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PERMIAN MAYFLY Nymphs: NEW taxa AND SYSTEMATIC CHARACTERS

Michael D. Hubbard and Jarmila Kukalová-Peck
Laboratory of Aquatic Entomology
Florida A&M University
Tallahassee, Florida 32307 USA

ABSTRACT

Fossil insect nymphs with well-developed wings described as Ephemeroptera from the Lower Permian Period were later referred to the Archodonata. In view of the great amount of polygenetic information that these nymphs can yield, their taxonomic placement is important. We discuss the systematic characters available in these nymphs and their relationships with the Ephemeroptera and the Archodonata. We consider these nymphs to be true Ephemeroptera and transfer them all to the Protorheptomatoidea. One new family and one new genus are established and three new species are described.

INTRODUCTION

Six fossil insect nymphs described by Kukalová (1968) from Lower Permian beds in Moravia and Oklahoma were referred to the Ephemeroptera, five to the Protorheptomatoidea and one to a distinct but unnamed related family. The wing venation of most of these nymphs is remarkably well preserved and even the corrugations, or fluting, of the veins is discernable. Tracheal gills are present.

*Department of Geology, Carleton University, Ottawa, Ontario K1S 5B6 Canada
on abdominal segments I to IX and the nearly homonomous thoracic wing pads are attached to the thorax only along the articular area; they are independent of each other, bent, and project posteriorly at an oblique angle to the body. The mouthparts consist of large broad mandibles, with well-developed teeth. These nymphs could be of great importance in the study of mayfly evolution, and therefore, an understanding of their systematic position is crucial in evaluating the data which can be obtained from their study.

In a critical review of these nymphs, Demoulin (1970) removed them from the Ephemeroptera and considered them to belong in the order Archodonta. His argument that they are not Ephemeroptera depended primarily on the presence of segmented tarsi and double tarsal claws, and details of the wing venation, in particular a simple MA, separate R1 and R5, and the existence of a connecting vein between MP and CuA. He regarded this connecting vein between MP and CuA as a precursor of the capture of MP by CuA as described in the Permian archodont family Pseudmecistidae. Demoulin also takes into consideration the factor of the numerous small marginal forks of the longitudinal veins similar to those observed in adult archodontine wings.

However, to transfer these Permian nymphs from the order Ephemeroptera to any other pterygote order would necessitate the retention of two basic characters which are generally accepted as being uniquely ephemeropterans: the presence of 1) three caudal filaments, and 2) a well-developed "cortical brace". While the former character is pleiomorphic (primitive) and is shared with the most "primitive" insect order, the pterygote Archaeognatha, the costal brace may well be considered as one of the basic derivative (apomorph) characters of the order Ephemeroptera. The history of the costal brace is that of an ancient structure which became emphasized because of the involvement in a new special function. Morphologically, the brace is the convex anterior branch of the subcostal vein system that became engaged in the flight mechanics peculiar to the Ephemeroptera. It is presumed that the manner of flight is one of the basic agents, if not the basic agent.

* Appendages on the genital segments VIII and IX appear to be serial with the other tracheal gills. Recently, however, two pairs of gonopods complete with terminal double claws have been found in adult Pteronarcys by one of us (JMA). There is therefore, a certain possibility that the last pair, or last two pairs, of "tracheal gills" in the Paleozoic mayfly nymphs may belong to the gonopods protruding laterally from beneath the genital segments.
that triggered the early radiation of tana in the Paleozoic. While the more distant venation of the wing is often subject to convergence, the basal venation and the details of wing articulation are the most dependable and informative landmarks for discerning relationships at the higher taxonomic levels. Quite clearly, the presence of three caudal filaments and the costal brace within the Pterygota point to only one order: the Ephemeroptera.

Demoulin pointed out that the segmented tarsal and double tarsal claws of these Permian nymphs are not known to occur in any Recent mayfly nymphs. As is generally known, the embryonic, the juvenile, and the adult stages of the insects underrate different developmental pathways in the process of adapting to their special needs and conditions. Consequently, the more specialized, and the "younger" (in a phylogenetic sense) the stages are, the more liable they are to be mutually different. In the fossil record, the embryonic stage cannot be documented. However, there are certainly two distinctive, progressively diverging developmental lines, one for the juveniles and another for the adults, whenever both stages are found. In the Pterygota, the differences in morphology between juveniles and adults eventually become so deep that they have to be bridged by a metamorphic stage. In the Ephemeroptera, the origin of this metamorphic stage came only after the Paleozoic (Kukalová-Peck 1978). In the light of this fossil evidence, the difference in the leg morphology, viz., the presence of five tarsal segments and of double tarsal claws in the Permian nymphs, as well as the reduction to unsegmented tarsi and one claw in the modern mayfly nymphs is fully consistent with the other knowledge of the developmental process. It contributes evidence that the simple tarsi and single claw of the Recent mayfly nymphs are the derived and not the primitive condition. The reduction in tarsal segmentations and the presence of a single unga in modern mayflies is undoubtedly apomorphic characters derived from the primitive condition of double claws and segmented tarsi still manifested in the related Odonata, and are of more recent origin that the Permian Period.

