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Revision of the damsel-dragonfly family Campterothlebiidae (Odonata) from the Early Jurassic of England reveals a new genus and species

RICHARD S. KELLY and ANDRÉ NEL

KELLY, R.S. & NEL, A., October 2017. Revision of the damsel-dragonfly family Campterothlebiidae (Odonata) from the Early Jurassic of England reveals a new genus and species. *Alcheringa* 42, 87–93. ISSN 0311-5518.

Historical fossil insect collections from England were re-examined and the taxa revised. *Lateophlebia* gen. nov. is erected for *Liassophlebia anglicanopsis* (Zeuner) in Campterothlebiidae. *Petrophlebia anglicana* Tillyard is confirmed in this family and *Archithemis liassina* (Strickland) is transferred to this family. Lastly, *Archithemis brodiei* (Geinitz), *Archithemis Handlirsch*, and Architemistidae Tillyard (reduced to this sole species) are transferred to the Heterophlebioidea.

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Key words: Insecta, Mesozoic, Odonata, Eiproctophora, Architemistidae.

THE DAMSEL-DRAGONFLY family Campterothlebiidae is known from deposits ranging in age from the Late Triassic of Krygyzstan (Pritykina 1970) to the Early Cretaceous of China (Li *et al.* 2012a) and Russia (Pritykina 2006), and is relatively common in Jurassic assemblages from England, Germany, Kyrgyzstan, China and Russia (Nel *et al.* 1993, Nel & Weiss 2017). This family is currently represented in England by *Petrophlebia* Tillyard, 1925 (see below), *Dorsettia* Whalley, 1985, which had a wide geographical range also being found in northwestern China (Zheng *et al.* 2016) and *Hypsothemis* Pritykina, 1968 (*H. fraseri* Whalley, 1985).

Historical collections of English fossil insects from the Late Triassic and Early Jurassic have been re-examined and the taxa revised leading to the discovery of new taxa and the synonymisation of other taxa. In this paper we revise representatives of Campterothlebiidae, holotypes are redrawn and revised and non-holotype material is surveyed leading to the establishment of a new genus of damsel-dragonfly in this family. Additionally, we discuss the familial placement of *Petrophlebia*. Presently, the genus is assigned

to Campterothlebiidae, but Bechly (2016) suggested that it should be transferred back to Architemistidae where it was placed by Fraser (1957).

Geological setting

The specimens discussed are from the Early Jurassic: lower Lias of England and are, therefore, *ca* 190 million years old. The lower Lias in the midlands and south of England consists of the Blue Lias Formation, which spans from the Triassic/Jurassic boundary to the lower Sinemurian, and it is overlain by the Charmouth Mudstone Member, which extends into the Pliensbachian (Simms *et al.* 2004).

The specimen from Barrow-upon-Soar, Leicestershire (National Grid Reference SK 575 175) is Hettangian in age, being found in the Planorbis Chronozone (Blue Lias Formation: Wilmcote Limestone Member). The specimens from Stonebarrow, Dorset (SY 369 929) are from the slightly higher Sinemurian stage. They were collected from the 'flatstones', which is a local name for a horizon found in bed 83/83 h of the Obtusum Chronozone: Obtusum Subchronozone (Charmouth Mudstone Formation, Black Ven Mudstone Member) (Page 2010). The Stonebarrow site was discussed in more detail by Kelly *et al.* (2017); for an in-depth description of the stratigraphy of the Dorset coast Lias, see Page (2010); the Barrow-upon-Soar locality was discussed by Martin *et al.* (1986).

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Fig. 1. Location of collection sites discussed from England: 1. Barrow-upon-Soar, Leicestershire; 2. Stonebarrow, Dorset. Map in figure 1 was adapted from d-maps.com.

Materials and methods

The material is held in the collections of the Natural History Museum, London (NHMUK) and the Warwickshire Museum, Warwick (WARMS). The Dorset specimen is part of the Jackson collection from the Jurassic Coast of England (Fig. 1) collected in the mid-twentieth century, and the Leicestershire specimen is part of the Edgell collection from the late nineteenth century. The specimens were examined first-hand by the primary author and remotely by the co-author. They were examined dry using a light stereomicroscope. Photographs were taken under alcohol, where possible, using a Nikon D3300 with an AF-S Micro Nikkor 40 mm macro lens attached to a stand.

