

# A new interpretation of dragonfly wing venation based upon Early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings

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The oldest known odonatoid wings are described from the Namurian of Argentina: *Eugeropterum lunatum* Riek n.g. et sp. and *Geropterum arcuatum* Riek n.g. et sp. (Meganisoptera: Meganeurina: *Eugeropteridae* n. fam.). The wings are generalized and support a reinterpretation of the venation of living Odonata as being fully homologous to that of other pterygotes and closely related to Ephemeropteroidea, but different from Neoptera. Therefore, Paleoptera is a valid phylogenetic unit, and Odonatoidea and Ephemeropteroidea are sister groups.

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On trouvera ici la description des plus vieilles ailes odonatoides jamais rencontrées: il s'agit d'ailes d'*Eugeropterum lunatum* n. gen. et n. sp. et de *Geropterum arcuatum* n. gen. et n. sp. Riek (Meganisoptera: Meganeurina: *Eugeropteridae* n. fam.) provenant du Namurien d'Argentine. Les ailes suivent le plan de base et donnent lieu à une réinterprétation de la nervation des Odonates récentes selon laquelle les ailes des Odonates récentes seraient entièrement homologues des ailes d'autres ptérygotes, très rapprochées des ailes d'Ephemeropteroidea, mais différentes des ailes de Neoptera. L'appellation Paleoptera coiffe donc un ensemble phylogénétique valide et il est juste de considérer comme des groupes-soeurs les Odonatoidea et les Ephemeropteroidea.

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## Introduction

Most entomologists follow Martynov (1924) and agree that the pterygotes are naturally divided into Paleoptera and Neoptera (Hennig 1981). Nevertheless, some consider Paleoptera not to be a natural phylogenetic group, but rather a grade (Lemche 1940; Boudreaux 1979; Rohdendorf and Rasnitsyn 1980; Rasnitsyn 1980; Kristensen 1981; Matsuda 1970, 1981). Sometimes Odonata are assumed to be closer to Neoptera than to the Ephemeroptera (Kristensen 1981), while other times, the wings and wing articulation of Odonata are judged to be so different that insect wings are believed to have originated twice: in the pterygote ancestor and in the odonatan ancestor (La Greca 1980; Matsuda 1981).

These last two unorthodox evolutionary ideas find support in the erroneous belief that the odonate wing venation and wing articulation are unique and cannot be fully homologized with the other pterygote orders.

We contend that wings and wing articulation originated at the same time and brought winged insects into existence as a group; therefore, they are considered as the basic apomorphic characters of the pterygotes. It is believed that the split into Paleoptera, Neoptera, and the major ordinal evolutionary lineages was initiated mainly by the radiation of the pterygote proto-wings into diverse flight-adaptive structures (Martynov 1924; Kukalová-Peck 1978, 1983; Hennig 1981). If these conclusions are correct and wings are monophyletic, then odonatan wing venation and articulation must be fully homologous to that of the other pterygotes.

Pterygote wing articulation was recently studied by Kukalová-Peck (1983), who compared modern and Paleozoic dragonflies with modern and Paleozoic Ephemeroptera, Paleozoic Paleodictyopteroidea (Paleodictyoptera, Megasecoptera, Diaphanopteroidea, and Permothemistida (=Archodonata<sup>2</sup>)), and primitive modern Neoptera. Multiple comparisons of articular systems in different evolutionary stages showed that the odonatoid articulation evolved in a way similar to that of other Paleoptera, but unlike that of Neoptera.

The position of odonatoids *within* the Paleoptera, namely whether they are more closely related to the paleodictyopteroids or to the ephemeropteroids, is not clearly shown in the articulation (Kukalová-Peck 1983). However, the closer relationship to ephemeroids is evident in the veinal characters, if the odonatoid veinal system presently used is corrected according to the clues found in the fossil record.

The goal of this paper is to provide documentation that the odonatoid venational system does not lack any veins as is presently believed, and that it shares the ground plan with the ephemeroids.

## Odonatan wing venation

The interpretation of odonatan wing venation has a long history of disagreement. Comstock and Needham (1898, 1899) erroneously assumed that veins are formed around tracheae and

<sup>2</sup>We follow Sinichenkova (1980) in calling the order Permothemistida Martynov, 1938, rather than Archodonata Martynov, 1932, because the group belongs in the paleodictyopteroids and has no relationship to Odonata.

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that the nymphal tracheation recapitulates the ancestral venation of adults. In fact, the preveinal blood channels in juveniles are invisible but present, and tracheae penetrate into them secondarily and sometimes quite erratically. An erroneous tracheae-based veinal system was adopted for odonates by Needham (1903). Owing to vagaries of tracheation, the wings were interpreted as being completely unrelated to those of other pterygotes, i.e., RP (Rs)<sup>3</sup> was a convex vein crossed by M<sub>1</sub> and M<sub>2</sub>, etc. Later on, numerous attempts were made by a number of authors to provide a homologous veinal scheme, namely by Lameere (1922), Tillyard (1914, 1915, 1916, 1917, 1922a, 1922b, 1925a, 1925b, 1926, 1928, 1935), Tillyard and Fraser (1938–1940), Martynov (1924), Carpenter (1931, 1938, 1939, 1943a, 1943b, 1944, 1947, 1960), Forbes (1943), Zalessky (1944), Fraser (1938, 1948, 1957), Needham (1903, 1951), Hamilton (1971, 1972), and Carle (1982). The interpretations differ considerably, but none of them has been found to be correct in comparison with the venation of the oldest and most generalized fossil dragonflies, which are described in this paper. One reason why there are so many seemingly feasible interpretations of odonate venation lies in the fact that in modern dragonflies the primary veins alternate with the secondary intercalary veins and an occasional veinal supplement, and cannot be readily distinguished from each other. However, secondary veins are not fully tracheated and are sometimes missing in the more primitive fossil dragonflies. Another reason is the basal parallel alignment of the fused veinal stems, which in modern dragonflies is accompanied by disappearance of the original veinal crossings between these stems. If the crossings were present, they would indicate the pattern under which the original fusions took place. The contribution of the fossil dragonflies introduced here is that they (i) preserve ancestral character states of venation devoid of most secondary veins, and (ii) show the original pattern of veinal fusions before the crossings disappeared. Thus, generalized fossil dragonflies give clues to how the venation evolved.

Presently, the most widely followed odonatan veinal scheme is that of Tillyard and Fraser (1938–1940). This is based upon the veinal pattern of rather specialized Paleozoic dragonflies and shows the venation as being almost homologous to other pterygotes except for two main veins: the media posterior MP– and cubitus anterior CuA+, which are interpreted as missing. Beside this nonhomologous feature, the Tillyard–Fraser veinal system does not display any relationship between odonates and other pterygote orders. Conspicuously, there is no similarity between Odonata and the other surviving order of Paleoptera, the Ephemeroptera. Because of this theoretically insurmountable difference in an important set of apomorphic characters, some entomologists felt that the odonatoids cannot be classified with Paleoptera or even with Pterygota (La Greca 1980; Matsuda 1981). In contrast, theoretical cladists like Hennig (1981) assumed that dragonflies and mayflies are related, the differences in nomenclature of venation notwithstanding.

During the work with Upper Paleozoic and Triassic odonatoid wings, one of us (Riek) became convinced that two veins in Tillyard–Fraser veinal system, the media and cubitus, were misunderstood (Riek 1970, p. 173, Fig. 8.2). If the medial stem is interpreted as in Paleozoic Ephemeroptera (Figs. 10, 20), i.e., as fused near the base with the cubital stem instead

of with R, and the radial vein as the plesiomorphic double radius of primitive Paleodictyoptera (Figs. 6, 7) and fossil and living Ephemeroptera, i.e., composed of two radial stems RA and RP, the odonatan venation will lose its “strange” character and will become related to Ephemeroptera and Paleodictyoptera. Both “missing” veins MP– and CuA+ will then be present in the venation, and the scheme will be at last fully homologous with that in the other pterygote orders.

The original, generalized odonatan veinal scheme is indicated in many Paleozoic Meganisoptera, but especially informative are two highly generalized (and probably also the oldest known) dragonfly wings, which were recently found in the Early Upper Carboniferous deposits of Argentina. Their venation represents the “missing link” between the typical odonatoid pattern and that of the ephemero-odonatoid common ancestor. The Argentinian fossil dragonflies are described in the following text and their venation is compared with fossil and modern odonates, ephemeropteroids, and paleodictyopteroids.

### Occurrence of the fossils

Two very well preserved and almost complete insect wings were found near Malanzán, Cuesta de la Herradura, La Rioja, Argentina, in the carbonaceous group of the La Divisoria Member of the Malanzán Formation, by Drs. S. Archangelsky and R. Leguizamón. The insects were in association with a plant assemblage including *Vojnowskya argentina* Archangelsky & Leguizamón, *Ginkgophyllum diazii* Archangelsky & Arrondo, and *Botrychiopsis weissiana* Kurtz, as well as a number of as yet undescribed plant species (S. Archangelsky, personal communication).

Previous records of this fossiliferous horizon mentioned a Devonian or Early Carboniferous age, whereas Archangelsky and Leguizamón (1971) thought that the strata might be dated near the Westphalian–Stephanian boundary. Azcuy (1975) referred the horizon to the Namurian (Early Upper Carboniferous) after a palynological analysis.

Both fossil wings are very similar to the wing of *Erasipteron larischi* Pruvost, 1933: Meganisoptera (=Protodonata) from the Lower Westphalian A (Bashkirian) of Czechoslovakia, previously known as the oldest dragonfly, but they are more generalized. It seems, therefore, that the horizon may be older than early Westphalian, and may be at least of Namurian age, as shown by the palynological analysis. From a study of the insects alone, an even older age is not excluded. Presently, there are only about a dozen winged insects known with certainty to occur in Namurian strata. Thus, the primitive Meganisopterids from Argentina are among the earliest known pterygotes, if not actually the earliest ones now recorded in fossil collections.

### Systematics

Odonatoids form a very distinctive superorder including the diverse, mostly Paleozoic stem order Meganisoptera (=Protodonata), and the less diverse daughter order Odonata, which has survived until modern times. New, rich material of Meganisoptera and Mesozoic Odonata has been recently researched by L. N. Pritykina (Paleontological Institute, Academy of Sciences USSR, Moscow), but the results are only partly published (Pritykina cited in Rohdendorf and Rasnitsyn 1980; Pritykina 1981). The systematics of fossil odonatans was previously based almost entirely on wing venation (Carpenter 1939, 1943a, 1943b, 1954; Rohdendorf 1962), but in fossil collections from France and Russia, several specimens are pre-

<sup>3</sup>An emended veinal nomenclature, consistently using suffix A for anterior veinal sectors (i.e., RA), and suffix P for posterior sectors (i.e., RP), is used in this paper (see Kukulová-Peck 1983).

served with their bodies. The newly added characters, quite understandably, throw a different light on the systematics of Meganisoptera, as follows.

