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The first Symphrasinae (Neuroptera: Mantispidae) from Cretaceous Charentese amber (France)

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KEY WORDS
Mantispidae,
Europe,
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ABSTRACT
A new species of Symphrasinae, *Carentosymphrasites zhengi* n. gen., n. sp., is described and illustrated from Cenomanian Charentese amber. This taxon is classified within the crown group of the subfamily due to the presence of 3-5 trichosors between adjacent veins along the distal wing margin. The discovery of this species suggests that Symphrasinae had a relatively broad distribution during the mid-Cretaceous, but later went extinct in Europe and Asia.

MOTS CLÉS
Mantispidae,
Europe,
mantispidés,
biogéographie,
groupe couronne,
diversité,
genre nouveau,
espèce nouvelle.

RÉSUMÉ
Le premier Symphrasinae (Neuroptera: Mantispidae) de l'ambre charentais du Crétacé (France).
Une nouvelle espèce de Symphrasinae, *Carentosymphrasites zhengi* n. gen., n. sp., est décrite et illustrée à partir d'ambre cénomanien des Charentes. Ce taxon est classé dans le groupe-couronne de la sous-famille en raison de la présence de 3 à 5 trichosors entre les nervures adjacentes le long de la marge distale de l'aile. La découverte de cette espèce suggère que les Symphrasinae avaient une distribution relativement large au cours du Crétacé moyen, mais qu'ils ont ensuite disparu en Europe et en Asie.

INTRODUCTION

The superfamily Mantispoidea Leach, 1815 includes three extant families – Berothidae Handlirsch, 1906, Rhachiberothidae Tjeder, 1959, and Mantispidae Leach, 1815 – along with one extinct family, Dipteromantispidae Makarkin, Yang & Ren, 2013 (Engel *et al.* 2018; Ardila-Camacho *et al.* 2021; Li *et al.* 2023, 2024; Wang *et al.* 2024). The monophyly of Mantispoidea is well supported by phylogenetic analyses based on both morphological and molecular data. However, the phylogenetic relationships between its families remain contentious, particularly regarding the placement of Rhachiberothidae and Mantispidae (Liu *et al.* 2015; Wang *et al.* 2017; Engel *et al.* 2018; Winterton *et al.* 2018; Vasilikopoulos *et al.* 2020; Ardila-Camacho *et al.* 2021).

The fossil record of Mantispoidea is diverse, comprising over 80 species from the Lower Jurassic to the Miocene (Jepson *et al.* 2018; Lu *et al.* 2020; Nakamine *et al.* 2020; Baranov *et al.* 2022; Hart *et al.* 2024). This superfamily appears to have diversified rapidly during the Angiosperm Terrestrial Revolution (Benton *et al.* 2022), likely driven by an increase in prey abundance, particularly angiosperm-feeding insects. However, this hypothesis requires further testing, as the diversity dynamics of the superfamily are still poorly understood.

Among the raptorial mantispoids, Dipteromantispidae are exclusively known from Cretaceous deposits, with fossils recorded in China, Myanmar, and the United States (e.g., Makarkin *et al.* 2013; Liu *et al.* 2017; Azar *et al.* 2020). The greatest species diversity for this family comes from mid-Cretaceous Kachin amber (e.g., Li & Liu 2020). Rhachiberothidae have a fossil record extending from the Cretaceous to the Eocene, with their highest diversity also found in mid-Cretaceous Kachin amber (e.g., McKellar & Engel 2009; Makarkin & Kupryjanowicz 2010; Nakamine *et al.* 2020). The Mantispidae fossil record begins in the Jurassic, with the youngest occurrences documented in the Miocene (e.g., Khramov 2013; Hart *et al.* 2024). Like the other two families, Mantispidae fossil diversity is concentrated in mid-Cretaceous Kachin amber (e.g., Lu *et al.* 2020; Li *et al.* 2023). This exceptionally high diversity during the mid-Cretaceous likely reflects a Lagerstätte effect, influenced by the abundance of amber deposits worldwide and sedimentary deposits in Asia (e.g., Jepson *et al.* 2013; So & Won 2022; Delclòs *et al.* 2023).

