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Three new stoneflies (Insecta: Plecoptera) from Eocene Baltic amber

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Abstract. Three new stonefly species are described and illustrated from Eocene Baltic amber found in Lithuania: †*Palaeopsole spinosa* sp. nov. (family Leuctridae Klapálek, 1905), †*Podmosta biloba* sp. nov. (family Nemouridae Newman, 1853), and †*Isoperla lituana* sp. nov. (family Perlodidae Klapálek, 1909). The generic diagnosis of †*Palaeopsole* Caruso & Wichard, 2011 is also emended. These new fossils enhance the understanding of the extinct Plecoptera fauna in Baltic amber.

Keywords. Leuctridae, Nemouridae, Perlodidae, new species.

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Introduction

Taxonomic studies of the Plecoptera Burmeister, 1839 (stoneflies) preserved in Eocene Baltic amber began early in the history of paleoentomology but have often been limited by incomplete descriptions and the loss of holotype specimens. Pictet & Hagen (1856) first described 13 species from six extant genera, including *Taeniopteryx* Pictet, 1841 (Taeniopterygidae Klapálek, 1905), *Leuctra* Stephens, 1836 (Leuctridae Klapálek, 1905), *Nemoura* Latreille, 1796 (Nemouridae Newman, 1853), *Perla* Geoffroy, 1762 (Perlidae Burmeister, 1839), *Isoperla* Banks, 1906 (Perlodidae Klapálek, 1909), and *Perlodes* Banks, 1903 (Perlodidae). However, the holotype specimens of 10 of these species have been lost, and these species are considered incertae sedis (Caruso & Wichard 2010; Jouault *et al.* 2021). Similarly, Ricker (1936) described †*Megaleuctra neavei* Ricker, 1936, whose holotype is also missing (Caruso & Wichard 2010). Furthermore, the original descriptions of these early species were rudimentary, lacking critical details such as genitalia morphology, which is essential in modern taxonomic work.

Fossil Plecoptera from Baltic amber were reviewed by Caruso & Wichard (2010), who described three new species: †*Zealeuctra cornuta* Caruso & Wichard, 2010 (Leuctridae), †*Lednia zilli* Caruso & Wichard, 2010 (Nemouridae), and †*Podmosta attenuata* Caruso & Wichard, 2010 (Nemouridae). Subsequently, Caruso & Wichard (2011) introduced †*Palaeopsole weiterschani* Caruso & Wichard, 2011 (Leuctridae) and discussed the paleogeographic distribution of Leuctridae and Nemouridae.

More recently, Chen (2018a, 2018b, 2018c, 2018d) expanded the fossil record by describing a female of *Podmosta* Ricker, 1952 with a distinctive "rabbit-shaped" sclerite on sternum 8, and by establishing new leuctrid genera (†*Baltileuctra* Chen, 2018 and †*Euroleuctra* Chen, 2018) and the first Brachypterainae fossil (†*Balticopteryx* Chen, 2018, Taeniopterygidae). Additional contributions include the first fossil record of *Brachyptera* Newport, 1848 (Chen 2022a), †*Balticonemoura* Chen, 2022 (Nemouridae; Chen 2022b), and further studies on †*Baltileuctra* and its parasitic mites (Chen & Liu 2022).

However, the diversity of stonefly species in Baltic amber is still underestimated, and further discoveries are anticipated. In this study, three species from the Eocene Baltic amber are described, namely †*Palaeopsole spinosa* sp. nov. (Leuctridae), †*Podmosta biloba* sp. nov. (Nemouridae), and †*Isoperla lituana* sp. nov. (Perlodidae), contributing to a better understanding of the diversity of Plecoptera and evolutionary patterns in this region.

Material and methods

The amber specimens analyzed in this study were legally acquired from MB Amber Inclusions, Vilnius, Lithuania. Baltic amber is generally considered to date from the Eocene (Bartonian to Priabonian, ca 34–38 million years ago) (Kosmowska-Ceranowicz *et al.* 1997; Jouault *et al.* 2021). The amber pieces were polished using sandpaper and grinding paste to enhance visibility for observation. All measurements and observations were conducted using a SDPTOP SZM45 stereo microscope. Photographs were taken using a Canon EOS 5DSR digital camera with a Canon MP-E 65 mm 5× macro lens, and widefield fluorescence images were captured with an Olympus CX31 light microscope equipped with a fluorescence imaging system. Image processing and figure assembly were performed using Adobe Photoshop CS6. The type specimens are deposited in the Insect Collection of Jiangsu University of Science and Technology, Jiangsu Province, China (ICJUST). The examination of extant species of *Podmosta* Ricker, 1952 were conducted in the C.P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins, Colorado, USA (CSUC). Terminology of wing venation follows that of Béthoux (2005).

Abbreviations for morphological terms

AA1 = first anterior analis
AA2 = second anterior analis
an = antenna
ce = cercus
CuA = anterior cubitus
CuP = posterior cubitus
ep = epiproct
LFW = left forewing
LHW = left hind wing
M = media
mp = maxillary palp
pp = paraproct
RA = anterior radius
ra-rp = crossvein between RA and RP
RFW = right forewing
RHW = right hind wing
RP = posterior radius
ScP = posterior subcosta
st = sternum
t = tergum
ve = vesicle

Results

Taxonomy

Class Insecta Linnaeus, 1758
Order Plecoptera Burmeister, 1839
Family Leuctridae Klapálek, 1905
Subfamily Leuctrinae Klapálek, 1905

Genus †***Palaeopsole*** Caruso & Wichard, 2011

Type species

†*Palaeopsole weiterschani* Caruso & Wichard, 2011.

Emended diagnosis

Tergum 9 with one posteromedial spine; sternum 9 extended caudally forming rounded subgenital plate which undergirds sternum 10, basally with vesicle; lateral projections of tergum 10 ending caudad in a more or less concave margin; subanal lobes variable in shape and length; cerci short and unsegmented, apex variably modified; epiproct upturned and hook-shaped, basal cushion variably modified.

†***Palaeopsole spinosa*** sp. nov.
urn:lsid:zoobank.org:act:18C09F91-CCDA-44F6-9B37-94B2143CE78D
Figs 1–3

Diagnosis

Epiproct slender (wider in *P. weiterschani*); paraprocts sharp (rounded in *P. weiterschani*); cerci without humps (with humps in *P. weiterschani*); lateral projections of tergum 10 obtuse (pointed in *P. weiterschani*); ra-rp reaching RP after fork point (at fork point in *P. weiterschani*).

Etymology

The specific epithet refers to the spine-shaped epiproct of the holotype.

Type material

Holotype (Fig. 1A–B)
LITHUANIA • ♂; Lithuanian amber, Eocene, Bartonian to Priabonian, ca 34–38 Ma; beach collected; CZT-PLE-BA6, ICJUST.

Description

Male

Body. Slender (Fig. 1C–D), length (excluding antennae) ca 3.0 mm. Macropterous; generally dark brown.

Head. Dark and rounded, much wider than pronotum (Fig. 1C). Triocellate; compound eyes large and protruded. Antennae filiform and dark brown, preserved segments almost equal with body length, with about 29 segments plus scapus and pedicellus, each segment covered with short bristles. Maxillary palp four-segmented, basal segment shortest, apical three segments subequal in size. Labial palp extremely short.

