Earth and Environmental Science Transactions of the Royal Society of Edinburgh, **104**, 283–306, 2014 (for 2013)

Dragonflies and damselflies (Insecta: Odonata) from the Late Eocene of the Isle of Wight

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ABSTRACT: The odonatan fauna of the Late Eocene of the Isle of Wight is revised. The following taxa are revised or described: the gomphaeschnids *Oligoaeschna*? *anglica* Cockerell & Andrews, 1916 and *Anglogomphaeschna eocenica* gen. et sp. nov.; the aeshnids '*Oplonaeschna*' *vectensis* Cockerell & Andrews, 1916, *Aeschnophlebia andreasi* Nel *et al*., 2005, *Oligaeschna wedmanni* sp. nov., and a 'Gynacanthinae' species; *Neophya legrandi* sp. nov., first fossil representative of the Cordulephyidae; three undescribed 'Corduliidae'; *Eomacrodiplax incompleta* gen. et sp. nov., first fossil representative of the Urothemistidae; the second representative of the Palaeogene family Bolcathoridae; a Thaumatoneuridae Dysagrionini species A; the megapodagrionid *Oligoargiolestes oligocenum* Kennedy, 1925; the two hypolestids *Anglohypolestes fasciata* gen. et sp. nov. and *Eohypolestes hooleyi* gen. et sp. nov.; the coenagrionid '*Enallagma*' *oligocena* Cockerell & Andrews, 1916, and three other undescribed species; *Angloprotoneura emilielacroixi* gen. et sp. nov., first fossil European representative of the damselfly family Protoneuridae; and the lestid *Lestes* aff. *regina* Théobald, 1937. This fauna has strong similarities with the Recent Afrotropical and Indo-Malayan Odonata, suggesting a warm palaeoclimate for the Late Eocene of the Isle of Wight. '*Megalestes*' *anglicus* Cockerell, 1915 is a Zygoptera Lestiformia or Coenagrionomorpha of uncertain affinities.

KEY WORDS: Palaeobiogeography, palaeoclimate, revision of fauna

The Odonata from the German and French Oligocene are now relatively well known; however, little attention has been given to the dragonflies and damselflies of the Palaeogene of England (see Nel & Jarzembowski 1999). Thanks to the INTAS project, we had the opportunity to study the rich collection of Odonata from the Late Eocene Insect Bed of the Isle of Wight, stored in the Natural History Museum (London), and the Museum of Isle of Wight Geology (Isle of Wight). The fossils are preserved as imprints of separated wings, frequently fragmentary, and a few body structures. Fortunately, these wing fragments are generally in a good state with colour preserved. Surprisingly, this fauna is very diverse, with representatives of two Recent families previously not known in the fossil record and three others poorly known.

The insects are preserved in concretions or tabular bands of very fine-grained micrite, known as 'Insect Limestone' or 'Insect Bed', on the northwest and northeast coast of the Isle of Wight. The unit where these concretions/bands occur lies towards the base of the Bembridge Marls Member (Solent Group: Bouldnor Formation). The Bembridge Marls were considered to be early Oligocene in age (Gale *et al*. 2006), although more recent publications suggest that they could be latest Eocene in age (Hooker *et al*. 2007, 2009).

Most of the specimens at the Natural History Museum belong to the A'Court Smith (purchased 1877, 1883), P.B. Brodie (purchased 1898) and R.W. Hooley (purchased 1924) collections. They are labelled 'Gurnard Bay' or 'Gurnet Bay' (which is an old name for Gurnard Bay). However, Smith collected specimens all the way from West Cowes to Newtown River on the northwest side of the Isle of Wight (Jarzembowski 1980). Most of the specimens probably came from Thorness Bay (Jarzembowski 1976). Brodie and Hooley acquired parts of Smith's collection, so parts and counterparts of individual insects have turned up in all three collections. The parts and counterparts often have different numbers because they were registered at different times. An additional collection was discovered at the Sedgwick Museum, Cambridge by A. J. Ross. This collection has also yielded counterparts of specimens at the NHM, which indicates that this is another part of the Smith collection. A label with '1883' on it suggests that the Sedgwick Museum acquired this collection in 1883, the same year that the NHM purchased specimens from Smith.

In this work, we follow the wing venation nomenclature of Riek (1976), Riek & Kukalová-Peck (1984), emended by Kukalová-Peck (1991), Nel *et al*. (1993) and Bechly (1996). The higher classification of fossil and extant Odonatoptera is based on the phylogenetic system of Bechly (1996).

Institutional repository abbreviations. BMB, Booth Museum of Natural History, Brighton; CAMSM, Sedgwick Museum of Earth Sciences, University of Cambridge; IWCMS, Isle of Wight County Museum Service; MIWG, Museum of Isle of Wight Geology, Isle of Wight; MNEMG, Maidstone Museum & Bentlif Art Gallery; NHMUK, Department of Palaeontology, Natural History Museum, London; PORT, Department of Geology, University of Portsmouth; USNM, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

1. Systematic palaeontology

Order Odonata Fabricius, 1793
Suborder Anisoptera Selys in Selys & Hagen, 1854
Superfamily Aeshnoidea Leach, 1815
Family Gomphaeschnidae Tillyard & Fraser, 1940
(*sensu* Bechly 1996)
Genus *Oligoaeschna* Selys, 1889

doi:10.1017/S175569101400005X

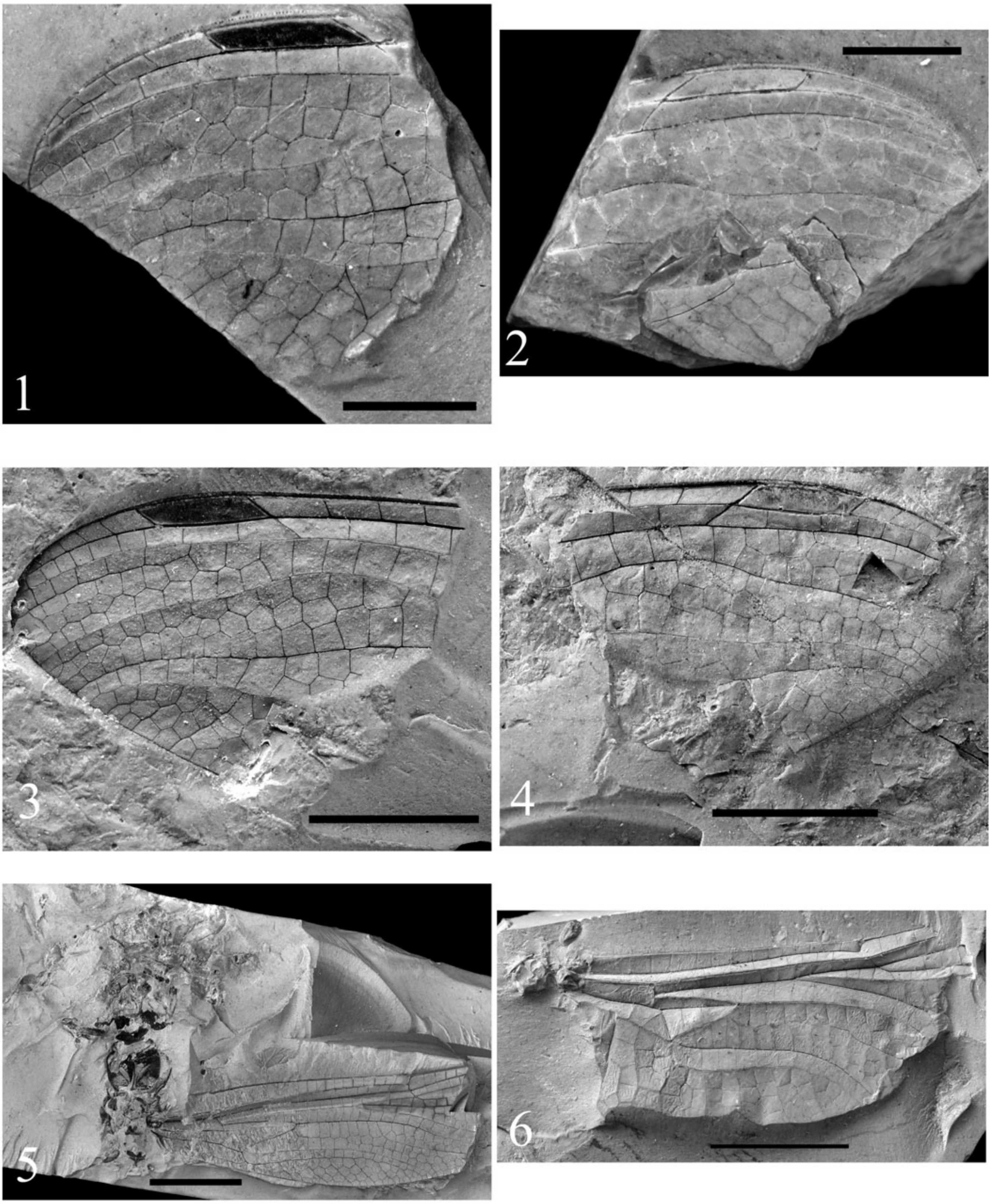
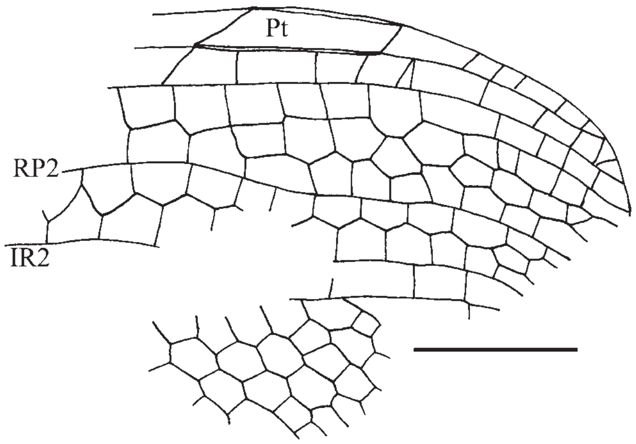


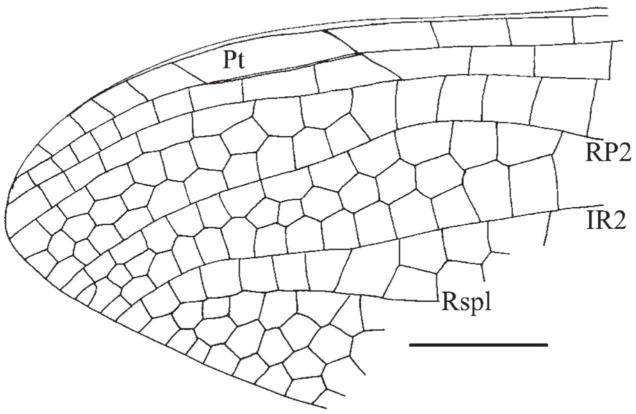
Plate 1 (1–4) *Oligoaeschna*? *anglica* Cockerell & Andrews, 1916, holotype: (1) part, NHMUK I.8649. Scale bar = 3 mm; (2) counterpart, NHMUK In.17266. Scale bar = 3 mm; (3) part, NHMUK In.17353. Scale bar = 3 mm; (4) counterpart, NHMUK In.17353. Scale bar = 3 mm. (5–6) *Anglogomphaeschna eocenica* gen. et sp. nov.: (5) holotype, NHMUK In.8793, forewing. Scale bar = 10 mm; (6) paratype, NHMUK In.17368, hindwing, male. Scale bar = 10 mm.

Oligoaeschna? *anglica* Cockerell & Andrews, 1916
(Plate 1, figs 1–4, text-figs 1–3)

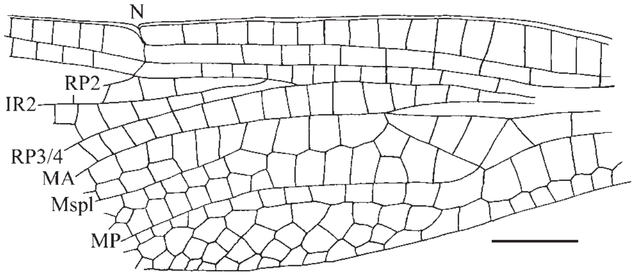
1916 *Oligoaeschna anglica* Cockerell & Andrews, p. 89, pl. 2, fig. 1.
1986 *Oligoaeschna anglica* Wighton & Wilson, pp. 507, 515.
1994 *Oligoaeschna*(?) *anglica* Nel *et al*., p. 163.
1999 ‘*Oligoaeschna*’ *anglica* Nel & Jarzembowski, p. 198.
2005 ‘*Oligoaeschna*’ *anglica* Nel *et al*., pp 150–152, fig. 3.



Text-figure 1 *Oligoaeschna*? *anglica* Cockerell & Andrews, 1916, holotype, NHMUK I.8649. Scale bar = 3 mm.



Text-figure 2 *Oligoaeschna*? *anglica* Cockerell & Andrews, 1916, NHMUK In.17353. Scale bar = 3 mm.



Text-figure 3 *Oligoaeschna*? *anglica* (?), NHMUK In.24756, forewing. Scale bar = 3 mm.

Holotype. NHMUK I.8649/In.17266 (Brodie/Smith coll., Plate 1, figs 1–2, Text-fig. 1), Insect Limestone, northwest Isle of Wight.

Other material. Specimen NHMUK In.17353 (Smith coll., Plate 1, figs 3–4, Text-fig. 2) is a more complete wing apex that we attribute to the same species. Nel *et al.* (2005) described a nearly complete hindwing.

The original description of Cockerell & Andrews (1916, p. 89, pl. 2, fig. 1) was based on the holotype. A. J. Ross found the counterpart, which is more complete. The Recent genera *Basiaeschna* Selys, 1883, *Oligoaeschna* Selys, 1889 and *Linaeschna* Martin, 1908 have very similar wing apices, with a posteriorly curved Rspl, two rows of cells between Rspl and IR2, IR2 unforked and weakly curved, three rows of cells between IR2 and RP2, RP2 with a distinct curve opposite the base of pterostigma, a short IR1, and a pterostigma covering 2–3 cells (Martin 1908). The hindwing described by Nel *et al.* (2005) is very similar to that of a Recent *Oligoaeschna*, but the generic attribution of this species remains uncertain because of the lack of body characters (see also Nel & Papazian 1983; Nel *et al.* 1994).

Specimen NHMUK I.8934/In.24756 (part and counter-part, Brodie/Hooley coll., Text-fig. 3) is the basal two thirds of a forewing that could also belong to the same species, because its dimensions are compatible with those of the wing apices attributed to *Oligoaeschna*? *anglica*, and its wing venation is consistent with the genus *Oligoaeschna*.

Genus *Anglogomphaeschna* gen. nov.

Type species. *Anglogomphaeschna eocenica* sp. nov.

Etymology. After *Anglia*, Latin name for England and *Gomphaeschna*.

Diagnosis. Wing characters only; antenodal cross-veins numerous; ‘cordulegastrid gap’ present; median space free; space between MP and CuA nearly as wide at basal third as at distal third in hindwing; MA and RP3/4 parallel to each other up to wing margin, MA without concave bend; Mspl and Rspl nearly parallel to MA and IR2 respectively; AA & AP and AA2 parallel before anal angle; anal triangle present; cubito-anal area broad; anal loop large and broad, transverse; two cross-veins in submedian area; discoidal triangle divided into five cells in forewing and three cells in hindwing.

Anglogomphaeschna eocenica sp. nov.
(Plates 1, figs 5–6, 2, figs 1–3; Text-figs 4–7)

Holotype. Specimen NHMUK I.8793 (Brodie coll., base of forewing, Plate 1, fig. 5, Text-fig. 4), Insect Limestone, northwest Isle of Wight.

Paratypes. NHMUK In.17368 (Smith coll., base of male hindwing, Plate 1, fig. 6, Text-fig. 5), NHMUK In.17330 (Smith coll., base of female hindwing, Plate 2, fig. 1, Text-fig. 6), NHMUK In.24649 (base of a hindwing, Text-fig. 7), NHMUK I.10390/In.24652(1) (base of a hindwing, on same piece as scarabaeid beetle abdomen, Plate 2, figs 2–3).

Etymology. After the Eocene period.

Diagnosis. As for genus.

Description. NHMUK I.8793. Forewing 14·3 mm wide, distance from wing base to arculus 8·1 mm, from arculus to nodus 25·8 mm, from base to Ax1 5·0 mm, from Ax1 to arculus 2·8 mm, from arculus to Ax2 4·8 mm; no secondary antenodal cross-vein basal of Ax1, four between Ax1 and Ax2, 14 distal of Ax2; 14 cross-veins between RA and RP basal of subnodus, with last cross-vein missing (‘cordulegastrid gap’); median area free; submedian + subdiscoidal area crossed by two veins; hypertriangle longer than anterior side of discoidal triangle, with three cross-veins; discoidal triangle elongate, with anterior side 8·3 mm long, posterior side 7·6 mm long, basal side 2·8 mm long, divided into five cells; two rows of cells in anal area; four rows of cells in cubito-anal area; postdiscoidal area with two rows of cells distal of triangle; Mspl straight, with two rows of cells between it and MA; opposite base of Rspl two rows of cells between MA and RP3/4, but these veins remain parallel; oblique vein just distal of base of RP2.

NHMUK In.17330. Hindwing. Distance from wing base to arculus 7·3 mm, from arculus to nodus 15·3 mm, from base to Ax1 4·6 mm, from Ax1 to arculus 1·4 mm, from arculus to Ax2 3·8 mm; no secondary antenodal cross-vein basal of Ax1, two between Ax1 and Ax2, eight distal of Ax2; six cross-veins between RA and RP basal of subnodus, with last cross-vein missing (‘cordulegastrid gap’); median area free;

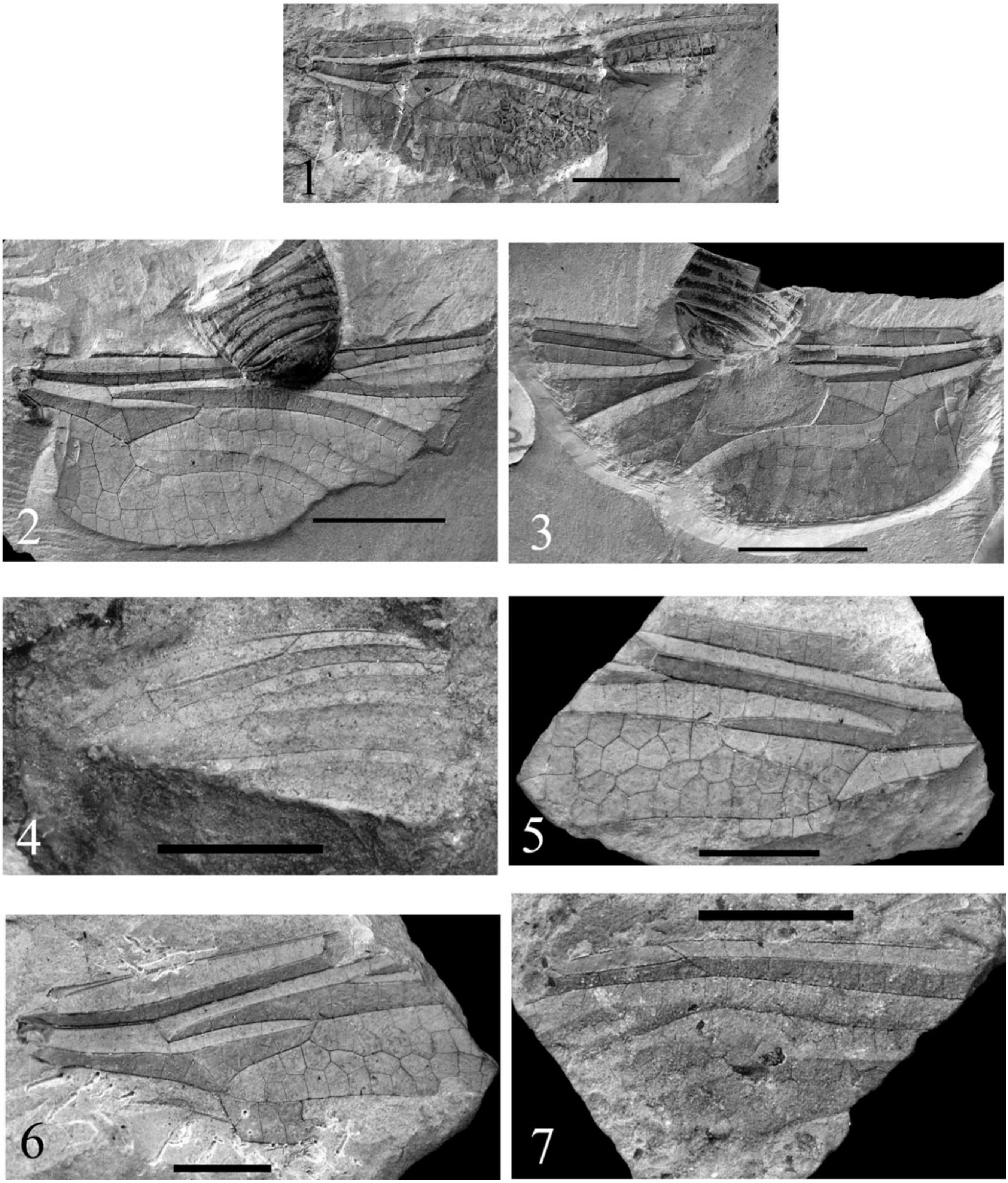
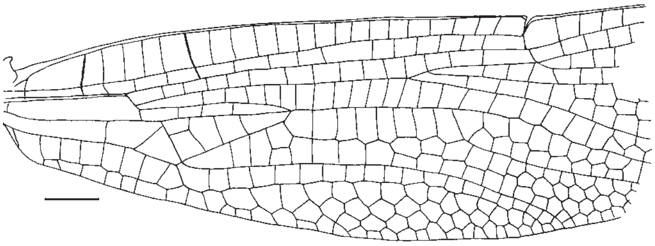
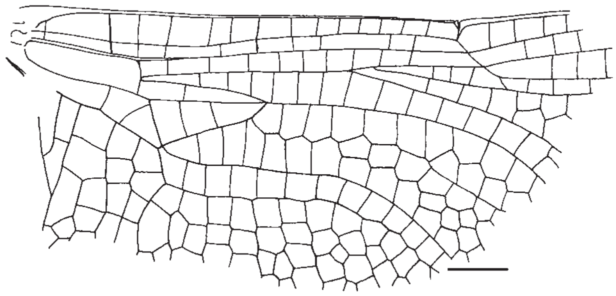


Plate 2 (1–3) *Anglogomphaeschna eocenica* gen. et sp. nov.: (1) paratype, NHMUK In.17330, hindwing. Scale bar = 10 mm; (2) paratype, NHMUK In.24652, hindwing, part. Scale bar = 10 mm; (3) paratype, NHMUK In.10390, counterpart. Scale bar = 10 mm. (4–7) '*Oplonaeschna*' *vectensis* Cockerell & Andrews, 1916: (4) holotype, NHMUK I.8572. Scale bar = 5 mm; (5) paratype, NHMUK I.8590, hindwing, part, probably related to *Oligaeschna wedmanni.* Scale bar = 5 mm; (6) paratype, NHMUK In.17369, counterpart, probably related to *Oligaeschna wedmanni*. Scale bar = 5 mm. (7) paratype, NHMUKI.8636, probably related to *Oligaeschna wedmanni*. Scale bar = 5 mm.



