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Short communication

New Coniopterygidae (Neuroptera) from the upper Cenomanian Nizhnyaya Agapa amber, northern Siberia

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ABSTRACT

Libanoconis siberica sp. nov. and two specimens of uncertain affinities (Neuroptera: Coniopterygidae) are described from the Upper Cretaceous (upper Cenomanian) Nizhnyaya Agapa amber, northern Siberia. The new species is distinguished from *L. fadiacra* (Whalley, 1980) by the position of the crossvein 3r-m being at a right angle to both RP1 and the anterior trace of M in both wings. The validity of the genus *Libanoconis* is discussed. It easily differs from all other Aleuropteryginae by a set of plesiomorphic character states. The climatic conditions at high latitudes in the late Cenomanian were favourable enough for this tropical genus, hitherto known from the Gondwanan Lebanese amber. Therefore, the record of a species of *Libanoconis* in northern Siberia is highly likely.

1. Introduction

The small-sized neuropteran family Coniopterygidae comprises ca. 570 valid extant species, and is distributed over much of the globe (Oswald, 2018). Thirty-two fossil species are known from the Late Jurassic to the Miocene (pers. data). Of these, sixteen species have been described from Cretaceous ambers, i.e., from Lebanese, Charentese, Burmese, New Jersey, Vendean and Taimyr ambers (Engel, 2016; Liu and Lu, 2017; Makarkin and Perkovsky, 2017).

The Taimyr amber localities are situated in northern Siberia, and of great importance for understanding the biota in the northern extremes of Cretaceous Laurasia. Five species belonging to three neuropteran families (i.e., Coniopterygidae, Sisyridae, and Hemerobiidae) are known from the Santonian Taimyr amber localities of Yantardakh and Ugolyak (Meinander, 1975; Makarkin, 1994; Perkovsky and Makarkin, 2015; Makarkin and Perkovsky, 2016, 2017). However, no Neuroptera have been described from the older (late Cenomanian) Taimyr amber locality of Nizhnyaya Agapa. Zherikhin (1978) reported on three specimens of Coniopterygidae, preliminarily assigning them to one undescribed species. Herein we describe these specimens.

2. Material and methods

This study is based on three specimens originally embedded in two pieces of amber from the Nizhnyaya Agapa locality in Taimyr Peninsula (northern Siberia). Its location is shown in the map in Gumovsky et al (2018, fig. 1). Amber was collected from the upper horizons of the Dolgan Formation (Zherikhin, 1978), and is dated to late Cenomanian, mainly by pollen (Saks et al., 1987; Babushkin et al., 2000; Lebedeva and Zverev, 2003; Lebedeva, 2008). Rasnitsyn et al. (2016) characterized this amber locality in more detail.

The photographs were taken by A.P. Rasnitsyn (PIN) using a Leica M165 stereomicroscope with an attached Leica DFC 425 digital camera. Line drawings were prepared by VM using Adobe Photoshop CS3.

The venational terminology follows Makarkin and Perkovsky (2017). Terminology of wing spaces and details of venation (e.g., traces, veinlets) follows Oswald (1993).

Abbreviations: AA1–AA3, first to third anterior anal vein; CuA, anterior cubitus; CuP, posterior cubitus; MA and MP, anterior and posterior branches of media; RA, anterior radius; RP, posterior radius; RP1, proximal-most branch of RP; ScP, subcosta posterior.

Institutional abbreviations: PIN, Paleontological Institute of the Russian Academy of Science, Moscow, Russia.

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3. Systematic paleontology

Order Neuroptera Linnaeus, 1758
Family Coniopterygidae Burmeister, 1839
Subfamily Aleuropteryginae Enderlein, 1905

Genus *Libanoconis* Engel, 2002

Revised diagnosis. In both wings, RP1 running smoothly towards wing margin (not strongly angled at 3r-m), and crossvein 3r-m in distal position connecting RP1 and M distad its fork; in hind wing, M bifurcate.
Species included. L. fadiacra (Whalley, 1980) (type species) from the lower Barremian Lebanese amber and *L. siberica* sp. nov. from the upper Cenomanian Taimyr amber.
Remarks. The genus is assigned to the subfamily Aleuropteryginae based on the branching of M in the forewing: it is trifurcate in most genera of Aleuropteryginae, whereas only bifurcate in all Coniopteryginae, both fossil and extant. In the single genus *Cretaconiopteryx* Liu and Lu, 2017 of the Cretaceous subfamily Cretaconiopteryginae, M is also bifurcate, but this genus strongly differs by other characters.

