Journal of Paleontology, 86(1), 2012, p. 81–104

0022-3360/12/0086-0081$03.00

SYSTEMATICS AND EVOLUTION OF PALEOZOIC AND MESOZOIC DAMSELFLY-LIKE ODONATOPTERA OF THE 'PROTOZYGOPTERAN' GRADE

ANDRÉ NEL,[1] GÜNTER BECHLY,[2] JAKUB PROKOP,[3] OLIVIER BÉTHOUX,[4] AND GUNTHER FLECK[5]
[1]CNRS UMR 7205, Muséum National d'Histoire Naturelle, CP 50, Entomologie, 45 rue Buffon, Paris F-75005, France, <anel@mnhn.fr>;
[2]Staatliches Museum für Naturkunde Stuttgart, Abt. Paläontologie, Rosenstein 1, Stuttgart D-70191, Germany, <guenter.bechly@smns-bw.de>;
[3]Charles University in Prague, Faculty of Science, Department of Zoology, Viničná 7, CZ-128 44, Praha 2, Czech Republic, <jprokop@natur.cuni.cz>;
[4]40 rue d'Aveillans, La Motte d'Aveillans F-38770, France, <obethoux@yahoo.fr>; and [5]<FleckGunther@gmail.com>

ABSTRACT—The Paleozoic to Mesozoic grade 'Protozygoptera' is revised. It appears to be composed of two main lineages, namely the superfamily Permagrionoidea, and the Archizygoptera. The latter taxon forms a monophyletic group together with Panodonata (=crown-Odonata plus their closest stem-relatives). Therefore, the 'Protozygoptera' as previously understood is paraphyletic. Diagnostic characters of the 'Protozygoptera', Permagrionoidea, and Archizygoptera are re-evaluated. The Permolestidae is considered as a junior synonym of the Permagrionidae. The following new taxa are described: *Permolestes sheimogorai* new species, *Permolestes soyanaiensis* new species, *Epilestes angustapterix* new species, *Solikamptilon pectinatus* new species (all in Permagrionidae); Lodeviidae new family (for *Lodevia*); Luiseiidae new family (including *Luiseia breviata* new genus and species); *Kennedya azari* new species, *Kennedya pritykinae* new species, *Kennedya ivensis* new species, *Progoneura grimaldii* new species (all in Kennedyidae); *Engellestes chekardensis* new genus and species (in Bakteniidae); and *Azaroneura permiana* new genus and species (in Voltzialestidae). The Kaltanoneuridae and Oboraneuridae are revised. The evolution of protozygopteran Odonatoptera during the transition from the Permian to the Triassic is discussed. The larger taxa of the permagrionoid lineage apparently did not cross through the Permian–Triassic boundary, unlike the more gracile Archizygoptera. This last group shows a remarkable longevity from the late Carboniferous to the Early Cretaceous. It also presents a great taxonomic and morphological stability, with genera ranging from the Permian to the Triassic, and a wing venation pattern nearly unchanged from the late Carboniferous to the Late Triassic. The mass extinction at the end of the Permian period seemingly had a minor effect on these tiny and delicate insects.

INTRODUCTION

THE PERMO–TRIASSIC is a key period for insect evolution, with the gradual development of typical Mesozoic lineages during the Permian (e.g., holometabolan groups Coleoptera, Neuroptera, and Antliophora; Ponomarenko, 2002a, 2002b), extinctions or sharp decrease of diversity of several 'ancient' lineages during the 20 million years around the Permian–Triassic boundary (e.g., Palaeodictyopterida), and lastly the Triassic diversification of Diptera and Hymenoptera (Shcherbakov et al., 1995; Lukashevich et al., 2010; Blagoderov et al., 2007; although the age of their most ancient stem-relatives remain controversial, see Wiegmann et al., 2009) (see also Béthoux et al., 2005). In this context, investigation of the evolution of a predatory group such as Odonatoptera is likely to complement our understanding of global changes that affected ecosystems during the late Paleozoic and early Mesozoic.

The 'traditional' pattern of major changes in Odonatoptera at the Permian–Triassic boundary (namely the extinction of Paleozoic Meganisoptera Martynov, 1932, and Protanisoptera Carpenter, 1931, and replacement by more advanced lineages) has been challenged by discoveries of Permian Triadophlebiomorpha and Odonata, and application of a new approach in palaeosynecology to the Odonatoptera (Nel et al., 1999a, 2001, 2010). A broader picture of the evolution of Odonatoptera at this period based on sound systematic data is needed.

Although it is one of the most diverse groups during the Paleozoic and the Mesozoic, the Protozygoptera Tillyard, 1925 has remained unrevised. Since 1997 data has been gathered and a revision of the majority of the taxa currently included in this 'group' is now possible. Herein we discuss the presumed non-monophyly and systematics of the 'Protozygoptera'.

MATERIAL AND METHODS

The great majority of the described specimens are isolated wings only, with their body structures unknown. Nevertheless, based on this data and on a few more complete specimens, we elaborate a new proposal for the relationships between the major groups currently included in 'Protozygoptera'. We refrained from producing a formal cladistic analysis because the available information is clearly too incomplete to assemble a useful data matrix. Within this context, we propose a taxonomic system based on a manual phylogenetic evaluation of the available data. Our proposal will be tested by future discoveries.

We follow the wing venation homologies proposed by Riek and Kukalová-Peck (1984), modified by Nel et al. (1993) and Bechly (1996). In agreement between the authors, the hypothesis on the course of the median anterior vein as proposed by Riek and Kukalová-Peck (1984) is followed herein. This does not imply support for this interpretation by AN and OB. Wing venation abbreviations are as follows: C (+ScA), costal vein; ScP, subcosta posterior; RA radius anterior; RP radius posterior; IR1, IR2, intercalary veins between branches of RP; MAa, anterior branch of media anterior; MAb, posterior branch of media anterior (indicated as * on figures); MP, media posterior; CuA, cubitus anterior; CuP, cubitus posterior; AA, analis anterior; AP, analis posterior (completely fused with posterior wing margin); Pt, pterostigma; Cr, nodal cross-vein; Sn, subnodal cross-vein; Ax1, Ax2, primary antenodal cross-veins; ASn, strong subantenodal cross-vein located in area between RA and RP, and between arculus and subnodus; N, nodus. Most drawings were prepared using an Olympus SZX9, except for the drawings made by GB at the Museum of Comparative Zoology.

The specimen referred to as MNHN is housed at the Palaeontology Department, Muséum National d'Histoire Naturelle (Paris, France). Specimens referred to as PIN are housed in the Arthropod Laboratory, Palaeontological Institute, Russian Academy of Science (Moscow, Russia). Specimens referred to as MCZ are housed in the Museum of Comparative Zoology (Cambridge, U.S.A.). The specimen referred to as NRPS is housed in the Naturhistoriska Riksmuseum Paleozoology (Stockholm, Sweden). The specimen referred to as Ld LAP is housed in the 'coll. Dr. Lapeyrie', Musée Fleury (Lodève, France). The specimen referred to as BMB is housed in the Booth Museum (Brighton, U.K.).

SYSTEMATIC PALEONTOLOGY

This section includes a discussion on the validity of the 'Protozygoptera' as a taxon, supplemented by new data on the Meganeuridae *Meganeura monyi* (Brongniart, 1884) (Fig. 1). The next part is composed of a revision of several previously described 'Protozygoptera', and description new taxa, supplemented by new illustrations (Figs. 1–17). The whole section is complemented by a summary of the proposed taxonomic and nomenclatural scheme (Fig. 18).

Taxon STIGMOPTERA Bechly, 1996

Discussion.—Bechly (1996) considered that the 'Protozygoptera' and Panodonata (Odonata plus Tarsophlebiidae) are grouped together within the Stigmoptera Bechly, 1996, characterized by several synapomorphies, the most prominent ones being the presence of a 'true' pterostigma, the capture of CuA by MP, and the reduction of CuP to a short vein between MP + Cu and AA. The group 'Protozygoptera' Tillyard, 1925 shares the apomorphies of the Stigmoptera. It is necessary to discuss the monophyly and composition of the former group.

Grade 'PROTOZYGOPTERA' Tillyard, 1925

Discussion.—Bechly (1996, 2009) proposed the following putative synapomorphies to characterize this assemblage: 'wing venation: strongly petiolated wings (convergent to Triadophlebiomorpha and many Zygoptera) with a very long petiolus; nodus shifted in a more basal position; regressive development of the nodus; number of antenodal cross-veins reduced to 2–3 that are more or less aligned (reversed in *Permepallage* Martynov, 1938); CuP-crossing (=anal crossing sensu Fraser, 1957) shifted in a very basal position. Other characters: not yet known'. The difficulty with this diagnosis is that all characters, except for the regressive development of the nodus (a state that could equally be interpreted as a plesiomorphy), are also present in at least some Zygoptera. Thus there is no known strict synapomorphy of the protozygopteran Odonatoptera.

Furthermore, compared to the Panodonata sensu Bechly (1996) (=Odonata and Tarsophlebiidae), protozygopterans have several plesiomorphic character states. The most prominent is the point of separation between CuA and MP not aligned with the posterior branch of MA (MAb). The reduction of CuA or complete disappearance of this vein in some Kennedyidae (see below) or Protomyrmeleontidae (see Nel et al., 2005) makes proper interpretation of this character difficult. However some taxa (e.g., *Progoneura* Carpenter, 1931, *Terskeja* Pritykina, 1981) clearly show an 'intermediate' condition for this character (i.e., CuA is not reduced, and its point of divergence with MP is not aligned with MAb), demonstrating that CuA is not of Odonata type in all protozygopterans, especially in Protomyrmeleontidae.

One potential derived character of the protozygopterans could have been the presence of a strong subantenodal cross-vein (ASn) located in the area between RA and RP, and between the arculus and the subnodus. However, as this cross-vein is absent in many Protozygoptera and Archizygoptera, it cannot constitute a strict synapomorphy of the whole protozygopterans. Furthermore, a similar cross-vein is known in the Triadophlebioptera Bechly, 1996, sister group of the Stigmoptera (e.g., Permophlebiidae Nel et al., 2001). It could well be a convergence due to similar strongly petiolated wings.

The permagrionid specimen PIN 1700/477 (Fig. 7.1; genus and species undetermined) is of particular interest for this discussion. This fossil clearly shows four tarsal segments (Fig. 7.3, 7.4), whereas tarsi have five segments in the Meganeuridae (Fig. 1), and three segments in Odonata. The Tarsophlebiidae (in Panodonata sensu Bechly, 1996) were also supposed to have tarsi with four segments, but Huang and Nel (2009) demonstrated that they possess three segments, as in other Odonata. Huang et al. (2010) also demonstrated that the 'protozygopteran' family Protomyrmeleontidae had tarsi with three segments. The number of tarsal segments remains unknown in the Permo–Triassic Triadophlebioptera Bechly, 1996 and in the Permian Protanisoptera Carpenter, 1931 (Huguet et al., 2002), but the presence of tarsi with four segments in a protozygopteran suggests that Triadophlebioptera and Protanisoptera also had a plesiomorphic state, namely four or five tarsal segments. The reduction of the number of tarsal segments from five to three is therefore a potential synapomorphy shared by Protomyrmeleontidae and Panodonata (Odonata plus Tarsophlebiidae). The presence of several wing venation synapomorphies of the Protomyrmeleontidae shared with the other families currently included in the Archizygoptera Handlirsch, 1906 (see below) suggests that this reduction of number of tarsal segments is a synapomorphy of a new taxon including Archizygoptera and Panodonata. This hypothesis implies that the 'Protozygoptera' is paraphyletic. Thus, the Stigmoptera includes a superfamily Permagrionoidea (see below) and a taxon composed of Archizygoptera and Panodonata. Test of this hypothesis will be possible if body structures of other Archizygoptera (Permepallagidae, Kennedyidae, etc.) are discovered.

Nevertheless, according to the most recent phylogenetic data at the base of Odonata, there could be a grade of damselfly-like groups with distinctly petiolated wings (Triadophlebiomorpha, Campylopterodea, Protozygoptera, Archizygoptera, Saxonagrionidae, Tarsophlebioptera, Zygoptera, Sieblosiidae) (Bybee et al., 2008). This suggests that Fraser's (1957) hypothesis of a stalked-wing origin of modern odonates could be correct, despite criticisms raised by Bechly (1996). Investigations of the evolution of groups with modern representatives provide relevant examples to consider. For example, broad-winged damselflies ('Calopterygoidea') were found to be nested as a subclade within petiolated damselflies (Dumont et al., 2010). Also, the Epiophlebiidae, i.e., the sister group of Anisoptera, and several other Mesozoic damsel-dragonfly taxa have narrow wing bases as well. However, several convergences between all these taxa with petiolated wings cannot be excluded, considering the homoplastic character distribution of narrow and broad wing bases within Odonatoptera, and the recent example of the polyphyly of the

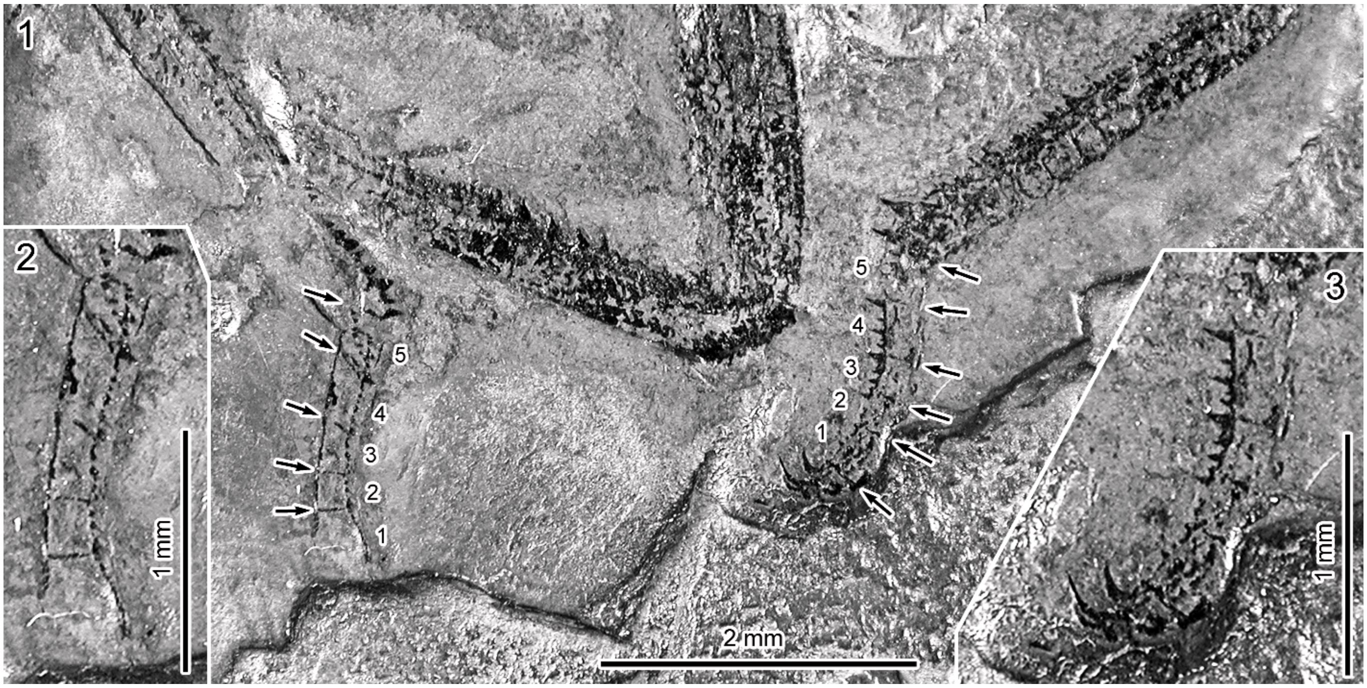

FIGURE *1*—*Meganeura monyi* (Brongniart, 1884), holotype specimen MNHN-LP-R52938: *1,* photograph of legs, with indication of the number of tarsal segments; *2, 3,* details of tarsi.

narrow winged ‘Tetrathemistinae’ within Libellulidae (Fleck et al., 2008). Wing petiolation is a very frequent phenomenon among insects, as it occurred in Megasecoptera, Odonatoptera, Mecoptera, Diptera, and Lepidoptera, etc. Therefore, convergencies affecting this character would not be very surprising within the Odonatoptera.

Another character typical of (at least) the archizygopteran family Protomyrmeleontidae is the absence of the subapical spine on tarsal claws (Huang et al., 2010), but this structure remains unknown in other Archizygoptera. The permagrionid specimen PIN 1700/477 (Fig. 7) had a tarsal claw similar to those of the Panodonata, but again the tarsal claws are unknown in Triadophlebioptera and Protanisoptera.

The presence of a complete meso-metathoracic interpleural suture in the specimen PIN 1700/477 (Fig. 7.1, 7.2) suggests that the (more or less important) reduction of this structure in modern Odonata and Protomyrmeleontidae (Huang et al., 2010) could be a potential apomorphy of Archizygoptera + Panodonata (but the Zygoptera: Calopterygidae, and at least some Isophlebioidea, have a complete suture as well).

The ventral projection at the base of the abdomen of PIN 1700/477 clearly is not a male secondary genital apparatus (probably an artifact), because it is situated between the short 1st and the long 2nd segment, and not between the two long segments 2 and 3. Nevertheless, the holotype specimen PIN 1700/3250 of the archizygopteran genus *Engellestes chekardensis* n. gen. n. sp. clearly has secondary male genital apparatus on the second abdominal segment. Also in the PIN collection, one of us (AN) and a colleague observed in 1997 two other specimens of Permagrionidae, from the same outcrop (late early Permian, Tshekarda) with body structures preserved and clear male secondary genital structures on the ventral part of abdominal segment 2 (unfortunately both specimens were lost during a loan shipment before they were properly documented). Therefore, we can consider that the secondary male genital apparatus is present in the Archizygoptera and probably also in the Permagrionoidea. This apparatus is absent in the protodonate *Namurotypus sippeli* Brauckmann and Zessin, 1989 according to Brauckmann (1991) and Bechly et al. (2001), and primitively developed in *Tarsophlebia eximia* (Hagen, 1862) according to Fleck et al. (2004). Nevertheless, we still do not know if this structure was present in groups like Protanisoptera or Triadophlebiomorpha.

In summary, the secondary male genital apparatus developed very early in the odonatopteran history as a representative of the Archizygoptera was already present during the late Carboniferous.

Finally, it must be mentioned that the exact position of the Tarsophlebiidae within the Panodonata is still disputed, as one of the arguments favouring a sister group relationships with the Odonata (Zygoptera + Epiproctophora) was the alleged presence of tarsi with four segments, which is no longer valid. However, the male secondary genital apparatus without intromittent organ, as well as the basally open discoidal cells in both pairs of wings are unique plesiomorphies that still could support an exclusion from crown-group Odonata (Fleck et al., 2004).

Superfamily PERMAGRIONOIDEA Tillyard, 1928

Type family.—Permagrionidae Tillyard, 1928 (=Permolestidae Martynov, 1932; see below) (monotypic superfamily).

