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Early Cretaceous Snakefly Larvae in Amber from Lebanon, Myanmar, and France (Raphidioptera)

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ABSTRACT

Snakefly (Raphidioptera) larvae are newly documented from the Early Cretaceous ambers of Lebanon, Myanmar (Burma), and France. Previously only two Cretaceous larvae had been documented, one in Late Cretaceous (Turonian) amber from New Jersey and another in Early Cretaceous (Albian) amber from Myanmar. The specimens discussed herein are likely representative of the extinct family Mesoraphidiidae, but definitive familial assignment is currently not possible. The new fossil material is described and placed into context with the known larval morphology of modern and fossil species, as well as with the geological history of the order as documented by the remains of adults.

RÉSUMÉ

De nouvelles larves de raphidioptères sont mentionnées dans les ambres du Crétacé inférieur du Liban, du Myanmar (Birmanie) et de France. Seules deux larves crétacées avaient été signalées jusqu'à présent, dans l'ambre crétacé supérieur (Turonien) du New Jersey et l'ambre crétacé inférieur (Albien) du Myanmar. Les spécimens discutés ici appartiennent probablement à la famille fossile Mesoraphidiidae, mais une attribution familiale certaine demeure actuellement impossible. Le nouveau matériel fossile est décrit et placé en regard de la morphologie des espèces modernes et fossiles, ainsi que de l'histoire géologique de l'ordre tel que documenté par les restes d'adultes.

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INTRODUCTION

Raphidioptera, or snakeflies, are presently classified into six families, four of which are extinct and known only from the Mesozoic. The families Alloraphidiidae Carpenter, Baissopteridae Martynova, and Mesoraphidiidae Martynov are known exclusively from the Jurassic and Cretaceous, whereas the Inocelliidae and Raphidiidae comprise all extant and some Tertiary species (Engel, 2002). Three other fossil families from the Cretaceous of China—Huaxiaraphidiidae Hong, Jilinoraphidiidae Hong and Chang, and Sinoraphidiidae Hong—are now considered synonyms of Mesoraphidiidae (Engel, 2002). The last family recognized, Priscaenigmatidae Engel, is segregated into a separate, basal suborder in some classifications and its attribution to Raphidioptera remains controversial (e.g., Willmann, 1994; Ponomarenko, 2002). This family contains only the enigmatic genera *Priscaenigma* Whalley and *Hondelagia* Bode from the Early Jurassic of Europe. Most recently, Aspöck and Aspöck (2004) dismissed the priscaenigmatids from the order since these fossils do not exhibit the entire suite of apomorphies in forewing venation that are used to define higher snakeflies. However, as noted by Engel (2002) and Grimaldi and Engel (2005), priscaenigmatids are likely stem-group Raphidioptera as evidenced by the hind-wing venation and would, therefore, not be expected to possess the complete suite of snakefly apomorphies as defined solely on the basis of more modern species. For now, the priscaenigmatids remain puzzling and it is greatly hoped that more complete material will eventually be recovered. A catalogue of all described fossil snakeflies was provided by Engel (2002) to which should be added *Sinoinocellia liaoxiensis* Wang (1987) and five fossils described subsequently from the Eocene-Oligocene of Florissant (Engel, 2003), in middle Eocene Baltic amber (Aspöck and Aspöck, 2004), and the Early Cretaceous of southern Korea (Engel et al., 2006). Table 1 summarizes the current classification of the order as well as the documented geological ranges of the included lineages.

Although adult snakeflies are uncommon, their immature stages are exceptionally rare in the fossil record, with specimens previously known only as inclusions in amber from the middle Eocene of the Baltic region (Hagen *in* Pictet-Baraban and Hagen, 1856; Weidner, 1958; Weitschat and Wichard, 1998) and two in amber from the Cretaceous (Grimaldi, 2000; Engel, 2002). Herein we provide descriptions of the remains of immature snakeflies preserved in Early Cretaceous amber from Lebanon (Neocomian, perhaps Barremian), northern Myanmar (Late Albian), and southwestern France (Late Albian). Several of the specimens are preserved only by their head capsules, while in two cases a single individual, in French and Burmese amber respectively, also preserves portions of the prothorax. Despite the fragmentary nature of some of the material, the

