NEUROPTERIDA OF THE LOWER CRETACEOUS OF SOUTHERN ENGLAND, WITH A STUDY ON FOSSIL AND EXTANT RAPHIDIOPTERA

A thesis submitted to The University of Manchester for the degree of PhD in the Faculty of Engineering and Physical Sciences

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ABSTRACT

The study of Neuropterida from the Lower Cretaceous Purbeck Limestone Group and Wealden Supergroup of southern England has shown that 13 families, 24 genera and 33 species are present. The majority of the taxa described are new to science with the exception of six genera and four species, which are redescribed. The Purbeck fauna consists of the families Kalligrammatidae, Psychopsidae, Osmyliidae, Prohemerobiidae, Chrysopidae, ?Hemerobiidae, Berothidae, Nymphidae, Mesoraphidiidae and one incertae sedis family. The Wealden contains Kalligrammatidae, Psychopsidae, Osmyliidae, Ithonidae, Mesoraphidiidae and two incertae sedis families. The psychopsoid families are the most dominant neuropterid in the Purbeck and Wealden neuropterid fauna. The discovery of the families Chrysopidae, ?Hemerobiidae, Osmyliidae, Ithonidae, Berothidae represent the first record in the Mesozoic of Britain. The ithonid also represents the oldest fossil record of that family. Megaloptera have not been found in these deposits. The neuropterids in both deposits would have lived in a distant wooded area based on modern analogues. On death they would have undergone disarticulation, decomposition/sorting and then deposition of wings only in the depositional basin. No body parts have been found associated with any neuropterid from these deposits. The climate change through the English Lower Cretaceous may have affected the neuropterid fauna in size (Raphidioptera) and family turnover (Neuroptera). Biogeographical links have been hinted at with Asia and South America with the occurrence of some of the same genera.

A preliminary key to the fossil raphidiopterans has been presented aiding identification to family and generic level. This is the first time such a key has been presented on fossil Raphidioptera. A cladistic study was undertaken (21 characters and 28 taxa) on the genera of fossil Raphidioptera with the inclusion of extant genera. Fifteen synapomorphies were found, but, relationships are largely unresolved, with few well-supported clades. Baissopteridae and Mesoraphidiidae were found to be paraphyletic. Baissopteridae is basal to all raphidiopterans. Both the key and cladistic study highlighted the need for a major taxonomic revision of fossil raphidiopterans.
Lay Abstract

Over thirty new species of fossil lacewings and snakeflies (insects) have been described from 145-125 million year old rocks from southern England. More species are now known to be present than previously thought and the older rocks in Dorset have yielded a higher number of lacewings than the younger rocks from the south east of England (Kent, Surrey and Sussex). The snakeflies are consistent across the whole of southern England. Fishflies and dobsonflies have yet to be discovered in England at this time. The lacewings and snakeflies would have lived in a distant forested environment far from the place where they were deposited. On death they would have decomposed and disarticulated before being washed into a watercourse. In the watercourse they would have become more disarticulated and at the place of deposition only their wings have been preserved. All of the wings show damage from the transportation process. Between 145-125 million years ago the climate changed from hot and dry to more humid and wet. This change had an effect on the snakeflies, which were smaller in the hot periods, and the lacewings, many of which became extinct when the climate became wetter.

An identification key for fossil snakeflies is presented and a study of the evolutionary relationships within snakeflies has been undertaken. The evolutionary relationships were largely unresolved. This work on fossil snakeflies has highlighted that this group of fossil insects has been poorly described over the years and a revision of the entire group needs to be undertaken before any other evolutionary study is undertaken.
DECLARATION

No portion of the work referred to in this thesis was submitted to support an application towards the obtainment of another degree of this or any other school or institute of learning.

James E. Jepson

2010
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ABOUT THE AUTHOR

As a child I was fascinated by the natural world. This fascination continued throughout my academic life. In 2005 I graduated from the University of Manchester with a B.Sc (Hons) in Geology, after which I found myself in the right place at the right time and ended up deciding to self fund a Ph.D. on neuropterids from the Purbeck and Wealden. A decision that has never been regretted.
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If it be now, 'tis not to come; if it be not to come, it will be now; if it be not now, yet it will come: the readiness is all.

William Shakespeare, from Hamlet (1600-1602)
CHAPTER 1. INTRODUCTION

This chapter gives an introduction to the aims of the project and why studying fossil insects (especially from the Mesozoic) is important.

1.1. The Project

Fossil Neuropterida (Megaloptera, Raphidioptera and Neuroptera) are an understudied group within the Lower Cretaceous rocks of southern England. With regards to Mesozoic British fossil neuropterids, only one major work has been completed on the Jurassic fauna (Whalley 1988). Prior to this study only four families and three species of Neuroptera had been recorded from the Purbeck and Wealden. There were no Megaloptera and only two Raphidioptera recorded, one from the Purbeck and one from the Wealden, which were mentioned but not described (Jarzembowski 1984, 2001; Clifford et al. 1994). After searching through many specimens, often uncatalogued in museum collections, many Neuropterida were discovered. The first aim of the project was to undertake a comprehensive survey of the Neuropterida from these deposits. From this study, the Neuropterida of southern England were able to be tracked across from the Purbeck into the Wealden in terms of evolution and adaptation with regards to the changing environment. This enabled a comparison with other neuropterid faunas from the Lower Cretaceous. There is also a study of the palaeoecology of these insects; how they interact and react to the flora and fauna in each deposit.

The second part of this thesis examines the fossil record of Raphidioptera, which includes an identification key to allow identification of fossil raphidiopterans to family and generic level. A cladistic study incorporating fossil raphidiopterans into a phylogeny with extant representatives; this study was undertaken at generic level. There have been few previous attempts at a cladistic analysis of fossil and extant raphidiopterans but these were not greatly successful (Ren & Hong 1994; Willmann 1994). It is hoped that this study will shed some light on the evolutionary relationships within fossil and extant raphidiopterans, or at least give a good starting point for future research.
1.2. The Importance of Studying Fossil Insects

Insects first appeared in the fossil record in the Devonian. In the Carboniferous winged insects such as the large dragonfly-like *Meganeura* are recorded, while the early members of most modern day Orders are found preserved in the rocks of the Permian and Triassic. The Cretaceous saw the beginnings of a modern biota evolving with many modern families appearing, in fact it has been estimated that over half of the Recent insect families evolved in the Cretaceous (Grimaldi & Engel 2005). The Cretaceous also has the advantage of having many fossil insect sites that have been subjected to fewer Earth processes, e.g. deformation and erosion. Also within the Cretaceous the evolution of the Angiosperms occurred, which had a major effect on insect evolution.

With regards to Neuropterida, the Cretaceous was a very important time. Effectively ‘the Golden Age’ of Neuropterida. Although Neuroptera and Megaloptera evolved in the Permian, and Raphidioptera in the Jurassic, great diversity of families and species was observed in a burst of evolutionary activity in the Mesozoic, particularly the Cretaceous. Therefore, to understand how the modern fauna evolved one needs to look at this all-important time in the evolution of this group. In particular in the Purbeck and Wealden there is a gap in our knowledge of Neuropterida with very little work previously undertaken; this study aims to fill that gap.

With regards to the integration of fossil insects with the extant to create a phylogeny, this is very important to get a fuller picture of the evolutionary history of a group.

1.3. Thesis Layout

This thesis is submitted under the ‘Alternative Format Regulations’, a collection of scientific papers that have been written as a result of the investigation carried out during the past years of the PhD (2005-2010). According to the regulations, the chapters, excluding the introductory and conclusive ones, have to be a paper submitted, published or in preparation.

The thesis is subdivided into two main parts comprising papers published and submitted. All papers were conceived by me. For each paper I carried out the bulk of the work, for example, descriptions, figures and writing the manuscripts. Co-author
contributions are given below. The introductory chapter (chapter 1), literature review (chapter 2) of extant and fossil neuropterids, geological settings, material and methods (chapter 3) precede the two parts. Part one focuses on the neuropterid assemblages of the Purbeck and Wealden: it is mainly a collection of systematic papers, giving an account of which Raphidioptera, Neuroptera and Megaloptera are present. It comprises nine chapters: the first of these chapters (chapter 4) is in collaboration with Drs Vladimir Makarkin (Institute of Biology and Soil Sciences, Vladivostock) and Edmund A. Jarzembowski (Maidstone Museum) on the Neuroptera fauna of the Purbeck. Dr Vladimir Makarkin is a major authority on Neuroptera, especially fossil taxa; his input was to clarify and aid in identification of the specimens, while EAJ helped with the geological setting and environment of the specimens. This paper has been submitted to Palaeontology. The next chapter (chapter 5) is on the Purbeck raphidiopteran fauna, written in collaboration with Drs Robert A. Coram (British fossils) and Edmund A. Jarzembowski. RAC collected the specimen and gave information on the geology of the deposit, EAJ gave general advice on the paper. The paper was published in Cretaceous Research (Jepson et al. 2009b). The next set of chapters are on the Wealden Neuropterida; the chapter (chapter 6) on the palaeodiversity predictions of the Neuroptera of the Wealden was written in collaboration with Dr Dave Penney (University of Manchester). DP gave assistance in implementing his predictive methods previously used on fossil spiders. This paper was published in Palaeogeography, Palaeoclimatology, Palaeoecology (Jepson & Penney 2007). The chapter (chapter 7) on the Neuroptera of the Wealden was written in collaboration with Drs Vladimir Makarkin and Edmund A. Jarzembowski. VN helped in clarifying and identification of the specimens and EAJ helped in the description of Psychopsites rolandi. The paper was published in Cretaceous Research (Jepson et al. 2009a). The next two chapters concentrate on the raphidiopteran fauna. The first of these (chapter 8) describes a new species from the Wealden, written in collaboration with Dr Edmund A. Jarzembowski. EAJ helped with the geological setting and partially with the description. The paper was published in Alavesia (Jepson & Jarzembowski 2008). The next chapter (chapter 9) describes more species from the Wealden in collaboration with Drs Jörg Ansource and Edmund A. Jarzembowski. JA supplied and helped in the identification of the Spanish specimens, EAJ helped with geological setting. The paper is in press in Palaeontology. The next chapter (chapter 10) of this section is on the neuropterid
palaeoecology and palaeoenvironment of the Wealden and Purbeck. This is a sole author work submitted to Palaeogeography, Palaeoclimatology, Palaeoecology. 

Part one ends with a conclusion (chapter 11) and future work (chapter 12) summing up the work completed on the neuropterid fauna of the Lower Cretaceous of southern England.

Part two (chapter 13) concentrates on Raphidioptera, in particular the systematics and evolutionary history of the group. The first section comprises an introduction, literature review which includes an in-depth look at raphidiopteran morphology, previous work on raphidiopteran systematics and evolutionary history. The main part consists of two sections, the first (13.3) being a key to the fossil families and genera of Raphidioptera. This is a sole authored paper, which will be submitted to Zootaxa. The next section (13.4) is a sole author paper on a cladistic analysis on fossil and extant raphidioptera. A discussion, conclusion and ideas for future work summarizes this study on raphidiopteran evolutionary history.
CHAPTER 2. LITERATURE REVIEW

This chapter introduces the Neuropterida: their systematics, life habits, fossil record and geological settings of the Purbeck and Wealden

2.1. What are the Neuropterida?

Neuropterida is a superorder of insects, which includes the Orders Megaloptera, Raphidioptera and Neuroptera (Fig 2.1).

Figure 2.1. Top left: Megaloptera, *Sialis lutaria* from Delamere, UK. (Photograph: Lisa Abbott). Top right: *Subilla confinis*, Belgium (species also found in the UK) (Photograph: J.K. Lindsey). Bottom centre: Neuroptera, *Chrysopa perla*, UK (Photograph: www.glaucus.org.uk).

Neuropterida is a member of the holometabolous insects which are insects that undergo complete metamorphosis (dramatic change from one developmental stage to another); they have a distinct larval, pupal and adult stage (Fig. 2.2) (Aspöck 2002b; Grimaldi & Engel 2005). The larval stage is soft-bodied, wingless and morphologically reduced and the pupal stage is mostly quiescent (inactive) (Grimaldi & Engel 2005). The adults are those individuals which are reproductively mature.
The defining feature of holometabolous insects is the larvae; the immature form is soft-bodied, slender, has six or no thoracic legs and no wing buds (Grimaldi & Engel 2005). The larval head is sclerotized with mandibles, palps, antennae and reduced eyes (or isolated ommatidia (conical structure of a compound eye) separated into stemmata (single facet of a compound eye)). When the insect is in its pupal stage metamorphosis occurs – the majority (or all) of the larval cuticle is replaced by adult cuticle, the new cuticle for legs, eyes, genitalia and wings derived from the imaginal discs (Fig. 2.3). Imaginal discs are specialized epidermal cells (histoblasts) under the cuticle (in neuropteroids the imaginal discs develop in the last larval instar); during the late larval and pupal stages the histoblasts increase and differentiate (Grimaldi & Engel 2005).
Figure 2.3. A schematic drawing showing the position of the imaginal discs (yellow) of the larva of *Drosophila* (Insecta: Diptera). A similar situation occurs in all holometabolous insects including the Neuropterida (redrawn from Grimaldi & Engel 2005 fig. 9.3 p. 334).

The Holometabola account for 85% of all Recent insects (Fig. 2.4) and the feature of complete metamorphosis is considered to be one of the two most important innovations of insect evolution (the other is the development of wings) (Grimaldi & Engel 2005). Holometabola is a considered to be a monophyletic group (Hennig 1981; Whiting *et al.* 1997; Whiting 2002b).
Figure 2.4. Pie chart showing the proportion of extant insects, based on described species. Although Holometabola are the dominant insect group, Neuropterida are only a very small proportion. Holometabola are dominated by Lepidoptera, Diptera and Coleoptera. (Chart drawn with data from Grimaldi & Engel 2005).

2.1.1. Neuropterida’s place within Holometabola

Neuropterida is a monophyletic superorder comprising three Orders Raphidioptera, Megaloptera and Neuroptera. The monophyly of Neuropterida is based upon rather inconspicuous characters in thoracic and abdominal structures, the musculature of the ovipositor and characters of the larval stemmata (Aspöck et al. 2003). Neuropterida’s relationships within Holometabola is as the sister-group to Coleoptera; this is based on the ovipositor structure and synapomorphies of the wing base (Mickoleit 1973; Hörnschmeyer 1998; Kristensen 1999; Aspöck et al. 2001; Aspöck et al. 2003; Grimaldi & Engel 2005). A mitochondrial genome phylogeny of the Neuropterida showed that Coleoptera and Neuropterida were sister-groups when run under a Bayseian hypothesis; however, when run under a parsimony analysis Neuropterida was found not to be monophyletic, Raphidioptera were placed as sister-group to all Holometabola, with the exception of Hymenoptera, and Neuroptera were shown as sister-group to Diptera (Cameron et al. 2009). This is an interesting outcome; however, the vast majority of evidence at the present time, which includes morphological and most molecular studies, shows that Neuropterida are
monophyletic and sister-group to Coleoptera. Figure 2.5 shows a phylogenetic tree of the relationships within Holometabola; other than the basal Coleoptera and Neuropterida there are the Orders Glosseltyrodea, Hymenoptera (e.g. bees, wasps and ants), Mecoptera (scorpionflies), Siphonaptera (fleas), Diptera (true flies), Strepsiptera (twisted wings), Trichoptera (caddisflies) and Lepidoptera (butterflies and moths) (Grimaldi & Engel 2005).

Figure 2.5. Phylogenetic tree of holometabolous insects, showing the relationship of Neuropterida with the other holometabolous insects (modified from Grimaldi & Engel 2005). The solid black lines indicate Order ranges based on fossil evidence; dashed lines indicate extrapolated ranges based on phylogenetic relationships.

2.1.3. Relationships of the three Orders within Neuropterida

All three Orders of Neuropterida are considered as monophyletic; Neuroptera and Raphidioptera have been rarely considered otherwise, Megaloptera, however, has had its monophyly debated (see Aspöck et al. 2001), but is now considered to be monophyletic (Aspöck et al. 2001; Aspöck et al. 2003; Aspöck & Aspöck 2008).
Neuroptera monophyly is based upon the character of complex sucking tubes of the larva and the silken cocoon of the pupa (Aspöck et al. 2003). Raphidioptera monophyly is based on the characters Sc running into C, third tarsale enlarged, tergite and sternite of abdominal segment 9 in male amalgamated to a ring, and ovipositor in female elongated to form a hose-like structure (Aspöck et al. 2003; Aspöck & Aspöck 2004). Monophyly of Megaloptera is supported by the organization of somatic ovarian tissues, tracheal gills of the larvae, and an often overlooked autapomorphy, the presence of eversible sacs with the fused gonocoxites 11 in Corydalidae and Sialidae (Aspöck et al. 2003; Aspöck & Aspöck 2008).

The proposed arrangement of the relationships within the superorder has changed over time. Traditionally it was thought that Neuroptera was sister-group to Raphidioptera + Megaloptera (Fig 2.6A). This hypothesis was based on symplesiomorphies, such as the gula, or on complex characters, for example, the postepimeron-complex, the polyintersegmental muscle between tergites 2 – 5, the reduction of tergite 2, and various oviarole concepts (Kristensen 1999; Aspöck et al. 2003). Molecular studies also arrived at this result using 18S and 28S ribosomal DNA (Whiting et al. 1997; Whiting 2002a, b). The superficial similarity may have been the inducement for this hypothesis (Aspöck et al. 2003).

Figure 2.6. Relationships of the Orders within Neuropterida. A is the traditional hypothesis (e.g. Whiting et al. 1997; Kristensen 1999; Whiting 2002a, b), which has
been superseded by hypothesis B based on more robust evidence (e.g. Aspöck 1995; Aspöck et al. 2001; Aspöck 2002b; Aspöck & Aspöck 2008).

Recent studies, however, have moved towards a Raphidioptera + (Megaloptera + Neuroptera) hypothesis (Fig 2.6 B). This is a revival of Boudreaux’s hypothesis (1979), which has corroboration mainly from the work of the Aspöcks (Aspöck 1995; Aspöck et al. 2001; Aspöck 2002b, c; Aspöck et al. 2003; Haring & Aspöck 2004; Aspöck & Aspöck 2008). The hypothesis is supported by characters from a morphological based study on larval characters, such as the head capsule, mouthparts, and primary aquatic lifestyle (Aspöck 1995), which was further corroborated by a cladistic approach based on numerous morphological characters (Aspöck et al. 2001; Aspöck & Aspöck 2008). It is additionally supported by molecular data (Haring & Aspöck 2004). The Raphidioptera are separated by autapomorphies, such as the tergite and sternite forming a ring in the male genitalia and the hose-like elongation of the ovipositor and the unpaired gonopophyses 8 of the same length (Aspöck & Aspöck 2008). Neuroptera and Megaloptera share the synapomorphies of an appendage-like gonocoxites and rosette arranged trichobothria on the ectoproct (in male and females) (Aspöck & Aspöck 2008). An autapomorphy of Neuroptera is the associated or amalgamated gonocoxites 9 with gonocoxites 11, and an autapomorphy of Megaloptera is the eversible sacs (Aspöck & Aspöck 2008). This relationship is the one accepted by most workers.

2.1.3. Relationships within the Orders

The relationships being reviewed in this section are at family level, while a more in depth review of Raphidioptera at generic level will be given in part 2 of this thesis.

There has been little doubt regarding the relationships within the Orders Raphidioptera and Megaloptera; both of these Orders have two families within, which comfortably form a sister-group relationship (Fig. 2.7). The evidence for the relationship Raphidioptera: Raphidiidae + Inocelliidae is based upon morphological evidence such as the absence of sternite 8 in the female terminalia Raphidiidae and fused sclerites in the parameres of the male terminalia (Aspöck et al. 1980; Aspöck et al. 2001). Molecular data also corroborate the sister-group relationship of these two families (Aspöck et al. 2003). The sister-group relationship of Megaloptera: Corydalidae + Sialidae is based on morphological evidence, for example, a paired
ectoproct in Corydalidae (unpaired in Sialidae), reduced trichobothria in Sialidae (organized into a rosette in Corydalidae) (Aspöck et al. 1980; Aspöck et al. 2001).

Figure 2.7. Relationships of the families in Raphidioptera and Megaloptera based on morphological and molecular evidence (e.g. Aspöck et al. 2001; Haring & Aspöck 2004; Aspöck & Aspöck 2008).

The phylogenetic relationships between Neuroptera have been long debated, with some relationships being better supported than others, based on weaker evidence. Recently U. Aspöck has done much work on the phylogeny of Neuroptera (Aspöck et al. 1980; Aspöck et al. 2001; Aspöck 2002b; Aspöck et al. 2003; Haring & Aspöck 2004; Aspöck & Aspöck 2008). Neuroptera can be divided into three suborders: Nevorthiformia, Myrmeleontiformia and Hemerobiiformia based primarily on the larval head capsule (Aspöck 2002b). The larval head capsule found in Nevorthiformia is considered archaic; it is compact with large gula, which is considered to be a pleisiomorphic state. The Nevorthiformia archaic larval head capsule gave rise to the derived maxillary head (Hemerobioid head of MacLeod 1964) of the Hemerobiiformia, which is composed mainly of elements of the maxillae, and the more derived, heavy and large inflated head capsule (Myrmeleontoid head of MacLeod 1964) of Myrmeleontiformia, the inflated size of the head provided space for the musculature of the huge sucking tubes (Aspöck et al. 2001; Haring & Aspöck 2004).
Nevrorthiformia is composed of just one family (Nevrorthidae), Myrmeleontiformia has five families (Nemopteridae, Psychopsidae, Nymphidae, Myrmeleontidae and Ascalaphidae), while the largest of three suborders is Hemerobiiformia, with 11 families (Polystoechotidae, Ithonidae (=Rapismatidae), Chrysopidae, Osmyridae, Hemerobiidae, Coniopterygidae, Sisyridae, Dilaridae, Mantispidae, Rhachiberothidae and Berothidae) (Aspöck et al. 2001; Aspöck 2002b; Grimaldi & Engel 2005). The monophyly of the suborders is based on the aforementioned structure of the larval head (Aspöck et al. 2001; Aspöck 2002b).

The relationships of the suborders are Nevrorthiformia + (Myrmeleontiformia + Hemerobiiformia) based on morphological evidence of the neuropteran larva (Aspöck et al. 2001; Aspöck 2002b) (Fig. 2.8A). The molecular and genital sclerite evidence, confirms the monophyly of Nevrorthiformia and Myrmeleontiformia, but splits Hemerobiiformia. The relationship of Nevrorthiformia + rest of Neuroptera still stands up to this new evidence, but, the division of Hemerobiiformia causes conflict (Aspöck et al. 2001; Aspöck & Aspöck 2008). The split of Hemerobiiformia puts Myrmeleontiformia as sister-group to part of Hemerobiiformia (Fig 2.8B)

![Figure 2.8. Relationships of the suborders of Neuroptera. A is based on morphological evidence (e.g. Aspöck et al. 2001) and B is based on morphological and in particular molecular evidence (e.g. Haring & Aspöck 2004; Aspöck & Aspöck 2008).](image)

The relationships within Myrmeleontiformia have caused one major debate, which is: Psychopsidae + (Nemopteridae + (Nymphidae + (Myrmeleontidae +
Ascalaphidae)) (Fig. 2.9A) or (Psychopsidae + Nemopteridae) + (Nymphidae + (Myrmeleontidae + Ascalaphidae))? (Fig 2.9B). The former hypothesis is the traditional and the move is towards the latter based on the presence of a *vena triplica* in the hindwing (Aspöck et al. 2001) and gonocoxites connected by a scleritized bridge (Aspöck & Aspöck 2008). However, the molecular data still support the former hypothesis (Haring & Aspöck 2004), therefore this relationship remains unresolved. The sister-group relationship of Ascalaphidae and Myrmeleontidae is corroborated by molecular data (Haring & Aspöck 2004) and morphological data including reduced trichobothria and a ventrolaterally divided tergite 9 (Aspöck et al. 1980; Aspöck et al. 2001; Aspöck 2002b). The sister-group relationship of Nymphidae + (Myrmeleontidae + Ascalaphidae) is supported by the presence of mandibles and grasping teeth (New 1989; Aspöck et al. 2001).

![Figure 2.9. Relationships of the families within Myrmeleontiformia. The two hypotheses are highlighted A and B, the relationships are still unresolved (e.g. Aspöck et al. 2001).](image)

Although the Myrmeleontiformia have unresolved relationships, it is nothing compared to the state of Hemerobiiformia. As mentioned before, conflicts have occurred between morphological characters, and morphological and molecular characters. It was previously thought that Hemerobiiformia was monophyletic, based primarily on the larval head capsule (Aspöck et al. 2001). The relationships of the
Orders from the first cladistic study are: (Ithonidae+Polystoechotidae) + ((Chrysopidae+Osmyliidae) + ((Hemerobiidae + (Coniopterygidae + Sisyridae)) + (Dilaridae + (Mantispidae + (Rhachiberothidae + Berotidae)))) (Fig 2.10) (Aspöck et al. 2001).

Figure 2.10. Relationships of the families within Hemerobiiformia. Based on morphological evidence of Aspöck et al. (2001).

The ithonid clade (Ithonidae + Polystoechotidae) is based on the synapomorphy of phytosuccivory of larva and the larval head morphology (MacLeod 1964; Aspöck et al. 2001; Aspöck & Aspöck 2008). The rest of the suborder is known as the ‘Higher Hemerobiiformia’, defined by the loss of the larval gula and the terminal constriction of the cardines (Aspöck et al. 2001). Within the ‘Higher Hemerobiiformia’ the dilarid clade (Dilaridae + (Mantispidae + (Rhachiberothidae + Berotidae))) receives strong support with the synapomorphies of the elongation of the postmentum, ventrally flat ‘maxillary head’ and the unpaired mediuncus, reduction of the transverse sclerite in gonocoxites 11 to an arch shape and the potential character of a long ovipositor (Aspöck et al. 2001; Aspöck & Aspöck 2008) and the reduction of the transverse sclerite into an arch-shape (Aspöck & Aspöck 2008). The internal relationships within the dilarid clade, however, have been sufficient to debate. Rhachiberothidae has been considered as a subfamily, Rhachiberothinae, within the family Mantispidae (Willmann 1990), but now the consensus is that it is a family in its own right (Aspöck & Mansell 1994). The sister-group relationships of the families Coniopterygidae and Sisyridae are weakly supported with the terminal
segment of the labial palps being enlarged (although this may have evolved independently) and narrowing of the cardines (Aspöck et al. 2001). Hemerobiidae is placed as sister-group to (Coniopterygidae + Sisyridae) + Dilarid clade based on the character of the cardines direction being parallel. The sister-group relationship of Osmylidae + Chrysopidae is based on the length of the cardines being shorter than half the length of the head capsule (Aspöck et al. 2001). The relationship of (Osmylidae + Chrysopidae) + rest of the ‘Higher Hemerobiiformia’ is based on the characters of the gula being reduced to a small triangle and a terminal constriction of the cardines (Aspöck et al. 2001).

The molecular data on the whole disagrees with the study of Aspöck et al. (2001) causing a major disruption of the Hemerobiiformia (Fig 2.11).

![Figure 2.11. Relationships of the families within Hemerobiiformia. Shows the disruption of the traditional view of the suborder with the use of molecular data (Haring & Aspöck 2004).](image)

Haring and Aspöck’s (2004) study separated Sisyridae and Osmylidae from the Hemerobiiformia. There is some corroboration for this with each having strong larval autapomorphies, however this arrangement is debatable. The dilarid clade, which gained strong support from morphological data is split with Coniopterygidae and Dilaridae forming a sister-group and the split of Berothidae and Mantispidae as a monophylum. Haring and Aspöck (2004) accept the split of the Dilaridae and they
reinterpret the former synapomorphies (secondary flat larval head, secondary broad insertion of the larval cardines) as sympleisiomorphies. The split of Berothidae and Mantispidae is still a problem as both have larval development is characterized by hypermetamorphosis (Haring & Aspöck 2004). Ithonidae came out as paraphyletic from the molecular study, which gave an arrangement of Australian Ithonidae + (American Ithonidae + Polystoechotidae); this may be due to the fact that the families are poorly. The placement of Hemerobiidae and Chrysopidae as a sister-group goes back to a traditional hypothesis based on larval similarities and the potential synapomorphy of the wing-like enlargement of the gonocoxites (Aspöck & Aspöck 2008).

The phylogeny of Neuroptera presently has many unresolved relationships, especially with the incorporation of molecular data and the Hemerobiiformia. Also, as yet no one has successfully created a phylogenetic tree comprising extant and extinct Neuropterida families; figure 2.12 incorporates some extinct families but not all.
Figure 2.12. Phylogenetic tree showing the relationship of the Neuropterida. All extant and some extinct families are shown (modified from Jepson & Penney 2007 fig. 2, using data from Grimaldi and Engel, 2005).

Other than the tree displayed in figure 2.12, little work has been done on incorporating fossil and extant neuropterans; the only other examples are Martynova (1949) and Schlüter (1986). However, these, like the tree from Grimaldi and Engel (2005), do not use all the extinct families, and unfortunately they do not give resolved relationships between the fossil and extant taxa. The reasons for this are most likely the lack of strong diagnostic characters within the fossil taxa, for example, the vast majority are recognized on wings only, whereas the extant forms have a wealth of characters, such as morphology, genitalia and the use of molecular data.
2.2. Developmental History of Neuropterids

Neuropterids can have varying time scales of development. This section reviews the current knowledge of development from egg to adult of each Order.

2.2.1. Neuroptera

Development of neuropterans from egg to adult lasts a few weeks (common) to a few years (rare). Most species undergo at least one complete generation each year; temperate species can have several generations in a limited time of the year, with a phenological break accompanied by a period of dormancy in winter (New 1989). Temperate Hemerobiidae tend to be univoltine (one generation), bivoltine (two generations) or multivoltine (many generations) with several overlapping generations during warm periods of the year. Neuropterans are generally multivoltine when conditions change, e.g. the environment (New 1989). Over-wintering occurs mainly as a pre-pupa within the cocoon (it is rare to have a pupa over-wintering). Adults and larva can overwinter and may even feed; fasting however, does occur (New 1989).

2.2.2. Raphidioptera

In Raphidioptera the egg stage lasts a few days to a few weeks and the pupal stage can last up to 10 months in some species. The number of larval instars is not fixed; it varies from 10–11 and may reach 15 (Aspöck 2002a). The larval period lasts from 1–6 years, but the majority are at the lower end of this range (Aspöck 2002a). Snakeflies hibernate in their last or penultimate larval stage or pupa (Aspöck 2002a). Larvae need low temperatures (near freezing) to induce pupation or hatching of the imago (final stage) (Aspöck 2002a; Grimaldi & Engel 2005).

2.2.3. Megaloptera

Few tropical megalopteran species have been studied in detail, and most of the present knowledge has been obtained from the study of Temperate region Megaloptera (New & Theischinger 1993). An aquatic larva is shared by all of the Order Megaloptera. Eggs of megalopterans tend to hatch in less than two weeks (New & Theischinger 1993). Adults are short-lived; however, this is not true for their larvae, which can last up to a few years, varying in different environments. For example, in the family Sialidae, Sialis lutaria has a one-year life-cycle in Denmark.
(Iversen & Thorup 1987), a two-year life-cycle in Britain (Elliott 1977; Brooker 1979) and up to a three-year life-cycle in high altitudes in the Pyrenees (Giani & Laville 1973). Larvae of some species of Sialis may only last 10–11 months (New & Theischinger 1993). The family Corydalidae has larvae that can last in excess of three years, Dysmicohermes disjunctus larvae have been estimated to need four years to develop, and Orohermes crepusculus requires an estimated five years for development (New & Theischinger 1993).

Megalopterans live their life as larvae in streams, rivers and lakes. Their development after hatching may be delayed if the water body dries up. In this situation aestivation (period of inactivity/dormancy) occurs; for example in Protochauliodes aridus the larvae burrow into gravel of the dry streambed and wait until water returns. Some water, however, is required otherwise the larvae will expire (New & Theischinger 1993).

Larvae of the family Sialidae have 10 instars; in Corydalidae the number of instars is unknown due to the longevity of the larvae (New & Theischinger 1993). The last instar is the over-wintering stage that finally develops in the following spring (New & Theischinger 1993).

Pupation occurs terrestrially in a pit dug into the soil, or under rocks or mosses. The chamber can be many metres away from the water habitat of the larvae. The pupa stage is fairly short-lived, lasting under a month (New & Theischinger 1993).

2.3. Extant British Neuropterida

All three Orders of Neuropterida are present in Britain today, with Neuroptera being the most diverse. They are found throughout Britain in varying habitats, but are most numerous in woodland areas.

2.3.1. Neuroptera

There are six families of Recent Neuroptera in Britain: Chrysopidae, Coniopterygidae, Hemerobiidae, Myrmeleontidae, Osmyidae and Sisyridae. The first three mentioned families, Chrysopidae, Coniopterygidae and Hemerobiidae, are the more common families in the Order. In Chrysopidae there are 18 species in 7 genera: Chrysopa, Chrysoperla, Chrysopida, Cunctochrysa, Dichochrysa, Nineta
and *Notochrysa* (Plant 1997). Coniopterygidae has 12 species in 6 genera: *Aleuropteryx*, *Coniopteryx*, *Conwentzia*, *Heliconis*, *Parasemidalis* and *Semidalis* (Plant 1997). Hemerobiidae is the most diverse neuropteran in Britain with 30 species in 7 genera: *Drepanepteryx*, *Hemerobius*, *Megalomus*, *Micromus*, *Psectera*, *Sympherobius* and *Wesmaelius* (Plant 1997). Myrmeleontidae, Osmylidae and Sisyridae are not as common in Britain as the other neuropterans. Myrmeleontidae is represented by one species in the genus *Euroleon*. Osmylidae is also represented by one species in one genus: *Osmylus*. Sisyridae has three species in one genus: *Sisyra* (Plant 1997).

### 2.3.2. Raphidioptera

Raphidiopterans are fairly uncommon in Britain; however, they are quite diverse at the generic level. The raphidiopterans are from one family, Raphidiidae, and they comprise four species in four genera: *Atlantaraphidia*, *Phaeostigma*, *Subilla* and *Xanthostigma* (Plant 1997).

### 2.3.3. Megaloptera

Only three species are found in Britain in one genus: *Sialis*, which belong to the family Sialidae (Plant 1997).

### 2.4. Fossil Record of Neuropterida

The world-wide fossil record of Neuropterida is reviewed below.

#### 2.4.1. Neuroptera

The first records of definitive Neuroptera date back to the Permian with the family Permithonidae, which are found in the former USSR (Martynova 1952), Siberia (Ponomarenko & Shcherbakov 2004), Urals (Novokshonov & Novokshonova 1997), Kansas (Tillyard 1937; Carpenter 1943a, 1976) and New South Wales, Australia (Tillyard 1926; Davis 1943). In the Triassic Neuroptera have been found in New South Wales, Australia: Prohemerobiidae, Psychopsidae, Osmylopsychopidae (Tillyard 1917, 1919, 1922, 1923), Queensland, Australia: Osmylidae (Lambkin 1988), Siberia: Archeosmylididae (Ponomarenko & Shcherbakov 2004) and Germany: Family *incertae sedis* (Brauckmann & Schlüter 1993). Neuroptera were widespread during the Permian and Triassic having been found in Russia, Australia and
America. However, it was during the Jurassic and especially the Cretaceous and into the ‘Tertiary’ that neuropterans had their ‘Golden Age’.

In the Jurassic species of Neuroptera are found in the Lias, of Britain: Permithonidae and Prohemerobiidae (Whalley 1988), from the Lias of Dobbertin, Germany: Chrysopidae, Prohemerobiidae (Ansorge & Schlüter 1990), Luxembourgh: Chrysopidae (Nel & Henrortay 1994; Ponomarenko 1995) in Solnhofen, Germany: Kalligrammatidae, Nymphitidae, Solenoptilidae, Mesochrysopidae, Myrmeleontidae, Hemerobiidae and Brongniartiellidae (Weyenbergh 1869; Meunier 1897; Carpenter 1929; Lambkin 1994; Ponomarenko 2003), Turkestan: Mesochrysopidae, Prohemerobiidae (Martynov 1927), Mongolia: Osmylidae, Prohemerobiidae, Mesithonidae, Kalligrammatidae and Mesochrysopidae (Ponomarenko 1992b), Karatau, Kazakhstan: Coniopterygidae, Mesithonidae, Promegalomidae, Kalligrammatidae, Psychopsidae, Mantispidae, Osmylidae, Episynmylidae, Grammosmylidae, Mesochrysopidae and Nymphidae (Meinander 1975; Panfilov 1980; Engel 2005) and China: Kalligrammatidae, Polystoechotidae, Grammotingidae, ‘osmylid-like’, Nymphidae, Osmylidae (Ren 2002; Ren et al. 2002; Ren & Oswald 2002; Ren & Yin 2003; Ren & Engel 2007).

There are many Cretaceous fossil insect localities, in both sediments and amber. Neuroptera were widespread and very diverse at this time, and many of the ‘modern’ families appeared in the Cretaceous. Neuropterans are found in the Lower Cretaceous of Britain: Kalligrammatidae, Psychopsidae, Brongniartielliidae and Nymphitidae (Jarzembowski 1984, 2001; Clifford et al. 1994), Transbaikalia: Nymphidae, Babinskaiidae and Myrmeleontoidea (Ponomarenko 1992a), Israel: Palaeoleontidae (Dobruskina et al. 1997), Mongolia: Kalligrammatidae, Prohemerobiidae, Hemerobiidae, Grammostylinidae, Mesochrysopidae, Myrmeleontoidea (Ponomarenko 1992b), Baissa, Siberia: Osmylidae, Mesithonidae, Nymphidae, Mantispidae, Psychopsidae, Chrysopidae (Makarkin 1990a, b, 1996, 1997a, b, 1999; Wedmann & Makarkin 2007), Yixian Formation, China: Myrmeleontoidea, Myrmeleontidae, Aetheogrammatidae, Kalligrammatidae, Osmylidae, Chrysopidae, Berothidae (Ren & Guo 1996; Ren & Yin 2002; Ren & Engel 2008a, b), Laiyang Formation, China: Chrysopidae, Allopteridae (Yang & Hong 1990; Zhang 1991), Crato Formation, Brazil: Nemopteridae, Ascalaphidae, Nymphidae, Myrmeleontidae, Palaeoleontidae, Araripeneuridae, Babinskaïidae,

Many Neuroptera are found in what was previously known as the ‘Tertiary’, which is now the Palaeogene and Neogene (Gradstein et al. 2005). Most Neuroptera from this time are found in amber deposits, but there are also numerous sedimentary deposits that yield neuropterans. In the Palaeogene neuropterans are found in the Palaeocene of Queensland, Australia: Osmyliidae (Lambkin 1987). Neuroptera are also found in the Eocene in the Fur Formation, Denmark: Polystoechotidae, Chrysopidae (Schlüter 1982; Willmann & Brooks 1991; Willmann 1993; Andersen 2001; Makarkin & Archibald 2003), British Columbia, Canada: Polystoechotidae (Makarkin & Archibald 2003), Parisian amber: Coniopterygidae, Rhachiberothidae, Sisyridae (Nel et al. 2003; Nel et al. 2005a; Nel et al. 2005c; Engel & Grimaldi 2007), Russian Far East: Ascalaphidae, Solenoptilidae, Chrysopidae (Makarkin, 1998), Baltic amber: Ascalaphidae, Nymphidae, Psychopsidae, Coniopterygidae, Dilaridae, Hemerobiidae, Nevrothidae, Osmyliidae, Rhachiberothidae, Sisyridae (MacLeod 1970; Meinander 1975; Engel 1999; Engel & Grimaldi 2007; Makarkin & Wedmann

2.4.2. Raphidioptera

The earliest definitive snakeflies recorded are Lower Jurassic (Engel, 2002a). Older Palaeozoic specimens assigned to Raphidioptera have now been placed in other Orders (Carpenter 1962, 1992; Sharov 1968; Storozhenko & Novokshonov 1995; Storozhenko 1998) their placement within Raphidioptera has been thought suspect for many years (see Carpenter 1967). The Palaeozoic family Permorrhaphidiidae is now placed in Orthoptera (Carpenter 1967, 1992; Sharov 1968), Sojanoraphidiidae is now placed within Grylloblattaria (Storozhenko & Novokshonov 1995), and Letopalopteridae with Protorthoptera (Novokshonov 1998); the family Fatjonopteridae was synonymized with the protorthopteran family Ampelipteridae (Scherbakov 1995). Aspöck and Aspöck (2004) debated the status of the family Priscaenigmatidae within Raphidioptera, based on the autapomorphies of the Order; they decided that this family was not raphidiopteran and called for the removal of it from the Order. Therefore the only true raphidiopteran families are Raphidiidae, Inocelliidae, Baissopteridae, Mesoraphidiidae and Alloraphidiidae.
Snakeflies were more diverse in the geological past than they are at present; the Mesozoic was their heyday and the Cretaceous itself was when great bursts of evolutionary activity took place. Mesoraphidiidae is the oldest family with species in the Lower Jurassic, while Baissopteridae, Alloraphidiidae and Inocelliidae are Cretaceous and Raphidiidae is ‘Tertiary’ in origin.

The oldest snakeflies are from the Lower Jurassic (Lias) of Britain and Germany comprising the species Metaraphidia confusa Whalley, 1988 and Metaraphidia vahldieki Willmann, 1994 respectively. Two Middle Jurassic species, Ororaphidia megaloccephala Engel and Ren, 2008 and Styporaphidia magia Engel and Ren, 2008, are found in Mongolia, China. In the Upper Jurassic snakeflies are found in Karatau, Kazakhstan: Proraphidia turkestanica Martynova, 1947, Mesoraphidia pterostigmalis Martynova, 1947, M. similis Martynova 1925b, M. parvula Martynov, 1925b, M. inaequalis Martynov, 1925b, M. elongata Martynova, 1925b and M. grandis Martynov, 1925a, and Mongolia M. gobiensis Ponomarenko, 1988.

In the Upper Jurassic–Lower Cretaceous boundary area of Gansu, China Sinoraphidia viridis Hong, 1982 is present.

deserta (Ponomarenko, 1988), Archeraphidia yakowlewi Ponomarenko, 1988, A. hosbayari Ponomarenko, 1988, and Alloraphidia petrosa Ponomareko, 1988. The oldest member of the family Inocellidae, Sinoinocellia liaoxiensis Wang, 1987, is from Xiaosershijiazi, China. The Purbeck and Wealden deposits prior to this study had only one specimen from each deposit mentioned but not described (Jarzembowski 1984; Clifford et al. 1994). The Lower Cretaceous of Montsec, Spain has a limited fauna including Proraphidia gomezi Jepson and Jarzembowski, 2008. Chinese Cretaceous deposits have yielded a diverse fauna of mesoraphidiids including Jilinoraphidia dalazensis Hong and Chang, 1989 (Zhixian, Jilin province), Kezuoraphidia kezuoensis (Hong 1992b), Xuraphidia liaoxiensis Hong, 1992b (Kezuo. Liaoning), Siboptera fornicata (Ren, 1994), Mesoraphidia sinica Ren, 1997, M. shangyuanensis (Ren, 1994), M. polyphlebia (Ren, 1994), M. myrioneura (Ren, 1997), M. obliquivenatica (Ren, 1994), M. heteroneura Ren, 1997, M. longistimosa (Ren, 1994), M. glossophylla (Ren, 1997), M. gaoi (Ren in Ren et al., 1995), M. furcivenata Ren in Ren et al., 1995, M. amoena Ren, 1997, Huaxiaraphidia shandongensis Hong, 1992a, H. sinensis Hong, 1992a, and baissopterids Baissoptera liaoningensis Ren, 1994, B. grandis Ren in Ren et al., 1995, B. euneura Ren, 1997 and one alloraphidiid Alloraphidia anomola Ren, 1997 (Beipiao, Liaoning). Two mesoraphidiid species have been discovered in the Cretaceous of South Korea, Mesoraphidia koreenensis Engel et al., 2006 and M. phantosma Engel et al., 2006. The Crato Formation, Brazil has yielded four species of snakefly, three baissopterids, Baissoptera pulchra (Martins-Neto and Nel, 1992), B. brasiliensis Oswald, 1990 and Austroraphidia brasiliensis (Nel et al., 1990), and one familia incertae sedis, Arariperaphidia rochai Martins-Neto and Vulcano, 1989.

The middle Cretaceous has only yielded one species, an alloraphid, Alloraphidia dorfi Carpenter, 1967 from Labrador, Canada. Two species are found in the Upper Cretaceous, both are mesoraphidiids, Nanoraphidia electroburmica Engel, 2002a, from Burmese amber, which is the smallest snakefly ever recorded, and Mesoraphidia luzzi Grimaldi, 2000 from New Jersey amber.

The Cenozoic raphidiopterans are represented by Raphidiidae and Inocellidae. The Mesozoic families Mesoraphidiidae, Alloraphidiidae and Baissopteridae became extinct at the Cretaceous-‘Tertiary’ boundary, and it has been hypothesized by Aspöck (1998) that these families died out for the same reasons as the other
unfortunate animals at the Cretaceous-‘Tertiary’ mass extinction. A small number of
snakeflies have been discovered in the Eocene Baltic amber, the raphidiid species are
*Raphidia baltica* Carpenter, 1956, and the inocellid species *Electroinocellia
peculiaris* (Carpenter, 1956) and *Fibla carpenteri* Engel, 1995. The main deposit in
the Cenozoic for snakeflies is Florissant at the Eocene-Oligocene boundary with the
mortua* Rohwer, 1909, *R. tranquilla* Scudder, 1890, *R. tumulata* (Scudder, 1890) and
*R. veterana* (Scudder, 1890). These species have been tentatively kept in *Raphidia* in
Engel’s (2002a) review of fossil snakeflies, but after revision he suggests that many
will be taken out of this genus and reassigned to others within Raphidiidae. Only two
inocelliid are known from Florissant, *Fibla exusta* (Cockerell and Custer, 1925) and
*Fibla erigena* (Menge, 1856). A few Upper Miocene deposits have yielded snakefly
species including the raphidiid *Ohmella coffini* Nel, 1993 from France and the
inocelliid *Fibla cerdanica* (Nel, 1993) from Spain.

