

# First discovery of Neazoniidae (Insecta, Hemiptera, Fulgoromorpha) in the Early Cretaceous amber of Archingeay, SW France

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## ABSTRACT

The extinct genus and species of planthopper family Neazoniidae, *Akmazeina santonorum* n. gen., n. sp., are described. This is the first record of the family in the Lower Cretaceous French amber of Archingeay. The new genus differs from *Neazonia* Szwedo, 2007 in subtriangular vertex, wider trigons; sensory pits only in upper portion of frons, fused submedian carinae, diverging only in upper portion of frons, slightly elevated disc of pronotum, delimited by semi-circular carinae, hind tibia with distinct, knee lateral tooth. The phylogenetic relationships of Neazoniidae and some other planthoppers families as well as their ecological affinities are discussed.

## RÉSUMÉ

*Première découverte de Neazoniidae (Insecta, Hemiptera, Fulgoromorpha) dans l'ambre crétacé inférieur d'Archingeay, SW France.*

Un genre et une espèce de fulgoromorpe de la famille Neazoniidae, *Akmazeina santonorum* n. gen., n. sp., sont décrits. Un représentant de la famille Neazoniidae est signalé pour la première fois dans l'ambre crétacé inférieur d'Archingeay. Le nouveau genre diffère de *Neazonia* Szwedo, 2007 par son vertex subtriangulaire, ses trigons plus larges, les fossettes sensorielles présentes uniquement dans la partie haute du front, un disque de pronotum légèrement élevé, délimité par un tasseau semi-circulaire, un tibia postérieur avec une dent de genou prononcée et latérale. Les relations phylogénétiques entre les Neazoniidae et d'autres familles de fulgoromorphes ainsi que leurs affinités écologiques sont discutées.

## KEY WORDS

Insecta,  
Hemiptera,  
Fulgoroidea,  
Neazoniidae,  
*Akmazeina santonorum*  
n. gen., n. sp.,  
Cretaceous amber,  
Albian,  
France,  
nymphs,  
phylogeny.

## MOTS CLÉS

Insecta,  
Hemiptera,  
Fulgoroidea,  
Neazoniidae,  
*Akmazeina santonorum*  
n. gen., n. sp.,  
ambre crétacé,  
Albien,  
France,  
nymphe,  
phylogénie.

## INTRODUCTION

The Fulgoromorpha is a very old and highly variable suborder of the Hemiptera, which comprises three superfamilies: Permian Coleoscytoidea Martynov, 1935, (Coleoscytidae Martynov, 1935), Permian and Triassic Surijokocixioidea Shcherbakov, 2000 (Surijokocixiidae Shcherbakov, 2000) and known since the Jurassic Fulgoroidea Latreille, 1807, with over 20 families extinct and extant (Szwedo *et al.* 2004; Bourgoïn & Szwedo 2007, 2008). Extinct families of Fulgoroidea are: Jurassic Fulgoridiidae Handlirsch, 1906, which seems to be paraphyletic, but believed to be ancestral to the other families of the superfamily, and Cretaceous Lalacidae Hamilton, 1990, Neazoniidae Szwedo, 2007, Perforissidae Shcherbakov, 2007 and Mimarachnidae Shcherbakov, 2007 (Hamilton 1990; Shcherbakov 2007a, b; Szwedo 2007). The monophyly, relationships, range and content of several extant families are also under discussion. The recently recognised extant Fulgoroidea families are: Achilidae Stål, 1866 + Achilixidae Muir, 1923, Caliscelidae Amyot et Serville, 1843, Cixiidae Spinola, 1838, Delphacidae Leach, 1815, Derbidae Spinola, 1839, Dictyopharidae Spinola, 1838, Eurybrachidae Stål, 1862 + Gengidae Fennah, 1949, Flatidae Spinola, 1838 + Hypochtonellidae China & Fennah, 1952, Fulgoridae Latreille, 1807, Issidae Spinola, 1838 + Acanaloniidae Amyot & Serville, 1843, Kinnaridae Muir, 1925 + Meenoplidae Fieber, 1872, Lophopidae Stål, 1866, Nogodinidae Melichar, 1898, Ricaniidae Amyot & Serville, 1843, Tettigometridae Germar, 1821 and Tropiduchidae Stål, 1866. Despite great interest to study phylogenetic relationships of Fulgoroidea the taxonomy of this unit is still not stable. Morphology-based hypotheses had been presented by Asche (1988), Emeljanov (1990, 1999) and Bourgoïn (1993). Several studies tested relative placement of particular families, e.g., Tettigometridae, Tropiduchidae, Caliscelidae or Achilixidae (Bourgoïn *et al.* 1997; Yeh *et al.* 1998; Liang 2002; Gnezdilov & Wilson 2006). Another attempt to present fulgoroid relationships (Bourgoïn & Campbell 2002) is based on combined morphology, molecular sequences and

palaeontological data. More recently, molecular phylogenetic studies were presented by Yeh & Yang (1999), Yeh *et al.* (2005) and Urban & Cryan (2007).

Nymphs of extant Fulgoroidea have been studied extensively in the last decades (Emeljanov 2001). In contrast, fossil nymphs have been studied very little (Szwedo *et al.* 2004). The oldest fossil nymph suggested to be related to Fulgoromorpha is *Knezouria unicus* Jell, 1993 reported from the Late Triassic, Carnian of Dinmore, Ipswich Basin, Queensland, Australia (Jell 1993). Other nymphs reported are *Perforissus muiri* Shcherbakov, 2007 (first instar?) and *Cretargus emeljanovi* Shcherbakov, 2007 (first instar) of the recently described family Perforissidae from the Upper Cretaceous Taimyr amber (Shcherbakov 2007a).

