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Lance lacewings of the world (Neuroptera: Archeosmylidae, Osmylidae, Saucrosmylidae): review of living and fossil genera

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Abstract

The genera of the lance lacewing family Osmylidae (Neuroptera) and extinct allied families (Archeosmylidae, Saucrosmylidae) are reviewed. A key to living Osmylidae genera of the world is presented. Each genus is diagnosed and figured with a checklist of species included for each. New, revised or support for previous taxonomic changes include the following: *Nuddsia* Menon & Makarkin, 2008 (= *Burmaleon* Myskowiak *et al.*, 2016 **syn. nov.**); *Kempynus* Navás, 1912 (= *Clydosmylus* New 1983a **syn. nov.**); *Osmylus* Latreille, 1802 (= *Hyposmylus* McLachlan; *Dictyosmylus* Navás, 1910; *Plesiosmylus*, Makarkin, 1985; *Plethosmylus* Krüger, 1913a); *Parosmylus* Needham, 1909 (= *Mesosmylus* Krüger, 1913c; *Phlebosmylus* Navás, 1928 **syn. nov.**); *Thaumatosmylus* Krüger, 1913a (= *Glenosmylus* Krüger, 1913a **syn. nov.**). New classification changes include: *Mesomylidus* Jepson, 2012 and *Petrushevskia* Martynova, 1958 are transferred to Protosmylinae; *Lahulul* Navás, 1930 is placed in Osmylinae; *Stenosmylina* Jepson *et al.*, 2009 is transferred to Eidoporisminae. *Cratovoluptia* Martins-Neto & Rodrigues, 2009 is removed from Osmylidae and transferred to Ithonidae, while *Cratosmylus* Myskowiak *et al.*, 2015 is transferred to Nymphidae. *Idiastogvia* Lin, 1986 and *Yanosmylus* Ren in Ren *et al.*, 1995 are excluded from Osmylidae and placed as *incertae sedis* in Neuroptera.

Key words: Osmlyloidea, fossil, lance lacewing, Neuroptera

Introduction

Lance lacewings (Neuroptera: Osmylidae) are represented by both living forms and a diverse fossil record extending back to the Early Jurassic. Two other related extinct families Archeosmylidae and Saucrosmylidae show the closest relationships with Osmylidae; Archeosmylidae have the oldest record of this lineage and date back to the Permian, while hitherto Saucrosmylidae are only found from the Middle Jurassic (Ren & Yin, 2003; Fang *et al.*, 2018). Adults of all three families range in size from medium to relatively large (wing span ranging from 15 mm to over 120 mm), often with broad, distinctively patterned wings (e.g., Figs. 25, 48). Larvae of Osmylidae are campodeiform in shape with dramatically elongate lance-like jaws that are typically much longer than the head length (Fig. 1). The larvae are generalist predators either in leaf litter and under bark in some subfamilies (e.g., Stenosmylinae, Porisminae), or in riparian lotic habitats where they are often found under rocks and amongst debris close to the water edge (e.g., Kempyninae, Osmylinae) (Winterton *et al.*, 2017; Martins *et al.*, 2018).



FIGURE 1. Larval stages of Osmylidae: A. *Kempynus* sp. (photo: Kristi Ellington); B. *Isostenosmylus* sp. (photo: Enio Branco); C. unidentified stenosmyline (photo: Kristi Ellington).

Osmylidae, Archeosmylidae and Saucrosmylidae represent a monophyletic lineage of lacewings that also includes two more distantly related extant families, Sisyridae and Nevrothidae (Winterton *et al.*, 2010; Wang *et al.*, 2016; Engel *et al.*, 2017; Winterton *et al.*, 2017, 2018). These five families comprise the superfamily Osmyloidea, a clade which diverged early in lacewing evolution and represents the second major diversification of lacewings after the origin of Coniopterygidae as the sister to the rest of the order (Engel *et al.*, 2017; Winterton *et al.*, 2018). Osmyloidea also share a plesiomorphic mitochondrial gene organization with Coniopterygidae which is also supportive of placement close to the base of the neuropteran phylogenetic tree (Zhao *et al.*, 2013; Wang *et al.*, 2016). Makarkin *et al.* (2013) and Yang *et al.* (2013) believed that the Jurassic families Panfiloviidae and Grammolingiidae are closely related to Osmylidae based on a common venational pattern, and therefore also belong to Osmyloidea; other authors however consider these families belong instead to Psychopsoidea (e.g., Engel *et al.*, 2018).

The putative stem-group of Osmyloidea is Archeosmylidae (Late Permian to Late Triassic). This family containing three genera (with seven species) represents the oldest definitive osmyloid lineage and exhibits many generalised wing venation traits, including a non-pectinately branched forewing CuP (Khramov, 2014).

Considered a subfamily of Osmylidae by some authors (e.g., Ren & Yin, 2003; Engel *et al.*, 2017), Saucrosmylinae was elevated to family rank by Fang *et al.* (2015). The likely sister family of Osmylidae, Saucrosmylidae (commonly called elegant lance lacewings) are relatively large neuropterans from the Middle Jurassic with dense wing venation and dramatically patterned wings. Eight genera (comprising 10 species) of Saucrosmylidae are recognised by their distinctive reticulated wing venation, including multiple rows of cells in the area between RA and RP in both wings. Yang *et al.* (2012) also considered Saucrosmylidae as a distinct family but suggested that it was more closely related to Psychopsidae and Grammolingiidae; this proposal has not been widely accepted by subsequent authors (e.g., Fang *et al.*, 2015; Winterton *et al.*, 2017).

Today, Osmylidae are present in all major biogeographical regions except notably the Nearctic, although there are Tertiary-aged fossils recorded from that region, indicating that the family only recently went extinct there (Carpenter 1953; New, 1989a). Herein we recognise 278 species in 25 living and 38 extinct genera; nine fossil genera are placed as *incertae sedis* in the family due to the incomplete nature of their preservation. The family is divided into eight extant subfamilies (Osmylinae, Kempyninae, Stenosmylinae, Gumillinae, Spilosmylinae, Eidoporisminae, Porisminae and Protosmylinae) and a single extinct subfamily Mesosmylininae (Krüger, 1912–1915b; Kimmins, 1940; New, 1986, 1989; Wang & Liu, 2009; Winterton *et al.*, 2017). Mesosmylininae comprise at least two genera known from Jurassic aged deposits (e.g., Jepson *et al.*, 2009, 2012; Khramov, 2014). Another extinct subfamily, Cratosmylinae, comprising the genus *Cratosmylus* Myskowiak *et al.*, 2015 from Early Cretaceous deposits in Brazil (Myskowiak *et al.*, 2015) was considered more appropriately placed in Nymphidae rather than Osmylidae by Winterton *et al.* (2017).

Internal relationships among the subfamilies and genera of Osmylidae have been obscure and had not been studied in detail previously. In a total evidence analysis using both DNA sequences and morphology for multiple exemplars from all major lineages, Winterton *et al.* (2017) presented a strongly supported phylogeny and time tree of relationships for the entire family. They recovered two major clades of extant taxa, one comprising the subfamilies Protosmylinae, Gumillinae and Spilosmylinae, while the other contained Porisminae, Stenosmylinae, Kempyninae, Osmylinae and Eidoporisminae. The placement of Mesosmylininae is unclear at this stage.

The first major taxonomic works on Osmylidae were published in a series of papers by Krüger (1912–1915b), representing a significant advance in our knowledge of the family. Unfortunately, few papers on the taxonomy of Osmylidae have been published since then. The proliferation of genera with ambiguous diagnoses erected by Krüger (1912–1915), as well as the rarity of specimens in collections has resulted in few publications on the family during the past 100 years, and none with an emphasis on the entire family. Indeed, the few papers published focussed instead only on small provincial faunas (e.g. Kimmins, 1942; New, 1983a,b, 1986a,b,c, 1989a,b, 1991; Tjeder, 1957; Wang, 2010; Ardila-Camacho & Noriega, 2014; Martins *et al.*, 2016; Badano & Winterton, 2017; Xu *et al.*, 2016, 2017). Only Kimmins (1940) and New (1983b) dealt with entire taxonomic subunits of the family, revising subfamilies such as Kempyninae, Stenosmylinae, Eidoporisminae and Porisminae. Moreover, numerous fossil taxa have been described from Paleozoic to Cenozoic deposits around the world, reflecting the rich history of Osmyloidea, particularly during the Jurassic and Cretaceous periods. Unfortunately, many were described based solely on single wings or wing fragments, and few diagnosed with reference to living taxa. As a follow-on from the phylogenetic studies of the family by Winterton *et al.* (2017) we present the first taxonomic treatment of all the genera of Osmylidae since Krüger (1912–1915), indeed in this case also reviewing the fossil genera of Osmylidae, Archeosmylidae and Saucrosmylidae. This study is an attempt to consolidate the disparate studies previously published on the extant members of the family, and importantly, integrate it with advances generated from the prolific fossil literature recently published. In this multi-authored work, we acknowledge at the onset that many workers on Neuroptera, and on Osmylidae in particular, have diverse opinions regarding the status and validity of various taxa within the family. The results presented here are, broadly speaking, a consensus amongst the listed authors, but different opinions still exist for various genera and we expect that while the overall framework presented here is robust, some changes will be necessary in the future as more taxa are discovered (both extinct and living) and our knowledge of the group improves. We diagnose the families Archeosmylidae, Osmylidae and Saucrosmylidae and all genera contained within. We also present a checklist of species (with synonyms) under the classification proposed here as well as a revised key to extant genera of Osmylidae.

Materials and methods

Morphological homology and terminology used here was recently addressed in Winterton *et al.* (2017) and follows the pragmatic and intuitive terminology of Tjeder (1957), Adams (1969) and Wang *et al.* (2011b), with modifications proposed by Winterton & Wang (2016) and Breitzkreuz *et al.* (2017), as implemented in Winterton *et al.* (2017) and Badano & Winterton (2017) (Figs 2–4). We follow Adams (1969) in the use of mediuncus for the primary intromittent organ, which is equivalent to the parameres of Tjeder (1957) or more recently the gonocoxite 10 complex of Martins *et al.* (2016) or gonocoxites by Ardila-Camacho & Noriega (2014). The baculum (*sensu* Tjeder, 1957) is the anterior arm of the gonarcus and is sometimes articulated anteriorly or even absent. The parameres referred to here are equivalent to the subarcus of Tjeder (1957) and are present only in Osmylinae, Gumillinae, Spilosmylinae and Protosmylinae. The parameres, when present, are always closely associated with the mediuncus (Fig. 2). In Osmylinae the parameres are separate, paired, rod-shaped sclerites, while in Gumillinae, Protosmylinae and Spilosmylinae they are fused medially as a single arched sclerite. The gonarcus is narrow and lacking setae in Protosmylinae and Spilosmylinae, while in Porisminae, Stenosmylinae, Kempyninae, Eidoporisminae and Osmylinae, it is broad and visible externally, with distinct setal pile. In Gumillinae, the gonarcus is narrowly sclerotised marginally with a large membranous area ventrally. Entoprocesses are fused laterally on the gonarcus and are equivalent to gonocoxite 9 (*sensu* Adams, 1969). They are narrow and curved (e.g., Spilosmylinae, Protosmylinae), broad and sub-triangular (e.g., Porisminae, Kempyninae, Stenosmylinae) or reduced to a small rounded process (e.g. Osmylinae, Gumillinae). Aspöck & Aspöck (2008) and Martins *et al.* (2016) interpreted the gonarcus and entoprocessus as a complex of gonocoxite 9 and gonopophyses 9, respectively. The hypandrium internum is of typical shape for neuropterans although it is unusually large compared with other families.

In female genitalia the structure of the sclerites is variable among subfamilies (Fig. 3). The enlarged gonocoxite 9 (=gonopophyses lateralis) is closely associated anteriorly with gonopophysis 9 in Protosmylinae, Spilosmylinae and Osmylinae, with two separate sclerites clearly visible. In the subfamilies Porisminae, Kempyninae, Eidoporisminae and Stenosmylinae, gonopophyses 9 is not closely associated as a regular sclerite with gonocoxite 9, but instead is more elaborately shaped (i.e., enlarged with multiple lobes) as a single articulating sclerite which acts upon sternite 8 during copulation. Sternite 8 has also been referred to as the subgenitale (*sensu* Tjeder, 1957), or as a fusion of gonocoxite 8+gonopophyses 8 by Aspöck & Aspöck (2008) and Martins *et al.* (2016). The shape and position of this sclerite is highly variable. In Osmylinae, Porisminae, Kempyninae, Eidoporisminae and Stenosmylinae it is a plate-like sclerite immediately posterior to sternite 7. In Kempyninae and Stenosmylinae it is frequently modified into a bowl-like structure. In Protosmylinae and Spilosmylinae, sternite 8 is much smaller in size and located posteriorly as a small process. The female genitalia are unknown for Gumillinae.

Based on recent studies by Breitzkreuz *et al.* (2017) using tracheation in mature adult wing venation we identify the medial vein as a separate field from the radius throughout its length (Fig. 4A). We disregard the assumption that the MA vein is fused anteriorly with R and dispute that it is represented in both wings as the posterior-most vein of the RP field (*sensu* Kukalov-Peck & Lawrence, 2004) (Fig. 4B). Consequently, we do not consider the sigmoid vein as the remnant of vein MA. The essential difference between the terminology used here and that used by some authors, is that the medial vein is separate from the radial vein and is forked into the MA and MP veins (Fig. 4A), while other authors consider this vein as MP, which then forks into MP1 and MP2 (Fig. 4B). Veins and subsequent branched veinlets (including end-twigging) are tracheated and usually longitudinally arranged along the wing to reach the wing margin; crossveins and trichosors lack trachea and are structural braces, usually interlinking veins and veinlets in the wing, and do not reach the wing margin. Note that the numerous branches arising along the length of the Sc are called veinlets here and not crossveins of many authors; crossveins may be present between veinlets in some osmylids (see Fig. 4). Veinlets may be forked but crossveins are never forked. Abbreviations (and figure colour scheme) used for wing veins are: 1-3A, anal veins (brown); C, costa; Cu, cubitus; CuA, cubitus anterior (red); CuP, cubitus posterior (purple); M, media; MA, media anterior (blue); MP, media posterior (orange); RA, radius anterior (green); RP, radius posterior (green); RP1, first (proximal-most) branch of RP; Sc, subcosta.

Genitalia were macerated in 10% KOH to remove soft tissue, then rinsed in distilled water and dilute glacial acetic acid, dissected in 80% ethanol and subsequently stained with a solution of Chlorazol Black in 40% ethanol. The dissected genitalia were placed in glycerine in a genitalia vial mounted on the pin beneath the specimen.

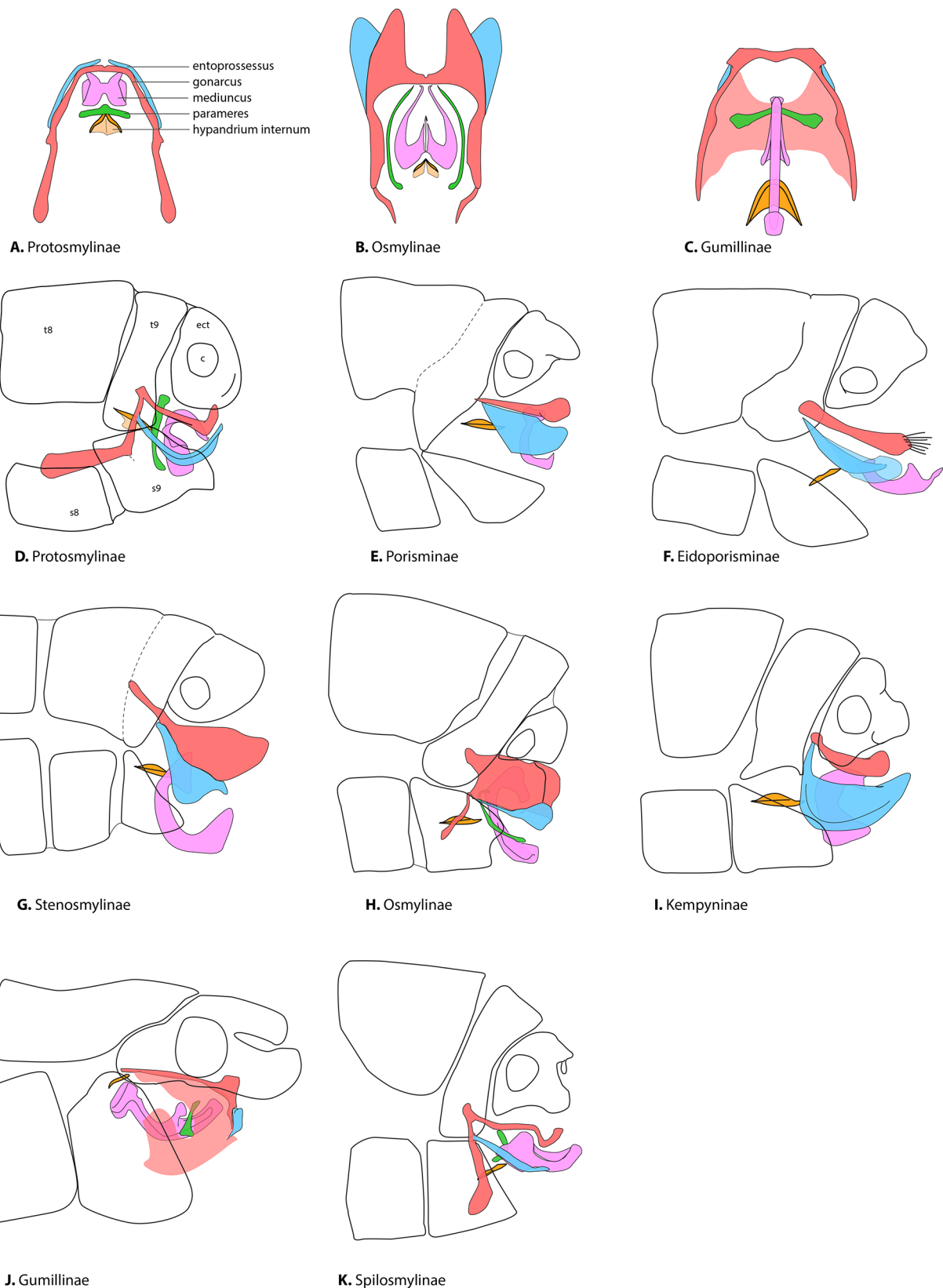


FIGURE 2. Male genitalic morphology amongst different subfamilies of Osmylidae. Colour code: gonarcus (red), entoprossessus (blue), parameres (green), mediuncus (purple), hypandrium internum (orange). Scale line: 0.5 mm.

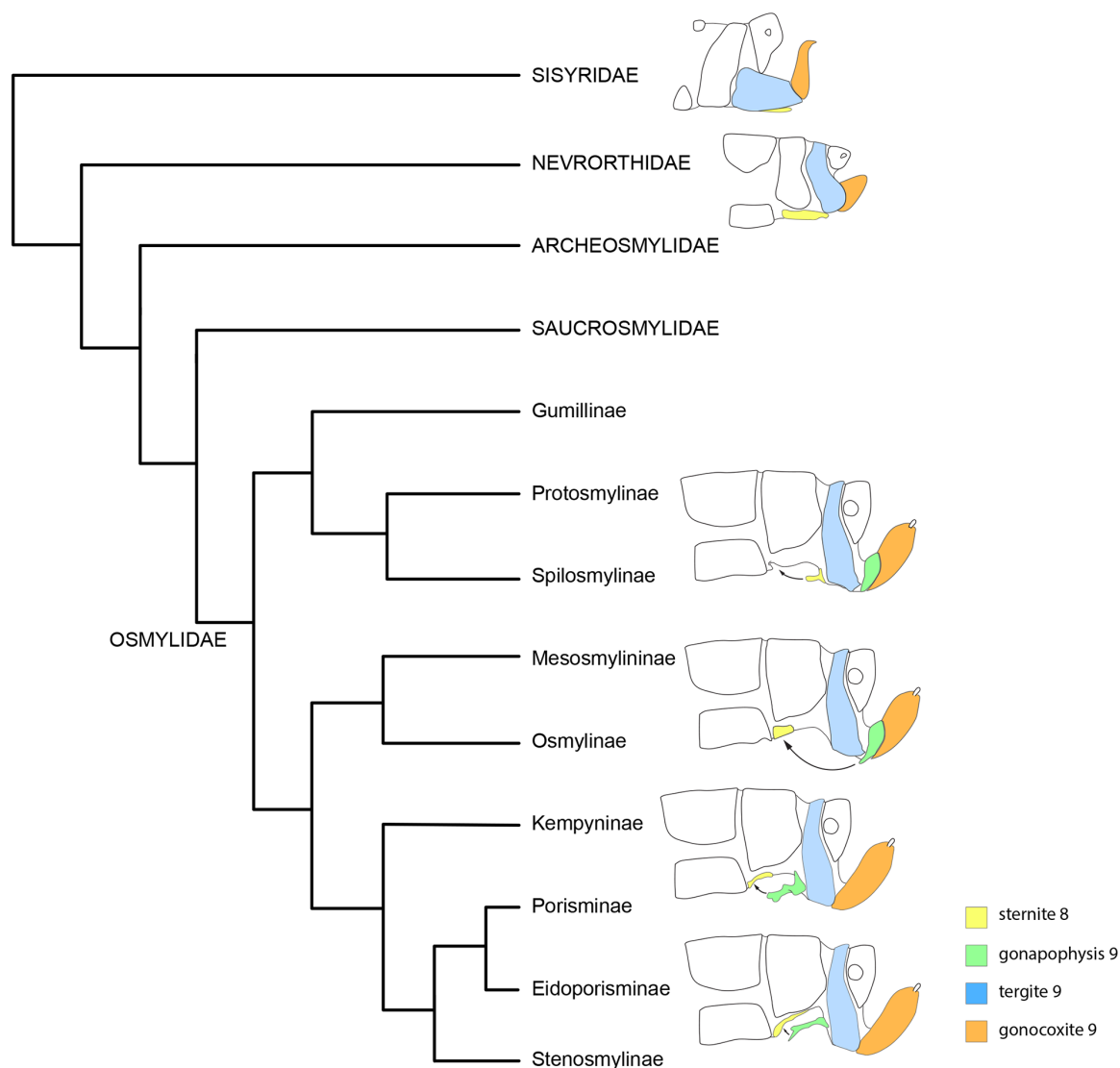


FIGURE 3. Distribution of female terminalia morphology on the hypothesised phylogenetic relationships amongst Osmyoidea families and subfamilies.

Taxonomy

Key to adults of families of Osmyoidea

1. Wing veins Sc and RA not fused apically, connected by a single crossvein; forewing subcostal veinlets typically simple, occasionally forked (fossil and living taxa known) NEVRORTHIDAE.
- Wing veins Sc and RA fused apically; forewing subcostal veinlets simple, occasionally forked 2.
2. Wing subcostal veinlets with numerous crossveins; RA-RP space with multiple rows of cells; RP1 divergent from RA in basal half of wing, strongly recurved in distal half of wing and convergent with RA (fossils only) (Fig. 65) SAUCROSMYLIDAE.
- Wing subcostal veinlets without crossveins (e.g., Fig. 12), or when present, fewer in number (Figs 18–19); RA-RP space with single rows of cells; RP1 subparallel with RA, not distinctly recurved anteriorly towards RA distally (e.g., Fig. 13) 3.
3. Wings medium to large (> 10 mm), crossveins often numerous; FW veins CuA, CuP and A1 strongly pectinately branched (frequently palisade-like arrangement) (e.g., Figs 9, 16, 29) (fossil and living taxa known) OSMYLIDAE.
- Wings relatively small (< 10 mm), crossveins largely absent or few in number; FW veins CuA, CuP and A1 weakly pectinately to dichotomously branched (e.g., Fig. 5) (fossil and living taxa known) 4.
4. Forewing with at least seven RP branches; outer gradate series present (Fig. 5) (fossils only known) ARCHEOSMYLIDAE.
- Forewing with fewer than four RP branches; outer gradate series absent (fossil and living taxa known) SISYRIDAE.

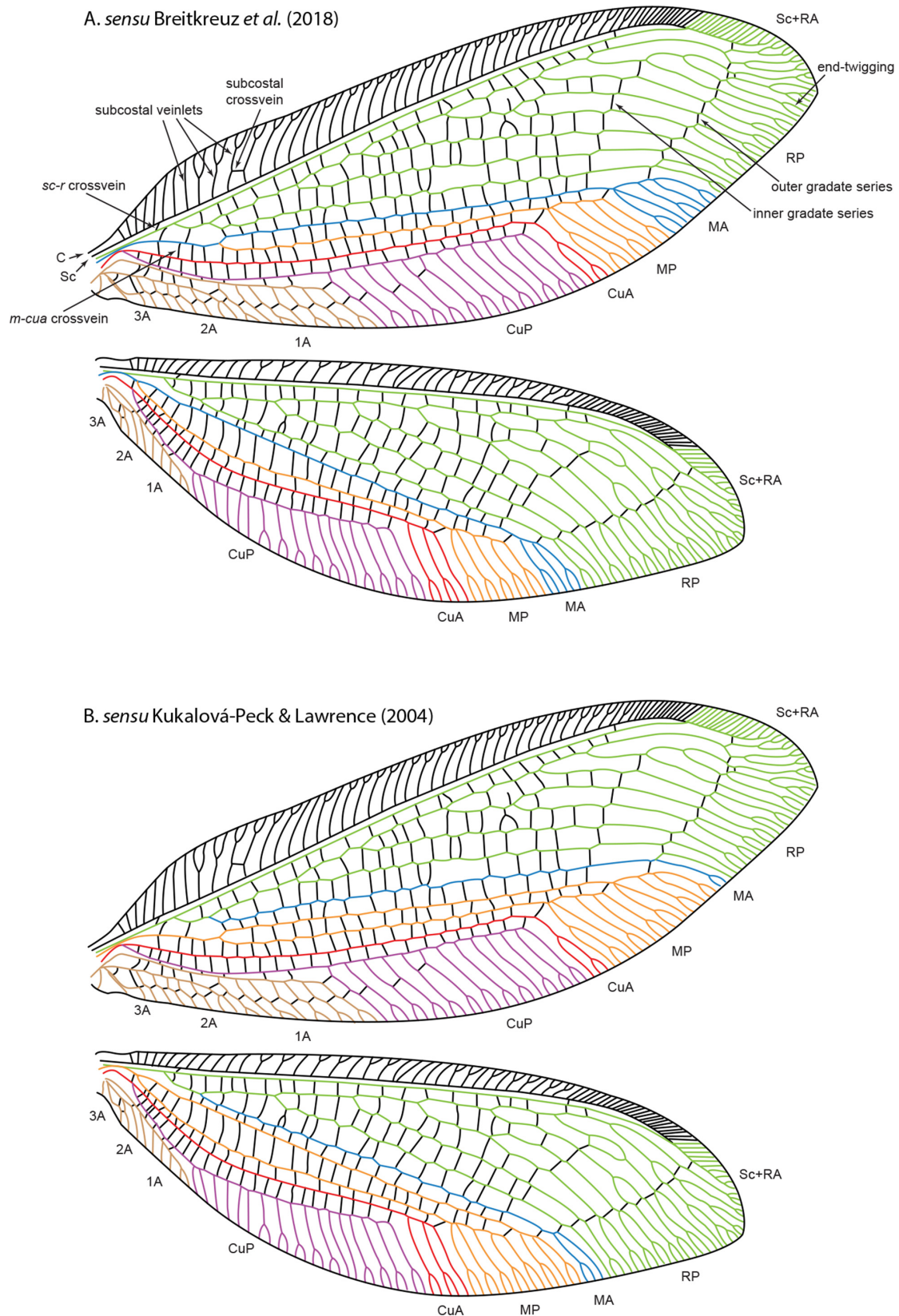


FIGURE 4. Fore- and hind wings of *Osmylus hyalinatus* McLachlan, presenting differing wing vein identities: A. *sensu* Breitkreuz et al. (2017); B. *sensu* Kukalová-Peck & Lawrence (2004) (trichosors and vestiture omitted). Labels: C: costal vein (black); Sc subcostal vein (black); Sc+RA: fusion of subcostal and anterior radial veins (green); RP: posterior radial vein (green); MA: anterior medial vein (blue); MP: posterior medial vein (orange); CuA: anterior cubital vein (red); CuP: posterior cubital vein (purple); 1A-3A: anal veins (brown).

ARCHEOSMYLIDAE Riek, 1953 (Permo-Triassic ‘stem lance lacewings’)

Type genus. *Archeosmylus* Riek, 1953: 85.

Diagnosis. Forewing ovoid, costal area relatively narrow, wider basally, subcostal veinlets mostly simple, more widely spaced basally; subcostal crossveins not detected (due to poor preservation); Sc and RA fused distally and thence slightly curved posteriorly, entering wing margin well before apex; RP with numerous branches (more than nine); crossveins in radial area scarce, dense end-twigging along posterior margin of wing; M fork into MA and MP distal to the origin of RP1; MA and MP mostly dichotomously branched; CuA, CuP and 1A few-branched, poorly pectinate with irregular forking, branches with distal angle relatively acute; HW known only from small fragment.

Comments. Archeosmylidae has been considered a synonym of Permithonidae by previous authors (e.g., Whalley, 1988; Makarkin & Archibald, 2003; Engel & Grimaldi, 2008). We agree with the placement of Archeosmylidae as closely related to Osmylidae and Saucrosmylidae and it indeed likely represents a Permo-Triassic-aged stem group for these younger crown group families (Riek, 1976; Makarkin *et al.*, 2014; Engel *et al.*, 2018). All three families have similar venation and differ mainly in the forewing configuration of the posterior vein fields. The veins CuA, CuP and A1 are weakly pectinate (weakly divergent branches) with few branches in Archeosmylidae while in osmylid genera these veins are more strongly pectinate with the branches strongly divergent and frequently arranged in a palisade-like pattern (see Makarkin *et al.*, 2014). A condition similar to Archeosmylidae is found in Saucrosmylidae, but these families differ widely in other venation characters, principally associated with the larger wings of the latter and the consequent proliferation of secondary veins and crossveins. All three families also share the condition where FW Sc is fused with RA apically, ending on costal margin well before the wing apex. Some fossil and living taxa now placed in families such as Nymphidae and Osmylitidae were previously considered as being in Osmyloidea (e.g., *Cratosmylus* by Myskowiak *et al.*, 2015), but all have the fused with Sc+RA vein joining the wing margin beyond the wing apex. Archeosmylidae have relatively few crossveins in the radial field, which are typically numerous in Osmylidae and Saucrosmylidae. Interestingly, the osmylid genus *Sinosmylus* is a typical member of Osmylinae but has secondarily convergent lack of radial crossveins except for two gradate series. Riek (1976) suggested that Archeosmylidae were stem group representatives of Osmylidae, although the absence of nygmata in Archeosmylidae is anomalous. Makarkin *et al.* (2014) discussed in detail the taxonomic composition and morphological characterisation of Archeosmylidae. Nygmata are widely considered as plesiomorphic for Neuroptera, being found in many distantly related lacewing families. The lack of nygmata in Archeosmylidae may represent a secondary loss in the clade, or simply even incomplete preservation in the compression fossil specimens of this family.

Genera included. *Archeosmylus* Riek; *Babykamenia* Ponomarenko & Shcherbakov; *Lithosmylidia* Riek.

Archeosmylus Riek, 1953

Type species. *Archeosmylus pectinatus* Riek, 1953: 86 (by original designation).

Diagnosis. Forewing relatively small (less than 11 mm), apex usually rounded; costal area expanded basally, narrowed towards apex; subcostal veinlets mostly simple; pterostigma long; Sc area narrow; RP arising near base of wing with numerous pectinate branches (7–11), end twigging dense; M forked after the origin of RP1; CuA deeply forked; CuA with at least four pectinate branches; 1A and 2A pectinately branched near apex, 3A less so, relatively short; pterostigma very long and narrow; CuA with at least six pectinate branches.

Comments. Members of *Archeosmylus* are relatively small species (wing length < 10 mm) with simplified venation and few medial vein branches. The absence of gradates is diagnostic for the genus although they are present in *A. costalis* (see Riek, 1955: fig. 21). The latter species is represented by an incomplete forewing and may belong to other genus and even family.

Included species.

A. costalis Riek, 1955 (Australia) (Late Triassic)

A. pectinatus Riek, 1953 (Australia) (late Permian)

A. stigmatus Riek, 1955 (Australia) (Late Triassic)

***Babykamenia* Ponomarenko & Shcherbakov, 2004**

Type species. *Babykamenia eskovi* Ponomarenko & Shcherbakov, 2004: S203 (by original designation).

