

Cretanallachiidae – a new family of the specialized Cretaceous Neuroptera



Vladimir N. Makarkin

Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, 690022, Russia

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ABSTRACT

The subfamily Cretanallachiinae is elevated to a family level, Cretanallachiidae, stat. nov. Its autapomorphies are bipectinate antennae in males and a long ventro-caudal extension of the 9th tergite in females. The family is known only from mid-Cretaceous Kachin amber. It is likely closely related to Dilaridae, an undescribed ithonoid-like taxon from the Middle Jurassic, and to a lesser extent Ithonidae. They lived in humid tropical forests with diverse angiosperms and probably fed on their flowers (nectar and/or pollen) using relatively long sucking mouthparts.

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1. Introduction

The order Neuroptera has been known since the Lower Permian, but it reached its peak diversity in the second half of the Mesozoic. Most extant families had appeared by this time, and 16 valid families restricted to the Mesozoic are recognized by most authors: Archoesmyliidae, Osmylopsychopidae, Kalligrammatidae, Aetheogrammatidae, Parakseneuridae, Prohemerobiidae, Sau-crosmyliidae, Panfiloviidae, Grammolungiidae, Mesochrysopidae, Ascalochrysidae, Palaeoleontidae, Babinskaiidae, Araripeneuridae, Cratosmyliidae and Dipteronotispidae (Ren and Makarkin, 2009; Yang et al., 2012; Makarkin et al., 2013, 2018; Lu et al., 2022).

Mid-Cretaceous Kachin amber contains numerous Neuroptera, some of which are amazing, quite unlike modern taxa (Lu and Liu, 2021). There are three taxonomic groups with long sucking mouthparts. Most are assigned to the Paradoxosyrrinae (presumed Sisyridae: Makarkin, 2016; Khrarov et al., 2019) and Cretanallachiinae, and one species belongs to the Kalligrammatidae (Z. Peng et al., 2024b).

The taxonomic placement of the subfamily Cretanallachiinae is controversial. It includes eleven species in six genera known only from Kachin amber (Huang et al., 2015; Lu et al., 2016a, b; Makarkin, 2017; Chang et al., 2018; Q. Liu et al., 2018; Z. Peng et al., 2024a, b). The first described genus of the group

(*Cretanallachius* Huang et al., 2015) was assigned to Nallachiinae, an extant subfamily of Dilaridae (Huang et al., 2015). The second (*Burmopsychops* Lu et al., 2016b) was attributed to an unclear family of Psychopsoidea (Lu et al., 2016a, b). Makarkin (2017) later established the new subfamily Cretanallachiinae in Dilaridae for these two genera. Chang et al. (2018) described the genus *Oligopsychopsis* Chang et al., 2018 and again considered Cretanallachiinae as belonging to an unclear family of Psychopsoidea. Liu et al. (2018) described two genera *Burmogramma* Liu et al. 2018 and *Cretogramma* Liu et al. 2018, and assigned this group to Kalligrammatidae as “a relatively advanced lineage within the family” (Liu et al., 2018, p. 9). Lastly, two new species of *Burmopsychops* (Z. Peng et al., 2024a), and the monotypic genus *Lasiorgramma* Z. Peng, Shi, Ren & Yang in Z. Peng et al. (2024b) have been described as belonging to Kalligrammatidae.

Therefore, Cretanallachiinae is currently thought to either belong to the Dilaridae or the Psychopsoidea, specifically the Kalligrammatidae. Here, I dispute a kalligrammatid (and generally psychopsoid) affinity of Cretanallachiinae and argue that this group is a family of its own, most probably closely related to Dilaridae or ithonoid-like taxa.

2. Material and methods

All Cretanallachiidae specimens (including those examined, mainly from high-resolution photographs) come from Kachin amber in northern Myanmar, estimated to be lowest Cenomanian

E-mail address: vnmakarkin@mail.ru.

(Shi et al., 2012; Smith and Ross, 2018) from the Hukawng Valley, the state of Kachin (see map in Makarkin and Staniczek, 2026, fig. 1).

Venational terminology follows Breitkreuz et al. (2017) except for details (e.g., spaces, veinlets) that follow Oswald (1993). Crossveins are designated by the longitudinal veins to which they connect and are numbered in sequence from the wing base, e.g., 1r-m, first (basal) crossvein between R/RP and M/MA.

Venational abbreviations: A1–A3, first to third anal veins; C, costa; CuA, anterior cubitus; CuP, posterior cubitus; dn, distal nygma; hv, humeral veinlet; MA and MP, anterior and posterior branches of the media; RA, anterior radius; RP, posterior radius; RP1, most proximal branch of RP; Sc, subcosta.

Institutional abbreviations: CNU, College of Life Sciences, Capital Normal University, Beijing, China; SMNS, State Museum of Natural History Stuttgart, Germany.

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3. Systematic palaeontology

Order Neuroptera Linnaeus, 1758.

Family Cretanallachiidae Makarkin, 2017, stat. nov.

Cretanallachiinae Makarkin, 2017: 13 [as a subfamily of Dilaridae]; Cretanallachiinae: Q. Liu et al., 2018: 2 [as a subfamily of Kalligrammatidae].

Type genus. *Cretanallachius* (by original designation).

Diagnosis. Small to medium-sized Neuroptera (forewings 6.5–32 mm long). Most antennal flagellomeres of male bipectinate except terminal (Fig. 1); flagellomeres of female moniliform or filiform, long (more than twice as long as wide). Mouthparts sucking with long galeae and ligulae; mandible and ligula completely reduced (Fig. 2). Both wings: distal nygma sometimes present; costal space broadened, mostly medially; subcostal crossveins numerous; Sc and RA widely separated distally; crossveins in radial space usually numerous, irregularly arranged with indistinctly formed outer gradate series; MP often with several anteriorly-directed pectinate branches. Forewing: humeral veinlet simple, straight; one to three basal branches of RP originating separately on RA in most genera; CuA simple or with few branches; CuP pectinately forked, often only distally. Hind wing: basal crossvein between R and M (if present) long, sinuous; CuA usually pectinately forked; CuP origins far from wing base, simple or at most bifurcated in most genera. Male (Fig. 3): 9th tergite divided dorsally, with caudally extending lobes bearing a row of short, strong setae; 9th sternite often with a long caudal projection. Female: 9th tergite divided dorsally, representing a paired structure with a long broad ventro-caudal extension; gonocoxites 9 broad, widely separated; gonostyli 9 well developed.

Genera included. Six genera from the mid-Cretaceous Kachin amber: *Cretanallachius* (monotypic), *Burmopsychops* (four species), *Burmogramma* (monotypic), *Cretogramma* (monotypic), *Lasiogamma* (monotypic), and *Oligopsychopsis* (three species).

4. Discussion

4.1. Diagnostic characters of Cretanallachiidae

4.1.1. Mouthparts

Cretanallachiidae are characterized by siphonate (sucking) mouthparts. The proboscis consists of eight long elements. Two

pairs are with certainty maxillary and labial palps covered with long setae. Two other pairs are slender structures lacking long setae, and their interpretation is ambiguous. One pair is interpreted as galea (Makarkin, 2017; Khramov et al., 2020) or the fused galea and laciniae (e.g., Lu et al., 2016a; Chang et al., 2018; Q. Liu et al., 2018). The latter interpretation is followed by those authors, who interpret another pair as the ligula. Makarkin (2017) considered the latter pair in *Oligopsychopsis groehni* (Makarkin, 2017) as laciniae, with the ligula completely reduced. This interpretation was based on the position of the prementum in front of the labium. This interpretation has been disputed by Q. Liu and coauthors based on their observation that in all specimens of *O. groehni* that they examined “the prementum is actually absent and the “prementum” illustrated in Makarkin (2017) is probably artificial” (Q. Liu et al., 2018, S1, p. 2). However, this appears to be untrue: first, the prementum is clearly discernible in *O. groehni* (see Makarkin, 2017, fig. 7A), and second, in other species of the genus (*Oligopsychopsis penniformis* Chang et al., 2018) and *Lasiogamma ooideum* Z. Peng, Shi, Ren et Yang in Z. Peng et al., 2024b the prementum is also well developed (Fig. 2C; Chang et al., 2018, fig. 4E). Unfortunately, photographs of the mouthparts in Lu et al. (2016a), Chang et al. (2018) and Q. Liu et al. (2018) are of poor quality and do not allow details to be discerned. Their interpretations are unreliable as their drawings are reconstructions with a large element of bias (see e.g., Lu et al., 2016a, fig. 4e; Chang et al., 2018, fig. 4e). For example, the reconstruction of the mouthparts of *O. groehni* shows two ‘ligulae’ being entirely separated and located in front of two galeae, not behind (Q. Liu et al., 2018, fig. 2i). A paired ligula is unknown in Neuroptera, but it can be reduced: entirely reduced to absence in Dilaridae (Shepard, 1967, fig. 45; Zimmermann et al., 2019, fig. 11.10c), and strongly reduced in some Ithonidae (e.g., Tillyard, 1919, fig. 6d; Shepard, 1967, fig. 13).

