Mesozoic Neuroptera and Raphidioptera (Insecta) in Britain

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Synopsis

The problems of identification and classification of the Neuroptera and Raphidioptera (Insecta) are discussed. Specimens from the British Mesozoic are reviewed and three new species (*Archeosmylus complexus*, *A. alysius* and *Prohemerobius aldertonensis*) are described. A type species for *Prohemerobius* Handlirsch, 1906, is designated.

Introduction

The present study of Mesozoic Neuroptera and Raphidioptera forms part of a project on the so-called 'Panorpoid complex' in Britain. Tillyard (1918–19) used the term to include the Neuroptera, Mecoptera, Trichoptera, Lepidoptera, Diptera and Siphonaptera. The Neuroptera *sensu* Tillyard included the Orders Megaloptera, Raphidioptera and Neuroptera (Planipennia). These are considered as a monophyletic group, the Neuropteridea (Neuropteroidea *sensu auctt.*), within the Holometabola (Kristensen 1975, Hennig 1981). The remainder of the Panorpoid complex *sensu* Tillyard is now placed in the monophyletic Mecopteroidea (Kristensen 1975). Boudreaux' (1981) emendations, Neuropterida and Panorpida, have not been widely accepted to replace the better-known Neuropteroidea and Mecopteroidea. The Mecopteroidea will be considered in a subsequent publication.

Martynova (1962) recognized three Orders within the Neuropteridea (Neuropteroidea) in her study of fossil insects and this classification is followed in the present paper. Although her work was primarily concerned with fossil insects in the U.S.S.R., she also considered fossil Neuropteridea from the rest of the world.

No comprehensive study of fossil Neuroptera and Raphidioptera in Britain has been made. Brodie (1845) figured a number of insects he considered neuropterous. Although he was the first to figure neuropterous insects from the Mesozoic rocks of Britain he did not provide names for them, describing them as '*Corydalis*' (a Recent genus of Megaloptera) or 'neuropterous insects'. Giebel (1856) provided names for many of Brodie's figures, including some listed as neuropterous, and these species were subsequently re-evaluated by Handlirsch (1906).

Table 1 gives the specimens figured by Brodie (1845) and Westwood (1854) as 'neuropterous insects' or '*Corydalis*' and indicates their current taxonomic position. All the specimens are in the collection of the British Museum (Natural History) unless otherwise stated.

Scudder (1886) described two fossil wings as Blattodea which Handlirsch (1906) recognized as Neuroptera.

Tillyard (1933) described two species of Neuroptera from the Lower Lias of Britain. He associated the Neuroptera *sensu stricto* with the Mecoptera and other orders of insects in the Panorpoid Complex although he expressed some reservation about this. He suggested that they were linked 'somewhat loosely with the Mecoptera through the ancient suborder Protomecoptera'. Nevertheless he went on to consider the Neuroptera as the 'most Primitive members of the Complex, and appear with the Mecoptera in the Lower Permian' (Tillyard 1933: 8). Kristensen (1975) pointed out that this association was based on the general phenetic resemblance of the more primitive members of the two orders, neither of which has greatly differentiated from their ancestral holometabolan type. No evidence has yet been presented of any synapomorphies from these orders which cannot, therefore, be considered to have a common ancestor separate from other Holometabola. Hennig (1981) considered that there was good

Table 1 Current systematic position of fossil insects described as 'neuropterous' or '*Corydalis*' by Brodie, 1845 and Westwood, 1854. (*Brodie (1845: 102) probably made a mistake in referring to fig. 15 (dragonfly abdomen) when he should have said fig. 16. Tillyard (1933: 64) synonymized *H. higginsi* with *Necrotaulius furcatus* Giebel on the basis that Brodie's references to figs 15 and 16 were mixed. A type designation for this species will be given in a subsequent publication on the Mecoptera.)

Plate number	Figure	Brodie's name (1845)	Current systematic position
5	2	*Corydalis*	Blattodea, *Nanoblattina similis* (Giebel)
5	3	*Corydalis*	Blattodea
5	12	Neuropterous (cf. *Orthophlebia*)	Mecoptera, *Orthophlebia bifurcata* (Giebel)
5	13	*Corydalis*	Orthoptera, *Zalamona brodiei* Giebel
5	14	*Corydalis*	Blattodea, *Blatta kollari* Giebel
5	16	*Corydalis*	Blattodea, *Nanoblattina brodiei* (Giebel)
5	18	Neuropterous (cf. *Orthophlebia*)	Mecoptera, *Stenopanorpa gracilis* (Giebel)
5	21	Neuropterous (cf. *Orthophlebia*)	Orthoptera, [*Bittacus dubius* Giebel][1]
6	22	*Hemerobius gigantea* Buckland	Odonata, *Isophlebia gigantea* (Buckland) (Handlirsch, 1906: 583)
8	10	Neuropterous	Hemiptera–Homoptera
8	11	Neuropterous	Orthoptera
8	16	Neuropterous	Odonata
9	15	*Hemerobius higginsi* (p. 102) (See * above)	
9	15	'abdomen of dragonfly' (p. 126) (See * above)	
9	16	Neuropterous (cf. *Panorpa*)	Mecoptera, *Necrotaulius furcatus* (Giebel)
9	17	Neuropterous (cf. *Panorpa*)	Mecoptera, *Necrotaulius liasina* (Giebel)

Plate number	Figure	Westwood's name (1854)	Current systematic position
15	16	*Termitidium ignotum*	Probably Orthoptera[2]
17	12	*Panorpidium tessellatum* var.	Probably Orthoptera[2]
18	24	*Sialium sipylus*	Nymphitidae[3]
18	39	*Agrionidium aetna*	Probably Orthoptera

[1] Giebel described this as a Mecopteran but it is Orthopterous.
[2] Specimens not examined.
[3] Specimen not examined. The marginal branching is more reminiscent of Neuroptera but from the figure little further can be determined.

evidence for believing that the Coleoptera (+ Strepsiptera) were more closely related to the Neuropteridea (Neuropteroidea) but he also suggested an alternative, that the Mecoptera and Neuroptera could be sister-groups. There is still no concensus on this.

The most primitive holometabolous insects occur in the Neuropteridea (Kristensen 1975) but the relationship of the three orders within the Neuropteridea (Neuroptera, Megaloptera, Raphidioptera) has not yet been resolved (Achtelig & Kristensen 1973).

In studying the neuropterous fossils, all the evidence for their identification is based on wing venation: very few bodies of neuropterous insects have been described. This creates a problem when detailed comparisons of fossil and Recent Neuropteridea are required. In the latter, although the venation of the wings is used in their major classification, other parts of the anatomy are extensively used both for this and the generic and specific classification. While a

general comparison of fossil and Recent wings can be made, the results may not always be significant. This is partly owing to the similarity of the wing venation in many Recent species which may currently be placed in different genera or even different families, and partly to the apparent lack of derived ground-plan characters in the wing.

The identification of a fossil wing as neuropterous is rarely difficult, although fragments have been described as cockroaches (Scudder 1886), but further identification is impeded by the limited number of taxonomic and classificatory characters in the wing venation. The recognition of the fossil as neuropterous is usually, in the first instance, based on the presence of a number of parallel branches of the radial sector (a condition also found in Orthoptera) and the presence of small end-branches ('apical twigging') at the wing margin. These first impressions can be confirmed on closer examination by the presence of trichosors (small structures on the wing margin between the veins). However, trichosors are not easily seen in fossils (and are absent in some Recent Neuroptera), but the presence of numerous subcostal veinlets will also help to confirm the identification.

The classification of the Neuropteridea into Neuroptera, Raphidioptera and Megaloptera, adopted by Martynova (1962), is followed here. There are two families in the Megaloptera. In the Sialidae there are three species in the Recent fauna in Britain but sialids have not been recognized in the British Mesozoic. The other family, Corydalidae, is known only from the New World and has not been found in the fossil record in Britain. The Permosialidae, listed by Martynova (1962) in the Megaloptera, are now considered to belong to Miomoptera.

Two species of Raphidioptera were recently described from the Dorset Lias (Whalley 1985) and there are four living species in Britain. The fossil species were placed in extinct families.

Martynova (1962) divided the Neuroptera into four superfamilies, Myrmeleontoidea, Polystoechotoidea, Hemerobioidea and Coniopterygoidea. (The spelling of these names has been emended from Martynova, 1962, to make the endings agree with the recommendations of the International Code for Zoological Nomenclature.) She defined these superfamilies on the basis of the characters given below and these are used in the current work to identify the British specimens. Because the definitions are based solely on the wings there is some overlap of characters between the genera listed by Martynova in the different groups. For example, the Berothidae (Hemerobioidea) have the subcostal and radial veins joined in many species (Tjeder 1969). Martynova considered that this was due to a cross-vein and that the subcostal vein does actually continue to the wing margin. While this may be true, it is rarely possible to decide from a study of the fossil whether the subcostal and radial veins are joined only by a cross-vein near the apex or whether they actually fuse, with the subcostal curving down to join the radial vein. Although there may be doubt over the interpretation of the origins of the apical anastamosis of the subcostal and radial, in the present study an anastamosis between the subcostal and radial veins (unless clearly due to a cross-vein) is used to make the primary taxonomic division to contrast with those where the subcostal and radial veins can be traced separately to the wing margin. All the specimens where the subcostal and radial can be traced separately to the outer wing margin are placed in the Hemerobioidea; the other specimens, where the subcostal and radial join, are placed in one of the two remaining groups (Myrmeleontoidea, Polystoechotoidea, *sensu* Martynova, 1962).

