Cretaceous Research 74 (2017) 11–22

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

New taxa of unusual Dilaridae (Neuroptera) with siphonate mouthparts from the mid-Cretaceous Burmese amber

Vladimir N. Makarkin

Institute of Biology and Soil Sciences, Far East Branch of the Russian Academy of Sciences, Vladivostok, 960022, Russia

ARTICLE INFO

Article history:
Received 3 November 2016
Received in revised form
28 December 2016
Accepted in revised form 29 December 2016
Available online 31 December 2016

Keywords:
Upper Cretaceous
Burmese amber
Dilaridae
Cretanallachiinae
Cretadilarinae

ABSTRACT

Cretadilar olei gen. et sp. nov. and *Burmopsychops groehni* sp. nov. (Neuroptera: Dilaridae) are described from the Late Cretaceous (earliest Cenomanian/late Albian) Burmese amber. Their dilarid affinities are supported by two autapomorphies of the family: the reduction of the ligula and the presence of pectinate antennae in males. They are considered to belong to two new subfamilies, Cretanallachiinae subfam. nov. and Cretadilarinae subfam. nov., respectively. These subfamilies are easily distinguished from other dilarids (Dilarinae, Nallachiinae, and Berothellinae) by possessing siphonate mouthparts; however they strongly differ from each other. In particular, the broad gonocoxites 9 of Cretanallachiinae females are not fused to form a distinct ovipositor, and bear long gonostyli, whereas a distinct saber-like ovipositor (short, lacking gonostyli) is present in Cretadilarinae. It is assumed that Cretanallachiinae primarily fed on pollen and Cretadilarinae on the nectar of flowers.

1. Introduction

The Dilaridae is a relatively small family of Neuroptera currently comprised of 98 valid species in four genera (Oswald, 1998; Machado and Rafael, 2010; Zhang et al., 2014a, 2014b, 2014c, 2015, 2016; Aspöck et al., 2015; Liu et al., 2017). Their larvae are predatory, which live in hidden habitats, e.g., in soil and decaying wood, under bark and in the galleries created by other insects in dead trees (Gurney, 1947; MacLeod and Spiegler, 1961; Ghilarov, 1962; Makarkin, 1993). The family is divided into three subfamilies, Dilarinae Newman, 1853, Nallachiinae Navás, 1914, and Berothellinae Liu, U. Aspöck and H. Aspöck in Liu et al., 2017 (Adams, 1970; Oswald, 1998; Liu et al., 2017). The extant dilarids are characterized by unipectinate antennae in males (except for *Berothella* Banks, 1934), and a long hose-like ovipositor in females.

Hitherto, three fossil species of typical Dilaridae (i.e., Dilarinae) has been described, i.e., *Cascadilar eocenicus* Engel, 1999 from the Eocene Baltic amber; this was later assumed to belong to the extant genus *Dilar* Rambur, 1838 (Grimaldi and Engel, 2005); and two species from the mid-Cretaceous Burmese amber (Liu et al., 2017). Recently however, many unusual dilarids have become known from that amber. Of these, *Cretanallachius magnificus* Huang et al., 2015 was initially interpreted as a member of Nallachiinae. Later it was removed from Dilaridae and assigned to an unnamed family within Psychopsoidea (Lu et al., 2016a). The latter authors described two other similar monotypic genera within this superfamily, i.e., *Fiaponeura* Lu et al., 2016b and *Burmopsychops* Lu et al., 2016b. All these genera are remarkable for possessing siphonate mouthparts, and differing greatly from typical dilarids by numerous characters. Nonetheless, all of them are considered herein as belonging to two new extinct subfamilies of Dilaridae, except *Fiaponeura* whose subfamily affinity is unclear.

In this paper, two new species are described: a new species of *Burmopsychops* and a new genus and species. In addition to the eight described specimens of these five species, approximately 15 other undescribed dilarids with siphonate mouthparts are known from Burmese amber in various collections, three of which were figured by Xia et al. (2015, figs. on pp. 90 and 91).

2. Material and methods

This study is based on two female specimens from Burmese amber. The amber pieces were collected in the Hukawng Valley (the state of Kachin in northern Myanmar). The precise mine from which these pieces originated cannot be determined, as they were

---

E-mail address: vnmakarkin@mail.ru.

http://dx.doi.org/10.1016/j.cretres.2016.12.019
0195-6671/© 2016 Elsevier Ltd. All rights reserved.

acquired from a fossil trader. The map of the Hukawng Valley is given by Grimaldi et al. (2002, fig. 1). The volcaniclastic matrix of the amber is estimated to be ~98.79 ± 0.62 million years old, i.e., near the Albian/Cenomanian (Early/Late Cretaceous) boundary (Shi et al., 2012), but the amber, however, is considered to be slightly older with a late Albian age. The biological inclusions of Burmese amber represent a sample of a tropical forest community in equatorial southeastern Asia at ~12°N paleolatitude (Grimaldi et al., 2002; Poinar et al., 2008).

The photographs were taken by Carsten Gröhn using a Zeiss stereomicroscope (modified with variable objectives: Nikon M Plan 5×, 10×, 20×, 40×; Luminar 18 mm, 25 mm, 40 mm) and an attached Canon EOS 450D digital camera; and by Valery Loktionov using a SteREO Discovery.V12 stereomicroscope. Line drawings were prepared using Adobe Photoshop CS3.

The venational terminology in general follows Kukalová-Peck and Lawrence (2004) as interpreted by Yang et al. (2012, 2014b). Terminology of wing spaces and details of venation (e.g., veinlets, traces) follows Oswald (1993a).

Abbreviations: AA1–AA3, first to third anterior anal vein; CuA, anterior cubitus; CuA1, proximal-most branch of CuA; CuP, posterior cubitus; MA and MP, anterior and posterior branches of media; RA, anterior radius; RP, posterior sector; RP1, proximal-most branch of RP; RP2, branch of RP distad RP1; ScA, subcosta anterior; ScP, subcosta posterior.

3. Systematic palaeontology

Order Neuroptera Linnaeus, 1758
Family Dilaridae Newman, 1853
Subfamily Cretadilarinae subfam. nov.

Type and only genus: *Cretadilar* gen. nov.

Diagnosis. Mouthparts siphonate [mandibulate in Dilarinae, Nallachiinae, Berothellinae]; in female, narrow gonocoxites 9 of female forms short ovipositor [long hose-like ovipositor in Dilarinae, Nallachiinae; broad non-fused gonocoxites 9 in Cretanallachiinae; unknown in Berothellinae]; and gonostyli 9 absent [shared with Dilarinae, Nallachiinae; present in Cretanallachiinae]; ScP, RA fused distally in both wings [separate distally in other subfamilies]; in forewing, RP1 independently originating from R before RP proper [shared with Dilarinae, Cretanallachiinae; all branches originating from RP in Nallachiinae, Berothellinae]; and CuP once shallowly forked [pectinate in most other Dilaridae, including Cretanallachiinae].

Genus ***Cretadilar*** gen. nov.
Type and only species. *Cretadilar olei* sp. nov.

Derivation of name. From the Cretaceous, and *Dilar*, a genus-group name. Gender masculine.
Diagnosis. As for the subfamily.

Cretadilar olei sp. nov.
Figs. 1–4

Derivation of name. From the first name of Ole Friedrich (Glinde, Germany), recognizing his help in examination of this amber piece.
Material. Holotype GPIH Typ. Kat. Nr. 4589 (collection of C. Gröhn, no. 11116), deposited in Centrum of Natural History [Centrum für Naturkunde] (formerly Geological-Paleontological Institute and Museum of the University of Hamburg [Geologisch-Paläontologisches Institut und Museum der Universität Hamburg]). A poorly preserved nearly complete female specimen. The amber is not completely translucent and there are several large air bubbles near the specimen, which preclude observation of some details.
Locality and horizon. Burmese amber (Northern Myanmar: Kachin State: Myitkyina District: Tanai Township: Hukaung Valley). Upper Cretaceous: lowest Cenomanian/uppermost Albian.
Description. Female. Head transverse, with large eyes. Face with median cuneal projection, laterally with dense, very long strong setae; genae with very long strong setae. Head behind antennae possesses calluses but their structure poorly visible: anterior rounded callus ('?median ocular pulvinus' in Fig. 2C) large, covered with long setae; other elongate callus on vertex near left eye covered with very long strong setae ('?vertex callus' in Fig. 2A); similar callus near right eye unclear. Antennae: scapus, pedicellus elongate, covered with elongate setae; flagellomeres short, covered with very short, sporadically spaced setae.

Mouthparts elongated, siphonate (poorly preserved). Mandibles not detected. Basal portion of maxillae not visible. Presumed galea poorly visible, long, rather broad and flat; setae probably absent. Presumed lacinia similar to galea but broader and shorter; lacinia and galea closely approach basally. Maxillary palpi elongate, with dense long setae; segmentation easily discernible (their orientation does not allow measurement of segments). Basal portion of labium short, poorly discernible; ligula not detected; labial palpi elongate, basally convergent, covered with long setae; their segmentation not clear.

Prothorax narrow, elongate; laterally with long setiferous process (apparently, this is strongly elongated anterior lateral cervical sclerite), which bears numerous apical, very long strong setae (Fig. 2A, B). Mesonotum covered with very long strong setae.

Foreleg, mid-leg poorly visible. Hind leg long; metatibia slender, with two apical spurs (one elongate, other very short), markedly longer than metafemur; metatarsus elongate (1.7 mm long), slender; relative length of left metatarsomeres: 5.5–2.5–1.4–1–1.4.

Abdominal segments (up to seventh) covered with very long setae. Eighth tergite extending to ventral surface, dilated ventrad, with rather long setae. Ninth tergite probably equally-broad dorsally and ventrally (upper borders not visible), extending to ventral surface (ventral border not clear), with relatively short setae. A structure lying above 9th tergite probably represents tenth tergite (unpaired ectoproct), but its callus cerci not detected due to crumpled condition. Gonocoxites 9 form relatively short, pointed apically ovipositor, covered with relatively short setae; gonostyli 9 not detected.

