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PERMIAN MAYFLY NYMPHS: NEW TAXA AND SYSTEMATIC CHARACTERS

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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 phylogenetic 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 Prottereismatoidea. 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 Prottereismatoidea 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

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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 Archodonata. 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 R₄ 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 archodonate family Permothemistidae. Demoulin also takes into consideration the factor of the numerous small marginal forks of the longitudinal veins similar to those observed in adult archodonate wings.

However, to transfer these Permian nymphs from the order Ephemeroptera to any other pterygote order would necessitate the refutation of two basic characters which are generally accepted as being uniquely ephemeropteran: the presence of 1) three caudal filaments, and 2) a well developed "costal brace". While the former character is plesiomorphic (primitive) and is shared with the most "primitive" insect order, the apterygote Archaeognatha, the costal brace may well be considered as one of the basic derivative (apomorphic) 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 *Protoneisma* by one of us (JKP). 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 taxa in the Paleozoic. While the more distal 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 tarsi 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 Insecta undertake 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 unguis in modern mayfly nymphs are 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 than 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 somehow expressed, in a subtle and inconspicuous way, in at least some living members of the same phylogenetic lineage. The reconstruction of the Permian nymph no. 1 from Oklahoma (*Kukalova 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 Ide (1936) in *Ecdyonurus venosus* (Fabricius) and are apparently also found in the nymph of *Dolanía americana* Edmunds and Traver.

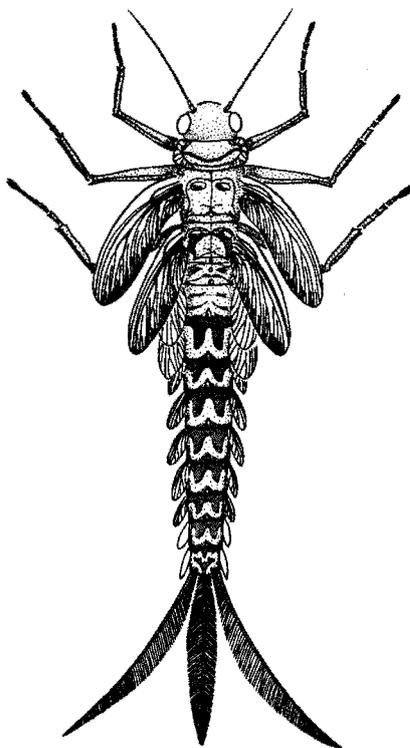


Figure 1. Nymph of *Kukulova americana*.

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 (Kulaková-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 *Analetris* 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 tarsi and double tarsal claws, this is a common condition in the adults. Rudimentary tarsal segmentation is found in some nymphs of the modern Siphlo-

nuridae (Edmunds 1972). The large mandibles of the Permian Oklahoma nymph are reminiscent of the mouthparts of some modern generalist feeders.

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 simple MA, separate R_4 and R_5 , and the presence of numerous small marginal forks (Recent mayflies have a forked MA, simple R_{4+5} , 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 primitively multiple-branched to supply blood to the alar appendage, 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 (Kukalová-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, Kukalová-Peck 1978, and Wootton 1976 for summaries). Therefore, since the appearance of Redtenbacher's paper (1886) 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 paleopterous lineage would precede the primarily forked MA in their descendants. The Carboniferous *Triplosoba* Handlirsch with its simple MA is most likely the representative of a blind evolutionary line (Carpenter 1963). Clearly, the Permian nymphs described by Kukalová (1968) either had forked MA, or they probably do not belong to the Protereisma-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 veinal systems was not capable of forming secondary connective veins, cross veins, braces, forks, and secondary branches. These last are sometimes formed along the crests of aerodynamic folds and flexion lines, like the well-known "spurious vein" 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.