Lasiogamma ooideum Z. Peng, Shi, Ren et Yang in Z. Peng et al., 2024b was recently described, in which the proboscis consists of four thin adjacent elements, and the palps are widely spaced (Figs. 2B, C; Z. Peng et al., 2024b, fig. 2C). These elements evidently originate from the maxillae and are undoubtedly the galeae and laciniae. In other known specimens, all elements of the proboscis are widely spaced and do not form a sucking tube, which indicates that they do not have a special connecting (coupling) mechanism.

Thus, the proboscis of Cretanallachiidae consists of two pairs of palps and probably galeae and laciniae; their ligula is completely reduced (until proven otherwise).

The terminal segments of the maxillary and labial palps possess a macula, which Lu et al. (2016a, fig. 4d) called an “ovoid sensory area”. It is unclear yet if these sensory areas in Cretanallachiidae and the palpimacula (see Crampton, 1921) of some extant Neuroptera (e.g., Hemerobiidae, Osmylidae, Mantispidae, Psychopsidae, Myrmeleontoidea) are homologous. The sensory areas of Cretanallachiidae are often not mentioned in descriptions, so information about them is incomplete.

Sucking mouthparts are detected in few fossil Neuroptera taxa, i.e., Aetheogrammatidae, Kalligrammatidae, Cretanallachiidae, Paradoxosyrrinae, the latter three in Kachin amber.

In Kalligrammatidae, the sucking mouthparts are known in Kalligrammatinae, Kallihemerobiinae, *Meioneurites spectabilis* Engel, 2005 and *Ithigamma multinervium* Yang et al., 2014; the mouthparts of Sophogrammatinae are chewing (mandibulate), and their structure is unknown in the basal Liassopsychopinae and *Protokalligamma* Yang et al., 2011; Makarkin and Ansorge, 2025. The proboscis of Kalligrammatinae and Kallihemerobiinae appears similarly constructed (see Labandeira et al., 2016, fig. S1). A maximum of six elements is visible: two pairs of elongate palps, and a pair of stylet-like elements, which usually treated as the

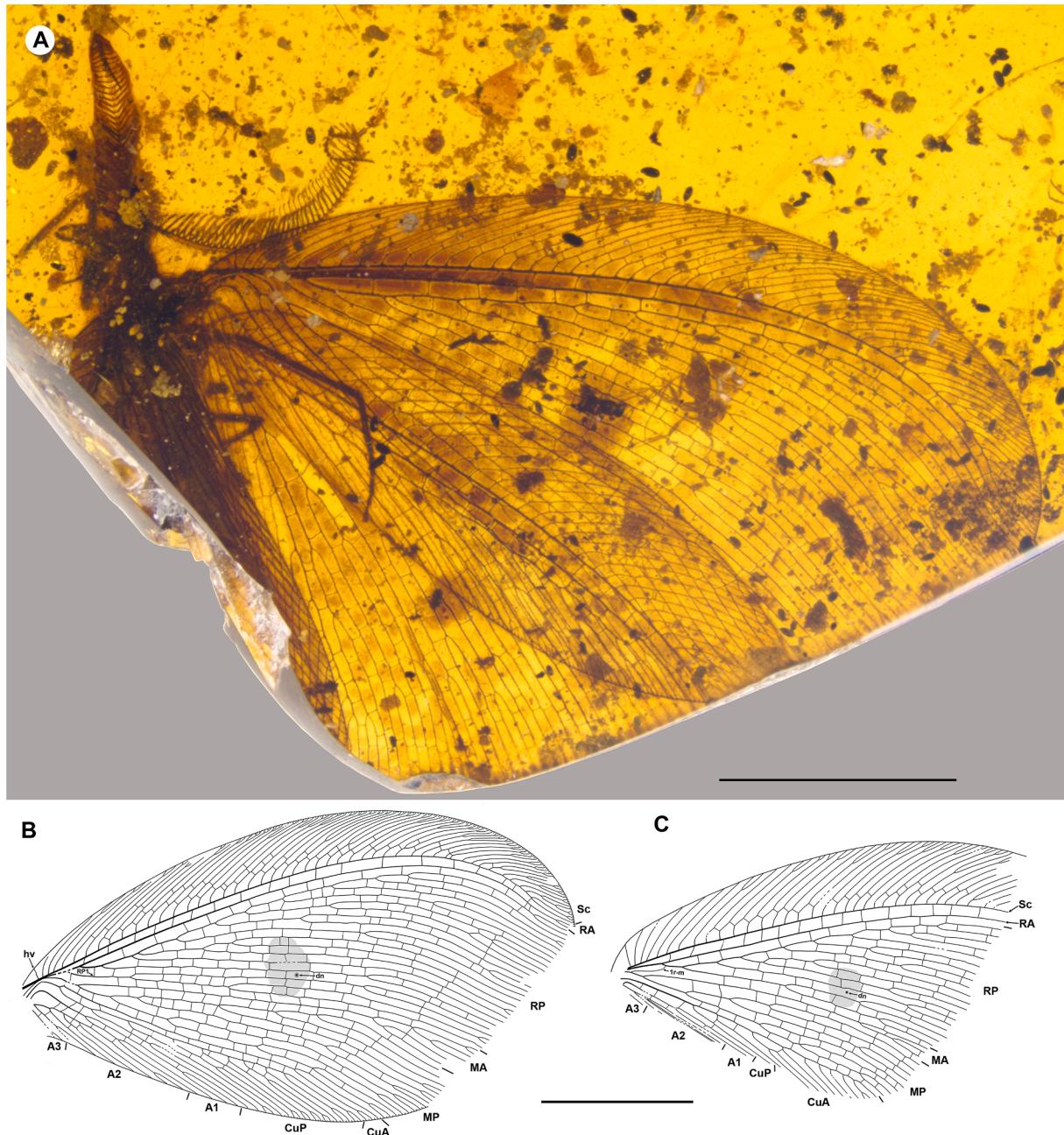


Fig. 1. *Oligopsychopsis grandis* Q. Liu et al., 2018, specimen SMNS BU-193. A, specimen as preserved (photo: H. Staniczek); B, forewing venation; C, hind wing venation. Scale bar is 5 mm (B, C, to same scale).

galeae (Labandeira, 2010, fig. 8B; Labandeira et al., 2016, fig. S1; Khramov et al., 2020, fig. 8.6), rarely as the ligula (Q. Liu et al., 2018, fig. S10c, d). Elements of the proboscis are usually conjoined to form a tube. As a result, its structure is often impossible to examine in detail.

The sucking mouthparts of Aetheogrammatidae are poorly known, but they appear generally similar to those of Kalligrammatinae (Khramov et al., 2020).

The sucking mouthparts of Paradoxosisyrrinae are generally similar to those of Cretanallachiidae, in which all elements of the proboscis are also widely spaced. But in addition to the eight elements, as in the Cretanallachiidae (i.e., two pairs of palps, a pair of galea and a pair of laciniae), there is a well-developed unpaired ligula, and the labrum is sometimes elongated (Makarkin, 2016, fig. 6A; Khramov et al., 2020, fig. 8.6).

The sucking mouthparts of three Neuroptera groups (Kalligrammatidae + Aetheogrammatidae, Cretanallachiidae and Paradoxosisyrrinae) most probably evolved independently.

4.1.2. Antennae

Pectinate antennae occur in Neuroptera only in male Cretanallachiidae and most Dilaridae. These are unipectinate in Dilaridae and bipectinate in Cretanallachiidae. However, the male antennae of the extant dilarid genus *Berothella* Banks, 1934 from south-eastern Asia are not pectinate (X. Liu et al., 2017). Makarkin (2016) considered the presence of pectinate antennae in males to be an autapomorphy of Dilaridae (including Cretanallachiinae), whereas Chang et al. (2018) and Q. Liu et al. (2018) believed that they evolved independently in these groups (i.e., Dilaridae and Cretanallachiidae).