Libanoconis siberica sp. nov.
Figs. 1–4

Derivation of name. From the Latin *Sibericus* [*-a*, *-um*], Siberian.
Material. Holotype PIN 3426/237-1, collected in 1973 during a PIN expedition; an incomplete specimen in amber broken into six pieces (Fig. 1A).
Locality and horizon. Russia: Krasnoyarskiy Krai: Taymyrsky Dolgano-Nenetsky District: western Taimyr Peninsula: Agapa River Basin: right bank of the Nizhnyaya Agapa River, 40 km below its source, Ladonnakh Lake; Nizhnyaya Agapa locality ("lens 16").
Diagnosis. May be easily distinguished from the type species of the genus by position of crossvein 3r-m at nearly a right angle to both RP1 and anterior trace of M in both wings (3r-m distinctly oblique in *L. fadiacra*).
Description. Head very poorly preserved, with eyes moderately large.

Legs not preserved except one of tarsi. Tarsus relatively short, covered with short, dense setae; basitarsus approximately as long as second and third tarsomeres together; fourth tarsomere flattened, strongly bilobed; terminal tarsomere slender; claw probably somewhat dilated basally.

Thorax very poorly preserved; details not discernible. Abdomen not preserved.

Forewing ca. 1.60 mm long as preserved (estimated complete length ca. 1.9 mm), 0.63 mm wide. Costal space very narrow medially, slightly dilated basally and distally. Basal subcostal veinlets poorly discernible. ScP, then presumable ScP1 stout, running nearly parallel to costal margin. Crossvein-like part of ScP2 located much proximad ra-rp. RA, then distal part of presumable ScP2 stout. Subcostal space very narrow basally, broad distad 1r-m; 1scp-r not detected (poorly discernible). RP originated very far from wing base, with one distal branch (RP1). RP1 space broad, with one crossvein connecting presumable ScP2 and RP distad origin RP1. M basally not fused with R. Anterior trace of M without long setae on weak thickenings, distally with two long, widely spaced pectinate branches (M1, M2). Three crossveins between M, R/RP: basal 1r-m short connecting R, M; 2r-m long connecting RP in proximal part, M; 3r-m long, connecting RP1 and M distad origin M2 at nearly right angle to both veins. Two crossveins between M, Cu: basal 1m-cu short, located slightly proximad 1r-m; 2m-cu long, located proximad 2r-m. Cu dividing into CuA, CuP near wing base, proximad 1m-cu. CuA, CuP long, simple, slightly divergent distally. Crossvein between CuA, CuP (1icu) slightly oblique, located approximately in middle position between 1r-m and 2r-m. Two crossveins between CuP, AA1 (1cu-a, 2cu-a), located relatively near to one another. AA1, AA2 long, connecting by long crossvein 1aa1-aa2. Crossvein 1aa2-aa3 not detected (poorly discernible). Setae of fringe along costal margin short, along basal posterior margin moderately long.

Hind wing incompletely preserved not allowing measurement. RP with one distal branch (RP1) which originates far from apical wing margin and running smoothly, not angled at 3r-m. RP1 space with one crossvein connecting ScP2, RP distad origin RP1. M bifurcate slightly distad fork of RP. 3r-m long, connecting RP1 and M far distad its fork at nearly a right angle to both veins. CuA, CuP, AA1, AA2 simple.

