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Re-description of *Grammapsychops lebedevi* Martynova, 1954 (Neuroptera: Psychopsidae) with notes on the Late Cretaceous psychopsoids

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Abstract

Grammapsychops lebedevi Martynova, 1954 from the Late Cretaceous (Cenomanian) of Siberia is re-described based on the holotype. The species is represented by a hind wing as its CuA is definitely concave, although the costal space is strongly dilated. This genus together with three other Cretaceous genera (i.e., *Embaneura* G. Zalessky, 1953, *Kagapsychops* Fujiyama, 1978, and probably *Pulchroptilonia* Martins-Neto, 1997) form the *Grammapsychops* genus-group. The hind wing of *Grammapsychops* may theoretically be associated with forewings of *Kagapsychops* or other closely related genera with similar forewing venation. The Late Cretaceous psychopsoids are critically reviewed. All known psychopsoid taxa from this interval are considered as belonging to Psychopsidae.

Key words: Psychopsidae, Osmylopsychopidae, Cretaceous

Introduction

The psychopsoids (i.e., the superfamily Psychopsoidea) comprise numerous taxa of Neuroptera with broad and multi-veined wings, among which are the largest species in the order. One hundred and forty-four fossil species of 80 psychopsoid genera have been described from the Middle Triassic to late Eocene/early Oligocene (pers. data), but today the superfamily is represented only by the small family Psychopsidae (28 species) distributed in southern Africa, southern Asia and Australia (Oswald 1993b; Wang & Bao 2006; Bakkes *et al*. 2017). The superfamily is now accepted to include Psychopsidae, Osmylopsychopidae, Kalligrammatidae and Aetheogrammatidae (Peng *et al*. 2016). Additionally, there are many fossil genera of uncertain family affinities; some of these may belong to Glottidiidae, whose status is yet unclear. Also, some authors consider the mid-Cretaceous Cretanallachiinae and related genera from Burmese amber as belonging to an unnamed family of Psychopsoidea (see Lu *et al*. 2016; Chang *et al*. 2018) or even to Kalligrammatidae (Liu *et al*. 2018). Actually, the affinity of this group is unclear. In particular, these were also assigned to Dilaridae (Huang *et al*. 2015; Makarkin 2017). At the very least, Cretanallachiinae is distantly related to typical psychopsoids, and not considered here within the superfamily. The Mesozoic Kalligrammatidae and Aetheogrammatidae are specialized families, easily differentiated from each other and the more typical psychopsoids, which belong to Psychopsidae and Osmylopsychopidae and related genera of unclear family affinities.

Psychopsoids were most abundant and diverse in the Late Triassic to the Early Cretaceous, and became rarer in the Late Cretaceous; only six species known from six specimens have been described from this interval. Of these, four species are known from the Cenomanian (i.e., *Litopsychopsis burmitica* Engel et Grimaldi, 2008 and *Electropsychops handlirschi* Lu *et al*., 2017 from of Burmese amber; *Embaneura vachrameevi* G. Zalessky, 1953 from western Kazakhstan; and *Grammapsychops lebedevi* Martynova, 1954 from Siberia), and two are from the Turonian (i.e., *Kagapsychops continentalis* Makarkin, 1994 from Kyzylzhar (Kazakhstan) and *Arctopsychops zherikhini* Makarkin, 1994 from the Arkagala Formation of north-eastern Siberia). In addition, psychopsoids have been reported from the Turonian New Jersey amber (Grimaldi 2000).

In this paper, *Grammapsychops lebedevi* is re-described based on the holotype and other psychopsoids known from the Late Cretaceous are reviewed.

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Material and methods

The holotype of *Grammapsychops lebedevi* was examined. The type locality is situated on the right bank of the Kem' River (left tributary of Enisey [=Yenisey] River), ca. 5 km upstream from the mouth of the Bol'shaya Belaya River [= Belaya River] in Siberia (Pirovskiy Rayon [District of Pirovskoe] of Krasnoyarskiy Kray [Krasnoyarsk Region]). The approximate coordinates of the locality are 57.971372°N 92.230036°E. The specimen is collected from the lower horizons of the Simonovo Formation, which represents alluvial and lacustrine-marsh deposits of a wide coastal lowland (Golovneva & Nosova 2012). The age of the formation is estimated to be Cenomanian based on the flora (Golovneva 2005; Golovneva & Nosova 2012).

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

Abbreviations: CuA, anterior Cubitus; CuP, posterior Cubitus; MA and MP, anterior and posterior branches of media; RA, anterior Radius; RP, posterior Radius; RP1, proximal-most branch of RP; ScP, posterior Subcosta.

Institutional abbreviations: CEATB, Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok; NMNS, National Museum of Nature and Science, Tsukuba, Japan; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia.

Systematic paleontology

Order Neuroptera Linnaeus, 1758

Family Psychopsidae Handlirsch, 1906

Genus *Grammapsychops* Martynova, 1954

Grammapsychops Martynova, 1954: 1167, 1169 [Psychopsididae (sic)]; Carpenter 1992: 351 [Psychopsidae]; Oswald 1993b: 48 [Psychopsidae]; Andersen 2001: 435 [Psychopsidae s.l.: Group IV]; Makarkin & Archibald 2003: 177 [Psychopsidae?]; Jepson *et al*. 2009: 1330 [Osmylopsychopidae]; Peng *et al*. 2011: 218, 221, 225 [Psychopsidae]; Makarkin *et al*. 2012: 59 [Psychopsidae]; Makarkin & Khramov 2015: 411 [Osmylopsychopidae?]; Peng *et al*. 2016: 262 [Osmylopsychopidae?].

Grammopsychops [sic, misspelled]: Martynova 1962: 278 [Psychopidae (sic)]; Martins-Neto 1997: 70, 71 [Psychopsidae]; Martins-Neto & Rodrigues 2010: 6 [Psychopsidae].

Type species. *Grammapsychops lebedevi* Martynova, 1954, by original designation.

Diagnosis. In hind wing, costal space extremely broad, with numerous crossveins arranged mainly in several gradate series; ScP and RA connected distally by relatively long crossvein; R then basal part of RP very stout; posterior trace of RA with three long distal anteriorly-directed branches; RA space very narrow; branches of RP deeply dichotomously branched; RP1–RP6 stout proximally; RP1 shallowly forked; M forked basally, only slightly distad origin of RP1; CuA strongly pectinately branched, with very oblique branches; CuP with three long, very oblique branches; many crossveins in radial to cubital spaces arranged mainly in irregular gradate series.

