

Discovery and Analysis of the Oldest Mayflies (Insecta, Ephemeroptera) Known from Amber

by W.P. McCafferty

Department of Entomology, Purdue University, West Lafayette, IN (USA) 47907

ABSTRACT

Conovirilus poinari (McCafferty n. gen. et n. sp. (family Leptophlebiidae) and Baetidae sp. 1 are described from adult mayfly fossils taken in Lebanese amber from the Lower Cretaceous. These mayflies represent the oldest mayflies known from amber and are significant in that they also represent the oldest corroborated fossils of their respective families. Baetidae sp. 1 cannot be resolved beyond family (obvious from its tarsal formula) because of the condition of the fossil specimen; however, genitalia, leg and hindwing characterization available on the fossil of *C. poinari* allows the taxon to be placed to a relatively ancient and plesiotypic Southern Hemisphere clade of Atalophlebiinae genera that also includes *Adenophlebia*, and *Aprionyx* and the *Atalophlebioides* complex. The distribution and age of *Conovirilus* is consistent with that of the clade as can be deduced from phylogeny and extant distributions. The study exemplifies the predictive value of phylogeny and how it can be tested with paleontological data.

Keywords : fossil mayflies, Leptophlebiidae, Baetidae, Lebanese amber, *Conovirilus*.

RÉSUMÉ

Découverte et analyse des plus anciens Ephémères (Insecta, Ephemeroptera) connus dans l'Ambre.

Conovirilus poinari McCafferty n. gen. et n. sp. (famille Leptophlebiidae) et Baetidae sp. 1 sont décrits à partir d'éphémères adultes pris dans l'ambre Libanais, daté du Crétacé Inférieur. Ce matériel représente les plus anciens Ephéméroptères connus dans l'ambre; sa portée apparaît aussi dans le fait qu'il s'agit également des plus anciens fossiles confirmés dans leurs familles respectives. Baetidae sp. 1 ne peut être résolu au delà de la famille (évidente par la formule tarsale) en raison de l'état du spécimen. En revanche, la caractérisation possible des genitalia, pattes et ailes postérieures du spécimen de *C. poinari* autorise à placer ce taxon dans un clade, relativement ancien et plésiotypique de l'Hémisphère Sud, de genres d'Atalophlebiinae qui inclut aussi *Adenophlebia*, *Aprionyx* et le complexe *Atalophlebioides*. La répartition et l'âge de *Conovirilus* sont compatibles avec ceux du clade ainsi qu'on peut le déduire de la phylogénie et des répartitions existantes. Cette étude met en évidence la valeur prédictive de la phylogénie et la façon dont cette dernière peut être testée par les données paléontologiques.

Mots clés : éphémères fossiles, Leptophlebiidae, Baetidae, ambre du Liban, *Conovirilus*.

INTRODUCTION

Previous to this report, the known mayfly fauna from fossilized resins has consisted of 31 nominal species, representative of 22 genera and 12 families. All of the families except Australiphemeridae are extant, and 10 of the genera previously known from amber are also extant (see asterisked genera, below). Other than one family, three genera, and five species, this fauna has been described from Baltic amber, which dates to the Oligocene and Eocene epochs [25-60 million years ago (mya)] although some of the Baltic amber ori-

ginally ascribed to the Oligocene may actually be Eocene (Schlüter 1975). Baltic amber genera include **Baetis* Leach (Baetidae), *Baltameletus* Demoulin (Siphonuridae *s.l.*), *Balticophlebia* Demoulin (Ameletopsidae), *Blasturophlebia* Demoulin (?Leptophlebiidae), *Brevitibia* Demoulin (?Ametropodidae), **Choroterpes* Eaton (?Leptophlebiidae), **Cinygma* Eaton (Heptageniidae), *Cronicus* Eaton (Coloburiscidae), *Denina* McCafferty (Ephemeridae), *Electrogenia* Demoulin (Arthropleidae), **Heptagenia* Walsh (Heptageniidae), **Metretopus* Eaton (Metretopodidae),

**Paraleptophlebia* Lestage (Leptophlebiidae), **Rhithrogena* Eaton (Heptageniidae), **Siphonurus* Eaton (Siphonuridae), **Siphloplecton* Clemens (Metretopodidae), **Succinogenia* Demoulin (Heptageniidae), **Timpanoga* Needham (Ephemerellidae), and **Xenophlebia* Demoulin (?Siphonuridae *s.l.*).

