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A review of the Late Jurassic *Promantispa* Panfilov (Neuroptera: Mantispidae), with description of a new species

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Abstract

The Late Jurassic genus *Promantispa* Panfilov, 1980 (Neuroptera: Mantispidae) is reviewed. *Promantispa similis* Panfilov, 1980 from the Aulie / Mikhailovka locality (Kazakhstan) is re-described based on the holotype and an additional specimen. *Promantispa rasnitsyni* **sp. nov.** is described from that locality based on a nearly complete forewing. The new species differs from *P. similis* in having a short distal crossvein in the subcostal space, a shallow terminal fork of A3, and a differently positioned 2r-m crossvein (its position between the basal branch of RP and MA has never been previously recorded in the family). The taxonomic affinities of *Promantispa* and *Liassochrysa* Ansorge & Schlüter, 1990 from the Early Jurassic of Germany are discussed. We argue that these two genera cannot be assigned to Drepanicinae as previously suggested, but that it is reasonable to provisionally consider them as subfamily *incertae sedis*.

Keywords: Drepanicinae, Doratomantispinae, Chrysopoidea, Karatau, Mesozoic insects, fossil, lacewings, Kazakhstan, Karabastau

Introduction

Mantispidae comprise nearly 400 extant species that are widely distributed (Oswald & Machado, 2018). During the 20th century, the family was known from only a few fossils (*e.g.*, Cockerell, 1921; Jarzembowski, 1980; Panfilov, 1980; Nel, 1989; Ansorge & Schlüter, 1990; Makarkin, 1990, 1997a). However, over the past two decades, many additional fossil species have been described, bringing their total current number to approximately 60 (Poinar, 2006; Engel & Grimaldi, 2007; Makarkin, 2019; Pérez-de la Fuente & Peñalver, 2019; Shi *et al*., 2019, 2020; Lu *et al*., 2020; Baranov *et al*., 2022; Jouault *et al*., 2022; Li *et al*., 2022, 2023; So & Won, 2022; Hart *et al*., 2024; Makarkin *et al*., 2025a, b; Makarkin & Perkovsky, 2026; Xiang *et al*., 2026).

In spite of this, the Jurassic mantispids remain poorly known. Two monotypic genera are currently assigned to the extant subfamily Drepanicinae: the Early Jurassic *Liassochrysa* Ansorge & Schlüter, 1990 and the Late Jurassic *Promantispa* Panfilov, 1980 (Liu *et al*., 2015). Five other Jurassic species are assigned to the extinct subfamily Mesomantispinae (Khramov, 2013; Jepson, 2015; Jepson *et al*., 2018a, b).

Extant Drepanicinae comprise five genera and 40 species from South America, Australia and southern Asia (Lambkin, 1986; Ohl, 2004; Liu *et al*., 2015; Li *et al*., 2020). Numerous fossil species have also been assigned to this subfamily (*e.g.*, Liu *et al*., 2015; Pérez-de la Fuente & Peñalver, 2019; Lu *et al*., 2020; So & Won, 2022). However, currently only two fossil species are confidently regarded as belonging to Drepanicinae: the Late Cretaceous *Gerstaeckerella asiatica* Makarkin, 1990 from Kzyl-Zhar (Kazakhstan), and the earliest Eocene *Danomantispa frandseni* Makarkin *et al*., 2025 from the Fur Formation of Denmark.

Here, we re-describe the type species of *Promantispa* based on the holotype and one other specimen, describe a new species of this genus, and discuss the subfamily affinities of *Promantispa* and the closely related *Liassochrysa* Ansorge & Schlüter, 1990.

Material and methods

The examined specimens of *Promantispa* were collected in the 1960s in the Upper Jurassic lacustrine deposits

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of the Karabastau Formation, exposed at the Aulie / Mikhailovka locality, 3 km southwest of Aktas village (Turkistan Region, Kazakhstan). The age of the deposit has been established as Oxfordian-Kimmeridgian based on palynology (Doludenko *et al*., 1990). The fossil-bearing layer consists predominantly of highly laminated claystone deposited in a freshwater lake (Dzik *et al*., 2010). The flora of the Karabastau Formation is dominated by Bennettitales and the conifers *Brachyphyllum* and *Pagiophyllum*, whose small, scale-like leaves are indicative of arid conditions. As Doludenko and Orlovskaya (1976) pointed out, "when judged by the composition and structure of the plants, the Karatau climate of this time [the Late Jurassic] was dry and hot". More than 18,000 fossil insects, including approximately 550 Neuroptera, have been collected from Aulie and adjacent localities (Jepson *et al*., 2018a).

Photographs of the specimens were taken using a Nikon SMZ25 stereomicroscope equipped with a Nikon DS-Ri2 camera. Line drawings were prepared from the photographs using Adobe Photoshop CS3.

Venational terminology follows Breitkreuz *et al*. (2017). Crossveins are designated by the longitudinal veins to which they connect and are numbered in sequence from the wing base, *e.g.*, 2r-m, crossvein in second gradate series between R/RP and M/MA; 2icu, crossvein in second gradate series between CuA and CuP. Contrary character states of compared taxa are provided in brackets.

