

REVISIONAL STUDY OF
THE ORDER PALAEODICTYOPTERA IN
THE UPPER CARBONIFEROUS SHALES
OF COMMENTRY, FRANCE
PART II¹

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An introductory discussion of the Palaeodictyoptera found in the Commeny shales and of the collection in the Institut de Paléontologie in Paris, as well as an account of the background of this investigation, was included in the first part of these studies. The present part deals with the following seven families: Homiopteridae, Lycocercidae, Graphiptilidae, Breyeriidae, Eugereonidae, Archaemegaptilidae and Megaptilidae. Compared with the Spilapteridae, considered in Part I, all of these families are small, consisting of only a few genera, at least from the Commeny shales. However, they show much diversity of structure and indicate the extensive range of wing modifications which occurred in the Palaeodictyoptera, including the reduction and shortening of the hind wings. The third part of this study will deal with the Dictyoneuridae, which provide us with more information about the body structure in this order of insects.

Family Homiopteridae Handlirsch

Homiopteridae Handlirsch, 1906: 91; Lameere, 1917: 102; Handlirsch, 1919: 16; Handlirsch, 1921: 133.

Roehlingiidae Guthörl, 1934: 188; Kukalová, 1960: 1.

Thesoneuridae Carpenter, 1944: 10.

Scepasmidae Haupt, 1949: 42.

Type genus: *Homioptera* Brongniart, 1893.

This family, as established by Handlirsch, included *Homioptera* Brongniart, *Graphiptiloides* Handlirsch (1906), *Homoeophlebia* Handlirsch (1906), all from Commeny; and *Anthracentomon* Handlirsch (1904) from Belgium. Of these genera, *Graphiptiloides* (= *Graphiptilus*) is here assigned to the Graphiptilidae; *Homoeo-*

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phlebia has already been synonymized with *Homoioptera* by Lameere (1917, p. 151); and *Anthracentomon*, on the basis of Handlirsch's figures, is also considered a synonym of *Homoioptera*.

The present revisional study of the Comentry material has brought new aspects to the family classification of the Palaeodictyoptera. The family Homiopteridae now appears to include several genera from localities other than Comentry. Three families, Roehlingiidae, Scepasmidae and Thesoneuridae, seem to be synonymous with the Homiopteridae; and the relationships of the Homiopteridae with the Graphiptilidae, Breyeriidae and Lycocercidae have become more obvious.

The wings of the Homiopteridae, as here treated, are the largest known in the Palaeodictyoptera. They are characterized especially by the following four features: (1) stems of main veins with a more or less pronounced bend in the basal third of the wings; (2) MA either simple or with very short branches and CuA always with branches (usually short ones); (3) CuA and CuP tending to be parallel to each other; and (4) a sclerotized strip with tubercles lying along the costa, just posterior to it. The cross veins are numerous, irregular and often connected.

The bending of the main veins basally is present in *Homoioptera*, *Boltopruvostia*, and to a lesser extent in *Thesoneura*; it also occurs in the related family Lycocercidae. MA is simple or has a little fork in *Homoioptera* (see left wing of the type specimen) and in *Thesoneura*; it gives rise to very short branches in *Boltopruvostia* (see *B. nigra* Kukalová, 1958). It is simple in the Breyeriidae but has a very short branch in *Graphiptilus* (type specimens of *heeri*). The branches on CuA are very short in *Homoioptera* and *Boltopruvostia*, longer in *Thesoneura* and completely reduced in Lycocercidae. In the Breyeriidae (*B. boulei*) and in *Graphiptilus* (*G. heeri*, specimen 19-12) CuA forms a short branch. The tendency for CuA and CuP to be parallel is a very persistent feature, common in all Homiopteridae and noticeable also in some Lycocercidae (*L. pictus*), Graphiptilidae (*Rhabdoptilus*) and some Breyeriidae (*B. barborae*). The cross venation of Homiopteridae and related families is very characteristic; it is readily distinguished from the more regular and rarely anastomosed venation of spilapterids and from the denser and usually relatively coarser pattern of the dictyoneurids.

From the foregoing account, it can be deduced that within the Homiopteridae and related groups the branches of MA and CuA

were in the process of reduction. The number of branches varies within the several genera of Homiopteridae, and twigs occasionally occur in related families, in which MA and CuA are generally simple. In my opinion the families Homiopteridae, Breyeriidae, Graphiptilidae and Lycocercidae form a phylogenetic unit, in which the Homiopteridae represent in many respects the most primitive series. It is to be emphasized that the simple form of CuA and MA does not necessarily represent the more primitive stage, as generally believed. This hypothesis was based by Handlirsch on the assumption that the most primitive Palaeodictyoptera were the Dictyoneuridae. However, this family, except for the archedictyon, is a very advanced one, with venation very specialized and already reduced. Of course, it is very difficult to determine, in our present state of meagre information of the body structures, which of the families has the most primitive features. The geological record seems to be indicating more and more that probably all the larger families of the Paleodictyoptera were present and already well developed at the base of the Upper Carboniferous and that their representatives evolved very little during the rest of that period. As a rule within the insects, the many morphological features of wing venation do not have equal significance for classification in all families of the orders. The presence or absence of branches of MA and CuA appears to be more stable for the spilapterid group than for the homiopterid group.

A remarkable feature, present to a more or less extent in all homiopterid specimens I have had occasion to study [*Homoioptera*, *Boltopruvostia*, *Amousus*, *Ametretus* and *Thesoneura*], is the sclerotized strip and tubercles strengthening the costal area. It is especially marked in the largest specimens of the family, i.e., in all species of *Boltopruvostia* and in *Homoioptera gigantea*.

This family includes the largest species of Palaeodictyoptera known. The wings are of nearly equal length, the hind wings being somewhat the broader. In addition to the venational characteristics discussed above, the following should be noted: postcostal area large, with several branches included; Sc long; area of Rs small; MA simple or with short branches; MP with several branches; CuA and CuP parallel to each other; CuA with several short branches directed anteriorly (usually), CuP with several branches.

Body structures: head small, with projecting eyes and large clypeus. Prothoracic lobes with radiating veins and many cross veins, often with undulated margins. Legs longer than in Spilapteridae, with elongate tibiae. Abdomen unknown.

The family Homiopteridae differs from the related families Lycocercidae, Breyeriidae, and Graphiptilidae in having CuA always branched and in possessing the sclerotized strip posterior to the costa. Only the genus *Homiooptera* is known from the Commeny shales. The following genera occur in other deposits: *Homiooptera* Brongniart (= *Anthracetomon* Handlirsch, 1904), Westphalian of Belgium; *Boltopruvostia* Strand, 1929 (*pro Boltonia* Pruvost, 1919) (= *Roehlingia* Guthörl, 1934, and *Ostrava* Kukulová, 1960), Westphalian of France, Westphalian C of Germany, Namurian C of Czechoslovakia. The following species appear to belong to the family Homiopteridae but the status and relationship of the genera established for them are uncertain: *Mammia alutacea* Handlirsch, 1906, *Scepasma gigas* Handlirsch, 1911, *Amouzus mazonus* Handlirsch, 1911, and *Ametretus laevis* Handlirsch, 1911, all from the Westphalian of Illinois.

Genus *Homiooptera* Brongniart, 1893

Homiooptera Brongniart, 1893: 353; Agnus, 1902: 259; Woodward, 1906: 28; Handlirsch, 1906: 91; Lameere, 1917: 151; Handlirsch, 1919: 16.

Homoeophlebia Handlirsch, 1906: 92; Handlirsch, 1919: 16.

Anthracetomon Handlirsch, 1904: 6; Handlirsch, 1906: 93.

Type species: *Homiooptera woodwardi* Brongniart, 1893 (OD).

A few years after Brongniart described *woodwardi*, Agnus (1902) added another species, *gigantea*; this Handlirsch (1906) later made the type of another genus, *Homoeophlebia*. As pointed out by Lameere (1917), the generic separation of *gigantea* seemed totally unnecessary. Meunier (1912, p. 5) added to the taxonomic confusion by the erection of a new species, *gaullei*, in another genus *Archaeoptilus*, basing it on the *counterpart* of Agnus' type specimen of *gigantea*! Handlirsch's *Anthracetomon*, based on *latipenne* from the Westphalian of Belgium, is actually inseparable from *Homiooptera*. The

following account is based on *woodwardi* and *gigantea*.
Wings relatively broad, almost identical, the hind pair being only a little broader than the fore; color markings in the form of numerous small, rounded spots. Precostal strip present (bordering the costal margin); anterior margin convex in the basal third of the wing; Rs with 3-4 branches, often forking; stem of M touching or nearly touching R near the base; M dividing near mid-wing, MA being simple and convex, MP with 3-4 branches; CuA and CuP with short branches, often originating at the same level. Anal veins 6-8 in number, sometimes forked. Cross veins often connected by numerous anastomoses, branched or forming a loose network.

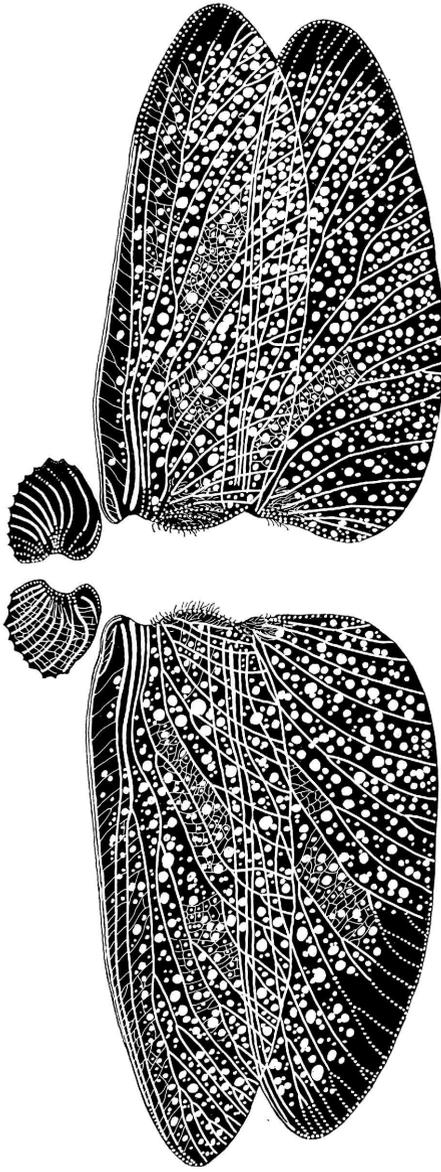


Figure 29. *Homioiptera woodwardi* Brongniart; specimen 20-10. Holotype.

thorax, their bases relatively near to each other.
 Body structures: prothoracic lobes relatively small, high on pro-
 strong femur, elongate tibia and narrow tarsus. Fore leg with

Homoioptera differs from the related genus *Boltopruvostia* Strand by having broader and shorter wings, smaller area of the radial sector, by more distal division of M (shortly before mid-wing), by MA being essentially simple and more convex, by CuP having fewer branches and by having a smaller anal area with less branching of the anal veins. All cross veins weak. From *Thesoneura*, *Homoioptera* differs in the more pronounced convex curvature of the main veins in the basal third of the wing and in having fewer branches on CuA.

The species included in the Commeny shales are *Homoioptera woodwardi* Brongniart and *H. gigantea* Agnus (= *Archaeomegaptilus gaullei* Meunier, obj. syn.). One other species, *latipenne*, from the Westphalian of Belgium, appears to belong here, as noted above.

Homoioptera woodwardi Brongniart

Figure 29

Homoioptera woodwardi Brongniart, 1893:354, fig. 15, pl. 20, fig. 10;
 Handlirsch, 1906: 91, pl. 11, fig. 1; Handlirsch, 1921: 134, fig. 61.

This species was based by Brongniart on one specimen (20-10), showing the fore and hind wings, prothoracic lobes and a fragment of fore leg. The wings present a remarkable color pattern of circular dots, a pattern which occurs repeatedly in the families related to the Homiopteridae. The shape of the prothoracic lobes probably has little taxonomic value other than at the specific level. Great variability in the shape of the lobes also occurs in the Spilapteridae. My study of the type specimen shows that the cross venation is much denser and is less regular than indicated in Brongniart's figure.

Fore wing: length 75 mm, width 27 mm. Wing membrane spotted by circular markings of varying diameters; wing uniformly broad in the proximal half, then abruptly narrowing; apex at about the wing axis; Sc, R and M almost parallel and convex at the end of the first quarter of the wing; M notably concave before the division into MA and MP; Rs with 3-4 branches, each forked several times; Rs area very small. Cross veins more simple in the areas of the subcosta, sc-r and r-rs, with much less anastomosis. A cluster of long hairs occurs at the bases of both fore wings. Hind wing: length 75 mm, width 31 mm. The sigmoidal curvature of the main

veins near the base is much less pronounced than in the fore wing; anal veins only rarely forked.

Body structures: prothoracic lobes with undulated margin, their veins S-shaped, about 11 in number. Numerous anastomoses of cross veins,

Homoioptera gigantea Agnus

Figure 30

Homoioptera gigantea Agnus, 1902: 259, pl. 1; Lameere, 1917: 151.

Homoeophlebia gigantea Handlirsch, 1906: 93, pl. 11, fig. 3.