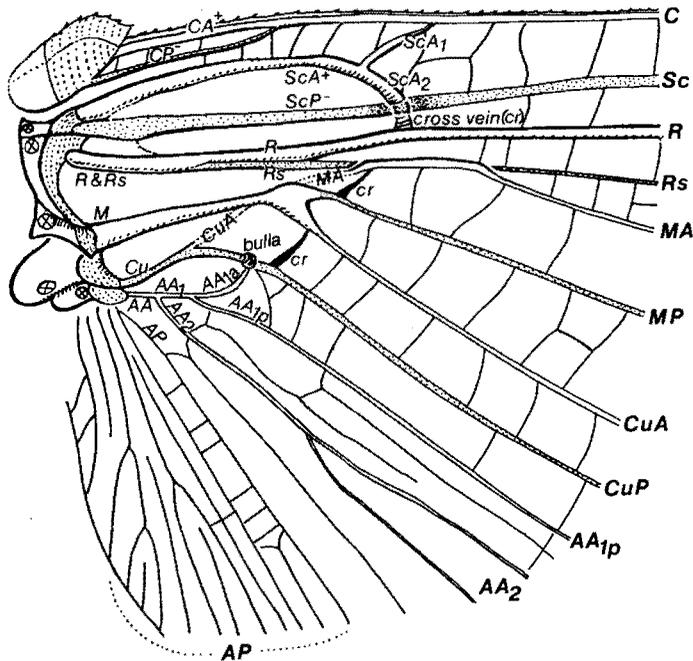


Figure 2. Adult *Prottereisma latum* (hind wing). Concave veins dotted. Veinal bases striped. (After J. Kukalová-Peck, unpublished figure from study on the Paleozoic wing bases, in prep.).

The puzzle of the inconsistent venation pattern of the Permian nymphs clearly has two different phylogenetic levels: the supposedly simple MA and separate (i.e., branched) R_4 and R_5 concern the primary branching of the primitive vein systems and reflect on the higher systematic categories such as superfamilies of the Recent Ephemeroptera; the numerous small marginal branches, forks, and secondary veinlets 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 (*Kukalova americana* Demoulin) is superbly three-dimensionally preserved with the natural pigment intact. Compared to it, the Permian nymphs from Obora 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. americana* Kukalova 1968, Pl. 29), 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 undetectable slip within the wing membrane may have masked the true, typically prottereismatoid venation.

The prottereismatoid 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 (JKP) and a paper is currently in preparation. The wing base pattern of adult *Prottereisma latum* Sellards (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 *Prottereisma* starts as a common stem with R and R_s . Soon, R_s is visible adjacent to R, but running distinctly at a lower level. After R_s diverges from R, it is met by MA which lies on top of it and completely covers R_s for a short distance. After that, R_s and MA separate and diverge as regular convex (MA) and concave (R_s) 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 R_s is weak and is discernable only in some specimens. There is a strong auxiliary cross vein which parallels distally the weak portion of MA and apparently takes over the bracing. 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 basianale, following the general trend of pterygote anal veins to form a fan-line pattern. It divided into two branches, AA₁ and AA₂, AA₁ and its upwardly continuing branch AA_{1a} form the mechanically important structure called the anal brace which prevents the anal area of the wing from buckling. AA_{1b} and AA₂ 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 anals and starting from an inconspicuous basijugale.

A detailed comparison of the wing bases of the nymphal *Kukalova americana* (Fig. 3) and the adult *Protereisma latum* (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 *Protereisma-toidea*.

SYSTEMATIC POSITION OF THE ARCHODONATA

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 (JKP, unpublished), is one of the basic apomorphic characters of the palaeodictyopteroid orders: the Palaeodictyoptera, the Megasecoptera, and the Diaphanopteroidea. 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 paleopterous 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

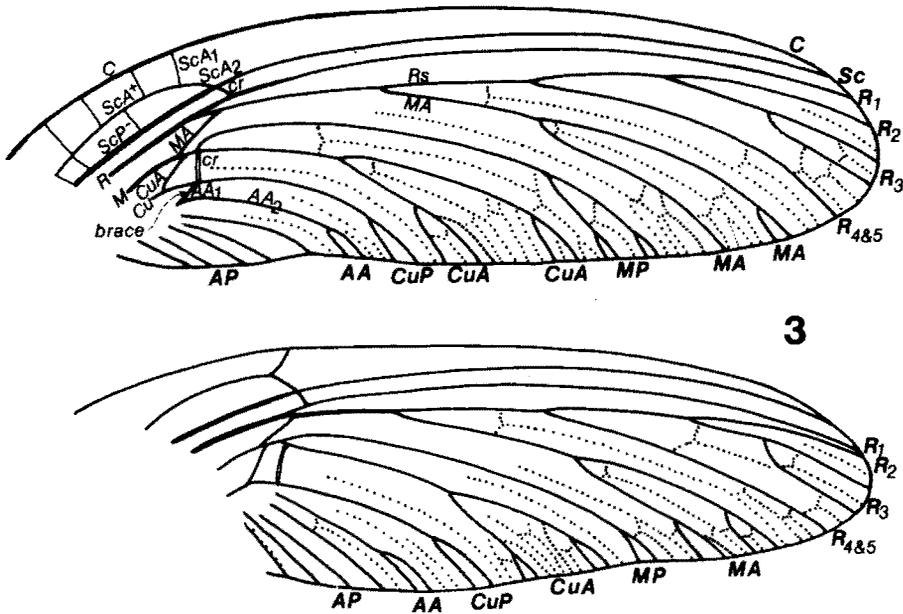


Figure 3. Fore and hind wings of nymph of *Kukulova americana*.

