ART. XX.—*Kansas Permian Insects. Part 4. The Order Paleodictyoptera;* by R. J. TILLYARD.

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As originally planned, this number of the series of studies dealing with the Kansas Permian insects included the actual description of the new Paleodictyopteron, *Dunbaria fasciipennis* Till., but this description was finally incorporated in Part 1 ("The Geologic Occurrence," by Carl O. Dunbar[1]). Owing to Lameere's recent work on the wing-venation of the Paleodictyoptera and allied orders,[2] it has become clear that a complete understanding of the venation of such orders as the Protodonata, Odonata and Plectoptera, to be discussed in later parts, can only be reached by making a careful comparison between them and the order Paleodictyoptera. Hence I propose to precede the description of these orders with the following further remarks and considerations on the genus *Dunbaria,* which will not only supplement my original description, but will also serve as a peg on which to hang a discussion of Lameere's new theory of wing-venation, and will provide the necessary foundation for the venational notations to be used in dealing with the Protodonata, Odonata and Plectoptera.

The genus *Dunbaria* belongs to the family Spilapteridæ, which Lameere, in his most recent work, appears to consider as belonging to the Plectoptera proper, rather than to the Paleodictyoptera. With this opinion I cannot agree. True Plectoptera are abundant in the Kansas Lower Permian, and differ markedly from the Spilapteridæ, notably in the abundant and strongly marked cross-venation, in the development of a unique system of triads on Rs, M and Cu_1, and in the origin of the radial sector and anterior median of Lameere from a common basal stalk. In contrast with true Plectoptera, *Dunbaria* exhibits an almost clear membrane between the branches of the main veins; only here and

[1] This Journal (5), 7, 171-209, 1924.

[2] A. Lameere, Sur la nervation alaire des insectes, Bull. Sci. Acad. Roy. Belg., 38-49, 1922 (English translation of same, by A. M. Brues, Psyche, 123-132, 1923).

there are to be made out a few weak cross-veins, while, in certain places, the remnants of the old Paleodictyopterous meshwork can also just be seen; the branches of Rs and Cu_1 are not triadic, but pectinate; and, finally, Rs and M are of the Paleodictyopteroid type, the former arising separately from the anterior median, which itself

FIG. 1.

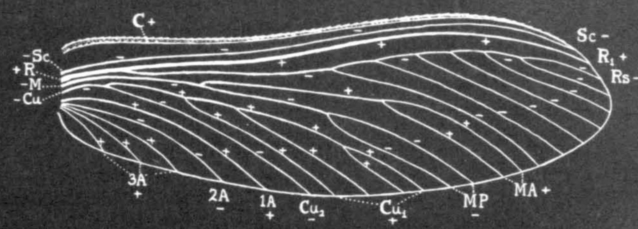

Fig. 1.—*Dunbaria fasciipennis* Till., venation of forewing, to illustrate some points in Lameere's theory of insect wing-venation. The usual Comstock-Needham notation is used except MA, anterior median of Lameere, MP, posterior median, or submedian, of Lameere. Convex veins are marked +, concave veins —.

forms a markedly convex anterior branch of M. Further important points of difference are the presence, in *Dunbaria,* of a very strong costal vein running nearly to apex of wing (text fig. 1), but not distinctly separated from the costal margin; in the Plectoptera, there is a short costal vein, distinctly separated from the costal margin in the Lower Permian forms; in *Dunbaria,* the costal vein is strongly serrated, as in some other Paleodictyoptera and all Protodonata, whereas in Plectoptera the costal margin is not serrated. The costal vein of Plectoptera is connected distally with Sc by a strong brace, which is absent in *Dunbaria* and all other Paleodictyoptera.

Lameere, in 1922, put forward a new theory of the wing-venation of insects in general, based chiefly on an extended study of the Paleodictyoptera. *Dunbaria* exemplifies the points made by Lameere so clearly that I do not hesitate to use it as a type with which to illustrate the main points of Lameere's theory, which must be clearly understood before any adequate descriptions of fossil wings belonging to the orders Protodonata, Odonata and Plectoptera can be made. Lameere's original paper is in French, but a translation of it was published by A. M. Brues in "Psyche," 1923, pp. 123-132; unfortunately, numerous errors of translation occur therein, and in several instances Lameere's meaning is either obscured or even reversed, so that those who have access to the original paper should read it for themselves.