The family Mantispidae includes two extinct subfamilies (Mesomantispinae Makarkin, 1996 and Doratomantispinae Lu, Wang, Zhang, Ohl, Engel & Liu, 2020) and four extant subfamilies (Symphrasinae Navás, 1909, Drepanicinae Enderlein, 1910, Calomantispinae Navas, 1914, and Mantispinae Leach, 1815) (Lai *et al.* 2024). The taxonomic position of Symphrasinae has been debated for decades, with conflicting results in the literature. Some researchers have placed it within Rhachiberothidae (e.g., Ardila-Camacho *et al.* 2021), while others classify it under Mantispidae (e.g., Liu *et al.* 2015; Li *et al.* 2024), or alternate between both families depending on the dataset analyzed (Cai *et al.* 2023). In this study, we provisionally follow the classification of Symphrasinae within Mantispidae (e.g., Lai *et al.* 2024), but emphasize the need for increased sampling and the generation of genomic data for Mantispoidea to resolve this issue.

Additionally, the discovery of more fossil taxa could help clarify the placement of Symphrasinae by providing further morphological evidence. Describing new taxa from deposits outside the most commonly studied regions (e.g., Kachin or Baltic ambers) could shed light on the past diversity of the family, refine the boundaries of its constituent lineages, and assess the diagnostic characters used to distinguish crown and stem groups. Following this approach, we describe the first representative of Symphrasinae from Cenomanian Charentese amber.

MATERIAL AND METHODS

Geological setting

The Charentes region in southwestern France has the highest concentration of amber deposits in France; most of them are of Albian or Cenomanian age (Perrichot *et al.* 2007a, 2010; Néraudeau *et al.* 2020). The piece of amber and specimen studied herein were found in the lignitic layers of the Font-de-Benon quarry, near the villages of Archingeay and Les Nouillers, which are dated as latest Albian-earliest Cenomanian (Néraudeau *et al.* 2002; Dejax & Masure 2005; Peyrot *et al.* 2019). The amber piece was collected from level A1sl-A (= A1sl2 sensu Néraudeau *et al.* 2002) of the 'lithological subunit A1', consisting of lignitic sand and clay lenses that range from 0.1 to 1 m in thickness (Fig. 1; see also 'Arc1' in Kania-Kłosok *et al.* 2022: fig. 1B). The resin pieces and the associated fossil woods were deposited, after short biostratinomic transport (parautochthony), in a coastal marine area, as indicated by sedimentary figures of tides and bioturbation, and the presence of oysters, teredinid bivalve holes in the woods, and marine foraminifera in the lignitic clay (Néraudeau *et al.* 2002; Perrichot 2005). However, the reduced abundance of burrows and oysters in amber levels suggests environments under continental influence (freshwater): the facies are compatible with those of an internal estuary (Dalrymple *et al.* 1992). Wood remains from Charentese amber outcrops have been associated with the morphogenera *Agathoxylon* Hartig, 1848, *Brachyoxylon* Hollick & Jeffrey, 1909, *Podocarpoxylon* Gothan, 1905, and *Protopodocarpoxylon* Eckhold, 1922, and the resin-producing tree has been related to Araucariaceae Henkel & W.Hochst. or Cheirolepidiaceae Turutanova-Ketova (Nohra *et al.* 2015).

Preparation and documentation of fossil material

The piece of amber was polished using thin silicon carbide papers on a Buehler Metaserv 3000 polisher and then embedded in epoxy resin (Araldite© 2020). The specimen was examined with a Zeiss Axio Zoom V16 stereomicroscope with an attached Zeiss AxioCam 512 color camera. All images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using Helicon Focus 6.7. The figures were composed with Adobe Illustrator CC2018 and Photoshop CC2018.