TABLE 1
Classification and Geological Distribution of Raphidioptera (updated from Engel, 2002)

Order RAPHIDIOPTERA Navás	
Suborder †PRISCAENIGMATOMORPHA Engel	
Family †Priscaenigmatidae Engel	Liassic
Suborder RAPHIDIOMORPHA Engel	
Family †Mesoraphidiidae Martynov	Liassic-Turonian
Family †Baissopteridae Martynova	Oxfordian-Cenomanian
Family †Alloraphidiidae Carpenter	Hauterivian-Cenomanian
Infraorder Neoraphidioptera Engel	
Family Raphidiidae Latreille	
Subfamily †Succinoraphidiinae Aspöck & Aspöck	Eocene
Subfamily Raphidiinae Latreille	Eocene-Holocene
Family Inocelliidae Navás	
Subfamily †Electrinocelliinae Engel	Eocene
Subfamily Inocelliinae Navás	Eocene-Holocene

high fidelity of preservation in amber permits a detailed description of the cephalic structures. Furthermore, characters of the head capsule alone permit positive identification as Raphidioptera (see Discussion, below). While previously the specimen reported by Engel (2002) in Burmese amber was the oldest immature snakefly in amber (other immatures are newly described from these deposits herein, see below), the specimen from Lebanon is now the oldest known snakefly larva.

For the descriptions we follow the format and terminology of Aspöck et al. (1991) and Engel (2002).

GEOGRAPHICAL AND GEOLOGICAL SETTING

Two specimens (see figs. 1–2) were excavated from the deposit of Archingeay/Les-Nouillers in Charente-Maritime (southwestern France), which already provided numerous fossils, principally insects (Perrichot, 2004, 2005; Perrichot et al., 2007). The amber is derived from alternating layers of estuarine or deltaic fine sand and clay containing mixed fragments of fossil plants (cuticles and lignitic wood). These amber-bearing strata were dated as latest Albian (ca. 100 Ma) by palynological studies (Néraudeau et al., 2002; Dejax and Masure, 2005). The corresponding paleoenvironment is estimated to have been a subtropical forest in estuarine or mangrove-like context, under a global warm-and-wet climate but with possible dry periods (Perrichot, 2004, 2005).

The densely fossil-packed Burmese amber has long been considered of Tertiary origin but was recently confirmed to be of middle Cretaceous age (reviewed in Zherikhin and Ross, 2000; Grimaldi et al., 2002; Cruickshank and Ko, 2003). The deposit is of Late Albian age (ca. 100 Ma) and was produced in a warm, moist tropical paleoclimate and with the most southerly paleolatitude of the three deposits discussed herein (Grimaldi et al., 2002).

The Lebanese specimen is fossilized in the Neocomian amber of Jezzine, which was, similar to the French amber, deposited in a deltaic plain under a tropical to subtropical climate (Azar, 2000).

The occurrence of these snakeflies in tropical or subtropical forests further attests to the fact that in the Cretaceous and Tertiary periods, Raphidioptera were not as climatically restricted as they are today. Although the order is today restricted to temperate to cold-temperate habitats or to high elevations where milder climates occur in otherwise warmer regions (e.g., some northern mountains of Central America), in the past snakeflies were found in a diversity of habitats and biogeographic regions (e.g., Engel, 1995, 2002).

SYSTEMATIC PALEONTOLOGY

Order RAPHIDIOPTERA Navás

French Specimens

Mesoraphidiidae? indet.