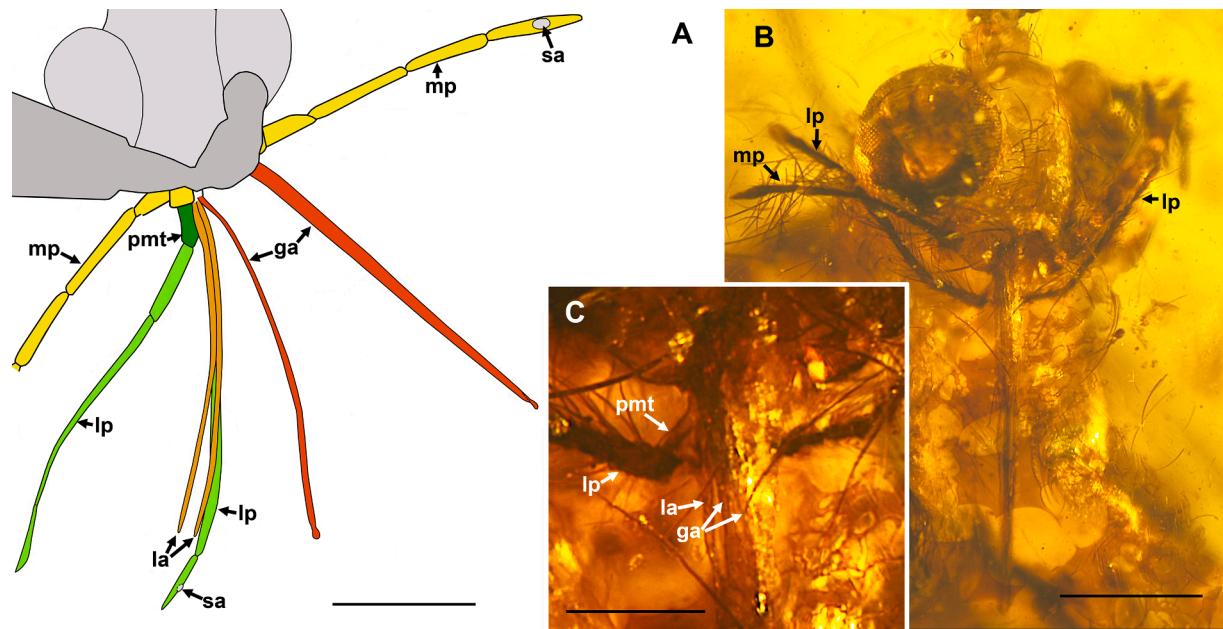


Fig. 2. Mouthparts of Cretanallachiidae. A, *Oligopsychopsis groehni* (Makarkin, 2017) (based on Makarkin, 2017, fig. 6B); B, *Lasiogramma ooideum* Peng, Shi, Ren and Yang in Z. Peng et al., 2024b, frontal view (photo: Z.H. Peng); C, same, enlarged portion of basal parts. ga, galea; la, lacinia; lp, labial palps; mp, maxillary palps; mpt, prementum; sa, sensory area. Scale bars are 0.5 mm (A, B), 0.2 mm (C).

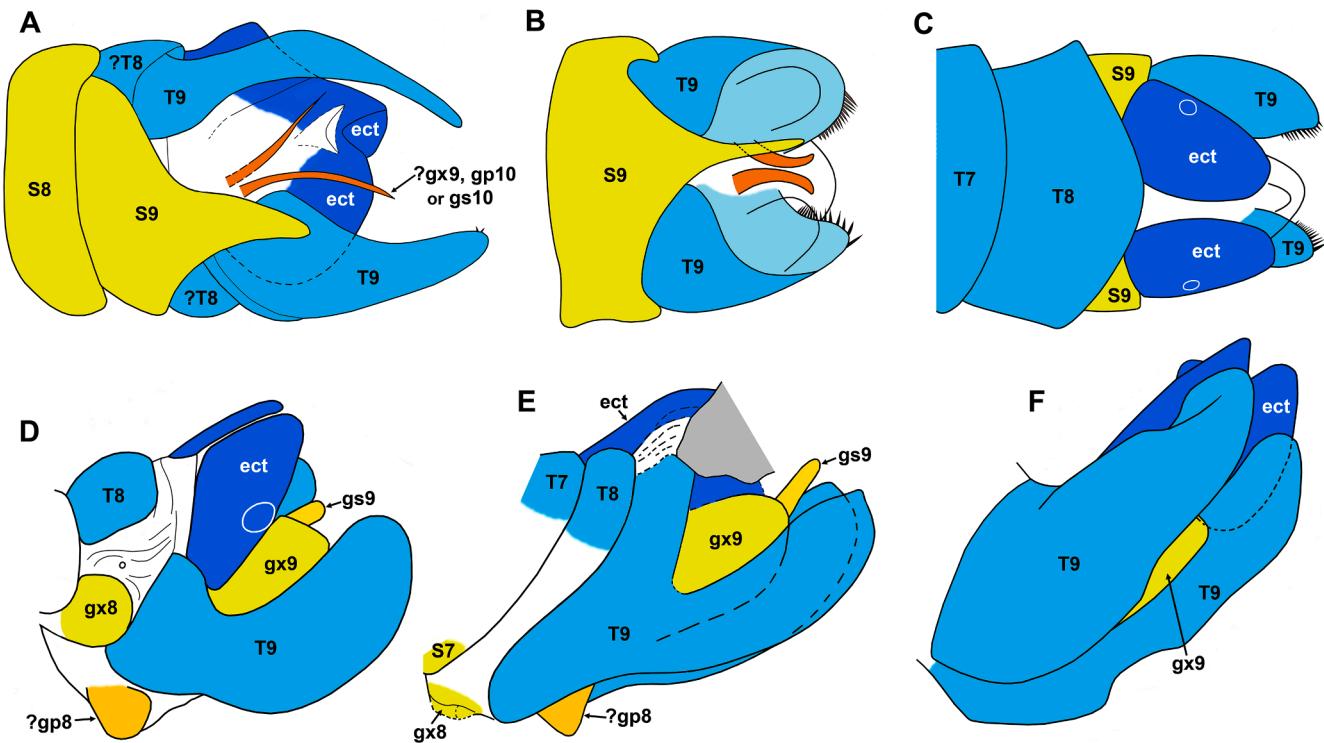


Fig. 3. Genital segments of Cretanallachiidae. A, male of *Cretanallachius magnificus* Huang et al., 2015, ventral view (based on Lu et al., 2016a, fig. 2b); B, male of *Burmopsychops shihi* Peng, Shi, Ren and Yang in Z. Peng et al., 2024, ventral view; C, same, dorsal view (based on Peng et al., 2024; fig. 3E, G); D, female of *Burmopsychops limoae* Lu et al., 2016b, lateral view (based on Q. Liu et al., 2018, fig. S2d); E, female of *Oligopsychopsis groehni* (Makarkin, 2017), lateral view (based on Makarkin, 2017, fig. 8B); F, female of *Burmogramma liui* Q. Liu et al., 2018, lateral view (Q. Liu et al., 2018, fig. S1i). ect, ectoproct; gp8, gonopophyses 8; gx8, gonocoxites 8; gs9, gonostyli 9; gx9, gonocoxites 9; S7 to S9, 7th to 9th sternites; T7 to T9, 7th to 9th tergites. All to not scale.

4.1.3. Male genitalia

The male genitalia of Cretanallachiidae are known in most genera (seven species, different in preservation): *Cretanallachius*

magnificus Huang et al., 2015, *Burmopsychops labandeirai* Q. Liu et al., 2018, *B. shihi* Peng, Shi, Ren et Yang in Z. Peng et al. (2024a), *Cretogramma engeli* Q. Liu et al., 2018, *Oligopsychopsis grandis* Q. Liu

et al., 2018, *O. penniformis*, *Lasiogramma ooideum* Peng, Shi, Ren et Yang in Z. Peng et al., 2024b (Huang et al., 2015, fig. 4c; Lu et al., 2016a, fig. 2d; Chang et al., 2018, fig. 5D; Q. Liu et al., 2018, figs. S3f,g; S4b,c; S6g; S8h; Z. Peng et al., 2024a, figs. 3D–G; Z. Peng et al., 2024b, fig. 4).

