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A new Liassophlebiidae (Odonata: Heterophlebioidea) from strata close to the Triassic-Jurassic boundary in Somerset, UK

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ABSTRACT

Liassophlebiidae is an extinct family of damsel-dragonflies found in Upper Triassic and Lower Jurassic strata of Europe, Asia and Antarctica. Whilst Liassophlebiidae is well represented by Lower Jurassic fossils, their lowest occurrence in the Upper Triassic has hitherto only been suggested by three fragmentary specimens. These were originally ascribed to two species: *Liassophlebia withersi* and *Liassophlebia batheri*, but the latter is now considered *nomen dubium*. Here we describe a fourth, better preserved specimen that is likely to be Rhaetian (Late Triassic) in age. The specimen, BRSMG Cg3101 a+b, was collected from Bowdens Quarry, Somerset, UK, from the lower part of the White Lias Formation. The specimen comprises an incomplete forewing attributed to *Liassophlebia* due to: the small number of antenodals, antesubnodals and crossveins between RP and MA based RP3/4 in the base of RP2 opposite the subnodus; a straight and elongate secondary longitudinal vein in the postdiscoidal area; numerous cells and secondary veins in radial and median areas. The specimen is likely to represent a new species and provides stronger evidence than the previous three specimens of the presence of Liassophlebiidae during the late Rhaetian. Its stratigraphical position suggests that Liassophlebiidae arose in the immediate aftermath of the Triassic-Jurassic mass extinction.

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Insecta; Odonatoptera; stem Anisoptera; diversity; Triassic; Triassic-Jurassic mass extinction

Introduction

The insect superorder Odonatoptera (damselflies and dragonflies) is one of the oldest groups of Pterygota (winged insects), and the earliest records of their occurrence are from the Serpukhovian Age of the Carboniferous Period (Jarzembowski and Nel 2002; Petrulevicius and Gutierrez 2016). The Carboniferous Odonatoptera include the well-known, large proto-odonates known as griffenflies (Meganisoptera: Meganeuridae) (Grimaldi and Engel 2005; Kohli et al. 2016), that had the largest wingspan (*c.* 71 cm) of all the insects that have ever lived (Prokop and Nel 2010; Nel et al. 2018). The Triassic was a pivotal period for Odonatoptera lineages (Jouault et al. 2022), with the diversification of the three groups 'Protozygoptera', Triadophlebiomorpha, and crown Odonata (Nel et al. 2012; Bechly 2016). These three groups first appeared during the Carboniferous-Permian and completely replaced the two strictly Palaeozoic groups Meganisoptera and Protanisoptera after the Permo-Triassic major crisis (Nel et al. 1999; Béthoux et al. 2005; Prokop et al. 2015; Deregnaucourt et al. 2023). During the Late Triassic, the first known representatives of the crown Odonata diversified. The appearance of the first Liassophlebiidae (Tillyard 1925), one of the crown Odonata lineages, is from strata close to the Triassic-Jurassic boundary, and likely to be of latest Triassic age.

Liassophlebiidae are a small extinct family of damsel-dragonflies known from the early Mesozoic of Western Europe, Central Asia, and Antarctica (Kelly and Nel 2018). The family is currently represented by the following five genera: *Bavarophlebia* (Nel and Petrulevičius 2005), *Ferganophlebia* (Pritykina 1970), *Grimmenopteron* (Ansorge 1996); *Rossiphlebia* (Kelly and Nel 2018), and *Liassophlebia* (Tillyard 1925); however, only the latter two genera are known from UK latest Triassic and Jurassic deposits (Kelly and Nel 2018). Liassophlebiidae were originally described from the type genus *Liassophlebia* Tillyard (1925) and were established for the following species that were identified at that time (Kelly 2018), based on incomplete wings (*L. magnifica* Tillyard 1925; *L. withersi* Tillyard 1925; *L. batheri* Tillyard 1925; and *L. westwoodi* (Hagen 1850)); and on incomplete abdomens: (*L.* (?) *clavigaster* Tillyard (1925); and *L.* (?) *hopei* (Brodie, 1845)). However, following a revision of Liassophlebiidae, Kelly and Nel (2018) considered *L. batheri* as *nomen dubium* due to the lack of diagnostic comparable characters in the holotype (NHMUK I.10434/10435). Kelly and Nel (2018) also re-assigned the second specimen (NHMUK I.10528) originally also attributed to *L. batheri* to *L. withersi*. Based on the fragmentary evidence, Liassophlebiidae (and *Liassophlebia*) is likely to be endemic to the UK in the Late Triassic but is observed to be more widespread in the Early Jurassic (Kelly 2018); with *Liassophlebia* known from the Hettangian of Germany (Kohli et al. 2016), and Liassophlebiidae from the Pliensbachian/Toarcian of Kyrgyzstan (Pritykina 1970) and the Toarcian of Germany (Ansorge 1996). Recent evidence suggests that Liassophlebiidae became extinct in the Toarcian (Nicholson et al. 2015, supplementary data).

