

STUDIES ON NORTH AMERICAN CARBONIFEROUS
INSECTS.

4. THE GENERA *METROPATOR*, *EUBLEPTUS*,
HAPALOPTERA AND *HADENTOMUM**

BY F. M. CARPENTER
Harvard University

The four genera treated in this paper, belonging to three different orders, have only one feature in common: all have been very difficult to interpret and to classify. *Metropator*, originally placed in the Palaeodictyoptera by Handlirsch (1906a), has subsequently been regarded as protorthopterous by some investigators and as mecopterous by others; *Eubleptus*, also placed by its author in the Palaeodictyoptera, has been made the type of a new order, Eubleptidodea, by Laurentiaux (1953); *Hapaloptera* and *Hadentomum*, originally designated by Handlirsch (1906a) as types of two new orders (Hapalopteroidea and Hadentomoidea), have subsequently been either assigned to these orders or placed with uncertainty in the Protorthoptera. Unfortunately, all of these genera are known only by their type-species, which are still represented solely by the unique type-specimens. From my study of these fossils, I am convinced that the species are not nearly so peculiar as has formerly been thought and that to a large extent their puzzling nature is the result of Handlirsch's unsatisfactory figures and descriptions. I believe that *Metropator* was based on the hind wing of a species of the order Miomoptera, that *Eubleptus* is very close to the family Spilapteridae of the order Palaeodictyoptera, and that *Hapaloptera* and *Hadentomum* are near relatives of other genera in the order Prothorthoptera. In the following account I have first redescribed the fossils in the taxa to which I consider them to belong and then have given the reasons for my conclusions on their affinities.

I am deeply indebted to Dr. G. A. Cooper of the U. S. National Museum for placing these type-specimens at my disposal on the several occasions during the past ten years when I have found it necessary to examine them. They have been studied under optimum conditions, with various types of illumination and with the use of alcohol-glycerine and with ammonium chloride, which has proven to be of the greatest

*This research is aided by Grant No. GB 2038 from the National Science Foundation. The previous part in this series was published in *Psyche*, 71: 117-124.

aid in working out venational details. I am also grateful to Dr. Jarmila Kukulová, of Charles University in Prague, who studied these fossils with me during her visit to Harvard University in 1964 and who prepared several of the drawings which are included in the present paper.

ORDER MIOMOPTERA MARTYNOV

This is an order of small insects, apparently related to the Prothoptera. The fore wings were membranous and the hind wings, which lacked an expanded anal area, had the media arising from the cubitus and had CuA and CuP anastomosed for their entire lengths, forming a strong concave vein. The order is known from Upper Carboniferous and Permian strata.

Family Metropatoridae Handlirsch

Metropatoridae Handlirsch, 1906, Proc. U.S.N.M., 29: 681
Metropatridae Martynova, 1962, Osnovy Paleont. :286¹

Related to the Archaemiopteridae and Palaeomanteidae. Hind wing nearly oval; Sc short, weakly developed and close to R, as in Palaeomanteidae; Rs forking before mid-wing, forming 6 terminal branches; MA arising independently of CuA at the base of the wing and forked almost to the level of origin of Rs; CuA + CuP with short terminal fork. Fore wing and body unknown.

Genus *Metropator* Handlirsch

Handlirsch, 1906, Proc. U.S.N.M., 29: 682

Hind wing: R₄+5 more deeply forked than R₂+3; R₃ with a deep fork, R₂ with a very shallow one; M₁+2 forked distally, M₃+4 forked twice. Type-species: *Metropator pusillus* Handlirsch

¹The generic name *Metropator* is obviously derived from the identical Greek word for "maternal grandfather". The genitive of this is *Metropatoros*, providing the root *Metropator-* and, therefore, the family name *Metropatoridae*.

In changing the name to Metropatridae, Dr. Martynova was apparently misled by the normal Greek word for father (*pater*), which ordinarily has the stem *patr-*; *pater*, however, as used in the compound *metropator*, does not follow *pater* in declension, although it means the same thing and is merely a collateral form of that word. Since Handlirsch used the generic name *Metropator*, there is no question about the root or the spelling of the family name. I am indebted to Mr. Charles C. Porter for providing me with this etymological information.

Metroptator pusillus Handlirsch

Figure 1

Handlirsch, 1906, Proc. U.S.N.M., 29: 682, fig. 8; 1906, Foss. Ins. :112, pl. 12, fig. 12.

Tillyard, 1926, Amer. Journ. Sci., 11: 161, fig. 19.

Martynova, 1962, Osnovy Paleont., Arthropoda: 286, fig. 892.

