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A new fossil genus and species of snakefly (Raphidioptera: Mesoraphidiidae) from Lower Cretaceous Lebanese amber, with a discussion of snakefly phylogeny and fossil history

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Abstract

Lebanoraphidia nana gen. et sp.n. is described from the Lower Cretaceous amber of Lebanon and represents the smallest known Raphidioptera. The new taxon is quite similar in its minute size, large compound eyes and wing venation to *Nanoraphidia electroburmica* (Mesoraphidiidae) from the Lower Cretaceous amber of Myanmar, as well as to '*Mesoraphidia*' *luzzii* from the Upper Cretaceous amber of New Jersey, and *Cantabroraphidia marcanoi* from the Lower Cretaceous El Soplao amber of Spain. For the species '*Mesoraphidia*' *luzzii* a new genus, *Grimaldiraphidia,* is erected, because it would otherwise render the genus *Mesoraphidia* paraphyletic. '*Mesoraphidia*' *durlstonenesis*, '*M.*' *gaoi*, '*M.*' *heteroneura*, '*M.*' *mitchelli*, '*M.*' *parvula* and '*M.*' *purbeckensis* are also transferred to this new genus *Grimaldiraphidia*. Four Cretaceous amber genera comprise minute specimens and represent a distinct clade within Mesoraphidiidae, for which a new tribe, Nanoraphidiini, is proposed. The phylogeny and fossil record of Raphidioptera is discussed and the suborders Priscaenigmatomorpha and Raphidiomorpha are supported. A revised definition and composition of Mesoraphidiidae (including *Cretinocellia*) is suggested. '*Siboptera*' *medialis* is transferred to the genus *Mesoraphidia*. The synonymy of Alloraphidiidae with Mesoraphidiidae is rejected and Alloraphidiinae is restored as separate subfamily that probably represents the sister group of Mesoraphidiinae. The genera *Caloraphidia*, *Styporaphidia* and *Ororaphidia* are transferred to a new subfamily Ororaphidiinae within Mesoraphidiidae. The genus *Metaraphidia* is excluded from Mesoraphidiidae and attributed to a new monotypic family Metaraphidiidae, which is considered as sister group of Neoraphidioptera (Raphidiidae+Inocelliidae) within the new taxon Euraphidioptera, which is the sister group to Mesoraphidiidae within the new taxon Raphidiformia. *Araripe raphidia rochai* is transferred to "Baissopteridae" that might rather be a paraphyletic grade of basal stem group representatives.

Keywords

Lebanoraphidia, *Grimaldiraphidia*, Nanoraphidiini, Mesoraphidiinae, Alloraphidiinae, Ororaphidiinae, Metaraphidiidae, "Baissopteridae", Euraphidioptera, Raphidiformia.

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Introduction

Several small raphidiopterans have recently been described from Cretaceous amber from New Jersey, Myanmar and Spain (Grimaldi 2000; Engel 2002; Pérez-de la Fuente et al. 2010), as well as from the Lower Cretaceous of Mongolia and Transbaikalia (Ponomarenko 1988, 1993), Korea (Engel et al. 2006), Spain and England (Jepson & Jarzembowski 2008; Jepson et al. 2009, 2011). They were all attributed to the extinct Mesozoic snakefly family Mesoraphidiidae. Here, we describe a further new genus and species from Lower Cretaceous amber of Lebanon, which actually represents the smallest snakefly currently known. The Lebanon amber was produced by kauri pines about 130 million years ago and ranks among the oldest known varieties of amber with fossil macro-inclusions (Schlee 1970; Azar 2000). The only previously known record of Raphidioptera from Lebanon amber was a fragment of a raphidiomorphan larva described by Perrichot and Engel (2007).

Materials and Methods

The morphological terminology of Raphidioptera follows Aspöck et al. (1991), and the taxonomy and phylogeny is expanded on the basis of Oswald (1990), Aspöck et al. (1991), Willmann (1994), Ponomarenko (2002), Engel (2002), Aspöck & Aspöck (2004), Grimaldi & Engel (2005) and Deflores & Nel (2006). The two type specimens have been embedded in two polished blocks of artificial resin for protection. The specimens were studied using a Leica M80 stereo microscope with 1.6 Plan Achromat lens, and drawings were made with a camera lucida. The macro photos have been made with a Leica DFC490 digital macro camera on a Leica Z16-Apo microscope with Synchroscopy AutoMontage software for focus stacking. All figure templates have been later edited with Adobe Photoshop CS3® image processing software.

Systematic Palaeontology

Lebanoraphidia gen.n.

Type species

Lebanoraphidia nana gen. et sp.n. by present original designation.

Diagnosis

Lebanoraphidia gen.n. is distinguished from the Mesozoic genera *Nanoraphidia* Engel, 2002, *Cantabroraphidia* Pérez-de la Fuente et al., 2010 and *Grimaldiraphidia* gen.n. by its very small size (forewing length <4 mm). It is distinguished from *Grimaldiraphidia* gen.n. and *Nanoraphidia* by the presence of 2 medial cells in the forewing (3 medial cells in *Grimaldiraphidia* gen.n., 1 medial cell in *Nanoraphidia*). *Lebanoraphidia* is distinguished from *Cantabroraphidia* as well as from *Nanoraphidia* by the following

characters: transverse head with eyes about 2 times as long as head posterior to eyes (eyes only slightly longer or as long as head posterior to eyes in *Cantabroraphidia* and *Nanoraphidia* respectively), ≥38 flagellomeres (only 20 or 26 flagellomeres in *Nanoraphidia* and *Cantabroraphidia*), r2 of forewing with one posterior cell immediately behind (two posterior cells in *Nanoraphidia* and *Cantabroraphidia*), arolium small or absent (arolium large in *Nanoraphidia* and *Cantabroraphidia*), and A2 not strongly arcuated (A2 strongly arcuated in *Nanoraphidia* and *Cantabroraphidia*).