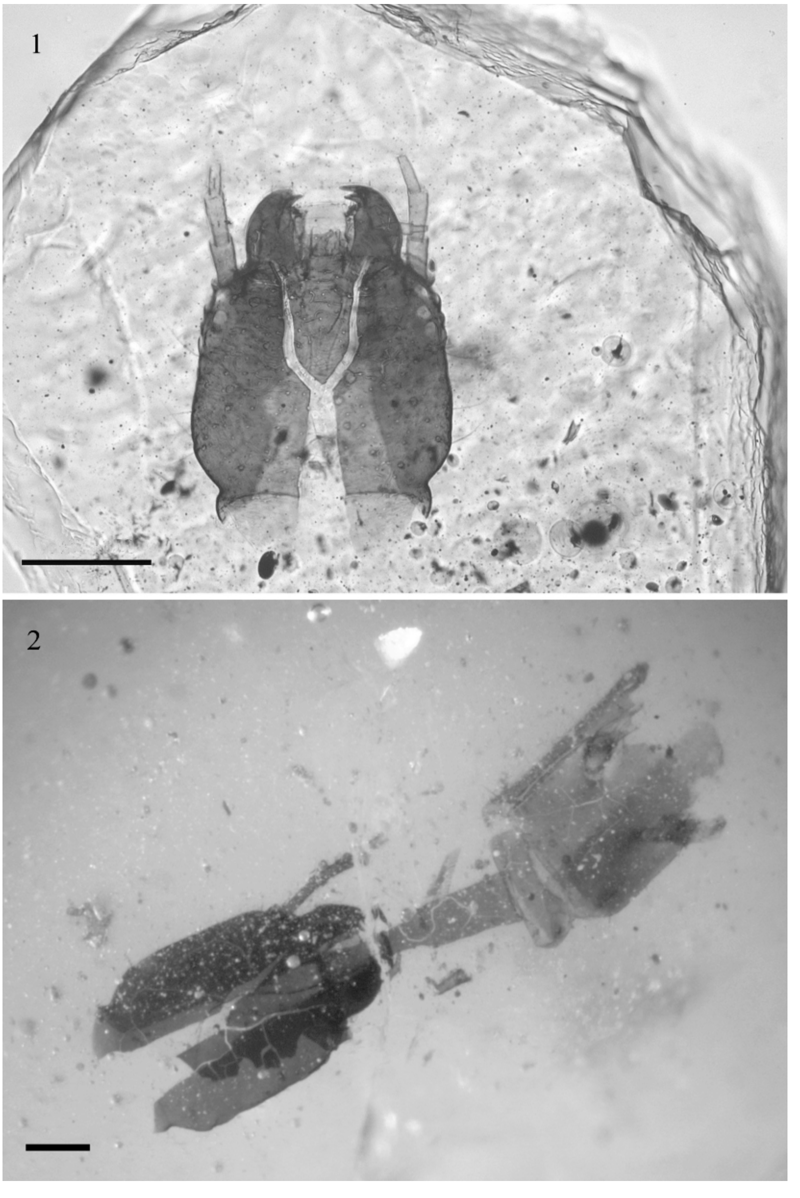
Figures 1–4

Material examined: Larval snakefly head capsule; MNHN-ARC-265.6 (figs. 1, 3); deposited in the Laboratoire de Paléontologie, Muséum national d'histoire naturelle, Paris, France.

Larval snakefly head capsule with prothoracic fragments; MNHN-ARC-328.4 (figs. 2, 4); deposited in the Laboratoire de Paléontologie, Muséum national d'histoire naturelle, Paris, France.

Occurrence: Archingeay/Les-Nouillers, Charente-Maritime, southwestern France; Early Cretaceous, Uppermost Albian (Néraudeau et al., 2002).

Description: **ARC-265.6.** Head slightly elongate, 0.4 mm in length (excluding mandibles), 0.3 mm in width; six stemmata disposed in circle at base of antenna (fig. 3); ocelli absent; seven fine, rather short setae on lateral margins of head; coronal ecdysial cleavage line complete, forking at about head midlength (fig. 3) (its fracturing and the separation of the head from other body sclerites suggest that this was a cast exuvium). Antennae short, about one-half length of head (ratio "antenna length/head length" = 0.625), with three cylindrical articles of 0.09/0.10/0.06 mm in length, respectively; only two fine setae at apex of second and third articles of right antenna (fig. 3). Mandibles with three distinct



Figs. 1–2. Photomicrographs of larval snakeflies in French amber. **1.** Head capsule of specimen MNHN-ARC-265.6 in dorsal view. **2.** Head capsule and prothorax of specimen MNHN-ARC-328.4. Scale bars = 0.25 mm.

teeth, third tooth biseriate, incisors asymmetrical; left apical tooth broken; clypeus and labrum trapezoidal or nearly subquadrate; a series of six fine setae on labrum, two lateral setae being twice length of other setae; two strong and short setae on each lateral margin of labium; labial palpus with three short palpomeres, palpomeres slightly tapering progressively in width; only right maxillary palpus preserved, with four short palpomeres, P_4 tapering to acute apex. Head with distinct narrowing and with minute lip posterior to this constriction representing raphidiopteran collar (figs. 1, 3).