This species is based on a unique specimen (type no. 38731, U.S.N.M.), consisting of an isolated wing, 7 mm. long and 3 mm. wide. It was collected near the Altamont Colliery, anthracite region, Pennsylvania (Namurian age). The preservation is fair; most of the main veins are clear, but the basal part of the wing is missing. Since this is one of about a dozen insects known from the lower part of the Upper Carboniferous, the oldest strata in which unquestionable insects have been found, its structure and affinities are of unusual interest. Some diversity of opinion exists about both aspects of the fossil. Handlirsch, who originally placed *Metroptator* in the Palaeodictyoptera, believed that the anterior margin of the wing was broken away, the front edge of the wing as preserved being the subcosta; he apparently reached that conclusion because he was unable to discern the subcosta as a submarginal vein. Tillyard in 1926, following his examination of the type specimen, concluded that the anterior margin of the wing was actually preserved and that Sc was discernible as a distinct vein between R₁ and the wing margin. In his description he points out that the subcosta is very faintly indicated, and that he could follow it out only with care by examining the fossil in a good oblique light. He also described and figured the cubito-median "Y-vein", this being much more strongly developed than most of the other veins of the wing. His conclusions were that *Metroptator* was a mecopteran, closely related to the Permopanorpidae. He did not discuss the detailed evidence for this, but simply asserted that the mecopterous affinities could readily be seen at once from the figures. His view of the position of *Metroptator* has been generally accepted subsequently, and it is the one presented in the Osnovy Paleontologii (Martynova, 1962).

The drawing included in figure 1 represents my own interpretation of this fossil and shows only those structures which I confidently believe are present. From my studies I am convinced that Tillyard was correct in his conclusion that the costal margin of the wing is actually present in the fossil, but I am also convinced that he was incorrect in his interpretation of the subcostal and cubital areas. The subcosta is discernible near the base of the wing, as noted by Tillyard, but that is the entire length of the vein; it extends only a short

distance beyond the origin of Rs. The ammonium chloride preparation brings this vein out clearly enough so that it is visible in photographs. On the other hand, the supposed branch of the media, which Tillyard showed as one arm of the cubital-median "Y-vein" and which was an important factor in his conclusions on the affinities of the fossil, cannot be seen — at least not by any techniques used by me. The cubital vein itself (labelled Cu1 in Tillyard's drawing) is, as mentioned by Tillyard, a distinct one, which stands out more strongly than any of the others excepting R1. It is, however, clearly *concave* in the fossil. This is important, since the supposedly homologous vein (CuA) in the mecopterous wings is strongly *convex*. I am convinced, therefore, that the venation of *Metropator* only superficially resembles that of the Mecoptera and that it does not have the essential features of the mecopterous venation.

I believe the type-specimen of *M. pusillus* can much more readily be interpreted as a hind wing of a miomopteron. In these wings the subcosta is very short (see figure 2), Rs arises close to the base of the wing, and CuA and CuP are completely coalesced, forming a strong *concave* vein. These are the outstanding features of *pusillus*. Unfortunately, since the base of the wing is missing in the type of *pusillus*, the precise relationship between Cu and M cannot be determined; however, there is no reason to assume that M does not join Cu near the basal part of the wing. The venation of *pusillus* shows more extensive branching than in the miomopteron illustrated in figure 2 [*Palaeomantis minuta* (Sellards)] but in other genera of Miomoptera (e.g., *Stefanomioptera* Guthörl and *Permonika* Kukalová) the radial sector has more branches than in *Palaeomantis*. It seems to me, therefore, that the available evidence, such as it is, indicates that *Metropator* is more likely a miomopteron than a mecopteran. The occurrence of several genera of Miomoptera in the Carboniferous deposits of Europe supports this probability. The Mecoptera, on the other hand, are otherwise unknown from beds earlier than the Permian and since these are endopterygote (holometabolous) insects, evidence for their presence in the lowest strata of the Upper Carboniferous should be really convincing before such a conclusion is reached. At present I believe the evidence points to a very different conclusion.