Etymology

Named after Lebanon, the country of origin, and the Recent snakefly genus *Raphidia*.

Remarks

With a forewing length of less than 4 mm this new taxon represents the smallest known member of the order Raphidioptera.

***Lebanoraphidia nana* sp.n.** (Figs 1-16)

Diagnosis

This species is distinguished from other minute Cretaceous amber species by the characters listed in Table 1.

Etymology

The species name *nana* (Greek "nanos", meaning "dwarf") refers to the minute size.

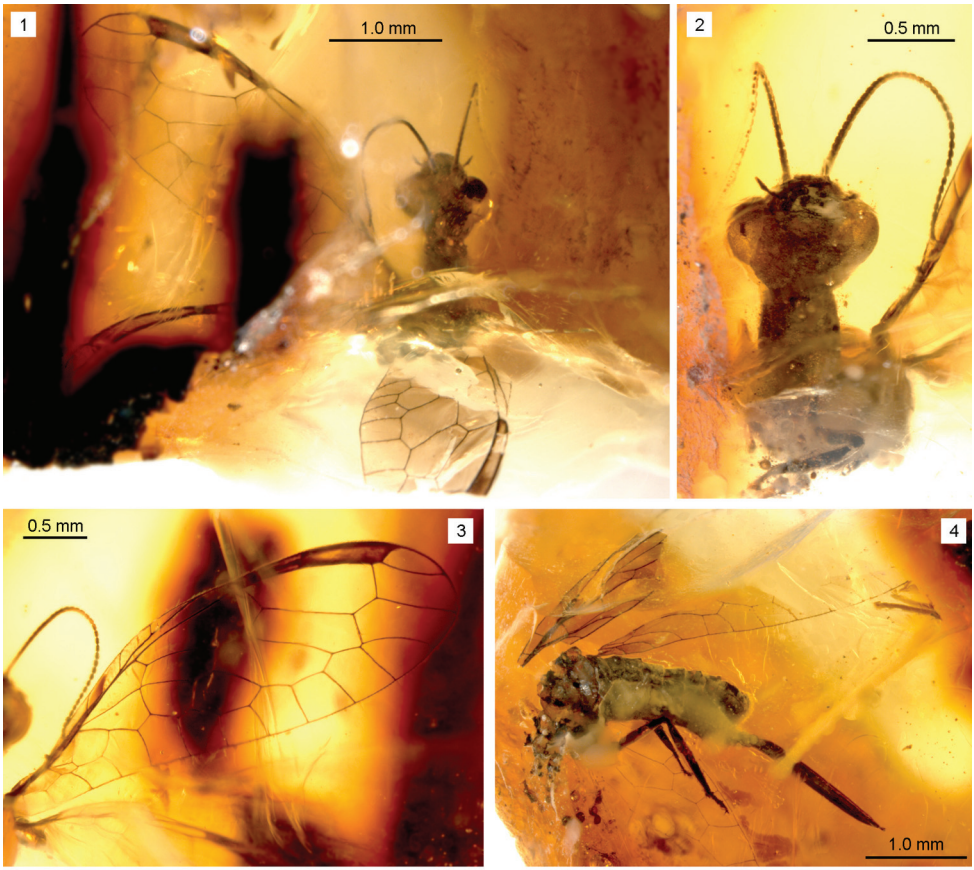
Description

Holotype. Head: transverse, rhomboidal, 0.76 mm long, 0.80 mm wide, compound eyes large, exophthalmic, about two times as long as head posterad posterior tangent of compound eyes (dorsal view), distance between inner margin of compound eyes 0.3 mm; ocelli not visible because of obfuscation by a "slimy" cover; maxillary palpus as long as width of compound eye (ventral view); Antennae: distance between antennal insertion about 0.1 mm, ≥ 38 flagellomeres with short setae, flagellomeres cylindrical, about 1.3 times as long as wide. Thorax: Pronotum length about 1 mm, width about 0.4 mm; Legs: only two incomplete legs present; Wings: left forewing complete, right forewing and left hind wing incomplete, right hind wing missing, forewing length=3.85 mm, width=1.28, stigma longer than either radial cell, without cross-veins, Sc terminating near middle of the wing, five costal cross-veins (c-sc), one sc-r cross-vein, veins at wing margins not apically bifurcate, two radial cells present with one posterior cell immediately behind, two medial cells present, M-CuA separation close to first cua-cup cross-vein, A2 straight, not arcuated proximally; hind wing length=3.2 mm, width approx. 1.2 mm, three radial cells present with one cell posterior r3, stigma about as long as r3. Abdomen: missing.

Table 1. Differential diagnosis of the minute raphidiopteran taxa hitherto known from Cretaceous amber (?=character state unknown)

