



Fossil record of the mayfly family Ephemerellidae (Insecta: Ephemeroptera), with description of new species and first report of Ephemerellinae from Baltic amber

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The fossil record of the mayfly family Ephemerellidae is reviewed. Of previously described fossil Ephemerellidae, all records but one are doubtful or erroneous. We reinvestigate the holotype of *Ephemerella viscata* Demoulin, 1968 from Eocene Baltic amber and confirm its previous placement within the subfamily Timpanoginae Allen, 1984, based on the presence of vestigial gill sockets on abdominal segments IV–VII only. It is transferred to the genus *Eurylophella* Tiensuu, 1935 [*Eurylophella viscata* (Demoulin, 1968) comb. nov.] based on proportions of the forelegs, elongated abdominal segment IX, and the shape of the subimaginal penis. Additionally, we describe two new specimens from Eocene Baltic amber: *Ephemerella trigonoptera* sp. nov. represents the first fossil record of subfamily Ephemerellinae. It can be separated from other representatives of *Ephemerella* Walsh, 1862 *sensu lato* by the shape of the hind wings, which are remarkably narrowed towards the apex, with a costal projection located rather proximally. The second new specimen, a male subimago, cannot be differentiated from other Ephemerellinae due to its poor preservation. The discovery of *Ephemerella trigonoptera* sp. nov., together with the taxonomic reassessment of *Eurylophella viscata* comb. nov., provide the first reliable evidence that both subfamilies of Ephemerellidae, Ephemerellinae and Timpanoginae, date back at least to the Palaeogene. The biogeographical and palaeological implications of these findings are discussed.

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Keywords: Ephemerellinae; Timpanoginae; Baltic amber; Eocene

Introduction

The fossil record of the mayfly family Ephemerellidae Klapálek, 1909 is very scarce, despite the fact that Ephemerellidae is a relatively speciose mayfly family of Holarctic and Oriental distribution with about 311 extant species described (Kluge 2017). There have been only five specimens from different geological periods suggested as fossil representatives of Ephemerellidae. Four out of those were described from China (Ping 1935; Hong 1979, 1983; Lin 1986). Their initial classifications within Ephemerellidae were either unsubstantial or erroneous, and by now they are either classified within different families (Jacobus & McCafferty 2006) or regarded as Ephemeroptera *incertae sedis* (Kluge 2004).

This leaves just a single fossil record that is reliably counted as Ephemerellidae: in a contribution on mayflies from Eocene Baltic amber, Georges Demoulin (1968, p. 270) described an evidently male ephemerellid

subimago as “*Ephemerella* (*Timpanoga*?) *viscata*.” He figured the entire type specimen in lateral left view and also figured a detailed left view of abdominal segments IV–VII (Demoulin 1968, p. 271, fig. 37a, b). While diagnostic characters of Ephemerellidae are easily recognizable in the specimen, its generic attribution is not obvious. Within various families of Ephemerelloidea, the presence and arrangement of paired larval gills (tergalii *sensu* Kluge 2004) on the first seven segments differs considerably (see Kluge 2004, p. 297, table 8): while in all ephemerelloid families but Ephemerellidae (a taxon referred to as Pantricrothyini by Kluge 2004) such gills are present on abdominal segment II, they are lacking on segment II in Ephemerellidae only. Moreover, within Ephemerellidae, the subfamilies differ in the presence (Ephemerellinae) or absence (Timpanoginae) of gills on abdominal segment III. Remnants of larval gill sockets may persist as vestiges in the winged stages. Demoulin’s specimen, a male subimago, shows finger-like gill sockets on

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abdominal segments IV–VII only, but the left view onto the first abdominal segments is obstructed. The original figures thus give no information on the presence or absence of gill sockets on abdominal segment III, which would be decisive for its attribution to a subfamily within Ephemerellidae. Nevertheless, Demoulin (1968) placed *Ephemerella* (*Timpanoga*?) *viscata* within a complex of subgenera of *Ephemerella*, later to be classified as subtribe Timpanogae Allen, 1984. McCafferty & Wang (1994, p. 569) referred to the latter as *Timpanoga* complex and subsequently classified it as subfamily Timpanoginae (McCafferty & Wang 2000). Kluge (2004, p. 301) referred to this taxon as *Timpanoga* fg1.

In subsequent publications and reviews on the fauna of Baltic amber (see list of synonymies below), this specimen was mostly considered belonging to the genus *Timpanoga*. However, Kluge (2004, pp. 296, 347) classified this species as Ephemerelloidea *incertae sedis*, given the fact that crucial information on the allocation of gill sockets cannot be confirmed from the figures in the original description. Given its importance as the sole hitherto known fossil representative of Ephemerellidae and its doubtful classification, the holotype of *Ephemerella* (*Timpanoga*?) *viscata* Demoulin, 1968 is reinvestigated in this contribution.

Additionally, we found a new winged specimen of fossil Ephemerellidae in the collection of the Museum of Amber Inclusions (Department of Invertebrate Zoology, University of Gdańsk), which is attributed within Ephemerellinae and described here as *Ephemerella trigonoptera* sp. nov. Yet another fossil male subimago of Ephemerellinae was discovered in the mayfly collection of the State Museum of Natural History Stuttgart, Germany, which is also documented here. The implications of the new findings in regard to the fossil history, biogeography and palaeoecology of Ephemerellidae are discussed.

Material and methods

The holotype of *Eurylophella viscata* comb. nov. is housed in the historical collection W. Simon at the Museum für Naturkunde, Berlin, Germany (MNB) under inventory no. MB.I.2238. The holotype of *Ephemerella trigonoptera* sp. nov. is deposited at the Museum of Amber Inclusions, Department of Invertebrate Zoology, University of Gdańsk, Poland (MAI) under inventory no. 2658. The second specimen, attributed to Ephemerellidae *incertae sedis* in this contribution, is deposited at the State Museum of Natural History Stuttgart, Germany (SMNS) under inventory no. SMNS BB-1401.

Line drawings were made using a WILD 308700 camera lucida on a WILD M3Z stereo microscope, and using a camera lucida on a Leica M205 C stereo microscope. Multiple photographs with different depth of field were taken through a Leica Z16 APO Macroscope using Leica

Application Suite v. 3.1.8. Photo stacks were processed with Helicon Focus Pro 6.4.1 to obtain combined photographs with extended depth of field, which were subsequently enhanced with Adobe Photoshop CS 5.0.

Systematic palaeontology

Class **Insecta** Linnaeus, 1758

Order **Ephemeroptera** Hyatt & Arms, 1890

Family **Ephemerellidae** Klapálek, 1909

Subfamily **Timpanoginae** Allen, 1984

Genus ***Eurylophella*** Tiensuu, 1935

Eurylophella viscata (Demoulin, 1968) comb. nov.
(Figs 1–4)

1968 *Ephemerella* (*Timpanoga*?) *viscata* Demoulin: 270, fig. 37a, b.

1978 *Ephemerella* (*Timpanoga*) *viscata* Demoulin; Larsson: 81.

1982 *Ephemerella* (*Timpanoga*) *viscata* Demoulin; Keilbach: 207.

1987 *Timpanoga viscata* (Demoulin); Hubbard 1987: 64.

1996 *Timpanoga viscata* (Demoulin); Wichard & Weitschat: 25.

1998 *Timpanoga viscata* (Demoulin); Weitschat & Wichard: 94.

2002 *Timpanoga viscata* (Demoulin); Weitschat & Wichard: 92.

2004 [*Ephemerella* (*Timpanoga*)] *viscata* Demoulin; Kluge: 296, 347.

2008 *Timpanoga viscata* (Demoulin); Jacobus & McCafferty: 189.

2009 *Timpanoga viscata* (Demoulin); Wichard, Gröhn, & Seredszus: 291.

Diagnosis. Body length 6.96 mm; length of forewings 8.10–8.14 mm. Eyes large, divided into two portions. Mesonotal suture transverse, stretched backward near crossing with medioparapsidal suture. Forewing with free marginal intercalary veins between iMP and CuA; CuP proximally connected with CuA by cross vein *cua-cup*; CuP connected with AA by cross vein *cup-aa*; *cua-cup* located distally from *cup-aa*. Hind wing of oval shape, as long as 0.26 of forewing length with distinct RS and MP bifurcation; costal projection rounded apically. First tarsomere of middle and hind legs fused with tibia; claws of all legs ephemeropteroid. Abdomen with vestigial gill sockets present on segments IV–VII only; segments VIII and IX with large posterolateral projections; segment IX 1.26× length of segment VIII. Gonostyli straight and short, covered by small setae; gonostylus segment III sub-ovoid. Penis short, expanded basally, apically broadly rounded with U-shaped incision. Paracercus well developed and slightly shorter than cerci.

