx. 5 mm), probably with 12 antennal segments, each much longer than wide. Mesosoma slender, twice as long as wide; pronotal collar longer than broad; legs long and slender; forecoxa elongate and contiguous, tibia and tarsus slender; hindleg extremely long, about equal to total body length (approx. 7.5 mm), coxa, trochanter, femur, tibia, tarsus as 0.9, 0.3, 0.9, 2.5, 3 (in mm), hind coxae contiguous. Metasoma with petiole cylindrical, petiole about twice as long as wide; with short longitudinal ridges on sterna 2.

DISCUSSION: It is tempting to refer this specimen to the Ampulicinae on the basis of the elongate habitus and distinct petiole. This fossil could just as well be placed within the subfamily Sphecinae, as a rather typical nonfossorial thread-waisted wasp. There is, however, little direct evidence to suggest that the specimen is a sphecid. The extremely long legs, in particular the tibiae and tarsi and the habitus, are suggestive of Dryinidae. Another possibility is Scolebythidae, which also has elongate proepisterna. A fossil species (*Cretabythus sibricus* Evans) was described from the Upper Cretaceous of Siberia (referred to ? Bethylidae in table 1), but none of the described species of Scolebythidae have a petiolate metasoma. Details of the wing venation and the antenna would permit the evaluation of these possibilities. Complete forewing venation, with 10 closed cells, would exclude the Chrysidoidea (i.e., the Scolebythidae and Dryinidae) and 10 antennal segments would be diagnostic for the Dryinidae (see Carpenter, 1986, for diagnoses of chrysidoid families). It should also be noted that the classification of this fossil in the Ampulicinae removes the apparent inconsistency noted by Lomholdt (1982) by placing the clade Ampulicinae + Sphecinae in the Lower Cretaceous, before the appearance of the more derived subfamily Pemphredoninae, which is first recorded from the Upper Cretaceous.

ACULEATA, Incertae Sedis

There are two additional specimens in this collection that cannot even be tentatively assigned to family level. Wings and antenna are missing in both specimens and these are regarded as aculeates on the basis of a distinct constriction between the mesosoma and metasoma, the lack of an exserted ovipositor, and a general robust wasplike habitus.

AMNH 43274 (fig. 20): Dorsal aspect,



Figs. 19–21. Aculeata incertae sedis. **19.** Sphecidae or Dryinidae (AMNH 44108). **20.** AMNH 45274. **21.** AMNH 44100. Scale lines, 5 mm.

poorly preserved, faint outlines of antenna, foreleg, and forewing. Body length, about 7 mm. Head wider than mesosoma; prothorax may be elongate. The antennae are probably filiform. There appears to be a distinct petiole but this may be an artifact of preservation, which is very poor in this region of the body.

AMNH 44100 (fig. 21): Dorsal aspect, body well preserved, but wings and all appendages missing. Although incomplete, what remains shows remarkable preservation; it is possible to discern the individual facets of the compound eyes. The head is rather broad, as wide as the mesosoma. The pterothorax is robust, indicating that the specimen was fully winged, a conclusion supported by the existence of an associated wing fragment. There are apparently 7 metasomal terga. The surface sculpture is apparently devoid of coarse punctures. It is possible that this specimen belongs to *Cretosphex parvus*. The body is about the right size, 8 mm total length.

DISCUSSION

One of the major goals of paleontology is to determine the phylogenetic implications of various fossil assemblages. The difficulties with this approach have been stressed by numerous neontologists who usually conclude that because of biases the fossil record can only provide information on the minimum age of a taxon (see Joysey and Friday, 1982).

Such reasoning makes it convenient to dismiss apparent discrepancies between the appearance and radiation of major groups in the fossil record and generally accepted views on phylogeny. For example, the traditional view of Hymenoptera diversification holds that the plant-feeding sawflies gave rise to parasitoids (parasitic Hymenoptera or Terebrantes), which in turn gave rise to solitary stinging wasps (Aculeata) and ultimately the highly social bees, ants, and wasps (Evans and Eberhard, 1970; Spradbery, 1973). This view, however, is not based on phylogenetic principles but rather on an anthropocentric view of the importance of social behavior. The fossil record is not consistent with this scenario; by the Lower Cretaceous, the Apocrita are highly diversified, including most of the major lineages of aculeates and parasitic wasps. Biases in the fossil record could be used as one convenient explanation.

Biased samples are a major problem in the study of fossil Hymenoptera because different fossilization processes preferentially preserve insects of different body sizes. Amber fossils tend to be smaller insects those that were not able to escape from the sticky resins, and mineral replacement and compression fossils tend to be larger insects, often with strong and complete wing venation. Robust insects are much more likely to withstand these fossilization processes. A systematic taxonomic bias can result because the major groups of Hymenoptera tend to differ dramatically in body size. In general, sawflies and aculeates are larger insects and body size reduction has been a recurrent theme in many of the parasitic superfamilies. Amber assemblages would be expected to contain a disproportionate number of parasitic Hymenoptera, even if sawflies and aculeates were abundant, and mineral replacement fossil beds would be expected to show a disproportionate representation of larger Hymenoptera, including sawflies and aculeates. Any bias would be accentuated in the study of Cretaceous Hymenoptera because of the fossil deposits that are available for study. The twelve mineral replacement sites from the Lower Cretaceous tend to have more specimens than do the six amber sites, all from the Upper Cretaceous; there is a definite bias toward larger Hymenoptera.

Recent phylogenetic studies have indicated that Symphyta are paraphyletic and that Ichneumonoidea + Aculeata forms the sister group of all other extant Apocrita (Mason, 1988; see also Gauld and Bolton, 1988 and Rasnitsyn, 1988a). This hypothesis would predict the occurrence of aculeates at about the same time as nonaculeate apocritans. Ichneumonoidea and Aculeata of large body size and more complete venation first appear in the Lower Cretaceous mineral replacement deposits, as do members of the basal lineages of the unnamed clade of the Apocrita exclusive of the Ichneumonoidea and Aculeata, e.g., the Megalyridae, Trigonalidae, and Gasteruptiidae. The Serphitidae, Mymarommatidae, Mymaridae, and Austroniidae are found for the first time in Upper Cretaceous amber. All of these species are of rather small body size and have weak, reduced wing venation and this is the most likely reason that these taxa have not been found in the earlier mineral replacement fossil beds. Lineages in the same clade but with larger body size are represented in the Lower Cretaceous beds (e.g., the Praeaulacidae and Mesoserphidae). In general, the appearance and distribution of taxa in the Cretaceous are more consistent with the recent phylogenetic hypothesis than with the gradual diversification of sawflies to parasitic wasps and finally to aculeates.

When possible biases that are related to the probability of fossilization are taken into account, the Hymenoptera fauna shows no dramatic changes at the level of higher taxonomic categories throughout the Cretaceous. This is rather surprising when it is realized that almost 40 million years, the duration of the Jurassic, separates the Brazilian collections (110 mybp) and the principal amber collections of Canada (72 mybp). The recent discovery of an advanced subfamily of bees from the Upper Cretaceous (Michener and Grimaldi, 1988a, b), the rapid and early diversification of the aculeates in the Lower Cretaceous, and the evolutionary stasis throughout the Cretaceous all question the importance of the rise of angiosperms as a causal factor in the evolution of the Hymenoptera. Clearly, a better understanding of the evolutionary history of the Hymenoptera is a prerequisite for causal explanations of their diversification, and progress will require the application of phylogenetic principles to data derived from both paleontology and neontology.

REFERENCES

Alekseev, V. N., and A. P. Rasnitsyn
1981. Late Cretaceous Megaspilidae (Hymenoptera) from amber of the Taymyr. Paleontol. J. 1981: 124–128.
Bohart, R. M., and A. S. Menke
1976. Sphecid wasps of the world. A generic revision. Berkeley: Univ. California Press.
Brothers, D. J.
1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Multillidae. Univ. Kans. Sci. Bull. 50: 483–648.
1976. Modifications of the metapostnotum and origin of the "propodeal triangle" in Hymenoptera Aculeata. Syst. Entomol. 1: 177–182.
Brown, W. L., Jr., and W. L. Nutting
1950. Wing venation and the phylogeny of the Formicidae (Hymenoptera). Trans. Am. Entomol. Soc. 75: 113–132.
Brues, C. T.
1937. Order Hymenoptera, Superfamilies Ichneumonoidea, Serphoidea, and Chalcidoidea. *In* F. M. Carpenter et al., Insects and arachnids from Canadian amber. Univ. Toronto Stud. Geol., ser. 40: 21–27.
Burnham, L.
1978. Survey of social insects in the fossil record. Psyche 85: 85–133.
Carpenter, J. M.
1986. Cladistics of the Chrysidoidea (Hymenoptera). J. New York Entomol. Soc. 94: 303–330.
Day, M.
1988. Hymenoptera, Pompilidae. Handbk. Ident. Br. Insects. 6(4).
Dlussky, G. M.
1975. Family Formicidae. *In* A. P. Rasnitsyn (ed.), Hymenoptera Apocrita of the Mesozoic. Trudy Paleontol. Inst. Akad. Nauk. SSSR 147: 114–122. [in Russian]
1983. A new family of Upper Cretaceous Hymenoptera: an "intermediate link" between ants and the scolioids. Paleontol. J. 1983: 63–76.
1987. New Formicoidea (Hymenoptera) of the Upper Cretaceous. Paleontol. J. 1987: 146–150.
Dlussky, G. M., and E. B. Fedoseeva
1988. Origin and early stages of evolution of ants (Hymenoptera: Formicidae). *In* A. G. Ponomarencho (ed.), [Biocenotic crisis in the Cretaceous and the Evolution of insects], pp. 70–144. Moscow: Nauka Press. [in Russian]
Evans, H. E.
1969. Three new Cretaceous aculeate wasps (Hymenoptera). Psyche 76: 251–261.
1973. Cretaceous aculeate wasps from Taimyr, Siberia (Hymenoptera). Psyche 80: 166–178.
Evans, H. E., and M. J. W. Eberhard
1970. The wasps. Ann Arbor: Univ. Michigan Press.
Gauld, I., and B. Bolton.
1988. The Hymenoptera. Oxford: Oxford Univ. Press.
Handlirsch, A.
1908. Die fossilen Insekten und die Phylogenie der rezenten. Leipzig: Formen. [in German]
Hong, Y.-C.
1975. Eine neue fossile Sinosiricidae (Hymenoptera: Siricoidea) in West-Weichangder Provinz Hebei. Acta Entomol. Sinica 18: 235–241. [in Chinese with German summary]
1982a. Fossil Insects. *In* The Mesozoic stratigraphy and paleontology of Guyang coal-bearing basin, Neimenggol Autono-

mous Region, China, pp. 85–100. Beijing: Geological Publishing House. [in Chinese]
1982b. Mesozoic fossil insects of Jiuquan Basin in Gansu Province. Beijing: Geological Publishing House. [in Chinese]
1984a. Insecta. *In* Palaeontological Atlas of North China. II. Mesozoic Volume. Beijing: Geological Publishing House. [in Chinese]
1984b. New fossil insects of Laiyang group from Laiyang Basin, Shandong Province. *In* Professional papers in stratigraphy and palaeontology, no. 11. Beijing: Geological Publishing House. [in Chinese, with English summary]

Jarzembowski, E. A.
1984. Early Cretaceous insects from southern England. Modern Geol. 9: 71–93.

Jell, P. A., and P. M. Duncan
1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. *In* P. A. Jell and J. Roberts (eds.), Plants and Invertebrates from the Lower Cretaceous Koonwarra Fossil Bed, South Gippsland, Victoria, pp. 111–205. Mem. Ass. Australas. Palaeontols. 3. Sydney: Association of Australasian Palaeontologists.

Joysey, K. A., and A. E. Friday (eds.)
1982. Problems of phylogenetic reconstruction. Syst. Assoc. Special Vol. No. 21. New York: Academic Press.

Kinsey, A. C.
1937. Order Hymenoptera, Family Cynipidae. *In* F. M. Carpenter et al., Insects and arachnids from Canadian Amber. Univ. Toronto Stud. Geol., ser. 40: 21–27.

Kozlov, M. A.
1974. An early Cretaceous ichneumon of the family Pelecinidae (Hym., Pel.). Paleontol. J. 1974: 136–138.
1975. Families Stigmaphronidae and Trupochalcididae. *In* A. P. Rasnitsyn (ed.), Hymenoptera Apocrita of the Mesozoic. Trudy Paleonol. Inst. Akad. Nauk SSSR 147: 75–83. [in Russian]

Kozlov, M. A., and A. P. Rasnitsyn
1979. On the limits of the family Serphitidae (Hymenoptera, Proctotrupoidea). Entomol. Obozr. 58: 402–415. [in Russian]

Krassilov, V. A., and A. P. Rasnitsyn
1982. A unique finding: pollen in the intestine of the early Cretaceous sawflies. Paleontol. J. 1982: 80–95.

Lanham, U. N.
1960. A neglected diagnostic character of the Apoidea (Hymenoptera). Entomol. News 71: 85–86.

Lin, Q.
1976. The Jurassic fossil insects from Western Liaoning. Acta Paleontol. Sinica 15: 97–118. [in Chinese, with English summary]

Lomholdt, O.
1982. On the origin of the bees (Hymenoptera: Apidae, Sphecidae). Entomol. Scand. 13: 185–190.

Mason, W. R. M.
1988. The phylogeny of the Apocrita. Unpublished lecture notes.

Meunier, F.
1903. Neuvas contribuciones á la fauna de los himerópteros fósiles. Mem. R. Acad. Cienc. Artes. Barcelona 4: 4–12.

Mckay, I. J., and R. J. Rayner
1986. Cretaceous fossil insects from Orapa, Botswana. J. Entomol. Soc. South Africa 49: 7–17.

Michener, C. D., and D. A. Grimaldi
1988a. A *Trigona* from Late Cretaceous amber of New Jersey (Hymenoptera: Apidae: Meliponinae). Am. Mus. Novitates 2917: 10 pp.
1988b. The oldest fossil bee: apoid history, evolutionary stasis, and antiquity of social behavior. Proc. Natl. Acad. Sci. USA 85: 6424–6426.

Muesebeck, C. F. W.
1963. A new ceraphronid from Cretaceous amber (Hymenoptera: Proctotrupoidea). J. Paleontol. 37: 129–130.

Olmi, M.
1984. A revision of the Dryinidae (Hymenoptera). Mem. Am. Entomol. Inst. (Ann Arbor) 37 (1–2) 1–1913.

Pate, V. S. L.
1947. A conspectus of the Tiphiidae, with particular reference to the nearactic forms (Hymenoptera, Aculeata). J. New York Entomol. Soc. 55: 115–145.

Ponomarenko, N. G.
1975. Family Dryinidae. *In* A. P. Rasnitsyn (ed.), Hymenoptera Apocrita of the Mesozoic. Trans. Paleontol. Inst. Acad. Sci. USSR, 147: 104–105. [in Russian]
1981. New Dryinidae (Hymenoptera) from the Late Cretaceous of the Taymyr and Canada. Paleontol. J. 1981: 115–120.

Rasnitsyn, A. P.
1965. Notes on the biology, systematics and phylogeny of Xyelinae (Hymenoptera,

Xyelidae). Pol. Pismo Entomol. 35: 483–519.

1968. New Mesozoic sawflies (Hymenoptera, Symphyta). *In* B. B. Rohdendorf (ed.), Yurskie nasekomye Karatau, pp. 190–236. Moscow: Nauka Press. [In Russian]

1969. Origin and Evolution of the Lower Hymenoptera. Trans. Paleontol. Inst. Acad. Sci. USSR, 147. [In Russian, translated in 1979 by Amerind Publishing Co., New Delhi]

1975. Hymenoptera Apocrita of the Mesozoic. Trans. Paleontol. Inst. Acad. Sci. USSR, 147: 1–134. [in Russian]

1977. New Hymenoptera from the Jurassic and Cretaceous of Asia. Paleontol. J. 1977: 349–357.

1980a. Origin and evolution of Hymenoptera. Trans. Paleontol. Inst. Acad. Sci. USSR 174: 1–192. [in Russian]

1980b. Contribution to the knowledge of the systematics of the family Aulacidae (Hymenoptera) in connection with a new find in the Neocom of Manlay. *In* Early Cretaceous Lake Manlay. Transactions of The Joint Soviet-Mongolian Palaeontological Expeditions 13: 65–67. [in Russian]

1983a. Fossil Hymenoptera of the superfamily Pamphilioidea. Paleontol. J. 1983: 56–70.

1983b. Ichneumonoidea (Hymenoptera) from the Lower Cretaceous of Mongolia. Contrib. Am. Entomol. Inst. 20: 259–265.

1985. *Eobraconus,* a substitute name of *Eobracon* Rasnitsyn (Hymenoptera, Braconidae). Psyche 92: 163.

1986a. Review of the fossil Tiphiidae, with description of a new species (Hymenoptera). Psyche 93: 91–101.

1986b. Order Vespida (=Hymenoptera). *In* A. P. Rasnitsyn et al. (eds.), Insects in the Early Cretaceous ecosystems of the West Mongolia. Transactions of The Joint Soviet-Mongolian Palaeontological Expeditions 28: 154–164. [in Russian]

1988a. An outline of evolution of the hymenopterous insects (Order Vespida). Oriental Insects 22: 115–145.

1988b. Sepulcidae and origin of Cephidae (Hymenoptera). *In* Taxonomy of the insects and mites. Trans. All-Union Entomol. Soc. 70: 68–73. [in Russian]

Rasnitsyn, A. P., and O. V. Kovalev

1988. The oldest Cynipoidea (Hymenoptera, Archaeocynipidae fam. n.) from the Early Cretaceous Transbaikalia. Vestn. Zool. 1988: 18–21. [in Russian]

Rasnitsyn, A. P., and M. Sharkey

1988. New Eoichneumonidae from Early Cretaceous of Siberia and Mongolia (Hymenoptera: Ichneumonoidea). Adv. Parasitic Hymenoptera Res. 1988: 169–197.

Ross, H. H.

1936. The ancestry and wing venation of the Hymenoptera. Ann. Entomol. Soc. Am. 29: 99–109.

Schlüter, T.

1978. Zur Systematik und Palökologie harzkonservierter Arthropoda einer Taphozönose aus dem Cenomanium von NW-Frankreich. Berliner Geowiss. Abh., ser. A, 9, 150S. [in German]

Sharov, A. G.

1957. First discovery of a Cretaceous stinging hymenopteron (Aculeata). Dokl. Akad. Nauk 112: 943–944. [in Russian]

Shaw, S. R.

1988. *Carminator,* a new genus of Megalyridae (Hymenoptera) from the Oriental and Australian regions, with a commentary on the definition on the family. Syst. Entomol. 13: 101–113.

Spradbery, J. P.

1973. Wasps. London: Sidgwick & Jackson.

Townes, H.

1973a. Two ichneumonids (Hymenoptera) from the Early Cretaceous. Proc. Entomol. Soc. Washington 75: 216–219.

1973b. Three tryphonine ichneumonids from Cretaceous amber (Hymenoptera). Proc. Entomol. Soc. Washington 75: 282–287.

1977. A revision of the Rhopalosomatidae (Hymenoptera). Contrib. Am. Entomol. Inst. 15: 1–34.

Whalley, P. E. S., and E. A. Jarzembowski

1985. Fossil insects for the Lithographic limestone of Montsech (late Jurassic-early Cretaceous), Lérida Province, Spain. Bull. Br. Mus. Nat. Hist. (Geol.) 38: 381–412.

