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A remarkable new genus of Symphrasinae (Neuroptera: Mantispidae) from mid-Cretaceous amber of Myanmar, and the problem of the phylogenetic affinities of Rhachiberothidae

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ABSTRACT

Rhachisymphrasis raehlei gen. et sp. nov. (Neuroptera: Mantispidae: Symphrasinae) is described from mid-Cretaceous Kachin amber. The genus is remarkable for possessing many character states which do not occur in other Symphrasinae: the profemur is slender; the protibia is very short; the lanceolate process of the probasitarsus arises from its tip and is relatively thin; the mesotibia is strongly expanded; and the forewing CuP is shallowly forked. The protarsus of *Rhachisymphrasis* gen. nov. is rather similar to that of Rhachiberothidae. However, it is unclear whether Rhachiberothidae is phylogenetically closer to Mantispidae or Berothidae. The most plausible hypothesis is that Rhachiberothidae constitute an ancient branch of Mantispoidea leading to Mantispidae (including Symphrasinae), but retaining many character states of Berothidae. The symphrasine affinity of *Sinomesomantispa* Jepson et al., 2013 from the Lower Cretaceous of China is confirmed.

1. Introduction

The Mantispidae constitute a relatively small family comprising nearly 400 extant and about 50 extinct species in six subfamilies: Mesomantispinae and Doratomantispinae (both Mesozoic), Drepanicinae and Symphrasinae (both Cretaceous to Recent), Calomantispinae and Mantispinae (both Eocene to Recent) (Jepson, 2015; Oswald and Machado, 2018; Lu et al., 2020; Li et al., 2023).

A diverse fauna of Mantispidae has been recently discovered in mid-Cretaceous Kachin amber comprised of 29 species in 14 genera. Six genera belong to Doratomantispinae: *Doratomantispa* Poinar and Buckley, 2011, *Paradoxomantispa* Lu et al., 2020, *Pectispina* Shi, Yang and Ren in Shi et al. (2020a), *Acanthomantispa* Lu et al., 2020, *Dicranomantispa* Lu et al., 2020, and *Psilomantispa* Lu et al., 2020; Li et al. (2025); the three latter genera were initially considered to belong to Drepanicinae by Lu et al. (2020). Six monotypic genera have been described in Symphrasinae: *Archaeosymphrasis* Shi et al., 2020b, *Habrosymphrasis* Shi et al., 2020b, *Haplosymphrasites* Lu et al., 2020, *Parasymphrasites* Lu et al., 2020, *Parvosymphrasites* Li et al., 2023, and *Proplega* Li et al., 2023. *Mesomantispoides* Li et al., 2023 and *Haplacantha* Li et al., 2023 were not assigned to a subfamily.

Most species in Kachin amber are represented by one specimen (but one species by three and two by two), which is typical for modern high diversity tropical ecosystems, i.e., there is a high frequency of 'singletons' in a sample (e.g., Coddington et al., 2009). Therefore, we may expect more species of Mantispidae to be found in Kachin amber, which sampled a mid-Cretaceous tropical forest.

Extant Symphrasinae include three genera (i.e., *Trichoscelia* Westwood, 1852, *Anchieta* Navás, 1909, and *Plega* Navás, 1928), and are distributed in America, from southern USA to Argentina. Besides these nine genera (Kachin amber and extant), one other fossil genus was described in the subfamily, i.e., the monotypic *Symphrasites* Wedmann and Makarkin, 2007 from the middle Eocene of the Messel Pit fossil site, Germany. Recently, the monotypic genus *Carentosymphrasites* Jouault et al., 2025 was recorded from the Cenomanian Charentese amber, France. Here, a symphrasine affinity of *Sinomesomantispa* Jepson et al., 2013 from the Lower Cretaceous Yixian Formation (China) is considered.

Here, a new genus and species of Symphrasinae is described from Kachin amber, which is one of minutest mantispids and superficially similar to Rhachiberothidae, the affinity of this family is discussed.

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2. Material and methods

This study is based on a single specimen of Mantispidae embedded in a relatively small, rectangular piece of Kachin amber about 15 × 10 mm. It was legally obtained before June 2017 (see Museum Catalogue Entry in Supplementary material) by Paul Miller, Contwig (Germany), who generously donated the amber piece to the State Museum of Natural History Stuttgart, Germany (SMNS) (inventory no. SMNS BU-341).

The male adult (SMNS BU-341-1) is embedded together with two insect specimens as syninclusions: a minute pirate bug (Heteroptera: Anthocoridae) (SMNS BU 341–2) and one small drain fly (Diptera: Nematocera: Psychodidae: Brichomyiinae) (SMNS BU 341–3).

Kachin amber originates from the Hukawng Valley in the state of Kachin in northern Myanmar (Fig. 1). The precise mine from which this piece originated cannot be determined. The age is currently considered to be earliest Cenomanian (Shi et al., 2012; Smith and Ross, 2018).

The specimen was examined under a Leica M205C stereo microscope. Serial photographs of SMNS BU-341-1 were taken and stacked using a Keyence VHX5000 microscope. Stacked photographs were optimised for sharpness, contrast and tonality with Adobe Photoshop CC. Line drawings were prepared by VM using Adobe Photoshop CS3.

Venation terminology follows Breitkreuz et al. (2017) except for details (e.g., spaces, veinlets), which follows 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; 2m-cu, second crossvein between MP and CuA.

Abbreviations: A1–A3, first to third anal veins; C, costa; CuA, anterior cubitus; CuP, posterior cubitus; hp, humeral plate; 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; RP2, branch of RP distad RP1; Sc, subcosta.

All taxonomic acts established in the present work have been registered in ZooBankLSID (see below), together with the electronic publication urn:lsid:zoobank.org:pub: C2E42FEF-F6C5–4B15-A8C3-AF738BBA5F08.

3. Systematic palaeontology

Order Neuroptera Linnaeus, 1758
Family Mantispidae Leach, 1815
Subfamily Symphrasinae Navás, 1909

Genus ***Rhachisymphrasis*** gen. nov.
(urn:lsid:zoobank.org:act:F121B1C5-6D4C-4D2A-B1FB-5E0E2E7ED93B).

Derivation of name. From *Rhachiberotha* and *Symphrasis*, genus-group names of Rhachiberothidae and Symphrasinae, referring to superficial similarity of the type species to Rhachiberothidae. Gender feminine.

Diagnosis. Pseudopenis (=penisfilum; = fused gonostyli 10) of males is basally stout and apically pointed, short curved, and far extending beyond ectoproct [a long (often very long), thin, for most portion coiled structure, located mostly within the abdomen in most other Symphrasinae]. Profemora narrow [distinctly dilated in other genera]; protibia very short, about 1/3 of femur length [long, 2/3 to 3/4 of femur length in other genera]; mesotibia distinctly expanded medially [not expanded in other genera (except some *Anchieta*)]. Forewing: Sc terminating on RA [Sc terminates on C connecting with RA by a crossvein in *Parvosymphrasites* and extant Symphrasinae]; RP with three branches [four in *Habrosymphrasis*, *Archaeosymphrasis*, *Carentosymphrasites*]; three crossveins between RA and RP [two in *Parvosymphrasites*, *Proplega* and extant Symphrasinae]; M basally closely approaching R (or fused with R) for a short distance so that 1m-cu connecting M (or point of approaching M to R) with CuA [fused for long distance so that 1m-cu connecting R + M with CuA in *Parvosymphrasites*, *Carentosymphrasites* and extant Symphrasinae]; CuP not forked [deeply forked in other genera]; crossveins between A2 and A3 present [absent in extant Symphrasinae and probably *Habrosymphrasis*, *Parasymphrasites*]. Hind wing: two crossveins between RA and RP [one in *Parvosymphrasites* and extant Symphrasinae]; RP with two branches [three-six in other genera except *Anchieta remipes* (Gerstaecker, 1888)].

Remarks. Two specimens assigned to *Habrosymphrasis xiai* Shi et al., 2020 by Shi et al. (2020b) and Lu et al. (2020) probably belong to different species. Both specimens have similar venation, but clearly differ by the structure of the pseudopenis: its shape in the holotype is similar to that of *Rhachisymphrasis raehlei* sp. nov., but the pseudopenis in the new specimen reported by Lu et al. (2020) is much longer, narrower and has a different shape (cf., Shi et al., 2020b, fig. 2C and Lu et al., 2020, fig. S2E).

Rhachisymphrasis raehlei sp. nov.
(urn:lsid:zoobank.org:act: act:535D31BB-6A19-418F–B414–24B97D2F501).
Figs. 2–7

Derivation of name. This species is dedicated to the memory of German malacologist and entomologist Dr. Wolfgang Rähle (19.3.1939–20.5.2019), former lecturer at Eberhard-Karls-University of Tübingen, Germany, and long-time honorary scientist at SMNS, in appreciation of his lifelong devotion to science, nature, and teaching.

Type material. Holotype SMNS BU-341-1, ex coll. P. Müller, deposited in the amber collection of Stuttgart State Museum of Natural History, Stuttgart, Germany. The specimen is complete and relative well preserved.

Type locality and horizon. Kachin amber (Northern Myanmar: Kachin State: Myitkyina District: Tanai Township: Hukawng Valley). Upper Cretaceous: lowest Cenomanian.