Text-figure 4 *Anglogomphaeschna eocenica* gen. et sp. nov., holotype, NHMUK I.8793, forewing. Scale bar = 3 mm.

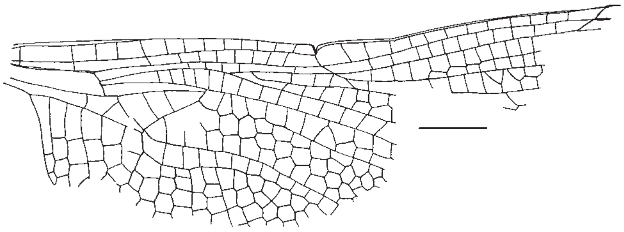


Text-figure 5 *Anglogomphaeschna eocenica* gen. et sp. nov., paratype, NHMUK In.17368, hindwing, male. Scale bar = 3 mm.

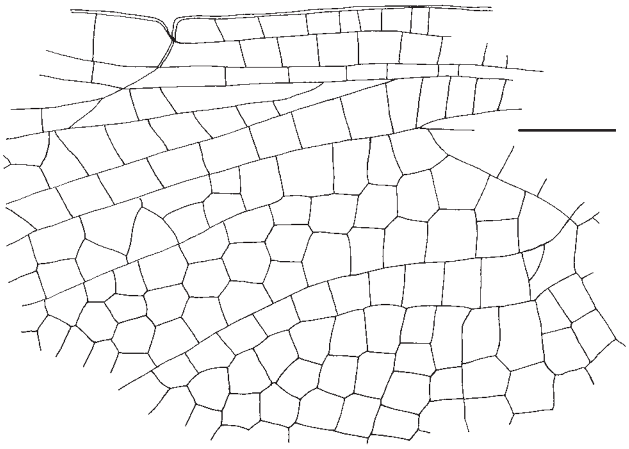
submedian + subdiscoidal area crossed by two veins; hypertriangle longer than anterior side of discoidal triangle, with at least one cross-vein; discoidal triangle elongate, with anterior side 6·0 mm long, posterior side 5·0 mm long, basal side 2·8 mm long, divided into three cells; space between MP and CuA nearly as wide at basal third as at distal third, with one row of cells; anal loop transverse, clearly defined, divided into five cells; cubito-anal area with at least five rows of cells between CuA and posterior wing margin; no anal angle and no anal triangle (female); 13 postnodal cross-veins; two rows of cells between Mspl and MA and Rspl and IR2; Mspl and Rspl straight.

NHMUK In.17368 mainly differs from In.17330 in the presence of an anal triangle and anal angle (male).

Discussion. The attribution of these forewing and hindwing fragments to the same species is based on the following characters: similar wing length; the differences between NHMUK I.8793 (forewing basal half) and NHMUK In.17330, NHMUK In.17368 and NHMUK In.24649 (hindwing basal halves) can be attributed to the normal differences between the forewings and the hindwings within the same species. They share in particular the same Mspl, distal part of area between MA and RP3/4; costal and subcostal area, median and submedian spaces. *Anglogomphaeschna* gen. nov. has a 'cordulegastrid' gap, *viz.* the distal part of antesubnodal area between RA and RP is free of cross-vein, which is an apomorphy of the clade Gomphaeschnidae, more pronounced in the numerous Mesozoic taxa, in the Paleocene genus *Alloaeschna* Wighton & Wilson, 1986, *Gomphaeschna* Selys, 1871 and *Sarasaeschna* Karube & Yeh, 2001 than in *Oligoaeschna*, and absent in *Linaeschna* Martin, 1908 (Wighton & Wilson 1986; Bechly *et al.* 2001, Ellenreider 2002). *Anglogomphaeschna* differs from the Mesozoic *Paramorbaeschna* Bechly *et al.*, 2001, *Progomphaeschnaoides* Bechly *et al.*, 2001, *Plesigomphaeschnaoides* Bechly *et al.*, 2001, *Gomphaeschnaoides* Carle & Wighton, 1990 and all the Recent gomphaeschnid genera in its larger and distinctly transverse anal loop. It differs from *Sinojagoria* Bechly *et al.*, 2001 in its forewing discoidal triangle divided into five cells. It differs from *Alloaeschna* in its more numerous antenodal cross-veins (21 instead of 13).



Text-figure 6 *Anglogomphaeschna eocenica* gen. et sp. nov., paratype, NHMUK In.17330, hindwing, female. Scale bar = 5 mm.



Text-figure 7 *Anglogomphaeschna eocenica* gen. et sp. nov., paratype, NHMUK In.24649, hindwing. Scale bar = 3 mm.

Anglogomphaeschna differs from all the genera of the '*Boyeria*' clade and the '*Brachytron*' clade (*sensu* Ellenreider 2002) in a series of characters depending on the genus, i.e. median space free; submedian space with only two cross-veins; space between MP and CuA nearly as wide at basal third as at distal third in hindwing; cubito-anal area broad.

Among the genera included within the Aeshnoidea, but still of uncertain position, *Austroaeschna* Selys, 1883, *Acanthaeschna* Selys, 1883 and *Planaeschna* McLachlan, 1896 also have a relatively similar wing venation, but they differ from *Anglogomphaeschna* in the absence of the 'cordulegastrid' gap, narrower cubito-anal area, less transverse anal loop, different anal triangle and presence of four cross-veins in submedian area. *Antipodophlebia* Fraser, 1960 and *Telephlebia* Selys, 1883 have their median space crossed. *Austrophlebia* Tillyard, 1916 has a very well-defined fork of IR2.

Lastly, *Anglogomphaeschna* differs from the third clade of Ellenreider (2002) (Aeshninae clade) in its MA without concave bend, and Mspl and Rspl straight.

Family Aeshnidae Leach, 1815

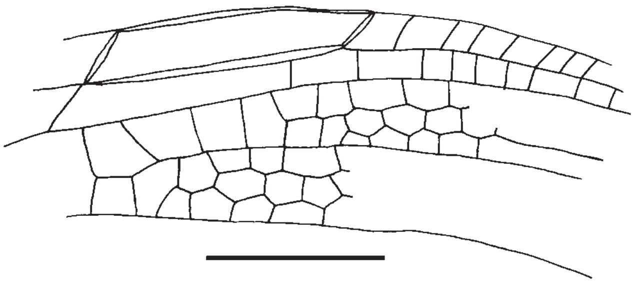
Genus undetermined

'*Oplonaeschna*' *vectensis* Cockerell & Andrews, 1916

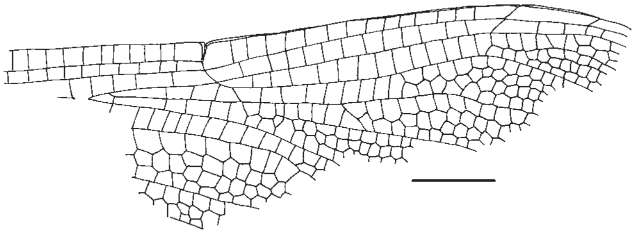
(Plates 2, figs 4–7, 3, fig. 1; Text-figs 8–9)

1916 *Oplonaeschna vectensis* Cockerell & Andrews, pp. 89–90, pl. 2 figs 2–4.
1986 *Oplonaeschna vectensis* Wighton & Wilson, p. 508.
1994 *Oplonaeschna vectensis* Nel *et al.*, pp. 170, 174.
1999 '*Oplonaeschna*' *vectensi*' Nel & Jarzembowski, p. 198.

Holotype. Specimen NHMUK I.8572 (Brodie coll., Plate 2, fig. 4, Text-fig. 8), Insect Limestone, northwest Isle of Wight. The type specimen of this species described by Cockerell & Andrews (1916, pp 89–90, pl. 2, fig. 2) is too fragmentary to be accurately attributed to a precise genus, according to Nel



Text-figure 8 '*Oplonaeschna*' *vectensis* Cockerell & Andrews, 1916, holotype, NHMUK I.8572. Scale bar = 3 mm.



Text-figure 9 '*Oplonaeschna*' *vectensis* Cockerell & Andrews, 1916, paratype, NHMUK In.17334 (conterpart), probably related to *Oligaeschna wedmanni*. Scale bar = 4 mm.

& Jarzembowski (1999). Furthermore, the paratype NHMUK I.8590/In.17369 (Brodie/Smith coll., Plate 2, figs 5–6) (figured in Cockerell & Andrews 1916, pp 89–90, pl. 2, fig. 3) is a costo-basal part of a hindwing that has strictly no structure in common with the holotype. Its attribution to the same species is impossible to justify (Plate 5, figs 2–3). Also the attribution of paratype NHMUK I.8636/In.17334 (Brodie/Smith coll., Plate 2, fig. 7, Plate 3, fig. 1, Text-fig. 9) (figured in Cockerell & Andrews 1916, pp 89–90, pl. 2, fig. 4) to the same species as the holotype cannot be demonstrated. This species is related to *Oligaeschna wedmanni* sp. n. (see below).

Clade '*Brachytron*' (*sensu* Ellenrieder 2002)
Genus *Aeschnophlebia* Selys, 1883

Aeschnophlebia andreasi Nel *et al*., 2005
(Plate 3, fig. 2; Text-figs 10–11)
2005 *Aeschnophlebia andreasi* Nel *et al*., pp 348–350, fig. 2

Holotype. Specimen IWCMS 2004.52, Insect Limestone, northwest Isle of Wight.

Other material. NHMUK In.17371 (Text-fig. 10) and NHMUK In.17395 (Plate 3, fig. 2, Text-fig. 11) (both wing apices, Smith coll.).

Description of the new specimens. NHMUK In.17371. Pterostigma 5·4 mm long, 1·0 mm wide, covering six cells; pterostigmal brace oblique; postnodal cross-veins numerous, more than 24; IR1 base in a very basal position, 10 cells basal of pterostigma; RP2 with a weak curve just basal of level of pterostigmal brace; IR2 with a distinct but weak anterior branch, three rows of cells between branches of IR2; Rspl straight, with two rows of cells between it and IR2.

Discussion. The attribution of NHMUK In.17395 (forewing apex) to the same species is based on its great similarity to NHMUK In.17371, except for the shorter basal part of IR1. The structures and dimensions of these two wing apices are nearly identical to those of the holotype (Nel *et al*. 2005).

Clade 'Aeshninae' (*sensu* Von Ellenrieder 2002)
Genus *Oligaeschna* Piton and Théobald, 1939

Oligaeschna wedmanni sp. nov.
(Plate 3, figs 3–4; Text-figs 12–13)

Holotype. Specimen IWCMS 2012.576 (forewing, Plate 3, fig. 3, Text-fig. 12), Insect Limestone, northwest Isle of Wight.

Paratype. Specimen NHMUK I.8636/In.17334 (forewing?, paratype of '*Oplonaeschna*' *vectensis*). A further specimen NHMUK I.10284 (Brodie coll., forewing, Plate 3, fig. 4, Text-fig. 13) and the paratype of '*Oplonaeschna*' *vectensis* NHMUK I.8590/In.17369 probably belong to the same species.

Etymology. Named after our colleague Dr Sonja Wedmann.

Diagnosis. Large wing; five rows of cells between RP2 and IR2 along wing margin; pterostigma covering three cells; one row of cells between MA and RP3/4 from the level of base of Rspl and posterior wing margin.

Description. Forewing hyaline, 50·0 mm long, 10·8 mm wide; distance from base to arculus 5·8 mm, from arculus to nodus 19·2 mm, from nodus to pterostigma 15·8 mm, from pterostigma to wing apex 5·7 mm; pterostigma 4·7 mm long, 0·8 mm wide, covering three cells; pterostigmal brace distinctly oblique; one antenodal cross-vein basal of Ax1, Ax1 is 4·6 mm from wing base and 1·7 mm from arculus, Ax2 3·7 mm distal of arculus; five antenodal cross-veins between Ax1 and Ax2; at least 15 secondary antenodal cross-veins distal of Ax2; 17 postnodal cross-veins; median space free of cross-veins; submedian space + subdiscoidal space crossed by five cross-veins (including CuP); hypertriangle 7·7 mm long, 0·8 mm wide, with four cross-veins; anterior side of discoidal triangle 6·3 mm long, posterior side 5·5 mm, basal side 2·5 mm, divided into five cells; 2–3 rows of cells in postdiscoidal area distal of triangle; Mspl curved with 3–4 rows of cells between it and MA; area between CuA and posterior wing margin 2·8 mm wide, with four rows of cells; MA with a slight curve opposite base of Rspl; at this level and for a distance of three cells, two rows of cells between MA and RP3/4, then one row until the posterior wing margin; Rspl strongly curved, with four rows of cells between it and IR2; IR2 with a distinct posterior curve; three rows of cells between IR2 and RP2 in the broadest part and five rows of cells along posterior wing margin; RP2 with a distinct but smooth curve below pterostigma.

Discussion. The attribution of the two wings IWCMS 2012.576 and NHMUK In.17334 to the same species is based on their nearly identical wing apices and similar dimensions. The possible attribution of NHMUK I.10284 is based on the very similar wing bases.

This fossil species clearly belongs to Aeshnidae and to the clade 'Aeshninae' *sensu* Ellenrieder (2002, fig. 20) after combination of the following apomorphic characters: MA and RP3/4 not parallel, MA with a marked concave bend; Mspl with a concave bend in its distal portion (homoplasy); Rspl not parallel to IR2, with a concave bend. It can be attributed to the group of the three genera *Oligaeschna*, *Kvacekia* Prokop & Nel, 2002 and *Oplonaeschna* Selys, 1883 on the basis of the following characters: pterostigmal brace clearly oblique; median space free; areas between Rspl and IR2 and between Mspl and MA with four rows of cells; absence of very strong bend of RP2; fork of IR2 absent. *Oligaeschna* and *Oplonaeschna* differ in the length of pterostigma, distinctly longer in the former than in the latter, and structure of discoidal triangle, longer and divided into five or more cells in *Oligaeschna*

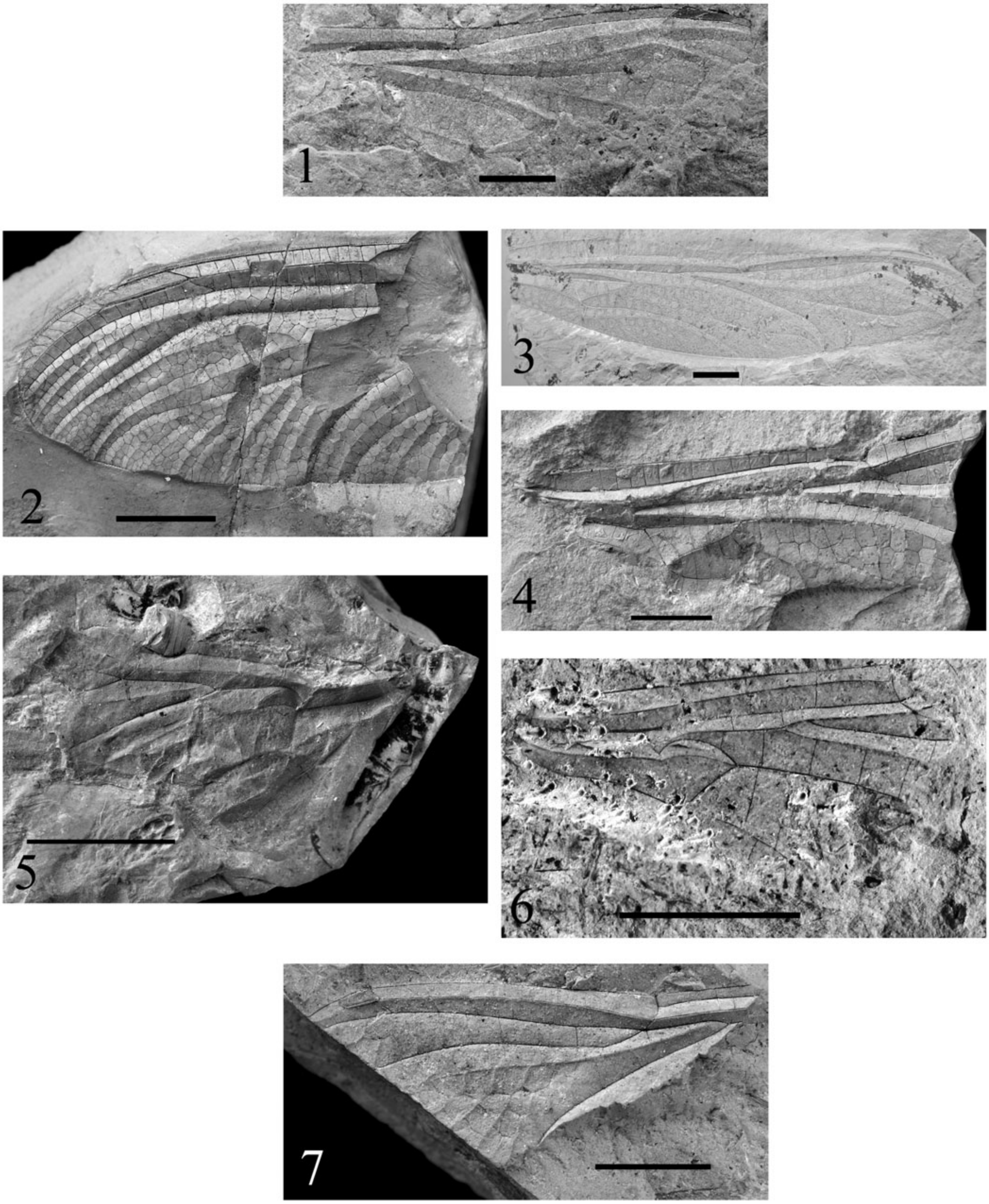
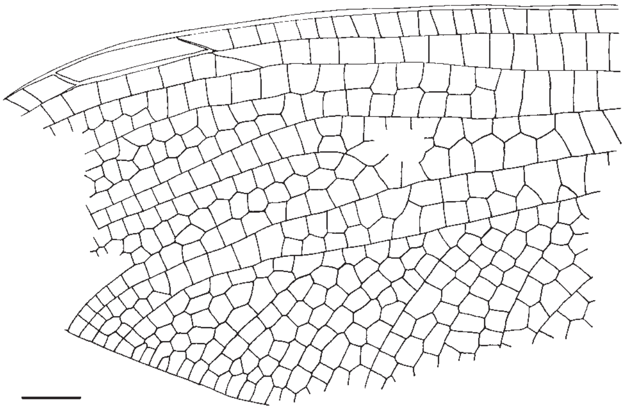
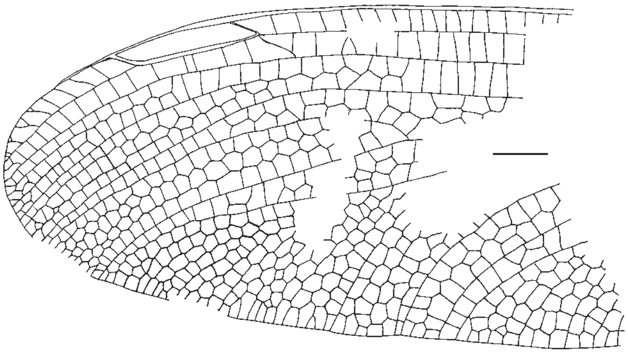


Plate 3 (1) ‘*Oplonaeschna*’ *vectensis* Cockerell & Andrews, 1916, paratype, NHMUK In.17334, probably related to *Oligaeschna wedmanni*. Scale bar = 5 mm. (2) *Aeschnophlebia andreasi* Nel *et al*., 2005, NHMUK In.17395, part. Scale bar = 5 mm. (3–4) *Oligaeschna wedmanni* sp. nov.: (3) holotype, IWCMS 2012.576, forewing. Scale bar = 10 mm; (4) paratype, NHMUK I.10284. Scale bar = 10 mm. (5–6) *Neophya legrandi* sp. nov.: (5) holotype, NHMUK In.24606, hindwing. Scale bar = 5 mm; (6) paratype, NHMUK II.2851a. Scale bar = 5 mm. (7) *Neophya legrandi* sp. nov., paratype, NHMUK In.24641. Scale bar = 5 mm.