Diagnosis.—As for the type family.

Discussion.—For this superfamily Bechly (1996, 2009) proposed as synapomorphy the arculus and Ax2 aligned, but this character is not present in some genera (*Permolestes* Martynov, 1932, see below). The presence of a strong and concave vein m-cu between MP and CuA (e.g., Cu) appears to be a more useful character state.

Family PERMAGRIONIDAE Tillyard, 1928

Type genus.—*Permagrion* Tillyard, 1928.

Other genera.—*Permolestes* Martynov, 1932, *Epilestes* Martynov, 1937, *Scytolestes* Martynov, 1937, *Solikamptilon* Zalessky, 1948.

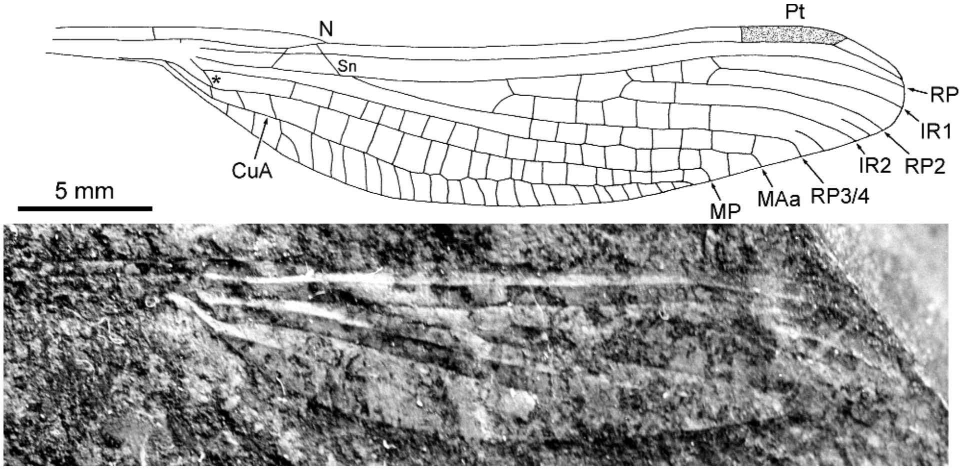

FIGURE 2—*Permagrion falklandicum* Tillyard, 1928, holotype specimen NRPS Ar 2168, drawing and photograph (negative imprint, reversed).

Diagnosis.—Wing elongate, with a long petiole; AA fused with posterior wing margin; CuP as a short cross-vein between MP + Cu and posterior wing margin; strong and concave vein m-cu between MP and CuA; numerous cross-veins between main longitudinal veins; nodal Cr and subnodus with a strong normal obliquity and generally well aligned; pterostigma very short to very long but sclerotized; primary antenodal cross-veins present, few (zero to two) secondary antenodals; MAb rather long and of normal obliquity; a strong subantenodal cross-vein (ASn) in area between RA and RP, arculus and subnodus, frequently of inverted obliquity.

Discussion.—Tillyard (1928, p. 56) erected the Permagrionidae. Bechly (1996) synonymized the Solikamptilonidae, originally described by Zalessky (1948, p. 49), with the Permagrionidae. Bechly (2009) proposed assigning *Lodevia* Nel et al., 1999 to the Permolestidae, but we consider this genus as an Archizygoptera (see below). The genus *Sushkinia* Martynov, 1930, based on fragmentary material, is of uncertain affinities but could be related to the Kennedyidae (see discussion in Nel et al., 1999b).

Regarding the diagnosis of Permagrionidae, Bechly (1996, 2009) proposed the following synapomorphies (based on Tillyard, 1928, and Fraser, 1957): apex of wing strongly falcate; basal and distal margin of pterostigma strongly oblique, so that the pterostigma is of rhomboidal shape; basal vestige of medial stem M suppressed; m-cu oblique and aligned with MAb. Our present revision of the type material of *Permagrion* demonstrates that all these characters are either erroneous (shape of wing or of pterostigma) or unknown (presence versus absence of medial stem M at wing base).

Bechly (1996, 2009) proposed no synapomorphy for the Permolestidae. After our revision, no significant difference can be found that would justify a separation between the two families Permagrionidae and Permolestidae. Thus we propose to synonymize the Permolestidae with the Permagrionidae. The rule of priority dictates that the genus *Permagrion* should be maintained as type genus of the family, even if it is one of the most poorly known genera in the family.

Genus PERMAGRION Tillyard, 1928

Type species.—*Permagrion falklandicum* Tillyard, 1928 (monotypic genus).

Diagnosis.—ASn aligned with a cross-vein, as in *Permolestes* spp.; pterostigma large and long, and area between CuA and posterior wing margin reduced with one row of cells, as in *Solikamptilon* spp.

PERMAGRION FALKLANDICUM Tillyard, 1928
Figure 2

Description.—Negative imprint of a mainly complete wing; 31.8 mm long, 6.2 mm wide; distance from wing base to nodus 10.0 mm, to arculus 5.0 mm, to pterostigma 15.4 mm; pterostigma 4.0 mm long, with proximal side vertical, distal side oblique; base of RP 0.5 mm distal to arculus; MA emerging 0.8 mm from RP; MAb 0.7 mm long; MP and CuA separating basally to RP; petiole and distal parts of wing badly preserved; ASn aligned with a cross-vein, and oriented towards wing base; antenodals and postnodals not preserved (except one antenodal); base of IR1 at 13.8 mm from subnodus, RP2 at 10.5 mm, IR2 at 6.2 mm, RP3/4 at 0.5 mm; secondary longitudinal veins between RP2 and IR2, and between IR2 and RP3/4; MAa zigzagged in its distal part; MP straight; m-cu 0.9 mm distal from MAb; one row of cells between RP3/4 and MAa, between MAa and MP, between MP and CuA; area between MP and CuA reduced in its distal third; area between CuA and posterior wing margin with one row of cells and only one cross-vein bifid at nodus level.

Type.—Specimen NRPS Ar 2168.

Occurrence.—Bodie Creek Head, Falkland Islands (Malvinas), Argentina; Upper Permian.

Discussion.—The original description and figure by Tillyard (1928) contains many mistakes, therefore we provide a revised description.

Genus PERMOLESTES Martynov, 1932

Type species.—*Permolestes gracilis* Martynov, 1932.

Other species.—*Permolestes sheimogorai* n. sp., *Permolestes soyanaiensis* n. sp.

Diagnosis.—Wing elongate and broad, pterostigma with the basal and distal sides trapezoidal with costal side longer than ventral side and basal side of inverted obliquity (synapomorphy); a very strong oblique ASn; AA completely fused with posterior wing margin; area between CuA and posterior wing margin with numerous rows of small cells; nodal Cr and subnodus aligned, strong and distinctly oblique; presence of supplementary longitudinal veins between main veins of median and radial areas; numerous small cells in distal half of wing.

PERMOLESTES GRACILIS Martynov, 1932
Figure 3.1

Diagnosis.—ASn perpendicular and more weakly developed than in the two new species.

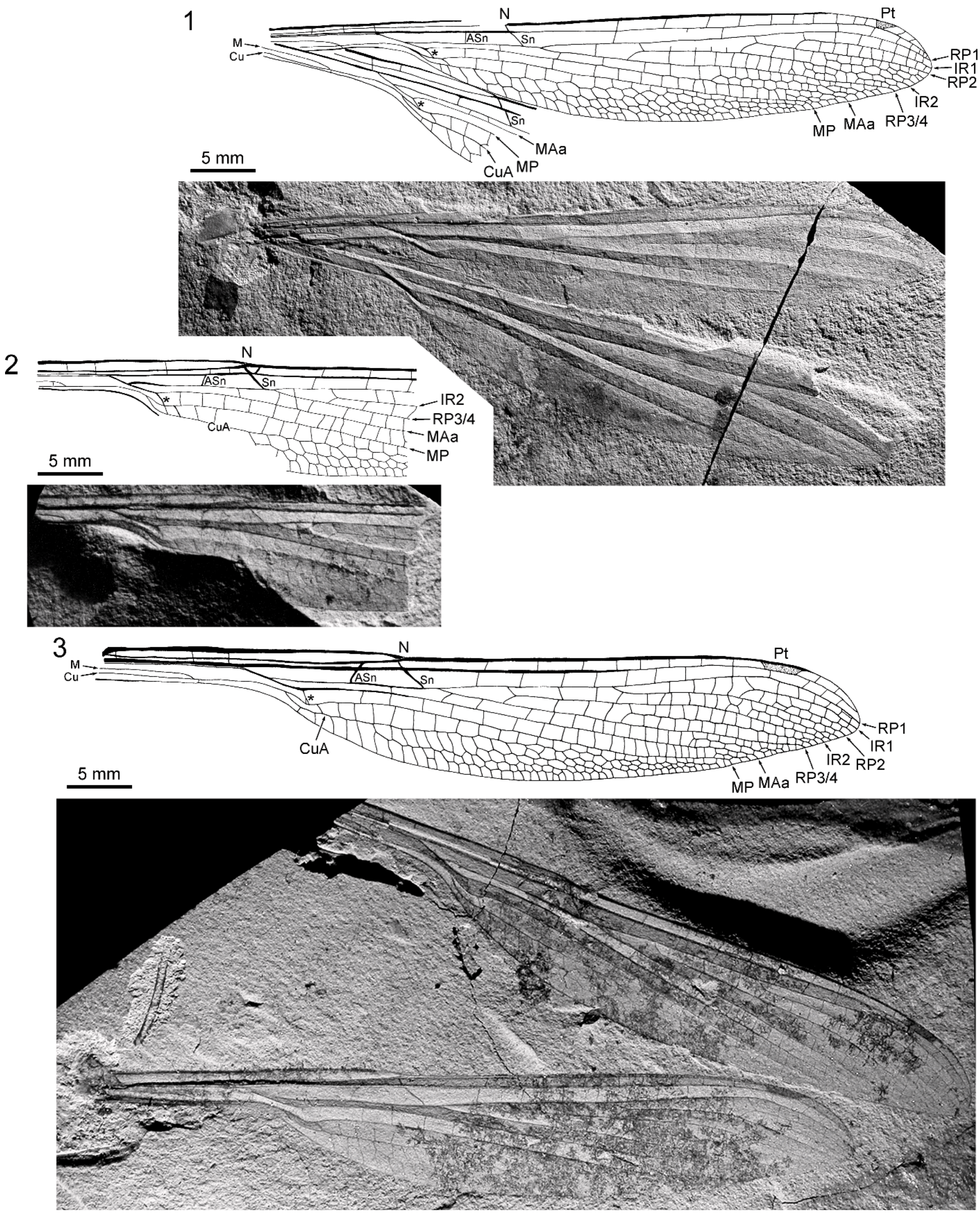

FIGURE 3—*Permolestes* spp.: *1, Permolestes gracilis* Martynov, 1932, holotype specimen PIN 2455/1, drawing and photograph (negative imprint of a left wing, and positive imprint of a right wing); *2, Permolestes sheimogorai* n. sp., holotype specimen PIN 8/117, drawing and photograph (negative imprint); *3*, *Permolestes soyanaiensis* n. sp., holotype specimen PIN 3353/63, drawing of the left forewing and photograph (positive imprint of a right wing, and negative imprint of a left wing).

Description.—Imprint and counter-imprint of both wings; wing 51.0 mm long, 8.1 mm wide; wing base and apex not well preserved; distance from base to nodus 18.1 mm, to pterostigma 46.8 mm, to arculus 8.1 mm; from arculus to base of RP 2.3 mm; MAa and MAb separated 1.6 mm from base of RP; MAb 0.9 mm long; MP and CuA separated just after separation of RP1 and MA; three visible antenodal cross-veins; Ax2 opposite arculus; Ax1 opposite CuP; one antenodal cross-vein more basal to Ax1, very far from wing base (thus it is probably not Ax0); Cr visible and aligned with subnodus; 10 postnodal cross-veins, first one aligned with a postsubnodal; cells delimited by postnodals of decreasing length from basal to distal parts; cross-veins delimiting five first postnodal cells oriented towards wing base; pterostigma very short and trapezoidal, with a costal side longer than others, 2.4 mm, posterior side the shortest, 0.4 mm long, basal side almost vertical, distal side very oblique; three cells between C and RA distal of pterostigma; base of IR1 30.7 mm from base of RP; RP2 26.9 mm, IR2 18.1 mm, and RP3/4 10.5 mm from subnodus; branches of RP straight and parallel; MP and Cu well separated at wing base, and fused 5.5 mm distally; CuP very short and ending on posterior wing margin perpendicularly; MAa simple and straight, very weakly zigzagged distally; a longitudinal supplementary vein between RP3/4 and MAa in distal third; MP divided in two strong concave veins MP and m-cu, 0.6 mm distal of MAb; m-cu very short; short longitudinal supplementary vein between MAa and MP just before wing margin; CuA zigzagged and very long, reaching wing margin 9.8 mm from wing apex; cubital area wide and long with four to five rows of cells between CuA and wing margin; AA completely fused with posterior wing margin.

Type.—Specimen PIN 2455/1–2.

Occurrence.—Soyana River, Arkhangelsk Region, north European Russia; early Kazanian, late Permian (Rasnitsyn and Zherikhin, 2002).

PERMOLESTES SHEIMOGORAI new species
Figure 3.2

Diagnosis.—This species differs from *Permolestes gracilis* in a stronger ASn, more antenodals, and the presence of a strong cross-vein just distal to subnodus.

Description.—Incomplete wing base; preserved length 29.1 mm; width 8.3 mm; distance from base to nodus 15.8 mm, to arculus 5.1 mm; RP emerging from MA at 1.5 mm distal to arculus; MAa and MAb bifurcating at 2.2 mm from base of RP; MAb 1.1 mm long and aligned to first cross-vein between MP and CuA; MP and Cu separated at wing base and fused 2.1 mm distally; one cross-vein between MP and CuA at 1.1 mm from wing base; MP and CuA separated at 7.7 mm from wing base, 1.5 mm distal to the RP-MA fork; m-cu and MP separated 2.3 mm from separation of MP and CuA; wing petiolated; three visible antenodals between C and ScP, the distal ones complete; distance from second antenodal to arculus 1 mm; two incomplete antenodals of second row between ScP and RA; a strong subantenodal cross-vein (ASn), oriented towards wing base, between RA (7.3 mm from its origin) and RP (5.1 mm from its origin); first postnodal cross-vein strong and oblique; four postnodals oriented towards wing base, third one aligned with a postsubnodal; base of IR2 and of RP3/4 15.1 mm and 11.2 mm from base of RP, respectiely; only one very oblique cross-vein between RP1/2 and RP3/4; MAa, MP and CuA simple and nearly straight; one row of cells between MAa and MP and between MP and CuA; CuP absent or not preserved; cubital area broad and with three rows of cells between CuA and wing margin.

Type.—Specimen PIN 8/117.

Etymology.—Named after the type locality.

Occurrence.—Soyana River, Arkhangelsk Region, north European Russia; early Kazanian, late Permian (Rasnitsyn and Zherikhin, 2002).

PERMOLESTES SOYANAIENSIS new species
Figure 3.3

Diagnosis.—This fossil differs from *Permolestes gracilis* and *P. sheimogorai* n. sp. in the presence of a strong ASn aligned with a cross-vein. Other differences with *P. gracilis* are as follows: presence of a secondary longitudinal vein between IR1 and RP2, a longer secondary longitudinal vein between IR2 and RP3/4, a shorter secondary longitudinal vein between RP3/4 and MAa. The pterostigma is longer, but organized in the same way as in *P. gracilis*.

Description.—Imprint and counter-imprint of two wings, 57.9 mm long, 9.3 mm wide; three complete antenodals; Ax2 at level of arculus; Ax0 present; ASn strongly developed, oblique, and aligned with one cross-vein; Cr aligned with subnodus; 10 postnodal cross-veins, first one nearly aligned with first postsubnodal; pterostigma short (but longer than in *Permolestes gracilis*) and trapezoidal with costal side longest; M and Cu separated at wing base but fused 7.2 mm distally; CuP very short and joining wing margin perpendicularly; MAa simple; longitudinal supplementary vein between RP3/4 and MAa in its distal fifth; MAb directed towards wing apex; MP bifurcating in MP and m-cu; m-cu short, concave, and strong, joining CuA; area between MAa and MP with one row of cells in its main part; cubital area very broad and long with four to five rows of cells between CuA and wing margin.

Type.—Specimen PIN 3353/63.

Etymology.—Named after the type locality.

Occurrence.—Soyana River, Arkhangelsk Region, north European Russia; early Kazanian, late Permian (Rasnitsyn and Zherikhin, 2002).

Genus SCYTOLESTES Martynov, 1937

Type species.—*Scytolestes stigmalis* Martynov, 1937 (monotypic genus).

Diagnosis.—This taxon shows great similarities with *Epilestes* spp. (three rows of cells in area between CuA and posterior wing margin; absence of secondary longitudinal veins between main veins of median and radial areas). The main difference between *Sc. stigmalis* and *Epilestes* spp. is the apparent fusion of RP2 with IR2 so that the 'true' base of RP2 looks like a transverse vein.

SCYTOLESTES STIGMALIS Martynov, 1937
Figure 4

Type.—Specimen PIN 100/21.

Occurrence.—Kargala, Orenburg region, Southern Ural, Russia; early Tatarian, late Permian (Rasnitsyn and Zherikin, 2002).

Discussion.—A new drawing of the holotype is provided to facilitate comparison between taxa. Several important details (vein ASn, etc.) are not indicated in the original description by Martynov.

Genus EPILESTES Martynov, 1937

Type species.—*Epilestes kargalensis* Martynov, 1937.

Other species.—*Epilestes gallica* Nel et al., 1999; *Epilestes angustus* n. sp.

