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Revision of some damsel-dragonflies (Odonata, Liassophlebiidae and Anglophlebiidae new family) from the Triassic/Jurassic of England and Antarctica

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Abstract.—Fossil insects from the Triassic-Jurassic boundary of England could provide an important resource for investigating the severity of extinction events in the terrestrial realm of the uppermost Triassic. However, the fossil record is poorly understood for this period even though there are abundant historical collections. Many of these collections are still in need of taxonomic revision before they can be used to reconstruct past entomofaunas and make inferences about diversity change through time. This paper is part of a larger project to revise the taxonomy of insects across the Triassic-Jurassic boundary of England to better understand changes in insect diversity through the Triassic-Jurassic boundary and associated extinction period. Herein, the damsel-dragonfly family Liassophlebiidae Tillyard, 1925 is revised and an additional specimen from the Early Jurassic of Antarctica is included. *Rossiphlebia* new genus is erected for *Liassophlebia jacksoni* Zeuner, 1962; *L. batheri* Tillyard, 1925 is considered nomen dubium and another specimen originally attributed to *L. batheri* is identified as *L. withersi* Tillyard, 1925. *Liassophlebia* (?) *clavigaster* Tillyard, 1925 and *L.* (?) *hopei* (Brodie, 1845) are considered incertae sedis at the generic level. *Liassophlebia gigantea* Zeuner, 1962 is based on a fragmentary specimen but has several unique key characteristics. We redescribe it in *Anglophlebia* new genus and tentatively in Anglophlebiidae new family in Heterophlebioptera. Also discussed are *L. magnifica* Tillyard, 1925, *L. withersi*, and *L. pseudomagnifica* Whalley, 1985, which are redescribed with updated figures. *Caraphlebia antarctica* Carpenter, 1969 was originally described from the Early Jurassic of Antarctica as being closely related to *Liassophlebia*; it is herein confirmed in Selenothemistidae Handlirsch, 1939.

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Introduction

The Late Triassic saw several periods of major biodiversity turnover, culminating in the End Triassic Extinction (ETE), described as one of the five largest mass extinction events in Earth history. Studies have suggested that >50% of genera from marine and terrestrial environments (Deenan et al., 2010), 23.4% of marine families, and 21.7% of terrestrial families (McGhee et al., 2004) went extinct (although insects were not counted in these studies). Nevertheless, there are current discussions on the severity of this event and whether it was one event or drawn out throughout the Rhaetian. The effects of this period on insect diversity are not well studied and large-scale datasets of insect diversity through time tend not to show an extreme event at the Triassic-Jurassic Boundary (TJB) (see Nicholson et al., 2015; Condamine et al., 2016). This paper is part of a larger study investigating the changes in insect diversity across the TJB to assess the impact of the ETE on insect diversity. Because there are few currently available rich insect outcrops, a large part of this project is the taxonomic revision of historical fossil insect collections from the Late Triassic to Early Jurassic at the species level to bring the taxonomy to current understanding. Herein, we revise Liassophlebiidae Tillyard, 1925, a family of damsel-dragonflies known from the Late Triassic and Early Jurassic of Europe, Central Asia, China, and Antarctica.

Liassophlebiidae is a small extinct family of damsel-dragonflies known from the early Mesozoic of western Europe, Central Asia, and Antarctica described in the suborder Epiprocta, which contains the extant dragonflies, similar in form to the other extant odonate suborder Zygoptera (damselflies). Most species are described from isolated wings or abdominal segments of adults and there are no known larval specimens, although it is difficult to compare adult and larval fossil specimens because they are so different morphologically. Only *Liassophlebia* Tillyard, 1925 and *Petrophlebia* Tillyard, 1925

(type species *P. anglicana* Tillyard, 1925) were included in the family by Tillyard (1925). *Liassophlebia* originally comprised four species based on wings: *L. magnifica* Tillyard, 1925, *L. batheri* Tillyard, 1925, *L. withersi* Tillyard, 1925, and *L. westwoodi* (Hagen, 1850), and two possible species based on partial abdomens: *L.* (?) *clavigaster* Tillyard, 1925 and *L.* (?) *hopei* (Brodie, 1845). *Liassophlebia westwoodi* was described from a specimen previously figured by Brodie (1845, pl. 10, fig. 8) and named *Heterophlebia westwoodi* by Hagen (1850, p. 359); it was later transferred to *Tarsophlebia* Hagen, 1866 by Hagen (1866). *Liassophlebia* (?) *hopei* was described from a specimen figured and named *Libellula hopei* by Brodie (1845, pl. 10, fig. 3); it was later transferred to *Heterophlebia* Westwood, 1849 by Selys-Longchamps and Hagen (1850) and then '(Anisozygopteron?)' by Handlirsch (1906). *Petrophlebia* was transferred to Architemistidae Tillyard, 1917 by Fraser (1957) and then to Campterophlebiidae Handlirsch, 1920 by Nel et al. (1993). Although Bechly (2016) proposed to transfer it back to Architemistidae, its position in the Campterophlebiidae was confirmed by revision of the family by Kelly and Nel (2017).

The diagnosis of Liassophlebiidae was slightly emended by Zeuner (1962) to include species with a discoidal cell closed basally. *Petrophlebia anglicanopsis* Zeuner, 1962, *Liassophlebia jacksoni* Zeuner, 1962, and *L. gigantea* Zeuner, 1962 were also described. Additional specimens were identified as *L. magnifica* from the Jackson collection of the lower Lias of Dorset. The Jackson collection was re-examined by Whalley (1985) who altered some of Zeuner's species descriptions, transferred *P. anglicanopsis* to *Liassophlebia* and described *L. pseudomagnifica* Whalley, 1985 from one of Zeuner's *L. magnifica* specimens. *Liassophlebia anglicanopsis* was considered an uncertain taxon in Liassophlebiidae by Nel et al. (1993).

Additional genera were included from continental Europe, Central Asia, China, and Antarctica, which are not known from the British deposits: (1) *Caraphlebia* Carpenter, 1969 from South Victoria Land, Antarctica was considered possibly referable to Turanothemistidae Pritykina, 1968 by Nel et al. (1993) but was transferred to Selenothemistidae Handlirsch, 1939 by Bechly (2016); (2) *Ferganophlebia* Pritykina, 1970 from the Early Jurassic of Kyrgyzstan; (3) *Paraliassophlebia* Hong, 1983 from the Middle Jurassic of China was considered as Epiprocta incertae sedis by Nel et al. (1993) but was tentatively transferred to Selenothemistidae by Bechly (2016); and (4) *Grimmenopteron* Ansorge, 1996 and *Bavarophlebia* Nel and Petrulevičius, 2005, both from the Toarcian of Germany, each with one associated species. A further specimen was identified as *Liassophlebia* sp. from the Early Jurassic of Austria by Kohli et al. (2016).

Liassophlebiidae was reported to be known from the Early Jurassic, Hettangian-Toarcian, by Nicholson et al. (2015, supplementary data) but this disregards the four species described by Tillyard (1925) from the Penarth Group of Strensham, England, which is Late Triassic: Rhaetian. This locality was reported as Rhaetian by Nicholson et al. (2015) for other families but Tillyard's book was not cited so these species must have been missed. The inclusion of this omission changes the dynamics of the family across the TJB because including these four species extends the family to before the boundary, indicating that the family survived the extinction event rather than originating in the subsequent stage.

Geological setting

The specimens discussed herein are from the Late Triassic to Early Jurassic of England (Fig. 1). They are mostly found in shallow marine limestones; these rocks are fine-grained enough to generally preserve insects well. The living insects were not necessarily associated with the marine environment but were transported from their terrestrial or freshwater habitat through fluvial systems to their final deposition in the marine shallows. The Late Triassic material was collected from bed 18 of the Penarth Group at the historical locality of Strensham in the county of Worcestershire (Brodie, 1845) and was updated to current geological nomenclature by Kelly et al. (2017) who found the horizon to lie within the Lilstock Formation, Cotham Member, which is Rhaetian in age. The Early Jurassic fossils were collected from three localities Binton in the county of Warwickshire, another historical locality, exposed several insect-bearing horizons, which Brodie (1845) originally described and Kelly et al. (2018) found to correspond to the Planorbis Chronozone (Blue Lias Formation, Wilmcote Limestone Member) of the Hettangian. The other two localities—Stonebarrow and Catherston Lane—are very similar and are found at or near the Dorset coast. Stonebarrow is still actively collected from and Catherston Lane was active for a short time during the construction of the Charmouth bypass. There are several insect-bearing horizons; the insects discussed herein were collected from the 'flatstones' (bed 83/83h), which is a local name for a horizon found in the Obtusum Chronozone, Obtusum Subchronozone (Charmouth Mudstone Formation, Black Ven Mudstone Member) (Page, 2010; Kelly et al., 2017).

