

CHAPTER 2. EPHEMEROPTERA

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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 *Siphogondwanus occidentalis*, new genus and species (Siphonuridae); alate forms of Siphonuridae (?) 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 Siphonuridae, Ephemeridae, and possibly Potamanthidae in Brazil indicate previous widespread distributions for these families (extant Neotropical ephemeroidea being of more recent north-temperate origin). The discovery of Hexagenitidae in the Southern Hemisphere indicates a widespread Pangaeian 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.

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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 Prottereismatoidea 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 Mesopleopteridae and Mesephemeridae continued into the Mesozoic.

Mesopleopteron (Mesopleopteridae) 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 ex-

tant taxa Behningiidae, Ephemerellidae, Coloburiscinae, Leptophlebiidae (Mesonetinae), Palingeniidae, and Siphonuridae. Of these extant groups, only Siphonuridae 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 Siphonuridae.

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* (Siphonuridae), *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 ad-

ditional 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 subimago 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

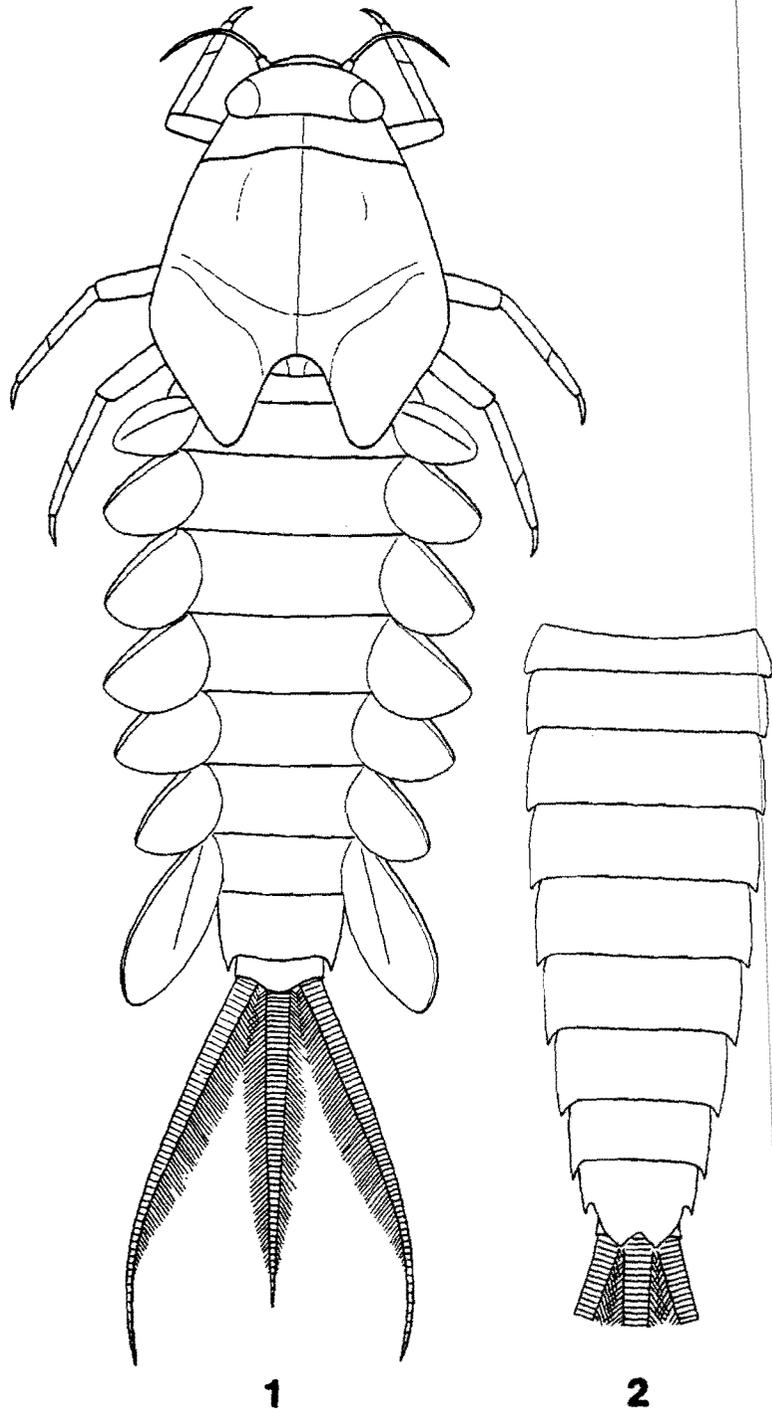
Baetidae (Siphonurinae), Costa Lima, 1950: 419.

Protoligoneuria limai Demoulin, 1955: 271.

Palaebaetodes 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 dorso-laterally; 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



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. $\frac{3}{4}$ 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 Siphonurinae (presently equivalent either to the family Siphonuridae or a complex of families including Siphonuridae). 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.

