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Evolution of the Order Odonata
Part I. Introduction and Early
History of the Order.

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THE EVOLUTION OF THE ORDER ODONATA.

PART I.—INTRODUCTION AND EARLY HISTORY OF THE ORDER.

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Recent discoveries in fossil insects have to a large extent bridged the great gaps which once obscured our view of the evolution of the principal Orders of Insects. The history of the winged Insects previous to the Upper Carboniferous is still obscure, although some light is necessarily thrown upon it by the discovery of what appear to be undoubted remains of Collembola in the Rhynie Chert of Scotland [Devonian: Old Red Sandstone; see Hirst and Maulik (1926) and Tillyard (1928*b*)]. It is logical to argue that if Collembola existed in the Old Red Sandstone so did Thysanura, which are in their morphological characters even more primitive. Indeed, a pair of insect mandibles preserved in these same beds may be placed with considerable probability as the mandibles of a young larval stage of some Thysanuran, probably belonging to the family Lepismatidae. If these fossils do really belong to the Apterygota, it gives much added weight to the theory that the Pterygota are descended from Apterygotan ancestors, and weighs equally strongly against Handlirsch's theory of the direct descent of Pterygota from Trilobites, with Apterygota as a debased side-branch.

But, however that may be, we are still faced with a complete gap in our knowledge as to how insect wings first arose. It is still quite legitimate to argue, purely on the evidence available from morphology and physiology of recent forms, that wings arose as specializations either from (a) paranotal expansions or (b) tracheal gills. All we can be certain of is that wings did arise, almost certainly by one or other of these methods, during the geological period between the Old Red Sandstone and the lower portion of the Upper Carboniferous. Judging by the wealth of forms and high comparative specializations displayed by the known Upper Carboniferous Insect Faunas, one would be inclined to expect the first winged Insecta at least as far back as the Lower Carboniferous.

The two great gaps in our knowledge of fossil insects which existed for so many years have now been almost completely filled by the discoveries made in the Permian and Trias. Before that, the Permian record was very poor indeed. Apart from a considerable number of Blattoids, Handlirsch in 1908 was only able to record one Protorthopteron, three Protoblattoidea, four Plectoptera, one Protodonaton, one Protohemipteron, two Homoptera and one doubtful member of the Perlaria. The discovery of a rich fauna in the Lower Permian of Kansas, and a more restricted though equally interesting fauna in the Upper Permian of Belmont and Newcastle, N. S. W., has changed the Permian from

one of the least known to almost the best known geological epoch as regards insect life. Much the same has been the case with the Trias. In 1908 Handlirsch listed only nineteen Triassic Coleoptera and two Neuroptera. Then came the discovery of the rich Upper Triassic fauna of Ipswich, Queensland, from which more than 120 species have already been described; and, much more recently, an older Triassic bed is being explored near Sydney, N. S. W. and has yielded a number of valuable discoveries not yet worked out or described.

Up to 1908, the oldest undoubted fossil Odonata belonged to the Lias, representing a period when the Suborder Anisozygoptera was dominant. At the present day, only a single genus (*Epiophlebia*) of that Suborder remains, with two species, one in Japan and one in the Himalayas. His analysis of the Liassic fossil record led Handlirsch to postulate the theory that the Anisozygoptera were the original stem of the Odonata, the Zygoptera being derived from them by reduction and the Anisoptera by amplification and addition.

The few Odonata discovered in the Upper Trias of Ipswich, Queensland, did not support this view, for they were all of simpler wing-structure than the Liassic Anisozygoptera, and the two forms in which the base of the wing was preserved (*Triassagrion* and *Triassolestes*) were both strongly petiolate. On Handlirsch's theory, these should have been later geologically, instead of earlier. It was still possible to argue, however, owing to the paucity of material, that these might have been very specializations, and that Anisozygopterous forms with non-petiolate wings existed in the Trias, though not yet discovered.

The next important discovery of fossil Odonata was made by myself when examining the great collection made by the Yale University Expedition, from the Kansas Lower Permian beds. Out of about two thousand specimens, two genera of undoubted Odonata were found. One of these, *Kennedyia* Till. (1925), was represented by both basal and distal portions of wings, and proved to be an exceedingly simplified type with strongly petiolate base. The other, *Ditaxineura* Till. (1926a), was only represented by the apical portion of the wing, but is nearly enough allied to *Kennedyia* to make it certain that it did not differ very greatly from it in the form of the basal portion of the wing. A third genus, *Opter* Sell., (poorly preserved), can be recognised as belonging to the same group, and is petiolate also.

With these discoveries, it seemed to me already clearly indicated that the original type of the Order Odonata was a very simple Zygopterous, or rather Protozygopterous, form in which the wings were definitely petiolate and the number of cross-veins was less than in any existing forms, however simple. This hypothesis forms the basis of the new classification of the Order which I have given in my "Insects of Australia and New Zealand" (1926b). The Lower Permian forms are definitely assigned to a new Suborder Protozygoptera, distinguished from true Zygoptera by the absence of any specialized discoidal cell, the absence of a subnodus, and the presence within the petiole of a remnant of the original convex vein Cu_1 , which is entirely absent from all other Odonata. The Triassic forms were true Zygoptera, still with petiolate wings. The Liassic Anisozygoptera form a complete series leading from petiolate

Zygoterous forms right up to true Anisopterous forms with broadened hindwings; this is clearly shown in my study of the British Liassic species (1925).

In the very restricted Upper Permian fauna from Belmont and Newcastle, N. S. W., no sign of Odonata has yet been seen. But, since true Odonata were present in the Lower Permian of Kansas, it was evident that such must also have been present somewhere on the earth in Upper Permian times. Either they had not yet reached Australia at that period, or else they are present at Belmont but not yet discovered. From a comparison of *Kennedyia* with the Triassic and Liassic forms, I concluded that one might expect the Upper Permian forms to be simple, true Zygotera with petiolate wings and an open discoidal cell not unlike that of the existing Australian genera *Hemiphlebia* and *Chorismagrion*; one would also expect Cu_1 to have vanished and at least some formation of a subnodus to be present.

Such an Upper Permian type has recently been unearthed in the genus *Permagrion* (Tillyard, 1928a.) from the Gondwana-formation of the Falkland Islands. This fine wing has proved to be almost exactly what I had anticipated for an Upper Permian type on the working hypothesis laid down. With its discovery, the chain of evidence for the internal evolution of the Order Odonata is practically complete. In this paper, I propose to set out the whole evolutionary history of the Order from the earliest known period, as far as we can trace it from the available palaeontological evidence.

It should be clearly understood that the great majority of fossil insect remains are impressions of wings only. All the Permian and Triassic Odonata so far discovered are wings only; but in the Lias some bodies also are known and in the Upper Jurassic many complete specimens. The classification of the Order being based mainly upon the wing-venation, the main lines of evolution are best indicated by following the venational changes. In a discussion of the evolution of other parts of the imago, or of the larva, more recourse must be had to the methods of comparative morphology, which experience has shown to be much less reliable than the palaeontological evidence.

EVOLUTION OF EARLY TYPES ANCESTRAL TO THE ORDER.