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 Palaeodictyoptera. The holotype of *L. lameerei* 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 palaeodictyopteroid 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 palaeodictyopteroid type; and the sclerites at the base of the wings were simple small specialized veinal bases characteristic of the Palaeodictyoptera. The Triassic *Litophlebia* Hubbard and Riek (= *Xenophlebia* 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 *Lithoneura* and *Litophlebia* - the costal brace. Consequently, we think that the association of the Litophlebiidae with the Ephemeroptera is doubtful and that it has to be referred to the Megasecoptera. One very important circumstance should be mentioned here: the recent discovery of a beautifully preserved wing of a member of the primitive Erasipteridae, an early odonatoid, from the Namurian (early Upper Carboniferous) of Argentina, the documentation of which one of us (JKP) was given the opportunity to study (courtesy of E.F. Riek). 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 Erasipterid. A paper discussing consequent changes in the odonatoid venational interpretation is in preparation by Riek.

Also of interest is the repeated tendency towards diptery which occurs both in the Ephemeroptera and in the Palaeodictyoptera (Kukalová-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 Paleoptera. It is therefore doubtful whether the diptery of the Archodonata justifies the separation of this group into a separate order apart from the Palaeodictyoptera.

TAXONOMY (see Table 1)

Nymph no. 1 of Kukalova (1968) was placed as the type-species, *Kukalova americana*, of a new genus, *Kukalova*, by Demoulin (1970). Nymph no. 2 of Kukalova was described as *Kukalova moravica*. Demoulin also referred nymphs nos. 3, 4, and 5 of Kukalova to this genus (as *Kukalova* spp.). The family Kukalovidae was established to contain this genus.

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

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

Kukalova moravica is placed as the type-species of a new genus,

Table 1. Taxonomic changes in the Protereismatoidea.

Protereismatidae Lameere, 1917.

= Kukulovidae Demoulin, 1970. NEW SYNONYMY.

Kukulova Demoulin, 1970.

Type-species: *Kukulova americana* Demoulin. (original designation)

Kukulova americana Demoulin.

Protereisma sp. (nymph no. 1) Kukulová, 1968:313,
figs. 1, 2, pl. 29.

Kukulova americana Demoulin, 1970:6.

Jarmilidae Demoulin, 1970. NEW PLACEMENT.

Jarmila Demoulin, 1970.

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

Jarmila elongata Demoulin.

Ephemeroptera inc. fam. (nymph no. 6) Kukulová, 1968:320,
fig. 7.

Jarmila elongata Demoulin, 1970:7.

Oboriphlebiidae Hubbard & Kukulová-Peck. NEW FAMILY.

Oboriphlebia Hubbard & Kukulová-Peck. NEW GENUS.

Type-species: *Kukulova moravica* Demoulin.

Oboriphlebia moravica (Demoulin).

Protereisma sp. (nymph no. 2) Kukulová, 1968:316, fig. 3.

Kukulova moravica Demoulin, 1970:6.

Oboriphlebia tertia Hubbard & Kukulová-Peck. NEW SPECIES.

Protereisma sp. (nymph no. 3) Kukulová, 1968:318, fig. 4.

Kukulova sp., larve no. 3 Demoulin, 1970:7.

Oboriphlebia quarta Hubbard & Kukulová-Peck. NEW SPECIES.

Protereisma sp. (nymph no. 4) Kukulová, 1968:318, fig. 5.

Kukulova sp., larve no. 4 Demoulin, 1970:7.

Oboriphlebia quinta Hubbard & Kukulová-Peck. NEW SPECIES

Protereisma sp. (nymph no. 5) Kukulová, 1968:318, fig. 6.

Kukulova sp., larve no. 5 Demoulin, 1970:7.

