Palaeoentomology 006 (6): 651–664
https://www.mapress.com/j/pe/

Article

ISSN 2624-2826 (print edition)
PALAEOENTOMOLOGY
ISSN 2624-2834 (online edition)

https://doi.org/10.11646/palaeoentomology.6.6.7
http://zoobank.org/urn:lsid:zoobank.org:pub:30BF283E-834F-47DE-A0AD-B1CB9E1EFF60

First green lacewing species of the tribe Chrysopini (Insecta: Neuroptera: Chrysopidae: Chrysopinae) from the Eocene Baltic amber and Miocene Mexican amber

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Abstract

The family Chrysopidae (green lacewings) is a highly diverse group of Neuroptera, with rich fossil records. The Cenozoic fossils of green lacewings currently comprise 21 genera and 42 species. Here we describe two new green lacewing species of the tribe Chrysopini, tentatively placed in the genus *Chrysopa* Leach, 1815, namely *Chrysopa*? *extensa* **sp. nov.** and *Chrysopa*? *prominenta* **sp. nov.** from Eocene Baltic amber and Miocene Mexican amber, respectively. These species represent the second chrysopid occurrence and the first record of the tribe Chrysopini from Baltic amber, and the first occurrence of Chrysopidae from Mexican amber, respectively. Both new species are assigned to Chrysopini based on the following characters: the intramedian cell eutriangular without crossvein, and the basal-most RP branch origins distal to the intramedian cell in the forewing.

Keywords: Chrysopinae, Chrysopini, *Chrysopa*, Baltic amber, Mexican amber

Introduction

Chrysopidae constitute a species-rich family of Neuroptera, which currently comprises at least 1,416 species assigned to 82 genera (Oswald, 2023). The family is divided into three extant subfamilies, *i.e.*, Apochrysinae, Chrysopinae, Nothochrysinae, and one extinct subfamily Limaiinae (Breitkreuz, 2018). The fossil record of Chrysopidae is rich, with about 79 species in 30 genera in the subfamilies Limaiinae, Nothochrysinae, and Chrysopinae (Table 1). However, all Mesozoic green lacewing fossils known to date probably belong to Limaiinae, and most Cenozoic fossils belong to Nothochrysinae (Cockerell, 1909, 1914; Carpenter, 1935; Statz, 1936; Adams, 1967; Schlüter, 1982; Nel & Séméria, 1986; Willmann & Brooks, 1991; Peñalver *et al*., 1995; Makarkin & Archibald, 2013; Makarkin, 2014; Archibald & Makarkin, 2017; Ngô-Muller *et al*., 2019; Huang *et al*., 2021; Makarkin *et al*., 2022). So far, only nine species in four genera belong to Chrysopinae, *i.e.*, *Paleochrysopa monteilsensis* Séméria & Nel, 1990 from the late Eocene of France; *Pseudosencera baltica* Makarkin *et al*., 2018 from the late Eocene Baltic amber; *Chrysopa sarmatica* Handschin, 1937 from the late Miocene of Romania; *Chrysopa martynovae* Makarkin, 1991, *Chrysopa miocenea* Makarkin, 1991 and *Chrysopa stavropolitana* Makarkin, 1991 from the middle Miocene of Russia; *Chrysopa glaesaria* Engel & Grimaldi, 2007, *Chrysopa vetula* Engel & Grimaldi, 2007 and *Leucochrysa prisca* Engel & Grimaldi, 2007 from the early-middle Miocene Dominican amber (Handschin, 1937; Séméria & Nel, 1990; Makarkin, 1991; Engel & Grimaldi, 2007; Makarkin *et al*., 2018). *Chrysopa*? *solenhofensis* Weyenbergh, 1869 from the Late Jurassic of Germany probably does not belong to Chrysopidae (see Weyenbergh, 1869: figs 11, 12).

Compared with the relatively rich records from the compression fossils, the adults of Chrysopidae are rarely found in amber. Hitherto, only two species have been described from the mid-Cretaceous Burmese amber, *i.e.*, *Parabaisochrysa xingkei* Lu *et al*., 2018 and *Mesypochrysa coadnata* Chen *et al*., 2022. Among the

Submitted: 30 Oct. 2023; accepted by D.-Y. Huang: 5 Dec. 2023; published: 18 Dec. 2023

TABLE 1. Fossil record of the family Chrysopidae.

Subfamily/Tribe/Genus	Species	Distribution	Age	Locality/Formation	Reference
Limaiinae Martins-Neto and Vulcano, 1989					
Aberrantochrysa Khramov, 2018	*A. buryatica* Khramov, 2017	Russia	Early Cretaceous	Khasurty	Khramov, 2018
	A. pulchella Khramov, 2017	Russia	Early Cretaceous	Khasurty	Khramov, 2018
Araripechrysa Martins-Neto & Vulcano, 1989	*A. magnifica* Martins-Neto & Vulcano, 1989	Brazil	Aptian	Santana do Cariri/Crato Formation	Martins-Neto & Vulcano, 1989
Baisochrysa Makarkin, 1997	*B. multinervis* Makarkin, 1997	Russian	Valanginian/ Barremian	Baissa/Zaza Formation	Makarkin, 1997
	B. pumila Khramov *et al*., 2016	Kazakhstan	Oxfordian/ Kimmeridgian	Karatau/Karabastau Formation	Khramov *et al*., 2016
Cretachrysa Makarkin, 1994	*C. martynovi* Makarkin, 1994	Russia	Cenomanian	Obeshchayushchiy	Makarkin, 1994
Drakochrysa Yang & Hong, 1990	*D. sinica* Yang & Hong, 1990	China	Barremian	Tuanwang Village/ Laiyang Formation	Yang & Hong, 1990
Limaia Martins-Neto & Vulcano, 1988	*L. adicotomica* Martins-Neto, 1997	Brazil	Aptian	Nova Olinda and Santana do Cariri/Crato Formation	Martins-Neto, 1997
	L. conspicua Martins-Neto & Vulcano, 1989	Brazil	Aptian	Santana do Cariri/Crato Formation	Martins-Neto & Vulcano, 1989
Mesypochrysa Martynov, 1927	*M. angustialata* Makarkin, 1997	Russia	Barremian	Baissa/Zaza Formation	Makarkin, 1997
	M. binervis Zhang *et al*., 2020	China	Barremian	Chaomidian Village/ Yixian Formation	Zhang *et al*., 2020
	M. cannabina Khramov, 2018	Russia	Early Cretaceous	Khasurty	Khramov, 2018
	M. chrysopa Makarkin, 1997	Russia	Barremian	Baissa/Zaza Formation	Makarkin, 1997
	M. chrysopoides Ponomarenko, 1992	Mongolia	Barremian/ Aptian	Bon Tsagaan/Dzun-Bain Formation	Ponomarenko, 1992
	M. coadnata Chen *et al*., 2022	Myanmar	Cenomanian	Hukawng/Burmese amber	Chen *et al*., 2022
	M. confusa Martins-Neto & Vulcano, 1989	Brazil	Aptian	Santana do Cariri/Crato Formation	Martins-Neto & Vulcano, 1989
	M. criptovenata Martins-Neto & Vulcano, 1989	Brazil	Aptian	Santana do Cariri/Crato Formation	Martins-Neto & Vulcano, 1989
	M. curvimedia Makarkin, 1997	Russia	Barremian	Baissa/Zaza Formation	Makarkin, 1997
	M. falcata Makarkin, 1997	Russia	Barremian	Baissa/Zaza Formation	Makarkin, 1997
	M. intermedia Panfilov, 1980	Kazakhstan	Oxfordian/ Kimmeridgian	Karatau/Karabastau Formation	Khramov *et al*., 2016
	M. latipennis Martynov, 1927	Kazakhstan	Oxfordian/ Kimmeridgian	Karatau/Karabastau Formation	Martynov, 1927
	M. magna Makarkin, 1997	Russia	Barremian	Baissa/Zaza Formation	Makarkin, 1997
	M. minima Makarkin, 1997	Russia	Barremian	Baissa/Zaza Formation	Makarkin, 1997
	M. miniscula Ren & Guo, 1996	China	Barremian	Chaomidian Village/ Yixian Formation	Ren & Guo, 1996
	M. minuta Jepson *et al*., 2012	United Kingdom	Berriasian	Durlston Bay/Durlston Formation	Jepson *et al*., 2012
	M. naranica Khramov, 2018	Russia	Early Cretaceous	Khasurty	Khramov, 2018
	M. nielseni Makarkin & Perkovsky, 2023	Denmark	Ypresian	Fur Formation	Makarkin & Perkovsky, 2023
	M. polyclada Ren & Guo, 1996	Kazakhstan	Oxfordian/ Kimmeridgian	Karatau/Karabastau Formation	Ren & Guo, 1996
	M. polyneura Ren & Guo, 1996	China	Barremian	Chaomidian Village/ Yixian Formation	Ren & Guo, 1996
	M. pusilla Zhang *et al*., 2020	China	Barremian	Huangbanjigou/Yixian Formation	Zhang *et al*., 2020
	M. reducta Panfilov, 1980	Kazakhstan	Oxfordian/ Kimmeridgian	Karatau/Karabastau Formation	Panfilov, 1980

