AMERICAN JOURNAL OF SCIENCE

FEBRUARY 1931

THE LOWER PERMIAN INSECTS OF KANSAS. PART 2. THE ORDERS PALEODICTYOPTERA, PROTODONATA, AND ODONATA.

F. M. CARPENTER*

The three orders treated in this part provide an interesting study in the evolution of wing venation. The Paleodictyoptera, which are known only from the Upper Carboniferous and Lower Permian, are recognized as possessing a venation more generalized than that of any other order. The Protodonata, confined to the same geological range, present a venational system which has certain specializations found only in the dragon-flies. In the Odonata, which are known from the Lower Permian to the present, we find a primitive but remarkably modified venation that has perplexed students of phylogeny for many years. Only by a comparison of the members of each of these groups, as both Tillyard and Lameere have shown, can we arrive at a correct understanding of the homologies of their wing veins.[1]

ORDER PALEODICTYOPTERA.

The Wellington shales of Kansas are the only Permian rocks to produce undoubted specimens of this order. In the Yale collection from these beds Tillyard found three specimens of the group, all belonging to a single species, *Dunbaria fascipennis* Till., of the family Spilapteridae. Two of these fossils were amazingly well preserved, showing all four wings and many parts of the body. In the Harvard collection there are

---

* National Research Fellow. These studies have also been aided by grant No. 280 of the Bache Fund, National Academy of Sciences, and a Sheldon Traveling Fellowship from Harvard University. Part 1 (Introduction and the Order Mecoptera) was published in the Bulletin of the Museum of Comparative Zoology, 70, No. 2, 1930.

[1] The Plectoptera should also be included here, but I shall postpone the discussion of the Kansan Permian may-flies until Tillyard has had an opportunity to describe those in the Yale collection.

also three specimens of this species: No. 3056ab (F. M. Carpenter, collector), consisting of a complete fore wing; No. 3057ab (J. W. Wilson, collector), consisting of the right fore and hind wings, the basal half of the left fore wing, and parts of the thorax; and No. 3058ab (W. S. Creighton, collector), consisting of a complete hind wing. All these wings are the same size as those of the holotype and have an identical color pattern.

Since none of the Harvard specimens are as complete as the holotype, I can add nothing to Tillyard's excellent description of this insect. It is interesting, however, to note the individual variations which occur in the venation. The holotype specimen possessed a 6-branched radial sector and a forked M4; the other two Yale specimens had a 9-branched Rs and an unbranched M4. Specimens No. 3056ab and 3057ab in the Harvard collection have a 9-branched Rs, but a simple M4; also Cu1a, which is forked in all the Yale specimens, is unbranched. The other Harvard fossil has a venation identical with that of the holotype.

Although the wings of *Dunbaria* are somewhat more highly specialized in shape than most of the Upper Carboniferous Paleodictyoptera, their venation is very typical of the order. As observed by Tillyard, this fossil illustrates very well Lameere's theory of wing venation, and I propose to use it also as an example of the primitive paradigm from which the Protodonate and Odonate types have been derived. Lameere's conception of wing venation (1922) is based upon the idea that in the Paleodictyoptera there were six main convex veins, each with a concave sector or posterior branch. Thus, the costa possessed a subcosta; the radius, a subradius (Rs); the media, a submedia, etc. Lameere believed that in all other insects the median sector or posterior media (MP) is either entirely absent or greatly reduced, Comstock's media (M) being Lameere's anterior media (MA). Tillyard, however, has subsequently pointed out (1925a) that the vein which Comstock designated as the media is concave in all recent orders except the Odonata and Plectoptera, and consequently must be the posterior media; in the two excepted orders the media is convex and is therefore the anterior media. Further research on the venation of the Carboniferous insects will probably throw much light upon the relationship between the anterior and posterior media, and may require some changes in our present conception of the nature of these veins in the

Paleodictyoptera; but for the purposes of this paper we can accept Lameere's theory, as modified by Tillyard, in its application to the Protodonata and Odonata.

ORDER PROTODONATA.

The order Protodonata was established by Brongniart in 1885 for the genus *Protagrion,* which he considered ancestral to the Odonata. Before his studies on the Commentry insects were completed, he had also found several other genera which appeared to belong to this group: *Meganeura, Titanophasma, Campyloptera,* and possibly *Brodia.* He also placed here Scudder's *Paralogus,* from the Carboniferous of Rhode Island. Brongniart's conception of the Protodonata was rather vague, however, and Handlirsch has since shown that *Titanophasma, Brodia,* and perhaps *Camyloptera* belong elsewhere. In more recent years other Carboniferous representatives of the order have been found in England and Pennsylvania. But it remained for the Wellington shales of Kansas to produce the first Permian insect definitely assignable to this order. In 1906 Dr. E. H. Sellards described his magnificent specimen of *Typus permianus* (Fig. 1), consisting of nearly all four wings outstretched and perfectly preserved. No other Protodonata are in the Sellards collection, but in the Yale material Tillyard found two other well-defined genera: *Megatypus,* allied to Sellards' species, and *Calvertiella,* a most aberrant and specialized group. Shortly after the appearance of Tillyard's paper, two species of Protodonata, very similar to and perhaps identical with *Typus,* were collected in the Permian (Hermit shale) of the Grand Canyon National Park, Arizona (Carpenter, 1928), and another species, *Tillyardiella distincta,* has recently been secured in the Permian of Russia (Martynov, 1930). In the Harvard collection from the Wellington shales I find one additional genus of the order, also related to *Typus,* but with much smaller species. It is very doubtful that the Protodonata persisted into the Mesozoic, although two fossils from this horizon have been placed here (Handlirsch, 1921). One of these, *Handlirschia galasii* Reis, from the Upper Triassic of Germany, is so fragmentary that nothing definite can be said of its affinities. The other fossil, *Piroutetia liasina* Meunier, is from the Upper Liassic of France and consists of a nearly complete wing, 42 mm. long. If Meunier's figure of the wing is correct, the insect certainly could not have been either a Protodonatan or an Odonatan, for R1 possesses at least six branches, and in all known species of both these orders R1 is always simple! It is possible, however, that the vein which Meunier has named the subcosta, extending to the apex of the wing, is actually R1; and that the subcosta is shorter and nearer the costal margin. If this were the case, one might have some basis for assuming the fossil to be Odonate.

The venation of the Protodonata, while diversified in many ways, is similar in fundamental respects throughout most of the genera. At the base of the wing there is a distinct precostal area, which may extend to the middle of the wing, as in *Meganeura,* or be restricted to the very base, as in *Typus.* In the few species where the precostal area has not been found, its absence can be traced to poor preservation, so it is very probable that all of the Protodonata possessed this feature. The anterior margin of the wings of most (and probably all) Protodonata was also peculiar in that it had a series of distinct serrations, which usually extended from the base to the middle of the wing or beyond. The Odonata is the only recent group where this trait is regularly found, but it was common in the Paleodictyoptera and Megasecoptera. The subcosta either terminates somewhere near the middle of the wing or extends to the apex; usually it terminates on the costa, but in the peculiar *Calvertiella* it ends on R1. The radius and its sector are well developed; R1 terminates at or close to the apex; Rs originates near the base, dividing into R2+3 and R4+5 before the middle of the wing; in *Meganeura* and its allies this division occurs just after the origin of Rs, but in *Typus* and related forms it does not take place before the middle of the wing. The structure of the media is more complicated. In *Meganeura* it is fused or almost fused with R basally, diverging from Rs just after the origin of this sector; in all these genera the media gives rise to a number of branches which terminate on the posterior margin of the wing. In *Calvertiella* and perhaps *Protagrion* the media consists of its two main branches, MA (+) and MP (–), but this does not seem to be the case with the other genera. Lameere found that in the type specimens of *Meganeura* there was a concave branch leading from MA near the middle of the wing; this he regarded as MP. Tillyard, however, has pointed out that where MP is present (as in *Calvertiella*), it diverges from MA at the very base of the wing, so that this concave vein in *Meganeura* is really only a branch of MA. In *Megatypus* and *Oligotypus,* new genus, there is a minute remnant of MP at the base of the wing, but in *Typus* not even this portion is preserved. The cubitus in *Protagrion* and *Calvertiella* also seems to be divided into an anterior and posterior branch, whereas in all the other Protodonata the anterior cubitus is either completely absent or reduced to a small remnant at the base of the wing. Cu2 is always a well developed vein and with the exception of *Calvertiella* and *Protagrion* is strongly undulated basally in all forms; it is always unbranched. 1A is a well developed vein also, sending a series of branches to the hind margin; it is usually undulated as much as Cu2. There is some doubt as to the presence of 2A. Tillyard recognized the presence of this vein in *Megatypus* when he described the genus (1925a), but in his recent account of the evolution of the Odonata (1928b) he states, "A glance at the whole of the known genera of Protodonata will show that, although they had broad hind wings, they possessed only one anal vein." Since he does not present any evidence to show why he reversed his interpretation, I fail to see reason for the change. Certainly there is a concave vein leading from 1A at the proper place in *Typus* and its relatives, as well as in *Paralogus* and *Meganeura.* In the new genus *Oligotypus* this vein is developed more extensively than in any of the other genera, and below 2A there is a shorter convex branch which I consider to be 3A; such a vein is present in a more reduced form in the other Protodonata.

There remains one other structure in the Protodonate wing to be considered. In his discussion of the wings of insects (1922, p. 10), Lameere pointed out that in *Meganeura* there is a short vein, resembling an oblique cross-vein at the base of the wing, between Cu2 and 1A. This vein was not shown in Brongniart's figure nor has it been represented in other reproductions of this insect. Lameere believed that this oblique vein was homologous to the one in the Odonata which Tillyard has termed the "anal crossing." This "crossing" has been supposed by Comstock and others to be the divergence of 1A from the common stem Cu2+1A. Consequently, that part of 1A basad of the anal crossing (AC) is not really a portion of this vein at all but a secondary development (A′)[2]. In his discussion of *Megatypus* and *Typus* Tillyard also noted the presence of this oblique vein and concluded that it was "almost

---

[2] See later for a complete discussion of this vein.

certainly homologous with AC of the true Odonata." By this interpretation, of course, the vein 1A in the Protodonate wing is actually 1A only as far back as the anal crossing; basad of that point it becomes A′ as in the Odonata. It is interesting to note that regardless of the high development of this oblique vein in certain of the Protodonata (as *Meganeura, Megatypus, Paralogus, Boltonites*) it is not so well developed in *Typus* and the new genus *Oligotypus*. In the latter genus there is a series of short cross-veins in this region, none of them oblique and none of them more strongly developed than the others. In *Typus* we find a variable condition: some specimens have a single, slightly oblique vein here, while others have *two* such veins. Now, the only reason that we have for supposing that this oblique vein in the Protodonata is the anal vein, rather than a cross-vein, is by analogy with the Odonata; for in the dragon-fly nymphs both Tillyard and Comstock have observed that the anal trachea crosses over at this point. But for reasons which I shall present later, I do not accept this interpretation of the nature of AC in the Odonata (the vein, not the trachea), but regard the anal crossing as merely a cross-vein. Consequently, of course, I also consider the oblique vein in the Protodonata to be a cross-vein, and do not recognize the existence of the secondary vein A′.