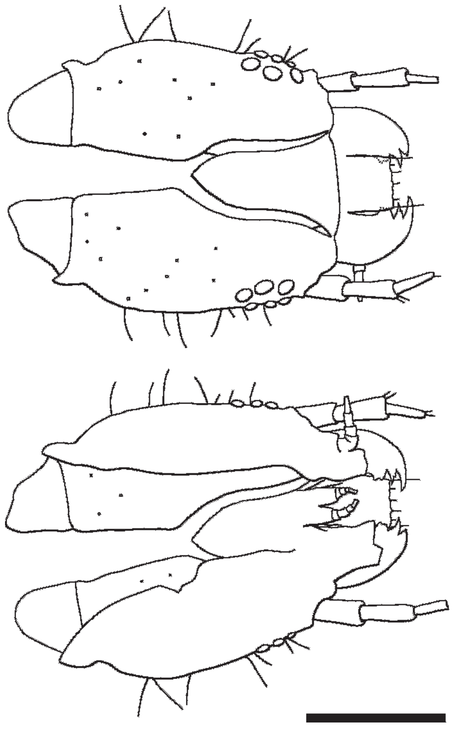


Fig. 3. Dorsal (top) and ventral (bottom) line illustrations of specimen MNHN-ARC-265.6 in French amber. Scale bar = 0.25 mm.

ARC-328.4. Nearly twice the size of ARC-265.6 but otherwise identical in features except that the antennae are slightly longer (whether this is enough to indicate that they were from different species is uncertain as the length is within the realm of natural size variation). Unlike ARC-265.6, ventral part of prothorax preserved (figs. 2, 4), nearly equal in length and width to that of head capsule.

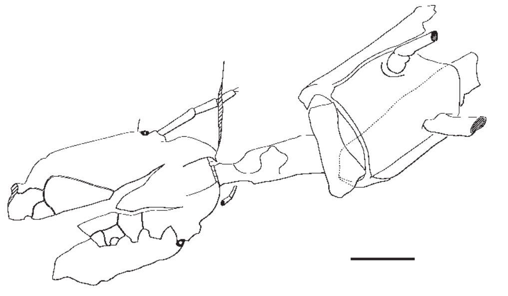


Fig. 4. Line illustration of specimen MNHN-ARC-328.4 in French amber. Scale bar = 0.25 mm.

Burmese Specimens

Mesoraphidiidae? indet. 1

Figure 5

Material examined: Snakefly larval head capsule, AMNH Bu-507, deposited in the Amber Fossil Collection, Division of Invertebrate Zoology, American Museum of Natural History, New York.

Occurrence: Northern Myanmar, Kachin, Tanai Village, 105 km Northwest of Myitkyna; Early Cretaceous, Upper Albian (Grimaldi et al., 2002; Cruickshank and Ko, 2003).