Venational abbreviations: A1–A3, first to third anal veins; CuA, anterior cubitus; CuP, posterior cubitus; MA, anterior media; MP, posterior media; RA, anterior radius; RP, posterior radius; RP1, proximal-most branch of RP; Sc, subcosta.

The type material is deposited at A.A. Borissiak Paleontological Institute of the Russian Academy of Sciences (Moscow, Russia), abbreviated as PIN.

This work and all nomenclatural acts contained therein are registered in ZooBank: urn:lsid:zoobank.org:pub:87EC4FB9-377F-4381-A84D-37076A264207.

Systematic palaeontology

Order Neuroptera Linnaeus, 1758
Family Mantispidae Leach, 1815
Subfamily *incertae sedis*

Genus *Promantispa* Panfilov, 1980

Type species. *Promantispa similis* Panfilov, 1980, by original designation.

Species included. *Promantispa similis* and *P. rasnitsyni* **sp. nov.** from the Late Jurassic of Kazakhstan.

Diagnosis. Forewing: crossvein 1r-m present [absent in all other genera, except some Doratomantispinae]; A3 forked [simple in all other genera, except one species of Doratomantispinae]; MA forked once distally [forked more than once in all Doratomantispinae].

Promantispa similis Panfilov, 1980
(Figs 1–3)

Material. Holotype PIN 2784/1080 (part, counterpart); a nearly complete forewing. Specimen PIN 2384/899 (part); a poorly preserved incomplete specimen. Both are deposited in PIN.

Diagnosis. May be easily distinguished from another species of the genus, described below, by a combination of the following forewing character states: crossvein 2r-m connects MA with stem of RP [with RP1 in *P. rasnitsyni*]; distal crossvein in subcostal space connecting pterostigma and RA long [short in *P. rasnitsyni*]; 'inner' (third) gradate series with two crossveins in radiomedial space [three in *P. rasnitsyni*]; terminal fork of A3 deep [relatively shallow in *P. rasnitsyni*].

Locality and horizon. Kazakhstan: Turkistan Region: Baydibek District; southern part of Karatau Range, Aulie / Mikhailovka locality. Late Jurassic (Oxfordian-Kimmeridgian; Karabastau Formation).

Description. *Holotype*. Forewing 10.5 mm long as preserved (estimated complete length 11 mm), 4.3 mm wide (length/width ratio 2.56). Costal space rather broad, most dilated proximad origin of RP; strongly dilated in pterostigmal area. Subcostal veinlets simple, widely spaced. Subcostal space relatively broad, slightly dilated before pterostigma; basal crossvein poorly preserved; intermediate crossvein not detected; one distal crossvein long, located slightly proximad middle of pterostigma. Pterostigma elongate oval, dark, with several poorly discernible incorporated veinlets of Sc. Posterior trace of RA forked distally, terminates at margin slightly before wing apex, with two forked veinlets. RA space relatively broad, with three crossveins: two proximad pterostigma, one distad. RP originates rather far from wing base (at 0.21 complete length), zigzagged, with four branches; posterior trace of RA and all its branches (except one) forked once. Four crossveins between RP and M: 1r-m very short, connecting R, M; 2r-m connects RP proximad RP1, and M distad its fork; two other crossveins between RP1, MA belong to third, fourth gradate series. M appears fused with R basally, forked far proximad origin of RP1 (proximad 2r-m). MA, MP similarly configured, forked once distally. Two crossveins between MA, MP belonging to third, fourth gradate series. Three crossveins between M/MP and Cu/CuA: 1m-cu slightly oblique, connecting M, Cu; 2m-cu, 4m-cu belonging to second, fourth gradate series, respectively. Cu dividing into CuA, CuP far from wing base (very far distad 1m-cu). CuA, CuP similarly configured, deeply forked. One crossvein between CuA,

