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Revision of Epigambriinae Handlirsch, stat. nov., a subfamily of Early Jurassic Ithonidae *s.l.* (Neuroptera)

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Abstract

We redescribe the holotype of *Epigambria longipennis* Handlirsch, 1939 from the Early Jurassic of Dobbertin (Germany), the type of the family Epigambriidae Handlirsch, 1939. Two other early Toarcian genera from Germany (*Polyosmylus* Ansorge, 1996 from Grimmen and *Rasnitsyneura* **gen. nov.**, the type species *R. aequabilis* (Bode, 1953), **comb. nov.** from Schandelach) are assigned to Epigambriidae, which we interpret as Epigambriinae, **stat. nov.**, a subfamily of Ithonidae *s.l.* The venation of Epigambriinae is most similar to that of the polystoechotid genus-group but may be distinguished from members of this group mainly by (1) a single gradate series between branches of RP in both the fore- and hind wings, and (2) the absence of crossveins between branches of MP and CuA in the forewing.

Keywords: Neuroptera, Ithonidae *s.l.*, polystoechotid genus-group, Epigambriinae, Early Jurassic, Dobbertin, Grimmen, Schandelah

Introduction

Many extinct families of Neuroptera have been described from the Jurassic to date. Those currently recognized to be valid are Kalligrammatidae Handlirsch, 1906, Mesochrysopidae Handlirsch, 1906, Prohemerobiidae Handlirsch, 1906, Panfiloviidae Makarkin, 1990a, Grammolingiidae Ren, 2002, and Saucrosmylidae Ren & Yin, 2003. Others are currently considered to be subfamilies of valid families or their synonyms, *i.e.*, Mesithonidae Panfilov, 1980 as a subfamily of Berothidae Handlirsch, 1906 (Makarkin *et al.*, 2012); Nymphitidae Handlirsch, 1906 a synonym of Nymphidae Rambur, 1842 (Shi *et al.*, 2013); Brongniartiellidae Martynova, 1949 a synonym of Osmylopsychopidae Martynova, 1949 (Peng *et al.*, 2016), Mesopolystoechotidae Martynova, 1949 a possible synonym of Polystoechotidae Handlirsch, 1906 (Makarkin & Archibald, 2003); Epiosmylidae Panfilov, 1980 a synonym of Gumillinae Navás, 1912 (Osmylidae Leach, 1815) (Menon & Makarkin, 2008); Promantispidae Panfilov, 1980 a synonym of Mantispidae Leach, 1815 (Lambkin, 1986); Promegalomidae Panfilov, 1980 a synonym of Hemerobiidae Latreille, 1802 (Oswald, 1993); and Liassochrysidae Nel *et al.*, 2005 a synonym of Mantispidae (Wedmann & Makarkin, 2007). Eomantispidae Bode, 1953 is an unavailable name as no genera were included in this family (Liu *et al.*, 2013). One new Jurassic family was recently described, namely Parakseneuridae Yang *et al.*, 2012.

However, the status and composition of four Jurassic families have not yet been clarified: Solenoptilidae Handlirsch, 1906, Epigambriidae Handlirsch, 1939, Osmylitidae Martynova, 1949, and Glottidiidae Bode, 1953 (Yang *et al.*, 2012).

The type genus of Epigambriidae is *Epigambria* Handlirsch, 1939 from the Early Jurassic (early Toarcian) of Dobbertin (Germany), based on a poorly preserved hind wing of its sole species, *Epigambria longipennis* Handlirsch, 1939. Handlirsch (1939) assumed that two other Mesozoic species might belong to this family, *i.e.*, *Osmylites protogaea* (Hagen, 1862) from the Late Jurassic of Eichstätt (Germany), and *Osmylopsis duplicata* (Giebel, 1856) from the Early Cretaceous (late Berriasian) of Durlston Bay (England). *Osmylites protogaea* is a *nomen nudum*; the valid name of this species is *Osmylites excelsa* (Oppenheim, 1888) (see Makarkin & Archibald, 2003). It is the type genus of

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Osmylitidae, but the status of this family is not clear (Yang *et al*., 2012). *Osmylopsis duplicata* is now considered to belong to Osmylidae (Jepson *et al*., 2012; Winterton *et al*., 2019).

Earlier, Martynova (1949, 1962), Makarkin (1990b) and Ross & Jarzembowski (1993) considered *Epigambria* to belong to Nymphitidae, which was subsequently synonymized with Nymphidae (Shi *et al*., 2013). However, the small size of *Epigambria* and other characters make it strongly dissimilar to other species of Nymphidae, whose wings are much larger and different in venation.

Here, we re-describe the holotype of *Epigambria longipennis* and show that Epigambriidae is a valid taxon, which we treat as Epigambriinae **stat. nov.**, a subfamily of Ithonidae *s.l.* We add to this subfamily two other monotypic genera from the Early Jurassic of Germany, *Polyosmylus* Ansorge, 1996 and *Rasnitsyneura* **gen. nov.**

Material and methods

Ten specimens of Neuroptera were examined from the Early Jurassic (early Toarcian) marine deposits of three localities in Germany (Dobbertin, Grimmen, and Schandelah), including the type specimens of *Epigambria longipennis* and *Polyosmylus excelsus* Ansorge, 1996. Detailed information on these localities may be found in a number of publications (see Ansorge, 1996, 2003; Ansorge & Obst, 2015; Ansorge & Makarkin, 2021).

We follow the wing venation terminology of Breitkreuz *et al*. (2017). Terminology of wing spaces and details of venation (*e.g*., traces, veinlets) follows Oswald (1993).

Venation abbreviations: A1 to A3, first to third anal veins; CuA, cubitus anterior; CuP, cubitus posterior; hv, humeral veinlet; M, media; MA, media anterior; MP, media posterior; RA, radius anterior; RP, radius posterior; RP1, proximal-most branch of RP; RP2, branch of RP distad RP1; Sc, subcosta.

Institutional and collections abbreviations: CNU, College of Life Sciences, Capital Normal University, Beijing, China; LGA, Lias Grimmen Ansorge collection in MNB; MNB, Museum für Naturkunde Berlin, Germany; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia.

Systematic palaeontology

Order Neuroptera Linnaeus, 1758
Family Ithonidae Newman, 1853, *s.l.*
Subfamily Epigambriinae Handlirsch, 1939, stat. nov.

Epigambridae [*sic*] Handlirsch, 1913: 813 (*nomen nudum*); Zittel, 1921: 679 (*nomen nudum*); Zittel, 1924: 700 (*nomen nudum*); Labandeira, 2002: 232 (fig. 4).

Epigambriidae Handlirsch, 1939: 76; Bode 1953: 18; Brues *et al*., 1954: 782, 817; Carpenter, 1992: 355; Makarkin & Archibald, 2003: 176; Engel & Grimaldi, 2008: 8 (Table 3); Jepson *et al*., 2012: 40; Yang *et al*., 2012: 2.

Type genus. *Epigambria* Handlirsch, 1939.

Diagnosis. May be distinguished from members of the polystoechotid genus-group of Ithonidae *s.l.* by a combination of the following character states: (1) a single gradate series between branches of RP in both fore- and hind wings [two series in genera of the polystoechotid genus-group (rarely: outer series distinct, proximal crossveins numerous, not arranged in inner series in forewing)]; (2) absence of crossveins between branches of MP and CuA in forewing [present in genera of the polystoechotid genus-group]; (3) several crossveins between RA and RP nearly perpendicular to these veins in hind wing [few and oblique in most members of the polystoechotid genus-group].

Included genera. *Epigambria*, *Polyosmylus*, and *Rasnitsyneura*, **gen. nov.**, all from the Early Jurassic (early Toarcian) of Germany.

Remarks. Handlirsch (1913) and Zittel (1921, 1924) mentioned the name 'Epigambridae', but no genera were included to this family until 1939.

Genus *Epigambria* Handlirsch, 1939

Epigambria Handlirsch, 1939: 76 [Epigambriidae]; Martynova, 1949: 151, 155 [Nymphitidae]; Bode, 1953: 18 [Epigambriidae]; Martynova, 1962: 274 [Nymphitidae]; Makarkin, 1990b: 125 [Nymphitidae]; Carpenter, 1992: 355 [Planipennia *incertae sedis*]; Makarkin & Archibald, 2003: 176 [Neuroptera *incertae sedis*].

Type species. *Epigambria longipennis* Handlirsch, 1939, by monotypy.

Emended diagnosis. Forewing: unknown. Hind wing: MA, MP deeply dichotomously forked [*Polyosmylus*: forked once, shallowly].