Forewing broadly oval, 8.0 mm long, 3.8 mm wide. Costal space moderately broad; strongly narrowed basally, moderately narrowed apically. Humeral veinlet simple, crossvein-like (poorly visible). Subcostal veinlets rather closely spaced, mainly simple; seven veinlets deeply forked. ScP, RA fused apically far from wing apex. ScP + RA entering margin well before wing apex; majority of its veinlets poorly discernible, probably simple. Subcostal space moderately broad; crossveins poorly discernible. RA space slightly wider than subcostal space, with three detected crossveins. Anterior trace of RP proper nearly straight for entire length, forked distally; with seven branches. RP1 originating from R proximad RP proper; deeply forked (proximad origin of RP2), both branches slightly arched; anterior branch one shallowly forked; posterior branch rather deeply forked. RP4 deeply forked in right wing; other RP branches shallowly forked once to three times. M forked relatively close to wing base, slightly proximad fork of RP1. Configuration and course of MA nearly identical with those of posterior branch of RP1. Posterior trace of MP and three of its branches arched, shallowly forked. Cu dividing into CuA, CuP near wing base. CuA in general pectinate, with four branches; CuA1 profusely branched, with three distally directed pectinate branches. CuP once shallowly forked. AA1 long, pectinately branched distally (poorly

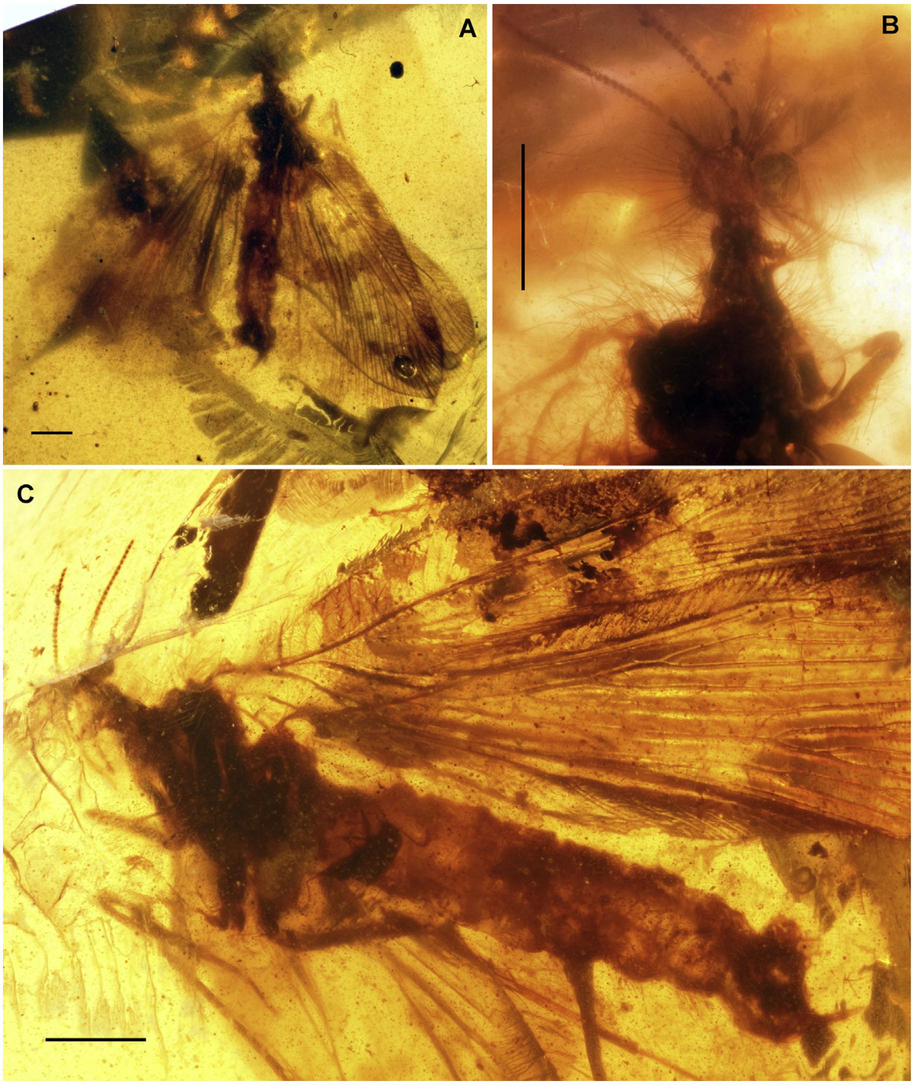

Fig. 1. *Cretadilar olei* sp. nov., holotype GPIH Typ. Kat. Nr. 4589, A, Specimen as preserved, dorsal view. B, Anterior part of body, dorsal view. C, Lateral view of the specimen. Scale bars represent 1 mm.

preserved). AA2 strongly pectinate, with seven, mostly simple branches. AA3 few branched (poorly preserved). Crossveins in radial and medial spaces rare, arranged mainly in three irregular gradate series. Color pattern mainly consists of three irregular dark transverse fasciae (Fig. 1A, C).

Hind wing ca. 7.5 mm long. Costal space relatively broad; slightly dilated apically. Subcostal veinlets rather closely spaced, simple. ScP, RA fused apically far from wing apex in left wing. ScP + RA entering margin well before wing apex; part of its veinlets poorly discernible, probably simple (in right wing one crossvein deeply forked). ScP, RA closely approach distally, but not fused in right wing. Subcostal space narrow; crossveins not detected. RA space nearly as wide as subcostal space, with two detected crossveins. RP with six branches. RP1 dichotomously forked distal to outer gradate series of crossveins. RP2 to RP4 shallowly forked (one or two times); RP5, RP6 probably simple (poorly preserved). M forked relatively close to wing base, slightly distad origin of RP1. Configuration of MA similar to those of RP1. MP poorly preserved (strongly folded), twice deeply forked. Cu dividing into CuA, CuP near wing base. CuA pectinate, with four forked branches. CuP poorly preserved, probably simple or once forked. Anal veins not visible. Crossveins in radial and medial spaces poorly visible, arranged in two regular gradate series. Area of basal 1r-m poorly preserved, but part of it appears visible, connecting RP1 and M.

Subfamily Cretanallachiinae subfam. nov.
Type genus: *Cretanallachius* Huang et al., 2015.

Diagnosis. Mouthparts siphonate [mandibulate in Dilarinae, Nallachiinae, Berothellinae]; proximal antennal fragellomeres of male bipectinate [monopectinate in Dilarinae, Nallachiinae; filiform in Berothellinae; male of Cretadilarinae unknown]; proximal fragellomeres of female long, more than twice as long as wide [very short, shorter than width in Cretadilarinae]; ninth tergite of female with long broad ventro-caudal projection [not developed in such extent in other subfamilies]; gonocoxites 9 of female broad, not fused with each other [narrow, fused to form long (Dilarinae, Nallachiinae) or short ovipositor (Cretadilarinae)]; gonostylus 9 well developed [lost in other subfamilies]; costal space (including distal portion) of both wings very broad [moderately broad narrowed towards wing apex in other subfamilies]; in forewing, CuA simple or few branched [usually pectinate in other subfamilies].

Genera included. *Cretanallachius* and *Burmopsychops* Lu et al., 2016b from Burmese amber.

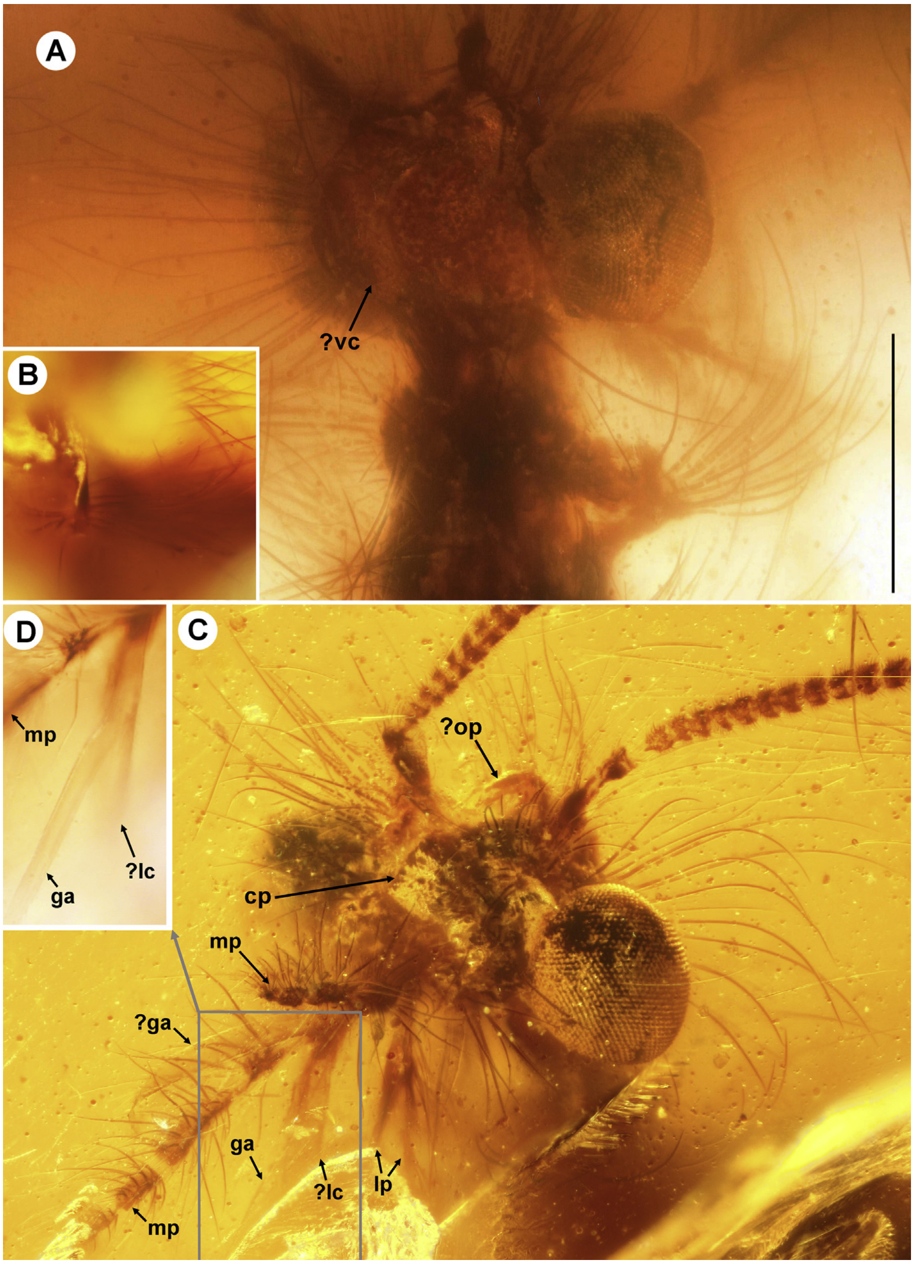

Fig. 2. *Cretadilar olei* sp. nov., holotype GPIH Typ. Kat. Nr. 4589. A, Head and pronotum, dorsal/slightly lateral view. B, Left setiferous process of prothorax, lateral view. C, Head, latero-ventral view. D, Fragment of right maxilla. cp, median cuneal projection; ga, galea; lc, lacinia; lp, labial palpus; mp, maxillary palpus; op, median ocular pulvinus; vc, vertex callus. Scale bar represents 0.5 mm (all to scale).