Thorax. Pronotum rectangular and dark brown, much longer than its width (Fig. 1C). Mesothorax and metathorax darkly sclerotized, much wider than prothorax. Legs generally brown (Fig. 1C–D); tibia

thinner and slightly longer than femur, ventroapically with two giant spurs. Tarsus with three segments; first and third segments subequal in length, second segment shortest.

Wings. Forewings length ca 4.0 mm (Fig. 1C–D). In forewings, ScP reaches RA before ra-rp; RP originated from near base of RA, forked before ra-rp and at near half length of the wing; M forked before the fork of RP; Cu basally forked to CuA and CuP; area between M and CuA with six crossveins in left forewing and seven crossveins in right forewing; area between CuA and CuP with ten crossveins in left forewing and seven in right forewing; AA1 curved, AA2 forked. Hind wings rolled, veins invisible.

Abdomen. Short, near ⅓ of body length (Fig. 1C–D). Terga 1–8 generally pale. Terga 9–10 sclerotized laterally and membranous medially (Fig. 2A–D). Posterior margin of tergum 9 projected with pale long spine, length of spine near half of tergum 9. Central area of tergum 10 generally pale, without obvious sclerite; lateral parts of tergum 10 rounded and unmodified, without projections. Epiproct hook-shaped

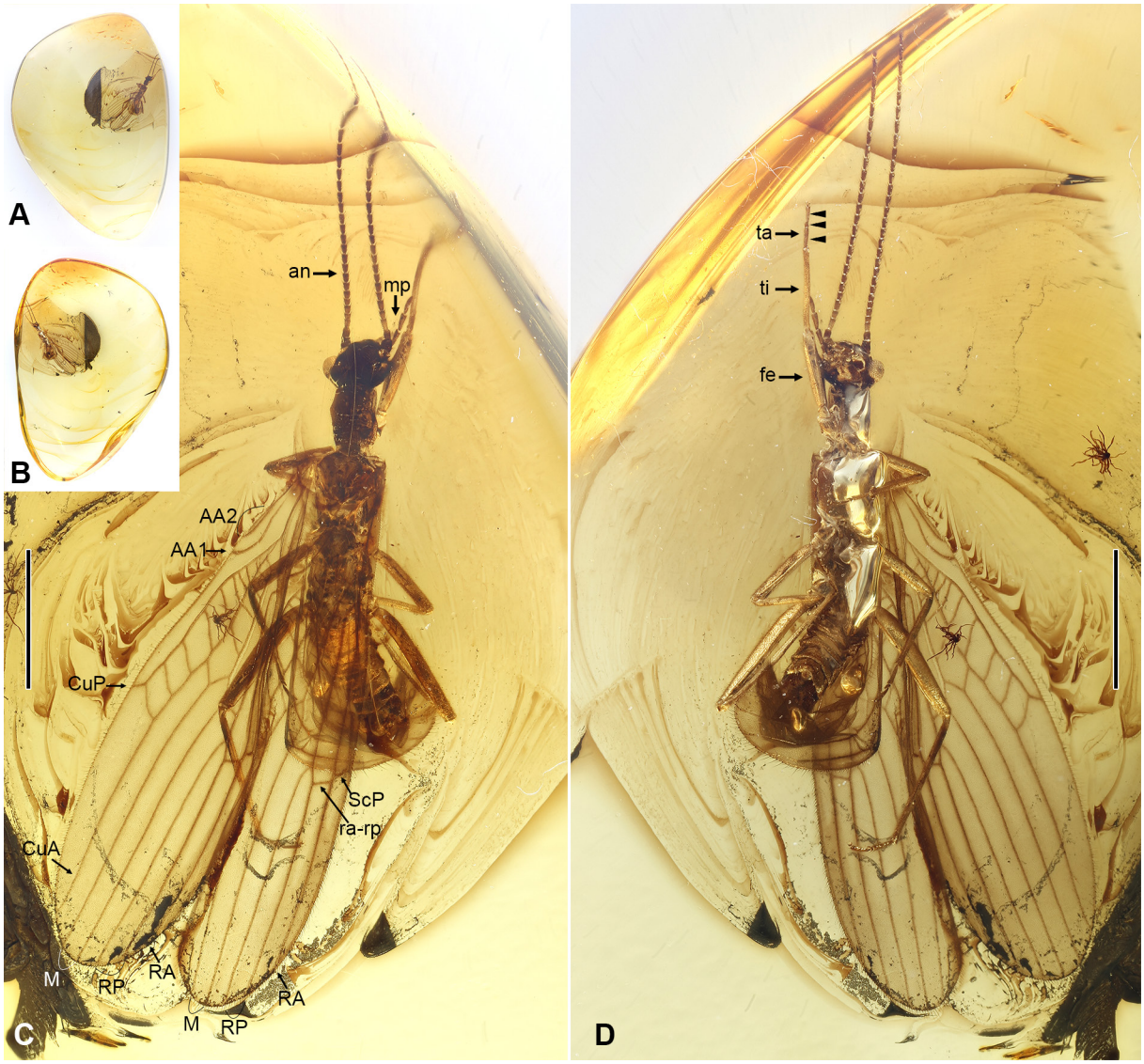

Fig. 1. †*Palaeopsole spinosa* sp. nov., ♂, holotype (CZT-PLE-BA6). **A**. Amber piece, dorsal view. **B**. Amber piece, ventral view. **C**. Habitus, dorsal view. **D**. Habitus, ventral view. Arrowheads = tarsal segments. Abbreviations: see Material and methods. Scale bars = 1 mm.

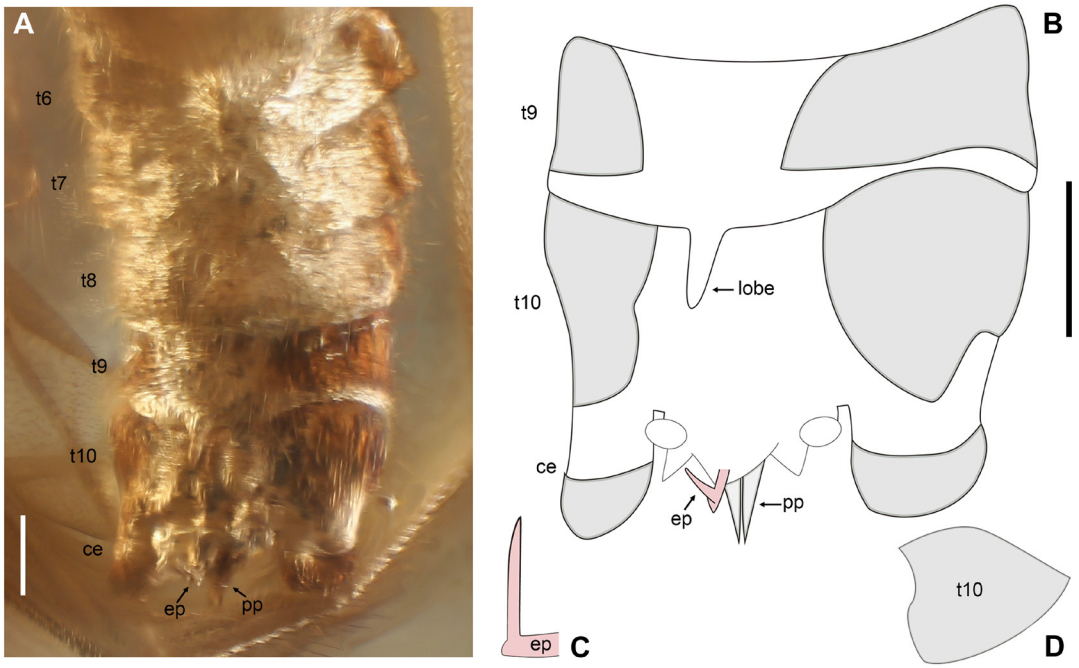

Fig. 2. †*Palaeopsole spinosa* sp. nov., ♂, holotype (CZT-PLE-BA6). **A**. Photo of terminalia, dorsal view. **B**. Drawing of terminalia, dorsal view. **C**. Drawing of epiproct, lateral view. **D**. Lateral part of abdominal tergum 10, lateral view. Abbreviations: see Material and methods. Scale bars = 0.1 mm.