Coniopterygidae indet.
Fig. 5

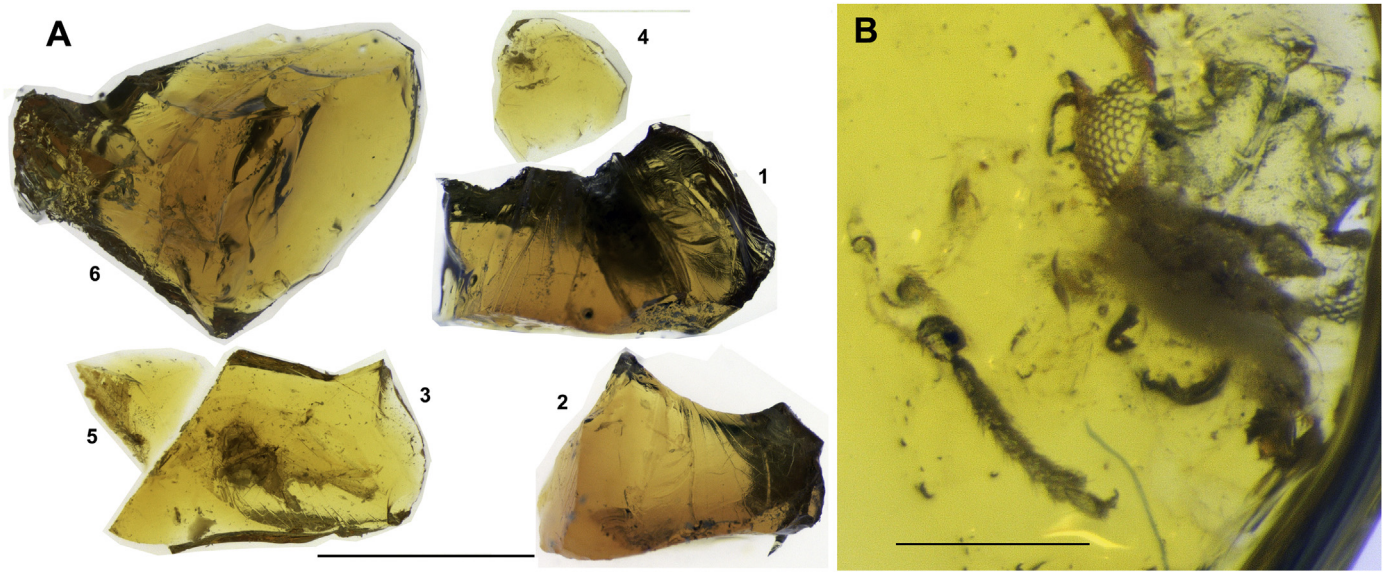

Fig. 1. *Libanoconis siberica* sp. nov. Holotype PIN 3426/237-1. A, specimen as preserved, broken into six pieces (##1–6); pieces ##5 and 6 lack parts of the specimen; B, head in dorso-frontal view and one of tarsi (piece #4). Scale bars represent 2 mm (A), 0.2 mm (B).