***Epigambria longipennis* Handlirsch, 1939**
(Fig. 1)

Epigambria longipennis Handlirsch, 1939: 76, Pl. 7, Fig. 119; Martynova, 1949: 167; Lambkin, 1988: 449, 453; Herrig & Nestler, 1989: 33; Carpenter, 1992: 355; Ross & Jarzembowski, 1993: 418; Makarkin & Archibald, 2003: 176.

Material. Holotype FGWG 123/51, deposited in the collections of the Institute of Geography and Geology,

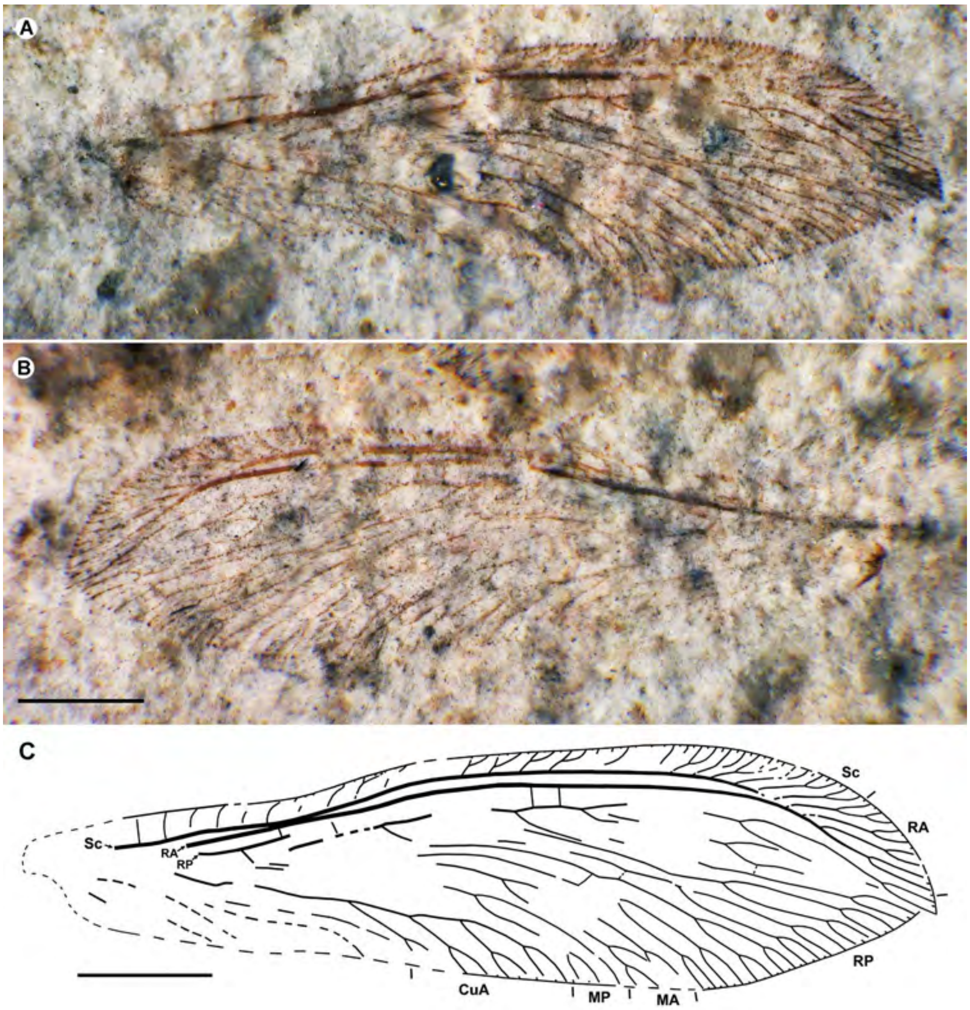

FIGURE 1. *Epigambria longipennis* Handlirsch, 1939, holotype FGWG 123/51. **A**, Part. **B**, counterpart. **C**, Hind wing venation. Scale bars = 1 mm (**A**, **B** to same scale).

University of Greifswald, Germany. A poorly preserved crumpled complete hind wing. Germany: Dobbertin. Early Jurassic (early Toarcian, "Grüne Serie", *Harpoceras falciferum* ammonite zone).

Re-description. Hind wing 6.9 mm long, 1.8 mm wide as preserved (estimated complete width ≥2 mm). Costal space relatively broad, slightly broadened proximally, moderately broadened distally. Subcostal veinlets widely spaced; basally simple, perpendicular to Sc; more proximally bent toward wing apex, simple or shallowly forked; distally once forked. Subcostal space moderately broad; crossveins not detected. Sc stout, approaching RA distally, with or without fusion unknown. RA stout, relatively long, entering margin somewhat proximad wing apex; with four long veinlets, once to twice forked. RA space narrow, with four preserved crossveins (nearly perpendicular to RA). RP originating relatively near wing base, with seven pectinate branches. RP1, RP3, RP4, RP6 deeply dichotomously forked; RP2 similarly (but not so deep) branched; RP5 once forked. Proximal part of M not preserved. MA, MP deeply dichotomously forked. CuA pectinately branched; its anterior trace, three branches once forked. CuP not clearly discernible (possibly few branched). Anal veins very poorly preserved. Crossveins in radial space very poorly preserved, probably forming one gradate series (three crossveins discernible).

Remarks. The drawing of Handlirsch (Handlirsch, 1939: Pl. 7, Fig. 119) is largely incorrect, especially in the area of the cubital space; we revise it here (Fig. 1).

Genus *Polyosmylus* Ansorge, 1996, sit. nov.

Polyosmylus Ansorge, 1996: 67 [Neuroptera *incertae sedis*].

Type species. *Polyosmylus excelsus* Ansorge, 1996, by original designation.

Emended diagnosis. Forewing: CuP deeply forked [shallowly forked in *Rasnitsyneura*]. Hind wing: MA, MP once forked, shallowly [*Epigambria*: deeply, dichotomously forked].

***Polyosmylus excelsus* Ansorge, 1996**
(Figs 2–4)

Polyosmylus excelsus Ansorge, 1996: 68, 107, Fig. 53; Pl. 10, Figs 7, 8; Ansorge, 2003: Fig. 3J.

Type material. Holotype LGA 1033 (part only), deposited in MNB. A well-preserved, nearly complete forewing overlapping an incompletely preserved hind wing.

Paratype LGA 540 (part only), deposited in MNB. A rather poorly preserved complete forewing. The same locality and horizon as the holotype.

Type locality and horizon. Germany: Grimmen. Early Jurassic (early Toarcian; "Grüne Serie", *Harpoceras falciferum* zone).

Re-description. *Holotype LGA 1033*. Forewing 8.7 mm long, 2.9 mm wide. Costal margin medially markedly concave. Costal space relatively narrow, broadened proximally and distally. Basal subcostal veinlets incompletely preserved; middle veinlets terminally curved to apex or forked with distal branch longer than proximal; some distal veinlets of Sc rather deeply once forked; some veinlets of RA twice forked. Subcostal space moderately broad distally; only basal crossvein detected located slightly proximad origin of RP. Sc, RA stout, distally approaching, probably not fused (Fig. 3A). RA space relatively narrow, nearly equal width throughout length; five, rather regularly spaced crossveins in middle part. RP originating near wing base; anterior trace forked distally, not zigzagged, with nine branches. RP1, RP3, RP4, RP9 dichotomously forked distad outer gradate series; RP2, RP5, RP6, RP8 once shallowly forked; RP7 simple. Two crossveins between R and M in basal part: 1r-m short, connecting R, M; 2r-m long, connecting RP proximad origin of RP1, MA. M basally not fused with R; forked far proximad origin of RP1. MA basally (proximad 2r-m) poorly discernible, forked distad outer gradate series (incompletely preserved). MP pectinately forked, with three long branches; each branch once shallowly forked. Crossveins in radial to medial spaces rare: two crossveins (between MA, MP and MP, CuA) form posterior part of inner gradate series; outer gradate series probably complete, eight crossveins detected from RP7 to CuA (some poorly preserved). Cu dividing into

