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REVIEW OF THE CALVERTIELLIDAE, WITH
DESCRIPTION OF A NEW GENUS FROM
PERMIAN STRATA OF MORAVIA
(PALAEODICTYOPTERA)

BY JARMILA KUKALOVÁ*
Charles University, Prague

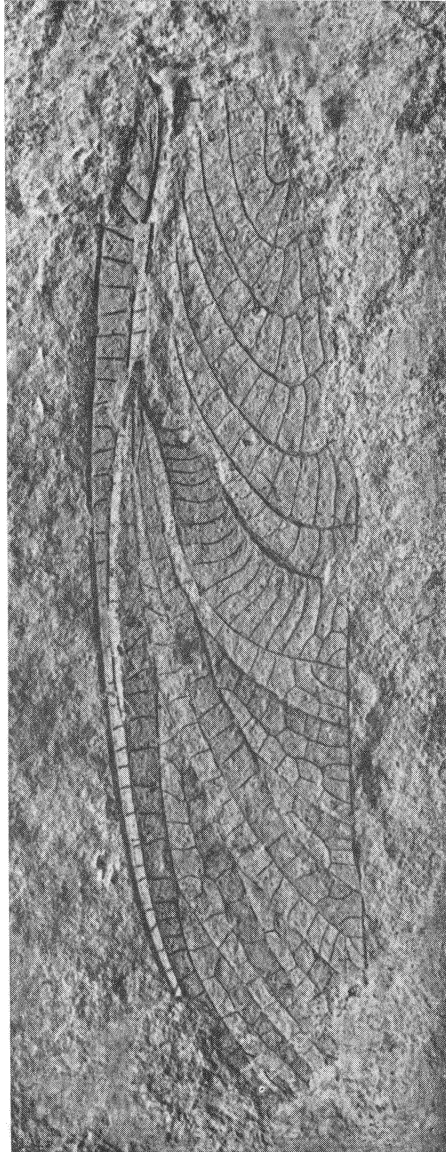
The extinct order Palaeodictyoptera now includes some twenty families, which appear to represent many lines of evolution radiating in different directions. Most of them resemble the Ephemeroptera, at least superficially, more than any other order of living insects but a few show some features highly suggestive of the Odonata and Protodonata.

The most notable of the latter is the family Calvertiellidae, now represented by *Calvertiella* Tillyard from Lower Permian deposits near Elmo, Kansas, and by *Moraviptera* Kukalová from the very base of the Lower Permian strata in Moravia (Zbýšov). Recently, some remarkably preserved fossils belonging to a new genus were found in Moravia at the Obora locality. Since both fore and hind wings are preserved, they add a great deal to our knowledge of this group of Palaeodictyoptera. The present paper consists of a review of the Calvertiellidae and the description of the new genus *Moravia* from Czechoslovakia.

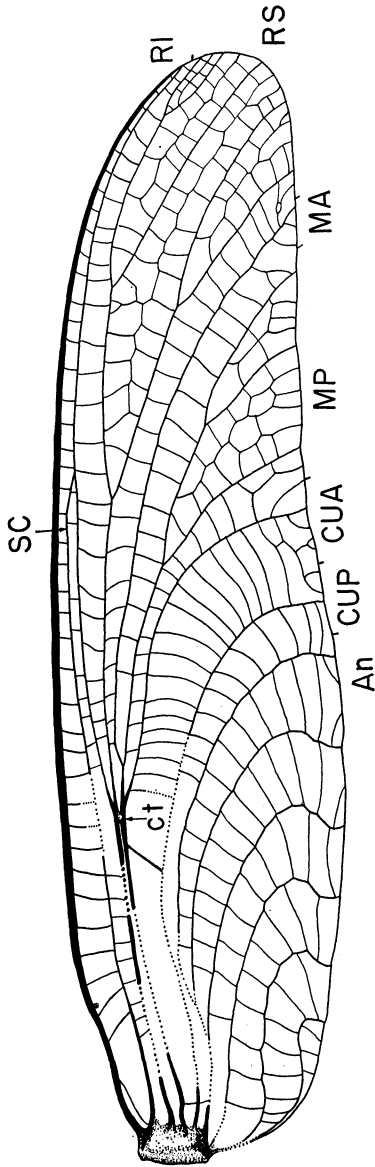
Calvertiella was originally (1925) placed by Tillyard in the family Protagrionidae within the order Protodonata, but this was before the Protodonata (as well as Odonata) were known to lack the veins MA and CuA. The family Calvertiellidae, established by Martynov in 1931, was transferred to the Palaeodictyoptera by

