ART. XXIV.—*Types of Permian Insects;* by E. H. SELLARDS.

IN the October, 1903, issue of this Journal the writer noted briefly the discovery of insects in the Permian of Kansas. The material is of exceptional interest as giving the most complete record of Permian insect life thus far obtained. Somewhat over two thousand specimens are now at hand and indicate the richness as well as the interesting character of the Permian insect fauna. For the present paper, leading types from the collection are selected for description, a full account of the fauna as a whole being reserved for subsequent monographic treatment. Unless otherwise indicated, the type specimens described are in the writer's collection.

PART I.—*Odonata.*

Odonata have not been obtained previously from the Permian. Several genera are known from the Coal Measures, those from the Commentry Coal Measures of France being particularly well known through the researches of Brongniart.* In the Mesozoic the group is fully represented by a rich series of specimens from the Solenhofen deposits. The American Permian specimens give, therefore, a welcome addition toward a fuller history of this interesting line of insect development.

The foundation studies of Comstock and Needham,† together with the special study of dragon-fly wing venation by Needham,‡ have afforded for the classification of the dragon-flies a basis much more secure than has been available heretofore. In seeking types among the living genera with which to compare the fossil forms, I have found it convenient to go repeatedly to Needham's paper, as being, in the absence of a large dragon-fly collection, the most accessible and most reliable source of detailed information regarding the wing venation of the modern forms. I very gladly express my indebtedness to these authors for their valuable investigations, without which a study of the Permian types would have been attended with much greater difficulties.

The following discussion is based, so far as it concerns Permian forms, on the exceptionally well-preserved specimen illustrated by the accompanying figures, 1 to 6. The genus and species are new and I suggest that this type be known as *Tupus permianus.*

* Récherches pour servir a l'Histoire des Insectes fossiles des Temps primaires, Charles Brongniart, pp. 394–406, 1893.

† The Wings of Insects, by J. H. Comstock and J. G. Needham, Amer. Nat., vol. xxxii, 1898, and vol. xxxiii, 1899.

‡ A Genealogical Study of Dragon-fly Wing Venation, Proc. U. S. Nat. Mus., vol. xxvi, pp. 703–764, pls. xxxi–liv.