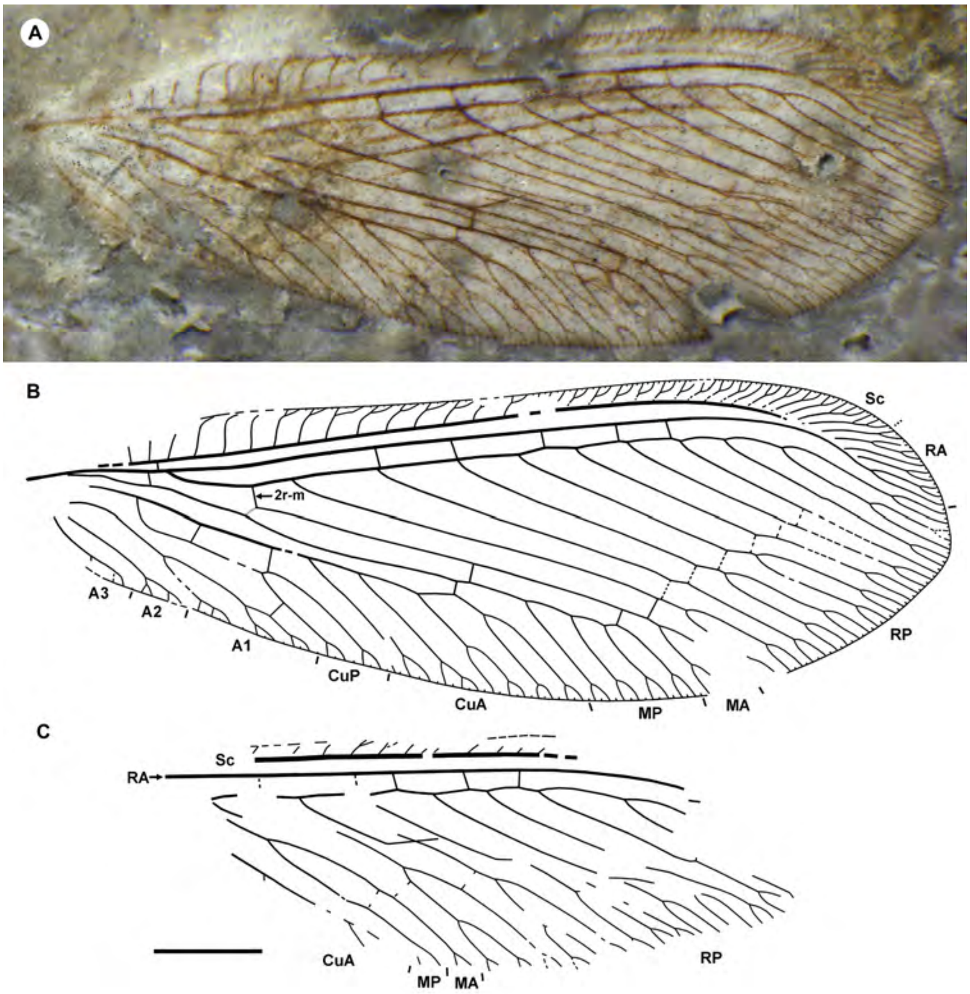

FIGURE 2. *Polyosmylus excelsus* Ansorge, 1996, holotype LGA 1033. **A**, Photograph. **B**, Forewing venation. **C**, Hind wing venation. Scale bar = 1 mm (all to same scale).

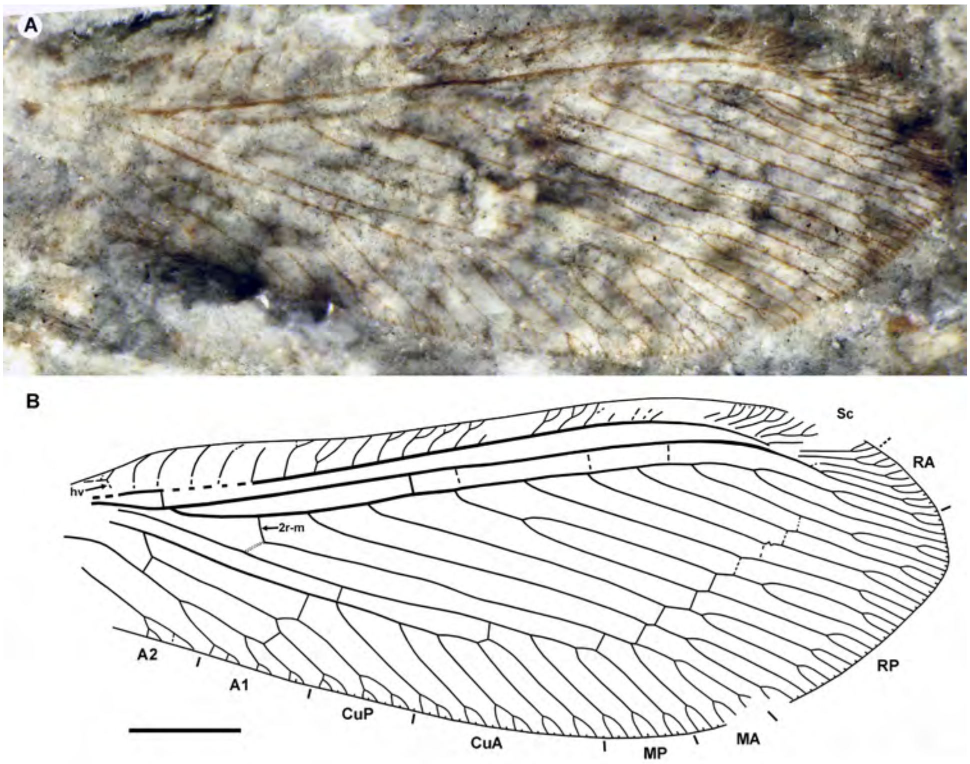

FIGURE 3. *Polyosmylus excelsus* Ansorge, 1996, paratype LGA 540. **A**, Photograph (wetted with ethanol). **B**, Forewing venation. Scale bar = 1 mm (both to same scale).

CuA, CuP relatively near wing base. CuA pectinately forked, with four long branches (three proximad distal crossvein between MP, CuA; one distad); each branch once or twice shallowly forked. CuP deeply forked, each branch shallowly once forked near margin. Two long crossveins between CuA, CuP. One long distal crossvein between CuP, A1 (basal crossvein not discernible). A1 dichotomously branched. A2, A3 similarly configured, with two to three very short branches.

Hind wing 5.9 mm long as preserved (estimated complete length *ca*. 7.0–7.5 mm), 2.1 mm wide as preserved (estimated complete width *ca*. 2.2 mm). Preserved portion of costal space narrow. Subcostal veinlets oblique, medially simple or once shallowly forked. Subcostal space rather broad, crossveins not detected. Sc, RA stout. RA space slightly wider than subcostal space; with five preserved crossveins nearly perpendicular to RA. RP with seven preserved branches (possibly eight in life). RP1–RP4 deeply dichotomously forked; RP5, RP6 shallowly forked. M forked far distad origin of RP1. MA, MP shallowly forked. Crossveins in radial to medial spaces poorly preserved; four crossveins partly preserved forming single gradate series. CuA pectinate, but only two branches fragmentarily preserved. CuP, anal veins not preserved.

Paratype LGA 540. Forewing 8.1 mm long, 3.0 mm wide. Costal margin medially markedly concave. Costal space relatively narrow, broadened proximally, distally. Humeral veinlet recurrent, with two very short branches; five basal subcostal veinlets simple, with their apices curved to wing apex; middle to distal veinlets bent toward apex, mainly once forked (often shallowly), rarely twice forked. Subcostal space moderately broad distally; only basal crossvein detected located slightly proximad origin of RP. Sc, RA stout, distally approaching, probably not fused (Fig. 3B). RA space relatively narrow, nearly equal width throughout length; four crossveins detected in middle part. RP originating near wing base; anterior trace forked distally, not zigzagged, with nine branches. RP3 dichotomously deeply forked far proximad outer gradate series; RP1, RP2, anterior branch of RP3, RP7 dichotomously forked distad outer series; posterior branch of RP3, RP4–RP6 once forked; RP8, RP9 simple. One long crossvein between R, M in basal part detected (2r-m), connecting RP proximad origin of RP1, MA. M basally not fused with R; forked far proximad origin of RP1. MA basally (proximad 2r-m) poorly discernible; pectinately forked distad outer gradate series with two forked branches. MP pectinately forked, with two long branches; each branch once shallowly forked. Crossveins of inner gradate series not detected; outer gradate series complete, nine crossveins detected from RP7 to CuA (some poorly preserved). Two crossveins detected between MP, CuA. Cu dividing into CuA, CuP relatively

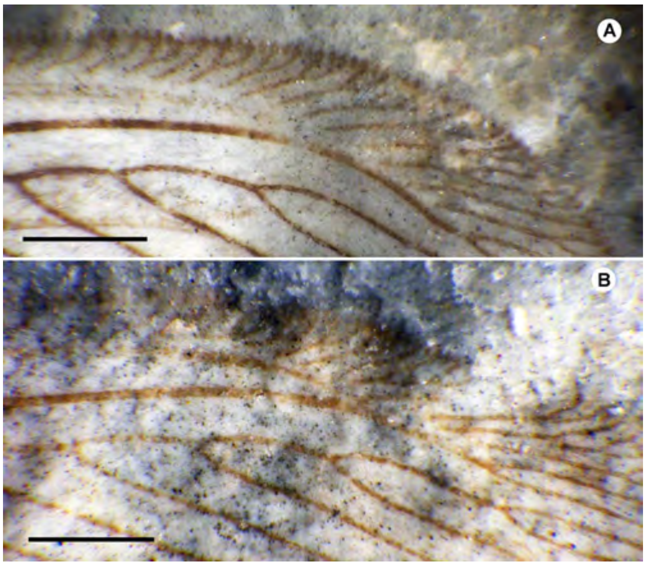

FIGURE 4. Apical portion of the forewing of *Polyosmylus excelsus* Ansorge, 1996. **A**, Holotype LGA 1033. **B**, Paratype LGA 540. Both wetted with ethanol. Scale bars = 0.2 mm.

near wing base. CuA pectinately forked, with four long branches (all proximad distal crossvein between MP, CuA); each branch once or twice shallowly forked. CuP deeply forked, each branch shallowly forked near margin (twice or three times). One long distal crossveins between CuA, CuP detected. Two long crossveins between CuP, A1. A1 dichotomously branched. A2 dichotomously branched near wing margin.