Wilson, E. O.

1985. Ants from the Cretaceous and Eocene amber of North America. Psyche 92: 205–216.

1987. The earliest known ants: an analysis of the Cretaceous species and an inference concerning their social organization. Paleobiology 13: 44–53.

Wilson, E. O., F. M. Carpenter, and W. L. Brown, Jr.

1967. The first Mesozoic ants, with the description of a new subfamily. Psyche 74: 1–19.

Yoshimoto, C. M.
1975. Cretaceous chalcidoid fossils from Canadian amber. Can. Entomol. 107: 499–528.

Zeuner, F. E., and F. J. Manning
1976. A monograph on fossil bees (Hymenoptera: Apoidea). Bull. Br. Mus. Nat. Hist. (Geol.) 27: 149–268.

Zhang, J.
1985. New data on the Mesozoic fossil insects from Laiyang in Shandong. Geol. Shandong, 1985, 1: 23–29. [in Chinese with English summary]

CHAPTER 8. RAPHIDIOPTERA

JOHN D. OSWALD[1]

ABSTRACT

Three adult snakefly specimens are recorded from the Lower Cretaceous Santana Formation, from near Nova Olinda, Ceará, Brazil. Two species are described and figured: *Baissoptera brasiliensis* n. sp. (Baissopteridae) and an unnamed species. These are the first authenticated records of Raphidioptera, fossil or extant, from South America and the Southern Hemisphere. A catalog of described Raphidioptera fossils (34 named species in 15 genera and 10 families) is presented.

INTRODUCTION

Three specimens representing two species of fossil snakeflies from the Lower Cretaceous Santana Formation of the state of Ceará, Brazil, were recently found in a collection of fossil insects belonging to the American Museum of Natural History (AMNH). These species are described and figured below. One species is assigned to the genus *Baissoptera,* originally described by Martynova (1961) from the Upper Jurassic of the USSR; the other species is poorly preserved and is left unnamed. These specimens authenticate the past presence of Raphidioptera in South America, and may have important zoogeographic implications for the order. For general accounts of the Santana Formation, its fossil biota and stratigraphy, see papers by Grimaldi and Maisey in this volume.

ACKNOWLEDGMENTS

I thank David A. Grimaldi of the American Museum for the opportunity to examine the material treated here, and H. Aspöck, F. M. Carpenter, and J. K. Liebherr for reviewing the manuscript.

TAXONOMY

FAMILY BAISSOPTERIDAE

Baissoptera brasiliensis, n. sp.

Figures 1, 3, 4

MATERIAL: Two specimens; AMNH 43287 (holotype female, exposed dorsally) and AMNH 44400/44407 (paratype, male?, complementary halves).

DESCRIPTION: Head: eyes hemispherical; postocular region elongate, abruptly narrowed posteriorly; three ocelli present, arranged in a triangular pattern; antennae filiform, scape enlarged; mouthparts concealed. Thorax: pronotum elongate, enclosing prothorax laterally; legs robust, tarsi 5-segmented; forewing as in figure 3; hindwing as in figure 4; wing bases mostly obscured; costal crossveins simple; remigial crossveins numerous, arranged posteriorly in well-developed gradate series; trichosores absent; Sc joining C just proximal to pterostigma; pterostigma large and opaque (reddish-brown as preserved). Abdomen: shorter than wings; parts of an elongate ovipositor are preserved in specimen AMNH 43287.

MEASUREMENTS (mm): AMNH 43287. Body length (excluding ovipositor) = ca. 19.5; forewing = ca. 14.5; hind wing = ca. 12.5. Body length of AMNH 44400/44407 also ca. 19.5.

DISCUSSION: I tentatively refer these two specimens to the genus *Baissoptera* Martynova based on the following venational characters: in the forewing and hind wing—remigial crossveins numerous and posteriorly arranged in well-defined series, Sc and C anastomosing just proximal to pterostigma, pterostigma long and opaque; in the hind wing only—MA inserting on Rs near divergence of Rs from R. The first of these four characters is particularly diagnostic. The venation of *B. brasiliensis* agrees extremely well with Martynova's figures of the venation of *B. martinsoni* (Martynova, 1961: fig. 6, forewing) and *B. kolosnitsynae* (Martynova, 1961:

---

[1] Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853.

Figs. 1, 2. Raphidioptera spp. **1.** *Baissoptera brasiliensis,* holotype female, dorsal habitus (AMNH 43287). **2.** Raphidioptera sp., female, dorsal habitus (AMNH 44406). Scale lines = 10 mm.

fig. 7, hind wing). With the exception of the prominent ocelli observable on AMNH 43287, the visible body characters of the present material are also consistent with Martynova's (1961, fig. 8) diagrammatic representation of the head and partial thorax of a *Baissoptera* sp. Martynova's figure differs by the lack of ocelli.

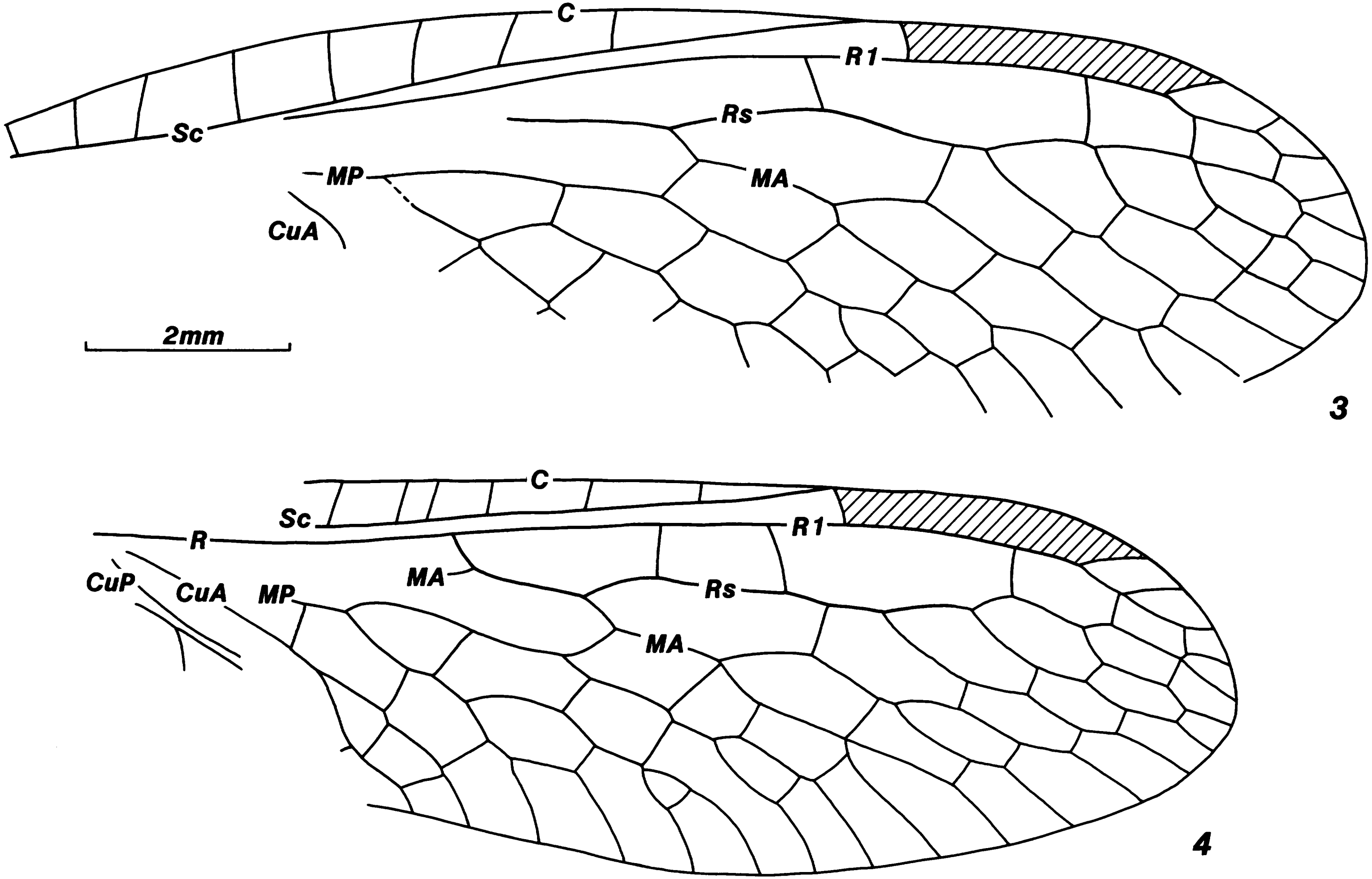
Raphidioptera sp.
Figure 2

MATERIAL: AMNH 44406 (female, exposed dorsally).

DESCRIPTION: Head: postocular region elongate, but proportionally shorter than in *Baissoptera brasiliensis*; ocelli apparently absent, but possibly lost with pieces of the fractured head capsule; antennae lost; labrum rectangular, mandibles large, other mouthparts concealed. Thorax: pronotum trapezoidal, elongate, enclosing prothorax laterally, covered sparsely with small tubercules (setal prominences?); legs represented only by fragments or impressions; wings all but lost, a single small venational fragment (right forewing?) is just visible, other wings each represented only by a short segment and collinear impression of a single prominent longitudinal vein (Sc?). Abdomen: position marked by a clear ventral impression, including the impression of the proximal portion of an elongate ovipositor; sclerites largely lost.

MEASUREMENTS: Body length (excluding ovipositor) = ca. 12.4 mm.

DISCUSSION: The form of the head and pronotum, together with the impression of an elongate ovipositor, clearly place this insect in the order Raphidioptera. The single visible fragment of venation is consistent with this determination, but is insufficient to allow more detailed taxonomic placement. The smaller size, shorter postocular head capsule



Figs. 3, 4. Reconstructed venation of *Baissoptera brasiliensis*. **3.** Forewing (AMNH 44400, converted to standard right dorsal view). **4.** Hind wing (AMNH 43287, converted to standard right dorsal view). Both to same scale. Pterostigmas hatched.

length, and apparent lack of ocelli differentiate this specimen from *Baissoptera brasiliensis* described above.

GENERAL DISCUSSION

The insect order Raphidioptera contains approximately 170 living species placed in two families, Raphidiidae [ca. 150 spp.] and Inocelliidae [ca. 20 spp.] (H. Aspöck, 1986). This small extant fauna is generally regarded as the relict of a once more diverse fauna (Carpenter, 1956), based on the relatively large number of described fossil Raphidioptera (presently 34 species placed in 15 genera and 10 families, see Appendix 1).

It has long been noted that living snakeflies are geographically restricted to the Northern Hemisphere. *Raphidia herbsti* Esben-Petersen (1912: 273), the only snakefly ever reported from the Southern Hemisphere [Chile], was treated by U. Aspöck and H. Aspöck (1969) as conspecific with *Agulla occidentis* Carpenter, a species of the western United States and southwestern Canada (U. Aspöck 1975). These authors regarded Esben-Petersen's record as erroneous or adventitious. Though the possibility of the existence of living snakeflies in South America cannot be entirely ruled out (H. Aspöck, personal commun.), extant New World Raphidioptera are presently known to occur south only to approximately 19°N in southern Mexico (H. Aspöck, 1986: figs. 4 and 5), where they appear to occur at high elevations.

Until now, all fossil snakeflies had also been recovered from Northern Hemisphere sites (North America—British Columbia, Colorado, Kansas and Labrador; Eurasia—Baltic Amber, China, England, and several localities in the USSR), supporting the hypothesis that Raphidioptera have always been restricted to northern latitudes. Immatures of living snakeflies appear to require a period of cold temperature to complete adult development (H. Aspöck, 1986). If one accepts a northern center of origin for the Raphidioptera, this requirement could explain (1) the absence of recent Raphidioptera from tropical regions, (2) the apparent restriction of Raphidioptera to high elevations at low northerly latitudes, and (3) the absence of extant snakeflies in the Southern Hemisphere, where suitable environmental conditions almost certainly exist.

The discovery of fossil snakeflies in Brazil (at ca. 7°S current latitude; ca. 9°S early Cretaceous latitude [Smith et al., 1981, map 30]) establishes the past presence of Raphidioptera in what is now South America. This occurrence extends the southern distributional limit of the order Raphidioptera into the Southern Hemisphere, approximately 25° farther south than any previously known fossil or extant snakefly. In addition, if the paleoclimatic conditions under which the Santana Formation formed were warm and arid (as suggested by Grimaldi and Maisey, this volume), the present find suggests that not all snakefly lineages have required cold temperatures to complete development. If so, other factors (e.g., low vagility, subsequent extinction) may be necessary to explain the apparent absence of snakeflies from Southern Hemisphere regions today.

The presence of fossil species of the family Baissopteridae in Asia and South America suggests that this family was broadly distributed throughout Laurasia and northern Gondwanaland during the Upper Jurassic and Lower Cretaceous. During this period South America and Africa were contiguous (Smith et al., 1981). *Baissoptera brasiliensis* likely represents a component of this ancestral fauna whose fossils have been displaced westward by the fragmentation of Gondwanaland.

Baissoptera brasiliensis does not appear closely related to extant North American Raphidioptera (H. Aspöck, personal commun.). This observation tends to refute the idea that North American snakeflies may have been derived from South American ancestors. But, it does not discriminate between two other hypotheses of the origin of the North American snakefly fauna: (1) that this fauna was derived solely from eastern Asian snakeflies which crossed the Bering land bridge sometime after the Miocene (Carpenter, 1936: 154), or (2) that this fauna was derived from the ancestors of a static remnant of an earlier Laurasian snakefly fauna (H. Aspöck, in press).

In conclusion, the discovery of Raphidioptera in South America is intriguing and raises a number of biogeographic questions. But, more detailed hypotheses of phylogenetic relationships among fossil and extant snakefly taxa will be required before a more complete hypothesis of raphidiopteran historical biogeography can be formulated.

CATALOG OF FOSSIL RAPHIDIOPTERA

The fossil Raphidioptera described approximately through 1987 are cataloged in Appendix 1. Bibliographic citations for all taxa are included in the References section. The family Permoraphidiidae, originally described in the order Raphidioptera, was placed in the Orthoptera by Sharov (1962, 1968) and Rohdendorf and Rasnitsyn (1980). Carpenter ([1968] 1967: 274–275) was more cautious, treating the Permoraphidiidae as only likely of orthopterous origin. Carpenter also regarded the ordinal affinities of the families Fatjanopteridae and Letopalopteridae as uncertain. These three poorly known Palaeozoic families have been provisionally retained in the present catalog for the sake of completeness.

The classification of extant Raphidioptera has been extensively revised over the last 25 years. During this period terminalic characters have replaced venational traits as the primary basis of the taxonomy of extant snakeflies. This is in sharp contrast to the taxonomy of snakefly fossils. Since the terminalia of fossil Raphidioptera are rarely sufficiently preserved to allow critical comparison, the taxonomy of snakefly fossils has remained based entirely on venational attributes. Furthermore, higher taxa (genera and groups of related genera) of recent snakeflies are known to have homogeneous venation and diverse terminalia. If this is a general feature of raphidiopteran evolution, the clustering of snakefly fossils solely on the basis of venational similarities would lead to generic concepts which are considerably broader than those currently in use for extant genera. Such concepts could mask considerable taxonomic diversity within fossil snakefly genera, particularly in those containing species from deposits widely disjunct geographically and/or temporally.

Today, fossil species based solely on venational traits cannot be accurately assigned to the extant genera more narrowly defined according to terminalia. Consequently, earlier assignments of Tertiary snakefly fossils to the recent genera *Raphidia, Fibla,* and *Inocellia* are now without critical support.

REFERENCES

Aspöck, H.

1986. The Raphidioptera of the world: a review of present knowledge. *In* J. Gepp, H. Aspöck, and H. Hölzel (eds.), Recent research in neuropterology. Proc. 2nd Int. Symp. Neuropterology, pp. 15–29. Austria: Graz.

In press. The Raphidioptera of Africa: a review of present knowledge (Insecta: Neuropteroidea). *In* M. W. Mansell and H. Aspöck (eds.), Advances in Neuropterology. Proc. 3rd Int. Symp. Neuropterology.

Aspöck, U.

1975. The present state of knowledge on the Raphidioptera of America (Insecta, Neuropteroidea). Polsk. Pismo Entomol. 45: 537–546.

Aspöck, U., and H. Aspöck

1969. Zur Frage des Vorkommens der Ordnung Raphidiodea auf der südlichen Hemisphäre. Beitr. Entomol. 19: 45–47.

Bode, A.

1953. Die Insektenfauna des ostniedersächsischen Oberen Lias. Palaeontographica, Beitr. Naturges. Vorz., ser. A, 103: 1–375.

Carpenter, F. M.

1936. Revision of the Nearctic Raphidiodea (recent and fossil). Proc. Am. Acad. Arts Sci. 71: 89–157.

1943. The Lower Permian insects of Kansas. Part 9. The orders Neuroptera, Raphidiodea, Caloneurodea and Protorthoptera (Probnisidae), with additional Protodonata and Megasecoptera. Proc. Am. Acad. Arts Sci. 75: 55–84.

1956. The baltic amber snake-flies (Neuroptera). Psyche 63: 77–81.

1967. Cretaceous insects from Labrador 2. A new family of Snake-flies (Neuroptera: Alloraphidiidae). Psyche 74: 270–275. [Psyche vol. 74, no. 4, was mailed 12 June 1968.]

Cockerell, T. D. A.

1907. Some fossil arthropods from Florissant, Colorado. Bull. Am. Mus. Nat. Hist. 23: 605–616.

1909. Fossil insects from Florissant, Colo-

rado. Bull. Am. Mus. Nat. Hist. 26: 67–76.
1912. A fossil *Raphidia* (Neur., Planip.). Entomol. News 23: 215–216.
1914. New and little-known insects from the Miocene of Florissant, Colorado. J. Geol. 22: 714–724.

Cockerell, T. D. A., and C. Custer
1925. A new fossil *Inocellia* (Neuroptera) from Florissant. Entomologist 58: 295–298.

Crowson, R. A., W. D. I. Rolfe, J. Smart, C. D. Waterston, E. C. Willey, and R. J. Wootton
1967. Arthropoda: Chelicerata, Pycnogonida, *Palaeoisopus,* Myriapoda and Insecta. *In* W. B. Harland et al. (eds.), The fossil record, pp. 499–534. London: Geological Society.

Esben-Petersen, P.
1912. A few new Neuroptera Planipennia. Entomol. Mitt. 1: 267–273.

Hagen, H. A.
1854. Ueber die Neuropteren der Bernsteinfauna. Verh. Zool.-Bot. Ver. Wien 4: 221–232.
1856. Die im Bernstein befindlichen Neuropteren der Vorwelt bearbeitet von F. J. Pictet-Baraban . . . und Dr. H. Hagen. *In* G. C. Berendt (ed.), Die im Bernstein befindlichen Organischen Reste der Vorwelt gesammelt in verbindung mit mehreren bearbeitet und herausgegeben von Dr. Georg Carl Berendt. Band 2: 41–125. Berlin.

Handlirsch, A.
1906–1908. Die fossilen Insekten und die Phylogenie der rezenten Formen. Leipzig: W. Engelmann.
1910. Canadian Fossil Insects. 5. Insects from the Tertiary lake deposits of the southern interior of British Columbia, collected by Mr. Lawrence M. Lambe, in 1906. Contrib. Can. Palaeontol. 2: 93–129.

