

KANSAS PERMIAN INSECTS. PART 13. THE NEW
ORDER PROTELYTROPTERA, WITH A DISCUSSION
OF ITS RELATIONSHIPS.

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The present Part deals with a small but extremely interesting group of the Lower Permian insect fauna of Kansas, which was not represented in the Sellards' Collection, and of which no descriptions have hitherto been given. The author has been studying these insects, on and off, as opportunity permitted, for the past four years, but since his removal to Australia the pressure of official work has been so heavy that little spare time has been available for this task. The difficulty of deciding what these insects are, combined with the lack of available time, is sufficient to explain the long gap which has intervened between the publication of Part 12 and the present Part.

At first sight, the insects comprised in this group appear to be true Coleoptera or Beetles. It might easily have happened, owing to the rarity of members of this group, that only elytra might have been discovered. In such a case, there can be little doubt that they would have been hailed as the elytra of Coleoptera: and, if forms carrying the complete venation had been amongst those discovered, this would have been taken as representing the original forewing venation of that order. But it has so happened that, of the seventeen specimens of this group present in the Yale University Collection, no less than four are more or less complete, and three of these reveal, either wholly or in part, the details of the delicate hindwing venation. In addition, another specimen shows the elytra more or less in the position of rest, with the hindwings folded beneath them. A careful study of these indicates that they are certainly not true Coleoptera, and most probably not even ancestral to such, though, on their general facies, they appear to approach this order even more closely than do the Proto-coleoptera of the Upper Permian of Australia. It would be difficult to conceive of a more puzzling problem than this in the whole range of palaeo-entomology. Workers on fossil insects try to avoid, as far as possible, the making of new orders, though their critics frequently fail to note this, and tax them with making new orders merely "for the fun of

the thing." Those critics should consider the stages by which a new fossil order is put on record. The first question which has to be answered is "Will the new form that is being studied classify into any existing order?" If, as sometimes happens, the answer to this is decidedly in the negative, another question has to be asked "Could any allowable stretching of the definition of an existing order be made to include this new type?" If this can be done without doing violence to the unity of concept for the order in question, then I venture to say that it usually *is* done. A good example of this is that of the Lower Permian Copeognatha, which are undoubtedly the ancestors of existing Copeognatha, and only require an enlargement of the present definition of the order to be included within it (Tillyard, 1926). But suppose this second question has also to be answered in the negative. Then we must ask a third, "Would it serve to leave this new group unclassified as to its order, placing it as a side-branch of less than ordinal value, but attached to some known order, without attempting to amend the definition of the existing order in any way?" This can occasionally be done in preference to the making of a new order. But it must always be borne in mind that it really leaves the case *sub judice* and cannot be a final decision. An example of this method may be found in my treatment of the Delopteridae in Part 12 of this series of papers (Tillyard, 1928).

Turning now to the new group here dealt with, it would be as well to present the difficult problem of classification just as I have had to face it, step by step. The first attempt, naturally enough, was to try to show that the fossils were true Coleoptera. As nobody knows what the original venation of the forewings of this order was like, before these organs became elytra, the presence of a complete venation on the elytra of the dominant members of the new group offered no obstacle to this solution. Nor did the form of the head or prothorax, or what little can be made out of the legs. But when I came to study the venation and method of folding of the hindwings, then I must confess that I could see very little indeed to connect these fossils with any known types of Coleoptera. The full discussion of this point must be left until later on; but, meanwhile, we must accept the statement that I have felt that the structure of the hindwing and its venation offer insuperable difficulties to any theory that these fossils can be ancestral to the Coleoptera.

The next idea that I tested out was that they might be very specialized Blattoidea. Here again, the form of the head, prothorax and legs would offer little opposition to the idea; but the venation of both fore and hind wings is entirely opposed to it.

Elytrophorous types are known in three other existing orders, viz., in the Neuroptera Planipennia, the Copeognatha and the Dermaptera. The first two can obviously be ruled out, since the new fossils do not approach them in any important character. The Dermaptera would appear to be a very ancient order of Hemimetabolous insects in which all existing forms are not only elytrophorous, but have reached a stage of evolution analogous to that of the Staphylinidae among the beetles. That is to say, the original form of elytron has become greatly shortened, and the folding of the hindwing correspondingly more complicated. Correlated with this complex mode of folding there is an extreme specialization of the hindwing venation, so much so that it is not at all easy to determine the homologies of those veins which are left. After long and careful consideration of the hindwing of the new fossil group, including the construction of a folding model, I have finally concluded that they represent the ancestors of the Dermaptera at the stage before the elytron began to be shortened. But they stand so far apart from true Dermaptera that they must receive ordinal rank. As the most suitable name, Protodermaptera, besides taking for granted the whole question of affinities, has already been used by M. Burr for a subordinate group within the order Dermaptera itself, I propose for the new order of fossil insects the name PROTELYTROPTERA.

The argument in favor of this order being the ancestral form from which the true Dermaptera have been derived is set forth later on in this paper, together with considerations of their possible relationships to Coleoptera and Protocoleoptera. For the present, we need only bear in mind that these fossils are the oldest known insects in which the forewing has become specialized as an elytron.

Order PROTELYTROPTERA n. ord.

Insects superficially resembling Coleoptera, but provided with short, jointed cerci and therefore probably not Holometabolous. Head broad, with lateral compound eyes wide apart.

Pronotum large and wide, with extended lateral portions. Forewing covering, or more than covering, the abdomen and specialized as a true elytron, markedly convex above, with granular or roughened surface and either with or without a definite venational scheme. Hindwing much larger than fore, greatly expanded transversely, and, in the position of rest, with apical portion folded under and inwards towards the inner or posterior side in a complicated manner; the main transverse line of folding is the *nodal fold* (Fig. 3, *nf*) beginning at a slight incision of the costal border near the end of R_1 , known as the *nodus* (*n*), and proceeding obliquely in a curved line across the wing; the folded apical portions then turn on a fulcral point (Fig. 3, *k*) situated at the end of the fused anal veins, a little below the nodus; the unfolded portion remaining is just long enough to be covered by the elytron, so that the whole hindwing fits neatly and closely beneath it. Thorax and abdomen fairly stout. Legs rather short, stoutly built, with broad, flattened femora and tibiae; the total number of tarsal segments is not known. Abdomen terminating in a pair of short cerci having only a few short segments.

Four distinct families can be recognized within the order, as follows:

1. Elytra with a complete or nearly complete venational scheme.2.
2. Elytra with the venational scheme greatly reduced or absent.3.
2. Sutural margin of elytron broad and evenly developed along the whole of the posterior border.Family 1. PROTELYTRIDAE.
Sutural margin of elytron broad or medium to about half-way along posterior border, thence either extremely narrow or obsolescent.Family 2. PERMELYTRIDAE.
3. Elytron with a distinct *vena dividens* (Cu_2) either wholly or partially developed as a deeply impressed concave vein.Family 3. BLATELYTRIDAE.
Elytron without such a *vena dividens*; venation either entirely absent or at most only vestigial.Family 4. ACOSMELYTRIDAE.

Family 1. PROTELYTRIDAE n. fam.

(Figs. 1-5, 14-15.)

Elytron with complete venation of a very primitive or simplified Orthopteroid type, in which all the main veins, Sc, R_1 , Rs, M, Cu_1 , Cu_2 and the three anals are simple veins, and there are no cross-veins at all. R_1 a strongly convex vein raised on a high ridge, with the costal field anterior to it forming a horizontal ledge at a much lower level, and carrying the weakened and barely concave Sc upon it. Along the

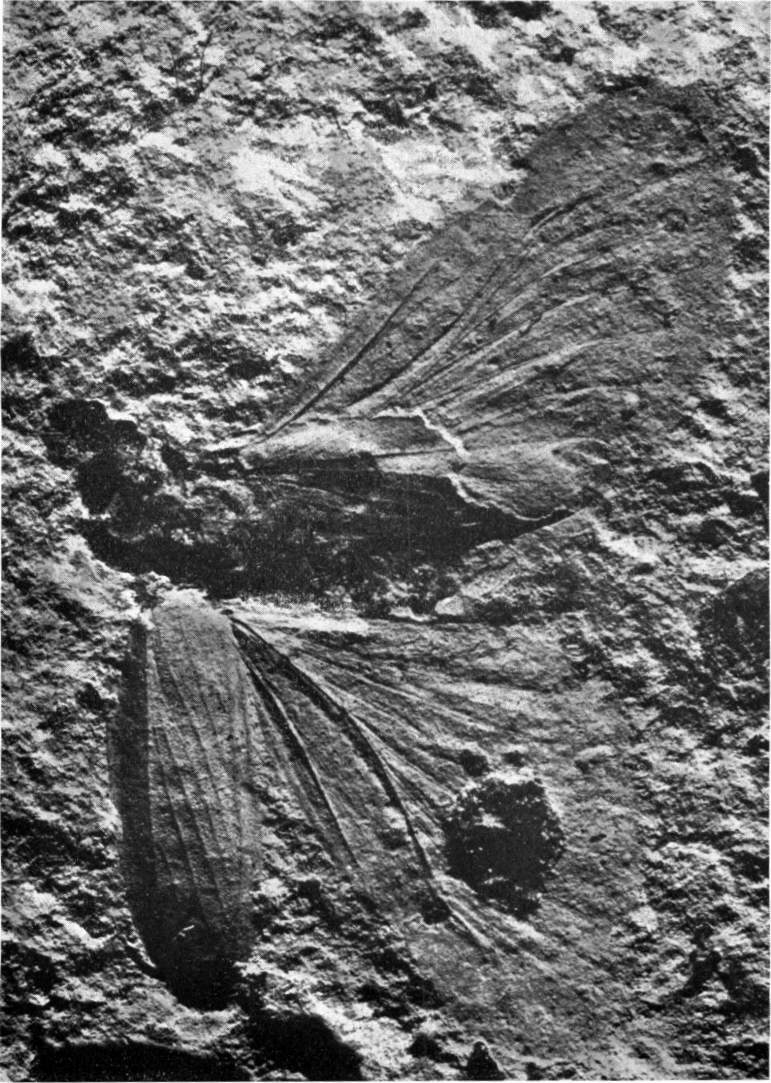


Fig. 1. *Protelytron permianum* n. g. et sp. Photograph of Specimen No. 1019a, enlarged. Actual length of elytron, 5.8 mm. W. C. Davies photo.

