



**The Mesozoic non-calopterygoid Zygoptera:
description of new genera and species from the
Lower Cretaceous of England and Brazil and
their phylogenetic significance (Odonata,
Zygoptera, Coenagrionoidea, Hemiphlebioidea,
Lestoidea)**

*E. A. Jarzembowski, †X. Martínez-Delclòs, ‡G. Bechly,
§A. Nel, ||R. Coram and ¶F. Escuillié

*Maidstone Museum & Art Gallery, St Faith's St, Maidstone, Kent, ME14 1LH and Postgraduate
Research Institute for Sedimentology, University of Reading, UK

†Departament Geologia Dinàmica, Geofísica i Paleontologia, Facultat de Geologia, Universitat de
Barcelona, Zona Universitària Pedralbes, E-08071, Spain

‡Institut und Museum für Geologie und Paläontologie, Eberhard-Karls-Universität, Sigwartstr. 10,
D-72076, Tübingen, Germany

§Laboratoire d'Entomologie, Muséum national d'Histoire naturelle, 45 Rue de Buffon, F-75005, Paris,
France

|| 6 Battlemead, Swanage, Dorset, BH19 1PH, UK

¶Rhinopolis, 58 Rue des Jonchères, F-03800, Gannat, France

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The earliest fossils which belong to the Coenagrionoidea (or Hemiphlebioidea), *Parahemiphlebia cretacea* gen. nov., sp. nov., and *P. allendaviesi* sp. nov., from the Lower Cretaceous of Brazil and southern England respectively, have non-petiolated wings. Consequently, a long wing petiolation may result from evolutionary convergence between different superfamilies of Zygoptera: Calopterygoidea, Lestoidea, Coenagrionoidea and (to a lesser degree) Hemiphlebioidea.

The phylogenetic relationships of the Lower Cretaceous subfamily Euarchistigmatinae Carle & Wighton 1990, based on *Euarchistigma atrophium* Carle & Wighton 1990 from Brazil (Araripe Basin), and the Triassic family Italophlebiidae Whalley 1986 (Italy) are discussed. The relationships of the extant family Hemiphlebiidae are also considered, as are those of the fossil genus *Eoprotoneura* Carle & Wighton 1990 (Lower Cretaceous of Brazil) which belongs to the Protoneuridae + Isostictidae. The low phylogenetic value of characters used in the current diagnosis of the Protoneuridae, Isostictidae and Platystictidae is demonstrated and a 'new' interpretation of the wing venation of the Platystictidae is proposed. The phylogenetic position of the Lower Cretaceous genus *Cretacoenagrion* Jarzembowski 1990 from the Wealden of the Weald is discussed and several new genera and species of Wealden Zygoptera are described from southern England, viz. *Cretarchistigma greenwoodi* gen. nov., sp. nov. (questionably placed in the subfamily Euarchistigmatinae), *Cretahemiphlebia rossi* gen. nov., sp. nov. (family undetermined) and *Cretalestes martinae* gen. nov., sp. nov. (lestoid?). A key is provided.

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KEY WORDS: fossil insects; Odonata; Triadophlebiomorpha; Zygoptera; Lestoidea, Coenagrionoidea; Hemiphlebioidea; Pseudostigmatidae; Cretacoenagrionidae, Coenagrionidae; Protoneuridae; Isostictidae; Platystictidae; Hemiphlebiidae; Italophlebiidae; Oreopteridae; Triassic; Lower Cretaceous; England; Brazil; Italy; gen. nov.; spp. nov.; phylogeny.

1. Introduction

Whilst Mesozoic dragonflies ('Anisozygoptera' + Anisoptera) are comparatively frequent in Western Europe, East Asia and Brazil, damselflies (Zygoptera) are rare. Four species have been described to date, from the Lower Cretaceous of Brazil and England, and the Lower Jurassic of Germany (Handlirsch, 1908, 1939; Carle & Wighton, 1990; Jarzembowski, 1990; Nel & Paicheler, 1993a, b, 1994a).

Amateur palaeontologists have recently discovered many new insect fossils in the Lower Cretaceous of England, including some undescribed damselfly wings. Fossil Odonata are diverse in the Lower Cretaceous of Brazil with eight anisopteran species, representing four families (Petaluridae, Gomphidae, Corduliidae and Aeschniidae), as well as two Zygoptera (Coenagrionoidea: ?Pseudostigmatidae, Protoneuridae) (Carle & Wighton, 1990; Nel & Escuillié, 1994; Nel & Paicheler, 1994b, 1995; Nel, Bechly, Jarzembowski & Martínez-Delclòs, in prep., Martill & Nel, in prep.). This odonatan palaeofauna is of great phylogenetic interest, because it includes some of the oldest representatives of these families. A new fossil zygopteran genus from Brazil and southern England (see below) may provide important data concerning the phylogeny of the Coenagrionoidea. This superfamily is poorly known in the fossil record, with only three described Mesozoic taxa and a few Cenozoic species (Nel & Paicheler, 1993b).

2. Systematic palaeontology

We follow the wing venational interpretation and terminology of Riek & Kukalová-Peck (1984), with slight modifications by Nel *et al.* (1993), Nel & Paicheler (1993a), and Bechly (1993, 1995). For vein abbreviations, see Figure 8.

Order Odonata Fabricius 1793, 1792–99

Suborder Zygoptera Selys 1853

? Superfamily Coenagrionoidea Kirby 1890

? Family Euarchistigmatidae Carle & Wighton 1990 (*sensu* Bechly, 1995) or

?(Pseudostigmatidae Tillyard 1917 + Coryphagrionidae Pinhey 1962)

? Subfamily Euarchistigmatinae Carle & Wighton 1990

Genus *Cretarchistigma* gen. nov.

Type species. Cretarchistigma greenwoodi sp. nov.

Etymology. The name refers to the Cretaceous age of the fossil and its plesiomorphic pterostigma.

Diagnosis. Small damselfly with a sigmoidal vein RA distal to the pterostigma and the veins RA, RP1, IR1 and RP2 converging towards the wing apex, as in Recent (and alleged fossil) genera of Pseudostigmatidae. There is also a braced, sclerotized pterostigma, few postnodal crossveins and IR2 is not fused with RP3/4.

Cretarchistigma greenwoodi gen. nov., sp. nov.

Figure 1A–1G, Table 1

1996 Zygoptera: family uncertain Jarzembowski & Nel, pl. 2, fig. 4.

Table 1. *Cretarchistigma greenwoodi* gen. nov., sp. nov. Dimensions of the apical portions of wings.

Specimen / dimension	Lpt	Wpt	Dpt-A
018754-5	1.3	0.6	2.0
018743-4	1.1	0.6	2.2
018745-6	?	0.7	2.5
018748-9	?	?	2.5
018777-8	?	?	2.7
018655-6	1.2	0.6	2.8
means	1.2	0.6	2.4

Lpt: length of the pterostigma. Wpt: width of the pterostigma. Dpt-A: distance between the pterostigma and the wing apex.

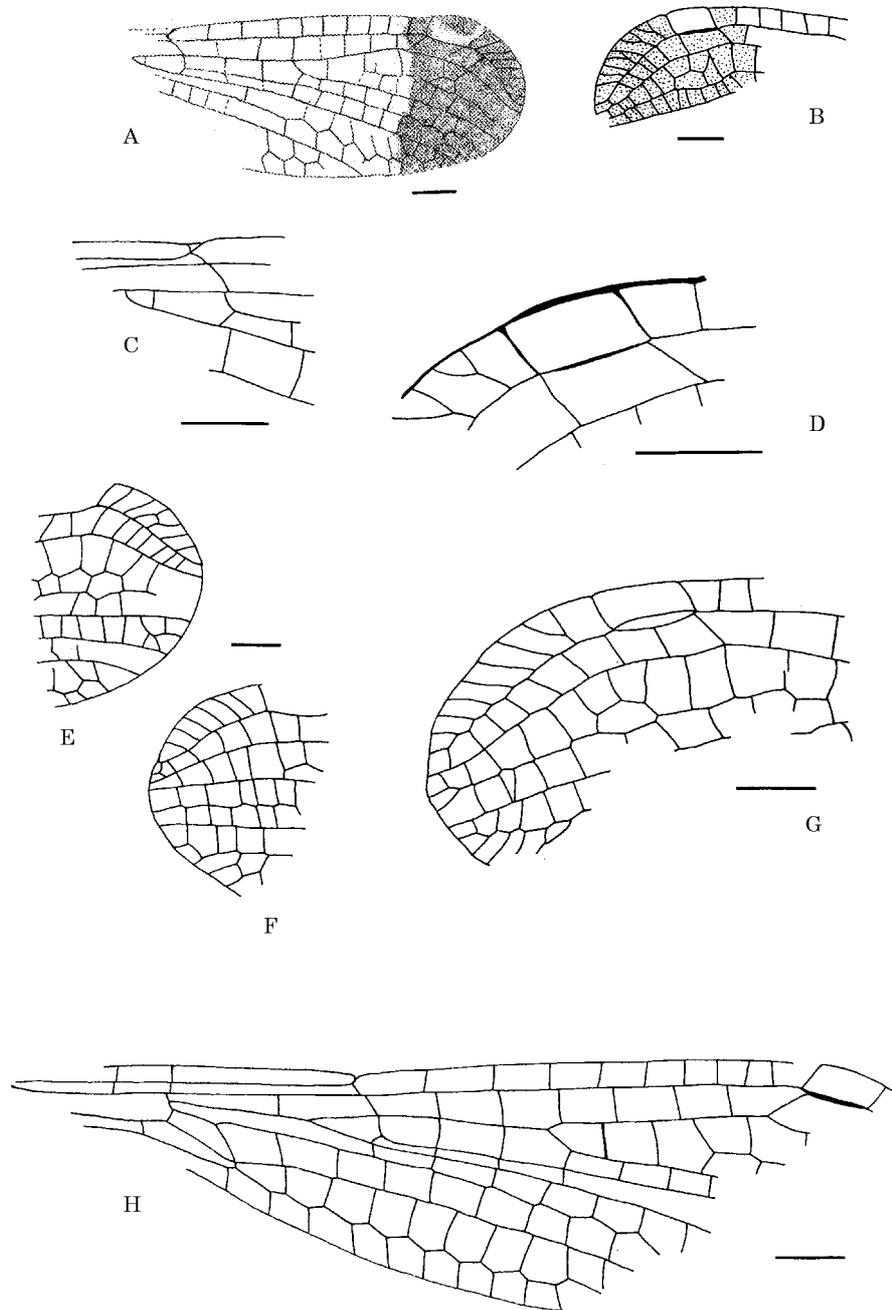


Figure 1. A–G, *Cretarchistigma greenwoodi*, venation. A, holotype 018754, -5. B, 018743, -4. C, 018754, -5 nodal region. D, 018743, -4, pterostigmal region. E, 018748, -9. F, 018745, -6. G, 018777, -8. (Scale bar = 1 mm). H, *Cretarchistigma greenwoodi*?, specimen no. 018658, venation. (Scale bar = 1 mm).

Etymology. After the fossil collector and geological reporter Mr J. Greenwood.

Diagnosis. As for genus.

Material. Holotype: 018754-5 (A. Ross). Paratypes: 018743-4 (C. Martin); 018745-6 (G. Bleach); 018748-9 (A. Ross); 018777-8 (R. Brunning); 018655-6

(A. Ross); 018780-1; 018797-8; Other (missing): B45 RGL; Booth Museum of Natural History, Brighton, UK. MNEMG 1996.229a/b; 1996.298a/b and 1997.183 (Jarzembowski coll.); Maidstone Museum & Art Gallery, UK.

Horizon and locality. Lower Cretaceous, Weald Clay, Surrey, UK. Hauterivian / Barremian (Allen & Wimbledon, 1991). All the specimens are from the Clockhouse (Butterley) Brickworks old pit except 018655-6, which is from the Auclay Brickworks pit, B45 RGL from Beare Green Brickworks and 1996.229 from Smokejacks Brickworks.

Description. All the fossils are parts and counterparts of the apical portions of wings. The holotype is the most complete specimen, with half of the wing preserved. Some specimens, including the holotype, have a dark spot covering the entire apical portion of the wing; other wings are apparently hyaline. All the wings are similar in shape and possess a relatively dense venation. The only major differences on the preserved portions are:

- (1) The pterostigma covers only one cell in 018754-5 and 018743-4, but in 018745-6, 018748-9 and 018777-8 it covers two cells;
- (2) There is a more or less well-developed vein IR1 in 018743-4, 018745-6 and 018655-6 but in the specimens 018754-5, 018748-9 and 018777-8, IR1 is a weak zigzagged vein.

These variations could be compatible with intraspecific variation, or with fore- and hindwing differences but there is no definite evidence for or against this. Thus, the present attribution of other specimens to this species is provisional. The description is based mainly on the holotype characters.

The holotype wing is 3.6 mm wide and the distance between the nodus and the pterostigma is 6.1 mm. The pterostigma is in a very distal position, six times nearer to the wing apex than to the nodus. The distance between the pterostigma and the apex is 2 mm. The area between RA and C distal to the pterostigma has six–nine transverse veins (seven in the holotype), which can be irregularly forked in some individuals. There are nine postnodal crossveins basal to the pterostigma, which are not aligned with the crossveins behind them in the area between RA and RP1. The maximum width of the latter area is 0.6 mm, near the base of RP2 (three cell-lengths and 2.3 mm distal to the subnodus), narrowing to 0.3 mm at the subnodus and the pterostigmal brace.

The pterostigmal brace is distinctly oblique. RP3/4 commences between the nodus and the arculus, 0.7 mm proximal to the nodus. IR2 begins opposite to the subnodus, two cells distal to the base of RP3/4. There are no visible antenodal crossveins in the distal part of the costal area. The obliquity of the subnodus is normal, viz. not very pronounced. Veins MP and RP3/4 are straight, MA and IR2 are distally zigzagged. The postdiscoidal area between MP and MA is not enlarged distally, with only one row of cells. The area between MA and RP3/4 widens towards the posterior wing margin. There is one row of cells between MA and RP3/4 opposite the base of RP2, and probably six rows near the wing margin. The area between RP3/4 and IR2 has one row of cells. There are three rows of cells in the area between RP2 and RP1, with one or two rows of cells between IR1 and RP1.

There is no oblique crossvein 'O' between RP2 and IR2. The longitudinal veins which reach the wing margin near the apex of the wing are distinctly convergent, especially veins RA, RP1, IR1 and RP2. Vein RA is strongly sigmoidal and RP1 is weakly sigmoidal distal to the pterostigma.

Discussion. This fossil species is assigned questionably to the Coenagrionoidea on the basis of the following characters: (1) the pterostigma is short; (2) there is an oblique pterostigmal brace; (3) vein RP2 commences well distal to the nodus; (4) vein IR2 commences immediately opposite the subnodus; (5) vein RP3/4 commences a little basal to the nodus.

However, these characters are of uncertain polarity (apomorphic or plesiomorphic) and of little use phylogenetically because they are developed in both the Coenagrionoidea and the Hemiphlebioidea. Nevertheless, the convergence of veins RA, RP1, IR1 and RP2 near the wing apex represents an apomorphy (specialised character) of the (Pseudostigmatidae [except *Anomisma*] + Coryphagrionidae) and Platystictidae (Münz, 1919; Carle & Wighton, 1990; p. 54), but the sigmoidal veins RA and RP1 distal to the pterostigma appears to be an apomorphic character only present in the (Pseudostigmatidae [except *Anomisma*] + Coryphagrionidae) (see Munz, 1919; Morton, 1924; Bechly, 1995).

The Coryphagrionidae *sensu* Bechly (1995) is a monogeneric family based on *Coryphagrion grandis* Morton 1924, considered to be a subfamily of the Megapodagrionidae by Davies & Tobin (1984) and Bridges (1993). Bechly (1995) considered it to be related to the Pseudostigmatidae. The Coryphagrionidae share with the Pseudostigmatidae many wing synapomorphies (shared apomorphies): (1) postnodals aligned with the crossveins below; (2) RP3/4 and IR2 basally running very close to each other for a considerable distance; (3) discoidal cell somewhat elongate; (4) MP and CuA very long, ending very distally at the posterior margin of the wing; (5) very slender wings; (6) nodus in a very basal position; (7) postnodal area hypertrophied; (8) apically convergent longitudinal veins; (9) curved and sigmoidal RA and RP1. Of course, these characters could be due to convergence related to the giant size, the elongate abdomen and the mode of oviposition in phytotelmata (small pools that collect on certain plants), but there is no firm evidence for this. *Coryphagrion* Morton 1924 is a Recent Afrotropical genus (from Uganda), but its venation is very similar to that of the Recent Neotropical pseudostigmatid *Mecistogaster*, which represents the most basal genus of the Pseudostigmatidae (Bechly, unpublished). The Pseudostigmatidae are currently divided into two subfamilies: the fossil Euarchistigmatinae Carle & Wighton 1990 (one genus and species, *Euarchistigma atrophium* Carle & Wighton 1990, see below) and the Recent Pseudostigmatinae (nine genera and subgenera). The family is known only from the Neotropical region. Bechly (1995) ranked the Euarchistigmatinae as a separate family that is unrelated to the Pseudostigmatidae. *Cretarchistigma greenwoodi* differs from the Pseudostigmatidae + Coryphagrionidae in the following features: (1) it has a normal, non-hypertrophied postnodal area, crossed by only nine postnodal veins (all known pseudostigmatids and coryphagrionids have a very long postnodal area crossed by more than twenty postnodal veins); (2) the cells between RA and RP1 opposite the pterostigma are simple, not divided (plesiomorphy); (3) the nodus is probably not very recessed proximally; (4) the pterostigma is well braced (the pterostigma of *Coryphagrion* is strongly braced); (5) the pterostigma is relatively long and sclerotized (among the Recent genera of Pseudostigmatidae, only *Mecistogaster* Rambur 1842 and *Megaloprepus* Rambur 1842 as well as the fossil genus *Euarchistigma* have a pseudo-pterostigma or a long and sclerotized pterostigma); (6) the crossveins are not aligned across main veins (as in *Euarchistigma*).

The preserved characters of *Cretarchistigma greenwoodi* all appear plesiomorphic (primitive) for the Pseudostigmatidae + Coryphagrionidae, even when compared with the Lower Cretaceous *Euarclistigma*. The attribution of *C. greenwoodi* to the Pseudostigmatidae + Coryphagrionidae is only based on one weak possible synapomorphy (the presence of a sigmoidal RA) and needs confirmation. *Cretarchistigma* could be related to *Euarclistigma* on the basis of wing venational similarities, e. g., the presence of a well sclerotized pterostigma.