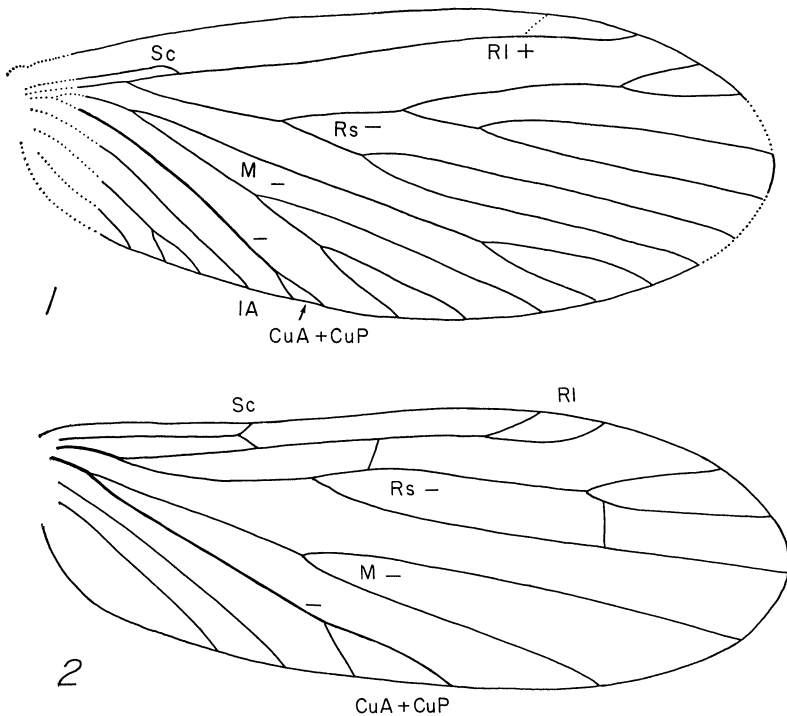
ORDER PALAEOICTYOPTERA GOLDENBERG

Family Eubleptidae Handlirsch

Handlirsch, 1906, Proc. U.S.N.M., 29: 679 (Order Palaeodictyoptera).
 Laurentiaux, 1953, In Piveteau, Traité de Paléontologie. 3: 423 (Order Eubleptidodea).

Fore wing: subcosta extending at least nearly to the wing apex; Rs with 4 terminal branches; MA forked, MP with at least 3 terminal branches; CuA with a short terminal fork; CuP more extensively developed, with a deep fork shortly after its origin; several anal veins; cross veins distributed generally over the wing, not arranged in rows; anterior margin of the fore wing nearly straight, at most very slightly concave. Hind wing: little-known; slightly broader than fore wing. Body structure: prothoracic lobes present; abdomen slender.

This family seems closely related to the Spilapteridae, from which it differs in having a less developed Rs and CuA. Lack of knowledge



Figures 1 and 2. Miomoptera. Figure 1. *Metroptator pusillus* Handlirsch. Drawing of holotype, no. 38731, U.S.N.M.; hind wing (original). Figure 2. *Palaeomantis minuta* (Sellards), hind wing (original). Lower Permian, Kansas. Lettering: Sc, subcosta; RI, radius; Rs, radial sector; M, media; CuA, anterior cubitus; CuP, posterior cubitus, 1A, first anal vein; +, convex veins; —, concave veins.

of the hind wings prevents more definite determination of the affinities, but all available evidence indicates that this is a group which fits readily within the Palaeodictyoptera; eventually the family may turn out to be inseparable from the Spilaptaridae.

Genus *Eubleptus* Handlirsch

Handlirsch, 1906, Proc. U.S.N.M., 29: 680

Fore wing: Rs arising slightly beyond mid-wing; M forked before the origin of Rs, and Cu forked even nearer the wing base; Rs forked and each of its branches forked; 1A simple, 2A forked. Type-species: *Eubleptus danielsi* Handlirsch.

Eubleptus danielsi Handlirsch

Figure 3

Handlirsch, 1906, Proc. U.S.N.M., 29: 680

Length of fore wing, as preserved 13 mm.; estimated total length 17 or 18 mm.; width of fore wing, 4 mm.; maximum width of hind wing (as preserved), 4.8 mm. Type no. 35576, U.S.N.M., collected near Morris, vicinity of Mazon Creek, Illinois (Westphalian age).

This species was originally based by Handlirsch on a single specimen consisting of obverse and reverse; the obverse specimen, according to Handlirsch's description, was contained in the Daniel's collection and the reverse in the U. S. National Museum. The counterpart in the National Museum has been studied in connection with the present account and is depicted in figure 3; the specimen in the Daniel's collection has not been found.

Handlirsch's figure, which has been reproduced many times in subsequent publications and which has been the basis for all discussions of the relationships of this fossil, was probably based to some extent on the counterpart in the Daniel's collection; at any rate the position of the body in Handlirsch's figure is the reverse of that in the counterpart in the National Museum. The Daniel's specimen presumably showed parts of the cerci, which are entirely missing in the National Museum fossil; also the Daniel's specimen probably showed a little more of the apical regions of the fore wings than the reverse half. The venation in the National Museum fossil is distinctly preserved and can be brought out even more clearly by the use of ammonium chloride. As shown in figure 3, it is only slightly different from that given in Handlirsch's figure; there are some differences in the positions of branches of the veins, but in general the patterns are very similar. Handlirsch apparently did not observe the basal connection between CuA and CuP, although this is clearly distinguishable in the National Museum specimen. His figure of the