Archaeoptilus gaullei Meunier, 1910: 233, fig. 1; Meunier, 1912: 5, pl. 6, fig. 1.

Homoeophlebia gaullei Handlirsch, 1919: 16, fig. 18.

This monotypic species was based by Agnus upon a remarkably well preserved, large fore wing, with a single prothoracic lobe and vague outlines of the head, including the base of the beak, and suggestions of the thorax and a fragment of a fore leg. The reverse, as already noted, was described by Meunier (1910) as *Archaeoptilus gaullei*.

Fore wing: length 187 mm, width 65 mm. Wing membrane spotted with (1) extremely dense, small, light markings, irregularly grouped into small clusters; (2) larger spots arranged into 4 transverse bands. Wing abruptly narrowed in the apical third, with the apex pointed and falcate. Anterior margin very convex in the basal third, the posterior margin S-shaped in the apical third. Sc, R, M following the convex curvature of the anterior margin. Sc somewhat shortened; subcostal area broad in the proximal half, then very narrow; stems of R and M touching near the base; M deeply concave before division into MA and MP; Rs with about four very oblique branches, the first of them long and forked. Anal area with about seven branches, the first forked several times. Cross veins parallel and directed in different directions, with much anastomosis. Long hairs are clustered at the base.

Body structures: prothoracic lobe length 27 mm, width 24 mm, with a complete covering of long hairs. Prothoracic lobe cordate, with seven radiating veins and densely arranged, simple cross veins; margin of lobe not undulated.

This species differs from *woodwardi* by its larger size, more specialized shape of the wing with its falcate apex, the larger rs area, the contact of the stems of R and M and the smoothly curved margins of the prothoracic lobes, as well as the color pattern of the wings.

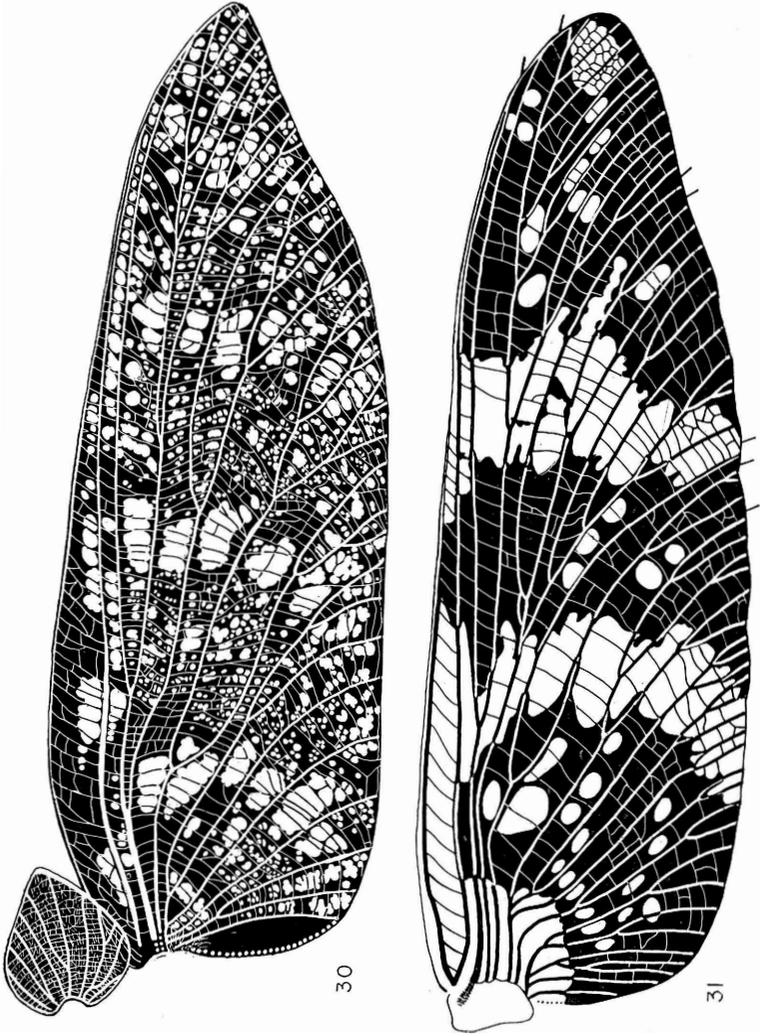


Figure 30. *Homoioptera gigantea* Agnus; prothoracic lobe, fore wing. Holotype.
Figure 31. *Lycocercus pictus* Handlirsch; fore wing. Holotype.

Family *Lycocercidae* Handlirsch, 1906

Lycocercidae Handlirsch, 1906: 675; Handlirsch, 1906: 88; Handlirsch, 1921: 133; Handlirsch, 1919: 15; Lameere, 1917: 102.

Polycraegridae Handlirsch, 1906: 110; Handlirsch, 1906: 678; Handlirsch,

Apopappidae Lameere, 1917: 42.

Patteiskyidae Laurentiaux, 1958: 302; Demoulin, 1958: 363.

Type genus: *Lycocercus* Handlirsch, 1906

The family *Lycocercidae* was established by Handlirsch for *Lycocercus* and was characterized as having more numerous branches than *Lithomanteidae*³ and as having cross veins forming at least partially a dense network of the dictyoneurid type. His interpretation of the fossils on which *Lycocercus* was based is only partly correct. The cross veins of the *Lycocercidae* are indeed denser, more irregular and more often connected by anastomoses than in *Lithomanteidae* but they do not form a real network of the dictyoneurid type.

This revisional study of the type material has revealed three additional and important features for the *Lycocercidae*: (1) the hind wing is as long as but narrower than the fore wing; (2) the MP area is of triangular shape, with many branches; (3) the origins of MA and the first fork of MP are very close.

The following families are considered by me to be synonymous with *Lycocercidae*: (1) *Polycraegridae* Handlirsch, 1906, based on the single genus *Polycraegra* Handlirsch, 1906; this genus differs from *Lycocercus* only by having more obliquely oriented branches, with longer forks and by having Rs more richly branched. (2) *Apopappidae* Lameere, 1917, based upon *Apopappus* Handlirsch, 1906, which differs from *Lycocercus* by having a more regular cross venation and by having CuP somewhat richer in branches. (3) *Patteiskyidae* Laurentiaux, 1958, based upon the oldest palaeodictyopteron so far known, *Patteiskya bouckaerti*⁴ (Namurian B, Germany), which differs from the other species of *Lycocercus* only in having M dividing more proximately; it is therefore inseparable from *Lycocercus*.

Wings about equal in length, hind pair narrower, similar in vena-

³The family *Lithomanteidae* is here understood to include the genus *Lithomantis* Woodward (syn. *Hadroneuria* Handlirsch and *Lithosialis* Scudder), *Macroptera* Laurentiaux (syn. *Lusiella* Laurentiaux and Texeira) and *Synarmoge* Handlirsch.

⁴In the figure published by Laurentiaux (1958, figure 1) Sc is correctly drawn but the subcostal area is broader proximally and is shaped as in *Lycocercus goldenbergi*. In the figure published by Demoulin (1958, p. 359, fig. 1) the vein designated as the costa is actually the subcosta. *Lycocercus bouckaerti* is not represented by a hind wing but by a fore wing.

tion; wing membrane usually dark, with light bands and spots. Fore wings resembling hind wings in outline but with broader subcostal area. Anterior margin nearly straight, often with precostal strip; stems of main veins convex in the basal third, as in Homiopteridae; Sc long; MA simple, curved, originating near the first fork of MP; MP with many branches, occupying a markedly triangular area; CuA simple and curved; CuP parallel to CuA, but with several branches. Anal area often large, with many branches. Cross veins fine, numerous, more or less irregular, sometimes connected.

Body structures: head small with conspicuous eyes and large clypeus. Prothoracic lobes with fan-like veins and many cross veins, often with undulated margins. Thorax broad, metathorax shorter than mesothorax; legs homonomous, not very short. Ovipositor not sculptured, stout and curved. Cerci robust, long.

The family Lycocercidae is related to the Homiopteridae in the characteristic curvature of stems of main veins near the base, in the late division of M, in the general character of cross veins, in the presence of many small forks along the posterior margin, etc. It differs from the Homiopteridae in the narrowed hind wing and more richly branched MP and CuP and simple CuA. Another related family is the Graphiptilidae, from which the Lycocercidae differ in the richly branched MP and CuP and the narrower hind wings.

Genera included in the Commeny shales: *Lycocercus* Handlirsch and *Aporappus* Handlirsch.

Occurrence in other deposits: *Lycocercus* Handlirsch, Namurian B, Germany.

Genus *Lycocercus* Handlirsch

Lycocercus Handlirsch, 1906: 89, Handlirsch, 1919: 15; Lameere, 1917: 153. *Patteiskya* Laurentiaux, 1958: 302; Demoulin, 1958: 360.

Type species: *Dictyoneura goldenbergi* Brongniart, 1893 (SD Handlirsch, 1922).

This genus was erected by Handlirsch for *goldenbergi* Brongniart, as represented by specimen 21-1. Specimen 21-2, correctly described by Brongniart under the same specific name, was erroneously referred by Handlirsch (1906, p. 90) to a separate species *brongniarti* (Lameere, 1917, p. 153). Meunier (1911, p. 121) described *Homioptera brongniarti*, which Handlirsch later (1919, p. 15) recognized as *Lycocercus*. The specific name having been preoccupied within the genus since 1906, Handlirsch (1919, p. 16) changed it to *Lycocercus pictus*. Though Lameere (1917, p. 153) believed that *pictus* was conspecific with *goldenbergi*, he was apparently incorrect.

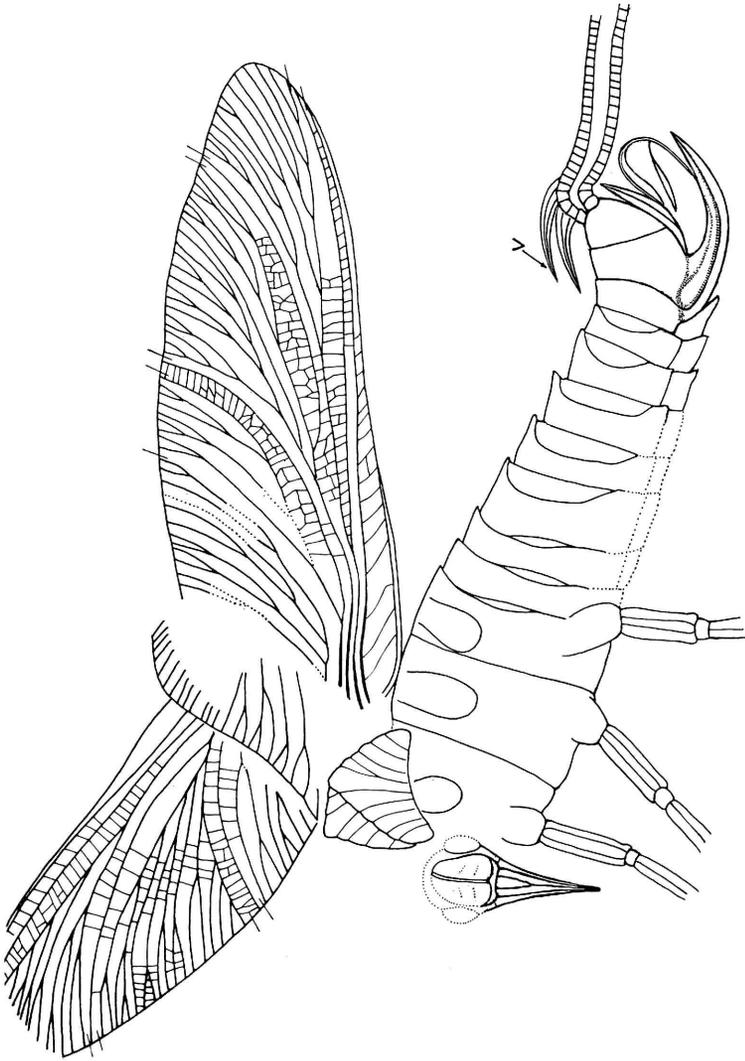
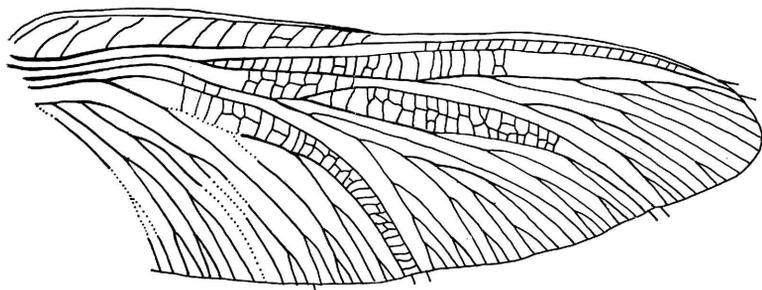
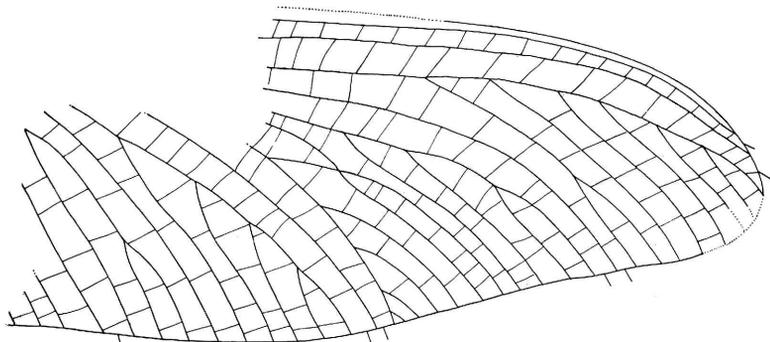
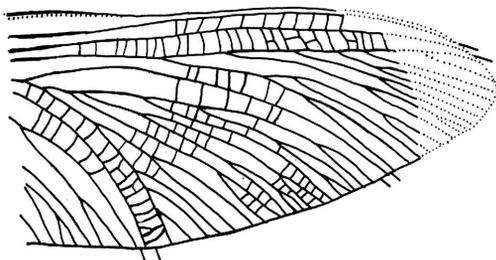


Figure 32. *Lycocercus goldenbergi* (Brongniart) ; specimen 21-1; v = separated valves of cast cuticle. Holotype.