Whilst evidence within the fossil record shows that Liassophlebiidae clearly diversified during the Early Jurassic (Nel and Petrulevičius 2005; Kelly and Nel 2018), the initial

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appearance of Liassophlebiidae has previously only been suggested from three very fragmentary specimens in strata interpreted to be latest Rhaetian in age at Strensham, Worcestershire, UK (Tillyard 1925; Kelly and Nel 2018). Thus any new fossils from this family, including the new specimen reported here, are important for better evaluating and understanding the diversification of the crown Odonata. Herein, we describe the fourth specimen and a potential new species of the damsel-dragonfly family Liassophlebiidae from strata that is likely to be Rhaetian (Late Triassic) in age, i.e. the oldest interval in which they are recorded to occur.

Material and methods

Bowdens Quarry (UK national grid reference: ST 41430 28846) is located approximately 1.7 km north of the small town of Langport in Somerset, UK (Figure 1B). The locality, also commercially known as the Somerset Lias quarry, is situated on private land and owned by Lovell Stone Group. The specimen comprises a partial forewing (BRSMG Cg3101 a+b) and was originally discovered in 2016 by Lee Riva, the quarry foreman, and was subsequently donated to the Bristol Museum & Art Gallery (BRSMG) by Simon Carpenter (Lovell Stone Group, n. d.). BRSMG Cg3101 a+b is the only fossil odonatan recorded from this locality to date. The quarry exposes the White Lias Formation of the Penarth Group and part of the overlying Blue Lias Formation of the Lias Group (Figure 1) (Gallois 2007, 2009). Whilst the fossil was not found in situ, the distinctive lithology surrounding the specimen shows that it was derived from one of the seven horizons of fine-grained crystalline limestone within the lower part of the White Lias Formation of the Penarth Group ('lower' White Lias; Figure 1C; *pers. comm.* Ramues Gallois). The fine-grained nature of this porcelaneous limestone has permitted high-quality preservation of this specimen.

The specimen was examined by author ES and remotely via photographs by co-author AN. BRSMG Cg3101 a+b was photographed by DH using a Nikon D5300 DSLR camera, and light sources were applied at various angles to best capture the preserved venation of the wing. In order to determine which half of the specimen was the part and counterpart, the two pieces were compared under magnification. The relief marginally changes across each half of the specimen, but the relief of leading edge of the wing indicates that BRSMG Cg3101a is the part. As the part and counterpart display different degrees of completeness, a line drawing was made of the better-preserved counterpart (BRSMG Cg3101 b; Figure 2). The line drawing was prepared by tracing over a photograph using the vector drawing