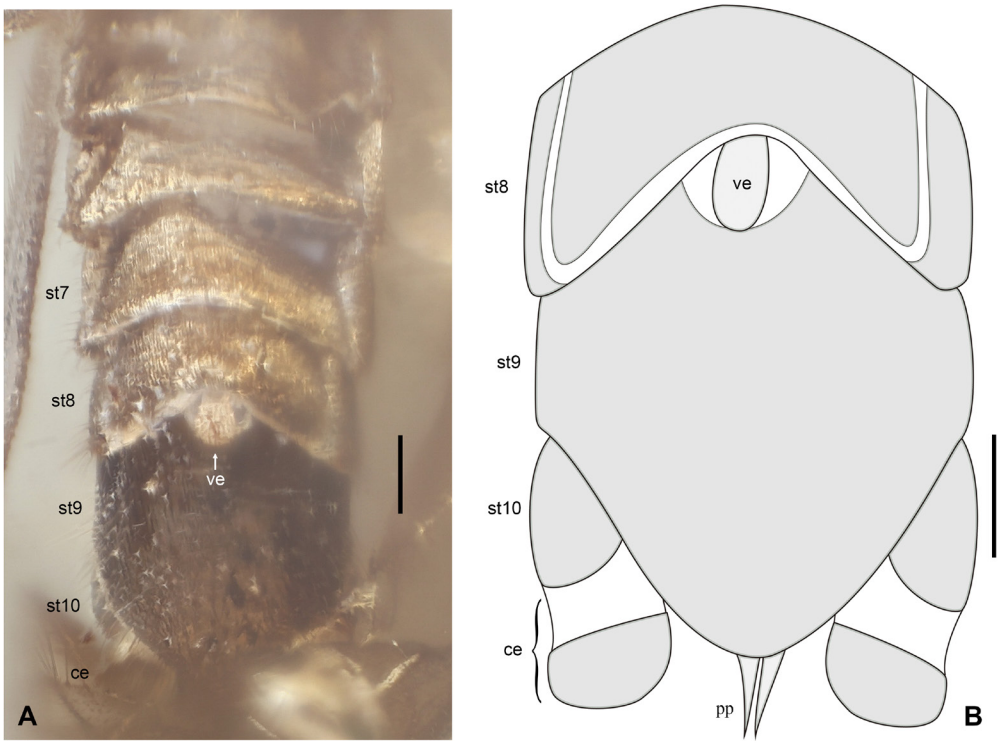

Fig. 3. †*Palaeopsole spinosa* sp. nov., ♂, holotype (CZT-PLE-BA6). **A**. Photo of terminalia, ventral view. **B**. Drawing of terminalia, ventral view. Abbreviations: see Material and methods. Scale bars = 0.1 mm.

with sharp apex, abruptly curved upwards; basal cushion of epiproct broad and wide, laterally with two bilobed plates. Paraprocts (subanal lobes) long, visible apical half semielliptical with sharp apex. Sternum 9 sclerotized, apically with distinct subgenital plate as wide as long and rounded apically, basally with oval vesicle (ventral lobe), which with length 1.5 × as long as its width (Fig. 3A–B). Cerci short and near cylindrical, apical half strongly sclerotized, hemispherical in shape.

Remarks

The slightly rolled wings, absence of the X-pattern of crossveins at the cord, and the unsegmented cerci collectively assign †*P. spinosa* sp. nov. to the family Leuctridae. The species' small and simple epiproct excludes its affiliation with the subfamily Megaleuctrinae (Zwick 2000). Its high morphological similarity to the extant genus *Rhopalopsole* Klapálek, 1912 suggests that it belongs to the subfamily Leuctrinae. The presence of a posteromedial spine on abdominal tergum 9, combined with its Eocene origin, confirms †*P. spinosa* as a member of the extinct genus †*Palaeopsole* Caruso & Wichard, 2011. The original definition of †*Palaeopsole* was based solely on the type species, †*P. weiterschani*, and several characters of †*P. spinosa* do not align with the type. Notably, the two long, triangular paraprocts of †*P. spinosa* resemble those in *Leuctra*, in which males have two slender median specilla adapted for sperm transfer (Pardo & Zwick 1993; Zwick 2000). The apical half of the cercus in †*P. spinosa* is strongly sclerotized into a distinct hemisphere, a feature absent in all known Leuctridae, including its only congener, †*P. weiterschani*.

Family Nemouridae Billberg, 1820
Subfamily Nemourinae Billberg, 1820

Genus ***Podmosta*** Ricker, 1952

Type species

Nemoura decepta (Frison, 1942).

†***Podmosta biloba*** sp. nov.
urn:lsid:zoobank.org:act:1850D232-C1D5-4A84-B1C3-F9EE6017FD40
Figs 4–7

Diagnosis

Vein ra-rp joining anterior branch of RP after fork point in both forewing and hind wings, without typical 'X-pattern' at cord. Posterior margin of abdominal sternum 7 membranous, extended backwards. Median sclerite on female abdominal sternum 8 subtriangular basally, apical half bilobed, each lobe slender, extending along lateral margin of sternum 8's anteromedial indentation.

Etymology

The specific epithet refers to the bilobed median sclerite on abdominal sternum 8.

Type material

Holotype

LITHUANIA • ♀; Lithuanian amber, Eocene, Bartonian to Priabonian, ca 34–38 Ma; beach collected; CZT-PLE-BA1, ICJUST.