Modern snakeflies have approximately 206 species in the families Inocelliidae (21
species) and Raphidiidae (185 species); there are 25 recognized genera in
Raphidiidae and 6 genera in Inocelliidae (Aspöck 2002b). They are restricted to the
Northern Hemisphere and in temperate latitudes, in areas where there is a cold winter
to help development (Aspöck 1998).

Raphidiopteran history spans the Jurassic to the present day. They are represented
throughout geological time as both larvae and adults. The earliest snakeflies from the
Jurassic already possessed synapomorphies of the Order suggesting an earlier origin,
perhaps Triassic or late Permain. The age of related clades, e.g. Neuroptera and
Megaloptera, would also suggest this, but fossil evidence is needed to support this
conjecture (Engel 2002a).

2.4.3. *Megaloptera*

Megaloptera have a sparse fossil record with very few species. The oldest
megalopterans are Permian in age and comprise *Parasialis dissedens* Ponomarenko,
1977 from Soyana River, *Parasialis ovata* Ponomarenko, 2000 (family Parasialididae)
and *Tychtodelopterum archaicum* Ponomarenko, 1977 from Kuznetsk Basin, Russia
(family Tychtodelopteridae).
No megalopterans have been found in the Triassic. In the Jurassic one species in the family Sialidae, *Dobbertina reticulata* Handlirsch, 1920, is found in Dobbertin Germany. The Lower Cretaceous has two sites where megalopterans have been found: *Cretochaulus lacustris* Ponomarenko, 1976 (family Corydalidae) from Baissa, Russia and unnamed specimens from the Crato Formation, Brazil (Martins-Neto *et al.* 2007). The Upper Cretaceous has one site at E. Taymyr, Russia with one species, *Chauliosalis sukatshevae* Ponomarenko, 1976, in the family Corydalidae.


There are approximately 270 species of extant Megaloptera belonging to two families, Corydalidae and Sialidae (Engel 2004b).

2.4.4. **Fossil British Neuropterida**

Fossil Neuropterida have been found in the ‘Tertiary’, Cretaceous, Jurassic and Triassic rocks in Britain. Little work has been done on these insects, and much of what has been done was undertaken in the 19th and early 20th Century. A note of warning is needed when referring to 19th Century literature, because terms such as ‘Neuroptera’, ‘Neuropterous’ and ‘*Sialis*’ were used as bucket terms for many insects with a dense venation pattern, for example, Odonata (dragonflies and damselflies) would be regarded as Neuropterous/Neuroptera. A notable example of this is in Brodie’s (1845) work on fossil insects in Britain.
There has yet to be any fossil representatives of Megaloptera found in Britain. Table 2.1 lists the localities with taxonomic data (at the family level) included when known.

<table>
<thead>
<tr>
<th>Age</th>
<th>Order</th>
<th>Family</th>
<th>Locality</th>
<th>Reference</th>
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<td>Alderton</td>
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<td>Dumbleton</td>
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<td></td>
<td>Raphidioptera</td>
<td>Mesoraphidiidae</td>
<td>Charmouth</td>
<td>(Whalley 1985, 1988)</td>
</tr>
<tr>
<td>Cretaceous</td>
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<td>Dorset (Purbeck)</td>
<td>(Whalley, 1988)</td>
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<td></td>
<td>Uncertain</td>
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<td>Dorset (Purbeck)</td>
<td>(Giebel 1856)</td>
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<td>(Westwood 1854; Giebel 1856; Scudder 1885; Whalley 1988)</td>
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<td>(Clifford et al. 1994)</td>
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<td>Isle of Wight</td>
<td>(Cockerell 1921; Jarzembowski 1980)</td>
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<td></td>
<td>Hemerobiidae</td>
<td>Isle of Wight</td>
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Table 2.1. The fossil record of neuropterids in Britain.
2.5. Environment and Ecology

This section comprises a review of the environment, ecology and plant and prey associations. The literature is reviewed with a view to using modern analogues for the fossil Neuropterida of the Purbeck and Wealden. With regards to Raphidioptera and Megaloptera the whole Orders will be investigated to gather modern analogues, because the fossils of these Orders are from families that are extinct. Some neuropteran families from the Purbeck and Wealden have persisted to the modern day; these include Chrysopidae, Berothidae, Nymphidae, Ithonidae, Psychopsidae, Osmylidae and Hemerobiidae, and these therefore have been the focus in the literature review.

2.5.1. Neuropterida

Many neuropterid taxa are associated with specific plants and vegetation. They use the plants and vegetation in a variety of ways, whether it is for a platform to lay eggs, protection for the larvae, food source or hunting ground (New 1989; Plant 1997; Grimaldi & Engel 2005). Prey plant specificity or preference can be a likely influence on habitat selection (New 1989).

Neuropterida are predators of small invertebrates making them of economic use; they are often used as pest control on crops (e.g. Wise 1995). Both larvae and adults are predators with the exception of the adults of some families who have taken to feeding upon pollen (Megaloptera, Nemopteridae, Sisyridae) (New 1989; New & Theischinger 1993; Grimaldi & Engel 2005). Some Neuropterida are generalist predators, feeding on any type of prey, while some are more specialized predators, restricted to one type. The neuropterids which are restricted to one type of prey tend to be found living in the same environments (New 1989).

Duelli et al. (2002) investigated Neuroptera and Raphidioptera habitats in forests. They found that it was the edges of forests rather than the forest interior that was the main habitat for many of them. The study, however, was based on a managed forest, and this therefore may not be true in a wild situation.

Microhabitats have scarcely been investigated, especially with regards to Neuroptera (New 1989). The little work done shows that different species of Neuropterida live in different areas on the same tree, with some being trunk dwellers and some being
canopy dwellers. The canopy dwellers themselves can live in different layers within the canopy (Barnard et al. 1986; New 1989). Trunk dwellers tend to be brown and mottled and the canopy dwellers are pale, demonstrating their different camouflage adaptations (Barnard et al. 1986).

2.5.2. Neuroptera

The life-cycle of most extant Neuroptera is in some way associated with vegetation. Below are some examples of the different ways in which the neuropteran families utilize this resource. The examples are illustrated with varied taxonomic rank; this has been done because of the great variation of plant utilization seen within families, genera and species.

Psychopsidae have predominantly arboreal larvae; living under or within deep crevices in the bark (Grimaldi & Engel 2005). Some subcortical larvae appear to be limited to Eucalyptus (New 1989). Immatures of the family Nymphidae live in leaf litter and under logs. Some larvae are arboreal and have become flattened to live under the bark or in crevices on the bark (Grimaldi & Engel 2005). Ithonidae (=Rapismatidae) larvae are associated with decaying bark and vegetation, which may form a source of food for them (Grimaldi & Engel 2005).

The majority of species in the family Hemerobiidae and Chrysopidae are arboreal (Grimaldi & Engel 2005). A great majority occur on vegetation, some having host-plant specificity (New 1989). The hemerobiid Wesmaelius is often associated with low-lying vegetation, others occur on all types of vegetation, with some being specialized on various trees, for example, Abies (Fir), Pinus (Pine), Quercus (Oak) and Populus (Poplar) (Monserrat & Marin 1996). European species of Wesmaelius are clearly associated with conifers (New 1989). Some hemerobiids and chrysopids feed on pollen and other plant substances (Monserrat & Marin 1996).

The family Osmylidae may possibly have an aquatic larva, although this has not been studied in detail. The adult osmylids have been consistently found near bodies of water; this behaviour is observed in most insects that have an aquatic larva, for example, megalopterans (New 1989; Grimaldi & Engel 2005).

The majority of neuropterans, both adults and larvae, are predators (New 1989; Grimaldi & Engel 2005). Hemerobiidae and Chrysopidae are found around prey
colonies such as aphids. They usually hunt by walking, but other hunting strategies are used such as ‘sit and wait’ and with the competent fliers, hunting on the wing (New 1989). The osmylid *Osmylus fulvicephalus* probes wet mud to feed on dipteran larvae. Cannibalism has been observed and predation of the first instar by siblings could be due to scarcity of prey (Duelli 1981). Berothidae is seen to hunt on termites, and this does seem to be a specialism (New 1989).

Little evidence of prey specificity within Neuroptera has been found and the prey is usually limited to what physically can be caught (New 1989). Most neuropterans have a varied diet, for example, the larvae of hemerobiids and chrysopids, which consume many small arthropods such as mites, aphids and other scale insects (Homoptera). Prey specificity has not been studied in great detail within Neuroptera. It may in fact be preferred prey of an insect as part of a varied diet (New 1989).

Some species of Neuroptera do seem to have prey specificity and this can be induced from the first meal the larvae feeds on; if changed after it could be fatal (Babrikova 1979). The work of Hydorn and Whitcomb (1979) and Canard (1970, 1973) on chrysopids has shown developmental abnormalities resulting from feeding on certain types of prey, e.g. failure to spin cocoons, death as pupa within the cocoon and males becoming sterile. Less fatal changes may occur such as a change in the weight of the cocoon (New 1989).

Miller *et al.* (2004) have undertaken work on the predator/prey relation of Neuropterida and Coccoidea (Hemiptera). This work lists numerous species of Hemerobiidae (Neuroptera), Inocelliidae and Raphidiidae (Raphidioptera) from the Afrotropical, Australasian, Nearctic (Greenland, highlands of Mexico and most of North America), Oriental and Palearctic (Europe, Asia north of Himalayas, northern Africa) regions and their Coccoidea prey. The study, however, was biased towards managed agricultural ecosystems.

Prey tends to be discovered at random by neuropterans. Some prey can be rejected by neuropterans on the basis of the prey’s physical characters, e.g. the hard cuticle of a gall wasp (Thorne 1972), the waxy cuticle of some aphids (Ru *et al.* 1975) and aphid cornicle excretions (Pupedis 1987).
Neuroptera are prey for many insects, for example, Odonata; the adults are caught on the wing by many species of dragonfly. The dipterans Empididae and Asilidae also feed on neuropterans, as do Hymenoptera (*Bembix*). Mites are known to eat neuropteran eggs (Killington 1925; Evans 1978; Evans *et al.* 1982; New 1989). Vertebrate predators of Neuroptera include birds and bats (New 1989; Szentkirályi & Kristín 2002)

2.5.3. *Raphidioptera*

Snakeflies (adults and larvae) live almost exclusively on trees, shrubs and bushes (Aspöck 1998, 2002a; Grimaldi & Engel 2005). They are found from sea level up to the timberline, in areas which have a cold winter period (Aspöck 1998, 2002a). The extant British fauna (Raphidiidae) have been recorded on various types of trees such as conifers, oak and willow (Plant 1997). Snakeflies use their long ovipositor to lay eggs in crevices in the bark or under it, and the larvae then live on or under the bark (Grimaldi & Engel 2005). Other species larvae live in the soil and leaf litter at the base of vegetation, and also in rock crevices (Aspöck 1998, 2002a; Grimaldi & Engel 2005). Their whole life is confined to the aboreal environment; they are poor fliers and often will not leave ‘their’ shrub or tree (Aspöck 1998).

The larvae of Raphidioptera are active predators hunting at night and feeding on a variety of invertebrates; their prey can include the larvae and eggs of other arthropods in particular Lepidoptera, Coleoptera and Hymenoptera. They will also feed on the larvae and adults of insects (e.g. Psocoptera, Auchenorrhyncha, Sternorrhyncha, Collombola, mites) and even spiders (Aspöck 2002a). There has been little field study on raphidipterans to determine their true diet and to investigate differences, if any, between the tree dwelling larvae and the leaf litter dwelling larvae; however, experiments in laboratory conditions have yielded no differences (Aspöck 2002a).

The adults of Raphidiidae are predacious with their main diet being aphids and other small arthropods; however, pollen has been eaten when in captivity and also has been found in the gut contents of wild raphidiids. The diet of Inocelliidae is virtually unknown; however, in captivity, as with Raphidiidae, pollen is taken as food, but pollen has not been found in the gut of wild inocelliids. (However, no extensive field research has been undertaken to discover the diet of the family (Aspöck 2002a)).
Raphidiopterans form food for predaceous insects, and other arthropods, for example, spiders, and they are often taken by birds (Szentkirályi & Kristín 2002).

2.5.4. Megaloptera

Adults of this Order utilize vegetation overhanging water to lay eggs, so that when the larva emerges it drops directly into the underlying water (Engel 2004b; Grimaldi & Engel 2005). Feeding strategies of adult Megaloptera is on the whole unknown (New & Theischinger 1993). It was thought that adult megalopterans did not feed, instead living on the reserves stored when feeding in the larval stage. However, adults of some species have been observed feeding on pollen and nectar, therefore suggesting that they must visit flowers to feed (Dubois & Geigy 1935; New & Theischinger 1993; Engel 2004b). Megalopterans in captivity have readily fed on honey-water solutions (Parfin 1952), fermented molasses and bananas with water and sugar (New & Theischinger 1993). *Protohermes grandis* has been observed feeding on tree sap (Yoshida *et al.* 1985). The feeding strategies above may be linked to the sex of the insect; females in laboratory conditions readily went for the sweet liquids, whereas males were content just drinking water. The large mandibles of the male corydalids also inhibit feeding as an adult (New & Theischinger 1993).

The larva of megalopterans are aquatic. Larva hatch from overhanging vegetation and drop into the underlying water where they live until they are ready to pupate, when they then leave the water for good (Grimaldi & Engel 2005). The aquatic habitat of Sialidae is diverse; they are found in freshwater, in small ponds and streams, lakes, and large slow-flowing rivers. Corydalidae are also found in diverse aquatic environments, but, the majority are to be found in streams (Grimaldi & Engel 2005). Some larvae (e.g. *Sialis lutaria*) when small live in the littoral zones (shallow water), moving when larger in their second year to the sub-littoral or profundal zone (deeper water) (New & Theischinger 1993).

The larvae can also inhabit microhabitats, for example, this has been observed when there are coexisting sialids and corydalids. The work of Evans (1972) on *Neohermes californicus* and *Protochauliodes aridus* in one stream in California, demonstrated the microhabitats of these two corydalids. *N. californicus* was always found in the deeper faster water, whereas *P. aridus* was found in the shallower water. Evans also observed another microhabitat choice for *N. californicus* and another species of
corydalid *P. spenceri*. These two species coexist in two small, connected intermittent streams, one with a soft substrate and the other with hard substrate. *N. californicus* was observed in the firm substrate stream and *P. spenceri* the soft substrate stream. This work, however, has not been verified in other streams inhabited by corydalids. Other factors can influence where various species are found; these include size of stream, water temperature, water pH and the level of pollution in the water (New & Theischinger 1993).

The larvae of Megaloptera are voracious predators of various aquatic invertebrates and vertebrates, and cannibalism is frequently observed (New & Theischinger 1993). They prey on larvae of mayflies, caddisflies, damselflies, dipterans (chironomids, *Simulium*), adult isopods, tadpoles and tubificid worms (New & Theischinger 1993). There are no links with prey interaction with plants and therefore they are not tied to any particular plant because of their prey.

Megaloptera are prey for other insects, for example, Trichoptera and Odonata, and their eggs form part of the diet of beetle larvae, the neuropteran family Sisyridae and slugs. Vertebrate predators include rodents and birds (New & Theischinger 1993).

2.5.5. *The Percentage of Neuropterida in Environments*

Neuropterida do not make up a large percentage of the insect fauna in specific habitats, neither extant nor fossil. This is probably due to the fact that they are predators and there are always fewer predators than prey. Below is the percentage of Neuropterida in various insect faunas.

In the Wealden there are 0.1–0.9% Neuroptera present (Jarzembowski 1995), while in the Purbeck Neuroptera and Raphidioptera are not as rare (Coram & Jarzembowski 2002). Less than 1% is normal in both extant and fossil habitats, higher proportions have been known, but they are rare. Examples of these are the Okanagan Highlands, British Columbia (1.5%) and the Fur Formation, Denmark (3.8–5%). In extant communities Neuroptera make up less than 1% of the insect fauna, for example, they are less than 1% in the tropical forests of Borneo; 0.45% in Queensland, Australia; and 0.25% in Primorye, Russia (Archibald & Makarkin 2006; Jepson & Penney 2007).
2.6. Geological Settings

The insects studied herein are from two Lower Cretaceous deposits in Britain, the Purbeck Limestone Group, and the Wealden Supergroup (Weald Sub-basin). This section gives the geological settings and palaeoenvironments of these two deposits. The climate change observed through the Purbeck into the Wealden will also be reviewed.

2.6.1. Mesozoic flora, a brief note

The flora of the Lower Cretaceous (Purbeck and Wealden), southern England is dominated by gymnosperms and pteridophytes (e.g. Francis 1983; Hill 1996). One putative Angiosperm has been identified from the Wealden (Hill 1996). Angiosperms first appeared around the Jurassic/Cretaceous boundary, but, their main radiation did not occur until ~115MA (phylogenetic tree in Grimaldi & Engel 2005 page 612). The main radiation took place ~5–10MA after the end of the Wealden, therefore not having a great effect on the entomofauna. Gymnosperms and pteridophytes, however, were present long before Purbeck and Wealden times (Thomas 1981).

2.7. Purbeck Limestone Group

The Purbeck Limestone Group is most dominant in present day Dorset and Wiltshire; this section will be looking at the deposit’s palaeogeography, palaeoclimate and palaeoenvironment. The majority of the neuropterid specimens are from the type area for the Purbeck Limestone Group, Durlston Bay, Swanage, Dorset.

2.7.1. Palaeogeography

The latitude of the Purbeck during deposition has been suggested as being 30–35°N (Ogg et al. 1994) (where the present day Mediterranean is situated). It lay between a complex of massifs (Fig. 2.13); Cornubia, Armorica, Londinia and the Irish and Welsh Massifs (Allen 1998). The massifs were bordered by the widening Protoatlantic to the west, the Boreal Sea to the northeast and the Tethys Sea to the south (Allen 1998). The sediment was deposited between the massifs in the Wessex sub-basin with Cornubia to the west and Armorica to the south (Hancock & Rawson
1992; Allen 1998). Purbeck sediments were also deposited in the Weald sub-basin (which yield little insect material) and the Midlands basin (very insectiferous deposits) (Brodie 1845; Coram 2005).

Figure 2.13. Palaeogeographic map at the time of the deposition of Purbeck and Wealden sediments (redrawn from Allen 1998).

The environment of deposition was originally thought to be estuarine (Brodie 1845; Fisher 1856), but has now been widely accepted (based on more complete geological evidence) to be lagoonal with intermittent connection to the sea. (Clements 1973). Lagoonal deposition dominates the Lower Purbeck, with little or no influence from the sea. The Middle and Upper Purbeck have much greater influence from the sea, observed by salinity changes and differences in the aquatic fauna (Clements 1973; Coram 2005). The lagoon was bordered (or broken up) by low-lying marshes, mudflats, shell beaches and sabkhas, and was also subjected to inundation, with subareial exposure observed by the presence of dinosaur footprints and desiccation cracks (Ensom 2002a). The exposed flats would have been several 10s of kilometres wide (limited in size in the north due to the South Dorset Swell) and they were probably unvegetated (scarcity of roots and plant remains) (Coram 2005). The present day Trucial Coast (Persian Gulf) and Laguna Madre (Texas/Mexico) have been cited as modern examples of such a landscape (Schreiber 1986; Eisma 1998; Coram 2005).
A marine regression is observed at the start of the Purbeck, going from the marine deposits of the Portland Beds (Jurassic) to the non-marine Purbeck Limestone Group (Lower Cretaceous). During this transition the region was gradually cut off from the open-sea (Batten 2002).

2.7.2. Palaeoclimate

The lower and middle Purbeck are now widely accepted as having a semi-arid, Mediterranean type climate, gradually becoming wetter towards the end of the Berriasian (Sladen & Batten 1984; Allen 1998; Batten 2002). This is reflected in the facies, with hypersaline deposits common in the lower Purbeck, and freshwater clastics dominating the upper part (Clements 1993; Batten 2002).

2.7.3. Palaeoenvironments

The Berriasian Purbeck Limestone Group consists of the Lulworth and Durlston formations (Fig 2.14). Below is an in-depth look at the stratigraphy and environments of deposition.
2.7.4. Lulworth Formation (Fig. 2.14):

The lower part of the Lulworth Formation is the Broken Beds Member, which was deposited in a hypersaline lagoon. The upper part of the member was deposited in a more shallow water environment (Batten 2002). Moving up through the succession the next member is the ‘Cypris’ Freestone (named after a genus of ostracod). This member is the oldest part of the Purbeck Limestone Group where fossil insects have been found (Coram & Jarzembowski 2002). It was deposited in a lagoonal environment in shallow water with varying salinity, which is now preserved as...
limestone (West 1975). The lagoon partly dried up in droughts in the summer months leaving evaporites such as halite within the fine carbonate sand (Batten 2002). The next unit, the Hard Cockle Member was deposited in a hypersaline environment, indicated by the presence of numerous evaporites. The overlying Soft Cockle Member has a similar environment, but with marls and shales in the upper part, with a sabkha facies common (Batten 2002). Moving into the Middle Purbeck from the Lower, one finds the penultimate member of the Lulworth Formation, the Marly Freshwater Member. This member was deposited in a shallow lake; and contains the well-known Mammal Bed (Batten 2002). The last member of the Lulworth Formation, the Cherty Freshwater Bed, was deposited in slight saline conditions with ‘seasonal’ droughts causing changes in salinity (Allen 1998).

2.75. Durlston Formation (Fig. 2.14):

The Durlston Formation begins in the Middle Purbeck with the Cinder Member the base of which formerly marked the Jurassic/Cretaceous boundary. (Coram & Jarzembowski 2002; Coram 2005). The member has been suggested to have been deposited in a fully marine environment (Batten 2002). Overlying the Cinder Bed is the Intermarine Member; the lower part of this member was deposited in a freshwater-slightly brackish lake, while the upper part was deposited in more saline conditions with some shell beaches (El-Shahat & West 1983; Batten 2002). Neither of these deposits have yielded any fossil insects (Coram 2005). Next is the Scallop Member, deposited in a marine environment, also devoid of insects. Overlying the Scallop Member is the Corbula Member (named after a genus of bivalve). This is one of the main insect-bearing units of the Purbeck (Batten 2002; Coram & Jarzembowski 2002), and was deposited in mainly near marine conditions (Batten 2002). Above the Corbula Member is the Chief Beef Member, which yields no fossil insects, and was deposited in brackish conditions (Batten 2002; Coram & Jarzembowski 2002). Overlying the Chief Beef Member is the Broken Limestone Member and Unio Member deposited in freshwater (Batten 2002). The transition from the Chief Beef to the Broken Limestone Member marks the change from Middle to the Lower Purbeck. The youngest unit of the Purbeck is the Upper ‘Cypris’ Clays and Shales Member (including the Purbeck Marble) which is overall non-marine and similar to the overlying Wealden Group (Batten 2002).
Coram’s (2003) work on the taphonomy and ecology of Purbeck insects splits the insects into an aquatic and terrestrial fauna. The articulated aquatic fauna lived in or quite near to the major bodies of water; being articulated shows evidence of little travel or little time to decay and disarticulate. The terrestrial fauna is on the whole disarticulated, which suggests that there has been an element of transport or period of decay. Distant woodland has been suggested for the disarticulated insects and for the better-preserved ones it is suggested that they may have lived on the sparsely vegetated lagoon margins (Coram 2003).

The environment proposed by Coram (Coram 2003, p. 316) is one of a brackish lagoon bordered by a shell beach or sabkha, with freshwater lake/marsh a damp forest/water margins and open glades with a distant forested region.

2.7.6. *Palaeoflora*

Algae, spores and pollen grains are present within the Purbeck. These are useful environment indicators (e.g. Batten 1982, 2002), but, it is difficult to link dispersed pollen and spores to their growth communities and parent plants, especially in the absence of macrofossils (Batten 2002).

There are few plant macrofossils in the Purbeck (Batten 2002). Cycadophyte remains have been found, as have conifers. Silicified pieces of coniferous trees have been found higher up in the succession, which are the same type as those that dominate the Lower Purbeck soil beds (Batten 2002). Foliage of different species have been discovered, but not yet studied, only an ‘*Equisetum*’ stem, coniferalean foliage and *Araucarites* cone have been described (Barker et al. 1975; Batten 2002). The palynological evidence from the Lower Purbeck suggests that gymnosperms dominated. Charcoal is present within the Purbeck indicating that wildfires burnt the vegetation. However, the fires do not seem to have affected the tree stumps, and therefore, they must have been of low intensity affecting the foliage only (Batten 2002).

The Purbeck vegetation is not very diverse; it is dominated by conifers (one or two species) and has less common bennititaleans, ferns, lycopods, mosses and liverworts. No angiosperms are present (Francis 1984).
2.7.7. Palaeofauna

The entomological fauna consists of Coleoptera, Hemiptera, Diptera, Orthoptera, Mecoptera, Heteroptera, Blattodea, Hymenoptera, Trichoptera, Odonata, Neuroptera, Raphidioptera and Megaloptera (Coram & Jarzembowski 2002).

The entomofauna is split into aquatic and terrestrial; the aquatic fauna can be fully preserved or disarticulated, reflecting transport, the disarticulated representing an allochthonous fauna and the articulated being autochthonous (Coram 2003). The terrestrial entomofauna are disarticulated, reflecting transport, e.g. Coram’s (2003) disarticulation on sabkha/shell beach, then after disarticulation the insect wings and sclerites being washed into pools or collected by the rising lagoon.

Bivalves, gastropods, ostracods, crustaceans, chelicerates, crocodiles, turtles, fish, dinosaurs, amphibians and mammals make up the rest of the fauna of the Purbeck Limestone Group (see papers in Milner & Batten 2002).

2.8. Wealden Supergroup (Weald Sub-Basin)

The Wealden Supergroup of southern England is a succession of Lower Cretaceous rocks deposited in two sub-basins the Weald and Wessex. This section concentrates on only one of these sub-basins, the Weald, because to date no Neuropterida have been discovered in the Wessex Sub-basin.

2.8.1. Palaeogeography

The distribution of land and sea from the Purbeck (Berriasian) to the Lower Weald Clay (mid-Hauterivian) did not change (Fig. 2.13); however, a gradual retreat of shorelines did occur (Hancock & Rawson 1992).

The Weald Sub-basin, as with the Purbeck Wessex Sub-basin was surrounded by a number of massifs: Londinia to the north, Cornubia to the west, Armorica to the south and the Welsh massif to the northeast (Hancock & Rawson 1992; Radley 2005).

The sediment (and derived fossils) in the Weald Sub-basin is largely from the Londinia massif (Allen 1975; Radley 2005), but, during Weald Clay times, sediment
especially sand, was occasionally washed in from the Cornubia massif (Radley 2005).

2.8.2. *Palaeoclimate*

Much work has been done on the climate of the Wealden, using evidence from various sources: palaeontology (e.g. fossil insects: Jarzembowski 1995), sedimentology (Allen & Wimbledon 1991; Allen 1998) and climate models (Haywood *et al.* 2005). This multi-disciplinary work suggests a sub-tropical/warm temperate ‘Mediterranean-like’ climate with the occurrence of wet and dry (commonly with wild fires) seasons. Also proposed is year-round precipitation with little evidence for prolonged drought; the apparent dry season is due to higher evaporation rates in the summer months (Batten 1998; Haywood *et al.* 2005). Average temperatures proposed by Haywood *et al.* (2005) are 4–8°C for cold months and 36–40°C for the warm months. Evidence for wildfires exists in the form of fusainized beetle elytra and plant remains (Watson & Alvin 1996; Batten 1998; Jarzembowski 2003).

2.8.3. *Palaeoenvironment*

The Wealden Supergroup consists of the Hastings Beds Group and the Weald Clay Group (Fig. 2.15). Below is an in depth look at the environments of the Wealden.
Figure 2.15. Stratigraphic column of the Wealden Supergroup modified from Rasnitsyn et al. (1998), with insect localities indicated.

The Hastings Beds and Lower Weald Clay groups (Fig. 2.15) represent three ‘megacycles’ (Allen 1975; Allen & Wimbledon 1991; Radley 2005). A megacycle consists of an alluvial deposit, Allen’s (1981) arenaceous formations. These deposits are observed in the Ashdown Beds, and the Lower and Upper Tunbridge Wells Sand. The alluvial formations are overlain by the second part of a cycle, the lake-lagoon clays, Allen’s (1981) argillaceous formations. These are observed in the Wadhurst, Grinstead and basal Weald Clays (Allen 1981; Radley 2005). The upper part of the
Weald Clays represent the bulk of the Weald Clay Group, and are dominated by lacustrine-lagoonal with distal alluvial facies (Allen & Wimbledon 1991).

Jarzembowski’s (1995) study on insect palaeoenvironment discusses a restricted freshwater fauna for insects dominated by Odonata adults with rare Trichoptera and Plecoptera. The restricted fauna ties in with sedimentological and palynological evidence, which suggests the water may have been brackish at times (Allen 1975; Batten 1982). This is further emphasized by the absence of larval Odonata and freshwater insects in the Wealden, suggesting that the aquatic fauna was not living in the main Wealden waterbody. (The majority of insects are not able to survive in water of over 0.2% salt, especially Odonata, Trichoptera and some Diptera.) Also the muddy water would not have favoured Ephemeroptera, which are absent from the Wealden; these favour clear, aerated water (Jarzembowski 1995).

The insect evidence suggests that the Wealden watercourses were bordered by woodland with occasional glades (Jarzembowski 1995). The evidence for this is a high number of wood associated insects, for example, Isoptera, Coleoptera and Hemiptera. The presence of Diptera suggests a damp woodland environment and the rarity of Orthoptera hints at a lack of open spaces (Jarzembowski 1995).

The insects are disarticulated with wings dominating the fossils and body parts being rare; the wings are also on the whole incomplete/damaged. The Wealden, as mentioned previously, has sediment derived mainly from Londinia (in the north) and it could be that the insects lived on the emergent ground of the south side of the Londinia massif, being washed into the area of deposition (the incompleteness of the wings is possibly due to damage during transport) (Jarzembowski 1995).

2.8.4. Palaeoflora

Much work has been done on the Wealden flora, most notably works by Watson and Alvin (1996 and references therein); their work demonstrated that the flora was dominated by gymnosperms and ferns (pteridophytes) with a possible eoangiosperm present (Hill 1996). Watson and Alvin (1996) give a floral list of all published flora up to 1996.

The ferns are dominated by Weichselia reticulata with fragmentary Flicopsida (Jarzembowski 1991; Ross & Cook 1995; Watson & Alvin 1996). The gymnosperms
from the Wealden are represented by horsetails, club mosses, conifer twigs and cones (Ross & Cook 1995; Watson & Alvin 1996).

The potential early angiosperm (*Bevhalstia pebja*) has been interpreted as being from a marshy or aquatic environment. The plant, having delicate structures preserved, means it has not been transported far from place of life to the place of fossilization (Hill 1996). *Bevhalstia pebja* has been found in abundance in the Weald Sub-basin in both Upper and Lower Weald Clay (Hill 1996).

2.8.5. *Palaeofauna*

The entomological fauna of the Wealden is diverse with the majority of extant Orders present. The Orders that have been recorded to date are Coleoptera, Odonata, Blattodea, Orthoptera, Hemiptera, Mecoptera, Diptera, Trichoptera, Hymenoptera, Raphidioptera, Neuroptera, Isoptera and Plecoptera (Jarzembowski 1984, 1995; Sinitshenkova 1998).

The woodland environment would have been dominated by the plant-feeding insects, the xylophagous (wood-eating) insects; the Isoptera would live in damp, fallen or standing trees and cupedoid Coleoptera would feed on dead wood. The coleopteran *Paleoscolytus sussexensis*, the aphid *Penaphis woolardi* and the fulgoroid Hemiptera would have fed on living trees. The lower vegetation was likely food for Orthoptera, Hymenoptera, some Coleoptera, Hemiptera, Psocoptera and some Diptera (Jarzembowski 1995). The Auchenorrhyncha (Homoptera) may have been associated with the numerous ferns at that time.

The insect predators (entomophagous) are Odonata, lower aculeate Hymenoptera, notonectoid Hemiptera, some Diptera, Raphidioptera and Neuroptera. Predators (with chewing mouthparts) include Odonata, Raphidioptera, adult Neuroptera and Hymenoptera, and predators (with sucking mouthparts) include Neuroptera larvae and some dipterans and hemipterans (Jarzembowski 1995). Aerial predators would be Odonata; arboreal predators would be Raphidioptera and Neuroptera; leaf litter predators would be some larval Raphidioptera, empidid and rhabionid Diptera (Jarzembowski 1995).
Jarzembowski (1995) summarized the anti-predation strategies of the insects, such as cryptic patterns on the wings of kalligrammatids (Neuroptera), wing shedding in Isoptera and a ‘click’ escape mechanism in elateriform Coleoptera.

Bivalves, gastropods, ostracods, conchostrachens, barnacles, foraminiferans, pterosaurs, isopods, echinoderms, fish, dinosaurs, sharks and reptiles are also present in the Wealden fauna (Gallois 1978; Jarzembowski 1991).

2.9. Climate and Environmental Change in the Purbeck and Wealden

The Purbeck and Wealden combined lasted for approximately 21 Ma and throughout that time the environment and climate underwent many changes. The main trend of change is from a semi-arid condition in the Lower Purbeck, becoming increasingly wetter through the Middle Purbeck onwards into the Wealden. This section reviews the published evidence for the Purbeck/Wealden climate change, with the divisions of Sedimentology and Palaeontological evidence.

2.9.1. Sedimentology

On a large scale the sedimentological evidence points to a lagoonal environment in the Purbeck, displayed by the characteristic lagoonal limestones. Evaporites are observed in the Lower Purbeck becoming less frequent and rare from the base of the Marly Freshwater Beds upwards (Coram 2005). The sedimentology of the Wealden indicates a fluvial/lacustrine dominated environment with cycles of sandstone and mudstone, with the mudstone becoming more dominant toward the end of Wealden times (the Weald Clays) (Allen 1998).

On a smaller scale clay minerals have highlighted a possible change in climate (tables 2.2 and 2.3).
### Table 2.2. Clay minerals with their environment preference (Hallam *et al.* 1991; Coram 2005).

<table>
<thead>
<tr>
<th>Mineral</th>
<th>Inferred Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kaolinite</td>
<td>Indicative of high temperature and high precipitation</td>
</tr>
<tr>
<td>Smectite</td>
<td>Indicative of warm conditions with seasonal variation in humidity</td>
</tr>
<tr>
<td></td>
<td>(also suggests a less pronounced wet and more pronounced dry season)</td>
</tr>
<tr>
<td>Palygorskite</td>
<td>Indicative of arid/semi arid conditions</td>
</tr>
<tr>
<td>Illite</td>
<td>No environment indication</td>
</tr>
</tbody>
</table>

### Table 2.3. Summarizing the clay mineralogy and the interpretation of climate (Sladen & Batten 1984; Ruffell & Batten 1990; Hallam *et al.* 1991; Coram 2005).

<table>
<thead>
<tr>
<th>Stratigraphy</th>
<th>Clay Minerals</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lulworth</td>
<td>Throughout formation</td>
<td>High smectite, some palygorskite and a lack of kaolinite</td>
</tr>
<tr>
<td>Durlston</td>
<td>Cinder Beds</td>
<td>Clay mineralogy changes</td>
</tr>
<tr>
<td></td>
<td>mid-Marly Freshwater Beds</td>
<td>Palygorskite is not seen any more</td>
</tr>
<tr>
<td></td>
<td><em>Intermarine Beds</em></td>
<td>Kaolinite reappears</td>
</tr>
<tr>
<td>Rest of Purbeck into the Wealden</td>
<td>Kaolinite is significant throughout (at the expense of smectite)</td>
<td></td>
</tr>
<tr>
<td>Late Wealden (late Barremian)</td>
<td>Reappearance of palygorskite</td>
<td>Indicates an increase in aridity</td>
</tr>
</tbody>
</table>

Other evidence suggesting a moistening of climate includes an increase of pyrite, sand, glauconite and reworked clastics in the higher Purbeck rocks (West 1979;
Coram 2005), the presence of siderite in the Wealden (Hallam 1984) and the character of palaeosols (Allen 1998).

2.9.2. *Palaeontological Evidence*

The types of aquatic biota are dependant on the water conditions; in the Purbeck the ostracods and molluscs have been used to demonstrate palaeosalinity (Horne 2002; Radley 2005). The palaeosalinity information obtained from these organisms reflects a change from a drier to a more humid climate.

Evidence from bioturbation, which appears at the base of the Marly Freshwater Beds, would suggest that the water was much fresher than previously in the Purbeck (Coram 2005).

Within the vertebrate fauna, the greatest diversity is seen in the Marly and Cherty Freshwater beds (Coram 2005). In the Middle and Upper Purbeck, dinosaur tracks, other vertebrate traces, crocodile and turtle remains are observed; these are rare or absent in the Lower Purbeck (see papers in Milner & Batten 2002). This may suggest a greater abundance of fresh water and food, reflecting a more tolerable ‘wetter’ climate (Coram 2005).

The evidence from palaeobotany is very limited with regard to plant macrofossils (Batten 2002). However, the miospore (spore or pollen grain less than 200 μm) record is very useful. For much of the Lower and Middle Purbeck the pteridophytes, characteristic of a ‘wetland’, were restricted and indeed confined to small damp habitats; later on they become more widespread and diverse up into lower Wealden times (change to a wetter climate) and then declined towards the end of Wealden times (return to a more arid environment) (Allen 1998; Batten 2002; Coram 2005).

It is difficult, however, to pinpoint the exact time of the change in climate in the Purbeck and Wealden, because the many studies on sedimentology and palaeontology give conflicting results (Norris 1969; Sladen & Batten 1984; Hunt 1985; Coram 2005).
CHAPTER 3. MATERIAL AND METHODS

3.1. Fossil acquisition

All the fossils were acquired from prior collected material such as museum collections and one private collection (where all described material has been, or will be, deposited in museum collections). The museums whose collections were used are the Booth Museum of Natural History, Brighton (BMB); Natural History Museum of London (BMNH Pal.), Maidstone Museum and Bentliff Art Gallery (MNEMG), Sedgwick Museum of Earth Sciences, Cambridge (CAMSM) and Devizes Museum, Wiltshire. The private collection used was that of Dr Robert Coram (Swanage), representing over 10 years of collecting.

3.2. Study of the fossils

The fossils were studied immersed under a 10% solution of ethanol to enhance fine detail. The microscope used was an Olympus SZH stereozoom microscope. An aeroneedle (Selden, 2003) was used when needed, to remove dust and small particles that obscured the wing. Line drawings were created using a camera lucida attachment. Where necessary the part and counterpart drawings were merged to form a composite image using a light-box, which gave a more complete venation drawing. The drawings were scanned into a computer to create a digital image, which was then labelled using Adobe Illustrator. Digital photographs were taken with a Nikon D1X SLR digital camera, and a Canon 450D SLR digital camera; the cameras were fitted with a macro lens and mounted on a rostrum stand.

3.3. Wing venation

Descriptions of the specimens were made using a modified version of the terminology of Comstock (1918) (Figs 3.1 and 3.2), with a few exceptions in accordance with current usage in neuropterology (e.g. Oswald 1993a; Archibald & Makarkin 2006).
Figure 3.1. The schematic wing venation diagram (Comstock 1918), which is used to name veins on the wings of all insects.

Figure 3.2. Modified venation diagram (modified from Comstock, 1918). The brackets show an alternative venation pattern sometimes used.

Wing vein abbreviations are as follows: C, costa; Sc, subcosta; R, radius; Rs, radial sector; Rs1, first branch of Rs; Rs2, second branch of Rs; M, media; MA, media anterior; MP, media posterior; MP1, first branch of MP; MP2, second branch of MP; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; A, analis; r, radial cell; dc, discal cell; mc, medial cell; ac, anal cell; p, pterostigma.
3.3. Problems Associated with Palaeoentomology

3.3.1. Fragmentary specimens

The majority of the specimens used in this study are of a fragmentary nature. The insects are represented by disarticulated wings with no body parts preserved. On rare occasions both fore and hind wings have been preserved, but, in the vast majority of cases only one wing is present. The wings are on the whole incomplete, for example, a wing may have a portion missing, or the specimen may be represented by a small fragment of the wing. The problems in identification that result from only having a wing of an insect will be discussed below in detail. The problem of having wing fragments are that one is unable to identify the specimen to lower taxonomic ranks such as family, genus or species and if the specimen is in a particularly bad state it may be impossible to say in which Order the specimen may belong. Therefore, many specimens were discarded and only the important/better-preserved specimens have been illustrated in this thesis.

3.3.2. The wing problem

The majority of extant Neuropterida species are described and diagnosed on the basis of morphology, in particular genital morphology (Aspöck & Aspöck 2008). As mentioned previously (Chapter 2.1.) the relationships of Neuropterida families/Orders have been studied using morphological and molecular data. The wings of Neuropterida are useful; they can be used to distinguish between Orders/families/genera and in some cases species (Plant 1997). Venation, however, is not just different between species, it can be different within species; this is called intraspecific variation, and examples of this and what can cause it are given below.

Sexual dimorphism (differences between the male and female of a species) can cause differences in the wing of the same species; the major difference observed in most species of Neuropterida is size, the female being larger than the male (Aspöck & Aspöck 1972).

Species of Raphidioptera can be identified on the basis of venation, for example, in Plant’s (1997) key for the differentiation of species of British Raphidioptera, venational features are used to distinguish between the four species (*Atlantoraphidia maculicollis, Phaeostigma notata, Xanthostigma xanthostigma* and *Subilla confinis*).
The keys use specific features to identify the species. A warning, however, has to be made; while some features are fixed, others are variable. Through my own observations of specimens in The Manchester Museum and through published literature that figures numerous specimens of the same species, I have seen that variations do occur that are intraspecific such as:

- Small variation is observed in the terminal forking of veins. Differences are seen in the male and female and even in the right and left wing in the same specimen (Aspöck et al. 1983)
- Angles of some veins also change between specimens from 1˚ to ~25˚
- Extra crossveins may be observed between specimens e.g. in the pterostigmal area

These differences can be ignored when one has the whole animal; they can be disregarded when, for example, genitalia between the specimens is the same. However, when one has only a fossil wing, this is more difficult.

Extant species of Megaloptera are not identified on the basis of venation, but are usually separated by the examination of genitalia. For example, the British species *Sialis lutaria*, *S. fulginosa* and *S. nigripes* are separated on genital morphology or in females on the anal plates. The venation of these three species of *Sialis* is very similar and unreliable as a method of identification (Plant, 1997).

A non-biological factor that can alter venation is post mortem deformation, for example tectonic (heat and pressure) distortion can occur. This is observed in Carboniferous insects (Jarzembowski, pers. com. 2008) and possibly in the Purbeck (Coram, pers. com. 2008). Softening of the cuticle causing wing distortion and wings settling at an angle onto soft sediment and being vertically compressed on the bedding planes may also have an effect on venation.

However, if one is cautious and takes these factors into account, and tries to be as conservative (without being over conservative) as possible when naming taxa, then no problems should arise. The fact is that true biological species cannot be described (as there is no way of knowing if fossil insects could have successfully mated, producing fertile offspring, especially when looking at just wings). Therefore one is
dealing with morphospecies, species that are described solely on morphological characters.
PART ONE A:

NEUROPTERIDA OF THE LOWER CRETACEOUS OF SOUTHERN ENGLAND
PURBECK LIMESTONE GROUP

And dead wings carried like a paper kite

Robert Frost, from Design (1936)
CHAPTER 4. LACEWINGS (INSECTA: NEUROPTERA) FROM THE LOWER CRETAEous PURBECK LIMESTONE GROUP OF SOUTHERN ENGLAND

(Jepson, J.E., Makarkin, V.N. and Jarzembowski, E.A. Lacewings (Insecta: Neuroptera) from the Lower Cretaceous Purbeck Limestone Group of southern England. Submitted to Palaeontology)

4.1. Abstract

Several new lacewing taxa are described from the Purbeck Limestone Group of southern England. *Sophogramma wimbledoni* sp. nov. (Kalligrammatidae), *Pterinoblattina purbeckensis* sp. nov., *P. fasciata* sp. nov., *Purbepsychops parallela* gen. et sp. nov. (Psychopsidae), *Ovalorobius purbeckensis* gen. et sp. nov. (Prohemerobiidae), *Mesosmylidus vulgaris* gen. et sp. nov., *Osmychrysa minima* gen. et sp. nov., *O. anomala* gen. et sp. nov., *Stenochrysa gradata* gen. et sp. nov. (Osmylidae), *Mesypochrysa minuta* sp. nov. (Chrysopidae), *Purbemerobius medialis* gen. et sp. nov. (?Hemerobiidae), *Epimesoberothus osmylodes* gen. et sp. nov. (Berothidae) and *Paraksneura alleni* gen. et sp. nov. (Incertae sedis) are described and figured. *Pterinoblattina pluma*, *P. penna* (Psychopsidae), *Osmylopsis duplicata* (Osmylidae) and *Sialium sipylus* (Nymphidae) have been redescribed and refigured with their family affinity being ascertained. The genus *Valdipsychops* has been synonymized with *Pterinoblattina* after the redescription of *P. pluma*.

*Key words:* Psychopsidae, Chrysopidae, Osmylidae, ?Hemerobiidae, Nymphidae, Kalligrammatidae, Dorset

NEUROPTERA along with the Orders Raphidioptera and Megaloptera make up the superorder Neuropterida. Neuropterida are holometabolous insects, undergoing complete metamorphosis (Grimaldi & Engel 2005). Neuropteran (lacewing) adults are mostly predators with biting mouthparts; some also consume pollen or honeydew. The generally terrestrial larvae are sucking predators in foliage, leaf litter and soil or, rarely, parasitic.