According to Kukalová-Peck (1983), large Meganisoptera are prognathous, and their prothoracic coxae are shifted far anteriorly under the head so that their long, strong, and spiny forelegs can reach forward (a paper documenting this is in preparation). In contrast, Odonata are hypognathous and have relatively weak and much shorter legs, which serve as a "fishing" basket. Pritykina (1981; and personal communication with Kukalová-Peck in Moscow, 1981) discovered that Meganisoptera had a deeply incised "unclosed thoracic pleural sulcus" with an additional inflexion running parallel to it anteriorly, while Odonata have a "closed pleural sulcus." The "double" pleural sulcus, which occurs in meganeurid, protanisopterid, protozygopterid, archizygopterid, and triadophlebiid ancestral dragonflies probably as a synapomorphy, is a unique feature in Pterygota and is a derived character. The "closed pleural sulcus" of living dragonflies developed perhaps by further invagination of the original pleural sulcus and of the parallel inflexion. This feature may well be the basic apomorphic character of the order Odonata as a daughter group.

The wings of Meganisoptera (Figs. 1–5, 11) lack an arculus and often lack a pterostigma, and the nodus is either completely absent or weakly indicated; venation is generally more primitive: the veins forming the costal margin (PC, CA, CP, and ScA) are basally separated from each other into PC and CA, CP, and ScA, and do not fuse into the basal costal triangle; the veinal stems are basally aligned in parallel more or less imperfectly, and include a free basal portion of convex medial stem (M+); CuP– is often recognizable between CuA+ and A branches; and the anal brace is often more or less concavely bent.

The wings of Odonata (Fig. 12A) have an arculus and a pterostigma and their nodus is pronounced. The costal margin is basally fused into the basal costal triangle (Fig. 12B); the veinal stems are basally well aligned in parallel; the basal portion of M is completely fused with Cu; CuP is not recognizable among the cubito-anal branches; the anal brace is aligned in parallel with other veinal stems basally; and secondary veinal supplements may occur in RP and MA–MP areas.

The oldest known dragonflies from the Namurian of Argentina, presented here (Figs. 1–3, 13–19), are members of the most primitive meganisopterid suborder Meganeurina and are closely related to *Erasipteron larischi* Pruvost, 1933 (Erasipteridae Carpenter, 1939) from the Westphalian A (Bashkirian) of Czechoslovakia (Fig. 4) and to *Erasipterella piesbergensis* Brauckmann, 1983 from the Westphalian of West Germany. Kukalová (1964, Fig. 2), found remnants of an archeductyon in the wing membrane.

ORDER Meganisoptera (=Protodonata)  
SUBORDER Meganeurina Handlirsch, 1906

Meganeurina is the most primitive odonatoid suborder containing medium-sized, large, and the largest known odonatoids with a wing span of 71 cm (in *Meganeuropsis permiana* Carpenter, 1939, from the Lower Permian of Kansas). Nodus, arculus, and costal triangle are missing, but a pterostigma may be indicated. In the most primitive new family Eugeopteridae and in related Erasipteridae, the venation carries relatively few branches and very few intercalary veins, and the membrane shows remnants of an archeductyon between the crossveins (Figs. 1–3, 4, 13). In the derived families with secondarily enlarged wings, namely in Meganeuridae, Paralogidae, and Triadotypidae, the venation is enriched by many additional intercalary branches and crossveins, which evolved secondarily from the membrane (Kukalová-Peck 1983) (Fig. 5). In meganeuromorph families the section of CuP between M and Cu stem and anal vein (CuP crossing) is usually well defined, long, oblique, and distinctly concave (Fig. 11). The free, basal portion of the medial stem (M+) is probably always present (Figs. 1–5, 11).

*Occurrence:* Tropical and probably temperate zone, Namurian to Triassic.

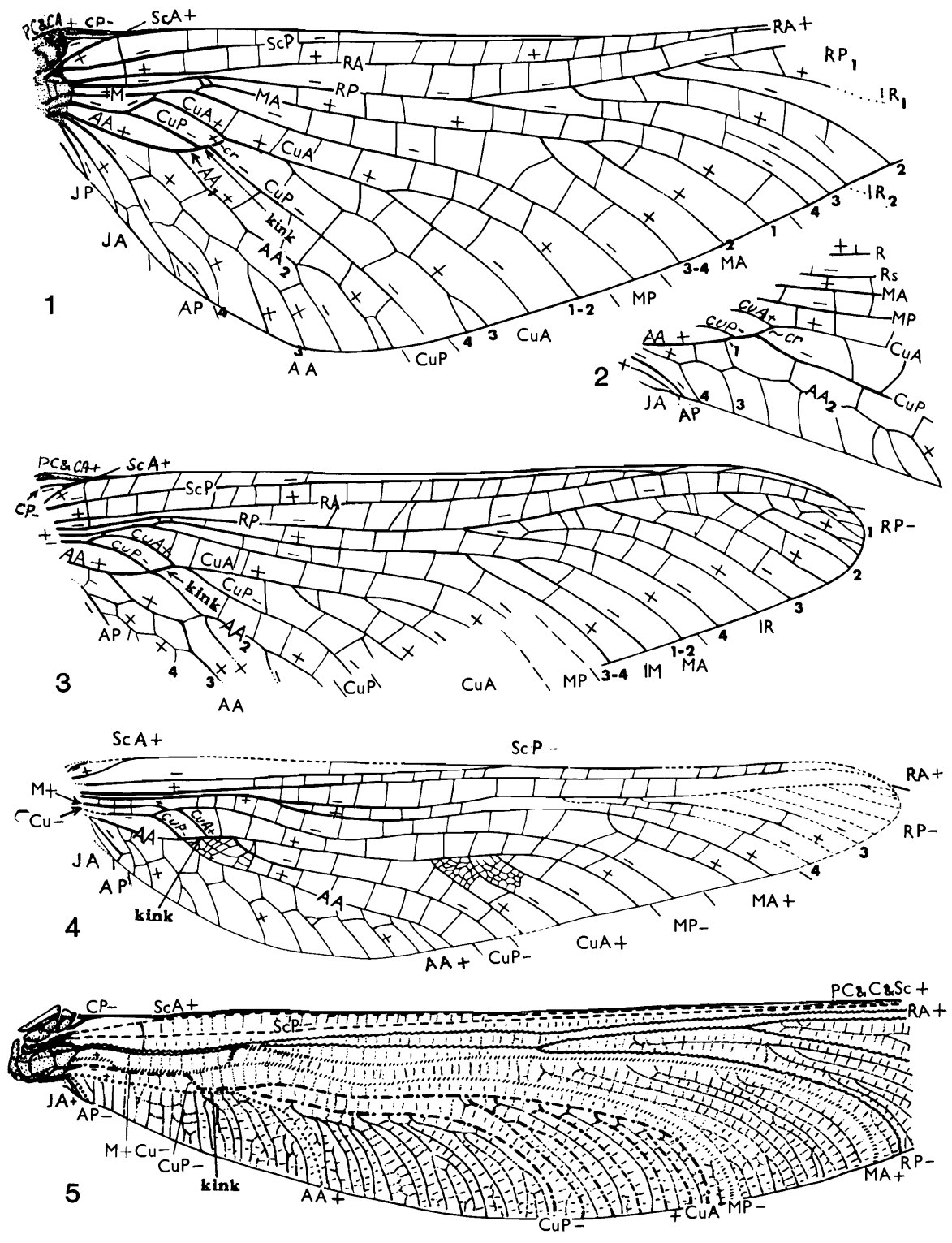
*Families included:* Eugeopteridae, Riek n. fam.; Erasipteridae Carpenter, 1939; Meganeuridae Handlirsch, 1906; Paralogidae Handlirsch, 1906; Triadotypidae Grauvogel & Laurentiaux, 1952.

**Eugeopteridae, Riek n. fam.**

*Type genus:* *Eugeopteron*, Riek n. gen.

*Diagnosis:* Eugeopteridae differ from the closely related family Erasipteridae in the veinal stems RA and RP running

FIG. 1. A generalized odonatoid wing showing the basic apomorphic character of odonatoid venation: the zig-zag kink in CuP, fused to AA<sub>1</sub> and connected by a crossvein (cr) to CuA. The odonatoid foci of reinforcement were marked by veinal arches and struts: MA and RP, and CuA and M. Veins of the costal margin (PC and CA+, CP–, ScA+) were separated basally; RA and RP were separated basally, not adjacent in a double radius; the anal brace was veinal, composed of AA, AA' and AA<sub>1</sub>; AP was branched and concave. Note the similarity to Carboniferous Ephemeroptera (Fig. 20) in all veinal features except the kink in CuP. Meganisoptera: Meganeuromorpha: Eugeopteridae n. fam.; *Eugeopteron lunatum* Riek n. gen. et sp. Holotype, hind wing fragment, length 35 mm, ?Lower Namurian of Argentina. Original drawing by E. F. Riek. FIG. 2. *Eugeopteron lunatum* Riek n. gen. et sp. Holotype, fore wing fragment, length 13.5 mm. ?Lower Namurian of Argentina. Original drawing by E. F. Riek. FIG. 3. A slightly more advanced odonatoid wing showing the zig-zag kink in CuP fused with the anal brace and also directly fused with CuA. This double fusion occurs in the wings of all recent Odonata. MA<sub>2</sub> is replaced by an intercalary vein. Meganisoptera: Meganeuromorpha: Eugeopteridae n. fam.: *Geropteron arcuatum* Riek n. gen. et sp. Holotype, hind wing fragment, length 45 mm. ?Lower Namurian of Argentina. Original drawing by E. F. Riek. FIG. 4. A still more advanced wing, in which veinal arches and struts are transformed by fusions: MA and RP, and M and CuA. CuP– and CuA+ crossings are both discernible but the MA crossing can hardly be distinguished from a crossvein. The wing is typically odonatoid in appearance. Note the similarity to Permian Ephemeroptera (Fig. 10) in all veinal fusions. Meganisoptera: Meganeuromorpha: Erasipteridae: *Erasipteron larischi* Pruvost, 1933, Westphalian A of Czechoslovakia. Holotype, fore wing fragment length 55 mm, total length ca. 64 mm. Figure after Kukalová 1964, with veinal nomenclature changed. FIG. 5. A still more advanced wing of a large meganeurid dragonfly, diagrammatically showing how the veins have fused. The MA crossing became fully aligned with the series of crossveins, the CuP crossing stayed deeply concave and well distinguishable, and the CuA crossing was no longer recognizable. The secondary branches, intercalary veins, and crossveins served to fill out the enlarged wings. Note the absence of the basal costal triangle, nodus, subnodus, and arculus, and the presence of a long, well-defined CuP. The composite anterior axillary plate shows deep grooves between articular sclerites. Meganisoptera: Meganeuromorpha: scheme based upon specimen No. 1/1983, Lower Permian of Obora, Czechoslovakia. Collection of and original drawing by J. Kukalová-Peck.



close but not adjacent to each other; stem of M closely approaching Cu but not fused with any part of Cu; MA arched towards RP but not fused with RP.

