KANSAS PERMIAN INSECTS. PART V. THE ORDERS PROTODONATA AND ODONATA.

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The two related orders Protodonata and Odonata are best dealt with together in a single article. Although the venational scheme in both orders is evidently closely related to that of the Paleodictyoptera and Megasecoptera, and can only be interpreted by reference to them, the differences are marked enough to make even fragmentary fossil wings in either order easily recognizable. The principal character by which the wings of Protodonata and Odonata can be distinguished from those of Paleodictyoptera and all other orders, except only the Plectoptera, is the arrangement of the system of cross-veins, which are, *in every part of the wing, including the costal space,* placed *at right angles* to the main veins and their branches. In all other densely-veined wing-types, the cross-veins either form an irregular meshwork, or are placed obliquely, *at least in the costal space,* where the apparent cross-veins are, strictly speaking, *veinlets,* i.e., short branches of Sc preceded by tracheæ in the larval wing-sheath, and thus differ from the true cross-veins in the other parts of the wing. From the Plectoptera, the two orders under consideration may be distinguished at once by the more robust development of the main veins, and by the absence, except on Rs, of the very special triadic type of branching of the veins characteristic of that order.

Up to the present time, the Protodonata have been known only from the Upper Carboniferous and Lower Permian, if we except the very remarkable and isolated genus *Aëroplana*, from the Upper Trias of Ipswich, Queensland, which I originally placed in this order but have since removed to a new order, Aëroplanoptera. The Odonata, on the other hand, are known from the Upper Trias to Recent times. In the Yale Collection of Kansas Permian insects, the Protodonata are well represented by several fine fossils. The Odonata are also

represented by a single beautifully preserved wing, while a more poorly preserved fossil can also be recognized as probably belonging to this order in the type described as *Opter brongniarti* Sellards and placed mistakenly by him in the order Megasecoptera.

It has generally been assumed that both Protodonata and Odonata are specializations from an older Paleodictyopterous type. The venation of the Protodonata is compared very carefully by Lameere with that of *Dictyoptilus* (*Cockerelliella*), a Paleodictyopteron of the family Dictyoneuridæ. A study of the new fossils appears to me to indicate the possibility that both orders are offshoots, not of the true Paleodictyoptera, but of the allied Megasecoptera.

No general agreement has been evidenced as to whether the Protodonata are actually the ancestors of the Odonata or not. Sellards, indeed, goes so far as to sink the Protodonata as a subordinate group within the Odonata[1]; but his arguments would certainly not be accepted by any student of Odonata at the present day, as they are based on assumptions concerning the radial sector and bridge-vein which no longer meet with general acceptance. The evidence brought forward in the following pages is all in favor of the two orders being quite distinct, and representing two separate lines of evolution, neither of which can be considered in any way ancestral to the other.

The two orders may be easily distinguished as follows:

Subcosta either very long, reaching nearly to apex of wing, or, if shorter, then not turned sharply upwards distally to meet costa; nodus and pterostigma always absent: precostal area frequently present. ..... Order Protodonata.

Subcosta always greatly shortened, and turning sharply upwards distally to meet costa at the point where the nodus is formed; nodus and pterostigma present; precostal area always absent. Order Odonata.

Order Protodonata.

Handlirsch recognizes four families in this order, viz. Protagriidæ,[2] Meganeuridæ, Typidæ and Paralogidæ.

[1] E. H. Sellards, This Journal (4), 22, 257-258, 1906.

[2] Genus *Protagrion* from Greek πρῶτος first and ἄγριον, a wild thing, neuter of ἄγριος; stem *agri-*, hence family name should be Protagriidæ, not Protagrionidæ as usually written.

The Typidæ are clearly only slightly specialized Meganeuridæ, and will be treated here as a subfamily of them. The Paralogidæ contain only the single genus *Paralogus* from the Upper Carboniferous of North America; the Protagriidæ and Meganeuridæ are both represented in the Lower Permian of Kansas. The three families may be distinguished as follows:

1. Both branches of M (i.e. MA and MP) and both branches of Cu (i.e. Cu_1 and Cu_2) present.
FAMILY PROTAGRIIDÆ.
Only the anterior convex branch of M (i.e. MA) and the posterior branch of Cu (i.e. Cu_2) present as free veins; the other two branches either obsolescent or absent.
2.
2. Sc long, ending towards apex of wing.
FAMILY MEGANEURIDÆ.
Sc short, ending about half-way along costa.
FAMILY PARALOGIDÆ.

FAMILY PROTAGRIIDÆ.[2]

This family is represented by the genus *Protagrion*[2] from the Upper Carboniferous of Commentry, France, and the new genus *Calvertiella*, described below, from the Lower Permian of Kansas. They may be distinguished as follows:

Precostal area present; Sc ending on costa near apex of wing; branches of 1A normal. .....Genus *Protagrion* Brongn.
Precostal area absent; Sc ending on R_1 a little beyond halfway; branches of 1A strongly arched. Genus *Calvertiella*, n. gen.

Genus *Calvertiella*, n. gen.
(Figs. 1, 2A.)

Wings of moderate size only (about an inch in length); costa strongly built and considerably arched from base to apex; precostal area absent. Only three free main veins arising from base, viz. Sc, R + M and Cu + 1A. Sc runs to a little beyond half-way beneath the costal margin, where it fuses with R_1; the latter continues just below costa to near apex. R and M are closely fused from base to about one-fourth of length of wing, where they separate; a little beyond this point, at about one-third of wing-length, Rs separates from R_1; at its origin,

Rs lies close above MA and is strongly connected with it by one or two short, stout cross-veins. Slightly before the level of the end of Sc, Rs divides into R_2 (anterior) and R_3 (posterior), both branches being concave; at about half-way between this point and apex of wing, R_2 again divides into R_{2a} and R_{2b}, both branches again

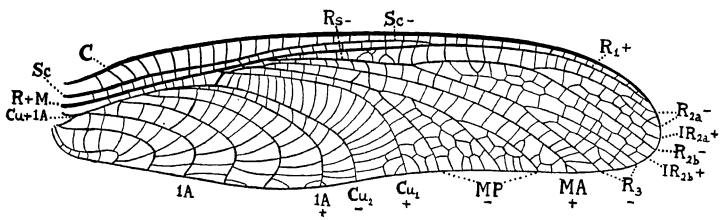

Fig. 1.—*Calvertiella permiana*, n. gen. et sp., order Protodonata, family Protagriidæ. Lower Permian of Kansas. Forewing. Length 26.5 mm. Specimen No. 5007*a*. Cf. fig. 2A. For lettering, see Table on p. 73. New Notation.

being concave. Between the three concave branches of Rs, convex intercalated sectors, IR_{2a} and IR_{2b}, are developed, somewhat irregular in form. Immediately on leaving R, M receives a strong convex cross-vein, somewhat oblique, from the vein below it; this is almost certainly the free basal portion of Cu_1, the rest of which forms a strongly arched vein lying below MP, but fused with M at base for a short length of less than one cellule; a little further distad, M divides into the convex anterior MA and the concave posterior MP; the former arches up at origin so as to come to lie close under Rs, and then runs as a simple, slightly arched vein to posterior margin at about one-sixth from apex; the latter continues the line of M straight on, finally branching into three, these concave branches being separated, as in the case of Rs, by interpolated convex sectors irregular and not very clearly defined. Cu_1 separated from Cu_2 by a wide and increasing space, filled with a single row of short, wide cellules. Cu and 1A fused together from close to base to about one-sixth of the wing-length, then diverging

very slightly; Cu runs on to a point below origin of M, where it gives off the strong cross-vein mentioned above as the probable free basal piece of Cu_1; Cu_2 continues straight on as a strongly curved vein ending up at right angles to the posterior margin of the wing and about half-way along it. 1A is an even more strongly arched vein, situated slightly basad from Cu_2 and diverging from it; between it and base of wing, five convex branches are given off, the first of which is sigmoidally curved and very short, the others gradually increasing in length and all strongly curved so as to end up either at right-angles to, or even making an obtuse angle with, the posterior margin.

The generic name is given in honor of my good friend and colleague, Dr. P. P. Calvert, Professor of Biology in the University of Pennsylvania, Philadelphia, and a leading authority on the Odonata.

Genotype.—Calvertiella permiana, n. sp.