There are approximately 6000 described species of extant Neuroptera in 17 families (Aspöck 2002b). In Britain today there are six families: Chrysopidae, Osmylidae, Coniopterygidae, Hemerobiidae, Myrmeleontidae and Sisyridae, and sixty-six species (Plant 1997). British Mesozoic Neuroptera are known from the Upper
Triassic (Tillyard 1932), from the Lower Jurassic, with genera attributed the families Prohemerobiidae, Mesopolystoechotidae [=Polystoechotidae], Brongniartiellidae, and Kalligrammatidae (Whalley 1988) and the Lower Cretaceous Wealden Supergroup, represented by the families Kalligrammatidae, Psychopsidae, Osmylidae, Ithonidae and two incertae sedis (Jarzembowski 2001; Jepson et al. 2009a (chapter 7)). The older Purbeck Limestone Group underlies the Wealden Supergroup; previously only four species of Neuroptera had been formally described: Sialium sipylus Westwood, Pterinoblattina pluma Giebel, P. penna Scudder and Osmylopsis duplicata Giebel (Westwood 1854; Giebel 1856; Scudder 1885; Whalley 1988). Herein we revise these species and describe 8 new genera and 12 new species.

4.2. Geological Setting

The Purbeck Limestone Group of southern England is a predominantly lagoonal succession currently considered to be basal Cretaceous (Berriasian) in age (c. 146 – 140 ma: Ogg et al. 1994). The Group is divided into a lower Lulworth Formation and upper Durlston Formation, attributed here to the Lower and Upper Berriasian respectively, although the precise position of the Jurassic/Cretaceous boundary is still in dispute, and may lie within the Lulworth Formation (Allen & Wimbledon 1991; Ensom 2002b; W. A. Wimbledon, pers. comm. 2009). Insect fossils are common and diverse in fine-grained fissile micrites in both the Lulworth and Durlston formations, comprising mainly disarticulated remains of terrestrial taxa.

With the exception of one specimen collected from a quarry near Teffont, in the Vale of Wardour, Wiltshire (National Grid Reference ST 991 310), all material described herein was collected from the coastal outcrop at Durlston Bay, near Swanage, Dorset (National Grid Reference SZ 035 780), the type section of the Purbeck Limestone Group and most prolific source of Purbeck fossil insect material. Fossil insects from this site were first studied and named in the mid 19th Century, principally by Prof. J. O. Westwood (1854). It remains highly productive and has provided the holotypes of approximately 200 insect species to date.

Fossils of Neuropterida are relatively uncommon in the Purbeck Limestone Group, comprising 1.4 per cent of identifiable insect wings from Durlston Bay (Coram
2005). Approximately three-quarters of these are Neuroptera, described below; the remainder are Raphidioptera, recently described by Jepson et al. (2009b (chapter 5)).

4.3. Material and Methods

The neuropteran material is deposited in the following collections: Devizes Museum, Wiltshire; MNEMG, Maidstone Museum and Bentlif Art Gallery, Kent; BMNH, the Natural History Museum, London; and CAMSM, the Sedgwick Museum of Earth Sciences, Cambridge.

The material was studied using an Olympus SZH stereomicroscope with a camera lucida attachment for producing drawings. Some drawings are composite, merging the part and counterpart to establish a more complete venation; this was achieved using a light box. 10% ethanol was used to enhance vein detail. Photographs were taken using a Canon EOS 450D digital SLR camera mounted on a rostrum stand, except the Natural History Museum, London specimens, which were photographed by Phil Crabb (NHM).

We follow the traditional (sensu Wootton 2002) venational terminology of Comstock (1918) with the recent interpretation of Oswald (1993b) and Archibald and Makarkin (2006). Wing vein abbreviations are as follows: C, costa; Sc, subcosta; R, radius; R1, first branch of R; Rs, radial sector; Rs1, most proximal branch of Rs; M, media; MA, media anterior; MP, media posterior; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; 1A–3A, first to third anal veins.

4.4. Systematic Palaeontology

Order NEUROPTERA Linnaeus, 1758

Family KALLIGRAMMATIDAE Handlirsch, 1906

Genus Sophogramma Ren et Guo, 1996


Type species. Sophogramma papilionaceum Ren et Guo, 1996, by original designation.
**Diagnosis.** Eye-spots absent in both wings; in forewing, Rs1 profusely branched distally; both MA and MP arched, not forked until terminal branching; in hind wing, costal space very broad; CuA dividing near wing base into 2 long branches; CuP appears to originating proximal to fork of CuA (Ren and Guo, 1996).

**Included species.** Six species from Lower Cretaceous of Eurasia: Lower Berriasian of England (new record), Valanginian/Barremian of Transbaikalia, Russia, and Barremian of the Yixian Formation, NE China (Ren & Guo 1996; Yang et al. 2009; Makarkin 2010; herein).

*Sophogramma wimbledoni* sp. nov.

1996 Kalligrammatidae; Ross and Jarzembowski, p. 113, text-fig. 5.

**Derivation of name.** After William Wimbledon


**Type locality and horizon.** Near Teffont, Wiltshire; Lulworth Formation; Lower Berriasian.

**Diagnosis.** Proximal branching of anterior branch of CuA in hind wing absent.

**Description.** Hind wing, 44 mm preserved length (estimated complete length about 60 mm), 36.8 mm preserved width. C not preserved, costal space incomplete, 11-12 subcostal veinlets (including perhaps humeral veinlet) and several crossveins.
between them preserved. Sc, R1 incomplete with many, rather regularly spaced crossveins preserved between them. Space between R1 and Rs nearly equal in width, with 16 r1-rs crossveins preserved. Rs origins very near to wing base, with 10 branches preserved, some forked distally. MA and MP appear originated separately from Rs (or M dividing into MA and MP very close to wing base). MA concave, simple for most length. MP with 3 anteriorly directed branches. Cu origin not preserved. CuA forked near to wing base, its anterior branch slightly concave, posterior branch strongly convex; both running parallel to each other, not branched before terminal branching. CuP strongly convex, pectinately branched distally. 1A very long, few branched distally. 2A long, running very close to 1A, pectinately branched. 3A poorly determinable, perhaps pectinate. Rather closely spaced numerous crossveins throughout wing. Wing membrane appears brown; eye-spot not detected.

*Remarks.* Four species of the genus *Sophogramma* are known only from forewings (Ren & Guo 1996; Makarkin 2010), but the fifth (*Sophogramma lii* Yang *et al.*) is a beautifully preserved complete specimen with open wings (Yang *et al.* 2009). The preserved hind wing venation of the Purbeck species is very similar to that of *S. lii*, particularly in the structure of the M and Cu systems. Cu of the new species has 3 long branches beginning near the wing base, and CuA is deeply forked and CuP not. Previously, only two genera were known whose Cu has 3 long branches, these were, *Limnogramma* Ren, 2003 (Makarkin *et al.* 2009) and *Kalligrammula* Handlirsch, 1919 (i.e., *Kalligrammula senckenbergiana* Handlirsch, 1919). The latter requires restudy, and the venation as figured in Handlirsch (1919, Fig. 1) does not allow the basal forking of Cu to be determined. In *Limnogramma*, CuP is deeply forked, and CuA is not (Makarkin *et al.* 2009). However, the assignment of this species to *Sophogramma* is somewhat tentative because of incompleteness and poor preservation of the holotype of *S. wimbledoni* sp. nov., but if our interpretation of the venation is correct, we can say with some confidence that it belongs to this genus.
Kalligrammatidae gen et sp. indet

Figure 4.2

Figure 4.2. Kalligrammatidae gen et sp. indet BMNH Pal. I. 3958. A. venation drawing. B. photograph. Scale bar = 1 mm.


Locality and horizon. Purbeck Limestone Group, Durlston Bay, Swanage.

Description. Wing 18.7 mm preserved length, 13.8 mm preserved width. Apparently only 6 branches of Rs partially preserved, two forked; numerous crossveins present throughout.

Remarks. A small fragment of a kalligrammatid wing, which unfortunately has no features preserved that allow identification to a lower taxonomic rank. It differs, however, from the other Purbeck kalligrammatid, particularly in its larger size.

Family PSYCHOPSIDAE Handlirsch, 1906

Genus PTERINOBLATTINA Scudder, 1885, sit. nov.

1885b Pterinoblattina; Scudder, p. 105.
2009b (chapter 7) Valdipsychops Jepson et al., p. 1330, syn. nov.

Type species. Blatta pluma Giebel, 1856, by subsequent designation (Handlirsch 1906–08: 607).

Diagnosis. In forewing, Rs dichotomously branched; several short gradate series of crossveins in radial space; CuA concave with relation to MP, pectinately branched; CuP non-pectinate.

Remarks. Examination of the type specimens of the Purbeck species of this genus (*P. pluma* and *P. penna*) shows with confidence that the genera *Pterinoblattina* and *Valdipsychops* are synonyms, and therefore belong to the family Psychopsidae. Unfortunately, the features of the type species are too vague to determine the family assignment with certainty. But other species of the genus having similar size, colour pattern and venation allow a confident placement within Psychopsidae. Previously, this genus had been placed within the family Brongniartiellidae. However, examination of photographs of the type species of the type genus of the family (i.e., *Brongniartiella gigas* (Weyenbergh)) shows that the latter has quite different venation from that of *Pterinoblattina* (Makarkin & Archibald 2005; Makarkin 2010). The assignment of *Pterinoblattina kobdoensis* Ponomarenko, 1986 (Lower Cretaceous of Mongolia) to this genus is doubtful.

*Pterinoblattina pluma* (Giebel, 1856)

Figure 4.3

1854 Unnamed neuropteran; Westwood, p. 394, pl. 15, fig. 14.
1856 *Blatta pluma* Giebel, p. 322 (Blattoptera).
1864 *Blattidium pluma*; Heer, p. 289 (Blattoptera).
1880 *Blatta pluma*; Geinitz, p. 520 (Blattoptera).
1885a *Pterinoblattina pluma*; Scudder, p. 755, fig. 935 (Blattoptera).
1885b *Pterinoblattina pluma*; Scudder, p. 105, 106 (Blattoptera).
1886 *Pterinoblattina pluma*; Scudder, p. 469, 470, pl. 48, figs 7, 8 (Blattoptera).
1906–08 *Pterinoblattina pluma*; Handlirsch, p. 608, pl. 48, fig. 7 (Prohemerobiidae).
1988 *Pterinoblattina pluma*; Whalley, p. 48, 56, 58, fig. 9 (Brongniartiellidae).

1993 *Pterinoblattina pluma*; Jarzembowski, p. 178 (Neuroptera).

1993 *Pterinoblattina pluma*; Ross and Jarzembowski, p. 418 (Brongniartiellidae).

**Figure 4.3.** *Pterinoblattina pluma* holotype, BMNH Pal. I. 3968. A. ?Forewing venation drawing. B. photograph. Scale bar = 1 mm.


**Type locality and horizon.** Durlston [= Durdlestone] Bay, Swanage, Dorset; Durlston Formation; Upper Berriasian.

**Diagnosis.** Several transverse costal gradate series.

**Description.** ?Forewing 8.8 mm preserved length (estimated length 20 mm), 5.2 mm preserved width. Costal space incomplete; 26 subcostal veinlets preserved, some forked near margin; costal gradate series present. Sc, R1, Rs incomplete. Subcostal and R1 spaces equal in width. Nine sc-r1 crossveins preserved. Rs with ten branches preserved, majority dichotomously forked, forming 30 branches distally. Few crossveins preserved in radial space. M, Cu, A not preserved.

**Remarks.** *Pterinoblattina pluma* is represented by a very fragmentary specimen and as such there are very few diagnostic characters preserved to allow a confident separation from the other species of *Pterinoblattina*. The main diagnostic character of *P. pluma* is the presence of several gradate series of costal crossveins.
Pterinoblattina penna Scudder, 1885b

Figure 4.4

1885b *Pterinoblattina penna* Scudder, p. 106, 108 (Blattoptera).
1886 *Pterinoblattina penna*; Scudder, p. 470, pl. 48, fig. 14 (Blattoptera).
1906–08 *Pterinoblattina penna*; Handlirsch, p. 608 (Prohemerobiidae).
1949 *Pterinoblattina penna*; Martynova, p. 168 (Brongniartiellidae).
1988 *Pterinoblattina penna*; Whalley, p. 48, 58, fig. 10 (Brongniartiellidae).
1993 *Pterinoblattina penna*; Jarzembowski, fig. 4 (Brongniartiellidae).

Figure 4.4. *Pterinoblattina penna* holotype, BMNH Pal. I. 12324. A. Forewing venation drawing. B. photograph. Scale bar = 1 mm.

*Holotype.* BMNH Pal. I.12324 (Brodie colln.). An incomplete forewing.

*Type locality and horizon.* Durlston [=Durdlestone] Bay, Swanage, Dorset; Lulworth Formation; Lower Berriasian.

*Diagnosis.* Absence of costal gradate series; reduced colour pattern.

*Description.* Forewing, preserved length 10.4 mm (estimated length 19 mm), preserved width 7.7 mm. C not preserved. Costal space wide, about 3 times wider than ‘vena triplica’, with 38 subcostal veinlets preserved, many forking towards anterior wing margin. ‘Vena triplica’, formed by Sc, R1 and Rs, runs parallel and straight, with 12 sc-r1 crossveins and three r1-rs crossveins preserved. Rs with 18 branches, many forked, some dichotomously, forking to 31 distally. Several crossveins preserved in radial space, forming two small gradate series. Fork of M not preserved; MA and MP (convex) appear simple before terminal branching; Cu incomplete, CuA pectinately branched, CuP and Anal veins not preserved.
Remarks. The wing of *Pterinoblattina penna* is interpreted as a forewing because of the extremely broad costal space, a posterior pectinate vein (CuA) and a convex vein anterior to it (MP). However, in this interpretation CuA is concave in relation to MP which is more characteristic of hind wings. But, in *P. purbeckensis*, sp. nov. the concavity/convexity relationships are the same (see below). Therefore, it is possible that these relationships are diagnostic of the genus, or these wings maybe hind despite their broad costal space. In *P. logunovi* (Jepson et al. 2009a (chapter 7)), the type species of *Valdipsychops* from the Wealden, these relationships appear the same: MP is clearly convex and CuA is slightly concave (Jepson et al. 2009b (chapter 7): fig. 7; anterior vein designated as ‘MA’ is MA, posterior is MP). Unfortunately, all psychopsid wings, from both the Purbeck and Wealden, are very incomplete with the basal forking of M and Cu not being preserved, which does not allow confident identification of the veins.

*Pterinoblattina purbeckensis* sp. nov.

Figure 4.5

Figure 4.5. *Pterinoblattina purbeckensis* sp. nov. holotype, DB175/NEUR 11. A. Forewing venation drawing. B. photograph. Scale bar = 1 mm.

Derivation of name. After the Isle of Purbeck, Dorset.

Holotype. MNEMG [DB175/NEUR 11]. An incomplete forewing, collected by R.A. Coram.

Type locality and horizon. Durlston Bay, Swanage, Dorset; Clements’ (1993) Bed DB175, Corbula beds, Durlston Formation; Upper Berriasian.

Diagnosis. Large size; spotted colour pattern.
Description. Forewing, 15 mm preserved length (estimated length 19 mm), 10 mm preserved width. C not preserved, costal area with 35 subcostal branches preserved and one gradate series of crossveins preserved. Sc, R1 and Rs forming ‘vena triplica’. Sc long curving, terminating on R1 distally. R1 long with eight preserved branches distally. Eight sc-r1 branches. Rs pectinately branched with 14 branches, many branches heavily forked. Crossveins preserved in radial space forming a few gradate series. M deeply forked (one-third of vein length), both branches appear simple. CuA pectinately branched, with seven branches. CuP non-pectinately branched with two primary branches, forking to four at posterior wing margin. 1A, forked with two primary branches, forking to four at posterior wing margin. 2A incomplete, with two branches. Six gradate series of crossveins preserved throughout radial, medial, cubital sector. Colour pattern preserved on wing.

_Pterinoblattina fasciata_ sp. nov.

Figure 4.6

![Figure 4.6](image)

Figure 4.6. _Pterinoblattina fasciata_ sp. nov. holotype, DB175/NEUR 1. A. Forewing venation drawing. B. photograph. Scale bar = 1 mm.

Derivation of name. From Latin _fascia_, band, in reference to the presence of pale band over fuscous forewing.

Holotype. MNEMG [DB59/NEUR 1]. An incomplete wing, collected by R.A. Coram.

Type locality and horizon. Durlston Bay, Swanage, Dorset; Clements’ (1993) Bed DB59, Soft Cockle beds, Lulworth Formation; Lower Berriasian.
Diagnosis. One costal gradate series; colour pattern: thick stripe basally and near apex.

Description. Forewing, preserved length 12.5 mm (estimated length about 18 mm), preserved width 11 mm. C not preserved, costal space with 40 subcostal veinlets preserved, majority forked, some dichotomously, closely spaced. One longitudinal costal gradate series of crossveins. Sc, R1 and Rs partially preserved; origin and termination not seen. Seven sc-r1 crossveins and three r1-rs crossveins preserved. Rs pectinately branched, many-forked dichotomously. Fork of M not preserved; configuration of MA unknown; MP convex, with terminal forking. CuA incomplete, pectinately branched. CuP and A not preserved. Colour pattern: thick stripes near base and apex.

Remarks. This species is placed in Pterinoblattina on the basis of the dichotomously branched Rs, pectinately branched CuA, and colour pattern. The colour pattern is similar to that of the Wealden species P. logunovi and P. proudlovei (Jepson et al. 2009b (chapter 7)).

Pterinoblattina sp. B

Figure 4.7

![Diagram of Pterinoblattina sp. B](image)

Figure 4.7. Pterinoblattina sp. B, BMNH Pal. I. 12311. A. forewing venation drawing. B. photograph. Scale bar = 1 mm.


Locality and horizon. Purbeck Limestone Group, Durlston Bay, Swanage, Berriasian.
**Description.** Forewing preserved length 10.5 mm (estimated length about 20 mm), preserved width 7.1 mm. C, Sc, R1 not preserved. Rs partially preserved, branches, some forked. Crossveins in radial space randomly arranged. M apparently two branched, origin not preserved; MA, MP fork not preserved. CuA convex, pectinately branched with six? branches. CuP partially preserved (two-four branches), apparently not pectinate. Anal veins not preserved.

**Remarks.** This species is assigned to *Pterinoblattina* because of the concave pectinately branched CuA, the Rs branching similar to that of some other species (e.g., *P. penna*, but not as multi-forked as in the majority of species placed in *Pterinoblattina*) and the radial crossveins are numerous and forming an irregular short series (with additional randomly arranged crossveins).

Genus **PURBEPYSCHOPSIS** gen. nov.

*Type and only species.* *Purbepsychopsis parallela* gen. et sp. nov.

*Derivation of name.* From Purbeck and *Psychopsis*, a genus-group name. Gender feminine.

*Diagnosis.* Elongate wing; parallel mostly simple branches of Rs; heavy distal forking of MA and MP; CuA dichotomous and CuP pectinate.

*Remarks.* The genus has been tentatively placed in Psychopsidae. The venation of this genus is mostly similar to that of *Epactinophlebia* (Upper Jurassic of Karatau, Kazakhstan) and several undescribed species from the Lower Cretaceous locality of Baissa (East Siberia) in general venational configuration and in the absence of crossveins, particularly in the radial space. The latter feature may be an artefact of preservation; but many Baissa specimens have no crossveins as well; therefore this is probably an autapomorphy of this genus (or genera group).
Purbepsychopsis parallela gen. et sp. nov.

Figure 4.8

Figure 4.8. Purbepsychopsis parallela gen. et sp. nov., CAMSM J58307. A. forewing venation drawing. B. photograph. Scale bar = 1 mm

Derivation of name. From Latin parallelus, parallel, in reference to the parallel branches of Rs.

Holotype. CAMSM [J58307]. A nearly complete forewing.

Type locality and horizon. Durlston Bay, Swanage, Dorset; Soft Cockle Beds, Lulworth Formation (interpreted from sediment by RAC), Lower Berriasian.

Diagnosis. As for genus.

Description. Forewing preserved length 15 mm (estimated length about 16-17 mm), preserved width 6.8 mm. C not preserved, costal space with 30 subcostal veinlets preserved. Subcostal and R1 spaces relatively narrow, equal in width. Rs with 25 parallel branches, vast majority not forked until end-twigging. M fork not preserved. MA concave, pectinately branched distally with five branches. MP convex, pectinately branched distally with four branches. Cu forked near wing base. CuA strongly convex proximal to distal dichotomous branching. CuP concave, pectinately branched with nine simple branches. 1A pectinately branched with four branches. 2A dichotomously forked. 3A incomplete, pectinately branched, with three branches preserved.
Family PROHEMEROBIIDAE Handlirsch, 1906

Genus OVALOROBIUS gen. nov.

*Type and only species. Ovalorobius purbeckensis* gen. et sp. nov.

*Derivation of name.* From Latin *ovalis*, oval, and –*robius*, a traditional ending of hemerobiid-like genera (from Hemerobius, a genus-group name), in reference to the oval shape of the type species forewing. Gender masculine.

*Diagnosis.* Large size; CuA dichotomously branched.

*Remarks.* The assignment of the genera *Liassopsychops* Bode and *Stenoleuta* Bode to Prohemerobiidae (Ponomarenko 1996) is very doubtful. *O. purbeckensis* gen. et sp. nov. has been placed within Prohemerobiidae on the basis of Sc not being fused distally.

Ovalorobius purbeckensis gen. et sp. nov.

Figure 4.9

Figure 4.9. *Ovalorobius purbeckensis* gen. et sp. nov., DB175/ NEUR 4. A. forewing venation drawing. B. photograph. Scale bar = 1 mm

*Derivation of name.* After the Isle of Purbeck, Dorset.

*Holotype.* MNEMG [DB175/NEUR4]. An almost complete forewing, collected by R.A. Coram.

*Type locality and horizon.* Durlston Bay, Swanage, Dorset; Clements' (1993) Bed DB175, Corbula beds, Durlston Formation; Upper Berriasian.
**Diagnosis.** As for genus.

**Description.** Forewing preserved length 10.9 mm (estimated length 12.2 mm), width 7.3 mm. C preserved, costal area with over 26 subcostal crossveins preserved, many forked near anterior wing margin. Sc preserved, termination not preserved. R1 preserved, forking distally. Rs pectinately branched, with 12 primary branches, many of which are forked, producing over 20 branches. M deeply forked 0.75 mm from origin. MA and MP both deeply forked, forking again near posterior wing margin. Cu appears deeply forked, fork not preserved. CuA simple for most of length, non-pectinate, forking to give seven branches at posterior wing margin. CuP heavily branched, with three primary branches, forking to give 17 branches, each with end-twigging. 1A deeply forked, with both branches forking. 2A forked, with both branches forking again giving seven branches at posterior wing margin. 3A incomplete.

Family OSMYLIDAE Leach, 1815

Subfamily ?MESOSMYLININAE Bode, 1953

Genus MESOSMYLIDUS gen. nov.

*Type and only species.* Mesosmylidus vulgaris gen. et sp. nov

*Derivation of name.* From the Mesozoic and Osmylidae. Gender masculine.

*Diagnosis.* Long, pectinately branched CuP, with up to ten branches.

*Remarks.* The subfamily classification of the fossil Osmylidae has not been studied. Mesosmylininae was created to include Mesosmylina exornata Bode, 1953 from the Lower Jurassic of Germany. In later work, Ponomarenko (1996) adequately redescribed this species. Three other species were included in this genus: M. mongolica Ponomarenko, 1984 (Lowet/ Middle Jurassic of Mongolia), M. sibirica Ponomarenko, 1985 (Middle Jurassic of Siberia) and M. falcifera Ansorge, 1996 (Lower Jurassic of Germany). M. sibirica is based on a poorly preserved specimen; its congeneric relationship with other species is impossible to confirm. The other three species may indeed belong to one genus. In particular, they share the few-pectinate CuP. The genus Jurosmylus [=Mesosmylus Panfilov, 1980] from the Upper Jurassic of Kazakhstan has similar venation, such as the structure of CuP (this genus
is probably not synonymous with *Mesosmylina*, being distinguished by other characters). These two genera may constitute the subfamily Mesosmylininae. It is unclear if *Mesosmylina*, as well as *Stenosmylina* Jepson *et al.*, 2009b from the Wealden Supergroup, belong to it, because they both possess a very long CuP.

*Mesosmylidus vulgaris* gen. et sp. nov.

Figure 4.10

![Figure 4.10. *Mesosmylidus vulgaris* gen. et sp. nov., DB175/NEUR9. A. forewing venation drawing. B. photograph. Scale bar = 1 mm](image)

*Derivation of name.* From Latin *vulgaris*, usual, in reference to generalised venation.

*Holotype.* MNEMG [DB175/NEUR 9]. An incomplete forewing, collected by R.A. Coram.

*Type locality and horizon.* Durlston Bay, Swanage, Dorset; Clements’ (1993) Bed DB175, Corbula beds, Durlston Formation; Upper Berriasian.

*Description.* Forewing preserved wing length 8.5 mm (estimated length 11-12 mm), preserved width 3.2 mm. Costal space rather broad, with 15 simple subcostal simple veinlets preserved, rather closely spaced. Subcostal space narrow, no sc-r1 crossveins detected. Rs originating from R near wing base; six r1-rs crossveins in proximal R1 space. Rs zigzagged, with two branches preserved; branches of Rs zigzagged. M deeply branched; MA simple for most of length, forked distally; MP forked many times distally, forming seven branches. Cu forked near wing base. CuA simple for most of its length, forking to four branches distally. CuP pectinately branched with 10 branches, some distal branches forked. Numerous crossveins
throughout radial to cubital spaces. One cup-1a crossvein preserved. 1A pectinately branched with six branches. Colour pattern consists of fuscous patches at ends of some crossveins proximally and fully dark-shaded crossveins distally.

Subfamily ?GUMILLINAE Navás, 1912

(=EPIOSMYLINAE Panfilov, 1980)

Genus OSMYLOCHRYSA gen. nov.

*Type species.* Osmylochrysa minima gen. et sp. nov.

*Included species.* Type species and Osmylochrysa anomalata gen. et sp. nov.

*Derivation of name.* Osmylo- (from Osmylus, a genus group name), and –chrysa, a traditional ending of chrysopoid genera (from Chrysopa, a genus group name [from Greek chrysos, gold, and opa, eyes]), in reference to osmylid affinity and superficial resemblance to chrysopids. Gender feminine.

*Diagnosis.* Presence of only one crossvein between R1 and Rs before origin of Rs1 in forewing.

*Included species.* Two species described below.

*Remarks.* The venation and wing size of this genus are most similar to those of the genus *Epiosmylus* Panfilov, 1980 (the subfamily Gumillinae). Unfortunately, the diagnosis of Gumillinae includes such features as very long antennae and enlarged scapus, which are not preserved in the specimen. Therefore, the subfamily affinity of the genus is preliminary.
*Osmylochrysa minima* gen. et sp. nov.

Figure 4.11

![A: Venation drawing. B: Photograph. Scale bar = 1 mm](image)

Figure 4.11. *Osmylochrysa minima* gen. et sp. nov., DB175/TM1096. A. forewing venation drawing. B. photograph. Scale bar = 1 mm

**Derivation of name.** From Latin *minimus*, smallest, in reference to smallest size of the holotype among gumillines.

**Holotype.** MNEMG [DB175/TM1096]. An incomplete forewing, collected by Mr A. A. Mitchell.

**Type locality and horizon.** Durlston Bay, Swanage, Dorset; Clements' (1993) Bed DB175, Corbula beds, Durlston Formation; Upper Berriasian.

**Diagnosis.** More distal branching of 1A [distal to the origin of Rs].

**Description.** Forewing, 12.7 mm preserved length (estimated length 13 mm), 3.3 mm preserved width. Costal space typical for osmylids; 35 subcostal veinlets, majority simple, more closely spaced and forked towards the apex. Trichosors present on anterior wing margin, towards apex. Sc and R1 fused distally; veinlets of Sc+R1 forked. Seven r1-rs crossveins. Rs pectinately branched, partially preserved; Rs1 originated far distal to origin of Rs. M partially preserved; its fork not visible. Four m-cua crossveins preserved. Cu forked near wing base; CuA and CuP incomplete, forking not preserved. 1A pectinately branched, with simple branches. One 1a-2a crossvein. 2A incomplete, probably pectinately branched, with one branch preserved.
Osmylochrysa anomalala gen. et sp. nov.

Figure 4.12

Figure 4.12. Osmylochrysa anomalala gen. et sp. nov., DB175/NEUR18. A. forewing venation drawing. B. photograph. Scale bar = 1 mm

Derivation of name. From Latin anomalus, anomalous, in reference to the presence of subcostal crossveins in the forewing.

Holotype. MNEMG [DB175/NEUR18]; a proximal half of the forewing, collected by R. A. Coram.

Type locality and horizon. Durlston Bay, Swanage, Dorset; Clements’ (1993) Bed DB175, Corbula beds, Durlston Formation; Upper Berriasian.

Diagnosis. Presence of subcostal crossveins and more proximal branching of 1A [proximal to the origin of Rs].

Description. Forewing, preserved length 5.4 mm (estimated length 11-12 mm) preserved width 3.1 mm. Costal space relative broad, dilated at basal c. one-fifth, narrowed basally, with 12 simple, widely spaced subcostal veinlets preserved. Subcostal space narrow, with four crossveins preserved. Three widely spaced rs-r1 crossveins preserved. Rs zigzagged, apparently pectinate with two branches partially preserved; one crossvein preserved between these. Origin of Rs1 distant from origin of Rs. One rs-m crossvein and two rs-ma crossveins preserved. M deeply forked; MA and MP simple for most of length, distal part of vein not preserved. Two ma-mp crossveins, four each m-cua and mp-cua crossveins. Cu dividing into CuA and CuP close to base. CuA pectinately branched distally with four simple branches. Four cua-cup crossveins. CuP pectinately branched with two branches. 1A pectinately branched with three branches.
Remarks. The venation of this species is somewhat ‘chrysopid-like’, especially in posterior portions of the wing (e.g., short CuA with simple, widely-spaced branches). In particular, it slightly resembles the chrysopoid family Mesochrysopidae, but the configuration of the venation is very different between them.

Subfamily UNCERTAIN

Genus STENOCHRYSA gen. nov.

Type and only species. Stenochrysa gradata gen. et sp. nov.

Derivation of name. From Greek stenos, narrow, and –chrysa, a traditional ending of chrysopoid genera (from Chrysopa, a genus group name), in reference to [presumable] narrow forewing of the type species. Gender feminine.

Diagnosis. Narrower R1 space [almost as wide as subcostal space] with widely-spaced crossveins.

Remarks. This genus may belong to Gumillinae, but the fragmentary nature of the wing does not allow a confident placement.

Stenochrysa gradata gen. et sp. nov.

Figure 4.13

Figure 4.13. Stenochrysa gradata gen. et sp. nov., DB175/NEUR12. A. forewing venation drawing. B. photograph. Scale bar = 1 mm

Derivation of name. From Latin gradatus, gradate, in reference to the presence of gradate series of crossveins in the radial space of the forewing.

Holotype. MNEMG [DB175/NEUR12], a fragmentary anterior portion of the forewing. Collected by R. A. Coram.
**Type locality and horizon.** Durlston Bay, Swanage, Dorset; Clements' (1993) Bed DB175, Corbula beds, Durlston Formation; Upper Berriasian.

**Diagnosis.** As for genus.

**Description.** Forewing, preserved length 27 mm (estimated length about 35 mm); preserved width 6.2 mm. Costal space relatively narrow; 25 simple subcostal veinlets preserved. Subcostal space comparatively broad, no subcostal crossveins detected. R1 space very narrow; six very widely spaced r1-rs crossveins preserved. Rs pectinately branched, with seven preserved branches. Twelve crossveins in radial space. Two rs-ma crossveins. M deeply forked, MA and MP incomplete, one ma-mp crossvein preserved. Two mp-cua crossveins preserved. Cu deeply forked, CuA and CuP incomplete; CuP pectinately branched, with 2 branches preserved. Three cu-a-cup crossveins; one cup-a1 crossveins. Anal veins not preserved.

Genus OSMYLOPSIS Handlirsch, 1906, sit. nov.

1906–08 Osmylopsis Handlirsch, p. 614.

**Type and only species.** Abia duplicata Giebel, 1856, by monotypy.

**Revised diagnosis.** Falcate hind wing; distal-most veinlets of Sc+R1 forked.

**Remarks.** The family affinity of this genus was hitherto unclear because of an inadequate original description. It was usually considered as Neuroptera incertae sedis (Handlirsch 1906–1908; Martynova 1949, 1962; Carpenter 1992). Handlirsch (1939) thought that Osmylopsis might be assigned to Epigambridae, a very poorly-defined family of Neuroptera. The hind wing of *O. duplicata* is poorly preserved but its examination shows with confidence that it belongs to the family Osmylidae (unknown subfamily).
Osmylopsis duplicata (Giebel, 1856)

Figure 4.14

1854 Unnamed orthopteran; Westwood, p. 390, 396; pl. 18, fig. 42.
1856 Abia duplicata Giebel, p. 264, 416 (Sialidae).
1886 Pterinoblattina? binneyi Scudder, p. 472, 473 (Blattoptera).
1887 Pterinoblattina? binneyi; Geinitz, p. 200 (Blattoptera; as a synonym of Abia duplicata).
1906–08 ?Osmylopsis duplicata; Handlirsch, p. 614; pl. 48, fig. 15 (Neuroptera incertae sedis).
1939 Osmylopsis duplicata; Handlirsch, p. 76 (?Epigambriiidae).
1949 Osmylopsis duplicata; Martynova, p. 169 (Neuroptera incertae sedis).
1993 Osmylopsis duplicata; Jarzembowski, p. 178 (Neuroptera).
2003 Osmylopsis duplicata; Makarkin and Archibald, 176 (Neuroptera familia incertae sedis).

Figure 4.14. Osmylopsis duplicata, holotype, BMNH Pal. I. 3954. A. forewing venation drawing. B. photograph. Scale bar = 1 mm


Type locality and horizon. Durlston [=Durdlestone] Bay, Swanage, Dorset; Lulworth Formation; Upper Berriasian.

Diagnosis. As for genus.

Description. Hind wing 10.4 mm preserved length (estimated length about 14 mm), width about 4.0 mm. C preserved; trichosors not detected. Costal space narrow, slightly dilated apically. Subcostal veinlets widely spaced proximally, more closely spaced distally; Sc+R1 veinlets closely spaced, four distal-most forking. Sc fused
with R1 far distal to wing apex; Sc+R1 entering margin well before wing apex. Subcostal space rather broad. Origin of Rs not preserved. Rs strongly zigzagged medially, smoother distally, with 12 branches, majority with terminal forking. R1 space (between R1 and Rs) rather narrow medially, very narrow distally; 6-7 r1-rs crossveins preserved. Crossveins in radial space poorly preserved, apparently rare. M incomplete, origin and fork of MA and MP not preserved. MA strongly concave, pectinately branched, with 4-5 branches, most (or all) with terminal forking. MP slightly convex, pectinately branched, with 5 branches, some with terminal forking. Two ma-mp, 3 mp-cua crossveins preserved. CuA pectinately branched, with 5 simple branches preserved. CuP, Anals veins not preserved.

Remarks. *Pterinoblattina? binneyi* is based on the same specimen as *Abia duplicata* (see Scudder 1886: 473).

Family CHRYSOPIDAE Schneider, 1851

Subfamily LIMAIINAE Martins-Neto and Vulcano, 1989

Genus MESYPOCHRYSA Martynov, 1927

*Type species.* Mesypochrysa latipennis Martynov, 1927 (Late Jurassic of Karatau, Kazakhstan), by monotypy.

*Diagnosis.* Complete fusion of basal portion of MA and R, then stem of Rs; MA appears as proximal branch of Rs.

*Included species.* Sixteen species from Late Jurassic (Oxfordian/ Kimmeridgian) to Early Cretaceous (Late Aptian) of Europe (1 species, herein), Kazakhstan (5 species), Russia (Transbaikalia; 6 species), Mongolia (1 species), China (1 species) and Brazil (2 species) (Makarkin 1997a; Nel et al. 2005b).
Mesypochrysa minuta sp. nov.

Figure 4.15

Figure 4.15. *Mesypochrysa minuta* sp. nov., holotype, DB175/NEUR 28. A. hind wing venation drawing. B. photograph. Scale bar = 1 mm

Derivation of name. From the Latin *minutus*, meaning minute, small.

Diagnosis. Broad mediocubital space in hind wing; small size.

Holotype. MNEMG [DB175/NEUR28]. A small poorly preserved hind wing, collected by R. A. Coram.

Type locality and horizon. Durlston Bay, Swanage, Dorset; Clements’ (1993) Bed DB175, Corbula beds, Durlston Formation; Upper Berriasian.

Description. Hind wing preserved length 6.7 mm (estimated length about 7 mm), width 2.7 mm. Costal space narrow, with seven preserved subcostal veinlets. Sc termination not observed. R1 long, termination not preserved. Two distal r1-rs crossveins preserved. Rs with six branches, most with terminal forks. Two gradate series of crossveins in radial to mediocubital spaces: inner with 4 crossveins and outer with 8 crossveins, both nearly parallel to each other and hind margin. M fork absent; MA appears from Rs like its proximal branch; MP appears fused with R basally; both simple most of length, forking terminally. Cu origin and fork not preserved. CuA pectinately branched with three simple branches. Distal portion of CuP partially preserved with one pectinate branch preserved. Mediocubital space (between MP and CuA) very broad. Distal cua-cup crossvein short. Anal veins not preserved.

Remarks. The specimen is very poorly preserved, with veins just visible under ethanol. Some features, however, are not observable; for example, the dense cross-
venation near the wing apex. This however, may be due to the poor preservation of the specimen, because other crossveins are not preserved, and the ones that are preserved are very faint. It has been confidently placed within the genus *Mesypochrysa* on the basis of the basal fusion of MA with R and then Rs in the hind wing. This is the smallest known fossil species of Chrysopidae, and first record of the family from the Mesozoic of Europe.

Family ?HEMEROBIIDAE Leach, 1815

Genus PURBEMEROBIUS gen. nov.

*Type and only species:* Purbemerobius medialis gen. et sp. nov.

*Derivation of name.* From Purbeck, and Hemerobius, a genus-group name. Gender masculine.

*Diagnosis.* Larg size; structure of Rs; CuA pectinately forked relatively close to posterior wing margin; CuP simple for most of length.

*Remarks.* The placement of this genus in the family Hemerobiidae is tentative due to the poor preservation of the wing. The character that suggests placement in this family is the anterior radial trace bearing 3 “radial-sectors”. Fossil hemerobiids are rare in the Mesozoic with only two confirmed taxa: *Promegalomus anomolous* from the Jurassic of Karatau, Kazakhstan, and *Cretomerobius disjunctus* from the early Cretaceous of Mongolia (Panfilov 1980; Ponomarenko 1992b). A hemerobiid-like species, *Protohemerobius perexiguus*, that has been described from the Wealden most likely represents an undescribed family (Jepson et al. 2009a (chapter 7)). *Mesohemerobius jeholensis*, from the Lower Cretaceous of China, was previously placed in Hemerobiidae, but was removed from the family by Makarkin et al. (2003) and placed as Neuroptera *incertae sedis*. Two species of hemerobiid have been described from the Lower Cretaceous Crato Formation of Brazil; however these are in need of redesription to confirm their placement in the family (Makarkin et al. 2003).
**Purbemerobius medialis** gen. et sp. nov.

Figure 4.16

![Figure 4.16](image)

Figure 4.16. *Purbemerobius medialis* gen. et sp. nov., holotype, DB175/NEUR5. A. hind wing venation drawing. B. photograph. Scale bar = 1 mm

Derivation of name. From *Media*, a median vein, in reference to the structure of the *Media* of the hind wing.

Holotype. MNEMG [DB175/NEUR 5]. An incomplete hind wing, collected by R. A. Coram.

Diagnosis. As for genus.

Type locality and horizon. Durlston Bay, Swanage, Dorset; Clements' (1993) Bed DB175, Corbula beds, Durlston Formation; Upper Berriasian.

Description. Hind wing preserved length 8.8 mm (estimated length 9.5 mm), width 4.5 mm. C preserved. Costal space narrow, 44 costal veinlets, majority simple. Sc long, forking before termination on wing margin. R1 long dichotomously forked distally 1.3 mm before wing apex, one r1-rs crossvein. Rs with three branches; Rs1 deeply forked, one crossvein preserved between branches, both branches forking distally, splitting to 12 branches at termination on posterior wing margin. Three rs1-rs2 crossveins. Rs2 branch simple most of length, dichotomously forked distally. Two rs2-rs3 crossveins preserved. Rs3 pectinately branched with seven branches, heavily damaged, simple most of length, forking distally. One rs1-ma crossvein. M deeply forked, origin not preserved. MA forks just before mid-point of vein, dichotomously branched, heavily damaged, one crossvein preserved between the branches. MP deeply forked, first branch simple most of length, forking before
termination at posterior wing margin, one crossvein preserved between branches. Second branch deeply forked, both branches simple for most of length, forking near termination, one crossvein preserved between branches. CuA origin not preserved, pectinately branched, 11 branches, mostly simple, some forked. One crossvein preserved within CuA. CuP simple most of its length, forking near termination at posterior wing margin. 1A pectinately branched, six branches preserved, one forked. 2A partially preserved, appears pectinately branched, three branches partially preserved.

Remarks. The wing appears to have been damaged prior to fossilization, with many veins being broken. This is observed especially around the mid-point of the wing, affecting mainly the lower half, towards the posterior wing margin. Purbemerobius medialis gen. et sp. nov. possibly represents the first Mesozoic fossil hemerobiid in Britain.

Family BEROTHIDAE Handlirsch, 1906

Genus EPIMESOBEROTHUS gen. nov.

Type and only species. Epimesoberothus osmylodes gen. et sp. nov.

Derivation of name. From Greek epi, near, and Mesoberotha, a genus-group name, in reference to mesoberothid appearance. Gender masculine.

Diagnosis. Simple subcostal veinlets; lack of recurrent humeral vein; forewing size (<4.5 mm); Rs with 6-7 branches; pectinately branched CuA; wide costal area.

Remarks. The forewing venation and size of the new genus are rather similar to those of the Burmese amber berothids (Engel & Grimaldi 2008), except for the pectinately branched CuA. In the latter genera, CuA is rather few-branched. Epimesoberothus gen. nov. is similar by the pectinately branched CuA to Sinosmylites Hong, 1983 from the Middle Jurassic of China, which was preliminarily assigned to the family Prohemerobiidae by Makarkin and Archibald (2005).
Epimesoberothus osmylodes gen. et sp. nov.

Figure 4.17

Figure 4.17. *Epimesoberothus osmylodes* gen. et sp. nov., holotype, USCDB/TM432. A. forewing venation drawing. B. photograph. Paratype, CAMSM TN272. C. forewing venation. D. photograph. Scale bar = 1 mm

Derivation of name. From *Osmylus*, a genus-group name, and Greek -*odes*, like or resembling, in reference to the superficial resemblance of the type species to minute osmylids.

Holotype. MNEMG [USCDB/TM432]. A nearly complete forewing, collected by Mr A. A. Mitchell.


Type locality and horizon. Holotype and paratype: Durlston Bay, Swanage, Dorset; Upper Soft Cockle beds, Lulworth Formation; Lower Berriasian.

Diagnosis. As for genus.
Description of the holotype. Forewing, length 3.7 mm, width 1.7 mm. C complete. 23 subcostal veinlets. Trichosors present on distal part of anterior margin. Sc incomplete, terminating on R1. R1 long with six branches distally. Two r1-rs crossveins. Rs with seven branches, all forking distally past mid-point of vein, forming 22 branches going into posterior wing margin. Seven crossveins in radio-media area, six forming gradate series. M deeply forked, both MA and MP fork distally 0.4 mm from posterior wing margin; MA forking to three branches, MP dichotomously branched. Cu deeply forked. CuA pectinately branched, with six branches, majority simple. CuP deeply forked. Anal veins not preserved.

Description of the paratype. Forewing, preserved length 3.8 mm (estimated length 4.5 mm), preserved width 2.1 mm. C incomplete, 20 subcostal veinlets preserved. Trichosors present on anterior wing margin. Sc terminates on R1. R1 with seven branches distally. One rs-rs1 crossvein past mid-point of wing. Rs pectinately branched, with eight branches forking distally after mid-point. Two crossveins preserved inn radial sector. One rs-m crossvein. M deeply forked (fork not preserved). MA and MP branching distally to give five branches going into posterior wing margin. CuA pectinately branched with six branches, majority simple. CuP incomplete forked to two branches. Anal veins incomplete.

Remarks. The paratype’s locality has been inferred by RAC, from the characteristic nature of the sediment (the light ‘chalky’ nature of the matrix, the abundant charcoal fragments and the small square halite (salt crystal) moulds), because no detailed locality information was present with the specimen.

Family NYMPHIDAE Rambur, 1842

Genus SIALIUM Westwood, 1854, sit. nov.

Type and only species. Sialium sipylus Westwood, 1854, by monotypy.

Diagnosis. Several subcostal veinlets forked proximal to pterostigmal region; 8 MP branches in the hind wing.

Remarks. Examination of the type species shows that the hind wing venation is typical for the family Nymphidae. In general, it is most similar to that of Mesonymphes, two species of which are known from the Late Jurassic of Germany.
and Kazakhstan (Carpenter 1929; Panfilov 1980). The latter genus is distinguished from *Sialium* as indicated in the diagnosis.

*Sialium sipylus* Westwood, 1854

Figure 4.18

1854 *Sialium Sipylus* Westwood, p. 390, 396, pl. 18, fig. 24 (Neuroptera, allied to *Sialis*).

1856 *Abia sipylus*: Giebel, p. 263, 416 (Sialidae).

1862a *Sialium Sipylus*: Hagen, p. 104 (Neuroptera).

1862b *Sialium sipylus*: Hagen, p. 10 (Neuroptera).

1884 *Syaliun [sic] Sipylus*: Geinitz, p. 571 (?Orthoptera).

1886 *Pterinoblattina ? Sipylus*: Scudder, p. 472 (Blattoptera).

1887 *Pterinoblattina ? Sipylus*: Geinitz, p. 200 (Blattoptera).

1891 *Sialium sipylus*: Scudder, p. 130 (Blattoptera).

1906–08 *Sialium sipylus*: Handlirsch, p. 609, pl. 48, fig. 10 (Nymphitidae).