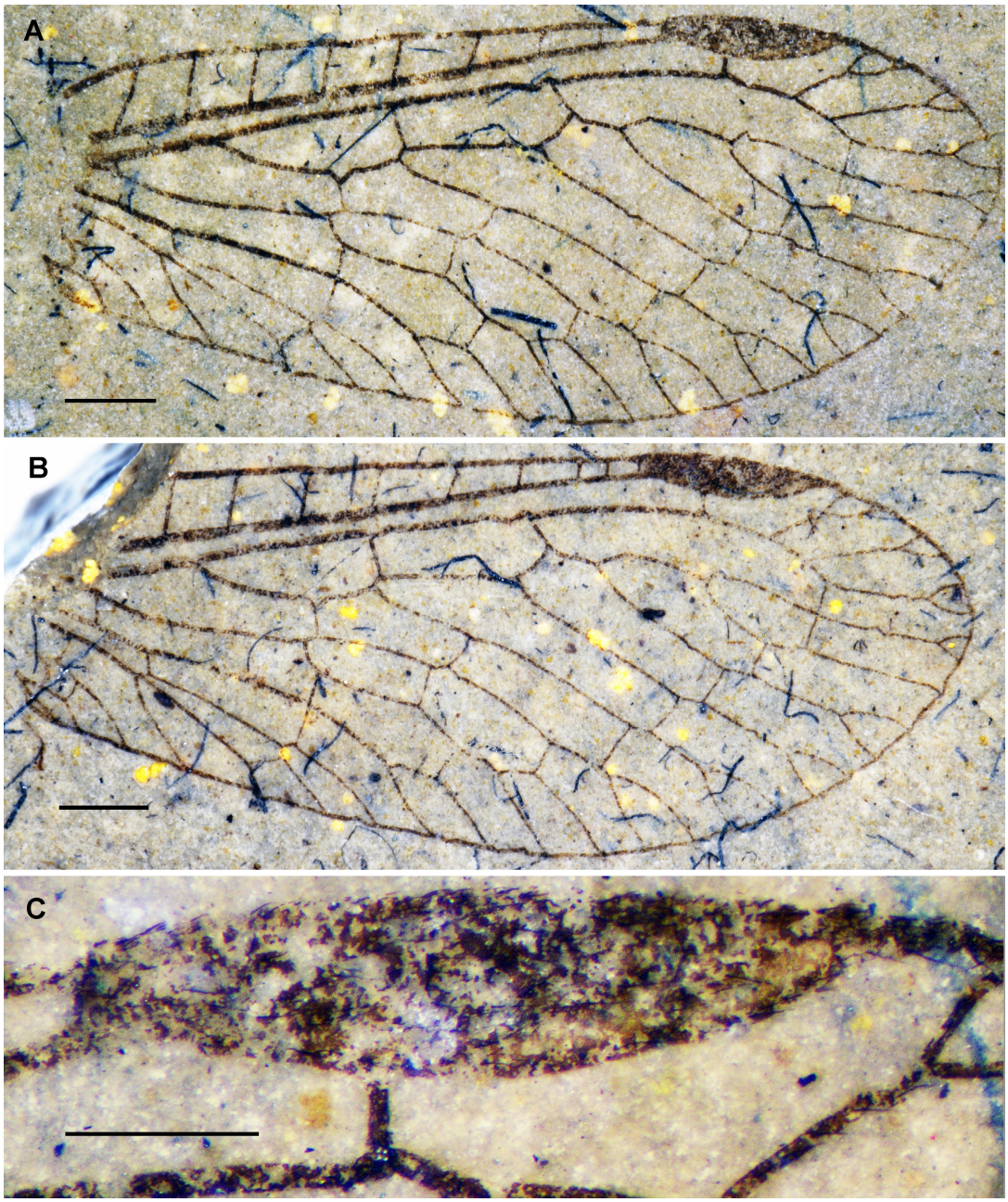


FIGURE 1. *Promantispa similis* Panfilov, 1980, holotype PIN 2784/1080. **A**, Part. **B**, Counterpart (mirrored). **C**, Pterostigma. Scale bars = 1 mm (**A**, **B**), 0.5 mm (**C**).

CuP belonging to second gradate series. Two crossveins between Cu and A1: 1cu-a1 connecting CuP with A1 nearly at the point of bifurcation of the latter; 3cu-a1 connecting terminal fork of CuP with anterior branch of A1. A1 deeply forked slightly proximad 1cu-1a; both branches simple. One long crossvein between A1, A2. A2 simple. One crossvein between A2 and A3. A3 deeply forked (alternatively: both A3 and A4 simple, fused basally). Four gradate series of crossveins: six crossveins in first series (1sc-r, 1r-m, 1m-cu, 1cu-a1, 1a1-a2, 1a2-a3); four crossveins in second series (2ra-rp, 2r-m, 2m-cu, 2icu); third series incomplete with four crossveins (3ra-rp, 3r-m, 3icu, 3cu-a1); four series complete, with eight crossveins between RA and CuA. Jugal lobe well developed, folded.

Specimen PIN 2384/899. Body poorly preserved. Prothorax very short, *ca*. 0.8 mm; forelegs missing. Meso- and metathorax, mid- and hind legs partly preserved, details indiscernible. Abdomen rather stout in dorsal view, *ca*. 5 mm long; details indiscernible.

Forewing *ca*. 5.7 mm long as preserved (estimated complete length *ca*. 7.5 mm), 3.1 mm wide. Preserved venation similar to that of holotype, differing as following: 3im slightly distad than 3r-m; 2icu slightly proximad than

