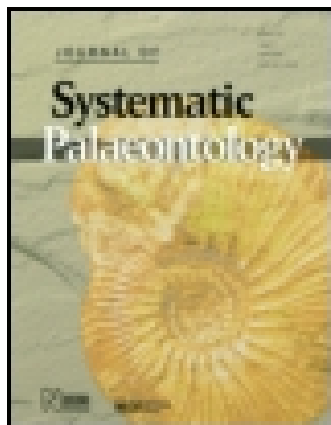


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First fossil record of Caliscelidae (Hemiptera: Fulgoroidea): a new Early Miocene Dominican amber genus extends the distribution of Augilini to the Neotropics

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First fossil record of Caliscelidae (Hemiptera: Fulgoroidea): a new Early Miocene Dominican amber genus extends the distribution of Augilini to the Neotropics

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A new extinct genus and new species, *Quizqueiplana alexbrowni* gen. et sp. nov. of the tribe Augilini Baker belonging to the family Caliscelidae Amyot & Serville (Hemiptera, Fulgoromorpha, Fulgoroidea), is described from Early Miocene Dominican amber. This is the first fossil record of this planthopper family and an unexpected occurrence of the tribe Augilini from the Neotropical region. Augilini are only known from extant taxa in South-East Asia and Madagascar, as shown in a checklist of taxa in the tribe with their distributions. Biogeographical consequences for the Augilini lineage, now with a so-called Gondwanian disjunction pattern, are discussed. Host-plant data suggest that ancestral Augilini fed on Bambusoideae. A Late Palaeocene Laurasian origin for the lineage with later dispersal events, or an older Indo-Malagasian lineage with an early vicariance and later dispersion events, remain two possible explanations of the origin of the Augilini.

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Keywords: Early Miocene; Caliscelidae; amber; biogeography; Gondwanian disjunction pattern; Laurasian origin

Introduction

The family Caliscelidae Amyot & Serville, 1843 is a small globally distributed group of planthoppers (Hemiptera, Fulgoroidea) that comprises 72 extant taxa with more than 200 species known to date (Gnezdilov 2013a; Bourgoïn 2015). The family is divided into two subfamilies with five tribes: the subfamily Caliscelinae Amyot & Serville, 1843 with the tribes Caliscelini Amyot & Serville, 1843 and Peltonotellini Emeljanov, 2008, and the subfamily Ommatidiotinae Fieber, 1875 with the tribes Ommatidiotini Fieber, 1875, Augilini Baker, 1915 and Adenissini Dlabola, 1980 (Emeljanov 1999, 2008, Gnezdilov & Wilson 2006; Gnezdilov 2011, 2013a). The tribe Adenissini includes four subtribes: Adenissina Dlabola, 1980, Bocrina Emeljanov, 1999, Coinquendina Gnezdilov & Wilson, 2006 and Pteriliina Gnezdilov & Wilson, 2006 (Gnezdilov 2008, 2013a).

The two newly discovered fossil specimens described below belong to the same taxon in the tribe Augilini, which was erected by Baker (1915) as a subfamily of the family Issidae Spinola, 1839. He did not indicate the type genus, but listed in the subfamily two genera – *Augila* Stål, 1870 and *Augilina* Melichar, 1914, previously placed

in Issidae (Caliscelinae) (Melichar 1906, 1914). The subfamily was subsequently transferred to the family Lophopidae Stål (Muir 1930), then considered as a tribe by Metcalf (1955), followed by Fennah (1963). Later, Fennah (1987) accommodated them in the subtribe Augilina of the tribe Ommatidiotini Fieber, subfamily Caliscelinae Amyot & Serville, of the family Issidae Spinola. Finally, Emeljanov (1999) suggested treating the group as a tribe within the subfamily Ommatidiotinae Fieber of the family Caliscelidae, based on the structure of larval sensory pits. This current point of view was confirmed by the structure of the ovipositor and supported by Gnezdilov & Wilson (2006) and Gnezdilov (2003, 2011).