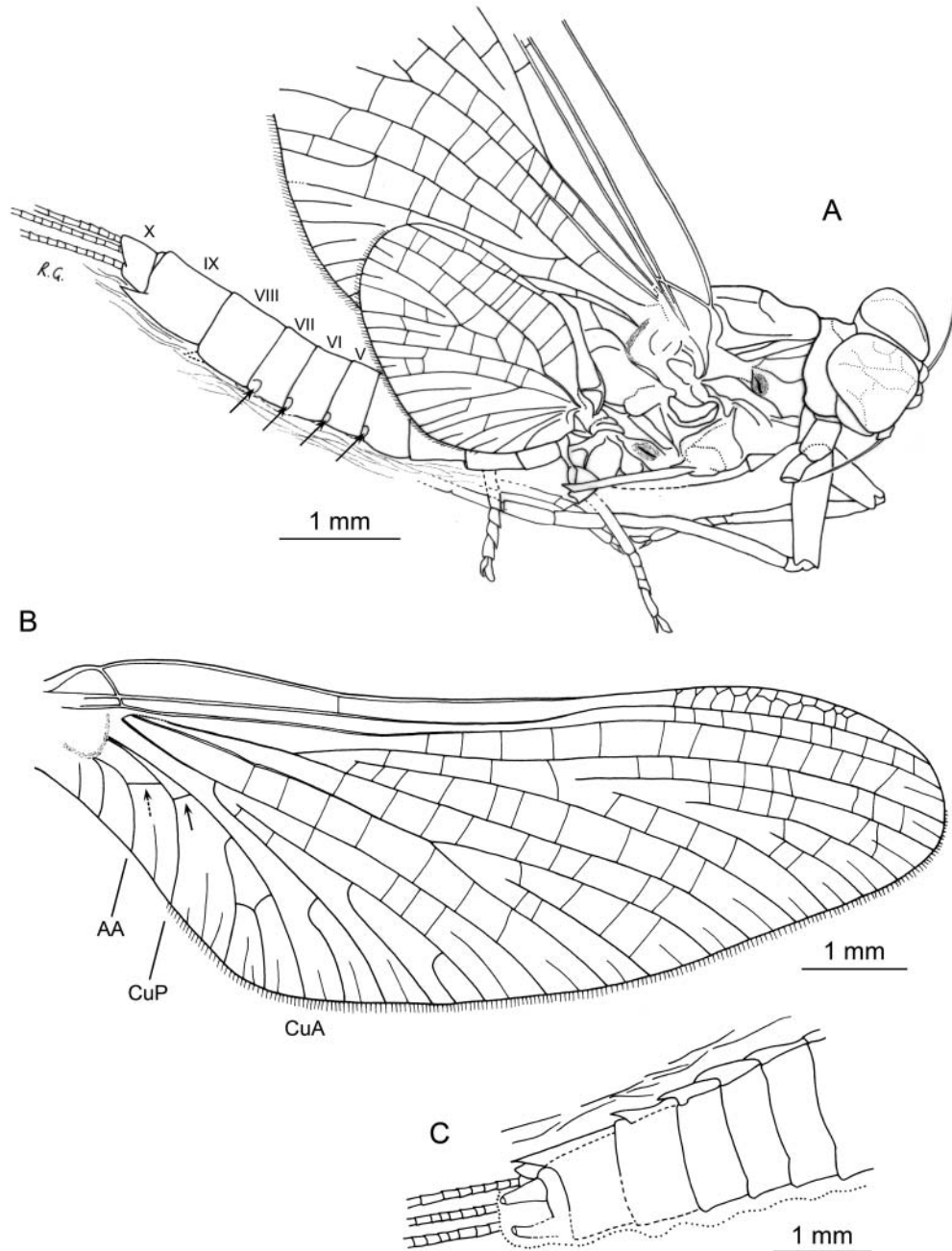


Figure 1. *Eurylophella viscata* (Demoulin, 1968), holotype, male subimago, MB.I.2238. **A**, dorsolateral right view; traces of gill sockets on abdominal segments IV–VII are marked by arrows; abdominal segments are indicated by Roman numerals; **B**, left forewing, ventral view; Cross veins *cua-cup* and *cup-aa* are marked by solid and dotted arrow, respectively; **C**, tip of abdomen, ventral view.

Material. Holotype: male subimago, MB.I.2238, Eocene, Baltic amber; originally labelled: “Holotype Fam. 3 Ephemeridae Orig. Demoulin, 1968, Dtsch. Ent. Z. Fig. 37”; “G. Demoulin det., 1966 *Ephemerella viscata* sp. n. ♂ subimago” MB.I.2238; housed in MNB, W. Simon collection.

Redescription of holotype. Male subimago, body length 6.96 mm; length of forewings 8.10–8.14 mm (Fig. 1A, B).

Well-preserved specimen embedded in resin in lateral position. Left side of body and most part of ventral side poorly visible because of ‘Verlumung’ (Figs 1C, 2A–E, 3A–E, 4A–E). Both forewings completely preserved, with setae along posterior margin; left hind wing bent; right foreleg lost. General colouration pale, yellowish-brown to brown. For measurements see Supplemental Table 1.

Head well preserved (Figs 1A, 2B, C). Eyes broad, flattened dorsally, medially contiguous; surface of ommatidia

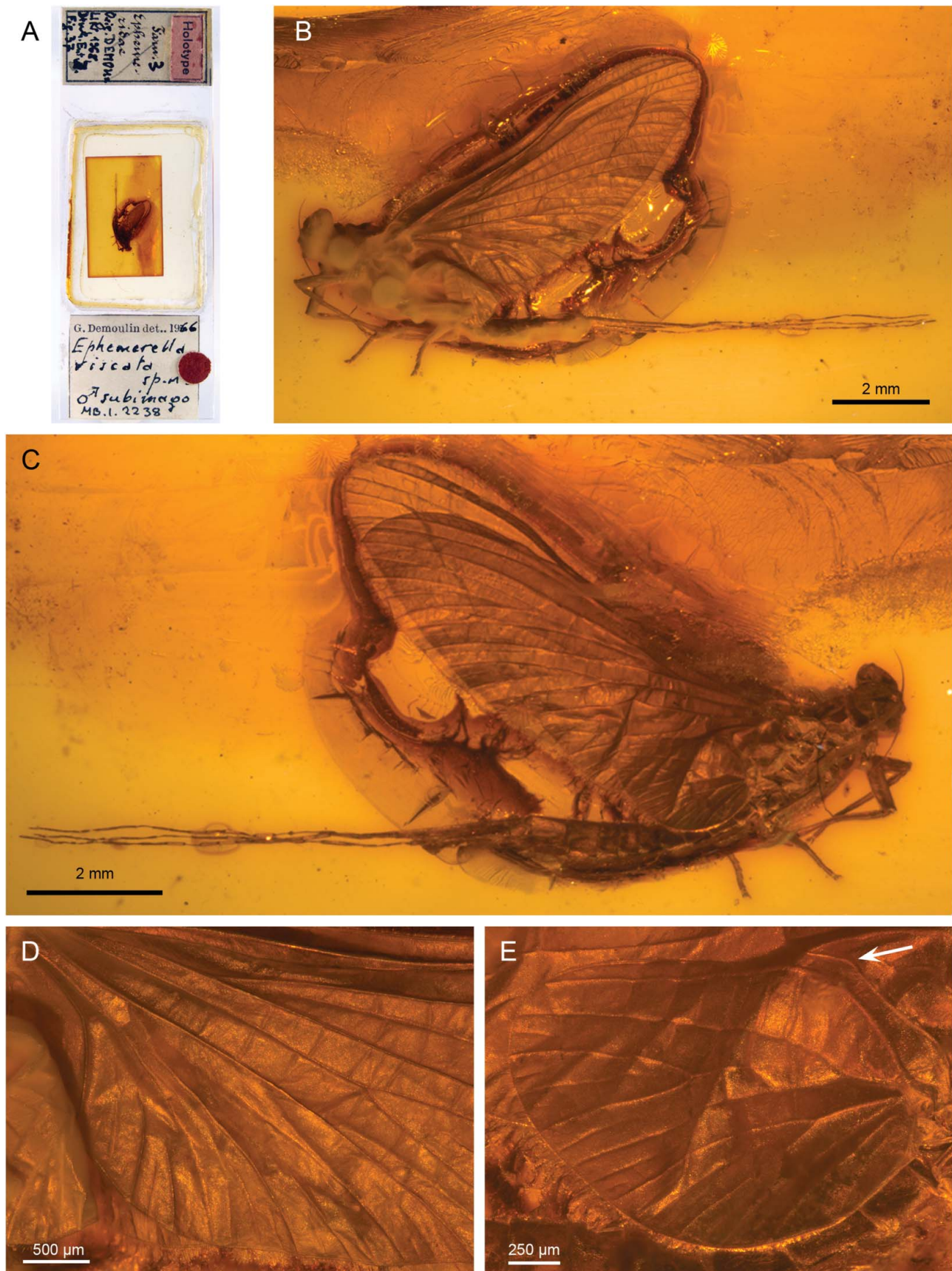


Figure 2. *Eurylophella viscata* (Demoulin, 1968), holotype, male subimago, MB.I.2238. **A**, view of embedded specimen mounted on a 76×26 mm microslide; **B**, general lateral view, left side; **C**, general lateral view, right side; **D**, base of left forewing, ventral view; **E**, right hind wing, ventral view. Costal projection is marked by arrow.