The most controversial part of the genitalia is a pair of large extended structures bearing a row of short strong setae ('teeth'). Superficially, these resemble the ectoproct of some Hemerobiidae (e.g., Oswald, 1993a, fig. 54), Psychopsidae (e.g., Oswald, 1993b, figs. 1, 6, 12, 17) and Ithonidae (e.g., Riek, 1974, figs. 4, 8, 39) or the 9th tergite of Dilaridae (see e.g., Zhang et al., 2016, figs. 11, 13). These genital segments are usually interpreted as gonocoxites 9 (Lu et al., 2016a, fig. 2d; Chang et al., 2018, fig. 5D; Q. Liu et al., 2018, figs. S3f, g; S4b, c), but the best preserved genitalia in *B. shini* certainly show that this is the 9th tergite (Fig. 3B, C). This tergite is entirely divided dorsally. Other well-developed segments are the 9th sternite, often with a caudal projection, and a paired ectoproct.

Internal genitalia are represented mainly by a pair of elongated divergent structures, which are usually interpreted as gonocoxites 10 (Chang et al., 2018; Q. Liu et al., 2018; Z. Peng et al., 2024a, b), but they can be interpreted also as gonocoxites 9, gonapophyses 10 or gonostyli 10. Other parts of inner genitalia do not allow even such an uncertain interpretation.

If this interpretation is correct, the male genitalia of Cretanallachiidae are most similar to those of Dilaridae (partly similar to *Berothella*, partly to *Nallachius* Navás, 1909; X. Liu et al., 2017, figs. 6, 11). In other families of Neuroptera, the 9th tergite is not so strongly extended in the caudal direction, including all genera of Psychopsidae (see Oswald, 1993b). Unfortunately, the male genitalia of Kalligrammatidae are unknown.

4.1.4. Female genitalia

Female genitalia are known in six species: *Burmogramma liui* Q. Liu et al., 2018, *Burmopsychops limoae* Lu et al., 2016b, *B. isodiametrus* Peng, Shi, Ren & Yang in Z. Peng et al., 2024a, *Cretanallachius magnificus* Huang et al., 2015, *Oligopsychopsis groehni* (Makarkin, 2017), and *O. grandis* Q. Liu et al., 2018 (Lu et al., 2016a; Makarkin, 2017; Chang et al., 2018; Q. Liu et al., 2018; Z. Peng et al., 2024a).

The most conspicuous part of the genitalia is the 9th tergite, which is elongated downwards with a long and wide ventro-caudal extension (Figs. 3D–F). Presumable gonocoxites 8 and presumable gonapophyses 8 are small structures, situated far from each other. Gonocoxites 9 are broad and elongate with well-developed gonostyli 9. The paired ectoproct is well developed, often elongate.

The genital segments of cretanallachiid females are in general more or less similar to those of some other families of Neuroptera, particularly Psychopsidae (Tjeder, 1960, figs. 257, 383), some Ithonidae (Penny, 1996, figs. 6, 7; Ardila-Camacho et al., 2020, figs. 3f, g), Polystoechotidae (Oswald, 1998, fig. 4), Hemerobiidae (Oswald, 1993, figs. 24, 68, 87, 93, 105, 137, 147, 151, 161, 169, 181), and some Chrysopidae (but gonostyli 9 in these are reduced: Aspöck and Aspöck, 2008, fig. 127; Tauber, 2019, figs. 9c, d, f). In these families, the 9th tergite is prolonged downwards, often reaching the ventral side, and is expanded ventro-caudally. But the ventro-caudal extension in Cretanallachiidae is much greater than in these families, and might be derived from any of them. The state of these genital characters in all these families is plesiomorphic in relation to the state that we find in the Cretanallachiidae.

The only known species of Kalligrammatidae with clearly visible female genitalia is *Oregramma illecebrosa* Yang et al., 2014 (Kalligrammatinae). Their structure is similar to that of Dilaridae, in particular bearing a long saber-like ovipositor being formed by two gonocoxites 9 with reduced gonostyli 9.

Thus, the female genitalia of Cretanallachiidae are similar to several families having plesiomorphic conditions, and dissimilar to those of known Kalligrammatidae and Dilaridae.

4.1.5. Wing venation

4.1.5.1. *Costal space*. The costal space of the fore- and hind wings is very broad in the medial and/or distal parts, but strongly narrowed in the proximal part, so that the costal margin is convex. Such a shape of the space is characteristic only of Cretanallachiidae, and is observed in all of its genera. The narrowing of the proximal part of the costal space is found in many families (e.g., Dilaridae, Chrysopidae, Myrmeleontoidea), but it is not so strongly broad (often narrow) medially and distally. The broad costal space occurs in some other families (Psychopsidae, Osmylopsychopidae, the chrysopid Apochrysinae, some Kalligrammatidae), but their proximal part is also broad.

4.1.5.2. *Humeral veinlet in the forewing*. The humeral veinlet is simple and crossvein-like in all Cretanallachiidae. This condition is present in all genera of many families (e.g., Sisyridae, Nevorthidae, Dilaridae, Osmylididae, Chrysopidae, Ascalaphidae, Myrmeleontidae, Nemopteridae) and some genera in many other families (e.g., Hemerobiidae, Berothidae, Mantispidae). However, this veinlet is recurrent and branched in most psychopsoids (all Psychopsidae and Osmylopsychopidae; many kalligrammatids: Liassopsychopinae, Sophogrammatinae, at least some Kallihemerobiinae, *Protokalligramma* Yang et al., 2011). In the Kalligrammatidae, it is simple and crossvein-like only in Kalligrammatinae.

4.1.5.3. *Distal relationships of ScP and RA*. Sc and RA are widely separated distally in all Cretanallachiidae. This condition is characteristic of many families (e.g., Dilaridae, Chrysopidae, Mantispidae, most Hemerobiidae, some Berothidae, Psychopsidae, Aetheogrammatidae). These veins are fused in most Kalligrammatidae, except Liassopsychopinae, in which Sc and RA approach apically, but are not fused (see Ansorge and Makarkin, 2021).

4.1.5.4. *Crossveins in the subcostal space*. Numerous crossveins in this space are present in all Cretanallachiidae as well as many other families (e.g., Kalligrammatidae, Psychopsidae, Osmylopsychopidae, Dilaridae, some Osmylididae, Parakseneuridae, some Nymphidae, few Berothidae). Numerous subcostal crossveins can be apparently developed in a few taxa of any family of Neuroptera.

4.1.5.5. *Media*. In Cretanallachiidae, M is divided into MA and MP relatively near wing base. MA is shallowly forked, dichotomously or pectinately. The posterior trace of the fore- and hind wing MP often have several anteriorly-directed pectinate branches. This condition is minimally developed in *Cretanallachius* where the posterior trace of M is forked only distally (see Huang et al., 2015, fig. 5b; Lu et al., 2016a, fig. 2b), and maximally in *Burmogramma*, *Burmopsychops* and *Oligopsychopsis*, where the posterior trace of MP bears up to seven anteriorly-directed branches (see Fig. 1A; Q. Liu et al., 2018, figs. S1b, f, S3b). The basal branch of MP is often again pectinately forked, with up to four branches (Fig. 1A).