The above definition of the genus is taken from an almost perfect wing, of which both obverse and reverse are preserved, and whose only defect is the loss of the high ridges of the main veins at one or two places near the base of the wing, as shown in Fig. 2A. Fortunately all the series of cross-veins are preserved; when these are mapped out, the courses of the lost portions of the main veins between them can be filled in with almost complete certainty, since there is not enough space between the series to admit of any alternatives. The only questions which might arise are as to whether, if the main veins had been fully preserved, a separate M might not have been visible running weakly just below R (as in Meganeuridæ) and a separate 1A running just below Cu. The decision that such was not the case has been arrived at partly because, where the main veins in question are preserved, no sign of such separation is to be found, and partly out of consideration of the space available between the series of cross-veins, which is so slight as scarcely to admit of two main veins running alongside, even if one of them were very slender.

Calvertiella must be regarded as a highly specialized off-shoot from the much older *Protagrion,* and undoubtedly presents to us one of the final stages reached by the family before its extinction. The general somewhat

bowed form of the wing, with the unique ending of Sc on R_1, the greatly curved Cu_1, Cu_2 and 1A, and, above all, the extraordinary form of the branches of 1A, are all high specializations, as are also the high degrees of fusion attained by the main veins near the base of the wing. For the purpose of comparison, the wing of *Pro-*

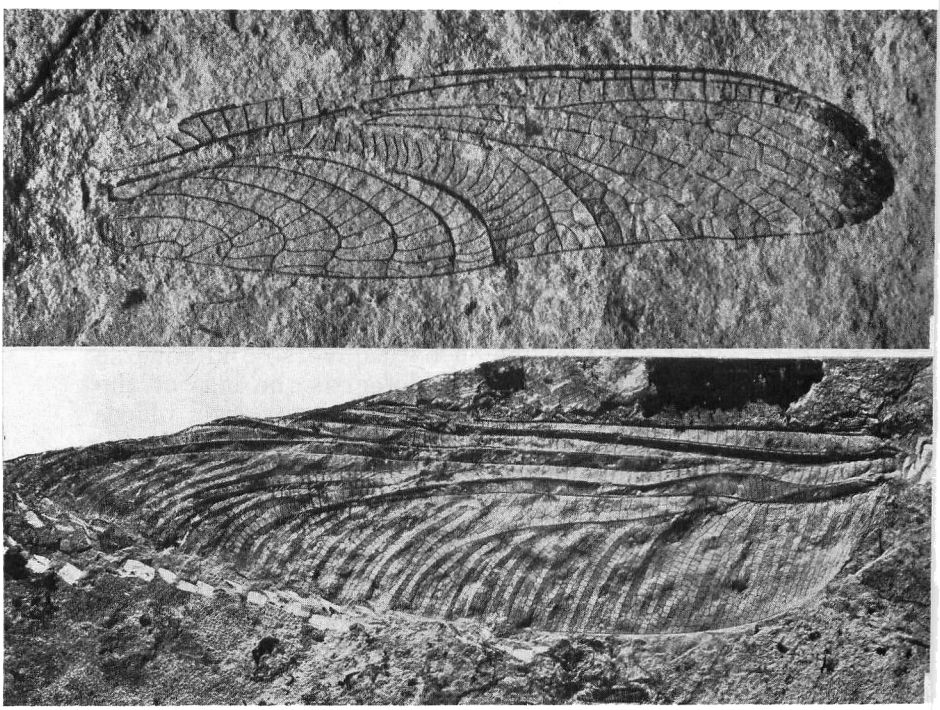

Fig. 2A.—*Calvertiella permiana*, n. gen. et sp., forewing; length 26.5 mm. Specimen No. 5007*a*. Cf. fig. 1.

Fig. 2B.—*Megatypus schucherti*, n. gen. et sp., hindwing; length 165 mm. Specimen No. 1021*a*. Cf. fig. 5. Photographed by Mr. W. C. Davies, Cawthron Institute, Nelson, New Zealand.

tagrion audouini Brongn. is shown in fig. 3; we should note, in particular, the close correspondence in the form of the origins of the free portions of Rs and M in *Protagrion* and *Calvertiella*, and the valuable evidence they supply of a condition intermediate between that of a

free MA, entirely unattached to Rs, as in Paleodictyoptera and most Megasecoptera, and the highly specialized stage reached by the next family, Meganeuridæ, in which MA has become secondarily attached to Rs, as in the true Odonata. We should also note that, in *Protagrion*, the branches of Rs are pectinately arranged and are all

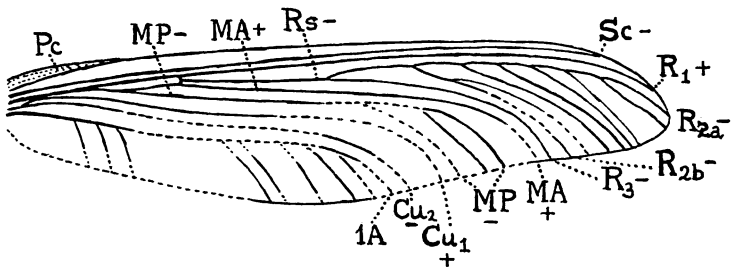

Fig. 3.—*Protagrion audouini* Brongn., order Protodonata, family Protagriidæ. Upper Carboniferous of Commentry, France. Forewing, for comparison with fig. 1. After Brongniart, with lettering of New Notation added, as in Table on p. 73, *Pc*, precostal area.

concave or true branches, as in Paleodictyoptera; whereas, in *Calvertiella,* as in Meganeuridæ and true Odonata, the number of true concave branches is reduced, and interpolated convex sectors are developed between them. In *Protagrion,* also, Cu_1 appears to have arisen by upward arching from Cu very close to the base, and has no point of fusion with M; also, 1A is not fused with Cu, and its descending branches are of normal form.

Calvertiella permiana, n. sp.

(Figs. 1, 2A.)

A beautifully preserved and practically complete wing, probably a forewing; *total length* 26.5 mm.; greatest breadth 6.5 mm. Pigmentation entirely absent, except for a slight infuscation of the apex of the wing. Costa very strongly formed and serrated almost to apex. All main veins strongly formed; in the fossil, the extreme base of the costa is covered by a small piece of the rock matrix, while the high ridges of R, from near base up to end of Sc, and of Cu_1 for a short distance, have been

irregularly broken away when the rock was split open. This type of breakage occurs only rarely in insect wings, and only in cases of highly convex and strongly developed veins. Extreme portion of free base of M missing for a short distance, apparently carried away by the breakage of the high ridges of R and Cu_1, between which it lies.

Of specific value only, we consider the following venational details:—the backwardly directed costal veinlets at the base of the wing (probably indicating a considerable amount of arching of the costa at the extreme base); the terminal forking of R_{2+3}; the forking of R_3, with development of an intercalated convex sector between the forks; and numerous details of the cross-venation shown in the figure but not important enough to mention here.

Types.—Holotype: Specimen No. 5007*a;* in Yale University Collection. Holotype counterpart: Specimen No. 5007*b;* in Cawthron Institute Collection. The holotype lies with its apex to the right, as shown in fig. 2A, and has R and Cu_1 convex; it is, therefore, an impression of a right wing, right way up.

Horizon.—Wellington shale, Lower Permian of Kansas.

Family 2. Meganeuridæ.

This family is represented by a number of closely allied genera in the Upper Carboniferous of Commentry, France, and by a single genus, *Boltonites,* from the Radstock Coal Measures, Somerset, England (the exact horizon of this specimen is doubtful). The genus *Typus,* described by Sellards from the Lower Permian of Kansas, and placed in a distinct family Typidæ, must, in my opinion, be considered as a member of this family.

The Meganeuridæ were large to gigantic insects, with wings measuring from about 4 to over 13 inches in length; the famous *Meganeura monyi* Brongn., with an expanse of about 700 mm., or nearly 28 inches, was the largest of all known insects. They are characterized by the hindwing being considerably wider than the fore, with larger anal area, by the presence of a precostal area, by the long, straight Sc, by the fusion of MA basally with Rs, the common stem of these two veins diverging from R not far from the base, by the loss

of MP and Cu_1 as free veins (both being either completely absent, or only present as short, obsolescent pieces attached basally to MA and Cu_2 respectively), by the free and characteristically waved Cu_2, and by the strongly developed, convex 1A, with attached concave sector 2A.