Philolimnias sinica was described by HONG (1979) from Chinese amber dating to the Eocene (ca 50-60 mya). The single specimen upon which its description was based can ostensibly be assigned to the Ephemerellidae based on wing venation. However, it should be noted that other interpretations of its morphology (e.g., mouthparts and abdominal terminalia) are clearly not consistent with Ephemeroptera and are misrepresentations of more obscure portions of the fossil, as can be seen from a whole-specimen photograph. Species of *Cretoneta* Tshernova and *Paleoanthus* Kluge are known from Taymyr retinite (Siberian) from the Upper Cretaceous (ca 70-100 mya). Kluge (1993) removed *Cretoneta* from the family Leptophlebiidae and placed it in Siphonuridae *s.l.* (viz., Pisciforma), and he placed *Paleoanthus* in a new family Paleoanthidae (Ephemeroidea). From its characterization, however, *Paleoanthus* actually falls within the context of the previously known extinct family Australiphemeridae (see McCAFFERTY 1990). There may be some other mayflies from Upper Cretaceous Siberian resins not accounted for here.

One of the least represented time periods in geologic history with respect to mayflies is the Lower Cretaceous (ca 120-135 mya). As pointed out by McCAFFERTY (1900), this period is critical for assessing the biogeographic history of mayflies because it was prior to the final breakup of major landmasses. It is also critical for assessing the fate of the Mesozoic fauna and origin of the Cenozoic fauna because it was just prior to the major biotic extinctions that took place by the end of the Cretaceous. Previous to this report only 13 nominal species in 12 genera, representative of at least seven families, were known from the Lower Cretaceous. Exemplifying the transitional nature of this fauna is the fact that all of the known Lower Cretaceous genera had disappeared by the Cenozoic, but three of the seven families presently known from the Lower Cretaceous record are present today. Australiphemeridae, Epeoromimidae, Hexagenitidae, and Pristiplociidae did not survive to the Cenozoic, but Leptophlebiidae, Oligoneuriidae and Siphonuridae did. Among other families known from the Mesozoic (Jurassic but not yet Cretaceous) several did not continue to the Cenozoic, but Coloburiscidae, Behningiidae, and Ephemerellidae survived to the present. Some other extant families not yet confirmed from the Mesozoic record can be assumed to have been present by the Lower Cretaceous based on their hypothesized phylogenetic positions relative to families known from the fossil record.

In this report, I describe and analyze the first mayflies (one leptophlebiid and one baetid) taken from Lebanese amber. Lebanese amber dates from the Lower Cretaceous (120-135

mya) (SCHLEE and DIETRICH 1970). The new data are significant because of the dearth of paleontological information from this period as explained above, and because the leptophlebiid fossil is in good enough condition to allow it to be precisely placed in the generic phylogeny of Leptophlebiidae. Furthermore, the evolutionary data have important biogeographic ramifications, as will be shown below.

RESULTS

1. *Conovirilus* McCafferty n. gen. (fam. Leptophlebiidae) : description

Male adult

Compound eyes (Figs. 1-3) large, meeting on meson of head, dorsal three-fourths missing (Fig. 3).

Frons with apical margin not deeply scalloped, shaped as in Figure 3.

Forelegs and midlegs incomplete. Hindlegs (Figs. 1, 2) with 4-segmented tarsus (Fig. 4) ; claws (Fig. 5) similar, each apically hooked and with smaller opposing hook.