Hong, Y.-C.
1982. Raphidioptera. *In* Mesozoic fossil insects of Jiuquan Basin in Gansu Province, pp. 152–155. Peking: Geological Publishing House. [in Chinese]

Lambkin, K. J.
1986. A revision of the Australian Mantispidae (Insecta: Neuroptera) with a contribution to the classification of the family. II. Calomantispinae and Mantispinae. Aust. J. Zool., suppl. ser. 117: 1–113.

Latreille, P. A.
1810. Considérations générales sur l'ordre naturel des animaux composant les classes des Crustacés, des Arachnides, et des Insectes; avec un tableau méthodique de leurs genres, disposés en familles. Paris: Schoell.

Larsson, S. G.
1978. Baltic Amber—a Palaeobiological Study. Entomonograph 1: 1–192.

Linnaeus, C.
1758. Systema natura per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1. Holmiae: Salvii. 10th ed., 824 pp.

Martynov, A. V.
1925a. To the knowledge of fossil insects from Jurassic beds in Turkestan. 1. Raphidioptera. Bull. Acad. Sci. Russie [= Izvestiya Akademii Nauk SSSR], ser. 6, 19: 233–246.
1925b. To the knowledge of fossil insects from Jurassic beds in Turkestan. 2. Raphidioptera (continued), Orthoptera (s.l.), Odonata, Neuroptera. Bull. Acad. Sci. Russie [= Izvestiya Akademii Nauk SSSR], ser. 6, 19: 569–598.

Martynova, O. M.
1947. Two new Raphidioptera from Jurassic shales of Karatau. Dokl. Akad. SSSR, n. ser., 56(6): 635–637. [in Russian]
1952. Permian Neuroptera of the SSSR. Akad. SSSR, Trudy Paleontol. Inst. 40: 197–237. [in Russian]
1961. Recent and fossil snakeflies (Insecta, Raphidioptera). Paleontol. Zh. 1961(3): 73–83. [in Russian]

Navás, L.
1913. Neurópteros del R. Museo Zoológico de Nápoles. Ann. Mus. Zool. R. Univ. Napoli, n. ser., 4(3): 1–11.
1915. Neurópteros nuevos o poco conocidos. (Quinta [V] serie). Mem. R. Acad. Cien. Artes Barcelona, ser. 3, 11: 455–480 [Separate: ser. 3, 11(27): 1–28].

Rohdendorf, B. B., and A. P. Rasnitsyn
1980. Istoricheskoe razvitie klassa nasekomykh [= Historical development of the insects]. Akad. SSSR, Trudy Paleontol. Inst. 175: 1–[269]. [in Russian]

Rohwer, S. A.
1909. Three new fossil insects from Florissant, Colorado. Am. J. Sci. 28: 533–536.

Schneider, W. G.
1843. Monographia generis Rhaphidiae Linnaei. Vratislaviae: Grassii, Barthii et Socii. 96 pp.

Scudder, S. H.
1890. Suborder Planipennia Burmeister. *In* Tertiary insects of North America. Rep. U.S. Geol. Geogr. Surv. Territories 13: 146–172.

Schummel, T. E.
1832. Versuch einer genauen Beschreibung der in Schlesien einheimischen Arten der Gattung *Raphidia,* Linn. Beiträge zur Entomologie besonders in bezug auf Schlesien, herausgegeben von T. E. Schummel. Breslau. No. 1. 16 pp.
Sharov, A. G.
1962. Otryad Orthoptera. Pryamokrylye (Saltatoria) [= Order Orthoptera]. *In* Yu. A. Orlov (ed.), Osnovy Paleontologii [= Fundamentals of Paleontology]. 9: 146–157 [in Russian]. Moscow: Izdatel'stvo Akademiia Nauk SSSR.
1968. Filogeniya orthopteroidnykh nasekomykh. Akad. SSSR, Trudy Paleontol. Inst. 118: 1–[217] [in Russian]. [English translation: 1971, Phylogeny of the Orthopteroidea, Israel Program for Scientific Translations Ltd., 251 pp.]
Smith, A. G., A. M. Hurley, and J. C. Briden
1981. Phanerozoic paleocontinental world maps. Cambridge: Cambridge Univ. Press.
Tillyard, R. J.
1932. Kansas Permian insects. Part 14. The order Neuroptera. Am. J. Sci., ser. 5, 23: 1–30.
Whalley, P. E. S.
1985. The systematics and palaeogeography of the Lower Jurassic insects of Dorset, England. Bull. Br. Mus. Nat. Hist., geol. ser., 39: 107–189.
Weidner, H.
1958. Einige interessante Insektenlarven aus der Bernsteininklusen-Sammlung des Geologischen Staatsinstituts Hamburg (Odonata, Coleoptera, Megaloptera, Planipennia). Mitt. Geol. Staatsinst. Hamburg 27: 50–68.

APPENDIX 1

FOSSIL RAPHIDIOPTERA

ANNOTATIONS

Abbreviations: A, adult; Dis, discussed, discussion; FW, forewing; HW, hind wing; L, larva; Lst, list, listed; OD, original description; RD, redescription; Syn, synonymy; Tax, taxonomy; W, wing(s). An asterisk (*) following an annotation indicates a figure, e.g., FW* = forewing figure.

FAMILY RAPHIDIIDAE LATREILLE, 1810 (Extant, Tertiary)

GENUS *RAPHIDIA* LINNAEUS (Extant, Tertiary)

Raphidia Linnaeus, 1758: 552. Type species: *Raphidia ophiopsis* Linnaeus, 1758, by monotypy.
Dictyoraphidia Handlirsch, 1910: 103. Type species: *Inocellia veterana* Scudder, by monotypy.
Archiraphidia Handlirsch, 1910: 103. Type species: *Inocellia tumulata* Scudder, by monotypy (*Raphidia tranquilla* Scudder and *Inocellia eventa* Scudder were only doubtfully included).

baltica Carpenter [Baltic Amber]

Raphidia baltica Carpenter, 1956: 78 (OD, FW*, HW*).

creedei Carpenter
[near Creede, Colorado, U.S.A.]

Raphidia creedei Carpenter, 1936: 150 (OD, FW*, HW*).

elegans (Cockerell)
[near Florissant, Colorado, U.S.A.]

Megaraphidia elegans Cockerell, 1907: 607 (OD, FW*). Handlirsch 1910: 104 (Lst).
Raphidia elegans (Cockerell). Carpenter 1936: 145–146 (Tax).

exhumata Cockerell
[near Florissant, Colorado, U.S.A.]

Raphidia exhumata Cockerell, 1909: 73 (OD). Carpenter 1936: 147 (RD, FW*, HW*).
Raphidia exhumata var. *a* Cockerell, 1912: 215 (OD, FW*).
Raphidia pulveris Cockerell, 1914: 714 (OD). Carpenter 1936: 147 (Syn).

mortua Rohwer
[near Florissant, Colorado, U.S.A.]

Raphidia mortua Rohwer, 1909: 533 (OD). Carpenter 1936: 148 (RD, FW*, HW*).

tranquilla Scudder
[near Florissant, Colorado, U.S.A.]

Raphidia tranquilla Scudder, 1890: 154 (OD, A*, FW*). Handlirsch 1907: 907 (Lst). Carpenter 1936: 150 (RD).
Inocellia somnolenta Scudder, 1890: 157 (OD, A*, W*). Handlirsch 1907: 908 (Lst). Handlirsch 1910: 104 (Lst). Carpenter 1936: 150 (Syn).
Archiraphidia tranquilla (Scudder). Handlirsch 1910: 104 (Lst, Tax). Carpenter 1936: 150 (Tax).

tumulata (Scudder)
[near Florissant, Colorado, U.S.A.]

Inocellia tumulata Scudder, 1890: 158 (OD, A*, W*). Handlirsch 1907: 907 (Lst).
Inocellia eventa Scudder, 1890: 160 (OD). Handlirsch 1907: 907 (Lst). Carpenter 1936: 149 (Syn).
Archiraphidia tumulata (Scudder). Handlirsch 1910: 104 (Lst, Tax).
Archiraphidia eventa (Scudder). Handlirsch 1910: 104 (Lst, Tax).
Raphidia tumulata (Scudder). Carpenter 1936: 149 (RD, FW*, Tax).

veterana (Scudder)
[near Florissant, Colorado, U.S.A.]

Inocellia veterana Scudder, 1890: 156 (OD, A*, W*). Handlirsch 1907: 907 (Lst).
Dictyoraphidia veterana (Scudder). Handlirsch 1910: 104 (Lst, Tax).
Raphidia veterana (Scudder). Carpenter 1936: 143–145 (Tax).

sp., larva [Baltic Amber]

Raphidia sp. Hagen 1856: 83 (OD, L*). Handlirsch 1907: 907 (Lst). Handlirsch 1910: 104 (Lst).

FAMILY INOCELLIIDAE NAVÁS, 1913
(Extant, Tertiary)

GENUS *FIBLA* NAVÁS
(Extant, Tertiary)

Fibla Navás, 1915: 477. Type species: *Fibla hesperica* Navás, 1915: 477, by original designation.

erigena (Hagen) [Baltic Amber]

Raphidia erigena Hagen, 1854: 228. Nomen Nudum.
Raphidia (*Inocellia*) *erigena* Hagen 1856: 83 (OD, A*, FW*, HW*). Handlirsch 1907: 907 (Lst).
Inocellia eogena [sic] (Hagen). Scudder 1890: 156.
Inocellia erigena (Hagen). Handlirsch 1910: 104 (Lst).
Fibla erigena (Hagen). Carpenter 1956: 79 (RD, FW*, HW*).
Rhaphidia [sic] (*Inocellia*) *erigena* Hagen. Larsson 1978: 162 (Dis).

exusta (Cockerell and Custer)
[near Florissant, Colorado, U.S.A.]

Inocellia exusta Cockerell and Custer, 1925: 296 (OD, HW*).
Fibla exusta (Cockerell and Custer). Carpenter 1936: 152 (RD, HW*, Tax).

GENUS *INOCELLIA* SCHNEIDER
(Extant, Tertiary)

Inocellia Schneider, 1843: 84. Type species: *Raphidia crassicornis* Schummel, 1832: 15, by monotypy.

peculiaris Carpenter [Baltic Amber]

Inocellia peculiaris Carpenter, 1956: 80 (OD, A*, FW*, HW*).

sp., larva [Baltic Amber]

Inocellia sp. Weidner 1958: 62 (OD, L*).

FAMILY ALLORAPHIDIIDAE CARPENTER [1968] 1967 (Cretaceous)

GENUS *ALLORAPHIDIA* CARPENTER
(Cretaceous)

Alloraphidia Carpenter, [1968] 1967: 270. Type species: *Alloraphidia dorfi* Carpenter, by original designation.

dorfi Carpenter
[near Schefferville, Labrador, Canada]

Alloraphidia dorfi Carpenter [1968] 1967: 271 (OD, FW*, HW*).

FAMILY BAISSOPTERIDAE MARTYNOVA, 1961 (Cretaceous, Jurassic)

GENUS *BAISSOPTERA* MARTYNOVA
(Lower Cretaceous, Upper Jurassic)

Baissoptera Martynova, 1961: 80. Type species: *Baissoptera martinsoni* Martynova, by original designation.

brasiliensis
[near Nova Olinda, Ceará, Brazil]

Baissoptera brasiliensis Oswald (this paper).

kolosnitsynae Martynova
[Buryatskaya A.S.S.R., USSR]

Baissoptera kolosnitsynae Martynova, 1961: 81 (OD, HW*).

martinsoni Martynova
[Buryatskaya A.S.S.R., USSR]

Baissoptera martinsoni Martynova, 1961: 80 (OD, FW*).

sp. [Buryatskaya A.S.S.R., USSR]

Baissoptera sp. Martynova, 1961: 82 (A*).

GENUS *PRISCAENIGMA* WHALLEY (Lower Jurassic)

Priscaenigma Whalley, 1985: 148. Type species: *Priscaenigma obtusa* Whalley, by original designation.

obtusa Whalley [Dorset, England]

Priscaenigma obtusa Whalley, 1985: 148 (OD, FW*).

FAMILY MESORAPHIDIIDAE MARTYNOV, 1925 (Jurassic)

GENUS *MESORAPHIDIA* MARTYNOV (Jurassic)

Mesoraphidia Martynov, 1925a: 235. Type species: *Mesoraphidia grandis* Martynov, by original designation.

Hondelagia Bode, 1953: 269. Type species: *Hondelagia reticulata* Bode, by original designation.

elongata Martynov
[near Galkino, Turkestan, USSR]

Mesoraphidia elongata Martynov, 1925a: 240 (OD, A*, FW*, HW*).

grandis Martynov
[near Galkino, Turkestan, USSR]

Mesoraphidia grandis Martynov, 1925a: 236 (OD, A*, FW*, HW*)

inaequalis Martynov
[near Galkino, Turkestan, USSR]

Mesoraphidia inaequalis Martynov, 1925b: 569 (OD, A*, FW*, HW*).

parvula Martynov
[near Galkino, Turkestan, USSR]

Mesoraphidia parvula Martynov, 1925a: 241 (OD, A*, FW*, HW*).

pterostigmalis Martynova
[Karatau Mts., Turkestan, USSR]

Mesoraphidia pterostigmalis Martynova, 1947: 635 (OD, A*, FW*, HW*).

reticulata (Bode) [Hondelage near Braunschweig, West Germany]

Hondelagia reticulata Bode, 1953: 269 (OD, FW*): Martynova in Rohdendorf and Rasnitsyn 1980: 87 (Syn). Lambkin 1986: 59 (FW*, Tax).

similis Martynov
[near Galkino, Turkestan, USSR]

Mesoraphidia similis Martynov, 1925a: 238 (OD, FW*, HW*).

GENUS *METARAPHIDIA* WHALLEY (Lower Jurassic)

Metaraphidia Whalley, 1985: 147. Type species: *Metaraphidia confusa* Whalley, by original designation.

confusa Whalley [Dorset, England]

Metaraphidia confusa Whalley, 1985: 148 (OD, FW*, HW*).

GENUS *PRORAPHIDIA* MARTYNOVA (Upper Jurassic)

Proraphidia Martynova, 1947: 636. Type species: *Proraphidia turkestanica* Martynova, by monotypy.

turkestanica Martynova
[Karatau Mts., Turkestan, USSR]

Proraphidia turkestanica Martynova, 1947: 636 (OD, HW*).

vitimica Martynova
[Buryatskaya A.S.S.R., USSR]

Proraphidia vitimica Martynova, 1961: 82 (OD, FW*).

FAMILY SINORAPHIDIIDAE HONG, 1982 (Jurassic)

GENUS *SINORAPHIDIA* HONG (Upper Jurassic)

Sinoraphidia Hong, 1982: 154. Type species: *Sinoraphidia viridis* Hong, by original designation.

viridis Hong [Gansu Province, China]

Sinoraphidia viridis Hong, 1982: 154 (OD, FW*).

FAMILY PERMORAPHIDIIDAE TILLYARD, 1932 (Permian)

GENUS *PERMORAPHIDIA* TILLYARD (Lower Permian)

Permoraphidia Tillyard, 1932: 6. Type species: *Permoraphidia americana* Tillyard, by original designation. Carpenter 1943: 67–68 (Dis). Carpenter [1968] 1967: 274 (Tax).

americana Tillyard
[near Elmo, Kansas, U.S.A.]

Permoraphidia americana Tillyard, 1932: 8 (OD, FW*). Carpenter 1943: 65 (RD, FW*, HW*).

grandis Carpenter
[near Elmo, Kansas, U.S.A.]

Permoraphidia grandis Carpenter, 1943: 66 (OD, FW*).

FAMILY LETOPALOPTERIDAE MARTYNOVA, 1961 (Permian)

GENUS *LETOPALOPTERA* MARTYNOVA (Upper Permian)

Letopaloptera Martynova, 1961: 77. Type species: *Letopaloptera albardiana* Martynova, by original designation. Carpenter [1968] 1967: 274–275 (Dis).

albardiana Martynova
[Arhangelskaja Oblast, USSR]

Letopaloptera albardiana Martynova, 1961: 77 (OD, A*, FW*, HW*).

carpenteriana Martynova
[Arhangelskaja Oblast, USSR]

Letopaloptera carpenteriana Martynova, 1961: 79 (OD, FW*).

FAMILY SOJANORAPHIDIIDAE MARTYNOVA, 1952 (Permian)

GENUS *SOJANORAPHIDIA* MARTYNOVA (Upper Permian)

Sojanoraphidia Martynova, 1952: 226. Type species: *Sojanoraphidia rossica* Martynova, by monotypy. Carpenter [1968] 1967: 274 (Dis).

rossica Martynova [USSR]

Sojanoraphidia rossica Martynova, 1952: 226 (OD, A*, FW*).

FAMILY FATJANOPTERIDAE MARTYNOVA, 1961 (Permian/Carboniferous)

GENUS *FATJANOPTERA* MARTYNOVA (Lower Permian/Upper Carboniferous)

Fatjanoptera Martynova, 1961: 76. Type species: *Fatjanoptera mnemonica* Martynova, by original designation. Carpenter [1968] 1967: 274–275 (Dis).

mnemonica Martynova
[Tunguska Basin,
Krasnoyarsk Region, USSR]

Fatjanoptera mnemonica Martynova, 1961: 76 (OD, FW*).

FAMILY INCERTA SEDIS

GENUS *ARCHIINOCELLIA* HANDLIRSCH (Tertiary)

Archiinocellia Handlirsch, 1910: 100. Type species: *Archiinocellia oligoneura* Handlirsch, by monotypy.

oligoneura Handlirsch
[British Columbia, Canada]

Archiinocellia oligoneura Handlirsch, 1910: 100 (OD, FW*, HW*). Carpenter 1936: 143–144 (Dis, Tax).

FAMILY AND GENUS INCERTA SEDIS

Raphidioptera sp. [near Nova Olinda, Ceará, Brazil] Oswald (this study).

CHAPTER 9. DIPTERA

DAVID GRIMALDI[1]

ABSTRACT

Twelve specimens of flies from the Santana Formation, Lower Cretaceous, of Brazil are known and belong to the following taxa: Tipulomorpha?, Tipulomorpha (Tipulidae; Limoniinae?), Culicomorpha (Chironomoidea), Bibionomorpha (Bibionidae, Mycetophilidae, and Sciaroidea), and Asiloidea (Asilidae, two species; and Therevidae?). This deposit contains the oldest known robber flies, for which the new genus and species *Araripogon axelrodi* is described. Figures and an account of the available diagnostic features of each taxon are provided. The records of known Cretaceous Diptera fossils are compiled and briefly discussed. It is hypothesized that the Brachycera originated in the Middle Jurassic.

INTRODUCTION

Many of the Cretaceous Diptera fossils, particularly midges and other small, primitive taxa, are known only from amber. The compression fossil Diptera from this period are virtually all Laurasian, and are mostly from the Soviet Union. Fine detail in the Diptera from the Santana Formation shows spines, setae, antennae, wing venation, and even eye facets. Because of some very comprehensive comparative studies, as in Hennig (1954) and especially in the Manual of Nearctic Diptera by McAlpine et al. (1981), venation and other taxonomically critical, fossilized features can now be better assessed in fossil Diptera.