The genus *Typus*, together with the allied *Megatypus*, n. gen., represented in the new material from the Kansas Lower Permian, form a distinct subfamily separated from the European genera (subfamily Meganeurinæ) as follows:

R_3 arising from Rs not far distad from origin of MA, i.e. between one-third and one-fourth of wing-length from base.
SUBFAMILY MEGANEURINÆ.

R_3 arising far distad from origin of MA, i.e. at some point nearly, or more than, half-way from base of wing.
SUBFAMILY TYPINÆ.

SUBFAMILY TYPINÆ.

The two genera comprising this subfamily may be distinguished as follows:

R_3 arising somewhat before half-way along the wing: Ac a simple cross-vein placed obliquely between two normal cross-veins; a single row of cellules between 1A and 2A: wings about 4 inches long. ..... Genus *Typus* Sellards.

R_3 arising distinctly beyond half-way: Ac a strongly formed oblique vein connecting Cu_2 with 1A and receiving upon itself a number of cross-veins above and below it; two or more rows of cellules between 1A and 2A; insects of larger size than *Typus*, the length of wing ranging from 7 to about 12 inches.
Genus *Megatypus*, n. gen.

Genus *Typus* Sellards.

"Types of Permian Insects," Part I, This Journal (4) **22**. 249-258, 1906.

Genotype.—Typus permianus Sell., from the Lower Permian of Kansas.

Typus permianus Sell.

(Fig. 4.)

Dr. Sellards very kindly sent me a photograph of his fine type specimen of this species, which shows portions of all four wings spread out, together with the head,

thorax, one fore leg, and base of abdomen. The drawing which he gives of it (p. 250, fig. 1 of his paper) is accurate as to the course of the main veins and the positions of most of the cross-veins; but I am unable to see, from the photograph, any sign of the alleged *oblique vein* which he uses as an argument in favor of considering this insect to be a true Odonate. I have not found this oblique vein present in any other Meganeurid; also, amongst true Odonata, it only occurs in the Anisoptera, and is entirely absent from the much older Zygoptera. Slight obliquity is shown by a number of cross-veins, chiefly in positions below the bases of branches of main veins where they are somewhat curved on leaving the main stem; but the only true *oblique vein,* as far as I can see in *Typus,* is the *anal crossing Ac,* which indicates the passage of a trachea across from Cu_2 to 1A, and is almost certainly homologous with *Ac* of the true Odonata. The strong alternation of convex and concave veins in the wings of this fine insect is not indicated in any way in Sellards' figure, which also fails to show the heavy calibre of most of the main veins, in contrast with the much slenderer cross-veins. In this connection, it seems necessary to point out how important it is that the convexity or concavity of the main veins in fossils of this type should be marked in some way. In this and succeeding parts, convex veins are marked +, concave veins —.

Lameere seems to have fallen into a somewhat serious error with regard to the composition of M in the Meganeuridæ, as he states[3] that the "median is divided into a high (i.e. convex) nervure, the anterior median (i.e. MA), and a low (i.e. concave) nervure, the posterior median (i.e. MP)". But in all the Meganeuridæ which I have examined, MP is entirely absent, and the posterior branch of MA, which arises a little before halfway along that vein in *Typus* and *Megatypus,* is clearly a convex vein, and is merely the first of a series of pectinately arranged branches of MA. The true MP, as we have seen in Protagriidæ, arises close to the origin of M, before the level of the origin of Rs, and, as it continues the line of the basal portion of M, not only in Protagriidæ but also in Paleodictyoptera and Megasecop-

[3] Psyche, 30, 129, 1923.

tera, it never takes any part in the fusion between M and Rs; this fact alone should have shown Lameere that he was not dealing with MP in the Meganeuridæ, since they have MA fused basally with Rs, and the alleged MP arises far distad from the fusion.

The new material from the Lower Permian of Kansas contains a well preserved fragment of a wing of *Typus*

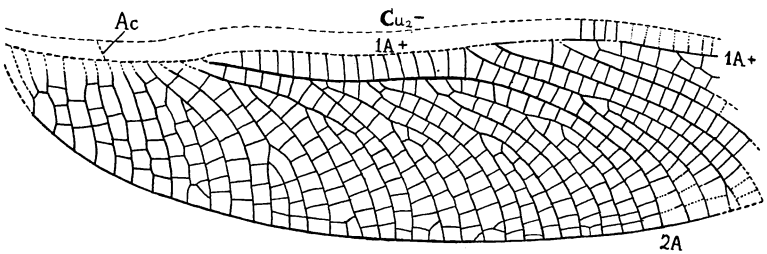

Fig. 4.—*Typus permianus* Sell., order Protodonata, family Meganeuridæ. Lower Permian of Kansas. Fragment of hindwing. Length 45 mm. Specimen No. 5008*a*. For lettering, see Table on p. 73, except Ac, anal crossing.

permianus Sell. (fig. 4) showing almost the whole of the anal area of a right hindwing. *Total length* of fragment, 45 mm., indicating a total length of wing of about 90 mm. or slightly smaller than the type specimen of *T. permianus*. A comparison of the venation of this fragment with that of the photograph of the type specimen shows so close a correspondence that I do not hesitate to assign the new fossil to *T. permianus*. The vein labelled 2A in fig. 4 is characteristic of all Meganeuridæ; being concave, whereas 1A itself is convex, it obeys Lameere's condition of being a posterior sector of opposite sign to the anterior vein from which it arises, and therefore merits the notation 2A, which I use throughout for the sub-penultimate of Lameere. It should be noted also that 1A, like MA and Cu_1, arches slightly upwards after the point of origin of 2A.

Types.—The type specimen of *T. permianus* is in Dr. Sellards' collection at Austin, Texas. Paratype (anal area of hindwing): Specimen No. 5008*a*; in Yale University Collection. Paratype counterpart: Specimen No. 5008*b*; in Cawthron Institute Collection. The paratype

lies with apex of 2A to the right, and therefore is an impression of a right hindwing, right way up.

Genus *Megatypus*, n. gen.

(Figs. 2B, 5-9.)

This genus differs from *Typus* Sell. by the much greater size of the wings and by the following venational characters: At base of wing, remnants of the obsolescent veins MP and Cu_1 are plainly visible, in the positions

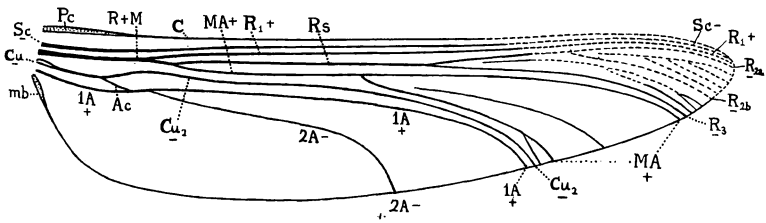

Fig. 5.—*Megatypus schucherti*, n. gen. et sp., order Protodonata, family Meganeuridæ. Lower Permian of Kansas. Hindwing. Length 165 mm. Specimen No. 1021*a*. Cf. fig. 2B. For lettering, see Table on p. 73, except Ac anal crossing, *mb* membranule, Pc precostal area. (Wing drawn with apex to right, to facilitate comparison with other figures.)

shown in fig. 6. R_3 arises about half-way between point of origin of Rs from Rs + M and apex of wing. Ac is a strongly developed oblique vein, receiving numerous cross-veins both above and below, and continued distad close alongside 1A for several cellules length beyond the point of origin of 2A; also it is markedly concave. Between 1A and 2A two or more rows of cellules are developed, increasing in number distally. Hindwing with a distinct membranule (fig. 6, *mb*) at base of posterior margin.

Genotype.—Megatypus schucherti, n. sp.

Two species of this fine genus are represented in the new material before us; they may be distinguished as follows:

Wings about 250 mm. or 10 inches long.
M. ingentissimus, n. sp.

Wings about 175 mm. or 7 inches long.
M. schucherti, n. sp.

Megatypus schucherti, n. sp.
(Figs. 2B, 5-8.)

This fine species is represented by an almost complete hindwing (obverse and basal third of reverse) beautifully preserved, and by a poorly preserved piece of a forewing.