Forewing venation indeterminate. Hindwing costal margin (Fig. 6) convex, with apex of convexity located slightly beyond one-third distance from base ; venation indeterminate.

Ninth abdominal sternum (Fig. 7) not enlarged posteriorly and not cleft medially.

Genitalia (Figs. 1, 7) with forceps 3-segmented ; segment 1 elongate, slightly thickened at base ; segments 2 and 3 short, together approximately one-sixth length of segment 1. Penes fused and conical ; apices obscured by exudate (Fig. 7. pointers).

Cerci and median caudal filament broken (median caudal filament represented by broken truncate stub (not tapered and rudimentary).

Larva and egg stages : Unknown.

2. Type species

Conovirilus poinari McCafferty n. sp.

3. Generic etymology

The generic nomen (formed from a combination of the Latin words *conus* and *virilis*) is an allusion to the unusual cone shaped penes.

4. *Conovirilus poinari* McCafferty n. sp. : description

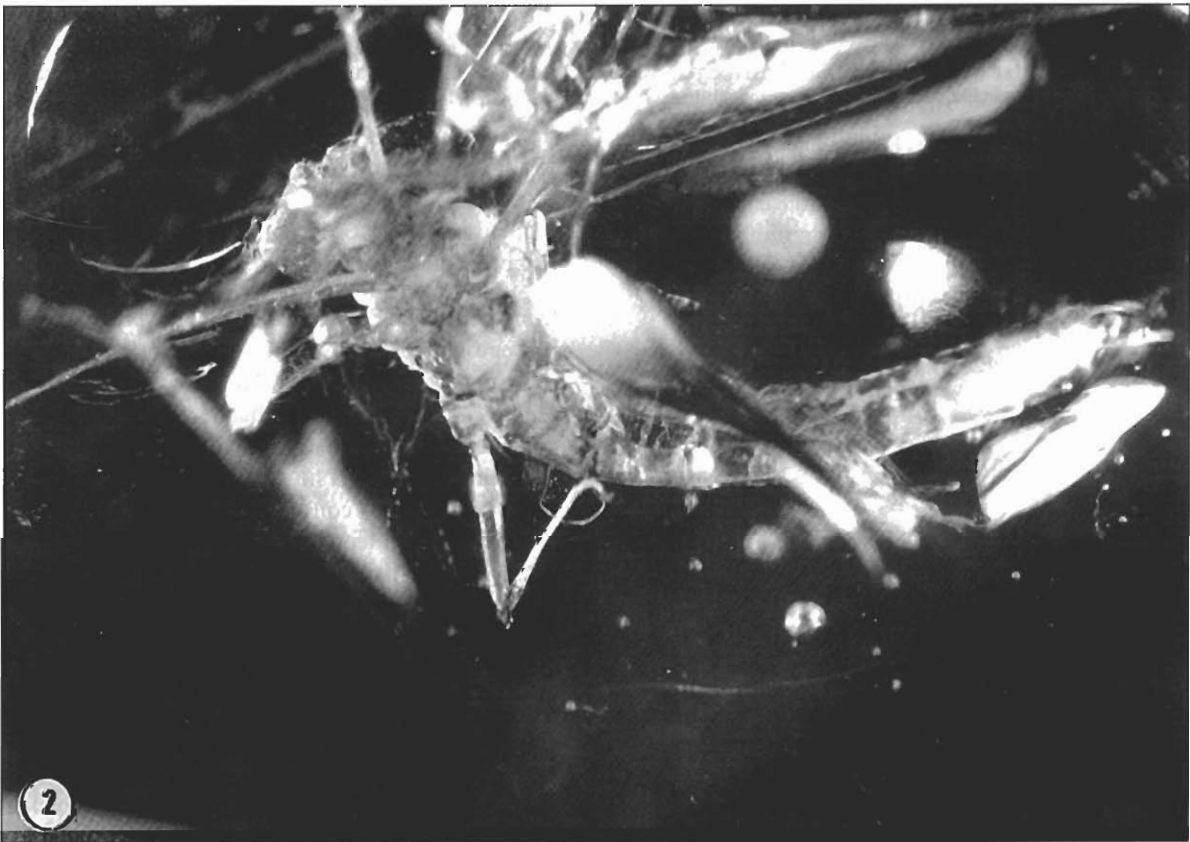
Male adult

Body (Figs. 1, 2) 4.3 mm long. Color patterns indeterminate, except where noted below.