Caraphlebia antarctica Carpenter, 1969 was described from the Jurassic 'Mawson Tillite' on Carapace Nunatak, South Victoria Land, Antarctica (Carpenter, 1969). Mawson Tillite is a historical name for the Mawson Diamictite of the Ferrar Group (Balance and Watters, 1971), now known as the Mawson Formation (Elliot and Hanson, 2001). Based on U/Pb and $^{40}Ar/^{39}Ar$ analysis of volcanic rocks in North Victoria Land, Musumeci et al. (2004) concluded that the pyroclastic event that led to the formation of the Prebble, Mawson, and Exposure Hill formations occurred between the Hettangian and lower Pliensbachian. However, given the sizable hiatus of Lower Jurassic rocks in South Victoria Land (Ribecai, 2007; Schöner et al., 2011), any fossils from the Mawson Formation in this area are likely to have been deposited later within this estimation.

The Mawson Formation is unconformably overlain by the Carapace Sandstone Formation, which is not present in all areas (Ribecai, 2007). However, the insect was collected on Carapace Nunatak where the formation is present and has been estimated to have been deposited during the upper Sinemurian to lower Pliensbachian (Ribecai, 2007). This means that the age estimation for the Mawson Formation in this area could lie within the later Hettangian to early late Sinemurian, making them of similar age to the English specimens.

Materials and methods

Collections of English material were examined from The Natural History Museum, London (NHMUK), the National Museum of

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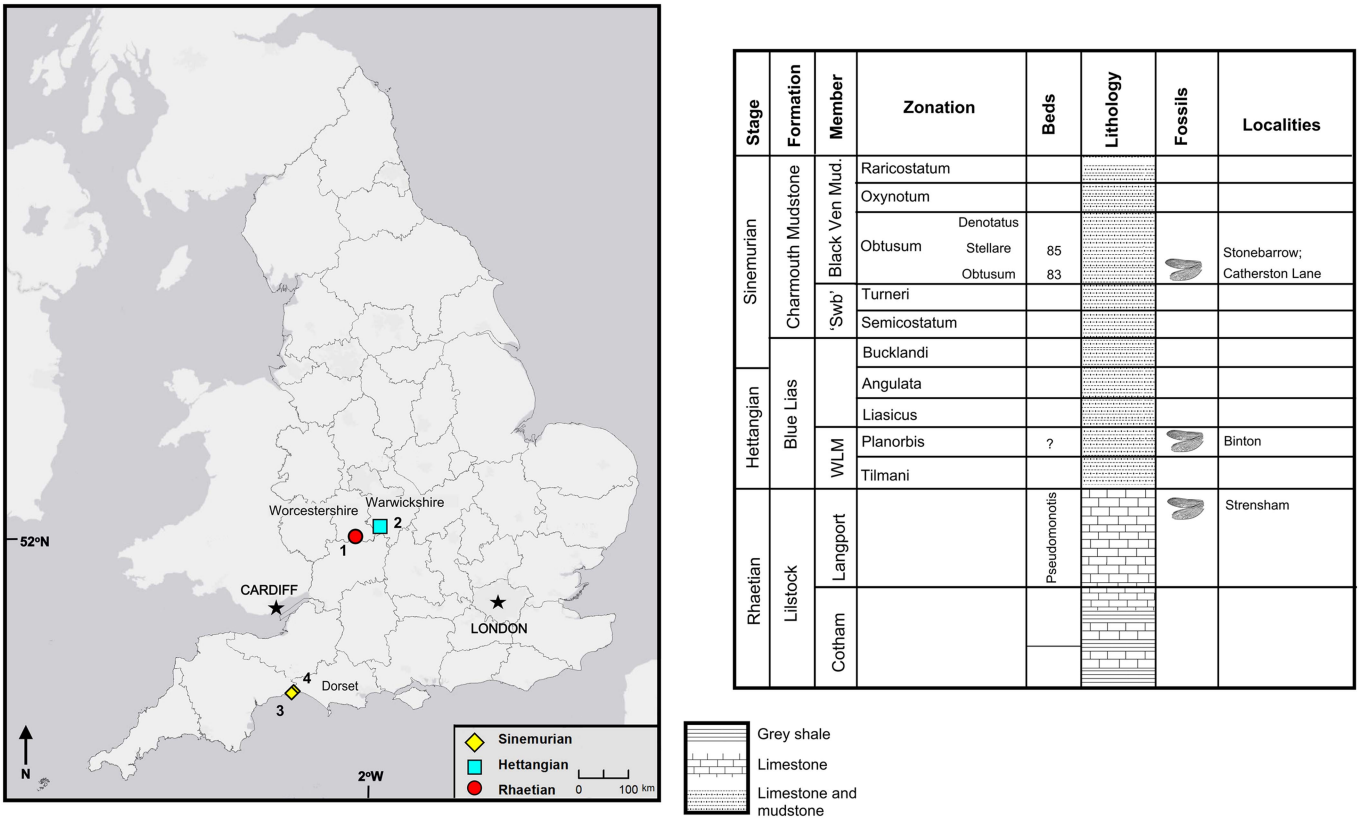

Figure 1. Locality map and stratigraphic chart for English specimens described herein. 1 = Strensham, Gloucestershire; 2 = Binton, Warwickshire; 3 = Stonebarrow, Dorset; 4 = Catherston Lane, Dorset; 'Swb' = 'shales-with-beef'; WLM = Wilmcote Limestone Member.

Wales, Cardiff (NMW), and the Oxford University Museum of Natural History (OUMNH). Photographs of the Antarctic specimen were examined from the National Museum of Natural History (United States National Museum), Smithsonian Institution, Washington, DC (USNM). All specimens from the English Midlands (Warwickshire and Worcestershire) were collected by the Rev. Peter Bellinger Brodie in the nineteenth century except for the OUMNH specimen, which was collected by the Rev. Frederick William Hope; all of the Dorset specimens were collected by James Frederick Jackson in the twentieth century except for the one collected from Catherston Lane, which was collected by a team of volunteers led by Kevin Page.

All specimens (except the holotype of *Caraphlebia antarctica*) were examined in person by the primary author and remotely via photographs by the co-author. Specimens were examined using the microscope equipment available at each museum and photographs were taken with a stand supporting a Nikon D3300 camera with AF-S Micro Nikkor 40-mm macrolens. Measurements were taken from photographs using the software package ImageJ (National Institutes of Health, ver. 1.51) and the scale of each image was calibrated using a standard ruler. Taxonomic figures were constructed in DrawPlus (Serif, version X8).

Venation nomenclature is based on the interpretations of Riek and Kukalová-Peck (1984), as modified by Nel et al. (1993) and Bechly (1996). Abbreviations are as follows: AA = anterior anal; AP = posterior anal; Arc = arculus; Ax = primary antenodal crossvein; Ax0 = first branch of primary antenodal crossvein; Ax1 = second branch of primary antenodal crossvein; Ax2 = third branch of primary antenodal crossvein; C = costal vein; Cu = cubitus; CuA = anterior cubitus; CuA1 = distal branch of anterior cubitus; CuA2 = proximal branch of anterior cubitus; CuP = posterior cubitus; DC = discoidal cell; Ht = hypertriangle; IM = intercalary medial vein; IR = intercalary radial vein; IR1 = intercalary radial vein 1; IR2 = intercalary radial vein 2; MA = anterior median; MA1 = anterior branch of anterior median; MA2 = posterior branch of anterior median; MP = posterior median; N = nodus; 'O' = oblique vein; Pt = pterostigma; RA = anterior radius; RP = posterior radius; RP1 = first branch of posterior radius; RP2 = second branch of posterior radius; RP3/4 = third/fourth branch of posterior radius; ScP = posterior subcostal; T = triangle. The higher classification of fossil and extant Odonatoptera is based on the phylogenetic system of Bechly (1996, 2016).

Repositories and institutional abbreviations.—NHMUK, The Natural History Museum, London, UK; NMW, National Museum of Wales, Cardiff, UK; OUMNH, Oxford University Museum of Natural History, Oxford, UK; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Systematic paleontology

Order Odonata Fabricius, 1793
Suborder Epiprocta Lohmann, 1996
Superfamily Heterophlebioidea Needham, 1903
Family Liassophlebiidae Tillyard, 1925

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Type genus.—*Liassophlebia* Tillyard, 1925.

Other genera.—*Ferganophlebia* Pritykina, 1970; *Grimmenopteron* Ansorge, 1996; *Bavarophlebia* Nel and Petrulevičius, 2005; *Rossiphlebia* new genus.

