

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 Weald 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.

KEY WORDS: Wealden Supergroup. Montsec. Early Cretaceous. southern England. Jurassic/Cretaceous transition. new species.

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 (Jarzembowski 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 (Jarzembowski 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 Grylloblatodea

(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

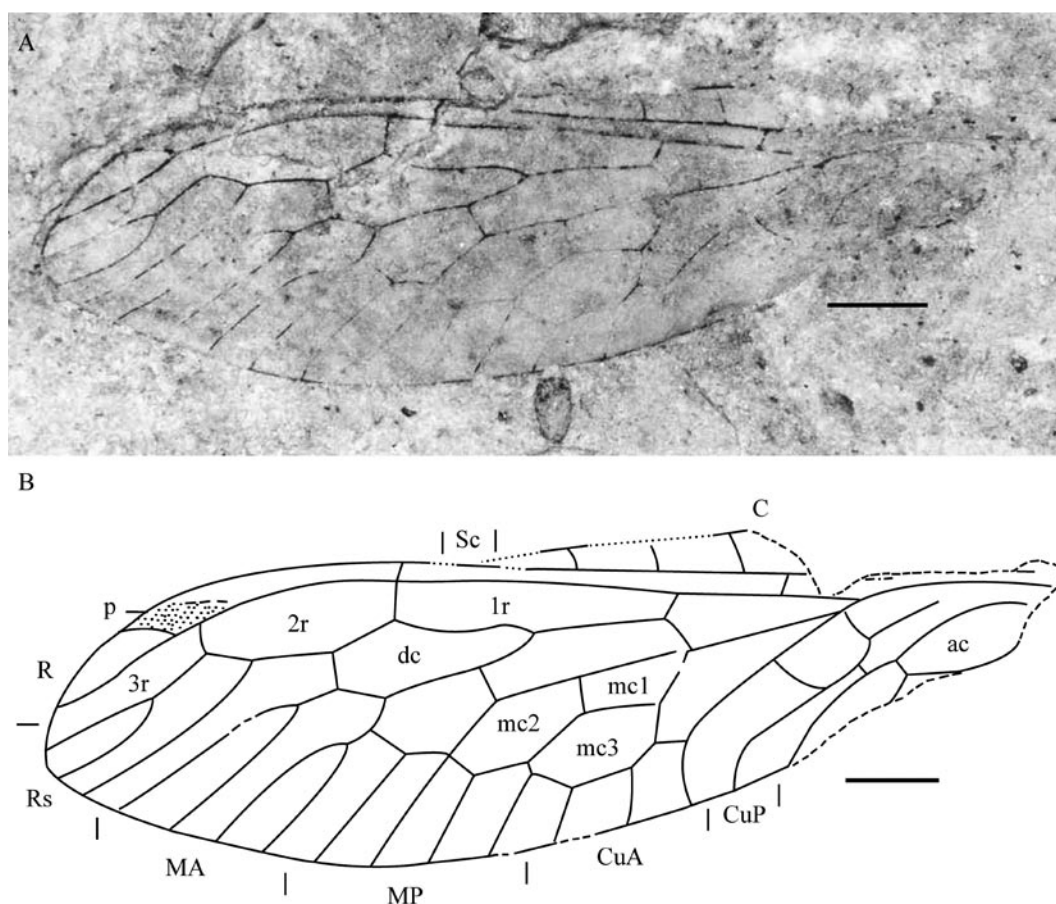


Figure 1. A. Photograph of the forewing of *Proraphidia hopkinsi* sp. nov. BMB 014915 [CH 879ia] B. Camera lucida drawing showing venation of *Proraphidia hopkinsi* sp. nov. Drawing convention as in Jarzembowski (1980). Scale bar = 1mm.

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 PALAEOONTOLOGY

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.

Holotype. BMB 014915, - 8 [CH 879ia,b] single left forewing. Deposited in the Booth Museum of Natural History, 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; Sc 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: 2.3mm 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 (*Mesoraphida* sp.) has been figured from the Purbeck Limestone Group of England (Jarzembowski 1993, Clifford et al. 1994). There are four species of the family Raphidiidae 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