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TABLE 1. (Continued)

Subfamily/Tribe/Genus	Species	Distribution	Age	Locality/Formation	Reference
	M. sinica Khramov *et al*., 2016	China	Bathonian/ Oxfordian	Daohugou/Tiaojishan Formation	Khramov *et al*., 2016
	M. skulda Martins-Neto, 2002	Brazil	Aptian	Nova Olinda/Crato Formation	Martins-Neto, 2002
Parabaisochrysa Lu *et al*., 2018	*P. xingkei* Lu *et al*., 2018	Myanmar	Cenomanian	Hukawng/Burmese amber	Lu *et al*., 2018
Protochrysa Willmann & Brooks, 1991	*P. aphrodite* Willmann & Brooks, 1991	Denmark	Ypresian	Fur/Fur Formation	Willmann & Brooks, 1991
	P. brevinervis Zhang *et al*., 2020	China	Barremian	Huangbanjigou/Yixian Formation	Zhang *et al*., 2020
	P. fuscobasalis Makarkin & Archibald, 2013	Canada	Ypresian	McAbee/Kamloops Group	Makarkin & Archibald, 2013
Nothochrysinae Navas, 1910					
Adamsochrysa Makarkin & Archibald, 2013	*A. aspera* Makarkin & Archibald, 2013	Canada	Ypresian	McAbee/Kamloops Group	Makarkin & Archibald, 2013
	A. wilsoni Makarkin & Archibald, 2013	Canada	Ypresian	McAbee/Kamloops Group	Makarkin & Archibald, 2013
Archaeochrysa Adams, 1967	*A. cockerelli* Makarkin *et al*., 2022	USA	Priabonian	Florissant/Florissant Formation	Makarkin *et al*., 2022
	A. creedei Carpenter, 1935	USA	Oligocene	Creede/Creede Formation	Carpenter, 1935
	A. fracta Cockerell, 1914	USA	Priabonian	Florissant/Florissant Formation	Cockerell, 1914
	A. paranervis Adams, 1967	USA	Priabonian	Florissant/Florissant Formation	Adams, 1967
	A. profracta Makarkin & Archibald, 2013	Canada	Ypresian	McAbee/Kamloops Group	Makarkin & Archibald, 2013
	A. sanikwa Archibald & Makarkin, 2015	Canada	Ypresian	Driftwood Canyon/Ootsa Lake Group	Archibald & Makarkin, 2015
Asiachrysa Makarkin, 2014	*A. tadushiella* Makarkin, 2014	Russia	Ypresian/Lutetian	Uglovi Stream/Tadushi Formation	Makarkin, 2014
Cimbrochrysa Schlüter, 1982	*C. americana* Makarkin *et al*., 2022	USA	Priabonian	Florissant/Florissant Formation	Makarkin *et al*., 2022
	C. major Makarkin *et al*., 2022	USA	Priabonian	Florissant/Florissant	Makarkin *et al*., 2022
	C. moleriensis Schlüter, 1982	Denmark	Eocene	Gallerup/Fur Formation	Schlüter, 1982
Danochrysa Willmann, 1993	*D. madseni* Willmann, 1993	Denmark	Ypresian	Sundby/Fur Formation	Willmann, 1993
Dyspetochrysa Adams, 1967	*D. vetuscula* Scudder, 1890	USA	Priabonian	Florissant/Florissant Formation	Adams, 1967
Hypochrysa Gould, 1866	*H. hercyniensis* Schlüter, 1982	Germany	Piacenzian	Willerhausen clay pit	Schlüter, 1982
Lithochrysa Carpenter, 1935	*L. borealis* Archibald & Makarkin, 2017	Canada	Eocene	Driftwood Canyon	Archibald & Makarkin, 2017
	L. concinnula Cockerell, 1909	USA	Priabonian	Florissant/Florissant Formation	Cockerell, 1909
	L. ferruginea Cockerell, 1909	USA	Priabonian	Florissant/Florissant Formation	Cockerell, 1909
	L. meyeri Makarkin *et al*., 2022	USA	Priabonian	Florissant/Florissant Formation	Makarkin *et al*., 2022
	L. wickhami Cockerell, 1914	USA	Priabonian	Florissant/Florissant Formation	Cockerell, 1914
Minimochrysa Jepson & Makarkin, 2023	*M. latialata* Jepson & Makarkin, 2023	USA	Lutetian	Coal Creek Member/ Kishenehn Formation	Jepson & Makarkin, 2023
Nothochrysa MacLachlan, 1868	*N. oligocenica* Ngô-Muller *et al*., 2019	France	Chattian	Aix-en-Provence/Aix-en-Provence Formation	Ngô-Muller *et al*., 2019
	N. praeclara Statz, 1936	Germany	Aquitanian	Rott	Statz, 1936
	N. stampieni Nel & Séméria, 1986	France	Chattian	Aix-en-Provence/Aix-en-Provence Formation	Nel & Séméria, 1986

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TABLE 1. (Continued)