	Lebanoraphidia nana sp.n.	*Cantabroraphidia marcanoi* Perez-de la Fuente et al. 2010	*Nanoraphidia electroburmica* Engel 2002	*Grimaldiraphidia luzzii* (Grimaldi 2000)
Head	transverse, rhomboidal	approx. quadrangular	ovoid	ovoid
Eyes	approx. 2× as long as head posterad eyes	slightly longer than head posterad eyes	nearly as long as head posterad eyes	?
Antenna	≥38 flagellomeres	26 flagellomeres	20 flagellomeres	23 flagellomeres
Pronotum	longer than head (approx. 0.25×)	subeaqual to head	subeaqual to head	as long as head
Tarsus	arolium small	arolium large	arolium large	?
Forewing	length 3.85 mm, width 1.28 mm	length 5.5 mm, width 1.8 mm	length 4.26 mm, width approx. 1.3 mm	length 6.13 mm, width approx. 1.8 mm
	5 costal cross-veins (c-sc)	4 costal cross-veins (c-sc)	5 costal cross-veins (c-sc)	5 costal cross-veins (c-sc)
	1 cell posterior r2	2 cells posterior r2	2 cells posterior r2	2 cells posterior r2
	2 medial cells	2 medial cells	1 medial cell	3 medial cells
	M-CuA separation close to cua-cup1	M-CuA separation closer to cua-cup2 than to cua-cup1	M-CuA separation near midpoint between cua-cup1 and cua-cup2	M-CuA separation close to cua-cup1
	A2 not arcuated	A2 strongly (?) arcuated	A2 strongly arcuated	A2 not arcuated
Hind wing	length 2.95 mm	?	length approx. 3.4 mm	length 5.3 mm
	1 cell posterior r3	?	2 cells posterior r3	2 cells posterior r3
	medial cell not divided	medial cell divided basad	medial cell not divided	medial cell divided basad
	MA and MP originate separately on R	?	MA and MP with common origin on R (?)	MA and MP originate separately on R
	CuA1+CuA2	CuA1+CuA2	CuA not branched	CuA1+CuA2
Abdomen	length 1.5 mm	crushed, length ?	crushed, length ?	?
	ovipositor 1.2× length of abdomen, straight	sex unknown	sex unknown	ovipositor 0.75× length of abdomen, curved gently upwards

Paratype. Head: missing; Thorax: incomplete, crushed; Legs*:* hind legs present, third tarsomere bilobed, claws non-toothed, arolium small (not visible); Wings*:* left and right forewing fragmentary, right hind wing almost complete, but anterior margin and base absent, radial cells as holotype, MA and MP originate separately on R, one medial cell present, medial cell not divided, two branches of CuA terminate at wing margin; Abdomen: length=1.5 mm; Female genitalia – Ovipositor straight, sword-like,



Figs 1–4. (1) *Lebanoraphidia nana* sp.n., holotype, photo of body in dorsal view. Scale bar=1 mm. (2) *Lebanoraphidia nana* sp.n., holotype, photo of head in ventral view. Scale bar=0.5 mm. (3) *Lebanoraphidia nana* sp.n., holotype, photo of left forewing in ventral view. Scale bar=0.5 mm. (4) *Lebanoraphidia nana* sp.n., paratype, photo of abdomen with ovipositor in lateral view. Scale bar=1 mm. This figure is published in colour in the online edition that can be accessed *via* http://www.brill.nl/ise

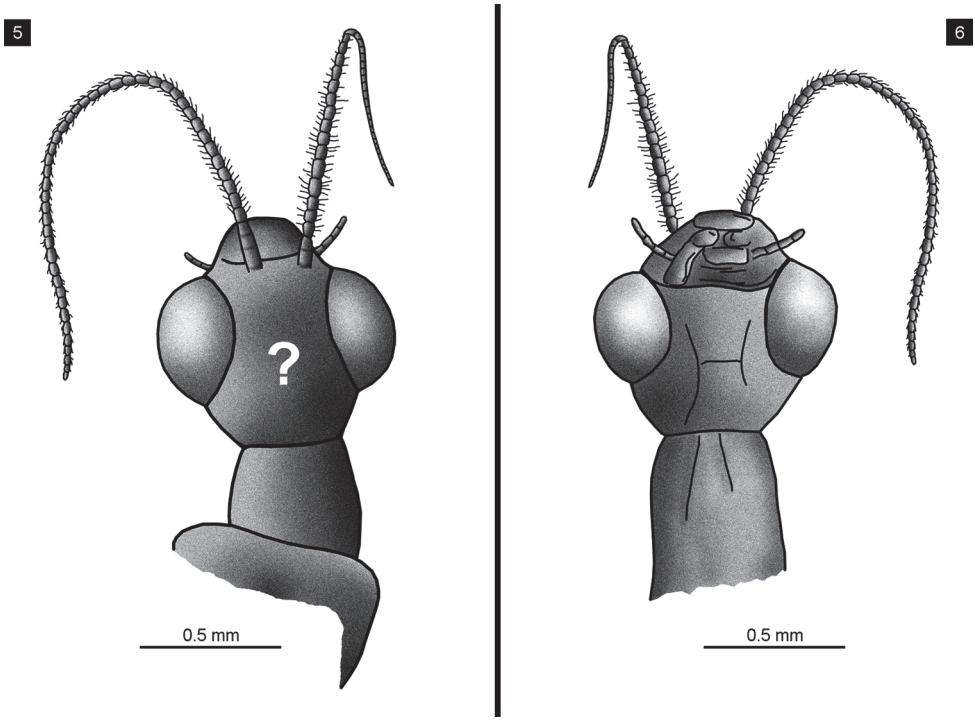
0.15 mm thick, 1.85 mm long. Because of the more or less identical dimension and visible venation of the wings, the paratype can be safely attributed to the same species as the holotype.

Type material

The holotype (SMNS LB-235-2) and the ♀ paratype (SMNS LB-235-1) are both deposited in the amber collection of the Staatliches Museum für Naturkunde Stuttgart in Germany.

Type locality

Jezzine, southern Lebanon.