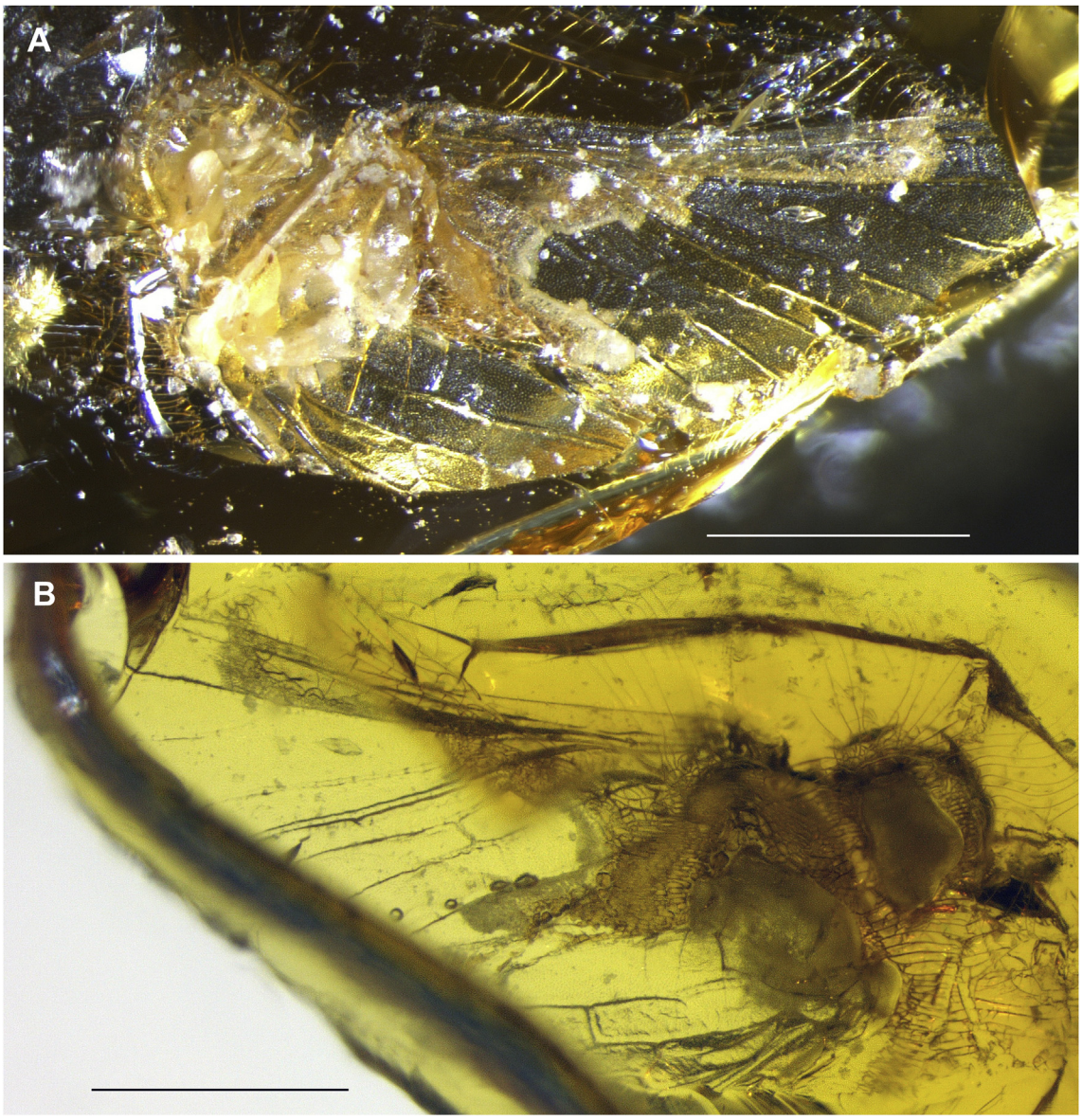

Fig. 2. *Libanoconis siberica* sp. nov. Holotype PIN 3426/237-1, piece #3. A, anterior part of specimen, dorsal view. B, same, ventral view. Scale bars represent 0.5 mm.

Material. PIN 3426/237-2, an anterior part of body, with fragmentarily-preserved and crumpled wings. PIN 3426/238, a fragmentary poorly-preserved specimen; both collected in 1973 during a PIN expedition.

Locality and horizon. Russia: Krasnoyarskiy Krai: Taymyrsky Dolgano-Nenetsky District: Taimyr Peninsula: Nizhnyaya Agapa locality ("lens 16").

Description. PIN 3426/237-2 (Figs. 5A, B). Head capsule dorsoventrally elongated, ca. 0.3 mm high; covered with short setae. Membranous antennal sockets large, with clearly visible boundaries. Eyes relatively small (eye height/head height ratio ca. 0.46). Terminal segment of maxillary and labial palpi fusiform, relatively slender (not especially swollen). Antennae 23-segmented, covered by short setae; scapus and pedicellus nearly equal in size, distinctly larger than flagellomeres; basal flagellomeres nearly as long as wide, distal flagellomeres slightly elongated.

Prothorax short, its proximal part covers occipital part of head. Legs typical for family, covered with relatively short setae. Profemur rather stout, nearly as long as protibia; protibia relatively slender. Meso- and metafemora more elongate and slender than profemur. Abdomen preserved incompletely, details not discernible.

Wings crumpled and very incomplete; diagnostic characters not discernible.

PIN 3426/238 (Figs. 5C, D). Very poorly-preserved specimen, whose only anterior part is more or less discernible, but no diagnostic characters are detectable.

Remarks. Both specimens are too fragmentary to assign them to a genus and species. Based on the 23-segmented antenna, specimen PIN 3426/237-2 is most similar to *Glaesoconis* Meinander, 1975 (24–32 antennal segments) and *Apoglaesoconis* Grimaldi, 2000 (23–25 antennal segments). However, this character state is unclear in *Libanoconis*, and therefore it may belong theoretically to this genus or even to the species *L. siberica* sp. nov.