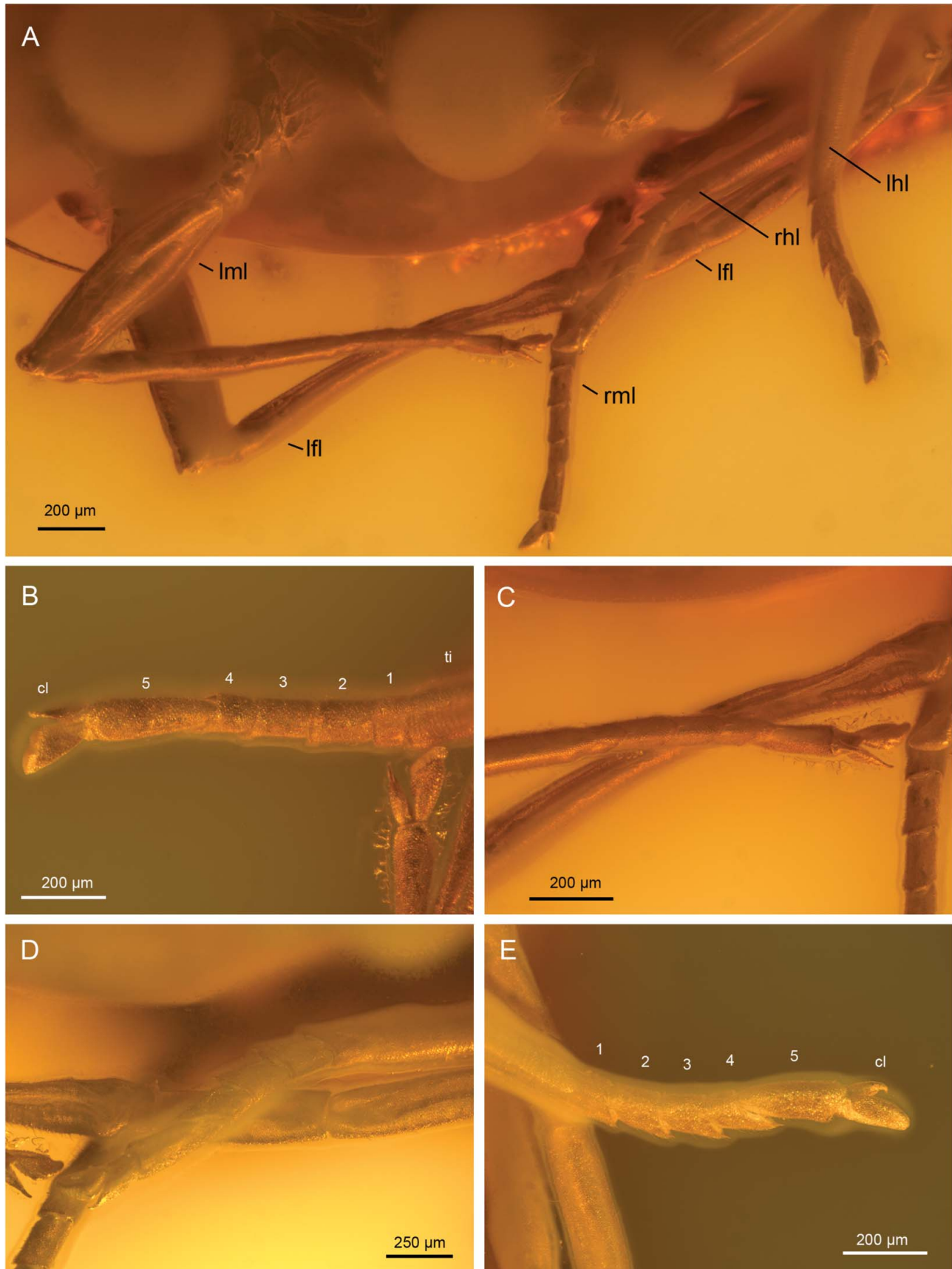


Figure 3. *Eurylophella viscata* (Demoulin, 1968), holotype, male subimago, MB.I.2238. **A**, legs in lateral view; **B**, right middle leg; tarsomeres 1–5 are indicated by Arabic numerals; **C**, left middle leg. **D**, right hind leg. **E**, left hind leg; tarsomeres 1–5 are indicated by Arabic numerals. Abbreviations: lfl, left foreleg; lml, left middle leg; rml, right middle leg; lhl, left hind leg; rhl, right hind leg.

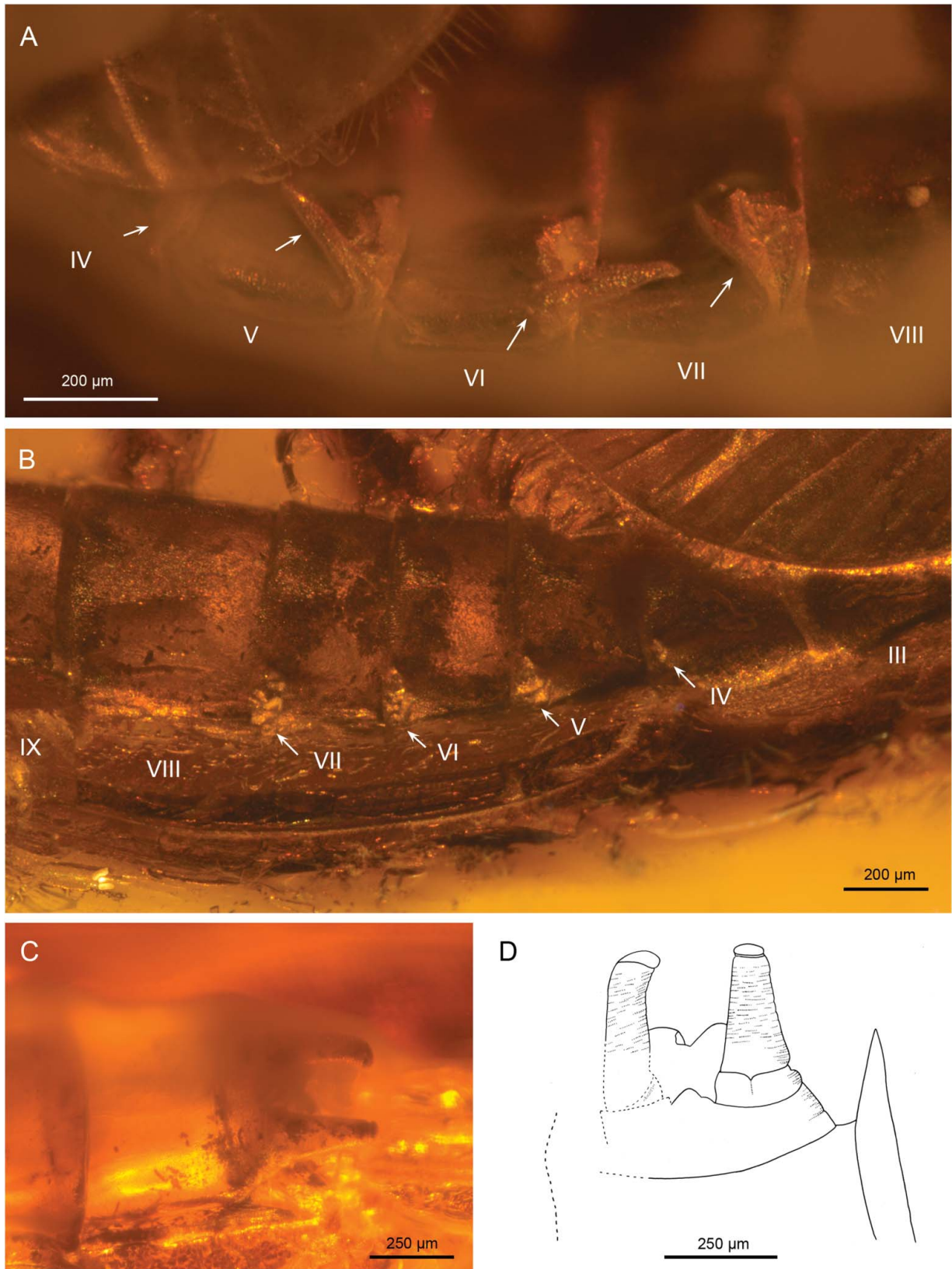


Figure 4. *Eurylophella viscata* (Demoulin, 1968), holotype, male subimago, MB.I.2238. **A**, abdominal segments IV–VIII, left lateral view; finger-like remnants of gill sockets on abdominal segments IV–VII are marked by arrows; numbers of respective abdominal segments are marked by Roman numerals; **B**, abdominal segments III–VIII, right lateral view; traces of gill socket attachments on abdominal segments IV–VII are marked by arrows; numbers of respective abdominal segments are marked by Roman numerals; **C**, male genitalia, ventral view; **D**, male genitalia, line drawing.

well preserved. Ocelli small, unicoloured brown. Antennae well preserved, longer than head.