Species included. Type species only.

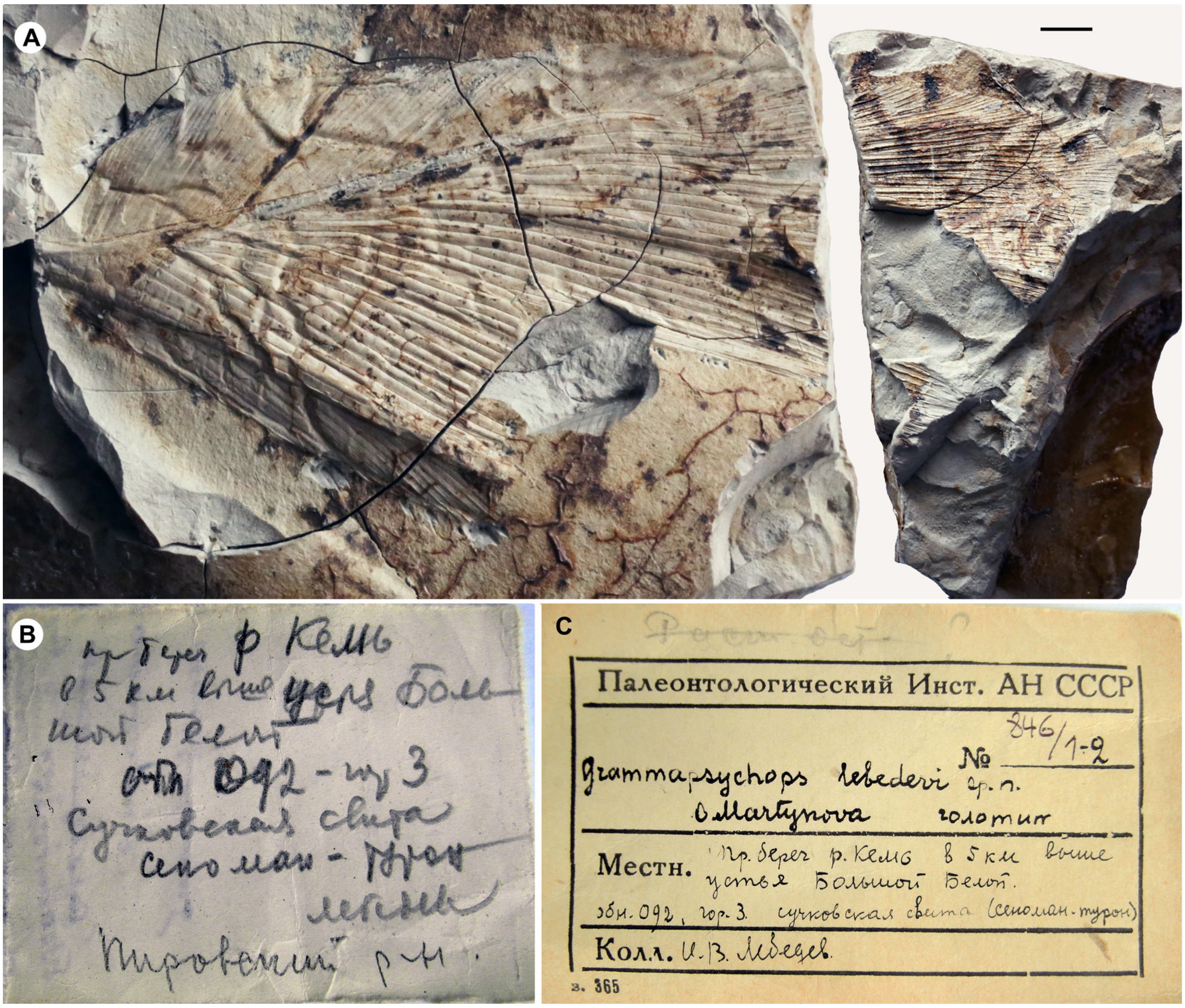
Comments. The venation of the hind wing of *Grammapsychops* is most similar to those of two Cretaceous genera, i.e., *Pulchroptilonia* Martins-Neto, 1997 and *Embaneura* Zalessky, 1953. Zalessky (1953) interpreted the only known wing of *E. vachrameevi* as a forewing, but judging from its venation this is most probably a hind wing. Unfortunately, this cannot be verified due to the current depository of the holotype of *E. vachrameevi* Zalessky, 1953 being unknown. *Grammapsychops* easily differs from these genera by the presence of numerous crossveins in the costal space of the hind wing (no crossveins are present in *Pulchroptilonia* and *Embaneura*).

The hind wing of *Grammapsychops* is also similar to that of *Alloepipsychopsis* Makarkin *et al*., 2012 from the Early Cretaceous (late Barremian) Yixian Formation, but the latter has its RP1 deeply forked.

The hind wing venation of other genera of Psychopsidae (and Osmylopsychopidae) is dissimilar to that of *Grammapsychops*. Unfortunately, however, the hind wings are not known in all fossil genera of these families.

Grammapsychops lebedevi Martynova, 1954
Figs 1–3

Grammapsychops lebedevi Martynova 1954: 1167–1169, Fig. 1; Rohdendorf 1957: 40, 88, Fig. 18 [Psychopidae (sic)]; Carpenter 1992: 351, Fig. 195,1; Engel & Grimaldi 2008: 13 (Tab. 6) [Psychopsidae s. str.]; Peng *et al*. 2011: 120 (Tabl. 1).
Grammopsychops [sic] *lebedevi*: Martynova 1962: Fig. 864; Kolosnitsyna 1964: 149 [Psychopsydidae (sic)]; Zherikhin 1978: 80 [Psychopsidae].