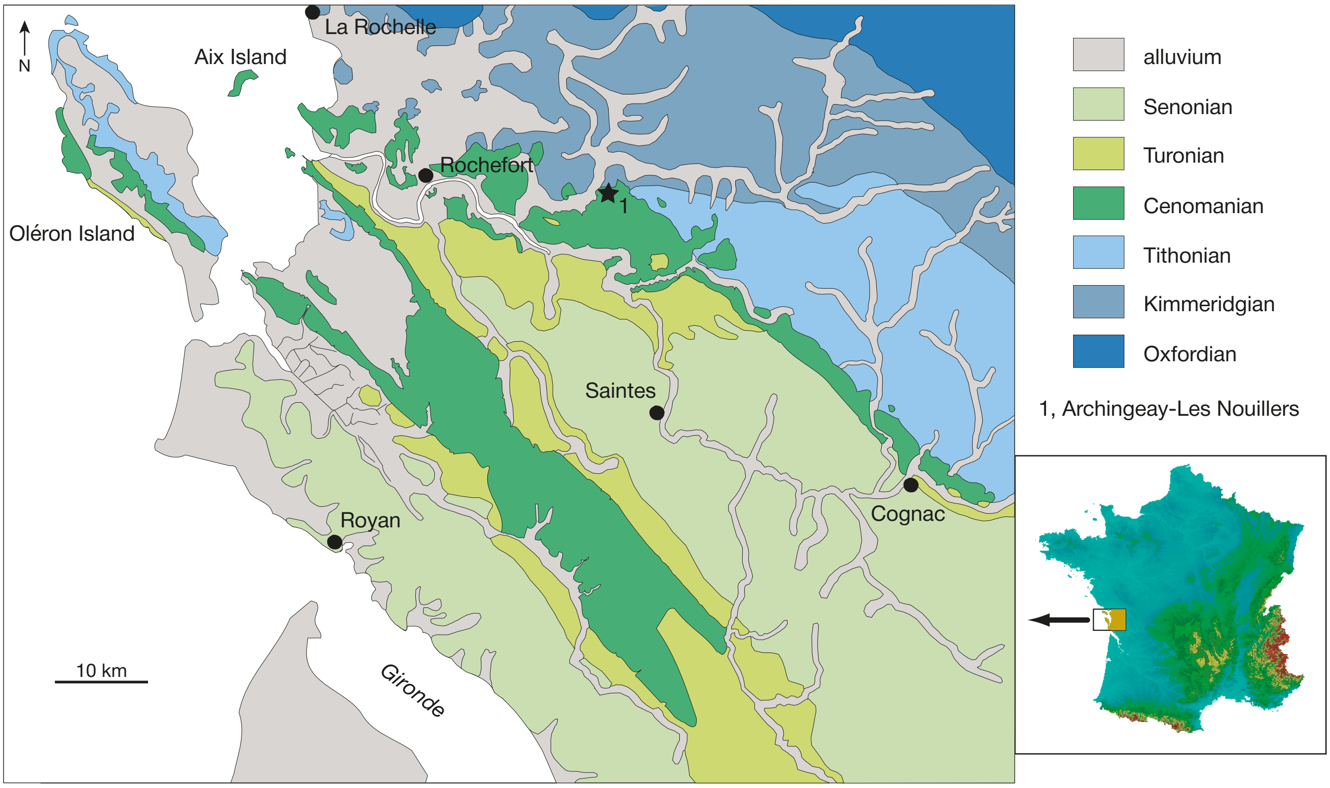

FIG. 1. — Geographical and geological settings of the Cretaceous Charentese amber deposit considered in the present study. Modified from Perrichot *et al.* (2007b).

TERMINOLOGY

The nomenclature of the wing venation is adapted from Li *et al.* (2023), and the nomenclature of the legs follows Ardila-Camacho *et al.* (2024). The holotype IGR.ARC-399 is housed in the Geological Department and Museum of the University of Rennes, France (IGR).

We follow standard wing venation terminology and abbreviations, as follows:

Institutional abbreviation

IGR Geological Department and Museum of the University of Rennes.

Collection abbreviation

ARC Specimen from Archingeay in IGR.

Other abbreviations

A analis;
Cu cubitus;
CuA cubitus anterior;
cua-cup first cross-vein in the area between CuA and CuP;
CuP cubitus posterior;
im intramedian cell;
M media;
MA media anterior;
MP media posterior;
1r first radial cell;
2r second radial cell;
3r third radial cell;
R radius;
RA radius anterior;
RP radius posterior;
rp-ma first cross-vein to connect RP and MA;
ScP subcosta posterior.

SYSTEMATIC PALAEONTOLOGY

Class INSECTA Linnaeus, 1758
Order NEUROPTERA Linnaeus, 1758
Family MANTISPIDAE Leach, 1815
Subfamily SYMPHRASINAE Navás, 1909

TYPE GENUS. — *Symphrasis* Hagen, 1877.

