

Ephemeroïd wing venation based upon new gigantic Carboniferous mayflies and basic morphology, phylogeny, and metamorphosis of pterygote insects (Insecta, Ephemera)

JARMILA KUKALOVÁ-PECK

Department of Geology, Carleton University, Ottawa, Ont., Canada K1S 5B6

Received June 4, 1984

KUKALOVÁ-PECK, J. 1985. Ephemeroïd wing venation based upon new gigantic Carboniferous mayflies and basic morphology, phylogeny, and metamorphosis of pterygote insects (Insecta, Ephemera). *Can. J. Zool.* **63**: 933–955.

Gigantic as well as very large mayflies from the middle Upper Carboniferous (Westphalian) strata of Europe and North America are described: the adult and nymph of *Bojophlebia prokopi* n. gen., n. sp. (**Bojophlebiidae** n. fam.) and the nymphs of *Lithoneura piecko* n. sp. and *Lithoneura clayesi* n. sp. (Syntonopteridae). Evolution of ephemeroïd wing venation during 300 million years is summarized. Autapomorphic, apomorphic, and plesiomorphic character states of venation are categorized. Venational nomenclature of Recent Ephemera is emended based on its evolutionary changes. Evidence that wing veins occurred primitively as a pair of fluted sectors is documented in Carboniferous mayflies in the costa, subcosta, radius, anal, and jugal. Ephemeroïds and odonatoïds are sister groups that share the veinal anal brace AA fused with CuP at an area important for flight. Ancestral Odonatoephemera are the sister group of the extinct haustellate Paleoptera. The Carboniferous nymphs bear three pairs of almost homonomous thoracic wings and, on the abdomen, nine pairs of legs and nine pairs of tracheal gills (wing homologues). This proves that abdominal legs have been totally reduced in Recent Ephemera except for the claspers (gonopods) and that tracheal gills are not flattened legs. The metamorphic instar probably originated in relatively young instars. Insectan cerci developed from segmented, arched, functional legs of abdominal segment 11, which were still present in this primitive condition in Carboniferous Monura.

KUKALOVÁ-PECK, J. 1985. Ephemeroïd wing venation based upon new gigantic Carboniferous mayflies and basic morphology, phylogeny, and metamorphosis of pterygote insects (Insecta, Ephemera). *Can. J. Zool.* **63**: 933–955.

On trouvera ici la description d'éphémères géants ou de très grande taille du milieu du Carbonifère supérieur (Westphalien) d'Europe et d'Amérique du Nord: adulte et larve de *Bojophlebia prokopi* n. gen., n. sp. (**Bojophlebiidae** n. fam.), larves de *Lithoneura piecko* n. sp. et de *Lithoneura clayesi* n. sp. (Syntonopteridae). L'évolution de la nervation des ailes d'éphémères au cours de 300 millions d'années est résumée ici. Les caractéristiques des nervations autapomorphe, apomorphe et plesiomorphe sont décrites également. La nomenclature des nervures des Ephemera récents a dû être amendée en fonction des changements apportés à l'interprétation évolutive de ces nervures. La morphologie de la costale, de la sous-costale, du radius, de l'anale et de la jugale chez les éphémères du Carbonifère indique que les nervures des ailes sont d'abord apparues sous la forme d'une paire de secteurs cannelés. Les Ephemera et les Odonata sont des groupes soeurs chez lesquels "l'arc-boutant" anal AA (veinal anal brace) est fusionnée à la cubitale postérieure CuP en un point crucial pour le vol. Les Odonatoephemera ancestraux constituent le groupe soeur des Paleoptera à trompe aujourd'hui disparus. Les larves du Carbonifère possédaient trois paires d'ailes thoraciques presque homonomes et, sur l'abdomen, neuf paires de pattes et neuf paires de branchies trachéennes (homologues des ailes). Cela prouve que les pattes abdominales sont totalement disparues chez les Ephemera récents, sauf les harpagones (gonopodes), et que les branchies trachéennes ne sont pas des pattes aplaties. Le stade métamorphique est probablement apparu chez des stades larvaires relativement jeunes. Les cerques des insectes se sont formés à partir des pattes fonctionnelles segmentées arquées du 11^e segment abdominale et ils existaient encore sous cette forme chez les Monures du Carbonifère.

[Traduit par le journal]

Introduction

In 1981, Dr. R. Prokop, the curator of the National Museum in Prague, brought to my attention a fossil Carboniferous mayfly nymph found in the central Bohemian coal basin of Czechoslovakia. This nymph is the largest and oldest known juvenile of the order Ephemera. The specimen was discovered by an amateur mineralogist, Mr. F. Janouš, near the town Tlustice, in tuffites of the middle Upper Carboniferous (Westphalian C). Recognizing the scientific importance of the find, Mr. Janouš gave the specimen to Mr. V. Petr (1981) of the County Museum in Beroun, who forwarded it to the National Museum in Prague and the care of Dr. Prokop.

The mayfly nymph has a body length (without appendages) of 10 cm and is not fully grown. It was preserved in kaolinized tuffites at the base of the "whetstone horizon" (brouskový horizont in Czech), which was deposited following a single volcanic eruption. The kaolinized tuffites form a distinctive key bed that marks the first eruption of a Carboniferous volcano located about 100 km from the site near the town Louny. The volcanic ashes spread quickly and evenly over a large area in an easily detectable bed that explicitly identifies

the simultaneous occurrence of all faunas found in the tuffites.

This last fact is important in supporting the close relationship between the gigantic nymph from Tlustice and a gigantic ephemeroïd adult, from nearby Vrapice, that had an astonishing 45-cm wingspan. The adult was found at the base of the whetstone horizon 28 years ago (Zázvorka 1956) but was not recognized as a mayfly.

Both the adult and nymphal gigantic mayflies are of comparable size, have compatible, extremely primitive morphological features and died simultaneously in an ashfall from the same volcanic eruption. It is, therefore, highly probable that they are closely related, even if direct proof will be always missing. Herein, they will be described as a new family, new genus, and new species.

During the Paleozoic, North America and Europe were parts of the Pangea supercontinent and were covered by a continuous belt of tropical vegetation that harboured a very similar entomofauna. North America, as well as Europe, had populations of very large mayflies, the Syntonopteridae, measuring up to 20 cm in wingspread. This family was recorded in the Westphalian D of Mazon Creek, Illinois, about 10 million years later

than related forms in Bohemia. The same Mazon Creek locality also has yielded two relatively large-sized, primitive mayfly nymphs, which are morphologically similar to the gigantic nymph of Czechoslovakia. These nymphs are the oldest ephemerid juveniles known so far from North America and are tentatively referred here to the family Syntonopteridae, genus *Lithoneura*. The material was assembled through the efforts of amateur paleontologists who devoted much of their time to systematic collecting in the vast spoil banks of old coal mines of Mazon Creek near Chicago. The specimens were made available by Mrs. Helen Piecko and by Mr. Walter Claves, both well-known collectors from Chicago.

Syntonopterid mayflies have had a tumultuous systematic past and have changed position several times between Paleodictyopteroidea and Ephemeroidea. The causes of the uncertain position were the numerous, exceedingly plesiomorphic "paleodictyopteroid" structures of body and wing venation, which made it doubtful whether or not the characters occurred in early Ephemera. In this paper an attempt is made to analyse the character states of Carboniferous, Permian, and Recent mayflies and to categorize them as constitutive, synapomorphic, autapomorphic, and plesiomorphic (Hennig 1981).

In Carboniferous mayflies, the plesiomorphic and autapomorphic characters of Ephemera stand out more clearly than in living mayflies. Comparisons between Carboniferous, Permian, and Recent veinal systems offer a rare opportunity to follow transformation of autapomorphic traits within an order for 300 million years.

Several emendations of presently used venational nomenclature resulted from the evolutionary aspect of this study (Fig. 39). Important morphological evidence found in the gigantic nymphs includes three pairs of almost homonomous thoracic wings and two pairs of appendages (tracheal gills and true abdominal legs) on each of the nine abdominal segments.

Systematics and descriptions

ORDER Ephemera Leach, 1817

Bojophlebiidae n. fam.

TYPE GENUS: *Bojophlebia* n. gen.

OCCURRENCE: Upper Carboniferous of Europe, tropical climatic zone.

GENERA: *Bojophlebia* n. gen.

DIAGNOSIS: Bojophlebiidae n. fam. differs from all ephemeroid families by its MA vein, which is arched towards but not fused with the RP vein, and in richer, dichotomous branching of veins MA, MP, CuA, AA, and AP. The new family shares with the closely related Carboniferous Syntonopteridae hind wings which are broader than the fore wings, and the following veinal characters: low arched and forked subcostal brace ScA+, CuA not fused to M but connected with M by a strut, AA1 completely fused with CuP in both fore and hind wings, AA2 diverging from CuP in an arch, the richer branching of almost all veins, and the presence of irregular, weak, anastomosed crossveins and archidictyon. The wing margin is scalloped; prothoracic wings are present and large. The head and body resemble those of Syntonopteridae and the Permian Prottereismatidae. The mouthparts were in all probability functional.

Relationships

The most remarkable feature of Bojophlebiidae is the gigantic dimensions, which exceed all expectations for the upper size

limit of Ephemera. In fact, bojophlebiids (45 cm in total wingspread!) are surpassed in size only by Paleozoic Paleodictyoptera (maximum 56 cm) and Protodonata (maximum 71 cm), while no species in Recent fauna comes close to these extraordinary proportions.

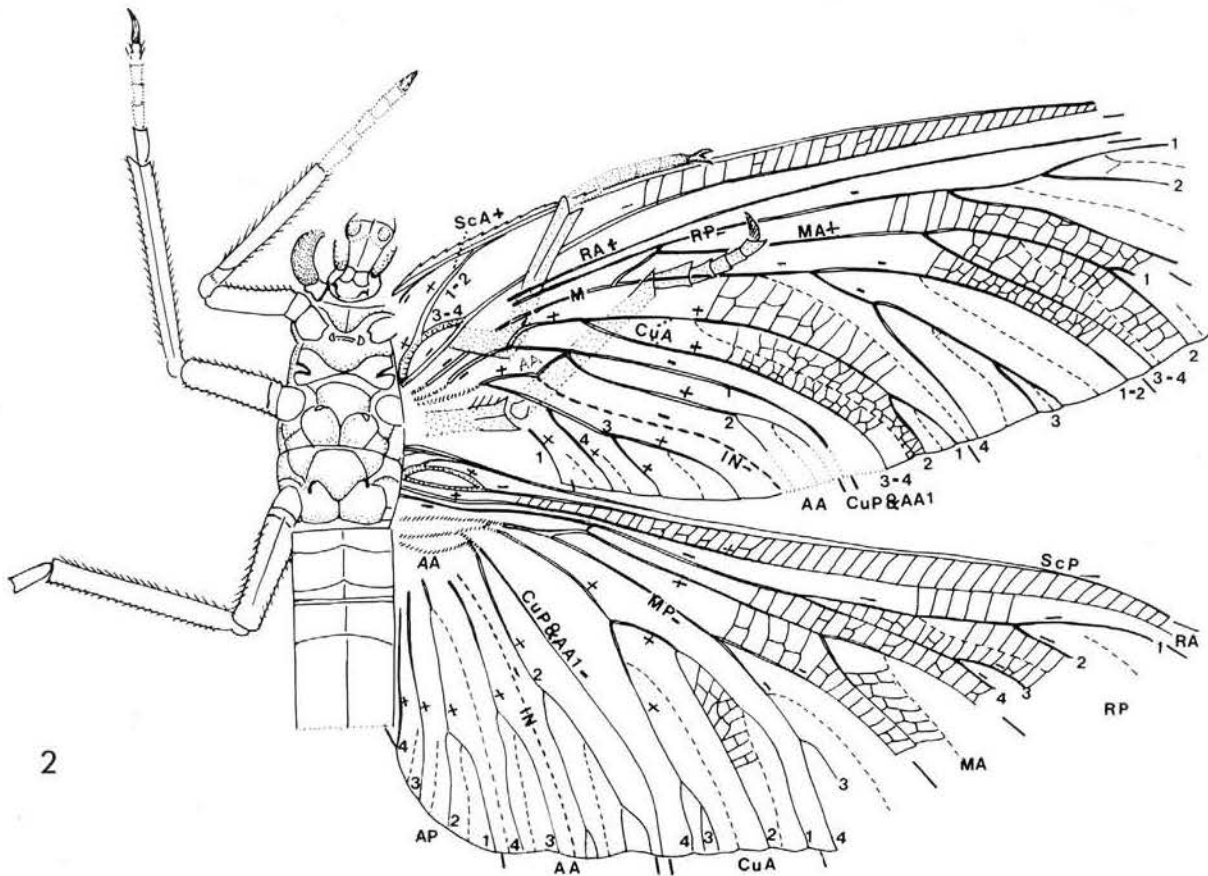
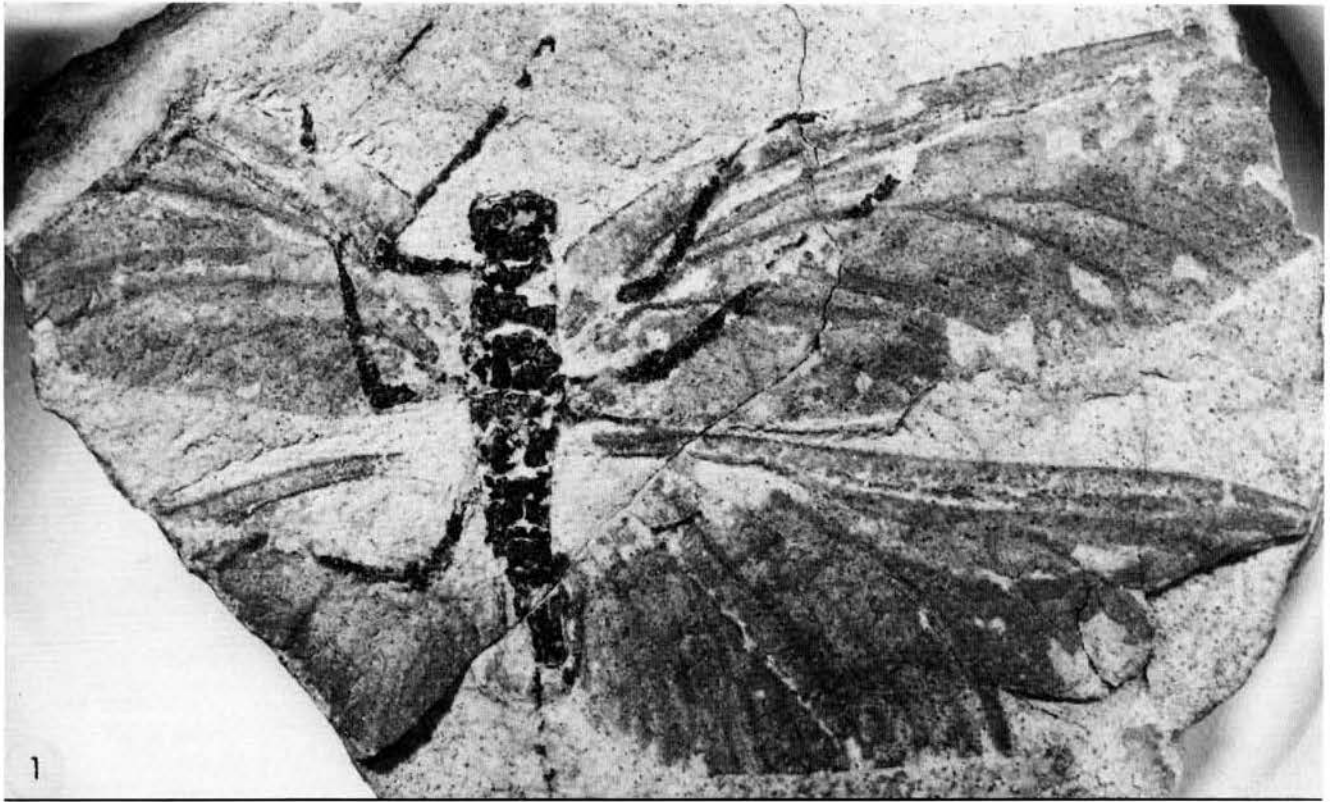
In living mayflies the hind wings are always smaller, even to the point of diptery, than the fore wings. Just the opposite is true for Bojophlebiidae, in which the hind wings are broader basally than the fore wings and triangular in shape as in most of the large Paleoptera, most notably the Paleodictyoptera. The related large Carboniferous mayflies, the Syntonopteridae (wingspread 8.5 cm to almost 20 cm), also have markedly broader hind wings, but the Permian Prottereismatoidea have hind wings subequal and slightly smaller. There are two possible interpretations for this: either, as in Paleodictyoptera, very broad hind wings were essential in very large insects to support the body in flight and the enlargement is secondary; or the oldest Ephemera originally had broad hind wings and the later reduction is entirely a matter of autapomorphic evolution of the order. Thus, we do not have an answer yet as to whether ancestral ephemeroids had homonomous wings, or whether the hind wings were broader than the fore wings.

The most interesting fact about bojophlebiid venation is that the typical ephemeroid pattern of vein fusion (MA & RP, CuA & M) is only indicated by veinal arches and struts, but the actual fusion is still lacking. A remarkably parallel gradual evolution from arch and strut to a true veinal fusion took place in odonatoid venation at homologous sites between MA & RP and CuA & M. This parallelism was recently documented in the fossil record in Eugeopteridae, Erasipteridae, and Meganeuridae in comparison with Recent Odonata (Riek and Kukalová-Peck 1984, Fig. 35).