33



34

Figure 33. *Lycocercus goldenbergi* (Brongniart); specimen 21-1; fore and hind wings. Holotype.

Figure 34. *Apopappus guernei* (Brongniart); specimen 19-3; fore wing. Holotype.

Although the differences in venation might conceivably be considered as due to individual variability and although the cross venation and color markings are almost identical, there is a marked difference in the length of the legs and probably also of the beak.

In *Lycocercus* the hind wings are like the fore wings in shape but are narrower. This assertion is based on specimen 21-2, in which the wings are preserved in their natural positions. If found isolated, a fore or hind wing can be recognized only by the width of the proximal part of the subcostal area, which is broader in the fore wings.

Fore wings unusually broad in the proximal half, shaped as hind wings. Hind wings similar but somewhat narrower. R₁ simple; R_s with six branches, first of them forked; MP forked 10-20 times. Number of CuP branches variable; about 8 anal veins, mostly forked. Cross veins dense, irregular, often connected.

Body structures: beak short or long. Legs stout but not very

short. *Lycocercus* differs from *Apopappus* in less regular anastomosing of cross veins, smaller CuP area and in the larger number of short branches of R_s and CuP. As a whole, the venation of *Lycocercus* is much less regular. From *Polycreagra* Handlirsch (Westphalian, Illinois) it differs in the less densely branched and less obliquely oriented branches of main veins.

Species included in the Commeny shales: *Lycocercus goldenbergi* Brongniart, 1893; *Lycocercus pictus* Handlirsch, 1919.

Occurrences in other deposits: *Lycocercus bouckaerti* (Laurentiaux, 1958) of Namurian B, Germany.

Lycocercus goldenbergi (Brongniart)

Figures 32, 33, 35

Dictyoneura goldenbergi Brongniart, 1883: 265 (for additional references see Handlirsch, 1922: 39).

Lithomantis goldenbergi, Brongniart, 1893: 369, pl. 21, fig. 1, 2.

Lycocercus goldenbergi, Handlirsch, 1906: 89, pl. 10, fig. 20; Handlirsch, 1921: 138, fig. 60; Handlirsch, 1919: 15, 16; Lameere, 1917: 101; Lameere, 1917: 153; Demoulin, 1960: 1-4, pl. 1.

Lycocercus brongniarti Handlirsch, 1906: 90, pl. 10, fig. 21; Handlirsch, 1919: 15, fig. 17.

This species was based by Brongniart on specimen 21-1, one of the most remarkable Palaeodictyoptera known, and on specimen 21-2, a fragment of fore and hind wing in natural positions. Handlirsch (1922) designated specimen 21-1 as the type; specimen 21-2, which is important for showing the wing shapes, was referred by Hand-

lirsch to a separate species, *brongniarti*, but was identified again as *goldenbergi* by Laneere (1917, p. 153).

The type specimen (21-1) has been discussed many times by various authors but of these only Brongniart and Laneere actually studied the fossil. Most interpretations are highly speculative and not worth discussing here. The fossil shows so many structures which are important for the whole order that it deserves the most detailed study. Actually, the specimen might contribute even more details than I was able to work out in my limited stay of several weeks at the Paris Museum. The following discussion is based mostly on the obverse, with the exception of the abdominal appendages, which are better preserved in the reverse. In figure 32, as usual, both obverse and reverse have been used.

The type specimen shows fragments of two twisted wings. The broad wing on the right side is a fore wing, having a broader subcostal and r-rs areas than the narrower hind wing on the left side. This conclusion was reached after noting that the second specimen (21-2, shown in figure 35), with fore and hind wings in natural positions, showed the same differences.

The body of specimen 21-1 is twisted in such a way that the thorax shows the dorsal side, while the abdomen shows the distal end in full lateral view. The head is in perfect frontal position. The insect apparently first rested with the beak oriented along the body axis; later the head became loose and shifted 90° to the left. The prothoracic lobes lifted from the pronotum and overlapped so that they are now in lateral position. Such preservation is unusual for the Palaeodictyoptera and proves beyond any doubt that (1) the prothoracic lobes were not fused together to form a pronotal shield, as claimed by Sharov (1966)⁵; and (2) that they were easily moveable. The legs of specimen 21-1 are extended on both sides of the body. All three right legs have a deep suture near the proximal end of the tibia, giving the impression of an extra segment fused with the tibia. I have observed similar sutures in *Stenodictya agnita* (Meunier) and *Stenodictya oustaleti* (Brongniart). It is of great interest that in Recent Ephemeroptera there is a marked bend in the same part of the tibia (e.g., *Ecdyonurus*). But the suture on the tibia does not seem to be present in the related orders Megasecoptera and Diaphanopteroidea and not even in all Palaeodictyoptera. At any

⁵The prothoracic lobes were attached to the pronotum by short cuticular ridges in the center of their basal part. The perfectly preserved prothoracic lobes of *Stenodictya* will be described in Part III of this series of papers.

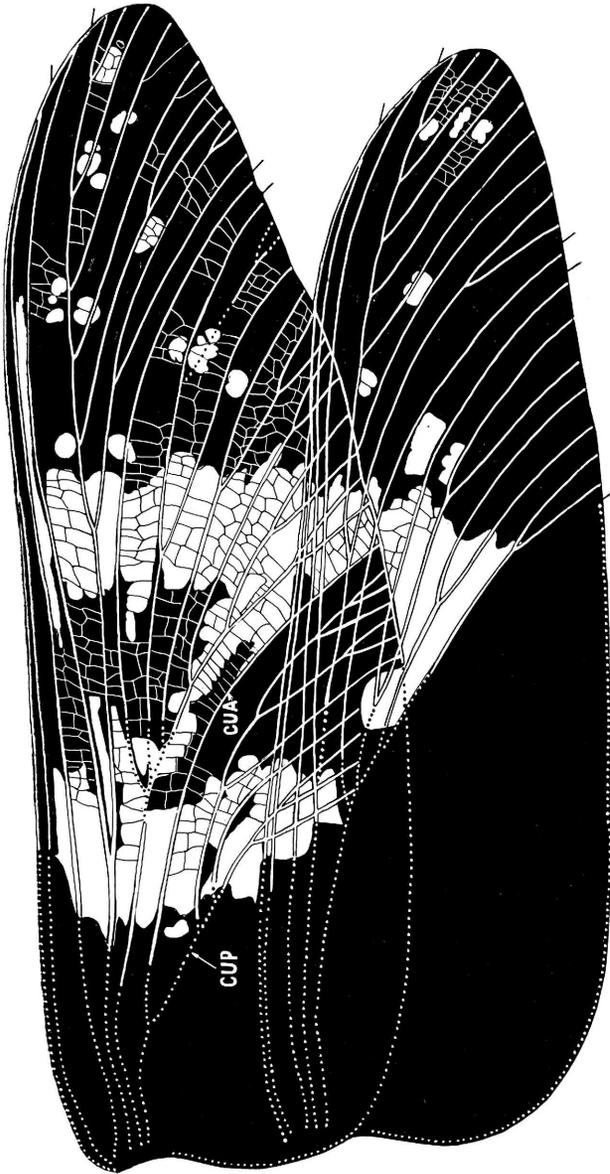


Figure 35. *Lycocercus goldenbergi* (Brongniart); specimen 21-2; fore and hind wings.

rate, the part divided by the suture makes a single piece with the tibia, so that it probably had hardly any functional significance.

The segments of the abdomen, undoubtedly because of decaying processes and distortion, show varying portions of the intersegmental membrane. The ovipositor is robust and opened widely. Between the ovipositor valves, a pair of sac-like cuticular structures appears to come from the abdomen. These have been incorrectly interpreted as gonapophyses by many authors. Demoulin (1960) considered them the evaginated cuticle of the oviduct and pointed to similar cases known in Recent Ephemeroptera after the laying of the eggs in paired large clusters (e.g., Polymitarciidae).

Above the end of the abdomen, twisted backwards, there are two structures described by Brongniart as "crochets dorsaux." Detailed examination shows that they are "attached" to the cercus. These seem like parts of a smaller and much less heavily sclerotized ovipositor and could be part of a cast cuticle. It is conceivable that the Palaeodictyoptera had an adult molt, in which case this "ovipositor" could have been part of the previously molted cuticle.

The ovipositor of *Lycocercus goldenbergi* resembles, in its broad attachment to the 9th segment, the ovipositors of certain dragonflies, such as the Zygoptera and some Anisoptera, especially those adapted for endophytic oviposition. Moreover, it resembles the ovipositor of some Diaphanopteroidea (Permian of Kansas and Czechoslovakia, unpublished material) in the prolongation of the lateral margin of the 9th tergite anteriorly. The surface of the gonapophyses does not show any sculpturing, whereas in *Asthenohymen* it is armed by ridges and even stout hairs directed backwards, as in the endophytic Hymenoptera.

The following account is based on the type specimen and on specimen 21-2.

Fore wing: length 73 mm, width 25 mm, broadest in the first third. Precostal strip extending to about the middle of the wing. Posterior margin with small convexities at the end of each area. Apex directed posteriorly, rounded. Rs with about 5 branches, the first two of them more or less richly branched; MA arising occasionally distally from the first branch of MP. MP forked 11-19 times. Cu dividing near the base, CuP with 3-5 posteriorly directed branches, often forked. Anal area moderately large with veins forked many times. Cross veins fine, dense, curved, sometimes branched and connected. Hind wing fragment: length 39 mm, width 22 mm.

Basic body structures: head small, with very large clypeus hav-

ing a median ridge. Beak relatively shorter than in any other known Palaeodictyoptera; length 11 mm. Labrum triangular, long. Thorax broad and robust. Mesothorax slightly longer than the metathorax and about the same length as the prothorax. Prothoracic lobes large, with fan-like veins and undulated margins. Legs stout, femur length 8.5 mm in all three pairs. Proximal end of tibia provided with a deep suture on all legs. Lengths of tibia and tarsi unknown. Abdomen relatively short and broad (length 48 mm), segments subequal, the first two being shorter than the following ones. Lateral margin of the 9th segment prolonged anteriorly. Ovipositor robust, heavily sclerotized, gonapophyses not sculptured; anterior valves arising from 8th segment, 8th sternite being shortened; 9th segment with the anterior margin concave; lateral valves much broader than the anterior ones. Cerci robust, multisegmented.

Lycocercus goldenbergi differs from the related species *bouckaerti* (Laurentiaux, 1958) of Namurian B, Germany (= *Patteiskya bouckaerti*) in the more distal division of the stem of M. From *Lycocercus pictus* Handlirsch, it differs in having shorter legs and probably also in having a shorter beak, having more numerous branches of CuP, smaller anal area; also, Cu divides more proximally and the cross venation is denser, with more numerous anastomoses.

Lycocercus pictus Handlirsch, 1919

Figures 31, 36

Homioptera brongniarti Meunier, 1911: 121, fig. 5; Meunier, 1912: 11, pl. 7, fig. 6 (*sec brongniarti* Handlirsch, 1908).
Lycocercus pictus Handlirsch, 1919: 15, fig. 17 (*pro brongniarti* Meunier).

This species is monotypic, based by Meunier (1911) upon a specimen showing both fore wings, prothoracic lobes, vague outlines of the beak and a fore leg and part of the head. Handlirsch (1919) correctly referred this species to *Lycocercus* using the name *pictus* for it to avoid homonymy. *Lycocercus pictus* was discussed in detail by Lameere (1917, p. 153-154), who erroneously assumed it to be conspecific with *goldenbergi*. Lameere in his account described the head and beak with a clypeus similar to that of the Fulgoridae and a trace of palpus on the side. Of all these structures I was able to see only weak outlines of the beak, which seemed to be longer than in *goldenbergi*.

The prothoracic lobes are aligned by their posterior margins with the posterior edge of the pronotum, giving the appearance of a shield. This is misleading, as shown by the related species, *goldenbergi*, in which both lobes are raised up above the pronotum.