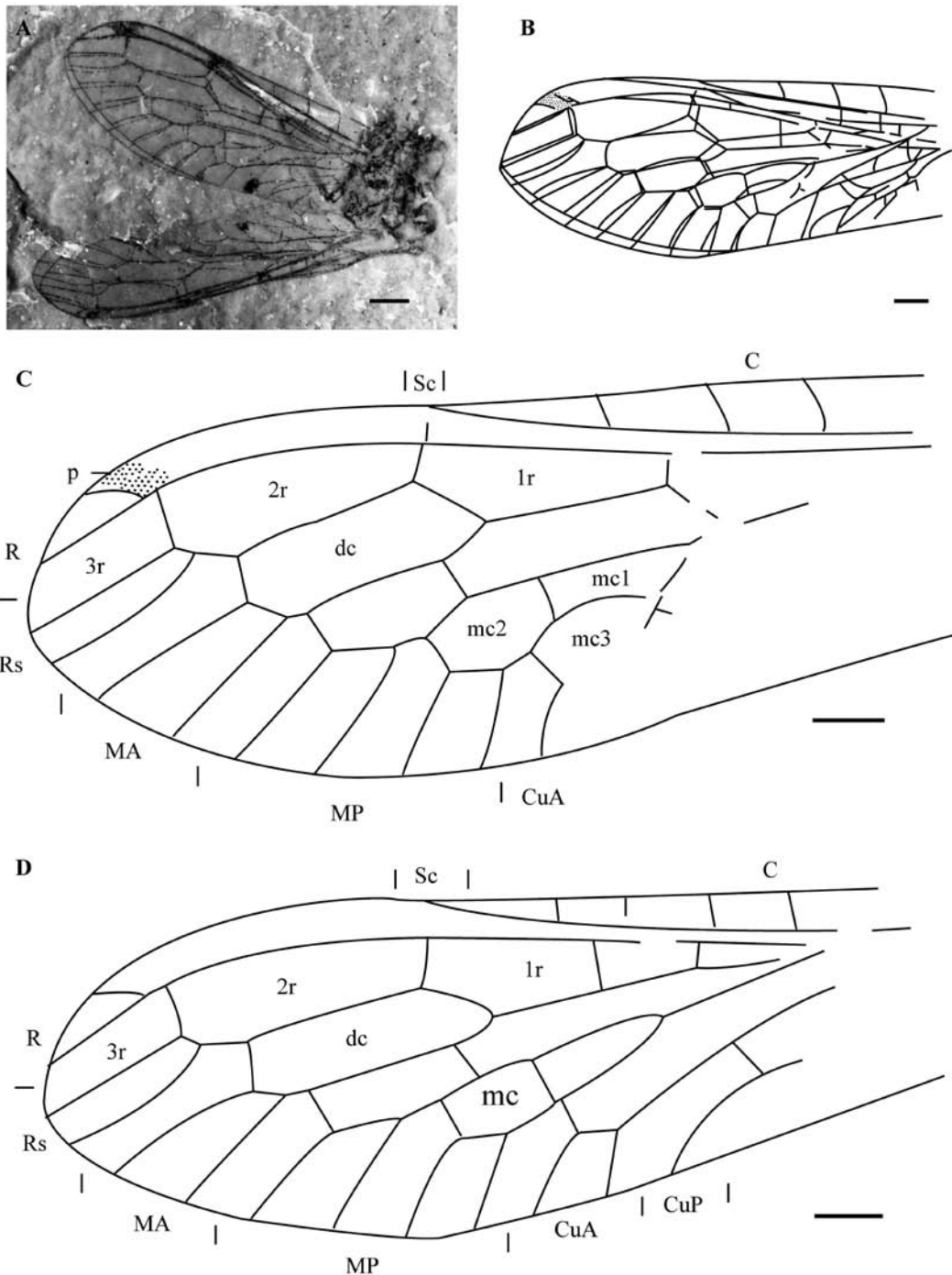


Figure 2. A. Photograph of *Proraphidia gomezi* sp. nov. [L. 29]. B Camera lucida drawing of overlapping wings. C. Camera lucida drawing of venation of forewing. D. Camera lucida drawing of venation of hindwing. Drawing convention as in Jarzembowski (1980). Scale bar = 1mm.

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 r-rs 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.fauna-ibericamncn.csic.es/faunaib/arthropoda/index.php>).

RAPHDIOPTERA 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/strad-

dled 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 (Martynov 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 *Creteraphidia* have been recorded in Baissa, 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 *Creteraphidiopsis* and *Lugala*) (Ponomarenko 1988, Willmann 1994, Engel 2002).