It has been already stated that the earliest known Odonata occur in the Lower Permian of Kansas. In order to trace the history of the Order further back, we begin by examining these beds for traces of insects allied to the Odonata, and we are at once struck by the fairly abundant remains of the closely allied Order Protodonata, previously only known from the Upper Carboniferous. Our first problem is to attempt to decide whether the Odonata proper are direct descendants of the Protodonata, or whether both have come from some older and less specialized common ancestor. If we can show that the Odonata are types modified from known members of the Protodonata by definite venational or other specializations, then we must accept the former alternative, but if we find that the Odonata are themselves more primitive in certain important characters than are the Protodonata, then the latter alternative is the only acceptable one.

The Protodonata differ from the true Odonata, as regards their venation, chiefly in the absence of any true nodus and pterostigma. The presence of the nodus is associated with a greatly shortened Sc, which turns slightly upwards distally to meet the costa at a point where the continuity of the line of the latter is definitely broken. In the Protodonata, most of the known types have Sc very long, running close above and parallel to R_1 nearly to the apex of the wing (*Protagrion*, *Meganeura*, *Typus*, etc.). But in *Paralogus* Sc is greatly shortened, while in *Calvertiella* it is not only considerably shortened but ends on R_1 ! This last genus was easily the smallest known member of the Order Protodonata, the total length of the wing being only 26 mm., while *Paralogus* had a wing-length of 60 mm. The other members of the Order were all huge insects, ranging from a wing-length of about 90 mm. for *Protagrion* and *Typus*, up to the enormous *Megatypus* and *Meganeura*, the largest of all known insects, with a wing-length ranging up to as much as 300 mm.! The Permian Odonata are all comparatively small insects, the wing of *Kennedyia* being about 33 mm. long and exceedingly narrow, while that of *Permagrion* is 34 mm. long. Thus we see that the shortened Sc is correlated, without exception, with the smaller-sized wings. It is not, therefore, a legitimate deduction to assume that the elongated Sc is primitive for Odonatoid insects. All we can say with certainty is that Sc was of a fixed, shortened form in the most primitive Odonata, while it remained in an unstable condition in the older Protodonata.

It is quite clear that the formation of a pterostigma was a specialization which followed the shortening of Sc and the development of a definite series of postnodal cross-veins. For the pterostigma, in Odonata, is a strongly chitinized cell lying towards the apex of the wing, between the costal margin and R_1 , and bounded basally and distally by cross-veins. In a Protodonate type with long Sc, two longitudinal veins, running parallel and close together (Sc and R_1), form the main support of this portion of the wing. With the reduction of Sc, this support is reduced to one vein only, viz., R_1 ; in spite of this, the smaller Protodonates, *Calvertiella* and *Protagrion*, remain without a pterostigma but all the early Odonata possess one. We may legitimately conclude, that, in this character, the Odonata are more specialized than the Protodonata and might have been derived from forms like *Protagrion*, though not from *Calvertiella* where Sc ends distally on R_1 .

But we meet with a grave difficulty when we come to consider the problem of petiolation. Is the petiolate wing primitive, or is it derived from a broad-based type? If we turn to the Upper Carboniferous forms, we find two very prominent groups of aerial insects: the Palaeodictyoptera with the wings comparatively broad at the base, and the Megasecoptera with the wings basally narrowed and usually sub-petiolate. Further, while the Palaeodictyoptera proper have three or more anal veins, the Megasecoptera have only a single anal, 1A, with or without a series of short descending branches. A glance at the whole of the known genera of Protodonata will show that, although they have broad wings, they possess only one anal vein, and that the branch veins descending from it are all specialized arrangements from this very simple Megasecopteroid type. We can only conclude that they have been derived

from an ancestor having an anal area similar to that of the Carboniferous Megasoptera, and not from the true Palaeodictyoptera.

The Odonata proper, or rather their early fossil forms, are evidently not derivable from any of the Protodonata as regards the form of their anal area. They all have Cu_2 and 1A fused throughout the petiole, and then diverging from one another distally as the wing widens. The series of descending veins from 1A is confined to the free portion of that vein distally from the petiole. All the Protodonata except *Calvertiella* have Cu_2 and 1A separate throughout. *Calvertiella* itself has the most highly specialized anal area to be found within this Order, and cannot be taken as the starting point of the Odonata. The only possible conclusion to come to in this case is that Protodonata and Odonata have both become specialized in the form of their anal area, but *in opposite directions*. For a common ancestor, then, we have to postulate a form with a subpetiolate wing and a single anal vein with or without descending branches (these latter would depend to a large extent upon the actual amount of petiolation in the ancestral wing).

In the true Odonata, both the concave median vein (MP) and the convex first cubitus (Cu_1) are absent, except in the single case of *Kennedya*, where a weak remnant of Cu_1 is preserved in the petiole. In the Protodonata, the highest forms (Meganeuridae) possess only small remnants of these two veins close to the base of the wing; but the older forms (Protagriidae) retain both MP and Cu_1 as complete veins. The common ancestor, therefore, must have agreed with the Protagriidae in this character.

Again, in the whole of the true Odonata, and also in the Meganeuridae within the Protodonata, Rs has been captured by MA, and the original basal piece of Rs has been lost. In Protagriidae Rs remains distinct from MA, but the latter arches up very close to it near its origin, and a short, strong cross-vein, uniting the two, shows clearly the method of capture in the higher forms. The common ancestor, therefore, must have had Rs distinct from MA.

There are two other characters common to the Protodonata and Odonata which need to be emphasized here. One is the character of the cross-vein system, which is, *in all parts of the wing including the costal areas*, at right angles to the veins which it connects. The only other insects with this very striking character are the May-flies (Plecoptera). The important point to notice is that, in those insects with true costal veinlets present, these are always *obliquely* placed. We may conclude that the cross-veins in the costal spaces of Odonata, Protodonata and Plecoptera are truly such, and not veinlets. Hence, in searching for a common ancestor, we should look for one *without costal veinlets*. The second point is of even greater importance, *viz.*, the extraordinary serrated condition of the very strongly formed costal margin of the wing. The larger forms, *i.e.*, all the Protodonata except perhaps *Calvertiella* (in which the extreme base of the costa is not well preserved) possess, in addition, a basal *precostal coriaceous area*, which must be regarded as a specialization due to size. In looking for a common ancestor, therefore, we should seek especially for some signs of this character, which is not to be found in any recent forms except Odonata.

Reviewing the above evidence, we conclude that the Protodonata cannot be the actual ancestors of the Odonata, as they are more specialized in the condition of their anal area and also in the possession of the precostal coriaceous area. But they agree so closely with them in other venational characters, that both must be considered as having arisen from a common ancestor at a time geologically not far back from the Upper Carboniferous. As we still have no records of winged insects earlier than this, the most we can do is to examine the lower or middle beds of the Upper Carboniferous for evidence of the existence of still more primitive types representing, or closely allied to, this common ancestor.

In this paper, I propose to analyse the characters common to the two Orders Protodonata and Odonata, and to attempt to deduce from them the common ancestral stock. From that stock we shall be able to follow the evolutionary stages of the Order Odonata right through to the present day. In this Part, the evolution will be followed up to the complete establishment of the most primitive existing Suborder, Zygoptera, in the Upper Permian, while the various lines of evolution from there onwards must be relegated to Part II.