abdomen is about as I have observed it, although this seems somewhat broader in the fossil than his drawing shows. As noted above, the National Museum specimen does not include the end of the abdomen and therefore lacks the cerci. Handlirsch's representation of the meso- and metothoracic segments is in agreement with mine; of course, considerable distortion undoubtedly occurred in the fossil and only the general form is indicated. The major difference between Handlirsch's figure and mine is in the structures which are anterior to the mesothoracic segment. Handlirsch was of the opinion that two large globular eyes could be distinguished, these being separated from the mesothorax by a structure which he interpreted as the prothorax. His figure in this area is slightly out of proportion; the structures which he shows as eyes are actually much closer to the mesothorax than indicated in his drawing. Furthermore the structures themselves do not have the regular, globular appearance which he depicts and they do not give any indication of being compound eyes. On the other hand, there are clearly visible radiating lines similar to those which occur on the paranotal lobes of many Palaeodictyoptera. The location of these structures and their details have convinced me that they are in fact small paranotal lobes. Between them and the mesothorax is a short segmented appendage, almost certainly a part of one of the legs; this is shown also in Handlirsch's figure.

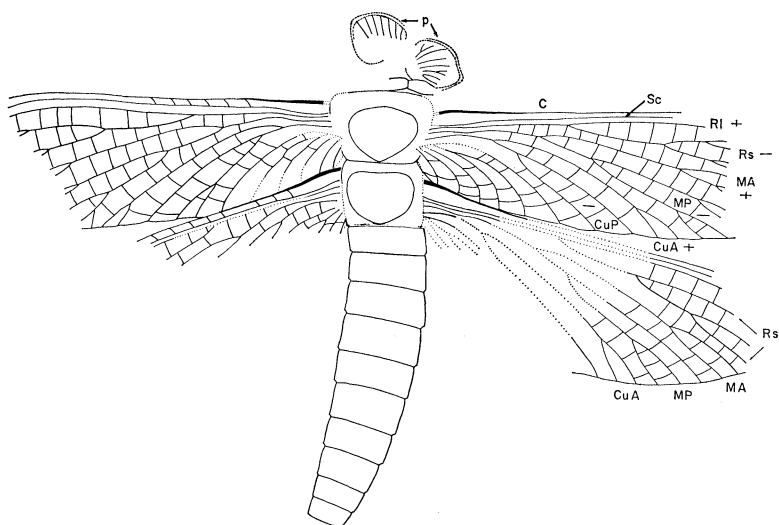


Figure 3. *Eubleptus danielsi* Handlirsch. Drawing of holotype, no. 35576, U.S.N.M. (original). p, paranotal lobes; other lettering as in figure 1.

The venation of the wings is actually typical of that of many Palaeodictyoptera, especially that of some of the Spilapteridae. The convexities and concavities of the veins, which are well preserved, have been marked in figure 3 in the usual manner. Perhaps the most distinct feature of the venation is the reduction of CuA to a single vein having a marginal fork; in the Spilapteridae this vein tends to be somewhat more extensively developed. There is a slight difference between the right and left wings so far as CuP is concerned; in one, CuP₂ is forked but in the other it is unbranched. The anal veins are slightly recurved, having the arched form occurring in many Palaeodictyoptera. The venation of the hind wing is very little-known but it appears to show no marked differences from the pattern in the fore wing; however, the wing itself is obviously somewhat broader than the fore wing.

Although the specimen of *Eubleptus* in the National Museum does not, presumably, show as much of the apical region of the wings as the counterpart in the Daniel's collection, I think there is no question that Handlirsch's figure is incorrect in showing the wings as very broadly and bluntly rounded. In that figure the left fore wing is completely restored, the apex being represented by dotted lines; but the drawing of the right wing shows an irregularity of the apex, which suggests that this is not the actual margin of the wing itself. In all probability, the apical region of the wing was shaped like that of spilapterids.

Handlirsch originally described *Eubleptus* in the Eubleptidae, as a palaeodictyopteron. However, his figure and description emphasized several peculiar features which actually do not exist in the fossil (such as the supposedly large eyes and the bluntly rounded wings). As a result of this, various workers on fossil insects who have not examined the type specimen have come to regard *Eubleptus* as a more peculiar and aberrant insect than it actually is. Martynov, in 1938, although placing the family Eubleptidae in the Palaeodictyoptera, stated that it could well belong to a distinct order; and in 1953 Laurentiaux established the order Eubleptidodea for it. He failed to indicate any characteristics by which he separated the order from the Palaeodictyoptera, although he referred to the eyes and the absence of lobes on the prothorax. In the *Osnovy Paleontologii*, Rohdendorf placed the Eubleptidae in a separate order, which he termed the Eubleptodea, presumably accepting Laurentiaux's ordinal status for the group although no reference is made to Laurentiaux's publication or to the change of spelling of the name.