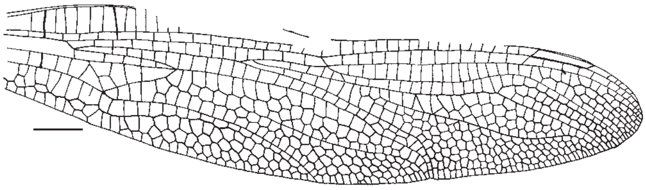
Text-figure 10 *Aeschnophlebia andreasi* Nel *et al.*, 2005, NHMUK In.17371. Scale bar = 2 mm.



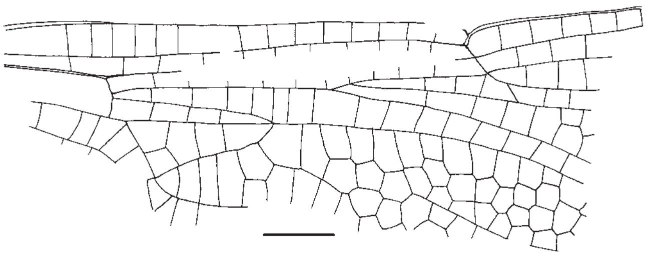
Text-figure 11 *Aeschnophlebia andreasi* Nel *et al.*, 2005, NHMUK In.17395. Scale bar = 2 mm.

(except for *O. saurai* Peñalver *et al.*, 1996), instead of four in *Oplonaeschna* (González-Soriano & Novelo Gutierrez 1998). *Kvacekia* differs from *Oligaeschna* and *Oplonaeschna* in the pterostigma covering 5–6 cells, and cubito-anal area of forewing with more than nine rows between CuA and posterior wing margin (Prokop & Nel 2002). On the basis of the combination of the above-mentioned characters we attribute our fossil to *Oligaeschna*.

All the fossil species currently attributed to the Recent genus *Oplonaeschna* are incertae sedis (Prokop *et al.* 2007 and see above). The genus *Oligaeschna* comprises seven described species from Oligocene and Miocene Eurasian and North American deposits. *O. jungi* Piton & Théobald, 1939 (Oligocene of Puy-de-Dôme, France, Oligocene of Enspel, Germany, Early Oligocene of Provence, France, Wedmann 2000; Nel *et al.* 2005) and *O. palaeocoerulea* (Timon-David 1946) (Oligocene, Bouches-du-Rhône, France) have circa ten rows of cells between RP2 and IR2 along wing margin instead of the five in *O. wedmanni* sp. n., and two rows of cells between MA and RP3/4 from the level of base of Rspl and posterior wing margin, as in *O. lapidaria* (Cockerell & Counts *in* Cockerell 1913) from the Late Eocene of Florissant (Colorado, USA) (Cockerell 1913). *O. moravica* Prokop *et al.*, 2007 (Middle Oligocene of northern Moravia), *O. separata* (Scudder 1890) (Florissant), and *O. ashutasica* (Martynov 1929) from the Paleocene to Oligocene of Ashutas mount (East Kazakhstan), differ from *O. wedmanni* in the presence of five cross-veins between RA and RP1 below pterostigma (Scudder 1890; Martynov 1929; fig. 4; Prokop *et al.* 2007). *O. saurai* Peñalver *et al.*, 1996, from the Early Miocene of Ribesalbes (Castellón, Spain), is a distinctly smaller species than all the other species (hindwing less than 30 mm long), and has two rows of cells between MA and RP3/4 from the level of base of Rspl and posterior wing margin.



Text-figure 12 *Oligaeschna wedmanni* sp. nov., holotype, IWCMS 2012.576, forewing. Scale bar = 4 mm.



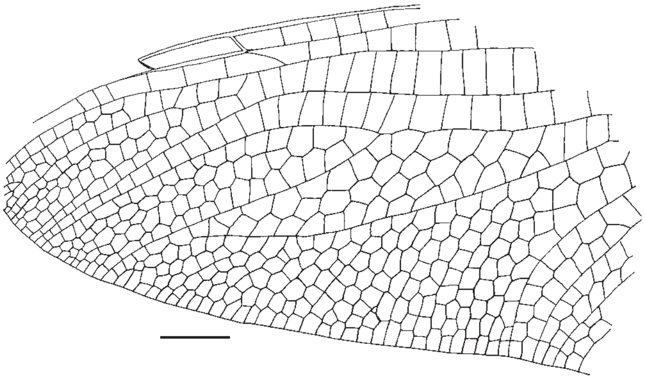
Text-figure 13 *Oligaeschna wedmanni* sp. nov., paratype, NHMUK I.10284. Scale bar = 3 mm.

Subfamily 'Gynacanthinae' Cockerell, 1913
'Gynacanthinae' species A
(Text-figs 14–15)

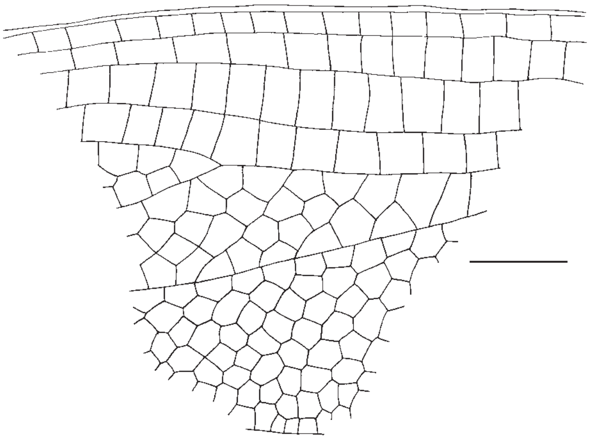
Material. NHMUK In.24638 (Hooley coll., Text-fig. 14) and NHMUK In.24751 (Hooley coll., Text-fig. 15), Insect Limestone, northwest Isle of Wight.

Description. It is not possible to decide if these fossils are fore- or hindwings. Wing hyaline; length of fragment NHMUK In.24638 30·0 mm, width of wing 17·5 mm; MA and RP3/4 parallel to each other up to wing margin, with two rows of cells between them distal of nodus level; Rspl with a strong curve, four rows of cells between Rspl and IR2, IR2 with a very strong fork; six cells basal of pterostigma, area between the branches of IR2 with 3–4 rows of cells, RP2 with a strong curve opposite base of pterostigma; one row of cells between IR2 and RP2; pterostigma 5·0 mm long, 1·0 mm wide, rather long, covering three cells; pterostigmal brace distinctly oblique and long; postnodal and postsubnodal cross-veins numerous.

Discussion. These two fossils can be attributed to the same species because their common wing venation structures are identical. Few Recent genera have a similar wing venation, *viz.* the 'gynacanthine' *Tetracanthagyna* Selys, 1883, *Triacanthagyna* Selys, 1883, *Plattycantha* Förster, 1908, *Gynacantha* Rambur, 1842, *Neuraeschna* Hagen, 1867, *Agyrtacantha* Lieftinck, 1937 and *Staurophlebia* Brauer, 1865: MA and RP3/4 parallel to each other up to wing margin, with two rows of cells between them distal of nodus level; Rspl with a strong curve, four rows of cells between Rspl and IR2, IR2 with a very strong fork basal of pterostigma, area between the branches of IR2 with 3–4 rows of cells, pterostigma rather long (Martin 1908; Lieftinck 1937; Ellenreider 2002). *Neuraeschna* and *Staurophlebia* could be excluded because their space between the branches of IR2 is narrower and the area between Rspl and IR2 is broader than in our fossil. The Recent *Gynacantha* also have a narrower space between the branches of IR2, and there is only one row of cells between MA and RP3/4. *Agyrtacantha* has a distinctly shorter pterostigma, its fork of IR2 is in a more basal position, and it has only one row of cells between MA and RP3/4. *Tetracanthagyna* would differ from our fossil in the distinctly broader areas between Rspl and IR2 and between the branches of IR2. All these differences are weak and are not sufficient to exclude one of these genera. It would be necessary to have information on the basal part of the wings



Text-figure 14 ‘Gynacanthinae’ species A, NHMUK In.24638. Scale bar = 3 mm.



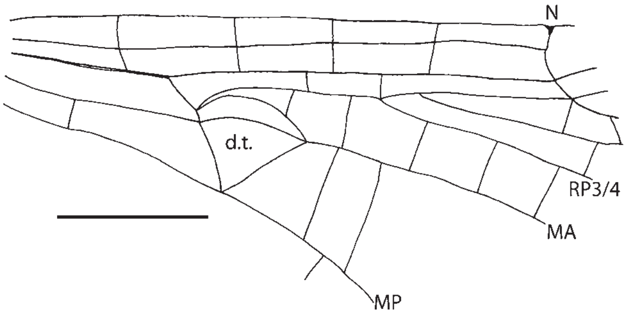
Text-figure 15 ‘Gynacanthinae’ species A, NHMUK In.24751. Scale bar = 3 mm.

of this fossil species. At this stage, it is not possible to attribute it to a precise ‘gynacanthine’ genus. Nevertheless, this fossil species is of great interest because all its closest living relatives live in warm to hot climates in Indo-Malaysia, South America and Australasia.

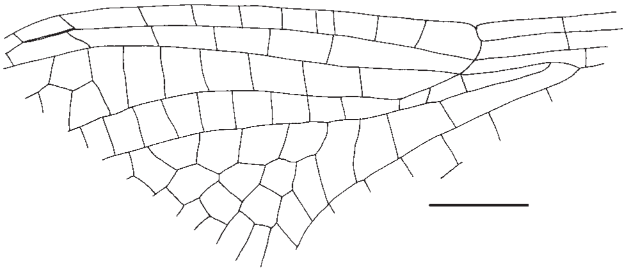
Very few fossils have been attributed to the ‘Gynacanthinae’ (Nel *et al.* 1994). *Gynacantha polydore* (Heer 1849) from the Miocene of Oeningen (Germany) needs revision. Martynov (1927) described *Heliaeschna parallela* from the Miocene of Azerbaijan. Nel & Petrulevičius (2010) synonymised the fossil genus *Epacantha* Martynov, 1929 (one species *E. magnifica* from the late Oligocene of Kazakhstan) with the Recent genus *Epiaeschna* Hagen, 1875. Lastly, the fossil genus *Necracantha* Martynov, 1929 (*N. composita* Martynov, 1929 and *N. proxima* Martynov, 1929 from the Late Oligocene of Ashutas mount (East Kazakhstan)) differs from our fossil in the straight Rspl and very long pterostigma covering six cells or more (Martynov 1929). *Necracantha* should be revised, because its wing venation has strong similarities with *Epiaeschna*.

Clade Cavilabiata Bechly, 1996
Family Cordulephyidae Tillyard, 1917
Subfamily Neophyinae Tillyard & Fraser, 1940
Genus *Neophya* Selys, 1881
Neophya legrandi sp. nov.
(Plate 3, figs 5–7; Text-figs 16–18)

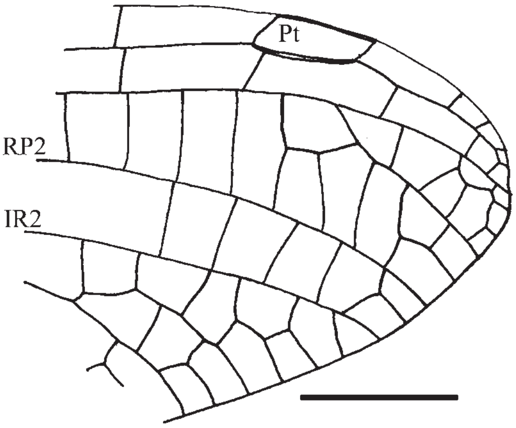
Holotype. Specimen NHMUK In.24606 (hindwing base, Hooley coll., Plate 3, fig. 5), Insect Limestone, northwest Isle of Wight.



Text-figure 16 *Neophya legrandi* sp. nov., paratype, NHMUK II.2851a. Scale bar = 3 mm.



Text-figure 17 *Neophya legrandi* sp. nov., paratype, NHMUK In.24641. Scale bar = 3 mm.



Text-figure 18 *Neophya legrandi* sp. nov., paratype, NHMUK In.24757. Scale bar = 2 mm.

Paratypes. Specimens NHMUK II.2851a,b (14/11/04) (hindwing base, Ross coll., Plate 3, fig. 6, Text-fig. 16), NHMUK In.24641 (costo-apical part of a wing, Hooley coll., Plate 3, fig. 7, Text-fig. 17), NHMUK In.24757 (wing apex, Hooley coll., Text-fig. 18).

Etymology. Named after our colleague, odonatologist Prof. Jean Legrand.

Diagnosis. Wing characters only; vein separating hypertriangle and discoidal triangle ending in MA at distal angle of discoidal triangle; only four antenodal cross-veins; two cross-veins in area between RA and RP basal of subnodus.

Description. Probable total length of hindwing 26·0 mm; Distance from wing base to arculus 3·3 mm, from arculus to nodus 7·4 mm, from nodus to pterostigma 12·3 mm; pterostigma 1·8 mm long, 0·5 mm wide, covering two-third of a cell; pterostigmal brace weak, not aligned with basal side of pterostigma; four antenodal cross-veins aligned with the subantenodal cross-veins; arculus between the two basal antenodal cross-veins, closer to first than to second; sectors of arculus stalked and strongly curved (costal side of hypertriangle very convex); trigonal vein that is separating the hypertriangle from the discoidal triangle, is distinctly curved; vein separating the hypertriangle and the discoidal triangle ending in MA at the distal angle of discoidal triangle; discoidal triangle nearly equilateral; median space free; submedian space crossed by CuP; anal loop elongate, with two rows of cells and a median rib (Cuspl); first cross-vein between MA and RP short and ending in anterior side of hypertriangle; two cross-veins in area between RA and RP basal of subnodus; one Bqr cross-vein; oblique vein 'O' just distal of base of RP2; postdiscoidal area with one row of large transverse cells distal of triangle; Mspl poorly preserved but probably rudimentary; Rspl absent; RP2 and IR2, as well as RP3/4 and MA probably distally converging, after their general shape and direction; IR1 short, with its base just distal of apex of pterostigma; eigth postnodal cross-veins not aligned with the four postsubnodal cross-veins.

Discussion. These three specimens can be attributed to the same species because of the identity of the shared parts of wings and very distinctive venation. The main remarkable structure of *Neophya legrandi* sp. nov. is the distinctly curved anterior side of hindwing discoidal triangle. Only few groups within the Cavilabiata have this character, viz. some Libellulidae, the Mesozoic Araripelibellulidae: Araripelibellulinae Bechly, 1996 (especially the English Wealdian *Cretaneophya strevensi* Jarzembowski & Nel, 1996), and the Recent *Neophya rutherfordi* Selys, 1881 (Cordulephyidae Tillyard, 1917 of the subfamily Neophyinae Tillyard & Fraser, 1940). The relevant Libellulidae (*Tetrathemis* Brauer, 1868, *Nannophlebia* Selys, 1878) have this vein less curved than in our fossil and a well defined Rspl, unlike our fossil (Ris 1909–1913). The main difference between *Cretaneophya* and *Neophya* is in the size and shape of the anal loop; 2–3 cells in *Cretaneophya* instead of transverse elongate with a median vein as in *Neophya* and in this fossil.

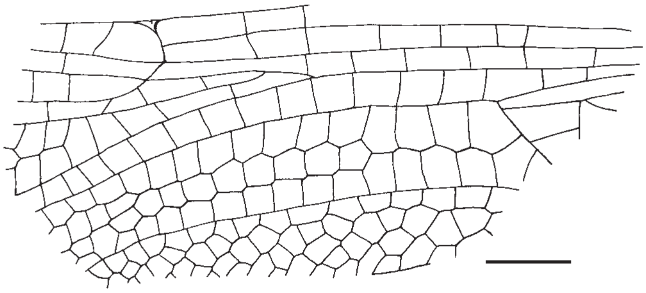
Furthermore, *N. legrandi* has the wing venation synapomorphies of the Neophyinae, i.e. sectors of arculus stalked and strongly curved (costal side of hypertriangle very convex); trigonal vein that is separating the hypertriangle from the discoidal triangle, is distinctly curved; Rspl absent; RP2 and IR2, as well as RP3/4 and MA distally converging. All the other characters present in *N. legrandi* are identical to those of *N. rutherfordi*, except for the vein separating the hypertriangle and the discoidal triangle ending in MA at the distal angle of discoidal triangle instead of before this angle as in *Neophya*, the presence of only four antenodal cross-veins instead of six as in *N. rutherfordi*, and two cross-veins in area between RA and RP basal of subnodus, instead of four as in *N. rutherfordi* (pers. obs.; Martin 1906).

The Palaeogene Argentinean *Palaeophya argentina* Petrulevičius & Nel, 2009 shares with *N. legrandi* the presence of only four antenodal cross-veins, but the former differs from the latter in the presence of four cross-veins in the area between RA and RP basal of the subnodus, instead of two, and of two rows of cells in postdiscoidal area opposite the base of RP3/4, instead of only one as in *N. legrandi*.

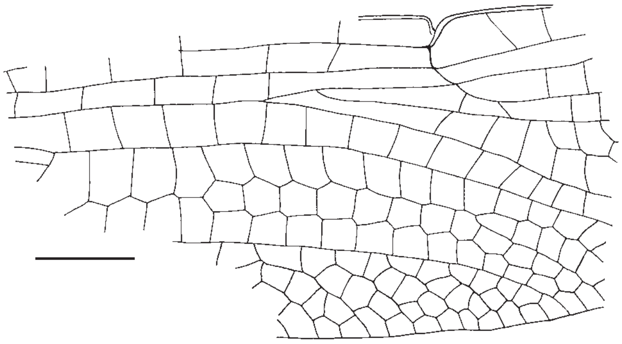
Clade Italoansida Bechly, 1996

'Corduliidae species A' *sensu* Nel & Jarzembowski (1999)
(Text-figs 19–20)

Material. This fossil 'species A' was originally described on the basis of an incomplete forewing (PORT 842245). A further fragmentary forewing can be attributed to the same species (NHMUK In.24654/In.24760, part and counterpart, Hooley coll., Text-figs 19–20, Insect Limestone, northwest Isle of Wight).