Subfamily/Tribe/Genus	Species	Distribution	Age	Locality/Formation	Reference
Okanaganochrysa Makarkin & Archibald, 2013	*O. coltsunae* Makarkin & Archibald, 2013	Canada	Ypresian	McAbee/Kamloops Group	Makarkin & Archibald, 2013
Palaeochrysa Scudder, 1890	*P. greenwalti* Jepson & Makarkin, 2023	USA	Lutetian	Coal Creek Member/ Kishenehn Formation	Jepson & Makarkin, 2023
	P. minor Jepson & Makarkin, 2023	USA	Lutetian	Coal Creek Member/ Kishenehn Formation	Jepson & Makarkin, 2023
	P. stricta Scudder, 1890	USA	Priabonian	Florissant/Florissant Formation	Makarkin *et al*., 2022
Pronothochrysa Peñalver *et al*., 1995	*P. vivesi* Peñalver *et al*., 1995	Spain	Burdigalian	La Rinconada	Peñalver *et al*., 1995
Pseudochrysopa Makarkin & Archibald, 2013	*P. harveyi* Makarkin & Archibald, 2013	Canada	Ypresian	Driftwood Canyon/Ootsa Lake Group	Makarkin & Archibald, 2013
Sinonothochrysa Huang *et al*., 2021	*S. zhangi* Huang *et al*., 2021	China	Paleocene	Sanshui/Buxin Formation	Huang *et al*., 2021
Stephenbrooksia Willmann, 1993	*S. multifurcata* Willmann, 1993	Denmark	Ypresian	Ejerslev/Fur Formation	Willmann, 1993
Tribochrysa Scudder, 1885	*T. firmata* Scudder, 1890	USA	Priabonian	Florissant/Florissant Formation	Makarkin *et al*., 2022
	T. inequalis Scudder, 1885	USA	Priabonian	Florissant/Florissant Formation	Makarkin *et al*., 2022
Chrysopinae Schneider, 1851					
Paleochrysopa Séméria & Nel, 1990	*P. monteilsensis* Séméria & Nel, 1990	France	Priabonian	Monteils	Séméria & Nel, 1990
Pseudosencera Makarkin *et al*., 2018	*P. baltica* Makarkin *et al*., 2018	Russia	Eocene	Baltic amber	Makarkin *et al*., 2018
Chrysopini Schneider, 1851					
Chrysopa Leach, 1815	*C. glaesaria* Engel & Grimaldi, 2007	Dominican Republic	Burdigalian/ Langhian	Dominican amber	Engel & Grimaldi, 2007
	C. martynovae Makarkin, 1991	Russia	Miocene	Vishnevaya Balka creek, outcrop 4, Stavropol	Makarkin, 1991
	C. miocenea Makarkin, 1991	Russia	Miocene	Vishnevaya Balka creek, outcrop 4, Stavropol	Makarkin, 1991
	C. sarmatica Handschin, 1937	Romania	Miocene	Magyar Sáros (=Delenii)	Handschin, 1937
	C. stavropolitana Makarkin, 1991	Russia	Miocene	Vishnevaya Balka creek, outcrop 3, Stavropol	Makarkin, 1991
	C. vetula Engel & Grimaldi, 2007	Dominican Republic	Burdigalian/ Langhian	Dominican amber	Engel & Grimaldi, 2007
Leucochrysini Adams, 1978					
Leucochrysa McLachlan, 1868	*L. prisca* Engel & Grimaldi, 2007	Dominican Republic	Burdigalian/ Langhian	Dominican amber	Engel & Grimaldi, 2007

Cenozoic green lacewing fossils, there has been only one species, *i.e*., *P. baltica*, recorded from the Eocene Baltic amber, while other amber green lacewings refer to those from the Miocene Dominican amber, *i.e*., *C. glaesaria*, *C. vetula*, and *L. prisca* (Engel & Grimaldi, 2007; Lu *et al*., 2018; Makarkin *et al*., 2018; Huang *et al*., 2021; Chen *et al*., 2022).

Here we describe two new species of Chrysopidae, *i.e*., *Chrysopa*? *extensa* **sp. nov.** and *Chrysopa*? *prominenta* **sp. nov.**, based on two specimens from the Eocene Baltic amber and Miocene Mexican amber, respectively. Notably, the former species represents the second chrysopid occurrence but the first record of the chrysopine tribe Chrysopini from the Eocene Baltic amber, while the latter species represents the first occurrence of Chrysopidae from the Miocene Mexican amber. The new fossils provide valuable new data for understanding the palaeodiversity and evolution of the Cenozoic green lacewings.

Material and methods

The Baltic amber sample in the present study is from the Samland area of Kaliningrad, Russia. All Baltic amber-bearing strata have been dated to be 48–23 million years old (late Eocene to late Oligocene), however, the age of inclusions is commonly assumed to be Priabonian (late Eocene; Sadowski *et al*., 2017). The Mexican amber sample in the present study is from the Simojovel region of Chiapas, Mexico (see Engel & Grimaldi, 2007), and has been dated to be 23–13 million years (early-middle Miocene) (Riquelme *et al*., 2014). The specimens are deposited in the Entomological Museum, China Agricultural University (CAU), Beijing, China.

Photographs and drawings were made by using a Zeiss SteREO Discovery V12 stereo microscope system. The figures were prepared with Adobe Photoshop CS6. The classification of Chrysopinae follows Breitkreuz (2018). Wing venation terminology generally follows Adams (1996) and Breitkreuz *et al*. (2017). Venational abbreviations: A, anal vein; *c1*, *c2*, first and second cubital cells; C, costa; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; *im*, intramedian cell; MA, media anterior; MP, media posterior; Psm, pseudomedia; Psc, pseudocubitus; RA, radius anterior; RP, radius posterior; Sc, subcosta.

Systematic palaeontology

Class Insecta Linnaeus, 1758
Order Neuroptera Linnaeus, 1758
Family Chrysopidae Schneider, 1851
Subfamily Chrysopinae Schneider, 1851
Tribe Chrysopini Schneider, 1851

Genus *Chrysopa* Leach, 1815

***Chrysopa*? *extensa* sp. nov.**
(Figs 1, 2, 5G)

Type material. Holotype: CAU-BLA-GY-23001: Four wings (distal parts of three wings are not preserved, only distal part of the right forewing is partially preserved), and incomplete head (only flagellum of antenna preserved) in an amber piece. It is polished in the form of a transparent elliptical cabochon, with length × width about 25.9 × 8.4 mm, and a height of about 7.4 mm.