In developping the argument set forth in this paper, the venational notation used must necessarily be that fully set forth in my recent work on the Insects of Australia and New Zealand (Tillyard, 1926). As far as the Odonata are concerned, this notation is the logical outcome of the evolutionary development indicated by the fossil history. One starts with the accepted notation for the Carboniferous Orders Palaeodictyoptera and Megasecoptera, with the recognized addition of a convex anterior median, MA, to the original Comstock-Needham system, as proposed by Lameere (1922). All the modifications in Odonate venational nomenclature necessarily follow from this.

The principal stages in the evolutionary history of the Order Odonata up to the formation of the true Zygoptera in the Upper Permian may be most clearly exhibited in four distinct stages, each dealt with in a separate Section. To these may conveniently be added, as a separate Section following on the first of the four dealing with Odonata, a short account of the evolution of the Order Protodonata. This gives us five Sections, as follows:—

- Section 1.*—Analysis of the Primitive Characters of the Common Ancestor of Protodonata and Odonata. (*Brodia* Stage: actual: Westphalian or middle part of Upper Carboniferous.)
- Section 2.*—Evolution of the Order Protodonata. (Upper Carboniferous and Lower Permian.)
- Section 3.*—Emergence of the Order Odonata from the ancestral stage. (*Protokennedyia* Stage: hypothetical: Stephanian or upper part of Upper Carboniferous.)
- Section 4.*—The first true Odonata. Suborder Protozygoptera. (*Kennedyia* Stage: actual: Lower Permian.)
- Section 5.*—Evolution of the Suborder Zygoptera. (*Permagrion* Stage: actual: Upper Permian.)

Section 1.—Analysis of the Primitive Characters of the Common Ancestor of Protodonata and Odonata. (*Brodia* Stage: actual: middle part of Upper Carboniferous.)

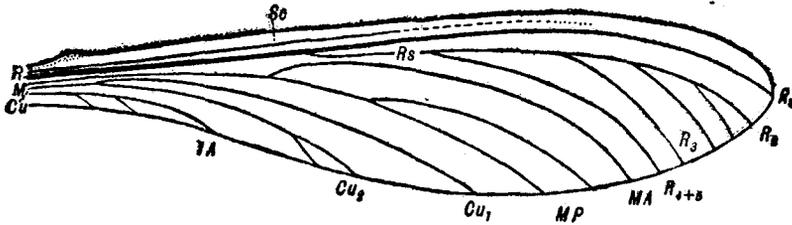


FIG. 1.—*Brodia priscotineta* Scudder, Order Megasecoptera. Upper Carboniferous of Europe. Wing. Length 58 mm. Cross-veins and transversely fasciated colour-pattern omitted.

The analysis of the ancestral characters common to both Protodonata and Odonata, already given above, supplies us with the following basis of venational requirements for the common ancestor of the two Orders:—

- (1) A hardened costal margin, with serrated edge.
- (2) A simple, concave subcosta (Sc).
- (3) A strong, convex radius (R), ending near apex of wing, and armed with reduced spines or serrations.
- (4) A concave radial sector (Rs), having a pectinate series of descending branches, all concave, of the type found in Palaeodictyoptera and Megasecoptera.
- (5) A simple or branched, concave, posterior median (MP), arising separately from the base of the wing, just below R.
- (6) A simple, convex, upwardly arching, anterior median (MA), not arising from the base of the wing, but originating from MP at or near the level of the origin of Rs, so that the highest point of the arch of MP comes very close up to Rs.
- (7) A concave second cubitus (Cu_2), with short descending branches distally, and ending up at about half-way along the posterior margin or less from the base of the wing.
- (8) A simple, convex first cubitus (Cu_1), not arising from the base of the wing, but branching anteriorly from Cu_2 very close to the base, definitely within the area of the subpetiole.
- (9) A single convex anal vein (IA), shorter than Cu_2 , but extending slightly beyond the subpetiole, with or without short descending veinlets.
- (10) An elongated, narrow form of wing, with the basal portion definitely compressed into a subpetiolate form.
- (11) A weak, unfixed system of cross-veins, all at right angles to the main veins.
- (12) Absence of costal veinlets, nodus and pterostigma.

When we compare these requirements with the venation exhibited by the Upper Carboniferous genus *Brodia* Scudder, (see Bolton, 1921, Handlirsch 1908, 1919), we find that they agree in all essential particulars. We do not require, in the ancestral form, the transversely fasciated colour-pattern of the wings of *Brodia priscotineta*, but all the other charac-

ters are needed. We may therefore speak of this earliest ancestral stage in the evolution of the two Orders Protodonata and Odonata as the *Brodia Stage*.

Age of the Brodia Stage.—It is interesting to note that, while the great majority of the Palaeodictyoptera and Megasecoptera occur in the Stephanian or upper division of the Upper Carboniferous, the genus *Brodia* occurs only in the Lower Coal Measures of England, *i.e.*, the Westphalian or middle division of the Upper Carboniferous, and possibly extends backwards even to the base of this division or beyond it. There is therefore no geological reason why this genus should not be regarded as the ancestor of both Protodonata and Odonata, since the former only appear in the Stephanian and the latter in the Lower Permian.

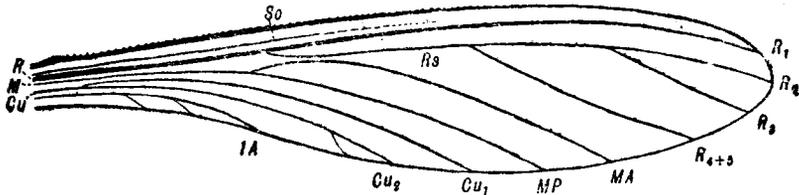


FIG. 2.—Hypothetical *Brodia* type of wing with the number of descending sectors of *Rs* reduced to two, *MP* unbranched, and no fasciated colour-pattern. Hypothetical ancestor of Odonata.

Classification of the Brodia Stage.—The genus *Brodia* will find its ordinal position according to the particular view-point of each author or student as to the limits and divisions of the great group Palaeodictyoptera. For the purposes of this paper, it does not seem necessary to discuss the proposals of Lameere for the sub-division of this Order. The only group which comes really into the question is that series of forms in which the anal area only carries a single vein, *IA*. I consider this to be the diagnostic character of the Order Megasecoptera, irrespective of whether the wings carried nygmata or not. The genus *Brodia* will then be classified as an early and slightly specialized form within this Order, characterized by the very strongly formed and serrately ridged costal margin, the subpetiolate, narrow wings with evenly rounded apices, the absence of nygmata and of specialized cross-veins.

It is also important to note that larval forms of this genus are known, and that the larval wings were held more or less vertically above the thorax in the position characteristic of Mayflies. In the last larval stage the wings are about two-fifths the length of those of the imago.

We may note three tendencies in the genus *Brodia* which are of importance in the later evolution of the groups which we are studying:—

- (a) The distal end of *Sc* is weakly formed and indeterminate.
- (b) *MA* is already upwardly arched so much that it tends to become connected with *Rs* close to its origin.
- (c) *IA* and *Cu₂* are already very close basally, owing to the subpetiolate condition of the wing, and are tending to unite.