The new taxon is the first fossil record of the family Caliscelidae and the first record of the tribe Augilini from the New World, known before only from the Oriental and Afrotropical regions (Gnezdilov & Bourgoïn 2009; Gnezdilov 2011). Global current distribution of the tribe Augilini is given in the Supplementary Material and currently covers: China (Guangdong, Guangxi, Hainan, Yunnan), southern India (Tamil Nadu, Karnataka), Sri Lanka, Vietnam, Thailand, Myanmar, Cambodia, Philippines (Luzon, Negros) and Madagascar. Modern fauna of the tribe comprises 13 genera with 26 species. Most of the genera (eight)

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are monotypic (*Anthracidium* Emeljanov, 2013, *Cano* Gnezdilov, 2011, *Cicimora* Emeljanov, 1998, *Discote* Emeljanov, 2013, *Pseudosymplanella* Che, Zhang & Webb, 2009, *Signoreta* Gnezdilov & Bourgoïn, 2009, *Symplanodes* Fennah, 1987, *Tubilustrium* Distant, 1916). Five genera (*Augila* Stål, 1870, *Augilina* Melichar, 1914, *Augilodes* Fennah, 1963, *Symplana* Kirby, 1894, *Symplanella* Fennah, 1987) include two to six species. Two monotypic genera are known from Madagascar (*Cano*, *Signoreta*), one monotypic genus is endemic to southern India (*Symplanodes*), and 10 genera with 23 species are known from Indochina and the Philippines.

Here we described the first Caliscelidae known in the fossil record and briefly explore the biogeographical consequences for the Augilini lineage that now has a so-called Gondwanian disjunction pattern.

Material and methods

The specimen was observed using a Zeiss Discovery V-12 stereomicroscope in normal reflected and transmitted light. Drawings were made using attached drawing tubes. Photographs of habitus were taken with a Canon EOS 50D digital camera associated with a Leica Z16 APO microscope. The digital images were then imported into Adobe Photoshop 8.0 for labelling and plate composition. Line figures were drawn with the aid of a camera lucida mounted on a Zeiss Discovery V-12 stereomicroscope.

The type specimens are deposited in the Muséum National d'Histoire Naturelle, Paris, France (MNHN). Morphological terminology follows that of Bourgoïn & Huang (1990) and Bourgoïn (1993) for male and female genitalia, respectively, and Bourgoïn *et al.* (2015) for vein nomenclature.

Systematic palaeontology

Family **Caliscelidae** Amyot & Serville, 1843

Subfamily **Ommatidiotinae** Fieber, 1875

Tribe **Augilini** Baker, 1915

Genus ***Quizqueiplana*** Bourgoïn & Wang gen. nov.

Type species. *Quizqueiplana alexbrowni* Bourgoïn & Gnezdilov sp. nov.

Etymology. The generic name is feminine and derived from the concatenation of the word *Quizqueia*, previous name of Hispaniola according to the first historian of the island Pietro Martire d'Anghiera (1457–1526), and the generic name *Symplana* Kirby.

Description. Head including the eyes slightly wider than pronotum (Figs 2A, 3A–C). Vertex strongly produced anteriorly in the shape of a long cephalic process, distinctly angulate apically, its lateral margins strongly ridged, hind margin angulately concave (Fig. 2A). Vertex with inconspicuous median carina which does not reach the level of the anterior margin of the eyes, disc of vertex strongly depressed. Frons elongate (Figs 2B, 3B), with median and lateral carinae; median carina running up to frontoclypeal suture, lateral carinae subparallel not reaching the frontoclypeal suture, but becoming indistinct above it; all carina distinctly elevated. Frontoclypeal suture slightly arched. Rostrum (Figs 1A–C, 2B) reaching between mid and hind coxae, its apical (third) segment slightly shorter than broad (0.86:1), distinctly shorter than the subapical (second) segment. Antennae (Fig. 2A–C) with scape short, ring-like; pedicel subcylindrical, covered with many microsetae extending to the base of the pedicel, widened in apical portion, apex with anterior portion distinctly produced over the subapical depression (Bourgoïn 1985); flagellum very long. Pronotum with its disc slightly elevated, strongly convex anteriorly and angularly emarginate posteriorly, delimited by weak, converging anteriorly lateral carinae (Fig. 2A, C). Mesonotum with its disc flattened (Fig. 2A, C), with lateral carinae; lateral areas obliquely depressed, nearly as broad as long at its middle. Legs relatively long. Lateral margin of hind tibia with a single spine medially. Apex of hind tibia with six spines. First metatarsomere with two lateroapical spines. Second metatarsomere without spines.

