



## New Protosmylinae (Neuroptera: Osmylidae) from the early Eocene of western North America, with taxonomic remarks

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### Abstract

The osmylid subfamily Protosmylinae is revised based on our emended diagnosis: *Petrushevskia* Martynova, 1958 and *Mesosmylidus* Jepson *et al.*, 2012 are excluded (both considered Osmylidae *incertae sedis*), and *Sogjuta* Martynova, 1958 is transferred to it from the Mesosmylininae. The late Eocene genus *Protosmylus* Krüger, 1913 is considered a junior synonym of *Osmylidia* Cockerell, 1908 based on a distinct apomorphy (deeply forked MA in the hind wing), **syn. nov.** Three new species of *Osmylidia* from the early Eocene of North America are described: *O. donnae* **sp. nov.** from Quilchena, *O. glastrai* **sp. nov.** from Republic, Washington, USA, and an unnamed species of *Osmylidia* is reported from Driftwood Canyon Provincial Park, British Columbia (all localities of the Okanagan Highlands series), and *O. taliae* **sp. nov.** from the Green River Formation of Colorado, USA.

**Key words:** Neuroptera, Osmylidae, Protosmylinae, Okanagan Highlands, Green River Formation, Baltic amber, Eocene.

### Introduction

The extant Osmylidae is a rather small neuropteran family of about 150 extant species distributed in warm-temperate to tropical forests globally except North America (Oswald 2021). Their absence in North America today is puzzling, as they are distributed in similar environments in Europe, East Asia and South America, and occurred in North America at least until the Oligocene.

Nine subfamilies are currently recognized, eight extant (Gumillinae, Kempyninae, Osmylinae, Protosmylinae, Spilosmylinae, Porisminae, Eidoporisminae, Stenosmylinae; the first five with a fossil record), and one extinct (Mesosmylininae) (Winterton *et al.* 2019).

The family has a rich fossil record with 62 fossil species described in 39 genera from the Early Jurassic to the Miocene (see Winterton *et al.* 2019; Khramov 2020; Ma *et al.* 2020a, b).

Only five of these species are from the Cenozoic, three of which belong to the Protosmylinae, all from the Priabonian (late Eocene): *Protosmylus pictus* (Hagen in Pictet-Baraban & Hagen, 1856) from Baltic amber (Pictet-Baraban & Hagen 1856; Krüger 1923; Wichard *et al.* 2009); *Osmylidia requieta* (Scudder 1890) and *Pseudosmylidia relictata* Makarkin, 2017 from Florissant, Colorado, U.S.A. (Scudder 1890; Cockerell 1908, 1913, 1914; Carpenter 1943; Makarkin 2017).

Here, we describe the Protosmylinae of the Ypresian (early Eocene) of North America and revise the composition of the subfamily.

## Materials and methods

We examined four fossils, one each from Ootsa Group shale at Driftwood Canyon Provincial Park near the village of Smithers and from the Coldwater Beds at Quilchena, near the town of Merritt, all in British Columbia, Canada; from an exposure of the Tom Thumb Member of the Klondike Mountain Formation in the town of Republic, Washington, USA, about 40 kilometers south of the international boundary, and from the Parachute Creek Member of the Green River Formation in the Piceance Basin (the eastern portion of Eocene Lake Uinta in northwestern Colorado). The first three are part of the Okanagan Highlands series of fossiliferous lacustrine shale deposits scattered across about a thousand kilometers between Driftwood Canyon, the northernmost site, to Republic (Archibald *et al.* 2011). They span the latter half of the Ypresian: Driftwood Canyon has an estimated age of  $51.77 \pm 0.34$  Ma by U–Pb zircon analysis (Mortensen and Archibald work in progress cited by Moss *et al.* 2005); Quilchena has an age of  $51.5 \pm 0.4$  Ma (Villeneuve & Mathewes 2005) and Republic of  $49.4 \pm 0.5$  Ma (Wolfe *et al.* 2003), both by  $^{40}\text{Ar}$ – $^{39}\text{Ar}$  analysis. All had montane forests and upper microthermal to lower mesothermal (Quilchena) climates (Archibald *et al.* 2011, Mathewes *et al.* 2016).

The fossil from the Parachute Creek Member of the Green River Formation in the Piceance Basin is from the so called ‘B-Groove’ exposure (D. Kohls, pers. comm.), 45 meters below the Mahogany Bed (see Young 1995: Fig. 4). The Green River Formation spans the latter half of the Ypresian, from about 48.5 to about 51 million years ago (Smith *et al.* 2003, 2008), and the fossil is in the upper horizons of the Parachute Creek Member, approximately 49 Ma old (Smith *et al.* 2008).

We also examined photographs of 17 fossils from Jurassic localities at Shar-Teg (Mongolia) and Daohugou (China), and from the Eocene of Florissant (Colorado, USA), and Baltic amber.

Drawings were done from the fossils and photographs. Photographs are composites of close-up images of the fossils wetted with ethanol.

We follow the wing venation terminology of Breitkreuz *et al.* (2017).

Venation abbreviations: 1A–3A, anal veins; C, costa; Cu, cubitus; CuA, anterior cubitus; CuP, posterior cubitus; dn, distal nygma; M, media; MA, anterior media; MP, posterior media; pn, proximal nygma; R, radius; RA, anterior radius; RP, posterior radius; RP1, most proximal branch of RP; Sc, subcosta.

Repositories and institutional abbreviations: GPIH, Geological-Palaeontological Institute and Museum, University Hamburg (now CeNak: Centrum of Natural History); MCZ, Museum of Comparative Zoology, Cambridge, MA, USA; RBCM, Royal British Columbia Museum, Victoria, BC, Canada; SFU, Simon Fraser University (Department of Biological Sciences), Burnaby, BC, Canada (“Q” number); SR, Stonerose Interpretive Center, Republic, Washington, USA; UCM, the Museum of Natural History of the University of Colorado, Boulder, USA.

## Systematic paleontology

### Class Insecta Linnaeus, 1758

### Order Neuroptera Linnaeus, 1758

### Family Osmylidae Leach, 1815

### Subfamily Protosmylinae Krüger, 1913

**Type genus.** *Protosmylus* Krüger, 1913 (= *Osmylidia* Cockerell, 1908).

**Emended diagnosis (based on wings).** Wings may be distinguished from those of other subfamilies of Osmylidae by a combination of the following.

Forewing: Subcostal veinlets almost always simple (very rarely some forked) [Osmylinae: mostly forked]; trichosors along almost entire wing margin [Gumillinae: restricted to apical region]; one subcostal crossvein, positioned basally [Porisminae: numerous along entire subcostal space]; all or nearly all crossveins in radial space forming three to four gradate series (except some *Lysmus*) [all or nearly all crossveins (Gumillinae, Porisminae, Eidoporisminae) or proximal crossveins (other subfamilies) irregularly arranged]; M forked at level or only slightly

proximal termination of A1 [Osmylinae, Kempyninae: much distad; Stenosmylinae, Porisminae, Eidoporisminae: much proximad]; between CuA, CuP  $\leq 5$  crossveins (up to 8 in some *Lysmus*) [Spilosmylinae: about 10 or more]; CuA pectinate, with 2–6 branches; CuP with 3–7 pectinate branches (up to 9 in some *Lysmus*) [Spilosmylinae: 8–15].

Hind wing: MP lacks anteriorly directed basal spur-like process [Spilosmylinae: present]; CuP relatively short, shallowly (not pectinately) branched or simple [Kempyninae, Osmylinae, Stenosmylinae, Porisminae, Eidoporisminae: long, pectinately branched].