1949 *Sialium siphlus [sic]*: Martynova, p. 167 (Nymphitidae).


Figure 4.18. *Sialium sipylus*, holotype, BMNH Pal. I. 13951ab. A. hind wing venation drawing. B. photograph. Scale bar = 1 mm.

*Holotype.* BMNH Pal. I. 13951ab. An almost complete hind wing.

*Type locality and horizon.* Durlston [=Durdlestone] Bay, Swanage, Dorset; Lulworth Formation; Lower Berriasian.

*Diagnosis.* As for genus.
**Description.** Hind wing, preserved length 21 mm (estimated length about 25 mm), preserved width 6.8 mm. C partially preserved, trichosors preserved apically. Subcostal space narrow, 21 subcostal veinlets preserved, becoming densely spaced distally, some forked. Sc curves towards R1 distally, (probably fused). R1 preserved only in distal part. Sc+R1 heavily forked with five preserved branches, forking to 11. Five r1-rs crossveins preserved. Rs pectinately branched with 12 branches, forking close to posterior wing margin. Numerous crossveins preserved in proximal part of radial sector in a random pattern. MA origin not preserved, forking towards posterior wing margin to give ten branches. Eight ma-rs crossveins preserved. MP simple for most of its length, dichotomously forking very close to posterior wing margin to give four branches. Six mp-ma crossveins preserved. Five mp-cua crossveins preserved. Cu origin not preserved. CuA pectinately branched, with nine branches, majority forked distally to give 22 branches at posterior wing margin. CuA terminates past mid-way point of wing. Four crossveins preserved within. Three cua-cup crossveins preserved. CuP pectinately branched with seven branches forking to 11 distally, no crossveins preserved within. Anal veins not preserved.

**Family NEUROPTERA familia incertae sedis**

Genus PARAKSENEURA gen. nov.

**Type and only species. Parakseneura alleni gen. et sp. nov.**

**Derivation of name.** From Greek paraksenos, strange, and Neuroptera, in reference to uncertain family affinity of the genus.

**Diagnosis.** Large size; broad proximal costal area; costal crossveins; dense arrangement of subcostal veinlets in distal part of wing.

**Remarks.** The systematic position of Parakseneura alleni gen. et sp. nov. is uncertain. However, it has similar venation to the younger Cratochrysa (Neuroptera familial incertae sedis) from the Crato Formation, Brazil, which was placed as basal with respect to Chrysopoidea (Nel et al. 2005b). Cratochrysa and P. alleni gen et sp. nov. also have a superficial similarity to the megalopteran family Corydasialidae Wichard et al., 2005, with regards to Sc and R1 not being fused, many crossveins between R1 and Rs, M and Cu not being fused near wing base, and CuA (in C. martinsnetoi, not preserved in P. alleni gen. et sp. nov.) and CuP being forked.
Therefore, it is possible that *Cratochrysa* and *Parakseneura* gen. nov. could be allied to Megaloptera, however, without body parts it is impossible to ascertain the true affinity of the fossil.

*Parakseneura alleni* sp. nov.

Figure 4.19

![Figure 4.19](image.png)

Figure 4.19. *Parakseneura alleni* gen. et sp. nov., holotype, HCSD NEUR 1. A. forewing venation drawing. B. photograph. Scale bar = 1 mm.

*Derivation of name.* After the late Professor Perce Allen.

*Holotype.* MNEMG [HCSD NEUR 1]. An almost complete forewing, collected by R. A. Coram.

*Diagnosis.* As for genus

*Type locality and horizon.* Durlston Bay, Swanage, Dorset; probably Hard Cockle Beds, Lulworth Formation; Lower Berriasian.

*Description.* Forewing, preserved length 23.3 mm (estimated total length 24.5 mm), width 8.3 mm. Costal area widened basally, with numerous crossveins. Gradate series of crossveins (eight preserved) in costal area near base of wing. Sc and R1 not fused apically. Three sc-r1 crossveins preserved; one at mid-point of wing and two in distal part of wing. Rs has five pectinate branches, splitting into seven. Rs branches from R1 5.0 mm from base of the wing. Eight crossveins present between R1 and Rs. M and CuA not fused basally. CuA incomplete, CuP long forking approximately 4 mm from posterior wing margin. Three cua-cup crossveins preserved. Three cup-1a crossveins. Anal veins straight; 1A forked 4.0 mm from posterior wing margin; 2A with four branches preserved. Two 1a-2a crossveins preserved. A small portion of the underlying other forewing is exposed, but provides no further information.
4.5. Discussion

Prior to this study only three species of neuropterans were known from the Purbeck Limestone Group of southern England, all of which were described in the 19th century and poorly illustrated. These species *Osmylopsis duplicata*, *Sialium sipylus* *Pterinoblattina pluma* and *P. penna* have now been thoroughly described and figured. The family affinity of these species has also been confirmed, with *Osmylopsis duplicata* being placed in Osmylidae, *Sialium sipylus* in Nymphidae and *Pterinoblattina pluma* and *P. penna* in Psychopsidae. The redescription of *Pterinoblattina* has shown the psychopsid genera *Valdipsychops* from the Wealden to be a synonym. The new families recorded within the Purbeck include Osmylidae, Chrysopidae, ?Hemerobiidae, Berothidae, Kalligrammatidae and Prohemerobiidae. A *familia incertae sedis* is also present. The psychopsoid neuropterans (Psychopsidae and Kalligrammatidae) make up the majority of the neuropteran fauna and the vast amounts of undescribed fragmentary material are also of psychopsoid affinity (JEJ pers. obs. 2008–2010). Osmylidae are the next dominant group after the psychopsoids. The chrysopids, nymphids, ?hemerobiids, berothids and prohemerobiids are represented by a single species each.

The dominance of the psychopsoids may be due to them being widespread and successful within the Cretaceous, being found in many other fossil deposits at that time. Alternatively it could be that their many veined wings make them more resilient to breaking down during transport. Human bias could also be a factor, psychopsoids are easily identified as neuropteran whereas other families may be overlooked or misidentified, therefore showing a bias. The high number of osmylids may be due to their lifestyle, it is possible that osmylid larva have a semi-aquatic lifestyle based on modern analogues, therefore if they are closer to water they would have a higher chance of being washed into the depositional area and a better chance of preservation, as opposed to the fully terrestrial fauna.

The first record of Chrysopidae, Berothidae and possibly Hemerobiidae in the Mesozoic of England has been recorded. The chrysopid is the smallest representative of the family recorded with an estimated wing length of 7 mm. The presence of Berothidae within England in the Lower Cretaceous extends the families
geographical range, with them known previously from Lebanon, China, Brazil, Burma, Russia, USA, Canada and Baltic amber (Engel & Grimaldi 2008).

The geographical ranges of the genera *Sophogramma* and *Mesypochrysa* have been extended with the discovery of them in the Purbeck. *Sophogramma* was previously only known from Russia and China (Ren & Guo 1996; Makarkin 2010). *Mesypochrysa* is more globally widespread with previous occurrences documented in Kazakhstan, Russia, Mongolia, China and Brazil (Makarkin 1997a; Nel *et al.* 2005b).

The neuropteran fauna of the Purbeck is more diverse than that of the younger Wealden having a higher number of families present [Wealden 4 (Jepson *et al.* 2009a (chapter 7)) and Purbeck 7 (herein)]. There are however similarities in each fauna, for example, the psychopsoids dominate in each, with Osmylidae being the next dominant. The family Brongniartiellidae has not been found in both the Purbeck and Wealden, with previously thought brongniartiellids being shown to be of the family Psychopsidae. Both the Purbeck and Wealden have genera which are present in the younger Crato Formation, Brazil; *Principiala* (Ithonidae) in the Wealden (Jepson *et al.* 2009a (chapter 7)) and *Mesypochrysa* (Chrysopidae) in the Purbeck (herein).

The neuropteran fauna of the Purbeck would have lived in the distant woodland area proposed by Coram (2003). On death they would have undergone disarticulation and transport before deposition, leaving only their wings. The proposed climate change within the Purbeck to the Wealden which affected the raphidiopterans (Jepson *et al.* 2009b (chapter 5)), seems to have had little affect on the neuropteran fauna, with the exception of Nymphidae being present in the Lulworth Formation. Nymphids are usually associated with arid/semi-arid environments and their presence in the hotter and drier Lower Purbeck, Lulworth Formation and not in the younger Durlston Formation and Wealden could be related to the change in climate.
1. **Raphidioptera (Insecta: Neuroptera) from the Lower Cretaceous Purbeck Limestone Group, Dorset, UK.**
Raphidioptera (Insecta: Neuropterida) from the Lower Cretaceous Purbeck Limestone Group, Dorset, UK

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ABSTRACT

Four new species of snakefly (Raphidioptera: Mesoraphidiidae): Mesoraphidia durstonensis sp. nov., Mesoraphidia purbeckensis sp. nov., Mesoraphidia websteri sp. nov. and Mesoraphidia mitchelli sp. nov., are described from the Lower Cretaceous Purbeck Limestone Group, southern England. This increases the number of described snakeflies from the Mesozoic deposits of Britain from two to five species, when the doubtful family Priscaenigmatidae is excluded.

1. Introduction

The order Raphidioptera has approximately 210 extant species in two families: Raphidiidae and Inocelliidae (Aspöck, 2002; Grimaldi and Engel, 2005; Engel et al., 2006). Raphidioptera is the least diverse order of the holometabolous insects, and is grouped within the superorder Neuropterida along with Neuroptera and Megaloptera (Aspöck, 2002). The distinctive features of the order include an elongated prothorax, a long female ovipositor, and typical venation (Engel, 2002). Four autapomorphies have been suggested for the order, but only one of which can be applied to fossil wings: the forewing subcosta running into the anterior margin (Aspöck and Aspöck, 2004). The habitat preference of extant snakeflies is arboreal, in areas of cool weather with at least some periods of near freezing temperatures. This restricts them to cold temperate regions and excludes them from areas with hotter climates (Grimaldi and Engel, 2005). Mesozoic raphidiopterans, however, have been discovered in much warmer conditions such as inferred tropical climates (Grimaldi and Engel, 2005). In Britain today snakeflies are rare, with four species in four genera in the family Raphidiidae; these are restricted to arboreal environments (Plant, 1997).

The Mesozoic raphidiopterans comprise three valid extinct families: Baissopteridae, Mesoraphidiidae and Alloraphidiidae, and one doubtful extinct family, Priscaenigmatidae (see Aspöck and Aspöck, 2004 for discussion). The Mesozoic raphidiopterans are very diverse at species level, supporting the idea that extant Raphidioptera are relict (Engel, 2002; Grimaldi and Engel, 2005).

Snakeflies from the Mesozoic of Britain are rare. Jarzembowski (1984) recorded a specimen from the Weald Clay (Lower Cretaceous, Hauterivian) of Surrey. Whalley (1985, 1988) described two raphidiopterans from the Lower Jurassic of Dorset: Metaraphidia confusa (Mesoraphidiidae) and Priscaenigma obtusa (Priscaenigmatidae). Priscaenigmatidae, however, has subsequently been excluded from the order (Aspöck and Aspöck, 2004). Clifford et al. (1994) figured a snakefly (Mesoraphidia sp.) from the Purbeck Limestone Group of Dorset. This specimen, described herein along with the other Purbeck specimens, brings the total number of described species from the Mesozoic deposits of Britain to five, all in the family Mesoraphidiidae.

2. Geological setting

The Purbeck Limestone Group of southern England is a predominantly lagoonal succession currently considered to be basal Cretaceous (Berriasian) in age, although the precise position of the Jurassic/Cretaceous boundary is still in dispute, and may in fact lie within the Purbeck (Allen and Wimbledon, 1991; Ensom, 2002). The
Group is divided into a lower Lulworth Formation and upper Durlston Formation; both of these have yielded fossils of Raphidioptera.

The type section of the Purbeck Limestone Group, and the source of all currently recognised Purbeck raphidiopeteran material, is Durlston Bay, near Swanage, Dorset (National Grid Reference SZ 035 780). Fossil insects from this site were first studied and named in the mid 19th Century, principally by Prof. J. O. Westwood (1854). It remains highly productive and has provided the holotypes of approximately 200 insect species to date.

3. Systematic palaeontology

The studied material is deposited in the following collections: Booth Museum of Natural History, Brighton (BMB) and Maidstone Museum and Bentifl Art Gallery, Kent (MNEMG).

The material was studied using an Olympus SZH stereomicroscope with a camera lucida attachment for producing drawings. Some drawings are composite, merging the part and counterpart to establish a more complete venation; this was achieved using a light box. 10% ethanol was used to view vein detail. Photographs were taken using a Nikon D1X digital SLR camera mounted on a rostrum stand.

Wing vein abbreviations are as follows: C, costa; Sc, subcosta; R, radius; Rs, radial sector; Rs1, first branch of Rs; Rs2, second branch of Rs, M, media; MA, media anterior; MP, media posterior; MP1, first branch of MP; MP2, second branch of MP; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; A, analis; r, radial cell; dc, discal cell; mc, medial cell; ac, anal cell; p, pterostigma.

Order: Raphidioptera Naváš, 1918
Family: Mesoraphidiidae Martynov, 1925
Genus Mesoraphidia Martynov, 1925

Type species. Mesoraphidia grandis Martynov, 1925 from Karatau, Kazakhstan (Upper Jurassic).

Diagnosis. Wings short to long (5–18 mm long) and elongate. Diagonal costal area. Costal veinlets not exceeding 10.5 terminating at costal margin near mid-point of wing. Pterostigma long. R runs parallel to costal margin and curves with it towards apex. Rs separates from R approximately one third of length of wing from base; it is then connected to R by two crossveins forming the three radial cells. Elongated dc. Two or three medial cells posterior to MP in forewing. Anal area similar to other raphidiopterans; elliptical ac.

Included species. In addition to the type species, 21 species from the Jurassic and Cretaceous of Europe, Asia and the USA (Engel, 2002; Engel et al., 2006), and four species described below.

Mesoraphidia durlstonensis sp. nov.
Figs. 1–3
1994 Mesoraphidia sp. Clifford et al.: p.143, fig. 1

Derivation of name. The species’ name refers to Durlston Bay.


**Fig. 1.** A, B. Mesoraphidia durlstonensis sp. nov., holotype forewing BMB 0183737; Durlston Bay, Upper Berriasian. A, venation drawing. B, photograph. Scale bar represents 1 mm.

**Diagnosis.** Larger than other Purbeck Mesoraphidia. dc narrower than that of M. purbeckensis sp. nov. Costal area shorter and narrower than in M. websteri sp. nov. CuA has fewer forks than M. gobiensis Pomomarenko, 1988. Differs from all other Mesoraphidia in the following combination of characters: many costal veinlets; long pterostigma, almost half length of wing; Rs2 exhibiting a kink in vein; three radial cells, 2r wide and 3r long; Rs and MA two branched, both branches simple; lack of a distinct fork for MA; MP two branched, both branches forking once.

**Description.** Holotype forewing (Fig. 1): narrow and elongate; 10.6 mm long and 2.9 mm wide. C complete; costal area preserved with seven crossveins. Sc terminates approximately 6 mm from wing base (just past mid-point of wing) on anterior wing margin. R complete and long, terminating near wing apex; one crossvein present between R and C. 9.0 mm from wing base. Pterostigma present; over 3 mm long; beginning of pterostigma difficult to determine as pigment fades towards wing base. Three radial cells present: 1r: 2.6 mm long and 0.5 mm wide; 2r: 2.4 mm long and 0.7 mm wide and 3r: 1.7 mm long and 0.4 mm wide. Rs arises from R approximately 3.5 mm from wing base. Rs two branched; Rs1 and Rs2 simple, Rs2 exhibits a kink in vein; both Rs1 and Rs2 arise in distal part of wing near apex. dc formed by a crossvein between Rs and MA; 2.4 mm long and 0.5 mm wide (at widest point). MA arises 1.7 mm from R where M forks into MA and MP; it then runs into Rs 0.6 mm from the split with MA. MA coalesced with Rs for 1.9 mm. MA two branched with both branches simple. One crossvein present between MA and MP. MP deeply forked with each branch forked near posterior wing margin. Three cells present between MP and CuA: mc1: 1.8 mm long, 0.4 mm wide; mc2: 1.4 mm long, 0.8 mm wide and mc3: 1.3 mm long, 0.6 mm wide. CuA coalesced with M for 0.6 mm. CuA forks near posterior wing margin; distal branch forked, basal branch simple. Two crossveins present between CuA and CuP; CuP simple. Anal area is preserved with 1A, 2A and 3A present. ac oval shaped, 1.4 mm long, 0.6 mm wide.

Paratype MNEMG 2007.46: hindwing lacking basal portion (Fig. 3). Length as preserved 8.0 mm; estimated total length 10.5 mm. Width 2.7 mm. C incomplete; costal area with three crossveins present but incomplete. Sc terminates approximately 4.4 mm from wing apex (before mid-point of wing) on anterior wing margin. R long, terminating near wing apex; one crossvein present between R and C, 1.0 mm from wing apex. Pterostigma...
(or pterostigma and dark membrane) long, from base of wing (as preserved) to r-c crossvein. Three radial cells present: 1r: 2.4 mm long and 0.5 mm wide, cut by crossvein; 2r: 2.3 mm long and 0.6 mm wide and 3r: 1.2 mm long and 0.3 mm wide. Rs arises 5.7 mm from wing apex; Rs two branched; Rs1 and Rs2 simple, Rs2 has a kink in vein; both Rs1 and Rs2 arise in distal part of wing near apex. MA origin not preserved, MA and Rs coalesced for 1.1 mm before separating. dc: 2.7 mm long and 0.6 mm wide (at widest point). MA two branched, both branches simple. Two crossveins present between MA and MP. MP origin 7.5 mm from wing apex; MP deeply forked with MP1 and MP2 branched. One cell present between MP and CuA; mc: 1.7 mm long, 0.5 mm wide. CuA forks near posterior wing margin. Two crossveins present between MP and CuA. One crossvein present between CuA and CuP; CuP forked. One crossvein present between CuP and 1A. Anal area poorly preserved; 1A present, but incomplete.

**Remarks.** Three specimens have been assigned to this species comprising two forewings and two hindwings. The paratype MNEMG 2007.45 shows slight differences in wing shape and vein proportions from the holotype. However, it has been assigned to *M. durlstonensis* sp. nov. on the basis of its similar size, overall venation pattern and comparable variation observed within extant species of snakeflies (e.g. species described in Aspöck et al., 1983; Rausch and Aspöck, 1993; pers. obs. JEJ). The overlapping fore- and hindwing of MNEMG 2007.45 indicates that the paratype MNEMG 2007.46 is of the same species due to similarities in venation and size. This is the only species from the Purbeck that has a pigmented pterostigma, but this may simply be fortuitous preservation. *M. durlstonensis* sp. nov. is the largest species of snakefly from the Purbeck, being almost twice the size of the other Purbeck raphidiopterans described herein.

*Mesoraphidia purbeckensis* sp. nov.

**Fig. 4**

**Diagnosis.** Forewing small compared to most species of *Mesoraphidia*. Few costal veinlets. Differs from *M. durlstonensis* sp. nov. in possessing narrower mc3, CuA forking more proximally, and most distal r-c crossvein being closer to termination of R. dc wider than in *M. durlstonensis* sp. nov., *M. websteri* sp. nov. and *M. mitchelli* sp. nov. 1A, 2A and 3A long compared to other Purbeck *Mesoraphidia*. Differences from other *Mesoraphidia* species as for *M. durlstonensis* sp. nov.
Description. Forewing: 4.9 mm preserved length, 5.1 mm estimated total length. Width 1.4 mm. C incomplete; costal area with four crossveins present but incomplete. Sc terminates approximately 2.3 mm from wing apex (just past mid-point of wing) on the anterior wing margin. R complete and long, terminating near wing apex; one crossvein present between R and Sc, 3.8 mm from wing apex; two crossveins present between R and C, 0.4 mm and 1.9 mm from wing apex. Pterostigma not preserved. Three radial cells present: 1r: 1.2 mm long, 0.3 mm wide; 2r: 1.0 mm long, 0.4 mm wide and 3r: 0.7 mm long, 0.2 mm wide. Rs arises approximately 3.1 mm from wing apex. Rs two branched; Rs1 and Rs2 simple; both Rs1 and Rs2 arise in distal part of wing near apex. dc: 1.2 mm long and 0.4 mm wide (at widest point). MA arises 2.2 mm from origin of M + CuA. MA coalesced with Rs for short distance (~0.2 mm). MP and CuA remain near wing apex. MP deeply forked with both branches simple. One crossvein present between CuA and CuP; CuP simple. Anal area poorly preserved; 1A, 2A and 3A present but incomplete.

Remarks. M. purbeckensis sp. nov. has the smallest wing length of the Purbeck Mesoraphidia and the second smallest wing length within Mesoraphidia. It is more typical of the size of Purbeck snakeflies, with the exception of M. durlstonensis sp. nov. The pterostigma is not present; this is most likely an artefact of preservation where the pigmentation has not been preserved.

Mesoraphidia websteri sp. nov. has been tentatively assigned to a new species as its small size and venation exclude it from M. durlstonensis sp. nov. and M. mitchelli sp. nov. Costal area longer than other Purbeck Mesoraphidia. R terminates further before apex than M. durlstonensis sp. nov. Differences from other Mesoraphidia species as for M. durlstonensis sp. nov.

Diagnosis. Hindwing: incomplete, 5.2 mm preserved length, 5.7 mm estimated total length. Width 2.1 mm. C incomplete; costal area poorly preserved and incomplete with two crossveins present. Sc terminates 2.1 mm from wing apex at two-thirds of wing length. R long, terminating 0.4 mm from wing apex. Pterostigma not preserved. Three radial cells present: 1r: 1.1 mm long and 0.4 mm wide; 2r: 1.6 mm long and 0.4 mm wide and 3r: 0.6 mm long and 0.3 mm wide. Rs and MA arise at different points. Rs and MA arise at different points, Rs 3.4 mm from wing apex, MA 4.3 mm from wing apex. Rs and MA coalesced for 0.6 mm before forking. Rs two branched; Rs1 and Rs2 simple; both Rs1 and Rs2 arise in distal part of wing near apex. dc 1.6 mm long and 0.5 mm wide (at widest point). MA two branched, both branches simple. MP deeply forked with MP1 and MP2 two branched. One cell present between MP and CuA: mc: 1.3 mm long, 0.4 mm wide. CuA forks near the posterior wing margin. Two crossveins present between MP and CuA. One crossvein present between CuA and CuP; CuP simple. Anal area poorly preserved; 1A, 2A and 3A present but incomplete.

Remarks. M. websteri sp. nov. has been tentatively assigned to a new species as its small size and venation exclude it from M. durlstonensis sp. nov. and its larger size excludes it from M. mitchelli sp. nov. The apparent lack of a pterostigma, as with M. purbeckensis sp. nov., is probably an artefact of preservation.

Mesoraphidia mitchelli sp. nov. has been tentatively assigned to a new species as its small size and venation exclude it from M. durlstonensis sp. nov. and M. mitchelli sp. nov. Costal area longer than other Purbeck Mesoraphidia. R terminates further before apex than M. durlstonensis sp. nov. Differences from other Mesoraphidia species as for M. durlstonensis sp. nov.

Diagnosis. Hindwing: incomplete, 5.2 mm preserved length, 5.7 mm estimated total length. Width 2.1 mm. C incomplete; costal area poorly preserved and incomplete with two crossveins present. Sc terminates 2.1 mm from wing apex at two-thirds of wing length. R long, terminating 0.4 mm from wing apex. Pterostigma not preserved. Three radial cells present: 1r: 1.1 mm long and 0.4 mm wide; 2r: 1.6 mm long and 0.4 mm wide and 3r: 0.6 mm long and 0.3 mm wide. Rs and MA arise at different points, Rs 3.4 mm from wing apex, MA 4.3 mm from wing apex. Rs and MA coalesced for 0.6 mm before forking. Rs two branched; Rs1 and Rs2 simple; both Rs1 and Rs2 arise in distal part of wing near apex. dc 1.6 mm long and 0.5 mm wide (at widest point). MA two branched, both branches simple. MP deeply forked with MP1 and MP2 two branched. One cell present between MP and CuA: mc: 1.3 mm long, 0.4 mm wide. CuA forks near the posterior wing margin. Two crossveins present between MP and CuA. One crossvein present between CuA and CuP; CuP simple. Anal area poorly preserved; 1A, 2A and 3A present but incomplete.

Remarks. M. mitchelli sp. nov. has been tentatively assigned to a new species as its small size and venation exclude it from M. durlstonensis sp. nov. and M. mitchelli sp. nov. Costal area longer than other Purbeck Mesoraphidia. R terminates further before apex than M. durlstonensis sp. nov. Differences from other Mesoraphidia species as for M. durlstonensis sp. nov.

Mesoraphidia mitchelli sp. nov. has been tentatively assigned to a new species as its small size and venation exclude it from M. durlstonensis sp. nov. and M. mitchelli sp. nov. Costal area longer than other Purbeck Mesoraphidia. R terminates further before apex than M. durlstonensis sp. nov. Differences from other Mesoraphidia species as for M. durlstonensis sp. nov.

Diagnosis. Hindwing: incomplete, 5.2 mm preserved length, 5.7 mm estimated total length. Width 2.1 mm. C incomplete; costal area poorly preserved and incomplete with two crossveins present. Sc terminates 2.1 mm from wing apex at two-thirds of wing length. R long, terminating 0.4 mm from wing apex. Pterostigma not preserved. Three radial cells present: 1r: 1.1 mm long and 0.4 mm wide; 2r: 1.6 mm long and 0.4 mm wide and 3r: 0.6 mm long and 0.3 mm wide. Rs and MA arise at different points, Rs 3.4 mm from wing apex, MA 4.3 mm from wing apex. Rs and MA coalesced for 0.6 mm before forking. Rs two branched; Rs1 and Rs2 simple; both Rs1 and Rs2 arise in distal part of wing near apex. dc 1.6 mm long and 0.5 mm wide (at widest point). MA two branched, both branches simple. MP deeply forked with MP1 and MP2 two branched. One cell present between MP and CuA: mc: 1.3 mm long, 0.4 mm wide. CuA forks near the posterior wing margin. Two crossveins present between MP and CuA. One crossvein present between CuA and CuP; CuP simple. Anal area poorly preserved; 1A, 2A and 3A present but incomplete.

Remarks. M. mitchelli sp. nov. has been tentatively assigned to a new species as its small size and venation exclude it from M. durlstonensis sp. nov. and M. mitchelli sp. nov. Costal area longer than other Purbeck Mesoraphidia. R terminates further before apex than M. durlstonensis sp. nov. Differences from other Mesoraphidia species as for M. durlstonensis sp. nov.

Mesoraphidia mitchelli sp. nov. has been tentatively assigned to a new species as its small size and venation exclude it from M. durlstonensis sp. nov. and M. mitchelli sp. nov. Costal area longer than other Purbeck Mesoraphidia. R terminates further before apex than M. durlstonensis sp. nov. Differences from other Mesoraphidia species as for M. durlstonensis sp. nov.

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Mesoraphidia mitchelli sp. nov. has been tentatively assigned to a new species as its small size and venation exclude it from M. durlstonensis sp. nov. and M. mitchelli sp. nov. Costal area longer than other Purbeck Mesoraphidia. R terminates further before apex than M. durlstonensis sp. nov. Differences from other Mesoraphidia species as for M. durlstonensis sp. nov.
4. Discussion

Prior to this research, there have been only five fossil snakefly specimens recorded in Britain from two families: Mesoraphidiidae and Priscaenigmatidae (Jarzembowski, 1984; Whalley, 1985, 1988; Clifford et al., 1994). The position of Priscaenigmatidae in Raphidioptera, however, has been questioned (see Aspöck and Aspöck, 2004 for discussion); therefore, if it is removed from the order, fossil snakeflies in Britain would only be represented by the family Mesoraphidiidae.

The most notable features shared by the Purbeck fauna are a more ‘simplified’ venation: veins Rs and MA are two branched with both branches forking close to the posterior wing margin and MP with a deep fork with both branches forking once near the posterior wing margin. M. purbeckensis sp. nov., M. websteri sp. nov. and M. mitchelli sp. nov. are very small, with estimated wing sizes ranging from 5.1–5.7 mm; they are a little larger than the smallest known snakefly, Nanoraphidia, from the Lower Cretaceous of Burma with a wing length of 4.5 mm (Engel, 2002). This small size separates them from the majority of other Mesoraphidia species (exceptions being M. parvula (5.5 mm) and M. gaoi (5 mm) (Martynov, 1925; Ren et al., 1995)) which are almost double or more the size of these snakeflies. M. durlstonensis sp. nov., however, is of a more average size for the genus. There are significant differences between the snakefly found in the older Upper Soft Cockle beds and the snakeflies from the younger Corbula beds. These differences are the distinct fork of MA and the two medial cells and the posterior fusion of CuA and MP.

The Purbeck climate is interpreted as having been seasonally semi-arid (Allen, 1998), providing further evidence that Mesozoic raphidiopterans were less climatically restricted than they are today. There is evidence that the climate became rather more humid midway through Purbeck times: for example, evaporites become much less frequent and there is a sustained increase in the clay mineral kaolinite (Deconinck, 1987), indicative of more intense weathering of the massifs supplying sediment to the depositional basin. The preserved material suggests that there may have been a raphidiopteran faunal change associated with this climate change, but more specimens are required to confirm this.

Extant raphidiopterans are predators of small arthropods both as larvae and adults and live exclusively on trees, the larvae very often developing under bark (Grimaldi and Engel, 2005). Purbeck raphidiopteran fossils are found alongside those of other tree-associated taxa (such as cupedoid beetles) and occasional remains of conifer foliage, all suggestive of a forested hinterland and a raphidiopteran habitat similar to that of today.

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References


PART ONE B:

NEUROPTERIDA OF THE LOWER CRETACEOUS
OF SOUTHERN ENGLAND
WEALDEN SUPERGROUP

And dead wings carried like a paper kite

Robert Frost, from Design (1936)
CHAPTER 6

2. NEUROPTERAN (INSECTA) PALAEODIVERSITY WITH PREDICTIONS FOR
   THE CRETACEOUS FAUNA OF THE WEALDEN
Neuropteran (Insecta) palaeodiversity with predictions for the Cretaceous fauna of the Wealden

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Abstract

The Wealden Group of southern England is a succession of non-marine sediments from the lower Cretaceous (c. 141–119 Ma), which also outcrop in Belgium and northwest Germany. Most insect orders are present as fossils, including Neuroptera, one of the most basal holometabolous orders. The fossil record of Neuroptera is diverse, spanning Permian–Recent, with all major family radiations having occurred prior to the Wealden. However, Wealden Neuroptera have received little attention to date, with only three families reported and one species described. The fossil record in general is notoriously incomplete, and palaeoenvironmental reconstructions can facilitate predictions of what other organisms were present in the habitat, but which were either not preserved or only occasionally preserved and yet to be found as fossils. We examine the Wealden palaeohabitat and global neuropteran palaeodiversity and consider these in relation to palaeo/biogeography of fossil and extant taxa (including habitat preferences). We predict that the following families will form components of the Cretaceous Wealden fauna: Nymphidae, Polystoechotidae, Chrysopidae, Hemerobiidae and Coniopterygidae.

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Keywords: England; Fossil; Lacewings; Mesozoic; Neuroptera; Palaeobiogeography

1. Introduction

The Wealden Group of southern England is a succession of non-marine sediments from the lower Cretaceous (c. 141–119 Ma) (Allen and Wimbledon, 1991), subdivided into the Wealden and Wessex sub-basins. The Wealden sub-basin consists of the Hastings Beds (Ashdown Beds, Wadhurst Clay, Lower and Upper Tunbridge Wells Sand, and the Grinstead Clay Formations) and the Weald Clay (Upper and Lower) (Allen and Wimbledon, 1991; Rasnitsyn et al., 1998). The Hastings Beds have been dated as Berriasian–Valanginian and the Weald Clays as Hauterivian–Aptian? (Allen and Wimbledon, 1991; Rasnitsyn et al., 1998). The Wessex sub-basin comprises the Wessex (Hauterivian) and Vectis Formations (Barremian–Aptian?) (Twitchett, 1994). In addition to the distal facies, there are two principle facies types in the Wealden: sediments of medial to proximal alluvial origin and sediments of lacustrine–lagoonal origin (Allen, 1981, 1989; Radley, 2005). The Wealden Group also outcrops in Western Europe: Belgium and northwest Germany (Allen and Wimbledon, 1991; Jarzembowski, 1995; Elstner and Mutterlose, 1996; Grimaldi and Engel, 2005) (Fig. 1).

Most insect orders are present in the Wealden Group, including Odonata, Blattodea, Orthoptera, Hemiptera, Neuroptera, Coleoptera, Mecoptera, Diptera, Trichoptera,
Hymenoptera, Isoptera, Raphidioptera (Jarzembowski, 1984, 1995) and Plecoptera (Sinitshenkova, 1998). However, the continental deposits have not been as well studied as the English deposits in terms of the insect fauna. The insects are preserved as uncrushed and unoxidized (Jarzembowski, 1984), disarticulated skeletal material (usually only wings, the reason for this sorting is unclear) in the calcareous (or ferruginous) siltstone developments or phosphatic or sideritic concretions in the clay formations. A subtropical/warm temperate (with seasonal rainfall) climatic reconstruction has been generated for the Wealden, based on the presence of certain insect orders (e.g. Isoptera) (Jarzembowski, 1995) and sedimentological evidence (Allen, 1998; Haywood et al., 2005). The occurrence of wet and dry (commonly with wild fires) seasons has been proposed, as has year round precipitation with little evidence for prolonged drought (Batten, 1998; Haywood et al., 2005). Evidence for wild fires exists in the form of fusainized elytra and plant remains (Watson and Alvin, 1996; Batten, 1998; Jarzembowski, 2003). The Wealden palaeohabitat consisted of woodland bordering Wealden water courses (Jarzembowski, 1995).

Neuroptera is one of the most basal orders of holometabolous insects (Ponomarenko, 2002; Grimaldi and Engel, 2005) and consists of approximately 6000 described extant species in 17 families (Aspöck, 2002). Their defining features include diaphanous wings with intricate, laced venation, larval sucking mouthparts formed by the maxillae and mandible, and the association of the ninth gonocoxites with the gonarcus (Grimaldi and Engel, 2005). They range in size from small (wing-span 5 mm) barklouse-like waxy lacewings, to large (wingspan exceeding 150 mm) damselfly-like antlions, and when at rest hold their wings in a roof-like position over their body. Most are poor fliers, however there are some exceptions e.g., the family Ascalaphidae, which represents the strongest and most agile fliers of the order (New, 1991). Neuroptera are widespread globally, but tend to be most abundant in the tropics, with several families having restricted distributions (New, 1991). Sixty-six extant species from six families (Chrysopidae, Coniopterygidae, Hemerobiidae, Myrmeleontidae, Osmylidae and Sisyridae) occur in Britain (Plant, 1997), with six additional families occurring on mainland Western Europe (Nevrorthidae, Berothidae, Ascalaphidae, Nemopteridae, Dilaridae and Mantispidae (Aspöck et al., 1980)). Presumably, a combination of both climatic and Channel barrier factors influence these distributions.

The fossil record of Neuroptera is diverse and spans a long period of geological time (Permian–Recent) with
all major family radiations having occurred prior to the Wealden (see later, and Ponomarenko, 2002; Grimaldi and Engel, 2005 for comprehensive reviews). However, the Neuroptera of the Wealden have received little attention to date, with only three myrmeleontiform families (†Brongniartiellidae, †Kalligrammatidae and Psychopsidae) reported (Jarzembowski, 1984) and only one species described (Jarzembowski, 2001). The absence of hemerobiiform families is enigmatic. One reason may be that the myrmeleontiform families recorded are very easily identifiable as neuropterans, whereas isolated wings from many hemerobiiform families would be considerably more difficult to attribute to Neuroptera by a non-specialist.

According to Jarzembowski (1995) the frequency of occurrence for Neuroptera in the Wealden fossil fauna is low, accounting for only 0.1–0.9% of a sample of 13,000 specimens. This is consistent with other fossil (and extant) assemblages. At least for the modern world and for Palaeogene lacustrine shales, less than 1% representation of Neuroptera is normal: Tadushi Formation, Primorye,

Fig. 2. Evolutionary tree of Neuroptera (after Grimaldi and Engel, 2005, based on Aspöck, 2002; updated to include Jarzembowski, 1980; Whalley, 1980; Schlüter, 1984; Ponomarenko, 1984; Lambkin, 1988; Makarkin, 1990a,b; Kukalova-Peck, 1991; Ross and Jarzembowski, 1993; Nel and Henrirotay, 1994; Ren and Guo, 1996; Makarkin, 1996, 1997b; Martins-Neto, 1997; Makarkin, 1998, 1999; Azar et al., 2000; Martins-Neto, 2000; Makarkin and Archibald, 2003).
Russia, about 0.3%; Bembridge Marls, about 0.1%; none are known from Eckfeld Maar, Germany; Messel, Germany; or the Bournemouth Group, England. Higher representations of Neuroptera in Palaeogene fossil assemblages are rare: about 1.5% at the Okanagan Highlands locality of McAbee; and approximately 3.8–5.0% of the Danish Fur Formation insects (depending on museum collection) (Archibald and Makarkin, 2006 and references cited therein). In modern forest communities Neuroptera have been consistently found to be less than 1% of insects: less than 1% in tropical forest canopy fogging samples in Borneo; 0.45% in window and Malaise trap samples in Queensland, Australia; and 0.25% in light trap samples in Primorye, Russia (Archibald and Makarkin, 2006 and references cited therein).

All forms of fossilization are subject to unique preservation biases. In sedimentary fossil deposits such as the Wealden, terrestrial invertebrates (Neuroptera do not have aquatic larvae, except for the families Nevrorthidae and Sisyridae) are usually allochthonous, and thus represent only a small fraction of the biota alive in the palaeohabitat. Given the incompleteness of the fossil record, it is equally important that we elucidate what other organisms were present in the environment at the same time as those preserved as fossils, but which did not get fossilized, or did so only occasionally and have yet to be found as fossils (e.g., Penney, 2005). Accurate palaeoenvironmental reconstructions based on a broad range of observed fossil taxa can facilitate this. Here, we examine the global neuropteran fossil record and consider it in relation to the palaeo/biogeography of fossil and extant taxa in order to make predictions for expected palaeodiversity of Wealden Neuroptera during the Cretaceous.

2. Methods

Palaeontological data are scarce by their very nature. New fossil Neuroptera species are often described based on singletons and only occasionally from a series of individuals, which are usually small in number. Thus, species numerical data are of limited value for quantitative assessments of palaeodiversity. Traditionally, analysis of terrestrial arthropod palaeocommunities has been at the family level, primarily as a result of a paucity of data, and has been applied extensively as the ‘higher taxon approach’ by neontologists charting the distribution, ecological correlates, and diversity patterns of extant tropical insect faunas (Labandeira, 2005). Here we use a similar approach with the fossil data.

The most recent evolutionary tree of the Neuroptera (Fig. 2) (Grimaldi and Engel, 2005; based on Aspöck, 2002, but with fossil taxa incorporated) was used to generate observed and predicted palaeodiversity spindle diagrams (Fig. 3) using the technique explained by Penney (2004a,b). This technique involves superimposing a cladogram over geological time and calibrating it using fossil data. Where a node, or new fossil record appears, the number of ranges of known taxa, based on direct fossil evidence, is counted to give an observed palaeodiversity value for that particular point in geological time. At the same point in time, a separate count is made of predicted taxa, from hypothesized range extensions, based on the presence of their sister taxon (derived from the cladogram) in the fossil record. Summing these two values gives a predicted palaeodiversity value. For details of tree construction methodology see Smith (1994); see also Lane et al. (2005). The observed palaeodiversity data were plotted over time (Fig. 4) and used to generate maximum and minimum predictions for global neuropteran family richness at the time of the Wealden. Most neuropteroid families were already widespread by the Cretaceous and adults of most families may be present in many different terrestrial environments (New, 1989), but not all can be expected to have existed in the Wealden environment. Thus, predictions specifically for the Wealden fauna were further refined based on closer scrutiny of fossil neuropteran palaeobiogeography (Fig. 5), in terms of taxa that had occurred in the region earlier in geological time and also

Fig. 3. Spindle diagrams of observed and predicted neuropteran family palaeodiversities based on data derived from the evolutionary tree (see Methods).
contemporaneous taxa from the proximate region of continental Europe.

3. Results

It is evident from the evolutionary tree (Fig. 2) that the major family radiations within Neuroptera had occurred by the time of the Wealden (see also Nel et al., 2005a). This is true for both observed and predicted palaeodiversity as demonstrated by the spindle diagrams (Fig. 3), which show barely any change over the past 100 million years. The increase of a taxon’s diversity over time is essentially a Markovian process, i.e., the newly evolved taxa are dependent on the presence of the ancestral taxa. Thus, the number of new taxa at any time is dependent, in part, upon the number of existing taxa. Therefore, the null model for the diversification process of a radiating group is a sigmoid curve with exponential increase during the incremental phase (Sepkoski, 1979). This is clearly evident in Fig. 4 and thus the palaeodiversity plot permitted accurate predictions for global neuropteran family richness values at the time of the Wealden sediments (c. 141–119 Ma), and produced a lower limit of approximately 15 and upper limit of approximately 17. However, it should be noted that no current phylogeny includes all fossil taxa, which may cast doubt on the accuracy of the above predictions. Unfortunately, this problem cannot be resolved until a thorough phylogenetic revision including all neuropteran fossil families is performed. Given the current state of taxonomic ‘chaos’ with regard to fossil Neuroptera, this does not seem likely to happen in the near future. Nonetheless, the palaeodiversity pattern in Fig. 4 is far from random, and fits perfectly that expected for diversification of a group through geological time (Sepkoski, 1979).

4. Discussion

Neuroptera are archaic insects and underwent their major family radiations during the Triassic and Jurassic, with all 17 extant families known or predicted as fossils by the Lower Cretaceous (Fig. 2). They may have been more diverse in the past than they are at present (Labandeira and Sepkoski, 1993; Grimaldi and Engel, 2005), a hypothesis supported by the presence of nine pre-Tertiary extinct families (Fig. 5). A number of additional fossil families, e.g. from the Crato Formation, were not included in the tree of Grimaldi and Engel (2005); these are poorly delimited taxonomically and systematically, and require revision (Ponomarenko, 2002; Makarkin and Archibald, 2003; Archibald and Makarkin, 2006), thus nine pre-Tertiary families represents a minimum number. The need for revision of these poorly delimited fossil families obviously creates difficulties with analyses such as we present here and this problem cannot be ignored. However, all the families we predict as undiscovered components of the Wealden fauna are extant and so this issue loses its importance. The only effect of inclusion or exclusion of these poorly defined families is likely to be a slight shift in the slope of the diversity plot during the incremental phase. This would change slightly the predicted global neuropteran palaeodiversity at the time of the Wealden, but it would not alter the family predictions we present here.

Neuroptera were widespread from the Permian onwards, constituting a significant element of the global
insect fauna, with Permian fossils recorded from South Africa, South America and Australia and Triassic fossils recorded from the former USSR and England (Fig. 5; Ross and Jarzembowski, 1993; Schlüter, 2003: Table 2 and references cited therein). There is unequivocal fossil evidence that the majority of neuropteran families had evolved by the Late Jurassic (c.155 Ma) when Pangea split to form Laurasia and Gondwana (Fig. 2). By the time of the Lower Cretaceous Wealden (c.141–119 Ma), many neuropteran families had a widespread distribution, particularly in Western Europe and Eurasia, e.g., the families †Brongniartiellidae, Nymphidae, Myrmecoleontidae, †Babinskaiidae, †Kalligrammatidae, Psychopsideae, Polystoechotidae, Chrysopidae, Osmylidae, Hemerobiidae and Coniopterygidae (Fig. 5).

It would be unrealistic to expect that all neuropteran families present globally in the Lower Cretaceous would occur in the Wealden palaeoenvironment. Indeed, numerous families have restricted distributions today and distribution ranges will have varied throughout their geological history. Therefore the predicted family palaeodiversity range of 15–17 for this period represents in excess of our upper predictable limit. Given that there are three families already recorded from the Wealden (which has been poorly studied with regard to Neuroptera), there are five extant families in southern England today that the other neuropteran families from these assemblages (†Permithonidae, †Osmynlopsychopidae, †Nymphitidae, Nymphidae and Polystoechotidae) should occur there too, although our current knowledge suggests the first two of these families may have become extinct by this time and the third may have been in decline (Fig. 5). Nonetheless, the remaining two families would almost double our predicted value from that already observed. Also, based on the extensive fossil record (including wide distributions, particularly in pre-Wealden continental European localities, see Fig. 5), and the known habitat preferences of extant species from the families Chrysopidae, Hemerobiidae, Coniopterygidae, and possibly also Mantispidae, it is difficult to exclude the probable occurrence of at least some of these families in the forests of the Wealden during the Cretaceous. However, we appreciate that our arguments here are not as strong as for the families mentioned previously because there is no evidence of their existence in England prior to the Wealden. Thus, to err on the side of caution, we cannot expect all of these families to have been present, so we restrict our predictions to those families common in southern England and adjacent warm temperate climates today: Chrysopidae, Hemerobiidae and Coniopterygidae. We appreciate that other factors may control distribution, such as the existence of water barriers, e.g. the English Channel at present, but this does not appear to have stopped these families reaching the UK, and the current absence of Wealden fossils is not evidence that they had not already done so by the Cretaceous. Thus, our minimum family palaeodiversity estimate for Wealden Neuroptera has risen to eight (including those already known), which based on our reasoning does not seem unreasonable.

The nature of predictions is that they cannot be made retrospectively and thus, they may be considered speculative axiomatically. However, given the incomplete nature of the fossil record, we feel such predictions as presented here, that are based on sound reasoning, may be important when considering biodiversity of palaeo-communities. This work forms the rationale behind a
research project being undertaken by the first author on Wealden Neuroptera, during which the predictions presented here will be evaluated. Such predictive techniques may prove useful for other insect groups and/or fossil localities.