*Current address: Biological Laboratories, Harvard University.

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Calvertiella permiana Tillyard (reverse of holotype). Lower Permian of Kansas. Original photograph, $\times 5$.



Text-figure 1. *Calvertiella permiana* Tillyard. Drawing of fore wing, based on obverse and reverse of the holotype. Lower Permian of Kansas. Original drawing.

Lettering: C, costa (+); Sc, subcosta (-); R, radius (+); Rs, radial sector (-); MA, anterior cubitus (+); MP, posterior cubitus (-); CuA, anterior cubitus (+), CuP, posterior cubitus (-); An, anal area (+); ct, cuticular thickening (+); (-) concave veins; (+) convex veins.

Handlirsch in 1937, along with the Protagrionidae. Since then, both families have been treated as Palaeodictyoptera.¹

ORDER PALAEO-DICTYOPTERA GOLDENBERG

Family Calvertiellidae Martynov, 1931

Calvertiellidae, Martynov, 1931, Bull. Acad. Sci. URSS, 1:146 [Protodonata (Meganisoptera)]; Handlirsch, 1937, Ann. Naturh. Mus. Wien, 48:32 [Palaeodictyoptera]; Martynov, 1938, Trav. Inst. paleont., 7(4):41 [Protodonata]; Carpenter, 1943, Bull. Geol. Soc. Amer., 54:536 [Palaeodictyoptera]; Laurentiaux, 1953, Traité de paléont.:424 [Palaeodictyoptera]; Carpenter, 1954, Bull. Mus. Comp. Zool., 108:786 [Palaeodictyoptera]; Kukulová, 1955, Sborník Ústř. Úst. geol., 21:571 [Palaeodictyoptera]; Rodendorf, 1962, Osnovy paleont.:52 [Palaeodictyoptera].

DIAGNOSIS. The following diagnosis of the family is based on a study of the type of *Calvertiella permiana* Tillyard, 1925, as well as on the material from Moravia.

Fore wing: a very short convex veinlet present at the basal part of the costal area; Sc terminating on R₁ slightly beyond mid-wing; R_s arising before the end of the first third of wing length, with 3-4 main branches; a cuticular thickening (ct)² between R and M, at about the level of the origin of R_s; stems of R and M independent at the wing base, but approaching each other near the point of origin of R_s; M forking near the level of the origin of R_s; MA unbranched, MP branched; stem of Cu independent, its branches simple and strongly curved towards posterior margin; CuA diverging towards M near the level of origin of R_s and fusing with it for some distance, or connected with it by means of a short, convex connecting vein; in its further course, CuA runs very near to the posterior branch of MP; area between CuA and CuP broad; 6 anal veins, at least the first 3 arising from one independent stem, all strongly arched, especially the proximal ones; cross veins more or less numerous, forming a reticulation in at least some areas of the wing; intercalary sectors more or less definitely indicated in the radial and medial areas.

Hind wing: broad basally and triangular in shape (*Moravia*, n.g.); anterior margin concave; basal veinlets in costal area somewhat better developed than in the fore wing; Sc terminating much

¹For a discussion of the nomenclatural problems involving the name Protodonata see Carpenter, 1943 and 1954.