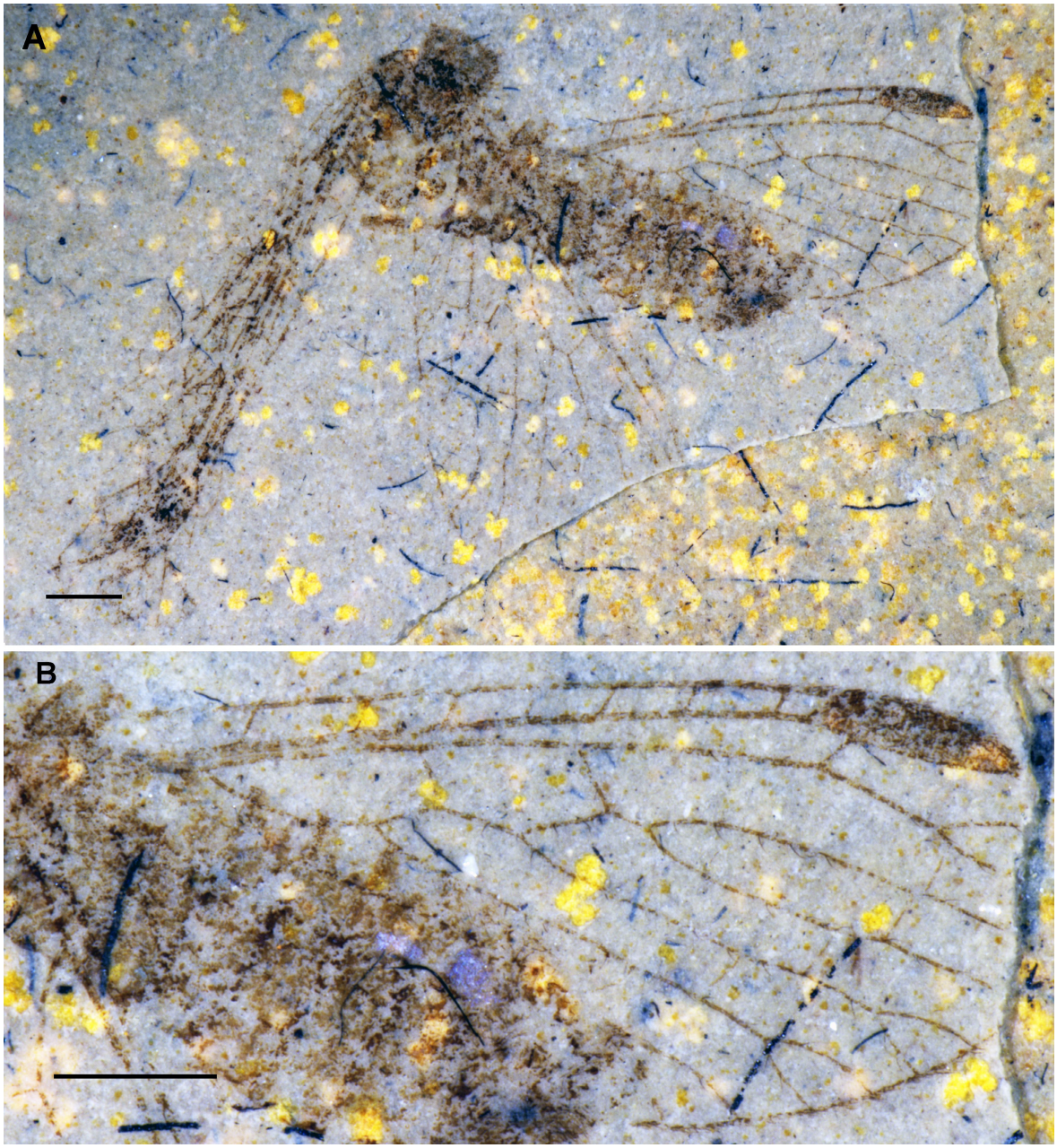


FIGURE 2. *Promantispa similis* Panfilov, 1980, specimen PIN 2384/899. **A**, Specimen as preserved. **B**, Hind wing. Scale bars = 1 mm.

2m-cu; 4im, 4m-cu not detected; 3cu-a1 absent; CuP very shallowly forked.

Hind wing 5.5 mm long as preserved (estimated complete length *ca*. 6.5 mm), *ca*. 2.6 mm wide. Costal space rather broad, slightly dilated proximad, strongly dilated in pterostigmal area. Subcostal veinlets widely spaced. Pterostigma similar in shape to that of holotype forewing; incorporated veinlets of Sc indiscernible. Subcostal space narrow basally, strongly dilated towards wing apex; distal crossvein long, oblique, located in proximal part of pterostigma. Distal part of RA incomplete, with one veinlet partially preserved. RA space relatively broad, with three crossveins (two proximad pterostigma, one distad), arranged similarly as in forewing. RP zigzagged, with three branches; RP1, RP2 forked distally; RP3 possibly simple (its apex not preserved). One (outer) gradate series of crossveins in radial space, with five preserved crossveins from RA to MA. MA partly preserved, forked once distally.

Remarks. The holotype and PIN 2384/899 differ in size, but this may reflect intraspecific variation, especially given that conspecific adults of extant Mantispidae may exhibit up to twofold differences in body size depending on the amount of food available during the larval stage (Redborg & MacLeod, 1985).