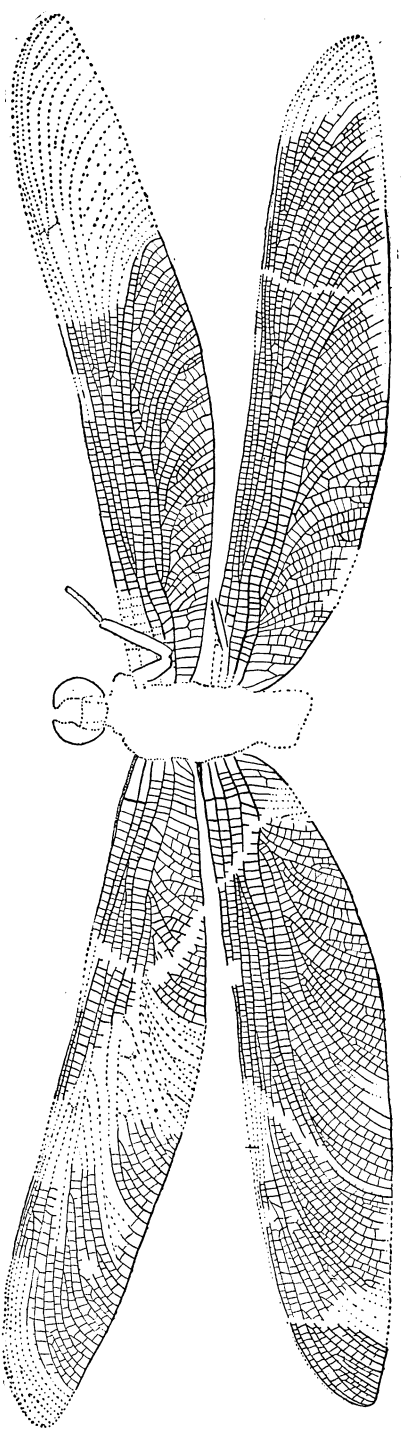

FIGURE 1.—*Tupus permianus* gn. sp. n. Type specimen slightly reduced. The specimen as illustrated is viewed from the ventral side, the base of the wings passing under the body. The strongly outlined structures on the under side of the head are apparently the mandibles, which in this as in European Paleozoic forms are unusually strong. The distal end of the femur, the tibia and a part of the tarsus of the left front leg is preserved, as is also a small part of the tibia of the second pair of legs. The tibia is spinous and the legs appear not to have been strong.

In the description to follow, the wing is considered by areas, as in this way its relations to earlier and to later forms are more readily indicated.

The base of the wing.—The base of the modern dragon-fly wing represents, as is well known, some very characteristic features. The costa is strong and marginal or with merely a narrow expanse of thickened membrane. The subcosta lies at the bottom of a deep fold. The radius and media are fused at the base and lie at the top of a corrugation. The cubitus appears in the basal part of the wing as a strong vein at the bottom of a furrow. The anal, also a strong vein, lies in turn at the top of a fold. Essentially the same features are presented by the base of the wing of Coal Measures and Permian dragon-flies, thus affording a starting point in homologizing the wing veins of Paleozoic and modern types. A clear recognition of the homologous parts at the base of the wing is of great importance in following the further interpretation of the veins throughout the wing, and I introduce here for comparison the base of the wing of a modern dragon-fly with that of the Permian form (figs. 2 and 3).

The costa.—The costa, as indicated, is in essential agreement with that of modern dragon flies. The genera thus far made known from the Commentry Coal Measures have, according to the illustrations of Brongniart, a more distinct precostal area than has *Tupus*. The one genus known from the American Coal Measures, *Paralogus* Scudder, in which this basal area is preserved, has, according to Scudder,* the subcosta (mediastinal) close to the margin.

The subcosta.—The subcosta continues simple, reaching usually beyond the middle line of the wing, gradually approaching and merging in the margin. In the modern forms the subcosta terminates at the strong cross vein forming the nodus. This special modification is concerned chiefly with the specialization of cross veins and will be considered under that head.

The radius and media.—The radius and media separate at a distance of from $1\frac{1}{2}$ to 2^{cm} from the base, the media going off at an oblique angle. $Radius_1$ continues as a simple vein to the apex of the wing. The media divides immediately after separating from the radius. The two resulting divisions admit of interpretation as the homologues of the veins marked in all of Needham's figures as M_{1-3}, and M_4, the upper division (M_{1-3}) falling into a furrow, the lower (M_4) topping a fold. Their subsequent divisions likewise admit of homologizing in the same way. M_4 runs in

* Insect Fauna of the Rhode Island Coal Field, Bull. U. S. Geol. Survey, No. 101, p. 20, pl. 1, figs. *a* and *b*, 1893.

a curved course and reaches the inner border well toward the apex, and has, as is usual with the general run of Odonata,

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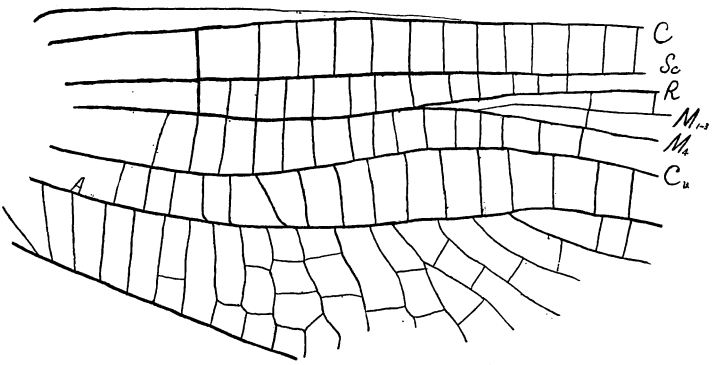