Diagnosis.—This genus differs from *Permolestes* in the longer pterostigma, with basal side perpendicular to costal

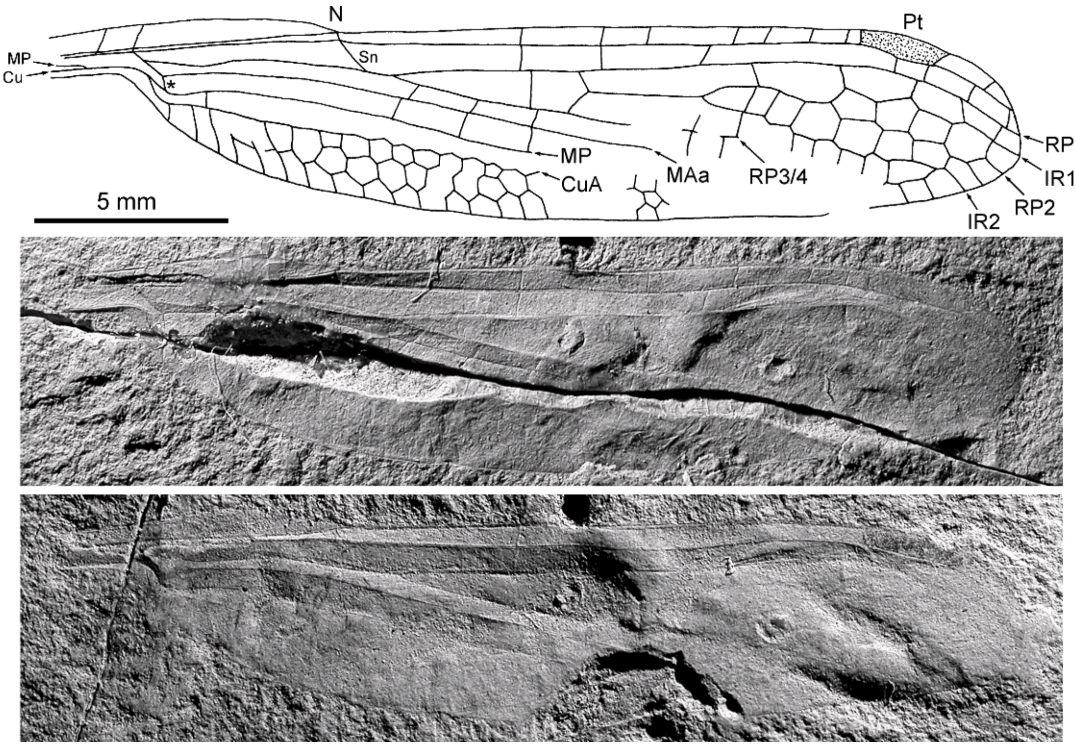

FIGURE 4—*Scytolestes stigmalis* Martynov, 1937, holotype specimen PIN 100/21, drawing and photographs (negative imprint, positive imprint reversed).

margin, and absence of secondary longitudinal veins between main veins of median and radial areas. It differs from *Permagrion* in the presence of two to three rows of cells in area between CuA and the posterior wing margin. It differs from *Scytolestes* in a different organization of the veins IR2 and RP2.

EPILESTES KARGALENSIS Martynov, 1937
Figure 5.1

Diagnosis.—Two rows of cells in cubital area.

Type.—Specimen PIN 100/0.

Occurrence.—Kargala, Orenburg region, Southern Ural, Russia; early Tatarian, late Permian (Rasnitsyn and Zherikin, 2002).

Discussion.—We provide new illustrations of the holotype to facilitate comparison.

EPILESTES ANGUSTAPTERIX new species
Figure 5.2

Diagnosis.—*Epilestes angustapterix* n. sp. differs from *E. kargalensis* in the narrower cubital area. *E. gallica* has three rows of cells in cubital area, instead of one to two in *Epilestes angustapterix*.

Description.—Imprint of an incomplete petiolated wing, 35.0 mm long, 5.0 mm wide; distance from base to arculus 5.4 mm, to nodus 12.1 mm, to pterostigma 29.0 mm; pterostigma 4.7 mm long; distance from RP to arculus 1.4 mm; bifurcation of MAa and MAb at 1.3 mm from base of RP; MAb 0.6 mm long and very oblique; a cross-vein closing basally dicoidal cell; MP and CuA bifurcating at 7.0 mm from wing base, opposite base of RP; two primary antenodal cross-veins, 1.5 mm apart; ASn perpendicular to RA and RP; Cr and subnodus oblique and aligned; RP3/4 emerging just distal subnodus, 6.0 mm from base of RP; only one aligned postnodal/postsubnodal cross-vein preserved; basal side of pterostigma vertical, distal side very oblique; only one cross-vein below pterostigma; only one cell distal to pterostigma between C and RA; base of IR1 not preserved; RP2 and IR2 not preserved; a very short secondary longitudinal vein between RP3/4 and MAa; MAa simple reaching wing margin at 4.6 mm from wing apex; MP reaching wing margin 6.3 mm from wing apex; one row of cells between MP and CuA; four cross-veins in area between MP and posterior wing margin; cubital area with one row of cells up to nodus level, more distally two rows, and only one row near apex of CuA.

Etymology.—Named after the narrow cubital area.

Type.—Specimen PIN 63/117.

Occurrence.—Soyana River, Arkhangelsk Region, north European Russia; early Kazanian, upper Permian (Rasnitsyn and Zherikhin, 2002).

Discussion.—This fossil can be placed in the genus *Epilestes* according to the following characters: no secondary longitudinal vein between all main longitudinal veins; very long pterostigma; two rows of cells in cubital area.

Genus SOLIKAMPTILON Zalessky, 1948

Type species.—*Solikamptilon remuliforme* Zalessky, 1948.

Other species.—*Solikamptilon pectinatus* n. sp.

Diagnosis.—This genus shares with *Scytolestes*, *Epilestes*, and *Permagrion* the absence of secondary longitudinal veins between main veins of median and radial areas. It differs from *Scytolestes* and *Epilestes* in the presence of only one row of cells in cubital area. It is very similar to *Permagrion*, from which it differs only in the veinlets of the cubital area, which are sigmoidal rather than straight.

SOLIKAMPTILON REMULIFORME Zalessky, 1948
Figure 6.1

Diagnosis.—Nodus and pterostigma distant; base of IR1 well basal of pterostigma.

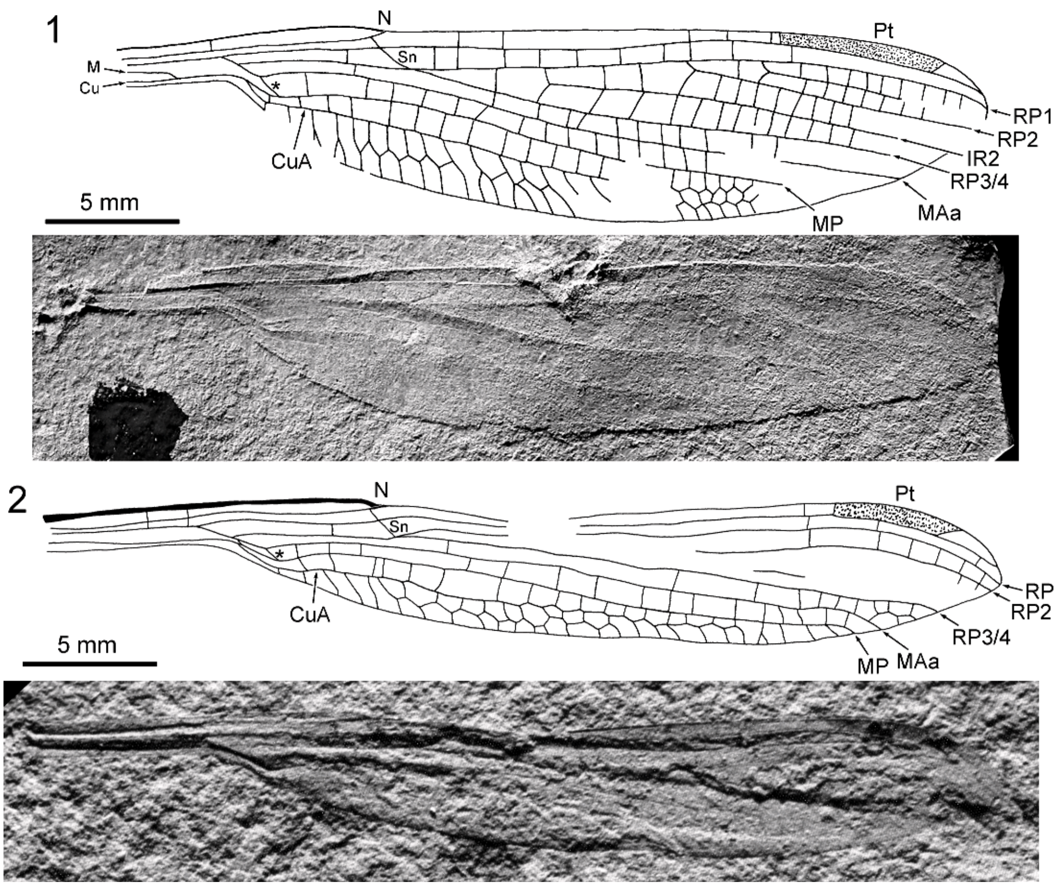

FIGURE 5—*Epilestes* spp.; *1, Epilestes kargalensis* Martynov, 1932, holotype specimen PIN 100/0, drawing and photograph (negative imprint, reversed); *2, Epilestes angustapterix* n. sp., holotype specimen PIN 63/117, drawing and photograph (positive imprint).

Description.—Distal two third of a wing, apparently hyaline; preserved part 32 mm long, 6 mm wide; distance from nodus to pterostigma about 22 mm; Cr and subnodus aligned and strongly oblique; only two postnodals; three postsubnodals, two of them being almost aligned with postnodals; base of RP3/4 aligned with subnodus; base of IR1 distinctly basal of pterostigma; longitudinal veins except CuA and MAa at their distal part, are straight; area between MP and CuA distally reduced; cubital area crossed by a series of sigmoidal cross-veins; pterostigma present, elongate but with its distal end not clearly indicated.

Type.—Specimen VI-200/3, Moscow, Vernadsky State Geological Museum (Gosudarstvennyi Geologicheskii Muzei imeni Vernadskogo), N VI-200, room 40, shelf 62, box 20 (A. Ponomarenko personal commun.).

Occurrence.—Tshekarda River, Ufa-Solikamsk Basin, Koshelevka Formation, Middle Urals, Russia; Kungurian, latest early Permian (Rasnitsyn and Zherikhin, 2002).

SOLIKAMPTILON PECTINATUS new species
Figure 6.2

Diagnosis.—The corresponding material could be assigned either to *Permagrion* or to *Solikamptilon* based on the absence of secondary longitudinal veins between main veins, and an area between CuA and posterior wing margin with one row of cells. However it shares with *Solikamptilon remuliforme* the presence of sigmoidal cross-veins in the cubital area, a character diagnostic of the corresponding genus. The distance between nodus and pterostigma is about 22 mm in *S. remuliforme*, and thus is distinctly longer than that of *Solikamptilon pectinatus* (Fig. 6.2). The second difference between the two species is that the base of IR1 is below the pterostigma in *S. pectinatus* whereas it begins well basal of it in *S. remuliforme*.

Description.—Imprint of a wing with apical part missing; 26.5 mm long, 5.0 mm wide; distance from base to nodus 9.2 mm, to pterostigma 23.4 mm, to arculus 3.9 mm; from nodus to pterostigma 14.2 mm; RP emerging from MA 1.0 mm distal base of arculus; MAa and MAb separating 1.0 mm from base of RP; MAb 0.6 mm long; MP reaching CuA 1.6 mm from base of CuA, base of CuA 4.4 mm from wing base, just before separation of RP from MA; wing petiolated; one complete antenodal preserved (Ax2?), 0.3 mm basal to arculus; Cr and subnodus aligned and strongly oblique; only two postnodals; three postsubnodals, two of them being almost aligned with postnodals; Asn present; base of IR1 17.1 mm distal of separation of RP and MA, base of RP2 14.3 mm, IR2 13.4 mm, RP3/4 7.1 mm, thus all distal of nodus; longitudinal veins except CuA and MAa at their distal part, are straight; area between MP and CuA distally reduced; cubital area crossed by a series of sigmoidal cross-veins.

Etymology.—Named after the structure of the wing.

Type.—Specimen PIN 13/117.

Occurrence.—Soyana River, Iva-Gora, Arkhangelsk Region, north European Russia; early Kazanian, upper Permian (Rasnitsyn and Zherikhin, 2002).

Family PERMAGRIONIDAE genus and species undetermined
Figure 7

Description.—Imprint and counter-imprint of a body in profile, with at least one fore- and one hind wing and legs

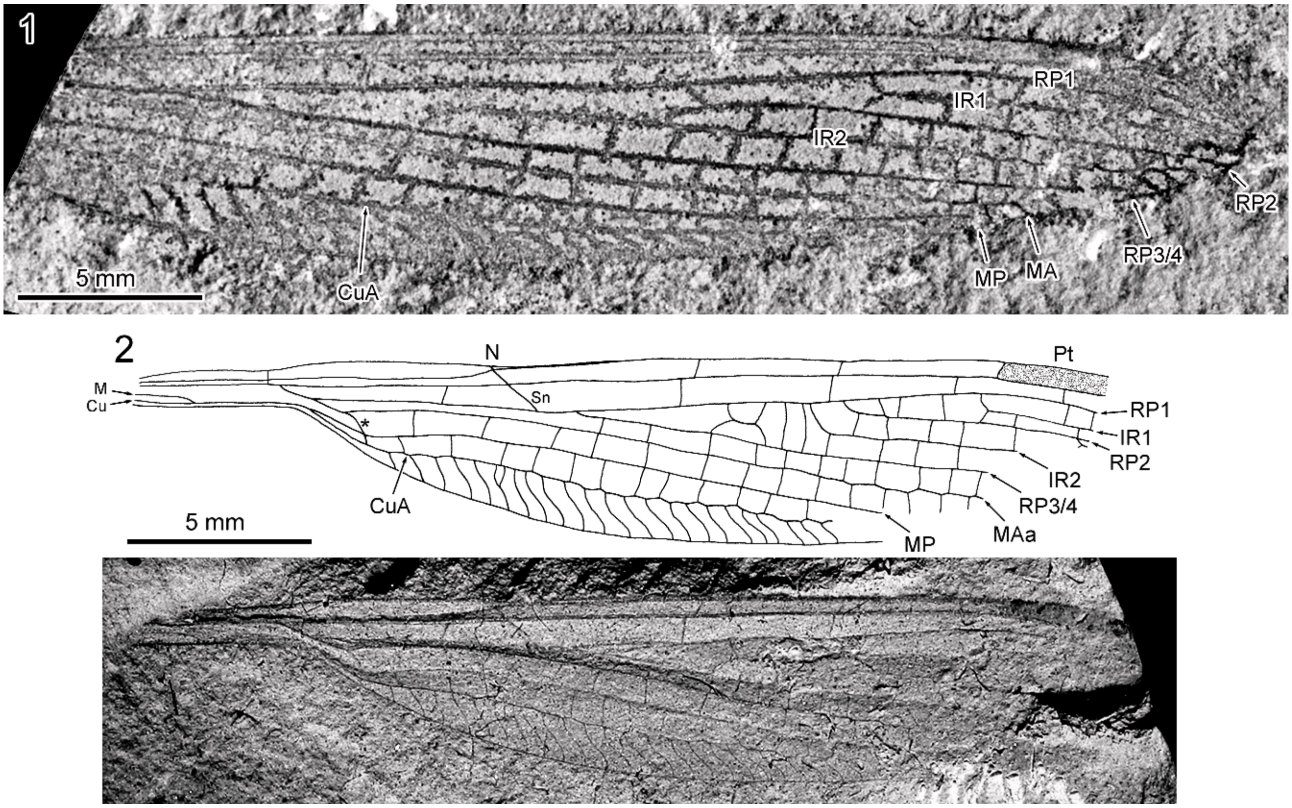

FIGURE 6—*Solikamptilon* spp.: *1, Solikamptilon remuliforme* Zalessky, 1948, holotype specimen VI-200/3, photograph (polarity unknown); *2, Solikamptilon pectinatus* n. sp., holotype specimen PIN 13/117, drawing and photograph (negative imprint, reversed).

connected, abdomen with four basal segments preserved. Body very strong; head small, 3.2 mm long, with eye large; antenna short and small; mouthparts orthognathous; prothorax broad, stronger than in recent Anisoptera, and comparable or slightly stronger than in Zygoptera, 1.3 mm long; pterothorax in profile, thoracic skewness not very pronounced (angle × approximately 30°, angle z approximately 40°) (sensu Needham and Anthony, 1903); meso-metathoracic interpleural suture complete; legs strong and of moderate length, with very strongly developed coxae (or possibly strong elongation of infra-episternum + coxa + part of trochanter); few short and strong spines on femora and tibias; tarsi four-segmented; claws very strong but with a stout subapical tooth, apparently no empodium; abdomen strong, 12.2 mm wide, first segment shorter than others that have a rather distinct median transversal carina; no trace of specialized genital structures on ventral part of second and third segment; wings overlapping with venation delicate to analyze; wing 36.4 mm long, ~6.4 mm wide, petiole 7.4 mm long; distance from wing base to nodus 14.5 mm, from nodus to pterostigma 14.5 mm, pterostigma 2.6 mm long, covering two cells with a cross-vein below its mid part; nodal Cr and subnodus distinctly oblique and aligned; area between CuA and posterior wing margin broad; CuA separating from MP opposite arculus; potsnodal cross-veins few, not aligned with postsubnodals; no antenodals visible, but they were probably very few (probably only Ax1 and Ax2).

Type.—Specimen PIN 1700/477a–b.

Occurrence.—Tshekarda River, Ufa-Solikamsk Basin, Koshelevka Formation, Middle Urals, Russia; Kungurian, latest early Permian (Rasnitsyn and Zherikhin, 2002).

Discussion.—Attribution of this fossil to the Permagrionidae is based on the long pterostigma covering one cross-vein, the petiolate wings, the base of CuA opposite arculus, the nodal Cr and subnodus aligned and oblique, and the few postnodals. It is not sufficiently well preserved to be attributed at the generic level.

This fossil is of great interest for the information on its body structures. In addition, the strong prothorax would allow a zygopterid type of mating, with the male grasping the prothorax of the female. Except for the meso-metapleural suture, the pterothorax is of anisopterid type, that is, strong and with a comparable skewness (Anisoptera between 19° and 38°, Zygoptera between 35° and 62°). The strong obliquity of the pterothorax in Zygoptera could be regarded as a possible apomorphy of the Zygoptera, but it is also (convergently?) present in the Archizygoptera: Protomyrmeleontidae (Huang et al., 2010). Also the presence versus absence of a distinct transverse carina near the middle of the abdominal segments is probably subject to homoplasies, as it is present in this Permagrionidae and the Anisoptera, whereas it is absent in Zygoptera and the Protomyrmeleontidae. Legs of this specimen differ from those of other Odonata in their relatively short and very strong femora and tibiae, and in that the coxae apparently much more developed (longer and stronger). Additionally, the Odonata have long and thin spines on tibiae (Anisoptera) and on tibiae and femora (Zygoptera). This is a potential apomorphy of Odonata (and maybe also Archizygoptera) because in the Protomyrmeleontidae both femora and tibia bear three pairs of long and sharp spines (Huang et al., 2010).

Taxon ARCHIZYGOPTERA + PANODONATA

Diagnosis.—Trimerous tarsi. Further potential apomorphy could be the reduction of the meso-metathoracic interpleural suture.

Discussion.—Trimerous tarsi have been reported in Archizygoptera such as the Protomyrmeleontidae (Huang et al., 2010).