пр берег р Кемь
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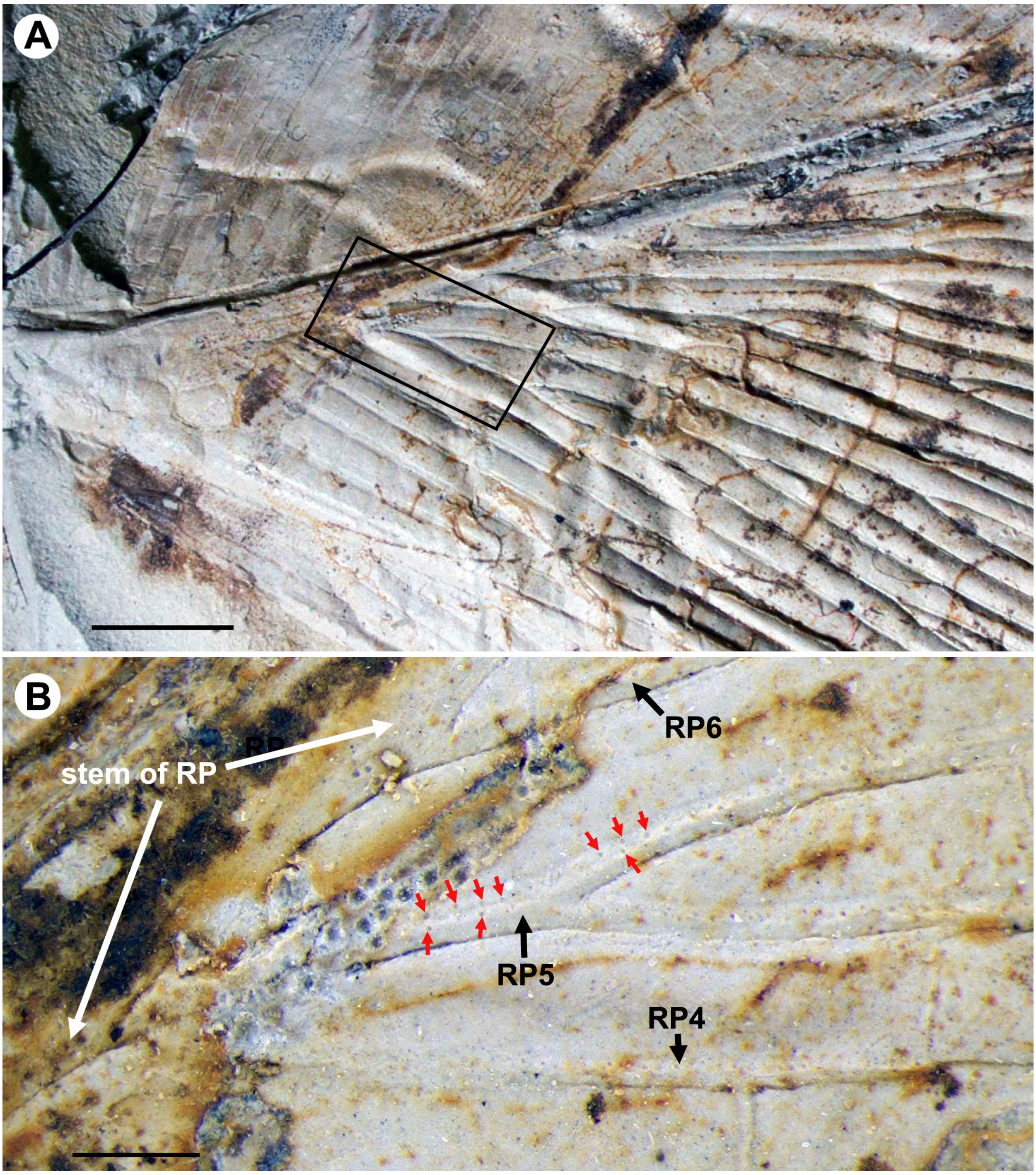
шой Белой
обн 092 - гор 3
Сучковская свита
сеноман - турон
[illegible]
Пировский р-н.

Палеонтологический Инст. АН СССР
№ 846/1-2
Grammapsychops lebedevi gр. n.
O. Martynova голотип
Местн. Пр. берег р. Кемь в 5 км выше
устья Большой Белой.
обн. 092, гор. 3. сучковская свита (сеноман-турон)
Колл. И. В. Лебедев.
з. 365

FIGURES 1. *Grammapsychops lebedevi* Martynova, 1954, holotype PIN 846/1-2. A, specimen as preserved; B, original field label; C, PIN label. Scale bar is 2 mm.

Re-description of the holotype. Hind wing ca. 41 mm long; maximum width (measured perpendicular to RA) 18.5 mm as preserved. Distal nygma absent; basal nygma not detected. Costal space strongly dilated along entire preserved length, slightly narrowed towards apex. Subcostal veinlets closely spaces, nearly all once to twice forked, becoming more oblique towards apex. Costal crossveins numerous, mainly arranged in gradate series orientated obliquely to anterior wing margin. Subcostal space narrow along entire length (its width in Fig. 3 is seen slightly narrower than in the reality as RA is convex and the space is at the angle); crossveins not preserved. ScP apically not fused with RA, entering margin well before wing apex. R broad; RA strongly convex, entering margin just before wing apex, with three long veinlets. RA (between RA and RP) space very narrow, slightly broadened distad; few distal crossveins detected. RP originates close to wing base, with 13 pectinate branches; broad proximally (up to origin of RP6). RP1–RP6 broad proximally; RP1–RP4 probably shallowly branched (their distal parts not preserved); RP5–RP11 deeply dichotomously branched; RP12, RP13 dichotomously branched, but more distally. Proximal branches of RP basally with setal sockets arranged mainly in two rows (Fig. 2B); distal parts of

RP branches appear thin as located in deep depressions, and setal sockets not detected. M forked slightly distad origin of RP1. MA, MP parallel, not branched for preserved proximal half (not preserved distally). Cu divided into CuA and CuP close to base of wing. CuA strongly concave, pectinately branched with nine preserved, very oblique branches (two of these deeply forked), their terminal parts not preserved. CuP with two anteriorly directed, parallel branches; their terminal parts not preserved. Anterior trace of AA1 fragmentarily preserved, close and parallel to posterior trace of CuP. Crossveins in radial to cubital spaces numerous, arranged mainly in many gradate series; distinct outer gradate series not detected; basal crossveins between R/RP and M/MA irregularly spaced. Distinct long convex fold between each vein and veinlet in their distal parts. Trichosors along costal and apical margins indistinct. Wing pattern not preserved, there are only small patches of dark pigmentation.