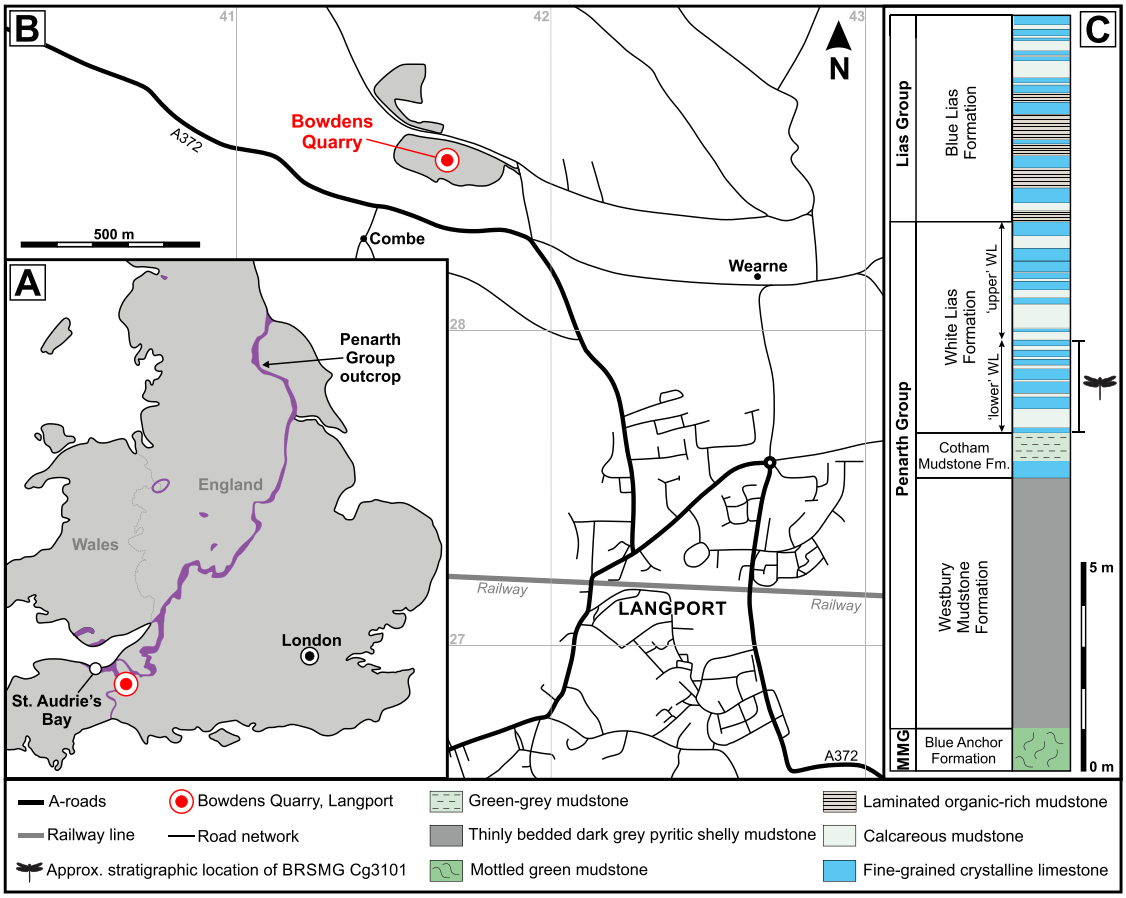

Figure 1. (A) A geographic map highlighting the extent of Penarth Group in England and Wales (outcrop shown in purple), and location of Bowdens Quarry (red circle). Note that the outcrop has been simplified for clarity. Modified from: Swift (1995); Swift and Martill (1999). (B) Close-up of the study area (Langport, Somerset), indicating the location of Bowdens Quarry. (C) Simplified stratigraphic log of the Late Triassic-Early Jurassic succession from the Langport-Somerton area (based largely on an unpublished log constructed by Ramues Gallois), showing the interval that BRSMG Cg3101 a+b came from. Based on lithology, the 'lower' White Lias is interpreted to be equivalent to the White Lias Formation on the Somerset coast and the 'upper' White Lias to the Watchet Mudstone Formation (Ramues Gallois pers comm). MMG denotes the Mercia Mudstone Group and WL the White Lias.