whole of the posterior border of the elytron there is developed a well marked sutural margin, also in the form of a horizontal shelf, contrasting with the markedly convex portion of the elytron lying between it and the costal field.

Hindwing much longer and wider than elytron, its costa broken by a notch at or close to the end of R_1 ; this notch, which may be called the *nodus* (Fig. 3, *n*), marks the beginning of the obliquely curved *nodal fold* (Fig. 3, *nf*), along which the apical portion of the wing is turned inwards in the position of rest. Venation very remarkable; Sc and R_1 well developed, but position of Rs doubtful. What appears to be

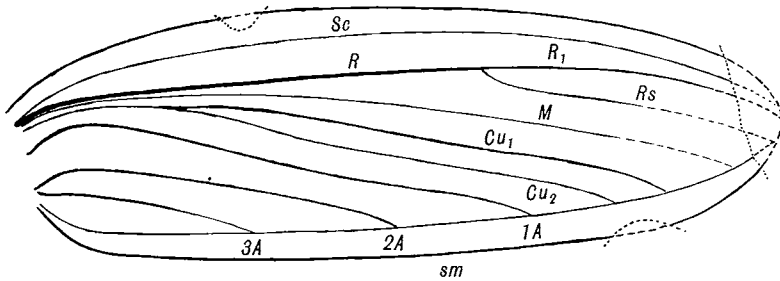


Fig. 2. *Protelytron permianum* n. g. et sp. Specimen No. 1019a-b. Elytron, with apex to right; actual length, 5.8 mm. 1A, 2A, 3A, the three anal veins; Cu₁ first cubitus; Cu₂ second cubitus; M media; R radius; R₁ its main stem; Rs radial sector; Sc subcosta; sm sutural margin.

the true M is fused basally with R_1 for nearly one-fourth the length of the wing and then leaves it at a slight angle, running to a point below the nodus, where it merges into the cubito-anal complex. What appears to be the true Cu arises with R at base of wing and leaves it immediately; it soon afterwards forks into a weakly chitinized convex vein which is probably Cu₁, and a deep furrow, barely if at all chitinized, which appears to represent the original course of Cu₂. These two branches form an enclosed fusiform space, with Cu₁ ending distally on the furrow vein at about half the length of the wing. Just below the furrow vein there is what appears at first sight to be a very strong, single, convex vein, curved markedly concavely to the anterior margin of the wing; in some well preserved specimens, this is seen to consist of two closely parallel convex veins, of which the anterior one is the weaker. This should be 1A, while the stronger posterior one should be 2A. The vein M, the furrow Cu₂ and the two

anals meet at the point already mentioned, where there are signs of considerable chitinization, and from this junction veins radiate out to the apical and posterior borders of the wing. The branches anterior to the apex appear to belong chiefly, if not entirely, to 1A, while those posterior to it all belong to 2A, with the possible exception of the first of the series. There are about eight of these radiating branches of 2A, followed on the posterior basal portion of the wing by two more which appear to have a separate origin at the base

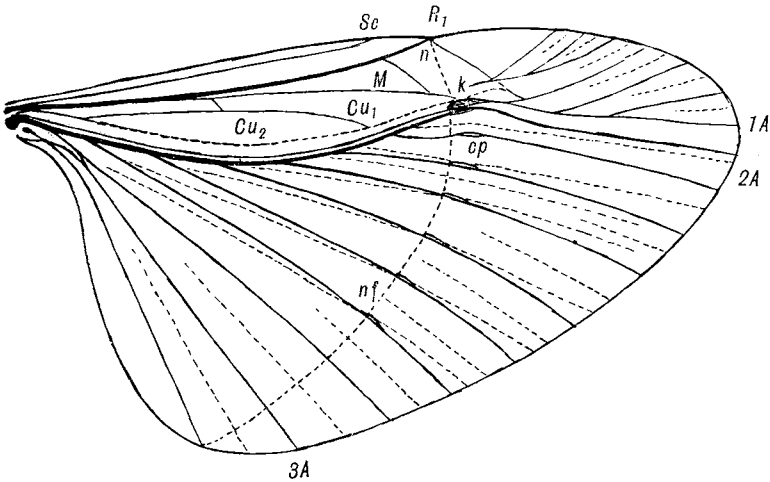


Fig. 3. *Protelytron permianum* n. g. et sp. Specimen No. 1019a-b. Hindwing, outspread; actual length 8.0 mm. Venation as in Fig. 2, except *k* fulcrum; *n* nodus; *nf* nodal fold; *cp* chitinous pad.

and represent either a two-branched 3A or possibly two simple veins, 3A and 4A.

Between these radiating veins there are developed, from the outer margin of the wing inwards, a series of intercalated concave folds, some short and some long; the latter mostly begin above a convex vein, gradually converge towards it at a very acute angle, cross it at or near the nodal line, and then continue basad on the other side of it. (Fig. 3.)

By drawing the wing on a large scale on stiff paper, and then creasing the paper convexly along the radiating veins and nodal fold, and also concavely along the intercalated folds, a model can be made for the testing of the method of folding. The first set of folds is made along the radiating veins and

the intercalated folds. It will then be seen that the folds must of necessity cross the veins somewhere, owing to the strong curve of the convex anal veins. When this folding is completed, all the radiating veins are gathered close together in a kind of closed fan, which is rigid up to the fulcral point *k*. At or near this point there is a definite pull of the folded apical portion downwards towards the posterior margin of the wing. By creasing the line of the nodal fold strongly, so as to bend the apical portion inwards (i.e. towards the tip of the abdomen if the wing were *in situ* on the insect), the whole of the already folded apical portion can be made to bend at right angles to the rest of the wing. This position is to be actually seen in the left hindwing of the fossil No. 5405a, where the apical folds, all closely crowded together, are seen projecting at right angles across the posterior end of the abdomen. The completion of the folding process can be done, of course, merely by pressing the folded apical part still further round, so that the apex comes to lie directed forwards and beneath the rest of the wing. In the living insect, this is probably accomplished by the hind legs.

It should be noted that the fulcral point *k* (Fig. 3) is distant only very slightly less from the base of the wing than the total length of the elytron, so that the folded hindwing lies neatly beneath it.

This family contains two genera, as follows:

Medium-sized insects, elytron 5 to 6 mm.; all main veins of elytron simple veins, with no cross-venation, meshwork or branches.

Genus PROTELYTRON n. g.

Large insects, elytron 10 to 12 mm., with the distal parts of the main veins becoming indistinct and merging in a weakly developed meshwork of irregular veins and cross-veins. Genus PROTELYTROPSIS n. g.

Genus *Protelytron* n. g.

(Figs. 1-4, 14-15.)

Head rather small, with button-like eyes placed antero-laterally.

Thorax and *abdomen* large and broad.

Elytron with costal field medium to broad, Sc and R₁ running almost or quite the full length of the elytron. Rs arising well beyond half-way along R. 1A ending up well beyond half-way along posterior margin, 2A at or near half-way, 3A shorter. Sutural margin broad.

Hindwing with narrower costal field, Sc ending up close to end of R_1 at half-way or more along the fully expanded wing. The veins in the trough between R and the anals are all weakly formed and differ according to the species. At the points where the radiating branch veins cross the nodal fold, just on the distal side of that fold, there are formed a series of weak, fusiform, flexible chitinous pads (Fig. 3, *cp*), not easy to be seen except in very well preserved specimens; they appear to serve the purpose of preventing the infolding distal portions of the radiating veins from buckling, and also allow the intercalated folds to cross without breaking the veins.

Genotype:—*Protelytron permianum* n. sp.

Horizon:—Lower Permian of Kansas.

The Yale Collection contains five specimens which belong to this genus. They apparently represent two distinct species, as follows:

Elytron with costal field relatively broad; hindwing with nodus only slightly incised and apex not very broadly and bluntly rounded.

P. permianum n. sp.

Elytron with costal field narrower; hindwing with nodus markedly incised and apex very broadly and bluntly rounded. *P. dunbari* n. sp.