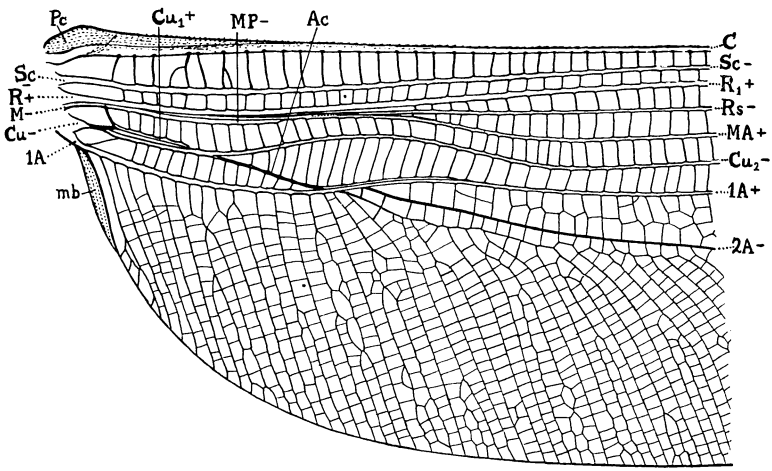

Fig. 6.—*Megatypus schucherti*, n. gen. et sp., order Protodonata, family Meganeuridæ. Basal portion of hindwing of Specimen No. 1021*a*, enlarged, and drawn with base to left, to show the composite structure of veins R + M and Cu + A. Ac, anal crossing; Cu_1, remnant of that vein situated above Cu_2 basally; *mb*, membranule; MP, remnant of that vein attached basally below MA. Other lettering as in Table on p. 73. Cf. fig. 7.

Hindwing.—Total length of nearly complete wing, 165 mm., representing a complete wing of approximately 7 inches in length; distance from base to end of 2A, 94 mm.; *greatest breadth* 94 mm. Pigmentation entirely absent. The impression is that of a right hindwing lying wrong side up, the concave veins appearing convex and *vice versa*. Fig. 5 shows the general venational scheme, with cross-veins omitted; the dotted portion at the apex is an attempted restoration of the miss-

ing part. *Precostal area* short and narrow, attached basally to the very stout *costa*, which is strongly serrated for the basal fourth of its length, but after that becomes rapidly thinner and loses its serrate character. Sc and R both strongly built; judging by their courses in the preserved portion, both probably run close

Fig. 7.—*Megatypus schucherti*, n. gen. et sp., hindwing, basal portion, enlarged, to show composite structure of basal parts of veins R + M and Cu + A. Specimen No. 1021*a*. Cf. fig. 6. Photograph by Mr. W. C. Davies, Cawthron Institute, Nelson, New Zealand.

together to near apex. Rs + M diverging very gradually from R at about one-sixth of wing-length, and almost then dividing into Rs and MA which run almost parallel to one another to a little beyond halfway, where the line of Rs is continued by R_3, converging very slightly towards the upper branch of MA distally, and ending with it far along posterior margin below apex. A short portion of R_2 is preserved, also the beginning of the first intercalated convex sector between it and R_3. Posterior branch of MA arising somewhat weakly and irregularly at about middle of wing. Cu_2 strongly waved sigmoidally in its basal third; 1A a strong, convex vein with well developed, concave 2A arising a little distad from Ac.

Probably owing to the exceptional state of preservation of this fossil, certain structures can be made out at the base which appear not to have been noticed in any other Meganeurid wing. These can be seen by comparing fig. 7 with fig. 6. A careful examination of R + M from base outwards shows that this vein begins as a *double vein,* consisting of the stout R with weaker M attached posteriorly, and very soon becomes a *triple vein* by addition of a fairly stout third vein attached to it posteriorly; this third vein only runs to a point just above the middle of Ac, when it ceases. There can be little doubt that this vein is the disappearing remnant of MP. A little beyond the end of MP, Rs + M begins to diverge very slightly from R_1, and almost immediately divides into Rs and MA, the latter arching slightly downwards as it leaves Rs. The first cross-vein situated basally below R + M is somewhat oblique and thickened; it appears to me probable that this is the homologue of M_5 in the Holometabola. Where this vein meets Cu, the latter is seen to have become a double vein; moreover, the two veins, though parallel and close together, are not actually attached to one another, as in the case of MP and MA, but a distinct space can be seen between them. This double condition continues to within two cellules' length of Ac, where the upper vein ends. The position of this upper vein with respect to M_5 and the main stem of Cu proves that it can be nothing else but the disappearing remnant of Cu_1; the condition of this vein should be compared with that to be seen in the new fossil Odonate wing described later on in this part.

What appears to be the first cross-vein basally between Cu and 1A is a very oblique, slender vein, arising from 1A and joining Cu_2 just distad from the origin of Cu_1. This oblique vein has quite the appearance of a weak chitinization over the course of an original trachea in the larval wing-sheath, and occupies the exact position of trachea 1A in the larval wing-sheaths of recent Odonata. Following Cu_2 to a point two cellules' width beyond the end of Cu_1, we meet with the remarkably specialized Ac which is one of the principal characters of the new genus *Megatypus;* it is a strong vein, very oblique, receiving upon its free portion between Cu_2 and 1A no less than six cross-veins above and six below. On reaching 1A,

Ac does not disappear at once, but can be seen to form with it a double vein similar to that shown by MA with MP, for about twelve cellules' length, after which it ends. The concave 2A arises below 1A at about three cellules distad from the point where Ac joins 1A; as Ac is also strongly concave, a strong impression is created

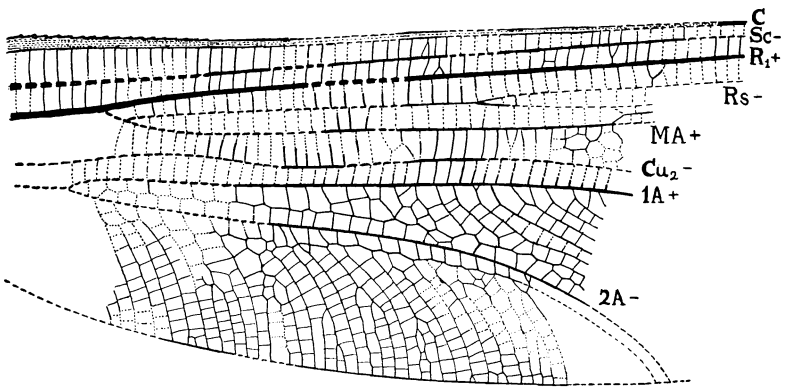

Fig. 8.—*Megatypus schucherti*, n. gen. et sp., order Protodonata, family Meganeuridæ. Fragment of forewing. Length 70 mm. Specimen No. 5009. Lettering as in Table on p. 73.

that the stout, convex 1A has somehow or other *cut across* a concave vein of which Ac is the basal and 2A the distal portion.

Finally, as a further somewhat unexpected occurrence in so primitive a wing, we must note the presence of a strong *membranule* at the extreme base of the posterior margin below 1A. This membranule (fig. 6, *mb*) is coriaceous, without cross-veins, and is exactly analogous to that found in recent Anisopterous Odonata.

The above details of the base of the wing have been described somewhat minutely, as they appear to me to be of very great importance in the consideration of the phylogeny of the two orders Protodonata and Odonata.

The *anal area* in the hindwing occupies more than half of the total width, and is formed by a series of very numerous, closely arranged, descending branches connected by cross-veins; these branches are alternately convex and concave, as in *Typus*, but are much more

numerous and closer together. Below 2A, the first of each set of cross-veins links up with short, bent portions of the descending branches, in such a way as to form a somewhat irregular *supplement* lying below and more or less parallel to 2A at one cellule's distance from it. Between 1A and 2A, except for three single cellules

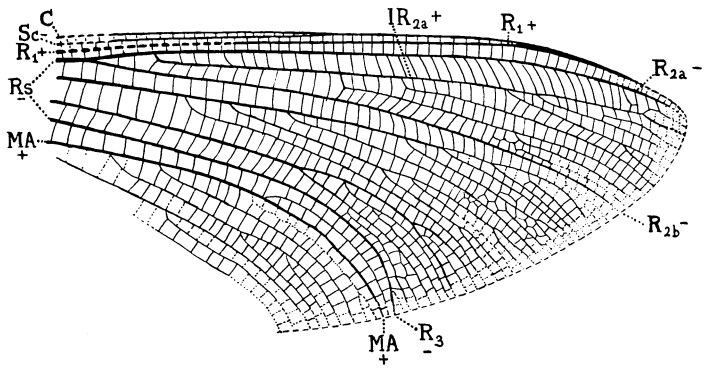

Fig. 9.—*Megatypus ingentissimus*, n. sp., order Protodonata, family Meganeuridæ. Lower Permian of Kansas. Apical fragment of hindwing. Length 54 mm. Specimen No. 5010*a*. Lettering as in Table on p. 73.

basally, there are two rows of cellules increasing distally to three or more; in *Typus*, this area contains a single row of cellules throughout.