FIGURES 2. *Grammapsychops lebedevi* Martynova, 1954, holotype PIN 846/1-2. A, proximal part of the forewing; B, a portion of RP and its branches (some setal sockets on veins are shown by red arrows). Scale bars are 2 mm (A), 0.4 mm (B).

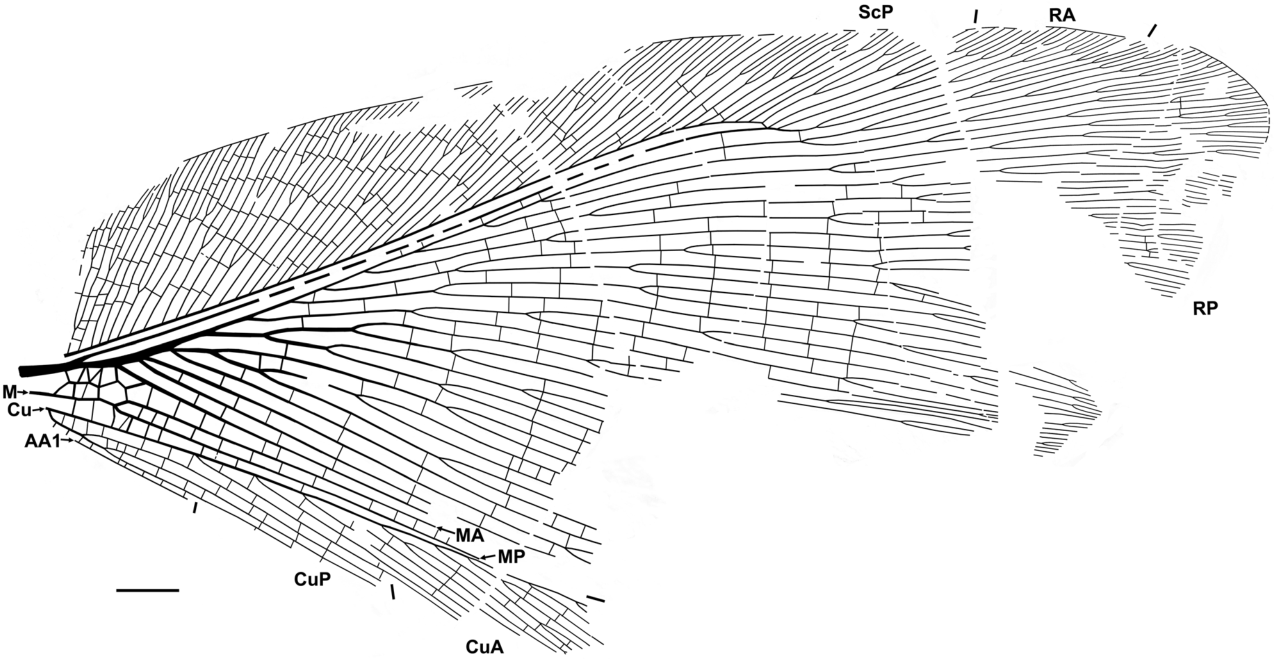
Holotype. Specimen PIN 846/1-2 (part only), collected by Ivan V. Lebedev in 1951. An incomplete hind wing.

Type locality and horizon. Russia: Krasnoyarsk Region: District of Pirovskoe: right bank of the Kem' River (left tributary of Yenisey River), ca. 5 km upstream from the mouth of the Belaya River [57.971372°N 92.230036°E]; exposure 092, horizon 3. Late Cretaceous: Cenomanian (Simonovo Formation).

Remarks. Martynova (1954) interpreted this wing as the left forewing, and she believed that its posterior margin is preserved (actually, it is not preserved, possibly inwardly folded). Based on this assumption, she designated veins accordingly and incorrectly, i.e., her M is actually five proximal branches of RP; Cu (CuA and CuP) is M (MA and MP); A1 is Cu (CuA and CuP); and A2 is AA1. The venation of the holotype shows that this is a hind wing because its CuA is clearly concave. Also, M is forked very proximally and the anterior trace of AA1 is proximally parallel to the posterior trace of CuP, which are more characteristic of the hind wing than of the forewing.

Martynova believed that the margins of the broad basal part of the vein R, then RP, are two parallel thin veins, i.e., R, then RP, and M in her interpretation (see Martynova 1954: Fig. 1). So, she considered 'M' running to the wing base as a separate vein and deeply forked into five branches (my RP1 to RP5). However, it is clearly visible that the basal parts of R and RP are broad and no break of RP between the origins of RP1 and RP6 exists (Fig. 2B).

The costal space of this wing is very broad assuming that it might be a forewing. However, the costal space of the hind wing of *Cretapsychops decipiens* Peng *et al*., 2010 is similarly configured to that of *Grammapsychops lebedevi*: it is very broad, wider than that of the forewing, and proximally more dilated than distally (see Peng *et al*. 2010: Fig. 3). Also, the costal spaces of the hind wing of *Pulchroptilonia espatifata* are configured rather similarly (see Martins-Neto 1997: Figs 8A, B).



FIGURES 3. Forewing venation of *Grammapsychops lebedevi* Martynova, 1954, holotype PIN 846/1-2. Scale bar is 2 mm.

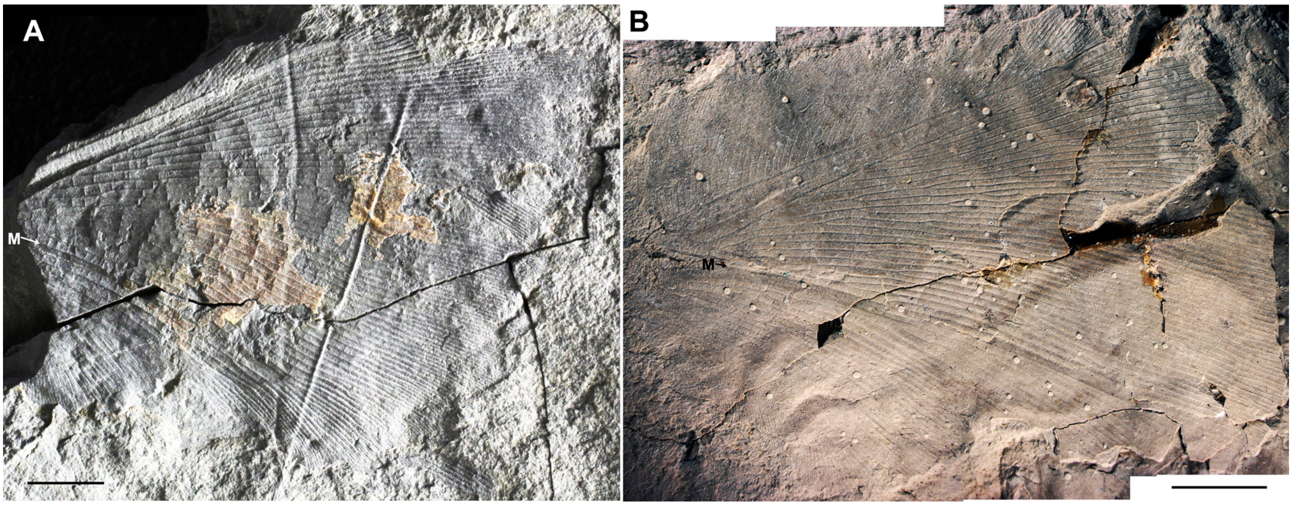
A review of the Late Cretaceous psychopsoids and their family affinities