Recent pseudostigmatid larvae live in very specialized habitats such as small pools in epiphytic bromeliads and tree-holes (Machado & Martinez, 1982; Fincke, 1984). Nothing is known about the larval habits of *Cretarchistigma*.

Cretarchistigma greenwoodi ?

Figure 1H

1996 Zygotera: Coenagrionidae Jarzembowski & Nel, pl. 1, fig. 3.

Material. Specimen no. 018658, Mrs P. Martin coll., Booth Museum of Natural History, Brighton, UK.

Horizon and locality. Upper Weald Clay, Barremian, Lower Cretaceous, Auclay Brickworks, Surrey, UK.

Description. The specimen is known from the part and counterpart of the basal two-thirds of the wing. Length of the preserved portion, 13.5 mm; width of wing, 3.9 mm. Distance between the wing base and the nodus, 5.0 mm; between the arculus and the nodus, 2.8 mm; between the nodus and the pterostigma, 7 mm. The pterostigma is 1.2 mm long and 0.6 mm wide; it probably covers one cell and its distal and proximal sides are slightly oblique. The pterostigmal brace is well defined and very oblique. The vein RP1 is distinctly angular beneath the pterostigmal brace. The 9 postnodal veins are not aligned with the crossveins behind them (between RA and RP1). The zigzagged vein IR1 commences $1\frac{1}{2}$ cells basal to the pterostigma. Vein RP2 commences just over 4 cells basal to the pterostigma and is a straight vein as far as it is preserved. IR2 and RP3/4 are also straight veins in their preserved portions. IR2 begins precisely opposite the subnodus and RP3/4 commences nearer to the nodus than to the arculus, 7.5 mm basal to the pterostigma. There is no oblique crossvein 'O' (between IR2 and RP2).

MA is a zigzagged vein two cells beyond the subnodus. Vein MP is straight. CuA is also a zigzagged vein with only one row of cells between MP and CuA, and between CuA and the posterior wing margin. Few transverse crossveins are aligned in the preserved portion of the wing. There are only two antenodal crossveins; distance between AX1 and AX2 is 0.85 mm. AX2 lies just distal to the arculus. CuP is about midway between AX1 and AX2. The discoidal cell is 1.2 mm long and 0.3 mm wide; its distal side is markedly oblique, not parallel to its proximal side. The length of the latter is 0.2 mm, that of the distal side 0.6 mm, the anterior side 0.7 mm, and the posterior side 1.2 mm. The wing petiole is poorly preserved, so it is not possible to determine if the wing was well petiolated or not.

Discussion. Veins IR2 and RP3/4 beginning near the nodus, the oblique distal side of the discoidal cell, the short pterostigma, the presence of an oblique pterostigmal brace and of a distinct angle in RP1 under the pterostigmal brace indicate that this specimen could be related to the Coenagrionoidea and maybe to

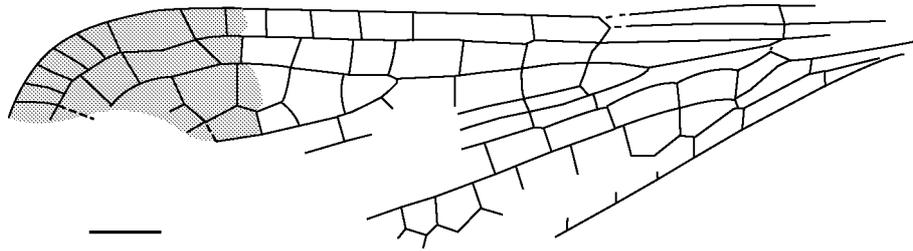


Figure 2. *Cretarchistigma greenwoodi*?, specimen no. 018767, -8, venation. (Scale bar = 1 mm).

the Coenagrionidae. This specimen differs from *Parahemiphlebia* gen. nov. (see below) in its discoidal cell being distinctly longer than broad and in its pterostigmal brace being less oblique. It differs from *Cretacoenagrion* in its postnodal crossveins not being aligned with the crossveins below them, in its pterostigma covering only one cell, and in its more oblique pterostigmal brace. It differs from *Cretahemiphlebia* gen. nov. (see below) in its vein IR1 whose base is only one and a half cells basal to the pterostigma (more than two cells in the latter), by its more oblique pterostigmal brace and more angular vein RP1. Differences from *Cretarchistigma greenwoodi* are distinctly fewer. Vein RP1 seems to be more angular opposite the base of IR1, but this could merely reflect differences between fore- and hindwing or male and female. Thus, we provisionally attribute this specimen to *C. greenwoodi*.

Cretarchistigma greenwoodi?

Figure 2

Material. Specimen no. BMB 018767, -8, Booth Museum of Natural History, Brighton, UK.

Horizon and locality. Lower Weald Clay; Lower Cretaceous; Hauterivian; Clockhouse (Butterley) Brickworks, Surrey, UK.

Description. The specimen is a nearly complete wing with the postero-apical part and the extreme base lacking. The apex is dark but the rest of the wing is hyaline. Wing length, 12.8 mm; width, about 3.5 mm; distance from the base of the wing to the nodus, 4.4 mm; distance from the nodus to the apex, 8.4 mm; the nodus is in a basal position; distance from the arculus to the nodus, 2.4 mm; distance from the nodus to the pterostigma, 5.7 mm; the pterostigma is about 1.1 mm long and 0.6 mm wide, covering exactly 1 cell; the pterostigma's distal and proximal sides are not very oblique; the pterostigmal brace is not very strong and weakly oblique; vein RP1 is not angular beneath the pterostigmal brace; the six/seven postnodal crossveins are not aligned with the subpostnodal crossveins (between RA and RP1); the zigzagged vein IR1 commences two cells basal to the pterostigma; vein RP2 commences four cells basal to the pterostigma and is a straight vein; IR2 and RP3/4 are straight veins in their preserved portions; IR2 begins exactly opposite the subnodus and RP3/4 commences nearer to the nodus than to the arculus, 0.9 mm basal to the subnodus; there is no clear oblique crossvein 'O' (between IR2 and RP2); MA is a weakly zigzagged vein; vein MP is straight; CuA is a zigzagged vein with only one row of cells between MP and CuA, and between CuA and the posterior wing margin; few transverse crossveins are aligned in the preserved portion of the wing; there were probably only two antenodal veins, only AX2 being preserved and lying opposite the arculus; CuP is

0.4 mm basal to AX2; the discoidal cell is 0.9 mm long and 0.3 mm wide, its distal side being markedly oblique and not parallel to its proximal side; the length of the latter is 0.2 mm, that of the distal side 0.4 mm, the anterior side of the discoidal cell is 0.5 mm and the posterior side 0.9 mm; the wing base is well preserved, the wing petiole being very reduced, with veins AA and AP separating at the extreme wing base; there are two crossveins in the anal area between AA and AP (as in *Parahemiphlebia cretacica* gen. nov., sp. nov.; see below).

Discussion. This specimen differs from *Cretarchistigma greenwoodi* in the following features: the pterostigmal brace is generally less oblique (variable in *C. greenwoodi*); there are only *c.*7 postnodal crossveins instead of 9 or 10; the preserved part of RA is less sigmoidal distal to the pterostigma; the base of RP2 is only four cells basal to the pterostigma instead of five cells; IR1 is closer to the pterostigma. The closest relative in the Wealden is specimen 018658 (Mrs P. Martin coll.) which we have provisionally attributed to *C. greenwoodi*. The shape of the discoidal cells, the organization of the main longitudinal veins and of the 'petiole' are similar in the two specimens. The main differences between their wings are: the pterostigmal brace of specimen 018658 is more oblique and vein RP1 distinctly angular beneath it; specimen 018658 also has 9 postnodal crossveins, the wing is distinctly longer (more than 13.5 mm compared with 12.8 mm), and the nodus more basally recessed. From the available characters, the two specimens seem to be closely related, although it is difficult to tell if inclusion within the same species is justified.

? Superfamily Coenagrionoidea Kirby 1890

Family Euarchistigmatidae Carle & Wighton 1990 (*sensu* Bechly, 1995) or

?(Pseudostigmatidae Tillyard 1917 + Coryphagrionidae Pinhey 1962)

Subfamily Euarchistigmatinae Carle & Wighton 1990

Genus *Euarchistigma* Carle & Wighton 1990

Type species. *Euarchistigma atrophium* Carle & Wighton 1990

Euarchistigma atrophium Carle & Wighton 1990

1990 *Euarchistigma atrophium* Carle & Wighton, pp. 52-54, figs 1-3.

1993b *Euarchistigma atrophium* Carle & Wighton; Nel & Paicheler, p. 61.

Material. Holotype adult reg. no. AMNH 44204, American Museum of Natural History.

Horizon and locality. Lower Cretaceous, Aptian, palaeolake sediments of the Crato Formation (Maisey, 1990; Martill *et al.*, 1993), Araripe Basin, NE Brazil.

Phylogenetic position. As already stated by Nel & Paicheler (1993b, p. 61), Carle & Wighton (1990, p. 54) have 'characterized' this fossil genus and subfamily within the Pseudostigmatidae on the basis of the presence of a sclerotized pterostigma and the basal fusion of IR2 and RP3/4. The sclerotized pterostigma is considered to be a plesiomorphy in the Pseudostigmatidae, not sufficient for the characterization of this subfamily. Carle & Wighton (1990, p. 54) also considered the basal fusion of IR2 with RP3/4 (IR3 and R4 + 5 *sensu* Carle & Wighton) to be a unique character within the suborder Zygoptera but this hypothesis is erroneous because several Recent and fossil genera of Thaumatoeuridae (*Thaumatoeuria* McLachlan 1897) and Megapodagrionidae also possess such a pronounced basal fusion of IR2 with RP3/4 (e.g., the Miocene genus *Vulgagrion* Nel & Paicheler

1994 and the Recent genera *Agnophilogenia* Kennedy 1941, *Agriomorpha* May 1933, and *Philosina* Ris 1917; Nel & Paicheler, 1994a).

Examination of specimens of the Recent pseudostigmatid species *Pseudostigma aberrans* Selys 1860 demonstrates that the relative positions of the bases of veins IR2 and RP3/4 are variable: these two veins can be very distinct basally, convergent or fused in the four wings of the same specimen. Thus, the fusion appears to be a rather uncertain character. Its stability in *Euarchistigma* needs confirmation by the discovery and study of new material. The genus *Coryphagrion* Morton 1924 (Coryphagrioninae) also has IR2 well fused basally with RP3/4. Thus this character is definitely not an autapomorphy of *Euarchistigma*.

Carle & Wighton's (1990) diagnosis of the Euarchistigmatinae appears inadequate because the given characters are either plesiomorphies or of uncertain phylogenetic polarity or probably homoplastic (convergent). They are summarized below: (1) crossveins not in alignment across main veins (uncertain polarity or plesiomorphy); (2) costal braces (Cb) present (these are the main antenodal crossveins which are always present in Zygoptera); (3) second costal brace at arculus (this character is present in many Recent Pseudostigmatidae like *Mecistogaster* or *Pseudostigma*); (4) nodus at slightly less than 1/4 of wing length (this character is also present in Recent Pseudostigmatidae and Coryphagrionidae); (5) pterostigma well developed and unbraced (the absence of a pterostigmal brace is an apomorphy of Recent Pseudostigmatidae, and the presence of a sclerotized pterostigma is a plesiomorphy); (6) R1 (RA), R2 (RP1), IR2 (IR1), and R3 (RP2) strongly convergent towards posterior wing margin (this is a synapomorphy of the Pseudostigmatidae and Coryphagrionidae); (7) IR2 (IR1) parallel to R3 (RP2) (this is a plesiomorphic character also present in the extant pseudostigmatids *Microstigma* and *Anomisma*, in contrast to the strongly convergent IR1 and RP2 of *Mecistogaster*); (8) IR3 (IR2) atrophied basally and in forewings fused to R4 + 5 (RP3/4) (the stability of this character needs confirmation); (9) discoidal cell rectangular (untypical for the Coryphagrionidae and Pseudostigmatidae).

There is still no evidence of an autapomorphic character that would characterize the subfamily Euarchistigmatinae, or a family Euarchistigmatidae, as proposed by Bechly (1995). It seems undesirable to create a new taxon based on plesiomorphic or uncertain characters. *Euarchistigma* and *Cretarchistigma* lack nearly all synapomorphies of the Pseudostigmatidae and Coryphagrionidae: (1) the giant size with extremely long and slender wings; (2) the strictly aligned crossveins in the hypertrophied postnodal area; (3) IR2 and RP3/4 running unfused but extremely closely parallel to each other for some distance distal to their origin; (4) MP and CuA very elongate and ending much nearer to the wing apex than usual. On the other hand, there is one possible synapomorphy of these two fossils with the Pseudostigmatidae + Coryphagrionidae, as already indicated for *Cretarchistigma*, i.e., the course of RA and RP1 at the wing apex, but this could be the result of convergence. A lack of synapomorphies is not sufficient reason for excluding these two fossils from the stem group of the Pseudostigmatidae + Coryphagrionidae, even if there is also no good reason for including them in that group!

In conclusion, the attribution of *Euarchistigma* and *Cretarchistigma* to the Pseudostigmatidae + Coryphagrionidae is at least very doubtful. *Euarchistigma* could belong to the stem group of the Pseudostigmatidae + Coryphagrionidae or

to the stem group of the Coenagrionoidea. All that is clear is that these two fossils are Zygoptera of uncertain position.

The exact relationships of Pseudostigmatidae and Coryphagrionidae with other Coenagrionoidea appear uncertain, even if Carle & Wighton (1990, p. 54) considered that this family group lies near the origin of the Coenagrionoidea (Protoneuridae + Platystictidae). Bechly (1995) considered that the Pseudostigmatidae and Coryphagrionidae could be the sister-group of the (Platystictidae + Platycnemididae + Protoneuridae [incl. Isostictidae] + Coenagrionidae).

Superfamily Coenagrionoidea Kirby 1890 (or Hemiphlebioidea Tillyard & Fraser 1938)

Family *incertae sedis*

Genus *Parahemiphlebia* gen. nov.

Type species. Parahemiphlebia cretacica gen. nov., sp. nov.

Etymology. After the Latin for like and the Recent genus *Hemiphlebia*.

Diagnosis. The wing venation has the following unique combination of characters among the Zygoptera non-Calopterygoidea: (1) the presence of an anal area crossed by two transverse veins between AA and AP (also present in *Cretarchistigma greenwoodi* ? specimen BMB 018767); (2) the wings are very briefly petiolated; (3) the pterostigmal brace is very oblique and nearly directly aligned with the proximal portion of vein RP1; (4) RP1 is strongly angular under the pterostigma; (5) postnodals are not aligned with crossveins below them.

Other distinctive characters are: (6) the pterostigma is quite short, covering a cell and a half (also in many Megapodagrionidae); (7) the nodus is not basally recessed (occurring at about 38% of the wing length and midway between the wing base and the pterostigma, as in *Hemiphlebia*); (8) the discoidal quadrangle is very short, its distal side being very oblique (as in Lestidae); (9) the forewing discoidal quadrangle is open or closed by a very weak vein, the hindwing one being distinctly closed; (10) RP3/4 separates from RP a little proximal to the nodus; (11) the base of IR2 is opposite the subnodus; (12) the abdomen is short, shorter than the wings; (13) the abdomen is apparently metallic-green coloured (see below).

Parahemiphlebia cretacica gen. nov., sp. nov.

Figures 3A–E, 4A–D

Material. Holotype, male specimen MNHN-LP-R.10451; allotype female specimen MNHN-LP-R.10452; paratype male specimen MNHN-LP-R.10453, all coll. Nel, Laboratoire de Paléontologie of the Muséum national d'Histoire naturelle, Paris. There is another specimen in the National Science Museum, Tokyo (no. 39, ex coll. Schwickert).

Holotype R. 10451: a small damselfly with the two wings exposed on each side of the body; the head is poorly preserved, but the abdomen and the venation are especially fine. Allotype R. 10452: the four wings overlap, but the body is well preserved, especially the abdomen and the female genital organs. Paratype R.10453: the body is in a good state of preservation but the four wings are rather poorly preserved, especially the right ones.

Horizon and locality. Lower Cretaceous, Aptian, Crato Formation (Maisey, 1990; Martill *et al.*, 1993), Araripe Basin, NE Brazil.

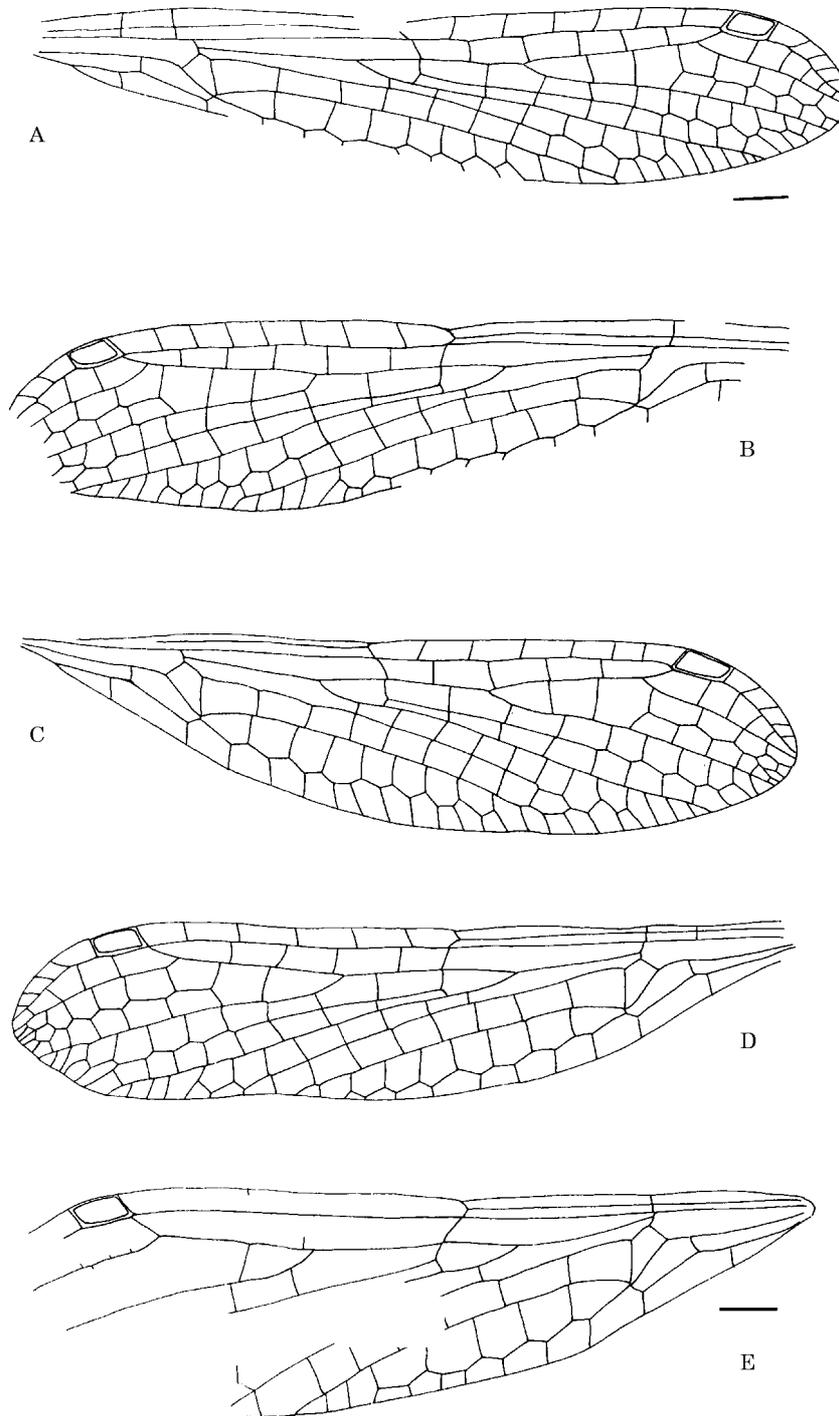


Figure 3. A–E, *Parahemiphlebia cretatica*. A, right forewing of holotype, R. 10451. B, left forewing of R. 10451. C, right hindwing of R. 10451. D, left hindwing of R. 10451. E, left hindwing of paratype R. 10453. (Scale bars = 1 mm).