The family Alloraphidiidae is the smallest of three raphidiopteran families with three genera *Alloraphidia*, *Archeraphidia* and *Pararaphidia* (Engel 2002). *Alloraphidia asiatica*, *Archeraphidia baisensis* and *Pararaphidia vitimica* are found in the Lower Cretaceous of Baissa, 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

Age	Family	Species	Locality/Deposit	Reference
Upper Cretaceous	Mesoraphidiidae	<i>Mesoraphidia luzzii</i> Grimaldi, 2000	New Jersey amber, USA	Grimaldi 2000
		<i>Nanoraphidia electroburmica</i> Engel, 2002	Myanmar amber	Engel 2002
Middle Cretaceous	Alloraphidiidae	<i>Alloraphidia dorfi</i> Carpenter, 1967	Labrador, Canada	Carpenter 1967
Lower Cretaceous	<i>Incertae sedis</i>	<i>Arariperaphidia rochai</i> Martins-Neto and Vulcano, 1990	Crato Formation, Brazil	Martins-Neto and Vulcano, 1990
	Baissopteridae	<i>Austroraphidia brasiliensis</i> (Nel, Séméria and Martins-Neto, 1990)	Crato Formation, Brazil	Willmann 1994
		<i>Baissoptera brasiliensis</i> Oswald, 1990	Crato Formation, Brazil	Oswald 1990
		<i>Baissoptera pulchra</i> (Martins-Neto and Nel, 1992)	Crato Formation, Brazil	Engel 2002
	Alloraphidiidae	<i>Alloraphidia anomala</i> Ren, 1997	Beipiao, Liaoning, China	Ren 1997
	Baissopteridae	<i>Baissoptera euneura</i> Ren, 1997	Beipiao, Liaoning, China	Ren 1997
		<i>Baissoptera grandis</i> Ren in Ren et al., 1995	Beipiao, Liaoning, China	Ren et al. 1995
		<i>Baissoptera liaoningensis</i> Ren, 1994	Beipiao, Liaoning, China	Ren 1994
	Mesoraphidiidae	<i>Huaxiaraphidia sinensis</i> Hong, 1992a	Beipiao, Liaoning, China	Hong 1992a
		<i>Huaxiaraphidia shandongensis</i> Hong, 1992a	Beipiao, Liaoning, China	Hong 1992a
		<i>Mesoraphidia koreenensis</i> Engel et al., 2006	Southern Korea	Engel et al., 2006
		<i>Mesoraphidia phantosma</i> Engel et al., 2006	Southern Korea	Engel et al., 2006
		<i>Mesoraphidia amoena</i> Ren, 1997	Beipiao, Liaoning, China	Ren 1997
		<i>Mesoraphidia furcivenata</i> Ren in Ren et al., 1995	Beipiao, Liaoning, China	Ren et al. 1995
		<i>Mesoraphidia gaoi</i> (Ren, 1995)	Beipiao, Liaoning, China	Engel 2002
		<i>Mesoraphidia glossophylla</i> (Ren, 1997)	Beipiao, Liaoning, China	Engel 2002
		<i>Mesoraphidia longistimosa</i> (Ren, 1994)	Beipiao, Liaoning, China	Engel 2002
		<i>Mesoraphidia heteroneura</i> Ren, 1997	Beipiao, Liaoning, China	Ren 1997
		<i>Mesoraphidia obliquivenatica</i> (Ren, 1994)	Beipiao, Liaoning, China	Engel 2002
		<i>Mesoraphidia myrioneura</i> (Ren, 1997)	Beipiao, Liaoning, China	Engel 2002
		<i>Mesoraphidia polyphlebia</i> (Ren, 1994)	Beipiao, Liaoning, China	Engel 2002
		<i>Mesoraphidia shangyuanensis</i> (Ren, 1994)	Beipiao, Liaoning, China	Engel 2002
		<i>Mesoraphidia sinica</i> Ren, 1997	Beipiao, Liaoning, China	Ren 1997
		<i>Siboptera fornicata</i> (Ren, 1994)	Beipiao, Liaoning, China	Ren 1997
		<i>Xuraphidia liaoxiensis</i> Hong, 1992b	Kezuo, Liaoning, China	Hong 1992b
		<i>Kezuoraphidia kezuoensis</i> (Hong, 1992c)	Kezuo, Liaoning, China	Willmann 1994
			<i>Jilinoraphidia dalaziensis</i> Hong and Chang, 1989	Zhixian, Jilin province, China
		<i>Proraphidia gomezi</i> sp. nov.	Lithographic Limestone, Montsec, Spain	Gómez-Pallerola 1986; herein
		<i>Proraphidia hopkinsi</i> sp. nov.	Wealden Supergroup, Southern England	herein
		<i>Mesoraphidia</i> sp.	Purbeck Limestone Group, England	Clifford et al. 1994
	Inocelliidae	<i>Sinoiocellia liaoxiensis</i> Wang, 1987	Xiaoershihazi, China	Wang, 1987
	Alloraphidiidae	<i>Alloraphidia petrosa</i> Ponomarenko, 1988	Mongolia	Ponomarenko 1988
<i>Archeraphidia hosbayari</i> Ponomarenko, 1988		Mongolia	Ponomarenko 1988	
<i>Archeraphidia yakowlewi</i> Ponomarenko, 1988		Mongolia	Ponomarenko 1988	
<i>Pararaphidia deserta</i> (Ponomarenko, 1988)		Mongolia	Willmann 1994	
Baissopteridae	<i>Cretinocellia cellulosa</i> Ponomarenko, 1988	Mongolia	Ponomarenko 1988	
	<i>Cretaraphidiopsis bontsaganensis</i> (Ponomarenko, 1988)	Mongolia	Engel 2002	
	<i>Lugala longissima</i> (Ponomarenko, 1988)	Mongolia	Willmann 1994	
Alloraphidiidae	<i>Cretoraphidia certa</i> Ponomarenko, 1993	Romanovka, Russia	Ponomarenko 1993	
	<i>Alloraphidia asiatica</i> Ponomarenko, 1993	Baissa, Buryat, Russia	Ponomarenko 1993	
	<i>Archeraphidia baisensis</i> Ponomarenko, 1993	Baissa, Buryat, Russia	Ponomarenko 1993	
	<i>Pararaphidia vitimica</i> (Martynova, 1961)	Baissa, Buryat, Russia	Engel 2002	
Baissopteridae	<i>Baissoptera martinsoni</i> Martynova, 1961	Baissa, Buryat, Russia	Martynova 1961	