The family Neazoniidae was recently described on the basis of a few nymphs preserved in Lower Cretaceous Lebanese amber (Szwedo 2007). Three species are included in the genus *Neazonia* Szwedo, 2007: *N. tripleta* Szwedo, 2007, *N. immatura* Szwedo, 2007 and *N. imprinta* Szwedo, 2007. The main feature distinguishing Neazoniidae from any other known nymphs of Fulgoroidea is the structure of the sensory pits placed on head, pronotum, mesonotum with wing pads, metanotum with wing pads and abdominal tergites including pygofer. Another feature of Neazoniidae is the extremely long rostrum, distinctly exceeding the body length.

The new specimen described below from the Early Cretaceous amber of SW France was firstly mentioned by Perrichot (2004, 2005).

## SYSTEMATICS

Order HEMIPTERA Linnaeus, 1758  
Suborder FULGOROMORPHA Evans, 1946  
Superfamily FULGOROIDEA Latreille, 1807  
Family NEAZONIIDAE Szwedo, 2007

Genus *Akmazeina* n. gen.

TYPE SPECIES. — *Akmazeina santonorum* n. sp.; here designated.

**ETYMOLOGY.** — Generic name is derived from Ancient Greek *akmazein*, be in the prime of the youth; gender feminine.

**DIAGNOSIS.** — Differs from *Neazonia* Szwedo, 2007 in subtriangular vertex (more pentagonal in *Neazonia*); wider trigons (trigons narrow in *Neazonia*); sensory pits only in upper portion of frons (two pairs of sensory pits in upper and lower portion of frons in *Neazonia*); submedian carinae fused, diverging only in upper portion of frons (submedian carinae diverging from frontoclypeal suture in *Neazonia*); disc of pronotum slightly elevated, delimited by semicircular carinae (carinae straight and diverging in *Neazonia*); hind tibia with distinct, knee lateral tooth (hind tibia lacking lateral teeth in *Neazonia*).

#### DESCRIPTION

Body slender, somewhat elongately ovoid. Head and thorax measured in midline shorter than abdomen with pygofer in midline; head and thorax with wing pads measured to the tips of wing pads about as long as abdomen with pygofer in midline. Vertex with distinct trigons, disc of vertex subtriangular, delimited by elevated carinae, posterior margin slightly elevated. Frons with distinct, subparallel lateral carinae; submedian carinae weak, slightly diverging near the margin of frons and vertex; quadruplet of sensory pits in upper portion, laterad of midline. Rostrum distinctly exceeding length of body.

Pronotum wider than head with compound eyes, with elevated disc delimited anteriolaterad by semicircular carinae; a pair of rosette-like triplets of sensory pits laterad of ecdysion line. Mesonotum with wing pads wider than pronotum; metanotum with wing pads about as wide as mesonotum with wing pads.

Fore and mid femora slightly flattened, carinate, fore and mid tibiae subquadrangular in cross section. Hind femur slightly flattened; hind tibia elongate, subquadrangular in cross section, with distinct knee tooth and rows of setae along margins.

Abdominal tergites IV-VII with single sensory pits near lateroposterior angle; tergite VIII with triplet of sensory pits. Pygofer triangular, with distinct median incision ventrally, reaching half of pygofer length; lateral lobes with triplets of sensory pits near half of pygofer length; posterior margins of pygofer lobes excavate, processes of IXth abdominal

sternite (“anal combs”) elongate, finger-like; Xth tergite plate-like, carinate.

#### *Akmazeina santonorum* n. sp.

(Figs 1-3)

**HOLOTYPE.** — Specimen MNHN ARC 186.2 (nymph of probable Vth instar), syninclusion: holotype of *Antodicranomyia azari* Perrichot, Nel & Krzemiński, 2007 (Perrichot *et al.* 2007). Deposited in the Muséum national d’Histoire naturelle, Paris (MNHN).

**ETYMOLOGY.** — Specific epithet is derived from Latin name of the Gallic tribe – Santones, inhabiting the area of Carantonus Maritimus – Gallia Celtica (present department Charente-Maritime) during Roman times.

**TYPE LOCALITY AND HORIZON.** — Archingey-Les Nouillers, Charente-Maritime, SW France. Lower Cretaceous, uppermost Albian, lithological subunit A1s2 (*sensu* Néraudeau *et al.* 2002).

**DIAGNOSIS.** — Body dorso-ventrally flattened, elongately ovoid. Lateral margins of vertex elevated; vertex in midline longer than pronotum in midline. Frontoclypeal suture nearly straight, with trapezoid process in the middle. Anterior margin of pronotum arcuate. Fore femur longer than fore tibia; mid-femur shorter than mid-tibia.

#### DESCRIPTION

Total length of body *c.* 4.55 mm. General shape elongately ovoid, flattened dorso-ventrally, with tip of rostrum exceeding apex of abdomen.