Description. Head poorly preserved; only parts of eyes, antennae and palpi well discernible. Four segments of maxillary palpi discernible: second, third segments short; fourth, fifth (terminal) segments very long (terminal segment narrowly conical, acute, dark); Two segments of labial palpi discernible; terminal segment fusiform, acute, brownish. Antenna short; basal flagellomeres transverse (i.e., their width greater than length); other preserved flagellomeres elongate, approximately twice as long as wide. Thorax very poorly preserved. Forelegs. Procoxa very long, slender, covered with rather scarce fine setae and several stronger setae. Protrochanter elongated, covered with dense, rather long setae. Profemur long, slender, slightly curved; densely covered with rather long fine setae; several stronger, longer setae proximally. Ventral processes arranged in two rows. Posteroventral row: ten strong, black spine-like setae ('thickened setae with globular base' of Ardila-Camacho et al., 2024) located for most length except proximally. Anteroventral row: six-seven longer, widely spaced 'spines' ('primary processes' of Ardila-Camacho et al., 2024) located along entire length, and numerous short 'spines' ('tubercle-shaped specializations' of Ardila-Camacho et al., 2024) located between longer 'spines for entire length (these are short, obtuse apically in distal part, and more elongate, pointed in proximal 2/3). Protibia very short, slightly curved, covered with short setae dorsally, and 13 prostrate setae ventrally. Protarsus: probasitarsus elongate, dark, covered with dense, rather stout, elongate pale setae; lanceolate process long, slender, slightly curved, appears located at

Fig. 1. Location of the Hukawng Valley amber mines in Myanmar.

tip of probasitarsus; other tarsomeres pale, its number cannot be counted; terminal tarsomere elongate, with several elongate pale setae; claws small, strongly curved.

Mid-legs. Mesocoxa not clearly discernible. Mesofemur long, slender, covered with dense long setae. Mesotibia strongly expanded medially, covered with scarce long setae (Fig. 5B). Metatarsus covered with dense long setae; metabasitarsus longest, approximately as long as three next tarsomeres together; terminal tarsomere elongated.

Hind legs. Metacoxa not clearly discernible. Metafemur very long, slender. Metatibia long, slightly expanded medially, covered with dense long setae. Metatarsus poorly preserved.

Abdomen (Fig. 7). Seventh to ninth tergite covered with relatively stout, long, scarce setae, eighth to ninth sternite narrow. Shape of ectoproct unclear, probably nearly quadrate in lateral view; covered with relatively long and dense setae. Fused gonostyli 10 form an unpaired, basally stout and apically tapering, strongly curved pseudopenis (penisfilum), far extending beyond ectoproct. A process (possibly membranous) lying ventral to pseudopenis is difficult to interpret (Fig. 7, labelled ‘?‘).

Forewing 4.3 mm long (left wing); 1.46 mm (left wing) and 1.54 mm (right wing) wide. Costal space most dilated at proximal 1/6 wing length. Subcostal veinlets very widely spaced proximally, moderately spaced distally; mostly simple, several forked very shallowly. Humeral veinlets recurrent with two simple branches. Sc apically abruptly turned to RA and fused with it. Sc + RA with five (proximad 4ra-rp), mostly well-discernible veinlets, three of which forked. Pterostigma indistinct. Subcostal space broad, with one crossvein located at origin of RP. RA space with three crossveins: two located proximad fusion of Sc, RA, and one distad. RP originates far from wing base (at 0.30 wing length), with three branches. RP1, RP2 dichotomously forked distad fourth gradate series; RP3 shallowly forked once (left wing) or twice (right wing). M basally appears to be closely approaching or fused with R for short distance; forked slightly distad origin of RP. MA, MP similarly dichotomously forked at fourth gradate series. CuA pectinately branched, with three short branches; proximal-most branch forked. CuP shallowly forked once, weekly sclerotized proximally. A1, A2, A3 simple. Crossvein between A2 and A3 long, curved. Jugal lobe well developed. Trichiation on veins and margins moderately long, rather scarce. One trichosor between ends of each two veins along apical half of wing; two along costal margin in proximal half and between ends of branches of Cu; seven between ends of CuP and A1; eight between ends of A1 and A2. Maculation absent.

Hind wing 3.6 mm long (left wing), 1.25 mm wide (right wing). Humeral plate and humeral lobe moderately developed. Costal space very narrow, with six proximal subcostal veinlets (stout, short) and three distal veinlets, of which distal-most is forked. Sc

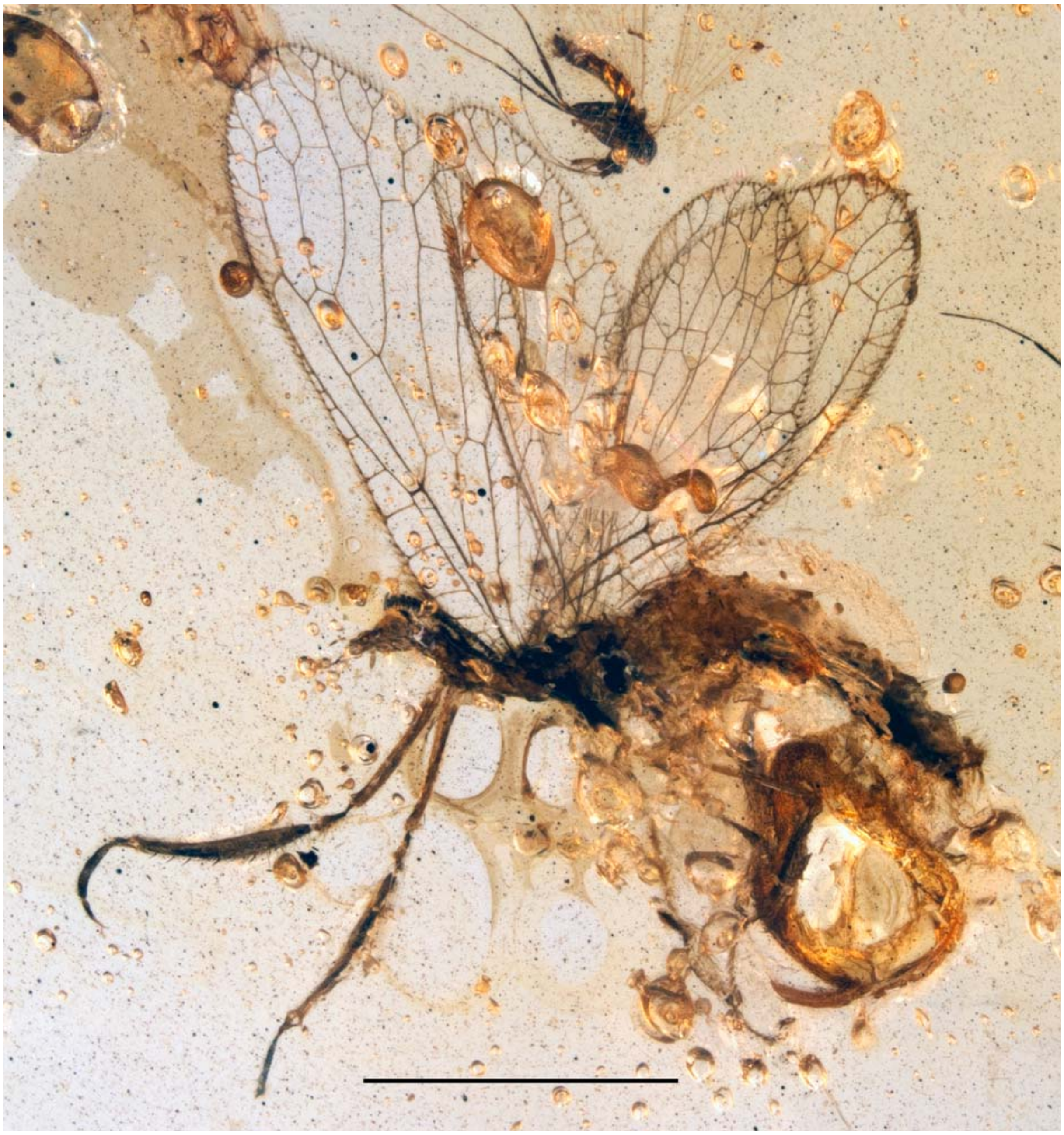

Fig. 2. *Rhachisymphrasis raehlei* gen. et sp. nov., holotype SMNS BU-341-1. Specimen as preserved. Scale bar represents 2 mm.

very closely approaching (or fused with) the costa for long distance, apically abruptly turned to RA and fused with it. Sc + RA long, with five (left wing) to seven (right wing) veinlets, mainly forked. Subcostal space broad for most part; no crossveins detected. RA space broad, with two crossveins: 2ra-rp located distad RP1, 3ra-rp distad RP2, proximad fusion of Sc, RA. RP originates relatively close to wing base (0.21 wing length), with two branches. RP1 pectinately forked distally, with four branches in right wing, three branches in left wing (proximal-most forked in both wings); RP2 forked twice near margin in right wing, dichotomously forked twice in left wing. One intraradial crossvein between RP1, RP2 belonging to outer gradate series. Two crossveins between RP and M/MA: 1r-m very long, sinuous connecting stem of R, M; 4r-m belongs to outer gradate series, connecting RP1, MA. M forked far from wing base, slightly proximad origin of RP1. MA pectinately forked, with four branches, proximal-most of these forked (in both wings); MP pectinately forked, with two (right wing) or three (left wing) simple branches. One intramedian crossvein belonging to outer gradate series. Two crossveins between M/MP and CuA: 1m-cu straight, located slightly proximad 1r-m; 4m-cu belongs to outer gradate series, connecting MP, CuA. Cu forked near wing base. CuA pectinately forked, with four branches (proximal-most branch forked). CuP incompletely discernible, probably with few branches. One intracubital crossvein (icu) long, with its anterior end inclined apicad. One rather short crossvein detected between Cu, A1, located near hind margin. A1, A2 long, simple. A3 much shorter, poorly discernible, without visible setae. Trichiation on veins rather long, scarce; along margin denser; along posterior basal margin very long. One trichosor between ends