Diagnosis. Forewing elongate with few crossveins present; trichosors and end-twigging present along posterior margin; costal area narrow; RA beyond junction with Sc only slightly arched along wing length; narrow terminal forks numerous along posterior wing margin although few amongst distal RP branches; RP origin towards base of wing; RP with twelve close-set branches, proximal ones almost parallel to longitudinal wing axis along most of length, not curving towards posterior wing margin in distal part of wing; M forked distal to origin of RP1 with numerous end-twigging; CuA pectinately branched around wing midpoint (distal to separation of MA and MP) closer to wing margin and comprising four branches; CuP forks proximal to CuA branching with anterior branch forking once more; 1A pectinate, with more branches than CuA or 2A; HW unknown.

Comments. Typical of stem group taxa, *Babykamenia* (like other Archaeosmylidae) exhibits plesiomorphic features such as RP originating basally in the wing and CuP forked with branches occupying a smaller area of the wing than M. These features lead Ponomarenko & Shcherbakov (2004) to suggest a closer relationship with Archeosmylidae and Permithonidae, although recent evidence suggests that while they are both stem group taxa, the resemblance is superficial. Permithonidae are older than Archeosmylidae and likely represent stem-group neuropteridans, while Archeosmylidae represent stem-group Osmylidae (see Engel *et al.*, 2018).

Included species.

B. eskovi Ponomarenko & Shcherbakov, 2004 (Russia) (Early Triassic)

***Lithosmylidia* Riek, 1955**

(Fig. 5)

Type species. *Lithosmylidia lineata* Riek, 1955: 678 (by original designation).

Diagnosis. Forewing medium sized; trichosors present; crossveins poorly preserved in wings of all specimens; costal area with veinlets widely spaced, mostly simple; subcostal area with *sc-r* crossveins not detected; crossveins in area between RA and RP few or absent (one detected in one specimen of *L. parvula*); RP originating close to wing base, with at least 10 branches, very slightly sinuous distally in some species; crossveins of RP field not well preserved in most material, but apparently restricted to a few random ones proximally and two widely separate and irregular gradate series; M forked close to wing base; CuA irregularly pectinate forked, with branches oblique. CuP dichotomously forked with few branches; 1A pectinate, length variable; 2A deeply forked; 3A short and apparently simple; HW unknown.

Comments. A specimen of *L. lineata* was considered by Riek (1955) as a hind wing, however Lambkin (1988) instead argued that it represented a forewing. Originally, *Lithosmylidia* was described by Riek (1955) belonging to Kempyninae, but Makarkin *et al.* (2014) argued that the genus belonged to Archeosmylidae. Characters such as Sc+RA joining the wing margin before the wing apex and the lack of RP crossveins support its placement in Archeosmylidae; unfortunately, important information about the hind wing cubital and anal vein fields were not preserved in any specimen.

Included species.

L. baronne Lambkin, 1988 (Australia) (Middle Triassic)

L. lineata Riek, 1955 (Australia) (Late Triassic)

L. parvula Riek, 1955 (Australia) (Late Triassic)

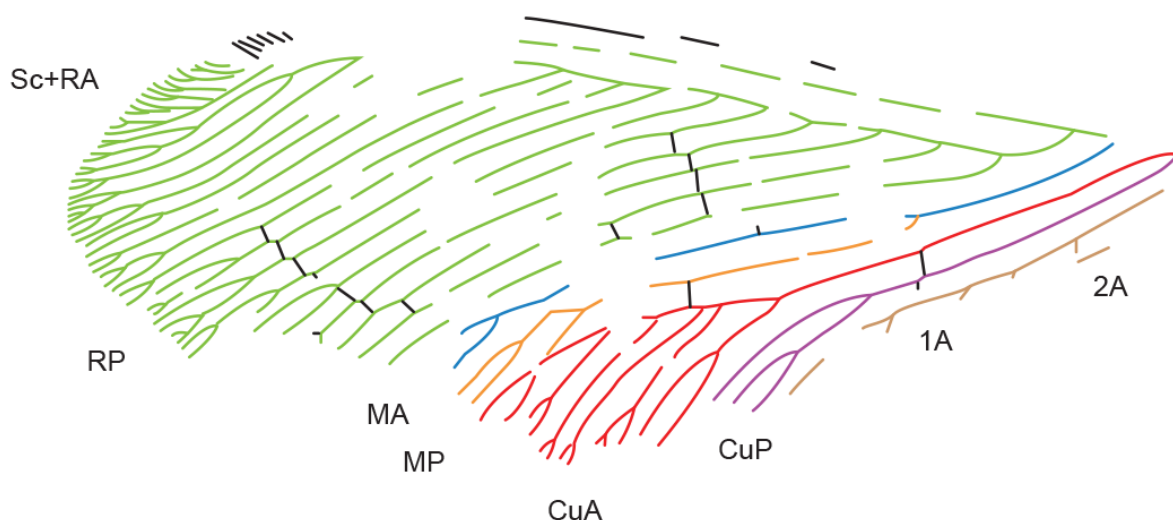


FIGURE 5. Archeosmylidae. *Lithosmylidia lineata* Riek, forewing (redrawn after Lambkin, 1988) (trichosors and vestiture omitted).

OSMYLIDAE Leach, 1815 ('lance lacewings')

Type genus. *Osmylus* Latreille, 1802: 289.

Diagnosis. Adult head with dorsal tentorial arms weakly developed; ocelli usually present, medial ocellus sometimes reduced (e.g., *Paryphosmylus*) or all ocelli completely absent (e.g., Gumillinae); palpmaculae absent; antennae filiform; wings with basal subcostal veinlet simple in costal area, sometimes forked but never recurrent; single basal crossvein (*sc-r*) between Sc and R, rarely more than one (e.g., *Porismus*, *Archaeosmylidia*); Sc and RA fused apically and joining costal margin before wing apex in both wings; single branch of RP, subsequently pectinately branched (5 or more branches); FW radial branches frequently curved posteriorly in apical half of wing, sometimes sinuous; FW medial vein fork variably placed along wing, HW medial vein fork near wing base; FW CuP pectinately (rarely dichotomously) branched; cubital field relatively large in both wings; nygmata typically present; trichosors present in both wings (rarely reduced to apical margin); end twigging along wing margin present, sometimes extensive and multi-layered; jugal lobe present; female gonocoxite 9 (gx 9) (i.e., gonopophysis lateralis) elongate and with terminal stylus; female with a pair of sclerotised spermathecae; male genitalia with well-developed arched gonarcus with paired entoprocesses fused laterally; mediuncus curved; parameres present or absent, sometimes fused into single arched sclerite; larva (Fig. 1) with straight, highly elongate jaws; gular-like sclerite absent; seven Malpighian tubules, of which five are incorporated into the cryptonephridium; eversible claws present on paired prolegs on last abdominal segment.

Comments. The monophyly of Osmylidae relative to other lacewings is unquestioned, based on a series of both adult and larval characters. The distinction of Osmylidae from Archeosmylidae and Saucrosmylidae is more problematic, and some authors consider the latter to be a subfamily of Osmylidae. Saucrosmylidae can be separated from Osmylidae based on the expanded area between veins RA and RP, with multiple rows of crossveins present. Archeosmylidae is differentiated from Osmylidae by the absence of pectinate branching in the posterior part of the wing and RP branches not sinuous distally. The larval characters listed here as synapomorphic for the family reflect our lack of knowledge of larval stages of closely related fossil families Saucrosmylidae and Archeosmylidae and the subfamily Mesosmylinae. Once larval stages are discovered for more Osmylidae and any of the fossil families, then the larval definition for Osmylidae may need modification. The family is divided into the nine subfamilies: Osmylinae, Kempyninae, Stenosmylinae, Gumillinae, Spilosmylinae, Eidoporisminae, Porisminae, Protosmylinae and Mesosmylinae. Beutel *et al.* (2010) provided a detailed study of the adult head morphology, MacLeod (1964) examined the head sclerites of the larva and Matsuno & Yoshitomi (2016) proposed terminology for the larval sclerites.

Key to Recent genera of Osmylidae

Lahululus Navás, 1930 is unknown beyond the original description and is not included at this time. All extant genera can be identified in the key primarily using wing characteristics, although genitalic characteristics are also provided where relevant. While fossil taxa with complete wing preservation can be identified to subfamily level using this key, genera are not included at this time as many are known only from wing fragments where important diagnostic features are not observable.

1. Hind wing (HW) CuP as a single branch, sometimes dichotomously forked along wing margin (Figs 9, 29, 42); female sternite 8 reduced to small knob-like sclerite located immediately anterior to the lower margin of tergite 9, distant from sternite 7 (note: female genitalia unknown in Gumillinae) 2.
- HW CuP greatly elongate and pectinately branched along wing margin (Figs 4, 16, 26, 53, 56, 59, 62); female sternite 8 located immediately posterior to sternite 7 9.
2. Antennae extremely long, exceeding the length of wing; ocelli absent; wings with fewer than five branches on RP before pterostigma; numerous radial crossveins present, gradate series absent (Brazil) (Figs 8–9) GUMILLINAE: *Gumilla* Navás.
- Antennae short and rarely extending beyond half-length of wing, never longer than wing; ocelli typically conspicuous but sometimes greatly reduced; wings usually with at least five branches on RP before pterostigma (Figs 30, 41); radial crossveins variable in number, inner gradate series distinct (Fig. 29) or indistinct (Fig. 42) 3.
3. RP crossveins relatively few in number aside from the gradate series, inner gradate series distinct and distant from crossveins in basal half of wing (Fig. 29) PROTOSMYLINAE: 4.
- RP crossveins numerous aside from the gradate series, inner gradate series often close to, and sometimes obscured by, irregular crossveins in basal half of wing (Fig. 42) SPILOSMYLINAE: 7.
4. Forewing (FW) with distinctive series of crossveins along wing margin in the radial field in addition to regular gradate series (New World: Ecuador) (Fig. 36) *Paryphosmylus* Krüger.
- FW without series of crossveins along wing margin in radial field (Old World) (Figs 29, 35) 5.
5. FW RP stem short, such that RP1 originates distinctly proximal to fork of M; FW with crossveins between M and stem of RP absent (Oriental, Eastern Palaearctic) (Figs 34–35) *Lysmus* Navás.
- FW with stem of RP long, such that RP1 originates on RP at, or more typically beyond, fork of MA and MP; FW with one or more crossveins between M and stem of RP, before origin of MA 6.
6. FW with costal area broad basally with basal subcostal veinlets radiating at divergent angles on Sc (Oriental Region) (Figs 27–29) *Gryposmylus* Krüger.
- FW with costal area narrow basally with basal subcostal veinlets equidistant and sub-parallel to each other (Oriental Region) (Figs 31–32) *Heterosmylus* Krüger.
7. FW with regular series of 2–4 basal m-cu crossveins before MA-MP fork (South East Asia) (Figs 43–44) *Thaumatomylus* Krüger.
- FW with single m-cu crossvein before MA-MP fork (Fig. 46) 8.
8. Numerous extensive markings on forewing, typically with a fenestrate patch present at the outer gradate series; embossed bulla absent along hind margin of FW (Madagascar, South East Asia) (Figs 45–47) *Thyridosmylus* Krüger.
- Forewing typically hyaline with markings much less extensive, embossed bulla usually present along hind margin of the FW in CuA region (sometimes absent) (Australasia, Madagascar, Africa, Oriental Region) (Figs 40–42) *Spilosmylus* Kolbe.
9. FW MA-MP fork in basal half of wing; few to many subcostal veinlets forked (rarely all simple) (Figs 4, 16); male with ever-scent glands between abdominal tergites 8 and 9. 10.
- FW MA-MP fork in the distal half of wing; subcostal veinlets all simple (rarely occasionally forked) (Figs 26, 53, 56); male abdominal tergites 8 and 9 fused into a single sclerite, lacking eversible scent glands 16.
10. HW area between MA-MP usually distinctly expanded, MP often forking in distal third (sometimes absent), branches of MP bifurcate near wing margin (Fig. 16); wing frequently falcate; male genitalia with parameres absent; female genitalia with gonapophysis 9 enlarged located anterior to ventral portion of tergite 9, often ornately modified and lobed (southern hemisphere) KEMPYNINAE: 11.
- HW area between MA-MP only slightly expanded, MP never forking in distal third, HW MP pectinately branched near wing margin (Fig. 4); wing never falcate; male genitalia with parameres present as paired rod-like structures lateral to mediuncus; female genitalia with gonapophysis 9 as regular sclerite closely associated to gonocoxites 9 and posterior to ventral region of tergite 9, unmodified and sometimes difficult to differentiate from gonocoxites 9 (northern hemisphere) OSMYLINAE: 13.
11. HW MA-MP fork relatively wide, crossveins between branches somewhat sinuous; large species (Australia, New Zealand and western South America) (Figs 13–16) *Kempynus* Navás.
- HW MA-MP fork narrower, cells between branches sub-quadrate; small to medium sized species (Figs 10, 12) 12.
12. Wings distinctly falcate; small species (forewing length <15.0 mm) (New Zealand) (Fig. 12) *Euosmylus* Krüger.
- Wings scarcely falcate; medium sized species (forewing length >20.0 mm) (Australia) (Fig. 10) *Australysmus* Kimmins.
13. FW with very sparse RP crossveins basal to the two distinct gradate series (China) (Fig. 23) *Sinosmylus* Yang.
- FW RP crossveins dense basal to the one or two distinct gradate series (Figs 18–22) 14.
14. Two distinct gradate series present; (Palaearctic) (Figs 18–21) *Osmylus* Latreille.
- One distinct gradate series, or gradates absent (eastern Palaearctic) (Fig. 22) 15.

15. FW relatively large (31–32 mm long) without maculation and with uniformly pale-brownish veins; gonarcus with paired long dorsal processes (each longer than the height of the gonarcus), each terminated by paired acute denticles *Grandosmylus* Makarkin.
- FW smaller (less than 30 mm long) with irregular mottled infuscation; veins with dark and pale sections; gonarcus dorsal process (when present) not as long and without terminal denticles (Fig. 22) *Parosmylus* Needham.
16. FW basal branch RP1 distant to the wing base (nearer to middle third of the wing), more than six *ra-rp* crossveins before origin of the basal RP branch (Figs 6, 26) (Australia) 17.
- FW basal RP1 branch diverging from RP closer to the wing base, fewer than four *ra-rp* crossveins before origin of branch RP1 (Figs 48–62) STENOSMYLINAЕ: 18.
17. FW with numerous *sc-r* crossveins (Australia) (Figs 24–26) PORISMINAE: *Porismus* McLachlan.
- FW with a single basal *sc-r* crossvein (Australia) (Fig. 6) EIDOPORISMINAE: *Eidoporismus* Esben-Petersen.
18. FW MA-MP fork near wing margin and containing few branches (usually 2–4) (Australia) (Note: some individuals of *Stenolysmus* and *Oedosmylus* appear to have this condition as MP is fused with CuA; in these cases the fork of MP is represented as an atypical oblique crossvein located around midpoint of wing and CuA having an unusually large number of branches (Fig. 59)) (Figs 60–62) *Stenosmylus* McLachlan.
- FW with distinct MA-MP fork at, or slightly beyond, midpoint of wing length; MA and MP fields both with numerous distinct branches (Figs 52, 56, 59) 19.
19. FW cubital space (bordered by CuA and CuP) curved sharply towards posterior wing margin around level of MA-MP fork (Figs 48, 50, 53) 20.
- FW cubital space straight along entire length, sometimes only slightly curved distally (Figs 56, 59) 22.
20. Wings extensively marked, dark brownish-black with contrasting white apical patches (Australia) (Fig. 48) *Euporismus* Tillyard.
- Wings markings not so extensive, lacking contrasting white apical patches 21.
21. Female with FW veins MP, CuA and/or A1 partially incrassate; male with ectoprocts rounded, not lobed (Australia) (Figs 51–53) *Oedosmylus* Krüger.
- Female with all FW veins of similar thickness, none incrassate; male with ectoprocts with distinct lobes or processes (South America) (Figs 49–50) *Isostenosmylus* Krüger.
22. FW falcate; FW stem of RP relatively short, such that length of RP stem shorter than distance between first and second branches of RP (South America) (Figs 54–56) *Phymatosmylus* Adams.
- FW rounded, not falcate; FW stem of RP length approximately equal to the distance between branches RP1 and RP2 (Australia) 23.
23. Body of living individual bright orange with dark legs; FW A1 and A2 with relatively few branches and with extensive end-twigging; FW A1 terminates in wing margin level with second branch of RP; female sternite 7 with narrow posterior margin; sternite 8 as broad plate; gonocoxites 9 with a ‘fringed’ row of stout, hooked setae (Australia) (Figs 57–59) *Stenolysmus* Kimmins.
- Body of living individual mottled brown; FW A1 and A2 with numerous branches and with extensive end-twigging; FW A1 terminates in wing margin level with fourth-fifth branch of RP; female sternite 7 with large keeled process; sternite 8 as lobed process; gonocoxites 9 without a row of stout setae (Australia) *Carinosmylus* New.

EIDOPORISMINAE Esben-Petersen, 1917

Type genus. *Eidoporismus* Esben-Petersen, 1917: 4.

Diagnosis. Antenna much shorter than forewing length; scape and flagellomeres not elongated; prothorax much longer than wide; single *sc-r* crossvein basally in both wings; RP sinuous distally, RP1 arising at ca. 1/3 wing length; FW vein M forking in distal half of wing, medial area not expanded; MP in both wings irregularly pectinate forked; trichosors present along entire margin of wings; hind wing CuP pectinately branched; male abdomen with tergites 8 and 9 closely associated and partially fused but retaining suture line, lacking eversible scent glands; male genitalia with parameres absent; gonarcus broad and arched; baculum absent; entoprocessus broad, subtriangular and not fused basally with gonarcus; female sternite 8 relatively large, concave, sculptured laterally, proximal to sternite 7; gonopophysis 9 enlarged, bilobed, anterior to ventral surface of tergite 9.

Comments. Eidoporisminae comprises a single living monotypic genus from eastern Australia and an extinct monotypic genus from England. Eidoporisminae and Porisminae share multiple features in common with Stenosmylinae suggesting a close relationship (New 1983b, Winterton *et al.*, 2017), including an elongate prothorax, medial vein forking in distal half of forewing and proximal branch of RP branching in the middle part of both wings. The phylogeny of the family by Winterton *et al.* (2017) suggests a possible paraphyly of Stenosmylinae relative to Eidoporisminae and Porisminae and the validity of the subfamily requires further investigation. Larvae are unknown for this subfamily.

Genera included. *Eidoporismus* Esben-Petersen, *Stenosmylina* Jepson *et al.*

Eidoporismus Esben-Petersen, 1917

(Fig. 6)

Type species. *Eidoporismus pulchellus* Esben-Petersen, 1917: 4 (by monotypy).

Diagnosis. Ocelli present; genal area not enlarged; wings relatively narrow, elongate, posterior margin straight distally, membrane hyaline with faint mottled markings; venation dark; costal area relatively narrow along length, crossveins simple, lacking interlinking crossveins; single sc-r crossvein basally; RP with 7–10 branches, crossveins numerous throughout both wings; distal part of radial field sinuous and lacking crossveins; FW RP1 arising distant from origin of RP, close to 1/3 of wing length; outer gradate series distinct, inner gradate series absent; FW vein M forking in distal half of wing and distal to origin of first branch of RP, medial area expanded only slightly; FW CuA with few dichotomous branches, CuP and 1A elongate and pectinately branched; HW CuA elongate, pectinately branched, CuP relatively short, ending before first RP branch origin; trichosors present along entire wing margin in both wings; female forecoxa with ventral spine-like process present but lacking patch of pedicellate setae. Male tergite 9 ventrally broad; gonarcus quadrangular with medial portion broad, setose at posterior angles, lacking anterior arm; posterior portion of entoprocessus subtriangular, widened distally and membranous; mediuncus with a narrow posteroventral extension. Female gonapophysis 9 with anteriorly directed, paired processes with distal half forked and multilobed; sternite 8 concave with a pair of lateral narrow arms; spermathecae spherical, spermathecal ducts short.

Comments. Esben-Petersen (1917) incorrectly attributed *Eidoporismus* to Krüger (in litt.) when describing *E. pulchellus*; here it is instead attributed to Esben-Petersen. Esben-Petersen (1917) described the genus based on a single female and New (1983b) described the male and discussed the close relationship of this taxon with Stenosmylinae and Porisminae; this conclusion was subsequently supported by Winterton *et al.* (2017) in their phylogeny of the family.

Included species.

E. pulchellus Esben-Petersen, 1917 (Australia)



FIGURE 6. Eidoporisminae. *Eidoporismus pulchellus* Esben-Petersen, dorsal view.

Stenosmylina Jepson *et al.*, 2009

Type species. *Stenosmylina medialis* Jepson *et al.*, 2009: 1327 (by original designation).

Diagnosis. Forewing narrowly ovoid; costal area relatively narrow, basal subcostal veinlets simple, relatively widely spaced; RP1 originating far from fork of RA-RP; M forked in distal part of wing; CuA pectinate; CuP strongly elongate and pectinately branched (14 branches); A1 pectinately branched; A2 with one short branch; preserved crossveins rather widely spaced and not forming gradate series; HW unknown.

Comments. This genus is known only from a single forewing fragment. Jepson *et al.* (2009) suggested that the genus most resembled members of *Mesosmylina* (Mesosmylininae). The fork of the forewing medial vein in the distal half of the wing, near the wing margin is a distinctive feature of members of Porisminae and Eidoporisminae, as noted by Jepson *et al.* (2009) as also occurring in *Stenosmylina*. This condition is also present in genera of Stenosmylinae. Another feature of the forewing of that *Stenosmylina* shares with Porisminae, Eidoporisminae and some genera of Stenosmylinae (e.g., *Stenosmylus*) is the origin of the first branch of RP near the middle part of the wing, distant from the origin of RP on RA. These aforementioned characters, as well as the overall venation shared by *Eidoporismus* and *Stenosmylina* support provisional placement of the latter in Eidoporisminae.

Included species.

S. medialis Jepson *et al.*, 2009 (England) (Early Cretaceous)

GUMILLINAE Navás, 1912

(= Epiosmylinae Panfilov in Dolin *et al.*, 1980. Type genus: *Epiosmylus* Panfilov in Dolin *et al.*, 1980: 100)

Type genus: *Gumilla* Navás, 1912: 57.

Diagnosis. Antenna longer than forewing, scape enlarged and flagellomeres slightly elongated; ocelli absent; prothorax length subequal to width; FW costal area relatively narrow along entire length, veinlets simple and lacking interlinking crossveins, widely spaced proximally; wing venation irregular, without inner or outer gradate series of crossveins (outer series sometimes poorly formed); FW with single basal crossvein *sc-r* (rarely more); RP branches straight, curved posteriorly apically, typically 5–7 branches of RP in both wings, rarely fewer or more; FW with RP1 originating distant from fork of RP; FW medial vein forked usually around wing length (rarely around); wing trichosors restricted to distal part of wing; both wings with end-twigging mostly absent along posterior margin; HW basal sinuate (sigmoid) crossvein (*1r-m*) absent; HW CuP simple and not pectinately branched, sometimes forked just before wing margin; male abdomen with tergites 8 and 9 appearing fused into single sclerite, male lacking eversible scent glands between abdominal tergites 8 and 9; gonarcus narrow with sparse pile; mediuncus narrow and arched; parameres into narrow, arched sclerite. Female genitalia unknown.

Comments. Menon & Makarkin (2008) provided an excellent characterisation of Gumillinae, including proposing the synonymy of Epiosmylidae. The feature unique to members of this subfamily is the greatly elongate antennal flagellum, exceeding the length of the forewing. Other important diagnostic features in the wings include the lack of well-defined gradate series, trichosors present only in the distal part of the wing margin, forewing medial vein forking in the basal half of the wing and the loss of the basal crossvein *1r-m* in the hind wing, although some of these are not unique to Gumillinae. The unbranched hind wing CuP unites this subfamily with Protosmylinae and Spilosmylinae (Winterton *et al.*, 2017) and is found in all genera conclusively placed in this subfamily. The only extant genus of Gumillinae is *Gumilla*, with male genitalia that appear highly divergent from other members of the family (Fig. 2C, J). The male abdominal tergites 8 and 9 are fused into a single sclerite and similar to the independently derived condition found in distantly related Stenosmylinae, Eidoporisminae and Porisminae. *Gumilla* is distributed in South America (see discussion by Martins *et al.*, 2016) while extinct members of the subfamily are more widely known from Jurassic to Cretaceous-aged deposits in Asia, Europe and South America. Wang & Ren (2010) presented a key to fossil genera of Gumillinae, although this is incomplete now as several genera have been described since. In addition, the distinction amongst the various genera of Gumillinae is problematic since most were established based on relatively few, rather minor venational features

(Table 1). Consequently, some characters used to distinguish fossil genera of Gumillinae are similar to the variation attributed as species-level characters in other subfamilies such as Osmylinae and Kempyninae. The status of some genera of Gumillinae should be re-evaluated in the future as more material is discovered and the description of new genera based solely on wing fragments or hind wings should be discouraged. Larvae are unknown for this subfamily.

Genera included. *Allotriosmylus* Yang *et al.*, *Enodinympa* Ren & Engel, *Epiosmylus* Panfilov in Dolin *et al.*, *Gumilla* Navás, *Kolbasinella* Khramov, *Nilionympha* Ren & Engel, *Nuddsia* Menon & Makarkin, *Osmylochrysa* Jepson *et al.*, *Tenuosmylus* Wang *et al.*

TABLE 1. Selected informative morphological characteristics of genera of Gumillinae.

	Number of FW RP branches	FW MA and MP branching pattern	Position of FW M fork
<i>Allotriosmylus</i>	Two	Extensive branches, MP area larger than MA	Close to origin of RP
<i>Enodinympa</i>	12–13	Few branches, subequal in area	Close to origin of RP
<i>Epiosmylus</i>	Six	Extensive branches, MP area larger than MA	Close to origin of RP
<i>Gumilla</i>	Six–seven	Extensive branches, MP area larger than MA	Between RP1 and RP2
<i>Kolbasinella</i>	unknown	unknown	unknown
<i>Nilionympha</i>	13–14	Few branches, subequal in area	Close to origin of RP
<i>Nuddsia</i>	Seven	Extensive branches, MP area larger than MA	Between origin of RP1 and RP2
<i>Osmylochrysa</i>	unknown	unknown	Close to origin of RP
<i>Tenuosmylus</i>	Eight	Few branches, subequal in area	Close to origin of RP

***Allotriosmylus* Yang *et al.*, 2010**

(Fig. 7A)

Type species. *Allotriosmylus uniramosus* Yang *et al.*, 2010: 856 (by original designation).

Diagnosis. Wings relatively narrow and small; wings with few longitudinal veins and crossveins, resulting in relatively large cells; end-twigging mostly absent; RP straight with one branch, originating at of wing length; FW M forked at 1/3 wing length; MA and MP pectinately branched, medial area enlarged; CuA, with relatively few pectinate branches; HW CuP short.

Comments. Known only from a single compression fossil specimen. Despite being very small and exhibiting the frequent reduction in wing cells associated with small wings found in other lacewings (e.g., *Turnerochrysa* Kimmins (Chrysopidae)), the venation of this genus is typical of Gumillinae. The single branch of RP and the expanded medial area is unique to this genus.

Included species.

A. uniramosus Yang *et al.*, 2010 (China) (Middle Jurassic)

***Enodinympa* Ren & Engel, 2007**

(Fig. 7C)

Type species. *Enodinympa translucida* Ren & Engel, 2007: 214 (by original designation).

Diagnosis. Antenna distinctly longer than forewing; scape elongate; wings narrow, medium sized; forewing with numerous crossveins throughout wing, regularly arranged but not forming gradates; RP with 12 branches; RP1 originating distant from origin of RP, approximately 1/3 wing length; M fork proximal to origin of RP1, closer to origin of RP, near 1/6 wing length; MA unbranched except for end-twigging near wing margin; MP with few pectinate branches near wing margin; CuA pectinately branched near wing margin, 4–5 branches, some with end-twigging; CuP strongly pectinate (nine simple branches); A1 pectinate with six branches; HW with numerous crossveins throughout wing; MP pectinate; CuA strongly pectinate (13 branches); CuP simple.

Comments. Placement of this genus in Gumillinae is clear based on the long antennae, narrow costal margin and distal origin of RP1. The forewing medial vein forking very close to the wing base is uncommon among genera of Gumillinae, as it typically forks closer to the middle of the wing. The relatively large number of RP branches (12) and numerous regular crossveins is also uncommon in Gumillinae, as most members of this subfamily have 5–7 (or fewer) branches and far fewer, irregular crossveins. This genus is likely closely related to *Tenuosmylus* and *Epiosmylus*. Li *et al.* (2018) recently transferred *Nilionympha imperfecta* to *Enodinympa*.

Included species.

E. imperfecta (Ren & Engel, 2007) (China) (Middle Jurassic)

E. translucida Ren & Engel, 2007 (China) (Middle Jurassic)

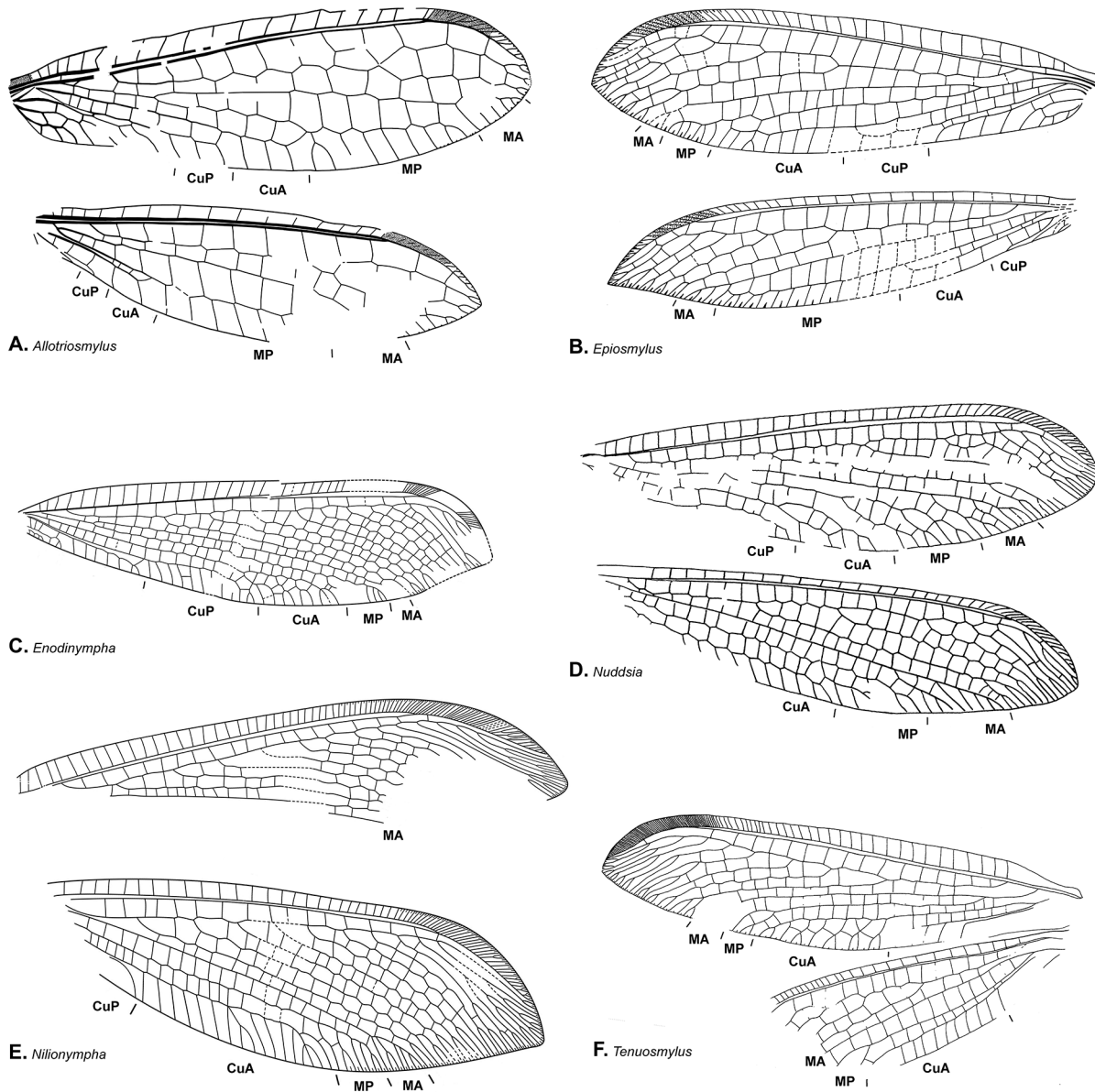


FIGURE 7. Gumillinae fossils. A. *Allotriosmylus uniramusus* Yang *et al.* (from Yang *et al.*, 2010); B. *Epiosmylus panfilovi* Ren & Yin (from Ren & Yin, 2002); C. *Enodinympa translucida* Ren & Engel (forewing); D. *Nuddsia longiantennata* Menon & Makarkin (from Menon & Makarkin, 2008); E. *Nilionympha pulchella* Ren & Engel (from Ren & Engel, 2007); F. *Tenuosmylus brevineurus* Wang *et al.* (from Wang *et al.*, 2009b) (figures not to scale).