**Relationships:** The odonatoid character of the new family Eugeopteridae is documented in the articulation by the fragments of two axillary plates of primitive odonatoid type in the holotype of *Eugeopteron lunatum* (compare Figs. 1, 13, 4 with 5 and 11), and in the venation by the presence of the typical odonatoid veinal anal brace<sup>4</sup> formed by AA and fused with a zig-zag kink in CuP, which in turn is fused with CuA (Figs. 1–3). A veinal anal brace of this type is limited to odonatoids, is found in venation of all representatives, and is, therefore, the basic apomorphic character of the superorder (Figs. 1–5, 11, 12). Early ephemeroids (Fig. 10) have a homologous anal brace formed by identical parts of anal branches, but instead of a kink in CuP there is a bulla. Very probably, the common ancestors of odonatoids and ephemeropteroids were gliding paleopterans, in which the meeting point of the anal brace, CuP, and CuA became very important for flight. When the structures responding to flight mechanics differentiated, ephemeropteroids retained a bulla in CuP, and odonatoids formed a kink in CuP.

In contrast to this, all paleodictyopteroids have a primitive, nonveinal, sclerotized anal brace, which is merely a thickening of the membrane in the basal corner of the anal area. Primitively, the anal branches crossing the sclerotization are visible (Figs. 6, 7), but in more advanced paleodictyopteroids they might be obliterated. The anal sclerotized brace is often posteriorly delimited by a convex bar (Figs. 6, 7, 9: S), which is variably shaped, straight, curved, or V-shaped (Kukalová-Peck 1969, 1970a, 1970b). The bar runs transversely across a varying number of anal branches, usually at the generic or specific levels.

The new family Eugeopteridae displays a venational pattern very similar to the related family Erasipteridae (Fig. 4) in the number of branches and type of crossveins. It differs in the primitive absence of veinal fusions: the RA and RP stems are basally close to each other but separated, not yet adjacent as in more advanced families; MA arches towards RP and is connected with it by two struts, but fusion has not yet occurred; CuA arches towards M and is connected with it by a short strut, but no fusion has yet occurred.

Except for the presence of an odonatoid basic apomorphic character, the kink in CuP, which is fused between the anal brace and CuA, the veinal pattern of Eugeopteridae is generalized (Figs. 1–3). In addition to the Ephemeroptera, it is also quite similar to that of the largest and most primitive Paleodictyoptera, the Homiopteridae (Fig. 6), and to Permothemistida (Figs. 8, 9). The Paleozoic order Permothemistida (=Archodonata) is a relatively small paleopterous order with haustellate, paleodictyopteroid type of mouthparts, and non-

foldable wings adapted for gliding. The wings show a relatively derived venation with intercalated veins and sclerotized anal brace.

It should be noted that venational fusions RP and MA or M, CuA and M (or Cu and M), and CuP and A (but not R and M at the wing base), occur repeatedly in all fossil paleopterous orders as well as in modern Paleoptera. Beside Odonata, they are present in advanced Paleodictyoptera (i.e., in some Calvertiellidae; Kukalová-Peck and Peck 1976, Fig. 2), Diaphanopteroidea (i.e., in Elmoidae; Kukalová-Peck 1974), Megaseoptera (i.e., in Alectoneuridae; Kukalová-Peck 1975, Fig. 12), Permothemistida (i.e., Permothemistidae; Sinichenkova 1980, Fig. 1), and in Ephemeroptera (Fig. 10). Likewise, intercalated veins occur not only in odonatoids and ephemeropteroids, but also in specialized Paleodictyoptera, Megaseoptera, and in Permothemistida (Figs. 8, 9) (Kukalová-Peck 1978, 1983).

The generalized venation found in Eugeopteridae provides a morphological missing link between the venation of Odonatoidea and that of Paleozoic Ephemeroptera (Figs. 1, 3, 4, 10, 11, 12, 13, 20) and of Paleodictyopteroidea. These characters include (i) plesiomorphic pterygote characters, such as the veins composing the costal margin (PC, CA, CP, and ScA) separated basally from each other, RA and RP stems separated basally from each other, and ScP fused with C distally without a nodus; (ii) characters acquired mostly by parallel evolution, typical for Paleoptera, such as MA arching towards RP, CuA arching towards M, and very pronounced, regular corrugation; and (iii) ephemero-odonatoid synapomorphic character, the veinal anal brace AA meeting CuP at a flight-important area. Eugeopteridae differ from all ephemeropteroids in the presence of the odonatoid basic apomorphic character, a zig-zag kink in CuP fused proximally with the veinal anal brace AA and distally with CuA, which is typical only for odonatoids.

### *Eugeopteron* Riek n. gen.

*Type species: Eugeopteron lunatum* n. sp.

**Diagnosis:** Hind wing: Sc ending on costal margin beyond midwing; stems of RA+ and RP- widely separated from each other basally, approaching each other at about one-sixth of the wing length; stem of M+ straight, aligned in parallel with RP; MA+ and MP- diverging from each other shortly before the point of divergence of RA+ from RP-; MA+ arched towards RP- and connected with it by two struts; MA+ with three branches; Cu+ stem concavely bent; CuA+ and CuP- diverging from each other close to base; CuA+ arched towards M+ and connected with it by a short strut; CuA+ and CuP- crossing cubito-anal area towards AA; CuP after fusing with AA turns immediately distally and then posteriorly in a zig-zag kink, and continues posteriorly as a simple vein; CuA connected with zig-zag kink in CuP by a crossvein, sending off two branches; AA'+ sending off AA<sub>1</sub> fused with CuP, and simple AA<sub>2</sub>; AA''+ divided into forked AA<sub>3</sub> and simple AA<sub>4</sub>; AP- starting from anal basivenale, with a short terminal fork; JA+<sup>5</sup> with a terminal fork; JP- simple; "first antenodal" crossvein running from costal margin to R and continued to RP; crossveins simple and openly spaced; intercalated veins few, including about 3–4 veins between RP branches, one between CuA

<sup>4</sup>The term "brace" defines a supporting, usually transverse structure, which evolved in the flying wing in response to aerodynamic forces. Braces can be formed by crossveins, veinal arches and struts, and by veinal crossings and fusions, or, can be formed by a sclerotization arising from the membrane. Bracing is opportunistic. Members of the same taxon usually have braces in similar position, but they can be formed by different elements, such as an arch and a crossvein, or by a direct veinal fusion. Braces are often composite and built from several elements, like sections of branches combined with crossveins. They are not always rigid, but may be cut by flexion lines, bullae, etc. The pattern of braces coincides with the pattern of foci of reinforcement needed to make the wing flightworthy.

<sup>5</sup>The presence of an all-apterygote, homologous jugal area with branching jugal veins was recently discovered in Paleoptera by Kukalová-Peck (1983). Therefore, a jugal area is plesiomorphic for the pterygotes.

branches, and one distally from AA<sub>2</sub>. Archedictyon reduced and barely noticeable.

*Fore wing remnant*: Kink in CuP flanked distally by a crossvein as in the hind wing; AA<sub>2</sub>+ with sub-branches, A<sub>3</sub> and A<sub>4</sub> simple; AP— simple; JA+ simple; crossveins fewer than in the hind wing.

*Wing articulation*: anterior axillary plate and posterior axillary plate of Meganisopterid type.

*Species*: *Eugeropteran lunatum*, n. sp., ?Lower Namurian of Argentina, probably temperate zone of the Pangean supercontinent.

***Eugeropteran lunatum* Riek n. sp.**

Figs. 1, 2, 13, 14, 15, 16

*Holotype*: Specimen No. 12886, Museo La Plata, Fossil Invertebrate Division, La Plata, Argentina. Fragment of fore wing showing portion of cubital and anal area (Fig. 2), hind wing with a fragment of wing articulation of Meganisopterid type, missing apical part (Fig. 1).

*Description*: By monotypy, the same as that of the genus. Fore and hind wings almost homonomous, hind wing slightly broader; AA<sub>2</sub> in the fore wing with 6 terminal branches distally from the zig-zag kink in CuP. Wing margin as well as membrane without obvious setae or spines. Hind wing fragment, length 35 mm; width 13 mm; total length ca. 38 mm.

*Occurrence*: ?Lower Namurian; Malanzán Formation, La Divisoria Member, Malanzán, Cuesta de la Herradura, La Rioja, Argentina.

***Geropteran* Riek n. gen.**

*Type species*: *Geropteran arcuatum*, Riek n. sp.

*Diagnosis*: Hind wing: Wing venation differs from the closely related new genus *Eugeropteran* in longer ScP— touching RA+ before terminating on costal margin at about three quarters of the wing length; MA+ with two primary branches and one intercalar vein; zig-zag kink on CuP more pronounced so that CuP first fuses shortly with the first branch of AA and then fuses shortly with CuA; CuP separates from CuA as a simple concave vein directed obliquely towards posterior margin; AA'+ sending off AA<sub>1</sub> fully fused with CuP, and forked AA<sub>2</sub>, with one intercalar vein; AP concave. Hind wing relatively narrower in the anal area.

*Relationships*: *Geropteran* is more advanced than the closely related genus *Eugeropteran* in having deeper zig-zag kink in CuP— fused directly with CuA+ instead of being connected with CuA by means of a crossvein. Anal brace of *Geropteran* is a morphological transition between that of *Eugeropteran* and *Erasipteron*.

*Species included*: *Geropteran arcuatum* Riek n. sp., ?Lower Namurian of the Pangean supercontinent.

***Geropteran arcuatum* Riek n. sp.** Figs. 3, 17, 18, 19

*Holotype*: Specimen No. 12885, Museo La Plata, Fossil Invertebrate Division, La Plata, Argentina. Hind wing without proximal part of posterior margin.

*Description*: By monotypy, the same as that of the genus. Wing margin and membrane without obvious setae or spines. There appears to be a bulla at the base of the first anterior branch of RP. Archedictyon reduced, indicated weakly between the branches of AA and elsewhere.

*Dimensions*: Hind wing length, 45 mm; width, 12 mm; total length, ca. 46 mm; total width, ca. 13 mm.

*Occurrence*: ?Lower Namurian, Malanzán Formation, La

Divisoria Member, Malanzán, Cuesta de la Herradura, La Rioja, Argentina.

**Why are Eugeropteridae true odonatoids?**

In the entomology of living insects, the whole animal is almost always available for morphological and systematic study. In paleoentomology, the material is often limited to wings, and many taxa are based solely upon wing venation. For more than a century, paleoentomologists have devoted attention to the characters of venation and searched for criteria to separate “stable” from “variable” characters. It has also been known for a long time that wing venation between and within orders is widely convergent. The development of venational convergence within separate orders was followed through time, because the fossil record provided the unique opportunity to examine character changes as they evolved. This research has brought abundant evidence that the clues to wing venation of recent orders lay with their Paleozoic stem groups.