Emended diagnosis.—Discoidal cell basally closed in hindwing, sometimes with incomplete veinlet between 'hypertriangle' and discoidal triangle; discoidal cell open in forewing; subdiscoidal cell closed in both; subdiscoidal cell widened in forewing, with convex posterior margin; MP + CuA with very strong posterior curve in discoidal cell, so that subdiscoidal space is rather transverse; hindwings with unicellular anal loop enlarged; few, if any, antefurcal crossveins between RP and MA from arculus to midfork; no secondary antenodal crossveins between C and ScP (first row).

Remarks.—A nearly straight, long secondary vein in the postdiscoidal space slightly distal of the triangle is present in *Liassophlebia* and *Rossiphlebia* n. gen., but this vein is absent in *Grimmenopteron*, *Ferganophlebia*, and *Caraphlebia*.

Genus *Liassophlebia* Tillyard, 1925

Type species.—*Liassophlebia magnifica* Tillyard, 1925.

Emended diagnosis.—Cubito-anal area of hindwing large and broad, with 5 or 6 rows of cells between CuA and posterior wing margin; subdiscoidal space not divided into two large cells by anterior branch of AA that ends on CuA, but divided into small cells; wings very large.

Liassophlebia magnifica Tillyard, 1925

1925 *Liassophlebia magnifica* Tillyard, p. 15, pl. 1, fig. 3, pl. 2, fig. 4, text-figs. 3, 4.
1939 *Liassophlebia magnifica*; Handlirsch, p. 23.
1957 *Liassophlebia magnifica*; Asahina, p. 1, figs. 1, 3.
1962 *Liassophlebia magnifica*; Zeuner, p. 162, pl. 27, fig. 1.
1993 *Liassophlebia magnifica*; Nel et al., p. 139, fig. 107.
1995 *Liassophlebia magnifica*; Bechly, p. 16.
1996 *Liassophlebia magnifica*; Trueman, p. 69.
2003 *Liassophlebia magnifica*; Fleck et al., p. 56, 86.
2003 *Liassophlebia magnifica*; Rehn, p. 212.

Holotype.—NHMUK I.6648/I.10462 (Fig. 2), 'Insect limestone' of the Planorbis Chronozone (Lias Group, Blue Lias Formation, Wilmcote Limestone Member); Early Jurassic, Hettangian; Binton, Warwickshire. Female according to lack of anal angle and anal triangle.

Emended diagnosis.—Female hindwing, anal branch forks into subdiscoidal space forming distinct structure (also seen in *Liassophlebia pseudomagnifica*, but see below).

Remarks.—The specimen NHMUK I.11089 was also attributed to this species (Tillyard, 1925) but only a partial abdomen is preserved and so it is impossible to link it with any species described from wings. Zeuner (1962) also attributed NHMUK In.64000, In.59106, and In.49213 to this species, but the first is the holotype of *L. pseudomagnifica* (see below); the second is the holotype of *Hypsothemis fraseri* Whalley, 1985, and the last is a fragment of the anterior margin of a wing and is not identifiable at the species level.

Liassophlebia withersi Tillyard, 1925

1925 *Liassophlebia withersi* Tillyard, p. 17, pl. 3, fig. 8.
1939 *Liassophlebia Withersi*; Handlirsch, p. 23.
1962 *Liassophlebia withersi*; Zeuner, p. 164.
1993 *Liassophlebia withers*; Nel et al., p. 142, fig. 106.

Holotype.—NHMUK I.10697 (Fig. 3), 'Insect limestone' of the Pseudomonotis beds (Penarth Group, Lilstock Formation); Late Triassic, Rhaetian; Strensham, Worcestershire.

Diagnosis.—Similar to *Liassophlebia magnifica* but smaller (distance from arculus to distal acute angle of discoidal cell = 5.6 mm, compare to >6 mm in *L. magnifica*). Two anal cells, compared to three in *L. magnifica*.

Additional material.—NHMUK I.10528, from Strensham.

Remarks.—The two specimens discussed here are forewings, whereas the other described species are known mostly from hindwings, except for the partial forewing in *Liassophlebia magnifica*. The differences between this partial forewing and that of the holotype of *L. withersi* are few and better-preserved specimens could lead to the synonimization of this species with *L. magnifica*, or with one of the other species currently only described from hindwings. NHMUK I.10528 is a forewing originally attributed to *L. batheri* (which is herein considered nomen dubium, see below). Upon examination, it is clear that there are few differences between this specimen and the holotype of *L. withersi* except for the aberration in the anal vein of the holotype NHMUK I.10697 and an additional crossvein in the area immediately basal to the subdiscoidal cell. There is also a size difference; NHMUK I.10697 is 10.1 mm in width when measured level with the distal point of the discoidal triangle, and I.10528 is 11.3 mm. The distance from the distal point of the discoidal triangle to the point at which the arculus meets the radial vein in I.10697 is 5.1 mm and in I.10528 is 6.4 mm. Upon further material being described, they might be recognized as separate species, but there is little justification to split them with the evidence available.

Liassophlebia pseudomagnifica Whalley, 1985

1962 *Liassophlebia magnifica* Tillyard; Zeuner, p. 162, pl. 27, fig. 1.
1985 *Liassophlebia pseudomagnifica* Whalley, p. 120, fig. 5a, b.
1993 *Liassophlebia pseudomagnifica*; Nel et al., p. 139, figs. 104, 105.
2003 Liassophlebia pseudomagnifica; Fleck et al., p. 56.

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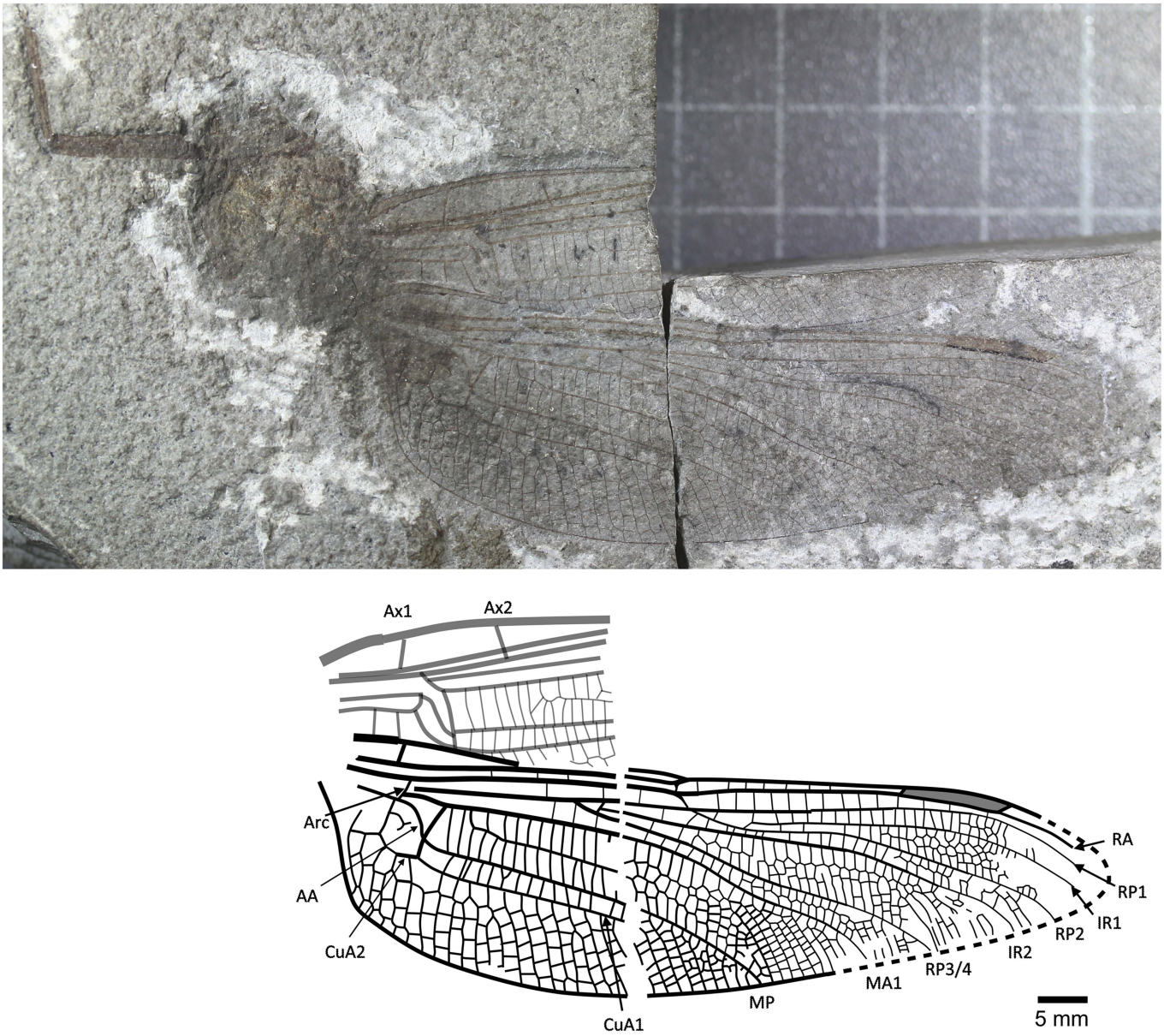