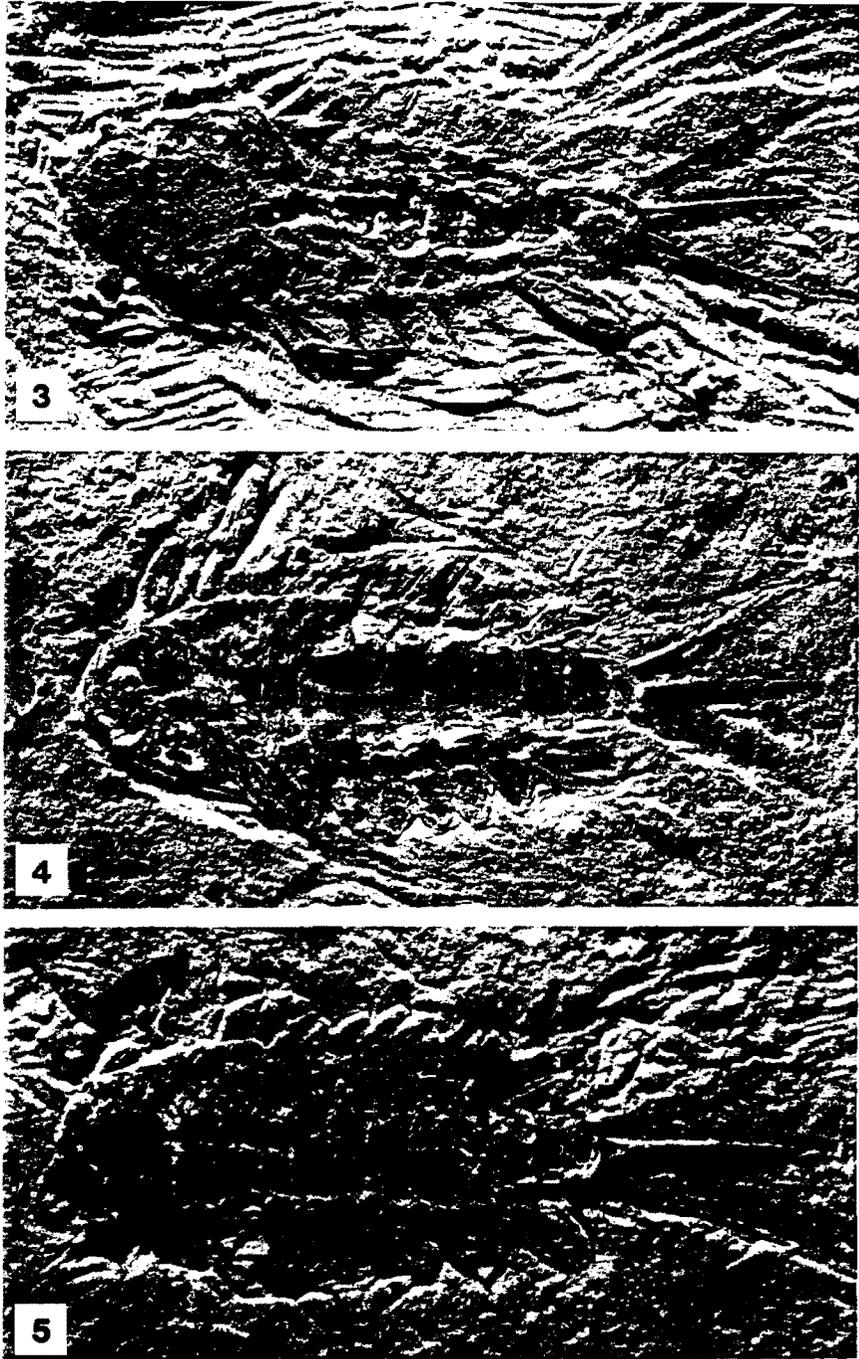
Demoulin (1955) subsequently proposed the new scientific name *Protoligoneuria limai* for these fossils based strictly on the description of Costa Lima (1950) and without designating types. Demoulin, believing Costa Lima's specimens to be members of the family Oligoneuriidae rather than Siphonuridae, devised his generic nomen to reflect this. This family reassignment was based entirely on the known distributions of the two families (siphonurids 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.