²Not known in *Moraviptera* because of poor preservation in the region of the origin of R_s.

as in fore wing; Rs arising slightly more basally than in the fore wing, with about 4 main branches; cuticular thickening as in fore wing; stem of M independent, forked near the level of origin of Rs; MA unbranched, MP branched; stem of Cu independent, dividing into two simple branches, arched strongly towards posterior margin; CuA diverging towards M as in the fore wing, and then continuing close to the posterior branch of MP; 4 anal veins, at least 3 arising from the base independently of each other, somewhat recurved; cross veins numerous, forming a reticulation over much of the wing; intercalary sectors in radial and medial area.

RELATIONSHIPS: The family *Calvertiellidae* clearly has a very specialized venation and seems far removed from most of the families of the order. This is shown by the short Sc, proximity of CuA and MP, the wide separation of CuA and CuP, the curved CuP, recurved anal veins (fore wing) and presence of intercalary sectors. Its closest relatives in the order seem to be the *Eugereonidae* (including *Dictyoptilidae*; see Carpenter, 1964, p. 104), which differ from *Calvertiellidae* in having Sc long and terminating on C, CuA more remote from the posterior branch of MP, CuP branched and less arched, area between CuA and CuP narrower, anal veins less arched, absence of intercalary sectors and of the cuticular thickening. The hind wing of *Calvertiellidae* is broader than that in the *Eugereonidae* and more triangular in shape.

It is interesting to find in the wings of the *Calvertiellidae* a short, simple or branched veinlet, which has now been noted in several families of *Palaeodictyoptera* (e.g. *Breyeriidae*, Kukalová, 1958; *Spilapteridae*, Carpenter, 1964). In *Calvertiella* it is a simple convex vein, but in the hind wing of *Moravia*, n.g., it is better developed, with a series of short veinlets. Although this vein may actually be a basal branch of the costa, since the area set off cannot reasonably be considered homologous with the precostal area of the *Orthoptera*, I have termed it the postcostal area (Kukalová, 1963). The vein seems more likely to be homologous with the costal brace of *Ephemeroptera*, resembling especially the Permian types.

Geological occurrence of family: Lower Permian of Kansas (USA) and *Moravia* (Czechoslovakia).

Genera included: *Calvertiella* Tillyard, 1925; *Moraviptera* Kukalová, 1955; *Moravia*, new genus (herein).

Genus *Calvertiella* Tillyard

Calvertiella Tillyard, 1925, Amer. Journ. Sci., 10:43; Tillyard and Fraser, 1938, Austral. Zool., 9(2):141-142; Fraser, 1957, Royal Zool. Soc. NSW:24.

DIAGNOSIS. Fore wing: long and slender, broadest before mid-wing; veins strong, wing membrane thin; anterior margin slightly concave near base, then almost straight; apex slightly directed posteriorly; posterior margin slightly concave at mid-wing; Sc terminating on R at about the end of the second third of the wing length; R₁ long; R_s originating before the end of the first third of the wing length, forming three branches, the first forked; an oblique cuticular thickening (ct) running from the very base of R_s to M + CuA; M close to R before, and branching slightly beyond, the level of the origin of R_s; MA simple; MP giving rise to two branches; Cu dividing before the origin of R_s, CuA fused with M for a short distance, then closely following MP; CuP simple, arched strongly backwardly; 6 anal veins arising perhaps from a common stem, recurved and slightly sigmoidal; cross veins not dense, mostly simple, forming little reticulation; intercalary sectors distinctly formed.

RELATIONSHIP: *Calvertiella* differs from *Moraviptera* (probably a hind wing) in having CuA more remote from MP, a three branched MP and more regular cross veins. From *Moravia*, n.g., it differs in the more slender fore wing, with only three branched MP, the fusion of CuA with M for some distance, the absence of supporting cross veins near origin of R₄ + 5, and in having far less dense cross venation and less reticulation.

Type-species: *Calvertiella permiana* Tillyard.

Calvertiella permiana Tillyard
Text-figures 1 and 4A; plate 19

Calvertiella permiana Tillyard, 1925, Amer. Journ. Sci., 10:43, figs. 1, 2A.