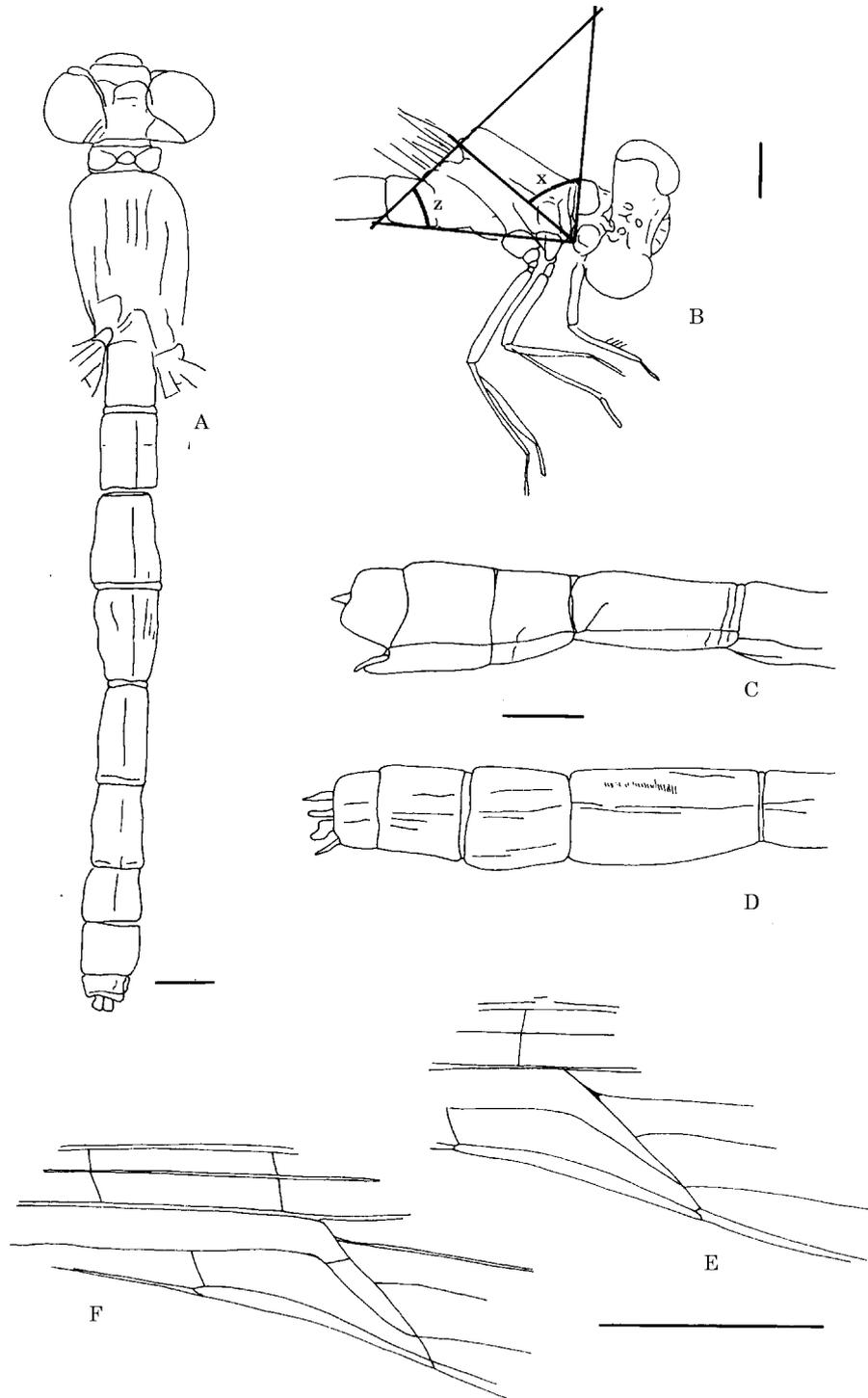


Figure 4. A–D, *Parahemiphlebia cretacica*. A, body of the male paratype R. 10453. B, head and thorax of the female allotype R. 10452. C, posterior abdominal segments of the female allotype R. 10452. D, posterior abdominal segments of the male holotype R. 10451. (Scale bars = 1 mm). E, F, *Hemiphlebia mirabilis* Selys 1869, female specimen, Nov Alexandra, Australia, coll. R. Martin, N Museum NH Paris. E, right forewing discoidal cell. F, left forewing discoidal cell. (Scale bar = 1 mm).

Etymology. After the age of the species.

Diagnosis. As for genus. This is the smallest known damselfly from the paleolake sediments of Araripe.

Description. The four wings are nearly identical and hyaline. Forewing length, 14.6 mm, width, 3.5 mm; distance from the base to the nodus, 6.6 mm; from the nodus to the apex, 8 mm; from the nodus to the pterostigma, 5.7 mm; from the nodus to the arculus, 3.7 mm; from the nodus to the base of RP3/4, 1 mm; from the nodus to the base of IR2, 0.2 mm, from the nodus to the base of RP2, 2.4 mm. Distance from the base of RP2 to the pterostigma, 3.5 mm.

Hindwing length, 14.1 mm, width, 3.6 mm; distance from the base to the nodus, 6.3 mm; from the nodus to the apex, 7.8 mm; from the nodus to the pterostigma, 5.4 mm; from the nodus to the arculus, 3.4 mm; from the nodus to the base of RP3/4, 0.9 mm; from the nodus to the base of IR2, 0.2 mm; from the nodus to the base of RP2, 2.2 mm; distance from the base of RP2 to the pterostigma, 3.2 mm.

The following characters are common to all wings: (1) RP3/4 separates from RP between the nodus and the arculus, nearer to the nodus. RP3/4 is a straight vein; (2) IR2 separates from RP opposite the subnodus. IR2 is straight in its proximal half and is zigzagged near the posterior wing margin. There is one row of cells between RP3/4 and IR2; (3) RP2 separates from RP two cells distal to the nodus. RP2 is a straight vein. There is one row of cells between RP2 and IR2 generally; (4) IR1 is a short, zigzagged vein which begins at least opposite the proximal portion of the pterostigma. There is one row of cells between RP2 and IR1, and between IR1 and RP1. There are two or three cells between the origins of RP2 and IR1; (5) the median and submedian spaces are free. Vein CuP, between MP + Cu and AA, is quite clear and perpendicular to MP + Cu and AA at 1.8 mm from the wing base. CuP is about midway between the two primary antenodal crossveins AX1 and AX2 in the forewings and nearer to AX1 in the hindwings; (6) AA and AP separate 0.6 mm distal to the wing base, so that the wings are very briefly petiolated; (7) the anal areas are very similar in the four wings, progressively widening medially, and they are crossed by two transverse veins between AA and AP proximal to the fusion of AA with CuA; (8) AA is fused with CuA exactly opposite the posterior angle of the discoidal quadrangle; (9) CuA is a rather long, zigzagged vein. There is only one row of cells in the cubito-anal areas between CuA and the posterior wing margin; (10) there is only one row of cells between MP and CuA and between MP and MA; (11) the postdiscoidal area is narrow distally; (12) MP and MA are straight veins, only zigzagged near the posterior wing margin; (13) the posterior portion of the nodus (Cr) is very oblique, distinctly more so than that of the subnodus; (14) the subnodus is well aligned with the nodal Cr; (15) there is no crossvein in the spaces between RA and RP basal to the nodus and between RP and MA proximal to RP3/4; (16) there are two primary antenodal crossveins. AX2 is in a proximal position, 0.3 mm proximad of the arculus. Distance between AX1 and AX2, 1 mm. In the hindwings, AX2 is nearly opposite the arculus and 0.9 mm from AX1; (17) there are 5 to 7 postnodal crossveins, which are not aligned with those between RA and RP1; (18) the short pterostigma is well-sclerotized, 0.9 mm long by 0.5 mm wide, and covering $1\frac{1}{2}$ cells; (19) the pterostigmal brace is very oblique and nearly aligned with the proximal portion of RP1. RP1 is strongly angular under the pterostigma. The area between RA and RP1 narrows opposite the

pterostigmal brace and widens distally for two cell lengths, before narrowing again towards the wing margin; (20) there are four or five cells in the area between RA and C distal to the pterostigma; (21) there is no oblique crossvein 'O' between RP2 and IR2; (22) the discoidal quadrangles are relatively broad and their distal sides are very oblique, distinctly longer than the anterior and proximal sides. The discoidal quadrangle in the left forewing of the holotype is open proximally, but closed in the right forewing by a weak but distinct vein. The hindwing discoidal quadrangles are all closed; (23) forewing discoidal quadrangle: length of the anterior side, 0.2 mm, of the distal side, 0.7 mm, of the posterior side, 0.7 mm, of the proximal side, 0.4 mm; (24) hindwing discoidal quadrangle: length of the anterior side, 0.3 mm, of the distal side, 0.7 mm, of the posterior side, 0.9 mm, of the proximal side, 0.3 mm.

Head: The eyes are rounded (diameter, 1.2 mm), 1.1 mm apart. There is no clear suture between the frons, vertex and occiput. Three triangular ocelli are visible on the allotype. The postocular lobes are well developed behind the eyes, and the occiput seems to be very reduced (cf. Lew, 1933). The epicranial suture is clearly visible. Length of the head, 1.4 mm; width, 2.9–3.0 mm.

Thorax: The prothorax is short (0.7 mm long) and narrow (1.3 mm wide). The thoraxes of the holotype and paratype are presented in dorsal aspect, their lateral structures not visible. However, the thorax of the allotype shows lateral sutures. Episternum 2 (0.5 mm wide) and the mesopleural suture (*sensu* Asahina, 1954) are clearly visible, but the median portions of epimeron 2 and episternum 3 are not preserved. The median portion of the interpleural suture between epimeron 2 and episternum 3 is also not preserved, so it is impossible to determine its exact length, or if it is complete or incomplete (cf. Asahina, 1957). Epimeron 3 is also visible and is 0.7 mm wide. Infraepisternum 2 is relatively long (0.5 mm) and wide (0.4 mm). Katepimeron 2, between the two coxae of the mesothoracic and metathoracic legs, is reduced and very small.

The thoracic skewness (*sensu* Needham & Anthony, 1903) is significant. The angle x , which represents the degree of inclination of the mesopleural suture, is 55° . The angle z , which represents the degree of inclination of the surface of wing insertion relative to the ventral portion of the thorax, is 50° . The distance between the head and forewing bases (3.0 mm) is about twice the head length. Following Needham & Anthony, the skewness of *Parahemiphlebia* is similar to that of Recent Lestoidea and Coenagrionoidea.

Legs: These are rather poorly preserved in the holotype and the paratype, but better preserved in the allotype. They are never widened or thickened. Their spines are 0.2 mm long and regularly disposed at 0.1 mm intervals. The fore trochanter and coxa are not preserved, but the mesothoracic and metathoracic trochanters and coxae are well preserved in the allotype.

Allotype: length of fore femur, 1.4 mm; of fore tibia, 1.5 mm; of fore tarsus, 0.4 mm; of mid coxa, 0.5 mm; of mid trochanter, 0.3 mm; of mid femur, 1.6 mm; of mid tibia, 1.6 mm; of mid tarsus, 0.7 mm; of hind coxa, 0.3 mm; of hind trochanter, 0.3 mm; of hind femur, 2.0 mm; of hind tibia, 2.0 mm; of hind tarsus, 0.7 mm.

Abdomen: This is always very short, 12 to 14 mm long, and less than twice the length of the thorax + head. The abdominal segments are all about the same width (1.4 mm). There is no perceptible difference between the abdomens of the male and female. Specimen 39 from the Schwickert collection (NSMT, Tokyo) has a metallic-green coloured second abdominal segment that clearly corresponds to its original coloration.

Sexual appendages. (1) Male: the sexual appendages of the last abdominal segments are visible on the holotype. The cerci seem to be small (0.2 mm long) and weak, and the paraprocts seem to be even smaller (0.15 mm long), shorter than the tenth abdominal segment. The secondary sexual organs of segment 2 are not visible on any specimen.

(2) Female: the ovipositor is well preserved on the allotype, in lateral aspect. Sternite 8, and the ventral and lateral valvulas cannot be distinguished, but the ovipositor (3.0 mm long) extends half way along the tenth segment. The very short stylus (0.4 mm long) is visible at the apex of the ovipositor. This ovipositor is of an endophytic type. One very short cercus, 0.4 mm long, is visible at the apex of the tenth segment. Length of segment 7, 3.2 mm; width, 1.4 mm; length of segment 8, 1.5 mm; width, 1.5 mm; length of segment 9, 1.7 mm; width, 1.5 mm; length of segment 10, 1.2 mm; width, 1.3 mm.

Discussion. This fossil damselfly can be easily recognized by its very reduced dimensions. All specimens show the same venation and very short abdomens, so they are probably conspecific. They are readily distinguished from *Eoprotoneura hyperstigma* Carle & Wighton 1990 (Protoneuridae) from the same outcrop by their non parallel-sided discoidal quadrangles and longer vein MP. The other described Araripe damselfly, *Euarchistigma atrophium* Carle & Wighton 1990 (Euarchistigmatidae), is a large species with densely reticulate wings.

The non-petiolated wings of *Parahemiphlebia cretatica* represent a plesiomorphic character at the base of the Coenagrionoidea when compared to the more or less petiolated wings of the non-calopterygoid Zygoptera and would contradict an ingroup position within the Coenagrionoidea. Within the Recent Zygoptera, only the Calopterygoidea possess basally separated veins AA and AP, but their anal areas are generally distinctly wider, with a more dense reticulation and secondary longitudinal veins. *Hemiphlebia* and *Parahemiphlebia* also exhibit open discoidal cells in the forewing (often in one wing only). The polarity of this character needs some consideration.

Polarity of the character: forewing discoidal cell open/closed

Fraser (1957) considered that an open discoidal cell was 'primitive' (plesiomorphic). However, Carle (1982) thought that it resulted from an apomorphic 'loss' of the posterior portion of the arculus which would have occurred convergently in *Hemiphlebia*, *Chorismagrion* Morton 1914 (Lestoidea: Synlestidae?) and the Oreopteridae. In fact, Carle revived an idea of Needham (1903, p. 749) who considered that this open discoidal cell resulted from the "loss of a cross vein that is elsewhere very constant—the cross vein forming the lower end of the arculus."

Riek & Kukalová-Peck (1984) considered that the basal side of the discoidal cell of the Odonata is a simple transverse vein ('Cr') between MP + CuA and MA which reinforces the structure of the arculus. This vein is absent in some of the older Odonatoptera: the Triassic Triadophlebiomorpha and Kennedyiomorpha *sensu* Pritykina (1981) and the Oreopteroidea: Oreopteridae Pritykina 1968 from the Upper Jurassic of Karatau (Turkestan, CIS).

The absence of this structure in all pre-Jurassic and many Mesozoic Odonata and its presence in almost all Recent Zygoptera + 'Anisozygoptera' + Anisoptera (except *Hemiphlebia* and *Chorismagrion*) suggest that the presence of this transverse vein reinforcing the arculus could be an apomorphy of the crown group of the Odonata.

Some specimens of *Hemiphlebia mirabilis* Selys 1869 show a closed forewing discoidal cell (see Figure 4E-F) in one wing and an open one in the other. This character is therefore of uncertain phylogenetic value.

The presence of an open discoidal cell in the genus *Chorismagrion* also suggests that some cases of reversion could have occurred in the Zygoptera. *Chorismagrion* has no affinity with Triassic Kennedyiomorpha but it could be more closely related to the Lestoidea and *Hemiphlebia* because the larval characters of *Chorismagrion* are very similar to those of *Hemiphlebia* and resemble those of *Synlestes* Selys 1869 (Fraser, 1956; Bechly, 1995). Also, the male secondary genitalia demonstrate that *Chorismagrion* is indeed a member of the Lestoidea.

The presence of an open discoidal cell in one forewing and of a closed one in the other forewing of the same specimen of *Parahemiphlebia cretacea* also shows how variable this character was in some Lower Cretaceous Zygoptera. Jarzembowski (1990, figs 2, 3) indicated a similar situation in the wings of some Recent specimens of *Agriocnemis* sp. (Coenagrionidae). Consequently, the character 'discoidal cell open' is of uncertain value, and the new suborder Archeoptera created by Belyshev & Haritonov (1985) for the two genera *Hemiphlebia* (Hemiphlebiidae) and *Chorismagrion* (Chorismagrionidae = Synlestidae: Chorismagrioninae *sensu* Davies & Tobin, 1984), based on the open discoidal cell in the forewing, is not well defined and of polyphyletic nature: it has to be rejected. Belyshev & Haritonov considered that the character is 'primitive': using a plesiomorphic character state to define a group does not make any sense from a cladistic point of view.