Compound eyes 0.6 mm diameter at base.

Antennae 0.7 mm long.

Forelegs incomplete ; femur 0.75 mm long. Midlegs incomplete ; femur 0.75 mm long. Hindlegs with femur 0.75 mm, tibiae 0.65 mm long, tarsi 0.38 mm long.

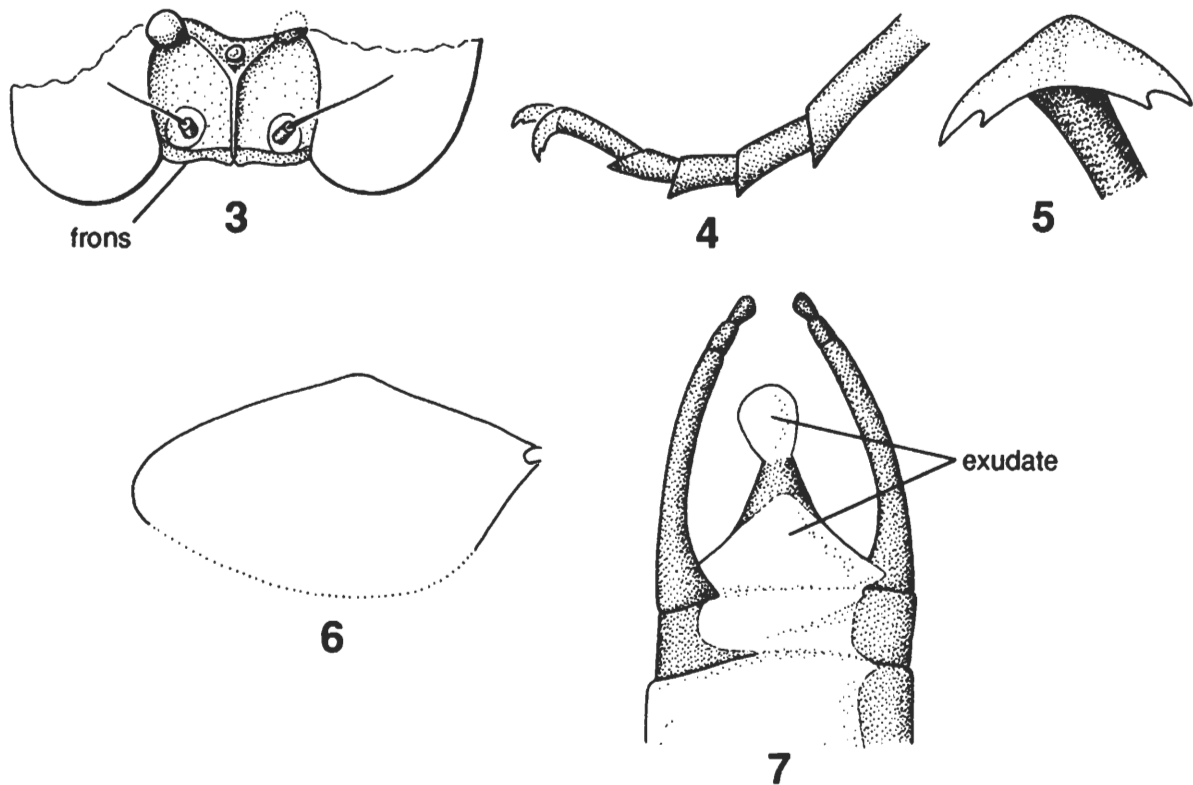


Figs. 1-2. *Conovirilus poinari* McCafferty, n. gen., n. sp.