Figure 2. Holotype of *Liassophlebia magnifica* Tillyard, 1925 (NHMUK I.6648), Binton, Warwickshire (Hettangian), photograph and reconstruction. AA = anterior anal; Arc = arculus, Ax1 = second branch of primary antenodal crossvein; Ax2 = third branch of primary antenodal crossvein; CuA1 = distal branch of anterior cubitus; CuA2 = proximal branch of anterior cubitus; IR1 = intercalary radial vein 1; IR2 = intercalary radial vein 2; MA1 = anterior branch of anterior median; MP = posterior median; RA = anterior radius; RP1 = first branch of posterior radius; RP2 = second branch of posterior radius; RP3/4 = third/fourth branch of posterior radius.

Holotype.—NHMUK In.64000 (Fig. 4), 'Flatstones' (bed 83) of the Obtusum Chronozone, Obtusum Subchronozone (Lias Group, Charmouth Mudstone Formation, Black Ven Mudstone Member); Early Jurassic, lower Sinemurian; Stonebarrow, Dorset.

Diagnosis.—Hindwing anal branch forking into subdiscoidal space similar to that seen in *Liassophlebia magnifica*; anal angle and triangle present.

Description.—See previous redescription by Nel et al. (1993).

Remarks.—This species was split from *Liassophlebia magnifica* based on a difference in the number of rows of cells between 'M and Cu' (Whalley, 1985), but it is clear from re-examination of the types that the numbers of rows are the same in the two specimens. Also, the peculiar shape of the anal vein in the subdiscoidal space is shared by *L. magnifica* and *L. pseudomagnifica*; this shape is not seen in any other species of liassophlebiid. The main differences between the two types of *L. magnifica* and *L. pseudomagnifica* are in the shape of the anal area, which is related to sexual dimorphism (presence of an anal angle and triangle in males), present in all Epiprocta (= 'Anisozygoptera' + Anisoptera). Another difference concerns the supplementary longitudinal vein in the basal part of the postdiscoidal area that begins three cells distal of the discoidal triangle in *L. magnifica* whereas it begins very close to it in *L. pseudomagnifica*. This difference could be due to intraspecific

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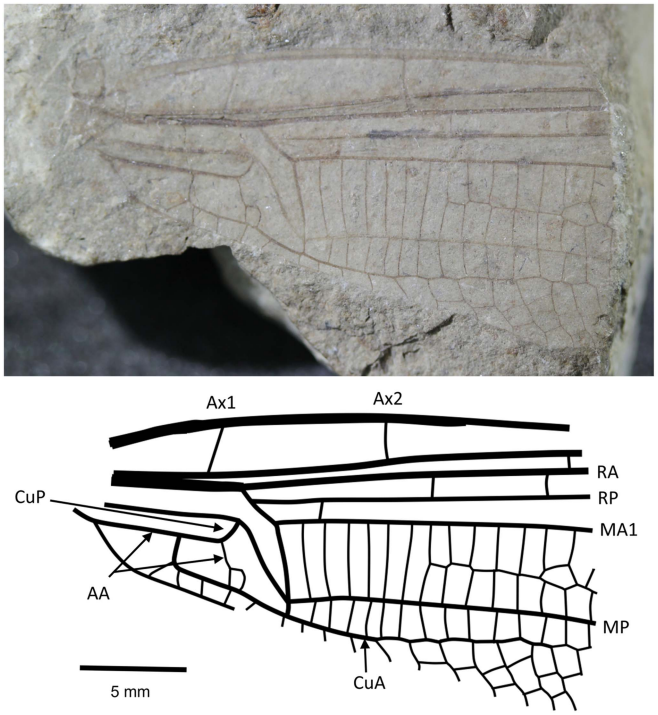

Figure 3. Holotype of *Liassophlebia withersi* Tillyard, 1925 (NHMUK I.10697), Strensham, Worcestershire (Rhaetian), photograph and reconstruction. AA = anterior anal; Ax1 = second branch of primary antenodal crossvein; Ax2 = third branch of primary antenodal crossvein; CuA = anterior cubitus; CuP = posterior cubitus; MA1 = anterior branch of anterior median; MP = posterior median; RA = anterior radius; RP = posterior radius.

variation. There is no way to determine whether they belong to the same species until better preserved specimens are found.

Liassophlebia batheri Tillyard, 1925, nomen dubium

1925 *Liassophlebia batheri* Tillyard, p. 16, pl. 2, figs. 5, 6, pl. 3, fig. 7.
1939 *Liassophlebia batheri*; Handlirsch, p. 23.
1993 *Liassophlebia batheri*; Nel et al., p. 142.

Holotype.—NHMUK I.10434/10435 (Fig. 5), 'Insect limestone' of the Pseudomonotis beds (Penarth Group, Lilstock Formation); Late Triassic, Rhaetian; Strensham, Worcestershire.

Remarks.—The holotype of this species is referable to Liassophlebiidae based on similarity to the holotype of the type species but there are few other diagnostic characters to separate this specimen from other liassophlebiids from the UK. Additionally, there are no comparable characters between this specimen and the forewing specimen previously attributed to this species, so it is impossible to say whether they are the same species. NHMUK I.10528 was found to be very similar to *Liassophlebia withersi* and has been attributed to this species herein. Compared to *L. magnifica* (the type species of *Liassophlebia*), the pterostigma of I.10434 is similar; there are two or three fewer postnodal veins and several crossveins can be slightly more or less oblique, leading to an assumption that they are similar. However, the diagnostic characters of *L. magnifica* are not present and so it is impossible to accurately attribute this specimen to that, or any other, species. Given the lack of diagnostic characters and the removal of the forewing from the type series, it is clear that this species name should be considered nomen dubium.

Genus *Rossiphlebia* new genus

Type species.—*Liassophlebia jacksoni* Zeuner, 1962.

Diagnosis.—Male hindwing characters known. Strong anterior branch of AA ending on CuA and splitting subdiscoidal cell into two relatively large cells; cubital area wide (six or seven rows of cells); anal triangle split into two large cells in male; base of RP2 aligned with subnodus. Well-defined supplementary longitudinal vein in basal part of postdiscoidal area, beginning very close to discoidal triangle (also present in *Liassophlebia pseudomagnifica*).

Etymology.—Named for Dr. Andrew Ross, British palaeoentomologist and supervisor to the senior author.

Remarks.—This genus is very interesting because it seems to exhibit characters of both Liassophlebiidae and Heterophlebiidae. It is a liassophlebiid according to the rudimentary discoidal triangle and the presence of a well-defined supplementary longitudinal vein in the basal part of the postdiscoidal area, but the division of the subdiscoidal cell is similar to that of heterophlebiids, with a strong anterior branch of AA, but in male heterophlebiids, the anal triangle is split into three cells. The new genus is based on hindwing characters, thus it is difficult to compare with *Ferganophlebia* and *Grimmenopteron*, which are based on forewings only (Pritykina, 1970; Ansorge, 1996). Nevertheless, it differs from both (and from *Caraphlebia*) in the presence of a well-defined supplementary longitudinal vein in the basal part of the postdiscoidal area. It is not comparable to *Bavarophlebia*, which is based on a forewing, but in the latter, the base of RP2 is distinctly distal to the subnodus, whereas it is well aligned with it in *Rossiphlebia* n. gen.

Rossiphlebia jacksoni (Zeuner, 1962)

1962 *Liassophlebia jacksoni* Zeuner, p. 162, pl. 25, figs. 1, 2.
1985 *Liassophlebia jacksoni*; Whalley, p. 121, fig. 6.
1993 *Liassophlebia jacksoni*; Nel et al., p. 139, figs. 102, 103.

Holotype.—NHMUK In.53999, part and counterpart (Fig. 6), 'Flatstones' (bed 83) of the Obtusum Chronozone, Obtusum Subchronozone (Lias Group, Charmouth Mudstone Formation, Black Ven Mudstone Member); Early Jurassic, lower Sinemurian; Stonebarrow, Dorset.

Diagnosis.—Nine antenodal crossveins of second row; two or three rows of cells between MA1 and the supplementary longitudinal vein.