However, in view of the structure of *Eubleptus danielsi*, as it now seems to be, there is no justification for the isolation or separation of

Eubleptus into a distinct order or even into a distinct suborder. It is, in fact, difficult to find significant differences in the venational patterns of the Spilapteridae and the Eubleptidae; ultimately these two families may turn out to be synonymous. However, I have not indicated such synonymy at this time since the name Eubleptidae would have priority, and to synonymize Spilapteridae with Eubleptidae seems inadvisable until the evidence for this is conclusive.

ORDER PROTORTHOPTERA HANDLIRSCH

Family Hapalopterae Handlirsch

Handlirsch, 1906, Die fossilen Insekten: 304 (Order Hapalopteroidea).

Fore wing: similar to that of the Cacurgidae but having fewer branches on the main veins and having CuP forking much further from the wing base; CuP₁ not branched except for forking at wing margin; cuticular swellings apparently absent. Hind wing unknown.

Genus *Hapaloptera* Handlirsch

Handlirsch, 1906, Proc. U.S.N.M., 29: 694

Fore wing: Sc extending nearly to wing apex; costal veinlets unbranched; Rs with four branches, MP forked to about mid-wing; CuA with a terminal fork only; cross veins numerous, weakly formed. Type-species: *Hapaloptera gracilis* Handlirsch.

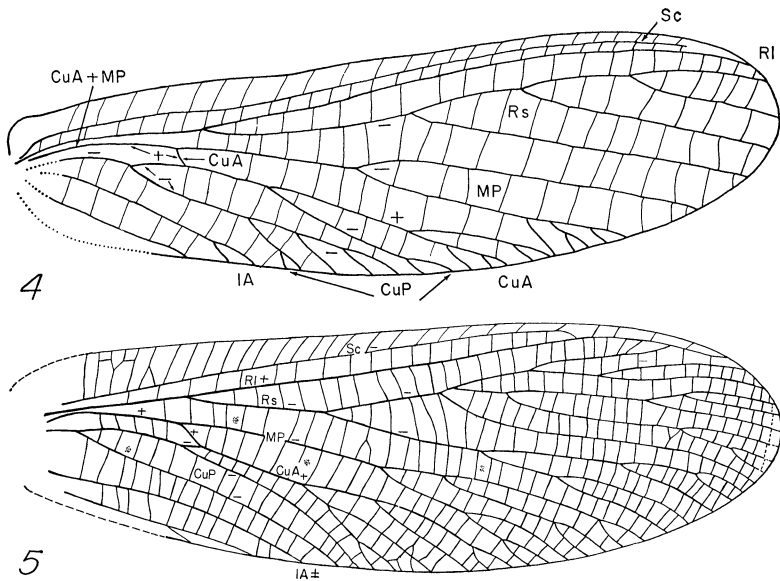
Hapaloptera gracilis Handlirsch

Figure 4

Handlirsch, 1906, Proc. U.S.N.M., 29: 694

Fore wing: length 14 mm., width 4.5 mm.; membranous and delicate; costal margin slightly concave, apex broadly rounded; R₂ forked, R₃, R₄ + 5, MP₁ and MP₂ unbranched; cross veins tending to be irregular, but not branched or forming a network. The holotype specimen, no. 38731, U.S.N.M., was collected at Sharp Mountain Gap, near Tremont, Pennsylvania (Stephanian age). The details of the venation are shown in figure 4.

This fossil consists of a fore wing, very nearly complete, with portions of a second wing. The venation is not distinct but use of ammonium chloride brings out most details clearly. Handlirsch had difficulty interpreting the venation, mainly because he failed to note that actually two wings are superimposed; his figure shows some veins which are in reality on the second wing. The distal part of the costal margin of the second wing can be clearly seen near the end of Sc of the complete wing, and part of its hind margin appears in the region of the end of MP. Handlirsch correctly recognized that



Figures 4 and 5. Protorthoptera. Figure 4. *Haploptera gracilis* Handlirsch. Drawing of holotype, no. 38731, U.S.N.M. (original) Figure 5. *Heterologus langfordorum* Carpenter. Drawing of holotype, Illinois State Museum (original). Upper Carboniferous, Illinois.

something was amiss with the venation for he represents one vein by a dotted line, which crosses over the basal part of another vein. With the use of ammonium chloride the actual venation of the upper wing becomes distinct and the pattern turns out to be very close to that of *Heterologus*, from the Upper Carboniferous of the Francis Creek Shales (Mazon Creek), Illinois (See figure 5). In *Haploptera gracilis*, as in *Heterologus*, the stem of CuA (which is strongly convex) is anastomosed with MP, but diverges away at about the level of the origin of Rs and then anastomoses with the concave CuP, only to separate again a short distance further. The main feature which distinguishes *Haploptera* from *Heterologus* and other Cacurgidae is the late forking of CuP and the absence of a long basal branch on CuP₁. My first thought on examining the fossil was that the wing membrane was extensively wrinkled but further study indicated that the wrinkles are in most cases actual cross veins between the veins. Although only a few cross veins are shown in Handlirsch's figure, they are almost uniformly distributed over the wing.