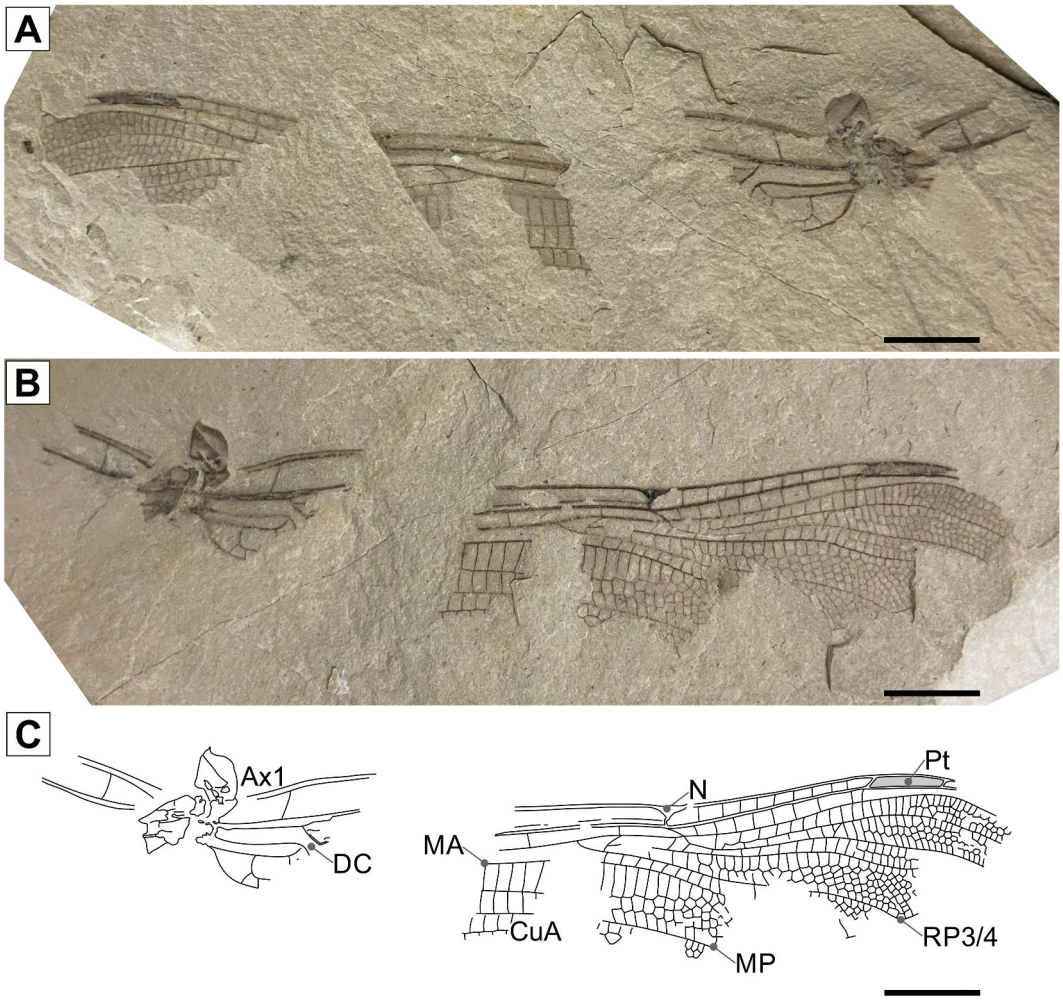

Figure 2. *Liassophlebia* sp., specimen BRSMG Cg3101 a+b: (A) BRSMG Cg3101 a, part; (B) BRSMG Cg3101 b, counterpart; (C) line drawing of BRSMG Cg3101 b, highlighting wing venation. Abbreviations: A×1= second branch of primary antenodal crossvein; CuA = anterior cubitus; DC = discoidal cell; MA = anterior median; MP = posterior median; N = nodus; Pt = pterostigma; RP3/4 = third/fourth branch of posterior radius. Scale bars = 5 mm. An artist's impression of *Liassophlebia* sp. is provided in Figure 3.

tools in CorelDRAW Graphics Suite X8. While some sections of the wing are obscured by matrix, Bristol Museum & Art Gallery (BRSMG) did not have the resources to further prepare the specimen for study.