Text-figure 19 'Corduliidae species A', NHMUK In.24654. Scale bar = 3 mm.

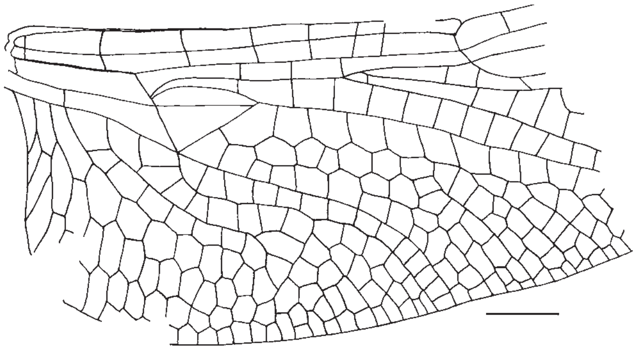


Text-figure 20 'Corduliidae species A', NHMUK In.24760. Scale bar = 3 mm.

Discussion. This fossil species belongs to the Italoansida Bechly, 1996 (Corduliidae + Anauriculida Bechly, 1996) (synapomorphies of forewing: discoidal triangle divided in the groundplan into two cells by a longitudinal cross-vein; subdiscoidal triangle divided into three cells in the groundplan; wings with a Mspl, that is still somewhat indistinct and more or less parallel to MA in the groundplan). The exact affinities of this fossil species cannot be ascertained within this group however, because we lack the hindwing structures and those of the distal third of the forewing (especially the Rspl). It is an Italoansida of uncertain position, probably not Libellulidae because its Mspl is not well defined.

'Corduliidae' species B
(Text-fig. 21)

Material. Specimen NHMUK In.17370/In.24763 (Smith/Hooley coll., Text-fig. 21), Insect Limestone, northwest Isle of Wight.



Text-figure 21 'Corduliidae' species B, NHMUK In.17370, hindwing, female. Scale bar = 3 mm.

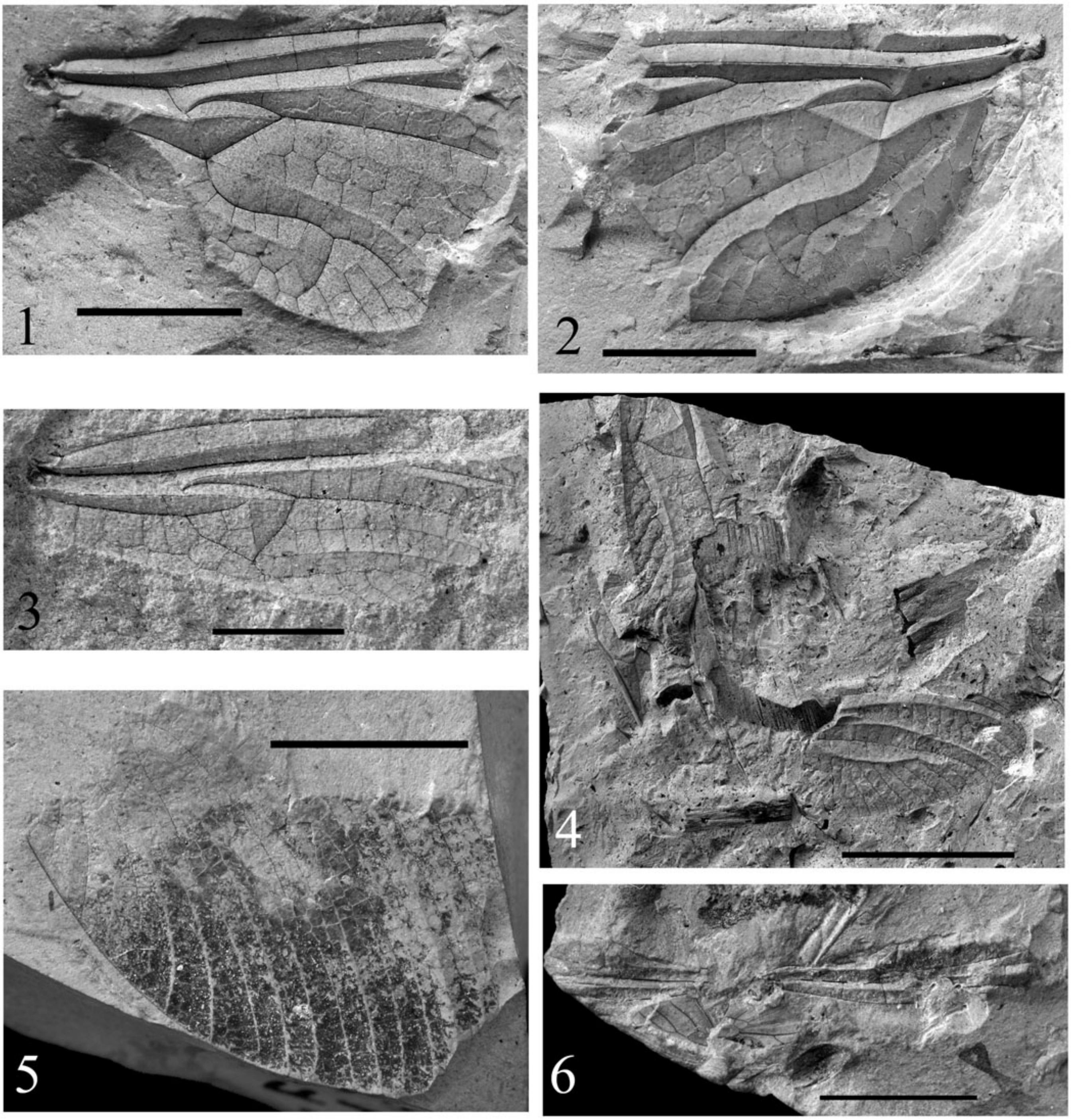
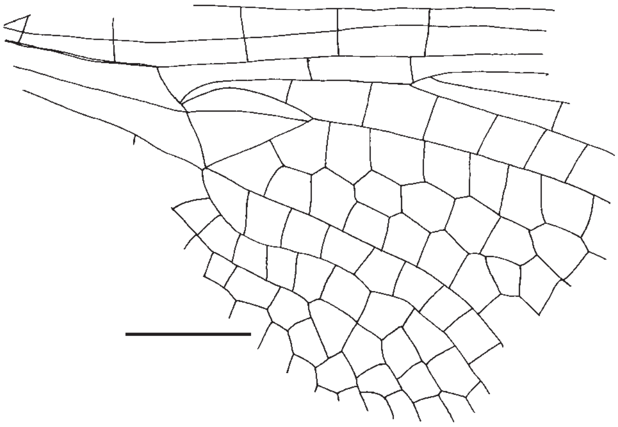


Plate 4 (1–2) ‘Corduliidae’ species C: NHMUK In.17324, hindwing, part. Scale bar = 5 mm; (2) NHMUK In.24771, counterpart. Scale bar = 5 mm. (3–4) *Eomacrodiplax incompleta* gen. et sp. nov. 1: (3) holotype, NHMUK In.24770, forewing. Scale bar = 5 mm; (4) paratype, NHMUK In.17333. Scale bar = 10 mm. (5) ?*Bolcathore* species A., NHMUK In.24648. Scale bar = 5 mm. (6) Dysagrionini species A, NHMUK I.9866. Scale bar = 5 mm.

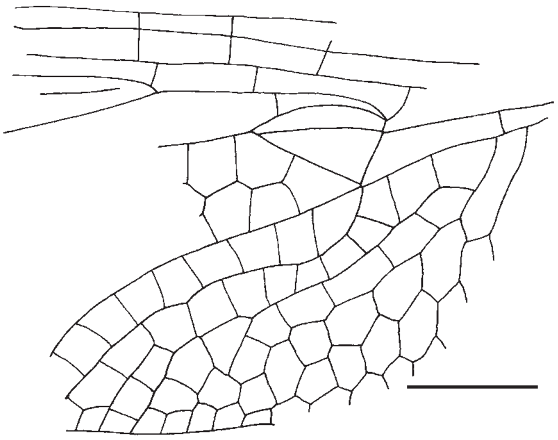
Discussion. This fossil could well correspond to the forewing of ‘Corduliidae species A’, because they have similar dimensions, but it is not possible to confirm this because we lack the wing apices of these fossils. The hindwing also fits into the Italoansida for the following reasons: hindwing discoidal triangle recessed to level of arculus; wings with a Mspl, that is still somewhat indistinct and more or less parallel to MA in the groundplan; hindwing with elongated and boot-shaped anal loop that nearly reaches the hind margin of the wing with its ‘toe’, and with a straight (non-zigzagged) and forked midrib (Cuspl) (Bechly 1996). Its rather poorly developed Mspl and sectors of arculus basally separated suggest that this fossil is not a Libellulidae, but rather a ‘Corduliidae’ or a Hemicorduliidae Bechly, 1996. The development of the anal loop and cubito-anal area of the Recent corduliid genus *Epitheca* Charpentier, 1825 is comparable to that of this fossil (Martin 1906, fig. 59).

‘Corduliidae’ species C
(Plate 4, figs 1–2; Text-figs 22–23)

Material. Specimen NHMUK In.17324/In.24771 (Smith/Hooley coll., Plate. 4, figs 1–2, Text-figs 22–23). Insect Limestone, northwest Isle of Wight.



Text-figure 22 'Corduliidae' species C, NHMUK In.17324, hindwing. Scale bar = 3 mm.



Text-figure 23 'Corduliidae' species C, NHMUK In.24771, hindwing. Scale bar = 3 mm.

Discussion. This hindwing base fits in the Italoansida and rather a 'Corduliidae' or a Hemicorduliidae for the same reasons as above for species B, except for those concerning the vein Mspl, unknown in this fossil. It corresponds to a different species because it is distinctly smaller, with a narrower cubito-anal area with only three rows of cells between the anal loop and the posterior wing margin, instead of four as in species B.

Family Urothemistidae Lieftinck, 1954
Genus *Eomacrodiplax* gen. nov.

Type species. *Eomacrodiplax incompleta* sp. nov.

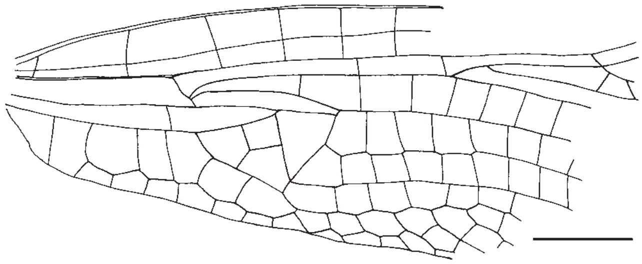
Etymology. Named after Eocene and *Macrodiplax*.

Diagnosis. Forewing base characters only. Subdiscoidal triangle divided into three cells; basal side of subdiscoidal triangle not perpendicular to anterior side; distal side of discoidal triangle distinctly angular; primary and secondary antenodal cross-veins identical; sectors of arculus not stalked; cubito-anal area broad with three rows of cells.

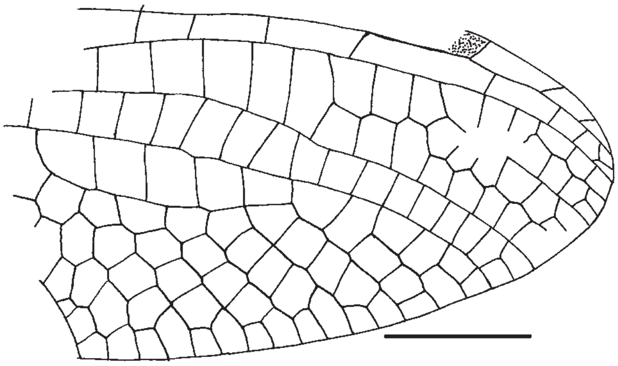
Eomacrodiplax incompleta sp. nov.
(Plate 4, figs 3–4; Text-figs 24–25)

Holotype. Specimen NHMUK In.24770 (forewing base, Hooley coll., Plate 4, fig. 3, Text-fig. 24), Insect Limestone, northwest Isle of Wight.

Paratype. Specimen NHMUK In.17333 (broken wing with separate base and apex, Smith coll., Plate 4, fig. 4, Text-fig. 25).



Text-figure 24 *Eomacrodiplax incompleta* gen. et sp. nov., holotype, NHMUK In.24770. Scale bar = 3 mm.



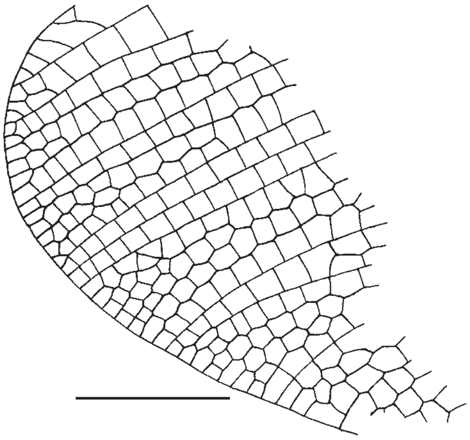
Text-figure 25 *Eomacrodiplax incompleta* gen. et sp. nov., paratype, NHMUK In.17333. Scale bar = 3 mm.

Etymology. Named after the incomplete state of preservation of the holotype forewing.

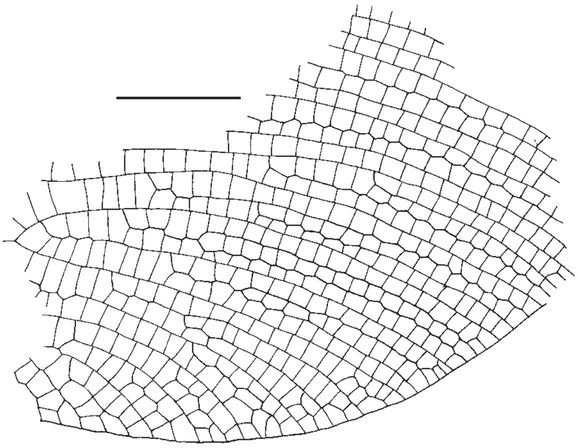
Diagnosis. As for the genus.

Description. Forewing hyaline, width of wing 8·0 mm; distance from base to arculus 3·0 mm, from arculus to nodus 12·3 mm, from arculus to base of RP3/4 7·7 mm, from wing base to Ax1 3·7 mm, from Ax1 to arculus 1·3 mm, from arculus to Ax2 1·5 mm; primary antenodal cross-veins identical to the secondaries; at least five antenodal cross-veins, probably seven or eight in the complete wing; only two cross-veins between RA and RP basal of subnodus; one Bqr cross-vein; oblique vein 'O' just distal of base of RP2; sectors of arculus not stalked; median area free of cross-vein; submedian area with only CuP; subdiscoidal area subdivided into three cells; hypertriangle free, 4·4 mm long, 0·5 mm wide; discoidal triangle free, with distal side with a strong angle; two rows of cells in postdiscoidal area distal of triangle; Mspl straight, with one row of cells between it and MA; anal area with two rows of cells; cubito-anal area with three rows of cells.

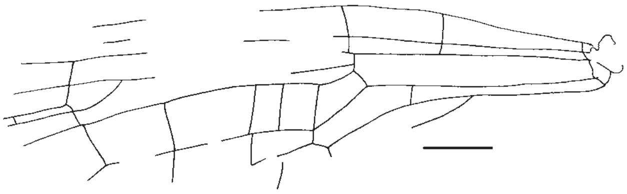
Discussion. The wing base of NHMUK In.17333 is identical to that of the holotype. The presence of the characteristical shape of Rspl, curved and distally rejoining the IR2, a distinct Mspl and the subdiscoidal triangle divided into three cells support affinities of this fossil with the Italoansida. Within this clade, affinities with the 'Corduliidae' and Hemicorduliidae are excluded because of the distinctly angular distal side of discoidal triangle. Its attribution to the Libellulida is supported by the two very distinct primary antenodal brackets Ax1 and Ax2. Affinities with the Eulibellulida are excluded because the sectors of arculus of this fossil are not stalked. The remaining family Urothemistidae Lieftinck, 1954 comprises the four Recent genera *Aethriamanta* Kirby, 1889, *Macrodiplax* Brauer, 1868, *Urothemis* Brauer, 1868 and *Selysiothemis* Ris, 1897. *Eomacrodiplax* gen. nov. shares with *Macrodiplax* and *Selysiothemis* the strong angle of distal side of discoidal triangle, but differs from *Selysiothemis* in its subdiscoidal triangle divided into three cells. *Eomacrodiplax* differs from *Macrodiplax* in the basal



Text-figure 26 Eucaloptera incertae sedis, NHMUK In.24759. Scale bar = 3 mm.



Text-figure 27 ?*Bolcathore* species A., NHMUK In.24648. Scale bar = 3 mm.



Text-figure 28 Dysagrionini species A, NHMUK I.9866. Scale bar = 1 mm.

side of its subdiscoidal triangle not perpendicular to its anterior side and its cubito-anal area broader with three rows of cells (Ris 1909–1913).

The Urothemistidae were previously unknown in the fossil record (Nel & Paicheler 1993b, 1994a). Despite the incomplete state of preservation of the type specimen, we consider this is the first fossil representative of this family and thus worthy of being named. The Urothemistidae are currently considered as the sister group of the Libellulida, whose oldest known representative is Turonian (Fleck *et al*. 1999). Thus the Urothemistidae are probably also at least Late Cretaceous, and their presence in the Palaeogene is not surprising. The Recent Urothemistidae are known from the Palaearctic, Nearctic, Oriental, Afrotropical and Australasian regions. It is not possible to infer significant palaeoenvironmental information from their discovery in the Late Eocene of the Isle of Wight.

Suborder Zygoptera Selys, 1854
Clade Eucaloptera Bechly, 1996
Subclade Calopterygiformia Bechly, 1996

Specimen NHMUK In.24759 (Hooley coll., Text-fig. 26, Insect Limestone, northwest Isle of Wight) belongs to the clade Eucaloptera (Amphipterygida and Calopterygomorpha), because of its very numerous cells and secondary longitudinal veins. It is not possible to ascertain its affinities.

Subclade Calopterygomorpha Bechly, 1996
Superfamily Polythoroidea Münz, 1919 (*sensu* Gentilini 2002)
Family Bolcathoridae Gentilini, 2002
Genus *Bolcathore* Gentilini, 2002
?*Bolcathore* species A.
(Plate 4, fig. 5; Text-fig 27)

Material. Specimen NHMUK In.24648 (Hooley coll., Plate 4, fig. 5, Text-fig 27), Insect Limestone, north-west Isle of Wight.

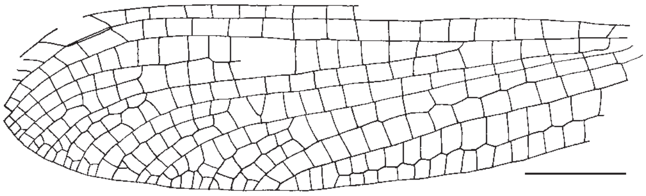
Remark. This fragment is a part of the medio-cubito-anal area, dark brown red. Although very incomplete, this fragment can be accurately attributed to the Eucaloptera because of its very numerous cells and secondary longitudinal veins. It has the typical polythoroid fork of CuA into CuAa and CuAb, with a concave intercalary vein between these branches (triadic branching), and the very broad cubito-anal area of the Bolcathoridae (Bechly 1996; Gentilini 2002). This family is recorded from the Middle Eocene of Monte Bolca (Italy) by *B. colorata* Gentilini, 2002. Our fossil is too fragmentary to be accurately compared to the Italian species. The Recent Polythoridae occur in the warm and humid Neotropical forests.

Subclade Amphipterygida Bechly, 1996
Superfamily Amphipterygoidea Tillyard, 1917
Family Thaumatoneuridae Tillyard & Fraser, 1938
Subfamily Dysagrioninae Cockerell, 1908
Dysagrionini species A

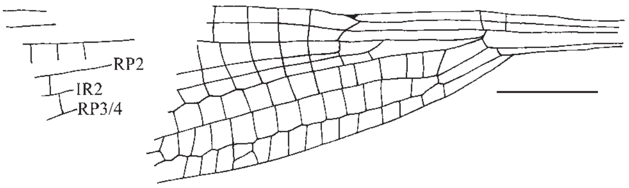
Material. Specimen NHMUK I.9866/I.9718 (part and counterpart of two wing bases, Hooley coll., Plate 4, fig. 6, Text-fig. 28), Insect Limestone, northwest Isle of Wight.