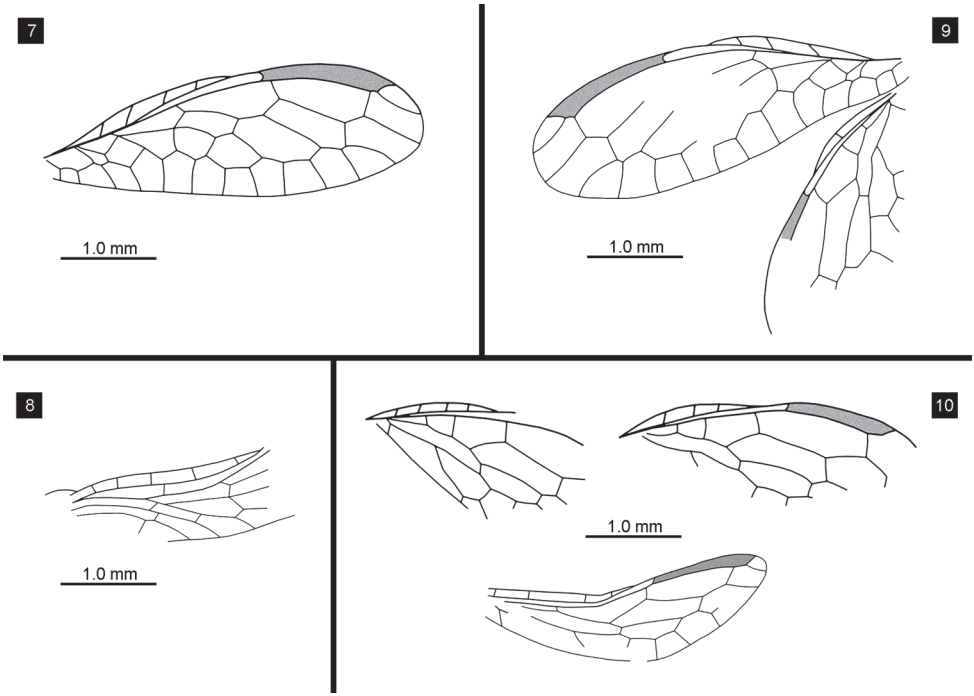
Figs 5–6. (5) *Lebanoraphidia nana* sp.n., holotype, head in dorsal view (ocelli not visible). Scale bar= 0.5 mm. (6) *Lebanoraphidia nana* sp.n., holotype, head in ventral view. Scale bar=0.5 mm.

Type stratum and age

Lebanese amber, Lower Cretaceous, Upper Neocomian (Barremian?) (Azar 2000).

Discussion

After having studied the complete available literature and the drawings of the wing venation of most genera and species of fossil Raphidioptera, our general impression is that the current classification is in great need of thorough revision. "Baissopteridae" and Mesoraphidiidae seem to be "wastebasket taxa" for fossil snakeflies from the Mesozoic. Drawings based on some Russian and especially Chinese fossils seem to be notoriously unreliable (e.g., suggested by the strange aberrant venation of *Sinoraphidia* Hong, 1982 and *Huaxiaraphidia* Hong, 1992, or the inconsistent drawing of stigmata with or without dividing cross-vein in some other taxa), so that the original type material would have to be revised. New fossil genera and species have often been attributed to certain families solely on the basis of superficial similarities with other fossils that themselves had been previously attributed to those families without sufficient or any evidence. Furthermore, new synonymies and re-classifications have recently been

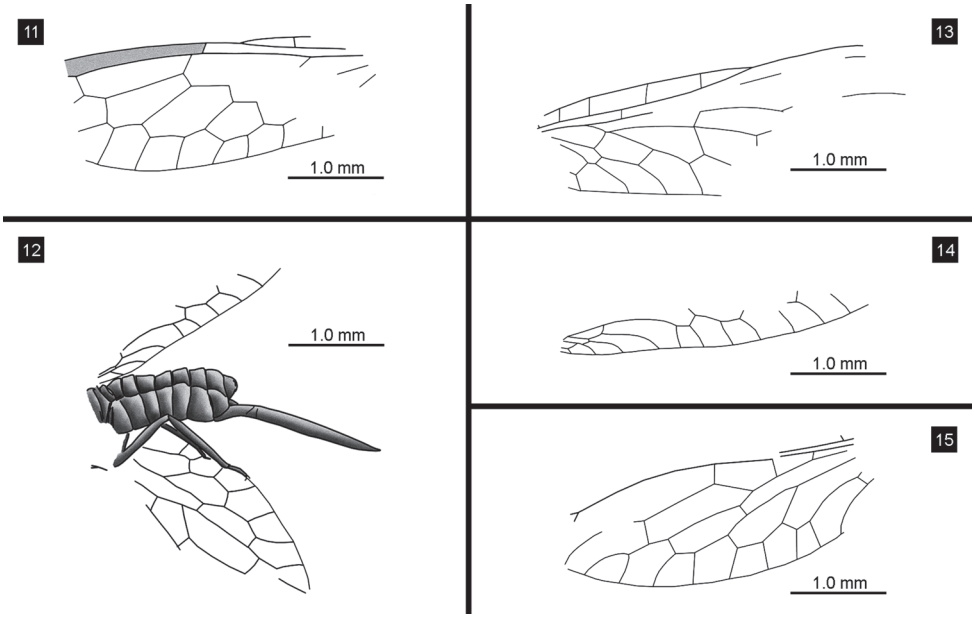


Figs 7–10. (7) *Lebanoraphidia nana* sp.n., holotype, wing venation, left forewing in ventral view. Scale bar=1 mm. (8) *Lebanoraphidia nana* sp.n., holotype, left forewing in ventral view from different angle (note the basal sc-r cross-vein that is invisible from other angles). Scale bar=1 mm. (9) *Lebanoraphidia nana* sp.n., holotype, left pair of wings in dorsal view. Scale bar=1 mm. (10) *Lebanoraphidia nana* sp.n., holotype, left hind wing from different views and angles. Scale bar=1 mm.

proposed without any discussion of arguments or without proper phylogenetic analysis. Unfortunately, the necessary large revision of all fossil Raphidioptera exceeds the scope of our paper. We, therefore, restrict our phylogenetic considerations to the following brief notes (we compared the fossil taxa with figures of the wing venation and head shape of all Recent species in Aspöck et al., 1991, and established the character polarity of mesoraphidiid fossils in using Recent snakeflies and the basal Priscaenigmatidae and "Baissopteridae" as outgroups).