Forewing.—Total length of fragment 70 mm.; *greatest breadth* 32 mm. This is a portion of a left forewing impressed wrong way up, with its apex to the right; the impression is poor and much obscured in places by vegetable remains. In fig. 8, the clearly preserved parts are drawn in by continuous lines, the missing or obscured adjacent parts being shown by dotted lines. By carefully measuring the parts and comparing with those of the hindwing above described, it is found that this fragment represents portion of a wing of about the same size; the venation only differs in the much narrower anal area, indicating a forewing. The supplement below 2A is well marked, and is, perhaps, characteristic of the species. The portion preserved consists of somewhat more than one-third of the wing, beginning at about one-

eighth of the wing-length from the base, and so missing Ac and the origins of Rs, M and 2A.

This species is dedicated to my friend Professor Charles Schuchert, Emeritus Professor of Paleontology, Yale University.

Types.—Holotype hindwing: Specimen No. 1021*a* in Yale University Collection; counterpart, Specimen No. 1021*b* in Cawthron Institute Collection. Holotype forewing: Specimen No. 5009*a*, in Yale University Collection: counterpart, Specimen No. 5009*b* in Cawthron Institute Collection. The hindwing counterpart has only the basal third of the wing, with the precostal area and basal portion of the costa missing, and a large hole, 7 mm. long by over 2 mm. wide, lying in the middle just below 2A and containing some dark plant remains with large cells.

Megatypus ingentissimus, n. sp.

(Fig. 9.)

This species is represented by a fragment 54 mm. long by 26 mm. wide at its greatest breadth, forming only the apical portion of a very large wing, and having the whole of the posterior margin broken away. In fig. 9, the probable position of this margin is indicated by the broken line. The fossil includes all that part of the wing which is missing in the type hindwing of *M. schucherti*, n. sp., together with a considerable distal portion of R_3 and MA. It is a fragment of a right wing, impressed right way up, with apex to right; whether it is part of a fore or hind wing is not certain, but the shape suggests the latter. By comparison of the distances between apex and end of R_3 in this fossil and in *Typus*, it can be seen at once that the complete wing must have measured well over 250 mm. in length, or more than 10 inches. The species, therefore, falls little short in size of the gigantic *Meganeura monyi* Brongn. of Commentry.

Sc lies very close to the costa, and ends up considerably before the apex. R_1 runs also very close to costa distally, and merges into it so imperceptibly that crossveins cannot be made out between them as the apex is approached. R_{2a} ends up about at apex. The fork of R_2 and R_{2a} is preserved, with a strong intercalated convex sector between them, viz. IR_{2a}. R_3 curves strongly downwards on approaching the posterior mar-

gin of the wing; between it and R_{2b} above, two strong convex sectors are interpolated, each of them branched distally. MA ends up very close to R_3, but not quite so arched distally. A peculiarity in the cross-vein system is the obliquity of the series between R_{2a} and IR_{2a} distally.

Types.—Holotype: Specimen No. 5010*a*; in Yale University Collection. Holotype counterpart: Specimen No. 5010*b*; in Cawthron Institute Collection. The counterpart is more fragmentary than the type, measuring only 37 mm. long, with all the apical portion missing.

Unnamed Fragments of the Family Megatypidæ.

Specimen No. 5011 in Yale University Collection consists of three well preserved abdominal segments of Odonate type, measuring 8.5 + 8.5 + 8 mm. in length; breadth 5 mm. If these were, as seems highly probable, three of the middle segments of the abdomen, say 4, 5 and 6, the total length of the abdomen would be a little over 60 mm., which would indicate that this specimen may well be portion of the abdomen of *Typus permianus* Sell.

Specimen No. 5023a in Yale University Collection, with its counterpart *5023b* in Cawthron Institute Collection, shows two abdominal segments of a Meganeurid, probably *Typus permianus* Sell., with tergites and pleural membrane complete; lengths 12 mm. and 9 mm. respectively; breadth 7 mm. They probably represent eithers segs. 2-3 or segs. 7-8.

Specimen No. 5024a in Yale University Collection, with its counterpart *5024b* in Cawthron Institute Collection, is the apical portion of a wing of *Typus permianus* Sell.; total length of fragment, 21 mm.

Specimens No. 5025a and *5026a* in Yale University Collection, with their counterparts *5025b* and *5026b* in Cawthron Institute Collection, are small fragments of a huge Meganeurid wing with exceptionally large cellules. They probably belong to *Megatypus ingentissimus,* n. sp.

Specimen No. 5012a in Yale University Collection with its counterpart *5012b* in Cawthron Institute Collection is a very poorly preserved fragment, much overlain with vegetable remains, showing about the apical two-thirds of a wing, probably the hindwing of *Typus permianus*

Sell. *Length* of fragment about 65 mm., *greatest breadth* 22 mm.

Specimen No. 5013a in Yale University Collection, and its more poorly preserved counterpart No. *5013b* in Cawthron Institute Collection, show the basal portion of a wing of *Typus permianus* Sell., including the costa, Sc, R + M, Cu_2 and 1A, with short portions of separate Rs and MA, but excluding 2A and the anal area. *Total length* 26 mm.

Specimens No. 5014*a*, 5015, 5016, 5017, 5018, 5019, 5027*a-b*, 5028*a-b*, 5029*a-b*, 5030, 5031*a-b*, 5032*a-b*, 5033*a-b*, 5034*a,b* are small fragments of Meganeurid wings which call for no special comment. All are in the Yale University Collection. The counterparts, denoted by the letter *b*, are in the Cawthron Institute Collection.

Order Odonata.

Until a few years ago, the oldest known Odonata were those from the Lias of England. Then followed the discovery of several new genera in the Upper Trias of Ipswich, Queensland, and these have remained to the present day the oldest known representatives of the order. From the Upper Trias back to the Lower Permian is a far cry, geologically, and the discovery of true Odonata in the Kansas beds is one of the most remarkable and unexpected results obtained from the Yale University expedition.

The specimen numbered 5005, which is the distal half of the wing of this new fossil, was one of the few specially selected examples originally sent to me by Dr. Dunbar soon after the expedition took place. The perfection of its preservation is only equalled by that of the wonderful Protohymenoptera already dealt with in Part III. The keenest disappointment was felt by me for many months, while studying this wonderful find, that there should have existed, so far back as the Lower Permian, an undoubted damsel-fly, of which Fate had, apparently, only allowed man to reclaim the distal half of one wing. What would not one have given for the basal half, with its hidden secret of quadrilateral and arculus formation! Then, one day, there arrived the two large crates containing the bulk of the fossils, and many days

were spent in unpacking them and making a rough preliminary classification. One whole crate was unpacked, and the specimens put away, without any sign of Odonate remains of any kind. Then the second crate was unpacked, and still there were no signs of dragonfly remains. At last, some 2,000 specimens having been unpacked and classified, my assistant remarked to me that the sorting was just about over, as there were only about a dozen specimens left. A moment later, he handed to me a specimen and its counterpart (Nos. 5006*a-b*), with the remark that they seemed a bit peculiar. On examining these, I at once recognized them as the basal portion of a petiolate damsel-fly wing, and proceeded to compare them with the distal half preserved on specimen No. 5005. Careful drawings of both specimens were made with the camera lucida; it was then found that, by placing the two drawings so that the preserved portions of the costa slightly overlapped, the series of postnodals could be arranged at equal intervals, and, at the same time, all the remaining veins fell into position, convex to convex and concave to concave. There was only one slight discrepancy, viz. that the width of the space between C and R_1 at the distal end of No. 5006 was slightly less than that of the same space in the overlapping portion of No. 5005. This led me to make careful measurements of this space in a large number of recent Zygoptera; the result was that, in almost every case, I discovered a similar slight difference between the widths of this space in fore and hind wings of the same specimen. There seems, therefore, no necessity to make two separate species for the two fossils under discussion; it is sufficient to satisfy all the facts of the case if we accept No. 5005 as the distal half of a forewing, and No. 5006 as the basal half of a hindwing, of one and the same species.