Thorax brown to dark brown, pigmentation around mesonotal suture not present or not preserved; details of prosternum not distinguishable. Lateral sides of thorax well visible, with characters typical for Ephemerellidae (Fig. 1A): mesonotal suture transverse, distinctly expressed and narrowly stretched backward near crossing with medioparapsidal suture; only proximal end of lateroparapsidal suture visible. Mesosternum hardly visible because of 'Verlumung', but apparently with separated furcasternal protuberances.

Wings opaque, not translucent, with setation on posterior margins. Longitudinal and cross veins unicoloured yellowish-brown. Costal field of forewing (Fig. 1B) with only one simple cross vein between costal brace and pterostigma, the latter with 11–12, apically bifurcated cross veins, not anastomosed. Free marginal intercalary veins between iMP and MP_2 , and between MP_2 and CuA ; CuP proximally connected with CuA by cross vein *cua-cup*; CuP connected with AA by cross vein *cup-aa*; *cua-cup* located distally from *cup-aa*; in cubital field one bifurcate vein arising from CuA (Figs 1B, 2D).

Hind wing (Figs 1A, 2E) relatively large, oval shape, distally broadly rounded, as long as 0.26 of forewing length; RS and MP with bifurcation. Sc terminating near apex; costal projection rounded apically, markedly protruding above anterior wing margin.

Legs (Fig. 3A–E) well preserved, except for right foreleg. For measurements of leg segments see Supplemental Table 1. Left foreleg (Fig. 3A): length ratio of femur/tibia/tarsus = 1/1.42/1.62; length ratio of tarsomeres: $2 > 4 > 3 > 5 > 1$. Left middle leg completely preserved (Fig. 3C): length ratio of femur/tibia/tarsus = 1/1.05/0.72; length ratio of tarsomeres: $5 > 2 > 4 > 1 = 3$. Left hind leg completely preserved (Fig. 3E): length ratio of femur/tibia/tarsus = 1/0.90/0.65. Length ratio of hind leg tarsomeres (Fig. 3D, E): $5 > 4 > 3 = 2 > 1$. First tarsomere of middle and hind legs fused with tibia. Patella-tibial suture present on middle and hind legs, absent on forelegs. Claws ephemeropteroid, outer claw hooked and inner claw blunt (Fig. 3A–E).

Abdominal segments completely preserved, brown to dark brown, covered with 'Verlumung' ventrally. Vestigial gill sockets on abdominal segments I–III absent (well visible on right side) (Figs 1A, 4B), left side of segments I–III invisible because of 'Verlumung', and additionally being covered by hind wing (Fig. 2B). Vestigial gill sockets present on four abdominal segments only, namely segments IV–VII (Fig. 4B); sockets IV smaller than on other segments; sockets V–VII well developed, finger-like, poorly visible from right side due to influx of resin (Fig. 4A). Abdominal segments VIII and IX with large, prominent posterolateral projections (largest on segment IX); segment IX slightly elongated, $1.26 \times$ length of

segment VIII (Fig. 1A, C). Abdominal sterna pale. Paracercus well developed, only slightly shorter than cerci (Figs 1A, 2B, C).

Genitalia mostly covered with 'Verlumung'. Styliiger with distinct median projection (Figs 1C, 4C–D). Gonostyli relatively straight and short, with small, irregular, pointed setae mainly on gonostylus segment II. Gonostylus segment I nearly rectangular; segment II evenly tapering to apex, relatively robust, not curved; segment III subovoid with length less than 3 times width. Penis relatively short, expanded basally, apically broadly rounded, with shallow, U-shaped incision (Fig. 4D). Details of lateral sides of penis not distinguishable; surface of penis without visible spination.

Occurrence. Baltic amber, middle Eocene (Lutetian Stage; 41.3–47.8 Ma).

Subfamily Ephemerellinae Lestage, 1917

Genus *Ephemerella* Walsh, 1862 s. l.

Ephemerella trigonoptera sp. nov.

(Figs 5, 6)

Diagnosis. Eyes relatively small, widely separated. Forewing with numerous free marginal intercalary veins between $RSa1$ and CuA ; CuP of forewing proximally connected with CuA by cross vein *cua-cup*; CuP connected with AA by cross vein *cup-aa*; *cua-cup* located distally from *cup-aa*. Hind wing narrow, narrowed towards apex, greatest width of wing at 0.2 of wing length; costal projection widely rounded apically, located close to wing base. First tarsomere of middle and hind legs fused with tibia; claws of all legs ephemeropteroid. Abdomen with vestigial gill sockets present on abdominal segments III–VII. Subanal plate apically smoothly rounded, not elongated.

Derivation of name. The species epithet *trigonoptera* (adjective) reflects the nearly triangular shape of the hind wings.

Material. Holotype: female imago, No. 2658, ex. SP 454, Eocene, Baltic amber; housed in MAI; donated to MAI by Stefan Plota on 16 December 1999.

Description. Female imago, body length 5.0 mm; length of forewings 7.0 mm (Fig. 5A). Incomplete specimen, embedded in resin in lateral position (Fig. 6A, B). Head slightly damaged. Left side of thorax and right foreleg lost. Forewings, ventral part and tip of abdomen partly covered by resin cracks (Figs 5A, 6A, B). Left hind wing bent. Abdomen partly flattened laterally. Cerci lost. General colouration yellow to brown; legs blackish basally. For measurements see Supplemental Table 2.

Head brown with blackish spots. Eyes relatively small, widely separated. Antennae shorter than length of head; with dark brown scape and pedicel, and paler flagellum.

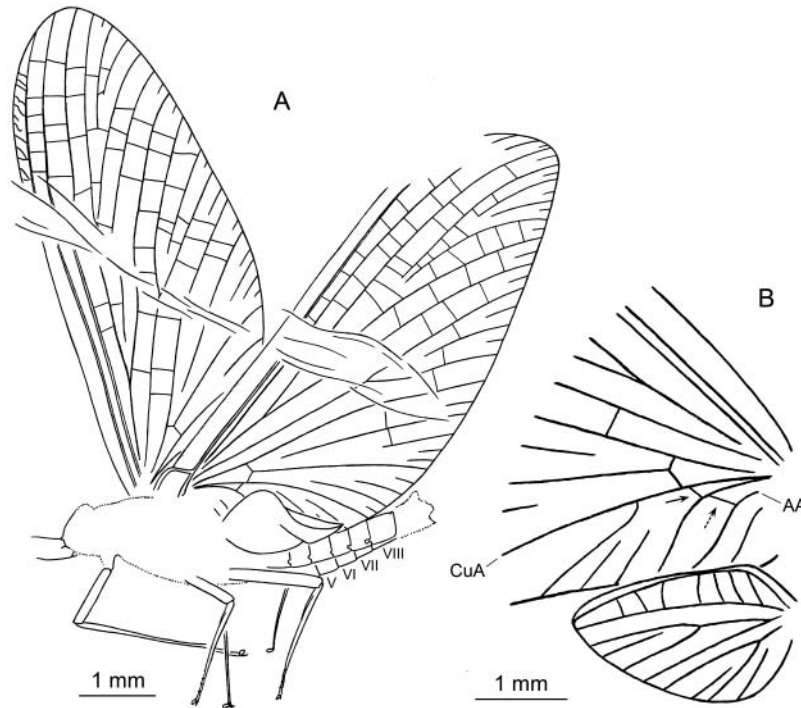


Figure 5. *Ephemerella trigonoptera* sp. nov., holotype, female imago, MAI, No. 2658, ex. SP 454. **A**, general lateral view, left side; abdominal segments V–VIII are marked by Roman numerals; **B**, right hind wing and base of right forewing, ventral view. Cross veins *cua-cup* and *cup-aa* are marked by solid and dotted arrows, respectively.

Thoracic characters hardly distinguishable; left side of mesothorax partly damaged, right side covered by resin influxes and cracks (Fig. 6A, B).