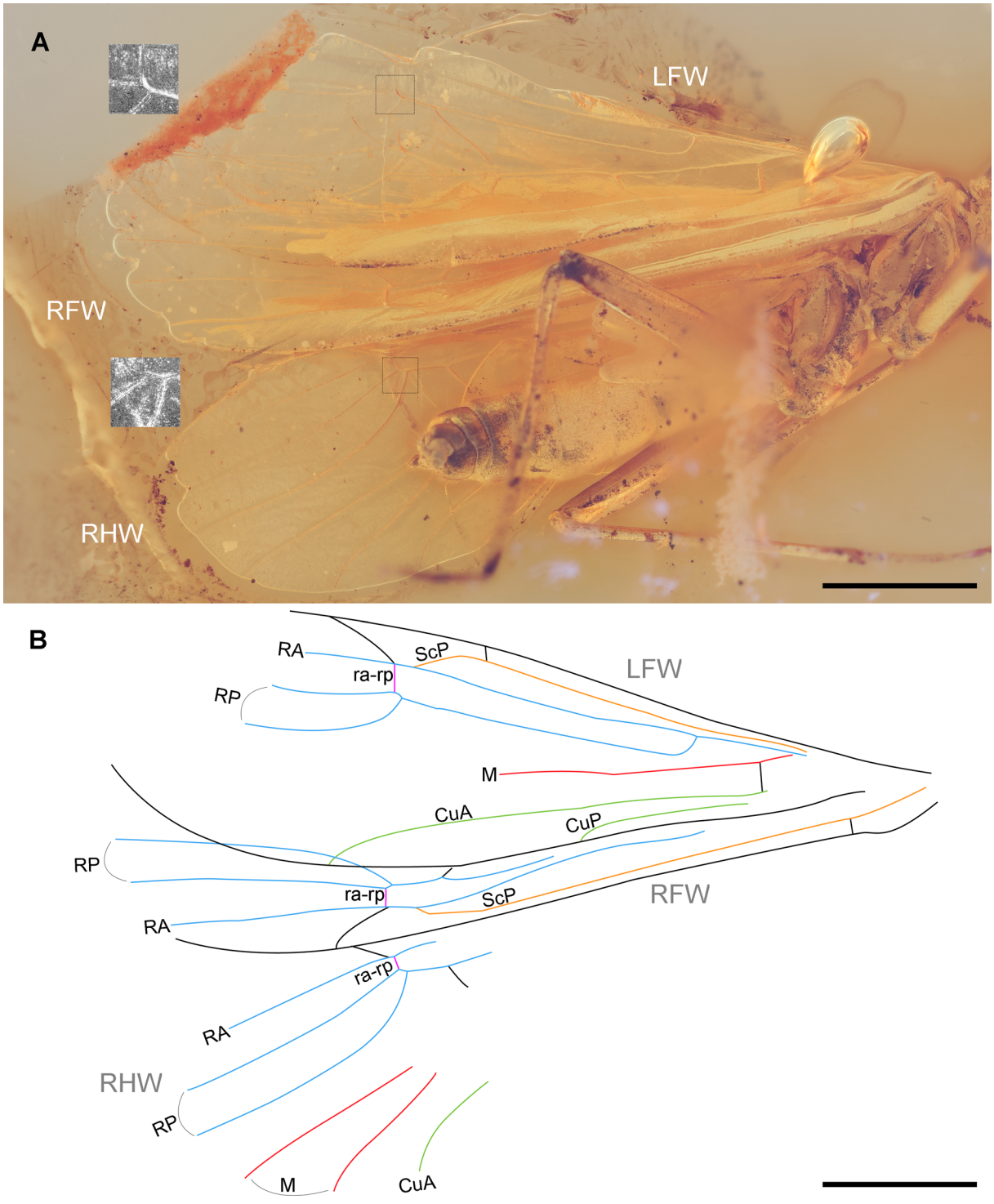

Fig. 4. †*Podmosta biloba* sp. nov., ♀, holotype (CZT-PLE-BA1). **A**. Photo of wings in right view. **B**. Drawing of wings in right view. Inset = joints of ra-rp and RP branches. Abbreviations: see Material and methods. Scale bars = 1 mm.

Description

Female

Wings. In forewing (Fig. 4A–B), terminal costal crossvein c-r joining RA near ra-rp; ScP reaching RA before ra-rp; RP forked; ra-rp joining anterior branch of RP, distal to RP fork point; CuA and CuP unforked. In hind wings (Figs 4A–B, 5A–B), terminal costal crossvein c-r joining RA shortly distal to a-rp; ScP reaching RA before ra-rp; RP forked; ra-rp joining anterior branch of RP, distal to RP fork point; CuA and CuP unforked; AA1 simple; AA2 with at least five branches.

Terminalia. Posterior margin of abdominal sternum 7 membranous, extended backwards (Figs 6A–B, 7A). Sternum 8 deeply indented anteromedially, posterior half folded, notched near posteromedial margin; median sclerite subtriangular basally, apical half bilobed, each lobe slender, extending along

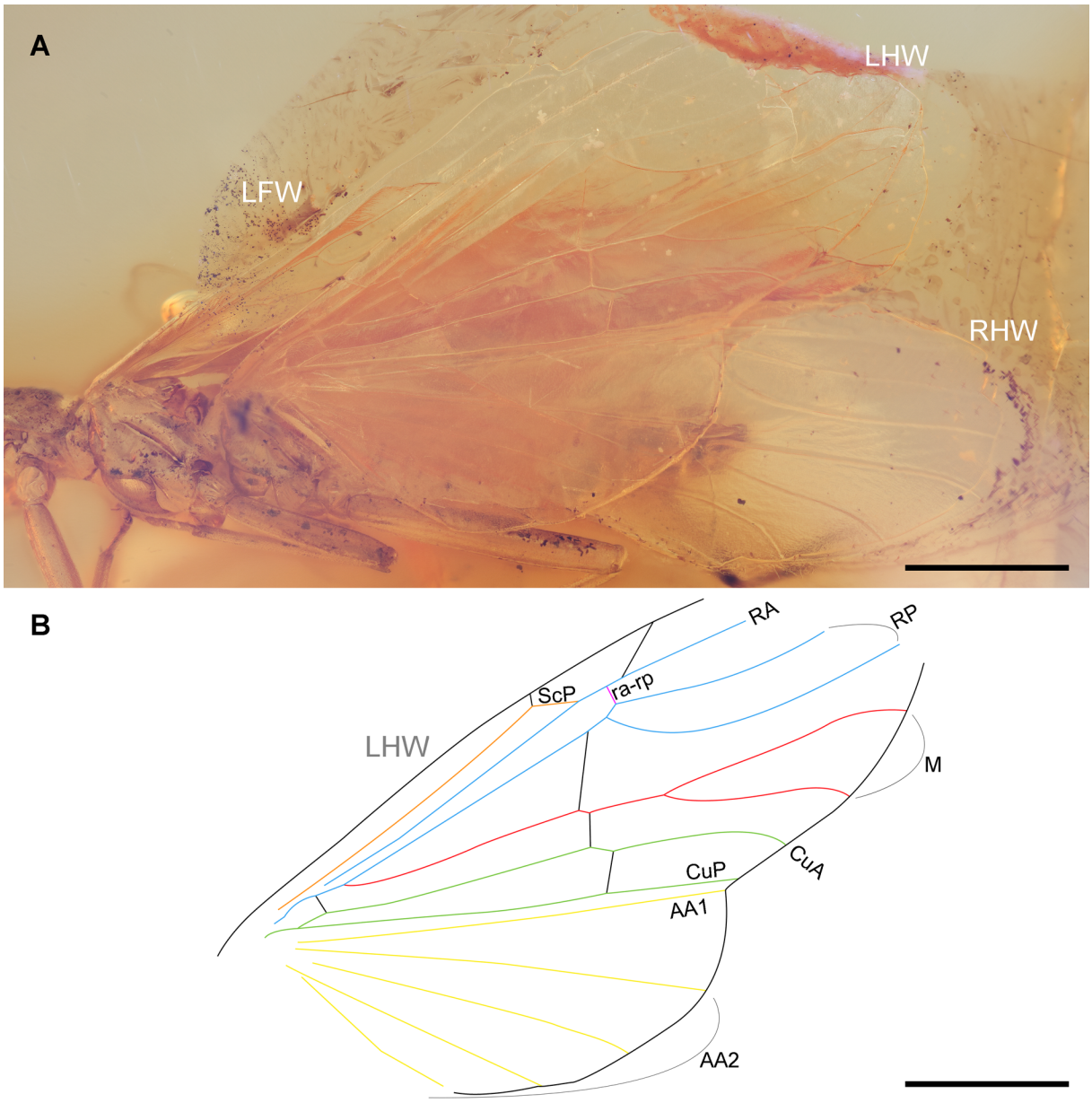

Fig. 5. †*Podmosta biloba* sp. nov., ♀, holotype (CZT-PLE-BA1). **A**. Photo of wings in left view. **B**. Drawing of wing in left view. Abbreviations: see Material and methods. Scale bars = 1 mm.