**Genera included.** Ten genera: †*Sogjuta* Martynova, 1958 (Early to Late Jurassic, Kyrgyzstan and Mongolia), **sit. nov.**; †*Juraheterosmylus* Wang *et al.*, 2010 (late Middle / early Late Jurassic, China); †*Jurosmylus* Makarkin & Archibald, 2005 (Late Jurassic, Kazakhstan); †*Protosmylina* Jepson *et al.* 2009 (Early Cretaceous, England); †*Osmylidia* (= *Protosmylus*, Priabonian, Baltic amber, **syn. nov.**), and †*Pseudosmylidia* Makarkin, 2017 (Priabonian, North America and Europe); *Heterosmylus* Krüger, 1913, *Gryposmylus* Krüger, 1913, and *Lysmus* Navás, 1911 (extant, all southeastern Asia); *Paryphosmylus* Krüger, 1913 (extant, Ecuador).

**Remarks.** The venation of some species of *Lysmus* is very similar to that of the Spilosmylinae, *e.g.*, *L. harmandinus* Navás, 1910 (see Makarkin 1985: Fig. 3; Winterton *et al.* 2019: Fig. 34). Moreover, this genus had long been considered a member of the Spilosmylinae. *Lysmus*, however, lacks an important synapomorphy of Spilosmylinae, the presence of an anteriorly directed basal spur-like process in the hind wing MP. Also, the male genitalia of *Lysmus* are typical for Protosmylinae (see Wang 2010).

According to Article 40.1 of ICZN, a family-group name is not replaced with a new family-group name when the name of its type genus is considered to be a junior synonym of another genus. Hence, Protosmylinae retains this name following designation of *Protosmylus* as a junior synonym of *Osmylidia*.

## Genus *Osmylidia* Cockerell, 1908

*Osmylidia* Cockerell, 1908: 342.

*Oligosmylus* Krüger, 1913: 34.

*Protosmylus* Krüger, 1913: 30, **syn. nov.**

**Type species.** *Osmylus requietus* Scudder, 1890, by monotypy.

**Included species.** *Osmylidia donnae* **sp. nov.**, (mid Ypresian, Quilchena), *O. glastrai* **sp. nov.** (late Ypresian, Republic), *O. taliae* **sp. nov.** (late Ypresian, Green River Formation); *Osmylidia* sp. (mid Ypresian, Driftwood Canyon), *O. requieta* (late Priabonian, Florissant), *O. picta* (Hagen in Pictet-Baraban & Hagen, 1856) (Priabonian, Baltic amber), **comb. nov.**

**Revised diagnosis.** Separated from other genera of the subfamily by hind wing MA deeply forked [shallowly forked in other genera (unknown in Mesozoic *Sogjuta*, *Jurosmylus* and *Protosmylina*)], female procoxa with a large process (clearly seen only in *O. picta*) [absent in other genera]. Forewing venation differs from that of other fossil genera by greater number of CuP branches (5–7) [ $\leq 4$  in *Sogjuta*, *Juraheterosmylus*, *Jurosmylus*, *Pseudosmylidia*; unknown in *Protosmylina*].

**Occurrence.** Eocene (Ypresian to Priabonian) of North America and northern Europe.

**Remarks.** The forewing character states of extant genera vary greatly among their species, covering almost the entire range of those of the family, but the shallowly forked hind wing MA is consistent in these genera.

The proximal crossveins in the forewing radial space of *Osmylidia requieta* are arranged rather irregularly (see *e.g.*, Carpenter 1943: Fig. 2). This is associated with at least eight and as many as ten crossveins between RA and RP while all other species of the genus possess at most six. We interpret this greater number of crossveins in these spaces and their arrangement as a species character.

### *Osmylidia glastrai* **sp. nov.**

Fig. 1

**Type material.** Holotype SR 02-22-15 (part) collected by Joshua Glastra, August 24, 2002; deposited in SR. A well-preserved almost complete forewing.

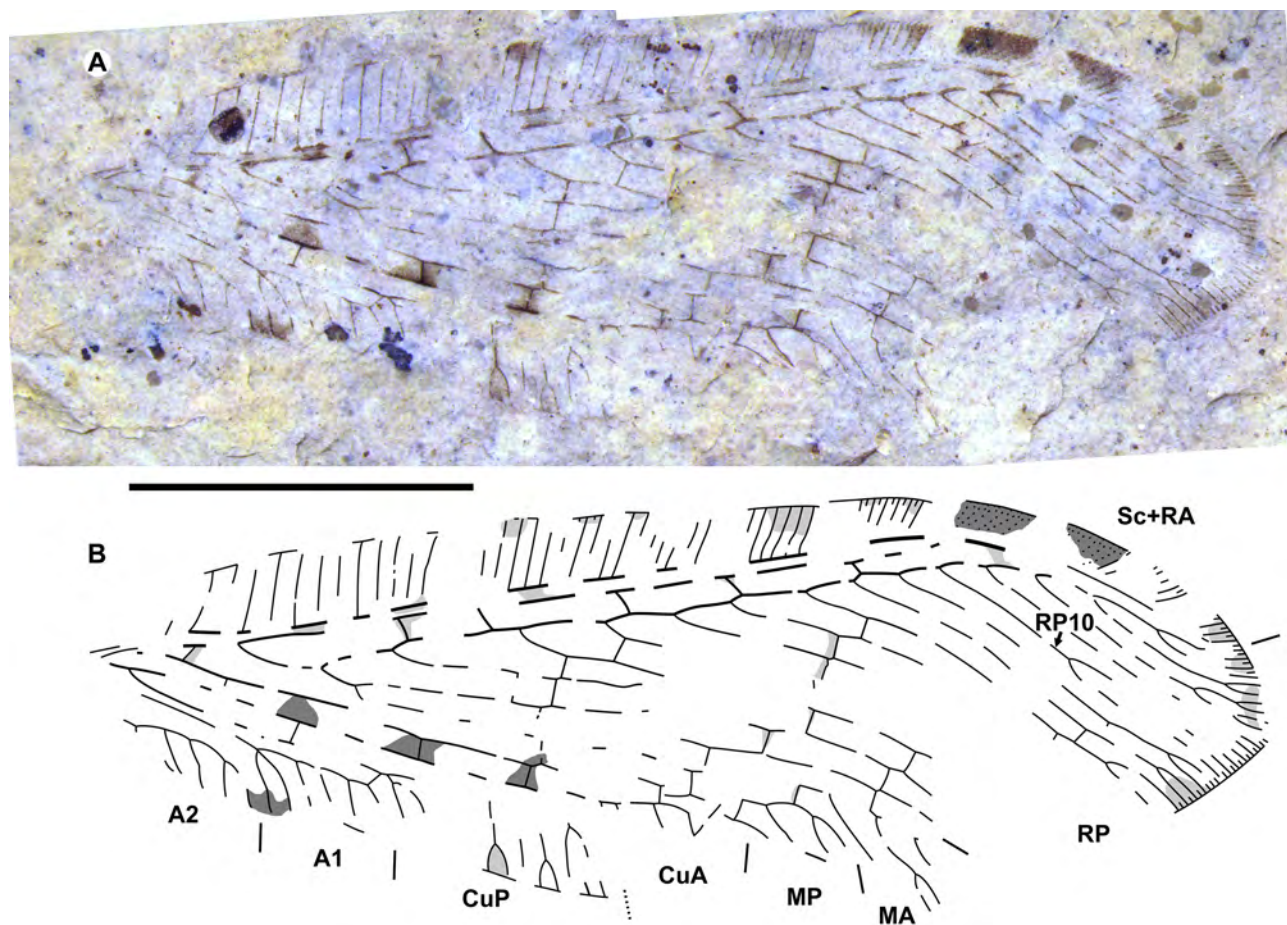
**Type locality and horizon.** Exposure B4131 of the Tom Thumb Member of the Klondike Mountain Formation in the town of Republic, Washington, U.S.A.; Eocene (late Ypresian).