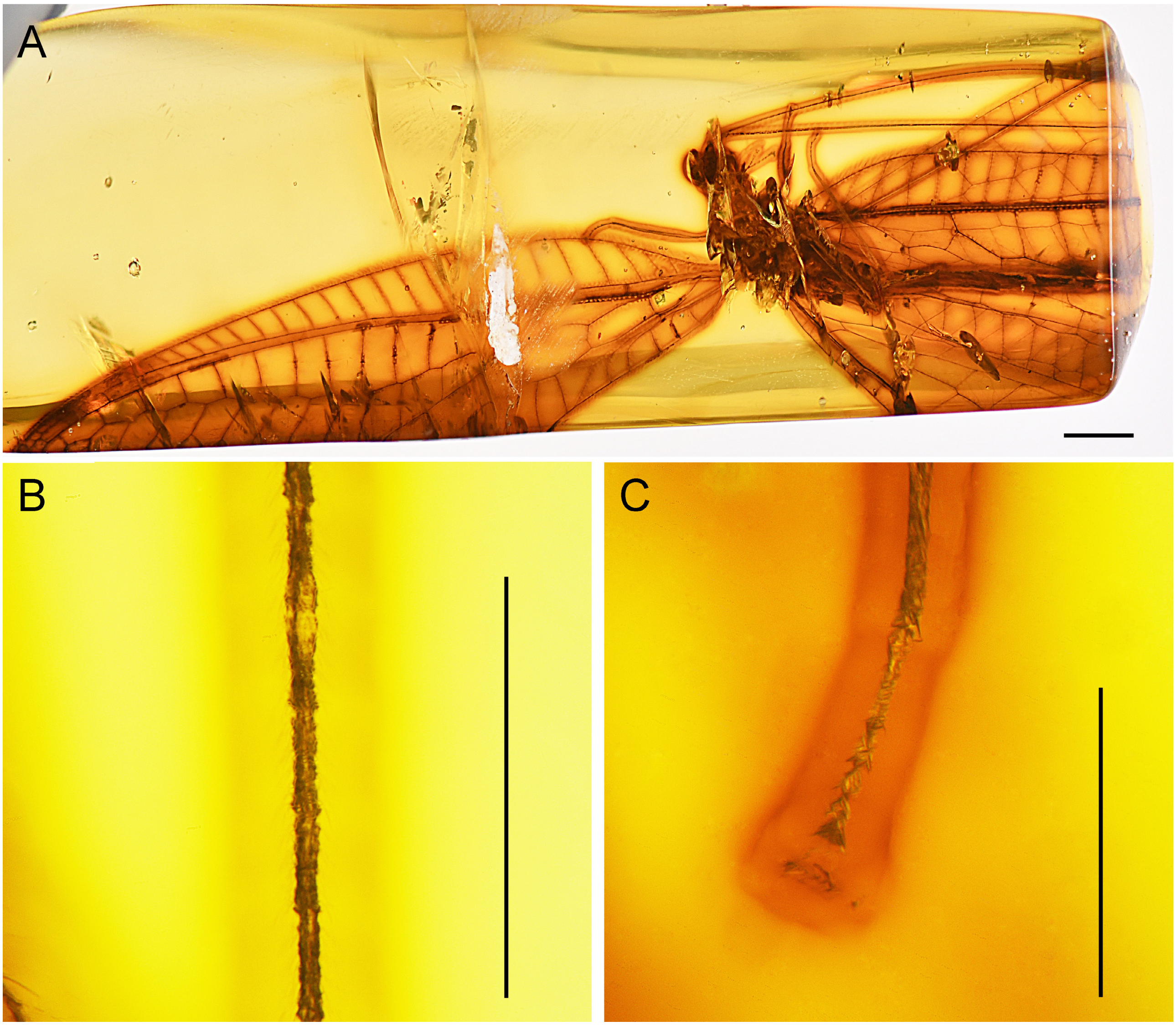

FIGURE 1. *Chrysopa*? *extensa* **sp. nov.**, holotype CAU-BLA-GY-23001. **A**, Habitus photo, dorsal view. **B**, Flagellomeres. **C**, Tarsus and pretarsus. Scale bars = 1.0 mm (**A**), 0.5 mm (**B**, **C**).

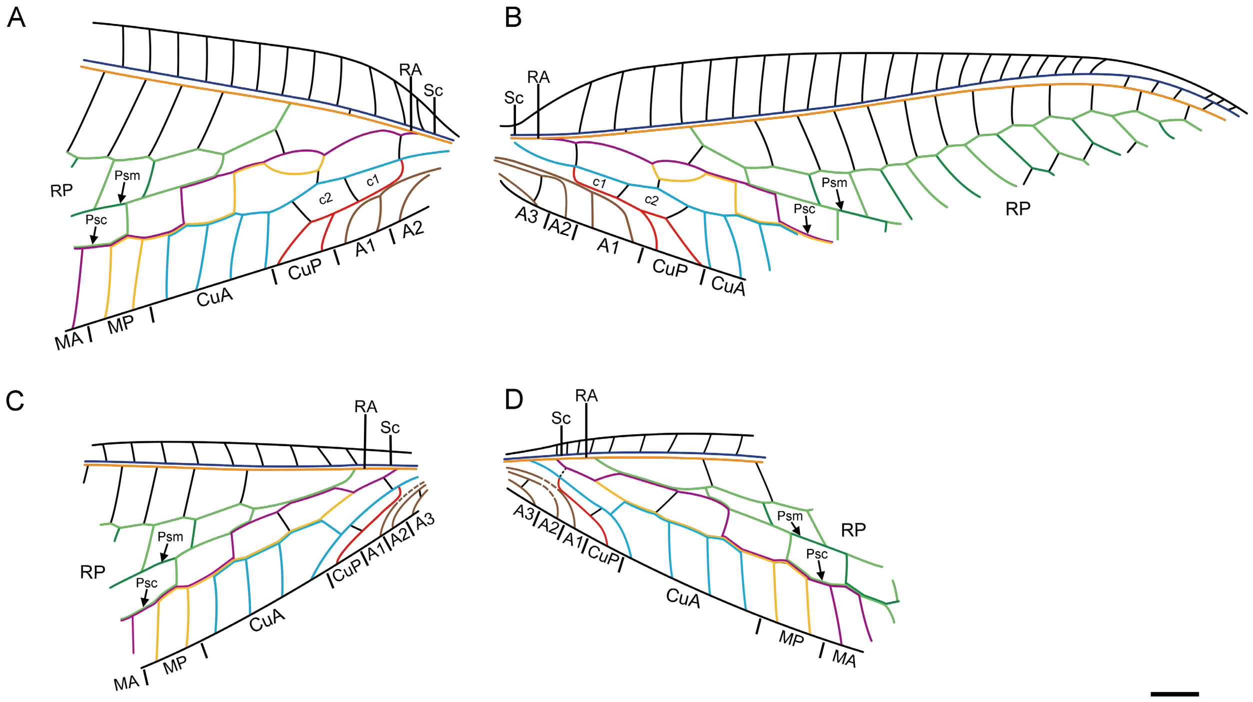

FIGURE 2. *Chrysopa*? *extensa* **sp. nov.**, holotype CAU-BLA-GY-23001. **A**, Drawing of left forewing. **B**, Drawing of right forewing. **C**, Drawing of left hind wing. **D**, Drawing of right hind wing. Scale bar = 1.0 mm.

Etymology. The specific epithet is derived from the Latin *extensus*, extended, referring to the inner gradate series distinctly extended anteriorly in the forewing of the new species.

Diagnosis. Forewing: 1sc-ra conspicuously distal to visible origin of M; inner gradate series distinctly extended anteriorly; RP with at least three branches enter Psm; 1r-m at about 2/3rd of *im*; *im* eutriangular; 1m-cu interstitial to separation of CuA and CuP; A1 distally bifurcated.

Type locality and horizon. Eocene Baltic amber, Kaliningrad, Samland area.

Description. Forewing 7.34 (left) and 15.49 (right) mm long and 5.96 (left) and 4.62 (right) mm wide as preserved; hind wing 7.13 (left) and 8.19 (right) mm long and 4.56 (left) and 4.29 (right) mm wide as preserved.

Head incompletely preserved. Flagellomeres narrow, setose, more than three times as long as wide (Fig. 1B).