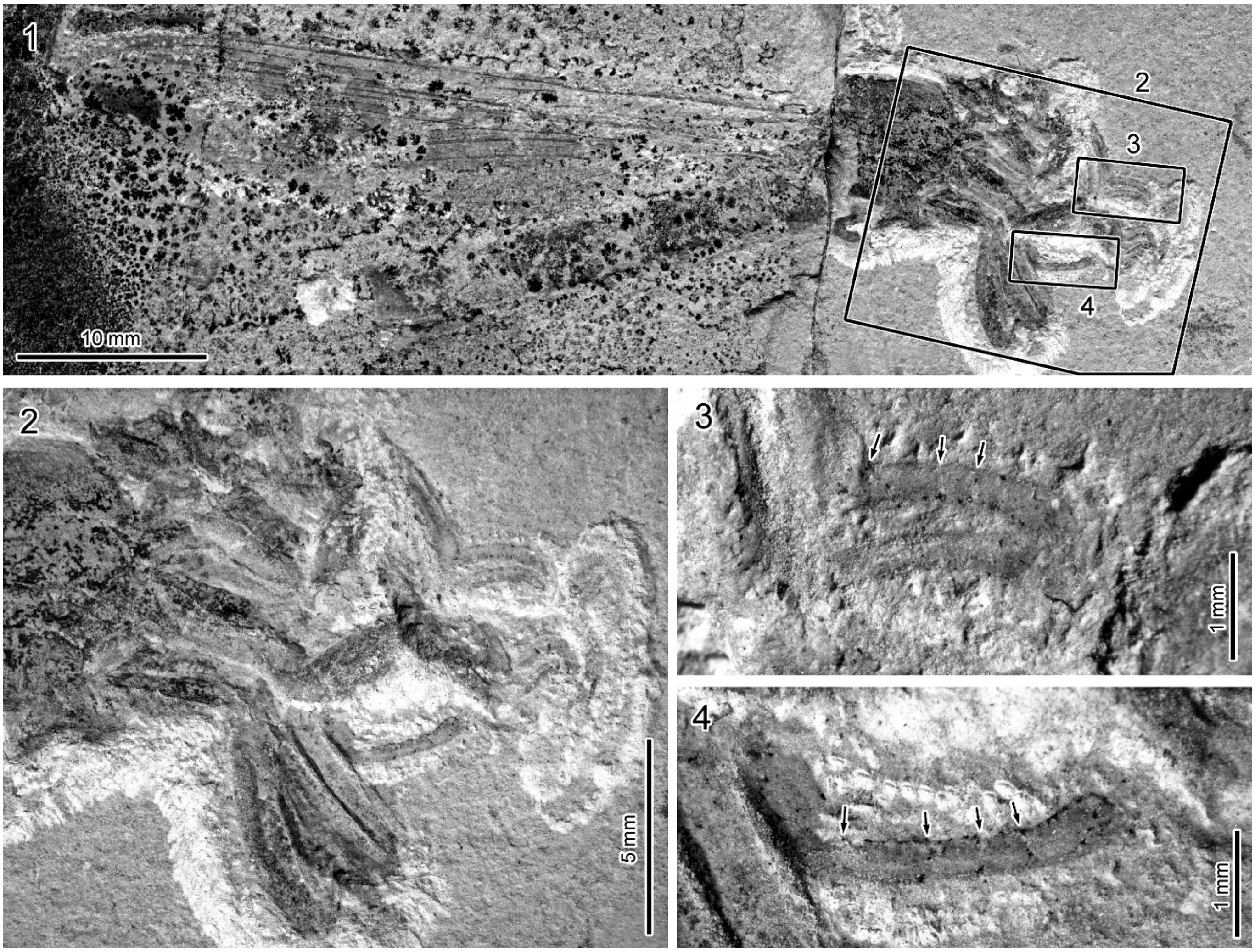

FIGURE 7—Permagrionidae gen. and sp. indet., specimen PIN 1700/477: *1,* photograph of the habitus (positive imprint, reversed); *2,* detail of head and appendages, as located on *1*; *3,* details of forelegs tarsi, as located on *1*; *4,* details of hind leg tarsus, as located on *1*.

Taxon PANODONATA Bechly, 1996
(Tarsophlebiidae plus Odonata Fabricius, 1793)

Diagnosis.—See Bechly (1996) for a list of defining apomorphies of this taxon (larval apomorphies unknown due to lack of material).

Discussion.—Bechly (1996) mentioned the suppression of the empodium as a putative apomorphy of Panodonata but this structure is apparently absent at least in the hind leg of PIN 1700/477. Thus this character is probably an apomorphy of the Stigmoptera at least. The empodia are also absent in the Protomyrmeleontidae (Huang et al., 2010). The position of the Tarsophlebiidae as sister group of Odonata is questionable because it is only supported by a single wing venation character state (discoidal cell basally open in both pairs of wings) and male secondary genitalia characters (ligula orimentary; vesicula spermalis still very short and flat with a very wide porus), which are very delicate and difficult to observe in fossils.

Taxon ARCHIZYGOPTERA Handlirsch, 1906

Diagnosis.—Nodal vein Cr and subnodus transverse, more or less vertical, not aligned, and shifted basally, so that they are nearly indistinguishable from other cross-veins between ScP and RA or RA and RP.

Discussion.—Bechly (1996) proposed the following additional synapomorphy: distal discoidal vein MAb not developed as an oblique secondary branch of MA but as short transverse ‘cross-vein’ between MA and MP. However, this character can no longer be considered as diagnostic of the whole Archizygoptera as we add the new family Lodeviidae, with a long MAb, to this taxon. Nevertheless, as shown below, *Permepallage angustissima* Martynov, 1938 has a very short MAa of inverted obliquity, very similar to that of *Kennedya mirabilis* Tillyard, 1925.

Composition.—The taxon Archizygoptera sensu Bechly (1996) comprises the Permepallagidae Martynov, 1938, Kennedyidae Tillyard, 1925, and Protomyrmeleontoidea Handlirsch, 1906 (Batkeniidae Pritykina, 1981 and Protomyrmeleontidae Handlirsch, 1906) (see also Nel et al., 1999b).

Family PERMEPALLAGIDAE Martynov, 1938

Type genus.—*Permepallage* Martynov, 1938 (monotypic family).

Diagnosis.—As for the type genus.

Genus PERMEPALLAGE Martynov, 1938

Type species.—*Permepallage angustissima* Martynov, 1938 (monotypic genus).

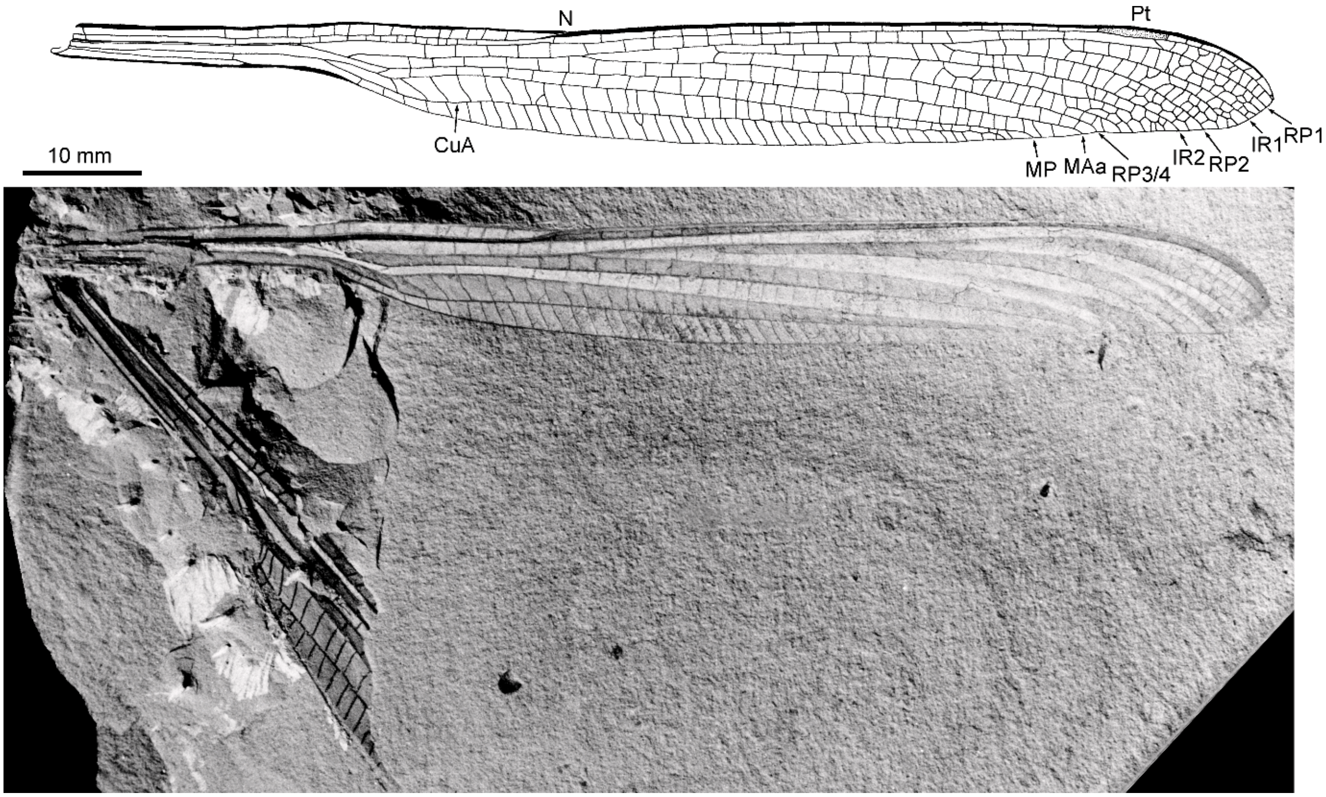

FIGURE 8—*Permepallage angustissima* Martynov, 1938, holotype specimen PIN 65/117, drawing of the right wing and photograph (negative imprint of a right wing and positive imprint of a left wing, reversed).

Diagnosis.—Wing narrow and elongate, rather falcate, with a very long petiole; main longitudinal veins parallel with no intercalary veins between them; numerous cells; nodal Cr and subnodus vertical; MAb very short and directed towards wing base; pterostigma very long and narrow, covering two long cells separated by a single cross-vein.

PERMEPALLAGE ANGUSTISSIMA Martynov, 1938
Figure 8

Description.—Imprint of two wings; wing petiolated, 101 mm long, 10.2 mm wide; distance from base to nodus 40.8 mm, from nodus to apex 60.2 mm, from arculus to wing base 19.4 mm, from pterostigma to nodus 45.0 mm; RP separated from MA 4.4 mm from base of arculus; MAa and MAb separated 3.5 mm from base of RP; MAb 1.0 mm long, with an inverted obliquity towards wing base; 14 antenodal cross-veins between C and ScP, with sixth and tenth antenodals aligned with those of second row between ScP and RA; nodal Cr with an inverted obliquity, directed towards wing base; subnodus not well defined and not aligned with Cr; postnodal cross-veins numerous, aligned with postsubnodals between RA and RP1; pterostigma long and narrow, 6.0 mm long, with basal and distal margins somewhat oblique; eight cells between C and RA distal of pterostigma; pterostigmal brace absent; a long cell beneath pterostigma; very oblique cross-vein between RA and RP below distal part of pterostigma; base of IR1 59.8 mm from base of RP, RP2 48.3 mm, IR2 30.6 mm and RP3/4 19.6 mm; a slight concavity in posterior margin at RP3/4 apex; area between IR2 and RP3/4 distally broadened and with a longitudinal secondary vein; presence of longitudinal veins between main veins of radial area; radial area covering 14.6 mm of posterior wing margin; wing apex pointed; MAa, MP and CuA straight and simple; apex of CuA at 22.5 mm from wing apex; area between MP and CuA very long, and getting narrower distally; AA separated from AP at wing base, but ending in petiole 15.0 mm distally; CuP reduced to a small cross-vein between Cu + MP and AA, just basal of apex of AA, at 13.5 mm of wing base; areas between RP3/4, MAa, MP, and CuA with one row of cells along posterior wing margin.

Type.—Specimen PIN 65/117.

Occurrence.—Tshekarda River, Ufa-Solikamsk Basin, Koshelevka Formation, Middle Urals, Russia; Kungurian, latest early Permian (Rasnitsyn and Zherikhin, 2002).

Discussion.—The main difference between *P. angustissima* and *Kennedya* spp. is the organization of the longitudinal veins in the petiole: AA is an independent vein with CuP being a cross-vein between MP + Cu and AA in *P. angustissima* whereas AA is completely fused with posterior wing margin in *Kennedya* spp.

We attribute a second specimen, PIN 66/117 (Early Kazanian, Letopala River, Iva-Gora limestones, Soyana River, Arkhangelsk Region, north European Russia, Martynov, 1938) to the same genus but it probably belongs to a different species. It differs from *P. angustissima* (Fig. 8) as follows: only three cells between C and RA distal of pterostigma, and three cells below this zone; no oblique cross-vein below pterostigma; base of IR1 below pterostigma instead of being more basal; five cells along posterior wing margin in area between MP and CuA instead of two. The incomplete preservation of this fossil prevented us from erecting a formal name for it.

Family BECHLYIDAE Jarzembowski and Nel, 2002

Type genus.—*Bechlya* Jarzembowski and Nel, 2002 (monotypic family).

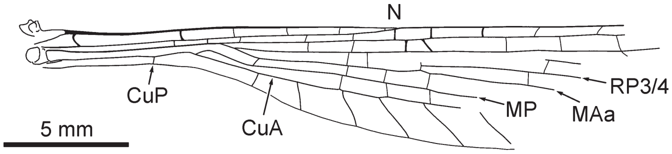

FIGURE 9—*Bechlya ericrobinsoni* Jarzembowski and Nel, 2002, holotype specimen BMB 018498 and 018499, drawing.

Diagnosis.—Three strong antenodal cross-veins present between C and ScP corresponding to Ax0, Ax1 and Ax2; antenodal cross-veins in second row (between ScP and RA) not well aligned with Ax1 and Ax2; Ax0 strongly curved; vein MAb strong but directed towards wing base and not aligned with free base of CuA; true nodus (N) present with nodal cross-vein Cr and oblique subnodus (Sn); all main longitudinal veins with no secondary branches except CuA; petiole long and narrow with AA completely fused with AP (A); CuP reduced to a short cross-vein between MP + CuA and anal margin; wing slender with few long cells.

Discussion.—An unexpected character state for a Carboniferous damselfly is the absence of a vestige of the medial stem M in the basal space of *Bechlya* (Fig. 9), because this vein is plesiomorphically present in the protodonate grade (Erasipteridae, Meganisoptera), Protanisoptera, Triadotypomorpha, Triadophlebiomorpha, Permagrionidae, and Kennedyidae, as well as in new fossils from Carrizo Arroyo (Fig. 10). *Bechlya* shows important similarities with *Permepallage*, especially in the relatively numerous secondary antenodal cross-veins, and comparatively long CuA. It shares with the *Permepallage*, and genera assigned to the Kennedyidae, a MAb vein that is short and vertical, or directed towards the wing base, but it differs from both of these taxa in the subnodus, which is distinctly oblique and directed towards the wing apex (Jarzembowski and Nel, 2002). *Bechlya* also differs from genera assigned to the Kennedyidae, and some other more derived genera, in the approximately equal width of the postnodal areas between C and RA and between RA and RP, respectively. The distinctiveness of *Bechlya* prompted us to erect a new family of this genus.

Bechlya is the oldest record of the Archizygoptera, otherwise known only in the Permian and the Mesozoic. If the Archizygoptera are considered as the sister group of the Panodonata, it implies that the latter taxon also originated in the Carboniferous, whereas the oldest record is from the middle Permian of France (namely the Saxonagrionidae Nel et al., 1999a).

Family Lodeviidae new family

Type genus.—*Lodevia* Nel et al., 1999 (monotypic family).

Diagnosis.—Wing venation similar to that of Permepallagidae, differing in: only one concave basal cross-vein between MP and CuA, instead of two; absence of intercalary veins between branches of RP; normal obliquity of subnodus; MAb short but with obliquity directed towards wing apex, instead of being directed towards base; pterostigma covering numerous small cells.

Discussion.—The position of the middle Permian genus *Lodevia* Nel et al., 1999 is problematic. Nel et al. (1999b) included it in the Permepallagidae but indicated that 'this is still open because the family characters of Permepallagidae are not at all clear'. Bechly (2009) considered that *Lodevia* could belong to the Permolestidae because it has a vein MAb of normal obliquity, unlike in the Archizygoptera sensu Bechly (1996). *Lodevia* also strongly differs from *Permepallage* in the number of cells covered by the pterostigma (four to five short cells instead two long) but these taxa have similar patterns of main longitudinal veins, with numerous cross-veins between them. *Lodevia* strongly differs from the Permolestidae in that the nodal Cr is not strongly oblique but nearly perpendicular to RA, as in the Archizygoptera. Thus we propose to consider *Lodevia* as a representative of the Archizygoptera that has not yet acquired a MAb of inverted obliquity, or perpendicular to MAa and MP. This implies that it cannot fit into any of the archizygopteran families, and it is probably the sister group of all other Archizygoptera. Then it is necessary to erect a new family Lodeviidae n. fam. for this taxon, with *Lodevia* as type genus.

Family Luiseiidae new family

Type genus.—*Luiseia* n. gen. (monotypic family).

Diagnosis.—As for the type genus.

Luiseia new genus

Type species.—*Luiseia breviata* n. sp. (monotypic genus).

Diagnosis.—As for type species.

Etymology.—Named after Maria Luise Bechly (Böblingen, Germany).

Luiseia breviata new species
Figure 10.1, 10.2

Diagnosis.—Wing elongate; pterostigma elongate and with both margins of similar obliquity; free vestige of medial stem M present in basal space; about 6 antenodal cross-veins; only few postnodal and postsubnodal cross-veins that are not aligned; MAb very short and perdendicular to MAa; MP short, ending at about midwing position; MAa short, ending far basal of pterostigma; CuA very short, ending basal of nodus; nodal and subnodal veinlets perdendicular to RA and RP; postnodal area between C and RA narrower than the postsubnodal area betwen RA and RP.

Description.—Imprint and counter-imprint of a nearly complete wing, apical part and distal hind magin missing, 17.8 mm long, ca. 2.5 mm wide; distance from wing base to nodus 7.6 mm, from base to pterostigma 15.3 mm; pterostigma elongate, 1.8 mm long, with basal side and distal side of equal obliquity; petiole very long; free vestige of medial stem M present in basal space; arculus 3.7 mm distal of wing base; base of RP 1.5 mm distal of arculus; MAa and MAb separating 0.25 mm distally; MAb very short and perdendicular between MAa and MP; MAa short, ending far basal of pterostigma; MP very short, ending at about midwing level; CuA very short, ending basal of nodus; area between CuA and posterior wing margin very narrow; AA fused with posterior wing margin; CuP cross-vein slightly distal of medial stem M; nodal and subnodal cross-vein at nodus and perpendicular to RA and RP; four antenodal cross-veins of first row and six of second row preserved; only two postnodals preserved, non-aligned to two postsubnodal cross-veins; postnodal area between C and RA is less wide than the postsubnodal area betwen RA and RP; IR1 not preserved; RP2 originates 1.6 mm distal of IR2, and IR2 3.5 mm distal of RP3/4; RP3/4 originates 0.9 mm distal of nodus; few aligned transverse veins; no longitudinal supplementary veins.

Etymology.—Named after the short wing veins CuA, MP and MA.