In Ephemera, the older Bojophlebiidae (Westphalian C) have MA & RP and CuA & M arched and connected by a strut, but unfused; the younger Syntonopteridae (Westphalian D) have MA & RP fully fused and CuA & M strongly arched and strutted but unfused; the still younger but deviant Triplosobidae (Stephanian) have MA arched or fused with R instead with RP and CuA & M possibly fused (Carpenter 1963); Permian Prottereismatidae have MA & RP fully fused and CuA & M sometimes fused and sometimes strutted. Prottereismatoids are generally considered as direct ancestors of Recent mayflies.

It should be noted that bracing and fusing of a section of M, or of MA & RP or R, Cu or CuA & M, and RA & RP occurs in most Paleoptera and is typical for the odonato-ephemeroid clade. A similar pattern of reinforcement, but usually accomplished in a more varied and complicated way and accompanied always by a fusion or by an extreme proximity of R & M stems immediately at the base, is characteristic for Neoptera. Hence, even if the wings of Paleoptera and Neoptera are exposed to the same physical laws of flight mechanics, there is a noticeable difference in the bracing at the areas of stress, so that the wings can be separated into two major subgroups (Kukalová-Peck 1983; Riek and Kukalová-Peck 1984).

The anal brace of Bojophlebiidae is typically ephemeroid and veinal (i.e., composed of sections of veins) and resembles closely that of Syntonopteridae. The veins involved are the AA stem and AA1-2. The distal end of the anal brace (AA1) is fused with CuP at a meeting point of four veins, AA1-2, AA2, Cu, and Cu & A1. This meeting point is prominent and became important in the ephemerid type of flight. In Prottereismatidae it carried a bulla (Kukalová-Peck 1983; Riek and Kukalová-Peck 1984).



FIGS. 1 and 2. *Bojophlebia prokopi* n. gen., n. sp. (Bojophlebiidae n. fam.) adult, the largest and oldest mayfly known, with a wingspread of 45 cm. Ventral side. The subcostal brace is gently arched (primitive), the typical ephemeroïd anal brace is present but inconspicuous, and radial sectors are independent. Holotype; fore wing fragment length 178 mm. Middle Upper Carboniferous, Westphalian C, Bohemia. Original drawing. (Abbreviations used in the figures are given in the Appendix.)

Bojophlebia n. gen.

TYPE SPECIES: *Bojophlebia prokopi* n. sp.

ETYMOLOGY: From Bojos, an ancient tribe of the kingdom Bojohemum. (This original name later became latinized and was changed to Bohemia.)

OCCURRENCE: Middle Upper Carboniferous (Westphalian C) of Central Europe.

SPECIES: *Bojophlebia prokopi* n. sp., adult and nymph.

Description

Body, adult: Head probably¹ with relatively long and thick antennae, large protruding eyes, and functional chewing mouthparts; body slender, legs probably long and comparatively stout; patello-tibia longer and femur shorter than basitarsus, tarsus and posttarsus combined; tarsus with four subsegments; cerci and paracercus probably with short hair, cerci shorter than paracercus.

Wings: Fore wing slightly longer and narrower than hind wing; hind wing triangular; prothoracic wings present as veined lateral lobes; precosta with serration; CA+ and CP- originating separately from costal basivenale, fusing together near base; subcostal brace forming low broad arch, ScA+ forked, ScA1-2 fusing with costal margin, ScA3-4 fusing with ScP; RA and RP originating separately from the base, running adjacent to each other as double radius; RP divided into 1, 2, 3, 4 branches; MA arched towards RP and strutted, MA divided into 1, 2, 3-4 branches, MP into 1-2, 3, 4, branches, CuA into 1, 2, 3-4 branches, AA and AP into 1, 2, 3, 4 branches and into subbranches; AA1 completely fused with CuP in both fore and hind wings. Intercalar veins alternate with all branches; crossveins irregular, archidictyon present, dense.

Bojophlebia prokopi n. sp.*Adult* (Figs. 1, 2, 3)

HOLOTYPE: Specimen No. 1/1985, Národní Museum, Prague, Czechoslovakia. Ventral side, head without antennae, thorax, two abdominal segments, bases of legs, four wings without apical parts.

ETYMOLOGY: The species is named in honor of Dr. Rudolf Prokop, a friend of many years, without whose initiative and generous help this paper would not be possible.

OCCURRENCE: Westphalian C, base of whetstone horizon, President Antonín Zápotocký mine near Vrapice, Central Bohemian Coal Basin, Bohemia.

Description

By monotypy, the same as that of the genus. Fore and hind wing almost equally broad but differently shaped; fore wing oval, hind wing slightly shorter and broader, triangular. Differences in venation between fore and hind wing include longer fork RP 3, 4 (hind wing), presence of fork CuA 3, 4 (hind

wing), A2 richer in branches (hind wing), and A3 richer in branches (fore wing).

Fore wing fragment: Length 178 mm, width 76 mm, total length ca. 215 mm.

Hind wing fragment: Length 175 mm, width 79 mm, total length ca. 20 cm.

Wingspread: About 45 cm. This may be the largest mayfly of all times.

Body: Head, length 20 mm, width ca. 30 mm; thorax (telescoped) length 50 mm; abdomen, first segment length 15 mm, second segment length 27 mm, maximum width 21 mm.

Legs: Fore leg, basitarsus through posttarsus 29 mm, patello-tibia 38 mm, femur 17 mm; middle leg, basitarsus through posttarsus 29 mm, patello-tibia 38 mm, femur 19 mm; hind leg, patello-tibia 48 mm, femur 30 mm.

Nymph (Figs. 4-10, 30)

PARATYPE: Specimen No. P27/80, Národní Museum, Prague, Czechoslovakia. Ventral side, head with antennae and mouthparts, body, four legs, abdominal tracheal gills, abdominal legs, male genitalia, and cerci and paracercus.

OCCURRENCE: Westphalian C, base of whetstone horizon, "Na Štilci" quarry near Tlustice, Central Bohemian Coal Basin, Bohemia.

DIAGNOSIS: *Bojophlebia prokopi* n. sp. differs from related syntonopterid nymphs in having relatively larger eyes, smaller prothorax, and possibly broader and larger plate gills. From protreismatid nymphs it differs in having a larger prothorax, larger prothoracic winglets, in relatively shorter and stouter legs, shorter and broader abdomen, and in cerci and paracercus with short, noninterlocking hairs.

Description

Head: Antennae similar to syntonopterid nymphs, longer and thicker than in protreismatid nymphs; eyes very large, protruding; head probably almost prognathous, mouthparts powerful, well sclerotized.

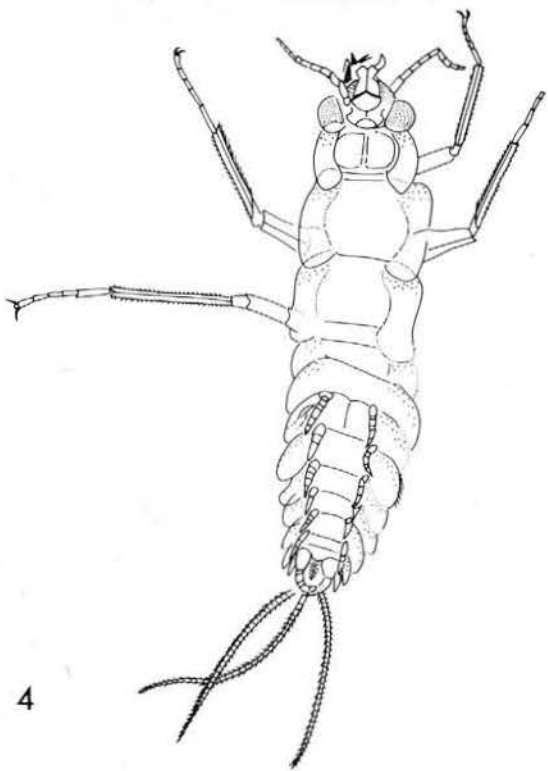
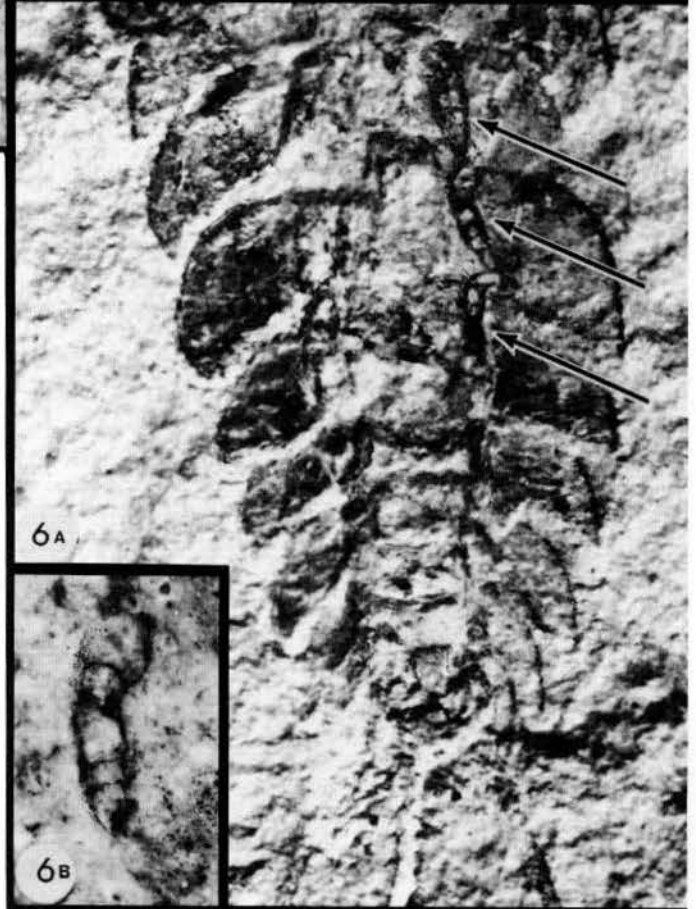
Thorax: Prothorax shortest, metathorax longest of thoracic segments; three pairs of wings equally shaped, curved strongly backwards; prothoracic wings slightly smaller than pterothoracic wings; legs similar to adults, not specialized for nymphal life, with femur short, basitarsus, tarsus and post-tarsus longer, and patello-tibia the longest part of each leg; double posttarsal claws present; legs comparatively long and strong, adapted to crawling.

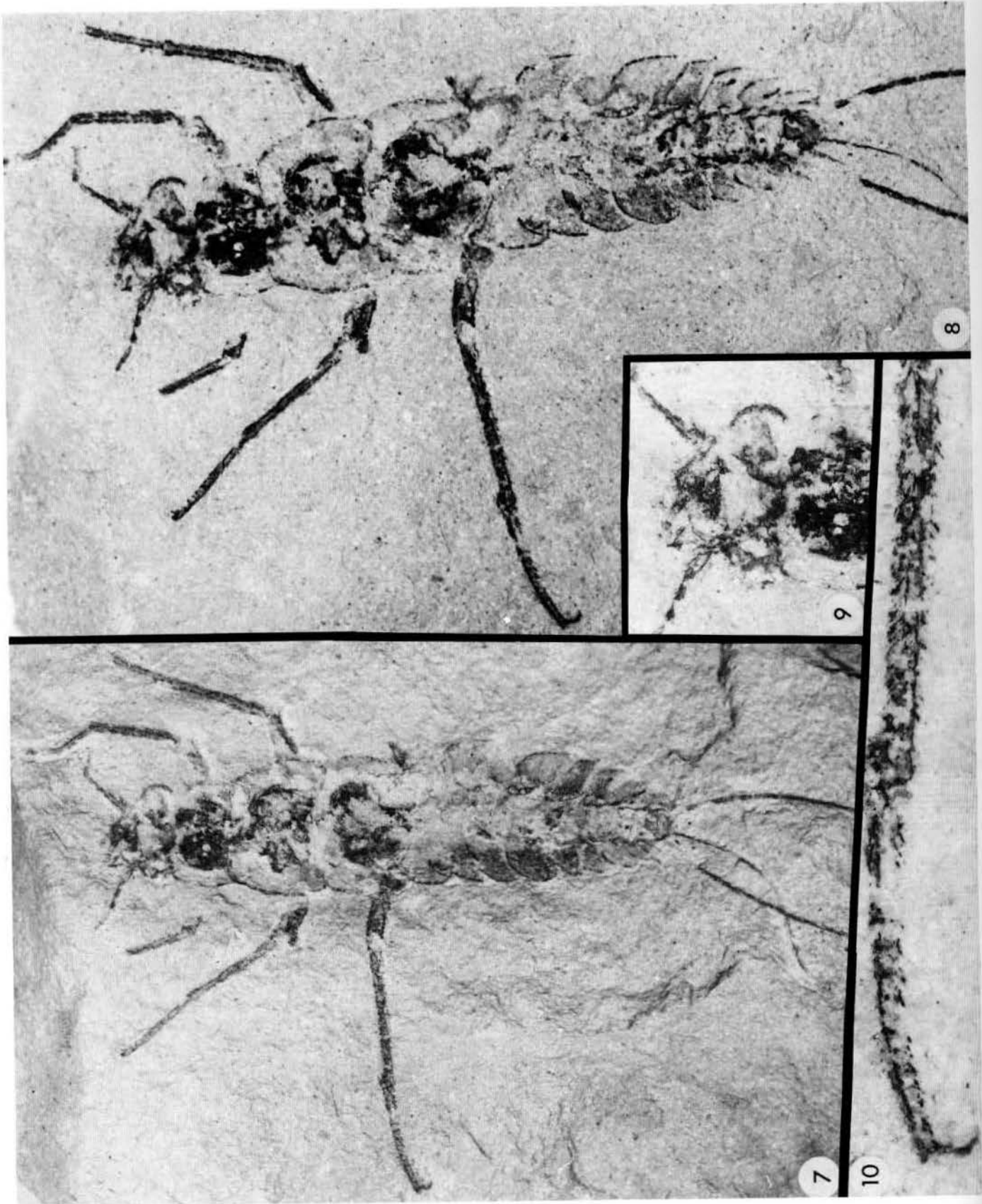
Abdomen: About as long as head and thorax combined, with 9 pairs of broad leaflike, veined tracheal gills slowly diminishing in size posteriorly; 9 pairs of abdominal legs (telopodites) composed of probably 7 segments; 9th pair of legs changed into claspers terminated in all probability by double claws²; cerci and paracercus thin, with short hairs at the end of each annulus; paracercus longer than cerci.

¹Character descriptions qualified by "probably" are found in the *Bojophlebia* nymph as well as in related Syntonopteridae but were not preserved in the *Bojophlebia* adult, and would in all probability be present in a complete specimen.

²The preservation of gonopodal claws in the *Bojophlebia* nymph is not very distinct, but remnants of claws are known in several male protreismatids from the Lower Permian strata of Elmo, Kansas, and in the males of other paleopterous orders (Kukalová-Peck 1983).

FIG. 3. *Bojophlebia prokopi* n. gen., n. sp., holotype; ventral side of head and telescoped thorax preserved in coarse-grained tuffite. Westphalian C, Bohemia. FIG. 4. *Bojophlebia prokopi* n. gen., n. sp., younger nymph of a gigantic mayfly. Ventral side showing 3 pairs of almost homonomous thoracic wings and co-occurrence of legs and tracheal gills on each of the 9 abdominal segments. Paratype; length without appendages 102 mm. Westphalian C, Bohemia. Original drawing. FIG. 5. Same specimen part of abdomen under alcohol showing pregenital leg with pigmented segments (arrow). FIG. 6. (A) Same specimen but with oblique lighting; part of abdomen showing remnants of 9 pairs of segmented pregenital legs (arrows) and 9 pairs of broad tracheal gills unevenly preserved in coarse-grained tuffite. (B) Best preserved pregenital abdominal leg of the 4th segment with natural dark pigmentation. Length 3 mm.





Body: Head length 11 mm, width 19 mm; prothorax length 8.5 mm, width 18 mm; mesothorax length 15 mm, width 24 mm; metathorax length 19.5 mm, width 24 mm; abdomen length 48 mm, width 24 mm.

Legs: Fore leg, basitarsus through posttarsus 11 mm, patello-tibia 16 mm, femur fragment 8 mm; middle leg, basitarsus through posttarsus 16 mm, patello-tibia 21 mm, femur fragment 7 mm; hind leg, basitarsus through posttarsus 20 mm, patello-tibia 25 mm, femur fragment 19 mm.

Relationships

The exposed, ventral side of the gigantic nymph shows a series of large, segmented abdominal legs ending with a pair of claspers (gonopods) on the 9th segment. The claspers are known in Permian protreismatoids to carry double claws, which documents that they are derived from the entire leg (Kukalová-Peck 1983). Dorsally, the same segments are provided with 9 pairs of tracheal plate gills. Until recently most entomologists believed, based on Snodgrass (1935), that ephemerid tracheal gills are flattened abdominal legs. The bojophlebiid nymph is an important proof that this interpretation is faulty. True abdominal legs were originally articulated much more ventrally than tracheal gills, at the same level as the claspers. They became reduced and disappeared in Recent mayflies.