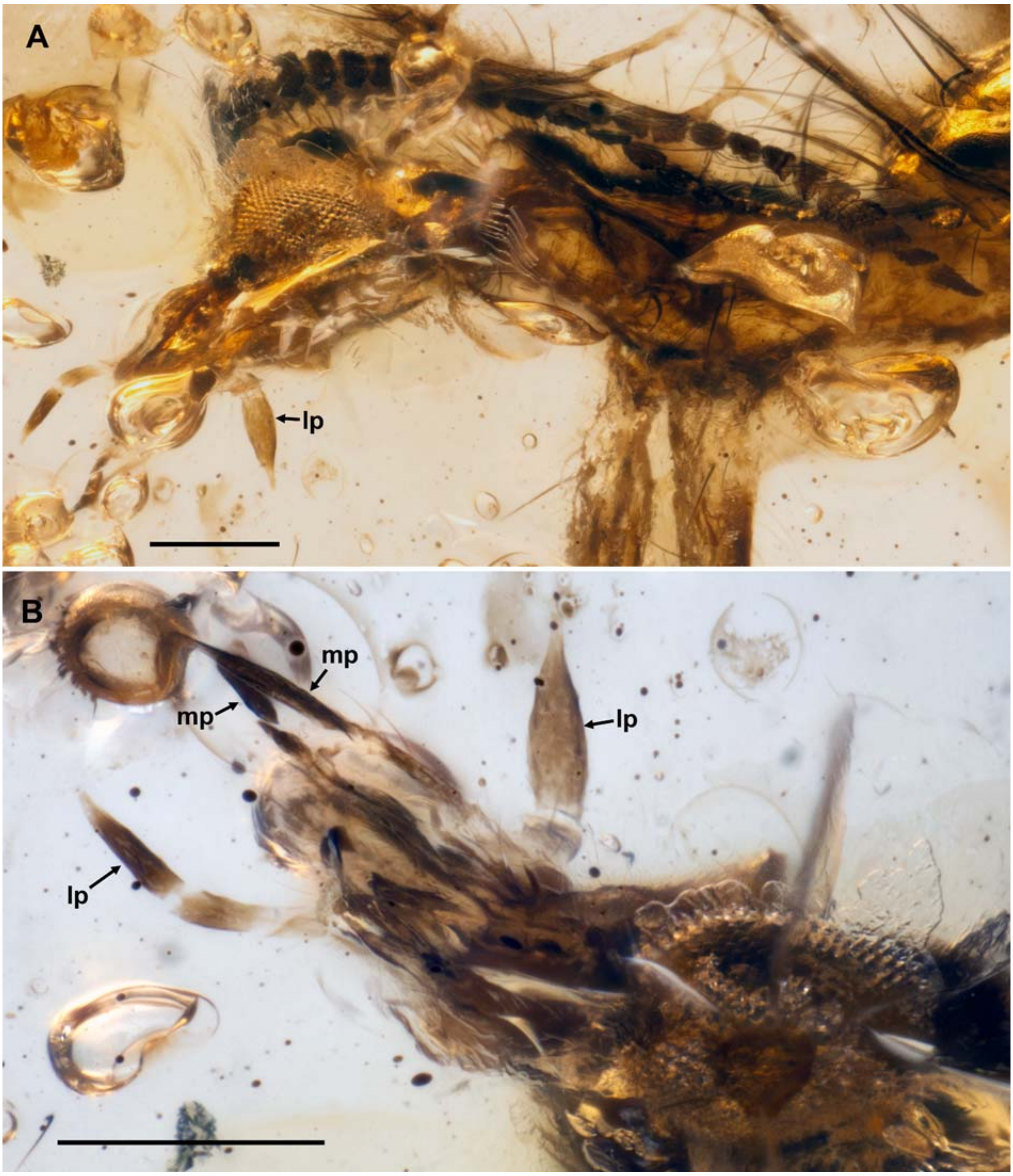

Fig. 3. Head and prothorax of *Rhachisymphrasis raehlei* gen. et sp. nov., holotype SMNS BU-341-1. A, left view; B, right view. lp, labial palpus; mp, maxillary palpus. Scale bars represent 0.2 mm.

of each two veins except basally; not detected along anterior basal margin; four to five along posterior basal margin between A1 to A3. Maculation absent.

4. Discussion

4.1. Diagnostic characters of Rhachisymphrasis

4.1.1. Size

With a forewing length of 4.3 mm, *Rhachisymphrasis raehlei* is one of smallest member of Symphrasinae and generally of Mantispidae. The smallest species is the Kachin amber *Parvosymphrasites aploneurus* with 3.95 mm forewing length (Li et al., 2023). The male forewing of *Plega duckei* Penny (1983) (5.5 mm long) is shortest among extant Symphrasinae (Penny, 1983). In general, all extant genera of the subfamily contain small species: in *Anchieta* the forewing ranges from 7 to 11.5 mm long, in *Plega* from 5.5 to 20.5 mm, and in *Trichoscelia* from 5.9 to 10.4 mm (based on various data). The forewings of six other symphrasine species from Kachin amber vary from 5.2 mm long in *Habrosymphrasis xiai* to 8.9 mm in *Archaeosymphrasis pennyi* (Lu et al., 2020; Shi et al., 2020b; Li et al., 2023).

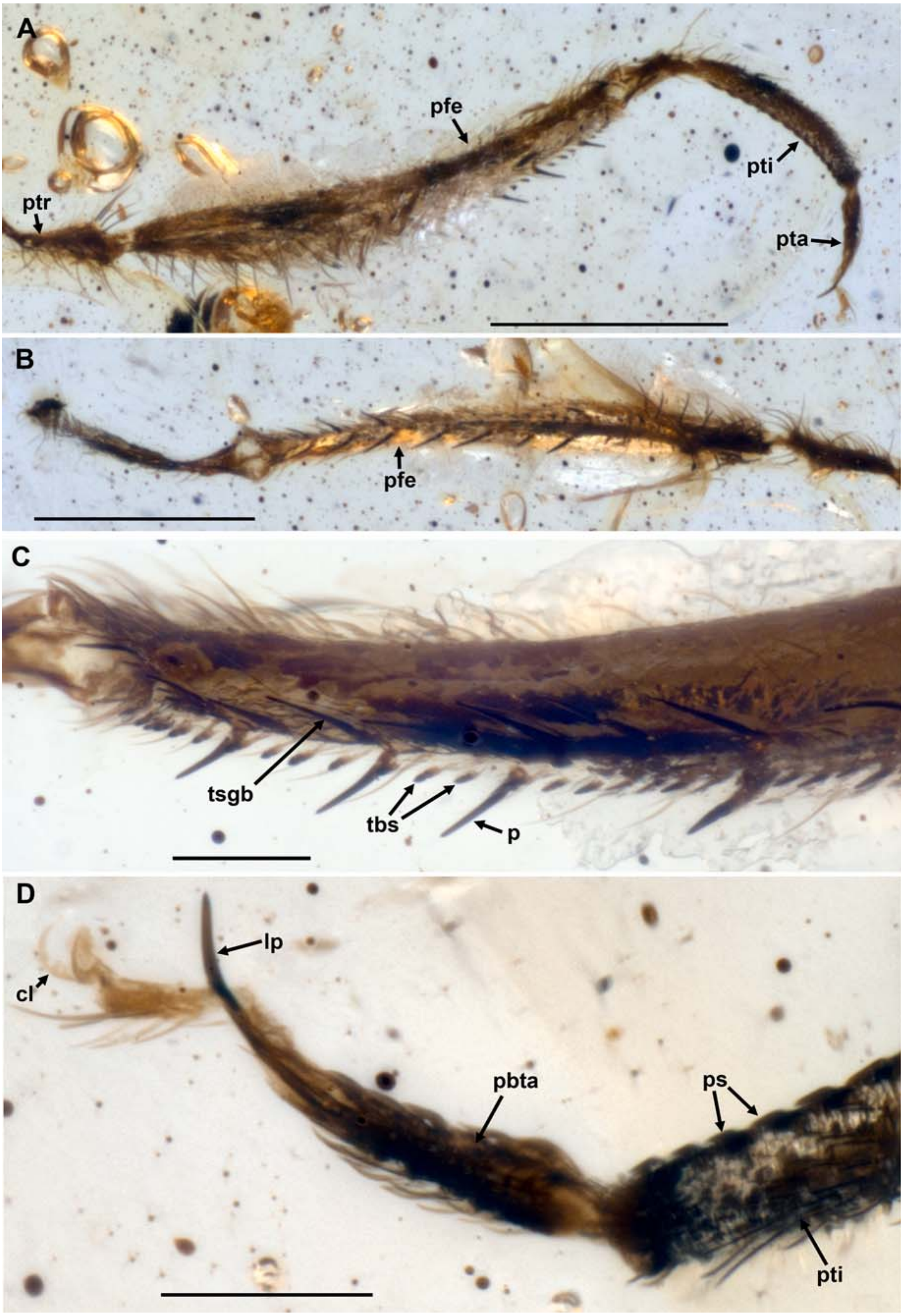

Fig. 4. Forelegs of *Rhachisymphrasis raehlei* gen. et sp. nov., holotype SMNS BU-341-1. A, right foreleg, lateral (outside) view; B, left foreleg, ventral view; C, distal part of right femur, lateral (inside) view; D, right protarsus, lateral (outside) view. cl, claw; lp, lanceolate process; p, primary process; pbtr, probasitarsus; pfe, profemur; pta, protarsus; pti, protibia; ps, prostrate setae; ptr, protrochanter; tbs, tubercle-shaped specializations; tsgb, thickened setae with globular base. Scale bars represent 0.5 mm (A, B), 0.1 mm (C, D).