Distribution and abundance of the fossils

Over 50 Mesozoic sites are currently known in Britain from which insect fossils have been found but fewer than ten of these have yielded any Neuropteridea. Neuroptera are recorded from the Permian (Martynova 1962) but are known only from the Upper Triassic to Lower Cretaceous in the British Mesozoic. Of the Recent families only the Coniopterygidae, Berothidae and Psychopsidae are known from the Mesozoic and few of these occur earlier than the Lower Cretaceous (Whalley 1980).

Fewer than 50 specimens, representing 11 species of Neuropteridea, are known from the British Mesozoic, a period of about 180 million years. Although relatively few specimens are known it is probably significant that these fossils represent eight families, only one of which is

extant. This compares with seven extant families of Neuropteridea in the British fauna and 20 extant families world-wide. In spite of the small numbers the data suggest that there was considerable diversity in Mesozoic Neuropteridea, although this diversity must be considered against the time-scale involved when making a comparison with the Recent fauna.

Fossil Neuropteridea are not common compared with some other insect orders. This either reflects their true status (i.e. they were actually less common), or they were living in areas where they had even less chance of being fossilized. There is no indication of a proportional change in abundance compared with Recent insects which can be seen in, for example, the Mecoptera which were more diverse and abundant in the Mesozoic than in the Recent fauna. Although Neuroptera are delicate insects, they are no more delicate than many of the other insects that were preserved in Mesozoic deposits. In an analysis of the various insect orders in four localities of early and late Jurassic age in Europe and Asia, Whalley (1985) quoted figures to show that Neuropteridea represent less than 7% of the total insect fauna at each of the four sites. Recent Neuroptera tend to be more numerous in woodlands but, being predatory insects, they are never as abundant as phytophagous insects.

In the British Mesozoic Neuropteridea it is evident that only one of the Lower Cretaceous specimens can be referred to a Recent family, the Psychopsidae (Jarzembowski 1984). However, by the Palaeocene (Tertiary) the Recent families Mantispidae (no longer occurring in Britain), Hemerobiidae, Chrysopidae and Sisyridae were all represented in the British fauna (Jarzembowski 1980).

Check list of British Mesozoic Neuropteridea

NEUROPTERA

Polystoechotoidea:

Permithonidae	*Archeosmylus complexus* sp. nov. (p. 50)
	Archeosmylus alysius sp. nov. (p. 50)
Mesopolystoechotidae	*Megapolystoechus magnificus* Tillyard

Hemerobioidea:

Brongniartiellidae	*Actinophlebia intermixta* (Scudder)
	Pterinoblattina pluma (Giebel)
	Pterinoblattina penna (Giebel)
Kalligrammatidae	*Paractinophlebia curtisii* (Scudder)
Prohemerobiidae	*Prohemerobius aldertonensis* sp. nov. (p. 60)
Psychopsidae	(figured in Jarzembowski, 1984: fig. 32)

RAPHIDIOPTERA

Mesoraphidiidae	*Metaraphidia confusa* Whalley 1985
	Mesoraphidia species
Baissopteridae	*Priscaenigma obtusa* Whalley 1985

MEGALOPTERA

No fossil record in Britain; not present in the Recent British fauna.

Subdivisions of the Neuroptera

The following list (after Martynova, 1962) includes all families currently recognized. (*Includes living species).

Coniopterygoidea. Very small insects. Venation very reduced from basic neuropterous plan, without additional marginal forks. Jurassic–Recent. Family Coniopterygidae*. Not known as fossils in Britain although occurring elsewhere in the Mesozoic (Whalley 1980). There are a number of Recent species in Britain.

Myrmeleontoidea. Long, narrow wings; distal part of Sc and R join; anterior branches of M merge with R; MP and Cu1 almost parallel; proximal branches of CuA thicker than the rest of the branches; CuP short. Jurassic–Recent. Families Ascalaphidae*, Myodactylidae*, Myrmeleontidae*, Nemopteridae*, Nymphidae*, Nymphitidae, Solenoptilidae. No Recent species in Britain.

Polystoechotoidea. Forewings more than twice as long as wide; Sc and R joined; MA usually many-branched, merging with Rs near base; MP with two branches; CuA and CuP long, with short, backward-directed, branches; anal veins often stepped. Permian–Recent. Families Archeosmylidae, Ithonidae*. Mesopolystoechotidae, Neurorthidae*, Osmylidae*, Osmylitidae, Permithonidae. One Recent species in Britain.

Hemerobioidea. Wings comparatively wide; Sc not merging with R; Sc, R and Rs approach (except in Chrysopidae, Mesochrysopidae); parallel Sc and R areas together narrower in width than costal area (except Chrysopidae); MA often joins R or Rs. Permian–Recent. Families Berothidae*, Brongniartiellidae, Chrysopidae*, Dilaridae*, Eomantispidae, Hemerobiidae*, Kalligrammatidae, Mantispidae*, Mesochrysopidae, Osmylopsychopidae, Palaemerobiidae, Proberothidae, Prohemerobiidae, Psychopsidae*, Rapismatidae*, Sialidopseidae, Sisyridae*. Recent species in the Hemerobiidae, Sisyridae and Chrysopidae occur in Britain.

Myrmeleontoidea do not occur in the Recent fauna and have yet to be found in the fossil record in Britain. British specimens with Sc and R joined have relatively short, broad wings and are all placed in the superfamily Polystoechotoidea.

Systematics

All numbers given are British Museum (Natural History) register numbers unless otherwise stated.

Order **NEUROPTERA**, lacewings

Superfamily **POLYSTOECHOTOIDEA**

Family **PERMITHONIDAE** Tillyard, 1922

1922 Permithonidae Tillyard: 289.
1953 Archeosmylidae Riek: 85; syn. nov.

DIAGNOSIS. Sc fused at two-thirds from wing-base or nearer centre of wing. Pterostigma long, often running round apex of wing. Radial area wider than subcostal. M branches towards centre of basal half of wing in some species. Rs with 7–10 branches. MA frequently well-branched. CuP simple or with short forks. Cross-veins not in even rows. Permian–Jurassic. (After Martynova, 1962, modified from Riek, 1955.)

DISCUSSION. The similarity between the Permithonidae and Archeosmylidae was mentioned by Martynova (1962) but she did not synonymize them. The separation of the Permithonidae from the Osmylitidae is based on the width of the radial area (radial field of Martynova, 1962) and from the Mesopolystoechotidae by the wing shape (figured in Martynova, 1962). The arrangement of the veins in *Osmylus* and some other genera in the Osmylidae, as in the Polystoechotidae, with cross-veins in the centre of the wing and a broad margin with only longitudinal veins, is used as a guide to these families. Most of the genera in the Permithonidae were from the Permian, but with the synonymizing of Riek's Triassic family the range is now extended. There are insufficient data on the British specimens to create a new genus for them and they are provisionally placed in *Archeosmylus*.

Genus ***ARCHEOSMYLUS*** Riek, 1953

1953 *Archeosmylus* Riek: 86.

TYPE SPECIES. *Archeosmylus pectinatus* Riek (1953: 86), by original designation.

DIAGNOSIS. Sc and R fused. Pterostigma long, curved round apex. Rs with 7–10 branches. Rs and MA fused for a short distance. CuA deeply forked. Anals simple except for marginal branches (after Riek, 1955: 677). Triassic, Australia; Jurassic, U.K.

Archeosmylus complexus sp. nov.
Figs 1, 3

DIAGNOSIS. As genus: each branch of the posterior radial sector divides well before the wing margin.

NAME. 'Complicated'.

DESCRIPTION. Sc and R join one-third from wing apex. Rs with 10 branches, posterior ones divide one-third from wing margin. Trichosors present. Broad subcostal area with numerous veinlets, many branched, R curves down below wing margin towards apex. Rs bifurcated at apex, 10 branches roughly parallel from Rs to wing margin; anterior branches simple, posterior ones branched one-third from margin with short marginal forks. Base of wing missing, MA and MP separate near base but may join together with base of R (area indistinct). Cu incomplete. Anal veins distinct. Few cross-veins preserved though some traces of them present.

MATERIAL. **Holotype**: I.11412, near Dumbleton, Gloucestershire; Brodie colln, 1896. Upper Lias. Dimensions: 9 × 4·5 mm; estimated wing length 9·5–10 mm. Paratype: I.3315, Alderton Hill, Gloucestershire; Slatter colln, 1898. Upper Lias. Other material: I.64664, Wainlode, Gloucestershire; Jarzembowski colln, 1984. Upper Trias.

DISCUSSION. This species has a broad costal area with long parallel veinlets. It is separated from *A. alysius* sp. nov. (below) by its size and by division of the branches of the posterior radial sector. There are other broadly similar species which have been described in the Proberothidae by Riek but these have series of well-preserved cross-veins. *A. complexus* resembles *A. stigmaticus* Riek (1955) from the Triassic of Australia, but the latter had only 9 branches from the radial sector. However, the poor state of preservation is such that a close comparison between these species is not practicable.

The diagnoses given by Riek and Martynova can be applied to a number of similar but probably unrelated fossils, particularly when the specimens are incomplete. The specimen from Wainlode is only provisionally placed here; it shows two overlying wings of the correct size for this species but the details of the costal, subcostal and radial areas are obscure.

Archeosmylus alysius sp. nov.
Figs 2, 4

DIAGNOSIS. As genus. Sc and R join one-third from apex of wing. Rs with 7–8 branches. Most branches of Rs with only small apical forks.

NAME. Arbitrary combination of letters.