ACKNOWLEDGMENTS

The following individuals contributed information to this paper and/or provided critiques on the manuscript, and for their valuable help I am grateful: Peter Cranston (CSIRO, Canberra), Frank Carpenter (MCZ, Harvard), Frank McAlpine (CNC, Ottowa), and especially Norman Woodley (USDA-ARS, Smithsonian) and Wiesław Krzeminski (Institute of Systematic and Experimental Zoology, Kraków, Poland).

TAXONOMY

TIPULIDAE

Figures 1, 2, 7

MATERIAL: Male, AMNH 43500.

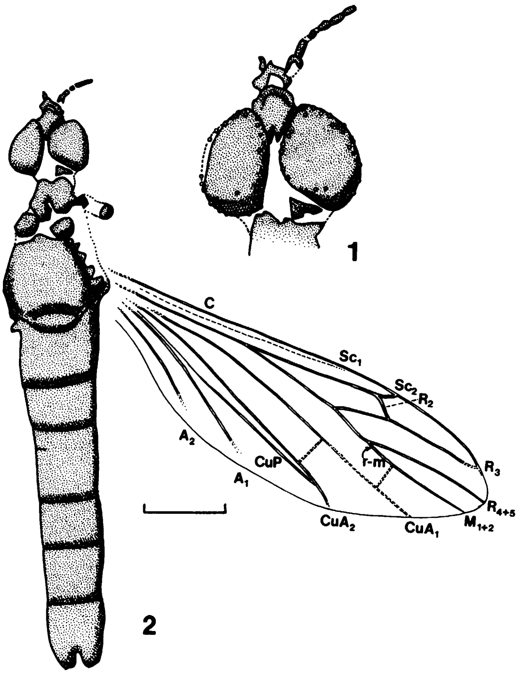
DESCRIPTION: Entire body with dorsal surface exposed. Eyes with facets preserved along some portions of the periphery. Eyes very close together, separated $<1/5$ eye width. Antennae not present. Clypeus protruding; right palp intact, with short basal segment; a long second segment plus 3 short terminal segments apparent. Preservation of mesonotum not sufficiently detailed to observe whether V-shaped mesonotal suture is present. Postpronotal lobes large. Legs, halteres not present. Right and left wings present, with much venation intact. Sc vein present; costal field darkly pigmented up to level of bifurcation of R_1 and R_2. R_1 extended to level of ca. R_4–R_5, nearly straight and parallel to M_1. Crossvein r-m at basal 1/3 of R_5. CuP extended past crossvein cu-a and intersected with CuA. A_1 and A_2 reaching margin; anal lobe small. No discal cell. Abdomen straight, with only 6 primary segments apparent. Terminal portion of abdomen with 2 lobes, its left lobe showing 2 segments, 1 being folded upon the basal segment, thus indicating a male.

MEASUREMENTS: (All measurements in mm.) Body length (excl. palps) = 6.6; wing length = 5.2 (r), 4.9 (l).

DISCUSSION: The terminal branching of R_1 with R_2 is perhaps the most diagnostic character of the specimen. The radial-medial branching is peculiar, even for some limoniines (segregated into a family from Tipulidae by many European workers) that also lack a discal cell, for crossvein r-m is in line with R_5 and perpendicular to m-cu. Also, the number of medial veins appears to be reduced to one, which occurs very rarely in the Tipulidae (e.g., *Phalacrocera*). Dr. Wiesław Krzeminski has examined these tipuloids, in-

---

[1] Assistant Curator, Department of Entomology, American Museum of Natural History.



Figs. 1, 2. AMNH 43500 (Tipulidae). **1.** Detail of head, showing facets. **2.** Habitus, with right wing a reconstruction of the venation seen in both wings. Scale lines in all figures are 1.0 mm; dashed and dotted lines represent extrapolations of absent portions of wing veins and structures based on depressions.

cluding AMNH 43500. He believes this particular specimen is a limoniine. Limoniines are well represented in Cretaceous ambers (e.g., Krzeminski and Teskey, 1987).

As one might expect based on their primitive attributes, the tipulids have the oldest fossil record of the true Diptera (Eudiptera). Rohdendorf (1974) mentioned the tipulomorphs as arising in the Late Triassic, as represented by the Architipulidae Handlirsch, 1906. Unfortunately, only venation survives in the most primitive Diptera fossils. No groups would benefit more in terms of phylogenetic understanding than for the Triassic-Jurassic "Archidiptera" and lower Eudiptera fossils to be studied firsthand and be compared cladistically with the Mecoptera and extant tipulomorphs (Tanyderidae and Tipulidae s.l.). Hennig's (1954) work represents the most comprehensive treatment toward this end, but he treated mostly the extant Tipulomorpha and did not examine the actual specimens described by Rohdendorf.

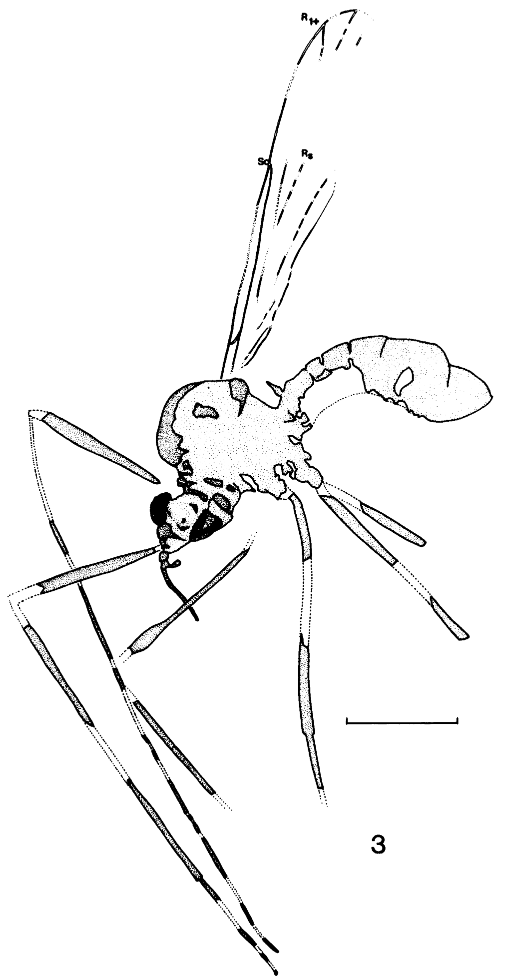


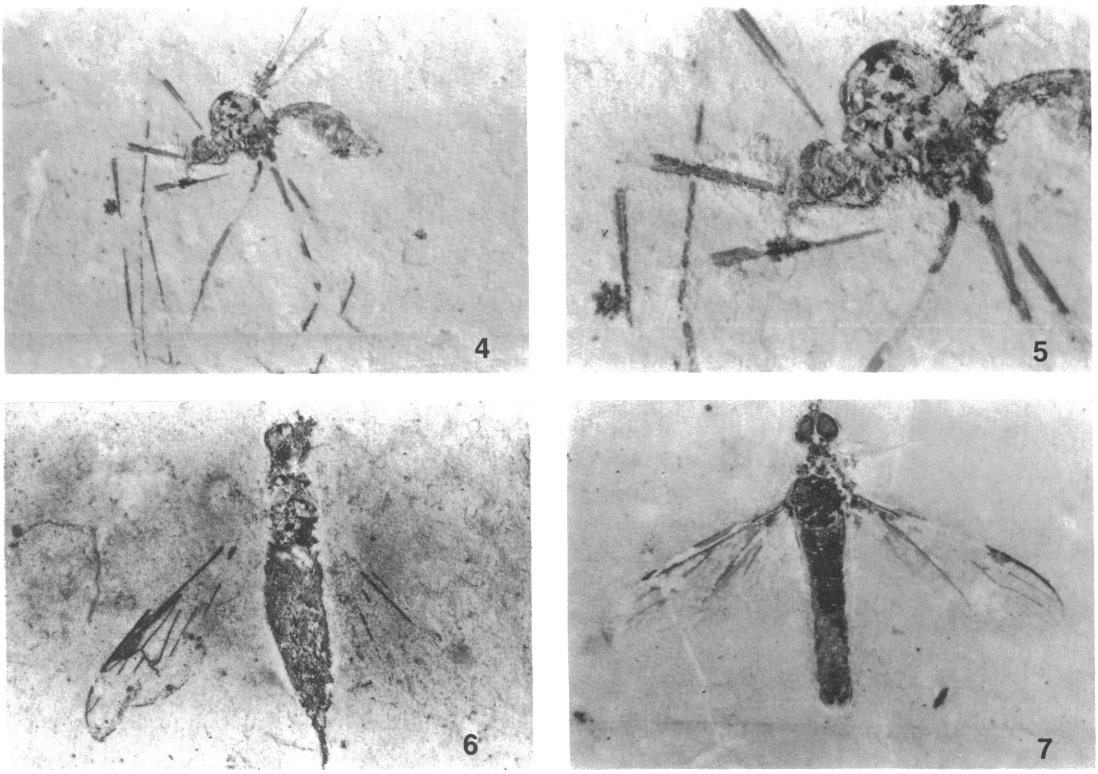
Fig. 3. AMNH 43501 (Tipulomorpha?). Habitus.

TIPULOMORPHA?

Figures 3–5

MATERIAL: AMNH 43501.

DESCRIPTION: Body in lateral repose, head in dorsal or ventral view. Some facets of eyes intact. Antennae not present. Portion of one palp and entire other palp visible; palp length ca. equal to length of head. Mesonotum considerably arched, almost hemispherical. Pronotum narrow. Femora and tibiae very long, most tarsi lost. Very little wing venation preserved, as follows: S_c, unbranched, meets



Figs. 4–7. Habitus photographs of fossil Tipulomorpha. **4, 5.** AMNH 43501, habitus and detail. **6.** AMNH 43513. **7.** AMNH 43500.

C slightly distal to midpoint of C; R_1 meets C with no terminal fork; only base of R_s present, R_s jointed to R_1 with an apparently gradual, acute angle. Genitalia and terminal portion of abdomen not present, but anterior portion is ca. ⅓ width of posterior portion of abdomen.

MEASUREMENTS: Body length = ca. 4.15; wing length = 3.9; midfemur = 2.4; hind femur = 3.0; foretibia = 3.6.

DISCUSSION: This specimen may be a small tipulid judging from the very long femora and tibiae, the long palp, the very round mesonotum and small pronotum, and by the shape of the abdomen. Trichoceridae is a family that the fossil habitus superficially resembles. However, the wing veins in Trichoceridae are heavily setulose; in the fossil some fine leg setulae are preserved, so if setulae were present on the veins there would probably be at least traces of them present in this fossil.

Records on the geological distributions of tipuloids are given in the Discussion under AMNH 43500 (Tipulidae). Specimen AMNH 43271 (fig. 6) may be the same species, judging from the very long, thin legs. Unfortunately this specimen has just portions of three legs intact, and a portion of the head, thorax, and base of one wing. Most of the wings and abdomen are lost.

CHIRONOMOIDEA

Figures 8, 18

MATERIAL: Male, AMNH 43503.

DESCRIPTION: Portions of head remain, especially the heavily sclerotized and rounded pedicel and some remains of densely plumose antennae. Anterior portion of notum strongly rounded; thorax in lateral view deep. Fragment of wing adpressed to body, no venation discernible. Scutellum and postscutellum not discernible. Forelegs long. Number of tarsal segments on each leg not apparent. Measurements in mm:

	Foreleg	Midleg	Hindleg
Femur	1.62	2.13	2.73
Tibia	1.44	1.91	2.26
Tarsus	1.34	2.40	2.05

Eight abdominal segments apparent, gonostylus remains as a depression.

OTHER MEASUREMENTS: Body length (excl. antennae) = 6.2; flagellum length = 1.7.

DISCUSSION: The straight abdomen, but especially the strongly arched anterior portion of the notum, the long, densely plumose antennae, and long forelegs are very suggestive of male Chironomidae. Chironomids have been reported from the Lower Cretaceous of China (Ping, 1928), but these records are difficult to evaluate in lieu of a modern study of the material, and because of a lack of sufficient taxonomic details in the original report such as structure of legs and wings. Two genera of Chironomidae were described from the Lower Cretaceous of Mongolia (Kalugina, 1986), but their familial and suprafamilial placements, too, are difficult to evaluate based on the published account and, no doubt, on the condition of the specimens as well.

Brundin's (1965) classic study hypothesized repeated vicariance events among some Podonominae from Austral South America, New Zealand, and Australia. Based on tectonic dates, Late Jurassic ages for these chironomids was proposed. It is not surprising, then, that a podonomine, for which the genus *Libanoclites* was described, occurs in the Early Cretaceous amber of Lebanon (Brundin, 1976) nor that AMNH 43503 may be a chironomid. The south temperate affinities of aphroteniine chironomids in the Siberian amber (Kalugina, 1978) are similar to the biogeographic affinities of *Libanoclites*. Kalugina mentioned 623 Orthocladiinae and 50 Aphroteniinae specimens as being in the Siberian amber, the vast majority of which are still unstudied. Eleven chironomid specimens are known from the Middle Cretaceous amber of Canada (McAlpine and Martin, 1969), three species are described based on six other Canadian specimens (Boesel, 1937), and an undescribed species, an orthocladiine, is represented by two specimens in Middle Cretaceous amber from New Jersey.

In Rohdendorf's (1974) review, the family Architendipedidae was proposed for wings from the Upper Triassic. Based on the figures, however, there is a very long R_{2+3}, R_1 is widely separated from R_{4+5}, and $CuA_1 + CuA_2$ are not forked, suggesting that the Architendipedidae is pleisiomorphic to the Chironomoidea. There is little reason to believe that the Chironomoidea has persisted since the Upper Triassic.

Chironomids inhabit a variety of media as larvae, but these are invariably aquatic or at least moist. They can be extremely abundant in the sediments of eutrophic lakes/ponds, about which the adults are found swarming.

BIBIONIDAE?

Figures 9, 10, 20

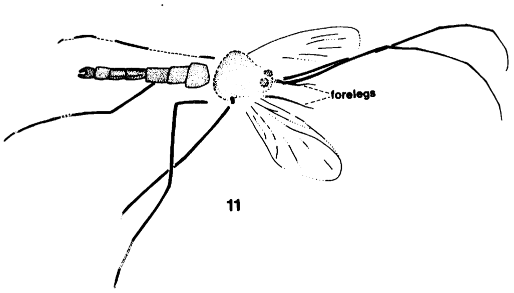
MATERIAL: AMNH 43504, sex unknown.

DESCRIPTION: Ventral portion of body exposed. Eyes large, separated by distance less than their width. One palp exposed, number of segments unapparent. Pedicel equal in size to first flagellomere. Twelve flagellomeres on each antenna; slightly tapered apically. Flagellomere width greater than length, except apical one which is twice as long as wide. Femora and tibiae present. Following portions of each wing remain (see reconstruction): short R_{2+3} present, length ca. ½ that of distance between R_{2+3} and end of R_{4+5}; S_c long, parallel to C for most of its length, ending near R_1; basal cell elongate, stem of $R_{2+3} + R_{4+5}$ attached to tapered apex of the cell; no stigma present at apex of R_1. Most of abdomen lost.

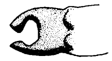
MEASUREMENTS: Lengths: head = 0.5; flagellum = 0.5; femora: fore = 0.8, mid = 0.6, hind = 1.0; wing = 3.5.

DISCUSSION: Twleve compact flagellomeres, large eyes, the short R_{2+3} vein, the very long S_c vein, and the long basal radial cell are indicative of the hesperiine and pleciine Bibionidae (the Bibioninae lack R_{2+3}). Shared between most of the Bibionidae and the Pachyneuridae is a stigma at the apex of R_1, which the fossil does not have. The specimen is surely not a pachyneurid for lack of two small cells apical to the basal cells (the discalmedial and radial cells). Presence of the radial cell is quite variable in Pachyneuridae and may even vary between both wings on the same individual. Pachyneurids also have a more elongate slender body than is present in

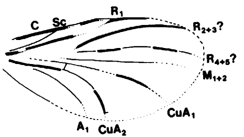
Figs. 8–10. Chironomoidea and Bibionidae. **8.** AMNH 43503 (Chironomoidea, male). Lateral habitus. 9, 10. AMNH 43504 (Bibionidae?). **9.** Habitus, ventral. **10.** Venation reconstructed from both wings.



11



12



13

Figs. 11–13. AMNH 43502 (Mycetophilidae: Macrocerinae?). **11.** Habitus. **12.** Detail of genitalia (male). **13.** Venation reconstructed from both wings.

this fossil. Bibionids have a rich and long fossil record compared to most Diptera fossils. Primitive forms undoubtedly assignable to the Bibionomorpha are known from the Jurassic (Rohdendorf, 1974), but the description of 11 extinct families in the Bibionomorpha (mostly by Rohdendorf) is excessive in light of the few available characters. A *Plecia* is known from Middle Cretaceous amber of Canada (table 1), so AMNH 43504 may be the earliest record for the family. Several bibionids have been reported from the Middle Cretaceous of Botswana, but several apparently well-preserved features, especially the venation, were not systematically studied (Rayner, 1987).

Bibionid larvae breed in decaying vegetation, and the adults are usually found in wet, heavily vegetated, but open, areas.

MYCETOPHILIDAE (MACROCERINAE?)

Figures 11–13, 19

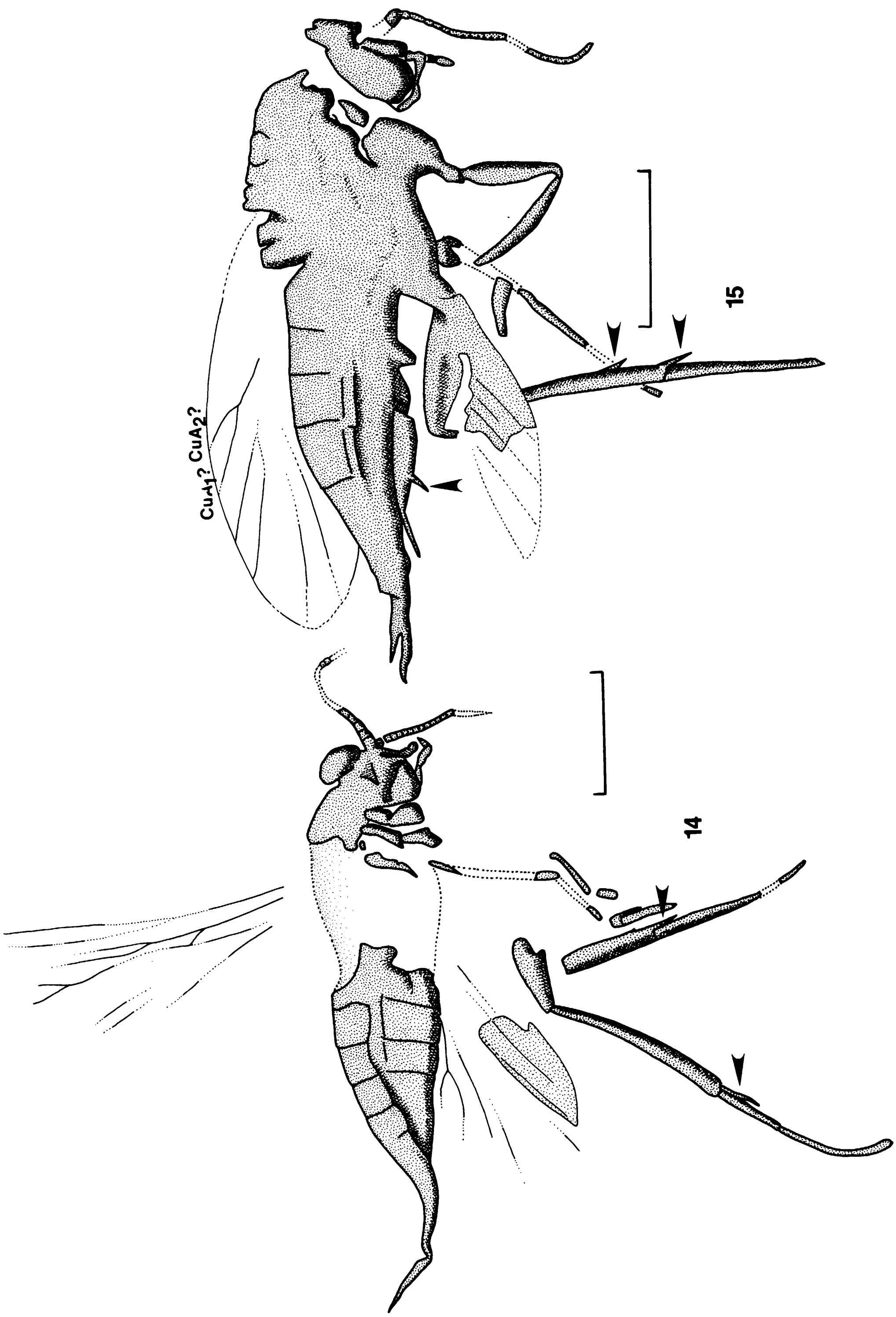
MATERIAL: Male, AMNH 43502.