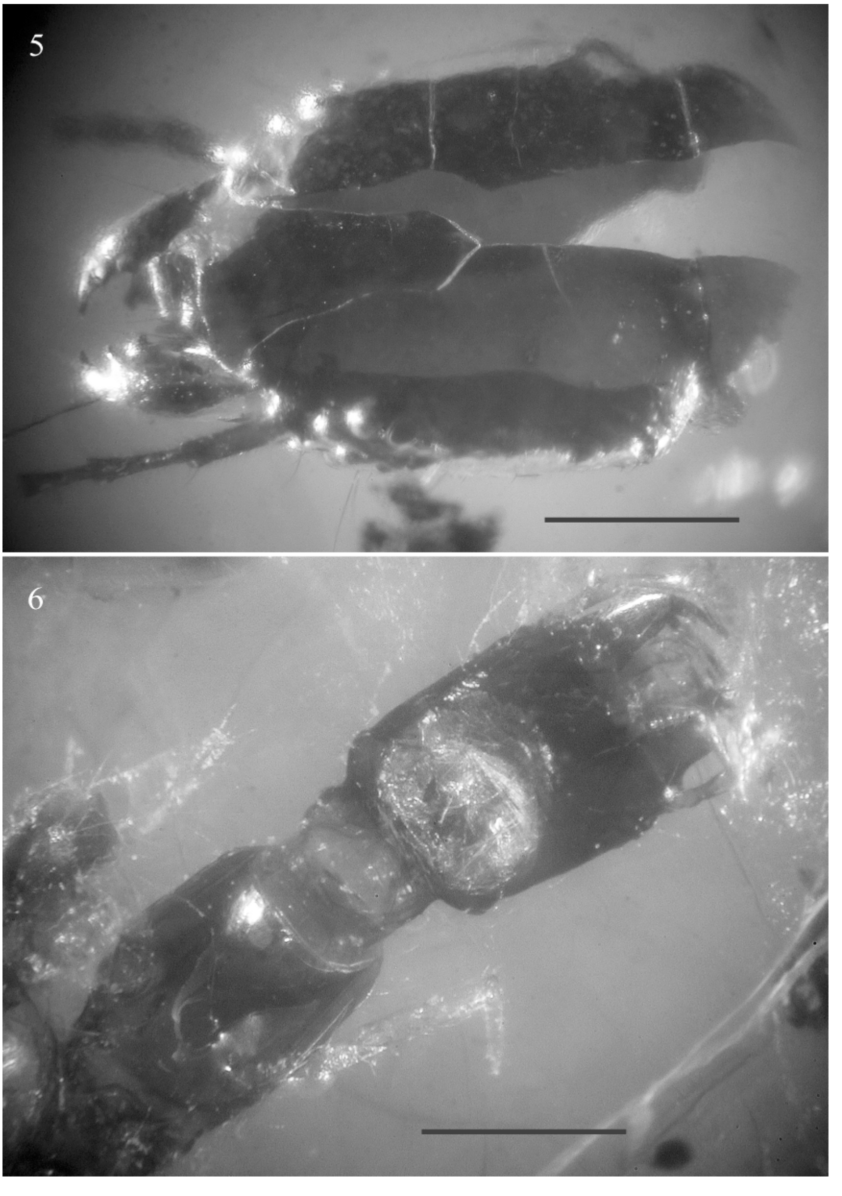
Description: **Bu-507.** Head slightly elongate, 1.6 mm in length (excluding mandibles), 1.3 mm in width; seven stemmata disposed in rough oval at base of antenna (fig. 5); ocelli absent; scattered, fine setae on lateral margins of head; coronal ecdysial cleavage line complete, forking just apical head midlength (fig. 5) (its fracturing and the separation of the head from other body sclerites, like ARC-265.6, suggest that this was a cast exuvium). Antennae about one-half length of head (ratio "antenna length/head length" = 0.456), with three cylindrical articles of 0.26/0.26/0.21 mm in length, respectively; a few, fine setae at apex of each antennal article. Mandibles with three distinct teeth, third tooth biseriate, incisors slightly asymmetrical, space between first and second tooth greater on left mandible, apical tooth largest in both mandibles; clypeus short, transverse; labrum short, transverse, with a few minute setae; labial and maxillary palpi not visible (ventral aspect of head obscured). Lateral margins of head slightly and gently convex; head with distinct posterior constriction forming posterior collar (fig. 5).

Mesoraphidiidae? indet. 2

Figure 6

Material examined: Snakefly larval head capsule and prothorax, AMNH Bu-644, deposited in the Amber Fossil Collection, Division of Invertebrate Zoology, American Museum of Natural History, New York.

Occurrence: Northern Myanmar, Kachin, Tanai Village, 105 km Northwest of Myitkyna;



Figs. 5–6. Photomicrographs of larval snakeflies in Burmese amber. **5.** Head capsule of AMNH Bu-507 (dorsal view). **6.** Head capsule and prothorax of AMNH Bu-644 (ventral view). Scale bars = 0.5 mm.

Early Cretaceous, Upper Albian (Grimaldi et al., 2002; Cruickshank and Ko, 2003).