Burmopsychops Lu et al., 2016

Burmopsychops Lu et al., 2016a: 6 [nomen invalidum]; Lu et al., 2016b: 325.

Revised diagnosis. Forewing RP1 originated from R proximad origin of RP proper [RP1 originated from stem of RP in *Cretanallachius*]; hind wing basal crossvein 1r-m absent [long, sinuate in *Cretanallachius*].

Species included. *B. limoae* Lu et al., 2016b and *B. groehni* sp. nov. from Burmese amber.

Burmopsychops groehni sp. nov.

Figs. 5–10, 11B

Derivation of name. The specific epithet is from the surname of Carsten Gröhn, in recognition of his efforts in the study of ambers.

Material. Holotype GPIH Typ. Kat. Nr. 4585 (collection of C. Gröhn, no. 11089), deposited in the Geological-Paleontological Institute and Museum of the University of Hamburg [Geologisch-Paläontologisches Institut und Museum der Universität Hamburg]. An incomplete female specimen in an amber piece with fissures and air bubbles, which preclude observation of some details. Syninclusions: a very small specimen of Hymenoptera (lost during preparation); a female of brachyceran Diptera.

Locality and horizon. Burmese amber (Northern Myanmar: Kachin State: Myitkyina District: Tanai Township: Hukaung Valley). Upper Cretaceous: lowest Cenomanian/uppermost Albian.

Diagnosis. Several costal crossveins present in forewing [at most one crossveins in *B. limoae*]; RP1 twice deeply forked in both wings [only once forked near margin in *B. limoae*]; gonocoxite 9 much

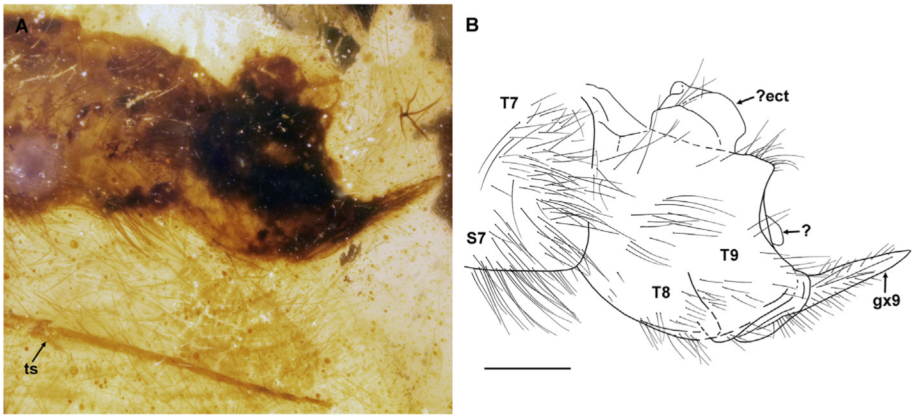

Fig. 3. *Cretadilar olei* sp. nov., holotype GPIH Typ. Kat. Nr. 4589, apex of the female abdomen and hind leg. A, Photograph. B, Line drawing, lateral view. ect, ectoproct; gx9, gonocoxites 9; S7, 7th sternite; 7T–9T, 7th to 9th tergite; ts, metatibial spur. Scale bar represents 0.5 mm (both to scale).

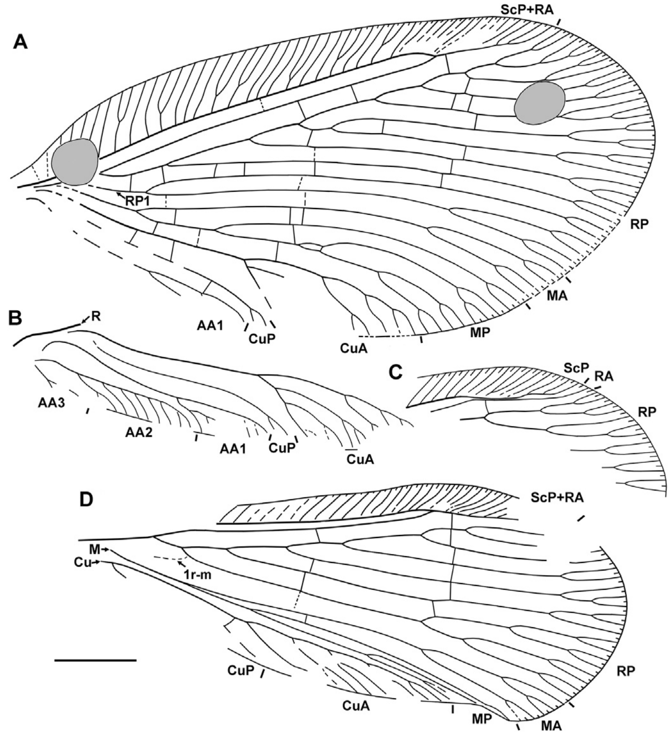

Fig. 4. *Cretadilar olei* sp. nov., wing venation of the holotype GPIH Typ. Kat. Nr. 4589. A, Right forewing. B, Cubital and anal spaces of left forewing. C, Apical part of right hind wing. D, Left hind wing. Scale bar represents 1 mm (all to scale).

shorter than ventro-caudal projection of ninth tergite [nearly equal in length in *B. limoae*].

Description. Head. Eyes large. Ocular pulvinae present: anterior median pulvinus, right posterior pulvinus strongly prominent covered with long setae (Fig. 6B, 'op'); left posterior pulvinus not clearly visible (hidden under air bubble), but identified by presence of bunch of long setae. Scapus rather long, stout, apically covered with long setae; pedicellus short, with dorso-apical projection; apically covered with long setae; flagellum with 40 flagellomeres; proximal flagellomeres elongated, more than twice as long as wide, each bears one row of very long setae; terminal flagellomeres short (only slightly longer than wider), with short setae.

Mouthparts elongated, siphonate. Labrum and possible mandibles not visible (obscured by abdomen of fly). Cardo, stypes of maxillae not visible, probably very short. Maxillary palpi long, five-segmented, covered with dense long setae, widely spaced (arranged at 180° to each other); basal segment shortest; second segment elongate; third, fourth segments longest, slender; terminal segment long, slightly fusiform, with dark macula medially (Fig. 7C, D, '?sa'). Presumable galeae long (left galea 1.35 mm), slender, flattened, with longitudinal ridges and very short, fine setae; apically rounded (Fig. 7B). Presumable laciniae long, very slender, closely approaching basally, slightly divergent distally; setae not detected (Fig. 7A). Labium: submentum, mentum of labium not visible, probably very short; prementum moderately elongated; labial palpi three-segmented, with all segments long; second segment longest; terminal segment slightly dilated apically, with small rounded convex macula (Fig. 7A, '?sa'); ligula not detected (probably reduced).

Prothorax elongate, with rare long setae. Meso- and metathorax poorly preserved.

Legs slender, covered with fine, rather long setae; tibial spurs absent; tarsi with small claws. Relative length of right mesotarsomeres: 4.3–2.0–1.5–1–1.5; of left metatarsomeres: 8.8–2.4–1.1–1–1.1.

Abdominal eighth tergite narrow, probably relatively short (judging from presence of setae), covered with long setae. A structure extending ventrally beyond abdomen interpreted as subgenitale (pseudosternite) (Fig. 8B, ?sg). Ninth tergite large, extending to ventral surface, with long, broad ventro-caudal projection covered with dense, very long setae; upper border of 9th tergite unclear. Gonocoxites 9 rather short, broad (in lateral view), setae not detected; apically bears long gonostyli, covered with rather short setae. Right ectoproct identified, as segment shifted proximally; left ectoproct not detected, possibly missing; alternatively, there is single tenth tergite ('fused ectoprocts'), which is shifted to anterior and right, but its callus cerci not detected as this segment is not clearly visible from right side (hidden under wings).

Forewing broad, ovate, with rounded apex; ca. 10 mm long, 5.6 mm wide. Costal space very broad, narrowed basally. Subcostal veinlets ca. 25 in number; mostly forked, deeply or shallowly. Humeral veinlet straight, crossvein-like. Several irregular crossveins detected in proximal half of costal space: five in right wing, four in left wing. Subcostal space equally broad for entire length except basally, with ≥12 crossveins. ScP, RA widely spaced distally. RA space as wide as subcostal space, with ≥11 crossveins. RP with six branches (right wing); RP1 originating from R proximad RP

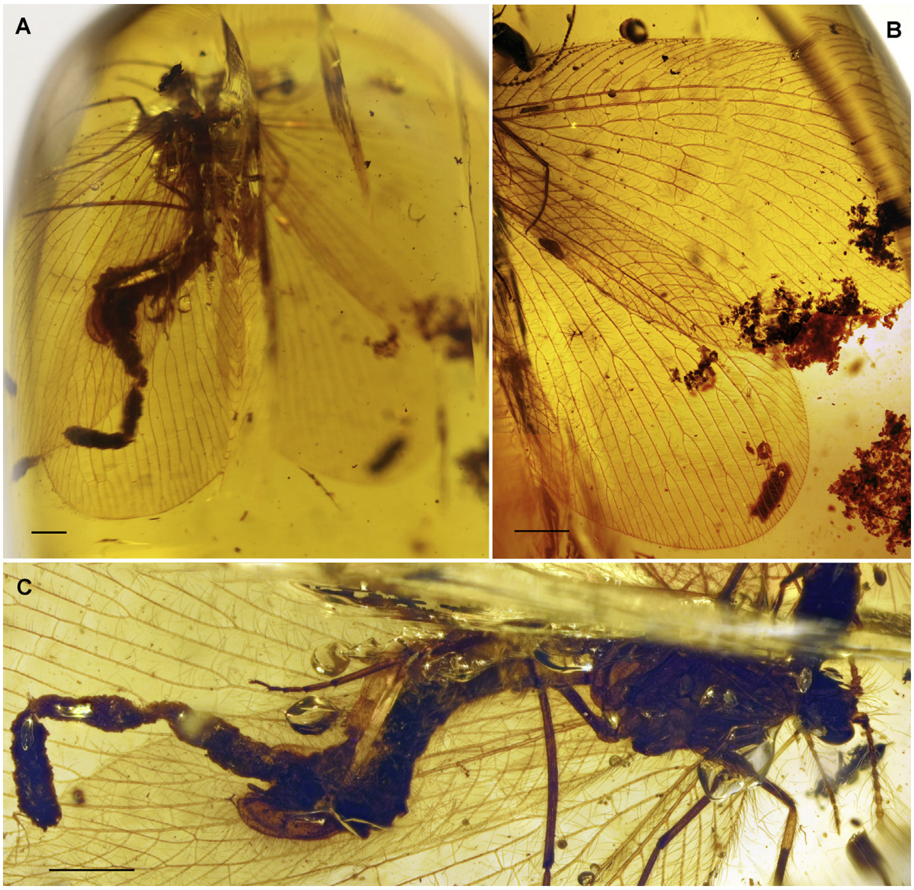

Fig. 5. *Burmopsychops groehni* sp. nov., holotype GPIH Typ. Kat. Nr. 4585. A, Specimen as preserved. B, Right wings. C, Lateral view of the body. Scale bars represent 1 mm.