Handlirsch placed the family Hapalopteridae in a separate order, Hapalopteroidea, although only one species, *H. gracilis*, was known at the time. His decision to establish this "provisional" order was undoubtedly the result of his misinterpretation of the venation of the unique specimen on which *gracilis* was based. In 1922 he placed another family, Emphylopteridae Handlirsch, in the order; this group was based on another monospecific genus, *Emphyloptera* Pruvost, from the Upper Carboniferous of Europe. The assignment of this genus to the Hapalopteridae obviously resulted once again from Handlirsch's misinterpretation of the venation of the type of *Hapaloptera*. Quite clearly, *Emphyloptera* shows no affinities with *Hapaloptera*, as now understood, and it is here assigned to family Incertae Sedis, order Protorthoptera, until the fossil on which it is based can be studied further. The genus *Ampeliptera* Pruvost (1927) from the Upper Carboniferous of Holland was placed in the Hapalopteroidea by Pruvost but removed to another extinct order, Protocicadida, by Haupt in 1941. The fossil on which *Ampeliptera* was based was studied by Kukalová (1958), who found that it was an unquestionable protorthopteron of the family Paoliidae.

As to the genus *Hapaloptera* itself, there is nothing known about it which eliminates it from the Protorthoptera. In fact, as noted above, it is very close to the Cacurgidae. Bolton (1934) described two species in the genus *Hapaloptera* from the Upper Carboniferous of South Wales. Neither of these fossils, however, has affinities with *Hapaloptera*, as can readily be seen from an examination of his figures; both of the species are known only from fragments of wings which, far from belonging to the same genus, represent at least separate families and may represent even separate orders. The order Hapalopteroidea is accordingly now placed in synonymy with the order Protorthoptera.

Family Protoperlidae Brongniart

Brongniart, 1893, Recherches l'histoire insectes fossiles: 407 [*nom. correct.*

Lameere, 1917, p. 197 (*pro* Protoperlida Brongniart, 1892)]

= Palaeocixiidae Handlirsch, 1919, Denkschr. Acad. Wiss. Wein, 92: 29

= Fayoliellidae Handlirsch, 1919, *ibid*: 48

= Hadentomidae Handlirsch, 1906, Die fossilen Insekten: 303 (Order Hadentomoidea)

Fore wing: costal area with numerous, simple veinlets; Sc extending well beyond mid-wing; R₁ unbranched; R_s arising at least slightly before mid-wing, unbranched; M forked; MP usually weaker than MA; CuA extensively branched; CuP straight or nearly so, unbranched; cross veins well developed; no reticulation but rarely two

rows of cells in a few areas. Hind wings (known only in *Protoperla*): Rs arising nearer the wing base than in the front wing; CuA fused with the very base of M; anal area expanded to form a distinct lobe.

From a study of the type material of *Protoperla*, *Palaeocixius*, *Fayoliella* and *Hadentomum*, I am convinced that these genera belong to one family, for which the oldest name is Protoperlidae. This family is now known from Upper Carboniferous deposits in Europe and North America.

Genus *Hadentomum* Handlirsch

Handlirsch, 1906, Proc. U.S.N.M., 29: 693

Fore wing: similar to that of *Palaeocixius* but having a coarse reticulation between R1 and Rs. Hind wing: incompletely known, but probably with a small, distinct anal lobe, as in *Protoperla*. Type-species: *Hadentomum americanum* Handlirsch.

Hadentomum americanum Handlirsch

Figure 6

Handlirsch, 1906, Proc. U.S.N.M., 29: 693, fig. 19-21.

Length of fore wing, 23 mm.; width of fore wing, 7.3 mm. Length of hind wing, 23 mm. Type, no. 35579, U.S.N.M., collected near Morris, Illinois (Westphalian age).

This species was based on a unique specimen consisting of the obverse, in the Daniel's collection, and the reverse in the U.S. National Museum. Since the location of the Daniel's collection is unknown, I have been able to study only the specimen in the National Museum. The preservation of this fossil is not very satisfactory; the two wings on one side, as shown in Handlirsch's figure, overlap in such a way as to interfere with the determination of the venational pattern. However, by tracing on photographs the veins of one wing with ink of a certain color and the veins which are apparently not related to that wing with ink of another color, I have found it possible to work out the venational patterns of the two wings satisfactorily. My interpretation of the wings is shown in figure 6. In most respects, the figure of the fore wing agrees with that of Handlirsch. However, the base of M, which Handlirsch shows fused with R, is distinctly free and independent; also, the fork of Cu is clearly preserved in the fossil, although it is not represented in Handlirsch's figure. The origin of R4 + 5 is not visible in the National Museum specimen; possibly it was preserved in the Daniel's specimen. The convexities and concavities of the veins are clearly preserved and are marked in figure 6. It will be noted that Rs is concave, the media is neutral (\pm), CuA