DESCRIPTION: **Bu-644.** Head slightly elongate, 0.64 mm in length (excluding mandibles), 0.53 mm in width; five stemmata disposed in semicircle at base of antenna; lateral margins of head with sparse, fine setae on lateral margins. Antennae of moderate length, about three-quarters length of head (ratio "antenna length/head length" = 0.734), with three cylindrical articles of 0.18/0.17/0.12 mm in length, respectively; sparse, fine setae at apex of articles (not discernible for third article). Mandibles strongly angulate in apical third, with three distinct teeth, third tooth biseriate, incisors asymmetrical, apical-

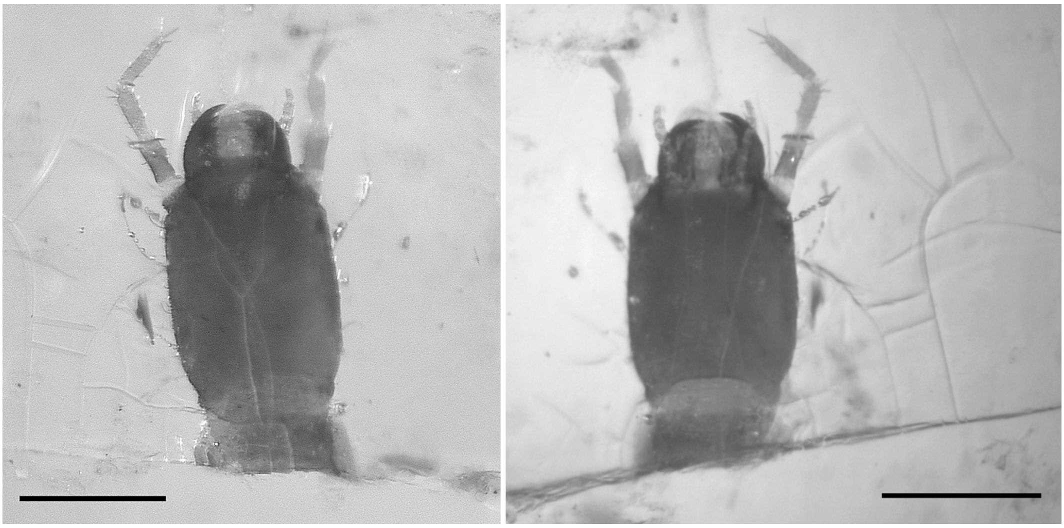


Fig. 7. Photomicrograph of head capsule (dorsal view left, ventral view right) of specimen JG-13 in Lebanese amber. Scale bars = 0.25 mm.

most incisor greatly elongate and sharply acute at apex, nearly twice as long as second incisor; base of mandibles unusually broad, giving mandibles a stout appearance. Mouthparts poorly preserved such that maxillary and labial palpi are indiscernible. Lateral margins of head relatively parallel, giving head quadrate appearance; head with strong posterior constriction and distinct lip representing raphidiopteran collar (fig. 6). Prothorax with proportions like those of head capsule (fig. 6), with sparse setae (unlike the specimens previously discussed, Bu-644 appears to be a deceased larva rather than a cast exuvium: fig. 6).

Lebanese Specimen

Raphidioptera: Raphidiomorpha indet.

Figures 7–8

Material examined: Larval snakefly head capsule; JG-13; provisionally deposited in the Laboratoire de Paléontologie, Muséum National d'histoire Naturelle, Paris, France.

Occurrence: Jezzine, southern Lebanon; Early Cretaceous, Upper Neocomian (Barremian?).

Description: **JG-13.** Head elongate and narrow, 0.4 mm in length, 0.28 mm in width; no visible stemmata or ocelli; a series of fine setae on lateral margins of head, two longer setae at base of antenna. Three antennal articles, articles progressively increasing in length from base to apex (lengths 0.07/0.08/0.1 mm, respectively) and together slightly shorter than head capsule (ratio "antenna length/head length" = 0.625); a minute but distinct spine on outer apex of second antennal article (visible on right antenna); a series of fine setae on each article. Mandibles tridentate, teeth distinct, third tooth biseriate,

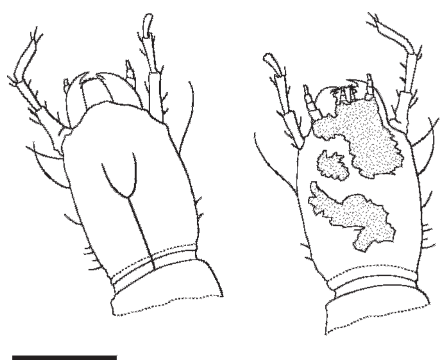


Fig. 8. Dorsal (left) and ventral (right) reconstruction of specimen JG-13 in Lebanese amber. Ventral surface partly covered by dust and microscopic bubbles (indicated by stippled areas). Scale bar = 0.25 mm.