**Etymology.** From the surname of Joshua Glastra, collector of this fossil.

**Diagnosis.** Forewings may be distinguished from those of other species of the genus by faint colour patterning (*O. picta*: strongly spotted; *O. requieta*: without spots).

**Description.** Forewing *ca.* 17 mm long, *ca.* 5.7 mm wide. Costal space broad, with subcostal veinlets simple, closely spaced. Sc fused with RA far from wing apex. Sc+RA veinlets simple, closely spaced. Subcostal space narrow; crossveins not detected. RA space relatively narrow, with five preserved crossveins, rather regularly spaced; one distal crossvein probably not preserved. RP originates rather close to wing base, with 14 pectinate branches, one of these (RP10) deeply forked. M forked distad origin of RP1, proximad origin of RP2. All crossveins (beside one proximal) in radial and radio-medial spaces arranged in three gradate series: proximal series with five crossveins; intermediate series with eight crossveins; outer series with seven preserved crossveins (partly fragmentarily preserved). Basal crossvein in radio-medial space connects R, M. Both MA, MP pectinately branched distally, with three branches. Four crossveins between MA, MP; five preserved crossveins between MP, CuA. CuA pectinately branched, with three branches. CuP pectinately branched, with five preserved branches (probably six or seven in life). One preserved crossvein detected between CuA, CuP. One distal crossvein between CuP, A1. A1 relatively long, with five pectinate, simple branches. A2 relatively long, with four preserved pectinate, simple branches. Wing colouration: irregular spots throughout wing (surrounding some crossveins, in subcostal space and along margin), most prominently three between MP, CuA, one along margin near termination of CuP, A1, and two on pterostigma.

**Remarks.** The species has a five-branched CuP and, therefore, is assigned to *Osmylidia* (see genus diagnosis) but only tentatively, as this character is unknown in one fossil genus, and *Osmylidia* is barely distinguished from extant genera solely by forewing venation.



**FIGURE 1.** *Osmylidia glastrai* sp. nov., holotype forewing SR 02-22-15. A, photograph; B, drawing. Scale bar = 5 mm.

*Osmylidia donnae* sp. nov.

Fig. 2

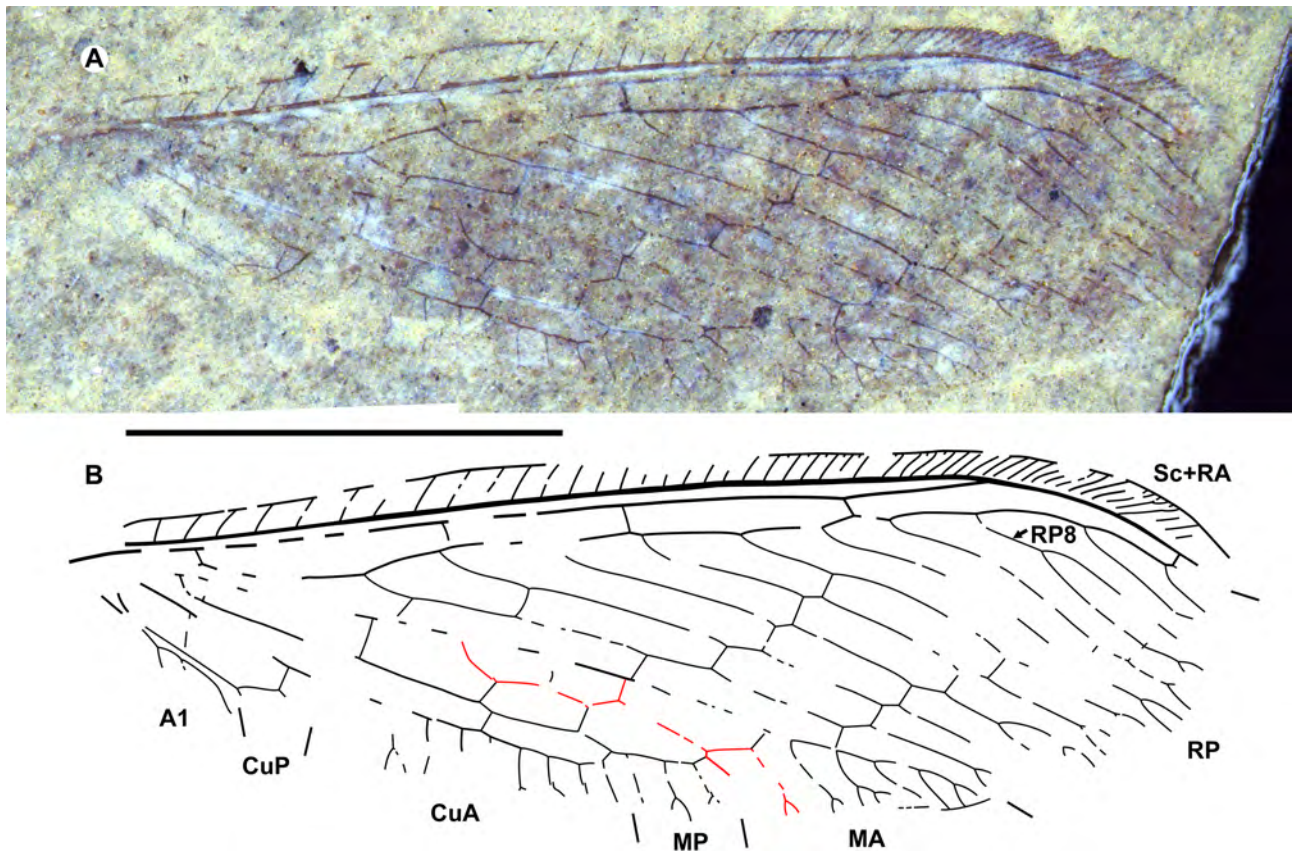
**Type material.** Holotype Q-0317, collected by RWM, October 2001; deposited in SFU. A rather well-preserved almost complete hind wing.

**Type locality and horizon.** Quilchena, British Columbia, Canada; Eocene (mid-Ypresian).

**Etymology.** From the first name of Donna Mathewes, for her support of fieldwork at Quilchena.

**Diagnosis.** May be distinguished from hind wings of other species of the genus by long distal crossvein between posterior branch of MA, MP [other species: this crossvein short or lacking as these veins fused for short distance], and membrane slightly infusate [other species: hyaline].

**Description.** Hind wing 13.5 mm as preserved (estimated complete length about 14 mm), 4.3 mm wide. Costal space relatively narrow, with simple, relatively closely spaced subcostal veinlets. Sc fused with RA far from wing apex. Sc+RA veinlets simple, closely spaced. Subcostal space narrow; crossveins not detected. RA space relatively narrow, with four widely spaced crossveins. RP with 10 branches, RP8 deeply forked, other branches shallowly forked. Basal crossvein 1r-m preserved fragmentarily, near RP. M forked near base wing, slightly proximad origin of RP. MA deeply forked, proximad level of proximal crossvein between RP1, RP2. All crossveins in radial, radio-medial spaces arranged in three gradate series: proximal series with two crossveins; intermediate series with five crossveins; outer series with eight preserved crossveins (region partly missing or damaged). Anterior branch of MA pectinately branched with four branches; posterior branch of MA with terminal fork, one incompletely preserved branch. MP pectinately branched with two branches. Two crossveins (one fragmentarily preserved) between MA, MP proximad forking of MA; three crossveins between anterior, posterior branches of MA, between posterior branch of MA, MP (including long distal crossvein, *i.e.*, posterior branch of MA, MP not fused). CuA strongly pectinately branched, with seven preserved branches (probably eight in life). CuP relatively short, forked once distally. Two crossveins between CuA, CuP. 1A with two pectinate branches. Membrane mostly slightly infusate (as preserved; perhaps uniformly infusate in life?).