DESCRIPTION. Costal margin with numerous veinlets. Trichosors present. R curves round below wing apex. Rs with 7–8 branches, with only small apical branches on wing margin. MP arises near base of MA; latter has two long branches. Cu with several branches. Head flattened anteriorly, broader than long. Head, prothorax and abdomen and part of hindwing preserved but with few details.

MATERIAL. **Holotype**: I.3318, Alderton Hill, Gloucestershire; Slatter colln, 1896. Upper Lias, part and counterpart. Dimensions: wing 4·3 mm (incomplete, estimated 5–5·5 mm). Head to tip of abdomen, 3 mm. Abdomen 2·5 mm. Paratypes: I.11416, near Dumbleton, Gloucestershire; Brodie colln, 1898. Upper Lias. I.11433, same data. Other material (incomplete, tentatively placed in this species): I.11281, Alderton, Gloucestershire; Brodie colln, 1898. Upper Lias. I.11375, Dumbleton, Gloucestershire; Brodie colln, 1898. Upper Lias. I.11402, same data.

DISCUSSION. One of the additional specimens has two overlying wings plus an impression of the shape of the head and thorax, but few details are preserved. All the specimens have a wing

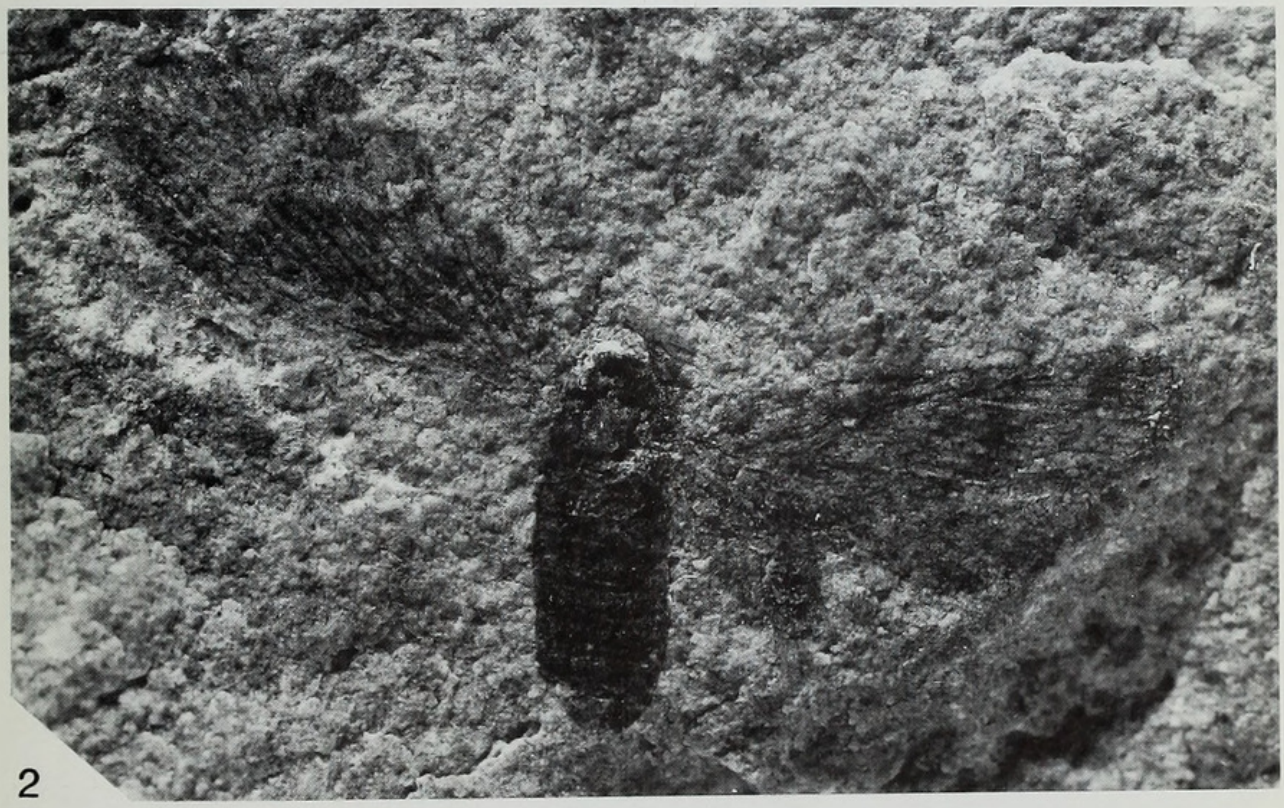


Fig. 1 *Archeosmylus complexus* sp. nov. **Holotype**, I.11412. Upper Lias, Gloucestershire (9 mm).
Fig. 2 *Archeosmylus alysius* sp. nov. **Holotype**, I.3318. Upper Lias, Gloucestershire (4·3 mm).

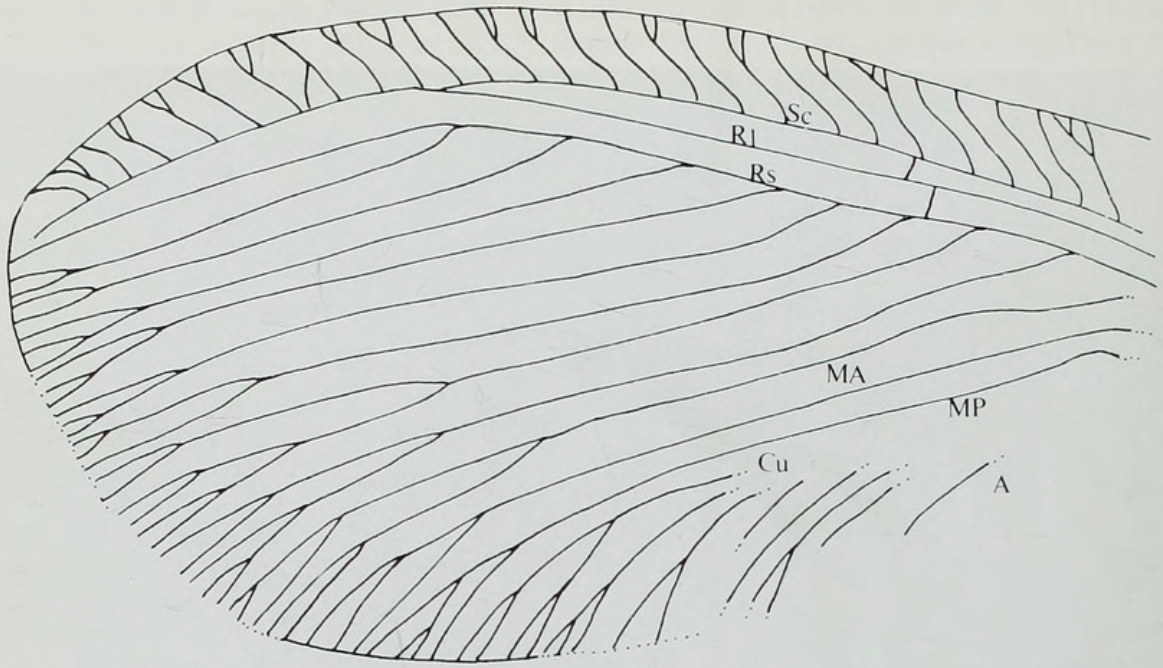


Fig. 3 *Archeosmylus complexus* sp. nov. Venation. A—Anal veins, Cu—Cubital vein, MA—Anterior medial, MP—Post medial, Sc—Subcostal, R1—First radial, Rs—Radial sector.

length of 4–5 mm (wingspan estimated 9–11 mm) and are smaller than the other neuropterous insects from the Mesozoic. Generally the branches from the radial sector remain unbranched themselves until they reach the margin where there are short marginal forks.

I.11281 has the base of the wing overlaid by a fragment of (?) hindwing. This effectively hides the subcostal vein towards the base and makes the specimen look very like a Recent species of *Hemerobius*. However, the base of the costal area of the wing has finely preserved hairs, unlike any of the other specimens, and there appears to be a change in the texture between the outer part of the wing with veinlets and the basal part of the costal area. Thus I think that the subcostal vein was probably present in this specimen, but is obscured. It is provisionally placed in *A. alysius* on the remaining characters and size of the wing.

Family **MESOPOLYSTOECHOTIDAE** Martynova, 1962

DIAGNOSIS. Apex of forewing tending to a point. Sc and R1 gradually merging. Branches of Rs without long forks. MP with two branches (Martynova 1962). Upper Triassic–Jurassic, Europe, Asia.

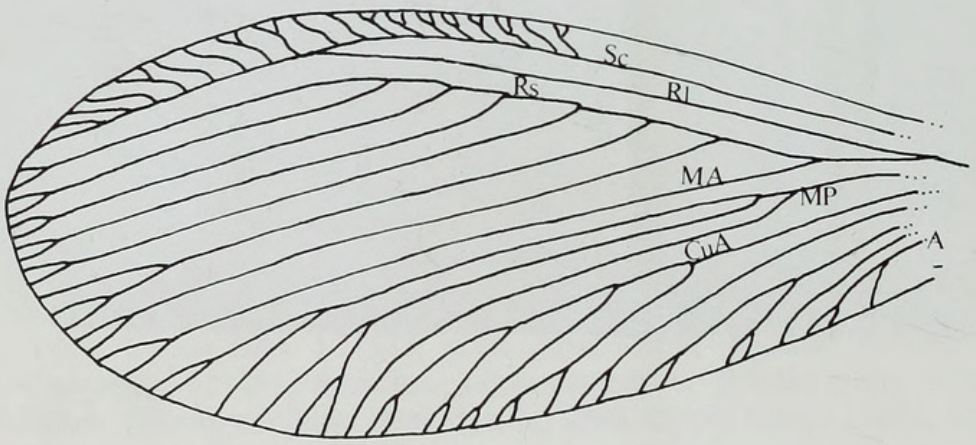


Fig. 4 *Archeosmylus alysius* sp. nov. Venation. A—Anal, CuA—Anterior cubital, MA—Anterior medial, MP—Post medial, Sc—Subcostal, R1—First radial, Rs—Radial sector.