Fore wing, 27.5 mm long, 7 mm broad; about 4 times longer than broad. Intercalary sectors well indicated, convex, irregular reticulation almost absent; first branch of R_s with a long fork, the third very short; anal area gradually broadening in the distally, the wing being broadest shortly before the middle.

Tillyard was apparently not aware, when he prepared his account of this fossil, that some tearing and distortion of the wing had taken place in connection with its preservation in the fossil state. In the basal third of the wing, the costal and subcostal areas are broken and pushed posteriorly over the stems of R. At the same time, the anal area was broken and pushed anteriorly over the stem of A₁. Careful removal of small pieces of matrix shows that all of the main veins have independent stems. The drawing in text-figure 1 depicts these veins restored to their normal positions. Clearing away of

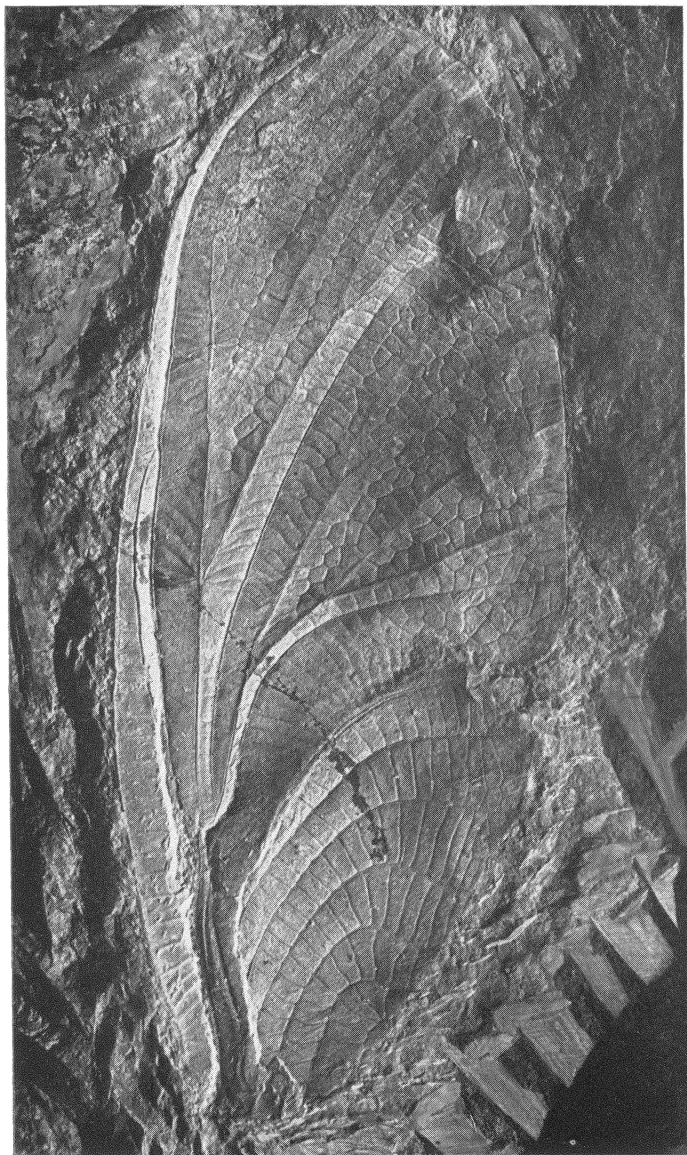
the matrix also revealed the complicated structure herein designated the cuticular thickening (ct, text-figure 4A). This does not resemble a vein but is a thick, cuticular band which extends from the stem of $M + CuA$ to the origin of Rs . It is much more extensively developed in the genus *Moravia*, described below.

Holotype: No. 5007 (obverse and reverse), Peabody Museum, Yale University; collected in the Wellington Shales, Elmo, Kansas. I am indebted to the authorities of the Peabody Museum for the opportunity of studying this fossil.