This structure of MP (i.e., anteriorly-directed pectinate branching) is rare in Neuroptera. It is found in many genera of Kalligrammatidae (Kalligrammatinae, Kallihemerobiinae, *Meioneurites spectabilis* and *Ithigrama multinervium*), the Triassic *Petropsychops superba* Riek, 1956 (Osmylopsychopidae), and a group of undescribed ithonoid-like Neuroptera from the Middle Jurassic of China (Fig. 4). However, the anteriorly-directed pectinate branching of the forewing MP is absent in the basal

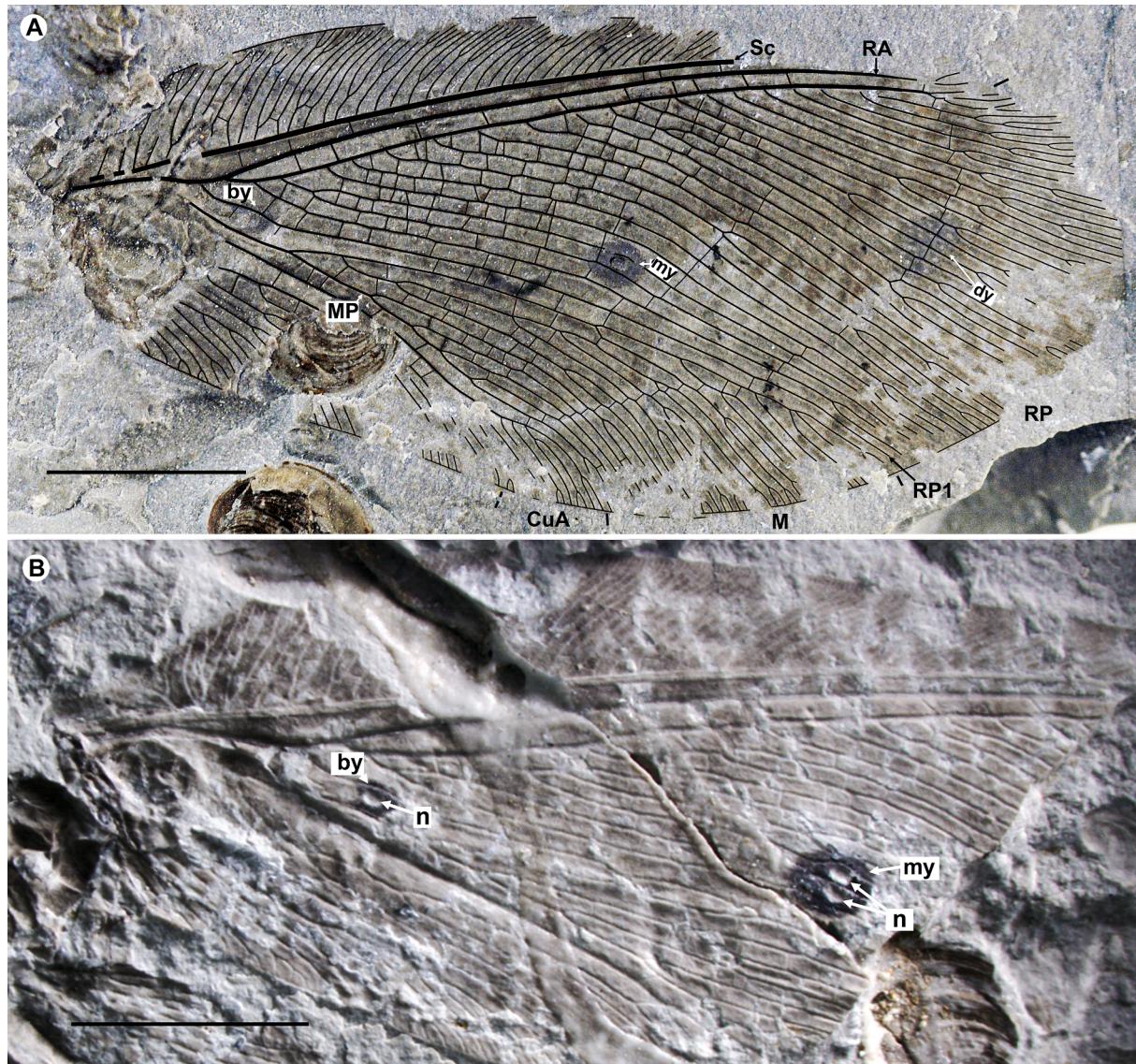


Fig. 4. Forewings of ithonoid-like Neuroptera from the Middle Jurassic of Daohugou (China). A, specimen CNU-NEU-NN2011062; B, specimen CNU-NEU-NN 2002005 (photo: Q. Yang). by, basal eyespot; dy, distal eyespot; my, middle eyespot; n, nygma. Scale bars are 5 mm.

Kalligrammatidae (i.e., *Protokalligramma* Yang et al., 2011, Liasopsychopinae and Sophogrammatinae: see Ansorge and Makarkin, 2021). M is dichotomously forked in these groups.

4.1.5.6. Distal nygma. Nygma are small sensory spots on wings, usually two in both fore- and hind wings or only in the hind wing: basal (between M and R/RP near the wing base) and distal (usually between RP1 and RP2 in the centre of the wing). The distal nygma is present in the following families of Neuroptera: some †Permithonidae (mainly in the hind wing), Nevorthidae, Osmylidae, Ithonidae, Polystoechotidae, most Dilaridae, †Osmylopsychopidae, and possibly some †Prohemerobiidae. In general, the presence of nygma is an indicator of the basal position of a family. The more advanced groups lack them (e.g., Chrysopoidea, Myrmeleontoidea, Mantispooidea, Kalligrammatidae, Hemerobiidae). The distal nygma is confidently detected in two genera of Cretanallachiidae, i.e., *Oligopsychopsis*

and *Cretogramma* (Fig. 1; Makarkin, 2017, fig. 10; Q. Liu et al., 2018).

4.1.5.7. Eyespots on wings. A well-developed eyespot in the centre of the wings is present only in one genus of Cretanallachiidae, i.e., *Burmogramma* (Q. Liu et al., 2018, figs 1g, h). Other species possess at most a brownish spot (often small) in that place, sometimes with a very small distal nygma (Fig. 1), or they lack spots (e.g., *Burmopsychops isodiametrus*, *Lasiogramma ooideum*).

Most Kalligrammatidae have eyespots (Ansorge and Makarkin, 2021). These are absent only in Sophogrammatinae and in some other genera (e.g., *Protokalligramma* Yang et al., 2011; *Abrigramma* Yang et al., 2014; not clearly discernible in *Affinigramma* Yang et al., 2014).

Eyespots are also present in the forewing of other Neuroptera: four eyespots in the large *Calopsychops extinctus* Panfilov, 1980 (Psychopsidae or Osmylopsychopidae) from the Upper Jurassic of Karatau (Kazakhstan); and up to three eyespots in a group of

undescribed ithonoid-like Neuroptera from the Middle Jurassic of China (Fig. 4) (see below for further details).

4.1.5.8. Proximal branches of RP in the forewing. Four genera of Cretanallachiidae possess one to three basal branches of RP originating separately on RA: *Cretogramma*, *Burmopsychops*, *Oligopsychopsis*, and *Lasiogramma* (Fig. 1). Such a condition (i.e., two or more branches of RP separately originating on RA) is characteristic of Hemerobiidae, Aetheogrammatidae, some Kalligrammatidae, some Dilaridae, some Ithonidae. A single RP (a plesiomorphic state) is present in *Cretanallachius* and *Burmogramma*, and in the vast majority of other Neuroptera.

4.1.5.9. CuA in the forewing. The forewing CuA of Cretanallachiidae is shallowly forked distally or even simple as in *Cretanallachius magnificus* and *Oligopsychopsis groehni* (Lu et al., 2016a, fig. 2b; Makarkin, 2017, fig. 9A). Its branching mode is unclear in *Burmogramma liui*. The forewing CuA of most other Neuroptera are pectinately forked distally, but shallowly forked in the advanced Kalligrammatidae (e.g., Kalligrammatinae), most Myrmeleontoidea (except †Babinskaiidae), and few taxa in other families (e.g., the dilarid *Neonallachius krooni* (Minter, 1986); Minter, 1986, figs. 3, 4).

4.1.5.10. CuP in the forewing. The forewing CuP in Cretanallachiidae is usually pectinately forked, having from eight branches located almost along entire anterior trace of the CuP (e.g., *Oligopsychopsis grandis*: Fig. 1) to two distal branches (e.g., *Cretanallachius magnificus*, *Burmopsychops shihi*). It is shallowly forked in *Lasiogramma* and unclear in *Burmogramma*. In most other Neuroptera it is similarly pectinately forked, often only distally (e.g., Nevrorthidae, Berothidae, Sisyridae, Ithonidae, Polystoechotidae, Dilaridae). In most Kalligrammatidae, the forewing CuP is shallowly forked, except basal Liassopsychopinae in which CuP is dichotomous (Q. Liu et al., 2014, fig. 2C; Ansorge and Makarkin, 2021, figs. 4C, 5C).

4.1.5.11. Crossveins in the radio-medial space. Crossveins in this space of Cretanallachiidae are usually numerous, irregularly arranged with indistinctly formed outer graduate series (except *Burmogramma liui*). Numerous irregularly-arranged crossveins are found in most families of Neuroptera (e.g., Osmylopsychopidae, some Dilaridae, Myrmeleontoidea, Osmyloidea). But the outer graduate series is present only in some of these (e.g., Osmylopsychopidae, some Osmylidae).