Oboriphlebia (named for Obora in Moravia), for which the family Oboriphlebiidae is established. Nymphs nos. 3, 4, and 5 of Kukalova (1968) are named as new species in *Oboriphlebia* (*O. tertia*, *O. quarta*, and *O. quinta*, respectively). The family Oboriphlebiidae and its included genus, *Oboriphlebia*, can be distinguished from the remainder of the Protereismatoidea 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 Protereismatoidea, bringing the total number of families in this superfamily to five.

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RESUME

Des fossiles de nymphes d'insectes à ailes bien développées, d'abord classés parmi les éphéméroptères du bas Permien ont sub-séquemment été rattachés aux archodonates. Étant donné la profusion 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 éphéméroptères et les archodonates. Nous considérons ces nymphes comme de véritables éphéméroptères et les rattachons toutes aux protéreismatoïdes. Une nouvelle famille et un genre nouveau sont reconnus dont trois nouvelles espèces seront décrites.

ZUSSAMENFASSUNG

Fossil Insektennymphen mit gut entwickelten Flügeln, beschrieben als Ephemeropteren der "Unteren Perm Periode", wurden später zu den Archodonaten gezählt. Im Hinblick auf die große Menge der phylogenetischen Information, die diese Nymphen liefern können, ist ihre taxonomische Einordnung von großer Bedeutung. In der vorliegenden Arbeit erörtern wir die systematischen Merkmale, die bei diesen Nymphen auftreten, sowie ihr Verhältnis zu den Ephemeropteren und Archodonaten. Wir halten die beschriebenen Nymphen für echte Ephemeropteren und rechnen sie alle zu den Protereismatoiden. Eine neue Familie und eine neue Gattung werden eingeführt, und drei neue Arten dargestellt.

REFERENCES

- Carpenter, F.M. 1963. Studies on Carboniferous insects from Commentry, France: Part IV. The genus *Triplosoba*. *Psyche* 70: 120-128.
- Carpenter, F.M. 1966. The Lower Permian insects of Kansas. Part II. The orders Protorthoptera and Orthoptera. *Psyche* 73: 46-88.
- Demoulin, G. 1970. Remarques critiques sur des larves "Ephemero-morphes" du Permien. *Bull. Inst. R. Sci. Nat. Belg.* 46(3): 1-10.
- Edmunds, G.F., Jr. 1972. Biogeography and evolution of Ephemeroptera. *Ann. Rev. Entomol.* 17: 21-42.
- Ide, F.P. 1936. The significance of the outgrowths on the prothorax of *Ecdyomurus venosus* Fabr. (Ephemeroptera). *Can. Entomol.* 68: 234-238.
- Kukalová, J. 1968. Permian mayfly nymphs. *Psyche* 75: 310-327.
- Kukalová, J. 1969a. Revisional study of the order Palaeodictyoptera in the Upper Carboniferous shales of Commentry, France. Part I. *Psyche* 76: 163-215.
- Kukalová, J. 1969b. Revisional study of the order Palaeodictyoptera in the Upper Carboniferous shales of Commentry, France. Part II. *Psyche* 76: 439-486.
- Kukalová, J. 1970. Revisional study of the order Palaeodictyoptera in the Upper Carboniferous shales of Commentry, France. Part III. *Psyche* 77: 1-44.
- Kukalová-Peck, J. 1974. Pteralia of the Paleozoic insect orders Palaeodictyoptera, Megasecoptera, and Diaphanopteroidea (Paleoptera). *Psyche* 81: 416-430.
- Kukalová-Peck, J. 1978. Origin and evolution of insect wings and their relation to metamorphosis, as documented by the fossil record. *J. Morphol.* 156: 53-126.
- Martynov, A.V. 1932. New Permian Palaeoptera with the discussion of some problems of their evolution. *Trudy Paleozool. Inst. Acad. Sci. USSR* 1: 1-44.
- Redtenbacher, J. 1886. Vergleichende Studien über das Flügelgeäder der Insekten. *Ann. K.K. Natur. Hofmus* 1: 153-232.
- Sharov, A.G. 1966. Basic arthropodan stock with special reference to insects. Pergamon Press, Oxford.
- Sharov, A.G. 1971. Morfologicheskie osobennosti i obraz zhizni paleodiktiopter. *Dok. 24 Chteniya Pamyati N.A. Khalodkovskogo Akad. Nauk SSSR*: 49-63.
- Wootton, R.J. 1976. The fossil record and insect flight. *Symp. R. Entomol. Soc. Lond.* 7: 235-254.