lateral margin of sternum 8's anteromedial indentation. Sternum 9 darkly sclerotized, slightly shorter than sternum 8, posteromedial margin slightly extended. Sternum 10 darkly sclerotized, near half length of sternum 9, posterior margin unmodified. Paraprocts subtriangular, with rounded corners. Cerci weakly sclerotized, 2 × as long as wide; apex rounded.

Remarks

†*Podmosta biloba* sp. nov. is easily distinguished from the five extant species of *Podmosta* (Fig. 7) by its uniquely shaped median sclerite on the female abdominal sternum 8 (Frison 1936; Ricker 1952; Baumann 1975; Chen 2018a; Grubbs & Baumann 2023). It differs from †*P. attenuata* in the structure of the ra-rp vein, which joins the anterior branch of RP after the fork point in both the forewing and hindwing, resulting in the absence of the typical X-pattern in the cord area. In contrast, in †*P. attenuata*, the ra-rp vein joins RP before the fork point in both wings, forming the characteristic X venation pattern found in extant species of *Podmosta* (Frison 1936; Caruso & Wichard 2010; Grubbs & Baumann 2023).

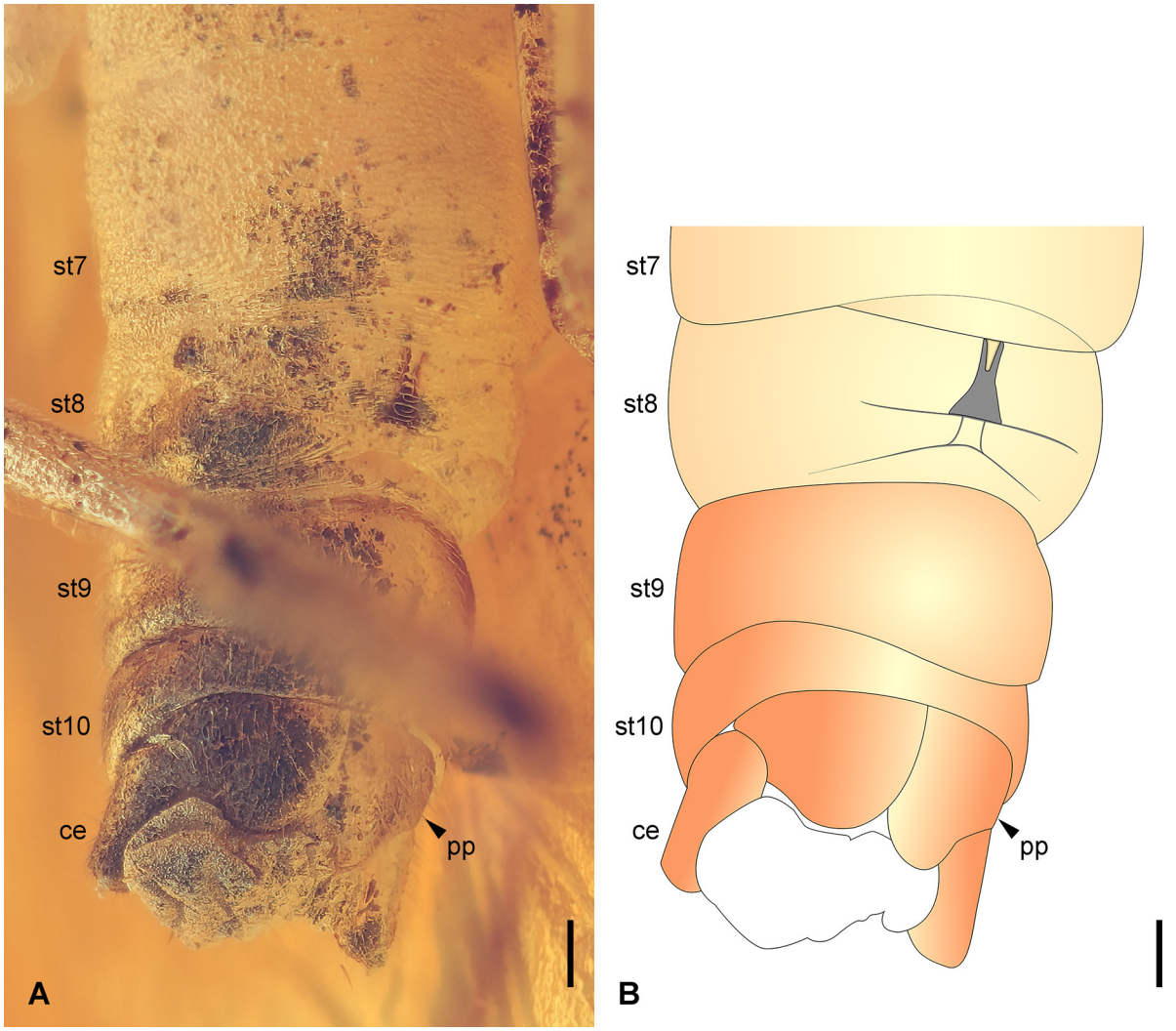

Fig. 6. †*Podmosta biloba* sp. nov., ♀, holotype (CZT-PLE-BA1). **A**. Photo of terminalia, ventrolateral view. **B**. Drawing of terminalia, ventrolateral view. Abbreviations: see Material and methods. Scale bars = 0.1 mm.