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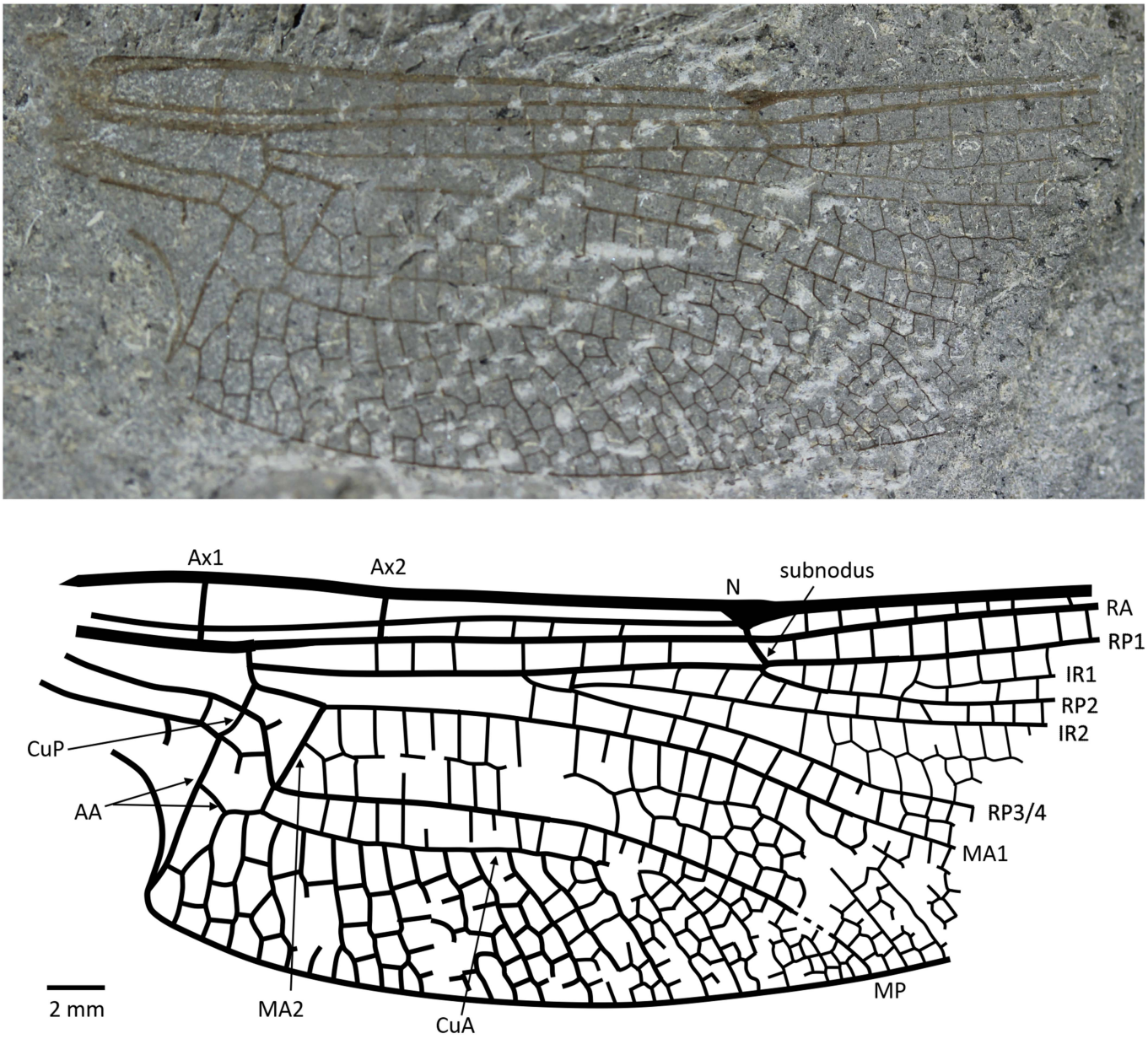

Figure 4. Holotype of *Liassophlebia pseudomagnifica* Whalley, 1985 (NHMUK I.64000); Stonebarrow, Dorset (Sinemurian); photograph and reconstruction. AA = anterior anal; Ax1 = second branch of primary antenodal crossvein; Ax2 = third branch of primary antenodal crossvein; CuA = anterior cubitus; CuP = posterior cubitus; IR1 = intercalary radial vein 1; IR2 = intercalary radial vein 2; MA1 = anterior branch of anterior median; MA2 = posterior branch of anterior median; MP = posterior median; N = nodus; RA = anterior radius; RP1 = first branch of posterior radius; RP2 = second branch of posterior radius; RP3/4 = third/fourth branch of posterior radius.

Description.—See original description by Zeuner (1962).

Additional material.—NMW 91.14G.1, Catherston Lane.

Remarks.—This species is transferred to the new genus *Rossiphlebia* based on hindwing characters; no forewings are yet known.

Family Anglophlebiidae new family

Type genus.—*Anglophlebia* new genus.

Diagnosis.—As for the type species, by monotypy.

Etymology.—*Anglo*, the Latin prefix for England, and *phlebiidae*, a common suffix for Liassic dragonfly families.

Genus *Anglophlebia* new genus

Type species.—*Liassophlebia gigantea* Zeuner, 1962.

Diagnosis.—As for the type species.

Etymology.—*Anglo*, the Latin prefix for England, and *phlebia*, a common suffix for Liassic dragonfly genera.

Anglophlebia gigantea (Zeuner, 1962)

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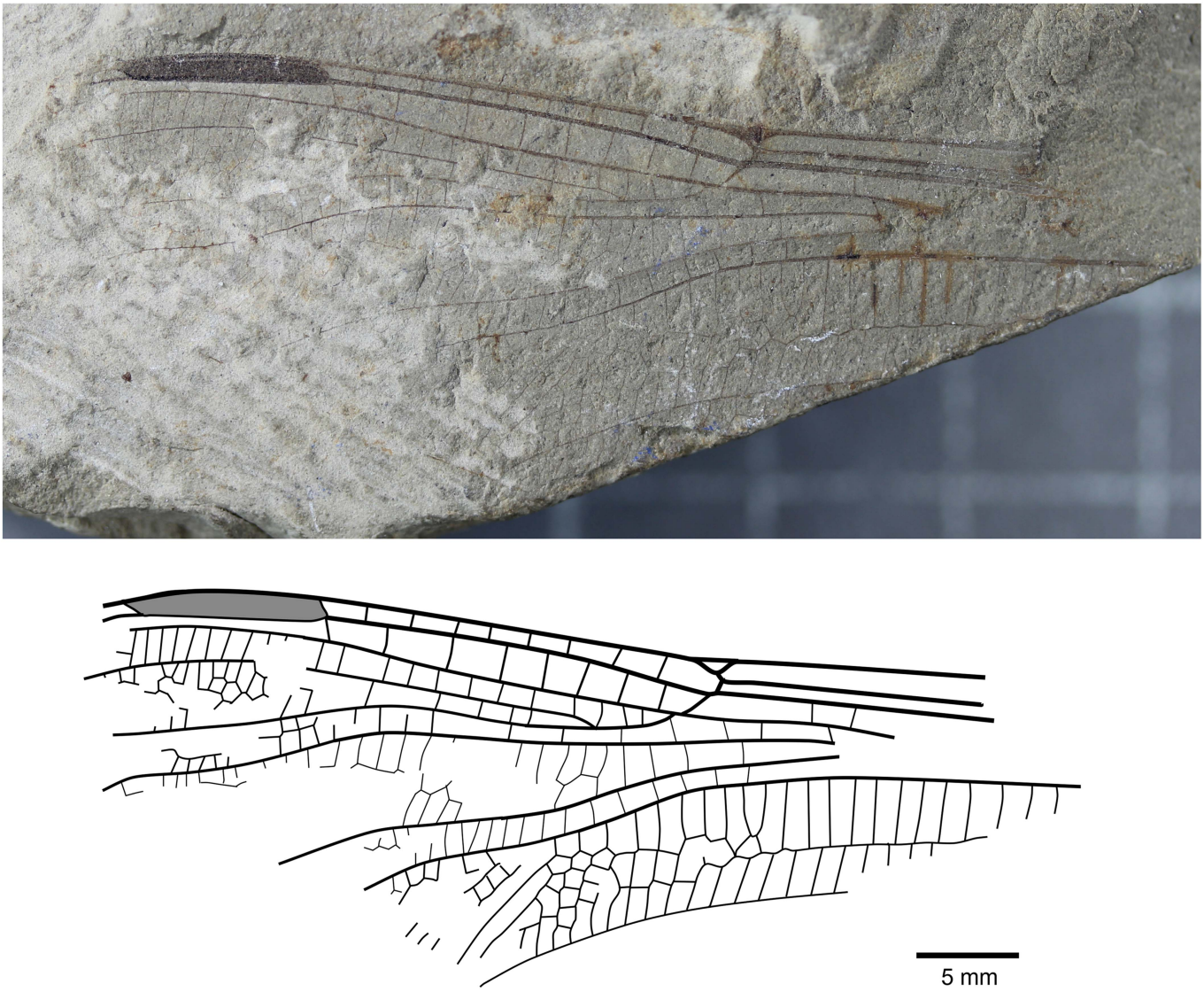

Figure 5. Holotype of *Liassophlebia batheri* Tillyard, 1925 (NHMUK I.10434), Strensham, Worcestershire (Rhaetian), photograph and reconstruction.