The venation nomenclature is based on the interpretations of Riek & Kukalová-Peck (1984), as modified by Nel *et al.* (1993) and Bechly (1996). The abbreviations are as follows: AA, anterior anal; AP, posterior anal; Ax, primary antenodal cross-vein; Arc, arculus; CuAa, distal branch of anterior cubitus; CuAb, proximal branch of anterior cubitus; CuP, posterior cubitus; DC, discoidal cell; MAa, anterior branch of anterior median; Mab, posterior branch of anterior median; MP, posterior median; RA, anterior radius; RP, posterior radius; ScP, posterior subcostal; IR, intercalary vein; 'O', oblique vein; Pt, pterostigma; T, triangle; Ht, hypertriangle; N, nodus. The higher classification of fossil and extant Odonatoptera is based on the phylogenetic system of Bechly (1996, 2016). Taxonomic figures were constructed in Serif DrawPlus X6.

Systematic palaeontology

Class INSECTA Linnaeus 1758

Order ODONATA Fabricius 1793

Clade ISOPHLEBIOPTERA Bechly 1996

Subclade ISOPHLEBIIDA Bechly 1996

Superfamily ISOPHLEBIOIDEA Handlirsch 1906

Family CAMPTEROPHLEBIIDAE Handlirsch 1920

Lateophlebia gen. nov.

Type species. *Lateophlebia anglicanopsis* (Zeuner, 1962).

Etymology. 'Lateo' is the Latin word for hidden, and 'phlebia' is a common odonatan suffix.

Diagnosis. Hindwing characters only (probably female owing to lack of anal angle and triangle). Anal vein completely separated from CuA; subdiscoidal area posteriorly open; CuAb distinctly curved; CuAa ending well distal of bases of RP3/4 and IR2, and basal of nodus level; RP3/4 and MAa nearly straight.

Lateophlebia anglicanopsis (Zeuner 1962)

1962 *Petrophlebia anglicanopsis* Zeuner, pp. 160–161, pl. 24, figs 1–2.

1985 *Liassophlebia anglicanopsis* (Zeuner, 1962); Whalley, pp. 122–123, fig. 8a.

1993 *Liassophlebia anglicanopsis* (Zeuner, 1962); Nel *et al.*, pp. 141–142.

Holotype. NHMUK In.49573 (Fig. 2).

Locality and age. Stonebarrow, Dorset. Sinemurian ('Flatstones', Bed 83, Obtusum Chronozone: Obtusum Subchronozone).

Diagnosis. Female hindwing; areas between CuAa and MP and between MP and MAa narrow; mostly only one row of cells in areas between MAa and MP, and between MP and CuAa; very few cells in subdiscoidal area below discoidal cell.

Redescription. This species is based on basal two-thirds of a single hindwing. Wing hyaline, preserved part 67.5 mm long and 20.0 mm wide. Distance between base and arculus 10.0 mm and between arculus and nodus 28.5 mm. Wing shortly petiolate; anal area poorly preserved but with irregular cells, some smaller than others; median space free, submedian space with curved vein CuP; curved cross-vein separates submedian and subdiscoidal spaces; subdiscoidal space posteriorly open and transverse, with AA making sub-right angle in basal part.

Discoidal cell free, closed basally, narrowly elongate, 3.5 mm long and 1.7 mm wide; RP and MA strongly separated at arculus; MAb less than twice as long as basal side of discoidal cell, which is 1.0 mm long; MAb well aligned with distal free part of CuA.