In contrast, *Hemiphlebia* has a more constant character which would appear to be apomorphic: the oblique alignment of the basal portion of the vein [MA + RP] with the basal portion of MA (MAB *sensu* Nel *et al.*, 1993) and the basal portion of vein CuA (Figure 4E, F) and the weakening of the main longitudinal branch of MA. The same type of alignment of these veins occurs in all taxa usually possessing a more or less constant open discoidal cell. This structure of an oblique, composite vein crossing the wing base is visible on the forewings of the Tarsophlebioidea (open discoidal cell) and the Epiophlebioidea (open or closed discoidal cell), and also on the forewings of the Heterophlebioidea (*sensu* Nel *et al.*, 1993). Furthermore, it is present in the forewings of *Hemiphlebia* and *Chorismagrion*. If this relatively rare structure is a plesiomorphic condition, it would imply many convergences between the major groups of Odonoptera. Also, the development of such a structure implies the replacement of the main branch of MA by the secondary vein MAB, which then becomes stronger and thicker than MA. So, it suggests an apomorphic condition, compared with the non-alignment of the veins RP + MA, MA, MAB and CuA of nearly all other Odonata. As the development of such a structure seems to be related to the weakening or absence of the proximal side of the discoidal cell in all the taxa concerned, it suggests that the presence of an open discoidal cell, together with the presence of an oblique composite transverse vein RP + MA - MA - MAB - CuA would be a composite apomorphic character. But its value is relative because, following Nel *et al.* (1993), this character occurred independently several times within the 'Anisozygoptera' + Anisoptera.

In conclusion, there are two possible scenarios for the evolution of the forewing discoidal cell: (1) presence of open discoidal cell both in fore- and hindwings in Triassic Odonoptera → the hindwing discoidal cell becoming closed once in the stem group of Zygoptera and once in the stem group of the

'Anisozygoptera' + Anisoptera, but the forewing one remained open in these stem groups, the discoidal cell being reinforced by the development of a specialized oblique composite transverse vein RP + MA - MA - MAb - CuA → the forewing discoidal cell becoming closed several times by convergence and the oblique composite transverse vein RP + MA - MA - MAb - CuA consequently became reduced in all taxa which had closed their forewing discoidal cell; (2) presence of open discoidal cell both in fore- and hindwing in Triassic Odonatoptera → both the fore- and hindwing discoidal cells becoming closed once in the stem group of Zygoptera and once in the stem group of the 'Anisozygoptera' + Anisoptera → occasionally, some reversions occurred in the forewing discoidal cell which became open again, this reversion being accompanied by the development of a specialized oblique composite transverse vein RP + MA - MA - MAb - CuA. This situation would have occurred by convergence in many groups of 'Anisozygoptera' and some Zygoptera.

Both these scenarios imply many convergences and reversions. The lack of knowledge concerning the structure of MA and MAb in the Triassic Odonatoptera does not allow us to choose between them at present. The phylogenetic value of the composite character 'presence of an open discoidal cell + presence of an oblique composite transverse vein RP + MA - MA - MAb - CuA' is very uncertain for the relationships of *Hemiphlebia* and *Chorismagrion*.

Phylogenetic relations between Parahemiphlebia and the Hemiphlebioidea

The Hemiphlebioidea Fraser 1960 are represented by only one Recent family, the monospecific Hemiphlebiidae Fraser 1960, based on *Hemiphlebia mirabilis* Selys 1869 from Australia. Whalley (1986) attributed the fossil family Italophlebiidae Whalley 1986 from the Italian Upper Triassic (Lower Rhaetian, 'Argilliti di Riva di Solto', Bergamo) to the Hemiphlebioidea. Fraser (1957, p. 53) considered the Hemiphlebioidea to be very 'primitive': "I cannot but think that its correct place in the order lies between the latter order (Protozygoptera) and the Coenagrionidea [*sic*], that is right at the base of the suborder Zygoptera". The Hemiphlebioidea (*Hemiphlebia*) were characterised, within the Zygoptera, by the following features: (1) the presence of the two primary antenodal crossveins; (2) an oblique composite transverse vein RP + MA - MA - MAb - CuA in the forewing and an open discoidal cell in the forewing but a closed discoidal cell in the hindwing; (3) postnodal crossveins that are not aligned with the corresponding crossveins between RA and RP1; (4) vein AA separated from AP just beyond the vein AX1, and the wing not well petiolated (the last character is not very constant; see Fraser, 1957, p. 32, fig. 12; Lindley, 1978); (5) the male penis more generalized than that of other Recent Zygoptera (Kennedy, 1920; Fraser, 1955b; Hennig, 1981; p. 356); (6) the male anterior hamuli trapezoidal as in the Megapodagrionidae (Fraser, 1955b); (7) the median lobe of the larval labial mask distinct from the mentum; (8) the gizzard very different from that of other Recent Zygoptera (considered as primitive by Tillyard, 1928); (9) well-developed male cerci and paraprocts (Fraser, 1955b, p. 112, fig. 1e, f); (10) female anal appendages very long and thick (Fraser, 1955b, p. 112, fig. 1g); (11) the white anal appendage of both sexes used for a unique and derived display behaviour (Sant & New, 1988).

Comments: character 1 is probably a synapomorphy of Zygoptera + 'Anisozygoptera' + Anisoptera; the polarity of character 2 is problematical. Even if it was apomorphic for *Hemiphlebia*, it is still impossible to use it for

phylogenetic purposes; characters 3, 4, 5, 7 and 8 are considered as plesiomorphies within the Zygoptera by Tillyard (1928), Fraser (1955b, 1957), Hennig (1981), Lindley (1978) and Davies (1981). Character 7 is more likely to be an autapomorphy, just like the alleged presence of paraglossae; character 6 is probably a symplesiomorphy; character 9 is probably a plesiomorphy of the Zygoptera + 'Anisozygoptera' + Anisoptera. The reduction of the zygopteran cerci and paraprocts seems to occur only within the Coenagrionoidea (Coenagrionidae + Platycnemididae) and *Parahemiphlebia*; the very long female anal appendages (character 10) are said to be a specialized character by Fraser (1955b) associated with the biology of *Hemiphlebia mirabilis*. *Parahemiphlebia* shares characters 1, 2 (in part ?), 3 and 4 with *Hemiphlebia*. These characters are ambiguous or clearly plesiomorphic. Characters 6, 7, 8 and 11 are unknown in *Parahemiphlebia*. Character 10 of *Hemiphlebia* is not present in *Parahemiphlebia*, which has female genital appendages similar to those of Recent Coenagrionoidea. The very small size and the lack of oblique vein perhaps represent shared derived characters states of *Hemiphlebia* and *Parahemiphlebia*, but these characters are often homoplastic in Zygoptera. *Parahemiphlebia* appears to share with *Hemiphlebia* its metallic-green coloured second abdominal segment, unlike the Coenagrionoidea, but the polarity of this character within Zygoptera remains undetermined.

The phylogenetic relationships between Parahemiphlebia and the Coenagrionoidea

Important characteristics are as follows: (1) the presence of a strong oblique pterostigmal brace and of a strongly angular RP1 which are apomorphies within the Coenagrionoidea: Coenagrionidae *sensu stricto*. The Platycnemididae, Protoneuridae, Isostictidae and the Hemiphlebioidea have a less angular RP1 and less oblique pterostigmal brace (see Figure 6A, B and Morton, 1914, pl. 9, fig. 4; Münz, 1919). The Pseudostigmatidae, Platystictidae and many 'Megapodagrionidae' have a very weak or no stigmal brace; (2) the short, nearly one-cell length pterostigma is probably apomorphic in the Coenagrionidae + Platycnemididae + Protoneuridae + Isostictidae, but this character is also present in *Hemiphlebia* and absent in several genera of Coenagrionoidea, especially most 'Megapodagrionidae' and Platystictidae: Palaemnematinae; (3) the development of a non parallel-sided discoidal quadrangle is probably a plesiomorphic or homoplastic apomorphic character (cf. quadrangle with a parallel distal side) but this character is present in all Lestoidea and most Coenagrionoidea (except for *Podopteryx* Selys 1871, Megapodagrionidae; *Lestoidea* Tillyard 1913, 'Pseudolestidae'; *Copera* Kirby 1890, Platycnemididae; *Chlorocnemis* Selys 1863, Protoneuridae). Some Recent platycnemidids have a non-parallel-sided discoidal cell (*Leptocnemis* Selys 1886 and *Melanesobasis* Donnelly 1984) while *Platycnemis* has a parallel-sided discoidal cell (Münz, 1919; Schmidt, 1951); (4) the polarities of the characters (a) base of RP3/4 a little proximal to the nodus, (b) base of IR2 opposite the subnodus and (c) absence of the oblique crossvein 'O' remain uncertain, but they are probable apomorphies of the Coenagrionoidea and Hemiphlebiidae because the presence of the opposite characters 'bases of RP3/4 and IR2 between the arculus and nodus', 'presence of 'O'' in groups as diverse as the Lestoidea and the 'Anisozygoptera' + Anisoptera would suggest that they are plesiomorphies (Nel *et al.*, 1993); (5) the very reduced male anal appendages of the last abdominal segments of *Parahemiphlebia* are an apomorphy within the Coenagrionoidea

(Coenagrionidae + Platycnemididae). On the contrary, the Lestoidea, Hemiphlebioidea, Calopterygoidea and other Coenagrionoidea families generally possess well-developed cerci and paraprocts (Fraser, 1933, 1955b, 1957) but these structures are very variable in these groups: *Coenagrion armatum* has giant inferior appendices (paraprocts) while *Enallagma signatum* and *Cercion lindeni* have large cerci. Also, the Calopterygidae: Philonganginae and many Megapodagrionidae (Coenagrionoidea) have the inferior anal appendage much reduced. As a result, the reduction of the male anal appendages is a homoplastic character (showing reversions and convergences); (6) the endophytic female ovipositor of *Parahemiphlebia* is similar to those of the Lestoidea, Coenagrionoidea and Hemiphlebioidea, but the female anal appendages of *Parahemiphlebia* are identical to those of the Coenagrionoidea; (7) the great development of the postocular lobes and the reduction of the occiput in *Parahemiphlebia* are probable synapomorphies of the Coenagrionoidea but, except for the work of Lew (1933), no extensive study has been made of these structures in the Lestoidea and Hemiphlebioidea. *Parahemiphlebia* had already acquired a specialized head similar to that of Recent Coenagrionidae; (8) the non-alignment of the postnodal crossveins with the crossveins between RA and RP1 of *Parahemiphlebia* is either a very basal, plesiomorphic character or a reversion (within the Coenagrionoidea) because this character is always absent in Recent Coenagrionoidea; (9) the non-dilated legs of the males of *Parahemiphlebia* is a plesiomorphic condition present in Coenagrionidae, but also in the subfamily Calicneminae of the Platycnemididae; (10) the polarity of the character 'presence of a very short abdomen, shorter than the wings' of *Parahemiphlebia* remains doubtful because little is known concerning the abdominal structures of the older, Triassic 'Odonata'. So it is impossible to use an outgroup method to determine the polarity of such a character. It is usually accepted that the evolution of the Odonata has led to longer abdomens. The Recent pseudostigmatids *Megaloprepus* spp. and *Mecistogaster* spp. have the longest abdomens and very special modes of oviposition by depositing their eggs in small tree holes. The length is said to be a specialisation linked to this peculiar mode of oviposition, but Fincke (1984) doubted this hypothesis, showing that the male of *Megaloprepus coerulatus* has a longer abdomen than the female. However, it seems that the relative dimensions of the abdomen and wings are more or less related to the biology or the flight mechanics of each species. Thus, convergences or reversions are likely for characters of this nature; (11) the very oblique pterostigmal brace, in direct alignment with the proximal portion of RP1, is a specialized feature, only present in *Parahemiphlebia*, and constitutes an autapomorphy for the genus.

Even if *Parahemiphlebia* looks like Recent *Hemiphlebia*, it only shares plesiomorphies and uncertain characters with it. In contrast, its male genital appendages and its pterostigmal characters show derived similarities with the Coenagrionoidea (Coenagrionidae + Platycnemididae).

Parahemiphlebia allendaviesi sp. nov.

Figure 5

Material. Holotype specimen MNEMG 1996.226a, b, R. Coram coll., Maidstone Museum, UK.

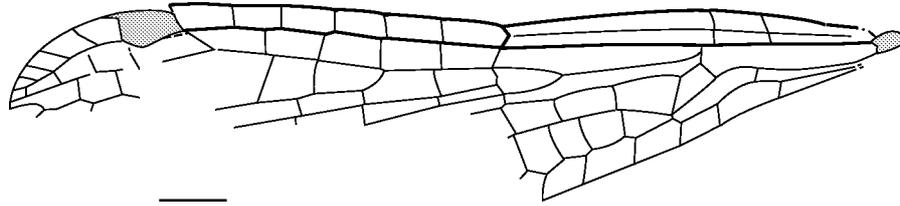


Figure 5. *Parahemiphlebia allendaviesi* sp. nov., holotype venation. (Scale bar = 1 mm).

Horizon and locality. Purbeck Limestone Group, Durlston Formation (Middle Purbeck beds), Clements' bed 175, Lower Cretaceous, Berriasian, Durlston Bay, Dorset, UK.

Etymology. After Dr Allen L. Davies, odonatologist.

Diagnosis. The wing is very briefly petiolated, with three crossveins between AA and AP in the anal area; the pterostigmal brace is very oblique and nearly directly aligned with the proximal portion of vein RP1; RP1 is strongly angular nearly opposite the pterostigma; the postnodal crossveins are not aligned with subpostnodal crossveins; the pterostigma is short and covers $1\frac{1}{2}$ cells; the nodus is not very basally recessed; the closed discoidal quadrangle is very short, with the distal side very oblique; RP3/4 separates from RP a little basal to the nodus; the base of IR2 is opposite the subnodus.

Description. The species is known from the impression of a nearly complete wing except for the posterior apical part; length, 12.8 mm; width, *c.* 2.7 mm; distance from base to nodus, 5.3 mm; distance from nodus to apex, 7.4 mm; distance from the arculus to nodus, 2.8 mm; distance from nodus to pterostigma, 4.8 mm. The pterostigma is about 0.9 mm long and 0.5 mm wide, covering 1.5 cells with its distal and proximal sides slightly oblique; the pterostigmal brace is well defined and very oblique. Vein RP1 is distinctly angular beneath the pterostigmal brace. The 5 postnodal crossveins are not aligned with the crossveins behind them (between RA and RP1). The zigzagged vein IR1 probably commences opposite the pterostigma; vein RP2 commences three cells basal to the pterostigma and is a straight vein. IR2 and RP3/4 are straight veins in their preserved portions; IR2 begins exactly opposite the subnodus and RP3/4 commences nearer to the nodus than to the arculus, 1.0 mm basal to the subnodus. There is no oblique crossvein 'O' (between IR2 and RP2). MA is a weakly zigzagged vein; vein MP is straight. CuA is a zigzagged vein; there is only one row of cells between MP and CuA and between CuA and the posterior wing margin. No transverse crossveins are aligned in the preserved portion of the wing. There are only two antennal crossveins; distance between AX1 and AX2, 0.8 mm. AX2 lies just basally of the arculus; CuP is between AX1 and AX2, nearer to AX1. The discoidal cell is 0.8 mm long and 0.3 mm wide, its distal side is markedly oblique, not parallel to its proximal side; the length of the latter is 0.3 mm, that of the distal side 0.5 mm, whereas the anterior side is 0.3 mm and the posterior side 0.8 mm. The wing base is well preserved, weakly petiolated, with veins AA and AP separating at the wing base; there are three crossveins in the anal area between AA and AP.

Discussion. This species shares the following characters with the Upper Aptian *Parahemiphlebia cretacica*: (1) the presence of an anal area crossed by two or more

crossveins (between AA and AP); (2) poorly petiolated wings; (3) pterostigmal brace very oblique and nearly aligned with the proximal portion of vein RP1; (4) RP1 distinctly angular near the pterostigma; (5) postnodal crossveins not aligned with the subpostnodal crossveins; (6) pterostigma covering $1\frac{1}{2}$ 'normal' cells; (7) nodus not very recessed basally (lying at about 41% of the wing length from base and nearly midway between the base of the wing and the pterostigma); (8) discoidal quadrangle very short, its distal side being very oblique (as in Lestidae); (9) discoidal quadrangle closed; (10) RP3/4 separating from RP a little basal to the nodus; (11) base of IR2 opposite the subnodus.

Apart from age and geographic considerations, the differences between the two species are very few: the discoidal cell is somewhat longer than that of *P. cretatica*; there are three crossveins between AA and AP, instead of only two in *P. cretatica*; the pterostigmal brace is less oblique. Thus, the Purbeck species is placed in *Parahemiphlebia* even if the polarities of the shared characters are not very clear, especially the weak petiolation of the wing. If *Parahemiphlebia* is indeed one of the oldest records of the Coenagrionoidea, then the very oblique pterostigmal brace and short pterostigma could be considered as synapomorphies of this genus, acquired convergently by other taxa within higher Coenagrionoidea: Coenagrionidae and Platycnemididae. *Parahemiphlebia allendaviesi* differs from *Cretarchistigma* in its vein RA being less strongly curved distal to the pterostigma, its more oblique pterostigmal brace and less numerous postnodal crossveins. It differs from *Cretacoenagrion* in the non-petiolated wing, proximally closed discoidal cell (hindwing ?) and non-aligned postnodal crossveins.

? Superfamily Coenagrionoidea Kirby 1890

Family *incertae sedis*

Genus and species undetermined

Martill *et al.* (1993: pl. 7, fig. 1) figured a small undescribed coenagrionoid-like damselfly from Araripe which belongs to a species (and probably genus) different from *Parahemiphlebia cretatica* because it possesses an abdomen longer than its wings. A description is awaited.

Superfamily Hemiphlebioidea Tillyard & Fraser 1938 or Coenagrionoidea Kirby 1890

Family undetermined

Genus *Cretahemiphlebia* gen. nov.

Type species. Cretahemiphlebia rossi gen. nov., sp. nov.

Etymology. In reference to similarities with the Recent genus *Hemiphlebia* Selys 1869 and to the age of the new genus.