Remarks. The holotype and paratype are certainly conspecific based on their very similar wing venation and their wings lacking spots.

Genus *Rasnitsyneura* gen. nov.

Type species. *Prohemerobius aequabilis* Bode, 1953.

Etymology. The genus is named in honor of Professor Alexander P. Rasnitsyn, a well-known Russian paleoentomologist; the ending -*neura* is from Neuroptera. Gender: feminine.

Diagnosis. Forewing: several brown spots [*Polyosmylus*: none]; CuP shallowly forked [*Polyosmylus*: deeply forked]. Hind wing: unknown.

Remarks. Bode (1953) described seven species of *Prohemerobius* with spotted forewings from two localities near Braunschweig in Germany (Hondelage and Schandelah): *Prohemerobius aequabilis*, *P*. *septemvirgatus* Bode, 1953, *P*. *succisus* Bode, 1953, *P*. *dispar* Bode, 1953, *P*. *sexfasciatus* Bode, 1953, *P*. *quatuorpictus* Bode, 1953, and *P*. *obliquevirgatus* Bode, 1953. Ponomarenko (1996) reexamined most of their types and assigned several additional specimens to them. He considered four species to be junior synonyms: *P*. *aequabilis*, *P*. *succisus*, and *P*. *dispar* to be synonyms of *P*. *septemvirgatus*; *P*. *obliquevirgatus* as a synonym of *P*. *quatuorpictus*. However, the situation is complicated by the fact that the present location of these types is unknown, the photographs of them provided by Ponomarenko (1996) are poor and not very informative, and their drawings by Bode (1953) and Ponomarenko (1996) are not accurate, at least in some details. Therefore, this synonymy is not well justified, and the actual number of these *Prohemerobius* species is unknown, as their diagnostic characters and generic affinities remain unclear. However, we may reasonably assume that *P*. *aequabilis*, *P*. *succisus*, *P*. *dispar* and *P*. *septemvirgatus* belong to *Rasnitsyneura* **gen. nov.** judging from the similar size, maculation and venation (but considering that their venations were drawn or interpreted somewhat incorrectly) to those of the specimens described here. Three other species (*P*. *sexfasciatus*, *P*. *quatuorpictus*, and *P*. *obliquevirgatus*) probably do not belong to Epigambriinae judging from their smaller sizes, stouter bodies, and differing maculations.

***Rasnitsyneura aequabilis* (Bode, 1953), comb. nov.**
(Figs 5–7)

Prohemerobius aequabilis Bode, 1953: 252, 257, 258; Pl. 12, Fig. 326; Ponomarenko, 1996: 75, 76, Figs 2, 10 (as a synonym of *Prohemerobius septemvirgatus* Bode, 1953).

Prohemerobius aequalibis [sic]: Ponomarenko, 1996: caption to Fig. 10.

Material. Specimen PIN 5552/34 (part only); a well-preserved, nearly complete forewing; deposited in PIN.

Locality and horizon. Germany: Schandelah. Early Jurassic (early Toarcian, *boreale* nodule, *Harpoceras falciferum* ammonite zone).

Description. *Specimen PIN 5552/34* (Fig. 5). Forewing 7.8 mm long, 2.6 mm wide. Costal margin medially markedly concave. Costal space relatively narrow, broadened proximally, distally. Humeral veinlet recurrent, with two short branches; terminal parts of proximal subcostal veinlets strongly bent toward wing apex, simple or with very shallow terminal fork; middle veinlets terminally curved to apex or forked with distal branch longer than proximal; distal veinlets of Sc, RA mainly once forked (two veinlets forked two or three times). Subcostal space moderately broad distally; only basal crossvein detected located slightly distad origin of RP. Sc, RA stout, distally approaching, probably not fused. RA space narrow, slightly dilated basally; five, rather regularly spaced crossveins in middle part. RP originating near wing base; anterior trace forked distally, not zigzagged, with seven branches. RP1, RP2, RP4

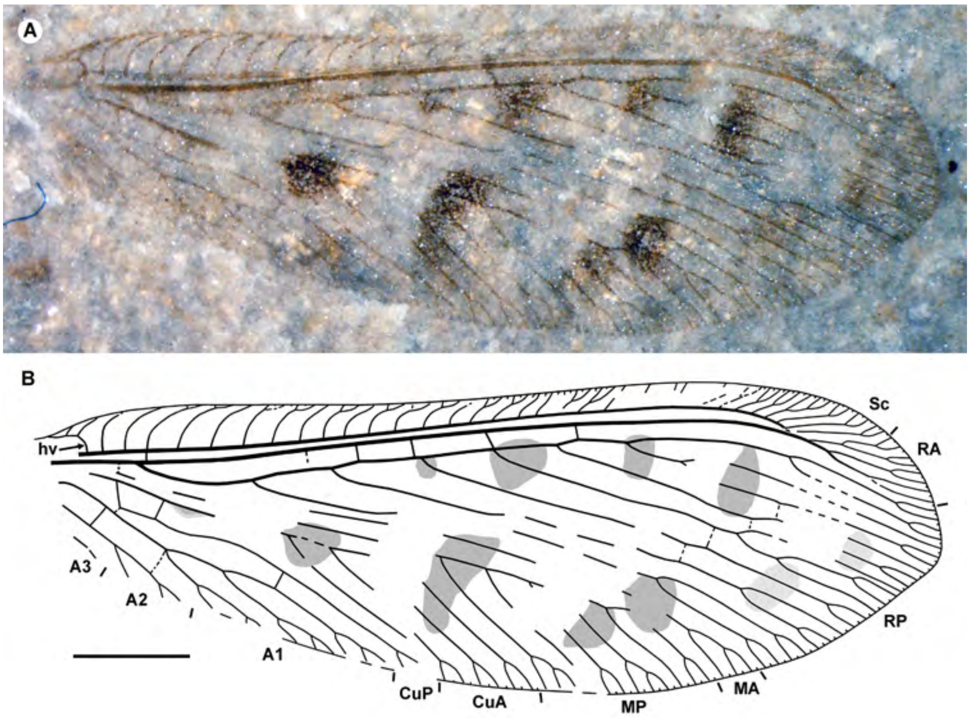

FIGURE 5. *Rasnitsyneura aequabilis* (Bode, 1953), specimen PIN 5552/34. **A**, Photograph. **B**, Forewing venation. Scale bar = 1 mm (both to same scale).

dichotomously forked distad outer gradate series; RP3, RP5, RP7 once shallowly forked; RP6 dichotomously forked far proximad outer gradate series. One short crossvein between R, M in basal part (1r-m) detected, connecting R, M. Fork of M not preserved. Anterior trace of MA forked distally, with one relatively short branch. MP pectinately forked, with five long branches, once to twice shallowly forked (one branch simple). Crossveins in radial to medial spaces poorly preserved; four crossveins (from RP2 to RP6) represented outer gradate series. Cu dividing into CuA, CuP relatively near wing base. CuA pectinately forked, with two, very long branches; each branch once shallowly forked. CuP shallowly once forked. One (proximal) crossvein between CuA, CuP detected. Two crossveins between CuP, A1: basal crossvein short; distal crossvein rather long. A1 profusely, pectinately branched, with two rather long branches, which are again pectinately or dichotomously branched. A2 pectinately forked, with two short branches. Two long crossveins between A1, A2. A3 fragmentarily preserved. Maculation: eight brown spots medially (different in size), two paler spots apically.