INCLUDED GENERA. — *Anchieta* Navás, 1909, *Archaeosymphrasis* Shi, Qiang, Winterton, Pang & Ren, 2020, *Habrosymphrasis* Shi, Qiang, Winterton, Pang & Ren, 2020, *Haplosymphrasites* Lu, Wang, Zhang, Ohl, Engel & Liu, 2020, *Parasymphrasites* Lu, Wang, Zhang, Ohl, Engel & Liu, 2020, *Proplega* Li, Zhuo, Wang, Nakamine, Yamamoto, Zhang, Ling, Ohl, Aspöck, Aspöck & Liu, 2023, *Parvosymphrasites* Ling, Liu & Wang, *in* Li *et al.* 2023, *Plega* Navás, 1928, *Sinomesomantispa* Jepson, Heads, Makarkin & Ren, 2013, *Symphrasites* Wedmann & Makarkin, 2007, *Trichoscelia* Westwood, 1852, *Carentosymphrasites* n. gen., and *Rhachisymphrasis* Makarkin & Staniczek, 2026. See the revision of the subfamily by Ardila-Camacho *et al.* (2024).

Genus *Carentosymphrasites* Jouault, Liu & Perrichot, n. gen.

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TYPE SPECIES. — *Carentosymphrasites zhengi* n. sp., by present designation and monotypy.

ETYMOLOGY. — From '*Carentonia*', the Latin name for the Charente River and Charentes region from which the type specimen originates, and *Symphrasites* (a generic name of fossil Symphrasinae), in reference to the origin of the specimen and its systematic placement. The gender is masculine.

DIAGNOSIS. — The new genus is characterized by the following characters: 1) fore femur anteroventral row complete with at least 14 stinger-shaped setae; 2) posteroventral row of processes reduced in apical portion, one primary process present plus at least five stinger-shaped setae; 3) fore tibia setose (vs glabrous in *Anchieta*); 4) fore wing ScP not fused with C (vs fused with C in *Haplosymphrasites*); 5) at least three ra-rp crossveins present in fore wing and two in hind wing; 6) most RP branches without marginal forks (vs many marginal forks present in *Plega* and *Trichoscelia*); 7) presence of 3-5 trichosors between neighbouring veins on distal margin of wing (similar to other crown group members of Symphrasinae); and 8) hind wing with 1r-m not distally connected to M stem by a short cross vein (vs connected in *Trichoscelia*)

REMARKS

The new genus differs from most fossil genera of Symphrasinae by the presence of 3-5 trichosors between neighbouring veins on distal margin of wings. The only fossil symphrasine with a similar arrangement of trichosors is *Haplosymphrasites* from the mid-Cretaceous of Myanmar (Lu *et al.* 2020). Unfortunately, the fore legs of the holotype of *Haplosymphrasites zouae* Lu, Wang, Zhang, Ohl, Engel & Liu, 2020 are not preserved, making direct comparison with *Carentosymphrasites* n. gen. impossible (Lu *et al.* 2020). Nevertheless, the wing characters, i.e., the configuration of fore wing ScP, and the number of radial crossveins, provide sufficient evidence to distinguish these two Cretaceous genera. Additionally, the genitalia of the holotype of *Carentosymphrasites* n. gen. are missing, which hinders more detailed comparisons with other crown group members of Symphrasinae, although the above-outlined wing and fore leg characters can be used to distinguish the new genus from those three extant genera. Due to the obscured condition of the amber piece encasing *Carentosymphrasites* n. gen., it is also impossible to confirm the presence or absence of tubercle-shaped processes (sensu Ardila-Camacho *et al.* 2024) on the posteroventral processes row.

Carentosymphrasites zhengi Jouault, Liu & Perrichot, n. gen., n. sp. (Figs 2; 3)

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TYPE MATERIAL. — **Holotype. France** • 1 specimen with one fore leg, parts of mid- and hind legs, one fore wing and one hind wing, and part of the abdomen preserved, adult – in syninclusion with one Hymenoptera (fragments) and one Diptera (indet.); Nouvelle-Aquitaine, Charente-Maritime Department, Archingeay-Les Nouillers, Font-de-Benon quarry; Cretaceous, uppermost Albian-lowermost Cenomanian (level A1sl); IGR.ARC-399.

ETYMOLOGY. — The specific epithet honors Yuchen Zheng, friend of CJ and PhD student of XL, for his contribution to Neuroptera systematics. It is to be treated as a noun in genitive case.

TYPE LOCALITY AND HORIZON. — Font-de-Benon quarry, Archingeay-Les Nouillers, Charente-Maritime Department (Nouvelle-Aquitaine, France); level A1sl, uppermost Albian-lowermost Cenomanian, Cretaceous (Néraudeau *et al.* 2002).