incisors slightly asymmetrical; labrum rectangular and longer than wide; ventral surface partly covered by dust and microscopic bubbles so that base of labial and maxillary palpi hidden, with three and four palpomeres visible, respectively. Distinct collar present; prothorax preserved by only a minute fragment of its anterior margin.

DISCUSSION

The head capsules are undoubtedly of raphidiopteran larvae as evidenced by the following characters: shape elongate and relatively narrow (more extreme in the Lebanese specimen and in the species described by Engel, 2002); antenna with three articles; head with fine, long setae near the lateral margins; distinct collar present. In addition, the specimens share the asymmetric development of the mandibles and relatively similar antenna/head ratios (i.e., antenna length/head length).

The Lebanese individual is not without its own peculiarities, differing from all other raphidiopteran larvae by the absence of stemmata, but also interesting for its relatively short antennae and the more developed collar. The absence of stemmata assuredly excludes placement in the Neoraphidioptera as all known larvae of Raphidiidae and Inocelliidae have stemmata (and furthermore these families are not known prior to the Tertiary as evidenced by relatively decent record of adult Raphidioptera: table 1). The Lebanese specimen differs most notably from the species in French amber by the absence of stemmata, a minute spine at the outer apex of the second antennal article (observable on the right antenna), longer maxillary palpi, and the more elongate head. In some of these attributes the Lebanese specimen is similar to the species described by Engel (2002) from Burmese amber. Both species have more strongly elongate heads, albeit even more strongly developed in the Burmese specimen. In addition, the coronal ecdysial cleavage lines are weak (nearly imperceptible or absent in the Burmese species: see Engel, 2002) or incomplete (in the Lebanese specimen) and the labrum is more rectangular with its longest axis oriented longitudinally (rather than the more subquadrate labra of other species). Naturally, there are just as many differences such as the vestigial collar, the greatly elongate antennal articles (lacking a minute outer, apical spine on the second article), and the elongate posterior setae in the Burmese species. The Burmese specimen was considered a putative mesoraphidiid and additional wing fragments subsequently discovered in Burmese amber are all of mesoraphidiids although of species larger and differing in venation from the adult described by Engel (2002) (Engel, unpubl. data). These observations of only mesoraphidiid fragments in Burmese amber further strengthen the possibility that the larvae are of the same family. By extrapolation, if the shared features between Engel's (2002) Burmese amber larva and the Lebanese specimen described herein are indicative of some degree of relationship, then it is possible that the latter is also representative of Mesoraphidiidae. A similar head shape is also seen in the New Jersey amber (Turonian) larval snakefly described by Grimaldi (2000) and which was assuredly a mesoraphidiid. While placement within Baissopteridae, which would certainly seem possible from a biogeographic perspective (e.g., Aspöck, 1998; Engel, 2002), cannot be excluded, it currently lacks any evidence. Naturally, an assignment to Mesoraphidiidae for the Lebanese specimen remains largely speculative but is not without some ancillary evidence, as we have noted (unlike the baissopterid possibility). Alloraphidiidae likely renders Mesoraphidiidae paraphyletic and is, therefore, not a viable "alternative" familial assignment as this would likely merely make the larva a particular form of mesoraphidiid.

The new larval material from Burmese amber differs considerably from the peculiar species described by Engel (2002) and the remains are more typical of the species in French amber. All can be readily distinguished from that species by the greatly elongate head and antennae in the former species (see Engel, 2002). Bu-507 is, of course, easily differentiated from Bu-644 as well as the French species by the significantly larger size, being nearly three times the length of the others. Aside from size, Bu-507 is generally quite similar to the French material differing most notably in the slightly more elongate antennal articles, the short and transverse clypeus and labrum (these are more subquadrate in the French species), and the presence of an additional stemma in the larval eye (seven in Bu-507, six in ARC-265.6). The second Burmese species (Bu-644), while of more diminutive proportions, has some additional differences from Bu-507 indicating that it was perhaps a separate species. Only five stemmata can be discerned in Bu-644 (a lateral view is not possible as the specimen is situated in a flow plane), the lateral margins of the head capsule are relatively straight and parallel, and the mandibles are more strongly angulate apically (this latter feature also serves to distinguish the species from all other Cretaceous snakefly larvae).