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CHAPTER 7

3. NEW LACEWINGS (INSECTA: NEUROPTERA) FROM THE LOWER CRETACEOUS WEALDEN SUPERGROUP OF SOUTHERN ENGLAND
New lacewings (Insecta: Neuroptera) from the Lower Cretaceous Wealden supergroup of Southern England

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ABSTRACT

Eight new genera and thirteen new species of lacewings (Neuroptera) are described from the Lower Cretaceous Wealden Supergroup, Weald Sub-basin: *Principiala rudwickensis* sp. nov. (Ithonidae), *Stenomylina medialis* gen. et sp. nov., *Protosmylina bifasciata* gen. et sp. nov. (Osmylidae), *Cretapsychops corami* gen. et sp. nov., *Micropsychops paralleus* gen. et sp. nov., *Valdipsychops logunovi* gen. et sp. nov., *V. brigidae* gen. et sp. nov., *V. maculosus* gen. et sp. nov., *P. pinnatifida* gen. et sp. nov., *Polyhemerobius perexiguus* gen. et sp. nov. (Psychopsidae), *Actinophlebioides valdensis* gen. et sp. nov. and *Protohemerobius perexiguus* gen. et sp. nov. (Neuroptera familia incertae sedis). Psychopsidae are shown to dominate the neuropteron fauna, while the presence of Brongniartiellidae has not been confirmed in the Wealden, due to previously thought representatives of this family being in fact psychopsids. This is the first fossil record of Ithonidae and Osmylidae in Britain. The range of Kalligrammatidae has been extended in the Cretaceous of Britain from the mid-Valanginian to early Barremian. © 2009 Elsevier Ltd. All rights reserved.

1. Introduction

Neuroptera (lacewings) is one of three orders that make up the superorder Neuroptera (Insecta: Holometabola) (Grimaldi and Engel, 2005) and consists of approximately 6000 described extant species in 17 families (Aspóck, 2002). They are widespread globally, but tend to be most abundant in the tropics, with several families having restricted distributions (New, 1991). Sixty-six extant species from six families: Chrysopidae (green lacewings), Coniopterygidae (wax flies), Hemerobiidae (brown lacewings), Myrmeleontidae (ant lions), Osmylidae and Sisyridae (spongillaflies) occur in Britain (Pond, 1997). Prior to this study, the presence of three psychopsoid neuropteran families were recorded in the Wealden: Psychopsidae (silky lacewings), and the extinct Brongniartiellidae and Kalligrammatidae (Jarzembowski, 1980). Neuroptera have a long and diverse fossil record from the Permian to Recent with all the major family radiations having occurred prior to the Lower Cretaceous (Ponomarenko, 2002; Grimaldi and Engel, 2005). In Britain, fossil Neuroptera have been found in the Triassic (Tillyard, 1933), Jurassic (Whalley, 1988), Cretaceous (e.g. Jarzembowski, 1984,1993) and Palaeogene (Jarzembowski, 1980).

2. Geological setting

The Lower Cretaceous Wealden Supergroup (c. 140–125 Ma: Gradstein et al., 2005) of southern England is subdivided into the Weald and Wessex Sub-basins (Allen and Wimbledon, 1991). The non-marine Weald Sub-basin has yielded the most insect remains and it is from this sub-basin that the specimens described herein have been collected (Fig. 1). The Weald Sub-basin consists of the Hastings Beds Group (Ashdown Beds, Wadhurst Clay, Lower and Upper Tunbridge Wells Sand, and the Grinstead Clay formations) and the Weald Clay Group (Upper and Lower Weald Clay formations) (Allen and Wimbledon, 1991; Rasnitsyn et al., 1998). The majority of insects and the specimens described herein are from the Weald Clay Group, which are dated as Hauterivian–Aptian? (Allen and Wimbledon, 1991; Rasnitsyn et al., 1998). The Weald Clays represent a lacustrine–lagoonal environment (Allen, 1981,1989; Radley, 2005). The insect orders that have so far been recorded in the Weald Sub-basin are Odonata, “Blattaria”, Orthoptera, Hemiptera, Neuroptera, Coleoptera, Mecoptera, Diptera, Trichoptera, Hymenoptera, Isoptera, Raphidioptera (Jarzembowski, 1984,1995) and Plecoptera (Sinitskenova, 1998). The insects are preserved as
uncrushed and unoxidized, disarticulated skeletal material, with isolated wings being the most common (Jarzembowski, 1984). They are found in the calcareous siltstone developments or phosphatic or sideritic concretions in the clay formations. The climate has been interpreted as subtropical/warm temperate with seasonal rainfall (Allen, 1998; Haywood et al., 2005). The occurrence of wet and dry (commonly with wild fires) seasons has been proposed, as has year-round precipitation with little evidence for prolonged drought but high evaporation (Batten, 1998; Haywood et al., 2005). Wildfire evidence exists in the form of fusainized coleopteran elytra and plant remains (Watson and Alvin, 1996; Batten, 1998; Jarzembowski, 2003).

3. Material and methods

The neuropteran material described herein was collected from the Weald Clay Group in various brickworks: Clockhouse (Lower Weald Clay Formation, Hauterivian), Auclaye, Rudgwick and Smokejacks (Upper Weald Clay Formation, Barremian) (locations labelled in fig. 1). The material is deposited in the following institutions: Booth Museum of Natural History, Brighton (BMB), Natural History Museum, London (BMNH Pal.) and Maidstone Museum and Bentlif Art Gallery, Kent (MNEMG).

The material was studied using an Olympus SZH stereomicroscope with a camera lucida attachment for producing drawings. Some drawings are composites, merging the part and counterpart to establish a more complete venation; this was achieved using a light box. 10% ethanol was used to enhance vein detail. Photographs were taken using a Nikon D1X digital SLR camera mounted on a rostrum stand, except *Psychopsites rolandi* gen. et sp. nov. which was drawn by EAJ using a camera lucida attachment on a M4A Wild microscope and photographed by Tony Mitchell (volunteer Maidstone Museum) using a Nikon Coolpix 5000 digital camera.

We follow the traditional (*sensu* Wootton, 2003) venational terminology of Comstock (1918) with the recent interpretation of Oswald (1993a) and Archibald & Makarkin (2006). Wing vein abbreviations are as follows: C, costa; Sc, subcosta; R, radius; R1, first branch of R; Rs, radial sector; Rs1, most proximal branch of Rs; M, media; MA, media anterior; MP, media posterior; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; 1A–3A, first to third anal veins.

4. Systematic palaeontology

Order: Neuroptera Linnaeus, 1758
Family: Ithonidae Newman, 1853 (¼ Rapismatidae Krüger, 1922)
Genus Principiala Makarkin et Menon, 2007

*Principiala rudwickensis* sp. nov.

**Fig. 2**

Derivation of name. After the Rudgwick Brickworks locality where the specimen was collected.

**Material.** Holotype BMB 025005, -6 (part and counterpart), an incomplete forewing. Rudgwick Brickworks, Upper Weald Clay, Lower Cretaceous, Barremian.

**Diagnosis.** May be distinguished from *Principiala incerta* by the following forewing character states [alternative character states are given in brackets]: most proximal branch of Rs terminated on MA long [very short in *P. incerta*]; numerous crossveins between proximal 5 branches of Rs: some veins having a ‘zig-zag’ appearance [not detected in *P. incerta*]; proximal 6 fused branches of Rs are straight [curved in *P. incerta*].

**Description.** Forewing shape indeterminate, preserved wing length 9.4 mm (estimated length about 11–12 mm). C not preserved. Few subcostal veinlets preserved. Gradate series of crossveins in costal space partially preserved. Sc partially preserved appearing to fuse with R1 distally; these veins at least, closely approach each other towards wing apex. 5 subcostal crossveins preserved. R incomplete, origin and termination not preserved. 2 r-rs crossveins preserved. Rs with 17 pectinate branches. Rs1 fuses with MA at approximately half

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**Fig. 1.** Geological map of the Wealden Supergroup, southeast England, with locations (brickworks) where Neuroptera have been found marked on. (Redrawn and modified from Gallois, 1978; Ross and Cook, 1995; Rasnitsyn et al., 1998).
MA length; other proximal 6 Rs branches fuse to form 1 vein, numerous crossveins between them forming polygonal cells. Majority of other Rs branches are simple, with few forked. 6 preserved r-ma crossveins. Origin of MA not preserved. MA long, reaching wing base distad of midpoint of wing, forked two-thirds along its length. 5 ma-mp crossveins at midpoint of MA detected. MP origin not preserved. MP with posterior pectination of anterior branch and anterior pectination of posterior branch, branches mainly with marginal forking, and with numerous crossveins between them. Cu poorly preserved. CuA incomplete, pectinately branched, with more than ten pectinate branches.

Remarks. Hitherto, only one fossil ithonid has been described, Principiala incerta Makarkin et Menon, 2007 from the Lower Cretaceous Crato Formation, Brazil (Makarkin and Menon, 2007). The general wing structure of Principiala rudgwickensis sp. nov. is very similar to that of P. incerta, so that the assignment of this new species to the genus Principiala seems to be undoubted despite its fragmentary condition. Both species share some important characters in the forewing, including the fusion of the proximal branches of Rs with MA and each other, the peculiar configuration of MP, narrow space between R1 and Rs, and the presence of numerous costal and subcostal crossveins. The ithonid affinity of the genus is based on a set of distinctive head and thoracic characters, as well as general ithonid features of the venation found in the type species. Principiala rudgwickensis sp. nov. is the oldest ithonid formally described, pre-dating P. incerta from the younger Crato Formation (Upper Aptian). A third fossil species of Ithonidae, having similar venation and belonging to the same species group,
**Diagnosis.** As for genus.

**Description.** Forewing 13 mm preserved length, 4 mm preserved width (estimated length about 15–16 mm). Costal space narrow, basal subcostal veinlets, all simple. Sc poorly preserved, appears very close to R1. Numerous (preserved), regularly spaced crossveins between R1 and Rs. 5 Rs branches preserved. Crossveins in radial space rather sparse, not forming distinct series. M not branched, simple for most of length, forking 2 mm from posterior wing margin. 11 crossveins between M and CuA. Origin of Cu not detected, close to wing base; CuA simple for most of length, branched at two-thirds of its length, with 6 pectinate branches. 9 crossveins preserved between CuA and CuP. CuP pectinately branched with 14 branches. 1 crossvein preserved between CuP and 1A. 1A pectinately branched with 3 branches. 2A with 1 branch. Trichosors present on posterior wing margin.

**Remarks.** One species of osmylid (Osmylus fulvicephalus Scopoli) is present in Britain today (Plant, 1997).

**Genus Protosmylina gen. nov.**

**Type and only species.** Protosmylina bifasciata gen. et sp. nov.

**Derivation of name.** From the Greek protos, before, and the genus Osmylus, reference to probable protosmyline subfamilial affinity of the genus. Gender feminine.

**Diagnosis.** Forewing venation is most similar to that of protosmyline genera, but may be distinguished from these by branches of Rs more numerous, closer spaced, more distal position of fork of M.

**Remarks.** The forewing venation of Protosmylina is particularly similar to that of Protosmylus Krüger, 1913 from the upper Eocene Baltic amber (see Pictet-Baraban and Hagen, 1856: Pl. 8, fig. 16), the type genus of the subfamily Protosmylinae. They are united by the following character states: Sc fused with R1 far distant from wing apex; subcostal crossveins (at least one) present; all crossveins in the radial space arranged in three gradate series; few, sparsely spaced crossveins between R1 and Rs; proximal crossvein between Rs1 and MA strongly oblique. It is probable that Protosmylina belongs to Protosmylinae; if so, this is the oldest known genus in the subfamily.

Protosmylina bifasciata gen. et sp. nov.

**Fig. 4**

**Derivation of name.** From the Latin bi, double, and fascia, band, in reference to the following colour pattern of the holotype.

**Material.** Holotype BMB 018569, -70 (part and counterpart), an incomplete forewing. Aucaye Brickworks, Upper Weald Clay, Lower Cretaceous, Barremian.

**Diagnosis.** As for genus.

**Description.** Forewing 9 mm preserved length (estimated length about 11 mm), 3.5 mm preserved width. Costal space broad, with 16 simple, closely spaced subcostal veinlets preserved. Sc fused with R distally, far distant from wing apex. 1 sc-r crossvein preserved at mid-point of wing. 5 r1-rs crossveins. Rs originates near base of wing, with 12 pectinate branches preserved. Majority of Rs branches simple for most of length; Rs5 forks at mid-point of vein, a few veins forked distally. 3 gradate series of crossveins in radio-medial space: 5 crossveins in most proximal series, 11 in middle series, and 8 in most distal series. Basal crossvein between stems of Rs and M present; basal crossvein connecting Rs1 and MA strongly oblique. M deeply forked far distal to origin of Rs1. MA with 4 pectinate branches, some branches forked distally. MP with 2 pectinate distal branches, of which proximal one deeply forked. 2 crossveins within pectinate branches of MA and 3 crossveins between MA and MP. Cu origin close to base of wing, deeply forked into Cu and CuP. CuA incomplete, pectinately branched distally. 4 branches preserved. CuP incomplete. Anal veins poorly preserved. Wing pattern consists mainly of 2 transverse, interrupted fuscous bands in middle and apical parts of wing.

**Family: Psychopsidae Handlirsch, 1906–1908**

**Remarks.** Psychopsidae is the only living family of the ‘psychopсид-like neuropterans’ (psychopsoids) which include in particular the extinct Osmypolopsychopidae, Brongniartiiellidae, and Kaligrammatidae. Psychopsoids are particularly diverse and abundant in the Mesozoic, but the taxonomy of this group has been very poorly studied. The Mesozoic psychopsids are often hard to distinguish from members of Osmypolopsychopidae and Brongniartiiellidae, especially if the wings are incomplete or fragmentary. The diagnoses and compositions of these families have not been well understood until now. A current study of very well preserved Triassic osmylopysychopids from the Madygen Formation (Central Asia) and the type species of Brongniartiiellidae from the Jurassic Solnhofen Limestone, show that Osmypolopsychopidae and Brongniartiiellidae might be readily distinguished from the Mesozoic Psychopsidae, and from this we can say that there is no definite evidence of these two families among the material examined here (VM, pers. obs., see also Makarkin, in press).

The forewings of extant Psychopsidae are characterized by the following character states [based on the reviews and revisions of Tillyard (1919), Kimmins (1939), Tjeder (1960), New (1989), and Oswald (1993b)]: wing broad with apex always broadly rounded; trichosors always present; “vena triplica” present (i.e., a complex character formed by Sc, R1, and Rs running parallel to “pterostigmal region”, then anastomosed or possessing 2 distal crossveins between them); pterostigma absent; humeral veinlets usually slightly recurrent, pectinately branched; costal space very broad throughout (width in “pterostigmal region” >2 times the combined width of the
adjacent subcostal and R1 spaces [1]); subcostal space with more than four crossveins (usually > 10) [2]; Sc and R1 distally connected by a strong crossvein or anastomosing; R1 (or Sc + R1) distally with few branches (if any), usually not pectinate [3]; branches of Rs mostly not forked before “pterostigmal region” and approximately parallel to the hind margin; crossveins in the radial space arranged in gradate series (mostly 2 or 3 series) [4]; M with two or more deep branches, none of them pectinately branched distally; CuA and CuP in most species pectinately branched [5]; 1A multi-branched.

The character states [1] and [2] are considered by Oswald (1993b) as synapomorphies of the Psychopsidae. The characters [3]–[5] are also characteristic of all (or the majority of) extant species. The typical “vena triplica” as described above is often absent in the fossil taxa. Therefore, the forewing of Psychopsidae may be characterized by a combination of the character states [1]–[5].

All the species described below are represented by incomplete or fragmentary wings, unfortunately lacking their basal portion. Nonetheless, the majority of the wings possess the characters [1]–[4]. Therefore, it seems most probable that the genera described, despite their fragmentary nature, are of psychopsid affinity. The structure of vein CuP, although not entirely preserved in any specimen, appears to be non-pectinate, at least in some species. However, because of problems with the identification of veins MA, MP, CuA and CuP due to the lack of a basal portion to the wings, these veins are often determined provisionally.

Genus Cretapsychops gen. nov.

**Type and only species.** Cretapsychops corami gen. et sp. nov.

**Derivation of name.** From Cretaceous and -psychops, a traditional ending of psychopsoid generic names. Gender masculine.

**Diagnosis.** May be distinguished from other psychopsid genera by the combination of non-pectinate structure of both CuA and CuP in the forewing.

**Remarks.** A similar structure of CuA is seen in Triassopsychops (Tillyard, 1922) and the non-pectinate CuP is observed in Baisopsychopteryx (Makarkin, 1997).

Cretapsychops corami gen. et sp. nov.

**Fig. 5**

**Derivation of name.** After Dr Robert A. Coram, British palaeontologist.

**Material.** Holotype BMNH Pal. PI II 1555a, an incomplete forewing. Smokejacks Brickworks, Upper Weald Clay, Lower Cretaceous, Barremian.

**Diagnosis.** As for genus

**Description.** Forewing 10.6 mm preserved length (estimated length about 15 mm), 8.2 mm preserved width. C not preserved. Costal space broad, over three times width of “vena triplica” (i.e., subcostal, R1 spaces together), with 29 subcostal veinlets mostly forked; 1 complete gradate series of 21 crossveins in costal space, running from its base to mid-point. 2 subcostal crossveins preserved. 4 r1-rs crossveins preserved. 20 pectinate branches of Rs preserved, mainly simple for most of their length, few forked at mid-point of vein. Few crossveins preserved forming 5 interrupted gradate series in radial to cubital spaces. M poorly preserved, with 2 branches. CuA peculiarly (in general, dichotomously) branched. CuP poorly preserved, probably dichotomously branched (possibly 4 branches forking terminally to form 9 branches). Anal veins poorly preserved, difficult to differentiate. Wing membrane mainly fuscous, paler basally and apically, with broad transverse pale patch at mid-point of wing.

Genus Micropsychops gen. nov.

**Type and only species.** Micropsychops parallelus gen. et sp. nov.

**Diagnosis.** May be distinguished from other psychopsid genera by having non-dichotomously branching (parallel for most of length) branches of Rs and presence of four (at least) transverse gradate series of crossveins in radial space.

**Remarks.** The genus possesses the wing venation typical of Psychopsidae (e.g., the broad costal space, the presence of “vena triplica”, the numerous subcostal crossveins, the gradate series of crossveins in the radial space), and it has been confidently placed in this family despite its small size.

Micropsychops parallelus gen. et sp. nov.

**Fig. 6**

**Derivation of name.** From Greek parallelos, parallel, in reference to the branches of Rs parallel for most of length.

**Material.** Holotype BMNH Pal. PI II 1518a, b (part and counterpart), an incomplete forewing. Smokejacks Brickworks, Upper Weald Clay, Lower Cretaceous, Barremian.
Description. Forewing 7.6 mm preserved length (estimated length about 9–10 mm), 5 mm preserved width. C not preserved. 33 subcostal veinlets, some forked. “Vena triplica” formed by Sc, R1, Rs configured nearly as in extant taxa being closed by 2 distal crossveins. 14 sc-r1 and 6 r1−rs crossveins preserved. R1 not branched, only with terminal fork. Rs pectinately branched, 17 branches, simple for most of lengths, forking distal to most distal gradate series. All crossveins arranged into 4 gradate series in radio-medial space. Origin of M not preserved; MA probably deeply forked, each branch forked distal to most distal gradate series of crossveins; MP pectinately branched distally, with 3 long branches. CuA pectinately branched with 3 long branches preserved. Anal veins not preserved.

Genus Valdipsychops gen. nov.

Type species. Valdipsychops logunovi gen. et sp. nov.

Derivation of name. From valdi-, the latinized name for the Wealden, in reference to the Wealden Supergroup, and -psychops, a traditional ending of the psychopsoid generic names. Gender masculine.

Species included. V. logunovi gen. et sp. nov., V. brigidae gen. et sp. nov., V. maculosus gen. et sp. nov., V. proutloveci gen. et sp. nov., V. minimus gen. et sp. nov., Valdipsychops sp., all from the Lower Cretaceous, Hauterivian and Barremian, Wealden Supergroup.

Diagnosis. May be distinguished from other genera by the combination of the following character states: branches of Rs dichotomously branched, CuA pectinate, CuP non-pectinate, and several (often numerous) short gradate series of crossveins in the radial space.

Remarks. This genus differs from other psychopsids mainly in having the combination of a strongly dichotomously branched Rs and the presence of several short gradate series of crossveins in the radial space. The other probable psychopsid genera that possess dichotomously branched branches of Rs are Triassopsychops Tillyard, 1922, and Angaropsychops Martynova, 1949; they differ from Valdipsychops gen. nov. by having a pectinate CuP (Triassopsychops) and having radial crossveins that are not arranged in series (Angaropsychops). Other fossil psychopsids, for example Propychopsis MacLeod, 1971 and Baisopsychops Makarkin, 1997, and extant genera have mostly unbranched veins of Rs before end-twigging, and two or three long gradate series of crossveins in the radial space. Some other Mesozoic genera usually ascribed to Psychopsoids that have a dichotomously branched Rs are Grammap-sychops Martynova, 1954, Eunemus Zalessky, 1953, Pulchriptionia Martins--Neto, 1997 and Kagapsychops Fujiyama, 1978; however, they may actually (partly confidently, partly very probably) belong to another psychopsid family, Osmolyspsychopidae. This is implied from their forewing characters, e.g. the subcostal space is narrow and lacks subcostal crossveins, Sc and R1 are fused, Rs1 is multibranch; all these features are very similar to those of osmolyspsychopidae (VM, ongoing research). The majority of the genera ascribed to the Bronngniartiellidae also have a dichotomously branched Rs. The examination of the type species of this family (Bronngniartiella gigas Weyenbergh) shows that all forewing character states of the Valdipsychops gen. nov. diagnosis are present also in B. gigas. However, other features found in B. gigas are not present in Valdipsychops gen. nov. (as well as in other psychopsids): the costal space is relatively narrow (width in the “pterostigmatic region” is equal to the combined width of the adjacent subcostal and R1 spaces); both subcostal and R1 spaces are broad; the crossveins are arranged mainly in long gradate series running from the cubital to radial spaces nearly parallel to the wing margin, like the ‘‘outer’’ gradate series of Hemerobiidae or Polystoechotidae (VM, pers. obs.). Therefore, the venation of Valdipsychops gen. nov. is superficially most similar to that of osmolyspsychopsid and bronngniartiellid genera, but it is separable from them by the presence of many subcostal crossveins and a broad costal space.

Valdipsychops logunovi gen. et sp. nov.

Fig. 7


Derivation of name. After Dr Dmitri V. Logunov, curator of arthropods at The Manchester Museum.

Diagnosis. May be distinguished from other species of the genus by scarce gradate crossveins in the radial space, and characteristic colour pattern.

Description. Forewing 14 mm preserved length (estimated length about 17–19 mm), 11 mm preserved width. C poorly preserved. Costal space very broad, approximately four times width of “vena triplica”, with 33 subcostal veinlets; costal crossveins not detected. Sc, R1, Rs parallel for most of length, forming “vena triplica”; Sc terminating on R1 (or connecting with R1 by short crossvein). R1 probably with only 1 distal branch. 10 subcostal crossveins, and 3 r1−rs crossveins preserved. Rs with 15 pectinate branches, dichotomously forked into 29 branches. Many Rs branches fork before mid-point of vein. Few preserved crossveins in radial space forming 3 interrupted gradate series. Origin of M not preserved. M probably forked at mid-point of vein (alternatively, forked near wing base, if apparent most proximal branch of Rs belongs actually to M). CuA with 6 pectinate branches, most proximal branches deeply forked. CuP poorly preserved, probably
not pectinate. Anal veins not preserved. Colour pattern mainly fuscous, paler horizontal bars at mid-point of wing.

**Valdipsychops brigidae** gen. et sp. nov.

*Fig. 8*


**Derivation of name.** After Mrs J. Brigid E. Jarzembowski, Wealden insect collector.

**Diagnosis.** May be distinguished from other species of the genus by having strongly curved branches in proximal parts of Rs, M, and Cu.

**Description.** ?Forewing 12.9 mm preserved length (estimated length about 20–22 mm), 10 mm preserved width. C partially preserved. Costal space broad, approximately four times width of “vena triplica”, with 30 subcostal veinlets preserved; 3 crossveins forming a gradate series are preserved in apical portion of wing connecting veinlets of R1. Sc terminating on R1. 10 subcostal crossveins preserved. Rs pectinate with 17 branches which are strongly dichotomously branched (up to 35 terminal branches). Many crossveins preserved in radio-cubital space forming up to 8 gradate series. Proximal branches of Rs curved. Origin of M not preserved; M slightly curved, forked at mid-point of vein (alternatively, forked near wing base, if apparent most proximal branch of Rs actually belongs actually to M). Cu origin not preserved. CuA curved, pectinately branched, with 7 branches preserved. CuP apparently deeply forked, both branches curved. 1A partially preserved, pectinately branched with 6 long branches.

**Valdipsychops maculosus** gen. et sp. nov.

*Fig. 9*

**Material.** Holotype BMB 018575, -6 (part and counterpart), an incomplete forewing. Auclaye Brickworks, Upper Weald Clay, Barremian.

**Derivation of name.** From the Latin *maculosus*, spotted, in reference to the forewing colour pattern.

**Diagnosis.** May be distinguished from the other species of the genus by the characteristic spotted forewing pattern.

**Description.** Forewing 12.9 mm preserved length (estimated length about 25 mm) and 8.4 mm preserved width. C partially preserved with trichosors present. Costal space broad, approximately four times the width of “vena triplica”, and with 38 subcostal veinlets preserved, many forked near anterior wing margin. Sc terminated on R1 (alternatively, these veins connected by rather long, oblique crossvein). 4 subcostal crossveins preserved. R1 incomplete. Rs pectinately branched, with 13 branches, which are dichotomously branched. Few crossveins preserved in radial space,
with 1 poorly developed potential gradate series. Origin and fork of M not preserved. Cu forked close to wing base. CuA pectinately branched, with 4 branches preserved. CuP few-branched, probably dichotomously branched. 1A few-branched. 2A well developed, pectinately branched. 3A not preserved. Colour pattern represented by small circular spots (diameter of about 0.3 mm) in radial to cubital spaces (over ten in number).

Remarks. The apparent absence of gradate series of crossveins in this species is possibly an artefact of preservation.

Valdipsychops proudlovei gen. et sp. nov.

Fig. 10
2003 Silky lacewing: Austen et al., p. 11, fig. 2.

Derivation of name. Named after the late Mr. William Proudlove, general manager, for facilitating fossil collecting at Smokejacks Brickworks.


Diagnosis. May be distinguished from the other species of the genus by the large size.

Description. 21.9 mm preserved length (estimated length about 40 mm) and 14 mm preserved width. C not preserved. Subcostal veinlets in distal portion of costal space mainly branched. Sc not fused with R1, connected apically by long crossvein; other subcostal crossveins not detected. R1 with 4 distal veinlets. 7 crossveins between R and Rs preserved. Rs probably pectinately branched, with 15 branches preserved, dichotomously branched (at least apically). Many crossveins preserved in distal portion of costal to radial spaces, arranged mainly into over 10 gradate series. Striped colour pattern is preserved. M, Cu and A not preserved.

Remarks. This specimen has been tentatively placed in Valdipsychops gen. nov. based on the dichotomously branched Rs and the presence of the gradate series of crossveins in the radial space. It has been assigned to a new species based on the large size of the specimen, which is more than twice the size of V. logunovi gen. et sp. nov.

Valdipsychops minimus gen. et sp. nov.

Fig. 11
1987 Psychopsoidea: Jarzembowski, fig. 9.5.

Derivation of name. From the Latin minimus, small, in reference to the small wing size of the holotype.


Diagnosis. May be distinguished from V. logunovi gen. et sp. nov., V. brigidae gen. et sp. nov., and V. maculosus gen. et sp. nov. by having fewer branches of CuA; the smaller size excludes it from V. proudlovei gen. et sp. nov.
Description. Forewing preserved length 12.5 mm (estimated length about 15 mm), preserved width 7 mm. C not preserved. 33 subcostal veinlets preserved, some forked. 3 crossveins preserved in costal space. Sc and R1 distally not fused, only slightly approaching each other towards wing apex. R1 with several anteriorly directed veinlets. 7 subcostal crossveins and 5 r1-rs crossveins preserved. R1 space (between R1 and Rs) narrow. Rs pectinately branched with 14 branches, many dichotomously forked before mid-way point of vein. Numerous crossveins preserved in radial space, forming at least 5 gradate series. M forked near mid-point of vein to give 2 branches. CuA pectinately branched with 3 branches preserved. CuP incompletely preserved, with 2 branches. Anal veins not preserved.

Valdipsychops sp.

Fig. 12


Description. Preserved length 9.9 mm (estimated length about 20–22 mm), preserved width 9 mm. C, Sc and R not preserved. Rs with more than ten dichotomously forked branches. Numerous crossveins, arranged in approximately eight–ten gradate series. Presumably M with two branches preserved. Presumably CuA pectinately branched with two branches preserved. Presumably CuP non-pectinately branched. Anal veins not preserved. Colour pattern preserved, mainly pale with light stripe thinning anteriorly.

Remarks. Tentatively placed in the genus Valdipsychops gen. nov. on the basis of having dichotomously branched Rs and the presence of the several gradate series of crossveins in the radial space. The venation of this fragmentary wing is most similar to that of V. minimus gen. et sp. nov. Unfortunately, in the latter species the colour pattern is not preserved.

Genus Psychopsites gen. nov.

Derivation of name. Psychops- (from Psychopsis, a psychopsid genus-group name), and -ites a traditional ending of fossil generic names. In reference to the similar forewing colouration of the type species of Psychopsis mimica Newman. Gender masculine.

Type and only species. Psychopsites rolandi gen. et sp. nov.

Diagnosis. Largest psychopsid (forewing of type species is 45–50 mm long), which may be distinguished from other genera by a combination of the following features: subcostal space very broad with densely spaced crossveins; Sc and R1 are distally fused; crossveins in radial space form >10 long gradate series.

Remarks. Comparison with Recent Psychopsidae in BMNH shows that the fossil cannot be assigned to a Recent genus. The fossil wing is larger than any extant psychopsid. Of Recent species, Mega-psychops illedgei (Froggatt) from Australia has the largest forewing which is only 30 mm. The fossil shows better developed gradate series than any extant species. The colour pattern resembles that of Psychopsis mimica Newman from Australia, but stripes are double in the latter. The affinities of Psychopsites gen. nov. are unclear.
compared with other fossil psychopsids due to the incompleteness of the wing. It is probably most closely related to two other Wealden genera, i.e. Valdipsychops gen. nov. and Cretapsychops gen. nov.

Psychopsites rolandi gen. et sp. nov.

1984 Psychopsidae: Jarzembowski, p. 82, fig. 32
1987 Psychopsidae: Jarzembowski, figs 9.9, 9.10
2006 Psychopsidites rolandi Jarzembowski and Makarkin, p. 29 (nomen nudum).

Derivation of name. After the late Prof. Roland Goldring, University of Reading.


Diagnosis. As for genus.

Description. ?Forewing preserved length 33 mm (estimated length about 45–50 mm), preserved width 24 mm. C partially preserved along costal margin. Costal space relatively narrow (for psychopsids), only two times wider than subcostal and R1 spaces combined. Preserved subcostal veinlets mainly forked, not connected by crossveins (except occasional one). Subcostal space very broad, twice wider than R1 space, with numerous closely spaced crossveins. Sc terminated on R1 distally; Sc + R1 lacking (or at most with 1–2) veinlets. Rs and R1 apparently not fused distally, but connected by oblique crossvein. Crossveins in R1 space poorly developed. Proximal branches of Rs and M difficult to separate because wing base not preserved. Rs apparently with c. 15 branches, distal branches inclined to Rs at acute angle; Rs branches dividing dichotomously. Crossveins in radial and medial spaces form 12–14 long transverse gradate series. Colour pattern preserved consisting of three oblique, brown stripes; the middle one interrupted posteriorly.

?Psychopsites sp.


Description. Partially preserved wing fragment, 14 mm long (estimated wing length over 40 mm). 4 parallel veins of Rs preserved. Preserved part of MA simple, concave. MP pectinately forked distally with 2 branches preserved. CuA pectinately branched with 5 branches, first dichotomously branched. CuP pectinately branched, with at least 10 branches preserved. Crossveins cover wing throughout, mostly arranged in series.

Remarks. This specimen resembles the family Kalligrammatidae due to the large size and numerous crossveins. However, the preserved venation and the crossveins arranged in numerous series clearly show that it belongs to the Psychopsidae. This specimen may belong to Psychopsites rolandi gen. et sp. nov. The fragmentary
nature of the specimen, however, does not allow us to associate them with certainty.

**Family: Kalligrammatidae Handlirsch, 1906–1908**

*Kalligrammatidae* gen. et sp. indet.

**Fig. 15**


**Description.** 21 mm preserved length (estimated length over 50 mm) and 9 mm preserved width. C not preserved. Costal space with 30 subcostal veinlets preserved of which 2 deeply forked. 7 crossveins preserved in costal space forming gradate series. Sc approaches R at wing base. 9 subcostal crossveins preserved basally. Origin of Rs 6.2 mm from origin of R. 6 crossveins preserved between R1 and Rs basally. Rs pectinately branched with 8 branches preserved in proximal portion of wing, Rs1 and Rs3 deeply forked. 17 crossveins randomly distributed in radial space basally. M fragment preserved. 7 randomly arranged crossveins preserved between R, Rs and M basally. Cu and A not preserved.

**Remarks.** The specimen has tentatively been placed in the family Kalligrammatidae based on the size of the wing and the dense pattern of crossveins in the subcostal to medial spaces. This is a small portion of a much larger wing indicated by the size of the fragment; it is much bigger than the psychopsid wings found in the Wealden, thus excluding it from this family.

**Family: Neuroptera familia incertae sedis**

**Genus** *Actinophlebioides* gen. nov.

**Derivation of name.** From *Actinophlebia*, a genus-group name, in reference to a superficial resemblance of the venation of the type species to that of *Actinophlebia*. Gender masculine.

**Type and only species.** *Actinophlebioides valdensis* gen. et sp. nov.

**Diagnosis.** May be distinguished from other neuropteran genera by the combination of the following character states: costal space broad, narrowed distally; Sc terminating on R1; Rs1 multi-branched, with four deep forks; M simple most of its length; CuA pectinately branched; CuP without deep forking; 1A pectinately branched; no crossveins present.

**Remarks.** In general, *Actinophlebioides* gen. nov. might be assigned to some psychopoid family, but its features do not fit confidently in any of them. The classification of psychopoids is generally very poorly understood. Superficially, this genus most closely resembles the genera usually treated as belonging to the Brongniarteliellidae (e.g. *Actinophlebia* Handlirsch, 1906–1908, *Pterinoblattina* Scudder, 1885), particularly in having the similar general venation pattern and in lack of crossveins. However, the brongniartellid affinities of these genera need confirmation, as the type genus *Brongniariella* Meunier, 1897 is inadequately described. At present, we cannot place this genus in a family with certainty.

**Actinophlebioides valdensis** gen. et sp. nov.

**Fig. 16**

**Derivation of name.** From vald, the latinized name for the Weald, in reference to the Weald Sub-basin.

**Material.** Holotype BMB 025007, -8 (part and counterpart), a nearly complete forewing. Clockhouse Brickworks, Lower Weald Clay, Lower Cretaceous, Hauterivian.

**Diagnosis.** As for genus.

**Description.** Forewing preserved length 7.4 mm (estimated length about 9 mm), preserved width 4.3 mm. C partially preserved with 24 subcostal veinlets, some forking towards anterior wing margin. Costal space broad, narrowed distally. Sc terminating on R1. R1 with some forked veinlets distally. Rs with 11 branches, many of them forked before mid-point of vein; Rs1 multi-branched, with 4 deep forks. M simple most of its length forking distally. CuA pectinately branched with 10 branches. CuP probably simple, or few-branched distally. 1A pectinately branched with 8 branches. 2A appears pectinately branched. No crossveins detected. Colour pattern faint and complex.
Remarks. The forewing of this species is noteworthy for the absence of crossveins. However, this may possibly be an artefact of preservation.

Genus Protohemerobius gen. nov.

Derivation of name. From the Greek protou, before, and Hemerobius, a genus–group name, in reference to the general similarity of the venation of the type species to that of Hemerobiidae. Gender masculine.

Type and only species. Protohemerobius perexiguus gen. et sp. nov.

Diagnosis. May be distinguished from other neuropteran genera by the combination of the following characters: very small wing size; subcostal veinlets forked once; Sc probably not terminating on R1; MA, MP and CuA pectinately branched distally; CuP probably dichotomously branched; 1A pectinately branched.

Remarks. The venation of this genus is similar (possibly superficially) to that of Hemerobiidae (brown lacewings), e.g. the similar branching of the subcostal veinlets together with the small size, the presence of trichosors, and the similar general configuration of the venation. Unfortunately, Protohemerobius gen. nov. lacks critical areas of the wing, and the determination of its family placement is not possible. However, the occurrence in the Chinese Jurassic (Daohugou) of taxa with rather similar venation (Ren, 2003) suggests that this genus may represent an undescribed family.

Protohemerobius perexiguus gen. et sp. nov.

Fig. 17

Derivation of name. From the Latin perexiguus, tiny, in reference to the tiny wing size of the holotype.

Diagnosis. As for genus.


Description. Forewing preserved length 4 mm (estimated length 4.6 mm); preserved width 2.5 mm. C partially preserved; trichosors present on anterior and posterior wing margin. 14 subcostal veinlets preserved, forking towards anterior wing margin. Sc curves towards R1 apically, apparently not terminating on it. No subcostal crossveins preserved. 1 crossvein between Rs and R1 preserved. Rs incomplete, pectinately branched, apparently with 8 preserved branches forking distally; 1 branch appears to be dichotomously branched. Crossveins in radial space poorly preserved, apparently present. M forked before mid-point of vein (fork not preserved); MA incomplete with 2 pectinate branches; MP pectinately branched with 3 branches. 1 crossvein between MA and MP, and 2 crossveins between MP and CuA preserved. CuA pectinately branched with 4 branches and 2 preserved crossveins between them. CuP incomplete, crumpled, probably dichotomously forked. 1A incomplete, pectinately branched.

5. Discussion

Prior to this study only a few neuropterans of the psychopsoid families Psychopsidae, Brongniartiellidae and Kalligrammatidae were recorded from the Wealden (Jarzembowski, 1984; Ross and Cook, 1995). It was predicted by Jepson and Penney (2007) that the families Nymphidae (split-footed lacewings), Polystoechotidae (giant lacewings), Chrysopidae (green lacewings), Coniopterygidae (wax flies) and Hemerobiidae (brown lacewings) should be present in the Wealden fauna (as well as the already recorded Psychopsidae (silky lacewings), Brongniartiellidae and Kalligrammatidae). This work, however, has not shown any of those predicted to be present: instead other neuropteran families have been recorded: Ithonidae, Osmyridae and at least one undescribed family. The predictive method may not have been successful because the predicted families have not yet been found, been preserved, or the analytical method that was successful for spiders may not be transferable to fossil insects.

The psychopsoids make up the majority of the neuropteran fauna of the Wealden, and among them the family Psychopsidae dominates. Genera from the family Psychopsidae are described herein (Cretapsychops gen. nov., Valdipsychops gen. nov., Micropsychops gen. nov. and Psychopsites gen. nov.). The vast majority of undescribed fragmentary specimens of Wealden Neuroptera from museum collections are also psychopsids (or have psychopsid affinities) (JEl, pers. obs.).

Kalligrammatids are now known to have persisted in the Wealden from the Valanginian Wadhurst Clay (Hastings Beds Group) to the Barremian Upper Weald Clay (Weald Clay Group). Kalligrammatidae are represented in the Wealden by small wing fragments. Kalligramma roycrowsoni Jarzembowski, 2001 defined by an impressive eyespot and fragmentary venation typical of the genus Kalligramma, was previously described from the Wadhurst Clay (Hastings Beds Group) (Jarzembowski, 2001). The specimen described herein, Kalligrammatidae gen. et sp. indet., is from the younger Upper Weald Clay, and is placed in the family on the basis of subcostal and medial space crossveins and the large size of the wing. The fact that a kalligrammatid has been observed in the Hastings Beds Group and Upper Weald Clay Formation suggests that the family Kalligrammatidae persisted from the mid-Valanginian to the early Barremian in the Wealden and should be present in the Grinstead Clay.

The occurrence of the family Brongniartiellidae has not been confirmed in the Wealden. Prior to this study, brongniartiellids were thought to be a major constituent of the Wealden insect fauna,
however, what was previously thought to be members of this family are in fact from the family Psychopsidae. For example, a fragmentary wing from Smokejacks Brickworks identified by Ross and Cook (1995: fig. 5) as the brongniartiellid *Pterinoblatina* sp., is most probably a representative of the genus *Valdipsychos* gen. nov., or some other psychopsid genus. There is no evidence that this family was present in the Wealden despite being recorded from the Lower Cretaceous of southern England by Martynova (1962).

The discovery of the ithoniid genus *Principalia* is most noteworthy. Hitherto, only one genus of Neuroptera was known with certainty to occur in both the European and South American Lower Cretaceous, i.e., *Triangulochrysopa* Nel et al., 2005 (Menon and Makarkin, 2008).

*Osmylidae* prior to this study were unknown in the Wealden; two genera have been described herein, *Stenosmylina* gen. nov. and *Protosmylina* gen. nov. The presence of *Osmylidae* in Britain has been extended back to the Lower Cretaceous. Both genera are closely related to those of the subfamilies Mesosmylininae and Protosmylinae, which are known to occur in the Jurassic to Eocene of continental Europe, and are very different to those of the subfamily Osmylinae, present in Britain today.

The two genera of uncertain placement might be representatives of undescribed families. Unfortunately, the poor state of preservation of these fossils prevents us from establishing new families.

The absence in the Wealden fauna of such groups as Chrysopidae and Myrmeleontoidea is important. Chrysopids often occur in Cretaceous deposits, and their absence in the Wealden is somewhat surprising. The myrmeleontoids are the dominant superfamily among Neuroptera in the Cretaceous of Brazil, indicative of arid and semi-arid conditions of the environment in the surrounding areas of the Crato lake/jagoon (*Martins Neto, 2006; Batten, 2008*). This group is also rarely recorded from other Cretaceous localities.

The Wealden Neuroptera would most likely have been arboreal, based on the habitat preferences of modern analogues. Modern psychopsids, ithoniids and hemerobids (potential modern analogues of *Prothomopera* gen. nov.) are often (but not always) found living in or around forested habitats, usually amongst the branches and trunks of trees (*New, 1989; Grimaldi and Engel, 2005*). This being the case, the neuropterans would probably have inhabited the woodland, which bordered the Wealden watercourses (*Jarzembowski, 1995*). The majority of modern osmylids have semi-aquatic larvae living in damp conditions (wet moss near water, under wet stones immediately adjacent to water); others occur in soil or under the tree bark (*Riek, 1970; New, 1986, VM, pers. obs.*). Their adults are often found close to water. Therefore if the Wealden osmylids had semi-aquatic larvae, the adults would be found near water, which compliments the suggestion that the neuropterans inhabited the woodland bordering water courses. The specimens of Neuroptera are all fragmentary and no body parts are present: this indicates that the insect bodies decayed, disarticulated and were sorted, most probably by fluvial process, prior to their deposition (*Jarzembowski, 1995*). The fragmentary nature of the wings may suggest a long transportation distance, a long decay period on land or on the water surface, or predation.

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4. TWO NEW SPECIES OF SNAKEFLY (INSECTA: RAPHIDIOPTERA) FROM THE LOWER CRETACEOUS OF ENGLAND AND SPAIN WITH A REVIEW OF OTHER FOSSIL RAPHIDIOPTERANS FROM THE JURASSIC/CRETACEOUS TRANSITION
Two new species of snakefly (Insecta: Raphidioptera) from the Lower Cretaceous of England and Spain with a review of other fossil raphidiopterans from the Jurassic/Cretaceous transition

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ABSTRACT
Two new species of snakefly (Insecta: Raphidioptera, Mesoraphidiidae) are described from the Wealden Clay of the Wealden Supergroup, southern England and the Lithographic Limestone of Montsec, Spain. Proraphidia hopkinsi sp. nov. is the first species of snakefly to be described from the Wealden and P. gomezi sp. nov. is the first snakefly to be formally described from Montsec. These species extend the range of the genus Proraphidia across the Jurassic/Cretaceous boundary and its geographical range from Kazakhstan to England and Spain. A review of the snakefly families and genera involved in the Jurassic/Cretaceous transition is given.


INTRODUCTION
Raphidioptera is the least diverse order of the holometabolous insects with approximately 210 extant species described in two extant families: Raphidiidae and Inocelliidae (Aspöck 2002, Grimaldi & Engel 2005, Engel et al. 2006). The order is distinctive with an elongated prothorax, a long ovipositor seen in females, and typical venation, although the true autapomorphies are not immediately clear (Engel 2002). However, Aspöck and Aspöck (2004) discussed and listed four autapomorphies of the order, but the only one that can be applied to fossil wings is the forewing subcosta running into the anterior margin. Extant snakeflies are arboreal, in areas of cold weather with near freezing winter temperatures. These cold temperatures are required for the insect to complete development before pupation or just before eclosion (Grimaldi & Engel 2005). Therefore they are found in cold temperate regions and are absent from hotter regions such as in South America, Australia and sub-Saharan Africa (loc cit.). However, some Mesozoic raphidiopterans are to be found in much warmer conditions such as inferred tropical climates (Engel 2002). Mesozoic raphidiopterans are divided into three definite extinct families: Baissopteridae, Mesoraphidiidae and Alloraphidiidae, and one debatable extinct family: Priscaenigmatidae. It is debated whether Priscaenigmatidae belongs in Raphidioptera because the subcosta runs into the wing apex and not the anterior margin (see Aspöck & Aspöck 2004). At species level, the Mesozoic raphidiopterans are very diverse, supporting the idea that extant Raphidioptera are relict (Engel 2002, Grimaldi & Engel 2005). Few attempts have been made at a cladistic study of fossil and extant raphidiopterans (e.g. Ren & Hong 1994, Willmann 1994) and the relationships have still not been satisfactorily resolved (see Engel 2002). Proraphidia hopkinsi sp. nov. and P. gomezi sp. nov. (Mesoraphidiidae) are the first species of Raphidioptera to be formally described from the Wealden Supergroup of southern England and the Lithographic Limestone of Montsec, Spain.