According to Lameere, in the original insect wing, the scheme of which is preserved completely in the Paleodictyoptera, each main vein consisted of an anterior convex[3] (*haut*) branch and a posterior concave[3] (*bas*) branch; in Lameere's nomenclature, the convex branch takes the name of the whole vein, while the concave branch is distinguished by adding the prefix *sub-*. Thus he speaks of the costa and subcosta, the radius and subradius, the median and submedian, the cubitus and subcubitus, and so on. In *Dunbaria* (text fig. 1), the costa (C) lies along the costal margin; the subcosta (Sc) is of normal form, but shows no sign of basal attachment to C; the radius (R_1) is normal; the subradius (Rs) is the branched vein known in the Comstock-Needham system as the radial sector. The anterior convex portion of the median vein we have distinguished in text fig. 1 as MA, while the posterior concave portion is called MP; this notation has been adopted because the ordinary Comstock-Needham notation will not apply in the case of this vein, as we shall discover when we follow out the course of its evolution in more specialized orders. The anterior convex branch of the cubitus is Cu_1 in text fig. 1, as in the Comstock-Needham system, and the posterior concave branch is Cu_2; we see no need to alter the well-established notation for these two veins, which keep the same clearly marked character throughout all the orders. As regards the so-called anal veins, Lameere would recognize four, viz. a penultimate (convex) with a concave branch called the subpenultimate; and an ultimate (convex) with a concave branch called the subultimate. In *Dunbaria*, as in recent insects, I prefer to keep to the Comstock-Needham notation, as it seems to me

[3] In A. M. Brues' translation, the words *haut* and *bas* are sometimes translated *high* and *low* respectively, sometimes *upper* and *lower*; the former is acceptable, the latter obscure and indefensible. It is better to keep to the well understood English equivalents *convex* and *concave*.

only possible to recognize *three* anal veins at the most, viz. 1A, 2A and 3A. 1A is the convex vein immediately below Cu_2; 2A in *Dunbaria* is the simple concave vein below 1A; 3A in *Dunbaria* is three-branched in both wings, all three branches being weakly convex.

Two main criticisms may be levelled against Lameere's theory, which, at the same time, must be admitted as a notable and valuable contribution to our knowledge of insect wing-venation:—

(1) The desire to make every main vein in the wing conform to a basic theoretical plan has apparently somewhat blinded the author to the facts of the case. While we may admit that the radius, media and cubitus do conform to the theoretical plan, surely the veins lying anterior and posterior to these, viz. the subcosta and the anals respectively, do not, or, at the most, do so only very incompletely.

(2) Lameere appears to have made a mistake in his interpretation of the fate of MA and MP in most recent insects. He states (translation in "Psyche," 1923, p. 124):—"The sector of the median is missing in the Perlids and consequently does not figure in Comstock's scheme" and he further states that this sector is the vein which I have called M_5 in the Holometabola. Now, in all recent insects, Comstock's media is a *concave vein*, while M_5, when it occurs (and it never occurs as a complete vein, only as a basal piece connecting M with Cu_1) is always *convex*. The obvious explanation, to me, is that Comstock's media is actually the homologue of the posterior median, MP (Lameere's submedian), while the vein M_5 is a new development, being merely an oblique strut designed to strengthen Cu_1 basally. Thus, it is actually not the posterior median which appears to be missing in recent insects, but the anterior median or convex portion of the media; this, as I shall hope to show in subsequent parts of this work, is not missing, but has become attached permanently to Rs, forming that portion of it which Comstock calls R_{4+5}.

An important point which has been entirely overlooked by Lameere is that, whereas, in the case of the radius, the basal piece is continued straight on by the convex branch R_1, in the case of the media and cubitus the basal piece is continued straight on by the concave or posterior branch, MP or Cu_2, as the case may be. This is as clearly to be seen in the case of *Dunbaria* and other Paleodictyoptera as it is in many recent insects. Further, MA had, from very early times, a tendency to become linked up with Rs instead of with M, while Cu_1 had a similar tendency to become linked up with M by means of the short oblique strut M_5 already mentioned above. The most obvious interpretation of these facts seems to me to be that, in some more ancient type of insect wing than any yet discovered, there was originally only one strong convex vein in the wing, viz. R_1, forming the main support of the wing membrane, with a number of weaker concave veins placed above or below it, viz. Sc running in a groove between C and R_1, Rs and its branches supplying the apical portion of the wing, and, below Rs, only MP, Cu_2 and 2A supplying the posterior part of the wing. The original tracheal supply of the developing wing would have followed the courses of these veins. As later developments, at first without fixed tracheal supplies, we may postulate the formation of MA, Cu_1, [illegible] and 3A as convex interpolated sectors, arising at first from the outer margin of the wing and running backwards between the original concave veins. When these sectors were sufficiently developed, they would receive tracheal supplies, and would tend to become permanently attached to one or other concave vein near its base; but there would always remain a tendency for this connection to vary, and, in many cases, we might expect to find a connection made with both the concave vein above and the one below. Also, when the connection was made, the interpolated vein would not continue the line of the original concave vein straight back, but would show a short curved basal portion at the connection. Now we actually find all these conditions fulfilled in a large number of instances; MA, attached to MP in Paleodictyoptera, is attached to Rs in most other orders, while Cu_1, usually attached to Cu_2 not only in Paleodictyoptera but also in most other insects, is yet frequently attached also, by means of M_5, to MP above it, and in some recent insects (e.g., Trichoptera and Lepidoptera) has a much stronger connection with MP than with Cu_2. Text fig. 2 shows the original plan of the insect wing on this theory, with the interpolated convex

sectors and their possible connections indicated as dotted lines. It will be seen at once that this type of vein-formation is the same as that of triad-formation in the Plectoptera (Tillyard, 1923),[4] except that, in a true triad, the interpolated vein separates two branches of a single main vein, whereas, in the figure, if the interpolated con-

FIG. 2.