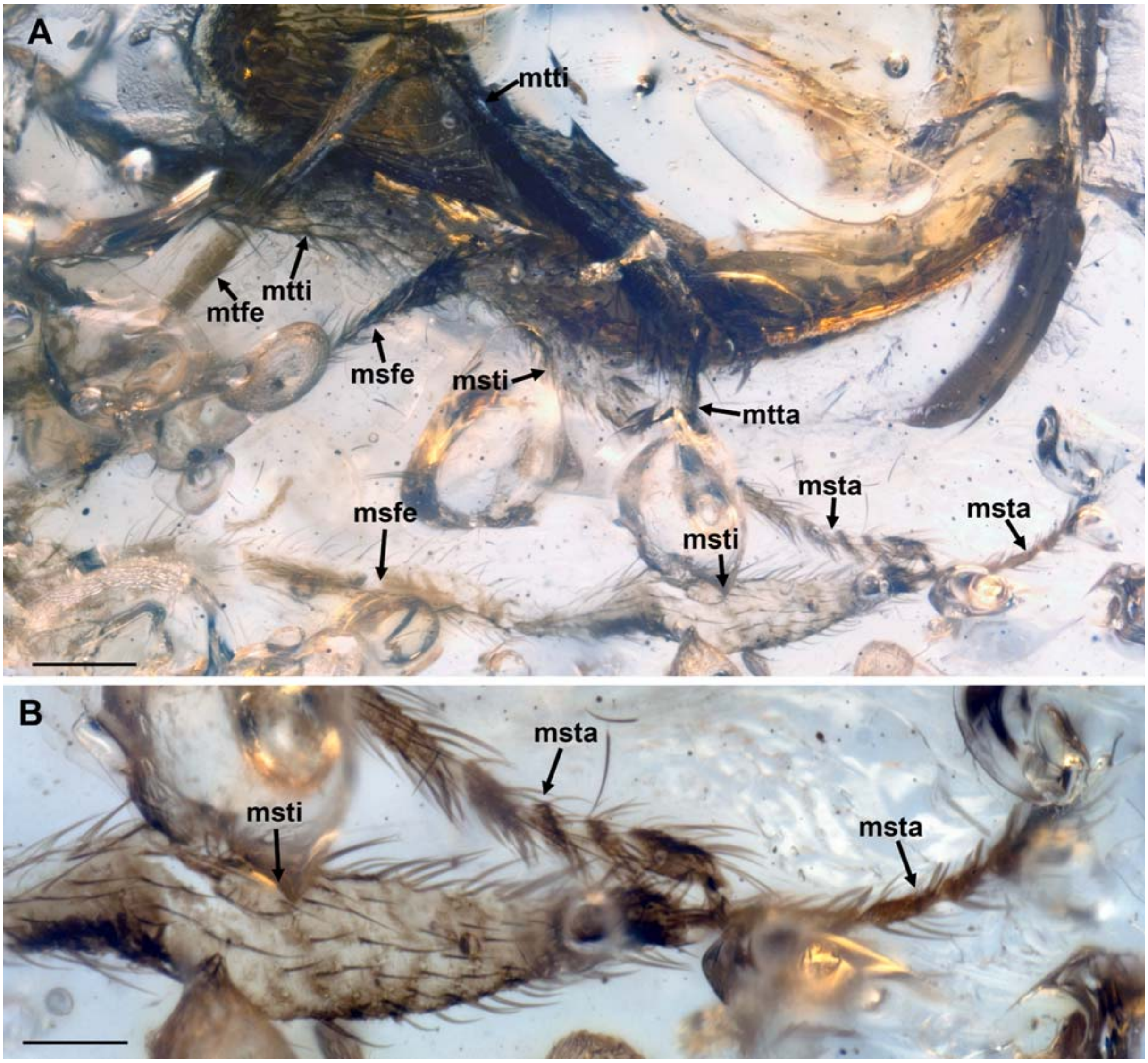

Fig. 5. Mid- and hind legs of *Rhachisymphrasis raehlei* gen. et sp. nov., holotype SMNS BU-341-1. A, parts of mid- and hind legs; B, distal parts of mid-legs. msfe, mesofemur; msta, mesotarsus; msti, mesotibia; mtfe, metafemur; mtta, metatarsus; mtti, metatibia. Scale bars represent 0.2 mm (A), 0.1 mm (B).

In comparison, the forewing length in Rhachiberothidae varies from 6 mm (several species of *Mucroberotha* Tjeder, 1959) to 8.8 mm (*Hoelzeliella manselli* Aspöck and Aspöck, 1997; Tjeder, 1959, 1968; Aspöck and Mansell, 1994; Aspöck and Aspöck, 1997).

4.1.2. Profemur

The slender shape of the profemur of *Rhachisymphrasis raehlei* is not known in any other species of Symphrasinae (and generally Mantispidae), but is characteristic of most Rhachiberothidae and Paraberothinae.

The profemur spination of *R. raehlei* differs from that of other Kachin Symphrasinae by its smaller number of primary processes and their absence in the proximal half (see Shi et al., 2020b, fig. 1F; Li et al., 2023, figs. 23C, 25G). In extant Rhachiberothidae these processes are absent (or are shorter) in the distal part of the profemur (e.g., Aspöck and Mansell, 1994, figs. 32, 38).

The arrangement of profemur spination in *R. raehlei* is generally similar to that of extant Symphrasinae in that it has all three types of ‘spines’ (primary processes; thickened setae with globular base; and tubercle-shaped specializations) arranged in two rows (see (Ardila-Camacho et al., 2024, fig. 1). However, the fine structure of primary processes and partly tubercle-shaped specializations is more similar to the spine-like setae of Paraberothinae (see Makarkin, 2025, fig. 2D) and Rhachiberothidae (to less extent) (see Ardila-Camacho and Contreras-Ramos, 2025, fig. 7) than those of Symphrasinae. In extant species of Symphrasinae, primary processes end in a very short Stitz organ (modified seta), while in *R. raehlei* each ends in a long, stout seta as in Paraberothinae and Rhachiberothidae.

4.1.3. Protarsus

The protarsus in *Rhachisymphrasis raehlei* is unusual for Symphrasinae, with the lanceolate process (=dorsal spine-like seta of Makarkin, 2015) of the probasitarsus being relatively thin and seta-like arising from its tip (see Fig. 4D). Unfortunately, it is impossible to confirm with certainty if this lanceolate process is entirely fused with the probasitarsus or not (i.e., is articulated) because of the vertical orientation of the tarsus to the visible plane

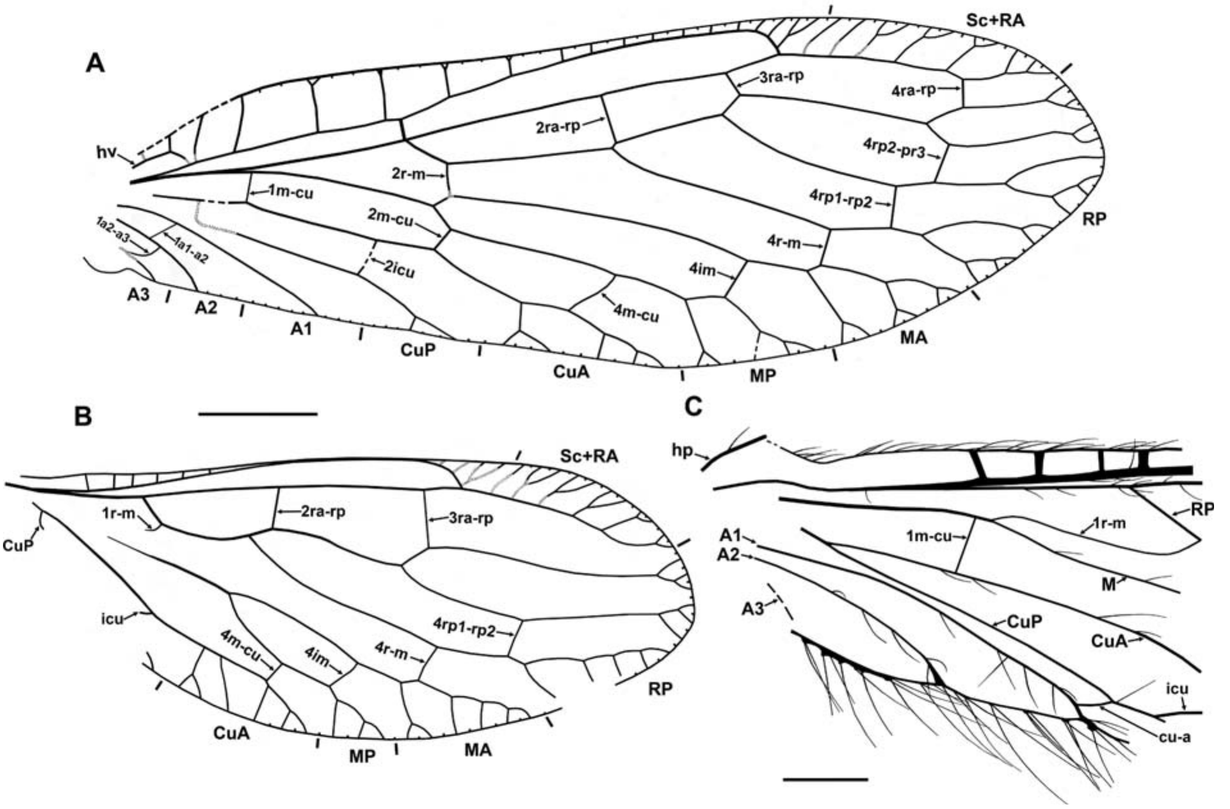

Fig. 6. Wing venation of *Rhachisymphrasis raehlei* gen. et sp. nov., holotype SMNS BU-341-1. A, left forewing; B, right hind wing; C, left hind wing. Scale bars represent 0.5 mm (A, B, to same scale), 0.2 mm (C).

and the probasitarsus being covered with dense setae. Superficially, however, the protarsus is similar to that of *Whalfera wiszniewskii* Makarkin and Kupryjanowicz, 2010 from Baltic amber, except by the absence of dense setae on the probasitarsus in the latter species (see Makarkin, 2015, figs. 7. 8B). In *W. wiszniewskii*, the lanceolate process is articulated, not fused, and arises from the tip of the probasitarsus.