GEOLOGICAL SETTINGS
The Wealden Supergroup is Lower Cretaceous in age (Berriasian-Aptian?); the supergroup consists of the Hastings Beds (Ashdown, Wadhurst Clay, Lower and Upper Tunbridge Wells Sand, and the Grinstead Clay formations) and the Weald Clay (Upper and Lower) (Allen & Wimbledon, 1991; Rasnitsyn et al. 1998). The insect remains are almost solely found in stone developments in the clays and most common in the Weald Clay (Jarzemowski 1984) in which the specimen below was found. Many of the insect orders are present: Odonata, Blattodea, Orthoptera, Hemiptera, Neuroptera, Coleoptera, Mecoptera, Diptera, Trichoptera, Hymenoptera, Isoptera, Raphidioptera (Jarzemowski 1984, 1995). The insects are usually represented...
by wing fragments and disarticulated body material; they are preserved as uncrushed and unoxidized elements in siltstones and early diagenetic concretions in the clay (Jarzembowski 1984). The palaeoenvironment is thought to have been woodland bordering watercourses (Jarzembowski 1995). The climate has been suggested as subtropical/warm temperate (with seasonal rainfall), based on the presence of certain insect orders (e.g. Isoptera) (Jarzembowski 1995) and sedimentological evidence (Allen 1998, Haywood et al. 2005). The occurrence of a distinct wet and dry season has been proposed, as well as year round precipitation with little evidence for prolonged drought (Batten 1998, Haywood et al. 2004). Wildfires are thought to have occurred due to the presence of fusainized elytra and plant remains (Watson & Alvin 1996, Batten 1998, Jarzembowski 2003).

The age of the Lithographic Limestone at Montsec is Early Barremian (Lower Cretaceous) (Soriano et al. 2006). The insects are preserved as impressions, sometimes showing traces of cuticle. They occur in well-cemented fine-grained brown limestone (Whalley & Jarzembowski 1985). Numerous insect orders have been found in the deposit: Blattodea, Odonata, Hemiptera, Coleoptera, Diptera, Hymenoptera, Ephemeroptera and Gryllloblattodea (Whalley & Jarzembowski 1985, Gómez-Pallerola 1986, Martínez-Delclòs 1989). The rocks were deposited in a lacustrine environment in subtropical conditions with alternating wet and not very pronounced dry seasons (Soriano et al. 2006).

**MATERIAL AND METHODS**

The Wealden holotype is preserved in a piece of siltstone concretion associated with Blattodea, Hemiptera, Mecoptera, Diptera, etc. and a crustacean antenna. The holotype is deposited in the collections of the Booth Museum of Natural History, Brighton (BMB).

The Montsec holotype is preserved on a piece of limestone. The holotype is deposited in the Institut d’Estudis Ilerdencs, Lérida, Spain [L. 29].

Drawings were made using a Wild Camera Lucida microscope attachment. Both halves were drawn separately and a composite drawing was produced through the use of a light-table. Photographs were taken using a Wild Photomicroscope using Ilford FP4 film. Wetting using a weak solution of ethyl alcohol was used to increase contrast.

Wing vein abbreviations are as follows: C, costa; Sc, subcosta; R, radius; Rs, radial sector; M, media; MA, media

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Figure 1. A. Photograph of the forewing of *Proraphidia hopkinsi* sp. nov. BMB 014915 [CH 879ia] B. Camera lucida drawing showing venation of *Proraphidia hopkinsi* sp. nov. Drawing convention as in Jarzembowski (1980). Scale bar = 1mm.
anterior; MP, media posterior; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; A, analis; r, radial cell; dc, discal cell; mc, medial cell; ac, anal cell; p, pterostigma.

SYSTEMATIC PALAEONTOLOGY

Order: Raphidioptera Navás, 1918
Family: Mesoraphidiidae Martynov, 1925

GENUS: Proraphidia Martynova, 1947

Type species: Proraphidia turkestanica Martynova, 1947. Upper Jurassic (Malm), Karatau, Chimkent Province, Kazakhstan, based on an isolated forewing.

Revised Diagnosis. Forewing. R close to Sc in proximal half of wing, dc short. Second branch of CuA forked, ac wide. Pterostigma short, basal border of pterostigma more distal than r-rs crossvein. Hindwing. Costal field narrow, dc long, MP deeply forked, Cu deeply forked, pterostigma probably as in forewing and strongly developed.

Included species. Proraphidia turkestanica, P. hopkinsi sp. nov. and P. gomezi sp. nov.

Proraphidia hopkinsi sp. nov.

Figure 1

1984 Mesoraphidiidae, Jarzembowski, pp. 82–83, fig. 30
1987 Proraphidia sp. nov., Jarzembowski, pp. 174–176, fig. 8.1
1988 Mesoraphidia sp., Whalley, pp. 48, 61
1990 Mesoraphidiidae, Nel, Séméria and Martins-Neto, p. 11

Etymology. Named after the late Dick Hopkins in recognition of his long voluntary service to museum geology at the Booth Museum, Brighton.


Type locality. Lower Weald Clay, Clockhouse Brickworks, Surrey, England. Lower Cretaceous (Late Hauterivian).

Diagnosis. Wing not as broad as in P. turkestanica; R not as close to Sc in proximal half of wing. Three crossveins between R and Sc; dc shorter. Both branches of MA forked; MP deeply forked with both branches forked. Second branch of CuA forked; ac much wider.

Description and measurements. Forewing: 11.5mm long and 3.2mm wide. C poorly preserved and incomplete; 3c incomplete, terminating approximately 4mm from the wing apex (slightly past the mid-point of the wing) on the anterior wing margin. Half of the subcostal area is preserved, with three crossveins present. R is complete and long terminating at the wing apex; in the radial area there are two crossveins preserved one 3.5mm from apex and the second 0.5mm. Pterostigma present terminating on third crossvein in radial space and terminating more distally than the most distal r-rs crossvein; pterostigma small, less than 1mm long. Three radial cells are present: 1r: 4mm long and 0.5mm wide; 2r: 2.5mm long and 0.7mm wide and 3r: 2.2mm long and 0.4mm wide. Rs and MA arise approximately 6.5mm from wing apex; they are coalesced for 1.6mm before forking. Rs2 is two branched forking from the stem of Rs 1.2mm from wing apex; both Rs1 and Rs2 arise in the distal part of the wing near the apex. The discal cell (dc) is formed by a crossvein between Rs and MA and is 2.2mm long and 0.7mm wide (at its widest point). MA is two branched with both branches being forked. MP is coalesced with CuA for a short distance (0.2mm). M and CuA arise 8.4mm from the wing apex. MP is deeply forked with each branch forked. Between MP and CuA three cells are present mc1, mc2 and mc3. CuA forks near the posterior wing margin; the first branch is simple, the second branch forks again. Two crossveins are preserved between CuA and CuP; CuP is simple. 1 crossvein is preserved between CuP and A. Anal area poorly preserved, only part of ac being present.

Remarks. The fossil has been placed in the genus Proraphidia on the basis of the small pterostigma (excluding it from Mesoraphidia with its long pterostigma), the pterostigma’s basal border being located more distally than the most distal r-rs crossvein, and the structure of M and Cu. There are three species in the genus Proraphidia: P. turkestanica, P. hopkinsi sp. nov. and P. gomezi sp. nov. Martynova (1961) identified a species Proraphidia vitimica; this, however, was transferred to Alloraphidia by Ponomarenko (1993) and later to Pararaphidia by Engel (2002). Proraphidia hopkinsi sp. nov. is the first species of snakefly to be described from the Early Cretaceous Wealden Supergroup. Snakeflies are present in the Jurassic in England, represented by the mesoraphidiid Metaraphidia confusa and the debatable raphidiopteran Priscaenigma obtusa (Whalley 1985, 1988, Willmann 1994, Engel 2002). A Cretaceous snakefly (Mesoraphidia sp.) has been figured from the Purbeck Limestone Group of England (Jarzembowski 1993, Clifford et al. 1994). There are four species of the family Raphidioptera in England today (Plant 1997).

Proraphidia gomezi sp. nov.

Figure 2

1986 Proraphidia sp., Gómez-Pallerola, p. 45, fig. 7, Photograph 46.

Etymology. After Mr Gómez-Pallerola, fossil collector and contributor to the Institut d’Estudis Ilerdencs, Lérida.

Holotype. [L. 29]. Overlapping fore- and hindwings and part of body. Deposited in Institut d’Estudis Ilerdencs, Lérida, Spain.

Type locality. Limestone, Pedrera de Meià, Rúbies, Spain, Lower Cretaceous, Early Barremian.

Diagnosis. Hindwing differs from P. turkestanica in length of the wing, having fewer costal veinlets, the
branches of Rs and MA being simple and mc being split into two.

**Description and measurements.** Forewing: 13mm long and 5.2mm wide. C is preserved with three costal veinlets; Sc terminating approximately 5.6mm from the wing apex (past the mid-point of the wing) on the anterior wing margin. R is complete and long terminating just before the wing apex; in the radial area there are two crossveins preserved one 5.6mm from apex of wing and the second 0.9mm from the wing apex. Pterostigma present terminating on the second crossvein in radial area and terminating more distally than the most distal r-rs crossvein; pterostigma small, less than 1mm long. Three radial cells are present: 1r: 3.7mm long and 1mm wide; 2r: 3.6mm long and 1.2mm wide and 3r: 2.2mm long and 0.7mm wide. Rs and MA arise approximately 9mm from wing apex; they are coalesced for 2.5mm before forking. Rs is two branched; Rs1 and Rs2 are simple; both Rs1 and Rs2

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Figure 2. A. Photograph of *Proraphidia gomezi* sp. nov. (L. 29). B Camera lucida drawing of overlapping wings. C. Camera lucida drawing of venation of forewing. D. Camera lucida drawing of venation of hindwing. Drawing convention as in Jarzembowski (1980). Scale bar = 1mm.
arise in the distal part of the wing near the apex. The discal cell (dc) is 3.5mm long and 1mm wide (at its widest point). MA is forked with both branches simple. Origin of MP not preserved. MP is deeply forked with each branch forked. Between MP and CuA three cells are present mc1, mc2 and mc3. Cu incomplete. CuA partially preserved. CuP and Analis not preserved.

Hindwing: 12.2mm long and 4.8mm wide. C is preserved with four costal veinlets; Costal area narrow. Sc terminating approximately 5.5mm from the wing apex (near the mid-point of the wing) on the anterior wing margin. R is complete and long terminating just before the wing apex; in the radial area there is one crossvein preserved 0.8mm from apex of wing. Three radial cells are present: 1r: 3.8mm long and 1.1mm wide; 2r: 4.5mm long and 1.1mm wide and 3r: 2.2mm long and 0.6mm wide. Cell 1r has a crossvein before mid-point. Rs arises approximately 9mm from wing apex and MA origin not seen. MA and Rs are coalesced for 3mm before forking. Rs is two branched; Rs1 and Rs2 are simple; both Rs1 and Rs2 arise in the distal part of the wing near the apex. The discal cell (dc) is 3.5mm long and 0.9mm wide (at its widest point). MA forks with both branches simple. MP origin not seen. MP is deeply forked with each branch forked. Between the branches of MP the medial cell (mc) is split in two by a crossvein. CuA forks once marginally; the origin of CuA is not preserved. CuP is partially preserved with a crossvein joining it to CuP at the vein’s mid-point. CuP is simple. Analis not preserved.

Remarks. This species has been placed in Proraphidia on the basis of the small pterostigma, the pterostigma’s basal border being located more distally than the most distal t-rrs crossvein, and the structure of M and Cu. This is the first species of snakefly to be formally described from the Spanish Cretaceous and Montsec. There are twelve species of snakeflies in Spain today in eight genera (http://www.faula-ibericamncn.csic.es/faunaib/arthropoda/index.php).

RAPHIDIOPTERA FROM THE JURASSIC/CRETACEOUS TRANSITION

A problem arises when one talks about a clear-cut Jurassic/Cretaceous boundary in continental deposits, because many are badly dated or the dates given are debatable. Here we have used the dates that are widely accepted by most workers.

There has only been one raphidiopteran family recorded, Mesoraphidiidae that ranges from the Jurassic into the Cretaceous. The family Raphidiidae has not been found in pre-Tertiary rocks (Engel 2002) and Inocelliidae has been recorded in Lower Cretaceous rocks (Wang 1987). Table 1 lists the families (with species) involved in the Jurassic/Cretaceous transition.

Mesoraphidiidae has two genera that crossed the transition, one genus that straddled the transition and one genus Metaraphidia that appears to have become extinct before the boundary. The three genera that crossed/straddled the Jurassic/Cretaceous boundary are Mesoraphidia, Proraphidia and Sinoraphidia. Out of these four genera, Sinoraphidia (one species) is known from the Upper Jurassic-Lower Cretaceous of Gansu, China (Hong 1982); Proraphidia crosses the boundary: P. turkestanica is known from the Upper Jurassic of Karatau, Kazakhstan (Martynova 1947), P. hopkinsi sp. nov. from the Lower Cretaceous Wealden Supergroup and P. gomezi sp. nov. from Montsec in the Lower Cretaceous; however, there is no evidence from the fossil record showing one good species continuing through the transition. Mesoraphidia shows a similar scenario to Proraphidia; there are no species that straddle the boundary. In the Jurassic, six species are known from Kazakhstan (Martynova 1925; Martynova, 1947) and one species from Mongolia (Ponomarenko, 1988; Willmann, 1994) has been described. In the Lower Cretaceous, eleven species have been recorded in China (Hong, 1992a; Ren et al. 1995; Ren, 1997; Engel 2002), one unnamed species from England (Jarzembowski, 1993; Clifford et al. 1994), two species from southern Korea (Engel et al. 2006) and one species has been recorded in the Upper Cretaceous New Jersey amber, USA (Grimaldi, 2000). The genus Metaraphidia, however, did not survive into the Cretaceous; the fossil record currently suggests that the genus became extinct in the Jurassic. It comprises two species from the Lower Jurassic of England and Germany (Whalley, 1988).

Baissopteridae have not been found in the Jurassic; however, they are found in the Lower Cretaceous. Five species of Baissoptera and four species of Cretoraphidia have been recorded in Baisa, Buryat Russia (Martynova 1961, Ponomarenko 1993, Engel 2002). The family has also been recorded in the Lower Cretaceous of Brazil (one species of Austroraphidia and two species of Baissoptera) (Oswald 1990, Willmann 1994, Engel 2002), China (three species of Baissoptera) (Ren 1994, 1997, Ren et al. 1995), and Mongolia (one species of Cretinocellia, Cretoraphidiopsis and Lugala) (Ponomarenko 1988, Willmann 1994, Engel 2002).

The family Alloraphidiidae is the smallest of three raphidiopteran families with three genera Alloraphidia, Archerraphidia and Pararaphidia (Engel 2002). Alloraphidia asiatica, Archerraphidia bainsensis and Pararaphidia vitimica are found in the Lower Cretaceous of Baisa, Buryat, Russia (Ponomarenko 1993, Engel 2002); other Cretaceous species are from Labrador, Canada (Carpenter 1967) and Mongolia (Ponomarenko 1988, Willmann 1994).

In the Cretaceous, raphidiopterans appear to be more widespread geographically than in the Jurassic; however, this may not be a true reflection because more fossil insect deposits are known in the Cretaceous than the Jurassic. In the Jurassic, the fossil evidence suggests that they were only present in Eurasia (England, Germany, Mongolia, Kazakhstan and China). In the Cretaceous, fossils have also been found in the USA, Canada and Brazil showing that they colonized the New World. The Jurassic, however, is thought to be the time when the major family radiations
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occurred (see phylogenetic diagram in Grimaldi & Engel 2005, fig. 9.4, p.336). However, the fact that there are no fossils of the families Alloraphidiidae and Baissopteridae in the Jurassic means that based on the current fossil evidence, the major radiation of raphidiopterans could not have been before the latest Jurassic. The Cretaceous saw the extinction of the fossil families Baissopteridae, Alloraphidiidae and Mesoraphidiidae (Engel 2002) and it is thought that snakefly biodiversity decreased around the middle Cretaceous (Aspöck 1998). Martynov (1925) suggested that the extinction of families such as Mesoraphidiidae was due to ‘disharmony’ in the degree of evolution of the wings and body. However, recently, the extraterrestrial impact at the end of the Cretaceous has been hypothesized as a reason for the extinction of the tropical snakeflies with only the cold-climate adapted snakeflies (Inocelliidae and Raphidiidae) surviving (Aspöck 1998). This would account for the absence of the order in warm-climate Palaeogene deposits such as the Bembridge Marls, southern England.

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Thanks to Dr John Nudds, Peter Falkingham and Karl Bates (University of Manchester) for discussion, Dr Dmitri Logunov (The Manchester Museum) for discussion and translation of the Martynova (1947) paper, Drs Jörg Ansorge and Vladimir Makarkin for helpful comments when reviewing the paper, Dr Carmen Soriano for information on Spain, and INTAS for supporting Fossilsx3.

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CHAPTER 9

5. NEW SNAKEFLIES (INSECTA: RAPHIDIOPTERA) FROM THE LOWER CRETACEOUS OF THE UK, SPAIN AND BRAZIL
NEW SNAKEFLIES (INSECTA: RAPHIDIOPTERA) FROM THE LOWER CRETACEOUS OF THE UK, SPAIN AND BRAZIL

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NEW SNAKEFLIES (INSECTA: RAPHIDIOPTERA) FROM THE LOWER CRETACEOUS OF THE UK, SPAIN AND BRAZIL

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Abstract: Several new taxa of snakeflies (Raphidioptera) are described from the Lower Cretaceous deposits of the Wealden, UK (Barremian), Montsec, Spain (Barremian) and the Crato Formation, Brazil (Aptian). Mesoraphidia ednae sp. nov. and M. hilli sp. nov. are described from the Wealden; Nanoraphidia lithographica sp. nov. and Iberoraphidia dividua gen. et sp. nov. are described from Montsec, and Baissoptera lisae sp. nov. is described from the Crato Formation. The geographical range of Nanoraphidia has potentially been extended.
**Key words:** Baissopteridae, Crato Formation, Mesoraphidiidae, Mesozoic, Montsec, Wealden, snakefly

RAPHIDIOPTERA are a member of the holometabolous superorder Neuropterida along with the orders Neuroptera and Megaloptera (Aspöck, U. 2002). Snakeflies are the least diverse order of the holometabolous insects with 225 extant species described in two families Raphidiidae Latreille, 1810 and Inocelliidae Navás, 1913 (Aspöck, U. and Aspöck, H. 2003; Engel et al. 2006). Extant snakeflies are arboreal and found in cold temperate regions; they require near-freezing temperatures to aid development (Aspöck, H. et al. 1991; Aspöck, H. 2002; Grimaldi and Engel 2005).


The fossil snakefly species, on the whole, are diagnosed on the basis of wing venation, whereas extant species are described on body morphology, in particular genitalic differences. In extant species wing venation is of little importance and it is likely that the venation-based species of the Mesozoic represent a complex of species, rather than a single species. This could mean that the Mesozoic diversity could be much greater than previously thought, thus supporting the idea that extant snakeflies are relict (Aspöck, H. et al. 1991; Engel 2002). This could also be true for other neuropterid groups (e.g. Myrmeleontiformia). Unfortunately, this is difficult to prove in the fossil record without preserved terminalia.

Only one other snakefly has been formally described from the Lower Cretaceous Wealden Supergroup, *Proraphidia hopkinsi* Jepson and Jarzembowski,
2008. *P. hopkinsi* belongs to the family Mesoraphidiidae and four species of the
nominotypical genus *Mesoraphidia* occur in the underlying Lower Cretaceous
Purbeck Limestone Group (Jepson *et al.* 2009). In addition, *Metaraphidia* is known
from the Jurassic of Dorset (Lower Lias, Charmouth) (Whalley 1988). Montsec has
had one species of snakefly formally described (*Proraphidia gomezi* Jepson and
Jarzembowski, 2008) in the family Mesoraphidiidae. The Crato Formation has four

**GEOLOGICAL SETTINGS**

*Upper Weald Clay, UK*

The Upper Weald Clay is the youngest formation of the Lower Cretaceous Wealden
Supergroup. The age of the Upper Weald Clay is Barremian, and the specimens
described herein were collected from two localities: Auclaye Brickworks, Surrey and
Rudgwick Brickworks, Sussex. The Upper Weald Clay represents a lacustrine-
lagooonal environment, with a warm-temperate to sub-tropical climate (Allen 1998;
Haywood *et al.* 2005). Many insects have been discovered in the Upper Weald Clay
including the orders Odonata, Grylloblattodea, Orthoptera, Neuroptera,
Montsec, Spain

The lithographic limestones of Sierra del Montsec outcrop at two sites in the mountain range Montsec de Rubies, Lerida Province, northeast Spain. The La Cabrua locality is situated at a steep local road near Santa Maria de Meia; the former quarry is near the abandoned village Rubies. The carbonate mud which builds up the lithographic limestones was deposited in the deepest parts of a fresh or brackish water lagoon without direct connection to the epicontinental sea (Ansorge 1993; Fregenal-Martinez and Melendez 1995). Deposition of charophytic limestones took place in shallow water. The age of the lithographic limestones has been determined as Lower Barremian based on the occurrence of the charophyte *Atopochara trivolis triquetra* Grambast, 1968 (morphotype ‘typique’) (Ansorge 1993; Martín-Closas and López-Móron 1995). The rich and well-preserved insect fauna of Montsec consists of aquatic larvae and imagines. Up to now representatives of the following insect orders have been recorded: Ephemeroptera, Odonata, Blattodea, Isoptera, Orthoptera, Hemiptera, Psocoptera, Trichoptera, Diptera, Hymenoptera, Coleoptera, Neuroptera and Raphidioptera (Ansorge 1993; Martínez-Delclos and Nel 1995; Whalley and Jarzembowski 1985). The most common fossil insect is the aquatic mayfly larva *Mesopalingea leridae* Whalley and Jarzembowski, 1985. Cockroaches and beetles are the most common flying insects. Together with the plant macrofossils (Barale 1995) the insects are typical of a drier climate with seasonal rainfall.

Crato Formation, Brazil
The specimen described herein is from the Nova Olinda Member of the Crato Formation, Brazil. This is the lowest unit of the formation, Aptian in age, consisting of finely laminated limestones deposited in a hypersaline lagoonal environment (Martill et al. 2007). The Crato Formation represents a Konservat Lagerstätte and is famous for its exceptionally preserved and diverse insect assemblage, with 21 hexapod orders present, including, Diplura, Zygentoma, Ephemeroptera, Odonata, Dermaptera, Mantodea, ‘Blattaria’, Isoptera, Chresmododea, Phasmatodea, Orthoptera, Hemiptera, Neuroptera, Raphidiptera, Megaloptera, Coleoptera, Hymenoptera, Mecoptera, Diptera, Trichoptera and Lepidoptera (see chapters in Martill et al. 2007).

MATERIAL AND METHODS

The studied material is deposited in the following collections: Booth Museum of Natural History, Brighton (BMB), Maidstone Museum and Bentlif Art Gallery, Kent (MNEMG), Sedgwick Museum of Earth Sciences, Cambridge (CAMSM), Institute of Geography and Geology, University of Greifswald (FGWG) and Geowissenschaftliches Zentrum der Universität Göttingen (GZG).

*Mesoraphidia ednae* sp. nov. was drawn by JEJ using an Olympus SZH stereomicroscope with a camera lucida attachment. The drawing is a composite, merging the part and counterpart to establish a more complete venation; this was achieved using a light box. 10% ethanol was used to enhance vein detail. Photographs were taken using a Canon EOS 450D digital SLR camera mounted on a rostrum stand.
The *Mesoraphidia hilli* sp. nov. holotype was drawn by Robert A. Coram (British Fossils) and EAJ using a camera lucida attachment on a Zeiss Stemi SVII microscope and photographed by JEJ using a Canon EOS 450D digital SLR camera mounted on a rostrum stand. The *M. hilli* sp. nov. paratype was photographed by Tony Mitchell (volunteer Maidstone Museum) using a Nikon Coolpix 5000 digital camera.

The Montsec specimens were drawn by JA using a camera lucida attached to a SM XX Zeiss stereomicroscope and photographed with a Nikon Coolpix 4500 mounted in a macrophotographic bellows.

Wing vein abbreviations are as follows: C, costa; Sc, subcosta; R, radius; Rs, radial sector; Rs1, first branch of Rs; Rs2, second branch of Rs; M, media; MA, anterior media; MP, posterior media; MP1, first branch of MP; MP2, second branch of MP; Cu, cubitus; CuA, anterior cubitus; CuP, posterior cubitus; A, analis; r, radial cell; dc, discal cell; mc, medial cell; ac, anal cell; p, pterostigma.

**SYSTEMATIC PALAEOONTOLOGY**

Order RAPHIDIOPTERA Navás, 1918

Family MESORAPHIDIIDAE Martynov, 1925

Genus MESORAPHIDIA Martynov, 1925

Type species: *Mesoraphidia grandis* Martynov, 1925 from the Late Jurassic of Kazakhstan.

*Mesoraphidia ednae* sp. nov.
Derivation of name. In honour of Edna Clifford who inspired the online EDNA fossil insect database.

Holotype. MNEMG 2009.42 [AY36a, b], disarticulated forewing, Auclaye Brickworks, Upper Weald Clay, Barremian.

Diagnosis. Separated from all other Mesoraphidia species by combination of MA bifurcating at exact point of fork of MP, long basal branch of MA, small size of mc3, wide distance between cua-cup crossveins, and 3A forking close to posterior wing margin.

Description. Holotype forewing (Text-fig. 1): narrow and elongate; 8 mm long and 2.6 mm wide. C complete; costal area preserved with five crossveins. Sc terminates approximately 3.4 mm from wing base (just past midpoint of wing) on anterior wing margin. R complete and long, origin 7.5 mm from wing apex, terminating near wing apex; three crossveins present between R and C, 0.8 mm, 1.1 mm and 2.8 mm from wing apex. Pterostigma present; over 1.7 mm long; beginning of pterostigma difficult to determine as pigment fades proximally. Three radial cells present: 1r: 1.6 mm long and 0.5 mm wide; 2r: 1.9 mm long and 0.9 mm wide and 3r: 1.3 mm long and 0.3 mm wide. Rs arises from R approximately 4.9 mm from wing base. Rs two branched; Rs1 and Rs2 simple; both Rs1 and Rs2 arise in distal part of wing near apex. dc formed by a crossvein between Rs and MA, 1.9 mm long and 0.5 mm wide (at widest point). MA arises 1.4 mm from R where M forks into MA and MP; it then runs into Rs 0.7 mm.
from fork with M. MA coalesced with Rs for 1.1 mm. MA two branched with both
branches simple. Two crossveins present between MA and MP. MP deeply forked
with each branch forked near posterior wing margin. Three cells present between MP
and CuA: mc1: 0.9 mm long, 0.5 mm wide; mc2: 1 mm long, 0.5 mm wide and mc3:
0.6 mm long, 0.3 mm wide. CuA coalesced with M for 0.1 mm. CuA forks near
posterior wing margin, distal branch forked, basal branch simple. Two crossveins
present between CuA and CuP; CuP simple. Anal area is preserved with 1A simple,
2A and 3A fused dividing 0.2 mm from posterior wing margin; 2A simple and 3A
forked near posterior wing margin. ac oval shaped, 1.1 mm long, 0.4 mm wide.

Remarks. Placed in Mesoraphidia Martynov, 1925 on the basis of typical venation,
having a long pterostigma and MA arising at the origin of MP.

Mesoraphidia hilli sp. nov.

Text-figs. 2–3

Derivation of name. In honour of the collector of the holotype, Prof. Chris R. Hill
(Nanjing Institute of Geology and Palaeontology).

Holotype. BMB 016381, 016382 (part and counterpart), disarticulated hind wing,
Rudgwick Brickworks, Upper Weald Clay, Barremian.

Paratype. BMB 025010, 025011 (part and counterpart), disarticulated wing, fragment
of apical half, Rudgwick Brickworks, Upper Weald Clay, Barremian.
Diagnosis. Separated from other *Mesoraphidia* species by the combination of Sc terminating well past midpoint of wing above centre of 2r, a near horizontal (relative to the anterior wing margin) cua-mp2 crossvein.

Description. Holotype hind wing (Text-fig. 2): narrow and elongate; 11.5 mm long and 7.1 mm wide. C incomplete; costal area preserved with four crossveins. Sc terminates approximately 4.3 mm from wing base (1.9 mm past mid-point of wing) on anterior wing margin. R complete and long, origin 7.5 mm from wing apex, terminating far from wing apex; two crossveins present between R and C, 2.7 mm and 3.6 mm from wing apex. Pterostigma present; over 0.9 mm long; beginning of pterostigma difficult to determine as pigment fades towards wing apex. Three radial cells present: 1r: 3.8 mm long and 0.9 mm wide with crossvein halfway; 2r: 3 mm long and 0.7 mm wide and 3r: 1.9 mm long and 0.3 mm wide curving towards anterior wing margin. Rs arises from R approximately 9.1 mm from wing apex. Rs two branched; Rs1 branches pectinately to form four branches at antero-posterior wing margin, Rs2 simple; both Rs1 and Rs2 arise in distal part of wing near apex. dc 3 mm long and 0.8 mm wide (at widest point). MA arises close to wing base, 10.9 mm from wing apex. MA runs into Rs, 2.2 mm from origin. MA coalesced with Rs for 2.2 mm. MA is dichotomously branched, splitting into four branches at posterior wing margin. Two crossveins present between MA and MP and MP1 and MP2. MP origin 11.4 mm from wing apex. MP appears to be deeply forked; however, fork not preserved. MP1 forks 3.6 mm from posterior wing margin, first branch forks 1.4 mm from posterior wing margin; second branch incomplete, however, most likely forked, based on vein fragment terminating on posterior wing margin next to first branch. MP2 forks 1.4 mm from posterior wing margin; first branch forks 1.62 mm from...
posterior wing margin, with most distal branch possibly forking again but incomplete.

Second branch forks 1 mm from posterior wing margin. Medial cell: 1.3 mm long, 0.5 mm wide; mc2: 1 mm long, 0.8 mm wide. One crossvein between CuA and MP and two crossveins between MP2 and CuA. CuA simple for most of its length forking 0.75 mm from posterior wing margin. CuP incomplete, termination on posterior wing margin preserved. Anal area not preserved.

Description of paratype. Apical wing fragment (Text-fig. 3): 6.4 mm preserved length, 4 mm preserved width. C incomplete, costal area incomplete. Sc incomplete, terminates 4.5 mm from wing apex, on anterior wing margin. R incomplete, terminating before wing apex. Three crossveins between R and C: 1.5 mm, 2.5 mm and 3.3 mm away from wing apex. Pterostigma preserved 1.9 mm long, faded towards beginning. Three radial cells, 1r: incomplete 1.5 mm preserved length, 0.8 mm width, 2r: 2.4 mm long, 0.8 mm wide and 3r: 2.2 mm long, 0.6 mm wide. Rs origin not preserved, Rs separates from MA 5.7 mm from wing apex. Rs two-branched, with Rs1 forking 1.8 mm from wing margin, first branch forking 0.8 mm from posterior wing margin, second branch simple. dc 2.5 mm long and 0.7 mm wide (at widest point). MA origin not preserved, dichotomously branched, first fork 3.2 mm from posterior wing margin, MA1 forks 1 mm from wing margin, and MA2 forks 1.8 mm from posterior wing margin. Two crossveins between MA and MP. MP incomplete, origin not preserved. MP1 dichotomously branched 2.5 mm from posterior wing margin, first branch forks 1.3 mm from posterior wing margin, second branch forks 0.8 mm from posterior wing margin. MP2 forks 1.7 mm from posterior wing margin, first branch forks 1 mm from posterior wing margin, second branch simple. Part of
Remarks. It is unsure whether the specimen represents a fore- or hind wing due to the fragmentary nature of the wing. The paratype has been provisionally attributed to *Mesoraphidia hilli* sp. nov. subject to more material being found. The provisional placement is on the basis of similarity in the structure of Rs, a dichotomously branched MA and the termination of Sc being well past the midpoint of the wing. The placement is tentative due to the fragmentary nature of the wing.

Genus *NANORAPHIDIA* Engel, 2002

Type species: *Nanoraphidia electroburnica* Engel, 2002 from the Lower Cretaceous Burmese amber.

*Nanoraphidia lithographica* sp. nov.

Text-Fig. 4

Derivation of name. The species epithet *lithographica* is derived from the rock source—a fine-grained lithographic limestone.

Holotype. FGWG 147 (MA 20 a,b, part and counterpart) disarticulated body with four overlapping wings, La Cabrua outcrop, Sierra del Montsec, Lower Barremian; for locality reference see Ansorge (1993, pp. 21–23) and Fregenal-Martinez and Melendez (1995).
Diagnosis. Differs from *N. electroburmica* in having larger size (*N. lithographica*, 5.3 mm, *N. electroburmica*, 4.26 mm), radial cells and dc narrower, CuA with one fork, forking further away from posterior wing margin.

Description. Holotype forewing (Text-fig. 4): 5 mm preserved length, estimated length 5.3 mm. C incomplete. Sc incomplete, termination not observed. R complete and long, terminating 0.4 mm from wing apex; one crossvein between R and C 0.6 mm from wing apex. Pterostigma not preserved, seems to be absent. Three radial cells present: 1r: incomplete, 0.4 mm wide; 2r: 1.1 mm long and 0.4 mm wide and 3r: 0.6 mm long and 0.2 mm wide. Rs two branched, both branches simple; both Rs1 and Rs2 arise in distal part of wing near apex. dc 1 mm long and 0.3 mm wide (at widest point). MA arises after fork of MP and CuA. MA coalesced with Rs for 1.2 mm. MA two branched with both branches simple. Two crossveins present between MA and MP. MP deeply forked with MP1 forking 0.8 mm and MP2 forking 0.7 mm from posterior wing margin. One medial cell posterior to MP between MP and CuA: mc1: 0.8 mm long, 0.4 mm wide and mc2: 0.8 mm long, 0.4 mm. CuA coalesced with M distally. CuA forks 0.6 mm from posterior wing margin. One cua-cup crossvein partially preserved before M-CuA separation. CuP, 1A, 2A and 3A incomplete.

Body parts. Poorly preserved; part of thorax and abdomen present. Thorax preserved length 2.3 mm. Abdomen preserved: length 1.8 mm.

Remarks. All four wings of the specimen are overlapping obscuring the venation, making it difficult to distinguish. The hind wing venation was indecipherable. The
specimen has been tentatively placed in the genus *Nanoraphidia* due to the combination of its small size and venation: the one medial cell (separating it from *Mesoraphidia*) and the first cua-cup crossvein occurring before the separation of M and CuA. Other diagnostic features are not preserved, e.g. the costal area and pterostigma (possibly an artefact of preservation); however, the pterostigmal area has no crossveins which is consistent with *Nanoraphidia*. *Nanoraphidia lithographica* sp. nov. has a larger wing size (estimated 5.3 mm) than *N. electroburmica* (4.26 mm); the size of the wing is similar to other snakeflies, e.g. *Mesoraphidia parvula* (wing length 5.5 mm (Martynov 1925)), *M. gaoi* (wing length 5 mm (Ren et al. 1995)), *M. mitchelli* (estimated wing length 5.4 mm), *M. purbeckensis* (estimated wing length 5.1 mm), *M. websteri* (estimated wing length 5.7 mm) (Jepson et al. 2009). However, the venation is sufficiently different from these species and closer to *Nanorapidia* to allow a tentative placement in the latter genus. The geographical disjunction of *N. lithographica* sp. nov. in Spain and *N. electroburmica* in Burma, again only supports a tentative and not a confident placement within *Nanoraphidia*.

Genus IBERORAPHIDIA gen. nov.

*Type and only species.* *Iberoraphidia dividua* gen. et sp. nov.

*Derivation of name.* After Iberia, the Iberian Peninsula comprising Spain and Portugal and *Raphidia*, a raphidiopteran genus.

*Diagnosis.* Divided pterostigma separates it from all other known snakeflies. MA separates distinctly prior to fork of MP, which separates it from almost all
Mesoraphidiidae and Alloraphidiidae - only Ororaphidia Engel and Ren, 2008 shows a similar shift of MA towards the wing base.

**Iberoraphidia dividua** sp. nov.

Text-fig. 5

**Derivation of name.** Meaning divided, in reference to the divided pterostigma.

**Diagnosis.** As for the genus.

**Holotype.** GZG.RF.7563 (part and counterpart), isolated forewing; La Cabrua outcrop, Sierra del Montsec, Lower Barremian, for locality reference see Ansorge (1993, pp. 21–23) and Fregenal-Martinez and Melendez (1995).

**Description.** Holotype forewing (Text-fig. 5): 12.5 mm long. C complete; costal area preserved with six crossveins (originally seven - basal one is extremely faint).

Macrotrichiae on C and the distal part of R (Text-fig. 5C). Sc terminates approximately 5.3 mm from wing apex (just past midpoint of wing) on anterior wing margin. R complete and long, terminating near wing apex; one crossvein between R and Sc 9.5 mm from wing apex, six crossveins present between R and C, 0.6 mm, 1.3 mm, 2.1 mm, 2.5 mm, 4.3 mm and 4.8 mm from wing apex. Pterostigma divided into two, over 1.7 mm long; beginning of first part of pterostigma 4.8 mm from wing apex, end of first part 4.3 mm, beginning of second part 2.5 mm and end 2.1 mm. Three radial cells present: 1r: 3.2 mm long and 0.9 mm wide; 2r: 2.5 mm long and 1 mm wide and 3r: 2.5 mm long and 0.6 mm wide. 3r narrows towards apex of wing. Rs
arises from R approximately 8 mm from wing apex. Rs two branched; Rs1 forks at its midpoint and first branch forks again 0.7 mm from wing margin; Rs2 is simple; both Rs1 and Rs2 arise in distal part of wing near apex. dc 2.5 mm long and 0.9 mm wide (at widest point). MA arises 3 mm from R, where M forks into MA and MP; it then runs into Rs 0.8 mm from split with M. MA coalesced with Rs for 2.1 mm. MA two branched with MA1 forking 2 mm from posterior wing margin; MA2 simple. Two crossveins present between MA and MP. MP deeply forked with MP1 forking 2 mm and first branch forking 1.8 mm from posterior wing margin; MP2 forks 1.2 mm from posterior wing margin. Three cells present between MP and CuA: mc1: 1.3 mm long, 0.5 mm wide; mc2: 1.6 mm long, 0.9 mm wide and mc3: 1.5 mm long, 0.8 mm wide. CuA coalesced with M for 1.7 mm. CuA forks near posterior wing margin; distal branchforked 0.7 mm from wing margin, basal branch simple. Two crossveins present between CuA and CuP; CuP simple. One crossvein between CuP and 1A at midpoint of these two veins. Anal area preserved with 1A simple, 2A and 3A present. ac oval shaped, 1.9 mm long, 0.7 mm wide.

Remarks. The species is excluded from the family Baissopteridae due to its less complex venation, and from Alloraphidiidae due to the basal shift of MA. It has been placed in Mesoraphidiidae due to the typical venation and long pterostigmal area. The divided pterostigma is a unique feature of *Iberoraphidia dividua* gen. et sp. nov. distinguishing it from all other Mesoraphidiidae.

Family BAISSOPTERIDAE Martynova, 1961

Genus BAISSOPTERA Martynova, 1961
Type species. *Baissoptera martinsoni* Martynova, 1961 from the Lower Cretaceous of Baissa, Russia.

*Baissoptera lisae* sp. nov.

Text-fig. 6

Derivation of name. Named after Lisa Abbott, geology student at the University of Manchester.

Holotype. CAMSM X.50155.2, female insect, some body parts preserved and fore- and hind wings overlapping on left and right side, Crato Formation, Brazil, Lower Cretaceous (Aptian). The provenance of the specimen has been inferred from the characteristic nature of the sediment and preservation of the insect. No provenance details were supplied with the specimen.

Diagnosis. Separated from other species of *Baissoptera* by a combination of Sc and C anastomising very proximally to pterostigma; few crossveins and cells in medio-radial area, but crossveins present forming two gradate series in posterior part of wing R forking distally in hind wing. Small body size (excluding ovipositor); head and pronotum, almost same size, head does not narrow posteriorly, separating it from *B. brasiliensis*.

Description. Holotype forewing (Text-fig. 6A): 12.4 mm preserved length, 3.7 mm preserved width. C complete; costal area poorly preserved with three crossveins. Sc terminates approximately 5.5 mm from wing apex (past mid-point of wing) on
anterior wing margin. R complete and long but terminating before wing apex; two
crossveins between R and C 1.8 mm and 4 mm from wing apex, one crossvein present
between R and Sc 11 mm from wing apex. Pterostigma preserved; 2 mm long, 0.3
mm wide between two r-c crossveins. Three radial cells present: 1r: 2.3 mm long and
0.7 mm wide; 2r: 1.3 mm long and 0.6 mm wide and 3r: 1.2 mm long and 0.3 mm
wide. 3r narrows towards apex of wing due to fork of Rs. Rs arises from R
approximately 8 mm from wing apex. Rs four branched; Rs1 forks near wing apex,
other branches simple. MA origin not preserved. MA coalesced with Rs for 0.8 mm.
MA simple most of length, forking close to posterior wing margin. Two crossveins
present between MA and MP. MP appears deeply forked, although point of forking
not preserved; both branches forked; cubital and anal veins not preserved.

Hind wing: 12.5 mm preserved length and 3.5 mm preserved width. C incomplete;
costal area preserved with three crossveins. Sc terminates approximately 5.7 mm from
wing base (past mid-point of wing) on anterior wing margin. R long, origin not
preserved, forking before termination, terminates away from wing apex. Two
crossveins preserved between R and C, 1.5 mm and 3.6 mm from wing apex.
Pterostigma present, incomplete. Three radial cells present: 1r: 2.6 mm long and 0.7
mm wide with crossvein halfway; 2r: 1.3 mm long and 0.4 mm wide and 3r: 1 mm
long and 0.3 mm wide. Rs arises from R approximately 7.9 mm from wing apex. Rs
four branched, Rs1 forking near wing margin. MA arises close to wing base, 10 mm
from wing apex. MA runs into Rs, 2.3 mm from origin. MA coalesced with Rs for 1
mm. MA dichotomously branched, splitting into four branches at posterior wing
margin. Four crossveins present between MA and MP. MP origin 10 mm from wing
apex, very close to MA. MP deeply forked. MP1 forks at 1.1 mm and 1.4 mm from
posterior wing margin. MP2 dichotomously forked, main fork 1.3 mm from posterior wing margin, both branches forking 0.5 mm from posterior wing margin. Three crossveins between CuA and MP. CuA incomplete. CuP and anal area not preserved.

**Head.** 2.9 mm long, 1.8 mm wide. Eyes partially preserved, left eye better preserved than right, 1 mm long, 0.5 mm wide. Three ocelli present and preserved in a triangular pattern close together. Antennae incomplete, partially preserved, scape 0.3 mm long, 0.2 mm wide.

**Thorax.** Pronotum elongate 3.1 mm long, 1.5 mm wide, enclosing prothorax. Meso- and metathorax poorly preserved, combined length 4.4 mm. Legs preserved, obscured by sediment (legs go down vertically into the rock).

**Abdomen.** Shorter than wings, 6 mm long (excluding ovipositor), 1.8 mm wide, poorly preserved; elongate ovipositor incomplete; preserved length 2.3 mm.

**Remarks:** The specimen is preserved in three-dimensions with many parts of the fossil (e.g. the legs) going down vertically into the rock concealing features of the body morphology. It is tentatively placed in the genus *Baissoptera* because of the numerous crossveins arranged in gradate series posteriorly, this being a diagnostic character of the genus (Oswald 1990). The wing venation is similar to the Crato Formation genus *Austroraphidia* Willmann, 1994; however, *B. lisae* sp. nov. differs from it in having arranged crossveins, more branches of Rs and MA, and having a more elongate wing. The absent/incomplete cubital and anal areas have meant only a tentative placement. *B. lisae* sp. nov. differs from the Brazilian *Baissoptera brasiliensis* in having a smaller
body length (B. lisae sp. nov. 16.5 mm, B. brasiliensis 19.5 mm), smaller wing size (B. brasiliensis larger), and the ratio of size of head to pronotum is greater in B. brasiliensis sp. nov. Also the head of B. lisae sp. nov. does not taper posteriorly.

DISCUSSION

This study has increased the number of species of snakeflies in the Wealden from one to three. The Cretaceous snakeflies in the UK are not diverse at family or generic level, being represented by only one family, Mesoraphidiidae, and two genera, Mesoraphidia and Proraphidia (Jepson and Jarzembowski 2008; Jepson et al. 2009). Mesoraphidiidae were present in the UK from the Jurassic (Lias) to the Cretaceous (Weald Clay: Barremian), with specimens found in between in the Purbeck Limestone Group (Berriasian) (Whalley 1988; Jepson et al. 2009). The genus Mesoraphidia has also had a long history in the UK, being recorded first in the Lower Berriasian of the Purbeck Limestone Group by Mesoraphidia mitchelli (Jepson et al. 2009) and last recorded in the Upper Weald Clay by Mesoraphidia ednae sp. nov. and M. hilli sp. nov. The genus developed from being small, just greater than 5 mm in wing length, e.g. M. mitchelli, M. purbeckensis, M. websteri, getting larger (over 10 mm wing length, a more normal size for the genus) in the later Berriasian M. durlstonensis and the Barremian M. ednae sp. nov. and M. hilli sp. nov., possibly linked to the changing climate from semi-arid to humid from the early Purbeck to Wealden (Jepson et al. 2009).