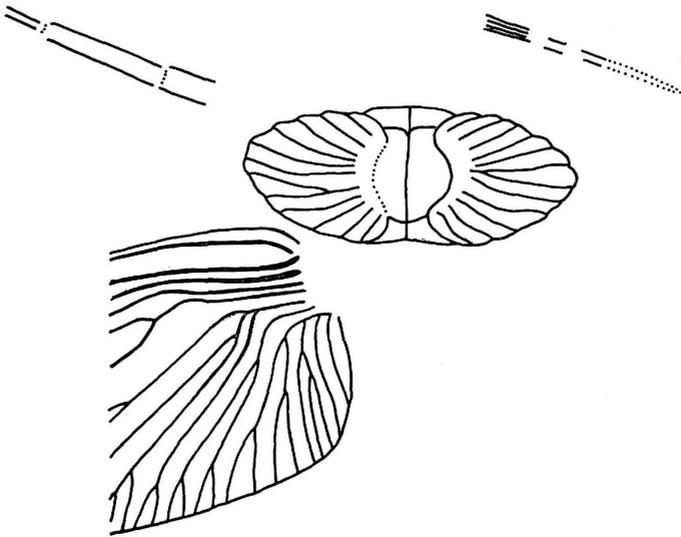


Figure 36. *Lycocercus pictus* Handlirsch; prothorax, basal part of fore wing, fragment of fore leg (l) and beak (b). Holotype.

Fore wing: 69 mm long, 22 mm broad, the wing uniformly broad in the proximal half. Anterior margin very slightly concave, posterior margin with a slight concavity also in the apical third; apex directed posteriorly, rounded. Precostal strip reaching to the end of the first third; subcostal area relatively narrow. Rs with 6 branches, mostly forked; MP forked 9 times; Cu dividing very distally, shortly before the origin of Rs; CuP as in *Homoioptera*, with a few terminal branches. Anal area very large, with 8 richly forked branches arising from separate stems. Cross veins dense, rather regular, sometimes connected.

Body structure: beak probably long (about 2.5 cm). Prothoracic lobes large, high on pronotum, their posterior margins corresponding to the posterior edge of the prothorax. Prothorax relatively long with median line. Legs longer than in *goldenbergi*, apparently with long tibia.

Lycocercus pictus differs from *goldenbergi* by the several venational traits and body structures already noted.

Apopappus Handlirsch, 1906

Apopappus Handlirsch, 1906: 100; Lameere, 1917: 149; Lameere, 1917: 103; Handlirsch, 1919: 20.

Type species: *Spilaptera guernei* (Brongniart, 1893) (OD).

This genus was erected by Handlirsch upon *Spilaptera guernei* Brongniart, specimen 19-3, because of a simple MA and CuA but it was erroneously classified with the family Graphiptilidae. Later, Lameere (1917, p. 103) suggested that *Apopappus* was a transitional form between the Spilapteridae and Ephemeroptera. Finally the same author (1917, p. 42) established for this genus a separate family, Apopappidae. With Triplosobidae, he referred this family to the Protephmeroidea because he believed that in the mp area of *guernei* there is the beginning of intercalary sectors, indicating its relationship to the Ephemeroptera.

The venation of *Apopappus* shows typical lycocercid features, such as the large triangular MP area, simple MA and CuA and fine but rather dense pattern of cross veins. The fusion of the distal branch of MP₁ with the proximal branch of MP₂, considered by Lameere as an intercalary sector, is in all probability an individual variation only.

Wing broad. Branches of main veins running parallel. Rs with 6 pectinate branches, most of them simple; MA arising near the first fork of MP; MP forked 9 times. CuP with a series of 6 branches. Anal area unknown. Cross veins fine, not very dense, mostly regular and simple.

Apopappus differs from *Lycocercus* in the regularly distributed branches of the main veins, in the very rich branches of CuP and in the more regular, less numerous and mostly simple cross veins.

Species included in the Commeny shales: *Apopappus guernei* (Brongniart, 1893).

Apopappus guernei (Brongniart)

Figure 34

Spilaptera guernei Brongniart, 1893: 341, pl. 19, fig. 3.

Apopappus guernei Handlirsch, 1906: 100, pl. 11, fig. 13; Handlirsch, 1919: 20; Lameere, 1917: 149.

This species is monotypic, based by Brongniart upon specimen 19-3, which I was not able to find in the collections of the Museum. This account has been made from a good photograph which Dr. Carpenter kindly placed at my disposal and which showed the venation very clearly.

As in other Lycocercidae, it is difficult to recognize the fore and hind wing if found isolated, especially if the subcostal area is missing. From the more pronounced convexity of posterior margin in the apical third and beyond the width, I believe the wing is probably the fore one.

Rs with 6 branches, the first of them with a small simple fork; MA curved as in other Lycocercidae; MP₁ sending off 4 branches posteriorly, MP₂ another four branches anteriorly. CuP with four simple branches, the fifth being forked several times. Cross veins tending to form rows in rs area.

Apopappus guernei is similar in the MP area to *Lycocercus pictus* but the forking of the last branch of CuP resembles the *Lycocercus goldenbergi*, specimen 21-2. The cross venation is slightly more simple and more regular than in *pictus*.

Family Graphiptilidae Handlirsch

Graphiptilidae Handlirsch, 1906: 99; Handlirsch, 1921: 136.

Rhabdoptilidae Handlirsch, 1919: 15.

Type genus: *Graphiptilus* Brongniart, 1893.

The family Graphiptilidae was erected on *Graphiptilus* but included *Apopappus* Handlirsch and *Spiloptilus* Handlirsch. The family, having been based upon an incomplete description and on a misinterpretation of the type specimens of *Graphiptilus*, represents a heterogeneous group, as treated by Handlirsch. The genus *Apopappus* belongs, in all probability, to the Lycocercidae; and *Spiloptilus*, having MA and CuA branched, has already been referred to the Spilapteridae (Kukalová, 1969). The structure of *Graphiptilus*, on the other hand, certainly justifies reference of the genus to a separate family.

Graphiptilus is known, so far only from the hind wing, which is markedly and broadly triangular in form. The principal characters of its venation are the very small rs area, simple MA and CuA, and the numerous weak cross veins. Within the Palaeodictyoptera only the genus *Rhabdoptilus* and representatives of the family Breyeriidae show similar venational features.

The relationship of *Graphiptilus* to *Rhabdoptilus*, though not previously mentioned, is obvious from the similarity not only of the venation and cross venation but even of the color pattern, which seems to be a more significant feature for the Graphiptilidae and Breyeriidae than for other families of the order Palaeodictyoptera. As noted by Professor Carpenter (1967, p. 61) the small circular spots on the wings of Breyeriidae are actually cuticular thickenings on the membrane. The well preserved Commeny material of *Breyeria* shows long hairs, probably macrotrichia, in clusters at these spots; similar structures may well have been present on the wings of the Graphiptilidae.

It is to be emphasized that the hind wings of both *Graphiptilus* and *Rhabdoptilus*, though broad and therefore relatively short, do not show any sign of reduction. This fact together with the venational pattern places them far from *Lithoptilus*, which has been erroneously associated with *Rhabdoptilus* (Demoulin, 1958).

The fore wing is unknown. The hind wing is of broadly triangular shape. Anterior margin almost straight; Sc long; Rs area reduced in size, with 3-4 branches; MA simple, MP with several branches; CuA simple, CuP branched several times; several anal veins. Cross veins dense, fine, long, sometimes connected by anastomoses. Color markings usually in the form of irregularly distributed larger spots and smaller rounded spots.

The family Graphiptilidae resembles Breyeriidae in several features, already noted above, including the wing markings. The graphiptilids differ from the breyeriids in having a denser pattern of cross veins and in having the branches of the main veins obliquely oriented (not perpendicular to posterior margin, as in some breyeriids) and in having these branches closer together. Among the Breyeriidae, the less specialized genus *Stobbsia* recalls most Graphiptilidae and may turn out to belong to that family.

Two genera are included in Commeny shales: *Graphiptilus* Brongniart, 1893; *Rhabdoptilus* Brongniart, 1893.

Genus *Graphiptilus* Brongniart

Graphiptilus Brongniart, 1893: 348; Handlirsch, 1906: 99; Handlirsch, 1919: 29; Lameere, 1917: 150.
Graphiptiloides Handlirsch, 1906: 92; Handlirsch, 19-9: 16.

Type species: *Graphiptilus heeri* Brongniart, 1893 (SD Handlirsch, 1906).

This genus was erected by Brongniart for *heeri*, *williamsoni* and *ramondi*. *Ramondi* was referred by Handlirsch (1906, p. 100) to a new genus *Spiloptilus*, which has been transferred to the Spilapteridae (Kukalová, 1969); *williamsoni* was assigned by Handlirsch (1906, p. 92) to a new genus *Graphiptiloides* and placed in the Homiopteridae. As mentioned already by Lameere (1917, p. 151) *heeri* and *williamsoni* are actually very close and they are undoubtedly conspecific; for some reason Lameere believed that *williamsoni* was based on a fore wing, though the unique type has the same wing form as *heeri*, characteristic for hind wings in this family.

A careful study of the specimens has made possible a reliable determination of the outline of the hind wings, their triangular

form becoming obvious. For the relationship of *Graphiptilus* (as well as for most other Palaeodictyoptera), the cross veins are most important. Those of *Graphiptilus*, being very fine and close together, have not been observed or at any rate mentioned by previous authors.

Hind wing very broad in proximal half; wing membrane usually with many elongate spots and small circular spots. Rs with four short branches; branches of main veins obliquely oriented to the posterior margin. Anal area reaching about midwing. Cross veins fine, dense, straight, regular.

Graphiptilus differs from the related genus *Rhabdoptilus* Brongniart by its fewer branches of MP, more obliquely oriented branching of main veins and in the more regular cross venation. The color pattern differs by the shape of the elongate spots.

Only the type-species is known from the Commeny shales.

Graphiptilus heeri Brongniart

Figure 37, 38

Graphiptilus heeri Brongniart, 1893: 349, pl. 19, fig. 13, Handlirsch, 1906:

100, pl. 11, fig. 12; Handlirsch, 1919: 20; Lameere, 1917: 150; Lameere, 1917: 131; *williamsoni* Brongniart, 1893: 350, pl. 19, fig. 12; Lameere,

Graphiptiloides williamsoni Handlirsch, 1906:92; Handlirsch, 1919: 16.

This species was based by Brongniart on a single specimen, 19-13, a hind wing without base but with a well preserved color pattern. As noted above, I consider the type of *williamsoni* (specimen 19-12) to be the same species.

Hind wing: length about 60 mm, width 27 mm, broadest at the end of the first third of the wing; light spots of diverse length are present, limited by cross veins, and in addition small round light spots irregularly distributed over the wing. Anterior margin straight, anal area moderately rounded. Apical half of wing abruptly narrowing distally, apex rounded, shifted anteriorly to the axis of the wing. R-rs area only a little broadened; anal area large with at least nine long branches reaching or extending beyond the middle of the wing; some cross veins in costal and subcostal area stronger than the others and more oblique.

The differences between specimens 19-13 (type of *heeri*) and 19-12 (type of *williamsoni*) are in the presence or absence of small forks on CuA and CuP, in one branch more or less on MP and CuP and in the relative lengths of the anal areas. None of these seem to be at the specific level.

Genus *Rhabdoptilus* Brongniart

Rhabdoptilus Brongniart, 1893: 266. Handlirsch, 1906: 88; Lameere, 1917:

Type species: *Rhabdoptilus edwardsi* Brongniart, 1893 (OD).

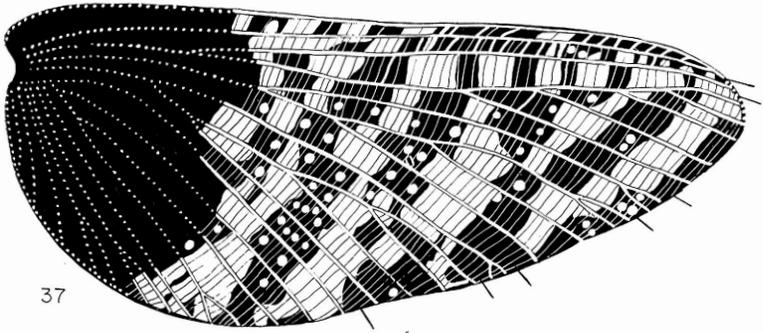
This genus is monotypic, erected by Brongniart upon a fragment of a large hind wing without base, apex or posterior margin. *Rhabdoptilus* was referred by Handlirsch first (1906) to the Lithoman-teidae and later (1919, p. 15) to a separate family Rhabdoptilidae, on the basis of its parallel, dense cross venation. Lameere (1917, p. 154) associated *Rhabdoptilus* with *Fouquea* in spite of the simple MA and CuA, because the cross veins in both genera seemed to him to be very much alike. Demoulin (1958) placed *Rhabdoptilus* with *Lithoptilus* and referred both genera to Handlirsch's family Rhabdoptilidae, which he thought was near to the Breyeriidae and Thesoneuridae.

I have explained above that Handlirsch's misinterpretation of *Graphiptilus* prevented recognition of the close relationship between *Rhabdoptilus* and *Graphiptilus*, despite the marked similarity in venation, cross veins and color markings. Nevertheless, there are some differences in wing membrane characters between these genera, most probably of functional significance, as noted below.