Description. Wing fragment hyaline, 8·7 mm long; distance from wing base to arculus 3·7 mm, from arculus to subodus 4·0 mm, from wing base to Ax1 2·5 mm, from Ax1 to Ax2 1·3 mm; Ax2 just distal of arculus; subnodus nearly vertical.

Discussion. Even if it is only a fragment of a wing base, this fossil can be attributed to the Dysagrioninae on the basis of the following characters: cubito-anal area very broad (inferred after the general shape of the wing); base of IR2 below nodus; base of RP3/4 between arculus and nodus, close to nodus; discoidal cell broad but broader in its distal part than in its basal part. The Petrolestini Cockerell, 1927 (*Petrolestes* Cockerell, 1927 and *Congqingia* Zhang, 1992) differ from this fossil in the base of IR2 in a more basal position. Several Dysagrionini Cockerell, 1908 are known from the Palaeogene of North America and Eurasia (*Dysagrion* Scudder, 1878, *Phenacolestes* Cockerell, 1908, *Primorilestes* Nel *et al*., 2005, *Electrophenacolestes* Nel & Arillo, 2006) (Nel & Paicheler 1994b; Bechly 1996; Nel *et al*. 2005; Nel & Arillo 2006). Our fossil differs from *Electrophenacolestes* in its subnodus nearly vertical. Our fossil is too incomplete to be compared with the three other genera. We consider it as a Dysagrionini of uncertain affinities. It confirms the presence of this group in the Late Eocene of Western Europe.



Text-figure 29 *Oligoargiolestes oligocenum* Kennedy, 1925, NHMUK I.8890. Scale bar = 3 mm.



Text-figure 30 *Oligoargiolestes oligocenum* Kennedy, 1925, NHMUK In.24645. Scale bar = 3 mm.

Remark. The fossil wing fragment MNEMG 1998.35 (= BLS 86a,b) that Nel & Jarzembowski (1999, pp 199–200, fig. 7) described under the label 'Odonata suborder uncertain, species A' could well belong to the same species as specimen NHMUK I.9866, because they have very similar discoidal and subdiscoidal cells, probably deformed in the latter.

Clade Coenagrionomorpha Bechly, 1996
Family Megapodagrionidae Calvert, 1913
Genus *Oligoargiolestes* Kennedy, 1925
Oligoargiolestes oligocenum Kennedy, 1925

1916 *Megalestes anglicus* Cockerell & Andrews, p. 90, pl. 2 fig. 5.
1925 *Oligoargiolestes oligocenicum* Kennedy, p. 299.
1994b *Oligoargiolestes oligocenicum* Nel & Paicheler, p. 46.
1999 *Oligoargiolestes oligocenicum* Nel & Jarzembowski, pp 195–197, figs 2–3.

Holotype. Specimen NHMUK I.8548 (Brodie coll., Plate 5, fig. 1), Insect Limestone, northwest Isle of Wight.

Other specimens. MNEMG 1998.36 figured in Nel & Jarzembowski (1999, pp 195–196, fig. 2), NHMUK I.8890 (Brodie coll., Text-fig. 29), and NHMUK In.24645 (Hooley coll., Text-fig. 30).

Description of new material (NHMUK I.8890 and NHMUK In.24645). Wing width 5.5 mm (I.8890), 5.2 mm (In.24645); distance from base to arculus 4.0 mm, from arculus to nodus 3.8 mm, from nodus to pterostigma 15.0 mm, pterostigma 2.1 mm long, 0.7 mm wide, covering 1.5 cell; pterostigmal brace oblique; basal and distal sides of pterostigma oblique; nodal Cr and subnodus distinctly oblique; Ax1 0.5 mm basal of arculus; Ax2 nearly opposite arculus; no secondary antenodal cross-vein; no antesubnodal cross-vein; median space free; CuP distal of base of AA; discoidal cell elongate, 1.7 mm long, 0.5 mm wide, with its anterior and posterior sides parallel, distal side oblique, 0.7 mm long; base of RP3/4 near subnodus, 1.0 mm basal of it; base of IR2 opposite subnodus; base of RP2 at about 5–6 cells distal of subnodus; base of IR1 7–8 cells distally; one row of cells between RP1 and IR1; three rows between IR1 and RP2, between RP2 and IR2, and between IR2 and RP3/4, five rows between RP3/4 and MA, one row between MA and MP, one row between MP and CuA and between CuA and posterior wing margin.

Discussion. Cockerell & Andrews (1916, p. 90, pl. 2, fig. 5) figured this fossil under the name '*Megalestes anglicus*' Kennedy (1925, pp 296–297, 299) created the genus *Oligoargiolestes* Nel & Paicheler (1994b, p. 46) and Nel & Jarzembowski (1999, pp 195–196, figs 2–3) discussed its family attribution and considered it could belong to the Megapodagrionidae or to the Pseudolestidae. This species can be separated from the Hypolestidae of the Isle of Wight (Late Eocene) on the basis of its very oblique distal side of pterostigma (see below). Both the type specimen and MNEMG 1998.36 are wing apices, but the two new specimens NHMUK I.8890, and NHMUK In.24645 are more complete wings. The attribution of these new specimens to the same species as the type is based on the exact identity in all their shared structures.

This species can be considered as a Coenagrionomorpha Bechly, 1996 because of the presence of their synapomorphies in the wing venation *sensu* Bechly (1996), i.e. pterostigma shortened; postnodal and postsubnodal cross-veins aligned; lestine oblique vein absent; basal closure of discoidal cell including the development of a dorsal arcular bracket. Within the Coenagrionomorpha, the Hypolestidae could be excluded because of their amphipterygid type of pterostigma (basal margin strongly slanting). The Coenagrioniformia Bechly, 1996 could also be excluded because of their suppressed intercalary veins (except IR1 and IR2) and the presence of only two rows of cells in the total wing space between RP1 and RP2 that are separated by the IR1. The last group within the Coenagriomorpha are the Megapodagrionidae. They have no known synapomorphies in the wing venation, after Bechly (1996), and could well be paraphyletic (Groeneveld *et al.* 2007).

Racenis (1959) proposed a division of the Megapodagrionidae into four subfamilies: Argiolestinae; Megapodagrioninae; Philosininae Ris, 1917; and Dysagrioninae Scudder, 1878 (transferred into the Thaumatoneuridae by Bechly 1996). Davies (1981) added the Tactonemidinae. Affinities with this last subfamily are excluded because they have veins RP3/4 and IR2 arising distal of the subnodus. *Oligoargiolestes* shares with *Philosina* Ris, 1917, the unique representative of the Philosininae, the structures of the petiole and anal and CuP veins, but differs in its straight CuA with a narrow cubito-anal area, and its distinctly shorter pterostigma (Ris 1917).

Oligoargiolestes could have some affinities with the Argiolestinae because of its longitudinal wing veins curved in their posterior part (convex), thus somewhat shortened (especially MA, MP and CuA) and the branches of RP (RP3/4 and IR2) distally diverging (Bechly, 1996). This author also considered that the character of 'more than one row of cells between CuA and the hind margin (reversal)' is a synapomorphy of the Argiolestinae, but this character is absent in some argiolestine genera as *Trineuragrion* and *Rhinagrion*. *Oligoargiolestes* shares with these last genera the presence of one row of cells between CuA and the hind margin. Nevertheless, all the argiolestine genera have their base of free AA opposite or distal of the arculus, unlike *Oligoargiolestes*.

The Megapodagrioninae have no known synapomorphies in the wing venation after Bechly (1996). Only the representatives of the tribe Megapodagrionini Racenis, 1959 have their CuP veins proximal of the arculus and distal of the base of AA (see list in Nel *et al.* 1997). Amongst them, *Megapodagrion* Selys, 1885 and *Priscagrion* Zhou & Wilson, 2001 have a CuP in a similar distal position relatively to base of AA, but *Priscagrion* has secondary antenodal cross-veins (Zhou & Wilson 2001; De Marmels 2002). *Oligoargiolestes* differs from *Megapodagrion* in its area between RP3/4 and IR2 being greatly broadened distally. Also, all the Recent Megapodagrioninae have their longitudinal veins (especially MA, MP and CuA) not curved in their posterior part.

Nel *et al*. (1997) listed and commented on the fossil megapodagrionid genera. Amongst them, *Oligoargiolestes* differs from *Eopodagrion* Cockerell, 1920 in that its subnodus is not vertical and it has more numerous postnodal cross-veins. *Melanagrion* Cockerell, 1907 has two rows of cells in the cubito-anal area and in the area between C and RA distal of the pterostigma, and its wing is petiolated distal of the CuP. *Miopodagrion* Kennedy, 1925 has two rows of cells in the area between C and RA distal of the pterostigma. *Vulcagrion* Nel & Paicheler, 1994b has its veins IR2 and RP3/4 fused basally distal of the subnodus and the wing petiolated distal of the CuP vein, as in *Lithagrion* Scudder, 1890. *Cerdanyagrion* Nel *et al*., 1996 differs from *Oligoargiolestes* in the presence of double rows of cells in the area between RA and RP1 and between C and RA (Nel *et al*. 1996). *Oligoargiolestes* differs from *Thanetophilosina* Nel *et al*., 1997 in the number of postnodal cross-veins (about 16 instead of 30) (Nel *et al*. 1997). *Oligoargiolestes* differs from *Furagrion* Petrulevičius *et al*., 2008 in having its pterostigma covering less than two cells and with a more oblique distal side. It differs from *Eckfeldia* Petrulevičius *et al*., 2008 in that its pterostigma covers less than two cells and it has a more oblique distal side (Petrulevičius *et al*. 2008). *Oligoargiolestes* differs from *Electropodagrion* Azar & Nel, 2008 having in its vein CuP in a more distal position, and in the presence of several secondary longitudinal veins in the areas between the branches of RP (Azar & Nel 2008).

Family Hypolestidae Tillyard & Fraser, 1938

Genus *Anglohypolestes* gen. nov.

Type species. *Anglohypolestes fasciata* sp. nov.

Etymology. Named after *Anglia*, Latin name for England and *Hypolestes*.

Diagnosis. Wing characters only; IR2 and RP3/4 bases basally recessed midway between nodus and arculus; no straight intercalary veins between RP1 and IR1; IR1, RP2 and IR2 nearly straight; a cross-vein between RA and RP just basal of subnodus; no cross-vein between basal side of pterostigma and costal margin; pterostigma covering three cells; CuA very long, weakly zigzagged; anal area present below discoidal cell; five rows of cells in area between IR2 and RP3/4, area between MP and CuA with one row of cells; area between IR1 and RP2 with four rows of cells along posterior wing margin; area between RP2 and IR2 with a very short secondary longitudinal vein; area between MA and MP broad, with six rows of cells along posterior wing margin.

Anglohypolestes fasciata sp. nov.

Holotype. Specimen NHMUK In.17373 (Smith coll., Plate 5, fig. 2, Text-fig. 31), Insect Limestone, northwest Isle of Wight.

Etymology. Named after the dark zone crossing the distal part of wing.

Diagnosis. As for the genus, a dark zone crossing distal part of wing.

Description. Wing hyaline except for a dark zone crossing distal part of wing; preserved part of wing 15·0 mm long, width 4·6 mm; distance between arculus and nodus 3·1 mm, between nodus and pterostigma 8·1 mm, between pterostigma and apex 2·1 mm; pterostigma 1·9 mm long, 0·5 mm wide, covering three cells, with basal margin strongly slanting; pterostigmal brace not very oblique; 11 postnodal and postsubnodal cross-veins aligned; no oblique vein ‘O’; Ax2 probably aligned with arculus; discoidal cell elongate, 0·37 mm wide and probably 0·8 mm long, with anterior side nearly as long as posterior side; subdiscoidal cell and anal area present below discoidal cell; subnodus oblique; one cross-vein in area between RA and RP basal of subnodus; bases of RP3/4 and IR2 midway between arculus and nodus; base of RP2 three cells distal of subnodus; base of IR1 two cells distally; all longitudinal veins straight or weakly curved and/or weakly zigzagged; distribution of intercalary rows of cells and veins between main veins as in diagnosis.

Discussion. This fossil could be considered as Coenagrionomorpha Bechly, 1996 because of the presence of their synapomorphies in the wing venation *sensu* Bechly (1996), i.e. pterostigma shortened; postnodal and postsubnodal cross-veins aligned; lestine oblique vein absent. Within the Coenagrionomorpha, the Coenagrioniformia Bechly, 1996 could be excluded because of their suppressed intercalary veins (except IR1 and IR2) and the presence of only two rows of cells in the total wing space between RP1 and RP2 that are separated by the IR1. The Megapodagrionidae Calvert, 1913 have no known synapomorphies in the wing venation (after Bechly 1996), but their IR2 and RP3/4 bases are below the nodus, not basally recessed as in this fossil. It shares with the Hypolestidae Tillyard & Fraser, 1938 the amphipterygid type of pterostigma, with basal margin strongly slanting. The Heteragrioninae Racenis, 1959 (*Heteragrion* Selys, 1862) and the Philogeniinae Racenis, 1959 (type genus: *Philogenia* Selys, 1862, other possible genus *Paraphlebia* Hagen, 1861) are excluded due to the positions of the bases of IR2 and RP3/4. *Anglohypolestes* gen. nov. belongs to the remaining subfamily Hypolestinae, in which the midfork is at least somewhat recessed basally, and the subnodus is located between the bases of RP2 and IR2 that are widely separated.

Within this subfamily, the Lestoideini Münz, 1919 (*Lestoidea* Tillyard, 1913) can be excluded, because *Anglohypolestes* has numerous intercalary longitudinal veins between the main veins, but lacks the two characteristic straight intercalary veins between RP1 and IR1.

The Hypolestini Tillyard & Fraser, 1938 (*Hypolestes* Gundlach, 1888) have a characteristic distal curvature of the veins IR1, RP2 and IR2, not present in *Anglohypolestes*. Also our fossil has a cross-vein in the area between RA and RP, just basal of the subnodus, which is absent in *Hypolestes*.

The Philosinini Kennedy, 1925 comprise the type genus *Philosina* Ris, 1917 and the sister-genera *Lestomima* May, 1933 and *Rhipidolestes* Ris, 1912, and maybe *Eolestes synthetica* Cockerell, 1940 and *Prohypolestes dauphinensis* Nel & Paicheler, 1994b (Bechly 1996). *Lestomima* and *Rhipidolestes* differ from *Anglohypolestes* in the shape of the CuA and the pterostigma (Münz 1919; May 1933). The base of IR2 is below the subnodus in *Philosina*, unlike in *Anglohypolestes*. *Eolestes* has one row of cells in the area between IR2 and RP3/4, and a very broad area between MP and CuA; the main differences from *Anglohypolestes* (Cockerell 1940). Differences from *Prohypolestes* are fewer, but nevertheless justify a generic separation; i.e. the area between IR1 and RP2 with two rows of cells along the posterior wing margin in *Prohypolestes*, instead of the four in *Anglohypolestes*; the area between RP2 and IR2 with a longer secondary longitudinal vein in *Prohypolestes* than in *Anglohypolestes*; the area between MA and MP narrower in *Prohypolestes* than in *Anglohypolestes*; and the pterostigma covering two cells in *Prohypolestes* instead of three as in *Anglohypolestes* (Nel & Paicheler 1994b).

Genus *Eohypolestes* gen. nov.

Type species. *Eohypolestes hooleyi* sp. nov.

Etymology. Named after Eocene and *Hypolestes*.

Diagnosis. Wing characters only; IR2 and RP3/4 bases basally recessed midway between nodus and arculus; no straight intercalary veins between RP1 and IR1; IR1 zigzagged; RP2

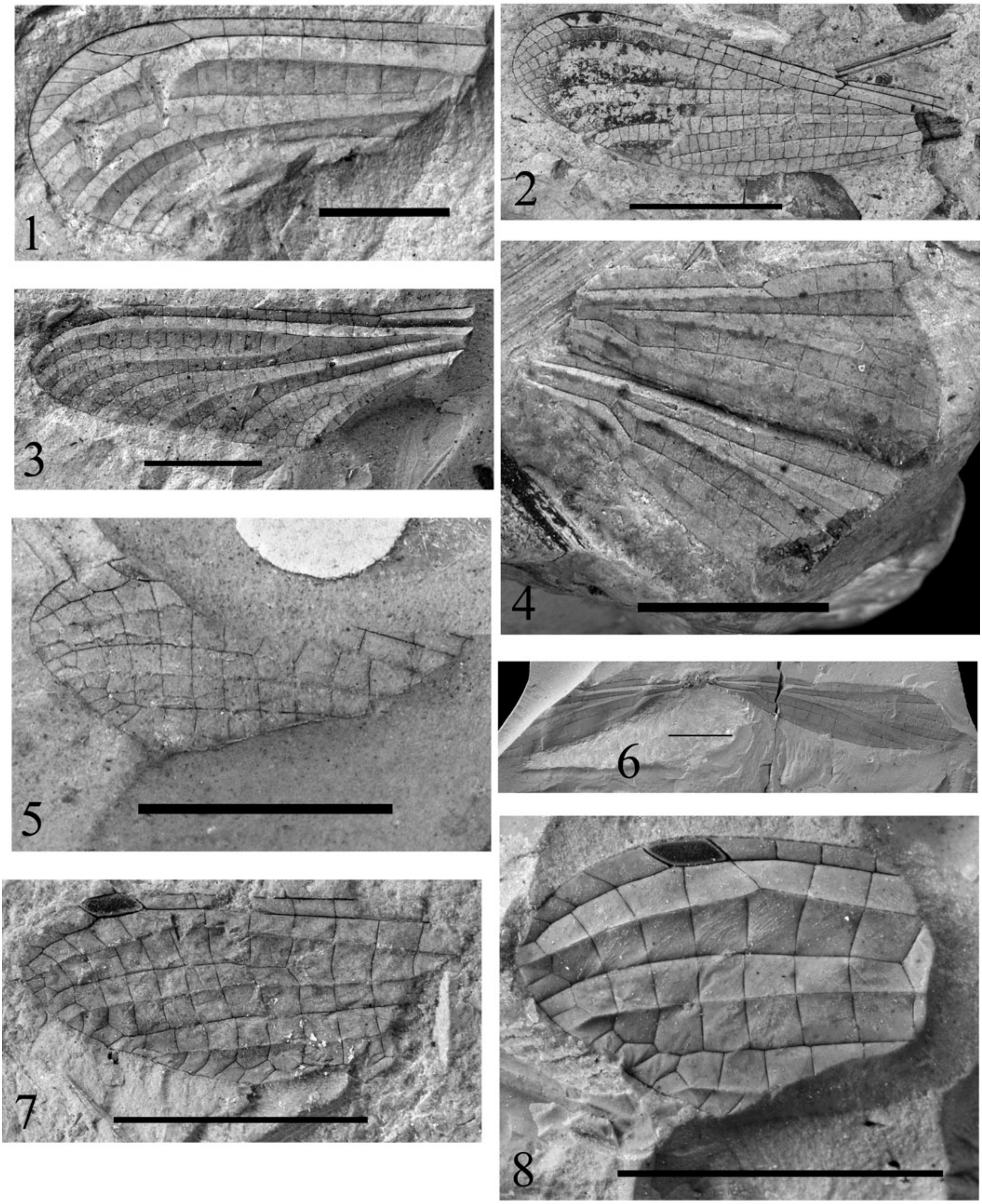
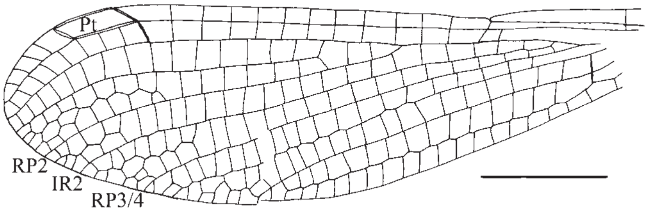
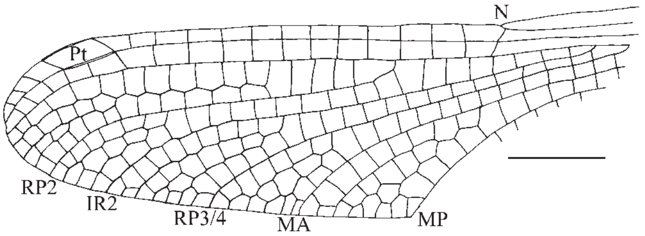


Plate 5 (1) *Oligoargiolestes oligocenum* Kennedy, 1925, holotype, NHMUK I.8548. Scale bar = 3 mm. (2) *Anglohypolestes fasciata* gen. et sp. nov., NHMUK In.17373. Scale bar = 5 mm. (3) *Eohypolestes hooleyi* gen. et sp. n., holotype, NHMUK In.24653. Scale bar = 5 mm. (4) '*Enallagma*' *oligocena* Cockerell & Andrews, 1916, holotype, NHMUK I.8631. Scale bar = 5 mm. (5) '*Enallagma*' *oligocena* Cockerell & Andrews, 1916, paratype, NHMUK I.8647. Scale bar = 5 mm. (6) Coenagrionidae genus and species B, specimen X.50140.143. Scale bar = 5 mm. (7) Coenagrionoidea undetermined, NHMUK In.24642. Scale bar = 5 mm. (8) Coenagrionoidea undetermined, NHMUK In.17372. Scale bar = 2 mm.