RESIDUAL PRIMITIVE FEATURES IN LIVING MAYFLIES

It is often the case, in the insects, that the ancestral condition documented by the fossils are somewhere expressed, in a subtle and inconspicuous way, in at least some living members of the same phylogenetic lineages. The reconstruction of the Permian nymph no. 1 from Oklahoma (Naakulona americana demoulin; Fig. 1) shows three pairs of thoracic wings. The rudimentary prothoracic wings are still in existence in a few modern mayflies: they were first recognized by Ise (1936) in Polyphemus ornatus (Fabricius) and apparently also found in the nymph of Poliana americana Edmonds and Traver.
The movable meso- and metathoracic wing pads of these Permian mayfly nymphs testify that the wing appendages of the Ephemeroptera in the Paleozoic were narrowly attached and independently articulated (Kukalová-Peck, in prep.). In modern nymphs, however, the attachment is usually very broad along the whole tergum and the articulation is completely obliterated. Thus, the wing pads are fused with the tergum into one inseparable unit. This is not, however, always the case. For example, the nymph of Aulestria Edmunds has the wing pads narrowly attached, similar to those of the Paleozoic mayflies, and the only difference is that the articulation in the Recent mayflies is obliterated.

In regard to residual primitive features in the legs, while no known Recent mayfly nymphs possess 5-segmented tarsai and double tarsal claws, this is a common condition in the adults. Rudimentary tarsal segmentation is found in some nymphs of the modern Siphlo-
The venation of Permian mayfly nymphs

Demoulin argued that the Permian nymphs could not belong to the Ephemeroptera because of the differences in venation, namely the single MA, separate R₁ and R₂, and the presence of numerous small marginal forks. Recent mayflies have a forked MA, simple R₄₊, and few marginal forks. This argument cannot be valid on the ordinal level, because of the reasons discussed above. It could, however, be of importance on sub-ordinal levels.

The vein systems are derived from the blood lacunae and were primarily multiple-branched to supply blood to the alar appendages, long before it became the wing. They also provided the "tunnels" for the tracheae that grew into the richly tracheated alar appendage. Since the original function of the venation was not to support the aerofoil but to evenly distribute the blood, the primitive condition of the venation in all pterygote orders is always the (symmetrically) branched venation. This includes even such notoriously simple veins as the costa, the sub-costa and the radius I.

Some of the primitively dichotomously symmetrical branching was lost under the rigid requirements of flight mechanics (Rukalová-Peck 1978) soon after the Paleoptera and the Neoptera started using their alar appendages for forward movement. However, remnants of the primitively branched condition of all veins are scattered throughout the ancient Paleozoic pterygotes. This residual branching gives evidence as to the original state and is well known to paleoentomologists (see Carpenter 1966, Sharov 1966, Rukalová-Peck 1978, and Iceton 1976 for summaries). Therefore, since the appearance of Hettich's paper (1816) most paleoentomologists have insisted that the richer branching of any particular vein system is principally the more primitive condition. Also, the loss of one branch is usually considered to be a one-way evolutionary step. Under these premises it is unlikely that the simple MA in any paleoentogoe lineage would precede the primarily forked MA in their descendant. The Carboniferous Diplacobi Hamburgesch with its simple MA is most likely the representative of a blind evolutionary line (Carpenter 1963).

Clearly, the Permian nymphs described by Rukalová (1968) either had forked MA, or they probably do not belong to the Proteroisma- toidea.*

* It should be noted that several of the Permian nymphs are older nymphs, the venation of which is expected to be reasonably close to that of the adults.
The small branches along the posterior margin, on the other hand, do not seem to be of much phylogenetic importance in the Paleozoic insects, certainly not on higher than generic levels. The use of wing venation in taxonomy would be much easier if the wing membrane between the basic hemocoel-based venal systems was not capable of forming secondary connective veins, cross veins, braces, forks, and secondary branches. These last are sometimes formed along the creases of aerodynamic folds and flexion lines, like the well-known "spurious veins" of the Diptera, or, they may simply connect together two neighboring veins and simulate the capture of veins (Fig. 2, cr). Occasionally, these secondary vein "additions" are so inconspicuous that they blend perfectly with the primary venation. If this is the case, argument may arise and the phylogeny of a particular group might linger unsolved for decades. The fossil record is of invaluable help, because it brings direct evidence of the ancestral stage, and may solve the problem.