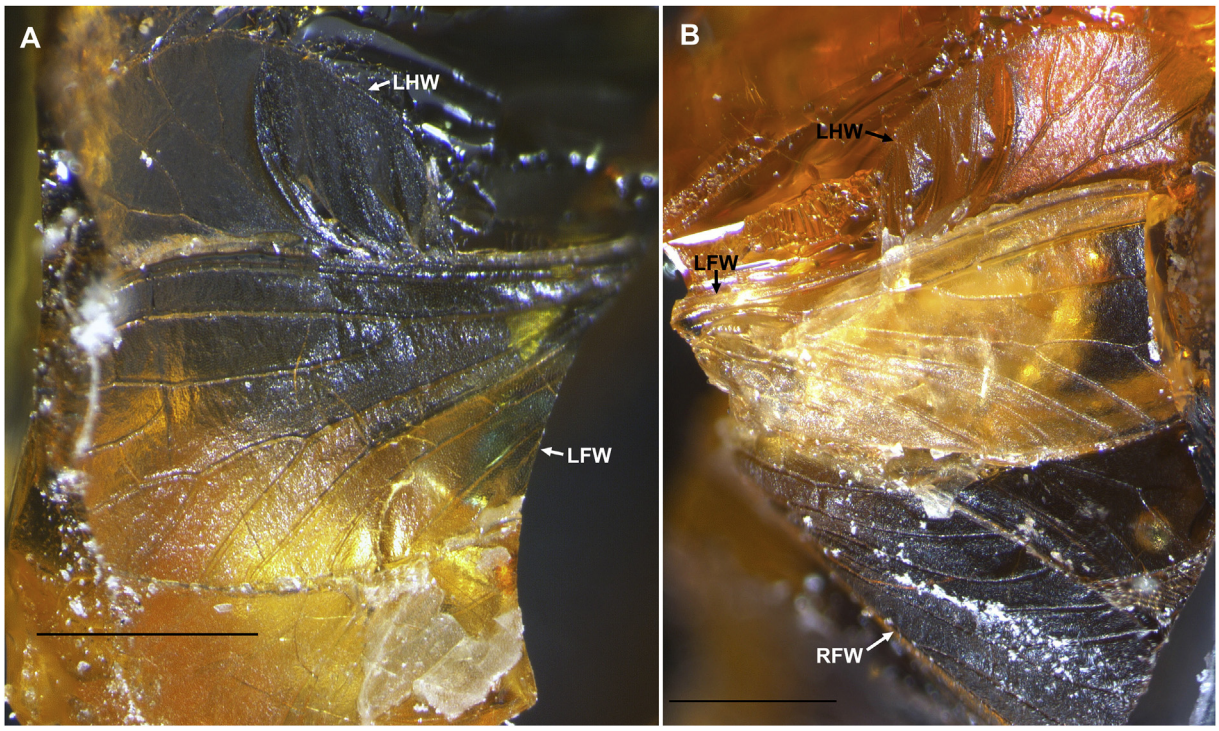

Fig. 3. *Libanoconis siberica* sp. nov. Holotype PIN 3426/237-1. A, wings, dorsal view (piece #2). B, same, ventral view (piece #1). Scale bars represent 0.5 mm. LFW, RFW, left and right forewings; LHW, left hind wing.

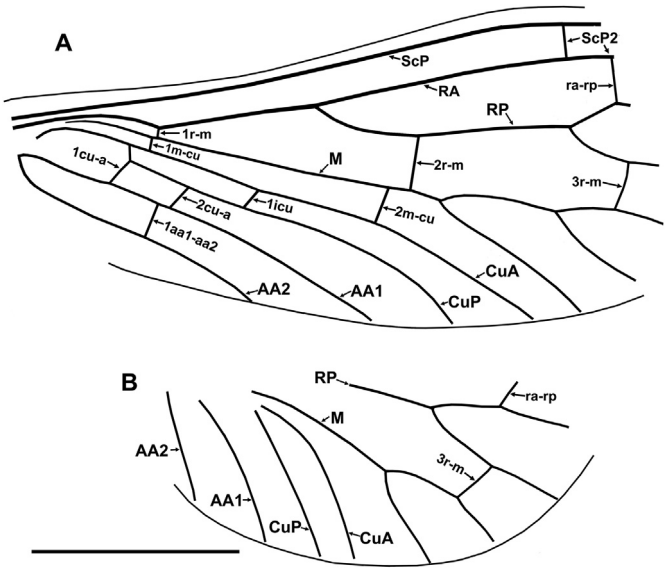

Fig. 4. *Libanoconis siberica* sp. nov. Wing venation of the holotype PIN 3426/237-1. A, forewing. B, hind wing. Scale bar represents 0.5 mm (both to scale).

4. Discussion

4.1. Validity of the genus Libanoconis

The genus *Libanoconis* Engel, 2002 contained hitherto only the type species, which was originally described as *Glaesoconis fadiacra* Whalley, 1980 from the Lebanese amber locality of Jouar-Es-Soûss (early Barremian or older: Maksoud et al., 2017). The original description was very incomplete and partly incorrect. Based on this description, Engel (2002) erected the new genus *Libanoconis*. Nel et al. (2005) examined the holotype, provided its new drawing (Nel et al., 2005, fig. 5), but did not re-describe the species. They analyzed Engel's diagnosis of the genus, and found that only one character allowed it to be distinguished from the other genera (i.e., RP1 running smoothly towards wing margin, not strongly angled at 3r-m). The other character states are either present in other genera or unclear. Nel et al. (2005) concluded that the validity of *Libanoconis* is provisional.