On the basis of the presence or absence of the posterior media and the anterior cubitus, Tillyard has separated the Protodonata into two distinct families,—Meganeuridae and Protagriidae. Although the characters involved in this division seem to me to be of subordinal rather than family rank, I adopt this same grouping here. The family Meganeuridae includes three subfamilies, Meganeurinae, Paraloginae, and Typinae. The Protagriidae, according to Tillyard, include two subfamilies, Protagriinae and Campylopterinae. The latter subfamily, based upon the Commentry genus *Campyloptera,* is characterized by petiolate wings and it plays an important part in Tillyard's theory of the evolution of the Odonata. He believes that it represents an annectant group between the Protodonata and the petiolate Megasecoptera. *Campyloptera,* in fact, furnished the only evidence which led Tillyard to the radical conclusion that the Protodonata were derived from the Megasecoptera. Unfortunately, Tillyard did not see the specimen of *Campyloptera* itself and was obliged to base his results entirely upon Brongniart's drawing and the discussion of Handlirsch. The former student placed the genus in the

Protodonata, as I have mentioned above, but he also placed here a number of other forms (e.g. *Brodia*) which we now recognize as true Megasecoptera. Handlirsch (1908) treated *Campyloptera* as a Megasecopteran, although he expressed himself as doubtful. Tillyard (1928) calls attention to the remarks of Handlirsch that the figure of Brongniart shows intercalated sectors similar to those of the Protodonata; and Tillyard himself points out that the presence of a precostal area in Brongniart's figure "clearly indicates the true Protodonate character of the genus." Tillyard, however, seems not to have considered Lameere's important revision of the Commentry fossils which was based upon his examination of Brongniart's types. For Lameere states that *Campyloptera* "is a Megasecopteran; *there is neither a precostal space nor intercalated sectors.*[3] The fossil is unfortunately too poor to determine its generic affinities." In view of this observation I exclude *Campyloptera* from the Protodonata, and I fail to see how we can regard it as evidence of the descent of the Protodonata from the Megasecoptera.

In the Wellington shales of Kansas both the Meganeuridae and the Protagriidae are represented, the former by three genera and five species, the latter by a single genus and species.

MEGANEURIDAE.

Typus Sellards.

Typus Sellards, this Journal, **22**, 249-258, 1906.
Typus Sellards, ibid., **27**, 157, 1909.
Typus Tillyard, ibid., **10**, 49, 1925.

Large insects, with an expanse of about 25 cm. Fore wing: Sc terminating on the costa a little beyond the middle of the wing; R1 extending to the apex; R3 originating at about the middle of the wing; obsolescent portions of Cu1 present at base; MA branched; oblique vein AC hardly differentiated from the cross-veins. Hind wing: much broader basally than the fore wing and a little longer, with a nearly identical venation.

---

[3] The italics are mine.

Typus permianus Sellards.

Fig. 1, *2*; Fig. 2, *1* and *2*.

Typus permianus Sellards, this Journal, **22**, 249-258, 1906.
Typus permianus Tillyard, ibid., **10**, 49-52, 1925.
Typus permianus Handlirsch, Denk. Akad. Wissen. Wien, Math-natur. Kl., **96**, 62, 1919.

Fore wing: length, 9-10 cm. Anterior margin very slightly concave, apex rather pointed; posterior margin markedly convex, the wing being broadest at about the middle. Precostal space short, not extending distad of the first cross-vein between Sc and C. Costa serrated for about half its length; Sc very remote from costa at base, converging toward it and meeting it a little beyond the middle of the wing. R+M curved at base; Rs+M diverging from R1 at about one-fourth the wing length from base; R1 approaching close to Sc near the middle of the wing, then diverging from it and continuing parallel to it up to the apex; Rs straight until its division into R2 and R3+4 at middle of wing; MA diverging posteriorly just after its origin, then continuing parallel to Rs; R4+5 undivided; R2+3 dividing into R2a, R2b and R3. Cu1 a weak, sigmoidal vein at the very base of the wing; Cu2 well developed and strongly arched; 1A also arched, but with a number of distal branches; 2A diverging from 1A a little basad of the origin of Rs. Cross-veins very numerous.

Hind wing: slightly shorter than the fore wing and much broader basally; anal area much enlarged; costal margin almost straight; apex pointed; posterior margin slightly convex, the wing being broadest near the base, about at the level of the origin of Rs; precostal area with a basal protuberance. Venation similar to that of the fore wing, differing only in that Rs+AM diverges from R nearer to the base, MA possesses fewer distal branches, and the arching of Cu2 is more pronounced.

Little of the body is known; the type specimen shows a rounded head, 5 mm. long, 8 mm. wide; and a slender thorax, 20 mm. long, 6.5 mm. wide.

Holotype.—No. 630, Sellards collection.

This interesting insect was described by Sellards from a magnificent specimen consisting of most of all four wings, as shown in Fig. 1, *2*. Dr. Sellards' description, although complete enough for the time when it was published, does not include any of the details which we now recognize as being most significant in the taxonomy of the Odonate insects.

Only a small fragment of a hind wing, consisting of part of the anal area, was secured by Dr. Dunbar for the Yale collection, so that Tillyard was not able to examine a good specimen of this species. In the Harvard collection there are, aside from unimportant fragments, six specimens of this species: No. 3052ab is the obverse and reverse of the basal two-thirds of a fore wing, exclusive of the anal area; No. 3050 and 3051ab are splendidly preserved bases of the hind wing, each about a third of the wing-length; Nos. 3053ab, 3054ab, and 3055ab are specimens of the anal area and surrounding regions (all specimens collected by F. M. Carpenter).

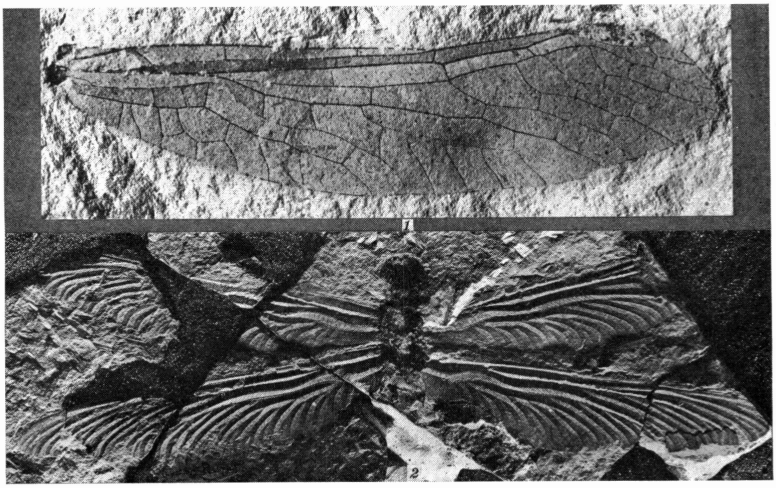

Fig. 1.

1. Photograph of wing of *Ditaxineura anomalostigma* Till., specimen No. 3046a, Mus. Comp. Zoölogy.
2. Photograph of *Typus permianus* Sell., type specimen No. 630 Sellards collection.

In addition to these fossils, I have also examined and photographed Dr. Sellards' type specimen, so that I have been able to present a complete account of the venation of this insect. There is no sign of the concave remnant of MP or of the membrule which are found in *Megatypus;* but the reduced M5 is identical in both genera. In Tillyard's figure of the Yale specimen of *T. permianus* (showing most of the anal area) the anal crossing is represented as an oblique vein, much like a cross-vein at a slant; but as a matter of fact the obliquity of this vein is quite variable. In the hind wing of Sellards' type and in specimen No. 3051ab (hind wing), as well as in No. 3051ab (fore wing), there are *two* such oblique veins here, instead of one; in the fore wing of the type and in specimen No. 3050ab (hind wing) there is only a single, slightly oblique vein here. The presence of two such veins in some specimens is especially interesting and has direct bearing on the question of the nature of the anal crossing, as I shall show later.

Megatypus Tillyard.

Megatypus Tillyard, this Journal, **10**, 52, 1925.

This genus was established for two well-defined species, *M. schucherti* Till. and *M. ingentissimus* Till. The first species was represented in the Yale collection by a nearly complete hind wing and a small fragment of a fore wing; in the Harvard collection I find only a basal piece of a fore wing (No. 3048), similar in venation to the hind wing, but somewhat narrower. *M. ingentissimus* Till. is known only from a fragment of the apical part of the hind wing, the type specimen in the Yale collection. There are no fossils of this species in the Harvard collection or in the Sellards collection. Tillyard's discussion of *Megatypus* is so complete that nothing can be added to it.

Oligotypus, new genus.

Medium-sized insects related to *Typus.* Fore wing: Sc terminating on the costal margin a short distance beyond the middle of the wing; R1 joining the costa well before the apex; obsolescent portions of MP present at the base of the wing; MA unbranched; "anal crossing" entirely unspecialized as an oblique vein. The hind wing is not known.

Genotype: *Oligotypus tillyardi,* new species.

Oligotypus tillyardi, new species.

Fig. 2, 3.

Described from a nearly complete fore wing, perfectly preserved. Length, 50 mm., width, 11 mm. Anterior margin concave; apex pointed; posterior margin markedly convex; precostal area not preserved; costa serrated, only one-third its length; Sc very remote from costa at base, but fusing with it at about two-

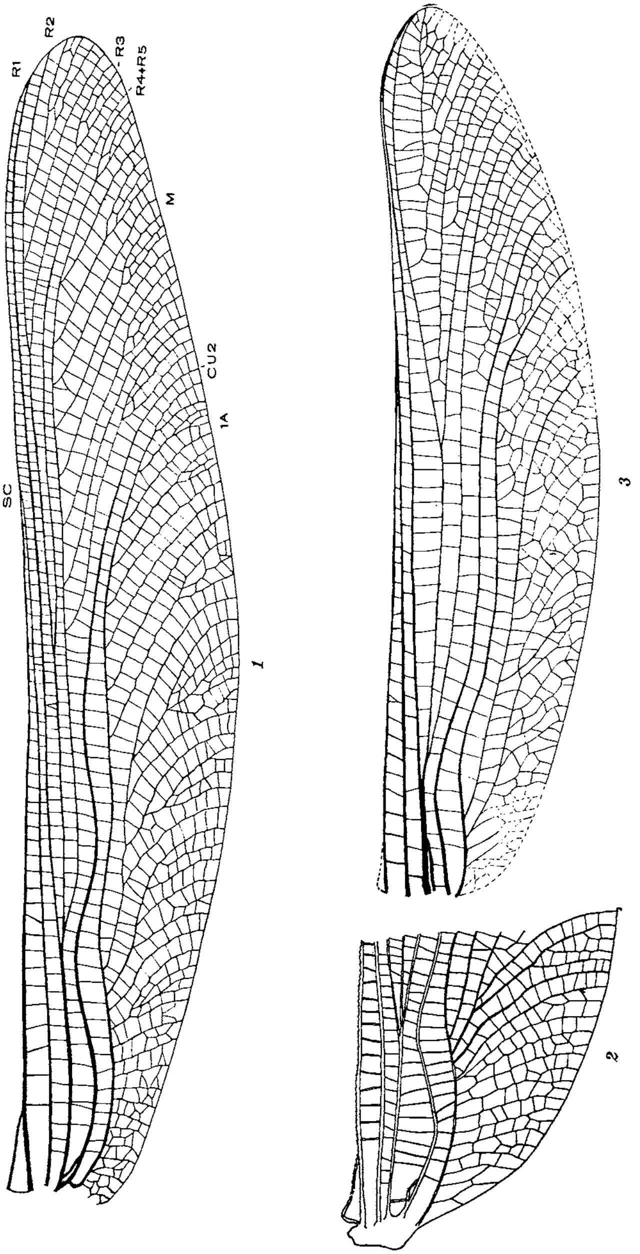

Fig. 2.