Type.—Specimen no. 1-1981, in 'coll. J. Kukalová-Peck', Department of Earth Sciences, Carleton University, (Ottawa, Canada).

Occurrence.—Carrizo Arroyo, Bursum Formation, Red Tanks Member, central New Mexico, U.S.A.; Carboniferous/Permian boundary (Schneider et al., 2004).

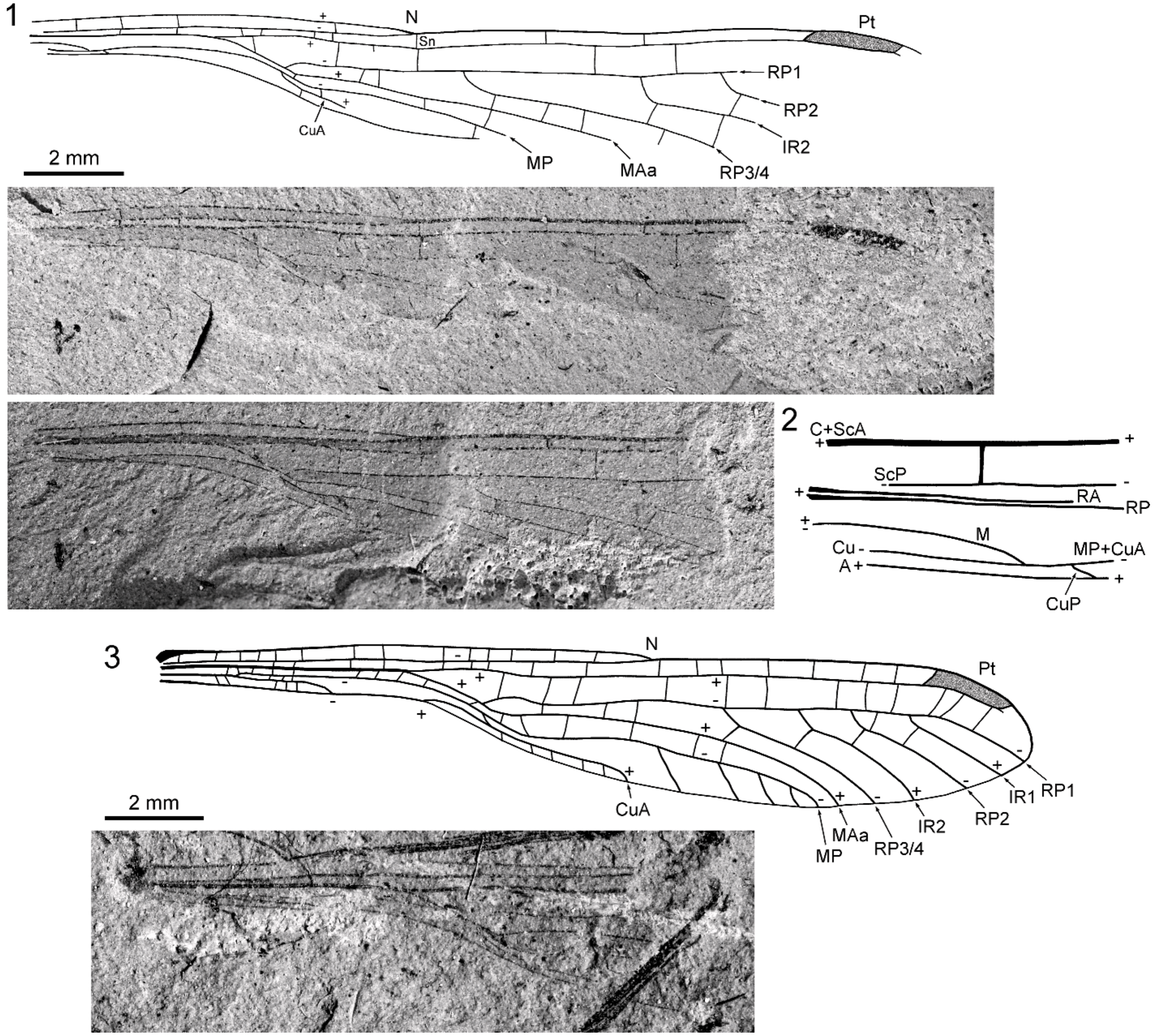

FIGURE 10—*1, 2, Luiseia breviata* n. gen. and sp.: *1,* holotype specimen no. 1-1981 ('coll. J. Kukalová-Peck', Department of Earth Sciences, Carleton University, Ottawa, Canada), drawing and photograph (positive imprint, and negative imprint, reversed); *2,* detail of wing base, drawing; *3,* undescribed new 'protozygopteran' of uncertain affinity from Carrizo Arroyo, specimen no. SDMNH 2927-20649, drawing and photograph (negative imprint, reversed).

Discussion.—This fossil shares with the Kennedyidae and some other 'higher' Archizygoptera the widened postsubnodal area between RA and RP, as well as a short and perpendicular nodus, subnodus and MAb. It shares with *Progoneura* spp. a very short CuA. However, the new taxon differs from other archizygopteran genera in the shape of the pterostigma, the number of antenodal cross-veins, and especially the very short veins MAa and MP. Therefore, we propose to erect a new genus and a new family for this new species. Together with *Bechlya* and another Carrizo Arroyo specimen (no. SDMNH 2927-20649), *Luiseia breviata* n. sp. is one of the oldest known damselfly-like odonates. Specimen no. SDMNH 2927-20649 (Fig. 10.3) at the San Diego Natural History Museum has a very unusual wing venation and is here tentatively considered as of uncertain position within the 'protozygopteran' grade. A formal description of the new taxon is projected by J. Kukalová-Peck.

Family KENNEDYIDAE Tillyard, 1925

Type genus.—*Kennedya* Tillyard, 1925.

Other genera.—*Progoneura* Carpenter, 1931.

Diagnosis.—Bechly (1996) proposed the following synapomorphies: CuA strongly reduced and very short; venation rather open with only few postnodal cross-veins; not more than one cross-vein beneath pterostigma; midfork distinctly distal of nodus. We add the following characters in the diagnosis: MAb very short; nodal Cr and subnodus short, perpendicular to C, RA and RP.

Discussion.—The genus *Sushkinia* Martynov, 1930 is very enigmatic and could well be related to the permagrionid genus

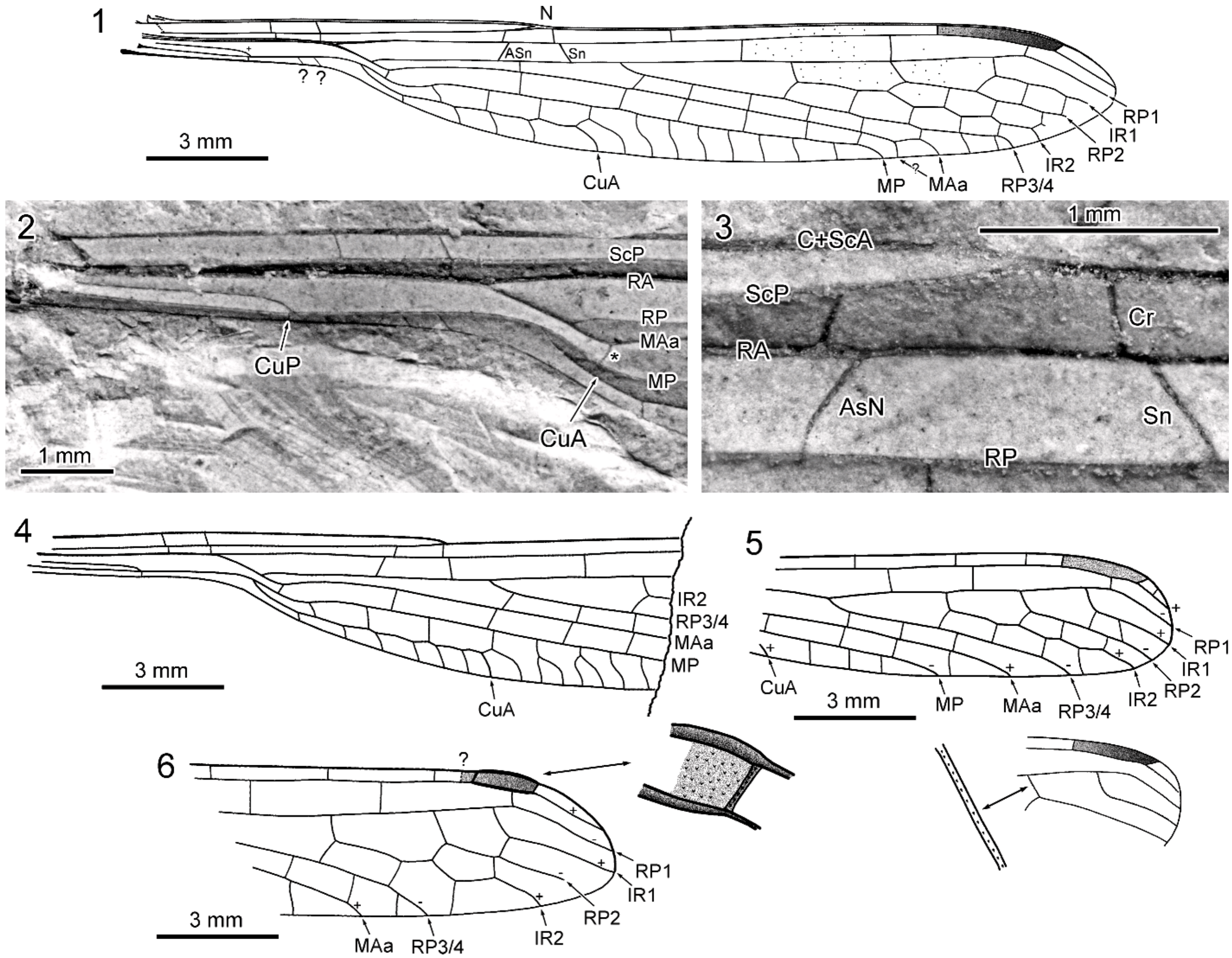

FIGURE 11—*Kennedya* spp.: *1–5*, *Kennedya mirabilis* Tillyard, 1925; *1–3*, specimen MCZ 3971: *1*, drawing; *2*, photograph of wing base (negative imprint); *3*, photograph of wing nodus area (negative imprint); *4*, specimen MCZ3220, drawing; *5*, specimen MCZ3174, drawings of wing and detail of spines on vein; *6*, *Kennedya reducta* Carpenter, 1939, holotype specimen MCZ 3973, drawings of wing and detail of pterostigma.

Scytolestes (see below). The Permian *Opter brongniartii* Sellards, 1909 is based on a very incomplete wing with important structures unknown (nodus, nodal Cr and subnodus). Its general shape suggests affinities with the Kennedyidae, but it differs from *Kennedya* and other kennedyid genera in a very long CuA (Sellards, 1909).

Genus KENNEDYA Tillyard, 1925

Type species.—*Kennedya mirabilis* Tillyard, 1925.

Other species.—*Kennedya tillyardi* Carpenter, 1939, *Kennedya reducta* Carpenter, 1939, *Kennedya fraseri* Carpenter, 1947, *Kennedya carpenteri* Pritykina, 1981, *Kennedya gracilis* Pritykina, 1981, *Kennedya* sp. (in Tasch and Zimmerman, 1959, 1962), *Kennedya azari* n. sp., *Kennedya pritykinae* n. sp., *Kennedya ivensis* n. sp.

Diagnosis.—Vein CuA comparatively long, ending on posterior wing margin opposite or distal to nodus; more cells than in *Progoneura*.

Discussion.—New figures of four specimens of the type species *K. mirabilis* in the collection of MCZ are provided (Fig. 11.1–11.6). A pattern of tiny dots visible on the distal wing membrane was observed (Fig. 11.1, 11.3), which could either represent denticles or the bases of sensorial hairs. Spines were observed on the wing veins (Fig. 11.5), and denticles on the surface of the pterostigmata (Fig. 11.6). A new drawing of the holotype of *K. tillyardi* is provided (Fig. 12.1). This species also has denticles on the surface of the pterostigma. The wing base is well preserved and shows the basal and radioanal plates of the articulation, as well as an oblique basal brace Ax0 (probably also present in *K. mirabilis*, Fig. 11.1), which is similar to Protanisoptera and thus seems to be a plesiomorphic state. *K. reducta* is based on an apical third of a wing (Fig. 12.2), easily characterized by the great reduction of the number of cross-veins (among others, only one cell between IR1 and RP1), but this fossil lacks the diagnostic characters that could exclude it from the genus *Progoneura*, i.e., the shape and length of CuA. Thus its attribution to *Kennedya* is only tentative. *K. reducta* has distinct spinelets on the surface of the pterostigma (Fig. 12.2). The stigma has an indistinct basal margin but seems to be shorter than in other species of *Kennedya*. It is best considered as a Kennedyidae genus undetermined.

KENNEDYA AZARI new species
Figure 13.1

Diagnosis.—Only two cross-veins between CuA and posterior wing margin and three between CuA and MP; three cells

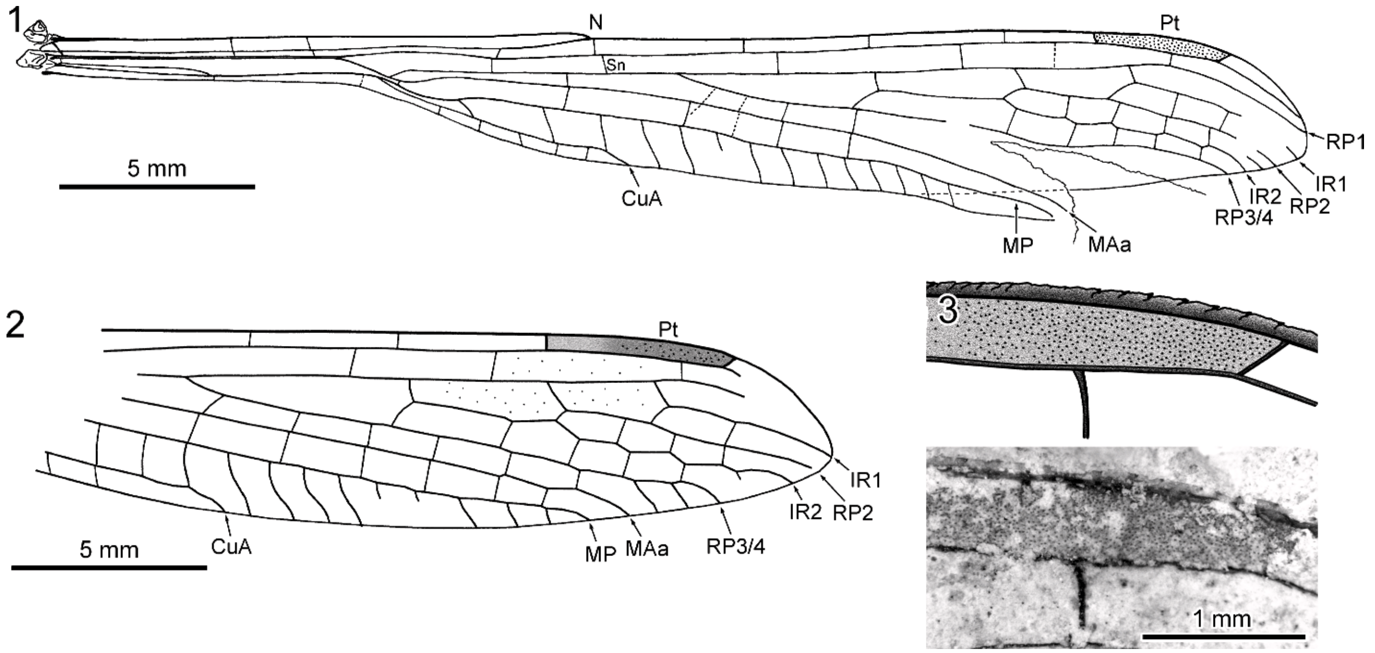

FIGURE 12—*Kennedya* spp.: *1*, *Kennedya tillyardi* Carpenter, 1939, holotype specimen MCZ 3970, drawing; *2*, *3*, *Kennedya mirabilis* or *K.* cf. *tillyardi* specimen MCZ (without no.): *2*, drawing; *3*, drawing of pterostigma and detail photograph (reversed).

between IR2 and RP3/4 and two cells between MAa and MP along posterior wing margin.

Description.—Imprint of a wing, base missing, preserved part 43.5 mm long, 7.0 mm wide; distance from wing base to arculus 7.0 mm, to nodus 15.9 mm, from nodus to pterostigma 20.2 mm; pterostigma 4.9 mm long; base of RP 2.8 mm from arculus; MAa and MAb separating 0.7 mm distally; MAb 0.3 mm long; MP and CuA separating opposite midway between base of arculus and base of RP; Ax2 opposite arculus; ASn weakly pronounced, not aligned with a cross-vein; Cr and Sn weakly oblique and not exactly aligned; few postnodal cross-veins (three), not aligned with postsubnodals; basal side of pterostigma vertical, distal side obliquely oriented toward wing base; two cells distal of pterostigma between C and RA; only one cross-vein between RA and RP below middle of pterostigma; base of RP3/4 10.5 mm from base of RP, that of IR2 at 16.9 mm, RP2 at 21.3 mm, IR1 at 23.6 mm; a very short secondary longitudinal vein between RP3/4 and IR2; few cross-veins in areas between main veins; MAb directed towards wing base; one or two rows of cells between MP and posterior wing margin; only two cross-veins between MP and CuA, and between CuA and posterior wing margin; CuA short ending at nodus level; CuP ending on AA just basal of fusion of AA with posterior wing margin; petiole long.

Etymology.—Named after our friend and colleague Dr. D. Azar.

Type.—Specimen PIN 1/276.

Occurrence.—Tshekarda River, Ufa-Solikamsk Basin, Koshelevka Formation, Middle Urals, Russia; Kungurian, latest early Permian (Rasnitsyn and Zherikhin, 2002).

KENNEDYA PRITYKINAE new species
Figure 13.2, 13.3

Diagnosis.—This species differs from other *Kennedya* species except *Kennedya azari* in the orientation of MAb, and the presence of only three cross-veins between CuA and MP. It differs from the latter in the more distal position of nodal Cr and subnodus.

Description.—Imprint of a wing with base missing; preserved part 32.9 mm long, 5.9 mm wide; Ax2 distinctly basal of arculus; ASn weakly pronounced, not aligned with a cross-vein; Cr et Sn nearly vertical, not exactly aligned; few (three) postnodals; basal side of pterostigma obliquely directed towards wing apex, distal side with an inverted obliquity; only one cross-vein below pterostigma; arculus elongate, distance between base of arculus and base of RP distinctly longer than distance between base of RP and base of MAb; MAb nearly vertical but slightly directed towards wing apex; wing petiolated but petiole broken.

Etymology.—Named after our Russian fellow paleoentomologist Dr. L.N. Pritykina.

Type.—Specimen PIN 3353/76.

Occurrence.—Soyana River, Iva-Gora outcrop, Arkhangelsk Region, north European Russia; early Kazanian, upper Permian (Rasnitsyn and Zherikhin, 2002).

