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THE FOSSIL LEPTOPHLEBIIDAE (EPHEMEROPTERA): A SYSTEMATIC AND PHYLOGENETIC REVIEW

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ABSTRACT—The fossil mayflies which have been referred to the Leptophlebiidae are reviewed; their taxonomic characters are examined, and their systematic placement is discussed. The possible phylogenetic importance of the fossil data is examined. Ten genera and fifteen species are included in the review.

INTRODUCTION

IN the past decade or so, knowledge of fossil mayflies has increased substantially, with many new forms being described. This has been accompanied by considerable taxonomic rearrangement as new data are interpreted. There are a number of problems inherent in the study of fossils, not the least of which is the paucity of specimens. Many fossil mayfly taxa are based on fragmentary or incomplete specimens, and usually only one life history stage is known. Many characters usually involved in the taxonomy of extant mayflies are unclear or lacking in most fossils. Accordingly, systematic placement of fossil mayflies is often with the tacit understanding that few characters have been concerned in this placement, and that it is likely that as knowledge increases, the placement will have to be re-examined.

Unfortunately, there is a tendency among non-paleoentomologists to accept uncritically the placement of fossils assigned to a particular group. The purpose of this paper is to re-examine the fossil mayflies referred to the Leptophlebiidae in light of knowledge of the extant members of this family. Selected references are listed in the synonymy of each species.

SYSTEMATIC PALEONTOLOGY

Class INSECTA Linnaeus, 1758
Order EPHEMEROPTERA Hyatt & Arms, 1891
Family LEPTOPHLEBIIDAE Banks, 1900
Subfamily LEPTOPHLEBIINAE Banks, 1900
Genus PARALEPTOPHLEBIA Lestage, 1917
(Synonym OLIGOPHLEBIA Demoulin, 1965)
PARALEPTOPHLEBIA PRISCA (Pictet, 1856)

Potamanthus priscus PICTET. PICTET-BARABAN & HAGEN, 1856, p. 41, Pl. 6, fig. 3.

Leptophlebia prisca (Pictet). EATON, 1871, p. 37, 87.

Oligophlebia calliarcys DEMOULIN, 1965, p. 147, fig. 2; DEMOULIN, 1968a, p. 266, figs. 33a, b.

Oligophlebia? longiceps DEMOULIN, 1965, p. 147, fig. 3a.

Oligophlebia? sp. 1 DEMOULIN, 1965, p. 149, fig. 3b.

Oligophlebia? sp. 2 DEMOULIN, 1965, p. 149, fig. 4.

Paraleptophlebia prisca (Pictet). DEMOULIN, 1968a, p. 263, 275, figs. 30, 31, 32, 33c, d, 39; DEMOULIN, 1970, p. 9, figs. 7, 8, 9.

Potamanthus priscus was described by Pictet (Pictet-Baraban & Hagen, 1856) for males and females from Baltic amber. This species was placed in *Leptophlebia* by Eaton (1871) and then in *Paraleptophlebia* by Demoulin (1968a).

In 1965, Demoulin established the genus *Oligophlebia* for four species from Baltic amber, and later (1970) synonymized all of these species with *Paraleptophlebia prisca*.

Paraleptophlebia prisca has vein CuA recurved in the fore wings, characteristic of the Leptophlebiidae, 3-segmented forceps, and a divided styliger plate. Based on the figures and descriptions of this species, there is little doubt that if it were alive today it would be placed without hesitation by most mayfly workers in the genus *Paraleptophlebia*.

Subfamily ATALOPHLEBIINAE Peters, 1980
Genus ATALOPHLEBIA Eaton, 1881
ATALOPHLEBIA CULLENI (Etheridge & Olliff, 1890)

Ephemera culleni ETHERIDGE & OLLIFF, 1890, p. 8.

Atalophlebia culleni (Etheridge & Olliff). RIEK, 1954, p. 159, Pl. 10, figs. 1, 2, 3, 4, 5.

Originally described as *Ephemera culleni* by Etheridge & Olliff (1890), these Pliocene(?)

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nymphs from New South Wales were transferred to *Atalophlebia* by Riek (1954). The general habitus of the depressed nymph with widely flattened femora is distinctly *Atalophlebia*-like, and the discernible morphological characters agree with this diagnosis rather well. Unfortunately, the gills are wanting on all 7 known nymphs. Until further specimens are known, we regard placement in *Atalophlebia* as provisionally correct.