Section 2.—Evolution of the Order Protodonata. (Upper Carboniferous and Lower Permian.)

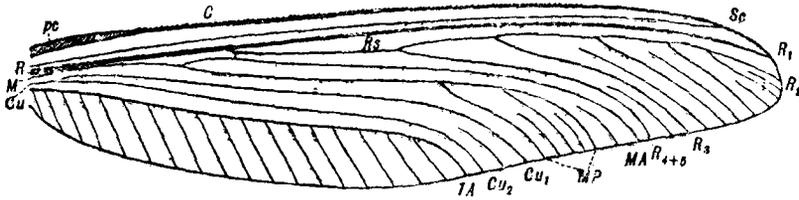


FIG. 3.—*Protagrion audouini* Brongn., Order Protodonata, family Protagriidae. Upper Carboniferous of Europe. Restoration of wing. Length about 90 mm. Cross-veins omitted, except the short one connecting Rs basally with MA.

When we come to analyse the known genera of Protodonata, we find that they fall conveniently into two distinct families, as follows:—

FAMILY PROTAGRIIDAE.—Posterior median (MP) and first cubitus (Cu_1) still existing as distinct veins running to the posterior margin of the wing. 1A with pectinate series of descending branches.

FAMILY MEGANEURIDAE.—Posterior median and first cubitus either entirely absent, or else only existing as short vestiges attached closely to MA and Cu_2 respectively near the base of the wing. 1A with a specialized concave sector (SA) as well as numerous convex descending branches.

On all points the family Protagriidae is seen to be the more primitive of these two groups. In looking, then, for the ancestral connecting link between Protodonata and the older *Brodia* Stage, we must first of all analyse the known genera of this family.

The fossil *Protagrion audouini* Brongn., from the Stephanian of Commeny, France (fig. 3) appears to be the oldest known type of Protodonate yet discovered. The actual specimen is not very well preserved, but I venture to give a restoration of the wing from a study of the fossil and a good photograph of it. This should be carefully compared with *Brodia* (fig. 1), when it will be seen to agree pretty closely with it in a number of important points:—

- (1) The radial sector (Rs) has a series of five or six descending, concave branches, pectinately arranged. But *Protagrion* has, in addition, somewhat irregular convex interpolated veins between these.
- (2) The anterior median (MA) is a simple convex vein, arching up so as nearly to meet the radial sector close to its origin. In *Protagrion*, however, it appears to be definitely connected by a short, strong cross-vein to Rs, whereas in *Brodia* it remains unconnected.
- (3) The posterior median (MP) is complete and is distally branched.
- (4) The first cubitus is a complete, simple, convex vein, arising from the stem of Cu not far from base.

Protagrion differs from *Brodia* as follows:—

- (1) Instead of a costal hump, there is a well developed precostal coriaceous area (*pc*).
- (2) The general shape of the wing is very different, and petiolation is absent.
- (3) The first anal (1A) is a much longer vein, reaching almost as far as the end of Cu_2 , and having a very complete series of descending branches, pectinately arranged.

In searching for a type which would connect *Protagrion* with *Brodia*, we should naturally look for one which included all four characters on which these two are agreed, but which also should show (*a*) a weak development of a precostal area, (*b*) some amount of petiolation of the wing, and (*c*) a shorter and less well developed anal vein than that of *Protagrion*.

The fossil genus *Campyloptera* Brongn., from the Stephanian of Commeny, agrees with these requirements in all respects except one, *viz.*, that the anterior median appears to be already fused with *Rs* for a short distance. As I have not studied the fossil, which appears to have been only moderately well preserved, I do not attempt to figure it here, but would simply refer to Handlirsch's figure (1908, Atlas, pl. xxxii, fig. 15). The general shape of the wing is that of *Kennedya* (fig. 6), but the basal portion is only subpetiolate and the apex is somewhat nodding, like that of *Permagrion* (fig. 8). The anal vein (1A) reaches to about two-fifths of the posterior margin from the base, and has a series of short, descending, pectinate branchlets. *Rs* appears to have had only two concave descending branches, separated by two interpolated convex veins, as in *Calvertiella* and all true Odonata. *MP* is distally forked much as in *Brodia*. There is a short but quite definite precostal area, and a poorly developed system of cross-veins at right-angles to the main veins. The total length of the wing was 65 mm. as against 58 mm. for *Brodia priscotineta* and about 90 mm. for *Protagrion audouini*.

Brongniart (1893, p. 527) placed the genus *Campyloptera* within the Order Protodonata, next to the genus *Brodia*, which he also included within that Order. Handlirsch (1908, p. 316) removed *Campyloptera* to the Megasecoptera, though his remarks on the point show that he was in considerable doubt about it. At the same time, he placed *Brodia* in the Order Palaeodictyoptera (1908, p. 113); but, in his more recent work (1919, p. 73) he again moves this genus to the Megasecoptera, where it clearly belongs.

Handlirsch placed considerable weight on the presence of "Schaltsectoren" or "intercalated sectors" as an ordinal character for the Protodonata, and he says of *Campyloptera* (l.c., p. 316) "Sollten die Adern, wie es auf dem Bilde den Anschein hat, wirklich den Character von Schaltsectoren haben, so durfte die Form wohl eher zu den Protodonaten gehören". Brongniart's original figure of the genus (1893, pl. 40, fig. 3) shows undoubted intercalated sectors present, and, if there were any doubt on the question, it seems to me that the presence of the precostal area clearly indicates the true Protodonate character of the genus.

It seems clear to me that the original ancestor of the Protodonata must have been the Westphalian form (not yet discovered) from which *Campyloptera* was directly descended, and that it only differed from that genus in having MA still unfused with Rs. Such a form, to which the name *Procampyloptera* might be provisionally given, would connect *Brodia* quite naturally with the family Protagriidae, and would allow us to envisage the change from Megasecoptera to Protodonata as having taken place through a subpetiolate form, which began to develop intercalated sectors a little prior to the first connection between Rs and MA by means of a cross-vein.

We may now indicate the general lines of evolution of the genera of Protodonata as follows:—

Family PROTAGRIIDAE.—Starting with the hypothetical *Procampyloptera* as the ancestral type, there are two lines of evolution:—

(Sub-family Campylopterinae.)

- (A) The *subpetiolate line* of descent, which ran to *Campyloptera* and then, as far as we know, died out in the Stephanian.

Sub-family Protagriinae.