1962 *Liassophlebia gigantea* Zeuner, p. 163, pl. 27, fig. 2.
1985 *Liassophlebia gigantea*; Whalley, p. 122, fig. 7a, b.
1993 *Liassophlebia gigantea*; Nel et al., p. 139, fig. 108.

Holotype.—NHMUK In.51030, part and counterpart (Fig. 7), 'Flatstones' (bed 83) of the Obtusum Chronozone, Obtusum Subchronozone (Lias Group, Charmouth Mudstone Formation, Black Ven Mudstone Member); Early Jurassic, lower Sinemurian; Stonebarrow, Dorset.

Diagnosis.—Narrow wing with characters of both fore- and hindwings of the Liassophlebiidae: AA strongly curved posteriorly and straight (typical of forewings); posterior margin of subdiscoidal cell not convex and forking, with Cu appearing to extend toward posterior margin; subdiscoidal cell widened distally as in Liassophlebiidae; discoidal cell basally closed, with shape reminiscent of that in liassophlebiid hindwings; subdiscoidal space divided into three or four cells; at least six cells between subdiscoidal cell and wing base; cubital area very narrow (forewing character); intercalary medial vein beginning at first crossvein after distal margin of discoidal triangle (MA2) and stronger and smoother than that of liassophlebiids; also more cells in postdiscoidal area with possible second posterior intercalary vein.

Remarks.—This is a peculiar specimen because it seems to exhibit characters traditionally indicative of both fore- and hindwings. With the shape of the discoidal cell and the presence of the intercalary vein in the postdiscoidal area, it could be identified as a hindwing, as indeed it was by Zeuner (1962). However, in the counterpart, the cubito-anal area is better preserved and exhibits characters of a forewing (AA curving strongly posteriorly; shape of anal area; narrow cubital area) and of a hindwing (discoidal cell basally closed; shape of discoidal cell; intercalary vein in postdiscoidal area; subdiscoidal cell divided).

There are two possible hypotheses based on the evidence: (1) that we have a hindwing with a reduced cubito-anal area, as

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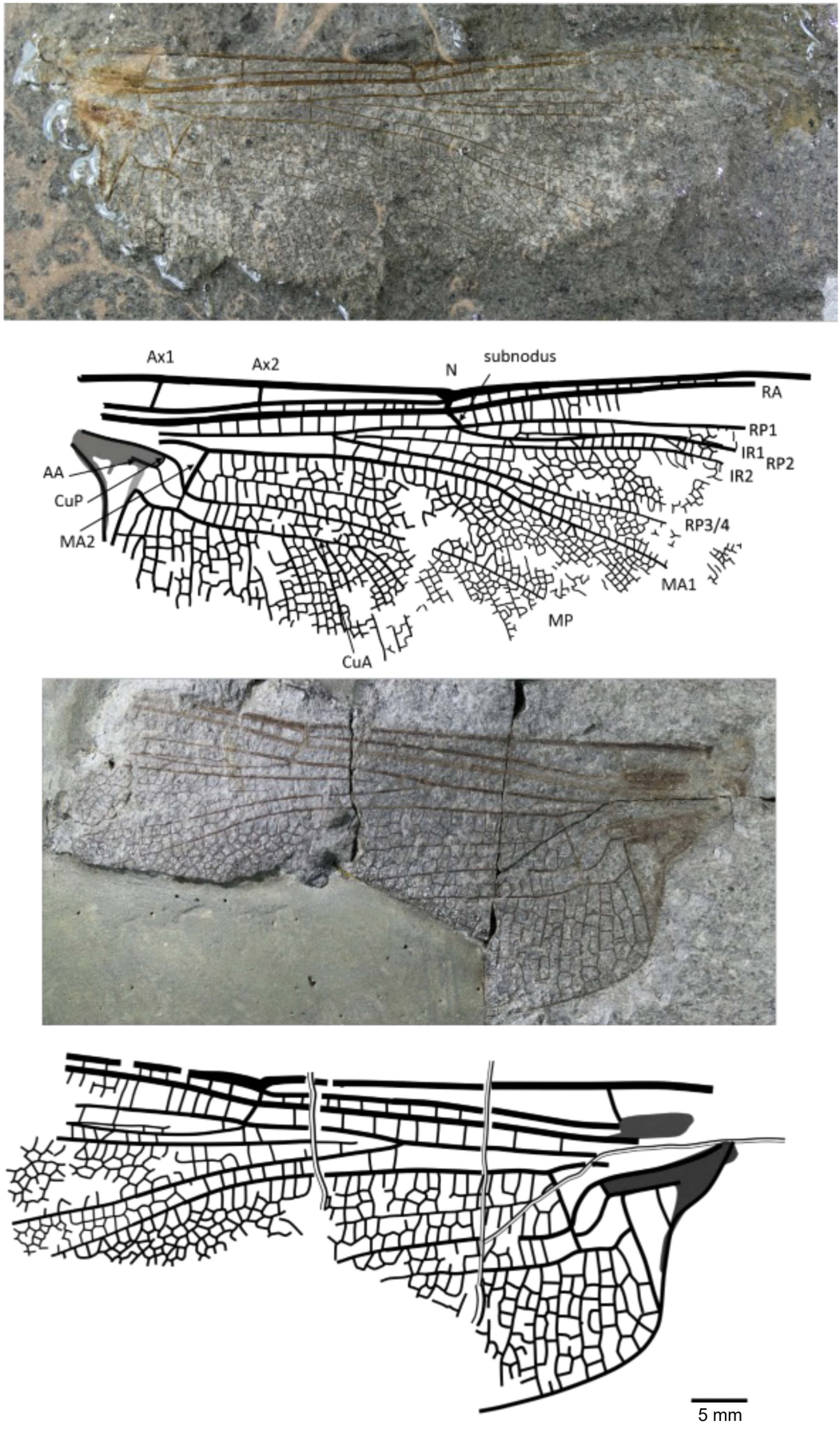

Figure 6. Holotype of *Rossiphlebia jacksoni* (Zeuner, 1962) (NHMUK In.53999, part and counterpart), Stonebarrow, Dorset (Sinemurian), photograph and reconstruction. AA = anterior anal; Ax1 = second branch of primary antenodal crossvein; Ax2 = third branch of primary antenodal crossvein; CuA = anterior cubitus; CuP = posterior cubitus; IR1 = intercalary radial vein 1; IR2 = intercalary radial vein 2; MA1 = anterior branch of anterior median; MA2 = posterior branch of anterior median; MP = posterior median; N = nodus; RA = anterior radius; RP1 = first branch of posterior radius; RP2 = second branch of posterior radius; RP3/4 = third/fourth branch of posterior radius.