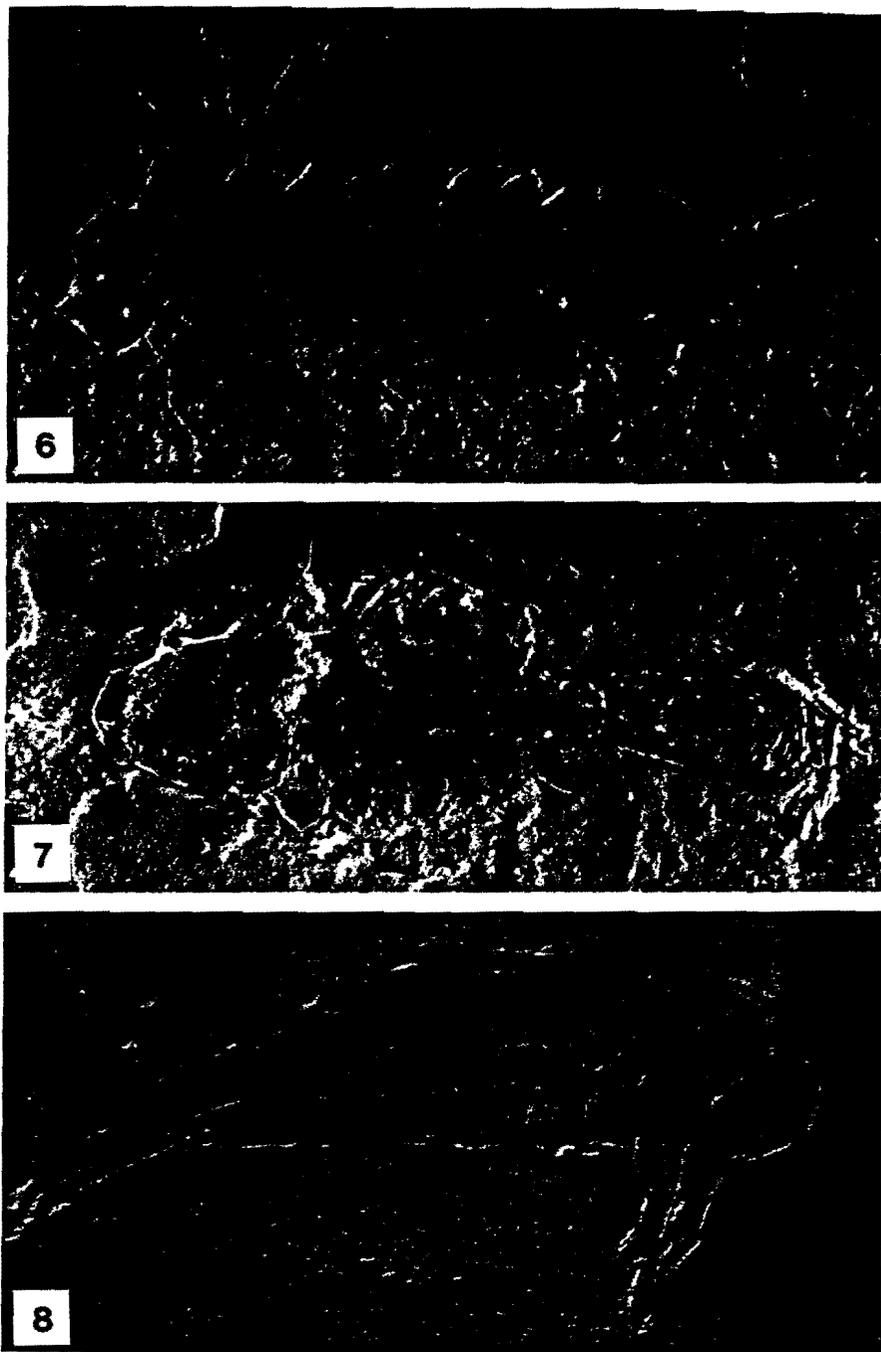
According to the International Code of Zoological Nomenclature [Art. 73b (i)], "Syntypes may include specimens . . . not seen by the author but which form the bases of previously published descriptions or illustrations upon which the author founded the new nominal species-group taxon. . . ." As such, 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 Siphonuridae or a complex of primitive families including Siphonuridae. 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.



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 Siphonuridae." 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 Siphonuridae, 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 Siphonuridae (in its broadest sense) is a "stem group" and that fossils are difficult to assign when they may belong to Siphonuridae 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 propor-

tionality. 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 Pangaeian 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 siphonurids 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-

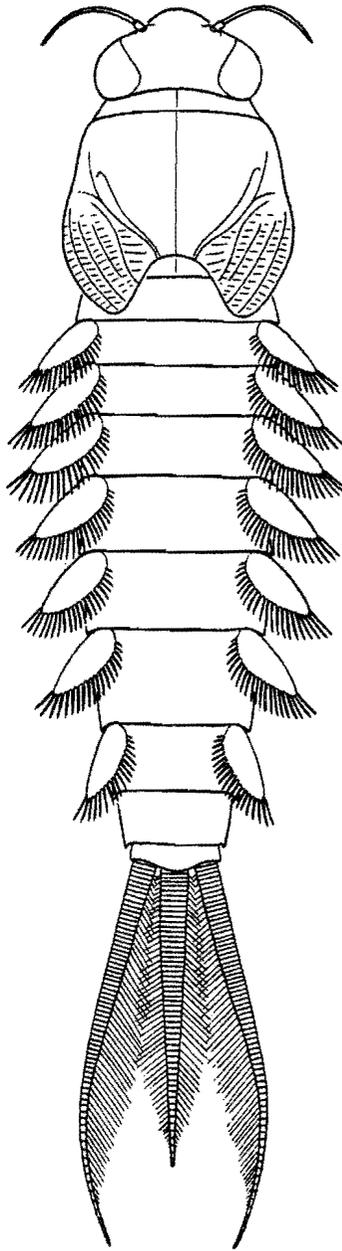


Fig. 9. *Siphondwanus occidentalis* larva, dorsal reconstruction without legs.