DISCUSSION. This family was erected for the genus *Mesopolystoechus* Martynov, 1937, from the Lower Jurassic of central Asia.

Genus **MEGAPOLYSTOECHUS** Tillyard, 1933

1933 *Megapolystoechus* Tillyard: 12, fig. 1.
1962 *Megapolystoechus* Tillyard; Martynova: 262 (Hemerobiidea, *incertae sedis*).

TYPE SPECIES. *Megapolystoechus magnificus* Tillyard, 1933, by original designation.

DIAGNOSIS. Sc and R merge gradually towards the apex of the wing. Branches of Rs without

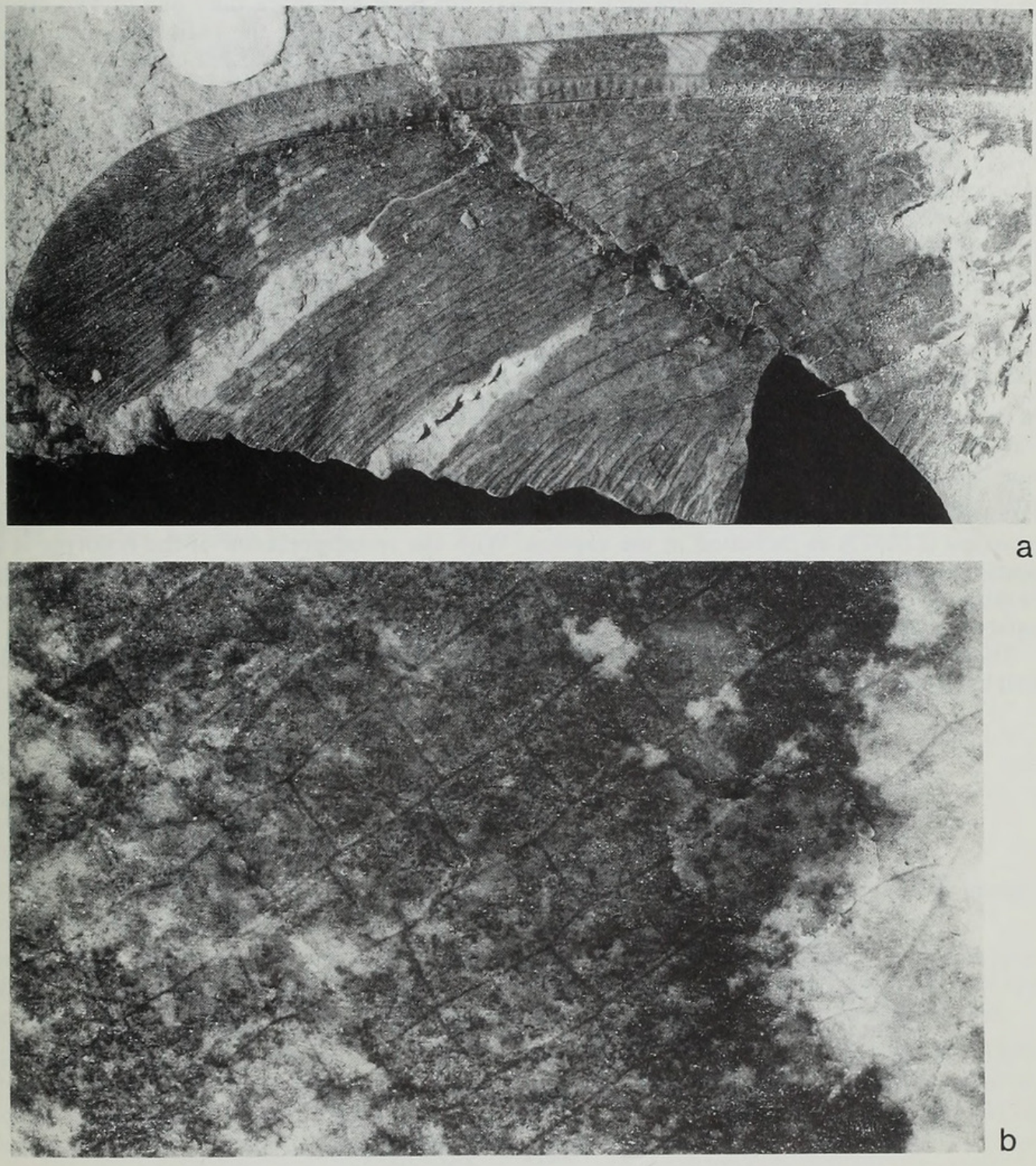


Fig. 5 *Megapolystoechus magnificus* Tillyard. Holotype, I.11027. Upper Trias, Worcestershire (30 mm). a, whole wing. b, wing, details of median and cubital areas.

long forks, Rs with numerous (at least 24) parallel branches. Many cross-veins on the branches of Rs, especially towards the centre of the wing.

DISCUSSION. In the original description and figure of the single species in this genus, Tillyard indicated that the subcostal and radial veins ran separately to the apex of the wing. Re-examination of the type specimen shows that only R runs to the wing apex while Sc curves towards R, joining it before the apex of the wing.

Tillyard's original description contained a number of other errors, apart from his interpretation of the anterior veins; see discussion below. The membrane was very wrinkled and on preservation these wrinkles gave the impression of many cross-veins, especially in the subcostal area; this area and the radial area have in reality nothing like as many cross-veins as indicated by Tillyard (1933: fig. 1). The subcostal area may not have had more than one or two cross-veins but the incomplete preservation makes interpretation difficult: the radial area may have had two or three cross-veins, possibly a few more, but not the 30–40 indicated by Tillyard. Upper Triassic–Upper Lias, U.K.

Megapolystoechus magnificus Tillyard, 1933
Figs 5a, 5b, 6

1933 *M. magnificus* Tillyard: 12.

DIAGNOSIS. As genus.

DESCRIPTION. Incomplete forewing, membrane dark. Branches of Rs may divide several times with narrow, U-shaped, branches to wing margin. R curves round below wing apex. Branches of Rs virtually parallel. Cross-veins preserved near centre of wing, not stepped. Subcostal and radial areas together equal in width to costal area.

MATERIAL. Holotype: I.11027, Strensham, Worcestershire; Brodie colln, 1898. Upper Trias. Paratype: I.10523, data as holotype. Other material: 1983/755, Aust, Gloucestershire; in Yorkshire Museum. Upper Trias.

DISCUSSION. The specimen illustrated by Tillyard (1933: fig. 1) is the holotype (I.11027), not the paratype (I.10523) as indicated in the caption. With the reinterpretation of the holotype it is possible to compare the genus with *Mesopolystoechus* Martynov, from which it differs in the number of cross-veins. There are two gradate series in *Mesopolystoechus* but these are alternately arranged, and more numerous, in *Megapolystoechus*.

Tillyard's estimated wing length of 37 mm may have been rather conservative and it could well have been 40 mm or more.

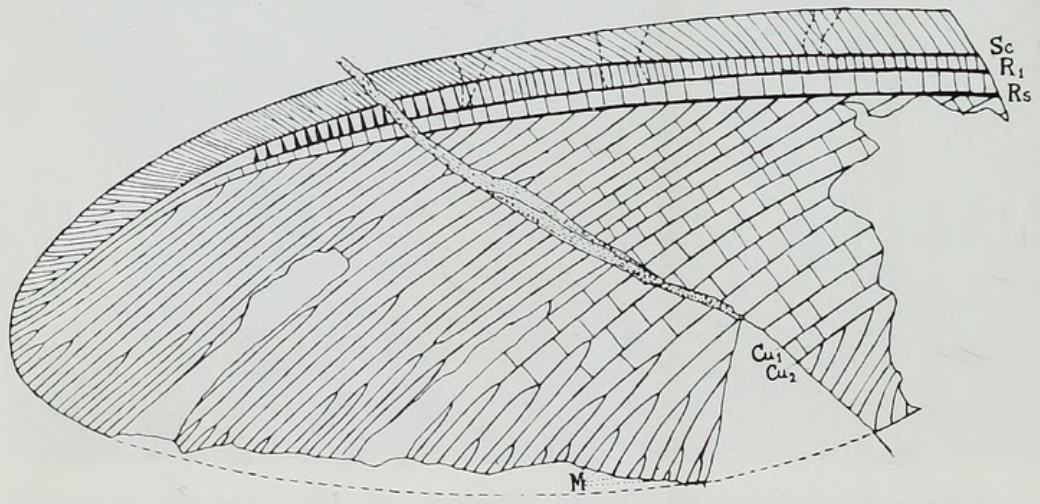


Fig. 6 *Megapolystoechus magnificus* Tillyard. Venation, from Tillyard, 1933: fig. 1.

Superfamily **HEMEROBIOIDEA**, brown lacewings

In all the remaining species the subcostal and radial veins run separately to the wing margin. There are 13 families (Martynova 1962) in the superfamily, ranging widely in size and shape. In Britain, examples of the families Brongniartiellidae, Kalligrammatidae and Psychopsidae have been found in the Lower Cretaceous (Wealden) deposits (Jarzembowski 1984). The superfamily is known from the Permian onwards and includes many living species.