Raphidioptera Handlirsch, 1908

Some of the characters that are diagnostic and synapomorphic for Recent snakeflies, e.g., the elongate prothorax and hypertrophied ovipositor, are also known from the fossil "Baissopteridae" and Mesoraphidiidae, but are not preserved in the most basal stem group representatives. Therefore, they could be autapomorphies of Raphidiomorpha rather than of Raphidioptera. Three autapomorphies that support the monophyly of Raphidioptera including the most basal Priscaenigmatidae are listed in Fig. 17.



Figs 11–15. (11) *Lebanoraphidia nana* sp.n., holotype, right forewing in ventral view. Scale bar=1 mm. (12) *Lebanoraphidia nana* sp.n., paratype, abdomen with ovipositor in lateral view. Scale bar=1 mm. (13) *Lebanoraphidia nana* sp.n., paratype, fragment of right forewing in dorsal view. Scale bar=1 mm. (14) *Lebanoraphidia nana* sp.n., paratype, fragment of left forewing in ventral view. Scale bar=1 mm. (15) *Lebanoraphidia nana* sp.n., paratype, right hind wing in ventral view. Scale bar=1 mm.

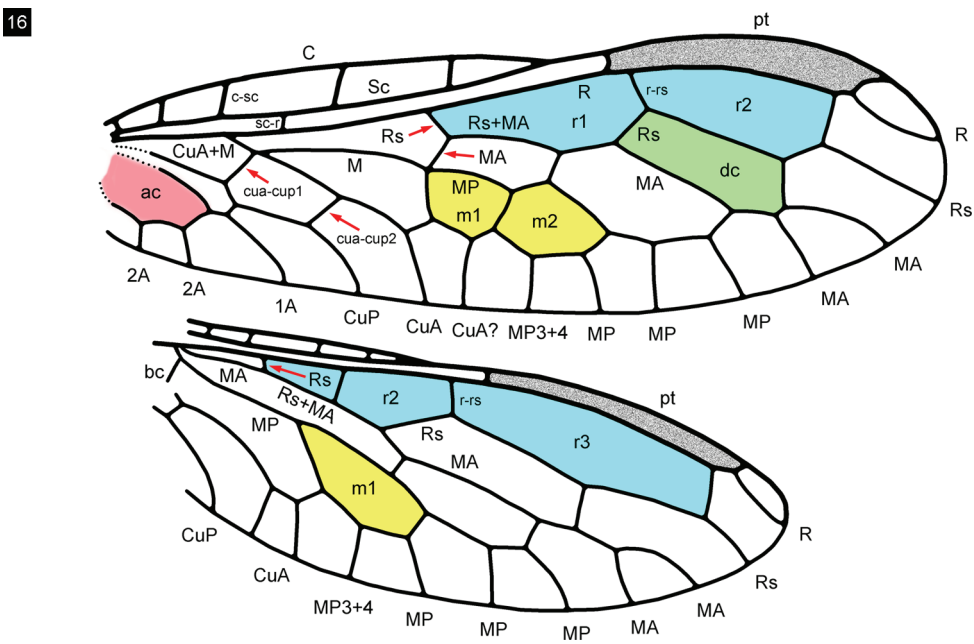


Fig. 16. *Lebanoraphidia nana* sp.n., reconstructed venation of fore- and hind wing, with a revised interpretation of the wing venation of Raphidioptera. This figure is published in colour in the online edition that can be accessed *via* http://www.brill.nl/ise