1. Fore wing of *Typus permianus* Sell.
2. Base of hind wing of *T. permianus* Sell.
3. Fore wing of *Oligotypus tillyardi*, n. sp.

thirds the wing length from the base; R+M straight at base; Rs+M diverging from R1 close to the base of the wing; R1 nearly parallel to Sc at first, then continuing parallel to the anterior margin until it terminates on the costa near the apex; Rs diverging downward from R1 near the middle of the wing, so that the space between these veins is unusually wide; Rs dividing into R2+3 and R4+5 at the middle of the wing; R2+3 at first diverges upwards and then terminates at the very apex; R4+5 appearing as a continuation of the stem of Rs, terminating on the posterior margin; MA is gently undulated, and between it and Cu2 there are several rows of cellules; Cu2 well developed and strongly undulated; 1A running very nearly parallel to Cu2; 2A quite straight, arising from 1A at the base of the wing and sending off a few branches to the posterior margin; 3A also present and well developed. The cross-veins, although strong and distinct, are not so numerous as in *Typus* and *Megatypus.*

Holotype: No. 3049ab, Museum of Comparative Zoölogy, J. W. Wilson, collector. The species is named for Dr. R. J. Tillyard, Entomologist of the Commonwealth of Australia, in recognition of his brilliant researches on recent and fossil insects.

This insect has many interesting features. It is by far the smallest of all the Meganeuridae known, and is second only to *Calvertiella* as the smallest of the Protodonata. It differs from *Typus* by having R1 terminate well before the apex of the wing, and MA unbranched. The remnant of MP at the base of the wing runs parallel to R+M, as in *Megatypus.* The wing is relatively shorter and broader than that of *Typus* or *Megatypus,* Rs and MA originating much nearer to the base than in the other two genera. There is no sign of the so-called anal crossing in *Oligotypus.*

Oligotypus species.

Fig. 3, *3.*

There is another specimen of Protodonata in the Harvard collection which probably belongs to *Oligotypus;* it consists only of the basal third of a fore wing. The long basal and unbranched part of 2A and the relative positions of the preserved parts of the main veins are nearly identical with those of *O. tillyardi.* But the wing must have been much larger, for the preserved area is about twice as large as the corresponding portion of the type of *tillyardi.* However, since the fragment is too small to show any good specific characters, I have not named the species; in all probability additional and more complete fossils of this insect will be found in the future.

ORDER ODONATA.

The order Odonata now consists of more than 2,500 species, which are widely distributed over all regions of the globe, although they are most abundant in the tropics. Structurally, these insects are essentially primitive and they have had a long geological history, which goes back, like that of so many of the other existing orders, to the Lower Permian.

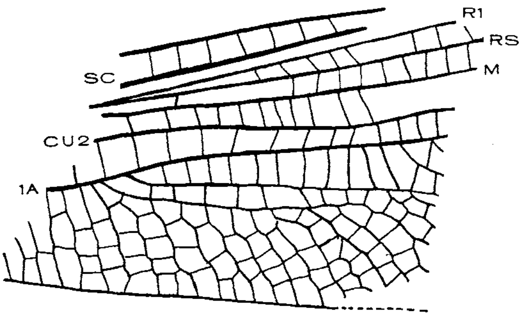

Fig. 3. Drawing of part of wing of *Oligotypus* sp., specimen No. 3041a, Mus. Comp. Zoölogy.

In the study of fossil dragon-flies we are greatly aided by the fact that the wing venation plays an important part in the taxonomy of existing species; indeed, the wings have furnished odonatologists with the most dependable characteristics in the formation of the major groups. But when we enter into a discussion of Odonate wings we at once find ourselves in the midst of a controversy which has been active for nearly eighteen years. This controversy is largely due to the diverse conclusions obtained in attempts to homologize the veins with those found in other insect orders, some of the resulting systems being quite unique and unlike those used for related groups. But as more and more research is carried out on the dragon-fly wings, it becomes increasingly evident that their venation is not so "queer" as previously supposed; and that, as expressed by Martynov, the apparent peculiarities of Odonate venation are rather the peculiarities of interpretation. The controversy which I have mentioned above has largely centered upon the question of the validity of the method which Comstock and Needham used to determine the homology of the veins. This method, which of course is familiar to all entomologists, depended upon the assumption that the main longitudinal veins in the wing of the adult insect "are formed along the courses of trachea" in the immature stages, and that the distribution of the trachea was less specialized than that of the veins in the perfected wing. Consequently, by studying the tracheal systems in the nymphal and pupal wings, one can determine the primitive condition of the venation in a particular group. Applying this method to the wings of the Odonata, Comstock and Needham observed that in the wings of the anisopterous nymphs the trachea corresponding to the radial sector crossed over the first two branches of the media, and they came to the conclusion that the vein Rs behaved in a similar fashion, terminating on the posterior margin between M2 and M3; they did not observe the same phenomenon in the zygopterous nymphs, but nevertheless extended that interpretation to Rs in this suborder. They also believed that the media was a well developed system with at least four branches, and that the cubitus was forked into Cu1 and Cu2. From 1899, when their work was published, until the present time this interpretation has been almost universally accepted.

In 1915 Dr. R. J. Tillyard expressed the first doubts that the radial sector in the Zygoptera crossed over the media as it did in the Anisoptera; from his studies on the trachea of the Zygoptera he concluded instead that there was no true radial sector and that in this suborder Rs of Comstock and Needham was really a branch of the media. But he continued to accept the latters' interpretation of Rs in the Anisoptera until 1922. In that year he began a series of investigations on Odonate venation which led him to believe that in the Anisoptera also the radius was unbranched, Rs of Comstock being termed the median sector; in addition he suggested, without advancing proof, that the vein usually named Cu1 in the Odonata was in fact Cu2 of the other insects. Early in the same year there appeared Lameere's important paper on the wing venation of insects, in which it was demonstrated that the radial sector was not only present in the Odonata, but was even well developed, arising near the base of the wing and sending off the four veins which Tillyard had been calling M1, M2, Ms, and M3; that the true media was represented by a single vein previously termed M4; that Cu1 of the authors was actually Cu2 in the other insects, as Tillyard had previously suggested. In the fall of the same year, 1922, Dr. A. V. Martynov, of the Zoological Museum at Leningrad, read a paper before the Russian Entomological Society on the "Venation of the Odonata and Agnatha."[4] In this work, which was prepared without knowledge of Lameere's researches of that year, Martynov proved that the distribution of the nymphal tracheation is dependent upon the arrangement of the veins as part of their environment. "Comstock and Needham supposed that the tracheation in the wing of a pupa and nymph reflects the primitive state of venation. Therefore one would suppose that in the forms with a venation which resembles especially closely the original plan of venation, we should expect a particularly complete parallelism of the tracheation with the venation. But this is not so. In *Hydropsyche*, which is a small caddis-fly with extremely primitive venation, Comstock and Needham found a complete uncomformity of the tracheation with the venation, which they interpret without regard for the direction of the trachea. These authors were obliged to do the same with the Hymenoptera and Diptera. Why should we rely so blindly upon the tracheation in the case of the dragon-flies . . . . and ignore the data of paleontology . . ? . . . . My investigation of the relation of the venation to the tracheation has led me to the conclusion that the formation of venation occurred under the influence of causes of mechanical character; the tracheation, adapting itself to a newly formed distribution of veins, often changed in a most original way; therefore one can interpret the venation by such an 'indirect' representation of it only with the utmost care." (Martynov, 1924, 150). Martynov then came to exactly the same conclusion as Lameere regarding the homology of the radial sector, the media, and Cu1. More recently Tillyard has also accepted Lameere's idea that Rs is well developed in the Odonata, and he has furnished additional evidence to substantiate the other results, with a few modifications.

At the present time, then, Lameere, Martynov, and Tillyard have agreed that certain changes must be made in the Com-

---

[4] Although written in 1922 this paper was not published until 1924 (Revue Russe d' Entomologie, **18**, (4), 145-172. The whole of this valuable work being in Russian (with the exception of a two-paged summary in French), it has received no recognition from students of wing venation or phylogeny; for this reason I have prepared an English translation of the article to be published in an early issue of Psyche.

stock-Needham interpretation of the Odonate venation: the radial sector is a well developed vein and does not cross over the branches of the media; the media is unbranched and is fused with Rs at the base; Cu1 is absent. I believe that there is another structure in the Odonate wing which has been erroneously interpreted also, not only by Comstock and Needham, but by the others mentioned above; this is the vein called the "anal crossing." The term was originally applied by Tillyard (1914, 168) to the "first cubito-anal cross-vein" of Needham (1903). Tillyard observed that in the nymphs of the Anisoptera the trachea Cu2 and the trachea 1A were fused together basally, 1A diverging from Cu at an angle of about 90 degrees and then separating into its branches (Tillyard, 1914, fig. 2, 169). He also maintained that the "anal vein" of Needham was not the true anal vein but a "secondarily formed bridge-vein from the lower end of AC backwards towards the wing bases." This vein he designated the secondary anal vein, A′. His conception of the nature of AC seems to have been generally accepted by all students of the Odonata, as well as by Lameere and Martynov. Very recently (1928) Tillyard has presented the most elaborate account of the part this structure seems to have played in the evolution of the Odonata; on this explanation rests his theory of the development of the Anisoptera from the Zygoptera. It is impossible to do justice to Tillyard's theory by attempting to reproduce it in a few words; I can only refer the reader to his complete account of it (1928b, 169-171, fig. 10). It will be seen that by this hypothesis Tillyard regards the Anisoptera, in which Cu2 and 1A *appear* to be independent, as a specialization over the Zygoptera, in which 1A is fused basally with Cu2 for some distance from the base. It is obvious that neither Comstock, Martynov, nor Lameere have realized the significance of the accepted interpretation of AC as fully as Tillyard has. These other authors have been led to their conclusions largely through the study of the tracheation of the nymphal wings; Tillyard also introduced the factors of paleontology and phylogeny, so that his outlook on the question is much broader. For my own part, however, I do not believe that either the tracheation of the nymphs or the data of paleontology have proved that AC is a portion of the true anal vein, 1A; on the contrary, for reasons discussed below, I consider the tracheal studies to be as negative as those on the radial sector and the media, and regard the paleontological evidence as positive proof against the accepted understanding of the anal crossing. By this new interpretation the Zygoptera must be looked upon as more highly specialized than the Anisoptera, not as more primitive. To these questions I shall return after the description of the Harvard fossils.

There are two large existing suborders of Odonata, the Anisoptera and Zygoptera. The former is characterized by having the discoidal cell divided into two triangles (h and t); their larvae are stout and breathe by means of tracheal gills in the rectum. This suborder goes back to the middle of the Jurassic. The Zygoptera are distinguished from the foregoing by having an undivided discoidal cell; the larvae are slender and breathe by means of three caudal gills. This group has been found as far back as the Upper Permian.

A third suborder, Anisozygoptera, reached its maximum development during the Mesozoic, but it is supposed to be still existing, represented by a single genus, *Epiophlebia*. The suborder was originally established by Handlirsch (1908) for several species from the Jurassic, as well as for *Epiophlebia*. Tillyard (1917) did not at first accept this suborder, but he subsequently obtained a peculiar dragon-fly larva from the Himalayas, which appeared to have a wing tracheation very similar to the venation of *Epiophlebia* (Tillyard, 1921). Although the nymph lacked the terminal portion of the abdomen, Tillyard believed that it possessed certain characteristics of both Zygoptera and Anisoptera and consequently he recognized Handlirsch's Anisozygoptera.