***Epiosmylus* Panfilov in Dolin *et al.*, 1980**

(Fig. 7B)

Type species. *Epiosmylus longicornis* Panfilov in Dolin *et al.*, 1980: 100 (by original designation).

Diagnosis. Wings narrow, subacute apically; RP with 5–6 branches; RP1 originating far from origin of RP (1/3–1/2 wing length); FW medial fork close to but distal to origin of RP; MA with few branches near wing margin in both wings; FW MP pectinately branched with 3–6 branches; HW MP elongate, pectinately branched; FW CuA pectinately branched (3–5 branches); FW CuP pectinately branched (3–7 branches); HW CuA elongate with widely spaced pectinately branches; HW CuP simple; FW A1 pectinate (3 widely spaced branches).

Comments. The genus is the type of the family Epiosmylidae Panfilov in Dolin *et al.*, 1980, which was synonymised with Gumillinae by Menon & Makarkin (2008). *Epiosmylus* is differentiated from most other gumilline genera by the first RP branch originating on RP at least 1/3 wing length and relatively few branches of RP (5–6). It appears closely related to *Enodinympha* and *Tenuosmylus*. The wings of these genera are relatively narrow compared to other genera (e.g., *Gumilla*).

Included species.

E. longicornis Panfilov in Dolin *et al.*, 1980 (Kazakhstan) (Late Jurassic)

E. longus Khramov, 2017 (Russia) (Middle Jurassic)

E. panfilovi Ren & Yin, 2002 (China) (Middle Jurassic)



FIGURE 8. Gumillinae. *Gumilla adpersus* Navás, wings.

***Gumilla* Navás, 1912**

(Figs 2C, J, 8–9)

Type species. *Gumilla adpersus* Navás, 1912: 189 (by original designation).

Diagnosis. Antenna longer than FW with elongated flagellomeres and elongated scape; ocelli absent; wings ovoid; subcostal veinlets not forked; subcostal area with single *sc-r* crossvein; RP with crossveins irregularly arranged, without distinct gradate series; FW RP1 originating at approximately 1/3 of wing length, M fork from opposite to slightly beyond origin of RP1; HW medial fork at 2/3 of wing length from base to apex; male genitalia with gonarcus narrow with sparse pile; mediuncus (complex of gonocoxites 10 *sensu* Martins *et al.*, 2016) narrow, arched, dorsomedially with a short subquadrate process; parameres (gonocoxites 11 *sensu* Martins *et al.*, 2016) narrow, slightly arched; female genitalia unknown.

Comments. Navás (1912) correctly placed *G. adpersus* in Osmylidae but a reference by Hagen (1861) to *Osmylus longicornis* as a chrysopid based on the elongate antennae proliferated in the literature (e.g., Banks, 1907); the issue was settled by Adams (1977) who affirmed the conclusions of Navás (1912) and Krüger (1913b) that the latter species belonged in *Gumilla*. Two extant species in this genus are known, although Adams (1977) suggested that these are likely synonymous. Martins *et al.* (2016) recently revised this genus and outlined the confusion regarding the type locality of *G. longicornis*, which is stated as Georgia, but no geographic locality in South America matches that name; it is considered most likely a mislabelling, with the actual type locality being in northern South America.

Included species.

G. adpersus Navás, 1912 (Brazil)

G. longicornis (Walker, 1853) (likely South America)

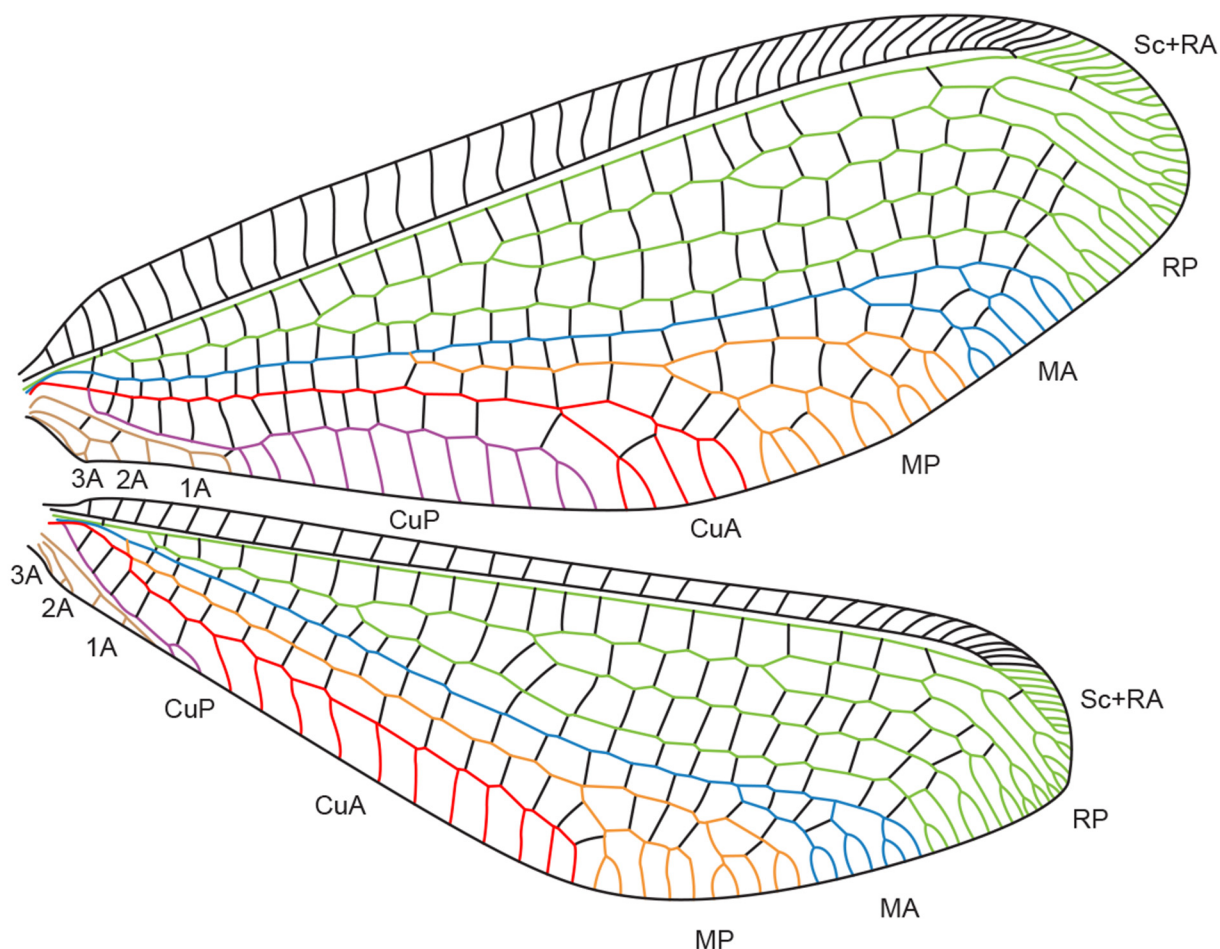


FIGURE 9. Gumillinae. *Gumilla longicornis* (Walker), wing venation (trichosors and vestiture omitted).

***Kolbasinella* Khramov, 2014a**

Type species. *Kolbasinella elongata* Khramov, 2014a: 304 (by original designation).

Diagnosis. Hind wing narrow; RP1 originating at approximately 1/5 wing length; RP with 12 branches MA pectinately branched near wing margin (7 closely spaced branches); numerous regularly arranged crossveins throughout wing, outer gradate series poorly formed near wing margin; MP with only a few pectinate branches; CuA strongly pectinate (*ca.* 19 very short branches); FW unknown.

Comments. *Kolbasinella* was placed in Gumillinae by Khramov (2014a) due to the crossvein density and lack of trichosors in the wing margin. While these are indeed traits exhibited (in part) by Gumillinae, they are not diagnostic of the subfamily; some Gumillinae do have trichosors in the distal part of the wing (e.g., *Gumilla*). Unfortunately, since *Kolbasinella* is only known from a hind wing, the justification presented by Khramov (2014a) for placement in Gumillinae is equivocal as important diagnostic antennal and forewing features are absent. The hind wing of *Kolbasinella* does not show the vein CuP but based on the shape of the other wing veins and the wing margin, it suggests that CuP is at least not elongate and pectinately branched, therefore placing it in one of three subfamilies, Spilosmylinae, Protosmylinae or Gumillinae. However, the genus is tentatively retained in Gumillinae here as its hind wing does not possess the basal sinuate crossvein *1r-m*, a state diagnostic for the subfamily (*1r-m* is present in Spilosmylinae and Protosmylinae). The lack of end-twigging in the posterior part of the wing is typical of Gumillinae but could also be due to the elongate shape of the wing and the proximity of the longitudinal veins (i.e., M and Cu) to the wing margin.

Included species.

K. elongata Khramov, 2014a (Kazakhstan) (Late Jurassic)

***Nilionympha* Ren & Engel, 2007**

(Fig. 7E)

Type species. *Nilionympha pulchella* Ren & Engel, 2007: 216 (by original designation).

Diagnosis. Wings relatively short and broad, apices slightly rounded; FW costal area narrow, subcostal veinlets widely spaced basally, denser distally, pterostigma relatively broad; FW RP1 originating relatively distant to origin of RP; both wings with numerous regular crossveins, outer gradate series absent; both wings with MA and MP with few irregular pectinate/dichotomous branches, MP area larger than MA; FW CuA irregularly dichotomously to pectinately branched, HW CuA more strongly pectinate and larger in area, with occasional end-twigging; FW CuP pectinately branched, HW CuP short, simple.

Comments. *Nilionympha* was originally described based on incomplete specimens of *N. pulchella* and *N. imperfecta* Ren & Engel, 2000). Li *et al.* (2018) recently revised the genus and transferred *N. imperfecta* to *Enodinympa* after a reappraisal of the type specimen and description of the forewing. Unfortunately, the hind wing venation of both *Nilionympha* and *Enodinympa* was misinterpreted by both Ren & Engel (2007) and Li *et al.* (2018), specifically the identity of the posterior veins. In both cases RP1 was misinterpreted as MA, MP as CuA, CuA as CuP. Indeed, their interpretation would actually preclude placement in Gumillinae as an interpretation of an elongate and pectinately branched CuP in the hind wing would place both genera in subfamilies such as Stenosmylinae. We identify the hind wing CuP as a short, simple vein basal to the elongate and pectinately branched CuA, which taken into consideration with characters such as the wing cell arrangement and highly elongate antennae, *Enodinympa* and *Nilionympha* clearly both belong to Gumillinae.

Included species.

N. pulchella Ren & Engel, 2007 (China) (Middle Jurassic)

N. shantouensis Li *et al.*, 2018 (China) (Middle Jurassic)

***Nuddsia* Menon & Makarkin, 2008**

(Fig. 7D)

(= *Burmaleon* Myskowiak *et al.*, 2016 syn. nov. Type species. *Burmaleon magnificus* Myskowiak *et al.*, 2016: 219)

Type species. *Nuddsia longiantennata* Menon & Makarkin, 2008: 151 (by original designation).

Diagnosis. Wings elongate and narrow; FW RP with five branches, RP1 originating far from origin of RP, close to wing length; FW M fork at to 1/3 wing length, slightly proximal origin of RP1; MA and MP each dichotomously branched apically in both wings; FW CuA with distal fork forming distinct loop; FW CuP and HW CuA elongate pectinate branched.

Comments. *Nuddsia* (late Aptian) and *Burmaleon* **syn. nov.** (earliest Cenomanian) are very similar in appearance and while being located on separate continents, are relatively close in age. Indeed, the only feature to distinguish between *Burmaleon* and *Nuddsia* is the slight difference in position of the forewing medial fork. This fork is close to, but just proximal to the origin of RP1 in *Burmaleon*, while in *Nuddsia* it is slightly more proximal. This distinction is relative and hardly significant at the generic level when compared to other genera of Gumillinae. The overall similarity of *Nuddsia* and *Burmaleon* is otherwise close enough to consider them congeneric and *Burmaleon* is herein synonymised with *Nuddsia*. Both Martins-Neto & Rodrigues (2010) and Myskowiak *et al.* (2016) describe the main difference between *Nuddsia longiantennata* and *Nuddsia repatriata* as being the medial fork of forewing being positioned at the base of the wing, slightly basal to the origin of RP. Yet, no other osmylid forewing has the medial fork this close to the base of the wing, although all osmylid hind wings do. The forewing and hind wing venation in Osmylidae is at times very similar, especially in Gumillinae where the costal area is not expanded in the forewing. We are sure therefore, that the forewing of *N. repatriata* presented in Martins-Neto & Rodrigues (2010: fig. 2) is instead a hind wing, although the placement in *Nuddsia* is still valid. *Nuddsia* is similar in wing venation to *Gumilla* but differs in the position of the forewing medial fork being distal to the origin of the first branch of RP.

Included species.

N. longiantennata Menon & Makarkin, 2008 (Brazil) (Early Cretaceous)

N. repatriata Martins-Neto & Rodriguez, 2010 (Brazil) (Early Cretaceous)

N. magnifica (Myskowiak *et al.*, 2016) **comb. nov.** (Myanmar) (Late Cretaceous)

***Osmylochrysa* Jepson *et al.*, 2012**

Type species. *Osmylochrysa anomala* Jepson *et al.*, 2012: 39 (by original designation).

Diagnosis. Forewing oval, relatively small; subcostal area with several *sc-r* crossveins at least in basal half of wing (preserved in *O. anomala*); RP with at least two branches (likely more), RP1 originating relatively close to origin of RP (only one *ra-rp* crossvein in this part of the wing); M fork basal to origin of first branch of RP and close to origin of RP; MA and MP branching pattern unknown; CuA and CuP with relatively few pectinate branches; A1 pectinately branched; crossveins scarce in proximal half of the wing. Hind wing unknown.

Comments. The genus is only known from a few fragmentary forewings and the placement in Gumillinae is tentative based on general appearance rather than identification of synapomorphies characteristic of the subfamily. The diagnosis here is based largely on *O. anomala*, as the specimen of *O. fragilis* is only known from a smaller wing fragment. *Osmylochrysa* displays a remarkable similarity in wing venation with *Allotriosmylus* and may indicate some relationship, although this could easily be convergence as both have highly reduced venation, likely associated with the small size of the wings (*ca.* 10 mm). *Osmylochrysa* is easily distinguished from all other gumilline genera by the multiple subcostal crossveins and from *Allotriosmylus* by the multiple branches of RP.

Included species.

O. anomala Jepson *et al.*, 2012 (England) (Early Cretaceous)

O. fragilis Jepson *et al.*, 2012 (England) (Early Cretaceous)

***Tenuosmylus* Wang *et al.*, 2009b**

(Fig. 7F)

Type species. *Tenuosmylus brevineurus* Wang *et al.*, 2009b: 558 (by original designation).

Diagnosis. Wings narrowly ovoid, medium length; crossveins irregularly spaced and few in number; FW RP with eight branches, RP1 originating relatively distant from wing base, approximately wing length in both wings; FW M fork close to origin of RP; MA, MP few branched close to wing margin; FW CuA pectinately branched, with six branches interlinked by crossveins, end-twigging present in most branches; HW CuA elongate pectinately branched but lacking interlinking crossveins and end-twigging; FW CuP and A1 with few pectinate branches.

Comments. The status of *Tenuosmylus* relative to *Epiosmylus* and *Enodinympa* is questionable, as the wings of all three genera are very similar in all significant respects, except that in *Tenuosmylus* and *Enodinympa* the forewing cubital vein has secondary crossveins interlinking the branches of CuA and end-twigging; these are lacking in *Epiosmylus*. Additionally, are eight branches of RP in *Tenuosmylus* compared with fewer than six in *Epiosmylus*. Presently, we maintain *Tenuosmylus* as distinct from *Epiosmylus*, but the status of the genus relative to *Enodinympa* requires further investigation.

Included species.

T. brevineurus Wang *et al.*, 2009b (China) (Middle Jurassic)

KEMPYNINAE Carpenter, 1943

(= Kalosmylinae Krüger, 1913a: 95. Type genus: *Kalosmylus* Krüger, 1913a: 96)

Type genus. *Kempynus* Navás, 1912: 191.

Diagnosis. Wings typically large with extensive contrasting markings; margin rounded or falcate posteriorly; antennae shorter than forewing length; prothorax length subequal to width, or slightly longer; trichosors present along most of wing margin; end-twigging extensive along much of posterior wing margin, often multi-layered; FW subcostal veinlets evenly and densely distributed along costal area, simple or irregularly forked, often extensively, sinuous, sometimes with secondary interlinking crossveins; single *sc-r* crossvein basally; RP1 originating near wing base in both wings, usually more than ten branches of RP, numerous crossveins in radial area with outer gradate series distinct (rarely absent), inner gradate series absent, RP branches sinuous in distal part of wing; FW medial fork in basal part of wing, beyond origin of RP1; FW CuA dichotomously or pectinately branched, extent of branching variable, usually with few branches, with numerous branches in some fossil genera; HW sigmoid crossvein *1r-m* typically distinct; HW intramedial area between MA and MP usually expanded; HW CuA and CuP veins elongate and pectinately branched; FW A1 elongate and pectinately branched; male abdominal tergites 8 and 9 separate sclerites with paired eversible scent glands present in intersegmental membrane; male genitalia with gonarcus as broadly arched sclerite often with sparse setal pile; baculum absent; entoprocessus broad and subtriangular; parameres absent; female genitalia with sternite 8 large, concave and immediately posterior to sternite 7; female gonopophysis 9 large, often multilobed process; spermathecae small with short spermathecal duct; larvae generally dark, often with sclerites metallic-like.

Comments. Kempyninae comprise three extant genera and five extinct genera. They are typically large lacewings, with wings that are often falcate with dark mottled markings; some of the largest osmylids are in this subfamily. The enlarged area between hind wing MA and MP is usually composed of irregularly arranged crossveins interlinked with secondary crossveins, although this is most distinct in *Kempynus* and various fossil genera, and not so distinct in *Euosmylus* or some *Australysmus*. The radial area in the distal part of the wing is also typically sinuate. Characters such as the arrangement of the forewing medial fork in the basal part of the forewing and elongate pectinately branched hind wing CuP, as well as abdominal scent glands in the male are shared only with Osmylinae, reflecting the close relationship between these subfamilies (see Winterton *et al.*, 2017). The wing venational characters do vary, making distinction between Kempyninae and Osmylinae difficult based on wing features only, especially in fossil taxa, but features in both the male and female genitalia are very distinct and

support them strongly as separate groups. Larvae are associated with riparian habitats close to water edge, usually along montane streams. They are found in leaf litter and under rocks.

Genera included. *Arbusella* Khramov, *Australysmus* Kimmins, *Cretosmylus* Makarkin, *Euporismites* Tillyard in Tillyard & Dunstan, *Euosmylus* Krüger, *Jurakempynus* Wang *et al.*, *Kempynosmylus* Makarkin, *Kempynus* Navás, *Ponomarenkius* Khramov *et al.*, *Sauktangida* Khramov.

***Arbusella* Khramov, 2014a**

Type species. *Arbusella bella* Khramov, 2014a: 307 (by original designation).

Diagnosis. Forewing oval shaped, medium length; costal area of both wings with subcostal veinlets interlinked by secondary crossveins arranged in a regular pattern; both wings with RP with numerous branches (18 or more), distal branches slightly sinuous, crossveins dense in basal half of wing, outer gradates present or absent; MP in both wings with few pectinate branches; HW intramedial area distinctly expanded with secondary crossveins; FW CuA, CuP, A1, A2 pectinate with relatively few branches; wing with distinctive dot-like markings.

Comments. The costal area with subcostal veinlets interlinked by secondary crossveins arranged in a regular pattern and lack of outer gradate series appear diagnostic for this genus. Khramov *et al.* (2018) recently described a new species.

Included species.

A. bella Khramov, 2014a (Kazakhstan) (Late Jurassic)

A. magna Khramov *et al.*, 2018 (China) (Middle-Late Jurassic)

***Australysmus* Kimmins, 1940**

(Fig. 10)

Type species. *Australysmus lacustris* Kimmins, 1940: 198 (by original designation).

Diagnosis. Ocelli present; wings elongate, narrow, posterior margin rounded or rarely slightly falcate; FW subcostal veinlets forked along length; FW RP with distal branches slightly sinuous, outer gradate series present; FW MP forked in distal part of wing; HW intramedial area typically not widely separated, crossveins between them basal to MP fork not sinuous and cells quadrate; male genitalia with tergite 9 often posterodorsally projected, gonarcus narrow, densely setose posterolaterally; entoprocessus elongate, subtriangular shaped, projecting posteriorly beyond gonarcus; female genitalia with tergite 8 anteroventrally possessing a hook-like process, tergite 9 anteroventrally projected into a broad lobe; gonapophyses 9 large, forked, modified, often with several lobes.

Comments. A genus endemic to Australia and atypical for the subfamily by lacking the broadly expanded area between MA and MP in the hind wing. The wings are typically elongate, narrow and ovoid (slightly falcate posteriorly in *A. nevoissi*).

Included species.

A. biproctus New, 1983a (Australia)

A. furcatus New, 1983a (Australia)

A. lacustris Kimmins, 1940 (Australia)

A. nevoissi New, 1983a (Australia)



FIGURE 10. Kempyninae. *Australysmus biproctus* New, dorsal view.

***Cretosmylus* Makarkin, 1990**

(Fig. 11B)

Type species. *Cretosmylus sibiricus* Makarkin, 1990: 102 (by original designation).

Diagnosis. Forewing medium length; costal area broad, subcostal veinlets dense and simple at least in basal half of wing; branches of RP in basal half of wing closely spaced (6–7 branches in basal half); M fork distant from origin of RP1, level with RP3; A1 and A2 weakly pectinate; hind wing unknown.

Comments. A compression fossil where the sole species is represented only by the proximal half of a forewing. Makarkin (1990) compared this genus with those of Kempyninae as the available venation is more similar to that of Kempyninae than other subfamilies. However, the apical part of the forewing and the hind wing are missing, which possess some diagnostic features of the subfamily such as the shape of the distal part of RP and CuA. The kempynine affinity of *Cretosmylus* should be considered as tentative and placement in Osmolinae is also plausible (see also Wang *et al.*, 2011a; Makarkin, 2014). The forking of the forewing medial vein is unique for this genus amongst genera in either subfamily.

Included species.

C. sibiricus Makarkin, 1990 (Russia) (Early Cretaceous)

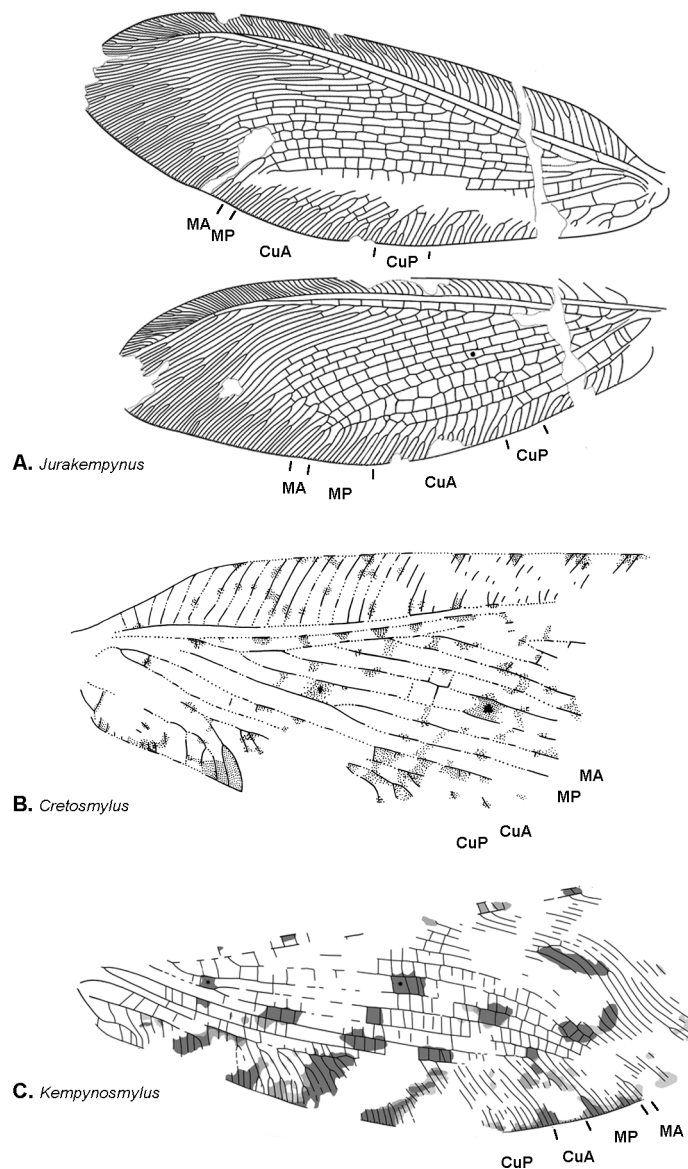


FIGURE 11. Kempyninae fossils. A. *Jurakempynus sinensis* Wang *et al.* (from Wang *et al.*, 2011a); B. *Cretosmylus sibiricus* Makarkin (from Makarkin, 1990) (forewing); C. *Kempynosmylus zherikhini* Makarkin (from Makarkin, 2014) (forewing) (figures not to scale).

Euosmylus Krüger, 1913a

(Fig. 12)

Type species. *Stenosmylus stellae* McLachlan, 1899: 259 (by monotypy) (New Zealand).

Diagnosis. Relatively small robust species; wings falcate, markings variable, hyaline to strongly patterned, contrasted dark areas with pale fenestrate areas; FW costal area relatively narrow, subcostal veinlets mostly simple, rarely forked; numerous branches of RP (10–12), outer gradate series present, extending from MA to pterostigma in both wings; FW M fork level with origin of RP₂; HW intramedial area expanded, but less than in other genera, cells between them quadrate and crossveins not sinuous; female genitalia with spermatheca constricted, hour-glass shaped.

Comments. Closely related to *Kempynus*, *Euosmylus* is a monotypic genus endemic to New Zealand which has very similar shaped male and female genitalia and wing venation. *Euosmylus stellae* is a relatively small, but robust species with distinctively patterned wings.



FIGURE 12. Kempyninae. *Euosmylus stellae* (McLachlan), dorsal view.

Included species.

E. stellae (McLachlan, 1899) (New Zealand).

***Euporismites* Tillyard in Tillyard & Dunstan, 1916**

Type species. *Euporismites balli* Tillyard in Tillyard & Dunstan, 1916: 44 (by original designation).

Diagnosis. Forewing costal area with subcostal veinlets simple; branches of RP numerous, strongly sinuous distally, radial crossveins dense, except in distal part; outer gradate series apparently absent; end-twigging largely absent in medial and cubital regions; HW with MP relatively deeply forked; CuA probably strongly pectinate.

Comments. The type species was described based on a compression fossil hind wing fragment. This was later re-examined by Riek (1952) who assigned to this species an apical 1/2 of a forewing from the same locality and horizon. Later, these two specimens were re-examined by Lambkin (1987) who assigned to the species another hind wing fragment from a nearby locality (i.e., Dinmore) of the same horizon. It is very possible that the holotype and additional specimen represent different species and maybe even subfamilies. Lambkin (1987) mentioned some differences between the two but consider them as examples of intraspecific variation. The hind wing venation of the holotype is similar to *Euporismus* (Stenosmylinae) as believed by Tillyard & Dunstan (1916) and Riek (1952) (cf. Tillyard, 1916, fig. 1, and Lambkin, 1987, fig. 1). The incomplete preservation of the holotype does not allow precise determination of the subfamily, but the venation of the Dinmore specimen certainly belongs to Kempyninae based on the presence of the basal sinuous crossvein *Ir-m* and the deeply forked MP.

Included species.

E. balli Tillyard in Tillyard & Dunstan, 1916 (Australia) (Paleogene)

***Jurakempynus* Wang et al., 2011a**

(Figs 11A)

Type species. *Jurakempynus sinensis* Wang et al., 2011a: 867 (by original designation).

Diagnosis. Forewing ovoid with posterior margin straight to slightly falcate; costal area broad basally, narrowing distally, subcostal veinlets mostly irregularly forked; RP with numerous branches (typically more than 15), distal branches slightly sinuous, crossveins numerous, irregularly spaced in basal half of wing, absent in distal half, RP branches with extensive multi-layered end-twigging extending deep into radial area of both wings, outer gradate series absent in both wings; FW M forked nearly level with origin of RP1; MA, MP with few pectinate branches apically; HW medial vein with expanded intramedial area with two rows of irregularly arranged cells; FW CuA strongly pectinate (seven forked branches; proximal branch profusely branched); HW CuA with 10–15 pectinate branches; FW CuP with 3–5 pectinate branches, HW CuP with 4–12 pectinate branches; A1 strongly pectinate in both wings (4–8 branches).

Comments. *Jurakempynus* is a typical kempynine osmylid distinguished from other genera by the expanded area in the hind wing medial vein with two rows of irregular cells, numerous RP branches in both wings with dense crossveins basally and the outer gradate series apparently lacking in radial field. The hind wing veins CuA and CuP both have fewer pectinate branches than most extant genera.

Included species.

J. bellatulus Wang et al., 2011a (China) (Middle Jurassic)

J. arcanus Khramov, 2014a (Kazakhstan) (Late Jurassic)

J. sublimis Khramov, 2014a (Mongolia) (Late Jurassic)

J. sinensis Wang et al., 2011a (China) (Middle Jurassic)

J. epunctatus Wang et al., 2011a (China) (Middle Jurassic)

***Kempynosmylus* Makarkin, 2014**

(Fig. 11C)

Type species. *Kempynosmylus zherikhini* Makarkin, 2014: 9 (by original designation).

Diagnosis. Forewing ovoid; RP with numerous branches (>16), strongly sinuate distally; numerous regularly arranged crossveins in basal half of wing, outer gradate series apparently absent; FW M forked nearly level with origin of RP2, approximately at level of A2 termination, MA few branched, MP pectinately branched (5–6 branches); FW CuA (3–4 branches) and CuP (11–12 branches) both pectinately branched; A1 elongate, strongly pectinate (≥ 13 branches) with some irregular end-twigging; A2 strongly pectinate (7 branches); A3 with a few pectinate branches; HW unknown.

Comments. Based on an incomplete forewing fragment, the apparent kempynine affinity of this genus (*cf.* Osmylinae) remains tentative. Characters such as the numerous basal crossveins, position of the medial fork and sinuate distal branches of RP suggest that it should be placed in Kempyninae but not conclusively and placement in Osmylinae cannot be ruled out. The wing venation of *Kempynosmylus* is similar to *Arbusella* and *Jurakempynus*, genera similarly lacking the outer gradate series. The status of the genus relative to these genera (and its subfamilial placement) will be clearer once additional, more complete material is discovered.

Included species.

K. zherikhini Makarkin, 2014 (Russia) (Early Cretaceous)

***Kempynus* Navás, 1912**

(Figs 13–16)

(= *Kalosmylus* Krüger, 1913a. Type species: *Osmylus incisus* McLachlan, 1873: 112)

(= *Osmylinus* Banks, 1913. Type species: *Osmylus longipennis* Walker, 1853: 235)

(= *Clydosmylus* New, 1983a. Type species: *Clydosmylus montanus* New, 1983a: 409) **syn. nov.**

Type species. *Osmylus incisus* McLachlan, 1873: 112 (by original designation).



FIGURE 13. Kempyninae. *Kempynus incisus* (McLachlan), dorsal view.