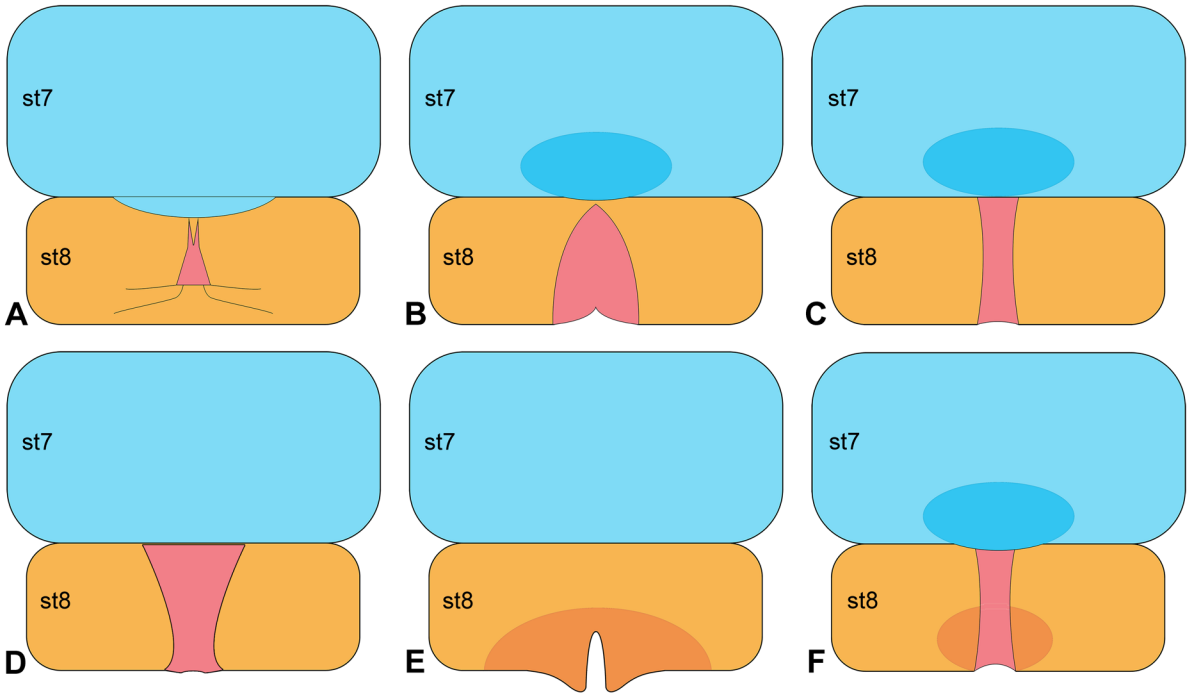

Fig. 7. Diagrams of female abdominal sterna 7–8 in species of *Podmosta*. **A**. †*Podmosta biloba* sp. nov. **B**. *Podmosta decepta* (Frison, 1942). **C**. *Podmosta delicatula* (Claassen, 1923). **D**. *Podmosta macdunnoughi* (Ricker, 1947). **E**. *Podmosta obscura* (Frison, 1936). **F**. *Podmosta weberi* (Ricker, 1952). Abbreviation: see Material and methods.

Family Perlodidae Klapálek, 1909
Subfamily Isoperlinae Frison, 1942

Genus ***Isoperla*** Banks, 1906

Type species

Isoperla bilineata (Say, 1823).

†***Isoperla lituana*** sp. nov.
urn:lsid:zoobank.org:act:0FE85367-E3C5-46C2-92F8-3FF11976E76E
Figs 8–11

Diagnosis

Head generally pale brown, with a light M-shaped pattern. Pronotum narrower than head, width ca 1.5 × as long as length, with angled corners, anterior margin convex, posterior margin almost straight, lateral margins slightly oblique; median suture distinct, lateral areas rugose. Macropterous. In forewing, ScP reaching RA before ra-rp; RP with two branches; CuA with two branches; AA1 simple, AA2 forked. In hind wing, ScP reaching RA before ra-rp; RP with two branches. Tibia with moderate apical spurs. Abdominal terga 1–8 unmodified. Tergum 9 with a subquadrate patch of short stout sensilla basiconica medially. Tergum 10 complete, with depressed, membranous, posteromedial area, anterior and lateral areas of the membrane surrounded by short stout sensilla basiconica similar to those on tergum 9. Paraprocts darkly sclerotized, upcurved, narrow, pointed apically. Sternum 7 with posteromedian

extension. Vesicle of sternum 8 absent. Sternum 9 greatly expanded backwards into hood exceeding basal cercal segment, posterolateral margins forming oblique ridges. Cerci slightly shorter than abdomen.

Etymology

The new species is named after Lithuania, where the piece of amber was obtained.

Type material

Holotype

LITHUANIA • ♂; Lithuanian amber, Eocene, Bartonian to Priabonian, ca 34–38 Ma; beach collected; CZT-PLE-BA9, ICJUST.

Description

Male

Body. Length (from anterior of head to posterior of abdomen) ca 9.5 mm. Body mostly pale brown (Fig. 8A–B).

Head. Generally pale brown, anteriorly with light M-shaped pattern (Fig. 9A). Triocellate, anterior ocellus near half in size of posterior ones. Compound eyes large and rounded. Antennae slender, generally dark brown, subequal in length to abdomen. Maxillary palps slender, five-segmented with

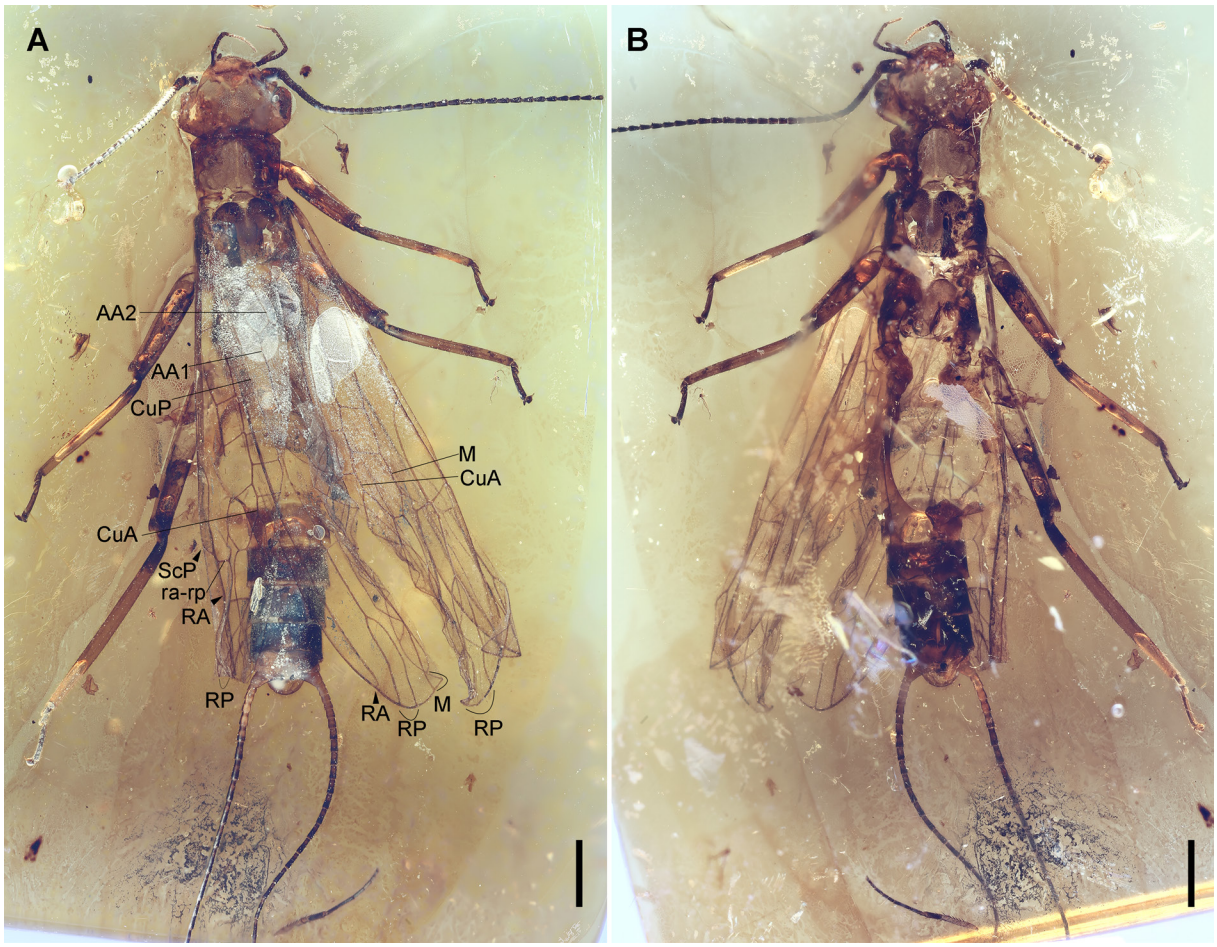

Fig. 8. †*Isoperla lituana* sp. nov., ♂, holotype (CZT-PLE-BA9). **A**. Habitus, dorsal view. **B**. Habitus, ventral view. Abbreviations: see Material and methods. Scale bars = 1 mm.