Tracheal gills are inserted by the leg musculature and are appendageal in character (Matsuda 1976). Therefore they cannot be explained merely as simple evaginations of the membrane as blood gills. Their musculature is serially homologous to that of the thoracic wings (subalare; Matsuda 1976, 1981) and their position on the abdominal pleuron is the same as that of the wings on the thoracic pleuron. They are homologous to wings and were probably derived from the outer exites articulated between the first and the second leg segment (epicoxa and subcoxa), which both became incorporated into the body wall in pterygotes (Kukalová-Peck 1983). In other Recent pterygote juveniles, surviving homologous equivalents of mayfly gills are the abdominal filaments of some dragonfly nymphs (Euphaeidae and Polythoridae of Zygoptera), some stonefly nymphs, dobsonfly and sisyrid larvae, and of some beetle larvae.

Relationship of the Syntonopteridae Handlirsch, 1911

TYPE GENUS: *Syntonoptera* Handlirsch, 1911

OCCURRENCE: Middle Upper Carboniferous (Westphalian D) to ?Lower Permian; tropical belt of North America and ?Europe.

GENERA: *Syntonoptera* Handlirsch, 1911; *Lithoneura* Carpenter, 1938.

Syntonopteridae are large Carboniferous mayflies with a wingspread from ca. 8.5 to ca. 19 cm, closely related to Bojophlebiidae. The family has had a tumultuous systematic history and has been shifted several times between Paleodictyopteroidea and Ephemera. Paleodictyopteroidea was preferred by Handlirsch (1911, 1919), Lameere (1917), Carpenter (1938, 1943), Richardson (1936), Hubbard and Kukalová-Peck (1980), and Kukalová-Peck (1978, 1983). Ephemera

was favored by Edmunds and Traver (1954) and Sharov (1966). Laurentiaux (1953) erected for the family a separate order, Syntonopteroidea.

The reason for this uncertainty lies in the numerous plesiomorphic characters that have been emphasized, as well as morphological peculiarities and artifacts. Syntonopteridae have well-developed prothoracic lobes, carry rather heavy, long antennae, the wing venation lacks fusion between CuA and M which is substituted by CuA arch and strut to M, the crossveins are very irregular, and the wing membrane is covered by a dense archidictyon. The holotype of *Lithoneura lameerei* Carpenter, 1938 (Figs. 11, 12, 13, 37) has a fold cutting basally across the cubito-anal area, which makes the veinal anal brace seem to resemble the typical secondary anal brace of Paleodictyoptera (cf. Fig. 22 in Kukalová-Peck and Richardson (1983)). The head is squashed in such a way that it is reminiscent of the heads of paleodictyopteroids with only the base of the haustellum preserved. All these morphological features were at one time believed to show the paleodictyopteroid rather than the ephemerid nature of the Syntonopteridae.

On the other hand, Syntonopteroidea have the typical slender ephemerid body, ephemerid veinal pattern of branching, braces, and near-braces, and a very regular, alternating system of intercalate veins. The anal area contains some characteristic "bundling" of anal branches by crossveins which probably occurs only in Ephemera. However, what ultimately convinced me about the ephemerid nature of the Syntonopteridae are two autapomorphic characters of venation: the incipient but already specialized gently arched and strong subcostal brace, which is a derivative character in Ephemera, and a composite veinal anal brace fused with CuP at an area important for flight, which is derivative in the ancestral Odonatoephemera. Both apomorphic characters are also present, in a very similar form, in the Bojophlebiidae (Fig. 2). In contrast, extinct haustellate Paleodictyopteroidea have an unspecialized, straight subcostal brace and a very different anal brace. The latter is merely a sclerotization of the membrane in the basal corner of the anal area and is frequently delimited by a secondary, transverse, or V-shaped bar (Kukalová 1969, Fig. 1-4; Kukalová-Peck 1970, Fig. 42).

It is possible that Syntonopteridae and Bojophlebiidae are not directly ancestral to Protreismatoidea but represent a side-branch, albeit not very specialized, of the ephemeroid stem group.

It seems that, in spite of the differences in the shape of the hind wing, the two families should be referred to the superfamily Syntonopteroidea, characterized by a broader hind wing than fore wing, a very gently-arched subcostal brace, an anal brace with AA1 fully fused with CuP, AA2 diverging from CuP as an arch, and the presence of many subbranches, irregular crossveins, and a dense archidictyon.

As a result of Hennig's work on theoretical systematics (1981), we are now provided with criteria for judging the systematic position of such enigmatic groups as the Syntonopteridae. Fossils, especially if they are very primitive, often carry unexpected plesiomorphic features, while the apomorphic characters are few and inconspicuous. However, it is

FIGS. 7-10. *Bojophlebia prokopi* n. gen., n. sp., younger nymph of the oldest known gigantic mayfly well adapted for aquatic life. Fig. 7. Dry specimen, ventral side. Note remnants of several pregenital abdominal legs, unevenly preserved in coarse-grained tuffite. Fig. 8. Specimen under alcohol; the dark pigmentation caused by residual dark chitin is accentuated. Fig. 9. Enlarged view of head showing bulging eyes with several preserved ommatidia. Fig. 10. Metathoracic leg, tibia, basitarsus, tarsus with 4 subsegments and large posttarsus, darkly pigmented as in life. Paratype, body length 10.3 mm. Westphalian C, Bohemia.

the apomorphic character that is decisive for classification. In the case of early fossils, autapomorphic characters are usually in the initial state of development. This circumstance makes the fossils especially interesting for Recent systematists because they may possess clues for the categorization of character states and may offer an opportunity to examine characters from an evolutionary perspective.

Body structure and wing base of *Lithoneura* Carpenter, 1938

I have studied the holotype of *Lithoneura lameerei* Carpenter, 1938 (Syntonopteridae) and have prepared parts of the body and the wing base, as shown in Figs. 11, 12, 13. The head is a composite impression of the dorsal and ventral head structures; the eyes are very large and bulging; and the antennae are long, multisegmented, and relatively thick. The prothorax carried two large prothoracic wings, which were noticed previously by Carpenter (1938). The mesothoracic and metathoracic tergal sulci are indistinct. The abdomen is narrow and typically ephemeroid.

Of these structures, the large prothoracic wings are particularly interesting. It has long been thought that they occur only in the Paleodictyoptera. However, they were recently also described in Diaphanopteroidea, Permothemistida, Ephemeroptera nymphs and adults, and in many extinct and extant groups of Neoptera (Kukalová-Peck 1978, 1983). Prothoracic wings are, therefore, a typical residual plesiomorphic structure which sometimes finds a new use in shielding the sides of the prothorax. In Ephemeroptera, prothoracic wings are now known to occur in adult Permian *Prottereisma* (Fig. 22; Museum of Comparative Zoology, Harvard University (MCZ) specimen 3405, personal observation), in nymphal prottereismatoids (Fig. 31; MCZ specimen 6311), in Carboniferous adult Syntonopteridae (Fig. 11), in nymphal Syntonopteridae (Fig. 17, 18, 28, 29), and in nymphal Bojophlebiidae (Figs. 4, 30). In Carboniferous nymphs, the prothoracic wings are very large, do not differ in shape and position from the mesothoracic and metathoracic wings, and on occasion may be even larger than the metathoracic wings (Figs. 18, 20). Quite clearly, prothoracic wings are serially homologous to pterothoracic wings and started in ancestral pterygotes as one of three pairs of homonomous proto-wings.

After preparation, the base of the wings of the *Lithoneura lameerei* holotype yielded the following two ephemerid constitutive characters crucial for the ordinal classification of Syntonopteridae: a gently arched but very strong subcostal brace and a veinal brace of ephemeroid type. The cubito-anal area basally is dissected by a fold (Figs. 12, 13f). An identical fold is still present in the same position in Recent mayflies (Fig. 39)

but is less apparent. The fold continues into the anal area as an intercalated vein IN-, immediately posterior to AA2, which is also present in Recent mayflies. A similar fold, but positioned between AA and AP basally, occurs by convergence in the haustellate order Permothemistida (Riek and Kukalová-Peck 1984, Figs. 8, 9). In my 1983 paper I was misled by this feature (and by the curiously crushed head) into believing that *Lithoneura* is a permothemistid.

In the fore wing, the intercalated vein IN- takes over the basal part of AA3-4 and reaches the posterior margin without interruption; in the hind wing, it ends at a bundle of branches and starts again from AA2 and then reaches posterior margin. In the hind wing of *Lithoneura mirifica* Carpenter, 1943 (Fig. 14) IN- runs without interruption through similar bundle of branches. Note that the "bundle of branches" in the anal area is typically ephemeroid.

The axillary plate of *Lithoneura* is plesiomorphic and reminiscent of the paleodictyopteroidea band of little diversified articular sclerites. In contrast, the axillary plate of later ephemeroids has a typically inflated radial basivenale and is flanked proximally by diversified fulcralia with muscular attachments (Kukalová-Peck 1983, Fig. 3). In light of this evidence, the inflated and specialized axillary plate in recent Ephemeroptera stands out as an autapomorphy that became pronounced mainly in the Permian. It is probably positively correlated with the increased arching of the subcostal brace. The small inflation of the radial basivenale was almost certainly already present in the earliest Ephemeroptera and most likely represents the constitutive character of the articulation. Arch and strut bracing between CuA & M is plesiomorphic and shows how veinal braces developed in the pterygote venation. CuA & M in homologous areas in Prottereismatoidea are often fully fused. Parallel, gradual development of veinal braces from arch and strut to direct fusion was recently described in the oldest fossil Odonatoidea by Riek and Kukalová-Peck (1984).

Syntonopteroidea incertae sedis

(Figs. 15, 16)

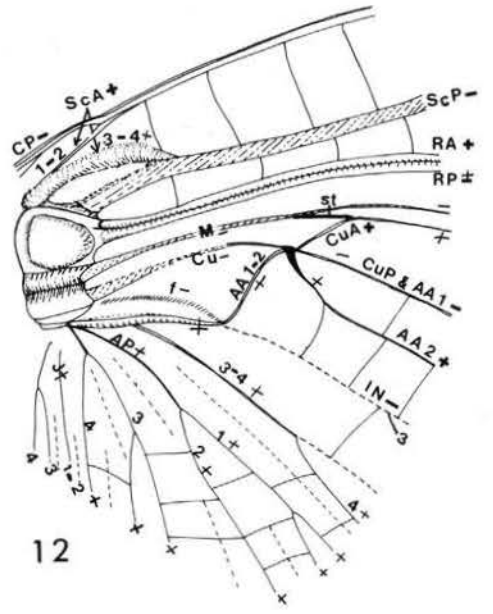
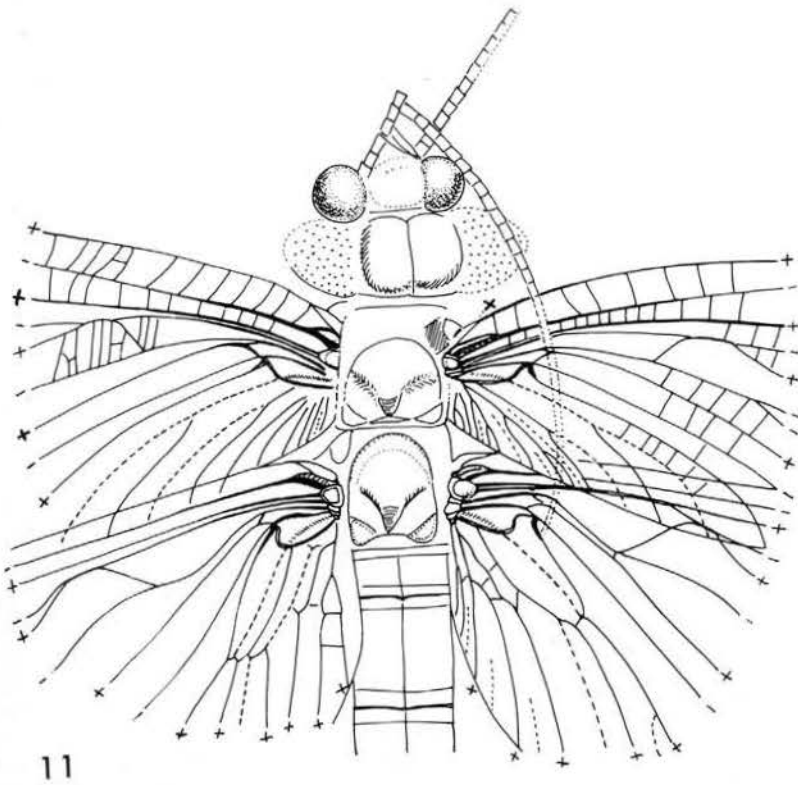
ORIGINAL SPECIMEN: No. 3/1985 in the collection of J. Kukalová-Peck, Carleton University, Ottawa, Canada. Apical half of hind wing.

OCCURRENCE: Lower Permian (Leonard), Obora, Czechoslovakia.

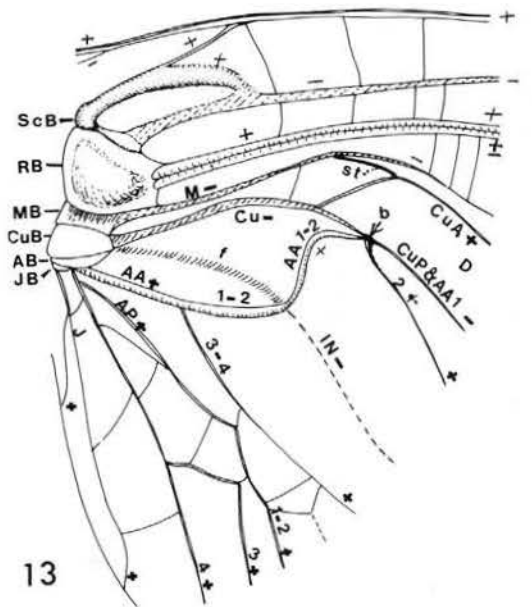
Relationships

This remnant of a large hind wing is difficult to classify. It probably belongs to Ephemeroptera, possibly to Syntonopteridae, or perhaps still more likely to a related but separate family. However, I am hesitant to base a new family on the distal half of one wing only. The fragment has a very fine archdictyon

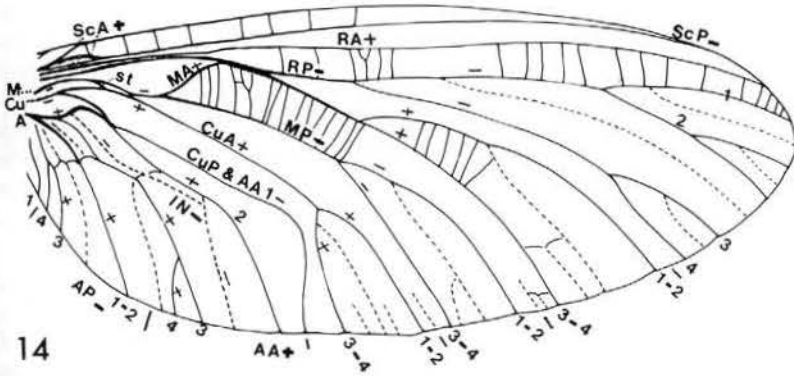
FIG. 11. *Lithoneura lameerei* Carpenter, 1938 (Syntonopteridae) with plesiomorphic long antennae and large prothoracic wings. Ephemeroid autapomorphic characters are the strong, arched subcostal brace, specialized anal brace, and pattern of venation, braces, and intercalated veins, as well as the presence of veinal "bundles" in the anal area. Wingspread ca. 8.5 cm. Westphalian D, Illinois. Original drawing from holotype. FIGS. 12 and 13. *Lithoneura lameerei*, bases of fore and hind wings. The enlarged radial basivenale (RB) and narrow, slanted medial basivenale (MB) are ephemeroid traits. The subcostal brace is gently arched but very strong, the radius is doubled as in Odonata, and the anal brace (AA & AA1-2) ends in CuP at an area important for flight (b). A strut (st) replaced fusion between CuA & M. Note concave fold (f) crossing the Cu-AA area, basally, which continues into the anal area as intercalary vein IN- posterior to AA2. Westphalian D, Illinois. Original drawings from holotype, composites of left and right fore and hind wing bases. FIG. 14. *Lithoneura mirifica* Carpenter, 1943, hind wing with plesiomorphic arch and strut (st) bracing between CuA & M and advanced arch and fusion bracing between MA & RP. Radial sectors are independent near the base as in Odonata. Ephemeroid traits are represented by arched subcostal brace ScA and by veinal anal brace AA & AA1-2. Wing length 85 mm. Westphalian D, Illinois. Original drawing. FIGS. 15 and 16. Syntonopteroidea incertae sedis, apical half of a large wing with ephemeroid type of intercalated veins and with color pattern. Figure corrects dislocation along breakage line. Length of fragment 29.5 mm. Lower Permian, Czechoslovakia. Original drawing.