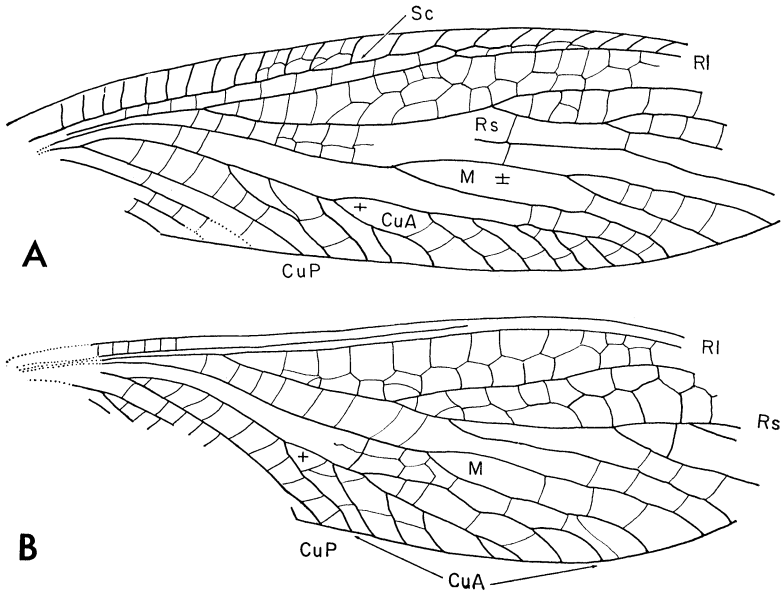


Figure 6. *Hadentomum americanum* Handlirsch. Drawing of fore wing (A) and hind wing (B). Holotype, no. 35579, U.S.N.M. (original).

strongly convex and CuP concave. Since there is no indication of a distinctly convex MA or concave MP, I have designated the media here simply as "M". It is possible that the vein that has been designated R₄ + 5 is actually MA, which may be fused basally with the radial sector; however, there is no indication of the free basal part of such a vein.

The anterior margin of the hind wing, which is not shown in Handlirsch's figure, can be made out without difficulty in the fossil by the use of ammonium chloride. The most significant difference between Handlirsch's interpretation of the hind wing and mine is in the nature of the hind margin of the wing. Handlirsch shows the hind margin continuing to the base with the uniform curvature of the apical region of the wing—that is without an anal lobe. This is particularly important, since the absence of an anal lobe would virtually eliminate the species from the Protorthoptera. However, the National Museum specimen does not show the hind margin basally of the termination of Cu₁; it is clearly broken away at this point. There is no reason, therefore, to assume that the anal lobe was absent, and in view of the affinities of the fossil as indicated by the fore

wing, there is every reason to assume that the anal lobe was present.

The body is only faintly indicated in the specimen of *americanum*. Handlirsch's figure depicts the abdomen and the thorax as they seem to me to be in the fossil, except that the prothorax is slightly shorter and somewhat broader than he has drawn it. I see no indications of the head as it was drawn by him; there are some irregularities in the rock which may possibly represent part of the head but no definite form can be made out and there are no suggestions of the eyes, so far as I can observe, in the National Museum specimen.

Handlirsch established the order Hadentomoidea (1906, p. 692) for this genus. He gave no definite diagnosis of the order, his account of the group being essentially a description of the individual specimen of *americanum*. However, it is clear from his discussion that he placed much emphasis on the apparent similarity of the fore and hind wings and on his conviction that the hind wing lacked an anal lobe. His conclusion was that the Hadentomoidea were probably closely related to the Embioptera, although showing some affinities with the Perlaria. I believe that his conclusions based on the apparent absence of the anal area are not valid. The reconstruction of *Hadentomum americanum*, which Handlirsch included in his account of fossil insects in Schröder's *Handbuch der Entomologie* (fig. 73, p. 143), is highly imaginary, since it shows the legs, antennae and mouth parts, none of which are even suggested in the fossil. The general effect of this figure, of course, is to increase the bizarre appearance of the insect, as conceived by Handlirsch. As a matter of fact, the fore wings of *Palaeocixius* and of *Hadentomum* show striking similarities, which I believe can only be explained by close relationship of these genera, at least to the family level. (See figures 6 and 7) The media seems somewhat more reduced in *Hadentomum* than in *Palaeocixius*, but the vein which is labelled R₄ + 5 in the accompanying figure of *Hadentomum* may actually be the anterior branch of the media (i.e., corresponding to the vein labelled MA in *Palaeocixius*). In the orthopteroids and the Perlaria there is much individual variation in the amount of fusion between branches of M and parts of the radial sector. Unfortunately, we do not know the hind wing of *Palaeocixius* or that of any of the other genera which I am now placing in the family Protoperlidae, with the exception of the type-species of *Protoperla* itself. The latter genus is based upon a single species known from the hind wing, which shows a definite anal lobe, although the lobe is not as large as in most of the Protorthoptera. The venation of the *Protoperla* hind wing is difficult to interpret on the basis of the single specimen known. The media is