Now the Mesozoic Anisozygoptera, as originally conceived by Handlirsch, included two distinct types of venation: in one the discoidal cell of the fore wing was identical with that of the hind wing; in the other this cell was much larger and more specialized in the hind wing than in the fore wing. After his study of the Anisozygoptera of the Liassic of England, Tillyard was led to exclude from this suborder the species with similar discoidal cells in the two pairs of wings; these he placed in the Anisoptera. Such a classification seems to be entirely justified and I believe that further restriction is needed. If we examine the wings of the more primitive Jurassic Anisozygoptera, we note that the arculus diverges abruptly from R1 and that the discoidal cell is already differentiated. There is, however, no cross-vein joining Cu2 to the arculus and closing the discoidal cell. This elementary condition is found in the fore wing of *Liassophlebia* (Lower Liassic of England), *Tarsophlebiopsis* (Jurassic of England), *Tarsophlebia, Isophlebia* (both Jurassic of Bavaria), and *Solenthemis* (Upper Liassic of Mecklenburg). Only in *Torsophlebia*[5] is the structure of the arculus and discoidal cell of the hind wing similar to that of the fore wing. In the hind wing of *Liassophlebia* there is a cross-vein closing the discoidal cell basally. Unfortunately, the hind wings of the other species with open discoidal cells in the fore wings are not known; probably they possessed a closed discoidal cell. All the other Anisozygoptera (as limited by Tillyard) had the discoidal cell of the fore wing closed, but in these the discoidal cell of the hind wing was divided into two sections or triangles (see *Heterophlebia buckmani* and *H. anglica,* Upper Liassic of England). That is, as previously observed by Tillyard, the hind wing of the Anisozygoptera seems to have been one step ahead of the fore wing in the evolution of the discoidal cell. For this reason, I do not believe that *Epiophlebia,* in which the discoidal cells of both pairs of wings are nearly identical, can belong to this suborder. It seems more likely to be a member of the Zygoptera, or, if the nymph described by Tillyard from Himalayas (*laidlowi*) really is an immature stage of *Epiophlebia*, to represent a new suborder.

Furthermore, I do not consider that there are sufficient facts to show that the Anisozygoptera were intermediate between the Anisoptera and the Zygoptera, as has been generally assumed. On the contrary, I believe that the Anisozygoptera were not related to the Zygoptera but were the annectant group between the Anisoptera and certain very primitive, broad-winged forms of the Lower Permian,—the Protanisoptera described below. To this subject I shall return after a discussion of the fossils themselves.

In addition to these suborders, two others, definitely extinct, have been recognized. The suborder Archizygoptera was established by Handlirsch to include his problematical genus *Protomyrmeleon,* and was also used by Tillyard for *Triassagrion* and *Triassolestes* from Australia, and by Martynov

---

[5] As a matter of fact, however, the discoidal cell of the hind wing of *Tarsophlebia* was probably closed as in *Liassophlebia*. Having seen the specimens on which Hagen based his figures of *Tarsophlebia,* I am convinced that the absence of the discoidal cross-vein in the hind wing is due to lack of preservation.

for several related genera from the Upper Jurassic of Turkestan. Although the exact affinities of these genera are uncertain, there are sufficient data to show that they represent an end branch of the Odonate types and had no part in the evolution of the modern forms. The other suborder, Protozygoptera, was established by Tillyard for *Kennedya* Till., *Opter* Sellards, and *Ditaxineura* Till., from the Wellington shales of Kansas. That the two former genera are of a general zygopterous nature, yet too primitive to be actually included within that suborder, cannot be questioned; but I shall demonstrate below that *Ditaxineura* is utterly different from what Tillyard supposed it to be, and that it is a representative of another suborder. As this paper goes to press, Martynov describes (1930) two other species of zygopterous insects from the Permian (Kazan) of Russia. He places them in the family Kennedyidae, but since they are very poorly preserved and especially since the bases of the wings are unknown, the correctness of this classification is questionable.

The following species of Odonata have been found in the Lower Permian of Kansas:

SUBORDER PROTOZYGOPTERA.

Damsel-flies with slender, petiolate wings, two or three antenodals and only a few postnodals, widely spaced; costal margin serrated; nodus incomplete, situated basad of the middle of the wing; subnodus absent; media and radius incompletely fused basally; arculus present, RS+MA diverging from R1 more or less abruptly; discoidal cell open basally; MA joined to Cu2 by a short stout cross-vein (mcu), forming the distal wall of the discoidal cell; Cu1 either entirely absent or present in a rudimentary state at the base of the wing, close to Cu2; Cu2 and 1A fused together for the length of the petiole, diverging just below the point of separation of Rs and MA; subquadrangular cell closed; anal crossing present or absent; pterostigma present, well developed; Rs with 5 branches; MA, Cu2, and 1A unbranched.

It should be noted that the above description differs somewhat from that originally given by Tillyard, e.g., in the number of antenodals. These changes have been made necessary by the discovery of a new species belonging to this suborder, but differing in minor points from *Kennedya*.

KENNEDYIDAE.

Wings very slender, the petiole extending nearly up to the arculus; pterostigma narrow, with parallel sides; main veins regular; postnodals not in line with the cross-veins below.

Genotype: *Kennedya mirabilis* Till.

Kennedya Tillyard.

Tillyard, this Journal, **10**, 63-65, 1925.

Genotype: *Kennedya mirabilis* Till.

Kennedya mirabilis Tillyard.

Fig. 4, 5.

Kennedya mirabilis Tillyard, this Journal, **10**, 66-72, 1925.

This species was based upon two fragments, one consisting of the basal half of a wing and the other of a distal half; but the two fossils were obviously not pieces of the same individual wing. In order to determine whether these fossils represented one or two species, Tillyard made careful, enlarged drawings of the veins; he found that when the drawings were placed together, with a part of the middle slightly overlapping, they fitted almost perfectly, each vein in its place. The only discrepancy was in the width of the space between C and R1, which was slightly broader in the distal fragments than in the basal one. From an examination of the wings of recent Zygoptera, Tillyard found that in most cases this space was slightly broader in the fore wing than in the hind, and so concluded that the distal fragment was a part of a fore wing, and the basal piece a portion of a hind wing of the same species. Whether or not these two fossils represent different parts of the same species is, of course, still open to question. But for the purposes of phylogeny the issue is not of the least significance, for even if two species are represented, these were obviously closely related, and the differences which may have existed between the species were of a minor specific nature only, not of subordinal or even family rank. Regarding these fossils as a single species, we have a wing about 44 mm. long and 5.8 mm. wide. This, as Tillyard pointed out, makes a more slender wing than that possessed by any other known Odonatan. The anterior margin of the petiole is straight; at the nodus there is a pronounced indentation, but the rest of the anterior margin is also very straight; the apex is pointed, and the posterior margin gently rounded; between Sc and R+M there are two short cross-veins, just below the antenodals (Ax1 and Ax2); between R and Sc another cross-vein, just basad to the nodus; between R1 and R2–5 there are 4 cross-

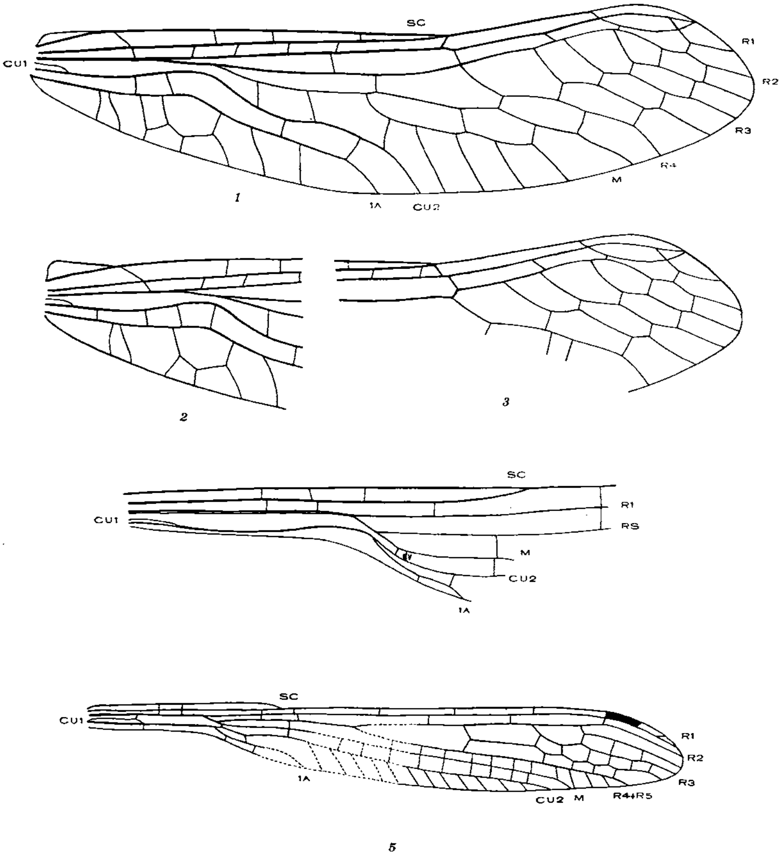

Fig. 4.

1. Wing of *Ditaxineura anomalostigma* Till., specimen No. 3046a, Mus. Comp. Zoölogy.
2. Basal part of wing of *D. anomalostigma* Till., specimen No. 3045a, Mus. Comp. Zoölogy.
3. Distal portion of wing of *D. anomalostigma* Till., specimen No. 3044a, Mus. Comp. Zoölogy.
4. Wing of *Progoneura minuta*, n. sp.
5. Wing of *Kennedya mirabilis* Till. (after Tillyard, with restored parts modified).

veins, widely spaced; the short remnant of Cu1 extends from the base to the middle of the petiole, terminating on Cu2+1A, just above AC. R3 arises well towards the apex of the wing; between it and R2 is a concave intercalated vein, and between it and R4+5 is another such vein; between MA and R4+5 there is a series of cross-veins, corresponding in position to a second series between Cu2 and MA.

The wing formed by placing these two fossils together is complete except for a small portion along the posterior margin, near the termination of 1A. Tillyard was therefore unable to determine just how far 1A extended. In his restoration of the wing, he showed 1A extending about half the wing length, but he admitted that this might be incorrect: "there is, on the one hand, the evidence of *Permagrion* in favor of it; but on the other hand the formation shown in the larval wing tracheation of *Hemiphlebia* points much more strongly to the existence of an original very short 1A, followed by a much longer Cu2 with numerous descending branches . . . . . The point must be left unsettled, pending the discovery of further fossil evidence." Although the Harvard collection contains no specimens of this species, it does include a related species, showing 1A complete. Here this vein is very short, as in the nymph of *Hemiphlebia*. I consider this to be conclusive enough to require a modification in Tillyard's restoration so that 1A terminates much as in the new species.

The type specimens of *K. mirabilis* are Nos. 5006a and 5005 in the Peabody Museum, Yale University. Since Tillyard has given an admirable discussion of the phylogenetic significance of this fossil, there is no need to repeat the subject here.

Opter Sellards.

Opter Sellards, this Journal, **27**, 151, 1909.
Opter Tillyard, ibid., **10**, 72, 1925.

Damsel-flies allied to *Kennedya,* but with a broader wing, longer arculus, and shorter subquadrangular cell.

Genotype: *Opter brongniarti* Sellards.

Opter brongniarti Sellards.

Opter brongniarti Sellards, this Journal, **27**, 151, 1909.
Opter brongniarti Tillyard, ibid., **10**, 72, 1925.