Legs long and slender; tarsus (Fig. 1C) five-segmented, tarsomere 1 much longer than other tarsomeres, tarsomeres 2–5 almost equal in length; pretarsal claws simple.

Forewing (Figs 2A, B, 5G) costal space dilated proximally, but strongly narrowed distad, with 25 simple crossveins preserved; Sc and RA long; subcostal space narrow, but dilated distad, with at least four sc-ra crossveins; 1sc-ra present; RP strongly zigzagged, with 13 branches preserved, at least three of them entering Psm; inner gradate series of crossveins in radial space with four crossveins preserved; Psm nearly straight, Psc slightly zigzagged; 1rp-m long, located much distal to separation of MA and MP; both MA and MP distally bifurcated; *im* eutriangular, without crossvein incorporated, proximal to basal-most RP branch; MA fused with MP on Psm and Psc; MP fused with CuA on Psc; 1m-cu located at separation of CuA and CuP; CuA with four pectinate branches; CuP distally bifurcated; *c1* slightly shorter than or as long as *c2*; A1 long and distally bifurcated; A2 and A3 simple; a2–a3 present.

Hind wing (Figs 2C, D, 5G) slightly narrower than forewing; costal space narrow, and costal crossveins simple; 1ra-rp slightly distal to origin of basal-most RP branch; RP strongly zigzagged, with three proximal branches preserved entering Psm; Psm nearly straight, Psc slightly zigzagged Psc; both MA and MP distally bifurcated; MA and MP forked slightly distal to origin of RP; MA fused with MP on Psc; MA fused with first RP branch on Psm and Psc; MP fused with CuA on Psc; CuA with four pectinate branches; CuP simple; A1, A2 and A3 simple; a2–a3 present.

Remarks. The new species is the first record of the tribe Chrysopini from the Eocene Baltic amber. It can be distinguished from the Baltic amber species *P. baltica* by the eutriangular forewing *im* (the forewing *im* is quadrangular in *P. baltica*) (see Makarkin *et al*., 2018: figs 4, 6). The new species differs from the late Eocene species *P. monteilsensis* by the one forewing ra-rp crossvein proximad basal-most RP branch (two crossveins proximad basal-most RP branch in *P. monteilsensis*) (see Séméria & Nel, 1990: fig. 1). The new species can be distinguished from the other fossil species of Chrysopinae by the long forewing inner gradate series distinctly extended anteriorly (the forewing inner gradate series is usually short, smooth and parallel to outer gradate series in the other species) (Handschin, 1937; Séméria & Nel, 1990; Makarkin, 1991; Engel & Grimaldi, 2007; Makarkin *et al*., 2018).

***Chrysopa? prominenta* sp. nov.**
(Figs 3, 4, 5H)

Type material. Holotype: CAU-MA-GY-23001: A nearly complete specimen of *C. prominenta* in the amber piece (the left wings, the distal part of the right forewing, and some genital parts are not preserved). It is polished in the form of an elliptical cabochon, transparent, with length × width about 28.3 × 9.3 mm, a height of about 6.3 mm.

Etymology. The specific epithet is derived from the Latin *prominens*, prominent, referring to the apical projection in the genitalia of the new species.

Diagnosis. Forewing: 1sc-ra slightly distal to visible origin of M; 1r-m in distal part of *im*; *im* eutriangular; 1m-cu slightly distal to separation of CuA and CuP; A1 distally bifurcated. Hind wing: ma-mp absent. Genitalia: pair of long and narrow apical projections present posterodorsad.

Type locality and horizon. Miocene amber of Mexico, Chiapas, near Simojovel.

Description. Body preserved part 7.99 mm long; forewing 10.58 mm long and 4.03 mm wide; hind wing 10.91 mm long and 3.14 mm wide.

Head (Fig. 3C) with vertex distinctly domed and ovoid. Compound eyes large, semi-globular. Antenna long filiform, setose; scape stouter than pedicel and flagellum, about three times as long as wide; pedicel smaller than scape, subcylindrical; flagellomere (Fig. 3D) narrower than scape and pedicel, more than three times as long as wide. Mouthparts chewing-mandibulate; maxillary palpus five-segmented, terminal segment elongate, fusiform; labial palpus three-segmented, terminal segment elongate, fusiform.

Prothorax about 1.5 times as long as wide; meso- and metathorax robust. Legs long and slender; tarsus (Fig. 3E) five-segmented, tarsomere 1 much longer than other tarsomeres, tarsomeres 2–5 almost equal in length; pretarsus with four apical setae, including two long setae, and pair of short setae; pretarsal claws simple, slender and long, with sharp tip.