**FIGURE 2.** *Osmylidia donnae* sp. nov., holotype hind wing Q-0317. A, photograph; B, drawing of venation (colouration omitted, refer to photograph). Posterior branch of MA in red. Scale bar = 5 mm.

*Osmylidia taliae* sp. nov.

Fig. 3

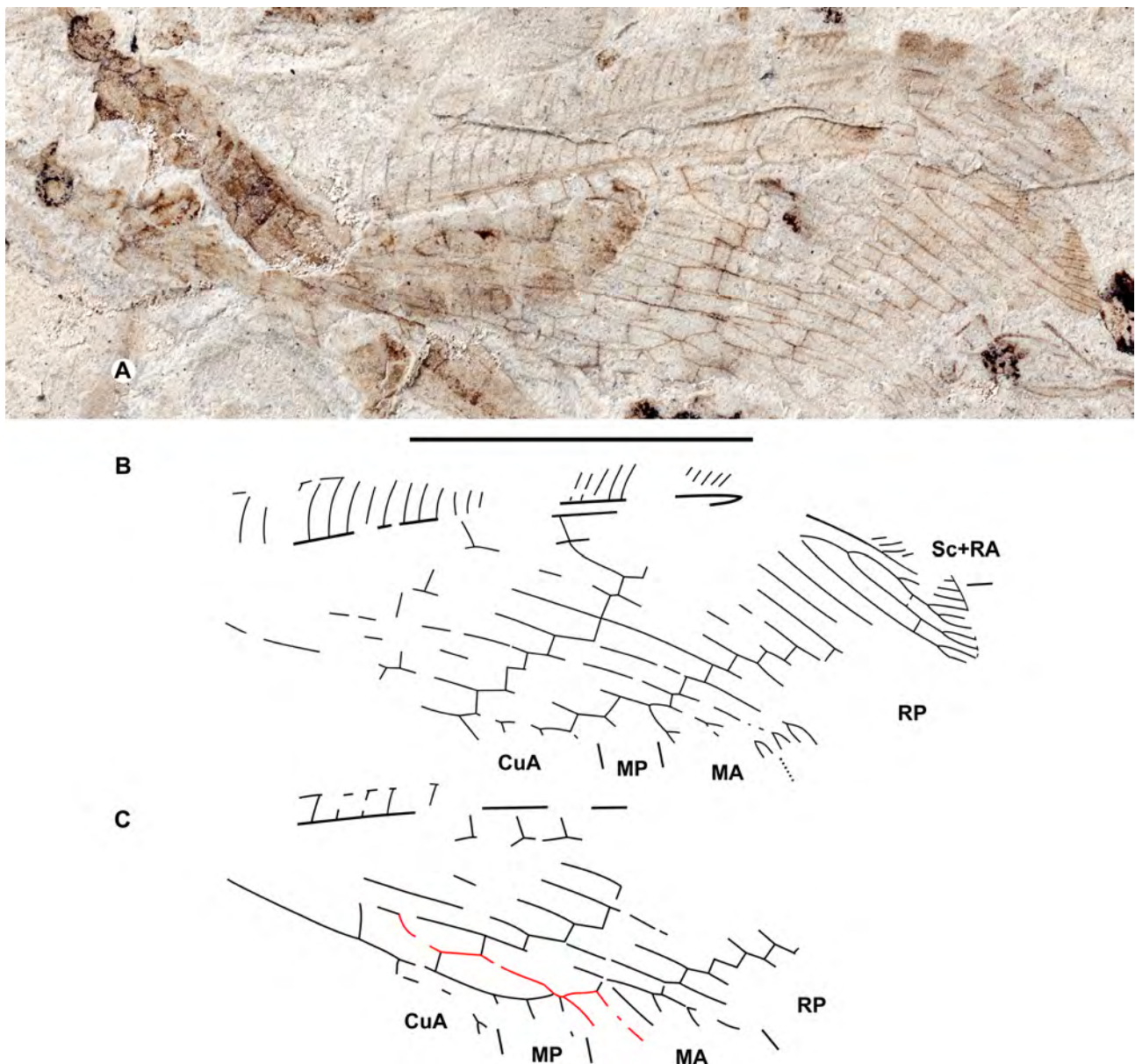
**Type material.** Holotype UCM 67996, collected by David Kohls, 4 March 2004; deposited in UCM. A poorly preserved incomplete specimen with at least small portions of all four wings.

**Type locality and horizon.** UCM locality 2005025 (Anvil Points Kohls site); Garfield County, Colorado, U.S.A. Parachute Creek Member of the Green River Formation; late Ypresian (early Eocene).

**Etymology.** From the first name of Talia Karim, for her long-standing helpful support of paleoentomology.

**Diagnosis.** May be distinguished from other species of the genus by forewing stem of RP distally pectinately branched [other species: dichotomously branched]; MP not branched at outer gradate series [other species: branched]; hind wing posterior branch of MA fused with MP for short distance [other species (except some specimens of *O. picta*): separate, connected by crossvein].

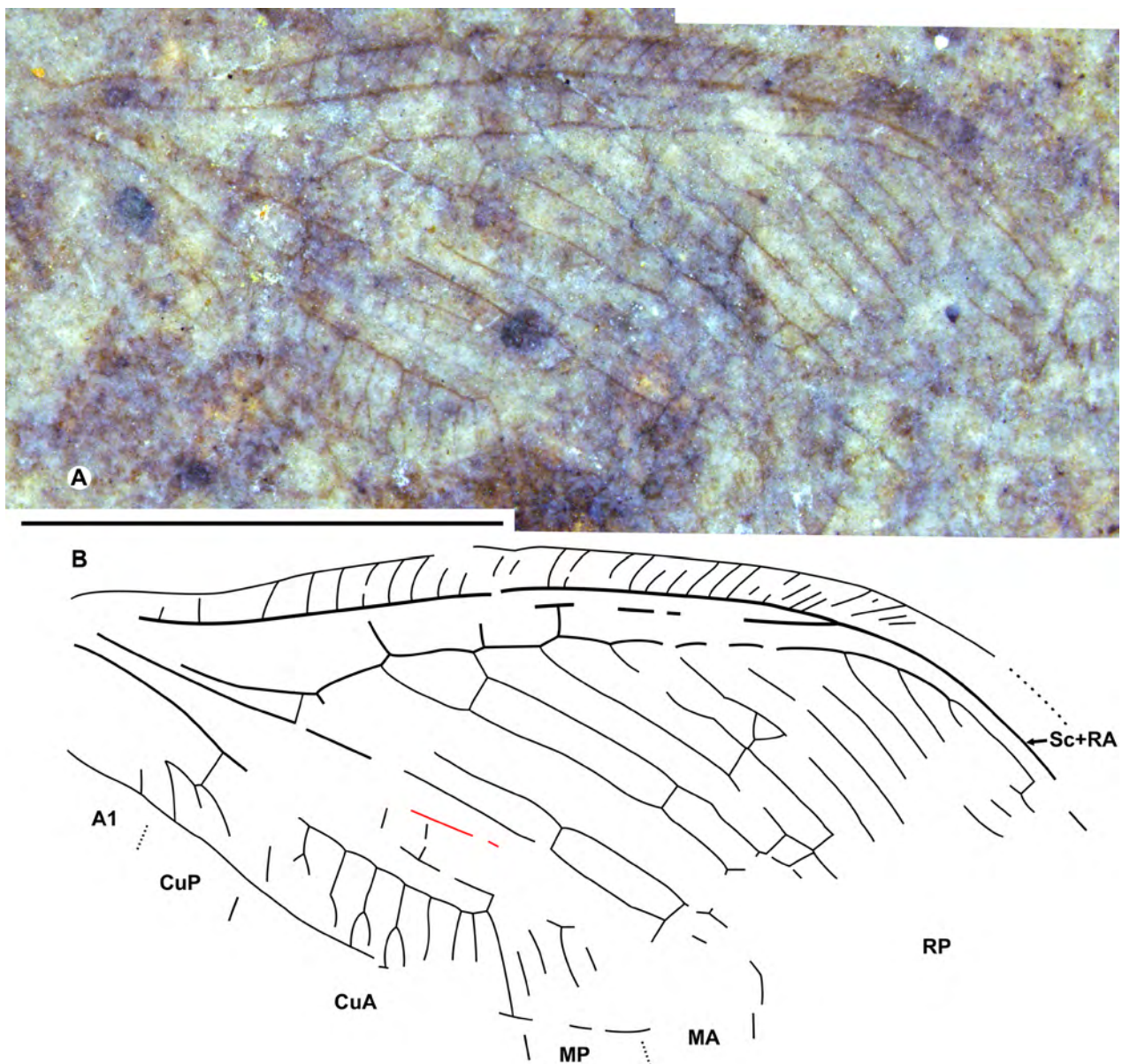
**Description.** Body poorly preserved, ca. 9 mm long; details not discernable.