Quizqueiplana alexbrowni Bourgoïn & Gnezdilov
sp. nov.

(Figs 1A–G, 2A–E, 3A–H)

Etymology. The specific name is dedicated to Mr Alex Brown who generously gave the two specimens described to the MNHN.

Material. Holotype: female, Dominican amber inclusion MNHN.F.A51125, La Búcara mine, Cordillera Septentrional, Dominican Republic, A. Brown Collection, 2012; amber piece with about 50 Collembola Entomobryomorpha specimens. Paratype: specimen with genital segments and apical area of left wings missing, same data, MNHN.F.A51126.

Occurrence. Amber from La Búcara mine belongs to the La Toca Formation group of mines. It is dated to the late Early to early Middle Miocene, around 16 Ma (Burdigalian), the first and longest warming period during the Miocene (Iturralde-Vinent 2001).

Description.

Size. Female only. Total length (from apex of vertex to tip of forewings): 4.65–5.43 mm (holotype, 4.65 mm,

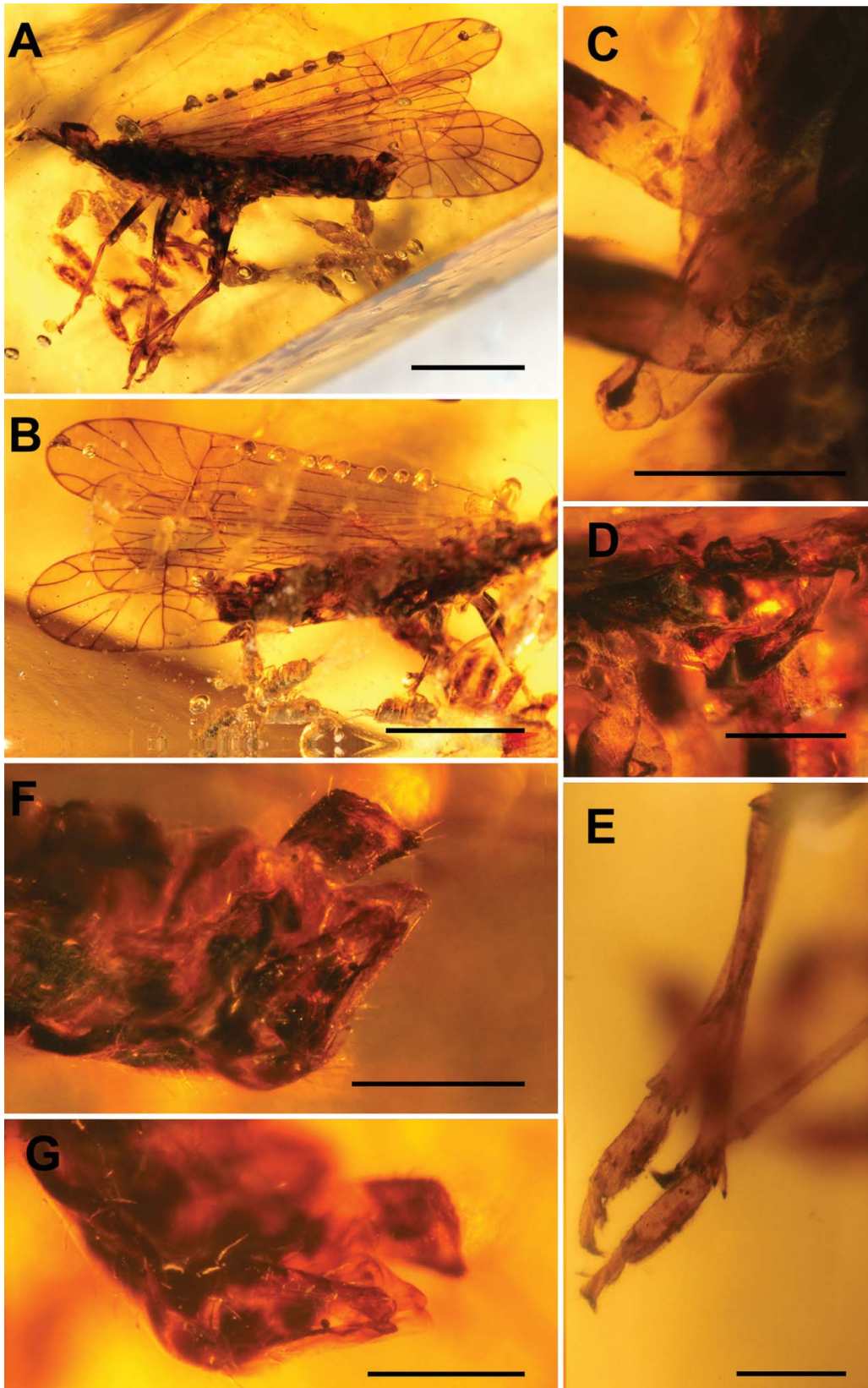


Figure 1. *Quizqueiplana alexbrowni* gen. et sp. nov., light stereomicroscope images of holotype. **A**, specimen, oblique ventral view; **B**, forewings and hind wings, oblique ventral view; **C**, apical part of labium, lateral view; **D**, post-coxal process, lateral view; **E**, legs, lateral view; **F**, female genitalia, left lateral view; **G**, female genitalia, oblique ventral view. Scale bars: A, B, D = 1 mm; C, E–G = 0.25 mm.