proper; RP1, RP3 deeply dichotomously branched; RP2, RP4, RP5 deeply forked before outer gradate series of crossveins. M not fused with R basally, forked slightly distad origin of RP proper. MA with three distal pectinate branches, two of these shallowly forked (left wing). MP deeply forked; MP1 pectinately branched, with two long branches (its proximal-most branch shallowly forked) (left wing); MP2 deeply forked, with both branches shallowly forked (left wing) or anterior branch simple and posterior branch twice shallowly forked (right wing). Cu dividing into CuA, CuP near wing base. CuA simple (right wing), rather deeply forked (left wing). CuP very shallowly forked apically, pectinately branched, with five oblique branches; proximal-most branches shallowly forked (right wing). AA1 deeply forked; anterior branch simple, posterior branch shallowly forked. AA2 deeply forked; anterior branch deeply (left wing) and rather shallowly (right wing) forked, posterior branch probably simple (indistinctly visible). AA3 fragmentarily visible. Crossveins in radial and medial spaces rather numerous, mostly not arranged in series except distal ones which form the outer gradate series. Distal nygma indistinct, located between RP1, RP2.

Hind wing broad, with rounded apex, ca. 9.5 mm long, 5.1 mm wide. Costal space very broad slightly narrowed basally. Subcostal veinlets 24 in number (right wing), mostly simple (one forked) proximally, mostly one or twice forked apically. Humeral veinlet straight, crossvein-like. No crossveins detected in costal space. Subcostal space probably equally broad for entire length except basally, with 12 crossveins. ScP, RA widely spaced distally. RA once shallowly forked. RA space slightly wider than subcostal space, with 9 crossveins. RP with six branches (right wing); RP1 deeply dichotomously forked; RP2, RP3 deeply forked before outer gradate series of crossveins; RP4–RP6 shallowly forked. M forked near wing base. MA distally twice forked (after outer gradate series). MP pectinately branched, with three branches before outer gradate series. CuA pectinate, with at least three branches. CuP, anal veins poorly preserved. Crossveins in radial and medial spaces rather numerous, mostly not arranged in series except distal ones which form distinct outer gradate series. Distal nygma indistinct, located between RP1, RP2.

4. Discussion

4.1. *Dilarid affinities of Cretadilarinae and Cretanallachiinae*

Dilarid affinities of the strongly specialized Cretadilarinae and Cretanallachiinae are not instantly obvious and require confirmation through an analysis of characters. The extant Dilaridae are characterized in particular by some distinctive character states, e.g., [1] unipectinate antennae in males; [2] long hose-like and saber-like ovipositor in females; and [3] three setose ocellar pulvinae (ocelli-like tubercles) on the head (Aspöck et al., 1980). Of these, character state [1] is considered an autapomorphy of the family (Aspöck and Mansell, 1994), and character state [2] may also be treated as such (see Aspöck and Aspöck, 2008). Wings of extant Dilaridae are generalized and do not possess clear apomorphic conditions at the family level, but they contain some important plesiomorphies. Below, these and other characters, which can help to clear up family affinities of these groups, are analyzed.

Antennae. All males of extant Dilaridae have unipectinate antennae and females non-pectinate (filiform/moniliform), except

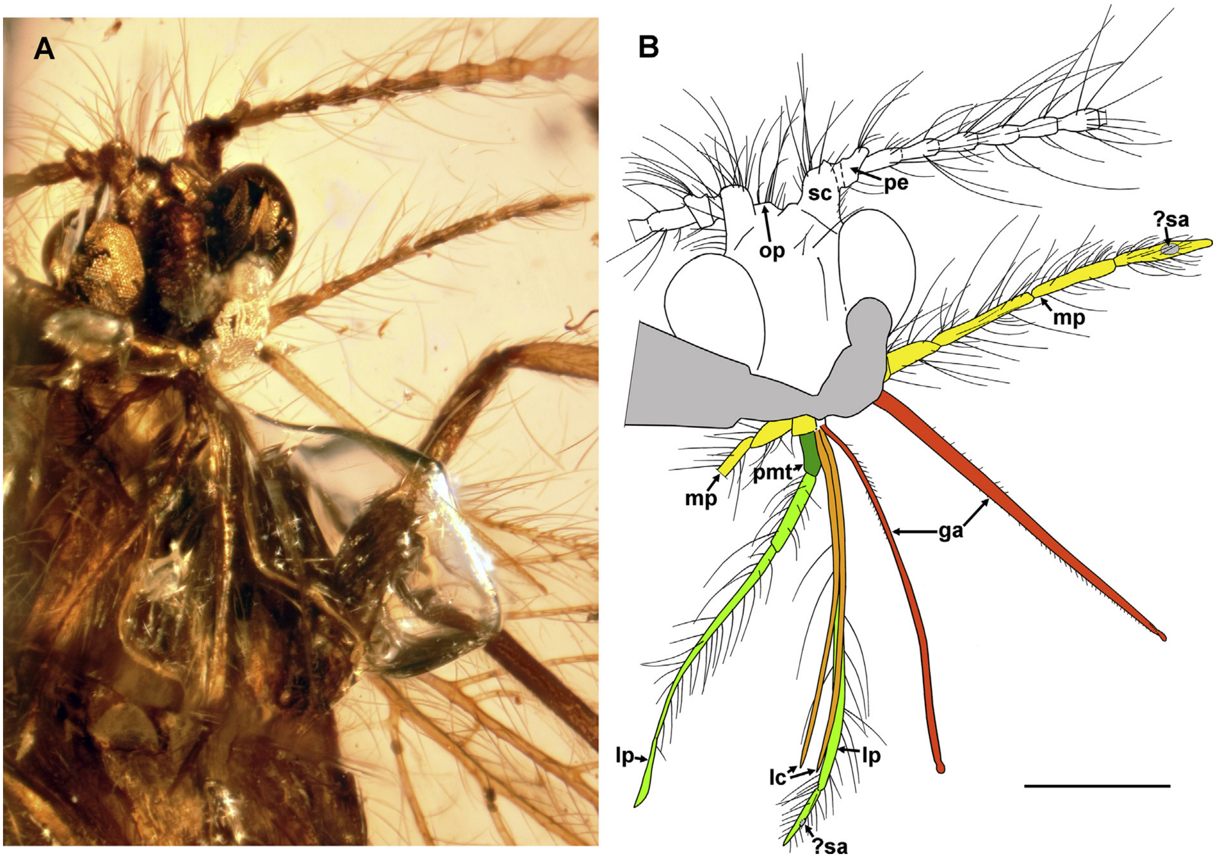

Fig. 6. *Burmopsychops groehni* sp. nov., head and mouthparts of the holotype GPIH Typ. Kat. Nr. 4585, A, Photograph, frontal view. B, Line drawing. ga, galea; lc, lacinia; lp, labial palpus; mp, maxillary palpus; op, median ocular pulvinus; pe, pedicellus; pmt, prementum; sa, sensory area; sc, scapus. Scale bar represents 0.5 mm (both to scale).

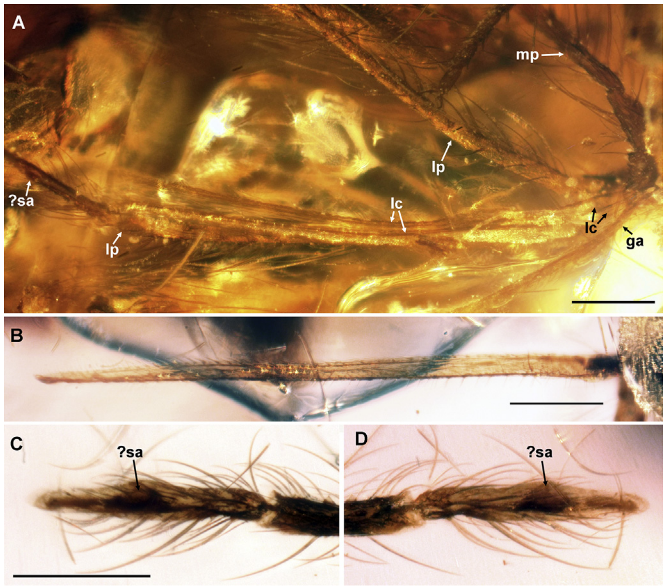

Fig. 7. *Burmopsychops groehni* sp. nov., mouthparts of the holotype GPIH Typ. Kat. Nr. 4585. A, Details showing labial palps and laciniae, frontal view. B, Left galea, frontal view. C, Terminal segment of left maxillary palpus, caudal view. D, Same, frontal view. ga, galea; lc, lacinia; lp, labial palpus; mp, maxillary palpus; sa, sensory area. Scale bars represent 0.2 mm.

the genus *Berothella*, whose males are characterized by filiform non-pectinate antennae (pers. obs.; Liu et al., 2017). In other Neuropterida, unipectinate antennae are present in one clade of Chauliodinae (Megaloptera: Corydalidae) (Liu and Yang, 2006), including fossil taxa (see Weitschat and Wichard, 1998, pl. 50). Males of Cretadilarinae are unknown, but males of Cretanallachiinae possess bipectinate antennae, which are not present in their females. The structure of the female fragellomeres of these taxa differs strongly: proximal fragellomeres of Cretanallachiinae are elongate with very long setae arranged mainly in one row (collar-like), and those of Cretadilarinae are short with very short setae not arranged in rows. Although males of Cretadilarinae are unknown, it is reasonable to assume that pectinate antennae in males (irrespectively, unipectinate or bipectinate) are an autapomorphy of Dilaridae at the order level. It is interesting to note that partly bipectinate antennae are known in males of one species of the Burmese amber trichopteran family Odontoceridae. Other taxa of Trichoptera have mostly non-pectinate antennae, and very rarely unipectinate (Wichard and Wang, 2016).