DIAGNOSIS. — As for the genus (*vide supra*), by monotypy.

MEASUREMENTS. — Fore wing length about 6.45 mm long and about 2.4 mm wide; hind wing about 4.95 mm long and about 2.05 mm wide.

DESCRIPTION

Head not preserved.

Thorax damaged; fore leg with femur at least 1.85 mm long (partially preserved), about 0.55 mm wide (maximal width), dorsal surface concave in lateral view, all surfaces setose, inner surface with three distinct rows of setae (see diagnosis for more details), mesal row developed near femur base then indistinct; tibia about 1.75 mm long and about 0.13 mm wide, subcylindrical, distinctively curved, entirely setose, with a row of 30(?) strong setae on inner surface (Fig. 3B), slightly tapering toward apex; clavate setae present at tibia apex; tarsus about 0.53 mm long, with tarsomere I spine like (Fig. 3B), terminating at level of tarsomere IV (about 0.09 mm long), apically with fore tarsal Stitz organ, tarsomere II arising midway along tarsomere I, pretarsal claw simple, arolium present; midleg with tibia about 1.4 mm long, widest at mid-length, tarsus about 0.6 mm long, tarsomeres bearing a couple of thickened setae, laterally on the distal margin of the plantar surface. Hind legs partially preserved.

Wings slightly broadened at distal ⅓, but again narrowed distad. Fore wing without distinct marking; trichosors present around entire wing margin, 3-5 trichosors present between two neighboring veins; costal space dilated proximally; recurrent humeral veinlet present, trifurcate; pterostigma not clearly discernible; costal space with ten(?) crossveins, mostly simple but one bifurcate; ScP distally broadly arched, reaching RA and fused with it; RA with at least four simple branches; subcostal space distinctly broadened distad; 2scp-r, located immediately after R fork, straight; RP with five main branches, most of which are bifurcate, some lack small marginal forks; 1r slightly less than twice 2r length; 3r maybe crossed by faint crossvein between third and fourth RP branches; one complete gradate series of crossveins present; one rp-m crossvein present, reaching M just anteriad its fork; M proximally fused with R for a short distance, deeply bifurcate into two main branches; MA forked, with four branches distad; MP forked, with four branches distad; im cell base slightly anteriad R fork, apex at level of 2r apex; 1m-cu distinctly anteriad fork of M; Cu diverging into CuA and CuP near wing base; CuA with four branches distad, anterior most with a small marginal fork; one