Diagnosis. Ocelli present; wings elongate, relatively large, slightly to strongly falcate, wing apices acute or rounded; FW subcostal veinlets often forked, usually strongly sinuous, interlinking crossveins rarely present; both wings with RP with *ca.* 11–20 branches, crossveins irregular, outer gradate series distinct, elongate and sinuous; FW M fork near origin of RP1 or RP2 RP; MP branching at or beyond of the mid-length of wing, sometimes with posterior branch partially fused to CuA; HW MA and MP relatively divergent, crossveins slightly sinuous; FW CuA with few branches, HW CuA elongate pectinately branched; CuP in both wings greatly elongate, pectinate branched; FW A1 and A2 elongate pectinate branched.

Comments. The largest genus in the subfamily, with species displaying a distinct austral distribution in Australia, New Zealand, Chile and Argentina. The typically falcate and strongly patterned wings, frequently sinuous crossveins throughout is typical for *Kempynus*. New (1983a) described the monotypic genus *Clydosmylus* New based on a large, sexually dimorphic species from eastern Australia. In their phylogenetic analyses Winterton *et al.* (2017) suggested that the differentiation of *Clydosmylus* from *Kempynus* is not supported and that *Clydosmylus* should be synonymised with *Kempynus*, which is done herewith. Lacewings with larger wings often develop additional vein branching and crossveins associated as a structural requirement to support the larger wing

membrane area. The main features separating *Clydosmylus* from *Kempynus* described by New (1983a) include the large wing size, more reticulate venation and more basal forking of vein MP in the FW; all these features could easily be ascribed to the larger wing area. The distinctive New Zealand *Kempynus incisus* (Fig. 14) was noted as also possibly being present in Australia by New (1983a) based on two specimens (lacking genitalia) collected in Queensland. No additional specimens have been collected so this record is yet to be confirmed.



FIGURE 14. Kempyninae. *Kempynus incisus* (McLachlan), courtship behaviour (photo: Gil Wizen).

Included species.

- K. acutus* New, 1986b (Australia)
- K. citrinus* (McLachlan, 1873) (New Zealand)
- K. crenatus* Adams, 1971 (Argentina; Chile)
- K. digoniostigma* Oswald, 1994 (Argentina; Chile)
- K. falcatus* Navás, 1912 (Argentina; Chile)
- K. incisus* (McLachlan, 1863) (Australia (?), New Zealand)
- K. kimminsi* New, 1983a (Australia)
- K. latiusculus* (McLachlan, 1894) (New Zealand)
- K. longipennis* (Walker, 1853) (Australia)
- K. maculatus* New, 1983a (Australia)
- K. millgrovensis* New, 1983a (Australia)
- K. montanus* (New, 1983a) **comb. nov.** (Australia)
- K. striatus* New, 1983a (Australia)
- K. thecatus* New, 1983a (Australia)
- K. tjederi* Oswald, 1994 (Chile)



FIGURE 15. Kempyninae. *Kempynus acutus* New, dorsal view.

***Ponomarenkius* Khrakov *et al.*, 2017**

Type species. *Ponomarenkius excellens* Khrakov *et al.*, 2017: 3 (by original designation).

Diagnosis. Wings elongate, relatively large, ovoid; FW subcostal veinlets occasionally forked, more frequent distally, usually sinuous distally, interlinking veinlets absent; both wings with RP with *ca.* 11–20 branches, crossveins irregular and dense in basal part of wing, absent in distal part of wing except for a distinct outer gradate series, RP branches elongate and sinuous distally; FW M fork near origin of RP; MP branching near base of wing, just beyond RP2; HW MA and MP both forked near base of wing, HW MP with multiple branches, area between MP and MP not greatly expanded compared with other veins; FW CuA with few branches, HW CuA elongate pectinately branched; CuP in both wings greatly elongate, pectinate branched; FW A1 and A2 elongate pectinate branched.

Comments. *Ponomarenkius* is spelt two different ways in Khrakov *et al.* (2017), including also ‘*Ponomarenkus*’. It is clear in the publication that the first and most frequent use of *Ponomarenkius* is the intended spelling and this is what is used herein. The multiple branches of MP in both wings is diagnostic for the genus.

Included species.

P. excellens Khrakov *et al.*, 2018 (China) (Middle-Late Jurassic)

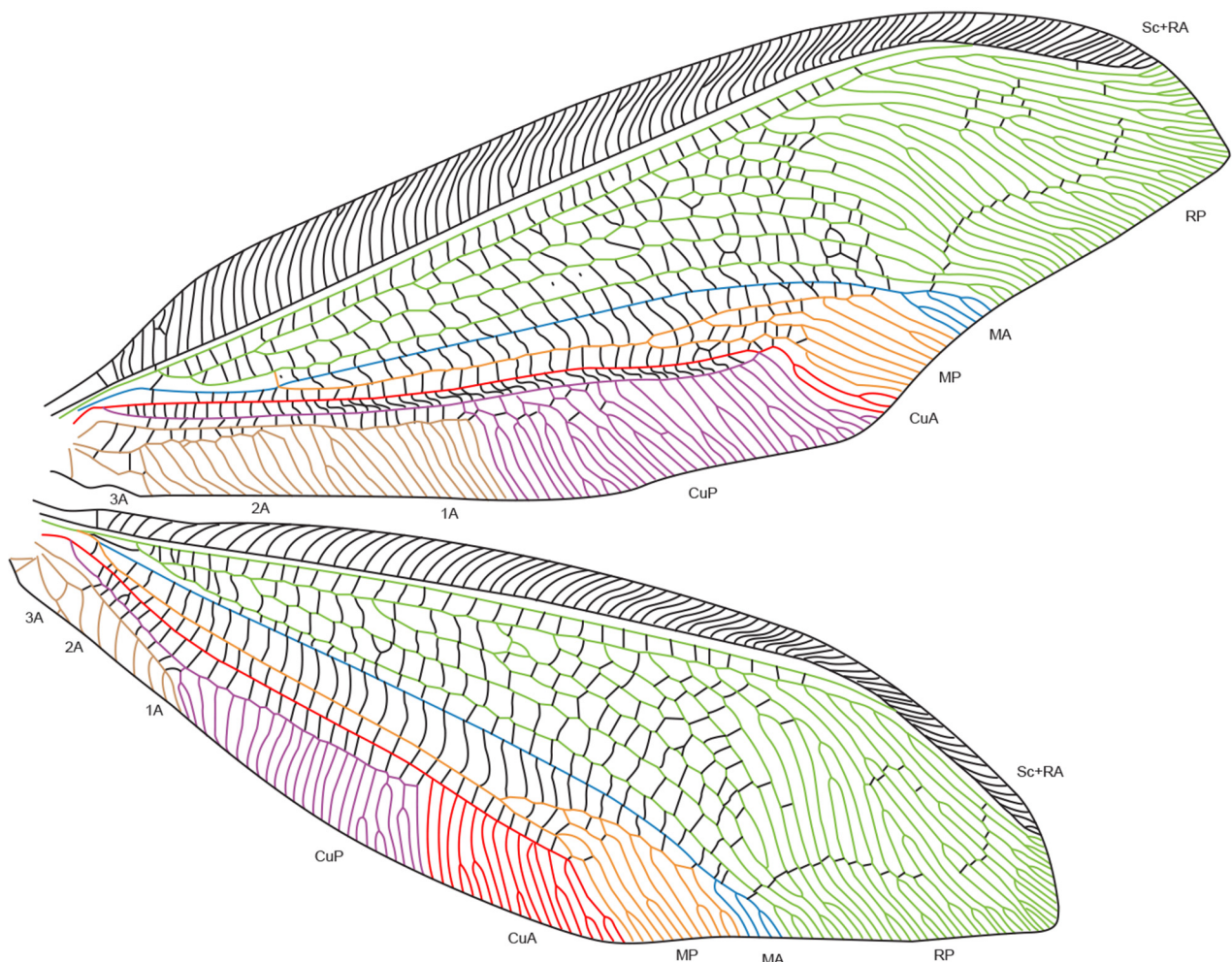


FIGURE 16. Kempyninae. *Kempynus incisus* (McLachlan), wing venation (trichosors and vestiture omitted).

Sauktangida Khamov, 2014b

Type species. *Sauktangida aenigmatica* Khamov, 2014b: 60 (by original designation).

Diagnosis. Hind wing relatively broad, medium length; subcostal veinlets forked distally; basal 1r-m sinuous, connecting M and RP1; RP field with numerous irregular crossveins throughout; wing with end-twigging extensive along posterior margin; intramedial area (between MA and MP) broad, with irregular crossveins and bisected to form 2–3 rows of cells; MP forked around wing length, dichotomously branched; CuA strongly pectinate (ca. 10 long, mostly forked branches); CuP pectinate (five long, mostly forked branches); A1, A2 pectinate with few branches; FW unknown.

Comments. The kempynine affinity of this genus is very probable due to the general venation of the hind wing, and its intramedial area is dilated with additional longitudinal rows of crossveins.

Included species.

S. aenigmatica Khamov, 2014b (Kyrgystan) (Early Jurassic)

MESOSMYLININAE Bode, 1953

Type genus. *Mesosmylina* Bode, 1953: 247.

Diagnosis. Forewing with trichosors present along most of wing margin (where known); wing ovoid, relatively small; costal area uniformly narrow to broad basally; relatively few medial and cubital branches that are usually irregularly branched to few pectinate and not palisade-like in arrangement along the wing margin; single sc-r crossvein basally, rarely more; FW CuP with few branches (not elongate pectinately branched); HW unknown.

Comments. Members of this Jurassic subfamily display a generalised forewing with MA-MP fork near the base of the wing. This is an apparent plesiomorphic feature for Osmylidae as more distal forking of the forewing medial vein is found in the middle of the wing in some Protosmylinae and in the distal half of the wing in Stenosmylinae. The non-palisade-like arrangement of pectinately branched veins along posterior margin of wing (especially MA and MP) is characteristic; this area is also smaller in area than in other subfamilies. The definition of Mesosmylinae is unclear at this stage, especially relative to Protosmylinae and Spilosmylinae. The shape, branching pattern and relative areas of the medial and cubital veins in both wings appear important in defining Mesosmylinae; this in turn may require some reconsideration of the membership of the subfamily. In particular the forewing CuP has only a few branches in Mesosmylinae, while in Protosmylinae and Spilosmylinae CuP is elongate and pectinately branched. Larvae are unknown for this subfamily.

Genera included. *Mesosmylina* Bode, *Sogjuta* Martynova.

***Mesosmylina* Bode, 1953**

Type species. *Mesosmylina exornata* Bode, 1953: 247 (by original designation).

Diagnosis. Forewing ovoid; costal area relatively broad basally and narrowed distally, subcostal veinlets simple, rather widely spaced basally, denser distally towards pterostigma, rarely forked; numerous crossveins in RA-RP area; RP branches numerous, dense and slightly sinuous distally; origin of RP1 variable, sometimes distant from origin of RP; MA-MP fork variable, usually before origin of RP1 but sometimes beyond RP1 and before RP2; MA few branched distally; MP slightly pectinate; crossveins in radial to intramedial spaces arranged in six gradate series, irregular proximally CuA pectinate; CuP with just a few pectinate branches (2–3); HW unknown.

Comments. The presence of multiple discreet gradate series throughout the radial and medial areas of the forewing, along with the pectinate CuP appears diagnostic. *Mesosmylina sibirica* Ponomarenko likely does not belong to this genus, and even its osmylid affinity needs a confirmation; it is only tentatively included here.

Included species.

M. angusta Khramov, 2014b (Kyrgyzstan) (Early/Middle Jurassic)

M. exornata Bode, 1953 (Germany) (Early Jurassic)

M. falcifera Ansorge, 1996 (Germany) (Early Jurassic)

M. mongolica Ponomarenko, 1984 (Mongolia) (Early/Middle Jurassic)

M. shurabica Khramov, 2014b (Kyrgyzstan) (Early/Middle Jurassic)

M. sibirica Ponomarenko, 1985 (Russia) (Middle Jurassic)

***Sogjuta* Martynova, 1958**

(Fig. 17)

Type species. *Sogjuta speciosa* Martynova, 1958: 77 (by original designation).

Diagnosis. Forewing ovoid, relatively small and rounded apically; costal area relatively narrow along entire length, subcostal veinlets mostly simple, widely spaced along entire wing; RP with 8–9 branches; RP1 originated relatively far from origin of RP; M forked basal to origin of RP1; MA and MP distally dichotomously branched; crossveins in radial to mediocubital spaces arranged in three regular gradate series; CuA with few pectinate branches (2–4); CuP pectinately branched (4–5); HW unknown.

Comments. Martynova (1958) originally placed *Sogjuta* in Nymphitidae and was later moved to Osmylidae by Lambkin (1988). Khramov (2011) described a second species and characterised the genus further. The small size and rounded shape of the forewing, along with the branching pattern of the medial and cubital veins supports

placement in Mesosmylinae (Khrmov, 2011; Makarkin *et al.*, 2014). Three gradate series in the forewing separates *Sogjuta* from *Mesosmylina*, which has 5–6 gradates.

Included species.

S. shartegica Khrmov, 2011 (Mongolia) (Late Jurassic)

S. speciosa Martynova, 1958 (Kyrgyzstan) (Early Jurassic)

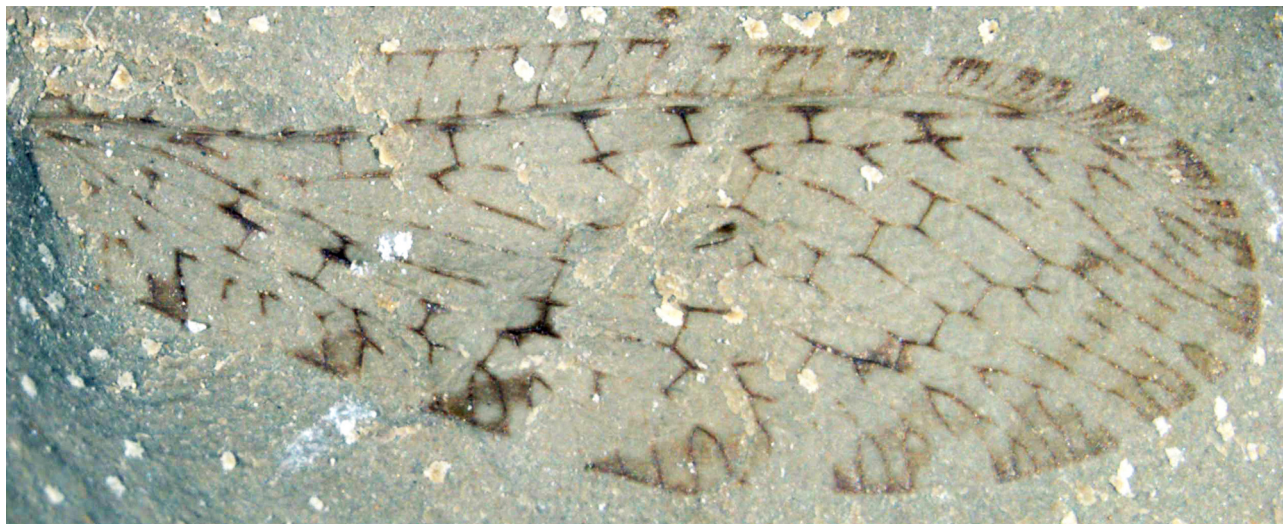


FIGURE 17. Mesosmylinae. *Sogjuta shartegica* Khrmov (photo: A. Khrmov).

OSMYLINAE Leach, 1815

Type genus. *Osmylus* Latreille, 1802: 289.

Diagnosis. Ocelli present, antennae shorter than half length of FW; prothorax width subequal to length; female forecoxae sometimes with narrow processes; trichosors present along most of wing margin; usually numerous FW forked subcostal veinlets, sometimes with interlinking crossveins; HW subcostal veinlets sometimes forked, particularly distally; single FW with single *sc-r* crossvein basally; RP with 10–17 branches, crossveins numerous and regularly spaced, rarely with crossveins almost completely absent in basal half of radial area (e.g., *Sinosmylus*), RP branches only slightly sinuous distally; RP with outer and inner gradate series distinct in both wings, although inner series sometimes absent (e.g., *Parosmylus*, *Lithosmylus*); FW M vein forked opposite or slightly distal (rarely basal, e.g., *Parosmylus*) to origin of RP1; HW medial area slightly expanded basally, narrowed distally; marginal branches of M and Cu near perpendicular to wing margin, palisade-like in arrangement; CuA with more branches in HW than in FW; CuP in both wings elongate with numerous pectinate branches; male abdominal tergites 8 and 9 as separate sclerites with eversible scent glands present on membrane between; male genitalia with enlarged gonarcus, externally visible with distinct setal pile, anterior apodeme narrow and articulated upon gonarcus; entoprocesses reduced and rounded; parameres narrow rod-shaped sclerites flanking mediuncus; female genitalia with sternite 8 plate-like, positioned immediately posterior to sternite 7; gonopophysis 9 as lateral sclerites anterior to and closely associated with gonocoxite 9, articulated with tergite 9 ventrally. Larvae typically have a dark brownish-black body colour.

Comments. Osmylinae are closely related to Kempyninae and Stenosmylinae and share many morphological similarities with Kempyninae, especially in wing venation. Indeed, this similarity in wing venation has been problematic for placing fossil genera (e.g., *Lithosmylus*) where typical discriminating wing vein characters at the subfamily level (e.g., branching pattern of subcostal veinlets, forewing media and hind wing cubitus) are the same in both Osmylinae and Kempyninae. Osmylinae occupy an intermediate position in the phylogeny of the family, sister to more derived subfamilies such as Kempyninae, Porisminae and Stenosmylinae and exhibit a variety of characters shared with other subfamilies (e.g., fusion of male tergites 8 and 9, eversible scent glands, presence of parameres, and position of female gonopophysis 9). Osmylinae comprise at least six morphologically similar

genera, although some authors recognise up to eight. Unfortunately, characteristics useful in defining genera in this subfamily are relatively few in number, and those used are not adequate. This has resulted in very little consensus amongst various authors regarding generic concepts (Banks, 1913; Nakahara, 1914; Kuwayama, 1953, 1962; Makarkin, 1985; Wang & Liu, 2009; Sekimoto, 2010; Xu *et al.*, 2016), even amongst authors of this present work. Moreover, in their phylogenetic analysis of both molecular and morphological data, Winterton *et al.* (2017) confirmed the uncertain status of most genera in the subfamily, with *Osmylus* rendered paraphyletic by all other osmyline genera included in the study (i.e., *Plethosmylus*, *Parosmylus* and *Sinosmylus*). Herein we diagnose the following genera but consider the status of all but the type genus *Osmylus* as uncertain and in need of further detailed study. Larvae are found in the air-water interface of riparian habitats.

Genera included. *Grandosmylus* Makarkin, *Lahulul* Navás, *Lithosmylus* Carpenter, *Osmylus* Latreille, *Parosmylus* Needham, *Sinosmylus* Yang.

***Grandosmylus* Makarkin, 1985**

Type species. *Grandosmylus centrasius* Makarkin, 1985: 41 (by original designation).

Diagnosis. Female forecoxae with strongly curved processes; wings elongate ovoid; FW largely hyaline and veins uniformly pale-brownish; subcostal veinlets mainly forked, without interlinking crossveins; RP with 9–10 branches, some of them deeply forked; RP branches only slightly sinuous distally; crossveins numerous in basal half of radial area, inner gradate series absent, outer series present; M vein forked slightly distal to origin of RP1; CuA, CuP, A1 strongly pectinate; branches of A1 long, without interlinking crossveins; male genitalia with large gonarcus bearing a pair of very long dorsal processes, each terminating in paired acute denticles; female genitalia sternite 8 very short with paired short processes.

Comments. This genus is distributed in mountains of Central Asia (at elevations up to 3800 m). Like *Parosmylus*, it lacks an inner gradate series and can be differentiated by male genitalic features, especially the enlarged dorsal processes on the gonarcus.

Included species.

G. centrasius Makarkin, 1985 (Tajikistan)

G. nubeculosus (Navás, 1910) (Afghanistan)

***Lahulul* Navás, 1930**

Type species. *Lahulul babaulti* Navás, 1930: 9 (by original combination).

Diagnosis. Prothorax slightly longer than wide; wings hyaline with yellow venation, narrow with obtuse apex, posterodistal wing margin convex; pterostigma with brown marks; outer gradate series distinct, remainder of crossveins irregularly arranged; Cu forked at wing base; FW RP with 13–15 branches, slightly curved with bifurcated apex; FW subcostal area with most veinlets forked, those in the distal half somewhat sinuous; a single crossvein between R and M veins; CuA with three branches; some maculae present in cubital region; HW costal area narrow at base with only few costal crossveins forked; RP with 13 branches; male ectoproct sub-triangular with hook shaped ventral projection; male abdomen yellow with yellow setae.

Comments. The monotypic genus *Lahulul* Navás is known only from the original description and neither the type or additional specimens of the sole species have been located in the Muséum National d'Histoire Naturelle, Paris. Little is discernible about this genus from the description by Navás (1930), but he does state a clear similarity with the genus *Hyposmylus* Krüger, a genus now considered a synonym of *Osmylus*. According to Navás description, *Lahulul* has the simpler costal area and more reticulated pterostigma when compared to *Hyposmylus*. We cannot immediately conclude *Lahulul* is a synonym of *Osmylus* though, as the male genitalic drawing by Navás (1930), albeit simplistic, is unlike any other found in the family; it will require further examination to determine the validity of the genus.

Included species.

L. babaulti Navás, 1930 (India).

***Lithosmylus* Carpenter, 1943**

Type species. *Osmylus columbianus* Cockerell, 1908: 758 (by original designation).

Diagnosis. Wings oval; FW costal area broad basally, subcostal veinlets closely spaced and mostly shallowly forked in both wings, veinlets simple at wing base and distally; first branch of RP originating near origin of RP on RA; FW RP with 16 branches, HW with 17 branches; both wings with outer gradate series well developed, inner gradate series absent, radial crossveins numerous in basal half of wing, slightly more irregularly arranged in HW; M forked slightly distal to origin of RP1; MA and MP with 2–4 branches distally in both wings; CuA and CuP strongly pectinately branched in both wings with shallow end-twigging very close to wing margin, FW with six branches in CuA and nine branches in CuP, HW with seven branches in CuA and 12 branches in CuP; FW A1 with seven pectinate branches, HW A1 with four pectinate branches; FW A2 with four pectinate branches, two in HW; A3 simple in both wings.

Comments. The venation of this fossil genus is relatively typical for Osmylinae and we agree with its placement in this subfamily by Lambkin (1987) and Wang *et al.* (2011a), although considering the wing venation similarity, Carpenter (1943) unsurprisingly regarded it as belonging to Kempyninae. Only the wings are known.

Included species.

L. columbianus (Cockerell, 1908) (U.S.A.) (late Eocene)

***Osmylus* Latreille, 1802**

(Figs 4, 18–21)

(= *Hyposmylus* McLachlan, 1870: 200. Type species: *Osmylus punctipennis* Walker, 1860: 183)

(= *Dictyosmylus* Navás, 1910: 189. Type species: *Dictyosmylus lunatus* Navás, 1910: 189)

(= *Plesiosmylus* Makarkin, 1985: 41. Type species: *Osmylus tessellatus* McLachlan, 1875: 36)

(= *Plethosmylus* Krüger, 1913a: 43. Type species: *Osmylus hyalinatus* McLachlan, 1875: 181)

Type species. *Hemerobius maculatus* Fabricius, 1787: 247 (by monotypy).

Diagnosis. Wings elongate, broad, posterior margin occasionally straight distally; FW typically with irregular mottled infuscation; HW mostly hyaline except for pterostigma wing margin and wing base; FW subcostal veinlets often forked near wing margin distally, interlinking crossveins present or absent; RP with at least two gradate series in both wings, dense crossveins in basal 3/4 of wing, RP1 originating close to origin of RP; FW M fork close to, or opposite to RP1; FW cubital area with crossveins present or absent; female forecoxa typically with a prominent process on the anterior surface; male tergite 9 with variably-shaped dorsal processes often present; gonarcus mainly external, enlarged, sclerotized and densely setose in lateral view; entoprocessus shape variable and poorly sclerotised. Female genitalia with sternite 8 variable in shape, sometimes with lateral processes; spermatheca oval or cylindrical.

Comments. Some authors further divide *Osmylus* into two subgenera (*Osmylus* and *Plesiosmylus*), although the basis for at least *Plesiosmylus* is problematic due to a lack of apomorphic characters (Makarkin 1985). Matsuno & Yoshitomi (2016) described the larvae of three Japanese species and found that larval characters also did not support the division of subgenera as proposed by Makarkin (1985). They also synonymised *O. kisoensis* Iwata with *O. pryori* McLachlan. Krüger (1915) erected *Plethosmylus* largely based on the interlinking of costal veinlets with crossveins, but this has not been accepted by some subsequent authors (e.g., Nakahara, 1914; Makarkin, 1985; Sekimoto & Yoshizawa, 2011). Xu *et al.* (2016) provided a key to species of *Osmylus*, but it requires examination of both male and female genitalic characters for an identification. The lack of external diagnosable features and limited specimens on which species have been described means that we do not fully understand the intraspecific

variability expressed in the genus and how it impacts the validity of all species described. *Osmylus* appears to mostly be distributed in the temperate Palaearctic region.



FIGURE 18. Osmylinae. *Osmylus atomatus* Yang *et al.*

Included species.

- O. angustimarginatus* Xu, *et al.*, 2016 (China)
- O. atomatus* (Yang *et al.* in Huang *et al.*, 1988) (China)
- O. biangulus* Wang & Liu, 2010 (China)
- O. bipapillatus* Wang & Liu, 2010 (China)
- O. cilicicus* Krüger, 1913c (Turkey)
- O. conanus* Yang, 1987 (China)
- O. decoratus* Nakahara, 1914 (Japan, Russia)
- O. elegantissimus* Kozhanchikov, 1951 (Azerbaijan, Georgia, Turkey, Ukraine, Russia)
- O. fuberosus* Yang, 1997 (China)
- O. fulvicephalus* (Scopoli, 1763) (Europe)
- O. hyalinatus* McLachlan, 1875 (Japan, Russia)
- O. lucalatus* Wang & Liu, 2010 (China)

O. maoershanicola Xu, *et al.*, 2016 (China)
O. megistus Yang, 1987 (China)
O. minisculus Yang, 1987 (China)
O. multiguttatus McLachlan, 1870 (Turkey, Ukraine)
O. pachycaudatus Wang & Liu, 2010 (China)
O. posticatus Banks, 1947 (China)
O. pryeri McLachlan, 1875 (Japan, Russia) (= *O. kisoensis* Iwata, 1928; = *O. shikokuensis* Kuwayama, 1953)
O. punctipennis Walker, 1860 (China, India)
O. shaanxiensis Xu, *et al.*, 2016 (China)
O. taiwanensis New, 1991 (China)
O. tessellatus McLachlan, 1875 (Japan, Russia)
O. wuyishanus Yang, 1999 (China)
O. xizangensis Yang *et al.* in Huang *et al.*, 1988 (China)
O. zheanus (Yang & Liu, 2001) (China)



FIGURE 19. Osmylinae. *Osmylus hyalinatus* McLachlan.

***Parosmylus* Needham, 1909**

(Fig. 22)

(= *Mesosmylus* Krüger, 1913c: 280. Type species: *Osmylus naevius* Navás, 1912: 184)

(= *Phlebosmylus* Navás, 1928: 94. Type species: *Phlebosmylus tancrei* Navás, 1928: 95) **syn. nov.**

Type species. *Parosmylus prominens* Needham, 1909: 209 (by original designation).

Diagnosis. Wings elongate, ovoid; FW with irregular mottled infuscation; HW mostly hyaline except for

pterostigma wing margin and wing base; FW subcostal veinlets often forked near wing margin distally, interlinking crossveins absent; RP with only outer gradate series present in both wings, sometimes not discernible; dense crossveins throughout much of both wings; RP1 originating on RP close to fork of RA; FW M fork close to, or opposite to origin of RP1; FW cubital area often with crossveins present; male gonarcus posteriorly strongly sclerotised, entoprocesses rounded, well sclerotised and projecting; female genitalia with spermathecae oval.

Comments. Some authors consider *Parosmylus* a synonym of *Osmylus* (e.g., Banks 1913; Nakahara 1914) but following Wang & Liu (2009) we consider it sufficiently different to keep it as separate for now. *Phlebosmylus* Navás is known only from the original description and the type of the sole species in the genus has been destroyed. Only some wings characteristics are discernible about this genus from the description by Navás (1928), including that the genus is similar to *Osmylus*, except for some wing characteristics such as the presence of one row of gradates, which supports placement in *Parosmylus*.



FIGURE 20. Osmylinae. *Osmylus maoershanicola* Xu *et al.*



FIGURE 21. Osmylinae. *Osmylus multiguttatus* McLachlan.

Included species.

- P. belaae* Ghosh & Sen, 1968 (India)
- P. brevicornis* Wang & Liu, 2009 (China)
- P. gussakovskii* (Kozhanchikov, 1951) **comb. nov.** (Tajikistan)
- P. jombai* Yang, 1987 (China)
- P. liupanshanensis* Wang & Liu, 2009 (China)
- P. prominens* Needham, 1909 (India) (= *Osmylus naevius* Navás, 1912)
- P. tancrei* (Navás, 1928) **comb. nov.** (Turkmenistan (?))
- P. tibetanus* Yang, 1987 (China)
- P. yadonganus* Yang, 1987 (China)

***Sinosmylus* Yang, 1992**

(Fig. 23)

Type species. *Sinosmylus hengduanus* Yang, 1992: 450 (by original designation).

Diagnosis. Wings elongate, ovoid; FW extensively mottled infusate; HW mostly hyaline except for pterostigma, wing margin and wing base; FW subcostal veinlets forked near wing margin distally, some veinlets forked at base, interlinking crossveins absent; RP diverging from RA close to wing base, FW RP1 originating close to origin of RP; RP with two distinct gradate series present in both wings, other crossveins largely absent, resulting in elongate radial cells; FW M vein forked slightly beyond origin of RP1; multiple crossveins present between MP and CuA in FW and CuA and CuP in both wings; female genitalia with spermathecae ovoid; male genitalia not known.

Comments. *Sinosmylus* is unique among Osmylinae for the scarce RP crossveins besides the gradate series. Hitherto no new material is collected except for the only one female specimen of the type species from southeastern China.

Included species.

S. hengduanus Yang, 1992 (China)



FIGURE 22. Osmylinae. *Parosmylus liupanshanensis* Wang & Liu.

PORISMINAE Krüger, 1913a

Type genus. *Porismus* McLachlan, 1867: 266.

Diagnosis. Ocelli present; antenna approximately half length of FW; prothorax elongate, much longer than wide; female forecoxae with narrow processes; costal area with subcostal veinlets simple; multiple *sc-r* crossveins in both wings; trichosors present along most of wing margin; numerous crossveins in both wings; both wings with RP sinuous in distal area of wing, RA-RP area wide with numerous crossveins, RP with ca. 8–10 branches, RP1 originating near middle of wing; gradate series absent; FW medial vein forking in distal half of wing; FW CuA with more branches than in HW, HW CuP elongate and pectinately branched; male with abdominal tergites 8 and 9 fused and eversible scent glands absent; male genitalia with parameres and baculum absent, gonarcus relatively narrow with setal pile; entoprocessus broadly triangular; female sternite 8 immediately adjacent to sternite 7, broadly concave; gonopophysis 9 relatively small and triangular, present as separate sclerite anteroventrally of tergite 9.



FIGURE 23. Osmylinae. *Sinosmylus hengduanus* Yang.

Comments. Porisminae comprises a single monotypic genus from eastern Australia. Eidoporisminae and Porisminae share features with Stenosmylinae suggesting a close relationship (New 1983b, Winterton *et al.*, 2017), including an elongate prothorax, fork of the medial vein in distal half of forewing and RP1 diverging in the middle part of both wings. Winterton *et al.* (2017) suggested a possible paraphyly of Stenosmylinae relative to Eidoporisminae and Porisminae and the validity of the subfamily requires further investigation.

Genera included. *Porismus* McLachlan.

***Porismus* McLachlan, 1867**

(Figs 24–26)

Type species. *Osmylus strigatus* Burmeister, 1839: 184 (by monotypy).

Diagnosis. Wings with highly distinctive contrasting colour pattern; wings ovoid; body glossy black with head bright orange; RP with numerous crossveins irregularly arranged; CuA and CuP strongly sinuous in both wings, branching near wing margin in FW; HW CuA with few dichotomous branches; female forecoxa with 11–15 short pedicellate setae and a prominent preapical process on dorsal surface; female tergite 9 strongly produced posteroventrally; sternite 8 with posterior end forked and with two small setose lobes; spermathecae rounded.