FIGURE 2.—Base of the right front wing of *Tupus permianus*. C, costa; Sc, subcosta; R, radius; M_{1-3}, branches 1 to 3 of media; M_4, fourth branch of media; Cu, cubitus; A, anal. Drawn with the camera lucida; enlarged four diameters.

particularly Odonata Anisoptera, a considerable number of veins from the lower side filling the space between itself and the cubitus. M_3 separates from M_{1-2}, and, again agreeing to a surprising degree with M_3 of Anisoptera, runs in a curved course parallel and close to M_4. No interpolated veins appear between M_3 and M_4. M_{1-2} divides opposite the subnodus; from this point both divisions continue as simple veins, presenting again an unexpected agreement with Odonata Anisoptera.

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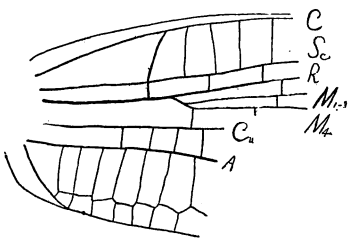

FIGURE 3.—Base of the wing of a modern dragon-fly. Lettering and enlargement as in figure 2. Both wings are viewed from the ventral surface, the body obscuring the extreme base of the wing.

Radial sector, subnodus, and oblique vein.—It is a well-known fact that to recognize the radial sector in the adult dragon-fly wing is often a matter of difficulty. With the Paleozoic forms, the adults only of which are available, we must therefore expect to recognize the radial sector, as a rule, from its relation to other veins rather than from any evidence in the sector itself. Fortunately, however, in most dragon-flies structural evidence bearing on the position of the radius is not wanting even in the adults. The keen observations of Need-

ham emphasized the fact that there exists in the wing of most adult dragon-flies a persistently oblique cross vein lying usually at or just beyond the separation of M_{1-2}; also a similar oblique vein above, uniting the radius and M_1. From the nymph wing it was found that the trachea of the radial sector crosses $M_{1\ 2}$, and that the oblique apparently cross veins are in fact parts of the sector. An examination of this region on the Permian genus *Tupus* reveals the presence of such an oblique vein arising from M_2 at a point just beyond the separation of M_1 and M_2; also an equally well-marked oblique vein, the subnodus, connecting the radius and media. Bearing in mind the complete agreement of all other veins of the radio-medial area with those of the same area in modern Odonata, there can

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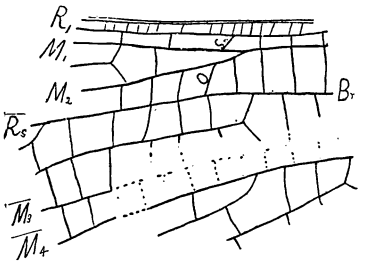

FIGURE 4.—Enlarged detail of the region of the subnodus of *Tupus permianus*, taken from the right front wing. Sn, subnodus; O, oblique vein; Br, bridge; R, radius; M_1, first main branch of media; M_2, second main branch of media; Rs, radial sector; M_3, third, and M_4, fourth main branches of media. Enlarged 4 diam.: drawn with camera lucida.

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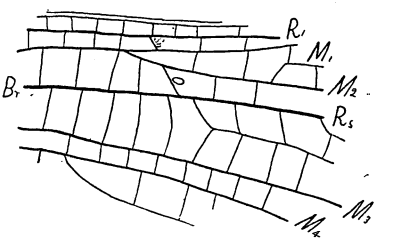

FIGURE 5 —Same area from the left hind wing of *Tupus permianus*. Enlargement and lettering as in figure 4. In this wing there is a slight depression (not shown in the figure) running from the subnodus toward the oblique vein.

scarcely remain a doubt as to the meaning of these two oblique cross veins. They clearly indicate a crossing of the radial sector. The area of the wing in the region of the crossing of the sector is shown enlarged in the accompanying camera lucida sketches. The fundamental significance of the crossing of the sector as a bond or relationship between Paleozoic and modern forms is too obvious to require further emphasis.*

It will be observed that in this Permian genus there is apparently a loss of that part of the sector lying between M_1 and M_2.