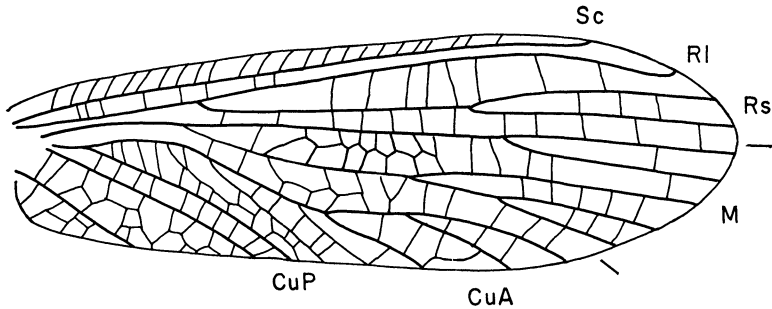


Figure 7. *Palaeocixius antiquus* Handlirsch. Drawing of holotype, in Laboratoire de Paleontologie, Paris, (original). Upper Carboniferous of Commentry, France.

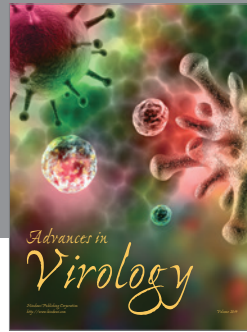
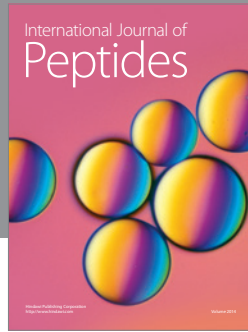
apparently coalesced at least in part with the radius or the radial sector, giving the impression that the radial sector occupies a very large area of the wing surface.

At the present time I believe that all the evidence at hand indicates that *Hadentomum* is a member of the family Protoperlidae, as here conceived. In any event, there is no evidence at hand to justify the retention of the order Hadentomoidea, which is here placed in synonymy with the Protorthoptera.

REFERENCES

- BOLTON, H.
1934. New forms from insect fauna of the British Coal Measures. Quart. Journ. Geol. Soc. **90**: 278-301.
- BRONGNIART, C.
1893. Recherches pour servi à l'histoire des insectes fossiles des temps primaires. Thèse Fac. Sci. Paris., No. 821: 1-494.
- HANDLIRSCH, A.
1906a Revision of American Palaeozoic insects. Proc. U.S.N.M., **29**: 661-820.
1906b Die fossilen Insekten. Leipzig.
1919. Revision der Paläozoischen Insekten. Denkschr. Acad. Wiss. Wien, Math.-Naturwiss. Class, **96**: 1-82.
1920. Paläontologie, in Schröder's Handb. Ent. **3**: 117-306.
1922. Fossilium catalogus (1): Animalia: Insecta palaeozoica. **16**: 1-230.
- HAUPT, H.
1941. Die ältesten geflügelten Insekten und ihre Beziehungen zur Fauna der Jetztzeit. Zeit. für Natur. Halle, **94**: 60-121.
- KUKALOVÁ, J.
1958. On the systematic position of *Ameliptera limburgica* Pruvost, 1927. Vestnik U.U.G. **33**: 377-379.

- LAMEERE, A.
1917. Revision sommaire des insectes fossiles du Stephanien de Commeny. Mus. Nat. Hist. Natur., Bull., 23: 141-201.
- LAURENTIAUX, D.
1953. Insects, in Piveteau, *Traité de Paléontologie*, 3: 397-527.
- MARTYNOV, A. V.
1938. Etudes sur l'histoire géologique et de phylogénie des ordres des insectes. *Trav. Inst. Paléont.* 7(4): 1-148.
- MARTYNOVA, O.
1962. *Osnovy Paleontologii, Mecoptera*, pp. 283-294.
- PRUVOST, P.
1927. Sur une aile d'insecte fossile trouvée au sondage de Gulpen. *Geol. Bur. Neded. Mijn. Heerlen*: 76-77.
- ROHDENDORF, B. B.
1962. *Osnovy Paleontologii, Eubleptodea*, p. 154.
- TILLYARD, R. J.
1926. Kansas Permian Insects. Part 7. The order Mecoptera. *Amer. Jour. Sci.* 11: 133-164.



Hindawi

Submit your manuscripts at
<http://www.hindawi.com>