Comments. Commonly called the ‘pied lacewing’ this highly distinctive species is placed in a separate subfamily based on a series of autapomorphies features in the wings such as the branching pattern of medial and cubital veins, lack of gradate series crossveins and multiple *sc-r* crossveins. *Porismus strigatus* is associated with *Eucalyotus* trees during the autumn months in eastern Australia when adults have been observed ovipositing under tree bark; larvae are sub-corticolous on these trees and not associated with riparian habitats (Winterton *et al.*, 2017). Krüger (1913) erected Porisminae along with Eidoporisminae as separate subfamilies based on distinctive venational characters, and although the male and female abdominal sclerites and genitalic morphology reflect a close relationship with Stenosmylinae, their status as separate subfamilies is maintained (discussed in New, 1983b). Winterton *et al.* (2017a,b) also concluded that Porisminae was closely related to Eidoporisminae and Stenosmylinae, consistent with previous proposals (Esben-Petersen, 1917, Kimmins, 1940, New, 1983b), but relationships amongst the three subfamilies were inconclusive.

Included species.

P. strigatus Burmeister, 1839 (Australia)



FIGURE 24. Porisminae. *Porismus strigatus* Burmeister (photo: Shaun L. Winterton).

PROTOSMYLINAЕ Krüger, 1913a

Type genus. *Protosmylus* Krüger, 1913a: 30.

Diagnosis. Ocelli present or variously reduced (medial ocellus sometimes reduced or absent), antennae shorter than forewing length; prothorax width subequal to length; pronotum length subequal to width; female forecoxae without processes (except *Protosmylus*); wings ovoid; costal area broad basally, subcostal veinlets simple, sometimes irregularly forked in FW; trichosors present along entire wing margin; single FW *sc-r* crossvein basally; both wings with RP with *ca.* 8-10 branches (rarely more), rarely sinuous distally, radial area with relatively few crossveins basally resulting in large and well defined cells; two (rarely one or three) gradate series present and well defined, often distant

from the other irregular radial crossveins in basal half of wing; FW M vein forked near wing base, near origin of RP1; CuA usually with more branches in HW than in FW; HW CuP simple and relatively short, not pectinately branched; male with abdominal tergites 8 and 9 as separate sclerites with eversible scent glands absent; male genitalia less sclerotised with gonarcus narrow, arched and not observable externally; parameres present, fused medially and arched; anterolateral arm of gonarcus non-articulating; female genitalia with gonopophysis 9 basally associated with gonocoxite 9 (not acting upon sternite 8); sternite 8 as small knob-like process located near anteroventral margin of tergite 9; spermathecae oblong and folded upon itself, spermathecae duct extremely long and coiled.



FIGURE 25. Porisminae. *Porismus strigatus* Burmeister.

Comments. Protosmylinae comprises four extant and six extinct genera. Three of the extant genera are found in the Oriental and Eastern Palearctic regions while the fourth genus is known only from a relatively small area in Ecuador. The six extinct genera are widely known from deposits throughout the Palearctic and one in the Nearctic, ranging in age from the Middle Jurassic to late Eocene. Based on a phylogenetic analysis *Lysmus* was recently placed in Protosmylinae by Winterton *et al.* (2017). This subfamily has attracted attention recently, with revisions by Wang *et al.* (2010) (*Juraheterosmylus*), Dong *et al.* (2016) (*Heterosmylus*) and Winterton & Wang (2016) (*Gryposmylus*) have resulted in new species being described in these genera. Wang *et al.* (2010) revised the diagnosis of Protosmylinae, updating the original concept by Krüger (1913). Protosmylinae is closely related to Spilosmylinae (Winterton *et al.*, 2017a,b) and the two subfamilies share features such as a single to few branched hind wing vein CuP, narrow gonarcus and fused parameres in the male terminalia, as well as sternite 8 migrated posteriorly into a small knob-like process in the female terminalia (Winterton *et al.*, 2017). The similarities between the two subfamilies are indeed striking and few reliable characters are known that separate them (Krüger, 1913; Wang *et al.*, 2010; Winterton *et al.*, 2017) resulting to problems for placing taxa (e.g., *Lysmus*), particularly for some fossils where only wing fragments are known. Within Protosmylinae, besides similarities in wing venation, male and female genitalic morphology is also relatively uniform, with only slight differences amongst genera and even some species. The distinction of various extant and extinct genera is reliant on minor wing venation differences that should be evaluated further in a comparative context to determine synonymies with the nominal genus *Protosmylus* (see comments below under *Protosmylus*). Important characters useful for

differentiating genera in this subfamily include the number of distinct gradate series, and the relative sizes and number of branches of CuP and CuA in the forewing (Table 2). Larvae are unknown for this subfamily.

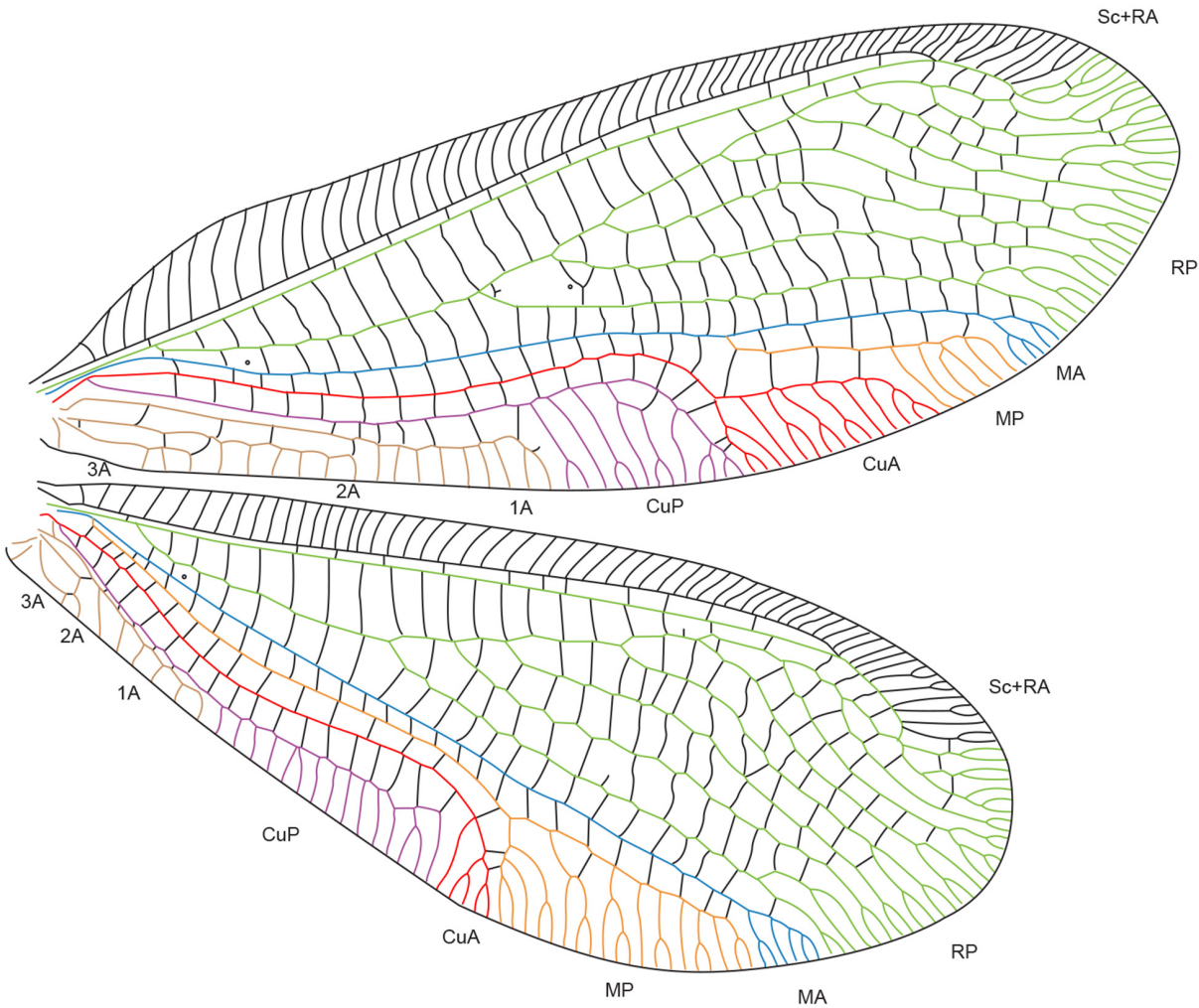


FIGURE 26. Porismyinae. *Porismus strigatus* Burmeister, wing venation (trichosors and vestiture omitted).

TABLE 2. Selected informative morphological characteristics of genera of Protosmylinae.

	Number and orientation of gradate series	Relative areas of FW CuA and CuP branching	Position of FW M fork
<i>Gryposmylus</i>	Two, divergent	CuA area smaller than CuP	Approx. level with RP1 fork
<i>Heterosmylus</i>	Three, subparallel	Subequal in area	Basal to RP1 fork
<i>Juraheterosmylus</i>	Three, subparallel	Subequal in area	Approx. level with RP1 fork
<i>Jurosmylus</i>	Three, subparallel	CuA area larger than CuP	Approx. level with RP1 fork
<i>Lysmus</i>	Two to three, subparallel	CuA area smaller than CuP	Approx. level with RP1 fork
<i>Mesosmylidus</i>	Unknown	CuA area smaller than CuP	Basal to RP1 fork
<i>Osmylidia</i>	Two, subparallel	Subequal in area	Approx. level with RP1 fork
<i>Paryphosmylus</i>	Three to four, subparallel	CuA area smaller than CuP	Approx. level with RP1 fork
<i>Petrushevskia</i>	One	CuA area smaller than CuP	Approx. level with RP1 fork
<i>Protosmylina</i>	Three, divergent	Unknown	Approx. level with RP2 fork
<i>Protosmylus</i>	Two, subparallel	Subequal in area	Approx. level with RP1 fork
<i>Pseudosmylidia</i>	Three, subparallel	CuA area larger than CuP	Approx. level with RP2 fork



FIGURE 27. Protosmylinae. *Gryposmylus pennyi* Winterton & Wang (photo: Steve Gaimari).



FIGURE 28. Protosmylinae. *Gryposmylus pubicosta* (McLachlan) (photo: Steve Gaimari).

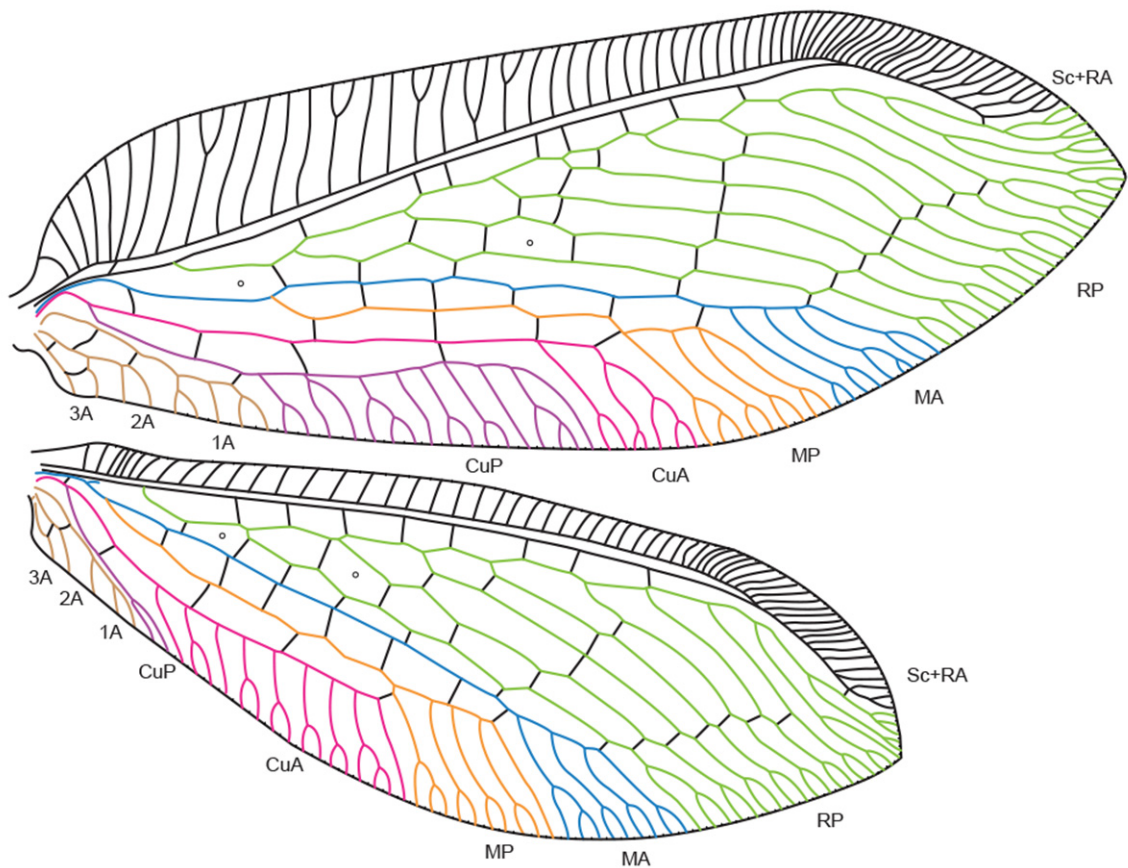


FIGURE 29. Protosmylinae. *Gryposmylus pennyi* Winterton & Wang, wing venation (vestiture omitted).

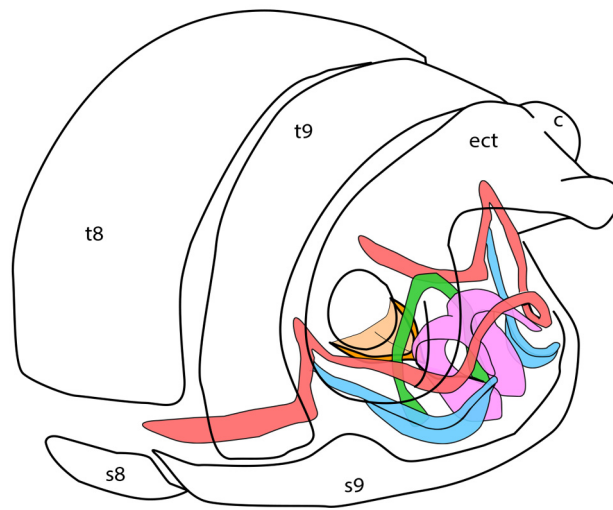


FIGURE 30. Protosmylinae. *Gryposmylus pennyi* Winterton & Wang, male genitalia, oblique view. Colour code: gonarcus (red), entoprocessus (blue), parameres (green), mediuncus (purple), hypandrium internum (orange).

Genera included. *Gryposmylus* Krüger, *Heterosmylus* Krüger, *Juraheterosmylus* Wang *et al.*, *Jurosmylus* Makarkin & Archibald, *Lysmus* Navás, *Mesosmylidus* Jepson *et al.*, *Osmylidia* Cockerell, *Paryphosmylus* Krüger, *Petrushevskia* Martynova, *Protosmylina* Jepson *et al.*, *Protosmylus* Krüger, *Pseudosmylidia* Makarkin.

***Gryposmylus* Krüger, 1913a** (Figs 27–30)

Type species. *Chrysopa pubicosta* Walker, 1860: 183 (by original designation).

Diagnosis. Three ocelli present; antennae less than FW length; wings ovoid, hyaline with dark markings; FW costal margin relatively broad basally, subcostal veinlets simple with occasional irregular forking, basal 6-7 veinlets arranged sub-radially; FW RP stem short, RP1 originating at, or after fork, of M vein; both wings with two distinct gradate series divergent in orientation; FW with CuA with fewer branches than CuP.

Comments. *Gryposmylus* is closely related to *Lysmus* (Winterton *et al.*, 2017) and differs only slightly in wing features such as the shape of the costal area and the orientation of the gradate series; the shape and orientation of the basal subcostal veinlets appears to be diagnostic for the genus. Winterton & Wang (2016) recently revised the genus, describing a second species.

Included species.

G. pennyi Winterton & Wang, 2016 (Vietnam, China, Malaysia)

G. pubicosta (Walker, 1860) (India, Malaysia)

***Heterosmylus* Krüger, 1913c** (Figs 31–32)

Type species. *Heterosmylus aspersus* Krüger, 1913c: 37 (by original designation).

Diagnosis. Three ocelli present; antennae less than FW length; wings ovoid, hyaline or FW weakly infusate; costal area relatively narrow, subcostal veinlets simple, occasionally forked, subparallel at base; FW RP stem

relatively long, RP1 originating distal to fork of M at approximately $\frac{1}{3}$ wing length; 8–16 branches of RP; FW with basal radial crossveins sometimes arranged into a third gradate series basal to inner series, both wings with regular gradate series elongated, parallel in orientation; area between R and M without crossveins near wing base; medial area with rarely more than four *ma-mp* crossveins; FW with CuA with similar number of branches to CuP.



FIGURE 31. Protosmylinae. *Heterosmylus processus* Dong *et al.* (photo: Jishen Wang).

Comments. Dong *et al.* (2016) recently revised this genus and described a new species from China. Dong *et al.* (2016) do not mention parameres in the male genitalia in their revision but the structure is present and evident as an unlabelled structure in some of their images (Dong *et al.*, 2016: e.g., figs 18, 35, 48). Members of this genus are often relatively large compared with other protosmylines but do not have denser wing venation. In some species, the semi-ordered arrangement of some of the basal radial crossveins gives the appearance of a third gradate series; this feature is common in many fossil protosmyline genera. The elongate stem of RP, with RP1 notably distal to the fork of M, is distinctive for the genus.

Included species.

- H. aspersus* Krüger, 1913c (India)
- H. curvagradata* Yang, 1999 (China)
- H. flavidus* Yang, 1992 (China)
- H. limulus* Yang, 1987 (China)
- H. primus* Nakahara, 1955 (China)
- H. processus* Dong *et al.*, 2016 (China)
- H. shennonganus* Yang, 1997 (China)
- H. wolonganus* Yang, 1992 (China)
- H. yunnanus* Yang, 1986 (China) (= *H. zhamanus* Yang, 1987)



FIGURE 32. Protosmylinae. *Heterosmylus wolonganus* Yang.

***Juraheterosmylus* Wang *et al.*, 2010**

(Fig. 33)

Type species. *Juraheterosmylus antiquatus* Wang *et al.*, 2010: 46 (by original designation).

Diagnosis. Antenna at least half FW length; wing weakly mottled infusate; wings narrowly ovoid, posterior margin straight distally; FW costal area relatively narrow, subcostal veinlets relatively widely spaced and simple proximally, and more closely spaced and sometimes forked distally; RP with rather dense (13–14) slightly sinuous branches; RP1 originating relatively far from origin of RP; 2–3 well defined gradate series in both wings, with few irregular crossveins basal to these; FW M fork at, or distal to, origin of RP1; MA and MP with few branches distally (mostly dichotomous); in both wings CuA and CuP with similar number of pectinate branches.

Comments. Wang *et al.* (2010) described this genus with three species based on a series of relatively complete compression fossils from Middle Jurassic-aged deposits in China. This genus has clear similarities to *Heterosmylus* and *Jurosmylus*, but some distinct branching patterns in the forewing, most notably in the higher number of well-defined gradate series crossveins and the distal branching patterns of the radial and medial veins.

Included species.

J. antiquatus Wang *et al.*, 2010 (China) (Middle Jurassic)

J. astictus Wang *et al.*, 2010 (China) (Middle Jurassic)

J. minor Wang *et al.*, 2010 (China) (Middle Jurassic)

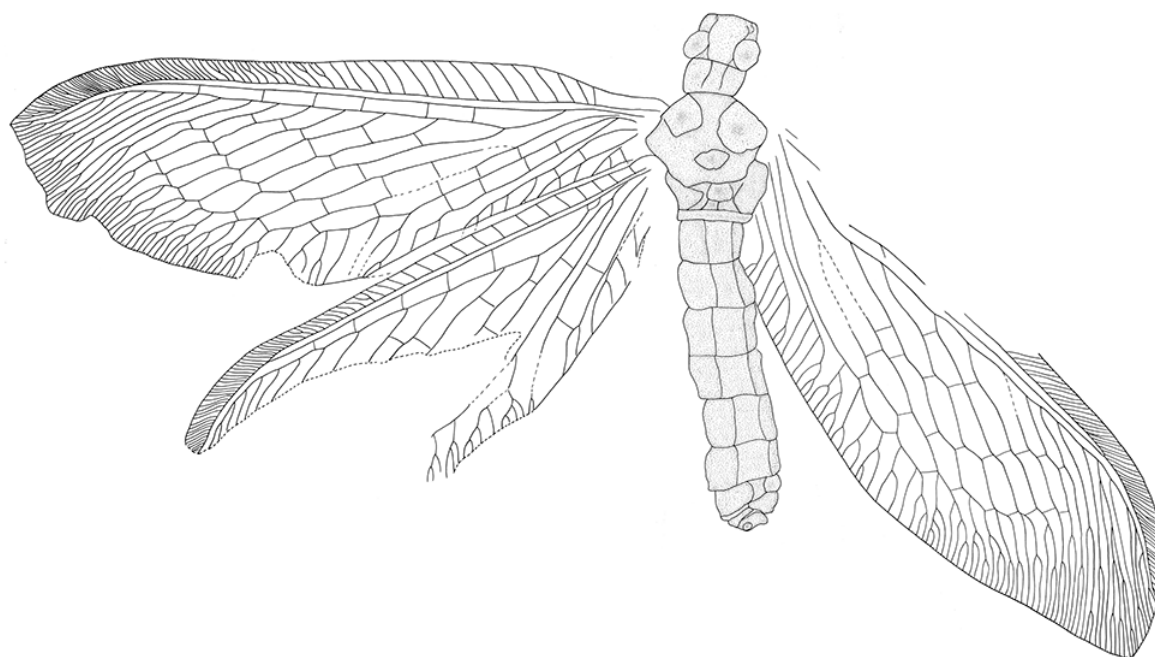


FIGURE 33. Protosmylinae. *Juraheterosmylus antiquatus* Wang *et al.*

***Jurosmylus* Makarkin & Archibald, 2005**

(= *Mesosmylus* Panfilov, 1980: 99. Type species: *Mesosmylus atalantus* Panfilov, 1980: 99) (preoccupied)

Type species. *Mesosmylus atalantus* Panfilov, 1980: 99 (by original designation).

Diagnosis. Wings narrowly ovoid, FW costal area relatively narrow, subcostal veinlets simple proximally, and more closely spaced and sometimes forked at mid-length; RP with 6–18 branches; RP1 originating relatively close to origin of RP, three distinct gradate series, sometimes with very few irregular crossveins basal to these; M fork at or distal to origin of RP1; MA and MP with few dichotomous branches distally; FW with CuA and CuP with similar number dichotomous branches; A1 strongly pectinate (4–6 branches); HW unknown.

Comments. *Jurosmylus* was proposed by Makarkin & Archibald (2005) as a replacement name since *Mesosmylus* Panfilov, 1980 was preoccupied by *Mesosmylus* Krüger, 1913c. The forewing venation of *Jurosmylus* is very similar to that of *Juraheterosmylus* and *Protosmylus*.

Included species.

J. atalantus (Panfilov in Dolin *et al.*, 1980) (Kazakhstan) (Late Jurassic)

J. parvulus Khranov, 2014a (Kazakhstan) (Late Jurassic)

***Lysmus* Navás, 1910**

(Figs 34–35)

(= *Eosmylus* Krüger, 1915: 73. Type species: *Spilosmylus nigricornis* Nakahara, 1914: 509)

(= *Neolysmus* Nakahara, 1955: 13. Type species: *Neolysmus ogatai* Nakahara, 1955: 13)

Type species. *Osmylus harmandinus* Navás, 1910: 190 (by original designation).

Diagnosis. Three ocelli present; antennae less than FW length; wings ovoid, hyaline, FW sometimes with dark markings; FW costal area broadened basally, subcostal veinlets simple, not arranged sub-radially at base (sometimes basal 2–3 arranged divergently); RP stem short; 10–13 RP branches present; end-twigging of radial and medial veins along wing margin regular and one level; FW with stem of RP relatively short, RP1 arising proximal to M fork; RP in both wings with two distinct gradate series, subparallel in orientation, more basal crossveins semi irregular in arrangement, sometimes with third poorly defined gradate series; FW M vein fork near base of wing, between first and second branches of RP; FW CuP with more branches than CuA.

Comments. *Lysmus* was previously placed in Spilosmylinae, underscoring the difficulties in differentiating and classifying members of both subfamilies. Winterton *et al.* (2017) recovered this genus as the sister to *Gryposmylus*, and Winterton & Wang (2016) noted that the genera are differentiated by features such as the orientation of the basal subcostal veinlets and gradate series crossveins, and by the position of the M fork relative to the origin of RP1. Considering the variability of some venational features in *Lysmus*, this genus should be a priority for revision to clarify its status relative to other genera in the subfamily, especially genera such as *Gryposmylus*, *Osmylidia* and *Protosmylus*.

Included species.

L. beccarii (Navás, 1929) (Indonesia, Japan)

L. canimaculatus Jia & Liu, 2005 (China)

L. harmandinus (Navás, 1910) (Japan, Russia) (= *Lysmus kurilensis* Kuwayama, 1956; = *Spilosmylus nigricornis* Nakahara, 1914)

L. oberthurinus (Navás, 1910) (China)

L. ogatai (Nakahara, 1955) (Japan, China)

L. pallidius Yang & Liu, 2001 (China)

L. qingyuanus Yang *et al.*, 1995 (China)

L. victus Yang, 1997 (China)

L. zanganus Yang *et al.* in Huang *et al.*, 1988 (China)



FIGURE 34. Protosmylinae. *Lysmus harmandinus* Navás.



FIGURE 35. Protosmylinae. *Lysmus victus* Yang.

***Mesosmylidus* Jepson *et al.*, 2012**

Type species. *Mesosmylidus vulgaris* Jepson *et al.*, 2012: 38 (by original designation).

Diagnosis. Forewing narrowly ovoid; costal area broad basally and likely narrowed distally, subcostal veinlets simple, relatively widely spaced; RP1 originating relatively far from origin of RP; M fork distinctly basal to origin of RP1; radial and medial crossveins in basal half of the wing not arranged in gradate series; MA field area smaller than MP field area; CuA with very few pectinate branches distally; CuP strongly pectinate (ca. 10 branches); A1 elongate and strongly pectinate (at least 4 branches); HW unknown.

Comments. Only known from a single forewing fragment, the subfamily affinity of this genus is unclear. Jepson *et al.* (2012) suggested that it may belong to Mesosmylinae, but its forewing crossveins are not arranged to series and the forewing CuP is greatly elongate and pectinately branched compared with CuA, precluding it from Mesosmylinae and indicating more appropriate placement in Protosmylinae.

Included species.

M. vulgaris Jepson *et al.* (England) (Early Cretaceous)

***Osmylidia* Cockerell, 1908**

(= *Oligosmylus* Krüger 1913: 19. Type species: *Osmylus requietus* Scudder, 1890: 164)

Type species. *Osmylus requietus* Scudder, 1890: 164 (by monotypy).

Diagnosis. Wings ovoid, mostly hyaline; FW costal area relatively narrow, subcostal veinlets simple throughout, sub-parallel in arrangement, relatively widely spaced basally, closely spaced distally; area behind Sc+RA distal to pterostigma relatively large, lacking crossveins to RP; FW RP with 9–10 branches, RP1 originating relatively close to origin of RP; both wings with two distinct gradate series, arranged subparallel, outer gradate series slightly longer than inner series, relatively few radial crossveins in basal half of wings; FW M forked just basal to origin of RP1; FW MA and MP with few distal branches (nearly dichotomous); FW CuP with more pectinate branches than CuA; FW A1 with relatively few branches.

Comments. Known from several, mostly incomplete compression fossils where the forewing is clearly represented, but the body and hind wing are not clear (Cockerell, 1913, 1914; Carpenter, 1943). Carpenter (1943) noted a close similarity to *Gryposmylus*, but *Osmylidia* shows greater similarity to genera such as *Lysmus* and *Protosmylus* based on characters of the forewing such as absence of forking of subcostal veinlets, number and arrangement of gradate series and relative proportions of branching patterns in CuA and CuP.

Included species.

O. requieta (Scudder, 1890) (U.S.A.) (late Eocene)

***Paryphosmylus* Krüger, 1913a**

(Fig. 36)

Type species. *Paryphosmylus ornatus* Krüger, 1913a: 33 (by original designation).

Diagnosis. Only two ocelli clearly evident, medial ocellus reduced and lateral ocelli widely separated; antennae less than FW length; wings relatively narrow, hyaline with dark mottled pattern, more pronounced in FW; costal area relatively narrow, subcostal veinlets almost all simple, sub-parallel, not divergent basally; FW RP stem relatively short (longer in HW); RP in both wings with approximately 12 branches, inner and outer gradate crossvein series elongate, sub-parallel and diverging distally towards wing apex, more basal RP crossveins arranged semiregularly in two short series; FW RP with distal branches interlinked by crossveins along wing margin; FW medial fork immediately distal to origin of RP1; MA and MP with regular pectinate branching distally in both wings; FW CuA and CuP with similar number of pectinate branches; FW A1 with at least five pectinate branches.

Comments. The only extant representative of Protosmylinae in the New World, *Paryphosmylus* is distinctive based on the presence of marginal crossveins along the posterior forewing margin, interlinking the end-twigging forks of the R and M branches. Additional diagnostic features of this genus are the relatively narrow wings and multiple elongated gradate series crossveins with outer gradates curved towards the wing apex. This species is known from only two specimens, both from Ecuador. The genitalia of both sexes is unknown at present.

Included species.

P. ornatus Krüger, 1913a (Ecuador)



FIGURE 36. Protosmylinae. *Paryphosmylus ornatus* Krüger.

***Petrushevskia* Martynova, 1958**

Type species. *Petrushevskia borisi* Martynova, 1958: 77 (by original designation).

Diagnosis. Forewing ovoid with broadly rounded apex; costal area relatively narrow along entire length, all subcostal veinlets simple; RP1 originating relatively close to origin of RP; RP with 10 closely spaced branches; M fork between origin of RP1 and RP2; MA, MP with few branches; CuA with single fork distally; crossveins in radial to mediocubital spaces randomly spaced except for a single outer gradate series; CuP pectinate, with six branches; A1, A2 pectinate, with 3-4 branches; HW unknown.

Comments. Makarkin *et al.* (2014) assumed that this genus may belong to Mesosmylininae. However, it is possible that it belongs to Protosmylinae as CuP is strongly pectinate, CuA has few branches, and crossveins in the radial to mediocubital spaces are largely randomly spaced (with only a single outer gradate series). In contrast, most genera of Mesosmylininae have multiple distinct gradates series throughout the wing.

Included species.

P. borisi Martynova, 1958 (Kyrgyzstan) (Early Jurassic)

***Protosmylina* Jepson *et al.*, 2009**

Type species. *Protosmylina bifasciata* Jepson *et al.*, 2009: 1328 (by original designation).

Diagnosis. Forewing hyaline with slight banding pattern; costal area broad at base with veinlets relatively closely spaced, apparently not forked; FW with subcostal crossvein present midway along wing; FW RP stem short, RP1 originating close to origin of RP; RP with 12 closely spaced branches; three distinct gradate series of crossveins in RP; inner and outer gradate series divergent; M fork level with origin of RP2; MA irregularly branched; MP dichotomously branched; CuA pectinately branched; HW unknown.

Comments. The protosmyline affinity of this genus is undoubted, although the holotype is only an incomplete forewing. Jepson *et al.* (2009) suggested that the wings of *Protosmylina* and *Protosmylus* were very similar, although *Protosmylina* resembles *Osmylidia* and *Pseudosmylidia* more closely. The divergent orientation of the forewing gradate series and the medial fork level with the origin of the second branch of RP are features shared by these two genera. The presence of a sc-r crossvein midway along the forewing in *Protosmylina* is highly unusual and may be a specific characteristic.

Included species.

P. bifasciata Jepson *et al.*, 2009 (England) (Early Cretaceous)

***Protosmylus* Krüger, 1913a**

(Figs 37–38)

Type species. *Osmylus pictus* Hagen in Berendt, 1856: 86 (by original designation).