It is interesting to note that the Burmese amber fauna consists of three distinct larval types (two described herein and a third by Engel, 2002) in addition to at least two species documented from adults (*Nanoraphidia electroburmica* Engel and another known only from wing fragments: Engel, unpubl. data). It would appear that the Burmese amber fauna may eventually rival in number of species that of the more well-studied Baltic amber fauna (Carpenter, 1956; Engel, 2002; Aspöck and Aspöck, 2004).

The French amber species is quite distinctive from the putative mesoraphidiid larva described previously from Burmese amber (see Engel, 2002: fig. 4) by its smaller size, a smaller ratio "antenna length/head length" (1.18 vs. 0.625 in Burmese and French specimens respectively), the presence of six stemmata, the more typical head shape that is slightly longer than wide (greatly elongate in the Burmese species), the more subquadrate labrum (elongate in the Burmese specimen), and the shorter antennae that just surpass the apices of the mandibles (the antennae are exceedingly elongate in the Burmese species, with the first article alone surpassing the mandibular apices: see Engel, 2002). The French amber material is more similar to the putative mesoraphidiid larva described from New Jersey amber (see Grimaldi, 2000: fig. 2) by its similar head and antennal sizes. A distinct collar is not visible in the New Jersey specimen, although it is likely hidden by froth and intersegmental membranes as suggested by Grimaldi (2000: 263). Unfortunately, mouthparts and all but one stemma also are hidden in this fossil by the froth of microscopic bubbles, which prohibit a more precise comparison with our specimen. The French species is also quite similar to the snakefly head capsule newly recorded herein from Burmese amber (fig. 5) as detailed in the preceding paragraph.

According to Aspöck et al. (1991: 74), the French specimen would fall into the modern family Raphidiidae rather than the Inocellidae owing to the absence of a short sclerite between the basal two articles of its antenna and the presence of six stemmata gathered at the base of its antenna (in contrast with the four present in inocelliids). However, each of these traits is considered plesiomorphic and likely represents the primitive condition for the clade Raphidiidae + Inocelliidae (i.e., the Neoraphidioptera: table 1), if not for raphidiomorphan snakeflies as a whole (interestingly, the family Raphidiidae itself is largely defined by plesiomorphies relative to Inocelliidae and the former may indeed eventually prove to be paraphyletic). Though the French specimen has strong similarities with some raphidiid larvae (cf. figs. 53–55 in Aspöck et al., 1991), the preservation of the head alone does not allow definitive assignment to this family. Moreover, larvae are unknown for the extinct families Alloraphidiidae and Baissopteridae, which are also known to have occurred during the Cretaceous. We therefore cannot make a definitive assignment as to family for our fossil. However, based on the biogeographic distribution of alloraphidiids, it is unlikely that the species belongs to this family (Carpenter, 1968; Engel, 2002) (plus the aforementioned possibility that alloraphidiids are derived mesoraphidiids partly vitiates this concern). Similarly, Baissopteridae are known only from the Late Jurassic of eastern Asia (Martynova, 1961) and the Early Cretaceous of Brazil (Martins-Neto and Vulcano, 1989; Oswald, 1990; Nel et al., 1990). Thus, it is perhaps most likely that the French specimen is representative of the Mesoraphidiidae, particularly given that raphidiids are entirely confined to the Cenozoic, the oldest being those preserved in middle Eocene Baltic amber (Carpenter, 1956; Aspöck and Aspöck, 2004). Mesoraphidiids, by contrast, are known from the Jurassic and Cretaceous of Eurasia (e.g., Martynov, 1925a, 1925b; Martynova, 1947; Hong, 1982, 1992; Hong and Chang, 1989; Ren, 1997; Engel, 2002; Engel et al., 2006) and the Late Cretaceous of North America (Grimaldi, 2000). Taken together, it seems most plausible that our specimen belongs to the Mesoraphidiidae.

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