**Research Article**

**Chrismooreia michaelbehei** gen. et sp. nov. (Insecta: Odonata: Asiopteridae), a new fossil damsel-dragonfly from the Early Jurassic of England

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**Abstract**

A new fossil damsel-dragonfly *Chrismooreia michaelbehei* gen. et sp. nov. (Insecta: Odonata: Asiopteridae) is described from the Early Jurassic of Charmouth in England. This fossil is the best preserved and first complete specimen of the Mesozoic family Asiopteridae, which was previously only known from isolated wings, and actually represents one of the most complete Liassic odonates known. Body characters are described for the first time and include compound eyes that meet dorsally, robust thorax, legs with short spines, and very long leaf-like cerci. The forewing venation features a short fusion of AA+Cu with MP near the tip of the discoidal cell, which is an absolutely unique character state within the order Odonata, here described for the first time. The wing venation shows a mixture of sphenophleboid and asiopterid characters, with the latter characters dominating. The classification of Sphenophlebidae is discussed and its synonymy with Asiopteridae is tentatively rejected, but not ruled out. As further addition to the Liassic odonate fauna from the Charmouth fossil locality, a specimen of *Protomyrmeleon cf. brunonis* is featured but not formally described as first record of the suborder Archizygoptera and the family Protomyrmeleontidae.

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**INTRODUCTION**

Fossil insects from the Early Jurassic (Liassic) of Europe are known from a variety of localities such as the Rhein-Main-Donau-Channel at Bachhausen, Kerkhofen, and Sulzkirchen (Frankonia, Bavaria, Germany), Holzmaden (Baden-Württemberg, Germany), Döbbertin and Grimmen (Western Pomerania, Germany), region of Braunschweig with Schandelah, Grassel, and Hondelage (Lower Saxony, Germany), Bascharage (Luxembourg), and Charmouth (Dorset, England) [1–2].

The calcareous mudstones exposed at cliffs along the coast of Dorset, especially at Charmouth, were formed in a marine deltaic environment about 191 million years ago. Fossil insects are allochthonous elements of the taphocoenosis, washed in from surrounding land [3–4], and thus are relatively rare with only some hundred specimens recovered from 11 orders and 66 species [5–6]. We here report two new fossil odonate specimens, of which the better preserved one is a damsel-dragonfly (= “anisozygopteran”) described as new genus and species of the family Asiopteridae, while the other represents the first record of Protomyrmeleontidae for this locality.

Like most fossil insects from the Liassic of Eurasia the family Asiopteridae was previously only known from isolated wings. Recently, a complete specimen of *Turanopteron pommerana* was reported and pictured in a museum flyer [7], but is not yet formally described. The present specimen therefore represents not only a new genus and species of Asiopteridae, but also by far the best-preserved and the first almost complete specimen of the whole family and actually of all Liassic odonates. Thus, it greatly enhances our knowledge about this extinct group of damsel-dragonflies.

**METHODS**

Observations and drawings were made using a Leica M80 (1.6 Plan Achromat lens) stereo microscope with camera lucida system. Macro photos were made with a Sony SLT A65 and Sigma 105mm/f2.8 macro lens with JJC LED macro ring light. Micrographs were taken with a Leica DFC490 digital macro camera on a Leica Z16-Apo Microscope, using Leica Application Suite 3.8.0 for focus stacking. All photos were polished with Adobe Photoshop CC 2018 imaging software on a MacBook Pro.
A new damsel-dragonfly from the Early Jurassic of England

Pro, but no parts of the fossil were manipulated except for overall hue, brightness, and contrast (some light reflexes on the stone matrix outside of the fossil wing were removed in Figure 13). Figures 5–13 were photographed with the fossil covered with ethanol alcohol for contrast enhancement.

The classification of odonates is mainly based on Bechly [8–10]. The terminology of odonate wing venation is based on Riek & Kukalová-Peck [11], modified by Nel et al. [12] and Bechly [8]. The abbreviations used are: AA = Anal vein, arc = arculus, ax = primary antenodal crossvein, C = Costal vein, Cu = Cubitus vein, CuA = Cubitus anterior vein, dc = discoidal cell, IR = Interradius intercalary vein, MA = Media anterior vein, MP = Media posterior vein, RA = Radius anterior vein, RP = Radius posterior vein, ScP = Subcostal vein.