Diagnosis. Antennae comparatively long (with 38–52 flagellomeres), approximately equal to $\frac{2}{3}$ – wing length; ocelli present; female procoxa with elongate, lobed process on anterior surface; wings ovoid, hyaline, FW with dark irregular mottling; costal area relatively broad basally, subcostal veinlets simple, relatively closely spaced; both wings with relatively few crossveins in RA-RP area, RP with 8–9 branches; HW with stem of RP relatively long and curved, shorter in FW; two distinct gradate series in both wings; FW M fork at level of origin of RP1; FW MA with 3–4 pectinate branches, MP with 2–3 pectinate branches; FW CuA and CuP pectinately branched, both subequal in area of branching along wing margin; FW A1 with three pectinate branches.

Comments. The genotype of the subfamily Protosmylinae, *Protosmylus* was originally described based on a single forewing (Pictet-Baraban & Hagen, 1856; Haug, 2003; Scheven, 2004; Wichard *et al.*, 2009). The holotype of *P. pictus* is presumed lost, although a number of more complete specimens matching this species (and other new species) exist in museums and private collections. The comparatively long antenna is unique among Protosmylinae genera, which typically have relatively shorter antennae. The presence of an elongate process on the female forecoxa is also unique to this genus and is a character typically found in other subfamilies (e.g., Osmylinae). *Protosmylus* belongs to a group of very similar genera comprising *Osmylidia*, *Pseudosmylidia*, *Protosmylina* and *Lymsus*, although it also has some features consistent with *Jurosmylus* and *Juraheterosmylus*, suggesting a slightly more distant relationship.

Included species.

P. pictus (Hagen in Berendt, 1856) (Europe) (late Eocene)



FIGURE 37. Protosmylinae. *Protosmylus pictus* (Hagen), photo of specimen in Baltic amber (photo: Jonas Damzen).



FIGURE 38. Protosmylinae. *Protosmylus* sp., photo of specimen in Baltic amber (photo: Marius Veta).

***Pseudosmylidia* Makarkin, 2017**

Type species. *Pseudosmylidia relictata* Makarkin, 2017: 582 (by original designation).

Diagnosis. Antennae less than FW length; wings ovoid, hyaline; costal area broad, basally and distally narrowed; subcostal veinlets simple basally and forked distally, sub-parallel and relatively widely spaced throughout; relatively few crossveins in RA-RP area; stem of RP relatively short, with 10 branches; end-twigging along posterior margin irregular and multi-layered; three distinct gradate series arranged in parallel through radial and medial areas; FW M fork at level with origin RP2; MA and MP with very few pectinate branches; FW CuA pectinately forked (four branches), area of branching of FW CuP smaller than area of CuA; A1 elongate and pectinate branched.

Comments: The forewing CuA with more branches than CuP is distinctive for this genus and suggests a close relationship to *Jurosmylus*, the only other protosmyline genus to exhibit this condition.

Included species.

P. relictata Makarkin, 2017 (U.S.A.) (late Eocene)

SPILOSMYLINAE Krüger, 1913a

Type genus. *Spilosmylus* Kolbe, 1897: 34

Diagnosis. Antenna shorter than FW; ocelli sometimes with median (or all) ocelli absent; pronotum length subequal to width; female forecoxa without processes; wing shape variable, including ovoid, sub-triangular, elongate or slightly falcate; costal area relatively narrow, subcostal veinlets simple (rarely forked) and without interlinking crossveins, densely spaced; trichosors present along entire wing margin; wings typically hyaline with dark pattern (especially FW) as mottling, bands, or fenestrations, sometimes with embossed spot present in FW CuP branches; FW with single sc-r crossvein basally; RP with 8-16 branches that may be slightly sinuous distally, 1-3 distinct gradate series in both wings, often dense crossveins in basal part of wing; FW M fork close to level with origin of RP1; MP base usually with a spur vein; HW medial area not expanded; CuA usually with more branches in HW than in FW; HW CuP short, simple, sometimes forked near wing margin; male abdominal tergites 8 and 9 as separate sclerites without scent glands, gonarcus narrow, arch-like and lacking setae, entoprocesses narrow and curved, mediuncus with a basal sclerotized arm, parameres present, fused medially as a single sclerite; female genitalia with sternite 8 as a small, knob-like process, located posteriorly proximal to gonocoxite 9, gonapophyses and gonocoxites 9 closely associated or appearing fused, spermathecal duct greatly elongate and coiled.

Comments. Spilosmylinae comprise three extant and two extinct genera widely distributed throughout tropical and subtropical parts of the Old World, ranging from southern Africa and Madagascar, throughout Asia and Australasia; while being found in Australia the subfamily is restricted to northern tropical regions. Spilosmylinae is by far the most species rich subfamily with 118 species, the bulk of which being placed in *Spilosmylus*. The distinction of *Spilosmylus* from *Thaumatomylus* and *Thyridomylus* is poorly defined and lacks characters which diagnose any one of these genera from the other two consistently across all species. Diagnostic characters presently used are themselves highly variable with multiple exceptions and species exhibiting apparent intermediate conditions. In their phylogenetic analysis, Winterton *et al.* (2017) recovered *Thaumatomylus* as sister to a clade containing *Spilosmylus* and *Thyridomylus*, with all three genera as monophyletic. Traditionally placed in Spilosmylinae (e.g., Krüger, 1913), *Lysmus* was instead recovered in Protosmylinae as sister to *Gryposmylus*. Spilosmylinae had been rarely treated since important taxonomic and faunistic revisions by Kimmins (1942) and New (1986, 1988, 1991), although several species of spilosmylines have been described recently (Xu *et al.*, 2017) (*Thyridomylus*) and Badano & Winterton (2017) (*Spilosmylus*) to complement phylogenetic studies of *Thyridomylus* by Wang *et al.* (2011) and Zhao *et al.* (2013). Larvae inhabit riparian zones of lotic watercourses.

Included genera. *Ensiosmylus* Khramov, *Imanosmylus* Makarkin, *Spilosmylus* Kolbe, *Thaumatomylus* Krüger, *Thyridomylus* Krüger.

Ensiosmylus Khramov, 2014a

Type species. *Ensiosmylus acutus* Khramov, 2014a: 302 (by original designation).

Diagnosis. Hind wing narrow, slightly falcate; subcostal veinlets relatively widely spaced; stem of HW RP relatively long, RP1 originates far from origin of RP; RP with 17 branches, slightly sinuous distally, crossveins semi-regular in arrangement with distinct outer gradate series present; HW MA with very few dichotomous branches close to wing margin, MP with five pectinate branches; HW CuA with ten regular pectinate branches, with few forks, CuP with single terminal fork; A1 with three pectinate branches; FW unknown.

Comments. Khramov (2014a) assigned this genus to Spilosmylinae based on the branching pattern of the anal veins and crossvein pattern in the radial and medial areas. However, a typical feature of Spilosmylinae (i.e., the presence of a spur-like process on the basal part of the hind wing MP directed proximally) is not discernible in the fossil. The hind wing figures presented by Khramov (2014a) have the veins identified following Kukalov-Peck & Lawrence (2004) (i.e., MA labelled as MP, MP as CuA, CuA as CuP and so on). The presence of a simple CuP vein in hind wing could place *Ensiosmylus* in Spilosmylinae, but the feature also occurs in Protosmylinae and Gumillinae; consequently, its placement in Spilosmylinae is tentative until a more complete specimen is known; placement in Gumillinae may be precluded by the presence of a well-defined outer gradate series.

Included species.

E. acutus Khramov, 2014a (Kazakhstan) (Late Jurassic)

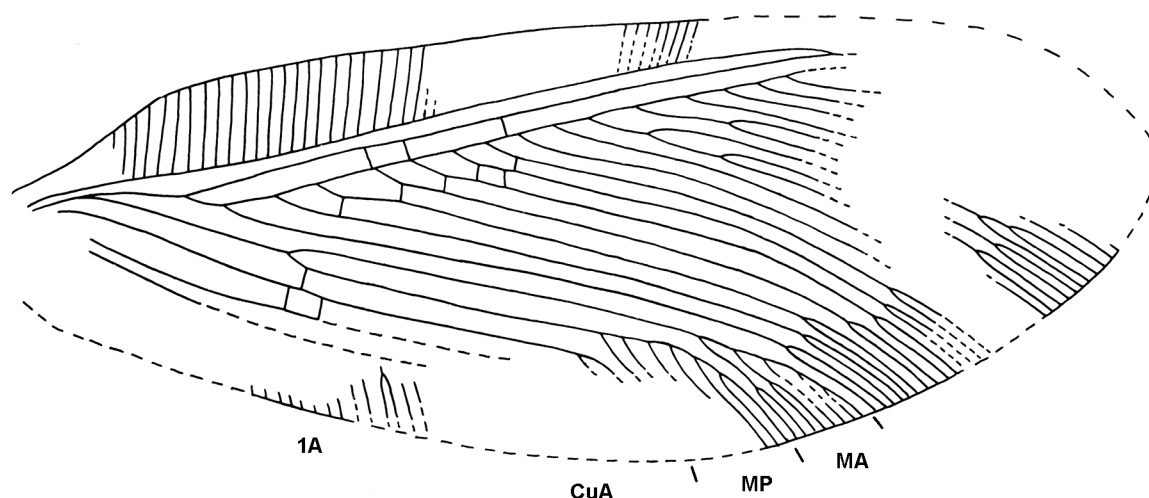


FIGURE 39. Spilosmylinae. *Imanosmylus ussurensis* Makarkin (from Makarkin, 1994) (forewing).

Imanosmylus Makarkin, 1994

(Fig. 39)

Type species. *Imanosmylus ussuriensis* Makarkin, 1994: 286 (by original designation).

Diagnosis. Forewing ovoid, costal area broad; subcostal veinlets simple, very closely spaced and nearly perpendicular to Sc; branches of RP numerous, dense; RP1 originated near origin of RP; M forked distal of origin of RP2; MA and MP pectinately branched; MA field slightly smaller area than MP field; CuA probably few pectinate; CuP likely pectinate and likely smaller in area than CuA; A1 pectinate; hind wing unknown.

Comments. Ren & Guo (1996) proposed that this genus belonged to Spilosmylinae. Indeed, the subcostal veinlets are simple and closely spaced as in most species of this subfamily. However, this character is not necessarily unique to Spilosmylinae and the shape of the subcostal veinlets in the costal area is different to that of spilosmylines. Moreover, overall wing shape in Spilosmylinae tends to be slightly narrower (especially basally) than exhibited by *Imanosmylus*, whose wing is more rounded. There is an important autapomorphy of Spilosmylinae that may be support this attribution, i.e., a spur-like process from the basal part of the hind wing MP. This is unfortunately not evident in the specimen of *Imanosmylus* although we do retain the placement of this genus in Spilosmylinae provisionally.

Included species.

I. ussuriensis Makarkin, 1994 (Russia) (Late Cretaceous)

***Spilosmylus* Kolbe, 1897**

(Figs 40–42)

(= *Ripidosmylus* Krüger, 1913a: 61. Type species: *Osmylus africanus* Kolbe, 1897: 33)

(= *Conchylosmylus* Krüger, 1914a: 20. Type species: *Spilosmylus aureus* Navás, 1912: 187)

(= *Kelidosmylus* Krüger, 1914a: 29. Type species: *Ripidosmylus togoensis* Krüger, 1913: 78)

(= *Ostreosmylus* Krüger, 1914a: 30. Type species: *Osmylus inquinatus* McLachlan, 1870: 200)

(= *Grammosmylus* Krüger, 1914a: 34. Type species: *Spilosmylus punctatus* Navás, 1912: 186)

(= *Stigmatosmylus* Krüger, 1914a: 32. Type species: *Stigmatosmylus ocellatus* Krüger, 1914a: 32)

Type species. *Osmylus tuberculatus* Walker, 1853: 235 (by original designation).



FIGURE 40. Spilosmylinae. *Spilosmylus arishensis* New.

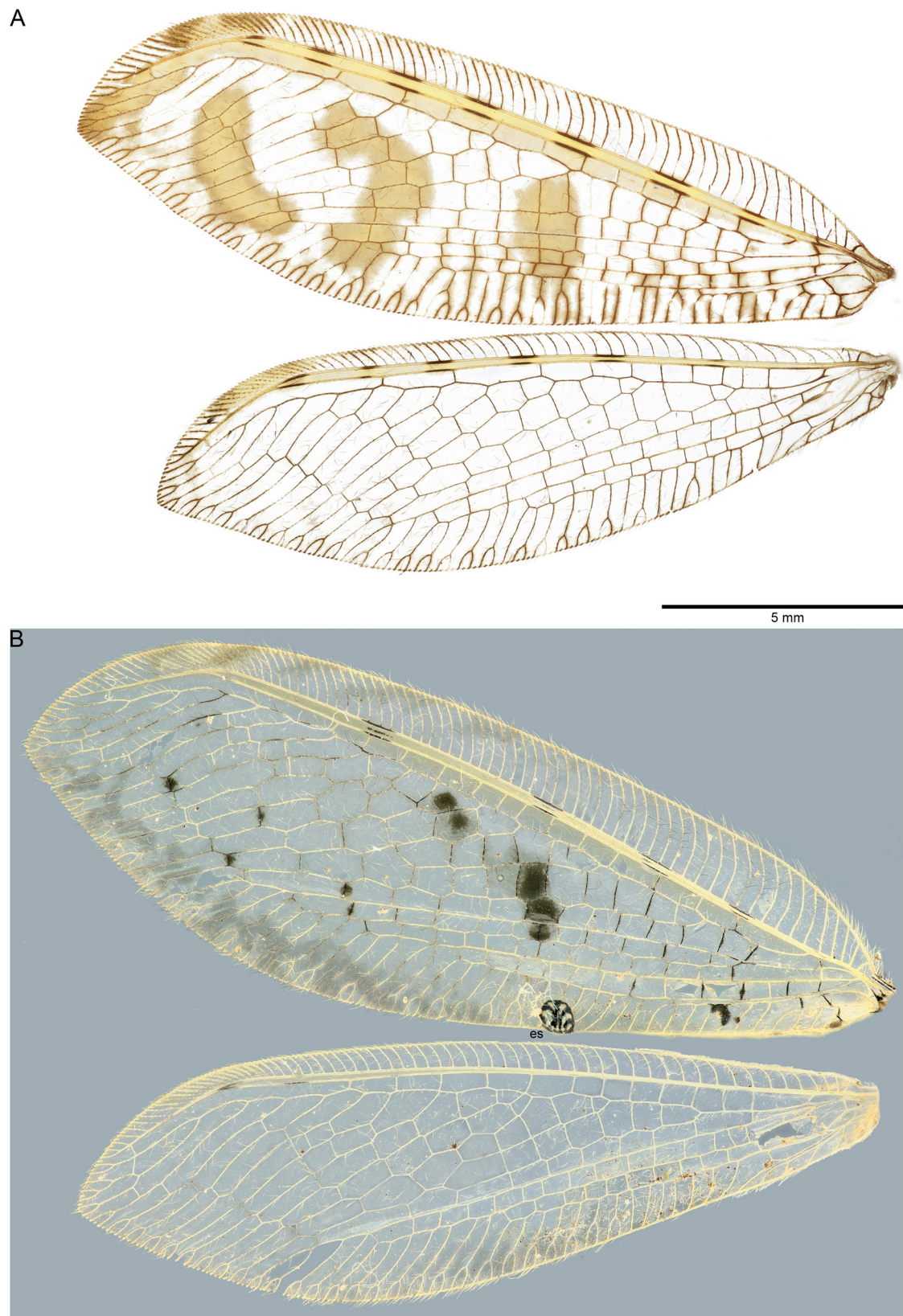


FIGURE 41. Spilosmylinae. A. *Spilosmylus spiloptyx* Badano & Winterton, wings; B. *S. tephrodestigma* Badano & Winterton, wings (from Badano & Winterton, 2017).

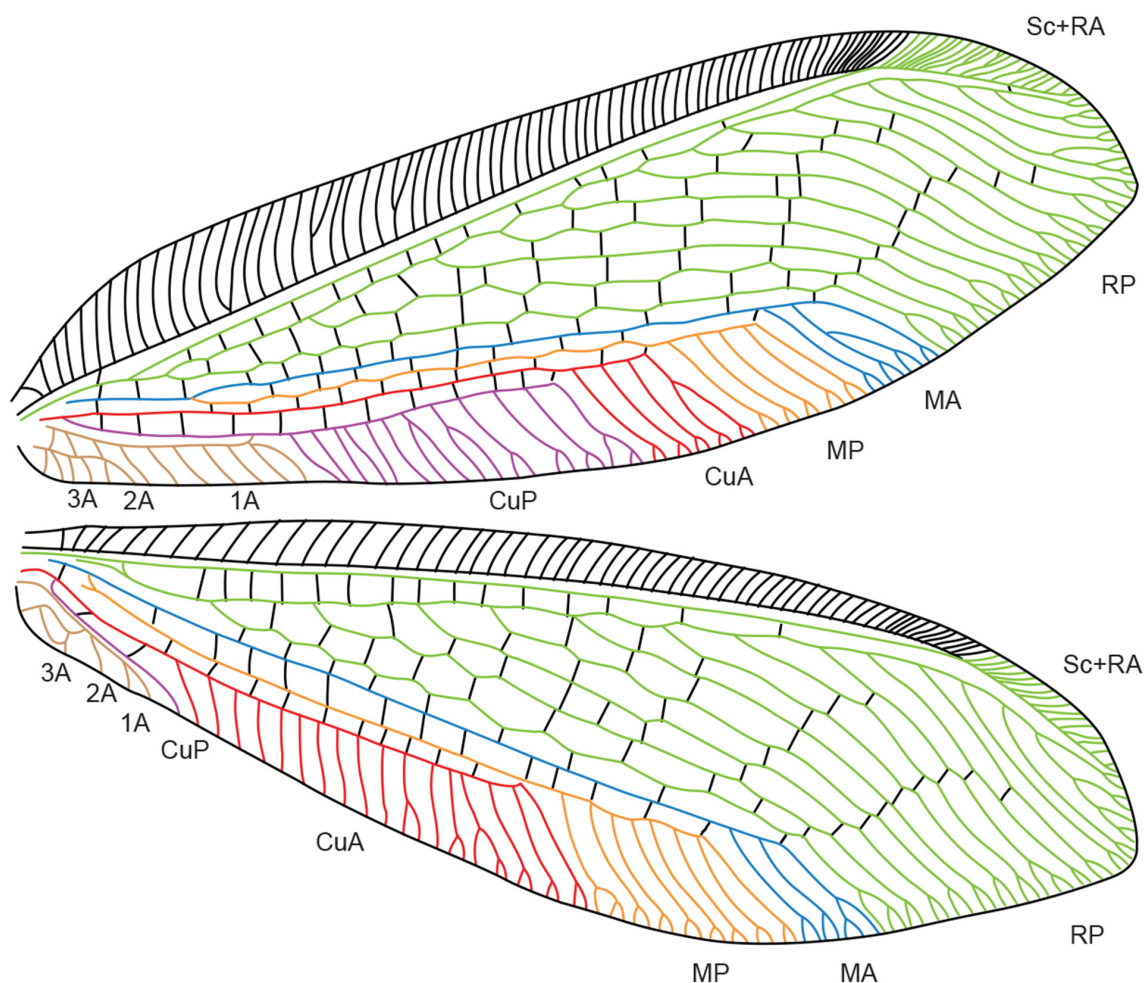


FIGURE 42. Spilosmylinae. *Spilosmylus* sp., wing venation (trichosors and vestiture omitted).

Diagnosis. Ocelli present or absent, sometimes only medial ocellus reduced or absent; wings ovate, posterior margin sometimes straight; wings typically hyaline with sparse patterning especially in FW, sometimes markings more extensive; FW costal area broad basally, subcostal veinlets mostly simple with occasional forked veinlet sometimes present; Sc and RA closely approximately along length in both wings, frequently with intermittent dark banding on veins and across area in between (appearing as dashes along wing); RP with 8–13 branches in both wings, crossveins numerous and semi-regularly arranged basally, more regular distally with outer gradate series distinct from other crossveins while inner gradate series is often not distinct from basal crossveins; FW RP stem relatively short; end-twigging regular and close to wing margin in radial and medial fields of both wings, end-twigging less extensive in cubital fields; FW with only one *m-cu* crossvein before M fork (rarely more); FW with embossed bulla usually located in CuP field along wing margin (absent in some species), rarely with a second bulla in A1 field; female spermatheca variable, sometimes with a complex of tubular accessory glands.

Comments. *Spilosmylus* is differentiated from *Thaumatomyzus* and *Thyridomyzus* by the presence in the forewing of an embossed spot along the posterior margin, dash-like bands in the Sc-RA area and only a single *m-cu* crossvein basally, although there are exceptions to these characters in some species (e.g., *S. gressitti*). Krüger (1913–1915) erected multiple genera in Spilosmylinae to accommodate the numerous species based on spurious wing venation features, which Kimmins (1942) subsequently synonymised with *Spilosmylus* (although also including *Lysmus*). We follow this more conservative classification of the extant Spilosmylinae and provide revised diagnoses of *Spilosmylus*, *Thaumatomyzus* and *Thyridomyzus*. Placement of species in each genus remains tentative though, as we have not examined representatives and types from all. A thorough revision of *Spilosmylus* relative to *Thaumatomyzus* and *Thyridomyzus* is needed to determine the generic limits and thus confirm placement of species in each.

Included species.

- S. africanus* (Kolbe, 1897) (Tanzania, Madagascar, western Afrotropics)
S. alleni New, 1991 (Thailand)
S. alticolus Banks, 1937 (Philippines)
S. amarillus New, 1989b (Indonesia)
S. analis New, 1989b (Indonesia)
S. annulatus Navás, 1923 (Gabon)
S. apoamus Banks, 1937 (Philippines)
S. araucariensis New, 1989b (Indonesia)
S. arishensis New, 1986c (Australia)
S. asahinai Nakahara, 1966 (China)
S. ateritriangulus New, 1986d (Papua New Guinea)
S. aureus Navás, 1912 (Indonesia)
S. basalis New, 1986d (Papua New Guinea)
S. bernhardensis New, 1989b (Indonesia)
S. bimaculatus New, 1986d (Papua New Guinea)
S. bossei (Navás, 1928) (Madagascar)
S. brandti New, 1986d (Papua New Guinea)
S. camerunensis (van der Weele, 1905) (Cameroon, Uganda)
S. ceyloniensis Esben-Petersen, 1927 (Sri Lanka)
S. collarti (Navás, 1930) (Democratic Republic of the Congo)
S. cornutus New, 1989b (Indonesia)
S. darjeelingensis Ghosh, 2000 (India)
S. elongatus New, 1989b (Indonesia)
S. epiphanes (Navás, 1917) (China)
S. flavicornis (McLachlan, 1875) (Japan) (= *Lysmus nikkoensis* Navás, 1911)
S. formosus Banks, 1924 (Philippines)
S. fumosus New, 1989b (Indonesia)
S. fuscomaculatus New, 1989b (Indonesia)
S. gressitti New, 1986d (Papua New Guinea)
S. griseofasciatus New, 1986d (Papua New Guinea)
S. hauginus (Navás, 1910) (Ivory Coast, Gabon)
S. inclytus (Navás, 1917) ('Indochina')
S. inquinatus (McLachlan, 1870) (Indonesia, Philippines)
S. interlineatus (McLachlan, 1870) (Madagascar, Mozambique, South African Republic)
S. inthanonensis New, 1991 (Thailand)
S. ismayi New, 1986d (Papua New Guinea)
S. javensis New, 1991 (Indonesia)
S. laetus Tjeder, 1957 (Zimbabwe)
S. latipennatus New, 1986d (Papua New Guinea)
S. leletensis New, 1986d (Papua New Guinea)
S. leucomatodes (Navás, 1911) (Democratic Republic of the Congo (?), Equatorial Guinea)
S. lichenoides Navás, 1913 (unknown)
S. lieftincki New, 1989b (Indonesia)
S. lineatocollis (McLachlan, 1870) (India)
S. loloensis (Krüger, 1914a) (Cameroon)
S. ludinganus Yang, 1992 (China)
S. majalis Navás, 1925 (Indonesia, Papua New Guinea)
S. malgassicus Fraser, 1951 (Madagascar)
S. misoolensis New, 1989b (Indonesia)
S. modestus (Gerstaecker, 1894) (Indonesia, Malaysia, Philippines)
S. monticolus (Banks, 1937) (Philippines)

S. navasi New, 1989b (Indonesia)
S. nebulosus New, 1989b (Indonesia)
S. neobritannicus New, 1986d (Papua New Guinea)
S. nephelius Navás, 1926 (Philippines)
S. nesaesus Navás, 1940 (Union of the Comoros, Madagascar)
S. nipponensis (Okamoto, 1914) (Japan)
S. obliquus New, 1986d (Papua New Guinea)
S. ocellatus (Krüger, 1914a) (Indonesia)
S. pictus New, 1989b (Indonesia)
S. pretiosus (Banks, 1931) (India (?), Malaysia)
S. proximus Banks, 1937 (Philippines)
S. punctatus Navás, 1912 (Indonesia)
S. pustulatus Navás, 1935 (Madagascar)
S. rattanensis New, 1989b (Indonesia)
S. reflexus New, 1986d (Indonesia, Papua New Guinea)
S. saishiuensis Okamoto, 1924 (Philippines)
S. sibilensis New, 1989b (Indonesia)
S. sigiensis New, 1989b (Indonesia)
S. sinuosus New, 1989b (Indonesia)
S. spilopteryx Badano & Winterton 2017 (Philippines)
S. subtilis New, 1986d (Papua New Guinea)
S. sumatranus Krüger, 1914a (Indonesia)
S. sumbanus Krüger, 1914a (Indonesia)
S. tephrodestigma Badano & Winterton, 2017 (Philippines)
S. tjederi New, 1989b (Indonesia)
S. togoensis (Krüger, 1914a) (Togolese Republic)
S. toxopeusi New, 1989b (Indonesia)
S. triseriatus Banks, 1913 (Australia, Indonesia)
S. tristis Tjeder, 1957 (Zimbabwe)
S. tuberculatus (Walker, 1853) (India, Asia (widespread))
S. vernans Navás, 1921 (Indonesia)
S. weiensis New, 1986d (Papua New Guinea)
S. xaverii Navás, 1928 (Indonesia, Papua New Guinea)

***Thaumatomyzus* Krüger, 1913a**

(Fig. 43–44)

(= *Glenosmylus* Krüger, 1913a: 91. Type species. *Glenosmylus elegans* Krüger, 1913a: 91) **syn. n.**

Type species. *Osmylus diaphanus* Gerstaecker, 1894: 168 (by original designation).

Diagnosis. Ocelli present; wings broad, ovoid to sub-triangular with expanded posterior margin at mid-length of wings; wings hyaline with sparse to dense patterning especially in FW; FW costal area relatively broad along entire length; subcostal veinlets simple and densely arranged; stem of RP short, RP with 11–15 branches, slightly sinuous distally; crossveins numerous and semi-regularly arranged in basal half of wings, more regular distally with outer gradate series distinct from other crossveins while inner gradate series (when present) is often not distinct from basal crossveins; end-twigging regular and close to wing margin in radial and medial fields of both wings, end-twigging less extensive in cubital field; M vein forked before of the origin of t RP1; FW with 2–4 *m-cu* crossveins before fork of M; FW lacking embossed bullae, and fenestrate areas absent in infusate areas of wing; male genitalia with ectoproct with one or two pairs of rounded lobes; gonarcus and entoprocessus narrow and joined by extensive membrane area; female spermatheca shape variable, often with only a few lobes.

Comments. *Thaumatosmylus* is distinguished by the presence of 2–4 *m-cu* crossveins before the fork of M in the forewing. Other characteristics include the lack of fenestrate spots in wing markings and lack of embossed bullae. Species from continental regions have relatively narrower wings, while those found on islands (e.g., Malaysia and Indonesia) tend to have broader wings. *Glenosmylus elegans* Krüger is moved to this genus based on the crossveins in the M-Cu area while *G. kruegeri* is transferred to *Thyridosmylus* (see below). *Spilosmylus fraternus* (Banks) and *S. conspersus* (Walker) are transferred from *Spilosmylus* since they have more than one forewing *m-cu* crossvein before the fork of MA-MP and lack an embossed spot along the posterior forewing margin.

Included species.

T. conspersus (Walker, 1853) (Malaysia) **comb. nov.**

T. delicatus Banks, 1931 (Malaysia)

T. diaphanus (Gerstaecker, 1894) (Indonesia)

T. elegans (Krüger, 1913a) (China) **comb. nov.**

T. fraternus (Banks, 1931) (Malaysia) **comb. nov.**

T. hainanus Yang, 2002 (China)

T. ornatus Nakahara, 1955 (China)

T. punctulosus Yang, 1999 (China)

T. raoengensis New, 1991 (Indonesia)

T. umbratus New, 1991 (Malaysia)

T. zheanus Yang & Liu, 2001 (China)



FIGURE 43. Spilosmylinae. *Thaumatosmylus delicatus* Banks.



FIGURE 44. Spilosmylinae. *Thaumatosmylus hainanus* Yang (photo: Shaun L. Winterton).



FIGURE 45. Spilosmylinae. *Thyridosmylus paralangi* Wang *et al.* (photo: Shaun L. Winterton).

***Thyridosmylus* Krüger, 1913a**

(Figs 45–47)

(= *Centrolysmus* Navás, 1917: 15. Type species: *Osmylus perspicillaris* Gerstaecker, 1884: 46)

(= *Heliosmylus* Krüger, 1915b: 80. Type species: *Glenosmylus kruegeri*, Esben-Petersen, 1914: 269) **syn. nov.**

Type species. *Osmylus langii* McLachlan, 1870: 197 (by original designation).

Diagnosis. Ocelli present, wings ovate, posterior margin sometimes straight to weakly falcate with apex slightly angular; FW typically with extensive dark markings and suffusions, some of these forming large macula and fenestrations, numerous crossveins bordered with brown; FW costal area slightly broader basally, veinlets simple, rarely with occasional forked veinlet; Sc and RA closely approximated along length in both wings, lacking intermittent dark banding in sc-r area; FW RP stem relatively short; RP with 10–15 branches in both wings, crossveins numerous and semi-regularly arranged basally, more regular arrangement distally with outer gradate series distinct from other crossveins, inner gradate series sometimes not distinct from basal crossveins; end-twigging regular and close to wing margin in radial and medial fields of both wings, end-twigging less extensive in cubital field; FW with only one *m-cu* crossvein before M fork (rarely more); FW without embossed bulla; female spermatheca variable, simple or with a complex of tubular accessory glands.



FIGURE 46. Spilosmylinae. *Thyridosmylus paralangi* Wang *et al.*

Comments. Kimmins (1942) incorrectly cited *C. epiphanes* Navás as the type species of *Centrolysmus* and considered *O. perspicillaris* to be congeneric with *O. langii*, but since he did not cite the correct type species the synonymy of *Centrolysmus* with *Thyridosmylus* was not formalised (Oswald & Penny, 1991). *Glenosmylus kruegeri* Esben-Petersen was originally placed in *Glenosmylus* and then as the type of *Heliosmylus* by Krüger (1915). It was subsequently moved to *Spilosmylus* by Kuwayama (1962) but is herein placed in *Thyridosmylus* based on the forewing having a single *m-cu* crossvein combined with the extensive markings and faint fenestrations. Wang *et al.* (2011) investigated the phylogeny of the genus using morphology. Based on the

placement of Malagasy species placed more basally in the phylogeny to the more species-rich Oriental members, they suggested that the genus evolved in Gondwanaland prior to rafting on the Indian subcontinent to subsequently diversify in the Oriental region during the Tertiary. A similar process has been suggested by Bakkes *et al.* (2018) based on molecular and morphological data for some genera of Psychopsidae with connections between the Afrotropical and the Oriental regions.



FIGURE 47. Spilosmylinae. *Thyridosmylus pustulatus* Kimmins.

Included species.