Diagnosis. The preserved structures of the distal half of the wing of the new genus and species are similar to the corresponding areas of the Recent *Hemiphlebia mirabilis* Selys 1869 (Figure 6A, B). The main differences are (1) the fossil's longer vein IR1, which begins more than two cells basal to the pterostigma compared with less than one cell in *Hemiphlebia mirabilis*; (2) vein RP2, which originates almost five cells basal to the pterostigma in *Cretahemiphlebia* but only two and a half cells in *Hemiphlebia*. *Cretahemiphlebia* differs from all Recent coenagrionoid genera in that the postnodal crossveins are not aligned with the crossveins of the area between RA and RP1. It differs from *Parahemiphlebia* gen. nov. in its less oblique pterostigmal brace and its longer vein IR1. It differs from

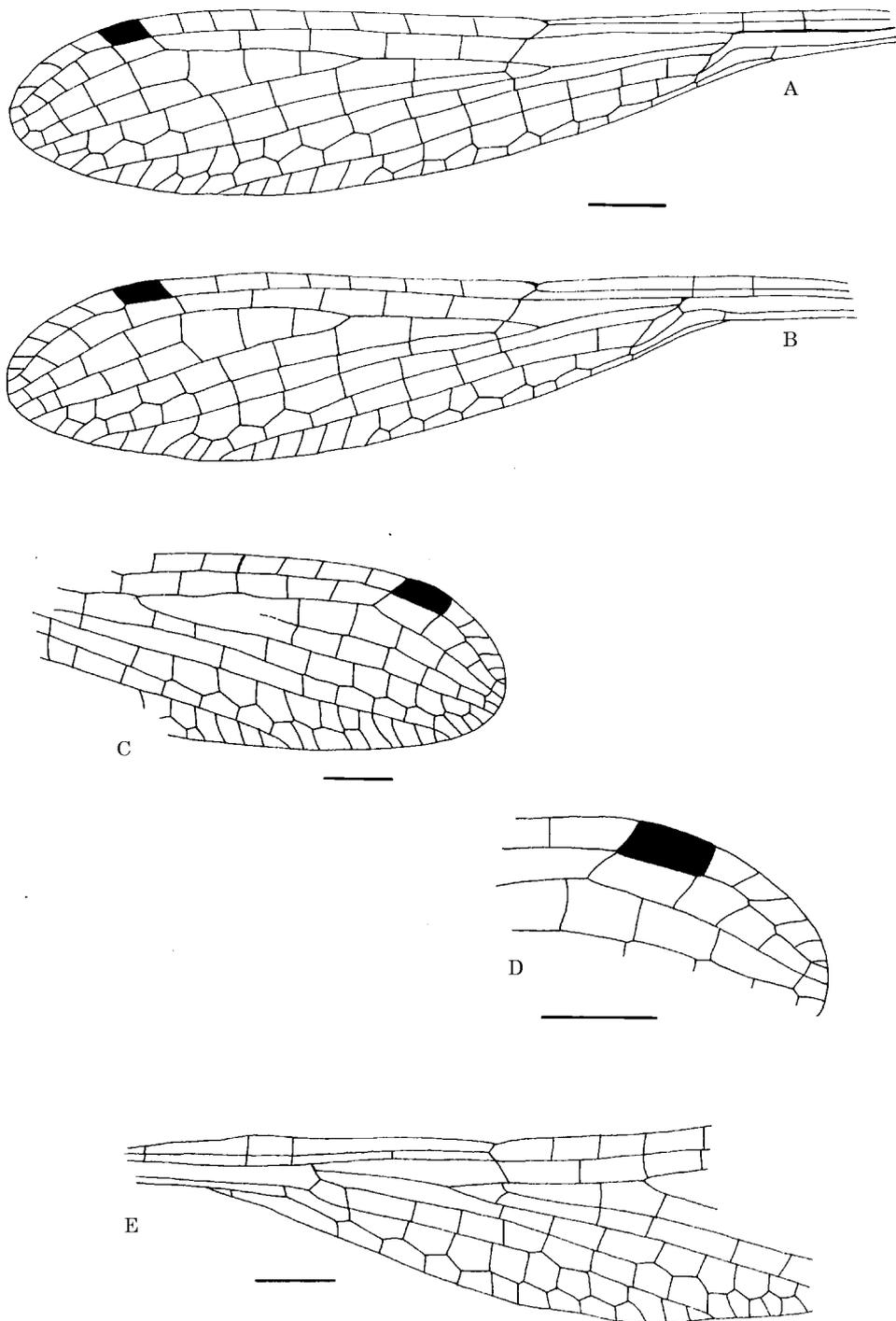


Figure 6. A, B, *Hemiphlebia mirabilis* Selys 1869, venation. A, forewing. B, hindwing. (Scale bar = 1 mm). C, D, *Cretahemiphlebia rossi*. C, venation of holotype. D, detail of pterostigmal region of holotype. (Scale bars = 1 mm). E, *Coenagrionoidea* or *Hemiphlebioidea*, species A, venation. (Scale bar = 1 mm).

Cretacoenagrion in its shorter pterostigma covering only one cell (two cells in *Cretacoenagrion*), in its angular vein RP1 under the pterostigmal brace (RP1 is a straight vein in *Cretacoenagrion*), and by its postnodal crossveins not being aligned with the corresponding crossveins between RA and RP1 (well aligned in *Cretacoenagrion*).

Cretahemiphlebia rossi gen. nov., sp. nov.

Figures 6C, D, 7

Material. Holotype specimen 016383, A. Ross coll., Booth Museum of Natural History, Brighton, U. K.

Horizon and locality. Lower Cretaceous, Weald Clay, Rudgwick Brickworks, Sussex, England.

Etymology. This species is dedicated to Mr A. Ross who discovered the unique type specimen.

Diagnosis. As for genus.

Description. The species is known from part of the apical portion of a wing. Length of the preserved portion, 7.0 mm; width of wing, 2.9 mm. The pterostigma is 0.9 mm long and 0.3 mm wide and covers exactly one cell. Its distal and proximal sides are nearly perpendicular to veins C and RA and are not oblique. The pterostigmal brace is well defined but not very oblique. Vein RP1 is moderately angular opposite the pterostigmal brace. The postnodal veins are not aligned with the crossveins behind them between RA and RP1. Vein IR1 begins more than two cells basal to the pterostigma. RP2 begins five cells (3.6 mm) basal to the pterostigma. IR1 and RP2 are straight veins. The nodus is not preserved. IR2 is a zigzagged vein only in its distal portion, near the posterior wing margin. RP3/4 is a straight vein. MA is a zigzagged vein only one cell distal to the origin of RP2. MA reaches the posterior wing margin near the pterostigma. MP is a straight vein, reaching the posterior wing margin a little beyond the origin of IR1. Only the very distal end of CuA is preserved. The transverse crossveins are generally not aligned in the preserved portion of the wing.



Figure 7. *Cretahemiphlebia rossi* gen. nov., sp. nov., holotype, $\times 18$.

Discussion. The preserved characters of the fossil wing are similar to the corresponding characters of the Recent genus *Hemiphlebia* Selys 1869. However, they are only symplesiomorphies (shared primitive characters), especially the non-alignment of the crossveins of the postnodal area with those of the area between RA and RP1, and also the non-alignment of the crossveins in the radial area. The main differences between the two genera are the lengths of veins IR1 and RP2, as mentioned earlier.

The exact affinities of *Cretahemiphlebia rossi* are not clear. It could be related to *Hemiphlebia* because of the similarities discussed above. But these characters cannot be considered to be synapomorphies of the Hemiphlebiidae because some are symplesiomorphies of the Zygoptera and others, like the angle of RP1 and the oblique pterostigmal brace, are convergent apomorphies present in the Hemiphlebiidae and in the 'higher' Coenagrionoidea, especially Coenagrionidae. *Cretahemiphlebia* could be related either to the Hemiphlebioidea or to the stem-group of the Coenagrionoidea. Its phylogenetic position remains uncertain because of the lack of information concerning the proximal portion of the wings (discoidal cell, arculus, antenodal area, petiole, and insertions of veins RP3/4 and IR2) and of its body characters (male and female genitalia).

Superfamily Hemiphlebioidea Tillyard & Fraser 1938 or Coenagrionoidea Kirby 1890

Family uncertain

Genus uncertain

Species A

Figure 6E

Material. Specimen no. 018531, Jarzembowski coll., Booth Museum of Natural History, Brighton, UK.

Horizon and locality. Lower Cretaceous, Lower Weald Clay, Clockhouse Brickworks, near Capel, Surrey, UK.

Description. The unique specimen shows only the basal two-thirds of a wing. Length of the preserved portion, 8.7 mm; width of the wing, 2.5 mm; distance from base to arculus, 2.3 mm; to nodus, 4.6 mm; distance between nodus and arculus, 2.3 mm. Only four postnodal crossveins are preserved, the two distal ones being nearly aligned with the crossveins behind them. Vein RP2 begins two cells (1.6 mm) beyond the subnodus. Vein IR2 begins opposite the subnodus and RP3/4 begins 0.6 mm basal to the nodus, nearer to the nodus than to the arculus. IR2 and RP3/4 are straight veins. There is no oblique vein 'O' between IR2 and RP2. MA is a zigzagged vein opposite RP2. MP is only slightly zigzagged. CuA is also a zigzagged vein. AA separates from AP well proximal to CuP, 1.0 mm from the wing base and 0.9 mm basal to CuP. There is a small, oblique vein between AA and AP in the anal area, very near to the base of AA. CuP is nearer to AX2 than to AX1. Distance between AX1 and AX2, 0.6 mm. The arculus is in a distinctly distal position, 0.2 mm beyond AX2. The discoidal cell is 0.5 mm long and 0.2 mm wide; its distal side is slightly oblique but not appreciably longer than its proximal side; length of proximal side, 0.2 mm; of distal side, 0.2 mm; of anterior side, 0.3 mm; of posterior side, 0.6 mm.

Discussion. This wing shows three characters common only to Hemiphlebioidea and Coenagrionoidea: (1) vein IR2 begins behind the nodus and the subnodus;

(2) the distal side of the discoidal cell is nearly as long as the proximal side and slightly oblique; (3) there is no oblique vein 'O'.

The exact phylogenetic relationships of this fossil species are undetermined because of the lack of pterostigmal characters (form of the pterostigma, pterostigmal brace and vein RP1 under the pterostigma). The non-alignment of at least some of the postnodal crossveins with the veins behind them, and the weak petiolation of the wing with the presence of a basal crossvein in the anal area, are characters of this fossil also found in the Recent genus *Hemiphlebia*. But these characters are plesiomorphic and present in *Parahemiphlebia* described above. The fossil could thus belong to the Hemiphlebioidea or the Coenagrionoidea.

Species A differs from *Cretarchistigma* described above because the discoidal cell is distinctly shorter and the arculus is in a more distal position relative to the second antenodal crossvein. However, comparison with *Cretahemiphlebia* (see above) is more difficult because species A is known from the wing base and *Cretahemiphlebia* is known from the wing apex. Both fossil wings resemble the wings of Recent *Hemiphlebia mirabilis* (Figures 6A, B) suggesting that they might represent the same fossil species but there is no direct evidence for this. However, the basal halves of the wings of *Parahemiphlebia cretacica* from Araripe also resemble species A. For the present, specimen no. 018531 is best considered to belong to an as yet undetermined genus and species.

Phylogenetic position of the Hemiphlebioidea within the Zygoptera

The superfamily Hemiphlebioidea is still mainly 'characterized' by plesiomorphies of the suborder Zygoptera, with the exception of the anal appendages, which show autapomorphies. The superfamily's position within the suborder is thus far from clear. Hennig (1981, p. 355) considered that "There may be a sister-group relationship between *Hemiphlebia* and the rest of the Recent Odonata...". This hypothesis is far from being confirmed. Carle & Wighton (1990, p. 52) considered that the Recent genera *Lestoidea* and *Hemiphlebia* are derived from amphipterygids. This assertion seems strange because Recent Amphipterygidae have numerous characters absent in *Hemiphlebia*, such as the presence of secondary antenodal crossveins, and a wide cubito-anal area. This hypothesis also implies that the Amphipterygidae are paraphyletic and that there are a great number of regressive characters in *Hemiphlebia*. Pfau (1991, fig. 12) considered that the phylogenetic position of the Hemiphlebiidae is still unresolved, although this group could be related to the Megapodagrionidae + Pseudolestidae. Bechly (1995) proposed that the Hemiphlebiidae are the sister-group of the Lestoidea (=Cretacoenagrionidae + Chorismagrionidae + Perilestidae + Synlestidae + Megalestidae - Lestidae), based on the following synapomorphies: (1) 'similar' and derived larval colour pattern and habitus; (2) derived microsculpture of the pterostigma; (3) metallic green body colour. Unique symplesiomorphies with *Chorismagrion* are: (4) open discoidal cell in forewing; (5) presence of a suture between the vertex and the occiput. *Hemiphlebia* shares in common with *Cretacoenagrion* and *Chorismagrion* the presence of an oblique, composite transverse vein RP +MA - MA - MAb - CuA, but, as discussed above, the value of this character is uncertain because it could be due to convergence. There is only weak evidence supporting the assumption of sister-group relationship with the Lestoidea, but it is the most parsimonious solution and there is no alternative hypothesis that is better supported. A complete revision of *Hemiphlebia*,

investigating further body characters, is now necessary to solve this phylogenetic problem. The current attribution of fossil Zygoptera to the Hemiphlebioidea is very difficult because the superfamily is characterised almost exclusively by plesiomorphies. The wings of *Cretarchistigma*, *Parahemiphlebia*, *Cretahemiphlebia*, sp. A and modern *Hemiphlebia* are clearly very similar in many respects, including characters (where preserved) which are not seen in modern Coenagrionoidea and Lestoidea, such as a poorly petiolated wing base, non-aligned postnodal crossveins, and relatively distally set nodus.

Whilst these characters could imply that the above genera are related, they are all primitive or of uncertain polarity, and thus not particularly useful for establishing phylogenetic relationships. This also has implications for the fossil family Italophlebiidae (see below).

Suborder Zygoptera

? Superfamily Hemiphlebioidea Tillyard & Fraser 1938

Family Italophlebiidae Whalley 1986

Genus *Italophlebia* Whalley 1986

Type species. Italophlebia gervasuttii Whalley 1986

Italophlebia gervasuttii Whalley 1986

1986 *Italophlebia gervasuttii* Whalley, pp. 52-57, figs 1-8.

Material. Holotype specimen no. 3460; paratype specimen no. 6678; other material: three specimens, nos 5115, 6677 and 6679, Coll. Museo Civico di Scienze Naturali 'E. Caffi', Bergamo, Italy.

Horizon and locality. Upper Triassic, Rhaetian (Stefani *et al.*, 1992), Riva di Solto, Bergamo, Italy.

Phylogenetic position of the Italophlebiidae Whalley 1986

Whalley (1986, 52-57, figs 1-8) considered *Italophlebia gervasuttii* Whalley 1986 to be a hemiphlebioid on the basis of the following characters: "Zygoptera with discoidal cell open in forewing, closed in hindwing. Postnodals not exactly aligned with the crossveins from R1 to R2 (RA and RP1) behind. Two antenodal veins". These symplesiomorphies (or uncertainly polarized characters) are not sufficient for an attribution of *Italophlebia* to the Hemiphlebioidea. In fact, *Italophlebia* does not share any definite synapomorphy with *Hemiphlebia*, so its allocation to the Hemiphlebioidea is not well founded and needs to be confirmed. Whalley's Italophlebiidae are 'characterized' by uncertain or plesiomorphic or homoplastic characters which are insufficient for a phylogenetic study. From Whalley's illustration (1986, fig. 1), the nodus of *Italophlebia* is very specialized: the vein ScP converges on RA and then diverges towards C (autapomorphy). There is no specialized Cr between ScP and RA, nor any thickening of C (plesiomorphies). The subnodus is directed towards the wing base (probable autapomorphy). The nodus of *Italophlebia* is quite different from the nodus of *Hemiphlebia*.

The Italophlebiidae could be related to the stem group of the 'Anisozygoptera' + Anisoptera because *Italophlebia* has a hindwing distinctly broader than the forewing, with a hindwing cubito-anal area distinctly wider than the forewing one. This character would be considered by Fraser (1957), Hennig (1981) and Nel *et al.* (1993) to be a synapomorphy of the 'Anisozygoptera' + Anisoptera, never found in *Hemiphlebia* or other Recent Zygoptera. But the very

different nodus of *Italophlebia* would imply that the development of the nodal structure is due to evolutionary convergence between the Zygoptera and the Italophlebiidae + 'Anisozygoptera' + Anisoptera. The development of a hindwing broader than the forewing could also be the result of evolutionary convergence between *Italophlebia* and the 'Anisozygoptera' + Anisoptera. In this case, no convergence is necessary to explain the development of the nodus within the Zygoptera + 'Anisozygoptera' + Anisoptera. Clearly, more material is needed. *Italophlebia* also shows some similarities in venation to *Triassolestodes* and the Japanese Triassic Triassoneuridae Riek 1976 described by Fujiyama (1991) in possessing a peculiar 'rudimentary' nodus with the same abnormal obliqueness of the subnodus, an open discoidal cell in the forewing, two antenodal crossveins, and relatively widened hindwings. The phylogenetic position of the Triassoneuridae is still unclear (Nel *et al.*, 1993).

Thus, the phylogenetic position of *Italophlebia* within the Odonata is uncertain. Until the body characters are studied, the Italophlebiidae have to be considered as Odonata *incertae sedis* that are unrelated to the Hemiphlebiidae.

? Superfamily Coenagrionoidea Kirby 1890 or Lestoidea Calvert 1901

Family Cretacoenagrionidae Bechly 1995

Genus *Cretacoenagrion* Jarzembowski 1990

Type species. Cretacoenagrion alleni Jarzembowski 1990

Cretacoenagrion alleni Jarzembowski 1990

1990 *Cretacoenagrion alleni* Jarzembowski, pp. 28–31, figs 1–4.

1990 *Cretacoenagrion alleni* Jarzembowski; Carle & Wighton, p. 57.

1993b *Cretacoenagrion alleni* Jarzembowski; Nel & Paicheler, p. 61.

1995 *Cretacoenagrion alleni* Jarzembowski; Bechly, pp. 192, 263, fig. 10.

Material. Holotype reg. no. 014884-5, Booth Museum of Natural History, Brighton; a single wing.

Horizon and locality. Lower Cretaceous, Lower Weald Clay, Late Hauterivian, Clockhouse (Butterley) Brickworks, near Capel, Surrey, UK.