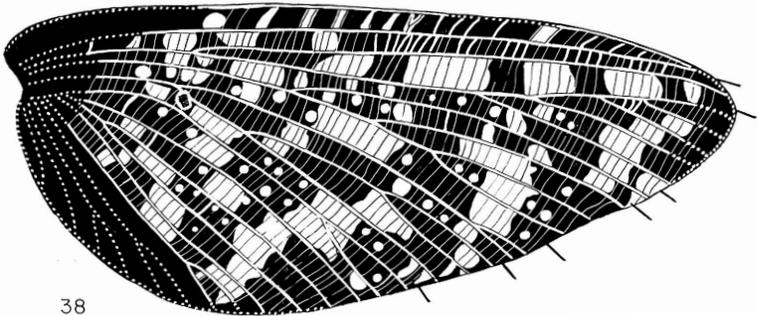
The wing area being large, the membrane thin, and cross veins weak, the wing tends to be strengthened in several ways. First, the membrane is heavily pigmented and the pigmentation even penetrates into light spots in the form of peculiar tooth-like projections; second, the membrane between the veins is rippled, producing a corrugated effect, and the thin cross veins usually run on the ridges of the ripples. These are probably functional structures and restricted to the genus and possibly to the type species. Lameere was not correct in considering the strong conspicuous cross veins of *Fouquea* to be like those of *Rhabdoptilus*.

In *Rhabdoptilus* the hind wing is not reduced in length and all branches of the main veins are fully developed. In *Lithoptilus* the hind wing, on the other hand, is greatly reduced with branching levels of R₁, R_s and M shifted distally. The cross venation of *Lithoptilus* is very dense, with numerous, coarse connections, distinctly different from *Rhabdoptilus*. For that reason I consider that Demoulin's conclusion about the relationship of these genera is in-supportable. In this paper, *Lithoptilus* is referred to Eugereonidae.

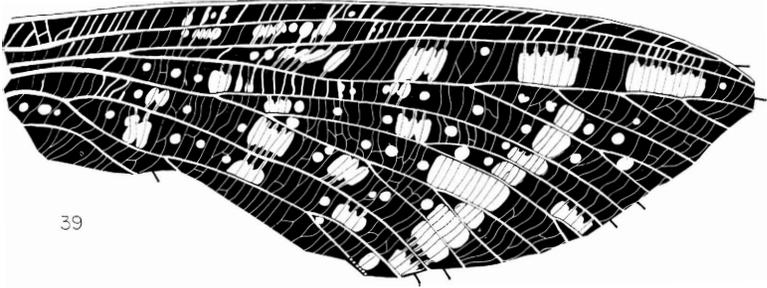
Hind wing: probably broadly triangular; markings forming large, elongate and small circular light spots. Anterior margin slightly convex. R_s originating in the basal third of the wing, with several



37



38



39

Figure 37. *Graphiptilus heeri* Brongniart; specimen 19-13; hind wing.

Figure 38. *Graphiptilus heeri* Brongniart; specimen 19-12; hind wing.

Figure 39. *Rhabdoptilus edwardsi* Brongniart; specimen 20-9; hind wing. Holotype.

short branches; MA simple; MP forked several times; CuA simple; CuP with few branches. Cross veins fine, dense, curved, rarely with anastomoses.

The distinctions between *Rhabdoptilus* and *Graphiptilus* have already been noted above.

Only the type species is known from the Commeny shales.

Rhabdoptilus edwardsi Brongniart

Figure 39

Rhabdoptilus edwardsi Brongniart, 1893: 365, pl. 20, fig. 9; Handlirsch, 1906: 88, pl. 10, fig. 19; Lameere, 1917: 154; Handlirsch, 1919: 15; Demoulin, 1958: 4.

This species is monotypic, being based by Brongniart upon specimen 20-9, a fragment of a large hind wing with the posterior margin missing. The preserved part of the wing is very clear and all details of venation and color pattern in the heavy pigmentation of the membrane are perfectly distinct.

Hind wing fragment: length 87 mm, width 29 mm. Light spots of diverse lengths, with rounded lateral margins, some with pigmentation penetrating into them, as shown in figure 39. Small rounded spots are numerous, irregularly distributed. R-rs area broadened; Rs with about 5 branches, first of them forked; MP forked about 5 times; CuP slightly concave near its origin, sending off several branches. Cross veins regularly distributed; in subcostal and sc-r1 areas they are not anastomosed, and they are unusually strong.

Family Breyeriidae Handlirsch

Breyeriidae Handlirsch, 1906: 95; Handlirsch, 1921: 135; Handlirsch, 1919: 18; Laurentiaux-Vieira and Laurentiaux, 1963: 173-8; Laurentiaux-Vieira and Laurentiaux, 1964: 1282-1284; Carpenter, 1967: 58.

Type genus: *Breyeria* Borre, 1875.

This family was established by Handlirsch on *Breyeria* Borre, *Borrea* Brongniart and *Megaptiloides* Handlirsch; three other genera were subsequently added to the family; *Pseudoborrea* Handlirsch, *Stobbsia* Handlirsch and *Breyeriopsis* Laurentiaux.

The family is represented in Upper Carboniferous strata of England, Belgium, Holland, France, Czechoslovakia and the United States (Tennessee) but despite that record no body structures are known so far. The uniformity of the venational pattern of the Breyeriidae being obvious, it does not seem possible to recognize more than two valid genera (Kukalová, 1959, p. 311; Laurentiaux, 1964, p. 3; Carpenter, 1967, p. 61): *Breyeria* Borre and *Stobbsia* Handlirsch.

Although specimens found in deposits other than Commentry are the better preserved, the Commentry material contributes some very interesting morphological details. Both *Breyeria lachlani* and *Breyeria boulei* show clusters of long hairs, in a dense pattern and extending along the anterior part of the proximal half of the wing membrane, long hairs at the wing base, and a border of long hairs along the anterior and posterior margins of the wing. In *lachlani* clusters of hairs have been observed also arising from some of the circular light spots in the cua-cup area.

The short hairs on the wings are now well known in Palaeodictyoptera. They are common on veins and cross veins, and in some families, as Dictyoneuridae, a dense covering of hairs can be seen over the entire wing and body surfaces. Clusters of long hairs on the wing base were found also in the related family Homiopteridae; similar hairs were noted in Archaemegaptilidae along the basal part of C, Sc and Cu. However, as far as I have been able to determine from the Commentry specimens, long hairs in clusters on the wing membrane and along the wing margin occur only in the Breyeriidae. In other Breyeriidae, outside of the Commentry deposit, traces of hairs have been described on the basal part of the costa and the posterior wing margin, as in *Breyeria barborae* (Kukulová, 1959) but the hairs themselves were not preserved. The clusters of long hairs on the wing membrane might be macrotrichia serving as sense organs, an hypothesis which seems to be supported by their presence in the light spots, which are actually cuticular thickenings of the wing membrane (Carpenter, 1967, p. 61).

Wings of large size, broad, equal in length, the hind pair broader. Sc shortened. Stems of R and M approaching or touching near the base. Branches of main veins few, widely separated from each other. CuA and MA simple; MP forked; CuP usually with a fork. Hind wings often broadly triangular in shape. Cross veins numerous, thin, irregular, often connected by anastomoses.

The family Breyeriidae seems related to the Graphiptilidae on the basis of the small rs area, simple MA and CuA, the few branches of MP and CuP, the presence of numerous long, fine cross veins and the triangular shape of the hind wings. Small circular spots frequently occur in color patterns of both groups.

Genera included in the Commentry shales: *Breyeria* Borre, 1875; *Megaptiloides* Handlirsch, 1906.

Other occurrences: *Breyeria* Borre (Westphalian-Stephanian of Europe, Westphalian of North America); *Stobbsia* Handlirsch (Westphalian of England).

Breyeria Borre, 1875: 7; Laurentiaux, 1953: 421.
Borrea Brongniart, 1893: 378; Handlirsch, 1906: 97; Handlirsch, 1919: 18.
Pseudoborrea Handlirsch, 1919: 18.
Breyeriopsis Laurentiaux, 1949: 47-54.
 Type species: *Pachytylopsis borinensis* Borre, 1875 (OD), Westphalian, Belgium.

(A revised figure of the type has been published by Laurentiaux (1949, p. 50, fig. 1a and 1953, p. 42, fig. 19b). In the Commeny shales two species have been found: *Breyeria lachlani* (Brongniart, 1893) and *Breyeria boulei* (Meunier, 1910), both based on slightly damaged hind wings. Laurentiaux (1949, p. 52) considered them to be conspecific and places *boulei* as a synonym

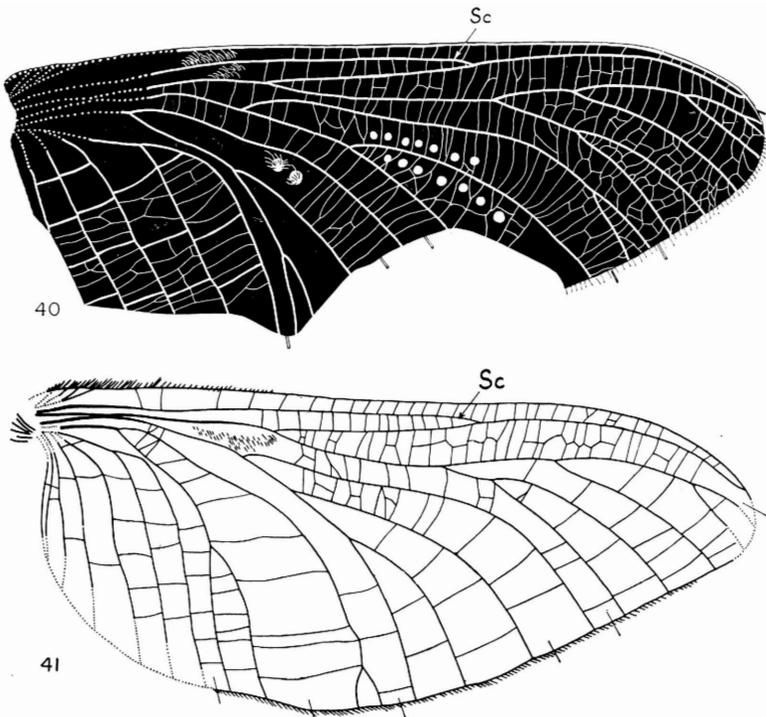


Figure 40. *Breyeria lachlani* (Brongniart); specimen 21-9; hind wing. Holotype.

Figure 41. *Breyeria boulei* (Meunier); hind wing. Holotype.

of *lachlani*. After having removed much matrix on the specimen of *boulei* I was able to see more details of its venation, including some which are specific differences and which eliminate the possibility of the synonymy with *lachlani*.

Specimen 21-5, designated by Handlirsch (1906, p. 97) as *Megaptiloides brodiei*, is too fragmentary for definite classification. It shows dense cross veins, richly anastomosed and tending to form short intercalary sectors. The hairs along the margin are absent. Handlirsch's classification of *brodiei* into a separate genus is probably justified.

The following account is based mostly on the details already published by Laurentiaux, Laurentiaux and Laurentiaux-Vieira, Carpenter and Kukulová.

Wings subequal, hind wing being somewhat shorter and broader. Hind wing sometimes very broad in the anal third and often of triangular shape. Postcostal area triangular, with several short branches. Sc terminating far before the apex, on R; Rs with 3-6 branches, the first of them often forked. Branches of M, Cu and the anals are curved sharply toward the posterior margin. MP with 1-5 broad forks; cua-cup area often markedly broad. CuP with 1-2 forks, seldom simple. Anal area either with a series of about 5 simple branches or with a series of simple long forks. Cross veins fine, irregular, rather dense, sometimes connected by irregular anastomoses. In the anal area, there are often present stronger and straighter cross veins (in addition to the finer ones) tending to be arranged in regular rows. Circular cuticular thickenings are often present in rows in the areas of m, rs and cu.

Breyeria Borre differs from *Stobbsia* Handlirsch by having Sc ending on R and by the branches of M, Cu and the anals abruptly curving toward the posterior margin.

Species included in the Commeny shales: *Breyeria lachlani* (Brongniart), *Breyeria boulei* (Meunier); *Megaptiloides brodiei* (Brongniart).

Species from other deposits: *Breyeria borinensis* (Borre) (Westphalian, Belgium); *Breyeria barborae* Kukulová (Westphalian A, Czechoslovakia); *Breyeria limburgica* Laurentiaux (Westphalian A, Holland); *Breyeria delruei* Laurentiaux (Westphalian B, France); *Breyeria wrankenii* Laurentiaux-Vieira and Laurentiaux (Westphalian B, Holland); *Breyeria rappi* Carpenter (Westphalian C, Tennessee); *Breyeria stopai* Laurentiaux and Laurentiaux-Vieira (Westphalian C, France); ?*Breyeria britannica* Laurentiaux and Laurentiaux-Vieira (Westphalian B, England).

Breyeria lachlani (Brongniart)

Figure 40

Borrea lachlani Brongniart, 1893: 379, pl. 21, fig. 9; Handlirsch, 1906: 97, pl. 11, fig. 8; Handlirsch, 1919: 18; Lameere, 1917: 157; Laurentiaux, 1949: 52.

This species was erected by Brongniart on specimen 21-9, a hind wing lacking the base and most of the posterior margin. The following account was completed after exposing additional features following the removal of substantial matrix.