Family **BRONGNIARTIELLIDAE** Martynova, 1949

DIAGNOSIS. Forewing with 12–16 branches to Rs. Wings roughly triangular. MP divides at base of wing, CuA and CuP often with many branches. Few cross-veins (Martynova 1962). Jurassic, Europe.

DISCUSSION. This family, together with the Psychopsidae and Kalligrammatidae, includes species where the relatively large wing size has resulted in an increased number of veins. The possession of large numbers of veins is generally considered a primitive feature (e.g. Imms 1970), presumably because many of the earliest known insects in the Carboniferous had many veins. It is difficult to see how the complicated venation in the three families mentioned above can be derived from the early Permian Neuroptera, or even from the Carboniferous insects, without considering it a specialization, since the venation is not based on the more typical reticulate venation of many Carboniferous insects. Presumably the more complicated venation of these large Neuroptera can be considered as an adaptation of the basic neuropterous venation plan to the structural needs of larger-sized wings.

Genus ***ACTINOPHLEBIA*** Handlirsch, 1906

1906 *Actinophlebia* Handlirsch: 476.

TYPE SPECIES. *Pterinoblattina megapolitana* Geinitz, by monotypy.

DIAGNOSIS. Forewing subtriangular with numerous costal veinlets. Sc, R and Rs close together, particularly below the pterostigma but running separately to the apex of the wing. Rs with 12–16 branches. Jurassic, Europe.

DISCUSSION. Martynova (1962) transferred this genus to the Brongniartiellidae from the Prohemerobiidae where it had been placed by Handlirsch.

Actinophlebia intermixta (Scudder 1885)
Figs 7, 8

1885 *Pterinoblattina intermixta* Scudder: 107.
1886 *Pterinoblattina intermixta* Scudder; Scudder: 471; pl. 48, fig. 9.
1890 *Pterinoblattina intermixta* Scudder; Scudder: 363; pl. 22, fig. 9.
1906 *Actinophlebia intermixta* (Scudder) Handlirsch: 476.
1933 *Actinophlebia anglicana* Tillyard: 14, fig. 2 (syn. n.).
1939 *Actinophlebia intermedia* (*sic*) (Scudder); Handlirsch: 75.

DIAGNOSIS. As type species of the genus, but smaller and with straight terminal wing margin and sigmoidally waved vein Cu (Tillyard 1933: 15).

DESCRIPTION. Forewing, Sc and R run close together along most of the wing but do not join. Many costal veinlets branched. Anal veins run parallel to hind margin for the first part of the length, ending with short branches on the hind margin. Both Rs and M have many branches.

MATERIAL. Holotype (of *intermixta*): I.3577, Alderton, Gloucestershire; Brodie colln, 1898. Upper Lias. Dimensions: forewing, 11–12 mm × 5·5 mm. Other material: I.11346, near Dumbleton, Gloucestershire; Brodie colln, 1898. Upper Lias (holotype, *anglicana*). I.11319 and I.1134, Dumbleton, Gloucestershire; Brodie colln, 1898. Upper Lias (paratypes, *anglicana*).

DISCUSSION. Scudder originally described *A. intermixta* as a cockroach but its neuropterous affinities were recognized by Handlirsch (1906). The outer (terminal) margin of the forewing

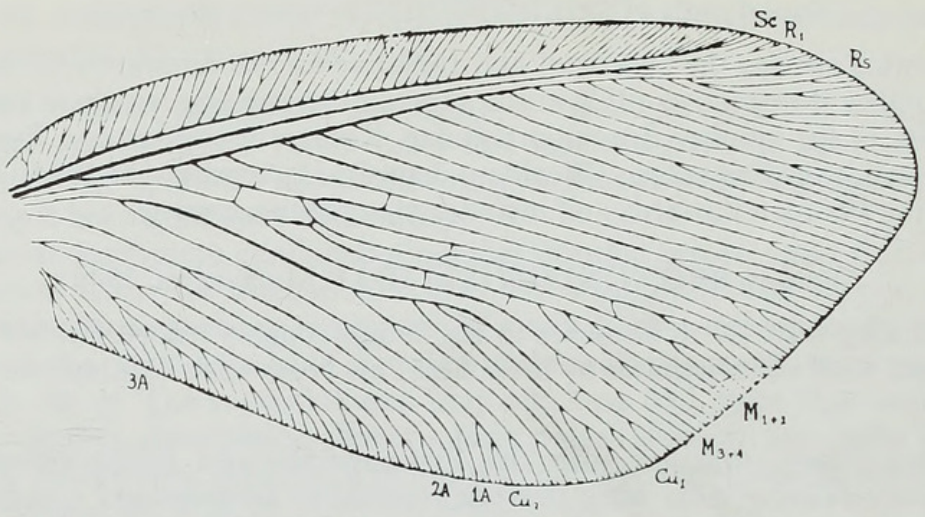


Fig. 7 *Actinophlebia intermixta* (Scudder). Venation, from Tillyard, 1933: fig. 2 (illustrated as *A. anglicana* Tillyard).

subtends an obtuse angle with the hind margin of the wing, which tends to have a pointed apex. Some trichosors are present in all the specimens but are not clearly visible all round the wing. The hindwing and the rest of the body are unknown.

Genus ***PTERINOBLATTINA*** Scudder, 1885

1885 *Pterinoblattina* Scudder: 105.
1886 *Pterinoblattina* Scudder: 486; pl. 22, fig. 7.
1890 *Pterinoblattina* Scudder: 360.
1906 *Pterinoblattina* Scudder; Handlirsch: 607.
1962 *Pterinoblattina* Scudder; Martynova: 279.

TYPE SPECIES. *Pterinoblatinna pluma* (Giebel), by subsequent designation by Handlirsch, 1906: 607.

DISCUSSION. *Pterinoblattina* was described by Scudder as a genus of Blattodea (cockroaches) but was transferred to the Neuroptera by Handlirsch (1906). This was followed by Martynova (1962) who placed the genus in the family Brongniartiellidae. Scudder's figure of the type species (1886: pl. 22, fig. 7) is accurate and examination of the specimen shows that the subcostal runs close to the first radial vein, particularly towards the apex of the wing, but then appears to stop and cannot be traced further forwards. It is probable that it curves down slightly but it does not appear to fuse with the radial vein. From the evidence available the genus is best left in the Brongniartiellidae.

Pterinoblattina pluma (Giebel 1856)
Fig. 9

1854 (unnamed) Westwood: 394; pl. 15, fig. 14.
1856 *Blatta pluma* Giebel: 322.
1885 *Pterinoblattina pluma* (Giebel) Scudder: 105.
1886 *Pterinoblattina pluma* (Giebel); Scudder: 469; pl. 48, figs 7, 8.
1890 *Pterinoblattina pluma* (Giebel); Scudder: 361; pl. 22, figs 7, 8.
1906 *Pterinoblattina pluma* (Giebel); Handlirsch: 607.

DIAGNOSIS. Sc ends abruptly, probably not joining R. Rs with 8–10 branches, each branch dividing either near or before the centre of the wing, producing some 20–30 marginal branches. Broad costal area, veinlets mostly unbranched, numerous, with fine, stepped cross-veins.

DESCRIPTION. Incomplete forewing. Probably slightly shrunken on preservation since all longitudinal veins are raised slightly. Very broad costal area with close, parallel, apparently

unbranched veinlets. Cross-veins present, slightly stepped, on these veinlets. Many of the branches from the Rs divide close to their point of origin, producing rows of parallel veins to the wing margin. Anal area not preserved.

HOLOTYPE. I.3968, Durdlestone Bay, Dorset: Brodie colln, 1898. Lower Cretaceous (Durlston formation). Dimensions: 12 mm (estimated wing length, 14 mm).

DISCUSSION. The specimen is preserved on a small piece of rock with several other insect fossils.

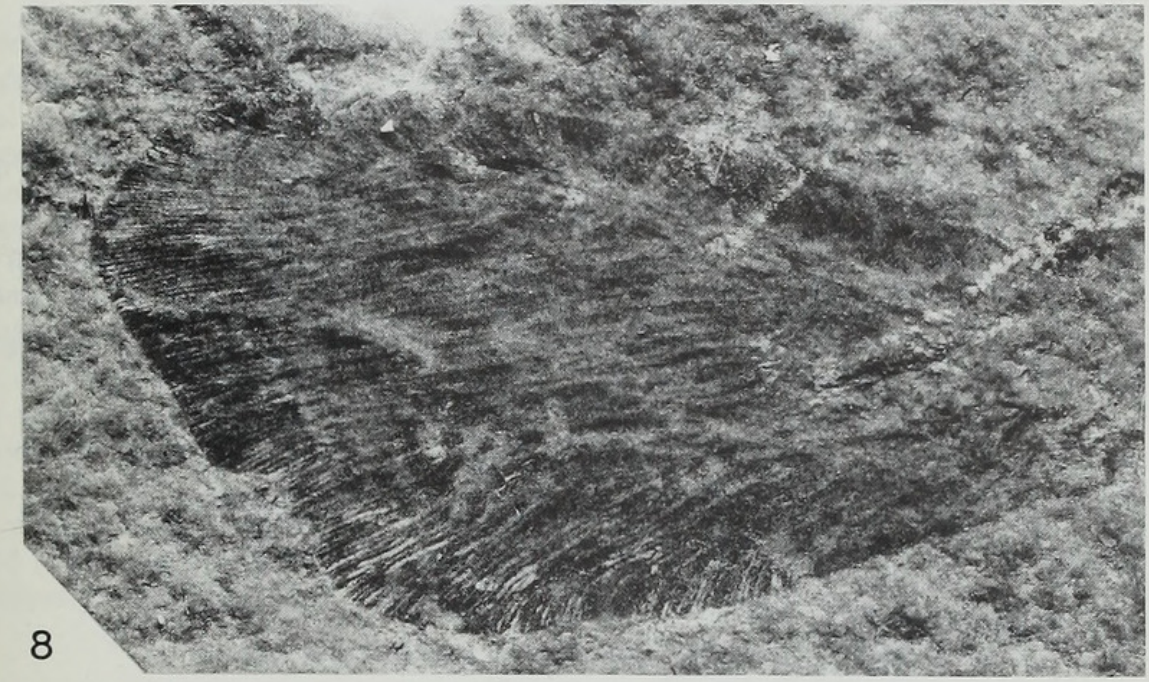


Fig. 8 *Actinophlebia intermixta* (Scudder). Holotype, I.3577. Upper Lias, Gloucestershire (11 mm).
Fig. 9 *Pterinoblattina pluma* (Giebel). Holotype, I.3968. Lower Cretaceous, Dorset (12 mm).