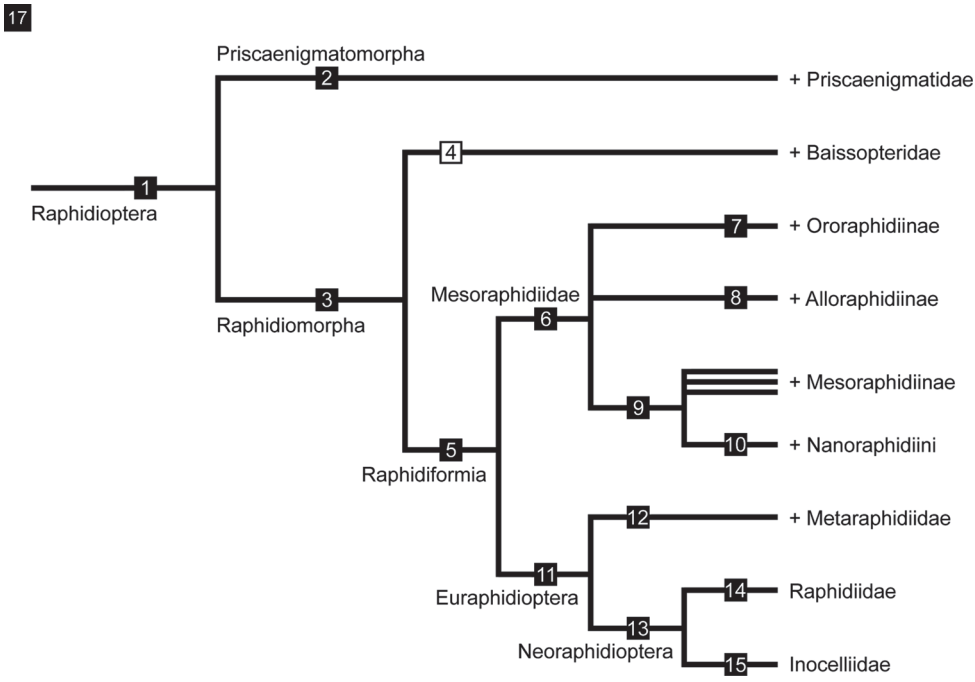


Fig. 17. Phylogenetic tree of fossil and extant Raphidioptera families. List of synapomorphies: (1) Raphidioptera: MP developed as oblique veinlet (bc) between MA and CuA in hind wing, elongate open cell between the basal parts of RS and M/MA in hind wing, stigma at least weakly developed; (2) Priscaenigmatomorpha: fusion of Sc with RA at least in forewing, very long and narrow cell between RA and RS, similar cell pattern in distal half of wing, MP unbranched or only apically forked in forewing; (3) Raphidiomorpha: more distinct stigma, parallel course of CuA and CuP, vein Sc shorter; (4) "Baissopteridae": only symplesiomorphies, possibly paraphyletic; (5) Raphidiformia taxon n.: reduction of number of cells and of distal branchings of veins; (6) Mesoraphidiidae: typical triangular arrangement of three median cells (m1 and m2 above, and m3 in the middle below them) in forewing; (7) Ororaphidiinae subfam.n.: long stigma with diffuse basal margin; (8) Alloraphidiinae stat. rest.: stigma very short, with distinct basal margin (transverse vein) and distal margin (oblique vein), traversed by a single oblique veinlet; apparent triadic branching of R, M, and CuA in the forewing; (9) Mesoraphidiinae: stigma without cross-veins (convergent to Inocelliidae); Sc ends at about midwing position; (10) Nanoraphidiini trib.n.: RS distally unbranched or only with single apical fork, stigma very long, postorbital region of head shortened, ovipositor short and conspicuously strong (?), minute size of body and wings; (11) Euraphidioptera taxon n.: fused origins of MA and MP in the hind wing; (12) Metaraphidiidae fam.n.: no cross-veins between CuA and CuP in forewing; (13) Neoraphidioptera: free base of RS shifted to midwing position in forewing; (14) Raphidiidae: cua-cup1 cross-vein originates on R instead of M-Cu in forewing, AA fused to CuP in hind wing, cross-vein that forms the basal margin of the stigma is shifted distally midway between the end of Sc and the wing apex; (15) Inocelliidae: hind wing arc (=MP3+4) extremely oblique (not yet in Electrinocellia), forewing with three radial cells r1, r2, and r3 (not reaching apical wing margin), in forewings the second cross-vein between Sc and RA is close to the end of Sc (homologous to the basal margin of the stigma in Mesoraphidiidae, thus the stigma is only dark pigmented in the distal half, but transparent in the basal half), RA apically unbranched in forewing, MA originates further basal and as transverse veinlet between M and R in forewing, stigma not divided by cross-vein (convergent to Mesoraphidiidae).

Priscaenigmatomorpha Engel, 2002 stat. rest.

Aspöck and Aspöck (2004) rejected the re-classification by Engel (2002) as unfounded, and considered neither the monophyly of Priscaenigmatomorpha and Priscaenigmatidae Engel, 2002, nor their attribution to Raphidioptera as established. This rejection was insufficiently grounded on arguments concerning the "desirable definition" of the order Raphidioptera (short Sc), and partly based on the circumstance that only two of the suggested autapomorphies of Raphidioptera could be preserved in petrified fossils (Sc ending on costal margin basal of apex, female ovipositor distinctly elongated), but are absent or invisible in the two Jurassic genera *Priscaenigma* Whalley, 1985 and *Hondelagia* Bode, 1953. Even though the visible characters do hardly allow a safe attribution of *Priscaenigma* to Raphidioptera based on convincing synapomorphies, the genus *Hondelagia* clearly shares previously overlooked synapomorphic states of the hind wing venation with Raphidioptera, such as the MP developed as oblique veinlet between MA and CuA, and the elongate open cell between the basal parts of RS and M/MA. Willmann (1994) suggested four putative synapomorphies of *Hondelagia* with other Raphidioptera under exclusion of *Priscaenigma*, which would imply the paraphyly of Priscaenigmatidae sensu Engel (2002). The first character (reduction of number of cells between R and RS) is weak because some "Baissopteridae" have six radial cells in the forewing, compared to 6–7 in *Priscaenigma*, and the other three characters are of rather dubious significance as well. We, therefore, do not consider the paraphyly of Priscaenigmatidae to be convincingly demonstrated. *Priscaenigma* and *Hondelagia* share in both wings a very similar cell pattern of the wing venation in the distal half of wing, as well as the very long cell between RA and RS, and a derived fusion of Sc with RA, which renders a close relationship very likely. Both genera differ from the more modern Raphidioptera in a somewhat longer vein Sc (symplesiomorphy) that fuses with RA (putative synapomorphy) instead of the costal margin. We, therefore, tentatively support the re-classification of Engel (2002) and retain the suborders Priscaenigmatomorpha and Raphidiomorpha, as well as the family Priscaenigmatidae (contra Willmann 1994; Ponomarenko 2002; Aspöck & Aspöck 2004).

Raphidiomorpha Engel, 2002

All fossil and Recent raphidiopterans, except *Priscaenigma* and *Hondelagia*, share a more distinct stigma and a parallel course of CuA and CuP (synapomorphy), and a shorter vein Sc (synapomorphy) that fuses with the costal margin (symplesiomorphy).