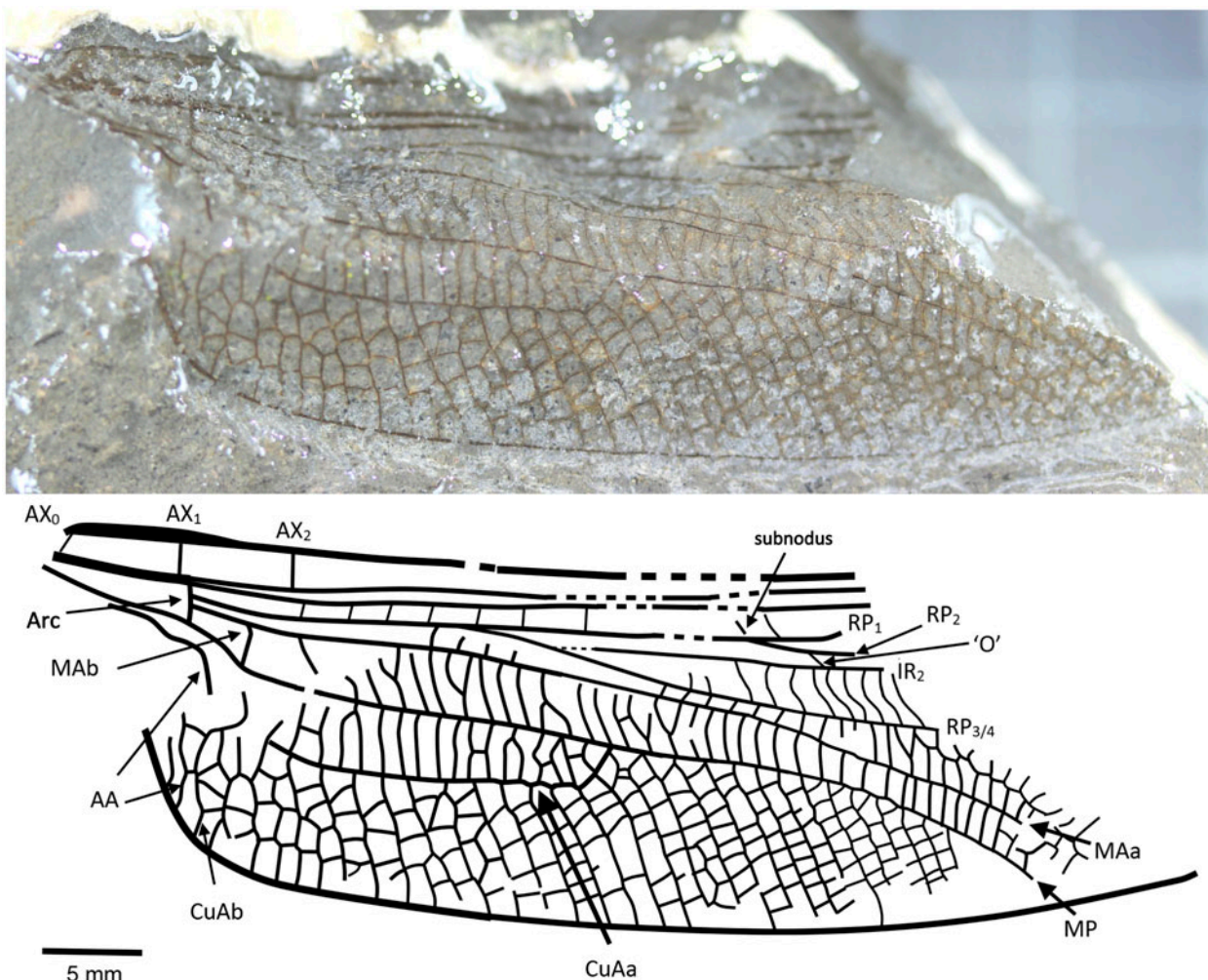


Fig. 2. Holotype of *Lateophlebia anglicanopsis* (NHMUK In.49573), photograph and reconstruction.

Distal free part of CuA is 3.5 mm long, dividing into CuAa and CuAb; CuAb 6.2 mm long, curved, directed towards posterior margin. CuAa relatively short, ending well basal of nodus level, with 12 posterior branches. CuAa and MP well-separated, clearly parallel for a long distance, one row of intervening transverse cells. Area between MP and CuAa 4.0 mm wide; MP weakly curved, reaching posterior margin well distal of nodus level, 61.2 mm from wing base; MAa nearly straight, more or less parallel to MP, with one row of cells in basal part of postdiscoidal area, 4.0 mm wide, narrower than area between MP and CuAa.