Spain has a slightly more diverse Cretaceous fauna with three genera of Mesoraphidiidae: Proraphidia (Jepson and Jarzembowski 2008), Nanoraphidia and Iberoraphidia gen. nov. herein. The discovery of a possible Nanoraphidia in Montsec...
could potentially mean that the genus is older and more geographically widespread
than previously thought. Originally the genus was only known from the younger
Burmese amber (Engel 2002). It is interesting to note that as yet no Mesoraphidia
have been found in Montsec.

The Brazilian snakefly is younger than the European ones being of Aptian age.

Other than Baissoptera lisa sp. nov., the Brazilian snakefly fauna includes other
baissopterids: Austroraphidia brasiliensis Nel et al., 1990, Baissoptera brasiliensis
Oswald, 1990, B. pulchra ( Martins-Neto and Nel, 1992); also familia incertae sedis
Arariperaphidia rochai Martins-Neto and Vulcano, 1990 and a Raphidioptera sp.
(Oswald 1990). The Brazilian snakeflies are very important from a historical
biogeography point of view, because prior to their discovery, snakeflies were only
observed in the northern hemisphere. The southernmost regions where extant
Raphidioptera are found are Mexico (Central America), north of the Sahara (Africa),
northern India, Burma and northern Thailand (Asia) (Aspöck, U. et al. 1992; Aspöck,
U. and Aspöck, H. 2003). The discovery of a snakefly fauna in the Crato Formation
extends their range to the southern hemisphere (Aspöck, H. 1986; Oswald 1990).

Aspöck, U. and Aspöck, H. (2004) supposed that the rich Mesozoic
raphidiopteran fauna ended dramatically through climatic changes caused by the end-
Cretaceous bolide impact. Snakeflies of tropical and subtropical regions died out, and
only those branches adapted to colder climates like Raphidiidae and Inocellidae
survived.

Acknowledgements
Thanks to John Cooper and Gerald Legg at the Booth Museum of Natural History, Brighton; also to Maidstone Museum and Bentlif Art Gallery and Dan Pemberton and Matt Riley at the Sedgwick Museum of Earth Sciences for loan of specimens, Robert Coram (British Fossils) for the drawing of *M. hilli* sp. nov., Tony Mitchell (Maidstone Museum) for the photograph of *M. hilli* sp. nov. paratype. Thanks to Ulrike Aspöck and Sam Heads for reviewing and improving the manuscript. JEJ acknowledges the Alkins Fund (The University of Manchester) and a Wingate Scholarship for financial support.

References


FIGURE CAPTIONS


TEXT-FIG. 5. *Iberoraphidia dividua* gen. et sp. nov. holotype GZG.RF.7563 A, venation drawing of the forewing. B, photograph of wing. C, photograph of wing tip showing macrotrichiae.
TEXT-FIG. 1. *Mesoraphidia ednae* sp. nov. holotype MNEMG 2009.42 [AY36a, b] A. composite venation drawing of the forewing. B. photographs part and counterpart, scale bar = 1 mm. 176x111mm (200 x 200 DPI)
TEXT-FIG. 2. *Mesoraphidia hilli* sp. nov. holotype BMB 016381. - A. composite venation drawing of the hind wing. B. photograph, scale bar = 1mm. 188x222mm (300 x 300 DPI)
TEXT-FIG. 3. *Mesoraphidia hilli* sp. nov. paratype BMB 025010–12. A. composite venation drawing. B. photograph, scale bar = 1 mm. 186x120mm (200 x 200 DPI)
TEXT-FIG. 4. *Nanoraphidia lithographica* sp. nov. holotype FGWG 174 (MA 20 a,b). A. venation drawing of the forewing. B. photograph part and counterpart.

131x177mm (200 x 200 DPI)
TEXT-FIG. 5. *Iberoraphidia dividua* gen. et sp. nov. holotype GZG.RF.7563. A. venation drawing of the forewing. B. photograph of wing. C. photograph of wing tip showing macrotrichiae. 189x263mm (300 x 300 DPI)
TEXT-FIG. 6. Baissoptera lisae sp. nov. holotype CAMSM X.50155.2. A. venation drawing of the forewing. B. venation drawing of the hind wings. C. drawing of body. D. photograph, scale bar = 1 mm.

180x167mm (200 x 200 DPI)
CHAPTER 10. PALAEOECOLOGY OF THE LOWER CRETACEOUS PURBECK AND WEALDEN NEUROPTERIDS (INSECTA: NEUROPTERA, RAPHIDIOPTERA)

(Jepson, J.E. Palaeoecology of the Lower Cretaceous Purbeck and Wealden neuropterids (Insecta: Neuroptera, Raphidioptera). To be submitted to *Palaeogeography, Palaeoclimatology, Palaeoecology*)

10.1. Abstract

The neuropterid fauna of the Lower Cretaceous Purbeck Limestone Group and Wealden Supergroup of southern England is discussed. The palaeoenvironment and palaeoecology are discussed and compared with other Lower Cretaceous deposits worldwide. The most dominant neuropterids in the Lower Cretaceous of England are the Psychopsoid neuropterans forming over 60% of the neuropterid fauna. Kalligrammatidae, Psychopsidae and Osmylidae persist from the Lower Purbeck to the Weald Clay. Some families differ between the deposits, some of which may be a function of the changing climate at this period in England’s history. The Purbeck and Wealden are now seen to be major deposits for the study of fossil Neuropterida, filling gaps in the knowledge of Neuropterida in Europe during the Cretaceous.

*Key words.* England, Lacewing, Neuropterida, Palaeoenvironment, Snakefly, Wealden, Purbeck

10.2. Introduction

Neuropterida are a superorder of insects comprising snakeflies (Raphidioptera), alderflies and dobsonflies (Megaloptera) and lacewings (Neuroptera) (Aspöck, 2002). Until recently little was known of the neuropterid fauna of the Lower Cretaceous Purbeck and Wealden of southern England. The neuropteran families Ithonidae, Berothidae, ?Hemerobiidae, Chrysopidae, Nymphidae, Prohemerobiidae, Osmylidae, Kalligrammatidae, Psychopsidae, an undescribed family possibly related to Hemerobiidae and the raphidiopteran family Mesoraphidiidae are now known to have been present, however, Megaloptera have not been discovered (Jepson & Jarzembowski 2008 (chapter 7); chapter 4; chapter 9; Jepson *et al.* 2009a (chapter 5); Jepson *et al.* 2009b (chapter 8)). A review of the published literature on the
palaeontology, geology and modern analogues will be used to interpret the environments in which these Lower Cretaceous neuropterids once lived.

10.3. Materials and Methods

The fossil specimens represent extinct species and finding a direct modern analogue (i.e. species and genera) is therefore difficult. However, with regards to Neuroptera from these deposits many of the families are still living today (for example, Psychopsidae, Berothidae, Chrysopidae, Nymphidae, ?Hemerobiidae, Ithonidae and Osmylidae) and therefore, information can be taken from modern analogues and the mode of life of the extinct can be interpreted using the extant. Problems do occur, however, when dealing with the extinct and the incertae sedis families. With some, for example, Protohemerobius it may be possible to use Hemerobiidae as an analogue due to their potential relationship (Jepson et al. 2009b (chapter 7)) and the Mesoraphidiidae could be interpreted from general extant raphidiopteran habits. With regards to the other extinct taxa it may be more difficult to interpret their mode of life, but not impossible because the fossils themselves can give information such as the eyespot on Kalligrammatidae which could be interpreted as having a similar function to that of extant Lepidoptera. With others however, it may be more difficult and only general neuropteran modes of life can be applied.

10.4. Geological Settings

The fossil neuropterids in the Lower Cretaceous are deposited in the Wessex Sub-basin (Purbeck Limestone Group) and the Weald Sub-basin (Wealden Supergroup). These two sub-basins were surrounded by four massifs, the Welsh massif to the north, the Armorica massif to the south, the Londinia-Brabant massif to the east and the Cornubian massif to the west (Fig. 10.1). Two of these massifs, the Londinia and Cornubia, are the most important as these are the areas were sediment was supplied to the sub-basins (Fig. 10.1).
Figure 10.1. The palaeogeography of the Lower Cretaceous of southern England showing the massifs, sub-basins and drainage pattern (Constructed with data from Sladen & Batten 1984; Hancock & Rawson 1992; Jarzembowski 1995; Allen 1998; Radley 2005).

10.4.1. Purbeck Limestone Group

The Purbeck Limestone Group is Lower Cretaceous (Berriasian) in age, consisting mainly of lagoonal sediments (Allen & Wimbledon 1991). The group is divided into two formations, the older Lulworth Formation and the younger Durlston Formation. The type locality at Durlston Bay was extensively logged by Clements (1993), who divided the group up into numerous beds. Fossil insects are found in many horizons in the Purbeck, and in some places there can be hundreds found on a single bedding plane (Coram 2003).

In the Lulworth Formation the climate was dry, with little evidence of fluvial activity; it has been interpreted as being semi-arid, based on sedimentological evidence, with hypersaline deposits common, for example, evaporites (Clements 1993; Allen 1998; Batten 2002; Coram 2005), and clay mineralogy such as the presence of the mineral palygorskite, which indicates an arid/semi-arid environment (Sladen & Batten 1984; Hallam et al. 1991; Ruffell & Batten 1994; Coram 2005). In contrast the Durlston Formation climate has been interpreted as being more humid,
shown by the lack of hypersaline deposits and the dominance of the clay mineral kaolinite (Deconinck 1987).

The neuropterid specimens are from Durlston Bay, Swanage, Dorset and Teffont, Wiltshire.

10.4.2. Wealden Supergroup, Weald Sub-basin

The Wealden Supergroup of southern England is Berriasian–Aptian in age; it is subdivided into the Weald and Wessex Sub-basin (Allen & Wimbledon 1991). The non-marine Weald Sub-basin has yielded the most insect remains and it is from this basin that the neuropterid fossils derive. The Weald Sub-basin consists of the Hastings Group (Ashdown Beds, Wadhurst Clay, Lower and Upper Tunbridge Wells Sand, and Grinstead Clay formations) and the Weald Clay Group (Upper and Lower Weald Clay formations) (Allen & Wimbledon 1991; Rasnitsyn et al. 1998). The neuropterids are from the Wadhurst Clay and Weald Clay Group (Jarzembowski 2001; Jepson & Jarzembowski 2008 (chapter 8); Jepson et al. 2009b (chapter 7)).

The Weald Clays represent a lacustrine–lagoonal environment (Allen 1981, 1989; Radley 2005). The climate has been interpreted as subtropical/warm temperate (with seasonal rainfall): the climatic reconstruction has been generated for the Wealden based on geological evidence, modelling (Allen 1998; Haywood et al. 2005) and the presence of certain insect Orders, for example, Isoptera (Jarzembowski 1995). The occurrence of wet and dry seasons (commonly with wild fires) has been proposed, as has year-round precipitation with little evidence for prolonged drought but high evaporation (Batten 1998; Haywood et al. 2005). Wildfire evidence exists in the form of fusainized elytra and plant remains (Watson & Alvin 1996; Batten 1998; Jarzembowski 2003).

The neuropterid specimens have been found in numerous localities: Hastings Beds, Wadhurst Clay, Quarry Hill, Tunbridge Wells and Weald Clay, Lower Weald Clay, Clockhouse Brickworks, and the Upper Weald Clay, Keymer Tileworks, Rudgwick, Auclaye, and Smokejacks Brickworks.

10.5. Taphonomy

The neuropterids from the Purbeck and Wealden are preserved as disarticulated (often fragmentary) wings; there have been no body parts of neuropterids found. The
The taphonomy of Purbeck insects was described in detail by Coram (2003). Herein only the information that is relevant to Neuropterida has been added. In the Purbeck it has been suggested that the neuropterids most likely lived in a distant forested land and on death they underwent disarticulation and transport, with their wings being deposited into the Purbeck lagoon (Coram 2003 Figure 6 p. 316). The long transport also manifests itself in the poor state of the wings, many of which are fragmentary, and in some cases they cannot be described to lower taxonomic levels.

The neuropterids in the Wealden, as mentioned previously, most probably lived in a distant wooded area, for example, on the south side of the Londinian massif (Jarzembowski 1995). The Purbeck and Wealden wings are of a similar fragmentary state and have both been interpreted as being transported from a distant wooded habitat. A schematic figure of the palaeoenvironment within the Wealden is shown in figure 10.2, showing a similar scenario to the Purbeck (Coram 2003 Figure 6 p. 316).
Figure 10.2. A schematic reconstruction of the Wealden showing the distant forested land and area of deposition

Most of the neuropterids in the Wealden are found in the localities close to the Londinia-Brabant massif (Smokejacks, Clockhouse and Auclaye, see Fig. 10.3), whereas they are very rare and fragmented in the most distant locality of Keymer Tileworks (Fig. 10.3). Being a further distance away means the neuropterid remains would have a higher chance of being destroyed by the longer period of transport. This long transport is also the reason why few fossil insects and no neuropterids have been found in the Wealden in the Wessex Sub-basin on the Isle of Wight, and also why the insects which have been found are in a poor fragmentary state dominated by the hard elytra of beetles.
Figure 10.3. Showing the position of the Wealden localities with respect to the massif. The furthest locality away from the massif, Keymer tileworks, has only one fragmentary neuropterid recorded (Constructed with data from Sladen & Batten 1984; Jarzembowski 1995; Allen 1998; Jepson et al. 2009b (chapter 7)).

There are numerous possible scenarios to explain why the insects in the Purbeck and Wealden are only represented by their wings. The insects could have died on the land, disarticulated, their bodies decomposing or forming food for predators, who often discard wings. Their wings would then be transported in the wet season to one of the watercourses, which would transport them, causing damage in the process, until deposition (in the Purbeck Lagoon, or Weald Sub-basin).

Alternatively the insect could have died and fallen into the watercourse or died on land and washed in whole into the watercourse. When on the water the insect disarticulated and decomposed. The decomposing body parts on the surface of the water would be an easy target for predation, again leaving just the wings.

Another scenario could be that the insect was alive and became trapped in the watercourse, for example, during heavy rain, or blown in during a storm. When on the water surface, if the insect could not escape it would eventually die through asphyxiation, either on the surface, or if it broke through the surface tension, within the water column. The insect would then disarticulate, due to decomposition or predation, separating the wings from the body, which eventually get deposited in the basin.
The neuropterid fossils in the Wealden are more fragmented than those of the Purbeck, indicating that they have undergone more disarticulation. The (estimated) wingsize range of the described taxa shows that the majority are between 6–25 mm, with 1–5 mm being very rare and few 40+ mm. The rarity of <5 mm and 40+ mm wingsized neuropterids, may be due to the fact that insects with these wing sizes find it hard to break through the water surface tension (Martínez-Delclos & Martinell 1993), and therefore are an easy target for predation and total decomposition on the water surface. This may be a reason why the family Coniopterygidae (very small wing sizes) predicted by Jepson and Penney (2007 (chapter 6)) to be in the Wealden, has not been discovered, and also why there are few large neuropterans.

It is difficult to state confidently which of the above scenarios are true for the Purbeck and Wealden. It is probably most likely that a mixture of all three took place. The fate of the neuropteran body parts is unknown; they could have decomposed, been consumed by predators, or separated during transport and deposited in another location awaiting discovery.

10.6. Lower Cretaceous Neuropterida from Britain

The knowledge of the neuropterid fauna of the Purbeck and Wealden within the last few years has increased significantly. Table 10.1 and 10.2 list the taxa described and undescribed (fragments from museum collections) from the deposits.
<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>Species</th>
<th>Formation</th>
<th>Bed</th>
<th>Locality</th>
<th>Age</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neuroptera</td>
<td>Kalligrammatidae</td>
<td>Sophogramma wimbledoni</td>
<td>Lulworth</td>
<td>?</td>
<td>Durlston, Wiltshire</td>
<td>Lower Berriasian</td>
<td>Jepson et al. submitted</td>
</tr>
<tr>
<td>Neuroptera</td>
<td>Ommatidae</td>
<td>Ommatius apiculate</td>
<td>Lulworth</td>
<td>?</td>
<td>Darlinton Bay, Dorset</td>
<td>Lower Berriasian</td>
<td>Jepson et al. submitted</td>
</tr>
<tr>
<td>Indet.</td>
<td>indet.</td>
<td>(DB59/Neur2)</td>
<td>?</td>
<td>Darlinton Bay, Dorset</td>
<td>Lower Berriasian</td>
<td>Jepson pers. obs.</td>
<td></td>
</tr>
<tr>
<td>Indet.</td>
<td>indet.</td>
<td>(DB175/Neur6)</td>
<td>?</td>
<td>Darlinton Bay, Dorset</td>
<td>Lower Berriasian</td>
<td>Jepson pers. obs.</td>
<td></td>
</tr>
<tr>
<td>Psychopsoida</td>
<td>Psychopsidae</td>
<td>Mesoraphidiidae</td>
<td>indet.</td>
<td>(DB175/Neur15)</td>
<td>Durlston Bay, Dorset</td>
<td>Lower Berriasian</td>
<td>Jepson pers. obs.</td>
</tr>
<tr>
<td>Psychopsoida</td>
<td>Psychopsidae</td>
<td>indet.</td>
<td>(DB6-8/Wing14)</td>
<td>?</td>
<td>Darlinton Bay, Dorset</td>
<td>Lower Berriasian</td>
<td>Jepson pers. obs.</td>
</tr>
</tbody>
</table>

Table 10.1. The specimens of Neuropterida from the Purbeck Limestone Group.


<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>Genus and Species Group</th>
<th>Formation</th>
<th>Locality</th>
<th>Age</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neuroptera</td>
<td>Kalligrammatidae</td>
<td>Kalligramma aequisfolia</td>
<td>Weald Clay</td>
<td>Smokejacks Brickworks, Surrey</td>
<td>Barremian</td>
<td>Jepson et al. submitted</td>
</tr>
<tr>
<td>Neuroptera</td>
<td>Ommatidae</td>
<td>Raphidioptera</td>
<td>Upper Weald Clay</td>
<td>Smokejacks Brickworks, Surrey</td>
<td>Barremian</td>
<td>Jarzembowski, 2008</td>
</tr>
<tr>
<td></td>
<td>Psychopsidae</td>
<td>Psychopsites rolandi</td>
<td>Upper Weald Clay</td>
<td>Clockhouse Brickworks, Surrey</td>
<td>Barremian</td>
<td>Jepson pers. obs.</td>
</tr>
</tbody>
</table>

Table 10.2. The specimens of Neuropterida from the Wealden Supergroup.

The neuropterid fauna of Britain comprises Raphidioptera and Neuroptera, with Megaloptera currently not having been found. Neuroptera are the most numerous representatives of the superorder, while Raphidioptera is only represented by one family and two genera. Figure 10.4 displays the percentages of the described species of each deposit and the percentages of families within the neuropterid fauna of the Purbeck and Wealden.
Within the described insect fauna of the Purbeck and Wealden, Neuroptera is shown as quite a high percentage. This unfortunately does not represent true diversity; instead it represents a bias to those insect groups which have been worked on in detail, for example, Hymenoptera (Rasnitsyn *et al.* 1998) and Orthoptera (Gorochov *et al.* 2006). With regards to the neuropterid fauna (Fig 10.4C) it is shown that the psychopsoid neuropterans dominate comprising 66%, with Osmylidae forming quite a high percentage.

The number of specimens found at each locality in the Purbeck and Wealden is shown in the spindle diagrams of figure 10.5. Neuropterans show an increase in number from the Lower Purbeck to the Upper Weald Clay (Wealden) (dashed line, Fig. 10.5), whereas the raphidiopterans remain approximately constant. However, little is known from the Middle Purbeck to the top of the Lower Weald Clay due to
poor preservation conditions and little work done, especially in the clay formations of the Hastings Group.

Figure 10.5. Spindle diagram showing the number of specimens from the fossil localities within the Purbeck and Wealden. The dashed lines shows an extrapolation through the areas of little information.

The increase in numbers could be due to the taphonomy of the deposits; the Purbeck is drier than the Wealden, and therefore there is less water to transport neuropterans from their distant habitat to the basin of deposition. Whereas the increased fluvial activity within the Wealden could have increased the chances of transport, deposition and therefore preservation. Although the number of specimens is higher in the Wealden the diversity of neuropterans is lower, with more families known in the Purbeck.

The geological ranges of the families of Neuropterida from the Purbeck into the Wealden are shown in figure 10.6.
Figure 10.6. The geological ranges of the neuropterid families in the Lower Cretaceous of Britain.

The families Mesoraphidiidae, Kalligrammatidae, Psychopsidae, Osmylidae and the indeterminate psychopsoid neuropterans are shown to have been present in the Lower Cretaceous of England from the Lower Purbeck into the Weald Clay (Fig. 10.6). The differences between the two deposits are that in the Purbeck the families Berothidae, Nymphidae, Prohemerobiidae, ?Hemerobiidae and Chrysopidae are recorded and in the Wealden Ithonidae is present. The fauna is discussed in detail below.

10.6.1. Raphidioptera

Raphidiopterans are found in both the Purbeck and Wealden; the oldest Cretaceous specimen is undescribed from the Lower Soft Cockle Beds, Lulworth Formation (Table 10.1). The next occurrence of raphidiopterans is in the Upper Soft Cockle
Bed (Lulworth Formation) with the species *Mesoraphidia mitchelli* (Jepson *et al.* 2009a (chapter 5)). This species is found with two other fragmentary specimens most likely of the same species. Raphidiopterans are then not observed until the Corbula Beds (Durlston Formation), where they are more diverse (at species level), and represented by *Mesoraphidia durlstonensis*, *M. purbeckensis* and *M. websteri* (Jepson *et al.* 2009a (chapter 5)). Snakeflies are next recorded in the top of the Lower Weald Clay, where they are represented by a larger species and a different genus *Proraphidia hopkinsi* (Jepson & Jarzembowski 2008 (chapter 8)), and their last occurrence is in the lower part of the Upper Weald Clay with *Mesoraphidia hilli* and *M. ednae* (chapter 9).

The Lower Cretaceous British raphidiopterans are not very diverse, and are represented by one family Mesoraphidiidae and only two genera, the dominant *Mesoraphidia*, and *Proraphidia*.

In the Lower Purbeck the snakeflies were much smaller than the subsequent fossils in the Purbeck and Wealden and their modern counterparts (Fig. 10.7). The oldest described snakefly from the Lulworth Formation of the Purbeck is *M. mitchelli* with an estimated wing length of 5.4 mm. Moving up through the Purbeck into the Durlston Formation there are still small raphidiopterans *M. purbeckensis* (5.1 mm) and *M. websteri* (5.2 mm), but there is a larger more dominant species *M. durlstonensis* (8–10.6 mm) represented by three specimens. The Wealden raphidiopterans are of a larger size; *Proraphidia hopkinsi* from the Lower Weald Clay has a wing length of 11.5 mm and in the Upper Weald Clay *Mesoraphidia hilli* and *M. ednae* have wing lengths 11.5 mm and 8 mm respectively.
A reason for the size differences could be due to the changing climate. The climate change has been interpreted by the presence of evaporites, lack of fluvial sediments in the Lower Purbeck, changing to a loss of evaporates and increase in fluvial sediments from the mid-Purbeck to the Wealden. The presence of certain clay minerals in the Purbeck and Wealden also indicate a change in climate, for example, palygorskite in the Lower Purbeck indicates arid/semi-arid conditions (Deconinck 1987). The snakeflies in the Lower-Mid Purbeck may have been small to cope with the harsher environment, e.g., high temperatures and lack of prey.

10.6.2. Neuroptera

There are 12 neuropteran families present in the Purbeck and Wealden; the most numerous representatives are the psychopsoid neuropterans (Table 10.1 and 10.2, Fig. 10.4).
The psychopsoid neuropterans are represented by the families Psychopsidae and Kalligrammatidae which are easily recognized by their dense venation in both fore- and hind wings.

Psychopsoid neuropterans are first recorded in the British Lower Cretaceous in the Lower and Upper Cypris Freestones (Lulworth Formation) with 2 indeterminate psychopsoids. They are next seen in the Lulworth Formation in the Upper Soft Cockle Bed, with 5 indeterminate psychopsid specimens. The kalligrammatid Sophogramma wimbledoni is found in the Lulworth Formation in Teffont, Wiltshire. Psychopsoids are next recorded in the Cherty Freshwater Beds in the Durlston Formation again with an indeterminate specimen. Numerous specimens are known from the Corbula Beds; with the species Pterinoblattina fasciata and P. purbeckensis and 1 indeterminate specimen and 10 psychopsoid neuropteran fragments.

The earliest record of a psychopsoid in the Wealden is the kalligrammatid Kalligramma roycrowsoni from the Wadhurst Clay, Hastings Group. The next records are the psychopsids, Pterinoblattina minimus, ?P. sp. A and Psychopsites rolandi and 5 indeterminate psychopsids and 1 indeterminate psychopsoid in the Lower Weald Clay, Clockhouse Brickworks. In the Upper Weald Clay psychopsids are recorded at Auclaye Brickworks with Pterinoblattina maculosus, P. sp., Psychopsites sp. and 2 indeterminate psychopsids. At Smokejacks Brickworks (Upper Weald Clay) there are numerous psychopsoids known (Cretapsychops corami, 2 ?Cretapsychops sp., Micropsychops parallelus, Pterinoblattina logunovi, P. brigidae, P.proudlovei, P. sp., 12 ?Pterinoblattina sp., 6 indeterminate psychopsids and an indeterminate kalligrammatid). An indeterminate psychopsid is also known from Keymer Tileworks (Jarzembowski 2001; Jepson et al. 2009b (chapter 7); Jepson pers. obs. 2009).

Osmylidae are fairly common within the neuropterid fauna of Lower Cretaceous Britain. They are first recorded in the Corbula beds (Durlston Formation) in the Purbeck, with the species Osmylopsis duplicata, Osmylochrysa minima, O. anomola, Mesosmylidus vulgaris and Stenochrysa gradata. Osmylids are then observed within the Weald Clay, represented by Stenosmylina medialis and Protosmylina bifasciata.
One species of ithonid is known from the Lower Cretaceous of Britain, *Principiala rudgwickensis*, which is of the same genus of *P. incerta* from the younger Crato Formation of Brazil (Makarkin & Menon 2007; Jepson et al. 2009b (chapter 7)). Extant ithonids may be broadly divided into arid and forest dwelling genera (Makarkin & Archibald 2009). It is most likely that the genus *Principiala* would have been a forest dweller in the Wealden, based on the assemblages of insects and interpreted palaeoenvironment (Jarzembowski 1995).

Nymphidae is the only myrmeleontoid known from the Lower Cretaceous of England. It is represented by the species *Sialium sipylus*, which was one of the first neuropterids described from the deposit (Westwood 1854). Unfortunately the locality information is unknown, except that it is from the Lulworth Formation, Purbeck Limestone Group and was collected at Durlston Bay.

Prohemerobiidae is only represented by the genus *Ovalorobius purbeckensis* in the *Corbula* Beds.

One species of ?Hemerobiidae is known from the *Corbula* Beds (Purbeck); *Purbemerobius medialis* is known from a poorly preserved hind wing. This is the first record of a potential hemerobiid in the fossil record of Britain.

Chrysopidae is represented by one species in the *Corbula* Beds (Purbeck); *Mesypochrysa minuta* is the smallest chrysopid known in the fossil record with an estimated wing span of ~ 7 mm. No other chrysopids are known in the fossil record of Britain.

Two specimens of Berothidae represent the species *Epimesoberothus osmylodes* known from the Purbeck Limestone Group. Both of the specimens are from the Upper Soft Cockle Beds (Lulworth Formation). These represent the smallest neuropterans in the Purbeck.

*Icertae sedis* neuropterans are found in both the Purbeck and Wealden. The only one in the Purbeck is the species *Paraksneura alleni* which may be related to chrysopoids or even megalopterans; unfortunately with no body parts preserved the true affinity of this species cannot be ascertained. The Wealden has two species that cannot be placed within a described family; *Actinophlebia valdensis*, is possibly from a psychopsoid family, for example Brongniartiellidae, but, due to the poor
taxonomy of these neuropterans it has been placed as *incertae sedis*. *A. valdenisis* is from the Lower Weald Clay. In the Upper Weald Clay *Protohemerobius perexiguus* is present and is superficially similar to Hemerobiidae; however, it is most likely a new family of Neuroptera as it is similar to an undescribed neuropteran family from China. The preservation of *P. perexiguus* is such that it cannot be described as a new family, because many of the diagnostic features required are not preserved.

Megalopterans have not yet been found in the Purbeck or Wealden.

10.7. **Neuropterid palaeoenvironment and palaeoecology**

Extant neuropterids of the families Psychopsidae, Ithonidae, Berothidae, Nymphidae, Hemerobiidae, Chrysopidae and the Order Raphidioptera are found in a variety of habitats; they are mainly arboreal, often (but not always) found living in or around forested habitats. They are quite often found living on the trunk, or amongst the branches. Many of the neuropterids are weak flyers and therefore do not travel far from their place of hatching. Some extant Osmylidae have a different habitat preference to the other neuropterids, tending to live close to water. It has been suggested that they may have a semi-aquatic larva, because of the habits the adult are similar to insects that have semi-/aquatic larva, for example, the megalopteran family Sialidae.

Neuropterans and raphdiopterans are on the whole entomophagous insects, but, some are known to feed on nectar and pollen, especially in their adult form (New 1989; Aspöck *et al.* 1991). The fact that they are predators means that they inhabit a higher trophic level in the food chain, and therefore will be fewer in number than phytophagous insects. This is reflected in their rarity in the insect fossil record of the Purbeck and Wealden and modern faunas. Extant neuropterids (both larva and adult) are predominantly generalist predators feeding on small invertebrates, for example, scale insects, aphids, bark lice, and mites. However, some families are more specialized feeding solely on termites, or ants, or sponges, or even spider egg cases (New 1989). They are generally active hunters, either seeking prey (for example, they can be observed walking through aphid colonies) or sit and wait predators, waiting for prey to come to them; or on the wing hunters, like dragonflies; scavenging has also been observed. Extant neuropterids have also been observed eating plant matter, such as pollen and honeydew, and in some cases the larva are
voracious predators, whereas the adult feeds only on pollen or honeydew (New 1989).

In the Purbeck it is likely that the neuropterans and raphidiopterans would have fed on the small invertebrate fauna, for example the smaller forest dwelling arthropods. In the distant forest, where the neuropterids have been proposed to have lived (Coram 2003), potential prey are also observed including fungus gnats, cupedoid beetles, aphids and other plant bugs. It is likely that these insects would have been the main food source for the majority of neuropterids. To add support to this the fossil raphidiopterans from the Purbeck have been found associated with these tree dwelling insects, for example cupedoid beetles (Jepson et al. 2009a (chapter 5)). With regards to the family Berothidae, the extant members of the family are specialized feeders on termites; however, no fossils of termites have been found within the Purbeck as yet, although they are present in the Wealden (Jarzembowski 1995).

The Wealden Neuroptera and Raphidioptera would have had similar prey such as barklice (producers of *Paleoscolytus*), aphids (e.g. the Wealden aphid: *Penaphis woolardi*), and other scale insects that are found in the deposit (Jarzembowski 1995).

The neuropterids from both localities would have been prey for other predatory insects, for example, the abundant dragonflies known from these deposits. There also would most likely have been predation by vertebrates, using the modern analogue of insects with cryptic colour patterns and in particularly eye-spots (e.g. on the wings of extant Lepidoptera). Kalligrammatids, which are observed in the Wealden, in particularly *Kalligramma roy crowsoni* has a well-preserved eyespot (a feature observed in the genus *Kalligramma*) (Jarzembowski 2001), and many of the psychopsoids from both the Purbeck and Wealden have cryptic wing patterns, which may indicate a defence against vertebrate prey (Jepson et al. 2009b (chapter 7)).

10.8. **Faunal change**

The major change from the neuropterid fauna of the Purbeck to the Wealden is the loss of some and gaining of other families. Only the families Psychopsidae, Kalligrammatidae, Osmylidae and Mesoraphidiidae persist from the Lower Purbeck up into the Weald Clay (Fig. 10.6). The change in fauna also represents the change in
climate to some extent. The change from small to larger snakeflies has already been mentioned, with regards to size in neuropterans there is little difference between the two deposits. Berothidae are the smallest neuropterans within the Purbeck and these happen to be from the same beds as the smallest raphidiopterans, but, little can be inferred from this because of the small sample size and the fact that other neuropterans are not of such a size. Also no berothids have been found in younger beds for comparison. The families themselves may indicate climate. Berothids and nymphids are usually found in arid/semi-arid environments in the present day, so their presence in the Lower Purbeck and not in the younger beds could be related to climatic change.

The Purbeck neuropterid fauna contains the families Chrysopidae, ?Hemerobiidae, Nymphidae, Berothidae and Prohemerobiidae, which are not present in the Wealden. Berothidae and Nymphidae has been excused on climatic grounds, but there is no reason why Chrysopidae and ?Hemrobiidae and even Prohemerobiidae should not be present in the Wealden and they may yet be discovered. Ithonidae is only present in the Wealden; again it may have been present in Purbeck times but not discovered because it has a wide habitat preference today from high altitudes to sandy desert environments (Menon & Makarkin 2008).

What has to be remembered is that the fossils from these distant woodland areas of the Purbeck and Wealden are just ‘snapshots’ of a habitat and not all the insects will survive transportation to be preserved.

10.9. Lower Cretaceous neuropterid faunas world-wide

Many neuropterids have been described from numerous localities in the Lower Cretaceous world-wide. Below is a review of some of these localities of a similar age to the Purbeck and Wealden (Berriasian–Aptian) which have a neuropterid fauna.

Baissa, Transbaikalia (Valanginian–Barremian): This is a very rich insect deposit comprised of the neuropteran families: Osmylidae, Mesithonidae, Nymphidae, Mantispidae, Psychopsidae, Chrysopidae, Babanskaiaidae, Brongniartiellidae and Myrmeleontoidea (Makarkin 1990a, b, 1996, 1997a, b, 1999, in press; Wedmann & Makarkin 2007). The Raphidiopterans are also diverse in this deposit, with all the extinct families represented: Mesoraphidiidae (genera: Siboptera, Baisoraphidia),

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Spain: Montsec and Las Hoyas (Barremian): The neuropteran families include *Mesochrysopidae, Incertae sedis* (Chrysopoid), and *Kalligrammatidae* (Martínez-Delclos & Martinell 1993; Nel et al. 2005). The snakefly fauna consists only of the family *Mesoraphidiidae* (genera: *Proraphidia, Iberoraphidia, Nanoraphidia*) (Jepson & Jarzembowski 2008 (chapter 8); chapter 9).

China: Yixian Formation (Barremian–Aptian): Another formation, which has an abundant neuropterid fauna, it comprises the neuropteran families: *Myrmeleontidae, Myrmeleontoidea, Aetheogrammatidae, Kalligrammatidae, Osmylidae, Chrysopidae* and *Berothidae* (Ren & Guo 1996; Ren & Yin 2002; Ren & Engel 2008a, b). The snakefly fauna is also very diverse with all extinct families present: *Mesoraphidiidae* (genera: *Siboptera, Mesoraphidia, Huaxiaraphidia*), *Baissopteridae* (genus: *Baissoptera*) and *Alloraphidiidae* (genus: *Alloraphidia*) (Ren 1994, 1997; Ren et al. 1995).


Lebanon: Lebanese amber (Barremian–Aptian) has few neuropterids. Neuropterans include *Coniopterygidae, Berothidae* and *Rhachiberthidae*, while snakeflies are only represented by a *Mesoraphidiidae* larva (Engel & Grimaldi 2007).

Brazil: Crato Formation (Aptian): the Crato Formation of Brazil has a very extensive and diverse neuropterid fauna. Neuropterans are represented by the families: Nemopteridae, Ascalaphidae, Nymphidae, Myrmeleontoidea, Berothidae, Palaeoleontidae, Araipeneuridae, Babinskaiidae, Chrysopidae, Mesochrysopidae, Hemerobiidae, Makarkiniidae, Brongniartiellidae, Kalligrammatidae, Ithonidae, Osmylidae, Sisyridae, and Limaiidae. The snakefly fauna consists of the family *Baissopteridae* (genus: *Baissoptera, Austroraphidia*), and one *familia incertae sedis*
(genus: *Arariperaphidia*) (Martins-Neto et al., 2007). Megalopterans are also known from this deposit (Martins-Neto *et al.* 2007; Jepson pers. obs.).

Lower Cretaceous localities with few neuropterids recorded:


South Korea: Jinju Formation: Mesoraphidiidae (genus: *Mesoraphidia*) (Engel *et al.* 2006).

Japan: Osmystalsophipidae (Fujiyama 1978).

Romanovka, Russia: Baissopteridae (*Cretoraphidia*) (Ponomarenko 1993).

10.9.1. *Palaeobiogeography*

Neuropterids are now a relict group of insects, but during the Cretaceous they were globally widespread. Further evidence for this has come from the study of the Purbeck and Wealden fauna, which shares genera with more geographically distant insect localities. For example, the genus *Sophogramma* is also present in Russia and China (Ren & Guo 1996; Yang *et al.* 2009; Makarkin in press; chapter 4), *Kalligramma* is widespread in Kazakhstan, Germany and China (Walther 1904; Panfilov 1980; Ren & Guo 1996), *Mesypochrysa* is also present in Kazakhstan, Russia, China and Brazil (Makarkin 1997b; Nel *et al.* 2005) and the genus *Principiala* is present in Brazil (Makarkin & Menon 2007).

10.10. *Discussion*

The Lower Cretaceous Purbeck and Wealden are important deposits for Neuropterida; there are 12 families, 22 genera and 31 species of Neuroptera, and 1 family, 2 genera and 7 species of Raphidioptera. The neuropterids can be tracked from the Berriasian to the Barremian, but, there is a gap of 3 million years, where little is known of the insects. This gap is due mainly to the sediment not being conducive to insect preservation, for example, the Hastings Group is dominated by
sands. Crowson (1946) mentioned the presence of some insects from the Wadhurst Clay, and Jarzembowski (2001) described *Kalligramma roycrowsoni* from this unit. It is more than likely that further examination of the clays in the Hastings Group could yield more insects, and decrease this large gap within the Wealden.

The most common neuropterids in the Lower Cretaceous are the psychopsoid neuropterans (which include Psychopsidae and Kalligrammatidae). These neuropterans were widespread throughout the Cretaceous and Mesozoic, and have appeared in the majority of the fossil insect localities. Why they are so numerous is difficult to answer, and could be due to many possible reasons. It could be that they were the most numerous and successful group of neuropterans at that time, and this success has been recorded in the fossil record; alternatively their dominance could be due to their wings having many veins. Since the neuropterans are thought to have been transported some distance before deposition, the numerous veins of psychopsoid neuropterans could have made them more resilient to breaking down, and therefore giving them a better chance of preservation than insects with fewer veins. Human bias could also be a factor; the fact that psychopsoid neuropterans are readily recognized by non-specialists, whereas other families may be overlooked, or misidentified, could lead to them appearing more numerous. Osmylidae are also well represented in the Purbeck and Wealden, which may be because of a semi-aquatic larva. If adults are found near to water they have a better chance of being washed into the depositional area.

There are some absences in the fauna of the Purbeck and Wealden, such as the Order Megaloptera, and the families Chrysopidae (in the Wealden), Myrmeleontoidea (Myrmeleontidae, Palaeoleontidae, Ascalaphidae, Nymphidae) and Brongniartiellidae. The absence of Megaloptera may be due to an absence in England at that time. In the Jurassic they were present in Germany and in the Cretaceous they are known from Baissa, so it may be possible that they did not inhabit England. The environment may not have been suitable for their aquatic larvae, due to the water having varying salinities in both the Purbeck and Wealden. However, other insects with aquatic larva are known, and therefore there was most likely a suitable freshwater environment available. The other alternative is that they have not been preserved; fossil megalopterans are very rare in the fossil record, and the larvae would most likely have not survived the transport distances for deposition.
in the Purbeck and Wealden. On the other hand it may be that they have yet to be found, and are awaiting discovery. The absence of Chrysopidae in the Wealden again is probably due to the fact that they are awaiting discovery, because chrysopids are common in many Cretaceous deposits, and a chrysopid is known from the Purbeck. Myrmeleontoidea are indicative of semi-arid conditions, and their absence in the more humid Wealden may be expected, but, the absence of all but Nymphidae in the Purbeck is more curious. Myrmeleontids are the major constituent in the neuropterid fauna of the Crato Formation of Brazil, but they are rare in the fossil record in the Cretaceous, with Palaeoleontidae being found in Israel and Brazil, Ascalaphidae in Brazil, Myrmeleontidae in China and Brazil. However, a species is known from the Jurassic of Germany, and therefore there may be a possibility of an English Cretaceous myrmeleontid being found. Brongniartiellidae was previously thought to have been present in the Lower Cretaceous of England, but the specimens assigned to this family are now known to be of the family Psychopsidae (Jepson et al. 2009b (chapter 7)) and therefore this family is not present.

Within the Purbeck and Wealden there is a very similar neuropterid fauna. Psychopsoids are dominant and osmylids and mesoraphidiids are present in each. They differ, however, with the families Berothidae, Chrysopidae, Prohemerobiidae, ?Hemerobiidae, Nymphidae (only found in the Purbeck) and Ithonidae (only found in the Wealden); the Incertae sedis families also differ between deposits. The Purbeck, with regards to Neuroptera, is more diverse than the Wealden, with more families present. Raphidioptera are more or less equal, the differences being that the Wealden has two genera (Mesoraphidia and Proraphidia), while the Purbeck is only represented by Mesoraphidia. The Purbeck raphidiopterans were also much smaller, than the Wealden. Neuropterids generally make up a small proportion of the insect fauna; extant neuropterids generally make up less than 1% of the insect fauna (for example, Borneo has less than 1%, and Queensland, Australia has ~0.45%) which is also consistent with Palaeogene fossil insect deposits (Archibald & Makarkin 2006). In the Purbeck the number of Neuropterids is ~1.5% of recognizable wings (Coram 2005) and in the Wealden they represent 0.1–0.9% from a sample of 13,000 specimens (Jarzembowski 1995) of the insect fauna. Therefore, their abundance in the Lower Cretaceous of Britain is consistent with the extant faunas.
The Purbeck and Wealden are amongst the better known neuropterid faunas, comparable to the diverse Asian faunas with regards to Neuroptera families. The snakefly fauna of the Lower Cretaceous of England, and indeed western Europe is not that diverse, compared to the Asian localities, such as Baissa, and China, for example. In western Europe only one family of snakefly has been recorded (Mesoraphidiidae) whereas the Asian localities have two or all three of the extinct families. The reason for this may be that more work is needed on these European deposits, and that more snakeflies could be found either in the field or in museum collections. It could also be a biogeographical reason; the families Alloraphidiidae and Baissopteridae may not have been present in Europe at that time, although this is unlikely because Baissopteridae and Alloraphidiidae at least must have been widespread because fossils of these families are recorded in the Lower Cretaceous of Brazil and the Middle Cretaceous of Canada respectively (Carpenter 1967; Oswald 1990).

The extant neuropterid fauna is very much a relict of their former diversity. Many families which had a global population are now restricted to isolated parts of the world. For example, the family Psychopsidae was widespread during the Cretaceous and it is now only found in isolated parts of the world (New 1988). Neuropterids were globally widespread into the ‘Tertiary’, after which they started to reduce in numbers, maybe as a result of the end Cretaceous extinction, or the climate change during the ‘Tertiary’.
CHAPTER 11. CONCLUSIONS

From the work on the fossil neuropterids from the Lower Cretaceous Purbeck and Wealden of southern England it has been found that:

1. There are 12 families, 22 genera, 33 species of Neuroptera and 1 family, 2 genera and 7 species of snakefly present in the Purbeck and Wealden.

2. In the Purbeck there are the families Kalligrammatidae, Psychopsidae, Osmylidae, Prohemerobiidae, Chrysopidae, ?Hemerobiidae, Berothidae, Nymphidae, *familia incertae sedis* and Mesoraphidiidae.

3. The Wealden has Kalligrammatidae, Psychopsidae, Osmylidae, Ithonidae, two *familia incertae sedis* and Mesoraphidiidae.

4. The fauna of the Purbeck is much more diverse at family level than that of the Wealden. However, in both deposits the psychopsoid neuropterans dominate.

5. The first Mesozoic records in England of the families Chrysopidae, Hemerobiidae, Osmylidae, Berothidae and Ithonidae are documented.

6. The family Brongniartiellidae and the Order Megaloptera have been shown to be absent from the Purbeck and Wealden.

7. The oldest fossil record of the family Ithonidae is *Principiala rudgwickenesis* from the Wealden. The chrysopid *Mesypochrysa minuta* is the first record of Chrysopidae in the Mesozoic of Europe.

8. Biogeographical links have been shown with the Lower Cretaceous of England and Brazil, China, Russia, Kazakhstan and Mongolia. These links are interpreted from the presence of the genera *Sophogramma, Mesypochrysa* and *Principiala*.

9. Both palaeoenvironments for the neuropterids of the Purbeck and Wealden are distant woodlands away from the depositional basin. The insects were transported after undergoing periods of disarticulation before deposition in the basin.

10. Climate change from the Lower Purbeck to the Wealden may have affected the neuropterid fauna. This is shown by the small raphidiopterans within the Lower
Purbeck and the loss of Myrmeleontoids in the Wealden, which prefer arid/semi-arid environments.
CHAPTER 12. FURTHER WORK

There is much further work to be done with regards to the Purbeck and Wealden. With regards to the palaeoenvironment and palaeoecology, a detailed study of the sediments themselves, such as petrological and geochemical investigations would give more information on provenance of sediment, climate and the environment reconstruction. Also experimental taphonomy would give information on, for example, the transport dynamics of the wings and the decay rate of neuropterids and if the amount of damage of the wings can be correlated to distance travelled to pinpoint a more accurate location of the distant habitat for these insects.

Other than Neuropterida, there are vast collections of Purbeck and Wealden insects which are awaiting description. Therefore further taxonomic studies on other insect groups would give a much fuller picture of the entomofauna of the Lower Cretaceous of England.
PART TWO:

A STUDY ON FOSSIL AND EXTANT RAPHIDIOPTERA

The best-laid schemes o’ Mice an’ Men Gang aft a-gley

Robert Burns, from To a Mouse (1785)
CHAPTER 13. A STUDY ON FOSSIL AND EXTANT RAPHIDIOPTERA

13.1. Introduction

The phylogeny of raphidiopterans has rarely been investigated. Aspöck et al. (1991) with modifications from Aspöck (1998) constructed a hypothesis for the relationships of extant genera; Willmann (1994) and Ren and Hong (1994) tried to incorporate fossil material into a phylogenetic analysis. Ren and Hong’s (1994) attempt was less successful than Willmann’s (1994), whose work provides a good foundation to build upon.