Wings partly translucent, hyaline with well-distinguishable longitudinal veins and cross veins. Basal part of forewings and most part of hind wings covered with blackish smudge. Forewing (Fig. 5A, B) with full set of longitudinal and intercalary veins, with numerous irregularly distributed cross veins, with free marginal intercalaries. CuP arising from CuA under acute angle and sharply bent posteriad, at point of bending connected with CuA by cross vein *cua-cup*, and more proximally connected with AA by cross vein *cup-aa* (Fig. 5B). Pterostigma with 12 irregularly curved, simple or branched, non-anastomosed oblique veins (Fig. 5A). Hind wings relatively narrow, narrowed towards apex, with costal projection and greatest width of wing at 0.2 of wing length; width/length ratio approximately 0.85 (Fig. 5B).

Legs well preserved, except right foreleg. For measurements of leg segments see Supplemental Table 2. Patella-tibial suture present on middle and hind legs, absent on forelegs. Tarsus of middle and hind legs shorter than half of tibia length; first tarsomere fused with tibia. Claws of all legs ephemeropteroid (inner claw blunt, outer claw pointed and hooked).

Abdominal segments well preserved, brown to blackish brown. Vestigial gill sockets on five abdominal segments

only, i.e. on segments III–VII (Fig. 6C). Subanal plate apically smoothly rounded, not elongated.

Occurrence. Baltic amber, middle Eocene (Lutetian Stage; 41.3–47.8 Ma).

Ephemerella sp. s. l.
(Fig. 7)

Material. Male subimago, SMNS BB-1401, housed in the SMNS amber collection.

Description. Male subimago. Body length 3.90 mm; length of forewing 4.20–4.25 mm (Fig. 7A, C). The specimen is completely embedded in resin in lateral position, but lateral and ventral side poorly visible because of ‘Verlummung’ and amber cracks (Fig. 7A). Both forewings completely preserved, but left wing bent. General colouration dark, yellow to dirty-brown.

Wings opaque, slightly translucent, with setation on posterior margins. In forewing, free marginal intercalary veins between iMP and CuA poorly visible, but present; CuP proximally connected with CuA by a crossvein *cua-cup*; CuP connected with AA by a crossvein *cup-aa* (Fig. 7B, C). Hind wing relatively large and of oval shape, distally broadly rounded, length 0.22 × forewing length, width/length ratio of hind wing approximately 0.50; RS and MP bifurcated; costal projection very small and slightly bent, slightly protruding

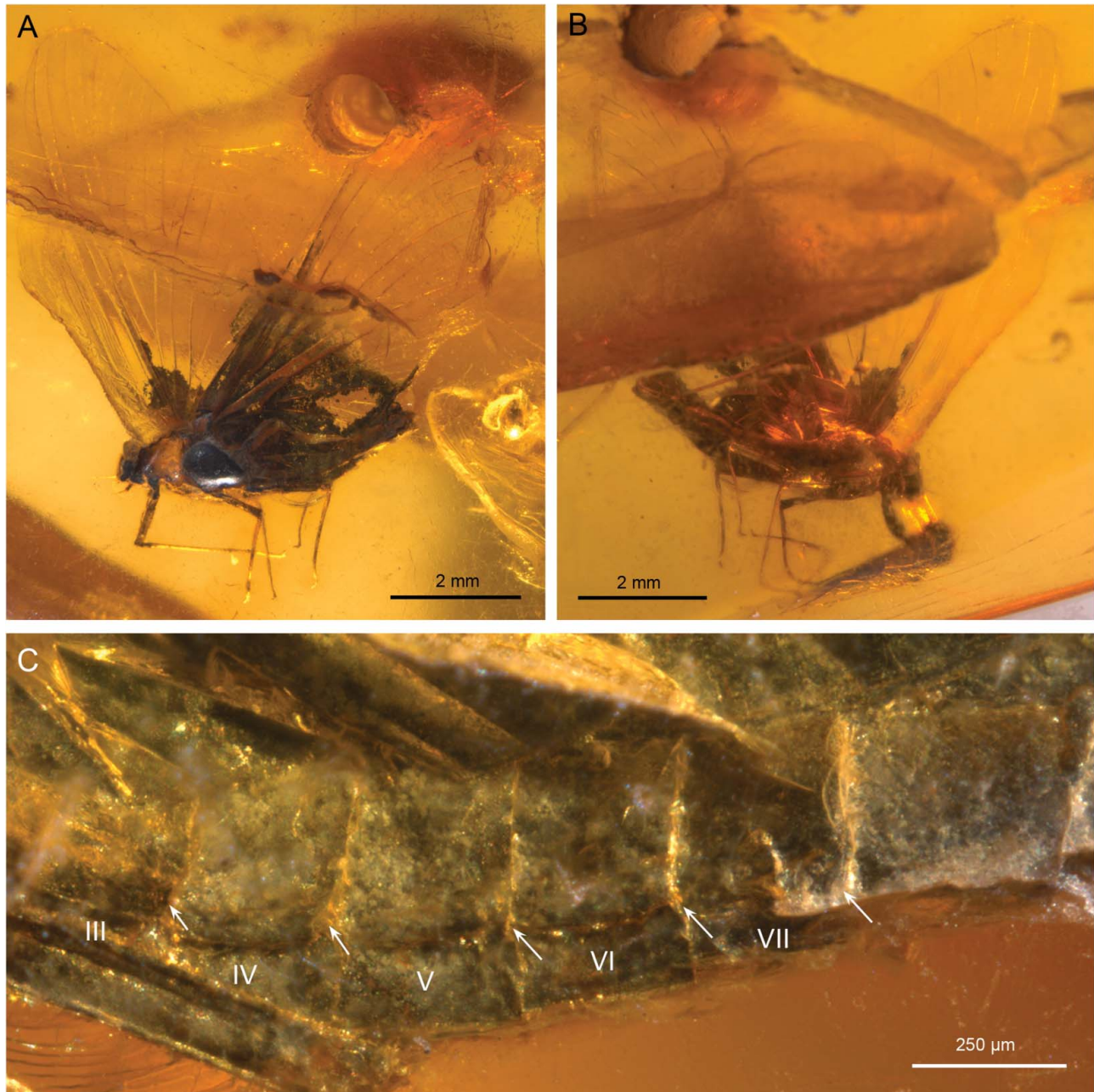


Figure 6. *Ephemerella trigonoptera* sp. nov., holotype, female imago, MAI, No. 2658, ex. SP 454. **A**, general lateral view, left side; **B**, general lateral view, right side; **C**, abdominal segments III–VII, left lateral view; traces of larval gill attachments on abdominal segments III–VII are marked by arrows; numbers of respective abdominal segments are marked by Roman numerals.

above anterior margin of wings (Fig. 7D). First tarsomeres of middle and hind legs fused with tibia. Claws of all legs ephemeropteroid (outer claw hooked and inner one blunt).

Abdominal segments completely preserved, covered with ‘Verlumung’; rudimentary gill sockets on abdominal segments III–VII. Paracercus well developed, slightly shorter than cerci.

Genitalia mostly covered with ‘Verlumung’ and not visible ventrally. In lateral view penis lobes slender, deeply separated. Gonostyli three-segmented, with sub-void segment III.

Occurrence. Baltic amber, middle Eocene (Lutetian Stage; 41.3–47.8 Ma).