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 edge-waters 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 Siphonuridae 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 (?)

Siphondwanus occidentalis, new genus, new species

Figures 9, 10

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

ETYMOLOGY: *Siphondwanus* is a masculine gender nomen comprised of an arbitrary combination of letters alluding to a siphonurid from Gondwana. The specific epithet *occidentalis* is from the Latin, meaning western. Thus the names together refer to a siphonurid 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 *Siphondwanus occidentalis*.

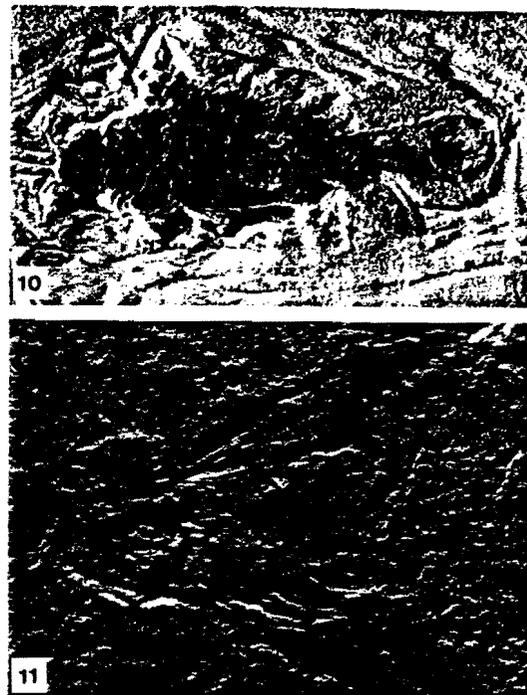
LARVA: Dorsal aspect with all legs and left abdominal gills missing, and mouthparts not discernible. Body minnowlike and 9.0 mm long. Head relatively small, broader than long but narrower than thorax, apparently hypognathous; antennae short, discernible portion very thin with length less than width of 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 Siphonuridae (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 Siphonuridae, 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 Siphonuridae in its broadest sense (e.g., McCafferty and Edmunds, 1979), the absence of synapomorphies in *Siphgondwanus* would additionally place it in the subfamily Siphonurinae. Characters that would allow more definitive subfamilial classification are, unfortunately, not represented on the fossil. It may be noted also that

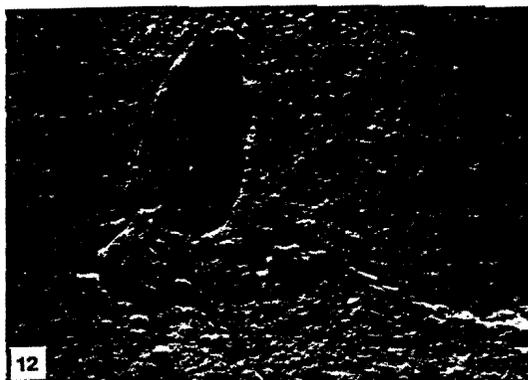


Figs. 10, 11. 10. *Siphgondwanus occidentalis* larva, dorsal habitus, AMNH 43404 (holotype). 11. Siphonuridae (?) sp. 1 alate stage, dorsal habitus, AMNH 44306.

the subfamilies of Siphonuridae are progressively becoming recognized at the family level by many Ephemeroptera workers, and such revision of rank status has become almost inevitable.

Little can be inferred about possible relationships with other siphonurid 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 siphonurid 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 Siphonuridae appear to be the Jurassic genera



Figs. 12, 13. Siphonuridae (?) 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 Siphonuridae, 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 siphonurids have been known mainly from the Northern Hemisphere, but also from Australia.

Extant Siphonuridae are not known from tropical South America, although three subfamilies are amphinotic. The presence of Siphonuridae 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 *Siphogondwanus*.

SIPHONURIDAE (?) 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; cross-venation well developed; Rs forked just basad of midlength of wing; MA fork in distal $\frac{1}{4}$ 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 siphonurid. 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.

SIPHONURIDAE (?) 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; cross-venation extensive; Rs forked in basal third; MA forked in distal $\frac{1}{4}$ 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 Siphonuridae but do not allow more than a preliminary classification.

SIPHONURIDAE (?) 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 MA₁, IMA, and MA₂ not discernible; MP₁ and IMP attached by crossvein near base, connection of MP₂ not discernible; CuA paralleling MP₂; 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 Siphonuridae (certain *Siphonurus*, e.g., have IMP and MP₂ attaching to MP₁ 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 Siphonuridae is tentative because the cubital region of the forewing is obscured.