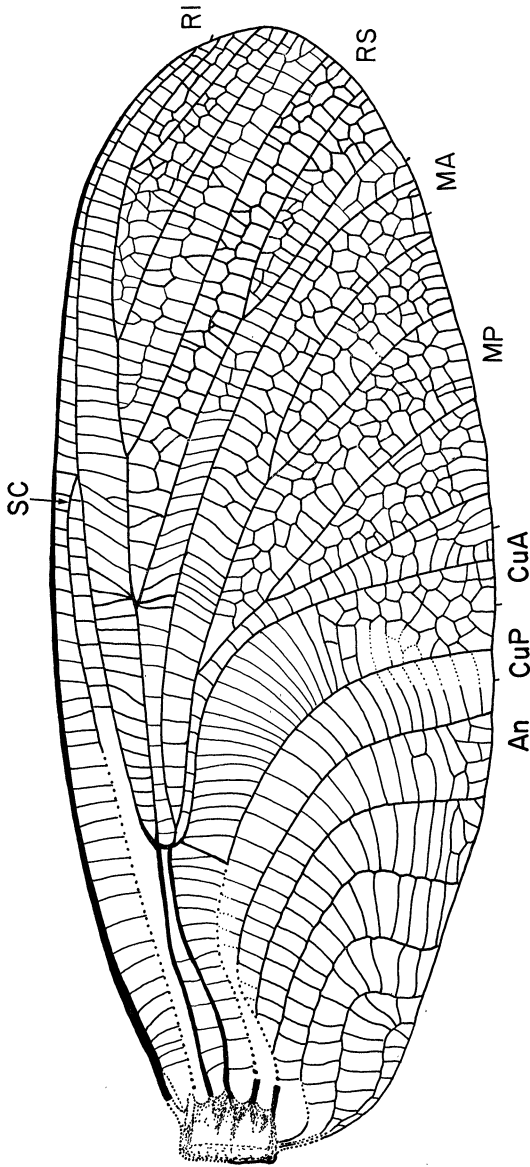
Genus *Moravia*, new genus

Fore wing: broad, almost oval. Apex very broadly rounded; anterior margin convex; posterior margin even more convex; postcostal area very small and indistinct; Sc terminating on R_1 before the end of the second third of the wing length; R_1 long; Rs originating before the end of the first third of the wing length, with four branches, the first of them forked; cuticular thickening (ct) arched, starting from R at the point of origin of Rs , crossing the stem of M and continuing by a convex connecting vein between M and CuA ; M approaching R before the origin of Rs , but not touching it, branching slightly behind the cuticular thickening; MA simple, MP forked three times; Cu dividing into CuA and CuP slightly before the level of the origin of Rs ; CuA approaching close to M , connected with M and with the cuticular thickening by a short connecting vein; in its further course, CuA follows MP closely; area between CuA and CuP with many cross veins and a reticulation; curvature of the 6 anal veins becoming more pronounced proximally; cross veins numerous, simple, reticulated in the radial, medial and cubital areas; several cross veins radiating from Rs to R and to MA in the proximity of the origin of the first branch of Rs ; intercalary sectors present in the radial area.

Hind wing: triangular, very broad basally; anterior margin slightly concave. Postcostal area larger than in the fore wing; Sc terminating on R somewhat beyond mid-wing. Rs originating at about the end of the first quarter of the wing length, giving rise to about four main branches, the first of them forked; cuticular thickening (ct) arched, starting from the very base of Rs and crossing M at the point where the short convex connecting vein between M and CuA is starting; stem of M approaching R before the origin of Rs , but not touching it, branching some distance beyond the cuticular thickening; MA simple, MP with 4 terminal branches; the stem of



Moravia convergens n.sp. (holotype, fore wing). Lower Permian of Czechoslovakia. Photograph by F. M. Carpenter, \times 3.7.



Text-figure 2. *Moravia convergens* n.sp. Drawing of holotype (fore wing). Lower Permian of Czechoslovakia. Original. Lettering as in text-figure 1.