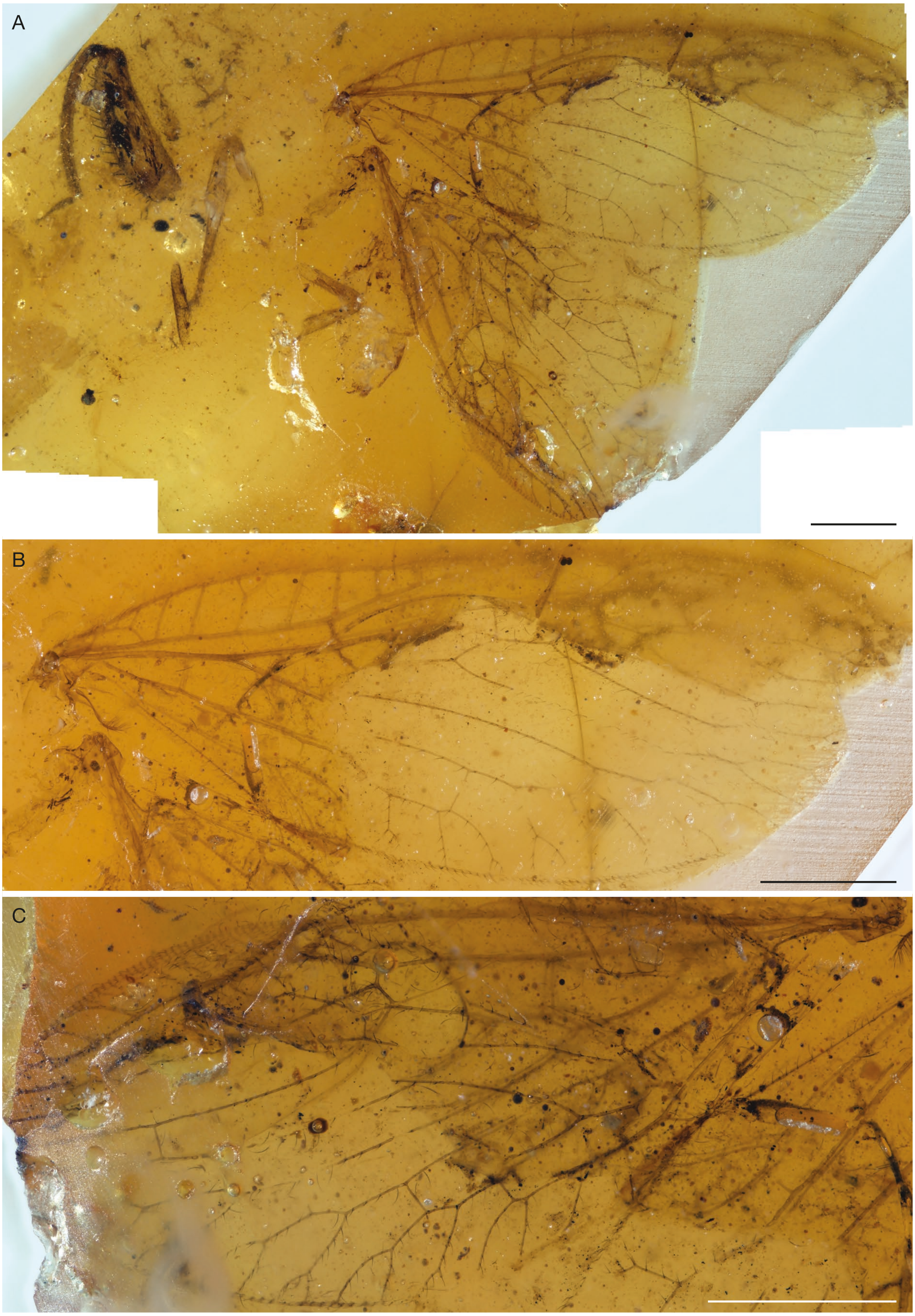

Fig. 2. — *Carentosymphrasites zhengi* n. gen., n. sp., holotype IGR.ARC-399: **A**, entire specimen; **B**, detailed view of fore wing; **C**, detailed view of hind wing. Scale bars: 1 mm. Photos: Corentin Jouault (OUMNH).

cua-cup crossvein present; CuP bifurcate distad; A1 simple, other anal veins poorly preserved.

Hind wing shape similar to fore wing, but markedly smaller; immaculate (if maculations are present they are indistinguishable from the amber color); trichosors present around entire wing margin; costal space markedly short and strongly narrowed, with at least three simple crossveins preserved proximally; pterostigma large, starting after ScP and RA meeting point and running up to level of RP4 fork; subcostal space broadened distad; radial space markedly wider than that in fore wing; two ra-rp crossvein present, first one between RP1 and RP2, second one connecting RP4, both slightly inclined; RP with four main branches, most of which are bifurcate but lack small marginal forks; 1r shorted than 2r; 3r not closed apically; one incomplete gradate series of crossveins present; rp-ma sigmoid; MA forked, with four branches distad; MP forked, with four branches distad; im cell base slightly anteriad first RP fork, apex at level of 2r apex; CuA pectinately branched into four branches; CuP and anal veins not preserved.

Abdomen not preserved.

DISCUSSION

The new fossil is readily assignable to the raptorial Mantispoidea (i.e. Rhachiberothidae, Dipteromantispidae, and Mantispidae) based on its distinct raptorial fore legs (Figs 2; 3). It can be excluded from Dipteromantispidae, as that family is characterized by reduced hind wings (only the fore wings are developed in Dipteromantispidae), whereas this specimen has fully developed fore- and hind wings (e.g., Makarkin *et al.* 2013; Li *et al.* 2020, 2023). Similarly, it cannot be placed in Rhachiberothidae (e.g., Jouault 2022; Li *et al.* 2023), which are currently divided into two valid subfamilies, Paraberothinae Nel *et al.*, 2005 (paraphyletic) and Rhachiberothinae Tjeder, 1959. Paraberothinae can be distinguished from Rhachiberothinae by the presence of at least two (and usually numerous) spines on the inner edge of the protibia, and the absence of the crossvein 2scp-r on the fore wing (Nakamine *et al.* 2020). Thus, if the specimen belongs to Rhachiberothidae, it would likely be classified under Rhachiberothinae. However, the morphology and wing venation of the new specimen exclude this possibility. According to the recently revised diagnosis of Rhachiberothinae by Li *et al.* (2023), the new specimen differs in key features: its profemur stout (vs weakly incrassate in Rhachiberothinae), its protarsus 4-segmented (vs 5-segmented, although sexually dimorphic), its fore wing with more than one trichosors between each adjacent veinlets (vs only one), at least three ra-rp crossveins (vs one or two), M fused with R for a long distance distad 1m-cu (vs separated from R proximad 1m-cu), and the hind wing with a sigmoid 1r-m crossvein (vs upright). Therefore, the new specimen cannot be placed in either Paraberothinae or Rhachiberothinae.