Text-figure 31 *Anglohypolestes fasciata* gen. et sp. nov., NHMUK In. 17373. Scale bar = 3 mm.



Text-figure 32 *Eohypolestes hooleyi* gen. et sp. nov., holotype, NHMUK In.24653. Scale bar = 3 mm.

and IR2 distally curved; no cross-vein between basal side of pterostigma and costal margin; pterostigma covering two cells; seven rows of cells in area between IR2 and RP3/4, area between RP3/4 and MA with six rows of cells; area between IR1 and RP2 with three rows of cells along posterior wing margin; area between RP2 and IR2 with two zigzagged secondary longitudinal veins.

Eohypolestes hooleyi sp. nov.

Holotype. Specimen NHMUK In.24653 (Hooley coll., Plate 5, fig. 3, Text-fig. 32), Insect Limestone, northwest Isle of Wight.

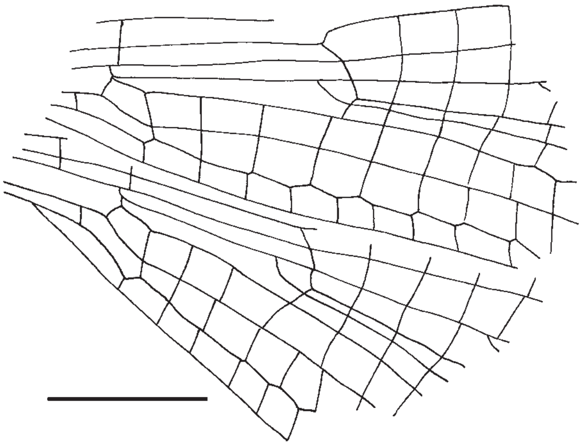
Paratype. Specimen NHMUK In.24769 (Hooley coll.).

Etymology. Named after Mr Hooley, collector of the type specimen.

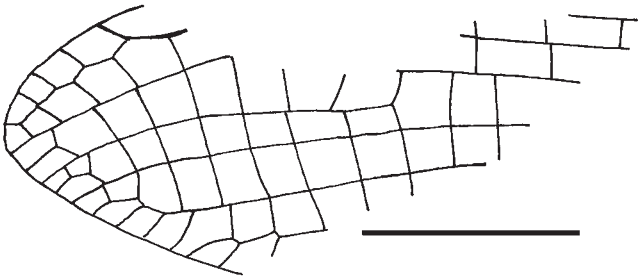
Diagnosis. As for the genus.

Description. Both specimens are distal two-thirds of wings. Wing hyaline (a dark zone is present in the holotype along the posterior wing margin, but this is probably due to taphonomy); preserved part of wing 19·3 mm long, width 5·9 mm; distance between nodus and pterostigma 11·7 mm, between pterostigma and apex 2·3 mm; pterostigma 2·1 mm long, 0·7 mm wide, covering two cells, with basal margin strongly slanting; pterostigmal brace not very oblique; 11 postnodal and postsubnodal cross-veins aligned, but no postsubnodal cross-vein corresponding to the most distal postnodal cross-vein; no oblique vein 'O'; subnodus oblique; bases of RP3/4 and IR2 midway between arculus and nodus, but well apart; base of RP2 three cells distal of subnodus; base of IR1 five cells distally; cubito-anal area with three rows of cells between CuA and posterior wing margin (visible in paratype); shape of main longitudinal veins and distribution of intercalary rows of cells and veins between main veins as in diagnosis.

Discussion. This fossil can be attributed to the Hypolestinae for the same reasons as above. Furthermore, affinities with the Lestida Bechly, 1996 are very unlikely, because this fossil has its postnodal and postsubnodal cross-veins well aligned and the bases of IR2 and RP3/4 more distant than in taxa of this clade. The Lestoideini, *Philosina*, *Lestomima* and *Rhipidolestes*, are excluded for the same reasons as above (the shape of the pterostigma in the cases of *Lestomima* and *Rhipidolestes*). The area between MA and MP is much narrower in *Prohypolestes* than in *Eohypolestes* gen. nov. *Eolestes* has one row of cells in the area between IR2 and RP3/4, unlike in *Eohypolestes*.



Text-figure 33 '*Enallagma*' *oligocena* Cockerell & Andrews, 1916, holotype, NHMUK I.8631. Scale bar = 3 mm.



Text-figure 34 '*Enallagma*' *oligocena* Cockerell & Andrews, 1916, NHMUK I.8647. Scale bar = 3 mm.

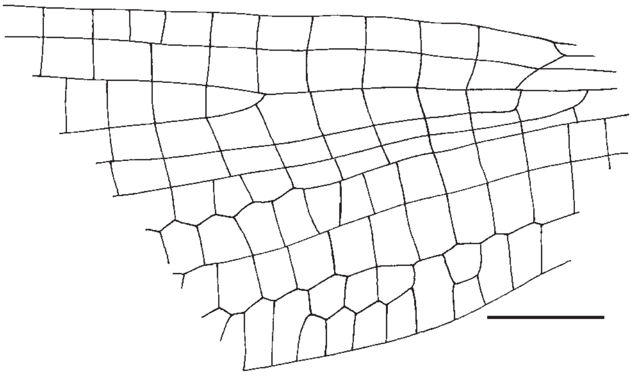
Eohypolestes shares with the Hypolestini and *Hypolestes* the characteristical distal curvature of RP2 and IR2, but not IR1, which is zigzagged in *Eohypolestes*. Other differences with *Hypolestes* are as follows: base of RP2 three cells distal of subnodus in *Eohypolestes*, instead of two cells; base of IR1 five cells distal of that of RP2 in *Eohypolestes*, instead of two; area between RP3/4 and MA with six rows of cells along posterior wing margin, instead of only one; area between IR2 and RP2 with four rows of cells and two long intercalary veins in *Eohypolestes*; three rows of cells in cubito-anal area. Thus we tentatively attribute *Eohypolestes* to the Hypolestini, but to a different genus from *Hypolestes*.

Remark. The family Hypolestidae was already known in the fossil record from several larvae and a possible adult in the Eocene Baltic amber, *Eolestes synthetica* Cockerell, 1940 (Eocene, USA) and *Prohypolestes dauphinensis* Nel & Paicheler, 1994b (Oligocene, France) (Nel & Paicheler 1994b; Bechly & Wichard 2009). Thus the present discovery of two new genera and species is not surprising.

Clade Coenagrioniformia Bechly, 1996
Family Coenagrionidae Kirby, 1890
Genus *Enallagma* Charpentier, 1840
'*Enallagma*' *oligocena* Cockerell & Andrews, 1916

1916 '*Enallagma*' *oligocena* Cockerell & Andrews, pp. 90–91, pl.2 figs 6,7.
1993 '*Enallagma*' *oligocenica* Nel & Paicheler, p. 60.
1999 '*Enallagma*' *oligocena* Nel & Jarzembowski, p. 197.

Note. This species was originally described on the basis of the holotype NHMUK I.8631 (Brodie coll., median part of two wings, Plate 5, fig. 4, Text-fig. 33, Insect Limestone, northwest Isle of Wight) (Cockerell & Andrews 1916, pp 90–91, pl. 2, fig. 6), and paratype NHMUK I.8647 (Brodie coll., a wing apex, Plate 5, fig. 5, Text-fig. 34) (Cockerell & Andrews



Text-figure 35 Coenagrionidae genus and species C, specimen NHMUK In.24762, drawing. Scale bar = 2 mm.

1916, pp 90–91, pl. 2, fig. 7). Nel & Paicheler (1993a) and Nel & Jarzembowski (1999) discussed the possible affinities of this taxon and indicated that the second specimen could well belong to a different species. *'E.' oligocena* is a Coenagrionidae of uncertain affinities.

Coenagrionidae genus and species A

Remarks. Nel & Jarzembowski (1999) described and figured this Coenagrionoidea on the basis of the distal two-thirds of a wing (MNEMG 1998.33, Insect Limestone, northwest Isle of Wight), mainly characterised by the shortened MP and a very short pterostigma covering less than one cell. Its affinities remain uncertain.

Coenagrionidae genus and species B

Remarks. This taxon is based on the basal two-thirds of two wings attached to a thorax (CAMSM X.50140.143, Smith Coll., Plate 5, fig. 6, Insect Limestone, northwest Isle of Wight), and differs from genus and species A in its elongate CuA and MP. It differs from '*Enallagma*' *oligocena* in its discoidal cell with a shorter anterior side. Nevertheless, its incomplete state of preservation does not allow further taxonomic placement within the Coenagrionidae.

Coenagrionidae genus and species C

Remarks. This taxon is based on the median half of a wing (specimen NHMUK In.24762, Hooley coll., Text-fig. 35, Insect Limestone, northwest Isle of Wight). It differs from the other coenagrionoid taxa from the Isle of Wight in the presence of two rows of cells in the distal part of the cubito-anal area.

Remarks. Several other fragments of wings attributable to the Coenagrionoidea have been found in the Isle of Wight outcrops (specimens NHMUK In.17372, In.17385 (Smith coll.), NHMUK In.24528, In.24640, In.24642, In.24755, (Hooley coll.) and MIWG 3602) (Plate 5, figs 7–8, Plate 6, fig. 1, Text-figs 36–41), but their exact affinities and identity cannot be determined.

Superfamily Platycnemidoidea Jacobson & Bianchi, 1905
Family 'Protoneuridae' Jacobson & Bianchi, 1905
Genus *Angloprotoneura* gen. nov.

Type species. *Angloprotoneura emilielacroixi* sp. nov.

Etymology. Named after *Anglia*, Latin name for England and *Protoneura*.

Diagnosis. Wing characters only; CuA lacking; AA lacking; only seven postnodal cross-veins; MP ending three cells distal of level of subnodus; pterostigma covering one cell and longer than broad; base of RP2 three cells distal of subnodus.

Angloprotoneura emilielacroixi sp. nov.

Holotype. Specimen NHMUK In.17246 (Smith coll., Plate 6, fig. 2, Text-fig. 42), Insect Limestone, northwest Isle of Wight.

Etymology. Named after the late Emilie Lacroix, friend of one of us (GF).

Diagnosis. That of the genus.

Description. An isolated wing, 12·3 mm long, 2·5 mm wide, probably hyaline, with dark pterostigma, the traces of coloration of some veins being probably due to diagenetic process; pterostigma 0·7 mm long, 0·25 mm wide, longer than broad, covering nearly one cell; petiole elongate and narrow, 1·75 mm long, 0·5 mm wide, but with its posterior part partly destroyed; nodus in the basal 32% of wing length, distance from wing base to arculus 1·75 mm, from arculus to nodus 2·3 mm, from nodus to pterostigma 6·5 mm, from pterostigma to wing apex 1·5 mm; antenodal area partly destroyed, with antenodal cross-veins not preserved; nodal Cr and subnodus distinctly oblique; seven postnodal cross-veins, aligned with postsubnodal cross-veins, except for the two distals; base of RP3/4 below nodus; base of IR2 aligned with subnodus; base of RP2 three cells and 2·4 mm distally; base of IR1 three cells and 2·3 mm distally; IR1, RP2, RP3/4, and MP nearly straight; IR2 and MA distally zigzagged; cross-veins of the radial area nearly aligned in transverse rows; discoidal cell partly destroyed but clearly narrow rectangular and elongate, 0·1 mm wide, 1·1 mm long; one row of cells in area between MP and posterior wing margin; MP ending three cells distal of level of subnodus, nearly below base of RP2; CuA lacking, AA lacking.

Discussion. The vein CuA completely fused with the posterior wing margin, thus only retained as subdiscoidal vein, is a specialised character that convergently developed between the Triassic Protozygoptera: Batkeniidae, and among the true Zygoptera, in the Platystictidae Laidlaw, 1924, *Disparocypha* Ris, 1916, the Lestoideini Münz, 1919 (*Lestoidea* Tillyard, 1913) and the Protoneuridae Jacobson & Bianchi, 1905 (Bechly 1996).

The Lestoideini have completely different positions of the bases of veins RP3/4 and IR2, well basal of nodus and a very short MP, not reaching the level of nodus (Fraser 1957). The rhinocyphine genus *Disparocypha* also has its bases of RP3/4 and IR2 basally recessed. The Platystictidae have their wings with a falcate apex, longitudinal veins RA, RP1, IR1, RP2 and IR2 strongly converging to the apex, the costal edge of the pterostigma much shorter than the radial edge, and the nodus in a very basal position (about 22% of wing length), unlike *Angloprotoneura* gen. nov. (Bechly 1996).

Bechly (1996) characterised the Protoneuridae by the following wing venational synapomorphies: 'discoidal cell rectangular (convergent to Lestoideini, Platystictidae and most Caloptera; maybe synapomorphic with Platycnemidinae); discoidal bracket (dorsal sclerotisation on MAb and the subdiscoidal vein) strongly reduced (convergent to Perilestidae and Anisoptera); CuA completely fused with the hind margin, thus only retained as subdiscoidal vein (convergent to Batkeniidae, Disparocypha, Lestoideini and Platystictidae).' None of these characters is strictly present in the Protoneuridae, but their combination present in *Angloprotoneura* gen. nov. occurs only in this family.

Fraser (1957) divided the Protoneuridae into Protoneurinae, Caconeurinae Fraser, 1957, Disparoneurinae Fraser, 1957, and Isostictinae Fraser, 1955. Watson (1992) synonymised the

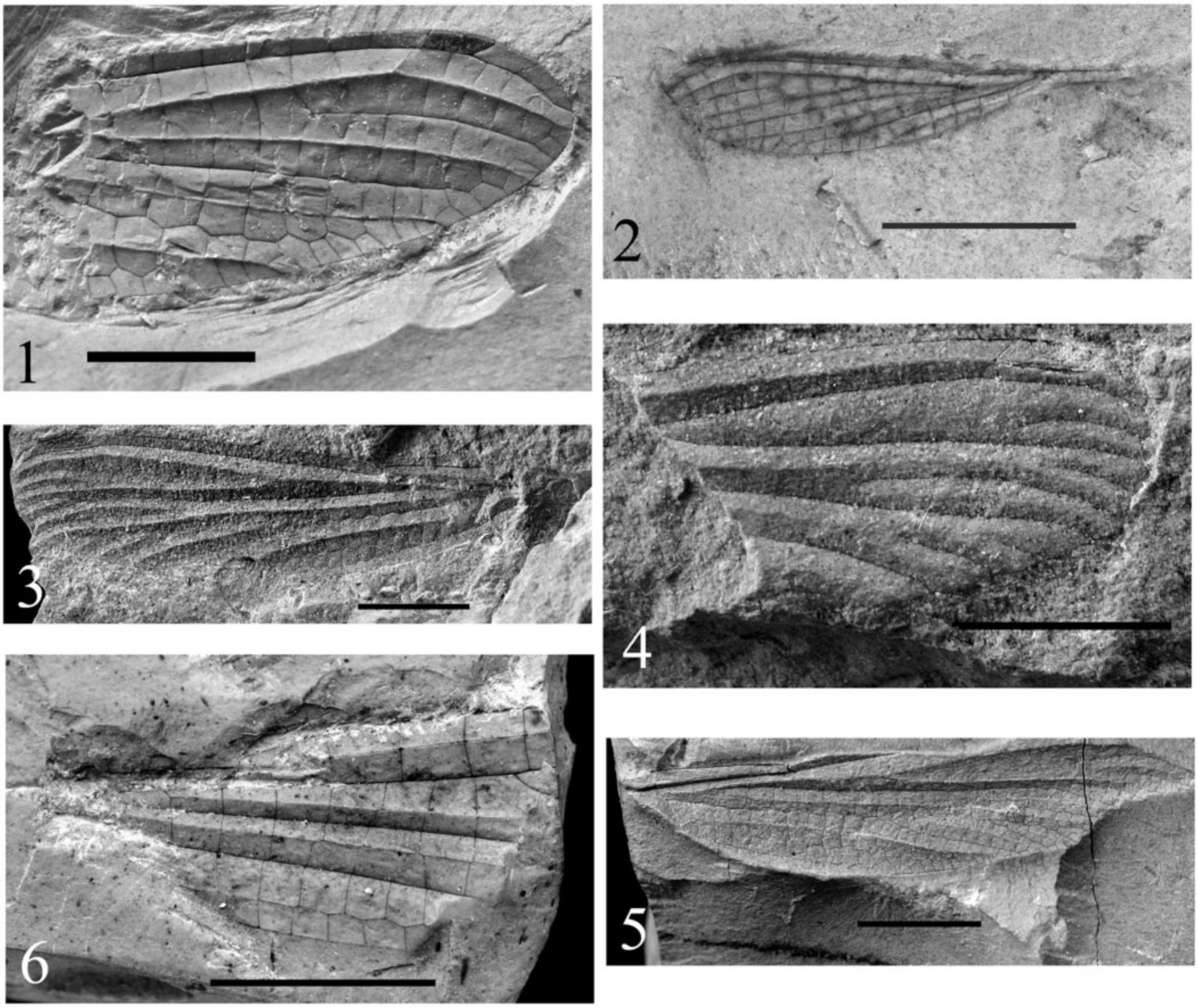


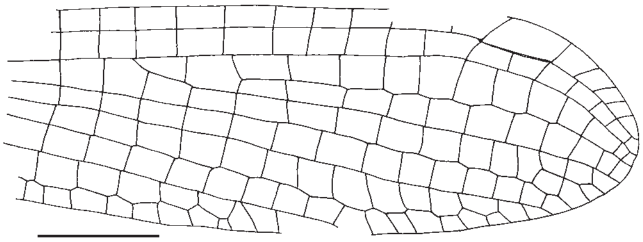
Plate 6 (1) Coenagrionoidea undetermined, NHMUK In.17385. Scale bar = 3 mm. (2) *Angloprotoneura eocenica* gen. et sp. nov., holotype, NHMUK In 17246. Scale bar = 5 mm. (3) *Lestes* aff. *regina* Théobald, 1937, NHMUK In.17408a, part. Scale bar = 5 mm. (4) NHMUK In.17408b, counterpart. Scale bar = 5 mm. (5) NHMUK In.24639. Scale bar = 5 mm. (6) '*Megalestes*' *anglicus* Cockerell, 1915, holotype, USNM No. 61449. Scale bar = 4 mm.

Disparoneurinae with the Protoneurinae. Later, Bechly (1996) divided the Protoneuridae into Protoneurinae (incl. Caconeurinae and Disparoneurinae), and Isostictinae, but he proposed no precise wing venational synapomorphy to support the Protoneurinae, and only one for the Isostictinae, i.e. arculus secondarily shifted distal of Ax2, but indicating it may be a synapomorphy with certain Protoneurinae. Pessacq (2008) concluded after a new phylogenetic analysis that the Protoneuridae as a whole is probably polyphyletic. Therefore, we have to compare *Angloprotoneura* gen. nov. to all the genera. The list of protoneurid genera up to 1993 is given in Bridges (1993).

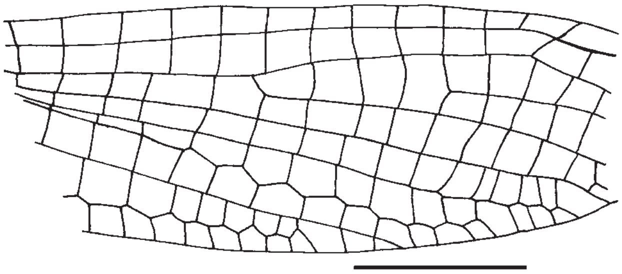
Angloprotoneura differs from *Chlorocnemis* Selys, 1863 and *Proneura* Selys, 1889 in its lacking CuA vein (Münz 1919, figs 130–131). It differs from *Elattoneura* Cowley, 1935, *Junix* Racenis, 1968, *Proneura* Selys, 1889, *Disparoneura* Selys, 1860, *Peristicta* Hagen, 1860, *Neoneura* Selys, 1860, *Caconeura* Kirby, 1890, *Esme* Fraser, 1922, *Phylloneura* Fraser, 1922, *Arabineura* Schneider & Dumont, 1995, *Lamproneura* De Marmels, 2003 and *Idioneura* Selys, 1860 in lacking its AA vein (Münz 1919; Fraser 1933; Cowley 1935; Schneider & Dumont 1995; De Marmels 2003).