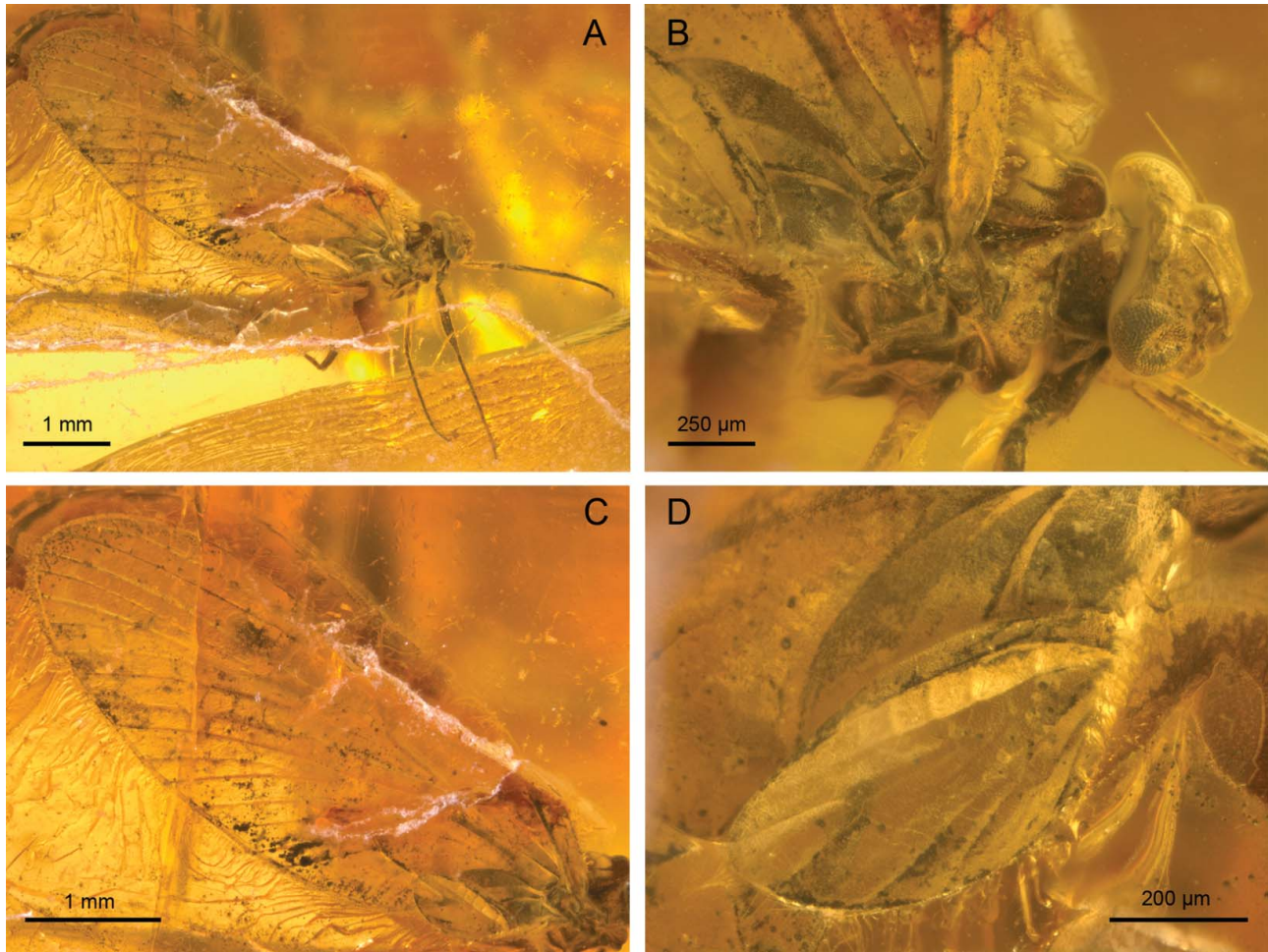


Figure 7. *Ephemerella* sp. *sensu lato*, female subimago, SMNS BA-1401. **A**, general dorsolateral view, right side; **B**, head, thorax and wing bases, dorsolateral view, both wings turned upwards; **C**, right forewing, ventral side; **D**, right hind wing, ventral side.

Discussion

Published records of fossil Ephemerellidae

An incomplete and badly preserved insect abdomen from the Chinese Late Jurassic was described as a mayfly nymph *Ephemeropsis tingi* by Ping (1935), which would imply its placement within the extinct mayfly family Hexagenitidae. However, larval stages of Hexagenitidae are characterized by a pisciform shape, and the abdomen bearing seven pairs of leaf-like gills, the seventh of which is considerably enlarged (Staniczek 2007). Neither the description nor the figure in Ping (1935) justifies such conclusions. Demoulin (1954) transferred it to *Turfanarella tingi* (Ping, 1935) suggesting a provisional placement within Ephemerellidae, thereby reinterpreting the lateral abdominal outgrowths on segments V–IX not as gills, but as posterolateral abdominal projections. However, Demoulin (1954) himself admitted that posterolateral projections are also present in other mayfly families, and Edmunds (1972) suggested that *Turfanarella* might

belong instead to Siphonuridae. In fact, such projections are also present in a variety of other Mesozoic and Palaeozoic insects (Rasnitsyn & Quicke 2002), and may even reflect a groundplan character of Pterygota (Staniczek *et al.* 2014). The lack of reliable autapomorphic characters of Ephemerellidae visible in this specimen prompted Kluge (2004) to place it within Euephemeroptera *incertae sedis*.

Philolimnias sinica Hong, 1979, a well-preserved imaginal specimen, was described from early Eocene Fushun amber, China, and was – without further reasoning – attributed to Ephemerellidae by Hong (1979). However, its actual description appears to be seriously flawed, depicting functional mouth parts and most unusual male genitalia in the specimen. Moreover, its forewing venation lacks cross veins *cua-cup* and *cup-aa* that are characteristic for all Ephemerelloidea (see below). Nevertheless, this specimen was included in a cladistic analysis of Ephemerelloidea by Jacobus & McCafferty (2006), where it nested as sister group to all other Ephemerelloidea (including

Vietnamella Tshernova, 1972 and *Austremerella* Riek, 1963). Thus, Jacobus & McCafferty (2006) erected a separate family Philolimnidae to accommodate this species. However, Kluge (2004) and Hubbard (1987) regarded it as Euephemeroptera *incertae sedis*, as this fossil does not match diagnostic features of Ephemerelloidea. We concur that its placement within Ephemerelloidea is doubtful, but its systematics needs further evaluation and will be treated elsewhere (Staniczek & Godunko in prep.).

Ephemerella shanwangensis Hong, 1983 was described from the middle Miocene of China, but later transferred to Heptageniidae by Zhang (1989). The figures provided with the original description, however, show a larva with allegedly flattened body, rectangular head, medially separated wing pads, posterior lateral projections on visible abdominal segments III–VII, and a well-developed paracercus. The entire habitus and visible characters point rather to a placement within Leptophlebiidae. Kluge (2004) attributed it to Euplectoptera *incertae sedis*.

Clephemera clava Lin, 1986 is another larval specimen with inadequate and insufficient description, described from the Middle Jurassic (Bajocian) terrestrial mudstone in the Shiti Formation of China. The sole line drawing figures the outline of a pisciform larva without any other phylogenetically informative characters visible, but just regarding its body shape it becomes obvious that its initial classification to Ephemerellidae is erroneous or at least very doubtful. Kluge (2004) placed it within Euephemeroptera *incertae sedis*.

This leaves the specimen described as *Ephemerella* (*Timpanoga*?) *viscata* by Demoulin (1968) as the only hitherto recorded fossil Ephemerellidae. Its attribution to Ephemerellidae is without any doubt, as it features the family's major diagnostic characters, such as: (1) male eyes large, divided into two portions (unlike Pantricyrithi *sensu* Kluge 2004); (2) distinct mesonotal suture (unlike Pantricyrithi); (3) forewing with free marginal intercalaries; (4) cubital field with long intercalary basally connected to CuA, and with successive, small proximal intercalaries; (5) hind wing well developed, with RS bifurcated; and (6) costal projection not prominent, with Sc terminating near apex (unlike *Teloganopsis* Ulmer, 1939 and *Hyratanella* Allen, 1980) (Kluge 2004). Its systematic position within Ephemerellidae, however, became apparent only after our reinvestigation (see below).

Generic characters available in winged stages of fossil Ephemerelloidea

The mayfly superfamily Ephemerelloidea (or *Ephemerella*/fg1 *sensu* Kluge 2004) is well characterized by its forewing venation: CuP in its proximal part is connected with CuA by a constant cross vein *cua-cup*, and with AA by a constant cross vein *cup-aa*; the vein *cua-cup* is located more distally than *cup-aa*; CuP arises from CuA

under acute angle and is sharply bent at the place of connection with *cua-cup* (Figs 1A, 5B). This wing venation is present in all representatives of Ephemerellidae and in those representatives of Pantricyrithi Kluge, 2004 whose wings are not highly modified.

Unlike in the general diagnosis of Ephemerelloidea, the majority of higher taxa within Ephemerelloidea are based on larval characters only. This applies for nearly all genus-group and family-group taxa within Ephemerellidae *sensu stricto* (or *Ephemerella*/fg2 *sensu* Kluge 2004). Unlike larval characters, the characters in winged stages (subimago and imago), such as wing shape and venation, cuticular pigmentation of subimaginal mesothorax, type of claws, length of paracercus, and genital structure, are either uniform among all Ephemerellidae, or are species specific. In most cases these characters do not allow a reliable determination of supra-specific taxa. This hampers a reliable determination of winged stages in fossil Ephemerellidae. However, some larval taxonomic characters are conserved in winged stages, especially so in the subimagines. While larval gills in mayflies are usually lost in the adult stages, in Ephemerellidae rudimentary gill sockets can be observed still in the subimago and sometimes also in the imago. The same applies for the length proportions of abdominal segments and the presence of posterolateral projections of abdominal segments VIII–IX, so examination of these characters can be helpful in assessing the systematics of fossil Ephemerellidae.

In larvae of all Ephemerelloidea, the first abdominal segment either bears a pair of stick-like gills on prominent sockets (thus appearing 'bipartite'), or lacks gills; in all cases winged stages have no sockets on the first abdominal segment. Lamellate gills in larval stages and their sockets in winged stages can be present from abdominal segment II onwards (in Pantricyrithi Kluge, 2004), or from abdominal segment III onwards (in Ephemerellinae, or *Ephemerella*/fg3 *sensu* Kluge 2004), or from abdominal segment IV onwards (in Timpanoginae, or *Timpanoga*/fg1 *sensu* Kluge 2004); the most posterior abdominal segment bearing gills in the larvae or corresponding vestigial sockets in winged stages is either segment VII, or one of the preceding ones (Kluge 2004, table 8). Using the segmental distribution of these sockets together with additional characters, we were able to attribute *Eurylophella viscata* comb. nov. and *Ephemerella trigonoptera* sp. nov. to subfamilies Timpanoginae and Ephemerellinae, respectively.