KENNEDYA IVENSIS new species
Figure 13.4

Diagnosis.—Area between CuA and posterior wing margin very narrow; petiole very long; MAb obliquely directed towards wing apex; nodal Cr and subnodus vertical; a long distance between bases of RP3/4 and IR2; base of IR1 below apical side of pterostigma; pterostigma very broad with a strong narrowing of area between RA and RP below it.

Description.—Imprint of a complete wing, 26.4 mm long, 3.2 mm wide; distance from base to arculus 6.9 mm, from arculus to nodus 4.4 mm, from nodus to wing apex 14.9 mm; from nodus to pterostigma 11.3 mm; pterostigma 2.3 mm long, with a cross-vein below it and very pronounced narrowing of area between RA and RP below it; one cell between C and RA distal of pterostigma; nodal Cr and subnodus well aligned and nearly vertical; roughly five to seven postnodal cross-veins not aligned with postsubnodals; although IR2 and RP2 are branching on RP, their bases are strongly approximate and their longitudinal parts are respectively closer to RP3/4, and IR2 than to main RP, as if they

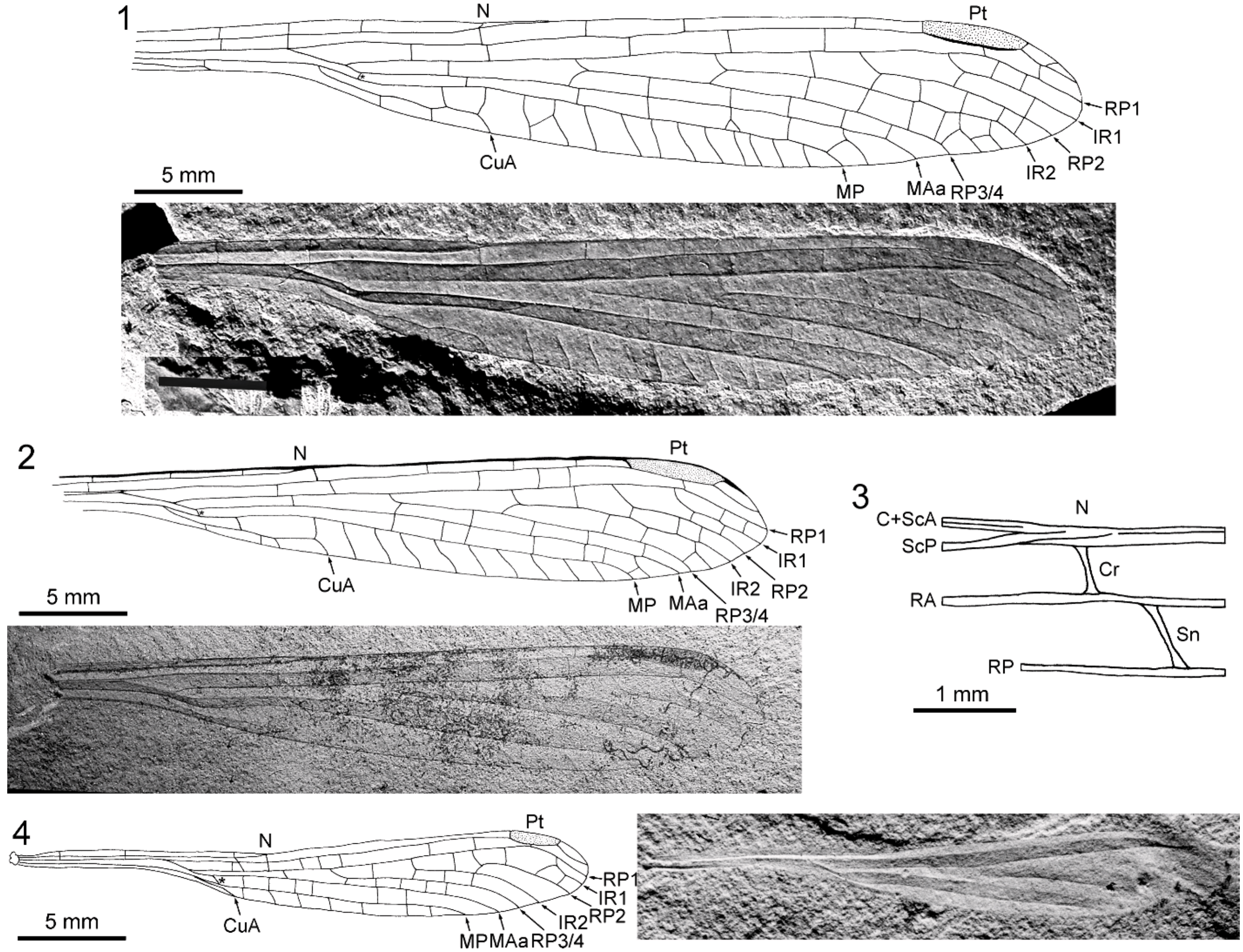

FIGURE 13—*Kennedya* spp.: *1*, *Kennedya azari* n. sp., holotype specimen PIN 1/276, drawing and photograph (positive imprint); *2*, *3*, *Kennedya pritykinae* n. sp., holotype specimen PIN 3353/76: *2*, drawing and photograph (positive imprint); *3*, drawing of nodus area; *4*, *Kennedya ivensis* n. sp., holotype specimen PIN 15/117, drawing and photograph (positive imprint).

were branching respectively on RP3/4 and IR2; distance from longitudinal part of IR2 to RP3/4 0.4 mm, to RP 0.6 mm, distance from longitudinal part of RP2 to IR2 0.4 mm, to RP 0.8 mm, distance from longitudinal part of IR1 to RP2 1.0 mm, to RP 0.4 mm; MP ending well distal of nodus level; area between MP and posterior wing margin very narrow; area between CuA and posterior wing margin very narrow; apex of CuA at level of nodus; AA absent, completely reduced; petiole very long and narrow.

Etymology.—Named after the Iva-Gora outcrop.

Type.—Specimen PIN 15/117.

Occurrence.—Soyana River, Arkhangelsk Region, north European Russia; early Kazanian, upper Permian (Rasnitsyn and Zherikhin, 2002).

Genus PROGONEURA Carpenter, 1931

Type species.—*Progoneura minuta* Carpenter, 1931.

Other species.—*Progoneura nobilis* Carpenter, 1947, *Progoneura venula* Carpenter, 1947, *Progoneura* sp. (in Carpenter, 1947), *Progoneura grimaldii* n. sp.

Diagnosis.—Vein CuA very short, ending on posterior wing margin basal of nodus, and with only one to two cross-veins between CuA and hind margin; less cells than in *Kennedya*.

Discussion.—A potentially important difference between *Progoneura* and *Kennedya* could have been the absence of nodal Cr and subnodus in the former genus. This structure is not illustrated for *P. nobilis* and *P. minuta* in Carpenter (1931, 1947). The complete reduction of these important veins would have been unique among the Protozygoptera and Odonata, but Carpenter (1947) illustrated these veins in his reconstruction of the wing of *P. venula*. As other differences between *P. venula* and *P. nobilis* are few (length of stem of arculus and position of base of RP3/4), these species certainly belong to the same genus, and the lack of nodal Cr and subnodus in Carpenter's figures of *P. nobilis* and *P. minuta* could have been due to improper observation and/or preservation biases. Our re-examination of three specimens of *P. minuta* at MCZ revealed that in two specimens (MCZ 3042a, MCZ 3975) there is indeed no nodal and subnodal vein visible (Fig. 14.1, 14.2), whereas in specimen MCZ 3221 (Fig. 14.3) there is a nodal and subnodal vein present, similar to those present in *Kennedya* (for comparison see also type specimen of *P. nobilis* [Fig. 14.4]). Therefore, the species *P. minuta* must be considered as polymorphic on this character.

Our re-examination shows that three to four antenodal cross-veins are present in *P. minuta* (Fig. 14.1, 14.3), which is a

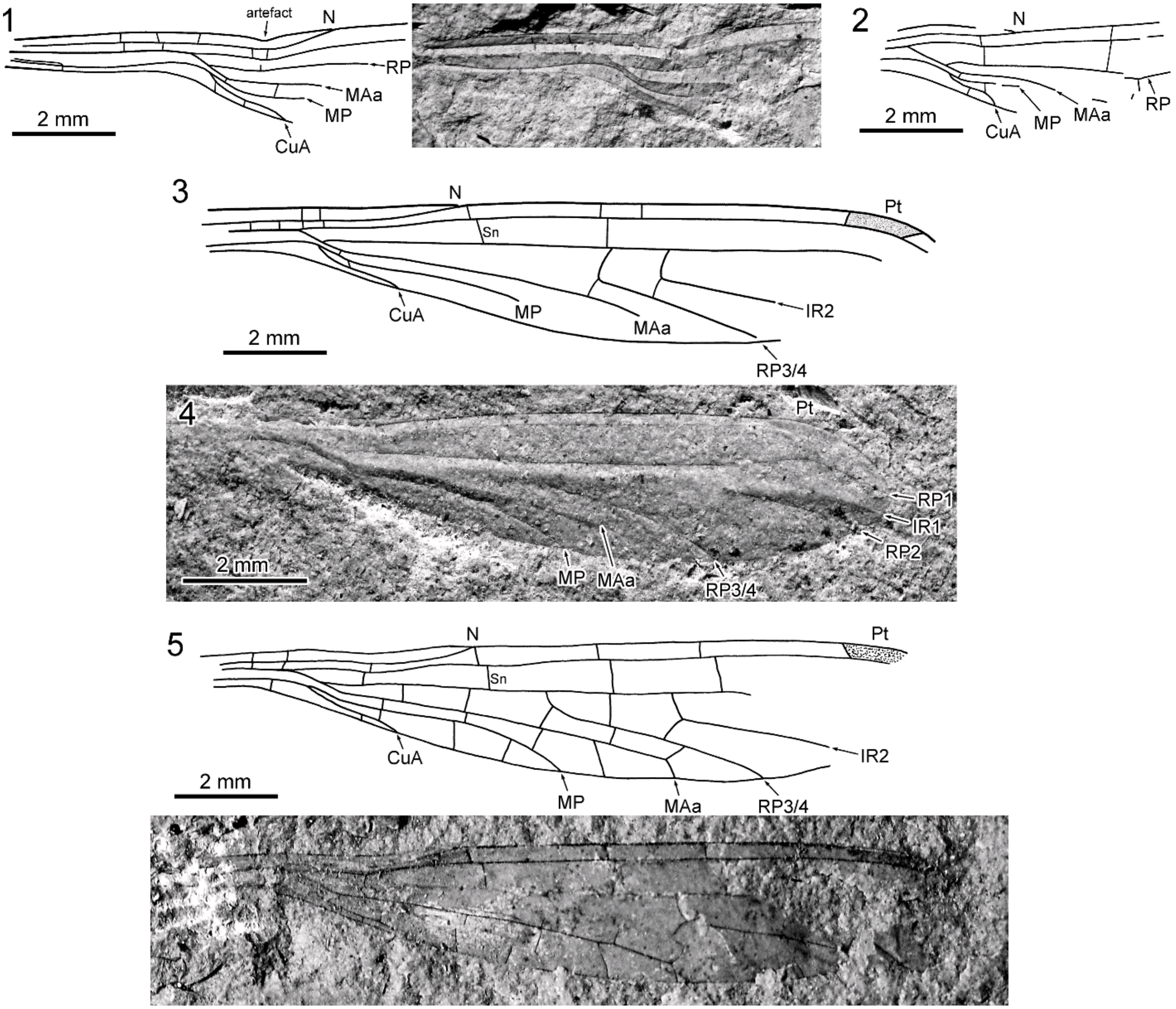

FIGURE 14—*Progoneura* spp.: *1–3*, *Progoneura minuta* Carpenter, 1931: *1*, specimen MCZ 3042a, drawing and photograph (positive imprint); *2*, specimen MCZ 3975, drawing; *3*, specimen MCZ 3221, drawing; *4*, *Progoneura nobilis* Carpenter, 1947, holotype specimen MCZ 4786, photograph (positive imprint); *5*, *Progoneura grimaldii* n. sp., holotype specimen No. 204-203, ACccn 7053, drawing and photograph (positive imprint, reversed).

significant difference to *Kennedya* where only two antenodal cross-veins, Ax1 and Ax2, are present.

PROGONEURA GRIMALDII new species
Figure 14.5

Diagnosis.—Ax2 opposite arculus; distance between arculus and nodus distinctly greater than distance between nodus and base of RP3/4; apex of CuA midway between nodus and base of RP.

Description.—Imprint and counter-imprint of a wing; wing petiolated, base missing; preserved part 13.9 mm long; width 2.6 mm; distance from base to arculus about 0.3 mm, from arculus to nodus 3.4 mm, from pterostigma to nodus 7.2 mm; RP separated from MA at 0.6 mm from base of arculus; MAa and MAb separated at 0.5 mm from base of RP; MAb 0.15 mm long reaching MP with a normal obliquity; two primary antenodal cross-veins between C and ScP, Ax1 0.7 mm basal of arculus and Ax2 opposite arculus; one cross-vein in antesubnodal space between subnodus and Ax2 aligned with one cross-vein in space between ScP and RA; nodal Cr with a normal obliquity; subnodus not aligned to Cr; two postnodal cross-veins, not aligned to three postsunodals between RA and RP1; pterostigma long and narrow with basal and distal margins poorly preserved, ~1.5 mm long; pterostigmal brace probably absent; IR1 and RP2 not preserved, base of IR2 at 3.9 mm and that of RP3/4 at 1.5 mm from subnodus; area between IR2 and RP3/4 getting broader but developing no longitudinal secondary vein; no longitudinal veins between main veins of radial area; MAa, MP and CuA straight and simple; CuA ends at 2.3 mm from arculus, well basal of nodus level; area between MP and CuA short; AA never separated from AP; areas between RP3/4, MAa, MP, CuA, and posterior wing margin all with only one row of cells.

Etymology.—Named after our colleague Dr. D. Grimaldi.

Type.—Specimen YPM 204203, Invertebrate Paleontology, Yale Peabody Museum, U.S.A.

Occurrence.—Sumner Group, Wellington Formation, site IPD-06359, Red Rock, Schultz's Hill, Noble County, Oklahoma, U.S.A.; Artinskian, early Permian (Rasnitsyn and Zherikhin, 2002).

Discussion.—This fossil differs from *P. nobilis* in the distance between arculus and nodus, distinctly greater than the distance between nodus and the base of RP3/4. It differs from *P. minuta* in that the apex of CuA is midway between the nodus and the base of RP, instead of being distinctly closer to nodus level. Both these characters are also present in *P. venula*. Differences with this last species are very few, the most significant being that Ax2 is opposite the arculus instead of being distinctly more basal. The main interest of this fossil is that it confirms the presence of true nodal Cr and subnodus in the genus *Progoneura* (already known in *P. venula*).

Genus SUSHKINIA Martynov, 1930

Type species.—Sushkinia parvula Martynov, 1930.

Other species.—Sushkinia elongata Martynov, 1930.

Diagnosis.—Base of IR1 basal of pterostigma; distal half of MAa zigzagged; pterostigma very elongate.

Occurrence.—Tikhiye Gory, Kama River, Baitugan Formation, Kazan region, Russia; early Kazanian, Permian (Rasnitsyn and Zherikhin, 2002).

Discussion.—This genus is based on two very incomplete fossil wings, with basal third missing. Martynov (1930) included them in Kennedyidae, but Carpenter (1992) transferred them into the Permagrionoidea. Nel et al. (1999b) proposed to restore them to Kennedyidae on the basis of two putative synapomorphies: no more than one cross-vein beneath the pterostigma, and few postnodals. However, these characters are also present in Permagrionidae. These two fossils lack decisive characters that would allow a positive attribution, namely those of the nodal structures, and shape of MAb. Therefore, we have to consider them 'protozygopteran' of uncertain position, even though *Sushkinia parvula* has a pattern of apparent branching of RP2 on IR2 similar to that of the genus *Scytolestes*, suggesting possible affinities of both genera.

Family KALTANONEURIDAE Rohdendorf, 1961

Type genus.—Kaltanoneura Rohdendorf, 1961 (monotypic family).

Diagnosis.—That of the type genus.

Genus KALTANONEURA Rohdendorf, 1961

Type species.—Kaltanoneura bartenevi Rohdendorf, 1961 (monotypic genus).

Diagnosis.—Pterostigma elongate and covering two cross-veins; area between C and RA very narrow and that between RA and RP much broader; CuA very reduced or absent.

KALTANONEURA BARTENEVI Rohdendorf, 1961.
Figure 15.1

Description.—Imprint and counter-imprint of a wing, with basal part missing; wing 14.4 mm long, 5.3 mm wide; distance from nodus to pterostigma 8.4 mm; pterostigma 3.4 mm long, covering two cross-veins, with its distal side oblique; area between C and RA very narrow, 0.2 mm wide, that between RA and RP distinctly broader; nodal Cr and subnodus nearly vertical and aligned; four postnodals, all nearly aligned with the postsubnodals; base of IR1 at 8.3 mm from subnodus, RP2 at 6.3 mm, IR2 at 4.3 mm, and RP3/4 at 1.6 mm; although RP3/4, IR2, RP2, and IR1 are branching on RP, their longitudinal parts are respectively very close to MA, RP3/4, IR2, and RP2 than to main RP; no supplementary longitudinal veins between main veins; area between MA and MP along posterior wing margin wide; area between MP and posterior wing margin with one row of cells; CuA not visible, either completely absent or very short.

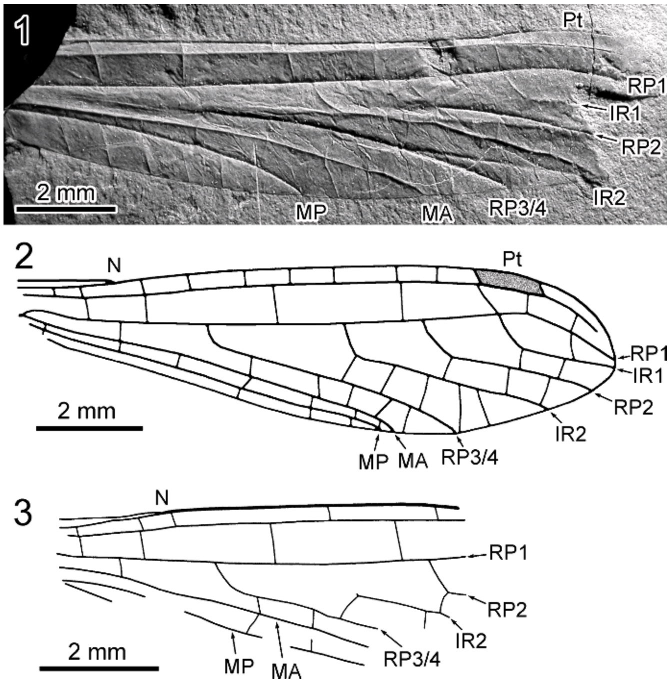

FIGURE 15—Archizygoptera: *1*, *Kaltanoneura bartenevi* Rohdendorf, 1961, holotype specimen PIN 600/485, photograph (positive imprint); *2*, *3*, *Oboraneura kukalovae* Zessin, 2008, holotype specimen (without coll. number): *2*, drawing (redrawn after Zessin, 2008); *3*, drawing (original drawing based on negative imprint only).