To satisfy the requirements of §8 and §21 of the 2012 ICZN Amendment to the International Code of Zoological Nomenclature for the availability of new scientific names and nomenclatural acts in electronic publications, the present work has been properly registered in ZooBank with the LSID http://zoobank.org/urn:lsid:zoobank.org:pub:A7376EE5-176F-410D-913B-4C898325B85E. The journal Bio-Complexity of Biologic Institute is independently archived digitally by CLOCKSS (https://www.clockss.org/clockss/Participating_Publishers), which is officially approved by the International Commission of Zoological Nomenclature [13].

RESULTS

The here described fossil insect can be classified as follows:
Order Odonata Fabricius, 1793
Clade Epiproctophora Bechly, 1996
(= Epiprocta Lohmann, 1996)
Suborder Isophlebiptera Bechly, 1996
Family Asiopteridae Pritykina, 1968
(= Oreopteridae Pritykina, 1968)

This new genus *Chrismoorea* gen. nov., is registered at http://zoobank.org/urn:lsid:zoobank.org:act:F85DAF93-B5CC-45E1-913B-4C898325B85E.

The type species (genotype) is *C. michaelbehei* sp. nov. by present designation.

Etymology: The new genus is named in honor of the collector Mr. Chris Moore (Charmouth) in recognition of his contributions to paleontology.

Differential diagnosis: The new genus is very similar to *Turanopteron*, but differing from this genus and all other Asiopteridae by the following set of characters: a very large size with

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**Figure 1:** Macro photo of *Chrismoorea michaelbehei* gen. et sp. nov. (*Asiopteridae*). The counter slab of the holotype without number in the private collection of Chris Moore, Liassic, Charmouth. Scale bar = 20 mm. Note the ammonite *Promicroceras planicosta* (*Eoderoceratidae*).

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A new damsel-dragonfly from the Early Jurassic of England

Figure 2: Macro photo of Chrismooreia michaelbehei gen. et sp. nov. (Asiopteridae). The positive slab of the holotype without number in the private collection of Chris Moore, Liassic, Charmouth. Scale bar = 10 mm. doi:10.5048/BIO-C.2018.1.f2


Holotype specimen: The holotype specimen is a fossil odonate without collection number in the private collection of Mr. Chris Moore (Charmouth, Dorset, England), who declared to the author that this specimen will be deposited in the projected museum for the Jurassic Coast UNESCO World Heritage Site in Charmouth. No other fossils of this species are known yet.


Holotype specimen: The holotype specimen is a fossil odonate without collection number in the private collection of Mr. Chris Moore (Charmouth, Dorset, England), who declared to the author that this specimen will be deposited in the projected museum for the Jurassic Coast UNESCO World Heritage Site in Charmouth. No other fossils of this species are known yet.

The type locality is Charmouth in Dorset, England, UK, and the type stratum is the Obtusum Zone of the Charmouth Mudstone Formation, which has been dated as Upper Sinemurian in the Early Jurassic / Liassic period, about 191 million years ago.

Etymology: The new species is named in honor of Professor Michael Behe (Lehigh University) for his groundbreaking contributions to intelligent design theory, which had great influence on the personal views of the author.

Differential diagnosis: The diagnosis is same as for the type genus since it is monotypic.

Description: The holotype specimen (illustrated in Figures 1–12) includes the positive slab (part) and counter slab (counter-part) of a very well-preserved and relatively complete fossil damsel-dragonfly with a total body length of 78.5 mm and an estimated wing span of about 114 mm. Please note that the animal is preserved in dorsal aspect on the positive slab, so that the anatomical left and right side are reversed on the counter slab, which shows most of the animal, while the positive slab only shows thorax, head and right forewing.

The head is only preserved in the positive slab; it is 6.2 mm wide and 3.0 mm long, with a large frons, basal 2 segments of the left antenna, tips of the left maxilla, and two large compound eyes visible, which are not separated but meet dorsally in a manner similar to modern Cordulegastridae. Ocelli are not preserved.

The prothorax is shield-like (maximally 4.4 mm wide and 2.6 mm long) and the pterothorax is relatively short and robust (10.4 mm long and 7.0 mm wide).