12



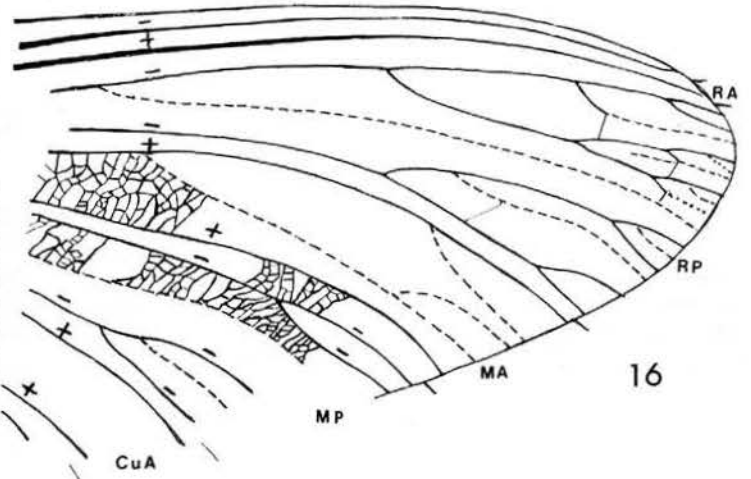
13



14



15



16

plus irregular crossveins similar to Syntonopteridae and Bojophlebiidae, but the first fork on MA and MP seems to be unusually long, a feature that might indicate an aberrant paleodictyopteroidean. Paleodictyoptera sometimes have intercalated veins, but these are usually less regular and are surrounded by a coarser reticulum. It is not particularly surprising that large Carboniferous mayflies would survive into the Permian at Obora, because this locality was at the bottom of a moist, deep graben and contained many elements of both Carboniferous flora and insect fauna.

Nymphs of Syntonopteridae

(Figs. 17, 18, 19, 20, 21, 28, 29)

Two very primitive ephemerid nymphs have been found in the middle Upper Carboniferous (Westphalian D) strata of Mazon Creek, Illinois, which show a close resemblance to the bojophlebiid nymph from Westphalian C of Czechoslovakia. Both represent younger stages of the developmental series and probably belong to the same family. Because the only family known so far from Mazon Creek is Syntonopteridae, the wings of Syntonopteridae are similar to those of Bojophlebiidae, and the nymphs of Bojophlebiidae are quite similar to the Mazon Creek nymphs, there is a chance that this placement is correct.

Comparisons between the nymphs are hampered by the facts that one is younger than the other and that the younger one is preserved on the dorsal side, while the older, on the ventral. Tracheal gills, which have the potential to provide a good comparative basis, are preserved only in the posterior abdomen, where they lose their characters as a result of small size. However, available fragments of tracheal gills make a close relationship seem plausible. The nymphs are tentatively referred to the genus *Lithoneura* and to two different species.

Lithoneura piecko n. sp.

(Figs. 17, 28)

HOLOTYPE: Specimen 4/1985, J. Kukalová-Peck collection, Carleton University, Ottawa, Canada. Dorsal view, head, antennae, body, three pairs of wings, bases of three legs, cerci and paracercus.

ETYMOLOGY: The species is named in honor of Helen Piecko, a devoted amateur paleontologist and prominent collector of fossils in the Mazon Creek area.

OCCURRENCE: Westphalian D, Mazon Creek, Illinois.

DIAGNOSIS: *Lithoneura piecko* n. sp. differs from the related *Lithoneura clayesi* n. sp. in its relatively shorter prothorax with relatively smaller prothoracic wings. From *Bojophlebia prokopi* n. sp. it differs in smaller eyes, much heavier cerci and paracercus, and possibly in narrower tracheal gills.

Remarks

The plesiomorphic nature of the nymphs is expressed in the long and rather heavy antennae; well-developed, large prothoracic wings identical in shape to the pterothoracic wings; the presence of tracheal gills on the 8th and 9th abdominal segment; and in the thick cerci and paracercus covered with short, noninterlocking hairs. The nymph is preserved in dorsal view and the pterotergal sulci are partly preserved. It is of interest that, in spite of the young stage of the nymph, the terga resemble those of adult Permian Prottereismatoidea (Fig. 22). The conspicuous arched ridges on the abdominal segments are also found in some Paleodictyoptera, most notably in *Lycocercus goldenbergi* (Kukalová 1969, Fig. 32).

Lithoneura piecko n. sp. is preserved in an ironstone con-

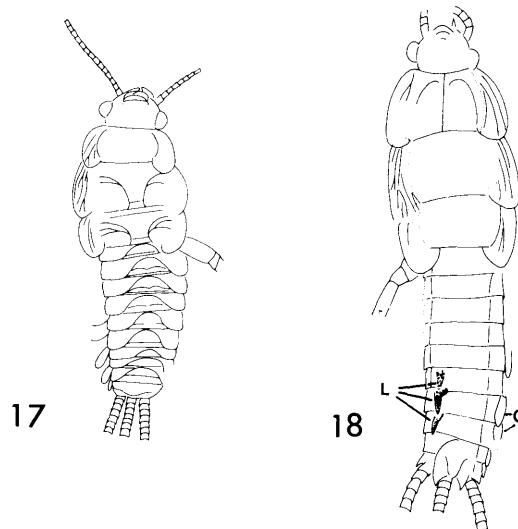


FIG. 17. *Lithoneura piecko* n. sp., very young nymph with three pairs of small, almost homonomous wings strongly curved backwards into a streamlined position. Thoracic terga with the adult pattern of sulci. Body length without appendages 17 mm. Westphalian D, Illinois. Original composite drawing of obverse and reverse from holotype. FIG. 18. *Lithoneura clayesi* n. sp., young nymph, male, ventral side. Prothoracic wings are larger than metathoracic wings. Abdomen showing remnants of tracheal gills (G) and of abdominal legs (L). Body without appendages 34 mm. Westphalian D, Illinois. Original composite drawing of obverse and reverse from holotype.

cretion and displays an unusual condition of preservation, because the obverse does not quite match the reverse. For example, the first abdominal segment is visible in the reverse but is missing in the obverse. This peculiar preservation happens when a multilayered specimen partly rotted, then was compressed, and then split at two different layers. In Mazon Creek concretions a similar type of preservation has been noticed in other insects as well, e.g., in *Herdina mirificus* by Carpenter and Richardson (1971).

Lithoneura clayesi n. sp.

(Figs. 18, 19, 20, 21, 29)

HOLOTYPE: Specimen No. 5/1985 in the private collection of Walter Clayes, Chicago. Ventral view, head, body with three pairs of wings and base of one leg, abdomen with five tracheal gills and three abdominal legs, remnant of male penes, cerci, and paracercus.

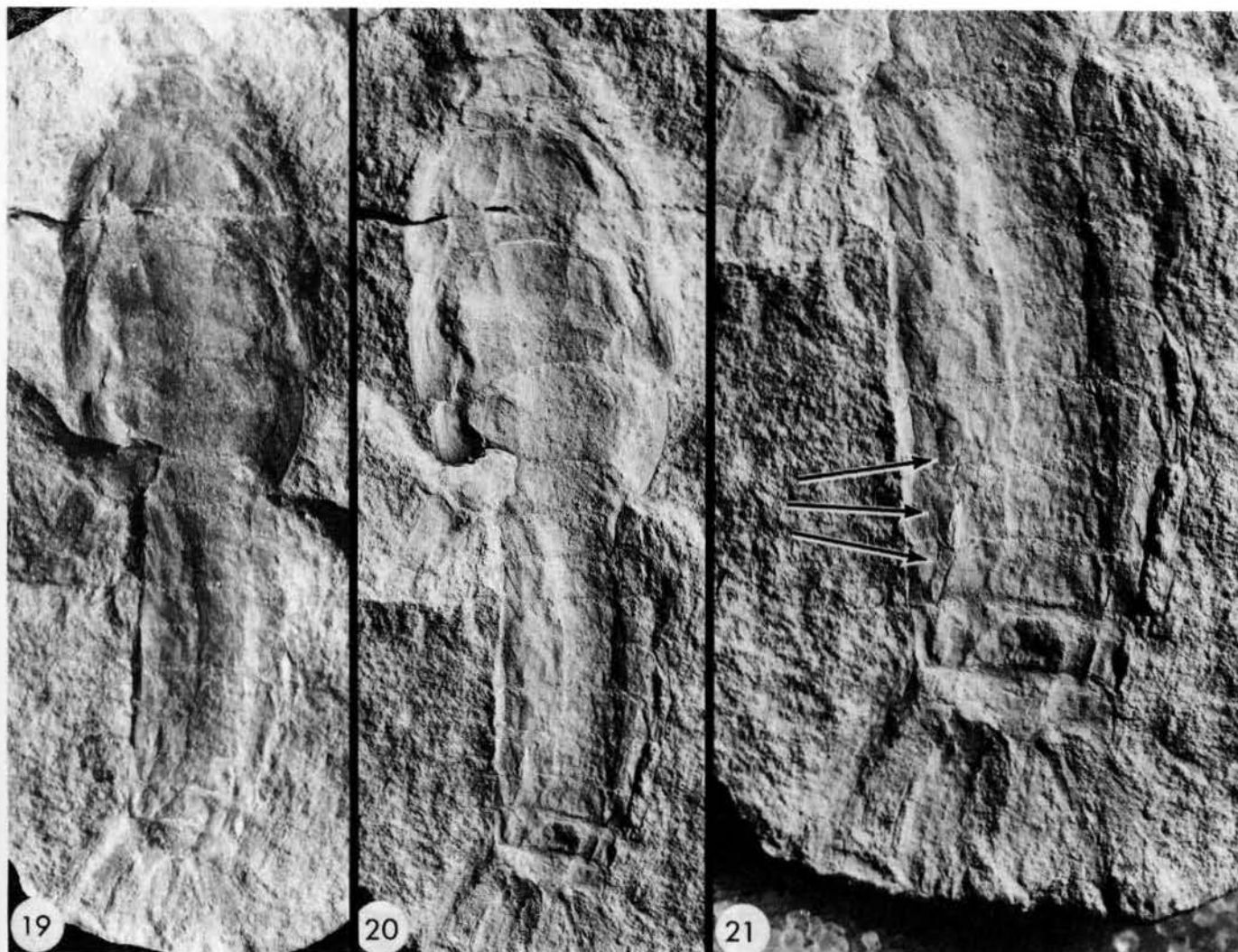
ETYMOLOGY: The species is named in honor of Walter Clayes, an amateur paleontologist who collected the holotype and offered it for scientific evaluation.

OCCURRENCE: Westphalian D, Mazon Creek, Illinois.

DIAGNOSIS: *Lithoneura clayesi* n. sp. differs from the related *Lithoneura piecko* n. sp. in the relatively longer prothorax with relatively larger prothoracic wings. It differs from *Bojophlebia prokopi* n. sp. in having smaller eyes, much heavier cerci and paracercus, and possibly in narrower tracheal gills. The prothorax in *Lithoneura clayesi* n. sp. is larger than metathorax.

Relationships

The most interesting morphological feature of the nymph is the unusually large prothorax and the large prothoracic wings. The evolutionary tendency in ephemerids is generally to diminish the size of prothorax and wings before diminishing the size of metathorax and wings. Even *Bojophlebia prokopi* n. sp.,



FIGS. 19–21. *Lithoneura clayesi* n. sp., young nymph, male, ventral side. Ventral surface irregular, showing more or less distinct traces of several serial abdominal legs (arrows). Body length 34 mm. Westphalian D, Illinois.

which is older, has a relatively smaller prothorax than metathorax.

In summary, the large prothorax with large wings that are similar in size and shape to pterothoracic wings is a plesiomorphy that is expressed in all the Carboniferous mayflies introduced here. Permian prottereismatoids already have a noticeably smaller prothorax (Fig. 31) and have quite inconspicuous prothoracic wings. In modern mayflies the prothorax is very small and prothoracic wings have disappeared, except in a single species, *Ecdyonurus venosus* (Fabricius) (Ide 1936).

Differences between Recent and Paleozoic nymphs

There are a number of differences between Paleozoic and modern ephememerid nymphs, which seem to be caused by an autapomorphic development (gradual accumulation of small character changes) rather than by major splitting of clades.

In modern nymphs, the head is usually hypognathous, antennae are short and thin, mouthparts are rather weak, and eyes are small and do not protrude much laterally. In *Bojophlebia*, the head is prognathous or almost so, the antennae are fairly thick and long, and mouthparts are well developed, sclerotized, and adapted for general feeding.

In modern nymphs by far the largest segment of the thorax

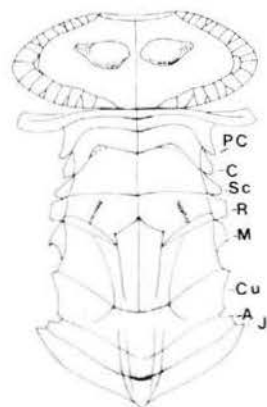


FIG. 22. *Prottereisma* sp. (Prottereismatidae), reconstruction of prothorax and mesothorax based upon specimen Nos. 3405, 3410, and 3411 deposited at MCZ, Cambridge. Note the presence of prothoracic wings in adults and rather symmetrically distributed tergal sulci. Total length ca. 6 mm. Lower Permian, Kansas. Original reconstruction.

is the mesothorax, while the prothorax and metathorax are shorter and narrower. The prothorax lacks wing pads with the exception of *Ecdyonurus venosus* (Ide 1936). In *Bojophlebia*, the largest segment is the metathorax, which also carries the

largest wing pads; the mesothorax is slightly smaller, and the prothorax is the smallest. All three segments have wings which are similar in shape and differ from each other only modestly in size.

In modern nymphs the wing articulation is always completely obliterated and the wings are "tucked away" on the back for protection and streamlining, the only exception being *Analetris* (Edmunds and Koss 1972). In *Bojophlebia*, the wing articulation was obscured because the nymph is preserved "belly up," but it was almost certainly present. Well-preserved articular sclerites in the wings of young protreismatid nymphs of Permian age are distinctly visible in the photographs published by Carpenter (1979, Figs. 10B, 10C). This nymphal articulation shows a close similarity to the adult articulation depicted by Kukalová-Peck (1983, Fig. 3) and presents important morphological evidence that pterygote nymphal wings were originally articulated and that some were still articulated in the Permian.

Legs of modern nymphs sometimes carry rudiments of tarsal segments (modern Siphonuridae; Edmunds 1972) but never exhibit double tarsal claws. In *Bojophlebia* the legs of nymphs and adults are similar: the patella is separated from the tibia by a suture, the basitarsus and four tarsal subsegments are fully preserved, and the posttarsal claws are double.

The abdomen of modern mayflies carries at most 7 pairs of tracheal plate gills while *Bojophlebia* has 9 pairs of gills. Of special interest is the occurrence of abdominal legs on segments 1 through 9 because these are always missing in modern mayflies. Only gonopods (claspers) of males survived from the primitively complete series of abdominal telopodites (Kukalová-Peck 1983). It is possible that pregenital abdominal legs were also present in the Permian mayfly nymphs but that they have been overlooked owing to their minute size. These inconspicuous, receding structures were detected in *Bojophlebia* because of their larger size (reaching 3 mm (!)) and the dark coloration of individual leg segments (Fig. 6B). It should be noted that serial abdominal legs are known to be present in Paleozoic Paleoptera other than juvenile Ephemera such as in many specimens of adult Diaphanopteroidea (Kukalová-Peck 1983, Fig. 1, and unpublished material) and in adult Permothemistida (specimen No. 11/168, Paleontological Institute (PIN), Moscow, personal observation in 1981). However, pregenital abdominal legs of *Bojophlebia* are less reduced and probably consisted of all 7 leg segments of the original abdominal telopodite (prefemur through posttarsus) as claspers of Protreismatoidea (personal observation, unpublished). The posttarsus might have carried two claws but the preservation is not good enough to observe this minute structure.

Cerci and paracercus

Cerci and the paracercus of primitive modern mayfly nymphs often bear lateral fringes of elongated interlocking

hairs, so that all the "tails" can move in unison like a paddle and propel the nymph forward in an undulating motion. The "paddle" arose very early in mayfly evolution in the Lower Permian Protreismatidae (Fig. 13) (Kukalová 1968). However, all Carboniferous mayflies known so far (*Bojophlebiidae*, *Syntonopteridae*, and *Triplosobidae*) had tails with only short hairs so that the paracercus and cerci could not interlock. Cerci of *Triplosoba* are distinctly shorter than the paracercus. This state is plesiomorphic and probably occurred in a somewhat more primitive version in the ancestral pterygotes, for the following reasons.

Cerci are derived from the legs of the 11th abdominal segment³ and their elongation and subsequent annulation is, therefore, secondary. According to Hennig (1981) Insecta Ectognatha can be divided into two sister groups, Monocondylia and Dicondylia. Monocondylia contain Archeognatha (machilids) with cerci shorter than the paracercus. Dicondylia include three major groups: primitive wingless Monura⁴ with a long paracercus and cerci still in the form of short, arched, segmented legs (Figs. 23–27); wingless Thysanura (= Zygentoma; silverfish), which have a long paracercus and shorter cerci; and Pterygota, with the most primitive order Ephemera which in the Paleozoic also had a long paracercus and shorter cerci. It is probable, therefore, that the early ancestral pterygotes had a paracercus and short, annulated cerci. If this interpretation is correct, then the abdominal legs of the 11th segment developed their specialized "cercal" articulation when they were still arched and functional. The transformation into cerci by reduction of segment number, elongation, and development of secondary annulation probably happened several times: in the ectognathous insects, in Monocondylia (Archeognatha, machilids), and again in the stem group of Dicondylia after Monura had separated from it.