Genus XENOPHLEBIA Demoulin, 1968

XENOPHLEBIA AENIGMATICA Demoulin, 1968

Xenophlebia aenigmatica DEMOULIN, 1968a, p. 268, fig. 35; DEMOULIN, 1970, p. 6, fig. 6.

This species is known from a male imago from Baltic amber. The wings show some details of venation. The presence of symmetrically forked MA and MP, paired ICuA, and apparent costal projection of the hind wings and 3-segmented forceps seem to indicate that placement within the Leptophlebiidae is correct. A second specimen of a male subimaginal exuvia from Baltic amber (Demoulin, 1970) may belong to the same species, but adds little to our understanding of its systematic position.

Genus BLASTUROPHLEBIA Demoulin, 1968

BLASTUROPHLEBIA HIRSUTA Demoulin, 1968

Ephemeride oder Eintagsfliege BACHOFEN-ECHT, 1949, p. 74, fig. 64.

Blasturophlebia hirsuta DEMOULIN, 1968a, p. 270, fig. 36.

This genus is known from a single specimen, a male subimaginal exuvia from Baltic amber. Nothing is known of the wings or of the penes. The specimen shows dissimilar claws, and 3-segmented forceps with the first segment expanded basally. In the figure by Demoulin, the forelegs are shown with four tarsal segments, but appear to have a weak indentation indicative of a fifth segment. If there are only four segments in the male fore tarsi, this would remove *Blasturophlebia* from consideration as a member of the Leptophlebiidae as currently defined.

Subfamily MESONETINAE Tshernova, 1969

Genus CRETONETA Tshernova, 1971

CRETONETA ZHERICHINI Tshernova, 1971

Cretoneta zherichini TSHERNOVA, 1971, p. 614, figs. 1, 2, 3, 4; DEMOULIN, 1979, p. 2.

Cretoneta zherichini was described by Tshernova (1971) from the Upper Cretaceous of Siberia. Both male and female imagoes are known. The figures show a distinctly leptophlebiid wing, although the cubital field is much narrower than in Recent Leptophlebiidae. Based on the figures of the wings and male genitalia, there is little doubt that this genus is properly placed in the Leptophlebiidae, although Demoulin (1979) considers *Cretoneta* to be a siphlonurid precursor of the Leptophlebiidae.

Tshernova (1971) transferred the family Mesonetidae to a subfamily of the Leptophlebiidae and placed *Cretoneta* in it along with the Jurassic *Mesoneta*.

Genus MESONETA Brauer, Redtenbacher & Ganglbauer, 1889

MESONETA ANTIQUA Brauer, Redtenbacher & Ganglbauer, 1889

Mesoneta antiqua BRAUER, REDTENBACHER & GANGLBAUER, 1889, p. 4, Pl. 1, figs. 2a, 2b; TSHERNOVA, 1969, fig. 79; DEMOULIN, 1968b, p. 1; TSHERNOVA, 1969, p. 159, fig. 5; DEMOULIN, 1969, p. 1; SINITSHENKOVA, 1976, Pl. 6, fig. 5; DEMOULIN, 1979, p. 3.

MESONETA LATA Sinitshenkova, 1976

Mesoneta lata SINITSHENKOVA, 1976, p. 90, Pl. 6, fig. 4.

MESONETA UNDINA Sinitshenkova, 1976

Mesoneta undina SINITSHENKOVA, 1976, p. 90, Pl. 6, fig. 3.

The genus *Mesoneta* was established by Brauer, Redtenbacher & Ganglbauer (1889) for nymphs of *Mesoneta antiqua* from the Jurassic of the Baikal Region. Two additional species of *Mesoneta* were described by Sinitshenkova (1976) from the Lower Cretaceous of Eastern Transbaikal.

Mesoneta has been variously placed over the years, more recently in the Ametropodidae by Demoulin (1968b). In 1969, Tshernova created the family Mesonetidae for *M. antiqua,* but later (1971) she changed this family to a subfamily of the Leptophlebiidae, and included the genus *Cretoneta*.

Demoulin (1979) has recently removed the Mesonetinae to the Siphlonuridae, and removed *Cretoneta* from the subfamily.