Fig. 1 : Male adult (photographed in amber), dorsal view. Fig. 2 : Male adult (photographed in amber), ventral view.

Figs 1-2. *Conovirilus poinari* McCafferty, n. gen., n. sp.

Fig. 1 : Adulte mâle (photographié dans l'ambre), vue dorsale. Fig. 2 : Adulte mâle (photographié dans l'ambre), vue ventrale.



Figs 3-7. *Conovirilus poinari* McCafferty, n. gen., n. sp.

Fig. 3 : Frontal view of head (frons indicated). Fig. 4 : Hindleg tarsus. Fig. 5 : Tarsal claws (spread in amber). Fig. 6 : Outline of hindwing (dotted line presumed). Fig. 7 : Terminalia, ventral view (obscuring white exudate from specimen indicated).

Figs 3-7. *Conovirilus poinari* McCafferty, n. gen., n. sp.

Fig. 3 : Vue frontale de la tête (front indiqué). Fig. 4 : Tarse postérieur. Fig. 5 : Griffes tarsales (déployées dans l'ambre). Fig. 6 : Contour de l'aile postérieure (tracé en pointillés présumé). Fig. 7 : Terminalia, vue ventrale (écran formé par l'exsudat blanc du spécimen indiqué).

Mesonotum white (or bleached) (Fig. 1).

Genital forceps (Fig. 7) with apical segment rounded ; penes broad at base and narrow apically, approximately one-half length of forceps.

Cerci white (or bleached).

Larva and egg stages : Unknown.

5. Material examined

Holotype : Male adult, Lebanese amber. Deposited in the Milki Collection, American University of Beirut, Beirut, Lebanon.

6. Species etymology

The species is named after George Poinar (see Acknowledgements).

7. Discussion of *Conovirilus*

The two recent subfamilies of Leptophlebiidae (Leptophlebiinae and Atalophlebiinae) have not heretofore been known from earlier than the Eocene. Some unnamed fossils

from the Lower Cretaceous of Brazil were tentatively placed in Leptophlebiidae by McCafferty (1990) on the basis of forewing impressions. Two Mesozoic genera (*Cretoneta* and *Mesoneta* Brauer, Redtenbacher and Ganglbauer) were considered in an extinct subfamily (Mesonetinae) of Leptophlebiidae by Tshernova (1971). Although Hubbard and Savage (1981) considered the Mesonetinae to be clearly related to recent leptophlebiids, Kluge (1993) removed the two genera historically placed in Mesonetinae from Leptophlebiidae and considered them in Siphonuridae *s.l.*, but only distantly related to each other.

Known characteristics of *Conovirilus* indicate that the genus belongs to the Atalophlebiinae, thus providing direct evidence that the Atalophlebiinae had originated by the Lower Cretaceous. Hubbard and Savage (1981) indicated that the Leptophlebiinae and Atalophlebiinae had originated by 50 mya, and in fact probably occurred much earlier, but Kluge (1993) concluded that the oldest leptophlebiid was represented by Baltic amber *Paraleptophlebia*, which he considered a subgenus of *Leptophlebia* Westwood (Lepto-

phlebiinae). The discovery of *Conovirilus* from Lebanese amber now confirms the date of the origin of the family to be much earlier, and, in particular, the origin of Atalophlebiinae to be at least 120–135 mya. Biogeographic inference (see below) suggests the date of origin to be even earlier.

Unfortunately, the wing venation of *Conovirilus* is indeterminate. However, based on genitalic characteristics of *Conovirilus*, the genus appears to be more comparable to certain recent African Atalophlebiinae than to any fossil genera of Atalophlebiinae that are known from alate stages [see review of HUBBARD (1987)], in particular *Atalophlebia* Eaton (RIEK 1954). Among recent Eastern Hemisphere Leptophlebiidae (see PETERS and EDMUNDS 1964, 1970), *Conovirilus* shares the following characteristics with the southern African genus *Aprionyx* Barnard: similarly hooked tarsal claws making up each pair of claws, shape of the costal margin of the hindwing, juxtaposed compound eyes (some but not all *Aprionyx*), and fused penes without subapical spines. The shape and relative size of the genital forceps segments of *Conovirilus*, which may or may not be good indicators of relationship, are most similar to those of *Castanophlebia* Barnard, another genus indigenous to temperate South Africa.