The right forewing is completely preserved on both the positive slab and counter slab, but the wing venation is more clearly visible in the positive slab. The left forewing is missing. The total forewing length is 54.4 mm, with a maximum width of 10.3 mm. Primary antenodal crossveins ax1 and ax2 are very distinct and slanted towards each other (5.2 mm apart along ScP); no secondary antenodal crossveins are present in the first row between C and ScP; no secondary antenodal crossveins are present in the second row between ax1 and ax2 either; 9 secondary antenodal crossveins are found in the second row between ScP and RA distal of ax2. The space between RA and RP basal of the subnodus is evenly crossed by 16 antsubnodal crossveins (with no cordulegastrid gap of antsubnodals near the subnodus). The nodus is situated at 51.5% of the wing length; ScP is without kink at the nodus; the nodal veinlet n is short and perpendicular; the subnodal veinlet sn is oblique. 12 postnodal crossveins are non-aligned with the 15 postsubnodal crossveins beneath them; there is no libellulid gap of postsubnodal crossveins near the subnodus. The pterostigma is 5.6 mm long and 1.0–1.2 mm wide, very elongate, with oblique sides and broadened margins; the pterostigmal brace is indistinct; there are only two crossveins (2–3 cells) beneath the pterostigma; crossveins between C and RA distal of the pterostigma are oblique and sigmoidally shaped. IR1 is long and not zigzagged, with a maximum of 5–6 rows of cells between it and RP1, and
with a maximum of 3–4 rows of cells between it and RP2; there is no secondary IR2 originating at the pterostigma; RP2 originates one cell (0.8 mm) distal of the subnodus; there is a single lestine oblique vein between RP2 and IR2 that is 6 cells (4.4 mm) distal of the subnodus. IR2 is basally fused to RP3/4, originating from a symmetrical furcation 3.0 mm distal of the origin of RP3/4; IR2 ends at the level of the distal side of the pterostigma; IR2 is parallel to RP3/4, with 2–5 rows of cells between their distal parts; no radial supplement Rspl exists. RP3/4 is widely divergent from MA. The midfork is 8.6 mm distal of the arculus; no antefurcal crossveins are present between RP and MA. MA is gently curved, distally zigzagged, and distally strongly converging to MP with always only a single row of cells between them; no median supplement Mspl exists. MP is gently curved, reaching far beyond the level of the nodus. CuA is strongly zigzagged, so that its branches can hardly be distinguished from the cross-venation in the cubital field, but CuA seems to be short and not reaching beyond the level of the nodus. AA+Cu fuses to MP shortly basal of the tip of the discoidal cell, and CuA unfuses from MP shortly distal of the tip of the discoidal cell. The CuP-crossing (= anal crossing) is not preserved. The discoidal cell is triangular with a very acute angle, free, and basally wide open, with a straight upper portion of the arculus (origins of RP and MA) aligned with the distal discoidal vein; the arculus is incomplete and situated between ax1 and ax2, only 1.4 mm distal of ax1; an oblique subdiscoidal vein is present between the tip of the discoidal cell and the hind margin of the wing; a subdiscoidal cell is absent due to the fusion of AA+Cu with MP. The basal space is free.

Figure 3: Macro photo of habitus of *Chrismoorea michaelbehei* gen. et sp. nov. (Asiopteridae). The counter slab of the holotype. Scale bar = 10 mm. doi:10.5048/BIO-C.2018.1.13
A new damsel-dragonfly from the Early Jurassic of England

The right hind wing is completely preserved on the counter slab, but the posterior wing margin is only preserved in the apical region. Of the left hind wing only a fragment of the apical region is visible on the counter slab. No hind wings are visible on the positive slab. Total hind wing length is 49.1 mm, the maximum width is unclear because of a poorly preserved posterior wing region, but it is about 10 mm in the cubital region. Primary antenodal crossveins ax1 and ax2 are very distinct and parallel to each other (5.1 mm apart along the ScP); there are no secondary antenodal crossveins in the first row between C and ScP, and no secondary antenodal crossveins between ax1 and ax2 in the second row either; there are several (probably about 7) secondary antenodal crossveins in the second row between ScP and RA distal of ax2, but only three of them are clearly visible. The space between RA and RP basal of the subnodus is evenly crossed by 12 antesubnodal crossveins (no cordulegastrid