The *Grammapsychops* genus-group. The genus *Grammapsychops* together with three other Cretaceous genera form a distinct genus-group, the *Grammapsychops* genus-group, in which the following taxa are included: *Kagapsychops* Fujiyama, 1978 with *K. araneus* Fujiyama, 1978 from the Barremian of Kaseki-kabe (Kuwajima Formation, Japan; the age is according to Sano 2015) and *K. continentalis* Makarkin, 1994 from the Turonian of Kyzylzhar, southern Kazakhstan; *Embaneura* with *E. vachrameevi* from the Late Cretaceous (Cenomanian) of Terekty-say, western Kazakhstan, and probably *Pulchroptilonia* with *P. espatifata* Martins-Neto, 1997 from the Early Cretaceous (late Aptian) of the Crato Formation, Brazil. Three of these five species are from the early Late Cretaceous.

The *Grammapsychops* genus-group may be characterized by a set of following character states: forewings range from 40 to 50 mm long, and hind wings from ca. 35 to ca. 48 mm long; in both wings, costal space broad; ScP and RA distally not fused, at most only approach; RA with one to three long distal veinlets; branches of RP deeply dichotomously branched; branches of CuA and CuP very oblique; crossveins form many short gradate series in the radial to cubital spaces (not detected in *P. espatifata*); in the forewing, numerous subcostal crossveins (not detected in *P. espatifata*); RP1 deeply branched (multi-branched) (unclear in *P. espatifata*); in the hind wing, basal parts of proximal branches of RP direct to CuA.

Kagapsychops araneus is represented by an incomplete forewing (Fig. 4A). Its venation was figured in general adequately (Fujiyama, 1978: Fig. 6), except for the subcostal crossveins, which were not depicted by Fujiyama (1978) but are easily distinguishable (see Fig. 4A). The estimated complete forewing is ca. 50 mm long. ScP is likely not fused with RA: either it is connected with it by an oblique crossvein or touching it (not clearly discernible). It is very likely that RP1 is deeply dichotomously branched, but the proximal-most part of RP is not preserved.

Kagapsychops continentalis is also known from an incomplete forewing (Fig. 4B). Its venation was figured by Makarkin (1994: Fig. 1); the estimated complete length is ca. 40 mm long.



FIGURES 4. Forewings of *Kagapsychops* Fujiyama, 1978. A, holotype of *K. araneus* Fujiyama, 1978 (NMNS PM12004); B, holotype of *K. continentalis* Makarkin, 1994 (PIN 2383/496, counterpart). Scale bars are 5 mm.

These two species were treated as possibly belonging to different genera and even families by Makarkin & Khramov (2015). However, it is clear now that these species may belong to the same genus. Differences between them are too weak and therefore not generic, e.g., CuA of *K. araneus* possesses a few terminal branches, whereas it is clearly pectinate with five long branches in *K. continentalis*, and the former species is clearly broader than the latter. The other preserved parts of the venation of both are in general similar.

Pulchroptilonia espatifata was described from two specimens: the holotype, which was adequately figured by Martins-Neto (1997: Fig. 8), and an additional specimen (which is named "paratype" in the caption of Plate 2), which was initially provided only with a photograph (see Martins-Neto 1997: Pl. 2B), and later with an inadequate line drawing (see Martins-Neto & Rodrigues 2010: Fig. 5). The holotype is represented by an incomplete specimen with fore- and hind wings partly preserved (its forewing length is 40 mm according to Martins-Neto (1997), and the estimated length of the hind wing is ca. 35 mm), and the paratype by an incomplete thorax with an incomplete forewing.

Embaneura vachrameevi is represented by a nearly complete, likely hind wing of ca. 48 mm long (estimated). The hind part of the wing (its medial to anal spaces) is probably inadequately figured (see Zalessky 1953: Fig. 1a; refigured in Martynova 1962: Fig. 863).

Theoretically, the hind wings of *Grammapsychops* or *Embaneura* may be associated with the forewings of *Kagapsychops*. At least, the shape, size and venation of *G. lebedevi*, *E. vachrameevi* and *K. continentalis* are similar enough, and they all lived in nearby regions of central Asia.

FIGURES 5. Larvae of Psychopsidae. A, presumed second-instar larva (probably exuvia) from Burmese amber (type A; *Acanthopsychops triainus* Badano et Engel in Badano *et al*., 2018); scale bar is 2 mm (courtesy of Arnold Staniczek, Staatliches Museum für Naturkunde Stuttgart, Germany); B, presumed mature larva from Burmese amber (type B), ca. 10 mm long including mandibles (courtesy of Sieghard Ellenberger, Burmese-amber.com); C, mature larva of the extant Australian *Psychopsis* sp., ca. 10–12 mm long (courtesy of Shaun L. Winterton).

Species of the *Grammapsychops* genus-group are superficially similar to that of Osmylopsychopidae. Indeed, Osmylopsychopidae and Psychopsidae are certainly closely related families. Peng *et al*. (2016) provided the diagnoses of Osmylopsychopidae and Psychopsidae. The authors stated that the wings of Psychopsidae may be distinguished from those of Osmylopsychopidae by a combination of the following character states: in both wings, [1] the costal space is very broad distally; [2] RP1 is not deeply forked; [3] the distal nygma is lost; [4] the distal RA is straight, not curved posteriad (its posterior trace continues the course of proximal RA); in the hind wing, [5] the crossvein 1r-m is short and straight.