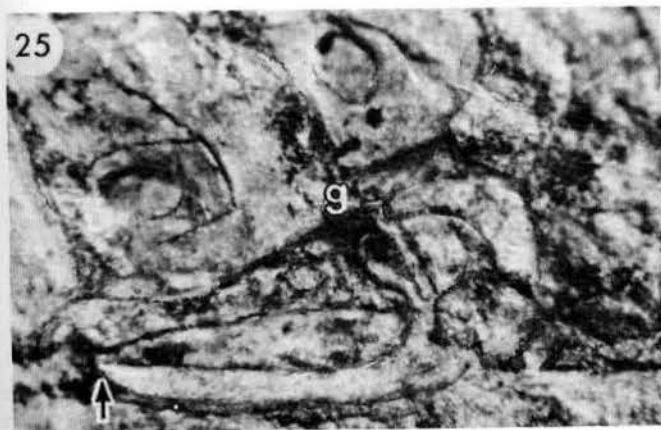
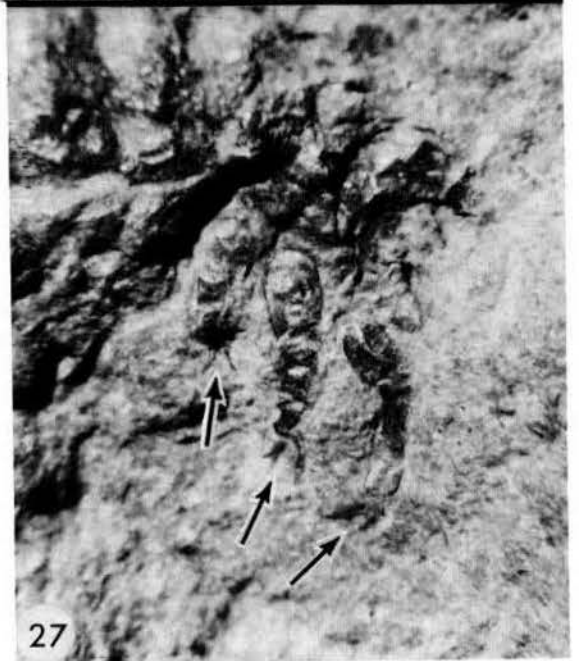
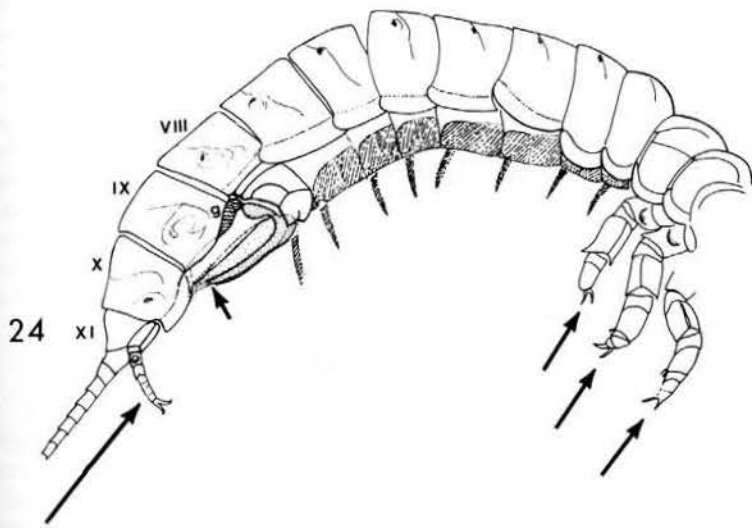
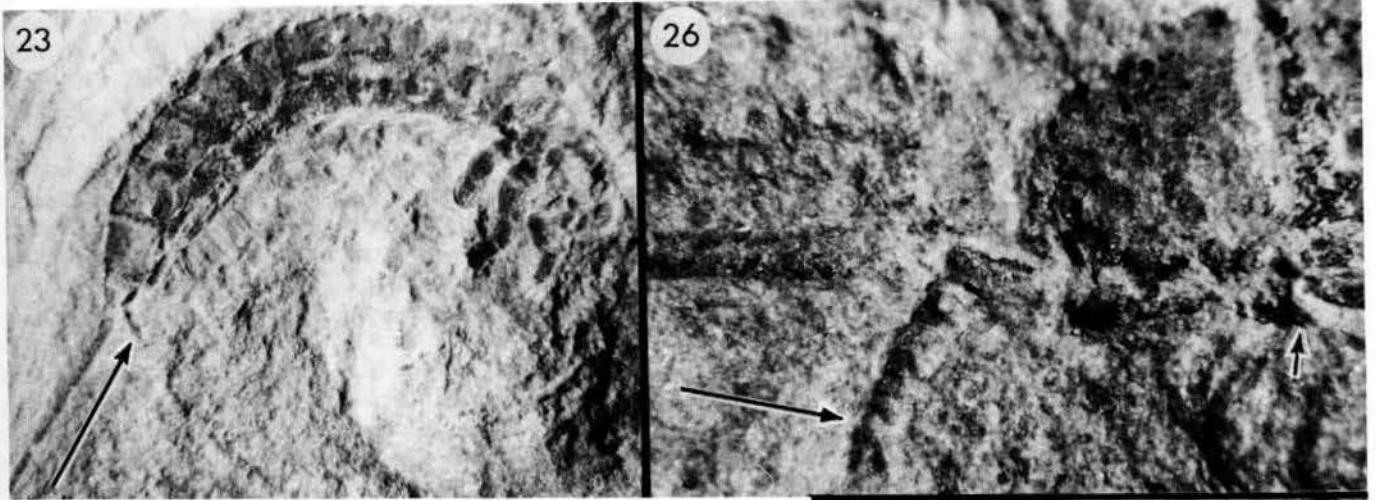
Carboniferous mayfly nymphs and metamorphosis

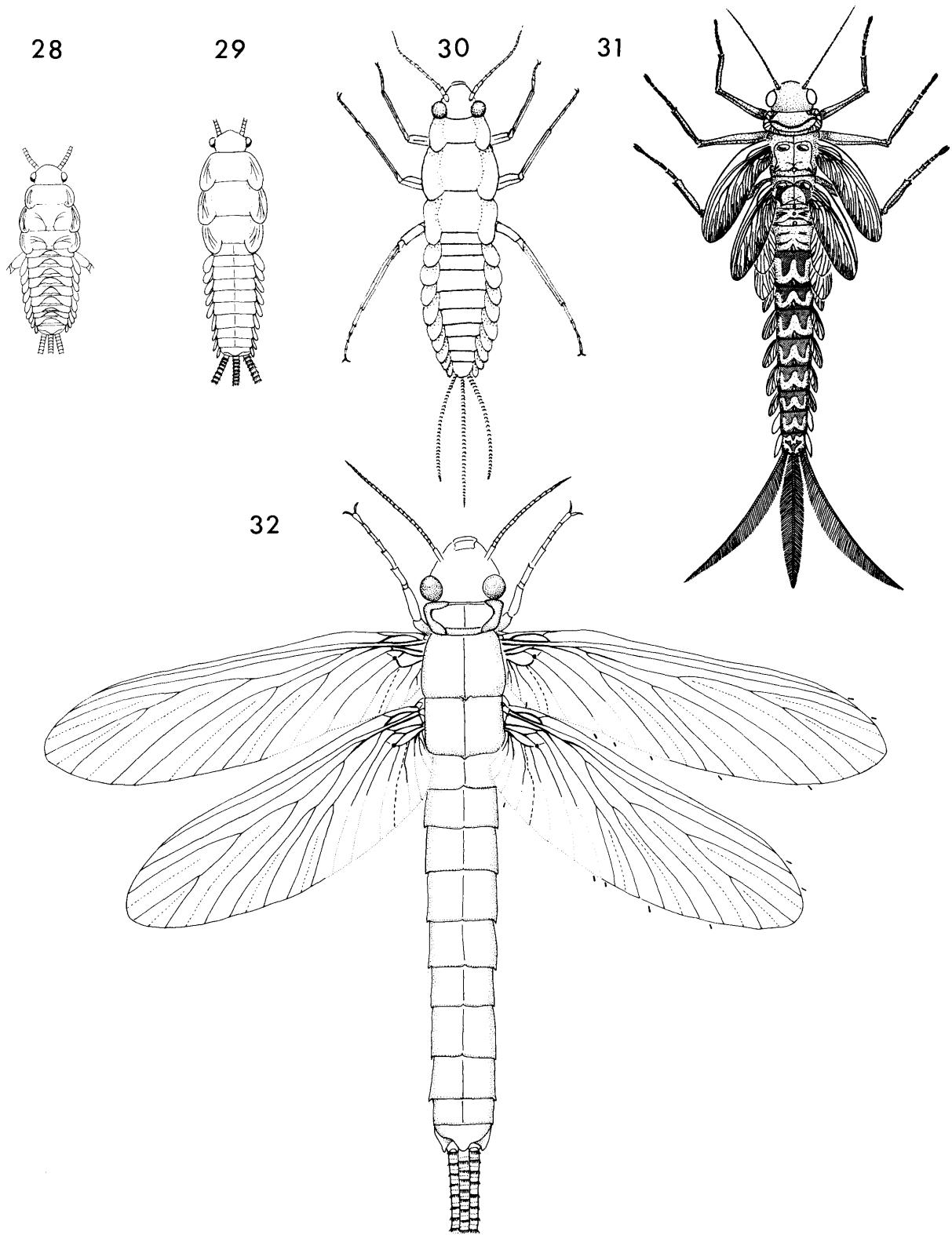
Progressive adaptation of wings towards the needs of a juvenile, pursuing mainly a better hiding ability and more stream-

³The specialized articulation of cerci originated only once in ancestral hexapods; this is shown in an extensive, as yet unpublished comparative morphological study by Edward L. Smith, California Academy of Sciences, San Francisco (E. L. Smith, personal communication).

⁴The presence of segmented cercal legs instead of annulated cerci seems to indicate that Monura were derived from the stem group of Dicondylia as an early side branch. Monura have broad, symmetrical, well-sclerotized thoracic subcoxae embedded in the body wall, a gonangulum, and a broadly triangular mandible with an interior mandibular articulation (Mazon Creek specimens: L 1658, Lietz collection; A3, Agazzi collection; P11E 757, Cozart collection; PE 39270, Field Museum of Chicago collection (Figs. 23–27)). These important characters indicate the relationship to Dicondylia rather than Monocondylia.

FIGS. 23–27. Monura, an extinct, wingless, probably largely amphibious, and primitive insect order, bear a long paracercus and arched cercal legs, ending in double claws, on the 11th abdominal segment instead of filamentous cerci. Cercal legs are also preserved in specimen Nos. 1197/595 and 598, PIN, Moscow; in specimen A3 of the Agazzi collection and in specimen PE 39270, Field Museum of Natural History, Chicago, both from Mazon Creek, Illinois; and in undescribed monurans from Carrizo Arroyo, New Mexico, author's collection. Monura are probably a sidebranch of the Dicondylia stem group. Note the pleuron of the 8th abdominal segment, gonangulum (*g*) on the 9th segment, and ovipositor, all closely resembling those of primitive Pterygota. Resemblance of body form to machilids is plesiomorphic and misleading. Fig. 23. Cast cuticle of *Dasyleptus* sp., Cozart specimen No. P11E 757, length 18 mm, without paracercus. Westphalian D, Mazon Creek, Illinois. Fig. 24. Same specimen, original drawing. Fig. 25. Same specimen, detail of ovipositor showing triangular gonangulum (*g*). Fig. 26. Same specimen, showing enlarged cercal leg with segments and little claws. Fig. 27. Thoracic legs ending in double claws. Long arrows (Figs. 23, 26) indicate the arched cercal leg of segment 11; medium arrows (Fig. 27) point out the double claws on the thoracic legs; short arrows (Figs. 25, 26) indicate where both valves of the ovipositor broke off.





FIGS. 28–31. Developmental changes in size and position of wings in late Paleozoic juveniles. Younger nymphs (Figs. 28, 29, 30) have strongly curved, probably afunctional wings with weakly formed articulation; older nymphs (Fig. 31) have widely spread, fully articulated wings engaged in underwater flying; and subadults (Fig. 32) have flying wings with a residual nymphal bend. Fig. 28. *Lithoneura piecko* n. sp., youngest nymph. Fig. 29. *Lithoneura clayesi* n. sp., young nymph. Fig. 30. *Bojophlebia prokopi* n. gen., n. sp., young nymph. Fig. 31. *Kukalova americana* Demoulin, 1970, older nymph. Fig. 32. *Misthodotes delicatulus* (Tillyard) subadult with delicate wings bearing residual bend and not fully developed genitalia. All original reconstructions based upon holotypes.

lined contours, first occurs in Paleozoic ephemerids in the younger instars. In sharp contrast to the streamlined young nymphs (Figs. 28, 29, 30), older nymphs (Fig. 31) and subadults (Fig. 32) had their wings widely spread laterally (in a functional position) and had adultlike wing articulation (Kukalová-Peck 1978; Carpenter 1979, Figs. 10B, 10C). It seems that the adaptation towards a better hiding ability started in the most vulnerable young instars and progressed so quickly that it eventually required a metamorphic instar still within the juvenile stage. Occurrence of adaptive "Recent juvenile" changes first in the young instars was also observed in Paleozoic Neoptera (Rasnitsyn 1981) and in specialized Paleodictyoptera (Kukalová-Peck 1983). The most probable implication is that the metamorphic instar, present in all Recent pterygotes, originated *between relatively young instars* of the primitive developmental series rather than near the end of the series, as is often assumed. Metamorphic instars originated independently in all major evolutionary lineages (Kukalová-Peck 1978); therefore, the original number of instars that preceded and followed the metamorphic instar is bound to be more or less different in these lineages.

The metamorphic instar probably originated to bridge the gap caused by the progressive adaptation of younger instars mainly for hiding. In the course of this adaptation, the wings became entirely immobilized, reduced, and tucked away on the back or invaginated. Restoration of the wings to a larger size and mobility remained a gradual process for some time in the Paleozoic, with many ecdyses. Still later, the metamorphic instar occurred and postmetamorphic instars fused into the adult stage as we know it in Recent insects. The fossil record seems to indicate that (i) in Recent insects the nymphal or larval stages represent only part of the original developmental series further reduced in number of instars, and (ii) the Recent adult stage is a varied fusion of older nymphal, subadult, and adult instars of the original developmental series.

Emendations of venational nomenclature

The venational nomenclature used in this paper in labeling veins and numbering branches conforms to a veinal system that can be homologized, as proposed by Kukalová-Peck (1983). The ultimate goal of this system is to reflect the way venation evolved, to clearly define the nature of character states, and to improve comparisons between taxa.

As indicated by the fossil record and the venation of primitive living orders, the nonflying proto-wings were almost symmetrical, with homonomous, dichotomously branched veins. Each original vein started branching immediately after leaving a blood sinus (basivenale) and was composed of two (fluted) sectors: the convex anterior (A+), and the concave posterior (P-). As the wings progressively responded to flight-induced asymmetrical forces, the veins in the anterior and posterior parts of the wings became strongly modified. Anteriorly, they lost their branches and became crowded, braced, and fused into the costal margin (precosta PC, costa C, and subcosta anterior ScA+); posteriorly, they spread into a pliable fan which was braced only near the base (anal A and jugal J). Contrary to this, the middle veins (radius R, media M, and cubitus Cu), more or less retained their original, paired, and dichotomously branched condition; the basal sectoral stems RA & RP, MA & MP, and CuA & CuP usually became fused together into one veinal stem R, M, and Cu. All the above-mentioned changes towards asymmetry are adaptive because

all wing veins, with the one exception of M⁵, have at times been documented to be preserved in the original state as two completely independent veinal sectors, forming a true veinal pair starting from the wing base. The original pair is preserved in Paleozoic mayflies in the following veins: CA and CP, ScA and ScP, RA and RP, AA and AP, and JA and JP. The implication is that the original veinal system and, consequently, also the proto-wing were largely symmetrical.

To be able to trace the intricate and varied phylogenetic changes in the venation of pterygote orders, an evolution-based nomenclature is essential. Typological elements in nomenclature are highly undesirable, because they prevent comprehension of character states. Wing veins should be labeled in accordance with the way they evolved between the ancestral symmetrical and the flight-adapted asymmetrical veinal systems. The two primitively separated veinal sectors, anterior and posterior, should be designated as such whenever they are still preserved in their original form, and the substitute terms that are used for them in several living order should be avoided. This concerns, for example, the subcostal brace ScA+ present in Ephemera and several other living orders, as follows.

Primitively, the ScA+ sector starts from a subcostal basivenale, runs obliquely anterodistally, and fuses with the costal margin, thus forming a brace. In fossil orders, ScA+ is always well preserved and sometimes very long in Paleodictyoptera and in most Paleozoic Neoptera (Kukalová-Peck 1983, Fig. 17C). In recent orders, the ScA brace is usually close to the wing base and is no longer discernible, but it is strong and well preserved in Ephemera, Megaloptera (Kukalová-Peck 1983, Figs. 17A, 17B), some Neuroptera, Odonata, Blattodea, and in the primitive Orthoptera (misinterpreted as "ambient costa").

In this evolutionary setting, the ScA brace stands out clearly as part of the primary veinal system that was used in several orders for a new purpose. In Ephemera, it was forked and arched as ScA & ScA3-4 (Figs. 36, 37), and the arch became increasingly more involved in the ephemeroid type of flight (Brodski 1974), representing the constitutive character of this order (Hubbard and Kukalová-Peck 1980); in Orthoptera, ScA+ was primitively long and strengthened the flanks of the rooflike arrangement of folded wings; in Blattodea, ScA+ fortified the "shoulders" of flexed wings; in Odonata, ScA provided a flexible brace between the axillary plate and the costal triangle, and so on.