4.1.5.12. Basal crossvein between R and M in the hind wing. The basal crossvein 1r-m is long and sinuous in some Cretanallachiidae. It is observed in *Cretanallachius magnificus* and *Oligopsychopsis grandis* (Fig. 1C), absent in *Burmopsychops shihi*, *B. isodiametru*s, and probably absent *Burmogramma liui*.

This plesiomorphic character state is very important, since its reversion is extremely unlikely, if not impossible, at least it has never been reported by any author. It occurs in most basal families of the order (e.g., †Permithonidae, Nevrorthidae, Sisyridae, Osmylidae, Ithonidae, Polystoechotidae, and some Dilaridae). In most known Kalligrammatidae, 1r-m is straight, not distinguished from other basal crossveins (e.g., Makarkin et al., 2009, figs. 1A, 2C; Q. Liu et al., 2015, figs. 2.3, 4.2). However, in a recently discovered hind wing of the basal Lower Jurassic subfamily Liassopsychopinae, it is longitudinal (but not so long), similar to its state in the Jurassic Parakseneuridae (Yang et al., 2012, figs. 15C; pers. obs.). This condition is intermediate from plesiomorphic to apomorphic in these two taxa.

4.1.5.13. CuA in the hind wing. The hind wing CuA of Cretanallachiidae is usually pectinately forked, having from three (e.g., Z. Peng et al., 2024a, figs. 2D, 3D) to ten branches (e.g., Fig. 1C; Q. Liu et al., 2018, fig. S1d). However, it is shallowly forked in *Cretanallachius* (Lu et al., 2016a, fig. 2b) and *Lasiogramma* (Z. Peng et al., 2024b, figs. 3F, H). The hind wing CuA is also pectinately forked in many families of Neuroptera (most Dilaridae, Nevrorthidae, Berothidae, Polystoechotidae, some Kalligrammatidae, and others). Therefore, this condition is typical for the order.

4.1.5.14. CuP in the hind wing. The hind wing CuP of most Cretanallachiidae is relative short, simple or at most terminally bifurcated, and originates far from the wing base. This vein appears to be the most proximal branch of CuA and undoubtedly represents an apomorphic condition. It is clearly observed in *Cretanallachius magnificus* (Lu et al., 2016a, fig. 2b) and *Oligopsychopsis grandis* (Fig. 1C). The hind wing CuP of *Burmopsychops shihi* and probably *Burmogramma liui* originates rather near the wing base, but is weakly branched and not parallel to CuA (i.e., this state is more plesiomorphic).

The similar apomorphic state of CuP occurs only in Dilaridae among Neuroptera (all three their subfamilies), and one species of Ithonidae (i.e., *Oliarces clara* Banks, 1908).

The CuP of *Nallachius* Navás, 1909 originates far from the wing base, and is often pectinately forked with short simple branches (see e.g., Carpenter, 1947, fig. 2; Adams, 1970, figs. 1, 11, 12, 14D; Penny, 2002, figs. 435–437; Martins and Amorim, 2015, fig. 2A; Martins and de Araújo, 2016, fig. 3; Lara and Perioto, 2017, fig. 2). In some *Neonallachius* Nakahara, 1963 (Nallachiinae), CuP is considered absent (X. Liu et al., 2017). Although a complete reduction of CuP in these species cannot be ruled out, CuP may be represented by a proximal-most simple branch of the apparent CuA, which in this case differs little from the state of *Nallachius*. Such an apomorphic condition is also present in the monotypic Berothellinae (see X. Liu et al., 2017, fig. 5I). In *Neonallachius sinuolatus* Li and Liu, 2021, the very weak CuP is depicted in a drawing as originating relatively close to the wing base (Li and Liu, 2021, fig. 2A), but it is not discernible in the photograph (Li and Liu, 2021, fig. 1C). It is possible that all of this “CuP” or only its proximal portion is a flexion fold.

Most species of *Dilar* Rambur, 1838 (Dilarinae) exhibit the plesiomorphic condition of CuP (i.e., originating near the wing base with long forked branches), but some species of this genus have an apomorphic condition similar to that of *Neonallachius* (see e.g., Monserrat, 1988, figs. 17, 18). A similar plesiomorphic condition as found in *Dilar* is present in many taxa of Neuroptera.

The hind wing CuP of all Kalligrammatidae is fundamentally different in configuration from that of Cretanallachiidae. It is a long vein originating near the wing base, and parallel (or nearly so) to CuA for a long distance (see e.g., Ren and Oswald, 2002, fig. 2; Makarkin et al., 2009, figs. 1, 2; Yang et al., 2014, figs. 10C, 13C, 14D; Q. Liu et al., 2015, figs. 2–4). In other Psychopoidea (including fossils), this vein also does not resemble a branch of CuA, as it originates near the wing base with at least a few long, often pectinate branches (see e.g., Khramov and Makarkin, 2015, figs. 9, 10; Y. Peng et al., 2016, figs. 13B, 15B, 19D, 23B).

4.2. Monotypy of Cretanallachiidae

The analysis here supports genera of Cretanallachiidae as a monophyletic group: all males have bipectinate antennae, the structure of the mouthparts and the venation are similar, and the genital segments of males and females have a similar configuration. The bipectinate antennae in males and the long ventro-

caudal extension of the 9th tergite of females are unique among Neuroptera and, therefore, are autapomorphies of the family.

Oligopsychopsis grandis Q. Liu et al., 2018 is one of most typical representatives of Cretanallachiidae (Fig. 1). Its basal crossvein 1r-m is long and sinuous, CuP is simple, originating far from the wing base in the hind wing, and the distal nygma is present in both the fore- and hind wing.

Burmogramma is most unlike the other genera of Cretanallachiidae, and the family was assigned to Kalligrammatidae by Q. Liu et al. (2018) mainly based on the configuration of the forewing MP and the presence of eyespots. Indeed, its eyespot more or less resembles that of Kalligrammatidae. However, it has no swellings (embossed structures in the central pigmented disk of an eyespot), which are often present in all subfamilies that have an eyespot, i.e., Liassopsychopinae, Kalligrammatinae and Kallihereroobiinae (Ansorge and Makarkin, 2021). The eyespot in *Burmogramma* is located where the brownish spot is in other genera and may have developed independently of the eyespots in Kalligrammatidae.

Burmogramma is larger and has denser venation, which is not fundamentally different from that of other genera of the family. Its proboscis does not form a sucking tube, unlike that of all known Kalligrammatidae. Also, the female genitalia of *Burmogramma* does not principally differ from those of other Cretanallachiidae, although in this genus some segments (gonocoxites 8, gonaphophyses 8, gonostyli 9) are not preserved.

Thus, *Burmogramma* certainly belongs to the family Cretanallachiidae, the most distant from its other genera.

4.3. Systematic position of Cretanallachiidae

The presence of two important plesiomorphic features of some genera (the long and sinuous basal crossvein 1r-m in the hind wing, and at least the distal nygmata in both wings) indicates a basal position of Cretanallachiidae. These two conditions are present in †Permithonidae, Nevorthidae, Ithonidae s. str., Polystoechotidae, Dilaridae, Osmylididae, and †Osmylopsychopidae. The sinuous 1r-m is present in †Prohemeroobiidae, Sisyridae, Rhachiberothidae, few Berothidae (mainly the Mesozoic †Mesithoninae), Mantispidae (only Symphrasinae) and Hemerobiidae, but the nygmata are absent in these. A proximal nygma is present in Psychopsidae, but its hind wing 1r-m is straight. The basal Lower Jurassic Kalligrammatidae (Liassopsychopinae) and the Jurassic †Parakseneuridae have similar venation, but this is strongly dissimilar to that of Cretanallachiidae. Both lack nygmata, but their 1r-m is in an intermediate condition, from plesiomorphic to apomorphic, being relatively short but oriented longitudinally (Yang et al., 2012, fig. 15C; pers. obs.). Advanced Kalligrammatidae do not possess both of these plesiomorphic character states.

The venation of two superfamilies is strongly dissimilar to that of Cretanallachiidae, including the loss of these two plesiomorphies: Myrmeleontoidea (Nymphidae, †Palaeoleontidae, †Arripeneuridae, †Babinskaiidae, †Cratosmylididae, Nemopteridae, Myrmeleontidae, Ascalaphidae) and Chrysopoidea (†Meso-chrysopidae, †Ascalochrysidae, Chrysopidae). It is clear that Cretanallachiidae are very distantly related to these families.