The nymphs of *Mesoneta* were associated by Tshernova (1971) with the adults of *Cretoneta* in large part by the great similarity of

their male genitalia, which are also quite like those of some Recent *Leptophlebia*. If this somewhat tenuous association of the two genera within the Mesonetinae is correct, then *Mesoneta* must be considered to belong in the Leptophlebiidae as Tshernova has placed them. Until adults of *Mesoneta* or the nymphs of *Cretoneta* become known, this matter must remain unresolved.

Subfamily INCERTIS

Genus LEPISMOPHLEBIA Demoulin, 1968

LEPISMOPHLEBIA PLATYMERA (Scudder, 1890)

Lepisma platymera SCUDDER, 1890, p. 102, Pl. 12, fig. 18.

Mesobaetis platymera (Scudder). DEMOULIN, 1956, p. 263.

Lepismophlebia platymera (Scudder). DEMOULIN, 1968b, p. 7.

In 1890, Scudder described an arthropod from the Florissant Miocene which he considered a thysanuran, and named *Lepisma platymera*. Demoulin (1956) recognized this as a nymph of Ephemeroptera, and placed it in the genus *Mesobaetis,* which he at that time considered to belong in the Leptophlebiidae. When Demoulin later (1968b) removed *Mesobaetis* to the Baetidae, he established a new genus, *Lepismophlebia,* for this species which he left in the Leptophlebiidae.

From the description and figure of Scudder (1890), it is obvious that this specimen is indeed an ephemeropteran nymph, and the ovate femora, glabrous caudal filaments, and bi- or trifid gill lamellae agree well with the placement in the family Leptophlebiidae by Demoulin, although, without knowledge of the mouthparts, subfamilial placement is uncertain.

INCERTAE SEDIS

Genus CHOROTERPES Eaton, 1881

CHOROTERPES sp. Demoulin, 1968

Choroterpes sp. DEMOULIN, 1968a, p. 267, fig. 34.

A female subimaginal exuvia from Baltic amber was placed by Demoulin (1968a) in the genus *Choroterpes,* on the basis of the sole systematic character which he could find on the twisted specimen: the subanal plate. The shape of the subanal plate is quite consistent with placement in a number of other genera, some of them Leptophlebiidae. We see no reason to assign this specimen to *Choroterpes* and would even be reluctant to insist that it belongs in the Leptophlebiidae.

Genus MESOBAETIS Brauer, Redtenbacher & Ganglbauer, 1889

MESOBAETIS SIBIRICUS Brauer, Redtenbacher & Ganglbauer, 1889

Mesobaetis sibirica BRAUER, REDTENBACHER & GANGLBAUER, 1889, p. 5, Pl. 1, fig. 3; DEMOULIN, 1954, p. 326; TSHERNOVA, 1962, p. 62, fig. 76; DEMOULIN, 1968b, p. 5; TSHERNOVA, 1970, p. 126.

In 1954, Demoulin considered these Lower Jurassic nymphs from Irkutsk to belong in the Leptophlebiidae, an opinion concurred in by Rohdendorf (1957) and Tshernova (1962). However, Demoulin (1968b) later pointed out that the new figure given by Tshernova (1962) showed a great difference in the gills from what was thought to be the case from the description given by Brauer, Redtenbacher and Ganglbauer. Gills are apparently present only on abdominal segments II–VII (rare, but not unknown in the Leptophlebiidae), and are simple, and elliptical in shape. He removed this genus to the Baetidae. Tshernova (1970) considered this genus to be of uncertain taxonomic position. We agree that there is little reason to consider *Mesobaetis* to belong in the Leptophlebiidae.

PHYLOGENETIC INFERENCES

Representatives of both the subfamilies Atalophlebiinae and Leptophlebiinae are present in Baltic amber. Traditionally considered Oligocene in origin, Baltic amber is now thought by many authorities (Schlüter, 1975; N. D. Sinitshenkova, personal commun.) to date from the Eocene. This fossil data means that the separation of the two extant subfamilies of the Leptophlebiidae had definitely already occurred more than 50 m.y. B.P., and, in fact, probably occurred very much earlier. The subfamily Mesonetinae, clearly related to the Recent leptophlebiids, existed at least 130 m.y. B.P.

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