1. *Protelytron permianum* n. sp.

(Figs. 1-3, 14-15.)

Total length approximately 6 mm.; *head* 1 mm. wide; *prothorax* 1.8 mm. wide; length of *elytron* 5.8 mm.; length of *hindwing* 8.0 mm.

Fig. 1 is a photograph of the reverse impression of the type specimen, which is the most complete and best preserved specimen of the whole order. We are indebted to Mr. W. C. Davies for the fine photograph of this specimen. The *head* lies slightly to the right, with the antennae missing; the eyes are small, and the mouth-parts not at all prominent. The *pronotum* is broad, with well developed lateral expansions. *Prothorax*, *meso-* and *metathorax* and *abdomen* appear to have been equally broad, the abdomen gradually tapering very slightly to the anal end. *Cerci* not visible. The sex of the specimen is not determinable, but it should be noted that the deceptive appearance of an ovipositor seen in Fig. 1 is due to the sharp edge of the right elytron, which is impressed upon and beyond the abdomen, and is not nearly so marked in the specimen as in the photograph. The legs are mostly

missing, but indications of the fore femora can be made out alongside the deep impression of the pronotum.

The left elytron is practically perfect and is figured in Fig. 2. The specific characters are the broad costal field, with well curved costa, Sc well curved concavely to R and closer to the costa than to R, this latter vein very nearly straight for most of its length, with Rs arising at about two-thirds, Cu dividing at about one-fifth and with its two branches not as far apart as M and Rs, 1A with strong basal arch, 2A and 3A arising close together far below 1A. The sutural margin is broad except at its two ends, and becomes broadest below Cu; it curves from a point just below the origin of 2A and 3A to the rounded anal angle, then runs practically straight to below Cu, where it begins to turn upwards again, narrowing until it ends on or near Rs. The whole elytron is delicately granulated or shagreened all over.

The right elytron is impressed partly upon the abdomen and partly upon the right hindwing, so that its details are not clearly to be seen.

Both right and left hindwings are beautifully preserved, though the basal posterior portion of the latter is missing where it has broken away and exposed the elytron beneath it, while a large rounded hole is to be seen near the middle of the left elytron. Much of the venation and all the complex folds are very delicate and not at all easy to make out even in such an excellent specimen, but by combining the preserved portions of both wings the whole can be made out with fair accuracy. The complete wing is shown in Fig. 3. The costal field is much narrower than in the elytron, and only very slightly convex along the costa. Sc is almost straight and lies very close to the costa. R is slightly curved concave to the costa, and ends at the nodus (*n*), which is only very slightly incised. The nodal fold (*nf*) can be faintly traced in a curve across the wing as indicated by the curved dotted line in the figure. From the nodus, and also from a point somewhat basad from it on R, two faintly marked descending veins can be made out with difficulty: one ends on M just before the fulcrum *k* and one on the stalk of the first radiating vein anterior to the apex. I am not able to determine whether either of these veins is possibly Rs, but the more basally situated one might well be that vein. Just after leaving R, the very faint concave vein M sends off a faint oblique vein to join Cu₁; this might be interpreted as a vestige of an

original M_5 , or it may be merely a weak cross-vein. Cu_1 is a weak vein but quite markedly convex. Cu_2 is a deep and scarcely chitinized furrow. The double convex anal vein made up of 1A and 2A is very markedly curved concavely to the costal margin. At the fulcrum k there is a group of three weak veins on a common stalk, arising from the end of 1A, and another group of four veins arising from a short stalk leaving the fulcrum itself distally; the most posterior of these four may be said to end on the true apex of the wing, and continues the line of the main stalk of the four. Just below this is a much stronger vein, slightly diverging, and apparently arising from the fusion of 1A and 2A just below the fulcrum k ; posterior to this there are nine radiating anal branches, all of which except the last two appear to arise from 2A. On the six of these next below the main stem of 2A there are indications of flexible chitinous pads (cp) just distad from the nodal fold. The intercalated folds are very faintly marked and very difficult to make out accurately; Fig. 3 gives the best interpretation of them that I can make out with good oblique lighting.

Fig. 15 shows the hindwing in the position in which the apical portion is very nearly folded backwards. The apical folds are imbricated one upon another at approximately equal intervals, while the curious curve of the two main anal veins ensures that the radiating branches, when folded, shall make a straight edge, as the figure clearly shows. It is clear that the hindwing, when fully folded, can be securely tucked beneath the elytron.

Types:—*Holotype, complete insect*, Specimen No. 1019a (reverse impression, Figs. 1-3) in Yale University Collection; counterpart (obverse) No. 1019b. The reverse is chosen as the type, as it is the better impression of the two, particularly as regards the venation.

2. *Protelytron dunbari* n. sp.

(Fig. 4.)

Total length 7.0 mm.; *elytron* 5.2 to 5.5 mm.; *hindwing* 7.2 mm.

This species differs from *P. permianum* in its somewhat smaller size and markedly narrower elytra; in particular, the costal field of the elytron is narrow in comparison with that of *P. permianum*, and the elytron appears barely long enough to

cover the whole of the abdomen. The hindwing is remarkable in being much more widely and bluntly rounded than that of *P. permianum* and in having a more definitely incised nodus. These characters are probably correlated with the shortening of the elytron. The venation of the elytron is similar to that of *P. permianum*, but R_1 does not reach the apex, and Sc is indistinct; R_s arises nearer half-way along R. All the specimens have the elytra folded back along the abdomen, and hence

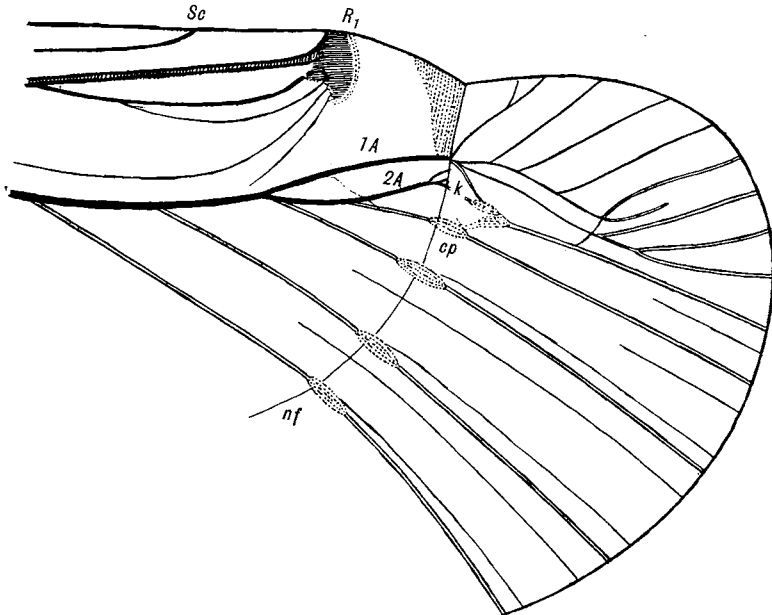


Fig. 4. *Protelytron dunbari* n. sp. Specimen No. 5405a-b. Distal portion of hindwing, outspread. Venation as in Figs. 2 and 3.

the venation cannot be made out as clearly or completely as is desirable. Fortunately, however, in two of the specimens, one of the hindwings projects out beyond the elytron, so that the whole of its distal portion can be studied (Fig. 4). The nodal fold is very strongly marked, and, when followed backwards from the costa, is seen to pass exactly under the extreme apex of the elytron, thus proving clearly that it represents the major fold of the wing and that the folded wing is just the right length to be completely covered by the elytron. The details of venation in the region of the nodal fold and the

apex are strikingly different from those of *P. permianum*. Sc lies further from the costa; R_1 stops short of the nodus and is separated from it by a small pigmented area which is possibly also chitinized. Below the distal portion of R_1 there appears to be a short, weak R_s which loops up distally with the rather indefinite end of R_1 itself. The region on both sides of the nodus is pigmented and perhaps also chitinized. The two strong anals, 1A and 2A, appear to be almost entirely fused into a single convex vein, except as they approach the nodal fold, when they separate slightly, forming a narrow oval loop which ends on the nodal fold itself. From this point there springs a complex of radiating veins not easy to interpret, but about nine separate branches can be made out, of which the most posterior appears to be separated entirely from all the rest and apparently belongs to 2A. I can find no trace of the distal portion of M, but the furrow of Cu_2 can be made out just anterior to the anals. The shape of the apical portion of the wing is very remarkable, being much broader and blunter than in *P. permianum*. The radiating branches of 2A stand more widely apart, and the chitinous pads just distad of the nodal fold are clearly marked. There appear to be two sets of intercalated folds, one lying just anterior to each vein and one posterior but more widely separated.

In Specimen 5405a there is, to the left of the head, a slight impression of what may be a small portion of the antenna, showing three or four apparently short, moniliform segments.