Recent orders are offshoots of a very limited number of Paleozoic insects and are usually not older than the Permian or Triassic. This also includes the order Odonata. As a rule, the stem groups show more varied venation (at higher systematic levels), which is richer in branches. Instead of fused veins, this venation frequently has unfused veins, arched veins, and struts, or shows easily interpretable fusions.

For understanding veinal evolution at ordinal levels, the recognition of ordinal basic apomorphic characters is crucial. The theoretical presumption is that each order group originated by the development of at least one, but usually several, new character states, by which the group is defined. A basic apomorphic character is distinguished from all other apomorphic characters by the fact that it occurred earlier and that it is shared by all members of the group, extinct as well as extant. It should be noted that insect wings evolved from veined, movable proto-wings that were not flight adapted (Kukalová-Peck 1978, 1983). Changing nonflying flaps into a flight organ required a regrouping of the veins into a pattern that would be flightworthy. Therefore, wings of all pterygotes are a combination of symmetrical (nonadaptive) and asymmetrical (flight-adapted) veinal elements (Kukalová-Peck 1983).

In all flying insect wings, there is a certain pattern of areas or foci that have to be reinforced for flight. The reinforcements are often provided by fusions among veins, which originated partly at the very beginning of flight, but mostly in the process of diversification of orders. Since adaptation for flight was orchestrated by identical aerodynamic laws, veinal fusions within orders formed in parallel, with the result that they became widely convergent. Because of this convergence, the wings of many pterygote orders look alike to an untrained eye. Many times it was also observed that the older the wings are, the less distinguishable they become (Figs. 1, 2, 6–11). The best example of an increasing similarity is the well-known Paleozoic wing-based “waste-basket” order Protorthoptera, which contains stem groups of plecopteroids, orthopteroids, blattopteroids, hemipteroids, and neuropteroids, not because they had not been well separated from each other, but because the wing venation is still very little differentiated. Eventually, even venational differences between Paleoptera and Neoptera tend to disappear (Kukalová-Peck 1983). This process of “vanishing characters,” theoretically, should continue until the ultimate ancestor would have only the basic (definitive) apomorphic characters plus plesiomorphic (ancestral) characters. This “reversed evolutionary process” as documented by fossils

is, of course, in accord with the evolutionary basis of systematics, and provides a definitive proof to the monophyly of insect wings.

Recent entomologists, who have the luxury of examining the whole organism, sometimes tend to mistrust the capacity of wing venation to provide reliable criteria for taxonomic work. This is true in some insect groups (i.e., the fore wings of cockroaches have very variable venation), but in other groups the venation is like a thumbprint and provides reliable characters from ordinal down to specific levels. It is a well-known fact that Odonatoidea, Ephemeropteroidea, and Paleodictyopteroidea have a very characteristic wing venation and that they can often be identified even when the body parts are not examined or not available. A trained entomologist can readily recognize a wing of any recent or Mesozoic dragonfly based on the wing veins. Late Upper Carboniferous and Permian meganeurid odonatoids still "look" like dragonflies, even if they lack the nodus, subnodus, costal triangle, veinal supplements, arculus, alignment of veinal stems, and have a well pronounced CuP (compare Fig. 5 with Fig. 12). Because of this obviously more primitive, but not very "strange" set of characters, a rigorous recent taxonomist might be tempted to regard the meganeurid veinal pattern as original for odonatoids. However, this presumption is not at all probable. Compared with the wings of the most primitive Paleodictyoptera (Figs. 6, 7) as well as Ephemeroptera (Figs. 12, 20) and Neoptera, the meganeurid wing venation is highly derived in many characters. Interpreting the origin of such a complex change by a megamutation, as may be favored by some authors, is highly unlikely.

It is a well-known fact, based upon the comparative study of many groups of Paleozoic insects, that the stem groups of living orders may have unfused veins, or that the fusions are sometimes preshadowed by veinal arches and struts. The Argentinian ancestral dragonflies (Eugeropteridae) occur in the Namurian and they may be the oldest known pterygotes. Their wings show a combination of the odonatoid basic apomorphic veinal character and the incipient pattern of odonatoid apomorphic veinal fusions, represented by veinal arches and struts. These are a kink in CuP fused between the veinal anal brace and CuA, and the arched MA to RP and CuA to M. However, we know that arches and struts are interchangeable with veinal fusions, because braces are opportunistic. This archetypal odonatoid pattern revealed a hidden character of basic importance, which could not have been deduced from recent and Mesozoic dragonfly venation: the kink in CuP built between AA and CuA and its fusion with both of these veins. This discovery made homologization of odonatoid venation with that of all other pterygotes smooth and easy.

While additional fusion (a brace) between CuP and AA is present in all pterygotes except most Paleodictyopteroidea, CuA and CuP separate usually at or near the cubital basivenale, and then no longer brace with each other. However, the presence of a bracing CuA and CuP in the Odonatoidea is by no means unique. It occurs also in some primitive Paleozoic Neoptera and is well developed especially in Geraridae (Protorthoptera), recently revised by Burnham (1983, Figs. 17a, 19, 25). In the large fore wings of this family, CuP is forked and CuP<sub>1-2</sub> fuses temporarily with CuA+ and separates from it again as a concave branch, simple or forked. While the presence of a CuA and CuP brace is convergent among pterygote orders, the bracing by means of a kink in CuP is unique and a hallmark of the Odonatoidea.

As expected from theoretical considerations, the archetypal odonatoid foci of wing reinforcement are identical to those present in the ephemeropteroids. In addition, in Carboniferous Ephemeroptera (the most primitive known, Fig. 20), the wings show a strikingly parallel pattern of arches and struts as in Eugeropteridae (Figs. 1-3), while Permian Ephemeroptera (Fig. 10) have them replaced by fusions as in Erasipteridae (Fig. 5). Note that "double radius" is very pronounced in Carboniferous mayflies, less visible in Permian forms, but still recognizable in well-sclerotized modern forms. Also note that the stem of M starts in mayflies well posteriorly from the "double radius," and therefore the latter cannot be interpreted as R and M as it is in some contemporary publications.

Ephemero-odonatoids share a basic synapomorphy, which is the veinal anal brace AA meeting CuP at a flight-important area. In contrast, all paleodictyopteroids have a sclerotized anal brace. From an evolutionary viewpoint, Eugeropteridae are an excellent example of a missing link and are probably very close to a hypothetical early odonate. They seem to be generalized in all aspects except, perhaps, in the paucity of veinal branches, because other primitive Paleoptera as well as Neoptera have richly dichotomously branched veins.

The venational pattern of Eugeropteridae provides an outstanding example of a succession of characters, theoretically formulated by Hennig (1981). While the odonatoid nature is established by the presence of a basic apomorphic character, the future apomorphic characters are only suggested and become more pronounced later through a process of the autapomorphic accumulation of small character changes. Autapomorphy in odonatoids is extremely pronounced and is at the root of all problems with homologization to other insects.

The transformation of veins from separated to arched and then to fused, and of veinal crossings from discernible to lost, is an evolutionary process observed in all Paleozoic paleopterous orders and is demonstrably parallel. This fact indicates that ancestral pterygotes diverged very early, probably already during the transition of proto-wings to flying wings. Major pterygote lineages probably started with venation virtually devoid of fusions, except perhaps the veins reinforcing the anterior wing margin. This consideration is important for systematic evaluations of recent wings, because it implies that the veinal patterns mostly evolved at lower than ordinal levels. To estimate which way the adaptation was directed in a particular post-Paleozoic group, it was suggested that one compare a given specimen first with the model of the proto-wing, then with the model summarizing wing adaptations during the Paleozoic, and finally with the key representatives of the particular living order. In this way, the Paleozoic phase of evolution, which is so important for correct evaluation of character states, can be incorporated into phylogenetic considerations and systematic decisions (Kukalová-Peck 1983, Figs. 13-15).

Further evidence that Eugeropteridae are true odonatoids, even if they do not "look" like recent Odonata, is found in the remnants of the wing articulation attached to the wing base (Figs. 1, 13, 14). In contrast to other insects, this articulation includes two axillary plates, the anterior and the posterior. The posterior axillary plate is present also in other gliding Paleoptera, but is absent from the Neoptera, which have axillary sclerites of a different composition (Kukalová-Peck 1983). The anterior axillary plate is a complex supersclerite formed by fusions of four dorsal articular sclerites with ventral articular sclerites, the basalaria (Kukalová-Peck 1983, Figs. 16B, 16E, 21). This plate is unique to odonatoids and, in all proba-

bility, is the basic apomorphic character of the odonatoid articulation. The four articular sclerites that compose the odonatoid anterior axillary plate are movably hinged to each other in ephemeropteroids, paleodictyopteroids, and in Neoptera. While the anterior axillary plate of recent odonatoids shows almost no sutures among the original sclerites, meganeurids have deeply incised and partly flexible grooves separating the four dorsal sclerites and the ventral basalaria (Figs. 5, 11) (detailed report in preparation by J. Kukalová-Peck). Eugeopteridae show the remnant of an odonatoid anterior axillary plate, which is, quite predictably, close to the meganeurid type (Figs. 1, 5, 11, 13, 14, 15).

### Fluting of basal veinal stems

It should be noted that under the generalized condition present in the Eugeopteridae, radial sectors are completely separated and the entire posterior radius (RP) is concave, contrary to that in all other odonatoids, in which radial sectors are adjacent and RP is always convex. In the adjacent basal stems of the radial sectors (double radius) of Ephemeroptera and