DESCRIPTION: Head and thorax lost, their position marked by depressions. Position of eyes apparent where 2 dark spots lie at antennal bases. Antennae slightly longer than length of body, very thin, bases separated by distance equal to width, with ca. 7 long segments decreasing in length distad. Forelegs much thinner and ca. ⅓ the length of other legs. Wing broad, width ca. ½ wing length. Venation not complete, but the following are apparent: costa (C) heavy; S_c apparently short and fused with basal third of C; R_1 unbranched; R_{4+5} and M_{1+2} separated by distance from at least level of bm-cu; CuA_1, CuA_2, and A_1 apparent, as is bm-cu (present as a depression). Mid and hind legs each equal in length; number and lengths of tarsal segments not apparent. Seven abdominal segments present, including hypopygium. Gonostyli present, slightly curved medially, length ca. twice their width, separated by distance ca. twice their width.

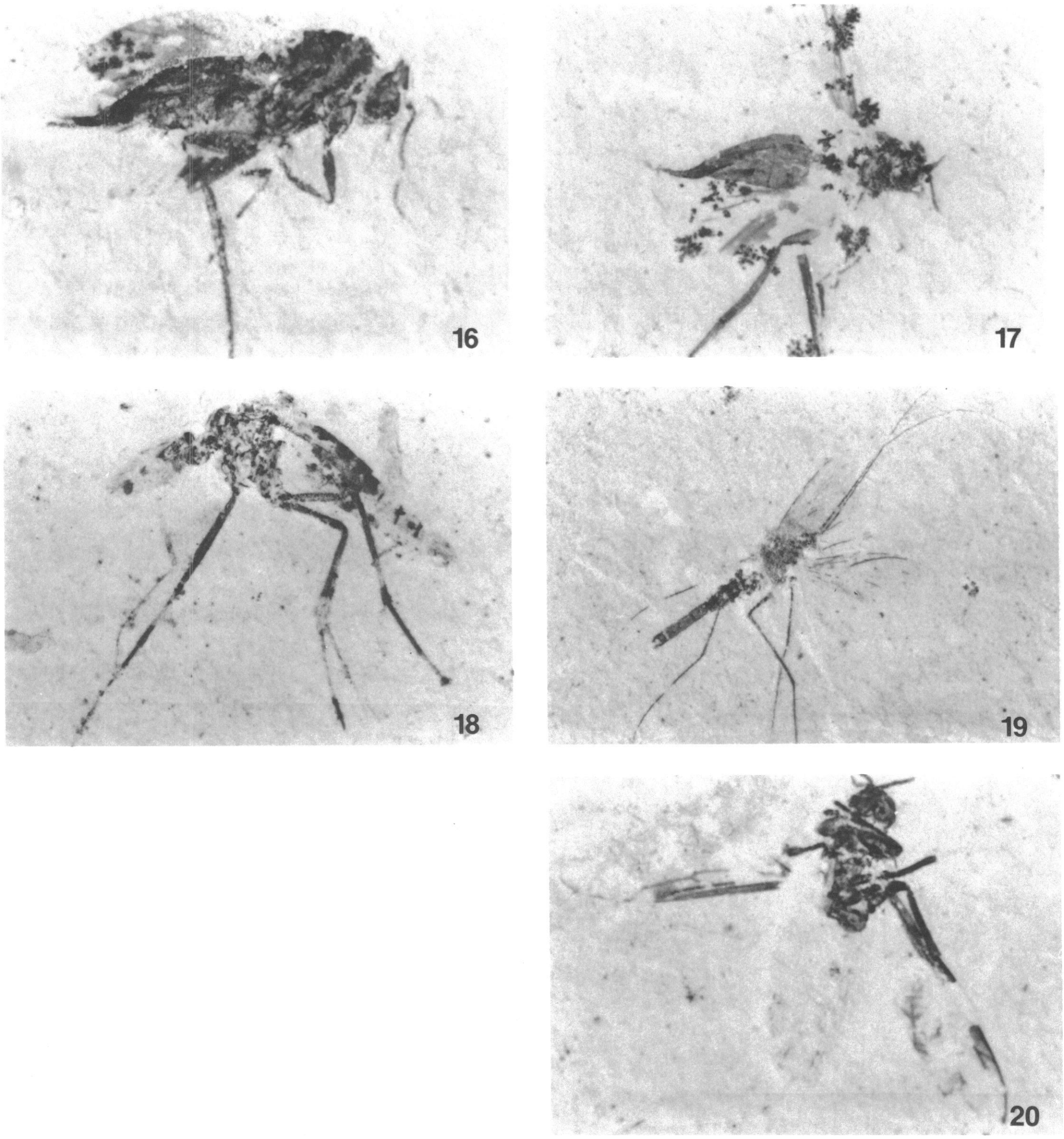
MEASUREMENTS: Lengths: body (excl. antennae) = 4.3; abdomen = ca. 2.7; antenna = 5.2; wing = 2.7 (r); midtibial = 1.8; tarsi: mid = 2.4, hind = 2.4.

DISCUSSION: The long, thin, and tapering antennae with long segments are suggestive of Deuterophlebiidae, but the antennae are considerably shorter than ones in this family. The notum is not strongly arched, and the fossil has a much more primitive venation than is seen in the Blephariceridae. Also, no large pretarsi were apparent in the fossil. Elongate antennae with long flagellomeres are also seen in the macrocerine Mycetophilidae, but in the fossil there is no evidence of elongate coxae, tibial spines, a short R_{2+3} vein, and forked $M_1 + M_2$, which is probably due to the quality of preservation. Antennae similar to the ones in the fossil have been reported in *Mangas* Kovalev (Mycetophilidae), but in *Mangas* there is a stigma at the apex of vein R_1. Because of a lack of detail in the basal portion of the wing in AMNH 43502, it is not apparent if there is a basal cell whose distal border is formed by a Y-branch of R_{4+5}. Despite the completely different habitus (as figured), *Mangas* venation resembles that of *Mycetobia* (Anisopodidae) except that in *Mangas* there is the primitive condition wherein vein CuA_2 begins near the middle of the basal cell.

Matile (1981) gave the most recent and comprehensive review of fossil Mycetophilidae sensu lato and the description of a primitive new genus, *Schlueterimyia*, most closely related to the Macrocerinae. *Schlueterimyia* is from Late Cretaceous (Cenomanian, ca. 95 mya) amber of France. Based on this fossil, on some older sciaroid fossils represented



Figs. 14, 15. Sciaroidea. **14.** AMNH 43505. **15.** 43506. Both are lateral habitus. Arrows point to tibial spurs.



Figs. 16–20. Habitus photographs. **16, 17.** AMNH 43505, 43506 (Sciaroidea). **18.** AMNH 43503 (Chironomoidea). **19.** AMNH 43502 (Mycetophilidae: Macrocerinae?). **20.** AMNH 43504 (Bibionidae?).

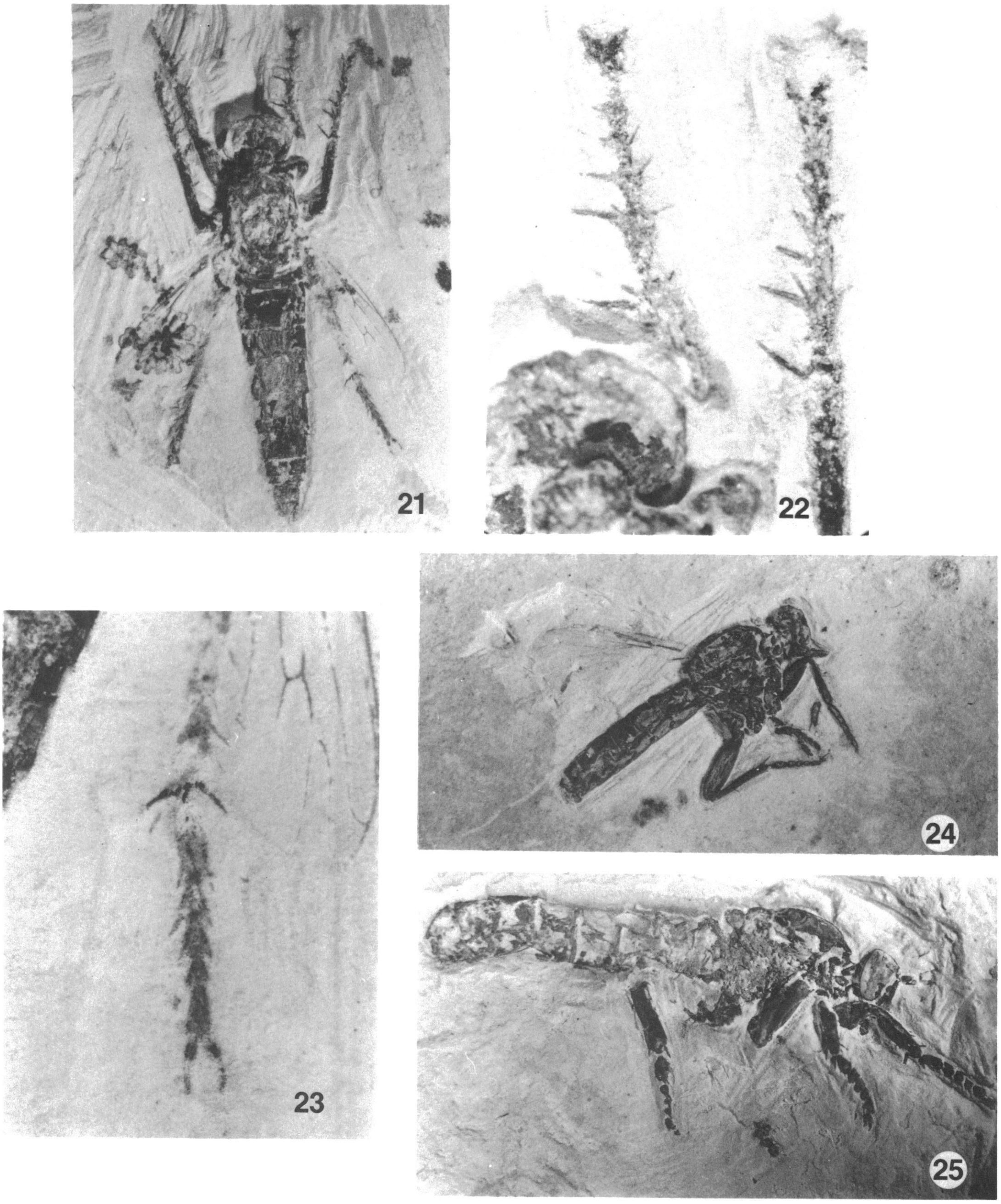
mostly as wings from Jurassic rocks, and the cladistic relationships of these fossils and living keroplatid subfamilies, Matile hypothesized an origin of the Keroplatidae in the Middle Jurassic.

SCIAROIDEA

Figures 14–17

MATERIAL: 2 females; AMNH 43505, AMNH 43506.

DESCRIPTION: Both specimens with right lateral surface exposed. Antennae multiarticulate; flagellomeres equal in width and length, pedicel ca. twice the size of flagellomeres; AMNH 43505 has a nearly complete antenna with 23 flagellomeres. Palps intact in AMNH 43506, 1 palp shows 4 segments: 1 short basal segment, 2 longer terminal segments of equal length. Halteres not present in either specimen. Only fragments of wings present in each specimen; no diagnostic venation apparent



Figs. 21–25. Habitus photographs of fossil Asilidae. 21–23. AMNH 43507 (*Araripogon axelrodi,* paratype). **21.** Habitus. **22.** Detail of right fore and midlegs. **23.** Detail of right hind leg. **24.** Lateral habitus of AMNH 43514 (*Araripogon axelrodi,* holotype). **25.** Lateral habitus of AMNH 43512 (*Araripogon,* sp. 2?).

except perhaps for a forked CuA$_1$–CuA$_2$; wings heavily pigmented. At least fore and midcoxa long, nearly equal to length of forefemur and wider. Hind femur stout, spindle-shaped, width ca. 2½ times that of hind tibia. Hind tibia with apical spur, length ca. ¼ that

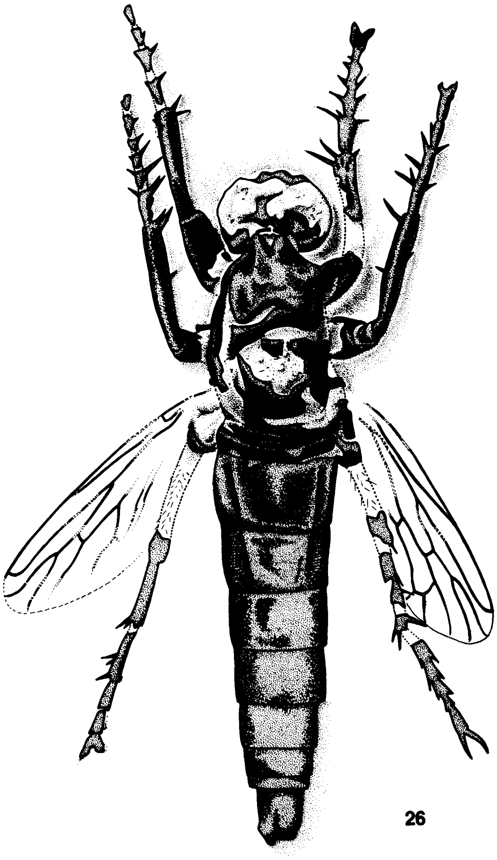


Fig. 26. AMNH 43507 (*Araripogon axelrodi*, paratype). Habitus, dorsal.

of tibia, and a slightly longer preapical spur. Midtibia with apical and a longer preapical spur. Most tarsi lost, hind tarsus of AMNH 43505 complete, but tarsomeres not distinct. Most of abdomen complete. Lateral folds apparent, suggestive of membrane; 5 to 6 tergites and 4 to 5 sternites apparent; terminal part of abdomen with elongate and narrow tapering.

Measurements: Body length (excl. flagella) = 4.2 (43505), 4.7 (43506); forecoxa = 0.5 (43505); forefemur = 0.6 (43505); hind femur = 0.8 (43505); hind tibia = 1.4 (43505), 1.4 (43506); hind tarsi = 1.4 (43505), 1.5 (43506).

Discussion: Despite the paucity of available details on these two specimens, there are several definite taxonomic conclusions to be drawn. The presence of multiarticulate antennae exclude them from the Brachycera. On the basis of the apical tibial spurs and the long coxae, the specimens can be placed in the Sciaroidea. In addition, heavily pigmented wings are common in the Sciaridae, although a forked CuA_1–CuA_2 is not (but is more common in Mycetophilidae). The long, tapering abdominal apex gives an indication of a telescoping ovipositor, which is found in the Cecidomyiidae (the third family in the Sciaroidea, sensu McAlpine et al., 1981) and Sciaridae.

Probably the oldest known sciaroids are the Archizelmiridae Rohdendorf 1962, Pleciofungivoridae Rohd. 1946, and Fungivoritidae Rohd. 1964. There are no tibial spurs in these groups, but R_{2+3} branches from R_{4+5} distally, approximately where the apex of R_1 meets the C vein (at least in *Archizelmira* and *Pleciofungivorella*).

ASILIDAE

Araripogon, new genus

Diagnosis: Forelegs with very stout spines; venation primitive, consisting of arcuate discal cell; R_{2+3} free from R_1 and turned costad; R_4 turned slightly costad; and veins M_1, M_2, M_3 arising separately from distal apex of discal cell.

Etymology: A combination derived from Araripe Plateau, and a common suffix in asilid names.

Type Species: *A. axelrodi*, new species.

Araripogon axelrodi, new species

Figures 21–24, 26–28, 34

Diagnosis: Same as for genus.

Etymology: Named for Dr. Herbert Axelrod, whose generosity with his personal collection made this entire study possible.

Holotype: AMNH 43514 (AMNH 43507 is paratype).

Description: Entire body and most of the wing preserved in both specimens, dorsal surface exposed in 43507, lateral surface in 43514. For AMNH 43507: head is facing down into matrix, posterior surface exposed, area just behind eyes concave. Pronotum with narrow saddle extended beyond anterior margin of notum by distance about equal to width of pronotum. Legs heavily spinose; fore and midlegs with sharp spines pointed mediad; lengths of spines up to twice the width of leg segments.

No. spines:	Foreleg	Midleg
Tibia	2 medials (apical)	2 apical medials
	1 smaller lateral	1 middle medial
Tarsomere-1	1 large medial	2 large medials
	1 smaller lateral	1 small lateral
Tarsomere-2	1 large medial	1 large medial
	1 smaller lateral	1 small lateral

Spines mostly at apices of tarsomeres. Pulvilli of fore and midlegs large. Five tarsomeres on each pair of legs. Three stout spines at apex of hind tibia; hind tarsomere-1 and -2 with 1 or 2 heavy spines on lateral surface. Length of hind pretarsal claws about equal to that of pretarsus. Femora short, barely exposed; stout, widths ca. twice that of tibiae. Wings relatively small: see reconstructed venation in figure 31. S_c long, parallel to R_1 for most of S_c length; apices of R_1 and R_{2+3} very close, apex of R_{2+3} abruptly turned costad (that of R_4 slightly less so); crossvein r-m at about middle of discal (d) cell; posterior margin of basal-radial cell nearly straight, discal cell curved posteriad and giving rise to M_1, M_2, and M_3; not apparent if A_1 intercepts CuA_2 before they meet margin of wing. Nine heavily sclerotized abdominal segments apparent, gradually tapered apicad. Segment 1 ca. ⅓ length of segment 2; segment 8 ca. ½ length of segment 7. Genitalia not apparent.

For 43514: 8 abdominal segments clearly visible. Hind and forelegs entirely preserved, heavily spinose. Head capsule partly collapsed and fragmentary, but a heavily sclerotized proboscis pointed forward and stout facial hairs are present. Venation very similar to that of AMNH 43507 except that R_{2+3}, R_4, and R_5 are apically more curved.