Types.—*Holotype*, complete insect, Specimen 5418 (obverse impression) in Yale University Collection. The elytra lie slantingly on either side of the abdomen, with the right one covering the basal and posterior portions of the outspread right hindwing; left elytron with distal portion missing. *Paratypes*.—Specimens 5405a and 5417 (both obverses) in Yale University Collection; counterpart No. 5405b. No. 5405a is an almost complete specimen having the two elytra lying nearly parallel alongside the abdomen; the left hindwing is spread out, while the right is *in the half-folded position*, with the radiating veins folded closely together and the apical portion beyond the nodal fold turned in at right angles and projecting from under the apex of the elytron across the end of the abdomen. No. 5417 has the elytra folded back almost into the actual resting position, but slightly diverging distally; the hindwings are evidently folded beneath them.

Genus *Protelytroptis* n. g.

(Fig. 5.)

This genus differs from *Protelytron* in the much larger size of the elytron, the narrower sutural margin and the slightly more pointed apex. The main veins, as they approach the distal end of the elytron, lose their distinct courses and become merged into a weak, obsolescent meshwork of zigzagging veins and cross-veins. The elytron is finely granulose or shagreened.

Genotype:—*Protelytroptis grandis* n. sp.

Horizon:—Lower Permian of Kansas.

There is only a single species in this genus.

3. *Protelytroptis grandis* n. sp.

(Fig. 5.)

Specimen No. 5420 represents the obverse of the distal half only of a large elytron, approximately 11 mm. in length. Length of preserved portion 5.5 mm.; greatest breadth 3 mm.

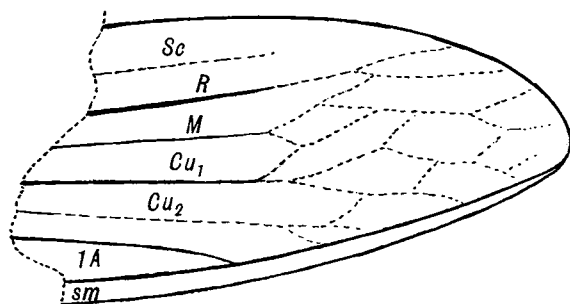


Fig. 5. *Protelytroptis grandis* n. g. et sp. Specimen No. 5420. Distal half of elytron; actual length 5.5 mm. Venation as in Fig. 2.

Before the apex, the costal margin is more curved than the posterior, giving the apex a very slightly nodding aspect. The costal field is very broad, with R_1 strongly marked up to a point about 3 mm. from apex, when it degenerates and merges into the obsolescent apical meshwork. All the other main veins do likewise except one which can be seen to end definitely at a point about 4 mm. from apex on the posterior margin; this is evidently 1A. Between this and R_1 there is another strong vein, Cu_1 . M is a weak vein lying between R_1 and Cu_1 , and Cu_2 is an even less distinct vein between Cu_1 and 1A. Sutural margin well developed and tapering evenly to a point

just below apex, but not at all broad; greatest breadth in preserved portion about 0.3 mm.

Type:—*Holotype elytron* (obverse), Specimen No. 5420 in Yale University Collection.

Family 2. PERMELYTRIDAE n. fam.

(Figs. 6-8.)

Elytron with venation incomplete, the main veins either becoming obsolescent before reaching the distal margin, or else merging into a weakly formed meshwork of veins and cross-veins. Along the basal half of the posterior border the sutural margin is well developed, but along the distal half it is either very narrow or absent.

(Hindwing not preserved.)

There are two genera in this family, distinguished as follows:—

Elytron oval, bluntly pointed at apex; distal half of sutural margin narrow but distinct. Genus PERMELYTRON n. g.
Elytron with very broadly rounded apex; no sutural margin along distal half of posterior border. Genus MEGELYTRON n. g.

Genus *Permelytron* n. g.

(Fig. 6.)

Elytron of moderate size, about 8 mm. long, elongate oval in shape, with apex narrowing to a blunt point. Costal margin very convex. Of the main veins, only Sc, R, M and Cu₁ are at all well marked, and these all become obsolescent long

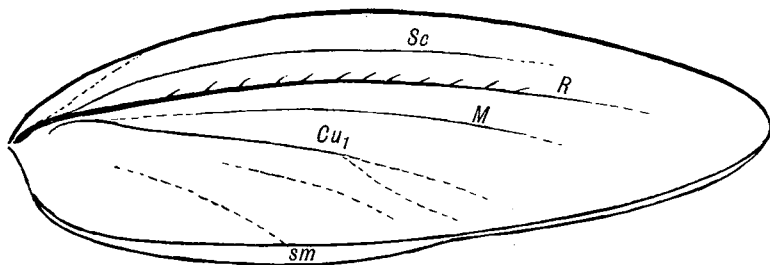


Fig. 6. *Permelytron schucherti* n. g. et sp. Specimen No. 5411a. *Elytron*; actual length 8.0 mm. Venation as in Fig. 2.

before reaching the distal margin. No sign of Rs. R provided with a row of strong setae. No distal meshwork of veins. Sutural margin narrow basally, then widening out con-

siderably up to half-way along posterior margin, where it narrows to less than half its previous width and runs evenly to just below apex.

Genotype:—*Permelytron schucherti* n. sp.

Horizon:—Upper Permian of Kansas.

This genus contains only a single species.

4. *Permelytron schucherti* n. sp.

(Fig. 6.)

Specimen No. 5411 *a-b* is a complete elytron of this species, of *total length* 8.0 mm., *greatest breadth* 2.6 mm. The surface of the elytron is finely granulate all over. The impressions of fairly large setae can easily be made out along R, and there is a suspicion of the presence of smaller setae along part of Sc and M. The convexity of the elytron is rather slight.

Type:—*Holotype elytron* (obverse), Specimen No. 5411*a* in Yale University Collection; No. 5411*b* (reverse).

Genus *Megelytron* n. g.

(Figs. 7-8.)

A genus containing larger insects, elytron about 11 mm. long, and of robust build. *Head* rather small, short, with small laterally placed eyes. *Pronotum* large, with rounded lateral margins. *Elytron* with only moderately convex costal margin and with the posterior margin practically straight, the apex very broad and bluntly rounded; venation fairly complete and strongly marked, but the main veins merging distally into an obscure meshwork. Cu_2 and anal veins apparently irregular, indistinct and merging into one another. A distinct but short Rs arising far distad along R.

(Hindwing not preserved.)

Genotype:—*Megelytron robustum* n. sp.

Horizon:—Lower Permian of Kansas.

There is only one species in this genus.

Megelytron robustum n. sp.

(Figs. 7-8.)

Total length 14 mm.; *elytron* 11 mm. long by 3 mm. wide.

Specimen No. 5406 *a-b* represents a large and almost complete insect very suggestive of a true Coleopteron. Only a part of the rather small head is present, but the small, button-

like, laterally placed compound eye can be seen on the right side of it. *Pronotum* (Fig. 7) complete, measuring only 1.3 mm. long by 2.9 mm. wide; its anterior border is straight and in contact with the head, its posterior border slightly convex, and its lateral lobes well rounded and evidently projecting

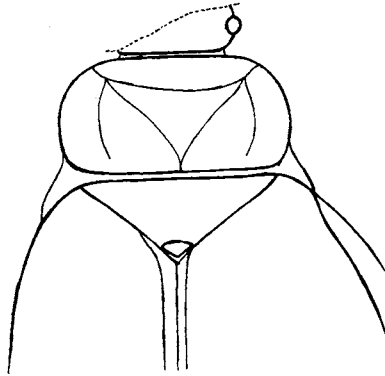


Fig. 7. *Megelytron robustum* n. g. et sp. Specimen No. 5406a. Elytron; actual length 11 mm. Venation as in Fig. 2.

beyond the body proper. Just posterior to the pronotum and between the bases of the elytra there can be seen the exposed, broad, triangular mesonotum, apparently ending posteriorly in a small, triangular scutellum.

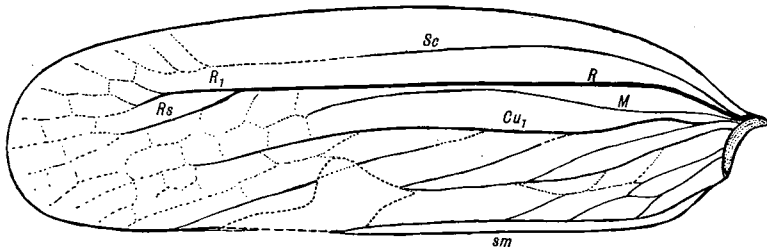


Fig. 8. *Megelytron robustum* n. g. et sp. Specimen No. 5406a-b. Head, pronotum and mesonotum. Actual width of pronotum 2.9 mm.

The *elytron* itself is attached to the mesonotum by a strong hinge, with the costal margin springing away in a strong arch, as in many Coleoptera; for the greater part of its length, the costal margin is only slightly curved and the width of the

elytron is consequently almost the same until nearing the broad, bluntly rounded apex. The sutural margin is well marked but rather narrow for the basal half of the elytron, after which it either disappears or is so narrow as not to be clearly visible. Sc is at first closer to the costa than to R, but at about one-fourth of its length it curves slightly and then runs closer to R than to the costa; distally it is weakly chitinized and merges into the obsolescent meshwork of veins that is to be found throughout that part of the elytron. R is a strong vein, strongly curved near its origin, then running almost straight at a distance of about one-third of the total breadth of the wing from the costa. At one-fourth from apex, it gives origin to a short Rs, and soon afterwards both R₁ and Rs merge in the distal meshwork. M is a weak vein which at first diverges from R but approaches it again quite closely at about one-third of the wing-length, after which it diverges from R again to a little beyond half-way, when it merges into the meshwork. Cu₁ is a strong vein with an irregular course which can be followed to within about one-fifth from the apex, when it is lost in the meshwork. This vein has several posterior branches, weakly formed and irregular; the courses of these and of the anal veins cannot be made out with certainty owing to this portion of the elytron overlying the partially decomposed abdomen, but they appear to anastomose with one another freely.