- (B) The *non-petiolate line* of descent, which gave origin in the Stephanian to *Protagriion* through strong development of the anal area, with a cross-vein connection between Rs and MA and a fairly strong development of intercalated sectors between the branches of Rs, M and Cu. This line carried on into the Lower Permian in North America, where we find the very highly specialized genus *Calvertiella* (Tillyard, 1925, pp. 43-48, figs. 1,2A) with the anal area still more highly specialized, IA partially fused with Cu₂ and all its descending branches strongly curved, MP still branched and with intercalated sectors, and Rs with only two concave descending branches, but with the intercalated sectors already taking on very strongly the form of the two interpolated convex veins IR₂, IR₃, characteristic of the true Odonata,

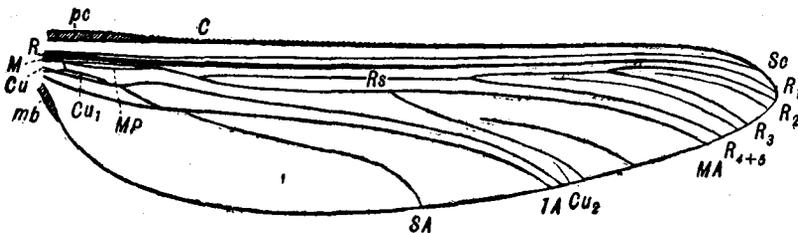


FIG. 4.—*Megatypus schucherti* Till., Order Protodonata, family Meganeuridae. Lower Permian of North America. Length about 250 mm. Cross-veins and intercalated Sectors omitted. Note the remnants of MP and Cu₁ near base of wing.

Family MEGANEURIDAE.—This was the most highly successful specialization within the Order, and gave rise, in both Stephanian and Lower

Permian times, to the largest insects ever evolved. Three main lines of descent can be distinguished :—

- (A) Sub-family Paraloginae, of moderate size (wings about 60 mm. long), with the bases somewhat narrowed, Sc shortened, and the precostal area very slightly formed. (Genera *Paralogus* Scudder and *Paralogopsis* Handl., both from the Upper Carboniferous of North America).
- (B) Subfamily Meganeurinae, of large to very large size (wings from 120 up to 300 mm. in length), with the bases not narrowed, Sc very long, and R_4+5 arising close to origin of MA, and the precostal area well developed. (Genera *Meganeura* Brongn., *Meganeurula* Handl., *Meganeurella* Handl., *Meganeurina* Handl., *Meganeurites* Handl., *Boltonites* Handl. and *Gilsonia* Meun., all from the Upper Carboniferous of Europe.)
- (C) Sub-family Typinae, differing only from (B) in having R_4+5 arising far distad from origin of MA. (Genera *Typus* Sell. and *Megatypus* Till., both from the Lower Permian of North America.)

Section 3.—Emergence of the Order Odonata from the ancestral stage. (*Protokennedy* Stage: hypothetical: Upper Carboniferous.)

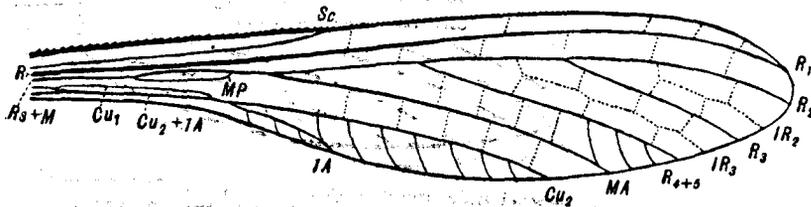


FIG. 5.—Wing of *Protokennedy*, a hypothetical type intermediate between the *Brodia* Stage (Order Megasecoptera) and the *Kennedy* Stage (Order Odonata, sub-order Protozoptera). Note the beginnings of the two interpolated convex veins IR_2 and IR_3 , formed from the alignment between two sets of cross-veins.

While the Protodonata reached the summit of their short but glorious evolutionary career in the Stephanian or upper division of the Upper Carboniferous, and died out in the Permian, we now have to indicate the hypothetical connecting link which serves to bring *Kennedy* and its allies into evolutionary connection with *Brodia*. This stage, which may conveniently be termed the *Protokennedy* Stage, is reached from *Brodia* by the following specializations :—

- (1) Sc becomes much shortened, ending on costa.
- (2) R and M approach very close basally.
- (3) MA captures R_s close to its origin, and the original basal piece of R_s becomes aborted.
- (4) R_s becomes fixed with two descending concave branches in addition to its apical portion, and the beginnings of interpolated convex veins appear between them.

(5) Vein MP becomes reduced to a short basal portion lying close below MA and attached again to it distally.

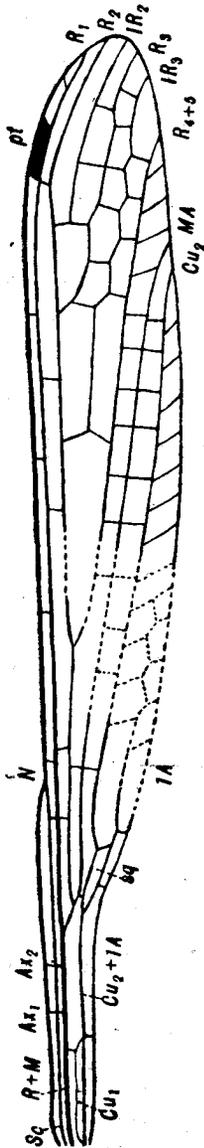


FIG. 6.—*Kennedyya mirabilis* Till., Order Odonata, suborder Protozygoptera. Lower Permian of North America. Wing, with missing parts restored by dotted lines. Length 44 mm.

(6) Vein Cu_1 likewise becomes reduced to a short basal portion lying close above Cu_2 and attached again to it distally.

(7) Cu_2 and IA become fused for a short distance close to the base, within the subpetiole.

(8) The cross-vein system becomes more definite, consisting of a fair number of cross-veins at right angles to the main veins and fairly evenly spaced; in particular, double series of cross-veins develop between R_2 , R_3 and R_4+5 , forming the beginning of interpolated longitudinal veins.

(9) The subpetiolate form of wing becomes more marked, tending to complete petiolation; at the same time, the wing is becoming excessively narrowed, this condition being correlated with (5), (6) and (7).

This stage may be taken as the *annectant* stage between the two Orders Megasecoptera and Odonata. The actual fossil form which seems to lie closest to it appears to me to be *Campflyoptera eatoni* Brongn., from the Stephanian of Commenyry, but I have not been able to study this fossil in detail.

Section 4.—The first true Odonata. Suborder Protozygoptera. (*Kennedyya* Stage: actual: Lower Permian.)

The first true Odonata recognizable in the fossil record belong to the Lower Permian of Kansas, and consist of the three genera *Kennedyya* Till., *Opter* Sell. and *Ditaxineura* Till. Of these, the only one that is approximately complete is *Kennedyya* (fig. 6). The *Kennedyya* Stage, representing the Suborder Protozygoptera, is reached from the *Protokennedyya* Stage by certain very definite specializations, as follows:—

(1) 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.

- (2) 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.
- (3) Development of a series of evenly spaced *postnodals*, probably originally six or seven in number only.
- (4) 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*).
- (5) Complete formation of a petiolate base or stalk to the wing.
- (6) Almost complete fusion of R and M basally within 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 remnant of Cu₁, which becomes very weakly chitinized and only about half the length of the petiole.
- (11) Complete fusion of Cu₂ and 1A throughout whole length of petiole.
- (12) Fixation of the cross-vein *dv* (discoidal cross-vein) between MA and Cu₂ in region of arculus.
- (13) Fixation of the cross-vein *Sdv* (subdiscoidal cross-vein) between Cu₂ and 1A distally from arculus, with upward arching of Cu₂ from that point.
- (14) First formation of the *subdiscoidal cell* (*sq*) by strengthening and obliquity of *Sdv*.
- (15) Increase in number of cross-veins so that the total number of closed cells in the wing now numbers somewhere about one hundred, but without any very definite transverse alignments of such cross-veins.