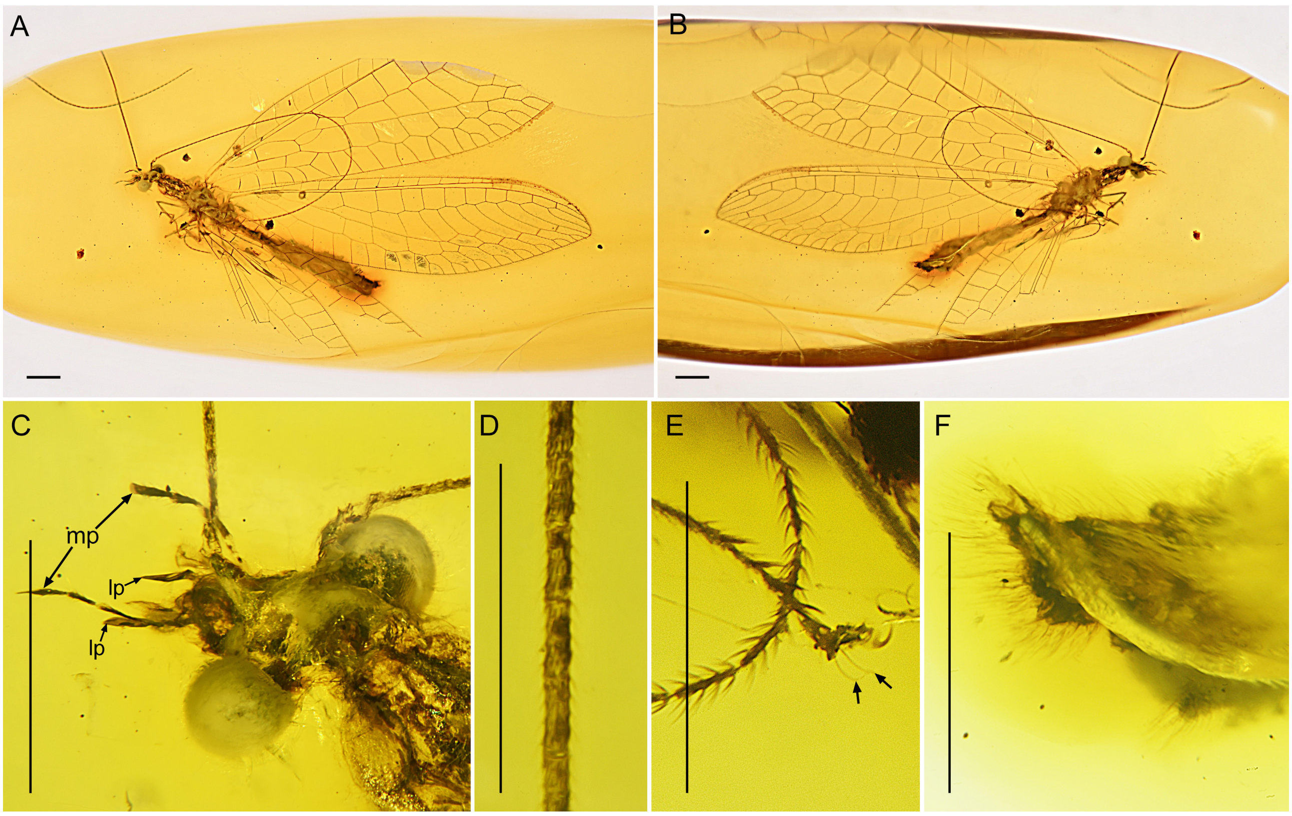

FIGURE 3. *Chrysopa*? *prominenta* **sp. nov.**, holotype CAU-MA-GY-23001. **A**, Habitus photo, dorsal view. **B**, Habitus photo, ventral view. **C**, Head, dorsal view. **D**, Flagellomeres. **E**, Tarsus and pretarsus. **F**, Abdominal terminalia, lateral view; lp, labial palps; mp, maxillary palps. Scale bars = 1.0 mm (**A**, **B**, **C**, **F**), 0.5 mm (**D**, **E**).

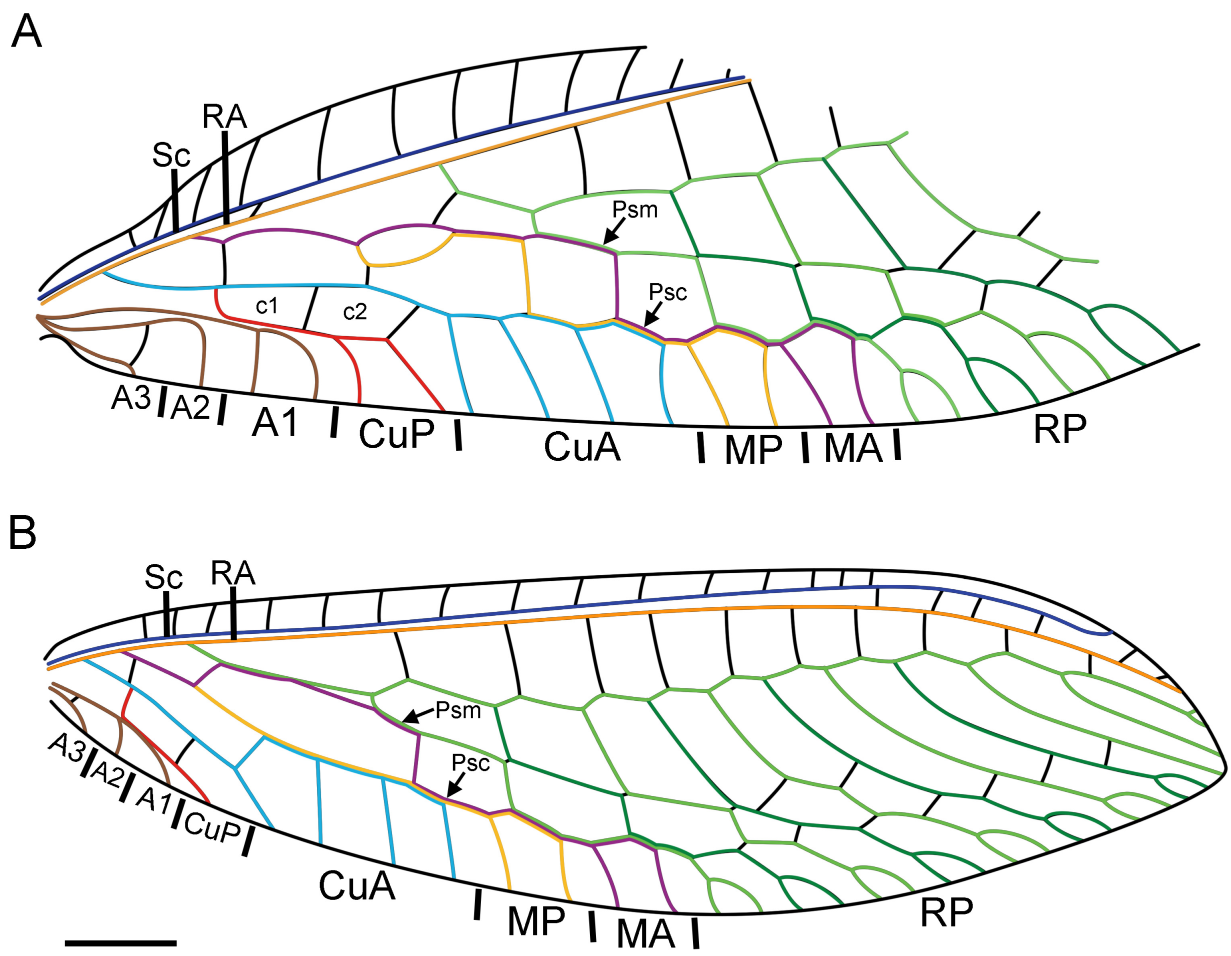

FIGURE 4. *Chrysopa*? *prominenta* **sp. nov.**, holotype CAU-MA-GY-23001. **A**, Drawing of right forewing. **B**, Drawing of right hind wing. Scale bar = 1.0 mm.

Forewing (Figs 4A, 5H) costal space dilated proximally, but narrowed distad, with 12 simple crossveins preserved; distal part of Sc and RA not preserved; subcostal space narrow; 1sc-ra present, slightly distal to visible origin of M; RP strongly zigzagged, with five branches preserved, four of them entering Psm, and distally bifurcated; two gradate series of crossveins present in radial space (incompletely preserved); basal crossvein of inner gradate series enters Psm; Psm continuous with outer gradates; Psm nearly straight, Psc slightly zigzagged; 1r-m long, located in distal part of *im*; both MA and MP distally bifurcated; *im* eutriangular, without crossvein incorporated, proximal to basal-most RP branch; MA fused with MP and first RP branch on Psm and Psc; MP fused with CuA on Psc; 1m-cu located slightly distal to separation of CuA and CuP; CuA with four pectinate branches; CuP distally bifurcated; *c1* slightly shorter than *c2*; A1 long, distally bifurcated; A2 and A3 simple; a2–a3 long.

Hind wing (Figs 4B, 5H) slightly narrower than forewing; costal space narrow, and costal crossveins simple; 1ra-rp slightly distal to separation of basal-most RP branch; RP strongly zigzagged, with 12 branches, most of them distally bifurcated, and three of them entering Psm; two gradate series of crossveins present in radial space, nearly parallel to each other; two crossveins in inner series anterior to Psm, and five crossveins in outer series anterior to Psc; Psm nearly straight, Psc slightly zigzagged; both MA and MP distally bifurcated; MA and MP forked slightly distal to origin of RP; MA fused with MP on Psc; MA fused with first RP branch on Psm and Psc; MP fused with CuA on Psc; CuA with four pectinate branches; CuP simple; A1 simple, coalescent with A2 for some distance; A2 and A3 simple; a2–a3 short.