**FIGURE 3.** *Osmylidia taliae* sp. nov., holotype UCM 67996 from the Green River Formation. A, photograph of the part; B, drawing of forewing venation; C, drawing of hind wing venation. Posterior branch of MA in red. Scale bar = 5 mm (all to scale).

Forewing *ca.* 14 mm long, *ca.* 4.8–5.0 mm wide. Costal space broad, with subcostal veinlets simple, closely spaced. Sc fused with RA far from wing apex. Subcostal space narrow in distal portion; crossveins not detected. RA space relatively broad medially, with two preserved crossveins. RP with 11 pectinate branches, all shallowly forked. All preserved crossveins in radial to medio-cubital spaces arranged in three gradate series: proximal series with three preserved crossveins; intermediate series with eight preserved crossveins; outer series with 11 preserved crossveins (probably 14 in life). MA pectinately branched distally, probably with three branches. MP probably shallowly branched (apex not preserved), at least not branched at outer gradate series or proximad it. CuA pectinately branched, with three preserved branches. Wing colouration: faint spots at pterostigma and along apical margin; some crossveins in gradate series appear surrounded by fuscous colouration.

Hind wing 7.5 mm long as preserved (estimated complete length *ca.* 13 mm), *ca.* 3 mm wide as preserved (estimated complete width *ca.* 3.5 mm). Costal space moderately broad, with simple, relatively closely spaced preserved subcostal veinlets. Three closely spaced crossveins preserved in RA space medially. RP with five partially preserved branches. MA deeply forked, distally pectinately forked, with at least three branches. MP pectinately forked with two branches. CuA fragmentarily preserved. Crossveins in radial, radio-medial spaces arranged in two preserved gradate series: intermediate series with four preserved crossveins; outer series with six preserved crossveins. Two preserved crossveins between posterior branch of MA, MP.



**FIGURE 4.** *Osmylidia* sp., hind wing specimen RBCM P1567. A, photograph; B, drawing. Posterior branch of MA in red. Scale bar = 5 mm.

## *Osmylidia* sp.

Fig. 4

**Material.** Specimen RBCM P1567, collected by SBA July 23, 2001; deposited in RBCM. A poorly preserved incomplete hind wing on a piece of shale with a heteropteran (Hemiptera), a syrphid (Diptera), and two nematoceran pupae (Diptera).

**Locality and horizon.** Ootsa Group shale exposed at Driftwood Canyon Provincial Park, British Columbia, Canada; Eocene (mid-Ypresian).

**Description.** Hind wing 10.9 mm long as preserved (estimated complete length about 11.5 mm), *ca.* 5 mm wide (actual width probably less, wing deformed). Costal space relatively broad, with simple, relatively closely spaced subcostal veinlets. Sc fused with RA far from wing apex. Subcostal space incompletely preserved, narrow distally; crossveins not detected. RA space relatively narrow for most length, basally broadened, with three detected crossveins in proximal half. RP with 11 branches, all probably shallowly forked (their deep forks absent, distal portions not preserved). Fork of M not detected. MA probably deeply forked, MP probably pectinate (both fragmentarily preserved). Nearly all preserved crossveins in radial, radio-medial spaces arranged in intermediate, outer gradate series (both series incomplete) or single crossvein in position of proximal gradate series in other Protosmylinae; one crossvein in intermediate series adventitiously forked. Two preserved crossveins between posterior branch of MA, MP. CuA strongly pectinately branched, with eight branches. CuP relatively short, forked twice distally.

**Remarks.** Although it differs from other species by its arrangement of crossveins between RA and RA, this incomplete specimen lacks many potentially diagnostic characters (*e.g.*, the configuration of M), and we, therefore, do not name a species based on it.

## Discussion

Extant Osmylidae are divided into two distinct groups by morphology of their hind wing CuP (Winterton *et al.* 2017: Fig. 6): long, subparallel to the hind margin and pectinately branched (Osmylinae, Kempyninae, Stenosmylinae, Porisminae, Eidoporisminae), or relatively short, inclined to the hind margin and with few or no branches (Gumillinae, Spilosmylinae and Protosmylinae).

**Protosmylinae and Mesosmylinae.** The forewing venation of the Protosmylinae is most similar to that of the Early-Middle Jurassic subfamily Mesosmylinae Bode, 1953, but their relationship remains unclear, as hind wings of Mesosmylinae are unknown. The type species of the type genus (*Mesosmylina exornata* Bode, 1953, re-described by Ponomarenko 1996) is a nearly complete forewing from the Early Jurassic of Hondelage, Germany. Although its venation is rather similar to that of Protosmylinae in many ways, its crossvenation is denser, more like that of the Spilosmylinae. The CuA of *M. exornata*, however, has only four branches and Spilosmylinae have 8–15. Further, the crossveins between branches of CuA and CuP in *M. exornata* are absent in both Protosmylinae and Spilosmylinae.

The other three Early or Middle Jurassic species of *Mesosmylina* have similar forewing venation (*M. mongolica* Ponomarenko, 1984 from Mongolia, *M. angusta* Khramov, 2014 and *M. shurabica* Khramov, 2014 from Kyrgyzstan). All possess crossveins between branches of CuA (and probably between branches of CuP in most) which is diagnostic for *Mesosmylina* and Mesosmylinae as treated here. Assignment of the poorly preserved *M. falcifera* Ansoerge, 1996 from the Early Jurassic of Germany (Grimmen) to this genus might then be incorrect according to the published wing drawing (Ansoerge 1996: Fig. 51).

Makarkin *et al.* (2014) included three genera in the Mesosmylinae (*Mesosmylina*, *Sogjuta* and *Petrushevskia* Martynova, 1958), and Winterton *et al.* (2019) two (*Mesosmylina* and *Sogjuta*) (*Sogjuta* and *Petrushevskia* from the Early Jurassic Dzhil Formation at Sogyuty, Kyrgyzstan). Here, we transfer *Sogjuta* to the Protosmylinae (below).