Head with compound eyes 1.06 mm wide. Vertex subtriangular, a bit shorter (0.43 mm) than wide at base (0.54 mm), anterior margin acutely converging, posterior margin arcuate, lateral margins elevated. Disc of vertex slightly concave; mid-dorsal ecdysial line distinct. Trigons distinct, delimited by elevated carinae, with posterior angle reaching anterior  $\frac{1}{4}$  of length of compound eye. Frons about 1.76 times as long as broad at frontoclypeal suture, 0.86 mm long in midline, slightly wider at level of sensory pits (0.51 mm) than at frontoclypeal suture (0.43 mm), angularly rounded at apex, with lateral margins subparallel. Lateral carinae slightly elevated laterad, extending to level of frontoclypeal suture and continuing only in very basal portion of clypeus. Submedian carinae fused since the frontoclypeal suture, slightly diverging in upper portion at level

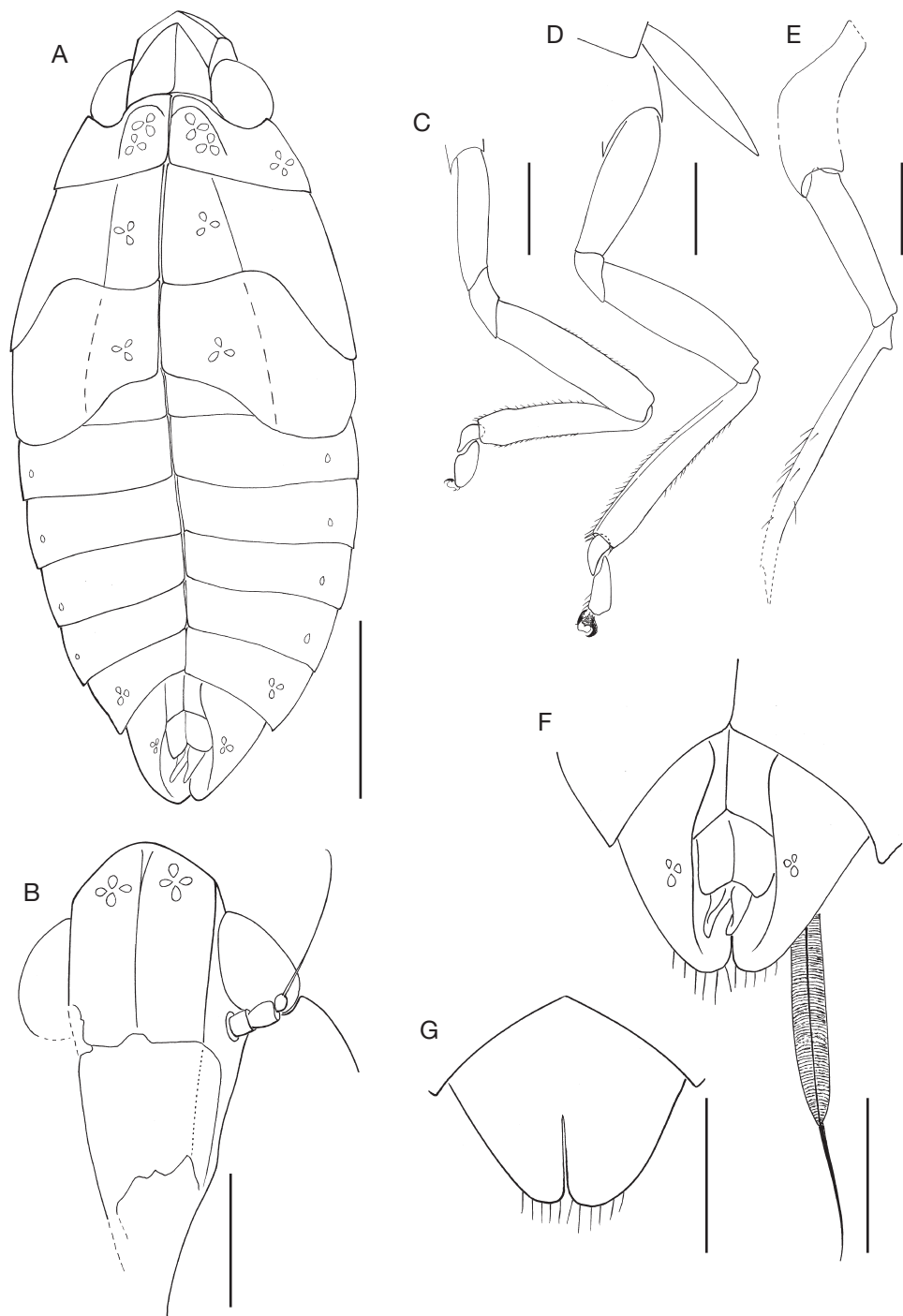


FIG. 1. — *Akmazeina santonorum* n. gen., n. sp.: **A**, body; **B**, face; **C**, left fore leg; **D**, left middle leg; **E**, left hind leg (incomplete, tip of tibia and tarsus missing); **F**, pygofer in dorsal view; **G**, lobes of pygofer in ventral view. Scale bars: A, 1 mm; B-G, 0.5 mm.