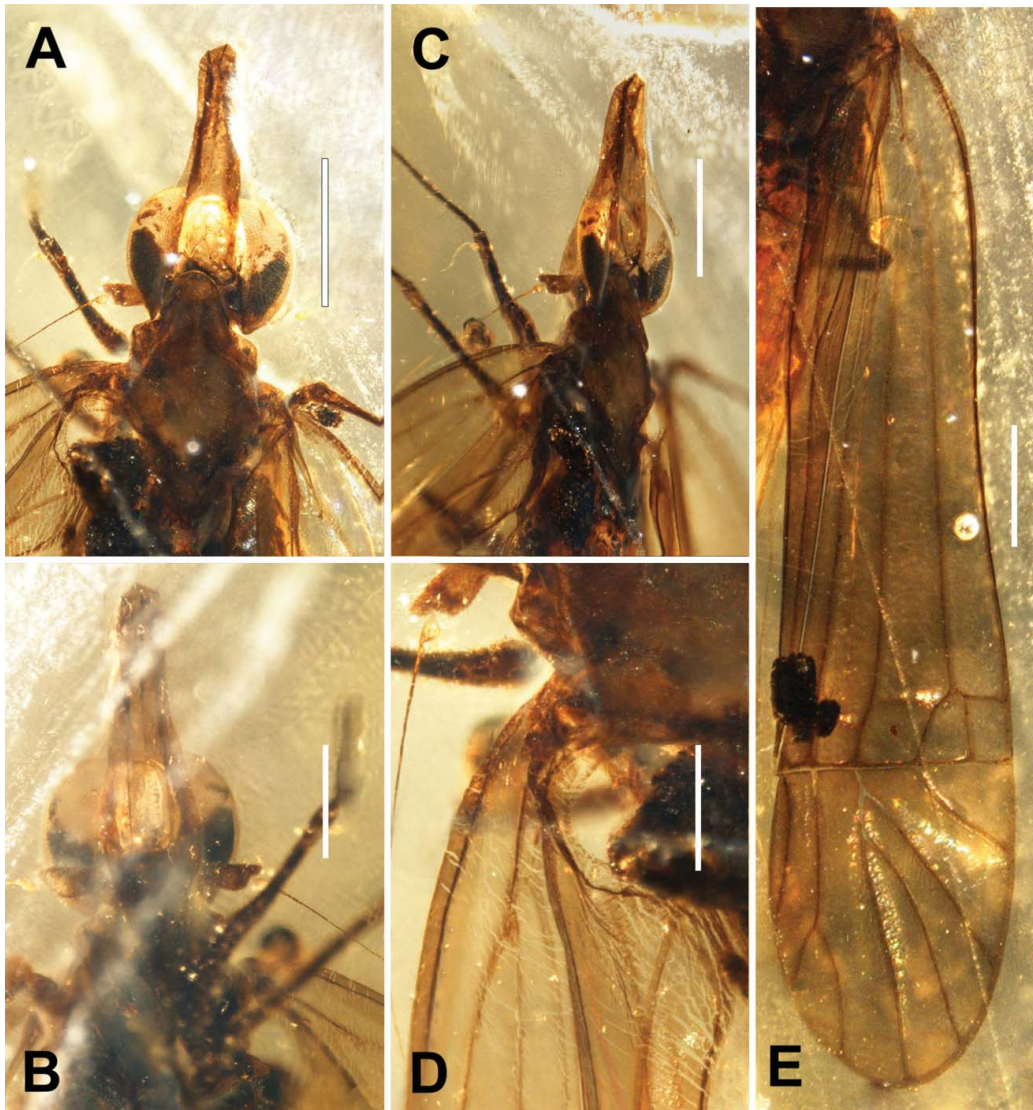


Figure 2. *Quizqueiplana alexbrowni* gen. et sp. nov., light stereomicroscope images of paratype. **A**, head, pronotum and mesonotum, dorsal view; **B**, head, ventral view; **C**, head, pronotum and mesonotum, oblique lateral view; **D**, base of left forewing; **E**, right forewing; Scale bars: A–C, E = 1 mm; D = 0.25 mm.

paratype, 5.43 mm); body length (from apex of vertex to tip of anal tube): 3.40 mm (holotype, 3.40 mm, abdomen of paratype is destroyed apically); forewing length: 3.35–4.07 mm (holotype, 3.35 mm, paratype, 4.07 mm).

Colouration. General colouration yellowish brown.

Head and thorax. As mentioned above for the genus. Head including the eyes (Figs 2A–C, 3A–C) slightly wider than pronotum (1.36:1). Vertex (Figs 2A, 3A) projecting beyond the eyes (1.59 times longer than length of eye), in a shape of a long cephalic process, angulate apically, nearly four times as wide as long in midline (3.7:1); its lateral margins slightly converging apically (Fig. 2A). Pronotum (Figs 2A, 3A–C) 0.26 times longer in midline than vertex, distinctly shorter than mesonotum in midline

(0.33:1); lateral carinae slightly keeled, converging anteriorly, anterior margin in median portion strongly convex; disc of pronotum elevated, without median carina, hind margin angulately concave. Mesonotum (Figs 2A, 3A) with anterior margin clearly produced medially, with lateral carinae; 0.97 times wider at widest part than its medial length. Pronotum and mesonotum together medially 1.06 times as long as median length of the vertex.

Forewings. Subhyaline, long and narrow, 4.2 times longer than its widest part, with slightly concave costal margin, costal area thin without cross veins; nodal line present at distal seven-tenths of forewing; basal cell triangular, elongated and truncated distally; claval suture distinct; Sc + R separating in a two branched ScP + RA1