Remarks. We assign this specimen to *Rasnitsyneura aequabilis* judging from the drawings of the holotype by Bode (1953: Fig. 326) and Ponomarenko (1996: Fig. 10, which we consider mostly correct). Both specimens have relatively narrow forewings, almost identical maculation shown by Bode (1953), and similar venation as shown by Ponomarenko (1996) if the anterior branch of M is interpreted as RP1, the posterior branch of M as MA, CuA as MP, and CuP as CuA. The holotype of *R. aequabilis* is also from Schandelah.

***Rasnitsyneura* sp.**
(Figs 6, 7)

Material. Specimens PIN 5552/36, PIN 5552/37, PIN 5552/38, PIN 5552/39, PIN 5552/40; incomplete crumpled forewings; all deposited in PIN.

Locality and horizon. Germany: Schandelah. Early Jurassic (early Toarcian, *boreale* nodule, *Harpoceras falciferum* ammonite zone).

Description. *Specimen PIN 5552/36* (Fig. 6A, B). Forewing 5.7 mm long as preserved (estimated complete length *ca*. 7–7.5 mm), 2.1 mm wide as preserved (estimated complete width *ca*. 2.5). Costal space broadened proximally, distally. Proximal subcostal veinlets bent toward wing apex, simple or with very shallow terminal fork; distal veinlets of Sc, RA mainly once forked. Subcostal space moderately broad distally; crossveins not detected. Sc, RA stout, distally approaching, probably not fused. RA space narrow; crossveins not detected. RP with eight branches, mostly once forked. Three crossveins detected in radial space. MA probably twice forked distally. MP pectinately forked, with three long branches, one of which is deeply forked. CuA pectinately forked, with two very long branches; each branch once or twice shallowly forked. CuP shallowly once forked.

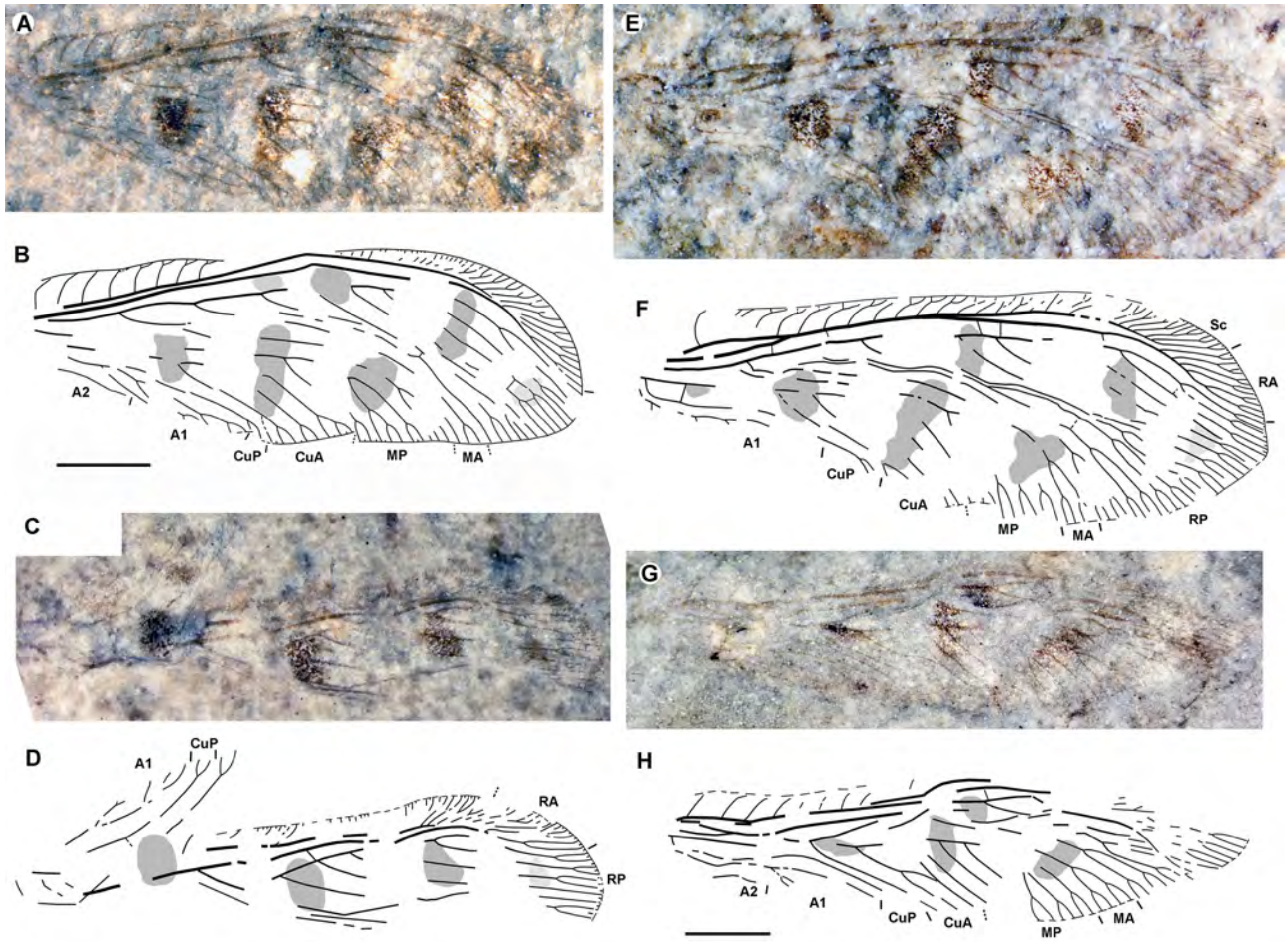

FIGURE 6. *Rasnitsyneura* sp., forewings. **A** and **B**, PIN 5552/36. **C** and **D**, PIN 5552/39. **E** and **F**, PIN 5552/38. **G** and **H**, PIN 5552/40. Scale bars = 1 mm (**A** and **B**, **C**–**H** to same scale).

A1 pectinately branched, probably with three branches. A2 fragmentarily preserved. Maculation: six brown spots medially (different in size), one paler spot apically.

Specimen PIN 5552/39 (Fig. 6C, D). Forewing *ca*. 7 mm long as preserved (estimated complete length *ca*. 7.5 mm), *ca*. 1.5 mm wide as preserved. Costal space broadened distally. Distal subcostal veinlets of Sc, RA mainly once forked. Subcostal space moderately broad. Sc, RA stout, distally approaching, probably not fused. RA space narrow, with one detected crossveins in middle part. RP with five preserved branches, which mainly once forked distally. CuP once shallowly forked. One crossvein between CuA, CuP detected. A1 pectinately branched, with two/three branches. Maculation: three brown spots preserved medially (all rounded, similar in size), one paler spot apically.

Specimen PIN 5552/38 (Fig. 6E, F). Forewing 7.4 mm long as preserved (estimated complete length *ca*. 8 mm), 2.7 mm wide as preserved (estimated complete width *ca*. 3 mm). Costal space relatively narrow, broadened distally. Terminal parts of middle subcostal veinlets strongly bent toward wing apex, with shallow terminal fork; distal veinlets of Sc, RA mostly forked once. Subcostal space narrow as preserved. Sc, RA stout, distally slightly approaching, not fused. RA space narrow; five, irregularly spaced crossveins detected. Anterior trace of RP forked distally, not zigzagged, with probably ten branches. RP1-RP4 dichotomously forked distad outer gradate series; other preserved branches once shallowly forked. One crossvein in radial space detected. Fork of M not preserved. MA dichotomously forked distally (like RP1). MP pectinately forked, with five/six long branches (forked once if preserved). CuA pectinately forked, with two, very long branches. CuP shallowly forked once. One (proximal) crossvein between CuA, CuP detected. A1 pectinately forked (branches incompletely preserved). Maculation: five brown spots medially (different in size), one small spot basally, one paler spot apically.