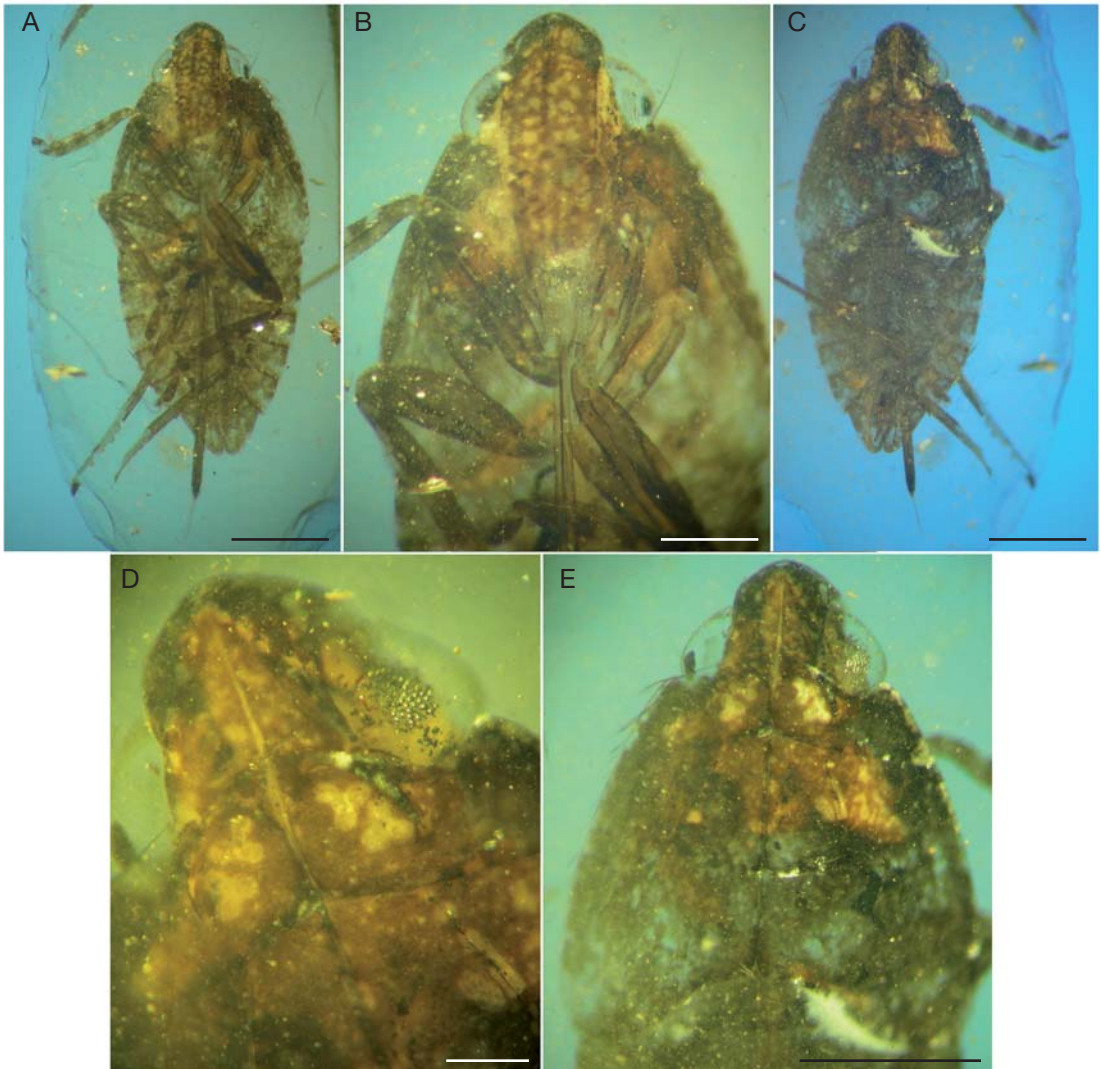


FIG. 2. — *Akmazeina santonorum* n. gen., n. sp.: **A**, general ventral view; **B**, face; **C**, general dorsal view; **D**, head and pronotum; **E**, head and thorax. Scale bars: A, C, 1 mm; B, E, 0.5 mm; D, 0.2 mm.

of sensory pits. Disc of frons slightly concave. Two quadruplets of sensory pits in upper portion of frons, slightly below anterior margin of head. Clypeus about 0.83 mm long in midline, without median carina; obsolete lateral carination only as continuation of lateral carinae of frons near frontoclypeal suture. Lora narrow, not distinctly delimited from clypeus, about as wide as gena. Antennal fovea

distinct, with margin not distinctly elevated; scape subcylindrical, wider than long (0.08 mm), shorter than pedicel; pedicel elongate, subconical, about 0.1 mm long; first flagellomere globular, narrower than pedicel; arista elongate, about 0.51 mm long. Rostrum with tip exceeding apex of the body, subapical segment about 1 mm long, apical segment about 1.6 mm long.

Thoracic nota divided by longitudinal mid-dorsal ecdysial line into three pairs of plates. Pronotum wider than head with compound eyes, anteriorly produced to the level of basal  $\frac{1}{4}$  of compound eyes length, with distinct anteromedian lobes, anterior angle slightly protruding anteriorly, lateral margins distinctly diverging posteriorly, posterior margin weakly triangularly incised. Pronotum in midline 0.36 mm long, shorter than vertex in midline, 0.57 mm as whole, 1.12 mm wide between anteromedian lobes, 1.58 mm wide at posterior angles. Disc of frons delimited by semicircular, elevated carinae anteriorly; two pairs of triplets of sensory pits present laterad of mid-dorsal ecdysial line, one in anteromedian portion, second in posterolateral portion of disc. Pair of triplets of sensory pits present in posterolateral angle of pronotum.