At first sight, the restored wing of this wonderful fossil seems to be of true Zygopterous type, only requiring a new family for its reception. The slender petiolate base of the wing, the presence of only two antenodals, the position of the nodus at about one-third of the wing-length from base, and the general arrangement of the veins and cross-veins, all indicate a true Zygopteron, and, indeed, not only that but definitely a representative

of the superfamily Cœnagrioidea (Agrionidæ of Selys) as against the Agrioidea (Calopterygidæ of Selys). There are, however, three important characters in which the new fossil differs from all known Odonata, viz. in the nodus being incomplete, in the peculiar formation of the arculus and discoidal cell, and in the presence of an extra longitudinal vein basally between R + M and Cu + 1A, in the basal half of the basilar or median space. The first two of these characters are clearly much more primitive formations than any so far known for the order. As regards the extra vein, it is convex but of very weak calibre compared with the other main veins; basally it is connected with Cu, not with R + M, and distally it again ends on Cu, just above Ac. It is therefore a closely similar formation to that described above in *Megatypus schucherti,* n. sp., and can be nothing else than the obsolescent remnant of Cu_1, entirely lost in all other Odonata.

On the above evidence, the fossil will be placed in a new suborder, Protozygoptera, as the first representative of a new family Kennedyidæ containing the new genus *Kennedya* with the single species *K. mirabilis,* n. sp. The generic name is already well known as that of a group of Australian climbing plants of the natural order Leguminosæ, but does not appear to have been so far used in the Animal Kingdom; it is given in honor of my good friend and colleague, Dr. Clarence H. Kennedy, Professor of Entomology in the State University of Ohio at Columbus, whose work on the male genitalia of Zygoptera was one of the chief causes which led me to question the accuracy of the settled convictions which I had held for many years, in company with all other Odonatologists, on the subject of the lines of evolution of Odonate wing-venation.

Suborder Protozygoptera, n. subord.

Damsel-flies of Cœnagrioid facies, with slender, petiolate wings, only two antenodals and few postnodals placed wide apart; nodus incomplete, i.e. formed simply by the upturned end of Sc without supporting cross-vein beneath and without any subnodus, and situated well before half-way along the costa. M attached to R bas-

ally as far as arculus as a very slender but distinct vein (see fig. 11); at arculus, Rs + MA diverges obliquely downwards and soon divides into the two "sectors of the arculus," viz. Rs above and MA below. Arculus incomplete posteriorly; no closed discoidal cell present, but MA connected with Cu_2 in this region by a single, short cross-vein *mcu*. Cu_1 present as a slender convex vein lying between R + M and Cu_2 + 1A in the basal half of the basilar space, and ending up on the latter vein just above Ac. Cu_2 and 1A completely fused to end of petiole, but separating just before the level of *mcu* into the concave Cu_2 above and the convex 1A below; a strong, somewhat oblique cross-vein closes off a triangular *subquadrangle* (*sq*) between them. Anal crossing (*Ac*) present below Cu_2 + 1A. No trace of anal bridge (*Ab* in recent Odonata) or of any other specialized structures between subquadrangle and posterior margin of wing. Pterostigma present. Rs with five branches, three of which (viz, R_{2a}, R_{2b}, R_3) are original, concave branches of the type found in Paleodictyoptera, while two (viz. IR_{2a}, IR_{2b}) are interpolated convex sectors; the complete arrangement of branches of Rs is that of a double negative triad with middle members attached anteriorly. MA, Cu_2 and 1A unbranched.

Family Kennedyidæ, n. fam.

Damsel-flies with long and slender, petiolate wings, the petiole reaching as far as the origin of the arculus or further; pterostigma narrow, elongate, parallel-sided. Main veins not zig-zagged, except IR_2 and, very slightly, R_2 above it. Antenodals placed fairly close together, Ax_2 before origin of arculus. Postnodals few in number, at equal intervals apart, not in line with the cross-veins beneath them. Cu_1 ending on Cu_2 + 1A halfway along petiole, with Ac beneath it.

Genus *Kennedya*, n. gen.

(Figs. 10-12.)

Nodus at about one-third of wing-length from base, formed by the convergence, at equal obliquities, of C and end of Sc; unspecialized cross-veins present on

either side of nodus both above and below R_1. Postnodals four, placed at wide, equal intervals; below them between R_1 and Rs, only three cross-veins. Pterostigma about one-fifth as long as wide, with a hypostigmatic cross-vein supporting it from beneath near base, but not obliquely braced; R_{2a} bent at this cross-vein. R_3 aris-

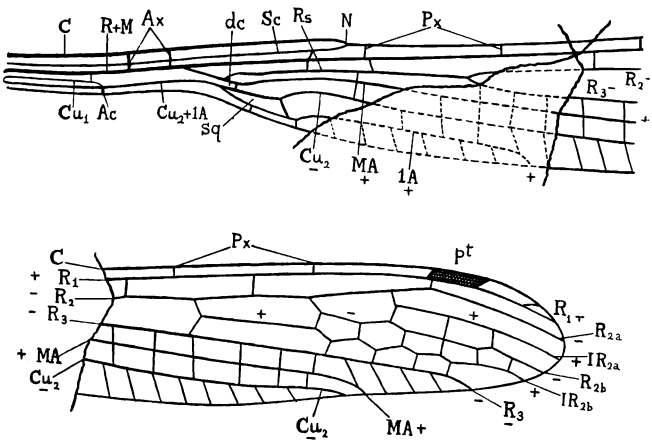

Fig. 10.—*Kennedya mirabilis*, n. gen. et sp., order Odonata, family Kennedyidæ. Lower Permian of Kansas. Above, basal half of hindwing, showing distally the manner in which the distal half of forewing, figured below, can be fitted on. Below, distal half of forewing, with space between C and R_1 slightly narrowed so as to fit hindwing, and apex turned to right. Cf. fig. 12. Lengths:— basal half 25.6 mm., distal half 19.5 mm. Lettering as in Table on p. 73, except Ac anal crossing, Ax antenodals, *dc* discoidal cell, N nodus, *pt* pterostigma, Px postnodals, *sq* subquadrangle.

ing well distad from arculus; the other branches of Rs all arising in the distal part of the wing. MA and Cu_2 converging distally; 1A fairly short. Arculus with a long common stem, from which the two sectors diverge strongly at first (fig. 11) and then approach one another again; the lower sector (MA) supported at its point of greatest curvature by the cross-vein *mcu* below it. Cu_2 and 1A diverging from their common stem at a point slightly basad from the level of the origin of the sectors of the arculus, and forming, with the strong cross-vein *cua*, a long, triangular subquadrangle (*sq*) with anterior and posterior sides both curved. Cu_2 strongly upcurved

after leaving *cua;* 1A also upcurved after leaving the short posterior cross-vein just distad from the end of *cua.*

Genotype.—Kennedya mirabilis, n. sp.

Kennedya mirabilis, n. sp.
(Figs. 10-12.)

This species is represented by two fragments, viz. No. 5005, showing the whole of the distal half of a forewing, and No. 5006, showing most of the basal half of a hindwing. These will be described separately, taking the basal portion first.

Specimen No. 5006a-b (figs. 10, upper fig., and 11; fig. 12A).—The impression is on a greyish-buff rock, not very smooth, and not strongly visible to the naked eye like No. 5005. On examination with a lens, the slender venation is seen to be quite perfect, even down to the very base of the wing. Along the costa, the wing is preserved for a length of 25.6 mm. from base to a point well beyond the second postnodal; along the posterior margin, the preserved portion measures only 12.5 mm., i.e. from base to a little beyond distal end of subquadrangle. The break cuts off all the intermediate veins very obliquely, passing Rs just distad from its first dichotomy. The preserved portion thus includes the whole of the petiole, the two antenodals, the nodus, the arculus, the discoidal cell area, the subquadrangle and the arched portions of Cu_2 and 1A.

In addition to the characters already given under subordinal, family and generic headings, we may note the following as having only specific value:

In the petiole, a very weak cross-vein is just visible, placed above the bent apex of Cu_1 just before it rejoins Cu_2. Two cross-veins are present, one almost exactly above the other, above and below R_1 respectively, somewhat basad from nodus. First postnodal is placed only slightly distad from nodus, and has an oblique cross-vein below and slightly distad from it. A little basad from this, a cross-vein descends from Rs to MA and continues straight on to Cu_2. From middle of posterior side of subquadrangle, a short cross-vein descends to posterior margin of wing, and a second similar cross-

vein lies just distad from the subquadrangle, at the point where 1A arches upwards.