- T. fuscomarginatus* Xu, Wang & Winterton, 2017 (Madagascar)
- T. fuscus* Yang, 1999 (China)
- T. kruegeri* (Esben-Petersen, 1914) (China, Japan) **comb. nov.**
- T. langii langii* (McLachlan, 1870) (China, India)
- T. langii angustus* Kimmins, 1942 (China, India)
- T. longiprocessus* Xu, Wang & Winterton, 2017 (Madagascar)
- T. maolanus* Yang, 1993 (China)
- T. marmoratus* Fraser, 1955 (Madagascar)
- T. medoganus* Yang *et al.* in Huang *et al.*, 1988 (China)
- T. pallidus* Yang, 2002 (China)
- T. paralangii* Wang *et al.*, 2011b (China)
- T. perspicillaris perspicillaris* (Gerstaecker, 1885) (India)
- T. perspicillaris fenestratus* Kimmins, 1942 (India)
- T. perspicillaris minor* Kimmins, 1942 (China, India) (= *T. similaminor* Yang, 1992)
- T. polyacanthus* Wang *et al.*, 2008 (China)
- T. pulchrus* Yang *et al.* in Huang *et al.*, 1988 (China) (= *T. minoroides* Yang, 1987)
- T. punctulatus* (Navás, 1933) (Madagascar)
- T. pustulatus* Kimmins, 1942 (India)
- T. qianus* Yang, 1993 (China)

T. trifasciatus Yang, 1993 (China)
T. trimaculatus Wang *et al.*, 2008 (China)
T. triypsiloneurus Yang *et al.*, 1995 (China) (= *T. vulgatus* Yang, 1999)

STENOSMYLINAЕ Krüger, 1913a

Type genus. *Stenosmylus* McLachlan, 1867: 267.

Diagnosis. Ocelli present; antennae length variable, often between half and full length of FW; pronotum length longer than width; female forecoxa sometimes with narrow process and/or pedicellate setae; wings with subcostal veinlets simple, rarely occasionally forked; trichosors present around entire margin of both wings; FW with single *sc-r* crossvein basally; FW RP crossveins dense, semi-regularly arranged, lacking distally with distal RP branches variably sinuous; outer gradate series distinct, inner gradate series absent; FW M vein forked at, or beyond the mid-length of wing; medial area between MA-MP not expanded and crossveins not sinuous; CuA with more branches in HW than in FW; HW CuP elongate and pectinately branched; female sometimes with FW veins MP, CuA and/or A1 partially incrassate; male abdominal tergites 8 and 9 partially or completely fused, scent glands absent; gonarcus enlarged, subtriangular with setal pile, entoprocesses broad; parameres absent; female sternite 8 modified into a large concave sclerite that acts as a receptacle for gonapophysis 9; gonapophysis 9 enlarged, complex, variously bilobed, located anteriorly to ventral part of tergite 9, not closely associated with gonocoxite 9; gonocoxite 9 often with dark longitudinal stripe; spermatheca ovoid to spherical. Larvae typically have a pale to cream colouration with light brown sclerites (Fig. 1B, C).

Comments. In their phylogenetic analyses Winterton *et al.* (2017) supported previous contentions (e.g., Krüger 1913a; Esben-Petersen, 1917; Kimmins, 1940; New, 1986) that Stenosmylinae are closely related to Kempyninae, and also Porisminae and Eidoporisminae. In fact, Winterton *et al.* (2017) could not recover reciprocal monophyly of Stenosmylinae, Porisminae or Eidoporisminae in their phylogeny, thus calling into question the validity of all three as separate subfamilies. It is plausible that the monotypic Porisminae and Eidoporisminae each simply represent highly derived and autapomorphic forms of Stenosmylinae. Stenosmylinae comprise five Australian genera and two genera in South America. No definitive fossil taxa have been discovered, although Jepson *et al.* (2009) placed *Stenosmylina* in the subfamily based on an incomplete forewing; herein we consider this genus better placed in Eidoporisminae (see above). Stenosmylinae represent a truly southern hemisphere fauna, with connections between the Australian and South American forms likely pre-dating any trans-Antarctic connection during the Late Cretaceous-Early Paleogene (Winterton *et al.*, 2017). Larval stages are terrestrial, living under bark of trees, in leaf litter and on foliage (Winterton *et al.*, 2017; Martins *et al.*, 2018).

Included genera. *Carinosmylus* New, *Euporismus* Tillyard, *Isostenosmylus* Krüger, *Oedosmylus* Krüger, *Phymatosmylus* Adams, *Stenolysmus* Kimmins, *Stenosmylus* McLachlan.

Carinosmylus New, 1986a

Type species. *Carinosmylus durus* New, 1986a: 448 (by original designation).

Diagnosis. Female forecoxa with patch of pedicellate setae, anteroventral process absent; wings elongate, narrow ovoid, FW hyaline with mottled brown venation; FW stem of RP short, RP originating close to wing base, RP1 originating close to origin of RP; RP branches sinuous distally; FW M forked at approximately 2/3 wing length, MA and MP parallel until close to wing margin, both pectinately branched; female with FW veins regular, not incrassate; FW CuA not strongly arched towards posterior wing margin; FW 2A terminates in wing margin level with origin of first RP branch; male tergites 8 and 9 partially fused; ectoprocts without posterior processes; female sternite 7 highly modified with prominent posteroventral keel; sternite 8 bilobed; gonapophysis 9 bilobed with a pair of ventral arms, gonocoxite 9 slender; spermathecae spherical.

Comments. *Carinosmylus* is monotypic genus where the female genitalia are highly modified (New, 1986a). New (1986a) suggested that *Carinosmylus* was closely related to *Stenosmylus* and *Stenolysmus* and possibly

represented an unusual species of *Stenosmylus*. Winterton *et al.* (2017) similarly recovered *Carinosmylus* as sister to a clade comprising *Stenosmylus*, *Stenolysmus* and *Oedosmylus*, or as sister to *Euporismus*. The status of the genus is maintained here pending additional studies of this group of genera.

Included species.

C. durus New, 1986a (Australia)

***Euporismus* Tillyard, 1916**

(Fig. 48)

Type species. *Euporismus albatrox* Tillyard, 1916: 41 (by original designation).



FIGURE 48. Stenosmylinae. *Euporismus albatrox* Tillyard (photo: Ken Walker).

Diagnosis. Female forecoxa with numerous weakly pedicellate setae arranged into irregular rows along outer ventral edge, anteroventral process absent; wings relatively broad and slightly falcate; both wings dark infusate with stark contrasted white mottled markings and large irregular white patches apically; FW stem of RP short, RP originating close to wing base, RP1 originating close to origin of RP; RP branches strongly sinuous distally in both wings; FW end-twigging irregular and intermittent along posterior margin of wing; FW M forked midway along wing, both MA and MP pectinately branched; female with FW veins regular, not incrassate; FW CuA and CuP distally strongly arched towards posterior wing margin; FW 2A very short, terminates in wing margin level with origin of RP1; male tergites 8 and 9 entirely fused, ectoproct without angular process; gonarcus apex broadly truncate; entoprocesses curved and apically clubbed; female spermatheca spherical.

Comments. *Euporismus* is a monotypic genus from Southern Queensland with spectacularly marked wings. It is represented by very few specimens in collections; collection labels indicate that this species was found sitting on large rocks in a river bed (Tillyard, 1916), which is unusual for a member of Stenosmylinae as species of this subfamily are typically found far from water (Winterton *et al.*, 2017). Certain wing characters in *Euporismus* are

very similar to *Oedosmylus* and *Stenosmylus*, suggesting a close relationship with these genera (Tillyard, 1916; Kimmins, 1940).

Included species.

E. albatrox Tillyard, 1916 (Australia).



FIGURE 49. Stenosmylinae. *Isostenosmylus* sp. (photo: Steve Marshall).

***Isostenosmylus* Krüger, 1913a**

(Figs 49–50)

Type species. *Osmylus pulverulentus* Gerstaecker, 1894: 166 (by monotypy).

Diagnosis. Female forecoxa with or without pedicellate setae (occasionally numerous), sometimes with preapical process; wings broadly ovoid, membrane hyaline with irregular suffusion and small dark markings along wing veins; FW costal area relatively broad basally, subcostal veinlets rarely forked; FW stem of RP short, RP originating on RA close to wing base, first branch of RP originating close to origin of RP; RP branches strongly sinuous distally in both wings; end-twigging mostly regular and very close to margin of wing; FW M fork just beyond midpoint of wing, MA and MP regularly pectinately branched; female with all FW veins regular, not incrassate; FW CuA and CuP distally strongly arched towards posterior wing margin; FW 2A very short, terminates in wing margin before origin of first branch of RP; male tergites 8 and 9 entirely fused with distinct sulcus, ectoproct apex with angular posterior processes or lobes; gonarcus with anterior apodeme present; entoprocesses curved and apically clubbed; female sternite 8 flat and plate-like, gonapophysis 9 usually with apex

bilobed.

Comments. *Isostenosmylus* is the most species rich genus of Stenosmylinae, with 10 described species and more undescribed species in collections (Kimmins, 1940; Ardila-Camacho & Noriega, 2014; Martins *et al.*, 2016; Martins, unpublished data). Species of this genus are distributed in south Brazil, and along the Andes from Argentina and Bolivia to Venezuela, with many of them having an apparent predilection to montane forests. This suggest that the many species are locally endemic, with their diversification likely related to the geological uplifting of the Andes. The larvae of this genus are recorded as arboreal (Martins *et al.*, 2016; Winterton *et al.*, 2017).

Included species.

I. bifurcatus Ardila-Camacho *et al.* in Martins *et al.*, 2016 (Colombia)

I. contrerasi Ardila-Camacho & Noriega, 2014 (Colombia)

I. fasciatus Kimmins, 1940 (Bolivia, Peru, Venezuela)

I. fusciceps Kimmins, 1940 (Peru)

I. irroratus Ardila-Camacho *et al.* in Martins *et al.*, 2016 (Venezuela)

I. julianae Aspöck *et al.* in Martins *et al.*, 2016 (Peru)

I. morenoi Navás, 1928 (Ecuador)

I. nigrifrons Kimmins, 1940 (Ecuador)

I. pulverulentus (Gerstaecker, 1894) (Brazil, Paraguay)

I. septemtrionalandinus Ardila-Camacho & Noriega, 2014 (Colombia)



FIGURE 50. Stenosmylinae. *Isostenosmylus fusciceps* Kimmins.

***Oedosmylus* Krüger, 1913a**

(Figs 51–53)

Type species. *Oedosmylus tasmaniensis* Krüger, 1913a: 106 (by original designation).

Diagnosis. Female forecoxa with pedicellate setae either as larger setae in small patch, or as smaller setae more widely distributed, preapical anteroventral process absent; wings relatively narrow and ovoid, to broad and slightly falcate; FW venation dark, membrane markings variable, from mostly hyaline to mottled and darkly suffused; FW costal area relatively narrow; FW stem of RP short, RP originating close to wing base, RP1 originating close to origin of RP; RP branches strongly sinuous distally in both wings; FW end-twigging irregular and intermittent along posterior margin of wing; FW M forked midway along wing, both MA and MP pectinately to dichotomously branched; female with FW MP, CuA and/or 2A veins incrassate; CuA and CuP curved towards posterior wing margin distally; FW 2A terminating in wing margin before origin of first branch of RP; male tergites 8 and 9 entirely fused with sulcus evident; gonarcus usually with an apical acuminate prominence and densely setose, anterior apodeme of gonarcus short and narrow; entoprocessus broad and subtriangular; female sternite 8 flattened to concave, often with narrow lateral processes.

Comments. *Oedosmylus* is closely related to *Stenosmylus* and *Stenolysmus*, sharing a variety of wing venation and male and female genitalic characters (Kimmins, 1940; New 1990; Winterton *et al.*, 2017). The apical acuminate process of the male gonarcus found in most species is apparently unique to *Oedosmylus*.



FIGURE 51. Stenosmylinae. *Oedosmylus latipennis* Kimmins (photo: Shaun L. Winterton).

Included species.

O. brevis New, 1990 (Australia)

O. latipennis Kimmins, 1940 (Australia)

O. montanus Kimmins, 1940 (Australia)

O. nebulosus New, 1990 (Australia)

O. pallidus (McLachlan, 1863) (Australia)

O. parvus New, 1990 (Australia)

O. sclerotus New, 1990 (Australia)
O. tasmaniensis Krüger, 1913a (Australia)



FIGURE 52. Stenosmylinae. *Oedosmylus latipennis* Kimmins.

***Phymatosmylus* Adams, 1969**

(Figs 54–56)

Type species. *Phymatosmylus caprorum* Adams, 1969: 5 (by original designation).

Diagnosis. Female forecoxa with anterior patch of pedicellate setae; wings elongate and falcate with acute apex, highly variably in colour and extent of markings; female with FW CuP and 1A veins incrassate, male with all FW veins generally thicker than in HW; costal area relatively narrow; FW stem of RP short, RP originating close to wing base, RP1 originating close to origin of RP; RP branches strongly sinuous distally in both wings; end-twigging irregular and intermittent along posterior margin of wing; FW M forked midway along wing, both MA and MP dichotomously branched; CuA and CuP only slightly arched towards posterior wing margin beyond of M fork; FW 2A terminates in wing margin at level of origin of first branch of RP; male tergite 8 partially fused to tergite 9, and in turn tergite 9 partially fused to ectoproct; ectoproct without angular process; gonarcus rounded, anterior apodeme present, narrow; entoprocesses curved and apically rounded; female sternite 8 concave with posterolateral setose process; gonapophysis 9 short, bilobed; spermatheca spherical.

Comments. A highly variable monotypic genus likely closely related to *Isostenosmylus*; while the large falcate wings with dense venation show a superficial similarity to *Kempynus*, *Phymatosmylus* is clearly placed in Stenosmylinae. Adams (1969) suggested that this genus displayed an intermediate position in Stenosmylinae, exhibiting a series of ‘generalised’ features, including the more proximal fork of the forewing medial vein and only partial fusion of the male abdominal tergites 8 and 9. Individuals examined by Adams (1969) and in this study exhibit tremendous variation not only in pigmentation, but also vein branching, notably in the position of the

medial fork, presence or absence of forking in various RP branches and partial fusion of MP branches with CuA. The latter vein fusion is rare and when present it not symmetrical in individuals. See Cousin & Béthoux (2015) for discussion of this phenomenon in other Stenosmylinae.

Included species.

P. caprurum Adams, 1969 (Argentina, Chile)

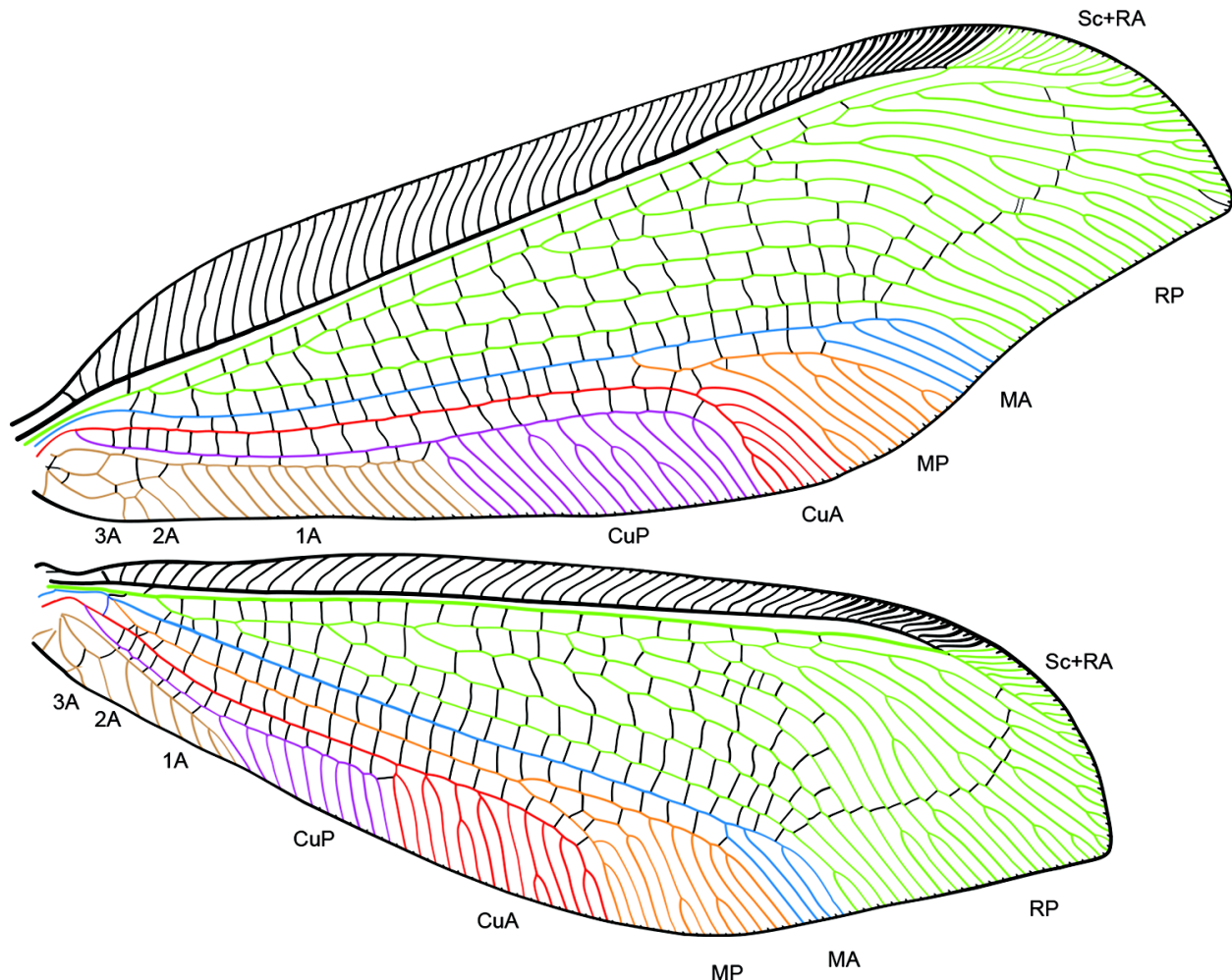


FIGURE 53. Stenosmylinae. *Oedosmylus brevis* New, wing venation (after Cousin & Béthoux, 2015) (vestiture omitted).

Stenolysmus Kimmins, 1940

(Figs 57–59)

Type species. *Nymphes extranea* Walker, 1853: 230 (by original designation).

Diagnosis. Antennae elongate, ca. FW length; female forecoxa without pedicellate setae, anteroventral process absent; wings elongate, narrowly ovoid, hyaline with dark venation and pale pterostigma; costal area relatively narrow; FW stem of RP relatively short, RP1 originating close to origin of RP; RP branches weakly sinuous distally in both wings; end-twigging mostly irregular and multi-layered along posterior margin of wings; FW M fork just beyond midpoint of wing, MA and MP dichotomously or pectinately branched, M fork sometimes obscured as MP may be fused to CuA distally (when this occurs there is an apparent oblique ‘*m-cua* crossvein’ (inset in Fig. 58)); female with all FW veins regular, not incrassate; FW CuA and CuP not strongly arched towards posterior wing margin distally; A2 elongate, terminating more or less level with origin of RP1; male tergites 8 and 9 and ectoprocts mostly fused; ectoproct apically rounded; gonarcus large and subtriangular, lobed dorsally,

anterior apodemes absent; entoprocessus short, broadly rounded; female sternite 7 with posteroapical corners produced; sternite 8 concave with rounded posterolateral processes with setal pile; gonapophysis 9 broadly lobed and truncate with internal sculpturing; gonocoxites 9 with distinct posteroventral fringe with stout hooked setae.



FIGURE 54. Stenosmylinae. *Phymatosmylus caprorum* Adams (photo: Steve Marshall).



FIGURE 55. Stenosmylinae. *Phymatosmylus caprorum* Adams.

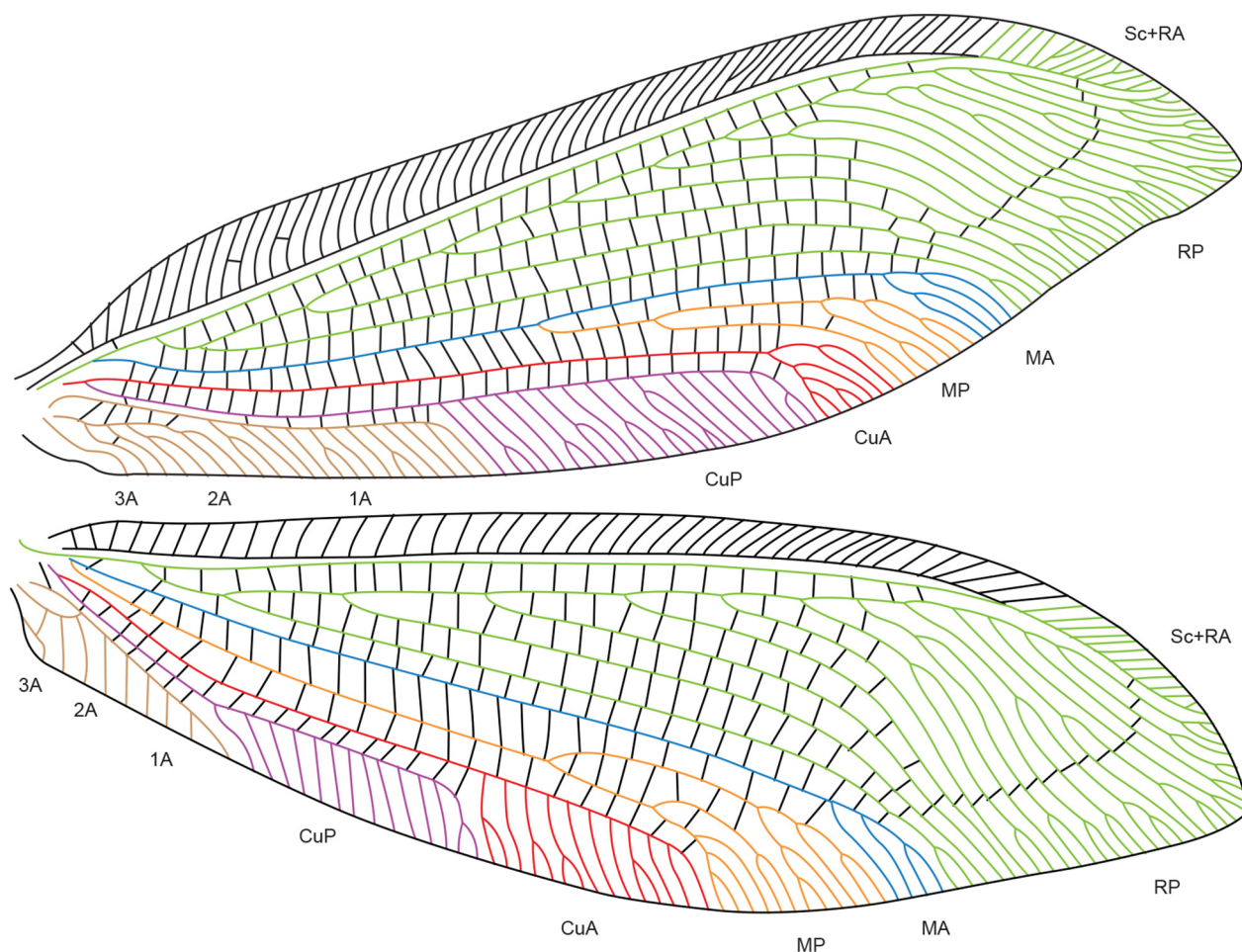


FIGURE 56. Stenosmylinae. *Phymatosmylus caprorum* Adams, wing venation (trichosors and vestiture omitted).

Comments. *Stenolysmus extraneus* is bright orange when living, and along with the unusual wing venation, was likely the reason for the original placement in *Nymphes* Leach by Walker (1853), a nymphid genus where many species are also bright orange in colour. Indeed, *S. extraneus* has been placed by various authors in Osmylidae (i.e., *Osmylus sensu lato* and *Stenosmylus*) and Nymphidae (i.e., *Nymphes*, *Myiodactylus* Brauer) (e.g., Walker 1853; Hagen 1866; McLachlan, 1867; Banks 1913). The unusual ‘oblique *m-cua* crossvein’ in the forewing of some individuals of various genera of Stenosmylinae, including some individuals of *S. extraneus* has created some confusion regarding the identity and homology of certain wing veins (New, 1986; Cousins & Béthoux, 2015). New (1986) and Cousins & Béthoux (2015) studied the forewings of various genera of Stenosmylinae and proposed that the oblique crossvein in the forewing of some individuals represented a fusion of MP (as MP2) with CuA. Following the method of identifying wing veins in lacewings used recently by Breitkreuz *et al.* (2017) we examined the wing tracheation of different individuals of *S. extraneus* without (Fig. 59) and with (Fig. 59, inset) the ‘oblique *m-cua* crossvein’ to identify veins and their points of apparent fusion. The forewing tracheation of both forms of *S. extraneus* clearly show that the oblique vein is indeed the stem of MP which fuses with CuA for a short length, and then separates again, supporting the contention that the oblique vein is the stem of MP and not a crossvein (New, 1986; Cousins & Béthoux, 2015).



FIGURE 57. Stenosmylinae. *Stenolysmus extraneus* (Walker) (photo: Reiner Richter).



FIGURE 58. Stenosmylinae. *Stenolysmus extraneus* (Walker).

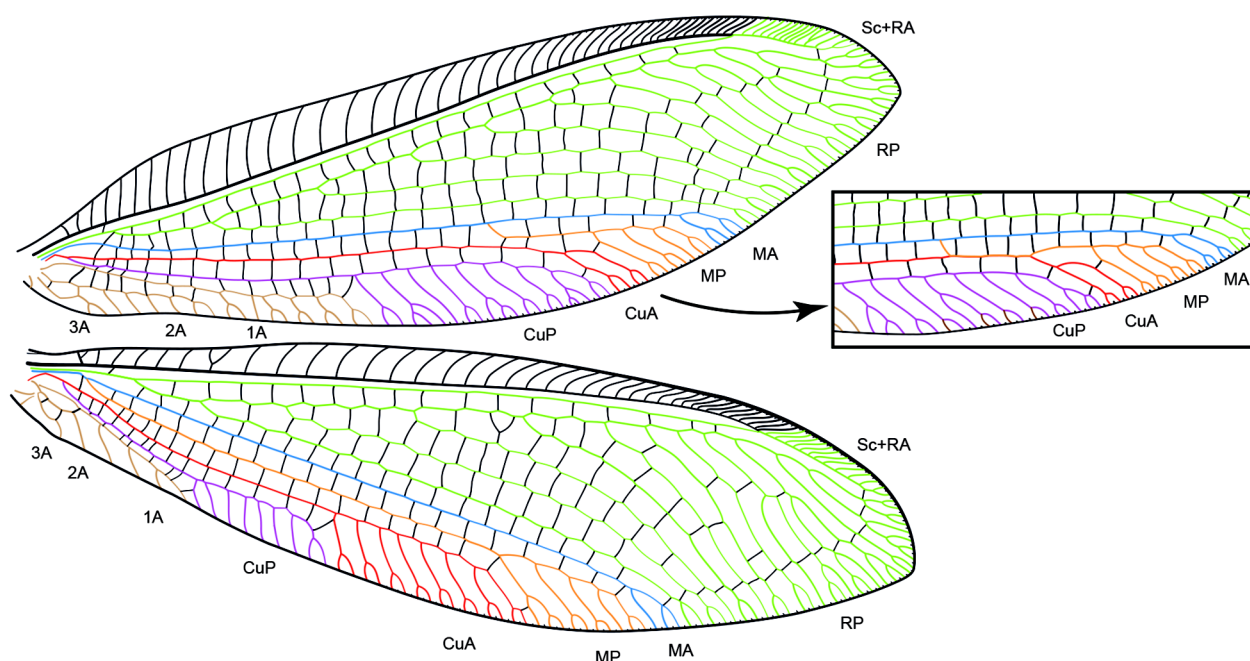


FIGURE 59. Stenosmylinae. *Stenolysmus extraneus* (Walker), wing venation (after Cousin & Béthoux, 2015) (vestiture omitted), alternative MP venation exhibited by some individuals shown as inset.

Included species.

S. extraneus (Walker, 1853) (Australia)

Stenosmylus McLachlan, 1867

(Figs 60–62)

Type species. *Osmylus tenuis* Walker, 1853: 234 (by subsequent designation).

Diagnosis. Antennae length ca. FW length; female forecoxa without pedicellate setae or anteroventral process; wings narrow, hyaline with dark mottled venation and irregular suffusions; costal area relatively narrow, subcostal veinlets rarely forked; FW stem of RP long, RP originating distant from wing base, RP1 originating far from origin of RP; RP branches slightly to strongly sinuous distally in both wings; end-twigging mostly regular but intermittent, very close to margin of wing; FW M fork well beyond midpoint of wing, close to wing margin, pectinately branched (ca. 4–5 branches), MP rarely fused to CuA (see discussion under *Stenolysmus*); female with all FW veins regular, not incrassate; FW CuA and CuP not arched towards posterior wing margin distally; FW 2A very short, terminates in wing margin before origin of first branch of RP; male tergites 8 and 9 fused, ectoproct rounded; gonarcus medially rounded or with medial process; entoprocessus short and broad. female with sternite 8 concave with posterolateral lobes rounded and setose; gonapophysis 9 slender, bifid at apex; tergite 9 ventrally broad; gonocoxites 9 lacking fringing row of setae.

Comments. *Stenosmylus* is recorded from eastern Australia (New 1986), although *S. tenuis* is the only Osmylidae known also found in Western Australia (unpublished data). The setose posterolateral lobed processes of the female sternite 8 are similarly found in *Phymatosmylus*, *Isostenosmylus*, *Oedosmylus* and *Stenolysmus* and may indicate the basic form for the subfamily. The fork of the forewing medial vein in the distal part of the wing is characteristic for the genus.

Included species.

S. stenopterus McLachlan, 1867 (Australia)

S. tenuis (Walker, 1853) (Australia)

S. turneri Kimmins, 1940 (Australia)



FIGURE 60. Stenosmylinae. *Stenosmylus stenopterus* McLachlan.

GENERA OF UNCERTAIN PLACEMENT IN OSMYLIDAE

Numerous fossil genera and species have been described based on incomplete specimens, most often from only one wing or fragments of wings. Since characters important for placement to family and constituent subfamilies are found in both wings and in the genitalia, and should be considered in combination, many taxa based on these incomplete specimens are presently unable to be confidently placed in any subfamily of Osmylidae, and in some cases their inclusion in Osmylidae is questionable.

Archaeosmylidia Makarkin *et al.*, 2014

(Fig. 63)

Type species. *Archaeosmylidia fusca* Makarkin *et al.*, 2014: 210 (by original designation).

Comments: The Mid Jurassic-aged *Archaeosmylidia* was considered by Makarkin *et al.* (2014) to be the intermediate between Archeosmylidae and Osmylidae. Known only from a single forewing, this genus has a unique combination of characteristics compared with other Osmylidae, including multiple *sc-r* crossveins (typically one), RP branches largely straight (frequently sinuous), CuP with few branches and dichotomously branched (commonly CuP is larger in area than CuA, with pectinate branching), and radial and medial crossveins are few in number (typically numerous). In a phylogenetic analysis by Winterton *et al.* (2017) *Archaeosmylidia*

was weakly supported as sister to Osmylinae rather than as sister to the rest of Osmylidae as proposed by Makarkin *et al.* (2014). The phylogenetic position of this genus remains uncertain.



FIGURE 61. Stenosmylinae. *Stenosmylus tenuis* (Walker).