Discussion: Jarzembowski (1990) considered that *Cretacoenagrion* could belong to the Coenagrionidae. The same year, Carle & Wighton (1990, p. 57) considered it to be "an apparent megapodagrionid" without any explanation. Nel & Paicheler (1993b) returned *Cretacoenagrion* to the Coenagrionidae. Bechly (1995) suggested that it could belong to the stem-group of the Lestoidea, as the sister group of the (Chorismagrionidae + Perilestidae + Synlestidae + Megalestidae - Lestidae). Like Bridges (1993), Bechly also separated the genus *Chorismagrion* from the Synlestidae to form a monogeneric family Chorismagrionidae. *Cretacoenagrion alleni* has an oblique, composite transverse vein RP + MA - MA - MAb - CuA and an open discoidal cell. Jarzembowski (1990, p. 31) based his discussion on these characters. As we have discussed above, their polarities are now rather uncertain and difficult to use, although Nel & Paicheler (1993b) and Bechly (1995) regarded the open discoidal cell as plesiomorphic.

The arculus and the open discoidal cell in *Cretacoenagrion* are nearly identical to those of *Chorismagrion* because there is no angle between RP + MA, the basal portion of MA and the oblique transverse vein MAb (*sensu* Nel *et al.*, 1993). This character is probably apomorphic but is also present in the wings of groups which

are obviously not related to the Hemiphlebioidea + Lestoidea, such as the 'Anisozygoptera': Tarsophlebioidea and Heterophlebioidea.

Jarzembowski (1990) placed *Cretacoenagrion* in the Coenagrionoidea: Coenagrionidae on a combination of the following characters: (1) the wing is petiolate. This character is also present in Lestoidea and Hemiphlebioidea and, as we suggest herein, could be the result of convergence; (2) the wing is hyaline. This character is also present in Lestoidea and Hemiphlebioidea and is probably a plesiomorphy; (3) only the two primary antenodal crossveins AX1 and AX2 are present. This character is also present in Lestoidea and Hemiphlebioidea and its polarity is still rather uncertain (probably apomorphic); (4) the arculus is aligned with AX2. This character is also present in many Lestoidea; (5) the postnodal crossveins are aligned with crossveins behind them. This character is also present in many Lestoidea; (6) IR2 and RP3/4 arise nearer the nodus than the arculus. This character is also present in many Lestoidea: Synlestidae; (7) MA and IR2 are zigzagged distally. This character is also present in many Lestoidea: Lestidae.

Thus, the attribution of *Cretacoenagrion* to the Coenagrionidae, although possible, is not based on sufficient synapomorphies. Bechly's (1995) placing is also not founded on strong synapomorphies of *Cretacoenagrion* with the Lestoidea. His characters are discussed as follows: (1) in *Cretacoenagrion*, the vein MAb is distinctly longer than the basal portion of MA. This character is present in *Chorismagrion* and also in the Tarsophlebioidea and Heterophlebioidea with open discoidal cells. Some Recent Coenagrionidae, e.g., *Zonagrion* Kennedy 1917, also have a vein MAb distinctly longer than the basal portion of MA. This character is thus not a unique synapomorphy of the Lestoidea; (2) the character 'pterostigma covering two cells' of *Cretacoenagrion* is probably a symplesiomorphy of the Zygoptera because it is present in the Calopterygoidea, the Lestoidea and the Coenagrionoidea. Even if it was apomorphic, Nel & Martínez-Delclòs (1993) have suggested that the evolution of the odonatan pterostigma is very complicated and that many reversions and parallelisms have occurred. The polarity of this character is thus uncertain; (3) the presence of a moderately oblique pterostigmal brace, as in *Cretacoenagrion*, is probably plesiomorphic in the Zygoptera + 'Anisozygoptera' + Anisoptera because this character is present in nearly all the major odonatan divisions. Its reduction in obliqueness probably occurred several times and may be related to the reduction of the pterostigma and/or to the development of the postnodal area. Nevertheless, the type of pterostigmal brace seen in *Cretacoenagrion* is present in some Coenagrionoidea and Lestoidea + Hemiphlebioidea; (4) the absence of any angle in RP1 under the pterostigmal brace of *Cretacoenagrion* is a plesiomorphy; (5) the veins RP3/4 and IR2 arising opposite the nodus of *Cretacoenagrion* is a character shared by the Coenagrionidae and some Lestoidea; (6) the very oblique vein MAb is present in many Lestoidea but also in Coenagrionidae; (7) the vein AA (which separates from AP just proximal to the transverse vein CuP) and the moderately petiolated wing are features found in many Lestoidea and Coenagrionoidea; (8) *Cretacoenagrion* has a weakly oblique vein 'O' between RP2 and IR2 but the polarity of this character is still uncertain. It is present in the wings of the 'Anisozygoptera' + Anisoptera and of some Lestoidea. As these groups are not closely related, it is probably a symplesiomorphy, or due to convergence; (9) the postnodals are aligned (also in Coenagrionoidea).

Other recognized venational characters of *Cretacoenagrion*, like the structure of the median and radial areas, are common to Coenagrionoidea, Lestoidea and

Hemiphlebioidea. In conclusion, we have failed to find any certain synapomorphy of *Cretacoenagrion* shared with either the Coenagrionoidea or the Lestoidea. Since the Lestoidea ground plan does not have any synapomorphic venational characters, that conclusion was predictable. Still, the position of *Cretacoenagrion* as basal Lestoidea is more parsimonious than any other. *Cretacoenagrion* has to be considered as Zygoptera superfamily undetermined belonging to one of the stem groups of the Lestoidea or Coenagrionoidea, more probably the former. However, it is possible to calculate a probability of the two opposing hypotheses: *Cretacoenagrion* is a basal lestoidean and *Cretacoenagrion* is a basal coenagrionoidean. For each determining character, we have to consider that the cases of homoplasy have a null probability and that all the other options are equally probable. In consequence, the probability of one of the possible hypotheses is the ratio of the number of favourable cases to the total number of cases.

If we consider only character (A) (viz. presence of an oblique vein) either it is a plesiomorphy or an apomorphy for the relationship of *Cretacoenagrion*. Within that hypothesis, if we consider that *Cretacoenagrion* is a basal lestoidean, the two possibilities do not imply any homoplasy. If we consider that *Cretacoenagrion* is a basal coenagrionoidean, the hypothesis 'presence of an oblique vein is an apomorphy' implies a convergence with the Lestoidea but the hypothesis 'presence of an oblique vein is a plesiomorphy' implies no homoplasy. In consequence, there are only three 'possible' cases and two of them agree with the attribution of *Cretacoenagrion* to the basal Lestoidea. So, the probability p (*Cretacoenagrion* is basal Lestoidea) = 2/3.

If we add character (B) (viz. presence of an oblique, composite transverse vein RP + MA - MA - MAb - CuA and an open discoidal cell), exactly the same situation occurs; if we consider that the two characters (A) and (B) are independent, in a probability sense, the total of the possible cases is [total of the possible cases for (A)] \times [total of the possible cases for (B)] with five possible cases: (A and B apomorphic, with *Cretacoenagrion* is basal Lestoidea); (A apomorphic, B plesiomorphic, with *Cretacoenagrion* is basal Lestoidea, etc.) and (A and B plesiomorphic, with *Cretacoenagrion* is basal Coenagrionoidea). Four of them correspond to (*Cretacoenagrion* is basal Lestoidea). The probability p (*Cretacoenagrion* is basal Lestoidea) = 4/5. This attribution is highly probable but not certain. Also, the definition of a fossil family Cretacoenagrionidae, based on *Cretacoenagrion*, does not appear very well founded because *Cretacoenagrion* does not possess any clearly autapomorphic character. Nevertheless, monotypic taxa that can be diagnosed with unique plesiomorphies do not necessarily need autapomorphies since they are monophyletic by monotypy. *Cretacoenagrion* differs greatly from the Lower Cretaceous coenagrionoid *Parahemiphlebia* gen. nov. on the basis of the following main features: (1) the pterostigmal brace of *Cretacoenagrion* is just slightly oblique, not directly aligned with RP1, so that the corresponding state of the character is plesiomorphic compared to *Parahemiphlebia* gen. nov.; (2) the wing of *Cretacoenagrion* is more petiolated than in *Parahemiphlebia* gen. nov. to a point just distal to the first antenodal crossvein; (3) the nodus of *Cretacoenagrion* is recessed toward the wing base, with a much greater distance between the nodus and the pterostigma than between the nodus and the wing base (apomorphic character state); (4) postnodals are aligned with crossveins below. *Cretacoenagrion* is clearly not directly related to *Parahemiphlebia*

gen. nov., even if they share an at least occasionally open discoidal cell in the forewing.

? Superfamily Lestoidea Calvert 1901

Family *incertae sedis*

Genus *Cretalestes* gen. nov.

Type species. Cretalestes martinae sp. nov.

Etymology. based on the Recent genus *Lestes* and the Cretaceous Period.

Diagnosis. The postnodal crossveins are not aligned with the corresponding subpostnodal crossveins between RA and RP1; the anterior side of the closed discoidal cell is very short and distal side very oblique, distinctly longer than the proximal side; the wing is well petiolated with AA and AP separating just basal to vein CuP; AX2 is more or less opposite the arculus; veins IR2 and RP3/4 begin between the arculus and the nodus, nearer to the arculus; vein IR1 is very long; the pterostigma is long, its brace weakly oblique; no secondary longitudinal vein is present in the main areas.

Cretalestes martinae sp. nov.

Figure 8

Material. Holotype specimen no. MNEMG 1996.227, Jarzembowski coll., Maidstone Museum and Art Gallery, UK.

Horizon and locality. Lower Weald Clay, Lower Cretaceous, Clockhouse Brickworks, Surrey, UK.

Etymology. After Mrs P. Martin, fossil collector.

Description. The species is known from the impression of a nearly complete wing. Length, 28.6 mm; width, 4.4 mm; distance from the wing base to the nodus, 10.7 mm; distance from the arculus to the nodus, 5.6 mm; from the nodus to the pterostigma, 14.1 mm. The pterostigma is 2.3 mm long and 0.6 mm wide; it covers 3.5 cells; its distal and proximal sides are slightly oblique; the pterostigmal brace is oblique; vein RP1 is not angular but curved beneath the pterostigmal brace; the seventeen postnodal crossveins are not aligned with the subpostnodal crossveins between RA and RP1; the weakly zigzagged, very long vein IR1 commences eleven cells beyond and 8.1 mm basal to the pterostigma; the base of vein RP2 is very poorly preserved but this vein seems to commence opposite the subnodus and is a straight vein; IR2 and RP3/4 are straight veins in their preserved portions, beginning between the nodus and the arculus, closer to the latter; distance from the nodus to the base of IR2, 3.7 mm; the oblique crossvein 'O' (between IR2 and RP2) is not preserved or absent; MA is proximally straight and distally zigzagged; vein MP is straight; CuA is a zigzagged vein with only one row of cells between it, MP and the posterior wing margin; virtually no crossveins

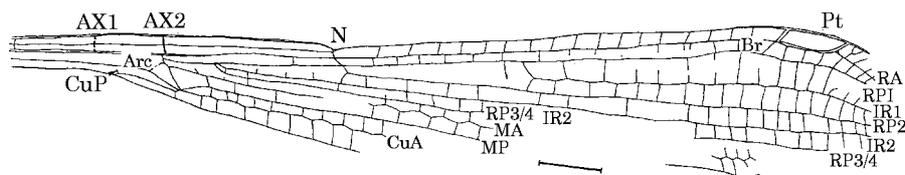


Figure 8. *Cretalestes martinae* gen. nov., sp. nov., holotype. (Scale bar = 2 mm).

are aligned in the preserved portion of the wing; there are apparently only two antenodal crossveins; the distance between AX1 and AX2 is *c.* 2.2 mm; AX2 lies opposite the arculus; CuP is between AX1 and AX2, nearer to AX1; CuP reaches vein AA just distad of its base; the discoidal cell is 1.1 mm long and 0.4 mm wide: its distal side is markedly oblique, not parallel to its proximal side and its anterior side is apparently very short; length of proximal side 0.4 mm, distal side 0.8 mm, anterior side 0.2 mm, posterior side 1.1 mm; the wing base is well preserved and distinctly petiolated, with veins AA and AP separating 3.5 mm distal to the base of the wing; there is one crossvein in the anal area between AA and AP; there are no secondary longitudinal veins between the main veins.

Discussion. RP3/4 and IR2 beginning between the nodus and the arculus is suggestive of Lestoidea but it is a character present in many groups of Odonata including the 'Anisozygoptera' + Anisoptera, and also some Zygoptera: Pseudolestidae, Amphipterygidae, Dysagrionidae, Calopterygoidea and higher Lestoidea such as Perilestidae, Synlestidae, Megalestidae, Lestidae and Sieblosiidae. This widespread character might be a symplesiomorphy of Zygoptera + 'Anisozygoptera' + Anisoptera; the reverse hypothesis would imply at least four cases of convergence.

The position of the arculus is also of little systematic value. In the oldest known odonatan, an undescribed Westphalian 'Protozygoptera-like' wing (Jarzembowski & Nel, in prep.), the arculus lies between AX1 and AX2, but in Permian and Triassic Protozygoptera and Liassic Archizygoptera which may be considered as the sister-groups of the Zygoptera + 'Anisozygoptera' + Anisoptera, the arculus is found distal to AX2. This would imply that AX2 lying opposite or basal to the arculus is a possible symplesiomorphy of the Zygoptera, with the arculus lying between AX1 and AX2 in the 'Anisozygoptera' + Anisoptera being a reversal. Nevertheless, the only known 'Anisozygoptera' + Anisoptera having a similar wing venation to the Wealden fossil are the Epiophlebioidea (= Epiophlebiidae + Asiapteridae, Nel *et al.*, 1993, Nel *et al.*, in press) and any attribution of *Cretalestes* to these families would imply a further reversal concerning the relative positions of the arculus and AX2. However, the discoidal cell of *Cretalestes* has several apomorphic characters not found in Epiophlebioidea but present in some Lestoidea: Lestidae and Megalestidae and some Coenagrionoidea: Coenagrionidae such as *Ceriagrion* and *Telebasis*, viz. the anterior side of the discoidal cell is very short and the distal side very long and oblique. Whether these characters of the discoidal cell are synapomorphies of higher Lestoidea and Coenagrionoidea or were convergently acquired within these two superfamilies remains undecided, but these characters exclude any attribution of *Cretalestes* to the 'Anisozygoptera' + Anisoptera and Calopterygoidea. Also, the lack of any secondary antenodal crossveins and of any secondary longitudinal veins between the main veins are characters not found in Calopterygoidea. The vein AA separating from AP just basally of the transverse vein CuP and the petiolated wing are features found in many Lestoidea and Coenagrionoidea but rarely in Calopterygoidea. *Cretalestes* has a long pterostigma and a 'straight' vein RA (plesiomorphies) unlike the angled RA and short pterostigma of Coenagrionidae; thus any attribution of *Cretalestes* to Coenagrionidae would necessitate a very basal position which would contradict the highly specialised discoidal cell shared with the more advanced Coenagrionidae. In short, *Cretalestes* shares nearly all its venational characters with Lestoidea and shows much similarity to wings of

Recent Lestidae and Synlestidae. The plesiomorphic condition of the postnodal crossveins not being aligned with the corresponding subpostnodal crossveins between RA and RP1 is still seen in some Synlestidae and would imply that *Cretalestes* has a rather basal position within the Lestoidea because the Cretacoenagrionidae, Chorismagrionidae and Perilestidae have well aligned postnodals. A higher position within Lestoidea would imply three cases of convergence in these families or a reversed condition for the postnodal crossveins in *Cretalestes*. We cannot exclude this last possibility because *Chlorolestes* and *Synlestes* (Synlestidae, sister-group of Megalestidae and Lestidae) also have poorly aligned postnodal crossveins. If we assume that the poorly aligned postnodals of Synlestidae are a reversal, then *Cretalestes* could be a synlestid. The lack of information concerning the oblique crossvein in *Cretalestes* precludes a more definite assignment of this taxon within Lestoidea. However, *Cretalestes* differs from all Recent taxa in the lack of secondary longitudinal veins in all the main areas, and in RP2 being aligned with the subnodus.

Superfamily Coenagrionoidea Kirby 1890
 Family Protoneuridae Jacobson & Bianchi 1905
 Subfamily Eoprotoneurinae Carle & Wighton 1990
 Genus *Eoprotoneura* Carle & Wighton 1990

Type species. Eoprotoneura hyperstigma Carle & Wighton 1990

Eoprotoneura hyperstigma Carle & Wighton 1990

1990 *Eoprotoneura hyperstigma* Carle & Wighton, pp. 56-57, figs 7, 8.

1991 'adult damselfly' Grimaldi, p. 380, unnumbered fig.

1993b *Eoprotoneura hyperstigma* Carle & Wighton; Nel & Paicheler, p. 61.

Material. Holotype male adult specimen AMNH 44203, paratypes female adult specimens AMNH 44201 and AMNH 44202. One other female specimen in coll. Nel, also a figured female in Martill *et al.* (1993, pl. 7, fig. 2), a specimen in the Kitakiushu Museum of Natural History (pers. comm., K. Ueda) and an undescribed male in the Martins-Neto coll.

Horizon and locality. Lower Cretaceous, Aptian, Crato Formation (Maisey, 1990; Martill *et al.*, 1993), Araripe Basin, NE Brazil.

Discussion. Carle & Wighton (1990, p. 56) considered that *Eoprotoneura* belonged to a monogeneric fossil subfamily Eoprotoneurinae Carle & Wighton 1990. Nel & Paicheler (1993b, p. 61-62) indicated that this subfamily could be related to the Protoneurinae but seems to be 'characterized' within the Protoneuridae only on the basis of plesiomorphies: (a) the pterostigma covering two cells, and (b) the crossveins not aligned in the posterior half of the wings.

Nevertheless, *Eoprotoneura* is of great phylogenetic interest because it has a highly specialized petiole, with the vein AA completely fused with AP, the vein CuA reduced to a simple crossvein and the vein MP extending for only one cell distal to the posterior angle of the discoidal cell, exactly opposite the vein descending from the subnodus; from the wing base to its apex, MP + Cu subtends three cells in both fore- and hindwings. Following Fraser's (1957) definition of the three subfamilies of Protoneuridae and Watson's (1992) revision, these venational apomorphic characters would imply that *Eoprotoneura* is related to the Recent genera of the 'Protoneurinae' Fraser 1957. The two other

subfamilies, the 'Caconeurinae' Fraser 1957 and the 'Disparoneurinae' Fraser 1957, would be more or less 'characterized' by the corresponding plesiomorphic characters of the veins AA, CuA and MP. The genital and prothoracic characters (apomorphies?) of some genera of the 'Caconeurinae' and 'Disparoneurinae', given by Watson (1992), are not preserved in any known specimen of *Eoprotoneura*. The study of the phylogenetic position of *Eoprotoneura* is complicated because of the inadequate definitions of the three subfamilies proposed by Fraser (1957) and subsequent classification of the Coenagrionoidea with evanescent veins AA, CuA and MP (Platystictidae, Protoneuridae and Isostictidae as well as *Lestoidea* Tillyard 1913, *Disparocypha* Ris 1916). That character is also present in Triassic Protozygoptera: *Batkenia* Pritykina 1981. The three families are therefore considered below.