FAMILY OLIGONEURIIDAE

SUBFAMILY COLOCRURINAE,

NEW SUBFAMILY

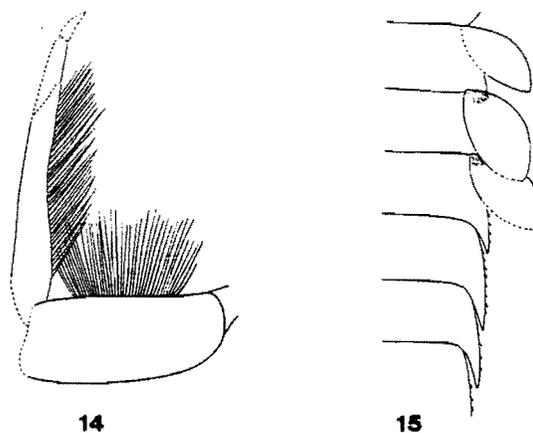
Colocrus indicum,

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 *indicum* is from the Latin *indicus*, meaning in-

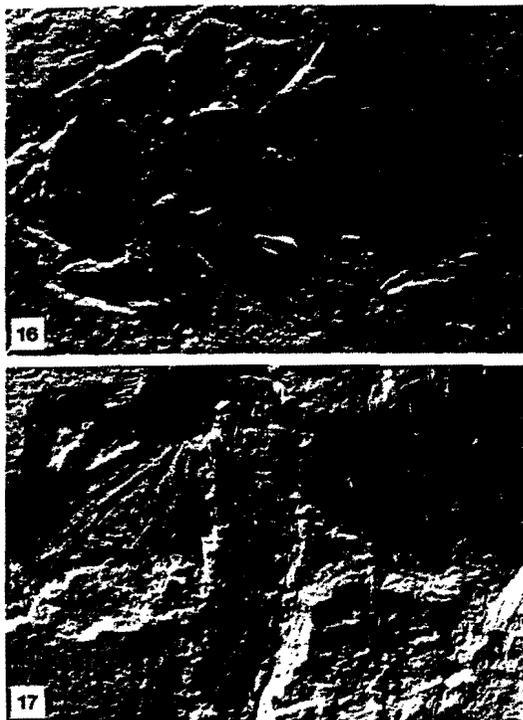


Figs. 14, 15. *Colocrus indicum* larva, dorsal aspect. 14. Left foreleg. 15. Right half of partial abdomen, with gills 1–3 present, gills 4–7 missing.

dicative. It alludes to the indication of phyletic relationships that this species provides with respect to the Oligoneuriidae.

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 indicum* 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. $\frac{1}{2}$ length of segment 5, 5 and 6 extended ca. $\frac{1}{2}$ 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. $\frac{1}{2}$ as wide as head. Forewing ca. 11.0 mm long, longitudinal veins

consisting of C, Sc, R₁, Rs (giving rise to at least R₂, ?R₃, and R₄₊₅), MA₁, MA₂, MP₁, IMP, MP₂, CuA₁, CuA₂, CuP, A₁, A₂, and A₃ (fig. 19); crossveins apparent only in costal region and distal R₁ and R₂ areas; Rs forked at ca. $\frac{1}{3}$ distance from base; other major forks near base; cubital region with one and possibly more intercalaries; R₄₊₅ and MA₁ running near each other; MA₂ and MP₁ geminating very near each other for entire length; MP₂ and CuA₁ forming close paralleling pair for entire length. CuP paralleling CuA basally and CuA₂ 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 siphonurid-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 Siphonuridae 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 Siphonuridae 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 siphonurine 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