The Odonata wing venation nomenclature used in this paper is based on the interpretations of Riek and Kukalová-Peck (1984), as modified by Nel et al. (1993) and Bechly (1996). The abbreviations are as follows: AA = anterior anal; AP = posterior anal; Arc = arculus; Ax = primary antenodal crossvein; A×0= first branch of primary antenodal crossvein; A×1= second branch of primary antenodal crossvein; A×2= third branch of primary antenodal crossvein; C = costal vein; Cu = cubitus; CuA = anterior cubitus; CuP = posterior cubitus; DC = discoidal cell; IM = intercalary medial vein; IR = intercalary radial vein; IR1 = intercalary radial vein 1; IR2 = intercalary radial vein 2; MA = anterior median; Maa = anterior branch of MA; 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. The higher classification of fossil and extant Odonatoptera is based on the phylogenetic system of Bechly (1996, 2016).

Institutional abbreviations: **BRSMG**, Bristol Museum & Art Gallery, Bristol, UK; **NHMUK**, Natural History Museum, London, UK; **OUMNH**, Oxford University Museum of Natural History, UK.

Systematic Palaeontology

Order Odonata Fabricius, 1793

Suborder Epiprocta Lohmann, 1996

Superfamily Heterophlebioidea Needham, 1903

Family Liassophlebiidae Tillyard (1925)

Type genus

Liassophlebia (Tillyard 1925). Rhaetian – Sinemurian (Late Triassic – Early Jurassic) of England (UK); and Hettangian (Early Jurassic) of Germany.

Family diagnosis *(from Kelly and Nel 2018).*

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).

Genus *Liassophlebia* Tillyard (1925)

Type species

Liassophlebia magnifica (Tillyard 1925); Hettangian (Early Jurassic) of Binton, Warwickshire (UK).

Genus diagnosis *(emended from Kelly and Nel 2018).*

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; fore- and hind-wings very large; base of RP2 opposite to subnodus; numerous rows of cells between main longitudinal veins, and presence of an intercalary longitudinal vein in postdiscoidal; several antesubnodal crossveins; presence of several secondary antenodal crossveins between ScP and RA; a straight elongate secondary longitudinal vein present in postdiscoidal area.

Liassophlebia sp.

(Figure 2)

Material examined

Specimen BRSMG Cg3101 a+b (part and counterpart of an incomplete forewing), stored in the palaeontology collection in the Geology Department at the Bristol Museum & Art Gallery, UK.

Type stratum

White Lias Formation, Penarth Group; likely Rhaetian, Late Triassic in age.

Type locality

Bowdens Quarry (commercially called the Somerset Lias quarry), near Langport, Somerset, UK (ST 41430 28846).