Generic attribution of *Eurylophella viscata*

Demoulin (1968) analysed the possible generic position of this fossil species within Timpanoginae. The extant genus *Attenella* Edmunds, 1971 (in Demoulin's paper treated as *Attenuanella* Edmunds, 1959 nom. praecoc.; for details see Edmunds 1971, p. 152), was excluded based on the

shape of the apical gonostylus segment. However, Demoulin neither provided a detailed description nor figured male genitalia. *Dannella* Edmunds, 1959 was also excluded by Demoulin based on leg proportions. However, we could not confirm Demoulin's leg measurements in our reinvestigation. Furthermore, Demoulin (1968) did not consider *Eurylophella* Tiensuu, 1935 in his considerations at all, but suggested close affinities to *Timpanoga* Needham, 1927 instead. This was based on the presence of prominent posterolateral projections of abdominal segments VIII and IX, and finger-like gill sockets on abdominal segments IV–VII. However, these characters are present also in other recent representatives of Timpanoginae. Moreover, further taxa of Timpanoginae, such as *Dentatella* Allen, 1980, were not yet known at that time and thus could not be considered by Demoulin (1968), which left the generic position of *Ephemerella* (*Timpanoga*?) *viscata* in limbo.

Studying the taxonomic and phylogenetic relationships of Timpanoginae, McCafferty (1977, 2000) and McCafferty & Wang (1994, 2000) suggested two distinct 'Dannella-Timpanoga' and 'Dentatella-Eurylophella' lineages. Burian (2002) assumed the synonymy of *Dentatella* and *Eurylophella*, because their divergence was based on larval characters only. However, this argument is not valid, as two clades may very well only differ in larval characters. Indeed, McCafferty *et al.* (2003) discussed *Dentatella* as the sister group of *Eurylophella*. Using combined molecular and morphological characters in a cladistic analysis of Ephemerellinae, Ogden *et al.* (2009) suggested monophyletic Ephemerellinae and Timpanoginae, the latter with the branching sequence *Timpanoga*+(*Dannella*+(*Dentatella*+*Eurylophella*)). *Attenella* nested within Ephemerellinae in the combined cladogram, but clearly grouped within Timpanoginae based on morphological characters only (Jacobus & McCafferty 2008; Ogden *et al.* 2009).

Demoulin (1968) attributed '*Ephemerella* (*Timpanoga*?) *viscata*' to the complex of subgenera corresponding to Timpanoginae (or *Timpanoga*/fg1 *sensu* Kluge 2004); this conclusion was based on the presence of gill sockets on abdominal segments IV–VII. However, he only figured the left side of the specimen, where the view of proximal abdominal segments is obstructed (see our Fig. 4A), and from his description the absence of gill sockets on abdominal segments II and III is not evident. Our examination of the opposite, right side of this specimen indeed revealed the absence of these sockets in question, so Demoulin's placement of this specimen within Timpanoginae is confirmed. The following considerations allow the attribution of this species to the genus *Eurylophella*:

1. We do not concur with Demoulin's (1968) assessment of foreleg proportions in this specimen, and also cannot confirm that its second tarsomere is longer than the third one. Our own measurements

reveal that the protibia is shorter than the protarsus, and the third tarsomere of the foreleg is slightly shorter than the second one (Fig. 3A; Supplemental Table 1). The same foreleg proportions are reported for *Eurylophella* (Allen & Edmunds 1963, p. 598).

2. Demoulin (1968) tentatively assigned the specimen to *Timpanoga* based on the presence of vestigial gill sockets on abdominal terga IV–VII and enlarged posterolateral projections on abdominal segments VIII and IX (Figs 1A, 4A, B). However, these characters are also present in the subimagines of recent species of *Eurylophella* (Keffermüller & Da Terra 1978, p. 31, figs 2, 3; McCafferty 1977, p. 885, fig. 12; Studemann & Tomka 1987, p. 370, fig. 21).
3. Abdominal segments VIII and IX of *E. viscata* are elongated, with segment VIII being significantly longer than segment VII, and segment IX being longer than segment VIII (Fig. 1A, C). This is characteristic for larvae and winged stages of the genus *Eurylophella* (or *Eurylophella*/fg2 *sensu* Kluge 2004), and allows this taxon to be distinguished from all other Timpanoginae (Kluge 2004).
4. Demoulin (1968) did not describe the genitalia in detail, as they are covered by 'Verlumung' except for the apical segments of gonostyli. The styliiger with its median projection is typical for Timpanoginae: the shape of gonostylus segment III is close to recent taxa of this subfamily, except for *Attenella* (whose attribution to Timpanoginae is questionable anyway) with its distinctly elongated apical segment (see for comparison our Figs 1C, 4C, D; Edmunds 1959, p. 543, fig. 1; McCafferty 1977, p. 885, fig. 11; McCafferty & Wang 1994, p. 576, fig. 11). The gonostyli of *E. viscata* are covered with small irregular spines, which are lacking in *Timpanoga*.
5. Subimaginal penes in general are shorter than their imaginal counterparts, but their apical part still can be useful for comparison. Its shape in *E. viscata* comb. nov. resembles that of recent species of *Eurylophella*, *Dentatella*, *Dannella* and *Attenella* in being apically broadly rounded with shallow incision, in contrast to the deeply incised, prominent and apically expanded penis of *Timpanoga*. Moreover, the penis has no visible spination, in contrast to *Timpanoga*.

Thus, the elongation of abdominal segments VIII and IX, foreleg proportions, shape of subimaginal penis, and genital spination do not support a generic placement of this specimen within *Timpanoga*, but rather support its transfer to the genus *Eurylophella*.

Within *Eurylophella*, *E. viscata* comb. nov. differs from most Recent species of *Eurylophella* by its significantly smaller size: its wing length is 8.10–8.14 mm, while in *E.*

karelica Tiensuu, 1935 forewing length is 11.5–12.5 mm, in *E. iberica* Keffermüller & Da-Terra, 1978 forewing length is 8.2–9.5 mm, and in *E. korneyevi* Martynov, Palatov & Godunko, 2015 (winged stages unknown), the larval body length is 9.7–12.5 mm. The size of *E. viscata* agrees with the total range size among Recent *Eurylophella*, with forewing lengths of 6–12.5 mm (Allen & Edmunds 1962). It can be separated from other small-sized species of *Eurylophella* (e.g. *E. iberica*, and other small Nearctic species) by the enlarged apical portion of the penis lobes.

Generic attribution of *Ephemerella trigonoptera* sp. nov.

The forewing venation of *E. trigonoptera* matches all diagnostic characters of Ephemerelloidea (see Discussion above: Generic characters) and moreover resembles the wing venation characteristics of Ephemerellidae (Fig. 5A, B).

The preserved part of the abdomen bears paired lateral gill sockets on five successive segments. The first of these sockets is situated so far from the hind leg base that it cannot belong to abdominal segment II. Thus, it is most likely that these sockets belong to segments III–VII. Abdominal segments I and II are not visible. Within Recent Ephemerelloidea, the occurrence of abdominal gills varies among different taxa: gills on abdominal segment I–VII are present only in *Vietnamella* Tshernova, 1972; *Austremerella* Riek, 1963 has gills on segments II–VII (Suter 1979; Suter & Mynott 2013; Hu *et al.* 2017), and gills on abdominal segments III–VII are present only in Ephemerellinae (*Ephemerella*/fg3 sensu Kluge 2004, p. 297, table 8).

The extant genus *Vietnamella* includes only a few species, with a distribution limited to the Oriental Region. Unlike *Vietnamella*, *Ephemerella trigonoptera* sp. nov. has free marginal intercalaries in the forewing, and its peculiar hind wing also differs from that of *Vietnamella* (see Kluge 2004, p. 318, fig. 95B, Hu *et al.* 2017, p. 385, figs 4B, 5B).

From the monotypic genus *Austremerella* with the single extant Australian species *A. picta* Riek, 1963, the fossil specimen differs in several thoracic and wing characters: (1) no long fine filaments on posterior margin of mesonotum (in contrast to a pair of filaments in *A. picta*) (Riek 1963, p. 50; Suter & Mynott 2013, p. 239, fig. 3b); (2) pterostigma of forewing with mostly simple and few branched, non-anastomosed cross veins (in contrast to numerous cross veins forming a double series of cellules in *A. picta*) (Riek 1963: 49, 50, fig. 10); (3) no cross veins between C and Sc in distal half of hind wing (in contrast to 8–9 cross veins in *A. picta* situated mainly distally); (4) at least seven cross veins between Sc and RA of hind wing (in contrast to 3–5 veins in *A. picta*); (5) costal process of hind wing situated more proximally (in contrast to *A. picta* with costal process situated more

distally); and (6) hind wing with triangular outline (in contrast to oval outline in *A. picta*).