Mesonotum with wing pads 0.72 mm long in midline, 2.29 mm wide at posterior angle of wing pads, disc slightly elevated, delimited by lateral carinae diverging posteriad, anterior margin widely triangular anteriorly, lateral margins diverging posteriad, posterior margin deeply excavate, with posterior margin of disc slightly convex posteriad; pair of triplets of sensory pits present on disc, near laterodiscal carina.

Metanotum with wing pads in midline shorter (0.5 mm) than mesonotum, as wide as mesonotum with wing pads, posterior margin distinctly excavate; disc of metanotum with pair of triplets of sensory pits.

Prothoracic leg with coxa shorter (0.71 mm) than femur (1 mm), femur slightly flattened, longer than tibia (0.88 mm), tibia subquadrangular in cross section, with margins with short setae along, first tarsomere short (0.14 mm), shorter than apical tarsomere (0.25 mm), apical tarsomere with distinct pulvillus and tarsal claws.

Mesothoracic leg with coxa shorter (0.83 mm) than femur (0.93 mm), femur slightly flattened, shorter than tibia (1.14 mm), tibia subquadrangular in cross section; tarsus 0.43 mm long, first tarsomere shorter (0.14 mm) than second tarsomere (0.33 mm), tarsal claws and arolium distinct.

Metathoracic coxa about 0.75 mm long, conical, femur 0.71 mm long, tibia slender elongate over 1.43 mm long, with distinct knee lateral

tooth, rounded in cross section with short setae along.

Abdomen with pygofer 2.3 mm long in midline, 1.85 mm wide, 9-segmented, slightly narrower at base than preceding thoracic segment. Abdominal tergites IV-VII with single sensory pit at posterolateral angles, elevated near mid-dorsal ecdysial line, delicately carinate at  $\frac{1}{2}$  of distance from midline to lateral margin. Abdominal tergite VIII with pair of triplets of sensory pits at posterolateral angle. Abdominal sternites subrectangular, sternite VIII more chevron-shaped, with posterior margin triangularly incised.

Pygofer (segment IX) triangular, 0.74 mm long in midline, 0.8 mm wide, with posterior margin dorsally excavate, with distinct, narrow median incision on ventral margin, reaching  $\frac{1}{2}$  of its length; pair of triplets of sensory pits on lateral lobes, about  $\frac{1}{2}$  of pygofer length. Pair of finger-like processes of IXth abdominal sternite ("anal combs") visible. Anal segment (segment X), subrectangular, with distinct median carination.

## DISCUSSION

### PLACEMENT OF NEAZONIIDAE WITHIN FULGOROIDEA

First attempts to present phylogenetic tree of extant Fulgoroidea based on nymphal characters was given by Yang & Fang (1993) and Chen & Yang (1995). Nymphal features had been also used by Yang & Chang (2000) in their Fulgoroidea families relationships scheme. However, relationships among the evolutionary lineages suggested a polarity reversal relative to the other morphology-based hypotheses (Bourgoin 1993; Bourgoin *et al.* 1997; Urban & Cryan 2007). The monophyly of several fulgoromorph families (extant and extinct as well) is questioned, their range and content is under debate (Emeljanov 1999; Holzinger *et al.* 2001; Gnezdilov 2007; Bourgoin & Szwedo 2007, 2008). Unfortunately nymphs of extinct groups, crucial for reconstruction of relationships, are not known or were not included to the analysis. Very little is still known on biology of nymphs of recent Fulgoroidea and only a few hypotheses had been