Following the homologous veinal system, the "costa" of previous authors is composed of the PC (the serration in fossil mayflies), CA, CP (basally separated in fossil mayflies), and ScA1-2 and is called here the costal margin. The "costal brace" of previous authors is composed of ScA & ScA3-4 and is called the subcostal brace; "Sc" here is labeled ScP-, "R1" is RA, "Rs" is RP, and M and Cu veins are unchanged.

The traditional nomenclature of anal veins in Ephemera is typological in that it uses simple successive numbering of branches. However, the anal vein did not originate differently from other veins and therefore must not be *labeled differently* from other veins! Also, simple numbering cannot describe the composition of the anal brace, thus concealing the important relationship of ephemerids to odonates. Finally, it misses the

⁵Almost surely, sectors MA and MP, completely separated basally, were present in the Early Carboniferous (Mississippian) pterygotes which, alas, are still undiscovered. Basal fusion of MA & MP must have been essential for flight and, therefore, occurred very early in evolution.

fact that the first anal branch is fused with CuP, again an important constitutive character.

As far as fluting is concerned, AA and AP sectors in Ephemera were convex already in the Carboniferous mayflies and stayed that way up to Recent times. Consequently, all concave elements in the anal area are concave intercalated veins (IN-). Note that in the whole history of venation, the anterior anal (AA) never changed position from convex to completely concave. It is, therefore, highly unlikely that the deeply concave "2A" (Borror and DeLong 1971, Fig. 94) should be a primary vein. In opposition to this, the AP sector in the proto-wing was mildly concave and stayed concave in many fossil (Fig. 35) and some Recent insects, including some Recent odonates. The level or convex position of AP is always secondary but occurs frequently, as would be required by flight mechanics. In Ephemeroptera, AP is consistently level or mildly convex since the Late Carboniferous.

Nomenclature of branches

As documented earlier in fossil and primitive Recent insects (Kukalová-Peck 1983), both veinal sectors (A+ and P-) of each vein originally were branched dichotomously about *four times*. In Recent insects, veinal sectors usually branch only twice or less, by reduction. To correctly label the *twice* dividing branches, so that veinal systems can be compared with each other as well as with the reduced state, requires using four digits: 1, 2, 3, 4. In the case of only one branch, hyphenated numbers are recommended, 1-2 and 3-4 (also to express uncertainty as to which one of the two branches was reduced). Labeling branches haphazardly as they reach the wing margin does not help phylogenetic considerations, in fact, it may easily disguise a relationship.

In Ephemera, it is currently customary to label the anterior radius sector RA as "R1" and the subsequent branches of RP as "Rs2," "Rs3," "Rs4," and "Rs5." This numbering fails to reflect the fact that the anterior radius RA is a veinal component equivalent to the posterior radius RP. The proof that RA and RP of the odonatoephemeroid clade indeed are not one branching vein but two independent sectors of a veinal pair is presented in this paper and in Riek and Kukalová-Peck (1984). Note that bojophlebiid and syntonopterid mayflies figured here have the RA sector basally fully separated from the RP sector. Adjacent, incompletely superimposed stems of RA and RP can still be distinguished from each other in large Recent mayflies. All Recent dragonflies have a characteristic "double radius" which consists of the adjacent, parallel sectoral stems RA and RP (see discussion on double radius in Paleoptera by Kukalová-Peck (1983)). The emended labeling of RP branches in Ephemera proposed and used in this paper is RP1, RP2 (forked), and RP3-4 (Fig. 39).

Thus, according to the veinal system of Carboniferous and Permian mayflies, the MA in Recent mayflies divides into MA1-2 and MA3-4. MP divides into MP1-2 and MP3-4 with several secondary intercalary veins as medial supplement Mspl; CuA divides into CuA1-2 and CuA3-4 (if present). The rest of the CuA branches belong to secondary cubital supplement Cuspl.

The typological, successive numbering of anal branches as currently used by other workers provides no labels for an analysis of the anal brace. Yet this brace expresses the relationship between Ephemeroidea and Odonatoidea! The entire Paleoptera can then be subdivided according to the form of anal braces, as will be shown later, but none of these properties can

be described with simple numbering. As introduced here, the anal brace of Ephemera is composed of aligned veinal sectors connecting the anal basivenale with CuP, namely of AA & AA1-2, while A1 is fused with CuP at a flight-important meeting point of veins. In recent Ephemera, AA1 is fused with CuP, the first free anal branch is AA2 ("1A" of authors), followed by concave intercalary vein IN- ("2A" of some authors), followed by the remaining anals, as shown in Fig. 39.

Systematic position of Ephemera

Presently, most entomologists agree that the Pterygota formed as a group by the adaptation of proto-wings and wing articulation for flapping and consider the pterygotes to be monophyletic. This concept recently received strong support in the fossil record and in comparative morphology, anatomy, physiology, and genetics (Kukalová-Peck 1983).

Within the system of Recent pterygotes, Ephemera are usually considered to be related to Odonata and are classified as one of the two surviving orders of Paleoptera. All other insects are grouped into Neoptera. The former division of Pterygota into Hemimetabola and Holometabola is now believed to be typological because metamorphosis arose several times convergently after Pterygota had already radiated into distinctive lineages (Kukalová-Peck 1978 and references therein). The Paleoptera contain the orders Ephemera, Protodonata, and Odonata with chewing mouthparts, and at least four extinct orders with elongated, haustellate mouthparts of the piercing-sucking type, namely Diaphanopteroidea, Paleodictyoptera, Megasecoptera, and Permothemistida (Figs. 33A, 33B). The haustellate Paleoptera were the most prominent and abundant component of entomofauna in the Carboniferous and Lower Permian tropical belt, and declined in the Upper Permian. Haustellate mouthparts (Fig. 33B) are homologous to the primitive ephemeroid type (Figs. 34A, 34B) with the anterior mandibular articulation converted into a slider that was further specialized for lengthwise sliding. Propped against the long palps ending in two claws, the mouthparts were able to tear apart fructifications and imbibe the whole contents of the strobili, including spores or pollen, which are on occasion found in the guts of insect fossils (personal observation, unpublished). Wings of haustellate Paleoptera are very varied, ranging from flexing over the abdomen (Diaphanopteroidea) to permanently stretched to the sides (Paleodictyoptera, Megasecoptera, Permothemistida), from broadly attached basally (Paleodictyoptera) to a very narrow petiolate base (some Megasecoptera), and from broader hind wings or homonomous size of wings (Paleodictyoptera) to near diptery (Permothemistida). The wings share as synapomorphy the simple type of anal brace (secondary sclerotization of the membrane in the basal corner of the anal area) and have the plesiomorphic, simple, oblique subcostal brace.

The relationship between Ephemera and Odonata has always been considered to be rather enigmatic. They have been designated as sister groups by Sharov (1966), Kukalová-Peck (1978, 1983), and Hennig (1981). This conclusion was challenged by Boudreaux (1979) who presumed Ephemera to be closer to Neoptera than to Odonata and argued that the group Paleoptera does not exist. Recently, much new evidence has emerged in the fossil record on venational systems, providing strong support to the sister-group relationship.

The major obstacle in stating clearly the relationship between Ephemera, Odonata, and the four extinct haustellate orders was always the typological nomenclature of dragonfly

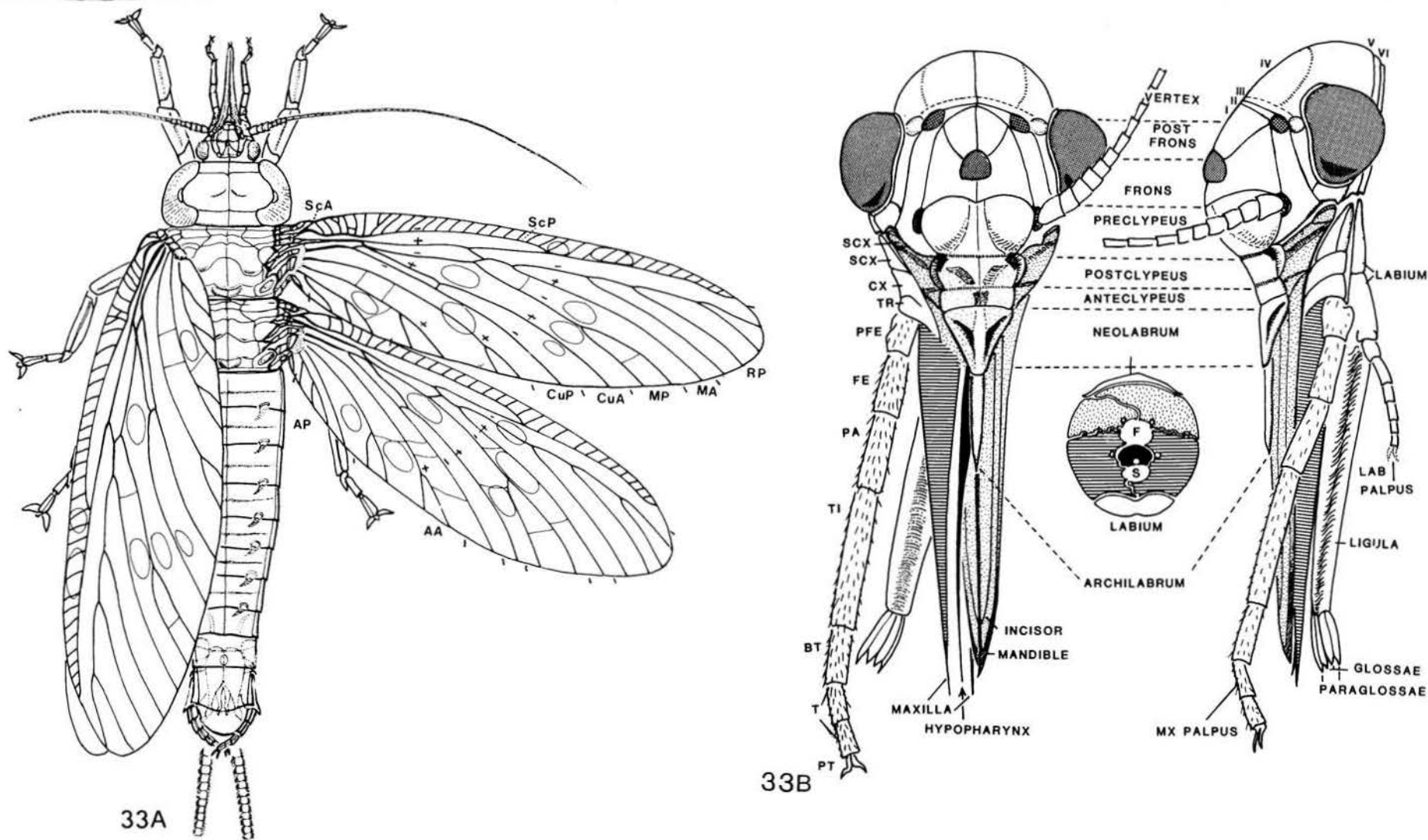


FIG. 33. (A) Haustellate Paleoptera, the most primitive order Diaphanopteroidea, male. This "see-through" reconstruction shows the reduced prothoracic wings and 9 pairs of abdominal legs ending with claspers. Wings have a bandlike articulation composed of unfused sclerites, which allow wings to be flexed backwards. Undescribed material from Lower Permian, Urals. Reconstruction based mainly on specimen Nos. 1700/488, 493, 494, and 495, PIN, Moscow. Original reconstruction. (B) Head of haustellate Paleoptera. Reconstruction based upon the same specimens as those indicated in A and on broken beaks of *Homaloneura dabasinskasi* Carpenter & Richardson, 1971 and *Monsteropterum moravicum* Kukalová-Peck, 1972, and on about 20 heads from Mazon Creek, Illinois, Elmo, Kansas, and Obora, Czechoslovakia. Mouthparts are very similar to Recent mayfly nymphs but have elongated stylets. Head bears 6 horseshoe-shaped head segments (I–VI) and 5 stylets modified for piercing and sucking: two mandibles, two maxillae, and one hypopharynx. Mandibles lack the molar lobe and the anterior and posterior articulation is changed into sliders. The anterior slider shown in outline under the postclypeus and anteclypeus. Maxillary stylets are lacinio-galeae. Labium served as a trough for stylets and must have folded up like a Z as the stylets penetrated plant tissue. Enlarged cibarial sucking muscles account for the inflated preclypeus. The archilabrum and tip of labium probably served as clamps. The orientation of the head was more or less hypognathous. This interpretation is the result of my collaboration with Dr. Edward L. Smith, California Academy of Sciences, San Francisco.

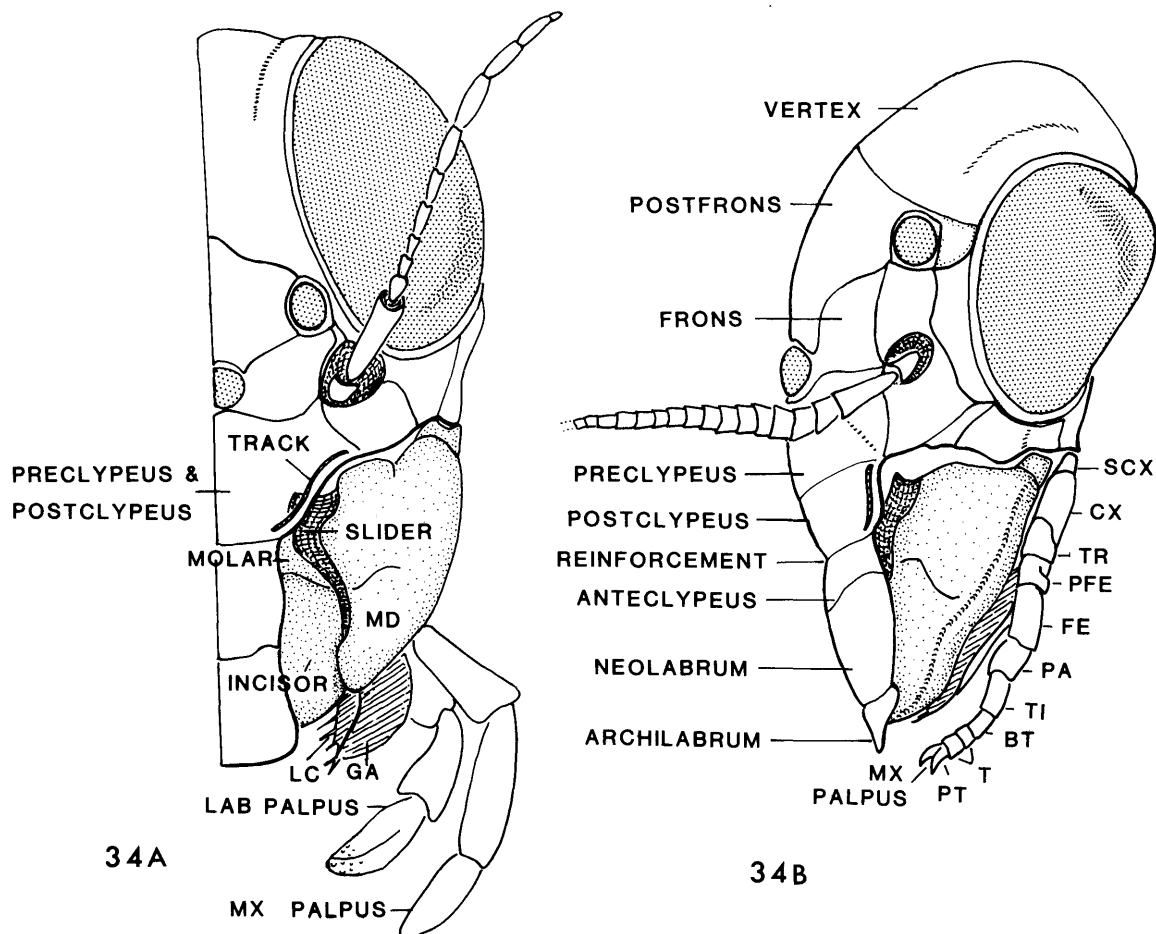


FIG. 34. (A) Head of a Recent primitive mayfly nymph showing a mandibular slider replacing anterior articulation and the inside clypeo-antennal track. Based on the unpublished figure of Dr. Edward L. Smith (California Academy of Sciences) but simplified. (B) Head of a Paleozoic mayfly adult. Composite of eight specimens of *Protereisma* (mainly No. 4374) and *Misthodotes* (mainly No. 4389) from Lower Permian of Kansas, MCZ, the Peabody Museum, Yale University, New Haven, and three specimens of *Misthodotes* (PIN No. 1700/371, 1700/388, 212/26) from Lower Permian, USSR. Note that mouthparts were functional, the presence of a mandibular slider, a primitive archilabrum, and the maxillary palpus represented by a complete leg. Original head segmentation was still partly preserved; the curious bulge between the antennal ocellus and the eye may be a reduced remnant of the postantennal ocellus. This interpretation is the result of my collaboration with Dr. Edward L. Smith (California Academy of Sciences). Original reconstruction.

venation, which did not allow comparison with either Ephemeroptera or with the rest of Paleoptera and Neoptera. The odonatan veinal system appeared to be unique in all Pterygota in lacking two complete primary veins, sectors MP- and CuA, while the rest of venation branched in a way which did not show any relationship to other pterygote orders. The inescapable theoretical outcome was that winged insects are a grade and not a clade, and consequently that the wings developed twice. Some entomologists accepted this interpretation (La Greca 1980; Matsuda 1981). However, this solution to the problem is contradicted by the sharp and general increase in similarity of wing characters in all insect stem groups in the Paleozoic. This increase includes odonatoids and is massively documented.