P. pluma differs from *Actinophlebia* in the extensive branching of the radial sector branches close to their point of origin. The large costal area has apparently unbranched veinlets on which there are some cross-veins.

Pterinoblattina penna Scudder 1885
Fig. 10

1885 *Pterinoblattina penna* Scudder: Scudder: 106 (Blattodea).
1886 *Pterinoblattina penna* Scudder: 470; pl. 48, fig. 14.
1890 *Pterinoblattina penna* Scudder: 361; pl. 22, fig. 14.
1906 *Pterinoblattina penna* Scudder; Handlirsch: 608 (Neuroptera).

DIAGNOSIS (from illustration). Large costal area with branched veins. Sc and R close (it is difficult to see in the illustration if they join); Scudder wrote that they 'approach each other very gradually'. Rs has about 18 branches.

HOLOTYPE. I.12324, Durdlestone Bay, Dorset; Brodie colln (specimen not traced). Purbeck. Dimensions: 13 mm × 9 mm, estimated wing length 15 mm.

DISCUSSION. This species is retained in the genus *Pterinoblattina* pending examination of the holotype. There are, however, some basic differences between Scudder's figure of *P. penna* and *P. pluma*; for example, the figure shows many more branches on the radial sector vein and that the costal veinlets are clearly branched.

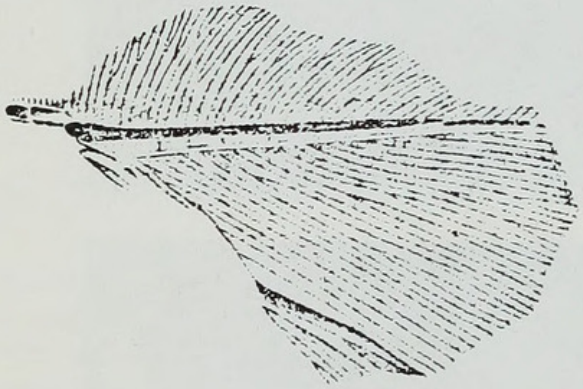


Fig. 10 *Pterinoblattina penna* Scudder. Venation, from Scudder, 1886: fig. 14.

Family **KALLIGRAMMATIDAE** Handlirsch, 1906

This is a group of large (wingspan 80–200 mm) neuropterous insects in which the hind wing is narrower than the much-enlarged forewing. The costal area is twice as wide as the subcostal and radial areas together. Cross-veins are usually numerous and a large eye-spot is often present on the forewing. Apical branches of MA form rows in front of MP, running to the outer (terminal) margin.

Genus ***PARACTINOPHLEBIA*** Handlirsch, 1906

1906 *Paractinophlebia* Handlirsch: 477.

TYPE SPECIES. *Pterinoblattina curtisii* Scudder, 1886, by monotypy.

DISCUSSION. This genus was proposed by Handlirsch for an incomplete forewing, described by Scudder as a cockroach. There is insufficient preserved to decide on its affinities within the Neuroptera and it is only transferred provisionally to the Kalligrammatidae on grounds of size and arrangement of the few preserved veins. No significant definition of this monotypic genus, based on the single incomplete specimen, can be given.

Paractinophlebia curtisii (Scudder 1886)
Fig. 12

1886 *Pterinoblattina curtisii* Scudder: 471; table 48, fig. 16.
1890 *Pterinoblattina curtisii* Scudder: 363; pl. 22, fig. 16.
1906 *Paractinophlebia curtisii* (Scudder); Handlirsch: 477.
1939 *Paractinophlebia curtisii* (Scudder); Handlirsch: pl. 6, fig. 115.

DESCRIPTION. (Wing too incomplete for diagnosis). Forewing, small apical part of R and Sc preserved, running close together. All radial veins branch near wing margin, actual margin not preserved. Rs with many parallel veins, cross-veins numerous.

HOLOTYPE. I.3585, Alderton, Gloucestershire; Brodie colln, 1898. Upper Lias. Dimensions: Wing 25 mm × 13 mm, incomplete, estimated wing length 35–40 mm.

DISCUSSION. This is placed in the Kalligrammatidae because of its size and the numerous parallel veins with cross-veins. These are regarded as diagnostic and are used to separate the Kalligrammatidae from the Psychopsidae. It differs from *Megapolystoechus* Tillyard in the main longitudinal veins which run more towards the outer (terminal) margin rather than the posterior margin as they do in *Megapolystoechus*.

Family **PROHEMEROBIIDAE** Handlirsch, 1906

Although Tillyard suggested that this family was characterized by a large number of branches on the radial sector ('immense development of parallel branches', Tillyard, 1933: 11) this does not fit the original concept proposed by Handlirsch (1906). Tillyard placed genera in Prohemerobiidae where there were 20–27 branches on the radial sector, whereas in Handlirsch's original description, and his later usage in 1939, only species with 7–11 branches on the radial sector were included. Martynova (1962) recognized this and removed the genera placed by Tillyard (1933) in Prohemerobiidae. The original definition proposed by Handlirsch is used here with slight modification.

Genus ***PROHEMEROBIUS*** Handlirsch, 1906

1906 *Prohemerobius* Handlirsch: 474.

TYPE SPECIES. *Prohemerobius dilaroides* Handlirsch, here designated. Upper Lias. Germany.

DIAGNOSIS. Forewing rounded, not triangular in outline. Sc free from R, reaching nearly to apex of wing. R branched near apex. Rs with 6–10 parallel branches. Branches of Rs divide near wing margin; posterior branches of Rs sometimes with forks one-third from wing margin. M close to (? joins) R. MP usually forked. Cu divided, often with long CuP. Anal veins roughly parallel, curve towards wing margin. Jurassic, Europe.

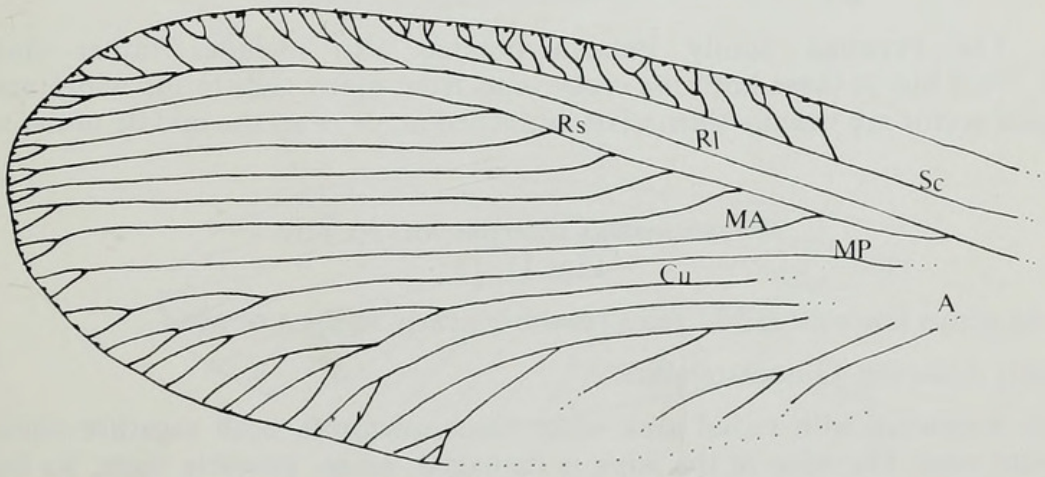
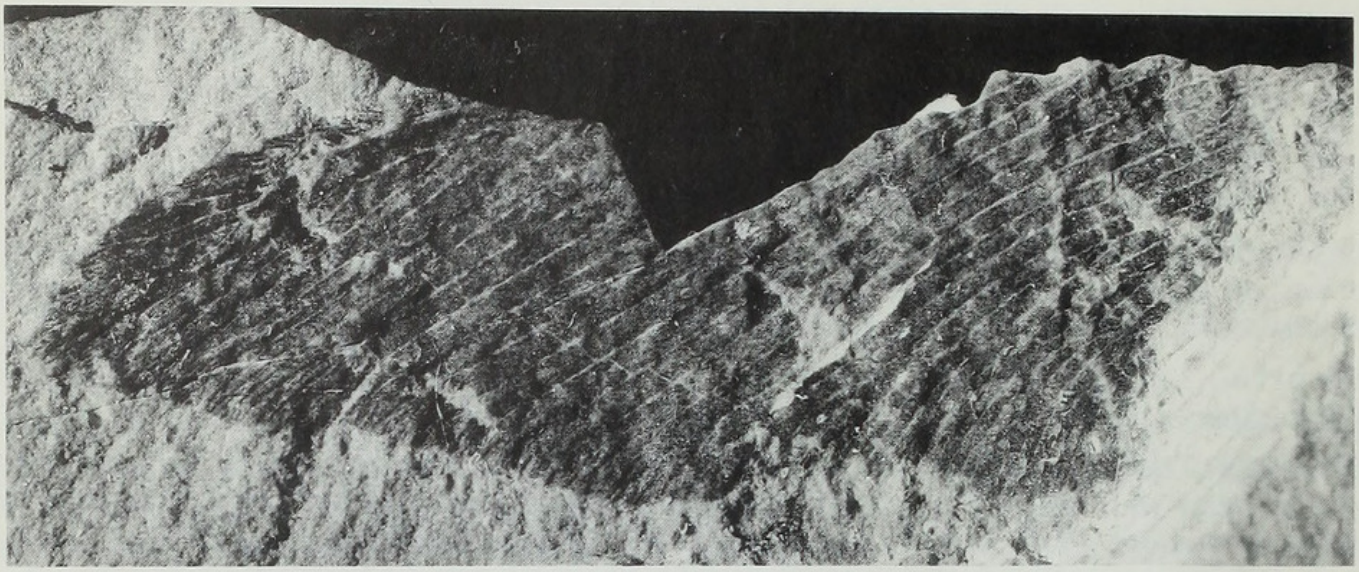