The protarsus of *Archaeosymphrasis, Habrosymphrasis* and *Carentosymphrasites* appears to be similar to that of extant Symphrasinae, i.e., the probasitarsus and its lanceolate process appears to be entirely fused to form a single tarsomere terminating with a spine, and the second tarsomere originates from its distal half, not from its tip (see Shi et al., 2020b, figs. 1f, 2c). The probasitarsus in the male of *Parvosymphrasites aploneurus* appears to be similar to that of Paraberothinae having five ventral specialized setae (the lanceolate process is not mentioned in the description, and not discernible in the photographs: Li et al., 2023, figs. 23A–C). The structure of the protarsus of three genera of Kachin amber Symphrasinae (*Haplosymphrasites*, *Parasymphrasites* and *Proplega*) is unclear (Lu et al., 2020; Li et al., 2023).

Males of three extant species of Rhachiberothidae are known. In these, the protarsus is four-segmented and the probasitarsus is specialized, whereas females of the subfamily have a five-segmented unspecialized protarsus (a plesiomorphy). The male protarsus of four species is constructed in a generally similar manner to that of extant Symphrasinae, with their probasitarsus terminating in a spine bearing a seta homologous with the Stitz organ of Symphrasinae, i.e., *Rhachiberotha sheilae*, *Mucroberotha vesicaria* Tjeder, 1968, *M. aethiopica* Aspöck and Mansell, 1994, and *Rhachiella malawica* Aspöck et al., 2020; Tjeder, 1968, fig. 1; Aspöck and Mansell, 1994, figs. 12, 21; Aspöck et al., 2020, fig. 3; Ardila-Camacho et al., 2021b, fig. 23f; Ardila-Camacho and Contreras-Ramos, 2025, fig. 9a). The structure of the protarsus of *R. sheilae* especially resembles that of extant Symphrasinae in that the probasitarsus is elongated and the second tarsomere originates far from the end of the probasitarsus.

The structure of the male protarsus in *Mucroberotha minteri* Aspöck and Mansell (1994) is simplest in Rhachiberothidae: the second tarsomere originates from the tip of the probasitarsus, and a terminal spine-like seta is more like ordinary sensilla chaetica, but thicker (Aspöck and Mansell, 1994, fig. 38).

The lanceolate processes of the probasitarsus is also present in five genera of Upper Cretaceous Paraberothinae: *Rhachibermissa* Grimaldi, 2000, *Albertoberotha* McKellar and Engel, 2009, *Acanthoberotha* Nakamine et al., 2020, *Creagroparaberotha* Makarkin, 2015, *Micromantispa* Shi et al., 2015 (see Grimaldi, 2000, fig. 17; McKellar and Engel, 2009, fig. 2; Shi et al., 2015, fig. 5B; Makarkin, 2015, fig. 6; Nakamine et al., 2020, figs. 2b, 9d, 11c, 13c). However, these ‘processes’ are more like ordinary setae, but thicker. All Paraberothinae have a five-segmented protarsus in both males and females, and the second tarsomere originates from its tip. In general, the protarsus of this subfamily differs from that of Berothidae with cursorial forelegs only by the presence of several stronger setae. Moreover, the protarsus of some Paraberothinae does not bear any such setae and, therefore, does not differ from that of Berothidae with cursorial forelegs (see e.g., Makarkin, 2025, fig. 2B). The protarsus of Paraberothinae is clearly relatively plesiomorphic compared to those of Symphrasinae and some Rhachiberothidae.

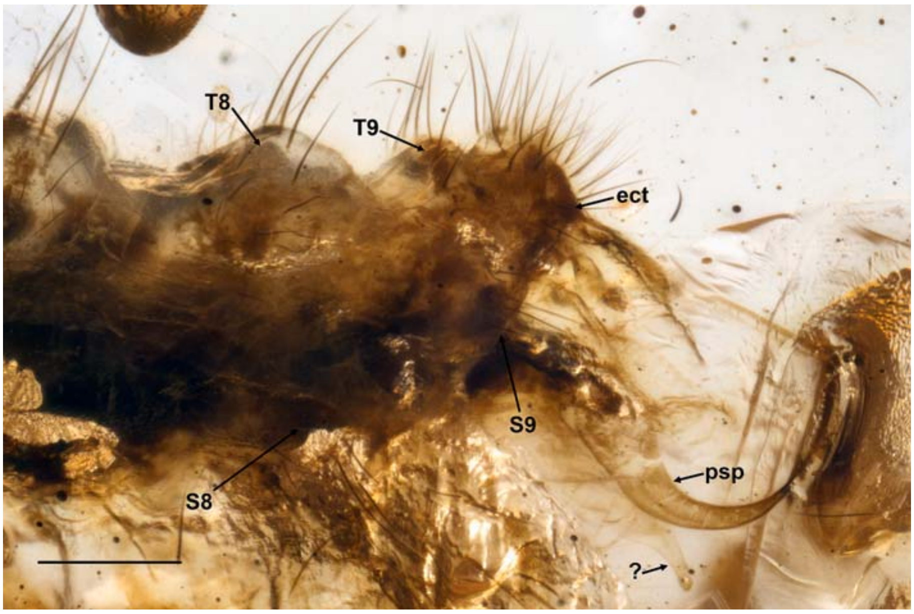

Fig. 7. Apex of abdomen of *Rhachisymphrasis raehlei* gen. et sp. nov., holotype SMNS BU-341-1. ect, ectoproct; psp, pseudopenis; S8, S9, 8th and 9th sternites; T8, T9, 8th and 9th tergites. Scale bar represents 0.2 mm.

In summary, the protarsus of *Rhachisymphrasis raehlei* is most plesiomorphic in Symphrasinae (in species where it is clearly visible), and more like that of Rhachiberothidae (especially *Whalfera* Engel, 2004).

4.1.4. Mesotibia

The mesotibia of *Rhachisymphrasis* is strongly expanded medially (Fig. 5B), while it is normal, not expanded in *Parasymphrasites*, *Parvosymphrasites* and most extant Symphrasinae (except *Anchieta*), and unclear in *Habrosymphrasis*, *Archaeosymphrasis* and *Proplega*.

4.1.5. Metatibia

The metatibia of *Rhachisymphrasis* is slightly expanded, while it is not in other Kachin amber species. It is strongly expanded and flattened laterally (oar-shaped) in most species of the extant genus *Anchieta* (see e.g., Ardila-Camacho, Garcia, 2015, figs. 2h, i, 3d; Ardila-Camacho et al., 2024, figs. 4F, 12G, 14F, 16G, H, 18F, 20G, H, 24F). Penny (1983) assumed that “the small size and swollen orange and black hind tibiae of some species give these mantispids the appearance of stingless bees (Meliponini), which are common in the region” (p. 418).

4.1.6. Multiple trichosors

The presence of two or more trichosors between the tips of two veins (i.e., multiple trichosors) as detected in *Rhachisymphrasis raehlei* is a typical character state for Symphrasinae and occurs in several other families of Neuroptera: Babinskaiidae, Nymphidae, Chrysopidae (Jurassic Limaiinae, some lower Eocene Nothochrysinae), and the Eocene genus *Whalfera* (Rhachiberothidae) (see details in Makarkin, 2017). One trichosor between the tips of each two veins is present in all extant Rhachiberothidae.

4.1.7. Distal relationships of the forewing Sc and RA

Sc and RA are distally fused in *Rhachisymphrasis* (the distal part of Sc is bent towards RA). Such a condition is found in many fossil taxa of Mantispidae (most Kachin amber genera of Symphrasinae, all Mesomantispinae and Doratomantispinae except some drepanicine-like genera: Li et al., 2025), all Paraberothinae and Mesithoninae. In the mantipid Drepanicinae, Calomantispinae and Mantispinae (and fossil genera associated with these), Sc and RA are distally not fused, but these veins usually closely approach in the pterostigmal area. In extant Symphrasinae, the Kachin amber *Haplosymphrasites* and *Parvosymphrasites*, and the middle Eocene *Symphrasites*, these veins are widely separated. In extant Symphrasinae Sc is often considered to be distally fused with RA (e.g., Tjeder, 1959; Ardila-Camacho et al., 2024). Indeed, the distal part of Sc and veinlets of RA incorporated in the pterostigma are very poorly discernible. However, the portion of Sc located immediately distal to the distal crossvein is clearly visible in some species (see Ardila-Camacho et al., 2024, figs. 10B, 12B, 38B).

In the majority of Rhachiberothidae (including the upper Eocene *Whalfera*) Sc and RA are widely separated distally (Fig. 8B). The single exception is the lower Eocene *Oisea celinea* (Nel et al., 2005a), in which Sc is distally fused with RA (Nel et al., 2005a, fig. 23).

In general, the distal fusion of Sc and RA is characteristic of Mesozoic members of those families whose Cenozoic and extant members have these veins separated (e.g., Hemerobiidae, Mantispidae, Chrysopidae). So, this is the common situation in Symphrasinae.

4.1.8. Crossveins between RA and RP in the forewing

Two of these crossveins are present in all extant Symphrasinae and the Kachin amber *Parvosymphrasites* and *Proplega*, but there are three in most fossil genera of Symphrasinae (four genera in Kachin amber including *Rhachisymphrasis*, and one from the middle Eocene), and most other Mantispidae (fossil and extant), except for their secondary proliferation in some Mantispinae (e.g., the extant *Eumantispa* Okamoto, 1910). One genus in Kachin amber Symphrasinae (*Haplosymphrasites*) has one ra-rp crossvein, and some Kachin amber genera of Doratomantispinae have two (Lu et al., 2020, fig. S1G, S4H, S8E, F, S11D).