The new specimen possesses most of the diagnostic character states proposed by Li *et al.* (2023) to delineate the mantispid subfamily Symphrasinae. It can be easily distinguished from Doratomantispinae by the configuration of its profemoral spines, which are extremely long and often bifurcated in doratomantispine species (e.g., Lu *et al.* 2020; Jouault *et al.* 2022; Li *et al.* 2020, 2022). Additionally, the new specimen differs from Mesomantispinae by the ScP and RA fused distally (vs not fused in Mesomantispinae) and by fewer branches on the CuA of the fore wing (vs profusely and pectinately branched) (Jepson *et al.* 2018; Lu *et al.* 2020). Affinities with Mantispinae and Calomantispinae are excluded due to the specimen's broad wings, with numerous RP veins, the ScP not meeting C, and its overall pattern of the wing venation (e.g., Snyman *et al.* 2018; Reynoso-Velasco & Contreras-Ramos 2019). The diagnosis of Drepanicinae was recently revised (Lu *et al.* 2020), several diagnostic features for that subfamily are absent in the new specimen: fore femur with one row of integumentary processes present (vs with at least two rows of integumentary processes in the new specimen); trichosors usually absent or occasionally present and restricted to wing apex (vs trichosors present along the entire wing margin); fore wing at most with a suggestion of recurrent humeral veinlet (vs fore wing with a humeral veinlet). Therefore, the specimen cannot be assigned to Drepanicinae. Its classification within Symphrasinae is further supported by the configuration of its tarsomere I, which is spine-like, its tarsomere II arising midway, and the absence of a basal integumentary process (i.e., a prominent basal spine) (Lu *et al.* 2020; Ardila-Camacho *et al.* 2024).

Currently, the genera *Sinomesomantispa*, *Parasymphrasites*, *Archaeosymphrasis*, *Proplega*, *Parvosymphrasites*, *Symphrasites*, and *Habrosymphrasis* are considered as part of the stem groups of Symphrasinae (Wedmann & Makarkin 2007; Lu *et al.* 2020; Shi *et al.* 2020; Li *et al.* 2023). In a recent cladistic analysis, the genus *Clavifemora* Jepson, Heads, Makarkin & Ren, 2013, was found to be sister group to the rest of Symphrasinae (Li *et al.* 2024). However, it is currently classified within the subfamily Mesomantispinae (Jepson *et al.* 2013). Only the genus *Haplosymphrasites* is classified within the crown group of Symphrasinae, due to the presence of two to four trichosors between longitudinal veins along the distal wing margin (Lu *et al.* 2020). This character, which is also found in the new specimen, supports its placement within the crown group of Symphrasinae (Fig. 3E). Thus, the crown group of Symphrasinae now includes *Haplosymphrasites*, the new genus described herein, and the extant genera *Anchieta*, *Plega*, and *Trichoscelia* (Ardila-Camacho *et al.* 2024).