Figure 2. Adult Protoreptoptera Latum (hind wing). Concave veins dotted. Veinal bases striped. (After J. Kukalova-Peck, unpublished figure from study on the Paleozoic wing bases, in prep.).
The puzzle of the inconsistent venation patterns of the Permian nymphs clearly has two different phylogenetic levels: the supposedly simple MA and separate (i.e., branched) R₉ and R₁₀ concern the primary branching of the primitive vein system and reflect on the higher systematic categories such as superfamilies of the Recent Ephemeroids; the numerous small marginal branches, forks, and secondary veinslets are less important and apparently operate on the specific or, at most generic, levels. This dilemma raises one obvious question: was the venation of the Permian nymphs correctly identified by Kukalova in 1968? Regrettably, the answer must be that it was not.

The Oklahoma Permian nymph (Kukalovia cremacularis Demoulin) is superbly three-dimensionally preserved with the natural pigment intact. Compared to it, the Permian nymphs from Ebora are only flat and colorless imprints of the body structures and venation in the soft mud, while the chitin is completely dissolved. The venation of the freely articulated wing pads of K. cremacularis Kukalova 1968, Pl. 39, is darkly pigmented, distinct, and even fluted. However, the wing pads are damaged by the irregular splitting of the rock. The venation shown by Kukalova (1968, Fig. 2) is the composite of the obverse and the (unfigured) reverse. In spite of the fact that the venation on the photograph looks like that figured, we believe that the split of the rock and perhaps an indestructible slip within the wing membrane may have masked the true, typically proteresimatoïd venation.

The proteresimatoïd wing base and articulation of the nymphs and adults, in comparison with those of the modern "primitive" mayflies, have been studied lately by one of us (JEP) and a paper is currently in preparation. The wing base pattern of adult Proteresimat simus Jellon Sellaris (Fig. 2) and 25 related forms provides new aspects for a better understanding of the Permian nymphal venation and, perhaps, offers a solution to this problem.

As shown in Fig. 2, the radius in adult Proteresimatos starts as a common stem with R₁ and R₉. Soon, R₉ is visible adjacent to R₁, but running distinctly at a lower level. After R₉ diverges from R₁, it is met by MA which lies on top of it and completely covers R₉ for a short distance. After than, R₉ and MA separate and diverge as regular convex (MA) and concave (R₉) veins. The media also starts as a common and well-defined stem. MA separates inconspicuously; the portion between the stem of M and the point of its superimposition on R₉ is weak and is discernable only in some specimens. There is a strong auxiliary cross vein which parallels dis tally the weak portion of MA and apparently taken over the branching. The cubitus also starts as a common stem which is well-defined. CuA separates early and inconspicuously, and fuses laterally with the stem of M, leaving no trace of fusion. Like the initial portion of MA, CuA is also very weak and paralleled by an auxiliary cross vein which
acts as the mechanical brace. CuP carries a distinct bulla at the point where it is met by the anal brace. The anterior anal vein starts immediately from the basistyles, following the general trend of pterygote anal veins to form a fan-like pattern. It divided into two branches, \( A_2 \) and \( A_3 \), and its upwardly continuing branch \( A_{2,3} \) forms the structurally important structure called the anal brace which prevents the anal area of the wing from buckling. \( A_{1,2} \) and \( A_3 \) are branched and run parallel with CuP. The posterior anal vein (AP) has lost its basal stem and starts immediately as a group of branches. The number of AP branches seems to be variable on the specific level. There may be a special jugal vein independent of the anal and starting from an inconspicuous basijugal.

A detailed comparison of the wing bases of the nymphal *Kukalovia americana* (Fig. 3) and the adult *Proteresima lutum* (Fig. 2) shows a close similarity, probably at the family level. A major peculiarity of apparently all of the nymphal wings (not suspected when the wings were first described) is that MA seems to stay on top of Rs for a surprisingly long distance. This deviation from the adult pattern of all known mayflies, extinct or extant, is apparently due to the fact that the wings were simultaneously moving and bent backwards at a seemingly awkward angle. If the wing venation is reconstructed with this new interpretation of MA in mind, as is done here in Fig. 3, it becomes quite similar to the pattern of the adult Proteresimatoidea.