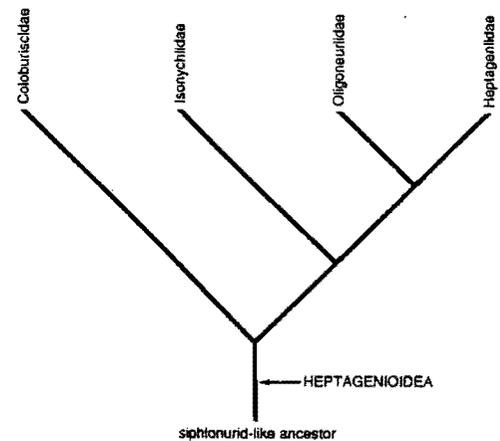
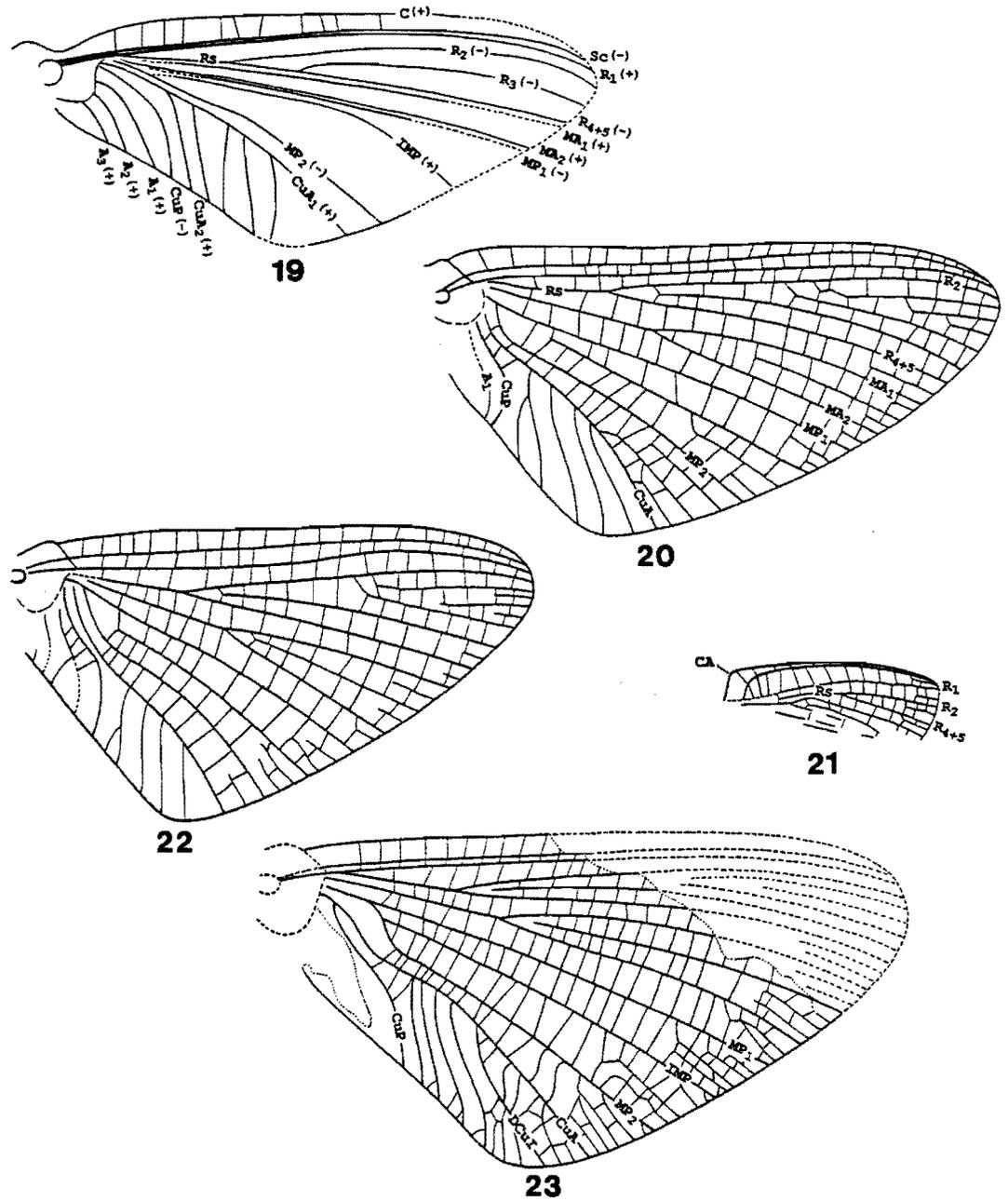


Fig. 18. Cladogram of the families of Heptagenioidea.

ancestral passive filtering capacity and associated foreleg characteristics and became highly depressed dorsoventrally and oriented to bottom feeding in streams.

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 indicivum*, 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 R_s , MA, and MP forked near the base, and R_{4+5} -MA₁, MA₂-CuA₁, and CuA₂-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 MA₁, MA₂ and MP₁, and MP₂ and CuA₁ (fig. 19). This pairing corresponds to those major geminated pairs in oligoneuriine wings (see e.g., Crass, 1947; Edmunds et al., 1976). Vein MA₁ (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 MA₁ and MA₂, MP₁ and IMP, and IMP and MP₂. 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 de-

rived 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), *Siphurites* 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 *Siphurites* 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

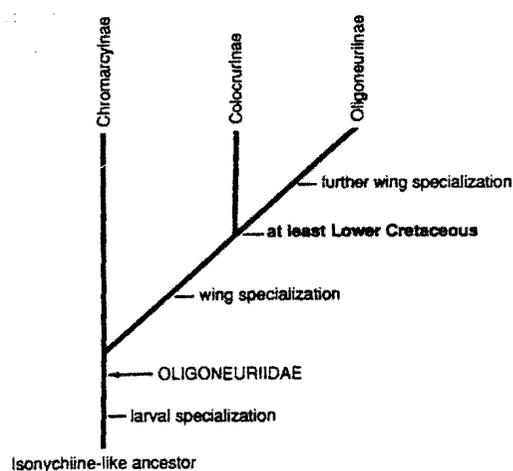


Fig. 24. Cladogram of the subfamilies of Oligoneuriidae.

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 Colocurinae 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 Colocurinae 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 Colocurinae 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 Siphonuridae 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 siphonurid-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 Pan-tropical. 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.