MEASUREMENTS: All are lengths. For 43507: body = 12.8; wing = 5.3 (r), 5.6 (l); thorax = 3.7; abdomen = 7.6; tibiae: fore = 2.0 (r), 2.1 (l), mid = 2.5 (r + l); tarsi: fore = 1.7, mid = 2.5 (r). Specimen 43514: body = 10.3; wing = 5.6 (r); thorax = 3.3; hind femur = 2.41; hind tibia = 2.21.

DISCUSSION: Despite the very primitive venation, there is virtually no doubt as to the familial assignment of the two specimens. AMNH 43507 and 43514 are conspecific judging from the similar body size and proportions and the venation. The following are apomorphies for the Asilidae which are present in the fossils: stout, sharp, medial spines on fore and midlegs; large pulvilli on fore pretarsi; large claws on hind pretarsi; postocular region concave; proboscis sclerotized and projecting; well-developed facial hairs. The primitive nature of the venation can be seen in figures 32–34, which compares Therevidae (fig. 33) with AMNH 43507 (fig. 34) and a Miocene (Florissant shale) asilid, *Senoprosopis eureka* (fig. 32). The venational resemblance of AMNH 43507 to *Psilocephala hypopygaea* (Therevidae) (another Florissant shale species) is very striking but is symplesiomorphic at the family level for the Asilidae. The diversity of the Florissant asilids is quite impressive, including at least 23 species placed in 15 genera, among which are some forms with very recently derived venation.

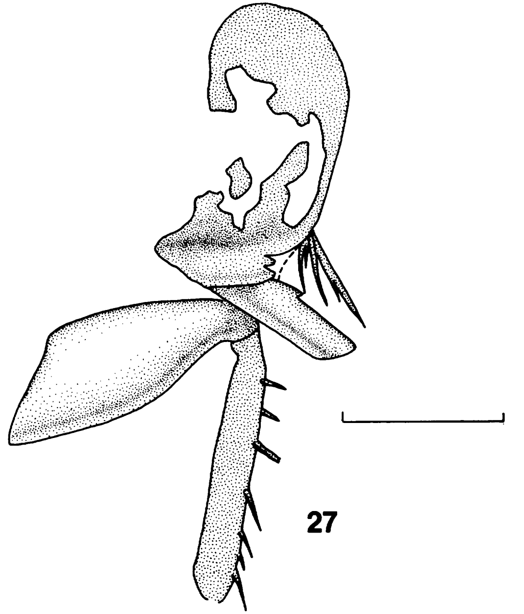
A probable origin near the Jurassic–Cretaceous boundary for the asilomorphs is indicated by the modern diversity during the Miocene and by the Cretaceous specimens present here, and perhaps by an Upper Liassic specimen (Bode, 1953). The Eremochaetidae was described by Ussatchov (1968) for several Upper Jurassic specimens from Karatau, Soviet Union. It was included in the Asilomorpha by Ussatchov and by Kovalev (1986), but in this infraorder both workers likewise included the Tabanoidea. Eremochaetidae may be synonymous with the Vermileonidae because, according to Kovalev's illustration (Kovalev, 1986: 150, fig. 120a), the abdomen is long and slender, the eyes are rather large, and the wings (although apparently lacking a discal cell in *Eremochaetosoma* Kovalev) possess the following features: wing petiolate (anal lobe small), R_{2+3} turned costad near apex (almost intercepting R_1 in *Eremochaetosoma,* and actually intercepting R_1 in *Eremochaetus asilicus* Ussatchov), ends of CuA_2 and A_1 nearly touching, and R_{4+5} forked apically. Specimens AMNH 43507 and 43514, and, of another species, AMNH 43512, are the oldest known specimens definitely assigned to the Asilidae.

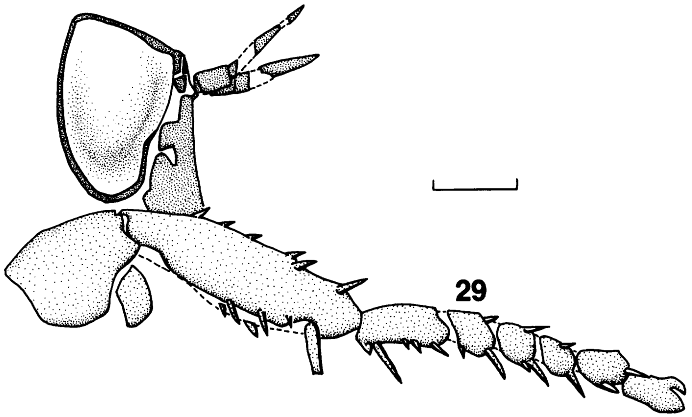
Araripogon, sp. 2?

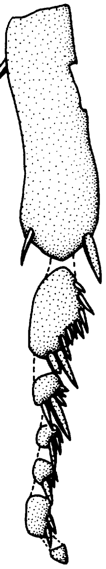
Figures 25, 29, 30

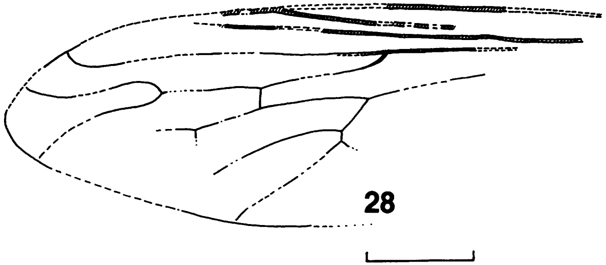
MATERIAL: AMNH 43512, sex unknown.

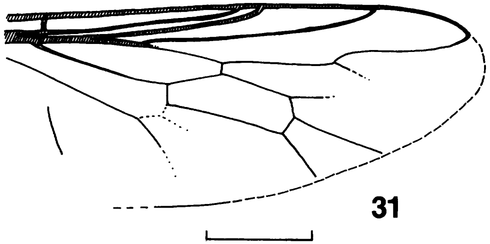
DESCRIPTION: Habitus in lateral repose,











Figs. 27–31. Asiloidea. 27, 28. AMNH 43514 (*Araripogon axelrodi,* holotype). **27.** Head and forefemur and tibia. **28.** Wing. 29, 30. AMNH 43512 (*Araripogon* sp. 2?). **29.** Head and forelegs. **30.** Hind tibia and tarsi. **31.** Wing of AMNH 43511 (Therevidae?).

nearly completely preserved save for loss of wings. Dorsal surface of notum and scutellum intact. Eye large, nearly the full width and length of the head. Face long. Antennae apparently porrect. Pedicel about ½ length of flagellum. Most of right 3 legs intact: forefemur very short and stout, about ½ length of midfemur (which is fragmentary). Foretibia nearly equal in length to foretarsus. Tibiae and tarsi heavily spinose, as illustrated. Five tarsomeres on all legs, pretarsus bearing large claws on fore and midlegs. Tarsomere-1 is longest one on fore and midtarsi. Hind tarsus with combs of short, stout spines on anterior surface of tarsomeres-1 and -2. Eight abdominal segments clearly visible.

Measurement: Total body length = 20.1 mm.

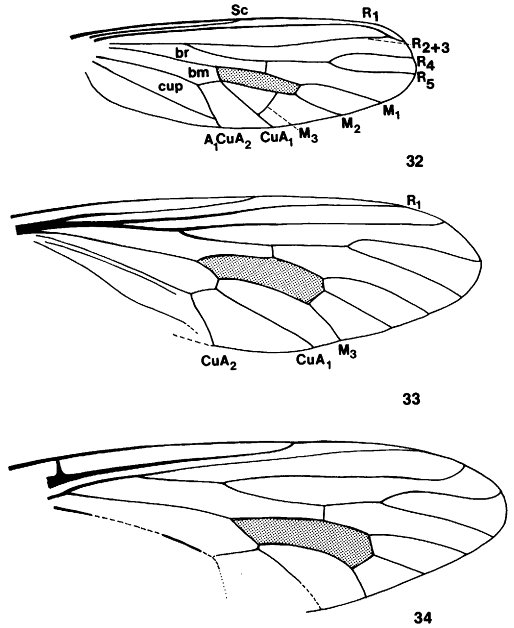
Discussion: The size and general habitus, but particularly the spination of the legs and proportions of leg segments, including the raptorial forelegs, indicate that this specimen is an asilid. Unfortunately, the proboscis, facial hairs, and the wings are missing, which would be needed to corroborate this. Some asilids have a rather marked sexual dimorphism in size (the female being the larger sex, as in most flies), which usually does not extend to the magnitude of difference between AMNH 43512 and the other two *Araripogon* fossils from the same deposit. However, in lieu of wings and other diagnostic features on this specimen, I am hesitant to name another species.

THEREVIDAE?

Figure 31

Material: AMNH 43511, sex unknown.

Description: Specimen very fragmentary; remaining are only portions of thorax, head, abdominal tergites 1–3, and wings. Right wing is preserved best (fig. 31 is a composite of both wings). Humeral vein present. Subcosta extended to ½ length of wing. Costa reaching to R_4. R_1 and base of R_s are thickest veins. Vein R_{2+3} originating from slightly beyond middle of br cell. End of cell bm proximal to that of br by distance about 5 times the length of crossvein r-m. Veins R_5, M_1 and cubitals not completely preserved. Discal cell about ⅘ length of cell br, nearly straight. Crossvein r-m just slightly proximal to middle of discal cell.



Figs. 32–34. Wings of fossil Asiloidea, all to same scale. Discal cell is stippled. **32.** *Senoprosopis eureka* Melander, holotype (AMNH FI 26602: Florissant [Miocene]) (Asilidae). **33.** *Psilocephala hypopygaea* Cockerell, holotype (AMNH 18853: Florissant) (Therevidae). **34.** AMNH 43507, *Araripogon axelrodi* (paratype), venation reconstructed from both wings.

Measurements: Approximate body length = 8.5; length of wing = 4.8–5.0.

Discussion: The very incomplete preservation makes a familial assignment tenuous. If the comparative wing study by Hennig (1954) is used, several things become apparent. Wing shape is most like that seen in the Asilidae, Athericidae, Therevidae, Tabanidae, and Pelecorhynchidae. The last two can be ruled out since the medial veins in the fossil are not directed strongly posteriad and the apex of R_{2+3} is only slightly distal to the fork of $R_4 + R_5$. Dr. Rafael Martins-Neto has supplied me with a figure of a specimen in his collection, which has the body almost entirely intact (ventral side up) and a venation identical to that of AMNH 43511. The large eyes and stout, truncate abdomen indicated in the drawing do, however, suggest Tabanidae. If this specimen is eventually studied, a detailed examination should be made of the antennae and proboscis, if preserved at all. The Athericidae have the apices of R_1 and R_{2+3} joined before meeting or approximately near the costa, unlike the plesiomorphic condition in the fossil. The salient features in the venation are the relatively short cell bm, and the crossvein r-m located very near the middle of the discal cell, which is a feature widespread in Therevidae and Asilidae. I would hesitate to assign the specimen to the Asilidae for it does not possess a vein R_1 which has a length at least three-quarters the wing length, as is found in most asilids (including the Cretaceous asilids in this study), as well as in a few other primitive Brachycera such as *Xylomya* (Xylomyidae).

DISCUSSION

Table 1 is a compilation of the published and unpublished records of the known Cretaceous Diptera fossils. Not included are very general identifications, such as "dipteran" from the Orapa, Botswana deposit (McKay and Rayner, 1986), or the larvae discussed by Bode (1953). For some papers that list the fauna of a particular deposit (e.g., McAlpine and Martin, 1969), the reference in the table gives the most recent systematic treatment of the particular taxon in question.

Also not included in the table are some of the families first reported to have been found in the Cretaceous ambers of Taymyr, Siberia (Zerikhin et al., 1973). There apparently is an ongoing study of these specimens by the Soviets. The classification of families in table 1, as in the taxonomic text, follows McAlpine et al. (1981), with a few minor exceptions (e.g., Limoniidae instead of limoniine Tipulidae).

The great majority of Cretaceous Diptera records represent species in the paraphyletic suborder "Nematocera." The only known Cretaceous Muscomorpha are Platypezoidea, a few Syrphoidea, and one reference each to a calliphorid and, recently, a milichiid from New Jersey amber. The extant families of lower Brachycera represented as fossils in the Cretaceous are the Stratiomyidae, Rhagionidae, Asilidae, Bombyliidae, Empididae (s.l.), and Dolichopodidae (s.l.). One of the most remarkable sets of fly fossils is the Nemestrinidae collection from the Upper Jurassic of South Kazakstan, Karatau, Soviet Union (Rohdendorf, 1968). The venation of the Soviet specimens is virtually complete, and the upturned distal portions of the radial and medial veins and closed cell just below the discal cell seen in the specimens are diagnostic of the family. Hong (1982) described the family Protabanidae for a Cretaceous compression fossil from China with most of the wings, abdomen, legs, and a portion of the head intact. The presence of a bulbous, large clypeus, large beak, the general shape of the abdomen and legs, and especially the series of parallel medial cells in the wing show the specimen not to be a fly, but a homopteran! In only a few phylogenetic studies on extant taxa have there been incorporated some Cretaceous specimens, such as Stratiomyidae (Woodley, 1986); Empidoidea (Hennig, 1971); and Sciadoceridae, later placed in the Phoridae by Hennig (1973) (but see Grimaldi [1988]), which occur in ambers from Canada (mid-Cretaceous) (McAlpine and Martin, 1966) and Lebanon (Lower Cretaceous) (personal obs.). For most of these three instances the specimens are cladistically basal in a familial scheme. (In the case of the Sciadoceridae, the fossil and extant species purportedly form a monophyletic sister group to the large cosmopolitan family, the Phoridae.)

Kovalev (1985) mentioned several Early Jurassic rhagionids; until a critical stratigraphy of the site and the details of the specimen morphology are published, I find his view of the Brachycera having originated in the Early Jurassic (195–175 mya) as more opinion than fact. I have seen a rhagionid wing from the Early Cretaceous (Neocomian) amber from Lebanon, provided by Mr. Fadi Acra. Also, the presence of the bombyliid subfamilies Phthiriinae, Cyrtosiinae, and Platypyginae in the Lower Cretaceous suggests an origin of the Bombyliidae in the Jurassic (Zaitzev, 1986). However, the monophyly of this heterogenous family is in serious question, for lack of a consistent synapomorphy. The best

TABLE 1
Known Cretaceous Diptera
(A = amber, M = mineral replacement)

Taxa	A/M		Source	Reference
			Tipulomorpha	
Tipuloidea				
Tipulidae	M	1	England	Jarzembowski, 1984
Unnamed	M	2	Brazil	this study
Limoniidae				
Cretolimonia$^+$ (1 sp.)	M	3	Mongolia	Kalugina, 1986
Nemumeia$^+$ (1 sp.)	M	3	Mongolia	Kalugina, 1986
?*Eotipulina*$^+$ (1 sp.)	M	3	Mongolia	Kalugina, 1986
?Limoniidae, incertae sedis	M	3	Mongolia	Kalugina, 1986
Limonia albertensis	A	4	Canada	Krzeminski & Teskey, 1987
Trichoneura canadensis	A	4	Canada	Krzeminski & Teskey, 1987
Macalpina incomparabilis	A	4	Canada	Krzeminski & Teskey, 1987
			Bibionomorpha	
Bibionoidea				
Bibionidae	M	2	Brazil	this study
	M	14	Botswana	Rayner, 1987
Plecia myersi	A	4	Manitoba	Peterson, 1975
Sciaroidea				
3 genera, incertae sedis	M	3	Mongolia	Kovalev, 1986
	M	2	Brazil	this study
Sciaridae				
Undescribed	A	4	Manitoba	McAlpine & Martin, 1969
Mycetophilidae				
Undescribed	M	1	England	Jarzembowski, 1984
Macrocerinae:	M	2	Brazil	this study
Schlueterimyia$^+$ (1 sp.)	A	5	France	Matile, 1981
Sciophilinae:				
Undescribed	A	4	Manitoba	Vockeroth, 1981
Bolitophilinae:				
Mangas$^+$ (1 sp.)	M	3	Mongolia	Kovalev, 1986
?Mesosciophilidae				
Mesosciophilites$^+$ (1 sp.)	M	3	Mongolia	Kovalev, 1986
Cecidomyiidae				
Cretocatocha$^+$ (1 sp.)	A	7	Alberta	Gagné, 1977
Cretocordylomia$^+$ (1 sp.)	A	4	Manitoba	Gagné, 1977
Cretomiastor$^+$ (1 sp.)	A	4, 7	Alberta & Manitoba	Gagné, 1977
Cretowinnertzia$^+$ (1 sp.)	A	4	Manitoba	Gagné, 1977
Undescribed	A	8	Lebanon	Schlee & Dietrich, 1970
	A	6	New Jersey	unpubl.
			Psychodomorpha	
Psychodidae				
Phlebotomites$^+$ *brevifilis*	A	8	Lebanon	Hennig, 1972
Phlebotomites longifilis	A	8	Lebanon	Hennig, 1972
Trichoceridae				
Paleotrichocera$^+$ (1 sp.)	M	3	Mongolia	Kalugina, 1986
Trichonomites$^+$ (1 sp.	M	3	Mongolia	Kalugina, 1986
Anisopodidae				
Undescribed	A	4, 7	Canada	McAlpine & Martin, 1969
6 genera, incertae sedis	M	3	Mongolia	Kovalev, 1986
Pachyrhyphus$^+$ (2 spp.)	M	3	Mongolia	Kovalev, 1986

TABLE 1—(*Continued*)

Taxa	A/M		Source	Reference
Scatopsoidea				
2 "genera"$^+$, undescribed	M	3	Mongolia	Kovalev, 1986
Scatopsidae				
Undescribed	A	4	Manitoba	McAlpine & Martin, 1969
Culicomorpha				
Chaoboridae				
Chironomaptera$^+$	M	3	Mongolia	Kalugina, 1986
Astrocorethra$^+$ (3 spp.)	M	3	Mongolia	Kalugina, 1986
Simuliidae				
Simuliites$^+$ (1 sp.)	M	3	Mongolia	Kalugina, 1986
Liauningius$^+$	M	16	China	Hong, 1982
Ceratopogonidae				
Undescribed	A	8	Lebanon	Schlee & Dietrich, 1970
Undescribed	A	4	Manitoba	McAlpine & Martin, 1969
Lasiohelea cretea	A	4, 7	Canada	Boesel, 1937
Lasiohelea globosa	A	4, 7	Canada	Boesel, 1937
Atrichopogon canadensis	A	4, 7	Canada	Boesel, 1937
Ceratopogon aquilonius	A	4, 7	Canada	Boesel, 1937
Protoculicoides depressus	A	4, 7	Canada	Boesel, 1937
Culicoides casei	A	6	New Jersey	Grogan & Szadiewski, 1988
Chironomoidea				
Mesotendipedidae$^+$	M	16	China	Hong, 1982
	M	3	Brazil	this study
Chironomidae				
Undescribed	A	4, 7	Canada	McAlpine & Martin, 1969
Chironomaptera$^+$ *gregaria*	M	9	China	Ping, 1928
Chironomaptera melanura	M	9	China	Ping, 1928
Chironomopsis$^+$ *gracilis*	M	10	China	Ping, 1928
Gurvanomyia$^+$ (2 spp.)	M	3	Mongolia	Kalugina, 1986
Libanochlites$^+$ *neocomicus*	A	8	Lebanon	Brundin, 1976
Aphroteniinae:				
Electrotenia$^+$ *brundini*	A	15	Siberia	Kalugina, 1978
Orthocladiinae:				
Undescribed	A	6	New Jersey	unpubl.
Metriocnemus cretatus	A	4, 7	Canada	Boesel, 1937
Spaniotoma conservata	A	4, 7	Canada	Boesel, 1937
Spaniotoma (*Smittia*) *veta*	A	4, 7	Canada	Boesel, 1937
Shinlustia$^+$ (1 sp.)	M	3	Mongolia	Kalugina, 1986
Perissomatidae				
Gurvaniella$^+$ (1 sp.)	M	3	Mongolia	Kovalev, 1986
Tabanomorpha				
Stratiomyoidea				
Stratiomyidae				
Cretaceogaster$^+$ *pygmaeus*	A	4	Manitoba	Teskey, 1971; Woodley, 1986
Tabanoidea				
Batgana$^+$ (1 sp.)	M	3	Mongolia	Kovalev, 1986
Shulmas$^+$ (1 sp.)	M	3	Mongolia	Kovalev, 1986
Rhagionidae				
Undescribed	M	1	England	Jarzembowski, 1984
Undescribed	A	12	Siberia	Zerikhin et al., 1973
Mongolomyia$^+$ (1 sp.)	M	3	Mongolia	Kovalev, 1986
Ptiolinites$^+$ (1 sp.)	M	3	Mongolia	Kovalev, 1986
2 "genera," incertae sedis	M	3	Mongolia	Kovalev, 1986