Ocellar pulvinae (ocelli-like tubercles). Burmopsychops groehni possesses three setiferous tubercles on the head; those tubercles (calluses) in *Cretadilar* are larger. The head of some extant Neuroptera also possess three setiferous tubercles dorsally, which Tjeder (1960) called 'ocellar sclerites', and Oswald (1993b) 'ocellar pulvinae': one anterior median and two posterior lateral. They occur in extant Osmylidae (but each ocellar pulvinus also bears one cornea (oculus), except Gumillinae), Psychopsidae, Dilaridae, and some Berothidae (including Rhachiberothinae), and are located in those

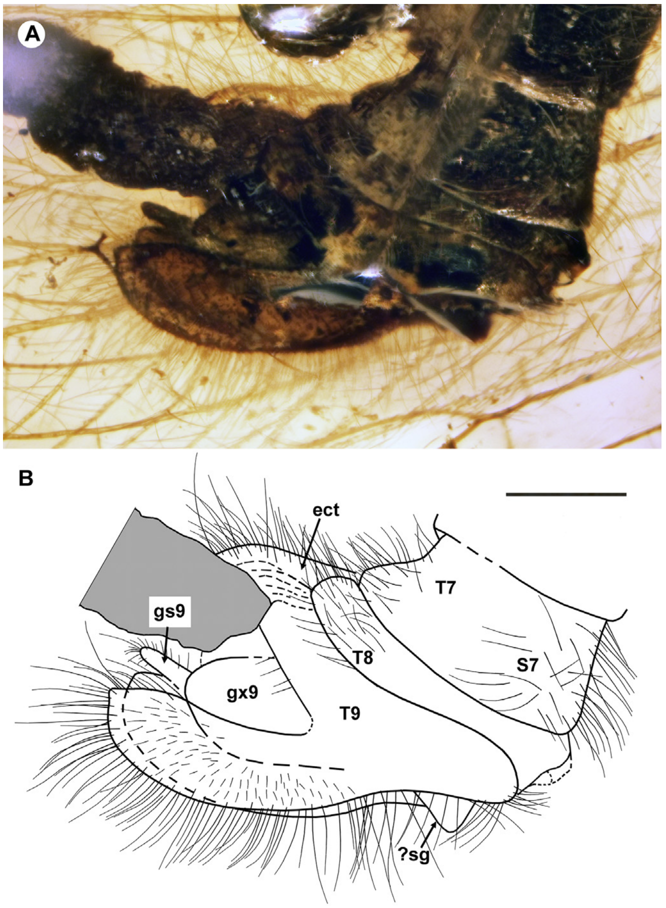

Fig. 8. *Burmopsychops groehni* sp. nov., apex of the female abdomen of the holotype GPIH Typ. Kat. Nr. 4585. A, Photograph. B, Line drawing, lateral view. ect, ectoproct; gs9, gonostylus 9; gx9, gonocoxites 9; S7, 7th sternite; sg, subgenitale; 7T–9T, 7th to 9th tergite. Scale bar represents 0.5 mm (both to scale).

places where three corneae (ocelli) are found in Raphidioptera and Megaloptera. This indicates that ocellar pulvinae in these neuropteran families are probably homologous and primarily ocelli-bearing structures (Oswald, 1993b; Beutel et al., 2010). Their presence is therefore a plesiomorphic condition in Neuroptera. Setiferous tubercles of *Burmopsychops groehni* are certainly ocellar pulvinae, but those of *Cretadilar* are dissimilar to those, and probably secondarily derived from ocellar pulvinae.

Mouthparts. The mouthparts of Cretadilarinae and Cretanallachiinae are greatly specialized, siphonate (i.e., haustellate). Both taxa have short cardo/stipes (presumably, these are poorly visible); long maxillary and labial palpi covered with long setae; widely spaced long galeae; and their ligula and probably their mandibles are reduced. The structure of laciniae in these taxa appears to differ: they are broad and located near each galea in Cretadilarinae, and slender, and dislocated far from the galeae in Cretanallachiinae. Lu et al. (2016a) suggested that the structures, which are interpreted herein as laciniae, represent a paired ligula, and the lacinia and galea are fully fused with each other (this structure is interpreted here as the galea). The interpretation herein is supported by the fact that the presumable laciniae are remain paired for the entire visible part, i.e., it is much more basad than the presumable ligula would have adjoined to the prementum (Fig. 7A).

From how the mouthparts have been interpreted in this paper, the ligula has not been detected in *Cretadilar* gen. nov. and *Burmopsychops*. It is worth noting that the ligula and anterior part of the prementum are reduced in extant Dilaridae. At least, these were not detected in some species of *Dilar* and *Nallachius* Navás, 1909 (pers. obs.; S. Randolf, pers. comm.). In other Neuroptera, the ligula and/or anterior part of the prementum is usually well developed. Moreover, the distinctly enlarged anterior part of the

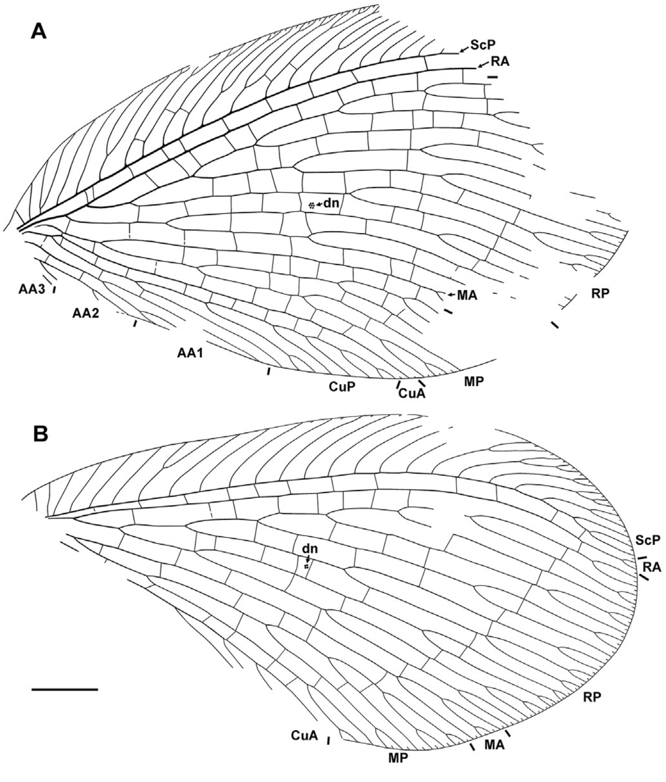

Fig. 9. *Burmopsychops groehni* sp. nov., wing venation of the holotype GPIH Typ. Kat. Nr. 4585. A, Right forewing. B, Right hind wing. Scale bar represents 1 mm (both to scale).

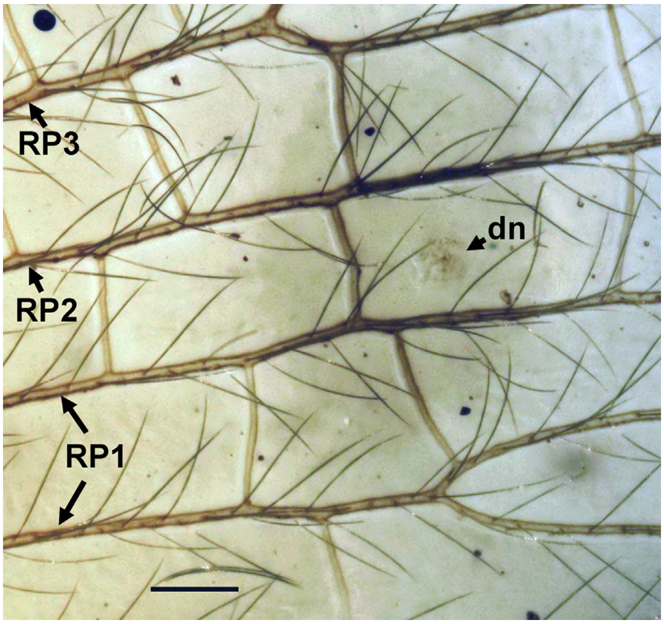

Fig. 10. *Burmopsychops groehni* sp. nov., holotype GPIH Typ. Kat. Nr. 4585, fragment of right forewing showing the distal nygma (dn). Scale bar represents 0.2 mm.

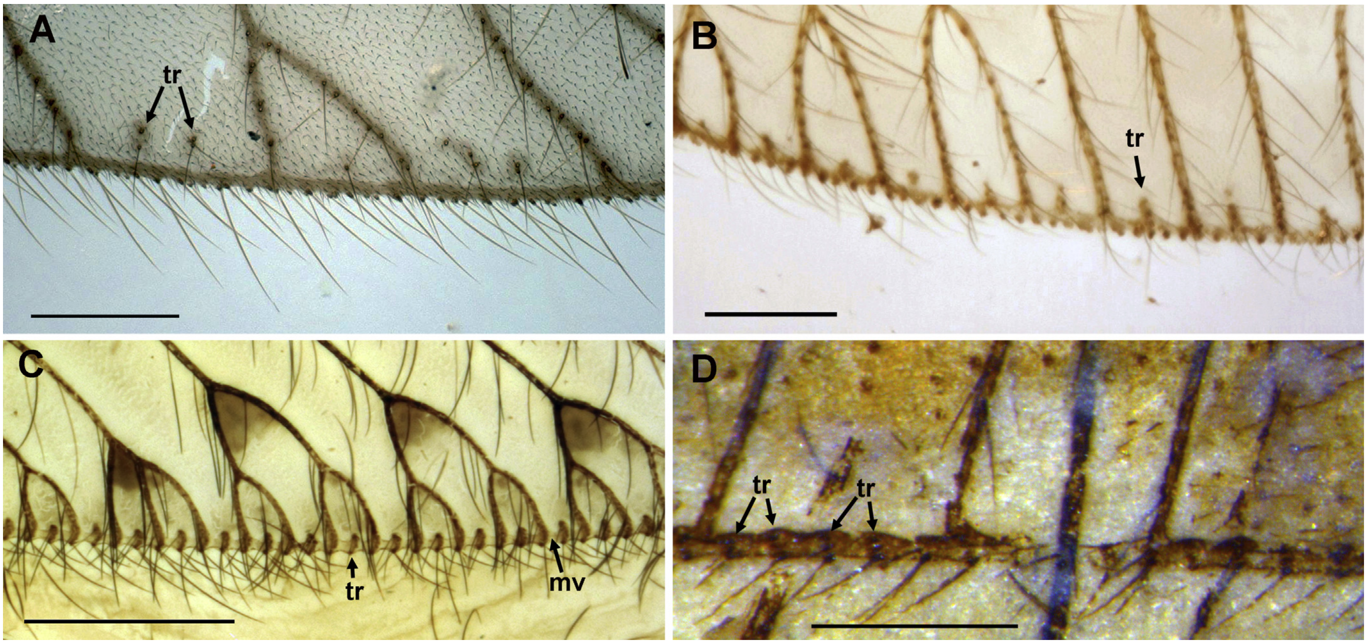

Fig. 11. Different types of trichosors in Neuroptera. A, Extant *Sisyra nigra* (Retzius, 1783) (Sisyridae), the hind wing posterior margin; trichosors are only represented by thickenings of membrane. B, *Burmopsychops groehni* sp. nov. (holotype GPIH Typ. Kat. Nr. 4585), the hind wing outer margin. C, *Elektroberotha groehni* Makarkin and Ohl, 2015 (Berothidae) from Baltic amber, the forewing posterior margin; trichosors are mainly represented by thickening of the marginal 'vein'. D, *Adamsochrysa* sp. (Chrysopidae: Nothochrysinae) from early Eocene of Republic (U.S.A.), the forewing posterior margin. mv, marginal 'vein'; tr, trichosor. Scale bars represent 0.2 mm (A, B), 0.5 mm (C), 0.3 mm (D).