Postdiscoidal area becoming narrower below nodus but broader near posterior wing margin with four rows of small cells present; Ax0 visible, very near to wing base; two primary antenodal veins very strong, Ax1 1.2 mm basal of arculus and Ax2 5.7 mm distal of arculus, Ax1 nearly perpendicular to ScP and R+MA, Ax2 more oblique; no secondary antenodal cross-vein visible; about seven preserved antesubnodal cross-veins between arculus and subnodus; base of RP3/4 10.5 mm distal of arculus, closer to arculus than to nodus; base

of IR2 very close to that of RP3/4, 2.5 mm distally, originating distinctly from RP; nodal crossing and subnodus oblique; postnodal and postsubnodal cross-veins not preserved; RP2 aligned with subnodus; first oblique vein 'O' two cells and 3.7 mm distal of base of RP2; area between MAa and RP3/4 widened distally; area between RP3/4 and IR2 strongly widened distally.

Remarks. *Lateophlebia anglicanopsis* differs greatly from the hindwings of Heterophlebiomorpha (including those of Liassophlebiidae) in the shape of the discoidal cell, which is narrowly elongate, with posterior side straight and distal side not twice as long as basal side. Neither is there a cross-vein, complete or incomplete, in the discoidal cell. Furthermore, the shape of the cubito-anal area differs strongly from those in Heterophlebiomorpha. Vein AA is not fused with CuA, and the area between MP and CuAa is broader than the postdiscoidal area. These characters are apomorphies of Isophlebioidea. Thus, this species does not belong to *Liassophlebia*.

The species was originally attributed to *Petrophlebia* (placed here in the isophlebiomorphan family

Architemistidae Tillyard 1917; see below). However, it differs from *Petrophlebia* and Architemistidae in the veins AA and CuAb being completely separated. Within Isophlebioidea, *Lateophlebia* can be attributed to Campterophlebiidae rather than to Isophlebiidae based on the following characters: opposite curvature of MA and MP constricting the area between them (apomorphy); basal part of area between MP and CuAa less than twice as wide as basal part of area between MAa and MP (plesiomorphy); distal side (MAB) of discoidal cell and gaff (basal CuA before its furcation) not orientated in one transverse axis (plesiomorphy).

Within Campterophlebiidae, *Lateophlebia* belongs to the group of genera that have the AA vein completely separated from CuA so that the subdiscoidal area is open posteriorly, viz., *Campterophlebia* Bode, 1905, *Pritykinia* Nel *et al.*, 2009, *Pternopteron* Pritykina, 1970, *Oreophlebia* Pritykina, 1985, *Amnifleckia* Zhang *et al.*, 2006, *Qibinlina* Nel *et al.*, 2009, *Dorsettia* Whalley, 1985, and *Gallodorsettia* Nel & Weis, 2017, plus possibly *Sibirioneura* Pritykina, 1985 (Nel *et al.* 1993, 2009, Zhang *et al.* 2006, Zheng *et al.* 2016, Nel & Weis 2017).

Lateophlebia differs from *Gallodorsettia* and *Oreophlebia* in the distinctly curved CuAb and narrower areas between CuAa and MP, and between

MP and MAa. *Lateophlebia* differs from *Dorsettia*, *Amnifleckia*, *Qibinlina* and *Pternopteron* in the longer CuAa, which ends distal to the bases of RP3/4 and IR2. It also differs from *Sibirioneura* in the nearly straight RP3/4 and MAa. All these characters are shared with *Campterophlebia* but it differs from this genus in the presence mostly of a single row of cells in the areas between MAa and MP, and between MP and CuAa, plus the presence of very few cells in the subdiscoidal area below the discoidal cell, as in *Pritykinia*. *Lateophlebia* differs from *Pritykinia* in the curved MAB and the presence of only one row of cells in the area between CuAa and MP. Therefore, we consider that it corresponds to a new genus.

A second specimen (NHMUK In. 59376) was attributed to *Petrophlebia anglicanopsis* by Zeuner (1962). However, this specimen corresponds to the distal half of a wing and, therefore, there is little similarity with the holotype (basal portion). This fossil is probably referable to Campterophlebiidae, as there is a long pterostigma present, which is basally recessed, but its attribution to the same species is questionable.