Most other families, some which have these plesiomorphic traits, are also distant to Cretanallachiidae (i.e., Nevorthidae, Sisyridae, Osmylididae, †Saucrosmylididae, †Panfiloviidae, †Grammalingiidae, †Osmylopsychopidae, Psychopsidae, and Mantispidae). These families have either genital or venational (or both) characters that differ greatly from those of the Cretanallachiidae.

Only a few families can be considered closely related to Cretanallachiidae.

Q. Liu et al. (2018) regarded Cretanallachiinae “a relatively advanced subfamily” within Kalligrammatidae, and in their cladogram, the subfamily represents the youngest and most advanced group (Q. Liu et al., 2018, fig. 3). However, this contradicts the basal position of the family based on the presence of nygmata and a long sinuous 1r-m, as these characters are apomorphic in other Kalligrammatidae. Even if we accept Cretanallachiinae as a subfamily of Kalligrammatidae, it represents the earliest divergence of the family, but early Kalligrammatidae probably had chewing mouthparts (detected in *Sophogramma* Ren and Guo, 1996; but possibly in more genera). Of course, it is plausible that siphonate mouthparts evolved independently in Cretanallachiinae and other Kalligrammatidae. However, this would mean that Cretanallachiinae and other Kalligrammatidae represent two lineages that diverged at least in the Lower Jurassic, consistent with the family status of Cretanallachiinae. Some venational character states of Kalligrammatidae are completely different from those in Cretanallachiinae. For example, the structure of the hind wing Cu as found in Cretanallachiinae (the combination of a strongly pectinate CuA and a relatively short, simple or little-branched CuP) never occurs in Kalligrammatidae. Thus, a kalligrammatid affinity of Cretanallachiinae cannot be confirmed. Their siphonate mouthparts and eyespots most likely evolved independently in these groups.

The venation and other characters of other psychopsoid families (Osmylopsychopidae and Psychopsidae) are so different from that of the Cretanallachiidae that they may be immediately discounted as close relatives. A putative psychopsoid affinity of Cretanallachiidae (see Lu et al., 2016a; Chang et al., 2018) appears to be based on superficial similarities.

The Cretanallachiidae are likely most closely related to Dilaridae. These taxa share many venation character states: nygmata are present in both fore- and hind wings; Sc and RA are widely separated distally, subcostal crossveins are numerous, crossveins in the radial space are irregularly arranged, the humeral veinlet is simple, the forewing RP1 originates separately on RA in some taxa, the basal crossvein 1r-m is sinuous, and the hind wing CuP originates far from the wing base in most genera. The 9th tergite of males in both families is similarly constructed.

Cretanallachiidae were initially considered to be a subfamily of Dilaridae (Makarkin, 2017), for which there was a precedent. Although the long, saber-shaped ovipositor of Dilaridae and the peculiar genitalia of female Cretanallachiidae are very different, this cannot serve as the sole basis for classifying them into different families. In the family Mantispidae, Symphrasinae possess a long ovipositor, while female genitalia in other taxa of the family plesiomorphically lack such an ovipositor.

Cretanallachiidae may theoretically be descendants of ancient Dilaridae, which had a long ovipositor. However, dilarids are unknown before the mid-Cretaceous, probably originating in the Jurassic. In this regard, a group of undescribed ithonoid-like Neuroptera from the Middle Jurassic of China (Daohugou) deserve special consideration most promising as possible ancestors of Cretanallachiidae (Fig. 4).

First, their forewing venation is similar to that of Cretanallachiidae, e.g., the subcostal crossveins are numerous; RP1 originates separately on RA; the crossveins in the radial space are arranged irregularly proximally and form the outer gradate series distally; the pectinate branches of the posterior trace of M are anteriorly directed; and CuA has few distal branches.

Secondly, they possess eyespots, but with a different structure. The basal and medial eyespots are situated at the location of the basal and distal nygmata, respectively, and contain in the centre one (basal) and one to two (medial) circular embossed structures, which are undoubtedly large nygmata similar to the swellings of

Kalligrammatidae ('n' in Fig. 4). The wing shown in Fig. 4B is particularly indicative, showing that the origin of the swellings of Kalligrammatidae from nygmata is very plausible. The distal eyespot is a large flat dark spot with several small pale spots. Although its structure rather resembles that of eyespots of some Kalligrammatidae, its location in the distal part of the wing suggests that the distal eyespot of this itonoid-like group and the eyespots of Kalligrammatidae are convergent.

Therefore, Cretanallachiidae are more similar to this taxon than they are to Kalligrammatidae, and they may be theoretically descendants of this itonoid-like group. If so, the taxon should have been widespread in the Jurassic to Lower Cretaceous, including Gondwana (see below, Biogeography).

Further, the venation of Cretanallachiidae is rather similar to that of extant Ithonidae s. str., which also has Sc and RA widely separated distally; radial crossveins irregularly arranged; RP1 separately originating on RA in the forewing (some genera); and the hind wing CuP originating far from the wing base in one genus. The ligula of Ithonidae is similarly strongly reduced.

Thus, considering all of this evidence, Cretanallachiidae are likely closely related to Dilaridae, a Middle Jurassic itonoid-like taxon, and Ithonidae. While many venational characters support this, the configuration of the hind wing CuP is particularly important, as this condition is present only in Cretanallachiidae, most Dilaridae, and one genus of Ithonidae.

4.4. Biogeography

It is well known that the West Burma Block (West Burma Terrane), where Kachin amber was found, was formerly a part of Gondwana, namely Australia (Metcalfe, 2017; Poinar, 2019; Westerweel et al., 2019, 2025). The fact that the family has only been found in Kachin amber suggests that it may have formed from a proto-cretanallachiid Gondwanan taxon during the drift of the West Burma Block from Australia to Asia. The Burma Block, as expected, separated from Australia in the Upper Jurassic (Fig. 5) and was located almost on the equator during the time of the Kachin amber forest (Westerweel et al., 2025). Long-term island isolation in an equatorial climate has resulted in the formation of many endemic (often bizarre) family-group taxa, not only Cretanallachiidae (e.g., Rasnitsyn and Öhm-Kühnle, 2018; Ogaza et al., 2025).

What Gondwanan taxon might be ancestral to the Cretanallachiidae? The single known Jurassic Gondwanan Neuroptera is an unnamed small wing from the Upper Jurassic of Telengana (India) deposited in the Museum of Comparative Zoology (Harvard University, 2018). The neuropteran assemblage of the Crato Formation of Brazil is numerous and diverse, but it is Aptian, i.e., significantly younger than the separation of the Burma Block. The assemblage is dominated by Myrmeleontoidea and has lesser amounts of Ithonidae, Kalligrammatidae, Psychopsidae,