prementum is considered to be an autapomorphy of the order (Beutel et al., 2010). Irrespectively of whether or not the latter is correct, the reduction of the ligula and anterior part of the prementum is an important synapomorphy of Dilaridae. This part of the labium is also strongly reduced in extant Ithonidae (see Tillyard, 1919, fig. 6d), whose labium appears generally to be similar to that of Dilaridae.

The terminal segment of the maxillary palpus possesses an indistinct dark macula (Fig. 7C), and the terminal segment of the labial palpi possess a small rounded, slightly convex structure. Such structures in *Burmopsychops limoae* were called by Lu et al. (2016a, fig. 4d) an "ovoid sensory area". Similar sensory areas on the outer surface of the terminal segments of the labial palpus carry minute setae; these were called palpimacula by Crampton (1921). These are present in some extant families of Neuroptera (e.g., Hemerobiidae, Osmylidae, Mantispidae, Psychopsidae, Myrmeleontidae, Ascalaphidae, and Nymphidae). It is unclear yet if these sensory areas in *Burmopsychops* and the palpimacula are homologous; probably not as the latter is usually a depression, which is densely lined with minute recumbent setae, but the sensory area of *Burmopsychops* is slightly convex lacking setae, at least on the labial palpus of *B. groehni*.

Tibial spurs. In both genera of Cretanallachiinae these spurs are absent; this is also observed in some extant *Dilar* (Vshivkova and Makarkin, 2010). The spurs are also lost in some Ithonidae, Coniopterygidae, Berothidae, and Nymphidae. In *Cretadilar*, there are two spurs of different sizes (very small and normal), at least in the hind tibia (Fig. 3A). In *Fiaponeura*, a single spur on each tibia is thought to be present (Lu et al., 2016a); but it is possibly that a very small spur has not been detected. Unfortunately, the presence and structure of tibial spurs in extant Dilaridae has been poorly studied.

Male terminalia. Males of Cretadilarinae are unknown. Male genitalia of Cretanallachiinae (known only in *Cretanallachius*) consist of an unpaired ectoproct; enlarged ninth tergite; a pair of slender elongate and spinous structures (putative gonostyli 10, which were originally interpreted as gonocoxites 10 by Lu et al. (2016a)); ninth sternite strongly projecting medially into a horn-like process (see Lu et al., 2016a, fig. 2d).

The homologization of an enlarged caudal segment of *Cretanallachius* (which is here interpreted as the 9th tergite) with gonocoxites 9 is unreasonable (see Lu et al., 2016a). In most families of Neuroptera, gonocoxites 9 are part of the internal genitalian complex (except Nevrorthidae and Sisyridae), and are often small to very small (see e.g., Aspöck and Aspöck, 2008, figs. 33, 35, 40, 65, 94, 97). Previously, this enlarged segment was misinterpreted as being an ectoproct (Huang et al., 2015), but, as noted by Lu et al. (2016a) this could not be the case because a true ectoproct is found in this genus. The male genitalia of Cretanallachiinae are most similar to those of Dilarinae by the presence of an enlarged ninth tergite and an unpaired ectoproct.

Female terminalia. Those of Cretanallachiinae are peculiar, consisting of an enlarged ninth tergite, ventrally expanded in a caudally-directed long and broad lobe ('putative fused 9th tergite and ectoprocts' of Lu et al., 2016a); the ectoproct is probably represented by an unpaired dorsal segment (this is not clearly visible in *Burmopsychops groehni*); the enlarged gonocoxites 9 bearing rather long terminal gonostyli represents the ovipositor. This ovipositor of Cretanallachiinae is most similar to that of Osmylidae, which is considered an ancestral type of ovipositor among Neuroptera (Aspöck and Aspöck, 2008). Based on their similarity to those of Psychopsidae, the genera of Cretanallachiinae (together with the genus *Fiaponeura*) were assigned to an unnamed family within Psychopsoidea (Lu et al., 2016a, 2016b). However, the ovipositor of Psychopsidae and Cretanallachiinae has certainly evolved independently from an ancestral type of neuropteran ovipositor. In Psychopsidae, the ninth gonostylus always arises subapically from the ventral surface of the 9th gonocoxites, and bears a ventral field of highly modified "digging" setae (Oswald, 1993b), but the 9th gonocoxites and gonostyli of Cretanallachiinae are much more similar to those of Osmylidae.

Female genitalia of Cretadilarinae are most similar to those of extant Dilaridae (see description above); the gonocoxites 9 form a short acute (saber-like) ovipositor, which lacks gonostili. In Neuropterida, the saber-like long ovipositor is present in all Raphidioptera and some Neuroptera, i.e., Kalligrammatidae (found in the Early Cretaceous *Oregramma illecebrosum* Yang et al., 2014a), Dilaridae (Dilarinae and Nallachiinae), and Mantispidae (Symphrasinae). The ovipositor of extant Dilaridae is lined by closely-spaced transversal furrows, giving it a hose-like appearance. The ovipositor of Cretadilarinae is saber-like, but not hose-like; it appears to possess few longitudinal furrows.

Nygmata. The structure of the distal nygma in *Burmopsychops* is similar to that of some extant *Dilar*: it is very indistinct, and veins around the nygma are not curved (Fig. 9). The distal nygma is detected in some families of Neuroptera: Permithonidae, some Prohemerobiidae, Osmylopsychopidae, Nevrorthidae, Ithonidae s.l., and Dilaridae. Although the presence of nygmata is a plesiomorphic feature, their structure may be helpful for family determination; however this has been poorly studied.

Trichosors. The presence of trichosors in the wings of Neuroptera is one of the most striking apomorphies of this order (Hennig, 1981). The term was proposed by Killington (1936) for "small setigerous swellings between the tips of the veins and veinlets" (p. 34). Earlier, Comstock (1918) called these structures "marginal dots or dashes", and defined them similarly, i.e., as "small thickened areas alternating with the tips of veins" which "bear one or more groups of setae" (p. 166). The complete reduction of trichosors is probably an apomorphic condition in the order, and occurs in Coniopterygidae, Dipteromantispidae, Mesochrysopidae, Ascalochrysidae, Myrmeleontidae, Ascalaphidae, Araripeneuridae, Palaeoleontidae, Nemopteridae, and Aetheogrammatidae.

From the examination of both extant and fossil taxa of Neuroptera at least three distinct types of trichosors are observed: (1) 'primitive', (2) typical (single), and (2) multiple trichosors.

(1) 'Primitive' trichosors: setae on the marginal 'vein' (i.e., the costal vein along the anterior margin and the false 'vein' along the outer and posterior margins) are more or less regularly or randomly spaced, and not only restricted to the trichosors and the tips of veins; the thickening of the marginal 'vein' is absent, and trichosors (often long) are formed by the thickening of the membrane bearing one or more setae (except for Nevrorthidae in which one-sided (inner) thickening of that vein forms the major part of the trichosors); each marginal seta is basally thickened (except for some Dilaridae). This type of trichosors is most probably plesiomorphic, and occurs in Sisyridae, Nevrorthidae, and Dilaridae (Fig. 11A). The trichosors of *Cretadilar* gen. nov. and *Burmopsychops* belong to this type (Fig. 11B).

The thickening of the membrane constituting the trichosors in Sisyridae rarely touches the marginal 'vein', especially along the posterior margin (Fig. 11A). Such trichosors are considered to be the most primitive in extant Neuroptera, and therefore may be considered as ancestral in the order. The trichosors of Nevrorthidae and Dilaridae (including Cretadilarinae and Cretanallachiinae) are more advanced, but the setation of their marginal 'vein' remains plesiomorphic.

(2) Typical trichosors: single distinct thickening of the marginal 'vein' between the tips of two veins, which may continue onto the membrane for a short distance; the marginal 'vein' between such a trichosor and the end of the veins appears to be thinner and lacks setae (Fig. 11C). This type of trichosors is widely distributed within the order, and occurs in Ithonidae, Polystoechotidae, Osmylidae, Berothidae, Hemerobiidae, Psychopsidae, Osmylopsychopidae, and probably Prohemerobiidae.

(3) Multiple trichosors: two or more (up to six in Mantispidae) weak thickenings between the tips of two veins, all bearing setae (i.e., all setae of the marginal 'vein' are located only on these thickenings and the tips of the veins), and the thickening of the membrane between the tips of veins is absent (Fig. 11B). These trichosors usually occur along the posterior wing margin, rarely along the anterior (costal) margin, and are found in Mantispidae (Drepanicinae and Symphrasinae) (see e.g. Willmann, 1990, fig. 11), some Nymphidae, including fossil taxa (e.g., Archibald et al., 2009, fig. 2; Shi et al., 2013, fig. 5), Babinskaiidae (pers. obs.), and some fossil Chrysopidae (some early Eocene Nothochrysinae and Middle Jurassic Limaiinae) (Makarkin and Archibald, 2013, figs. 25.3–25.11; pers. obs.).

A condition of "more than one trichosor between each two veins" (Willmann, 1990, p. 254) or "paired trichosors" (Aspöck and Mansell, 1994, p. 205) is considered to be an autapomorphy of Mantispidae by these authors. However, "paired trichosors" may be regarded as a sub-type of multiple trichosors. They are located only along the wing apices in some Drepanicinae and Symphrasinae in species which bear multiple trichosors along the posterior margin.