*Petrushevskia* lacks some forewing diagnostic characters of both the Mesosmylinae (*e.g.*, crossveins between branches of CuA and CuP absent) and the Protosmylinae (*e.g.*, CuA not pectinate; eleven crossveins between CuA and CuP) and we, therefore, consider it to be Osmylidae *incertae sedis* until its type is further examined or well-preserved specimens are found.

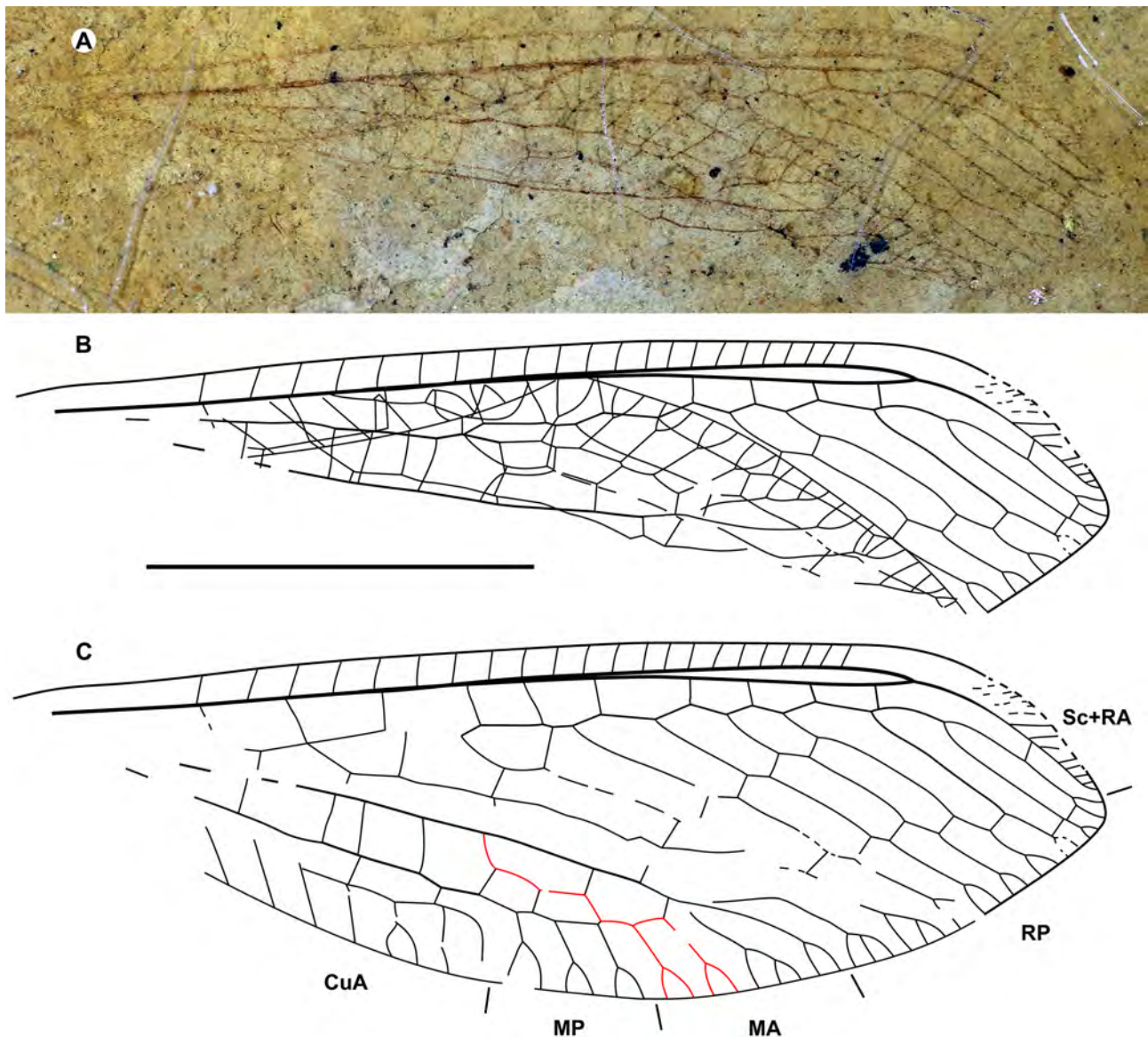
Therefore, Mesosmylinae here includes only the genus *Mesosmylina*, and may be closely related to the Gumillinae, as its diagnostic character state (above) is present also in some Gumillinae (*e.g.*, the Jurassic *Tenuosmylus*