**SYSTEMATIC POSITION OF THE ARCHIODONATA**

The order Archodonata was established by Martynov (1932) to harbor dipterous Paleoptera with a primitive venation pattern, nine apparent abdominal segments, no prothoracic lobes, and a richly branched anal area. Nevertheless, as additional data on the group are added, it becomes more and more evident that the Archodonata are synonymous with the Palaeodictyoptera. The Archodonata have been found to have a prominent haustellate beak (Sharov 1971). This sucking beak, composed of mandibular stylets, maxillary stylets, and the hypopharynx, all resting on the trough of the labial ligula (MLP, unpublished), is one of the basic apomorphic characters of the palaeodictyopteroid orders: the Palaeodictyoptera, the Megasecoptera, and the Blanphonopterodea. It is of interest that these mouthparts are derived from the "mayfly pattern" as preserved in Recent mayfly nymphs and Paleozoic nymphs and adults. However, the elongation of the parts into stylets is very distinctive and no palaeodictyopteroid is known so far to carry the "regular" jaws. Apparently, the adaptation of the basic palaeopterous mouthparts (which resembled those of living mayfly nymphs) for sucking, happened very early. The sucking beak became very narrowly bound with the palaeodictyopterous flight mechanics and with typically palaeodictyopterous wing articulation. As shown by Kukalová-Peck (1974) the articulation is
quite distinctively different from the mayfly base. Therefore, either the beak, or the peculiar articulation, are decisive enough for the classification of a fossil. On the other hand, the wing venation by itself can be very misleading because the ephemeropteran "pattern" occurred repeatedly in different groups. Thus, Lithoneura Carpenter, which has often been considered a mayfly of a monotypic superfamily, is a Palaedicyoptera. The holotype of L. Jameseri Carpenter has been studied by one of us (JKP) and found to be strongly convergent in venation and in the body shape to mayflies. However, the head is palaedicyopteroid with long heavy antennae, bulging eyes, outlines of the swollen clypeus where the cibarial muscles were attached, and with small remnants of a beak; the prothorax carried a pair of large prothoracic winglets of the palaedicyopteroid type; and the sclerites at the base of the wings were single small specialized vein bases characteristic of the Palaedicyoptera. The Triassic Lithophlebia Hubbard and Riek (=Kosmophlebia Riek) also has wings with strikingly mayfly-like venation. They have been placed as a separate family. Since no
body is attached and the articulation is missing, there are few clues for a decision. However, one important apomorphic ephemeropteroid feature is missing in both Lithobates and Lithophanes - the coxal brace. Consequently, we think that the association of the Lithobatesidae with the Ephemeroptera is doubtful and that it has to be referred to the Megaleuroptera. One very important circumstance should be mentioned here: the recent discovery of a beautifully preserved wing of a member of the primitive Eupteroidae, an early odonatoid, from the Namurian (early Upper Carboniferous) of Argentina, the documentation of which one of us (JRF) was given the opportunity to study (courtesy of S.F. Rick). It becomes quite clear that the basic ephemeroid pattern is also at the base of the odonatoid venation. Indeed, there is a striking similarity and parallel between the Paleozoic mayfly wing (Fig. 2) and the Argentine Eupteroid. A paper discussing consequent changes in the odonatoid venational interpretation is in preparation by Rick.

Also of interest is the repeated tendency towards diptery which occurs both in the Ephemeroptera and in the Paleocaducipterygidae (Kukalova-Peck, 1969a, b, 1970). Unlike the neopterous Diptera, the switch to two-winged flight did not bring major changes in the flight-related morphological structures and in the flight pattern in the Paleocaducipterygidae. It is therefore doubtful whether the diptery of the Archolenata justifies the separation of this group into a separate order apart from the Paleocaducipterygidae.

TAXONOMY (see Table 1)

Nymph no. 1 of Kukalova (1999) was placed as the type-species, Kukalovia koreanensis, of a new genus, Kukalovia, by Demoulin (1970). Nymph no. 2 of Kukalova was described as Kukalovia noravun. Demoulin also referred nymphs nos. 3, 4, and 5 of Kukalova to this genus (as Kukalovia spp.). The family Kukaloviidae was established to contain this genus.

Nymph no. 6 of Kukalova was made the type-species, Jarvilleia elongata, of a new genus, Jarvilleia, by Demoulin, for which the family Jarvilleiidae was established. Demoulin suggested that all of these nymphs belonged to the Archolenata.