Fig. 11 *Prohemerobius aldertonensis* sp. nov. Venation. A—Anal, Cu—Cubital, MA—Anterior medial, MP—Post medial, Sc—Subcostal, R1—First radial, Rs—Radial sector.



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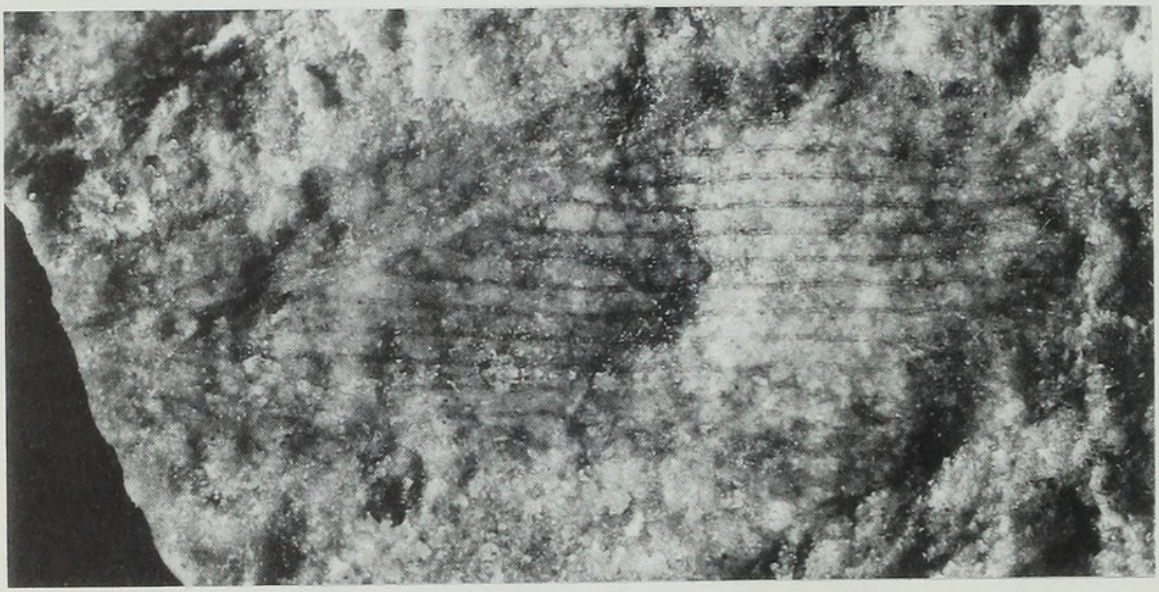

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Fig. 12 *Paractinophlebia curtisii* (Scudder). Holotype, I.3585. Upper Lias, Gloucestershire (25 mm).
Fig. 13 *Prohemerobius aldertonensis* sp. nov. **Holotype**, I.11304. Upper Lias, Gloucestershire (4.7 mm).

DISCUSSION. The Permian family Palaemerobiidae also includes rather small species (Martynova 1962) but in these both the cross-veins from many cells in the wings and branches from the radial sector are usually themselves branched at, or near, the middle of the wing.

Prohemerobius aldertonensis sp. nov.
Figs 11, 13

DIAGNOSIS. As genus but with radial veins reaching nearly to apex of wing.

NAME. Locality Alderton, Gloucestershire.

DESCRIPTION. Forewing with radial area wider than subcostal, both together about equal to width of costal area. The base of the wing is damaged; seven, possibly eight, Rs branches. M branched, possibly with short unbranched second cubital. Anal veins obscured. Trichosors present.

HOLOTYPE. I.11304, Alderton, Gloucestershire; Brodie colln, 1898. Upper Lias. Dimensions: 4·7 mm × 1·9 mm.

DISCUSSION. This species has fewer branches on the radial sector than the species of *Prohemerobius* described by Handlirsch (1906, 1939) or Bode (1953) from the Upper Lias of Germany; otherwise the venation is broadly similar.

Family **PSYCHOPSIDAE** Handlirsch, 1906

A single forewing of a psychopsid has been identified in a collection of Wealden (Lower Cretaceous) insects (Jarzembowski 1984: fig. 31).

MATERIAL. In.64632, Clockhouse Pit, near Dorking, Surrey. Weald Clay. Dimensions: wing 32 mm.

Order **RAPHIDIOPTERA**, snakeflies

Two specimens were found in the Lower Lias of Dorset (Whalley 1985) and one from the Lower Cretaceous of Surrey (Jarzembowski 1984: fig. 30).

Family **MESORAPHIDIIDAE** Martynov, 1925

Genus ***MESORAPHIDIA*** Martynov, 1925

Mesoraphidia sp.

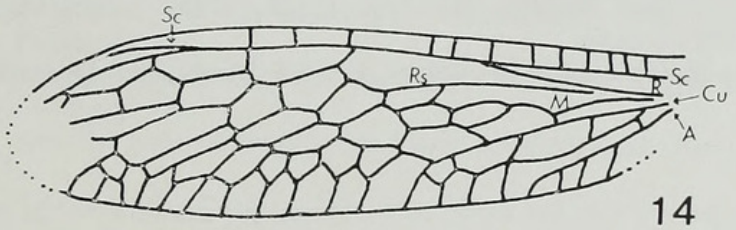
1984 Mesoraphididae Jarzembowski: 82; fig. 30 (unnamed).

MATERIAL. In.64633, near Dorking, Surrey. Lower Cretaceous. Dimensions: wing 11 mm.

Mesoraphidia confusa (Whalley 1985)
Figs 15, 16

1985 *Metaraphidia confusa* Whalley: 148; figs 44, 45.

HOLOTYPE. GSM 117552, Charmouth, Dorset; in British Geological Survey colln. Lower Jurassic. Dimensions: wing 14·5 × 4·8 mm.



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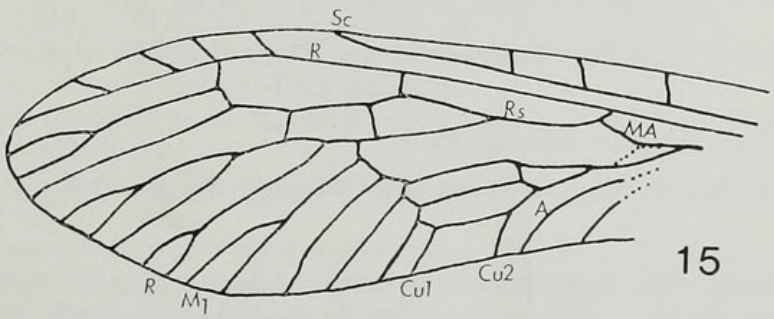

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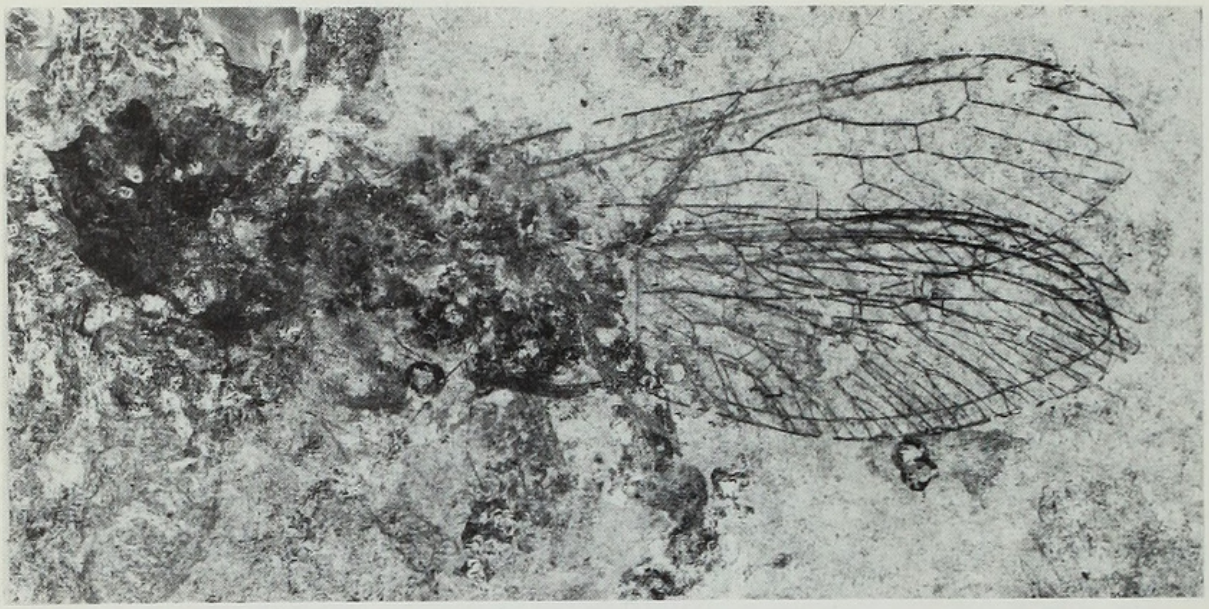
Fig. 14 *Priscaenigma obtusa* Whalley. Venation.
Fig. 15 *Metaraphidia confusa* Whalley. Venation.