Cu parallel with the stem of M, dividing well before the origin of Rs; CuA diverging towards M and connected to it by a short connecting vein; in its further course, CuA parallel with MP; both cubital branches sigmoidal, directed almost perpendicularly to the posterior margin; area between CuA and CuP not broadened; four anal veins, arising independently from the base, arched, rarely branched; cross veins numerous, forming a reticulation in radial, medial, cubital and anal areas; several supporting cross veins radiating from Rs to R₁ and from Rs to MA in about the level of the origin of the first branch of Rs; intercalary sectors well developed in the radial area.

Moravia differs from *Calvertiella* in the broader and shorter fore wing; Sc is shorter, Rs gives off four main branches, the cuticular thickening is arched, M does not touch R, MP is forked three times, CuA does not fuse directly with M and the cross veins and reticulation are much more dense.

From *Moraviptera* Kukalová (1955)⁴, which is apparently a hind wing, it differs in the broader wing, a broader area between MP and CuA and in presence of more numerous cross veins and a denser reticulation.

Moravia is in many features the most specialized of all the genera of Calvertiellidae, known so far. Its cuticular thickening is highly convex, and continues as a convex connecting vein, forming a transverse "bridge" between R and CuA. It may have had a function like the arculus in Recent Odonata. The function of the radiating cross veins near the origin of R₄+5 was probably that of support.

Both fore and hind wing of *Moravia* are known. Coloration in the fore wing is absent, but in the hind wing there are irregular pigment spots. The wings differ also little in length, and their venational patterns are very similar. It is impossible to determine whether the fore and hind wings belong to one species, but they are here treated as such.

Stratigraphic occurrence: Lower Permian (Upper Autunian) of Czechoslovakia.

Type-species: *Moravia convergens* n. sp.

***Moravia convergens* n. sp.**

Text-figures 2, 3, 4B, 4C; plates 20 and 21.

Fore wing: 38 mm long and 15 mm broad, about 2.5 times

⁴In the figure of *Moraviptera reticulata* Kukalová, (1954, p. 548, fig. 3) the origin of Rs is not correctly shown; it arises directly from R, just before the forking of M.

longer than broad. Coloration completely absent; postcostal area short and indistinct; length of Sc slightly variable, as well as the length of the forks on Rs and MP, the width of area between MP and CuA, and the curvature of the anal veins.

Hind wing: about 43 mm long and 20 mm broad, about 2.1 times longer than broad; triangular in shape. Postcostal area broad and long, with a series of short branches directed towards costa; irregular colored spots concentrated mainly in the posterior half of the wing; fork on the first branch of Rs relatively broad, as well as the fork on MP; area between CuA and CuP not very wide, but area between CuP and 1A broad; anal veins arising mostly independently from the base, curving slightly backwards; first two anal veins simple, the third one with a long fork, the fourth simple; reticulation dense, filling the area between CuP and 1A and the anal veins.

Holotype (fore wing): No. 1/1965, Department of Palaeontology, Charles University, Prague; collected by Anna Havlatová in Lower Permian shales (Upper Autunian), Obora, Moravia, Czechoslovakia.

Paratype (hind wing): No. 3/1965; collected by Jarmila Kukalová, at the same locality.