Insight into the puzzling relationship within the Paleoptera was recently provided by the fossil record. It was documented that Paleoptera, including Odonatoidea (Protodonata and Odonata), share numerous veinal characters and a certain type of bandlike wing articulation linearly fused into axillary plates, which is very different from the neopterous, clusterlike articulation with axillary sclerites and a characteristic revolving element 3Ax (Kukalová-Peck 1983; Kukalová-Peck and Richardson 1983). At the same time, the veinal nomenclature system of Odonatoidea was emended with the help of two

extremely primitive dragonflies (Protodonata: Eugeopteridae) from the Namurian of Argentina (Riek and Kukalová-Peck 1984). After this correction, the dragonfly veinal system lost its unique character and was shown to be completely homologous to other pterygote veinal systems. In particular, it became very similar to that of Paleozoic mayflies (Figs. 35, 36, 37). The similarity includes veinal branching pattern, fluting, and bracing pattern (identical braces and struts between MA & RP and between CuA & M), type of intercalary veins, type of crossveins, dense archidictyon, and especially the shared presence of the veinal anal brace. The anal brace is composed of AA & AA1-2 and is fused to CuP in an area important for flight. This unique feature distinguishes odonatoephemerids not only from the haustellate Paleoptera but also from all Neoptera.

If they are superficially inspected, the oldest odonatooid and ephemeroid wings seem to be very similar.⁶ However, this is

⁶The oldest odonatooids, the Eugeopteridae, also had two axillary plates, which is a convincingly odonatooid type of wing articulation (Fig. 35). Development of differences in powered flight between ephemeroids and odonatooids must have been well under way already in the Early Carboniferous.

what should be expected in sister groups which, 300 million years ago, were near their divergence from a common ancestor. Following Hennig's theoretical systematics, sister groups must differ in at least one apomorphic character. In the wings of the oldest fossil representatives, two veinal characters are very different: ephemeroids have the ScA brace arched and very strong as an apomorphy and a bulla in CuP at the end of the anal brace as a plesiomorphy, while odonatoids have the straight ScA brace as a plesiomorphy and a kink in CuP at the end of the anal brace as an apomorphy. These characters separate the two superorders till the Recent times.

In spite of the fact that the observable differences in venation seem inconspicuous, they actually mark the beginning of two unique autapomorphic trends, which ultimately took the sister groups far apart from each other. In this respect, they are true constitutive characters at an ordinal level as defined by Hennig (1981). The initial solitary kink in CuP, which only occurred in the eugropterid dragonflies (Fig. 35), was gradually followed in the late Paleozoic and early Mesozoic by several additional kinks: in ScP (nodus), RP & MA (arculus), MP (part of triangle), and in CuA (at the triangle) (Riek and Kukalová-Peck 1984). Ultimately, the wings of Recent dragonflies became ridden with kinks and extremely autapomorphic, unlike any other winged insects. The evolutionist, however, must be aware of the fact that for comparison only one, the initial, kink in CuP is meaningful. The wings of Recent dragonflies certainly look quite different from those of recent mayflies (even if they do bear some overall similarity), but this difference was not present when the sister groups separated.

The veinal system of large Carboniferous mayflies is "stripped" of most autapomorphies; there is no desclerotization of M and Cu basal stems, the ScA brace is arched very gently so that costa and precosta (serration) are fully visible, and the veinal anal brace is not very conspicuous (Figs. 2, 11-14). In this state of development, ephemerid venation is extremely similar to that of the oldest odonatoids. Later, autapomorphic evolution took ephemeroids towards an ever stronger and more highly arched subcostal brace, and towards a stronger and larger anal brace, while the veinal stems of M and Cu became desclerotized along with sections of veins close to the anal brace (Figs. 36-39).

There is a well-pronounced parallel evolution in early ephemeroids and odonatoids during which arch and strut braces between MA & RP and CuA & M changed into real fusions; another parallelism is in RA & RP sectoral stems, which became adjacent in a more or less perfect "double radius."

Hypothetical ancestral Odonatoephemerida

Considering all the new information that is now known from the fossil record, it is possible to reconstruct a hypothesis of a set of characters occurring in the ancestral Odonatoephemerida, as in the following discussion.

The wing articulation was bandlike, the axillary plate was enlarged, radial sectors were fused together with several articular sclerites so that gliding was effortless and wings could not be flexed over the abdomen. The precosta in the anterior margin was serrated. The subcostal brace was oblique, long, and forked: one branch (ScA1-2) was fused with the costal margin, the other branch (ScA3-4) was directed posteriorly and fused with ScP. RA and RP veinal stems were completely separated from each other basally and did not touch. RA was weakly branched at the end, RP was dichotomously branched several times. All veinal sectors were dichotomously branched except

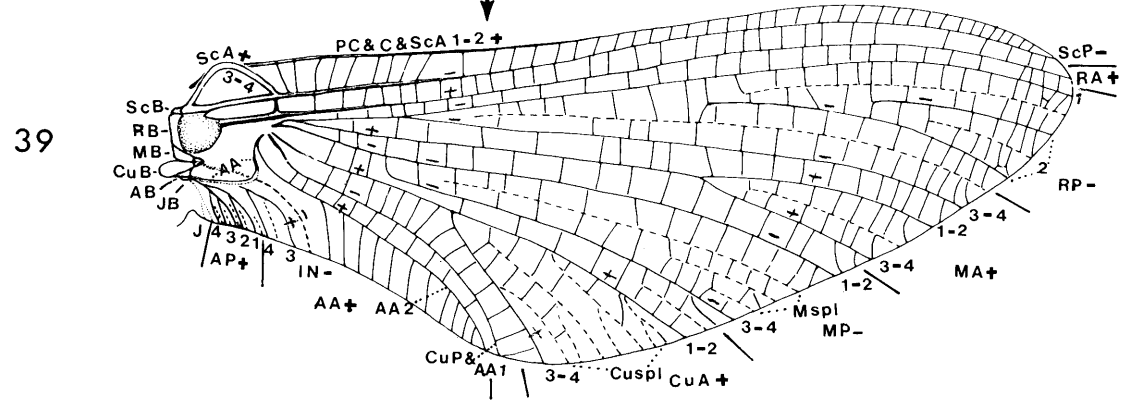
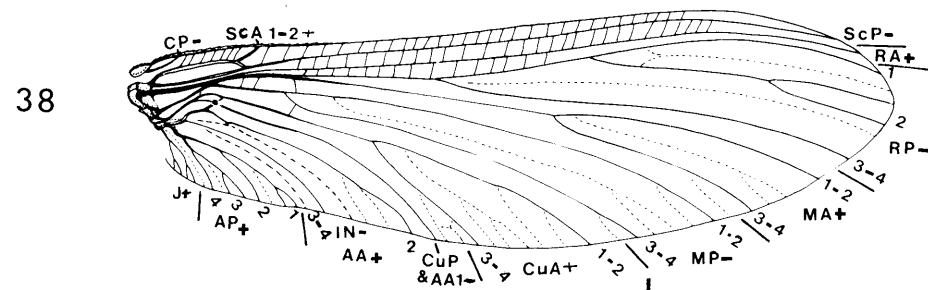
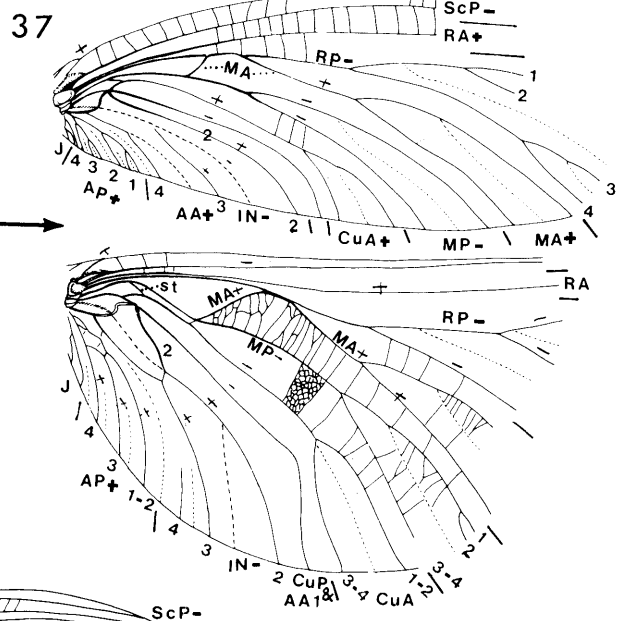
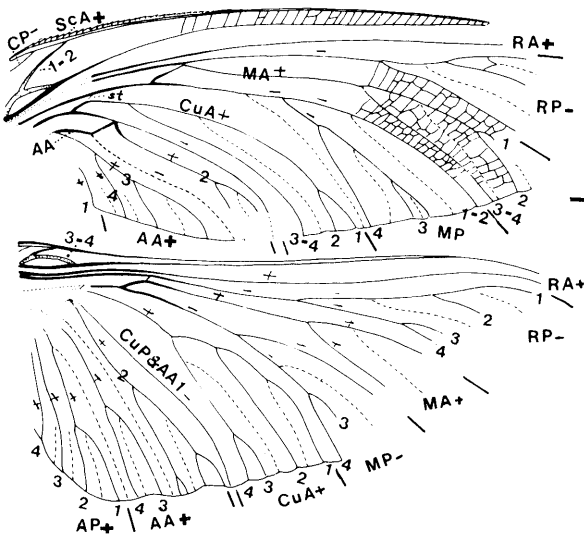
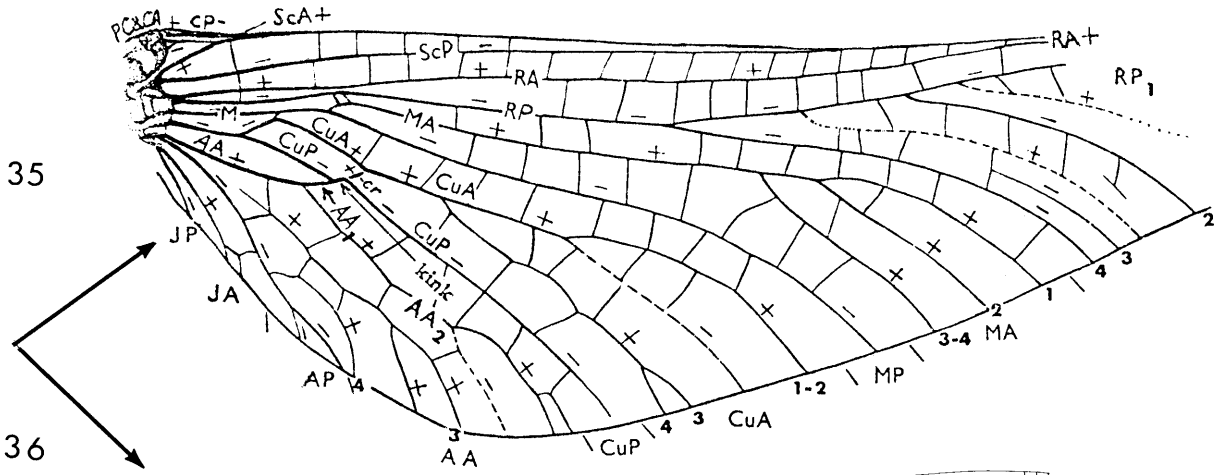
CuP, which was probably already devoid of branches. MA was arched to RP, CuA was arched to M, and both arches were braced by struts. The anal brace was concavely bent, veinal, extending between the anal basivenale and CuP, and was composed of AA & AA1-2 & AA1. Branch AA1 was fused with CuP at an area important for flight. Jugal veins were branched and the jugal area was small. There were prominent intercalary veins regularly alternating with the veinal branches. The wing membrane was covered with a dense and fine archdictyon and irregular crossveins.

Body structures of Odonatoephemerida were as follows. The head was probably mildly hypognathous with long antennae and functional mouthparts that resembled those of fossil mayflies (and extinct paleodictyopteroids) in lacking a permanent mandibular anterior condyle (Figs. 33A, 33B and 34A, 34B). The mouthparts⁷ were adapted for general feeding and survived in a nearly primitive condition until Recent times in ephemerid nymphs. Odonatoids developed a permanent anterior condyle in the mandible as they shifted towards predatory feeding. The abdomen was probably long and relatively narrow, with short cerci and paracercus. Females had an ovipositor similar to recent damselflies but with a long, segmented gonopod ending in two little claws. Males had fully segmented gonopods (claspers) also ending in two claws. Nymphs were aquatic general feeders and had three pairs of homonomous wings in young instars and two pairs of appendages on 9 abdominal segments: 9 pairs of epicoxal exites, and 9 pairs of segmented legs, each probably ending with two little claws. Exites were probably tubelike and annulated and functioned mainly as movable breathing devices (gills), thus resembling homologous filaments of polythorid and euphaeid damselflies and some primitive stonefly nymphs.

Older nymphs had the thoracic wings curved and spread laterally in a functional position and perhaps used them at first for underwater movement and respiration. After emergence from water, the short stubs of wings may have been used for hopping as in living brachypterous insects and for thermoregulation, before they could have been used in full flapping flight.⁸ It is not excluded that some instars were amphibiotic and used short wings both for swimming and hopping. Younger subimagos had wings curved backwards and the curve became gradually straightened with each ecdysis (Kukalová-Peck

⁷Research on Recent insectan heads and mouthparts and a detailed comparative study of mandibular articulation and function was done by Dr. Edward L. Smith (California Academy of Sciences) and will be documented in his forthcoming book, *Atlas of Arthropods*.

⁸New research on flight of birds, using models that apply aerodynamic principles, suggests that controlled fall from trees (gliding) could not have preceded flapping flight (Lewin 1983). Instead, flight started in all probability as a series of hops, probably while chasing insects, aided by a flap of (feathered) forelimbs. Hence, from the point of view of aerodynamics, the active use of insectan proto-wings in short hops for escape, food gathering, and dispersal seems to be the most probable evolutionary stimulus for their evolving into flying wings. The hypothesis that insects developed flapping wings by jumping off trees is not likely, especially since adult protopterygotes started leaving water (in the Silurian?) when there were no trees. Wind transport is likewise improbable. Primitive Paleozoic insects were large, with a very rich and primitive wing venation and body morphology. This richness would not be present if the ancestral insects developed from small individuals adapted as aerial plankton. Structures, that become reduced in small animals generally do not return to their original state with a secondary increase in size, especially if they are deeply plesiomorphic and very complex.



1978). There was no metamorphic instar and development was entirely confluent, with many instars of older nymphs, subimagos, and possibly also imagoes. The split into ephemeroid and odonatoid clades probably happened before the mode of flight was fully established, i.e., at some time in the conversion from proto-wings to wings when insects were flying by short hops. This early divergence accounts for the differences in wing articulation and wing musculature engaged in powered flight (Kukalová-Peck 1983, Fig. 16, and references therein).

Veinal system of Odonatoephemerida, haustellate Paleoptera, and Neoptera

Veinal systems of Odonatoephemerida and haustellate Paleoptera share the following features: a similar pattern of braces (if present), which includes arch and strut support or direct fusion between RP or R & M or MA, and between CuA or Cu & M; stems of R and M originating apart from each other from the basivenalia (except in petiolate and very small wings); similar, regularly alternating fluting of veins and branches (convex veins formed as ridges largely in the dorsal wing membrane and concave veins formed as ridges largely in the ventral wing membrane). A double radius (RA and RP running more or less parallel to each other in the proximity of the base) occurs in Ephemerida, Odonatoidea, and in the most primitive Paleodictyoptera (Kukalová-Peck 1983; Kukalová-Peck and Richardson 1983; Riek and Kukalová-Peck 1984).

In contrast, Neoptera have a more complicated system of braces, the veinal stems of R & M are always either fused or at least closely adjacent *immediately at the wing base*, and fluting of RP and of M branches is either lowered, levelled, or even reversed to a uniformly convex position (Kukalová-Peck 1983, Figs. 13, 14). Almost all veins in neopterous wings are formed in both the dorsal as well as the ventral membrane (Kukalová-Peck 1978). There is no double radius, only a fused radial veinal stem or fused or adjacent R & M stems.

Odonatoephemerida differ from the haustellate Paleoptera in venation mainly in the structure of the anal brace, which functionally means that they differ in their way of flight. Articulation has a relatively larger, more specialized axillary plate than in haustellate Paleoptera (Kukalová-Peck and Richardson 1983, Fig. 11). Specialization for flight probably provided the basic evolutionary impulse for early divergence of odonatoephemerids from the paleopterous stock. In haustellate Pale-

optera the anal area is braced by a sclerotization of the anal fan in the basal corner adjacent to the anal and jugal basivenale. This is sometimes delimited posterodistally by a bar that is either straight, bent, or V-shaped. Contrary to this, Odonatoephemerida have a veinal anal brace composed of strong, aligned sections of AA & AA1-2 & AA1, extending between the anal basivenale and CuP and bracing the anal area against buckling. This connects to CuP at a meeting point of several veins, a feature which is important for flight. All haustellate Paleoptera lack this connection between the anal brace and CuP. Neoptera also have a veinal anal brace, but its adjoinment to CuP is unimportant for flight and is always inconspicuous. It has not been noticed by most students of insect wing venation.