Figure 4: Camera lucida drawing of Chrismooreia michaelbehei gen. et sp. nov. (Asiopteridae). Composite of counter slab and positive slab of the holotype without number in the private collection of Chris Moore, Liassic, Charmouth. Scale bar = 10 mm. doi:10.5048/BIO-C.2018.1.f4
A new damsel-dragonfly from the Early Jurassic of England

A gap of antsubnodals is found near the subnodus. The nodus is situated at 45.5% of the wing length; ScP is without kink at the nodus; the nodal veinlet n is short and perpendicular; the subnodal veinlet sn is oblique. 12 postnodal crossveins are non-aligned with the 11 postsubnodal crossveins beneath them; there is no libellulid gap of postsubnodal crossveins near the subnodus. The pterostigma is 6.4 mm long and 0.8–1.0 mm wide, very elongate, with oblique sides and broadened margins; the stigmal brace is not precisely aligned with the anterior margin of the pterostigma; there are only two crossoves (2–3 cells) beneath the pterostigma; crossoves between C and RA distal of the pterostigma are oblique and sigmoidally shaped. IR1 is long and not zigzagged, with a maximum of 5–6 rows of cells between it and RP1, and with a maximum of 3–4 rows of cells between it and RP2; there is no secondary IR2 originating at the pterostigma; RP2 originates one cell (0.5 mm) distal of the subnodus; a single lestine oblique vein o lies between RP2 and IR2, five cells (4.3 mm) distal of the subnodus. IR2 is basally fused to RP3/4, originating from a symmetrical furcation 3.2 mm distal of the origin of RP3/4. RP3/4 is widely divergent from MA. The midfork is 5.6 mm distal of the arculus; no antefurcal crossoves are found between RP and MA. The MA is gently curved, distally zigzagged, and distally strongly converging to MP with only a single row of cells between them. MP is relatively straight, reaching far beyond the level of the nodus. CuA is strongly zigzagged, so that its branches can hardly be distinguished from the cross-venation in the cubital field, but CuA seems to be short, not reaching the level of the nodus. AA+Cu are not fused to MP near the tip of discoidal cell (this is different than the forewing). The CuP-crossing (= anal crossing)
is short and oblique. The discoidal cell is quadrangular and free
(unicellular, 1.7 mm long), basally closed, with a short basal
side (basal width 0.2 mm) and long distal side (distal width
0.9 mm), thus strongly widened distally, and correlated with
a basally widened postdiscoidal field; the arculus is complete
and broken (kinked), and is situated between ax1 and ax2, only 0.8
mm distal of ax1; a long subdiscoidal vein delimits a widened
subdiscoidal cell that seems to be free. The basal space is free.
The anal margin is not preserved, so that it is not visible if there
was an anal angle or not.

The femur of the left foreleg and the femur and tibia of the
right foreleg are preserved in the positive slab (the femur is
5.8 mm long and 1.0 mm wide, the tibia 5.5 mm long and
0.4–0.5 mm wide, with a row of tiny spines), while a dislocated
left middle leg (the femur is 7.8 mm long and 1.1 mm wide,
the tibia is 7.7 mm long, 0.5–0.6 mm wide, with row of short
spines) is preserved on the counter slab. No tarsi are preserved.

The complete abdomen is preserved (with a total length of
50.6 mm without terminal appendages, and a width of 2.2–3.9
mm), except for parts of segment 7 (the respective lengths are:
I = 1.6 mm; II = 2.5 mm; III = 7.8 mm, IV = 7.8 mm, V =
8.2 mm, VI = 7.9 mm, VII = 8.4 mm, VIII = 2.1 mm, IX =
1.9 mm, and X = 1.8 mm). No genitalia (neither male second-
ary genital apparatus on segments II+III nor female ovipositor
on segments VIII+IX) are visible, because the abdomen is pre-
served in dorsal aspect.

At the end of the abdomen two extremely elongate leaf-
like cerci are visible (with a length of 11.9 mm, and a median
width of 1.6 mm), which have a median longitudinal keel. No
epiproct or paraprocts are visible.