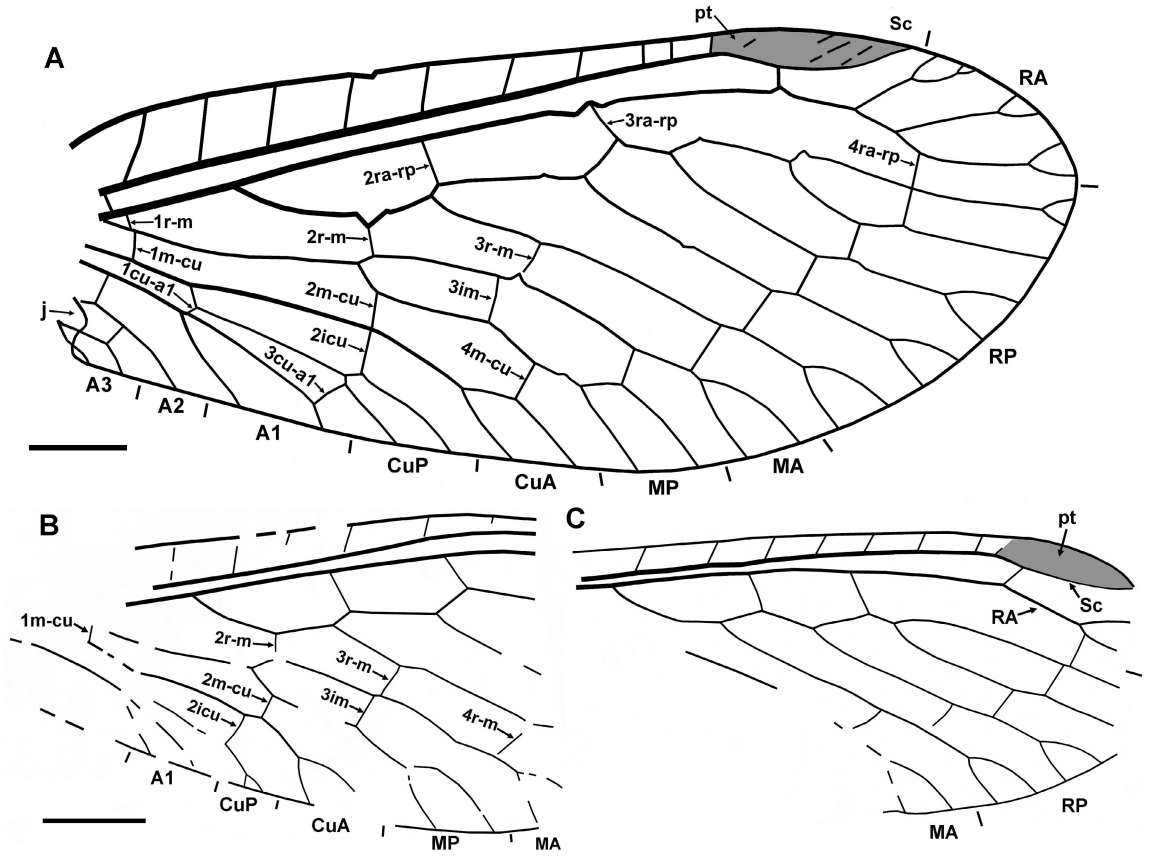


FIGURE 3. Wing venation of *Promantispa similis* Panfilov, 1980. **A**, Forewing of holotype PIN 2784/1080. **B**, Forewing of specimen PIN 2384/899. **C**, Hind wing of specimen PIN 2384/899. Scale bars = 1 mm (**B**, **C** to the same scale).

***Promantispa rasnitsyni* sp. nov.**

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(Fig. 4)

Material. Holotype PIN 2784/1115 (part), a nearly complete forewing, deposited in PIN.

Etymology. The species is named in honour of Prof. Alexandr P. Rasnitsyn, a leading Russian expert on fossil insects, on the occasion of his 90th birthday.

Diagnosis. May be easily distinguished from *P. similis* (its character conditions shown in brackets) by the following forewing character states: crossvein 2r-m connects MA with RP1 [connects with stem of RP]; distal crossvein in subcostal space connecting pterostigma and RA short [long]; 'inner' (third) gradate series with three crossveins in radial and medial spaces [two crossveins]; terminal fork of A3 relatively shallow [distinctly deep].

Locality and horizon. Kazakhstan: Turkistan Region: Baydibek District; southern part of Karatau Range, Aulie / Mikhailovka locality. Late Jurassic (Oxfordian-Kimmeridgian; Karabastau Formation).

Description. Forewing 8.9 mm long as preserved (estimated complete length 9.1 mm), 3.8 mm wide (length/width ratio 2.39). Costal space rather broad, most dilated distad origin of RP and in pterostigmal area. Subcostal veinlets simple, widely spaced. Subcostal space relatively broad, slightly dilated before pterostigma; basal crossvein indiscernible; intermediate crossvein located distad origin of RP; one distal crossvein rather short, located in proximal part of pterostigma. Pterostigma elongate oval, rather dark, with several long closely spaced incorporated veinlets of Sc. Posterior trace of RA terminates at wing margin slightly before apex, forked distally with two forked veinlets (posterior branch of each forking shallowly forked). RA space broad, with three crossveins: two proximad pterostigma, one distad (3ra-rp oblique). RP originates rather far from wing base (at 0.22 complete length), with three branches before outer gradate series; anterior trace of RA rather deeply forked with both branches shallowly forked; all branches forked once. Four crossveins between RP and M: 1r-m very short, connecting R, M; 2r-m connects RP1, M distad its fork; two other crossveins belong to third, fourth gradate series. M appears fused with R basally, forked at level of origin of RP1. MA, MP similarly configured, once forked distally; anterior branch of MA shallowly forked. Two crossveins between MA and MP, belonging to third, fourth gradate series. Three crossveins between M/MP and Cu/CuA: 1m-cu oblique, connecting M, Cu; 2m-cu, 4m-cu