Type.—Specimen PIN 600/485.

Occurrence.—Kuznetsk Basin, Kaltan, Kemorovo, West Siberia, Russia; Kazanian or Ufimian, late Permian (Rasnitsyn and Zherikhin, 2002).

Discussion.—Rohdendorf (1961) originally included *Kaltanoneura* spp. and the corresponding genus and family in the Protanisoptera Carpenter, 1931, but Huguet et al. (2002) transferred these taxa to the Protozygoptera, according to the pterostigma of odonatan-type. Zessin (2008) listed these taxa in Archizygoptera. The wing venation of *Kaltanoneura* spp. is similar to that of *Kennedya* spp. or *Progoneura* spp., especially in the narrow area between C and RA and broad area between RA and RP distal of nodus, and distal position of bases of radial branches. The lack of information concerning the basal part of the wing prevents us from being positive on a possible attribution of *Kaltanoneura* spp. to the Kennedyidae, and a synonymy between Kaltanoneuridae and this last family.

Family OBORANEURIDAE Zessin, 2008

Type genus.—Oboraneura Zessin, 2008 (monotypic family).

Diagnosis.—That of the type genus.

Genus OBORANEURA Zessin, 2008

Type species.—Oboraneura kukalovae Zessin, 2008 (monotypic genus).

Diagnosis.—That of the type species.

OBORANEURA KUKALOVAE Zessin, 2008
Figure 15.2, 15.3

Diagnosis.—Very narrow area between MA and MP and between MP and hind margin.

Type.—Specimen without collection number in coll. Kukalova-Peck (Carleton Univ., Ottawa), composed of positive and negative imprints.

Occurrence.—Obora, Boskovice Furrow, Moravia, Czech Republic; late Sakmarian to early Artinskian (Schneider et al., 2004).

Discussion.—The original description of this species was published in a periodical difficult to access, with comparatively poor illustration, and based on an erroneous interpretation. Therefore, we provide a new drawing of the holotype (Fig. 15.2), and an original drawing of the counterpart (Fig. 15.3). The species shares with species assigned to the Kaltanoneuridae and Kennedyidae a narrow area between C and RA, a broad area between RA and RP, three big cells in the interradial field between RP3/4 and IR1, and apically converging veins RA and IR1. These apomorphies suggest that this set of species form a monophyletic group within Archizygoptera. *Oboraneura kukalovae* differs from species assigned to the Kennedyidae and Kaltanoneuridae in the general shape of the wing, the shape of the short pterostigma with an oblique cross-vein below its base, aligned with IR1. A unique character state is the very narrow area between MA and MP, and between MP (erroneously termed CuA in the original description) and the hind margin, which suggests a reduced CuA (not preserved).

Family BAKTENIIDAE Pritykina, 1981

Type genus.—*Baktenia* Pritykina, 1981.

Other genera.—*Paratriassoneura* Bechly, 1997, *Engellestes* n. gen.

Diagnosis.—CuA strongly reduced and very short; rather numerous postnodal cross-veins; midfork opposite or distinctly basal of nodus. RP3/4, IR2, RP2, and IR1 originating on RP, unlike in Protomyrmeleontoidea.

Discussion.—Bechly (1997, 2009) assigned the following additional Triassic genera in the Bakteniidae: *Terskeja* Pritykina, 1981 (transferred below in Voltzialestidae n. fam.), *Paratriassoneura* Bechly, 1997 (all in Batkeniinae), and *Voltzialestes* Nel et al., 1996 (in Voltzialestinae, considered below as a separate new family). Bechly (1996) considered the Bakteniidae as the sister group of Protomyrmeleontidae (within the Protomyrmeleontoidea) on the basis of the following synapomorphies: 'IR1 apparently originating on RP2 or even fused to it; RP2 apparently originating on IR2 or even fused to it; IR2 apparently originating on RP3/4 or even fused to it; MA and RP3/4 distinctly curved towards posterior wing margin, so that both veins are distinctly shortened'. However *Baktenia* and *Paratriassoneura* do not show these characters, contrary to *Terskeja* and other taxa formerly currently included in Batkeniidae. *Baktenia* and *Paratriassoneura* have a CuA that is strongly reduced, such as in *Kennedya*, and nodal Cr and subnodus similar to that observed in Kennedyidae. Nevertheless, *Baktenia* and *Paratriassoneura* differ from all Kennedyidae in that the bases of RP3/4 and IR2 are basal of the nodus, and postnodal cross-veins are more numerous than in Kennedyidae. Thus we propose to maintain the family Bakteniidae.

Genus ENGELLESTES new genus

Type species.—*Engellestes chekardensis* n. sp. (monotypic genus).

Etymology.—Named after Dr. M. S. Engel, and *Lestes*.

Diagnosis.—That of the type species.

ENGELLESTES CHEKARDENSIS new species
Figure 16

Diagnosis.—Wings very narrow; MP + CuA extremely reduced, ending on posterior wing margin at the level of the arculus; no secondary longitudinal vein between main veins; pterostigma long, with one cross-vein below it; a long cell between RP1 and IR1 below pterostigma; MAb very short, directed towards wing base; nodal Cr oblique but subnodus perpendicular to RA and RP; base of RP3/4 (midfork) opposite subnodus.

Description.—Holotype PIN 1700/3250 (Fig. 16.1, 16.2): imprint and counter-imprint of two forewings attached to thorax together with base of abdomen, base of left wing missing: preserved part 24.8 mm long, 4.1 mm wide; distance from base to arculus 6.0 mm; from base to nodus (on right wing) 11.3 mm; from subnodus to apex 15.3 mm; from subnodus to pterostigma 11.7 mm; pterostigma elongate, 2.3 mm long, with distal side strongly oblique and covering two long cells; a long petiole; RP and MA separating 0.2 mm from base of arculus, MAa and MAb separating 0.2 mm distally; MAb directed towards wing base, 0.1 mm long; MP + Cu ending on posterior wing margin 6.5 mm from wing base; two complete antenodal cross-veins well basal of arculus; Ax1 4.5 mm and Ax2 2.0 mm from arculus; two cross-veins between ScP and RA basal of nodus; nodal Cr and Sn more or less aligned, Cr weakly oblique and subnodus nearly perpendicular to RA and RP; seven postnodal cross-veins, not aligned to subpostnodals; one to two cells between C and RA, distal of pterostigma; base of IR1 11.9 mm from base of RP, RP2 9.3 mm, IR2 6.8 mm, RP3/4 4.2 mm; MAa zigzagged distal of nodus level, with its apex at 4.6 mm from wing apex; a long and large cell below pterostigma between RP1 and IR1; no secondary longitudinal vein between main veins.

Paratype PIN 1700/3249 (Fig. 16.3): distal two-third of a wing, preserved part 17.9 mm long, 4.1 mm wide; distance from subnodus to pterostigma 11.4 mm.

Paratype PIN 1700/454 (Fig. 16.4): distal two-third of a wing, preserved part 20.4 mm long, 4.8 mm wide; distance from subnodus to pterostigma 13.1 mm.

Etymology.—Named after the type locality.

Types.—Holotype specimen PIN 1700/3250; paratype specimens PIN 1700/3249 and PIN 1700/454.

Occurrence.—Tshekarda River, Ufa-Solikamsk Basin, Koshelevka Formation, Middle Urals, Russia; Kungurian, latest early Permian (Rasnitsyn and Zherikhin, 2002).

Discussion.—The three specimens are nearly of the same sizes and proportions, so we propose to include them in the same species. The nodal vein (Cr) and subnodus (Sn) being nearly vertical, and MAb directed towards wing base, together with the absence of intercalary longitudinal veins, are characters of Kennedyidae and Bakteniidae. *Engellestes chekardensis* n. sp. shares with species of the latter family the relatively basal position of base of RP3/4, located opposite the subnodus. The strongly reduced MP + CuA without any independent CuA or AA veins is a very particular structure, unique among the protozygopterans. The complete reduction of AA and CuA also occurs in the protomyrmeleontoid families Voltzialestidae Bechly, 1996 (see below, in *Terskeja*) and Protomyrmeleontidae Handlirsch, 1906, but this last superfamily is characterized by a particular pattern of the bases of branches of RP, namely, RP2 apparently originating on IR2 or even fused to it (plus in many taxa, IR1 apparently originating on RP2 or even fused to it; and IR2 apparently originating on RP3/4 or even fused to it). *Engellestes chekardensis* n. sp. does not have this pattern of venation.

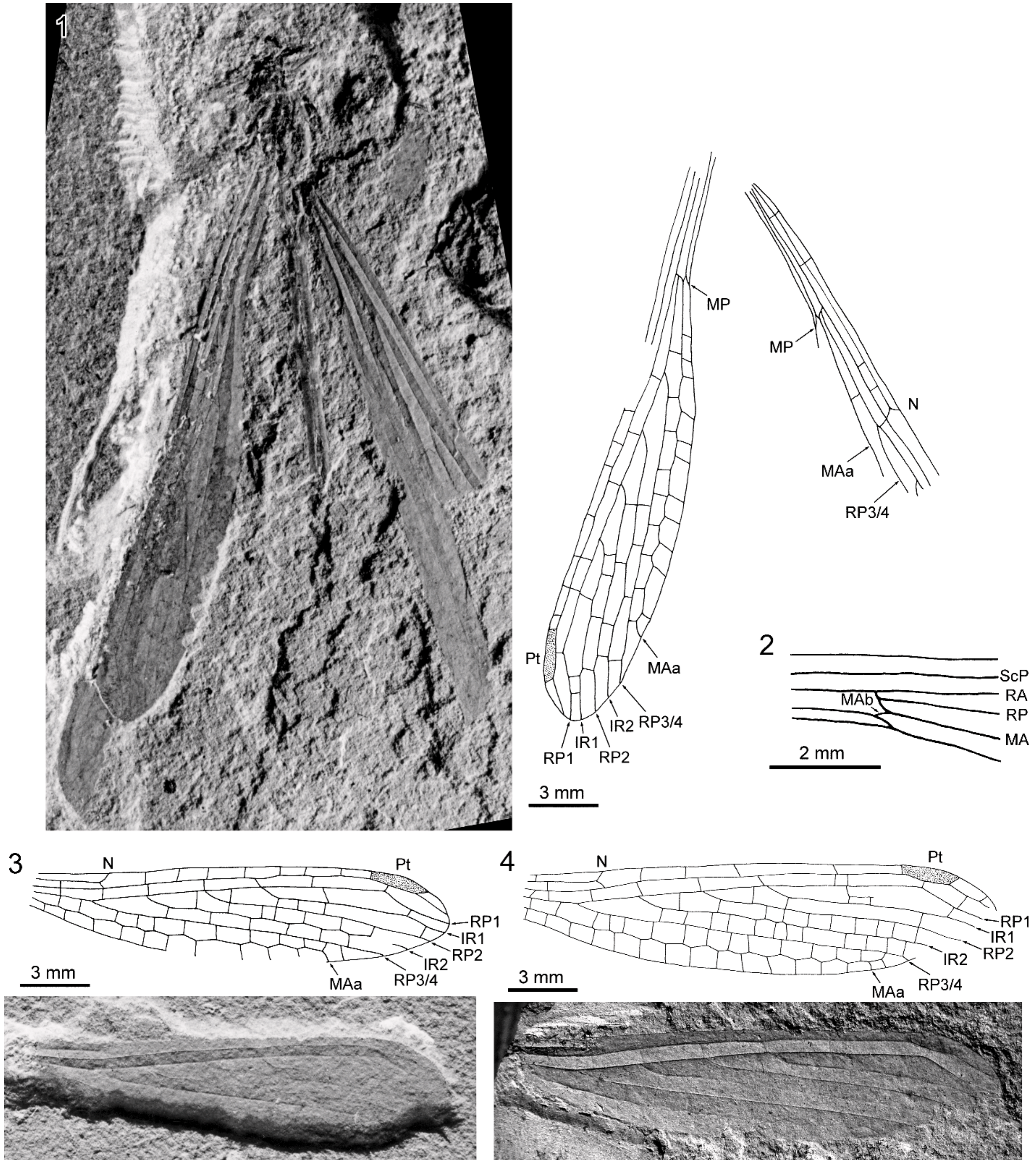

FIGURE 16—*Engellestes chekardensis* n. gen. and sp.: *1*, *2*, holotype specimen PIN 1700/3250: *1*, drawing and photograph of imprint; *2*, drawing of arculus area; *3*, paratype specimen PIN 1700/3249, drawing and photograph (positive imprint, reversed); *4*, paratype specimen PIN 1700/454, drawing and photograph (negative imprint, reversed).

Thus, we can conclude that the reduction of the veins AA, CuA and MP occurred convergently in Kennedyidae, Bakteniidae, and some Protomyrmeleontoidea. The first step of this reduction is present in *Progoneura* spp. (CuA very short), and the second step in *Engellestes chekardensis* n. sp. (CuA absent and MP just reaching arculus).

Superfamily PROTOMYRMELEONTOIDEA Handlirsch, 1906

Type family.—Protomyrmeleontidae Handlirsch, 1906.

Other families.—Voltzialestidae Bechly, 1996.

Diagnosis.—To include the genus *Azaroneura* n. gen., we modify the diagnosis proposed by Bechly (1996) as follows: RP2 apparently originating on IR2 or even fused to it (main synapomorphy). Other synapomorphic characters (IR1 apparently originating on RP2 or even fused to it; IR2 apparently originating on RP3/4 or even fused to it) are not shared by this genus but by other taxa currently included in it.

Family VOLTZIALESTIDAE Bechly, 1996

Type genus.—*Voltzialestes* Nel et al., 1996.

Other genera.—*Terskeja* Pritykina, 1981, *Azaroneura* n. gen. (Permian).

Diagnosis.—RP2 not secondarily forked into RP2a and RP2b (plesiomorphy).

Discussion.—Bechly (1996) proposed the following putative synapomorphies for his 'Bakteniidae' (*Voltzialestes* and *Terskeja*, plus *Baktenia* and *Paratriassoneura* that are excluded from the Voltzialestidae herein): 1) MP more or less shortened; and 2) CuA completely fused with the hind margin, only retained as apparent cross-vein between MP and hind margin, that is aligned with the distal discoidal vein MAb. The first character is rather variable and not very different from the situation in Protomyrmeleontidae. The second character is also present in Protomyrmeleontidae. Thus there is no clear synapomorphy supporting the group of genera *Terskeja*, *Voltzialestes*, and *Azaroneura* n. gen., which is mainly 'characterized' by the absence of the synapomorphies of the Protomyrmeleontidae. Consequently, this 'family' might rather represent a grade between the highly derived Protomyrmeleontidae and the other Archizygoptera, but in the absence of definite evidence showing the paraphyly of this group we prefer to classify the three genera in one taxon.

Genus AZARONEURA new genus

Type species.—*Azaroneura permiana* n. sp. (monotypic genus).

Diagnosis.—That of the type species.

Etymology.—Named after Dr. Dany Azar and 'neura' (Latin for 'nervature').

AZARONEURA PERMIANA new species
Figure 17

Diagnosis.—CuA probably completely absent; nodal Cr and subnodus vertical; a very short distance between bases of RP3/4 and IR2; base of IR1 below apical side of pterostigma.

Description.—Imprint of a wing, base missing; preserved length 15.2 mm, width 3.0 mm; distance from nodus to pterostigma 8.5 mm; pterostigma 2.4 mm long, with a cross-vein below it; one cell between C and RA distal of pterostigma; nodal Cr weakly oblique, subnodus nearly vertical, not aligned with Cr; four postnodal cross-veins not aligned with postsubnodals; although RP2 is branching on RP, its base is strongly approximate and its longitudinal part is closer to IR2 than to main RP, as if it was branching on IR2; distance from RP3/4 to IR2 3.3 mm, distance from IR2 to RP2 0.9 mm, distance from RP2 to IR1 3.5 mm; a distinct widening of area between MAa and MP along wing margin; MP ending well distal of nodus level; area between MP and posterior wing margin very narrow; no trace of CuA.

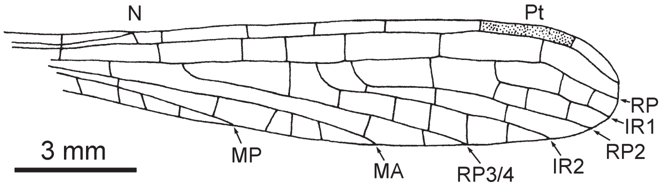

FIGURE *17*—*Azaroneura permiana* n. gen. and sp., holotype specimen PIN 1700/473, drawing.

Etymology.—Named after the Permian period.

Type.—Specimen PIN 1700/473.

Occurrence.—Tshekarda River, Ufa-Solikamsk Basin, Koshelevka Formation, Middle Urals, Russia; Kungurian, latest early Permian (Rasnitsyn and Zherikhin, 2002).

Discussion.—This new species represents the first record of Protomyrmeleontoidea in the Paleozoic. The species has RP2 apparently originating on IR2, which is a synapomorphic character of the Protomyrmeleontoidea (Bechly, 1996; Nel et al., 2005). *Azaroneura permiana* n. sp. is characterized by the base of RP3/4 close to nodus. It shares the reduction of the area between MP and the posterior wing margin with species assigned to the genera *Engellestes* and *Oboraneura*. Because of the shape of the area between MP and the posterior wing margin, *Azaroneura permiana* n. sp. probably had a completely reduced CuA, similarly to species assigned to the genera *Engellestes* and *Terskeja*.

DISCUSSION

Our systematic treatment allows the evolution of the 'Protozygoptera' to be investigated in greater detail. In the first place this assemblage appears to be paraphyletic: it is composed of the Permagrionoidea and the Archizygoptera. The latter group represents the sister group of the Panodonata that comprises 'true', modern damselflies, damsel-dragonflies, and dragonflies. As the Archizygoptera is recorded in the late Carboniferous, the Panodonata should have been of the same age, even if its oldest representative is middle Permian (see above; Nel et al., 1999a).

The Archizygoptera and Panodonata have acquired trimerous tarsi (in contrast to five or four tarsal segements in more basal groups). This change in the adult leg morphology probably had an impact on the type of prey these insects could have captured. Carboniferous and Permian Archizygoptera and Panodonata were relatively small insects with petiolate wings, compared to the distinctly larger Meganeuridae, Protanisoptera and Permagrionoidea, which probably had tarsi with four or five segments and stronger legs. These delicate Archizygoptera and Panodonata were probably capturing small prey and were probably able to diversify significantly during the Permian because they did not compete with the larger griffenflies. In addition, the male secondary genital apparatus, correlated with the well-known odonate mating wheel, appeared during the late Carboniferous as we detected evidence of the presence of this structure in the Archizygoptera.