Together with the fossil damsel-dragonfly there is a small
ammonite (diameter 39.2 mm) completely preserved on the
same counter slab, belonging to the species Promicroceras plani-
costa (Eoderoceratidae), which is the most common ammonite
in the Liassic of Dorset.

DISCUSSION

The sex of the specimen cannot be determined with cer-
tainty, but the very elongate leaf-shaped and keeled cerci are
very similar to the females of a few recent Aeshnidae species
(e.g., Heliaeschna uninervulata Martin, 1909 or Oligoaeschna
foliacea (Lieftinck, 1968)), suggesting that it might be a female
specimen. Furthermore, the visible appendages would hardly
be suited for grasping a female head or prothorax as would be
required for a male specimen.

The strange fusion of AA+Cu with MP near the tip of the
forewing discoidal cell is a very remarkable feature never seen
before in any living or fossil dragonfly. This character state
might be a teratology, but given the fact that there is only a
very short subdiscoidal veinlet in the most similar asiopterid
Turanopteron major [14], it is here considered as a diagnostic
trait of the new genus and species.

Taxonomic attribution

The extinct odonate suborder Isophlebioptera also includes
the enigmatic Mesozoic families Euthemistidae, Spheno-
phlebiidae, Oreopteridae, and Asiopteridae [8-10, 15-16].
Oreopteridae has been considered a synonym of Asiopteridae
by Bechly [9–10].

Ansorge [17] attributed the genus Sphenophlebia to Ore-
opteridae, mainly based on his discovery of the new species
Sphenophlebia pomerana and his observations on the para-
type of Sphenophlebia interrupta. Sphenophlebia pomerana
was transferred to the asiopterid genus Turanopteron by Bechly
[9] because of the nearly identical venation that was already
mentioned by Ansorge [17]. A synonymizing of Sphenophle-
biaeidae with Asiopteridae, implied by Ansorge [17], would be
problematic since he has only seen the paratype of S. interrupta
and therein observed a lack of secondary antenal crosses
between C and ScP, while Bode [18] in his original descrip-
tion explicitly described and pictured 20 antenal crosses

Figure 9: Micro photo of hind wing discoidal area of Chrismoorea michaelbehei gen. et sp. nov. (Asiopteridae). Counter slab of the holotype. Scale bar = 1 mm. Note the broadened subdiscoidal cell. doi:10.5048/BIO-C.2018.1.f9

Figure 10: Micro photo of head of Chrismoorea michaelbehei gen. et sp. nov. (Asiopteridae). Positive slab of the holotype. Scale bar = 2 mm. Note the compound eyes meet dorsally. doi:10.5048/BIO-C.2018.1.f10
between C and ScP for the holotype specimen. As mentioned by Li et al. [15], Bode’s description remains doubtful. This is also suggested by his drawing of *Ensphingophlebia* with the basal space divided by 2–4 crossveins, which seems highly unlikely. Without a proper revision of the holotype of *S. interrupta* the family Sphenophlebiidae cannot be safely synonymized with the family Asiopteridae, which always lacks secondary antenodal crossveins between C and ScP and also always lacks antefurcal crossveins.


According to Bechly [1] *Eosagririon risi* Handlirsch, 1920 (Eosagririonidae) from the Liassic of Dobbentin is either closely related to or belongs within Sphenophlebiidae. *Eosagririon* was pictured by Handlirsch [20] with secondary antenodal crossveins between C and ScP, but this may be erroneous as it was in many of the older descriptions of fossil dragonflies. But it seems to share with *Chrismooreia* gen. nov. the fusion of IR2 with RP3/4. *Euphaeopsis multinervis* (Hagen, 1862) from the Upper Jurassic of Solnhofen was redescribed and attributed to Isophlebioidea by Fleck et al. [21], but transferred to Sphenophlebiidae by Bechly [22], because of the pattern of intercalary veins.