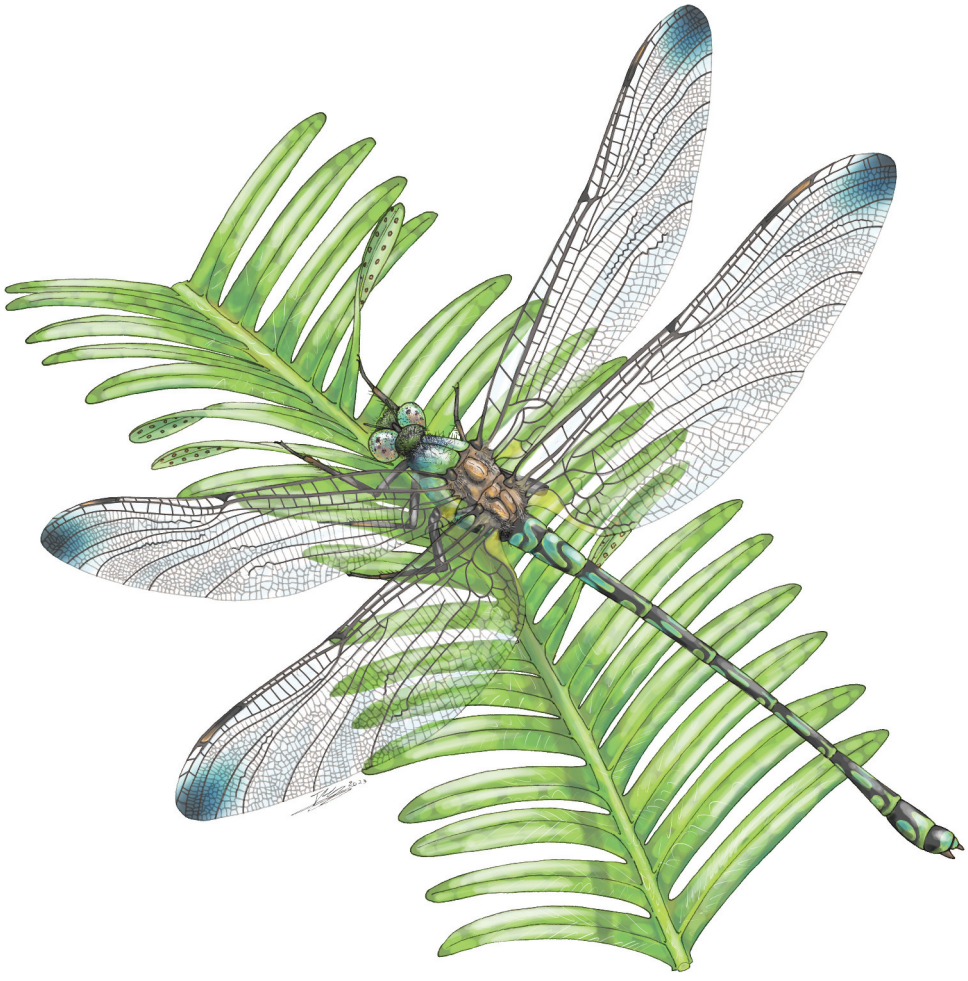

Figure 3. An artist's impression of *Liassophlebia* sp., resting on a frond of the palaeofern species *Phlebopteris muensteri*. the forewings are based on the specimen BRSMG Cg3101 a+b described herein. As the new specimen is incomplete, other specimens within the genera were used to create this artist's impression as follows: the hindwing is based on the holotype specimen of *Liassophlebia magnifica* (NHMUK I.6648/I.10462); and the body proportions are based on the incomplete abdomens of the holotypes *'Liassophlebia' clavigaster* (NHMUK I.10433) and *'Liassophlebia' hopei* (OUMNH J.55084 a and b). The colour and body morphology, including resting wing posture is inferred from present day Anisoptera. © Jules Kiely and Bristol Museum & Art Gallery.

Description

Forewing characters only. Wing more than 42.5 mm long (taking into account that the wing is broken and the distal part slightly displaced); wing *c*. 10.0 mm wide; distance between base and arculus 4.7 mm, between arculus and nodus *c*. 18.3 mm, between nodus and pterostigma 10.8 mm, between pterostigma and apex *c*. 7.0 mm; pterostigma 4.7 mm long, 0.8 mm wide; wing very shortly petiolate; 1–2 rows of cells between posterior wing margin and AA; AA nearly parallel to MP+CuA, making a very strong distal angle; median area free of crossveins, no crossvein in submedian area; a curved strong vein CuP separating submedian and subdiscoidal areas; subdiscoidal space probably free, large, elongate, broad and transverse, with its posterior margin convex; discoidal cell basally opened, transverse and narrow; RP+MA separated at nearly right angles from RA, straight; area between MP and CuA with one row of cells in preserved part; MA and MP weakly curved; a straight and elongate secondary longitudinal vein in postdiscoidal area; two rows of cells in postdiscoidal area distad discoidal space; a longitudinal secondary vein between MAa and MP, parallel to MP, basally straight and distally weakly zigzagged; A×0 preserved at wing base; A×10.8 mm basad arculus, weakly oblique; in preserved parts, no antenodal crossveins between C and ScP and between ScP and RA; nine postnodal crossveins between C and RA; nine postsubnodal crossveins between RA and RP1 basad pterostigma, not aligned with postnodals; only two visible crossveins in area between RA and RP, between arculus and nodus; base of RP3/4 4.6 mm basad subnodus, closer to nodus than to arculus; in preserved part no crossveins between MA and RP basad RP3/4; base of IR2 1.4 mm distad that of RP3/4; IR2 apparently branching on RP3/4; pterostigmal brace present, aligned with basal side of pterostigma but perpendicular to RA and RP1; pterostigma with only one crossvein below it; subnodus oblique; one crossveins in Bqr space between RP, IR2 and subnodus; base of RP2 opposite subnodus; no oblique vein 'O'; RP2 weakly undulate; base of IR1 three cells distad base of RP2; IR1 smoothly curved, area between RP3/4 and IR2 with more than eight rows of cells; area between IR2 and RP2 with two rows of cells in preserved part; area between RP2 and IR1 with four rows of cells; area between IR1 and RP1 with three rows of cells below pterostigma.