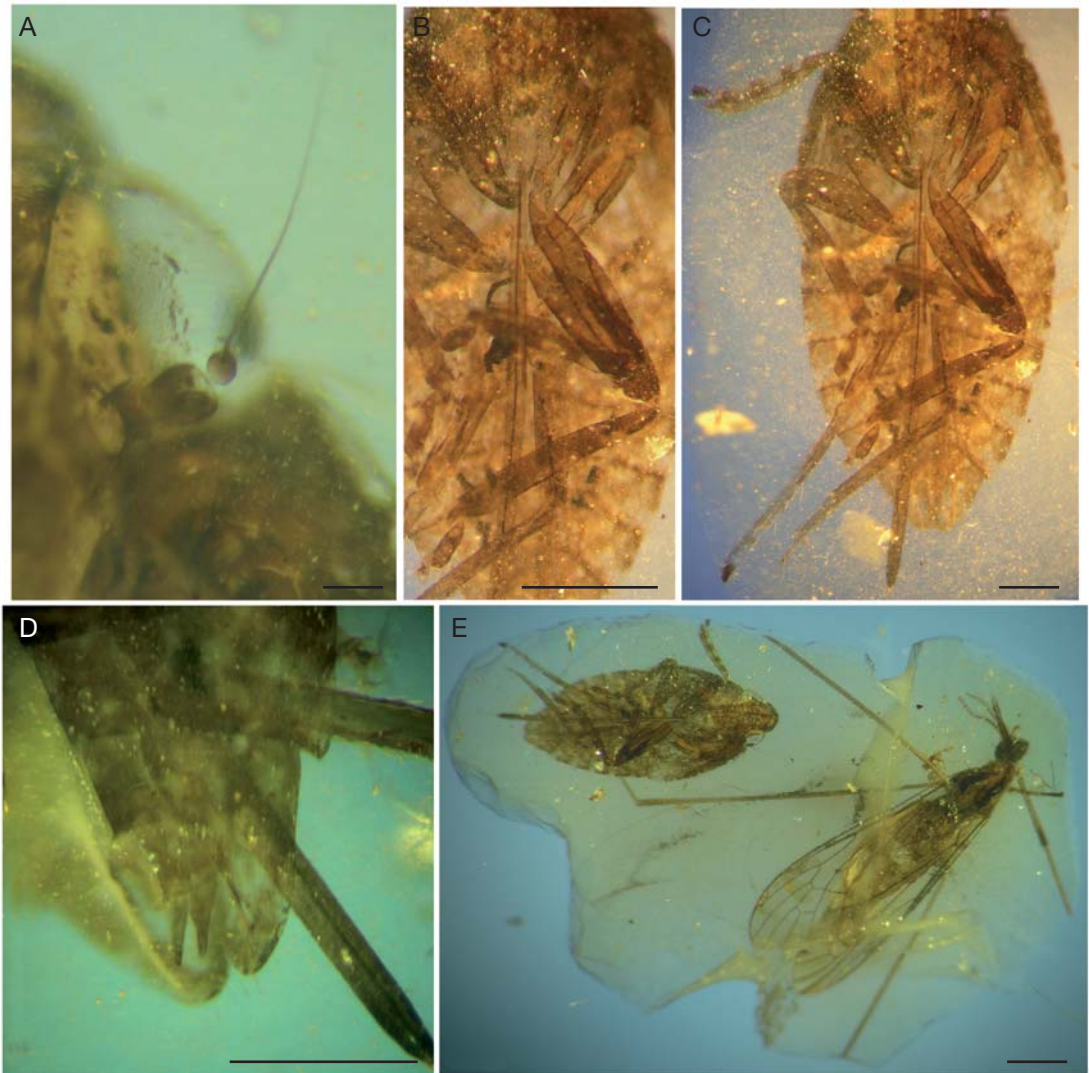


FIG. 3. — *Akmazeina santonorum* n. gen., n. sp.: **A**, antenna; **B**, fore and middle legs; **C**, legs; **D**, pygofer in posterodorsal view; **E**, situation of the specimen in piece of amber (note Limoniidae fly – *Antodicranomyia azari* Perrichot, Nel & Krzemiński, 2007). Scale bars: A, 0.1 mm; B-D, 0.5 mm; E, 1 mm.

given on biology of the extinct lineages. According to Shcherbakov & Popov (2002) nymphs of the earliest Fulgoromorpha are supposed to live in soil or other concealed places, maybe they were sessile, non free-living. Nymphs of the Jurassic Fulgoridiidae (a paraphyletic group being believed as ancestral to extant families of Fulgoroidea) are not known, but it seems reasonable to assume that they were

cryptic, flattened, biscuit-like creatures with short legs, small frontoclypeus and long rostrum, as the first free-living, adult-like nymphs are known since the mid-Cretaceous (Shcherbakov & Popov 2002). They might have fed on phloem of rather thick stems or in bark cavities (Shcherbakov & Popov 2002; Bourgoïn & Campbell 2002). Adult Fulgoridiidae had very long rostra, suggested by

Shcherbakov & Popov 2002 as feature indicating that they were more often associated with arboreal gymnosperms, sucking from trunks and thick branches, than were extant planthoppers. Very long rostra are found also among representatives of the other families from particular times, e.g., among Eocene Achilidae, while in extant Achilidae the tip of rostrum reaches or merely exceeds hind coxae. Extremely long rostra, exceeding length of body are known also among other hemipterans, e.g., in the Eocene extinct aphid genus *Germaraphis* Heie, 1967 (Pemphigidae Herrich-Schaeffer *in* Koch, 1857) and in unrelated recent aphid genus *Stomaphis* Walker, 1870 (Lachnidae Herrich-Schaeffer *in* Koch, 1857). Species of *Stomaphis* lives in bark crevices and crannies, feeding on phloem, such behaviour is also postulated for *Germaraphis* (Larsson 1978). The clypeus of Fulgoridiidae was not hypertrophied, suggesting phloem-feeding for these planthoppers. Late Fulgoridiidae or their descendants, lacking the filter chamber of coexisting plant sucking lineages (Sternorrhyncha, Cicadomorpha) probably found fine roots and/or fungal hyphae with relatively nutritious cells that were easily attacked and that had relatively high soluble nitrogen content (Szwedo 2005). Transition from gymnosperms to angiosperm host plants (and also probably to fungal hyphae, as new types of mycorrhizas appeared at this time) could be related to the appearance of the first angiosperms approximately 140 Ma (Valanginian) and their major radiation leading to a global distribution during the Albian-Cenomanian, i.e. c. 100-90 Ma (Brundrett 2002; Willis & McElwain 2002).