The type of trichosors in some fossil families is unclear (i.e., Permithonidae, Archeosmylidae, Kalligrammatidae, Parakseneuridae, Grammolingiidae, Panfiloviidae, and Saucrosmylidae).

Venation. The venation of Cretadilarinae does not principally differ from that of Dilarinae, especially *Dilar*. This includes, in particular, the similar branching of RP (including a separate origin of RP1), M, AA1, and AA2 in the forewing, RP, CuA and CuP in the hind wing. Only the distal fusion of ScP and RA may be considered an autapomorphy of the subfamily; in other Dilaridae these veins are distally separated.

The venation of Cretanallachiinae is more specialized. The broad costal space in both wings and the simple (or at most once forked) CuA in the forewing are noteworthy. This venation is superficially similar to that of the extant *Nallachius hermosa* (Banks, 1913) from Colombia, whose wings are the broad and relatively large (the wing expanse of the female holotype is 25 mm: Banks, 1913), and RA and ScP nearly reach the wing apex (see Carpenter, 1947, fig. 5).

The costal space in Cretanallachiinae and Cretadilarinae is basally narrowed, and the humeral veinlet is not recurrent and unbranched, conditions that are also found in Dilaridae. The crossvein-like humeral veinlet is thought as primary in the order (characteristic of several basal families), and as a secondary simplification in some others, including Dilaridae (see Makarkin et al., 2013, fig. 7). It is possible, however, that this condition of the basal costal space as found in Dilaridae (and Cretanallachiinae and Cretadilarinae) is also primary, not a secondary simplification; this is because the phylogenetic relationships of the family are not known.

In the forewing of *Burmopsychops* and *Cretadilar*, RP1 originates from R before RP proper. Normally, this condition is present in all species of *Dilar* in the forewing, as well as in many species in the hind wing (e.g., Nakahara, 1955, figs. 1, 3, 4; Zhang et al., 2014c, fig. 3). In other Dilaridae, RP1 in both wings always originates from the stem of RP. The separate origin of RP1 is also characteristic of some Ithonidae and most Osmylopsychopidae, and the separate origin of several branches of RP from R occurs in all Aetheogrammatidae, most Hemerobiidae, and some Kalligrammatidae.

In summary, the dilarid affinities of Cretadilarinae and Cretanallachiinae are supported by two autapomorphies of the family, i.e., the loss of the ligula and pectinate antennae in males. The Cretadilarinae are most similar to Dilarinae possessing similar venation and the presence of a saber-like ovipositor that lacks gonostyli. Cretanallachiinae possesses important plesiomorphies such as the presence of three ocular pulvinae, distal nygma, and 'primitive' trichosors. This set of character states occurs only in Dilaridae. Taking these together with the aforementioned autapomorphies shared by Cretanallachiinae and extant Dilaridae, the family affinity of the subfamily may be considered as confident. Also, Cretanallachiinae possess a number of other (although homoplasious) character states, which are characteristic of most/some extant Dilaridae, i.e., the absence of tibial spurs; the costal space being basally narrowed; the humeral veinlet not being recurrent and unbranched; RP1 originating from R before RP proper.

The presence of the primitive ovipositor in Cretanallachiinae and the saber-like ovipositor in Cretadilarinae is important. It is possibly that Cretadilarinae constitute single clade with Dilarinae and Nallachiinae having similar ovipositor, and therefore the siphonate mouthparts in Cretanallachiinae and Cretadilarinae may have evolved independently.

The genus *Fiaponeura* Lu et al., 2016b from Burmese amber probably belongs to Dilaridae, but its subfamily placement is unclear. Its mouthparts are similar to those of Cretanallachiinae, and wings are more or less similar to those of Cretadilarinae. Male genitalia are unknown, and those of the female are unclear. Therefore, additional specimens are needed to determine its affinities.

4.2. *Feeding habit of Cretanallachiinae and Cretadilarinae*

The excrement of the holotype of *Burmopsychops groehni* consists most probably of pollen grains; at least it consists of small rounded particles and does not contain any arthropod fragments. Such a large amount of presumable pollen grains shows that this species primarily fed on pollen. But this type of feeding is hard to assume judging from the structure of their mouthparts, which imply nectar feeding. Recently, spongilla-flies (Neuroptera: Sisyridae: Paradoxosisyrinae) with long siphonate mouthparts were discovered in Burmese amber, these are assumed to have been nectarivorous (or less likely hematophagous) (Makarkin, 2016). The structure of siphonate mouthparts in Dilaridae (Cretanallachiinae) and Sisyridae (Paradoxosisyrinae) differ in some important details: the galeae are widely spaced in all examined specimens of Cretanallachiinae while those of Paradoxosisyrinae are not, implying that they may form a sucking tube together with laciniae in the latter. In general, the galeae, maxillary, and labial palpi of all known Cretanallachiinae are widely spaced, implying that they are more suitable for collecting pollen than for nectarivory.

The mouthparts of Cretadilarinae are not clearly visible, but their galeae and laciniae appear to be more similar to those of Paradoxosisyrinae than Cretanallachiinae. Therefore, the feeding habit of Cretadilarinae is likely to be similar to that of Paradoxosisyrinae, i.e., nectarivorous.

Cretanallachiinae, Cretadilarinae and Paradoxosisyrinae probably fed on nectar and pollen of flowers, as their mouthparts were relatively short, suitable to exploit the shallow calyx (often less than 1 mm) of many Burmese amber flowers (see e.g., Grimaldi et al., 2002, fig. 13; Poinar et al., 2007, fig. 2). It may be assumed that these Burmese amber sisyrids and dilarids were among the first specialized groups of insect pollinators, which occupied the newly formed niche provided by flowers as a source of food. Some other groups of insects also fed on pollen of flowers in the Burmese amber forest (e.g., first bees and the psocopteran-like order Permopsocida), but these possessed relatively unspecialized mouthparts (Danforth and Poinar, 2011; Huang et al., 2016).

5. Conclusion

Two new subfamilies of Dilaridae with siphonate mouthparts have been described herein (i.e., Cretanallachiinae and Cretadilarinae) from the earliest Cenomanian/late Albian Burmese amber. They have been assigned to Dilaridae due to the presence of two dilarid autapomorphies at the order level: the entire reduction of the ligula, and the presence of pectinate antennae in males. Females of Cretanallachiinae have been shown to differ from those of other subfamilies by the presence of a primitive ovipositor: their gonocoxites 9 are broad, bear long gonostyli and are not fused to form a distinct ovipositor, while in other dilarid subfamilies a saber-like ovipositor is present (although it is short in Cretadilarinae). It is assumed that Cretanallachiinae primarily fed on pollen and Cretadilarinae on nectar of flowers.

Acknowledgements

I thank Carsten Gröhn and Alex Friedrich (Glinde, Germany) for allowing study the specimens and providing huge numbers of photographs, and answering numerous questions; Philip Perkins (Museum of Comparative Zoology, Harvard University, U.S.A.) for photographs of *Berothella pretiosa*; Susanne Randolf (Naturhistorisches Museum, Wien, Austria) for helpful discussion on mouthparts of extant Dilaridae; Valery M. Loktionov (Institute of Biology and Soil Sciences, Vladivostok, Russia) for help in photography; James Jepson (University College Cork, Ireland) for editing of the English. The study is supported by Grant Nos. 16-04-00053 and 14-04-00649 of the Russian Foundation for Basic Research.

References

Adams, P.A., 1970. A review of the New World Dilaridae. Postilla 148, 1–30.

Archibald, S.B., Makarkin, V.N., Ansorge, J., 2009. New fossil species of Nymphidae (Neuroptera) from the Eocene of North America and Europe. Zootaxa 2157, 59–68.

Aspöck, U., Aspöck, H., 2008. Phylogenetic relevance of the genital sclerites of Neuropterida (Insecta: Holometabola). Systematic Entomology 33, 97–127.

Aspöck, U., Mansell, M.W., 1994. A revision of the family Rhachiberothidae Tjeder, 1959, stat. n. (Neuroptera). Systematic Entomology 19, 181–206.

Aspöck, H., Aspöck, U., Hölzel, H., 1980. Die Neuropteren Europas, vol. 1. Goecke and Evers, Krefeld, Germany, 495 pp.

Aspöck, U., Liu, X.Y., Aspöck, H., 2015. The Dilaridae of the Balkan Peninsula and of Anatolia (Insecta, Neuropterida, Neuroptera). Deutsche Entomologische Zeitschrift 62, 123–135.

Banks, N., 1913. Synopses and descriptions of exotic Neuroptera. Transactions of the American Entomological Society 39, 201–242.

Banks, N., 1934. Supplementary neuropteroid insects from the Malay Peninsula, and from Mt. Kinabalu, Borneo. Journal of the Federated Malay States Museums 17, 567–578.

Beutel, R.G., Zimmermann, D., Krauss, M., Randolf, S., Wipfler, B., 2010. Head morphology of *Osmylus fulvicephalus* (Osmylidae, Neuroptera) and its phylogenetic implications. Organisms Diversity & Evolution 10, 311–329.

Carpenter, F.M., 1947. Taxonomic notes on the Dilaridae (Neuroptera). Psyche 54, 100–109.

Comstock, J.H., 1918. The Wings of Insects: An Exposition of the Uniform Terminology of the Wing-veins of Insects and a Discussion of the more General Characteristics of the Wings of the Several Orders of Insects. Comstock Publishing Company, Ithaca, NY, ix + 430 pp.

Crampton, G.C., 1921. The sclerites of the head, and the mouthparts of certain immature and adult insects. Annals of the Entomological Society of America 14, 65–110.

Danforth, B.N., Poinar Jr., G.O., 2011. Morphology, classification, and antiquity of *Melittosphex burmensis* (Apoidea: Melittosphecidae) and implications for early bee evolution. Journal Paleontology 85, 882–891.

Engel, M.S., 1999. The first fossil of a pleasing lacewing (Neuroptera: Dilaridae). Proceedings of the Entomological Society of Washington 101, 882–826.

Ghilarov, M.S., 1962. The larva of *Dilar turcicus* Hag. and the position of the family Dilaridae in the order Planipennia. Entomologicheskoe Obozrenie 41, 402–416.

Grimaldi, D.A., Engel, M.S., 2005. Evolution of the Insects. Cambridge University Press, Cambridge, UK, xv + 755 pp.

Grimaldi, D.A., Engel, M.S., Nascimbene, P.C., 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. American Museum Novitates 3361, 1–72.

Gurney, A.B., 1947. Notes on Dilaridae and Berothidae, with special reference to the immature stages of the Nearctic genera (Neuroptera). Psyche 54, 145–169.