Summary and conclusions

Detailed comparisons between the earliest fossil mayflies, dragonflies, extinct haustellate Paleoptera, and Neoptera showed that the wings evolved only once, the Pterygota are a monophyletic group, and the first major division was into Paleoptera and Neoptera.

Paleoptera are a clade which shares, among others, a number of characters in wing venation, namely the pattern of veinal braces, R and M separated from each other basally, a strong type of fluting, and veins largely formed in either the dorsal or ventral membrane (in Neoptera, veins are formed mostly in both membranes). The last two characters of Paleoptera are apomorphic.

Paleoptera are composed of two sister groups that were derived from unknown, common, paleopterous ancestors: one with haustellate, sucking mouthparts, now extinct, including order Diaphanopteroidea, Paleodictyoptera, Megasecoptera, and Permothemistida; and the other with chewing mouthparts, including the living orders Ephemerida and Odonata and the extinct Protodonata. The apomorphic character occurring in all types of mouthparts is the fused laciniogalea. Ancestral Paleoptera are the sister group of Neoptera.

Ephemeroida and Odonatoidea are sister groups which share the following synapomorphic character of the venation: the veinal anal brace AA & AA1-2 and AA1 fused with CuP at an area important for flight.

The sister groups diverged when the veinal anal brace became fused to CuP at a kink in CuP in Odonatoidea. In Ephem-

FIGS. 35-39. Relationship and evolution of ephemeroid wing venation in the past 300 million years. Fig. 35. As a sister group of ephemeroids, the oldest odonatoids bear wing venation very similar to that of Carboniferous mayflies, except that the arched subcostal brace is missing and the anal brace is fused to a kink in CuP instead of a bulla in CuP. *Eugeropteron lunatum* Riek, 1984 (Protodonata: Eugeropteridae). Hind wing fragment length 35 mm. Early Upper Carboniferous, Namurian, Argentina. After Riek and Kukalová-Peck (1984). Fig. 36. The oldest known mayfly, *Bojophlebia prokopi* n. gen., n. sp. (Bojophlebiidae), showing plesiomorphic precosta as serration, CA and CP separated basally, two independent radial sectors, the gently arched subcostal brace, arch and strut brace between MA & RP and between CUA & M, and richly branched venation. The hind wing is very broad and triangular as in Paleozoic dragonflies. Natural wing length ca. 21.5 cm. Westphalian C, Bohemia. Original drawing from holotype. Fig. 37. The Carboniferous mayfly, *Lithoneura lameerei* (Syntonopteridae) has lost some branches, the subcostal brace became stronger, and MA & RP fused together, while the hind wing is still broader than the fore wing. Natural wing length ca. 35 mm. Westphalian D, Illinois. Original drawing from holotype. Fig. 38. Ancestors of Recent mayflies, *Protereisma* sp. (Protereismatidae), with hind wings smaller than fore wings and simplified primary branching. The arch of the subcostal brace is higher, MA or M & MA are always fused to RP, and the CuA & M brace is either an arch and strut or a true fusion. The jugal area is larger than in Recent mayflies. The bulla marks the end of the anal brace in CuP. Stems M and Cu are not yet desclerotized. Fore wing length 23 mm. Lower Permian, Kansas. Original drawing based mainly on specimen No. 3411, MCZ, Cambridge. Fig. 39. The veinal system of Recent mayflies with emended labeling based upon the evolutionary aspects shown in Figs. 36-38. The veinal nomenclature and numbering of branches have been chosen to allow comparisons and homologization of veinal elements within all pterygotes. The fossil record gives clues that all veins were originally in pairs, including subcosta (ScA, ScP), radius (RA, RP), and anal (AA, AP); the subcostal brace is composed of ScA & ScA3-4; the anal brace of AA & AA1-2; RP2 is forked; MP and CuA areas may have secondary veinal supplements Mspl and Cuspl; AA1 is fused with CuP; stems of M and Cu are desclerotized; concave IN is not a primary vein "2A" but a secondary intercalated sector in continuation of a basal fold; and there is a small jugal area with a reduced, barely visible jugal vein J. Original composite drawing based on ephemerid, siphonurid, and baetid Recent mayflies.

eroidea the same area was marked by a bulla in CuP.

The relationship between the wing venation of Recent Ephemera and Odonata is evident only if the faulty odonatoid Tillyard-Fraser (1938-1940) veinal system that is now in use is replaced by the new veinal nomenclature system proposed by Riek and Kukulová-Peck (1984).

A constitutive character of ephemeroidean wing venation is the arched, strong subcostal brace. This is positively correlated with special flight mechanics leading to progressive desclerotization of parts of venation near the wing base and enlargement of the anal brace.

Most veins in ephemeroidean stock separate into two sectors at the very base of the wing, namely the costa, subcosta, radius, anal, and jugal, which proves that wing veins occurred primitively as a pair of two independent, fluted sectors. The implication of this primitive veinal symmetry is that the proto-wing itself must have been nearly symmetrical.

Comparisons between wing venation of Carboniferous, Permian, and Recent mayflies confirm that the evolution of wing venation proceeded from richly branched to poorly branched, from regular to asymmetrical, and from dichotomous to non-dichotomous. The vein radius was found in Carboniferous mayflies in the plesiomorphic form as two independent sectors RA and RP originating next to each other from the wing base (double radius). This primitive character state is still fully present in Recent dragonflies.

The advantages of labeling wing venation according to its evolution and several adjustments of the currently used, partly nonhomologous ephemeroidean veinal system are advocated (Fig. 39).

Cerci originated from the segmented, arched, functional legs of the 11th abdominal segment. The specialized cercal articulation probably developed at this early stage, and only once. On the other hand, elongation and annulation of cerci are secondary and may have developed several times. Monura share three synapomorphic characters with Zygentoma and Pterygota (thoracic subcoxae fully embedded in the pleural body wall, gonangulum, and secondary anterior mandibular articulation) but have segmented cercal legs, instead of annulated filamentous cerci, and a long paracercus. The latter features clearly are extremely primitive. Therefore, the strong indication is that the longer paracercus and shorter cerci, wherever present in the ephemeroidean clade, are a primitive character state.

Carboniferous ephemeroidean nymphs originally had 3 pairs of almost homonomous thoracic wings, 9 pairs of abdominal winglets (tracheal gills), and 9 pairs of segmented abdominal legs. This proves that tracheal gills in Recent mayflies are not flattened legs, as was previously presumed; they are wing homologues with leg musculature and, in all probability, originated from leg exites.

The metamorphic instar probably occurred repeatedly, in several lineages, between young instars and the rest of the nymphal stage, subadults, and adults rather than near the end of the nymphal stage, as is often presumed. The Recent adult stages are probably a fusion of older nymphal, subadult, and adult stages. In Ephemera older nymphal and early subadult stages were fused into a subimago. There is much evolutionary plasticity in metamorphosis because of its polyphyletic nature and because some metamorphic instars (i.e., those of Ephemera) did not develop until the end of the Paleozoic or early Mesozoic. It should be noted that the original number of instars before and after the metamorphic instar was probably different in separate pterygote lineages.

Further characters separating ephemeroideans and odonatoids are the following: one axillary plate in mayflies and two axillary plates in dragonflies, both fused from the original bandlike sclerites of ancestral Paleoptera, which were unfused. The original pterygote voluntary anterior mandibular articulation turned into a mandibular slider in mayflies but was transformed into a permanent anterior mandibular articulation in dragonflies.

Acknowledgements

I am deeply obliged to amateur collectors in Bohemia, namely František Janouš, Václav Tobiáš, Karel Havlata, and Anna Havlata, as well as to amateur paleontologists in the Chicago area, Helen Piecko, Walter Clayes, C. Cozart, W. H. Lietz, G. Agazzi, and Mary Phillips, whose devotion to nature and collecting has made it possible to follow mayfly evolution through 300 million years. My thanks go also to mine engineer Jan Lukeš, custodian Václav Petr, and especially custodian Dr. Rudolf Prokop, who spent much time and effort in getting specimens to me. I was helped and encouraged in the study of Recent mayflies by ephemeroidean Professor William L. Peters and Dr. Michael D. Hubbard. Professor Frank M. Carpenter, Museum of Comparative Zoology, Harvard University, Cambridge, gave me the opportunity to study in detail the holotype of *Lithoneura lameerei*, which helped much in evolutionary considerations. The sister-group relationship between Ephemera and Odonata would have remained veiled if Dr. Edgar F. Riek had not shared with me his material of Namurian dragonflies from Argentina in a joint study that resulted in full homologization of mayfly and dragonfly venation. I am most indebted to Russian paleoentomologists from the Paleontological Institute of the Academy of Sciences, Moscow, especially to Dr. A. P. Rasnitsyn who let me study in detail their magnificently preserved material of haustellate Paleoptera which, after several years of comparisons, has resulted in an almost complete reconstruction of the body, genitalia, head, and mouthparts, including the mode of their function. The interpretation of these structures was difficult and complex, but I received invaluable help from the experience of Recent morphologist Dr. Edward L. Smith (California Academy of Sciences, San Francisco), who is preparing a detailed study on primitive structures of arthropods. This will be published in a book, *Atlas of Arthropods*, and will contain full documentation of some structures that could not be introduced in this paper (this concerns especially the general interpretation of the head). Last but not least I am grateful to Dr. Stewart B. Peck for improving the text. The photographs were made with the professional help of Rober Fee; the Bohemian specimens were photographed by my friend Karel Drábek as a great favor. The text was typed with speed and skill by Elaine Quehl. The research was generously supported by operating grants from the Natural Sciences and Engineering Research Council of Canada. Facilities and work space were provided by the Department of Geology, Carleton University, Ottawa.

BORROR, D. J., and D. M. DELONG. 1976. An introduction to the study of insects. 4th ed. Holt, Rinehart and Winston, Toronto. pp. 1-852.

BOUDREAUX, H. B. 1979. Arthropod phylogeny, with special reference to insects. John Wiley & Sons, New York. pp. 1-320.

BRODSKII, A. K. 1974. Evolution of the wing apparatus in the Ephemeroptera. Entomol. Obozr. 53(2): 291-303.

CARPENTER, F. M. 1938. Two Carboniferous insects from the vicinity of Mazon Creek, Illinois. Am. J. Sci. 36: 445-452.

- . 1943. Carboniferous insects from the vicinity of Mazon Creek, Illinois. Ill. State Mus. Sci. Pap. **3**(1): 9–20.
- . 1963. Studies on Carboniferous insects from Commentry, France: Part IV. The genus *Triplosoba*. *Psyche*, **70**(2): 120–128.
- CARPENTER, F. M., and E. S. RICHARDSON. 1971. Additional insects in Pennsylvanian concretions from Illinois. *Psyche*, **78**(4): 267–295.
- EDMUNDS, G. F., JR. 1972. Biogeography and evolution of Ephemeroptera. *Annu. Rev. Entomol.* **17**: 21–42.
- EDMUNDS, G. F., JR., and R. W. KOSS. 1972. A review of the Acanthametropodinae with a description of a new genus (Ephemeroptera, Siphonuridae) Pan-Pac. *Entomol.* **48**: 136–144.
- EDMUNDS, G. F., JR., and J. R. TRAVER. 1954. The flight mechanics and evolution of the wings of Ephemeroptera, with notes on the archetype insect wing. *J. Wash. Acad. Sci.* **44**(12): 390–400.
- HANDLIRSCH, A. 1911. New Paleozoic insects from the vicinity of Mazon Creek, Illinois. *Am. J. Sci.* **31**: 297–326, 353–377.
- . 1919. Revision der paläozoischen Insekten. *Denkschr. Akad. Wiss., Wien, Math. Naturwiss. Kl.* **96**: 1–82.
- HENNIG, H. 1981. *Insect phylogeny*. John Wiley & Sons, New York. pp. 1–514.
- HUBBARD, M. D., and J. KUKALOVÁ-PECK. 1980. Permian mayfly nymphs: new taxa and systematic characters. In *Advances in Ephemeroptera biology*. Edited by J. F. Flannagan and K. E. Marshall. Plenum Publishing Corp., New York. pp. 19–31.
- IDE, F. P. 1936. The significance of the outgrowths on the prothorax of *Ecdyonurus venosus* Fabr. (Ephemeroptera). *Can. Entomol.* **68**: 234–238.
- KUKALOVÁ, J. 1968. Permian mayfly nymphs. *Psyche*, **75**(4): 310–327.
- . 1969. Revisional study of the order Palaeodictyoptera in the Upper Carboniferous shales of Commentry, France. Part I. *Psyche*, **76**(2): 163–215.
- KUKALOVÁ-PECK, J. 1970a. Revisional study of the order Palaeodictyoptera in the Upper Carboniferous shales of Commentry, France. Part II. *Psyche* **76**(4): 439–486.
- . 1970b. Revisional study of the order Palaeodictyoptera in the Upper Carboniferous shales of Commentry, France. Part III. *Psyche* **77**(1): 1–44.
- . 1978. Origin and evolution of insect wings and their relation to metamorphosis, as documented by the fossil record. *J. Morphol.* **15**: 53–126.
- . 1983. Origin of the insect wing and wing articulation from the arthropodan leg. *Can. J. Zool.* **61**: 1618–1669.
- . 1984. Insect beaks and coevolution in Carboniferous communities. Proceedings of the 9th International Congress of Carboniferous Stratigraphy and Geology, May 1979, Urbana, IL. American Geological Institute, Falls Church, VA. In press.
- KUKALOVÁ-PECK, J., and E. S. RICHARDSON, JR. 1983. New Homiopteridae (Insecta: Paleodictyoptera) with wing articulation from the Upper Carboniferous of Mazon Creek, Illinois. *Can. J. Zool.* **61**: 1670–1687.
- LA GRECA, M. 1980. Origin and evolution of wings and flight in insects. *Bull. Zool.* **47**(Suppl.): 65–82.
- LAMEERE, A. 1917. Revision sommaire des insectes fossiles du Stephanien de Commentry. *Bull. Mus. Paris*, **23**: 141–200.
- LAURENTIAUX, D. 1953. Classe des insectes. In *Traité de paléontologie*. Tome 3. Edited by J. Piveteau. Masson, Paris. pp. 397–527.
- LEWIN, R. 1983. How did vertebrates take to the air? *Science* (Washington, D.C.), **221**: 38–39.
- MATSUDA, L. 1976. Morphology and evolution of the insect abdomen. Pergamon Press, Elmsford, N.Y. pp. 1–534.
- . 1981. The origin of insect wings (Anthropoda: Insecta). *Int. J. Insect Morphol. Embryol.* **10**(5/6): 387–398.
- PETR, V. 1981. First find of insect in the quarry "Na Štilci" near Tlustice in Žebrák Basin (Upper Carboniferous, Westphalian C). *Casop. Nar. Mus.* **150**(3/4): 152.
- RASNITSYN, A. P. 1981. A modified paranotal theory of insect wing origin. *J. Morphol.* **168**: 331–338.
- RICHARDSON, E. S. 1956. Pennsylvanian invertebrates of the Mazon Creek Area, Illinois. *Fieldiana, Geol.* **12**(3/4): 1–76.
- RIEK, E. F., and J. KUKALOVÁ-PECK. 1984. A new interpretation of dragonfly wing venation based upon early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic characters states in pterygote wings. *Can. J. Zool.* **62**: 1150–1166.
- SHAROV, A. G. 1966. *Basic arthropodan stock*. Pergamon Press, New York. pp. 1–271.
- SINICHENKOVA, N. D. 1980. Revision of the order Permothemistida (Insecta). *Paleontol. Zh.* **4**: 91–106.
- SNODGRASS, R. F. 1935. *Principles of insect morphology*. McGraw-Hill, New York. pp. 1–667.
- TILLYARD, R. J., and F. C. FRASER. 1938–1940. A reclassification of the order Odonata based on some new interpretations of the venation of the dragonfly wing. *Aust. Zool.* **9**: 125–169.
- ZÁZVORKA, V. 1956. Find of Upper Carboniferous dragonfly in the Coal Basin of Kladno. (In Czech.) *Casop. Mineral. Geol.* **1**(2): 122–126.

Appendix: List of abbreviations

A	anal	MA	media anterior (sector)
AA	anal anterior (sector)	MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
AP	anal posterior (sector)	MD	mandible
B	basal articular sclerite, usually basivenale and fulcalare	MP	media posterior (sector)
b	bullae, or flight important area	MX	maxilla
BT	basitarsus	PA	patella
C	costa	PC	precosta
CA	costa anterior (sector)	PFE	prefemur
CP	costa posterior (sector)	PIN	Paleontological Institute of the Academy of Sciences USSR, Moscow
cr	cross vein	PT	posttarsus
Cu	cubitus	R	radius
CuA	cubitus anterior (sector)	RA	radius anterior (sector)
CuP	cubitus posterior (sector)	RP	radius posterior (sector)
CX	coxa	Sc	subcosta
FE	femur	ScA	subcosta anterior (sector)
G	tracheal gill, winglet, leg exite	ScP	subcosta posterior (sector)
GA	galea	SCX	subcoxa (= pleuron)
g	gonangulum	st	strut
J	jugal	T	tarsus
JA	jugal anterior (sector)	TI	tibia
JP	jugal posterior (sector)	TR	trochanter
L	abdominal leg		
LC	lacinia		
M	media		