Specimen PIN 5552/40 (Fig. 6G, H). Forewing 6.7 mm long as preserved (estimated complete length *ca*. 7.5 mm), 1.8 mm wide as preserved (estimated complete width *ca*. 2.5 mm). Subcostal veinlets incompletely preserved, bent toward wing apex. RP1, RP2, MA dichotomously forked distad outer gradate series. MP pectinately forked, apparently with four long branches. CuA pectinately forked, with two, very long branches (one branch deeply

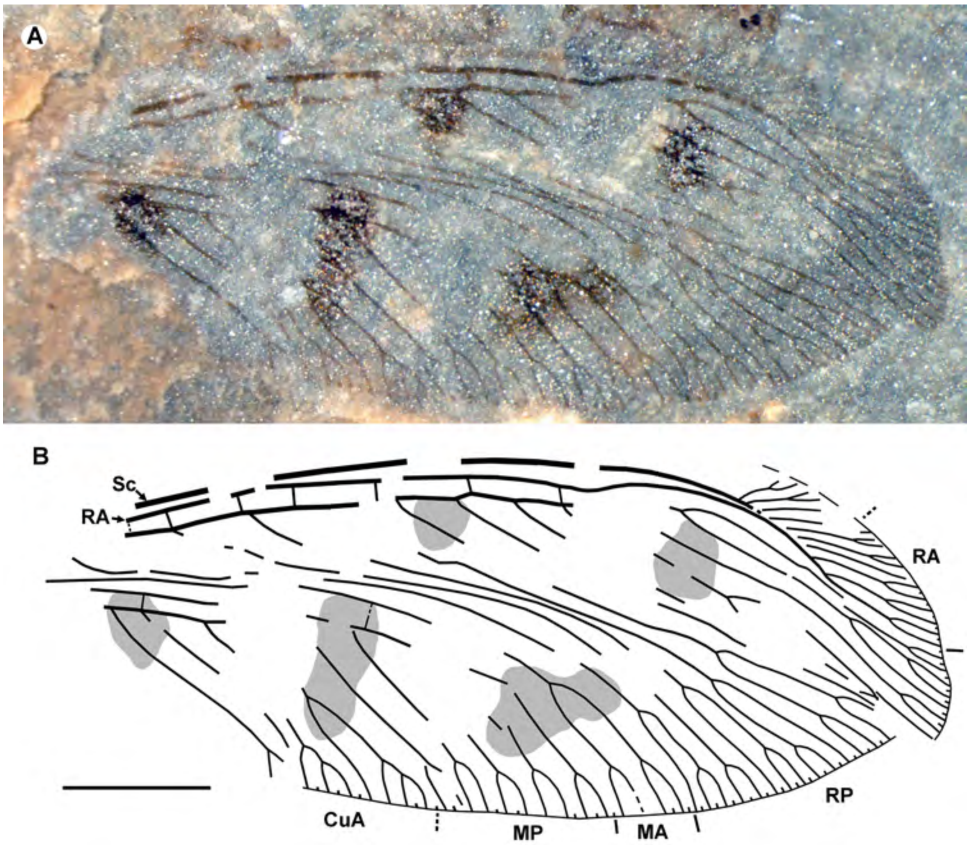

FIGURE 7. *Rasnitsyneura* sp., specimen PIN 5552/37. **A**, Photograph. **B**, Forewing venation. Scale bar = 1 mm (both to same scale).

forked). CuP incompletely preserved, apparently forked once. A1 probably pectinately branched. A2 fragmentarily preserved. Maculation: five brown spots medially (different in size) preserved.

Specimen PIN 5552/37 (Fig. 7). Forewing 6.1 mm long as preserved (estimated complete length *ca*. 7.6–7.8 mm), 2.4 mm wide as preserved (estimated complete width *ca*. 2.7 mm). Costal space preserved only distally. Distal veinlets of Sc, RA forked once. Subcostal space narrow as preserved. Sc, RA stout, distally approaching, probably not fused. RA space narrow; five/six rather regularly spaced crossveins detected. RP with ten branches. RP1, RP3–RP5, RP10 dichotomously forked distad outer gradate series; RP8 dichotomously forked proximad outer gradate series; RP2, RP9 once shallowly forked. MA rather deeply, dichotomously forked. MP pectinately forked, with four long branches (once shallowly forked). CuA incompletely preserved, pectinately forked, with three/four long branches. Maculation: five dark-brown spots medially (different in size).

Remarks. The specimens PIN 5552/36, PIN 5552/38, PIN 5552/39, and PIN 5552/40 may be conspecific and assigned to *Rasnitsyneura aequabilis* as their forewing maculation, size, and preserved venation are similar to those of specimen 5552/34 (however, the number of the RP branches varies, from seven to ten).

Specimen PIN 5552/37 differs from the others by the absence of apical paler spots and by its broader forewing, suggesting that it may not belong to *R. aequabilis*.

Epigambriinae gen. et sp. indet.
(Fig. 8)

Material. PIN 5552/48, deposited in PIN. An incomplete crumpled hind wing.

Locality and horizon. Germany: Schandelah. Early Jurassic (early Toarcian, *boreale* nodule, *Harpoceras falciferum* ammonite zone).

Description. Hind wing 5.8 mm long as preserved (estimated complete length *ca*. 6.2–6.5 mm), 2.3 mm wide as preserved (estimated complete length *ca*. 2.5). Preserved portion of costal space relatively broad; broadened distally. Subcostal veinlets mainly oblique; simple or once shallowly forked medially; once to twice forked distally. Subcostal space rather narrow as preserved. Sc, RA stout. RA space narrow, with three preserved crossveins nearly perpendicular to RA (distal slightly oblique). RP with seven branches. RP1–RP3 deeply dichotomously forked; other branches shallowly forked or their terminations not preserved. MA, MP dichotomously forked. CuA pectinate with at least five branches. CuP not completely preserved, probably few branched. Presumed A1, A2 each shallowly

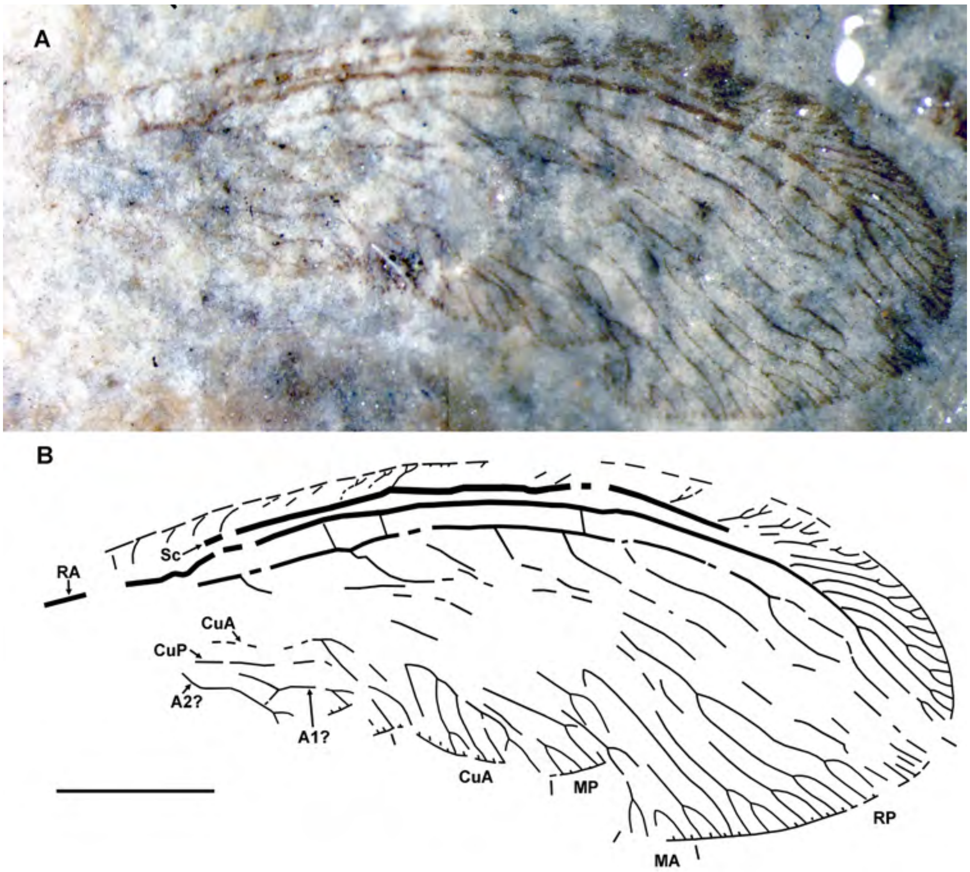

FIGURE 8. Epigambriinae gen. et sp. indet., PIN 5552/48. **A**, Photograph. **B**, Hind wing venation. Scale bar = 1 mm (both to same scale).

forked once (alternatively, A1 dichotomously forked, A2 not preserved). One distal crossvein between presumed A1, A2.

Remarks. The venation of this hind wing is very similar to that of *Epigambria longipennis* and is clearly distinguished from that of *Polyosmylus excelsus* by its dichotomously branched M. Judging from its size, this wing might also belong to *Rasnitsyneura* **gen. nov.**

Discussion

The monophyly of a group comprising Epigambria, Polyosmylus and Rasnitsyneura **gen. nov.**

The genera *Polyosmylus* and *Rasnitsyneura* **gen. nov.** are certainly closely related by their almost identical forewing venations (*cf*. Figs 2, 5). These genera differ only in small details (see the diagnosis of *Rasnitsyneura* **gen. nov.**).