Peristicta, *Caconeura*, *Phylloneura* and *Esme* also differ from *Angloprotoneura* gen. nov. in their great number of postnodal cross-veins (more than 12, instead of seven). *Ellatoneura* has more than nine postnodals (Cowley 1936). *Junix* and *Neoneura* have a very short MP, not surpassing the level of the nodus (Racenis 1968). *Lamproneura* has also a very short MP, unlike *Angloprotoneura*.

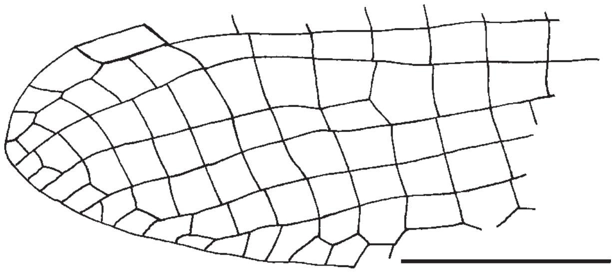
Among the taxa with AA completely lacking, *Angloprotoneura* gen. nov. differs from *Roppaneura* Santos, 1966 in its pterostigma of 'normal' size and shape, covering one cell and longer than broad; in its longer MP, reaching the posterior wing margin 3–4 cells distal of the level of the nodus, instead of 2–3 cells; and in its base of RP2 three cells distal of the subnodus, instead of two (see Santos 1966, figs 1, 3–5). *Angloprotoneura* gen. nov. differs from *Idioneura* Selys, 1860, *Epipleoneura* Williamson, 1915, *Epipotoneura* Williamson, 1915, *Nososticta* Selys, 1860, *Prodasineura* Cowley, 1934, *Psaironeura* Williamson, 1915, *Protoneura* Selys, 1857, *Phasmoneura* Williamson, 1916, *Forcepsioneura* Lencioni, 1999 and *Drepanoneura* Ellenrieder & Garrison, 2008 in its distinctly longer MP, reaching the posterior wing margin 3–4 cells distal of the level of the nodus, instead of none, one, two, or three (Münz



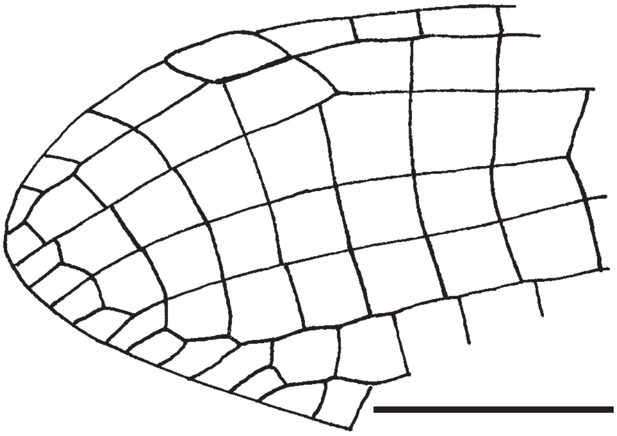
Text-figure 36 Coenagrionoidea undetermined, NHMUK In.24640. Scale bar = 2 mm.



Text-figure 37 Coenagrionoidea undetermined, NHMUK In.24755. Scale bar = 3 mm.



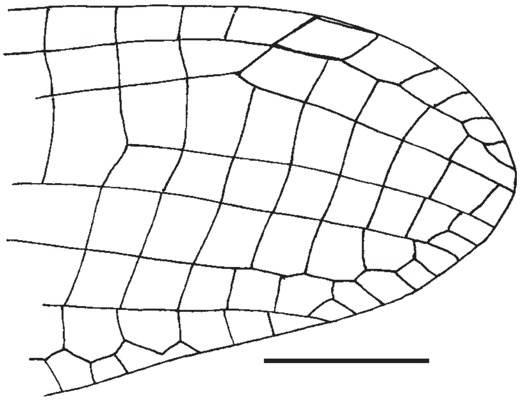
Text-figure 38 Coenagrionoidea undetermined, NHMUK In.24642. Scale bar = 3 mm.



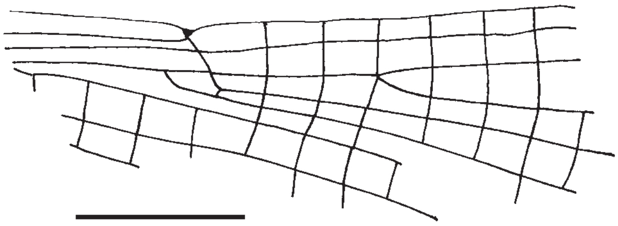
Text-figure 39 Coenagrionoidea undetermined, NHMUK In.17372. Scale bar = 2 mm.

1919; Cowley 1936; Lencioni 1999; Machado 2004; Ellenrieder & Garrison 2008). *Angloprotoneura* gen. nov. differs from *Microneura* Hagen, 1886, *Melanoneura* Fraser, 1922 and *Amazoneura* Machado, 2004 in its smaller number of postnodal cross-veins (around 20 in the latters) (Fraser 1933; Cowley 1935).

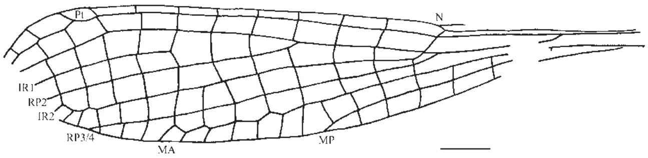
The genus *Eoprotoneura*, originally attributed to the Protoneuridae: Eoprotoneurinae Carle & Wighton, 1990, and latter transferred to the Isostictinae: Eoprotoneurini, differs from *Angloprotoneura* in its very short MP, just reaching the nodus level, base of IR2 well distal of the subnodus, and in its pterostigma covering one cell and a half (Carle & Wighton 1990; Bechly 1996).



Text-figure 40 Coenagrionoidea undetermined, NHMUK In.24528. Scale bar = 2 mm.



Text-figure 41 Coenagrionoidea undetermined, MIWG 3602. Scale bar = 3 mm.



Text-figure 42 *Angloprotoneura eocenica* gen. et sp. nov., holotype, NHMUK In.17246. Scale bar = 1 mm.

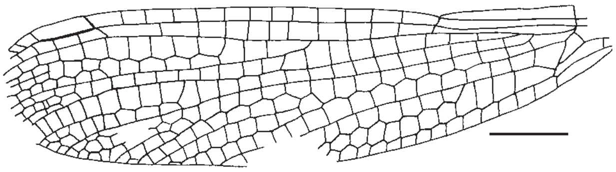
The fossil record of the small damselfly family Protoneuridae is so far reduced to the sole genus *Eoprotoneura* Carle & Wighton, 1990 from the Early Cretaceous of Brazil. Piton (1940) described a very poorly preserved and enigmatic fossil from the Paleocene of Menat (France), which he attributed to the Ephemeroptera family Protoneuridae (*sic*), under the name *Archaeophlebia enigmatica*. Nel & Roy (1996) revised this taxon and concluded that it is not an Odonata or an Ephemeroptera, but a Mantodea of uncertain family, probably a Chaeteessidae.

Clade Lestomorpha Bechly, 1996
Family Lestidae Calvert, 1901
Genus *Lestes* Leach, 1815
Lestes aff. *regina* Théobald, 1937
(Plate 6, figs 3–5; Text-figs 43–44)

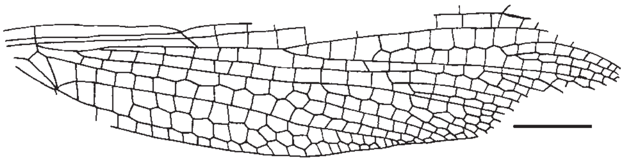
Previously described material. Specimen BMB 018808/-9, Insect Limestone, northwest Isle of Wight.

New material. NHMUK In.17408 (Smith coll., Plate 6, figs 3–4, Text-fig. 43); NHMUK In.24639 (Hooley coll., Plate. 6, fig. 5, Text-fig. 44).

Discussion. Nel & Jarzembowski (1999, pp 193–195, fig. 1a–b) described and figured the specimen BMB 018808/-9.



Text-figure 43 *Lestes* aff. *regina* Théobald, 1937, NHMUK In.17408. Scale bar = 3 mm.



Text-figure 44 *Lestes* aff. *regina* Théobald, 1937, NHMUK In.24639. Scale bar = 3 mm.

They considered that this species is very close, if not identical, to *Lestes regina* from the Late Eocene of Gard (France). The new specimens can be attributed to the same species as BMB 018808/-9 on the basis of the same wing venation, especially the presence of three rows of cells in the cubito-anal area (first group of Nel & Paicheler 1994b). NHMUK In.17408 and NHMUK In.24639 are slightly larger wings (respective widths 5·7 mm and 5·3 mm, instead of 4·9 mm for BMB 018808/-9).

Note. The type specimen of '*Megalestes*' *anglicus* Cockerell, 1915 (USNM No. 61449) is the middle part of a wing (see Plate 6, fig. 6) that could correspond to the same species as *Anglohypolestes fasciata*, to *Eohypolestes hooleyi*, or to another taxon belonging to a different family (Cockerell 1915, pp 498–499, pl. 61, fig. 9; Nel & Paicheler 1994b, pp 3–4, fig. 2; Nel & Jarzembowski 1999, p. 195). It is a Zygoptera Lestiformia, or a Coenagrionomorpha of uncertain affinities.

2. Palaeoclimatic implications

With nearly 20 different species distributed in 11 different families, the Isle of Wight fauna is one of the most diverse of the European Palaeogene, comparable to that of Aix-en-Provence. The family profile of the Isle of Wight differs strongly from those of the Oligocene of France, in the presence of Corduliphyidae, Urothemistidae, Bolcathoridae and Protoneuridae; but also in the absence of the Libellulidae. This last family dominates the diversity of nearly all the Middle to Late Oligocene outcrops of France and Germany. The Libellulidae are recorded from the Late Cretaceous and the Early Eocene. It is possible that they began to diversify only after the Eocene but, unfortunately, the present knowledge on the odonatan fauna of the Palaeocene–Eocene remains very incomplete.

The 'Gynacanthinae' species A is of great interest because all its closest living relatives live under warm to hot climates in Indo-Malaysia, South America and Australasia. *Neophya rutherfordi* is an Afrotropical taxon, living in forests along rivers and small streams in the warm to hot intertropical zone. This discovery of a *Neophya* is the second case of the presence of an Afrotropical insect genus in the Western European Palaeogene. The first one was the presence of the calopterygid genus group *Sapho* + *Umma* in the Late Oligocene of Aix-en-Provence and Armissan (Nel 1987; Nel & Paicheler 1992; Nel & Petrulevičius 2010). The presence of these Afrotropical insects in the Palaeogene of Western Europe could correspond to multiple contacts between these areas during the Cretaceous–Palaeogene (Gheerbrant & Rage 2006). The presence of *Palaeophya* Petrulevičius & Nel, 2009 in the Palaeogene of Argentina rather supports a great antiquity for the Cordulephyidae. The presence of *Palaeophya* in Argentina and of a *Neophya* species in the UK suggests relict taxa of a widely distributed family during the Late Cretaceous–Palaeogene.

The 'Protoneuridae' is a circumtropical family, known from the Neotropical, Afrotropical (also a genus from Arabia), Australo-Papuan and Indo-Malaysian regions. As the exact affinities of *Angloprotoneura* cannot be accurately established, its main interest is to demonstrate the presence of this 'group' of intertropical Zygoptera in Europe during the Palaeogene. The Recent representatives live in a warm climate, but not always very humid, and their larvae inhabit small streams and rivers, suggesting a warm palaeoclimate for the Isle of Wight Eocene palaeobiota.

3. Acknowledgements

We sincerely thank the staff of the Dinosaur Isle Museum for their kind help. We also acknowledge the INTAS Project 03-51-4367 'The terrestrial fauna and flora of the Insect Bed, Isle of Wight: interpreting the climate near the Eocene/Oligocene boundary'; Phil Crabb for the photographs of the material from the NHM; Scott Moore-Fay (NHM) for the preparation of specimen X.50140.143; and Bill Crighton (NMS volunteer) for checking the English.

4. References

Azar, D. & Nel, A. 2008. First Baltic amber megapodagrionid damselfly (Odonata: Zygoptera). *Annales de la Société Entomologique de France*, (N.S.) **44**, 451–57.

Bechly, G. 1996. Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata), unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der Odonata. *Petalura* Special Volume **2**. 402 pp.

Bechly, G., Nel, A., Martínez-Delclòs, X., Jarzembowski, E. A., Coram, R., Martill, D., Fleck, G., Escuillié, F., Wisshak, M. M. & Maisch, M. 2001. A revision and phylogenetic study of Mesozoic Aeshnoptera, with description of several new families, genera and species (Insecta: Odonata: Anisoptera). *Neue Paläontologische Abhandlungen* **4**. 219 pp.

Bechly, G. & Wichard, W. 2009. Damselfly and dragonfly nymphs in Eocene Baltic amber (Insecta: Odonata), with aspects of their palaeobiology. *Palaeodiversity* **1**, 37–74.

Brauer, F. 1865. Vierter Bericht über die auf der Weltfahrt der kais. Fregatte Novara gesammelten Neuropteren. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien*, (*Gesellschaft*) **15**, 903–08.

Brauer, F. 1868. Verzeichnissder bis jetzt Bekannten Neuropteren in Sinne Linne's. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien*, (*Gesellschaft*) **18**, 711–42.

Bridges, C. A. 1993. *Catalogue of the family-group, genus-group and species-group names of the Odonata of the World*. Second edition. Urbana, Illinois: C. A. Bridges. 950 pp.

Calvert, P. P. 1901. *Odonata, Biologia Centrali Americana: Insecta Neuroptera*. London: R. H. Porter and Dulau & Co. v–xxx + 17–342.

Calvert, P. P. 1913. The fossil odonate *Phenacolestes*, with a discussion of the venation of the legion Podagrion Selys. *Proceedings of the Academy of Natural Science of Philadelphia* **65**, 225–72.

Carle, F. L. & Wighton, D. C. 1990. Chapter 3. Odonata. *In* Grimaldi, D. A. (ed.) *Insects from the Santana Formation, Lower Cretaceous, of Brazil. Bulletin of the American Museum of Natural History* **195**, 51–68. 191 pp.

Charpentier, T. de. 1825. *Horae Entomologicae (Neuroptera, Orthoptera, Coleoptera)*. Wratislawiae: Gosohorsky. xvi + 255 pp.

Charpentier, T. de 1840. *Libellulinae europaeae descriptae ac depictae*. Lipsiae: L. Voss. 1–180.

Cockerell, T. D. A. 1907. Fossil dragonflies from Florissant. *Bulletin of the American Museum of Natural History* **23**, 133–39.

Cockerell, T. D. A. 1908. Fossil insects from Florissant, Colorado. *Bulletin of the American Museum of Natural History* **24**, 59–69.

Cockerell, T. D. A. 1913. Two fossil insects from Florissant with a discussion of the venation of the aeschnine dragon-flies. *Proceedings of the United States National Museum* **45**, 577–83.

Cockerell, T. D. A. 1915. British fossil insects. *Proceedings of the United States National Museum* **49**, 469–99.

Cockerell, T. D. A. 1920. Eocene insects from the Rocky Mountains. *Proceedings of the United States National Museum* **57**, 233–60.

Cockerell, T. D. A. 1927. A new fossil dragonfly from the Eocene of Colorado. *The Entomologist* **60**, 81–82.

Cockerell, T. D. A. 1940. A dragon-fly from the Eocene of Colorado (Odonata, Agrionidae). *Entomological News* **51**, 103–05.

Cockerell, T. D. A. & Andrews, H. 1916. Dragon-flies from the English Oligocene. *Proceedings of the Biological Society of Washington* **29**, 89–92.

Cowley, J. 1934. Changes in the generic names of the Odonata. *The Entomologist* **67**, 200–05.

Cowley, J. 1935. A new generic name in the Protoneuridae (Odonata). *Entomologists' Monthly Magazine* **71**, 14–15.

Cowley, J. 1936. The *Disparoneura* complex: generic characters and lists of species (Odonata). *Annals and Magazine of Natural History* **17**(10), 509–26.

Davies, A. L. 1981. A synopsis of the extant genera of the Odonata. *Societas Internationalis Odonatologica, Rapid Communications* **3,** 1–59.

De Marmels, J. 2002. Phylogenetic relationships of *Priscagrion* Zhou & Wilson, 2001, with a description of *Teinopodagrion croizati* spec. nov. from Ecuador (Zygoptera: Megapodagrionidae). *Odonatologica* **31**, 389–94.

De Marmels, J. 2003. *Lamproneura lucerna* gen. nov., sp. nov. from Venezuela, and *Cyanallagma ferenigrum* sp. nov., a remarkable new species from Brazil (Odonata: Protoneuridae, Coenagrionidae). *International Journal of Odonatology* **6**, 99–107.

Ellenrieder, N. von. 2002. A phylogenetic analysis of the extant Aeshnidae (Odonata: Anisoptera). *Systematic Entomology* **27**, 437–67.

Ellenrieder, N. von & Garrison, R. W. 2008. *Drepanoneura* gen. nov. for *Epipleoneura letitia* and *Protoneura peruviensis*, with descriptions of eight new Protoneuridae from South America (Odonata: Protoneuridae). *Zootaxa* **1842**, 1–34.

Fabricius, J. C. 1793. 1792–1799. *Entomologia Systematica Emedau et Aucu. Secundum classes, ordines, genera, species, adjectis synonymis, lods, observationibus, descriptionibus*. Copenhagen: C. G. Proft.

Fleck, G., Nel, A. & Martínez-Delclòs, X. 1999. The oldest record of the Libellulidae from the Upper Cretaceous of Kazakhstan (Odonata, Anisoptera). *Cretaceous Research* **20**, 655–58.

Förster, F. 1908. Neue Aeschniden. *Annales de la Société Entomologique de Belgique* **52**, 213–18.

Fraser, F. C. 1922. New and rare Indian Odonata in the Pusa collection. *Memoirs of the Department of Agriculture of India, Entomological Series* **7**, 39–77.

Fraser, F. C. 1933. Odonata. *In* Stephenson, J. (ed.). *The fauna of British India, including Ceylon and Burma* 1, i–xiii + 1–423. London: Taylor and Francis.

Fraser, F. C. 1955. A new isostictine dragonfly from Australia with some remarks on the subfamily Isostictinae nov. (Odon., Protoneuridae). *Entomologists' Monthly Magazine* **91**, 7–230.

Fraser, F. C. 1957. A reclassification of the order Odonata, based on some new interpretations of the venation of the dragonfly wing. *Handbook of the Royal Zoological Society of New South Wales* **12**, 1–133.

Fraser, F. C. 1960. A handbook of the dragonflies of Australia with keys for the identification of all species. *Royal Zoological Society of New South Wales*, 1–67.

Gale, A. S., Huggett, J. M., Pälike, H., Laurie, E., Hailwood, E. A. & Hardenbol, J. 2006. Correlation of Eocene–Oligocene marine and continental records: orbital cyclicity, magnetostratigraphy and sequence stratigraphy of the Solent Group, Isle of Wight, UK. *Journal of the Geological Society, London* **163**, 401–15.

Gentilini, G. 2002. Fossil damselflies and dragonflies from the Eocene of Monte Bolca, Italy (Insecta: Odonata). *Studi e Ricerche sui Giacimenti Terziari di Bolca, Museo Civico di Storia Naturale di Verona* **9**, 7–22.

Gheerbrant, E. & Rage, J-C. 2006. Paleobiogeography of Africa: how distinct from Gondwana and Laurasia? *Palaeogeography, Palaeoclimatology, Palaeoecology* **241**, 224–46.

González-Soriano, E. and Novelo Gutierrez, R. 1998: *Oplonaeschna magna* sp. nov. (Odonata: Aeshnidae), from Mexico with a description of its larva. *Revista de Biologia Tropical* **46**, 705–15.