* Handlirsch's statement, Revision American Paleozoic Insects, p. 689, with reference to the Protodonata, that the "intersection of the longitudinal veins" is "still entirely wanting," can not, I feel sure, be maintained in view of the evidence here presented. The agreement of the veins of the entire radio-median area is altogether too complete to admit of explanation on any grounds other than that of strict homology.

In the left hind wing there is a slight depression not shown in the illustration, continuing the subnodal vein and running toward the oblique vein, indicating possibly the position of the vein or trachea. A comparison of the position of the subnodus

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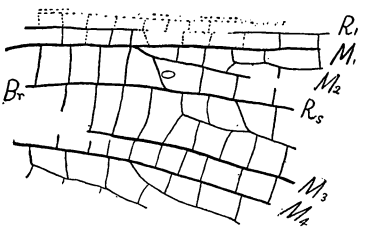

FIGURE 6.—Same area from the right hind wing of *Tupus permianus*. Dotted lines indicate restored border of the wing lost from the breaking of the matrix. Enlargement and lettering as in figures 4 and 5,

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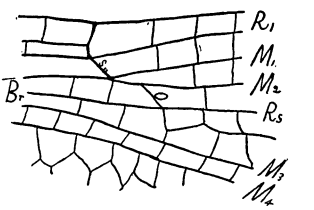

FIGURE 7.—Same area from the wing of a modern dragon fly. Enlargement and lettering as in former figures.

and oblique vein as seen in *Tupus* with the position of the trachea as seen in many modern nymphs is instructive. From the nymphs it will be seen that the trachea often lies across the media beyond the separation of M_1 and M_2, occupying approximately the position of the subnodus and oblique vein of *Tupus*. In the adult condition of modern dragon-flies the subnodus, as a rule, meets the media just at the point of separation of M_1 and M_2. It is probable that the subnodus has migrated in modern adult dragon-flies to its present position from an earlier primitive position, sometimes beyond the forking of M_{1-2}, sometimes perhaps basad of that point. As a result of its important function as a brace the subnodus is held firmly in place, while the oblique vein, serving no such responsible function, is much less constant in position.

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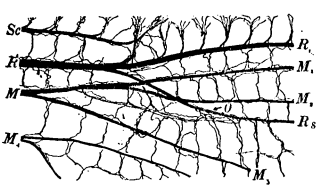

FIGURE 8.—Position of trachea of same area of modern nymph dragon-fly, genus *Didymops;* after Needham. Lettering as above. The indistinct trachea preceding the bridge is present, although not lettered.

The cubitus.—Cu_1 continues from the strong basal origin as a simple sinuous vein meeting the inner border slightly beyond the middle line of the wing. It is observed that the various genera of modern dragon-flies differ not a little among them-

selves in the disposition of the cubitus. With the advanced Anisoptera there is, as demonstrated by Needham, an abrupt bend in the cubitus just back of the arculus, the bend thus made forming the base of the triangle. With the Zygoptera the bend is much less conspicuous and the sinuous or uniformly curved type of Cu_1 is the rule. The Zygoptera have thus retained a cubitus much less differentiated from that of the Permian form than have the Anisoptera. The course of Cu_2 in the Odonata is one of the highly characteristic peculiarities of that unique order. Its distinctive feature lies in the fact that immediately after leaving Cu_1 it fuses with the first anal, continuing that vein and giving in the adult the appearance of a single strong vein from the base of the inner border. In those advanced Anisoptera in which the cubitus is most abruptly bent, Cu_2 is given off at the point of closest approach to the anal. With those more generalized Odonata in which the cubitus has a sinuous course, the basal part of Cu_2 appears as a cross vein. It is hardly to be expected that the particular cross vein representing the basal part of Cu_2 can in all cases be recognized in the fossil genera. It is to be noted, however, that in the Permian genus *Tupus* a cross vein some distance from the base becomes conspicuous by its strongly slanting position (fig. 2). A similar slanting cross vein is seen in Scudder's careful illustration of the Coal Measures genus *Paralogus*.*