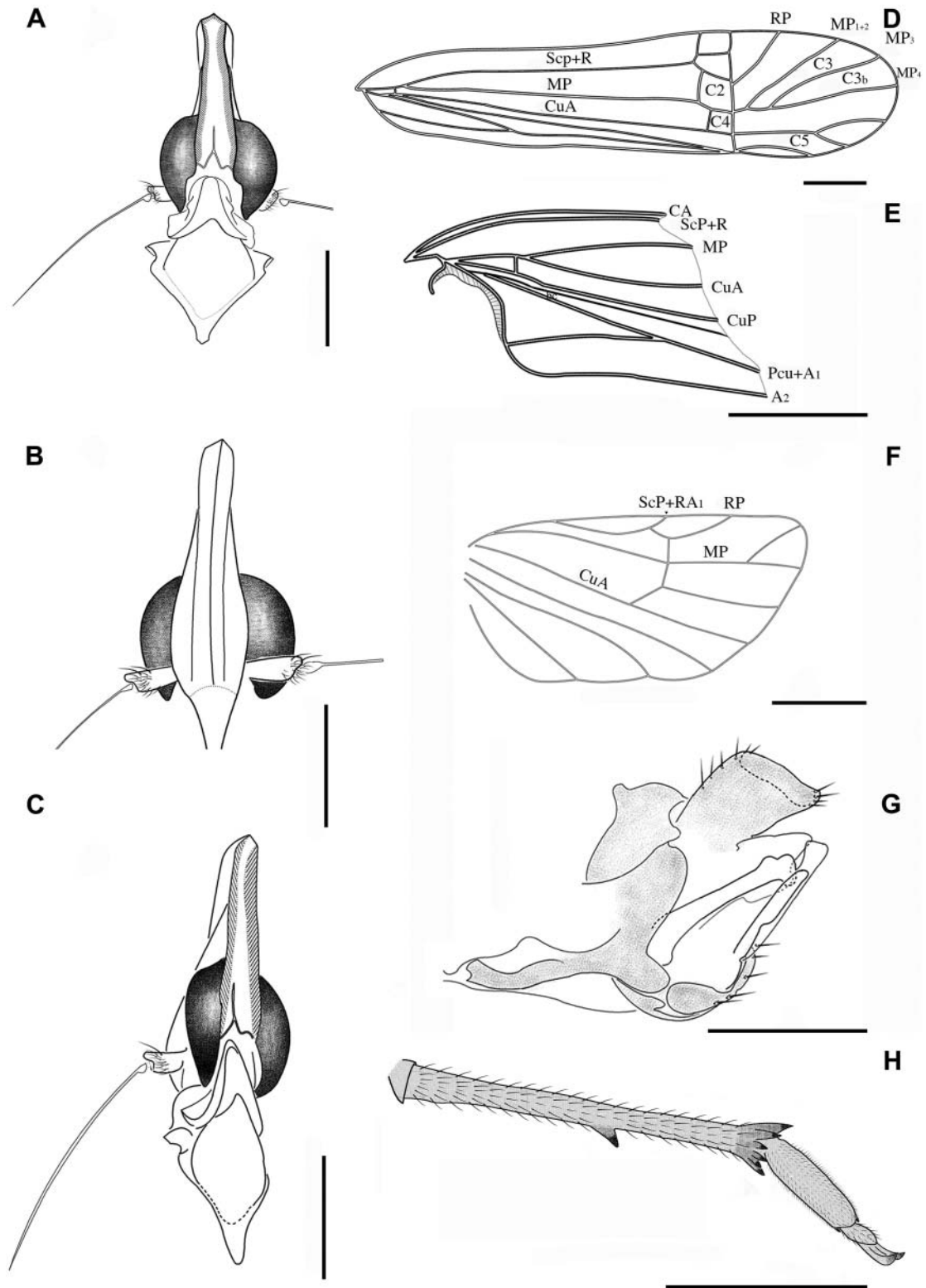


Figure 3. *Quizqueiplana alexbrowni* gen. et sp. nov., paratype. **A**, head, pronotum and mesonotum, dorsal view; **B**, head, ventral view; **C**, head, pronotum and mesonotum, oblique lateral view; **D**, right forewing; **E**, base of right forewing; **F**, right hind wing (reconstruction from the folded wing); **G**, female genitalia; **H**, metathoracic tibia and tarsi. Scale bars: A–C, E = 0.5 mm; D = 1 mm; F–H = 0.25 mm.

and a monobranched RP; these 3 branches united by *ir* closing at antenodal C1 and aligned with second half of RA forming a nodal line; Sc + R and M with a short common stem after the basal cell, two *r-m* veinlets enclosing C2, the distal one at the nodal line; M simple before nodal line, forking in 3 branches M_{1+2} , M_3 , M_4 (holotype as M_1 , M_2 , M_{3+4} on the left side; Fig. 1A, B); C3 and C3b open (C3a also open in holotype; Fig. 1A, B), both post-nodal cells; C4 antenodal, closed by 2 *m-cua* veinlets, the distal one at the nodal line; CuA forking at nodal line in a 2-branched CuA1 and CuA2 joining the tegmen margin; Pcu uniting A_1 at basal 2/5 of clavus; corium with 3 closed subapical prenodal cells C1, C2, C4, and 9 apical post-nodal open cells, distinctly longer than the subapical ones.