Petrophlebia Tillyard 1925

Type species. Petrophlebia anglicana Tillyard, 1925

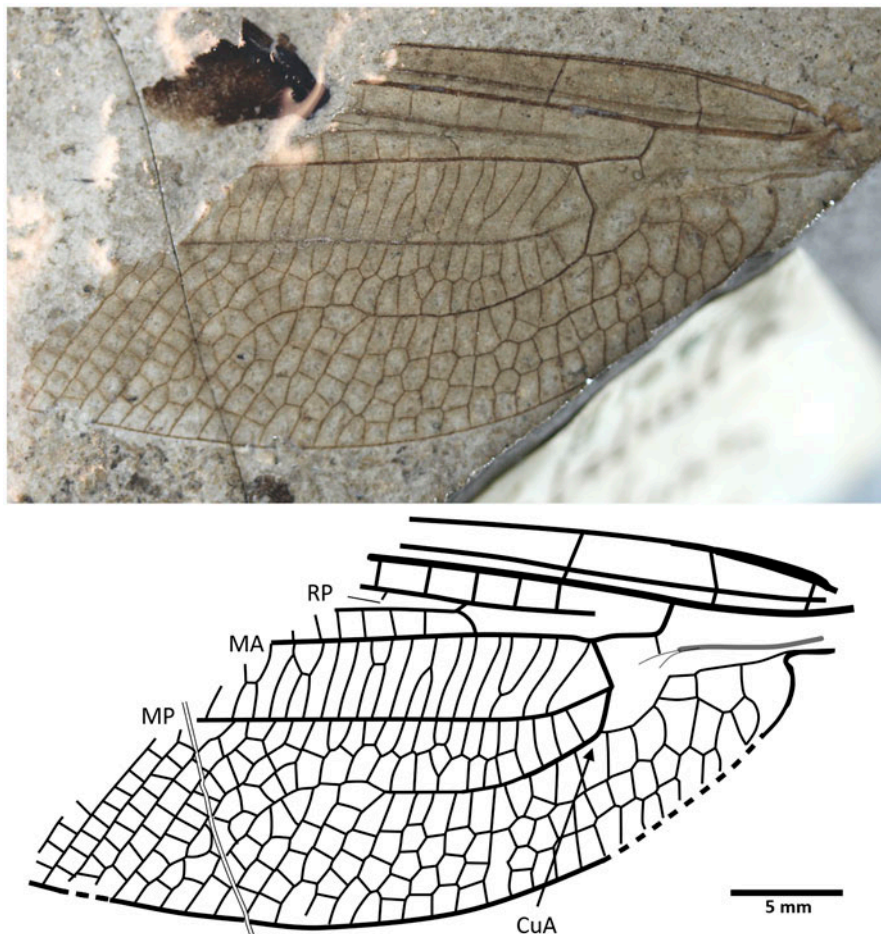


Fig. 3. Holotype of *Petrophlebia anglicana* (NHMUK I.10494), photograph and reconstruction.

Petrophlebia anglicana Tillyard 1925

1925 *Petrophlebia anglicana* Tillyard, p. 13, pl. 1, fig. 2, text-fig. 2.

1993 *Petrophlebia anglicana* Tillyard; Nel *et al.*, p. 236, fig. 195.

2011 *Petrophlebia anglicana* Tillyard; Petrulėvičius *et al.*, p. 736.

2012b *Petrophlebia anglicana* Tillyard; Li *et al.*, p. 66.

Holotype. NHMUK I.10494 (Fig. 3).

Locality and age. Barrow-upon-Soar, Leicestershire; Hettangian (Planorbis Chronozone).

Remarks. This taxon was originally placed in Liasophlebiidae but was later transferred to Architemistidae Tillyard 1917 by Fraser (1957); and then Campterothlebiidae by Nel *et al.* (1993) where it was retained by Petrulėvičius *et al.* (2011). Bechly (2016) proposed to restore it to Architemistidae on the basis of two putative synapomorphies: a single row of very long transverse and oblique cross-veins in the postdiscoidal area of the hindwing and IR2 originating on RP3/4. The first character is of relatively little value because it is also present in some campterothlebiid genera, e.g. *Sogdophlebia*, *Angaroneura* and *Sibirioneura amurica*. The second character is of greater value because it is more rarely distributed in these Odonata. Moreover, the comparable parts of the hindwing venation of *Petrophlebia anglicana* and of *Archithemis liassina* (Strickland,

1840) (after the reconstruction proposed by Tillyard 1917) are nearly identical. However, the holotype of *A. liassina* (specimen WARMS G 307 from the Hettangian Planorbis Chronozone of Nook quarry, Bickmarsh, Warwickshire) is rather poorly preserved (Fig. 3). If what is now visible is congruent with the characters of *Petrophlebia*, the most important structures are very poorly visible.