Epigambria longipennis is, however, represented by a hind wing. Although its venation is incomplete and crumpled, it has important similarities to that of an incomplete hind wing of the *Polyosmylus excelsus* holotype, sharing the following character states: (1) apices of the middle subcostal veinlets are bent toward wing apex and some are terminally forked; (2) the RA space is rather narrow, not dilated proximally; (3) there are several crossveins between RA and RP which are more or less perpendicular to them; (4) a single gradate series (although poorly preserved); (5) a similar forking of RP branches; (6) a pectinate CuA; (7) and are of similar size. No strongly dissimilar character states are found in these species. Character state (4) is only shared by these genera among Ithonidae *s.l.* (see below).

As well as these genera, there is an isolated crumpled hind wing described above as Epigambriinae gen. et sp. indet. whose venation is very similar to that of *Epigambria*. This wing shares all of the character states mentioned above except (4), probably due to poor preservation.

Therefore, we may reasonably assume that all three of these genera form a single suprageneric taxon: *Polyosmylus* associated with *Rasnitsyneura* **gen. nov.** by forewing venation and *Epigambria* associated with *Polyosmylus* by hind wing venation.

Nevertheless, the venation of the type genus *Epigambria* should also be compared with that of other families to which it may theoretically belong.

The hind wing venation of *Epigambria* belongs to the so-called 'hemerobiid type', an informal group comprising taxa with hind venation similar to that of Hemerobiidae (Hemerobiidae, Permithonidae, Nevrorthidae, Sisyridae, Dilaridae, Berothidae, Prohemerobiidae, and Ithonidae *s.l.*). The venations of most of these families are strongly dissimilar to that of *Epigambria* by their general configuration as well as by some individual characters. In particular, CuA of Nevrorthidae and Berothidae is long, running near and parallel to the hind margin, with short branches. The hind wings of the typical extant and Cretaceous Sisyridae are also greatly distinguished from those of *Epigambria* by their relatively reduced venation (two to three branches of RP) and their strongly dilated basal RA space (see Perkovsky & Makarkin, 2015; Yang *et al*., 2018). Although the mid-Cretaceous Paradoxosisyrinae have more complex venation, they have few crossveins between RA and RP (see Khramov *et al*., 2019: Figs 1F, 5B, 6D). Of Dilaridae, the hind wing venation of Dilarinae is somewhat similar to that of *Epigambria*, however, their Sc and RA are widely separated distally, and the radial crossveins are irregularly arranged.

The hind wing venation of the other five families is more or less similar to that of *Epigambria*, differing only in details.

The hind wings of the Permian/Triassic Permithonidae occur rarely. *Permopsychops saurensis* Novokshonov & Vilesov in Vilesov & Novokshonov, 1994 and *Permorapisma fragmentatum* Vilesov & Novokshonov, 1994 from the late Permian of Karaungir (Kazakhstan) are the best preserved among them. These have strongly oblique crossveins between RA and RP, and radial crossveins arranged in at least two gradate series.

The hind wings of Hemerobiidae have few (one to three) or no crossveins between RA and RP, even in such a densely veined genus as *Drepanepteryx* Leach, 1815; the RA space is usually dilated basally; and CuA is configured differently (see *e.g*., Oswald, 1993: Fig. 183).

The family Prohemerobiidae is poorly known. Here, we consider it to include only the heterogeneous Jurassic genus *Prohemerobius* Handlirsch, 1906, which strongly needs revision. Its type species (*P. dilaroides* Handlirsch, 1906) is represented by a forewing (see Ansorge & Obst, 2015: Fig. 19d). The holotypes of *Prohemerobius liasinus* Handlirsch, 1906 (certainly), and *P. latus* Handlirsch, 1920 (probably) are represented by hind wings; their prohemerobiid affinities, however, need confirmation. The vast majority of Prohemerobiidae fossils are isolated wings. The first photograph of a whole specimen was published by Ilger (2014: Fig. 27) as "Chrysopidae indet." (see Fig. 9A). This specimen is very important as its forewing venation is similar to that of the type species, and therefore its hind wing venation should be also similar. Also, several unreported hind wings are known; one is shown here for the first time in Fig. 9B.

In general, the hind wing venation of Prohemerobiidae is similar to that of Hemerobiidae, but differs from that of *Epigambria* in particular by having few crossveins (two to three) between RA and RP, and a basally dilated RA space (Fig. 9).

The hind wing venation of Ithonidae *s. str*. (*i.e*., excluding those genera that previously constituted Polystoechotidae) differs from that of *Epigambria* by the presence of numerous, irregularly spaced crossveins in the radial space, and Sc and RA are clearly separate distally.

The hind wing venation of the polystoechotid genera-group of Ithonidae *s.l.* is very similar to that of *Epigambria* but differs from it by the presence of two gradate series of crossveins.

The systematic position of Epigambriidae and its status

The forewing venation of *Polyosmylus* and *Rasnitsyneura* **gen. nov.** is most similar to that of the polystoechotid genera-group of Ithonidae *s.l.* They share with this group practically all of the diagnostic character states of the former family Polystoechotidae except the absence of nygmata (see Archibald & Makarkin, 2006). However, the distal nygma is also absent in both species of extant *Polystoechotes* Burmeister, 1839, and has not been detected in the Jurassic *Jurapolystoechotes* Ren *et al*., 2002 (see Fig. 10B).

The hind wing venation of Epigambriidae is not informative and is more or less similar to that of some families, including Ithonidae *s.l.*, Prohemerobiidae, Permithonidae and Hemerobiidae (see above). But if we consider both fore- and hind wings together, only the polystoechotid genera-group of Ithonidae *s.l.* may be a potential candidate for these genera, or perhaps as close relatives to this group if Epigambriidae is interpreted as a family. At least, they certainly belong to ithonoids.

The Ithonoidea are a diverse group with a long paleontological history and poorly defined families. A phylogenetic study of extant ithonoids (Ithonidae *s.l.*) indicates that this group is divided into two clades, one composed of the three Australian genera of Ithonidae, and the other composed of all genera of Polystoechotidae and Rapismatidae, and some Ithonidae, *i.e*., Ithonidae is then paraphyletic (Winterton & Makarkin, 2010). Later, Zheng *et al*. (2016a) identified three genus-groups within Ithonidae *s.l.*, *i.e*., the ithonid, polystoechotid, and the heterogeneous rapismatid groups. Makarkin *et al*. (2014) provided a list of fossil species assigned to Ithonidae *s.l.* to that date. A revision of Ithonoidea is necessary to clarify this situation. Until accurate descriptions of the Jurassic and Cretaceous ithonidoids are done, a satisfactory classification of this group is impossible, as relatively few extant taxa are relicts of the Mesozoic.