Of the above characters, I would single out as diagnostic for the Order Odonata the *nodus*, the *pterostigma* and the *arculus-formation*. The first and third of these are never again lost. The *pterostigma* is almost as constant, but we must remember that the males of certain highly specialized genera of Agrioidea lose it entirely, while other forms may have it hypertrophied.

With the emergence of the group into a recognizable Odonate stage, we now have to consider certain specializations in the larval wing which must of necessity have taken place concurrently with those of the imago.

The first of these is the evolution of the peculiar condition found in all Odonate larvae, in which the hind wing-sheaths come to overlie the fore. This is, of course, correlated with the adoption of the obliquely placed thorax in the imago. Let us study the two together.

If we consider the Mayfly larva and imago, we find that the thorax remains normal in form, and the fore wing-sheaths of the larva overlie the hind. It seems manifestly impossible for such a larval form as this to have been the ancestor of one in which the positions of the wing-sheaths are reversed.

But we know that, in the *Brodia* stage, the wing-sheaths did *not* lie flatly down upon the thorax of the larva at all; instead, they stood out more or less vertically from it, much as the imaginal wings of Mayflies do to-day. Now let us try to conceive the effect of a gradually increasing petiolation on such a type, with correlated increase in the obliquity of the thorax. It seems logical to suppose that, as the wings narrowed basally, the notal areas also narrowed, thus allowing for the expansion of the pleural areas in front of them. As this progresses, the wings of the imago and the wing-sheaths of the larva would both tend to project backwards at a steadily decreasing angle to the abdomen. It is a verifiable fact that most Zygopterous Odonata rest with the anterior portions of their hindwings more or less enveloping the posterior portions of the fore, and it seems logical to assume that this position was also a primitive one in the arrangement of the larval wing-sheaths. Once this slight envelopment is attained, it will easily be seen that as flattening of the sheaths is attained, it is inevitable that the hind wing-sheath must come to overlies the fore, and not *viceversa*.

The second point of importance is the consideration of the primitive condition of the tracheal system of the larval wing. We have to start with the Megasecopterous condition, which we may provisionally assume had, in the larval wing, a complete series of main tracheae along the courses of the main veins, and therefore must have had tracheae MP, Cu₁ and 1A complete, but no tracheae IR₂ or IR₃, since these veins had not then been formed.

When Rs was captured by MA, trachea Rs might have retained its primitive connection with R, or it might have become aborted basally, leaving trachea M in possession of the whole tracheal system supplying Rs. We know, from actual study of Odonate larval wings, that the later is the universal condition throughout the Order.

With the loss of vein MP, and, a little later, of vein Cu₁, it might be expected that the tracheae belonging to these veins would also abort. This also we know has actually happened.

We know also that no existing Odonate larva has a trachea along the course of IR₂. IR₃, on the other hand, has secondary tracheal

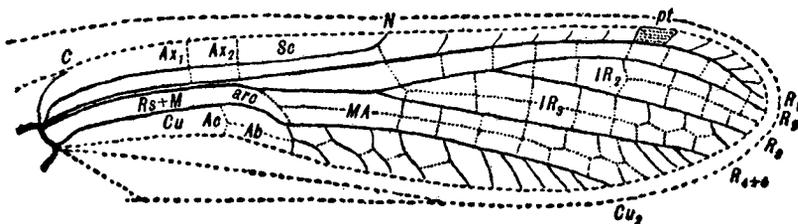


FIG. 7.—*Hemiphysbia mirabilis* Sel., Order Odonata, suorder Zygoptera, family Hemiphysbiidae. Recent. Wing of last larval instar, showing tracheation (complete lines) and pigment-bands of veins and cross-veins of imaginal wing (dotted lines).

supplies of varying types. Only in the very archaic genus *Hemiphysbia* does it possess no tracheal supply at all, and this genus also has a larval

wing without any tracheal supply to either MA or 1A. MA we know must have been an interpolated vein at one stage of its development, since a very large number of insects never possessed it. It would appear, therefore, as if its trachea did not develop until the Order Odonata was well under way, and the primitive genus *Hemiphlebia* must have been evolved before this happened. The original trachea 1A was almost certainly suppressed during the process of petiolation and of fusion of 1A with Cu₂. A new secondary anal trachea appears to have developed again very slowly in the Odonata as the anal area also developed, but its tortuous course betrays its secondary origin. Many primitive Zygoptera show little or no signs of such a trachea.

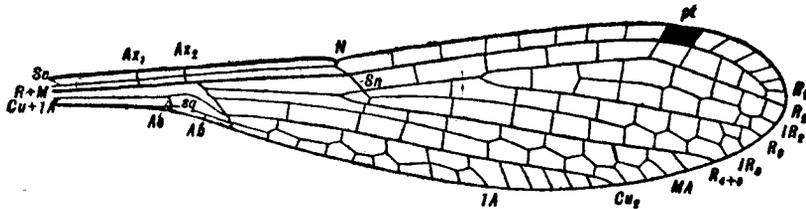


FIG. 7a.—Forewing of imago of *Hemiphlebia mirabilis* Selys.

The larval tracheation of *Hemiphlebia mirabilis* Sel. is shown in fig. 7 to illustrate the most archaic condition still extant within the Order Odonata. In tracing the evolution of the chief existing groups, the additions made to this simple type will also be figured.

Section 5.—Evolution of the Suborder Zygoptera. (*Permagrion* Stage: actual: Upper Permian).

Very few additional specializations are required to change the Protozygopterous *Kennedy*-type into a true Zygopteron. This change took place during the Permian. The Lower Permian Odonata were all Protozygoptera. The only Upper Permian (Gondwanan) form yet discovered is *Permagrion* from the Falkland Islands, and this is a true Zygopteron. The evolution of the *Permagrion* Stage (most primitive Zygopteron) from the *Kennedy* Stage was brought about as follows:—

- (1) Complete loss of Cu₁.
- (2) Completion of nodus and formation of subnodus by alignment and obliquity of two cross-veins, that between Sc and R₁ completing the nodus and that between R₁ and R_s forming the subnodus (Sn).
- (3) Completion of basal fusion of R and M (these are still slightly separated basally in *Kennedy*).
- (4) Specialization of the discoidal cross-vein *dv* as an oblique vein continuing the line of the arculus above it, and hence.—
- (5) First formation of a recognisable open discoidal cell or quadrilateral (*q*) with more or less acute distal angle.
- (6) Fixation of subdiscoidal cross-vein *Sdv* obliquely in line with and immediately below *dv*.

(7) Differentiation of the original free basal portion of 1A, after its fusion with Cu_2 , into the anal crossing (Ac) and anal bridge (Ab) with supporting cross-veins.

(8) Extension of 1A distally by alignment of portions of the descending branches of Cu_2 and their connecting cross-veins.

(9) Increase in the number of postnodals and cross-veins generally, with beginnings of tendency to transverse alignment of cross-veins, and with zigzagging of distal portions of the convex veins IR_3 , MA and 1A.

(10) Precession of branches of Rs basad; in particular, the origin of $R_4 + 5$ moves close to Sn though still distad from it.