Hind wings. Translucent, well developed, 0.9 times as long as forewings, posterior margin sinuate; Sc + R single, forking apically into ScP + RA and RP, median *r-m* veinlet single, M and CuA each with 2 branches, median *m-cua* veinlet single, CuP, Pcu and A_1 simple.

Legs. Elongate, simple (not dilated or flattened); the post-coxal processes (Fig. 1D) spine-like, outgrowth from the posterior surface of the postcoxa, thin, spatulate and papery; hind tibia with single lateral spine medially and six spines apically; first metatarsomere with 2 lateroapical spines and sole with pad of dense and short setae; second metatarsomere shorter than first, without spines and its sole with hair-shaped setae; first metatarsomere twice as long as second and third metatarsomeres combined.

Female terminalia. Anal tube approximately 1.48 times as long as medial width in ventral view, truncate apically; in lateral view narrow basally, expanded to its apex, ventral margin relatively straight and long, ventrolateral angle of anal tube slightly produced; epiproct is very short and small, not surpassing posterior margin of anal tube in dorsal view. Gonoplasts triangularly elongate, far surpassing the apex of anal tube. Female sternum VII with hind margin weakly concave.

Remarks. *Quizqueiplana* is closely related to the Oriental genus *Symplana* (southern India, Sri Lanka and southern China) according to its long vertex, and is closely related to the genera *Symplana* and *Symplanella* according to its forewing venation (Fennah 1963, fig. 1a–e, 1987, fig. 6). However *Quizqueiplana* differs from *Symplana* by its subparallel lateral carinae of the frons (converging above the frontoclypeal suture in *Symplana*) and the pedicel clearly extending beyond the subapical depression (not so in *Symplana*). The new genus differs from *Symplanella* by its long vertex.

In the holotype (Fig. 1A, B), M is 3-branched as M_{1+2} , M_3 , M_4 on one side and as M_1 , M_2 , M_{3+4} on another side. As this last figure is also observed in the paratype, this is the one we retain in the species description. Media characters are however difficult to evaluate as an important

disparity is observable in Augilini genera for the terminal branches of the media (from 3 to 6 branches or even with a net of apical veinlets in *Cicimora*, *Augilodes* and *Dis-cote*) and interpretation of homologies between species is rather difficult. Following the first principle of Bourgoïn *et al.* (2015) in which vein forks should guide the priority of recognition of vein branches rather than their number and topology, various patterns can be observed in Augilini, such as: M_{1+2} , M_3 , M_4 in *Symplana viridinervis* Kirby (Fennah 1963), *Signoreta*, *Augilina* and *Pseudosymplanella*; M_{1+2} , M_3 , M_4 , M_5 or M_1 , M_2 , M_3 , M_4 as in various *Symplanella* species; M_1 , M_2 , M_3 , M_4 , M_5 in *Symplana*, *Tubilustrium* and *Cano*; M_1 , M_2 , M_3 , M_4 , M_5 , M_6 in *Symplanodes*; or even M_1 , M_2 , M_{3a} , M_{3b} , M_{4a} , M_{4b} as in *Symplana major* Fennah, 1963. The M_1 , M_2 , M_{3+4} pattern of *Quizqueiplana* gen. nov. is also observable in *Anthracidium*.