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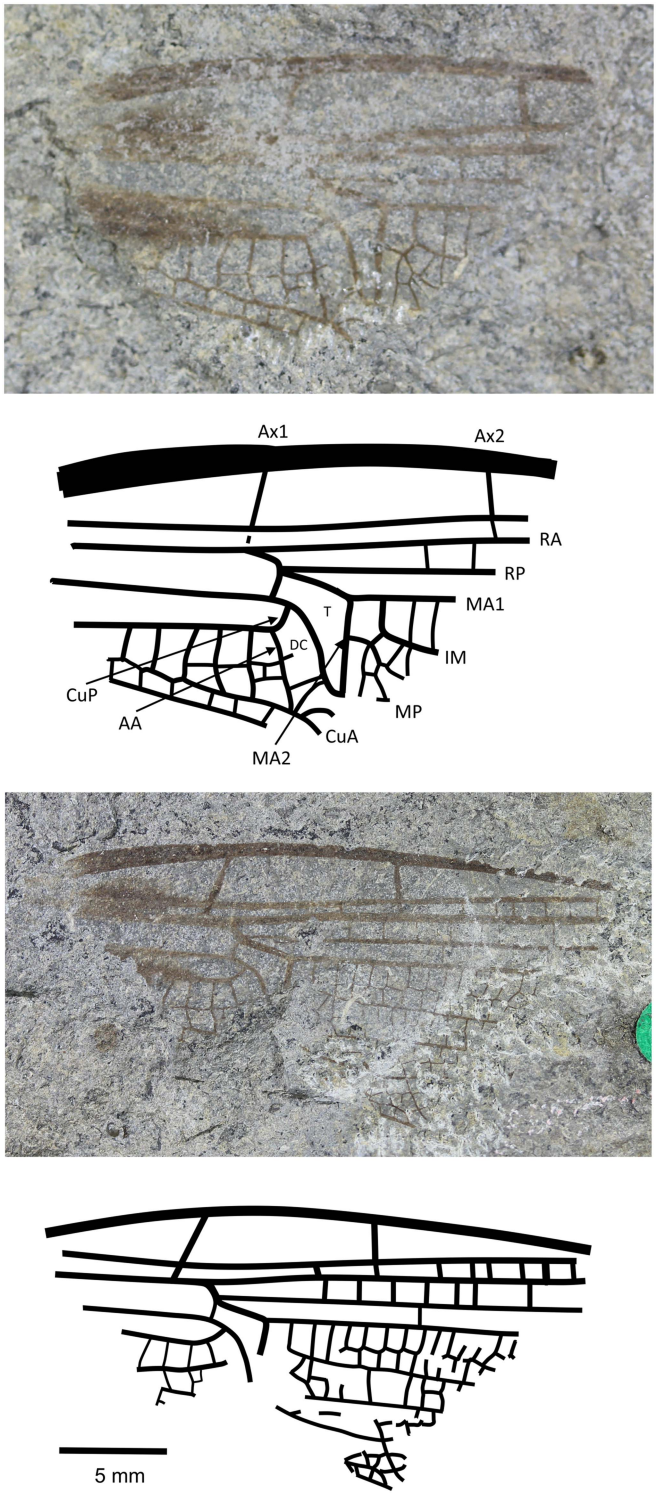

Figure 7. Holotype of *Anglophlebia gigantea* (Zeuner, 1962) (NHMUK In.51030 pt and cpt); Stonebarrow, Dorset (Sinemurian); photograph and reconstruction. AA = anterior anal; Ax1 = second branch of primary antenodal crossvein; Ax2 = third branch of primary antenodal crossvein; CuA = anterior cubitus; CuP = posterior cubitus; DC = discoidal cell; IM = intercalary medial vein; MA1 = anterior branch of anterior median; MA2 = posterior branch of anterior median; MP = posterior median; RA = anterior radius; RP = posterior radius; T = triangle.

in some Campterophlebiidae (Nel et al., 2008), or (2) that we have a forewing with some hindwing characters (as in the Liassogomphidae Tillyard, 1935 and modern Anisoptera in which the discoidal cell is divided into a hypertriangle and a discoidal triangle in the forewings, compared to the Heterophlebiidae Handlirsch, 1906, in which this is only true in the hindwings). Either way, and although the specimen is only the basal fragment, it is unique among the British materials (checked at all known repositories of British Late Triassic–Early Jurassic material in the UK and the USA), the Liassic

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material held in Paris at the Muséum National d'Histoire Naturelle (examined by AN), the Late Triassic–Early Jurassic Russian and Central Asian material (checked at the Paleontological Institute of the Russian Academy of Sciences in Moscow by RSK and Dmitry Vassilenko), and the Late Triassic–Early Jurassic material from China held at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (examined by RSK). The specimen does not fit with any family diagnosis already described and so we tentatively erect a new family for this species in the hope that further, better-preserved specimens will be found and described in the future.

Clade Isophlebioptera Bechly, 1996
Family Selenothemistidae Handlirsch, 1939

Genus *Caraphlebia* Carpenter, 1969

Type species.—*Caraphlebia antarctica* Carpenter, 1969.

Diagnosis.—A very well-defined CuA2 directed toward posterobasal side of hindwing.

Caraphlebia antarctica Carpenter, 1969

1969 *Caraphlebia antarctica* Carpenter, p. 419, fig. 1.
1993 *Caraphlebia antarctica*; Nel et al., p. 259, fig. 221.

Holotype.—USNM 165874, part and counterpart (Fig. 8), Ferrar Group, Mawson Formation; Early Jurassic, lower Lias (possibly Hettangian–Sinemurian); Carapace Nunatuk, South Victoria Land, Antarctica.

Diagnosis.—Hindwing CuA2 quite distinct, directed toward posterobasal margin of wing.

Description.—Primary antenodals present, Ax1 basal to arculus, Ax2 distal to it, arculus closer to Ax1 than to Ax2. Crossveins between RA and RP basal to expected position of subnodus; postnodal crossveins not visible. Pterostigma very long and narrow, but apparently distally incomplete. Postdiscoidal area not distally narrowed. Area between RP3/4 and IR2 apparently distally broadened. Oblique veins not preserved. Nodal structures very poorly preserved. RP2 and IR1 not discernible. Discoidal cell poorly preserved, but quite short and with distal side MA2 twice as long as basal side (without any trace of subdivision into hypertriangle and triangle, as figured by Carpenter, 1969). Subdiscoidal space broad, with posterior side (AA and CuA) convex. Basal part of CuA short, CuA2

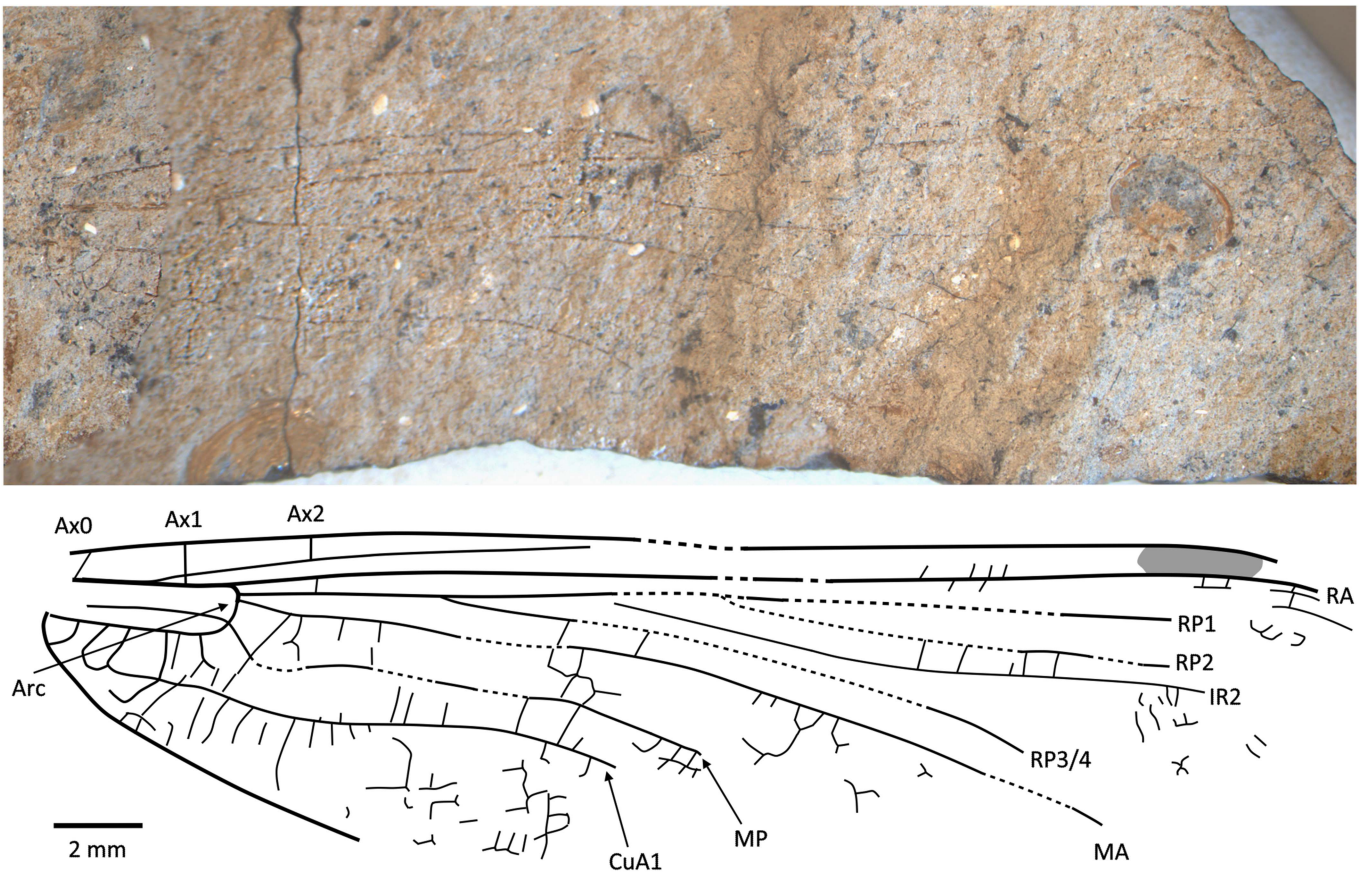

Figure 8. Holotype of *Caraphlebia antarctica* Carpenter, 1969 (USNM 165874), Carapace Nunatak (Hettangian to Sinemurian), photograph and reconstruction. Ax0 = first branch of primary antenodal crossvein; Ax1 = second branch of primary antenodal crossvein; Ax2 = third branch of primary antenodal crossvein; Arc = arculus; CuA1 = distal branch of anterior cubitus; IR2 = intercalary radial vein 2; MA = anterior median; MP = posterior median; RA = anterior radius; RP1 = first branch of posterior radius; RP2 = second branch of posterior radius; RP3/4 = third/fourth branch of posterior radius.