Hind wing: length 65 mm; preserved width 26.5 mm. Anterior margin straight, strongly curved towards apex; apex broadly rounded. Sc terminating at the end of the second third of the length of the wing on R; Rs with 3 branches, first of them forked; MA slightly concave soon after its origin with a small fork at the end; MP probably with 2 branches extending anteriorly; CuA slightly concave in the first third of its course, CuP twice forked; anal area with 6 widely spaced branches. Cross venation dense, sometimes the cross veins connected, forming a network in the rs area. Strong, regular cross veins present in anal area. Long hairs occur in two clusters in the subcostal and sc-r areas, arising in circular, cuticular thickenings in cua-cup area and bordering the posterior margin. Small rounded cuticular thickenings forming rows between some branches.

Breyeria lachlani (Brongniart) differs from *boulei* in its denser and more reticulated cross venation and in the widely spaced anal veins, resembling those of the fore wing. It is similar to many other species, such as *delruei*, *vrankeni*, *rappi*, etc.

Breyeria boulei (Meunier)

Figure 41

Borrea boulei Meunier, 1910: 236, fig. 4; Meunier, 1912: 7, pl. 7, fig. 1.

Pseudoborrea boulei Handlirsch, 1919: 18, fig. 20.

Borrea lachlani Laurentiaux, 1949: 52.

Breyeria (*Borrea*) *lachlani* Laurentiaux and F. Laurentiaux-Vieira, 1951: 590.

This species was erected by Meunier upon a nearly complete hind wing. In comparison with all other hind wings of the genus, *boulei* does not have a very broad anal area and consequently it lacks the typical triangular shape.

Hind wing: length 59 mm, width 25 mm, broadest at about the first third of the wing length. Anterior margin, strongly curved towards the apex. Apex directed posteriorly, slightly pointed. Posterior margin as a whole convex, slightly concave in the cua-cup

area and slightly convex just before the apex. Sc terminating at the end of the second third of the wing on R; Rs with 3 branches, first of them forked; MA slightly concave soon after its origin; MP with 2 branches arising anteriorly. CuA slightly concave in the first third of its course, CuP forked; cua-cup area very broad; anal area with about six parallel branches, not widely spaced. Cross veins not very dense, sometimes connected. Stronger and more regular cross veins in the anal area and also in rs and m areas. Long hairs are present in a cluster in the r-m area at the base and bordering the proximal part of the anterior margin and the whole posterior margin. Cuticular thickening in rows probably present.

Breyeria boulei differs from *lachlani* as previously indicated.

Family Eugereonidae Handlirsch

Eugereonidae Handlirsch, 1906: 388; Carpenter, 1964: 104.

Dictyoptilidae Lameere, 1917: 194.

Peromapteridae Handlirsch, 1906: 79; Handlirsch, 1919: 11; Handlirsch, 1921: 130.

Type genus: *Eugereon* Dohrn, 1866 (Lower Permian of Germany).

The family Eugereonidae has been recently (1964) reviewed by Professor Carpenter, who synonymized the Dictyoptilidae with it and discussed *Eugereon* and the Commentry genus *Dictyoptilus*. Details of that study are not repeated here. On the basis of my own studies of Commentry material, I am adding certain details on the structure of the wing base of Eugereonidae and the related family Calvertiellidae which were not included in previous papers (Carpenter 1964, Kukalová 1964). To keep the revisional study as nearly complete as possible I am including in this paper figures of all Commentry Eugereonidae (Figures 42, 43, 44, 45).

The Eugereonidae are made spectacular by the more or less pronounced reduction of the hind wings, which often (to varying degrees) differ from the fore wings in shape and venation. The tendency to reduce the hind wings apparently occurred repeatedly in families of Palaeodictyoptera. Sometimes, the hind wings are broader but slightly shorter (Dictyoneuridae, Mecynostomatidae, some Spilapteridae) while in others the hind wings are as long as the fore wings but are narrower (Lycocercidae). Extremely shortened hind wings are so far known in two families — Eugereonidae and Megaptilidae.

Within the Eugereonidae, as understood in this paper, the

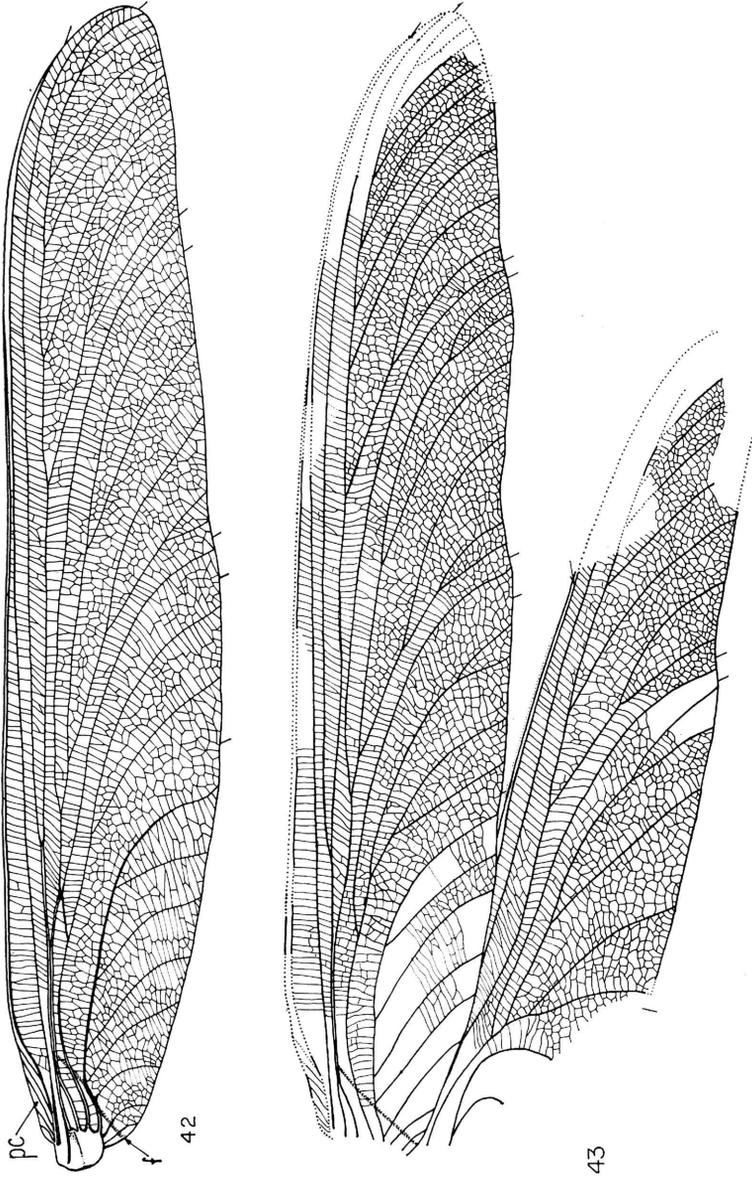


Figure 42. *Dictyoptilus sepultus* (Meunier); fore wing. Holotype. pc = precostal area; f = furrow.

Figure 43. *Dictyoptilus peromapteroides* (Meunier); fore and hind wings. Holotype.

amount of variability in the hind wing shape and venation seems to be very great. Nevertheless, I do not consider it practical, at least at our present stage of knowledge, to separate into different families those genera in which the fore wings are much alike. In my opinion, the hind wings representing reduced structures may have been variable in form. The most modified hind wing of the Palaeodictyoptera occurs in *Peromaptera* Brongniart, the wing being very short, broad and having an extremely reduced rs area. The hind wing of *Valdeania* Teixeira is very short and broad also but the venation is similar to that of its fore wing (according to Teixeira, 1941, fig. 1). In both *Eugereon* and *Dictyoptilus* (fig. 43) the hind wing is less shortened and narrow, approximately of the same width as the fore wing; the venation is modified more in the basal third, that is in the anal and cubital areas; the rs area is relatively well developed (Carpenter, 1964). So far, I consider these differences of generic level.

Another remarkable morphological feature of Eugereonidae is the precostal area. This was mentioned for the first time by Lameere (1917, p. 160) in *Dictyoptilus sepultus* (Meunier) and later in the same species by Laurentiaux (1953, p. 423). As far as I am aware, the largest precostal area is present in both fore and hind wings of the families Eugereonidae and Calvertiellidae; a narrower precostal area occurs in the related family Archaemegaptiidae. It was probably present also in Protagrionidae.

The precostal area of the families mentioned above is comparable with that of the Orthoptera, being formed by a series of short branches coming out anteriorly from a strong costa at its very base. It continues distally, forming a long membranous precostal strip. However, a precostal strip, not broadened basally to form a precostal area, is common in Palaeodictyoptera, being especially pronounced in the Dictyoneuridae, Lycocercidae, Homiopteridae and some Spilapteridae. In families with the precostal area well developed, the postcostal area is completely missing.

The postcostal area, as far as I was able to observe it in the specimens, is present in all families of Palaeodictyoptera without a precostal area. Besides the Palaeodictyoptera, I was able to see it in those Megaseoptera which did not have the wings very narrowed basally. The postcostal area was first described by me in the Breyeriidae (1959) and in the Roechlingiidae (1960), under the inappropriate term "precostal area." It is formed by a short vein, often branched, arising from the very base of the costa and oriented obliquely, finally terminating again on the costa after a

short distance. To avoid confusion and to emphasize the postcostal position of this area, I changed (1964) the term to postcostal area and pointed out its probable homology with the so-called costal brace of Ephemeroptera.⁶ The interesting and intermediate condition between the well developed triangular postcostal area and its complete reduction and replacement by the precostal area is present in Dictyoneuridae. In this family, which has a broad precostal strip and which is very probably related to Eugereonidae and Calvertiellidae, there is only one weak postcostal vein, oriented along the wing axis and ending usually on Sc, recalling the costal brace of the mayflies more than structures in other Palaeodictyoptera.

The origin of the costal brace-postcostal area probably goes back to the common ancestors of Palaeodictyoptera, Megasecoptera, Diaphanopteroidea and Ephemeroptera. The strongly developed costal brace has been found in aquatic Permian mayfly nymphs (Kukalová, 1969) probably helping to support the obliquely oriented and independent wing pads. In adult Permian mayflies the costal brace was less developed than in the nymph and probably non-functional. On the other hand, the terrestrial (apparently) nymphs of Megasecoptera (Carpenter, 1969) and Palaeodictyoptera (undescribed material from Westphalian, Illinois) have a vestigial postcostal area very much as in the adults. It is possible that in ancestral palaeopterous nymphs there was a selective trend towards the ability to hold the wings in a more posterior position. The costal brace-postcostal veins possibly helped to hold the wings in this favorable position.

The other striking morphological feature of the Eugereonidae is the presence of a deep furrow crossing the anal area obliquely and ending on the stem of M. It has been found in *Dictyoptilus*, *Eugereon* and very probably also in *Peromaptera*. This feature is best developed, though not unique, in this family and apparently developed independently in the very thin wings or very large wings, so-called, in addition to Eugereonidae and is most pronounced in the Calvertiellidae (thin wings) and Homiopteridae (very large wings). The function of this furrow is very puzzling, since the wings

⁶New and undescribed material of Calvertiellidae from the Lower Permian of Czechoslovakia shows beyond any doubt that in all known specimens of this family (including *Calvertiella*, which I had an opportunity to restudy recently) there is a well developed, large precostal area; the postcostal area is completely missing, as in the Eugereonidae. In this respect my account on Calvertiellidae (1964) has to be corrected.

of Palaeodictyoptera break off easily along this line. Thus, Calvertiellidae are usually found with the base of the anal area broken away. In Homiopteridae the anal veins and cross veins are distinctly different before and behind the furrow, which thus forms some type of a separate basal area. The high percentage of palaeodictyopterous wings with similarly broken bases indicates the presence of the basal furrow in many families. At the present time I am not able to explain this structure.

Wings unequal in length, the fore pair being longer. Hind wings shortened, with modified venation, different from that of the fore wings. Wing membrane usually dark with very small light spots restricted to individual cells of the reticulation. Fore wings long and very narrow, with the precostal area and precostal strip present; deep furrow obliquely crossing the anal area and terminating on R; Sc terminating before apex; stems of R and M arising separately but touching for some distance beyond the base; MA simple, MP with 2-4 branches; CuA usually simple, CuP usually with one branch only. Anal area long and narrow with pectinate and widely separated veins. A very dense pattern of coarse cross veins present, often with anastomoses and sometimes forming a network.

The nearest relatives of the Eugereonidae appear to be the Archaeomegaptilidae, Calvertiellidae and Protagrionidae; more distantly related are the Dictyoneuridae. All these affinities have at least partially been mentioned by previous authors (Handlirsch 1906, 1937; Lameere 1917, 1935; Martynov 1932; Tillyard and Fraser 1938; Laurentiaux 1953; Carpenter 1964; Kukalová 1964). There is also, in my opinion, a more distant relationship with another family that has markedly shortened hind wings — Megaptilidae. This family differs in having much broader and shorter fore wings, with a very large rs area but it recalls the Eugereonidae in having the branches of the main veins often arranged perpendicularly to the posterior margins; also in the simple MA and CuA, the branching of MP and in the very dense, richly anastomosing cross venation. The families mentioned above probably form a related group within the order.

Genera included in commentry shales: *Dictyoptilus* Brongniart, 1893; *Peromaptera* Brongniart, 1893.

Other genera in other deposits: *Eugereon* Dohrn, 1866 (Lower Permian of Germany; *Valdeania* Teixeira, 1941 (Stephanian, Portugal).