"Baissopteridae" Martynova, 1961

The family "Baissopteridae" is not supported by synapomorphies. We concur with Willmann (1994) that it most probably is a paraphyletic grade of basal stem group representatives of Raphidioptera. However, the four characters suggested by Willmann (1994) as evidence for the paraphyly of "Baissopteridae", like many of the other characters in his analysis, are rather weak and homoplastic. In the absence of a proper phylogenetic re-evaluation of the relationship of all included taxa of "Baissopteridae"

we here refrain from any change in classification and composition of this fossil family. Because *Arariperaphidia rochai* Martins-Neto & Vulcano, 1989, previously considered as Raphidioptera incertae sedis, shares with some "Baissopteridae" (e.g., *Baissoptera grandis* Ren, 1995, *B. euneura* Ren, 1997 and *B. brasiliensis* Oswald, 1990) the typical pattern of short cells near the wing apex, this taxon is here transferred to "Baissopteridae" and the genus *Arariperaphidia* is considered as a subjective junior synonym of *Baissoptera* Martynova, 1961, because there are no distinguishing characters preserved.

Raphidiformia taxon n.

Ororaphidiinae subfam.n., Alloraphidiinae, Mesoraphidiinae, and Metaraphidiidae fam.n. share with Neoraphidioptera a reduction of the number of cells and of the distal branchings of veins as putative synapomorphies in the wing venation.

Mesoraphidiidae Martynov, 1925 sens.n.

The six characters given in the original diagnosis of the family Mesoraphidiidae by Martynov (1925) were rightfully criticized by Willmann (1994). Nevertheless, we also reject the characters suggested by Willmann (1994) as putative evidence for the paraphyly of Mesoraphidiidae as unconvincing, because they only include a few homoplastic minor features of the wing venation, and are partly based on dubious or even clearly incorrect interpretations of the wing venation (Engel 2002).

Ororaphidiinae subfam.n., Alloraphidiinae, Mesoraphidiinae (including *Cretinocellia* Ponomarenko, 1988) and *Iberoraphidia* Jepson et al., 2011 share a typical triangular arrangement of three median cells (m1 and m2 above, and m3 in the middle below them) in the forewing as putative synapomorphy in the ground plan (secondarily reduced in some genera of Nanoraphidiini, who only have 1–2 median cells), because this state is absent in all Priscaenigmatidae, "Baissopteridae" and Recent snakeflies. They also share with "Baissopteridae" the separate origins of MA and MP on R in hind wings, which obviously represents a symplesiomorphy.

Ororaphidiinae subfam.n. (within Mesoraphidiidae)

Type genus

Ororaphidia Engel & Ren, 2008.

Diagnosis

Very long stigma with diffuse basal margin (apomorphy), divided by 1-2 cross-veins (plesiomorphy).

Remarks

The two genera *Ororaphidia* and *Styporaphidia* were recently described as Raphidioptera familia incertae sedis by Engel & Ren (2008). Because they lack the autapomorphies

of Alloraphidiinae as well as those of Mesoraphidiinae, and are quite similar to each other (esp. hind wings are nearly identical except for the apical branchings of RS and MA), they are here classified in a new subfamily within Mesoraphidiidae.

We reject the synonymy of *Caloraphidia* Ren, 1997 with *Mesoraphidia*, because *C. glossophylla* Ren, 1997 shares neither of the two autapomorphies of Mesoraphidiinae, and is here tentatively transferred to Ororaphidiinae subfam.n., because of the similar venation, even though a position at the very base of Alloraphidiinae or Mesoraphidiinae cannot be excluded.

Alloraphidiinae Carpenter, 1967 stat.rest. (within Mesoraphidiidae)

The subfamily Alloraphidiinae is characterized by the two putative autapomorphies listed for Fig. 17. These two characters are also shared by *Archeraphidia* Ponomarenko, 1988 and by *Pararaphidia* Willmann, 1994, which are, therefore, correctly placed in Alloraphidiinae (contra Willmann, 1994). The very elongate and slender shape of the wing in *Alloraphidia dorfi* Carpenter, 1967, correlated with a very short Sc, is absent from most other Alloraphidiinae and clearly does not belong to the ground plan characters of this family. Because of the plesiomorphic presence of a cross-vein in the stigma, that is absent in Mesoraphidiinae, we reject the proposed synonymy of these two families and restore Alloraphidiinae as a distinct subfamily within Mesoraphidiidae, most probably representing the sister group of Mesoraphidiinae s.str. (including *Cretinocellia*, excluding *Metaraphidia*).

Mesoraphidiinae Martynov, 1925 sensu n.

This subfamily includes the genera *Baisoraphidia* Ponomarenko, 1993, *Cantabroraphidia* Pérez-de la Fuente et al., 2010, *Cretoraphidia* Ponomarenko, 1993, *Cretinocellia* Ponomarenko, 1988, *Grimaldiraphidia* gen.n., *Huaxiaraphidia* Hong, 1992, *Jilinoraphidia* Hong & Chang, 1989, *Kezuoraphidia* Willmann, 1994, *Lebanoraphidia* gen.n., *Mesoraphidia* Martynov, 1925 s.str., *Nanoraphidia* Engel, 2002, *Proraphidia* Martynova, 1947, *Siboptera* Ponomarenko, 1993 (=*Liaoraphidia* Ren, 1994), *Sinoraphidia* Hong, 1982, *Xuraphidia* Hong, 1992, *Xynoraphidia* Ren, 1997, and *Yanoraphidia* Ren, 1995. These genera share two derived similarities as putative synapomorphies (see Fig. 17).

Neither of these two character states is shared by *Metaraphidia confusa* Whalley, 1985 and *M. vahldieki* Willmann, 1994, who share the fused origin of hind wing MA and MP with crown-group Raphidioptera (=Neoraphidioptera) as putative synapomorphy with the latter. Therefore, the genus *Metaraphidia* is here excluded from Mesoraphidiidae and transferred to a new monotypic family Metaraphidiidae. However, both characters are synapomorphically shared by *Cretinocellia cellulosa* Ponomarenko, 1988 which was previously classified in "Baissopteridae", but is here transferred as the most basal genus to Mesoraphidiinae.