The psychopsid affinity of the *Grammapsychops* genus-group is supported by character states [1] and [3], and the osmylopsychopid affinity by [2]; character states [4] and [5] are unclear in this generic group.

Character state [2] appears to be the most distinct feature of Osmylopsychopidae. However, it does not only occur in this family. The hind wing of the psychopsid *Alloepipsychopsis lata* Makarkin *et al*., 2012 possesses such a character state (see Makarkin *et al*., 2012: Figs 1, 2).

Character state [4]. The distal RA is not strongly straight, and it is slightly curved posteriad in the *Grammapsychops* genus-group. However, what is more important is that RA possesses only a few distal (one to three) veinlets. In Osmylopsychopidae, ScP+RA has numerous veinlets.

Character state [5]. The venation in the basal area between R/RP and M is very complicated in the *Grammapsychops* genus-group, and it is impossible to distinguish the crossvein 1r-m among other crossveins. Such a situation is also present in the psychopsid *Alloepipsychopsis lata* (see Makarkin *et al*., 2012: Figs 1, 2). At the very least, the *Grammapsychops* genus-group does not possess the long sinuate crossvein 1r-m as found in the Jurassic *Nematopsychops unicus* Peng *et al*. 2016 (see Peng *et al*. 2016: Figs 15B, 22F), which is characteristic of Osmylopsychopidae.

In all genera of Osmylopsychopidae, ScP and RA are fused and ScP+RA has many veinlets. A single exception is the Jurassic genus *Eupypsychops* Peng *et al*., 2016 in which these veins are separate, but it possesses the distal nygma. In the *Grammapsychops* genus-group, ScP and RA are not fused (when the wing apex is clearly discernible), which is characteristic of most fossil Psychopsidae.

Therefore, the assignment of the *Grammapsychops* genus-group to Psychopsidae is most probable.

Burmese amber psychopsoids. Two psychopsoids species have been described from Burmese amber, i.e., *Litopsychopsis burmitica* and *Electropsychops handlirschi* (Engel & Grimaldi 2008; Lu *et al*. 2017). Their placement in Psychopsidae is doubtless, although *L. burmitica* is known only from the distal portions of one pair of wings. These two genera only slightly differ from the extant and Baltic amber taxa, e.g., some branches of RP in the *E. handlirschi* forewing is deeply forked, its CuP is not strongly pectinate, and its costal space is slightly narrowed towards apex. However, these features are inessential for family assignation. Moreover, the hind wing venation of *E. handlirschi* is typical for Psychopsidae. One other (undescribed) specimen in a private collection, whose photograph I have seen, also belongs to *E. handlirschi*. The preserved venation of *L. burmitica* is typical for Psychopsidae.

The psychopsoid larvae are rather common in Burmese amber. Five larvae of Psychopsidae have been described (Engel & Grimaldi 2008; Badano *et al*. 2018), and I have seen photographs of nine other larvae. All these larvae do not principally differ from those of both the extant and Baltic amber Psychopsidae (see Fig. 5C and Tillyard 1919: Figs 2–9; Pl. 79, Figs 2–5; MacLeod 1964: Figs 66–72; 1971: Figs 12–14; Gepp 1984: Fig. 15; Ross 1998: Fig. 134). They have a similarly constructed large head with long, smoothly curved jaws lacking teeth; long, slender antennae; extended labrum; and papillae on the head capsule. Three main types of these larvae may be distinguished: (1) the first type (type A) is shown in Figure 5A (recently named *Acanthopsychops triainus* Badano et Engel in Badano *et al*., 2018: Fig. S1f, g); its labrum possesses three slender acute processes, of which the middle is longest; (2) the presumable mature larva represents type B (Fig. 5B, 6); its extended labrum possesses a three-lobed margin; this type is especially similar to larvae of extant species (cf. Figs 5B, 6 and 5C); (3) the third type (type C) is similar to the second but differs from it by possessing a one-lobed margin of the labrum, which terminates with a pair of strong setae, four-segmented antennal flagellum with its terminal segment bearing a cluster of three spicule-like setae. This larva has been firstly described by Engel & Grimaldi (2008: Figs 5, 6), and later named as *Aphthartopsychops scutatus* Badano & Engel in Badano *et al*. (2018: Fig. 3b). It is 1.03–2.87 mm long, and therefore a first-instar larva. It might be assumed however that type C is transformed to type B when the larva becomes mature, and it would support in particular the fact that there are several larvae whose labrum are intermediate in shape between types B and C. Unfortunately, setation of the terminal antennal segment is unclear on the photographs that I have seen. However, in the larvae of the extant Australian *Psychopsis elegans* (Guérin-Méneville, 1844), a single species whose larval instars are all known, such a great change of the labrum shape during larval development from the first to the third instar does not occur (cf. Tillyard 1919: Figs 2, 3, 5). All larvae of the extant and Baltic amber species of Psychopsidae, including a first-instar larva, and type B (Fig. 6), possess single spicule-like seta on the terminal antennal segment (often accompanied with one or more much shorter fine setae). Therefore, it is more probable that there are several closely related species with their labrum more or less similar to that of the extant and Baltic amber species of Psychopsidae.

Larval type A is dissimilar to the larvae of the extant species and the Baltic amber Psychopsidae, by the structure of the labrum and the weak-developed papillae, however it is similar to those taxa in possessing many-segmented antennae with a single spicule-like seta on its terminal segment. Theoretically, it may belong to a distantly-related taxon of Psychopsidae rather than to a group similar to these typical psychopsids.

Engel & Grimaldi (2008: Figs 7, 8) also described a first-instar larva of a putative Psychopsidae, ca. 0.6 mm long. Although its morphology is generally similar to that of a first-instar larva of the extant African *Silveira rufus* Tjeder, 1960, it is much shorter: a first-instar larva of *S. rufus* is 3.25 mm long (see Bakkes *et al*. 2017: Figs 109–111). The larva of *S. rufus* was found inside the maternal abdominal chamber (Bakkes *et al*. 2017), and so it is surely newly hatched. The forewing of this species is 15–18 mm long, and therefore the forewing of this putative Psychopsidae from Burmese amber should be much shorter than 15 mm. Therefore, a first-instar larva described in Engel & Grimaldi (2008: Figs 7, 8) does probably not belong to Psychopsidae.