The venation of *Libanoconis siberica* sp. nov. provides new evidences on the validity of the genus. Besides the course of RP1, characteristic of the genus, we found that in this species the hing wing M is bifurcate. This is also observed in *L. fadiacra*, judging from its drawing (see Nel et al., 2005, fig. 5). Besides *Libanoconis*, the hind wing M is bifurcate only in one Cretaceous aleuropterygine genus, i.e., *Garnaconis* Perrichot and Nel in Perrichot et al. (2014) from the Cenomanian/Turonian of Vendean amber (France), but in this genus RP1 is angled, M is bifurcate in the forewing and there are long setae on the thickenings of M (see Perrichot et al., 2014, fig. F2). The M is trifurcate in all other known genera of the Cretaceous Aleuropteryginae (i.e., *Achlyoconis* Engel, 2016; *Alboconis* Nel et al., 2005; *Apoglaesoconis*; and *Glaesoconis*).

A combination of the bifurcate M in the hind wing (#1), the smooth course of RP1 (#2) and the distal position of the crossvein 3r-m connecting RP1 and M distad its fork in the forewing (#3) allow *Libanoconis* to be easily distinguished from all other Aleuropteryginae, both extant and fossil.

However, the bifurcate M in the hind wing is also present in all extant Aleuropteryginae and *Archiconis* Enderlein, 1930 from Baltic amber, and most extant and fossil Coniopteryginae (e.g., in *Libanosemidalis* Azar et al., 2000 from Lebanese amber). Additionally, this condition occurs in *Cretaconiopteryx* from mid-Cretaceous Burmese amber belonging to the subfamily Cretaconiopteryginae, which might represent the basalmost lineage of the family (Liu and Lu, 2017). Therefore, character state 1 is certainly plesiomorphic.