Our discovery of *Azaroneura permiana* n. sp. as a Permian protomyrmeleontoid is of great interest, as this group was

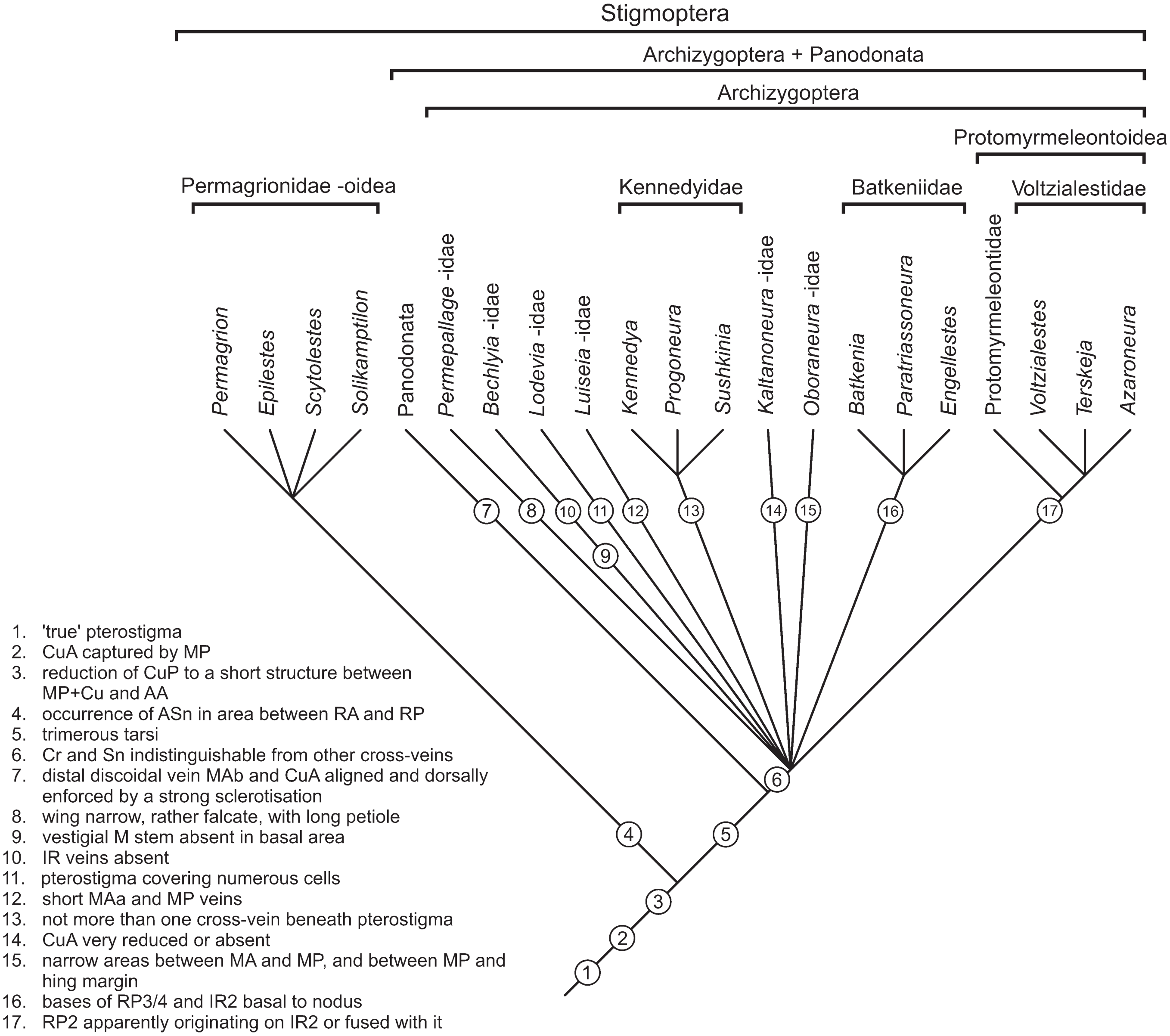

FIGURE *18*—Summary of proposed relationships withing the 'protozygopteran' grade, with most relevant diagnostic characters.

previously only known from the Mesozoic (Nel et al., 2005). The large stratigraphic range of the Archizygoptera between the Carboniferous and the Early Cretaceous indicates that this group of gracile damselfly-like Odonatoptera successfully endured several global changes that occurred during this time period, i.e., the major Permian–Triassic crisis, and changes in ecosystems related to the diversification of other aquatic predators (beetles and bugs), and new terrestrial and/or aquatic prey (Neuroptera, Trichoptera, Diptera, etc.). Some genera (*Kennedya*) are even present over a long period of time between the Permian and Triassic. In contrast, the Permagrionoidea, sister group of the (Archizygoptera + Panodonata), are to date only recorded in the Permian, together with the Protanisoptera. This suggests the presence of rather particular paleobiotas during the early to middle Permian when these two groups of large damsel-dragonfly-like Odonatoptera were flourishing. The period of extinction of these two groups remains uncertain, ranging from the late Permian to the Early Triassic.

ACKNOWLEDGMENTS

We thank our colleague J.F. Petrulevičius (Museo de La Plata, La Plata), whose important contribution to this article could not be indicated by authorship due to diplomatic reasons. We thank the President and Fellows of Harvard College for permission to use MCZ copyrighted material. Authors are grateful to A. Rasnityn and D. Vasilenko (Laboratory of Palaeoentomology at Russian Academy of Sciences, Moscow, Russia) for photos of two specimens at PIN, and to T. Deméré (San Diego Natural History Museum, San Diego, U.S.A.) for photos of the Carrizo Arroyo specimen represented on Fig. 10.3. Authors are grateful to J. Kukalová-Peck (Carleton Univ., Ottawa) for allowing them to describe a specimen from her collection in the present contribution. The second author (GB) is very grateful to J. Kukalová-Peck and to P.D. Perkins (MCZ, Cambridge, U.S.A.) for their hospitality and friendly support during his research visit in 1996. The third author (JP) is very grateful to

J. Kukalová-Peck for her generous hospitality and fruitful research visits, to S. Butts (Peabody Museum of Natural History Yale University, New Haven, U.S.A.) and to A. Rasnitsyn for their kind help and access to collections they are in charge of. The third author (JP) acknowledges the research support from the Grant Agency of the Czech Republic No. P210/10/0633, and Ministry of Schools MSM 0021620828. We sincerely thank the two anonymous referees and the editorial board of the journal for their helpful comments on an earlier version of the paper. We thank T. Brend for polishing of English language.

REFERENCES

BECHLY, G. 1996. Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata), unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der Odonata. Petalura, Special Vol. 2, 402 p.

BECHLY, G. 1997. New fossil odonates from the Upper Triassic of Italy, with a redescription of Italophlebia gervasuttii, and a reclassification of Triassic dragonflies (Insecta: Odonata). Rivista del Museo Civico di Scienze Naturali 'Enrico Caffi', 19:31–70.

BECHLY, G. 2009. Phylogenetic classification of fossil and extant odonates. Internet site: http://www.bernstein.naturkundemuseum-bw.de/odonata/system.htm

BECHLY, G., C. BRAUCKMANN, W. ZESSIN, AND E. GRÖNING. 2001. New results concerning the morphology of the most ancient dragonflies (Insecta: Odonatoptera) from the Namurian of Hagen-Vorhalle (Germany). Journal of Zoological Systematics and Evolutionary Research, 39:209–226.

BÉTHOUX, O., F. PAPIER, AND A. NEL. 2005. The Triassic radiation of the entomofauna. Comptes Rendus Palevol, 4:541–553.

BLAGODEROV, V. A., D. GRIMALDI, AND N. C. FRASER. 2007. How time flies for flies: diverse Diptera from the Triassic of Virginia and early radiation of the order. American Museum Novitates, 3572:1–39.

BRAUCKMANN, C. 2004. Arachniden und Insekten aus dem Namurium von Hagen-Vorhalle (Ober-Karbon; West-Deutschland). Veröffentlichungen aus dem Fuhlrott-Museum, Band 1, 275 p.

BYBEE, S. M., T. H. OGDEN, M. A. BRANHAM, AND M. F. WHITING. 2008. Molecules, morphology and fossils: a comprehensive approach to odonate phylogeny and the evolution of the odonate wing. Cladistics, 23:1–38.

CARPENTER, F. M. 1931. The lower Permian insects of Kansas. Pt. 2. The orders Palaeodictyoptera, Protodonata, and Odonata. American Journal of Science, (serie 5), 21:97–139.

CARPENTER, F. M. 1939. The lower Permian insects of Kansas. Pt. 8. Additional Megasecoptera, Protodonata, Odonata, Homoptera, Psocoptera, Plecoptera, and Protoperlaria. Proceedings of the American Academy of Arts and Sciences, 73(3):29–70.

CARPENTER, F. M. 1947. Lower Permian insects from Oklahoma. Pt. 1. Introduction and the orders Megasecoptera, Protodonata, and Odonata. Proceedings of the American Academy of Arts and Sciences, New York, 76:25–54.

CARPENTER, F. M. 1992. Superclass Hexapoda. *In* R. C. Moore and R. L. Kaesler (eds.), Treatise on Invertebrate Paleontology. Geological Society of America and University of Kansas, Boulder, Colorado, (R), Arthropoda 4, 3/4, xxii + 655 p.

DUMONT, H. J., A. VIERSTRAETE, AND J. R. VANFLETEREN. 2010. A molecular phylogeny of the Odonata (Insecta). Systematic Entomology, 35:6–18.

FLECK, G., G. BECHLY, X. MARTÍNEZ-DELCLÒS, E. JARZEMBOWSKI, AND A. NEL. 2004. A revision of the Upper Jurassic–Lower Cretaceous dragonfly family Tarsophlebiidae, with a discussion on the phylogenetic positions of the Tarsophlebiidae and Sieblosiidae (Insecta, Odonatoptera, Panodonata). Geodiversitas, 26:33–60.

FLECK, G., M. BRENK, AND B. MISOF. 2008. Larval and molecular characters help to solve phylogenetic puzzles in the highly diverse dragonfly family Libellulidae (Insecta: Odonata: Anisoptera): The Tetrathemistinae are a polyphyletic group. Organisms Diversity & Evolution, 8:1–16.

FRASER, F. C. 1957. A reclassification of the order Odonata, based on some new interpretations of the venation of the dragonfly wing. Handbook of the Royal Zoological Society of New South Wales, 12:1–133.

HAGEN, H. A. 1862. Über die Neuropteren aus dem lithographischen Schiefer in Bayern. Palaeontographica, 10:96–145.

HANDLIRSCH, A. 1906. Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen. Wilhelm Engelmann, Berlin, 1430 p.

HUANG, D.-Y. AND A. NEL. 2009. The first Chinese Tarsophlebiidae from the Lower Cretaceous Yixian Formation, with morphological and phylogenetic implications (Odonatoptera: Panodonata). Cretaceous Research, 30:429–433.

HUANG, D.-Y., J. F. PETRULEVIČIUS, AND A. NEL. 2010. New morphological data from the Jurassic of Inner Mongolia confirms the damsel-fly aspect of Protomyrmeleontidae (Insecta: Odonatoptera). European Journal of Entomology, 107:615–620.

HUGUET, A., A. NEL, X. MARTÍNEZ-DELCLÒS, G. BECHLY, AND R. MARTINS-NETO. 2002. Preliminary phylogenetic analysis of the Protanisoptera (Insecta: Odonatoptera). Geobios, 35:537–560.

JARZEMBOWSKI, E. A. AND A. NEL. 2002. The earliest damselfly-like insect and the origin of modern dragonflies (Insecta: Odonatoptera: Protozygoptera). Proceedings of the Geologist's Association, 113:165–169.

LUKASHEVICH, E. D., A. A. PRZHIBORO, F. MARCHAL-PAPIER, AND L. GRAUVOGEL-STAMM. 2010. The oldest occurrence of immature Diptera (Insecta), Middle Triassic, France. Annales de la Société Entomologique de France, (N.S.), 46:4–22.

MARTYNOV, A. 1930. New Permian insects from Tikhie Gory, Kazan province. 1. Palaeoptera. Trudy Geologicheskovo Muzeya, Akademii nauk SSSR, 6:69–86.

MARTYNOV, A. 1932. New Permian Paleoptera with the discussion of some problems of their evolution. Trudy Paleozoologicheskovo Instituta Akademii Nauk SSSR, Moskva, 1:1–44.

MARTYNOV, A. 1937. Permian fossil insects from Kargala and their relationships. Trudy Paleontologicheskovo Instituta Akademii Nauk SSSR, Moskva, 7:8–92. (in Russian).

MARTYNOV, A. 1938. Ocherki geologicheskoj istorii i filogenii otryadov nasekomykh (Pterygota). 1. Palaeoptera i Neoptera–Polyneoptera [Essays on the geologic history and phylogeny of insect orders (Pterygota)]. Trudy Paleontologicheskovo Instituta Akademii Nauk SSSR, Moskva, 7:1–149. (In Russian)

NEL, A., O. BÉTHOUX, G. BECHLY, X. MARTÍNEZ-DELCLÒS, AND F. PAPIER. 2001. The Permo–Triassic Odonatoptera of the 'protodonate' grade (Insecta: Odonatoptera). Annales de la Société Entomologique de France, (N.S.), 37:501–525.

NEL, A., G. GAND, G. FLECK, O. BÉTHOUX, AND J. LAPEYRIE. 1999a. Saxonagrion minutus nov. gen. et sp., the oldest damselfly from the upper Permian of France (Odonatoptera, Panodonata, Saxonagrionidae nov. fam.). Geobios, 32:883–888.

NEL, A., G. GAND, J. GARRIC, A. E. JARZEMBOWSKI, AND J. LAPEYRIE. 1999b. The first recorded protozygopteran insects from the upper Permian of France. Palaeontology, 42:83–97.

NEL, A., P. NEL, J. F. PETRULEVIČIUS, V. PERRICHOT, J. PROKOP, AND D. AZAR. 2010. The Wagner Parsimony using Morphological Characters: A new method for palaeosynecological studies. Annales de la Société Entomologique de France, (N.S.), 46:276–292.

NEL, A., X. MARTINEZ-DELCLOS, J.-C. PAICHELER, AND M. HENROTAY. 1993. Les 'Anisozygoptera' fossiles. Phylogénie et classification (Odonata). Martinia, Special Issue, 3:1–311.

NEL, A., F. PAPIER, L. STAMM-GRAUVOGEL, AND J.-C. GALL. 1996. *Voltzialestes triasicus*, n. gen., n. sp., le premier Odonata fossile du Trias des Vosges (France). Morphologie, affinités et phylogénie. (Odonatoptera, Odonata, Protozygoptera). Paleontologia Lombarda, (N.S.), 5:25–36.

NEL, A., J. F. PETRULEVICIUS, AND X. MARTINEZ-DELCLOS. 2005. New Mesozoic Protomyrmeleontidae (Insecta: Odonatoptera: Archizygoptera) from Asia with a new phylogenetic analysis. Journal of Systematic Palaeontology, 3:187–201.

PONOMARENKO, A. G. 2002a. Superorder Scarabaeida Laicharting, 1781. Order Coleoptera Linné, 1758. The beetles, p. 164–176. *In* A. P. Rasnitsyn and D. L. J. Quicke (eds.). History of Insects. Kluwer Academic Publishers, Dordrecht.

PONOMARENKO, A. G. 2002b. Superorder Myrmeleontidea Latreille, 1802 (=Neuropteroidea Handlirsch, 1903), p. 176–189. *In* A. P. Rasnitsyn and D. L. J. Quicke (eds.). History of Insects. Kluwer Academic Publishers, Dordrecht.

PRITYKINA, L. N. 1981. Novye triasovye strekozy srednej Azii, p. 5–42. *In* V. N. Vishniakova, G. M. Dlussky, and L. N. Pritykina (eds.), Novye iskopaemye nasekomye s territorii SSSR. Trudy Paleontologicheskovo Instituta Akademii Nauk SSSR., 183:5–42. (In Russian)

RASNITSYN, A. P. AND V. V. ZHERIKHIN. 2002. Impression fossils, p. 437–444. *In* A. P. Rasnitsyn and D. L. J. Quicke (eds.), History of Insects. Kluwer Academic Publishers, Dordrecht.

RIEK, E. F. AND J. KUKALOVÁ-PECK. 1984. A new interpretation of dragonfly wing venation based upon early Carboniferous fossils from

Argentina (Insecta: Odonatoidea) and basic characters states in pterygote wings. Canadian Journal of Zoology, 62:1150–1166.

ROHDENDORF, B. B. 1961. Podklass Pterygota, p. 69–88. *In* B. B. Rohdendorf, E. E. Becker-Migdisova, O. M. Martynova, and A. Sharov (eds.), Paleozojskie nasekomye kuznetskogo bassejna. Trudy Paleontologicheskovo Instituta Akademii Nauk SSSR, 85:1–705.

SCHNEIDER, J. W., S. G. LUCAS, AND J. M. ROWLAND. 2004. The blattida (insecta) fauna of Carrizo Arroyo, New Mexico—Biostratigraphic link between marine and non-marine Pennsylvanian/Permian boundary profiles. *In* S. G. Lucas and K. E. Zeigler (eds.), Carboniferous–Permian transition at Carrizo Arroyo, Central New Mexico, Bulletin of the New Mexico Museum of Natural History and Science, 25:247–261.

SELLARDS, E. H. 1909. Types of Permian insects. Pt. 3: Megasecoptera, Oryctoblattinidae, Protorthoptera. American Journal of Sciences, 4, 27:151–173.

SHCHERBAKOV, D. E., E. D. LUKASHEVICH, AND V. A. BLAGODEROV. 1995. Triassic Diptera and initial radiation of the order. International Journal of Dipterological Research, 6:75–115.

TASCH, P. AND J. R. ZIMMERMAN. 1959. New Permian insects discovered in Kansas and Oklahoma. Science, 130:1656.

TASCH, P. AND J. R. ZIMMERMAN. 1962. The Asthenohymen-Delopterum bed—A new Leonardian insect horizon in the Wellington of Kansas and Oklahoma. Journal of Paleontology, 36:1319–1333.

TILLYARD, R. J. 1925. Kansas Permian insects. 5. The orders Protodonata and Odonata. American Journal of Science, (5), 9:40–73.

TILLYARD, R. J. 1928. A Permian fossil damselfly wing from the Falkland Island. Transactions of the Entomological Society of London, 76: 55–63.

WIEGMANN, B. M., M. D. TRAUTWEIN, J.-W. KIM, B. K. CASSEL, M. A. BERTONE, S. L. WINTERTON, AND D. K. YEATES. 2009. Single–copy nuclear genes resolve the phylogeny of the holometabolous insects. BMC Biology, 7:1–16.

ZALESSKY, G. 1948. Nasekomye iz Permskikh otlozhenij Solikamskovo i Cherdynoskovo rajonov. Voprosy Teoreticheskoj i Prikladnoj Geologii, 5:44–52. (In Russian)

ZESSIN, W. 2008. Überlick über die paläozoischen Libellen (Insecta, Odonatoptera). Virgo, Mitteilungsblatt des Entomologischen Vereins Mecklenburg, 11:5–32.

ACCEPTED 7 JULY 2011