Rhachiberothidae and at least some Mesithoninae have three crossveins, while the vast majority of Paraberothinae have two. The number of these crossveins varies in other fossil Berothidae, from one (Makarkin, 2018) and two (Makarkin, 2015) to four (Makarkin and Ohl, 2015). Similarly, there are usually two or three

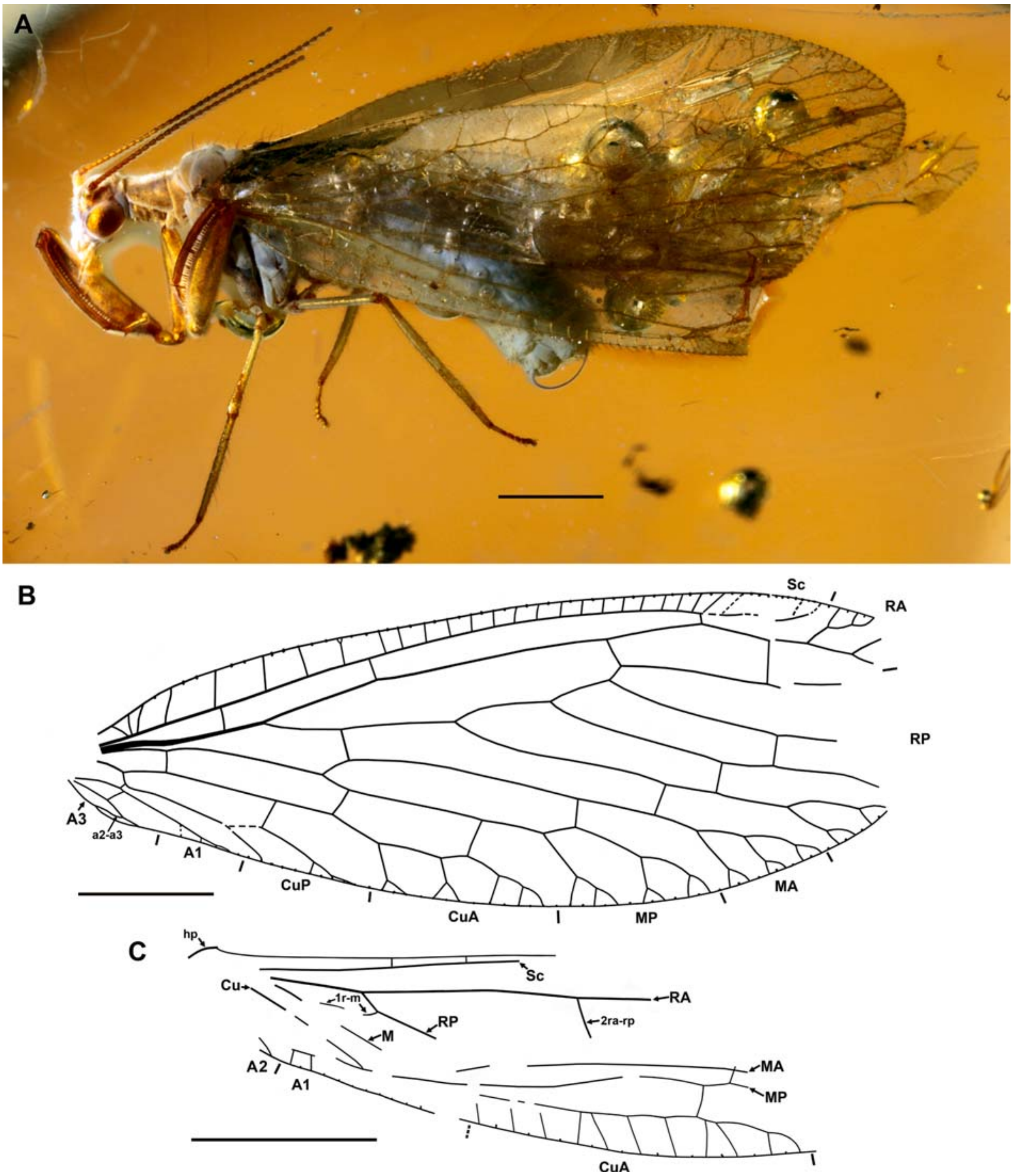

Fig. 8. Baltic amber *Whalfera wiszniewskii* Makarkin and Kupryjanowicz (2010) from the upper Eocene Baltic amber, holotype MZ 24203. A, whole specimen (photo: J. Kupryjanowicz); B, forewing venation; C, hind wing venation. Scale bars represent 1 mm.

crossveins in extant taxa, except for their secondary proliferation in some genera. The presence of three crossveins between RA and RP in the forewing is probably a plesiomorphic state at the level of Mantispoidea, and their reduction or proliferation is apomorphic.

4.1.9. Forewing M

The forewing M of *Rhachisymphrasis* appears to be fused with R (or perhaps only closely approaches) basally slightly proximad 1m-cu. A similar condition is seen in *Habrosymphrasis* and *Proplega* (Shi et al., 2020b, fig. 3a; Li et al., 2023, fig. 26A, B). In *Archaeosymphrasis* these veins are not fused (Shi et al., 2020b, fig. 1d). This plesiomorphic condition is also present in all Mesozoic Mantispidae, including the Lower Jurassic *Liassochrysa stigmatica* Ansorge and Schlüter (1990), the oldest member of the family. In these, M appears to be fused only basally with R (or only approaches R), so that the basal crossvein 1m-cu connects Cu and M (see e.g., Panfilov, 1980, fig. 96; Ansorge and Schlüter, 1990, fig. 3; Jepson et al., 2013, fig. 1C; Poinar and Buckley, 2011, fig. 9). On the contrary, M is fused with R for a long distance in all extant Mantispidae (including Symphrasinae), so that 1m-cu connects Cu and

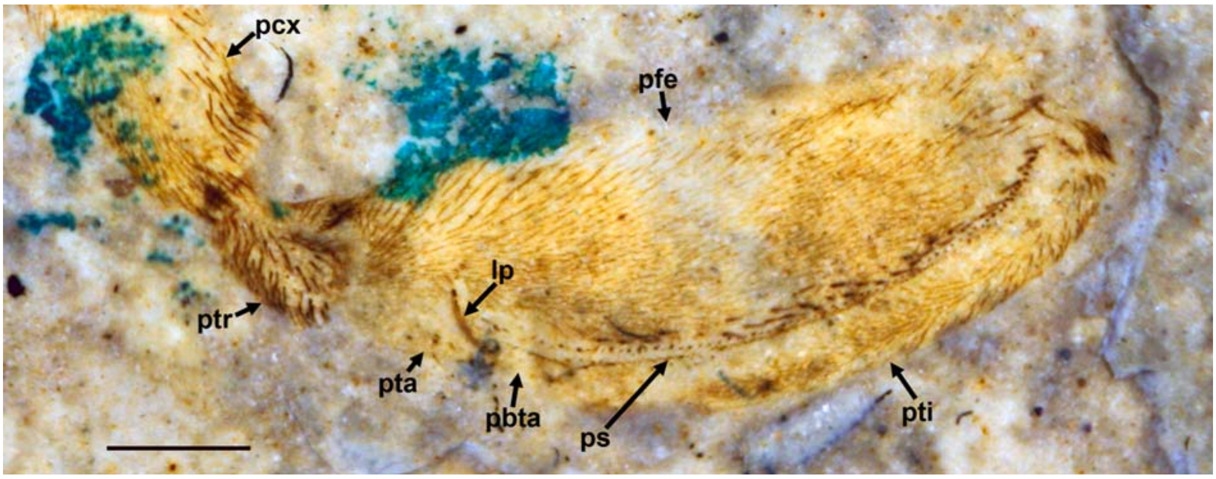

Fig. 9. Foreleg of *Sinomesomantispa microdentata* Jepson et al. (2013) from the Lower Cretaceous Yixian Formation (China), holotype CNU-NEU-2011006P/C (photo: J. Jepson). lp, lanceolate process; pbtr, probasitarsus; pcx, procoxa; pfe, profemur; ps, prostrate setae; pta, protarsus; pti, protibia; ptr, protrochanter. Scale bar represents 1 mm.

R + M (see e.g., Ardila-Camacho et al., 2018, figs. 1a, 4a, 7a; Li et al., 2023, fig. 24). Such an apomorphic condition is also present in the Kachin amber *Parvosymphrasites* and *Haplosymphrasites*.

The forewing M and R are basally separate in Paraberothinae and Rhachiberothidae, including the upper Eocene *Whalfera* (Fig. 8B) (except for *Mucroberotha* in which these are fused slightly proximad or distad 1m-cu).

4.1.10. Forewing CuP

The shallowly forked forewing CuP as found in *Rhachisymphrasis raehlei* occurs extremely rarely in Mantispidae. We know of only a few species with a simple CuP, all in advanced taxa, e.g., the Oligocene *Prosagittalata oligocenica* Nel (1989) (fig. 3), the extant *Leptomantispa chaos* Hoffmann (2002) (fig. 587) (both Mantispinae), and the genus *Nolima* Navás, (1914) (Calomantispinae) (Reynoso-Velasco et al., 2019, fig. 4A). All hitherto known Symphrasinae have a deeply forked CuP.

CuP is deeply forked in all Rhachiberothidae and most Berothidae. A shallowly forked and simple forewing CuP are apomorphic conditions in Mantispoidea.