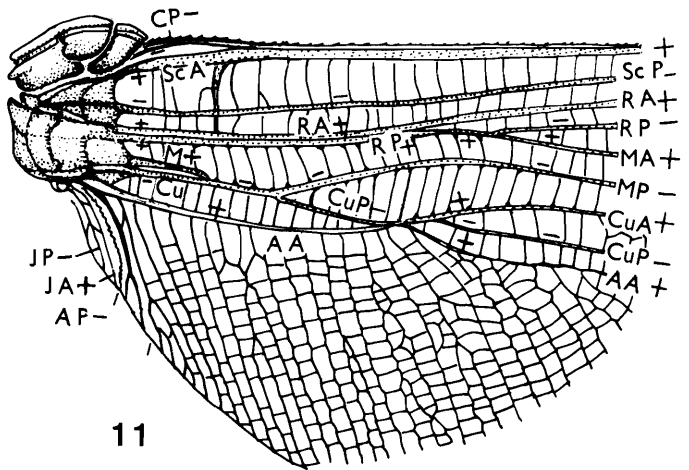
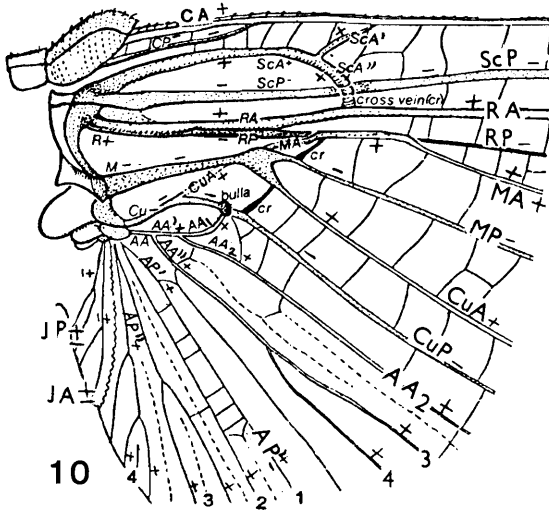
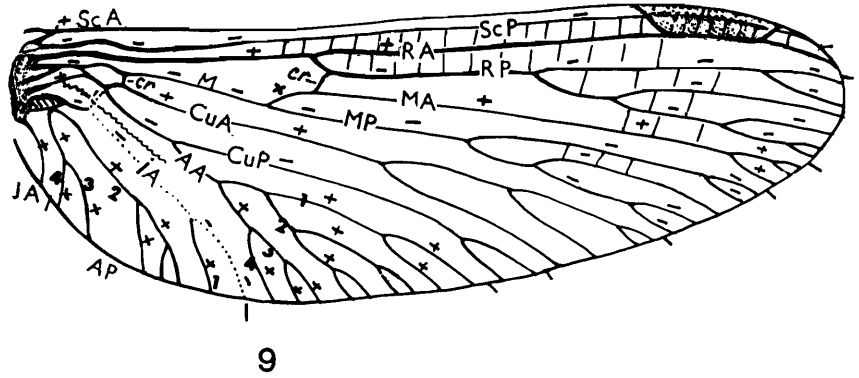
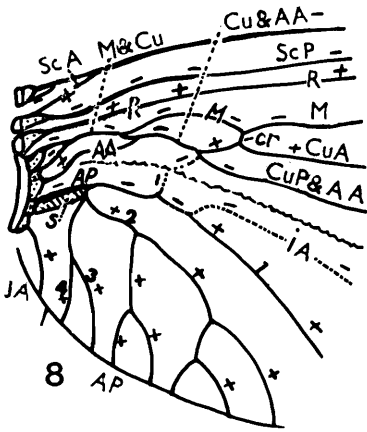
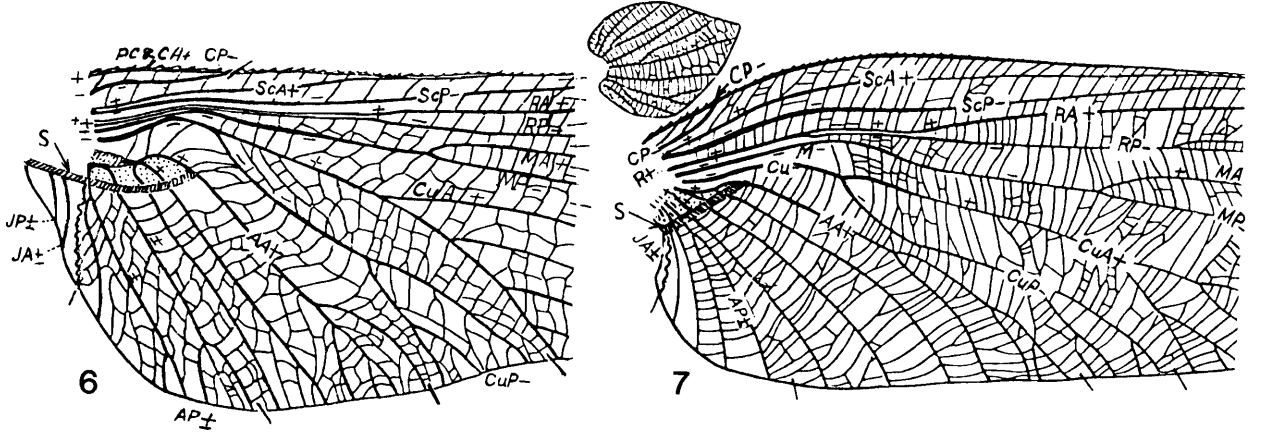
Paleodictyoptera, RA is always convex, while RP is either concave or levelled, but never convex. There is no doubt that the concave position of the basal stem of RP is primitive. The problem is how to explain the convexity of RP stem in *Erasipteron* and all younger odonatoids.

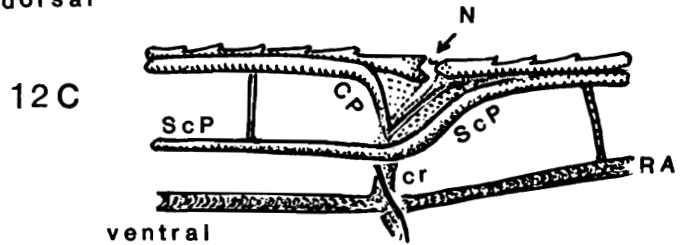
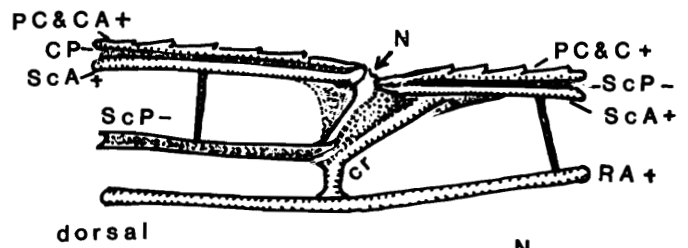
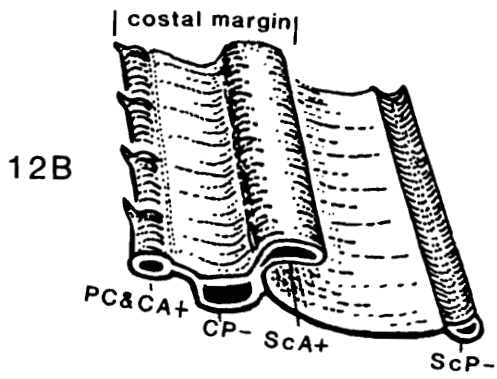
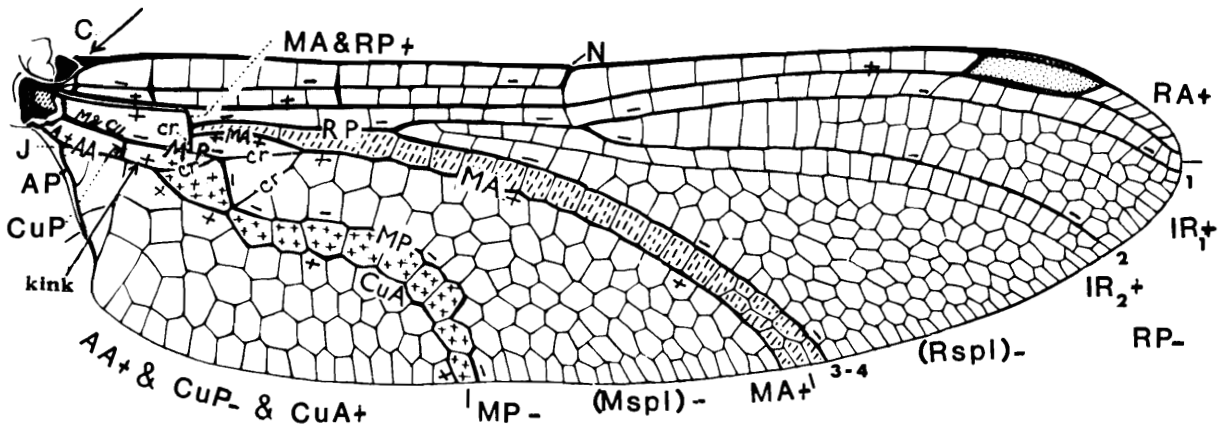
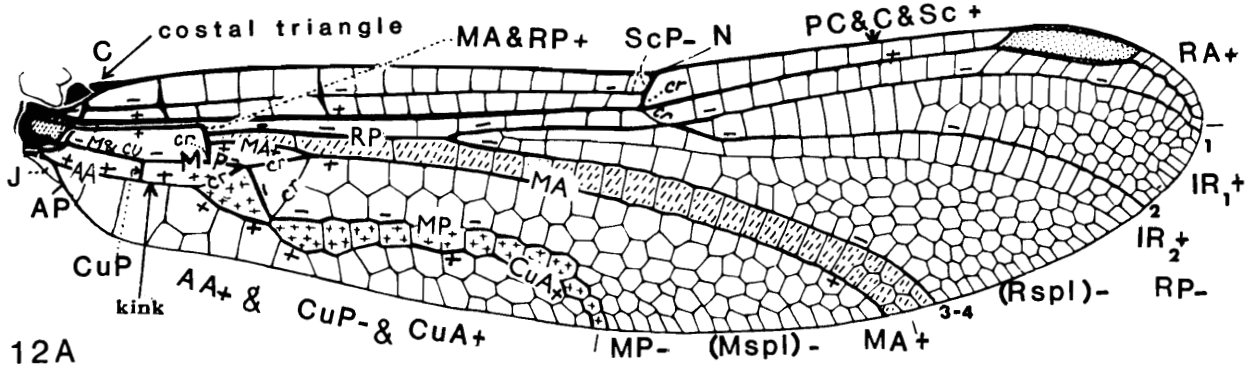
Recently, Kukalová-Peck (1983) provided evidence that the fluting of veinal stems near the base may be variable at lower than ordinal levels, especially in Paleozoic insects. While ScP is always concave and R (or RA) always convex, the stem of M can be convex, levelled, or concave, and very short or long; the stem of Cu convex, concave, or missing; and the stem of A very short and convex or missing. There is little doubt that changes in fluting, presence of stems, and length of stems are derived and are controlled by aerodynamic laws, but the cause and effect are only superficially known.