The adult characteristics of the abdominal sternum 9 being neither enlarged nor cleft distally in the male, the lack of a distinctive costal process in the hindwing, and the fused penes found in *Conovirilus* place it in a grouping of genera including *Aprionyx*, *Adenophlebia* Eaton, and *Atalophlebioides* Phillips, according to the phylogram of PETERS and EDMUNDS (1970). The latter generic concept should now be considered a complex including also *Deleatidium* Eaton (TOWNS and PETERS 1978). Although the phyletic analysis of PETERS and EDMUNDS (1970) was not entirely cladistic (it was based in part on symplesiomorphies), there can be little doubt that the fused condition of the penes in Ephemeroptera, which generally retain the plesiotypic paired external genitalia, is a compelling synapomorphy. *Aprionyx* and *Adenophlebia* [diagrammed as the apotypic pair in the group by PETERS and EDMUNDS (1970)] occur in Africa, and the more basally derived *Atalophlebioides* complex is known from Australia, Chile, Madagascar, and New Zealand. On the basis of biogeographic inference alone—from the distribution of the *Atalophlebioides* complex—this clade would date to a time when West Gondwana and East Gondwana were connected, i.e., approximately 150 mya or earlier. The age of *Conovirilus* (120–135 mya) is consistent with this hypothesized age of the clade, and the continental distribution of *Conovirilus* is consistent with the distribution of the genera *Aprionyx* and *Adenophlebia*. Certainly, the plesiotypic position of the group as shown by Peters and Edmunds (1970) is also consistent.

This is a prime example of how data from paleontology and phyletic data from neontology can be complementary (McCAFFERTY 1991). In this case, the congruence of the data from separate evidentiary sources (paleontology and pa-

leogeography) clearly corroborates the phyletic deductions of PETERS and EDMUNDS (1970).

8. Baetidae sp. 1 : description

Female adult

Body 3.0 mm long

Forelegs 2.6 mm long ; femur 0.88 mm long ; tibia 0.63 mm long ; 4-segmented tarsus 0.76 mm long ; tarsi 4 segmented.

Midtarsi 3 segmented.

Hindleg 1.88 mm long ; femur 0.76 mm long ; tibia 0.68 mm long ; 3-segmented tarsus 0.38 mm long ; tarsi 3 segmented.

Wing venation indeterminate, hindwings present.

9. Material examined

One female adult from Lebanese amber. Deposited in the Milki Collection, American University of Beirut, Beirut, Lebanon.

10. Discussion of Baetidae sp. 1

The tarsal formula of four segments in the foretarsus and three each in the mid- and hindtarsus is indicative of the family Baetidae (LUGO-ORTIZ and McCAFFERTY 1996). Unfortunately, this fossil is not entire enough to allow assignment to any genus. The family Baetidae is very poorly known from the fossil record, previously consisting of two species from Baltic amber assigned to *Baetis* and one species from the Pliocene of Australia assigned to *Cloeon* Leach. Assignments to *Baetis* and *Cloeon* must be considered speculative in light of recent research on the systematic diversity of Baetidae (e.g., McCAFFERTY and WALTZ 1990). The original consideration of Jurassic genus *Mesobaetis* Brauer, Redtenbacher and Ganglbauer in the family Baetidae has been more appropriately considered in the Siphonuridae s. l. by SINITSHENKOVA (1985) and McCAFFERTY (1990). The new discovery of the family Baetidae from the Lower Cretaceous is significant because of the earlier historical date that can now be associated with the family.

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