TABLE 1—(*Continued*)

Taxa	A/M	Source	Reference
		Asilomorpha	
Eremochaetoidea			
Eremochaetidae⁺			
Eremochaetosoma⁺ (1 sp.)	M 3	Mongolia	Kovalev, 1986
Asiloidea			
Asilidae: *Araripogon axelrodi*	M 2	Brazil	this study
	M 11?	Germany, Upper Liassic	Bode, 1953
Bombylioidea			
Bombyliidae			
Undescribed	A 12	Siberia	Zerikhin et al., 1973
2 "genera," incertae sedis (see attached)	M 3	Mongolia	Kovalev, 1986
Empidoidea			
Microphorites⁺ *extinctus*	A 8	Lebanon	Hennig, 1971
Proplatypygus⁺ *rohdendorfi*	A 12	Siberia	Zaitzev, 1986
Procyrtosia⁺ *sukatshevae*	A 12	Siberia	Zaitzev, 1986
Zarzia⁺ *zherichini*	A 12	Siberia	Zaitzev, 1986
Empididae			
Undescribed	A 4, 7	Canada	Legg, 1942
1 "genus," incertae sedis	M 3	Mongolia	Kovalev, 1986
Trichinites⁺ *cretaceous*	A 8	Lebanon	Hennig, 1970
Cretomicrophorus⁺ *rohdendorfi*	A 12	Siberia	Negrobov, 1978
Archichrysotus⁺ *hennigi*	A 12	Siberia	Negrobov, 1978
Archichrysotus⁺ *minor*	A 12	Siberia	Negrobov, 1978
Tachydromiinae:			
Cretoplatypalpus⁺	A 15	Siberia	Kovalev, 1978
Archiplatypalpus⁺	A 12	Siberia	Kovalev, 1974
Empis orapaensis	M 14	Botswana	Waters, 1989
Dolichopodidae			
Undescribed	A 4	Manitoba	McAlpine & Martin, 1969
?Dolichopodidae			
Retinitus⁺ *nervosus*	A 12	Siberia	Negrobov, 1978
"Hybotidae"			
1 "genus," incertae sedis	M 3	Mongolia	Kovalev, 1986
		Muscomorpha	
Platypezoidea			
Platypezidae			
Undescribed	A 4	Manitoba	McAlpine & Martin, 1969
Undescribed	A 12	Siberia	Zerikhin et al., 1973
Ironomyiidae	A 4	Manitoba	McAlpine & Martin, 1969
Sciadoceridae			
Sciadophora bostoni	A 7	Alberta	McAlpine & Martin, 1966
Prioriphora canadambra	A 4	Manitoba	McAlpine & Martin, 1966
Phoridae			
Metopina	A 6	New Jersey	Grimaldi, 1988
Syrphoidea			
Pipunculidae?			
Undescribed	A 4	Manitoba	McAlpine & Martin, 1969
Syrphidae	A 12	Siberia	Kovalev, 1985

TABLE 1—(*Continued*)

Taxa	A/M	Source	Reference
	Muscomorpha-Schizophora		
Calliphoridae			
Cretaphormia+ *fowleri*	M 13	Alberta	McAlpine, 1970
Milichiidae	A 6	New Jersey	Grimaldi et al., 1989

Formations: 1. Clay, Wealden Beds, Berriasian-Barremian, 119–144 mya (Lower Cretaceous); 2. Limestone, Santana Formation, Aptian, 110 mya (Lower Cretaceous); 3. (w. Mongolia); 4. Amber, Cedar Lake, same as Alberta amber? 5. Amber, d'Ecommoy, Sarthe; Cenomanian, 80 mya (Middle Cretaceous); 6. Amber, New Jersey, Raritan-Magothy Formation, 80–95 mya (Middle Cretaceous); 7. Amber, Medicine Hat, Foremost Formation, Belly River Series, 72–73 mya (Upper Cretaceous); 8. Amber, Lebanon (Lower Cretaceous); 9. Shale, Laiyang Formation (Lower Cretaceous); 10. Shale, Upper Volcanic Series (Lower Cretaceous); 11. Upper Liassic, Germany? 12. Amber, Siberia, ? Santonian (Upper Cretaceous); 13. Ironstone, Edmonton Formation, 70 mya (Upper Cretaceous); 14. Kimberlite and mudstone; Cenomanian/Turonian, 82–95 mya; 15. Amber, Siberia; Upper Cenomanian (Upper Cretaceous, 95 mya); 16. Stratum in Cretaceous unknown.

indications are that Brachycera origins are in the Middle Jurassic, and the various groups of "Nematocera" of ranks higher than the suborder Brachycera certainly have origins in the Early Jurassic. Given this antiquity, the influence of continental tectonics on distributions must be regarded, at least at the outset of biogeography studies on flies, as anything but trivial.

Despite the very incomplete nature of the record, there is, in general, a positive relationship in the Diptera between the sequence of appearance in the fossil record and the sequence of branching of a cladogram of the families, which is an observation first documented by Hennig (1954; his fig. 272). In fact, Hennig's impetus for doing such comprehensive studies on Eocene and Cretaceous amber Diptera (briefly reviewed by Larsson, 1978) was to correlate an approximate absolute age of a group with its taxonomic rank.

REFERENCES

Bode, A.
1953. Die Insektenfauna des ostniedersachsischen Oberen Lias. Paleontographica, ser. A, 103: 1–375.

Boesel, M. W.
1937. Order Diptera, family Chironomidae. *In* F. W. Carpenter et al. (eds.), Insects and arachnids from Canadian amber. Univ. Toronto Stud. Geol. 40: 44–55.

Brundin, L.
1965. On the real nature of transantarctic relationships. Evolution 19: 496–505.
1976. A Neocomian chironomid and Podonominae-Aphroteniinae (Diptera) in the light of phylogenetics and biogeography. Zool. Scripta 5: 139–160.

Case, G. R.
1982. A pictoral guide to fossils. New York: Van Nostrand Reinhold.

Gagné, R. J.
1977. Cecidomyiidae (Diptera) from Canadian amber. Proc. Entomol. Soc. Washington 79: 57–62.

Grimaldi, D. A.
1988. The genus *Metopina* (Diptera: Phoridae) from Cretaceous and Tertiary ambers. J. New York Entomol. Soc. 97: 65–72.

Grimaldi, D. A., C. W. Beck, and J. J. Boon
1989. Occurrence, chemical characteristics, and paleontology of the fossil resins from New Jersey. Am. Mus. Novitates 2948: 28 pp.

Grogan, W. L., Jr., and R. Szadiewski
1988. A new biting midge from Upper Cretaceous (Cenomanian) amber of New Jersey (Diptera: Ceratopogonidae). J. Paleontol. 62: 808–812.

Hennig, W.
1954. Flugelgeader und System der Dipteren. Beitr. Entomol. 4: 17–387.
1970. Insektenfossile aus der Unteren Kreide, II. Empididae (Diptera, Brachycera). Stutt. Beitr. Naturk. 214: 1–12.
1971. Insektenfossile aus der Unteren Kreide, III. Empidiformia ("Microphorinae")

aus der Unteren Kreide und aus dem Baltischen Bernstein. Stutt. Beitr. Naturk. 232: 1–28.

1972. Insektenfossile aus der Unteren Kreide, IV. Psychodidae (Phlebotominae) mit einer kritischen Ubersicht uber das phylogenetische System der Families und die bisher beschrieben Fossilien (Diptera). Stutt. Beitr. Naturk. 241: 1–69.

1973. Ordnung Diptera (Zweiflugler). Kukenthal's Handbk. Zool. 4(2): 1–337.

Hong, Y-C.

1982. Mesozoic fossil insects of Jiuquan Basin in Guasn Province. Peking: Geological Publishing House, 187 pp. [In Chinese]

Jarzembowski, E. A.

1984. Early Cretaceous insects from southern England. Mod. Geol. 9: 71–93.

Kalugina, N. S.

1978. Cretaceous Aphroteniinae from North Siberia (Diptera, Chironomidae, *Electrotenia brundini* nov., sp. nov. Acta Univ. Carolinae—Biol. 1978: 89–93.

1986. Insects in the Early Cretaceous ecosystems of the West Mongolia. Trans. Paleontol. Inst. (USSR) 28: 112–127. [In Russian]

Kovalev, V. G.

1974. A new genus of the family Empididae (Diptera) and its phylogenetic relationships. Paleontol. Zh. 2: 84–94.

1978. A new fly genus (Empididae) from Late Cretaceous retinites of the Taymyr. Paleontol. Zh. 3: 351–356.

1985. Main aspects in the evolution of Diptera Brachycera in the Mesozoic Era. *In* O. A. Skarlato (ed.), Systematics of Diptera (Insecta), ecological and morphological principles, pp. 56–59 (translated from Russian). New Dehli: Amerind Publ., 185 pp.

1986. Insects in the Early Cretaceous ecosystems of western Mongolia. Trans. Paleontol. Inst. (USSR) 28: 127–154. [In Russian]

Krzeminski, W., and H. J. Teskey

1987. New taxa of Limoniidae (Diptera: Nematocera) from Canadian amber. Can. Entomol. 119: 887–892.

Larsson, S. G.

1978. Baltic amber: a paleobiological study. Entomonograph 1: 1–192. Klampenbørg, Denmark: Scandinavian Science Press.

Legg, W. M.

1942. Collection, preparation and statistical study of fossil insects from chemawinite. Senior thesis, Dept. Biol., Princeton Univ., Princeton, N.J.

Matile, L.

1981. Description d'un Keroplatidae du crétacé moyen et donées morphologiques et taxonomiques sur les Mycetophiloidea (Diptera). Ann. Soc. Entomol. France 17: 99–123.

McAlpine, J. F.

1970. First record of calypterate flies in the Mesozoic era (Diptera: Calliphoridae). Can. Entomol. 102: 342–346.

McAlpine, J. F. et al.

1981. Manual of Nearctic Diptera, vol. 1. Agric. Can. Monogr. 27: 1–674. Ottawa: Ministry of Supply and Services.

McAlpine, J. F., and J. E. H. Martin

1966. Systematics of Sciadoceridae and relatives with descriptions of two new genera from Canadian amber and erection of family Ironomyiidae (Diptera: Phoroidea). Can. Entomol. 99: 225–336.

1969. Canadian amber—a paleontological treasure-chest. Can. Entomol. 101: 819–838.

McKay, I. J., and R. J. Rayner

1986. Cretaceous fossil insects from Orapa, Botswana. J. Entomol. Soc. South Africa 49: 7–17.

Negrobov, O. P.

1978. Flies of the superfamily Empidoidea (Diptera) from Cretaceous retinite in northern Siberia. Paleontol. Zh. 1978 (2): 81–90.

Peterson, B. V.

1975. A new Cretaceous bibionid from Canadian amber (Diptera: Bibionidae). Can. Entomol. 107: 711–715.

Ping, C.

1928. Cretaceous fossil insects of China. Paleontol. Sinica, ser. B, 13: 1–50.

Rayner, R. J.

1987. March flies from an African Cretaceous springtime. Lethaia 20: 123–127.

Rohdendorf, B.

1968. New Mesozoic Nemestrinidae (Diptera, Nemestrinidae). *In* B. B. Rohdendorf (ed.), Jurassic insects of Karatau, pp. 180–189. [In Russian]

1974. The historical development of Diptera. (English translation.) Edmonton: Univ. Alberta Press.

Schlee, D., and H. G. Dietrich

1970. Insektenfuhrender Bernstein aus der Unterkreide des Libanon. N. Jahrb. Geol. Palaeontol. Monatsh. 1970: 40–50.

Teskey, H. J.

1971. A new soldier fly from Canadian amber (Diptera: Stratiomyidae). Can. Entomol. 103: 1659–1661.

Ussatchov, D. A.
1968. New Jurassic Asilomorpha (Diptera) in Karatau. Entomol. Rev. (USSR) 47: 617–628.

Vockeroth, J. R.
1981. Mycetophilidae. *In* J. F. McAlpine et al. (eds.), Manual of Nearctic Diptera, vol. 1. Agric. Can. Monogr. 27: 223–248. Ottawa: Ministry of Supply and Services.

Waters, S.
1989. A Cretaceous dance fly (Diptera: Empididae) from Botswana. Syst. Entomol. 14: 233–241.

Woodley, N. E.
1986. Parhadrestiinae, a new subfamily for *Parhadrestia* James and *Cretaceogaster* Teskey (Diptera: Stratiomyidae). Syst. Entomol. 11: 377–387.

Zaitzev, V. F.
1986. New species of Cretaceous fossil bee flies and a review of paleontological data on the Bombyliidae (Diptera). Entomol. Obozr. 4: 815–824.

Zerikhin, A. A., P. Sukacheva, A. G. Sharov, V. N. Vishnykova, A. G. Ponomarenko, and P. Becker-Migdisova
1973. Insects from the Cretaceous retinite of northern Siberia. 24th Ann. Rept. on Lectures in Memory of N. A. Kolodovsky (April, 1971), Leningrad.

GENERAL INDEX

acetic acid, 12
alate, 22, 47
Albian, 5, 15, 16, 76
algae, 17
Alianca formation, 15
amber, 8, 164, 177
Amber, Baltic, 21, 68
  Canada (Manitoba), 165, 169, 181
  France, 169, 181
  Lebanese, 177, 181
  New Jersey, 167, 177, 181
  Siberian, 167, 181
Amphinotic distribution, 30
apatite, 9
Aptian, 5, 15, 16, 76
Araripe basin, 15
Araripe Plateau, 5, 15, 17, 79
ashing technique, 9
Austral, 9, 24, 167
Australia, 5, 9, 24, 74, 123
Australian Plate, 74

Berremian, 16
Beriasian, 76
Berriasian-Berremian, 5
biogeography, 157
Botswana, 5, 177
Brotas group, 15, 16
burrow, 39, 41

calcar, 145, 146
calcite, 9
calcrete, 16
caliche layer, 16, 18
Canada, 150
carbon, 9
carbonate, 9, 17, 18
Carboniferous, 21
catalogs, fossil Diptera, 178
  fossil Ephemeroptera, 21
  fossil Hymenoptera, 124
  fossil Raphidioptera, 158, 160
Ceará, Brazil, 5
Cenomanian, 76
Cenozoic, 76
cerci, 9, 71, 72, 79
cervical sclerites, 71, 72
Chile, 123
China, 5, 68
circumtropical, 73, 74
cladogram, 33, 36, 38, 73
Codo Formation, 8
Crato Member, 5, 8, 15, 16
Cretaceous Period, 5, 21, 74, 76, 174, 177
  Early, 167
  Middle, 169
  Upper, 16

damselflies, 52
deposition, 17
dimorphism, 40
dragonflies, 57

earwigs, 68
East Berlin formation, 17
elytra, 9, 10, 12, 71
England, 5
Eocene, 20, 76
eutrophic lake, 12, 167
evaporites, 17, 18
Exu Formation, 5, 16

filter feeders, 33, 47
filtering setae, 24, 33, 37
fine morphology, 9, 12
fish concretions, 12
flies, oldest, 165
Florissant, 68, 174
fluting, 35
forewing, 9, 77, 80
fossorial habit, 39
freshwater lakes, 12

Gansu, China, 5
geminating veins, 35
genual plates, 135, 136
geographical extinctions, 9, 73, 154, 157
goethite, 9
Gondwanaland, 20, 30, 45, 46, 74, 76, 157
Green River formation, 17

Hautervian, 76
hind wing, 77, 80
Holarctic distributions, 9, 24
hydrochloric acid, 9

imago, 76

Jurassic, 5, 15, 21, 24, 27, 29, 35, 38, 45–47, 68, 74, 123, 131, 150, 154, 165, 167, 169, 171, 177
Jurassic-Cretaceous boundary, 174

karst, 18
Kimberlite, 181
Koonwarra fossil bed, 123

Labrador, 76
lacustrine, 13, 15, 17, 18, 28, 47
lamination, 17
larva, larvae, 27

Laurasia, 21, 27, 157, 164
Lebanese amber, 76
lentic, 28
Lérida, Spain, 5
limestone, 16
littoral, 13, 28, 47
Lower Cretaceous, 5, 15

Madagascar, 74
manganese oxide, 9
matrix, 9
mesosternal plates, 145
mesosternum, 136, 145
Mesozoic, 5, 15, 21, 47, 76, 136, 145
metapostnotum, 145
micrites, 17
microtrichia, 12
minnow-like mayflies, 24, 30, 33
Miocene, 157, 174
Mongolia, 5

Nearctic, 123, 129
Neocomian, 76
New Jersey, 145
North America, 157
Northern Hemisphere, 157

oldest representatives, 8, 174
Oligocene, 123, 136
Oriental Region, 74
ostracods, 15, 16, 17
oxidation, 13

Paleocene, 9
Paleoenvironment, 12
Paleozoic, 5, 21, 46, 76
palynology, 15, 16
Pangaea, 21, 46
Pangaean distribution, 27
pannote mayflies, 47
Pantropical, 36, 41, 46
parallelism, 66, 67
parasites, 9
Permian, 9, 21, 76
petiolate wings, 52–57
phylogeny, 136, 149
phytophagous insects, 13
plants, 13, 17
pollen, 16, 18
polycolpate, 16
preservation, 9, 12
proepisterna, 147
propodeal triangle, 145
pterostigma, 9
pterothorax, 148
pyrite, 17
pyrolusite, 9

Queensland, 123

relict distributions, 9, 157
rheophilic, 27, 28
robber flies, 172–176
Romualdo member, 16

saline, 13
sandstone, 16
Santana Formation, 5, 15, 16, 76
scanning electron microscopy, 9, 12
schistonotes, 46
sculling, 35
Seki, 68
Senonian amber, 76
Sergi formation, 15
Sergipe-Alagoas basin, 16
shales, 17
Siberia, 147
snakeflies, 154
social behavior, 149
South Africa, 74, 123
South America, 9, 20, 74, 154
Southern continents, 74
Southern Hemisphere, 20, 74, 157
Soviet Union, 68, 164
Spain, 5, 76
stratigraphy, 15
stream, 47
subimaginal stage, 22, 35
swimming, 27, 30, 47

tarsal reduction 74
termite, 76
Tertiary, 21, 76
Transbaikalia, 123
Triassic, 21, 46, 76, 165

USSR, 123

Valanginian, 76
venation, 10
vertebrates, 15
vicariance, 27, 42, 46, 167
Victoria, Australia, 5, 123

Wealden Clay, 76, 181
Wealden series, 5
wing vein, reconstruction, 156
wing venation, 27

x-ray diffraction, 9
xerophilic arthropods, 13

TAXONOMIC INDEX

Asterisks (*) indicate new taxa. Numbers in bold refer to the page of description or major discussion for that taxon.