Fig. 11 shows the more minute structure of the veins forming the petiole; the fine denticulation of the somewhat flat costal and posterior margins of the wings is omitted from this drawing, but it should be noted that

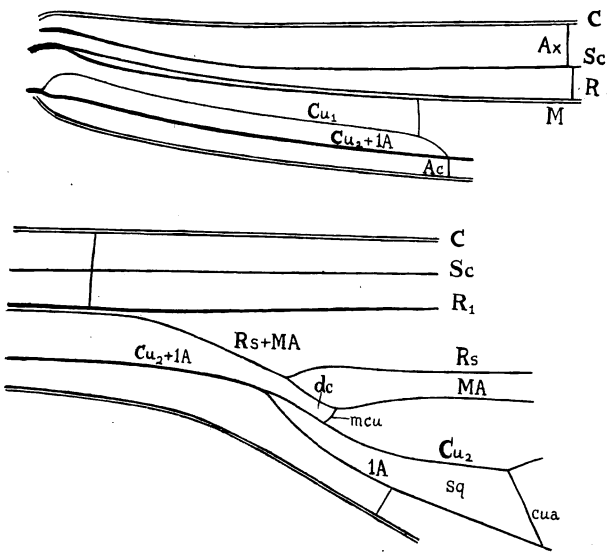

Fig. 11.—*Kennedya mirabilis*, n. gen. et sp., order Odonata, family Kennedyidæ. Enlargements of basal portions of wing, drawn from Specimens No. 5006*a-b*. Above, basal half of petiole, showing composite structure of vein R + M and course of the obsolescent Cu_1. Below, region of arculus and discoidal cell. Lettering as in Table on p. 73, except Ac anal crossing, Ax antenodal, *cua* cubito-anal cross-vein, *dc* discoidal cell (open), *mcu* medio-cubital cross-vein, *sq* subquadrangle.

the structure of the costa and posterior margin of recent Zygoptera is closely similar to it. The chief point of interest is the beautifully preserved R + M, which arises from a rather narrow swelling or callus at the extreme base, and almost immediately divides into R above and M below (Rs being attached to M further distad); for a little distance, these veins run quite markedly apart, but then approach so closely to one another that they appear as a single, two-ridged vein right up to arculus, where

the lower vein diverges without any sharply marked angle. The archings of Rs and MA repeat on a wider scale the basal arching of R and M, i.e. they diverge markedly at first and then approach one another again, running fairly close and parallel to one another until the level of the nodus is reached, when they diverge from

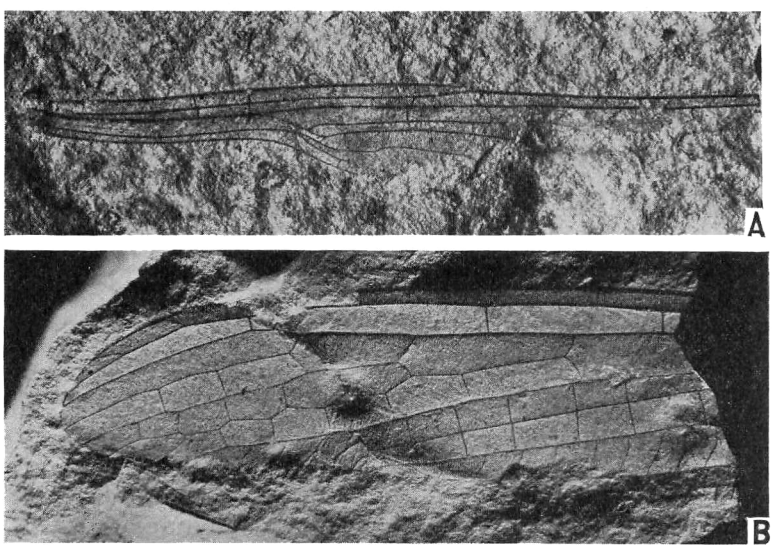

Fig. 12A.—*Kennedya mirabilis*, n. gen. et sp., basal half of hindwing; length 25.6 mm. Specimen No. 5006*a*. Cf. fig. 10, upper figure.
Fig. 12B.—*Kennedya mirabilis*, n. gen. et sp., distal half of forewing; length 19.5 mm. Specimen No. 5005. Cf. fig. 10, lower figure. Photographed by Mr. W. C. Davies, Cawthron Institute, Nelson, New Zealand.

one another gradually. From its origin to the cross-vein *mcu* the arculus is very nearly straight, thus inviting comparison with the straight arculus and open discoidal cell of the forewings of *Hemiphlebia* (fig. 14) and *Chorismagrion*.

The chitinization of Cu_1 is weak and barely visible in the photograph in fig. 12A, owing to the position of the lighting, but it is quite easily visible with an ordinary lens. Cu_2, on the other hand, is a strong, though concave, vein; when it branches, its upper branch is concave and lower convex, a condition comparable with that of

Calvertiella in the Protodonata, but differing from that in the Meganeuridæ, where Cu_2 is unbranched. As Lameere has already shown, the convex lower branch can be nothing else except 1A, and hence the correct notation for the common basal stem is not Cu_2, but $Cu_2 + 1A$. The anal crossing, Ac, indicates, as is well known, the point at which trachea A diverges from trachea Cu_2 in the larval wing-sheath of recent Odonata, and there is no reason to suppose that it does not indicate exactly the same thing in *Kennedya.*

The obverse of this specimen, No. 5006*a,* is beautifully preserved; the reverse, No. 5006*b,* in which the convex veins appear concave and *vice versa,* is not suite so clear except at the extreme base, where the connections of the main veins are fairly easy to make out. The impression is that of a right hindwing, the base being to the left in the obverse, which is right way up.

Specimen No. 5005 (fig. 10, lower fig.; fig. 12B).—This specimen is the reverse impression of the distal half of a right forewing, with the apex to the left and the convex veins apparently concave, and *vice versa* (fig. 12B). The rock on which it is impressed is pale greyish white and very irregularly broken, but the part of the wing preserved is complete except for a small portion of overlying rock hiding the base of the pterostigma and about 3 mm. of the costa basad from it. The impression is remarkably clear, resembling that of the Protohymenoptera described in Part III, and evidently indicating that the wing-membrane was of the same tough, hyaline consistency as that of recent Odonata. *Total length* of fragment 19.5 mm.; *greatest breadth* 5.8 mm.

The costal portion of this fragment begins just before the second cross-vein lying between R_1 and Rs distad from the nodus; some distance further along, the third postnodal is to be seen, between C and R_1. It thus happens that a small portion of the costa preserved on this specimen is also preserved distally on No. 5006 (though not, of course, belonging to the same wing). Thus, by placing the third postnodal in line with the second postnodal preserved in No. 5006, and at the same distance from it that the second is away from the first, the two preserved portions can be brought into very close alignment. After allowing for the already mentioned slightly greater

width between C and R_1 shown in the distal fragment (but not indicated in the somewhat diagrammatic fig. 10), it will be seen that the two parts of the wing are such that the prolongations of the broken veins of No. 5006 distad run simply and naturally into the corresponding veins preserved in No. 5005. So striking is this agree-

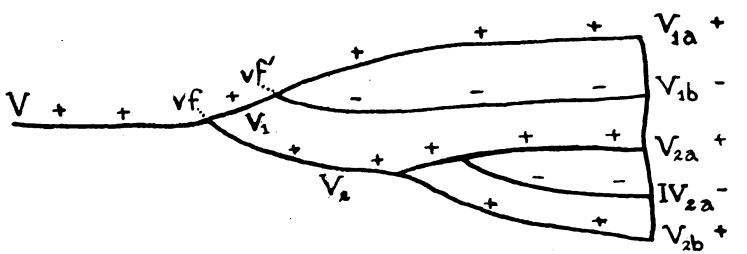

Fig. 13.—Diagram to show system of triadic branching of main veins. For explanation, see text, 73.

ment, that I do not hesitate to treat the two fragments as belonging to one and the same species, and possibly even to fore and hind wings of the same individual specimen!

