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, 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-Malagasy lineage with an early vicariance and later dispersion events, remain two possible explanations of the origin of the Augilini.


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

Introduction


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 & Bourgoin 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)

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 Bourgoin & Huang (1990) and Bourgoin (1993) for male and female genitalia, respectively, and Bourgoin et al. (2015) for vein nomenclature.

**Systematic palaeontology**

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**Family Caliscelidae** Amyot & Serville, 1843

**Subfamily Ommatidiotoidea** Fieber, 1875

**Tribe Augilini** Baker, 1915

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

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**Type species.** *Quizqueiplana alexbrowni* Bourgoin & 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.

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**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 1B, 2B, 3B) 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 subeylindrical, 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 (Bourgoin 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.

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*Quizqueiplana alexbrowni* Bourgoin & 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 Búcarca 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 Búcarca 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.
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

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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.
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 tarsa. 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 M1+2, M3, M4 (holotype as M1, M2, M3+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 related to the genera Quizqueiplana with hind margin weakly concave. Female sternum VII anal tube in dorsal view. Gonoplacs triangularly elongate, very short and small, not surpassing posterior margin of its apex, ventral margin relatively straight and long, ventrally furred apically; in lateral view narrow basally, expanded to 1.48 times as long as medial width in ventral view, trun-
cated. Tarsi are however difficult to evaluate as an important character. 

**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, Cu,P, Pcu and A1 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, ventral lateral angle of anal tube slightly produced; epiproct is very short and small, not surpassing posterior margin of anal tube in dorsal view. Gonopods triangularly elongate, far surpassing the apex of anal tube. Female sternum VII 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 foroventer vertex (Fennah, 1963, fig. 1a–e, 1987, fig. 6). However Quizqueiplana differs from *Symplana* by its subparallel lateral cariniae of the frons (converging above the frons of *Symplanella* and the pedi-
cel 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 M1+2, M3, M4 on one side and as M1, M2, M3+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 *Discote*) and interpretation of homologies between species is rather difficult. Following the first principle of Bourgoin *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: M1+2, M3, M4 in *Symplana viridinervis* Kirby (Fennah 1963), *Signoreta, Augilina* and *Pseudosymplanella*: M1+2, M3, M4 or M1, M2, M3, M4 as in various *Symplanella* species; M1, M2, M3, M4, M5 in *Sym-
plana, Tubilustrium* and *Cano*: M1, M2, M3, M4, M5, M6 in *Symplanodes*; or even M1, M2, M3a, M3b, M4a, M4b as in *Symplana major* Fennah, 1963. The Mt, M2, M3+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 isidiod group of families of Fulgoroida 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 Palaearctic region and Taiwan in the Old World, and also in the New World. In the subfamily Ommatidiotinae (24 genera), the tribe Adenissini Diabola is distributed in the Palaearctic, the north-east of Afrotropical and in Oriental regions; the monogeneric tribe Ommatidiotini is endemic to the Palaearctic 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 & Bourgoin 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 & Bourgoin 2009). If this last hypothesis would fit with a relatively young isidiod 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 fossi-
tal 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 Palaeocene by dispersions 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 Coloppterinae (Nogodinidae) known from the Neotropics and southern Africa (Gnezdilov 2012). Such a hypothesis would also imply that Augilini would be at least a Late Palaeocene–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-Malagasy lineage, but would exclude an older Gondwanan 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

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References