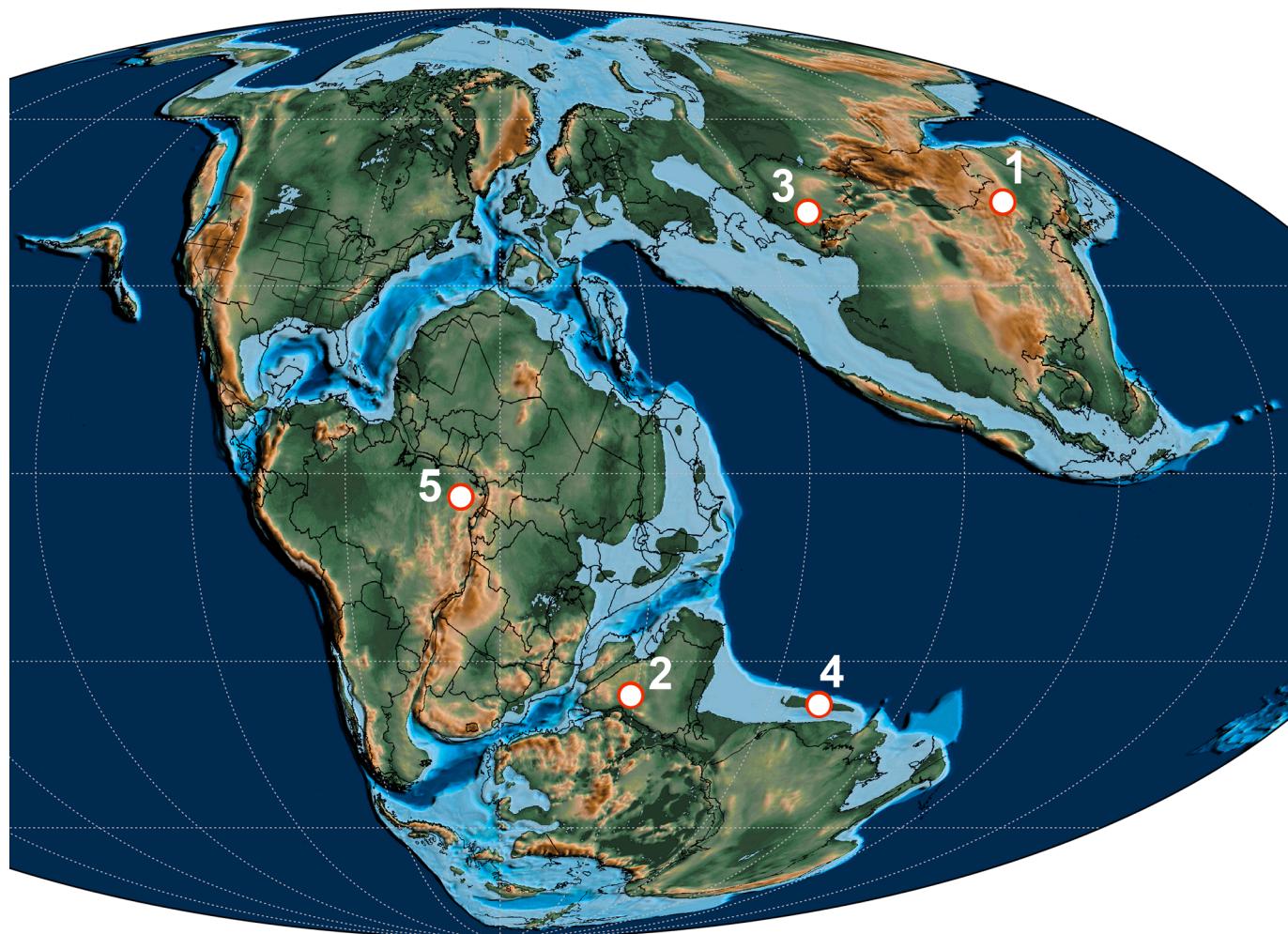


Fig. 5. A paleogeographical map of Earth in the Upper Jurassic (155 Ma) showing localities mentioned in the text (after Scotese et al., 2024). 1, Daohugou, China (Middle Jurassic); 2, Telengana, India; 3, Karatau, Kazakhstan; 4, West Burma Block; 5, Crato Formation, Brazil (Lower Cretaceous, Aptian).

Osmylidae, Chrysopidae, Mesochrysopidae, Berothidae and possibly Sisyridae (Martins et al., 2022). Of these, only Ithonidae and Kalligrammatidae can be considered close to the Cretanallachiidae. These families are represented in the Crato Formation by one to two genera. Three species of the kalligrammatid genus *Makarkinia* Martins-Neto, 1997 are fragmentarily preserved (Bechly and Makarkin, 2016; Machado et al., 2021). The genus is tentatively assigned to the subfamily Kalligrammatinae, not basal Kalligrammatidae. Of Ithonidae, *Principiala* Makarkin and Menon, 2007 belongs also to the advanced *Principiala* genus-group which is represented in Kachin amber (X. Liu et al., 2025); *Crato-voluptia* Martins-Neto and Rodrigues, 2009 is inadequately described.

Thus, no proto-cretanallachiid candidates have yet been found in Gondwana, but dilarid-like and ithonoid taxa might be found there in future.

4.5. Habitats

Most authors interpret the Myanmar palaeoenvironment during amber deposition as a humid, warm tropical forest (e.g., Grimaldi et al., 2002; Xing et al., 2018; Lu et al., 2019b, 2020). Although many fossil organisms found there are indeed moisture-loving (e.g., ferns, bark-growing liverworts, Onychophora, cockroaches), there is some evidence of dry conditions: fire-adapted angiosperms with needle-like xeromorphic leaves (Shi et al., 2022); the presence of Nemopteridae (Lu et al., 2019b), indicators of arid or semiarid environment; the occurrence of some Araripeneuridae that are very similar to those inhabited semi-arid ecosystems of the Aptian Brazil (Lu et al., 2019a). These dry conditions could have been seasonal, but it cannot be ruled out that semi-arid ecosystems existed alongside humid forests. So that the palaeoenvironment of the West Burma Block in that time was more reminiscent of extant equatorial Africa than Kalimantan or Malaysia.

Cretanallachiidae probably lived in humid tropical forests dominated by gymnosperms, accompanied by diverse angiosperms (Shi et al., 2022).

4.6. Feeding habits

Based on the structure of their mouthparts, Cretanallachiidae probably fed on flowers, nectar and/or pollen, or both. Their proboscis was short, from less than 1 mm (*Cretanallachius*) to about 3 mm (*Burmogramma*) long, excluding palpi, which are somewhat longer. Diverse angiosperm flowers in Kachin amber were mostly very small, with a calyx of 0.3–2 mm in diameter, often shallow (Poinar and Chambers, 2005, 2007, 2017, 2020a, b; Poinar et al., 2007a, b, 2008, 2013; Z. Liu et al., 2018; Chambers and Poinar, 2020; Shi et al., 2022). So that the proboscis of Cretanallachiidae would have been suitable to feed on nectar from these flowers.

A fairly large number of Paradoxosisyrrinae had a proboscis that was similarly short, with a length ranging from 0.6 mm to approximately 1 mm (Makarkin, 2016; Khramov et al., 2019, 2020). They likely share the same ecological niche with Cretanallachiidae, although they possibly divided it in some way, although there is no evidence yet of this.

Cretanallachiidae and Paradoxosisyrrinae may have theoretically fed on liquid pollination drops of some gymnosperms (e.g., Cycadales and Bennettitales), but this is rather unlikely. The proboscises of small Mecoptera from Kachin amber (Aneuretopsychidae, Pseudopolycentropodidae) were short, similar in length to the proboscises of these Neuroptera, and these scorpionflies are thought to be associated with both flowers and gymnosperms (Lin et al., 2019). However, these families of Mecoptera lived before the

emergence of angiosperms, and they may have retained their dietary preferences into the mid-Cretaceous. Cretanallachiidae and Paradoxosisyrrinae emerged when angiosperms were beginning their great diversification. Their feeding on flowers may then have followed this early phase of their rise to ecological dominance.

The only species of Kalligrammatidae known from Kachin amber (*Eletrogramma transformatum* Z. Peng et al., 2024b) is represented by incomplete wings, and its mouthparts are unknown. The extinct Bennettitales were found in Kachin amber (Shi et al., 2022). They are suggested to have been one of the gymnosperms that kalligrammatids with sucking mouthparts fed on (Labandeira et al., 2010, 2016). However, the venation of this species is most similar to that of *Sophogramma* (see Makarkin and Ansorge, 2025), which possesses mandibulate (chewing) mouthparts. Thus, *E. transformatum* may not have fed on nectar and/or pollen, but was carnivorous.

Other flower visitors among Kachin amber Neuroptera are pollen feeders. At least two genera are found here: *Cretocroce* Lu et al., 2019b (Nemopteridae) and *Rhynchoberotha* Wang et al., 2025 (Berothidae). The mouthparts are chewing in these genera, but their rostrum is similarly elongated (Lu et al., 2019b, fig. 3A; Wang et al., 2025, fig. 7A). All extant Nemopteridae and some Berothidae (e.g., *Nyrma kervillea* Navás, 1933) are specialized pollen feeders.

5. Conclusions

Cretanallachiidae constitute a distinct family, autapomorphies of which are the bipectinate antennae in males and the long ventro-caudal extension of 9th tergite in females. The family is likely closely related to Dilaridae, a Middle Jurassic ithonoid-like taxon, and to a lesser extent to Ithonidae, but the relationship between these remains unclear. This raises a new question: are these four taxa really closely related? To answer this, new fossil species and their detailed, accurate descriptions are needed.

CRediT authorship contribution statement

Vladimir N. Makarkin: Writing – review & editing, Writing – original draft, Investigation.

Declaration of competing interest

The author declares that he has no any competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data was used for the research described in the article.

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