The characters thus far discussed are those which concern the distribution of the main veins of the wing, and as such are without doubt the structurally more important characters of the wing. In these characters there is found to exist essential agreement throughout between Paleozoic, Mesozoic, and modern dragon-flies. That there are differences, many and obvious, scarcely needs stating. Such differences as exist, however, are associated almost wholly with the specialization of cross veins and as such are of secondary importance. They are conveniently discussed under the heading of cross veins.

Cross veins.—Specialization of cross veins plays a leading part in the development of mechanical strengthening devices with which the wings of modern dragon-flies are so richly supplied. With the Paleozoic dragon-flies, however, the cross veins are but little differentiated among themselves. Such specialization as has occurred has taken the direction principally of the matching of cross veins and is most advanced in the basal and dorsal part of the wing. In the Permian genus *Tupus* there is observed near the base a strong brace corresponding to the triangular brace at the base of the wing of

* Bull. U. G. S., No. 101, pl. i, fig. a.

many modern genera. Lines of matched cross veins are seen also in the basal part of the wing (fig. 2).

Nodus and stigma.—On the Paleozoic genera thus far known, both nodus and stigma are apparently lacking. Since the nodus is recognized as merely a strongly developed cross vein running from the costa to the radius, at which cross vein the subcosta usually terminates, the existence of a weak nodus on some of the more specialized late Paleozoic genera need occasion no surprise. It is to be expected that the subcosta will in early types reach beyond the cross vein, the nodus appearing simply as a strong cross vein from costa to subcosta, matched with a similar strong cross vein from subcosta to radius. Much the same may be said of the stigma, a strengthening structure thus far not observed to occur on these early Odonates.

The arculus.—A very conspicuous structural feature of the modern dragon-fly wing is the arculus. As is well known, the arculus of this, as of other orders in which it occurs, consists in part of the media directed obliquely at its point of origin from the radius, and in part of a strong cross vein from the media to the cubitus. The arculus, as a conspicuous feature, is absent from the wings of Paleozoic dragon-flies; yet the elements which compose it are there and in their respective positions. For the formation of a characteristic arculus there is needed scarcely more than a slightly accentuated bend of the media at its separation from the radius and a correlated strengthening of the cross veins bearing the chief stress in the support of the media. Along with this will go naturally the more or less complete disappearance of the now unnecessary accessory cross veins.

Triangle and quadrangle.—The structures known as triangle in the Anisoptera and as quadrangle in Zygoptera result, as in the case of the arculus, from specialized cross veins in conjunction often with a modified course of the adjoining main veins. The base of the triangle of the Anisoptera is formed by the cubitus, and results from an abrupt bend of that vein just beyond the arculus. The sides of the triangle are formed each by a cross vein running from the cubitus to the media. With the Zygoptera, in which the bend of the cubitus is less abrupt, there is naturally a less well-marked structure in this region, and as the arrangement of cross veins gives to this area a quadrangular rather than a triangular shape, Needham has proposed to designate it as the *quadrangle.* As has been noted above, the cubitus of the known Paleozoic forms agrees with that of the generalized modern Odonates in its sinuous, rather than abruptly bent course. With the most generalized of modern Odonates the quadrangle or triangle, as conspicuous

features, can scarcely be said to exist. To this extent they approach the Permian type.*

The bridge.—To the supplementary longitudinal vein interpolated between M_{1-2} and M_3 and connecting with the radial sector, Needham has applied the term *bridge*. The bridge appears as a normal feature in *Tupus*. A part of the bridge is seen also in *Paralogus*. Unfortunately the tip of the wing of that genus is not preserved. The crossing of the radial sector has doubtless promoted the early development of this structure.