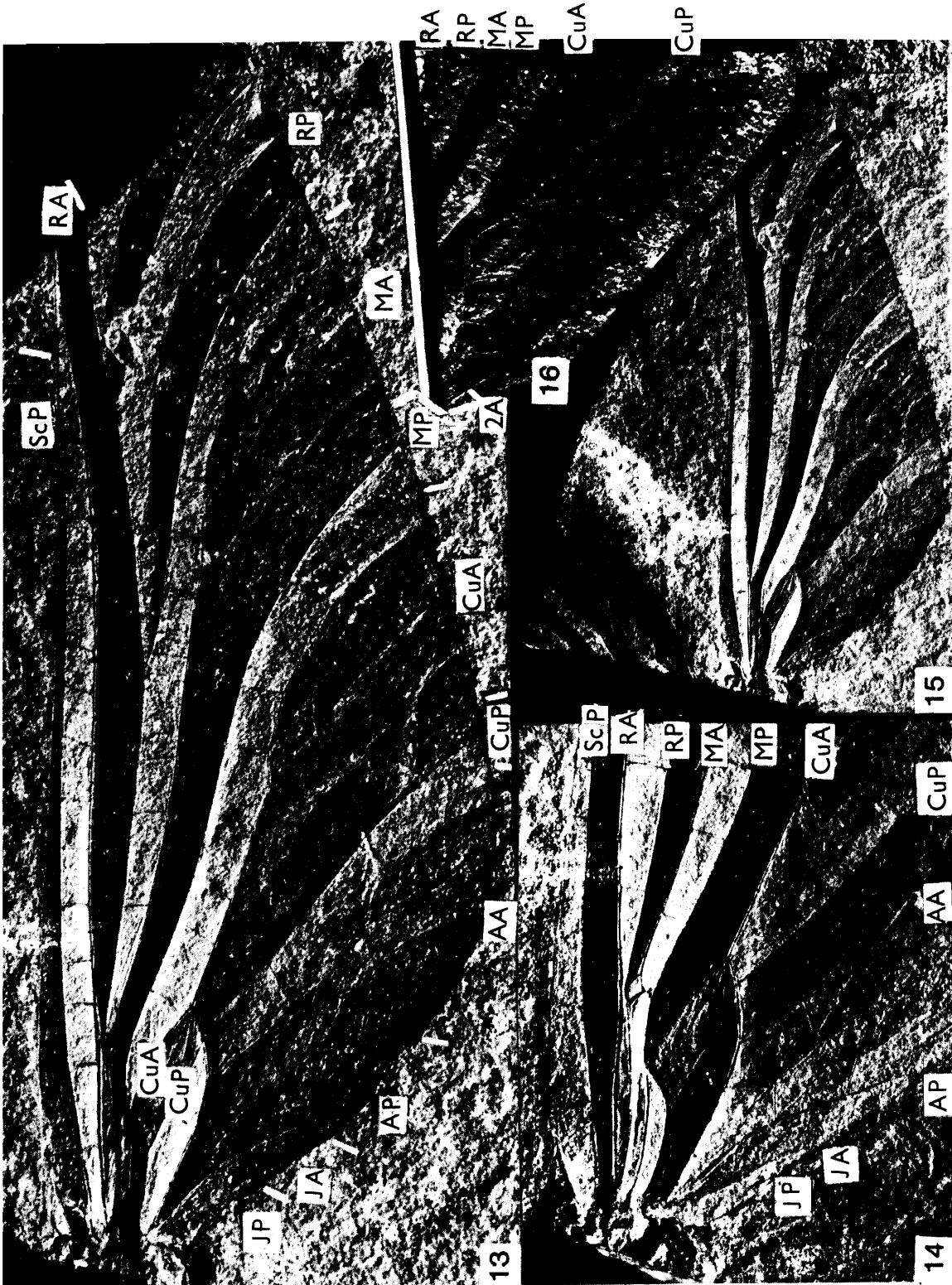
Seven pairs of wing veins have been found by now, one at a time, to be completely separated basally into two sectors, namely PC, C, Sc, R, Cu, A, and J (Kukalová-Peck 1983). The only exception is M, which always has at least a short basal stem. Very probably, it is only a question of time before M will

FIG. 6. Primitive Paleodictyoptera with two radial sectoral stems RA+ and RP± adjacent in a double radius. Venational foci of reinforcement were M and RP, and Cu and M, both placed distally from the wing base. The anal brace was a sclerotized basal corner of the anal area (dotted) delimited by a convex bar (S). Note the lack of a brace between AA and CuP and the presence of a well-defined jugal area with two jugal veins. Paleodictyoptera: Homiopteride: *Thesoneura americana* Carpenter, 1943, Westphalian C-D of Illinois. Holotype, hind wing, total length 110 mm. Original drawing from holotype, Kukalová-Peck and Richardson 1983. FIG. 7. A paleodictyopterid wing documenting the transition between a double (primitive) and a single (derived) radial stem: RA+ was superimposed on RP- basally, but the sectoral stems were adjacent as a double radius more distally before they diverged. AP was preserved in the primitive concave position within the sclerotized anal brace, but became secondarily levelled (±) after crossing the convex bar (S). Paleodictyoptera: Homioptera: *Homioptera gigantea* Agnus, 1902, Stephanian of Commeny, France. Holotype, prothoracic and mesothoracic wing, total length of the latter 187 mm. After Kukalová-Peck and Richardson 1983. FIGS. 8 and 9. Advanced paleodictyopteroid Permothemistida had an identical ground plan of veinal foci of reinforcement as did the ephemero-odonatoids (MA and RP, CuA and M, AA and CuP), but had paleodictyopteroid type of sclerotized anal brace (S). Note the highly specialized, intercalated vein IA (dotted) replacing part of AA and of AP, which is probably indicative of a unique style of flight. FIG. 8. Permothemistida: Diathemididae: *Diathemidia monstruosa* Sinichenkova, 1980; Lower Permian of Perm, U.S.S.R. Holotype, fore wing, total length 17.2 mm. FIG. 9. Permothemistida: Permothemistidae: *Permothemis libelluloides* (Martynov, 1932), Upper Permian, SE of European U.S.S.R. Holotype, fore wing length 17.3 mm. Original drawings from holotypes by J. Kukalová-Peck. FIG. 10. Permian mayflies had the anal brace AA and AA' and AA<sub>1</sub> fused with CuP at a bulla, and extended to CuA by a crossvein. The identical veinal anal brace, the veins of the costal margin separated basally, the double radius, and the pattern of veinal fusions MA and RP, and CuA and M, demonstrate the close relationship to early Odonatoidea. Ephemeroptera: Prottereismatidae: *Prottereisma* sp., Lower Permian of Kansas. Hind wing, total length ca. 20 mm. After Kukalová-Peck 1983. FIG. 11. The giant meganeurid dragonflies had a composite anterior axillary plate differently shaped than that of recent odonates, with deeply incised grooves between articular sclerites. Veins composing the costal margin (PC and CA+, CP-, ScA+) were always separated basally. The double radius resembled that of the odonates, but the stems of M+ and Cu- were basally separated, the MA crossing was rarely discernible and the CuA crossing was not discernible from crossveins, while the CuP crossing was always concave and well pronounced. Note the primitively concave AP and presence of convex and concave jugal veins. Meganisoptera: Meganeuromorpha: Meganeuridae: *Megatypus schucherti* Tillyard, 1925, Lower Permian of Kansas. Holotype, hind wing, maximum width 35 mm. Original drawing from holotype by J. Kukalová-Peck.

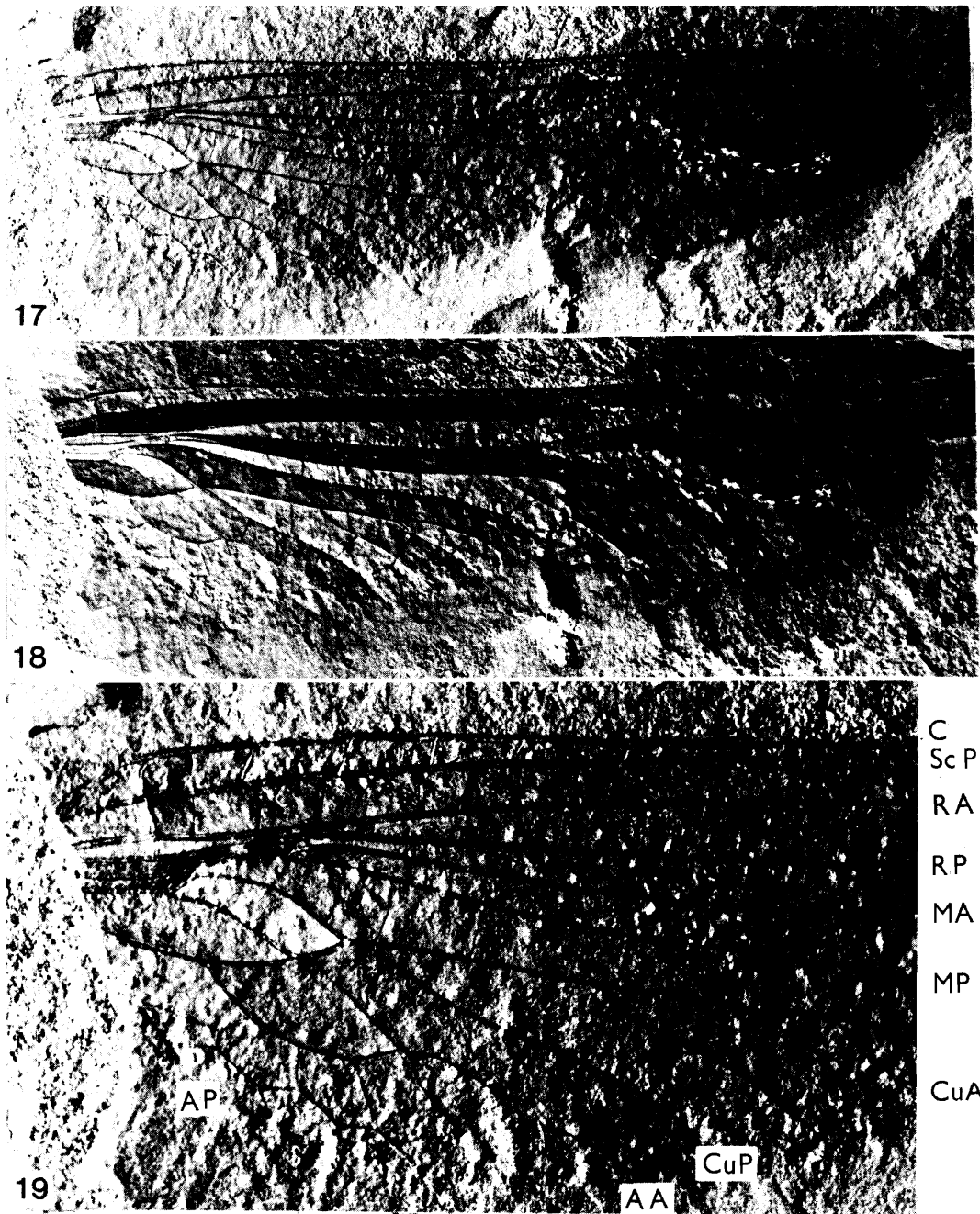
FIG. 12A. A corrected interpretation of the venation of recent dragonflies. The veins of the costal margin PC and CA and CP and ScA are fused basally into a costal triangle; ScP forms a kink at the nodus (N) and fuses with the costal margin; RA is convex, simple; RP is basally secondarily convex and adjacent to RA, then shortly superimposed by MA+ and forming a kink RP and MA+, from which RP emerges as a concave sector; RP is dichotomously branched into RP<sub>1</sub>, RP<sub>2</sub>, and RP<sub>3-4</sub>; M and Cu are fused basally into a concave stem M and Cu-, then CuP diverges posteriorly as the CuP crossing, then CuA diverges posteriorly but the crossing is lost, then MA diverges anteriorly towards RP and the crossing is lost; RP and MA+ form a kink, from which MA emerges as a convex, simple sector; MP runs posteriorly from the arculus, forms a kink and continues as a concave, simple sector towards posterior margin; the arculus is composed of a kink in RP and MA+, MA+, and of a crossvein; CuP fuses with AA<sub>1</sub>, forms a kink and fuses again with CuA; CuA sends off several pectinate branches; CuP probably does the same; AA and AP are shortly fused basally into A, AA is branched and convex, and AA<sub>1</sub> fuses with CuP; AP is simple and either concave (primitive), or levelled, or convex (derived). Jugal veins are lost and the jugal area is almost completely reduced. The odonatoid basic apomorphic character is the veinal anal brace fused with the kink in CuP and this in turn with CuA, so that resulting convex vein is composed of portions of A, AA, AA', AA<sub>1</sub>, CuP, CuA, and sends off a (pectinate) series of CuA, CuP, and AA branches, which cannot be distinguished from each other. Note many additional kinks, which in odonate venation followed the kink in CuP, and which were built up through the accumulation of small evolutionary changes (autapomorphies). Odonata: Gomphidae: *Austrogomphus* sp., Recent, Australia. Original drawings by the authors. FIG. 12B. Basal transverse section through the costal triangle of recent dragonflies showing the original veins PC and CA+, CP-, and ScA+, which became sclerotized next to each other, through autapomorphy. After Kukalová-Peck 1983. FIG. 12C. Dorsal and ventral view of nodal region in recent dragonflies showing differences in veinal patterns. The V-shaped indentation of CP- forming reinforcement of the nodal break and then fusing into PC and C, as well as the kink in ScP supporting distally the nodal break (N), are visible only ventrally. Anisoptera: Petaluridae: *Uropetala carovei* (White), New Zealand. Original drawing by Kukalová-Peck.