Preliminary analysis of the nymphal and imaginal (Perforissidae, Mimarachnidae) characters of extinct families Neazoniidae and Perforissidae allowed to place them among families regarded as “basal” lineage of Fulgoroidea (Fig. 4). Placement of Mimarachnidae could only be given tentatively – it seems it was a specialised group, with some features shared with Perforissidae (e.g., type of tegmen venation, presence of sensory pits in imagines), but on the other hand, it (superficially?) resembles Fulgoridae. Placement of Perforissidae is not fully clear, as the nymphs are highly derivative and weakly known. However, after analysis of features given by Shcherbakov (2007a)

and undescribed nymphs from Lower Cretaceous Lebanese amber, it seems that Perforissidae could be placed rather near Cixiidae and Delphacidae and Kinnaridae + Meenoplidae. Features shared by these groups (e.g., sensory pits on face arranged in rows, nymphal metatarsal segments with more than three apical teeth) seem to be plesiomorphic condition, according to Emeljanov (2001) statement. On the other hand, presence of sensory pits on the meso- and metanotum could be treated as synapomorphy for the group of families. A sensory pit is defined as “a small hole with horizontal seta directed inwards and diverging from its border; the length of the seta is not greater than diameter of the hole” (Emeljanov 2001; Gnezdilov & Wilson 2007). The sensory pits are specific organs in fulgoroidean larvae and are very rare in adults (Emeljanov 2001), usually placed on head and thorax. Recently Gnezdilov & Wilson (2007) described also sensory pits placed on abdominal sternites in some genera of Nogodinidae tribe Mithymini. Similar analogous sensory organs are known also for Cixiidae (Benini Metcalf, 1938 and Bennarellini Emeljanov, 1989), Achilixidae (Achilixinae Muir, 1923 and Bebaiotinae Emeljanov, 1991) and Tropiduchidae (*Alleloplasis* Waterhouse, 1839). Then, more data must be collected and more detailed morphological and ultrastructural studies are necessary. For example, Emeljanov (2001) suggested that sensory pits arranged in rows, with setiform sensilla directed to adjoining carina is the plesiomorphic condition of Fulgoroidea as a whole. Contrary, Gnezdilov & Wilson (2006) suggested that lack of sensillae on the border of sensory pit may be treated as a plesiomorphic character.

These doubts are also true for Neazoniidae which seems to be a derivative group of Fulgoroidea (head with distinct trigons, subtriangular shape of pygofer could be regarded as apomorphies), but in respect to some features (excavation of dorsad margin of pygofer, finger-like processes of IXth abdominal tergite) it seems it could be placed rather near Kinnaridae + Meenoplidae unit, than near other Fulgoroidea. Nymphs of other families, e.g., Tettigometridae, seem also to be derivative (Yang & Yeh 1994), as these planthoppers seems to be an attempt to create “leafhopper-like” planthoppers. Shcherbakov’s



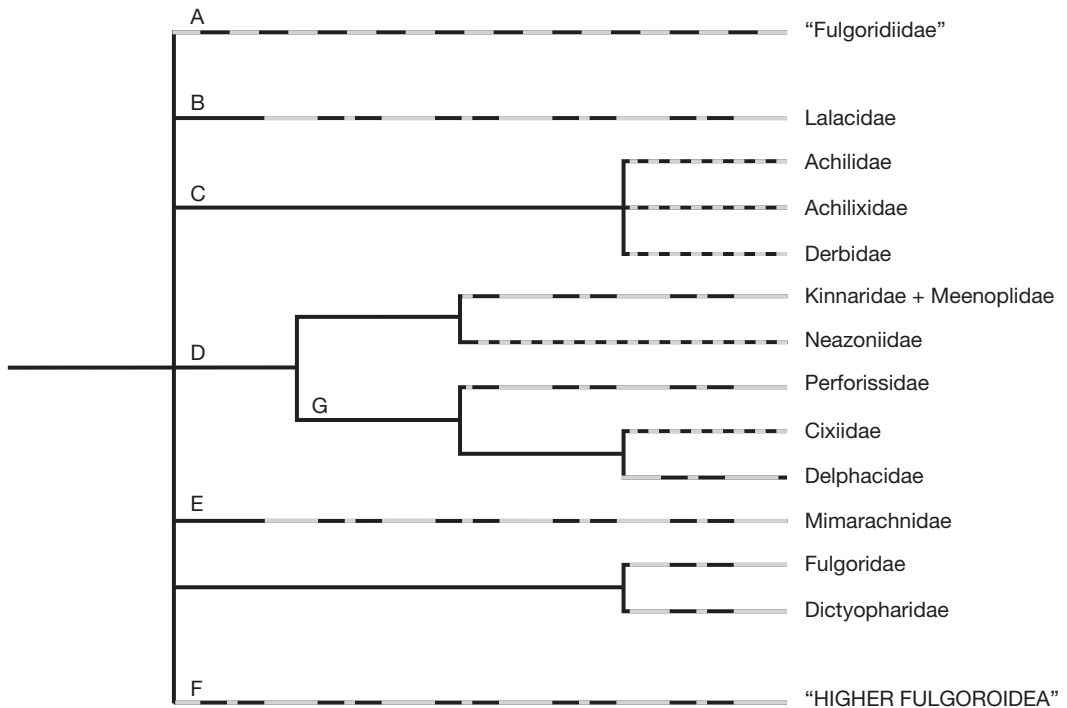


FIG. 4. — Hypothetic framework of Fulgoroidea families relationships inferred from interpretation of palaeontological and morphological, nymphal and imaginal, and molecular data, including their biology: **dotted lines**, nymphs cryptobiontic, feeding on fungal hyphae; **dashed lines**, nymphs not known; **dotted-dashed lines**, nymphs free living, on host plants; **A**, "Fulgoridiidae" is a paraphyletic unit, but believed to be ancestral for other Fulgoroidea lineages; **B**, Lalacidae is one of the "short living" families from the times of mid-Cretaceous biotic turnover, the relationship of the family is not clear, it is one of the first units with adult-like, free-living nymphs (not formally described); **C**, this clade seems to be monophyletic, however both molecular and morphological data suggest non-monophyly of the families; **D**, this clade comprises "Cixiidae-like" groups, its monophyly is weakly supported, and some not formally described units are being placed there; **E**, placement of Mimarachnidae is tentative, it is another "short living" family from the Lower Cretaceous, being extinct at mid-Cretaceous biotic turnover; **F**, so-called "higher Fulgoroidea" (families Acanaloniidae, Calicelidae, Eurybrachidae, Flatidae, Gengidae, Hypochthonellidae, Issidae, Lophopidae, Nogodinidae, Ricaniidae, Tetigometridae and Tropiduchidae) seems to be not monophyletic, the relationships of particular lineages and lower rank units within are not resolved.