The specimen lies with the two elytra folded backwards over the abdomen in the position of rest, so that the hindwing cannot be seen. Apparently the sutural margin of the right elytron overlapped that of the left. The costal field is broad and flat, with R raised up well above it and the rest of the elytron moderately convex.

Type:—*Holotype*, nearly complete insect, Specimen No. 5406a (obverse) in Yale University Collection; No. 5406b (reverse).

Family *Blattelytridae* n. fam.

(Figs. 9-11.)

Elytron without any definite venational scheme, at the most with only traces of Sc, R, M and Cu₁, but with a complete and strongly marked *vena dividens* (Cu₂) present, ending half-way or more along the posterior border.

(Hindwing not preserved.)

This family contains two genera, which may be distinguished as follows:—

Vena dividens of Blattoid type, strongly arched from base to tip.

Genus BLATTELYTRON n. g.

Vena dividens straight or nearly so for most of its length, only curved towards its tip. Genus PARABLATTELYTRON n. g.

Genus *Blattelytron* n. g.

(Fig. 9.)

Characters as given in the Key above. Elytron oval, with well rounded apex; moderately convex.

Genotype:—*Blattelytron permianum* n. sp.

Horizon:—Lower Permian of Kansas.

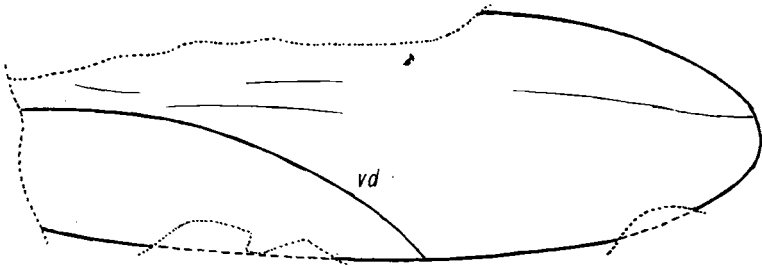


Fig. 9. *Blattelytron permianum* n. g. et sp. Specimen No. 5409a-b. Elytron; actual length 8.0 mm. *vd* vena dividens.

Blattelytron permianum n. sp.

(Fig. 9.)

Specimen No. 5409 *a-b* is a rather poorly preserved and somewhat broken elytron of this species. *Length* of specimen 8.0 mm., indicating a total length of the complete elytron of about 9 mm.; *breadth* about 2.5 mm.

The impression is on a rather rough-grained piece of rock. The basal two-thirds of the costal margin is broken away and so is the whole of the extreme base. Elytron moderately convex and apparently finely granulate. There are faint traces of R, especially towards the apex, which is clearly preserved and evenly rounded. The only outstanding feature of the elytron is the deeply incised and strongly curved *vena dividens*, which arises not far below R, somewhat closer to costal than to posterior margin, and proceeds in a strong arch to a point

on the posterior border about 3.5 mm. from apex. There is no clear indication of a sutural margin.

Type:—*Holotype elytron* (reverse). Specimen No. 5409*a* in Yale University Collection; No. 5409*b* (obverse), not so well preserved.

Genus *Parablattelytron* n. g.

(Figs. 10-11.)

Elytron with R strongly marked for at least its basal half; *vena dividens* straight or nearly so for most of its length. Apex narrowly rounded. Sutural margin present.

Genotype:—*Parablattelytron subincisum* n. sp.

Horizon:—Lower Permian of Kansas.

Two species belonging to this genus may be distinguished as follows:

Elytron 7 mm. long, with *vena dividens* deeply incised for a short distance from base only, slightly curved. *P. subincisum* n. sp.
Elytron 5.5 mm. long, with *vena dividens* well marked and quite straight for about two-thirds of its length. *P. rectum* n. sp.

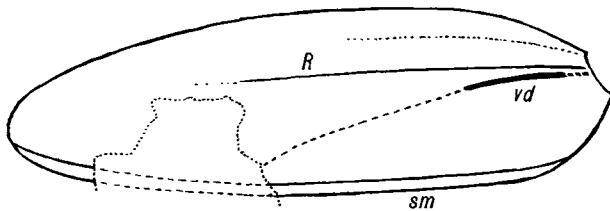


Fig. 10. *Parablattelytron subincisum* n. g. et sp. Elytron, Specimen No. 5408*a*; actual length 7.0 mm. *sm* sutural margin; *vd* vena dividens.

Parablattelytron subincisum n. sp.

(Fig. 10.)

Specimen No. 5408 *a-b* shows a complete elytron of this species except for a deep, irregular break inwards from the distal portion of the posterior margin. Length 7.0 mm., breadth 2.1 mm. The elytron is markedly convex, with broad costal margin and well developed sutural margin, the former lying at a much lower level than the raised middle part. Faint traces of R can be seen at about one-third of the width from costal margin. Close below the base of R arises the deeply incised *vena dividens*, curving gently away from it for a short distance only and then quite suddenly becoming obsolescent. Sutural margin only of moderate width but well marked.

Type:—*Holotype elytron* (obverse), Specimen No. 5408a in Yale University Collection; No. 5408b (reverse).

Parablattelytron rectum n. sp.

(Fig. 11.)

Specimen No. 5413 *a-b* represents a perfect elytron of this rather small species. *Length* 5.5 mm., *breadth* 1.5 mm. The elytron is fairly convex, but the costal margin is not as flatly

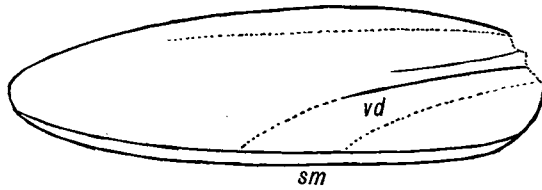


Fig. 11. *Parablattelytron rectum* n. sp. Elytron, Specimen No. 5413a. Actual length 5.5 mm. R radius; *sm* sutural margin; *vd* vena dividens.

differentiated off as in the previous species. *Vena dividens* running straight from immediately below origin of R and deeply incised for nearly two-thirds of its length, then becoming suddenly obsolescent. Sutural margin rather narrow but distinct.

Type:—*Holotype elytron* (obverse), Specimen No. 5413a in Yale University Collection; No. 5413b (reverse).

Family ACOSMELYTRIDAE n. fam.

(Figs. 12-13.)

In this family I propose to include all those types of Protelytroptera in which neither a definite venational scheme nor a distinct, incised *vena dividens* can be seen. There may be a trace of R or of Cu_1 or one of the anal veins. A sutural margin is also present.

The hindwing, lying spread out below the elytron in the genotype, has the venation very faintly marked, but as far as it can be made out it agrees closely with the scheme of venation in the hindwings of the Protelytridae.

Other details available for this family are the form of the head, which is large, the pronotum fairly broad, the legs stout with flattened femora and tibiae, the abdomen markedly shorter than the elytron, and the cerci present, short, five-segmented.

There is only a single genus.

Genus *Acosmelytron* n. g.

(Figs. 12-13.)

Characters as given for the family. The elytra in this genus are distinctly convex, with costal margin more or less clearly differentiated and sutural margin generally well marked also.

Genotype:—*Acosmelytron elongatum* n. sp.

Horizon:—Lower Permian of Kansas.

There are three species of this genus, which can be recognized as follows:

1. Elytron elongate oval, apex not sharply pointed; length 8 mm.
A. elongatum n. sp.
2. Elytron pointed at apex 2.
Elytron about 8 mm. long *A. acutum* n. sp.
- Elytron about 6 mm. long, very narrow *A. delicatum* n. sp.

Acosmelytron elongatum n. sp.

(Fig. 12.)

Specimen No. 5415 shows the obverse of a complete elytron together with the hindwing of the same side (left) spread out below it, but with the apical portion not exposed. The elytron is markedly convex, with fairly wide costal margin and well-

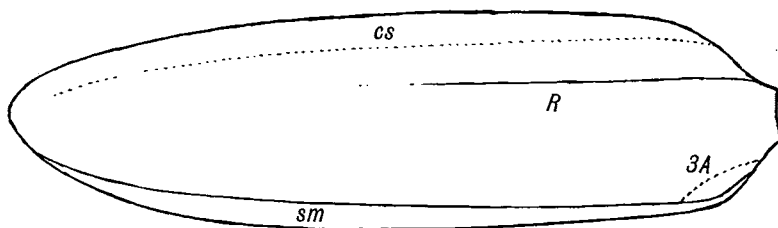


Fig. 12. *Acosmelytron elongatum* n. sp. et sp. Elytron, Specimen No. 5415. Actual length 8.0 mm. 3A, third anal; cs costal shelf; R radius; sm sutural margin.

developed sutural margin widest at about its middle. Traces of R and Sc can be made out as very faint veins, and there is also, near the anal angle, a short, faint vein which is probably 3A. In shape the elytron is elongated, with the two sides almost parallel for a considerable distance, then ending in a rather narrowly rounded apex. Length 8.0 mm., greatest breadth 2.4 mm.