strongly shortened apical segment; labial palps much shorter, three-segmented with slightly shortened apical segment (Fig. 9A–B).

Thorax. Pronotum narrower than head (Fig. 9A), width ca 1.5 × as long as length, with angled corners, anterior margin convex, posterior margin almost straight, lateral margins slightly oblique; median suture distinct, lateral areas rugose. Macropterous; wings hyaline, veins brown (Fig. 8A–B). Forewings length ca 8.0 mm, hindwings length ca 6.5 mm. In forewing, ScP reaching RA before ra-rp; RP with two branches; CuA with two branches; AA1 simple, AA2 forked. In hind wing, ScP reaching RA before ra-rp; RP with two branches; anal area large and folded. Legs mostly brown, darker at joints of femur and tibia; tibia with moderate apical spurs.

Abdomen. Abdominal segments mostly dark brown. Terga 1–8 unmodified. Tergum 9 with subquadrate patch of short stout sensilla basiconica medially (Fig. 10A–C). Tergum 10 complete, with elliptical, depressed, membranous, posteromedial area, anterior and lateral areas of membrane surrounded by short stout sensilla basiconica similar to those on tergum 9. Paraprocts darkly sclerotized, upcurved, narrow, pointed apically. Sternum 7 with short but wide posteromedian extension (Fig. 11A–B). Vesicle of sternum 8 less developed, indistinguishable from sternum. Sternum 9 greatly expanded backwards into hairy, rounded hood exceeding basal cercal segment; posterolateral margins of sternum 9 forming

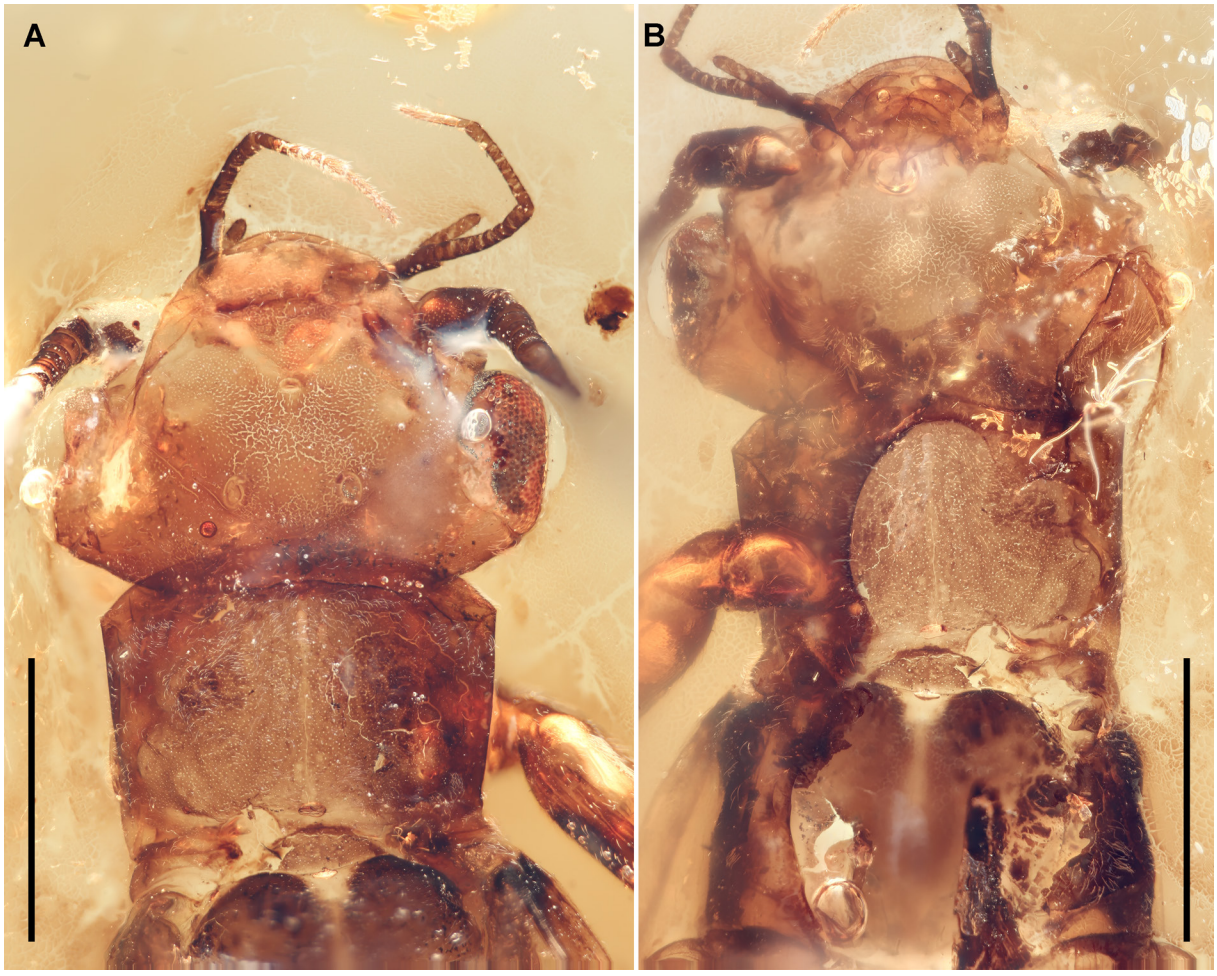

Fig. 9. †*Isoperla lituana* sp. nov., ♂, holotype (CZT-PLE-BA9). **A**. Head and thorax, dorsal view. **B**. Head and thorax, ventral view. Scale bars = 1 mm.