Based upon a poorly preserved specimen consisting of the basal third of a wing. Length of fragment, 9.0 mm.; width, 2.5 mm. The anterior margin is straight; there is only a slight indentation at the nodus; subcostal space narrow; only one antenodal is preserved, close to the nodus; 3 postnodals present, much nearer to the nodus and closer together than in *Kennedya;* 1A+Cu2 remote from the stem of R+M. From the structure of the preserved portion of this fossil one would assume that the whole wing would be about the same size as *K. mirabilis,* though perhaps a little longer and broader.

Holotype: No. 1286, Sellards collection.

This insect was originally placed by Sellards in the extinct order Megasecoptera. The poorly preserved and fragmentary condition of the fossil prevented him from recognizing the true position of the insect, but the allied fossils in the Yale collection convinced Tillyard that it really belonged to the Odonata. Through Dr. Sellards' kindness I have been able to examine and photograph his type and to substantiate Tillyard's conclusion. Sellards' figure of the fossil is not correct in showing the subcosta extending the full length of the fragment, parallel to the costa; instead, this vein terminates much as in *Kennedya.* Sellards did not show 1A in his figure, but it is undoubtedly, though faintly, preserved in the wing. It is perfectly possible that this fossil may be the hind wing of *Kennedya,* for in the Anisozygoptera the arculus and related structures were quite different in the fore and hind wings. But until this relationship can be definitely proved by the discovery of a fossil with both wings attached, it is better to consider *O. brongniarti* as a distinct species.

Progoneura, new genus.

Allied to *Kennedya.* Nodus much basad of the middle of the wing, formed only by Sc turning upward to meet the costa, there being no break in the anterior margin; 3 antenodals; arculus with a very long stem; Rs arising almost at the middle of the arculus, MA continuing the stem of the arculus; Cu2 and 1A diverging directly below the point of origin of Rs; subquadrangle (sq) very long and narrow; 1A+Cu2 strongly undulated in the petiole.

Genotype: *Progoneura minuta,* new species.

Progoneura minuta, new species.

Fig. 4, *4*.

Based upon a well preserved basal half of a wing. Length of fragment, 8.0 mm.; greatest width, 2.0 mm. Anterior margin straight or nearly so; the three antenodals equally spaced; Ax1 and Ax3 perpendicular to the costa; Ax2 oblique; 2 cross-veins between R+M and Sc, one just a little distad of Ax1, the other a little distad of Ax2; Sc bends upward gently to meet the costal margin; half-way between Ax3 and the nodus, there is a stout cross-vein joining Sc to R1; only one postnodal preserved and this is well beyond the nodus; R+M straight in the petiole, about as far from Sc as Sc is from the costa; at the beginning of the arculus R is slightly indented; R1 straight basally but bending upward very slightly after the termination of Sc; arculus very straight; Rs parallel to R1 basally and about as far from R1 as it is from MA; a single cross-vein between R1 and Rs, just below the first postnodal; between Rs and MA another cross-vein; Cu1 faintly preserved as a thin chitinous line at the very base of the wing; Cu2+1A remote from the posterior margin at the base of the petiole, but at about the middle of the petiole it almost touches the posterior margin, then it curves upward so that it almost touches the arculus; Cu2 continues the downward curve of the stem of Cu2+1A beyond the arculus; mcu cross-vein short, placed as far distad from the point of origin of MA as the origin of Ma is from the origin of Rs; 1A diverges from Cu2 directly below the origin of MA and then terminates on the posterior margin a short distance further on; 1A joined to the hind margin by a cross-vein midway between its origin and termination; the subquadrangle cell is exceedingly slender, the distal wall close to the end of 1A, and the anterior and posterior walls distinctly curved.

Holotype: No. 3042ab, Museum of Comparative Zoölogy. Collector, F. M. Carpenter.

That portion of *Kennedya mirabilis* which corresponds to the preserved part of *P. minuta* is 19 mm. long and 3.8 mm. wide. Since these dimensions are twice those of *minuta* we are justified in concluding that the whole wing of the latter must have been about half the size of that of *mirabilis*, or approximately 21 mm. long and 3 mm. wide. Accordingly, this fossil ranks with the smallest of the known damsel-flies, although some of the recent Australian species are even smaller. But what a great contrast *Progoneura* must have been to its coexistent neighbor, *Megatypus ingentissimus,* with a wing length of over 250 mm.!

In comparing the wings of *Progoneura* and *Kennedya,* we find several important differences:

1. The nodus in *Progoneura* is obviously much more primitive than that of *Kennedya.* Tillyard has demonstrated that the nodus of the Odonata consists of three parts: a) the costal break, b) the small distal part of the subcosta leading from this break to c), the nodal cross-vein. In *Kennedya* there is a decided break in the costal margin at the termination of Sc, and the nodal cross-vein is also present between Sc and R1 just basad of the nodus. Hence, all three of these structures are present in *Kennedya.* In *Progoneura,* on the other hand, there is absolutely no break in the costal margin, Sc turning upward gradually to merge with the costa; the only cross-vein between Sc and R1 is far basad of the termination of Sc. With regard to all of the above points, therefore, the nodus of Progoneura is more primitive than that of *Kennedya;* it is, in fact, the most primitive type of nodus which has been found in the Odonata, recent and fossil. The nearest approach is found in *Triassagrion,* from Australia.

2. While the origin of the arculus is essentially the same in both of these genera, there are a few significant differences in structure. In *Progoneura* R1 continues as a straight vein, instead of bending upward directly after its origin, as it does in *Kennedya.* More interesting, however, is the fact that in *Progoneura* MA is very little affected by the cross-vein, mcu, for it continues the stem of the arculus almost in a uniform curve. In *Kennedya* MA is pulled downward by the cross-vein, so that there is a sharp bend in MA at this point; the intensity of this bend increases as we ascend the scale of the existing genera of Zygoptera. On the whole, therefore, I consider that the arculus of *Progoneura* is more primitive than that of *Kennedya.*

3. Perhaps the most striking difference is in the stem of the composite vein, Cu2+1A, in the petiole. In *Kennedya* the vein is very close[6] to the posterior margin throughout the entire petiole; just a suspicion of an upward bend can be discerned near the arculus. In *Progoneura* this vein is undulated to a

---

[6] Tillyard's figures of *Kennedya* in this Journal, **10**, 64, and in the Records of the Indian Museum, **30**, 163, differ in a few details. The former is far more accurate.

marked degree, almost touching the posterior margin of the petiole at its mid point, and then rising again upwards towards the arculus. No recent or fossil Zygopteran has this vein similarly waved within the petiole, but most of the Protodonata, Anisozygoptera and Anisoptera, as well as *Ditaxineura,* have this same undulation of Cu2 and 1A. As I shall demonstrate later, this undulation in the ancient forms of Odonata was exaggerated in the evolutionary progression and was largely responsible for the unusual development of venational structure at the base of the wings in Anisoptera.

From the above discussion it is clear that on the whole *Progoneura* is more primitive than *Kennedya,* and consequently the most primitive of all the known Odonata with petiolate wings.

PROTANISOPTERA, new suborder.

Dragon-flies, with moderately broad fore wings, 4 antenodals, no postnodals; precostal area present; nodus incomplete, situated beyond mid wing; MA attached to R weakly at the base; arculus very incomplete; no discoidal cell; MA with a posterior, convex, interpolated branch; Cu1 present in the form of a weak chitinous line attached to Cu2; Cu2 and 1A separate for their entire lengths; pterostigma present; Rs with 5 branches, of which three are the original concave branches of Rs, and the others convex interpolated branches; cross-veins very few.

DITAXINEURIDAE.

Anterior margin with a distinct break at the nodus; pterosstigma slender, rounded posteriorly; main veins more or less "zigzagged," especially the branches of Rs; antenodals widely spaced; nodal cross-vein at the termination of Sc; R4+5 arising directly beneath nodus; R1 terminating at about the apex of the wing, beyond the pterostigma.

Ditaxineura Tillyard.

Ditaxineura Tillyard, this Journal 11, 69, 1926.

Nodus a little distad of mid wing; 5 oblique, short crossveins between R1 and Sc, basad of the nodus; Rs extending close to nodus and joined to it by a short cross-vein; pterostigma about three times as long as wide; posterior branch of MA with several branchlets terminating on the hind margin; Cu2 extending to near the middle of the wing; 1A terminating close to Cu2; arculus diverging off only very slightly from R+M; R3 and MA arising almost as a bifurcation.

Ditaxineura anomalostigma Tillyard.

Fig. 1, *1*, Fig. 4, *1, 2, 3.*

Ditaxineura anomalostigma Tillyard, this Journal **11**, 71-73, 1926.

Length of wing (fore): 2.1 mm.; maximum width (just beyond nodus) 5 mm.; precostal area small, not extending as far distally as the first antenodal (Ax1); anterior margin from the base to the nodus slightly convex; at the nodus the margin takes an abrupt turn forwards and then continues straight up to the pterostigma; from the base of the pterostigma to the apex the margin is regularly rounded; from the apex to the base, the posterior margin traces a smooth curve; Ax1 very oblique, with the top nearer to the base; Ax2, Ax3, and Ax4, perpendicular to Sc, the space between Ax4 and Ax3 nearly twice that between Ax2 and Ax3; Sc straight; a short, slightly oblique cross-vein joins Sc to R+M; the cross-veins between Sc and R1 are more oblique and inclined in the opposite direction; the nodal cross-vein is strong and oblique, the angle of its inclination being variable; R+M straight, R1 continuing the stem in a straight line to the nodal cross-vein, where it makes a slight curve posteriorly and then continues parallel to the anterior margin until it reaches the pterostigma; it passes through the pterostigma and terminates near the apex of the wing; M+Rs arises just a little distad of Ax1 and continues for a short distance *almost parallel to the longitudinal axis of the wing;* just below Ax2 it divides into Rs and MA; Rs is unbranched up to the region of the nodus, where R4 separates from R2+3; R3 diverges from R2 midway between the nodus and the pterostigma; R2 approaches close to the pterostigma and then terminates at the very apex of the wings; there is a concave, intercalated vein between R2 and R3, and another one between R3 and R4; between Rs and R1 there is a long cross-vein, well basad of the nodus; just at the origin of R4 there is another cross-vein joining R1 to Rs and corresponding to the subnodus of the recent Odonata; there are two cross-veins joining R1 to R2, one near the origin of

R3, the other near the apex of the wing; R2 is joined to the pterostigma by a short cross-vein; between consecutive branches of Rs there are only two cross-veins; MA unbranched for some distance after its origin, the posterior concave branch diverging just below Ax4; MA itself terminating directly on the posterior margin; the posterior branch sending off 4 long branchlets to the margin; MA joined to Rs by a long cross-vein a little distad of the level of Ax4; Cu1 extending for about one-half the length of the precostal area; Cu2 straight basally, then rising upward into a broad curve close to the arculus, after which it turns posteriorly; below Ax3 it again curves anteriorly, only to turn back shortly after and terminate on the margin; between Cu2 and MA there are two long, well developed cross-veins; 1A diverges from Cu2 at the base, then continues more or less parallel to it; between Cu2 and 1A there are 4 cross-veins, two close together near the arculus and the other two more distad; between 1A and the posterior margin there are 5 slightly irregular cross-veins, and two other very irregular ones, joined together and forming a primitive anal loop.