Hindwing with the general venational scheme of *Protelytron* n. g. but with most of the veins weaker. Nodus and nodal fold clearly visible at a distance from the base slightly less than length of elytron.

Type:—*Holotype elytron and hindwing* (obverse), Specimen No. 5415 in Yale University Collection.

Acosmelytron acutum n. sp.

Specimen No. 5414 *a-b* is a very poorly preserved elytron of this species. *Length* 7.5 mm. with the extreme tip broken off; *greatest breadth* 2 mm. Shape narrowly oval, with apex obviously pointed, though the actual tip is missing. Basal half of R visible and also a fairly well developed Cu_1 , somewhat curved. Indications of a narrow sutural margin can be made out near the base

Type:—*Holotype elytron* (obverse), Specimen No. 5414*a* in Yale University Collection; No. 5414*b* (reverse).

Acosmelytron delicatum n. sp.

(Fig. 13.)

Specimen No. 5416 represents a lateral view of a fairly complete specimen of a small, beetle-like insect with large head, lateral compound eyes, fairly large prothorax, rather short

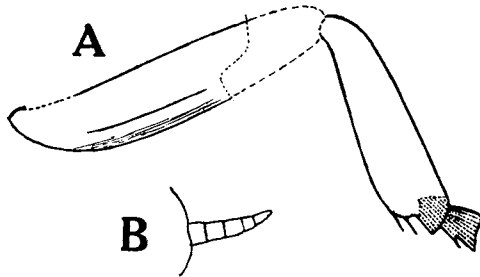


Fig. 13. *Acosmelytron delicatum* n. sp. A, hind leg, showing femur, tibia and basal tarsal segment. B, cercus. Specimen No. 5416. Both figures $\times 24$.

abdomen and long, slender, pointed elytron projecting well beyond the end of abdomen. *Elytron* about 6 mm. long, apparently without any sign of venation. What appears to be the folded apical portion of the hindwing projects downwards at right angles to the elytron from below its tip. The speci-

men is of particular value in showing two characters not visible in any other specimen, viz. the *hind leg* (Fig. 13, A) and the *cercus* (Fig. 13, B).

Hind leg with broad, flattened *femur*, 1.9 mm. long; *tibia* also flattened, 1.4 mm. long, narrow basally but broader distally, and having the distal end excised ventrally and armed with two short spines; *tarsus* with first segment short, broad, armed ventrally with a sharp spine. Rest of tarsus missing, as are also the coxa and trochanter.

Cercus 0.5 mm. long, five-segmented, the segments subequal, tapering to a point.

The abdomen, cerci, mesothorax, part of the head, apical portion of the tibia and the whole of the tarsal first segment are deeply pigmented; the elytron is pale.

Type:—*Holotype*, complete insect, Specimen No. 5416 in Yale University Collection.

SPECIMENS INCERTAE SEDIS.

Specimen No. 5407 a-b shows the head, pronotum and one damaged elytron of a type that probably belongs to the genus *Acosmelytron*, but is not well enough preserved to name.

Specimen No. 5410 a-b is a very poorly preserved elytron, probably also belonging to *Acosmelytron*, but with no definite characterization.

Specimen No. 5412 a-b is a very poorly preserved elytron about 7 mm. long, showing a faint longitudinal vein R, ending at apex, and a fairly definite Cu_2 of the type indicated in the genus *Parablattelytron*, to which it probably belongs.

Specimen No. 5419 is a poorly preserved specimen showing parts of fore and hindwing, only doubtfully referable to this order, possibly referable to the Copeognatha.

Specimen No. 5421 shows portion of a poorly preserved elytron probably referable to the genus *Protelytron* as there are clear indications of a definite venational scheme similar to the one in that genus.

RELATIONSHIPS OF THE NEW ORDER PROTELYTROPTERA.

1. *Relationship with the Order Dermaptera.*

We have already seen how the solution of the problem of the relationships of the new order is bound up with the venational scheme and method of folding of the hindwing. The only

type of hindwing now existing which at all invites comparison with that of the Elytroptera is the hindwing of the order Dermaptera or earwigs. In considering the line of evolution of this latter order, we have to concentrate on the obvious fact that they are a specialized Orthopteroid group which has not only completely achieved the transformation of the forewing into a true elytron, but has also progressed, *as an order*, to a stage closely analogous to that of the Staphylinidae amongst the Coleoptera. The three principal stages in this line of evolution may be briefly stated as follows:—

- Stage A.* ORTHOPTEROID STAGE. Forewing much longer than abdomen, of equal length to, or slightly longer than hind, tegminous. Hindwing with broad anal fan and with the preanal part of the wing comparatively narrow. The forewings in the position of rest form either a roof or hood over the hind, the latter being folded radially in the region of the anal fan only.
- Stage B.* ELYTRIFORM STAGE. Forewing forming a true convex elytron of hard texture, somewhat longer than the abdomen, but markedly shorter than the hindwing. Hindwing folding not only radially in the region of the anal fan, but also inwards from the apex along the nodal fold, so as to fit neatly beneath the shorter elytron. The two elytra meet along their posterior margins in the mid-longitudinal line of the abdomen, with or without development of a sutural margin.
- Stage C.* STAPHYLINOID STAGE. The elytron shortened to less than half the length of the expanded hindwing, and much shorter also than the length of the abdomen. The two elytra still meet in the middle line along their posterior margins. The hindwings now fold not only along the radiating veins of the anal fan, longitudinally, but *twice* transversely, the more basal fold being inwards and the more distal outwards.

As the order Elytroptera is obviously at evolutionary Stage B, while the order Dermaptera is equally obviously at Stage C, only these two stages now come into the discussion. To facilitate this, we must compare, side by side, the expanded hindwings and their methods of folding in the two orders (Figs. 14-17).

Fig. 14 shows the expanded hindwing of *Protelytron permianum*, which has already been fully described in this paper. Fig. 15 shows the left hindwing of the same species, partially folded, and viewed from beneath. The first folding is along the radiating veins of the anal fan, longitudinally; the second folding is transversely, about the fulcrum *k*, using the line from nodus (*n*) to *k* as a convex fold. The partially folded condition of the hindwing is actually preserved in the specimens numbered 5405 (*Protelytron*) and 5416 (*Acosmelytron*) so that there can be no doubt as to what actually took place.

If we consider, as seems highly probable, that the hindwing, in the initial stages of the mechanics of shortening and folding, was helped into its final resting position by the action of the

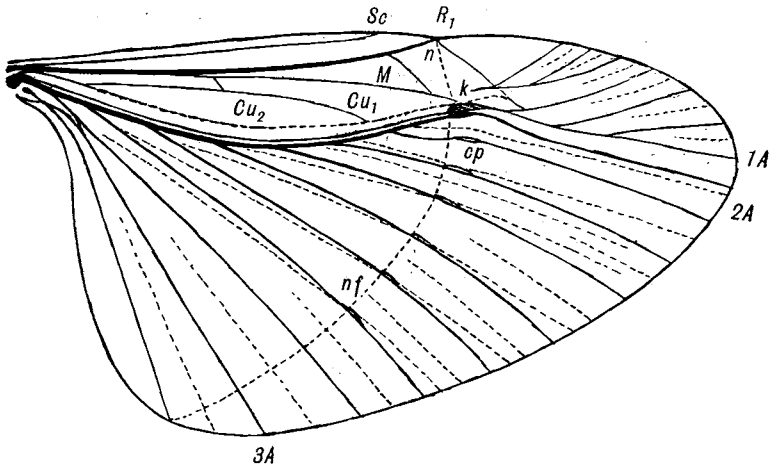


Fig. 14. *Protelytron permianum* n. g. et sp. Order Protelytroptera. Right hindwing, expanded. Venation as in Fig. 2, except *k* fulcrum; *n* nodus; *nf* nodal fold; *cp* chitinous pad.

hind legs, we can see how it was that the apical portion must have become folded *under*, and not *over* the rest of the wing; for, the wing being straight and the abdomen markedly convex,

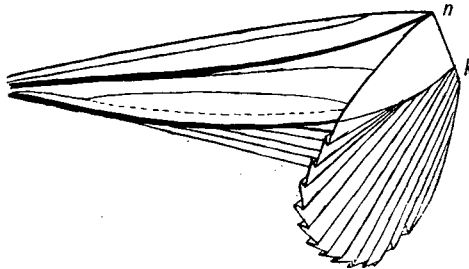


Fig. 15. *Protelytron permianum* n. g. et sp. Order Protelytroptera. Left hindwing, ventral view, in partially folded position. *k* fulcrum; *n* nodus.

there already existed a space suitable to receive the infolded portion *beneath* the rest of the wing, while the tegmen or incipient elytron fitted too closely on top of the hindwing to allow of the apex being pushed in between it and the hind.