All six genera currently classified in Sphenophlebiidae share with other Parazygoptera within Isophlebioptera the unusual origin of RP2 distal of the subnodus, contrary to Euthemistidae and Isophlebioidea, but it must be noted that a cladistic study by Nel et al. [16] challenged the validity of the taxon Parazygoptera as only weakly supported by this single homoplastic character. *Sphenophlebia interrupta*, *Ensphingophlebia undulata*, *Eosagririon risi* and maybe *Euphaeopsis multinervis* would share the presence of secondary antenodal crossveins between C and ScP with Euthemistidae, contrary to most other Isophlebioptera (with a few exceptions like *Isophlebia aspasia*, *Pseudotriassothe- nis minensis*, *Mesoplebia antinodalis*, *Italophlebia gerasuvtii*, and maybe *Progonophlebia cromptoni*), but only if the original descriptions of Bode [18] and Handlirsch [20, 23] are correct. Two of the three syntype specimens of *Ensphingophlebia* described and pictured by Bode [18] have IR2 fused to RP3/4 very similar to *Chrismooreia* gen. nov. described above, but they all differ very much in the shape of the discoidal cell, the presence of two rows of cells between the distal parts of MA and MP; and of course the second antenodal crossveins and crossed basal space. *Mesoepiophlebia veronicae* shares with Asiopteridae a lack of secondary antenodal crossveins between C and ScP, but differs in the not zig-zagged distal MA and IR2 as well as the presence of a few antefurcal crossveins (just as pictured by Bode [18] for *Sphenophlebia interrupta* and *Ensphingophlebia undulata*). *Proeuthemis pritykinae* shares with Asiopteridae a lack of secondary antenodal crossveins between C and ScP and the zig-zagged distal MA, but it lacks the distally zigzagged IR2 and also has a few antefurcal crossveins (like *Euthemis*, but unlike *Sinoeuthemis*) [24]. The overall character pattern obviously is very much incongruent (homoplastic). To avoid weakening the well-established diagnosis of Asiopteridae I here prefer to retain Sphenophlebiidae as a distinct family, also because all four included genera share with Euthemistidae ( contrary to Asiopteridae) several long intercalary veins between IR1 and RP1, and between IR1 and RP2, as well as between RP3/4 and IR2, and between IR2 and RP2.

The body characters of Asiopteridae, here described for the first time, differ very much from the recently first described body fossil of Euthemistidae [15], which has distinctly separated compound eyes and very short female cerci.

Figure 11: Micro photo of right foreleg of *Chrismooreia michaelbehei* gen. et sp. nov. (Asiopteridae). Positive slab of the holotype. Scale bar = 2 mm. Note the short spines on tibia. doi:10.5048/BIO-C.2018.1.f11

Figure 12: Micro photo of cerci of *Chrismooreia michaelbehei* gen. et sp. nov. (Asiopteridae). Counter slab of the holotype. Scale bar = 5 mm. Note the median keel on the extremely elongate cerci. doi:10.5048/BIO-C.2018.1.f12
In any case the high degree of homoplasy shows that the overall pattern of similarity is very incongruent and does not readily align with a hierarchical system required by evolutionary classification. While surprising from the perspective of common ancestry, such incongruences would not be surprising from the perspective of common design. To avoid a dilemma here, I recommend basing classification on maximum similarity rather than assumed common descent. Also on this basis I here tentatively retain Sphenophlebiidae as a distinct family and attribute the new taxon to Asiopteridae, with which it shares most features of the wing venation (the only known character complex in the other genera of Asiopteridae).

First record of Protomyrmeleontidae for Charmouth

In addition to the new genus described above, I also received in 2011 a slab with an isolated fossil damselfly wing from the Liassic of Charmouth. This fossil is from the private collection of Mr. Thomas Bastelberger, who happens to be the grandson of the well-known German lepidopterologist Max Bastelberger. He collected this fossil (coll. no. AR 428) himself while searching the burden pile at Charmouth, and declared that the fossil will be donated to the State Museum of Natural History Stuttgart (SMNS) in Germany [25]. It turned out to be a Protomyrmeleontidae of the genus *Protomyrmeleon* (*P. cf. brunonis* Geinitz, 1887). It has a wing length of about 22.5 mm, but a detailed drawing of the venation was not feasible because there are at least three wings superimposed to each other (Figure 13). This is the first fossil record of the suborder Archizygoptera and the family Protomyrmeleontidae for the Liassic of Charmouth and documents the wide distribution of the genus *Protomyrmeleon* in Europe and NE Asia during the Mesozoic era.

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A new damsel-dragonfly from the Early Jurassic of England