Age	Family	Species	Locality/Deposit	Reference
		<i>Baissoptera cellulosa</i> Ponomarenko, 1993	Baissa, Buryat, Russia	Ponomarenko 1993
		<i>Baissoptera elongata</i> Ponomarenko, 1993	Baissa, Buryat, Russia	Ponomarenko 1993
		<i>Baissoptera kolosnitsynae</i> Martynova, 1961	Baissa, Buryat, Russia	Martynova 1961
		<i>Baissoptera minima</i> Ponomarenko, 1993	Baissa, Buryat, Russia	Ponomarenko 1993
		<i>Baissoptera sibirica</i> Ponomarenko, 1993	Baissa, Buryat, Russia	Ponomarenko 1993
		<i>Creteraphidia macrocella</i> Ponomarenko, 1993	Baissa, Buryat, Russia	Ponomarenko 1993
		<i>Creteraphidia magna</i> Ponomarenko, 1993	Baissa, Buryat, Russia	Ponomarenko 1993
		<i>Creteraphidia reticulata</i> Ponomarenko, 1993	Baissa, Buryat, Russia	Ponomarenko 1993
	Mesoraphidiidae	<i>Baissoraphidia glossopteron</i> Ponomarenko, 1993	Baissa, Buryat, Russia	Ponomarenko 1993
		<i>Baissoraphidia orientalis</i> Ponomarenko, 1993	Baissa, Buryat, Russia	Ponomarenko 1993
		<i>Siboptera eurydictyon</i> Ponomarenko, 1993	Baissa, Buryat, Russia	Ponomarenko 1993
		<i>Siboptera medialis</i> Ponomarenko, 1993	Baissa, Buryat, Russia	Ponomarenko 1993
Upper Jurassic – Lower Cretaceous	Mesoraphidiidae	<i>Sinoraphidia viridis</i> Hong, 1982	Gansu, China	Hong 1982
Upper Jurassic	Mesoraphidiidae	<i>Mesoraphidia gobiensis</i> Ponomarenko, 1988	Mongolia	Ponomarenko 1988
		<i>Mesoraphidia grandis</i> Martynov 1925	Karatau, Kazakhstan	Martynov 1925
		<i>Mesoraphidia elongata</i> Martynov, 1925	Karatau, Kazakhstan	Martynov 1925
		<i>Mesoraphidia inaequalis</i> Martynov, 1925	Karatau, Kazakhstan	Martynov 1925
		<i>Mesoraphidia parvula</i> Martynov, 1925	Karatau, Kazakhstan	Martynov 1925
		<i>Mesoraphidia similis</i> Martynov, 1925	Karatau, Kazakhstan	Martynov 1925
		<i>Mesoraphidia pterostigmalis</i> Martynova, 1947	Karatau, Kazakhstan	Martynova 1947
		<i>Proraphidia turkestanica</i> Martynova, 1947	Karatau, Kazakhstan	Martynova 1947
Lower Jurassic	Mesoraphidiidae	<i>Metaraphidia confusa</i> Whalley, 1985	England	Whalley 1985
		<i>Metaraphidia vahldieki</i> Willmann, 1994	Germany	Willmann, 1994

Table 1. Extinct taxa of raphidiopterans known from the Jurassic and Cretaceous.

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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