Achilidae, 9, 82, 96, **97**, 98, 116
*_Acixiites_, **97**, 98, 119
Acridoidea, 9
Aculeata, 123, 135, 136, 139, 147, **149**
Aenigmephemeridae, 20
*Aeschnidioidea, **64**
Aeschnidiopsis, **64**, 66
Aeschnidium, **64**
Aeshnidae, 58, **64**
Aeshnidiidae, **64**
Aeshnoidea, **64**
Afromera, 39
Aleurodes, 96
Aleyrodidae, 113
Aleyrodoidea, 82, 95, **96**, 115
Alloambria, 113
Allostethinae, 74
Amberaphis, 113
Ameletus, 27, 29
Amphipterygidae, 52, 56
Amphipteryx, 52
Ampulicinae, 140, 145, 146, **147**
Anacanthotermes, 80
Anaxyelidae, 123, **129**
Ancorale, **101**, 102, 103, 120
*Ancoralinae, **101**, 103
*Ancoralini, 101
Angarosphecidae, **140**
Angarosphex, **140**
Aniferella, 113
Anisolabidae, 72
Anisopodidae, 178
Anisoptera, **57**
Anisozygoptera, 54, 57
Annulaphis, 113
Anthoboscinae, **135**, 136
Antonaphis, 113
Apachyinae, 74
Aphidoidea, 113, 115, 116
Aphrodini, 88
Aphroteniinae, **167**, 179
Apidae, **145**
Apocrita, **130**, 149
Araripechrysa, 9
Araripegryllus, 9
*_Araripogon_, **173**–176
Archaeobehningia, 39
Archijassidae, 115
Archisphex, **140**
Architendipedidae, **167**
*_Architettix_, **91**, 93, 94, 113, 115, 119
Architiphia, **135**, **136**
Architipulidae, 165
Archotermopsis, 77, 79
Asilidae, 9, 13, 172, **173**–176, 180
Asiloidea, 180
Asilomorpha, 174, 180
Atalophlebia, 43
Athericidae, 176, 177
Australiphemera, 34, **37**, 38, 39, 40, 42
Australurus, 21, 30
Austrogomphinae, 57, 62
Austroniidae, **149**

Baetidae, 22, 24, 29, 31, **47**
Baetiscidae, 47
Baetoidea, 24
Baissodidae, **140**
Baissoptera, 9, 154
Bathysmatophorini, 82, 85
Behningiidae, 21, 39, 46
Belostomatidae, 6, 8
Bernaea, 113
Bibionidae, **167**–169, 178
Bibioninae, **167**
Bibionoidea, 178
Bibionomorpha, 178
Blandicinae, 74
Blattodea, 8, 9, 10, 76
Blephariceridae, 169
Bolitophilinae, 178
Bombyliidae, **177**, 180
Bombylioidea, 180
Boreoscytidae, 82, **96**
Borinquena, 44
Brachycera, 181, 177
Brachylabinae, 73, 74

Caelifera, 9
Caenidae, 47
Caenoidea, 38
Caliphaea, 52
Calliphoridae, 181
Calopterygidae, 52, 54
Campylocia, 41
Canadaphis, 113
Canteronecta, 8
Carabidae, 8
Carcinophoridae, 72, 73
Carcinophorinae, 73, 74
Careospina, 44
Caririchrysa, 9
Carpododus, **108**, 110–112, 121
*Carpopodini, 106, **108**, 111, 113

Carsonus, 82
Cecidomyiidae, 178
Ceratopogonidae, 179
Cercopidium, 115
Cercopion,* **93, 95
Cercopionidae, 82, **93**
Cercopoidea, 82, 85, 91, **93**, 95, 113, 115
Chalybion, **147**
Chaoboridae, 179
Chelisochidae, 74
Chiliocyclidae, 115
Chironomidae, **167**
Chironomoidea, **166**–168, 179
Chlorocyphidae, 52
Chromarcyidae, 36
Chromarcyinae, 36, 45, 46
Chromarcys, 36, 45
Chrysidoidea, **147**
Chrysomelidae, 7
Chrysopidae, 9
Cicadellidae, 82, 83, **85**, 87, 93, 99, 113, 116
Cicadellinae, 83, **85**, 86
Cicadidae, 91, 116
Cicadoidea, **91**, 115
Cicadomorpha, 115, 116
Cicadoprosbole, 91
Cicadoprosbolidae, 82, **91**, 94, 115
Cimicomorpha, 6, 8
Cixiidae, 82, 96, **97**, 98, 99, 113, 115, 116
Cixius, 103, 111
Coccoidea, 113
Coenagrionidae, 52, 54
Coleoptera, 7, 8, 13
Coloburiscidae, 29, 32, 33, 45
Coloburiscinae, 21, 32, 35, 45
*Colocrurinae, **31**, 32–37, 45–47
Colocrus,* **31, 32–36, 45–47
*Cordulagomphinae, **58**, 62
Cordulagomphus,* **58
Cordulegastridae, 58, 62
Corduliinae, 59
Corixidae, 6
Cranopygia, 71
Cretabythus, **147**
Cretaceimelittommoides, 8
Cretatermes, 76, 77, 79
Cretatermitinae, 76, 79, 80
**Cretolabia,* 68, 72, 73, 74
Cretoneta, 21, 39
Cretophasma, 8
Cretophasmidae, 8
Cretosphex, **140**, 141, 143, 144, 149
Cronicus, 35
Culicoides, 179
Culicomorpha, 179
Curculionoidea, 7, 8, 13

Dastilbe, 13, 17
Delphacidae, 97, 98, 99
Delphacoides, 97
Delphax, 99
Derbidae, 97, 116
Dermaptera, 8, **69**
Dermapteron, 74
Deuterophlebiidae, 169
Dictyopharidae, 105, 113, 116
Dictyoptera, 74
Diplatyinae, 74
Diptera, 8
Disparocypha, 52
Dolichopodidae, 180
Dryinidae, 106, **147**
Dulcimanna, 21
Dysagrion, 52
Dysmorphoptiloidea, 115
Dytiscidae, 7, 8

Echinopsallus, 73
Echinosomatinae, 73, 74
Elassoneuria, 37
Electrococcus, 113
Ellinaphis, 113
Empididae, 180
Empidoidea, 180
Empis, 180
Endopterygota, 74
Ensifera, 9
Eoprotoneura,* **56
*Eoprotoneurinae, **56**
Epeoromimidae, 21, 30, 32, 33
Epeoromimus, 21, 32, 33
Ephemera, 38, 39, 46
Ephemerellidae, 21, 47
Ephemeridae, **37**, 38–40, 42, 45–47
Ephemeroidea, 29, **38**, 39, 41–43, 45
Ephemeropsis, 27, 28
Ephemeroptera, 8, 9, 13
Ephialtitidae, **130**
Epigomphinae, 57, 62
Eremochaetidae, **174**, 180
Eremochaetoidea, 180
Esphaleminae, 74
Euarchistigma,* **52
*Euarchistigmatinae, **52**
Eudiptera, 165
Euthyplocia, 41
Euthyplociidae, 9, 38–41, 45–47
Euthyplociinae, 41
Evaniomorpha, **135**

Foliomimus, 32
Forficulidae, 74
Forficula, 71
Forficuloidea, 72, 73
Formicidae, 123, **139**, 140
Fulgoridiidae, 96, 115

Fulgoroidea, **96**, 97, 101, 103, 106, 108, 111, 113, 115, 116
Fulgoromorpha, 82, 115

Gasteruptiidae, **149**
Gerromorpha, 6
Geotiphia, **136**
Gomphaeschna, 63
Gomphaeschninae, 64
Gomphaeschnoides, **63**
Gomphidae, **57**, 58, 62
Gomphinae, 57
Gomphoidea, 57
Gonolabia, 71
Gonolabididae, 73
Govanogomphus, 57
Granulidae, 115
Gryllidae, 9
Gryllinae, 9, 11
Gryllospeculinae, 9

Hageniinae, 57, 58
Hagenulus, 44
Haglidae, 2
Hallex,* 86, **88, 89–92, 118, 119
Hallicini, 88
Heidea, 113
Hemimerina, 73
Hemiphlebia, 52
Hemiptera, 74
Heptageniidae, 32, **33**, 37, 45, 46
Heptagenioidea, 32, **33**, 35, 36, 45
Heteroptera, 6, 8, 13
Hexagenia, 39
Hexagenitidae, 21, **22**, 27, 29, 36, 46
Hexameropsis, 21, 27
Hodotermes, 80
Hodotermitidae, 76, 77, 79, 80
Hodotermitinae, 76, 77, 79, 80
Hodotermopsis, 79
Homoeneuria, 36
Homoptera, 8, 13
Hybotidae, 180
Hydradephaga, 8
Hylaeoneura, 91, 113
Hymenoptera, 8, **123**, 149, 150

Iassinae, 85
Ichneumonoidea, **149**
Ichneumonomorpha, **135**
Ichthybotus, 39, 40
Idiocerini, 115
Ilerdocossus, 115
Ipsviciidae, 115
Ipsvicioidea, 115
Ironomyiidae, 180
Isonychia, **27**, 35
Isonychiidae, 32, **33**, 45
Isoptera, 8, 74, 76
Isostictidae, 54

Jantardakhia, 113
Jascopidae, **82**, 83, 84, 85, 115
Jascopus, 113
Jassidae, 86
Jassus, 86
Juraphis, 113
Jurocallis, 113

Karataus, **130**, 131
Keroplatidae, **171**
Khatangaphis, 113
Kinnara, 103
Kinnaridae, 97, 99
*Kinnarocixiini, **103**
Kinnarocixius,* **103, 104, 105, 121, 122
Kisylia, 91

Labiduridae, 74
Labiidae, 73, 74
Labiinae, 74
Labioidea, 72, 74
*Lalacidae, 82, **98**
*Lalacinae, 105
*Lalacini, 105
Lalax,* 98, 105, **106, 107, 108, 112, 122
Larridae, **145**
Latiscutellidae, 8
Ledrinae, 85
Lepidoptera, 8
Leptophlebiidae, 21, 39, **43**, 44
Leptophlebioidea, 38, 45
Leptoprosbole, 91
Lestinae, 56
Lestoidea, 52, 57
Liadopsylla, 120
Liassocicada, 120
Liassogomphus, 57
Libellulidae, 58
Libelluloidea, 62
Limaia, 9
Limaiinae, 9
Limoniidae, 164, 178
Limoniinae, 164, 165
Lindeniinae, 57, 62
Liosphex, 138, **139**
Lisponema, **147**
Lithotiphia, **136**
Lygaeoidea, 8

Macrocerinae, **169**, 178
Macromia, 67
Macromiidae, **66**, 67
Mallophaga, 74
Mangas, **169**, 178
Mastotermitidae, 79, 80

Mecoptera, 8, 165
Meenoplidae, 97, 99
Megaleurodes,* 95, **96
Megalyridae, 135, **149**
Megapodagrionidae, 52, 54, 56
Meiatermes, 76–80
Membracidae, 116
Membracoidea, **82**, 113, 115
Mesephemeridae, 21
Mesephemeroidea, 21
Mesobaetis, 30
Mesodiphthera, 91, 115
Mesogenesia, 38, 39
Mesojassoides, 113
Mesojassula, 93, 115
Mesoneta, 21, 39
Mesonetinae, 21
Mesoplectopteridae, 21
Mesoplectopteron, 21
Mesoplocia, 38
Mesorhopalosoma, **136**, 138, 139
Mesosciophilidae, 178
Mesoserphidae, **133**, 149
Mesoserphinae, **135**
Microhodotermes, 80
Microphemera,* **39, 40, 42
Milichiidae, 181
Mogzonurella, 35, 45
Mogzonurus, 35, 45
Mongologenites, 21, 27
Montsecocossus, 115
Mundopoides, 113
Muscomorpha, 177, 181
Mycetobia, 169
Mycetophilidae, **169**, 178
Myerslopiinae, 86
Mymaridae, **149**
Mymarommatidae, **149**
Myrmeleontidae, 13
Myzinninae, **136**

Nannogomphus, 58
Naucoridae, 6, 8
Nemestrinidae, **177**
Neohagenulus, 44
Neopetaliidae, 58, 62
Neophemeridae, 38, 47
Nepomorpha, 8
Netutela, 113
Neuroptera, 8
Nitidulidae, 8
Notonectidae, 8
Nyssoninae, **140**

Octogomphinae, 57, 58, 62
Odonata, **51**, 8, 13
Oecanthinae, 9
Olgisca, 30
Oligoneuriidae, 9, 24, **31**–33, 35–37, 45, 46
Oligoneuriinae, 35, 36, 45
Oligoneurisca, 36
Onychogomphinae, 57, 62
Oreopteron, 58
Orthocladiinae, **167**, 179
Orthoptera, 8, 9, 11, 74
Oviparosiphum, 113
*Ovojassini, 86
Ovojassus,* **86, 88, 89, 118
Oxycorynidae, 8

Pachyneuridae, 167
Palaeoaphis, 113
Palaeobaetodes, 22, 24
Palaeoforda, 113
Palaeontinidae, 115
Palaeontinoidea, 115
Palingeniidae, 21, 38, 46
Palingeniinae, 38
*Paracarsonini, 82
Paracarsonus,* **82, 83, 84, 85, 118
Paraleptophlebia, 43
Paraprosbole, 91
Parasitica, **123**
Parisolabidinae, 73, 74
Parisolabis, 71
Passalidae, 8
Patulopes,* **106, 108, 109, 122
Peloridiomorpha, 6
Pemphredoninae, 140, **147**
Pentatomorpha, 6, 8
Perissommatidae, 179
Petalocephala, 83
Petropteron, 113
Phalacrocera, 164
Phasmatodea, 8, 73
Phoridae, 180
Phylloscelis, 101
Phyllogomphinae, 57, 62
Pincombeoidea, 115
Pipunculidae, 180
Pittoecus, **147**
Platycnemididae, 54
Platyjassites,* **83, 84, 85, 118
Platyjassus, 83
Platypezidae, 180
Platypezoidea, 180
Platystichtidae, 52, 54, 57
Plecia, **169**, 178
Plecoptera, 8, 73, 74
Polymitarcyidae, 38, 41
Polyplocia, 41
Pompilidae, **139**
Ponerinae, **140**
Porotermes, 77, 79
Porotermitinae, 76, 77, 79

Potamanthidae, 9, 38, 39, **42**, 46, 47
Potamanthus, 42
Praeaulacidae, **149**
Pricecoridae, 8
Pristiplocia, **40**, 41, 42, 46
Proameletus, 21, 30
Procercopidae, 115
Proctotrupidae, **132**
Proctotrupomorpha, 126
*Proerrhomini, 85
Proerrhomus,* **85, 86, 87, 118
Projagoria, 64
Promirara, 21
Prophalangopsidae, 2
Prosbolidae, 91
Prosopistomatidae, 47
Prosyntexis, **129**
Protabanidae, 177
Protelytroptera, 9
Protereismatoidea, 21
*Protodelphacinae, 99
*Protodelphacini, 99
Protodelphax,* **99, 100, 101, 120
Protodiplatys, 73, 74
Protoephemeroptera, 21
Protoligoneuria, 21, **22**, 23–28, 30, 47
Protoneuridae, 52, 54, **56**, 57
Protoprocto, **132**, 133
Protozygoptera, 52, 54, 57
Psestocixius,* **111, 112, 121
Pseudambria, 113
*Pseudomacromiidae, 64, 65, **66**
Pseudomacromia,* 64, 65, **66
Pseudostigmatidae, **52**, 54
Psilocephala, **174**
Psocoptera, 8
Psychodidae, 178
Psyllidae, 113
Psylloidea, 115, 116
Psyllomorpha, 115
Pterygota, 74
Pygidiocranidae, 72, 73, 74
Pygidiocraninae, 73, 74
Pygidiocranoidea, 72, 73
Pyragrinae, 73

Ranunculus, 13
Raphidioptera, 8, 9, 154
Reduviidae, 6, 8
Retinaphis, 113
Rhagionidae, 177, 179
Rhopalosoma, **138**, 139
Rhopalosomatidae, 9, 123, **136**, 138, 139
Ricaniites, 101, 115
Roproniidae, **133**

Saldidae, 6, 8
Scarabaeoidea, 8
Scarabaeidae, 7
Scarinae, 85
Scatopsoidea, 179
Scatopsidae, 179
Sceliphron, **146**
Schlueteromyia, 169
Sciadoceridae, **177**, 180
Sciaridae, 178
Sciaroidea, 170, **171**, 178
Sciophilinae, 178
Scolioidea, **140**
Scolobythidae, **147**
Scorpionida, 13
Semenoviola, 74
Senoprosopsis, **174**
Serpentivenidae, 115
Serphitidae, **149**
Shaposhinkovia, 113
Shuraboprosbole, 91
Siberiogenites, 27
Sieblosia, 52
Simuliidae, 179
Sinocercopis, 93
Siphgondwanus,* **28, 29, 30
Siphlonuridae, 9, 21, 22 24, 27, **28**, 29–32, 44
Siphlonurinae, 22, **28**, 31
Siphlonurus, 35
Siphlurites, 74
Siphonaptera, 9
Siricidae, 36
Sphecinae, 140, **145**, 146, 147
Sphecoidea, **140**
Sphex, 146
Spongiphoridae, 73
Stackelbergisca, 30
Stangeella, **147**
Staphylinidae, 7, 8
Stolotermes, 77, 79
Stolotermitinae, 77, 79
Stratiomyidae, 179
Stratiomyoidea, 179
Symphyta, 123, **129**, 149
Syntexinae, 123, **129**
Syntexis, **129**
Syntonopteridae, 21
Syrphidae, 180
Syrphoidea, 180

Tabanidae, 176
Tabanoidea, 174, 179
Tachydromiinae, 180
Tajmyraphis, 113
Tajmyrella, 113
Terebrantes, **149**
Termopsidae, 77
Termopsinae, 76, 77
Termopsis, 77, 79
Tettigarctidae, 91, 115

Tettigonioidea, 9, 11, 13
Thaumatoneura, 52
Therevidae, **176**, 178
Thraulodes, 44
Thysanoptera, 74
Tiphiidae, 9, **135**, 136
Tipulidae, **164**, 166, 178
Tipuloidea, 178
Tipulomorpha, **165**, 178
Traverina, 44
Trichoceridae, **166**, 178
Trichoptera, 8, 115
Tricorythidae, 47
Tridactylidae, 9, 11
Trigona, 145
Trigonalidae, **149**
Trigonopsis, 147
Turanopteron, 58
Turutanovia, 91
Ulmeriella, 79
Ulopinae, 85
Urogomphus, 64, 67

Valditermes, 76, 80
Vermileonidae, 174
Vitimosphex, **140**
Vulcanoia, 106, **111**, 113, 114, 121, 122

Wightonia,* **66
Wonnacottella, 115

Xestocephalus, 88
Xylomyidae, 177

Zootermopsis, 79
Zygoptera, **52**

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.