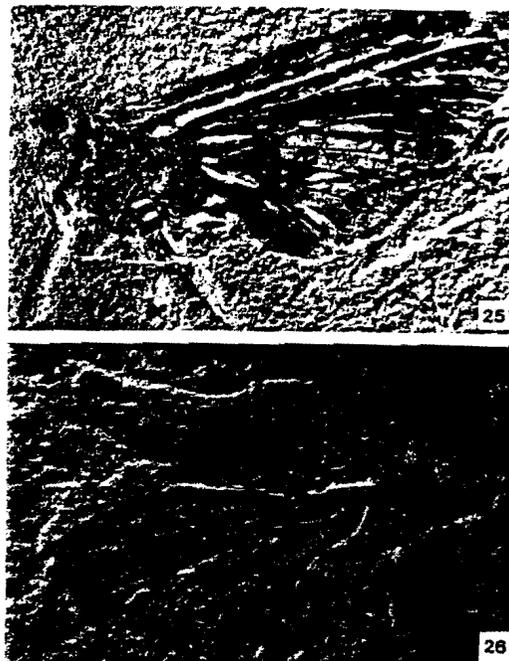
FAMILY EPHEMERIDAE

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 ephemeropterid from the Southern Hemisphere. The specific epithet *revelata* is from the Latin, meaning revelatory, an allusion 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 ephemeropterid forewing, and with MA



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

forked at midlength, a relatively distinct distal arch of CuP, A₁ nearly straight, and no cubital intercalaries; and a hindwing with a well-developed costal angulation, and Rs much shorter than R₂ and R₄₊₅.

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; MP₂ 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-

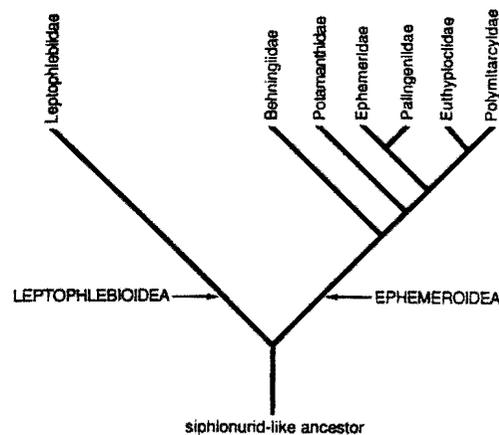


Fig. 27. Cladogram of Leptophlebioidea and Ephemeroidea.

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; crossveination moderately to well developed; basal attachment of R_1 apparently at wing base; R_s 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 crossveination of the forewings as well as the quadrate costal arch and short R_s 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), Polymitarciidae, 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 impor-

tant 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, R_s of the hindwing is shorter than R_2 and R_{4+5} (a plesiomorphic trait). A R_s 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 in-

dicating 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 ephemeroïd larvae. The larva described as *Archaeobehningia* (Behningiidae) from the Palearctic Upper Jurassic by Tshernova (1977) is not convincingly an ephemeroïd 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 Mesonetiinae 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 *Mesogenesis* is an ephemeroïd, 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 *Afro-mera* are represented in the Afrotropics by a few species, and, although the genus *Ichthybotus* occurs in New Zealand, ephemeroïds are absent from Australia. One may assume from the presence of *Australiphemera* and other ephemeroïds reported below from Brazil that some early stock was widespread (perhaps Pangaeon) 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 ephemeroïds 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 Polymitarciids, 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

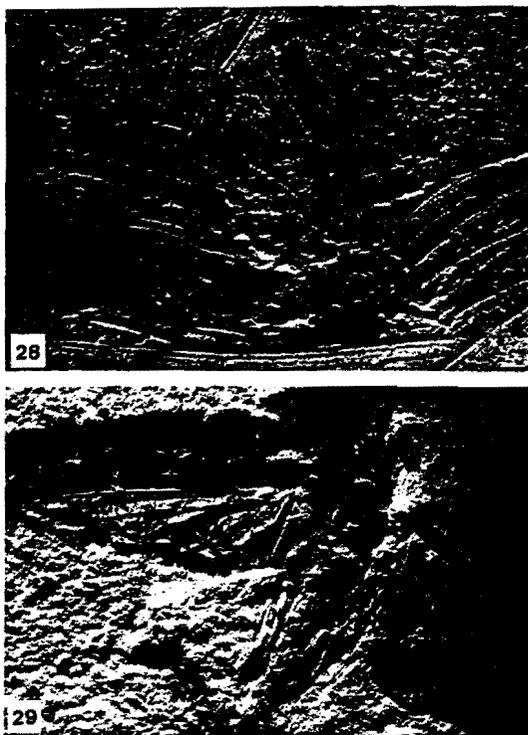
TYPE: Adult (sex?) 43301 (fig. 28).

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 ephemeroïd 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 A₁ 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. ¾ distance from wing base; MP₂



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 $\frac{1}{4}$ distance from base; MA fork in basal $\frac{1}{3}$ 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 *Polyploccia*). 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 Pan-tropical 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

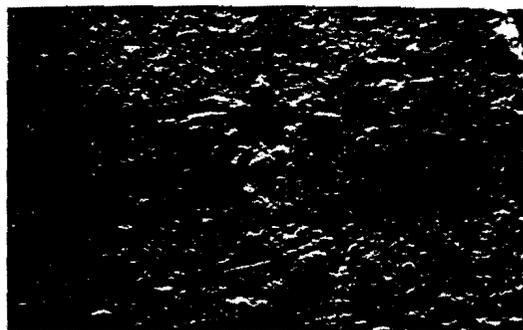


Fig. 30. Potamanthidae (?) sp. 1 alate stage, dorsal habitus, AMNH 44311.