Groeneveld, L. F., Clausnitzer, V. & Hadrys, H. 2007. Convergent evolution of gigantism in damselfies of Africa and South America? Evidence from nuclear and mitochondrial sequence data. *Molecular Phylogenetics and Evolution* **42**, 339–46.

Gundlach, J. C. 1888. *Contribution a la entomologia Cubana*. Neuropteros **2**, 189–281. Habana: Alvarez & Co.

Hagen, H. A. 1860. Dernière légion. *In* Selys-Longchamps, E. de. (ed.) *Synopsis des Agrionines. Bulletin del'Académie Royale de Belgique* **10**(2), 431–62.

Hagen, H. A. 1861. Synopsis of the Neuroptera of North America, with a list of the South American species, prepared for the Smithsonian Institution, Washington. *Smithsonian Miscellaneous Collections* **1**, 1–347.

Hagen, H. A. 1867. Notizen beim Studium von Brauer's Novara-Neuropteren. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft, Wien* **17**, 31–62.

Hagen, H. A. 1875. Synopsis of the Odonata of America. *Proceedings of the Boston Society of Natural History* **18**, 20–96.

Hagen, H. A. 1886. *In* Selys-Longchamps, E. de. Révision du synopsis des Agrionines. Première partie comprenant les légions Pseudostigma, Podagrion, Platycnemis et Protonevra. *Mémoire de l'Académie Belgique (Classe des Sciences)* **38**(4), i–iv, 1–85.

Heer, O. 1849. Die Insektenfauna der Tertiärgebilde von Œningen und von Radoboj in Croatien. Zweite Abtheilung: Heuschrecken, Florfliegen, Aderflüger, Schmetterlinge und Fliegen. *In* Englemann, W. (ed.) *Neue Denkschriften Allgemeinen Schweizerischen Gesellschaft für die Gesammten Naturwissenschaften, Zurich* **11**. iv + 264 pp.

Hooker, J. J., Collinson, M. E., Grimes, S., Sille, N. & Mattey, D. 2007. Discussion on the Eocene–Oligocene boundary in the UK, *Journal of the Geological Society, London* Vol. 163, 2006, pp 401–415. *Journal of the Geological Society, London* **164**, 685–86.

Hooker, J. J., Grimes, S., Mattey, D., Collinson, M. E. & Sheldon, N. D. 2009. Refined correlation of the UK Late Eocene–Early Oligocene Solent Group and timing of its climate history. *In* Koeberl, C. & Montanari, A. (eds) *The Late Eocene Earth – hothouse, icehouse and impacts. Geological Society of America Special Papers* **452**, 179–95.

Jacobson, G. & Bianchi, V. 1905. [*Die Orthopteren und Pseudoneuropteren des Russischen Reiches und der angrenzenden Gebiete*], 635–846. St. Petersburg: A. F. Dewrien. [In Russian.]

Jarzembowski, E. A. 1976. Report of Easter field meeting: the Lower Tertiaries of the Isle of Wight, 27–31.III.1975. *Tertiary Research* **1**, 11–16.

Jarzembowski, E. A. 1980. Fossil insects from the Bembridge Marls, Paleogene of the Isle of Wight. *Bulletin of the British Museum, Natural History*, (A), *Geology* **33**, 237–93.

Jarzembowski, E. A. & Nel, A. 1996. New fossil dragonflies from the Lower Cretaceous of SE England and the phylogeny of the superfamily Libelluloidea (Insecta: Odonata). *Cretaceous Research* **17**, 67–85.

Karube, H. & Yeh, W.-C. 2001. *Sarasaeschna* gen. nov., with descriptions of female *S. minuta* (Asahina) and male penile structures of *Linaeschna* (Anisoptera: Aeshnidae). *Tombo* **43**, 1–8.

Kennedy, C. H. 1925. New genera of Megapodagrioninae, with notes on the subfamily. *Bulletin of the Museum of Comparative Zoology* **67**, 291–311.

Kirby, W. F. 1889. A revision of the subfamily Libellulinae, with descriptions of new genera and species. *Transactions of the Zoological Society, London* **12**, 249–348.

Kirby, W. F. 1890. *A synonymic catalogue of Neuroptera Odonata, or dragonflies. With an appendix of fossil species*. London: Gumey & Jackson. ix + 202 pp.

Kukalová-Peck, J. 1991. Fossil history and the evolution of hexapod structures. *In* Naumann, I. D. (ed.) The insects of Australia, a textbook for students and research workers **1**, 141–79. Melbourne: Melbourne University Press.

Laidlaw, F. F. 1924. A catalogue of the dragonflies (Odonata) recorded from Ceylon, based on material collected by Mr. E.E. Green, with description of a new species. *Spolia Zeylanica* **12**, 335–74.

Leach, W. E. 1815. Entomology. *In* Brewster, D. (ed.) *The Edinburgh Encyclopaedia* **9**, 57–172.

Lencioni, E. A. A. 1999. The genus *Phasmoneura*, with description of *Forcepsioneura* gen. nov. and two new species (Zygoptera: Protoneuridae). *Odonatologica* **28**, 127–37.

Lieftinck, M. A. 1937. The dragonflies (Odonata) of New Guinea and neighbouring islands. *Nova Guinea*, (N.S.) **1**, 1–82.

Lieftinck, M. A. 1954. Handlist of Malaysian Odonata. A catalogue of the dragonflies of the Malay Peninsula, Sumatra, Java and Borneo, including the adjacent small islands. *Treubia* **22** (Suppl.). xiii + 202 pp.

Machado, A. B. M. 2004. Studies on Neotropical Protoneuridae. 15. *Amazoneura* gen. nov. with description of *A. juruaensis* sp. nov. (Odonata, Zygoptera). *Revista Brasileira de Zoologia* **21**, 333–36.

Martin, R. 1906. Cordulines. *In*: *Collections zoologiques du Baron Edm. de Selys Longchamps, Catalogue systématique et descriptif* **17**, 1–98. Bruxelles: Haye.

Martin, R. 1908. Aeschnines. *In*: *Collections zoologiques du Baron Edm. de Selys Longchamps, Catalogue systématique et descriptif* **18,** 1–84; **19**, 85–156. Bruxelles: Haye.

Martynov, A. 1927. On two Tertiary fossil dragonflies from the Caucasus. *Russkoe Entomologicheskoe Obozrenie* **21**, 1–5.

Martynov, A. 1929. Fossil insects from Tertiary deposits in Ashutas Saisan district. *Trudy Geologicheskogo Muzeya Akademii nauk SSSR* **5**, 173–216.

May, E. 1933. Zwei neue Genera der Legion *Podagrion* (*Agriomorpha* und *Lestomima*). *Senckenbergiana* **15**, 340–45.

McLachlan, R. 1896. On some Odonata of the subfamily Aeschnina. *Annals and Magazine of Natural History* **17**(6), 409–25.

Münz, P. A. 1919. A venational study of the suborder Zygoptera (Odonata) with keys for the identification of genera. *Memoirs of the Entomological Society* (*of the Academy of Natural Sciences*) **3**, 1–78.

Nel, A. 1987. Un nouveau Calopterygidae fossile des laminites oligocène d'Armissan (Aude, France) (Odonata). *Revue Française d'Entomologie*, (N.S.) **9**, 147–48.

Nel, A., Martínez-Delclòs, X., Paicheler, J.-C. & Henrotay, M., 1993. Les 'Anisozygoptera' fossiles. Phylogénie et classification (Odonata). *Martinia*, Numéro Hors Série **3**, 1–311.

Nel, A., Martinez-Delclòs, X., Escuillié, F. & Brisac, P. 1994. Les Aeshnidae fossiles: Etat actuel des connaissances (Odonata, Anisoptera). *Neues Jahrbuch für Geologie und Paläontologie*, *Abhandlungen* **194**, 143–86.

Nel, A., Martinez-Delclòs, X., Papier, F. & Oudard, J. 1997. New Tertiary fossil Odonata from France. (Sieblosiidae, Lestidae, Coenagrioniidae, Megapodagrionidae, Libellulidae). *Deutsche Entomologische Zeitschrift* **44**, 231–58.

Nel, A., Petrulevičius, J. F. & Jarzembowski, E. A. 2005. New fossil Odonata from the European Cenozoic (Insecta: Odonata: Thaumatoneuridae, Aeshnidae, ?Idionychidae, Libellulidae). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **235**, 343–80.

Nel, A. & Arillo, A. 2006. The first Baltic amber dysagrionine damselfly (Odonata: Zygoptera: Thaumatoneuridae: Dysagrioninae). *Annales de la Société Entomologique de France* **42**, 179–82.

Nel, A. & Jarzembowski, E. A. 1999. Fossil damselflies and dragonflies (Insecta: Odonata) from the Late Upper Eocene of southern England. *Proceedings of the Geologists' Association* **110**, 193–201.

Nel, A., Arillo, A. & Martínez-Delclòs, X. 1996. New fossil Odonata (Insecta) from the Upper Miocene of France and Spain. (Anisoptera and Zygoptera). *Neues Jahrbuch für Geologie und Paläontologie*, *Abhandlungen* **199**, 167–219.

Nel, A. & Paicheler, J.-C. 1992. Les Odonata fossiles: état actuel des connaissances. Huitième partie: Les Calopterygoidea fossiles [Odonata, Zygoptera]. *Bulletin de la Société Entomologique de France* **97**, 381–96.

Nel, A. & Paicheler, J.-C. 1993a. Les Odonata fossiles: état actuel des connaissances. Septième partie: les Coenagrionoidea fossiles (Odonata, Zygoptera). *Entomologica Gallica* **4**, 59–63.

Nel, A. & Paicheler, J.-C. 1993b. Les Libellulidae fossiles. Un inventaire critique (Odon., Anisoptera, Libelluloidea). *Entomologica Gallica* **4**, 166–90.

Nel, A. & Paicheler, J.-C. 1994a. Les Libelluloidea fossiles autres que Libellulidae. Un inventaire critique (Odonata, Corduliidae, Macromiidae, Synthemistidae, Chlorogomphidae et Mesophlebiidae). *Nouvelle Revue d'Entomologie* (N.S.) **11**, 321–34.

Nel, A. & Paicheler, J.-C. 1994b. Les Lestoidea (Odonata, Zygoptera) fossiles: un inventaire critique. *Annales de Paléontologie* **80**, 1–59.

Nel, A. & Papazian, M. 1983. Description d'une nouvelle espèce d'Odonate fossile du Stampien d'Aix-en-Provence. *L'Entomologiste* **39**, 119–22.

Nel, A. & Petrulevičius, J. F. 2010. Afrotropical and Nearctic genera of Odonata in the French Oligocene: biogeographic and paleoclimatic implications (Insecta: Calopterygidae and Aeshnidae). *Annales de la Société Entomologique de France* (N.S.) **46**, 228–36.

Nel, A. & Roy, R. 1996. Revision of the fossil "mantid" and "ephemerid" species described by Piton from the Palaeocene of Menat (France) (Mantodea: Chaeteessidae, Mantidae; Ensifera: Tettigonioidea). *European Journal of Entomology* **93**, 223–34.

Peñalver, E., Nel, A. & Martínez-Delclòs, X. 1996. Insectos del Mioceno inferior de Ribesalbes (Castellón, España): Paleoptera y Neoptera Poli- y Paraneoptera. *Treballs Pedagògics del Museu de Geologia de Barcelona* **5**, 15–95.

Pessacq, P. 2008. Phylogeny of Neotropical Protoneuridae (Odonata: Zygoptera) and a preliminary study of their relationship with related families. *Systematic Entomology* **33**, 511–28.

Petrulevičius, J. F., Wappler, T., Wedmann, S., Rust, J. & Nel, A. 2008. New megapodagrionid damselflies (Odonata: Zygoptera) from the Paleogene of Europe. *Journal of Paleontology* **82**, 1173–81.

Petrulevičius, J. F. & Nel, A. 2009. First Cordulephyidae dragonfly in America: a new genus and species from the Paleogene of Argentina. *CR Palevol* **8**, 385–88.

Piton, L. 1940. Paléontologie du gisement éocène de Menat (Puy-de-Dôme), flore et faune. *Mémoire de la Société d'Histoire Naturelle d'Auvergne* **1**, 1–303.

Piton, L. & Théobald, N. 1939. Poissons, crustacés et insectes fossiles de l'Oligocène du Puy-du-Mur, Auvergne. *Mémoires de la Société Scientifique de Nancy*, 1–47.

Prokop, J., Přikryl, T., Dostál, O. & Nel, A. 2007. *Oligaeschna kvaceki* sp. nov., a new fossil dragonfly (Odonata: Aeshnidae) from the Middle Oligocene of northern Moravia (Western Carpathians). *Geologica Carpathica* **58**, 181–84.

Prokop, J. & Nel, A. 2002. New Tertiary dragonflies from Lower Oligocene of the Ceské středohoři Mts and Lower Miocene of the Most Basin in the Czech Republic (Odonata: Anisoptera). *Acta Societatis Zoologicae Bohemicae* **66**, 141–50.

Racenis, J. 1959. Notas taxonomicas sobre la familia Megapodagrionidae (Odonata: Zygoptera) con la sinopsis de las especies venezolanas. *Acta Biologica Venezolana* **2**, 335–67.

Racenis, J. 1968. Dos nuevos generos de los Zigopteros (Insecta: Odonata) de la Amazonia venezolana. *Publicaciones Ocasionales del Museo de Ciencia Naturales*, Caracas, Venezuela (*Zoologia*) **11**, 1–15.

Rambur, J. P. 1842. *Histoire naturelle des insectes. Névroptères. (Suites à Buffon)*. Paris: Roret. xvii + 534 pp.

Riek, E. F. 1976. A new collection of insects from the Upper Triassic of South Africa, *Annals of the Natal Museum* **22**, 791–820.

Riek, E. F. & Kukalová-Peck, J. 1984, A new interpretation of dragonfly wing venation based upon early Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings, *Canadian Journal of Zoology* **62**, 1150–66.

Ris, F. 1897. Notes sur quelques Odonates de l'Asie centrale. *Annales de la Société Entomologique de Belgique* **41**, 42–50.

Ris, F. 1909–1913. Libellulinen monographisch bearbeitet. *In*: *Collection Zoologique du Baron Edm. de Selys Longchamps. Catalogue systématique et descriptif*, **9–16 bis**, 1–1278.

Ris, F. 1916. Zwei Notizen über Calopterygiden (Odonata) vom Malaiischen Archipel. *Entomologische Mitteilungen* **5**, 303–18.

Ris, F. 1917. Eine neue Agrioniden-Gattung der "Légion *Podagrion*" (Odonata) aus China. *Tijdschrift voor Entomologie* **60**, 185–91.

Santos, Dos N. D. 1966. Contribuição ao conhecimento da região de poços de caldas, MG, Brasil. *Roppaneura beckery* gen. nov., sp. nov. (Odonata, Protoneuridae). *Boletim do Museu Nacional*, *Rio deJaneiro* (N.S.) **256**, 1–4.

Schneider, W. & Dumont, H. J. 1994 [1995]. *Arabineura* n. gen., a new protoneurid genus from Arabia, with the description of the hitherto unknown female of *Arabineura khalidi* (Schneider, 1988) comb. nov. (Insecta: Odonata: Protoneuridae). *Biologisch Jaarboek* **62**, 114–20.

Scudder, S. H. 1878. An account of some insects of unusual interest from the Tertiary rocks of Colorado and Wyoming. *Bulletin of the United States Geological and Geographical Survey of the Territories* **4**, 519–43.

Scudder, S. H. 1890. The fossil insects of North America (with notes on some European species). 2. The Tertiary insects. *Report of the United States Geological Survey of the Territories* **13**, 1–734.

Selys-Longchamps, E. de. 1854. Synopsis des Gomphines. *Bulletin de l'Académie Royales des sciences et belles-lettres de Bruxelles* **21**, 23–114.

Selys-Longchamps, E. de. 1857. Neuroptères de l'isle de Cuba. *In* de la Sagra, R. (ed.) *Histoire physique, politique, et naturelle de l'Ile de Cuba* **8**, 435–73. Paris: A. Bertrand.

Selys-Longchamps, E. de. 1860. Synopsis des Agrionines. Deuxième légion: Protoneura. *Bulletin de l'Académie Royale de Belgique* **10**(2), 431–62.

Selys-Longchamps, E. de. 1862. Synopsis des Agrionines. Troisième légion: Podagrion. *Bulletin de l'Académie Royale de Belgique* **14**(2), 5–44.

Selys-Longchamps, E. de. 1863. Synopsis des Agrionines. Quatrième légion: Pseudostigma. *Bulletin de l'Académie Royale de Belgique* **16**(2), 147–76.

Selys-Longchamps, E. de. 1871. Aperçu statistique sur les Névroptères Odonates. *Transactions of the Entomological Society of London* **19**, 409–16.

Selys-Longchamps, E. de. 1878. Odonates de la région de la Nouvelle-Guinée. 1. Considérations sur la faune de la Nouvelle Guinée, des Moluques et de la Célèbes. *Mitteilungen aus dem Königlich Zoologischen Museum zu Dresden* **3**, 289–322.

Selys-Longchamps, E. de. 1881. *Neophya* Selys, nouveau genre de Cordulines. *Comptes Rendus de la Société Entomologique de Belgique* **25**, xv–xviii.

Selys-Longchamps, E. de. 1883. Synopsis des Aeschnines. Première partie: classification. *Bulletin de l'Académie Royale de Belgique* **5**(3), 712–48.

Selys-Longchamps, E. de. 1885. Programme d'une révision des Agrionines. *Comptes Rendus de la Société Entomologique de Belgique* **29**, cxli–cxlvi.

Selys-Longchamps, E. de. 1889. Odonates de Sumatra comprenant les espèces recueillies à Pulo Nias par M. le Dr. E. Modigliani. *Annali del Museo Civico di Storia Naturale di Genova* **27**, 444–84.

Selys-Longchamps, E. de & Hagen, H. A. 1854. Monographie des Caloptérygines. *Mémoires de la Société des Sciences de Liège* **9**. i–xi + 291 pp.

Theobald, N. 1937. Les insectes fossiles des terrains oligocènes de France. *Bulletin Mensuel (Mémoires) de la Société des Sciences de Nancy* **1**, 1–473.

Tillyard, R. J. 1913. On some new and rare Australian Agrionidae (Odonata). *Proceedings of the Linnean Society of New South Wales* **37**, 404–79.

Tillyard, R. J. 1916. Life history and descriptions of Australian Aeschnidae, with a description of a new form of *Telephebia* by Herbert Campion. *Linnean Journal of the Zoological Society*, *London* **33**, 1–83.

Tillyard, R. J. 1917. On some new dragonflies from Australia and Tasmania. *Proceedings of the Linnean Society of New South Wales* **42**, 450–79.

Tillyard, R. J. & Fraser, F. C. 1937–1940. A reclassification of the order Odonata based on some new interpretations of the venation of the dragonfly wing. *The Australian Zoologist* **9**, 124–396.

Timon-David, J. 1946. Insectes fossiles de l'Oligocène inférieur des Camoins. 3. Description d'une nouvelle espèce d'Odonate. *Bulletin de la Société Entomologique de France* **51**, 94–96.

Watson, J. A. L. 1992. The subfamilies of Protoneuridae (Zygoptera). *Odonatologica* **21**, 195–201.

Wedmann, S. 2000. Die Insekten der oberoligozänen Fossillagerstätte Enspel (Westerwald, Deutschland). Systematik, Biostratinomie und Paläoökologie. *Mainzer Naturwissenschaftliches Archiv* **23**, 1–154.

Wighton, D. C. & Wilson, M. V. H. 1986. The Gomphaeschninae (Odonata: Aeshnidae): new fossil genus, reconstructed phylogeny, and geographical history. *Systematic Entomology* **11**, 505–22.

Williamson, E. B. 1915. Notes on Neotropical dragonflies, or Odonata. *Proceedings of the United States National Museum* **48**, 601–38.

Williamson, E. B. 1916. A new dragonfly genus of the legion *Protoneura*. *Entomological News* **27**, 30–33.

Zhang, J.-F. 1992. *Congqingia rhora* gen. nov., spec. nov. – a new dragonfly from the Upper Jurassic of Eastern China (Anisozygoptera, Congquingiidae fam. nov.). *Odonatologica* **21**, 375–83.

Zhou, W.-B. & Wilson, K. D. P. 2001. *Priscagrion kiautai* gen. nov., spec. nov. and *P. pinheyi* spec. nov., new damselflies from Southwestern China (Zygoptera: Megapodagrionidae). *Odonatologica* **30**, 117–21.

MS received 4 October 2012. Accepted for publication 31 January 2014.