The type species *Archithemis brodiei* (Geinitz, 1884) of Architemistidae was originally named *Libellula (Aeschna) brodiei*, and designated after the original figure of Brodie (1845, pl. 8, fig. 1). Handlirsch (1906–1908, pl. 42, fig. 1) later considered it as the type species of *Archithemis* Handlirsch, 1906–1908. The specimen was figured by Brodie (1845, pl. 8, fig. 1) under the label ‘*Libellula Brodiei* (Buckman. Geol. Proc. vol. iv. p. 211), Upper Lias, Dumbleton’, yet the figure by Handlirsch (1906–1908) shows a discoidal cell divided into a hypertriangle and a triangle by a cross-vein, IR2 on RP3/4 is not branched, and a subdiscoidal space is present, which is very similar to those of Heterophlebiomorpha, and not to those of Isophlebioptera. The specimen in Brodie’s figure was found to correspond to the specimen WARMS G 8079 (Fig. 4). Buckman (1843, p. 212) indeed named a fossil *Libellula (Aeschna) brodiei* from the county of Gloucestershire, but without describing it. Tillyard (1917, fig. 157) figured (apparently after Handlirsch) the basal part of the wing with structures completely different, viz., a one-celled discoidal rectangle, IR2 beginning on RP3/4 and a subdiscoidal cell of isophlebiopteran type.

It is clear from the photograph of the holotype of *Libellula (Aeschna) brodiei* (Fig. 4) that the specimen is a hindwing with a clear division of the discoidal space into a hypertriangle and a discoidal triangle, plus a subdiscoidal space of the heterophlebioid type. This fossil seems to have no supplementary antenodal cross-veins in the space between C and ScP, which would suggest a position in Heterophlebiidae. Nevertheless, this fossil is too incomplete to allow a precise comparison with the other taxa in this family. As a result, *Archithemis brodiei* is a Heterophlebioidea incertae sedis. *Archithemis* and Architemistidae must be transferred to this superfamily.

Brodie (1845, pl. 10, fig. 4) figured another hindwing that corresponds exactly to the pattern of venation of *Petrophlebia* and was named by Brodie as ‘Wing of Mr. Strickland’s *Aeschna liassina* drawn from the original’, which corresponds to the original figure of Strickland (1840, fig. 11). *Archithemis liassina* (Strickland, 1840) differs markedly from *Archithemis brodiei* in the absence of division of the discoidal space into a hypertriangle and a triangle (Fig. 5). Thus, it does not belong to Heterophlebioidea. It does not belong to *Archithemis* and Architemistidae, which must be reduced to the sole *Archithemis brodiei*, as *Petrophlebia anglicana* is referable to Campterothlebiidae (see above). *Archithemis liassina* also belongs to Campterothlebiidae, but its

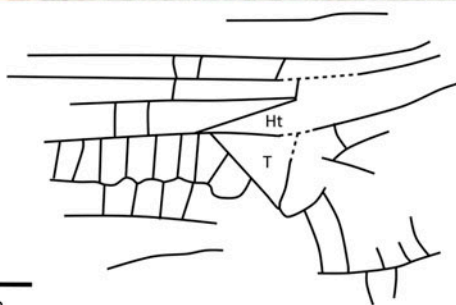
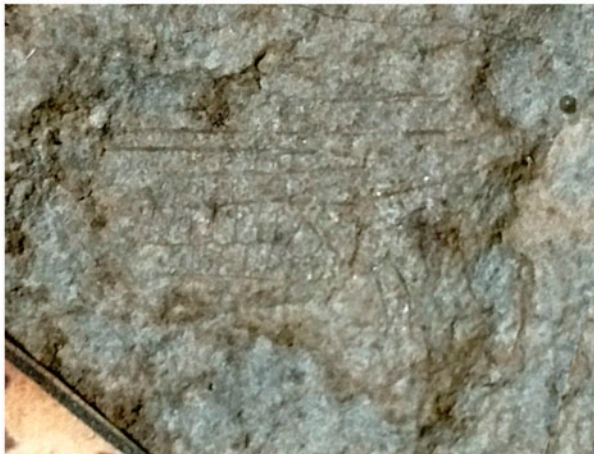


Fig. 4. Holotype of *Libellula (Aeschna) brodiei* (WARMS G 8079), photograph and reconstruction.