Discussion

Although fragmentary, this forewing can be attributed to the family Liassophlebiidae based of the following characters: subdiscoidal cell widened, with a convex posterior margin (visible even though only partly preserved); no antefurcal crossveins between RP and MA from the arculus to the midfork; discoidal space basally open, narrow, and transverse; no secondary antenodal crossvein of first row; few antesubnodal crossveins; an elongate and narrow pterostigma; no oblique pterostigmal brace; IR1 apparently emerging from RP2 very close to its base.

The new specimen is distinct from the Liassic genus *Bavarophlebia* Nel and Petrulevičius (2005) because the base of RP2 is opposite to the subnodus vs. well distad (Nel and Petrulevičius 2005). The specimen also differs from the Liassic genera *Grimmenopteron* Ansorge (1996) and *Ferganophlebia* Pritykina (1970) in the numerous rows of cells between the main longitudinal veins, and the presence of an intercalary longitudinal vein in the postdiscoidal area (Pritykina 1970; Ansorge 1996). The Liassic genus *Rossiphlebia* Kelly and Nel (2018) is based on a hind wing, but differs from BRSMG Cg3101 a+b as it has less crossveins in the antesubnodal space (four in distal part, distad the base of RP3/4 in new specimen vs. only one in *Rossiphlebia*), and the presence of secondary antenodal crossveins between ScP and RA (Kelly and Nel 2018). The new specimen fits well in the genus *Liassophlebia* due to the following preserved characteristics: (1) the base of RP2 opposite the subnodus; (2) there are very few antenodals, antesubnodals, and crossveins in area between RP and MA basad RP3/4; (3) a straight and elongate secondary longitudinal vein is present in postdiscoidal area; (4) there are numerous cells and secondary veins between main veins of radial and median areas (Kelly and Nel 2018).

As previously mentioned, the genus *Liassophlebia* currently comprises the following three species: *L. magnifica* Tillyard (1925) (Hettangian), *L. pseudomagnifica* Whalley (1985) (Sinemurian), and *L. withersi* Tillyard (1925) (Rhaetian). The holotype of *L. withersi* (NHMUK I.10697), the additional specimen of *L. withersi* (NHMUK I.10528), and the now unassigned specimen (NHMUK I.10434/10435) were all collected from the 'Insect limestone' (bed 18) of the *Pseudomonotis* beds that form the upper part of the Penarth Group in Strensham, Worcestershire, UK (Kelly and Nel 2018). All three of these specimens consist of fragmentary wings, suggesting that the assignment of species was overly ambitious (Kelly and Nel 2018).

The new specimen, BRSMG Cg3101 a+b, described herein contains several distinct features that differ from these other specimens. BRSMG Cg3101 a+b differs from *L. magnifica*, *L. pseudomagnifica*, and the unassigned specimen NHMUK I.10434/10435 (previously the holotype of *L. batheri*) due to the presence of only one antesubnodal crossvein distad the base of RP3/4. It also differs from *L. magnifica* because of the absence of crossvein between RP and MA just basad the base of RP3/4. *Liassophlebia magnifica* has much larger wings (70 mm long vs. 42.5 mm). *Liassophlebia batheri* has a pterostigma 9.5 mm long vs. 4.7 mm in the new specimen (Tillyard 1925). *Liassophlebia withersi* is based on the part of a forewing basad the base of RP3/4 and is different to BRSMG Cg3101 a+b. Nevertheless, the distance from wing base to arculus is 6.25 mm in *Liassophlebia withersi* vs. 4.7 mm in the new specimen, strongly suggesting that the type specimen of *L. withersi* is a forewing larger than BRSMG Cg3101 a+b. If the proportions between the wing lengths and distance between base and arculus are respected, *L. withersi* would have a wing *c*. 56.5 mm long, much longer than that of the new specimen. Thus BRSMG Cg3101 a+b probably corresponds to a different species. Nevertheless, as *L. withersi* is based on a very incomplete and poorly preserved fossil we prefer here to avoid assigning a species name to the new fossil.