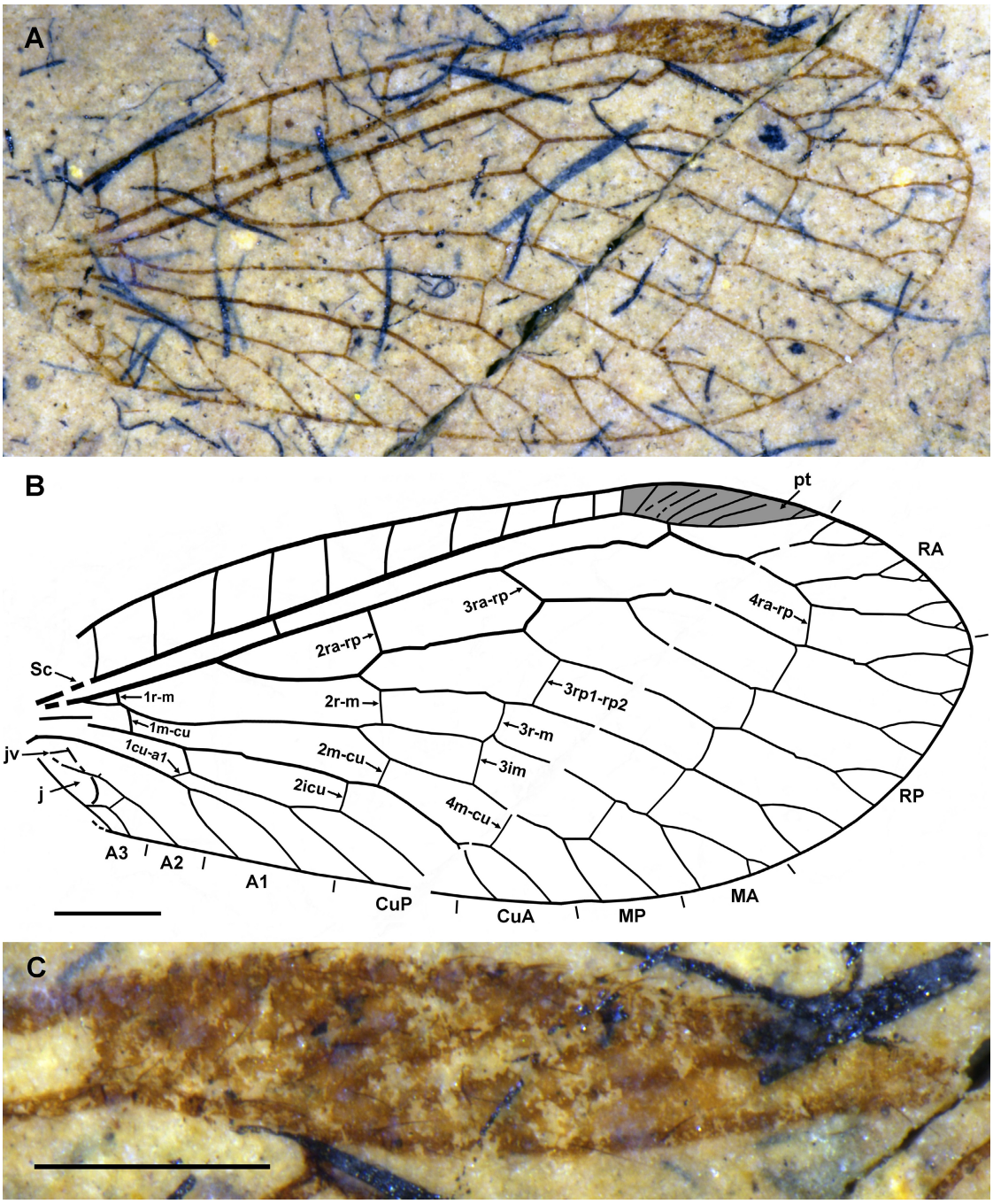


FIGURE 4. *Promantispa rasnitsyni* **sp. nov.**, holotype PIN 2784/1115. **A**, Specimen as preserved. **B**, Forewing venation. **C**, Pterostigma. Scale bars = 1 mm (**A**, **B** to the same scale), 0.5 mm (**C**).

belonging to second, fourth gradate series. Cu dividing into CuA, CuP far from wing base (very far distad 1m-cu). CuA, CuP similarly configured, deeply forked (fork of CuP markedly deeper than that of CuA). One crossvein belonging to second gradate series between CuA, CuP. One oblique, relatively long crossvein between Cu, A1 connecting CuP, A1 proximad its fork. A1 deeply forked, distad 1cu-a1; both branches simple. Probably one long crossvein (fragmentarily preserved) between A1, A2. A2 simple. One crossvein between A2, A3. A3 forked (alternatively: A3, A4 simple fused basally). Four gradate series of crossveins: five crossveins in first series (1r-m, 1m-cu, 1cu-a1, 1a1-a2, 1a2-a3); four crossveins in second series (2ra-rp, 2r-m, 2m-cu, 2icu); third series incomplete with four crossveins (3ra-rp, 3rp1-rp1, 3r-m, 3im); fourth series complete, with seven crossveins from RA to CuA. Jugal lobe well developed, folded; jugal vein incompletely preserved.

Remarks. This specimen was erroneously treated as the holotype of *Promantispa similis* by Jepson & Ohl (2019: fig. 3C).