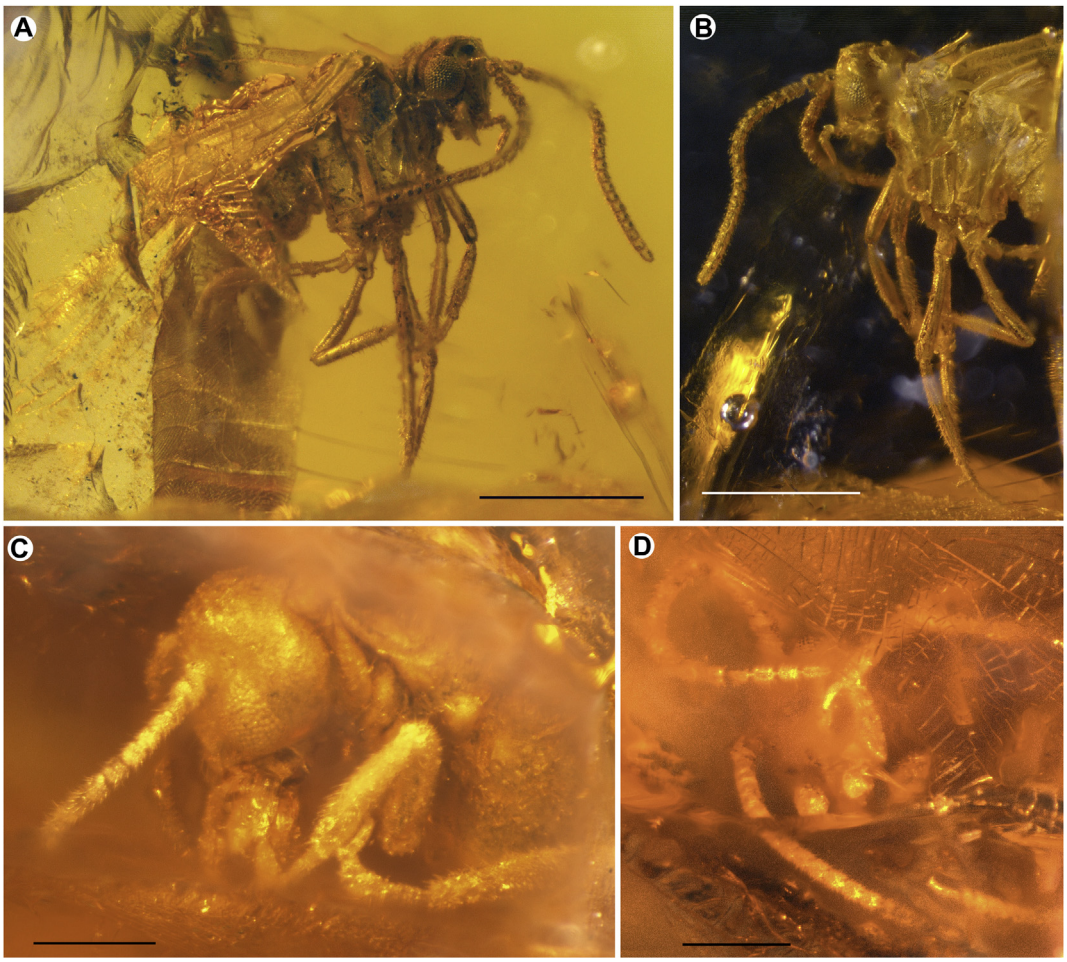

Fig. 5. Coniopterygidae indet. A, PIN 3426/237-2, lateral view of specimen, right side; B, PIN 3426/237-2, lateral view of specimen, left side; C, PIN 3426/238, anterior part of specimen, lateral view; D, PIN 3426/238, anterior part of specimen, frontal view. Scale bars represent 0.5 mm (A, B), 0.2 mm (C, D).

Character state 2 (i.e., smooth course of RP1) is most probably plesiomorphic as it is present in *Cretaconiopteryx* and many extant Coniopteryginae.

Character state 3 (i.e., distal position of 3r-m) is present in *Cretaconiopteryx* and the vast majority of fossil and extant Aleuropteryginae and Coniopteryginae, and therefore is certainly plesiomorphic (see Meinander, 1972).

Therefore, all these diagnostic character states (##1–3) are plesiomorphic and only allow *Libanoconis* to be distinguished from the other Aleuropteryginae, but not from every genus of the family. For example, all these conditions are present in *Cretaconiopteryx*.

4.2. Paleobiogeographical implications

The Lebanese amber *Libanoconis fadiacra* lived in dense tropical or subtropical forests in a moderate to hot and humid climate (Azar et al., 2003, 2010). This territory belonged in the early Barremian to northern Gondwana (Azar, 2007; Peris et al., 2016) (Fig. 6). We assigned the new Taimyr species *L. siberica* sp. nov. to the same genus. But could a Gondwanan Lebanese amber genus occur in northern Siberia in the late Cenomanian? There are climatic and paleobiogeographical data that would support a positive answer to this question.

(1) During the Cenomanian there was a progressive long-term warming trend with a thermal maximum in the latest Cenomanian–early Turonian. In this period, climate changed from warm greenhouse conditions with moderately low latitudinal thermal gradients to hot greenhouse conditions with temperatures at high latitudes approaching those of low latitudes (Huber et al., 1995, 2002; Clarke and Jenkyns, 1999; Jenkyns and Wilson, 1999; Pucéat et al., 2003; Keller, 2008). Therefore, the climate in northern Siberia in the late Cenomanian was favourable enough for the tropical genus.

(2) There are many examples of wide distribution of closely related insect taxa in the Early or Late Cretaceous. In particular, the extant dipteran genus *Leptoconops* Skuse, 1889 (Ceratopogonidae), most species of which today occur in tropical and subtropical regions, and during the Early and Late Cretaceous it was widely distributed across Laurasia (including Taimyr amber localities Nizhnyaya Agapa and Yantardakh) and northern Gondwana (including Lebanese amber) (Szadziewski, 1996; Szadziewski et al., 2015). In general, some other genera of Ceratopogonidae known from Lebanese amber (e.g., *Austroconops* Wirth and Lee, 1958, *Protoculicoides* Boesel, 1937) are also distributed in many Lower and Upper Cretaceous Laurasian localities, including Taimyr (Nizhnyaya Agapa and Yantardakh) amber (Szadziewski, 1996, 2018). The genus *Dryinus* Latreille, 1804 (Hymenoptera: Dryinidae) distributed today mainly in tropical regions was recorded in Cenomanian from both the northern Siberian Nizhnyaya Agapa and Myanmar tropical forests (Ponomarenko, 1981; Guglielmino et al., 2018).