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Figure 9. Holotype of '*Liassophlebia*' *clavigaster* Tillyard, 1925 (NHMUK I.10433), Strensham, Worcestershire (Rhaetian), photograph.

Figure 10. Holotype of '*Liassophlebia*' *hopei* (Brodie, 1845) (OUMNH J.55084); Strensham, Worcestershire (Rhaetian); photograph.

quite distinct, directed toward posterobasal margin of wing, with AA ending within it. Cubital area broad with ~5 or 6 rows of cells between CuA and posterior wing margin. Anal area broad with two rows of large cells. Anal margin rounded, without any angle; no anal triangle (female).

Remarks.—The original description and figure (Carpenter, 1969) shows an almost complete and supposedly well-preserved fossil. However, the type specimen (Fig. 8) is not as well-preserved with most of the apical half of the wing missing, although fortunately most of the major veins are preserved though slightly warped by the structure of the rock. The numerous secondary antenodal crossveins figured by Carpenter (1969, fig. 1) are not discernible. The pattern of the longitudinal veins, i.e., postdiscoidal space not narrowed and RP3/4 not parallel to IR2, corresponds to Liassophlebiidae and Selenothemistidae. However, the shape of the discoidal cell differs from that of liassophlebiids in that it is relatively short and without any trace of division into a hypertriangle and discoidal triangle. The probable absence of secondary antenodal crossveins and veins in the basal area between RA and RP also supports attribution to the Selenothemistidae. The quite well-defined CuA2, curved toward the posterobasal side of the wing, is very particular and probably is an autapomorphy of the genus.

Odonata incertae sedis, fam. indet.
'*Liassophlebia*' *clavigaster* Tillyard, 1925

1925 *Liassophlebia* (?) *clavigaster* Tillyard, p. 19, pl. 3, fig. 9, text-fig. 5.
1939 (Anisozygopteron) *clavigaster*; Handlirsch, p. 29.
1978 *Liassophlebia clavigaster*; Lindley, p. 344.
1993 *Liassophlebia* (?) *clavigaster*; Nel et al., p. 142, fig. 109.

Holotype.—NHMUK I.10433 (Fig. 9), 'Insect limestone' of the Pseudomonotis beds (Penarth Group, Lilstock Formation); Late Triassic, Rhaetian; Strensham, Worcestershire.

Remarks.—This specimen and the other identified as this species (NHMUK I.475) are known only from abdominal segments. Liassophlebiid higher taxonomy is based on wings so it is impossible to attribute this specimen to a genus or family. Therefore, we consider this species to be incertae sedis at those levels until a better-preserved specimen allows identification.

'*Liassophlebia*' *hopei* (Brodie, 1845)

1845 *Libellula hopei* Brodie, p. 71, pl. 10, fig. 3.
1892 *Libellula hopei*; Woodward, p. 195.
1879 *Libellula hopei*; Goss, p. 129.
1850 *Petalura liassina* (Strickland); Hagen, p. 359.
1850 *Heterophlebia hopei*; Selys-Longchamps and Hagen, p. 359 (footnote).
1906 (Anisozygopteron ?) *hopei*; Handlirsch, p. 470.
1939 (Anisozygopteron) *hopei*; Handlirsch, p. 29.
1925 *Liassophlebia* (?) *hopei*; Tillyard, p. 19.
1993 *Liassophlebia hopei*; Nel et al., p. 143.

Holotype.—OUMNH J.55084 a and b, 'Insect Limestone' of the Pseudomonotis beds (Penarth Group, Lilstock Formation); Rhaetian; Strensham, Worcestershire.

Remarks.—Same reasoning as for '*Liassophlebia*' *clavigaster*, above.

Discussion

Examination of the fossil material from the Late Triassic and Early Jurassic of England has led to several major changes to the taxonomy of Liassophlebiidae and changes to the diversity estimates of insects across the TJB. The new family Anglophlebiidae is tentatively erected for a specimen previously attributed to the liassophlebiid species *Liassophlebia gigantea* by Zeuner (1962). This specimen is only a fragment of a wing, and it is expected that future changes to the taxonomy of this family will be required as and when better-preserved specimens are found. However, the characters that are preserved are of sufficient uniqueness that it is important to draw attention to the specimen. This taxon is of particular interest because it appears to exhibit characters traditionally attributed to both fore- and hindwings, respectively narrow cubito-anal area vs. discoidal cell basally close and nearly divided into two parts by an incomplete crossvein.

Rossiphlebia n. gen. is erected for a species previously attributed to *Liassophlebia jacksoni* by Zeuner (1962). This species is clearly not attributable to *Liassophlebia* because the subdiscoidal space is subdivided into two large cells by a branch of AA. This genus is particularly interesting because it seems to exhibit characters of both Liassophlebiidae and Heterophlebiidae. As the taxonomy of these groups is revised, it is also important to consider the bigger picture and the effects of such findings on previous phylogenies (e.g., Nel et al., 1993). With the new characters described since 1993, the topography of a Jurassic Odonata phylogeny would probably look much different.

Two specimens—a forewing and a hindwing—were originally attributed to *Liassophlebia batheri* by Tillyard (1925).

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Because these are isolated wings, it is impossible to ascertain whether they belong to the same species without a specimen that preserves both fore- and hindwings together. Moreover, the forewing was found to be very similar to the holotype of *L. withersi*, which is described from a forewing. The only real difference is an aberration in the anal area of the holotype and a size difference that is not sufficient to split them into separate species, so the forewing previously attributed to *L. batheri* is herein transferred to *L. withersi*. This leaves only the hindwing holotype of *L. batheri*, which is not of sufficient preservation for description and so the species is herein considered nomen dubium.

Two species—*Liassophlebia (?) clavigaster* and *L. (?) hopei*—were described from isolated abdominal segments. However, liassophlebiid higher taxonomy is described from isolated wings and there are yet to be any specimens described with both wing and abdomenal characters, so it is impossible to attribute isolated abdomens to the same taxa. The taxonomy of these specimens is not clear higher than family level because members of Stenophlebiidae also have apically widened abdomens similar to *L.* (?) *clavigaster*; it is therefore not yet possible to attribute these fossils to a precise higher group (e.g., Stenophlebiomorpha, Heterophlebioptera, etc.).

Taxonomic revision of historical collections is important because it increases our understanding of past diversity and allows us to better reconstruct palaeoentomofaunas. There are also implications for our understanding of insect phylogenies because several of the species described herein exhibit characters from traditionally separate families. The current revision did not however have much of an effect on our understanding of the impact of the ETE on insect diversity. We consider *L. batheri* to be nomen dubium and we transferred the other specimen identified as this species to *L. withersi*; this reduced the species richness of insects in the Rhaetian by one (*L. batheri*) but did not affect the ranges of other species or the genus. There were no taxonomic changes to *L. magnifica* and no further specimens were found, so there were no changes to the range of this species and so it still seems to have originated in the Hettangian following the ETE. Selenothemistidae was previously only known from the Toarcian of Germany (Handlirsch, 1939) so the confirmation of *Caraphlebia* in this family increases the range of the family back to the Hettangian or Sinemurian, indicating that the family originated closer to the TJB and prior to the early Toarcian mass extinction. *Rossiphlebia* n. gen. and Anglophlebiidae n. fam. are newly described but are only known from the Sinemurian. Their description increases the diversity of insects in the Sinemurian but does not affect the range of Liassophlebiidae or *Liassophlebia* across the TJB.

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Data statement.— This study did not involve any underlying data. All specimens are available for re-study in the public institutions indicated in the text.

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