In comparing the Protozygopterous type with the Zygopterous, we may with advantage concentrate on the important changes which took place in two special regions of the wing:—

(A) *The Nodus* (fig. 9). The Protozygopterous nodus, as already pointed out, was incomplete, being merely the point at which a definite bend in the costal margin had been formed by the fusion with it of the slightly upturned end of Sc (fig. 9, A). In *Kennedy* we note the presence of an unspecialized cross-vein basad from the nodus between Sc and R_1 and another unspecialized cross-vein below this, between R_1 and Rs. It seems clear that the Zygopterous nodus was first completed by the movement distad of these two cross-veins, which, at the same time, became somewhat oblique in position. The term nodus in the Odonata is generally used to include the whole formation at and below the costal break or bend, from C down to R_1 ; that is to say, it consists of three parts (a) the costal break or bend, (b) the small distal piece of Sc from this bend back to the origin of the cross-vein, and (c) the *nodal cross-vein* (nv) itself. As the nodal cross-vein is placed at a more or less marked angle to Sc, the typical form

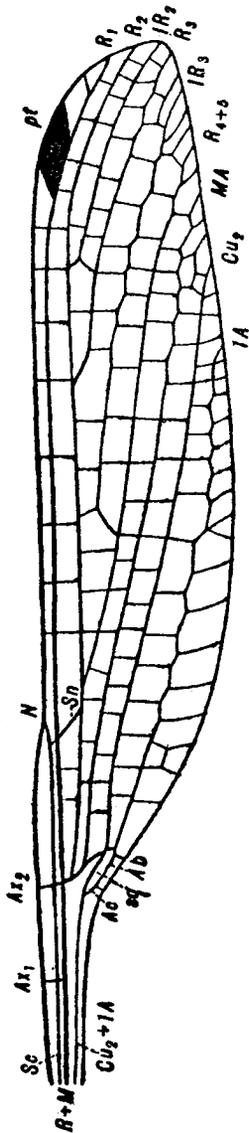


FIG. 8.—*Permagrion falklandicum* Till., Order Odonata, suborder Zygoptera, family Permagriidae. Upper Permian (Gondwanan) of the Falkland Islands. Wing Length 34 mm.

of Odonate nodus is V-shaped, tending to become more and more obtuse as evolution progresses and finally blending

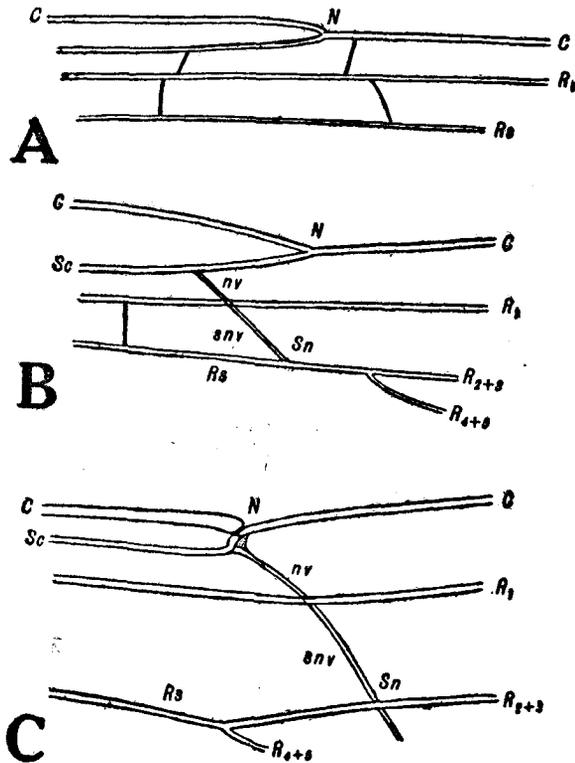


FIG. 9.—Evolution of the Nodus in Odonata. A. Primitive formation of end of subcosta in *Kennedya mirabilis* Till., suborder Protozygoptera. B. Formation of the nodal area in *Permagrion falklandicum* Till., suborder Zygoptera, showing completion of subnodus (Sn) by alignment of the nodal (nv) and subnodal (snv) cross-veins. C. Complete nodal formation in a recent Zygopteron, *Hemiphlebia mirabilis* Sel., with flexible joint on costa at nodus (N).

into a sort of arch concave to the base of the wing (fig. 9). The *Subnodus* (Sn) continues this formation directly downwards by means of the second or subnodal cross-vein (snv) between R_1 and R_s . This fixed area of nodus plus subnodus is one around which important evolutionary changes later on took place, helping to differentiate the main groups within the Order.

(B) *The Arculus and Discoidal Cell* (fig. 10). In the Protozygoptera (fig. 10,A) there was merely a gentle divergence of $R_s + MA$ from its common stalk with R_1 ; this formed the *anterior arculus* of Comstock. Except for a greater degree of divergence, this incomplete arculus formation remained throughout the Permian, and is still to be seen in the forewings of *Hemiphlebia* (fig. 10, C) and *Chorismagrion*. But, while little change was going on in this area, a most interesting series of changes was taking place in the region just pos-

terior to it. Here, as we can see from *Kennedyya* (fig.10,A) the early development of a specialized cross-vein, the subdiscoidal cross-vein, *sdv*, formed a closed triangular cell, the subdiscoidal cell, or subquadrangle (*sq*), long before the more typi-

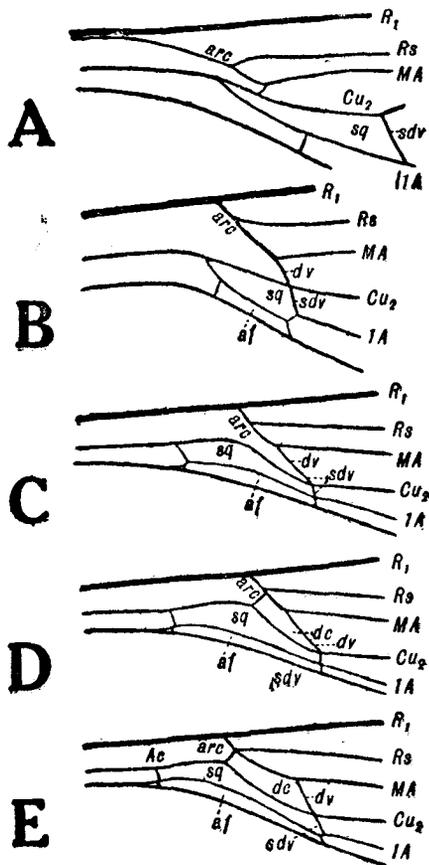


FIG. 10.—Evolution of the Arculus, Discoidal Cell, Subdiscoidal Cell and Anal Field in Odonata. A. Primitive condition in *Kennedyya mirabilis* Till. B. First alignment of discoidal (*dv*) and subdiscoidal (*sdv*) cross-veins in *Permagrion falklandicum* Till. C. Normal formation of open discoidal cell in *Hemi-plebia mirabilis* Sel., forewing. D. Abnormal closure of discoidal cell from the other forewing of same specimen as C. E. Closed discoidal cell of hindwing of same specimen as C.