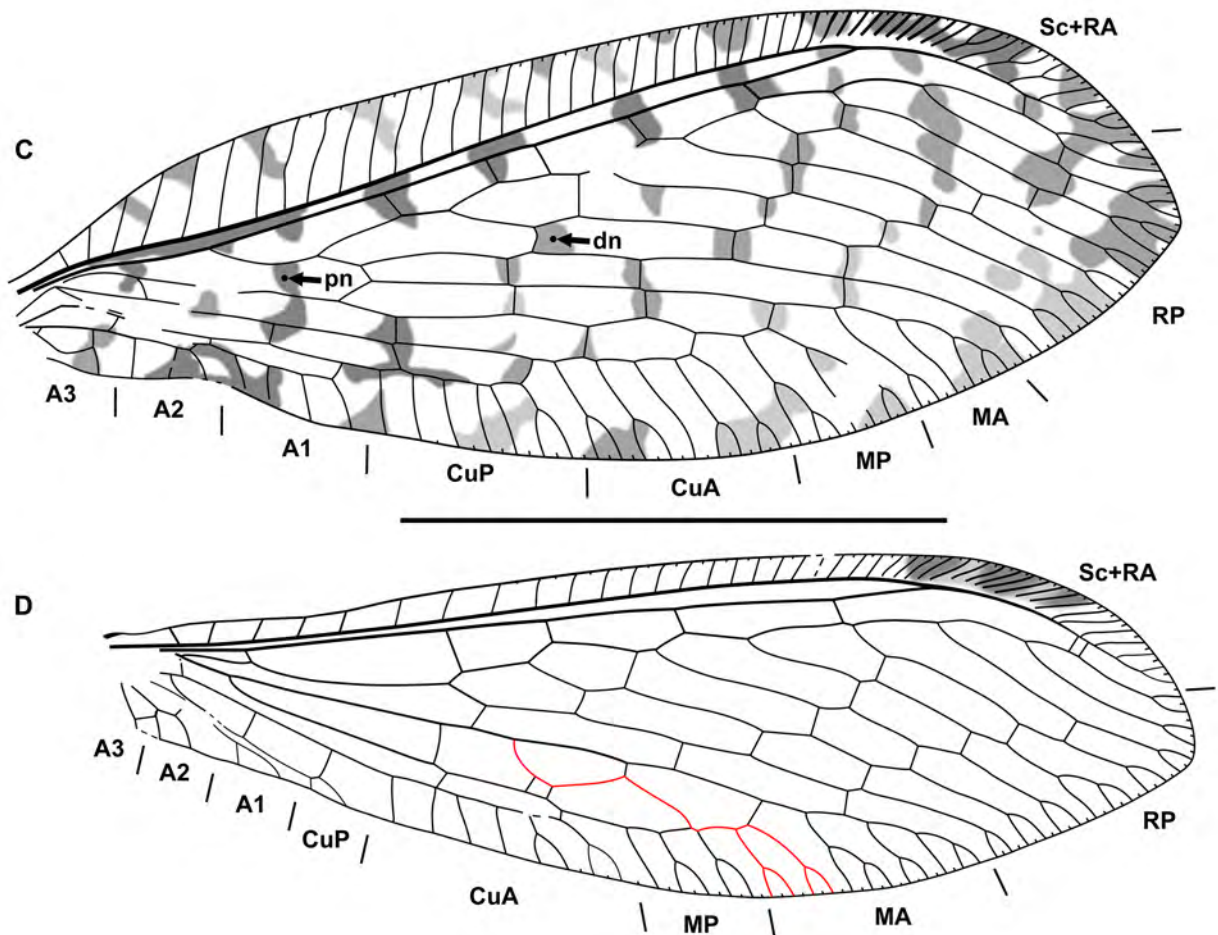
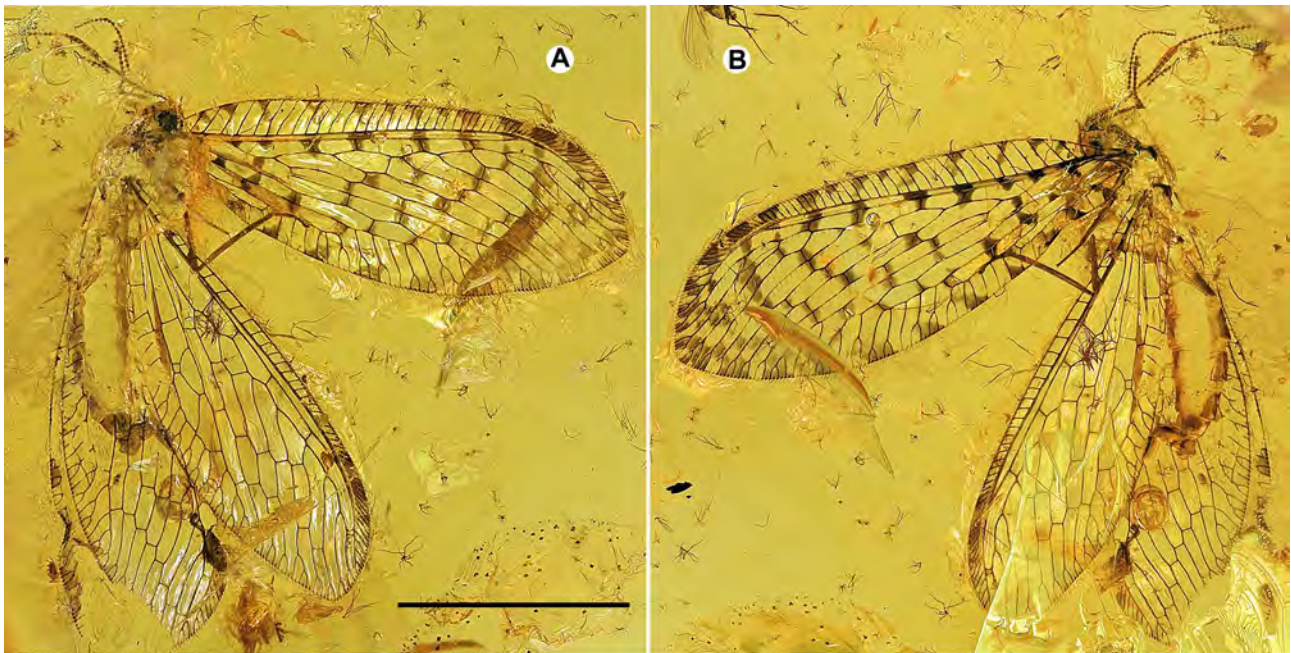
*brevineurus* Wang *et al.*, 2009, the extant *Gumilla adspersus* Navás, 1912: Winterton *et al.* 2019: Figs 7F, 8). It is still unclear if crossveins between branches of CuA in these species indicate a close relationship of these subfamilies (if so, these crossveins are lost in other species of Gumillinae) or if this is a convergence. This may be resolved when fossils of Mesosmylinae bodies are found with antennae and hind wings.

**Protosmylinae and Spilosmylinae.** The male and female genitalia of Protosmylinae indicate a close relationship with the Spilosmylinae, sharing several synapomorphies (Winterton *et al.* 2017, 2019). They are separated by wing venation (see emended diagnosis of Protosmylinae, above). Although Winterton *et al.* (2017) assumed that Protosmylinae and Gumillinae diverged from Spilosmylinae in the Middle Triassic, Osmylidae are unknown before the Early Jurassic. Further, the two fossil genera assigned to the Spilosmylinae are only provisionally so, as the anteriorly directed basal spur-like process of MP in the hind wing diagnostic of the subfamily remains unknown in their only specimens by preservation.

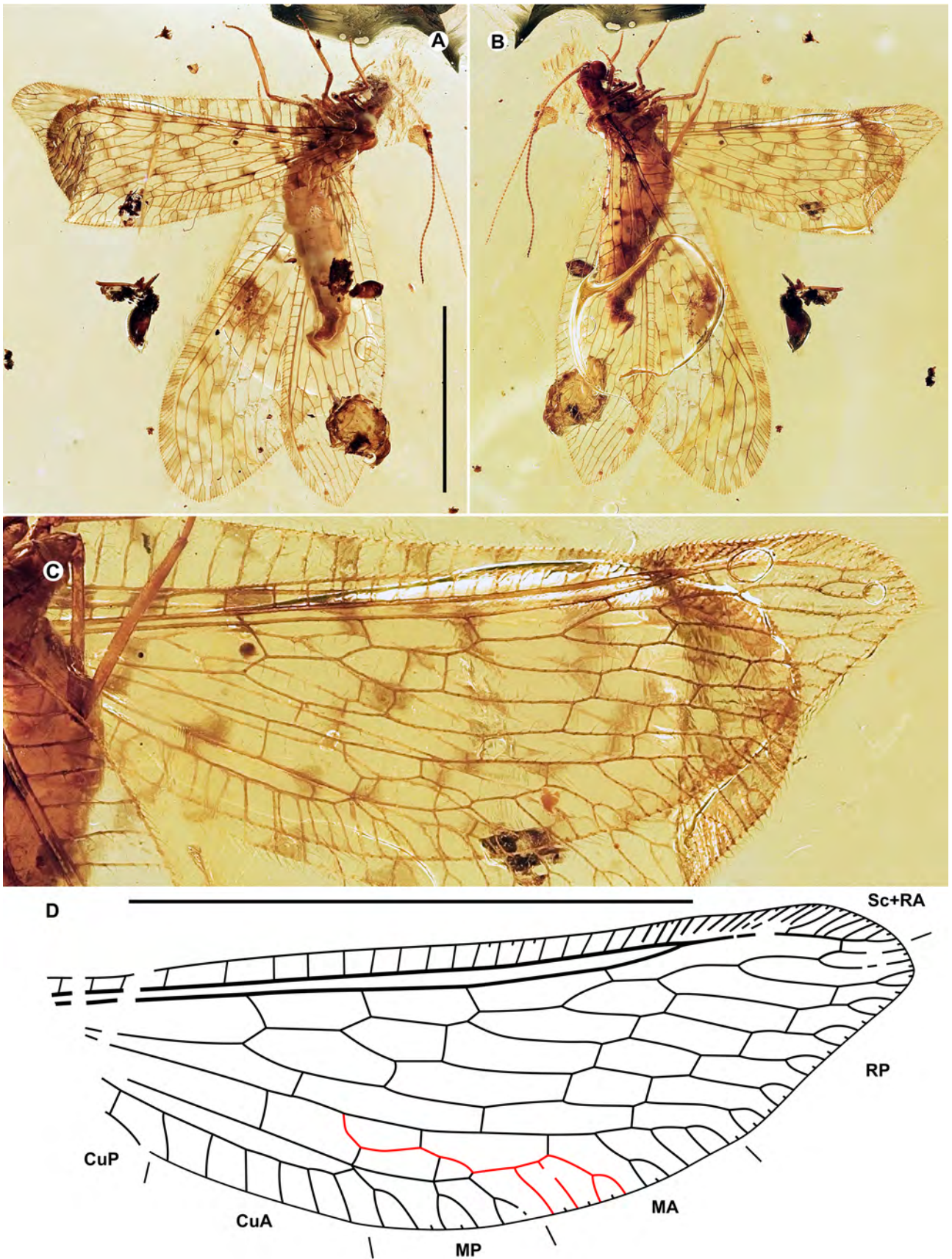
**The composition of Protosmylinae.** The Protosmylinae is currently thought to include eight fossil genera: *Petrushevskia*, *Juraheterosmylus*, *Jurosmylus*, *Mesosmylidus* Jepson *et al.*, 2012, *Protosmylina*, *Osmylidia*, *Pseudosmylidia*, and *Protosmylus* (Winterton *et al.* 2019).