In terms of the age of the specimen, it was found in strata close to the Triassic-Jurassic boundary. However, there is some uncertainty about the exact position of the base of the Jurassic in the UK and, as the only age indicators for Bowdens Quarry are lithostratigraphical, further uncertainty with respect to correlation to this location. The Global Stratotype Section and Point (GSSP) for the base of the Hettangian Stage and therefore the Jurassic System is in Austria, but the ammonite faunal succession including the primary marker is not easily correlated to the UK (Hillebrandt et al. 2013). It is also relevant here that the formal positioning of GSSP places the maximum of the Triassic-Jurassic mass extinction in the latest Triassic (Hillebrandt et al. 2013). Within the broad biostratigraphical correlation, the distinctive carbon isotope signature over the Triassic-Jurassic boundary interval as summarised in Hillebrandt et al. (2013) currently provides the most unequivocal means of high-resolution correlation between the GSSP and the UK. The carbon isotope signature at St Audrie's Bay, Somerset, UK, 40 km to the north of Bowdens Quarry (Figure 1A), indicates that the White Lias Formation (formerly the lower part of the Langport Member) and, by inference the equivalent 'lower' White Lias at Bowdens Quarry where

specimen BRSMG Cg3101 a+b was found (Figure 1C), was deposited during the very latest part of the Rhaetian. However, recently, poorly preserved ammonites were found at the very top of the White Lias at Lavernock, Wales (Hodges 2021) which suggest that the top of the White Lias Formation at that location (and therefore the top of the 'lower' White Lias at Bowdens Quarry) could be Jurassic in age. As the exact bed within the 'lower' White Lias at Bowdens Quarry that the *Liassophlebia* specimen came from is unknown, and the relative age is based on lithostratigraphical correlation to Bowdens Quarry, it is therefore just possible, taking into account Hodges (2021), that the specimen is of Jurassic age. Using the carbon isotope signature and the other evidence at St Audrie's Bay, the maximum of the Triassic-Jurassic mass extinction (Hillebrandt et al. 2013) was close to the boundary between the Cotham and White Lias formations (Figure 1C). Assuming that the White Lias Formation at St Audrie's Bay and the 'lower' White Lias at Bowdens Quarry are stratigraphically equivalent and, that the specimen is from within the 'lower' White Lias, this indicates that the *Liassophlebia* specimen reported here is most likely from the short interval between the maximum of the Triassic-Jurassic mass extinction and the base of the formally defined Jurassic. Based on the lithostratigraphy and in the absence of other high resolution stratigraphical markers, the other three *Liassophlebia* specimens from Strensham, Worcestershire, UK (reported in Kelly and Nel 2018) are likely to be from the same stratigraphical interval. This implies that Liassophlebiidae evolved in the immediate aftermath of the Triassic-Jurassic mass extinction.

Conclusion

In this study, we describe the fourth specimen and most likely a new species of the damsel-dragonfly family Liassophlebiidae from the UK. While previous fossils attributed to *Liassophlebia* (Liassophlebiidae), most likely from the Rhaetian, were fragmentary and incomplete, this new specimen confirms the presence of Liassophlebiidae very close to the Triassic-Jurassic boundary in strata that is likely to be of Rhaetian age. Although BRSMG Cg3101 a+b possibly corresponds to a new species, we prefer not to establish a new name, due to the incomplete preservation of the other specimens and species of *Liassophlebia*. Thus, BRSMG Cg3101 a+b is assigned to *Liassophlebia* sp. The discovery of this new specimen enriches our knowledge of Odonata diversity at this time and indicates that Liassophlebiidae is likely to have originated immediately after the Triassic-Jurassic mass extinction.

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Disclosure statement

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