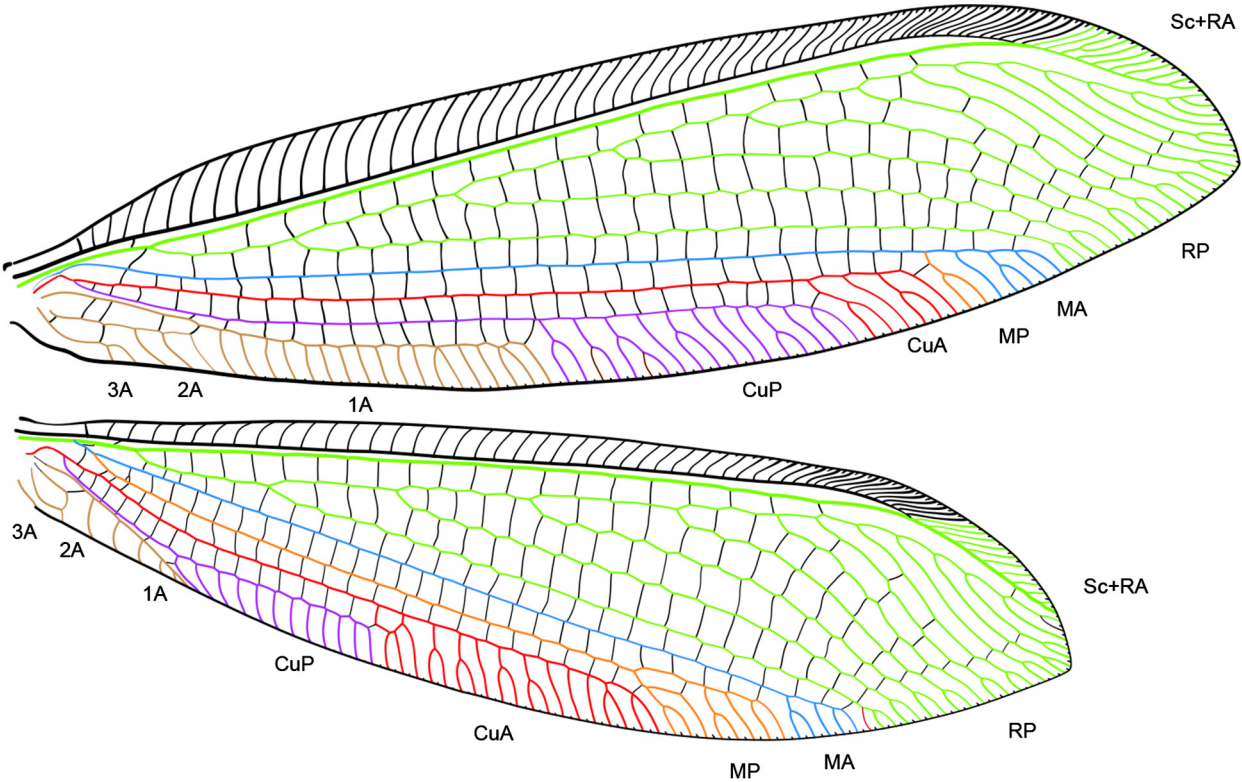


FIGURE 62. Stenosmylinae. *Stenosmylus stenopterus* McLachlan, wing venation (after Cousin & Béthoux, 2015) (vestiture omitted).

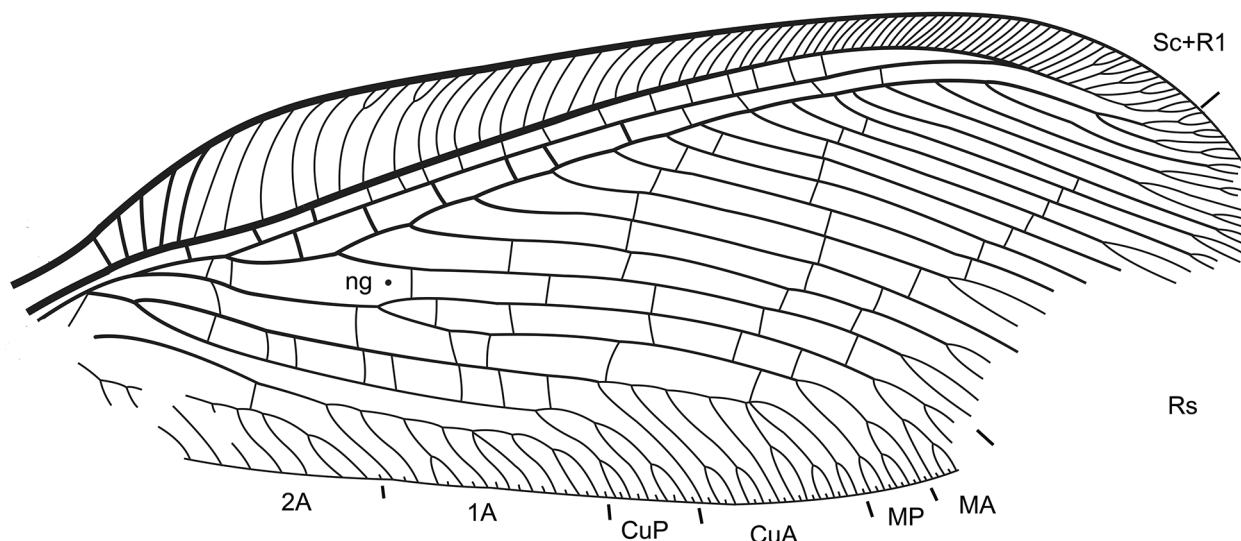


FIGURE 63. *Archaeosmylidia fusca* Makarkin *et al.* (from Makarkin *et al.*, 2014) (forewing).

***Dimidiosmylus* Khrakov in Ponomarenko *et al.*, 2014**

Type species. *Dimidiosmylus ramosus* Khrakov in Ponomarenko *et al.*, 2014: 1672 (by original designation) (Mongolia) (Late Jurassic).

Comments. The only known species is represented by a well-preserved basal half of a forewing. The genus was originally not assigned to any family of Neuroptera (Ponomarenko *et al.*, 2014), although it was compared with subfamilies of Osmylidae. The venation in general is typical for Osmylidae except some character states, which are not characteristic of the family, i.e., the proximal branches of RP, MA and MP are deeply forked. We consider these conditions as autapomorphies of the genus. The venation is in general most comparable to that of Kempyninae.

***Erlikosmylus* Khrakov, 2014b**

Type species. *Erlikosmylus obscurus* Khrakov, 2014b: 56 (by original designation) (Kyrgyzstan) (Early Jurassic-Middle Jurassic).

Comments. Based on a forewing fragment, the basal part of the wing is missing and thus obscuring the identity of some of the posterior veins important for placing the taxon to subfamily. Overall, the venation of *Erlikosmylus* is most similar to that of *Mesosmylina*, and likely it belongs in Mesosmylinae. These genera are distinct if we compare the venation of their type species (*cf.* Ponomarenko, 1995: fig. 77 and Khrakov, 2014b: fig. 3).

***Kubekius* Khrakov, 2017**

Type species. *Kubekius multiramosus* Khrakov, 2017: 64 (by original designation) (Russia) (Middle Jurassic).

Comments. Based on a single forewing, *Kubekius* is distinguished by the paucity of crossveins, especially the lack of any gradate series in the radial field. Only *Sinosmylus* is similar in this lack of radial crossveins, although this genus retains two gradate series. According to Khrakov (2017) the absence of crossveins gradates series in the wing of *Kubekius*, plus the straight branches of RP are evidence of a primitive state. However, the highly pectinate CuP differs from that found in Archeosmylidae. At present, *Kubekius* cannot be assigned to any of known

subfamilies of Osmylidae.

***Osmylopsis* Handlirsch, 1906**

Type species. *Abia duplicata* Giebel, 1856: 614 (by monotypy) (England) (Early Cretaceous).

Comments. This genus is based on a poorly preserved fragment of the apical half of the hind wing. The family affinity of which was hitherto unclear due to an inadequate original description and fragmentary nature of the specimen. Jepson *et al.* (2012) redescribed *O. duplicata* and assigned to Osmylidae although the subfamily placement cannot be determined.

***Palaeothyridosmylus* Wang *et al.*, 2009a**

(Fig. 64)

Type species. *Palaeothyridosmylus septemaculatus* Wang *et al.*, 2009a: 67 (by original designation).

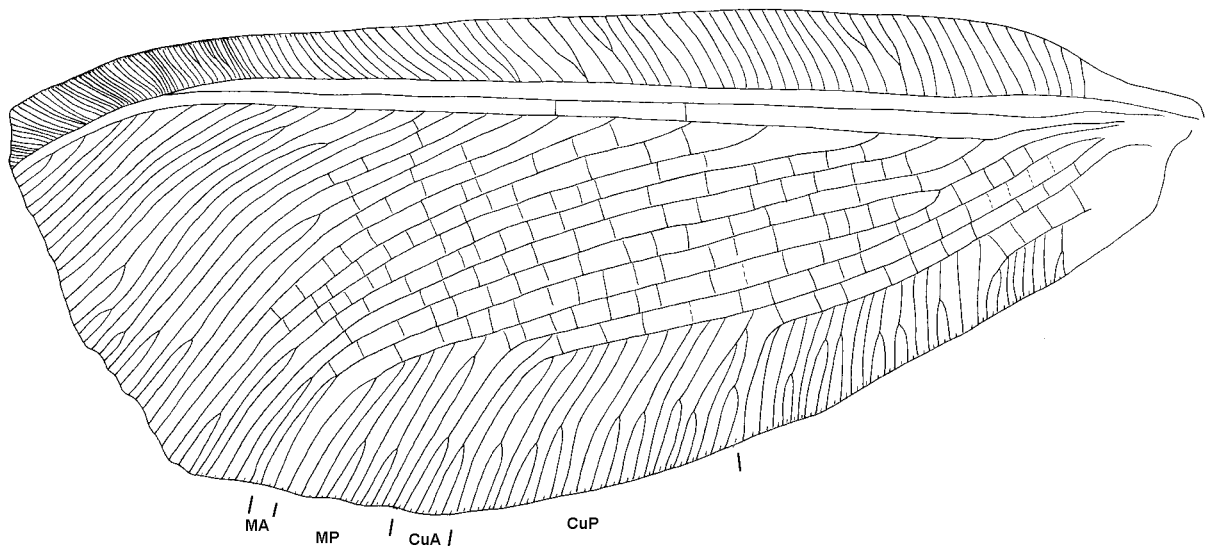


FIGURE 64. *Palaeothyridosmylus septemaculatus* Wang *et al.* (from Wang *et al.*, 2009a) (forewing).

Comments. The forewing figures presented by Wang *et al.* (2009a) have the veins identified following Kukalov-Peck & Lawrence (2004) (i.e., MA labelled as MP, MP as CuA, CuA as CuP and so on). The hind wing described and figured by Wang *et al.* (2009a: figs 3–4) as ‘*Palaeothyridosmylus* sp.’ is most likely the forewing as the M vein is forked near origin of the first branch of RP; osmylids typically have the hind wing medial fork closer to the origin of RP. Indeed, the wing is very similar in venation to the forewing described for *P. septemaculatus*. The specimen described by Wang *et al.* (2009a) is a hind wing overlaying (or underneath) a forewing, and the authors had some difficulty attributing the patterning of the wing to either. Considering the branching pattern of the wing figured (especially M), it seems that this specimen is a composite of wing venation from the forewing and hind wing. Moreover, the wing venation figured as ‘*Palaeothyridosmylus* sp.’ has an elongate and highly pectinately branched CuP, which would actually preclude placement in Spilosmylinae if it was a hind wing. Wang *et al.* (2009a) tentatively assigned this genus to Spilosmylinae, however, the genus does lack some important venational features characteristic of Spilosmylinae, such as at least one RP gradate series crossveins or a spur-like process on the basal part of the hind wing MP directed proximally (an important synapomorphy of Spilosmylinae). Based on

this, as well as the branching pattern the M, Cu and A1 veins, it was prudent of the authors not to formally describe the specimen as it likely represents a composite of both fore and hind wings. At present the subfamilial placement of this genus is undetermined until more material is available.

***Stenochrysa* Jepson *et al.*, 2012**

Type species. *Stenochrysa gradata* Jepson *et al.*, 2012: 40 (by original designation) (England) (Early Cretaceous).

Comments. Based on a single forewing fragment, most of the diagnostic features of the wing are not present to place this genus to subfamily. Jepson *et al.* (2012) suggested that this genus may belong to Gumillinae, a decision followed by Khrakov (2014a), but the fragmentary nature of the wing does not allow for confident placement in any subfamily.

***Tengriosmylus* Khrakov, 2014b**

Type species. *Tengriosmylus magnificus* Khrakov, 2014b: 56 (by original designation) (Kyrgyzstan) (Early Jurassic / Middle Jurassic).

Comments. This genus is based on a single almost complete forewing. It is most similar to genera of Mesosmylinae, but it likely does not belong to this subfamily.

***Tetanoptilon* Bode, 1953**

Type species. *Tetanoptilon brunsvicense* Bode, 1953: 266 (by original designation) (Germany) (Early Jurassic).

Comments. The genus is represented only by a single hind wing which was redescribed by Ponomarenko (1995). This specimen does not allow us to determine the systematic position of the genus since it is represented only by a hind wing with a set of unusual characteristics (e.g., *1r-m* is crossvein-like; subcostal veinlets arising nearly perpendicular to Sc; the proximal branches of RP are widely spaced; intracubital area is broad basally). Based on the elongate and densely pectinate branching pattern of the hind wing CuP, we can preclude placement in Gumillinae, Spilosmylinae and Protosmylinae. The density of crossveins and pectinate branching of the posterior wing veins likely also reflected in the unknown forewing of this genus, which would also suggest that it cannot be placed in Mesosmylinae or Archeosmylidae. While we agree with its placement in Osmylidae, we cannot definitively place it in any of the remaining subfamilies (e.g., Stenosmylinae, Osmylinae, Porisminae, Eidoporisminae).

TAXA EXCLUDED FROM OSMYLIDAE

***Cratovoluptia* Martins-Neto & Rodrigues, 2009**

Type species. *Cratovoluptia criptoneura* Martins-Neto in Martins-Neto & Rodrigues, 2009: 16 (by original designation) (Brazil) (Early Cretaceous).

Comments. Martins-Neto & Rodrigues (2009) assigned this genus to Osmylidae. However, based on the drawings provided it shows that this fossil more appropriately belongs to Ithonidae (*Rapisma*-genus group) based on features such as rounded wings, very broad costal area, and branching pattern of forewing medial vein.

***Cratosmylus* Myskowiak *et al.*, 2015**

Type species. *Cratosmylus magnificus* Myskowiak *et al.*, 2015: 28 (by original designation) (Brazil) (Early Cretaceous).

Comments. Cratosmylinae (containing only *C. magnificus*) is herein excluded from Osmylidae and placed in Nymphidae following Winterton *et al.* (2017). In the absence of ocelli or thyridiate crossveins evident in the specimen, Myskowiak *et al.* (2015) noted that *Cratosmylus* could be placed in either Osmylidae or Nymphidae, and despite the clear similarity to Nymphidae wings, they proposed inclusion in Osmylidae rather than Nymphidae based on two characters. They argue that two features found in *Cratosmylus* that would otherwise place it in Nymphidae (i.e., Sc+RA with long forked veinlets and, that Sc+RA terminates beyond the apex of the wing), are also present in Osmylidae. Examining the examples given they are either incorrect, or not particularly convincing as apomorphies justifying placement in Osmylidae compared with Nymphidae. Firstly, Sc+RA with long forked veinlets is a character typical of nymphids in the subfamily Myiodactylinae and is also present not only in *Porismus* (Fig. 26) and in some Protosmylinae and Stenosmylinae genera, but also present in various families of Neuroptera (e.g., Hemerobiidae, Chrysopidae); it appears therefore to be rather labile as phylogenetic character. Secondly, Sc+RA does not terminate beyond the wing apex in the lance lacewings and examples of exceptions they provide (i.e., *Heterosmylus* (Fig. 32) and *Arbusella*) do not exhibit this state. Indeed, this appears to be a useful diagnostic character that separates early lacewings like Osmylidae from highly derived members of Myrmeleontoidea. Myskowiak *et al.* (2015) do identify a mark which they interpret as nygma in the forewing. Their figure of the structure (Myskowiak *et al.*, 2015: fig. 6) is not very clear, nor convincing as a nygma, but if it is indeed found to be a nygma, it would better support placement of *Cratosmylus* in Osmylidae rather than Nymphidae. While the wing of *Cratosmylus* is similar to Gumillinae some respects as Myskowiak *et al.* (2015) suggest, the venation is more similar to Nymphidae genera in Myiodactylinae. The remaining characters in the wing could easily be autapomorphies. Makarkin *et al.* (2017, 2018) considered Cratosmylinae (containing two Cretaceous genera from Brazil, *Cratosmylus* and *Araripenymphes* Menon *et al.*) as a separate family closely related of Nymphidae.

***Idiastogyia* Lin, 1986**

Type species. *Idiastogyia fatisca* Lin, 1986: (China) (Early Jurassic).

Comments. *Idiastogyia* is described from a single fragment of the basal half of the hind wing. The venation is clear but distorted, and most of the important diagnostic characteristics of the family are not evident. At this stage we consider *Idiastogyia* as *incertae sedis* in Neuroptera.

***Yanosmylus* Ren in Ren *et al.*, 1995**

Type species. *Yanosmylus rarivenatus* Ren in Ren *et al.*, 1995: 101 (China) (Early Cretaceous).

Comments. *Yanosmylus* is described from a single fragmentary hind wing. The size of the wing is very small (8.0 mm), with simple venation and is unusually small for an osmylid. The branching pattern of the venation presented by Ren *et al.* (1995) is difficult to reconcile with any group of Osmylidae, and it exhibits few of the diagnostic characteristics of the family that would place it there. At this stage we consider *Yanosmylus* as *incertae sedis* in Neuroptera.

SAUCROSMYLIDAE Ren & Yin, 2003 ('elegant lance lacewings')

Type genus. *Saucrosmylus* Ren & Yin, 2003: 3 (by original designation).

Diagnosis. Antenna filiform, shorter than half of FW length; wings broad, ovoid to subtriangular, often with the

posterior margin sinuate distally (in either wing) and often with distinct markings; costal area relatively narrow; nygmata present; venation dense with numerous longitudinal veins, veinlets and crossveins present; venation in FW and HW remarkably similar in the size and branching pattern of vein fields; end-twigging along posterior margin dense multi-layered and irregular; trichosors present apparently around entire wing margin; costal area relatively narrow, subcostal veinlets simple to forked, interlinked by crossveins; single basal subcostal crossvein present; Sc and RA fused apically and curved posterior to enter margin before wing apex; area between RA and RP wide, with 2–7 irregular rows of cells; RP divergent from RA in basal half of wing, convergent with RA distally; RP branches numerous, distal forking irregular and angled toward posterior margin of wing, occasionally with secondary vein fusion, branches slightly curved posteriorly in distal part of wing; gradate absent; FW M fork close to wing base, usually between origin of RP1 and RP2; MP pectinately branched, sometimes irregularly with extensive secondary branching; CuA pectinately branched (sometimes irregularly) in middle of wing, larger in area than CuP in both wings.

Comments. Saucrosmylidae is an extinct family of Mesozoic lance lacewings originally described as a subfamily of Osmylidae (Ren & Yin, 2003) based on a series of symplesiomorphic characteristics found throughout Neuroptera. Of these, the most distinctive (although not necessarily unique to Saucrosmylidae) is the presence of multiple irregular rows of cells between RA and RP. Although the wing shape may vary between the forewing and hind wing, the wings are remarkably homogeneous in vein branching pattern and the size of vein fields. The density of vein branching and crossveins is typical of distantly related families in Myrmeleontoidea (e.g., Kalligrammatidae), although other families with such dense venation frequently have quite different branching patterns between the fore- and hind wings (i.e., various Myrmeleontoidea). Following the unpublished thesis study by Wang (2010) some authors have considered Saucrosmylidae as a distinct family, either closely related to Osmylidae (Makarkin *et al.*, 2013; Liu *et al.*, 2014; Khramov, 2017), or closer to Myrmeleontoidea (i.e., psychopsid-clade) (Yang *et al.*, 2012), while others have continued to treat it as a subfamily of Osmylidae (Liu *et al.*, 2013). Saucrosmylidae was finally elevated to family rank formally by Fang *et al.* (2015) and we follow this decision herein. Genera within Saucrosmylidae have distinctive variations in wing markings and wing shape, but tend to be homogeneous amongst genera, indicating a preponderance of genera based on species-level characteristics (e.g., nine species in eight genera). For example, while features such as shape of RP and posterior margin of the wing may be typically useful generic level characters in osmyloid genera, wing markings and rows of cells are usually not. Moreover, only the hind wing is known for *Rudiosmylus* and *Daohugosmylus* (see Fang *et al.*, 2016), while the forewing is only known for *Huiyingosmylus* and likely *Thaumatomerobius*. As discussed in Winterton & Brooks (2002), the erection of numerous monotypic genera based on spurious species-level characters results in the continued proliferation of monotypic genera for any newly discovered taxa as the previously described genera are too narrowly defined. Similarly, the limits of the various genera of Saucrosmylidae require re-evaluation in a phylogenetic context, for example, based on more stable features such as the shape of RP in both wings. The shape of RP in both wings suggests that there are two groups of taxa, including those with a relatively straight RP (i.e., *Huiyingosmylus*, *Daohugosmylus*, *Rudiosmylus*, *Saucrosmylus*, *Ulrikezza*) and those with an RP that is arched anteriorly (i.e., *Bellinympha*, *Laccosmylus* and *Thaumatomerobius*). Various keys to species are presented by Liu *et al.* (2013, 2014) and Fang *et al.* (2016). Larvae are unknown for this family.

Included genera. *Bellinympha* Wang *et al.*, *Daohugosmylus* Liu *et al.*, *Huiyingosmylus* Liu *et al.*, *Laccosmylus* Ren & Yin, *Rudiosmylus* Ren & Yin, *Saucrosmylus* Ren & Yin, *Thaumatomerobius* Ponomarenko, *Ulrikezza* Fang *et al.*

***Bellinympha* Wang *et al.*, 2010**

(Figs 65E–F)

Type species. *Bellinympha filicifolia* Wang *et al.*, 2010: 1 (by original designation).

Diagnosis. Wings subtriangular, posterior margin irregularly sinuous distally in FW, mostly straight in HW; both wings with distinct markings or infuscation, FW with prominent pinna-shaped markings along entire length centred along medial vein; FW subcostal veinlets irregularly forked; both wings with RP arching in apical part of wing, two to five regular rows of cells present in RA area, distal branches of RP apically curving toward posterior

margin, RP with six branches before distal curve anteriorly; MP with numerous pectinate branches; CuA with regular pectinate branches.

Comments. This genus has apically truncated, subtriangular wings where the forewing has a sinuate posterior margin. The disruptive pattern of colouration that resemble leaf pinnae, as well as thickened MP vein superficially resembles a leaf rachis (see discussion by Wang *et al.*, 2010) makes this genus readily distinguishable from other genera in the family. There is an appendage close to the caudal segment that resembles the female gonocoxite 9 of Osmylidae, lending additional support to the close relationship of these two families.

Included species.

B. dancei Wang *et al.*, 2010 (China) (Middle Jurassic)

B. filicifolia Wang *et al.*, 2010 (China) (Middle Jurassic)

***Daohugosmylus* Liu *et al.*, 2014**

Type species. *Daohugosmylus castus* Liu *et al.*, 2014: 302 (by original designation).

Diagnosis. HW broad with rounded posterior margin; RA area with at most six rows of cells; RP only slightly curved anteriorly towards RA in distal part of wing, RP with six branches before distal curve anteriorly; most vein areas subdivided with additional rows of cells in RP, medial and cubital field in middle part of wing; end-twigging greatly elongate with forks originating relatively distant from wing margin; FW unknown.

Comments. The only known specimen consists of an almost complete hind wing. *Daohugosmylus* appears to be closely related to *Ulrikezza* and *Laccosmylus* based on the degree of secondary rows of cells and arched branching pattern of CuP.

Included species.

D. castus Liu *et al.*, 2014 (China) (Middle Jurassic)

***Huiyingosmylus* Liu *et al.*, 2013**

Type species. *Huiyingosmylus bellus* Liu *et al.*, 2013: 388 (by original designation).

Diagnosis. FW broadly subtriangular, posterior margin strongly and regularly sinuate distally; RA area with six oblique, irregularly arranged rows of cells, RP with seven branches before distal curve anteriorly and with numerous distal branches angled posteriorly and densely arranged; area between multiple longitudinal veins among radial medial and cubital fields with additional rows of cells; area between 1A and 2A with more than two rows of cells; end-twigging greatly elongate with forks originating relatively distant from wing margin; HW unknown.

Comments. The only known specimen is a well-preserved forewing with distinctive markings, including multiple spots. Similar spots are found in *Daohugosmylus* and *Ulrikezza*.

Included species.

H. bellus Liu *et al.*, 2013 (China) (Middle Jurassic)

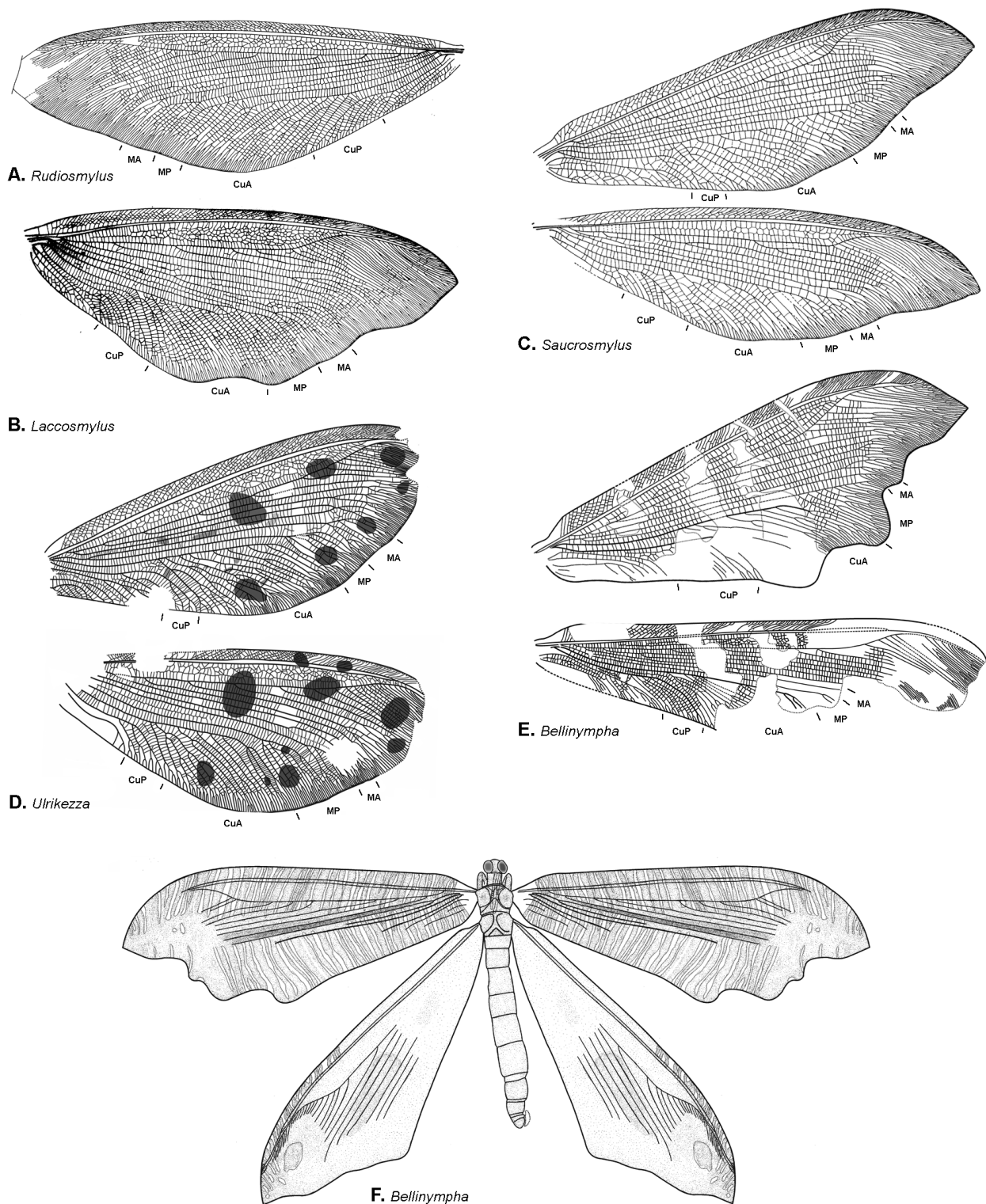


FIGURE 65. Saucrosmylidae fossils. A. *Rudiosmylus ningchengensis* Ren & Yin (from Ren & Yin, 2003), hind wing; B. *Laccosmylus calophlebius* Ren & Yin (from Ren & Yin, 2003), hind wing; C. *Saucrosmylus sambneurus* Ren & Yin (from Ren & Yin, 2003); D. *Ulrikezza aspoeckae* Fang *et al.*, 2015 (from Fang *et al.*, 2015); E. *Bellinympha filicifolia* Wang *et al.*, 2010 (from Wang *et al.*, 2010); F. same (figures not to scale).

***Laccosmylus* Ren & Yin, 2003**

(Fig. 65B)

Type species. *Laccosmylus calophlebius* Ren & Yin, 2003: 8 (by original designation).

Diagnosis. Wings broadly sub-triangular with undulate distal posterior margin, FW narrower than HW, both wings with extensive dark markings; both wings with RA area with 4–7 poorly formed rows of cells, RP sharply curved anteriorly in distal part of wing, RP with 5–7 branches before distal curve anteriorly; 1–2 rows of cells between MA and MP; end-twigging greatly elongate with forks originating relatively distant from wing margin.

Comments. *Laccophlebius* comprises three distinctive species with wings dark markings and undulate posterior margins distally (Ren & Yin, 2003; Fang *et al.*, 2018).

Included species.

L. calophlebius Ren & Yin, 2003 (China) (Middle Jurassic)

L. latizonus Fang *et al.*, 2018 (China) (Middle Jurassic)

L. cicatricatus Fang *et al.*, 2018 (China) (Middle Jurassic)

***Rudiosmylus* Ren & Yin, 2003**

(Fig. 65A)

Type species. *Rudiosmylus ningchengensis* Ren & Yin, 2003: 6 (by original designation).

Diagnosis. Hind wing relatively narrow, subtriangular, slightly curved posteriorly with a narrow apex; subcostal veinlets rather dense, forked, with many interlinking crossveins; RA area with at most four rows of irregular cells; RP very slightly curved anteriorly, and with seven branches before distal curve anteriorly distal branches of RP with some crossveins and irregular forking; end-twigging irregular, elongated with forks originating relatively distant from wing margin; area between MA and MP with two rows of cells. CuA and CuP deeply forked, branches of CuA forming a large triangular area; FW unknown.

Comments. Only known from the holotype, which consists of an almost complete and well-preserved hind wing.

Included species.

R. ningchengensis Ren & Yin 2003 (China) (Middle Jurassic)

***Saucrosmylus* Ren & Yin, 2003**

(Figs 65C)

Type species. *Saucrosmylus sambneurus* Ren & Yin, 2003: 3 (by original designation).

Diagnosis. Forewing narrow, subtriangular with posterior margin straight to very slight falcate, apex distinctly angular, wing markings extensive with irregular banding pattern; subcostal veinlets dense and irregularly forked, with mostly regular rows of interlinking crossveins; RA area with 1–3 regular rows of cells; RP in both wings sharply curved anteriorly in distal part of wing, FW RP with six branches before RP anterior curve; distal RP branches only slightly angled posteriorly and lacking crossveins; end-twigging irregular; single row of cells between MA and MP; CuA fork forming large triangular area.

Comments. *Saucrosmylus* is the type genus of Saucrosmylidae, described based on two well-preserved specimens with distinctive wing banding.

Included species.

S. sambneurus Ren & Yin, 2003 (China) (Middle Jurassic)

***Thaumatomerobius* Ponomarenko 1985**

Type species: *Thaumatomerobius mirabilis* Ponomarenko, 1985: 92 (by original designation).

Diagnosis. Wing subcostal veinlets dense and irregularly forked; RA area with at least three irregular rows of cells; RP sharply curved anteriorly in distal part of wing, distal RP branches slightly angled posteriorly and lacking crossveins.

Comments. This monotypic genus is known only from two wing fragments. Originally placed in Prohemerobiidae, Khamov (2017) appropriately argued that it is better placed in Saucrosmylidae based on the rows of cells in the expanded area between RA and RP, and the convergence of RP with RA in the distal part of the wing.

Included species.

T. mirabilis Ponomarenko, 1985 (Russia) (Middle Jurassic)

***Ulrikezza* Fang *et al.*, 2015**

(Figs 65D)

Type species. *Ulrikezza aspoeckae* Fang *et al.*, 2015: 4 (by original designation).

Diagnosis. Wings ovoid and relatively broad; wing markings extensive with distinct spots in distal half of wing; subcostal veinlets dense and irregularly forked distally, with irregular rows of dense interlinking crossveins; RA area with 4–5 rows of irregular rows of cells; RP in both wings only slightly curved anteriorly in distal part of wing, FW RP with six branches before RP anterior curve, distal RP branches only slightly angled posteriorly and lacking crossveins; end-twigging irregular and dense; single row of cells between MA and MP; CuA fork forming large triangular area with extensive irregular crossveins.

Comments. Fang *et al.* (2015) described *Ulrikezza* as a monotypic genus, but also informally described another specimen based only on a single forewing; despite some subtle differences, the additional specimen is very similar to *U. aspoeckae*.

Included species.

U. aspoeckae Fang *et al.*, 2015 (China) (Middle Jurassic)

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