Family Platystictidae Laidlaw 1924 *sensu* Fraser (1957): Fraser (1957) characterized the Platystictidae by the presence of a basal crossvein, proximal to the 'anal-crossing vein' *sensu* Fraser (1957) in the submedian space. He considered that this character was very primitive and demonstrated the affinities of the Platystictidae and the 'ancient zygopteroid stock' and the absence of any relations between Platystictidae and Protoneuridae. Fraser's theory is erroneous for two reasons (Bechly, 1995): (1) the 'basal crossvein' *sensu* Fraser is in fact the genuine vein CuP which is basally recessed and this recession is very probably apomorphic; (2) the 'anal-crossing vein' *sensu* Fraser is not homologous with CuP but is a simple crossvein. The basal position of CuP is found in some specimens of other Recent Coenagrionoidea, such as *Isomecocnemis* Cowley 1936, and is not an unequivocal synapomorphy of the Platystictidae. Fraser (1957) supposed that the vein AA is fused with the vein MP + CuA in the posterior part of the discoidal cell, forming a 'subdiscoidal cell'. This character is erroneous because the alleged subdiscoidal cell is a pseudo-subdiscoidal cell that is formed by three ordinary crossveins (Figure 9). AA is never fused with MP + CuA but with the hind margin. In the Recent genus *Protosticta* Selys 1885, the pseudo-discoidal cell is secondarily absent. The lateral labial lobes of *Protosticta* spp. (and other Platystictidae ?) are of 'gomphine-shape' (Fraser, 1919, 1933, 1943) and the median lobe is flat, produced apically and deeply fissured. These characters are most probably plesiomorphic.

Family Protoneuridae Jacobson & Bianchi 1905 *sensu* Fraser (1957): Fraser (1957) characterized this family on the basis of some venational characters,

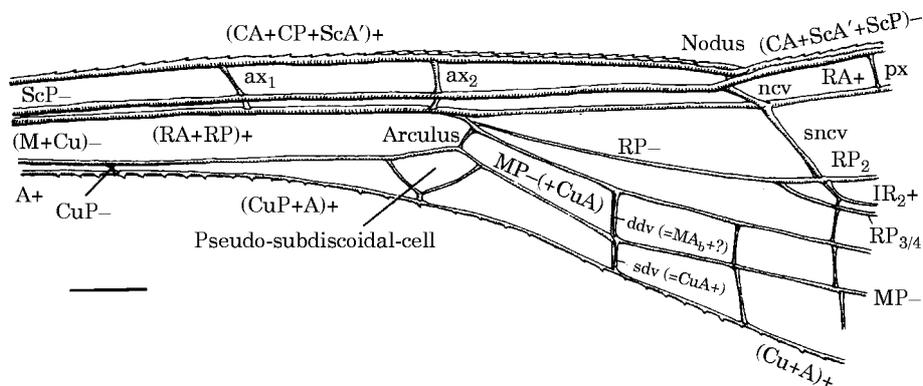


Figure 9. *Palaemnema clementina* (Zygoptera: Platystictidae), basal region of the left forewing. (Scale bar = 1 mm).

especially the shortening of the veins AA, CuA and MP, but these characters are also present in the families Isostictidae and Platystictidae. The MP is normally long in *Palaemnema* Selys 1860; thus, at least the reduction of this vein must be due to convergence. The larval characters of the Protoneuridae are not well known but seem to be very similar to the Platycnemididae, and also the Isostictidae. Watson (1992) showed that the protoneurid subfamilies are not very well defined.

Family Isostictidae Fraser 1955 *sensu* Lieftinck (1975): Fraser (1955a) first proposed a family group (subfamily) rank but Lieftinck (1951) suggested that the constituent genera could belong to a "complex" within the Protoneuridae. The same author (1975) separated them from the Protoneuridae on the basis of the structure of the saccoid, with a subapical constriction, rather than flat larval caudal gills (see Tillyard (1917) and Lieftinck (1953) for the larvae of the Recent genera *Selysioneura* Förster 1900, *Neosticta* Tillyard 1913 and *Isosticta* Selys 1885; and Fraser (1956) for the larva of *Oristicta* Tillyard 1913). But the polarity of this character has never been established, even if Lieftinck (1953) considered this type of gill to be very 'primitive'. If that was the case, this supposed plesiomorphic character would not be sufficient for a phylogenetic definition of the Isostictidae. The larvae of some isostictid genera are still unknown. *Nososticta* Selys 1890 (Recent Protoneuridae: Disparoneurinae) also has a constricted saccoid type of gill (Tillyard, 1917). This would not be an adequate character to define the Isostictidae if *Nososticta* Selys 1890 is really a protoneurid. However, because this character is only present in the Isostictidae and one protoneurid, it could be a synapomorphy of the group and needs further investigation. Fraser (1957, p. 44) suggested that the Isostictidae could be related to the Platycnemididae on the basis of derived 'similarities' in the setal pattern of the labial mask. Some Platycnemididae, for example *Chlorocnemis nubilipennis* Karsch 1893, tend to show a reduction of the veins AA, CuA and MP, resembling Isostictidae and Protoneuridae. However, the polarities of the characters of the labial mask have never been clarified, and the reduction of the veins AA, CuA and MP could have occurred independently in many groups. Watson (1992) showed that the male anal appendages are rather variable in shape in different genera of each family and are nearly useless for a redefinition of the groups proposed by Fraser (1957). The superior anal appendages are forcipate in the Platystictidae and some genera of Isostictidae, Protoneuridae: 'Caconeurinae' and 'Disparoneurinae'. Even some species of the same genus, such as *D. quadrimaculata* (Rambur 1842), the type-species of *Disparoneura* Selys 1860, has forcipate superior anal appendages of 'Caconeurinae' type whereas others do not, for example, *D. atkinsoni* Selys 1886. Fraser (1957, p. 43) indicated that the superior anal appendages of the Protoneuridae: 'Disparoneurinae' could be "trigger-shaped" in profile but this character also occurs in the 'Caconeurinae'. Watson (1992) also showed that the female prothoracic structures, if highly specialized in the 'Disparoneurinae' and 'Protoneurinae', are very variable at the species level even in these two subfamilies.

The above discussion demonstrates that the present definitions of these families are not satisfactory and insufficient for phylogenetic study. It is highly probable that some families, especially the Protoneuridae, are paraphyletic. An attempt at a phylogenetic classification of the Recent and fossil genera of these three groups (see Table 2 for list of taxa; for character polarities see Tables 3, 4) shows that the divisions proposed by Fraser (1957) cannot be justified on the venational

Table 2. List of Recent genera of Protoneuridae, Platystictidae and Isostictidae used in the phylogenetic analysis (Tables 3, 4), partly based on Davies (1981), Watson (1992) and Bridges (1993).

Protoneuridae Jacobson & Bianchi 1905
 Caconeurinae Fraser 1957
Caconeura Kirby 1890 (= *Alloneura* Selys 1860, = *Hypostrophoneura* Münz 1919)
Esme Fraser 1922
Indoneura Laidlaw 1917 [considered by Davies (1981) to be a synonym of *Caconeura*]
Melanoneura Fraser 1922 [considered by Davies (1981) to be a synonym of *Esme*]
Phylloneura Fraser 1922
 Disparoneurinae Fraser 1957
Chlorocnemis Selys 1863
Disparoneura Selys 1860
Elatoneura Cowley 1935
Isomecrocnemis Cowley 1936
Nososticta Selys 1890 (= *Risioneura* Münz 1919)
‘*Notoneura*’ Tillyard 1913 [considered by Davies (1981) to be a synonym of *Nososticta*]
Prodasineura Cowley 1934
 Protoneurinae Jacobson & Bianchi 1905
Epipleoneura Williamson 1915
Epipotoneura Williamson 1915
Idioneura Selys 1860
Junix Racenis 1968
Microneura Selys 1886
Neoneura Selys 1860 (= *Caenoneura* Kirby 1890)
Peristicta Selys 1860
Phasmoneura Williamson 1916
Proneura Selys 1889
Protoneura Selys 1857
Psainoneura Williamson 1915
Ropponeura Santos 1966
Platystictidae Laidlaw 1924
 Palaemnematinae Tillyard & Fraser 1938
Palaemnema Selys 1860
 Platystictinae Laidlaw 1924
Drepanosticta Laidlaw 1917 (including *Ceylonosticta* Fraser 1931)
Platysticta Selys 1870
Protosticta Selys 1885
Isostictidae Fraser 1955
Amphisticta Sjöstedt 1917
Austroticta Tillyard 1908
Cnemisticta Donnelly 1993
Eurysticta Watson 1969
Isosticta Selys 1885
Labidosticta Watson 1991
Lithosticta Watson 1991
Neosticta Tillyard 1913
Oristicta Tillyard 1913 (including *Phasmosticta* Lieftinck 1951)
Rhadinosticta Watson 1991
Selysioneura Förster 1900
Tanymecosticta Lieftinck 1935 (= *Stenosticta* Lieftinck 1932 as preoccupied)
Titanosticta Donnelly 1993

characters. Our attempt has been mainly limited to venation because it is all that is available for the fossil genus *Eoprotoneura*, which is therefore of little use for clarifying phylogenetic relationships. We have considered the Megapodagrionidae as the outgroup for determining character polarities.

As several genera possess the same venational characters, we have considered them as ‘groups’ for the present phylogenetic study: viz. the *Amphisticta* group for *Amphisticta* and *Austroticta*; the *Protoneura* group for *Phasmoneura*, *Epipleoneura*, *Epipotoneura*, *Microneura* and *Protoneura*; the *Idioneura* group for *Idioneura* and

Table 3. List of polarized characters used in phylogenetic analysis.

-
- | | |
|----|---|
| 1 | 0.- The pterostigma is long, distinctly longer than wide, covering more than one cell;
1.- The pterostigma is short, covering little more than one cell;
2.- The pterostigma is very short, covering less than one cell. |
| 2 | 0.- Vein CuA separates from MP in the posterior angle of the discoidal cell and is more than one cell long;
1.- CuA is one cell long;
2.- CuA is only a crossvein between MP and the posterior wing margin. |
| 3 | 0.- Vein AA separates from AP in the wing petiole and is one cell long or more;
1.- AA separates from AP in the wing petiole but is less than one cell long;
2.- AA never separates from AP. |
| 4 | 0.- No pseudo-subdiscoidal cell ;
1.- A pseudo-subdiscoidal cell present closed by two crossveins between AA + AP and MP + CuA. |
| 5 | 0.- MP is a long vein, beyond the posterior angle of the discoidal cell and extending well beyond the subnodus;
1.- MP extends only two or three cells beyond the subnodus;
2.- MP extends only one or half of a cell beyond the subnodus;
3.- MP only extends to opposite the subnodus;
4.- MP stops basad of the subnodus;
5.- MP is just a crossvein between the posterior angle of the discoidal cell and the posterior wing margin. |
| 6 | 0.- The vein CuP is not basally recessed;
1.- The vein CuP is basally recessed (Bechly, 1995). |
| 7 | 0.- The crossveins between the main longitudinal veins of the radial area are not aligned in the distal half of the wing;
1.- The crossveins between the main longitudinal veins of the radial area are well aligned. |
| 8 | 0.- IR1 begins only a short distance basal to the pterostigma;
1.- IR1 begins more than ten cells basal to the pterostigma. |
| 9 | 0.- The postnodal crossveins are not very numerous (less than sixteen);
1.- The postnodal crossveins are numerous (between sixteen and twenty);
2.- The postnodal crossveins are very numerous (more than twenty). |
| 10 | 0.- MA is a straight vein;
1.- MA is a zigzagged vein near the posterior wing margin, beyond RP2;
2.- MA is a zigzagged vein opposite or basal to RP2. |
| 11 | 0.- MA extends well beyond vein IR1;
1.- MA extends to opposite IR1;
2.- MA stops proximad of IR1. |
| 12 | 0.- The arculus is opposite AX2;
1.- The arculus is distal to the vein AX2. |
-

Neoneura; and the *Nososticta* group for *Nososticta* and '*Notoneura*'. The phylogenetic value of these groups needs further investigation.

Minimal trees have been obtained using the computer programme MacClade version 3.04, 1992, of Maddison & Maddison. Because there is a greater number of taxa than the number of available characters, there are many trees of minimal length, differing in the position of many terminal branches and indicating the presence of unresolved trichotomies concerning the relative positions of genera within the higher divisions. These trees have a medium consistency index (C.I., 0.64; R.I., 0.69, tree length, 69), indicating the presence of many homoplasies, mainly convergences in venational structures, suggesting that venational characters are of relatively little value in these families of the Coenagrionoidea (see figure 10). The minimal trees clearly show that it is impossible to justify, on the basis of the venational characters only, the monophyly of any of the Recent families or subfamilies, except Platystictidae. Isostictidae, Protoneuridae: Caconeurinae, Protoneurinae and Disparoneurinae would appear completely polyphyletic. These conclusions, although based on a very partial selection of

Table 4. Character states in the genera of Isostictidae, Protoneuridae and Platystictidae

taxa / characters	1	2	3	4	5	6	7	8	9	10	11	12
<i>Amphisticta</i>	2	2	2	0	1	0	1	0	0	2	0	0
<i>Austroticta</i>	2	2	2	0	1	0	1	0	0	2	0	0
<i>Cnemisticta</i>	1	2	2	0	0	0	1	0	0	2	0	0
<i>Eurysticta</i>	2	2	2	0	4/5	0	1	0	0	0/1	0	0
<i>Isosticta</i>	2	2	2	0	3	0	1	0	0	2	0/1	1
<i>Neosticta</i>	2	2	2	0	1	0	1	0	0	2	0	0
<i>Oristicta</i>	2	2	2	0	4	0	1	0	0	1	0	0
<i>Selysioneura</i>	2	2	2	0	5	0	1	0	1	2	0	0
<i>Titanosticta</i>	1	2	2	0	2	0	1	0	1	2	0	0
<i>Tanymecosticta</i>	1	2	2	0	2/3	0	1	0	0	?	0	0
<i>Palaemnema</i>	0	2	1	1	0	1	1	1	2	1	0	0
<i>Drapanosticta</i>	0/1	2	1	1	0	1	0	1	1	2	0	0
<i>Platysticta</i>	0	2	1	1	0/1	1	0/1	1	2	1	0	0
<i>Protosticta</i>	1	2	2	0	0/1	1	0	1	1	2	0	0
<i>Caconeura</i>	1	2	1	0	0/1	0	1	0	0	2	0	0
<i>Esmé</i>	0/1	2	1	0	0	0	1	1	2	1	0	0
<i>Indoneura</i>	0/1	2	1	0	0	0	1	1	2	1	0	0
<i>Melanoneura</i>	0/1	2	2	0	1	0	1	0/1	2	1	0	0
<i>Phylloneura</i>	0	2	1	0	0	0	1	1	2	1	0	0
<i>Chlorocnemis</i>	1	1	0	0	0	0	1	0	1	1	0	0
<i>Disparoneura</i>	0	2	1	0	0	0	1	0	1	2	0	0
<i>Elatoneura</i>	0	2	1	0	0/1	0	1	0	0/1/2	2	0	0
<i>Isomecocnemis</i>	1	2	1/2	0	0/1	0/1	1	0	0/1	1	0	0
<i>Nososticta</i>	1	2	2	0	5	0	1	0	0	2	0	0
<i>Prodasineura</i>	1	2	2	0	3	0	1	0	1	2	0	0
<i>Epipleoneura</i>	2	2	2	0	2	0	1	0	0	2	0	0
<i>Epiprotoneura</i>	2	2	2	0	2	0	1	0	0	2	0	0
<i>Idioneura</i>	2	2	1	0	2	0	1	0	0	2	0	0
<i>Junix</i>	2	2	1	0	3/4	0	0/1	0	0	0	1/2	0
<i>Microneura</i>	2	2	2	0	2	0	1	0	0	2	0	0
<i>Neoneura</i>	2	2	1	0	2	0	1	0	0	2	0	0
<i>Peristicta</i>	2	2	1	0	1	0	1	0	0	2	0	0
<i>Phasmoneura</i>	2	2	2	0	2	0	1	0	0	2	0	0
<i>Proneura</i>	2	1	1	0	1	0	1	0	0	2	2	2
<i>Protoneura</i>	2	2	2	0	2	0	1	0	0	2	0	0
<i>Psainoneura</i>	1	2	2	0	3	0	1	0	0	1	0	0
<i>Ropponeura</i>	2	2	2	0	1	0	1	0	0	1	0	0
<i>Eoprotoneura</i>	0	2	2	0	3	0	0	0	0	2	0	1

characters, confirm the views of Watson (1992) who suggested that the subfamilies of the Protoneuridae *sensu* Fraser (1957) are not tenable.

Nevertheless, we have failed to show synapomorphies for the Isostictidae and Protoneuridae, so their monophyly needs confirmation. Future research using body and larval characters is necessary to verify these hypotheses. Finally, *Eoprotoneura* appears to be related to several Recent genera of Protoneuridae belonging to the 'Protoneurinae' and the 'Disparoneurinae'. There is no longer any reason for considering *Eoprotoneura* to be a fossil representative of an extinct subfamily Eoprotoneurinae on the basis of the known venational characters. *Eoprotoneura* is a very old, but not basal representative of the Protoneuridae. It is impossible to synonymise Eoprotoneurinae with a Recent subfamily because all of them are very badly defined.