Abdomen (Fig. 3F) subcylindrical, setose. Genitalia incompletely preserved, with a pair of sclerites (putatively part of ectoprocts), which are slightly prolonged into narrow apical projections posterodorsad.

Remarks. Among the fossil green lacewing species of *Chrysopa sensu lato*, the new species is distinguished from *C. martynovae* by the forewing 1sc-ra located

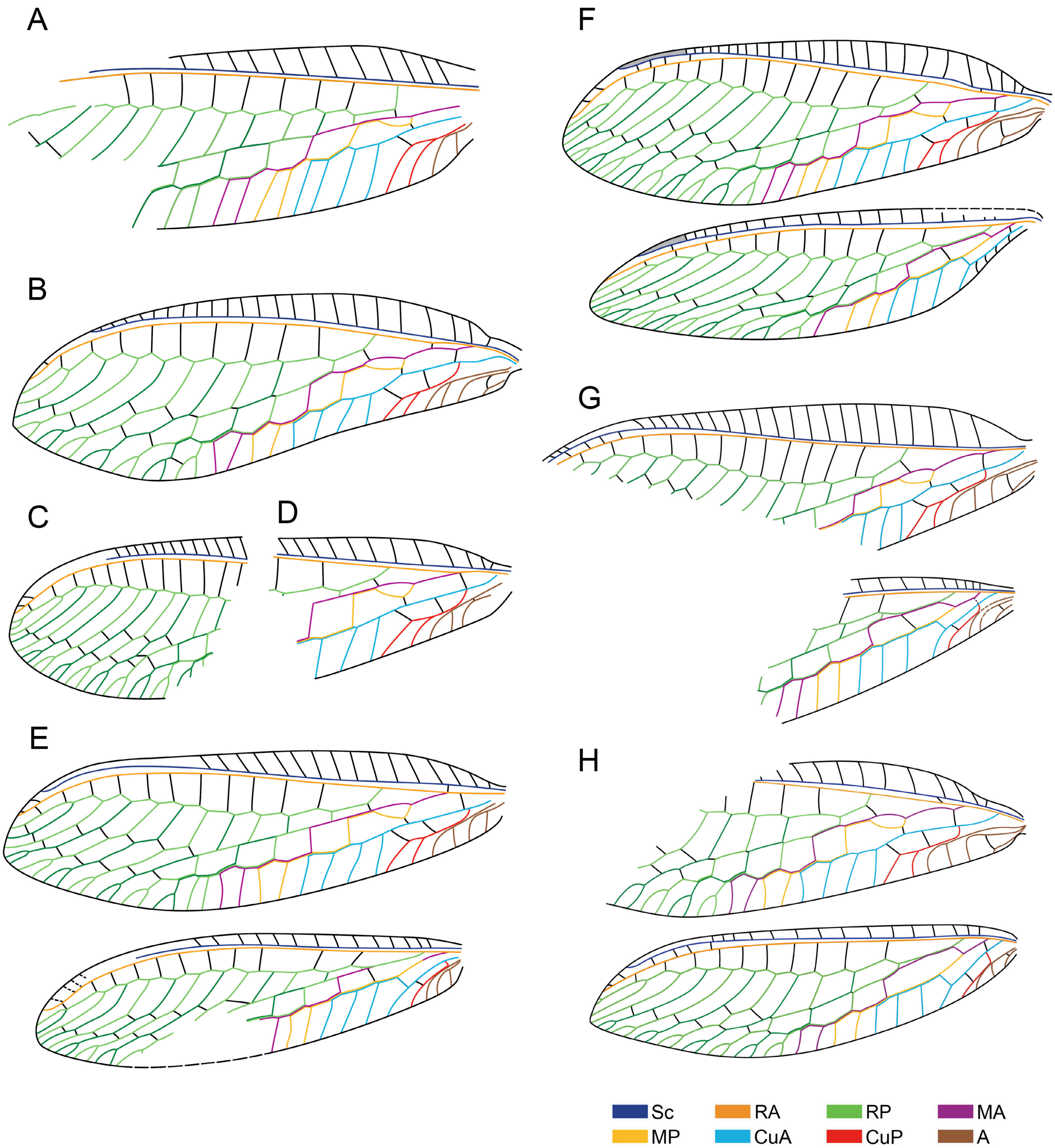

FIGURE 5. Comparison of the wing venations in the Cenozoic fossil species of *Chrysopa*. **A**, *Chrysopa sarmatica* (modified after Handschin, 1937: fig. 1). **B**, *Chrysopa vetula* (modified after Engel & Grimaldi, 2007: fig. 29). **C**, *Chrysopa miocenea* (modified after Makarkin, 1991: fig. 6); **D**, *Chrysopa stavropolitana* (modified after Makarkin, 1991: fig. 6). **E**, *Chrysopa martynovae* (modified after Makarkin, 1991: fig. 4, 6). **F**, *Chrysopa glaesaria* (modified after Engel & Grimaldi, 2007: figs 27). **G**, *Chrysopa*? *extensa* **sp. nov. H**, *Chrysopa*? *prominenta* **sp. nov.**

slightly distal to the visible origin of M (the forewing 1sc-ra is located at or proximal to the visible origin of M in *C. martynovae*) and the forewing 1r-m is located proximad the outer apex of *im* (the forewing 1r-m is located at or distad the outer apex of *im* in *C. martynovae*) (see Fig. 5E or Makarkin, 1991: figs 4, 6). The new species is distinguished from *C. sarmatica* by the forewing RP with three branches entering Psm (the forewing RP with at least five branches entering Psm in *C. sarmatica*) (see Fig. 5A or Handschin, 1937: fig. 1). The new species is distinguished from *C. glaesaria* by the forewing A1 distally bifurcate (the forewing A1 is simple in *C. glaesaria*) (see Fig. 5F or Engel & Grimaldi, 2007: fig. 27). The new species differs from *C. stavropolitana* and *C. vetula* by the forewing CuA and CuP diverged at a right angle (the forewing CuA and CuP are diverged at an acute angle in *C. stavropolitana* and *C. vetula*) (see Fig. 5D or Makarkin, 1991: fig. 6; Fig. 5B or Engel & Grimaldi, 2007: fig. 29). The new species differs from *C. miocenea* by the forewing RP with no branch entering Psm (the forewing RP with at least two branches entering Psm in *C. miocenea*) (see Fig. 5C or Makarkin, 1991: fig. 6). The new species can be separated from *C. extensa* **sp. nov.** by the hind wing ma-mp absent (the hind wing ma-mp present in *C. extensa* **sp. nov.**). In addition, the new species is distinguished from *P. monteilsensis* and *L. prisca* by the relatively narrow distance between forewing inner and outer gradate series (the distance between forewing inner and outer gradate series is relatively wide in the latter two species) (see Séméria & Nel, 1990: fig. 1; Engel & Grimaldi, 2007: fig. 33).

Discussion

The two new Tertiary green lacewing species are placed in Chrysopinae because they are clearly different from the other three chrysopid subfamilies. On one hand, they are distinguished from Apochrysinae by the presence of the basal 1sc-r crossvein, the presence of *im*, and the broadly separated Psm and Psc in the forewing, and from Nothochrysinae and Limaiinae by the well pronounced Psm, and the eutriangular *im* without crossvein in the forewing. On the other hand, they have the typical diagnostic characters of Chrysopinae, *i.e.*, the Psm continuous with the outer gradates (here visible only in *C. prominenta* **sp. nov.**), and the *im* eutriangular without crossvein in the forewing.