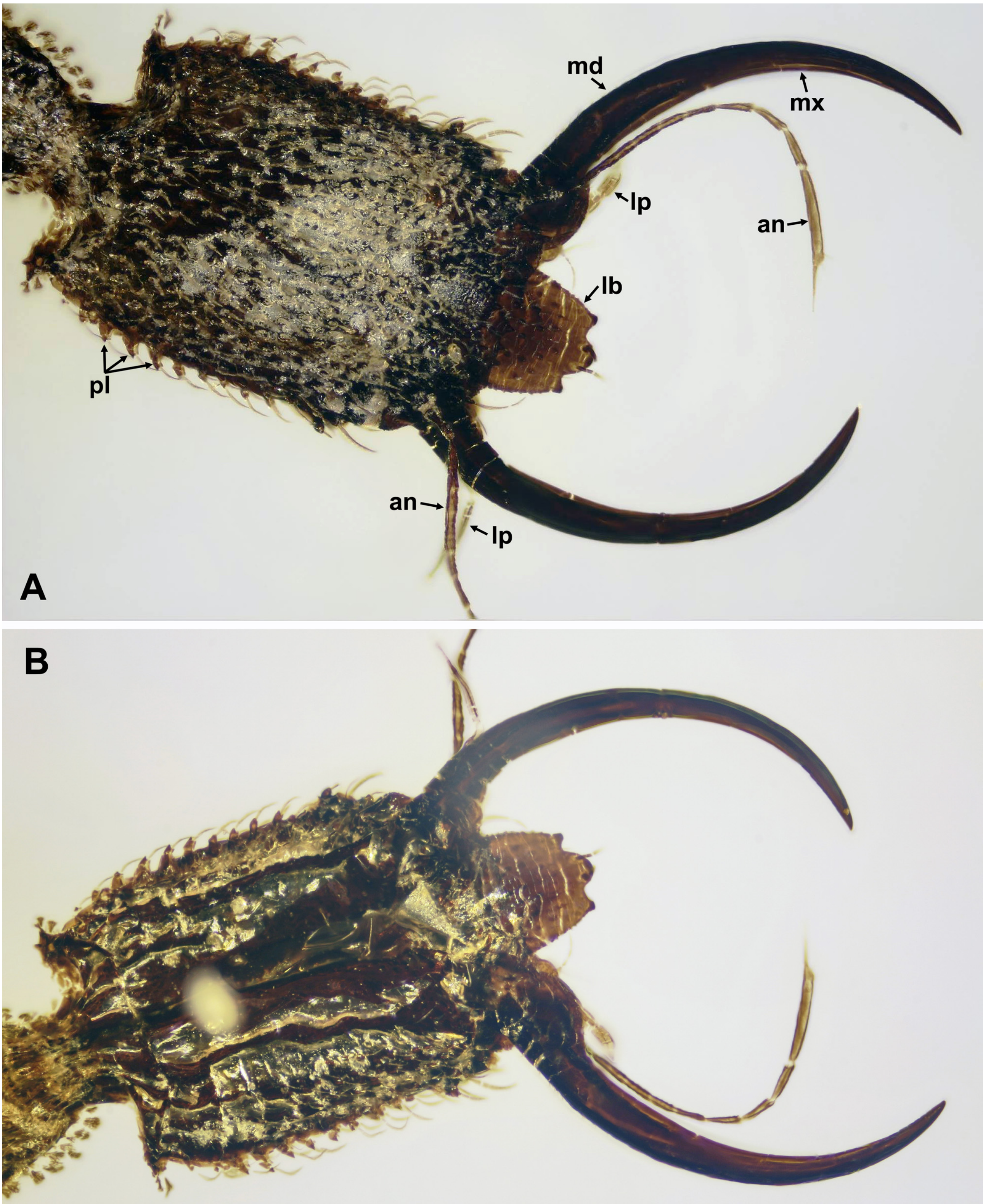
The larvae of extant psychopsids are arboreal, they live under bark and in crevices of trees, but may be found also in the leaf litter surrounding trees (Tillyard 1919; Gallard 1923; Bakkes *et al*. 2017). It is therefore not surprising that psychopsid larvae are rather common in Burmese amber.

Arctopsychops zherikhini. This species is represented by a fragmentary forewing in blackish aleurolite sediment (Fig. 7) from the late Turonian locality at Tal-Yuryakh, Magadan Region of Russia (Arkagala Formation) (see Makarkin & Khramov 2015 for more details on the formation). The venation is figured by Makarkin (1994: Fig. 3). It is characterized by closely spaced subcostal veinlets lacking crossveins between these; the preserved branches of RP are nearly parallel, not deeply forked; RP1 or anterior branches of MA possibly multi-branched, i.e., deeply forked; MA (alternatively, M) strongly concave; MP (alternatively, CuA) with few branches distally; CuA (alternatively, CuP) strongly pectinate; CuP (alternatively, AA1 or basal branches of CuA) few branched, probably with three long branches; AA1 (alternatively, AA2) strongly pectinate. Crossveins are not detected in the subcostal and RA spaces, probably due to poor preservation. Although the wing is preserved incompletely this is the most probable designation of veins. Alternative designation of veins (in brackets) is less probable, however possible.