In light of the previous discussion, we refer all of these nymphs to the Ephemeroptera and place them in the superfamily Protereismatidae. Kukalovia is placed in the Protereismatidae as a monotypic genus containing only the type-species, Kukalovia koreanensis, and the family Kukaloviidae is synonymized with the Protereismatidae. The genus Kukalovia may prove to be synonymous with Protereismatidae when further specimens are available for study.

Kukalovia noravun is placed as the type-species of a new genus,
Table 1. Taxonomic changes in the Proteresimataidae.

Proteresimataidae Lanceere, 1917.
- Kukalovidae Demoulin, 1970. NEW SYNONYM.

Kukalovidae Demoulin, 1970.
Type-species: Kukalovia americana Demoulin. (original designation)

Kukalovia americana Demoulin.
Proteresima sp. (nymph no. 1) Kukalová, 1968:313, figs. 7, pl. 29.

Jarmilidae Demoulin, 1970. NEW FAMILY.

Jarmila Demoulin, 1970.
Type-species: Jarmila elongata Demoulin. (original designation)

Jarmila elongata Demoulin.
Epimeroptera Lac. (nymph. no. 5) Kukalová, 1968:320, fig. 7.

Oboriphielidae Hubbard & Kukalová-Peck. NEW FAMILY.

Oboriphielida Hubbard & Kukalová-Peck. NEW GENUS.
Type-species: Eukukalovia novarior Demoulin.

Oboriphielida novarior (Demoulin).
Proteresima sp. (nymph no. 2) Kukalová, 1968:216, fig. 3.

Oboriphielida tertia Hubbard & Kukalová-Peck. NEW SPECIES.
Proteresima sp. (nymph no. 3) Kukalová, 1968:318, fig. 4.
Kukalovia sp., larvae no. 3 Demoulin, 1970:7.

Oboriphielida quarta Hubbard & Kukalová-Peck. NEW SPECIES.
Proteresima sp. (nymph no. 4) Kukalová, 1968:318, fig. 5.
Kukalovia sp., larvae no. 4 Demoulin, 1970:7.

Oboriphielida quinta Hubbard & Kukalová-Peck. NEW SPECIES.
Proteresima sp. (nymph no. 5) Kukalová, 1968:318, fig. 6.
Kukalovia sp., larvae no. 5 Demoulin, 1970:7.
Gotherphlebia (named for Obora in Norway), for which the family
Gotherphlebiidae is established. Nymphs nos. 3, 4, and 5 of
Kukalova (1968) are named as new species in Gotherphlebia
(O. tertia, O. quartza, and O. quintia, respectively). The family
Gotherphlebiidae and its included genus, Gotherphlebia,
are distinguished from the
remainder of the Proterelemastideae by the combination of the
nymphal mesothorax slightly longer than the metathorax and
the divergent wing pads. The holotypes of the new species are the
specimens figured by Kukalova (1968).

The monobasic family Jarmilidae is also transferred to the
Proterelemastideae, bringing the total number of families in this
superfamily to five.

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RESUME
Des fossiles de nymphes d'insectes a allies bien developpees,
d'abord classées parmi les épénochrotères du bas Paléozoïque ont sub-
sequemment été rattachés aux archosomatidés. Étant donné la pro-
fusion de renseignements phylogénétiques que ces larves fournissent,
leur classement taxonomique est important. Nous parlerons donc de
leurs caractéristiques systématiques disponibles et des rapports
qui existent entre les épénochrotères et les archosomatidés. Nous
considérons ces nymphes comme des véritables épénochrotères et les
rattachons toutes aux protéolesmatidés, une nouvelle famille
et un genre nouveau sont reconnus dont trois nouvelles espèces
seront décrites.

ZUSAMMENFASSUNG
Fossil Insektennymphen mit gut entwickelten Flügeln, beschrie-
ben als Ephemeropteren der "Unteren Perm Periode", wurden später
zu den Archosomatiden gezählt. Im Hinblick auf die große Menge der
Phylogenetischen Information, die diese Nymphen liefern können, ist
eine taxonomische Einordnung von großer Bedeutung. In der verliehen-
den Arbeit erstreben wir die systematischen Merkmale, die bei diesen
Nymphem auftreten, sowie ihr Verhältnis zu den Ephemeroparten und
Archosomatiden. Wir halten die beschriebenen Nymphen für echte
Ephemeropteren und rechnen sie alle zu den Proterelemastiden. Eine
neue Familie und eine neue Gattung werden eingeführt, und drei neue
Arten dargestellt.
REFERENCES


PERMIAN MAYFLY NYMPHS 31