Within Chrysopinae, the two new species differ from the tribe Ankylopterygini by the forewing costal space relatively narrow basally, and the presence of tibial spurs. In typical Ankylopterygini, the forewing costal space is broad basally, and the tibial spurs are absent, but the *Nineta*-group and *Signochrysa* Brooks & Barnard, 1990 currently placed in this tribe show these two characters similar to Chrysopinae. However, the two new species differ from the subgenus *Chrysopidia* Navás, 1910 of the *Nineta*-group by the forewing 2m-cu located in the proximal part of *im* (the forewing 2m-cu is located in the middle part of *im* in some species of *Chrysopidia*, *i.e.*, *C. flavilineata* Yang & Wang, 1994, *C. jiriana* Hölzel, 1973 and *C. junbesiana* Hölzel, 1973), the forewing 1r-m located proximad the outer apex of *im* (the forewing 1r-m at or distad the apex of *im* in *C. orientalis* Hölzel, 1973), and by two gradate series of crossveins in the hind wing (in *C. prominenta*) (three hind wing gradate series of crossveins in *Chrysopidia*) (Hölzel, 1973; Ma, 2021). The two new species differ from the subgenus *Chrysotropia* Navás, 1911 of the *Nineta*-group by the forewing *c1* slightly shorter than or as long as *c2* (the forewing *c1* is distinctly shorter than *c2* in *Chrysotropia*), and the narrow distance between inner and outer gradate series in the hind wing (detected in *C. prominenta*) (the distance between inner and outer gradate series is relatively wide in the hind wing of *Chrysotropia*) (Hölzel, 1971, 1973; Ma, 2021). The two new species differ from the subgenus *Nineta* Navás, 1912 of *Nineta*-group by the forewing inner gradate series distinctly extended anteriorly (detected in *C. extensa*) (the forewing inner gradate series is smooth and parallel to outer gradate series in *Nineta*), and the distance between inner and outer hind wing gradate series narrow (detected in *C. prominenta*) (the distance between hind wing inner and outer gradate series is relatively wide in *Nineta*) (Aspöck *et al*., 1980; Garland, 1981; Canbulat & Kiyak, 2003; Canard *et al*., 2014; Ma, 2021). The two new species differ from the subgenus *Tumeochrysa* Needham, 1909 of the *Nineta*-group by the forewing distal cubital cell (between the basal-most CuA branch and CuP) open, and the hind wing with two gradate series of crossveins (detected in *C. prominenta*) (the forewing distal cubital cell is closed, and three or more hind wing gradate series of crossveins are present in *Tumeochrysa*) (Navás, 1910; Hölzel, 1973; Hassan & Liu, 2022). The two new species differ from *Signochrysa* by the forewing inner gradate series distinctly extended anteriorly (detected in *C. extensa*) (the forewing inner gradate series is smooth and parallel to the outer gradate series in *Signochrysa*), and the fore- and hind wing basal crossvein of inner gradate series entering Psm (detected in *C. prominenta*) (the fore- and hind wing basal crossvein of inner gradate series do not enter Psm in *Signochrysa*).

The two new species differ from the species of the tribe Belonopterygini by the forewing *c1* slightly shorter than or as long as *c2*. In typical Belonopterygini, the forewing *c1* is longer than *c2*, but this character in some genera of this tribe, *i.e.*, *Belonopteryx* Gerstaecker, 1863 and *Vieira* Navás, 1913, is similar to that in the two new species. However, the two new species differ from *Belonopteryx*, at least because of their forewings without conspicuous narrowing of the costal space at about mid-length (*vs*. conspicuously narrowing), with a more rounded shape (*vs*. unmistakably lanceolate in *Belonopteryx*), with the cell *im* eutriangular (*vs*. trapezoidal), and flagellomeres distinctly longer than wide (the flagellomeres are wider than or as wide as long in *Belonopteryx*) (Brooks & Barnard, 1990: fig. 133). The two new species differ from *Vieira* by the forewing 1r-m connecting RP and M, and the absence of wing maculation (the forewing 1r-m connects RA and M, and the wing maculation is well developed in *Vieira*) (Tauber, 2006; Sousa & Tauber, 2017; Tauber, 2021).

The two new species differ from the species of the tribe Leucochrysini by their forewing with *im* triangular without crossvein. In Leucochrysini, *im* is quadrangular with a crossvein in the most genera, but some genera, *i.e.*, *Berchmansus* Navás, 1913 and *Nuvol* Navás, 1916, and some species of *Leucochrysa* McLachlan, 1868, *e.g.*, *Leucochrysa amazonica* Navás, 1913, *Leucochrysa affinis* Freitas & Penny, 2001 and *Leucochrysa floridana* Banks, 1897, this character is similar to that in the two new species. The two new species differ from *Berchmansus* by the forewing 1r-m connecting RP and M (the forewing 1r-m connecting RA and M in *Berchmansus*) (Tauber, 2007). The two new species differ from *Nuvol* by the forewing *c1* shorter than or as long as *c2* (the forewing *c1* is slightly longer than *c2* in *Nuvol* Navás, 1916) (Brooks & Barnard, 1990). In the two new species, the forewing 2m-cu is located in the proximal part of *im*, but in some aforementioned species of *Leucochrysa*, the forewing 2m-cu is located in the middle part of *im* (Freitas & Penny, 2001; Penny, 2002; Tauber, 2004).

The two new species differ from the species of the tribe Nothancylini by the forewing costal space relatively narrow basally, and the forewing 1sc-r present (in Nothancylini, the forewing costal space is broad basally, and the forewing 1sc-r is absent) (Breitkreuz, 2018). According to the aforementioned comparative analysis between the two new species and four tribes, these new species are very likely to be assigned to the tribe Chrysopini. In Chrysopini, the two new species are tentatively assigned to the genus *Chrysopa s.l.* because of their two gradate series of crossveins, and the basal crossvein of the inner gradate series entering Psm (in *C. prominenta*) in the fore- and hind wings (Brooks & Barnard, 1990; Breitkreuz, 2018).

The new green lacewing species provide valuable evidence documenting the evolutionary history of Chrysopidae. Notably, the finding of Chrysopini in the Eocene having typical venation for the tribe supports the previously estimated divergence time of this tribe during the early Paleogene or even earlier based on molecular data (Garzón-Orduña *et al*., 2019; Winterton *et al*., 2019). The taxonomy of most Chrysopinae, even the generic identification (especially within *Chrysopa s.l.*), largely relies on the genital characters, which, however, can be hardly used for our new fossil species. As such, the generic affiliation of the new green lacewings is tentative. However, although there are few specific diagnostic characters in these species, the naming of them as new species is justified because they are less likely to be conspecific with any extant species due to their old age. The Cenozoic green lacewings from amber inclusions are very rare, and any finding in either fine or poor preservation is worth describing.

Acknowledgements

We thank the anonymous reviewers for their comments to improve the manuscript. This research was supported by the National Natural Science Foundation of China (No. 31972871). The research of VNM was carried out within the state assignment of Ministry of Science and Higher Education of the Russian Federation (theme No. 121031000151-3).

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