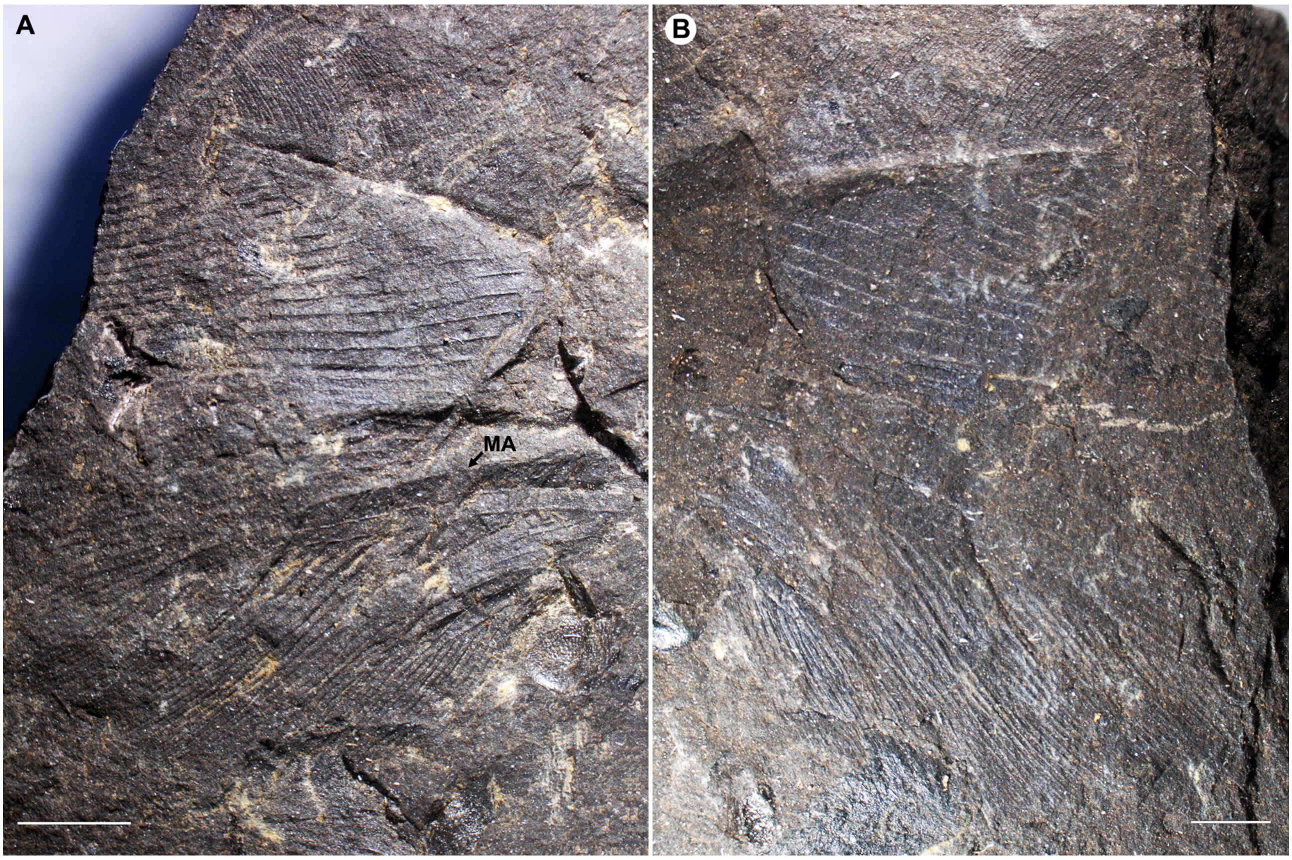
The venation of *A. zherikhini* is dissimilar to that of most other psychopsoids, especially in configuration of CuA. Such a strongly-pectinate CuA rarely occurs in Psychopsidae and Osmylopsychopidae. CuA of the Middle Jurassic Chinese psychopsid species *Gigantopsychops reticulatus* Peng *et al*., 2016 (16 branches) is most similar to that of *A. zherikhini* (14 branches). Also, an unnamed psychopsid species from New Jersey amber has a similar strongly pectinate CuA (see below). The CuP of *G. reticulatus* also has a few branches, like the CuP of *A. zherikhini*. Given this as well as other venational characters (e.g., the closely spaced subcostal veinlets lacking crossveins between these, the non-deeply forked branches of RP, and the possible multi-branched MA), these two species appear to be closely related, and thus the Psychopsidae affinity of *A. zherikhini* is most probable.

If the alternative version of the designation of veins is correct then the venation of *A. zherikhini* is dissimilar to that of any genus of Psychopsidae and Osmylopsychopidae: such a combination of a so few-branched CuA and so strongly-pectinate CuA is still unknown. Anyway, its venation is generally rather similar to that of the *Grammapsychops* genus-group in the shallowly branched M and CuA (as found in *Kagapsychops araneus*). The Psychopsidae affinity of *A. zherikhini* is again most probable.

New Jersey amber psychopsoids. One species of Psychopsidae has been described (but not named) by Grimaldi (2000) based on an adult from the Turonian New Jersey amber (see Grimaldi & Nascimbene 2010 for details of this amber). Also, a first-instar larva (2.5 mm long) was preliminary referred to Psychopsidae (Grimaldi 2000: Figs 3, 22c). This larva is very similar to the larvae of extant psychopsids, but possessing however some characters that are absent in those, e.g., relatively stout antennae whose distal segment terminates with a cluster of spicule-like setae, similar in that to the larval type C from Burmese amber (see above). It is probably that this larva belongs to the stem group of Psychopsidae, e.g., to the unusual 'adult' species, which is represented by proximal portions of fore- and hind wings (Grimaldi 2000: Fig. 4). Its hind wing is much shorter (at least twice) than the forewing, and the venation of both is peculiar. In the forewing, the presumable CuA is strongly pectinate, the presumable CuP is multi-veined, and the anal space occupies a very restricted area. The venation of the hind wing is strongly specialized in many characters. Although this venation is specialized, its placement in Psychopsidae is much more probable than it belonging to Osmylopsychopidae: no venational conditions typical of Osmylopsychopidae are found in this species.



FIGURES 6. Head of larva of Psychopsidae (type B) from Burmese amber (the same specimen as in Fig. 5B). A, dorsal view; B, ventral view (courtesy of Sieghard Ellenberger, Burmese-amber.com). an, antenna; lb, labrum; lp, labial palpus; md, mandible; mx, maxillary blade; pl, papillae.



FIGURES 7. Forewing of *Arctopsychops zherikhini* Makarkin, 1994, holotype PIN 1832/135. A, counterpart; B, part. Scale bars = 2 mm.

Conclusions

It can be preliminary concluded that all known psychopsoids from the Late Cretaceous belong to Psychopsidae. However, some of these strongly differ from the extant and Baltic amber taxa, i.e., from typical members of the family, although Burmese amber taxa may belong to the stem lineage leading to extant Psychopsidae. There is no clear evidence of the record of Osmylopsychopidae from this interval: no species are found with wings having the distal nygma, ScP and RA clearly fused, and ScP+RA with numerous veinlets.

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