This chapter will investigate the fossil raphidiopterans, producing a key for identification of all fossil families and genera, and a cladistic study to attempt to determine relationships between fossil taxa and extant genera.

13.2. Literature review

This section reviews the literature of relevance to the systematic and phylogenetic study of Raphidioptera. A review of raphidiopteran life-cycle, morphology and phylogeny will be given.

13.2.1. Raphidioptera

Raphidioptera (snakeflies) are a relict Order of insects, which along with Neuroptera and Megaloptera make up the superorder Neuroptera. Raphidioptera are holometabolous insects, which means they have a distinct larval, adult and pupal stage (Aspöck 2002) (Fig 13.1).
Raphidioptera are considered to be the sister-group of Megaloptera + Neuroptera (see Chapter 2.1 and below for detailed discussion). Extant raphidiopterans are split into two families Raphidiidae and Inocelliidae. Raphidiidae has been further subdivided into seven groups which are monophyletic (see below), while Inocelliidae relationships still require much study. There are an estimated 260 species of extant Raphidioptera, with currently 185 species in Raphidiidae, and 21 species in Inocelliidae (Aspöck 2002). Raphidioptera are considered relicts, or ‘living fossils’, because they had a higher biodiversity in the Mesozoic, with many different types being found in the Lower Cretaceous (e.g. Aspöck et al. 1991; Aspöck 2002; Engel 2002a). In the Mesozoic they were divided up into three extinct families Baissopteridae, Alloraphidiidae and Mesoraphidiidae, with their first appearance in the fossil record in the Lower Jurassic of Europe. It was previously thought that the family Priscaenigmatidae belonged to the raphidiopterans, but, this family was removed from the Order on the basis of the subcosta not running into the costa (Aspöck & Aspöck 2004).

13.2.2. Raphidioptera morphology

The majority of systematic studies of raphidiopterans are based upon morphology of the body and in particular the terminalia and genitalia of the males. The body of raphidiopterans is easily identifiable from the combination of elongate pronotum and
long ovipositor in females. Figure 13.2 shows the morphology of an adult raphidiopteran.

Figure 13.2. A labelled photograph of an adult female raphidiopteran *Phaeostigma notata* (specimen in Manchester Museum collection).

The genitalia are of particular interest to raphidiopteran systematics, and allow division of raphidiopterans into families, genera and species. Figure 13.3 shows the labelled genital morphology of adult raphidiopterans.
Figure 13.3. Genital morphology of Raphidioptera. A, lateral view of male; B, ventral view of male; C, ventral view of hypandrium internum; D, lateral view of female; E, sternite 7 showing position of bursa copulatrix; F, ventral view of bursa copulatrix (redrawn from Pantaleoni et al. 2004).

Raphidioptera have four wings; which are held roof-like over the body when at rest. Figure 13.4 shows a labelled fore- and hind wing; the vein abbreviations are as follows: C, costa; Sc, subcosta; R, radius; Rs, radial sector; M, media; MA, media anterior; MP, media posterior; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus
posterior; A, analis; 1-3A, anal veins 1-3; dc, discal cell; 1r, first radial cell; 2r, second radial cell; 3r, third radial cell; ac, anal cell.

Figure 13.4. The labelled fore- and hind wing venation of a raphidiopteran *Phaeostigma notata* (specimen from the Manchester Museum collection).

13.2.3. Potential problems of using wings for phylogenetic studies

As mentioned in chapter 3, there can be problems in using wing venation as a way of identifying species, because there is not the wealth of information in wing venation as there is in genital morphology, and the wing venation can vary within a species (sexual dimorphism) and even within an individual. Therefore, when dealing with an extant insect, the wing venation is of limited use. However, when dealing with an extinct insect, where the vast majority of fossils are wings, the venation becomes very important, as genitalia and body morphology are rarely preserved. Therefore care is needed to find informative characters in the venation and not ones which can be attributed to sexual dimorphism, or changes within an individual.

13.2.4. Phylogeny of the Raphidioptera

Much work has been done on the phylogeny of extant Raphidioptera at family level, which splits the raphidiopterans into two families; Raphidiidae and Inocellidae, with
a sister-group relationship. The apomorphies of the Order were discussed in detail by Aspöck and Aspöck (2004), who listed four: Sc running into the anterior wing margin (Fig. 13.5A), the ninth gonocoxites (ovipositor) of the female terminalia is elongate and tube shaped (Fig. 13.5B), imaginal tarsi with third tarsomere bilobed (Fig. 13.5C), and segment 9 in the male genital sclerites: the tergite and sternite form a ring (Fig. 13.5D). Other characters shared by extant raphidiopterans are the trichobothria in the male terminalia loosely forming a band (Fig. 13.5E) and the labial palp of the prementum in the larva is segment-like (Fig. 13.5F) (Aspöck et al. 2001; Aspöck & Aspöck 2004, 2008).
The apomorphies of the family Raphidiidae are: the lateral margins of the pronotum are bent down over to the ventral side, where they almost overlap in the middle (Fig. 13.6A), in Inocellidae the pronotum is rectangular and it does not appear ventrally, and the sternal sclerites are fused in the prothorax forming to large plates (Fig. 13.6B), in Inocellidae the sclerites are not fused medially.
The apomorphies of Inocellidae are an absence of ocelli (Fig. 13.6C), shortening and funnel-like shape of the second tarsi (Fig. 13.6D).

![Figure 13.6. The apomorphic characters of Inocellidae and Raphidiidae. A. the Pronotum (redrawn and modified from figs. 9 and 33 Aspöck et al. 1991), B. The sternal sclerites (redrawn and modified from figs. 9 and 33 Aspöck et al. 1991), C. The ocelli (redrawn and modified from figs. 1 and 27 Aspöck et al. 1991), D. The 2nd tarsomere (redrawn and modified from figs. 17 and 42 Aspöck et al. 1991).](image)

Other characters, which separate Raphidiidae and Inocellidae from each other are: sternite 8 being absent in Raphidiidae, is present in Inocellidae, the sclerites are fused in the paramere (Aspöck et al. 2001). Molecular data has corroborated the existence of the two raphidiopteran families (Haring & Aspöck 2004).

At generic level little work has been done on the relationships of extant Raphidioptera. Aspöck et al. (1991) proposed a hypothesis for a phylogeny based upon morphological characters (Fig 13.7 and 13.8). The extant raphidiopteran genera of Raphidiidae are split into 8 groups: Group I – Phaeostigma, Dichrostigma,
Tjederiraphidia, Turcoraphidia, Iranoraphidia, Tauroraphidia, Subilla, Ornatoraphidia, Xanthostigma, Parvoraphidia, Ulrike, Raphidia; Group II – Atlantoraphidia, Harrarphidia, Hispanoraphidia, Africoraphidia, Ohmella, Italoraphidia, Puncha, Group III – Venustoraphidia, Mauroraphidia; Group IV – Tadshikoraphidia; (Group V – Usbekoraphidia, synonymized with Mongoloraphidia (Aspöck et al. 1998), Group VI – Mongoloraphidia; Group VII – Agulla; Group VIII – Alena (Aspöck et al. 1991).

The characters used for Aspöck et al.’s (1991) hypothesis are entirely based upon the morphology, in particularly the majority are based upon the genitalia and terminalia, especially of the male. Listed below are the characters used by Aspöck et al. (1991), which have been listed and numbered, the numbers corresponding to the character on the phylogenetic trees figures 13.7 and 13.8.

Figure 13.7. Aspöck et al.’s (1991) hypothesis of relationships of Raphidiidae, with the characters numbered (key to the numbers in text) (modified and redrawn from Scheme 1, 2 and 3 Aspöck et al. 1991).
Raphidiidae characters (from Aspöck et al. 1991):

1. Median unpaired hypovalva
2. Massive sclerotization of parameres
3. Rod shaped parameres
4. Disc-shaped parameres
5. Lateral membranous hypovalva
6. Basally shortened ectoproct
7. Paramere-Hypovalva complex
8. Strengthening and dorsal shift of the stylus of the gonocoxites in the male
9. Narrow connection of the 7th sternite and 8th sternite in females
10. Large styli
11. Strong modification of stylus carrying part of the gonocoxites
12. Enlargement of the ectoproct
13. Differentiation of the paired contact places to the 9th sternite in males
14. Enlargement of the hypandium inturnum in the male
15. Shortening of MA in the hind wing
16. Pigmentation pattern in the larvae
17. Presence of intersegmental sternite 7/8 in females
18. Triangular, tapering head of the male
19. Reduction of hypovalva
20. Reduction of the gonocoxites base in males, breaking the connection with the hypovalva base.
21. Hypovalva with paired sclerites
22. Narrow coupling of the 8th sternite and the 9th sternite in males
23. Differentiation of the parameres
24. Anterior strongly convex in 8th tergite in the female
25. Paramere sclerite lying over hypovalva
26. Sclerite lying between styli in paramere
27. Enlarged ectoproct male
28. Strongly reduced paramere
29. Forked styli in the male
30. Poorly shaped apex of gonocoxites
31. Forked styli in the male
32. The form of the bursa copulatrix in the female
33. Terminal divergence of apices in hypovalva
34. Strongly sculptured ductus receptaculi in the female
35. Reduced gonocoxites
36. Large styli
37. Narrow coupling of the 8th sternite and 9th segment
38. Lack of parameres
39. Reduction of the ectoprocts
40. The obliteration of the 9th sternite
41. Trapezoid form of the 9th tergite
42. Lack of unambiguous trichobothria on the ectoproct of the male
43. Coupling of the 8th sternite at the 9th segment of the male
44. Paramere equipped with denticle sculpture
45. Possession of paramere
46. Paired differentiated hypovalva
47. Fusion of the basal sclerite with the gonocoxites in the male
48. Curved hypovalva
49. Tunnel-like merged parameres
50. The ‘hook and loop-fastener’ connection
51. Bent styli
52. The apices of the gonocoxites arranged proximally, and black pronotum.
53. Fusion of the parameres arch with the hypovalva
54. Long sickle-shaped styli; unusually longer, positioned far forwards passing sacculus bursae
55. Hypovalva sunken base
56. Reduction of the parameres
57. 7th sternites with bristles in the female
58. Long, slender head
59. Long, slender pronotum
60. Construction of parameres
61. Strong extension of the 7th sternites of the female
62. Pigmentation pattern of the abdominal segments of larvae
63. The dorsal, plate-like extension of the stylus base
64. Construction of the parameres
65. The dentition of hypovalva
66. The highly developed intersegmental S 7 / 8 of the females.
67. Long yellow pterostigma
68. The shape of the parameres
69. Male: paired 8th Sternites
70. Ventral expansion of the ectoprocts
71. Glandular ducts of the seminal receptacle with spherical sections in the female
72. Modified Gonocoxites: the dorsal part with a ‘lever-like’ stylus, while the ventral part is reduced almost completely
73. Reduction of the pterostigma
74. The unpaired, reduced parameres
75. The gonocoxites-apex ventrozephale
76. The bulge of the 8th tergite in the females
77. Dorsal transformation of the 9th tergites
78. U-shaped posterior border of gonocoxites
79. Tendency to a latero-caudal widening of the ectoprocts in males
80. A distinct, narrow ductus sacculi in females
81. The capsule-sclerotised bursa copulatrix of the female
82. Extension of the ductus receptaculi in females
83. The loss of the parameres in males
84. The widely divergent base of the hypovalva
85. The loss of the gonarcus
86. The loss of the parameres
87. The sclerotised, serrated hypovalva of the male
88. The huge schlid shaped parameres of male
89. The long sculpted receptaculi duct
90. The terminal cone on the spermatheca of the male
91. The angle of anterior apices of hypovalva and the associated median, large-sized and paired parameres in male
92. Paired sclerites in the bursa copulatrix
93. Stalked glandular ducts of the seminal receptacle in the female
94. Apex development on 9th tergite
95. Reduction of 9th sternites, linking the styli
96. Rod-shaped parameres in the male
97. A ring-shaped connection between the tergite and sternite of 8th segments among males
98. The long slender pronotum
101. The poor-shaped processus of the gonocixites of the male
102. Tendency to the obliteration of the crossveins vein in the pterostigma
103. The lightening of the abdominal sclerite
104. The form and dentition of parameres and gonarcus and their ‘hook-and-loopfastener-like’ connections
105. The separation of gonocoxites of the 9th tergite and 9th sternite
106. Adhesion and fusion of atrium bursae and receptaculum seminis in females

*Calabroraphidia* was not included in Aspöck *et al.*’s (1991) the study, because it was only described in 2004 (Rausch *et al.* 2004).

![Figure 13.8. Aspöck et al.’s (1991) hypothesis of inocelliid relationships, with the characters numbered (key to numbers in text) (modified and redrawn from Scheme 4 Aspöck et al. 1991).](image)

**Inocellidae characters** (from Aspöck *et al.* 1991):

1. MA base in the hind wing not as a crossvein
2. MA base in hind wing cryptic
3. Serratulum absent
4. Strongly differentiated styli
5. 8th tergite divided, appearing lateral in females
6. Bristle platelets and groups in the endophallus base and inside of the gonocoxites
7. Hook-shaped pseudostyli
8. Monofiliform antennae with bristles in male
9. Paired arcessus

**Sinoinocellia:** No male specimen therefore difficult to place within a phylogeny.

Aspöck *et al.*, (1991) stress that these are only working hypotheses of the relationships within Raphidioptera, with many of the relationships not being strongly supported. For example, the inocelliid sister-group relationships are not based on very strong synapomorphies, and even the genera themselves are given tentative apomorphies (Aspöck *et al.* 1991). However, the hypotheses given do form an admirable starting point.

When it comes to incorporating fossils into the raphidiopteran phylogeny, very little has been done, with only two attempts made. One of these attempts is at the family level (Ren & Hong 1994) and the other at the generic level (Willmann 1994). Ren and Hong’s (1994) attempt was strongly criticized by Engel (2002) for not being very rigorous, with only 6 characters used, and the characters themselves were dubious with no quantification given in many cases, for example, Prothorax: (0) shorter, (1) longer and Rs of forewing originates (0) just before midwing. (1) distad of midwing.

Two of Ren and Hong’s (1994) taxa used have been synonymized; Jilionraphidiidae and Huaxiaraphidiidae are considered to be in the family Mesoraphidiidae (Engel 2002).

The characters used in this study were:

1. Oblique vein in the pterostigma
2. MA in hind wing arises from R or M
3. R and M regions with more crossveins or less
4. Prothorax (shorter or longer)
5. In forewing: MA arises from M before or after MP, or originates well beyond forking of MP
6. RS of forewing originates just before, or distad of midwing

Figure 13.9. Ren and Hong’s (1994; Engel 2002) phylogeny of Raphidioptera families (redrawn from Ren & Hong 1994).

Willmann (1994) created a phylogeny based on selected extinct genera of Raphidioptera, as well as the two extant families Raphidiidae and Inocelliidae. Willmann’s efforts are more robust than that of Ren and Hong (1994), using 36 characters to construct his phylogeny, all based on variations within the wing venation

Characters used:

1. Decrease in number of cells between R and RS.
2. Base of cell between Rs and M is shortened by the change in the base of MA.
3. The free base of M, between RS and M, and the proximal m-cu crossvein is shortened (later becoming reversed).
4. The 3rd m-cua crossvein (counted from the wing base) leads to the formation of a large cell behind M.
5. Sc runs into C.
6. Rs separates from R near the end of the first wing third (original state R-Rs fork near the wing base. Leads to a shortening of the radial cell.
7. The first cell between the Media branches, expands basalwards.
8. Basal stem of M becomes inverse
9. Lengthening of the basal m-cu crossvein.
10. Basal cell between M and Cu extended distally
11. Anal loop in hind wing
12. Length of prothorax with regard to head
13. Two Cu crossveins present in hind wing
14. Three rs-m crossveins
15. Lengthening and re-orientation of basal m-cu crossvein
16. Four crossveins between R and Rs in hind wing
17. Short basal m-cu crossvein slightly curved in hind wing
18. Formation of 2r and discal cell
19. Loss of one of three rs-m crossveins
20. Extension or shortening of r-rs crossvein
21. A) A3 merged with the rear curve of the anal loop. B) Comb-like arrangement of the rear branches of A2 and A3.
22. Hind wing: partial coalescence of CuA1 and M3+4, if divergent the cell gets lost
23. Narrow wing
24. Wing with narrow base. Intramedian cell lies basalwards of R/Rs fork and basal cell between Rs+M.
25. Hind wing: Cu2 partially fused with A1
26. Hind wing with only 3 r-rs crossveins
27. Broad wing
28. M and CuA touch
29. Basal cut-off of Rs is midwing
30. Hind wing: basal cut-off of Rs (basal branch of MA of some authors) arises from proximal part of M not R.
31. Disappearance of the basal cells behind the Intramedian cell
32. Disappearance of the Intramedian cell
33. Basal cell between Rs and M, misaligned in the direction of the wing apex
34. Crossvein present between R, M and Cu (basal segment of M).
35. Another crossvein between R and Rs
36. Hind wing: cell between M3+4 and CuA1 present
Figure 13.10. Willmann’s (1994) raphidiopteran phylogenetic tree. A. Willmann’s complete phylogenetic tree with characters (defined in text) (redrawn from fig. 7 Willmann 1994), B. Alternative arrangement for basal groups (redrawn from fig. 10 Willmann 1994), C. Alternative arrangement for younger groups (redrawn from fig. 11 Willmann 1994).

Aspöck et al. (1991), Ren and Hong (1994) and Willmann (1994) represent the only work as yet completed on trying to resolve the relationships of raphidiopterans. The work of Aspöck et al. (1991) is a preliminary working hypothesis, the work of Ren and Hong (1994) is unfortunately full of problems, and only based on family relationships. Willmann’s (1994) work is a good foundation to build on, but, there may be some doubt as to his character choices, and he does not use all genera, just a select few. Hopefully the study herein will be able to shed some light upon the generic relationships within the Order Raphidioptera.
13.3. **Keys to the Families and Genera of Fossil Snakeflies (Insecta: Raphidioptera)**

(Jepson, J.E. Keys to the Families and Genera of Fossil Snakeflies (Insecta: Raphidioptera). To be submitted to *Zootaxa*)

13.3.1. *Abstract*

Identification keys have been constructed for the first time on all fossil raphidiopterans described to date. The keys offer an identification to family level, for all the five families (extant and extinct) and generic level within these families. All of the keys are primarily based upon the wing venation, which is predominantly used as the method of identification of the fossil taxa.

*Keywords*: Identification keys, Neuropterida, Raphidiidae, Inocelliidae, Alloraphidiidae, Mesoraphidiidae, Baissopteridae.

13.3.2. *Introduction*

The first record of Raphidioptera in the fossil record is from the Lower Jurassic with two species of *Metaraphidia* (Mesoraphidiidae) currently in the Lias of Britain and Germany (Whalley 1985; Willmann 1994). There are five families of Raphidioptera, both extant and extinct; these are the extinct Baissopteridae, Alloraphidiidae, Mesoraphidiidae and the extant Raphidiidae and Inocellidae (Engel 2002a). The family Priscaenigmatidae was previously thought to be raphidiopteran, however, it has now been removed from the Order (Aspöck & Aspöck 2004). There are approximately 32 genera and 96 species of fossil Raphidioptera described to date. For a review of fossil Raphidioptera see Engel (2002a) and Jepson and Jarzembowski (2008).

This study is the first attempt at a construction of an identification key for the families and genera of Raphidioptera. The keys are focused on the wings of fossil Raphidioptera, with some morphological data added. The keys to the families and genera are based on all the fossil raphidiopterans described to date.

The wings are the most diagnostic feature of fossil raphidiopterans; therefore they are the main focus of these keys. The vast amount of morphological data, especially the male genitalia used in the identification of extant species is very rarely preserved.
in the fossil record to allow it to be of any use in identification.

Figure 13.11. The labelled wing venation of the fore- (top) and hind (bottom) wing of *Mesoraphidia luzzi* Grimaldi, 2000.

Figure 13.11 shows the venation of a fore- and hind wing of a fossil raphidiopteran (*Mesoraphidia luzzi* Grimaldi *et al.* 2000) with the terminology used in the keys below, other features are highlighted in figures referenced in the keys. The abbreviations are C, costa; Sc, subcosta; R1 radius; Rs, radial sector; M, media; MA, media anterior; MP, media posterior; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; A, analis; 1A, first branch of analis; 2A, second branch of analis; 3A, third branch of analis; 1-3r, radial cells; dc, discal cell; mc1-3, medial cells; ac, anal cell.

13.3.3. Key to families

Included families: Baissopteridae, Alloraphidiidae, Mesoraphidiidae, Raphidiidae and Inocelliidae.

1. Sc terminating on the anterior wing margin, females with long ovipositor
Figure 13.12. Displaying the termination of Sc. A. is a raphidiopteran, B. is a neuropteran.

Yes.........2 (Fig. 13.12A)

No..........Not Raphidioptera (Fig. 13.12B)

2. Wings long and slender

Figure 13.13. Displaying the different wing shapes within Raphidioptera. A. elongate, B. non-elongate.

Yes.........3 (Fig 13.13A)

No..........4 (Fig 13.13B)

3. Forewing: Many cells between Rs and MA (15+) in the forewing
Figure 13.14. Displaying the cells between Rs and MA. A many, B few.

Yes.........Baissopteridae (Fig. 13.14A)

No.........5 (Fig. 13.14B)

4. Separation of CuA from M very close to the stem of R forming a trifurcation in forewing

Figure 13.15. Showing the trifurcation of R1, M and CuA.

Yes.........Alloraphidiidae (Fig. 13.15)

No.........5

5. Free branch of MA fuses with R1 for short period in forewing (Fig 13.16A) and free analis in the hind wing (Fig 13.16B)
Figure 13.16. Displaying the fusion of MA with R1 (A) and the free analis in the hind wing (B).

Yes..........Inocelliidae
No..........6

6. A combination of 2 medial cells in the forewing and a short pterostigma (pterostigma shorter or same size as 2r) (Fig 13.17)

Figure 13.17. Displaying the medial cells and short pterostigma.

Yes..........Raphidiidae
No..........Mesoraphidiidae

Any specimens that do not fit the above key = incertae sedis

13.3.4. Key to Genera

Baissopteridae Key:

Included genera: Baissoptera, Cretinocellia, Lugala, Cretoraphidia, Austroraphidia and Cretoraphidiopsis.

1. Number of medial cells (m, Fig. 13.11)
Few (3) .......... *Cretinocellia*

Many (4+).........2

2. Origin of the free base of MA with respect to the fork of MP in forewing

![Figure 13.18](image)

Figure 13.18. The origin of the free branch of MA with respect to the fork of MP. After (A), at (B) and before (C).

At or just before........3 (Fig. 13.18B, C)

After........4 (Fig. 13.18A)

3. Wings narrow and elongate, especially hind wing (see Fig. 13.13). Two cua-cup crossveins in hind wing (Fig. 13.19).

![Figure 13.19](image)

Figure 13.19. Showing the cua-cup crossveins in the hind wing.

Yes.........*Lugala*

No.........5
4. Many branches of the radial sector (greater than 3) (Rs, Fig. 13.11), many medial cells (greater than 5) (m, Fig. 13.11), costal area broader than pterostigma in forewing.

Yes...........\textit{Cretoraphidia}

No...........\textit{Austroraphidia}

5. First cu-crossvein after fork of CuA and MP (Fig 13.20)

![Figure 13.20. Showing the relationship between the first cu crossvein and the fork of CuA and MP.](image)

Yes...........\textit{Cretoraphidiopsis}

No...........\textit{Baissoptera}

Any specimens that do not fit the above key = \textit{incertae sedis}

\textbf{Alloraphidiidae Key:}

\textbf{Included genera: \textit{Alloraphidia}, \textit{Archeraphidia} and \textit{Pararaphidia}.}

1. Both fore- and hindings very thin and slender (see Fig. 13.13)

Yes...........\textit{Alloraphidia}

No.........2

2. MA arising at or before the fork of MP in forewing (see Fig. 13.18)

Yes...........\textit{Archeraphidia}

No.........3

3. Distal part of fore- and hind wings broad and rounded at apex, 1r and 2r broad.
Yes........Pararaphidia
No........Alloraphidia

Any specimens that do not fit the above key = incertae sedis

Mesoraphidiidae Key:

Included genera: Mesoraphidia, Proraphidia, Baisoraphidia, Siboptera, Huaxiaraphidia, Sinoraphidia, Kezuoraphidia, Xuraphidia, Metaraphidia, Nanoraphidia, Iberoraphidia and Cantabrorphidia.

Wing length below 6 mm:

Yes........1
No........3

1. Medial cells (m, Fig. 13.11):

Three........Mesoraphidia
Two........2
One........Nanoraphidia

2. 1r and 2r same width and thickness (Fig. 13.11):

Yes........Cantabrorphidia
No........Mesoraphidia

3. Pterostigma (pt, Fig. 13.11):

Short (same size or shorter than 2r, origin in the final wing third).........Proraphidia
Divided........Iberoraphidia
Long (longer than 2r)........4

4. M horizontal (~ parallel to R) before forking, after split with CuA (Fig. 13.21), Rs originates at mid-wing in the forewing, MA free branch originates very distal from M-CuA fork in the forewing
Figure 13.21. Showing the horizontal M ~parallel to R, origin of Rs, and the distal free branch of MA.

Yes........ *Siboptera*

No......... 5

5. Medial cells (m, Fig. 13.11) enlarged, and the discal cell ~one third of wing length (Fig. 13.22).

Yes............ *Kezuoraphidia*

No............. 6

6. Origin of MA very distal of fork of MP (see Fig. 13.18); MP forking close to R1

Yes......... 7

No......... 8

8. CuA pectinately branched (greater than 3)

Yes......... *Sinoraphidia*

No......... *Xuraphidia*
9. Numerous cup-a1 crossveins (greater than 3) and cua-cup crossveins, the presence of cua-m crossveins, and crossveins forming small cells between A2 and A3, ± pectinate A1 (Fig. 13.23):

Figure 13.23 showing the cup-a1, cua-cup and cua-m crossveins, small cells and pectinate A1.

Yes.........Huaxiaraphidia

No..........10

10. A2 and A3 not fused in the forewing, 4 r1-c crossveins in final wing third (pterostigmal area) (Fig. 13.24):

Figure 13.24. Displaying the rs-c crossveins and not fused A3

Yes.........Metaraphidia

No..........11

11. Pterostigma (pt, Fig. 13.11) starts before final wing third
Yes........*Mesoraphidia*

No........*Baisoraphidia*

Any specimens that do not fit the above key = *incertae sedis*

*Incertae sedis* key:

1. 2 r-sc (pterostigmal crossveins), extra rs-r1 crossvein, and lack of crossveins in radial and medial areas (this may be a preservational artefact) (Fig. 13.25)

![Figure 13.25](image1.png)

Figure 13.25. Showing MA fused with R, the extra rs-r1 crossvein and the r-sc (pterostigmal) crossveins.

Yes........*Styporaphidia*

No........2

2. 1 pterostigmal crossvein, cua-a1 crossvein in forewing and single medial cell in hind wing (Fig. 13.26).

![Figure 13.26](image2.png)

Figure 13.26. Showing the r-sc and cup-a1 crossvein in forewing and medial cell in hind wing.

Yes........*Ororaphidia*
No.........3

3. Long pterostigma (longer than 2r), 3r small, MA and MP with gradate series of crossveins parallel to posterior wing margin. Head round and pronotum smaller than mesothorax.

Yes.........Arariperaphidia (based on fragmentary wing venation)

No.........4

4. Less than 3 medial cells (m, Fig. 13.11) in forewing

Yes.........Archiinocellia

Raphidiidae Key:


1. Short branch of M (before MA and MP split) in hind wing (Fig. 13.27)

![Figure 13.27. Showing the stem of M in the hind wing. A, long; B, short.](image)

Yes.........2 (Fig. 13.27B)

No.........3 (Fig. 13.27A)

2. Gonapophyses 9 of the male: rod-like, not being connected ventrally.

Yes.........Succinoraphidia

No.........‘Raphidia’*

Note: Difficult to differentiate venationally.
3. Highly branched (over 2) apical terminus of R in hind wing, radial area not narrowed proximally (Fig. 13.28)

Figure 13.28 displaying the proximal radial area and apical terminus of R.

Yes........‘Agulla’*  
No......... ‘Ohmella’*

*The placement of specimens represented by just wings in the extant genera Raphidia, Ohmella, and Agulla cannot be convincingly supported by wing venation (Aspöck & Aspöck 2004).

Inocelliidae Key:

Included genera: ‘Fibla’, Electrinocellia, Succinofibla

1. Narrow costal area in forewing; MP 3+4 not bifurcated in fore- and hind wing; MP with 2 medial cells in hind wing (Fig. 13.29)

Figure 13.29. Showing the features of Electrinocellia
Yes.........Electrinocellia

No........2

2. Wide costal area in forewing; second rs-sc before termination of Sc (Fig. 13.30)

![Second sc-r crossvein](image)

Figure 13.30. Showing the second sc-r crossvein terminating before the termination of Sc.

Yes.........‘Fibia’*

No.........Succinofibla

Note: Succinofibla is diagnosed on the basis of the Gonocoxites 9 of the male with an armlike processus in a terminal position and wartlike tubercles at the inner side.

*The placement of specimens represented by just wings in the extant genus Fibla cannot be convincingly supported by wing venation (Aspöck & Aspöck 2004).
13.4. A Cladistic Study on Fossil Snakeflies (Insecta, Neuropterida, Raphidioptera)

(Jepson, J.E. A Cladistic Study on Fossil Snakeflies (Insecta, Neuropterida, Raphidioptera). To be submitted to Systematic Entomology)

13.4.1. Abstract

A cladistic analysis of fossil snakeflies using 21 characters and 28 genera has been undertaken. The characters are based upon wing venation with some easily preserved body morphology. Little resolution has been obtained between the genera. The families Baissopteridae and Mesoraphidiidae have shown to be paraphyletic. Some poor to well supported clades have been resolved. The baissopterids are placed basally to the rest of the snakeflies, as expected and observed in previous cladistic studies. Fifteen synapomorphies have been established from the analysis. The problems of cladistic analyses upon fossil and extant snakeflies is also discussed.

Keywords. Cladistics, Snakeflies, Mesoraphidiidae, Baissopteridae, Alloraphidiidae, Raphidiidae, Inocelliidae

13.4.2. Introduction

Very few cladistic or phylogenetic studies have been completed on raphidiopterans. Aspöck et al. (1991), gave hypotheses on the relationships of the extant raphidiopterans, and also highlighted the problems associated with finding strong synapomorphies to support many of the relationships of the genera. They divided the extant Raphidiidae into eight groups; the largest group, group I contains the genera Phaeostigma, Dichrostigma, Tjederiraphidia, Turcoraphidia, Iranoraphidia, Tauroraphidia, Subilla, Ornatoraphidia, Xanthostigma, Parvoraphidia, Ulrike, and Raphidia, group II consists of Atlantoraphidia, Harraraphidia, Hispanoraphidia, Africoraphidia, Ohmella, Italoraphidia, and Puncha, group III has the genera Venustoraphidia and Mauroraphidia, group IV contains only one genus; Tadshikoraphidia, group V has Usbekoraphidia, group VII Agulla and group VIII Alena (Aspöck et al. 1991). Usbekoraphidia was synonymised with Mongoloraphida, therefore removing group V (Aspöck 1998). Aspöck et al. (1991) also did a tentative phylogenetic tree on the extant Inocelliidae. The Aspöcks’
hypotheses, however, did not take into account the fossil raphidiopterans, the only two attempts of working out the relationships of fossil and extant are Ren and Hong (1994), who worked at the family level, and Willmann (1994), who used a selection of the genera. Ren and Hong’s (1994) attempt at a phylogeny was not as rigorous as that of Willmann’s (1994) whose phylogeny has created a good foundation to build upon.

This study is intended to give an updated starting point for the difficult task of incorporating fossil and extant raphidioptera into a phylogeny, however, the focus is on fossil raphidiopterans, with the relationships of extant genera being taken from the hypotheses put forward by Aspöck et al. (1991), Aspöck and Aspöck (1994), and Aspöck (1998).

13.4.3. Material and Methods

13.4.3.1. Body and wing morphology

The characters used in this study are a combination of both body and wing morphology; however the primary focus is on wing venation. This is because the fossil taxa are for the most part, described by their wing venation, because diagnostic body parts are rarely preserved. Genitalia characters are used to separate the extant taxa into their hypothesized relationships (Aspöck et al. 1991; Aspöck 1998); these however, are of little use for fossil raphidiopterans, which are usually preserved as isolated wings.

13.4.3.2. Taxa

The taxa used in this study are all the genera of Raphidioptera described, both extinct and extant. The extant taxa have been studied through the use of Aspöck et al.’s (1991) monograph on the world fauna of Raphidioptera, with updates of revised taxonomic position and new genera (Aspöck & Aspöck 1994; Aspöck 1998; Rausch et al. 2004). The fossil material is studied from the numerous published work on Raphidioptera. The majority of the measurements have been taken from drawings, therefore, inaccuracies in drafting may give errors however, photographs have been used when they can. The taxa used with geological ranges are listed in table 13.1.
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<th>Family</th>
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<th>Extinct/Extant</th>
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<td>Recent</td>
</tr>
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</tr>
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<tr>
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<td>Sinoraphidia</td>
<td>Extinct</td>
<td>Upper Jurassic–Lower</td>
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</table>
The outgroup taxa is the genus *Permoberotha* (Glosselytrodea: Permoberothidae) chosen because of its basal position to Neuropterida. (Carpenter 1943a; Grimaldi & Engel 2005). The genus *Permoberotha* (Fig. 13.31) is from the Permian of Kansas. It is likely that the Permoberothidae are stem-group Neuropterida (Grimaldi & Engel 2005).

Figure 13.31. The fore- and hind wing venation of the *Permoberotha*, the outgroup taxa of the study (after Carpenter 1943a).

13.4.3.3. Potential problems

The major problem with the incorporation of fossils into a phylogeny with extant raphidiopterans is that the vast amount of diagnostic characters are not preserved within the fossils. Most of the extant raphidiopteran species are diagnosed by the form and structure of the genitalia, or other body morphology, which very rarely get preserved in the fossil record, the rare occurrences are most often than not in amber fossils. For example, Aspöck and Aspöck (2004) were able to get many diagnostic characters from *Succinofibla* and *Succinoraphidia* in Baltic amber, than are normally
found in fossils. The majority of snakefly fossils are described based on wing venation, which in extant snakeflies can be very variable within genera, species and in some cases the individual. Therefore, how reliable the taxonomy of fossil snakeflies is, is debatable, many taxa in recent years have been synonymised (Engel 2002a).

Another problem which includes the extant taxa; is that apomorphies are very hard to decipher for genera, and when constructing relationships, synapomorphies are difficult to determine, and many of the resulting relationships are tentative. With fossil taxa the taxonomy of many groups is in need of revision, for example the genus Mesoraphidia appears to be a bucket group for many species, and some genera are in need of revision, and are possible synonyms of previously described genera. This therefore can cause erroneous results of any phylogenetic study, and care must be taken in interpreting the results.

13.4.4. Cladistic study

13.4.4.1. Characters

The characters used in the analysis are listed below with their coding (Table 13.2). They are mainly based upon wing venation, however some commonly preserved morphological characters are used. A labelled figure of raphidiopteran wing venation is given (Fig. 13.32).
Figure 13.32. Showing the venation of a fore- and hind wing of a raphidiopteran
(Mesoraphidia luzzi after Grimaldi 2000)

1: Number of cells of Rs and M in the forewing
   [0] Many (>17), [1] Few (<17)

2: Number of medial cells in the forewing

3: Trifurcation of R, M and Cu in the forewing
   [0] absent, [1] present

4: Presence of a gradate series of crossveins in the forewing
   [0] present, [1] absent

5: Pterostigma

6: Head
   [0] quadrato, [1] triangular
7: Number of cells of R and Rs in the forewing

8: The 2r and discal cell in forewing
[0] present, [1] absent

9: Number of r-rs crossveins in forewing
[0] many (>3), [1] few (<3)

10: Termination of Sc on C in both fore- and hind wings
[0] absent, [1] present

11: The presence of ocelli on the head capsule
[0] absent, [1] present

12: Basal cut off of Rs at the mid wing
[0] no, [1] yes

13: M and Cu touch
[0] no, [1] yes

14: ma-mp crossveins in the forewing
[0] >2, [1] <2

15: 2 cu-m crossveins in the hind wing
[0] no, [1] yes

16: r-rs crossveins in hind wing
[0] >4, [1] <4

17: Pterostigma
[0] not divided, [1] divided

18: Wing shape
[0] non-elongate, [1] elongate

19: Cubital area crossveins
[0] >2, [1] <2

20: M base
[0] at an angle, [1] horizontal

21: Wing size
[0] > 6 mm, [1] < 6 mm
The cladistic analysis was undertaken on the 28 genera of snakefly using 21 characters (Table 13.2) using PAUP 4.0 beta 10 (Swofford 2002). A heuristic search resulted in 891 parsimonious topologies with little resolution. The 50% majority rule consensus tree showed some resolution with some well supported clades (Fig. 13.33).
Figure 13.33. Strict consensus Tree. The percentage support for each node is given in an oval (Consistency Index: 0.815, Retention Index: 0.934, Homoplasy Index: 0.185.). Synapomorphies are indicated by a black bar and number (numbers refer to characters in data matrix (Table 16.2) and are explained below).

13.4.4.3. Synapomorphies

Very few synapomorphies were found for raphidiopterans through this analysis giving very little resolution within the cladogram (Fig. 13.33). The synapomorphies found are listed below:
1: Termination of Sc on C in both fore- and hind wings

2: 3-6 cells of Rs in forewing

3: less than 4 r-rs crossveins in hind wing

4: less than 2 rs-m crossveins in the forewing

5: less than 5 medial cells in the forewing

6: less than 17 cells of Rs and M in the forewing

7: No gradate series of crossveins in forewing

8: less than 3 r-rs crossveins in forewing

9: 3 or less cells of Rs in forewing (loss of Rs cells)

10: less than 2 cubital area crossveins

11: less than 6 mm wing size

12: pterostigma shorter than 2r

13: triangular head

14: Basal cut off of Rs at the mid wing

15: M and Cu touch

Very few sister-group relationships were resolved with many polytomies existing. However, there are some well supported clades (Fig. 13.33). Figure 13.34 shows a composite of the analysis presented herein and the work on extant raphidiopterans by Aspöck et al. (1991), Aspöck and Aspöck (1994), Aspöck (1998), Rausch et al. (2004) with the addition of the fossil genera of Raphidiidae and Inocelliidae.

Figure 13.34. (Overleaf). Showing all raphidiopteran (fossil and extant) with the results of the analysis herein and the works of Aspöck et al. (1991), Aspöck and Aspöck (1994), Aspöck (1998), Rausch et al. (2004).
13.5. Discussion

The construction of the fossil raphidiopteran key and the cladistic study on fossil raphidiopterans has highlighted further the problems of finding defining and diagnostic characters of fossil raphidiopterans. The key is a good preliminary starting point which can aid the worker in identifying any fossil raphidiopteran to family and generic level. The keys are based upon few defining characters and if any of these characters are not preserved within the fossil the identification cannot be made. However, if the wing is well preserved then identification should be possible. At generic level the characters used are sometimes quite weak and it may be that they are the products of natural variation which could occur within different species in the same genus, therefore weakening the key. This however can only be tested when more material is described, because at the present time many of the genera are monospecific.

The cladistic study on raphidiopterans further highlighted the problems associated with raphidiopteran characters. Numerous characters were investigated on all the species to try to find phylogenetic informative characters. Many characters were rejected, most of them on the basis of variation between and within species of the same genus. All manner of characters were attempted from the position of the crossveins within the wings, angles between the veins, termination of veins and number of branches, to name a few. From over 40 potential characters, only 21 were used in the analysis. Another problem was that the photographs of the fossil specimens were often of such poor quality that the venation drawings were used to get character information. This is problematic because it relies on the authors creating an accurate representation of the fossil, especially when investigating characters such as angles between veins. Another subtle factor which could cause erroneous characters is the fact that slight post mortem deformation could take place on the wing causing slight changes in venation. There is also the fact that many of the wings are partially preserved and only represented by an isolated fore- or hind wing, which may lead to potential characters not being preserved in fossils, leading to unresolved relationships.

The first attempt of the cladistic study had every genus of snakefly both fossil and extant incorporated into the analysis. The characters used were based on wing
venation and easily preserved body morphology and the genitalia and body morphology from Aspöck et al., (1991) to resolve the relationships of the extant taxa. When running this analysis no resolution was found; the wing venation and easily preserved body morphology varied very little between the extant taxa and this caused an almost infinite number of trees to be generated, ultimately causing PAUP’s memory to be exhausted, even after over 3 hours of running time. Therefore the extant taxa were condensed into the families Raphidiidae and Inocelliidae, which reduced dramatically the number of parsimonious topologies (to 897). When the 50% majority rule strict consensus tree was created, the work of Aspöck et al. (1991) with the additions of fossil raphidiid and inocelliid genera were incorporated to give a full view of raphidiopteran relationships at generic level. The analysis on the fossil raphidiopterans created little resolution of the relationships and only 15 potential synapomorphies were recovered. The families Baissopteridae and Mesoraphidiidae were shown to be paraphyletic and Alloraphidiidae was shown to be monophyletic, but forming a clade with incertae sedis genera and the mesoraphidiid Proraphidia. Baissopteridae was shown to be the basal family of Raphidioptera, as expected due to the dense venation pattern similar to that of the outgroup Permoberotha. The majority of genera within all families were resolved as polytomies, with few resolved clades. Some interesting relationships were shown such as the two Chinese taxa Huaxiaraphidia and Sinoraphidia forming a basal sister-group to the other mesoraphidiids, maybe reopening the possibility of a separate family placement for the genera. However this was only based upon a symplesiomorphy. There is also the dubious accuracy of the drawings as highlighted by Engel (2002a); therefore redescription is needed before anything can be interpreted about their taxonomic position.

On the whole the cladistic analysis agreed to some extent with Willmann (1994), with regards to the basal placement of Baissopteridae, the paraphyletic arrangement of Baissopteridae and Mesoroaphidiidae, and the sister-group relationship of Raphidiidae and Inocelliidae. Alloraphidiid genera grouped into a monophyletic clade in the analysis herein, however, was shown to be paraphyletic in Willmann (1994). This is most probably due to the fact that Willmann used fewer taxa in his analysis, and many of the characters he used are variable within taxa of the same family, such as in Alloraphidiidae.
After completing extensive work looking at all the species of fossil raphidioptera and in compiling a key and analysing relationships the major problem observed time and again is the lack of defining/diagnostic characters. One problem is that fossil snakeflies are generally only represented by isolated wings with only rare occurrences of body parts. With extant genera the male genitalia holds a wealth of information that allows identification of species, genera and their potential relationships (Aspöck et al. 1991). This information is only very rarely found in fossil material, for example the Baltic amber taxa *Succinoraphidia* and *Succinofibia* had visible terminalia, which allowed a more detailed description and diagnosis. When it comes to wings very little information can be ascertained. Another problem is the lack of synapomorphies that have been found within extant taxa; therefore even the hypotheses of extant relationships are only tentative. The comparing of morphospecies (such as the fossil raphidiopterans) and biological species also causes problems, because it is likely that fossil species represent a complex of biological species, as opposed to just one. Therefore comparing these two different species concepts may always give unresolved relationships.

To find useful defining/diagnostic characters within fossil raphidiopterans a large scale taxonomic review is needed. Many genera and species are defined on very poor weak characters and the only way to sort out this confusion is for the redescriptions of type specimens. Some genera and families are used as ‘bucket’ groups where many species are placed, based on dubious characters, such as the genus *Mesoraphidia* and the family Mesoraphidiidae. Engel (2002a) in his catalogue made a good start at sorting out the taxonomic confusion synonymizing many genera, families and bringing a more conservative systematic account of the Order. Until a major review is undertaken there is little hope in creating an accurate phylogenetic history of fossil Raphidioptera.
13.6. Conclusions

The work on raphidiopterans has shown that:

1. It is possible to complete a preliminary key at both family and generic level, which will help in avoiding errors when describing new taxa.

2. It may be premature to consider reconstructing the phylogenetic relationships of extant and fossil raphidiopterans. The characters that are useful for identifying fossil species are of little use at present to allow extant taxa at generic level to be placed into the same analysis. The problem of lack of variability within extant genera compared to extinct means that there are an infinite possibility of tree topologies, which cannot be resolved.

3. The phylogenetic relationships of fossil genera of raphidiopterans can give a preliminary hypothesis, but there is little resolution. There are only a few well supported clades.

4. Only 15 synapomorphies were found in the cladistic study of fossil raphidiopterans, out of the 21 characters used in the analysis.

5. Families of fossil raphidiopterans are on the whole paraphyletic, for example Baissopteridae and especially Mesoraphidiidae. Alloraphidiidae was shown to be monophyletic, but, only weakly supported. Baissopteridae however, are again shown to be basal with respect to all other raphidiopterans.

6. Much more work is needed on fossil raphidiopterans before their relationships and taxonomy can be fully understood.
13.6.1. *Further Work*

The first step for any further work on the fossils of Raphidioptera is a full world-wide taxonomic revison of all families, genera and species. Clear diagnoses at all taxonomic levels are needed, which will mean a complete redescription of all fossil material. Some taxa are very poorly described and figured, and they are diagnosed on either weak or dubious characters. To create a complete and accurate key to all raphidiopterans this revision needs to take place. With regards to phylogenetic studies, again the taxonomic revision will be required to find useful characters and synapomorphies, which will elucidate relationships between groups. It may also be worthwhile considering new techniques in identifying characters, due to the problems of wing venation. A possibility could be geometric morphometrics, which could help find more elusive characters within the wing venation.
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