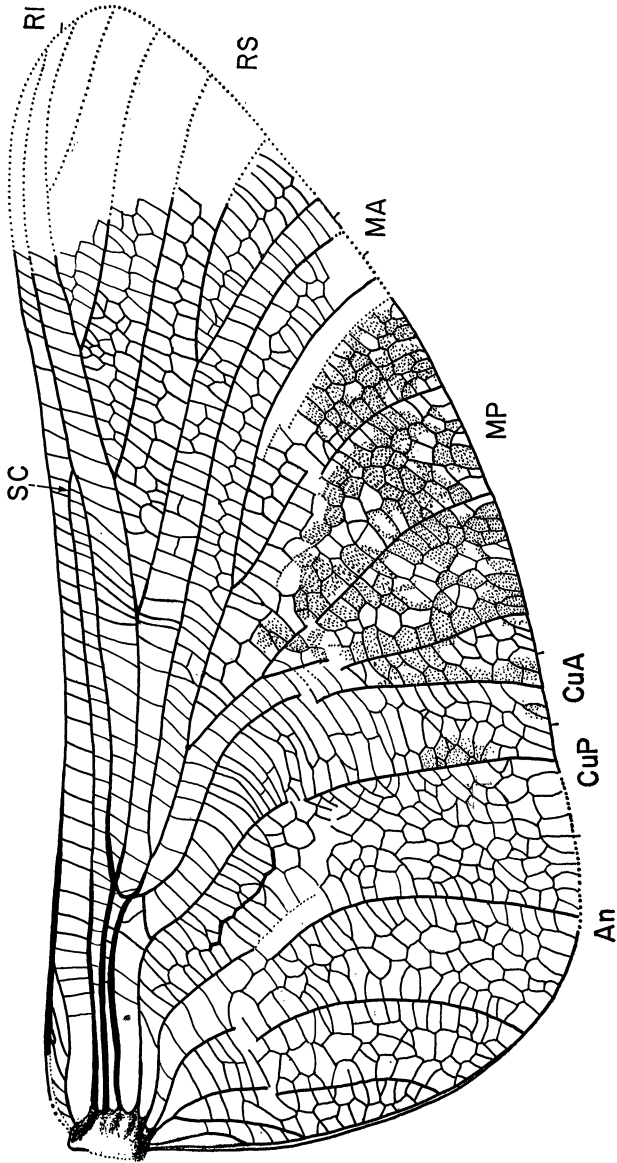
Another specimen of a fore wing (No. 2/1965), showing the basal part of the wing especially clearly, also collected at the Obora locality. Its venation is very similar, even in detail, to that of the holotype.

The holotype specimen was apparently distorted in preservation in much the same way as the type of *Calvertiella*. The wing is broken along Sc and the costal area has shifted towards R, while the anal area is drawn anteriorly across the stems of Cu and A. Nevertheless, the independent nature of the stems of the main veins can be seen. In text-figure 2, the veins have been restored to their original positions. The dotted lines representing the stems of Cu and A have been restored on the basis of those clearly preserved in specimen No. 2/1965.