FIGS. 13-15. Meganisoptera: Eugeroteridae Riek n. fam.: *Eugeroteron lunatum* Riek n. gen. et sp. Holotype, fragment of fore and hind wing. ?Lower Namurian of Argentina. Fig. 13. Hind wing, length of fragment 35 mm, maximum width 13 mm. Fig. 14. Hind wing base in different lighting. Fig. 15. Fore and hind wing in natural position. Fig. 16. Fore wing, length of fragment 13.5 mm. Photographed by E. F. Riek.



FIGS. 17–19. Meganisoptera: Meganeuromorpha: Eugeopteridae Riek n. fam.: *Geropteran arcuatum* Riek n. gen. et sp. Holotype, fragment of hind wing, ?Lower Namurian of Argentina. Fig. 17. Hind wing, length of fragment 45 mm, width of fragment 12 mm. Fig. 18. Hind wing in different lighting. Fig. 19. Enlarged hind wing base. Photographed by E. F. Riek.

also be found starting from a medial basivenale as two independent sectors, + and –, possibly in some Namurian or older fossils. Fluting of RP has the capacity to change from concave to levelled and to convex by thickening of the dorsal wing cuticle when there is an aerodynamic need, because the RP stem is known to have changed from concave to levelled in fossil and recent Ephemeroptera (Fig. 10) and in some Paleodictyoptera (Fig. 6). Other than that, RP branches in Neoptera are known to have changed from a mildly concave position in very primitive Paleozoic Neoptera, to a levelled or even convex position in many recent Neoptera, etc. Other veinal stems, M and Cu, are also known to change fluting from convex to concave at subordinal levels; veinal stems proximally from the

“wall” of braces are fluted so that their individual position is built into a fluted pattern of a higher rank, thus forming the special fluting of the wing base (Kukalová-Peck 1983).

Wing venation, articulation, and the alar musculature of odonatoids diverged from the pterygote ground plan more than in any other order, and the chain of transformations had already started in the Early Carboniferous. The change in convexity of RA is seen here as one of the many autapomorphies. It occurred in Westphalian A in *Erasipteron*, together with fusions between RP and MA and M and CuA, which replaced arches and struts. These innovations gave *Erasipteron* the odonatoid appearance in spite of the fact that other veinal characters remained very primitive. Change of fluting of RP in advanced

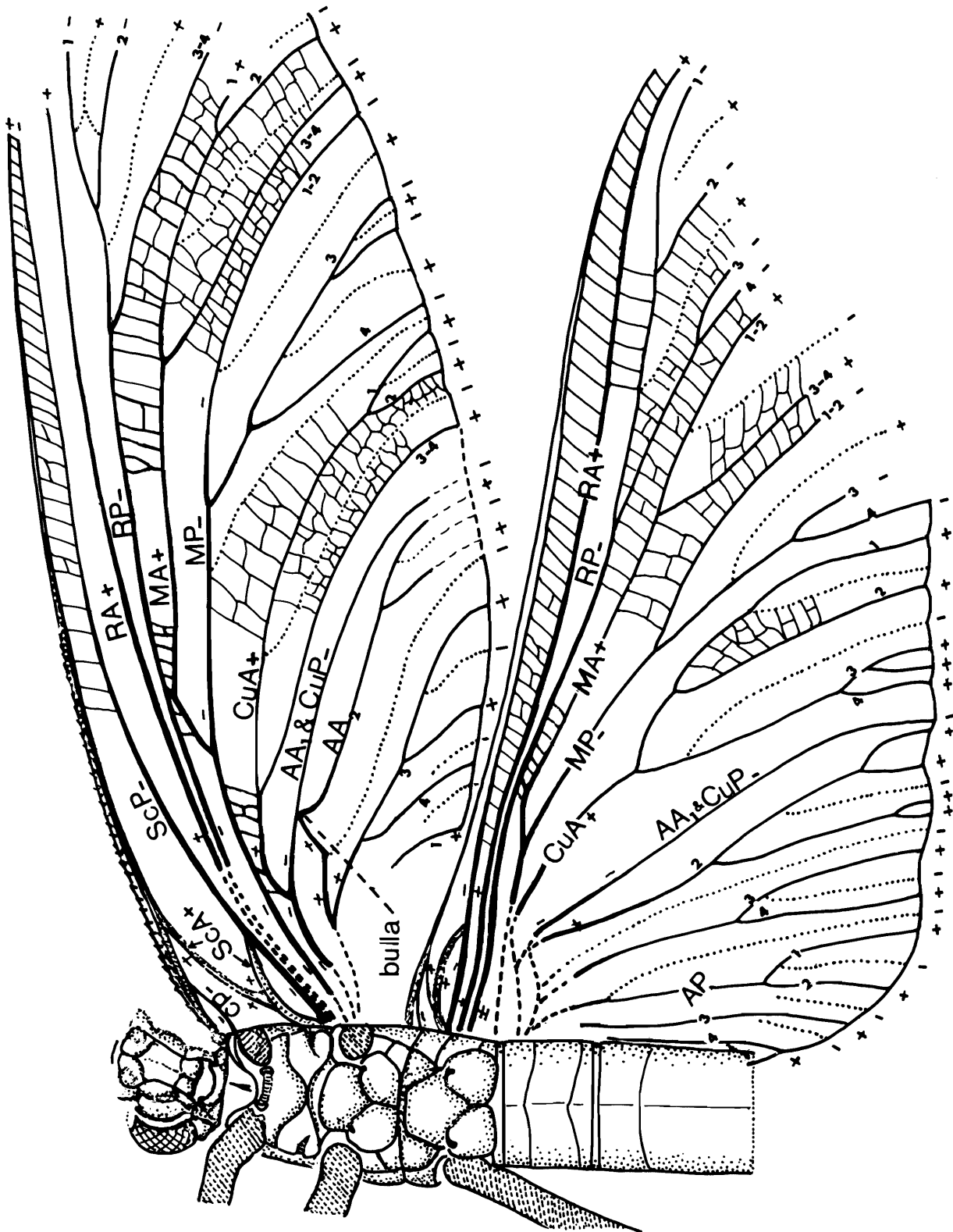


FIG. 20. Generalized ephemeropteroid wings were extremely similar to generalized eugeopterid odonateoids (Figs. 1-3) in that the foci of reinforcement MA and RP, and CuA and M were in both marked by veinal arches and struts, which preceded veinal fusions; the shared apomorphy was the veinal anal brace AA and AA' and AA, fused with CuP in an area important for flight; in mayflies this was probably expressed as a bulla. Note that the ephemeroid intercalary veins are already formed, but crossveins are still very irregular, with residual archidictyon as in early odonateoids, and the presence of large hind wings. This giant, oldest known mayfly had a wing span of ca. 42 cm and was found in the same thin layer of volcanic ash as a giant, young mayfly nymph 10 cm long (measured without caudal filament and cerci). Ephemeroptera, undescribed family, from a paper in preparation by J. Kukulová-Peck. Middle Upper Carboniferous (Westphalian C) of Central Bohemia. Ventral view. Original drawing by J. Kukulová-Peck.

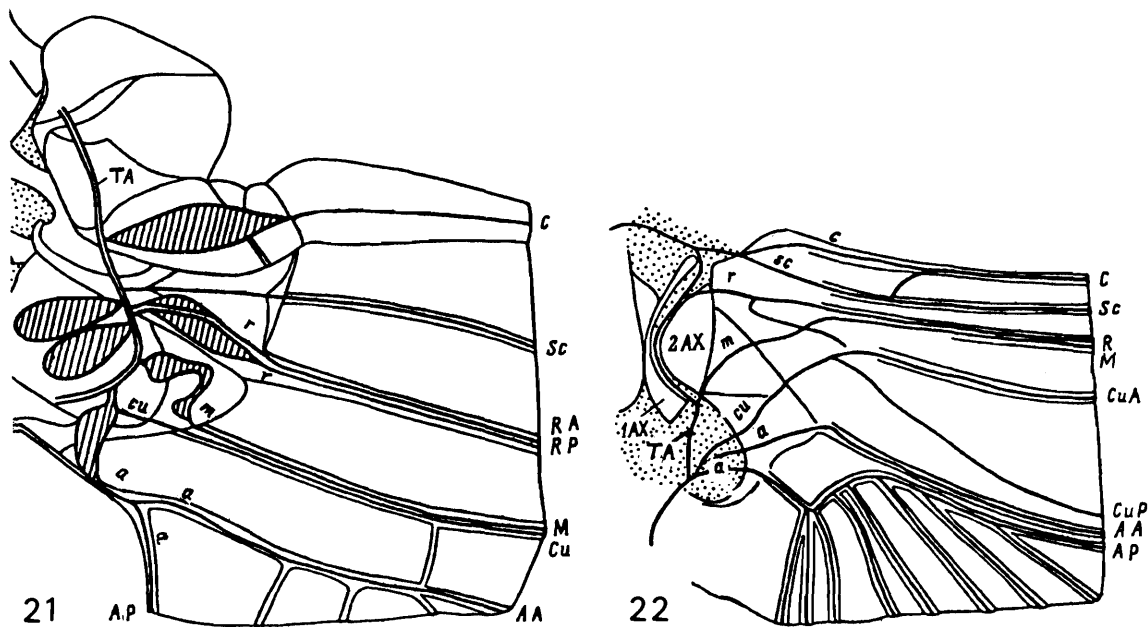


FIG. 21. Tracheae in the wings of recent dragonflies simulate the venational pattern of Paleozoic odonatoids. Note the medial trachea *m* starting in the middle between *r* and *cu* tracheae and then diverging posteriorly towards Cu. The anal and cubital tracheae are close basally. Odonata: *Tramea abdominalis*, hind wing, dorsal view. TA, tracheal arch; air sacks hatched. After Brodskiy 1981 with lettering changed. FIG. 22. Trachea in the wings of recent cockroaches show a very similar start of *sc*, *r*, *m*, *cu*, and *a* tracheae from the tracheal arch as in Odonata, but the medial trachea *m* diverges anteriorly towards R as typical for Neoptera. Blattodea: *Panchlora antillarum*, hind wing, dorsal view. After Brodskiy 1981 with lettering changed.

odonatoids was probably useful in strengthening the basal stems of the radial axial vein, which in odonates is fused to the posterior axillary plate (other veins are mostly hinged) and is responsible for effortless gliding (Kukalová-Peck 1983). Modern dragonflies often alternate quick wingbeats with gliding intervals, especially while hunting over large expanses of water.