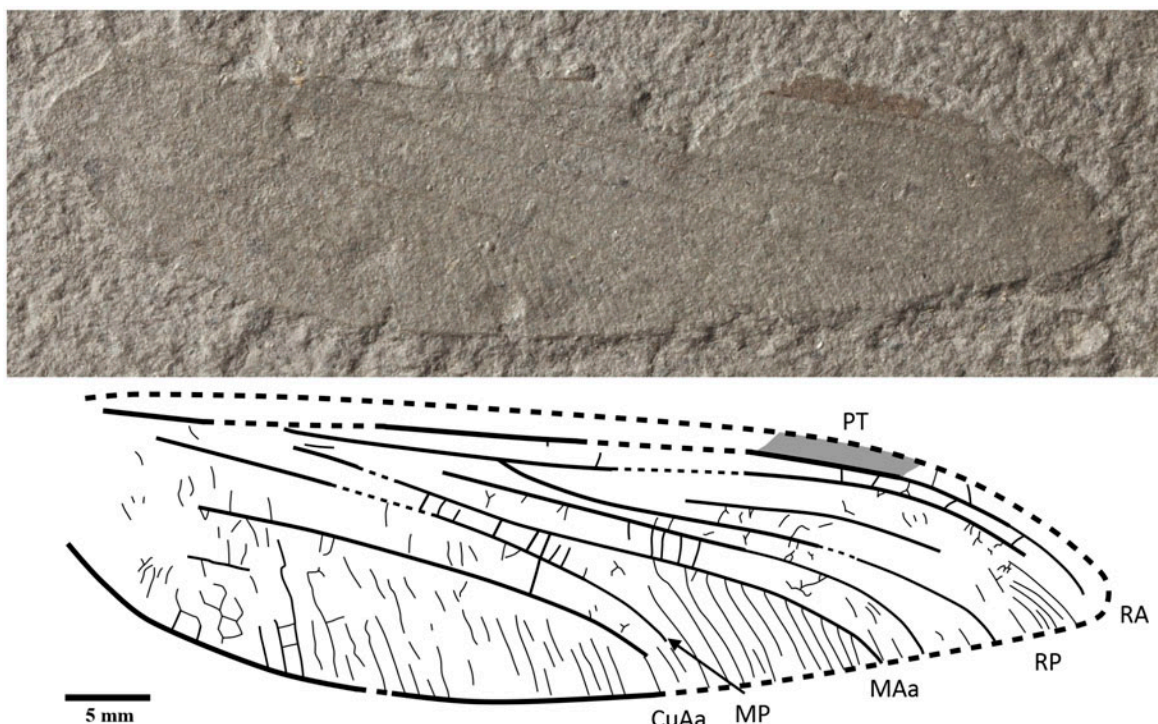


Fig. 5. Holotype of *Archithemis liassina* (WARMS G 307), photograph and reconstruction.

exact generic position remains uncertain because of its poor preservation.

Discussion

Lateophlebia is the fourth and one of the oldest representatives of Campterothlebiidae in the Liassic of Europe, after *Campterothlebia* and *Gallodorsettia* from the Toarcian of Germany and the Grand-Duchy of Luxembourg, and *Dorsettia*, which is contemporaneous with *Lateophlebia* also found in the ‘flatstones’ of Stonebarrow (Whalley 1985). All European specimens were collected from facies associated with shallow marine palaeoenvironments. In contrast, campterothlebiids from Asia were preserved in deposits associated with freshwater environments, and are much more common and diverse.

As well as describing *Lateophlebia* in Campterothlebiidae in this paper, we have discussed the status Archithemistidae. Based on the holotype of the type species *Archithemis brodiei* it is clear from the preserved characters that it is closer to Heterophlebiomorpha, and not to Isophlebioptera. However, owing to the poor preservation of the specimen, it has been designated as Heterophlebioidea incertae sedis, and the genus and family transferred to this superfamily.

Data access statement

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

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Disclosure statement

No potential conflict of interest was reported by the authors.

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