Hennig, W., 1981. Insect Phylogeny. John Wiley & Sons, New York, 514 pp.

Huang, D.Y., Azar, D., Cai, C.Y., Garrouste, R., Nel, A., 2015. The first Mesozoic pleasing lacewing (Neuroptera: Dilaridae). Cretaceous Research 56, 274–277.

Huang, D.Y., Bechly, G., Nel, P., Engel, M.S., Prokop, J., Azar, D., Cai, C.Y., van de Kamp, T., Staniczek, A.H., Garrouste, R., Krogmann, L., dos Santos Rolo, T., Baumbach, T., Ohlhoff, R., Shmakov, A.S., Bourgoin, T., Nel, A., 2016. New fossil insect order Permopsocida elucidates major radiation and evolution of suction feeding in hemimetabolous insects (Hexapoda: Acercaria). Scientific Reports 6, 23004. http://dx.doi.org/10.1038/srep23004.

Killington, F.J., 1936. A monograph of the British Neuroptera, vol. 1. Ray Society, London, xi + 269 pp.

Kukalová-Peck, J., Lawrence, J.F., 2004. Relationships among coleopteran suborders and major endoneopteran lineages: evidence from hind wing characters. European Journal of Entomology 101, 95–144.

Linnaeus, C., 1758. Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, tenth ed. vol. 1 Salvii, Holmiae, 824 pp.

Liu, X.Y., Yang, D., 2006. Phylogeny of the subfamily Chauliodinae (Megaloptera: Corydalidae), with description of a new genus from the Oriental Realm. Systematic Entomology 31, 652–670.

Liu, X.Y., Aspöck, H., Winterton, S.L., Zhang, W.W., Aspöck, U., 2017. Phylogeny of pleasing lacewings (Neuroptera: Dilaridae) with a revised generic classification and description of a new subfamily. Systematic Entomology. http://dx.doi.org/10.1111/syen.12225.

Lu, X.M., Zhang, W.W., Liu, X.Y., 2016a. New long-proboscid lacewings of the Early Cretaceous provide insights into ancient plant-pollinator interactions. Scientific Reports 6, 25382. http://dx.doi.org/10.1038/srep25382.

Lu, X.M., Zhang, W.W., Liu, X.Y., 2016b. Nomenclatural validation of new genera and species of the superfamily Psychopsoidea (Insecta: Neuroptera) from the mid-Cretaceous amber of Myanmar. Zoological Systematics 41, 323–326.

Machado, R.J.P., Rafael, J.A., 2010. Two new species of Dilaridae (Insecta: Neuroptera) with additional notes on Brazilian species. Zootaxa 2421, 61–68.

MacLeod, E.G., Spiegler, P.E., 1961. Notes on the larval habitat and developmental peculiarities of *Nallachius americanus* (McLachlan) (Neuroptera: Dilaridae). Proceedings of the Entomological Society of Washington 63, 281–286.

Makarkin, V.N., 1993. Some peculiarities of the structure of the soil insect community in oak forests of extreme south Primorye. In: Artamonov, S.D. (Ed.), Seventh Arseniev's Readings. Ussuriysk State Pedagogical Institute, Ussuriysk, pp. 47–51 (in Russian).

Makarkin, V.N., 2016. Enormously long, siphonate mouthparts of a new, oldest known spongillafly (Neuroptera: Sisyridae) from Burmese amber imply nectarivory or hematophagy. Cretaceous Research 65, 126–137.

Makarkin, V.N., Archibald, S.B., 2013. A diverse new assemblage of green lacewings (Insecta: Neuroptera: Chrysopidae) from the Early Eocene Okanagan Highlands, western North America. Journal of Paleontology 87, 122–145.

Makarkin, V.N., Ohl, M., 2015. An important new fossil genus of Berothinae (Neuroptera: Berothidae) from Baltic amber. Zootaxa 3946 (3), 401–415.

Makarkin, V.N., Yang, Q., Shi, C.F., Ren, D., 2013. The presence of the recurrent veinlet in the Middle Jurassic Nymphidae (Neuroptera) from China: a unique condition in Myrmeleontoidea. ZooKeys 325, 1–20.

Nakahara, W., 1955. The Dilaridae of Japan and Formosa (Neuroptera). Kontyû 23, 133–142.

Navás, L., 1909. Monografía de la familia de los Diláridos (Ins. Neur.). Memorias de la Real Academia de Ciencias y Artes de Barcelona (3) 7, 619–671.

Navás, L., 1914. Family Dilaridae. Neuroptera. Genera Insectorum 156, 1–14.

Newman, E., 1853. Proposed division of Neuroptera into two classes. Zoologist 11 (Appendix), clxxxi–cciv.

Oswald, J.D., 1993a. Revision and cladistic analysis of the world genera of the family Hemerobiidae (Insecta: Neuroptera). Journal of New York Entomological Society 101, 143–299.

Oswald, J.D., 1993b. Phylogeny, taxonomy, and biogeography of extant silky lacewings (Insecta: Neuroptera: Psychopsidae). Memoirs of the American Entomological Society 40, i–iii + 1–65.

Oswald, J.D., 1998. Annotated catalogue of the Dilaridae (Insecta: Neuroptera) of the world. Tijdschrift voor Entomologie 141, 115–128.

Poinar Jr., G.O., Chambers, K.L., Buckley, R., 2007. *Eoëpigynia burmensis* gen and sp. nov., an Early Cretaceous eudicot flower (Angiospermae) in Burmese amber. Journal of the Botanical Research Institute of Texas 1, 91–96.

Poinar Jr., G.O., Buckley, R., Brown, A.E., 2008. The secrets of Burmite amber. MAPS Digest 20, 20–29.

Rambur, M.P., 1838. Faune entomologique de l'Andalousie, vol. 2. Pl. 9. Paris.

Retzius, A.J., 1783. Caroli lib. bar. De Geer… Genera et species insectorvm e generosissimi avctoris scriptis extraxit, digessit, latine qvoad partem reddidit, et terminologiam insectorvm linneaum addidit Anders Iahan Retzivs. Siegfried Lebrecht Crvsivm, Lipsiae, 220 pp.

Shi, G.H., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M.C., Lei, W.Y., Li, Q.L., Li, X.H., 2012. Age constraint on Burmese amber based on U–Pb dating of zircons. Cretaceous Research 37, 155–163.

Shi, C.F., Makarkin, V.N., Yang, Q., Archibald, S.B., Ren, D., 2013. New species of *Nymphites* Haase (Neuroptera: Nymphidae) from the Middle Jurassic of China, with a redescription of the type species of the genus. Zootaxa 3700 (3), 393–410.

Tillyard, R.J., 1919. Studies in Australian Neuroptera. No. 8. Revision of the family Ithonidae, with descriptions of a new genus and two new species. Proceedings of the Linnean Society of New South Wales 44, 414–437.

Tjeder, B., 1960. Neuroptera-Planipennia. The Lace-wings of Southern Africa. 3. Family Psychopsidae. In: Hanström, B., Brinck, P., Rudebec, G. (Eds.), South African Animal Life. Results of the Lund University Expedition in 1950–1951, vol. 7. Swedish Natural Science Research, Stockholm, pp. 164–209.

Vshivkova, T.S., Makarkin, V.N., 2010. Ultrastructural morphology of leg cuticle derivatives useful for phylogenetic study of Neuropterida (Insecta: Megaloptera, Neuroptera): preliminary report. In: Devetak, D., Lipovšek, S., Arnett, A.E. (Eds.), Proceedings of the Tenth International Symposium on Neuropterology. Piran, Slovenia, 2008. Maribor, Slovenia, pp. 287–300.

Weitschat, W., Wichard, W., 1998. Atlas der Pflanzen und Tiere im Baltischen Bernstein. Dr. Friedrich Pfeil Verlag. München, 256 pp., 92 pls.

Wichard, W., Wang, B., 2016. A remarkable caddisfly with bipectinate antennae in Cretaceous Burmese amber (Insecta, Trichoptera). Cretaceous Research 69, 198–203.

Willmann, R., 1990. The phylogenetic position of the Rhachiberothinae and the basal sister-group relationships within the Mantispidae (Neuroptera). Systematic Entomology 15, 253–265.

Xia, F.Y., Yang, G.D., Zhang, Q.Q., Shi, G.L., Wang, B., 2015. Amber: Lives Through Time and Space. Science Press, Beiping, 197 pp. (in Chinese).

Yang, Q., Makarkin, V.N., Winterton, S.L., Khramov, A.V., Ren, D., 2012. A remarkable new family of Jurassic insects (Neuroptera) with primitive wing venation and its phylogenetic position in Neuropterida. PLoS One 7 (9), e44762.

Yang, Q., Wang, Y.J., Labandeira, C.C., Shih, C.K., Ren, D., 2014a. Mesozoic lacewings from China provide phylogenetic insight into evolution of the Kalligrammatidae (Neuroptera). BMC Evolutionary Biology 14, 126.

Yang, Q., Makarkin, V.N., Ren, D., 2014b. Two new species of *Kalligramma* Walther (Neuroptera: Kalligrammatidae) from the Middle Jurassic of China. Annals of the Entomological Society of America 107, 917–925.

Zhang, W., Liu, X.Y., Aspöck, H., Aspöck, U., 2014a. Revision of Chinese Dilaridae (Insecta: Neuroptera) (Part I): species of the genus *Dilar* Rambur from northern China. Zootaxa 3753, 10–24.

Zhang, W., Liu, X.Y., Aspöck, H., Aspöck, U., 2014b. Revision of Chinese Dilaridae (Insecta: Neuroptera) (Part II): species of the genus *Dilar* Rambur from Tibet. Zootaxa 3878, 551–562.

Zhang, W., Liu, X.Y., Aspöck, H., Winterton, S.L., Aspöck, U., 2014c. Species of the pleasing lacewing genus *Dilar* Rambur (Neuroptera, Dilaridae) from islands of East Asia. Deutsche Entomologische Zeitschrift 61, 141–153.

Zhang, W., Liu, X.Y., Aspöck, H., Aspöck, U., 2015. Revision of Chinese Dilaridae (Insecta: Neuroptera) (Part III): species of the genus *Dilar* Rambur from the southern part of mainland China. Zootaxa 3974, 451–494.

Zhang, W., Liu, X.Y., Winterton, S.L., Aspöck, H., Aspöck, U., 2016. A review of the pleasing lacewing genus *Dilar* Rambur (Neuroptera, Dilaridae) from Southeast Asia. Zootaxa 4105 (2), 124–144.