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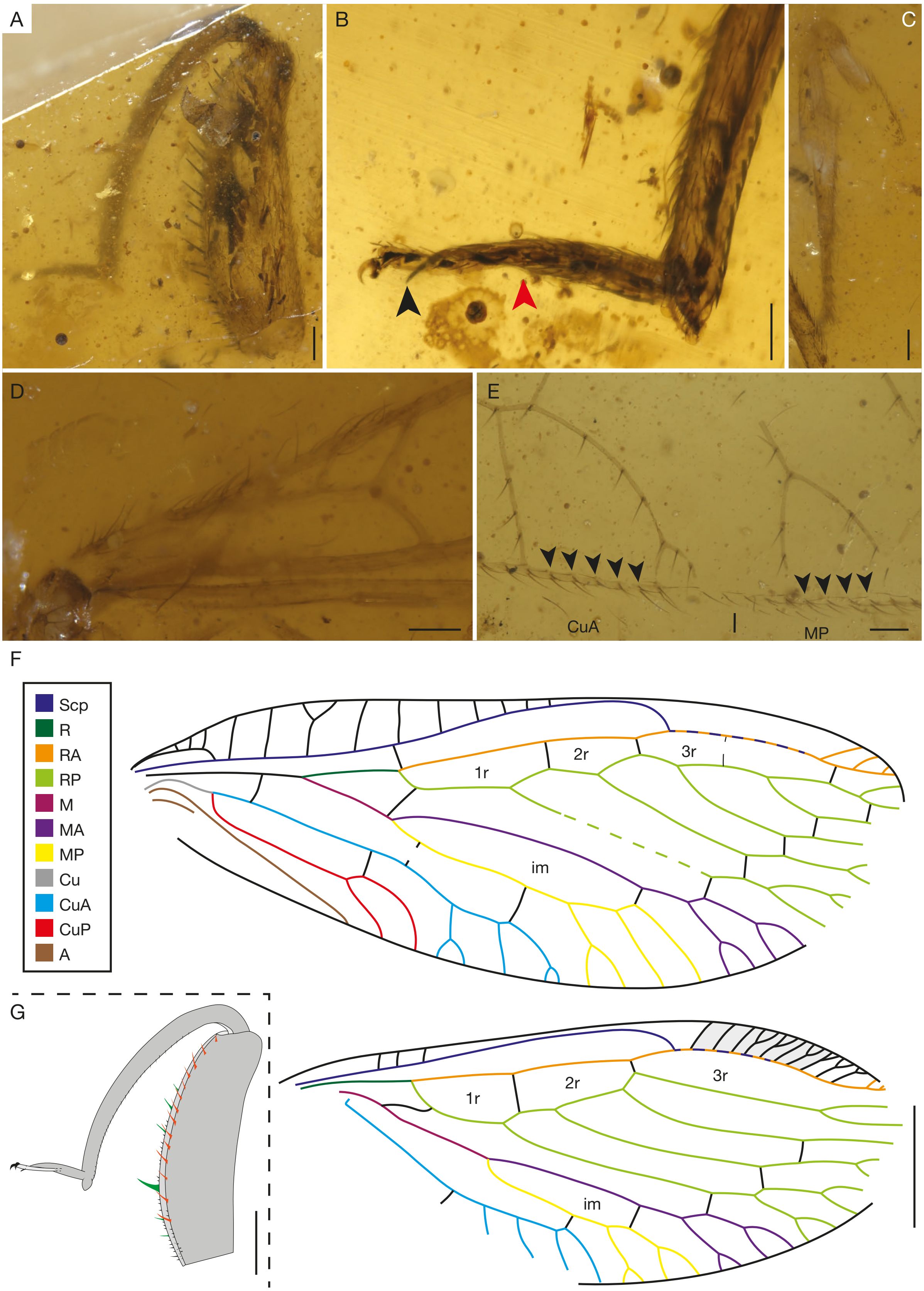

Fig. 3. — Detailed view and interpretative drawing of *Carentosymphrasites zhengi* n. gen., n. sp., holotype IGR.ARC-399: **A**, fore leg; **B**, tarsus (**black arrow** pointing at fore tarsal Stitz organ; **red arrow** pointing at tarsomere II insertion); **C**, midleg; **D**, fore wing humeral veinlet; **E**, apex of CuA anterior branch (**black arrows** pointing at trichosors); **F**, wing venation with names of cell labeled and veins colored; **G**, preserved part of fore leg (**orange**, anteroventral processes row; **green**, posteroventral processes row). Scale bars: A, C, 0.2 mm; B, D, E, 0.1 mm; F, 1 mm; G, 0.5 mm. Photos and drawings: Corentin Jouault (OUMNH).

Competing interests

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: CJ and VP; Investigation: CJ and XL; Resources: VP; Writing – original draft preparation: CJ; writing – review and editing: CJ, XL, VP; visualization: CJ; supervision: VP; project administration: CJ and VP; funding acquisition: VP. All authors have read and agreed to the published version of the manuscript.

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