Holotype: No. 5054a, Peabody Museum; counterpart, No. 5054b, Cawthron Institute. Unfortunately, the holotype fossil, the only specimen of this species in the Yale collection, is but a distal fragment of a wing. One naturally regrets that Tillyard should have attempted to describe a species from such an incomplete specimen, especially since the species turns out to be one of the most remarkable and unexpected fossil insects ever discovered.

The foregoing specific description is based on specimen No. 3046ab in the Harvard collection. This fossil consists of a complete wing, preserved with the perfection that only the Elmo limestone has given (see Fig. 1, *1*). There are also three other Harvard specimens which belong to this same species. Each one possesses a few venational traits not found in the others, but these peculiarities are of such a nature that they can only be regarded as individual variations. Some of these variations, however, are very interesting and are worthy of detailed consideration. Specimen No. 3044 consists of nearly the whole wing, only the posterior margin being obliterated. The most obvious differences between the venation of this fossil and that of No. 3046 are as follows:

1. The pre-costal area is somewhat larger and more projecting.

2. Ax2 and Ax3 are slightly oblique.
3. The basal cross-vein between R+M and Sc, just below Ax1, is more oblique than in the previous fossil.
4. Between 1A and Cu2, joining the peaks of the upward curves, there is a long cross-vein; another cross-vein unites Cu2 to 1A near the base of the wing. This latter cross-vein occupies the same position as the so-called anal crossing in the Anisoptera, but it is not found in any of the other specimens of *Ditaxineura.*
5. There are several differences in the cross-veins forming the anal loop.
6. The most interesting difference is at the nodus. The nodal cross-vein is inclined in the opposite direction than it is in No. 3046, and directly below it the subnodal cross-vein stands at the same slant, so that these two cross-veins form a straight line, as in modern Anisoptera. R4 diverges from R2+3 exactly at the subnodus.

Specimen No. 3045ab, consisting of the apical two-thirds of a fore wing, differs as follows:

1. The intercalated vein IR2 arises from R2 much more basally than in No. 3046; and as a consequence R3 joins R2 basad of the short cross-vein between R1 and Rs.
2. The nodal cross-vein is situated as in No. 3044, but the subnodal vein is more distad, so that these two cross-veins do not form a straight line. Also there is a deep indentation in Rs close to the origin of R4+5; this gives the appearance of two subnodal veins. An extra cross-vein, not found in the other fossils, joins R1 to Sc very close to the nodus.

Specimen No. 3043 consists only of the distal part of the wing, nearly the same area as the Yale holotype. But even here there are a few differences: IR2 meets R2 as in the previous fossil, but R3 meets R2 as in No. 3046; also between IRs and R4+5 there are three cross-veins, instead of two.

I have already called attention to the instability of the venation of the Wellington Mecoptera in Part 1 of this series, and Tillyard has demonstrated that great variability also occurs in the Protoperlaria. Now we find a similar variation in the few specimens of the Odonata of the same period. These variations are not sufficient to rank as specific characteristics, yet they are much more pronounced than in the recent Odonata.

The phylogenetic significance of *Ditaxineura* will be discussed below, but at this point I wish to call attention to the similarities and differences between the Protanisoptera (as represented by *Ditaxineura*) and the Protozygoptera. These groups possess two important features in common: a short remnant of Cu1 at the base of the wing; and five branches on Rs, of which two are intercalated. Both of these structures have played an important part in the evolution of the Odonata, and their common presence and nearly identical formation show that the Protozygoptera and Protanisoptera were more closely allied than one might suppose from the general appearance of the wings. But there are nevertheless striking differences between these suborders, as follows:

1. In the Protanisoptera the nodus is well developed, with a distinct nodal cross-vein; in the Protozygoptera the nodus is extremely primitive, without a specialized nodal cross-vein. In *Ditaxineura* we also find the subnodus, which is entirely absent in *Progoneura* and *Kennedya*. There can be no doubt therefore that the nodal region of the Protanisoptera is much more highly developed than that of the Protozygoptera.
2. In the Protanisoptera there is a strongly formed precostal area, but in the Protozygoptera this is absent. The existence of such a structure in *Ditaxineura* is unexpected, for it has not previously been found similarly developed in any Odonatan. As we have mentioned above, however, the precostal area was well developed in most of the Protodonata. The presence of this area in *Ditaxineura* indicates that the broadened costal margin at the base of the wing in *Petalura* and its allies is really the remnant of the precostal area. I am inclined to the conclusion also that the common ancestor of the Protodonata and Odonata possessed this same structure, which has disappeared in the higher Anisoptera, and of course in the Zygoptera during the process of petiolation. If this was the case, then the precostal space of *Ditaxineura* is a primitive feature lost in the Protozygoptera.
3. In the Protanisoptera there are four antenodals, whereas in *Kennedya* there are two, and in *Progoneura* three. Tillyard regards the condition found in *Kennedya* as the most primitive, but I do not believe that there is sufficient evidence to warrant this conclusion. At any rate the difference of one antenodal between *Ditaxineura* and *Progoneura* is not any indication of the relative position of the two suborders.
4. In *Ditaxineura* there are no postnodals; in the Protozygoptera there are four. But I consider that the number of postnodals is closely associated with the number of cross-veins in the entire wing. Tillyard has pointed out that as

we go down the genera of Odonata we find that the number of closed cells decreases. Thus he found that in the zygopterous *Permagrion* (Upper Permian) there were 162 closed cells and 8 postnodals; in *Kennedya* there were about 100 cells and 4 postnodals. In *Ditaxineura* we find only 60 cells and no postnodals! This certainly indicates that the cross-vein system of *Ditaxineura* is much more primitive than that of the Protozygoptera.

5. The arculus of *Ditaxineura* is extremely simple, hardly an arculus at all; and there is no specialized discoidal cross-vein. In both *Kennedya* and *Progoneura* the arculus, although more primitive than that of the true Zygoptera, arises with usual abruptness; and there is a definite, fixed discoidal cross-vein. Hence the arculus system of *Ditaxineura* is far and away the most primitive of all.

6. In the Protanisoptera we find a concave posterior branch on MA. This is not, of course, the posterior media of Lameere's system of nomenclature, for whenever that vein is present, it originates at the very base of the wing before the origin of RS+MA. This concave branch (IMA) of the media in *Ditaxineura* is an intercalated vein like IR2 and IR3; like these two veins also it is represented in the recent Anisoptera by a weak, "zigzagged" vein. But whereas both IR2 and IR3 are usually found in the Zygoptera, this IMA is absent in the Permian damsel-flies. Whether or not the presence of this branch is a primitive condition in the Odonata as a whole may consequently be open to question. I suspect that it is a primitive trait and believe that the branch existed in the original zygopterous forms before they reached the high degree of petiolation exemplified by *Kennedya*.

7. Finally, in the Protanisoptera the wing is broad at the base, Cu2 and 1A being widely separated for their entire lengths; in the Protozygoptera the wing is narrowly petiolate, Cu2 and 1A being fused for the length of the petiole and up to the arculus. We meet these same conditions in the Anisoptera and Zygoptera, respectively. Now as I have explained above, Tillyard and the others who have worked on Odonate venation do not regard 1A in the Anisoptera and Anisozygoptera as extending to the base of the wing in the form of a free vein. They believe that it is fused with Cu2 for some distance at the base of the wing, and that its abrupt departure from Cu2 forms the so-called "anal crossing." The straight vein (A′) at the base, appearing as the continuation of 1A,

they consider to be a secondary development. Tillyard, in fact, argues that this A′ has actually been formed from a short cross-vein in the Zygopteran wing (see his "Evolution of the Odonata," p. 170). In this way he derives the anisopterous from the zygopterous venation, making the petiolate wing the precursor of the normally broad wing. His whole theory of the evolution of the Odonata, deriving the Anisoptera from the Zygoptera, is therefore based upon the belief that 1A is fused with Cu2 in the Anisoptera and Anisozygoptera. This latter conception of the relation between Cu2 and 1A depends entirely upon the nature of the nymphal tracheation for its support. In the wing buds of the Anisoptera the trachea 1A is fused with the trachea Cu2 for some distance; it diverges off abruptly, however, forming the part known as the anal crossing, AC, and then divides into its several branches. Tillyard, Comstock, and the others have assumed that the anal vein of the adult wing followed the course of the anal trachea and was hence fused with Cu2 at the base. This is precisely the same method which led Comstock and Needham to the conclusion that Rs in the Odonata crossed over M1 and M2; it is the same method which Tillyard, Lameere, and the others have rejected, because they found that the tracheation of the radial sector had become specialized independently of the venation, and the venation modified independently of the tracheation. Is it not possible, then, that similar changes have taken place in the anal vein? This was the original opinion of Needham, who believed that in the anisopterous nymphs the trachea 1A became fused with Cu2 at the base, diverging away from it along the "cubito-anal cross-vein,"—the "anal crossing" of Tillyard's nomenclature. According to this explanation the anal crossing was originally nothing but a cross-vein, similar to the others in that region of the wing; secondarily, the path of the cross-vein was utilized by the anal trachea as it diverged from Cu2. However, I do not insist at this point that this interpretation is the correct one; I merely wish to point out that any conclusions based solely upon the assumption that the veins follow the nymphal tracheas are apt to be hasty. As Martynov has expressed it, "One can interpret the venation by such an 'indirect' representation of it only with the utmost care."

Now can we interpret the anal vein of *Ditaxineura* as it has been interpreted in the Anisoptera? Is the basal part of the apparent 1A in reality a secondary vein, A′, and is the corresponding part of the true 1A fused with Cu2? A moment's consideration will show that all of these questions must be answered negatively. Since *Ditaxineura* is too primitive to be derived from the Protozygoptera or Zygoptera, then the apparent basal part of 1A (= A′) could not have been derived from a cross-vein in the wing of either of these two latter suborders. Moreover, if any one of the veins between 1A and Cu2 at the base were actually the part of 1A bending downward from Cu2, we should expect to find this vein very oblique in such a primitive wing, and stronger than the other cross-veins in the wing. But such is not the case. In two of the specimens of *Ditaxineura anomalostigma* there are two veins joining 1A and Cu2 at the base; neither of these is especially oblique or stronger than the other. In the third specimen there is an additional vein between 1A and Cu2, much closer to the base of the wing; this is also developed as the others and is perpendicularly placed. I therefore believe that in *Ditaxineura* the anal vein is free from Cu2 for its entire length; and that all the veins between 1A and Cu2 are typical cross-veins. The application of this interpretation to the Anisozygoptera and Anisoptera will be discussed later.

PHYLOGENETIC RESULTS.

We may divide our discussion of the phylogeny of the Odonata into two parts, one dealing with the origin of the order and the other with the evolution within the order. Naturally enough, our data on the former subject are very meagre and largely dependent upon the results which we obtain by the study of the second topic. For this reason, therefore, I propose to reverse the natural order, by considering first the phylogeny within the Odonata.

Two views have been advanced concerning the relationship of the Zygoptera, Anisozygoptera, and Anisoptera. The older of these, proposed by Handlirsch (1908), contends that the Anisozygoptera were the common stem from which both the Anisoptera and Zygoptera were derived. This theory has been accepted by most entomologists for the past twenty years. However, the more recent discovery of true Zygoptera in the Upper Permian requires us to reject this theory, for these Permian damsel-flies are more primitive than any of the Anisozygoptera. The presence of the Protozygoptera in the Lower Permian is an added factor to be considered in this respect. The other view was set forth by Tillyard in his recent paper on the evolution of the Odonata (1928). He derives the whole series of Odonata from the Protozygoptera, the latter giving rise to the true Zygoptera, which in turn produced the Anisozygoptera; from these the Anisoptera were developed. *Kennedya* being his starting point of this phylogenetic series, Tillyard begins the true Odonata with the following venational structure.[7]

(1) Complete formation of a petiolate base or stalk to the wing.