Classification.

In the scheme of classification of Paleozoic insects proposed by Professor Samuel H. Scudder, the Paleozoic dragon-flies were disassociated from their modern descendants and placed along with all other Paleozoic insects in the Paleodictyoptera. Brongniart (Récherches des Insectes fossiles) places the Protodonata as a family group under the large order of Neuroptera. Professor Anton Handlirsch, in his recent publication (Revision of American Paleozoic Insects) has advanced the Protodonata to ordinal rank to stand as a Paleozoic order coördinate with the Odonata of Mesozoic and modern times.

It will be remembered that Professor Scudder, in defense of his general plan of classification, has urged repeatedly that the insects of the Paleozoic were more closely related *inter se* than to their descendants of the Mesozoic and later times. A classification based upon Scudder's principle must, in the nature of the case, break down with the advance of knowledge of extinct forms, for as the life history of the various lines of descent is continuous, it necessarily follows that the artificially placed dividing line between the Mesozoic and Paleozoic can remain a distinct break only so long as there remains time for a considerable development between the earliest known Mesozoic and the latest known Paleozoic representative of that particular line. In Scudder's classification emphasis is thrown on the interrelation of associated but diverging groups, or what may be called the lateral relation of organisms, rather than on the lineal or phylogenetic relations. In this connection I have urged a principle of classification† by no means new in its application, as follows:—"Any natural group of organisms should be recognized as extending back in time until a point is reached at which that group coalesces with a group or groups of coördinate rank, or unites with the parent stock." The principle proposed by Scudder necessitates breaking phyla,

* As a genus with cubitus unexpectedly similar to that of *Tupus*, compare *Pseudophœa*.

† This Journal, vol. xviii, p. 121, 1904.

the earlier members to be grouped with the parent or associated phyla, while the later stand in our classification under distinctive names. The line selected as the point at which to break the various insect phyla was the imaginary line dividing Paleozoic and Mesozoic—a line subject to change with the advance of stratigraphy and paleontology and in any case confessedly a line of convenience. A more natural classification is attained by recognizing under a single head an entire phylum. Difficulties will be met in applying the principle, owing to the near approach of the first ancestor of a phylum to the parent phylum (unless the origin of phyla should prove to be much more sudden than has been heretofore generally supposed). In practice it is clearly safe to recognize a phylum under a common head as far toward its point of origin as the evidence available permits the line to be with certainty determined. Thus, with the dragon-flies, there is apparently no doubt of the origin of the phylum as a distinct line in Carboniferous or pre-Carboniferous time and continuing to the present time. They are therefore entitled to a group name distinctive of the phylum as a whole.

Regarding the relative rank to be assigned the Protodonata, whether ordinal as proposed by Handlirsch* or subordinal, I would urge again what has been shown above, namely, that the main veins of the wings of the Coal Measures and Permian dragon-flies present an arrangement in agreement in their major characters with that of both Mesozoic and modern dragon-flies. The differences found are due to the specialization of cross veins, with which are associated minor changes in the direction of some of the main veins. These secondary differences are to my mind insufficient characters on which to base ordinal rank. The characters which are now known to exist entitle the Protodonata in my view to not more than subordinal rank. According to this view the order Odonata consists of three suborders, as follows: Protodonata, Zygoptera, and Anisoptera. The term Odonata is thus still available as an ordinal term, covering the Odonate phylum as a whole.

* Revision of American Paleozoic Insects, Proc. U. S. Nat. Museum, vol. xxix, p. 689, 1906.