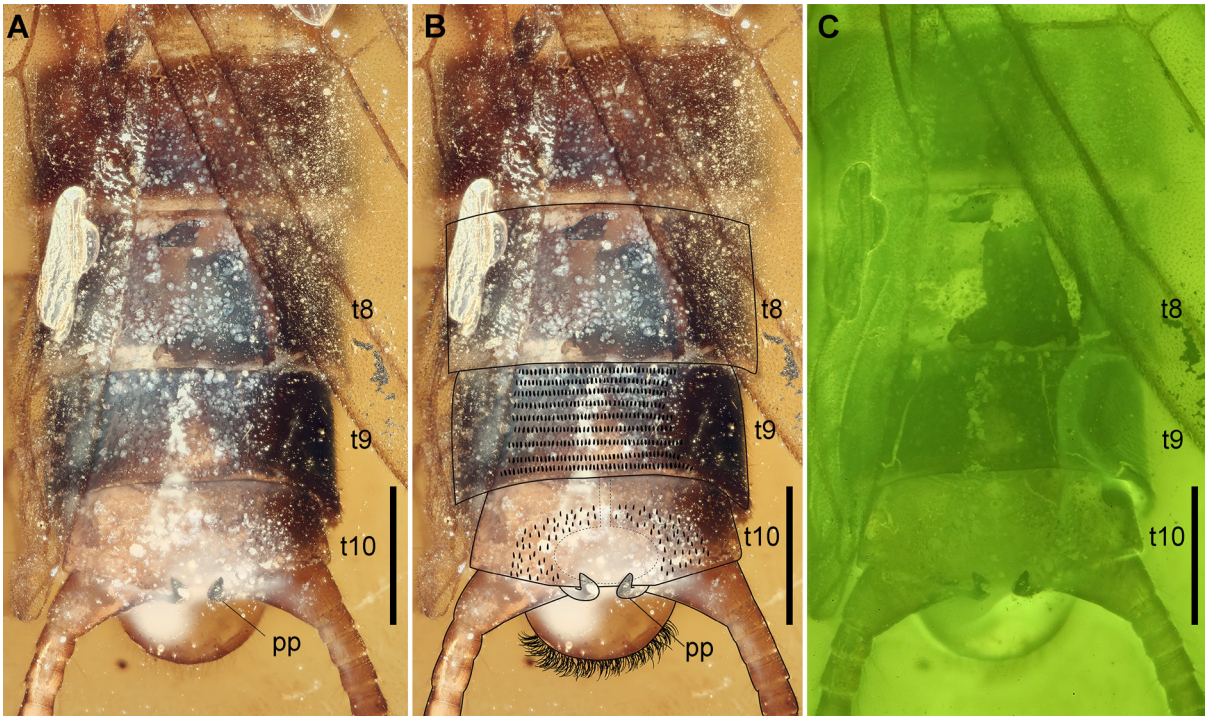

Fig. 10. †*Isoperla lituana* sp. nov., ♂, holotype (CZT-PLE-BA9). **A**. Photo of terminalia, dorsal view. **B**. Drawing of terminalia, dorsal view. **C**. Fluorescence image of terminalia, dorsal view. Abbreviations: see Material and methods. Scale bars = 0.5 mm.

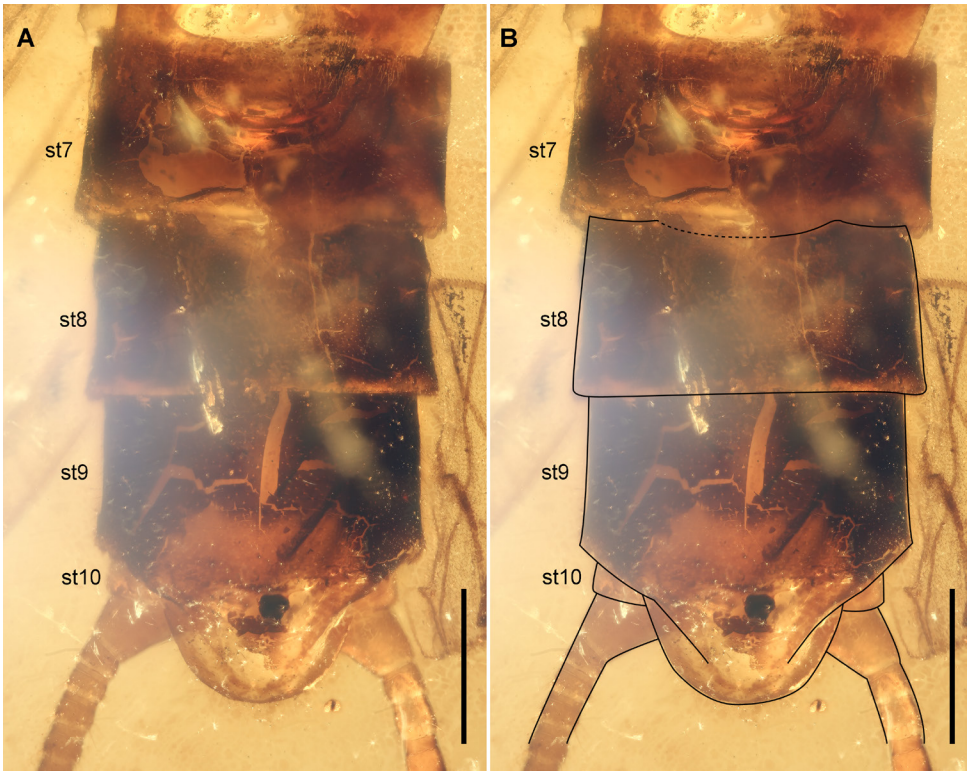

Fig. 11. †*Isoperla lituana* sp. nov., ♂, holotype (CZT-PLE-BA9). **A**. Photo of terminalia, ventral view. **B**. Drawing of terminalia, ventral view. Abbreviation: see Material and methods. Scale bars = 0.5 mm.

oblique ridges. Cerci slender, preserved parts slightly shorter than abdomen, basal segments pale, apical segments dark.

Remarks

Compared with †*Isoperla succinica* Hagen, 1856, whose holotype is lost and whose status has been treated as incertae sedis (Caruso & Wichard 2010; Jouault *et al.* 2021), †*I. lituana* sp. nov. can be distinguished by the 8th cercomere, which is more than 2 × as long as broad (vs barely 2 × as long as wide in †*I. succinica*), and by the absence of a median cleft in tergum 10 (vs presence of a cleft in †*I. succinica*) (Jouault *et al.* 2021). The new species can also be differentiated from †*I. baltica* by several features, including: the forewing with ScP reaching RA before ra-rp (vs after ra-rp), CuA with two branches (vs three branches), abdominal sterna 9 and 10 with patches of sensilla basiconica (vs lacking sensilla basiconica), and an elongated sternum 9 that exceeds the basal cercal segment (vs not exceeding the basal cercal segment) (Jouault *et al.* 2021). In addition to these distinguishing traits, †*I. lituana* differs from extant species by its unique combination of characters, as outlined in the diagnosis.

Discussion

To date, the stonefly fauna in Baltic amber includes one species within a single genus of Perlidae, four species within two genera of Perlodidae, four species within three genera of Taeniopterygidae, eight species within four genera of Nemouridae, and eleven species within six genera of Leuctridae. The diversity of extinct stoneflies in Baltic amber is likely underestimated in comparison to their extant diversity. The newly described species contribute to our understanding of extinct stonefly diversity in the Eocene. These species offer important calibration points for phylogenetic analyses and illuminate the functional morphology, historical distribution, and dispersal history of early stoneflies. The morphological differences observed between these new species and their extant relatives underscore the complexity of stonefly evolution and suggest that Baltic amber may preserve a much more diverse Plecoptera fauna than currently recognized. Future discoveries, particularly of male specimens, will likely refine the phylogenetic relationships and enhance our understanding of Plecoptera evolution during the Eocene.

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Competing interests

The author declares that he has no competing interests.

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