The synonymy of *Phiradia* and *Xynoraphidia* with *Mesoraphidia* as proposed by Engel (2002) is well justified, because the type species have a nearly identical wing

venation. The validity of some of the other genera of Mesoraphidiidae (espically from Russia and China, see discussion above) is rather doubtful, and we concur with Engel (2002) that a thorough revision will probably demonstrate their synonymy with *Mesoraphidia* or *Baisoraphidia*. The separate genus *Siboptera* is at least justified by a typical (probably autapomorphic) pattern of the cells in the wing venation. However, the species '*Siboptera*' *medialis* Ponomarenko, 1993 is here transferred to the genus *Mesoraphidia*, because the wing venation lacks the characteristic and unique pattern of *Siboptera fornicata* (Ren, 1994) and *S. eurydictyon* Ponomarenko, 1993, and mostly resembles that of *Mesoraphidia grandis* Martynov, 1925.

Nanoraphidiini trib.n. (within Mesoraphidiinae)

Type genus

Nanoraphidia Engel, 2002.

Other included genera

Lebanoraphidia, *Grimaldiraphidia* gen.n. and *Cantabroraphidia.*

Diagnosis

The new species Lebanoraphidia nana gen. et sp.n. shares with the other three small Cretaceous amber taxa (*Nanoraphidia electroburmica* Engel, 2002, *Grimaldiraphidia luzzii* (Grimaldi, 2002) and *Cantabroraphidia marcanoi* Pérez-de la Fuente et al., 2010) several diagnostic synapomorphies that are listed in Fig. 17.

Remarks

The polarity of the synapomorphic character states of the four nanoraphidiine genera is established by the different condition that is equally developed in the more primitive fossil "Baissopteridae" and the modern Raphidiidae and Inocelliidae. Some of the proposed synapomorphies (e.g., reduced branchings of RS) may be related to small size and therefore cannot be considered as strong evidence.

The short and conspicuously strong ovipositor (instead of long and thin) is currently only known from the two new genera *Lebanoraphidia* and *Grimaldiraphidia*. A comparison of the ovipositor size of some representatives of Recent Raphidioptera with that of the Cretaceous amber specimens suggests that the ovipositor of the fossils is only ≤13-times as long as wide, whereas in Recent Raphidioptera it is about 20-times as long as wide. It is also long and thin in "Baissopteridae". Unfortunately, the ovipositor is not yet known from many other Mesoraphidiidae.

'*Mesoraphidia*' *luzii* Grimaldi, 2000 shares all synapomorphies of Nanoraphidiini trib.n. and therefore has to be removed from the genus *Mesoraphidia* to avoid its paraphyly. Consequently, we here erect *Grimaldiraphidia* gen.n. as new genus.

***Grimaldiraphidia* gen.n.**

Type species

Grimaldiraphidia luzii (Grimaldi, 2000) by present designation.

Other included species

Several species that were previously classified in the genus *Mesoraphidia*' ('*M.*' *durlstonensis* Jepson et al., 2009, '*M.*' *gaoi* (Ren, 1995) '*M.*' *heteroneura* Ren, 1997, '*M.*' *mitchelli* Jepson et al., 2009, '*M.*' *parvula* Martynov, 1925, and '*M.*' *purbeckensis* Jepson et al., 2009) also share the synapomorphic characters of Nanoraphidiini trib.n. as well. To avoid a paraphyletic genus *Mesoraphidia* these species are here transferred to the genus *Grimaldiraphidia* gen.n., with which they share the symplesiomorphic presence of three median cells in the forewing.

Diagnosis: This new genus can be easily distinguished from the other three genera within Nanoraphidiini trib.n. by the presence of three median cells in the forewing; for further characters see diagnosis of the type species in Grimaldi (2000).

Etymology: Named after Dr David Grimaldi (AMNH) and the genus name *Raphidia*.

Euraphidioptera taxon n.

The fossil genus *Metaraphidia* (previously classified within Mesoraphidiinae) and the two extant families Raphidiidae and Inocelliidae synapomorphically share the fused origins of MA and MP in the hind wing. For this clade the new taxon Euraphidioptera is here proposed.

Metaraphidiidae fam.n.

Type genus

Metaraphidia Whalley, 1985; monotypic.

Diagnosis

Forewing: stigma divided by two cross-veins (plesiomorphy); A2 and A3 not fused (plesiomorphy); no cross-veins between CuA and CuP (apomorphy).

Remarks

Metaraphidia is here excluded from Mesoraphidiinae for the reasons mentioned above, and recognized as sister-group of Neoraphidioptera.

Neoraphidioptera Engel, 2007 (=Raphidioidea Latreille, 1810)

Raphidiididae Latreille, 1810 and Inocelliidae Navás, 1913 share several symplesiomorphic character states, such as Sc ends distal of midwing position, Y-shaped vein

between MA and MP (branched in Raphidiidae, unbranched in Inocelliidae), and CuA is apically branched in forewings. However, they also share at least one potential synapomorphy (see Fig. 17). The other two putative synapomorphies listed by Willmann (1994: 185) could not be confirmed by us, and rather have to be considered as dubious or incorrect.

Aspöck and Aspöck (2004) only provided two body characters as autapomorphies of Raphidiidae and Inocelliidae respectively, which are hardly visible in fossils (except amber inclusions). Fossil Raphidiidae and Inocelliidae can be recognized based on the putative wing venational autapomorphies listed in Fig. 17. Furthermore, Raphidiidae is of course characterized by a stigma that is divided by a cross-vein, but this clearly seems to be a retained plesiomorphic state that is also present in many fossil groups like "Baissopteridae" and Alloraphidiinae.

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