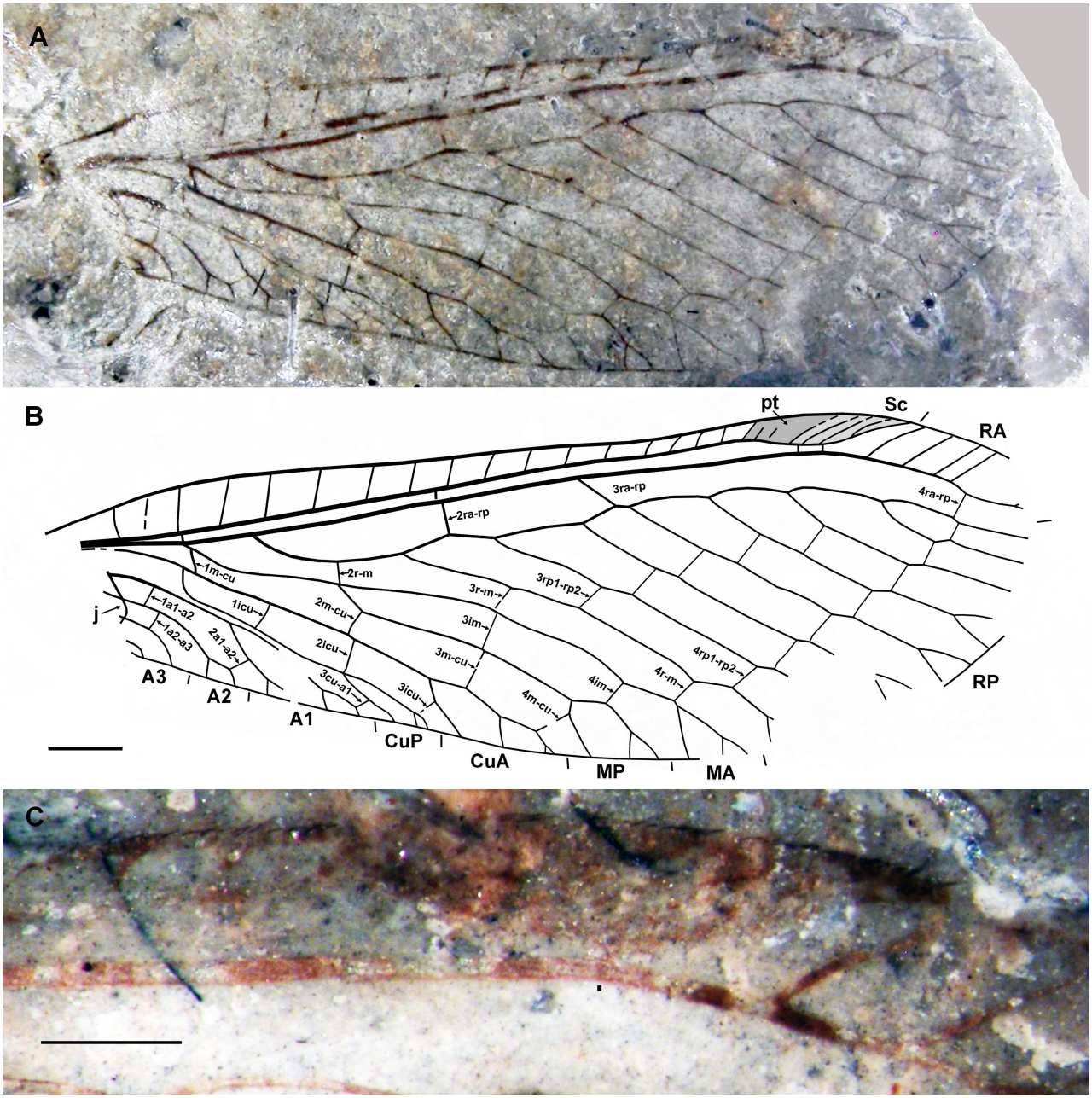


FIGURE 5. *Liassochrysa stigmatica* Ansorge & Schlüter, 1990, holotype MB.I 5046. **A**, Specimen as preserved. **B**, Forewing venation. **C**, Pterostigma (all converted to standard right view). Scale bars = 1 mm (**A**, **B** to the same scale), 0.5 mm (**C**).

Discussion

The genus *Promantispa* was described by Panfilov (1980) as the sole member of the new family Promantispidae, which was later synonymized with Mantispidae by Lambkin (1986). The subfamily placement of the genus remained uncertain (see, *e.g.*, the discussion in Wedmann & Makarkin, 2007) until Liu *et al*. (2015) assigned it, together with another Jurassic genus, *Liassochrysa* Ansorge & Schlüter, 1990, to Drepanicinae in their phylogenetic analysis. However, Liu *et al*. (2015) did not provide any character states of *Promantispa* and *Liassochrysa* that could be regarded as drepanicine synapomorphies. Moreover, the assignment of these two genera to Mantispidae has recently been considered "dubious" (Li *et al*., 2025: p. 397).