**FIGURE 5.** *Osmylidia requieta* (Scudder, 1890), hind wing specimen MCZ 4500 from Florissant, USA. A, specimen as preserved (counterpart); B, drawing of wing venation; C, venation of ‘graphically unfolded’ hind wing. Posterior branch of MA in red. Scale bar = 5 mm.



**FIGURE 6.** Probable *Osmylidia picta* (Hagen in Pictet-Baraban & Hagen, 1856), specimen from Baltic amber (GPIH no. 4974, collection of C. Gröhn, no. 7311). A, right side; B, left side; C, drawing of forewing; D, drawing of hind wing. Posterior branch of MA in red. Photo: Jonas Damzen. Scale bar = 5 mm (A, B and C, D to scales).



**FIGURE 7.** Probable *Osmylidia picta* (Hagen in Pictet-Baraban & Hagen, 1856), specimen from Baltic amber (GPIH no. 4971, collection of C. Gröhn, no. 7310). A, left side; B, right side; C, left wings; D, drawing of hind wing venation. Posterior branch of MA in red. Photo: Jonas Damzen. Scale bar = 5 mm (A, B and C, D to scales).

The forewing of *Petrushevskia* excludes it by its shallow, not pectinate branching of CuA and by 11 crossveins between CuA and CuP (see above). *Mesosmylidus* is also excluded from the Protosmylinae by forewings with crossveins in the radial space mostly not arranged in a gradate series, CuP with ten branches, 12 crossveins between CuA and CuP, and other traits. We treat *Mesosmylidus* as *Osmylidae incertae sedis*.

We add *Sogjuta* to the Protosmylinae by agreement of its forewing with the emended diagnosis. It is then the oldest known genus of the subfamily, with two described species: *S. speciosa* Martynova, 1958, and *S. shartegica* Khramov, 2011 from the Late Jurassic of the Shar-Teg Sequence (Mongolia).

**The composition of *Osmylidia*.** *Osmylidia requieta* from Priabonian Florissant is the type species of the genus. It is known by six published specimens (Scudder 1890; Bather 1909; Cockerell 1908, 1913, 1914; Carpenter 1943). Scudder (1890) noted that it bears some resemblance to “*Osm. pictus* of the Prussian amber” (p. 163) (considering both to be species of *Osmylus*) and Cockerell erected the genus *Osmylidia* for it (1908) while suspecting that it might be congeneric with *Protosmylus pictus* (still then in *Osmylus*). To our knowledge, the hind wings in all specimens of *O. requieta* are poorly visible and/or strongly crumpled, and so the branching of MA has not been evaluated. We find its deeply forked MA to be the single diagnostic character state defining *Osmylidia*, a character state not previously mentioned (see our emended diagnosis, above). The published drawing of the crumpled hind wing (Cockerell 1914: Fig. 1; MCZ 4500) was incomplete, not showing this. We examined a photograph of this hind wing and here graphically unfold it in our drawing to show this portion of the wing (Fig. 5). We found that it bears the deeply forked MA that we consider diagnostic of *Osmylidia*. It also shows that its venation largely agrees with known hind wing visible portions of *Osmylidia* specimens articulated to bodies with forewings.

Specimens of *Protosmylus* are not rare in Baltic amber; we know of more than ten, deposited mainly in private collections. The type specimen of *P. pictus*, its only described species, is now lost. It is unknown if the original drawing of its forewing is accurate (Pictet-Baraban & Hagen 1856: Pl. 8, Fig. 16). Krüger (1923) re-described the type, but without illustration. Photographs of *Protosmylus*-like osmylids were published as *P. pictus* (e.g., Scheven 2004: Fig. on p. 72; Wichard *et al.* 2009: Figs 07.02a, b) or were unnamed (e.g., Weitschat & Wichard 1998: Pl. 55, Figs d, f, h; Gröhn 2020: p. 262, upper figure). These appear accurately identified to genus or very probably so. We examined well-preserved specimens of probable *P. pictus*, where the deep branching of MA is visible and well-developed (GPIH no. 4974, collection of C. Gröhn, no. 7311, Fig. 6; GPIH no. 7410, collection of C. Gröhn, no. 7310, Fig. 7; other photographs of these previously published by Gröhn 2020: p. 262).

Their species affinities, however, are not so clear; they may or may not belong to *P. pictus* or perhaps other, unnamed species due to variation of colour pattern. For example, the forewing colour pattern of the specimen figured here (Fig. 6) is similar in most known specimens attributed to the genus, but in this specimen it differs slightly from that of the type as figured by Pictet-Baraban & Hagen (1856: Pl. 8, Fig. 16) (e.g., by the absence of spots around the proximal nygma, crossveins between RA and RA, and two distal crossveins in the intermediate gradate series), and the maculation in some specimens is less developed (see e.g., Scheven 2004: Fig. on p. 72). It is unclear if such differences constitute intraspecific variation or indicate that they are closely related species. A revision of the Baltic amber osmylids is necessary to clarify this.

Based on its deeply forked MA in the hind wing, we synonymize *Protosmylus* with *Osmylidia*. This condition is clearly apomorphic. In other Protosmylinae whose hind wings are preserved (i.e., *Juraheterosmylus*, *Pseudosmylidia* and all extant genera) MA is plesiomorphically shallowly forked (see Wang 2010: Figs 69–81; Wang *et al.* 2010: Figs 1–4; Martins *et al.* 2016: Figs 5A, 6A, B; Winterton & Wang 2016: Fig. 4; Winterton *et al.* 2019: Figs 29, 32, 34, 35; pers. obs. based on examination of extant specimens from Nepal and the Russian Far East, and re-examination of photographs of *Pseudosmylidia relictata*). Hind wings of the Mesozoic *Sogjuta*, *Jurosmylus* and *Protosmylina* are unknown.

The hind wing posterior branch of MA is zigzagged in all examined species of *Osmylidia*. In *O. donnae* **sp. nov.** from the middle Ypresian it is connected with MP by a long distal crossvein (Fig. 2B), which is very short in *O. requieta* about twenty million years later in the Priabonian (Fig. 5C). This crossvein is lost in the late Ypresian *O. taliae* **sp. nov.** (Fig. 3C) and the Priabonian *O. picta* (Fig. 6D), where the posterior branch of MA is usually fused with MP for a short distance. Individual specimens of *O. picta* show a lot of variation, however, sometimes possessing a short connecting crossvein (Fig. 7D), in one specimen that we examined it was incomplete in one hind wing (Fig. 7A).

The *Osmylidia* as constituted here is then the most widely distributed and diverse genus of the family during the Eocene, which includes five species occurring in the Okanagan Highlands (one tentatively), Green River Formation

and Florissant of North America, and Baltic amber of Europe. This is the second genus of Neuroptera known to occur in Baltic amber and the Okanagan Highlands after *Proneuronema* Makarkin *et al.* 2016 (Hemerobiidae).

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