(2) Fixation of a primitive nodus through the upturning end of Sc meeting the costal margin at a point not far distad from the end of the level of petiolation, in such a way that a definite *bend* of the costa is produced.

(3) Fixation of two specialized cross-veins connecting C, Sc and R well basad from the nodus, so as to form the two original *antenodals*, Ax1 and Ax2.

(4) Development of a series of even spaced *postnodals*, probably originally six or seven in number only.

(5) Chitinization of the cell between C, R1 and two of these postnodals at the point of greatest wing-impact during flight, *viz.*, somewhat before the apex. This chitinized cell is called the *pterostigma* (*pt*).

(6) Almost complete fusion of R and M basally within the petiole, and, consequently—

(7) Formation of a true *arculus* (*anterior arculus* of Comstock only).

(8) Complete loss of remnant of MP.

(9) Complete formation of the interpolated convex veins, IR2 and IR3.

(10) Last stage of reduction of Cu1, which becomes very weakly chitinized and only about half the length of the petiole.

(11) Fixation of the cross-vein *Sdv* (subdiscoidal cross-vein) between Cu2 and 1A distally from the arculus, with upward arching of Cu2 from that point.

(12) Fixation of the cross-vein *dv* (discoidal cross-vein) between MA and Cu2 in region of arculus.

(13) First formation of the *subdiscoidal cell* (*sq*) by strengthening and obliquity of *Sdv.*

(14) Increase in the number of cross-veins so that the total number of closed cells in the wing now numbers somewhere

---

[7] This list is taken *verbatim,* with slight change of order only, from Tillyard's paper (1928b).

about one hundred, but without any very definite transverse alignments of such cross-veins.

(15) Complete fusion of Cu2 and 1A throughout the whole length of petiole.

From these Protozygoptera Tillyard derives the true Zygoptera by the addition of a few specializations in the region of the nodus and the arculus. In a similar manner only a few modifications seem to have taken place in passing from the primitive Zygoptera, such as *Permagrion*, to the more highly specialized genera now existing. According to Tillyard, the most significant changes have occurred in the region of the discoidal cell. The subquadrangular cell lengthens; 1A diverges from Cu2 more and more to the perpendicular, until it resembles a cross-vein (AC). As this anal crossing reaches that condition, the cross-vein (A′) below it, forming the basal wall of the anal field, becomes "longitudinally placed," as if it were the extension of 1A basally. In the highest Zygoptera, as the Agriidae, this cross-vein (A′) becomes so well developed that it has all the characteristics of the basal part of 1A. Now from one of the more primitive Zygoptera, not unlike *Permagrion*, Tillyard derives the Anisozygoptera, by the broadening of the wing bases and slight differentiation of the discoidal cell in the fore and hind wings. In the most generalized of the Anisozygoptera the cross-vein A′ has already attained its longitudinal position, as in the highest Zygoptera. In the hind wing of the more highly developed genera, the discoidal cell is divided into triangles by a cross-vein. From these latter types Tillyard derives the true Anisoptera, by further broadening of the wing and the division of the discoidal cell in the fore wings, as well as the hind wings, into triangles.

A full account of Tillyard's theory will be found in his paper on the evolution of the Odonata, and it must be admitted that his arguments are very ingenious and striking. But are his conclusions consistent with our new Lower Permian fossils? That the Zygoptera are derived from the Protozygoptera cannot be doubted; and that a similar relationship exists between the Anisoptera and Anisozygoptera is equally certain. The only questionable part in Tillyard's theory, therefore, is the origin of the Anisozygoptera from the Zygoptera. In his foregoing list of the characteristics of the first true Odonata, there are obviously a few statements which require modification, as a result of more recent discoveries:

In (1) Tillyard asserts that in the first true Odonata there was a complete formation of a petiolate wing. The only evidence which he had for such a conclusion was negative: no Odonata with broad wings basally had been found in the Permian. It is very unfortunate that only the distal part of the wing of *Ditaxineura* was present in the Yale collection; for, as we have seen above, this Odonatan had a wing with as broad a base as the typical Anisoptera. We must therefore change Tillyard's statement to the effect that in the earliest Odonata known to us we find petiolate and normal wings developed.

In (3) the number of antenodals is fixed at two; but in *Progoneura* there are three, and *Ditaxineura*, four.

In (4) Tillyard states that these earliest Odonata possessed a series of equally spaced postnodals, probably six or seven in number; but in *Ditaxineura* there are none at all.

In (11) and (12) there is mentioned the fixation of the discoidal and the subdiscoidal cross-veins; but neither of these cross-veins are specialized or "fixed" in *Ditaxineura.*

In (13) Tillyard asserts that the subdiscoidal cell had been formed in the Lower Permian Odonata, but this is another feature absent in *Ditaxineura.*

In (14) the number of closed cells is stated to be about a hundred; but in *Ditaxineura* there are less than sixty.

In (15) we find "a complete fusion of Cu2 and 1A throughout the whole length of the petiole." There can not, of course, be any doubt that Cu2 and 1A are fused in *Kennedya* and *Progoneura.* But in *Ditaxineura,* as shown above, we see two independent veins in this region, 1A and Cu2. Consequently, the clause quoted must be entirely eliminated and we must substitute in its place the statement that of the earliest Odonata Cu2 and 1A were fused at the base in the Protozygoptera, but were free from each other in the Protanisoptera.

From this discussion I believe that it is evident that instead of all the Odonata of the Lower Permian being zygopterous, as Tillyard supposed, there were two different lines already established. One of these, exemplified by *Kennedya*, possessed narrow, petiolate wings, a very primitive nodus, the elements of a discoidal cell and arculus, and a fused Cu2 and 1A basally; the other line, represented by *Ditaxineura,* possessed normally shaped wings, a well-developed nodus, no true discoidal or arculus system, and an independent 1A. The first group, as

Tillyard has shown, gave rise to the Zygoptera, and the second group, in my opinion, produced the Anisozygoptera.

Let us now consider the possibility of deriving the Anisozygoptera from the Zygoptera. Unfortunately, the second part of Tillyard's study on the evolution of the Odonata, treating the Anisozygoptera and the Anisoptera, has not yet been published, and we are accordingly somewhat in the dark as to the evidence which led him to derive the Anisozygoptera from the Zygoptera. However, he does give us in other works two arguments in favor of this conception. One is the nature of the anal vein. As mentioned above, he regards the structure of 1A in the Anisozygoptera and Anisoptera as more highly specialized than that in the Zygoptera; this decision is based entirely upon the nature of the trachea 1A in the nymphal wing. But I have shown under my description of *Ditaxineura* that the recent investigation of the tracheation of wings proves that evidence derived from such sources is very untrustworthy and cannot have weight by itself in a phylogenetic discussion. Tillyard also suggests (1923, p. 295) that the structure of the male genitalia of the recent Odonata, as investigated by Dr. C. H. Kennedy, shows that the petiolate Zygoptera are more primitive than the Anisoptera and that the anisopterous type was directly derived from the zygopterous one. However, Professor Kennedy, to whom I referred the question, tells me that there is nothing in the genitalia to indicate that the Anisoptera were derived from the Zygoptera or any other stalked-wing forms.

Since these are the only reasons which Tillyard has given for concluding that the Anisozygoptera were descended from the Zygoptera, I believe that we should abandon this theory until additional and more positive evidence has been advanced.

Now if the Anisozygoptera were not derived from the Zygoptera of the Protozygoptera, from what group might they have originated? Certainly the most logical one to consider is that represented by *Ditaxineura*,—the Protanisoptera. A survey of the wings of the Anisozygoptera of the Jurassic points to several features which we require in their immediate ancestors: 1) A well-developed nodus with a more or less distinct subnodus, both situated at about the middle of the wing or somewhat more distally; 2) a primitive arculus (anterior part only), arising from R1 at a small angle; 3) an open discoidal cell, with an unspecialized distal cross-vein, at the most; 4) a waved or undulated Cu2 and 1A, with the curves distinct but not abrupt: 5) Cu2 and 1A independent basally; 6) a normally broad wing basally. Since I have described *Ditaxineura* above, one needs only to refer to this part to observe how well that insect meets the requirements. The exact steps which have led to the typical Anisoptera from this ancient *Ditaxineura*-like forms are not nearly so complicated as those postulated by Tillyard in his theory of the evolution of the Odonata. In passing from the Protanisoptera to the Anisozygoptera we have only the following:

1) The precostal area becomes less pronounced.

2) The subcosta terminates on the nodal cross-vein, instead of on the costa, and the relationship between the subnodus and the nodus becomes more definite.

3) The branches of Rs recede from the distal part of the wing and become more equally distributed.

4) Cu1 is completely lost.[8]

5) The anterior arculus is perfected by being shortened and by the change in the angle by which Rs+MA originates from R; the portion of MA between the origin of Rs and the discoidal cross-vein becomes aligned with the anterior arculus.

6) IR2 and IR3, as well as IMA, become "zigzagged" and lose their definite origins.

7) The first downward curves in Cu2 and 1A become more abrupt and more pronounced.

8) The number of cross-veins increases and postnodals are formed.

These modifications bring us to the venational structure found in the fore wings of the more primitive Anisozygoptera, such as *Liassophlebia, Tarsophlebia, Karatowia,* etc. Passing from these lower forms of the suborder to the higher (see Fig. 5) we find two additional steps: 1) closing of the discoidal cell basally by a cross-vein (fore wing of *Heterophlebia*), and 2) division of discoidal cell in hind wing by a cross-vein (*Heterophlebia, Gomphites,* etc.). The true anisopterous wing is easily derived from the latter type by very slight changes: 1) The discoidal cell of the fore wing is divided into triangles, just as the hind wing of the Anisozygoptera; 2) the cross-vein joining the arculus to Cu2 becomes perpendicular to Cu2, and that portion of MA between Rs and dv (discoidal cross-vein) is elongated and becomes more nearly longitudinally arranged.

---

[8] The remnant of Cu1 may be preserved, however, in Tarsophlebiopsis; see Tillyard 1923, p. 149.

To recapitulate, I believe that the known fossils of the order Odonata indicate that zygopterous and anisopterous lines of descent were already differentiated by the Lower Permian[9]; that the former group was more specialized in the region of the arculus and the anal vein, whereas the latter group was more highly developed at the nodus and subnodus; that the true Zygoptera have been descended directly from the Protozygoptera; and that the Anisozygoptera, which later produced the Anisoptera, were derived from the Permian Protanisoptera, and had no relationship with the Zygoptera. This scheme of descent is illustrated in Fig. 6C.