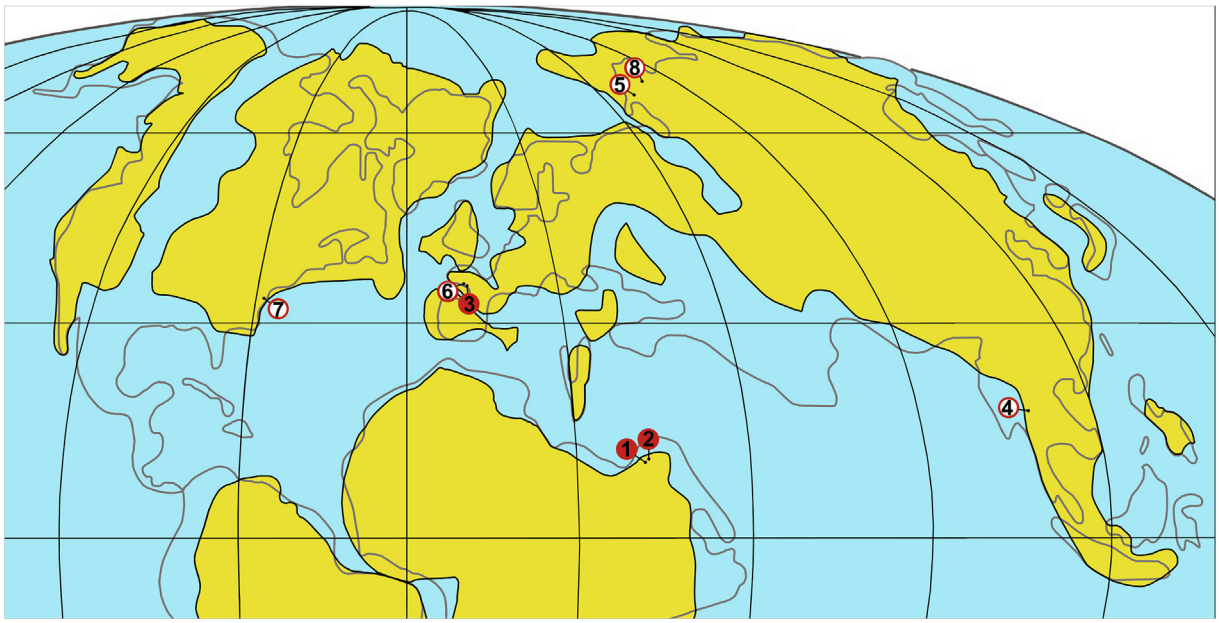

Fig. 6. Palaeomap of the late early Albian (redrawn from Smith et al., 1994) showing known localities of the Cretaceous Coniopterygidae. 1, Lebanese amber (Jouar-Es-Soûss), lower Barremian; 2, Lebanese amber (Hammana), upper Barremian; 3, Charentese amber (Archingeay), uppermost Albian; 4, Burmese amber, lowest Cenomanian; 5, Taimyr amber (Nizhnyaya Agapa), upper Cenomanian; 6, Vendean amber, Cenomanian–Turonian; 7, New Jersey amber, Turonian; 8, Taimyr amber (Yantardakh), Santonian. The Lower Cretaceous localities are shown by red circles, the Upper Cretaceous localities by white circles. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Unfortunately, Neuroptera are represented in Lebanese amber by only a few species, all belonging to monotypic genera unknown from other faunas (except *Libanoconis*). However, some neuropteran taxa were widely distributed; e.g., the definitely closely related species of the *Principiala* genus-group (Ithonidae) were distributed in the Gondwanan Brazil (late Aptian of the Crato Formation: Makarkin and Menon, 2007) and the Laurasian China (Barremian of the Yixian Formation: Makarkin et al., 2012) and Europe (Barremian of Upper Weald Clay, England: Jepson et al., 2009). This genus-group is also found in mid-Cretaceous Burmese amber (Lu et al., 2017).

Therefore, the record of a Lebanese amber genus from the late Cenomanian of Taimyr can be easily enough explained.

5. Conclusions

We assigned the new species *Libanoconis siberica* sp. nov. from the late Cenomanian of northern Siberia to the Barremian genus *Libanoconis* known hitherto from the Gondwanan Lebanese amber. The characters of *L. siberica* sp. nov. confirm the validity of the genus. Climatic conditions at high latitudes in the late Cenomanian were favourable enough for the tropical genus, and therefore its record there is highly likely.

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