4.1.11. Crossveins between A2 and A3 in the forewing

This crossvein (1a2-a3) is present in many Mantispidae (Kachin amber *Rhachisymphrasis*, *Proplega*, and *Parvosymphrasites*; Drepanicinae including the Jurassic *Liassochrysa stigmatica* Ansorge and Schlüter, 1990 and *Promantispa similis* Panfilov, 1980; Calomantispinae), Rhachiberothidae and Mesithoninae (e.g., the Upper Jurassic *Berothone protea* (Panfilov, 1980) and *B. gracilis* (Panfilov, 1980; Khramov, 2015, figs.1a–d), but absent in all extant Symphrasinae, Mantispinae, and fossil Paraberothinae. This crossvein is usually absent also in Berothidae with cursorial forelegs; it is present in the only extant species – *Manselliberotha neuropterologorum* Aspöck and Aspöck, 1988), and in a few fossils, e.g., the Lower Cretaceous *Sibelliberotha rihanensis* Azar and Nel (2013).

Its configuration in *Rhachisymphrasis* (i.e., long and sinuously curved) is very similar to that of some Rhachiberothidae, e.g., *Whalfera wiszniewskii* and the extant *Mucroberotha angolana* Aspöck and Mansell (1994); Aspöck and Mansell (1994), fig. 29, labelled as ‘A3’; Makarkin and Kupryjanowicz (2010), fig. 3, labelled as ‘3A’). We tend to believe that the presence of 1a2-a3 is a plesiomorphic condition; its reduction probably occurred independently in several lineages.

4.1.12. Basal crossvein between R and M in the hind wing

This crossvein in *Rhachisymphrasis* is long and sinuous. Such a condition is present in all Rhachiberothidae and Symphrasinae. This character state is probably a symplesiomorphy of Mantispoidea. In Berothidae, this condition is detected only in two Cretaceous genera, *Oloberotha* Ren and Guo, 1996 (Mesithoninae) from the Yixian Formation (China), and *Osmyloberotha* Khramov, 2021 from Kachin amber (Li et al., 2023, figs. 2A, B, 5A, 7A, C, D; VNM, pers. obs.). In other Berothidae (including the Cretaceous Paraberothinae) and other Mantispidae, 1r-m is crossvein-like or lacking (apomorphic states).

4.1.13. Male pseudopenis (=penisfilum, = fused gonostyli 10)

The visible portion of the male genitalia of *Rhachisymphrasis* is mainly an unpaired, very stout basally and strongly curved structure extending far beyond the ectoproct. This is most probably the pseudopenis (according to the terminology of Lambkin, 1986a), and may be interpreted as the fused gonostyli 10 according to the terminology of Aspöck and Aspöck (2008), i.e., a terminal portion of the fused gonocoxites 10 or of the paramere-mediuncus complex according to Aspöck and Nemeschkal (1998). A similar pseudopenis is found in the *Habrosymphrasis* and *Parvosymphrasites* from Kachin amber (Lu et al., 2020, fig. S2E; Li et al., 2023, fig. 23F), but these are more slender and longer than in *Rhachisymphrasis*. The pseudopenis of extant Symphrasinae is mostly very thin, often very long, and sometimes folded several times within the abdomen, and it almost doesn't extend beyond the ectoproct. Its simplest construction occurs in *Plega spinosa* Ardilla et al. (2019) (see Ardilla et al., 2019, fig. 9a; Ardilla et al., 2024, figs. 70a–e), which is most like the pseudopenis of *Parvosymphrasites*.

In general, the pseudopenis of Kachin amber genera is like that of some other Mantispidae (Drepanicinae, Calomantispinae, Mantispinae) and basal Berothidae. In different groups of mantispoids there are species with a relatively long pseudopenis, e.g., in Drepanicinae (Lambkin, 1986a, fig. 301), Mantispinae (Lambkin, 1986b, fig. 679; Aspöck and Aspöck 2008, fig. 40; Dobosz, 2008, figs. 3, 5), and Berothidae (e.g., the extant *Cyrenoberotha* MacLeod and Adams, 1968, and the lower Eocene *Microberotha* Archibald and Makarkin, 2004).

The long, coiled pseudopenis is also present in some Rhachiberothidae (e.g., *Mucroberotha*: Aspöck and Mansell, 1994, fig. 26) and in many Berothidae (e.g. Aspöck and Aspöck, 1980, figs. 4, 5, 10, 11).

4.2. The systematic position of *Rhachisymphrasis*

The genus *Rhachisymphrasis* is confidently referred to Mantispidae by the presence of prostrate setae on its forelegs, and to Symphrasinae by the structure of the protarsus. Our analysis shows that the genus is remarkable in possessing many character states that do not occur in any other Symphrasinae: the profemur is slender; the protibial is very short; the lanceolate process of the probasitarsus is relatively thin, arising from its tip; the mesotibia is strongly expanded (except in some Anchieta); the forewing CuP is shallowly forked; and the pseudopenis is very stout basally.

Although the new genus is so unique, it is generally like other genera in Kachin amber, and dissimilar to extant genera in many characters, especially pseudopenis structure, the location of crossvein 1m-cu, the presence/absence of a crossvein between A2 and A3, and the number of crossveins between RA and RP.

The forelegs of *Rhachisymphrasis* are more like those of Rhachiberothidae than to extant Symphrasinae (see above). The new genus shares two plesiomorphic forewing venation character states with Rhachiberothidae that are apomorphic in extant Symphrasinae: the crossvein 1m-cu connects M and CuA, and the crossvein 1a2-a3 between A2 and A3 is present. It is unclear whether this similarity is only superficial (is convergent) or a result of a close phylogenetic relationship between Rhachiberothidae and Symphrasinae (is homologous).

4.3. Composition of Rhachiberothidae

Four genera with fourteen extant species are known from Africa: *Rhachiberotha* Tjeder, 1959, *Mucroberotha*, *Hoelzeliella* Aspöck and Aspöck, 1997, and *Rhachiella* Aspöck et al., 2020; Aspöck and Mansell (1994); Aspöck and Aspöck (1997); Aspöck et al. (2020). Two fossil genera belong to this taxon, i.e., the monotypic *Oisea* Nel, 2005b from the lower Eocene of France, and the upper Eocene *Whalfera* with two described species, *Whalfera venatrix* (Whalley, 1983) from British amber (Norfolk, Great Britain), and *W. wiszniewskii* Makarkin and Kupryjanowicz (2010) from Baltic amber (Poland coast).

Oisea celinea is represented by a complete female from Oise amber. Its characters are generally concordant with those of extant taxa except two, i.e., ScP and RA are distally fused in both fore- and hind wings and two crossveins are present between RA and RP (see Nel et al., 2005a, fig. 23).

The systematic position of *Whalfera* has been extensively discussed. It was originally assigned to Mantispidae by Whalley (1983), belonging or closely related to Symphrasinae. Grimaldi (2000) also considered it to be closely related to this subfamily. Willmann (1994) provided a most comprehensive and accurate analysis of characters of *Whalfera venatrix*. He considered the genus to be within the family and concluded that it is the sister group of 'higher' Mantispidae (i.e., Symphrasinae + Drepanicinae + Calomantispinae + Mantispinae). Ohl (2004) listed the genus in the catalogue "as a possible mantispid with unknown affinities" (p. 261). But Aspöck and Mansell (1994), Engel (2004) and Grimaldi and Engel (2005) tentatively transferred *Whalfera* to Rhachiberothidae without serious analysis. Wedmann and Makarkin (2007) stated that "although there is a theoretical possibility of assigning this genus to a stem group of Mantispidae, the probability is greater that it belongs to Rhachiberothidae" (p. 710). Makarkin and Kupryjanowicz (2010) analysed the characters of *Whalfera* (mainly based on *W. wiszniewski*) and concluded that it is the only fossil genus of Rhachiberothidae as a subfamily of Berothidae. Jepson (2015) believed that "the position of *Whalfera venatrix* in Rhachiberothidae is still debatable", its type "requires restudying to confirm its family placement" (p. 425), and that the placement of *W. wiszniewskii* in the genus is tentative.

We examined high resolution photographs of *W. wiszniewskii* to reveal hind wing venation, which has previously not been described. It is incompletely visible, but two character states have been reliably established: the long and sinuous basal crossvein 1r-m, and CuP is long, parallel, and rather close to the hind margin (Fig. 87C). The preserved hind wing venation is fully concordant with that of extant Rhachiberothidae.

On the other hand, *Whalfera* shares one apomorphic character state with Symphrasinae, i.e., the presence of multiple trichosors in the forewing (see Makarkin, 2017), a condition which is absent in all extant Rhachiberothidae and the lower Eocene *Oisea* as well as in Berothidae and other Mantispidae (in these, there are single trichosors between each two veins). However, multiple trichosors are present in a number of other families (see above), so this support is weak.

The systematic position of the taxon Paraberothinae is unclear. It was established as a subfamily of Rhachiberothidae by Nel et al. (2005a) and most authors follow this treatment (e.g., Nakamine et al., 2020; Li et al., 2023, 2025), but sometimes is treated as a subfamily of Berothidae (Makarkin and Kupryjanowicz, 2010; Makarkin, 2015, 2025) as it lacks key character states of Rhachiberothidae (e.g., in Paraberothinae, the additional posterior section of the prothorax is absent; the antennal scapus is long; and the basal crossvein 1r-m in the hind wing is straight).

4.4. Possible phylogenetic relationships of Symphrasinae and Rhachiberothidae

4.4.1. Mantispoidea and Mantispidae

The monophyly of the clade Mantispoidea is accepted by all recent authors. The superfamily includes Berothidae, Rhachiberothidae, Mantispidae, the Cretaceous Dipteromantispidae, and possibly the Triassic Mesoberothidae (however, this group is poorly known). The loss of the basal subcostal crossvein in the hind wing and the presence of an elongated pseudopenis (i.e., fused gonostyli 10) are putative synapomorphies of Mantispoidea (Ardila-Camacho et al., 2021b; VNM, pers. obs.). Raptorial forelegs are characteristic of most Mantispoidea, occurring in all families in which forelegs are known: all Mantispidae, Rhachiberothidae, and Dipteromantispidae, Mesithoninae (Berothidae), and Paraberothinae. Although the phylogenetic relationships between these taxa with raptorial forelegs are considered well resolved (see Li et al., 2025), the position of some taxa (especially Mesithoninae and Paraberothinae) are controversial and unclear.