Future work is needed to solve the problem of the monophyly of the Protoneuridae, Isostictidae and Platystictidae, although recent work (Bechly, in prep.) suggests some phylogenetic changes: (1) to make Protoneuridae

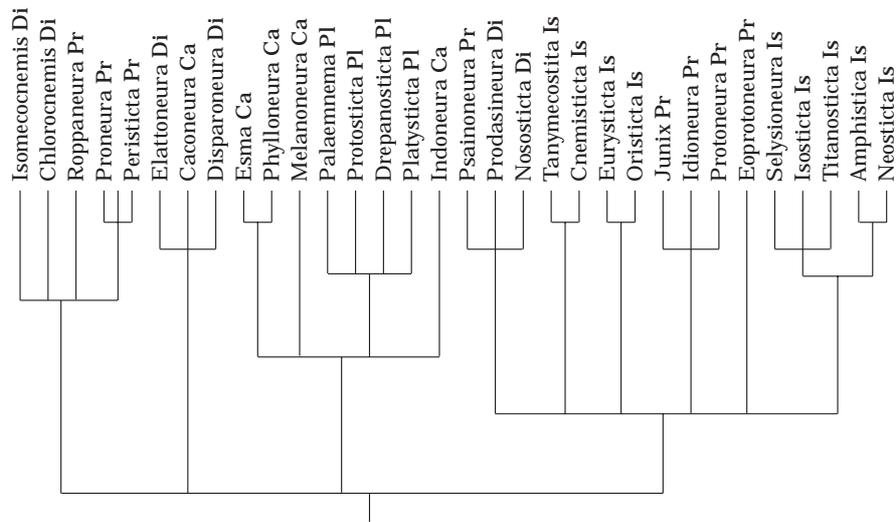


Figure 10. Consensus tree showing the unresolved polytomies in Protoneuridae, Isostictidae and Platystictidae.

monophyletic, it could be necessary to re-include Isostictidae as a subfamily; (2) the monophyly of the Platystictidae could be demonstrated by the following characters: very basal position of the vein CuP, presence of a pseudo-subdiscoidal cell (secondarily absent in *Protosticta*), pyramid type of microsculpture of the pterostigma (Bechly, 1995) and a falcate wing apex; (3) the Platystictidae could not be related to the Protoneuridae; (4) Protoneuridae, Isostictidae, Platynemididae and Coenagrionidae form a monophyletic group.

Table 5. Key to Cretaceous damselflies

(1).	Pterostigma unbraced	<i>Euarchistigma atrophium</i> .
	Pterostigma braced	(2)
(2).	Vein MP short, ending approximately at level of nodus	<i>Eoprotoneura hyperstigma</i> .
	Vein MP long, extending considerably beyond nodus	(3)
(3).	Pterostigma covers more than three cells	<i>Cretalestes martinae</i> .
	Pterostigma covers fewer than three cells	(4)
(4).	The postnodal crossveins are well aligned with the subpostnodal crossveins (between RA and RP1) basal to the pterostigma	<i>Cretacoenagrion alleni</i> .
	The postnodal crossveins are not aligned with the subpostnodal crossveins	(5)
(5).	Vein IR1 begins less than one cell basal to pterostigmal brace	(6)
	Vein IR1 begins more than one cell basal to pterostigmal brace	(7)
(6).	Two crossveins between AA and AP	<i>Parahemiphlebia cretacica</i> .
	Three crossveins between AA and AP	<i>Parahemiphlebia allendaviesi</i> .
(7).	IR1 straight and separated from RP1 by one row of cells	<i>Cretahemiphlebia rossi</i> .
	IR1 less straight and separated from RP1 by two cell rows for short distance level with distal end of pterostigma	<i>Cretarchistigma greenwoodi</i> .

3. Conclusion

Long wing petiolation is a 'specialized' apomorphic character present in the Zygoptera: Lestoidea and Coenagrionoidea, but also in certain Calopterygoidea, in the Epiophlebioidea (Odonata: 'Anisozygoptera' + Anisoptera, Nel *et al.*, 1993) as well as in the Triadophlebiomorpha Pritykina 1981, Protozygoptera and Archizygoptera. In these latter groups, the petiolation is markedly developed because Cu and MP are sometimes fused with AA + AP at the wing bases (Pritykina, 1981; Nel *et al.*, in press). If *Parahemiphlebia* proves to be basal Coenagrionoidea and *Hemiphlebia* basal Lestoidea (both with briefly petiolated wings) then the subsequent development of long wing petiolation would be the result of convergence between the two superfamilies. The wing petiolation of the Permo-Triassic Triadophlebiomorpha, Protozygoptera, Archizygoptera and Epiophlebioidea (Lower Jurassic-Recent) also resulted from a convergence with true Zygoptera: Calopterygoidea + Coenagrionoidea + (Lestoidea + Hemiphlebioidea). Within the Coenagrionoidea, the specialized structure of the pterostigmal brace and of RP1 in *Parahemiphlebia* which suggests affinities with the Coenagrionidae, also suggests that the phylogenetic relationships between the diverse families of Coenagrionoidea are rather complicated. Schmidt (1951) considered that the Coenagrionidae were 'ancestral' to Platynemididae, while Donnelly (1984) has taken a reverse view on the basis of a study of the Recent genus *Melanesobasis* Donnelly 1984. Neither of these authors polarized the characters they used, and the term 'ancestor' makes no sense for extant taxa from a cladistic point of view. The presence of two coenagrionoids of exactly the same age, one with a very plesiomorphic condition of the petiole, and the other a protoneurid with the opposite apomorphic character state, partly corroborates the hypothesis of Carle & Wighton (1990, p. 54) that the Coenagrionoidea had divided, very early in superfamily history, into a Pseudostigmatidae ? + Protoneuridae + Platystictidae ? group and a Coenagrionidae + Platynemididae ? group. Carle & Wighton (1990) considered that such parallel evolution would have occurred in the Southern Hemisphere for the Protoneuridae + Platystictidae ? and the Northern Hemisphere for the Coenagrionidae + Platynemididae ?. The presence of a Coenagrionidae-like form and genuine Protoneuridae in the same Lower Cretaceous Brazilian outcrop suggests that the palaeogeographical hypothesis is doubtful and needs further evidence. A phylogenetic study of the Coenagrionoidea remains to be undertaken. Even the monophyly of the diverse families has to be demonstrated, as already suggested by Donnelly (1984) for the Coenagrionidae. Not only the problem of the monophyly of the Zygoptera, but also of the diverse superfamilies within that suborder, appears increasingly acute following the study of the new fossil damselflies in this paper (cf. Bechly, 1995).

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References

- Allen, P. & Wimbledon, W. A. 1991. Correlation of the NW European Purbeck - Wealden (nonmarine Lower Cretaceous) as seen from the English type-areas. *Cretaceous Research* 12, 511-526.

- Asahina, S. 1954. *A morphological study of a relict dragonfly* *Epiophlebia superstes* Selys (Odonata, Anisozygoptera), 153 pp. (The Japan Society for the Promotion of Science Tokyo).
- Asahina, S. 1957. On the pterothoracic interpleural suture of Mesozoic and Recent Odonata. *Journal of the Faculty of Sciences, Hokkaido University, Zoology* (6) **13**, 1–7.
- Bechly, G. 1993. A brief report of an ongoing cladistic study on the phylogenetic relationships of the fossil and extant odonate family group taxa. *Petalura* **1**, 19–20.
- Bechly, G. H. P. 1995. 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* **1**, 1–341.
- Belyshev, B. F. & Haritonov, A. Yu., 1985. New relict suborder of dragonflies (Insecta, Odonata). *Izvestiya Sibirskogo Otdeleniya Akademii Nauk SSSR (Seriya Biologicheskikh Nauk)* **18**, 51–53. [In Russian, English summary]
- Bridges, C. A. 1993. *Catalogue of the family-group, genus-group and species-group names of the Odonata of the World*. Second edition, 950 pp. (C. A. Bridges, Urbana, Illinois).
- Carle, F. L. 1982. The wing vein homologies and phylogeny of the Odonata: a continuing debate. *Societas Internationalis Odonatologica, Rapid Communications* **4**, 1–66.
- Carle, F. L. & Wighton, D. C. 1990. Chapter 3. Odonata. In *Insects from the Santana Formation, Lower Cretaceous, of Brazil* (ed. Grimaldi, D. A.). *Bulletin of the American Museum of Natural History* **195**, 51–68.
- Davies, A. L. 1981. A synopsis of the extant genera of the Odonata. *Societas Internationalis Odonatologica, Rapid Communications* **3**, 1–59.
- Davies, A. L. & Tobin, P. 1984. The dragonflies of the world: a systematic list of the extant species of Odonata. Vol. 1, Zygoptera, Anisozygoptera. *Societas Internationalis Odonatologica, Rapid Communications (Supplement)* **3**, 1–127.
- Donnelly, T. W. 1984. *Melanesobasis* gen. nov., a new genus of Fijian damselflies: a possible link between the platycnemidid *Lieftinckia* and certain coenagrionids (Zygoptera). *Odonatologica* **13**, 89–105.
- Fincke, O. L. 1984. Giant damselflies in a tropical forest: reproductive biology of *Megaloprepus coerulatus* with notes on *Mecistogaster* (Zygoptera: Pseudostigmatidae). *Advances in Odonatology* **2**, 13–27.
- Fraser, F. C. 1919. Descriptions of new Indian Odonate larvae and exuviae. *Records of the Indian Museum* **16**, 459–467.
- Fraser, F. C. 1933. Odonata 1. In *The fauna of British India, including Ceylon and Burma* (ed. Stephenson, J.), xiii + 423 pp. (Taylor & Francis, London).
- Fraser, F. C. 1943. New Oriental Odonate larvae. *Proceedings of the Royal Entomological Society of London (B)* **12**, 81–93.
- Fraser, F. C. 1955a. A new isostictine dragonfly from Australia with some remarks on the subfamily Isostictinae nov. (Odon., Protoneuridae). *Entomologist's Monthly Magazine* **91**, 227–230.
- Fraser, F. C. 1955b. A study of *Hemiphlebia mirabilis* Selys (Odonata), a survival from the Permian. *Entomologist's Monthly Magazine* **91**, 110–113.
- Fraser, F. C. 1956. The nymphs of *Synlestes tropicus* Tillyard, *Chorismagrion risi* Morton, *Oristicta filicicola* Tillyard and *Lestoidea conjuncta* Tillyard with description of the female of the latter and further notes on the male. *Australian Journal of Zoology* **12**, 284–292.
- 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, Sydney* **12**, 1–133.
- Fujiyama, I. 1991. Late Triassic insects from Miné, Yamaguchi, Japan. Part 1. Odonata. *Bulletin of the National Science Museum (C)* **17**, 49–56.
- Grimaldi, D. A. 1991. The Santana Formation insects. In *Santana fossils: an illustrated atlas* (ed. Maisey, G. J.), pp. 379–406. (TFH Publications, New Jersey).
- Handlirsch, A. 1908. *Die fossilen Insekten und die Phylogenie der rezenten Formen*, 1433 pp. (W. Engelmann, Leipzig).
- Handlirsch, A. 1939. Neue Untersuchungen über die fossilen Insekten mit Ergänzungen und Nachträgen sowie Ausblicken auf phylogenetische, palaeogeographische und allgemeine biologische Probleme. *Annalen des Naturhistorischen Museums in Wien* **49**, 1–240.
- Hennig, W. 1981. *Insect phylogeny*, 514 pp. (J. Wiley & Sons, Chichester).
- Jacobson, G. & Bianchi, V. 1905. *Die Orthopteren und Pseudoneuropteren des Russischen Reiches und der angrenzenden Gebiete*, pp. 635–846 (A. F. Dewrien, St. Petersburg). [In Russian]
- Jarzembowski, E. A. 1990. Early Cretaceous zygopteroids of southern England, with the description of *Cretacoenagrion alleni* gen. nov., spec. nov. (Zygoptera: Coenagrionidae; 'Anisozygoptera': Tarsophlebiidae, Euthemistidae). *Odonatologica* **19**, 27–37.
- Jarzembowski, E. A. & Nel, A. 1996. Geology and fossil record. In Follett, P., *Dragonflies of Surrey*, pp. 5–11, pls 1–3 (Surrey Wildlife Trust, Woking).
- Kennedy, C. H. 1920. The phylogeny of the zygopterous dragonflies as based on the evidence of the penes. *Ohio Journal of Science* **21**, 19–29.

- 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**, 335–374.
- Lew, G. T.-W. 1933. Head characters of the Odonata with special reference to the development of the compound eye. *Entomologica Americana* **14**, 41–96.
- Lieftinck, M. A. 1951. Results of the Archbold expeditions. No. 64 Odonata of the 1948 Archbold Cape York expedition, with a list of the dragonflies from the peninsula. *American Museum Novitates* **1488**, 1–46.
- Lieftinck, M. A. 1953. The larval characters of the Protoneuridae (Odon.), with special reference to the genus *Selysioneura* Förster, and with notes on other Indo-Australian genera. *Treubia* **21**, 641–684.
- Lieftinck, M. A. 1975. The dragonflies (Odonata) of New Caledonia and the Loyalty Islands. Part 1, imagines. *Cahiers de l'ORSTOM, Série Hydrobiologie* **9**, 127–166.
- Lindley, R. P. 1978. Some armchair thoughts on the dragonfly wing. *Odonatologica* **7**, 323–351.
- Machado, A. B. M. & Martinez, A. 1982. Oviposition by egg-throwing in a zygopteran, *Mecistogaster jocaste* Hagen, 1869 (Pseudostigmatidae). *Odonatologica* **11**, 15–22.
- Maisey, J. G. 1990. Stratigraphy and depositional environment of the Crato Member (Santana Formation, Lower Cretaceous of N. E. Brazil), Chapter 1. In *Insects from the Santana Formation, Lower Cretaceous, of Brazil* (ed. Grimaldi, D. A.). *Bulletin of the American Museum of Natural History* **195**, 15–19.
- Martill, D. M., Brito, P. M., Wenz, S. & Wilby, P. R. 1993. Fossils of the Santana and Crato Formations, Brazil. *Palaeontological Association Field Guides to Fossils* **5**, 1–159.
- Morton, K. J. 1914. A remarkable new genus and new species of Odonata, of the legion *Podagrion*, Selys, from North Queensland. *Transactions of the Entomological Society of London* **62**, 169–172.
- Morton, K. J. 1924. A new genus and new species of dragonfly from East Africa belonging to the legion *Podagrion* (Odonata). *Entomologist* **57**, 217–220.
- 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.
- Needham, J. G. 1903. A genealogic study of dragonfly wing venation. *Proceedings of the United States National Museum* **26**, 703–764.
- Needham, J. G. & Anthony, M. H. 1903. The skewness of the thorax in the Odonata. *Journal of the New York Entomological Society* **11**, 117–123.
- Nel, A. & Escuillié, F. 1994. A new dragonfly from the Lower Cretaceous of Brazil (Odonata, Anisoptera). *Palaeontology* **37**, 923–930.
- Nel, A. & Martínez-Delclòs, X. 1993. Essai de révision des Aeschnidoidea (Insecta, Odonata, Anisoptera). *Cahiers de Paléontologie CNRS*, **1993**, 1–99.
- 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. & Paicheler, J.-C. 1993a. Les Odonata fossiles: état actuel des connaissances. Huitième partie: les Calopterygoidea fossiles (Odonata, Zygoptera). *Bulletin de la Société Entomologique de France* **97**, 381–396.
- Nel, A. & Paicheler, J.-C. 1993b. Les Odonata fossiles: état actuel des connaissances. 7. Les Coenagrionoidea (Odon., Zygoptera). *Entomologica Gallica* **4**, 59–63.
- Nel, A. & Paicheler, J.-C. 1994a. Les Lestoidea (Odonata, Zygoptera) fossiles: un inventaire critique. *Annales de Paléontologie* **80**, 1–59.
- Nel, A. & Paicheler, J.-C. 1994b. Les Gomphidae fossiles. Un inventaire critique (Odonata, Gomphidae). *Annales de la Société Entomologique de France, Nouvelle Série* **30**, 55–77.
- Nel, A. & Paicheler, J.-C. 1995. Les Libelluloidea fossiles autres que Libellulidae. Un inventaire critique (Odonata, Corduliidae, Macromiidae, Synthemistidae, Chlorogomphidae et Mesophlebiidae). *Nouvelle Revue d'Entomologie, Nouvelle Série* **11**, 321–334.
- Nel, A., Papier, F., Stamm-Grauvogel, L. & Gall, J.-C. (in press). *Voltzialestes triasicus*, gen. nov., sp. nov., le premier Odonata fossile du Trias des Vosges (France). Morphologie, affinités et phylogénie. [Odonatoptera, Odonata, Protozygoptera]. *Paleontologia Lombarda, Nuova Serie* **9**.
- Pfau, H. K. 1991. Contributions of functional morphology to the phylogenetic systematics of Odonata. *Advances in Odonatology* **5**, 109–141.
- Pritykina, L. N. 1968. Strekozy Karatau (Odonata). In *Yurskie Nasekomye Karatau* (ed. Rodendorf, B. B.), pp. 26–55 (Nauka, Moscow). [In Russian]
- Pritykina, L. N. 1981. New fossil Odonata from Central Asia. In *New fossil insects from the Territory of the U. S. S. R.* (eds Visnyakova, V. N., Dlusskiy, G. M. & Pritykina, L. N.), *Trudy Paleontologicheskogo Instituta* **183**, 5–42. [In Russian]
- Riek, E. F. & Kukulová-Peck, J. 1984. A new interpretation of dragonfly wing venation based upon Early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character stages in pterygote wings. *Canadian Journal of Zoology* **62**, 1150–1166.

- Sant, G. J. & New, T. R. 1988. The biology and conservation of *Hemiphlebia mirabilis* Selys (Odonata: Hemiphlebiidae) in Southern Victoria. *Arthur Rylah Institute for Environmental Research, Technical Report Series* **82**, v + 35 pp.
- Schmidt, E. 1951. Über neue und weniger bekannte afrikanische Platycnemididen (Odon.). *Mitteilungen Münchener Entomologische Gesellschaft* **41**, 217–240.
- Sjöstedt, Y. 1917. Results of Dr E. Mjöberg's Swedish scientific expeditions to Australia 1910–1913. 16. Odonaten. *Arkiv för Zoologi* **11**, 29–44.
- Stefani, M., Arduini, P., Garassino, A., Pinna, G., Teruzzi, G. & Trombetta, G. L. 1992. Palaeoenvironment of extraordinary fossil biotas from the Upper Triassic of Italy. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* **132**, 309–335.
- Tillyard, R. J. 1917. On the morphology of the caudal gills of the larvae of zygopterid dragonflies. *Proceedings of the Linnean Society of New South Wales* **42**, 72–111.
- Tillyard, R. J. 1928. The larva of *Hemiphlebia mirabilis* Selys (Odonata). *Proceedings of the Linnean Society of New South Wales* **53**, 193–206.
- Watson, J. A. L. 1992. The subfamilies of Protoneuridae (Zygoptera). *Odonatologica* **21**, 195–201.
- Whalley, P. 1986. Insects from the Italian Upper Trias. *Rivista del Museo Civico di Scienze Naturali 'E. Caffi', Bergamo* **10**, 51–60.