As a consequence, we attribute this fossil specimen to Ephemerellinae (*Ephemerella*/fg3 sensu Kluge 2004), as all other known characters are also in agreement with the diagnosis of this taxon.

Ephemerellinae (*Ephemerella*/fg3 sensu Kluge 2004) includes *Torleya* Lestage, 1917, *Serratella* Edmunds, 1959, *Teloganopsis*, *Hyrtanella*, *Crinitella* Allen & Edmunds, 1963, *Drunella* Needham, 1905, *Cincticostella* Allen, 1971, *Caudatella* Edmunds, 1959, *Ephemerella sensu stricto* Eaton, 1883, and some other taxa regarded by different authors either as genera or subgenera (see McCafferty & Wang 2000; Kluge 2004; Jacobus & McCafferty 2008).

Within Ephemerellinae, the various genera can only be differentiated in the larval stage, so there is no reliable generic attribution possible for our specimen. However, in order to be able to name this specimen, we refer to the different genera of Ephemerellinae here as *Ephemerella sensu lato*, and place *E. trigonoptera* sp. nov. within this taxon.

The new species *E. trigonoptera* sp. nov. differs from other species of Ephemerellinae by the shape of the hind wing, which is markedly narrowed towards the apex and has a costal projection located more proximally than in most other *Ephemerella sensu lato* (Fig. 5B).

Taxonomic position of SMNS specimen

The fossil specimen can be excluded from *Vietnamella* by the shape and venation of the hind wings. The absence of fine filaments on the posterior margin of the mesonotum and the simple pterostigmatic venation of the forewing clearly separates *Ephemerella* sp. sensu lato from *Austremerella*. Moreover, its relatively small and widely separated eyes are in contrast to the large and medially contiguous eyes of male *A. picta* (Fig. 7B; Suter & Mynott 2013, p. 239, figs 2, 3A). The subimaginal genitalia of *Ephemerella* sp. sensu lato are poorly visible in dorsal and ventral view. However, a lateral view reveals slender penis lobes that are mostly separated (in contrast to the bulbous penis of *A. picta*, which is fused along almost its entire length). Finally, the terminal gonostylus segment is nearly conical in *Ephemerella sensu lato spec.* (in contrast to a subovoid segment III in *A. picta*; see Suter & Mynott 2013, p. 241, fig. 7a–c).

On the other hand, wing venation and allocation of rudimentary gill sockets on abdominal segments III–VII clearly point to a species within Ephemerellinae. However, we cannot attribute this fossil specimen with certainty to a described genus within Ephemerellinae. As it is poorly preserved and subimaginal genitalia are not well visible due to ‘Verlummung’, which makes it impossible to differentiate this specimen from other Ephemerellinae, we refrain from naming this specimen and treat it here as *Ephemerella* sp. sensu lato.

Biogeographical considerations

The extant worldwide distribution of Ephemerelloidea is in sharp contrast to its almost complete absence in the fossil record. Likewise, other panotote mayflies are also only rarely recorded, and most records are confined to the Neogene. Within Protopistomatoidea, only Baetiscidae are known both from Eocene Baltic amber (Staniczek & Bechly 2002; Godunko & Krzemiński 2009) and the Lower Cretaceous of Brazil (Staniczek 2007; Pescador *et al.* 2009). Within Caenoidea, there are records of Neophemeridae from the Oligocene of Montana (Lewis 1977; Bae & McCafferty 1998); and fossil Caenidae are reported from the Miocene of Japan (Fujiyama & Nomura 1986). Likewise, they are also present in Miocene Dominican amber (authors' pers. obs.).

The discovery of Ephemerellinae and Timpanoginae in Baltic amber confirms their existence at least back to the Palaeogene. Within Ephemerellidae, most genera of Timpanoginae are confined to the Nearctic Region. *Eurylophella* is the only genus of Holarctic distribution, but with 15 Recent Nearctic species and only three Recent species in the Western Palearctic, its centre of distribution is likewise the Nearctic Region (Martynov *et al.* 2015). However, the Recent diversity of Timpanoginae in the Nearctic does not necessarily imply its Nearctic origin. The discovery of *Eurylophella viscata* in Baltic amber at least confirms that the presence of Timpanoginae in the Palearctic Region dates back to the Palaeogene, so the biogeographical origin of this taxon remains uncertain. There are also other Recent mayfly taxa either confined to the Nearctic or having a Nearctic centre of species distribution, e.g. Baetiscidae or Metretopodidae. However, new findings over the last decade revealed that Baetiscidae had stem-group representatives in Baltic amber (Staniczek & Bechly 2002; Godunko & Krzemiński 2009), and the fossil species diversity of Metretopodidae in the Palearctic by now equals its extant diversity in the Nearctic (Staniczek & Godunko 2012, 2014, 2016; Godunko & Staniczek in prep.). This may point to rather recent geological and palaeoclimatic processes that shaped the present distribution and biodiversity of Timpanoginae, and Holarctic mayfly taxa in general.

Palaeoecological considerations

Due to the specific fauna and flora discovered in Baltic amber along with investigations on Eocene climate, it is generally assumed that Baltic amber forests were present in a paratropical to subtropical environment (Weitschat & Wichard 1998, 2002). As first pointed out by Wheeler (1914) for ants, the faunal composition in Baltic amber indicates a strange mixture of thermophilic species and species rather adapted to a temperate climate. Archibald & Farrell (2003) referred to this phenomenon as 'Wheeler's Dilemma' and hypothesized the specific

faunal composition may be due to a rising cold month mean and may not necessarily be an indicator of raised mean annual temperature, thus indicating early Tertiary equability with milder winters, and not necessarily tropical or subtropical climate.

Another explanation for the presence of genera adapted to temperate regions was put forward by Ulmer (1912), who investigated the faunal composition of caddisflies in Baltic amber. He assumed the presence of mountainous regions in the Baltic amber forests including cool streams and rivers to accommodate the observed species, which are bound to these habitats. This assumption was further elaborated and supported by Ander (1942). The discovery of ground beetles belonging to the genus *Trechus* Clairville, 1806 in Baltic amber (Schmidt & Faille 2015; Schmidt *et al.* 2016) gave further recent support to this theory.

However, the aquatic mayfly fauna in Baltic amber raises even more questions. It is possible to find genera of Recent boreal distribution, such as *Ameletus* sp. (Ameletidae, see Godunko *et al.* 2008) that are today confined to cold creeks at higher altitudes (Buffagni *et al.* 2009). A number of other species recorded from Baltic amber represent Recent genera (e.g. *Heptagenia* Walsh, 1863, *Rhithrogena* Eaton, 1881, and *Ecdyonurus* Eaton, 1868, all Heptageniidae; see Demoulin 1968; Godunko 2004, 2007) that today are mainly found in epirhithral river sections, although they are reported to have a wider ecological plasticity and occasionally also can be found in other ecological stream zones (Buffagni *et al.* 2009). For those genera, it might have been possible to migrate to higher altitude in order to escape higher water temperatures. However, there were also some genera present in streams of Eocene amber forests that today inhabit predominantly metarhithral to epipotamal river sections in temperate regions. *Kageronia fuscogrisea* (Retzius, 1783) (Heptageniidae), *Analetris secundus* Godunko & Kłonowska-Olejniki, 2006 (Acanthametropodidae), *Balticobaetisca* spp. (Baetiscidae), *Siphloplecton* spp. (Metretopodidae), and now also *Eurylophella* (Ephemerellidae) are all reported from Baltic amber (Kluge 1986; Staniczek & Bechly 2002; Godunko & Kłonowska-Olejniki 2006; Godunko & Krzemiński 2009; Staniczek & Godunko 2012, 2015, 2016). These species generally prefer medium- to large-sized lowland rivers and can only occasionally be expected in first- or second-order streams in both lowland and mountainous areas (e.g. some Nearctic *Eurylophella*; Dr L. M. Jacobus, pers. comm.).

While we may explain the occurrence of some rhithral genera with the presence of higher mountains in the Baltic amber forest, this becomes difficult when it comes to presumably metarhithral to epipotamal species that need to meet their ecological requirements in lowland rivers and thus would not easily have had the chance to migrate upstream to higher altitudes in order to escape subtropical temperatures. Either these genera had different thermal regimes and different ecological preferences back in the

Eocene, or there were indeed epipotamal river sections present at higher altitude, i.e. high mountain plateaus that provided suitable refugia for epipotamal species, among them most likely *Eurylophella viscata*.

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Supplemental data

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