Genus *Peromaptera* Brongniart

Peromaptera Brongniart, 1893: 391; Handlirsch, 1906: 79; Lameere, 1917:

^{160; Handlirsch 1919: 11}
Type species: *Peromaptera filholi* Brongniart, 1893. (OD)

This genus is monotypic, based upon a single specimen with fore and hind wings preserved. Unfortunately, this remarkable fossil, showing a greatly reduced hind wing with the venation modified to the highest degree among Palaeodictyoptera, could not be found in the collection in Paris since I began this study. The following account is based on Lameere's revision (1917) and on photographs which Professor Carpenter made in 1938, when the specimen was in the collection.

Peromaptera was referred by Brongniart to the Dictyoneuridae. Handlirsch (1906, p. 79) erected for it a separate family on the basis of the shortened hind wing. Lameere (1917, p. 160) considered this separation as unnecessary because of the obvious relationships of the genus to *Dictyoptilus*.

From my studies of the photographs, I consider that Lameere's conclusions are correct: not only fore wing venation and cross venation but also all basal structures of the wing seem to be very similar in both *Peromaptera* and *Dictyoptilus*. The hind wing, on the other hand, is very different from that of both *Eugereon* and *Dictyoptilus*, being shorter and broader with a modified venation. But since we do not know the amount of individual and specific variation of the hind wing among the Eugereonidae and since the fore wing is almost indistinguishable from that of *Eugereon*, I do not consider it practical at this time to put *Peromaptera* in a separate family.

Fore wing narrow, broadening at the middle part. MP with few branches, CuP forked. Cross veins dense. Hind wing much broader than fore wing, extending almost to $2/3$ of the fore wing length, with broad apical part. Sc probably long; sc-r area broad; R1 ending relatively far before apex; Rs originating very basally, rs area being very small; M probably dividing beyond midwing, giving rise to simple MA and forked MP; CuA simple, CuP forked; anal area probably large, extending beyond midwing. Cross venation as in fore wings, in sc-r and r-rs areas much less dense than on the rest of the wing.

Peromaptera differs from *Eugereon* and *Dictyoptilus* in the shape of the hind wing. From all other genera of Eugereonidae the hind wing differs in the extreme modification of the hind wing venation.

Species included in Commeny shales: *Peromaptera filholi* Brongniart.

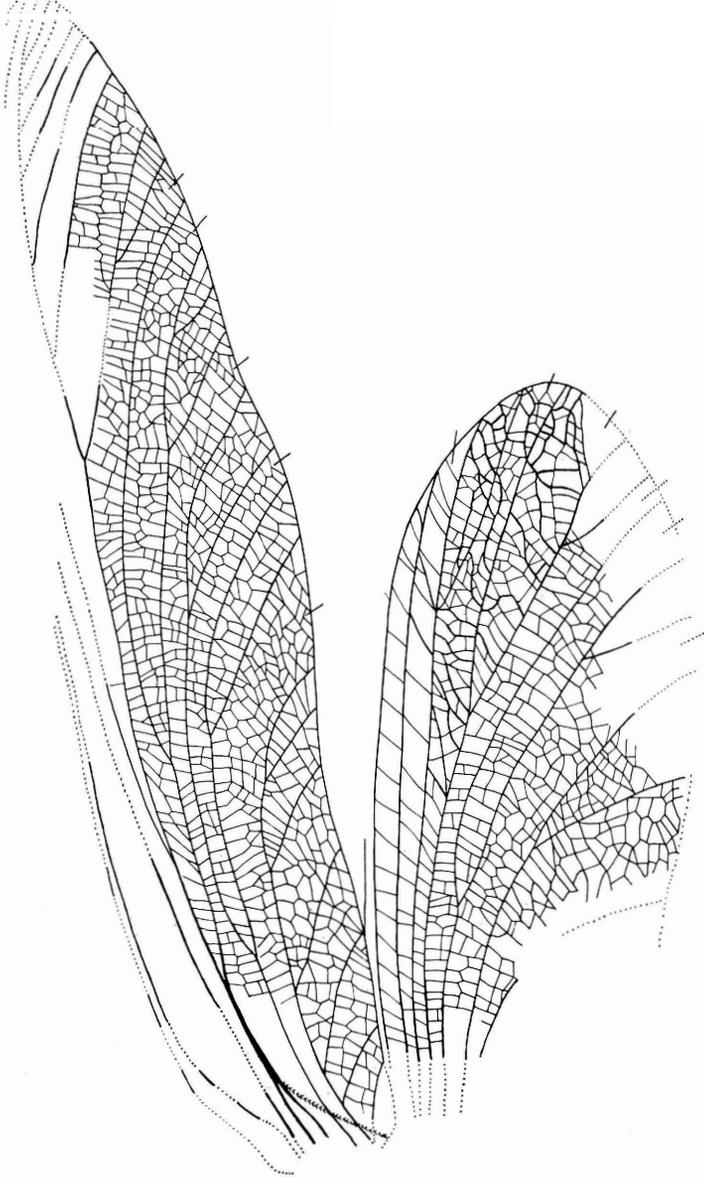


Figure 44. *Peromaptera filholi* Brongniart; fore and hind wings; Holotype.

Peromaptera filholi Brongniart

Figure 44

Peromaptera filholi Brongniart, 1883: 393, pl. 22, fig. 15; Handlirsch,

1906: 80, pl. 10, fig. 8; Lameere, 1917: 160.

This species is monotypic, based by Brongniart upon specimen 22-15, which was represented by a fore and a hind wing. For the drawing given here only the photograph was at my disposal. The base shows almost surely the stems of R and M touching as in *Dictyoptilus*. The precostal area being only fragmentary in the fossil is not so distinct. The hind wing venation unfortunately does not show convexities and concavities and has been interpreted according to Lameere (1917, p. 160).

Fore wing: length about 60 mm, width about 13 mm (according to Brongniart, 1893). Anterior margin unknown, posterior margin concave in the middle part of the wing. Subcostal area broad basally; Rs with about 7 branches, first of them forked; MA approaching the stem of Rs but not touching it; MP with two short branches; CuA independent from the stem of M but approaching it to some extent. Six anal veins.

Hind wing: length about 40 mm, width about 16 mm. Anterior margin straight; apical part shortened, apex obtusely rounded, located at about the wing axis. Rs very long, with short single branch; MP with a short fork at the end. Cu dividing proximally from M, occupying a narrow area. Anal veins far distant from each other, probably pectinate. Cross venation in hind wing with irregular thickening in the apical part.

The fore wing of *Peromaptera filholi* differs from that of all other species of Eugereonidae in the much less developed MP. The branch of CuA is probably an individual variation only, formed by the thickened reticulation which is frequently noted in the related family Dictyoneuridae. Also, CuA is simple in the hind wing. The shape of shortened hind wing recalls that of *Valdeania medeirosi* Teixeira, 1941 but the venation is completely different from that of the fore wing.

Family Archaemegaptilidae Handlirsch

Archaemegaptilidae Handlirsch, 1919: 13.

Type genus: *Archaemegaptilus* Meunier, 1908

This family, being based on a wing fragment, was erected by Handlirsch with some uncertainty as to its affinities. Lameere (1918,

p. 160), however, considered *Archaemegaptilus* related to *Dictyoptilus* (Eugereonidae).

Archaemegaptilus is known by a hind wing, which is not shortened and which has a venation similar to that of the fore wing of *Dictyoptilus*. In all genera of Eugereonidae, so far as we know, the hind wing is shortened and its venation is modified. The cross venation *Archaemegaptilus* is much coarser than in *Dictyoptilus* and forms intercalary sectors along the posterior margin, as in another related family, Calvertiellidae. Sc is almost as long as in Eugereonidae but terminates in a fork, forming thus an intermediate stage leading to an Sc which is short and which ends on R, as in Calvertiellidae. The stems of R and M are touching near the base as in Eugereonidae. The precostal area is very narrow and the wing venation less specialized than in both Eugereonidae and Calvertiellidae. In this way, *Archaemegaptilus* represents to some extent a combination of morphological features of both families being at the same time more primitive than any of them. I believe, therefore, that Handlirsch was probably correct in establishing a separate family for *Archaemegaptilus*. *Dictyoneurella perfecta* Laurentiaux, 1949 (Westphalian of France), should be referred to the same family, in my opinion; it is a fore wing with a long narrow precostal area, intercalary sectors and a venation and cross venation very similar to those of *Archaemegaptilus*.

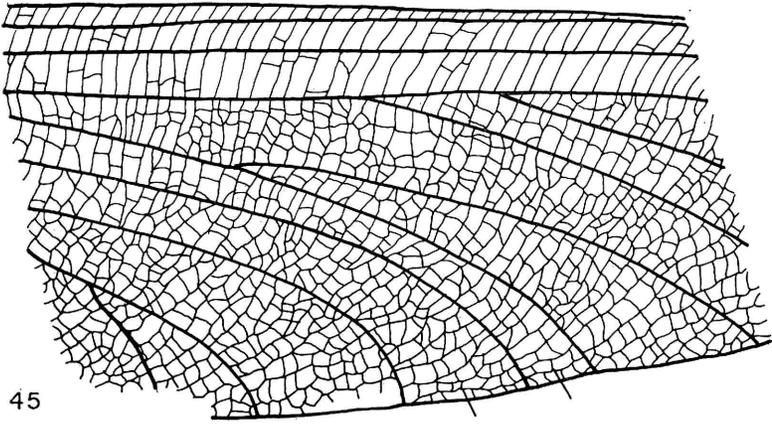
The following account is based on *Dictyoneurella* (fore wing) and the completed figure of *Archaemegaptilus* (hind wing).

Wings probably equal in length, hind pair broader. Venation in fore and hind wings alike. Wing membrane thin, with darker venation or dark with small light spots. Precostal area narrow, postcostal area completely missing. Sc more or less shortened. Stems of R and M close together or touching for some distance near base. Rs area small with few branches. MA simple, MP branched several times. CuA simple, CuP with several branches. Anal area with pectinate series of branches. Cross veins strong but not dense, forming a loose reticulation and convex intercalary sectors.

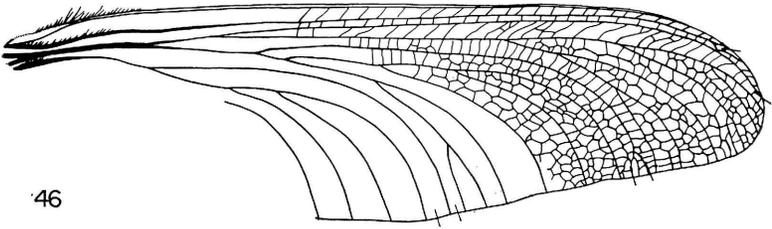
The family Archaemegaptilidae is closely related to the Eugereonidae, Calvertiellidae and Protagrionidae, from all of which it differs in its more primitive venation with independent branches and many-branched CuP.

Genus included in Commentary shales: *Archaemegaptilus* Meunier, 1908.

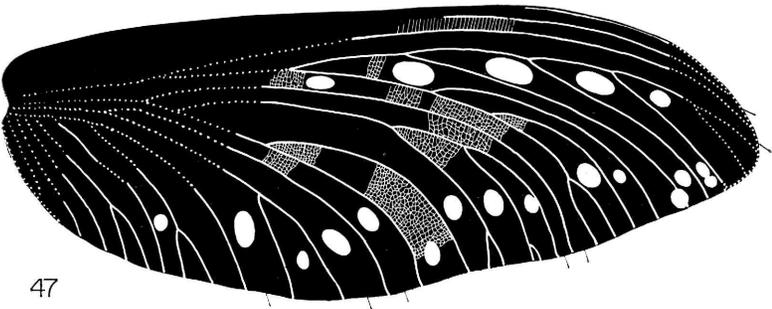
Genus from other locality: *Dictyoneurella* Laurentiaux, 1949 (Westphalian, France).



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Figure 45. *Dictyoptilus renaulti* Brongniart; fore wing. Holotype.
 Figure 46. *Archaemegaptilus kiefferi* Meunier; hind wing. Holotype.
 Figure 47. *Megaptilus blanchardi* Brongniart; fore wing. Holotype.

Genus *Archaemegaptilus* Meunier

Archaemegaptilus Meunier, 1908: 155; Meunier, 1908: 175; Meunier, 1909: 138; Händlirsch, 1919: 13; Lameère, 1917: 103; Lameère, 1917: 160.

Type species: *Archaemegaptilus kiefferi* Meunier, 1908 (OD).

This genus is monotypic, based by Meunier on the reverse of a hind wing. As Lameère (1917, p. 160) correctly noted, the obverse specimen, which was apparently not seen by Meunier, is more nearly complete; it is figured here for the first time. The following account is based on both parts of the type specimen.

Hind wing: long, broadening basally. Precostal strip pronounced, broadened at the base to form a narrow precostal area; Sc slightly shortened, terminating by a fork on C and R; stems of R and M touching for a long distance just beyond the base; CuA simple, curved, not approaching the stem of M; CuP with several branches occupying a large area. Cross venation coarse, consisting of cross veins connected by anastomoses, becoming a network. Intercalary sectors, short.

Archaemegaptilus differs from *Dictyoneurella* by its longer Sc and denser cross venation.