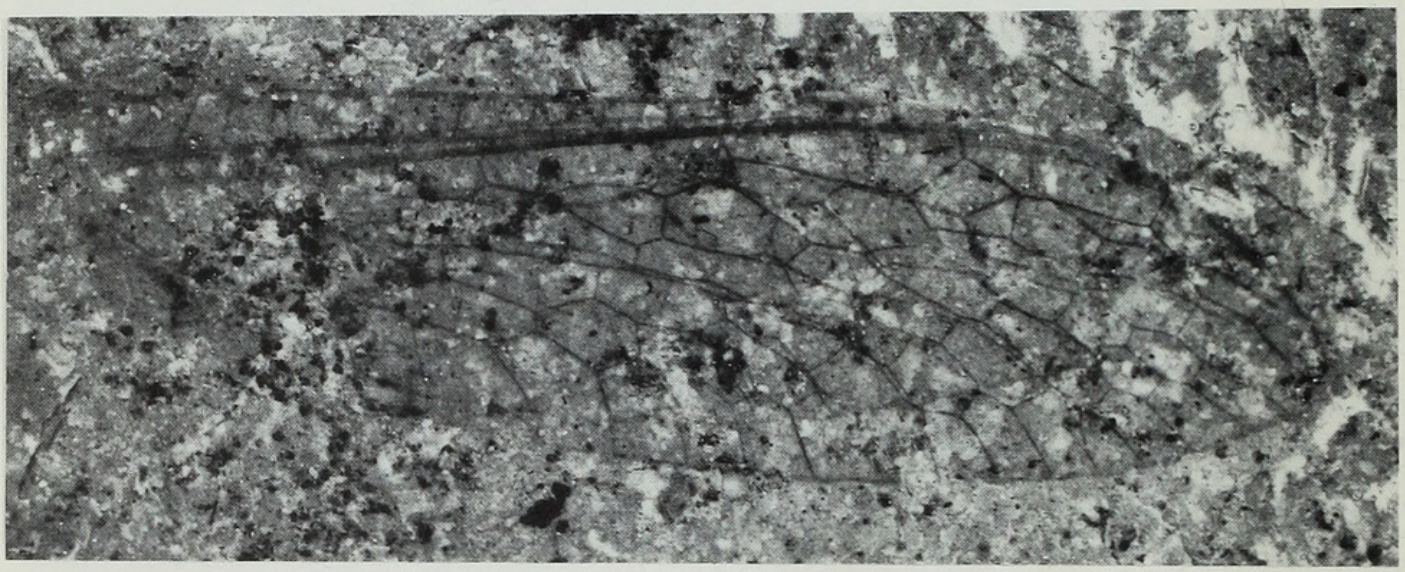


Fig. 16 *Metaraphidia confusa* Whalley. Holotype, GSM 117552. Lower Lias, Dorset (14·5 mm), in British Geological Survey colln.
Fig. 17 *Priscaenigma obtusa* Whalley. Holotype, I.53898. Lower Lias, Dorset (12·6 mm).

Family **BAISSOPTERIDAE** Martynova, 1961

Genus ***PRISCAENIGMA*** Whalley, 1985

Priscaenigma obtusa Whalley 1985
Figs 14, 17

1985 *Priscaenigma obtusa* Whalley: 148; figs 43, 46.

HOLOTYPE. In.53898, Black Ven, Charmouth, Dorset. Lower Jurassic. Dimensions: wing 12·6 mm.

DISCUSSION. Some doubt was expressed in the original description of the correct family for this species. It differs from the type of Baissopteridae in the number of cells in the median area and has longer subcostal veins and a longer radial cell. Since no further material is available the species is retained in the Baissopteridae.

Acknowledgements

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References

Achtelig, M. & Kristensen, N. P. 1973. A re-examination of the relationships of the Raphidioptera (Insecta). *Z. Zool. Syst. EvolForsch.*, Frankfurt a.M., **11:** 268–274.

Bode, A. 1953. Die Insektenfauna des ostniedersächsischen Oberen Lias. *Palaeontographica*, Stuttgart, (A) **103** (1–4): 1–375, pls 1–15.

Boudreaux, H. B. 1981. About the Panorpoid complex. *Ann. ent. Soc. Am.*, Washington, **74:** 155–157.

Brodie, P. B. 1845. *A history of the fossil insects in the Secondary rocks of England.* 130 pp., 11 pls. London.

Giebel, C. G. 1856. *Fauna der Vorwelt mit steter Berücksichtigung der lebenden Thiere*, **2** (1). 511 pp. Leipzig.

Handlirsch, A. 1906–08. *Die fossilen Insekten und die Phylogenie der rezenten Formen.* ix + 1430 pp., 13 tabs, 14 figs, 51 pls. Leipzig.

—— 1939. Neue Untersuchungen über die Fossilen Insekten. 2. *Annln naturh. Mus. Wien* **49:** 1–240, pls 1–16.

Hennig, W. 1981. *Insect phylogeny* (transl. Pont, A. with additional footnotes). xxii + 514 pp. Chichester.

Imms, A. D. 1970. *A general textbook of Entomology* (9th edn, Ed. Richards, O. W. & Davies, R. G.). x + 886 pp. London.

Jarzembowski, E. A. 1980. Fossil insects from the Bembridge Marls, Palaeogene of the Isle of Wight, Southern England. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **33** (4): 237–293, 77 figs.

—— 1984. Early Cretaceous insects from Southern England. *Mod. Geol.*, London, **9:** 71–93, 55 figs, 1 pl.

Kristensen, N. P. 1975. The phylogeny of the Hexapod 'Orders'. A critical review of recent accounts. *Z. Zool. Syst. EvolForsch.*, Frankfurt a.M., **13:** 1–44.

Martynov, A. 1925. To the knowledge of fossil insects from Jurassic beds in Turkestan. 1. Raphidioptera. *Izv. ross. Akad. Nauk*, Leningrad, (6) **19** (6–8): 233–246.

—— 1937. Liasovÿe nasekomÿe Shuraba i Kizil-Kii [Liassic insects from Shurab and Kisyl-Kiya]. *Trudÿ paleont. Inst.*, Moscow, **7** (1): 7–180, 5 pls.

Martynova, O. M. 1949. Mezozoiskie setchatokrÿlÿe (Neuroptera) i ikh znachenie dla ponimaniya i sistematikh otryada. *Trudÿ paleont. Inst.*, Moscow & Leningrad, **20:** 150–170.

—— 1962. [Arthropoda, Tracheata and Chelicerata]. *In* Rohdendorf, B. B. (ed.), *Osnovÿ Paleontologii*, Moscow, **9.** 560 pp. [In Russian].

Riek, E. F. 1953. Fossil Neuropteroid insects from the Upper Permian of New South Wales. *Rec. Aust. Mus.*, Sydney, **23:** 55–87, 67 figs, 1 pl.

—— 1955. Fossil insects from the Triassic beds at Mt Crosby, Queensland. *Aust. J. Zool.*, Melbourne, **3** (4): 654–691.

Scudder, S. H. 1885. Notes on Mesozoic Cockroaches. *Proc. Acad. nat. Sci. Philad.*, **1885** (2): 105–115.

—— 1886. A review of Mesozoic Cockroaches. *Mem. Boston Soc. nat. Hist.* **3:** 439–485.

—— 1890. *The fossil insects of North America, with notes on European species*, **1** (Pretertiary). 455 pp., 35 pls. New York.

Tillyard, R. J. 1918–19. The Panorpoid Complex. 1, Introduction. *Proc. Linn. Soc. N.S.W.*, Sydney, **43:** 265–319, 16 figs, 2 pls (1918). 3, Wing venation. *Loc. cit.* **44:** 533–718 (1919).

—— 1922. Some new Permian insects from Belmont, New South Wales, in the collection of Mr John Mitchell. *Proc. Linn. Soc. N.S.W.*, Sydney, **47:** 279–292.

—— 1933. The Panorpoid Complex in the British Rhaetic and Lias. *Fossil Insects* **3.** 79 pp., 1 pl. London, British Museum (Natural History).

Tjeder, B. 1969. Neuroptera Plannipennia, the Lacewings of Southern Africa. 2. Family Berothidae. *S. Afr. anim. Life*, Stockholm, **6:** 256–314.

Westwood, J. O. 1854. Contributions to fossil Entomology. *Q. Jl geol. Soc.*, London, **10:** 378–396.

Whalley, P. E. S. 1980. Neuroptera (Insecta) in amber from the Lower Cretaceous of Lebanon. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **33** (2): 157–164, 6 figs, 1 pl.

—— 1985. The systematics and palaeogeography of the Lower Jurassic Insects of Dorset, England. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **39** (3): 107–189.