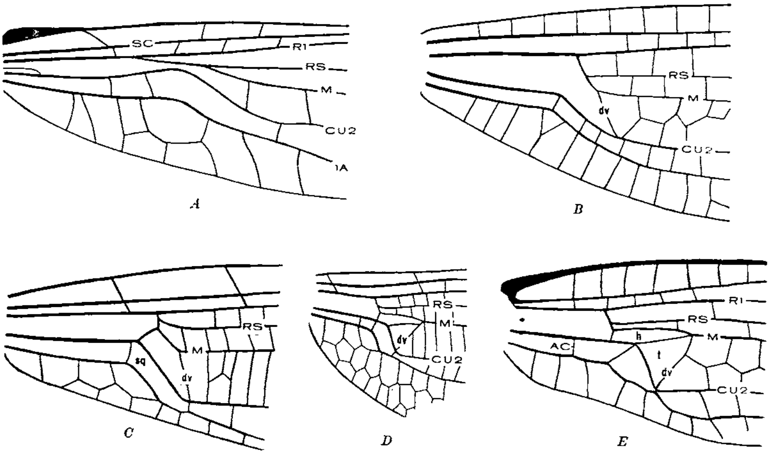

Fig. 5. The evolution of the arculus and discoidal cell in the anisopterous Odonata. A, Protanisoptera, *Ditaxineura;* B, Anisozygoptera, *Tarsophlebia;* C. Anisozygoptera, *Heterophlebia* fore wing; D, Anisozygoptera, *Heterophlebia* hind wing; E, *Gomphus exilis* fore wing (recent). C and D after Tillyard. Dv, discoidal cross-vein; sq, subquadrangular cell; h, supratriangular; t, triangle.

We are now in a position to consider the question of the ancestry of the Odonata as a whole. Only two views have been advanced. The older of these, which has been generally accepted, advocates that the order was derived directly from the Protodonata. However, both Tillyard (1925a) and Martynov (1924) have shown that the Protodonata were

---

[9] As this paper goes to press, Dr. Martynov tells me (*in littera*) that he has discovered a true Anisozygopteran in the Permian (Kazan) of Russia! This substantiates my statement regarding the antiquity of the anisopterous branch.

specialized in certain features in which the Odonata were primitive, and the more recent Permian discoveries substantiate their conclusions. In particular, *Ditaxineura* demonstrates that the number of cross-veins in the primitive Odonata was much smaller than even Tillyard supposed; all the Protodonata are characterized by a large number of cross-veins, much more than found in the higher Odonata of to-day. The alternative view has been proposed by Tillyard, who believes that the petiolate Megasecoptera were the common ancestors of both the Odonata and the Protodonata (Fig. 6B). According to this view, the Protozygoptera were derived from the Megasecoptera through some *"Prokennedya"* type not yet found; and the Protodonata were connected to the Megasecoptera by such a form as *Campyloptera.* I have shown above that Lameere's study of the fossil on which the genus *Campyloptera* was based proved that the genus was a true Megasecopteran, without any Protodonate features as supposed by Tillyard. Since this insect was the only evidence which Tillyard had to support his theory of the origin of the Protodonata from the Megasecoptera, I believe that we should have more proof before accepting such conclusions. As to the descent of the Odonata from the Megasecoptera, we must bear in mind that

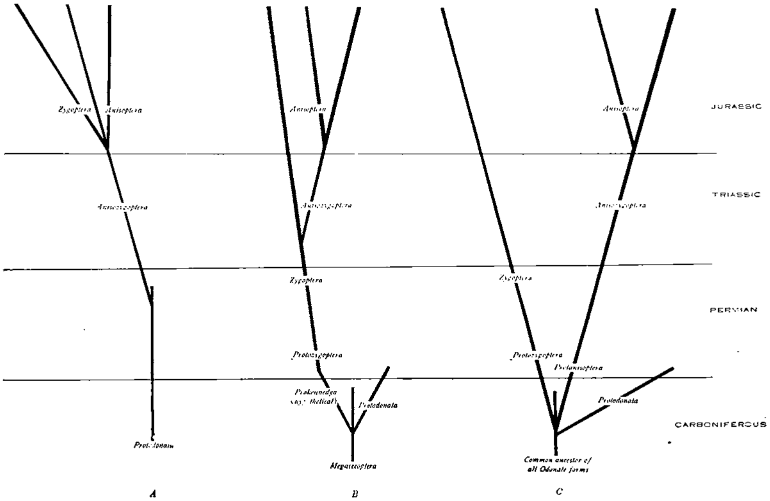

Fig. 6. The Phylogeny of the Odonata according to (A) Handlirsch, (B) Tillyard, and (C) the views expressed in this paper.

this hypothesis depends entirely upon the assumption that the petiolate Protozygoptera were the ancestors of all other suborders of the group, including the Anisoptera. I have shown above, however, that the Protanisoptera with normally shaped wings, were even more primitive than the Protozygoptera and could not have been derived from them. These facts lead me to the conclusion that such a theory of the origin of the Odonata does not satisfy our present requirements.

Now if my deduction that the anisopterous and zygopterous lines (represented by Protanisoptera and Protozygoptera, respectively) were established in the Lower Permian is correct, then we should be able to determine something of the nature of the *immediate* common ancestor of the two suborders, by a consideration of the primitive characteristics present in each line. The nodus of the Protozygoptera is obviously much more primitive than that of the Protanisoptera, so that we can conclude that the common ancestral group possessed (1) a nodus fully as primitive as that of *Progoneura,* where there is no costal break, nor a nodal cross-vein. In a similar manner we can designate the following features in the ancestors:

2) A simple arculus, diverging from R at a very small angle, and without a specialized discoidal cross-vein.
3) R and M close together at the base, but not fused.
4) A normally shaped wing, not petiolate.
5) 1A and Cu2 independent, with prominent undulations. (Note that these undulations are present in *Progoneura,* although the veins are fused.)
6) Cu1 present, but more or less reduced.
7) A small number of cross-veins, probably less than 60.
8) A pterostigmatic area, if not a perfect pterostigma.
9) MP absent or greatly reduced.
10) Probably two intercalated veins, IR2 and IR3.
11) Probably a precostal area.

No such insect has been found up to the present time, but this is not surprising when we consider that it would occur in Carboniferous rocks, since the Wellington shales are at the base of the Permian series. Our knowledge of Carboniferous insects is very meagre and mostly limited to large forms, although, as I have pointed out elsewhere (1930), several existing orders of small insects (Homoptera, Psocoptera, Mecoptera, and Neuroptera) must have existed in the Upper Carboniferous regardless of the fact that none of them have been actually found.

It is obvious from the characteristics in the foregoing list that the Protodonata were closely related to the group ancestral to the anisopterous and zygopterous lines, for in them we find the precostal area and the undulations of Cu2 and 1A, which I regard as important features. But none of the known Protodonata are primitive enough in other respects to represent this ancestral group. I am inclined to the opinion, however, that the families of Protodonata known to us are really highly specialized members of the order, and that the earliest and most primitive representatives were much more like the forms which we postulate as ancestors of the true Odonata. Just where the Megasecoptera fit into the picture is not at all clear. In the light of the fossils now known, I consider them to be entirely outside of direct descent of the Odonata. But until we know more of the smaller insects of the Carboniferous strata, all discussion of the phylogenetic relationships of the orders of that horizon will be pure speculation.

BIBLIOGRAPHY.

BOLTON, H.
1921. A Monograph of the Fossil Insects of the British Coal Measures. Part 1. Paleontological Society, 1919 (1921), pp. 1-80.
BRONGNIART, C.
1893. Etudes sur le terrain houillier de Commentry. Livre 3me. Faune Entomologique. St.-Etienne.
CARPENTER, F. M.
1928. A New Protodonatan from the Grand Canyon. Psyche, **35** (3): 186-190.
1930. A Review of Our Present Knowledge of the Geological History of the Insects. Ibid., **37**, (1): 15-34.
COMSTOCK, J. H.
1918. The Wings of Insects. Ithaca, pp. 1-430.
COMSTOCK, J. H., and NEEDHAM, J.
1898, The Wings of Insects. American Naturalist, **32**: 903-911.
HANDLIRSCH, A.
1906-1908. Die fossilen Insekten und die Phylogenie der rezenten Formen. Leipzig.
1919. Revision der Paläozoischen Insekten. Denks. Akad. Wiss. Wien, Math.—Nat. Kl., **96**, 1-82.
1920. Palaentologie, *in* Schröder's "Handbuch der Entomologie," III: 118-306.
LAMEERE, A.
1917. Revision sommarie des Insectes fossiles du Stéphanien de Commentary. Bull. Mus. Nat. Hist. Paris, **23**: 141-201.
1922. Sur la nervation alaire des insectes. Bull. Classe sc. Belgium, 1922 (4): 138-149.
MARTYNOV, A. V.
1924. Sur l'interpretation de la nervuration et de la tracheation des ailes des Odonates et des Agnathes. Revue Russe d'Entom., **18**: 145-174 (Russian).
1925. Contribution to the Knowledge of Fossil Insects from Jurassic Beds in Turkestan. Part 2. Bull. Acad. Sci. USSR., 1925: 5.

1927. Jurassic Fossil Insects from Turkestan. Part 7. Ibid., 1927: 757-768.
1930. New Permian Insects from Tikhie Gory, Kazan Province, Trav. Mus. Géol. Acad. Sci. USSR., **6**: 69-86.

NEEDHAM, J.
1903. A Genealogic Study of Dragonfly Wing Venation. Proc. U. S. Nat. Mus., **26**: 703-764.

SCHMIEDER, R. G.
1922. The Tracheation of the Wings of the Early Larval Instars of Odonata Anisoptera. Ent. News, 33 (9) : 257-262; (10) : 299-303.

SELLARDS, E. H.
1906. Types of Permian Insects. This Journal (4) **22**: 249-258.

TILLYARD, R. J.
1914. On Some Problems Concerning the Development of the Wing-venation of Odonata. Proc. Linn. Soc. N. S. W., **39** (1) : 163-216.
1915. On the Development of the Wing Venation in Zygopterous Dragonflies, with Special Reference to the Calopterygidae. Ibid., **40** (2) : 212-230.
1916. Mesozoic and Tertiary Insects of Queensland and New South Wales. Queensland Geol. Surv., publ. No. 253: 11-47.
1917. Mesozoic Insects of Queensland. No. 2. *Aeschnidiopsis flindersiensis* Woodw. Proc. Linn. Soc. N. S. W., **42** (3) : 676-692.
1918. Mesozoic Insects of Queensland. No. 3. Odonata and Protodonata. Ibid., **43** (3) : 417-436.
1921. On an Anisozygopterous Larva from the Himalayas (Order Odonata). Records of the Indian Museum, 22 (12) : 93-107.
1922. Mesozoic Insects of Queensland. No. 9. Orthoptera and Additions to Protothoptera, Odonata, Hemiptera and Planipennia. Proc. Linn. Soc. N. S. W. **47** (4) : 448-470.
1922a. New Researches on the Wing Venation of the Odonata. Ent. News, **33**: 1-7; 45-51.
1923. *Tarsophlebiopsis mayi* n.g. et n.sp., a Dragon-fly, found in the Body-Chamber of a Corallian Ammonite. Geol. Mag., **60** (706) : 146-152.
1923a. The Lower Permian Insects of Kansas. Preliminary Announcement. Ent. News, **34**: 292-295.
1925. The British Liassic Dragon-flies. Publ. British Museum Fossil Insects No. 1: 1-38.
1925a. Kansas Permian Insects. Part V, the Orders Protodonata and Odonata. This Journal, **10** (55) : 42-73.
1926. Kansas Permian Insects. Part 6. Additions to the Orders Protohymenoptera and Odonata. Ibid., 11 (61) : 58-73.
1926a. Insects of Australia and New Zealand. Sydney, 1926: 560 pp. Odonata, pp. 65-86.
1928. A Permian Fossil Damselfly wing from the Falkland Islands. Trans. Ent. Soc. London, 1928 (1) : 55-63.
1928b. The Evolution of the Order Odonata. Part 1. Introduction and Early History of the Order. Records of the Indian Museum, **30** (2) : 151-172.

MUSEUM OF COMPARATIVE ZOOLOGY,
CAMBRIDGE, MASS.