statement (2007a) that Perforissidae were an attempt to create "leafhopper-like" forms (quasi-leafhoppers) seems to be justified too. The Perforissidae (both adults and nymphs) look more "leafhopper-like" than any other planthopper group, with exception of Tettigometridae. This group presumably went extinct being outcompeted by Cicadellidae, known since the Early Cretaceous (Shcherbakov & Popov 2002). Other possible cause of their extinction is that they were trophically associated with some earliest angiosperm or proangiosperm lineages not surviving into the Cainozoic. It could be speculated that they lived on low herbaceous and/or brachyphyllous plants (Shcherbakov 2007a).

Several families known since the Cretaceous – Neazoniidae, Achilidae, Cixiidae – had the nymphs cryptobiontic or are supposed to have cryptobiontic nymphs, like the recently described family Mimarachnidae. These groups are believed to be descendants of Fulgoridiidae (Shcherbakov 2007b), but the relationships are still not established as Fulgoridiidae is a paraphyletic unit (Bourgoin & Szewo 2007, 2008). Shcherbakov (2002) and Shcherbakov & Popov (2002) assumed that until the mid-Cretaceous most fulgoroid nymphs dwelled in the soil or were cryptic on their host plants. Sorensen *et al.* (1995) suggested that early Fulgoroidea initially evolved to feed on roots and

fungal hyphae, which existed in subterranean/semisubterranean (duff) niches, much as many of their immatures do now (Wilson *et al.* 1994). It was postulated that the first fulgoroidea with mycetophagous nymphs were Achilidae (Shcherbakov 2002; Shcherbakov & Popov 2002). A cryptic nymph of Neazoniidae, with flattened shape and long rostrum, suggests that they could live under bark and also could be mycetophagous (Szwedo 2007). Nymphs with cryptic coloration, flattened body, similar to nymphs of Neazoniidae, are present in most of cixioid lineage families: Cixiidae, Achilidae, Derbidae, Meenoplidae. The Cixiidae and Derbidae – other families with mycetophagous nymphs, together with Achilidae, form an entity based on nymphal features (Yang & Yeh 1994). Very probably Neazoniidae, as preliminary analysis suggests, also could be placed in this lineage. The Neazoniidae may have lived in gymnosperm forests, which diversified during the Late Jurassic and Early Cretaceous (Taylor 1988). Particular types of mutualistic relationships between plant roots and fungi (e.g., ectomycorrhizal, ericoid and orchid mycorrhizas) originated in the Jurassic or Cretaceous (Brundrett 2002) and evolved during the period of rapid angiosperm radiation in the Cretaceous (Willis & McElwain 2002). These events could be a trigger for origination of new groups and new trophic relationships. The Neazoniidae could represent an early stage of development of free-living (but still cryptobiotic), jumping planthopper nymphs. The oldest families of Fulgoroidea with free-living, adult-like nymphs whose hind legs became elongate for jumping are Perforissidae – Lower and Upper Cretaceous, Lalacidae – Lower Cretaceous, Dictyopharidae – Upper Cretaceous, and Tropiduchidae – Upper Cretaceous (Shcherbakov & Popov 2002; Szwedo *et al.* 2004; Shcherbakov 2007a and unpublished data).

The Lalacidae, Mimarachnidae, Neazoniidae, Perforissidae and some undescribed fossils could be representatives of the period of intense faunistic reorganisation of insect assemblages, known as the “mid-Cretaceous biocoenotic crisis” (Zherikhin 1978, 1993, 2002; Rasnitsyn 1988). The mid-Cretaceous appearance and disappearance of families in the fossil record (faunistic turnover) is clearly demonstrated by palaeontological data. This

record may be interpreted as an endogenous community crisis evoked by competitive replacements in the early successive vegetation (Zherikhin 1993, 2002). During mid-Cretaceous, angiosperms were more frequent and abundant at lower latitudes in a dry (sub)tropical zone, at that time mainly tropical Gondwanaland, though gymnospermous forests prevailed in wetter climates in the higher latitudes of northern Laurasia and southern Gondwanaland (Anderson *et al.* 1999; Scotese 2003). At this time, about 100 Ma, also the first moist megathermal forests appeared for the first time in mid-latitudes (Maslin *et al.* 2005). Drastic vegetational changes in mid-Cretaceous times, during which the gymnosperm- and fern-dominated flora were replaced by angiosperm-dominated communities, was of great importance for Fulgoroidea history and evolution, greater than the Mesozoic/Cainozoic boundary with its extinction event. It resulted in the presence of number of short-living, extinct groups of Fulgoroidea as well as in origination of extant lineages.

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