cal discoidal cell, or quadrangle, *dc*, became differentiated. The later history of this sub-discoidal cell is very interesting, particularly as it lays an important part in the evolution of the Anisoptera. In *Kennedyya* (fig. 10,A) we see it in its most primitive form, viz., as a closed triangular cell formed by closure of the space between the two diverging veins *Cu*₂ and *1A*; at this stage, the cross-veins below *sq* are unspecialized. In the *Permagrion* Stage, (fig. 10, B), these two cross-veins have moved up to positions of greater advantage, strutting the cell on to the posterior margin and making

it more of an elongate pentagonal form than a triangle. As we shall see later, all *Anisopterous anal areas have arisen as specializations from this basic type*. As soon as this flattened pentagonal form is reached, we are able to divide the basal piece of IA, which formed the original posterior side of *sdv*, into two parts separated by an angle, *viz.*, the short basal portion from Cu_2 to the first cross-vein, which we can now recognize as the primitive *anal crossing* (Ac), and the rest of IA as far as *sdv*, which is the primitive *anal bridge* (Ab). Without the fossil record, it would have been impossible to discover that these two formations were originally parts of the same longitudinal vein; but such was undoubtedly the case. It is of special importance that we should now recognize that those forms of *Zygotera* in which Ac tends to be obliquely placed to Cu_2 , while the cross-vein below it remains still at right-angles to the posterior margin, are more archaic than those in which Ac takes on the appearance of a cross-vein, while the original cross-vein below it tends to become longitudinally placed, as if it were the true extension of Ab basad.

We now need a name for this important cross-vein below Ac, and we need not look far for one, for a little thought will show us that it is the first beginnings of the formation called the *secondary anal* or A^1 (fig. 10, C) in more highly evolved forms, both *Zygotera* and *Anisoptera*! The various lines of evolution of Ac, A^1 and Ab will be followed out in detail in a subsequent Part of this work.

Having now completed our survey of the subdiscoidal cell and its supporting cross-veins, let us return to the discoidal cell, which, as we have already seen, lags behind the subdiscoidal in evolutionary development. We can start with the very primitive position which we find in *Kennedya* (fig. 10, A), when the discoidal vein, *dv*, is merely an ordinary cross-vein, and not even in line with the subdiscoidal vein *sdv*. By the time the *Permagrion* Stage is reached (fig. 10, B), the two cross-veins *dv* and *sdv* are practically in line with one another, and this alignment is retained *without a single exception* throughout the whole of the three Suborders, *Zygotera*, *Anisozygotera* and *Anisoptera*, into which the Order *Odonata* subsequently became divided. Once this stabilized position is reached, it is easy to recognize the existence of a specialized *discoidal cell* (*dc*), even though that cell remained open basally for a very long period of geological time.

At first sight, it would seem only necessary to add here that the evolution of the discoidal cell into a complete quadrilateral was brought about (as it clearly was) by the development of an additional cross-vein below the anterior arculus, forming the *posterior arculus* of Comstock (fig. 10, D, E). This bare statement, however, does not suffice to set out the evolutionary history of this area. If we examine the existing archaic *Zygoterous* genera *Hemiphlebia* (fig. 10, C-E) and *Chorismagrion*, we note that *the discoidal cell of the forewing remains open, while that of the hindwing is already closed*, whereas, in all other known *Zygotera*, the discoidal cells of both fore and hind wings are closed quadrilaterals. This differentiation between fore and hind wings in *Hemiphle-*

bia and *Chorismagrion* was, in actual fact, *the first step towards anisoptery*; it persisted (with increasing divergence in form) in all the Liassic members of the derived Suborder Anisozygoptera, and may be recognised throughout all its stages as *a strong tendency for the development of the hindwing to outrun that of the fore.* In the Zygoptera, this tendency was checked before it had acquired momentum; after a long evolutionary interval, the discoidal cell of the forewing became closed like that of the hind, and from that point onwards the two wings developed at equal rates.

We still have one other important change to follow up in the region below the arculus, *viz.*, the fate of the *distal* portion of 1A. Most unfortunately, this has been almost wholly lost in *Kennedyia*. In my original restoration (1925, p. 64, fig. 10) I carried 1A distally almost to the limit of the gap between the two fossilized portions of the wing. This may, or may not, be correct. There is, on the one hand, the evidence of *Permagrion* (fig. 8) in favour of it; but, on the other hand, the formation shown in the larval wing-tracheation of *Hemiphebia* (fig. 7) points much more strongly to the existence of *an originally very short 1A, followed by a much longer Cu₂ with numerous descending branchlets.* This may, of course, have been due entirely to the loss of the original tracheation of 1A, and the zig-zagging of that vein distally may be due to its receiving a whole series of secondary tracheae as descending branchlets from Cu₂. To me, however, the previous supposition appears the more likely, and also it agrees most closely with our knowledge of the basic form *Brodia*, in which 1A was always very short, not extending very far beyond the subpetiole. The point must be left unsettled, pending the discovery of further fossil evidence; but, in the meanwhile, fig. 7 is given as indicating the probable course of evolution of the distal parts of Cu₂ and 1A.

We have now carried the account of the evolution of the Odonata as far as the Upper Permian, by which time true Zygoptera had appeared (*Permagrion* Stage). In Part II, we shall endeavour to trace the main lines of evolution within the Order subsequently to this.

SUMMARY.

In this paper the basic characters of the two related Orders Protodonata and Odonata are analysed and the conclusion is reached that the common ancestor is to be found in the Westphalian genus *Brodia* of the Order Megasecoptera. The Evolution of the group from this starting point is divided into five sections, *viz.*, (1) Analysis of the Primitive Characters of the common Ancestor of the Orders Protodonata and Odonata. (2) Evolution of the Order Protodonata. (3) Emergence of the Order Odonata from the ancestral stage. (4) The first true Odonata; Suborder Protozygoptera, and (5) Evolution of the Suborder Zygoptera. The stages corresponding to (1), (3), (4) and (5) respectively in the evolution of the Odonata are called the *Brodia*, *Protokennedyia*, *Kennedyia* and *Permagrion* Stages, the second of these being hypothetical but the other three based on actual fossil genera. The paper brings the evolution of the Order down to the formation of true Zygoptera in the Upper Permian, leaving the evolution throughout Mesozoic and Tertiary times to be dealt with in Part II.

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VENATIONAL NOTATION OF FIGURES.

1A, anal vein. Ab, anal bridge. Ac, anal crossing. *af*, anal field. *arc*, arculus. Ax_1 , Ax_2 , the two antenodals. C, costa. Cu, cubitus. Cu_1 , first cubitus. Cu_2 , second cubitus. *dc*, discoidal cell. *dv*, discoidal cross-vein. IR_2 , IR_3 , the two interpolated convex branches of Rs. MA, anterior median. MP, posterior median. *mb*, membranule. N, nodus. *nv*, nodal cross-vein. *pc*, coriaceous precostal area. *pt*, pterostigma. R, radius. R_1 , its main stem. Rs, radial sector, with its branches R_2 , R_3 , R_4+5 . Sc, subcosta. *sdv*, subdiscoidal cross-vein. Sn, subnodus. *snv*, subnodal cross-vein. *sq*, subquadangle.

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