Now let us compare the above wing with that of a modern earwig. Fig. 16 shows the expanded hindwing of *Forficula*

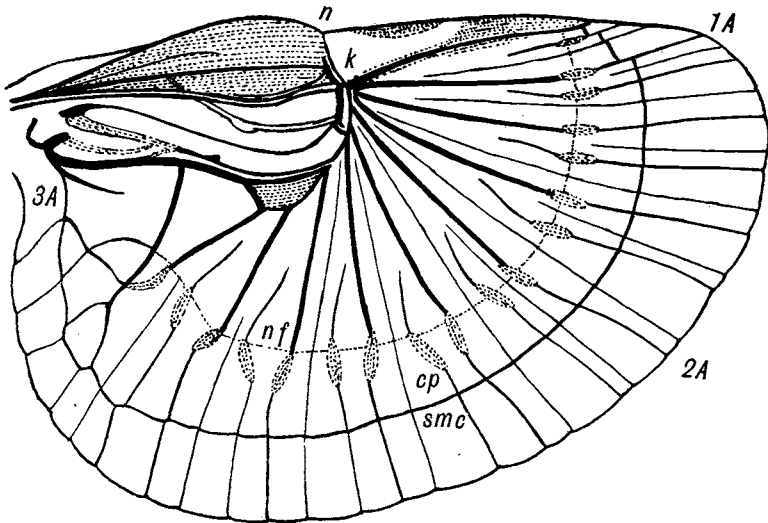


Fig. 16. *Forficula auricularia* L. Order Dermaptera. Right hindwing, completely expanded. *cp* chitinous pad; *k* fulcrum; *n* nodus; *nf* nodal fold; *smc* submarginal cord.

auricularia, the common European earwig. Fig. 17 shows the left hindwing of the same insect, viewed from beneath, and in

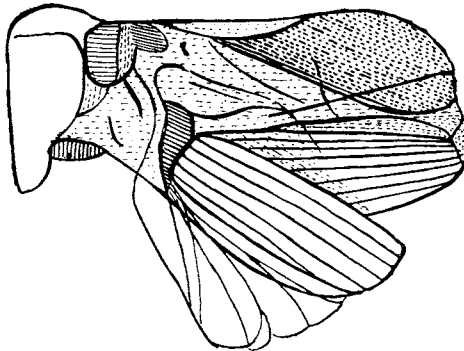


Fig. 17. *Forficula auricularia* L. Order Dermaptera. Left hindwing, nearly completely folded.

the position of nearly complete folding. The method of folding is so complex that it is not at all easy to examine it

accurately. I have found the best way to be the dissecting out of the metathorax of the earwig with the two hindwings still attached; this piece is then pinned, under water, on to paraffin wax in a small dissecting dish, by means of fine cabinet points, and the method of opening and shutting of the wings can then be tested with fine needles.

When this is done, it will be seen that the method of folding of this extremely specialized and complex wing consists essentially of three series of foldings, assisted by secondary stresses caused by the peculiar structure of the veins and the widening of the base of attachment of the wing to the thorax. Starting with the expanded wing, which, by the way, can only be kept expanded with the greatest difficulty, we note that the wing is first folded longitudinally along the outer radiating veins of the fan, and at the same time the strong spring action exercised by the specialized basal part of the wing pulls the distal part inwards and downwards. This pull, however, appears to be resisted, in the far distal portion of the wing, by the elasticity of the submarginal cord (*smc*), and the antagonistic strain put on this part of the wing by this cord offsets the inward pull on the fulcrum. Thus there is an inward bend of the part distad from the fulcrum, accompanied by an outward bend of the extreme apical portion distad from the nodal line, or line of chitinous pads.

It is not easy to construct all the intermediate stages by which this highly complex mechanism could have been evolved from a type similar to that found in the hindwing of the Protelytroptera; but I think the key to it lies in the recognition that, during the gradual reduction of the elytron from the original to the Staphylinoid stage, the recession of the nodus towards the base carried with it the upper portion of the nodal fold, from nodus to the fulcrum *k*, while the rest of the nodal line tended to move distad and to arrange itself concentrically with the more and more curved outer margin of the wing. Possibly the very first stage in this double movement can actually be seen in the species *Protelytron dunbari* (Fig. 4), in which, as I have already noted, the comparatively wide and bluntly rounded hindwing is probably correlated with the slight shortening of the elytron. Now, in this wing, the end of R_1 has already moved slightly basad from the original nodus, while the first of the chitinous pads appears irregularly placed somewhat distad from the nodal line. If the next stage of evolution included a slight regression of the fold from nodus

to k basad, following the movement of the end of R_1 , then the two differential tendencies would have been set in motion, and the final result would be obtained by allowing them to evolve to their limits, as shown in *Forficula*.

The working out of the correlated new strains and stresses which resulted in the peculiar condition of the more basally placed radiating veins of the anal region, together with the development of the complete submarginal cord, is, I think, somewhat beyond the scope of this paper. The main facts emerge that the original transverse folding of the Elytrophorous wing was along a nodal line just distad of which a series of chitinous pads was already in process of formation, and that there is still a fold in the corresponding position in the Dermapterous wing, though the actual bending is now in the outward direction instead of the inward. At first sight this appears to involve a contradiction; but I suggest that this secondary direction of bending may have first been given effect to by the hind legs, and later on stabilized by the development of the strongly elastic submarginal cord.

We see, then, from the above study of the evolution of the folding of the hindwing, that the Dermaptera might well be the direct descendants of the extinct order Elytroptera. Let us now examine the venational scheme to see how strong this probability really is.

Turning once more to the hindwing of *Protelytron* (Fig. 14), and comparing it with other more normal types of hindwing, the first thing that we note about it is that it is definitely an Orthopteroid type, but far more advanced in specialization even than the hindwing of such an order as the Protoperlaria. The essential line of evolution of the Orthopteroid hindwing is the narrowing of the original preanal portion and the steady enlargement of the anal fan. Analysis of the tracheation of almost any Orthopteroid type will show clearly that the chief contributor to the venation of the fan is the vein 2A (cf. hindwing tracheation of Perlaria and true Orthoptera, also venation of the fossil order Protoperlaria). This is equally true of the new order Elytroptera; only, in this case, the gain of actual area of the anal fan at the expense of the preanal region is well in advance of most Orthopteroid types.

Comstock (1918, p. 295, Fig. 305) interprets the radiating anal veins of the hindwing in Dermaptera as branches of 1A. But it seems clear, from his figure of the tracheation (op. cit., Fig. 306), that the stout anal trachea must be either 2A or else

two anal tracheae fused together. But, whatever may be our interpretation of the venation of the anal fan, it is at any rate quite clear that the Dermapterous wing represents, in its venation, simply a further evolutionary advance from a type either closely similar to, or actually the same as, that shown in *Protelytron*. The presence of the nodus, nodal line, flexible chitinous pads and intercalated marginal folds in both types proves their close affinity. The Dermapterous type is greatly in advance of the Elytropterous type through the further shortening of the preanal area, the recession of the nodus towards the base, the much greater curvature of the strong main anal vein, the more extensive development of flexible chitinous pads, which now appear not only on the radiating veins but also on the intercalated folds, which are also chitinized, and finally by the complete development of the submarginal cord.

Let us now consider the forewing. In the Elytroptera, this is already a true elytron, convex, hard, and shorter than the expanded hindwing, which it entirely covers in the position of rest. In the Dermaptera, the forewing is also a true elytron of the same type and serving the same function, but very much shortened. In the same manner that it is certain that the shortened elytron of a Staphylinid beetle must have been derived from a more normal elytron of the Silphid type, so it is clear that the shortened elytron of the Dermaptera must be descended from a more normal elytron, i.e. from a stage resembling that to be found in the Elytroptera.

Unfortunately not much evidence is to be obtained from the other parts of the body. As far as it goes, there is nothing in the body-structure of the Elytroptera which does not fit in with the hypothesis that they are ancestral to the Dermaptera. The form of head, with small laterally placed eyes, is quite suitable, while the large pronotum, with expanded lateral margins, is still met with in the Dermaptera. The form of the antennae and number of tarsal segments of the legs are not known for Elytroptera, but these should not in any case prove stumbling-blocks, particularly when we remember that the Coleoptera show all gradations from a primitive five-segmented tarsus to a highly specialized three-segmented type, and that the Dermaptera are throughout only trimerous types. As regards the cerci, if again we are agreed that the trend of evolution was towards reduction, then it is clear that the unsegmented forceps of the earwig can easily be derived from the short seg-

mented cercus of the Elytroptera, and not the other way round.

The totality of evidence stated above forms a strong case for regarding the Elytroptera as the ancestral order from which the present Dermaptera have arisen, probably as a highly reduced and specialized remnant of an originally more extensive and diverse group.