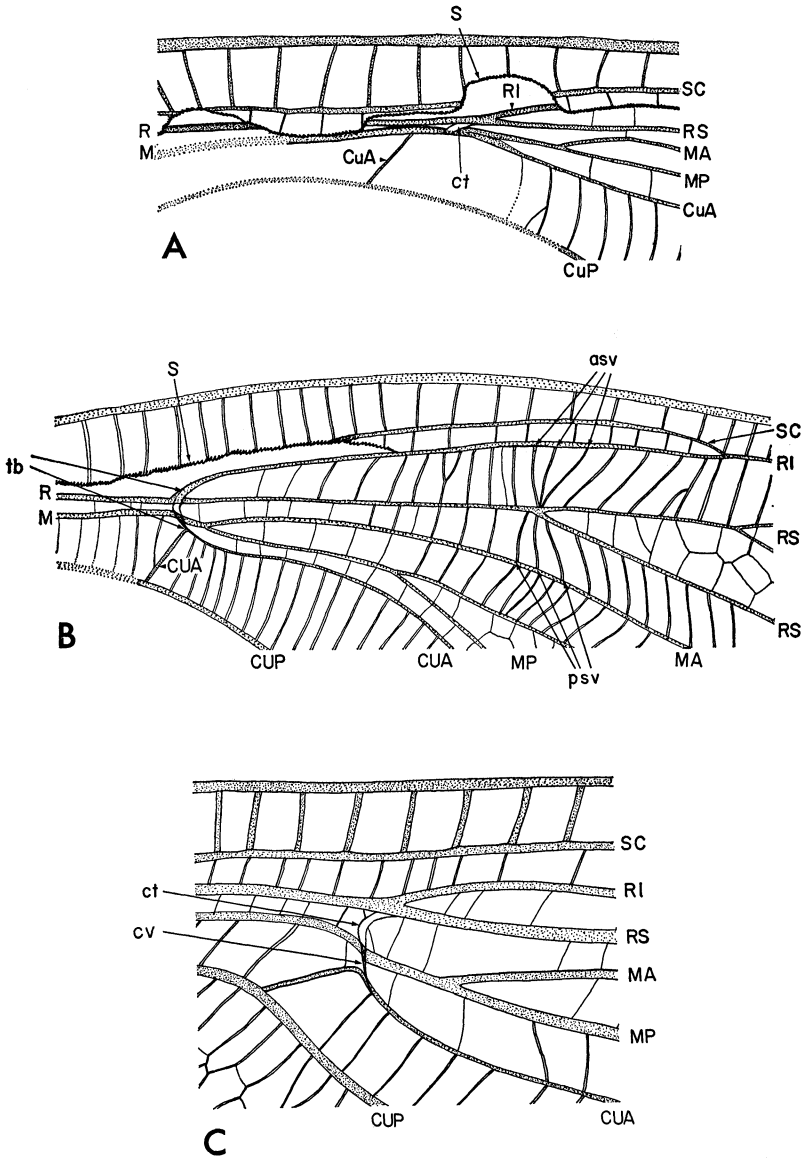
DISCUSSION: One of the remarkable features of *Moravia* is the peculiar cuticular thickening, which conceivably acts as a support between R and M at a point where most of the veins of the wing actually diverge. It is clearly developed in *Calvertiella* (see text-figure 4A), although very short—probably because of the close proximity of R and M + CuA at this point. It is more extensive in the fore wing of *Moravia convergens*, and much more so in the hind wing. In both wings the cuticular thickening is slightly curved



Moravia convergens n.sp. (paratype, hind wing). Lower Permian of Czechoslovakia. Photograph by F. M. Carpenter, $\times 4$.



Text-figure 3. *Moravia convergens* n.sp. Drawing of paratype (hind wing). Lower Permian of Czechoslovakia. Original. Lettering as in text-fig. 1.



Text-figure 4

and seems to lead into the base of R_1 , at least in the fore wing, where it is more convex. It continues posteriorly, seeming to cross M , and finally joins the angle of CuA , which is directed anteriorly. This cuticular arch is herein designated the *transverse bridge* (tb) and its posterior portion, the *connecting vein* (cv). It is highly probable that this whole structure functioned in much the same way as the arculus complex in the Odonata. Very different veins are involved in the Odonata, which lack MP and CuA .

The presence of the several radiating cross veins near the origin of R_4+5 is another notable feature of *Moravia convergens*. As can be seen in text-figure 4B, one group of three veins (asv) runs from R_s to R_1 , and the second group (psv) from R_s to MA just below the last group; the cross veins between MA and MP are much closer together than are the others. This structure also looks much like a supporting or strengthening device and recalls to mind the subnodal complex of the Odonata, although the locations of the two sets of structures are very different.

The enlarged anal area of the hind wing of *M. convergens*, as well as the triangular shape of the wing, also recalls the Odonata and, indeed, makes it difficult to realize that this insect, possessing all main veins including MP and CuA , was a palaeodictyopteron, not an odonate. Moreover, the similarities of the Calvertiellidae to the Eugereonidae make it nearly certain that the Calvertiellidae were haustellate, with a long and highly specialized beak.

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Text-figure 4. Details of venational structures in Calvertiellidae:

- A. Oblique cuticular thickening (ct) in *Calvertiella permiana* Till.
 B. Arched "transverse bridge" (tb), anterior supporting cross veins (asv) and posterior supporting cross veins (psv) in *Moravia convergens* n.sp. (fore wing).
 C. Arched "transverse bridge", composed of cuticular thickening (ct) and convex connecting vein (cv) in *Moravia convergens* n.sp. (hind wing). Lettering as in text-fig. 1. S = broken edge of wing.

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