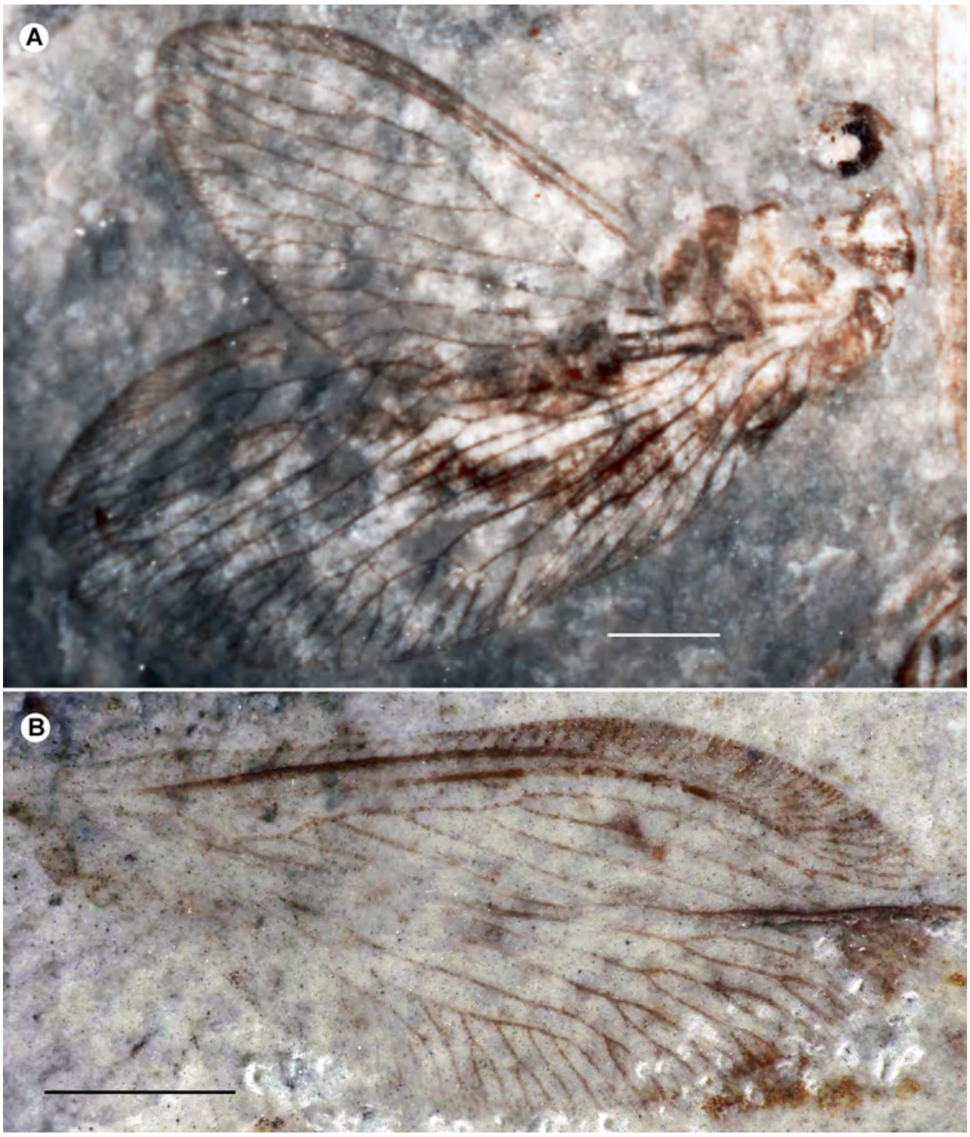

FIGURE 9. The Early Jurassic (early Toarcian) Prohemerobiidae. **A**, A specimen very similar to *Prohemerobius dilaroides*, the type species of the family, from Schandelah (Germany), coll. Thilo Lampe, Vechelde (Germany). **B**, A hind wing of presumed Prohemerobiidae from Grimmen (Germany), LGA 2310. Scale bars = 1 mm.

Nevertheless, the strong similarity in hind wing venation between an undescribed Early Jurassic taxon from Sogyuty (Fig. 10A), the Middle Jurassic *Jurapolystoechotes* (Fig. 10B) and the extant genus *Polystoechotes* (the type genus of Polystoechotidae) indicates that this lineage is very old and has conservative venation. Therefore, this lineage may be monophyletic that include also other genera: *Puripolystoechotes* Yang *et al*., 2019 (late Middle–early Late Jurassic of Daohugou, China); *Palaeopsychops* Andersen, 2001 (early Eocene of Europe and North America: Archibald & Makarkin, 2006); and two extant genera (*Platystoechotes* Carpenter, 1940 and *Fontecilla* Navás, 1932). Unnamed genera of similar appearance are known from the Early Cretaceous of Baissa (Transbaikalian Russia) and the Yixian Formation, China (Makarkin *et al*., 2012: Fig. 3E; pers. obs.)

Taxa resembling extant Ithonidae are unknown from the Early Jurassic. *Guithone* Zheng *et al*. (2016a) from the late Middle–early Late Jurassic of Daohugou (China) is believed to be the earliest known true Ithonidae. However, this fossil is poorly preserved and its forewing venation differs from that of extant taxa (*e.g*., the humeral veinlet is not branched and recurrent and CuA is dichotomously branched). An undescribed genus from the Lower Cretaceous Yixian Formation (China) is apparently the single fossil taxon similar to true (extant Australian) Ithonidae (pers. obs.). Epigambriidae is dissimilar in venation to this and the extant Australian genera of Ithonidae.

Other fossil ithonoids which differ in some important ways from extant Ithonidae (including Rapismatidae) include undescribed numerous and diverse taxa from Daohugou (Xu *et al*., 2021; VNM, pers. obs.); three genera from the Late Jurassic of Karatau (Kazakhstan) described

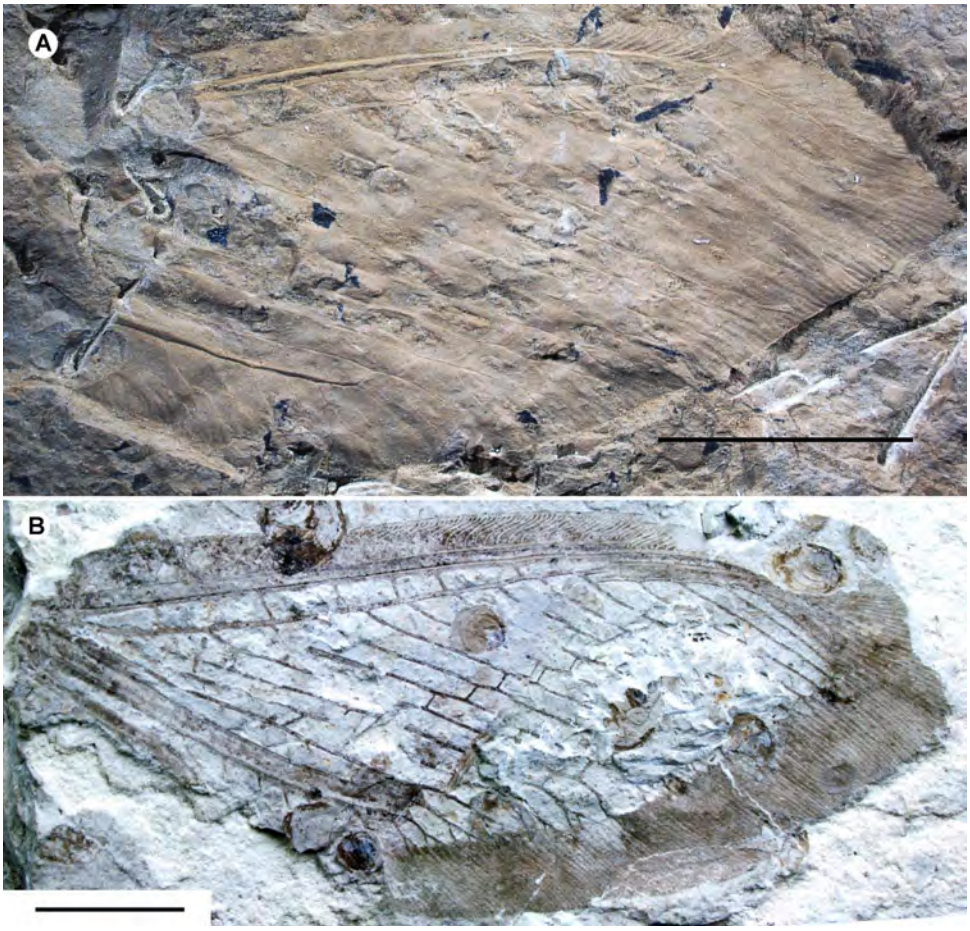

FIGURE 10. The hind wings of the Jurassic Polystoechotidae. **A**, An undescribed species of Polystoechotidae from the Early Jurassic (Sinemurian/ Hettangian) of Sogyuty (Kyrgyzstan), incorrectly assigned to *Mesopolystoechus apicalis* Martynov, 1937 by Martynova (1949: Fig. 8), PIN 371/323. **B**, The holotype of *Jurapolystoechotes melonolomus* Ren *et al*., 2002 from the late Middle Jurassic / early Late Jurassic of Daohugou (China), CNU-NEU-NN99021. Scale bars = 5 mm.

by Panfilov (1980); taxa from the Early Cretaceous of the Yixian Formation, China (see Makarkin *et al*., 2012) partly described by Zheng *et al*. (2016b); *Principiala* Makarkin & Menon, 2007 from the Early Cretaceous of Brazil and England; *Burmithone* Lu *et al*., 2017 from the mid-Cretaceous Burmese amber; *Allorapisma* Makarkin & Archibald, 2009 from the early Eocene of North America, and *Elektrithone* Makarkin *et al*., 2014 from late Eocene Baltic amber. This group of genera needs revision for better understanding of their relationships; at least Epigambriidae are more distantly related to these diverse ithonoids than to the polystoechotid genus-group.

Thus, we find that Epigambriidae are most closely related to the polystoechotid genus-group of Ithonidae *s.l*. However, it is currently difficult to evaluate the status of this group, as a family on its own or as a subfamily of Ithonidae *s.l*. We tend to consider it a subfamily, as it differs from other taxa of the family only by the presence/ absence, number and orientation of crossveins.

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