#### Corrected interpretation of odonatoid venation

According to clues found in the wing venation of the oldest, most generalized odonatoids of Namurian, Westphalian, and Lower Permian age, the veinal pattern of modern dragonflies is derived from the same ground plan as in other pterygotes, all veins are fully homologous to other pterygote orders, and none of them is missing. The presently used Tillyard-Fraser (1938–1940) venational system, which interprets two veins as absent, is incorrect.

The generalized venation of Egeropteridae, Erasipteridae, and Meganeuridae provides valuable clues for the interpretation of venation in modern Odonata (Fig. 12), as follows. The costal triangle is formed by veins composing a costal margin (PC, CA, CP, and ScA), which are fused basally (Fig. 12B); on the underside of the wing CP forms a V-shaped indentation forming a ventral reinforcement of the nodal break before it fuses with PC and CA into PC and C, and Sc forms a kink under the nodal break before it joins the costal margin (Fig. 12C); sectorial stems RA and RP are adjacent to each other basally; sectorial stem of RP acquired secondarily a convex position; M is fused basally completely with Cu and with a short section of CuA; MA is arched anteriorly and shortly fused with RP (MA crossing is not discernible); CuP and CuA diverge posteriorly towards AA (CuA crossing is not discernible; CuP crossing is sometimes preserved as a so-called "anal

crossing"); CuP becomes shortly fused with A and forms a zig-zag kink; anteriorly, CuP fuses shortly with CuA; the anal brace is composed of AA starting from the axillary plate and AA<sub>1</sub> fused to a kink in CuP, which in turn is fused to CuA, and all veinal sections (AA, AA<sub>1</sub>, CuP, and CuA) are aligned so that they form a single, composite, convex vein; branches of this composite vein are often pectinate, alternating with intercalary veins, so that original branches of CuA, CuP, and AA cannot be distinguished from each other any more (Fig. 12).

#### Tracheation of adult Odonata

The emended interpretation of odonatoid venation offered here finds support in the pattern of tracheation in the adults of living Odonata (Fig. 21). While tracheae are no longer considered to be predecessors to veins, they are often helpful in detecting the original veinal pattern, because they tend to be conservative in their course (Whitten 1961). While tracheae of juveniles are frequently variable in subsequent instars, tracheation of adults is more stable and meaningful for wing venation (Brodskii 1981). In the tracheal pattern of both Paleoptera and Neoptera, the cubital and anal tracheae tend to start close to each other, while the M trachea starts apart, at about midway of R (Figs. 21, 22). In modern Odonata, the M trachea follows a similar path as the vein M in ancestral Odonatoidea, Paleozoic Ephemeroptera, some Paleodictyoptera, and Permothemistida and approaches CuA or Cu (Figs. 6–11). It does not approach R, and veinal fusion of R and M basally does not occur in Paleoptera. In Neoptera, the M trachea is directed obliquely anteriorly and approaches R (Fig. 22). In contrast to the Paleoptera, R and M veinal stems in all known Neoptera are either very close, or adjacent, or fused at the immediate wing base.

As shown in Fig. 21, the double radius of Odonata is pene-

trated by two tracheal stems. This fact supports a conclusion that the radius was originally a veinal pair, as were the other wing veins, and that the veins in the proto-wing diverged dichotomously from each other immediately at their start from the basivenale (Kukulová-Peck 1983). The double radius, to our knowledge, never occurs in Neoptera, but it is present as a plesiomorphy in Odonatoidea, Ephemeroptera, and in some Paleodictyoptera. Since all these orders also became specialized very early in their evolution for effortless gliding, it is very probable that the double radius was advantageous for some types of flight involving gliding, and that this quality "saved" this primitive character from complete disappearance from pterygote wings.

### Evolution of odonatoid venation

Venation of Paleozoic odonatoids is similar to that of other paleopterous orders of the same era. Veinal characters such as separated radial stems and similar pattern of short veinal fusions (M, or MA and RP, M and CuA, or M and Cu, and AA and CuP) are present or indicated also in some Paleodictyoptera, Megaseoptera, Permothemistida, Diaphanopteroidea, and Ephemeropteroidea (Figs. 6–10).

In contrast to this, the pattern of fusions and braces in Neoptera is distinctly different. The most important features of neopterous venation are the stems of R and M adjacent or fused near the wing base representing, in all probability, one of the basic apomorphic characters of Neoptera. The neopteroid anal brace is veinal, composed of sections of the AA vein as in ephemero-odonatoid group, but its fusion with CuP is inconspicuous and not important for flight as in the latter (Kukulová-Peck 1983, Figs. 17A, 17B). In fact, the last leg of AA is weak and sometimes crossed by a claval fold. However, the neopterous anal brace developed a new and important function: to protect the anal area when the wings are folded in the resting position on the back. For that purpose, it often acquired additional sclerotization. Again, this adaptation of the anal brace is unknown in Paleoptera, even if they fold their wings completely backwards as do some Diaphanopteroidea (Kukulová-Peck 1983). The neopterous pattern of veinal fusions is rich and varied, in fact, much more varied than that of the Paleoptera. In addition to characteristic fusion of R and M basally, there is usually present an M and Cu brace executed by a crossvein, a bar, or by a veinal fusion of some sort. However, there are also primitive neopterous wings which completely lack this character (i.e., some Paleozoic Liomopteridae of the plecopteroid stem group). In Paleoptera, fusion between the stems R and M at the base is absent from the wings of gliding Paleoptera, Paleodictyoptera, Permothemistida, primitive Megaseoptera, Ephemeroptera, and Odonata (Figs. 6–11). R and M stems in Paleoptera became adjacent basally only in limited circumstances, namely if the veins are crowded in the petiolate wings of specialized Megaseoptera, or in the wings of some Diaphanopteroidea, which are small and fold backwards at rest.

In comparison with primitive Paleodictyoptera, venation of the oldest presently known odonatoids is not as rich in branches and is comparable to more advanced Paleodictyoptera. There is little doubt that gigantism of Late Paleozoic Meganisoptera is secondary, because the wings are "filled out" by numerous secondary branches and crossveins, which formed from the membrane (Fig. 5).

In addition to the plesiomorphic–paleopterous veinal pattern, Odonatoidea and Ephemeropteroidea share an apomorphic veinal anal brace AA reaching from the axillary plate

to CuA+, with a built-in bulla in CuP (Ephemeropteroidea) or a kink in CuP (Odonatoidea). The orders of the Paleodictyopteroidea share instead a different basic apomorphic character: a sclerotization in the basal corner of anal area, which is sometimes delimited by an oblique or a V-shaped bar. Anal branches crossing the sclerotization vary in number (Figs. 6, 7) and sometimes are not discernible.

The autapomorphic evolution towards a distinctly odonatoid venation, only indicated in (?Lower) Namurian, gathered momentum, and in Lower Westphalian fossils the "odonatoid type" of wing was almost formed (Fig. 4). Basic apomorphic character changes typical for Odonata, such as the shift toward direct flight musculature or fusion of sclerites into two axillary plates, probably somewhat preceded the changes in venation; Namurian, Westphalian, Stephanian, and Lower Permian dragonflies already have a typically odonatoid articulation with anterior and posterior axillary plates (Figs. 1, 5, 11). While the prey was increasing in size during the Westphalian and Stephanian, so were the odonatoid predators.

Modern odonatoid venational pattern is dominated by "kinks." While generalized Carboniferous dragonflies had only one zig-zag kink in CuP, Mesozoic and Cenozoic dragonflies also developed a kink in ScP (at nodus), a kink in MA and RP (at arculus), a kink in MP (at triangle), and a kink in CuA (beyond subtriangle) (Fig. 12). Succession in development of kinks during the Mesozoic should be of great help to taxonomists studying the Recent epoch, but this is beyond the realm of this paper.

As proposed by several previous authors and documented by various morphological characters (Sharov 1966; Kukulová-Peck 1978, 1983; Hennig 1981) Odonatoidea and Ephemeropteroidea are probably sister groups; the ephemero-odonatoid stem group and the paleodictyopteroid stem-group are also believed to be sister groups. This conclusion is supported by the present study of odonatoid venation. It also leads to the conclusion that gliding in Paleoptera (and all other Pterygota) is a grade and evolved twice, in ephemero-odonatoids and gliding paleodictyopteroids.

From the findings documented in this paper and summarized above, it is concluded that (i) insect wings are monophyletic, (ii) Paleoptera is a valid phylogenetic unit and not merely a grade, (iii) Odonatoidea are to be referred to Paleoptera, (iv) Odonatoidea and Ephemeropteroidea are sister groups, and (v) gliding in Paleoptera, as well as in Neoptera, is a grade.

The Tillyard–Fraser interpretation of odonatoid venation led, unfortunately but inevitably, to the erroneous conclusion of some authors that odonatoid venation and tracheation is similar neither to that of the Paleoptera nor the Neoptera, and that insect wings are thus polyphyletic. However, from the point of view of general evolutionary evidence, this idea is no more acceptable than a polyphyletic origin of tetrapod vertebrate limbs. Insect wings and limbs of vertebrates have two features in common: their morphology is fully homologous in all taxa and the similarity of their morphology increases in the fossil ancestors of living groups. It should always be kept in mind that fossil evidence records actual states of characters, as they passed through successive previous stages. Therefore, the gradual increase of overall similarity in older and older ancestors provides direct evidence of their monophyletic origin. In spite of its defects and the many artifacts of preservation, the fossil record provides a unique factual basis against which an evolutionist can test interpretations and from which he or she can improve an understanding of evolution.

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