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 cross-venation well developed; Sc visible for entire length; longitudinal veins not geminating; venation of radial triad not discernible; Rs forked in basal 1/4 of wing; MA forked slightly less than midlength of wing; MP₂ 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; A₁ apparently forked, with no veinlets.

DISCUSSION: This fossil is clearly an ephemeroidean as per *Australiphemera* and *Microphemera*, discussed above, but has general plesiomorphic wing venation found in both the Ephemeroidea and Potamanthidae. The placement to one or the other of these fam-

ilies is problematic. The anal area of the forewings is difficult to interpret. A₁ is evident and no veinlets can be seen. A second vein that is proximal and posterior to A₁ is nearly straight for its visible length, but is slightly curved in much the same manner as A₁. It could be interpreted as A₂, in which case an argument could be made for placing the fossil in the Ephemeroidea. 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 A₁. 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 A₁ anal veinlet of *Microphemera* bends in an opposite direction at its base and forms an abrupt angle with A₁ (fig. 22). The anal veinlet of *Microphemera* is thus typical of ephemeroidean attaching veinlets in this region and not like Potamanthidae, wherein the inner branch of A₁ follows a continuous line (no abrupt angles) with the stem of A₁, and the outer branch is most divergent from the line of the stem of A₁. The small laterally oriented eyes of the fossil, particularly if it is a male, would lend some support to the tentative potamanthid classification.

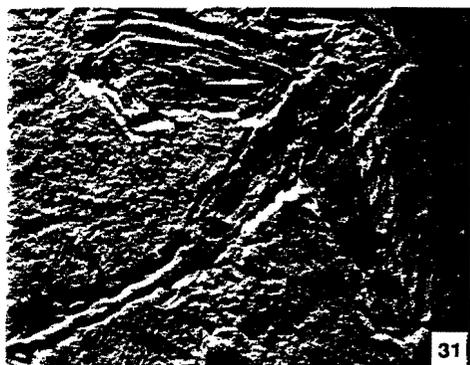
If this fossil is indeed a potamanthid, it would be the first fossil known of this family. The fossil from Baltic amber described as *Potamanthus priscus* was correctly shown to be a member of the Leptophlebiidae by Demoulin (1968). Extant Potamanthidae are restricted to the Holarctic and Oriental realms. 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; cross-venation 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; R_s forked at ca. $\frac{1}{4}$ 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 Siphonuridae, 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.

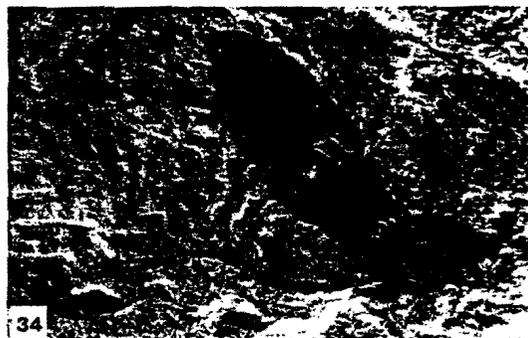
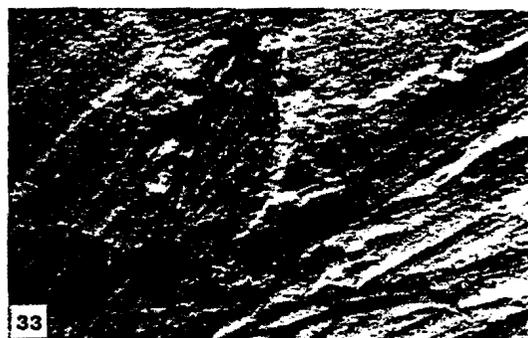
Leptophlebiidae (?) sp. 3

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. $\frac{1}{2}$ 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. $\frac{1}{4}$ 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, non-minnowlike 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 Siphonuridae. The family Oligoneuriidae, which is represented among the fossils studied, is shown to be phylogenetically 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, Colocurinae, and Chromarcyinae in the Oligoneuriidae. Although Colocurinae 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 siphonurid like ancestor, and siphonurid 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 tenta-

tive 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 Colocurinae 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 rep-

resented 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 Siphonuridae.

Although the family Siphonuridae (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 siphonurids 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 Colocurinae (Oligoneuriidae).

Of the higher taxa found to have existed or possibly existed in West Gondwana during the Lower Cretaceous, Hexagenitidae and Colocurinae are now extinct, and Siphonuridae 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 Quaternary 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 Colocurinae 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, Neophemeridae, 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 Siphonuridae, 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 siphonurid 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.

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