Liassochrysa, represented by an isolated forewing from the Early Jurassic of Dobbertin (Germany) (Fig. 5), is the oldest known genus of the family. The genus was originally described as a representative of Chrysopidae (Mesochrysopinae) and considered in this status for some time (Adams & Penny, 1992; Willmann, 1993; Martins-Neto, 1994; Nel & Henrotay, 1994), before being transferred to Mesochrysopidae by Makarkin (1997b). Later, Nel *et*

al. (2005) established a separate family Liassochrysidae (Chrysopoidea) for this genus, and this placement was accepted by some subsequent authors (*e.g*., Pérez-de la Fuente *et al*., 2012; Buscalioni & Poyato-Ariza, 2016). Wedmann & Makarkin (2007) re-examined the holotype and assigned the genus to Mantispidae, whereas Liu *et al*. (2015) then assigned it to the subfamily Drepanicinae.

But are *Liassochrysa* and *Promantispa* really members of Drepanicinae? Their forewing venation is indeed very similar to that of the subfamily, especially in the structure of the pterostigmal area (*cf*. Figs 3, 4 and Lambkin, 1986: fig. 34; Liu *et al*., 2015: fig. 2). However, a similar pterostigmal area has recently been discovered in some genera of Doratomantispinae, including *Acanthomantispa* Lu *et al*., 2020, *Dicranomantispa* Lu *et al*., 2020, *Psilomantispa* Lu *et al*., 2020, and *Pectispina* Shi *et al*., 2020. Most of these genera were originally assigned to Drepanicinae (Lu *et al*., 2020), but were later interpreted as representing a derived lineage within Doratomantispinae (Li *et al*., 2025).

Doratomantispinae are known exclusively from mid-Cretaceous amber of northern Myanmar and include 22 species in seven genera (Poinar & Buckley, 2011; Shi *et al*., 2019, 2020; Lu *et al*., 2020; Li *et al*., 2022; Xiang *et al*., 2026). Their foreleg femur bears a set of enlarged spines that differs markedly from those of other mantispids. In addition, four monotypic genera from the same amber deposit are currently regarded as subfamily *incertae sedis* (see Xiang *et al*., 2026), although the arrangement of spines on their forelegs is similar to that of Doratomantispinae.

The forewing venation of Doratomantispinae is denser than that of *Promantispa* and *Liassochrysa*. However, it possesses at least two character states that are present in these genera (in both or in one of them) but absent in other Mantispidae: the basal crossvein 1r-m and the forked A3.

The basal crossvein 1r-m, as found in *Promantispa*, has so far been detected only in Doratomantispinae, including most Kachin drepanicine-like genera (Lu *et al*., 2020: figs S7C, D; S9G, M; S10E, F; S11D; Xiang *et al*., 2026: figs 8B, 10A). This crossvein is absent in other Mantispidae (and generally in Mantispoidea), including fossil taxa. More broadly, it is absent in most Neuroptera. For example, 1r-m occurs in a few Berothidae (see, *e.g*., Makarkin & Ohl, 2015: fig. 1) and has been detected in only one genus of Hemerobiidae, the Eocene *Archibaldia* Makarkin, 2023. In some Hemerobiinae, however, 2r-m is shifted proximally, connecting R and M and thus resembling 1r-m, as in *Hemerobius* Linnaeus, 1758; while it is located more distally in *Wesmaelius* Krüger, 1922, connecting RP1 and M/MA (VM, pers. observ.).

A deeply forked A3 has been detected in one species of Doratomantispinae, *Paradoxomantispa hongi* (Shi, Yang & Ren, 2019) (Shi *et al*., 2019: fig. 3). A similar condition is present in *Liassochrysa* (Fig. 5). In *Promantispa*, however, the fork of A3 is less deep (Figs 3, 4).

Therefore, *Liassochrysa* and *Promantispa* could in principle belong to Doratomantispinae as their basal-most members. Only the discovery of their forelegs may clarify the situation. At least, two characters found in *Promantispa* (the basal crossvein 1r-m and the forked A3 in the forewing) preclude assigning it to Drepanicinae. Thus, until more information is available, it is reasonable to consider these genera as subfamily *incertae sedis*.

As to *Liassochrysa*, its forewing venation is generally similar to that of *Protoaristenymphes bascharagensis* Nel & Henrotay, 1994 (Chrysopoidea: Mesochrysopidae) from the same horizon of Early Jurassic (early Toarcian of Bascharage (Luxembourg) and Dobbertin (Germany), respectively). They share many character states, including the absence of trichosors, the unbranched humeral veinlet, simple subcostal veinlets, two gradate series in the radial space, similar configuration of RP branches, M, Cu and the anal veins, and similar arrangement of basal crossveins (see Nel & Henrotay, 1994: fig. 1). The wing apex is missing in the holotype of *P. bascharagensis*, but it is present in another species of the genus from the Middle/Late Jurassic of Daohugou (China), *i.e*., *P. daohugouensis* Yang *et al*., 2012 (see Yang *et al*., 2012: figs 1–4).

In some recent phylogenies of the order, Chrysopidae and Mantispoidea have been recovered as sister groups (*e.g*., Vasilikopoulos *et al*., 2020; Cai *et al*., 2023; Lai *et al*., 2025). Therefore, the similarity in wing venation between the earliest Mesochrysopidae and Mantispidae, such as *Protoaristenymphes* and *Liassochrysa*, may not be convergent, but may instead indicate a close relationship between these lineages. However, at present we do not have enough fossil evidence to support this conclusion.

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