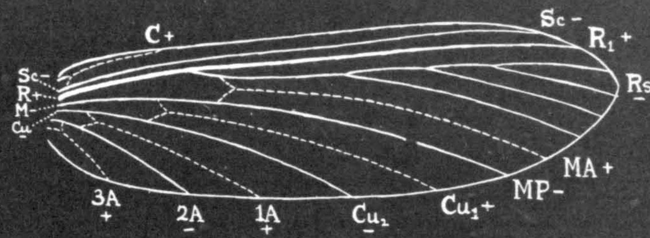

Fig. 2.—Diagram of an insect wing to illustrate the hypothetical formation of the venation suggested in this paper. The original system of veins, consisting of convex radius (R_1) and a system of concave veins, is fully lined in; the interpolated convex sectors and their possible basal connections are indicated by dotted lines. Convex veins are marked +, concave veins —.

vex veins are considered as the middle members of negative triads, then each of them separates two *separate* concave veins. But the underlying principle is the same in both cases, and leads to the type of wing in which convex and concave veins occur alternately.

The above remarks will, it is hoped, help to make clear the position as regards the outlook on insect wing-venation modified by Lameere's theory, and considerations which arise from it. In Part 5, we shall consider the problem of the venations of the orders Protodonata and Odonata in relation to what has already been stated here.

The only other point of interest which has not been fully discussed in the study of *Dunbaria* is the terminal portion of the abdomen and its appendages. Text fig. 3 shows an enlargement of this part of the allotype female specimen, as far as it can be made out (the greater portion of the immensely long cerci being omitted). Two

[4] R. J. Tillyard, The wing-venation of the order Plectoptera or mayflies, Journ. Linn. Soc. London, Zool., 35, 143-162, 1923.
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abdominal segments (IX and X) are shown; the tergites and sternites, if separate, cannot be clearly made out, as the segments have been somewhat twisted sideways during fossilization. Below these, a portion of a primitive ovipositor can clearly be seen, consisting, apparently, of a pair of gonocoxites (*gcx*) carrying a pair of terminal

Fig. 3.

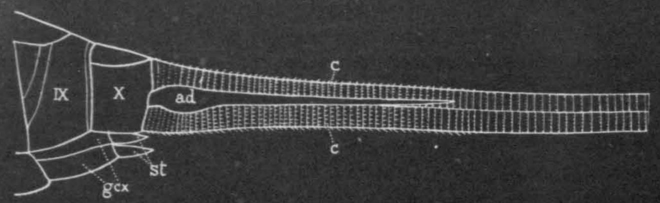

Fig. 3.—*Dunbaria fasciipennis* Till., end of abdomen and appendages of allotype female (about x 6. *ad* appendix dorsalis, *c* cercus, *gcx* gonocoxite, *st* style, IX, X, abdominal segments).

styles (*st*); if these are rightly interpreted, they indicate a relationship rather with Odonata than with Plectoptera. The immensely long and strong *cerci* (*c*) are beautifully preserved and closely similar to those of Plectoptera and Perlaria at the present day. Each cercus is made up of innumerable tiny segments or annuli, much shorter than wide, and provided with a ring of short cilia; near the base of the cercus, the first five or six annuli are more or less indistinctly marked off and without cilia; then follow some forty or more very short annuli with very distinct cilia, and these gradually merge into somewhat longer annuli in which the minute sockets of the rings of cilia are distinctly visible apart from the distal margin of each annulus. As in recent insects with long cerci, the annuli tend to increase in length and distinctness as one passes from base to distal end of the cercus.

The two cerci are pressed down, in the type fossil, so as to lie alongside one another and perhaps slightly overlap for most of their length. But, for the first sixty annuli or thereabouts, they are separated by a definite space in which practically no annulation or ciliation can be seen (the rock surface being irregular in this space), and which ends in a slender apex definitely lying upon

the upper cercus in text fig. 3. It seems highly probable that this space represents the position of the short *appendix dorsalis* (*ad*), and that the impression made by it has been lost when the fossil was broken from the rock, just as the impressions of a number of highly convex veins have been lost in a similar manner in other fossils. This appendix dorsalis was evidently considerably swollen basally, and then tapered gradually to a very slender apex. Similar types of appendix dorsalis can be found in a number of recent Plectoptera.

NOTE:—Specimen No. 5020 *a b*, is an additional paratype forewing of *Dunbaria fasciipennis* Till., not previously mentioned; it has the apex and extreme base missing, and the pigmentation very strongly marked. The obverse (No. 5025 *a*) is in Yale University Collection, the reverse (No. 5020 *b*) in Cawthron Institute Collection. *Specimen No. 5021a* in Yale University Collection, with its counterpart *5021b* in Cawthron Institute Collection, is a fragment of a hindwing, with dark pigmentation and narrow fasciae. *Specimen No. 5022* in Yale University Collection is a fragment of a hindwing with wider fasciae.

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