Origin of the Caliscelidae and Augilini lineages

According to molecular phylogenies (Urban & Cryan 2007), the family Caliscelidae might represent a relatively young group, and accordingly Gnezdilov (2013c) hypothesized a rapid evolution of the issidoid group of families of Fulgoroidea to which Caliscelidae belongs. Within the family and the subfamily Caliscelinae, only the tribe Caliscelini Amyot & Serville (28 genera) is distributed worldwide; the tribe Peltonotellini Emeljanov (19 genera) is known from the Palearctic region and Taiwan in the Old World, and also in the New World. In the subfamily Ommatidiotinae (24 genera), the tribe Adenissini Dlabola is distributed in the Palearctic, the north-east of Afrotropical and in Oriental regions; the monogeneric tribe Ommatidiotini is endemic to the Palearctic region; and Augilini are known from the Oriental region and Madagascar (see Supplementary Material). The new fossil genus *Quizqueiplana* is unexpected in enlarging the distribution of Ommatidiotinae into the New World with particular importance for the Augilini.

The recent discovery of Augilini in Madagascar raised the question of the origin of the Caliscelidae lineage (Gnezdilov & Bourgoïn 2009). Three scenarios were suggested to explain their current Gondwanian disjunction pattern: (1) a 160 Ma Gondwanian Caliscelid lineage; (2) a 70 Ma old Indian lineage; and (3) a 55 Ma Laurasian caliscelid lineage (Gnezdilov & Bourgoïn 2009). If this last hypothesis would fit with a relatively young issidoid lineage as recently suggested (Gnezdilov 2013a), none of these scenarios would be exclusive and a combination between older vicariance patterns with more recent dispersal events would still be possible (Sanmartin & Ronquist 2004). Unfortunately, this first Caliscelidae fossil taxa does not allow us to answer this question, as it

dates back only to the Miocene. Nevertheless it considerably extends the distribution of Augilini and helps to improve dating of this clade, which is at least 16–20 million years old.

Augilini is a tropical group. Accordingly in the Laurasian caliscelid origin hypothesis, the disjunct distribution of Augilini (Neotropical and Oriental regions and Madagascar) might have resulted from the reduction of an originally wider area of distribution attained during the Late Paleocene by dispersals and migrations (Davis *et al.* 2002) when the climate was warmer and more uniform (Zachos *et al.* 2001, 2008), through land connections between North America and Europe, covered with tropical forest. The separation of the Old and New World and the global cooling and drying that took place after the Middle Miocene Climatic Optimum have therefore isolated the lineages and fragmented their areas of distribution, as already hypothesized for other groups of animals (Eskov 1984). A similar scenario was suggested for another planthopper taxon, the Colpopterinae (Nogodinidae) known from the Neotropics and southern Africa (Gnezdilov 2012). Such a hypothesis would also imply that Augilini would be at least a Late Paleocene–Early Eocene lineage. Unfortunately, such a distribution pattern explained by dispersal events is not falsifiable and remains only an ad hoc explanation.

Most Augilini are recorded only from bamboo (Poaceae, Bambusoideae): *Anthracidium albosignatum* Emeljanov, 2013 and *Discote scutifer* (Fennah, 1963) (Emeljanov 2013), *Augilina namboina* Gnezdilov, 2013 (Gnezdilov 2013b), *Pseudosymplanella nigrifasciata* Che, Zhang & Webb, 2009 (Che *et al.* 2009); and from *Neosinocalamus* sp., another Bambusoideae host plant also recorded for *Symplanella recurvata* Yang & Chen, 2014 (Yang & Chen 2014). Accordingly and in a parsimonious scenario excluding subsequent or ad hoc host plant shifts, the Augilini ancestor would therefore have been a Bambusoideae feeder not older than the host plant group. Bambusoideae are now dated back to the latest Cretaceous before the loss of the land bridge between India and Madagascar (Prasad *et al.* 2011) and thus remain in agreement with a Laurasian origin for the Augilini or an Indo-Malagasian lineage, but would exclude an older Gondwanian origin of the tribe.

Only a phylogenetic analysis at genus level (including *Quizqueiplana*), providing a succession of the different lineages in time with their distributions, will be able to clarify these questions in the future and test the proposed scenarios to explain this unexpected distribution of the Augilini.

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Supplemental material

Supplemental material for this article can be accessed here: <http://dx.doi.org/10.1080/14772019.2015.1032376>

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