The pterostigma is beautifully marked and its pigmentation is still preserved; it was evidently of a pale brownish color between black nervures. The basal side is just hidden beneath the superincumbent rock (fig. 12B) and could probably be easily exposed with a penknife by a careful worker. Estimated dimensions of complete pterostigma, 2.3 mm. long by 0.4 mm. wide. Hypostigmatic cross-vein evidently close below base of pterostigma, but not quite at the basal posterior angle, nor slanted obliquely so as to form a brace-vein. R_2 bends considerably at the point where this cross-vein meets it.

In order to understand the interesting mode of branching of Rs, reference should be made to my paper on the Wing-Venation of Mayflies[4] in which the *triadic system* of branching is fully discussed. The primitive triad is there defined as follows (with reference to fig. 13 in this paper):

[4] Jour. Linn. Soc. London, 143-162, 1923

"V is a convex vein which divides at its primary fork *vf* into two equally convex branches V_1 and V_2. In the diverging angle between these two, a concave vein arises from either V_1 or V_2, its point of origin being not far distad from *vf;* this secondary fork is termed *vf'*. In the illustration before us, the concave vein is made to arise from V_1, so that the branches of this vein become V_{1a} (+), V_{1b} (—) and V_2 (+). If, instead of being a convex vein, V were a concave vein, then the two branches V_1 and V_2 would be concave, and the intermediate vein V_{1b} would be convex. The two cases can be distinguished by calling the triad developed from an originally convex vein a *positive triad,* that from an originally concave vein a *negative triad.* Further branching may take place from any one of the three veins, and usually consists of further triads. In the figure, a further triad is seen developed from V_2, viz. the positive triad V_{2a} (+), IV_{2a} (—) (originally written V_{2a}') and V_{2a} (+). If a triad had been developed from V_{1b}, it would have been a negative triad."

"The above definition needs slight modification for the case of the Odonata, as it seems certain, from a study of the Protodonata, that triads, when developed in either of these orders, have their middle veins formed as *intercalated sectors,* not as branches from either of the dichotomic veins enclosing them. That being so, the notation adopted for the middle member of a triad will be to affix "I" to the notation for the anterior vein of the triad, as in the case of IV_{2a} in fig. 13. Applying this to the case of Rs in the Protodonata and Odonata, we can see clearly, both in *Calvertiella* (fig. 1) and *Kennedya* (fig. 10) that the first branching of Rs into R_2 and R_3 has become a negative triad, by development of the middle intercalated sector IR_{2b}, and that a further negative triad is developed more distally on R_2 by its branching into R_{2a} and R_{2b}, with intercalated sector IR_{2a} between them.

When the middle member of a triad is developed as an intercalated sector, the attachment basally to either or both of the other members of the triad is of a secondary nature; it will therefore be easily seen that a certain amount of variability remains at such points, and that tracheal connections in the larval wing-sheath are

secondary and liable to vary also. This is actually what we find in the case of recent Odonata; for instance, IR_{2b} usually connects basally with R_2, but in the genus *Synlestes* and others it connects with R_3 instead.

Another interesting point about the wing of *Kennedya* is the marked convergence of MA and Cu_2 distally. Such

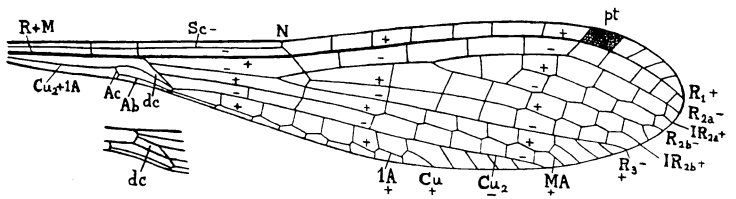

Fig. 14.—*Hemiphlebia mirabilis* Sell., order Odonata, family Hemiphlebiidæ. Recent. Forewing, length 12 mm., showing open discoidal cell (*dc*). Below, closed discoidal cell (*dc*) of hindwing of same. Lettering as in fig. 10 and Table on p. 73, except Ab, anal bridge.

convergence is not met with in most Zygoptera, but is well marked in the family Synlestidæ, which is in many respects one of the most archaic groups of existing Odonata.

The Restored Wing.—The wing of *Kennedya,* as restored by fitting the two preserved portions together after slightly reducing the actual width of the costal space distally, so as to form a hindwing, and after filling in the missing portions, is excessively long and narrow, its general form being that of the family Protoneuridæ, but differing from them in having 1A present and well developed. *Total length* approximately 44 mm.; *greatest breadth* only 5.8 mm.; ratio of breadth to length, 0.13, or less than that of any known recent Zygopterous wings; even in the narrowest wings of the Protoneuridæ, the ratio of breadth to length is 0.15, while the average ratio for petiolate Zygoptera is about 0.20 or 0.21. This is a very remarkable fact, and appears to indicate that the Zygoptera as a whole have been evolved from very narrow-winged ancestors.

The number of cellules in the wing, counting those in the restored portion, is only slightly over a hundred, or about the same as in such a tiny wing as that of *Hemiphlebia* (fig. 14), and far less than the number to be

found in any recent Zygopterous wing of a size corresponding with that of the fossil. When we consider that, in the wing of such a highly organized Libellulid as the male of *Neurothemis,* about 3,000 cellules can be counted, we see again how strong a case is here presented for acceptance of the view that addition, and not reduction (with the sole exception of the loss of 1A in Protoneuridæ) has been the chief factor in the evolution of Odonate wing-venation.

Types.—Holotype, basal half of hindwing: Specimen No. 5006*a,* in Yale University Collection; counterpart: No. 5006*b,* in Cawthron Institute Collection. Holotype, distal half of forewing: Specimen No. 5005, in Yale University Collection.

Opter brongniarti Sell.

Sellards, "Types of Permian Insects," Part III, this Journal (4), 27, 151 and 155, fig. 7, 1909.

This rather poorly preserved fragment was placed by Sellards in the order Megasecoptera, and later removed by Handlirsch to the Protorthoptera or Protoblattoidea (with some doubt), on the suggestion that it had the true anal area absent. Sellards' figure shows three of the main characters of Kennedyidæ, viz. the petiolate base, the arculus, and the characteristic formation of Cu_2 and 1A at the subquadrangle; he also indicates the position of one of the antenodals. This being so, I suggest that *Opter* is in reality a second genus of Kennedyidæ, distinguished from *Kennedya* itself, amongst other characters, by the much greater width of the wing. If this be so, it is probable that Sellards' indication of Sc as running far distad is incorrect, and the specimen should be re-examined, and, if possible, photographed, to determine this and other doubtful points.

Type.—Holotype fragment: No. 1286 in Sellards Collection.

A full discussion of the evidence offered by the new fossils described in this part as to the lines of evolution of the wing-venation in the orders Protodonata and Odonata would take us beyond the scope of this paper, and must be reserved for a later date. We add, however, a

table giving, in parallel columns, the new notation used in this part, the Comstock-Needham notation, and the Selysian system of nomenclature, to facilitate comparison with other works.

Table of Comparison of Venational Systems in the Orders Protodonata and Odonata.

(Convex veins marked +, concave veins —.)

New Notation.		Comstock-Needham.	Selysian.
Costa (+)	C	C	Costal Nervure.
Subcosta (—)	Sc	Sc	Subcostal Nervure.
Radius (+)	R	R	Median Nervure.
Main Stem (+)	R_1	R	Median Nervure.
Radial Sector (—)	Rs	M	Upper Sector of Arculus.
	R_2 (—)	M_{1+2}	Principal Sector.
	R_{2a} (—)	M_1	Principal Sector.
	IR_{2a} (+)	M_{1A}	Postnodal Sector.
	R_{2b} (—)	M_2	Nodal Sector.
	IR_{2b} (+)	Rs (Ms)	Subnodal Sector.
	R_3 (—)	M_3	Median Sector.
Media (—)	M	M	
		(fused basally with R to form Median Nervure or R + M)	
Anterior Branch (+)	MA	M_4	Lower Sector of Arculus.
Posterior Branch (—)	MP	(absent, except in Protagriidæ).	
Cubitus (—)	Cu	Cu	Submedian Nervure.
Anterior Branch (+)	Cu_1	(absent except in Protagriidae, *Megatypus* and *Kennedya*).	
Posterior Branch (—)	Cu_2	Cu_1	Superior Sector of Triangle.
Analis (—)		(fused basally with Cu_2, forming the submedian nervure, Cu_2 +1A).	
Anterior Branch (+)	1A	Cu_2	Inferior Sector of Triangle.
Posterior Branch (—)	2A	(absent in Odonata).	

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