Two synapomorphies are characteristic of Mantispidae: [1] the presence of the additional posterior section of the prothorax (i.e., the prolongation of the prothorax behind the articulation of the forelegs), and [2] the presence of the prostrate setae on ventral edges of the protibia and protarsus (Liu et al., 2015). Two other synapomorphies of Mantispidae were identified by these authors (i.e., the pronotum is ventrally closed, and third and fourth segments of the mid- and hind tarsi are subequal in length) are less important. The ventrally closed pronotum is mainly characteristic of higher Mantispidae, and the third and fourth segments of the hind tarsi are equal in length also at least in Paraberothinae (see Makarkin, 2015).

[1] The prothorax of extant Symphrasinae consists of a short saddle-shaped pronotum covered with long setae, ventral and lateral sclerites, and the short additional posterior section (see Ardila-Camacho et al., 2021b, 2024). The terminology of this section is not yet established. Ardila-

> Camacho and Contreras-Ramos (2025) named the entire posterior section the postfursternum, although it consists of two sclerites, dorso-lateral and ventro-lateral. Previously, however, Ardila-Camacho et al. (2021b) had used the term postfursternum for only the ventro-lateral sclerite, following the terminology of Crampton (1928) for Raphidioptera. The latter definition is rather reasonable as this structure in Raphidioptera is ventral, and it was considered a sternite by Ferris and Pennebaker (1939). Makarkin (2025) named the dorso-lateral sclerite the posterior postcoxal sclerite. Both the posterior postcoxal sclerite and the postfursternum are present in Symphrasinae; the posterior section is ventrally open in all genera except *Plega* (Ardila-Camacho et al., 2024). The posterior section of the prothorax in more derived Mantispidae consists of the fused posterior postcoxal sclerite and postfursternum.

Ferris (1940) assumed that the posterior section of the prothorax “may be formed by a secondary sclerotization of the intersegmental membranes” (p. 35). This is a quite reasonable assumption.

The forelegs are articulated to the prothorax anterior to the additional section, usually in the posterior part of the pronotum, rarely in its middle (e.g., Machado, 2018, fig. 1) or anterior (Ardila-Camacho et al., 2018, fig. 3a).

In advanced subfamilies (especially Mantispinae), the additional posterior section is often very long and tabular (i.e., entirely closed ventrally without a discernible line of contact). However, the forelegs articulate also in the anterior/middle part of the short pronotum (located in the anterior part of the prothorax), which is entirely fused with the posterior section (e.g., see Snyman et al., 2018, figs. 4c, 6c, 10b, 12c).

The additional posterior section is also present in Rhachiberothidae, including the Baltic amber *Whalfera wiszniewskii* (see Aspöck et al., 2020, fig. 7; Ardila-Camacho et al., 2021b, figs. 20a, b; Ardila-Camacho and Contreras-Ramos, 2025, figs. 6a–c). It is ventrally open in extant taxa and appears to be open in *W. wiszniewskii*.

The typical (plesiomorphic) articulation of the forelegs of all other Neuroptera is exemplified in Hemerobiidae, where there is no additional posterior portion of the prothorax and the forelegs articulate in the posterior part of the pronotum (see Killington, 1936, fig. 7).

> [2] Prostrate setae are considered a synapomorphy of Mantispidae (Liu et al., 2015), but these are secondarily lost in Mantispinae. All Mesozoic Mantispidae with preserved forelegs have these setae (see Pérez-de la Fuente and Peñalver, 2019), but all Berothidae, including the oldest (Middle Jurassic) Mesithoninae, Rhachiberothidae and Dipteromantispidae lack these (VNM, pers. obs.).

4.4.2. *Symphrasinae and Rhachiberothidae*

The Symphrasinae strongly differ from other Mantispidae by many character states (see detailed analysis in Ardila-Camacho et al., 2021b), but they have the two abovementioned synapomorphies of the family.

The monophyly of extant Symphrasinae is well supported (Liu et al., 2015; Lu et al., 2020). Recently, two Lower Cretaceous genera previously considered in Mesomantispinae (i.e., *Clavifemora* Jepson et al., 2013 and *Sinomesomantispa* Jepson et al., 2013) were transferred to Symphrasinae as its earliest branches: *Clavifemora* + [*Sinomesomantispa* + Kachin amber, Eocene and extant genera] (Li et al., 2025, fig. 2). Our examination of high resolution photographs of *Sinomesomantispa microdentata* Jepson et al. (2013) shows that its protarsal structure is indeed very similar to that of Symphrasinae by its elongate basiprotarsus bearing terminal lanceolate process (Fig. 9). This lanceolate process is rather similar to that of *Rhachisymphrasis*. The small prostrate setae are poorly seen in the distal part of inner edge of tibia. The primary processes of the profemur are short and seta-like. All legs are covered with dense short setae. Unfortunately, the wing venation of the only specimen of *S. microdentata* is poorly preserved and incomplete. In any case, we confirm that *Sinomesomantispa* may be a member of Symphrasinae, the oldest known genus of the subfamily.

In general, the body and foreleg structure of Mesomantispinae and Symphrasinae are similar, particularly in their short prothorax and similar profemur spination (see Jepson et al., 2013; Khramov, 2013). Their forewing venation is also rather similar, although it is much denser in Mesomantispinae. Unfortunately, the hind wing venation of this subfamily is unknown. It is, therefore, reasonable to assume that some Mesomantispinae were the ancestors of Symphrasinae.

On the other hand, the similarity of Mesomantispinae and Mesithoninae venation is obvious (see Khramov, 2013; Jepson, 2015). Mesozoic Mesithoninae, however, do not belong to Mantispidae, as this taxon does not possess mantispid synapomorphies (i.e., the presence of the prothoracic posterior section and prostrate setae) (Makarkin, 2025). Nevertheless, the taxa Mesithoninae, Mesomantispinae and Symphrasinae appear to form one phylogenetic lineage. In this lineage, however, it is hard to understand the position of Rhachiberothidae as they have not yet been discovered in the Mesozoic.

Rhachiberothidae and Symphrasinae are similar by a number of characters, and many authors have discussed this similarity since Tjeder (1959). Aspöck and Nemeschkal (1998) treated the similar structure of male forelegs in Symphrasinae and Rhachiberothidae as a synapomorphy. The taxon Rhachiberothidae + Symphrasinae was considered to be the sister group of other extant Mantispoidea (Winterton et al., 2018). Finally, the Symphrasinae were included in Rhachiberothidae as a subfamily based on two synapomorphies: the presence of a foretarsal Stitz organ on forelegs and a polygonal ninth sternite of the male (Ardila-Camacho et al., 2021b, 2024; Ardila-Camacho and Contreras-Ramos, 2025). However, both of these characters are weak. The foretarsal setae of Rhachiberothidae do not bear the Stitz organ characteristic of Symphrasinae, although these setae are homologous (see Makarkin, 2025). The shape of a sternite is also a weak character as it is very variable.

The probability of a close relationship of Rhachiberothidae with Berothidae and Mantispidae appears almost equal.

The berothid affinity of Rhachiberothidae is supported by a similar larval morphology (see Makarkin and Perkovsky, 2025), female genitalia (in particular, the presence of long pseudohypocaudae), the long hind wing CuP nearly parallel and rather close to the hind margin, and the presence of the tubercles on the vertex. In Symphrasinae, the larvae have a typical mantispid appearance (see Ardila-Camacho et al., 2021a); the pseudohypocaudae are absent; the hind wing CuP is short; and the tubercles on the vertex are absent.

A mantispid affinity of Rhachiberothidae is supported by foreleg morphology (in particular, the presence of the lanceolate process) and the presence of the prothoracic posterior section. If we assume that the presence of the latter indicates an inclusion to the family Mantispidae, then Rhachiberothidae belong to it (as a separate subfamily or a part of Symphrasinae), as proposed by Willmann (1990). Prostrate setae could have been secondarily lost in Rhachiberothidae as in Mantispinae. The discovery of *Rhachisymphrasis* provides further arguments in favor of this hypothesis.

It is currently impossible to determine which alternative is correct. In our view, the most plausible hypothesis is that

Rhachiberothidae constitutes an ancient branch of Mantispoidea leading to Mantispidae but which retains many character states of Berothidae. However, until Mesozoic fossils of Rhachiberothidae are found, further speculation is pointless. The idea that Rhachiberothidae represents a transitional lineage between Berothidae and Mantispidae remains most reasonable (Liu et al., 2017).

5. Conclusions

Rhachisymphrasis raehlei gen. et sp. nov. is unique in many character states within the Symphrasinae. The structure of its protarsus is particularly important, as it is similar to that of Rhachiberothidae, indicating that this family and the Symphrasinae might be closely related. However, the analysis shows that we cannot currently say with any certainty which families are closer to the Rhachiberothidae, the Mantispidae (and hence the Symphrasinae) or the Berothidae. Until Mesozoic Rhachiberothidae are found, this question remains open. It is only clear that both Rhachiberothidae and Symphrasinae are ancient branches of Mantispoidea, whose roots go back to the Jurassic.

CRediT authorship contribution statement

Vladimir N. Makarkin: Writing – review & editing, Writing – original draft, Investigation. **Arnold H. Staniczek:** Writing – review & editing, Writing – original draft, Investigation.

Declaration of competing interest

The authors declare that they have no known 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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2025.106243.