Species included in the Commeny shales: *Archaemegaptilus kiefferi* Meunier, 1908.

Archaemegaptilus kiefferi Meunier

Figure 46

Archaemegaptilus kiefferi Meunier, 1908: 155; Meunier, 1908: 175, fig. 3; Meunier, 1909: 138, pl. 2 fig. 2; Händlirsch, 1919: 13, fig. 15.

Although this species was erected by Meunier on a fragment of the reverse of a hind wing, the following account is based on the obverse as well.

Hind wing: length 105 mm, width 27 mm. Anterior margin straight, slightly concave near the base, separating off a narrow precostal area. Wing broadened in the middle part of its length, narrowing behind the CuA area. Apex directed backward, rounded; C, Sc and Cu covered by long hairs near the base. M touching the stem of R, near the base, but diverging from it again; r-rs area somewhat broadened, with oblique cross veins; Rs with 3 branches, first of them forking twice; MA originating near the first fork of MP; MP forked 5 times; CuP with 4 branches. Color marking in the form of small light spots.

Archaemegaptilus kiefferi shows very similar color patterns to *Dictyoptilus sepultus* (Eugereonidae) and to *Moravia convergens* Kukulová (hind wing, Calvertiellidae). *Dictyoneurella perfecta*

has dark veins very similar to those of *Calvertiella permiana* and *Moraviptera reticulata* Kukalová (Calvertiellidae).

Family Megaptilidae Handlirsch

¹³⁰Megaptilidae Handlirsch, 1906: 80; Lameere, 1917: 102; Handlirsch, 1921:

Anaxionidae Handlirsch, 1919:19.

Lithoptilidae Handlirsch, 1922: 44.

Type genus: *Megaptilus* Brongniart, 1885.

The family was based by Handlirsch on a fragment of a large fore wing of spectacular character, showing extremely dense cross venation and a large rs area, with curved Rs branches. Professor Carpenter has kindly given me for study another (undescribed) specimen of *Megaptilus* from the Westphalian of Rhode Island, represented by a hind wing. Surprisingly enough, this hind wing turns out to be extremely shortened, reaching about only half of the fore wing length. This unexpected discovery throws more light on the obscure relationships of the Megaptilidae. The peculiar type of reduction of the hind wing venation, suggestive of some Eugereonidae (e.g., *Peromaptera*), together with a general pattern of venation and cross venation, brings this family close to the Eugereonidae - Archaemegaptilidae - Dictyoneuridae - Protagrionidae - Calvertiellidae group.

The finding of this wing of *Megaptilus* enables us to solve the systematic position of another puzzling fossil — *Lithoptilus* Lameere, from Commeny. It probably represents a shortened hind wing of the same family Megaptilidae. The following account is based on *Megaptilus* (fore and hind wings) and *Lithoptilus* (hind wing).

Wings very unequal. Fore wings large and broad, hind wing somewhat narrow, reaching only about half of the fore wing length. Branches of Rs, M and Cu in fore wing curve posteriorly. Rs area very large; MA simple, MP forked several times; CuA simple; CuP and anal area with several branches. Hind wing with a very reduced rs and mp area, with curved branches of M and Cu. Cross veins in both pairs of wings extremely dense, connected by numerous anastomoses.

The family Megaptilidae is related to the Eugereonidae, as indicated by the shortened hind wings, curved branches of the main veins, nature of the branching of MP and the presence of extremely dense cross veins with numerous anastomoses.

Genera included in the Commeny shales: *Megaptilus* Brongni-

art, 1893; *Lithoptilus* Lameere, 1917. No other genera are known except for an undescribed specimen of *Megaptilus* in the Museum of Comparative Zoology from the Westphalian of Rhode Island.

Megaptilus Brongniart

Megaptilus Brongniart, 1885: 61; Brongniart, 1893: 373; Handlirsch, 1906: 80; Lameere, 1917: 156.

Type species: *Megaptilus blanchardi* Brongniart, 1885 (SD Handlirsch, 1906).

This genus was established by Brongniart for three species, *Megaptilus blanchardi*, *brodiei* and *scudderi*. Handlirsch (1906, p. 98) referred *brodiei* to a new genus, *Megaptiloides*, and placed it in the family Breyeriidae; he referred *scudderi* (1906, p. 118) to another new genus, *Paramegaptilus*, and transferred it to the Palaeodictyoptera incertae familiae; and he erected a new family, Megaptilidae, for *blanchardi*.

The following account is based on the type species (fore wing) and a hind wing of *Megaptilus* species (Westphalian of Rhode Island).

Wing membrane usually dark, sometimes with light oval spots arranged in longitudinal rows. Fore wings broad and short, broadest at about the middle. Sc long, remote from C in the apical third; first branch of Rs originating before the middle of the wing, forked several times; m area much larger than cu area. Anal area relatively small, with several branches. Hind wing with obtuse apical part and with very narrowed rs and mp areas. Cross venation equally dense in both wings.

Megaptilus (hind wing) differs from *Lithoptilus* Lameere (hind wing) by Sc, R, and stem of Rs being parallel and curved, with the more dense cross venation with more anastomoses.

Species included in the Commeny shales: *Megaptilus blanchardi* Brongniart, 1885. Occurrence elsewhere: *Megaptilus* species (Westphalian, Rhode Island).

Megaptilus blanchardi Brongniart

Figure 47

Megaptilus blanchardi Brongniart, 1885: 61; Brongniart, 1893: 374; pl. 21, fig. 3; Handlirsch, 1906: 80, pl. 10, fig. 9; Handlirsch, 1921: 130, fig. 56; Handlirsch, 1919: 13.

This species was erected by Brongniart upon specimen 21-3, a large fore wing fragment. Using glycerin, I was able to work out

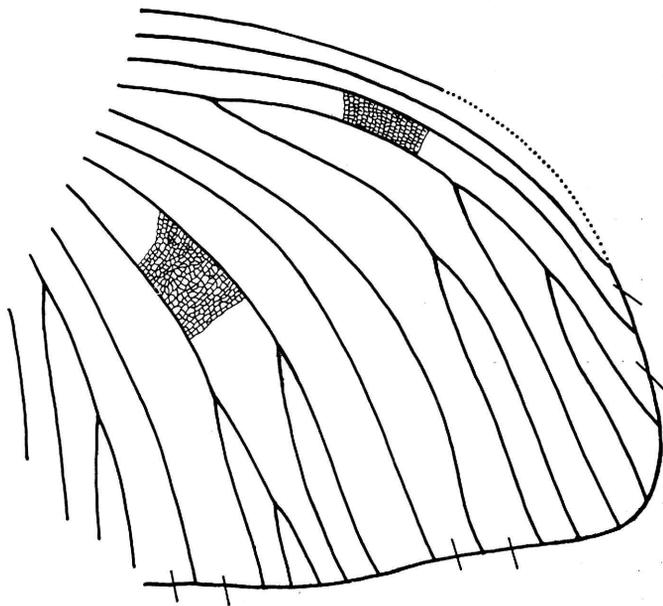


Figure 48. *Megaptilus* sp.; hind wing; Westphalian, Rhode Island.

a larger part of the anal area than shown in Brongniart's original figure.

At first, Brongniart believed that the wing of *blanchardi* belonged to the large insect's body described by him (1882) as *Titanophasma fayoli* but in 1893 (p. 374) he expressed doubt about that. Lameere (1917, p. 156) considered the small wing fragment designated as *Titanoptera maculata* Brongniart, 1893, as part of the anal area of *M. blanchardi*. Unfortunately, he did not find this fragment in the collections at the Paris Museum.

Fore wing fragment: length 144 mm, width 51 mm. Color markings light, oval, distributed along the stem of Rs between the branches and forming an irregular row in the posterior third of the wing. Wing broadest at the end of CuA, narrowing towards the base. Posterior margin concave at CuA and MA. Apex directed backwards. Subcostal area and sc-r area equally broad in the apical third; Sc, R and stem of Rs parallel and curved in the distal half; Rs with a long row of about 5 curved branches, widely distant from each other. First branch of Rs forked three times; MP forked 5

times, with widely separated branches; CuP with only one, wide fork. Branches of main veins near posterior margin S-shaped. Anal area with about 7 relatively densely arranged branches, some of them with short forks. Cross veins in sc-r area dense but simple, not connected by anastomoses.

Megaptilus blanchardi recalls *Dictyoptilus sepultus* (Eugereonidae) by its posteriorly curved veins with S-shaped tips along the posterior margin, by the fore wing broadening at the end of CuA and by the wide fork of MP. Also, the cross venation, though denser, is not very different from that of *sepultus*, either. The hind wing of *Lithoptilus boulei* (Meunier, 1908) shows the same S-shaped tips of M and Cu branches along the posterior margin as the fore wing of *blanchardi*.

Genus *Lithoptilus* Lameere

Lithoptilus Lameere, 1917: 157; Demoulin, 1958: 3.

Anaxion Handlirsch, 1919: 19.

Type species: *Lithoptilus boulei* (Meunier, 1908) (OD)

This genus was erected by Lameere (1917, p. 157) for *Archaeoptilus boulei* Meunier, 1908. Lameere noted that this genus seemed closely related to *Homoioptera*, differing only in the shorter and broader wings but he could not determine to which pair of wings the type specimen belonged. Handlirsch, noting the broad subcostal area, assumed the type specimen to be a fore wing and, having overlooked Lameere's paper, erected a new genus for *boulei*, *Anaxion* (Anaxionidae), which he associated with the Breyeriidae. Finally, Demoulin (1958) without seeing any of the specimens, concluded that *Lithoptilus* was based on a hind wing, vestigial as in most recent Ephemeroptera. As the closest related genus he suggested *Rhabdoptilus* and referred both genera to the Rhabdoptilidae Handlirsch. Demoulin's statement about the vestigial hind wing character of the type specimen of *Lithoptilus* is correct but there is no indication of relationship to *Rhabdoptilus*.

The systematic position of *Lithoptilus* becomes much clearer after the shortened hind wings of Eugereonidae and Megaptilidae are studied. Although *Lithoptilus* recalls some Eugereonidae by the shape of the hind wing (e.g., *Peromaptera*), the venational pattern and cross veins are most like those of *Megaptilus*. The range of variation of the hind wing shape seems to have been wide in the Eugereonidae and it probably was also in the Megaptilidae.

The following account is based upon the hind wing of *Lithoptilus boulei* (Meunier).

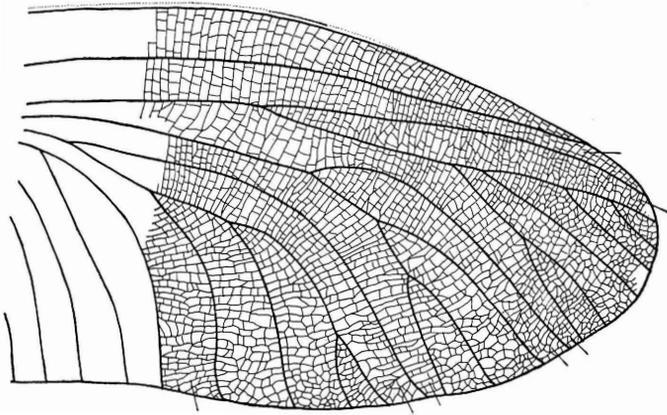


Figure 49. *Lithoptilus boulei* (Meunier); hind wing. Holotype.

Hind wing very shortened and broad, especially in the apical part. Anterior and posterior margins almost parallel. Sc long, subcostal area broad; Rs originating at about midwing; Rs area extremely small; M dividing at the level of the origin of Rs, MA simple, MP forking; Cu dividing within the first third of the wing length; CuA simple; CuP with several branches. Cross veins coarse and very dense, connected by numerous anastomoses, sometimes turning into a network.

Lithoptilus Lameere differs from *Megaptilus* (in the hind wing) by the broad subcostal area, straight Sc, R and Rs; by M dividing more distally; and by the somewhat less dense cross venation.

Species included in Commentry shales: *Lithoptilus boulei* (Meunier, 1908).

Lithoptilus boulei (Meunier)

Figure 49

Archaeoptilus boulei Meunier, 1908: 153; Meunier, 1908: 35, fig. 1; Meunier, 1909: 131, pl. 1, fig. 1.

Lithoptilus boulei Lameere, 1917: 157; Demoulin, 1958: 1-5.

Anaxion boulei Handlirsch, 1919: 19, fig. 21.

This species is monotypic, based by Meunier on a vestigial hind wing of a large palaeodictyopteron. Following the weak imprint of the veins on the matrix, I was able to work out some of the more proximal part of the type specimen.

Hind wing fragment: length 66 mm, width 40 mm. Anterior

margin abruptly curved towards the apex. Posterior margin convex at the end of the anal area. Apex rounded, directed somewhat anteriorly. Subcostal and sc-r areas broad; RI straight, Rs sending off 4 very short oblique branches, the first of them being forked. MP twice forked; CuP with a series of four branches. Anal area relatively large with long branches, perpendicular to posterior margin. Branches of M and Cu with S-shaped ends. Cross veins forming a network along the posterior part of the wing.

The broad subcostal and sc-r areas, together with straight course of Sc and R are very unusual for a hind wing. Nevertheless, the same straightening of Sc and R and broadening of sc-r area are present in the very shortened hind wing of *Peromaptera filholi* Brongniart, also.

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