2. *Relationship with the Order Coleoptera.*

Attractive as the idea of affinity with the Coleoptera appears at first sight, owing to the obviously Coleopteroid appearance of the complete insects of the order Elytroptera, and more

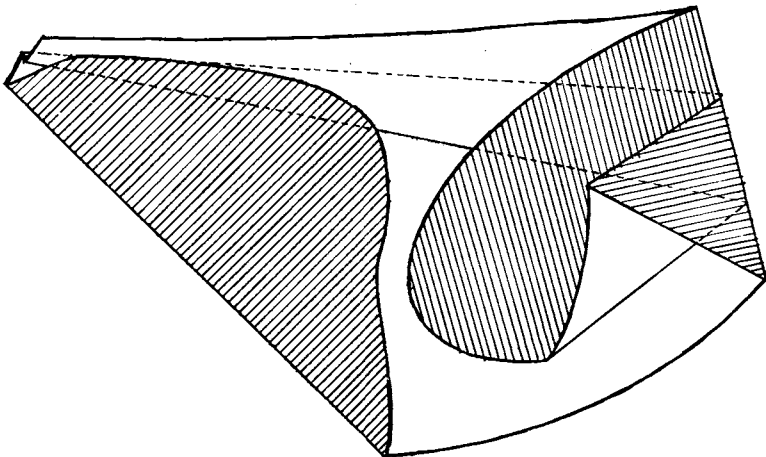


Fig. 18. Schematic diagram of the folding of the hindwing in the order Coleoptera, Suborder Polyphaga, according to d'Orchymont. The wing represented is a left hindwing, viewed from beneath, with the venation omitted. The shaded portions represent those portions which, on folding, expose their upper surface to ventral view.

particularly of the forewing, I am not able to find any clear indications of close affinity between them. Both d'Orchymont (1920, 1921) and Forbes (1924) have dealt very fully with the problem of the Coleopterous hindwing and its methods of folding, and the former author has analyzed the various types of folding found in the order, and has reduced them to a simple original type. Fig. 18 shows d'Orchymont's schematic diagram of a simple Polyphagous type of folding. The figure is that of a left wing, viewed from below, and the shaded

portions indicate those parts of the wing that are so folded that their upper surface appears in the figure. Comparing this type of wing with that of the Elytroptera, we can pick out the points in which they agree and disagree, as follows:—

Characters in which Coleoptera and Elytroptera agree:

- (1) Infolding of apical area backwards by a convex nodal fold.

Characters in which Coleoptera and Elytroptera disagree:

- (2) Folding of basal portion of anal area forwards and under in Coleoptera has no counterpart in Elytroptera.
- (3) Venation of anal area of Coleopterous wing not of Orthopteroid type, and lacking the important development of a large series of radiating branches.
- (4) No longitudinal fan-like folding in the Coleopterous wing.
- (5) Much greater area of wing occupied by preanal veins in the Coleopterous wing.

Analyzing these five points, we see at once that the only one which is common to the two orders is just that one which might most logically be expected to develop, during the course of evolution, more than once; for if it is true that the action of the hind legs first brought about the inpushing of the apical part of the hindwing when the forewing began to shorten, then this might surely happen in *any* type of insect, and is not therefore any proof at all of community of descent. On the other hand, in character (2) we find the Coleoptera evidently more advanced than the Elytroptera, while in (3), (4) and (5) they appear to be more primitive, but not lying along the Orthopteroid line at all.

Turning next to the elytron, we have to admit that here the correspondence between the two orders is a close one. The two types of elytron resemble one another in the development of the sutural margin, in their mode of folding when at rest, in their convexity, hardness and tendency to become granulose. There is, however, no evidence that any primitive type of Coleopteron ever possessed a simple type of Orthopteroid venational scheme on its elytron, and there is a good deal of evidence against it.

As regards the general form of body, head, pronotum, legs, etc., the Coleoptera could evidently easily have been derived from the Elytroptera. Only in two points are there apparent difficulties, viz. in the presence of short, segmented cerci in the Elytroptera, and in the fairly obvious fact that this order was not Holometabolous. The cerci could, of course, have been lost during evolution; they almost certainly were so lost by Coleoptera and other Holometabola which do not possess

them; for the most primitive Holometabolous group, the Mecoptera, still possess them in very shortened form. Also Holometabolism may have been evolved more than once in the Insecta; indeed, there is as yet very little evidence in favor of the Coleoptera having any very close relationship with other Holometabolous orders.

If, then, we wish to derive the Coleoptera from the Elytroptera, it can only be done by a somewhat devious method. We must imagine that the group represented in the fossil order Elytroptera by the family Acosmelytridae either possessed, or evolved later, very small, simplified types in which the whole of the elytral venation was lost and the hindwing became so reduced in its venational scheme that only a few elements of the original anal fan survived. Possibly from such an ancestor as this one might construct an evolutionary line leading to the Coleopterous hindwing. But personally I cannot offer much support to such a view, for I think the mass of evidence is quite against it. Only, for what it may be worth, we must recall that the first true Coleoptera, found in the Upper Permian of Australia, are indeed very small forms with elytra having practically no true venation, and therefore it is highly probable that this order, like all other Holometabola, has been evolved from very small ancestors.

My own conclusion is that no true relationship can be proved to exist between Elytroptera and Coleoptera, and that we must postulate two quite distinct main lines of evolution of Elytrophorous types, one running from the Elytroptera to the Dermaptera, and the other, starting from some still unknown type of ancestor and ending in the Coleoptera.

3. *Relationship with the Protocoleoptera.*

The fossil order Protocoleoptera (Tillyard, 1924) was formed by me to include a series of Upper Permian fossil elytra of large size which occurred alongside true Coleoptera in the Belmont and Warner's Bay Beds of N. S. W., but which were evidently not true Coleoptera. They had flattened, tegminous elytra with straight sutural margin and a complete and often very complex venational scheme, with the spaces between the veins strongly punctate. I stated that these forms could not be the true ancestors of Coleoptera, since they occurred in the same beds as the latter, but that they must belong to the more ancient group from which true Coleoptera had been

derived, in the same sense that Protodonata are related to true Odonata. Hence came the name Protocoleoptera.

The type of Elytropteron which comes closest to the Upper Permian Protocoleoptera is, I think, undoubtedly the genus *Megelytron* (Fig. 8) which should be compared with both *Protocoleus* and *Permofulgor*. Other more recently discovered types of Protocoleoptera, not yet described, appear to come fairly close to *Permelytron* (Fig. 6).

Bearing in mind the new evidence offered by the discovery of the order Elytroptera, I think it possible that the Upper Permian Protocoleoptera may indeed prove in the end to have had no connection at all with true Coleoptera, but rather to have been an archaic remnant of the older Elytroptera, at a stage when the elytron was still more tegminous and less convex. This remnant must, on this hypothesis, have reached Australia some time in the Permian and remained there more or less unchanged, while the main stem of the order advanced beyond them in the Northern Hemisphere. This supposition is not improbable; but until a hindwing of the order Protocoleoptera is found, the true relationships of that order cannot be determined.

SUMMARY.

1. The new order Elytroptera is defined and classified, with the following families, genera and species:—

Family 1. PROTELYTRIDAE.

Genus 1. *Protelytron* n. g.

1. *Protelytron permianum* n. sp. (Genotype).

2. *Protelytron dunbari* n. sp.

Genus 2. *Protelytroopsis* n. g.

3. *Protelytroopsis grandis* n. sp. (Genotype).

Family 2. PERMELYTRIDAE.

Genus 3. *Permelytron* n. g.

4. *Permelytron schucherti* n. g. (Genotype).

Genus 4. *Megelytron* n. g.

5. *Megelytron robustum* n. sp. (Genotype).

Family 3. BLATELYTRIDAE.

Genus 5. *Blattelytron* n. g.

6. *Blattelytron permianum* n. sp. (Genotype).

Genus 6. *Parablattelytron* n. g.

7. *Parablattelytron subincisum* n. sp. (Genotype).

8. *Parablattelytron rectum* n. sp.

Family 4. ACOSMELYTRIDAE.

Genus 7. *Acosmelytron* n. g.

9. *Acosmelytron elongatum* n. sp. (Genotype).

10. *Acosmelytron acutum* n. sp.

11. *Acosmelytron delicatum* n. sp.

2. The order Elytroptera represents the ancestral group from which the existing order Dermaptera has been derived.

3. There is no definite relationship between the Elytroptera and the true Coleoptera.

4. The Protocoleoptera may have been a remnant of the older Protelytroptera which found a refuge in Australia and remained there unchanged in the Upper Permian.

REFERENCES.

- COMSTOCK, J. H., 1918. *The Wings of Insects*. Ithaca, N. Y. See p. 295 and Figs. 305, 306.
- D'ORCHYMONT, A., 1920. *La Nervation alaire des Coléoptères*. *Ann. Soc. Ent. France*, **89**, 50 pp. 3 pls.
- , 1921. *Aperçu de la Nervation alaire des Coléoptères*. *Ann. Soc. Ent. Belg.*, **61**, 23 pp.
- FORBES, W. T. M., 1924. How a Beetle folds its Wings. *Psyche*, **31**, No. 6, pp. 254-258.
- TILLYARD, R. J., 1924. Upper Permian Coleoptera and a new Order from the Belmont Beds, New South Wales. *Proc. Linn. Soc. N. S. W.*, **49**, pt. 4, pp. 429-435, pls. xlv-xlvi.
- , 1926. *Kansas Permian Insects*. Part 8. The Order Copeognatha. *This Journal*, **11**, 315-349.
- , 1928. *Kansas Permian Insects*. Part 12. The Family Delopteridae, with a Discussion of its Ordinal Position. *This Journal*, **16**, 469-484.

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